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Validation of specimen-level phylogenetics in extinct and extant lacertid lizards (Squamata, Lacertoidea) based on osteology

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I

I, Lukardis Charlotte Marie Wencker, hereby declare that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the text. "Trust in what you love, continue to do it, and it will take you where you need to go."

Natalie Goldberg

Table of contents

Abstract	1
Organisation of the thesis	2
1. Introduction	3
1.1. Phylogenetic analyses	3
1.2. Obstacles in palaeontological phylogenies	5
1.2.1. Data problem	5
1.2.1.1. Abstract	6
1.2.1.2. Introduction	6
Institutional Abbreviations	9
1.2.1.3. Materials and methods	
Studied material	
Geological background	11
Character matrix construction	
Phylogenetic analysis	14
Jaw element comparison	15
Character testing	15
Morphotype testing	
1.2.1.4. Results	
Morphotype descriptions	
Premaxillae	
Maxillae	20
Dentaries	25
Phylogenetic analysis	
Premaxillae	
Maxillae	
Dentaries	

Fossil wild card taxa	35
Jaw element comparison	35
Character testing	35
Morphotype testing	
1.2.1.5. Discussion	45
Dataset comparison	46
Possible phylogenetic position of mOTUs	48
Premaxilla mOTUs	49
Maxilla mOTUs	50
Dentary mOTUs	51
Possible phylogenetic positions of the eight fossil wild card taxa	53
Species diversity of the morphotypes	54
1.2.1.6. Conclusions	59
1.2.2. Dataset composition problem	60
1.3. Specimen-level phylogeny	61
1.3.1. Concept and application of specimen-level phylogeny	61
2. Methods	66
2.1. Main matrix construction	66
2.2. Matrix construction with continuous character states	68
2.3. Simulated fossil dataset construction	69
3. Results	72
3.1. Matrix constitution	72
3.2. Comparison of weighting strategies	79
3.2.1. Introduction	79
3.2.2 Materials and methods	
3.2.2.1. Phylogenetic analyses	82
3.2.2.2. Tree comparison	83

Overall tree resolution	83
Clade delimitation	85
Symmetric resampling and jackknife	86
Robinson-Foulds distances and Distortion-Coefficients	86
3.2.3. Results	87
3.2.3.1. Accuracy measurements	87
Main matrix	88
45-fossil matrix	91
65-fossil matrix	93
Cd matrix	96
45-fossil-cd matrix	99
65-fossil-cd matrix	102
3.2.3.2. Best ranked trees	105
Main matrix	105
45-fossil matrix	108
65-fossil matrix	110
Cd matrix	112
45-fossil-cd matrix	114
65-fossil-cd matrix	116
3.2.4. Discussion	118
3.2.4.1. Species-structures derived from OTU positions	118
3.2.4.2. Correlation of accuracy measurements	119
3.2.4.3. Impact of weighting strategy on tree accuracy	120
3.3. Quantitative characters: continuous vs. discrete character states	123
3.3.1. Introduction	123
3.3.2. Material and methods	124
3.3.3. Results	125

3.3.3.1. Main matrix vs. cd matrix	
3.3.3.2. 45-fossil matrix vs. 45-fossil-cd matrix	
3.3.3.3. 65-fossil matrix vs. 65-fossil-cd matrix	
3.3.4. Discussion	
4. Discussion and Conclusions	131
4.1. Informative value of the data	131
4.2. Does the specimen-level approach work?	131
4.3. Recommendations for selection of tree search strategy	134
5. Acknowledgements	136
6. References	138
7. Index of figures	158
8. Index of tables	166
9. Appendices	169
Appendix 1	169
Appendix 2	173
Appendix 3	
Appendix 4	
Appendix 5	219
Appendix 6	
Appendix 7	
Appendix 8	227
Appendix 9	246
Appendix 10	
Appendix 11	

Abstract

Specimen-level phylogenetic analysis provides useful information about intraspecific relationships and can help delimiting species. Its importance is getting more and more also into the focus of vertebrate palaeontology, but it is still rarely used in this context. Therefore, a validation of this method is overdue and crucial. This thesis aims at evaluating different analytical (maximum parsimony) approaches to identify a general approach which creates the most reliable results for a specimen-level analysis depending on the properties of the dataset such as the amount of missing data and character type. Therefore, a real-life osteological dataset containing 252 characters coded for 120 specimen-level taxonomic units was used. The ingroup of the dataset is comprised of the lacertilian genera Lacerta and Timon, represented by 69 specimens. Derived from this dataset, two fossil-simulation matrices with different stages of incompleteness (45% and 65%) were created. In addition, for each matrix, a second version was built with continuous character states coding for the quantitative characters. Hence, a total of six character matrices with the same specimens and characters were analysed to test 36 different weighting strategies. Subsequently, tree accuracy for the resulting phylogenetic trees was measured based on six criteria (such as clade delimitation and support metrics), and final rankings of the 36 weighting strategies for each matrix based on the criteria were constructed. To test furthermore the impact of continuous character states on tree accuracy, the trees of the best ranked weighting strategy were compared. The highest ranked weighting strategy was in all cases an analysis under extended implied weights with K-values between 50 and 200 and an assumed homoplasy for missing entries between 50% and 100%. Quantitative continuous and quantitative discrete character states performed equally well; an advantage of continuous character states was observed for the highly incomplete matrices (65% incompleteness). The specimen-level approach failed to recover correct species clades which might be a problem of the dataset or the data itself. Hence, further investigations to explore those problems are needed. Nonetheless, the obtained results allow for making recommendations concerning the decision on what weighting strategy to use to gain more accurate phylogenetic tress when analysing a specimen-level (possibly also species-level) dataset with certain dimensions.

Organisation of the thesis

The presented thesis is structured in: 1) a general introduction chapter; 2) a method chapter that explains the construction of the datasets; 3) a result chapter that is divided into three parts: i) a description of the datasets being used in special regard to the distribution of incompleteness; ii) a comparison of 36 different weighting strategies applied to the datasets with its own introduction, methods, results, and discussion section; iii) a comparison between quantitative continuous and quantitative discrete character statements using phylogenetic trees obtained from the previous part with its own introduction, methods, results, and conclusion chapter.

1. Introduction

1.1. Phylogenetic analyses

Phylogeny, derived from the Greek "phylé/phylon" for tribe, clan, race, and "genetikós" for source, origin, birth, is the field of systematics which aims to solve and understand the evolutionary relationships and history of organisms.

At the base of systematics lies the theory of classifying organisms into species which had its early beginnings approximately 2,400 years ago with Aristotle's Historia animalium (Balme and Gotthelf, 2002). For a long time, species were classified and defined by different given and static properties of an organism (e.g., Carl von Linné). The evolutionary concept behind species was developed later; Charles Darwin stated in his On the Origin of the species (1859) that organisms or species have the possibility to change their properties as an adaptation to their environment. But according to him, species would remain unmodified for long periods. Wiley (1975) defined three axioms of phylogenetic systematics: 1. evolution takes place, 2. all organisms share one common ancestor, and 3. characters are passed, modified or unmodified, from one to the other generation. Nowadays, species are generally understood as independently and continuously evolving lineages. The process of speciation itself is understood to underlie two factors: phyletic evolution, which is the gradual change from one species into another, and geographic speciation, which is caused by the geographic separation of one species into two groups and a following independent evolution leading to two different species (e.g., Gingerich, 1976). Hence, species are understood as consistently evolving, and a phylogeny is always an approximation to a "snapshot" of a specific stage in the speciation process of certain organisms. It is a hypothesis which cannot be experimentally proven. But it is (at present) the best tool to understand the relationships between species, to get, for instance, an idea of the evolutionary and paleogeographic conditions that lead to the speciation (see Ritz et al., 2007; Rheindt et al., 2009; Ahmadzadeh et al., 2016).

Consequently, to create a phylogeny that is as close as possible to the true tree, subjective opinions (of the observer) must be reduced to a minimum and analyses should be standardised and reproducible. First of all, the data itself has to be organised or managed in a comparable and coherent way. The data management is depending on the type of data being used, molecular or morphological. The generally accepted way of treating data of morphological/osteological nature for phylogenetic analysis is the character matrix. Here, the taxa of interest, also called operational taxonomic units (OTUs), are scored for a set of predefined characters by allocating

them to character statements; those character statements are expressed numerically. The OTUs can be of different levels, for instance genus-, species- or specimen-level, with one OTU representing a single genus, species, or specimen, respectively. For the reconstruction of phylogenies, different approaches, or optimality criteria to determine the relationships between taxa exist. The most common approaches used are maximum parsimony, maximum likelihood, and Bayesian inference. While maximum likelihood and Bayesian inference are model-based methods, maximum parsimony is an optimality criterion that finds as optimal tree the one which describes the data with the minimal number of character changes. For morphological datasets, it is currently debated which optimality criterion finds trees that are closest to the true tree (e.g., Wright and Hillis, 2014; O'Reilly et al., 2016; Goloboff et al., 2018; Puttick et al., 2019; Vernygora et al., 2020). For probabilistic methods (Bayesian inference and maximum likelihood), a character evolution model is needed to calculate phylogenetic trees. The most frequently used character evolution model for morphological data is that by Lewis (2001) which suggested a Markov k (Mk) model with its conditional version for variable character states, known as the Mkv model (e.g., Simões et al., 2018; Cau, 2017, 2019; Groh et al., 2020). Goloboff et al. (2019) discuss the adequacy of the Mkv model for morphological datasets because the model stems from the "common mechanism" (CM) which assumes the probability of character change to occur for all characters at the same time in different parts of the tree. According to them, also a gamma distribution which enables heterogeneity of rate evolution among the character, still leads to a correlation of change rate between faster and slower evolving characters in the same areas of the tree. However, simulations performed with MrBayes demonstrated that it is rather robust to the assumed CM (Goloboff et al., 2019). In the following, the focus is set only on maximum parsimony. Moreover, because this thesis thematically belongs to the field of palaeobiology, only osteological data is going to be included, which is in most cases the only source of information as DNA decays through time and is rarely available in fossils.

During the last decades, computing power has drastically increased and so has the capacity of data to be processed for a phylogenetic analysis. This allowed for character matrices to become extremely large over the last years (Murphy *et al.*, 2021). Godefroit *et al.* (2013), for instance, published a matrix consisting of 101 OTUs and 992 morphological characters. Previous studies observed an increase of homoplasy as a result from the growth of datasets (Kluge and Farris, 1969; Archie, 1989, 1996; Sanderson and Donoghue, 1989, 1996; Klassen *et al.*, 1991; Archie and Felsenstein, 1993; Lamboy, 1994; Givnish and Sytsma, 1997; Hauser and Boyajian, 1997;

Wiens, 2004). However, the increase in size of the character matrix seems not to be linked to a general decrease of the phylogenetic signal (Wiens, 2004; Murphy *et al.*, 2021). Moreover, homoplasy can be tackled by weighting characters inversely to it. Farris (1969) and Goloboff (1993, 1997, 2014), for instance, established several methods to weight characters according to their homoplasy.

1.2. Obstacles in palaeontological phylogenies

Incorporating fossils in phylogenetic analyses helps understanding evolutionary processes in deep time (Raup and Sepkoski, 1982), because fossils can be used for the calibration of molecular clocks (e.g., Pyron, 2011). Also, fossil taxa can break long branches, reducing the misleading phenomenon of long-branch attraction, and by that improve phylogenetic analyses (Donoghue *et al.*, 1989; Wiens, 2005; Legg *et al.*, 2013).

Thus, palaeontological material is an essential and inevitable source of information for the reconstruction of the history of life, but its usage bears certain obstacles which have to be taken into account.

1.2.1. Data problem

A major obstacle for fossil phylogenetic analyses is the often fragmentary or deformed condition of many fossils (e.g., McIntosh, 1990; Madsen *et al.*, 1995). Hence, the low information preserved in the data minimises the phylogenetic signal, and it can lead to high numbers of missing entries in the datasets. This, in turn, can result in the recovery of several conflicting most parsimonious trees (MPTs; Gauthier, 1986; Huelsenbeck, 1991; Wilkinson and Benton, 1995; Pol and Escapa, 2009). Hence, the phylogenetic position of those fragmentary fossils can remain uncertain.

This problematic positioning of fragmentary fossils needs a careful evaluation. An example for such an evaluation of phylogenetic results based on fragmentary fossils is given in the following part of the chapter which is published as an open access paper in *Cladistics* as:

Lukardis C. M. Wencker, Emanuel Tschopp, Andrea Villa, Marc L. Augé, Massimo Delfino (2021). Phylogenetic value of jaw elements of lacertid lizards (Squamata: Lacertoidea): A case study with Oligocene material from France. *Cladistics*. 37 (6): 765–802. https://doi.org/10.1111/cla.12460

1.2.1.1. Abstract

Several extinct species are known from the family Lacertidae, but due to poor preservation, many of them are based on single bones. Here, we compare phylogenetic signals of disarticulated premaxillae, maxillae and dentaries of lacertids from four French Oligocene localities (Coderet, La Colombière, Roqueprune 2, Mas de Got B). We identified five morphotypes among the premaxillae, six among the maxillae, and ten among the dentaries. These morphotypes were scored as individual taxa per locality into three separate character matrices with the same 246 characters, one matrix for each jaw element. Subsequently, the phylogenetic position of the morphotypes was tested using maximum parsimony. The consensus trees with the dentaries and the maxillae found a large polytomy including all taxa except the outgroup taxon Gekko gecko. The consensus tree with the premaxillae showed a considerably more resolved topology but found all morphotype taxa outside Lacertidae. In a second step, we compared the constitution of our three datasets and the morphotype taxa. Our results suggest that a combination of convergent characters and missing data led to the outgroup position of the premaxilla morphotype taxa. The poor resolution of the maxillae strict consensus is likely a consequence of their fragmentary preservation. For the dentaries, a high amount of missing data due to the high number of morphotype taxa most likely caused the poor tree resolution. Indeed, tests with fewer morphotypes found tree resolutions comparable to the premaxilla data. When linking the morphotypes, five possible lacertid "species" were found. Comparison with already known French Oligocene lacertid species points to a slightly higher species richness of Lacertidae at that time than known before. Reliable species classification based on phylogeny only seems possible when combining the jaw elements or in association with other cranial and postcranial material, putting some doubt on species identifications based on single bones.

1.2.1.2. Introduction

The family Lacertidae constitutes the taxonomically dominant reptile group in Europe (Arnold *et al.*, 2007; Sillero *et al.*, 2014; Speybroeck *et al.*, 2016; Villa and Delfino, 2019a; Speybroeck *et al.*, 2020). These small to medium-sized lizards are represented by >300 extant species from Eurasia and Africa (Arnold *et al.*, 2007; Uetz *et al.*, 2018). Lacertidae includes endemic "island giants" such as *Gallotia stehlini* and *Gallotia simonyi* from the Canary Islands (Arnold, 1973),

but also the widely distributed species *Lacerta agilis*, which occurs from Western Europe all the way east to Mongolia (Arnold *et al.*, 2007).

The place and time of origin of Lacertidae are still being debated. Their geographical origin was suggested to be located in Europe (Estes, 1983a; Fu, 1998). Also, crown-group lacertids are thought to have originated in Europe, based on the fact that fossils considered to be close to or at the base of the crown group were found on this continent (Borsuk-Bialynicka et al., 1999; Čerňanský and Augé, 2013). Moreover, the lacertid sister clade Eolacertidae is also known from the Eocene of Europe (Čerňanský and Smith, 2018). In terms of timing, molecular clock analyses identified a middle Cretaceous age for the most recent common ancestor of Lacertidae and Amphisbaenia (98 Myr old; Wiens et al., 2006) but the calibration date used has since been questioned (Hipsley et al., 2009). The earliest putative crown-lacertid was Plesiolacerta from the middle Eocene of Lissieu (Mammal Palaeogene zone (MP) 14; Augé, 2005; Čerňanský and Augé, 2013). Additionally, a recent study found strong morphological similarities between modern Lacertidae and skeletal material from the early Eocene of Mutigny, France (MP 8–9; Čerňanský et al., 2020). These studies are further supported by molecular clock analyses yielding estimates for the split between Lacertinae and Gallotiinae during the late Paleocene (58-56 Ma; Hipsley et al., 2009). Challenges regarding the interpretation of the time of origin of Lacertidae also derive from the difficulties in resolving higher-level phylogenetic relationships.

Molecular and morphological data have created contradictory relationships among major clades within Squamata (Losos *et al.*, 2012). Morphological studies recovered Iguania as sister to all other squamates (Scleroglossa), and Lacertidae as sister to Scincoidea within Scincomorpha (Estes *et al.*, 1988; Conrad, 2008; Gauthier *et al.*, 2012). However, molecular-based phylogenies found Iguania nested more crown-ward within Squamata and Lacertidae as sister to Amphisbaenia (Townsend *et al.*, 2004; Vidal and Hedges, 2005; Wiens *et al.*, 2012; Pyron *et al.*, 2013). Attempts with total-evidence analyses including fossils found tree topologies within Squamata that were congruent with relationships among higher-level clades recovered based on molecular data only, implying that differences between morphological and molecular phylogenies are the result of convergence, and confirming the close relationship of Lacertidae and Amphisbaenia (Wiens *et al.*, 2010; Müller *et al.*, 2011; Reeder *et al.*, 2015). Only recently, two studies found for the first time morphological phylogenies that were in agreement with molecular and combined analyses, as they recovered Gekkota as the earliest

squamate crown clade and Iguania further up in the tree: one study was performed with a subset of morphological characters (vertebrae) (Augé and Guével, 2018); the second study had a larger outgroup sampling compared to earlier morphological analyses (and the whole skeleton considered) and found Lacertidae as sister to Amphisbaenia (Simões *et al.*, 2018). Additional challenges impacting studies of the origin of Lacertidae derive from the state of preservation of early extinct members of the group.

Taxonomic and systematic studies are greatly complicated because fossil squamates generally are found disarticulated (Rage, 2013). Disarticulation can result both from preservation and collection bias, and is especially widespread among Palaeogene lacertid lizards, so information about their early history is limited (Čerňanský and Augé, 2013). Among the few exceptions of articulated fossil lacertids worth mentioning are exceptional cases of preservations in amber, on slabs/blocks and in dry environments. An almost complete specimen preserved in Baltic amber has been referred to Succinilacerta succinea by Borsuk-Bialynicka et al. (1999). Thanks to a block containing an almost complete and previously unpublished skull with a few associated postcranial bones, the osteology and phylogenetic relationships of the Oligocene lacertid Dracaenosaurus croizeti is now known in detail (Čerňanský et al., 2017). Janosikia *ulmensis* has been revisited and redescribed on the basis of two partially preserved individuals represented by several cranial and some postcranial elements embedded in early Miocene slabs from Germany (Čerňanský et al., 2016). Two mummified and therefore articulated partial skeletons of giant lacertids, coming from the Quaternary filling of a basaltic cavity on the Canary Islands, have been originally described by Castillo et al. (1994), and were subsequently used to extract ancient mtDNA by Maca-Meyer et al. (2003). However, the majority of extinct lacertid species were erected based on single bones only, mostly tooth-bearing bones (maxillae and dentaries in particular) as well as parietals (for European post-Palaeogene taxa, see Villa and Delfino, 2019a, and references therein; for the osteology of European lizards, see Villa and Delfino 2019b, and references therein). These are generally considered as being the most diagnostic elements and thus having the highest taxonomic value in the lacertid skull. However, such an approach to taxonomy can be problematic. Species descriptions and identifications based on highly fragmentary material can lack true diagnostic features. An example is the species Lacerta altenburgensis. This species was described by Rauscher (1992) based on a single maxilla with a uniquely shaped zygomatic process. However, personal observation of the type maxilla by one of us (E. Tschopp in 2016) revealed that the proposed diagnostic shape of the dorsal edge of the zygomatic process is most likely the result of damage because the

orbital margin of the zygomatic process seems to have sharp edges derived from breakage. The validity of other species is more difficult to test because they are based on subtle differences in shapes or ratios of completely preserved bones or teeth, without a detailed assessment of variability of these traits in a fossil sample or among extant species. This issue obviously impacts any further analysis using species occurrences to reconstruct evolution and/or study biodiversity through time.

Species identifications are crucial to understand the systematics of a particular group, as well as its evolutionary history. Assessments of evolutionary patterns and rates within clades generally rely on the number of reported species or genera (Barrett and Upchurch, 2005; Pereira, 2015; Wiens, 2015; Tennant et al., 2016), which can then be tested for correlations with ecology, palaeoenvironmental or climatic changes in order to understand potential drivers of biodiversity. A great study system to analyse the impact of climatic changes on lacertid evolution is the Oligocene with its abruptly cold temperatures after the Paleocene-Eocene Thermal Maximum (PETM) (Zachos et al., 2001, and references therein) and the warm period registered in the Eocene (Prothero, 1994) leading to the so called "Grande Coupure Eocène/Oligocène" (Stehlin, 1909). The response of the lacertids to these climatic and environmental changes is of high interest, especially considering the assumed close temporal association with the origin of crown-group lacertids. However, in order to understand how these climatic changes influenced taxonomic diversity, it is of crucial importance to assess the validity of the species that occurred during that period of time, as well as the methodology that was used to distinguish them at first place (see also Tschopp et al., in press). Here, we test the latter by comparing the phylogenetic signal of three tooth-bearing jaw elements of lacertid lizards that often were used to distinguish and erect new species from that period: premaxillae, maxillae and dentaries.

Institutional Abbreviations

BSPG, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; CIPA, Osteoteca, Laboratorio Arqueociencias, Lisbon, Portugal; COMGR, Collezione Osteologica Mauro Grano, Rome, Italy; FMNH, Field Museum of Natural History, Chicago, USA; GMZ, Grant Museum of Zoology and Comparative Anatomy, University College London, UK; HUJ-OST, Osteological Collections, Hebrew University of Jerusalem, Israel; ICP, Institut Català de Paleontologia Miquel Crusafont, Barcelona, Spain; IRSNB, Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; MDHC, Massimo Delfino Herpetological Collection in the Museum of Geology and Paleontology of the Department of Earth Sciences of the University of Turin, Italy; MNCN, Museo Nacional de Ciencias Naturales, Madrid, Spain; MNHN, Muséum National d'Histoire Naturelle, Paris, France; MRAC, Musée Royal de l'Afrique Centrale, Tervuren, Belgium; NHMUK, Natural History Museum, London, UK; NHMW, Naturhistorisches Museum Wien, Austria; PIMUZ, Paläontologisches Institut und Museum der Universität Zürich, Switzerland; SRK, Sammlung Ralf Kosma, Staatliches Naturhistorisches Museum Braunschweig, Germany; UAM, Universitad Autónoma de Madrid, Spain; UCBL, Université Claude Bernard, Lyon, France; YPM, Yale Peabody Museum, New Haven, USA; ZZSiD, Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Krakow, Poland.

1.2.1.3. Materials and methods

Studied material

The studied material from four Oligocene localities in France (Coderet, La Colombière, Roqueprune 2, Mas de Got B; Figure 1.1) was initially assigned to Lacertidae and is stored in the collections of the MNHN in Paris. All studied remains are associated with preliminary collection numbers which include a code indicating the collecting site (e.g., MdGB-1, MdGB-2, ... for remains from Mas de Got B). We studied a selected set of samples containing 156 disarticulated jaw elements from these localities. Although for La Colombière, Roqueprune 2 and Mas de Got B one single sample from each locality was selected, we had six samples from Coderet: Fouilles Viret, Coderet Couche 1 sup, Coderet Couche Verte sup 1-25, Coderet E1-0, Coderet H1-100 and Coderet H1-75. Each sample of Coderet corresponds to a different spot or stratigraphic layer within the locality. The latter three samples were taken during excavations in the 1960s (Hugueney, 1969). The labelling of those samples corresponds to the excavation grid, which was numbered A to J from East to West, and 0 to 2 from South to North. Samples were taken from different stratigraphic levels in those sectors, dividing them into increments of 0.25 m from the surface level downwards (e.g. Coderet E1-0 was taken from sector E1 at a depth of 0-0.25 m below surface; Hugueney, 1969; de Bonis et al., 1999). We have no information on the precise place and stratigraphic layer for the other samples. In order to keep the information gained from the sample sets separated, we did not create one large set for Coderet but instead retained the original subsamples.



Figure 1.1. Map of France indicating the geographical positions of the four Oligocene localities with black stars. Cod, Coderet; LaC, La Colombière; Roq2, Roqueprune 2; MdGB, Mas de Got B.

Geological background

In the South of France, Roqueprune 2 is located in the Département Tarn-et-Garonne and Mas de Got B in the Département Lot; both are approximately 100 km N of Toulouse. They belong to the karstic phosphate deposits of Quercy (Phosphorites du Quercy; Vianey-Liaud, 1974; Vianey-Liaud and Wood, 1976) and originated from slow fissure fillings. In most cases, the deposits of Quercy did not retain the original order of sedimentation and younger layers are mixed with older ones (Vianey-Liaud and Marivaux, 2016). Therefore, the precise age of the

fossils often is uncertain (de Bonis, 1974, 2011, and references therein). However, the sediments of Mas de Got B were correlated with the MP 22, and thus represent the oldest of the fossil localities studied herein; Roqueprune 2 was correlated with the slightly younger MP 23 (Schmidt-Kittler *et al.*, 1987; Aguilar *et al.*, 1997). Therefore, both localities represent Rupelian deposits.

Coderet is located at the northern part of the Allier basin in the Département Allier, 30 km SW of Moulins at Limagne bourbonnaise. Limagne is a collapsed basin orientated in a N–S direction (Hugueney, 1969; de Bonis *et al.*, 1999). It is backfilled with detrital and carbonate sediments (lacustrine and local forest resources). The quarry of Coderet is in contact with the western border fault of Limagne (Hugueney, 1969; de Bonis *et al.*, 1997) and is therefore of Chattian age.

La Colombière is located in the Département Hérault in the suburbs of the city of Montpellier. It is a depositional group of narrow fissure fillings (Thaler, 1966). It belongs to the Coderet zone and is, therefore, of Chattian age as well (MP 30; Thaler, 1966; Schmidt-Kittler *et al.*, 1987).

Character matrix construction

The three lacertid jaw elements on which we focused (premaxilla, maxilla, dentary) were classified into individual morphotypes based on morphological differences such as, for example, the complexity of their tooth crowns, which were based on the character matrix explained below. These morphotypes were divided into single morphotype operational taxonomic units (mOTUs) based on their respective localities. We minimized the amount of missing data and kept the geographical and stratigraphic information separated by creating those bone-specific mOTUs. This procedure of treating disarticulated elements for phylogenetic analysis is, to our knowledge, performed here for the first time in squamates. To label the mOTUs, we used the names for the morphotypes, which contain the letter P for premaxilla, M for maxilla and D for dentary plus a successive cipher, and combined it with an abbreviation of the locality (FV: Fouilles Viret; CC1sup: Coderet Couche 1 sup; CCVsup: Coderet Couche Verte sup 1-25; CE1-0: Coderet E1-0; CH1-100: Coderet H1-100; CH1-75: Coderet H1-75; LaC: La Colombière; Roq2: Roqueprune 2; MdGB: Mas de Got B). For instance, the mOTU identified as premaxilla morphotype P1 from the sample of Fouilles Viret was given the name P1 FV.

We then created three phylogenetic matrices with the same 246 osteological characters (180 cranial and 66 postcranial ones), each of which included the morphotypes of a single jaw element. In this way, we avoided potential problems for the algorithm resulting from lacking anatomical overlap among the elements under study (Tschopp et al., 2018a). The matrices were created with MESQUITE (v.3.51, build 898; Maddison and Maddison, 2018). They are based on the matrix of Tschopp et al. (2018b), which was, in turn, an updated version of the matrix used by Villa et al. (2017). Twenty-four characters were added based on literature (including one that was used by Villa et al., 2017, but excluded in Tschopp et al., 2018b) and on personal observations (see Appendix 1 and references therein). We excluded one character from the original matrix of Tschopp et al. (2018b) (Character 217: Inscriptional ribs: absent (0); present (1)) because it had the same character state for all scored taxa and was, therefore, uninformative in our specific case. Moreover, we added seven outgroup and 11 ingroup operational taxonomic units (OTUs). The matrix consists mostly of extant species, with the addition of extinct lacertid species known from the Oligocene: Ligerosaurus pouiti (Augé, 1993), Mediolacerta roceki Augé, 2005, Plesiolacerta lydekkeri Hoffstetter, 1942, Pseudeumeces cadurcensis (Filhol, 1877), Dracaenosaurus croizeti Gervais, 1848-1852, and "Lacerta" filholi Augé, 1988. We created two separate locality-level OTUs for Dracaenosaurus croizeti, one representing the material found in Cournon (approximately 10 km E of Clermont-Ferrand; MP 28; Schmidt-Kittler et al., 1987; Čerňanský et al., 2017), and the other including material from Coderet. The same strategy was applied for "Lacerta" filholi, with one OTU representing the material found in Pech-du-Fraysse (including the holotype; approximately 30 km SE from Aurillac; Quercy Phosphorites; MP 28; Schmidt-Kittler et al., 1987), and the other combining the information from material from Coderet (see the Supplementary material for a complete list of taxa and characters).

The outgroup now comprises *Gekko gecko* (Linnaeus, 1758) as a representative of the most basal squamatan clade Gekkota (molecular, total-evidence and morphological analyses agree on Gekkota being one of the most basal groups within Squamata; Gauthier *et al.*, 2012; Reeder *et al.*, 2015; Zheng and Wiens, 2015; Simões *et al.*, 2018). Where specimens were available for first-hand scoring, the more derived outgroups were represented by more than one species, following the recommendations by Brusatte (2010) and Tschopp and Upchurch (2019). Squamatan clades represented in this updated matrix are the Scincoidea, Anguimorpha, Teiidae and Amphisbaenia. Scincoidea is represented by *Chalcides ocellatus* (Forskal, 1775), *Broadleysaurus major* (Duméril, 1851) and *Ablepharus kitaibelii* (Bibron and Bory de Saint-

Vincent, 1833). The position of Scincoidea is unclear, with molecular data indicating a position near the base of the squamate tree as the sister taxon to Lacertoidea + Toxicofera (Pyron et al., 2013; Reeder et al., 2015; Zheng and Wiens, 2015), and morphological data recovering the group close to Lacertoidea, with which it forms the clade Scincomorpha (Estes et al., 1988; Conrad, 2008; Gauthier et al., 2012). Anguimorpha is represented herein by Varanus exanthematicus (Bosc, 1792), Anguis veronensis Pollini, 1818, and Pseudopus apodus (Pallas, 1775). The relative position of this clade is unclear too, being recovered in the opposite positions compared to Scincoidea. Molecular and morphological data find Anguimorpha within a clade that includes also Iguania and Serpentes (among other groups), and which forms the sister taxon to Lacertoidea (Reeder et al., 2015; Zheng and Wiens, 2015; Simões et al., 2018). Within Lacertoidea, Teiidae are represented by Salvator merianae Duméril and Bibron, 1839. Amphisbaenia is represented by Blanus rufus (Hemprich, 1820) and Blanus strauchi (Bedriaga, 1884) and is thought to be the sister taxon of Lacertidae based on molecular data (Zheng and Wiens, 2016). The ingroup Lacertidae is scored at species-level herein, mostly based on observations of ten or fewer specimens per species by one or more of the authors. In order to accurately represent intraspecific polymorphisms, we used majority scoring for polymorphic characters, following Wiens (1995). Where an equal number of specimens showed different character states, we scored the species as polymorphic. Hence, variation of character states that occurred only in a minority of the specimens belonging to one species was not factored in, this should be born in mind during data interpretation.

Phylogenetic analysis

For the species-level phylogenetic analysis with a maximum parsimony approach, we used the software TNT (v.1.5; Goloboff and Catalano, 2016). Extended implied weighting with a K-value of 5, 12 and 20, and the default setting for assumed homoplasy for missing entries was applied to reduce the influence of highly variable characters and missing data (Goloboff, 2014; Goloboff *et al.*, 2018; see also recommendations in Tschopp and Upchurch, 2019). The tree search was performed using the New Technology search, enabling all algorithms with their default settings, and stabilizing the consensus tree five times with a factor of 75. The resulting best-fitting trees were used as a starting point for a second iteration of tree bisection and reconnection (traditional heuristic search) to ensure a better tree space coverage. Twenty-seven

multistate characters were treated as ordered, as they were either quantitative characters or formed a morphocline (Brazeau, 2011).

Preliminary analyses recovered vast polytomies in the strict consensus trees, most likely due to the highly incomplete state of many of the fossil OTUs to be tested herein. Therefore, the analyses were run with 13 constraints to ensure the generally accepted basic structure of the trees (as obtained from molecular data; Zheng and Wiens, 2016). The constraints defined Scincoidea (Chalcides, Broadleysaurus, Ablepharus), Lacertoidea (Amphisbaenia, Lacertidae, Teiidae), Anguimorpha (Varanus, Anguis, Pseudopus), Amphisbaenia (Blanus), Lacertidae (Gallotiinae and Lacertinae), Gallotiinae (Gallotia and Psammodromus), Lacertinae (Eremiadini and Lacertini), Eremiadini (Acanthodactylus, Eremias, Mesalina, Ophisops), Anatololacerta. Archaeolacerta. Lacertini (Algyroides, *Iberolacerta*. Lacerta. Phoenicolacerta, Podarcis, Takydromus, Timon, Zootoca), and the genera Podarcis, Algyroides, Iberolacerta and Lacerta. We excluded the French mOTUs, and the extinct species Dracaenosaurus croizeti, Ligerosaurus pouiti, Mediolacerta roceki, Pseudeumeces cadurcensis, Plesiolacerta lydekkeri and "Lacerta" filholi from all constraints, as no molecular data for those taxa are available. Therefore, they are considered to be "wild card taxa" and could be recovered at any position in the tree by the analysis. It should be noted that the constrained clades might only be recovered partly or not at all in the resulting strict consensus tree as a consequence of conflicting tree topologies in some cases.

Jaw element comparison

Character testing

In order to be able to compare the phylogenetic values of the three different jaw elements (premaxilla, maxilla, dentary) we had to ensure the comparability of the three datasets. To do so, we used both a quantitative and a qualitative approach for character comparison. First, we compared the number of characters existing in the matrix for each jaw element individually; characters scored for two or more elements at once were counted multiple times (e.g., characters that code for maxillary and dentary teeth).

In a second step, the characters describing the three jaw elements were classified into "quantitative" and "qualitative" characters, with a further subdivision of the quantitative characters into "meristic" and "morphometric", and of qualitative characters into "countable/measurable" and "shape-describing" characters (Table 1.1; classifications of the

individual characters can be found in the Supplementary material). The distribution of the different character types then was expressed as a percentage of the total number of characters for each jaw element.

Character type	Character subtype	Definition	Example
quantitative	meristic	character states are countable	Maxilla, number of labial foramina: 6 or less (0); >6 (1).
	morphometric	character states are measurable	Premaxilla, tooth-bearing portion, curvature, anterior-posterior length to transverse width: <0.2 (wide) (0); 0.2-0.4 (intermediate (1); >0.4 (narrow) (2).
qualitative	countable/ measurable	character states are neomorphic (absent/present; Sereno, 2007) or have a "countable" state	Premaxilla, ascending nasal process, posterior end of medial ridge, shape in lateral view: bifid, with dorsal and ventral spurs (0); single (1).
	shape describing	character states are transformational (Sereno, 2007): they describe shapes that are not "measurable"/ "countable"	Dentary, subdental ridge, shape: straight (0); concave (1).

Table 1.1. List of character types and subtypes used for the quantitative approach of jaw element comparison with their definitions and examples.

Morphotype testing

Based on the number of characters describing the premaxilla, maxilla and dentary obtained from the first part of the character testing, we took into account the preservation state or "specimen" completeness of the individual mOTUs. We calculated the actual percentages of scorable characters among the previously regarded characters describing the individual jaw elements.

The three jaw elements were represented by different numbers of morphotypes for each sample, changing the number of total OTUs, and thus effectively the taxon sampling among the three

matrices. In order to avoid a potentially confounding impact on the analysis based on the number of OTUs, we ran the phylogenetic analysis ten times per jaw element under the same conditions as stated above, with subsampled datasets reduced to five randomly picked mOTUs for each analysis and ensuring that each mOTU was picked at least once.

In addition, we tested the stability of the mOTUs with respect to their tree position. We followed the procedure for rogue taxa identification used in Pei *et al.* (2020) with minor modifications to their TNT script (*improvecombin.run*). In a first step, unstable (rogue) taxa were identified heuristically (*prune nelsen*). We allowed a maximum of n + 1 taxa to be pruned at the same time (n = number of mOTUs per jaw element). In a second step, the heuristically identified unstable taxa were checked by testing the tree resolution when adding or removing the unstable taxa in different combinations (*prune-up-and-down*). Here, combinations of up to n + 1 taxa could be reinserted in the tree and the pruning was evaluated with a factor F of 0.9. Factor F defines the penalty for the removal of a taxon, it varies between 0 and 1; the higher the number the more costly the removal. Given that our mOTUs were very fragmentary, we decided to select a higher factor F to identify the taxa whose removal increased the tree resolution the most. We identified unstable taxa for all analyses of the complete datasets (K = 5, 12 and 20). As last, we included only the stable mOTUs of each jaw element dataset. The analyses were run under the same parameters as before.

As a last test, we merged the locality-level mOTUs belonging to the same morphotype into a single cross-regional mOTU by following the majority rule. In this way, the amount of missing data could be reduced in some cases. Consequently, we created, in congruence with the number of observed morphotypes, five cross-regional mOTUs for the premaxilla, six for the maxilla and ten for the dentary dataset. The following morphotypes were present only in a single locality and therefore were kept as they were: P4 CE1-0, M2 CC1sup, M5 CE1-0, M6 CE1-0, D5 CE1-0, D6 CE1-0 and D10 Roq2. We reran the analyses in two steps: first, using only one cross-regional mOTU at a time, and then using all cross-regional mOTUs per jaw-element-dataset. The analysing parameters were the same as before.

1.2.1.4. Results

Morphotype descriptions

Among the jaw elements in our sample, the dentaries were the most abundant representing 68%, with maxillae and premaxillae comprising 23% and 9% of the sample, respectively. In general, the sample from Coderet contained the highest number of jaw elements with 91% of the studied jaw elements coming from this locality. The distribution for Coderet was 66% dentaries, 25% maxillae and 9% premaxillae. For the localities La Colombière and Mas de Got B, neither premaxillae nor maxillae were present. The sample from Roqueprune 2 included 10% premaxillae and 90% dentaries.

Premaxillae

Five different lacertid morphotypes for the premaxilla were identified among the sample of Roqueprune 2 and five subsamples of Coderet (Table 1.2). The preservation of the studied elements generally comprises the tooth-bearing portion with partially preserved teeth, and the anterior part of the ascending nasal process, whereas the posterior end of the nasal process plus the articulation with the nasal are never preserved.

Morphotype P1 (Figure 1.2A) is characterized by seven tooth positions, of which the median tooth is enlarged. The preserved teeth are monocuspid and somewhat globose with narrow longitudinal striae. In one specimen, we observed some indication of bicuspidity in one of the posterior-most teeth (within the sample from Fouilles Viret). The facets for articulation with the maxillae are large. The palatine processes bordering the depression on the horizontal plate are preserved in about half of the specimens. A small pit can be present at the transition of the tooth-bearing portion to the ascending nasal process. The ascending nasal process has a circular cross-section at its base. The ethmoidal foramina at the base of the ascending nasal process are not situated within fossae. The medial ridge on the ventral side of the preserved part of the ascending nasal process is not visible and it therefore probably does not reach far anteriorly.

Morphotype P2 (Figure 1.2B) is rather slender, with seven tooth positions accommodating pencil-shaped teeth, which all seem to be of the same size. The tooth crowns are monocuspid with relatively less dense, narrowly spaced striae, compared to morphotype P1. Large maxillary facets are present, and the ethmoidal foramina are situated within fossae, which are posteriorly bordered by a ridge. Palatine processes were never preserved, so their real absence or presence cannot be confirmed. The horizontal plate seems to have no depression. The ascending nasal

Table 1.2. Occurrences of morphotypes and their abundance given in absolute numbers. P1–P5, premaxillary morphotypes; M1–M6, maxillary morphotypes; D1–D10, dentary morphotypes; Cod, Coderet; FV, Fouilles Viret; CC1sup, Coderet Couche 1 sup; CCVsup, Coderet Couche Verte sup 1–25; CE1–0, Coderet E1–0; CH1–100, Coderet H1-100; CH1–75, Coderet H1–75; LaC, La Colombière; Roq2, Roqueprune 2; MdGB, Mas de Got B.

Locality		P1	P2	Р3	P4	Р5	M1	M2	М3	M4	M5	M6	D1	D2	D3	D4	D5	D6	D7	D8	D9	D10
Cod	FV	1				1	4						2	5								
	CC1sup	2	1				4	3	4	1			21	10	6							
	CCVsup	1					5			1				4		1			6	3		
	CE1-0	2	2	1	1		7			2	1	1	5	6		3	2	3	5			
	СН1-100						1		1	1				3	2					1		
	СН1-75					1								2	2	1						
LaC																					2	
Roq2				1																1	7	1
MdGB																2						

process is very slender, dorsoventrally higher than wide, and the medial ridge on its ventral side does not reach far anteriorly.

Morphotype P3 (Figure 1.2C) has an overall shape which is similar to morphotype P2. It has seven tooth positions with monocuspid, rounded and narrowly striated teeth. The maxillary facets on the tooth-bearing portion are smaller than in morphotype P2 but still large. The ethmoidal foramina are situated within fossae, which are not completely closed and delimited posteriorly by a ridge. A pit at the base of the ascending nasal process can be present. Palatine processes might be absent or broken off, and the horizontal plate has no depression. The preserved part of the ascending nasal process has parallel lateral margins and the medial ridge on its ventral side does not seem to reach far anteriorly, as it is not visible on the preserved part of the ascending nasal process.

Morphotype P4 (Figure 1.2D) differs from the other morphotypes in having nine teeth. The teeth are slender, rather fang-like and curved posteriorly. Their tooth crowns show no sign of striation. The tooth-bearing portion is relatively wide and straight with steep and small maxillary facets. The ethmoidal foramina are located lateral to the ascending nasal process, penetrating the horizontal lamina. The ascending nasal process is wider than dorsoventrally high and seems to be straight throughout its entire length with the medial ridge probably being restricted to the posterior part.

Morphotype P5 (Figure 1.2E) has seven tooth positions with monocuspid, globose-like teeth which bear narrowly spaced, longitudinal striae. The maxillary facets are deep and large. The horizontal plate is depressed and continues into two palatine processes. At the base of the ascending nasal process, two pairs of ethmoidal foramina are present; they are not situated within fossae. The ascending nasal process has parallel margins and is wider than dorsoventrally high. The medial ridge is not reaching far anteriorly on its ventral side.

Maxillae

The preservation of the maxillae was rather fragmentary. Less than 50% of a single element was preserved on average, mostly representing isolated anterior, central and posterior parts. Anterior parts were generally preserved without the facial process and with broken anteromedial/-lateral premaxillary processes. In total, six morphotypes among the maxillae were identified in five subsamples of Coderet (Table 1.2).



Figure 1.2. Overview of premaxilla morphotypes. A, Morphotype P1, premaxilla from Coderet Couche 1 sup (CC1sup-1) in posterior view. B, Morphotype P2, premaxilla from Coderet Couche 1 sup (CC1sup-3) in posterior view. C, Morphotype P3, premaxilla from Coderet E1-0 (CE1-0-5) in anterior view. D, Morphotype P4, premaxilla from Coderet E1-0 (CE1-0-6) in posterior view. E, Morphotype P5, premaxilla from Fouilles Viret (FV-2) in right lateral view. The arrowheads mark important diagnostic structures: 1, enlarged median tooth; 2, ethmoidal foramen within fossa which is not completely closed and bordered posteriorly by a ridge; 3, fang-like, pointed tooth; 4, ethmoidal foramen without fossa; 5, second ethmoidal foramen without fossa. anp, ascending nasal process; et.f, ethmoidal foramen; mf, maxillary facet; pp, palatine process. Scale bar 1 mm. Individual and more detailed figures of the morphotypes can be found in the Supplementary material.

Morphotype M1 (Figure 1.3A) has a maximum of 12 tooth positions preserved in a single element, the total number of teeth in one element is probably between 16 and 20. Most teeth seem to be tricuspid with smooth tooth crowns. In the anterior half, large and robust teeth are present, followed by abruptly smaller teeth in the central part, which are relatively consistent in size. The tooth size increases gradually posteriorly, where the most robust teeth are located. The tooth row is straight in ventral view. For the articulation of the palatine, a slight medial extension is present. The anterolateral premaxillary process has a concave ventral edge. The facial process has a uniform external surface with a well-developed dermal ornamentation. The anterior margin of the facial process is perpendicular to the dental crest for some distance and a small subtriangular process projects anteriorly from the anterodorsal corner of the facial process. On the medial side, the anterior margin is connected with the carina maxillaris by a small ridge. There is no step visible at the orbital margin of the zygomatic process.

Morphotype M2 (Figure 1.3B) was never preserved with a facial process. An indication of dermal ornamentation is present. The maximum number of observed teeth in a single element is 12, whereas the total number is probably approximately 16–20 teeth. The majority of the tooth crowns seem to be tricuspid with widely spaced striae, but bicuspid teeth do occur in the anterior part. The four posterior-most teeth are significantly smaller and less robust than the succeeding ones in the posterior half. Teeth in the central part decrease gradually in size and robustness. The tooth row is straight in ventral view, and the supradental shelf extends slightly for the articulation with the palatine. The orbital margin of the zygomatic process seems to be smooth.

Morphotype M3 (Figure 1.3C) was always preserved without the premaxillary processes, but the nasal recess and central-posterior parts were present. The facial process is incomplete in all elements. Its anterior margin is clearly perpendicular to the dental crest and connected with the carina maxillaris on the medial side by a small ridge. The lateral surface is uniform without a distinct groove, but with well-developed dermal ornamentation. The zygomatic process seems to be slightly undulating, but without a distinct step. The development of tooth size and robustness throughout the tooth row is similar to morphotype M1, but the tri- and bicuspid teeth have widely spaced striae instead of being smooth. The preserved teeth in the anterior half are more robust than the posteriorly succeeding teeth, whereas the posterior-most teeth seem to be the most robust.

Morphotype M4 (Figure 1.3D) is more robust and larger than morphotypes M1, M2 and M3, as well as M6. Only the anterior part is preserved. The lateral surface has no groove that would separate the ventral and dorsal portions, but a well-developed dermal ornamentation is present. The anterior margin of the partly preserved facial process is perpendicular to the dental crest for some distance. On the medial side, the anterior margin is connected with the carina maxillaris by a small ridge. The anterolateral premaxillary process has a concave ventral edge in lateral view. The anteromedial premaxillary process bears a dorsomedially projecting spur close to the anterior end. The three to four anterior-most teeth are smaller and less robust than the (approximately) two succeeding ones, which are then followed by again less robust teeth; the increase in size seems to be gradual. The teeth are slightly fang-like with tooth apices pointing posteriorly. The tooth crowns are mostly mono- or bicuspid with widely spaced striae; there is some indication of tricuspidity present in the more posterior teeth.

Morphotype M5 (Figure 1.3E) is relatively robust with a uniform external surface and no dermal ornamentation. The anterior margin of the facial process is perpendicular to the dental crest and does not bear a subtriangular process. On the medial side, the anterior margin is connected to the carina maxillaris by a small ridge. The preserved onset of the anterolateral premaxillary process shows a concave ventral edge. The teeth are similar to the ones of the premaxilla morphotype P1 in being monocuspid and globose-like with narrowly spaced striae on the tooth crowns. In general, the tooth size seems to increase distinctly posteriorly.

Morphotype M6 (Figure 1.3F) has a rather slender shape with a uniform external surface and no dermal ornamentation. The teeth are monocuspid and fang-like with strongly backwards curved apices. The crown surfaces have no striation.



Figure 1.3. Overview of maxilla morphotypes. A, Morphotype M1, left maxilla from Coderet E1-0 (CE1-0-7) in lateral view. B, Morphotype M2, right maxilla from Coderet Couche 1 sup (CC1sup-8) in medial view. C, Morphotype M3, right maxilla from Coderet Couche 1 sup (CC1sup-11) in lateral view. D, Morphotype M4, left maxilla from Coderet Couche 1 sup (CC1sup-15) in lateral view. E, Morphotype M5, right maxilla from Coderet E1-0 (CE1-0-16) in medial view. F, Morphotype M6, right maxilla from Coderet E1-0 (CE1-0-17) in medial view. The arrowheads mark important diagnostic structures: 1, subtriangular process; 2, facial process which is perpendicular to dental crest; 3, dermal ornamentation; 4, concave ventral edge of anterolateral premaxillary process; 5, slight medial extension for articulation with palatine; 6, abruptly smaller and less robust posterior-most teeth; 7, larger tooth in anterior-half; 8, globose-like, monocuspid tooth; 9, fang-like, pointed tooth. alp, anterolateral process; ca.m, carina maxillaris; fp, facial process; ps, palatine shelf; zp, zygomatic process. Scale bar 1 mm. Individual and more detailed figures of the morphotypes can be found in the Supplementary material.

Dentaries

The dentaries always lack the angular process, and for most of the elements, either only the posterior or only the anterior part is preserved. However, one almost complete mandible and some almost complete dentaries were among the samples. In total, ten morphotypes could be identified among the studied bones from all four localities (Table 1.2).

Morphotype D1 (Figure 1.4A) is slender, but continuously broadens dorsoventrally towards its distal end. The maximum number of teeth observed in a complete tooth row is 23. Most of the teeth seem to be bicuspid and no striation is visible. However, tricuspid teeth are present in the posterior half. The change in tooth size is gradual with the most robust teeth being located in the posterior part. The subdental ridge is concave; its thickness increases anteriorly. A distinct splenial facet is present, which indicates a splenial extending for approximately ³/₄ of the tooth row. The anterior-most teeth are strongly tilted anteriorly. The Meckelian canal is triangular and reaches the symphysis, which seems to have a distinct articular facet. The coronoid facet is distinct.

Morphotype D2 (Figure 1.4B, C) is very similar to morphotype D1. Its shape also is rather slender, but continuously broadening distally. The majority of the preserved teeth are bicuspid, a few tricuspid teeth occur in the posterior half. At the tip of the dentary, the teeth are procumbent. The tooth crowns have widely spaced striae. The Meckelian canal reaches the symphysis. The articulation facet of the symphysis seems to be distinct. The subdental ridge is concave and thickens anteriorly. Two elements are preserved with parts of the splenial (among the sample of Fouilles Viret, Coderet E1-0), which has a bifid anterior end. The extent of the splenial seems to be approximately ³/₄ of the tooth row with a distinct splenial facet. The coronoid facet is distinct.

Morphotype D3 (Figure 1.4D, E) is more robust than the other dentary morphotypes. The concave subdental ridge is very thick, with the greatest thickness anteriorly, and a well-developed splenial facet. Teeth at the tip of the dentary are tilted anteriorly. The most robust teeth in the posterior part of the dentary show clear tricuspidity, whereas bicuspid teeth are present in the anterior part. The tooth crowns have widely spaced longitudinal striae. The coronoid facet is distinct. The Meckelian canal is triangular and open until the symphysis, which seems to have a distinct articulation facet.

Morphotype D4 (Figure 1.4F, G) is similar to the morphotypes D1 and D2. The element is continuously broadening with the most robust teeth in the posterior part. The tooth size gradually decreases anteriorly. Tricuspid teeth are present in the posterior part, whereas the teeth become bicuspid anteriorly and might be monocuspid close to the symphysis. The anterior-most teeth are strongly anteriorly tilted. The tooth crowns have narrowly spaced striae. The subdental ridge is concave and its thickness is increasing anteriorly. The splenial facet is distinct and the posterior end of the splenial is single and pointed. The articulation facet of the symphysis and the coronoid facet are distinct. The angular process is exceeding the apex of the coronoid.

Morphotype D5 (Figure 1.4H-J) has, on the contrary to all other morphotypes, a Meckelian canal which is closed in the anterior part for approximately ¹/₄ of the dental shelf, and that opens again at the very tip. It is situated rather ventrally. The articulation of the symphysis is fairly indistinct, and the teeth do not seem to be tilted anteriorly. The tooth crowns have widely spaced striae and are at least bicuspid. The tooth size increases posteriorly. The subdental ridge is rather straight. The dentary seems to be rather sickle-shaped. No distinct splenial articulation facet is visible. However, only the anterior part of this morphotype is preserved.

Morphotype D6 (Figure 1.5A) is very slender and fragile. It appears to be sickle-shaped with a slightly concave subdental ridge and a weakly developed splenial facet. The preserved teeth are bicuspid with smooth tooth crowns.

Morphotype D7 (Figure 1.5B-D) is slender, but its shape is continuously broadening posteriorly. The subdental ridge is similar to morphotype D6, and less strongly concave than in morphotypes D1, D2, D3 and D4. The splenial facet is distinct, but the splenial seems to extend less far anteriorly than in the other morphotypes (approximately ²/₃ of tooth row). Therefore, the triangular Meckelian canal appears to be narrower than in the aforementioned morphotypes. The open portion of the canal reaches the symphysis, which has a distinct facet. The teeth at the

tip are procumbent. In the posterior part, teeth with very distinct tricuspidity are present with widely spaced striae. The striation is less distinct in the specimens found in Coderet Couche Verte sup 1–25. The tooth size gradually decreases anteriorly. The coronoid facet is distinct.

Morphotype D8 (Figure 1.5E, F) is similar to the morphotype D3. The subtriangular element has a concave subdental ridge that thickens anteriorly. The splenial facet is distinct; it probably extended for approximately ³/₄ of the tooth row. The most robust teeth are present in the posterior part, but the two or three posterior-most teeth are significantly less robust than their neighbouring teeth. Tooth size gradually decreases anteriorly. The tooth crowns have narrowly spaced striae and show tricuspidity in the posterior half, whereas bicuspid teeth are present in the anterior half. The coronoid facet is distinct, whereas the symphysis is relatively indistinct. The teeth at the tip do not seem to be tilted anteriorly.

Morphotype D9 (Figure 1.5G) is similar to morphotype D7. It is relatively slender, with a concave subdental ridge. The teeth have bicuspid tooth crowns, and no indication of tricuspid teeth is visible. The tooth crowns appear to be smooth. The coronoid facet is very distinct. The splenial probably extended for approximately $\frac{2}{3}$ of the tooth row, based on the distinct facets. The Meckelian canal is open until it reaches the seemingly indistinct symphysis. The most robust teeth are present in the posterior part of the dentary, but the two posterior-most teeth seem to be a bit less robust than their anterior neighbours. The teeth at the tip are procumbent.

Morphotype D10 (Figure 1.5H, I) is preserved only as a single anterior tip. The teeth are upright, bulky and globose, with monocuspid tooth crowns bearing narrowly spaced striae. The anterior-most tooth also is the most robust one and the tooth size seems to decrease abruptly posteriorly. The Meckelian canal seems to be triangular (but is not preserved entirely), and reaches the symphysis, which has a distinct articulation facet. The teeth overtop the dental crest by approximately ²/₃, whereas in all other observed dentaries the teeth overtop the dental crest by less than half of their height.

Figure 1.4. Overview of dentary morphotypes D1–D5. A, Morphotype D1, right dentary from Coderet Couche 1 sup (CC1sup-16) in medial view. B, C, Morphotype D2, right dentary from Coderet Couche Verte sup 1-25 (CCVsup-8) in medial view (B), tooth of a left dentary from Coderet Couche 1 sup (CC1sup-46) in medial view (C). D, E, Morphotype D3, right dentary from Coderet Couche 1 sup (CC1sup-47) in medial view (D), teeth of a left dentary from Coderet H1-100 (CH1-100-7) in medial view (E). F, G, Morphotype D4, right dentary from Coderet E1-0 (CE1-0-29) in medial view (F), tooth of a left dentary from Coderet E1-0 (CE1-0-31) in medial view (G). H-J, Morphotype D5, right dentary from Coderet E1-0 (CE1-0-32) in medial (H) and ventral (I) view, tooth of a left dentary from Coderet E1-0 (CE1-0-33) in medial view (J). The arrowheads mark important diagnostic structures: 1, tricuspid tooth crown; 2, distinct articular facet on symphysis; 3, distinct splenial facet; 4, widely spaced striae; 5, narrowly spaced striae; 6, bicuspid tooth crown; 7, Meckelian canal that opened up at the tip. mk.c, Meckelian canal; spl.ft, splenial facet; sy, symphysis. Scale bars 1 mm. Individual and more detailed figures of the morphotypes can be found in the Supplementary material.








Figure 1.5. Overview of dentary morphotypes D6–D10. A, Morphotype D6, right dentary from Coderet E1-0 (CE1-0-34) in medial view. B-D, Morphotype D7, left dentary from Coderet E1-0 (CE1-0-37) in medial view (B), left dentary from Coderet E1-0 (CE1-0-38) in medial view (C), tooth of a left dentary from Coderet Couche Verte sup 1-25 (CCVsup-14) in medial view (D). E, F, Morphotype D8, right dentary from Coderet H1-100 (CH1-100-9) in medial view (E), tooth of a left dentary from Coderet Couche Verte sup 1-25 (CCVsup-19) in medial view (F). G, Morphotype D9, left dentary from La Colombière (LaC-1) in medial view. H, I, Morphotype D10, right dentary from Roqueprune 2 (Roq2-10) in medial view (H), tooth of the right dentary from Roqueprune 2 (Roq2-10) in lateral view (I). The arrowheads mark important diagnostic structures: 1, weakly developed splenial facet; 2, very distinct tricuspid tooth crown; 3, distinct splenial facet; 4, distinct articular facet on symphysis; 5, widely spaced striae; 6, smaller and less robust posterior-most teeth; 7, narrowly spaced striae; 8, large and globose-like monocuspid tooth. Scale bars 1 mm. Individual and more detailed figures of the morphotypes can be found in the Supplementary material.

Phylogenetic analysis

Premaxillae

The analysis of the complete premaxilla dataset produced by far the best strict consensus tree resolution among the three jaw elements. However, all mOTUs were recovered outside Lacertidae (Figure 1.6). A polytomy was present at the base of the tree. It was composed of four OTUs (P1 CCVsup, *Ablepharus kitaibelii, Chalcides ocellatus* and *Varanus exanthematicus*) and four branches: (1) a partly recovered Anguimorpha clade with ((P4 CE1-0, *Anguis veronensis*), *Pseudopus apodus*); (2) a smaller polytomy with ((*Broadleysaurus major*, P3 Roq2), (P2 CC1sup, P2 CE1-0), P3 CE1-0)); (3) a second smaller polytomy with ((*Dracaenosaurus croizeti* (Cod), *Dracaenosaurus croizeti* (Cou), P1 FV, P1 CC1sup, P1 CE1-0), (P5 FV, P5 CH1-75)); and (4) an entirely resolved clade of Lacertoidea.

When applying a K = 5, higher taxonomic relationships were almost completely resolved, showing the general topology of (Gekkota, (Anguimorpha, (Scincoidea, Lacertoidea)))). The mOTUs P3 Roq2 and P4 CE1-0 were recovered within the same clades as stated before. The other mOTUs were recovered as part of Lacertoidea with P1 CCVsup at the base forming a polytomy with two other branches: (1) a smaller polytomy (*Dracaenosaurus croizeti* (Cod), *Dracaenosaurus croizeti* (Cou), P1 FV, P1 CC1sup, P1 CE1-0, P5 FV, P5 CH1-75, (*Blanus rufus, Blanus strauchi*)); and (2) (P2 CC1sup, P2 CE1-0, P3 CE1-0, (*Salvator merianae* + Lacertidae).



Figure 1.6. Strict consensus tree of analysis of the complete premaxilla dataset using a value of K = 20 based on six most parsimonious trees (MPTs). Length of strict consensus: 1547 steps; CI of strict consensus: 0.180; RI of strict consensus: 0.441. Length of MPTs: 1499 steps; CI of MPTs: 0.186; RI of MPTs: 0.462. Arrowheads indicate the premaxilla mOTUs; daggers show the fossil OTUs; locks mark clades with fulfilled constraining. Black branches, non-crown-lacertids; blue branches, Gallotiinae; green branches, Lacertinae. FV, Fouilles Viret; CC1sup, Coderet Couche 1 sup; CE1-0, Coderet E1-0; CH1-75, Coderet H1-75; CCVsup, Coderet Couche Verte sup 1-25; Roq2, Roqueprune 2; PdF, Pech-du-Fraysse; Cod, Coderet; Cou, Cournon. Strict consensus trees of K = 5 and 12 can be found in the Supplementary material.

Maxillae

The strict consensus trees with the maxilla mOTUs recovered a large polytomy, which consisted of all OTUs but the outgroup taxon *Gekko gecko* (Figure 1.7). No further resolved subclades including any of the mOTUs were recovered, but two clades involving mOTUs within the large polytomy were found only for the analysis with K = 5: (1) a polytomy with (M3 CC1sup, M3 CH1-100, M4 CC1sup, M4 CE1-0, M4 CH1-100, "*Lacerta*" *filholi* (PdF)); and (2) a clade with (M2 CC1sup, *Ligerosaurus pouiti*).

Dentaries

Similar to the recovered trees based on the maxilla mOTUs, the strict consensus trees with the dentary mOTUs included a large polytomy consisting of all OTUs but the outgroup taxon (Figure 1.8). Four resolved clades (three for K = 5) comprising mOTUs were found within the polytomy: (1) (*Iberolacerta cyreni* (Müller and Hellmich, 1937), D5 CE1-0), *Iberolacerta monticola* (Boulenger, 1905)); (2) (*Algyroides nigropunctatus* (Duméril and Bibron, 1839), D6 CE1-0), *Algyroides fitzingeri* (Wiegmann, 1834)); (3) (*Blanus strauchi, Blanus rufus*), D10 Roq2); and (4) (D9 LaC, *Podarcis tiliguerta* (Gmelin, 1789)) (only for K = 12 and 20).

Figure 1.7. Strict consensus tree of analysis of the complete maxilla dataset using a value of K = 20 based on more than 100 000 MPTs (overflow). Length of strict consensus: 2269 steps; CI of strict consensus: 0.123; RI of strict consensus: 0.112. Length of MPTs: 1499 steps; CI of MPTs: 0.186; RI of MPTs: 0.455. Arrowheads indicate the maxilla mOTUs; daggers show the fossil OTUs; black locks mark clades with fulfilled constraining, the two grey connected locks represent a single constraint which split up into two clades during analysis. Black branches, non-crown-lacertids; blue branches, Gallotiinae; green branches, Lacertinae. FV, Fouilles Viret; CC1sup, Coderet Couche 1 sup; CE1-0, Coderet E1-0; CH1- 100, Coderet H1-100; CCVsup, Coderet Couche Verte sup 1-25; PdF, Pech-du-Fraysse; Cod, Coderet; Cou, Cournon. Strict consensus trees of K = 5 and 12 can be found in the Supplementary material.





Figure 1.8. Strict consensus tree of analysis of the complete dentary dataset using a value of K = 20 based on more than 100 000 MPTs (overflow). Length of strict consensus: 2074 steps; CI of strict consensus: 0.135; RI of strict consensus: 0.215. Length of MPTs: 1505 steps; CI of MPTs: 0.185; RI of MPTs: 0.464. Arrowheads indicate the dentary mOTUs; daggers show the fossil OTUs; locks mark clades with fulfilled constraining. Black branches, non-crown-lacertids; blue branches, Gallotiinae; green branches, Lacertinae. FV, Fouilles Viret; CC1sup, Coderet Couche 1 sup; CE1-0, Coderet E1-0; CH1-100, Coderet H1-100; CH1-75, Coderet H1-75; CCVsup, Coderet Couche Verte sup 1-25; LaC, La Colombière; Roq2, Roqueprune 2; MdGB, Mas de Got B; PdF, Pech-du-Fraysse; Cod, Coderet; Cou, Cournon. Strict consensus trees of K = 5 and 12 can be found in the Supplementary material.

Fossil wild card taxa

The positions of the eight extinct taxa were not consistent throughout. Resolved positions for *Mediolacerta roceki* and *Pseudeumeces cadurcensis* were observed only for the analysis with the premaxillae. They were recovered at the base of Lacertidae with *Pseudeumeces cadurcensis* being more basal. Also, *Ligerosaurus pouiti* was only recovered at a resolved position when analysing the premaxilla dataset. It was found within the clade of *Iberolacerta* (K = 12 and 20) or within Gallotiinae (K = 5). For *Plesiolacerta lydekkeri* only the analyses with premaxillae and maxillae resulted in a resolved position within *Timon*, as sister to *Timon lepidus* (Daudin, 1802) (K = 12 and 20) or as sister to *Timon pater* (Lataste, 1880) (K = 5). The two *Dracaenosaurus croizeti* OTUs (from Cournon and Coderet) were always sister to each other, and for analyses with dentaries and maxillae they were recovered within Anguimorpha. In the case of the premaxilla dataset, the two taxa were found outside of Lacertoidea without further resolution (K = 12 and 20) or in close relationship to Amphisbaenia (K = 5). The two OTUs of *"Lacerta" filholi* (from Pech-du-Fraysse and Coderet) were found, for the analysis with premaxillae, nested within Gallotiinae. For the analysis with dentaries, only the taxon from Coderet was found sister to *Gallotia caesaris* (Lehrs, 1914).

Jaw element comparison

Character testing

Our character matrix contains 32 characters coding for premaxillae, 28 characters for maxillae and 24 characters for dentaries from the total number of 180 cranial characters. The classification of the characters describing the premaxilla, maxilla and dentary into quantitative, qualitative and their subtypes, showed that the majority of the characters are qualitative (84% of the premaxillary characters, 89% of the maxillary characters and 92% of the dentary characters; Table 1.3). When comparing the distribution of characters among the subtypes "countable/measurable", and "shape-describing", a smaller number of characters is attributed

to the subtype "shape-describing" (31% in the premaxillae, 32% in the maxillae and 41% in the dentaries). The character distribution among the subtypes of quantitative characters shows that maxillary and dentary characters are exclusively meristic in the used dataset, whereas for the premaxillae 60% of the quantitative characters are attributed to morphometric characters.

Table 1.3. Distribution of character types coding for premaxillae, maxillae, and dentaries. The distribution is given in absolute numbers and relative percentages in brackets (rounded to the nearest integer). morph, morphometric; c/m, countable/measurable; shape, shape describing.

	quantitative			qualitative		
	total	meristic	morph	total	c/m	shape
premaxilla	5 (16%)	2 (6%)	3 (9%)	27 (84%)	17 (53%)	10 (31%)
maxilla	3 (11%)	3 (11%)	0 (0%)	25 (89%)	17 (61%)	8 (28%)
dentary	2 (8%)	2 (8%)	0 (0%)	22 (92%)	13 (54%)	9 (38%)

Morphotype testing

The state of completeness was calculated based on the number of applicable characters describing the premaxilla, maxilla and dentary. However, for some dentary morphotypes we were also able to score characters describing the splenial and/or coronoid, given that they were found articulated. Nonetheless, only characters describing the dentary were included in the calculation here. Therefore, the preservation state of the premaxillae, maxillae and dentaries allowed us to score the respective mOTUs for an average of 68% (range 59%–75%), 39% (25%–61%) and 64% (38%–79%) of the available characters, respectively (for state of completeness of the individual mOTUs and their individual positions during analyses, see Appendix 2).

The analysis of the reduced datasets with the premaxillae generally recovered the same tree topologies as seen for the complete dataset. In 80% of the cases, the higher systematic topologies were resolved (as seen in complete premaxilla analysis under K = 5). The mOTUs of P1, P4 and P5 were all recovered within Anguimorpha with mOTU P4 always being sister to *Anguis veronensis*. Under K = 5, the P5 mOTUs and P1 CE1-0 fluctuated between Anguimorpha and a basal position within Lacertoidea with the P5 mOTUs being in a clade with

Amphisbaenia. mOTUs P1 FV and P1 CC1sup were always found in a clade with Amphisbaenia when applying K = 5. The mOTUs P2 and P3 were recovered within the clade of Scincoidea, with P3 Roq2 being consistently found as the sister taxon to *Broadleysaurus major*. But P2 mOTUs and P3 CE1-0 were also found as sister to or in polytomy with *Salvator merianae* + Lacertidae (K = 5).

The analyses with the reduced maxilla datasets still resulted in strict consensus trees with large polytomies. However, 30% of the trees had the clade of Anguimorpha resolved, and in another 30%, the large polytomy was restricted to Lacertidae. Within the polytomies, some smaller clades were found. mOTUs M5 CE1-0 and M6 CE1-0 were never found in a resolved position. The M1 mOTUs were mostly recovered within Lacertidae, with M1 CCVsup (K = 5) and M1 CH1-100 found within *Podarcis*. Among the M1 mOTUs only M1 FV (K = 12 and 20) and M1 CC1sup were positioned in the clade of Gallotiinae. mOTU M2 CC1sup was always recovered as Gallotiinae. The mOTU M3 CC1sup was found within Gallotiinae (K = 5), and M3 CH1-100 was either recovered as sister to "*Lacerta*" filholi (from Pech-du-Fraysse) within the unresolved Lacertoidea clade (K = 5 and 12) or as well within Gallotiinae (K = 20). The M4 mOTUs were found unresolved within Lacertidae, and M4 CC1sup also was recovered as Gallotiinae (K = 5). Only M4 CCVsup was found in no further resolved position within Lacertoidea.

When analysing the reduced dentary datasets, remarkably better resolved strict consensus trees were obtained than for the complete dataset. The resolution of the reduced dentary datasets was comparable to the one of the premaxilla datasets, and the same general tree topology was observed. However, larger polytomies were still present in about half of the cases. The three mOTUs D5 CE1-0, D6 CE1-0 and D10 Roq2 were recovered at the same positions as when analysing the complete dataset. The D1 mOTUs fluctuated between the clade of Gallotiinae and *Lacerta*, with only D1 FV being consistently found within *Lacerta*. Among the D2 mOTUs, D2 FV and D2 CCVsup were always recovered within *Lacerta*. MOTU D2 CE1-0 switched between a position within Gallotiinae (all *K*-values), *Podarcis* (K = 5), or as sister to *Timon* + *Lacerta* (K = 12 and 20), D2 CH1-100 was found unresolved within Lacertidae (K = 5 and 12) and Gallotiinae (K = 20) or *Lacerta* (all *K*-values). All D4 mOTUs were recovered as Lacertoidea, with D4 CE1-0 being found within Gallotiinae (all *K*-values), *Podarcis* (K = 5), or as sister to *Timon* + *Lacerta* (K = 12 and 20), and D4 MdGB being found as part of *Podarcis* (K = 5) or as

sister to *Timon* + *Lacerta* (K = 20). The mOTU D4 CCVsup switched between a position within Lacertoidea or Scincoidea. mOTU D7 CE1-0 was consistently found within *Lacerta*, whereas D7 CCVsup was found in an unresolved position within Lacertoidea. Among the D8 mOTUs, only D8 CH1-100 was found further resolved in a clade with Gallotiinae, the others were found only as Lacertoidea (D8 CCVsup) or in no resolved position at all (D8 Roq2). The D9 mOTUs were found either within *Podarcis* or as sister to *Timon* + *Lacerta*, and in a few cases (under K = 20) within Gallotiinae.

The stability tests identified in total three of 11 premaxillae, eight of 14 maxillae and seven of 26 dentary mOTUs as unstable (Appendix 2). After excluding the unstable mOTUs and rerunning the analyses, the tree resolution improved significantly compared to the analyses with the complete datasets, and all three datasets resulted in trees with a similar general tree topology. The remaining stable premaxillary mOTUs generally were recovered in the same positions as in the analyses of the reduced datasets with their respective K-value. For the maxilla dataset, the new analyses recovered all stable mOTUs within crown-Lacertidae, except for mOTU M5 CE1-0, which formed a grade with Salvator merianae being more basal to it, and the lacertids Pseudeumeces cadurcensis, Ligerosaurus pouiti and Mediolacerta roceki as successively more derived branches. Under K = 5, all stable maxilla mOTUs were either recovered within Gallotiinae or forming a sister clade to it. With K = 12 and 20, the maxilla mOTUs were found in a polytomy within Lacertidae and only M1 CC1sup was found as Gallotiinae. The analyses with the stable dentary mOTUs found the mOTU D10 Roq2, D5 CE1-0 and D6 CE1-0 in the same positions as in the previous analyses. All remaining stable dentary mOTUs were recovered within Podarcis, except that D8 CH1-100 was found within Gallotiinae (K = 5 and 12) or as sister to *Ligerosaurus pouiti*, together forming the sister clade to Timon. For a tabular summary of the mOTU positions for the complete, reduced and only-stable-mOTUs analyses, see Appendix 2.

The analysis with the cross-regional mOTUs of the premaxillae found, when including only one at a time, the cross-regional mOTUs P1, P2 and P5 within Anguimorpha as sister taxon to the two *Dracaenosaurus croizeti* OTUs. Only when applying K = 5, the cross-regional mOTU P1 was found as sister to the two *Blanus* taxa. mOTU P4 (no cross-regional OTU; P4 occurs in a single sample only) was recovered as sister to *Anguis veronensis* within Anguimorpha. The cross-regional mOTU P3 was found as sister to *Broadleysaurus major* within Scincoidea. For the analysis including all premaxilla cross-regional mOTUs at the same time (including also P4), the strict consensus tree found all mOTUs recovered in the same positions as before, except for P2, which was now found within Scincoidea, in a polytomy with cross-regional mOTU P3 and *Broadleysaurus major* (Figure 1.9; for the trees of the cross-regional mOTUs analysed individually, see Supplementary material). For the analysis of the cross-regional mOTUs under K = 5, the clade of Scincoidea collapsed into the following polytomy: (P2, P3, *Ablepharus kitaibelii, Broadleysaurus major, Chalcides ocellatus*, (P1, (*Blanus strauchi, Blanus rufus*)), (*Salvator merianae*, Lacertidae)).



Figure 1.9. Strict consensus tree of the premaxillary cross-regional analysis using a value of K = 20 based on two MPTs. Length of strict consensus and MPTs: 1494 steps; CI of strict consensus and MPTs: 0.187; RI of strict consensus and MPTs: 0.456. Arrowheads indicate the premaxilla (cross-regional) mOTUs; daggers show the fossil OTUs; locks mark clades with fulfilled constraining. Grey dashed-line arrow indicates the position of the cross-regional mOTU when analysing it individually (K = 20). Black branches, non-crown-lacertids; blue branches, Gallotiinae; green branches, Lacertinae. CE1-0, Coderet E1-0; PdF, Pech-du-Fraysse; Cod, Coderet; Cou, Cournon. Strict consensus trees of K = 5 and 12 can be found in the Supplementary material.

When analysing the single maxilla cross-regional mOTUs, the cross-regional mOTU M1 was found in a clade with Zootoca vivipara, Takydromus sp. and Phoenicolacerta troodica, as the sister taxon to Zootoca vivipara. The mOTU M2 (no cross-regional OTU; M2 occurs in a single sample only) was found as sister to Ligerosaurus pouiti, within a clade composed of the two *Iberolacerta* species and *Archaeolacerta bedriagae*. Under K = 5, it was found in polytomy with Ligerosaurus pouiti as part of Gallotiinae. The cross-regional mOTUs M3 and M4 were both found as sisters to the clade Timon + Lacerta. The analysis including only morphotype M5 (no cross-regional OTU; M5 was found in a single sample only) recovered it in a grade with Salvator merianae as more basal, and the lacertids Pseudeumeces cadurcensis, Ligerosaurus pouiti and Mediolacerta roceki in successively more derived positions. The strict consensus tree of the analysis with mOTU M6 (no cross-regional OTU; M6 is represented in a single sample only) was poorly resolved with a large polytomy excluding only the outgroup taxon Gekko gecko but including mOTU M6. When including all cross-regional maxilla mOTUs simultaneously (including M2, M5 and M6), the tree topology showed the same large polytomy as found by the analysis restricted to the mOTU M6 (Figure 1.10; for the trees of the cross-regional mOTUs analysed individually, see Supplementary material). The cross-regional mOTUs M1 and M3 were found in a smaller polytomy within the large polytomy, including the "Lacerta" filholi OTU from Pech-du-Fraysse. The cross-regional mOTU M4 was found at the same position as when analysed alone. The other cross-regional mOTUs were not found in a resolved position in the strict consensus tree. For the analysis under K = 5, the clade of Gallotiinae was resolved in the larger polytomy and included the cross-regional mOTUs M1, M2, M3 and M4.



Figure 1.10. Strict consensus tree of the maxillary cross-regional analysis using a value of K = 20 based on 20 MPTs. Length of strict consensus: 1739 steps; CI of strict consensus: 0.160; RI of strict consensus. Length of MPTs: 1498 steps; CI of MPTs: 0.186; RI of MPTs: 0.452. Arrowheads indicate the maxilla (cross-regional) mOTUs; daggers show the fossil OTUs; locks mark clades with fulfilled constraining. Grey dashed line arrows indicate the position of the (cross-regional) mOTUs when analysing them individually (K = 20). Grey asterisk marks the mOTU which was found at a resolved position when analysed individually, but still as non-lacertid. Black branches, non-crown-lacertids; blue branches, Gallotiinae; green branches, Lacertinae. CC1sup, Coderet Couche 1 sup; CE1-0, Coderet E1-0; PdF, Pech-du-Fraysse; Cod, Coderet; Cou, Cournon. Strict consensus trees of K = 5 and 12 can be found in the Supplementary material.

The separate analyses for the dentary cross-regional mOTUs found D1 and D7 within Gallotiinae, as sister taxa to a clade including the three taxa of Gallotia and the two "Lacerta" filholi OTUs. The analysis with the cross-regional mOTU D2 recovered it within Lacerta, as sister to the clade Lacerta media + L. schreiberi. The cross-regional mOTU D3 was recovered within Lacerta as well, but in a polytomy with L. media and L. schreiberi. The analysis including the cross-regional mOTU D4 found it within Gallotiinae, as sister to the clade Gallotia stehlini + G. simonyi. mOTU D5 (no cross-regional OTU; D5 occurs only in a single sample) was found as part of Iberolacerta, forming the sister taxon to I. monticola. As before, mOTU D6 (no cross-regional OTU; D6 occurs only in a single sample) was found within Algyroides, forming the sister taxon to A. nigropunctatus. The cross-regional mOTU D8 and *Ligerosaurus pouiti* were found as sister clade to *Timon*. Under K = 5, D8 was still close to Ligerosaurus pouiti but those two were positioned within Gallotiinae. The cross-regional mOTU D9 was recovered as sister to Timon + Lacerta, or in a polytomy with Podarcis and *Timon* + *Lacerta* (K = 5). As already observed in the trees of the previous analysis, mOTU D10 (no cross-regional OTU; D10 occurs only in a single sample) was positioned as sister to the clade *Blanus strauchi* + *B. rufus* (Amphisbaenia). When including all cross-regional dentary mOTUs at the same time (including D5, D6 and D10), D5, D6, D8 and D10 were recovered at the same positions as before (Figure 1.11; for the trees of the cross-regional mOTUs analysed individually, see Supplementary material). By contrast, the other cross-regional mOTUs (D1, D2, D3, D4, D7, D9) were recovered in different positions, namely within Podarcis, where D9 was sister to P. tiliguerta. Under K = 5, the cross-regional mOTU D8 was found within Gallotiinae.



Figure 1.11. Single MPT of the dentary cross-regional analysis using K = 20. Length: 1504 steps; CI: 0.186; RI: 0.456. Arrowheads indicate the dentary (cross-regional) mOTUs; daggers show the fossil OTUs; locks mark clades with fulfilled constraining. Grey dashed-line arrows indicate the position of the cross-regional mOTUs when analysing them individually (K = 20). Black branches, non-crown-lacertids; blue branches, Gallotiinae; green branches, Lacertinae. CC1sup, Coderet Couche 1 sup; CE1-0, Coderet E1-0; PdF, Pech-du-Fraysse; Cod, Coderet; Cou, Cournon. Strict consensus trees of K = 5 and 12 can be found in the Supplementary material.

During morphotype testing, the eight other extinct taxa, which were treated as wild card taxa, were found mostly in the same positions as recovered by analyses with the complete datasets. Mediolacerta roceki and Pseudeumeces cadurcensis were always found close to each other. They were positioned at the base of Lacertidae with Pseudeumeces cadurcensis being more basal (all datasets: all K-values), within Gallotiinae (premaxilla and dentary datasets: K = 20) or as sister to Timon+ Lacerta (dentary datasets: K = 20). Ligerosaurus pouiti was found at the base of Lacertidae, between Pseudeumeces cadurcensis and Mediolacerta roceki (maxilla dataset: all K-values; dentary dataset: K = 20), as part of Gallotiinae (premaxilla datasets: K = 5 and 20; maxilla datasets: K = 5; dentary dataset: all K-values), within *Iberolacerta* (premaxilla dataset: K = 12 and 20; maxilla datasets: K = 12 and 20; dentary datasets: K = 12) or as sister to Timon + Lacerta (dentary datasets: K = 20). *Plesiolacerta lydekkeri* was found within *Timon*, as sister to *Timon lepidus* (all datasets: K = 12and 20) or to *Timon pater* (premaxilla and maxilla datasets: K = 5; dentary datasets: all K-values). The two Dracaenosaurus croizeti OTUs (Cournon and Coderet) were almost exclusively found in a sister relationship to each other within Anguimorpha (all datasets: all K-values); in some cases, the two taxa were found in close relationship to Amphisbaenia (premaxilla datasets: K = 5). The two OTUs of "*Lacerta*" filholi (Pech-du-Fraysse and Coderet) were consistently found within Gallotiinae.

1.2.1.5. Discussion

The recovered trees for premaxillae, maxillae and dentaries from our analyses with the complete datasets displayed different degrees of resolution, implying that the phylogenetic signal of tooth-bearing elements is incongruent within Lacertidae. This means that premaxillae, maxillae and dentaries alone are not equally suited for species identification based on phylogenetic analysis, and that taxa represented by single bones only often cannot be placed in a well-resolved position in a phylogenetic tree. Likewise, different bones from the same species, when found disarticulated, can be recovered in different positions along the tree. Here, we explore

the possible reasons for this issue, and what this could mean for the systematics of extinct lacertids from the Oligocene of France.

Dataset comparison

The quantitative comparison of the characters showed no significant overrepresentation of any of the three elements compared to the other two. Concerning the qualitative character comparison, our dataset displayed only relatively few differences in character type distribution among premaxillary, maxillary and dentary characters. On the one hand, it has been argued that a high amount of "shape-describing" characters makes the analysis more error-prone, because state definitions in this kind of character often are vague and could thus be interpreted differently by different researchers. Consequently, qualitative, shape-describing characters often were regarded as less objective than "countable/measurable" qualitative characters (Catalano et al., 2010). However, qualitative characters in general have been interpreted to be less objective than quantitative characters by some phylogeneticists (e.g., Poe and Wiens, 2000). On the other hand, quantitative characters with discrete character states, as are being used in our dataset, can be problematic because the definition of their state boundaries may be subjective (Archie, 1985; Rae, 1998). Indeed, if a range of values is discretized into two distinct character states, taxa with significantly different values can be grouped together, whereas taxa displaying similar values, but on the two sides of the state boundary, will be scored differently (Farris, 1990). Therefore, several authors have suggested the use of continuous (Rae, 1998; Goloboff et al., 2006) or even morphometric characters (Catalano et al., 2010), which can both now also be scored and implemented directly in TNT (Goloboff et al., 2006; Goloboff and Catalano, 2016). However, discretizing continuous characters is a very straightforward approach, and the scoring of the OTUs into discrete states is easily reproducible. Discretizing continuous character states, as was done in our dataset, can also partially address the problem of outliers in the dataset, which can result from abiotic causes such as taphonomic deformation (Tschopp and Upchurch, 2019) that almost always affects fossils (Arbour and Currie, 2012; Tschopp et al., 2013). Nevertheless, among continuous characters, only the morphometric characters are affected by taphonomic deformation, given that meristic characters cannot logically be altered in this way. Although differences in the relative amount of different character types in our dataset are low (Table 1.3), they indicate that quantitative characters were slightly less error-prone and more reliable than qualitative characters in terms of recovering resolved phylogenetic trees. It seems unlikely, though, that these were the only factors impacting tree resolution and/or causing the sometimes conflicting positions of the morphotypes.

Morphological variability differs between tooth-bearing elements, the impact of which was tested with the analyses with a reduced mOTU sampling. When simply comparing the number of observed morphotypes, the premaxillae and maxillae had a similar number of morphotypes, whereas the dentaries represent the most variable jaw element (see also Table 1.2). The dentary also was the most frequent element in our sample at 68% of the material, whereas the maxillae and premaxillae constituted 23% and 9%, respectively. This distribution of the three jaw elements is comparable to other localities with squamate remains (e.g., Monte Tuttavista, Sardinia, Italy: 65% dentaries, 32% maxillae, 3% premaxillae, Tschopp *et al.*, 2018b; Maramena, northern Greece: 73% dentaries, 25% maxillae, 2% premaxillae (considering only the squamate remains), Georgalis *et al.*, 2019), indicating that the dentaries have a higher preservation probability compared to the relatively thin, and thus more fragile maxillae and premaxillae (and assuming that they are equally recognizable during picking and sorting activities). It also should be kept in mind that dentaries and maxillae twice as likely to be preserved. Hence, the observed higher variability might be due to preservation bias.

Missing scores in the mOTUs appear to have had a more profound impact on tree topology than character number and definition, because the possibility of determination and positioning of the taxa within the phylogenetic tree decreases with an increasing number of missing entries (Wiens, 2003). The resultant instability of the incomplete OTU leads to a recovery of a high number of conflicting most parsimonious trees (MPTs), and consequently to a poorly resolved strict consensus tree (Gauthier, 1986; Huelsenbeck, 1991; Wilkinson and Benton, 1995; Pol and Escapa, 2009).

The state of completeness of the various morphotypes (quantified by the relative number of characters that were scorable for the individual morphotypes of the tooth-bearing elements) showed remarkable differences. Whereas the premaxilla and the dentary mOTUs displayed comparable average percentages, the portion of scorable characters for the maxilla morphotypes was significantly lower (most complete maxilla mOTU: 61%; most incomplete premaxilla mOTU: 59%). This degree of "specimen" incompleteness in the case of the maxilla probably is the main reason for the poorly resolved strict consensus trees. Such an interpretation is also supported by the resolution of the strict consensus trees of analyses with the reduced datasets.

The resolution of the strict consensus trees with the dentaries was slightly lower than the one of the premaxillae, probably owing to the somewhat lower "specimen" completeness. However, when a larger polytomy occurred, the dentary mOTUs were mostly recovered in the resolved part of the strict consensus trees. By contrast, the reduced datasets with the maxillae still recovered larger polytomies with the majority of mOTUs involved. The stability tests revealed a strong correlation of stability and completeness of the mOTUs. Generally, the higher the completeness of a mOTU, the more stable its position among the MPTs, regardless of the weighting strength. However, some mOTUs with low completeness values were nonetheless identified as stable, implying the importance of not only the number of scored characters, but also the character itself (e.g., an apomorphic feature for a specific group in the dataset).

By creating the cross-regional mOTUs, the amount of missing data was reduced without deleting taxa, as mOTUs of the same morphotype but with different states of preservation were merged. Moreover, a possible ecomorphological signal (i.e., directed noise) was weakened as data from different localities were combined and, thereby, the real phylogenetic signal was enhanced. The analyses did not result in completely different positions, but especially in the case of the maxillae, the morphotypes were recovered at much more resolved positions. The different morphotype testing methods also can be seen as a less laborious approach to test alternative tree hypotheses. Of course, it is less powerful than using completely different datasets as done by Scarpetta (2020). But, by testing the different *K*-values and combinations of taxa, the general value of a taxon's position in the phylogenetic tree can readily be appraised. If needed, more rigorous methods could be used in a subsequent iteration.

Possible phylogenetic position of mOTUs

The phylogenetic positions found for the various mOTUs varied considerably in the different analyses, rendering taxonomic interpretations difficult for some morphotypes. Concerning the influence of the weighting strength applied to the maximum parsimony analyses, we generally observed poorer tree resolutions with K = 5, whereas K = 12 and 20 created better resolved tree topologies. Even though the latter two weighting strengths showed quite similar results, K = 20 generated the best tree resolution. The somewhat better performance of the milder downweighting against homoplastic characters, represented by the higher *K*-values (12 and 20), agrees with results from analyses with simulated data (Goloboff *et al.*, 2018).

Premaxilla mOTUs

Even though all premaxilla mOTUs were recovered outside of Lacertidae, the outgroup position of the mOTUs belonging to morphotypes P1 (Figure 1.2A), P2 (Figure 1.2B), P3 (Figure 1.2C) and P5 (Figure 1.2E), is highly questionable and likely inaccurate. Several morphological features that generally are regarded to be diagnostic for Lacertidae are present in these morphotypes, supporting an assignment of these premaxillae to the ingroup. The observed number of teeth ranging from six to nine fits the range found in extant and extinct lacertids (Barahona Quintana, 1996; Barahona and Barbadillo, 1998; Evans, 2008; Khosravani et al., 2011; Čerňanský and Augé, 2013; Čerňanský et al., 2016; Čerňanský and Syromyatnikova, 2019; Villa and Delfino, 2019b). Moreover, the tooth arrangement and composition are lacertidlike with closely spaced teeth and rounded tooth apices (Villa and Delfino, 2019b). However, the prominent enlarged median tooth observed in P1 previously was regarded as an unambiguous synapomorphy for the clade composed of Amphisbaenia + Dibamidae (Gauthier et al., 2012), and probably impacts our analyses as well. Other features found in the premaxillae morphotypes also may be unusual in lacertids generally, but can be observed in some taxa. The slender ascending nasal process and the teeth of morphotype P2 are similar to the extant species Lacerta strigata Eichwald, 1831 (e.g., Čerňanský and Syromyatnikova, 2019, therein figure 12), and the extinct species Lacerta poncenatensis Müller, 1996, from the Miocene of Poncenat, France (e.g., Müller, 1996, therein figure 5). The unclosed fossae around the ethmoidal foramina present in P3 (Figure 1.2C), is a feature that also occurs in *Lacerta bilineata* Daudin, 1802 (MNCN-16505) and Podarcis muralis (MDHC 311). A second pair of ethmoidal foramina was present in P5. We observed this state also in the OTUs in our dataset: Anguis veronensis (MDHC 102; Anguimorpha), Blanus strauchi (MDHC 287; Amphisbaenia), Gallotia simonyi (NHMW 849), Acanthodactylus erythrurus (UAM.R. Ac-VII) and Iberolacerta monticola (UAM.R. Lm77; all three are lacertids). It also is known as a rare feature in Podarcis muralis (Laurentini, 1786) (Barahona Quintana, 1996; Villa and Delfino, 2019b). It seems that convergently acquired features pull the mOTUs of the aforementioned morphotypes out of the ingroup and overrule the real phylogenetic signal. Hence, they are likely representing lacertid remains.

Only the position of mOTU P4 (Figure 1.2D), which was always recovered as sister to the anguimorph *Anguis veronensis*, seems to be plausible, and it was suggested to indeed represent an anguid (Rage, 2016, pers. comm.). It resembles the extinct anguid species *Pseudopus laurillardi* (Lartet, 1851) in terms of the dorsal shape of the tooth-bearing portion

that is almost rectangular and quite robust, looking like the crossbar of the letter "T" (e.g., Klembara *et al.*, 2010, therein figure 3).

Maxilla mOTUs

All maxilla mOTUs generally were recovered within Lacertidae, except for morphotypes M5 and M6. The morphotypes M1 (Figure 1.3A) and M3 (Figure 1.3C) could represent the same species owing to their similar appearance; they differ only in the presence or absence of striae on their tooth crowns. Additionally, morphotypes M4 (Figure 1.3D) and M3 also show similarities and differ (mostly) in their size. Also, phylogenetic analyses (individual crossregional analyses) recovered them in the same position, as sister to *Timon + Lacerta*. It is possible that these two either represent different species or that the size difference originates from sexual dimorphism or ontogeny, because variation in the size of the skull between adult males and adult females or juveniles is common among lacertids (e.g., Klemmer, 1957; Darevsky, 1967), and it is usually male-biased (Vincent and Herrel, 2007, and references therein). The smaller morphotype M3 might represent the adult female or juvenile, and the larger morphotype M4 the adult male version of a single species. A classification of the three morphotypes to Lacertidae (maybe Lacertini) seems plausible, based on the tooth arrangement especially in the anterior part, with the small anterior teeth having slightly posteriorly pointing tooth apices. Adding to this, the texture of the dermal ornamentation is also similar to the one seen in Lacerta (e.g., Čerňanský and Syromyatnikova, 2019, therein figure 13).

Morphotype M2 (Figure 1.3B) with the abrupt change from smaller posterior-most teeth to preceding larger teeth in the posterior half which also had been observed in specimens belonging to the large-sized lacertid genus *Timon* and the extinct species *"Lacerta" siculimelitensis* Böhme and Zammit-Maempel, 1982 (Böhme and Zammit-Maempel, 1982; Mateo Miras, 1988; Tschopp *et al.*, 2018b), can also be an identified as an indeterminate lacertid but the poor preservation renders a more precise classification difficult.

Morphotype M5 (Figure 1.3E) has globose teeth with deep striae, which are similar to the teeth preserved in premaxillary morphotype P1; thus, the two may belong to a single species. Also, the two morphotypes overlap geographically (see Table 1.2). The phylogenetic position of morphotype M5 was never further resolved than basal most Lacertidae (or Lacertoidea), which makes a more specific classification speculative.

Morphotype M6 (Figure 1.3F) is unlikely to represent a lacertid because of its fang-like, slender teeth. These characteristics appear to be shared with varanids (e.g., Georgalis *et al.*, 2017, therein figure 1; Villa *et al.*, 2018; Villa and Delfino, 2019a, therein figure 11). Our analysis did not recover M6 at any resolved position. Hence, based on our observations, the morphotype likely does not represent a lacertid, but rather an anguimorph. Given that mOTU P4 is also thought to be an anguimorph, and they both come from the same locality and sample (Coderet E1-0), those could represent the same (non-lacertid) species. Alternatively, they could be palaeovaranids, which also share a similar tooth morphology, but their tooth crowns have longitudinal striae (Georgalis, 2017). Their presence is not reported from Coderet, but they are well-known from the Quercy phosphorites (Georgalis, 2017, and references therein).

Dentary mOTUs

Except for morphotype D10, all dentary morphotypes were generally recovered as lacertids. The dentary morphotypes D1 (Figure 1.4A), D2 (Figure 1.4B, C) and D4 (Figure 1.4F, G) are highly similar in their overall shape, with the only differences being the presence or absence of either widely or narrowly spaced striae. Their phylogenetic position was mainly within Gallotiinae or at different positions within Lacertini. Considering that the three morphotypes are rather slender, an identification of the three morphotypes as Lacertini rather than Gallotiinae might be reasonable but remains speculative.

The morphotypes D3 (Figure 1.4D, E) and D8 (Figure 1.5E, F) are similar in being rather robust. The two are distinguished by the distinctly smaller teeth of D8 in the posterior-most part of the jaw, with the most robust teeth preceding those. This morphology also was observed in the maxillary morphotype M2, which also was relatively robust. The peculiar tooth morphology resembles certain specimens of *Timon* and the extinct species *"Lacerta" siculimelitensis* (Böhme and Zammit-Maempel, 1982; Mateo Miras, 1988; Tschopp *et al.*, 2018b). Based on the aforementioned observations, the two morphotypes may or may not represent the same species, but their identification as lacertid is very likely.

The very slender morphotype D6 (Figure 1.5A) from Coderet E1-0 always was recovered as part of the *Algyroides*-clade. However, its high incompleteness raises doubts on such a specific identification. In any case, a referral to Lacertidae and, given the slender morphology and its biogeography, to Lacertini seems to be plausible.

The morphotype D7 (Figure 1.5B-D) has a very distinctly developed tricuspidity of the tooth crowns which is an attribute that was formerly used as a diagnostic feature for the extinct species *Miolacerta tenuis* (Roček, 1984). However, strong tricuspidity also has been observed in the lacertid genera *Takydromus* and *Gallotia*, in the gerrhosaurid *Tracheloptychus madagascariensis* Peters, 1854 (Barahona *et al.*, 2000; Kosma, 2004), and in specimens of *"Lacerta" filholi* (Augé and Smith, 2009, therein figure 2). Moreover, the overall appearance is *"Lacerta" filholi*-like with the rather slender subtriangular shape, the distinct coronoid facet and the posteriorly reduced subdental shelf (e.g., Augé and Smith, 2009). Hence, morphotype D7 might belong to *"Lacerta" filholi*, but currently available data only seem to allow for a classification as Lacertidae indet.

Morphotype D9 (Figure 1.5G) also has strong similarities with "*Lacerta*" *filholi* in terms of shape, but tricuspid teeth as seen in "*Lacerta*" *filholi* (Augé, 2005) are absent. Morphotype D9 represents in all probability a lacertid and probably a member of the tribe Lacertini, as it has a fairly slender appearance.

Morphotype D10 (Figure 1.5H, I) differs in its morphology from the other dentaries, because of the globose, very robust teeth that are distinctly different in size from each other and have narrowly spaced striae. This was also observed in morphotypes P1 and M5. A similar tooth morphology has been reported for the extinct lacertids *Pseudeumeces cadurcensis* (e.g., Augé and Hervet, 2009, therein figure 2) and *Dracaenosaurus croizeti* (e.g., Müller, 2004; Čerňanský *et al.*, 2017, therein figure 9). It should be noted that there is no geographical or stratigraphic overlap of P1 and M5 with D10 (see Table 1.2). All phylogenetic analyses found the mOTU D10 forming a clade within Amphisbaenia. However, only the very tip of the dentary was preserved, which makes an identification barely possible, but a referral to lacertids might be plausible, also in consideration that *Dracaenosaurus croizeti* was as well recovered outside Lacertidae (see discussion below).

Morphotype D5 (Figure 1.4H-J) was present only in the sample from Coderet E1-0. It was always recovered within the clade of *Iberolacerta*. However, a Meckelian canal which is closed in the anterior quarter and opening up at the tip was never detected by any of us in *Iberolacerta* (or lacertids in general). Instead, such a morphology is reported in skinks, for instance in *Trachylepis aurata* (Linnaeus, 1758) and *Chalcides ocellatus* (e.g., Caputo, 2004; Villa and Delfino, 2019b, therein figure 43). Based on these data, the position of the morphotype remains uncertain. Because in lacertids, the Meckelian canal is known to be completely open (e.g., Estes

et al., 1988), an identification of morphotype D5 as lacertid is highly unlikely. It might represent a skink or even some other, unidentified taxon.

Possible phylogenetic positions of the eight fossil wild card taxa

Regardless of the weighting strength and number of taxa (including mOTUs) in the dataset, Plesiolacerta lydekkeri was always recovered within the genus Timon, either as sister to Timon lepidus or Timon pater. Previous studies (e.g., Čerňanský and Augé, 2013; Čerňanský and Syromyatnikova, 2019) have already noticed shared features between Plesiolacerta and Timon. However, several issues render a close relationship of Plesiolacerta lydekkeri and Timon lepidus or Timon pater questionable. Molecular analysis of the six extant species of *Timon* have shown that they form a monophyletic group (Pyron *et al.*, 2013). The genus can be subdivided into two subclades that are geographically separated into an eastern and a western clade. Timon kurdistanicus (Suchow, 1936) and Timon princeps (Blanford, 1874) form the eastern clade with a distribution across Turkey, northern parts of Iraq and Iranian areas (Zagros Mountains) (Eiselt, 1968; Anderson, 1999; Ilgaz and Kumlutaş, 2008; Ahmadzadeh et al., 2012). The western clade is composed of two subclades: one is formed by Timon pater and Timon tangitanus (Boulenger, 1889), both from northwestern Africa (Paulo et al., 2008; Perera and Harris, 2010), whereas the second is formed by Timon lepidus and Timon nevadensis (Buchholz, 1963), which are distributed across southwestern Europe (Miraldo et al., 2012). Divergence time of the sister genera Lacerta and Timon has been estimated to 18.6 Ma (95% highest posterior density (HPD) interval: 17.5-20.6 Ma) and the split between the western and eastern clade of Timon to 7.4 Ma (HPD interval: 5.9-9.0 Ma; Ahmadzadeh et al., 2016). Plesiolacerta lydekkeri is known from the middle Eocene (Lutetian; MP 14) until the early Oligocene (Rupelian; MP 21) (Augé, 2005; Čerňanský and Augé, 2013 and references therein), which pre-dates these estimated divergence times considerably. Therefore, although a close relationship of *Plesiolacerta* and *Timon* seems plausible, the position of *Plesiolacerta lydekkeri* within *Timon*, as recovered by our analyses, is here regarded questionable.

Estes (1983b) proposed a close relationship between the amblyodont lacertid species *Pseudeumeces cadurcensis* and *Dracaenosaurus croizeti*, suggesting they may form a morphological series. Based on similarities in tooth shape, a lacertid lineage from *"Lacerta" filholi* via *Mediolacerta roceki* and *Pseudeumeces cadurcensis* to *Dracaenosaurus croizeti* was hypothesized (Hoffstetter, 1944; Rage, 1987; Augé, 2005). To

knowledge, phylogenetic our analyses have been carried out only with Pseudeumeces cadurcensis and Dracaenosaurus croizeti so far. Their position was consistently found within Gallotiinae (Čerňanský et al., 2016, 2017; Tschopp et al., 2018b; Garcia-Porta et al., 2019). In our analyses, only the two "Lacerta" filholi OTUs were found consistently within Gallotiinae. Pseudeumeces cadurcensis and Mediolacerta roceki were almost always found at the base of Lacertidae, with few analyses recovering them within Gallotiinae or Lacertini. In an even stronger contrast to earlier analyses, the two Dracaenosaurus croizeti OTUs were either part of Anguimorpha or forming a clade with Amphisbaenia (for some premaxillae analyses). Hence, our analyses did not recover the hypothesised lacertid amblyodont lineage, suggesting that amblyodonty evolved several times independently. Nevertheless, the position of Dracaenosaurus croizeti outside Lacertidae remains questionable, given that other analyses found it consistently within Gallotiinae (Čerňanský et al., 2017; Garcia-Porta et al., 2019).

The Miocene taxon *Ligerosaurus pouiti* was first described as part of the genus *Pseudeumeces* (Augé, 1993) and later assigned to its own genus despite superficial similarities in the dentition (Augé *et al.*, 2003). Our analyses found it mostly within Gallotiinae or the genus *Iberolacerta*. In very few cases, *Ligerosaurus pouiti* also was recovered as sister to *Timon* + *Lacerta* and at the base of Lacertidae, with *Pseudeumeces cadurcensis* being more basal. The very inconsistently recovered closer relationship to *Pseudeumeces cadurcensis* seems to confirm the referral of *Ligerosaurus pouiti* to a different genus. The controversial or rather unstable positions of these wild card taxa in our analyses were likely also caused by the other added extinct mOTUs, which potentially render their recovered positions less reliable.

Regarding the completeness of the wild card taxa, *Mediolacerta roceki* and *Ligerosaurus pouiti* were the most incomplete taxa (9% and 6%, respectively), whereas *Plesiolacerta lydekkeri* was the most complete one (39%). This highlights again how specimen incompleteness and tree resolution are correlated.

Species diversity of the morphotypes

Given the observed morphological similarities and the phylogenetic positions of the fossil material in the several analyses, there is support for probably three lacertid and one anguimorphan species among the premaxillae, about four lacertid and one anguimorphan species among the maxillae, and about five lacertid and one non-lacertid species among the dentaries.

The disparity between the premaxilla morphotypes is quite distinct, but the number of different morphotypes was rather low. By contrast, the number of dentary morphotypes was relatively high, but the differences between those were less distinct. In the case of the maxilla, the number of morphotypes and the distinctness was in between those of the two other jaw elements. The variation in size observed in the dentary and maxilla morphotypes probably results from either sexual dimorphism (Klemmer, 1957; Darevsky, 1967; Vincent and Herrel, 2007 and references therein; Ljubisavljević *et al.*, 2010; Borczyk *et al.*, 2014) or ontogeny (Roček, 1980).

Considering possible connections between the jaw elements resulting from their morphological similarities, at least five different lacertid species (Figure 1.12) and two non-lacertid species are present in our sample. The first lacertid species ("species 1") probably comprises the premaxilla morphotypes P1 and P5, the maxilla morphotype M5, and the dentary morphotype D10, as they share the same morphology of globose teeth with dense, narrowly spaced striae. A similar tooth morphology occurs in the species Pseudeumeces cadurcensis and Dracaenosaurus croizeti (Augé, 2005); the two could thus be plausible candidates for a species referral of morphotypes P1, P5, M5 and D10. The second lacertid species ("species 2") is likely represented by the maxilla morphotype M2 and the dentary morphotype D8. They have the same distribution of robust teeth with the most robust teeth being located in the posterior half followed by significantly less robust and smaller teeth in the posterior-most part of the jaw element (maxilla, dentary) which is also known in the extant genus Timon and the Pleistocene species "Lacerta" siculimelitensis (Böhme and Zammit-Maempel, 1982; Mateo Miras, 1988; Tschopp et al., 2018b). However, M2 has narrowly spaced striae, whereas D8 has widely spaced striae on their tooth crowns. Given that similarities of the two mentioned species with Plesiolacerta lydekkeri were reported already (e.g., Čerňanský and Augé, 2013; Čerňanský and Syromyatnikova, 2019), "species 2" might be closely related with it or even belong to Plesiolacerta lydekkeri. As a third lacertid species ("species 3"), the two dentary morphotypes D1 and D9 may be conspecific with the maxilla morphotype M1, given that they all have smooth tooth crowns and a similar overall robustness. The fourth lacertid species ("species 4") may be represented by the maxilla morphotypes M3 and M4, which possibly show ontogenetic variation or sexual dimorphism, with the less robust M3 potentially showing the adult female or juvenile constitution. Those two maxilla morphotypes might be linked to the dentary morphotypes D2 and D3, which also might show a sexual dimorphism or variation in size due to ontogeny, with the slenderer morphotype D2 possibly representing the adult female or juvenile state. It is possible that the dentary morphotypes D4 and D7 also are referable to this species, because the differences among the four dentary morphotypes are quite small. However, all morphotypes assigned to this species have widely spaced striae on their tooth crowns, except for D4, which has narrowly spaced striae. Therefore, the informative character on the constitution of striae on tooth crowns (when present) seems to be questionable, as also seen in the previously mentioned "species 2". Apart from these minor differences, the morphotypes resemble "*Lacerta*" *filholi*, a species which is known already from Coderet, La Colombière, Mas de Got B and Roqueprune 2 (Augé, 2005). The fifth species ("species 5") is represented by dentary morphotype D6, which was the most fragile element in the sample; no comparable maxilla or premaxilla was observed for this species. It resembles *Algyroides* in its delicateness. The two premaxilla morphotypes P2 and P3 probably represent two separate species, but those are likely linked to some of the already defined five lacertid species. Both have tooth crowns with narrowly spaced striae, but as seen above, the condition of the striae might not be taxonomically significant at the species level.

One of the non-lacertid species probably consists of the premaxilla morphotype P4 and the maxilla morphotype M6, and are most plausible referred to an anguimorphan species. The second non-lacertid species is represented by the dentary morphotype D5, which may be a skink or some other "scincomorphan" lizard. However, it should be kept in mind that the dataset that we used was created specifically for lacertids, and therefore, it has a rather low taxon sampling for the outgroups. Because of this, the phylogenetic position of possible non-lacertid taxa is not very reliable.

During the Oligocene in France, five lacertid species are certainly known to have occurred: *Plesiolacerta lydekkeri*, "*Lacerta*" *filholi*, *Mediolacerta roceki*, *Pseudeumeces cadurcensis* and *Dracaenosaurus croizeti* (Augé, 2005; Augé and Hervet, 2009). In the four localities from where our samples are (Coderet, La Colombière, Roqueprune 2, Mas de Got B), "*Lacerta*" *filholi* is known to have been present in all of them, *Mediolacerta roceki* is reported from Roqueprune 2 and Coderet, *Dracaenosaurus croizeti* occurred only in Coderet, and no remains of *Plesiolacerta lydekkeri* and *Pseudeumeces cadurcensis* have been found in any of the four localities, although *Pseudeumeces cadurcensis* overlaps in age with Coderet and La Colombière (Augé, 2005). The last occurrence of *Plesiolacerta lydekkeri* was in the early Oligocene in the MP 21 (Augé, 2005), hence, there is no chronological overlap with our four four french localities, as the oldest one is correlated to MP 22 (Mas de Got B). With respect to time, an increase in species variability is observable from the Rupelian to the Chattian. When reconciling our previously identified five lacertid "species" with the five already known ones,

"species 5" seems to be unique. It is present in the sample from Coderet (Figure 1.12), but it does not resemble any of the five known species due to its delicateness. However, ontogeny or sexual dimorphism might also play a role here. "Species 1" was found in the samples from Coderet and Roqueprune 2 (Figure 1.12) and resembles or is related to the amblyodont species Pseudeumeces cadurcensis and Dracaenosaurus croizeti. The stratigraphic range of Pseudeumeces cadurcensis and Dracaenosaurus croizeti fits the age of Coderet (MP 30), but remains from this locality are reported only for Dracaenosaurus croizeti (Augé, 2005). However, Roqueprune 2, which was correlated to MP 23, pre-dates the first occurrences of the two amblyodont species (Pseudeumeces cadurcensis: MP 25; Dracaenosaurus croizeti: MP 28; Augé and Hervet, 2009). "Species 2" occurs in the samples from Coderet and Roqueprune 2 (Figure 1.12). It might resemble or be related to Plesiolacerta lydekkeri, which last occurred in MP 21 (Augé, 2005); this pre-dates Coderet (MP 30) and Roqueprune 2 (MP23). "Species 4" was found in the samples from Coderet and Mas de Got B (Figure 1.12), and probably represents "Lacerta" filholi, which has been reported from these localities before. "Species 3" was found in Coderet, La Colombière and Roqueprune 2 (Figure 1.12). It could represent any of the five known species from the Oligocene of France except for the two amblyodont species (Pseudeumeces cadurcensis and Dracaenosaurus croizeti). Therefore, the species variability of lacertid lizards in the Oligocene of France seems to be somewhat greater than recognised previously with possibly six different species: Plesiolacerta lydekkeri, "Lacerta" filholi, Mediolacerta roceki, Pseudeumeces cadurcensis, Dracaenosaurus croizeti and "species 5". Possibly, the stratigraphic range of *Plesiolacerta lydekkeri* extends further into the Oligocene, whereas the first occurrence of Pseudeumeces cadurcensis or Dracaenosaurus croizeti might date further back than previously thought.

1. Introduction | 1.2. Obstacles in palaeontological phylogenies



Figure 1.12. Distribution pattern and constitution of the possible five lacertid species among the four French localities indicated by black stars. Although the morphotypes P2 and P3 were classified as lacertids, they are not included here, because a referral to one of the five "species" is too speculative. Cod, Coderet; LaC, La Colombière; Roq2, Roqueprune 2; MdGB, Mas de Got B.

1.2.1.6. Conclusions

Assessing the phylogenetic value of lacertid premaxillae, maxillae and dentaries is only possible to a limited extent. The phylogenetic trees resulting from three individual datasets of jaw elements show remarkable differences in terms of resolution of the strict consensus trees and number of MPTs. Also, analyses of the same dataset but with different weighting strengths and methods often led to conflicting positions of the single-bone morphotypes.

However, based on observations of the morphotypes, possibly five lacertid "species" could be identified in our samples from the four French localities. Reconciliation with the already known lacertid species in France during the Oligocene suggests a larger species diversity than thought previously, with six species in total, indicating a more rapid radiation of Lacertidae following the abrupt shift to colder temperatures after the Paleocene–Eocene Thermal Maximum (PETM) and the warm period during the Eocene. However, various iterations of phylogenetic analyses with modified datasets failed to recover clear and consistent phylogenetic positions for most morphotypes, demonstrating the weakness of their phylogenetic signal. Also, a highly resolved tree does not necessarily imply that there was a reliable phylogenetic signal in the dataset. Therefore, it is important to be aware of the constitution of the data being used and to test the robustness of the taxa's positions. A precise classification at species-level of the individual jaw elements was not possible based on the phylogenetic analysis. Hence, species descriptions and classification based on single tooth-bearing elements should be treated with caution. Although real autapomorphic features may be present in some of these elements, these seem to be difficult to interpret as such, and if identified correctly, they do not seem to provide enough information to consistently reveal their true phylogenetic position, and so phylogenetic trees should undergo a conscientious "test of robustness".

Supporting Information

A .zip file including the following supplementary material can be downloaded here: https://doi.org/10.6084/m9.figshare.13277564

- File S1. Nexus file of the premaxilla taxon-character matrix (.nex format).
- File S2. Nexus file of the maxilla taxon-character matrix (.nex format).
- File S3. Nexus file of the dentary taxon-character matrix (.nex format).
- File S4. List of characters including their character classifications (.xlsx format).

File S5. List of studied specimens (.xlsx format).

File S6. List of references for File S4 and File S5 (.pdf format).

File S7. List of figured mOTUs including their preliminary collection numbers (.xlsx format).

File S8. TNT input files and tree files (.tre format) of analyses of complete premaxilla, maxilla and dentary datasets (K = 5, 12, 20) (.zip format).

File S9. TNT input files and tree files (.tre format) of analyses of reduced premaxilla, maxilla and dentary datasets (K = 5, 12, 20) (.zip format).

File S10. TNT tree files (.tre format) of stability analyses of premaxilla, maxilla and dentary datasets (K = 5, 12, 20), including the script for taxa pruning (.zip format).

File S11. TNT input files and tree files (.tre format) of analyses of cross-regional premaxilla, maxilla, and dentary datasets (K = 5, 12, 20) (.zip format).

File S12. Single MPTs or strict consensus trees of the phylogenetic analyses testing the positions of the cross-regional mOTUs individually (.pdf format).

File S13. Strict consensus trees of analyses of complete premaxilla, maxilla and dentary datasets (K = 5, 12) (.pdf format).

File S14. Individual figures of morphotypes (.zip format).

File S15. Table of completeness of the eight fossil wild card taxa (.pdf format).

This is the end of the published section of the chapter.

1.2.2. Dataset composition problem

Another challenge is the composition of the dataset itself: often, the individual OTUs represent information taken from different quantities of specimens. Thus, one OTU may stand for only one specimen whereas other OTUs in the dataset represent a larger group of specimens belonging to the same species or genus (e.g., López-Arbarello and Wencker, 2016; Vlachos and Rabi, 2018; Simões *et al.*, 2020). As with the data problem, this is a result of the fragmentary condition of the fossil record.

With different quantities of specimens being represented by the individual OTUs, factors such as intraspecific variation impact the analyses unequally, because approaches such as majority scoring (Wiens, 1995) takes only the main constitution of a character into account, not the variations. For example: there are two OTUs, OTU1 and OTU2. OTU1 stands for five specimens and for character X two specimens show state 1 and three specimens show state 0;

according to the majority scoring, only state 0 is considered to be present in character X for OTU1. OTU2 is represented by a single specimen and has state 1 for character X. Even though specimens within the two OTUs actually share the same character state for character X, this information is not present in the final analysis, as intraspecific variation for OTUs representing several specimens is more or less ignored under the majority scoring approach.

A second issue belonging to the dataset composition problem stems from the "species delimitation problem" which in turn results from the "species problem" (term introduced by Trueman, 1924; see also Tschopp et al., in press). The "species problem" describes the hurdle in defining species in a consistent and comparable way, and the "species delimitation problem" is the difficulty of defining species in a consistent way throughout the different fields of biological sciences (Palaeontology - Neontology; see Tschopp et al., in press and references therein). In solely palaeontological datasets, the individual species definitions, represented by species OTUs, can be based on diverging "species frames" which can be set narrower (little variation accepted within species) or wider (some variation accepted within species), depending on the researcher (see also Tschopp et al., in press). This "species comparability problem" can become more severe when mixing neontological and palaeontological data, because differential concepts of species delimitation can be used for neontological data compared to palaeontological data, such as reproductive isolation (see also Tschopp et al., in press and references therein). The usage of specimen-level OTUs circumvents the "species comparability problem" as no (species) definitions are needed. Moreover, human errors, concerning misidentifications of specimens that lead to chimeric OTUs, can be avoided. However, the actual "species delimitation problem" is not solved by using the specimen-level approach, but just ignored until the evaluation of the resulting phylogeny.

1.3. Specimen-level phylogeny

1.3.1. Concept and application of specimen-level phylogeny

The concept of specimen-level phylogeny is treating specimens as individual OTUs, as opposed to other levels of phylogeny where OTUs (mostly species or genera) are generally representing a group of specimens. Thus, specimen-level phylogenies are independent of previously made identifications or classifications made to the individual OTUs, and errors resulting from wrong taxonomic allocation or chimeric taxa are circumvented.

Specimen-level phylogenetic analyses not only provide valuable data which can be used for a re-evaluation of species-level taxonomy (e.g., Upchurch *et al.*, 2004; Tschopp *et al.*, 2015; Cau, 2017; Villa *et al.*, 2017). But this method can also be considered a bottom-up approach for species determination, it can provide information about relationships between individuals. Moreover, it may help to highlight the importance and the state of variation of a particular character through the evolutionary history of a certain taxon (speciation processes). In combination with well-dated stratigraphy, specimen-level phylogenetics can become a powerful tool to pinpoint occurrences of diagnostic characters to a certain locality and time. Further correlations with palaeoclimatic, palaeoenvironmental, or molecular data can then yield information on evolution in preeminent detail (Tschopp and Upchurch, 2019).

However, a major challenge with specimen-level phylogenetic analysis is anatomical overlap (Tschopp et al., 2015, 2018a; Tschopp and Upchurch, 2019). Anatomical overlap is created when at least two OTUs preserve the same skeletal regions, which allows the scoring of the same characters. It is crucial for the comparison of OTUs, but incomplete specimens lower the anatomical overlap (Tschopp et al., 2015). This is why the specimen-level approach is only rarely used in phylogenies that are based on morphological and/or palaeontological data, but broadly used for molecular-based phylogenies (e.g., Dettman et al., 2003; Godinho et al., 2005; Mayer and Pavlicev, 2007; Bacon et al., 2012; Ahmadzadeh et al., 2013b; Jiménez-Mejías et al., 2016; Marzahn et al., 2016). In higher-level phylogenies, data of several fragmentary specimens are combined to form a more or less complete "picture" of an OTU, whereas in specimen-level phylogenies, a fragmentary specimen will remain an incomplete OTU. However, specimen-level phylogeny based on osteological morphology has been performed, for instance, within Diplodocidae (Upchurch et al., 2004; Tschopp et al., 2015), Triceratops (Scannella et al., 2014), Mosasaurinae (Lively, 2016), Colubridae (Racca et al., 2020), and Lacertidae (Villa et al., 2017). Noteworthy is also a study by Gee (2020) in which he used the specimen-level approach to test the effect of ontogenetic differences on the phylogeny of Trematopidae by utilizing maximum parsimony and Bayesian Inference as optimality criteria, and two studies by Cau (2017, 2019) that also analysed specimen-level datasets under Bayesian Inference. Besides those intentional usages, specimen-level data are often present in specieslevel palaeontological analyses without the authors being aware of it or without proper consideration, because a fossil species might only be composed of a single specimen, while more specimens are present for other species. This leads to a mixing of the specimen- and species-level approach which can be problematic, as the intraspecific signal for the specieslevel OTUs is weakened due to the majority scoring, but not for the specimen-level OTUs (see also 1.2.2. Dataset composition problem).

Therefore, a validation of this method which addresses the problematics of specimen incompleteness and homoplastic characters is timely, and crucial. In this thesis, different methodological approaches were evaluated by utilizing a real-life dataset, instead of the commonly used simulated character matrices, in order to find a general method able to create the most reliable results for specimen-level data analysis depending on the properties of the dataset such as the amount of missing data and character distribution. For the construction of the real-life character matrix, the European squamate genera Lacerta and Timon were selected as the ingroup. The genus Lacerta is currently composed of ten extant species: Lacerta agilis Linnaeus, 1758 (Figure 1.13), Lacerta bilineata Daudin, 1802, Lacerta citrovittata Werner, 1935, Lacerta diplochondrodes Wettstein, 1952, Lacerta media (Lantz and Cyrén, 1920), Lacerta pamphylica Schmidtler, 1975, Lacerta schreiberi Bedriaga, 1878, Lacerta strigata Eichwald, 1831, Lacerta trilineata Bedriaga, 1886, and Lacerta viridis (Laurenti, 1768) (Speybroeck et al., 2020 and references therein). For reasons of accessibility, the following seven species of Lacerta were included in this thesis: L. agilis, L. bilineata, L. media, L. schreiberi, L. strigata, L. trilineata, and L. viridis. Noted here, because the species L. trilineata was just recently split into three species: L. trilineata, L. citrovittata, and L. diplochondrodes (Kornilios et al., 2020), it is possible that our data includes also specimens of the latter two newly erected species which were previously identified as *L. trilineata*. In total, six extant species belong to the genus Timon: Timon kurdistanicus (Suchow, 1936), Timon lepidus (Daudin, 1802), Timon nevadensis (Buchholz, 1963), Timon pater (Lataste, 1880), Timon princeps (Blanford, 1874), and Timon tangitanus (Boulenger, 1889) (Ahmadzadeh et al., 2012, 2016; Speybroeck et al., 2020 and references therein). Due to availability, the following four species were incorporated in this thesis: T. lepidus, T. kurdistanicus, T. pater, and T. princeps. The monophyletic state of the genus Lacerta in sister relationship to the genus *Timon* was recognised by molecular phylogenies (Figure 1.14; e.g., Ahmadzadeh et al., 2012; Pyron et al., 2013). However, phylogenies based on morphology find the genus *Timon* nested as a clade within *Lacerta*, and the sister relationship of the two genera is then forced by the usage of clade constraints during analysis (e.g., Tschopp et al., 2018b; Wencker et al., 2021).


Figure 1.13. Photograph of a (presumably) female specimen of *Lacerta agilis* from Röhnberg, Thuringia. Photograph taken by Andrea Villa.

The decision to use *Lacerta* and *Timon* as the ingroup was made based on its accessibility and an easy handling of the material due to the small body size of up to 21 cm (tail not included) of the individuals. Also, several molecular phylogenies (e.g., Godinho *et al.*, 2005; Ahmadzadeh *et al.*, 2012, 2013b; Pyron *et al.*, 2013; Sagonas *et al.*, 2014; Ahmadzadeh *et al.*, 2016; Marzahn *et al.*, 2016; Mendes *et al.*, 2016; Saberi-Pirooz *et al.*, 2021), including *Lacerta* and *Timon* can help during the evaluation process of the phylogenetic trees based on morphology. When testing different data compositions and analysing strategies which result in several phylogenetic trees, an idea of how the true tree might look like is crucial.

The evaluation or validation of the different analytical methods with specimen-level datasets is needed to identify specific settings which are optimal for specimen-level phylogenetic analysis based on osteology. Eventually, the aim is to establish a guideline upon which the best setting for the individual dataset can be selected leading to more accurate and reliable trees based on osteology.



Figure 1.14. Phylogenetic relationship of the genera *Lacerta* (orange rectangle) and *Timon* (blue rectangle) based on molecular data (modified from Kornilios *et al.*, 2020 and Saberi-Pirooz *et al.*, 2021).

2. Methods

2.1. Main matrix construction

The matrix used in this study is based on the one from Wencker *et al.* (2021; see also chapter 1.2.1. Data problem) which is an updated version of the matrix in Villa *et al.* (2017) and Tschopp *et al.* (2018b). It was initially constructed using the programme MESQUITE (v. 3.51, build 898; Maddison and Maddison, 2018), but then transferred to and managed through the web application MorphoBank (project: 3412, not published yet; O'Leary and Kaufman, 2012). The characters in the matrix were checked for clarity in phrasing, reproducibility of scorings, and dependencies among those characters following Simões *et al.* (2017). Eventually, the changes made to the matrix in Wencker *et al.* (2021) led to the exclusion of 14 characters, the modification (mostly wording modifications) of 11 characters, and the addition of 17 new characters based on personal observations (see Appendix 3 for a list of changes). The final matrix consists of 252 characters; all of them focused on the osteological morphology (for a complete character list including their sources see Appendix 4). Among them, 165 characters describe the cranial, 18 the dental, and 69 the postcranial elements of the skeleton. In respect to the character constitution, 215 qualitative and 37 quantitative characters are present in the matrix, which all have discrete character statements (Table 2.1).

Table 2.1. Character type distribution. Integers and percentages of the complete number of characters in the dataset given in brackets. Abbreviations: QN, quantitative; QL, qualitative; C, cranial; D, dental; P, postcranial.

Character type	QN-C	QN-D	QN-P	QL-C	QL-D	QL-P
Number of characters	17 (7%)	4 (2%)	16 (6%)	148 (59%)	14 (6%)	53 (21%)

The OTUs incorporated in the dataset are at the specimen-level and exclusively extant. The majority of the skeletons are from the collections of the Museo di Geologia e Paleontologia at the Università degli Studi di Torino. Before skeletonisation, the specimens were identified at species level on the basis of their external morphology and provenance according to Sindaco *et al.* (2008 and references therein) and Sillero *et al.* (2014). An exception is represented by the lacertine lacertid *Takydromus* that was positively identified at genus level only. Additional specimens were added based on personal observations from various collections (see 1.2.1. Data problem for institutional abbreviations). The species identifications of those specimens are assumed to be correct and were most probably made based on soft tissue morphology as in the case of the specimens at the Università degli Studi di Torino.

The specimen scoring is an ongoing joint effort together with Emanuel Tschopp, Andrea Villa, Marco Camaiti, and Letizia Ferro, with the majority of specimens in the dataset being checked for correct character scoring or newly added by me. The total number of OTUs (synonymous with specimens) is 120 (for a complete list of OTUs see Appendix 5) belonging to 45 different species. Every effort was made to include a mixture of female, male, and juvenile specimens (see Appendix 6 for information about the sex and ontogeny of the *Lacerta* and *Timon* OTUs). The number of OTUs per species ranges between one and 12.

The outgroup is composed of Gekko gecko (Linnaeus, 1758) as the most basal squamate (the clade of Gekkota was shown through molecular, total-evidence, and morphological analyses to be one of the most basal groups within Squamata; Gauthier et al., 2012; Reeder et al., 2015; Zheng and Wiens, 2015; Simões et al., 2018). Less basal outgroup OTUs are representatives of Scincoidea, Anguimorpha, Teiidae, Amphisbaenia, and Lacertidae. Scincoidea is formed by OTUs of Chalcides ocellatus (Forskal, 1775), Broadleysaurus major (Duméril, 1851), and Ablepharus kitaibelii (Bibron and Bory de Saint-Vincent, 1833). The position for Scincoidea is debated: molecular data indicate a position as the sister taxon to Lacertoidea + Toxicofera at the base of Squamata (Pyron et al., 2013; Reeder et al., 2015; Zheng and Wiens, 2015), whereas morphological data suggest the group to form the clade Scincomorpha together with Lacertoidea (Estes et al., 1988; Conrad, 2008; Gauthier et al., 2012). The clade of Anguimorpha is formed by OTUs of Varanus exanthematicus (Bosc, 1792), Anguis veronensis Pollini, 1818, and Pseudopus apodus (Pallas, 1775). The position of Anguimorpha is unclear as well; it is found as part of Toxicofera, a clade including, among other groups, Iguania and Serpentes, by molecular and morphological data. The clade of Toxicofera itself is found as sister to Lacertoidea (Reeder et al., 2015; Zheng and Wiens, 2015; Simões et al., 2018). As part of Lacertoidea, Teiidae are represented by specimens of Salvator merianae Duméril and Bibron, 1839 and Tupinambis teguixin (Linnaeus, 1758). The amphisbaenian clade is composed of OTUs of Blanus rufus (Hemprich, 1820) and Blanus strauchi (Bedriaga, 1884). Molecular analysis recovered it as sister of Lacertidae (Zheng and Wiens, 2016). The clade of Lacertidae is represented by the two subfamilies Gallotiinae and Lacertinae which are sister taxa (Arnold et al., 2007; Pyron et al., 2013). The clade of Gallotiinae is composed of specimens belonging to Gallotia caesaris (Lehrs, 1914), Gallotia simonyi (Steindachner, 1889), Gallotia stehlini (Schenkel, 1901), and *Psammodromus algirus* (Linnaeus, 1758). The subfamily Lacertinae is further divided into the African monophyletic tribe Eremiadini and the European monophyletic tribe Lacertini as sister taxa (Arnold et al., 2007; Pyron et al., 2013). Eremiadini are composed of OTUs of Acanthodactylus boskianus (Daudin, 1802), Acanthodactylus erythrurus (Schinz, 1833), Eremias velox (Pallas, 1771), Mesalina guttulata (Lichtenstein, 1823), and Ophisops elegans Ménétries, 1832. Lacertini is composed of specimens representing Algyroides fitzingeri 1834), Algyroides (Duméril Bibron, 1839), (Wiegmann, nigropunctatus and Anatololacerta danfordi (Günther, 1876), Archaeolacerta bedriagae (Camerano, 1885), Iberolacerta cyreni (Müller and Hellmich, 1937), Iberolacerta monticola (Boulenger, 1905), Phoenicolacerta troodica (Werner, 1936), Podarcis hispanicus (Steindachner, 1870), Podarcis muralis (Laurenti, 1768), Podarcis siculus (Rafinesque-Schmaltz, 1810), Podarcis tiliguerta (Gmelin, 1789), Podarcis waglerianus Gistel, 1868, Takydromus sp. Daudin, 1802, and Zootoca vivipara (Lichtenstein, 1823).

The ingroup is formed of 69 OTUs that belong to the two lacertine genera *Lacerta* and *Timon*. It contains 12 OTUs of *Lacerta agilis*, 12 of *L. bilineata*, three of *L. media*, six of *L. schreiberi*, two of *L. strigata*, eight of *L. trilineata*, 11 of *L. viridis*, ten of *T. lepidus*, one of *T. kurdistanicus*, three of *T. pater*, and one OTU of *T. princeps* (see Appendix 5 for collection numbers of ingroup and outgroup OTUs).

2.2. Matrix construction with continuous character states

A second matrix based on the main matrix was constructed. It consists of the same 120 OTUs and 252 characters, but the 37 quantitative characters, which had discrete character statements in the main matrix, were coded as continuous characters here.

For matrix construction, the web application MorphoBank was used (project: 3412, not published yet; O'Leary and Kaufman, 2012). The aim was to obtain a precise value for the quantitative characters for all OTUs, which had been assigned to a discrete character state in the main matrix; ranges were given when bilateral asymmetry occurred. In some cases, exact measurements or counts were not possible, because of inaccessibility of certain areas in the skeleton due to bone articulation or inaccessibility of the material itself. The characters were then also coded with a range of values; the ranges were based on the original discrete character scorings. As example, for character 3: Teeth, crown complexity, maximum number of cusps in a single toot: 4 or more (state 0); 3 (state 1); 2 or less (state 2), an inaccessible OUT that was scored as having state 2 (2 or less) would receive as continuous character state the range "1-2"; another inaccessible OUT with the discrete character state 0 (4 or more), would receive as continuous character state the range "4–5" because for the upper boundary the maximum

number of observed cusps in the whole dataset would be selected. Hence, also the number of missing entries was the same for the main matrix and the continuous-discrete matrix; the continuous-discrete matrix is in the following referred to as "cd matrix".

2.3. Simulated fossil dataset construction

To generate results which are also meaningful for fossil OTUs, simulated fossil datasets based on the main matrix and the cd matrix were created. It was decided against using real fossil OTUs to ensure (better) comparability with the results of the extant analyses because critical factors such as a varying number of specimens per species were minimised.

As fossil OTUs have generally a lower specimen completeness than extant ones, the number of missing entries had to be higher in the simulated datasets than in the two extant datasets (main matrix, cd matrix) which were used as starting points. But not only the number of missing entries, but the distribution pattern of such needed to be considered to generate a realistic fossil dataset as well.

Hence, as the basis for the distribution pattern of missing values for the simulated dataset, fossil OTUs scored for the main matrix in a different context (but not included in the dataset here; Wencker *et al.*, 2021; Tschopp *et al.*, in press) were used as a fossil model (for a list of fossil OTUs see Appendix 7). In total, 41 specimens belonging to seven extinct species comprised the fossil model matrix: *Dracaenosaurus croizeti* (seven specimens), "*Lacerta*" siculimelitensis (five locality level OTUs treated as specimens), "*Lacerta*" filholi (four specimens), *Ligerosaurus pouiti* (one specimen), *Mediolacerta roceki* (four specimens), *Plesiolacerta lydekkeri* (12 specimens), and *Pseudeumeces cadurcensis* (eight specimens).

Therefore, a custom python script ("25-imcompleteness script") was created utilising the Anaconda distribution with the software library Pandas (python v. 3.7.9) in the integrated development environment (IDE) Spyder (v. 4.2.2; the script is published in the supplementary material of Tschopp *et al.*, in press; available also in Appendix 8). The script divided the matrix into 25 sections with ten characters each (12 characters in the last section) and calculated the percentage of missing values per character section. The incompleteness percentages per character section and by that the distribution of missing values was calculated for the extant matrices (the two have the same distribution pattern) and the fossil model matrix.

In the next step, a second custom python script ("fossil-simulation script") was created to randomly delete a predefined percentage of scored character states within the specific character sections (see above at 25-incompleteness script) of the extant matrices (the script is published in the supplementary material of Tschopp *et al.*, in press; available also in Appendix 8). For the predefined percentage to be deleted in the specific character sections, the incompleteness percentages calculated for the fossil model dataset with the first python script were taken as a starting point to calculate a target value for the simulated fossil datasets. As target values for overall incompleteness percentage of the simulated datasets an incompleteness of 45% and 65% was chosen. The latter percentage appears to be a relatively high overall completeness even for fossils and was for instance observed in the dataset used in Tschopp *et al.* (2015). The lower percentage, 45%, was chosen as an intermediate incompleteness between the extant matrices with an incompleteness of 30% and the other simulated target value. In the case of the target incompleteness of 45%, for two sections (characters 11-20 and characters 241-252) the percentage of the extant matrices was kept as it is, because the calculated target value was lower than the extant/original one (Table 2.2).

Eventually, four simulated datasets were generated: 1) 45-fossil matrix (45% incompleteness, based on the main matrix); 2) 45-fossil-cd matrix (45% incompleteness, based on the cd matrix); 3) 65-fossil matrix (65% incompleteness, based on the main matrix); and 4) 65-fossil-cd matrix (65% incompleteness, based on the cd matrix).

Additionally, a third custom python script ("3-imcompleteness script") was created to calculate the percentage of missing entries for three matrix partitions which each code for a specific skeletal region: cranial (excluding characters that code for dentition), dental, and postcranial. The three partitions were further subdivided into quantitative and qualitative characters (the script is published in the supplementary material of Tschopp *et al.*, in press; available also in Appendix 8).

Table 2.2. Incompleteness of extant matrices, fossil model matrix, and the simulated matrices per character section (25-imcompleteness script) and the overall incompleteness percentage. Asterisks indicate sections where the percentage of the extant matrix was kept because the target value was lower than the extant one. Cell colours indicate low incompleteness (green shades) to high incompleteness (red shades) of the individual section. Abbreviation: incomp., incompleteness.

	Extant matrices	Fossil model matrix	45-fossil matrices	65-fossil matrices
Overall incomp. (in %)	30	90	45	65
Incomp. per section (in %)			
characters 1 - 10	32	83	41	60
characters 11 - 20	50	95	50*	68
characters 21 - 30	39	93	46	67
characters 31 - 40	39	94	47	68
characters 41 - 50	22	89	44	64
characters 51 - 60	38	90	45	65
characters 61 - 70	20	84	42	61
characters 71 - 80	32	89	44	64
characters 81 - 90	31	94	47	68
characters 91 - 100	26	92	46	66
characters 101 - 110	24	95	47	68
characters 111 - 120	27	93	46	67
characters 121 - 130	19	91	46	66
characters 131 - 140	21	93	46	67
characters 141 - 150	17	97	48	70
characters 151 - 160	17	92	46	66
characters 161 - 170	25	62	31	45
characters 171 - 180	18	90	45	65
characters 181 - 190	35	96	48	69
characters 191 - 200	14	60	30	43
characters 201 - 210	38	100	50	72
characters 211 - 220	33	96	48	69
characters 221 - 230	44	93	46	67
characters 231 - 240	36	95	47	68
characters 241 - 252	53	98	53*	71

3. Results

3.1. Matrix constitution

In total, six character matrices, all consisting of the same 120 OTUs and 252 characters, form the basis of this thesis (see Appendix 9 for matrices). Three of them contain only characters with discrete character statements: main matrix, 45-fossil matrix, and 65-fossil matrix. The other three matrices contain 37 characters with continuous and 215 characters with discrete character statements: cd matrix, 45-fossil-cd matrix, and 65-fossil-cd matrix. Next to the character statement type, the main dividing factor among the matrices is their amount of missing data. Two matrices each share the same percentage of missing data, forming matrix pairs: main matrix and cd matrix, 45-fossil matrix and 45-fossil-cd matrix, 65-fossil matrix and 65-fossil-cd matrix. Even though the matrix pairs share the same percentage of incompleteness, the absolute number of missing values slightly varies for the simulated fossil dataset matrix pairs (Table 3.1). Because the deletion of entries was performed based on percentages of missing values to be created and not on absolute numbers (see also 2.3. Simulated fossil dataset construction).

In regard to the three character matrix partitions (according to the skeletal regions which the characters describe), cranial (excluding characters coding for dentition), dental, and postcranial, all matrices show a similar distribution pattern of missing values, with the highest completeness in the dental partition and the lowest in the postcranial partition (Table 3.1).

Table 3.1. List of created matrices, including their percentages of incompleteness in respect to the three matrix
partitions. Absolute numbers of characters coding for specific partitions and character types given in brackets after
the subcategories of partitions. Absolute numbers of missing entries given in brackets after the overall
incompleteness percentages. Grey shaded fields indicate different incompleteness values among the matrix pairs.
Abbreviations: Incomp., incompleteness; QN, quantitative; QL, qualitative; T, total; c, characters.

Character	Overall	Cranial			Dental			Postcrar	Postcranial		
matrix	incomn	QN	QL	Т	QN	QL	Т	QN	QL	Т	
matrix	meomp.	(17 c)	(148 c)	(165 c)	(4 c)	(14 c)	(18 c)	(16 c)	(53 c)	(69 c)	
Main matrix	30%	4106	24%	26%	50/2	17%	15%	53%	4196	110/2	
	(9,118)	-170	2470	2070	570	1770	1370	5570	4170		
45-fossil	45%	15%	11%	15%	18%	330/2	20%	50%	10%	51%	
matrix	(13,687)	-J /0		4370	1070	5570	2770	5770		5170	
65-fossil	65%	65%	65%	65%	15%	40%	18%	73%	60%	70%	
matrix	(19,657)	0370	0570	0570	4370	1970	1070	1570	0770	7070	
Cd matrix	30%	4106	24%	26%	5%	17%	15%	53%	419/2	119/2	
Cumatrix	(9,118)	41%	2470	20%	570	1/%0	1370	33%0	41%	44%	
45-fossil-cd	45%	46%	44%	45%	18%	33%	30%	59%	49%	51%	
matrix	(13,715)	1070		1570	10/0	5570	5070	3970	1270	3170	
65-fossil-cd	65%	65%	65%	65%	15%	10%	18%	73%	60%	70%	
matrix	(19,675)	0570	0570	0570	J/0	770	7070	1370	0770	/0/0	

The main matrix and the cd matrix have an overall percentage of 30% of missing data (nonapplicable characters were treated as scored characters; Figure 3.1). The distribution of missing values throughout the three matrix partitions are identical for the two matrices (Table 3.1). The dental, as the most completely scored partition, had an incompleteness of 15%, the cranial of 26%, and the postcranial of 44%. For the cranial and postcranial partitions, the qualitative characters were more complete, whereas for the dental partition, the quantitative characters were the ones with a higher completeness. In the cranial, the incompleteness of the quantitative characters is 41% and for the qualitative characters 24%. For the dental, 5% missing entries in the quantitative and 17% in the qualitative characters were observed. The quantitative postcranial characters show an incompleteness of 53%, whereas the qualitative characters have 41% of missing entries.



Figure 3.1. Composition of the main matrix in respect to missing data (matrix dimensions 120 OTUs x 252 characters). Black areas: scored characters; grey areas: missing characters. The cd matrix is not depicted, because it shows an almost identical distribution pattern of missing data. Abbreviations: QN, quantitative characters; QL, qualitative characters.

The 45-fossil matrix and the 45-fossil-cd matrix have an overall percentage of 45% of missing entries (Figure 3.2). The two matrices show an identical distribution of missing entries for the postcranial partition with 51% of total incompleteness. For the cranial and dental partition, the differences in the distribution pattern are marginal with 29% of incompleteness for the dental partition in the 45-fossil matrix and 30% of incompleteness in the 45-fossil-cd matrix, respectively. The percentage of missing entries in respect to the subcategories quantitative and qualitative characters, is quite similar for the cranial partition, but slightly different values were observed for the two matrices, with 45% of incompleteness in the quantitative and 44% in the qualitative characters for the 45-fossil matrix, and 46% in the quantitative and 44% in the qualitative characters for the 45-fossil-cd matrix. In the dental partition, the quantitative characters have an incompleteness of 18% and the qualitative characters of 33%. The quantitative postcranial characters have a proportion of 59% of missing values, whereas the qualitative characters have 49% of missing entries. The small differences observed between the percentages of missing values between the two matrices (cranial, quantitative; dental, total) is due to the slight difference in absolute numbers of missing entries (see Table 3.1 and text above).



Figure 3.2. Composition of the 45-fossil matrix in respect to missing data (matrix dimensions 120 OTUs x 252 characters). Black areas: scored characters; grey areas: missing characters. The 45-fossil-cd matrix is not depicted, because it shows an almost identical distribution pattern of missing data. Abbreviations: QN, quantitative characters; QL, qualitative characters.

The 65-fossil matrix and the 65-fossil-cd matrix have an overall incompleteness of 65% (Figure 3.3). The observed percentage of missing entries in the three matrix partitions is identical for the two matrices. The cranial, dental, and postcranial partitions show an incompleteness of 65%, 45%, and 70%, respectively (Table 3.1). Among the subcategories quantitative and qualitative characters, the two matrices show quite similar patterns of incompleteness: for the cranial partition, both categories have 65% of missing values. In the dental partition, the quantitative characters have an incompleteness of 45% and the qualitative of 49%, respectively. The proportion of missing values among the postcranial characters are 73% for quantitative characters.



Figure 3.3. Composition of the 65-fossil matrix in respect to missing data (matrix dimensions 120 OTUs x 252 characters). Black areas: scored characters; grey areas: missing characters. The 65-fossil-cd matrix is not depicted, because it shows an almost identical distribution pattern of missing data. Abbreviations: QN, quantitative characters; QL, qualitative characters.

As an additional measurement of completeness, the two overlap indices, All Characters Overlap Index (AOI) and Comparable Characters Overlap Index (COI), following Tschopp *et al.* (2015) were calculated utilising the Microsoft Excel® template provided by Tschopp *et al.* (2018a). The AOI indicates how many characters of the whole character set have an overlap in a specific group. Hence, it can give an idea how much support based on anatomical overlap is present in the specific group. The COI is expressing the mean of overlaps of characters which have an anatomical overlap within a specific group. Hence, a minimum of two taxa has to be part of the group (for AOI and COI), the COI is always higher than the AOI, and if only two taxa form a group, the COI is per definition 100%.

The two indices were calculated for 12 groups: two genus groups including all OTUs assigned to *Lacerta* or *Timon*, respectively, one group for each species of *Lacerta* and *Timon*, whereas *T. princeps* and *T. kurdistanicus* were combined in a single group (Table 3.2) because for the calculation of the overlap indices, the minimum number of taxa in a group is two, and molecular and morphological data suggest a monophyletic state for the two species (e.g., Ahmadzadeh *et al.*, 2012, 2016; Wencker *et al.*, 2021).

The AOI ranges for the main matrix and cd matrix, from 28% (*Lacerta media*) to 76% (*L. trilineata*), for the 45-fossil matrix from 19% (*L. media*) to 56% (*L. agilis*, *L. trilineata*), for

the 45-fossil-cd matrix from 17% (L. media) to 57% (L. trilineata), for the 65-fossil matrix from 8% (L. media) to 33% (Lacerta), and for the 65-fossil-cd matrix from 10% (L. media) to 32% (Lacerta) (Table 3.2). Because the L. strigata and T. princeps/kurdistanicus group consisted only of two OTUs, their COI was per definition 100%. When considering only the other ten groups, the COI has a range of 59% (Timon) to 80% (L. trilineata) in the main matrix and cd matrix, of 44% (Timon) to 65% (L. media) in the 45-fossil matrix, of 45% (Timon) to 65% (L. media, T. pater) in the 45-fossil-cd matrix, of 27% (Timon) to 60% (T. pater) in the 65-fossil matrix, and of 28% (Timon) to 60% (L. media) in the 65-fossil-cd matrix (Table 3.2). Differences in the AOI and COI between the discrete and continuous-discrete simulated fossil matrices can be explained by the fact that the index calculation programme treats a missing value ("?") and a non-applicable character ("-") in the same way, whereas the fossil-simulation script (see 2.3. Simulated fossil dataset construction) with which the simulated fossil datasets have been created, treats non-applicable characters as a scored character. The deletion of characters with the python script is performed randomly within the defined sections (see 2.3. Simulated fossil dataset construction). Hence, for the discrete matrix, the python script could have deleted the state of a character that was scored as non-applicable, whereas for the continuous-discrete matrix, a character state could have been deleted that had a numeric character state or vice versa.

In summary, the missing values are rather equally distributed among the OUTs, but a pattern is visible for the character sections or rather skeletal regions with the highest incompleteness among postcranial characters and the lowest among dental characters. In regard to the character type, only in the case of the dental partition was the incompleteness of qualitative characters higher than the one of the quantitative characters. This focused distribution of missing entries in the same areas is also reflected by the overlap indices which are quite similar for all tested groups.

Table 3.2. Overlap indices of the six character matrices following Tschopp et al. (2015) and Tschopp et al. (2018).
Overlap indices are calculated for two genus groups (Lacerta and Timon) and ten species groups individually (all
species of Lacerta and Timon). Numbers in brackets after group names indicate number of specimens forming the
group. Grey shaded fields indicate different incompleteness values among the matrix pairs. Abbreviations: AOI,
All Characters Overlap Index; COI, Comparable Characters Overlap Index.

	Main	matrix/	45-fossi	1	65-fossi	1	45-fossi	l-cd	65-fossi	l-cd
Group/matrix	cd matrix		matrix		matrix		matrix		matrix	
	AOI	COI	AOI	COI	AOI	COI	AOI	COI	AOI	COI
Lacerta (54)	67%	67%	52%	53%	33%	33%	52%	52%	32%	33%
L. agilis (12)	71%	72%	56%	57%	31%	33%	54%	55%	31%	34%
L. bilineata (12)	66%	68%	49%	51%	31%	35%	49%	51%	30%	34%
L. media (3)	28%	72%	19%	65%	8%	53%	17%	65%	10%	60%
L. schreiberi (6)	47%	65%	35%	54%	18%	38%	35%	55%	18%	37%
L. strigata (2)	62%	100%	40%	100%	15%	100%	38%	100%	16%	100%
L. trilineata (8)	76%	80%	56%	60%	32%	38%	57%	61%	30%	37%
L. viridis (11)	60%	63%	45%	48%	26%	31%	45%	49%	25%	31%
Timon (15)	58%	59%	43%	44%	25%	27%	44%	45%	26%	28%
T. lepidus (10)	57%	60%	42%	45%	23%	28%	43%	46%	25%	31%
<i>T. pater</i> (3)	46%	74%	29%	64%	13%	60%	30%	65%	13%	58%
T. princeps/ kurdistanicus (2)	63%	100%	35%	100%	13%	100%	34%	100%	14%	100%

3.2. Comparison of weighting strategies

3.2.1. Introduction

Whether or not to apply differential weights to characters during morphological phylogenetic analyses is a controversial topic (Farris, 1969, 1983; Neff, 1986; Wheeler, 1986; Carpenter, 1988; Bryant, 1989; Goloboff, 1993, 1995, 2014; Thiele, 1993; Chippindale and Wiens, 1994; Turner and Zandee, 1995; Allard and Carpenter, 1996; De Laet, 1997; Kluge, 1997; Emerson and Hastings, 1998; Haszprunar, 1998; Wiens and Servedio, 2000; Wiens, 2001; Vogt, 2002; Goloboff *et al.*, 2008; Prevosti and Chemisquy, 2010; Brazeau, 2011). However, it should be born in mind, that already the character selection process is a form of character weighting, as weight is given to included/described features whereas excluded/undescribed features are given no weight at all (Neff, 1986; Wheeler, 1986; De Laet, 1997; Haszprunar, 1998; Vogt, 2002). Hence, an equal weighted morphological phylogenetic analysis does not exist, because the inclusion of all possible features into a dataset is impossible, may the character selection be intentional. Therefore, all phylogenetic analyses are already weighted per default (Haszprunar, 1998). Haszprunar (1998) even stated that a combination of character selection and an equal weighted analysis is representing the strongest unequal weighting possible.

In general, phylogeneticists agree that phylogenetically significant traits should have a higher weight than insignificant, usually homoplastic, traits (Farris, 1969; Kluge and Farris, 1969; Platnick et al., 1991), but a consensus on how to achieve such a weighting scheme does not exist (Farris, 1969, 1983; Neff, 1986; Wheeler, 1986; Carpenter, 1988; Bryant, 1989; Goloboff, 1993; Chippindale and Wiens, 1994; Allard and Carpenter, 1996; De Laet, 1997; Emerson and Hastings, 1998; Haszprunar, 1998; Vogt, 2002). There are three basic concepts for the implementation of character weighting: 1) prior knowledge of the character variability through time and taxonomic group (Felsenstein, 1981; Sober, 1986); 2) character compatibility during tree search (Penny and Hendy, 1985; Sharkey, 1989); 3) and observed homoplasy (Farris, 1969). The first iterative approach to downweigh homoplastic characters was proposed by Farris (1969) as the so-called successive weighting; it is based on the concept of observed homoplasy. It was further developed by Goloboff (1993) and implemented in the programme Pee-Wee (Goloboff, 1994) and later in TNT (Goloboff and Catalano, 2016) as an automated method called implied weighting. Here, the weight of a character is adjusted based on its homoplastic fit on the possible trees during the tree search analysis, and eventually the tree with the highest implied weights is retained (Goloboff, 1993). Hence, the human impact on the process of character weighting is restricted to the character selection. Thus, the extreme scenario of equal weighting and character selection (see above) is circumvented. As proposed by Farris (1969), for successive weighting, also the implied weighting uses a weighting function with a concave shape. A concave weighting function is weighing strongly in favour of reliable characters, whereas a convex function weighs strongly against unreliable characters (Farris, 1969). The extent of the concavity, i.e., the strength of downweighting homoplastic characters can be adjusted through the concavity constant K, also called the K-value (see Goloboff, 1993 for the mathematical bakground). Simply put, the weighting function f can be explained as f = K + (K/es) where es is the number of extra steps (Goloboff, 1995). Accordingly, the smaller the K-value, the less weight is given to a homoplastic character during tree search, and the downweighting is thus stronger. A K-value which approaches infinity corresponds to equalweighting approaches (Wheeler, 1986; Turner and Zandee, 1995; De Laet, 1997; Mirande, 2009) and a K-value approaching 0 converges with a priori exclusion of homoplastic characters (Carpenter, 1988; De Laet, 1997). Since simulations have shown that homoplastic characters actually increase phylogenetic accuracy (Chippindale and Wiens, 1994), by possibly adding information at a lower taxonomic level (Farris, 1969; Haszprunar, 1998), downweighting these characters seems more useful than a priori exclusion, especially when analysing specimen-level data (Tschopp and Upchurch, 2019). However, the choice of an adequate K-value remains unclear (Turner and Zandee, 1995; Meszaros et al., 1996), even though suggestions of using rather higher K-values (greater than the default setting in TNT of K = 3) have been made (Goloboff et al., 2008, 2018). In fact, one major critique on implied weighting is that the choice of the K-value has no biological grounds and remains thus arbitrary (Turner and Zandee, 1995; Emerson and Hastings, 1998). Källersjö et al. (1999) noticed based on observations of the third codon position in plants that downweighting of homoplastic characters might not be suitable. However, for morphological datasets, weighting against homoplasy led to an increase in average jackknife frequencies and an improvement of other resampling measures were observed (Goloboff, 1997; Goloboff et al., 2008). De Laet (1997) and Kluge (1997) discussed that the method of weighting characters as proposed by Goloboff (1993) finally maximizes fit instead of minimizing homoplasy, and is thus not in agreement with the main idea behind parsimony methods. Even though fittest trees and MPTs might coincide, it seems not to be the general case according to De Laet (1997).

Implied weighting is infrequently used in palaeontological phylogenetic analyses (Congreve and Lamsdell, 2016) or if used, researchers often apply the default setting of K = 3 (e.g.,

Mannion *et al.*, 2013; Tschopp *et al.*, 2015), which seems to downweigh homoplastic characters too strongly (Goloboff *et al.*, 2018). A rare exception is, for instance, Groh *et al.* (2020) who tested next to K = 3, also K = 12. A possible reason for the infrequent usage of implied weights in palaeontological phylogenies could have been the influence of missing entries in a dataset on the observed homoplasy: characters with high numbers of missing entries display (on average) less homoplasy than completely scored characters, which leads to higher weights given to those incompletely scored characters, even though their true homoplasy might be different than the observed one (Goloboff, 2014). To address this problem, Goloboff (2014) developed and implemented in TNT a method called extended implied weighting. Here, the observed homoplasy in the scored entries of a character is taken as a starting point for the assumption of the homoplasy, which might be present in the missing entries. The implementation allows to set the assumed homoplasy for the missing entries to be from 0% to 100% of the observed homoplasy is theoretically resulting in a simple implied weights analysis.

Previous studies trying to evaluate the performance of implied weights were mainly based on simulations (Congreve and Lamsdell, 2016; O'Reilly *et al.*, 2016; Goloboff *et al.*, 2018; Puttick *et al.*, 2019; Smith, 2019). Some estimates of phylogenetic accuracy of implied weights in real morphological datasets were either testing a very small range of *K*-values (Prevosti and Chemisquy, 2010; Sansom *et al.*, 2018) or presented results which did not distinguish between the different *K*-values (Goloboff *et al.*, 2008). However, no study has ever explored the capacities of different weighting strategies, including extended implied weighting, to recover real taxonomic groupings based on actual morphological data.

Presented herein is a first case study using a real morphological specimen-level dataset with the aim to investigate the impact of implied weights and extended implied weights on tree accuracy in order to find the best fitting weighting strategy. Additionally, investigations were expanded to datasets containing continuous data treated as such and/or simulated fossil datasets which were all based on the same initial real morphological specimen-level dataset.

3.2.2 Materials and methods

3.2.2.1. Phylogenetic analyses

The six character matrices (main matrix, 45-fossil matrix, 65-fossil matrix, cd matrix, 45-fossilcd matrix, 65-fossil-cd matrix; see also 2. Methods and 3.1. Matrix constitution) were used for the case study. The specimen-level phylogenetic analyses with the maximum parsimony approach were performed with the software TNT (v. 1.5; Goloboff and Catalano, 2016). In all cases, a traditional heuristic search with 10,000 replications and 50 trees saved per replication was conducted. For a better tree space coverage, the resulting MPTs were used as a starting point for a second round of tree bisection and reconnection (TBR). When more than one MPT was recovered, a strict consensus tree was calculated.

The analyses were performed with differential weighting strategies: 1) all characters equally weighted (equal weights); 2) implied weights with seven different *K*-values (5, 10, 20, 50, 100, 150, 200); and 3) extended implied weighting with the same seven *K*-values as for strategy 2, but with four different settings or percentages of assumed homoplasy for the missing entries based on the observed homoplasy for each *K*-value (25%, 50%, 75%, 100%, for each *K*-value; see also Figure 3.4). This procedure was applied to each of the six matrices. Hence, a total of 216 phylogenetic analyses were performed (36 per matrix).



Figure 3.4. Scheme visualising the tested weighting strategies. The six character matrices: main matrix, 45-fossil matrix, 65-fossil matrix, cd matrix, 45-fossil-cd matrix, 65-fossil-cd matrix, were used to test the three weighting strategy approaches: equal weights, implied weights, and extended implied weights. For implied weights and extended implied weights different values for K (5, 10, 20, 50, 100, 150, 200) and percentages for the assumed homoplasy for missing entries (25%, 50%, 75%, 100%) were tested. Hence, one analysis under equal weights, 7 under implied weights, and 28 under extended implied weights were preformed which sums up to a total of 36 analyses per matrix.

3.2.2.2. Tree comparison

The resulting trees (single MPT or strict consensus) were compared based on six accuracy measurements: 1) the overall tree resolution; 2) clade delimitation; 3) average group support for symmetric resampling; 4) average group support for jackknife resampling; 5) Robinson-Foulds distances (Robinson and Foulds, 1981); and 6) Distortion-Coefficients (modified after Farris, 1973 by Goloboff *et al.*, 2018). Except for the overall tree resolution and clade delimitation, which were conducted manually, all other accuracy measurements were calculated with the implementations provided in TNT. The results of the six accuracy measurements were normalised to values from 0 to 1 with one representing the best score, and those normalised scores were then combined into a final ranking. The comparison of the trees resulting from the different weighting strategies was done separately for each character matrix (noted here, the process of normalising the values of the individual accuracy measurements eliminates the possibility to compare the values of one matrix with another). A scheme summarising the whole work flow from matrix construction to final ranking is depicted in Figure 3.5.

Overall tree resolution

The overall tree resolution was determined manually by observing each strict consensus tree or MPT (if only a single one was obtained) resulting from the 216 different analytical procedures. The resolution of the trees could generally be divided in six stages of resolution: 1) polytomy involving ingroup and outgroup; 2) polytomy involving the complete ingroup; 3) polytomy involving major part of the ingroup; 4) polytomy involving half or less of the ingroup; 5) only smaller polytomies present involving the ingroup; 6) completely resolved tree with no polytomy involving the ingroup. Accordingly, for the rating of the overall tree resolution, a range of values from 0 to 5 was selected, where 0 corresponds to stage 1 and 5 corresponds to stage 6. If within the observed polytomies some branches were recovered, hence, if the polytomy was actually between two stages, a score of 0.5 was added to the initial score. The final overall tree

resolution score was then normalised to values from 0 to 1 (1 is best) and considered in the final ranking of the individual character matrices.



Figure 3.5. Scheme summarising the work flow performed for the comparison of weighting strategies. 1. Matrix construction of six character matrices (main matrix, 45-fossil matrix, 65-fossil matrix, cd matrix, 45-fossil-cd matrix, 65-fossil-cd matrix; 2. Phylogenetic analysis using equal weights, implied weights and extended implied weights (see also Figure 3.4) resulting into 36 different weighting strategies applied to each of the six character matrices; 3. Accuracy measurements -including overall tree resolution, clade delimitation, symmetric resampling frequencies, jackknife frequencies, Robinson-Foulds distances, and Distortion Coefficients- that were estimated for the 36 different weighting strategies per character matrix; 4. Final ranking for each of the six character matrices based on the accuracy measurements. Abbreviations: ew, equal weights; iw, implied weights; eiw, extended implied weights; otr, overall tree resolution; clade delimitation; sr, symmetric resampling; jk, jackknife; RF, Robinson-Foulds distances; DC, Distortion Coefficients.

Clade delimitation

In the case of clade delimitation, the previously made species identifications of the OTUs based on the soft parts (see 2.1. Main matrix construction) were considered for the evaluation. Two approaches for the determination of clade delimitation were combined: 1) counting cladeintruding OTUs on higher-taxonomic levels and 2) enumerating OTUs correctly forming a clade on lower-taxonomic levels.

Clade intruding OTUs were identified for the tribe Lacertini, the genus *Lacerta*, and the genus *Timon*. But, as stated in chapter 1.3.1. Concept and application of specimen-level phylogeny, in morphological analyses, *Timon* is recovered nested within *Lacerta* which was also the case in this study. Therefore, for *Lacerta*, the *Timon* clade with its intruders was ignored to avoid double counts. The counts from the three clades were first normalised individually to values from 0 to 1 with one representing the best score, hence, the fewer intruding OTUs the better, and then summed to a final clade intruder score, this score was again normalised to values from 0 to 1.

Correct clade formation was determined for the seven species of *Lacerta* and the four species of *Timon*. For this purpose, the number of correctly placed OTUs forming the largest species clade was enumerated. To also consider cases when all OTUs of one species were placed correctly in their species-clade, but intruding OTUs were "destroying" the clade, a bonus 0.5 was added to the initial count. However, this was only done if the number of intruding OTUs was no more than the number of OTUs actually belonging to the species clade. In cases where the largest clean species-clade was a polytomy, a minus point of 0.25 was given, and when another intruding OTU was part of the polytomy the number of correctly placed OTUs minus 0.5 was taken as the final score for the clade formation. In a second step, the individual species-clade values were converted into proportion-scores, for instance, the final score for the species *Lacerta agilis* was 3, the proportion-score would be 3 (the final score) divided by 12 (the

number of OTUs identified as *L. agilis*) which is 0.25. Those proportion-scores were then summed up. In the case of the genus *Timon*, 1 additional point was given, if the complete genus clade structure was recovered correctly with *Timon lepidus* + *T. pater* forming sister to the clade of *T. princeps* + *T. kurdistanicus*. The final clade formation score was then normalised to values from 0 to 1 with 1 representing the best values, hence, the more correctly placed OTUs in a clade the better.

Eventually, the normalised final clade intruder score and the normalised final clade formation score were added together to the final clade delimitation score. It was then again normalised to values from 0 to 1 (1 is best) and considered in the final ranking of the individual character matrices.

Symmetric resampling and jackknife

Jackknife resampling is a widely used support metric which was already used to compare group supports of different analytical strategies (Källersjö *et al.*, 1999; Goloboff *et al.*, 2008). However, Goloboff *et al.* (2003) reported that jackknife frequencies might produce distorted support values when comparing between analyses with different weighting strategies, and suggested using the symmetric resampling method. However, a case study could not show a consistently better performance of one or the other method (Kopuchian and Ramírez, 2010). Hence, there is no clear preference for either traditional jackknife or symmetric resampling (see also Tschopp and Upchurch, 2019, and references therein). Therefore, both support metrics were used here; they were calculated with the implementation in TNT. In both cases, the default settings were chosen, with the number of replicates set at 10,000. For the final ranking, the average group support of all groups was taken as value. The values for the symmetric resampling and jackknife were normalised to values from 0 to 1 (1 is best) and considered separately for the final ranking of accuracy measurements.

Robinson-Foulds distances and Distortion-Coefficients

The Robinson-Foulds distances are a symmetric tree topology comparison metric that measures the differences between a pair of trees by comparing bipartition splits of two trees; it differs between identical and not-identical branches (Robinson and Foulds, 1981).

The Distortion-Coefficient is also a symmetrical and pairwise comparison of trees, it is calculated in а similar way as the Retention Index (RI; Farris, 1989): DC = (Ga + Gb - Sab - Sba) / (Ga + Gb - Ma - Mb) with G as the maximum number of possible steps for tree a and b, S is the observed number of steps when mapping tree a on tree b (and vice versa), and M as the minimum number of possible steps for tree a and b (see Goloboff et al., 2018). Thus, the stepwise differences between branches are considered.

Both methods have been used to calculate the differences between a modelled "true tree" and a tree resulting from analysis of a simulated dataset (e.g., Goloboff *et al.*, 2018). In the present study, a real dataset was used and, thus, no "true tree" is present to compare it with the trees resulting from the analyses with the different weighting strategies. Hence, the basic idea to use the Robinson-Foulds distances and the Distortion-Coefficients in this context as accuracy measurement is that theoretically topological structures that are shared by several trees should be more likely to have a larger support or seem to derive from a true signal than topologies that occur only in one or few trees.

The Robinson-Foulds distances and the Distortion-Coefficients were both calculated with the implementations in TNT. Here, each tree (single MPT or strict consensus, resulting from the individual analyses with 36 different weighting strategies) was compared to every other tree (single MPT or strict consensus, resulting from the individual analyses with 36 different weighting strategies). Then the sum of the resulting distance values for each tree was calculated. The values for each tree (or weighting strategy) were then normalised to a range of 0 to 1, with 1 representing the best score. In the case of the initial Robinson-Foulds distances, smaller (distance) values are better, whereas for the Distortion-Coefficients, greater values express higher similarity between the trees. The scores of the Robinson-Foulds distances and the Distortion-Coefficients were considered separately for the final ranking.

3.2.3. Results

3.2.3.1. Accuracy measurements

Here, the final rankings of the 36 different weighting strategies are presented. The different weighting strategies were applied to each of the six character matrices (main matrix, 45-fossil matrix, 65-fossil matrix, cd matrix, 45-fossil-cd matrix, and the 65-fossil-cd matrix). The rankings, which are based on the six accuracy measurements, are kept separately for each character matrix.

Main matrix

Based on the six accuracy measurements, the best weighting strategy for the main matrix is an extended implied weighting with K = 150 and the assumed homoplasy for missing entries to be 50% of the observed one; identified as worst weighting strategy was an implied weighting with K = 5 (Table 3.3). The top ten ranked weighting strategies use an extended implied weighting with a *K*-value between 20 and 200, except for implied weight with K = 50 which was ranked 5th. Among the ten worst weighting strategies are all strategies using K = 5, the equal weights analyses, and all strategies using K = 10 except for the extended implied weighting with an assumed homoplasy of 75% which is ranked as 25th of 36.

Table 3.3. Final ranking of the 36 different weighting strategies applied to the main matrix. Cell colours indicate low accuracy (red shades) to high accuracy (green shades) of the individual accuracy measurements and their final score. Abbreviations: RF, Robinson-Foulds distances; DC, Distortion-Coefficients; sr, symmetric resampling; jk, jackknife; cld, clade delimitation; otr, overall tree resolution; iw, implied weights; ew, equal weights (for the non-normalised accuracy measurement values see Appendix 10).

#	Weighting strategy	RF	DC	sr	jk	cld	otr	Final score
1	<i>K</i> = 150, 50%	0.779	0.821	0.955	0.935	0.949	1.000	5.439
2	K = 20, 50%	1.000	0.989	0.932	0.957	0.514	1.000	5.391
3	<i>K</i> = 200, 100%	0.894	0.784	0.977	0.935	0.774	1.000	5.364
4	<i>K</i> = 50, 25%	0.888	0.968	0.955	0.935	0.611	1.000	5.357
5	K = 50, iw	0.960	0.951	0.909	0.891	0.645	1.000	5.356
6	<i>K</i> = 20, 75%	0.939	0.971	0.932	0.978	0.514	1.000	5.335
7	<i>K</i> = 50, 50%	0.729	0.947	0.977	0.957	0.689	1.000	5.300
8	<i>K</i> = 200, 25%	0.889	0.813	0.932	0.913	0.735	1.000	5.283
9	<i>K</i> = 150, 75%	0.841	0.751	0.977	0.935	0.754	1.000	5.258
10	<i>K</i> = 100, 100%	0.799	0.755	1.000	0.957	0.744	1.000	5.254
11	<i>K</i> = 200, 75%	0.822	0.821	0.977	0.935	0.697	1.000	5.252
12	<i>K</i> = 50, 100%	0.856	0.949	1.000	1.000	0.436	1.000	5.242
13	<i>K</i> = 50, 75%	0.850	0.896	1.000	0.978	0.517	1.000	5.240
14	<i>K</i> = 150, 100%	0.697	0.592	0.977	0.957	1.000	1.000	5.223
15	<i>K</i> = 200, 50%	0.656	0.675	0.977	0.935	0.959	1.000	5.202
16	<i>K</i> = 100, 25%	0.890	0.915	0.955	0.913	0.517	1.000	5.189
17	<i>K</i> = 100, 75%	0.653	0.910	0.977	0.957	0.676	1.000	5.173
18	<i>K</i> = 200, iw	0.734	0.892	0.932	0.870	0.735	1.000	5.163
19	<i>K</i> = 20, 100%	0.773	0.962	0.955	1.000	0.414	1.000	5.103
20	<i>K</i> = 150, 25%	0.585	0.863	0.932	0.913	0.608	1.000	4.900
21	<i>K</i> = 150, iw	0.793	0.701	0.909	0.870	0.573	1.000	4.846
22	<i>K</i> = 100, iw	0.830	0.859	0.909	0.870	0.351	1.000	4.819
23	<i>K</i> = 20, iw	0.738	0.925	0.795	0.826	0.488	1.000	4.773
24	K = 100, 50%	0.591	0.346	0.977	0.935	0.676	1.000	4.525

#	Weighting strategy	RF	DC	sr	jk	cld	otr	Final score
25	K = 10,75%	0.755	0.897	0.705	0.783	0.354	1.000	4.493
26	<i>K</i> = 20, 25%	0.989	1.000	0.886	0.913	0.352	0.250	4.391
27	ew	0.859	0.863	0.864	0.783	0.745	0.250	4.364
28	<i>K</i> = 10, 25%	0.652	0.790	0.636	0.717	0.334	1.000	4.131
29	<i>K</i> = 10, iw	0.500	0.461	0.523	0.587	0.372	1.000	3.443
30	<i>K</i> = 10, 100%	0.518	0.603	0.705	0.761	0.266	0.250	3.103
31	K = 5,75%	0.175	0.531	0.159	0.239	0.460	1.000	2.565
32	K = 5, 50%	0.147	0.500	0.182	0.239	0.402	1.000	2.470
33	<i>K</i> = 5, 100%	0.055	0.450	0.136	0.217	0.477	1.000	2.335
34	K = 5, 25%	0.245	0.401	0.136	0.196	0.296	1.000	2.274
35	<i>K</i> = 10, 50%	0.000	0.036	0.682	0.761	0.000	0.000	1.479
36	K = 5, iw	0.172	0.000	0.000	0.000	0.187	1.000	1.359

3. Results | 3.2. Comparison of weighting strategies

When plotting the 36 weighting strategies (ordered from strongest to lowest downweighting) against their normalised scores resulting from the six accuracy measurements, a general increase of the scores with a decrease of the weighting strength is observable (Figure 3.6).

However, for the overall tree resolution, this is not the case. The score of overall tree resolution is for all weighting strategies high (completely resolved trees), except for equal weights, extended implied weights with K = 10 and an assumed homoplasy for missing entries of 50% (absolute minimum) and 100%, and extended implied weights with K = 20 and an assumed homoplasy for missing entries of 25% (Figure 3.6A). The clade delimitation score, which improved with decreased weighting strength, shows the three highest scores for extended implied weights with K = 150 and an assumed homoplasy for missing entries of 50% and 100%, and extended implied weights with K = 150 and an assumed homoplasy for missing entries of 50% (Figure 3.6A). The lowest clade delimitation score is found for extended implied weights with K = 10 and an assumed homoplasy for missing entries of 50% (Figure 3.6A).

The plotted scores of symmetric resampling and jackknife frequencies follow a very similar pattern with a gradual increase with the decrease of the weighting strength (Figure 3.6B). The two support measures reach a plateau when K is equal or greater than 20, no clear increase is then visible. However, the weighting strategies with implied weights (K = 20, 50, 100, 150, and 200) and the equal weights form relative minima in this plateau area, and an increase of the percentage of the assumed homoplasy for missing entries lead to an improvement of tree accuracy relative to the implied weights analysis with the respective K-value (Figure 3.6B).

The plots of the Robinson-Foulds distances and the Distortion-Coefficients increase strongly with decreasing downweighting strength until they reach their absolute maximum with K = 20 (Figure 3.6C). The weighting strategies with weaker downweighting strength led to somewhat lower scores for Robinson-Foulds distances and Distortion-Coefficients which were still generally high, only the Distortion-Coefficient for extended implied weights with K = 100 and an assumed homoplasy for missing entries of 50% was remarkably low, being the second lowest for the main matrix (Figure 3.6C).

The plot of the final score increases until reaching a plateau at K = 20, and besides smaller fluctuations, it remains quite stable with the decrease of the weighting strength (Figure 3.6D). Relative minima in the plateau area are extended implied weights with K = 20 with 25% assumed homoplasy, K = 100 and 50% assumed homoplasy, K = 150, with 25% assumed homoplasy, implied weights with K = 100 and 150, and equal weights (Figure 3.6D).



Figure 3.6. Graphs of the normalised scores of the six tree accuracy measurements and their final score which are plotted against the individual weighting strategies that were applied to the main matrix. A, plotted clade delimitation and overall tree resolution; B, plotted symmetric resampling and jackknife frequencies; C, plotted Robinson-Foulds distances and Distortion-Coefficients; D, plotted final score. Abbreviations: RF, Robinson-Foulds distances; DC, Distortion-Coefficients; sr, symmetric resampling; jk, jackknife; cld, clade delimitation; otr, overall tree resolution.

45-fossil matrix

The best-ranked weighting strategy for the 45-fossil matrix is an extended implied weighting with K = 200 and for the missing entries a homoplasy which is assumed to be 100% like the observed one (Table 3.4). The approach with extended implied weighting with K = 5 and an assumed homoplasy of 100% for missing entries was ranked last. The worst ten weighting strategies for the 45-fossil matrix are strategies using K = 5, equal weights, and K = 10 except for the extended implied weights with 25% for the homoplasy assumption of missing entries which is ranked 25th of 36. Among the top ten ranked are only strategies using an extended implied weighting with a *K*-value between 50 and 200.

Table 3.4. Final ranking of the 36 different weighting strategies applied to the 45-fossil matrix. Cell colours indicate low accuracy (red shades) to high accuracy (green shades) of the individual accuracy measurements and their final score. Abbreviations: RF, Robinson-Foulds distances; DC, Distortion-Coefficients; sr, symmetric resampling; jk, jackknife; cld, clade delimitation; otr, overall tree resolution; iw, implied weights; ew, equal weights (for the non-normalised accuracy measurement values see Appendix 10).

#	Weighting strategy	RF	DC	sr	jk	cld	otr	Final score
1	<i>K</i> = 200, 100%	0.900	0.902	0.857	0.929	1.000	1.000	5.589
2	<i>K</i> = 150, 100%	0.883	0.900	0.857	0.929	1.000	1.000	5.569
3	K = 200, 50%	0.873	0.886	0.857	0.857	0.977	1.000	5.450
4	<i>K</i> = 150, 75%	0.809	0.841	0.857	0.929	0.988	1.000	5.424
5	<i>K</i> = 100, 100%	0.635	0.887	0.929	1.000	0.956	1.000	5.406
6	<i>K</i> = 150, 25%	0.884	0.926	0.786	0.857	0.873	1.000	5.325
7	K = 50, 50%	0.796	0.816	0.857	0.929	0.839	1.000	5.237
8	<i>K</i> = 150, 50%	0.723	0.783	0.857	0.857	0.928	1.000	5.149
9	<i>K</i> = 50, 25%	0.803	0.788	0.857	0.929	0.771	1.000	5.148
10	K = 200, 75%	0.663	0.815	0.857	0.929	0.828	1.000	5.092
11	<i>K</i> = 20, 100%	0.512	0.761	0.929	1.000	0.850	1.000	5.052
12	<i>K</i> = 200, iw	0.826	0.847	0.786	0.714	0.856	1.000	5.029
13	K = 200, 25%	0.798	0.874	0.786	0.857	0.711	1.000	5.027
14	<i>K</i> = 50, iw	0.700	0.753	0.786	0.786	0.848	1.000	4.872
15	<i>K</i> = 50, 75%	0.589	0.800	0.929	0.929	0.763	0.750	4.760
16	<i>K</i> = 100, 75%	1.000	1.000	0.857	0.929	0.687	0.250	4.723
17	<i>K</i> = 100, 25%	0.786	0.638	0.857	0.857	0.531	1.000	4.669
18	<i>K</i> = 100, 50%	0.680	0.625	0.857	0.929	0.562	1.000	4.652
19	<i>K</i> = 50, 100%	0.788	0.954	1.000	1.000	0.650	0.000	4.391
20	<i>K</i> = 20, 50%	0.530	0.699	0.857	0.857	0.427	1.000	4.370
21	<i>K</i> = 100, iw	0.608	0.731	0.786	0.714	0.508	1.000	4.348
22	K = 20,75%	0.421	0.584	0.929	0.929	0.404	1.000	4.267
23	<i>K</i> = 150, iw	0.735	0.655	0.714	0.714	0.406	1.000	4.224
24	K = 20, 25%	0.702	0.810	0.714	0.786	0.602	0.500	4.115

#	Weighting strategy	RF	DC	sr	jk	cld	otr	Final score
25	<i>K</i> = 10, 25%	0.512	0.695	0.786	0.357	0.543	1.000	3.893
26	K = 20, iw	0.668	0.733	0.571	0.643	0.610	0.500	3.725
27	<i>K</i> = 10, 50%	0.341	0.604	0.714	0.714	0.490	0.750	3.614
28	<i>K</i> = 10, 75%	0.353	0.514	0.786	0.786	0.538	0.250	3.226
29	ew	0.717	0.628	0.357	0.143	0.847	0.500	3.192
30	<i>K</i> = 10, iw	0.445	0.585	0.286	0.286	0.517	0.750	2.869
31	<i>K</i> = 10, 100%	0.175	0.201	0.786	0.714	0.354	0.500	2.731
32	K = 5, 50%	0.100	0.246	0.286	0.357	0.361	0.750	2.101
33	K = 5, 25%	0.100	0.094	0.286	0.286	0.463	0.500	1.729
34	<i>K</i> = 5, 75%	0.000	0.054	0.286	0.286	0.000	1.000	1.625
35	K = 5, iw	0.069	0.000	0.000	0.000	0.161	1.000	1.230
36	K = 5, 100%	0.063	0.027	0.214	0.214	0.029	0.500	1.048

3. Results | 3.2. Comparison of weighting strategies

The graphs of the accuracy measurement scores plotted against the 36 weighting strategies show a general increase with a decrease of downweighting strength, only for the overall tree resolution this correlation is not visible (Figure 3.7).

The overall tree resolution has its absolute minimum for extended implied weights with K = 50 and an assumed homoplasy of 100%. Thus, the overall tree resolution is generally high for weighting strategies with *K*-values of 20 and higher (Figure 3.7A). The clade delimitation graph increases slightly with a decrease in weighting strength; the two absolute maxima are reached for extended implied weights with K = 150 and 200 and an assumed homoplasy for missing entries of 100% (for both; Figure 3.7A).

The graphs of the symmetric resampling and the jackknife frequencies have a very similar trend (Figure 3.7B). They increase with a decrease of downweighting strength and reach a plateau of generally high scores for weighting strategies with a *K*-value of 20 or higher. However, within this plateau, the implied weights strategies (K = 20, 50, 100, 150, 200) form relative minima, and the tree accuracy is improving for extended implied weights with an increase of the percentage for the assumed homoplasy for missing entries relative to the respective *K*-value (Figure 3.7B). Equal weights reaches similar scores as strategies using K = 5 or 10 (Figure 3.7B).

The plotted Robinson-Foulds distances and Distortion-Coefficients follow a similar trend and gradually increase with decreased weighting strengths (Figure 3.7C). Though, a plateau is reached for strategies with *K*-values of 50 and greater (Robinson-Foulds distances) and strategies with *K*-values of 20 and greater (Distortion-Coefficients) (Figure 3.7C).

The graph of the final score plotted against the 36 weighting strategies, is gradually increasing with a decreased weighting strength, but equal weights is not following this progression, it forms a relative minimum which is similar to the scores of weighting strategies using K = 10 (Figure 3.7D).



Figure 3.7. Graphs of the normalised scores of the six tree accuracy measurements and their final score which are plotted against the individual weighting strategies that were applied to the 45-fossil matrix. A, plotted clade delimitation and overall tree resolution; B, plotted symmetric resampling and jackknife frequencies; C, plotted Robinson-Foulds distances and Distortion-Coefficients; D, plotted final score. Abbreviations: RF, Robinson-Foulds distances; DC, Distortion-Coefficients; sr, symmetric resampling; jk, jackknife; cld, clade delimitation; otr, overall tree resolution.

65-fossil matrix

For the 65-fossil matrix, the highest ranked weighting strategy is an extended implied weighting with K = 200 and for the missing entries an assumed homoplasy of 75% (Table 3.5). An extended implied weighting with K = 5 and an assumed homoplasy of 100% for the missing entries was ranked in last place. Among the ten worst ranked are all strategies using K = 5, equal weights, implied weights with K = 10 and 50, and an extended implied weighting with K = 200 and an assumed homoplasy of 100% for the missing entries. The top ten ranked weighting strategies are exclusively extended implied weights with K-values between 20 and 200.

Table 3.5. Final ranking of the 36 different weighting strategies applied to the 65-fossil matrix. Cell colours indicate low accuracy (red shades) to high accuracy (green shades) of the individual accuracy measurements and their final score. Abbreviations: RF, Robinson-Foulds distances; DC, Distortion-Coefficients; sr, symmetric resampling; jk, jackknife; cld, clade delimitation; otr, overall tree resolution; iw, implied weights; ew, equal weights (for the non-normalised accuracy measurement values see Appendix 10).

#	Weighting strategy	RF	DC	sr	jk	cld	otr	Finale score
1	<i>K</i> = 200, 75%	0.724	0.848	1.000	0.750	0.993	1.000	5.315
2	K = 20, 25%	0.623	0.905	1.000	0.750	1.000	1.000	5.278
3	K = 50, 50%	0.735	0.762	1.000	0.750	0.997	1.000	5.244
4	K = 200, 50%	0.672	0.933	1.000	0.750	0.771	1.000	5.126
5	<i>K</i> = 20, 75%	0.782	0.823	1.000	0.750	0.741	1.000	5.096
6	<i>K</i> = 100, 50%	0.487	0.704	1.000	0.750	0.754	1.000	4.694
7	<i>K</i> = 150, 75%	0.625	0.782	1.000	0.750	0.720	0.750	4.627
8	<i>K</i> = 100, 100%	0.565	0.594	1.000	0.750	0.620	1.000	4.529
9	<i>K</i> = 150, 25%	0.690	1.000	0.667	0.750	0.411	1.000	4.518
10	<i>K</i> = 150, 100%	0.705	0.791	1.000	0.750	0.467	0.750	4.463
11	<i>K</i> = 100, 75%	0.453	0.903	1.000	0.750	0.286	1.000	4.393
12	<i>K</i> = 20, 50%	0.716	0.770	1.000	0.750	0.330	0.750	4.317
13	<i>K</i> = 50, 100%	1.000	0.567	1.000	1.000	0.123	0.500	4.190
14	<i>K</i> = 200, iw	0.472	0.675	0.667	0.750	0.593	1.000	4.157
15	<i>K</i> = 200, 25%	0.481	0.716	0.667	0.750	0.492	1.000	4.106
16	<i>K</i> = 100, iw	0.550	0.631	0.667	0.750	0.463	1.000	4.061
17	<i>K</i> = 50, 75%	0.698	0.613	1.000	0.750	0.491	0.500	4.052
18	<i>K</i> = 150, 50%	0.485	0.689	1.000	0.750	0.304	0.750	3.979
19	<i>K</i> = 20, iw	0.748	0.917	0.667	0.750	0.239	0.500	3.821
20	<i>K</i> = 20, 100%	0.573	0.701	1.000	0.750	0.272	0.500	3.796
21	<i>K</i> = 10, 75%	0.526	0.705	0.667	0.750	0.583	0.500	3.732
22	<i>K</i> = 10, 100%	0.586	0.694	0.667	0.750	0.466	0.500	3.663
23	<i>K</i> = 150, iw	0.933	0.676	0.667	0.750	0.119	0.500	3.645
24	<i>K</i> = 50, 25%	0.937	0.576	0.667	0.750	0.179	0.500	3.608
25	<i>K</i> = 10, 25%	0.241	0.486	0.667	0.750	0.433	1.000	3.576
26	<i>K</i> = 100, 25%	0.953	0.361	0.667	0.750	0.318	0.500	3.549
27	<i>K</i> = 200, 100%	0.675	0.135	1.000	0.750	0.480	0.500	3.541
28	<i>K</i> = 10, iw	0.457	0.727	0.667	0.500	0.385	0.750	3.486
29	<i>K</i> = 50, iw	0.632	0.576	0.667	0.750	0.179	0.500	3.304
30	<i>K</i> = 10, 50%	0.722	0.276	0.667	0.500	0.197	0.500	2.861
31	<i>K</i> = 5, 75%	0.000	0.270	0.333	0.250	0.991	0.750	2.594
32	<i>K</i> = 5, 50%	0.341	0.547	0.333	0.250	0.605	0.500	2.577
33	<i>K</i> = 5, 25%	0.474	0.386	0.333	0.250	0.632	0.500	2.575
34	K = 5, iw	0.537	0.831	0.000	0.250	0.418	0.500	2.536
35	ew	0.726	0.479	0.333	0.000	0.413	0.000	1.951
36	<i>K</i> = 5, 100%	0.015	0.000	0.333	0.250	0.000	0.750	1.348

For the 36 weighting strategies, applied to the 65-fossil matrix, and plotted against the six accuracy measurements, no clear general trend is visible (Figure 3.8).

The graph of the overall tree resolution is following no clear trend and there seems to be no increase; remarkable is only the absolute minimum which is formed by the score for equal weights (Figure 3.8A). The plotted clade delimitation scores show no clear trend either, the absolute minimum is formed by the extended implied weights with K = 5 and an assumed homoplasy of 100% (Figure 3.8A). The absolute maximum is formed by extended implied weights with K = 20 and an assumed homoplasy of 25%; three weighting strategies are very close to the absolute maximum: extended implied weighting with K = 5 and 200 and an assumed homoplasy of 75% and with K = 50 and an assumed homoplasy of 50% (Figure 3.8A).

Only for the graph of the symmetric resampling and the jackknife frequencies a trend increase with decreasing weighting strength is detectable (Figure 3.8B). The graph of the symmetric resampling frequencies has an absolute minimum for implied weights with K = 5, followed by an increase, and then stable values for the other weighting strategies using K = 5, the graph increases again to reach another plateau with weighting strategies with K = 10 and implied weights with K = 20, and finally reaches a plateau of absolute maxima beginning with extended implied weights with K = 20 and an assumed homoplasy of 25% and continuing for weaker downweighting strengths (Figure 3.8B). Relative minima are only formed by implied weights for K = 50, 100, 150, and 200, extended implied weights for K = 50, 100, 150, and 200 and an assumed homoplasy of 25%, and equal weights (Figure 3.8B). The jackknife frequencies are stable for all weighting strategies using K = 5, then the graph increases and reaches a plateau starting with extended implied weights with K = 10 and an assumed homoplasy of 25% (Figure 3.8B). The jackknife frequencies are then stable for the other weighting strategies, except for a relative minimum formed by extended implied weights with K = 10 and an assumed homoplasy of 50% (value higher than for K = 5), an absolute maximum formed by extended implied weights with K = 50 and an assumed homoplasy of 100%, and an absolute minimum formed by equal weights (Figure 3.8B).

For the plotted Robinson-Foulds distances and Distortion-Coefficients no clear trend is visible, the graph is fluctuating without generally decreasing or increasing (Figure 3.8C). The absolute minimum for the Robinson-Foulds distances is formed by extended implied weights with K = 5and an assumed homoplasy of 75%, the absolute maximum is formed by extended implied weights with K = 50 and an assumed homoplasy of 100%, three relative maxima are formed by extended implied weights with K = 50 and 100 and an assumed homoplasy of 25%, and implied weights with K = 150 (Figure 3.8C). The graph of the Distortion-Coefficients has the absolute minimum formed by extended implied weights with K = 5 and an assumed homoplasy of 100%, a relative minimum is formed by extended implied weights with K = 200 and an assumed homoplasy of 100% (Figure 3.8C).

The graph of the final score shows a slight increase with a decrease of weighting strength (Figure 3.8D).



Figure 3.8. Graphs of the normalised scores of the six tree accuracy measurements and their final score which are plotted against the individual weighting strategies that were applied to the 65-fossil matrix. A, plotted clade delimitation and overall tree resolution; B, plotted symmetric resampling and jackknife frequencies; C, plotted Robinson-Foulds distances and Distortion-Coefficients; D, plotted final score. Abbreviations: RF, Robinson-Foulds distances; DC, Distortion-Coefficients; sr, symmetric resampling; jk, jackknife; cld, clade delimitation; otr, overall tree resolution.

Cd matrix

The best-ranked weighting strategy for the cd matrix is extended implied weights with K = 100 with an assumed homoplasy of 100% for missing entries (Table 3.6). The worst-ranked weighting strategy is implied weights with K = 5. Ranked in the top ten are extended implied weights with *K*-values between 20 and 150, and implied weights with K = 100. Among the worst ten, are all weighting strategies using K = 5, equal weights, extended implied weights

with K = 200 and an assumed homoplasy for missing entries of 25%, 75%, and 100%, and extended implied weights with K = 10 and an assumed homoplasy of 25 %.

Table 3.6. Final ranking of the 36 different weighting strategies applied to the cd matrix. Cell colours indicate low accuracy (red shades) to high accuracy (green shades) of the individual accuracy measurements and their final score. Abbreviations: RF, Robinson-Foulds distances; DC, Distortion-Coefficients; sr, symmetric resampling; jk, jackknife; cld, clade delimitation; otr, overall tree resolution; iw, implied weights; ew, equal weights (for the non-normalised accuracy measurement values see Appendix 10).

#	Weighting strategy	RF	DC	sr	jk	cld	otr	Final score
1	<i>K</i> = 100, 100%	0.971	0.927	0.805	0.778	0.944	1.000	5.425
2	<i>K</i> = 100, 75%	0.979	0.931	0.780	0.778	0.649	1.000	5.117
3	K = 20, 100%	0.625	0.888	0.951	0.978	0.542	1.000	4.984
4	<i>K</i> = 150, 50%	1.000	0.943	0.683	0.667	0.649	1.000	4.942
5	<i>K</i> = 10, 50%	0.863	1.000	0.707	0.778	0.580	1.000	4.928
6	K = 50, 25%	0.787	0.857	0.878	0.889	0.501	1.000	4.913
7	<i>K</i> = 150, 100%	0.749	0.762	0.707	0.689	0.968	1.000	4.876
8	<i>K</i> = 100, iw	0.741	0.762	0.707	0.711	0.947	1.000	4.869
9	K = 20, 50%	0.577	0.898	0.927	0.956	0.474	1.000	4.831
10	K = 20,75%	0.694	0.876	0.951	0.978	0.316	1.000	4.815
11	<i>K</i> = 200, 50%	0.725	0.755	0.683	0.644	1.000	1.000	4.807
12	<i>K</i> = 100, 50%	0.800	0.885	0.780	0.756	0.510	1.000	4.731
13	<i>K</i> = 10, 75%	0.722	0.969	0.707	0.778	0.535	1.000	4.711
14	<i>K</i> = 50, 100%	0.378	0.709	1.000	1.000	0.595	1.000	4.682
15	K = 20, 25%	0.667	0.893	0.854	0.889	0.371	1.000	4.674
16	K = 20, iw	0.727	0.925	0.780	0.778	0.440	1.000	4.651
17	<i>K</i> = 150, 75%	0.828	0.881	0.683	0.667	0.541	1.000	4.600
18	K = 50, 75%	0.391	0.793	0.976	0.978	0.430	1.000	4.568
19	<i>K</i> = 10, 100%	0.722	0.969	0.707	0.756	0.409	1.000	4.562
20	<i>K</i> = 100, 25%	0.633	0.686	0.732	0.733	0.721	1.000	4.506
21	K = 50, iw	0.459	0.880	0.854	0.844	0.404	1.000	4.442
22	<i>K</i> = 150, iw	0.698	0.741	0.634	0.600	0.721	1.000	4.394
23	<i>K</i> = 50, 50%	0.391	0.663	0.951	0.933	0.418	1.000	4.356
24	<i>K</i> = 150, 25%	0.374	0.617	0.659	0.622	0.930	1.000	4.201
25	<i>K</i> = 10, iw	0.706	0.923	0.537	0.533	0.348	1.000	4.047
26	<i>K</i> = 200, 100%	0.503	0.613	0.683	0.667	0.566	1.000	4.032
27	<i>K</i> = 200, 25%	0.529	0.596	0.634	0.622	0.612	1.000	3.993
28	<i>K</i> = 200, 75%	0.482	0.543	0.659	0.667	0.612	1.000	3.962
29	<i>K</i> = 10, 25%	0.495	0.593	0.683	0.711	0.250	1.000	3.732
30	<i>K</i> = 200, iw	0.452	0.550	0.634	0.622	0.075	1.000	3.334
31	K = 5, 50%	0.277	0.790	0.146	0.311	0.451	1.000	2.976
32	K = 5, 100%	0.391	0.695	0.122	0.244	0.441	1.000	2.894
33	K = 5,75%	0.390	0.707	0.146	0.289	0.298	1.000	2.831

#	Weighting strategy	RF	DC	sr	jk	cld	otr	Final score
34	ew	0.000	0.000	0.854	0.822	0.000	1.000	2.676
35	K = 5, 25%	0.110	0.568	0.146	0.222	0.042	1.000	2.089
36	K = 5, iw	0.183	0.544	0.000	0.000	0.289	1.000	2.016

The graphs with the six accuracy measurements plotted against the different weighting strategies do not share a general trend.

The plotted overall tree topology has no slope because for all weighting strengths, the trees are completely resolved (Figure 3.9A). The graph describing the clade delimitation scores has a slightly increasing trend with decreasing weighting strengths, but the absolute minimum is formed by equal weights and a relative maximum is formed by implied weights with K = 200 (Figure 3.9A). The absolute maximum is formed by extended implied weights with K = 200 and an assumed homoplasy of 50% (Figure 3.9A).

The plotted symmetric resampling and jackknife frequencies follow a very similar pattern to each other, they increase with a decrease of weighting strength with the highest values for weighting strategies using K = 20 and 50, for higher *K*-values the graph decreases (Figure 3.9B). For the weighting strategies using implied weights, the frequencies were relatively lower than the ones of the extended implied weights for their respective *K*-values; weighting strategies with a higher percentage for the assumed homoplasy for missing entries had relatively higher frequencies (Figure 3.9B).

The graph of the Robinson-Foulds distances does not have a clear trend. Generally, weighting strategies using a *K*-value greater than 5 have higher scores, and the absolute minimum is formed by equal weights (Figure 3.9C). The Distortion-Coefficients when plotted against the weighting strategies does not show a clear trend, either (Figure 3.9C). However, weighting strategies with K = 10, 20, 50, 100, and 150 showed generally high values. The absolute maximum is formed by extended implied weights with K = 10 and an assumed homoplasy of 50%, the absolute minimum is formed by equal weights (Figure 3.9C).

The plotted final scores show that generally *K*-values between 10 and 200 have the highest values which are quite similar (Figure 3.9D).



Figure 3.9. Graphs of the normalised scores of the six tree accuracy measurements and their final score which are plotted against the individual weighting strategies that were applied to the cd matrix. A, plotted clade delimitation and overall tree resolution; B, plotted symmetric resampling and jackknife frequencies; C, plotted Robinson-Foulds distances and Distortion-Coefficients; D, plotted final score. Abbreviations: RF, Robinson-Foulds distances; DC, Distortion-Coefficients; sr, symmetric resampling; jk, jackknife; cld, clade delimitation; otr, overall tree resolution.

45-fossil-cd matrix

For the 45-fossil-cd matrix, the ranking of the six accuracy measurements identified an extended implied weighting with K = 50 and an assumed homoplasy for the missing entries of 100% as best (Table 3.7). Ranked as last was the extended implied weighting with K = 5 and an assumed homoplasy for missing entries of 100%. Among the top ten ranked weighting strategies for the 45-fossil-cd matrix are extended implied weighting with K-values of 10, 50, 100, 150 and 200, and implied weights with K = 100. The ten worst weighting strategies are all strategies using K = 5, implied weights with K = 10 and 20, extended implied weights with K = 50 and an assumed homoplasy for missing entries of 25% and 75%, and extended implied weights with K = 10 and an assumed homoplasy for missing entries of 25%.
Table 3.7. Final ranking of the 36 different weighting strategies applied to the 45-fossil-cd matrix. Cell colours indicate low accuracy (red shades) to high accuracy (green shades) of the individual accuracy measurements and their final score. Abbreviations: RF, Robinson-Foulds distances; DC, Distortion-Coefficients; sr, symmetric resampling; jk, jackknife; cld, clade delimitation; otr, overall tree resolution; iw, implied weights; ew, equal weights (for the non-normalised accuracy measurement values see Appendix 10).

#	Weighting strategy	RF	DC	sr	jk	cld	otr	Final score
1	<i>K</i> = 50, 100%	0.415	1.000	0.727	0.743	0.899	1.000	4.784
2	K = 200, 75%	0.917	0.746	0.879	0.943	0.294	1.000	4.778
3	K = 200, 100%	0.998	0.629	0.909	0.943	0.268	1.000	4.747
4	<i>K</i> = 10, 75%	0.685	0.985	0.455	0.486	1.000	1.000	4.610
5	K = 200, 50%	0.584	0.892	0.879	0.914	0.311	1.000	4.580
6	<i>K</i> = 200, 25%	0.877	0.592	0.879	0.886	0.337	1.000	4.570
7	<i>K</i> = 150, 50%	0.791	0.780	0.818	0.886	0.277	1.000	4.551
8	<i>K</i> = 150, 100%	0.645	0.851	0.848	0.886	0.309	1.000	4.539
9	<i>K</i> = 100, 50%	1.000	0.661	0.727	0.771	0.337	1.000	4.497
10	<i>K</i> = 100, iw	0.746	0.815	0.697	0.743	0.486	1.000	4.487
11	ew	0.371	0.600	1.000	1.000	0.747	0.667	4.385
12	<i>K</i> = 150, iw	0.529	0.698	0.788	0.829	0.515	1.000	4.359
13	<i>K</i> = 100, 100%	0.738	0.639	0.758	0.800	0.309	1.000	4.244
14	K = 20, 50%	0.289	0.932	0.636	0.686	0.503	1.000	4.046
15	<i>K</i> = 200, iw	0.572	0.339	0.848	0.886	0.383	1.000	4.028
16	<i>K</i> = 150, 25%	0.710	0.310	0.818	0.857	0.320	1.000	4.016
17	<i>K</i> = 10, 50%	0.678	0.847	0.455	0.486	0.516	1.000	3.982
18	<i>K</i> = 150, 75%	0.899	0.000	0.848	0.914	0.320	1.000	3.982
19	<i>K</i> = 10, 100%	0.605	0.735	0.424	0.457	0.726	1.000	3.948
20	<i>K</i> = 20, 75%	0.536	0.783	0.667	0.686	0.468	0.667	3.806
21	<i>K</i> = 20, 25%	0.449	0.565	0.576	0.629	0.531	1.000	3.750
22	<i>K</i> = 100, 75%	0.687	0.480	0.758	0.800	0.309	0.667	3.700
23	<i>K</i> = 50, 50%	0.469	0.838	0.636	0.657	0.085	1.000	3.685
24	<i>K</i> = 100, 25%	0.559	0.160	0.727	0.771	0.365	1.000	3.582
25	<i>K</i> = 20, 100%	0.990	0.863	0.667	0.686	0.376	0.000	3.582
26	K = 50, iw	0.733	0.499	0.515	0.543	0.540	0.667	3.497
27	<i>K</i> = 50, 25%	0.600	0.514	0.606	0.600	0.326	0.667	3.313
28	<i>K</i> = 50, 75%	0.554	0.372	0.697	0.686	0.000	1.000	3.308
29	<i>K</i> = 10, 25%	0.685	0.619	0.424	0.486	0.427	0.667	3.307
30	<i>K</i> = 20, iw	0.650	0.434	0.515	0.543	0.331	0.667	3.139
31	<i>K</i> = 10, iw	0.400	0.970	0.364	0.429	0.420	0.333	2.915
32	<i>K</i> = 5, 25%	0.484	0.589	0.121	0.114	0.559	1.000	2.868
33	<i>K</i> = 5, 50%	0.418	0.376	0.091	0.086	0.395	1.000	2.365
34	<i>K</i> = 5, iw	0.000	0.424	0.061	0.086	0.249	1.000	1.819
35	K = 5, 75%	0.358	0.041	0.030	0.029	0.338	1.000	1.796
36	K = 5, 100%	0.307	0.089	0.000	0.000	0.250	1.000	1.646

The graphs describing the progression of the accuracy measurements with a decrease of weighting strength do not have a clear common trend (Figure 3.10).

The overall tree resolution is generally high, and values are on the same level (Figure 3.10A). However, the absolute minimum is formed by extended implied weights with K = 20 and an assumed homoplasy of 100%, and eight other weighting strategies have lower values than the other strategies: implied weights with K = 10, 20, and 50, extended implied weights with K = 10 and 50 and an assumed homoplasy of 25%, K = 20 and 100 and an assumed homoplasy of 75%, and equal weights (Figure 3.10A). There is no clear trend visible for the plotted clade delimitation (Figure 3.10A). The absolute maximum is formed by extended implied weights with K = 10 and an assumed homoplasy of 75%, and the absolute minimum is formed by extended implied weights with K = 10 and an assumed homoplasy of 75%, and the absolute minimum is formed by extended implied weights with K = 50 and an assumed homoplasy of 75% (Figure 3.10A).

The symmetric resampling and jackknife frequencies are described by graphs that follow a very similar trend (Figure 3.10B). An increase of the graphs with decreasing downweighting strength is visible with the maximum reached for equal weights and the absolute minimum is formed by extended implied weights with K = 5 and an assumed homoplasy for missing entries of 100% (Figure 3.10B).

The plotted Robinson-Foulds distances seem to slightly increase with decreasing weighting strengths, but equal weights is forming one of the lowest relative minima (Figure 3.10C). The absolute minimum is formed by implied weights with K = 5, and the three absolute maxima are formed by extended implied weights with K = 20 and 200 and an assumed homoplasy of 100%, and with K = 100 and an assumed homoplasy of 50% (Figure 3.10C). The graph of the Distortion-Coefficients does not seem to follow a trend, the absolute minimum is formed by extended implied weights with K = 150 and an assumed homoplasy for missing entries of 75% (Figure 3.10C).

The graph of the final scores shows a general increase with a decreasing of the weighting strength (Figure 3.10D).



Figure 3.10. Graphs of the normalised scores of the six tree accuracy measurements and their final score which are plotted against the individual weighting strategies that were applied to the 45-fossil-cd matrix. A, plotted clade delimitation and overall tree resolution; B, plotted symmetric resampling and jackknife frequencies; C, plotted Robinson-Foulds distances and Distortion-Coefficients; D, plotted final score. Abbreviations: RF, Robinson-Foulds distances; DC, Distortion-Coefficients; sr, symmetric resampling; jk, jackknife; cld, clade delimitation; otr, overall tree resolution.

65-fossil-cd matrix

For the 65-fossil-cd matrix, the best ranked weighting strategy is an extended implied weighting with K = 200 and an assumed homoplasy for missing entries of 100% (Table 3.8). Ranked as the worst weighting strategy is an extended implied weighting with K = 5 and an assumed homoplasy for missing entries of 75%. The top ten weighting strategies are extended implied weighting with a *K*-value between 100 and 200. Ranked as the worst ten weighting strategies for the 65-fossil-cd matrix are all strategies using K = 5 and 10.

Table 3.8. Final ranking of the 36 different weighting strategies applied to the 65-fossil-cd matrix. Cell colours indicate low accuracy (red shades) to high accuracy (green shades) of the individual accuracy measurements and their final score. Abbreviations: RF, Robinson-Foulds distances; DC, Distortion-Coefficients; sr, symmetric resampling; jk, jackknife; cld, clade delimitation; otr, overall tree resolution; iw, implied weights; ew, equal weights (for the non-normalised accuracy measurement values see Appendix 10).

#	Weighting strategy	RF	DC	sr	jk	cld	otr	Final score
1	K = 200, 100%	0.783	0.970	1.000	1.000	0.466	1.000	5.219
2	<i>K</i> = 150, 25%	0.802	0.810	1.000	0.933	0.436	1.000	4.982
3	K = 200, 75%	0.714	0.933	1.000	1.000	0.580	0.667	4.894
4	<i>K</i> = 100, 25%	0.913	0.909	0.929	0.933	0.505	0.667	4.855
5	<i>K</i> = 150, 100%	0.838	0.938	1.000	0.933	0.353	0.667	4.729
6	<i>K</i> = 200, iw	0.527	0.653	1.000	1.000	0.547	1.000	4.728
7	<i>K</i> = 100, 100%	0.950	0.915	0.929	0.867	0.399	0.667	4.727
8	<i>K</i> = 150, 50%	0.635	0.592	1.000	1.000	0.434	1.000	4.661
9	<i>K</i> = 200, 50%	0.770	0.653	1.000	1.000	0.531	0.667	4.621
10	<i>K</i> = 150, 75%	0.795	0.938	1.000	0.933	0.281	0.667	4.614
11	<i>K</i> = 150, iw	0.989	0.845	1.000	0.933	0.471	0.333	4.572
12	<i>K</i> = 100, iw	0.825	0.670	0.929	0.933	0.480	0.667	4.504
13	<i>K</i> = 50, 100%	0.898	0.966	0.714	0.733	0.496	0.667	4.475
14	<i>K</i> = 50, 75%	0.713	0.754	0.714	0.733	0.519	1.000	4.434
15	<i>K</i> = 100, 75%	0.998	0.960	0.929	0.933	0.602	0.000	4.421
16	ew	0.644	0.809	1.000	1.000	0.623	0.333	4.409
17	<i>K</i> = 50, iw	0.656	0.904	0.786	0.800	0.553	0.667	4.366
18	<i>K</i> = 50, 50%	0.721	0.913	0.786	0.733	0.507	0.667	4.326
19	<i>K</i> = 50, 25%	0.660	1.000	0.786	0.733	0.472	0.667	4.317
20	<i>K</i> = 200, 25%	0.583	0.566	1.000	1.000	0.479	0.667	4.295
21	<i>K</i> = 100, 50%	0.887	0.944	0.929	0.933	0.371	0.000	4.064
22	<i>K</i> = 20, 50%	0.742	0.954	0.500	0.533	0.441	0.667	3.837
23	<i>K</i> = 20, iw	0.759	0.912	0.500	0.533	0.665	0.333	3.703
24	<i>K</i> = 20, 25%	0.582	0.733	0.500	0.533	0.909	0.333	3.590
25	<i>K</i> = 20, 75%	0.667	0.945	0.429	0.467	0.648	0.333	3.488
26	<i>K</i> = 20, 100%	1.000	0.759	0.429	0.467	0.532	0.000	3.187
27	<i>K</i> = 10, 50%	0.253	0.657	0.286	0.267	0.708	1.000	3.170
28	<i>K</i> = 10, iw	0.710	0.868	0.286	0.267	1.000	0.000	3.130
29	<i>K</i> = 10, 25%	0.525	0.864	0.286	0.333	0.388	0.667	3.062
30	<i>K</i> = 10, 100%	0.583	0.825	0.214	0.200	0.676	0.333	2.832
31	<i>K</i> = 10, 75%	0.312	0.542	0.214	0.267	0.551	0.667	2.552
32	K = 5, iw	0.220	0.643	0.143	0.067	0.768	0.667	2.507
33	<i>K</i> = 5, 50%	0.317	0.473	0.071	0.067	0.681	0.667	2.276
34	<i>K</i> = 5, 25%	0.526	0.505	0.143	0.067	0.659	0.000	1.900
35	<i>K</i> = 5, 100%	0.000	0.000	0.000	0.000	0.341	0.667	1.008
36	K = 5,75%	0.096	0.049	0.071	0.000	0.000	0.667	0.883

Generally, the six accuracy measurements which are plotted against the weighting strategies are not following a common trend (Figure 3.11).

For the plotted overall tree resolution and the clade delimitation no clear trend is visible (Figure 3.11A). The absolute minimum of the clade delimitation is formed by extended implied weights with K = 5 and an assumed homoplasy of 100%, whereas the absolute maximum is formed by implied weight with K = 10 (Figure 3.11A).

The plotted symmetric resampling and jackknife frequencies follow a similar pattern, they increase with a decrease of weighting strength (Figure 3.11B). The graph of symmetric resampling is reaching a plateau of highest values for weighting strategies with K = 150 and weaker downweighting strengths (Figure 3.11B). The plotted jackknife frequencies reach their plateau for strategies with K = 200 and equal weights (Figure 3.11B). For weighting strategies using a *K*-value between 5 and 50, the extended implied weights with an assumed homoplasy for missing entries between 75% and 100% had relatively lower values compared to the other strategies using the respective *K*-values (Figure 3.11B).

The graph of the Robinson-Foulds distances shows slightly higher values for weighting strategies with *K*-values of 20 and greater (Figure 3.11C). For the Distortion-Coefficients, no clear trend of the graph is visible (Figure 3.11C). The absolute maximum of the Robinson-Foulds distances and the Distortion-Coefficients is formed by extended implied weights with K = 5 and an assumed homoplasy of 100% (Figure 3.11C).

The trend of the plotted final scores shows a general increase with decreasing weighting strengths (Figure 3.11D).



Figure 3.11. Graphs of the normalised scores of the six tree accuracy measurements and their final score which are plotted against the individual weighting strategies that were applied to the 65-fossil-cd matrix. A, plotted clade delimitation and overall tree resolution; B, plotted symmetric resampling and jackknife frequencies; C, plotted Robinson-Foulds distances and Distortion-Coefficients; D, plotted final score. Abbreviations: RF, Robinson-Foulds distances; DC, Distortion-Coefficients; sr, symmetric resampling; jk, jackknife; cld, clade delimitation; otr, overall tree resolution.

3.2.3.2. Best ranked trees

Here, the phylogenetic trees (single MPT or strict consensus tree) resulting from the analysis of the six character matrices when using the best suiting weighting strategy, according to the accuracy measurements, are presented and described with regard to the position of the *Lacerta* and *Timon* OTUs (for all single MPTs or strict consensus trees resulting from analyses with the less accurate weighting strategies see Appendix 11).

Main matrix

The analysis of the main matrix when applying extended implied weights with K = 150 and an assumed homoplasy for missing entries of 50% recovered a single MPT (Figure 3.12). At the base of the *Lacerta*-clade only one intruder is present, *Podarcis waglerianus* MDHC 390. The basal-most OTU of *Lacerta* is *L. bilineata* AMNH R109472. The species-clades of *L. media* and *L. strigata* are completely resolved. The OTUs belonging to *L. trilineata* are recovered in one clade but five OTUs of *L. viridis* and one of *L. bilineata* intrude the species-clade.

Eventually, the largest clean clade is composed of three *L. trilineata* OTUs (of a total of eight OTUs). The largest clade of *L. schreiberi* is formed by five (out of six) OTUs but the clade is not recovered within the *Lacerta*-clade. It intrudes the *Timon*-clade together with the *Gallotia simonyi* OTU. However, the species-relationships within the *Timon*-clade are correctly recovered with *T. lepidus* + *T. pater* forming sister to *T. princeps* + *T. kurdistanicus*. Also, the species-clades themselves are completely found. Even though, not all OTUs of *Lacerta* are recovered in their correct species-clade, a general structure of the individual *Lacerta*-species seems to be present with (*L. agilis* + *L. media*), ((*L. bilineata* + *L. strigata*), ((*L. trilineata* + *L. viridis*), (*Timon* including *L. schreiberi*)).



Figure 3.12. Single MPT resulting from the highest ranked weighting strategy for the main matrix, an extended implied weights analysis with K = 150 and an assumed homoplasy for missing entries of 50%. Length: 2663 steps; adjusted homoplasy: 14.39578; CI: 0.105; RI: 0.520. Displayed here is only the part of the tree including the ingroup OTUs (the complete tree is available in Appendix 11). Black rectangle indicates the *Timon*-clade.

45-fossil matrix

A single MPT resulted from the analysis of the 45-fossil matrix when using an extended implied weight with K = 200 and an assumed homoplasy for missing entries of 100% (Figure 3.13). L. bilineata AMNH R109472 is found as the basal-most OTU of Lacerta. The genus clade is intruded by two Podarcis tiliguerta, two Podarcis siculus, one Podarcis muralis, the Podarcis hispanicus, and the Podarcis waglerianus OUT(s) at its base. The OTUs belonging to L. agilis are found in one clade; the largest correctly recovered clade of this species consists of nine (out of 12) OTUs, because the species-clade is intruded by the Gallotia stehlini OTU, all four Psammodromus algirus, the Algyroides nigropunctatus, one L. viridis, and two L. schreiberi OTUs. Also, the clade of L. trilineata is recovered, but it is intruded by three L. viridis, two L. media, and one L. bilineata OTU; the largest correct clade of L. trilineata is formed by four (out of eight) OTUs. The species-clade of L. strigata is completely recovered. Close to the base of the Timon-clade, the Gallotia simonyi OTU intrudes the genus clade of Lacerta. The Timonclade has no intruders, but the species-structure is not correct and one T. lepidus OTU intrudes the species-clade of T. pater. Although, the OTUs of Lacerta and Timon are only partly recovered in their correct species-clades, a general structure is recognisable: (L. agilis, (L. strigata, ((L. media + L. trilineata), (L. viridis, (L. bilineata, (L. schreiberi, (T. pater, (*T. lepidus*, (*T. kurdistanicus* + *T. princeps*)))))))))).



Figure 3.13. Single MPT resulting from the highest ranked weighting strategy for the 45-fossil matrix, an extended implied weights analysis with K = 200 and an assumed homoplasy for missing entries of 100%. Length: 2127 steps; adjusted homoplasy: 8.48916; CI: 0.130; RI: 0.512. Displayed here is only the part of the tree including the ingroup OTUs (the complete tree is available in Appendix 11). Black rectangle indicates the *Timon*-clade.

65-fossil matrix

The strict consensus tree resulting from the analysis of the 65-fossil matrix when using extended implied weights with K = 200 and an assumed homoplasy of 75% is based on 1038 MPTs (Figure 3.14). A larger polytomy is present that involves major parts of *Lacerta* and *Timon* but some smaller clades are still recovered within the polytomy.

At the base of *Lacerta*, the *Podarcis waglerianus*, one *Podarcis tiliguerta*, and one *Podarcis siculus* OTU intrude the species-clade. One OTU of *L. agilis* (MNHN 1963-49) is found further outside of the *Lacerta*-clade, as sister to the *Archaeolacerta bedriagae* OTU. The largest clade of the species *L. agilis* consists of five OTUs. As intruders of the *Lacerta* clade, the *Gallotia stehlini* OTU is recovered close to the OTUs of *L. agilis*, and the *Gallotia simonyi* OTU is found in the polytomy. The largest species-clades represent the following species and consist of two OTUs each: *L. schreiberi* (out of six), *L. strigata* (clade complete), *L. viridis* (out of 11), and *T. pater* (out of ten).



Figure 3.14. Strict consensus tree based on 1038 MPTs resulting from the highest ranked weighting strategy for the 65-fossil matrix, an extended implied weights analysis with K = 200 and an assumed homoplasy for missing entries of 75%. Length: 1614 steps; adjusted homoplasy: 6.15637; CI: 0.160; RI: 0.380. Displayed here is only the part of the tree including the ingroup OTUs (the complete tree is available in Appendix 11).

Cd matrix

When analysing the cd matrix under extended implied weights with K = 100 and an assumed homoplasy for missing entries of 100%, a single MPT was recovered (Figure 3.15). The OTU *L. bilineata* AMNH R109472 is recovered as the basal-most *Lacerta*. Two OTUs of *Podarcis tiliguerta*, two of *Podarcis siculus*, and the OTU of *Podarcis waglerianus* intrude the *Lacerta*clade at the base. The OTUs of *L. agilis* are found in one clade, but three OTUs of *L. bilineata*, three of *L. viridis*, and one of *L. schreiberi* intrude the clade. Thus, seven (out of 12) OTUs of *L. agilis* form a correct clade. The species-clade of *L. trilineata* is also found, but it is intruded by the *Broadleysaurus major* OTU, and three OTUs of *L. viridis*. The largest correct clade of *L. trilineata* consists of four (out of eight) OTUs. The *L. strigata*-clade is completely recovered. For *Timon*, the species-clade to *T. princeps* + *T. kurdistanicus*. But the genus-clade is intruded by a clade of five OTUs of *L. schreiberi* and a clade consisting of the OTUs of *Gallotia simonyi*, *Gallotia stehlini*, and *Gallotia caesaris*. The general structure of the species of *Lacerta* seems to be (*L. agilis*, ((*L. strigata* + *L. bilineata*), (*L. media*, (*L. viridis* + *L. trilineata*)), (*Timon* including *L. schreiberi*))).



Figure 3.15. Single MPT resulting from the highest ranked weighting strategy for the cd matrix, an extended implied weights analysis with K = 100 and an assumed homoplasy for missing entries of 100%. Length: 2963.965 steps; adjusted homoplasy: 20.95485; CI: 0.125; RI: 0.516. Displayed here is only the part of the tree including the ingroup OTUs (the complete tree is available in Appendix 11). Black rectangle indicates the *Timon*-clade.

45-fossil-cd matrix

The analysis of the 45-fossil-cd matrix under extended implied weights with K = 50 and an assumed homoplasy of 100% found one MPT (Figure 3.16). At the base of *Lacerta*, all four OTUs of *Psammodromus algirus*, the *Podarcis waglerianus* OTU, one OTU of *Podarcis muralis*, two of *Podarcis siculus*, and two of *Podarcis tiliguerta* are recovered as intruders. Another intruder is the OTU of *Gallotia stehlini*, it is found with OTUs of *L. bilineata*. The species-clade of *L. schreiberi* is recovered, but it is intruded by one OTU of *L. media*. Five (out of six) OTUs of *L. schreiberi* eventually form a correct clade. Also, the OTUs of *L. trilineata* are recovered in one clade, with three OTUs of *L. viridis* intruding it. A correct clade is formed by three (out of eight) OTUs of *L. trilineata*. The species-clade of *L. strigata* is completely recovered. For *Timon*, the species-relationships are not correctly recovered. The OTUs of *T. pater* oTUs form a correct clade. The *Timon*-clade is also intruded by the OTU of *Gallotia simonyi*. The general species-structure seems to be (*L. agilis*, (*L. strigata*, (*L. bilineata*, ((*L. trilineata* + *L. viridis*), (*L. media*, (*L. schreiberi*, (*T. lepidus*, (*T. pater*, (*T. princeps* + *T. kurdistanicus*)))))))).



Figure 3.16. Single MPT resulting from the highest ranked weighting strategy for the 45-fossil-cd matrix, an extended implied weights analysis with K = 50 and an assumed homoplasy for missing entries of 100%. Length: 2420.910 steps; adjusted homoplasy: 27.97690; CI: 0.150; RI: 0.499. Displayed here is only the part of the tree including the ingroup OTUs (the complete tree is available in Appendix 11). Black rectangle indicates the *Timon*-clade.

65-fossil-cd matrix

A single MPT was found by the analysis of the 65-fossil-cd matrix when using extended implied weights with K = 200 and an assumed homoplasy for missing entries of 100%. Even though the tree is completely resolved, no *Lacerta* or *Timon* species-clade is completely recovered. The largest clades of *L. agilis* and *L. trilineata* are composed of four OTUs each (out of 12 and eight OTUs, respectively). The basal-most *Lacerta* is *L. viridis* MNHN 1888-139, it is found with the four OTUs of *Psammodromus algirus*, and the OTU of *Algyroides nigropunctatus*. Further, the *Lacerta*-clade is intruded at its base by the *Podarcis waglerianus* OTU, the *Podarcis hispanicus* OTU, two OTUs of *Podarcis tiliguerta*, one of *Podarcis siculus*, and the OTUs of *Gallotia caesaris*, *Gallotia stehlini*, and *Gallotia simonyi*. Even though the species-structure within the *Timon*-clade is not correctly recovered, there are no intruders present. The general species-structure appears to be (*L. agilis*, (*L. schreiberi*, ((*L. strigata* + *L. bilineata*), (*L. media*, ((*L. trilineata* + *L. viridis*), (*T. lepidus*, (*T. pater*, (*T. princeps* + *T. kurdistanicus*)))))))).



Figure 3.17. Single MPT resulting from the highest ranked weighting strategy for the 65-fossil-cd matrix, an extended implied weights analysis with K = 200 and an assumed homoplasy for missing entries of 100%. Length: 1553.309 steps; adjusted homoplasy: 5.48032; CI: 0.216; RI: 0.514. Displayed here is only the part of the tree including the ingroup OTUs (the complete tree is available in Appendix 11). Black rectangle indicates the *Timon*-clade.

3.2.4. Discussion

3.2.4.1. Species-structures derived from OTU positions

The phylogenetic trees resulting from the different weighting strategies which were ranked as best for the individual character matrices shared common structures which are highlighted here regarding the genera *Lacerta* and *Timon*. The tree resulting from analysis of the 65-fossil matrix is excluded here, because no species structure was visible due to the large polytomy (Figure 3.14).

General species relationships derived from the positioning of the Lacerta-OTUs were possible, though, the species-clades were in the majority of the cases not completely recovered. The species-clade of L. agilis was always placed as most-basal Lacerta-species. The main part of the OTUs of L. trilineata and L. viridis were always found grouped together, except for the best ranked tree of the 45-fossil matrix. Here, L. trilineata OTUs were grouped with L. media OTUs (Figure 3.13). The latter grouping is in agreement with phylogenies based on molecular data, where L. trilineata is consistently found in sister relationship to L. media (Godinho et al., 2005; Ahmadzadeh et al., 2013a, 2013b; Pyron et al., 2013; Sagonas et al., 2014; Marzahn et al., 2016; Saberi-Pirooz et al., 2021). However, Tschopp et al. (2018b) and Wencker et al. (2021) found, based on earlier versions of the current, morphology-based dataset, L. trilineata in sister relationship to L. viridis (see also 2.1. Main matrix construction). Hence, it is not clear whether this structure is due to a general incongruence between morphological and molecular data or a problem of the character matrix itself. A comparison with other morphology-based phylogenies remains difficult, because they often include only one or two species of Lacerta (mostly L. agilis and/or L. viridis) (e.g., Gauthier et al., 2012; Čerňanský et al., 2016, 2017; Cruzado-Caballero et al., 2019). Molecular phylogenies find L. bilineata and L. viridis in sister relationship (Godinho et al., 2005; Pyron et al., 2013; Sagonas et al., 2014). The best ranked weighting strategy for the 45-fossil-cd matrix recovered OTUs of L. bilineata in close relationship to the grouped OTUs of L. viridis and L. trilineata (Figure 3.16).

For *Timon*, the main matrix and the cd matrix recovered a species-structure that is in congruence with molecular phylogenies (Ahmadzadeh *et al.*, 2012, 2016) with *T. lepidus* + *T. pater* as sister to *T. princeps* + *T. kurdistanicus*. For the other matrices, only the sister relationship of *T. princeps* and *T. kurdistanicus* was recovered correctly. However, it should be born in mind that only two OTUs were involved here. Furthermore, the generally better resolution of the *Timon*-clade is likely due to the lower number of OTUs compared to *Lacerta*.

3.2.4.2. Correlation of accuracy measurements

The individual accuracy measurements resulted in sometimes conflicting rankings for the different weighting strategies. Hence, the highest ranked weighting strategy is not necessarily the one which is the best in all criteria, but rather the one which is generally good. Here, possible correlations of the accuracy measurements with the weighting strategies also with regard to the different constitutions of the six character matrices are explored.

The overall tree resolution did not show a correlation with the weighting strategy. Though, analyses that use implied weights and extended implied weights tend to find fewer MPTs than equal weights (Goloboff, 2014). Hence, analyses with equal weights comparatively find more MPTs, this can result in low strict consensus tree resolution when conflicting structures are present (Gauthier, 1986; Huelsenbeck, 1991; Wilkinson and Benton, 1995; Pol and Escapa, 2009), although in this study, only when using the 65-fossil matrix, the equal weights approach resulted in the worst overall tree resolution compared to the other weighting strategies (Figure 3.8A). However, it is important to note that tree resolution is not necessarily correlated with phylogenetic information or vice versa (e.g., Wencker et al., 2021; see chapter 1.2.1. Data problem), as was observed in the case of the 65-fossil-cd matrix under implied weights with K = 10, which had the worst overall tree resolution score but was ranked highest for clade delimitation (Table 3.8). The clade delimitation showed indeed in some cases a correlation with the weighting strategy. It improved with decreasing weighting strength. For the matrices with continuous and discrete character statements, this correlation was generally not present. It was only weakly observable for the cd matrix (Figure 3.9A). For the matrices with discrete character statements only, the correlation of the clade delimitation values was present for the main matrix and the 45-fossil matrix.

The normalised values of the symmetric resampling and jackknife frequencies showed that both support measures identify the tree accuracy in a very similar way: for five of the six character matrices, the plotted normalised frequencies followed an almost identical (overlapping) trend. Only for the 65-fossil matrix, the trend of the two graphs differed (Figure 3.8B). Here, the normalised values of the jackknife frequencies seem to be more stable ($K \ge 20$). In contrast, the symmetric resampling frequencies had some variation depending on the weighting strategy ($K \ge 20$: values for implied weights and extended implied weights with 25% assumed homoplasy were lower than for other weighting strategies using the same *K*-values). Generally, there seems to be no advantage of one support measure over the other, a result in agreement with Tschopp and Upchurch (2019 and references therein). An improvement of the 119

significance of these two accuracy measurements might be gained by only taking the group support values of the (correct) ingroup clades of *Lacerta* and *Timon* OTUs instead of all group support values. Because in this way, the accuracy values would reflect more precisely the actual support of the ingroup OTUs and the impact of the weighting strategy on those.

The Robinson-Foulds distances and Distortion-Coefficients rated quite similarly the weighting strategies for the main matrix (Figure 3.6C), the 45-fossil matrix (Figure 3.7C), and the 65-fossil-cd matrix (Figure 3.11C), whereas for the cd matrix (Figure 3.9C) and the 65-fossil matrix, the two tree distance measures showed partly diverging results (Figure 3.8C). But for the 45-fossil-cd matrix, the two tree topology measurements showed no similarities regarding the ranking of the weighting strategies (Figure 3.10C). A correlation of the Robinson-Foulds distances and the Distortion-Coefficients with the weighting strategies with higher normalised scores, while the weighting strength decreased, was present for the main matrix (Figure 3.6C), the 45-fossil matrix (Figure 3.7C), the 65-fossil-cd (Figure 3.11C), and to some degree for the 65-fossil matrix (Figure 3.8C). In the case of the 45-fossil-cd matrix, only the Robinson-Foulds distances seem to have a correlation with the weighting strategy, whereas the Distortion-Coefficients show a random distribution (Figure 3.10C). The two tree topology distance measures showed no correlation to the weighting strategies for the cd matrix (Figure 3.9C). The main criticism with the Robinson-Foulds distances is that already small differences between the trees due to floating taxa that move between the clades would lead to large distances, though, the trees do not differ much from each other (Goloboff et al., 2018). In the present case, the Robinson-Foulds distances did generally rate the tree distances in a similar manner as the Distortion-Coefficients. This might indicate that the data itself, on which the character matrices are based, does not contain much conflicting information. It is further supported by the fact that, as stated above, analyses with equal weights did not produce a lot of (conflicting) MPTs.

3.2.4.3. Impact of weighting strategy on tree accuracy

In all cases, weighting strategies using the strongest weighting strength in the study with K = 5 were producing the least accurate trees. Hence, with *K* equal to or greater than 10, generally more accurate phylogenetic trees were found. This is partly in agreement with Goloboff *et al.* (2018), who found the best results for analyses using a *K*-value between 10 and 20. However,

slight differences of the tree accuracy depending on the weighting strategy were present for the individual character matrices which are highlighted here.

The main matrix and the 45-fossil matrix produced best results with weighting strengths between K = 20 and 200. However, the differences in accuracy between K = 20 and 200 were quite small. The analysis of the 65-fossil matrix resulted in somewhat better tree accuracies with *K*-values between 10 and 200. But the tree accuracy for the 65-fossil matrix was generally low and quite similar for the different weighting strengths. Hence, the tree accuracy suffers most likely from the high incompleteness of the dataset, and even the best fitting weighting strategy seems not to be able to detect the low phylogenetic signal properly.

The cd matrix showed good tree accuracies for weighting strategies using weighting strengths between K = 10 and 200. The differences of tree accuracies within this range were small. This was also the case for the ranges for the 45-fossil-cd matrix with best accuracy for weighting strategies with *K*-values between 100 and 200 and the 65-fossil-cd matrix with best tree accuracies for weighting strategies with *K*-values between 50 and 200.

Although, analyses with equal weights were not resulting in the least accurate trees, implied weights and extended implied weights with high *K*-values (at least > 5), outperformed equal weights in most cases. This agrees with other studies that conclude that analyses under implied weights produce less accurate trees than analyses under equal weights, because those only tested quite strong weighting strengths with *K*-values not greater than 10 (Congreve and Lamsdell, 2016; Puttick *et al.*, 2017). The results here confirm that these lower *K*-values are indeed resulting in the least accurate trees, but the accuracy for implied weights and extended implied weights with higher *K*-values generally resulted in more accurate trees than analyses under equal weights.

Differences between implied weights and extended implied weights were quite small. However, the symmetric resampling and jackknife frequencies detected better tree accuracies for analyses under extended implied weights, especially when the homoplasy for missing entries was assumed to be at least 50% of the observed one. This effect was stronger for the simulated fossil matrices 45-fossil matrix and 65-fossil matrix than for the more complete main matrix and cd matrix. This highlights that the observed homoplasy in characters with several missing entries is generally lower than the homoplasy that is actually present (Goloboff, 2014). Hence, the low percentage for the assumed homoplasy of missing entries leads to an even lower considered homoplasy during analyses. However, the simulated fossil datasets with continuous and discrete

character states did not respond in this way to the implied weights and extended implied weights: in the case of the 45-fossil-cd matrix, no real difference between implied weights and extended implied weights was observable. But for the 65-fossil-cd matrix, the extended implied weights with 75% and 100% of missing entries had lower tree accuracies than extended implied weights with a lower assumed homoplasy or implied weights with the respective *K*-value. However, this only applied to K = 5, 10, 20, and 50, for *K*-values greater than 50, no differences between implied weights and extended implied weights were visible. Due to the high incompleteness of the 65-fossil-cd matrix, it is not clear whether this is an artefact or a true signal.

Consequently, the results show that extended implied weights and implied weights with higher K-values (greater than 10) generally outperform analyses under equal weights. The best ranked weighting strategy was consistently an extended implied weights analysis, regardless of the dataset's state of incompleteness. This confirms the benefits of weighted analyses also for incomplete fossil datasets.

3.3. Quantitative characters: continuous vs. discrete character states

3.3.1. Introduction

Generally, phylogenetic characters can be divided into two basic types: qualitative and quantitative characters (e.g., Sereno, 2007). However, Baum (1988) and Stuessy (2009) argued that theoretically all characters could be transformed into quantitative characters. Qualitative characters describe shapes and forms and their states are expressed with words, whereas quantitative character states are mostly expressed by numbers which are based on measurements and counts. According to Sereno (2007) qualitative characters can be further subdivided into the five groups: 1) "form" (e.g., shape of a process), 2) "appearance" (e.g., dermal ornamentation), 3) "topology" (e.g., position of a ridge), 4) "composition" (e.g., fused elements), and 5) "ontogeny" (variation during development). The character state of a qualitative character is always discrete. A further subdivision of the quantitative characters can be made into "quantitative-absolute" (or meristic; e.g., tooth count), "quantitative-relative/geometric" (e.g., ratio of length to width) characters (Sereno, 2007). Their character states are naturally continuous but traditionally they have been discretised, also because until recently phylogenetic programmes could not handle this type of data (Goloboff *et al.*, 2006).

The process of discretisation of a quantitative character is a straightforward approach and scoring of OTUs is quick and reproducible. Especially, for palaeontological data which is often affected by abiotic factors resulting in deformation (Arbour and Currie, 2012; Tschopp *et al.*, 2013), the discretisation of morphometric characters can be beneficial. Because in this way, the effects of outliers resulting from taphonomic deformation can be minimised (Tschopp and Upchurch, 2019). Several approaches have been proposed to discretise quantitative characters, such as gap coding (Mickevich and Johnson, 1976), generalised gap coding (Archie, 1985), segment coding (Colless, 1980; Thorpe, 1984; Chappill, 1989) or the more widely used gap weighting (Thiele, 1993). However, defined state boundaries may still remain subjective (Archie, 1985; Rae, 1998). Farris (1990) raised criticism based on the fact that OTUs with significantly different values can be grouped in the same character state, whereas OTUs with similar values can be assigned different character states.

Thus, the usage of quantitative characters with their (natural) continuous character states was proposed by several researchers (Rae, 1998; Goloboff *et al.*, 2006). A bit more than a decade ago, an implementation of algorithms in TNT was made, which allows the processing of

continuous data (Goloboff et al., 2006; Goloboff and Catalano, 2016). Here, differences between the character states of the OTUs are calculated during tree search based on the actual values (Goloboff *et al.*, 2006). In case of overlapping intervals, as defined by Farris (1970), those are considered not to be different (Goloboff *et al.*, 2006).

Since the implementation, continuous character states have been increasingly integrated in palaeontological datasets, and phylogenetic analyses were performed including those, for instance, for Heterostraci (Randle and Sansom, 2017), Stegosauria (Maidment *et al.*, 2008; Raven and Maidment, 2017), Sauropodomorpha (Upchurch, 2009; Mannion *et al.*, 2013), Pterosauria (Andres *et al.*, 2014), Plesiosauria (Ketchum and Benson, 2010), Crocodylia (Groh *et al.*, 2020), Caseidae (Brocklehurst *et al.*, 2016), Dicynodontia (Kammerer *et al.*, 2011), Canidae (Prevosti, 2010), and Trilobita (Hopkins, 2011).

Here, the impact of continuous character states versus discretised character states for quantitative characters on the tree resolution are compared. To do so, two versions of a real morphological specimen-level dataset were used, one with only discrete character states and the other with continuous character states for the quantitative characters. Moreover, two simulated fossil matrices, respectively, with different degrees of incompleteness that were derived from the two versions of the real morphological specimen-level dataset, were included to explore also the effects of continuous character states on incomplete datasets.

3.3.2. Material and methods

For the comparison of the phylogenetic signal of quantitative continuous versus quantitative discrete characters, the six character matrices -main matrix, 45-fossil matrix, 65-fossil matrix, cd matrix, 45-fossil-cd matrix, and 65-fossil-cd matrix- were used.

All matrices are derived from the main matrix, and contain the same 252 characters of which 37 are quantitative and 215 are qualitative (see also 2.1. Main matrix construction). Here, the main matrix (only discrete character states) was compared with the cd matrix (quantitative continuous character states). For the simulated fossil matrices, the 45-fossil matrix was compared to the 45-fossil-cd matrix (both have an incompleteness of 45%) and the 65-fossil matrix was compared to the 65-fossil-cd matrix (both have an incompleteness of 65%). For the comparison, the phylogenetic trees that were recovered by the weighting strategy which was previously identified as the best fitting one for the individual matrices were used (see 3.2.

Comparison of weighting strategies). The trees were compared based on resolution and general tree topology. The weighting strategies used to create the individual trees were the following:

- Main matrix: extended implied weighting with K = 150 and an assumed homoplasy for missing entries of 50%
- Cd matrix: extended implied weights with K = 100 and an assumed homoplasy for missing entries of 100%
- 45-fossil matrix: extended implied weights with K = 200 and an assumed homoplasy for missing entries of 100%
- 45-fossil-cd matrix: extended implied weights with K = 50 and an assumed homoplasy for missing entries of 100%
- 65-fossil matrix: extended implied weights with K = 200 and an assumed homoplasy for missing entries of 75%
- 65-fossil-cd matrix: extended implied weights with K = 200 and an assumed homoplasy for missing entries of 100%

3.3.3. Results

Here, the differences between the phylogenetic trees in regard to the clade structure of the two ingroup genera *Lacerta* and *Timon* are explored.

3.3.3.1. Main matrix vs. cd matrix

The two trees share generally the same topology (Figure 3.18). However, they differ in the number of OTUs intruding the *Lacerta*-clade: the main matrix recovers just the *Podarcis waglerianus* OTU (Figure 3.18A), whereas for the cd matrix, two additional OTUs of *P. tiliguerta* and two of *P. siculus* are present at the base of the *Lacerta*-clade. Moreover, the *L. trilineata*-clade is intruded by the OTU of *Broadleysaurus major* which is a Scincoidea and thus part of a rather basal clade within the outgroup (Figure 3.18B). In terms of species-clade resolution, the main matrix recovered a complete *L. media*-clade (three OTUs), whereas the cd matrix finds just two *L. media* forming a clade. However, the cd matrix, recovered all 12 *L. agilis* OTUs in a single clade (with intruders), whereas the largest clade of *L. agilis* for the main matrix is consisting of five OTUs. Both matrices recover the species-structure of *Timon* correctly, but in the tree resulting from the main matrix, the clade is intruded only by the

Gallotia simony OTU, whereas in the case of the cd matrix, also the OTUs of *Gallotia stehlini* and *Gallotia caesaris* are found as part of *Timon* (all *Gallotia* from a clade).



Figure 3.18. Comparison between the most accurate trees resulting from analyses of the main matrix (A) (extended implied weights with K = 150, assumed homoplasy for missing entries of 50%) and the cd matrix (B) (extended implied weights with K = 100, assumed homoplasy for missing entries of 100%). Blue tree branches indicate an identical recovery of structures; grey rectangles highlight more accurately resolved clades compared to the other tree; orange arrowhead point to outgroup intrudes that were not shared with the other tree. Displayed here is only the part of the trees including the ingroup OTUs (the complete trees are available in Appendix 11).

3.3.3.2. 45-fossil matrix vs. 45-fossil-cd matrix

The trees resulting from the analyses of the 45-fossil matrix and the 45-fossil-cd matrix are less similar than the main matrix and the cd-matrix, but generally share a common topology (Figure 3.19). The basal-most *Lacerta* OTU for the 45-fossil matrix is *L. bilineata* AMNH R109472 (Figure 3.19A); for the 45-fossil-cd matrix, the basal-most is *L. viridis* MNHN 1887-810 (Figure 3.19B). The *Lacerta*-clade is in both cases intruded by the same OTUs, but for the 45-fossil matrix, also the OTUs of *Algyroides nigropunctatus*, *Podarcis hispanicus*, and

Gallotia simonyi are found as part of it. The *Timon*-clade is without intruders when analysing the 45-fossil matrix, whereas for the 45-fossil-cd matrix, the OTUs of *Gallotia simonyi* and *Gallotia caesaris* are found within *Timon*. Also, the species-clades found for the 45-fossil matrix in *Timon* are more accurate. For *Lacerta*, the analyses of the 45-fossil matrix found all OTUs of *L. agilis* in one clade (with intruders), whereas the largest clade of *L. agilis* for the 45-fossil-cd matrix contains four OTUs. However, for the 45-fossil-cd matrix, the clade of *L. schreiberi* is found with a single intruder, whereas for the 45-fossil matrix the largest *L. schreiberi*-clade has two OTUs.



Figure 3.19. Comparison between the most accurate trees resulting from analyses of the 45-fossil matrix (A) (extended implied weights with K = 200, assumed homoplasy for missing entries of 100%) and the 45-fossil-cd matrix (B) (extended implied weights with K = 50, assumed homoplasy for missing entries of 100%). Blue tree branches indicate an identical recovery of structures; grey rectangles highlight more accurately resolved clades compared to the other tree; orange arrowhead point to outgroup intrudes that were not shared with the other tree. Displayed here is only the part of the trees including the ingroup OTUs (the complete trees are available in Appendix 11).

3.3.3.3. 65-fossil matrix vs. 65-fossil-cd matrix

The phylogenetic tree of the 65-fossil matrix has a much lower tree resolution than the one resulting from analysis of the 65-fossil-cd matrix (Figure 3.20). Therefore, also differences in clade-recovery are larger. Though, for the 65-fossil-cd matrix, the tree resolution is better, the *Lacerta*-clade is intruded by more OTUs than the tree of the 65-fossil matrix. OTUs additionally intruding the 65-fossil-cd matrix are all four OTUs of *Psammodromus algirus*, the *Algyroides nigropunctatus* OTU, the *Gallotia caesaris* OTU, one OTU of *Podarcis tiliguerta*, the *Acanthodactylus erythrurus*, and the *Zootoca vivipara* OTU (Figure 3.20B). For the 65-fossil-cd matrix, the basal-most *Lacerta* OTU is *L. agilis* MNHN 1963-49 (Figure 3.20A); for the 65-fossil-cd matrix, the basal-most OTU is *L. bilineata* MDHC 48. Several species-clades of *Lacerta* were recovered for the 65-fossil-cd matrix: *L. agilis* with five OTUs (with intruders), *L. schreiberi* with five OTUs (with intruders), and *L. media* with two OTUs. For the 65-fossil matrix, a clade of *L. agilis* with nine OTUs (with intruders) was found. The *Timon*-clade of the 65-fossil-cd matrix, was recovered without intruders, whereas for the 65-fossil matrix, some OTUs of *Timon* were found in a resolved clade and the OTU of *Gallotia caesaris* intruding one of them.



Figure 3.20. Comparison between the most accurate trees resulting from analyses of the 65-fossil matrix (A) (extended implied weights with K = 200, assumed homoplasy for missing entries of 75%) and the 65-fossil-cd matrix (B) (extended implied weights with K = 200, assumed homoplasy for missing entries of 100%). Grey rectangles highlight more accurately resolved clades compared to the other tree; orange arrowhead point to outgroup intrudes that were not shared with the other tree. Displayed here is only the part of the trees including the ingroup OTUs (the complete trees are available in Appendix 11).

3.3.4. Discussion

Based on the differences observed between the main matrix and the cd matrix, no clear superiority of one over the other is present. Although, the cd matrix recovers a member of a distant outgroup (*Broadleysaurus major*) within the *Lacerta*-clade, it also finds all *L. agilis* OTUs in one clade (Figure 3.18), which was not the case when analysing the main matrix. Hence, they seem to be equally well fitting.

The comparison between the 45-fossil matrix and the 45-fossil-cd matrix, showed that the matrix with only discrete character states (45-fossil matrix) appears to result in a slightly better

fitting tree, because the *Timon*-clade showed a slightly better resolution, and a clade containing all OTUs of *L. agilis* was found (Figure 3.19).

The 65-fossil matrix had a significantly worse tree resolution than the 65-fossil-cd matrix. However, the *Lacerta*-clade in the 65-fossil-cd matrix recovered more intruders, but those are positioned rather at the basal node. Additionally, the 65-fossil-cd matrix found more clades that grouped OTUs of the same *Lacerta*-species, and the *Timon*-clade was without intruders (Figure 3.20). Hence, the matrix with continuous and discrete character states (65-fossil-cd matrix) seems to have found the better fitting tree.

When deciding whether to incorporate continuous characters in the dataset, the additional amount of work must be considered: taking exact measurements (which should actually also be done for discrete character states), the dataset management, and data input is a time-consuming process. Hence, one should ask: Is the additional work worthwhile? In the present study, only for the most incomplete simulated fossil datasets (65-fossil matrix and 65-fossil-cd matrix), an advantage of incorporating continuous character states was present. However, due to the fact that the 65-fossil-cd matrix is a simulation, the data and its measurements are derived from extant, mostly completely preserved specimens, which were not affected by taphonomic distortion. Real fossils are exposed to taphonomic processes (Arbour and Currie, 2012; Tschopp et al., 2013), resulting in incomplete and deformed specimens. These factors complicate or hinder taking exact measurements and positive effects of continuous character states due to added precision can be minimised. Phylogenies including continuous data derived from fossils show indeed improved tree resolution (e.g., Goloboff et al., 2006; Randle and Sansom, 2017; Raven and Maidment, 2017). However, this is also expected because the fewer overlaps between the exact continuous character states lead to the recovery of fewer equally long trees (e.g., Mannion et al., 2013; Mongiardino Koch et al., 2015).

Hence, the results confirm that continuous characters carry useful phylogenetic information, and for incomplete fossil datasets, incorporation of these types of data can be a beneficial tool to increase tree resolution.

4. Discussion and Conclusions

4.1. Informative value of the data

The results and interpretations made are based on a specific dataset (and its derived versions) with a stable number of characters and OTUs which was created with a focus on lacertid lizards. Hence, it remains to be understood if the significance of the study is limited to this case study or if it may have wider implications for the analysis of biological and palaeontological datasets. Generally, the results are in agreement with other studies that examine vertebrates and datasets of different sizes (see 3.2.4. Discussion of weighting strategy comparison and 3.3.4. Discussion of continuous vs. discrete character states). This suggests that the recommendations based on this study can also be applied to other vertebrate groups and possibly also for phylogenetic analyses at higher taxonomic levels than just at specimen-level.

For a more general validation, the same assessment of testing different weighting strategies and/or the impact of continuous character states on phylogenetic analyses should also be applied to other (vertebrate) taxa. Additionally, other distribution patterns of missing entries could be tested that are not evenly allocated to the OTUs but focused on few OTUs in the dataset.

4.2. Does the specimen-level approach work?

In this specific case, the specimen-level approach was not able to delimitate correctly the species of *Lacerta* and *Timon* in most of the cases. Also previous studies that use the specimen-level approach had problems with the delimitation of OTUs on the species level (e.g., Cau, 2017, 2019; Gee, 2020). The phylogenies of Cau (2017) and Gee (2020) resulted in large polytomies that are probably due to the incompleteness of the fossil OTUs and the number of OTUs in relation to the number of characters. The low resolution is similar to that observed for the ingroup when analysing the 65-fossil matrix, although the dataset of Cau (2017) and Gee (2020) have an incompleteness of 20% and 38%, respectively. Concerning the relation of OTUs to characters, Cau (2017) had a matrix consisting of 53 OTUs and 43 characters, whereas Gee (2020) had 51 OTUs and 85 characters, which are low character/OTU ratios compared to the dataset used in the present study which had about twice as many characters in relation to OTUs (252 characters for 120 OTUs). An example of a specimen-level phylogeny that found species clades correctly is shown in Villa *et al.* (2017). Here, there were 37 OTUs and 159 characters, indicating the importance of a high proportion of characters compared to OTUs. However, it should be noted that Villa *et al.* (2017) constrained the ingroup (*Lacerta*) to be monophyletic.

Although species were not precisely delimitated, it was shown that some weighting strategies resulted in more accurate trees, and general species structures were visible. This might be a problem of the dataset or of the data itself, here the selected group, Lacerta and Timon. The two genera are part of Lacertidae, which underwent several taxonomic and systematic revisions in the past years primarily with the help of analytical methods using DNA (e.g., Brückner et al., 2001; Godinho et al., 2005; Arnold et al., 2007; Ahmadzadeh et al., 2012; Mendes et al., 2016; Saberi-Pirooz et al., 2021). For this study, the species identification of the individuals was done before skeletonisation with the help of soft part morphology (such as coloration) and geographic distribution (see 2.1. Main matrix construction). It seems that the interspecific differences between the studied species are only reflected to a certain extent in the osteological parts, and that some species lack distinctive osteological characters (see also Villa et al., 2017). Frost et al. (1998) noted if morphological features that are a result of environmental adaptations evolve slower than molecular features, then the morphological information is retained longer than the molecular one. Hence, especially rather recently occurred species split-ups, which are already detectable on DNA-level, might be not yet manifested in the skeletal bauplan (see also Wiens and Penkrot, 2002). This might explain the poor species delimitation of L. viridis and L. bilineata whose OTUs were often found mixed in one clade. In previous times, the two were identified as L. viridis, but genetic investigations revealed the presence of two separate species (Rykena, 1991; Amann et al., 1997; Marzahn et al., 2016). For future work, it might be interesting to identify fast evolving skeletal areas and test what effect on the tree topology it has when given higher weight to those fast evolving areas and lower to the slowly evolving one. Does this lead to an enhancement of species delimitation, hence, to phylogenies that are congruent to molecular phylogenies on lower taxonomic levels?

For the genus *Lacerta*, even molecular data do not completely agree on all interspecific relationship of *Lacerta*, e.g., for *L. strigata* (Godinho *et al.*, 2005; Pyron *et al.*, 2013; Marzahn *et al.*, 2016), whereas for *Timon* interspecific relationships are better understood (Pyron *et al.*, 2013; Ahmadzadeh *et al.*, 2016). Also in the present study, species delimitation for *Timon*, at least for the most complete datasets (main matrix and cd matrix), was quite accurate, but intruding OTUs were present. The common intruders of the *Timon*-clade were the OTUs of *Gallotia* and *L. schreiberi*. However, this does not seem to be a problem of the analytical approaches in the specimen-level analysis, but rather derives from the included morphological characters. Indeed, *Timon* and *Gallotia* share a quite similar morphology, such as heavy dermal ornamentation and both are rather large-sized (e.g., Barahona *et al.*, 2000; Arnold *et al.*, 2007;

see also Figure 4.1). When OTUs of *L. schreiberi* intruded *Timon*, they formed a large clade on their own, indicating that also on species-level *L. schreiberi* might be recovered as part of *Timon*. Generally, Lacertini seem to have a fast radiation (Mendes *et al.*, 2016) which makes the construction of phylogenies more difficult. Hence, slower evolving groups might be less problematic for the specimen-level approach.



Figure 4.1. CT-scans of the skulls in dorsal view of (A) *Timon lepidus* (NHMW 10921-1) and (B) *Gallotia stehlini* (NHMW 11031-1) with a well-visible dermal ornamentation. Modified from Čerňansky and Syromyatnikova (2019; therein Figs. 34A and 40A). Scale bar 7.5 mm.

The present study highlights the disparity between osteology, soft parts, and molecules in terms of their eligibility for species delimitation, which possibly stems from their different evolutionary rates with the lowest rates in osteological features. However, for palaeontological studies bones are in the majority of the cases the only source of information. Hence, modifications of how osteological data are processed should be implemented in order to gain

results that are more in agreement with species delimitations based on soft parts and molecules. The inclusion of landmark data might be also an interesting topic to explore here.

Moreover, in regard to the general testing of specimen-level phylogenies, further investigations, by using other groups of taxa need to be done. The usage of TNT scripts, as was in Pei et al. (2020), could be taken in consideration to accelerate the analysing process. Also, the accuracy measurement criteria could be further improved. For instance, a refinement of the support measurements could be applied, by considering only the support frequencies of the ingroup (see 3.2.4.2. Correlation of accuracy measurements). In addition, the inclusion of more tree distance metrics, such as the subtree pruning and regrafting (SPR) distance (Penny and Hendy, 1985) which calculates the SPR rearrangements needed to get from one tree to another, might help to better explore the impact of intruding OTUs. For the improvement of the whole evaluation process, it would be very useful to develop an automated process because clade delimitation is especially time-consuming. Such increased speed would allow testing more matrix compositions such as different distribution patterns of specimen incompleteness (see also 4.1. Informative value of the data) and numbers of OTUs assigned to the same species. Also, the problem of directed noise (due to the OTUs' ecology, body size, ontogeny and sex) could be an interesting field to be explored for specimen-level analyses. Finally, guidelines need to be developed, defining at what point a phylogenetic relationship between OTUs is intra- or interspecific/-generic. This could also help addressing the problem of incomparability of palaeontological and neontological species (see also Tschopp et al., in press).

4.3. Recommendations for selection of tree search strategy

As shown above, analyses using extended implied weights generally outperform equal weights and implied weights for all character state types and states of incompleteness.

As a general guideline to generate the most accurate results for a specimen-level dataset, when using maximum parsimony, it seems that for the setting of the *K*-value, a large range from 10 or 20 to 200 is creating the best results for all matrices regardless of the incompleteness or the character state type. However, a *K*-value of 100 or 150 appears to represent a universally applicable weighting strength to gain accurate results. *K*-values lower than ten should be avoided. In regard to the assumed homoplasy of missing entries based on the observed homoplasy, at least the percentage of 50 which is set by default in TNT, should be selected. But especially for matrices with a higher state of incompleteness, the percentage for the assumed

homoplasy should be set to 100%. The usage of continuous character states in a specimen-level analyses do not be avoided, and for rather incomplete datasets it can even lead to an improvement of tree resolution and accuracy. However, datasets with too low phylogenetic signal (e.g., due to high incompleteness) will not, also with the best-fitting weighting strategy, recover highly accurate phylogenetic trees. These suggestions are probably not just valid for specimen-level analyses but also for analyses on higher levels.
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7. Index of figures

Chapter 1

Figure 1.1. Map of France indicating the geographical positions of the four Oligocene localities with black stars. Cod, Coderet; LaC, La Colombière; Roq2, Roqueprune 2; MdGB, Mas de Got B.11 Figure 1.2. Overview of premaxilla morphotypes. A, Morphotype P1, premaxilla from Coderet Couche 1 sup (CC1sup-1) in posterior view. B, Morphotype P2, premaxilla from Coderet Couche 1 sup (CC1sup-3) in posterior view. C, Morphotype P3, premaxilla from Coderet E1-0 (CE1-0-5) in anterior view. D, Morphotype P4, premaxilla from Coderet E1-0 (CE1-0-6) in posterior view. E, Morphotype P5, premaxilla from Fouilles Viret (FV-2) in right lateral view. The arrowheads mark important diagnostic structures: 1, enlarged median tooth; 2, ethmoidal foramen within fossa which is not completely closed and bordered posteriorly by a ridge; 3, fang-like, pointed tooth; 4, ethmoidal foramen without fossa; 5, second ethmoidal foramen without fossa. anp, ascending nasal process; et.f, ethmoidal foramen; mf, maxillary facet; pp, palatine process. Scale bar 1 mm. Individual and more Figure 1.3. Overview of maxilla morphotypes. A, Morphotype M1, left maxilla from Coderet E1-0 (CE1-0-7) in lateral view. B, Morphotype M2, right maxilla from Coderet Couche 1 sup (CC1sup-8) in medial view. C, Morphotype M3, right maxilla from Coderet Couche 1 sup (CC1sup-11) in lateral view. D, Morphotype M4, left maxilla from Coderet Couche 1 sup (CC1sup-15) in lateral view. E, Morphotype M5, right maxilla from Coderet E1-0 (CE1-0-16) in medial view. F, Morphotype M6, right maxilla from Coderet E1-0 (CE1-0-17) in medial view. The arrowheads mark important diagnostic structures: 1, subtriangular process; 2, facial process which is perpendicular to dental crest; 3, dermal ornamentation; 4, concave ventral edge of anterolateral premaxillary process; 5, slight medial extension for articulation with palatine; 6, abruptly smaller and less robust posterior-most teeth; 7, larger tooth in anterior-half; 8, globose-like, monocuspid tooth; 9, fang-like, pointed tooth. alp, anterolateral process; ca.m, carina maxillaris; fp, facial process; ps, palatine shelf; zp, zygomatic process. Scale bar 1 mm. Individual and more detailed figures of the morphotypes can be found in

Figure 1.4. Overview of dentary morphotypes D1–D5. A, Morphotype D1, right dentary from Coderet Couche 1 sup (CC1sup-16) in medial view. B, C, Morphotype D2, right dentary from Coderet Couche Verte sup 1-25 (CCVsup-8) in medial view (B), tooth of a left dentary from Coderet Couche 1 sup (CC1sup-46) in medial view (C). D, E, Morphotype D3, right dentary from Coderet Couche 1 sup (CC1sup-47) in medial view (D), teeth of a left dentary from Coderet H1-100 (CH1-100-7) in

medial view (E). F, G, Morphotype D4, right dentary from Coderet E1-0 (CE1-0-29) in medial view (F), tooth of a left dentary from Coderet E1-0 (CE1-0-31) in medial view (G). H-J, Morphotype D5, right dentary from Coderet E1-0 (CE1-0-32) in medial (H) and ventral (I) view, tooth of a left dentary from Coderet E1-0 (CE1-0-33) in medial view (J). The arrowheads mark important diagnostic structures: 1, tricuspid tooth crown; 2, distinct articular facet on symphysis; 3, distinct splenial facet; 4, widely spaced striae; 5, narrowly spaced striae; 6, bicuspid tooth crown; 7, Meckelian canal that opened up at the tip. mk.c, Meckelian canal; spl.ft, splenial facet; sy, symphysis. Scale bars 1 mm. Individual and more detailed figures of the morphotypes can be found in the Supplementary material.

Figure 1.5. Overview of dentary morphotypes D6–D10. A, Morphotype D6, right dentary from Coderet E1-0 (CE1-0-34) in medial view. B-D, Morphotype D7, left dentary from Coderet E1-0 (CE1-0-37) in medial view (B), left dentary from Coderet E1-0 (CE1-0-38) in medial view (C), tooth of a left dentary from Coderet Couche Verte sup 1-25 (CCVsup-14) in medial view (D). E, F, Morphotype D8, right dentary from Coderet H1-100 (CH1-100-9) in medial view (E), tooth of a left dentary from Coderet Couche Verte sup 1-25 (CCVsup-19) in medial view (F). G, Morphotype D9, left dentary from La Colombière (LaC-1) in medial view. H, I, Morphotype D10, right dentary from Roqueprune 2 (Roq2-10) in medial view (H), tooth of the right dentary from Roqueprune 2 (Roq2-10) in lateral view (I). The arrowheads mark important diagnostic structures: 1, weakly developed splenial facet; 2, very distinct tricuspid tooth crown; 3, distinct splenial facet; 4, distinct articular facet on symphysis; 5, widely spaced striae; 6, smaller and less robust posterior-most teeth; 7, narrowly spaced striae; 8, large and globose-like monocuspid tooth. Scale bars 1 mm. Individual and more Figure 1.6. Strict consensus tree of analysis of the complete premaxilla dataset using a value of K =20 based on six most parsimonious trees (MPTs). Length of strict consensus: 1547 steps; CI of strict consensus: 0.180; RI of strict consensus: 0.441. Length of MPTs: 1499 steps; CI of MPTs: 0.186; RI of MPTs: 0.462. Arrowheads indicate the premaxilla mOTUs; daggers show the fossil OTUs; locks mark clades with fulfilled constraining. Black branches, non-crown-lacertids; blue branches, Gallotiinae; green branches, Lacertinae. FV, Fouilles Viret; CC1sup, Coderet Couche 1 sup; CE1-0, Coderet E1-0; CH1-75, Coderet H1-75; CCVsup, Coderet Couche Verte sup 1-25; Roq2, Roqueprune 2; PdF, Pech-du-Fraysse; Cod, Coderet; Cou, Cournon. Strict consensus trees of K = 5 and 12 can be Figure 1.7. Strict consensus tree of analysis of the complete maxilla dataset using a value of K = 20based on more than 100 000 MPTs (overflow). Length of strict consensus: 2269 steps; CI of strict consensus: 0.123; RI of strict consensus: 0.112. Length of MPTs: 1499 steps; CI of MPTs: 0.186; RI of MPTs: 0.455. Arrowheads indicate the maxilla mOTUs; daggers show the fossil OTUs; black locks mark clades with fulfilled constraining, the two grey connected locks represent a single constraint which split up into two clades during analysis. Black branches, non-crown-lacertids; blue branches, Gallotiinae; green branches, Lacertinae. FV, Fouilles Viret; CC1sup, Coderet Couche 1 sup; CE1-0, Coderet E1-0; CH1- 100, Coderet H1-100; CCVsup, Coderet Couche Verte sup 1-25; PdF, Pech-du-Fraysse; Cod, Coderet; Cou, Cournon. Strict consensus trees of K = 5 and 12 can be found in the Supplementary material.

Figure 1.9. Strict consensus tree of the premaxillary cross-regional analysis using a value of K = 20 based on two MPTs. Length of strict consensus and MPTs: 1494 steps; CI of strict consensus and MPTs: 0.187; RI of strict consensus and MPTs: 0.456. Arrowheads indicate the premaxilla (cross-regional) mOTUs; daggers show the fossil OTUs; locks mark clades with fulfilled constraining. Grey dashed-line arrow indicates the position of the cross-regional mOTU when analysing it individually (K = 20). Black branches, non-crown-lacertids; blue branches, Gallotiinae; green branches, Lacertinae. CE1-0, Coderet E1-0; PdF, Pech-du-Fraysse; Cod, Coderet; Cou, Cournon. Strict consensus trees of K = 5 and 12 can be found in the Supplementary material.......41 Figure 1.10. Strict consensus tree of the maxillary cross-regional analysis using a value of K = 20 based on 20 MPTs. Length of strict consensus: 1739 steps; CI of strict consensus: 0.160; RI of strict consensus. Length of MPTs: 1498 steps; CI of MPTs: 0.186; RI of MPTs: 0.452. Arrowheads indicate the maxilla (cross-regional) mOTUs; daggers show the fossil OTUs; locks mark clades with fulfilled constraining. Grey dashed line arrows indicate the position of the (cross-regional) mOTUs when analysing them individually (K = 20). Grey asterisk marks the mOTU which was found at a resolved position when analysed individually, but still as non-lacertid. Black branches, non-crown-lacertids;

blue branches, Gallotiinae; green branches, Lacertinae. CC1sup, Coderet Couche 1 sup; CE1-0, Coderet E1-0; PdF, Pech-du-Fraysse; Cod, Coderet; Cou, Cournon. Strict consensus trees of K = 5Figure 1.11. Single MPT of the dentary cross-regional analysis using K = 20. Length: 1504 steps; CI: 0.186; RI: 0.456. Arrowheads indicate the dentary (cross-regional) mOTUs; daggers show the fossil OTUs; locks mark clades with fulfilled constraining. Grey dashed-line arrows indicate the position of the cross-regional mOTUs when analysing them individually (K = 20). Black branches, non-crown-lacertids; blue branches, Gallotiinae; green branches, Lacertinae. CC1sup, Coderet Couche 1 sup; CE1-0, Coderet E1-0; PdF, Pech-du-Fraysse; Cod, Coderet; Cou, Cournon. Strict Figure 1.12. Distribution pattern and constitution of the possible five lacertid species among the four French localities indicated by black stars. Although the morphotypes P2 and P3 were classified as lacertids, they are not included here, because a referral to one of the five "species" is too speculative. Cod, Coderet; LaC, La Colombière; Roq2, Roqueprune 2; MdGB, Mas de Got B.58 Figure 1.13. Photograph of a (presumably) female specimen of Lacerta agilis from Röhnberg, Figure 1.14. Phylogenetic relationship of the genera Lacerta (orange rectangle) and Timon (blue rectangle) based on molecular data (modified from Kornilios et al., 2020 and Saberi-Pirooz et al.,

Chapter 3

Figure 3.4. Scheme visualising the tested weighting strategies. The six character matrices: main matrix, 45-fossil matrix, 65-fossil matrix, cd matrix, 45-fossil-cd matrix, 65-fossil-cd matrix, were used to test the three weighting strategy approaches: equal weights, implied weights, and extended implied weights. For implied weights and extended implied weights different values for K(5, 10, 20, 10, 20)50, 100, 150, 200) and percentages for the assumed homoplasy for missing entries (25%, 50%, 75%, 100%) were tested. Hence, one analysis under equal weights, 7 under implied weights, and 28 under extended implied weights were preformed which sums up to a total of 36 analyses per matrix......83 Figure 3.5. Scheme summarising the work flow performed for the comparison of weighting strategies. 1. Matrix construction of six character matrices (main matrix, 45-fossil matrix, 65-fossil matrix, cd matrix, 45-fossil-cd matrix, 65-fossil-cd matrix; 2. Phylogenetic analysis using equal weights, implied weights and extended implied weights (see also Figure 3.4) resulting into 36 different weighting strategies applied to each of the six character matrices; 3. Accuracy measurements -including overall tree resolution, clade delimitation, symmetric resampling frequencies, jackknife frequencies, Robinson-Foulds distances, and Distortion Coefficients- that were estimated for the 36 different weighting strategies per character matrix; 4. Final ranking for each of the six character matrices based on the accuracy measurements. Abbreviations: ew, equal weights; iw, implied weights; eiw, extended implied weights; otr, overall tree resolution; cld, clade delimitation; sr, symmetric resampling; jk, jackknife; RF, Robinson-Foulds distances; DC, Distortion Coefficients.

matrix. A, plotted clade delimitation and overall tree resolution; B, plotted symmetric resampling and jackknife frequencies; C, plotted Robinson-Foulds distances and Distortion-Coefficients; D, plotted final score. Abbreviations: RF, Robinson-Foulds distances; DC, Distortion-Coefficients; sr, Figure 3.9. Graphs of the normalised scores of the six tree accuracy measurements and their final score which are plotted against the individual weighting strategies that were applied to the cd matrix. A, plotted clade delimitation and overall tree resolution; B, plotted symmetric resampling and jackknife frequencies; C, plotted Robinson-Foulds distances and Distortion-Coefficients; D, plotted final score. Abbreviations: RF, Robinson-Foulds distances; DC, Distortion-Coefficients; sr, Figure 3.10. Graphs of the normalised scores of the six tree accuracy measurements and their final score which are plotted against the individual weighting strategies that were applied to the 45-fossilcd matrix. A, plotted clade delimitation and overall tree resolution; B, plotted symmetric resampling and jackknife frequencies; C, plotted Robinson-Foulds distances and Distortion-Coefficients; D, plotted final score. Abbreviations: RF, Robinson-Foulds distances; DC, Distortion-Coefficients; sr, symmetric resampling; jk, jackknife; cld, clade delimitation; otr, overall tree resolution.102 Figure 3.11. Graphs of the normalised scores of the six tree accuracy measurements and their final score which are plotted against the individual weighting strategies that were applied to the 65-fossilcd matrix. A, plotted clade delimitation and overall tree resolution; B, plotted symmetric resampling and jackknife frequencies; C, plotted Robinson-Foulds distances and Distortion-Coefficients; D, plotted final score. Abbreviations: RF, Robinson-Foulds distances; DC, Distortion-Coefficients; sr, symmetric resampling; jk, jackknife; cld, clade delimitation; otr, overall tree resolution.105 Figure 3.12. Single MPT resulting from the highest ranked weighting strategy for the main matrix, an extended implied weights analysis with K = 150 and an assumed homoplasy for missing entries of 50%. Length: 2663 steps; adjusted homoplasy: 14.39578; CI: 0.105; RI: 0.520. Displayed here is only the part of the tree including the ingroup OTUs (the complete tree is available in Appendix 11). Black rectangle indicates the Timon-clade......107 Figure 3.13. Single MPT resulting from the highest ranked weighting strategy for the 45-fossil

Figure 3.17. Single MPT resulting from the highest ranked weighting strategy for the 65-fossil-cd matrix, an extended implied weights analysis with K = 200 and an assumed homoplasy for missing entries of 100%. Length: 1553.309 steps; adjusted homoplasy: 5.48032; CI: 0.216; RI: 0.514. Displayed here is only the part of the tree including the ingroup OTUs (the complete tree is available Figure 3.18. Comparison between the most accurate trees resulting from analyses of the main matrix (A) (extended implied weights with K = 150, assumed homoplasy for missing entries of 50%) and the cd matrix (B) (extended implied weights with K = 100, assumed homoplasy for missing entries of 100%). Blue tree branches indicate an identical recovery of structures; grey rectangles highlight more accurately resolved clades compared to the other tree; orange arrowhead point to outgroup intrudes that were not shared with the other tree. Displayed here is only the part of the trees including the ingroup OTUs (the complete trees are available in Appendix 11)......126 Figure 3.19. Comparison between the most accurate trees resulting from analyses of the 45-fossil matrix (A) (extended implied weights with K = 200, assumed homoplasy for missing entries of 100%) and the 45-fossil-cd matrix (B) (extended implied weights with K = 50, assumed homoplasy for missing entries of 100%). Blue tree branches indicate an identical recovery of structures; grey

rectangles highlight more accurately resolved clades compared to the other tree; orange arrowhead

Chapter 4

8. Index of tables

Chapter 1

Table 1.1. List of character types and subtypes used for the quantitative approach of jaw element
comparison with their definitions and examples16
Table 1.2. Occurrences of morphotypes and their abundance given in absolute numbers. P1-P5,
premaxillary morphotypes; M1-M6, maxillary morphotypes; D1-D10, dentary morphotypes; Cod,
Coderet; FV, Fouilles Viret; CC1sup, Coderet Couche 1 sup; CCVsup, Coderet Couche Verte sup 1
-25; CE1-0, Coderet E1-0; CH1-100, Coderet H1-100; CH1-75, Coderet H1-75; LaC, La
Colombière; Roq2, Roqueprune 2; MdGB, Mas de Got B19
Table 1.3. Distribution of character types coding for premaxillae, maxillae, and dentaries. The
distribution is given in absolute numbers and relative percentages in brackets (rounded to the nearest
integer). morph, morphometric; c/m, countable/measurable; shape, shape describing

Chapter 2

Chapter 3

Table 3.3. Final ranking of the 36 different weighting strategies applied to the main matrix. Cell colours indicate low accuracy (red shades) to high accuracy (green shades) of the individual accuracy measurements and their final score. Abbreviations: RF, Robinson-Foulds distances; DC, Distortion-Coefficients; sr, symmetric resampling; jk, jackknife; cld, clade delimitation; otr, overall tree resolution; iw, implied weights; ew, equal weights (for the non-normalised accuracy measurement values see Appendix 10).

Table 3.7. Final ranking of the 36 different weighting strategies applied to the 45-fossil-cd matrix. Cell colours indicate low accuracy (red shades) to high accuracy (green shades) of the individual accuracy measurements and their final score. Abbreviations: RF, Robinson-Foulds distances; DC,

9. Appendices

All appendices are also available via Figshare under the following private link:

https://figshare.com/s/c4f60604a2a013f6a86d

Appendix 1

From Wencker et al. 2021: List of newly inserted characters, including their states and sources.

No.	New character	Source (and original character numbers)
12	Premaxilla, tooth-bearing portion: curvature, anteroposterior length to transverse width: <0.2 (wide) (0); 0.2-0.4 (intermediate) (1); >0.4 (narrow) (2).	LCMW, pers. obs., 2018
36	Premaxilla, tooth row, shape: U-shaped (0); V- shaped (1).	LCMW, pers. obs., 2018
40	Premaxilla, second pair of ethmoidal foramina: absent (0); present (1).	LCMW, pers. obs., 2019
41	Premaxilla, ascending nasal process, posterodorsal end, shape in anterior view: pointed (0); widely rounded (1).	Barahona & Barbadillo (1997; C3.1), modified (split in two) by Villa et al. (2017; C23)
47	Premaxilla, ascending nasal process, length of articulation with the nasals: less than half nasal length (0); more than halfway to frontal between nasals (1).	modified after Gauthier et al. (2012; C10; exclusion of character state (2): nearly to, or articulates with frontals); Quadros et al. (2018; C3)
48	Premaxilla, ascending nasal process, constriction at the base: absent (0); present (1).	wording modified from Quadros et al. (2018; C4); Brizuela (2010; C3)
62	Maxilla, anteromedial premaxillary process lying between vomers and premaxilla: absent, vomers contact premaxilla (0); present, vomers do not contact premaxilla (1).	Estes et al. (1988; C12); Denton and O'Neill (1995; C4); Nydam and Cifelli (2002; C4); Nydam et al. (2007; C4); Conrad (2008; C25); Quadros et al. (2018; C13)
73	Nasals, anterior width: exceeds nasofrontal joint width (0); is subequal to nasofrontal joint width (1); less than anterior frontal width (2).	Gauthier et al. (2012; C18); Quadros et al. (2018; C6)
74	Nasal, anterior border: nasolateral process present, forming the posterior border and part of the labial border of the external nares (0); nasolateral process absent (1).	Quadros et al. (2018; C7); modified from Conrad (2008; C22); Gauthier et al. (2012; C22)

No.	New character	Source (and original character numbers)
77	Dermal skull bone ornamentation, frontal/parietal: absent, dermal skull roof smooth (0); present over dorsum (1); present on jugal postorbital bar (2).	modified after Quadros et al. (2018; C17; wording modified and exclusion of state (1): lightly rugose about frontoparietal suture); modified from Estes et al. (1988; C129); Conrad (2008; C10); Gauthier et al. (2012; C572)
93	Postorbital, overlapping of squamosal: dorsomedially as slender tapering rod attached superficially (0); dorsally (1); postorbital in long V- shaped trough dorsally and then rotating dorsolaterally posteriorly (2); squamosal lies in trough beneath postorbital (3).	modified from Gauthier et al. (2012; C78; exclusion of state (0): laterally into V-shaped recess in squamosal); Arnold (1998); Quadros et al. (2018; C35)
107	Quadrate, tympanic crest shape: straight or vertically developed (0); curved, forming "C" on outer line (1).	wording modified after Quadros et al. (2018; C78); modified from Brizuela (2010; C63)
109	Squamosal, base of temporal ramus: diverges from parietal (0); base lies against parietal (1).	Quadros et al. (2018; C46); Gauthier et al. (2012; C162)
110	Supratemporal position on parietal: partly ventral (0); partly ventrolateral (1); all lateral (2); dorsolateral (3).	De Queiroz (1987); Gauthier et al. (2012; C170)
127	Parietal, parasagittal crest strongly developed on the dorsolateral surface for the insertion of the adductor mandible musculature: absent (0); present (1).	Quadros et al. (2018; C22); modified from Denton and O'Neill (1995; C10); Nydam and Cifelli (2002; C10); Nydam et al. (2007; C10); Conrad (2008; C75); Gauthier et al. (2012; C9)
128	Epipterygoid-parietal contact: absent (0); overlaps parietal temporal muscle origin parietal downgrowths (1).	Gauthier et al. (2012; C294); Quadros et al. (2018; C84)
155	Dentary, subdental ridge, shape: straight (0); concave (1).	Bailon et al., 2014
159	Dentary, Meckelian canal, shape: triangular (0), tubular (1).	ET, pers. obs., 2018
160	Dentary, orientation of teeth at the anterior tip: upright (0); tilted anteriorly or procumbent (1).	LCMW, pers. obs., 2019
175	Coronoid-surangular articulation: coronoid restricted to medial aspect of mandible (0); coronoid extends onto dorsal surface of surangular (1); coronoid arches over dorsal margin of mandible to reach lateral surface of surangular (2).	Gauthier et al. (2012; C390); Quadros et al. (2018; C113)
184	Teeth, premaxillary, crown morphology (if	LCMW, pers. obs., 2018

No.	New character	Source (and original character numbers)
	monocuspid): fang-like/pointed (0); rounded (1).	
185	Teeth, premaxilla, median tooth: absent (0); present (1).	wording modified from Scanlon (1996; C4); Lee (1998; C154); Gauthier et al. (2012; C413)
186	Teeth, premaxilla, median tooth: same size as neighbouring premaxillary teeth (0); enlarged (1).	Lee (1998; C155); modified after Gauthier et al. (2012; C414; wording modified and exclusion of state (2) greatly enlarged median premaxillary tooth)
190	Teeth, maxilla and dentary, differences in tooth robustness: (0) absent to minimal; present not more than 50% different in robustness (1); (present, 50% or more difference in robustness (2).	LCMW, pers. obs., 2019

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Appendix 2

(Available also at https://figshare.com/s/c4f60604a2a013f6a86d)

From Wencker *et al.* 2021: Positions of premaxilla, maxilla, and dentary mOTUs in the trees with the complete and reduced datasets, and the analyses with the stable mOTUs only for each of the three K-values. Completeness scores for the individual mOTUs are given in brackets behind the taxon name. Abbreviations: FV: Fouilles Viret; CC1sup: Coderet Couche 1 sup; CE1-0: Coderet E1-0; CH1-100: Coderet H1-100; CH1-75: Coderet H1-75; CCVsup: Coderet Couche Verte sup 1-25; LaC: La Colombière; Roq2: Roqueprune 2; MdGB: Mas de Got B; PdF: Pech-du-Fraysse; Cod: Coderet; T+L: *Timon* + *Lacerta*.

mOTU	Analysis with a K-value of 5			Analysis with a K-value of 12			Analysis with a K-value of 20		
	complete	reduced	stable	complete	reduced	stable	complete	reduced	stable
P1 FV (66%)	Lacertoidea (clade with Amphisbaenia)	Lacertoidea (clade with Amphisbaenia)	Lacertoidea (clade with Amphisbaenia)	polytomy with D. croizeti	Anguimorpha	Anguimorpha	polytomy with D. croizeti	Anguimorpha	Anguimorpha
P1 CC1sup (72%)	Lacertoidea (clade with Amphisbaenia)	Lacertoidea (clade with Amphisbaenia)	excluded	polytomy with D. croizeti	Anguimorpha	excluded	polytomy with D. croizeti	Anguimorpha	excluded
P1 CE1-0 (75%)	Lacertoidea (clade with Amphisbaenia)	Lacertoidea (clade with Amphisbaenia)	Lacertoidea (clade with Amphisbaenia)	polytomy with D. croizeti	Anguimorpha	Anguimorpha	polytomy with D. croizeti	Anguimorpha	Anguimorpha
P1 CCVsup (59%)	Lacertoidea	Anguimorpha; Lacertoidea	Lacertoidea	-	Anguimorpha	excluded	-	Anguimorpha	excluded
P2 CC1sup (72%)	Lacertoidea (sister/polytomy to/with <i>S</i> .	Lacertoidea (sister/polytomy to/with <i>S</i> .	Lacertoidea (sister/polytomy to/with <i>S</i> .	clade with <i>B</i> . <i>major</i>	Scincoidea	Scincoidea	clade with <i>B</i> . <i>major</i>	Scincoidea	Scincoidea

mOTU	Analysis with a K-value of 5			Analysis with a K-value of 12			Analysis with a K-value of 20		
	complete	reduced	stable	complete	reduced	stable	complete	reduced	stable
	<i>merianae</i> + Lacertidae)	<i>merianae</i> + Lacertidae)	<i>merianae</i> + Lacertidae)						
P2 CE1-0 (75%)	Lacertoidea (sister/polytomy to/with <i>S.</i> <i>merianae</i> + Lacertidae)	Lacertoidea (sister/polytomy to/with <i>S.</i> <i>merianae</i> + Lacertidae)	Lacertoidea (sister/polytomy to/with <i>S.</i> <i>merianae</i> + Lacertidae)	clade with <i>B.</i> <i>major</i>	Scincoidea	Scincoidea	clade with <i>B.</i> <i>major</i>	Scincoidea	Scincoidea
P3 CE1-0 (69%)	Lacertoidea (sister to/polytomy with <i>S. merianae</i> + Lacertidae)	Lacertoidea (sister to/polytomy with <i>S. merianae</i> + Lacertidae)	Lacertoidea (sister to/polytomy with <i>S. merianae</i> + Lacertidae)	clade with <i>B</i> . <i>major</i>	Scincoidea	Scincoidea	clade with <i>B.</i> <i>major</i>	Scincoidea	Scincoidea
P3 Roq2 (59%)	Scincoidea (sister to <i>B. major</i>)	Scincoidea (sister to <i>B. major</i>)	Scincoidea (sister to <i>B. major</i>)	sister to <i>B.</i> major	Scincoidea (sister to <i>B. major</i>)	Scincoidea (sister to B. major)	sister to <i>B.</i> major	Scincoidea (sister to <i>B. major</i>)	Scincoidea (sister to <i>B.</i> <i>major</i>)
P4 CE1-0 (59%)	Anguimorpha (sister to <i>A.</i> <i>veronensis</i>)	Anguimorpha (sister to A. veronensis)	Anguimorpha (sister to A. veronensis)	sister to A. veronensis	Anguimorpha (sister to A. veronensis)	Anguimorpha (sister to A. veronensis)	sister to A. veronensis	Anguimorpha (sister to A. veronensis)	Anguimorpha (sister to <i>A</i> . <i>veronensis</i>)
P5 FV (66%)	Lacertoidea (clade with Amphisbaenia)	Anguimorpha; Lacertoidea (clade with Amphisbaenia)	excluded	clade with D. croizeti	Anguimorpha	Anguimorpha	clade with <i>D.</i> croizeti	Anguimorpha	Anguimorpha

mOTU	Analysis with a K-value of 5			Analysis with a K-value of 12			Analysis with a K-value of 20		
more	complete	reduced	stable	complete	reduced	stable	complete	reduced	stable
P5 CH1-75 (75%)	Lacertoidea (clade with Amphisbaenia)	Anguimorpha; Lacertoidea (clade with Amphisbaenia)	Lacertoidea (clade with Amphisbaenia)	clade with D. croizeti	Anguimorpha	Anguimorpha	clade with <i>D.</i> <i>croizeti</i>	Anguimorpha	Anguimorpha
M1 FV (29%)	-	Lacertidae	excluded	-	Gallotiinae	excluded	-	Gallotiinae	excluded
M1 CC1sup (36%)	-	Gallotiinae	Gallotiinae	-	Gallotiinae	Gallotiinae	-	Gallotiinae	Gallotiinae
M1 CE1-0 (61%)	-	Lacertidae	sister to Gallotiinae	-	Lacertidae	Lacertidae	-	Lacertidae	Lacertidae
M1 CH1-100 (25%)	-	Podarcis	excluded	-	Podarcis	excluded	-	Podarcis	excluded
M1 CCVsup (39%)	-	Podarcis	sister to Gallotiinae	-	Lacertidae	excluded	-	Lacertidae	excluded
M2 CC1sup (36%)	sister to <i>L. pouiti</i>	Gallotiinae	Gallotiinae	-	Gallotiinae	excluded	-	Gallotiinae	excluded
M3 CC1sup (50%)	polytomy with " <i>L</i> . " <i>filholi</i> (PdF)	Gallotiinae	sister to Gallotiinae	-	Lacertidae	Lacertidae	-	Lacertidae	Lacertidae
M3 CH1-100 (32%)	polytomy with <i>"L." filholi</i> (PdF)	Lacertoidea (sister "L." <i>filholi</i> (PdF))	sister to Gallotiinae	-	Lacertoidea (sister "L." <i>fìlholi</i> (PdF))	Lacertidae	-	Gallotiinae	Lacertidae

mOTU	Analysis with a K-value of 5			Analysis with a K-value of 12			Analysis with a K-value of 20		
	complete	reduced	stable	complete	reduced	stable	complete	reduced	stable
M4 CC1sup (32%)	polytomy with " <i>L</i> . " <i>filholi</i> (PdF)	Gallotiinae	sister to Gallotiinae	-	Lacertidae	excluded	-	Lacertidae	excluded
M4 CE1-0 (36%)	polytomy with " <i>L</i> . " <i>filholi</i> (PdF)	Lacertidae	sister to Gallotiinae	-	Lacertidae	Lacertidae	-	Lacertidae	Lacertidae
M4 CH1-100 (32%)	polytomy with " <i>L</i> . " <i>filholi</i> (PdF)	Lacertidae	sister to Gallotiinae	-	Lacertidae	excluded	-	Lacertidae	excluded
M4 CCVsup (25%)	-	Lacertoidea	excluded	-	Lacertoidea	excluded	-	Lacertoidea	excluded
M5 CE1-0 (50%)	-	-	Lacertoidea (sister to S. <i>merianae</i> + Lacertidae)	-	-	Lacertoidea (sister to <i>S. merianae</i> + Lacertidae)	-	-	Lacertoidea (sister to <i>S. merianae</i> + Lacertidae)
M6 CE1-0 (25%)	-	-	excluded	-	-	excluded	-	-	excluded
D1 FV (75%)	-	Lacerta	Podarcis	-	Lacerta	Podarcis	-	Lacerta	Podarcis
D1 CC1sup (75%)	-	Lacerta	Podarcis	-	Gallotiinae; Lacerta	Podarcis	-	Gallotiinae; <i>Lacerta</i>	Podarcis
D1 CE1-0 (63%)	-	Gallotiinae; <i>Lacerta</i>	Podarcis	-	Gallotiinae	Podarcis	-	Gallotiinae	Podarcis

mOTU	Analysis with a K-value of 5			Analysis with a K-value of 12			Analysis with a K-value of 20		
	complete	reduced	stable	complete	reduced	stable	complete	reduced	stable
D2 FV (71%)	-	Lacerta	Podarcis	-	Lacerta	Podarcis	-	Lacerta	Podarcis
D2 CC1sup (79%)	-	Lacerta	Podarcis	-	Lacerta	Podarcis	-	Lacerta	Podarcis
D2 CE1-0 (75%)	-	Gallotiinae; Podarcis	Podarcis	-	Gallotiinae; sister to <i>T</i> + <i>L</i>	Podarcis	-	Gallotiinae; sister to <i>T</i> + <i>L</i>	Podarcis
D2 CH1-100 (75%)	-	Lacertidae	Podarcis	-	Lacertidae	Podarcis	-	Gallotiinae	Podarcis
D2 CH1-75 (46%)	-	Lacertoidea	excluded	-	Lacertoidea	excluded	-	Lacertoidea	excluded
D2 CCVsup (63%)	-	Lacerta	Podarcis	-	Lacerta	Podarcis	-	Lacerta	Podarcis
D3 CC1sup (75%)	-	Lacerta	Podarcis	-	Lacerta	Podarcis	-	Gallotiinae; Lacerta	Podarcis
D3 CH1-100 (75%)	-	Lacertoidea	Podarcis	-	Lacertoidea	Podarcis	-	Lacertoidea	Podarcis
D3 CH1-75 (42%)	-	Lacertoidea	excluded	-	Lacertoidea	excluded	-	Lacertoidea	Excluded
D4 CE1-0 (79%)	-	Gallotiinae; Podarcis	Podarcis	-	Gallotiinae; sister to <i>T</i> + <i>L</i>	Podarcis	-	Gallotiinae; sister to <i>T</i> + <i>L</i>	Podarcis
D4 CH1-75 (50%)	-	Lacertoidea	excluded	-	Lacertoidea	excluded	-	Lacertoidea	excluded

mOTU	Analysis with a K-value of 5			Analysis with a K	C-value of 12		Analysis with a K-value of 20		
	complete	reduced	stable	complete	reduced	stable	complete	reduced	stable
D4 CCVsup (54%)	-	Lacertoidea; Scincoidea	excluded	-	Lacertoidea; Scincoidea	excluded	-	Lacertoidea; Scincoidea	excluded
D4 MdGB (75%)	-	Podarcis	Podarcis	-	Lacertoidea	Podarcis	-	sister to T+L	Podarcis
D5 CE1-0 (42%)	Iberolacerta (sister to I. cyreni)								
D6 CE1-0 (63%)	Algyroides (sister to A. nigropunctatus)								
D7 CE1-0 (75%)	-	Lacerta	Podarcis	-	Lacerta	Podarcis	-	Lacerta	Podarcis
D7 CCVsup (71%)	-	Lacertoidea	Podarcis	-	Lacertoidea	Podarcis	-	Lacertoidea	Podarcis
D8 CH1-100 (75%)	-	clade with Gallotiinae	Gallotiinae	-	clade with Gallotiinae	Gallotiinae	-	clade with Gallotiinae	sister to Timon
D8 CCVsup (38%)	-	Lacertoidea	excluded	-	Lacertoidea	excluded	-	Lacertoidea	excluded
D8 Roq2 (38%)	-	-	excluded	-	-	excluded	-	-	excluded

mOTU	Analysis with a K-value of 5			Analysis with a K-value of 12			Analysis with a K-value of 20		
	complete	reduced	stable	complete	reduced	stable	complete	reduced	stable
D9 LaC (67%)	-	Podarcis	Podarcis	sister to P. tiliguerta	Podarcis; sister to T+L	Podarcis	sister to P. tiliguerta	Gallotiinae; sister to <i>T+L;</i> <i>Podarcis</i> ;	Podarcis
D9 Roq2 (58%)	-	Podarcis	excluded	-	sister to T+L	excluded	-	Gallotiinae; sister to <i>T</i> + <i>L</i>	excluded
D10 Roq2 (54%)	clade with Amphisbaenia	clade with Amphisbaenia	clade with Amphisbaenia	clade with Amphisbaenia	clade with Amphisbaenia	clade with Amphisbaenia	clade with Amphisbaenia	clade with Amphisbaenia	clade with Amphisbaenia

(Available also at https://figshare.com/s/c4f60604a2a013f6a86d)

List of character changes

New characters

14. Nasal, length of nasal relative to length of articulation facet for premaxilla: less than one fourth (less than 0.25) (0); one-fourth and more but less than half (0.25-0.49) (1); half or more (more than 0.5) (2).

16. Nasal, facies dorsalis, outline shape, anterior edge relative to posterior edge: diverging anteriorly (more than 1.05) (0); subquadrangular to subrectangular (0.95 1.05) (1); converging anteriorly (less than 0.95) (2).

17. Vomer, maximum length in relation to maximum length of maxilla: shorter than maxilla (less than 1.0) (0); equal or longer than maxilla (1.0 or more) (1).

19. Frontal, anterior process, dorsoventral depth: less than 38% (0); 38-55% (1); 56-71% (2); 72-87% (3); more than 87% (4). (Gauthier, 1982); character 39 in Gauthier *et al.* (2012); modified to avoid gaps between states. Note: a CT scan is needed to apply the character.

26. Dentary, length compared to length of the rest of exposed lower jaw: equal to shorter (1.0 or less) (0); longer (more than 1.0) (1). Character 37 in Čerňanský et al. (2016); modified.

54. Premaxilla, ascending nasal process, thickness, in lateral view: thickness is retained from base until midway (0); thickness is gradually decreasing from base until posterior end (1).

55. Premaxilla, ascending nasal process, dermal ornamentation: weak to absent (0); present and well developed (1).

67. Maxilla, facial process, incisura nasalis: absent (0); present (1). (Rauscher 1992, p. 87).

82. Nasals, dermal ornamentation: weak to absent (0); present and well developed (1).

84. Prefrontal, dermal ornamentation: weak to absent (0); present and well developed (1).

93. Frontal, dermal ornamentation: weak to absent (0); present and well developed (1).

97. Postfrontal, dermal ornamentation: weak to absent (0); present and well developed (1).

101. Postorbital, dermal ornamentation: weak to absent (0); present and well developed (1).

108. Jugal, dermal ornamentation: weak to absent (0); present and well developed (1).

117. Squamosal, ascending process: present (0); absent (1). (Gauthier, 1982); character 165 in Gauthier *et al.* (2012).

122. Parietal, dorsal ornamentation: weak to absent (0); present and well developed (1).

151. Vomer, ventral longitudinal ridges: absent (0); present (1). Character 222 in Gauthier *et al.*(2012); modified to adapt to restricted taxon sampling.

Modified characters

28. Presacral vertebrae, width across postzygapophyses to greatest length: 0.7 or less (0); 0.71-0.89 (1); 0.9 or greater (2). (Barbadillo and Sanz, 1983); character 11 in Villa *et al.* (2017); character 22 in Tschopp *et al.* (2018), Wencker *et al.* (2021); modified to close gap between states.

80. Nasal, anterior border, nasolateral process: present (0); absent (1). Character 22 in Conrad
(2008), Gauthier *et al.* (2012); character 7 in Quadros *et al.* (2018); character 74 in Wencker *et al.*(2021); wording modified.

91. Frontal, prefrontal shield, impression (if present), shape: connected anteromedially (0); medially separated (1). Character 75 in Tschopp *et al.* (2018); character 84 in Wencker *et al.* (2021); wording modified.

103. Jugal, quadratojugal process (if present), shape: acute bony process (0); forms nearly a 90° angle (1). Character 84 in Tschopp *et al.* (2018); character 95 in Wencker *et al.* (2021); wording modified.

123. Parietal, dorsal ornamentation (if present): irregular (0); symmetrically subdivided by distinct grooves (1). (Rauscher 1992); character 70 in Villa *et al.* (2017); character 100 in Tschopp *et al.* (2018); character 114 in Wencker et al. (2021); wording modified.

128. Parietal, posterior margin, midline projection (if present): single (0); bifid (1). (Rauscher 1992, fig. 23.3); character 97 in Gauthier *et al.* (2012); character 74 in Villa *et al.* (2017), wording modified; character 105 in Tschopp *et al.* (2018); character 119 in Wencker *et al.* (2021); wording modified.

146. Sphenoid, ventral surface, depression close to base of basipterygoid processes (if present), shape: rounded (0); longitudinal trough (1). Character 122 in Tschopp *et al.* (2018); character 138 in Wencker *et al.* (2021); wording modified.

167. Dentary, tooth row, orientation in lateral view: tooth apices are on same level, forming nearly straight line (0); tooth apices form concave to S-shaped line with the distal most teeth reaching significantly dorsal to more mesial teeth (1). Character 143 in Tschopp *et al.* (2018); character 162 in Wencker *et al.* (2021), wording modified.

228. Postaxial, cervical intercentra, position: articulate with anterior element (0); between anterior and posterior centra (1); articulate only with more posterior element (2). Character 97-98 in Estes *et al.* (1988); characters 46 in Müller (2001); character 66 in Al-Hassawi (2004); modified after Al-Hassawi (2004) by reducing number of character states.

237. Caudal, autotomic vertebrae, transverse processes on posterior portion (if present), length compared to anterior process: shorter (0); longer (1). (Etheridge, 1967); character 12 (fig. 4) in Arnold (1973); character 31 (fig.11) in Arnold (1989); character 19 in Arnold *et al.* (2007); character 151in Villa *et al.* (2017), modified after Arnold *et al.* (2007) by splitting the character; character 208 in Tschopp *et al.* (2018); character 232 in Wencker *et al.* (2021); wording modified.

244. Sternal fontanelle (if present), shape: heart-shaped (0); oval (1). (Siebenrock, 1894); character 10 (fig. 3) in Arnold (1973); character 26 (fig. 10) in Arnold (1989); character 17 in Arnold *et al.* (2007); character 154 in Villa *et al.* (2017), modified after Arnold *et al.* (2007) by reversing polarity; character 215 in Tschopp *et al.* (2018); character 239 in Wencker *et al.* (2021); wording modified.

Deleted characters

Premaxilla, ascending nasal process, length of articulation with the nasals relative to length of ascending nasal process: less than or half nasal length (0); more than halfway to frontal between nasals (1). Character 10 in Gauthier *et al.* (2012); character 3 in Quadros *et al.* (2018); character 47 in Wencker *et al.* (2021). This character was replaced by character 14.

Premaxilla-maxilla contact: continuous (0); incomplete with opening between premaxillary processes of maxilla (1). Character 30 in Villa *et al.* (2017); character 46 in Tschopp *et al.* (2018); character 51 in Wencker *et al.* (2021).

Nasals, anterior width: exceeds nasofrontal joint width (0); width is subequal to nasofrontal joint width (1); width less than nasofrontal joint width (2). Character 18 in Gauthier *et al.* (2012); character 6 in Quadros *et al.* (2018); character 73 in Wencker *et al.* (2021), modified after Gauthier *et al.* (2012) to have the same reference point for all character states. This character was replaced by character 16.

Dermal skull bone, ornamentation: absent, dermal skull roof smooth (0); present (1). Character 129 in Estes *et al.* (1988); character 10 in Conrad (2008); character 572 in Gauthier *et al.* (2012); character 17 in Quadros *et al.* (2018); character 77 in Wencker *et al.* (2021). This character was replaced by characters 55, 82, 84, 93, 97, 101, 108, and 122.

Postorbital, anterolateral process, ventral extension compared to level of quadrate cephalic condyle: ventral (0); same level (1); dorsal (2). (Estes *et al.*, 1988); character 82 in *Gauthier et al.* (2012); character 82 in Tschopp *et al.* (2018), wording modified; character 92 in Wencker *et al.* (2021).

Postorbital, overlapping of squamosal: dorsomedially as slender tapering rod attached superficially (0); dorsally (1); postorbital in long V-shaped trough dorsally and then rotating dorsolaterally (2); posteriorly squamosal lies in trough beneath postorbital (3). (Arnold, 1998); character 78 in Gauthier *et al.* (2012); character 35 in Quadros *et al.* (2018); character 93 in Wencker *et al.* (2021), modified after Gauthier *et al.* (2012) to adapt to taxon sampling.

Quadrate, tympanic crest, shape: straight or vertically developed (0); curved, forming a "C" on outer line. Character 63 in Brizuela (2010); character 78 in Quadros *et al.* (2018), modified; character 107 in Wencker *et al.* (2021), wording modified after Quadros *et al.* (2018).

Squamosal, base of temporal ramus: diverges from parietal (0); base lies against parietal (1). Character 162 in Gauthier *et al.* (2012); character 46 in Quadros *et al.* (2018); character 109 in Wencker *et al.* (2021). This character was replaced by character 117.

Epipterygoid-parietal contact: absent (0); overlaps parietal temporal muscle origin (parietal downgrowths) (1). Character 294 in Gauthier *et al.* (2012); character 84 in Quadros *et al.* (2018); character 128 in Wencker *et al.* (2021).

Prootic-epipterygoid contact: absent (0); present, alar process of prootic reaches dorsal end of epipterygoid (1). Character 27 in Barahona and Barbadillo (1997); character 91 Villa *et al.* (2017), wording modified; character 127 in Tschopp *et al.* (2018); character 143 in Wencker *et al.* (2021).

Palatine-ectopterygoid contact: absent (0); present, anterolateral process of ectopterygoid reaches posterior extension of lateral process of palatine (1). Character 24 in Barahona and Barbadillo

(1997); character 93 in Villa *et al.* (2017), wording modified; character 129 in Tschopp *et al.* (2018); character 145 in Wencker *et al.* (2021).

Pterygoid, palatine processes, orientation in articulated skulls: parallel (0); convergent (1). Character 26 in Barahona and Barbadillo (1997); character 95 in Villa *et al.* (2017), wording modified; character 131 in Tschopp *et al.* (2018); character 147 in Wencker *et al.* (2021).

Dentary, orientation of teeth at the anterior tip: upright (0); tilted anteriorly or procumbent (1). Character 160 in Wencker *et al.* (2021).

Dentary, angular process, posterior extension: reaches below or exceeds coronoid apex (0); restricted anterior to coronoid apex (1); restricted anterior entire coronoid bone (2). (Gauthier, 1982); character 368 in Gauthier *et al.* (2012); character 39 in Čerňanský *et al.* (2015); character 149 in Tschopp *et al.* (2018); character 168 in Wencker *et al.* (2021).

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(Available also at https://figshare.com/s/c4f60604a2a013f6a86d)

Complete list of characters with indications on the character type and partition.

Abbreviations: QN, quantitative; QL, qualitative; C, cranial; D, dental; P, postcranial.

Quantitative characters

1. Premaxilla, number of teeth: 7 or less (0), 8 or more (1). Character 3.2 in Barahona & Barbadillo 1997; character 1 in Villa et al. (2017), Tschopp et al. (2018), Wencker et al. (2021). Character affiliation: QN-D

2. Maxilla, number of labial foramina, including only larger ones and the smaller ones which are on the same level with them: 6 or less (0); more than 6 (1). (Rauscher 1992); character 2 in Villa et al. (2017), Tschopp et al. (2018), Wencker et al. (2021, wording modified). Character affiliation: QN-

3. Teeth, crown complexity, maximum number of cusps in single tooth: 4 or more (0); 3 (1); 2 or less (2). (Müller, 1996); character 3 in Tschopp et al. (2018), Wencker et al. (2021). Character affiliation: QN-D

4. Teeth, number of maxillary teeth: less than 16 (0); 16 or more (1). (Rauscher, 1992); character 6 in Villa et al. (2017); character 4 in Tschopp et al. (2018), Wencker et al. (2021). Character affiliation: QN-D

5. Teeth, number of dentary teeth: less than 13 (0); 13 or more (1). (Rauscher, 1992); character 7 in Villa et al. (2017); character 5 in Tschopp et al. (2018), Wencker et al. (2021). Character affiliation: QN-D

6. Presacral vertebrae, number: less than 27 (0); 27 or more (1). Character 8 in Arnold (1973); characters 104-106 in Estes et al. (1988); character 48 in Müller (2001); character 13 in Arnold et al. (2007); character 8 in Villa et al. (2017, state boundary was adapted to taxon sampling); character 6 in Tschopp et al. (2018), Wencker et al. (2021). Character affiliation: QN-P

7. Presacral vertebrae, number of posterior elements with short ribs: 5 or fewer (0); 6 (1); 7 or more (2). (Siebenrock, 1894); (Arnold, 1989); character 14 in Arnold et al. (2007); character 9 in Villa et al. (2017, modified); character 7 in Tschopp et al. (2018), Wencker et al. (2021). Character affiliation: QN-P

8. Cervical intercentra, number: less than 7 (0); 7 or more (1). (Al-Hassawi, 2004); character 8 in Tschopp et al. (2018), Wencker et al. (2021). Character affiliation: QN-P

9. Xiphisternal ribs, number: 2 (0); 3 (1). (Arribas, 1998); character 15 in Villa et al. (2017). Character affiliation: QN-P

10. Anterior caudal vertebrae, number of non-autotomic elements: 4 or less (0); 5 (1); 6 (2); 7 or more (3). (Arnold, 1973); character 17 in Villa et al. (2017), modified; character 9 in Tschopp et al. (2018), Wencker et al. (2021). Character affiliation: QN-P

11. Premaxilla, ascending nasal process, cross section at base minimum, transverse width to anteroposterior length ratio: more than 1.1 (0); 0.9-1.1 (1); less than 0.9 (2). (Rauscher, 1992); character 22 in Villa et al. (2017, modified); character 10 in Tschopp et al. (2018), Wencker et al. (2021). Character affiliation: QN-C

12. Premaxilla, angle of ascending nasal process to horizontal plane: more than 70 (0); 50-70 (1); less than 50 (2). Character 5 in Čerňanský al. (2015); character 11 in Tschopp et al. (2018, wording modified), Wencker et al. (2021). Character affiliation: QN-C

13. Premaxilla, tooth-bearing portion, curvature, maximum anteroposterior length to maximum transverse width: wide, less than 0.2 (0); intermediate, 0.2-0.4 (1); narrow, more than 0.4 (2). Character 12 in Wencker et al. (2021). Character affiliation: QN-C

14. Nasal, length of nasal relative to length of articulation facet for premaxilla: less than one fourth (less than 0.25) (0); one-fourth and more but less than half (0.25-0.49) (1); half or more (more than 0.5) (2). Character affiliation: QN-C

15. Nasal, length relative to frontal length: less than 0.40 (0); 0.40-1.00 (1); more than 1.00 (2).
Character 17 in Čerňanský et al. (2015); character 12 in Tschopp et al. (2018, modified); character 13 in Wencker et al. (2021). Character affiliation: QN-C

16. Nasal, facies dorsalis, outline shape, anterior edge relative to posterior edge: diverging anteriorly (more than 1.05) (0); subquadrangular to subrectangular (0.95 1.05) (1); converging anteriorly (less than 0.95) (2). Character affiliation: QN-C

17. Vomer, maximum length in relation to maximum length of maxilla: shorter than maxilla (less than 1.0) (0); equal or longer than maxilla (1.0 or more) (1). Character affiliation: QN-C

18. Frontal, dorsal surface, anteroposterior length of frontoparietal shield to anteroposterior length of ornamented portion: 0.40 or less (0); more than 0.40 (1). (Čerňanský, 2010); character 24 in

Čerňanský et al. (2015); character 13 in Tschopp et al. (2018, modified); character 14 in Wencker et al. (2021). Character affiliation: QN-C

19. Frontal, anterior process, dorsoventral depth: less than 38% (0); 38-55% (1); 56-71% (2); 72-87% (3); more than 87% (4). (Gauthier, 1982); character 39 in Gauthier et al. (2012); modified to avoid gaps between states. Note: a CT scan is needed to apply the character. Character affiliation: QN-C

20. Frontal, transverse width, posterior end compared to midlength width: narrow, less than 1.8 (0); intermediate, 1.8-3.0 (1); widely expanded, more than 3.0 (2). (Estes *et al.*, 1988); character 49 in Gauthier et al. (2012); character 52 in Villa et al. (2017, quantitative boundaries were added); character 14 in Tschopp et al. (2018); character 15 in Wencker et al. (2021). Character affiliation: **QN-C**

21. Frontals, anterior transverse width, minimum transverse width: more than 1.20 (0); 1.20 or less (1). (Rauscher, 1992); (Barahona and Barbadillo, 1997); character 51 Villa et al. (2017, quantitative state boundaries were added); character 15 in Tschopp et al. (2018); character 16 in Wencker et al. (2021). Character affiliation: QN-C

22. Postorbital, length of contact with squamosal compared to total anteroposterior length: more than 0.41 (0); 0.41 or less (1). (Arribas, 1998); character 4 in Villa et al. (2017); character 17 in Tschopp et al. (2018); character 17 in Wencker et al. (2021). Character affiliation: QN-C

23. Parietal, interparietal shield, length compared to occipital shield: less than 0.95 (0); 0.95-1.05 (1); more than 1.05 (2). Character 30 in Čerňanský et al. (2015); character 19 in Tschopp et al. (2018, modified); character 18 in Wencker et al. (2021). Character affiliation: QN-C

24. Parietal, width of occipital shield compared to posterior width of ornamented portion: narrow, less than 0.40 (0); intermediate, 0.40-0.60 (1); wide, more than 0.60 (2). Character 2.6 in Barahona & Barbadillo (1997, fig. 2); character 71 in Villa et al. (2017); character 20 in Tschopp et al. (2018, modified); character 19 in Wencker et al. (2021). Character affiliation: QN-C

25. Parietal, length to width of ornamented part of dorsal surface: longer (0); equal to wider (1). Character 9 in Arnold (1989); character 5 in Villa et al. (2017, wording modified); character 18 in Tschopp et al. (2018); character 20 in Wencker et al. (2021). Character affiliation: QN-C

26. Dentary, length compared to length of the rest of exposed lower jaw: equal to shorter (1.0 or less) (0); longer (more than 1.0) (1). Character 37 in Čerňanský et al. (2016); modified. Character affiliation: QN-C

27. Presacral vertebrae, dorsoventral height to centrum length ratio: 1.1 or less (0); 1.2-1.3 (1); 1.4 or greater (2). Character 10 in Villa et al. (2017); character 21 in Tschopp et al. (2018), Wencker et al. (2021). Character affiliation: QN-P

28. Presacral vertebrae, width across postzygapophyses to greatest length: 0.7 or less (0); 0.71-0.89 (1); 0.9 or greater (2). (Barbadillo and Sanz, 1983); character 11 in Villa et al. (2017); character 22 in Tschopp et al. (2018), Wencker et al. (2021); modified to close gap between states. Character affiliation: QN-P

29. Axial, neural arch pedicels, minimum anteroposterior length to height of posterior edge: less than 1 (0); 1-1.4 (1); more than 1.4 (2). Character 12 in Villa et al. (2017); character 23 in Tschopp et al. (2018), Wencker et al. (2021). Character affiliation: QN-P

30. Axis, neural spine, height without pedicel to greatest height: less than 0.5 (0); 0.5 or greater (1).
(Barbadillo and Sanz, 1983); character 13 in Villa et al. (2017); character 24 in Tschopp et al.
(2018), Wencker et al. (2021). Character affiliation: QN-P

31. Postaxial, presacral centrum, length to posterior condyle height ratio: less than 2.5 (0); 2.5-3.5 (1); more than 3.5 (2). Character 14 in Villa et al. (2017); character 25 in Tschopp et al. (2018), Wencker et al. (2021). Character affiliation: QN-P

32. Sacral vertebra 1, greatest height to width across pleurapophyses: less than or equal to 0.38 (0); more than 0.38 (1). (Barbadillo and Sanz, 1983); character 16 in Villa et al. (2017); character 26 in Tschopp et al. (2018), Wencker et al. (2021). Character affiliation: QN-P

33. Interclavicle, length of anterior process compared to posterior process: less than 0.40 (0); 0.40 or greater (1). (Arribas, 1998); character 18 in Villa et al. (2017); character 27 in Tschopp et al. (2018), Wencker et al. (2021). Character affiliation: QN-P

34. Humerus, greatest length to maximum shaft diameter at midlength: less than 10 (0); 10 or greater (1). (Lécuru, 1969); character 28 in Tschopp et al. (2018), Wencker et al. (2021). Character affiliation: QN-P

35. Humerus, proximal transverse width to distal transverse width: less than 0.95 (0); 0.95-1.05 (1); more than 1.05 (2). (Lécuru, 1969); character 29 in Tschopp et al. (2018), Wencker et al. (2021). Character affiliation: QN-P

36. Humerus, minimum to maximum shaft diameter at midlength ratio: less than 0.82 (0); 0.82 or greater (1). (Lécuru, 1969); character 30 in Tschopp et al. (2018), Wencker et al. (2021). Character affiliation: QN-P

37. Tibia to femur length ratio: less than 0.70 (0); 0.70 or greater (1). Character 31 in Tschopp et al. (2018), Wencker et al. (2021). Character affiliation: QN-P

Qualitative characters:

38. Premaxilla, shape: two bilaterally symmetric elements (0); single midline bone (1). Character 1 in Estes et al. (1988), Müller (2001); character 32 in Tschopp et al. (2018), Wencker et al. (2021). Character affiliation: OL-C

39. Premaxilla, tooth bearing portion, shape in dorsal view: tapering laterally, anterior and lateral edges form an acute angle (0); retaining width along curvature, angle between anterior and lateral edges approaching 90° (1). (Rauscher, 1992); character 19 in Villa et al. (2017); character 33 in Tschopp et al. (2018), Wencker et al. (2021). Character affiliation: QL-C

40. Premaxilla, tooth bearing portion, dorsal surface: pierced by a circular pit close to origin of nasal process (0); no pits present (1). (Rauscher, 1992); character 20 in Villa et al. (2017); character 34 in Tschopp et al. (2018), Wencker et al. (2021). Character affiliation: QL-C

41. Premaxilla, tooth bearing portion, maxillary facet, size: small to absent (0); large, reaching almost base of nasal process (1). Character 35 in Tschopp et al. (2018), Wencker et al. (2021). Character affiliation: QL-C

42. Premaxilla, tooth row, shape: U-shaped (0); V-shaped (1). Character 36 in Wencker et al.(2021). Character affiliation: QL-C

43. Premaxilla, ascending nasal process, lateral margins: parallel (0); expanding transversely around midlength (1). (Rauscher, 1992); character 3.1 in Barahona & Barbadillo (1997); character 13 in Gauthier et al. (2012, appendix 2, fig. 13); character 21 in Villa et al. (2017, modified after Gauthier et al., 2012); character 36 in Tschopp et al. (2018); character 37 in Wencker et al. (2021). Character affiliation: QL-C

44. Premaxilla, ascending nasal process, ethmoidal foramen at base: situated within fossa (0); without fossa around foramen (1). Character 37 in Tschopp et al. (2018); character 38 in Wencker et al. (2021). Character affiliation: QL-C

45. Premaxilla, fossa around ethmoidal foramen (if present), delimitation: with distinct ridge posteriorly (0); with distinct ridge anteriorly (1). Character 38 in Tschopp et al. (2018); character 39 in Wencker et al. (2021). Character affiliation: QL-C

46. Premaxilla, second pair of ethmoidal foramina: absent (0); present (1). Character 40 in Wencker et al. (2021). Character affiliation: QL-C

47. Premaxilla, ascending nasal process, posterodorsal end, shape in anterior view: pointed (0); widely rounded (1). Character 3.1 in Barahona & Barbadillo (1997); character 23 in Villa et al. (2017, modified by splitting the character in two); character 41 in Wencker et al. (2021). Character

affiliation: QL-C

48. Premaxilla, ascending nasal process, shape in lateral view: relatively straight (0); convex (1). (Rauscher, 1992); character 24 in Villa et al. (2017); character 39 in Tschopp et al. (2018); character 42 in Wencker et al. (2021). Character affiliation: QL-C

49. Premaxilla, ascending nasal process, dorsoventral constriction in lateral view: present (0); absent (1). (Rauscher, 1992); character 25 in Villa et al. (2017); character 40 in Tschopp et al. (2018); character 43 in Wencker et al. (2021). Character affiliation: QL-C

50. Premaxilla, ascending nasal process, ventral surface, longitudinal medial ridge, development: extending nearly throughout entire length (0); restricted to posterior portion, accompanied laterally by two shallow fossae (1). (Rauscher, 1992); character 26 in Villa et al. (2017); character 41 in Tschopp et al. (2018); character 44 in Wencker et al. (2021). Character affiliation: QL-C

51. Premaxilla, ascending nasal process, ventral surface, longitudinal medial ridge, posterior end: fading (0); distinct (1). (Rauscher, 1992); character 27 in Villa et al. (2017); character 42 in Tschopp et al. (2018); character 45 in Wencker et al. (2021). Character affiliation: QL-C

52. Premaxilla, ascending nasal process, posterior end of medial ridge, shape in lateral view: bifid with dorsal and ventral spurs (0); single (1). (Rauscher, 1992); character 28 in Villa et al. (2017); character 43 in Tschopp et al. (2018); character 46 in Wencker et al. (2021). Character affiliation: QL-C

53. Premaxilla, ascending nasal process, constriction at the base, anterior view: absent (0); present (1). Character 3 in Brizuela (2010); character 4 in Quadros et al. (2018); character 48 in Wencker et al. (2021, wording modified after Quadros et al. 2018). Character affiliation: QL-C

54. Premaxilla, ascending nasal process, thickness, in lateral view: thickness is retained from base until midway (0); thickness is gradually decreasing from base until posterior end (1). Character affiliation: QL-C

55. Premaxilla, ascending nasal process, dermal ornamentation: weak to absent (0); present and well developed (1). Character affiliation: QL-C

56. Premaxilla, posterolaterally projecting palatine processes on horizontal plate: absent (0); present (1). (Rauscher, 1992); character 29 in Villa et al. (2017); character 44 in Tschopp et al. (2018, wording modified); character 49 in Wencker et al. (2021). Character affiliation: QL-C

57. Premaxilla, horizontal plate, medial depression: absent, plate straight (0); present, depression bordered by ridges that extend onto palatine processes (1). Character 45 in Tschopp et al. (2018); character 50 in Wencker et al. (2021). Character affiliation: QL-C

58. Snout, medial depression around premaxilla-nasal contact: present (0); absent (1). Character 23 in Barahona & Barbadillo (1997); character 31 in Villa et al. (2017, wording modified); character 47 in Tschopp et al. (2018); character 52 in Wencker et al. (2021). Character affiliation: QL-C

59. Maxilla, external surface of facial process: uniform, without distinct subdivisions (0); subdivided into dorsal and ventral halves by horizontal groove (1). (Rauscher, 1992); character 32 in Villa et al. (2017); character 48 in Tschopp et al. (2018, wording modified); character 53 in Wencker et al. (2021). Character affiliation: QL-C

60. Maxilla, dermal ornamentation: absent to weak (0); well-developed (1). Character 49 in Tschopp et al. (2018); character 54 in Wencker et al. (2021). Character affiliation: QL-C

61. Maxilla, anterolateral premaxillary process, shape of ventral edge in lateral view: straight to convex (0); concave (1). Character 33 in Villa et al. (2017); character 50 in Tschopp et al. (2018); character 55 in Wencker et al. (2021). Character affiliation: QL-C

62. Maxilla, anterior margin of facial process, orientation relative to dental crest: posteriorly inclined throughout (0); perpendicular for some distance (1). Character 51 in Tschopp et al. (2018); character 56 in Wencker et al. (2021). Character affiliation: QL-C

63. Maxilla, anterior margin of facial process, distinct, subtriangular process projecting anteriorly or anterodorsally: absent (0); present (1). Character 52 in Tschopp et al. (2018); character 57 in Wencker et al. (2021). Character affiliation: QL-C

64. Maxilla, prefrontal process on dorsal end of facial process: weakly developed (0); develops two distinct posterodorsally projecting spurs (1). (Rauscher, 1992); character 34 in Villa et al. (2017); character 53 in Tschopp et al. (2018); character 58 in Wencker et al. (2021). Character affiliation:

QL-C

65. Maxilla, bifid prefrontal process (if present), in lateral view: anterodorsal projection reaching considerably dorsal to posteroventral projection (0); both projections at subequal height (1).

(Rauscher, 1992); character 35 in Villa et al. (2017); character 54 in Tschopp et al. (2018); character 59 Wencker et al. (2021). Character affiliation: QL-C

66. Maxilla, facial process: straight, flat (0); curves considerably medially towards dorsal tip (1). Character 36 in Villa et al. (2017); character 55 in Tschopp et al. (2018); character 60 in Wencker et al. (2021). Character affiliation: QL-C

67. Maxilla, facial process, incisura nasalis: absent (0); present (1). (Rauscher, 1992, p. 87). Character affiliation: QL-C

68. Maxilla, nasal recess: absent (0); present (1). (Rauscher, 1992); character 37 in Villa et al. (2017); character 56 Tschopp et al. (2018); character 61 in Wencker et al. (2021). Character affiliation: QL-C

69. Maxilla, anteromedial premaxillary process (lying between vomers and premaxilla): absent (0); present (1). Character 12 in Estes et al. (1988); character 4 in Denton & O'Neill (1995); character 4 in Nydam & Cifelli (2002), Nydam et al. (2007); character 25 in Conrad (2008); character 13 in Quadros et al. (2018); character 62 in Wencker et al. (2021, modified after Quadros et al., 2018). Character affiliation: OL-C

70. Maxilla, dorsal margin of anteromedial premaxillary process: smooth (0); bears a dorsally or anterodorsally projecting spur close to anterior end (1). (Rauscher, 1992), character 4.3 in Barahona & Barbadillo (1997); character 38 in Villa et al. (2017); character 57 in Tschopp et al. (2018, wording modified after Villa et al., 2017); character 63 in Wencker et al. (2021). Character affiliation: QL-C

71. Maxilla, transition from orbital margin into posterior process: smooth (0); separated by step or spur (1). Character 17 in Arnold (1989, fig. 6); character 4.1 in Barahona & Barbadillo (1997); character 42 in Müller (2001); character 39 in Villa et al. (2017, modified after Müller, 2001); character 58 in Tschopp et al. (2018); character 64 in Wencker et al. (2021). Character affiliation: OL-C

72. Maxilla, morphology of separation of orbital margin and posterior process (if present): incipient step (0); distinct step, forming right angle (1); posteriorly projecting spur (2). (Rauscher, 1992); character 40 in Villa et al. (2017); character 59 in Tschopp et al. (2018, modified); character 65 in Wencker et al. (2021). Character affiliation: QL-C

73. Maxilla, posterior process, posterior extent: reaches mid orbit (0); posterior to mid orbit (1). Character 17 in Müller (2001); character 23 in Lee & Scanlon (2002); character 12 in Čerňanský et al. (2015, modified); character 60 in Tschopp et al. (2018); character 66 in Wencker et al. (2021). Character affiliation: QL-C

74. Maxilla, facial process, medial surface, anteroposterior ridge on supradental shelf connecting anterior margin of facial process with carina maxillaris: absent (0); present (1). Character 61 in Tschopp et al. (2018); character 67 in Wencker et al. (2021). Character affiliation: QL-C

75. Maxilla, supradental shelf, articulation facet for palatine, shape in dorsal view: slight medial extension (0); distinctly offset from crest (1). Character 62 in Tschopp et al. (2018); character 68 in Wencker et al. (2021). Character affiliation: QL-C

76. Maxilla, tooth row, shape in ventral view: curves laterally at distal end (0); straight (1). Character 41 in Villa et al. (2017); character 63 in Tschopp et al. (2018); character 69 in Wencker et al. (2021). Character affiliation: QL-C

77. Septomaxilla, anterolateral process: distinct (0); reduced (1). Character 2 in Arnold (1989, fig.
4); character 10.2 in Barahona & Barbadillo (1997); character 42 Villa et al. (2017, wording modified); character 64 in Tschopp et al. (2018); character 70 in Wencker et al. (2021). Character affiliation: QL-C

78. Septomaxilla, posteromedial process, length: scarcely developed (0); long (1). Character 2 in Arnold (Arnold, 1989, fig. 4); character 10.1 in Barahona & Barbadillo (1997); character 43 in Villa et al. (2017, modified after Barahona & Barbadillo, 1997 by splitting the character in two); character 65 in Tschopp et al. (2018); character 71 in Wencker et al. (2021). Character affiliation: OL-C

79. Septomaxilla, posterolateral corner: angular, projecting posterolaterally (0); rounded (1). Character 2 in Arnold (1989, fig. 4); character 10.3 in Barahona & Barbadillo (1997); character 44 in Villa et al. (2017, wording modified after Barahona & Barbadillo, 1997); character 66 in Tschopp et al. (2018); character 72 in Wencker et al. (2021). Character affiliation: QL-C

80. Nasal, anterior border, nasolateral process: present (0); absent (1). Character 22 in Conrad
(2008), Gauthier et al. (2012); character 7 in Quadros et al. (2018); character 74 in Wencker et al.
(2021); wording modified. Character affiliation: QL-C

81. Nasals, ventral contact beneath premaxillary nasal process: broad contact below (0); not in contact except near apex (1). Character 24 in Gauthier et al. (2012); character 45 in Villa et al. (2017); character 67 in Tschopp et al. (2018); character 75 in Wencker et al. (2021). Character

affiliation: QL-C

82. Nasals, dermal ornamentation: weak to absent (0); present and well developed (1). Character affiliation: QL-C

83. Prefrontal, dorsal process, length compared to length of orbitonasal flange: longer (0); equal to shorter (1). Character 68 in Tschopp et al. (2018); character 76 in Wencker et al. (2021). Character affiliation: QL-C

84. Prefrontal, dermal ornamentation: weak to absent (0); present and well developed (1). Character affiliation: QL-C

85. Frontals: paired (0); fused (1). (Boulenger, 1920); (Camp, 1923); character 6 in Estes et al (1988); character 4 in Arnold (1989, fig. 2, 3); character 1 in Müller (2001); character 46 in Villa et al. (2017, wording modified); character 69 in Tschopp et al. (2018); character 78 in Wencker et al. (2021). Character affiliation: QL-C

86. Frontal, anterior descending processes: reduced (0); long distinct (1). Character 9 in Estes et al. (1988); character 6 in Arnold (1989); character 8 in Arnold et al. (2007); character 38 in Gauthier et al. (2012); character 47 in Villa et al. (2017, wording modified); character 70 in Tschopp et al. (2018); character 79 in Wencker et al. (2021). Character affiliation: QL-C

87. Frontal, nasal margin: rather straight (0); highly irregular (1). (Rauscher, 1992); character 48 in Villa et al. (2017); character 71 in Tschopp et al. (2018); character 80 in Wencker et al. (2021). Character affiliation: QL-C

88. Frontal, medial and lateral processes: well-developed (0); reduced or absent (1). Character 49 inVilla et al. (2017, wording modified); character 72 in Tschopp et al. (2018); character 81 inWencker et al. (2021). Character affiliation: QL-C

89. Frontal, facet to accommodate dorsal process of maxilla: conspicuous (0); weak to absent (1). Character 1.4 in Barahona & Barbadillo (1997); character 50 in Villa et al. (2017, wording modified); character 73 in Tschopp et al. (2018); character 82 in Wencker et al. (2021). Character affiliation: QL-C

90. Frontal, prefrontal shield, impression: absent (0); present (1). Character 74 in Tschopp et al. (2018); character 83 in Wencker et al. (2021). Character affiliation: QL-C

91. Frontal, prefrontal shield, impression (if present), shape: connected anteromedially (0); medially separated (1). Character 75 in Tschopp et al. (2018); character 84 in Wencker et al. (2021); wording modified. Character affiliation: QL-C

92. Frontal, suture with parietal: interdigitating (0); rather straight (1). Character 7 in Arnold (1989, fig. 2, 3); character 65 in Müller (2001); character 1.3 in Barahona & Barbadillo (1997); character 53 in Villa et al. (2017, wording modified after Barahona & Barbadillo, 1997); character 76 in Tschopp et al. (2018); character 85 in Wencker et al. (2021). Character affiliation: QL-C

93. Frontal, dermal ornamentation: weak to absent (0); present and well developed (1). Character affiliation: QL-C

94. Postfrontal, maximum anteroposterior length to maximum anteroposterior length of postorbital: longer to subequal (0); distinctly shorter (1). (Arribas, 1998); character 3 in Villa et al. (2017); character 86 in Wencker et al. (2021). Character affiliation: QL-C

95. Postfrontal, anteromedial process: expanded (0); not expanded (1). Character 7.2 in Barahona & Barbadillo (1997); character 54 in Villa et al. (2017, wording modified); character 77 in Tschopp et al. (2018); character 87 in Wencker et al. (2021). Note: if the process is not visible in dorsal view, it is not expanded. Character affiliation: QL-C

96. Postfrontal, short, subtriangular, anterior projection close to suture with postorbital: absent (0); present (1). Character 78 in Tschopp et al. (2018); character 88 in Wencker et al. (2021). Character affiliation: QL-C

97. Postfrontal, dermal ornamentation: weak to absent (0); present and well developed (1). Character affiliation: QL-C

98. Postorbital-postfrontal suture: fused (0); separate (1). (Siebenrock, 1894); character 7 in Arnold (1973, fig. 2); character 14 in Estes et al. (1988); character 12 in Arnold (1989, fig. 2, 3); character 7.1 in Barahona & Barbadillo (1997); character 55 in Villa et al. (2017, wording modified); character 79 in Tschopp et al. (2018); character 89 in Wencker et al. (2021). Character affiliation: QL-C

99. Postorbital, anteromedial process: absent (0); present (1). Character 7.3 in Barahona & Barbadillo (1997); character 56 in Villa et al. (2017); character 80 in Tschopp et al. (2018); character 90 in Wencker et al. (2021). Character affiliation: QL-C

100. Postorbital-postfrontal impression of lateral shield, location: does not reach lateral margin (0); reaches lateral margin posteriorly (1); reaches lateral margin along most of its length (2). Character 39.1, 39.2 in Arnold (1989, fig. 14); character 21 in Arnold et al. (2007, fig. 15); character 81 in Tschopp et al. (2018); character 91 in Wencker et al. (2021). Character affiliation: QL-C

101. Postorbital, dermal ornamentation: weak to absent (0); present and well developed (1). Character affiliation: QL-C

102. Jugal, quadratojugal process: absent (0); distinct (1). (Siebenrock, 1894); character 15 in Arnold (1989, fig. 6); character 6.1 in Barahona & Barbadillo (1997, polarity reversed); character 57 in Villa et al. (2017); character 83 in Tschopp et al. (2018); character 94 in Wencker et al. (2021). Character affiliation: QL-C

103. Jugal, quadratojugal process (if present), shape: acute bony process (0); forms nearly a 90° angle (1). Character 84 in Tschopp et al. (2018); character 95 in Wencker et al. (2021); wording modified. Character affiliation: QL-C

104. Jugal, posterodorsal process, posterior margin, shape: distinctly curving posteriorly towards tip (0); nearly straight (1). Character 85 in Tschopp et al. (2018); character 96 in Wencker et al. (2021). Character affiliation: QL-C

105. Jugal, medial process on medial ridge: present (0); absent (1). Character 6.2 in Barahona & Barbadillo (1997); character 58 in Villa et al. (2017); character 86 in Tschopp et al. (2018); character 97 in Wencker et al. (2021). Character affiliation: QL-C

106. Jugal, posterodorsal process, position of medial ridge: on anterior half (0); on posterior half
(1). (Cerňanský *et al.*, 2014); character 22 in Čerňanský et al. (2015); character 87 in Tschopp et al.
(2018, modified); character 98 in Wencker et al. (2021). Character affiliation: QL-C

107. Jugal, maxillary facet on anterior process: large (0); small (1). Character 31 in Estes et al. (1988); character 16 in Arnold (1989, modified, fig. 6); character 6.3 in Barahona & Barbadillo (1997, polarity reversed); character 149 in Gauthier et al. (2012); character 16 in Arnold (1989); character 59 in Villa et al. (2017, modified after Arnold, 1989); character 88 in Tschopp et al. (2018); character 99 in Wencker et al. (2021). Character affiliation: QL-C

108. Jugal, dermal ornamentation: weak to absent (0); present and well developed (1). Character affiliation: QL-C

109. Lacrimal, orbital margin: forked with posterodorsal process (0); posterodorsal process, absent tapering to a pointed posteroventral end (1). Character 5 in Barahona & Barbadillo (1997); character 60 in Villa et al. (2017, wording modified); character 89 in Tschopp et al. (2018); character 100 in Wencker et al. (2021). Character affiliation: QL-C

110. Quadrate, anterior surface, pit above mandibular condyle: absent (0); present (1). (Rauscher, 1992); character 61 in Villa et al. (2017); character 90 in Tschopp et al. (2018); character 101 in Wencker et al. (2021). Character affiliation: QL-C

111. Quadrate, anterior margin, in medial view: angular (0); rounded (1). Character 9.1 in Barahona & Barbadillo (1997); character 62 in Villa et al. (2017); character 91 in Tschopp et al. (2018); character 102 in Wencker et al. (2021). Character affiliation: QL-C

112. Quadrate, anterior platform: concave (0); flat (1). Character 9.2 in Barahona & Barbadillo (1997); character 63 in Villa et al. (2017); character 92 in Tschopp et al. (2018); character 103 in Wencker et al. (2021). Character affiliation: QL-C

113. Quadrate, medial edge, pterygoid process: distinct (0); small to absent (1). Character 37 in
Estes et al. (1988); character 24 in Müller (2001); character 182 in Gauthier et al. (2012); character
93 in Tschopp et al. (2018, modified after Estes et al. 1988); character 104 in Wencker et al. (2021).
Character affiliation: QL-C

114. Quadrate, central pillar, position: at medial border only laterally accompanied by a flange (0); inset with flanges medially and laterally (1). (Rauscher, 1992); character 64 in Villa et al. (2017); character 94 in Tschopp et al. (2018); character 105 in Wencker et al. (2021). Character affiliation: OL-C

115. Quadrate, cephalic condyle, medial edge: straight (0); with distinct expansion accompanied by a short vertical ridge extending ventrally on medial surface of central pillar (1). Character 65 in Villa et al. (2017); character 95 in Tschopp et al. (2018, wording modified); character n 106 in Wencker et al. (2021). Character affiliation: QL-C

116. Squamosal, posterior end: medially expanded (0); slender, curving laterally (1). Character 34 in Estes et al. (1988); character 14 in Arnold (1989, fig. 5); character 8 in Barahona & Barbadillo (1997); character 21 in Müller (2001); character 66 in Villa et al. (2017, wording modified); character 96 in Tschopp et al. (2018); character 108 in Wencker et al. (2021). Character affiliation:

QL-C

117. Squamosal, ascending process: present (0); absent (1). (Gauthier, 1982); character 165 in Gauthier et al. (2012). Character affiliation: QL-C

118. Supratemporal, position on parietal: partly ventral (0); partly ventrolateral (1); all lateral (2); dorsolateral (3). (De Queiroz, 1987); character 170 in Gauthier et al. (2012); character 110 in Wencker et al. (2021). Note: CT needed! Character affiliation: QL-C

119. Parietal, anterior margin: small concavity near midline (0); straight (1). Character 2.5 in Barahona & Barbadillo (1997); character 67 in Villa et al. (2017, wording modified); character 97 in Tschopp et al. (2018); character 111 in Wencker et al. (2021). Character affiliation: QL-C

120. Parietal, parietal tabs: well-developed, projecting far anteriorly (0); reduced to absent (1). Character 22 in Estes et al. (1988, fig. 8A); character 13 in Müller (2001); character 68 in Villa et al. (2017); character 98 in Tschopp et al. (2018); character 112 in Wencker et al. (2021). Character affiliation: QL-C

121. Parietal, lappets, lateral expansion: present (0); absent (1). Character 2.4 in Barahona & Barbadillo (1997); character 69 in Villa et al. (2017, wording modified); character 99 in Tschopp et al. (2018); character 113 in Wencker et al. (2021). Character affiliation: QL-C

122. Parietal, dorsal ornamentation: weak to absent (0); present and well developed (1). Character affiliation: QL-C

123. Parietal, dorsal ornamentation (if present): irregular (0); symmetrically subdivided by distinct grooves (1). (Rauscher, 1992); character 70 in Villa et al. (2017); character 100 in Tschopp et al. (2018); character 114 in Wencker et al. (2021); wording modified. Character affiliation: QL-C

124. Parietal, facies dorsalis, outline, shape: strongly diverging anteriorly (0); subquadrangular to subrectangular (1); converging anteriorly (2). Character 101 in Tschopp et al. (2018); character 115 in Wencker et al. (2021). Character affiliation: QL-C

125. Parietal, posterior edge of parietal fossa: concave transversely (0); straight (1). Character 2.1 in Barahona & Barbadillo (1997); character 72 in Villa et al. (2017, modified); character 102 in Tschopp et al. (2018); character 116 in Wencker et al. (2021). Character affiliation: QL-C

126. Parietal, posterior margin, extension in dorsal view: not exceeding anterior margin of supraoccipital (0); extending over anterior margin of supraoccipital (1). Character 24 in Estes et al. (1988); character 25 in Barahona & Barbadillo (1997); character 73 in Villa et al. (2017, modified after Barahona & Barabadillo, 1997); character 103 in Tschopp et al. (2018); character 117 in Wencker et al. (2021). Character affiliation: QL-C

127. Parietal, posterior margin, single or bifid projection near midline: absent (0); present (1). Character 95 in Gauthier et al. (2012); character 104 in Tschopp et al. (2018, wording modified); character 118 in Wencker et al. (2021). Character affiliation: QL-C

128. Parietal, posterior margin, midline projection (if present): single (0); bifid (1). (Rauscher,1992, fig. 23.3); character 97 in Gauthier et al. (2012); character 74 in Villa et al. (2017, wording

modified); character 105 in Tschopp et al. (2018); character 119 in Wencker et al. (2021); wording modified. Character affiliation: QL-C

129. Parietal, postparietal processes: straight (0); twisted (1). (Rauscher, 1992); character 75 in Villa et al. (2017); character 106 in Tschopp et al. (2018); character 120 in Wencker et al. (2021). Character affiliation: QL-C

130. Parietal, ventral surface, anterolateral and posterolateral ventral crests, contact: absent (0); present (1). Character 2.2 in Barahona & Barbadillo (1997); character 76 in Villa et al. (2017); character 107 in Tschopp et al. (2018, modified after Villa et al. 2017); character 121 in Wencker et al. (2021). Character affiliation: QL-C

131. Parietal, ventral surface, anterolateral ventral crests, orientation: forming V-shape (0); forming U-shape, being subparallel anteriorly (1). Character 108 in Tschopp et al. (2018); character 122 in Wencker et al. (2021). Character affiliation: QL-C

132. Parietal, epipterygoid processes: absent (0); present (1). Character 23 in Estes et al. (1988); character 14 in Müller (2001); character 108 in Gauthier et al. (2012); character 109 in Tschopp et al. (2018, modified to include only the transformational component, following Estes et al., 1988); character 123 in Wencker et al. (2021). Character affiliation: QL-C

133. Parietal, ventral surface, bony structure between facies triangularis and parietal fossa, shape: wide shelf (0); narrow ridge (1). Character 110 in Tschopp et al. (2018); character 124 in Wencker et al. (2021). Character affiliation: QL-C

134. Parietal, ventral surface, parietal fossa, anterior end, shape: U-shaped to rectangular (0); triangular to trapezoid (1). (Barahona Quintana, 1996); character 77 in Villa et al. (2017, wording modified); character 111 in Tschopp et al. (2018); character 125 in Wencker et al. (2021). Character affiliation: QL-C

135. Parietal, parietal foramen, shape: circular (0); pear shaped (1). (Rauscher, 1992); character 78 in Villa et al. (2017); character 112 in Tschopp et al. (2018); character 126 in Wencker et al. (2021). Character affiliation: QL-C

136. Parietal, parasagittal crest, strongly developed on the dorsolateral surface for the insertion of the adductor mandible musculature: absent (0); present (1). Character 10 in Denton & O'Neil (1995); character 10 in Nydam & Cifelli (2002), Nydam et al. (2007); character 75 in Conrad (2008); character 93 in Gauthier et al. (2012); character 22 in Quadros et al. (2018, modified after Denton & O'Neill, 1995); character 127 in Wencker et al. (2021). Character affiliation: QL-C

137. Paroccipital, process length: long, exceeding posterior margin of otoccipital in lateral view (0); short (1). Character 14 in Barahona & Barbadillo (1997); character 79 in Villa et al. (2017, wording modified); character 113 in Tschopp et al. (2018); character 129 in Wencker et al. (2021). Character affiliation: QL-C

138. Supraoccipital, lateral margins of processus ascendens: parallel (0); converging (1). Character16.1 in Barahona & Barbadillo (1997); character 80 in Villa et al. (2017, wording modified);character 114 in Tschopp et al. (2018); character 130 in Wencker et al. (2021). Character affiliation:

QL-C

139. Supraoccipital, supraoccipital crest, shape: distinct crest (0); wide ridge (1). (Al-Hassawi, 2004); character 115 in Tschopp et al. (2018); character 131 in Wencker et al. (2021). Character affiliation: QL-C

140. Basioccipital, shape, in ventral view: subtriangular, exoccipital margin straight (0); mushroom shaped, exoccipital margin concave (1). (Rauscher, 1992); character 81 in Villa et al. (2017); character 116 in Tschopp et al. (2018); character 132 in Wencker et al. (2021). Character affiliation: QL-C

141. Basioccipital, cornua basisphenoidea: medially separated (0); medially co-ossified (1). (Rauscher, 1992); character 82 in Villa et al. (2017); character 117 in Tschopp et al. (2018); character 133 in Wencker et al. (2021). Character affiliation: QL-C

142. Basioccipital, occipital condyle, shape in ventral view: continuously rounded (0); bears weak recess (1). (Rauscher, 1992); character 83 in Villa et al. (2017); character 118 in Tschopp et al. (2018); character 134 in Wencker et al. (2021). Character affiliation: QL-C

143. Basioccipital, posterior process on lateral sinuses: absent (0); present, separating lateral sinus from exoccipital margin (1). (Rauscher, 1992); character 84 in Villa et al. (2017); character 119 in Tschopp et al. (2018); character 135 in Wencker et al. (2021). Character affiliation: QL-C

144. Basioccipital, dorsal surface, texture: smooth (0); ornamented (1). (Rauscher, 1992); character
85 in Villa et al. (2017); character 120 in Tschopp et al. (2018); character 136 in Wencker et al.
(2021). Character affiliation: QL-C

145. Sphenoid, ventral surface, depression close to base of basipterygoid processes: present (0); absent (1). Character 15.1 in Barahona & Barbadillo (1997); character 86 in Villa et al. (2017, modified); character 121 in Tschopp et al. (2018); character 137 in Wencker et al. (2021). Character

affiliation: QL-C

146. Sphenoid, ventral surface, depression close to base of basipterygoid processes (if present), shape: rounded (0); longitudinal trough (1). Character 122 in Tschopp et al. (2018); character 138 in Wencker et al. (2021); wording modified. Character affiliation: QL-C

147. Sphenoid, ventral surface, distinct longitudinal ridges or bosses at base of basipterygoid processes: absent (0); present (1). Character 87 in Villa et al. (2017); character 123 in Tschopp et al. (2018); character 139 in Wencker et al. (2021). Character affiliation: QL-C

148. Basipterygoid processes, shape at base: narrow, margins strongly concave (0); widened, margins nearly parallel (1). Character 15.2 in Barahona & Barbadillo (1997); character 88 in Villa et al. (2017, wording modified); character 124 in Tschopp et al. (2018); character 140 in Wencker et al. (2021). Character affiliation: QL-C

149. Prootic, alar process, development: weak, scarcely developed (0); well developed (1). Character 13.1 in Barahona & Barbadillo (1997); character 89 in Villa et al. (2017, wording modified); character 125 in Tschopp et al. (2018); character 141 in Wencker et al. (2021). Character affiliation: QL-C

150. Prootic, posterior process, length, in medial view: long (0); reduced (1). Character 13.2 in Barahona & Barbadillo (1997); character 90 in Villa et al. (2017, wording modified); character 126 in Tschopp et al. (2018); character 142 in Wencker et al. (2021). Character affiliation: QL-C

151. Vomer, ventral longitudinal ridges: absent (0); present (1). Character 222 in Gauthier et al. (2012); modified to adapt to restricted taxon sampling. Character affiliation: QL-C

152. Palatine, anterolateral process, shape: rounded margins (0); straight margins (1). Character 11 in Barahona & Barbadillo (1997); character 92 in Villa et al. (2017, wording modified); character 128 in Tschopp et al. (2018); character 144 in Wencker et al. (2021). Character affiliation: QL-C

153. Pterygoid recess, development: weak, angle between posteriormost point of recess and anteriormost points of anteromedial and lateral processes more than 90° (0); deep, angle 90° (1). Character 12.1 in Barahona & Barbadillo (1997); character 94 in Villa et al. (2017, modified by including angles); character 130 in Tschopp et al. (2018); character 146 in Wencker et al. (2021). Character affiliation: QL-C

154. Pterygoid, dorsal surface, crest separating concave area between columellar crest and transverse crest: absent (0); present (1). Character 132 in Tschopp et al. (2018); character 148 in Wencker et al. (2021). Character affiliation: QL-C

155. Pterygoid, quadrate process, pterygoid ridge on dorsolateral surface, development: weakly developed (0); laminar crest (1). Character 133 in Tschopp et al. (2018); character 149 in Wencker et al. (2021). Character affiliation: QL-C

156. Pterygoid, ventral surface, distinct ridge on transverse crest: present (0); absent (1). Character 96 in Villa et al. (2017); character 134 in Tschopp et al. (2018, wording modified); character 150 in Wencker et al. (2021). Character affiliation: QL-C

157. Pterygoid teeth: present (0); absent (1). (Boulenger, 1916); (Pregill *et al.*, 1986); character 40 in Müller (2001); character 267 in Gauthier et al. (2012, modified); character 97 in Villa et al. (2017); character 135 in Tschopp et al. (2018); character 151 in Wencker et al. (2021). Character affiliation: QL-C

158. Pterygoid teeth, arrangement (if present): patch (0); mostly in single line (1). Character 40 in Müller (2001); character 98 in Villa et al. (2017, modified); character 136 in Tschopp et al. (2018); character 152 in Wencker et al. (2021). Character affiliation: QL-C

159. Ectopterygoid, posterolateral process, length: long process (0); short knob (1). (Smith, 2009); character 283 in Gauthier et al. (2012); character 137 in Tschopp et al. (2018, modified to adapt to restricted taxon sampling); character 153 in Wencker et al. (2021). Character affiliation: QL-C

160. Dentary, shape: continuously broadening dorsoventrally towards distal (0); sickle shaped, subparallel in distal half, tapering mesially (1). Character 138 in Tschopp et al. (2018); character 154 in Wencker et al. (2021). Character affiliation: QL-C

161. Dentary, subdental ridge, shape in medial view: straight (0); concave (1). (Bailon *et al.*, 2014); character 155 in Wencker et al. (2021). Character affiliation: QL-C

162. Dentary, splenial facet on subdental ridge, development: weak (0); well developed (1). (Bailon *et al.*, 2014); character 139 in Tschopp et al. (2018); character 156 in Wencker et al. (2021).

Character affiliation: QL-C

163. Dentary, symphysis, distinct articular facet: absent (0); present (1). Character 42 in Čerňanský et al. (2015); character 140 in Tschopp et al. (2018, wording adapted to terminology proposed by Rauscher, 1992); character 157 in Wencker et al. (2021). Character affiliation: QL-C

164. Dentary, Meckelian fossa, anterior portion, shape: closed, open portion restricted posteriorly (0); open, portion nearly reaching symphysis (1). (Hoffstetter, 1944); character 30 in Müller (2001); character 141 in Tschopp et al. (2018, modified); character 158 in Wencker et al. (2021). Character

165. Dentary, Meckelian canal, shape: triangular (0); tubular (1). Character 159 in Wencker et al.(2021). Character affiliation: QL-C

166. Dentary, tooth row, differences in tooth size: significant (0); minimal (1). Character 142 in Tschopp et al. (2018); character 161 in Wencker et al. (2021). Character affiliation: QN-D

167. Dentary, tooth row, orientation in lateral view: tooth apices are on same level, forming nearly straight line (0); tooth apices form concave to S-shaped line with the distal most teeth reaching significantly dorsal to more mesial teeth (1). Character 143 in Tschopp et al. (2018); character 162 in Wencker et al. (2021, wording modified). Character affiliation: QL-C

168. Dentary, coronoid process, dorsal expansion: level with tooth row (0); strongly expanded above distal most teeth (1). Character 144 in Tschopp et al. (2018); character 163 in Wencker et al. (2021). Character affiliation: QL-C

169. Dentary, coronoid process, length: shorter than angular process (0); equally long to longer than angular process (1). (Rauscher, 1992); character 17.1 in Barahona & Barbadillo (1997); character 99 in Villa et al. (2017, modified); character 145 in Tschopp et al. (2018); character 164 in Wencker et al. (2021). Character affiliation: QL-C

170. Dentary, coronoid facet on labial surface, shape: shallow with indistinct margins (0); distinct (1). Character 146 in Tschopp et al. (2018); character 165 in Wencker et al. (2021). Character affiliation: QL-C

171. Dentary, surangular process: absent (0); present (1). (Rauscher, 1992); character 100 in Villa et al. (2017); character 147 in Tschopp et al. (2018); character 166 in Wencker et al. (2021). Character affiliation: QL-C

172. Dentary, angular process, posterior end: blunt (0); pointed (1). (Rauscher, 1992, figs. 16-19); character 101 in Villa et al. (2017); character 148 in Tschopp et al. (2018); character 167 in Wencker et al. (2021). Character affiliation: QL-C

173. Splenial, anterior extension relative to dentary tooth row: around one-third (or less) (0); about one-half (1); about two-thirds (2); three-fourths (or more) (3). Character 31 in Müller (2001); character 375 in Gauthier et al. (2012); character 102 in Villa et al. (2017, wording modified); character 150 in Tschopp et al. (2018); character 169 in Wencker et al. (2021). Character affiliation:



174. Splenial, anterior end: single (0); bifid (1). (Barahona Quintana, 1996); character 103 in Villa et al. (2017); character 151 in Tschopp et al. (2018); character 170 in Wencker et al. (2021). Character affiliation: QL-C

175. Splenial, medial surface, anterior to splenial anterior inferior alveolar foramen: flat or weakly concave (0); strongly concave dorsoventrally (1). Character 104 in Villa et al. (2017, wording modified); character 152 in Tschopp et al. (2018); character 171 in Wencker et al. (2021). Character affiliation: QL-C

176. Splenial, posterior end, shape: single (0); bifid (1). Character 105 in Villa et al. (2017, wording modified); character 153 in Tschopp et al. (2018); character 172 in Wencker et al. (2021). Character affiliation: QL-C

177. Coronoid, anteromedial process, anterior end, shape: pointed (0); blunt (1). Character 106 in Villa et al. (2017); character 154 in Tschopp et al. (2018); character 173 in Wencker et al. (2021). Character affiliation: QL-C

178. Coronoid, angle between anteromedial process and posteromedial process, in medial view: more open, larger than 50° (0); more acute, smaller than 50° (1). Character 42 in Čerňanský et al. (2015); character 155 in Tschopp et al. (2018, wording adapted to terminology proposed by Rauscher, 1992); character 174 in Wencker et al. (2021). Character affiliation: QL-C

179. Coronoid-surangular articulation: coronoid restricted to medial aspect of mandible (0); coronoid extends onto dorsal surface of surangular (1); coronoid arches over dorsal margin of mandible to reach lateral surface of surangular (2). Character 390 in Gauthier et al. (2012); character 113 in Quadros et al. (2018); character 175 in Wencker et al. (2021). Character affiliation:

QL-C

180. Surangular, labial surface, distinct horizontal crest: absent (0); present, delimits adductor fossa ventrally (1). Character 156 in Tschopp et al. (2018); character 176 in Wencker et al. (2021).Character affiliation: QL-C

181. Surangular, adductor fossa on labial surface of mandible: shallow, not extending further ventrally than midheight (0); deep, extending nearly to angular (1). (Gauthier, 1984); character 81 in Estes et al. (1988); character 399 in Gauthier et al. (2012); character 157 in Tschopp et al. (2018, wording modified); character 177 in Wencker et al. (2021). Character affiliation: QL-C

182. Articular, dorsal margin of anterior ramus: with distinct bulge (0); straight (1). Character 18 in Barahona & Barbadillo (1997); character 107 in Villa et al. (2017, wording modified); character
158 in Tschopp et al. (2018); character 178 in Wencker et al. (2021). Character affiliation: QL-C

183. Retroarticular process, dorsal surface posterior to articular facet: flat to weakly concave transversely (0); strongly concave transversely (1). Character 74 in Estes et al. (1988); character 34 in Müller (2001); character 159 in Tschopp et al. (2018, wording modified); character 179 in Wencker et al. (2021). Character affiliation: QL-C

184. Retroarticular process breadth (greatest width) relative to mandibular condyle (glenoid): narrower (0); wider (1). (Estes *et al.*, 1988); character 37 in Müller (2001); character 410 in Gauthier et al. (2012); character 160 in Tschopp et al. (2018); character 180 in Wencker et al. (2021). Character affiliation: QL-C

185. Palpebral, posterior margin: strongly concave, with elongate dorsoposterolateral process (0); relatively straight, palpebral outline subtriangular (1). Character 19 in Barahona & Barbadillo (1997); character 108 in Villa et al. (2017, wording modified); character 161 Tschopp et al. (2018); character 181 Wencker et al. (2021). Character affiliation: QL-C

186. Ossification of temporal scales: little or none (0); extensive (1). Character 5 in Arnold (1973); character 19 in Arnold (1989); character 12 in Arnold et al. (2007); character 109 in Villa et al. (2017, wording modified); character 162 in Tschopp et al. (2018); character 182 in Wencker et al. (2021). Character affiliation: QL-C

187. Teeth, premaxillary, crown morphology, bicuspid teeth: present (0); absent (1). Character 20.3 in Barahona & Barbadillo (1997); character 111 in Villa et al. (2017, modified); character 163 in Tschopp et al. (2018); character 183 in Wencker et al. (2021). Character affiliation: QN-D

188. Teeth, premaxillary, crown morphology (of monocuspid teeth): fang like, pointed (0); rounded(1). Character 184 in Wencker et al. (2021). Character affiliation: QN-D

189. Teeth, premaxilla, median tooth: absent (0); present (1). Character 4 in Scanlon (1996); character 154 in Lee (1998); character 413 in Gauthier et al.(2012); character 185 in Wencker et al. (2021, wording modified from Scanlon, 1996). Character affiliation: QN-D

190. Teeth, premaxilla, median tooth, size: same size as neighbouring premaxillary teeth (0); enlarged (1). Character 155 in Lee (1998); character 414 in Gauthier et al. (2012); character 186 in Wencker et al. (2021, modified after Gauthier et al. 2012). Character affiliation: QN-D
191. Teeth, maxillary, size compared to premaxillary teeth: significantly larger (0); similar (1). Character 112 in Villa et al. (2017); character 164 in Tschopp et al. (2018, wording modified); character 187 in Wencker et al. (2021). Character affiliation: QN-D

192. Teeth, maxillary, crown morphology in majority of teeth: monocuspid (0); bicuspid (1); tricuspid (2); more than 3 cusps (3). (Siebenrock, 1894); character 20.1 in Barahona & Barbadillo (1997); character 113 in Villa et al. (2017, modified); character 165 in Tschopp et al. (2018); character 188 in Wencker et al. (2021). Character affiliation: QN-D

193. Teeth, maxilla and dentary, location of most robust teeth: anterior half (0); central (1); distal half (2); distal-most (3). (De Stefano, 1903); character 114 in Villa et al. (2017); character 166 in Tschopp et al. (2018); character 189 in Wencker et al. (2021). Character affiliation: QN-D

194. Teeth, maxilla and dentary, differences in tooth robustness along tooth row: absent to minimal (0); present, not more than 50% different in robustness (1); present, 50% or more different in robustness (2). Character 190 in Wencker et al. (2021). Character affiliation: QN-D

195. Teeth, maxilla and dentary, distal transition from larger to smaller teeth: gradual (0); distinct (1). Character 115 in Villa et al. (2017); character 167 in Tschopp et al. (2018); character 191 in Wencker et al. (2021). Character affiliation: QN-D

196. Teeth, dentary, crown morphology in majority of teeth: monocuspid (0); bicuspid (1); tricuspid (2); more than 3 cusps (3). (Siebenrock, 1894); character 20.1 in Barahona & Barbadillo (1997); character 116 in Villa et al. (2017, modified); character 168 in Tschopp et al. (2018); character 192 in Wencker et al. (2021). Character affiliation: QN-D

197. Teeth, crown surface: smooth (0); with longitudinal striae (1). Character 169 in Tschopp et al. (2018); character 193 in Wencker et al. (2021). Character affiliation: QN-D

198. Teeth, crown surface, striae spacing (if present): wide (0); narrow (1). Character 170 in Tschopp et al. (2018); character 194 in Wencker et al. (2021, wording modified). Character affiliation: QN-D

199. Teeth, dentary, tooth crowns overtop dental crest: by less than half their height (0); by half their height or more (1). (Böhme, 2010); character 117 in Villa et al. (2017); character 171 in Tschopp et al. (2018); character 195 in Wencker et al. (2021). Character affiliation: QN-D

200. Atlas, foramen on lateral surface: absent (0); present (1). Character 118 in Villa et al. (2017); character 172 in Tschopp et al. (2018); character 196 in Wencker et al. (2021). Character affiliation:

201. Atlas, foramen on lateral surface (if present), position: centrum (0); neural arch (1). (Calori, 1858); character 119 in Villa et al. (2017); character 173 in Tschopp et al. (2018); character 197 in Wencker et al. (2021, wording modified). Character affiliation: QN-P

202. Atlas, intercentrum, ventral keel, dorsoventral height in comparison to centrum: subequal to smaller (0); considerably larger (1). Character 120 in Villa et al. (2017); character 174 in Tschopp et al. (2018); character 198 in Wencker et al. (2021). Character affiliation: QN-P

203. Atlantal intercentrum, ventral keel, anteroposterior length compared to centrum length: shorter to subequal (0); considerably longer (1). Character 121 in Villa et al. (2017); character 175 in Tschopp et al. (2018); character 199 in Wencker et al. (2021). Character affiliation: QN-P

204. Atlas, ventral keel, shape: confluent with centrum anteriorly and posteriorly (0); separated from centrum by transverse grooves (1). Character 122 in Villa et al. (2017); character 176 in Tschopp et al. (2018); character 200 in Wencker et al. (2021). Character affiliation: QN-P

205. Atlantal neural arches, anterior and posterior articular facets on base, dorsal separation: present (0); absent (1). Character 123 in Villa et al. (2017); character 177 in Tschopp et al. (2018); character 201 in Wencker et al. (2021). Note: Anterior articular facet is for occipital condyle; posterior articular facet is for odontoid process of axis. Character affiliation: QN-P

204. Atlantal neural arch, posterolateral projection on base: small tubercle (0); distinct projection (1). Character 124 in Villa et al. (2017); character 178 in Tschopp et al. (2018); character 202 in Wencker et al. (2021). Character affiliation: QN-P

207. Atlantal neural arch, dorsal process, width to length: wider than long (0); subequal to narrower (1). Character 125 in Villa et al. (2017); character 179 in Tschopp et al. (2018); character 203 in Wencker et al. (2021). Character affiliation: QN-P

208. Atlantal neural arch, dorsal process, medial edge, dorsoventral height: high, with distinct medial surface (0); tapering to a thin edge (1). Character 126 in Villa et al. (2017); character 180 in Tschopp et al. (2018); character 204 in Wencker et al. (2021). Character affiliation: QN-P

209. Atlantal neural arch, indentation of posterior margin of dorsal process: deep, forming distinct posterior extension (0); shallow (1). Character 127 in Villa et al. (2017); character 181 in Tschopp et al. (2018); character 205 in Wencker et al. (2021). Character affiliation: QN-P

210. Axial centrum, articular surface with odontoid process, dorsoventral midline groove, width: narrow (0); wide, approximately 1/3 of facet (1). Character 128 in Villa et al. (2017); character 182 in Tschopp et al. (2018); character 206 in Wencker et al. (2021). Character affiliation: QN-P

211. Axial centrum, depression on posterior articular condyle: absent (0); present (1). Character 129 in Villa et al. (2017); character 183 in Tschopp et al. (2018); character 207 in Wencker et al. (2021). Character affiliation: QN-P

212. Axial centrum, longitudinal ventral crest: absent (0); present (1). Character 130 in Villa et al. (2017); character 184 in Tschopp et al. (2018); character 208 in Wencker et al. (2021). Character affiliation: QN-P

213. Axial centrum, neural canal floor, longitudinal median ridge, shape: continuous (0); interrupted at midlength (1). Character 131 in Villa et al. (2017); character 185 in Tschopp et al. (2018); character 209 in Wencker et al. (2021). Character affiliation: QN-P

214. Axial intercentrum, ventral keel, anterior extension: absent (0); present (1). Character 132 in Villa et al. (2017); character 186 in Tschopp et al. (2018); character 210 in Wencker et al. (2021). Character affiliation: QN-P

215. Axial intercentrum, ventral keel, collateral posterior projections on proximal base: absent (0); present (1). Character 133 in Villa et al. (2017); character 187 in Tschopp et al. (2018); character 211 in Wencker et al. (2021). Character affiliation: QN-P

216. Axis, postzygapophyseal facets, shape in posterior view: straight (0); concave (1). Character 134 in Villa et al. (2017); character 188 in Tschopp et al. (2018); character 212 in Wencker et al. (2021). Character affiliation: QN-P

217. Axial, neural spine, posterior extension: terminates anterior to or at posterior end of centrum (0); exceeds posterior end of centrum (1). Character 135 in Villa et al. (2017); character 189 in Tschopp et al. (2018); character 213 in Wencker et al. (2021). Character affiliation: QN-P

218. Axial, neural spine, sprl, shape: simple (0); bifurcates ventrally, forming transverse ridge posterior to prezygapophyseal facet (1). Character 136 in Villa et al. (2017); character 190 in Tschopp et al. (2018); character 214 in Wencker et al. (2021). Note: Can have bilateral asymmetry. Character affiliation: QN-P

219. Axis, posteriorly projecting process dorsal to postzygapophysis: absent (0); present (1). Character 137 in Villa et al. (2017); character 191 in Tschopp et al. (2018, wording modified); character 215 in Wencker et al. (2021). Character affiliation: QN-P

220. Presacral centrum, posterior articular condyle, transverse expansion compared to centrum: wider (0); narrower, condyle circumscribed by distinct groove dorsally and laterally (1). (Hoffstetter

and Gasc, 1969); character 138 in Villa et al. (2017); character 192 in Tschopp et al. (2018); character 216 in Wencker et al. (2021). Character affiliation: QN-P

221. Cervical, neural spine, dorsal edge, shape: simple (0); with longitudinal groove resulting in slight bifurcation (1). Character 139 in Villa et al. (2017); character 193 in Tschopp et al. (2018); character 217 in Wencker et al. (2021). Character affiliation: QN-P

222. Postaxial, presacral neural spine, shape in lateral view: subparallel anterior and posterior edges (0); anterior edge much more inclined than posterior edge (1). Character 140 in Villa et al. (2017); character 194 in Tschopp et al. (2018); character 218 in Wencker et al. (2021). Character affiliation: QN-P

223. Postaxial, presacral neural arch, zygosphene-zygantrum articulation: absent (0); present (1). (Hoffstetter and Gasc, 1969); character 96 in Estes et al. (1988); character 195 in Tschopp et al. (2018, polarity reversed due to limited taxon sampling); character 219 in Wencker et al. (2021). Character affiliation: QN-P

224. Anterior postaxial, cervical neural spines, inclination of anterior edge in relation to neural canal floor: weak, less than 40° (0); strong, 40° (1). Character 141 in Villa et al. (2017); character 196 in Tschopp et al. (2018); character 220 in Wencker et al. (2021). Character affiliation: QN-P

225. Cervical vertebra 3, ossified cervical ribs: absent (0); present (1). (Arribas, 1998); character 142 in Villa et al. (2017); character 197 in Tschopp et al. (2018); character 221 in Wencker et al. (2021). Character affiliation: QN-P

226. Cervical ribs, expansion of distal end of anterior elements: wide (0); narrow, not significantly wider than anterior end (1). Character 143 in Villa et al. (2017); character 198 in Tschopp et al. (2018); character 222 in Wencker et al. (2021). Character affiliation: QN-P

227. Cervical intercentra, lateral crests: absent (0); present (1). (Al-Hassawi, 2004); character 199 in Tschopp et al. (2018); character 223 in Wencker et al. (2021). Character affiliation: QN-P

228. Postaxial, cervical intercentra, position: articulate with anterior element (0); between anterior and posterior centra (1); articulate only with more posterior element (2). Character 97-98 in Estes et al. (1988); characters 46 in Müller (2001); character 66 in Al-Hassawi (2004); modified after Al-Hassawi (2004) by reducing number of character states. Character affiliation: QN-P

229. Dorsal synapophyses, foramen on dorsolateral portion: absent (0); present (1). Character 145 in Villa et al. (2017); character 200 in Tschopp et al. (2018); character 224 in Wencker et al. (2021).

Character affiliation: QN-P

230. Dorsal vertebrae, posterior centrosynapophyseal lamina: absent (0); present (1). Character 146 in Villa et al. (2017); character 201 in Tschopp et al. (2018); character 225 in Wencker et al. (2021). Character affiliation: QN-P

231. Dorsal vertebral spines, foramina on lateral surface of spol: absent (0); present (1). Character 147 in Villa et al. (2017); character 202 in Tschopp et al. (2018); character 226 in Wencker et al. (2021). Character affiliation: QN-P

232. Posterior dorsal vertebral centra, ventral keel: absent (0); present (1). Character 144 in Villa et al. (2017); character 203 in Tschopp et al. (2018, modified); character 227 in Wencker et al. (2021). Character affiliation: QN-P

233. Posterior dorsal neural spines, development: distinct, elevated (0); reduced to a ridge (1). Character 148 in Villa et al. (2017); character 204 in Tschopp et al. (2018); character 228 in Wencker et al. (2021). Character affiliation: QN-P

234. Sacral vertebra 2, pleurapophyses, shape in dorsal view: curved (0); straight (1). Character 149 in Villa et al. (2017); character 205 in Tschopp et al. (2018, wording modified); character 229 in Wencker et al. (2021). Character affiliation: QN-P

235. Sacral vertebra 2, pleurapophyses, posterolateral projection on posterior edge: present (0);absent (1). Character 206 in Tschopp et al. (2018); character 230 in Wencker et al. (2021).Character affiliation: QN-P

236. Caudal, autotomic vertebrae, transverse processes on posterior portion: absent (0); present (1). (Etheridge, 1967); character 12 in Arnold (1973, fig. 4); character 31 in Arnold (1989, fig.11); character 19 in Arnold et al. (2007); character 150 in Villa et al. (2017, modified after Arnold et al., 2007 by splitting the character); character 207 in Tschopp et al. (2018); character 231 in Wencker et al. (2021). Character affiliation: QN-P

237. Caudal, autotomic vertebrae, transverse processes on posterior portion (if present), length compared to anterior process: shorter (0); longer (1). (Etheridge, 1967); character 12 in Arnold (1973, fig. 4); character 31 in Arnold (1989, fig.11); character 19 in Arnold et al. (2007); character 151 in Villa et al. (2017, modified after Arnold et al., 2007 by splitting the character); character 208 in Tschopp et al. (2018); character 232 in Wencker et al. (2021); wording modified. Character affiliation: QN-P

238. Caudal centra, pedicels for haemal arches: present (0); absent (1). (Pregill *et al.*, 1986); character 475 in Gauthier et al. (2012); character 209 in Tschopp et al. (2018, modified to adapt to restricted taxon sampling); character 233 in Wencker et al. (2021). Character affiliation: QN-P

239. Chevrons, articulation with caudal vertebrae: entirely with more anterior element (0); between anterior and posterior caudal centrum (1). (Hoffstetter and Gasc, 1969); character 210 in Tschopp et al. (2018); character 234 in Wencker et al. (2021). Character affiliation: QN-P

240. Scapulacoracoid, secondary ventral coracoid emargination: absent (0); present (1). (Lécuru, 1968); character 113 in Estes et al. (1988); character 51 in Müller (2001); character 211 in Tschopp et al. (2018, wording modified); character 235 in Wencker et al. (2021). Character affiliation: QN-P

241. Clavicle, medial loop: complete (0); interrupted posteriorly (1). (Boulenger, 1920); character 9 in Arnold (1973, fig. 3); character 22 in Arnold (1989, fig. 9); character 15 in Arnold et al. (2007); character 152 in Villa et al. (2017, modified after Arnold et al., 2017); character 212 in Tschopp et al. (2018); character 236 in Wencker et al. (2021). Character affiliation: QN-P

242. Interclavicle, transverse arms, orientation: perpendicular to sagittal axis or slightly curving forward (0); directed obliquely backwards (1). Character 11 in Arnold (1973, fig. 3); character 24 in Arnold (1989, fig. 10); character 16 in Arnold et al. (2007); character 153 in Villa et al. (2017, wording modified after Arnold et al., 2007); character 213 in Tschopp et al. (2018); character 237 in Wencker et al. (2021). Character affiliation: QN-P

243. Sternal fontanelle: absent (0); present (1). Character 121 in Estes et al. (1988); character 481 in Gauthier et al. (2012); character 214 in Tschopp et al. (2018); character 238 in Wencker et al. (2021). Character affiliation: QN-P

244. Sternal fontanelle (if present), shape: heart-shaped (0); oval (1). (Siebenrock, 1894); character 10 in Arnold (1973, fig. 3); character 26 in Arnold (1989, fig. 10); character 17 in Arnold et al. (2007); character 154 in Villa et al. (2017, modified after Arnold et al., 2007 by reversing polarity); character 215 in Tschopp et al. (2018); character 239 in Wencker et al. (2021); wording modified. Character affiliation: QN-P

245. Xiphisternal fontanelle: absent (0); present (1). Character 485 in Gauthier et al. (2012); character 216 in Tschopp et al. (2018); character 240 in Wencker et al. (2021). Character affiliation: QN-P

246. Inscriptional ribs: absent (0); present (1). (Arnold, 1973); character 30 in Arnold (1989); character 18 in Arnold et al. (2007); character 155 in Villa et al. (2017, modified after Arnold et al., 2007 by reversing polarity); character 217 in Tschopp et al. (2018). Character affiliation: QN-P

247. Humerus, area dorsal to deltopectoral crest: concave (0); flat to convex (1). Character 218 in Tschopp et al. (2018); character 241 in Wencker et al. (2021). Character affiliation: QN-P

248. Humerus, subcondylar and subtrochlear fossae, shape: form an m-shape, with a deep dorsal incision between them (0); conjoined completely medially (1). (Lécuru, 1969); character 219 in Tschopp et al. (2018); character 242 in Wencker et al. (2021). Character affiliation: QN-P

249. Manus and pes, distal-most non-ungual phalanx, length compared to preceding phalanx: equal to shorter (0); longer (1). (Arnold, 1998); character 157 in Villa et al. (2017); character 220 in Tschopp et al. (2018); character 243 in Wencker et al. (2021). Character affiliation: QN-P

250. Ilium, preacetabular process: present (0); absent (1). (Lee, 1998); character 521 in Gauthier et al. (2012); character 221 in Tschopp et al. (2018, wording modified); character 244 in Wencker et al. (2021). Character affiliation: QN-P

251. Ischium, posterior process, shape: subtriangular (0); pointed process, posteroventral edge of ischium is concave (1). Character 158 in Villa et al. (2017); character 222 in Tschopp et al. (2018); character 245 in Wencker et al. (2021). Character affiliation: QN-P

252. Ischium, posterodorsal edge, shape: straight to slightly concave (0); convex, or somewhat sinuous (1). Character 159 in Villa et al. (2017); character 223 in Tschopp et al. (2018); character 246 in Wencker et al. (2021). Character affiliation: QN-P

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(Available also at https://figshare.com/s/c4f60604a2a013f6a86d)

List of OTUs included in the study

Institutional abbreviations: AMNH, American Museum of Natural History; BSPG, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; CIPA, Osteoteca, Laboratorio Arqueociencias, Lisbon, Portugal; COMGR, Collezione Osteologica Mauro Grano, Roma, Italy; FMNH, Field Museum of Natural History, Chicago, USA; GMZ, Grant Museum of Zoology and Comparative Anatomy, University College London, UK; HUJ-OST, Osteological Collections, Hebrew University of Jerusalem, Israel; ICP, Institut Català de Paleontologia Miquel Crusafont, Barcelona, Spain; IRSNB, Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; MDHC, Massimo Delfino Herpetological Collection in the Museum of Geology and Paleontology of the Department of Earth Sciences of the University of Turin, Italy; MNCN, Museo Nacional de Ciencias Naturales, Madrid, Spain; MNHN, Muséum National d'Histoire Naturelle, Paris, France; MRAC, Musée Royal de l'Afrique Centrale, Tervuren, Belgium; NHMUK, Natural History Museum, London, UK; NHMW, Naturhistorisches Museum Wien, Austria; PIMUZ, Paläontologisches Institut und Museum der Universität Zürich, Switzerland; SRK, Sammlung Ralf Kosma, Staatliches Naturhistorisches Museum Braunschweig, Germany; UAM, Universitad Autónoma de Madrid, Spain; UCBL, Université Claude Bernard, Lyon, France; YPM, Yale Peabody Museum, New Haven, USA; ZZSiD, Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Krakow, Poland.

Outgroup taxa:

GEKKONIDAE

Gekko gecko (MDHC 112)

TEIIDAE

Salvator merianae (COMGR 235)

Tupinambis teguixin (AMNH R15524, ZMH R12172)

ANGUIMORPHA

Varanus exanthematicus (MDHC 335)

Anguis veronensis (MDHC 102)

Pseudopus apodus (MDHC 214)

SCINCOIDAE

Chalcides ocellatus (MDHC 193)

Broadleysaurus major (MDHC 164)

Ablepharus kitaibelli (MDHC 239)

AMPHISBAENIA

Blanus rufus (MDHC 156)

Blanus strauchi (MDHC 287)

LACERTIDAE

Gallotiinae

Gallotia caesaris (SRK 00.346)

Gallotia simonyi (NHMW 849)

Gallotia stehlini (MNCN-22226)

Psammodromus algirus (AMNH R5960, AMNH R9297, NHMW 788, UAM R PS-9)

Lacertinae

Eremiadini

Acanthodactylus boskianus (MDHC 276)

Acanthodactylus erythrurus (UAM R AC-VII)

Eremias velox (NHMW 822)

Mesalina guttulata (MDHC 272)

Ophisops elegans (MDHC 281, MDHC 282, AMNH R43265, AMNH R90235)

Lacertini

Algyroides fitzingeri (MDHC 351)

Algyroides nigropunctatus (NHMW 797)

Anatololacerta danfordi (MDHC 283, MDHC 284)

Archaeolacerta bedriagae (MDHC 167, SRK 00.120)

Iberolacerta cyreni (UAM R Lm-4)

Iberolacerta monticola (UAM R Lm-77, UAM R Lm-92)

Phoenicolacerta troodica (MDHC 318, MDHC 319)

Podarcis hispanicus (UAM R H-30)

Podarcis muralis (MDHC 311, MDHC 312, MDHC 313, NHMUK 1920.1.20.801)

Podarcis siculus (MDHC 25, MDHC 125, AMNH r110436)

Podarcis tiliguerta (MDHC 153, MDHC 154)

Podarcis waglerianus (MDHC 390)

Takydromus sp. (MDHC 151)

Zootoca vivipara (MDHC 179)

Ingroup taxa:

Timon lepidus (CIPA 761, MDHC 216, AMNH R57770, MNCN-41021, MNHN 1887-545, MRAC 3390, MRAC 92-050-R-1, NHMW 699, PIMUZ A/III 0965, GMZ VD. 36 XI.246)

Timon kurdistanicus (NHMW 18545)

Timon pater (NHMUK 1920.1.20.2722, NHMUK 1920.1.20.1259, GMZ D.36 X.171)

Timon princeps (NHMW 32881)

Lacerta agilis (AMNH R76854, CIPA 1550, MDHC 176, MDHC 177, MDHC 178, MDHC 230, MDHC 231, MNCN-15979, MNHN 1963-49, NHMW 802, PIMUZ A/III 0902, ZMH R12174)

Lacerta bilineata (MDHC 15, MDHC 48, MDHC 73, MDHC 77, MDHC 84, MDHC 381, MDHC 420, AMNH R1148, AMNH R109472, MNCN-16505, PIMUZ A/III 1276, UAM Q-21)

Lacerta media (NHMW 34809, HUJ-OST-Z-299, HUJ-OST-Z-396)

Lacerta schreiberi (CIPA 778, CIPA 1256, CIPA 1511, CIPA 1517, NHMUK 1906.10.30.14, UAM S-6)

Lacerta strigata (MDHC 304, NHMW 10918)

Lacerta trilineata (MDHC 240, MDHC 241, MDHC 295, MDHC 356, MRAC 95-050-R-0001, MRAC 95-050-R-0002, NHMUK 1914.1.12.1, ZZSiD R/235/76)

Lacerta viridis (AMNH R154761, AMNH R154762, MNCN-16504, MNHN 1888-139, MNHN 1887-813, MRAC 91-077R-76, NHMW 887, NHMW 906, NHMW 32879-3, ZZSiD R/287/80, ZZSiD R/463/87)

(Available also at https://figshare.com/s/c4f60604a2a013f6a86d)

Information about the ontogenetic state, sex, and geography of the ingroup OTUs of *Lacerta* and *Timon*.

Institutional abbreviations: AMNH, American Museum of Natural History; CIPA, Osteoteca, Laboratorio Arqueociencias, Lisbon, Portugal; GMZ, Grant Museum of Zoology and Comparative Anatomy, University College London, UK; HUJ-OST, Osteological Collections, Hebrew University of Jerusalem, Israel; MDHC, Massimo Delfino Herpetological Collection in the Museum of Geology and Paleontology of the Department of Earth Sciences of the University of Turin, Italy; MNCN, Museo Nacional de Ciencias Naturales, Madrid, Spain; MNHN, Muséum National d'Histoire Naturelle, Paris, France; MRAC, Musée Royal de l'Afrique Centrale, Tervuren, Belgium; NHMUK, Natural History Museum, London, UK; NHMW, Naturhistorisches Museum Wien, Austria; PIMUZ, Paläontologisches Institut und Museum der Universität Zürich, Switzerland; UAM, Universitad Autónoma de Madrid, Spain; ZZSiD, Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Krakow, Poland.

Taxonomy	Specimen number	Skeletal maturity	Sex	Geography
Lacerta agilis	AMNH R76854	?	?	?
	CIPA 1550	mature	f	Birkdale Dunes, Merseyside, England
	MDHC 176	mature	f	Poland
	MDHC 177	mature	f	Poland
	MDHC 178	mature	m	Poland
	MDHC 230	mature	?	Captivity
	MDHC 231	mature	?	Captivity
	MNCN-15979	mature	?	Krakow, Poland
	MNHN 1963-49	mature	?	?
	NHMW 802	mature	?	Reckawinkel, Austria
	ZMH R12174	?	?	Wehr, Germany
	PIMUZ A/III 0902	?	?	?
L. bilineata	MDHC 15	mature	m	Italy
	MDHC 48	immature	?	Italy
	MDHC 73	immature	?	Italy
	MDHC 77	mature	m	Italy
	MDHC 84	mature	f	Italy

Specimen number	Skeletal maturity	Sex	Geography
MDHC 381	?	?	Italy
			Vallone di Piantonetto, Piemonte,
MDHC 420	mature		Italy
AMNH R1148	?	?	Italy
AMNH R109472	?	?	Italy
			Santillana del Mar, Santander,
MNCN-16505	mature	f	Cantabria, Spain
PIMUZ A/III 1276	mature	?	Ticino, Switzerland
UAM Q-21	mature	?	?
NHMW 34809	?	?	Van, Turkey
HUJ-OST-Z-299	?	?	?
HUJ-OST-Z-396	?	?	?
CIPA 778	mature	?	Beira Alta, Portugal
CIPA 1256	mature	f	Minho, Portugal
CIPA 1511	mature	m?	Minho, Portugal
CIPA 1517	immature	?	Minho, Portugal
NHMUK		-	
1906.10.30.14	mature	m	Loroya Valley
UAM S-6	mature	m	?
MDHC 304	?	?	Georgia
NHMW10918	mature	m	?
MDHC 240	mature	f	Greece
MDHC 241	mature	f	Greece
MDHC 295	mature	?	Turkey
MDHC 356	mature	?	Croatia
MRAC 95-050-R-			
0001	mature	?	?
MRAC 95-050-R- 0002	mature	?	?
NHMUK			
1914.1.12.1	mature	m	Zara, Dalmatia
ZZSiD R/235/76	mature	m	Burgas, Bulgaria
AMNH R154761	?	?	Czechoslovakia
AMNH R154762	?	?	Czechoslovakia
MNCN-16504	mature	?	Bulgaria
MNHN 1887-813	immature	?	?
MNHN 1888-139	mature	?	?
MRAC 91-077-R-			
76	mature	?	Jugoslavia
NHMW 887	mature	?	Zara vecchia, Jugoslavia
NHMW 906	mature	?	Lussin, ?Jugoslavia
NHMW 32879:3	mature	?	?
ZZSiD R/287/80	mature	?	Bulgaria
77SD D/462/97	mature	2	2
	Specimen number MDHC 381 MDHC 420 AMNH R1148 AMNH R109472 MNCN-16505 PIMUZ A/III 1276 UAM Q-21 NHMW 34809 HUJ-OST-Z-299 HUJ-OST-Z-396 CIPA 778 CIPA 1256 CIPA 1511 CIPA 1517 NHMUK 1906.10.30.14 UAM S-6 MDHC 240 MDHC 241 MDHC 255 MDHC 356 MRAC 95-050-R-0001 MRAC 95-050-R-0002 NHMUK 1914.1.12.1 ZZSID R/235/76 AMNH R154761 AMNH R154762 MNCN-16504 MNHN 1887-813 MNHN 1887-813 MNHN 1887-813 MNHN 1887 MIMW 32879:3 ZZSID R/287/80	Specimen numberSkeletal maturityMDHC 381?MDHC 420matureAMNH R1148?AMNH R109472?MNCN-16505maturePIMUZ A/III 1276matureUAM Q-21matureNHMW 34809?HUJ-OST-Z-299?HUJ-OST-Z-396?CIPA 778matureCIPA 1511matureCIPA 1517immatureNHMUK1906.10.30.141906.10.30.14matureMDHC 304?NHMW10918matureMDHC 240matureMDHC 241matureMDHC 255matureMDHC 256matureMDHC 241matureMDHC 241matureMDHC 241matureMDHC 356matureMRAC 95-050-R- 0001matureMRAC 95-050-R- 0002matureMNHN 1887-813immatureMNHN 1887-813immatureMNHN 1887-813immatureMNHN 1887-813immatureMNHN 1887-813immatureNHMW 906matureNHMW 906matureNHMW 32879:3matureNHMW 32879:3mature	Specimen numberSkeletal maturitySexMDHC 381??MDHC 420mature?AMNH R1148??AMNH R109472??MNCN-16505maturefPIMUZ A/III 1276mature?UAM Q-21mature?NHMW 34809??HUJ-OST-Z-299??HUJ-OST-Z-396??CIPA 178mature?CIPA 1511maturem?CIPA 1517immature?NHMUKmaturem1906.10.30.14maturemUAM S-6maturemMDHC 304??NHMUK??MDHC 240maturefMDHC 255mature?MDHC 356mature?MRAC 95-050-R-mature?0001mature?MRAC 95-050-R-mature?MNHN 1847-813immature?MNHN 1887-813immature?MNHN 1887-813immature?MNHN 1887-813immature?MHMW 887mature?NHMW 887mature?NHMW 906mature?NHMW 906mature?NHMW 32879:3mature?XIANP 7207///////////////////////////////

Taxonomy	Specimen number	Skeletal maturity	Sex	Geography
Timon lepidus	CIPA 761	mature	?	Portugal
	MDHC 216	mature	?	?
	AMNH R57770	?	?	?
	MNCN-41021	mature	m	San Agustín de Guadalix, Madrid, Spain
	MNHN 1887-545	mature	?	?
	MRAC 3390	mature	?	Spain
	MRAC 92-050-R-1	mature	?	Piedrafita de Babia, Spain
	GMZ vd36.xi246	?	?	?
	NHMW 699	mature	?	?
	PIMUZ A/III 0965	mature	?	?
Timon pater	GMZ d.36_x.171	?	?	?
	NHMUK 1920.1.20.1259	mature	?	Lambessa, Algeria
	NHMUK 1920.1.20.2722	mature	m	Bougie, Algeria
Timon kurdistanicus	NHMW18545	mature	?	Turkey
Timon princeps	NHMW32881	mature	m	?

(Available also at https://figshare.com/s/c4f60604a2a013f6a86d)

List of fossil OTUs used as basis for the distribution pattern of missing values for the simulated datasets.

Institutional abbreviations: MNHN, Muséum National d'Histoire Naturelle, Paris, France; RH for Musée de Gannat, Gannat, France; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; UCBL, Université Claude Bernard, Lyon, France; USTL, Université Montpellier 2, Sciences et Techniques du Languedoc, Montpellier, France.

Dracaenosaurus croizeti (UCBL97682 den, UCBL97690 den, CodH1-75 pre, CodCoucheVerte E1-25 max, MNHN COR5, MNHN F COR7, MNHN COR4)

"Lacerta" siculimelitensis ("locality" samples from: Malta, Grotta di Spinagallo (Sicily), Contrada Fusco (Sicily), Gargano (Foggia), Orosei (Sardinia) without collection number)

"Lacerta filholi" (MNHN PFR11001 den, MNHN PFR11013 den, MNHN PFR11015 max, UCBL FSL97689 den coderet)

Ligerosaurus pouiti (MNHN-PtF 31374)

Mediolacerta roceki (MNHN-PFR 11006, SMNS 59446, MNHN pfr11002, MNHN QU17728)

Plesiolacerta lydekkeri (MNHN ECB1702, MNHN QU17179, MNHN QU17166, MNHN QU17676, MNHN QU17713, MNHN QU17727, MNHN QU17745, MNHN QU17168, MNHN SNM1, USTL BRT857, USTL LAV1274, USTL PRR20051)

Pseudeumeces cadurcensis (MNHN PFR11004, MNHN QU17169, MNHN QU17180, MNHN QU17749, RH B2 0023, RH B2 771, RH B2 775, RH B2 1179)

(Available also at https://figshare.com/s/c4f60604a2a013f6a86d)

Custom python scripts (also available in the supplementary material of Tschopp et al., in press)

Script 1: 25-incompleteness script

(calculation of incompleteness; overall incompleteness and incompleteness of the 25 character sections)

if __name__ == '__main__':

import pandas as pd

 $from_column_1 = 0$

 $to_column_1 = 10$

from_column_2 = 10

to_column_2 = 20

from_column_3 = 20

 $to_column_3 = 30$

 $from_column_4 = 30$

 $to_column_4 = 40$

 $from_column_5 = 40$

 $to_column_5 = 50$

from_column_6 = 50

 $to_column_6 = 60$

from_column_7 = 60
to_column_7 = 70
from_column_8 = 70
to_column_8 = 80
from_column_9 = 80
$to_column_9 = 90$
from_column_10 = 90
to_column_10 = 100
from_column_11 = 100
to_column_11 = 110
from_column_12 = 110
to_column_12 = 120
from_column_13 = 120
to_column_13 = 130
$from_column_14 = 130$
to_column_14 = 140
$from_column_15 = 140$
to_column_15 = 150

from_column_16 = 150

to_column_16 = 160
$from_column_17 = 160$
to_column_17 = 170
from_column_18 = 170
to_column_18 = 180
from_column_19 = 180
to_column_19 = 190
$from_column_20 = 190$
to_column_20 = 200
$from_column_21 = 200$
to_column_21 = 210
from_column_22 = 210
$to_column_22 = 220$
$from_column_23 = 220$
to_column_23 = 230
$from_column_24 = 230$
to_column_24 = 240
$from_column_25 = 240$
to_column_25 = 253

#insert name of file for calculation

input_matrix = pd.read_csv('[filename].csv', index_col=0)

matrix_part_to_sample_from_1 = input_matrix.iloc[:, from_column_1:to_column_1] matrix_part_to_sample_from_2 = input_matrix.iloc[:, from_column_2:to_column_2] matrix_part_to_sample_from_3 = input_matrix.iloc[:, from_column_3:to_column_3] matrix_part_to_sample_from_4 = input_matrix.iloc[:, from_column_4:to_column_4] matrix_part_to_sample_from_5 = input_matrix.iloc[:, from_column_5:to_column_5] matrix_part_to_sample_from_6 = input_matrix.iloc[:, from_column_6:to_column_6] matrix_part_to_sample_from_7 = input_matrix.iloc[:, from_column_7:to_column_7] matrix_part_to_sample_from_8 = input_matrix.iloc[:, from_column_8:to_column_8] matrix_part_to_sample_from_9 = input_matrix.iloc[:, from_column_9:to_column_9] matrix_part_to_sample_from_10 = input_matrix.iloc[:, from_column_10:to_column_10] matrix_part_to_sample_from_11 = input_matrix.iloc[:, from_column_11:to_column_11] matrix_part_to_sample_from_12 = input_matrix.iloc[:, from_column_12:to_column_12] matrix_part_to_sample_from_13 = input_matrix.iloc[:, from_column_13:to_column_13] matrix_part_to_sample_from_14 = input_matrix.iloc[:, from_column_14:to_column_14] matrix_part_to_sample_from_15 = input_matrix.iloc[:, from_column_15:to_column_15] matrix_part_to_sample_from_16 = input_matrix.iloc[:, from_column_16:to_column_16] matrix_part_to_sample_from_17 = input_matrix.iloc[:, from_column_17:to_column_17] matrix_part_to_sample_from_18 = input_matrix.iloc[:, from_column_18:to_column_18] matrix_part_to_sample_from_19 = input_matrix.iloc[:, from_column_19:to_column_19] matrix_part_to_sample_from_20 = input_matrix.iloc[:, from_column_20:to_column_20] matrix_part_to_sample_from_21 = input_matrix.iloc[:, from_column_21:to_column_21] matrix_part_to_sample_from_22 = input_matrix.iloc[:, from_column_22:to_column_22] matrix_part_to_sample_from_23 = input_matrix.iloc[:, from_column_23:to_column_23] matrix_part_to_sample_from_24 = input_matrix.iloc[:, from_column_24:to_column_24]

matrix_part_to_sample_from_25 = input_matrix.iloc[:, from_column_25:to_column_25]

control_result_1 = (matrix_part_to_sample_from_1.values == '?').sum() / (matrix_part_to_sample_from_1.shape[0] * matrix_part_to_sample_from_1.shape[1]) control_result_2 = (matrix_part_to_sample_from_2.values == '?').sum() / (matrix_part_to_sample_from_2.shape[0] * matrix_part_to_sample_from_2.shape[1]) control_result_3 = (matrix_part_to_sample_from_3.values == '?').sum() / (matrix_part_to_sample_from_3.shape[0] * matrix_part_to_sample_from_3.shape[1]) control_result_4 = (matrix_part_to_sample_from_4.values == '?').sum() / (matrix_part_to_sample_from_4.shape[0] * matrix_part_to_sample_from_4.shape[1]) control_result_5 = (matrix_part_to_sample_from_5.values == '?').sum() / (matrix_part_to_sample_from_5.shape[0] * matrix_part_to_sample_from_5.shape[1]) control_result_6 = (matrix_part_to_sample_from_6.values == '?').sum() / (matrix_part_to_sample_from_6.shape[0] * matrix_part_to_sample_from_6.shape[1]) control_result_7 = (matrix_part_to_sample_from_7.values == '?').sum() / (matrix_part_to_sample_from_7.shape[0] * matrix_part_to_sample_from_7.shape[1]) control_result_8 = (matrix_part_to_sample_from_8.values == '?').sum() / (matrix_part_to_sample_from_8.shape[0] * matrix_part_to_sample_from_8.shape[1]) control_result_9 = (matrix_part_to_sample_from_9.values == '?').sum() / (matrix_part_to_sample_from_9.shape[0] * matrix_part_to_sample_from_9.shape[1]) control_result_10 = (matrix_part_to_sample_from_10.values == '?').sum() / (matrix_part_to_sample_from_10.shape[0] * matrix_part_to_sample_from_10.shape[1]) control_result_11 = (matrix_part_to_sample_from_11.values == '?').sum() / (matrix_part_to_sample_from_11.shape[0] * matrix_part_to_sample_from_11.shape[1]) control_result_12 = (matrix_part_to_sample_from_12.values == '?').sum() / (matrix_part_to_sample_from_12.shape[0] * matrix_part_to_sample_from_12.shape[1]) control_result_13 = (matrix_part_to_sample_from_13.values == '?').sum() / (matrix_part_to_sample_from_13.shape[0] * matrix_part_to_sample_from_13.shape[1]) control_result_14 = (matrix_part_to_sample_from_14.values == '?').sum() / (matrix_part_to_sample_from_14.shape[0] * matrix_part_to_sample_from_14.shape[1])

control_result_15 = (matrix_part_to_sample_from_15.values == '?').sum() /
(matrix_part_to_sample_from_15.shape[0] * matrix_part_to_sample_from_15.shape[1])

<pre>control_result_16 = (matrix_part_to_sample_from_16.values == '?').sum() / (matrix_part_to_sample_from_16.shape[0] * matrix_part_to_sample_from_16.shape[1])</pre>
<pre>control_result_17 = (matrix_part_to_sample_from_17.values == '?').sum() / (matrix_part_to_sample_from_17.shape[0] * matrix_part_to_sample_from_17.shape[1])</pre>
<pre>control_result_18 = (matrix_part_to_sample_from_18.values == '?').sum() / (matrix_part_to_sample_from_18.shape[0] * matrix_part_to_sample_from_18.shape[1])</pre>
<pre>control_result_19 = (matrix_part_to_sample_from_19.values == '?').sum() / (matrix_part_to_sample_from_19.shape[0] * matrix_part_to_sample_from_19.shape[1])</pre>
<pre>control_result_20 = (matrix_part_to_sample_from_20.values == '?').sum() / (matrix_part_to_sample_from_20.shape[0] * matrix_part_to_sample_from_20.shape[1])</pre>
<pre>control_result_21 = (matrix_part_to_sample_from_21.values == '?').sum() / (matrix_part_to_sample_from_21.shape[0] * matrix_part_to_sample_from_21.shape[1])</pre>
<pre>control_result_22 = (matrix_part_to_sample_from_22.values == '?').sum() / (matrix_part_to_sample_from_22.shape[0] * matrix_part_to_sample_from_22.shape[1])</pre>
<pre>control_result_23 = (matrix_part_to_sample_from_23.values == '?').sum() / (matrix_part_to_sample_from_23.shape[0] * matrix_part_to_sample_from_23.shape[1])</pre>
<pre>control_result_24 = (matrix_part_to_sample_from_24.values == '?').sum() / (matrix_part_to_sample_from_24.shape[0] * matrix_part_to_sample_from_24.shape[1])</pre>
<pre>control_result_25 = (matrix_part_to_sample_from_25.values == '?').sum() / (matrix_part_to_sample_from_25.shape[0] * matrix_part_to_sample_from_25.shape[1])</pre>

miss = (input_matrix.values == '?').sum()

incompleteness = ((input_matrix.values == '?').sum()) / (input_matrix.shape[0] *
input_matrix.shape[1])

print(f'number of taxa: {input_matrix.shape[0]}, number of characters: {input_matrix.shape[1]}, number of '?': {miss}, overall percentage of missing values: {incompleteness}, percentage of missing values for partitions: columns 1 - 10: {control_result_1}, columns 11 - 20: {control_result_2}, columns 21 - 30: {control_result_3}, columns 31 - 40: {control_result_4}, columns 41 - 50: {control_result_5}, columns 51 - 60: {control_result_6}, columns 61 - 70: {control_result_7}, columns 71 - 80: {control_result_8}, columns 81 - 90: {control_result_9}, columns 91 - 100: {control_result_10}, columns 101 - 110: {control_result_11}, columns 111 - 120: {control_result_12}, columns 121 - 130: {control_result_13}, columns 131 - 140: {control_result_14}, columns 141 - 150: {control_result_15}, columns 151 - 160: {control_result_16}, columns 151 - 160: {control_result_16}, columns 171 - 180:

{control_result_18}, columns 181 - 190: {control_result_19}, columns 191 - 200: {control_result_20}, columns 201 - 210: {control_result_21}, columns 211 - 220: {control_result_22}, columns 221 - 230: {control_result_23}, columns 231 - 240: {control_result_24}, columns 241 - 253: {control_result_25}")

Script 2: fossil-simulation script	
(deletion of missing entries)	
ifname == 'main':	
import pandas as pd	
MISSING = "missing"	
$from_column_1 = 0$	
$to_column_1 = 10$	
percent_missing_1 = #insert percentage to be deleted from the fraction; e.	g., 0.4
from_column_2 = 10	
$to_column_2 = 20$	
percent_missing_2 = #insert percentage to be deleted from the fraction; e.	g., 0.4
from_column_3 = 20	
to_column_3 = 30	
percent_missing_3 = #insert percentage to be deleted from the fraction; e.	g., 0.4
from_column_4 = 30	
$to_column_4 = 40$	
percent_missing_4 = #insert percentage to be deleted from the fraction; e.	g., 0.4
from_column_5 = 40	
$to_column_5 = 50$	
percent_missing_5 = #insert percentage to be deleted from the fraction; e.	g., 0.4
from_column_6 = 50	
$to_column_6 = 60$	
percent_missing_6 = #insert percentage to be deleted from the fraction; e.	g., 0.4
from_column_7 = 60	
$to_column_7 = 70$	
percent_missing_7 = #insert percentage to be deleted from the fraction; e.	g., 0.4

from_column_8 = 70

$to_column_8 = 80$
percent_missing_8 = #insert percentage to be deleted from the fraction; e.g., 0.4
from_column_9 = 80
to_column_9 = 90
percent_missing_9 = #insert percentage to be deleted from the fraction; e.g., 0.4
from_column_10 = 90
$to_column_10 = 100$
percent_missing_10 = #insert percentage to be deleted from the fraction; e.g., 0.4
from_column_11 = 100
$to_column_11 = 110$
percent_missing_11 = #insert percentage to be deleted from the fraction; e.g., 0.4
$from_column_12 = 110$
to_column_12 = 120
percent_missing_12 = #insert percentage to be deleted from the fraction; e.g., 0.4
from_column_13 = 120
to_column_13 = 130
percent_missing_13 = #insert percentage to be deleted from the fraction; e.g., 0.4
$from_column_14 = 130$
$to_column_14 = 140$
percent_missing_14 = #insert percentage to be deleted from the fraction; e.g., 0.4
$from_column_15 = 140$
$to_column_15 = 150$
percent_missing_15 = #insert percentage to be deleted from the fraction; e.g., 0.4
from_column_16 = 150
to_column_16 = 160
percent_missing_16 = #insert percentage to be deleted from the fraction; e.g., 0.4

from_column_17 = 160

to_column_17 = 170
percent_missing_17 = #insert percentage to be deleted from the fraction; e.g., 0.4
$from_column_18 = 170$
to_column_18 = 180
percent_missing_18 = #insert percentage to be deleted from the fraction; e.g., 0.4
from_column_19 = 180
to_column_19 = 190
percent_missing_19 = #insert percentage to be deleted from the fraction; e.g., 0.4
from_column_20 = 190
to_column_20 = 200
percent_missing_20 = #insert percentage to be deleted from the fraction; e.g., 0.4
$from_column_21 = 200$
to_column_21 = 210
percent_missing_21 = #insert percentage to be deleted from the fraction; e.g., 0.4
$from_column_22 = 210$
to_column_22 = 220
percent_missing_22 = #insert percentage to be deleted from the fraction; e.g., 0.4
from_column_23 = 220
to_column_23 = 230
percent_missing_23 = #insert percentage to be deleted from the fraction; e.g., 0.4
from_column_24 = 230
to_column_24 = 240
percent_missing_24 = #insert percentage to be deleted from the fraction; e.g., 0.4
$from_column_25 = 240$
to_column_25 = 253
percent_missing_25 = #insert percentage to be deleted from the fraction; e.g., 0.4

#insert name of file for deletion of entries

input_matrix = pd.read_csv('[filename].csv', index_col=0)

matrix_part_to_sample_from_1 = input_matrix.iloc[:, from_column_1:to_column_1]

index_array_1 = matrix_part_to_sample_from_1.where(matrix_part_to_sample_from_1 != '?').stack().sample(frac=percent_missing_1).index.values

```
for i, j in index_array_1:
```

input_matrix.loc[i, j] = MISSING

matrix_part_to_sample_from_2 = input_matrix.iloc[:, from_column_2:to_column_2]

index_array_2 = matrix_part_to_sample_from_2.where(matrix_part_to_sample_from_2 != '?').stack().sample(frac=percent_missing_2).index.values

for i, j in index_array_2:

input_matrix.loc[i, j] = MISSING

matrix_part_to_sample_from_3 = input_matrix.iloc[:, from_column_3:to_column_3]

index_array_3 = matrix_part_to_sample_from_3.where(matrix_part_to_sample_from_3 != '?').stack().sample(frac=percent_missing_3).index.values

for i, j in index_array_3:

input_matrix.loc[i, j] = MISSING

matrix_part_to_sample_from_4 = input_matrix.iloc[:, from_column_4:to_column_4]

index_array_4 = matrix_part_to_sample_from_4.where(matrix_part_to_sample_from_4 != '?').stack().sample(frac=percent_missing_4).index.values

for i, j in index_array_4:

input_matrix.loc[i, j] = MISSING

matrix_part_to_sample_from_5 = input_matrix.iloc[:, from_column_5:to_column_5]

index_array_5 = matrix_part_to_sample_from_5.where(matrix_part_to_sample_from_5 != '?').stack().sample(frac=percent_missing_5).index.values

for i, j in index_array_5:

input_matrix.loc[i, j] = MISSING

matrix_part_to_sample_from_6 = input_matrix.iloc[:, from_column_6:to_column_6]

index_array_6 = matrix_part_to_sample_from_6.where(matrix_part_to_sample_from_6 != '?').stack().sample(frac=percent_missing_6).index.values

for i, j in index_array_6:

input_matrix.loc[i, j] = MISSING

matrix_part_to_sample_from_7 = input_matrix.iloc[:, from_column_7:to_column_7]

index_array_7 = matrix_part_to_sample_from_7.where(matrix_part_to_sample_from_7 != '?').stack().sample(frac=percent_missing_7).index.values

for i, j in index_array_7:

input_matrix.loc[i, j] = MISSING

matrix_part_to_sample_from_8 = input_matrix.iloc[:, from_column_8:to_column_8]

index_array_8 = matrix_part_to_sample_from_8.where(matrix_part_to_sample_from_8 != '?').stack().sample(frac=percent_missing_8).index.values

for i, j in index_array_8:

input_matrix.loc[i, j] = MISSING

matrix_part_to_sample_from_9 = input_matrix.iloc[:, from_column_9:to_column_9]

index_array_9 = matrix_part_to_sample_from_9.where(matrix_part_to_sample_from_9 != '?').stack().sample(frac=percent_missing_9).index.values

for i, j in index_array_9:

input_matrix.loc[i, j] = MISSING

matrix_part_to_sample_from_10 = input_matrix.iloc[:, from_column_10:to_column_10]

index_array_10 = matrix_part_to_sample_from_10.where(matrix_part_to_sample_from_10 != '?').stack().sample(frac=percent_missing_10).index.values

for i, j in index_array_10:

input_matrix.loc[i, j] = MISSING

matrix_part_to_sample_from_11 = input_matrix.iloc[:, from_column_11:to_column_11]

index_array_11 = matrix_part_to_sample_from_11.where(matrix_part_to_sample_from_11 != '?').stack().sample(frac=percent_missing_11).index.values

for i, j in index_array_11:

input_matrix.loc[i, j] = MISSING

matrix_part_to_sample_from_12 = input_matrix.iloc[:, from_column_12:to_column_12]

index_array_12 = matrix_part_to_sample_from_12.where(matrix_part_to_sample_from_12 != '?').stack().sample(frac=percent_missing_12).index.values

for i, j in index_array_12:

input_matrix.loc[i, j] = MISSING

matrix_part_to_sample_from_13 = input_matrix.iloc[:, from_column_13:to_column_13]

index_array_13 = matrix_part_to_sample_from_13.where(matrix_part_to_sample_from_13 != '?').stack().sample(frac=percent_missing_13).index.values

for i, j in index_array_13:

input_matrix.loc[i, j] = MISSING

matrix_part_to_sample_from_14 = input_matrix.iloc[:, from_column_14:to_column_14]

index_array_14 = matrix_part_to_sample_from_14.where(matrix_part_to_sample_from_14 != '?').stack().sample(frac=percent_missing_14).index.values

for i, j in index_array_14:

input_matrix.loc[i, j] = MISSING

matrix_part_to_sample_from_15 = input_matrix.iloc[:, from_column_15:to_column_15]

index_array_15 = matrix_part_to_sample_from_15.where(matrix_part_to_sample_from_15 != '?').stack().sample(frac=percent_missing_15).index.values

for i, j in index_array_15:

input_matrix.loc[i, j] = MISSING

matrix_part_to_sample_from_16 = input_matrix.iloc[:, from_column_16:to_column_16]

index_array_16 = matrix_part_to_sample_from_16.where(matrix_part_to_sample_from_16 != '?').stack().sample(frac=percent_missing_16).index.values

for i, j in index_array_16:

input_matrix.loc[i, j] = MISSING

matrix_part_to_sample_from_17 = input_matrix.iloc[:, from_column_17:to_column_17]

index_array_17 = matrix_part_to_sample_from_17.where(matrix_part_to_sample_from_17 != '?').stack().sample(frac=percent_missing_17).index.values

for i, j in index_array_17:

input_matrix.loc[i, j] = MISSING

matrix_part_to_sample_from_18 = input_matrix.iloc[:, from_column_18:to_column_18]

index_array_18 = matrix_part_to_sample_from_18.where(matrix_part_to_sample_from_18 != '?').stack().sample(frac=percent_missing_18).index.values

for i, j in index_array_18:

input_matrix.loc[i, j] = MISSING

matrix_part_to_sample_from_19 = input_matrix.iloc[:, from_column_19:to_column_19]

index_array_19 = matrix_part_to_sample_from_19.where(matrix_part_to_sample_from_19 != '?').stack().sample(frac=percent_missing_19).index.values

for i, j in index_array_19:

input_matrix.loc[i, j] = MISSING

matrix_part_to_sample_from_20 = input_matrix.iloc[:, from_column_20:to_column_20]

index_array_20 = matrix_part_to_sample_from_20.where(matrix_part_to_sample_from_20 != '?').stack().sample(frac=percent_missing_20).index.values

for i, j in index_array_20:

input_matrix.loc[i, j] = MISSING

matrix_part_to_sample_from_21 = input_matrix.iloc[:, from_column_21:to_column_21]

index_array_21 = matrix_part_to_sample_from_21.where(matrix_part_to_sample_from_21 != '?').stack().sample(frac=percent_missing_21).index.values

for i, j in index_array_21:

input_matrix.loc[i, j] = MISSING

matrix_part_to_sample_from_22 = input_matrix.iloc[:, from_column_22:to_column_22]

index_array_22 = matrix_part_to_sample_from_22.where(matrix_part_to_sample_from_22 != '?').stack().sample(frac=percent_missing_22).index.values

for i, j in index_array_22:

input_matrix.loc[i, j] = MISSING

matrix_part_to_sample_from_23 = input_matrix.iloc[:, from_column_23:to_column_23]

index_array_23 = matrix_part_to_sample_from_23.where(matrix_part_to_sample_from_23 != '?').stack().sample(frac=percent_missing_23).index.values

for i, j in index_array_23:

input_matrix.loc[i, j] = MISSING

matrix_part_to_sample_from_24 = input_matrix.iloc[:, from_column_24:to_column_24]

index_array_24 = matrix_part_to_sample_from_24.where(matrix_part_to_sample_from_24 != '?').stack().sample(frac=percent_missing_24).index.values

for i, j in index_array_24:

input_matrix.loc[i, j] = MISSING

matrix_part_to_sample_from_25 = input_matrix.iloc[:, from_column_25:to_column_25]

index_array_25 = matrix_part_to_sample_from_25.where(matrix_part_to_sample_from_25 != '?').stack().sample(frac=percent_missing_25).index.values

for i, j in index_array_25:

input_matrix.loc[i, j] = MISSING

incompleteness = ((input_matrix.values == 'missing').sum() + (input_matrix.values == '?').sum())
/ (input_matrix.shape[0] * input_matrix.shape[1])

print(f'number of taxa: {input_matrix.shape[0]}, number of characters: {input_matrix.shape[1]}, overall percentage of missing values: {incompleteness}")

#insert name for the newly created 'fossilised' file

input_matrix.to_csv(f'[filename]_{inc.round(0)}.csv')

Script 3: 3-incompleteness script

(calculation of incompleteness; overall incompleteness and incompleteness of the three anatomical partitions: cranial, dental, postcranial, also subdivided in quantitative and qualitative characters)

```
if __name__ == '__main__':
  import pandas as pd
  #1 character
  quan_den_1_from to = 0
  #1 character
  quan_cran_1_from to = 1
  #3 characters
  quan_den_2_from = 2
  quan_den_2_to = 5
  #5 characters
  quan_post_1_from = 5
  quan_post_1_to = 10
  #16 characters
  quan_cran_2_from = 10
  quan_cran_2_to = 26
  #11 characters
  quan_post_2_from = 26
  quan_post_2_to = 37
  #128 characters
  qual_cran_1_from = 37
  qual_cran_1_to = 165
  #1 character
  qual_den_1_fromto = 165
```

#20 characters qual_cran_2_from = 166 qual_cran_2_to = 186

#13 characters qual_den_2_from = 186 qual_den_2_to = 199

```
#53 characters
qual_post_from = 199
qual_post_to = 252
```

#insert name for the file for calculation
input_matrix = pd.read_csv('[filename].csv', index_col=0)

```
quan_cran_1 = input_matrix.iloc[:, quan_cran_1_fromto]
quan_cran_2 = input_matrix.iloc[:, quan_cran_2_from:quan_cran_2_to]
qual_cran_1 = input_matrix.iloc[:, qual_cran_1_from:qual_cran_1_to]
quan_cran_2 = input_matrix.iloc[:, quan_cran_2_from:qual_cran_2_to]
quan_den_1 = input_matrix.iloc[:, quan_den_1_fromto]
quan_den_2 = input_matrix.iloc[:, quan_den_2_from:quan_den_2_to]
qual_den_1 = input_matrix.iloc[:, qual_den_1_fromto]
qual_den_2 = input_matrix.iloc[:, quan_den_2_from:qual_den_2_to]
quan_post_1 = input_matrix.iloc[:, quan_post_1_from:quan_post_1_to]
quan_post_2 = input_matrix.iloc[:, quan_post_2_from:quan_post_2_to]
```

#cranial regions

try:

missing_quan_cran_1 = (quan_cran_1.values == '?').sum()
except:

 $missing_quan_cran_1 = 0$

print("NOTE: check if character 2 (quan_cran_1) without missing value is correct.")

try:

missing_quan_cran_2 = (quan_cran_2.values == '?').sum()
except:

```
missing_quan_cran_2 = 0
print("NOTE: check if characters 11-26 (quan_cran_2) without missing value is correct.")
missing_qual_cran_1 = (qual_cran_1.values == '?').sum()
missing_qual_cran_2 = (qual_cran_2.values == '?').sum()
```

```
cran_quan = (missing_quan_cran_1 + missing_quan_cran_2) / (input_matrix.shape[0] * (1 + 16))
```

cran_qual = (missing_qual_cran_1 + missing_qual_cran_2) / (input_matrix.shape[0] * (128 + 20))

cran_total = (missing_quan_cran_1 + missing_quan_cran_2 + missing_qual_cran_1 + missing_qual_cran_2) / (input_matrix.shape[0] * (1 + 16 + 128 + 20))

#dental regions

try:

```
missing_quan_den_1 = (quan_den_1.values == '?').sum()
```

except:

missing_quan_den_1 = 0

```
print("NOTE: check if character 1 (quan_den_1) without missing value is correct.")
```

try:

```
missing_quan_den_2 = (quan_den_2.values == '?').sum()
```

except:

 $missing_quan_den_2 = 0$

print("NOTE: check if characters 3-5 (quan_den_2) without missing value is correct.")

```
missing_qual_den_1 = (qual_den_1.values == '?').sum()
```

```
missing_qual_den_2 = (qual_den_2.values == '?').sum()
```

```
den_quan = (missing_quan_den_1 + missing_quan_den_2) / (input_matrix.shape[0] * (1 + 3))
den_qual = (missing_qual_den_1 + missing_qual_den_2) / (input_matrix.shape[0] * (1 + 13))
den_total = (missing_quan_den_1 + missing_quan_den_2 + missing_qual_den_1 +
missing_qual_den_2) / (input_matrix.shape[0] * (1 + 3 + 1 + 13))
```

#postcranial regions

try:

```
missing_quan_post_1 = (quan_post_1.values == '?').sum()
```

except:

```
missing_quan_post_1 = 0
```

print("NOTE: check if characters 6-10 (quan_post_1) without missing value is correct.")

try:

```
missing_quan_post_2 = (quan_post_2.values == '?').sum()
```

except:

 $missing_quan_post_2 = 0$

print("NOTE: check if characters 24-34 (quan_post_2) without missing value is correct.")

```
missing_qual_post = (qual_post.values == '?').sum()
```

post_quan = (missing_quan_post_1 + missing_quan_post_2) / (input_matrix.shape[0] * (5 + 11))

post_qual = missing_qual_post / (input_matrix.shape[0] * 53)

post_total = (missing_quan_post_1 + missing_quan_post_2 + missing_qual_post) / (input_matrix.shape[0] * (5 + 11 + 53))

total_incomp = ((input_matrix.values == '?').sum()) / (input_matrix.shape[0] *
input_matrix.shape[1])

miss = (input_matrix.values == '?').sum()

print(f'RESULTS: number of taxa: {input_matrix.shape[0]}, number of characters: {input_matrix.shape[1]}, number of '?': {miss}, total incompleteness: {total_incomp}, cranial quan: {cran_quan}, cranial qual: {cran_qual}, total cranial: {cran_total}, dental quan: {den_quan}, dental qual: {den_qual}, total dental: {den_total}, post quan: {post_quan}, post qual: {post_qual}, total post: {post_total}'')

Appendix 9

(Available also at https://figshare.com/s/c4f60604a2a013f6a86d)

Presented here are the six character matrices (main matrix, 45-fossil matrix, 65-fossil matrix, cd matrix, 45-fossil-cd matrix, 65-fossil-cd matrix) in .tnt-format

Main matrix

xread

252 120

Varanus_exanthematicus_335 112001?1?30211120-?110--10012121001011001001-0001010000001000000-0011010?00110111000011010-1010010?-10-11010100110011?11100000100000000011110001-01001100011-10101100010100100100200100??10100022001110-011101001011??100100001??101000010--001110-??00?000

Chalcides_ocellatus_193 002011?0?00201100-?01?--

Tupinambis_teguixin_amnh_r155248111010??030?1?1??1?100--1?112111002111010011-00100??1????10000111110100-0?001??01?1?000000-1?1???11-?0-101??111101?0?2010?00100-00110?-00001?01?0000111?0?001-101?1100000??131000??0-?10?0110-00[1 2]2001110-010?1011??1?00?0?000[0 1]110100001001011111?1111110011

Tupinambis_teguixin_ZMH_R12172

Broadleysaurus_major_164

Blanus_rufus_156 ?020???????2101-?01?---

???20?????????????????????????????00100001000-11?00100001010010000-00------

?001100???1110-20?0----000-0101?0?001-01011100001-

???????????00101110101??????00?0?0-

Blanus_strauchi_287 00200????011?10?-?01?????20?????10111100111101001011?00100111000-11?00100001010011000-00----------?001100???1110-20?11---000-01?10?1001-0101?100001-

?1101110010011????01110101??11110001[0 1]00-

Gallotia_caesaris_srk00_346

Gallotia_simonyi_nhmw849

Gallotia_stehlini_mncn22226

Psammodromus_algirus_amnh_r92976

Psammodromus_algirus_nhmw788

Psammodromus_algirus_uamr_ps_9

101110???102??0?10?200?11011111111110?100?000011???10?00010101?1?10-?111010???0?11000110?001?0?2?110001??1000000??101?111?0-

0010011?1100?100000110110[0

1]100110??01?1000101300000???110??1???022?02101?????????00100011110101?01?0101010 110?000????011011

Acanthodactylus_boskianus_276

011001010001013010011000100?11100120010-00-

Acanthodactylus_erythrurus_uamr_acvii 001111???202????1?200--

1?021110110111010?1011001011???10?00110101?1?00-?111001???0?110000-

Eremias_velox_nhmw822 0021102003121?10?0?200--11??????10111110011-

00010??0001?0000001010010100?000??0?010110?00-10000?110?0-

11000101100111?0?1?01001101?0??001101111?1-00001?0?111-

```
011?11010001013010011010100011100121010-10-00001010??0?00?11010100011001001100-
0100110010?0000
```

Mesalina_guttulata_272

11010?01100011?1010110?1101100100111001100001011110111-

```
111001010000011100000111100?111?1020-00-
```

01100000110?00110000011100?10?1000100111101?????10?001

Ophisops_elegans_281

001110???20?210000?20??0111000211??1111100000010101100011?0001010111100-?101101000100000-10010011-00-

10110?11100111?0110110?1101100010110001000001011110111-

11100101000001300000001110??11101120010-00-

???00011?00110010011100?1000000110111?000????10?000

Ophisops_elegans_282

11100101000101300000011101?111??120010-00-

010000111001100100111?0????00001101?11000????1??000

Ophisops_elegans_amnh_r43265

Ophisops_elegans_amnh_r90235

Algyroides_fitzingeri_351

Algyroides_nigropunctatus_nhmw797

1121101001121?10?0?101201?????102011100000[01]0000???0001100001110101100-1??11??0?11?110?011010?011011100101011110101??1111100-0??0?001011000?0001111?0?101-011?1101000?01201000001010101010-0121010-00-01000011??0?00?0?010110010000001100-0101011010?1001

Anatololacerta_danfordi_283

A_danfordi_284

Archaeolacerta_bedriagae_167

Archaeolacerta bedriagae srk00 120

01100?0?1110?0000001010?11011-

Iberolacerta_cyreni_uamr_lm4

00101010?00010001010110?11?0000111101?010????00?011

I_monticola_uamr_lm77

Iberolacerta_monticola_uamr_lm92

00001010?11-

10??01?1000110?0100??1?1?0?????021?0211111???10010?000101110101?0?1??10001110-1?010????0??011

Phoenicolacerta_troodica_318

P_troodica_319

Podarcis_hispanicus_uamr_h30

Podarcis_muralis_311

Podarcis_muralis_3120[0

11000101010??????????????????1??1000?11111?01?????10?010

Podarcis_muralis_313

Podarcis_muralis_nhmuk1920.1.20.801

Podarcis_siculus_25

Podarcis_siculus_125

Podarcis_siculus_amnh_r110436

Podarcis_tiliguerta_153

0010110?000111301[0 1]001111100??11?11???11000-

01001011101001011010111?00?1000010111?010????00?011

Podarcis_waglerianus_390

Takydromus_sp_151 1[0

1] 1111???1??11000011??0010210211???1111??0???101011???1??0000110101110-110-100-110-110-100-100-110-100-100-100-100-100-100-100-

?0011101101000000-

011111010000012000011100100?????221020-0??001101001001001101101?0?1??00001010-1?000????1??000

Zootoca_vivipara_179

Timon_pater_nhmuk1920.1.20.2722 1[0 1]1[0

T_pater_nhmuk1920.1.20.1259 111111200[1

10001???000??0100111101?0??000101?11?1000?11310100?10110?11110010?0[1 2]1000-01??0101??1?01?111111100?001000??10110000-111?1011

Timon_kurdistanicus_nhmw18545

Timon_princeps_nhmw32881 1[0

Timon_lepidus_cipa761

Timon_lepidus_216

Timon_lepidus_amnh_r57770

T_lepidus_mncn41021

11111????11?????11??20???21?0????1110?100?010011???1??1??10000?1?110??0?01 0?????01001??0??0?????1??0?00001????10111?1?0-

T_lepidus_mnhn1887_545

111111??021????1?11??20?2021111????1110?100?010011???10?[0

00001?1?000??1100111101?00000100???1?1000?113?00?1?10?10110???010?02110???1??????? 1????1?1?01?100?0????01?10??0??1??10?00??

T_lepidus_mrac92_050_r_1 1[0

1]1111???111??1?1?101110?102110011111111?100?010011???10?01010?10?1?110?010100???1 ?01001110?000?0?0?100000??100001???101?121?0-

T_lepidus_nhmw699 1[0

T_lepidus_pimuz_a_iii0965

11?11??10?1?????111?2?020210?????1?100?????1001??011?01??1?010?1?0100?0?1? ???1?10?????01???10??1111??110100?1?11??0?1??110-10????0?00???1100?????1????0?001?1??1001?00???00??11010??11??010?12??00-01?01111?01111111101?10?100101???????0101?110?????

Timon lepidus gmz vd36.x1246

Lacerta_agilis_amnh_r76854

1]01??101001?103?1?0??11?10??11100121010-10-

Lacerta_agilis_cipa1550

Lacerta_agilis_176 001[0

L_agilis_177

L_agilis_178

Lacerta_agilis_230 1[0

L_agilis_231

Lacerta_agilis_mncn15979

Lacerta_agilis_mnhn1963_49101[0

$L_agilis_nhmw802$

L_agilis_pimuz_a_iii0902

Lacerta_agilis_ZMH_R12174

0021112000??1???00?00?2011??????11?11??001???01????1?1??101010??1?1??121?01?? ?1?11101???1001??0111110100?1111100?0121??111000-

0??0??001100?1?000011?1?001001001??101010?013?1??1010??01?1110012?11??1???1??1010?? ??00???0?01?10110??0?0010-1101011110?00??

Lacerta_bilineata_15

111?1011?001001111101?1?110010101?0-??000110?000011

L_bilineata_48

?0201?????1??????10???01120111?????1110?100?0010010??10?10110001011111?0?1? ?????11010000-11?10111??1001001?111110???1011011?0-0?????0011?0?000??0110?100111-

101?110?0000113101?1000110??11??0121010-

L_bilineata_73 1[0

1011111?001?????10010100-

11010111?11001001?11101001?001101????0????001?????0?01???1?0011-

L_bilineata_77 1[0

L_bilineata_84

L_bilineata_381

Lacerta_bilineata_420

?01110011110111?00?1101011101?000????00?011

Lacerta_bilineata_amnh_r1148

10211????2?1????1?00?100???????????111001000001???0??1?011010??1?1??111?00?? ?1????01???0-0?000?110?10010???[0 1]101100?1100?11110-

Lacerta_bilineata_amnh_r109472

Lacerta_bilineata_mncn16505

Lacerta_bilineata_pimuz_a_iii1276

L_bilineata_uam_q21 1[0

1]??0?00?11110111??10110101110110001111100011

Lacerta_media_nhmw34809

10211?????12??1??0?1??2101????????111000??0?11???0????101110????111121?011? ?1????01?????100??110?100?0101?110111?????111110-

Lacerta_media_huj_ost_z_299

Lacerta_media_huj_ost_z_396

Lacerta_schreiberi_cipa778

Lacerta_schreiberi_cipa1256

L_schreiberi_cipa1511

Lacerta_schreiberi_cipa1517

??011[0 1]111?1?1?100001?10???10????????11

L_schreiberi_nhmuk1906.10.30.14

00??1001????00?111101?111???100010101?00011111??011

Lacerta_schreiberi_uam_s_6

Lacerta_strigata_304

Lacerta_trilineata_240

L_trilineata_295

L_trilineata_356

Lacerta_trilineata_mrac95_050_r_0001

 $101111???200??1??1?000200?202111110011110?100?000111???10001111101?1?112?101\\001?1?0?01010110?010?111?100001?11000011??101?120?0-$

L_trilineata_mrac95_050_r_0002

Lacerta_trilineata_nhmuk1914.1.12.1

0?000?111?101101??1111000??101?110?0-

0010100?0101?1100001101010010100??01?1000001?11101?10010??1???012?011010-01101111?01100001110111?11?0111011000????00?010

Lacerta_viridis_amnh_r154762

Lacerta_viridis_mncn16504

Lacerta_viridis_mnhn1888_139

1011112?01??????0??11?00?????11????1110?1???01?????1?00?01?101?1??11??01??? ??????1????0?00??11??1001?1?1111???0?????1?110-

Lacerta_viridis_mnhn1887_813 101[0

01??00?0?????11?10???01???0010110-???1011?10?0?11

Lacerta_viridis_mrac91_077_r_76

Lacerta_viridis_nhmw887

Lacerta_viridis_nhmw906

Lacerta_viridis_nhmw32879_3

Lacerta_viridis_zzsid_r_287_80

102111??0200?????0?010200?1111111111110?100????1????10?11110101?1?112?001? ?????0?01???100?000?111?100001??011100???101?111?0-

1000110?1101?1100001101?00100100??01?1000001??0001?11010??1???012?0111111???00101? ?0001111110111??1?11100111011000111100?001

Lacerta_viridis_zzsid_r_463_87

;

proc/;

45-fossil matrix xread	
252 120	
Gekko_gecko_112 11211????0201120-?200 1?????1?020111?0????01?0010101??00?01?-101100-?001?1?00?001??010-10?1000?- 00?1?110?10110011??1?0-?-?1?00110010010100000???1?0?? 00?1?110000000110?0?0?200101??1?100??100?100	
Varanus_exanthematicus_335 11200??1?30211120-?110 10012121001011001001-?001?100000010000?0?0?11010?0011011??000110?0-1?10010?-1?- 11??010?11001????1???010000?000?011110001- 0??011?0011?1010?1000?01??10?1??2?0100??1?1000220?111?- 0111??0010????100100001??101000010-??01110-??00?000	
Chalcides_ocellatus_193 ?11121?01?21001110000000?001010?1?000110?0??????? 0??1??0?01?11?011?1111?0??110101000011?0??00?101? 1011110101000?2??0?1?110?1??11?0?0?00011011???01? 00????01?110	00?011?0?00201100-?01? ?011?1?1011001?110-1?1?00??- ?0000??0?- ?101??0011?0111101?11000000?11?00?
Salvator_merianae_cmgr 1?????????111?0??0?0?????1???0?0011101?0101?0?(1?10?00010100?10???0?11?01??1??-1?001??????0111?1 ?01?11?0101?[01]13?01002?1?11???10?0???00111?????? ?????????	?0?0?????011?1??-?110 0????11?1?10?000-1???0?10-?0- 0010?- ??????????

Tupinambis_teguixin_ZMH_R12172

1?1??1000?0?01?0000120??1???01?00022100-

Broadleysaurus_major_164

Blanus_strauchi_287

00??????011?10?-

?0??????20?????10????00111101?01011?00??0111000-11?0010000101?0???0?-?0-??----?----

-??001100???1?1?-20?11???000?01?10?100??0101?100001-

?1?011100?0011????0111010???11110001[01]00-

Gallotia_caesaris_srk00_346

Gallotia_simonyi_nhmw849

1?0110200202??1??0?1110100?????010111?1000??1??1???0??1?1010101111?11101??10 ??1??1?011???00?00??0???1011???1?1??110???01?111??-00?0110?01011?0?0?01??1?0?1000011??10100??11?00000?1??101?0?1?0321030-0??01101010?????0?11010110?0100100010?111?[01]011010?0011

Gallotia_stehlini_mncn22226

Psammodromus_algirus_amnh_r59605

Psammodromus_algirus_amnh_r92976

????????0?1??0??0?1?0?11?01??0?001???01010110?1100??

Psammodromus_algirus_nhmw788

102?101?01121?01?0?10?201??????11?111000?0000?0????001?00?010101011?0-0??00??00100110??111?00??11?010??0????1100001?1??11?1?0-???0??00?1????1??001?1?????000101?010?0???01201001000???011110?121010-?0-000010?0???200?1?01011010010?010110100011010?1000

Psammodromus_algirus_uamr_ps_9

?11?010?????1?000110?00??0?2?1???0???1?0?000???01?111??-

Acanthodactylus_boskianus_276

10211????202211000?2?01111021?201??11111?0?01?00101100011?10?0010?0?1?10?011 ???0?00011?00?-10?1000?000-

Eremias_velox_nhmw822

002?102003121?10?0?200--

11??????1011111???1-

0001???0001?0?00001010?10?0????0??0?01011??00?10?0??110?0?1100010?1???11?0????10?1?0 1?0???0110?111??-?0?0??0????-????110100010???10?110?0?00011100121010??0-

Mesalina_guttulata_272

102?11???1121?1000?2?02011020020???111?100000?001?1100010??00?00010???0-?101?00??000100100-10010?10???-

?10?0?011?00?1?1??0????11011?0??0111?01???001?1?11???1?11001010000011?0?000111100? 111?1?20-0?-?1100000110?00110000011100?10?1000100111101?????10?001

Ophisops_elegans_281

001110???20?210000?20??0111000211??11?1100000?101?1100011??0?1??0?1?100-?1?110?01?001000?0-??0????-

00?10110?11100111?01????0??1011000?0110??1?00?0?01?110111-

?11001010000??300?000011?0??11101??0010-00-

???0?01???011?01?011100?1000000110111??00????10?000

Ophisops_elegans_282

?01110???2022???0??20?2?110200?1????11?10?10??001?110?011?0?0100?11?1?0-?10?101???00?00?00-

1?1001?100010?3?0??000?1101?1????120010-00-

01000?11?00110???011??0????0000?101?11000????1??000

Ophisops_elegans_amnh_r43265

Ophisops_elegans_amnh_r90235

Algyroides_fitzingeri_351

102?1????021?????2?0102??20??11?110?0?0000011100010??0??00?101100-?101?????10?????0??????111?0?0?11?0????1011111?0?0010000011100?0?1-01???10??01???1011010000??????00?01110???110112??10-0??001??????????????10110????000?1001?1?0?????10?011

Algyroides_nigropunctatus_nhmw797

1121101001121?10?0?101201?????102?11?00000[01]0??0???00011??00111?10110???? ?11??0??1??10?011????0?101?10??01?110101????1111100????0????010?1?0?????1111?0??01? 011??101?00?012?10??001??01011?-01210?0-00-010?00?1??0??0?0?0?0?0?0?10010000001100-0101011010?1001

Anatololacerta_danfordi_283

A_danfordi_284

?02111???10221?100?10??00?021010????1?100?0000000110001???000100?011111?101 ???11?10010?0?-0?0?0?1???1?10?101[01]1?001???1?11?1??10111??000?111??00??011????0??1-

Archaeolacerta_bedriagae_167

0010?0111??1101?0?10110?1??1000111101??10????10?010

Archaeolacerta_bedriagae_srk00_120

1?11101???1?01???110??1??12?10?10??1011?01???111??-111?-111??-11??-11??-11??-11??-11??-11??-111??-11??-11??-11??-11??-11??-1

0110??0?111??00000?1?1??11011-

Iberolacerta_cyreni_uamr_lm4

00101????000100?1010110?11?000?1111?1?010????00?011

I_monticola_uamr_lm77

Iberolacerta_monticola_uamr_lm92

0110????11???1001???001?1??1?-

10???1?100011???100??1?1?0?????021?0?11111?????010?000101?1010??0?1??10001110-1?010????0??011

Phoenicolacerta_troodica_318

?0111????11?11?100?10???010101211???111??000??0?0?1100010?00???1??011?0-??011?1010?101100?-?1010?1111?00?0?0?0010?01???01??1??0-???000?0?1?0???0?-

??0??11?1?1-

P_troodica_319

0??????001

Podarcis_hispanicus_uamr_h30

??0????111??0??01??00001??0???0???010??1???113??10-

Podarcis_muralis_311

?010?1?0?1?101100????11?101?1?0?1111010001??301?1???1?100?1110112?020?0????010?110 1100?101?01?0?1??110?01??11?010??????000

Podarcis_muralis_312

?100010??1?????????????????1??1000?11111?01?????10?010

Podarcis_muralis_313

00001011100110?101?0111?00?10001?????1?10????0?011

Podarcis_muralis_nhmuk1920.1.20.801

```
??1????1?00?113?1??1????1??0???0112?0?0-00-
```

Podarcis_siculus_25

?0?00100011??00??110010110??10000001111?10????10?011

Podarcis_siculus_125

?01?00?01??0010?0?0110?11??001?01111010000??3001?11111?00?1?1?112??1?00?????01011?1 ?001111101?1?0??1000011?11?010????1??001

Podarcis_siculus_amnh_r110436

00?1?1?0?????1??1?100?0??????????111?00??0001010???10001010????1?0?11?0???? ?0???01????-0?????12??00????11??0????????1?0-?0?0??0??1?11?1????01?????1?1-001?1101000?????1?11?10??1?101121010-10-

0?1?1????1?00????1?00?10100??0?0111?1?01?????00?0??

Podarcis_tiliguerta_153

Podarcis_tiliguerta_154

Podarcis_waglerianus_390

01100??111111010111111111?10?110?011111?000????11?000

Takydromus_sp_151

??1111???1??11000011??001?2102?1???111???0???1?1011???1??0000?10??1110-??01110?1?10?00000-

0?11?1010000012?00011100100??????21?20-0??0011?1?010??00110?101?0?1??00?010?0-1??00????1??000

Zootoca_vivipara_179

0110110100000121?11?110???0?111??221?21?10??011101??001?01?10?0??1??1?00001?0??1?00 0????01?011

Timon_pater_nhmuk1920.1.20.2722

01??01???????1?111?111100?0?10001?101?01011111?1011

T_pater_nhmuk1920.1.20.1259

Timon_pater_gmz_d.36_x.171

Timon_kurdistanicus_nhmw18545

Timon_princeps_nhmw32881

Timon_lepidus_cipa761

Timon_lepidus_216

Timon_lepidus_amnh_r57770

???01?10??0???0?010?1???1???00?0??11?1001??131???????10???1?-

T_lepidus_mncn41021

?1111????11?????11??20???21?0????1110?10???10?1????1??1????000?1?110????010 ?????0?001??0??0??????1??0?0??0?001?????0?11???0-

T_lepidus_mnhn1887_545

T_lepidus_mrac3390

0?01?1??0????100??1?01??0????00???1?1000?113??0???10?101?????010?02110???1??????1?? ????1?01?100?0????01?10??0??1??10?00??

T_lepidus_mrac92_050_r_1

1[01] 11? 1??? 111?? 1?? 1? 101? 1?? 1021100111? 1111? 100?? 10011??? 10? 010? 0? 10??? 110??? 0? 00???? 10000???? 10000???? 101?? 21?? -

0?0?1????0??1?001??1010???001?1??11?10010113??101?1?010??0???1?0?0??0011011001?1?00 11111110111?00?110100?1?11010????00?011

T_lepidus_nhmw699

T_lepidus_pimuz_a_iii0965

1??11???0?1?????111?2?020210?????1??????1?01??011?01?????10?1?010??0?1?? ??1?1???????1?1?????111???1?01???1?1????1???10-

0??011?1?01111???1101?1??1001?1?????0101?110?????

Timon_lepidus_gmz_vd36.x1246

Lacerta_agilis_amnh_r76854

Lacerta_agilis_cipa1550

Lacerta_agilis_176

L_agilis_177

L_agilis_178

102111???201111001?11?20?11111?111011?1100100??0111100011?010101????1?12?101 011101110100011?1?????011000001?11?0?10??1011111?0-0110000?110??100000?1?111?100[01]00111101001011?1000??10110??1?100111010-010?100101?1010??0111????1?0??1000?11101?010????10?011

Lacerta_agilis_230

L_agilis_231

Lacerta_agilis_mncn15979

Lacerta_agilis_mnhn1963_49

L_agilis_nhmw802

L_agilis_pimuz_a_iii0902

Lacerta_agilis_ZMH_R12174

0021112000??1???00?00?2011??????11?11???0????01????1?1???0101???1?12??01?? ?1?11101???10?1??01111??0100?1?1110???1?11?0?-

??????00?100?1?0??011????010?10?1??101010?013?1??1010???1?1?1?012?11??1???1??1010??? ?00???0?01?10110??0?00?0-1101011110?00??

Lacerta_bilineata_15

101110?00?01111000?11?20?11011111101?111??1??0?0?01100111?111101011??111?001 010???11?1?00110?000?11?1100101??1110?00????11?1??-0?00?1??01001?000??1??10000?0??1?1101001??13????10?0110??01?00?110110?0-1?1?1011?001?01111101?1?11001010??0-??000110?000011

L_bilineata_48

?0201?????1??????10???01120?11????11????00?00??0?0????0?1011000101?111?0?1?? ????1?010000-

L_bilineata_73

L_bilineata_77

L_bilineata_84

100???0?11101?1?0??110??1?????10??????011

L_bilineata_381

10?11?????11111000?11?200????????????0?010000110?1001111110?0?01?11112?001? 1111?1101??01101?00?1???1001001?1110?001?101111???-

Lacerta_bilineata_420

Lacerta_bilineata_amnh_r1148

Lacerta_bilineata_amnh_r109472

0??0??001100?0??000?1???10????1????01000?1[01]??0???2?1?10?1?10-
Lacerta_bilineata_mncn16505

Lacerta_bilineata_pimuz_a_iii1276

L_bilineata_uam_q21

Lacerta_media_nhmw34809

Lacerta_media_huj_ost_z_299

Lacerta_media_huj_ost_z_396

Lacerta_schreiberi_cipa778

Lacerta_schreiberi_cipa1256

L_schreiberi_cipa1511

Lacerta_schreiberi_cipa1517

L_schreiberi_nhmuk1906.10.30.14

00??100?????0?111101?111???100?10101??0011111??011

Lacerta_schreiberi_uam_s_6

101111??0101??1??1?0?1210??10111?10111110??00?011?11???1??011?0111?1?1?1?001? ??????010[01]?100??01?0?0?1?100????10001????0??111???000011????010?[01]00???1??11???0 100???1?100001??1?0?1???110??0???01?011010-????0???1000????10???11????11000111???010111?101011

Lacerta_strigata_304

L_strigata_nhmw10918

Lacerta_trilineata_240

L_trilineata_241

L trilineata 295

L_trilineata_356

Lacerta_trilineata_mrac95_050_r_0001

?011?1???200??1??1?000200??021111100?1?10???0?000111???1?00111110??1?112??0?0 ?1?1?0??1010?10?010?111?100001??1?0?01???101??20?0-

L_trilineata_mrac95_050_r_0002

00?1?1?01010110??01?11??10[01]101?11110????1?11?10?0-

?0?0110??1?1??1001??1?1?0?000?????01?1000011??00?1?110?0?10???012??111?11010?1?01?01 10?111110111?1101??10111?11000????000011

Lacerta_trilineata_nhmuk1914.1.12.1

010?1?01????01?11110111011???110?1101100011111?0011

Lacerta_trilineata_zzsid_r_235_76 102111????10?????1?101200?111111?111111??1-?0??101???1??110??1?1???11??[01]01?????1??100?0-

Lacerta_viridis_amnh_r154761

Lacerta_viridis_amnh_r154762

001?1101??1?0???11101?1010001?0?111?11?00????100001

Lacerta_viridis_mncn16504

Lacerta_viridis_mnhn1888_139

Lacerta_viridis_mnhn1887_813

Lacerta_viridis_mrac91_077_r_76

001??0???10???100?1??01100000100??11?1001011?10?????1010??1????12?111011111?01?01?? 000???1110111?0[01]0110??010-?1000????00?011

Lacerta_viridis_nhmw887

Lacerta_viridis_nhmw906

Lacerta_viridis_nhmw32879_3

Lacerta_viridis_zzsid_r_287_80

Lacerta_viridis_zzsid_r_463_87

???1????11??0?0??00?1?0?1??10??1[01]1?000???001?11110-

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proc/;

65-fossil matrix xread 252 120 Gekko gecko 112 1??11?????2?1?20-???0-?-????0?10??0??????0-0??100?1?0?-0??0?????0??0??0??0?1-???0???????000 Varanus exanthematicus 335 ?1??0????3??111?0-?110--??01??2??0?0110????1-00??010?00?0100??0???0?1010??0?1??1????01?0??-?010?1????0-??0??1?0??001?????0??1?00??00?0??11???0?-?100?10?0????10110??101?0???1?0200?0??????0220?1?10-0??10????0????100??????010?0???-?0?1110-??00?0?? 002011?0?00???10?-??1?-Chalcides ocellatus 193 ???0????0 Salvator merianae cmgr 10???????1??1?????10?-?0?????0???????101???1?1????0???????020??11?????-

Tupinambis_teguixin_ZMH_R12172

Pseudopus_apodus_214

Broadleysaurus_major_164

Ablepharus_kitaibelli_239

102??1???0???1?0-

Blanus_rufus_156

?02????????21?1-??1?-?-

Blanus_strauchi_287

00?0??????11????-

Gallotia_caesaris_srk00_346

Gallotia_simonyi_nhmw849

Gallotia_stehlini_mncn22226

Psammodromus_algirus_amnh_r59605

Psammodromus_algirus_amnh_r92976

???????011??????011???1????0?00?1?????1011??11?0??

Psammodromus_algirus_nhmw788

Psammodromus_algirus_uamr_ps_9

??110?0???0???00?1???0?1????1???0??????0?????01?11???-

Acanthodactylus_boskianus_276

Eremias_velox_nhmw822

???110?0?3??1?1??0??00-

Mesalina_guttulata_272

Ophisops_elegans_281

?01?10???20??10?0??2????1?000?1?????1110???0?101011??0????0???1011?10???10??? 1??0001??0?0?1??10?1?-??-

Ophisops_elegans_282

Ophisops_elegans_amnh_r43265

Ophisops_elegans_amnh_r90235

Algyroides fitzingeri 351

Algyroides_nigropunctatus_nhmw797

Anatololacerta_danfordi_283

A_danfordi_284

Archaeolacerta_bedriagae_167

Archaeolacerta_bedriagae_srk00_120

Iberolacerta_cyreni_uamr_lm4

I_monticola_uamr_lm77

Iberolacerta_monticola_uamr_lm92

Phoenicolacerta_troodica_318

P_troodica_319

Podarcis_hispanicus_uamr_h30

??2??????0???1??0???1?10??21??0????110?????00?0?????11?0?1??10??1?1?110???? ?????100?1??????2??110?1????0??1??????-

Podarcis_muralis_311

Podarcis_muralis_312

Podarcis_muralis_313

Podarcis_muralis_nhmuk1920.1.20.801

??????1000?1?301??1?01?10?01?10?1?????-

Podarcis_siculus_25

Podarcis_siculus_125

0??1?0???00??1?00??10???01???1??1?010???0?0110?1?0????1??01?1?111?10?01? ??111??????01?0?1??21?1???0?????1??1??1??0???1???0??????010??00?????1??00??011110 ?0?0??1??01?1?11???0?11??1121???00?????1??1??????1??1??01?1????1??0?????1?010????1??0? 1

Podarcis_siculus_amnh_r110436

Podarcis_tiliguerta_153

Podarcis_tiliguerta_154

Podarcis_waglerianus_390

Takydromus_sp_151

Zootoca_vivipara_179

?????11??010?1?1??011???1?00?0??0??1?0?????0????1

Timon_pater_nhmuk1920.1.20.2722

T_pater_nhmuk1920.1.20.1259

????0?01????01?1????1110??0??????011000?-?????01?

Timon_pater_gmz_d.36_x.171

Timon_kurdistanicus_nhmw18545

Timon_princeps_nhmw32881

Timon_lepidus_cipa761

Timon_lepidus_216

$Timon_lepidus_amnh_r57770$

T_lepidus_mncn41021

T_lepidus_mnhn1887_545

T_lepidus_mrac3390

$T_lepidus_mrac92_050_r_1$

T_lepidus_nhmw699

T_lepidus_pimuz_a_iii0965

Timon_lepidus_gmz_vd36.x1246

Lacerta_agilis_amnh_r76854

Lacerta_agilis_cipa1550

Lacerta_agilis_176

L_agilis_177

00?0?1???10?11100??????1101????1?2?1???0100?0??0?10?0???0?0????0?0?11?2??0?0?1 ?0????1?0??10??0011?0111??0????1?0?10??1???0-

??1??0?01?????00??1?0?11?1????011110100???13?00?1????0??111?0?21?1?1?0?01???01?1??0 ??0??01?111?00?000??111011??0????0??01

L_agilis_178

Lacerta_agilis_230

L_agilis_231

Lacerta_agilis_mncn15979

Lacerta_agilis_mnhn1963_49

L_agilis_nhmw802

L_agilis_pimuz_a_iii0902

Lacerta_agilis_ZMH_R12174

Lacerta_bilineata_15

1?1??01???01?0111110????10010?01?0???00??10?0??011

L_bilineata_48

L_bilineata_73

L_bilineata_77

L_bilineata_84

L_bilineata_381

Lacerta_bilineata_420

Lacerta_bilineata_amnh_r1148

Lacerta_bilineata_amnh_r109472

Lacerta bilineata mncn16505

Lacerta_bilineata_pimuz_a_iii1276

L_bilineata_uam_q21

Lacerta_media_nhmw34809

Lacerta_media_huj_ost_z_299

Lacerta_media_huj_ost_z_396

Lacerta_schreiberi_cipa778

Lacerta_schreiberi_cipa1256

L_schreiberi_cipa1511

Lacerta_schreiberi_cipa1517

L_schreiberi_nhmuk1906.10.30.14

Lacerta_schreiberi_uam_s_6

?0??00????00??[01]1???1??1???1100??11??10?011??1010??

Lacerta_strigata_304

L_strigata_nhmw10918

Lacerta_trilineata_240

L_trilineata_241

L_trilineata_295

L_trilineata_356

Lacerta_trilineata_mrac95_050_r_0001

L_trilineata_mrac95_050_r_0002

???1110111?1101??10?11011????????0011

Lacerta_trilineata_nhmuk1914.1.12.1

00?0??0?000??11???0???1?0?????01?1????11?????1?????1?0???1?0?12??1?-

Lacerta_trilineata_zzsid_r_235_76

Lacerta_viridis_amnh_r154761

1???112??1??????????????????????????11?0?10[01]0?1??????110??????11?1?????

?????1?1??1????????????10????00?1101?000??01001?01

Lacerta_viridis_amnh_r154762

Lacerta_viridis_mncn16504

Lacerta_viridis_mnhn1888_139

Lacerta_viridis_mnhn1887_813

Lacerta_viridis_mrac91_077_r_76

Lacerta_viridis_nhmw887

Lacerta_viridis_nhmw906

?1???1?1????01???1?1?1101????1?11100?1??0?0????

Lacerta_viridis_nhmw32879_3

Lacerta_viridis_zzsid_r_287_80

Lacerta_viridis_zzsid_r_463_87

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proc/;

Cd matrix

xread

252 120

&[cont]

Gekko gecko 112

??? 1.7 0.802851 0.16 0.42 0.58 0.7 0.45 ?? 4.6 2.2 0.44 ??? 1.6 ????? 0.48 ? 8.63 1.39 0.8 0.75

11.0 9.0 1.0 30.0-31.0 30.0 ? ?

 Varanus_exanthematicus_335
 9.0 7.0-8.0 1.0 9.0 10.0-11.0 28.0 ? 8.0

 ? 7.0-10.0 1.3 0.733038 0.24 0.49 0.62 0.9 0.75 ? ? 2.9 1.16 0.45-0.55 ? ? 0.69-1.0 0.97 1.1 0.77 2.3

 0.46 4.4 0.43 0.24-0.39 8.49 0.96 0.74 0.83

 Chalcides_ocellatus_193
 7.0 6.0 1.0 12.0-13.0 17.0-18.0 40.0 ?

 6.0 ? 4.0 1.5 0.436332 0.16 0.44 0.63 1.16 0.66 ? ? 1.66 1.08 ? ? ? 1.0 1.08 1.2 0.8 1.5 0.5 3.3 0.36

 0.96 11.44 1.08 0.92 0.57

 Tupinambis_teguixin_amnh_r155248
 8.0-11.0 7.0-10.0 3.0 3.0-15.0 13.0-33.0 24.0

 26.0 ? ? 2.0 7.0-10.0 1.11-3.9 ? 0.2-0.4 ? 0.4-1.0 ? ? 0.41-0.53 ? 1.8-3.0 1.21-2.27 0.42-0.56 ? ?

 0.69-1.0 ? 1.2-1.3 0.71-0.89 1.41-2.3 0.5-0.7 2.5-3.5 0.39-0.53 0.24-0.39 8.13-9.9 1.06-1.39 0.82

 1.11 0.7-0.89

Tupinambis_teguixin_ZMH_R121729.0 4.0-5.0 3.0 11.0 14.0-15.0 ? ? ? ? ? 1.98 ?0.29 0.25-0.49 0.62 1.06-1.92 0.34-0.99 ? ? 2.64 1.43 0.56 ? ? ? 1.01-1.6 ? ? ? ? ? ? ? ? ? ? ? ? ?

 Anguis_veronensis_102
 9.0 4.0 1.0 8.0-9.0 10.0 24.0 2.0 6.0 ?

 9.0-10.0 0.7 0.977384 0.13 0.24 0.7 0.82 0.63 ? ? 1.5 1.1 ? 2.0 0.43 1.0 0.86 0.62 0.72 0.73 0.54

 3.11 0.42 ? ? ? ? ?

 Pseudopus_apodus_214
 7.0 5.0 1.0 13.0 14.0-16.0 52.0 3.0-4.0

 6.0 ? 7.0-10.0 1.8 0.959931 0.38 ? ? ? ? ? 1.35 1.0 ? 1.25 0.7 1.1-1.97 0.98 0.81 0.85 1.38 0.52

 3.16 ? ? ? ? ? ?

Broadleysaurus_major_164 7.0 9.0-10.0 2.0 18.0 20.0-21.0 28.0 ? 7.0 ? 6.0 1.2 0.942478 0.17 0.21 0.6 1.41 0.56 0.37 ? 1.7 1.14 ? 2.0 0.3 0.69-1.0 0.98 0.87 0.94 1.86 0.5 3.0 0.45 1.1 11.0 1.17 0.9 0.59

 Ablepharus_kitaibelli_239
 8.0-10.0 3.0-4.0 1.0 13.0-14.0 18.0 33.0 ? ? ? ?

 3.9 1.134464 0.33 ? 0.65 ? 0.48 ? ? 2.8 1.4 ? ? ? ? 1.13 ? ? ? ? ? ? ? ? ? ? ? ?

 Blanus_rufus_156
 ? 2.0 1.0 3.0 ? ? ? ? ? ? ? ? ? 1.0 0.48

 1.33 1.09 ? ? 1.44 1.2 ? ? ? ? ? ? ? 2.1 0.47 ? ? ? ? ? ? ?

 Blanus_strauchi_287
 7.0 2.0 1.0 4.0 8.0 ? ? ? ? ? 2.0

 0.872665 0.33 ? 0.57 1.06-1.92 ? ? ? 1.7 1.05 ? ? ? ? ? ? 2.3 0.43 ? ? ? ? ? ? ?

 Gallotia_simonyi_nhmw849
 9.0 8.0-9.0 5.0 20.0 23.0-24.0 25.0 7.0 6.0 2.0

 6.0 1.27 0.855211 ? ? 0.58 ? ? 0.36 ? 1.85 1.08 0.32 0.81 0.46 1.2 1.07 ? ? ? ? ? ? 0.25-0.35 11.25

 0.93 0.95 0.72

 Psammodromus_algirus_amnh_r59605
 8.0-11.0 2.0-6.0 3.0 16.0-31.0 13.0-33.0 ? ? ? ?

 ? 1.11-3.9 ? 0.2-0.4 ? ? ? ? ? 1.8-3.0 ? 0.2-0.41 1.06-4.7 0.09-0.39 1.1-1.97 ? ? ? ? ? ? ? ? ? ? ? ? ? ?

 Psammodromus_algirus_amnh_r92976
 8.0-11.0 ? 3.0 16.0-31.0 13.0-33.0 27.0-52.0 ?

 5.0-6.0 ? 5.0 1.11-3.9 ? 0.2-0.4 ? ? ? ? ? 1.8-3.0 ? ? 1.06-4.7 0.09-0.39 0.69-1.0 ? ? ? ? ? ? 0.21

 0.38 ? ? ? ? ?

 Psammodromus_algirus_nhmw788
 11.0 4.0-5.0 2.0 19.0 22.0-23.0 26.0 6.0 6.0

 2.0 5.0 1.0 0.802851-0.925025 0.37 ? 0.38-0.39 1.0 ? 0.34 ? 2.62-2.64 1.27-1.32 0.39 1.53-2.04

 0.34-0.35 0.92 ? ? ? ? ? ? ? ? 15.0 0.95 0.83 0.72

 Psammodromus_algirus_uamr_ps_9
 9.0 4.0-5.0 3.0 19.0 23.0-25.0 26.0 ? ? ? 5.0

 1.8 0.698132-0.872665 ? ? 0.38 ? ? 0.34 ? 2.45 1.36 ? 1.81 0.39 1.2 ? 1.3 0.8 0.9 0.6 3.4 0.45 0.4

 1.1 14.14 0.96 0.86 0.73

 Acanthodactylus_boskianus_276
 8.0 5.0 2.0 20.0 25.0 26.0 ? ? ? 6.0 0.97

 0.663225 0.56 0.41 0.45 1.33 0.57 0.38 ? 4.27-4.37 2.27 0.48 1.0 0.55 0.8 1.25 1.1 0.93 1.1 0.56

 3.85 0.33 0.56 ? ? 0.84 0.82

Acanthodactylus_erythrurus_uamr_acvii 7.0 4.0 3.0 18.0-19.0 23.0 27.0 ? ? ? 6.0 1.27 0.436332-0.870919 ? ? ? ? 0.44 ? 4.0 2.0 0.52 ? ? 0.69-1.0 ? 1.13 0.92 1.12 0.5 3.21 0.31 0.47 13.55 0.93 0.88 0.8

 Eremias_velox_nhmw822
 7.0 4.0-6.0 2.0 18.0-19.0 22.0-24.0

 26.0 8.0 5.0-6.0 2.0 7.0 1.0 0.453786 0.3 ? 0.46 1.06-1.92 ? 0.37 ? 3.6 2.08-2.13 0.54 ? ? 0.91-0.92

 1.16 ? ? ? ? ? ? ? 14.9 0.91 0.88 0.89

 Mesalina_guttulata_272
 8.0-9.0 5.0 2.0 24.0 26.0-28.0 27.0 ? ?

 ? 5.0 1.0 0.715585 0.4 ? 0.41 1.06-1.92 0.59 0.36 ? 3.2-3.21 1.6 0.56 1.55 0.29 1.0 1.14 0.8 0.9 0.94

 0.48 3.86 0.37 ? ? ? 0.93 0.79

 Ophisops_elegans_281
 7.0 5.0-6.0 3.0 20.0-21.0 26.0-27.0

 24.0 ? ? ? 6.0 1.5 ? 0.5 0.42 0.31 1.4 0.5 0.4 ? 3.78-3.83 1.78 ? ? 0.22 0.8 1.57 1.16 0.74 0.64 0.45

 3.88 0.48 0.6 ? ? 0.93 0.89

 Ophisops_elegans_282
 7.0 5.0-6.0 3.0 17.0-18.0 22.0 24.0 ? ?

 ? 6.0 1.16 0.645772 0.45 ? ? ? 0.46 ? ? 3.4 1.78 0.39 1.44 ? 0.69 1.3 1.12 0.87 0.63 0.37 3.35 0.39 ?

 ? ? ? 0.86

? 2.0-6.0 3.0 16.0-31.0 13.0-33.0 ? ? ? ? ? ? ? ? ?

Ophisops_elegans_amnh_r43265

Algyroides_fitzingeri_35110.0 5.0 2.0 18.0-19.0 23.0 ? ? ? ? ? 1.50.7766715 0.33 ? ? ? ? ? ? ? ? ? 1.56 0.24 1.11 1.16 1.1 0.9 ? ? 3.6 0.32 ? ? ? 0.84 0.73

 Algyroides_nigropunctatus_nhmw797
 8.0 7.0 2.0 19.0-20.0 23.0 26.0 6.0 6.0 2.0 5.0

 1.0 0.575959 0.39 ? 0.43-0.47 1.06-1.92 ? 0.37 ? 2.13-2.28 1.36-1.42 0.34-0.41 1.26-1.33 0.34-0.36

 0.9 ? ? ? ? ? ? 0.6-0.8 8.75 1.24 0.75 0.85

 Anatololacerta_danfordi_283
 9.0 5.0-6.0 2.0 19.0-20.0 24.0 ? ? ? ? 6.0 1.0 ?

 0.41 0.4 ? 1.4 0.55 0.37-0.39 ? 2.78-3.0 1.68 ? ? 0.33 1.31 1.25 1.1 1.0 1.0 0.56 3.9 0.32 0.36 ? ? ? ?

A_danfordi_284 9.0 6.0 2.0 18.0-19.0 24.0 27.0 ? ? ? 5.0 1.3 0.802851 0.42 0.4 ? 1.0 0.56 0.38 ? 2.94 1.65 ? ? 0.24 1.2 ? 1.0 1.0 1.2 0.4 3.3 0.25 ? ? ? ? 0.78

 Archaeolacerta_bedriagae_167
 8.0 6.0 3.0 18.0-19.0 25.0 26.0 ? ? ? 4.0 1.16 ?

 0.46 0.34 0.47 1.57 0.6 0.35-0.39 ? 2.47-2.76 1.61 ? ? 0.29 1.12 1.11 1.0 0.93 0.88 0.5 4.0 0.21 0.27

 15.52 0.88 0.9 0.76

Appendix	9
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Archaeolacerta_bedriagae_srk00_120	8.0 5.0-6.0 2.0 16.0 20.0-22.0 ? ? ? ? ? 0.9
0.872665-1.22173 ? ? ? ? ? 0.37 ? 2.29 1.52 0.4	43 2.73 0.3 1.12 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?
Iberolacerta_cyreni_uamr_lm4	9.0 ? 3.0 ? 23.0 27.0 ? ? ? 5.0 0.88 0.872665-
1.22173?????0.39?2.08-2.51.6?1.790.1	9-0.25 1.0-1.4 ? 1.07 0.99 1.0 0.59 3.3 0.26 0.42 11.9
0.9 0.84 0.7	
I_monticola_uamr_lm77	8.0 ? ? ? ? 27.0 ? ? ? 5.0 2.08
0.872665-1.22173 ? ? 0.43 ? ? 0.36 ? 1.98-2.14 0.35 ? ? 0.88 0.71-0.73	4 1.43 0.43 2.36 0.29 1.2 ? 1.37 1.0 1.0 0.39 3.53 0.33
Iberolacerta_monticola_uamr_lm92 ?	5.0-6.0 3.0 17.0-18.0 21.0-22.0 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?
0.37 ? 2.18 1.21-2.27 ? ? 0.32 1.2 ? 1.0 0.99 0.	75 0.43 3.7 0.26 ? 12.03 0.9 0.8 0.68
Phoenicolacerta_troodica_318	9.0 5.0 3.0 16.0 22.0-23.0 ? ? ? ? 5.0 1.0 ? 0.27
0.44 ? 1.0 0.56 0.38 ? 2.69 1.56 ? ? 0.46 1.16 1	.2 1.1 0.8 0.7 0.5 4.5 0.4 0.48 ? ? ? 0.78
P_troodica_319	9.0 4.0-6.0 2.0 16.0-17.0 20.0
27.0????1.33?0.43??1.40.55??2.361.	5 ? ? 0.45 1.0 1.57 1.1 0.9 1.0 0.5 4.8 0.38 0.52 ? ? ? ?
Podarcis_hispanicus_uamr_h30	7.0 5.0 2.0 17.0 22.0 26.0 ? ? ? 5.0 1.3
0.872665-1.22173 ? ? 0.48 ? ? 0.38 ? 2.77 1.77	0.3 1.19 0.41 1.14 ? 0.9 0.9 1.2 0.4 4.3 0.28 0.44
14.68 0.91 0.97 0.75	
Podarcis_muralis_311	7.0 5.0-6.0 3.0 19.0 24.0 ? ? ? ? 6.0 1.3 ? 0.26
0.31 ? 1.05 0.45 0.37 ? 2.25 1.56 ? ? 0.43 1.2-1	1.5 1.14 1.3 0.9 0.9 0.6 3.0 0.36 0.43 ? ? ? 0.77
Podarcis_muralis_312	7.0 6.0-7.0 2.0 17.0 22.0 ? ? ? ? 5.0 1.2
0.977384 0.33 0.33 0.39 1.42 0.47 0.35 ? 2.38 0.79	1.56 ? 1.54 0.32 1.0 1.18 ? ? ? ? ? 0.42 ? ? ? 0.93
Podarcis_muralis_313	? 6.0 3.0 18.0 23.0 ? ? ? ? ? ? ? ? 0.29 ? 1.36 ?
? ? 2.67 1.53 0.43 ? 0.28 1.1 1.26 1.0 0.8 0.8 0	.6 3.1 ? 0.48 14.02 0.91 0.98 ?
Podarcis_muralis_nhmuk1920.1.20.801	7.0 6.0 3.0 17.0 22.0-23.0 27.0 6.0 6.0 2.0 6.0
??0.43??????????????????????????????????	??
Podarcis_siculus_25	7.0 4.0-5.0 3.0 16.0 20.0-21.0 28.0 ?
6.0 ? 5.0 2.0 1.01229 0.46 0.32 0.44 1.88 0.63	0.38 ? 2.33 1.33 0.41 1.64 0.33 1.0 1.22 1.2 0.8 1.2
0.5 3.8 0.4 ? 13.85 1.03 0.91 0.78	

Podarcis_siculus_125	7.0 4.0-6.0 3.0 18.0-19.0 23.0 26.0 ? ? ? 4.0
1.6 ? 0.39 0.37 ? 1.47 0.42 0.42 ? 2.23 1.64 ? ?	0.26 1.4 1.2 1.3 0.8 0.9 0.52 3.8 0.41 0.44 ? ? ? 0.77
Podarcis_siculus_amnh_r110436	5.0-7.0 2.0-6.0 3.0 16.0-31.0 13.0-33.0 27.0-
52.0 ? 5.0-6.0 ? ? ? ? ? ? 0.4-1.0 ? ? 0.41-0.53 ?	1.8-3.0 1.21-2.27 0.42-0.56 1.06-4.7 0.09-0.39 1.1-
1.97?????????????	
Podarcis_tiliguerta_153	7.0 6.0 3.0 19.0 24.0 ? ? ? ? 5.0 0.8
0.907571 0.28 0.3 0.47 1.47 0.49 0.35 ? 2.59 2	.0 ? 1.62 0.48 1.3 1.18 1.1 0.8 1.4 0.4 3.7 0.47 0.44
13.96 1.0 0.87 0.75	
Podarcis_tiliguerta_154	7.0 6.0-7.0 ? 17.0-18.0 22.0 25.0 ? ? ?
4.0 1.2 ? 0.26 0.38 ? 1.5 0.64 0.37 ? 2.22 1.44 ?	? ? 0.48 1.3 1.1 1.0 0.9 1.1 0.4 4.0 0.38 0.53 13.19
0.95 0.91 0.78	
Podarcis_waglerianus_390	7.0 6.0 2.0 17.0 22.0-23.0 27.0 ? ? ? 6.0 1.5
0.959931 0.37 0.38 0.45 1.47 0.55 0.38 ? 2.27	1.5 ? 1.71 0.24 1.4 1.22 1.3 0.8 1.7 0.5 3.4 0.45 0.49
13.78 0.98 0.87 0.78	
Takydromus_sp_151	9.0 6.0-7.0 3.0 30.0 29.0-33.0 27.0 ? ?
? 5.0 ? ? ? 0.38 0.6 1.4 0.54 0.31 0.1-37.9 2.6 1	.18 ? ? 0.09 1.2 1.34 1.0 0.86 1.1 0.43 3.8 0.4 0.58 ?
? ? 0.75	
Zootoca_vivipara_179	7.0 5.0 3.0 19.0-20.0 22.0 28.0 ? ? ?
3.0 1.3 1.18682 0.27 0.33 0.42 1.6 0.51 0.46 ?	2.35 1.35 ? 1.89 0.24 0.81 1.33 1.1 0.9 0.7 0.6 3.5
0.3-0.34 0.45-1.1 12.71 1.13 0.92 0.7	
Timon_pater_nhmuk1920.1.20.2722	9.0 5.0-7.0 3.0 14.0-16.0 21.0-22.0 27.0 7.0
6.0 2.0 5.0 ? ? 0.31 ? ? ? ? 0.53 ? 1.54 1.0-1.2 ?	? 0.6 1.1-1.97 ? ? ? ? ? ? ? ? ? 13.3 ? 0.83 0.68
T_pater_nhmuk1920.1.20.1259	9.0 6.0-8.0 3.0 18.0 22.0-23.0 27.0-
28.0 7.0-8.0 6.0 2.0 5.0-6.0 ? ? 0.35 ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ? ? ? ? 0.24 10.75 ? 0.75 0.8
Timon_pater_gmz_d.36_x.171	9.0 7.0-8.0 3.0 20.0-23.0 27.0-28.0 ? ?
?????0.36????0.48?1.821.36?0.820.7	9 0.69-1.0 1.05 ? ? ? ? ? ? ? ? ? ? ? ? ?
Timon_kurdistanicus_nhmw18545	9.0 7.0 3.0 15.0 22.0-23.0 ? ? ? ? ? 0.98
0.907571 0.27 ? 0.55 ? ? 0.36 ? 1.55-1.63 1.04-	-1.09 0.34 1.32 0.46-0.5 1.19 0.98 ? ? ? ? ? ? ? ? ? ? ? ? ?

 Timon_princeps_nhmw32881
 9.0 5.0-7.0 3.0 18.0 24.0-26.0 ? ? ? ? ?

 1.0 0.699877-0.837758 0.39 ? 0.52-0.54 1.06-1.92 ? 0.37 ? 1.54-1.64 1.03-1.2 0.39-0.4 1.08 0.5

 1.23 0.89 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?

? 7.0-9.0 3.0 22.0 ? 27.0 ? ? ? 5.0 ? ? ?

 Timon_lepidus_216
 9.0-10.0 8.0 3.0 19.0-20.0 27.0-28.0

 28.0 ? ? ? 5.0 0.9 0.890118 0.29 0.46 0.57 1.41 0.57 0.45 ? 1.8 1.49 0.38 0.93 0.68 1.09 1.3 1.1 0.7

 1.5 0.44 2.8 0.35 0.49 11.36 0.98 0.83 0.74

Timon_lepidus_amnh_r577708.0-11.0 2.0-6.0 3.0 16.0-31.0 13.0-33.0 27.0-52.0 7.0-8.0 5.0-6.0 2.0 6.0 ? ? 0.2-0.4 ? ? ? ? 0.41-0.53 ? 1.8-3.0 1.21-2.27 0.42-0.56 0.7-0.9 0.4-0.6 1.1-1.97 ? ? ? ? ? ? 0.39-0.53 0.24-0.39 10.0-15.52 0.78-0.94 0.82-1.11 0.7-0.89

 T_lepidus_mncn41021
 9.0 7.0 3.0 22.0 27.0-28.0 ? ? ?

 ? 5.0 0.9-1.1 ? ? ? ? ? ? ? ? 1.8-3.0 1.0-1.2 ? ? 0.61-0.79 1.1-1.97 ? ? ? 1.87 0.59 ? 0.37 ? ? ? ? ?

 T_lepidus_mnhn1887_545
 8.0 7.0 3.0 21.0-22.0 28.0 27.0 ? ? 2.0

 6.0 1.0 ? ? ? ? ? ? 0.4-0.43 ? 1.8-3.0 1.0-1.2 ? ? 0.61-0.79 1.8 ? 1.4 0.7 1.7 0.6 2.6 0.45 0.43 ? ? ? ?

 T_lepidus_mrac3390
 9.0 6.0 3.0 23.0-24.0 30.0-31.0 27.0

 7.0 ? 2.0 ? 1.2 0.872665-1.22173 ? ? 0.54 1.06-1.92 ? 0.44 ? 1.53 1.26 0.2-0.41 0.7 0.68 1.97 0.81 ?

 ? ? ? ? ? ? ? ? ? ? ? ? ?

 T_lepidus_mrac92_050_r_1
 9.0 6.0-7.0 3.0 22.0 30.0 27.0 ? ? ? 5.0 1.1

 0.872665-1.22173 ? ? 0.51 ? ? 0.45 ? 1.96 1.31 0.34 1.02 0.5 1.65 ? 1.3 0.7 2.0 0.6 3.3 0.38 0.34

 11.65 0.97 0.83 0.71

 T_lepidus_nhmw699
 9.0 5.0-7.0 3.0 21.0 28.0 27.0 ? ? ? ?

 1.0 0.959931-1.134464 0.31-0.35 ? ? ? ? 0.48 ? 1.76 1.5 0.34 0.78 0.81 1.3 1.0 1.25 0.78 1.67 0.47 ?

 0.4 0.38 ? ? ? 0.7

 T_lepidus_pimuz_a_iii0965
 8.0-11.0 7.0 ? 16.0-17.0 24.0-25.0 ? ? 8.0 2.0 ?

 0.9-1.1 ? ? ? ? ? ? ? ? 1.8-3.0 1.0-1.2 0.33 ? 0.61-0.79 ? 0.99 1.5 0.7 1.7 0.52 2.2 ? ? ? ? ?

 Lacerta_agilis_cipa1550
 9.0 5.0 2.0 16.0 20.0-21.0 28.0 ? ? ?

 4.0 1.38 0.977384 0.18 ? 0.48 ? ? 0.37 ? 2.0 1.04 ? 2.03 0.29 1.02 ? 0.73 0.66 1.28 0.5 3.07 0.39

 0.74 12.86 0.9 0.71 0.71

Lacerta_agilis_176 7.0 4.0-5.0 3.0 15.0-16.0 20.0-21.0 29.0 ? ? ? 4.0 1.81 0.959931 0.3 0.46 0.47 1.59 0.51 0.42-0.47 ? 1.85-2.15 1.2 ? 3.2 0.32 0.98 1.25 1.1 0.8 1.0 0.53 3.2 0.36 0.45 10.17 0.96 0.77 0.7

 Lacerta_agilis_mdhc_177
 7.0 5.0-6.0 2.0 15.0 20.0 28.0 ? ? ? 5.0

 1.3 1.047198 0.33 0.47 0.45 1.47 0.55 0.42 ? 1.8 1.33 0.46 2.75 0.37 1.04 1.14 1.1 0.8 1.1 0.61 3.3

 0.36 0.56 12.7 1.09 0.83 0.73

 Lacerta_agilis_mdhc_178
 9.0 5.0 2.0 16.0-17.0 18.0-20.0 27.0 ? ?

 ? 6.0 1.4 1.204277 0.33 0.34 0.54 1.32 0.62 0.41 ? 2.0 1.12 ? 2.62 0.3 1.2 1.05 1.2 0.8 1.3 0.61 3.1

 0.41 0.5 11.29 0.88 0.85 0.72

 Lacerta_agilis_230
 9.0 6.0-8.0 3.0 16.0-17.0 22.0 28.0 ? ?

 ? 4.0 1.5 1.22173 0.29 0.43 0.47 1.21 0.54 0.33 ? 2.18 1.23 ? 4.7 0.36 1.0 1.18 1.1 0.8 0.6 0.5 3.4

 0.37 0.66 11.69 0.78 0.87 0.67

 Lacerta_agilis_mdhc_231
 9.0 5.0-6.0 3.0 17.0 19.0 28.0 ? ? ? 4.0

 1.2 1.256637 0.24 0.46 0.48 1.0 0.54 0.39 ? 1.92 1.2 0.45 3.4 0.3 0.96 1.15 1.3 0.7 0.9 0.5 3.3 0.42

 0.68 13.67 1.13 0.81 0.68

 Lacerta_agilis_mncn15979
 9.0 6.0 2.0 16.0-17.0 18.0-19.0 27.0 ? ? ? 6.0

 1.11-3.9 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 1.1 ? ? ? 0.9 0.55 ? 0.39 ? ? ? ? ?

 Lacerta_agilis_mnhn1963_49
 9.0 4.0-6.0 3.0 15.0-16.0 19.0-21.0 28.0 7.0 ?

 2.0 4.0 ? ? ? ? ? ? 0.29 ? ? 1.0-1.2 ? ? ? 1.0 ? ? ? ? ? ? 0.35 ? ? ? ? ?

 Lacerta_agilis_nhmw802
 9.0 5.0-6.0 2.0 17.0-18.0 21.0-22.0

 28.0 7.0 6.0 3.0 4.0 1.33 0.7801622-0.785398 ? ? 0.49-0.56 1.06-1.92 ? 0.29 ? 1.93-2.01 1.32 0.29

 0.35 3.22-3.28 0.25-0.29 0.9 1.18 ? ? ? ? ? ? ? 11.0 1.03 0.88 0.68

 Lacerta_agilis_pimuz_a_iii0902
 7.0 2.0-6.0 3.0 ? 20.0 ? ? ? ? ? ? ? ? ? 0.53 ? ?

 0.29-0.4 ? 1.74 1.18 0.36 ? 0.25 0.9 1.1 ? ? ? ? ? ? ? ? ? ? ? ? ? ?

Lacerta_agilis_ZMH_R12174 7.0 4.0 2.0 16.0-17.0 20.0-22.0 29.0 7.0 5.0-6.0 2.0 4.0 ? ? 0.23 ? ? ? 0.34-0.99 0.37 ? 1.53 1.4 ? 3.1 0.27 0.69-1.0 1.01-1.6 ? ? ? ? ? ? ? ? 11.66 0.95-1.05 ? 0.71

L bilineata 48

Lacerta bilineata 15 11.0 5.0 3.0 19.0 24.0-25.0 25.0 ? 6.0 2.0 6.0 1.29 0.994838 0.29 0.43 0.44 1.6 0.58 0.37 ? 1.81 1.13 ? 1.8 0.28 1.28 1.07 1.3 0.7 1.2 0.6 3.2 0.48 0.5 13.99 0.89 0.96?

21.0?????0.9-1.1????????1.8-3.01.21-2.27???1.1-1.971.251.31.10.70.522.60.44?? ???

L bilineata 73 22.0????5.01.0?0.25???0.52??2.21.21???1.01.2????2.8?????

L bilineata 77 27.0???6.01.01.0471980.260.390.451.630.520.31?1.811.06?2.250.231.31.121.30.8 0.9 0.55 3.3 0.41 ? 13.56 1.06 0.67 0.8

L bilineata 84 9.0 5.0-6.0 3.0 17.0-18.0 23.0 27.0???6.01.0?0.280.380.541.50.340.37?1.91.17?2.750.231.261.151.30.81.50.543.4 0.41 0.53 8.13 1.1 0.75 0.76

L bilineata 381 10.0-11.0 5.0-6.0 2.0 20.0-22.0 26.0?????1.01.1868240.30.40.511.380.560.36?1.821.15?1.910.321.41.09????????????? ???

11.0 5.0-6.0 3.0 21.0 26.0-27.0 27.0 ? ? ? 6.0 ? Lacerta bilineata 420 ?????0.58??1.681.140.36?0.291.25?1.30.81.20.643.50.49?11.80.970.840.77

Lacerta bilineata amnh r1148 8.0-11.0 2.0-6.0 1.0-2.0 16.0-31.0 13.0-33.0 ? ????0.7-0.89?0.2-0.4????0.41-0.53?1.3-1.791.21-2.27?0.95-1.050.09-0.391.1-1.97??? ??????????

Lacerta bilineata amnh_r109472 5.0-7.0 7.0-10.0 1.0-2.0 16.0-31.0 13.0-33.0 ?

9.0 5.0-6.0 3.0 17.0-18.0 19.0-22.0 Lacerta bilineata mncn16505 28.0???6.00.9-1.1????????1.0-1.2???1.27?1.3?1.00.62.80.43????0.75

Lacerta bilineata pimuz a iii1276 7.0 7.0-8.0 3.0 17.0 21.0-22.0 ? ? ? ? 0.9-1.1 ? ? ? ? ????1.85 1.0-1.2??0.3 1.73 1.16 1.4 0.8 1.7 0.52 2.0??????

Cd matrix

8.0-9.0 6.0-7.0 2.0 15.0 21.0-

11.0 5.0-7.0 3.0 19.0 24.0-25.0

? 5.0-6.0 2.0 14.0-15.0 18.0-

9.0 6.0-7.0 3.0 16.0 21.0-22.0 26.0 ? L bilineata uam q21 6.0 2.0 5.0 1.52 0.872665-1.22173 ? ? 0.48 ? ? 0.39 ? 1.85 1.31 0.32 1.87 0.2 1.12 ? 1.2 0.9 1.8 0.7 3.2 0.48 ? ? 1.0 0.62 0.7 Lacerta media nhmw34809 9.0 6.0 2.0 22.0 27.0 ? ? ? ? ? 0.9-1.1 0.809833-0.855211??0.41-0.51??0.25-0.35?2.09??1.55-1.60.42-0.461.31.04??????????? ??? Lacerta media huj ost z 299 ? 2.0-6.0 3.0 16.0-31.0 13.0-33.0 27.0 ? Lacerta_media_huj_ost z 396 9.0 2.0-6.0 3.0 16.0-31.0 13.0-33.0 ? ? Lacerta schreiberi cipa778 9.0 5.0-6.0 3.0 18.0-19.0 21.0-23.0 27.0 ? ? ? 5.0 1.39 1.047198 0.27 ? 0.47 ? ? 0.43 ? 1.69 1.05 ? 1.3 0.46 1.1-1.97 ? ? ? ? ? ? ? ? 0.39 11.71 ? 0.9 0.72 9.0 6.0 1.0-2.0 16.0 ? 28.0 ? ? ? 5.0 1.11-3.9 ? Lacerta schreiberi cipa1256 9.0 5.0-6.0 3.0 16.0-18.0 23.0-24.0 ? ? L schreiberi cipa1511 Lacerta schreiberi cipa1517 9.0? 1.0-2.0? 21.0-22.0 27.0??? 5.0 1.11-L schreiberi nhmuk1906.10.30.14 ? 6.0 3.0 18.0 23.0-24.0 28.0 7.0 7.0 2.0 ? ? ? ? ????0.45?1.951.0-1.2??0.21.3??????0.450.31???0.72 Lacerta schreiberi uam s 6 8.0 5.0-6.0 3.0 17.0-18.0 21.0-22.0 27.0 ? ? 2.0 5.0 1.29 0.872665-1.22173 ? ? 0.43 ? ? 0.41 ? 1.68-1.81 1.13 0.4 1.14 0.52 1.34 ? 1.5 0.8 0.91 0.5 3.0 0.43 ? 14.01 0.84 0.85 0.72 Lacerta strigata 304 7.0 4.0 2.0 16.0-17.0 20.0-21.0 27.0 ? ? ? 5.0 0.9 1.15192 0.38 0.44 0.47 ? 0.61 0.39 ? 2.13 1.33 ? 1.75 0.4 1.2 1.25 1.3 0.8 1.3 0.53 2.9 0.45 0.57 14.92 0.88 0.92 0.83 L strigata nhmw10918 ? 6.0-7.0 2.0 17.0-18.0 22.0-24.0 ? ? ?

Lacerta_trilineata_240 11.0 6.0 2.0 20.0-21.0 26.0 28.0 ? ? ? ? ? ? 0.907571 ? 0.41 ? 1.68 0.67 ? ? 1.3-1.79 1.0-1.2 ? ? ? 1.1-1.97 1.19 1.4 0.8 1.3 0.56 3.1 0.44 ? ? ? ? ? ?

L trilineata 241

11.0 6.0 3.0 20.0-21.0 27.0 25.0 ? ? ? ?

? 0.942478 0.25 0.33 0.5 1.92 0.47 0.37 ? 1.74 1.6 ? 1.14 0.44 1.43 1.1 1.4 0.8 1.4 0.58 3.3 0.52 0.63 14.89 1.11 0.78 0.79

L_trilineata_295 9.0 5.0 3.0 18.0-19.0 23.0-24.0 ? ? ? ? ? 1.33 1.308997 0.26 0.34 0.54 1.67 0.6 0.47 ? 1.87 1.5 0.33 2.67 0.34 1.52 1.03 1.5 0.7 1.36 0.58 2.4 ? ? ? ? ? ?

L_trilineata_356 12.0 5.0-6.0 2.0 21.0 27.0 27.0 ? ? ? ? 1.2 1.064651 0.23 0.31 0.6 1.6 0.52 0.46 ? 1.75 1.38 ? 1.38 0.4 1.41 1.06 1.4 0.8 1.3 0.6 3.1 0.48 ? 12.31 1.07 0.9 0.77

Lacerta_trilineata_mrac95_050_r_0001 14.0 6.0 3.0 23.0 26.0-27.0 27.0 ? ? ? 6.0 1.2 1.223476-1.570796 ? ? 0.52 ? ? 0.44 ? 1.6 1.36 0.45 1.34 0.29 1.48 ? 1.4 0.7 1.6 0.6 3.1 0.47 0.57 12.02 0.87 0.81 0.79

L_trilineata_mrac95_050_r_0002 9.0 6.0 3.0 20.0-21.0 26.0-27.0 27.0 ? ? ? 6.0 1.0 1.223476-1.570796 ? ? 0.47 ? ? 0.46 ? 1.61 1.16 0.32 1.42 0.26 1.57 ? 1.3 0.8 1.8 0.6 3.2 0.53 0.56 13.77 0.99 0.91 0.73

Lacerta_trilineata_nhmuk1914.1.12.1 11.0 6.0 1.0-2.0 21.0 27.0 27.0 6.0 7.0 2.0 6.0 ? ? 0.3 ? ? ? ? 0.43 ? 1.7 1.0-1.2 ? ? 0.33 1.1-1.97 ? ? ? ? ? ? 0.5 0.42 ? ? ? 0.71

Lacerta_trilineata_zzsid_r_235_76 8.0 6.0 2.0 18.0-20.0 23.0-24.0 28.0 ? ? ? 6.0 1.0 1.223476-1.570796 ? ? ? ? ? 0.46 ? 1.9 1.39 0.4 2.73 0.25 1.43 ? 1.3 0.8 1.4 0.6 3.2 0.44 0.63 12.08 0.96 0.88 0.74

 Lacerta_viridis_mnhn1888_139
 9.0 5.0-6.0 3.0 19.0-20.0 24.0-25.0 27.0 8.0 ?

 2.0 5.0 ? ? ? ? ? ? 0.38 ? ? 1.0-1.2 0.2-0.3 ? 0.09-0.39 1.4 ? ? ? ? ? ? 0.5 0.46 ? ? ? ?

 Lacerta_viridis_mnhn1887_813
 9.0 3.0-4.0 3.0 14.0-16.0 19.0-20.0 27.0 ? ? 3.0

 5.0 ? ? ? ? ? ? 0.34 ? ? 1.0-1.2 0.25-0.35 ? ? 1.3 ? ? ? ? ? 0.41 ? ? ? ? ?

Lacerta_viridis_mrac91_077_r_76 8.0 5.0 2.0 19.0-20.0 24.0 27.0 ? ? ? 5.0 1.64 1.223476-1.570796 ? ? 0.52 ? ? 0.39 ? 1.69 1.22 0.43 1.88 0.32 1.33 ? 1.4 0.8 1.3 0.6 3.2 0.47 0.56 12.82 0.92 0.91 0.7

Lacerta_viridis_nhmw887 11.0 6.0 2.0 20.0-21.0 27.0-28.0 28.0 6.0 7.0 2.0 6.0 1.0 0.907571-0.994838 0.3 ? 0.52-0.53 1.06-1.92 ? 0.42-0.46 ? 1.73 1.26 ? 1.56-1.61 0.44-0.46 1.1 1.08 ? ? ? ? ? ? 0.58 11.2 0.88 0.82 0.74

Lacerta_viridis_nhmw906 11.0 5.0-6.0 2.0 21.0 29.0 28.0 6.0 7.0 2.0 6.0 1.04 0.8779006 0.3 ? 0.52 ? ? 0.41 ? 1.59 1.25 ? 1.32 0.38 1.15 1.07 ? ? ? ? ? ? ? 11.8 1.04 1.11 0.75

 Lacerta_viridis_nhmw32879_3
 11.0 5.0-6.0 3.0 18.0 24.0 ? ? ? ? ? 1.0

 0.977384 0.29 ? 0.57 ? ? 0.39 ? 1.46-1.52 1.0 ? 1.11 0.25-0.3 1.08 1.09 ? ? ? ? ? ? ? ? ? ? ? ? ?

 Lacerta_viridis_zzsid_r_287_80
 9.0 4.0 2.0 17.0 22.0 28.0 ? ? 2.0 6.0 1.61

 1.223476-1.570796 ? ? ? ? ? 0.37 ? 1.7 1.07 0.46 2.19 0.28 1.26 ? 1.3 0.8 1.1 0.5 2.9 0.4 0.47 12.49

 0.97 0.84 0.7

Lacerta_viridis_zzsid_r_463_87 9.0 5.0-6.0 3.0 17.0 21.0-22.0 28.0 ? 8.0 ? 6.0 1.33 1.223476-1.570796 ? ? 0.54 ? ? 0.38 ? 1.83 1.14 0.42 3.45 0.34 1.37 ? 1.4 0.8 1.4 0.5 3.1 0.44 ? 12.34 1.0 0.86 0.66

&[num]

Gekko gecko 112

11100001011100101010?001010-101100-?00111000000110010-10?1000?-00-

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011101001011??100100001??101000010--001110-??00?000

Chalcides_ocellatus_193

0111000000100101011?000110-

001100-?01101010110011110-11110010-00-

Salvator_merianae_cmgr

Tupinambis_teguixin_amnh_r1552481010011-00100??1???10000111110100-0?001??01?1?000000-1?1???11-?0-101??111101?0?2010?00100-00110?-00001?01?0000111?0?001-101?1100000??131000??0-?10?0110-00[12]2001110-010?1011??1?00?0?000[01]110100001001011111?1111110011010?1011??1?00?0?000[01]110100001001011111?1111110011

 Ablepharus_kitaibelli_239
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 01011000001

Blanus_strauchi_287

Gallotia_simonyi_nhmw849

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 Psammodromus_algirus_amnh_r92976
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Acanthodactylus_boskianus_276

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Acanthodactylus_erythrurus_uamr_acvii 1010?1011001011???10?00110101?1?00-

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Eremias_velox_nhmw822 1110011-00010??0001?00000010100100?000??0?010110?00-10000?110?0-11000101100111?0?1?01001101?0??00110111?1-00001?0?111-011?11010001013010011010100011100121010-10-00001010??0?00?11010100011001001100-0100110010?0000

Ophisops_elegans_281

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Ophisops_elegans_282

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Algyroides_fitzingeri_3511110000000011100010?0011001101100-?101?????10??????0???????1111010?11100011?1011111?0-00100000111001001-0101?100101-01101101000001???00001110?11101121010-0??001?????????????10110????00001001?1?0????10?011

A_danfordi_284

Archaeolacerta_bedriagae_167

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Iberolacerta_cyreni_uamr_lm4

I_monticola_uamr_lm77

 Iberolacerta_monticola_uamr_lm92
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1?010????0??011

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      Phoenicolacerta_troodica_318
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      01011110111-
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P_troodica_319

Podarcis_hispanicus_uamr_h30

Podarcis_muralis_311

Podarcis_muralis_312

Podarcis_muralis_313

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Podarcis_muralis_nhmuk1920.1.20.801

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Podarcis_siculus_125

Podarcis_siculus_amnh_r110436

111000000010100??100010101?1?110111?01????0???011??0-

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Podarcis_tiliguerta_153

00101101000011301000111110??011?0131011000-

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Podarcis_tiliguerta_154

Podarcis_waglerianus_390

101011010001113010000110101?111?0121010-

Takydromus_sp_151

111??0???101011???1??0000110101110-?00111011010000000-

011111010000012000011100100?????221020-0??001101001001001101101?0?1??00001010-1?000????1??000 Zootoca_vivipara_179

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Timon_pater_nhmuk1920.1.20.2722

T_pater_nhmuk1920.1.20.1259

Timon_kurdistanicus_nhmw18545

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Timon_princeps_nhmw32881

Timon_lepidus_cipa761

Timon_lepidus_216

Timon_lepidus_amnh_r57770

T_lepidus_mncn41021

T_lepidus_mnhn1887_545

1110?100?010011???10?[01]?011010?1?110?1??????01?0???0?00??0???1011?0?1100?100?? 101?1?1?0-

T lepidus mrac3390

1110011-

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T_lepidus_mrac92_050_r_1

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T_lepidus_nhmw699

T_lepidus_pimuz_a_iii0965

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Timon_lepidus_gmz_vd36.x1246

Lacerta_agilis_amnh_r76854

Lacerta_agilis_cipa1550

Lacerta_agilis_176

Lacerta_agilis_mdhc_177

Lacerta_agilis_mdhc_178

01100000110001000001101110100[01]00111101001011210001110110??11100111010-010010010101010000111101?1?0??1000011101?010????10?011

Lacerta_agilis_230

Lacerta_agilis_mdhc_231

Lacerta_agilis_mncn15979

1100?100?001001??011?00010001?1?112?0??110?????01011??0??0??????1?1?11100????101 ?1?1?0-

Lacerta_agilis_mnhn1963_49

Lacerta_agilis_nhmw802

Lacerta_agilis_pimuz_a_iii0902

Lacerta_agilis_ZMH_R12174 1??001???01????1?1??101010??1?1??121?01???11101???1001??0111110100?1111100?0121?

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Lacerta_bilineata_15

000011000100110000011011000000001?1101001?11310[01]?1010110??01100111011000-111?1011?001001111101?1?110010101?0-??000110?000011

L_bilineata_48

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101?110?0000113101?1000110??11??0121010-

L_bilineata_73

111000000?010??0?010?100100-1011111?001?????10010100-

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L_bilineata_77

L_bilineata_84

L_bilineata_381

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Lacerta_bilineata_amnh_r1148

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Lacerta_bilineata_amnh_r109472

Lacerta_bilineata_mncn16505

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Lacerta_bilineata_pimuz_a_iii1276

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 $L_bilineata_uam_q21$

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0?000?110?100101??1110000??101?110?0-0010000?110000001-

Lacerta_media_nhmw34809

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Lacerta_media_huj_ost_z_299

Lacerta_media_huj_ost_z_396

Lacerta_schreiberi_cipa778

L_schreiberi_cipa1511

Lacerta_schreiberi_cipa1517 111????011011???1??0?1?111?1?10-???1100?????01001??0??0??0???1??10??00???101?1?0?0-

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Lacerta_schreiberi_uam_s_6

1110?100?011011???10?01110111?1?111?001?????1?010[01]1100?001?0?0?101001??[01]10001 ???101?111?0-

Lacerta_strigata_304

L_strigata_nhmw10918

Lacerta_trilineata_240

L_trilineata_241

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L_trilineata_295

L_trilineata_356

Lacerta_trilineata_mrac95_050_r_0001

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L_trilineata_mrac95_050_r_0002

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Lacerta_trilineata_nhmuk1914.1.12.1

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Lacerta_viridis_amnh_r154761

Lacerta_viridis_amnh_r154762

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Lacerta_viridis_mncn16504

Lacerta_viridis_mnhn1888_139

Lacerta_viridis_mnhn1887_813

Lacerta_viridis_mrac91_077_r_76

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Lacerta_viridis_nhmw887

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Lacerta_viridis_nhmw906

Lacerta_viridis_nhmw32879_3

Lacerta_viridis_zzsid_r_287_80

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Lacerta_viridis_zzsid_r_463_87

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0?000?1?0?100101?1[01]11000???001?11110-

;

proc/;

45-fossil-cd matrix xread 252 120 &[cont] Gekko gecko 112 11.0 9.0 1.0 30.0-31.0 30.0 ? ? ???1.70.8028510.160.420.580.70.45??4.62.20.44???1.6?????8.631.390.8? Varanus exanthematicus 335 ? 7.0-8.0 1.0 ? 10.0-11.0 28.0 ? 8.0 ? 7.0-10.0 1.3 0.733038 0.24 0.49 0.62 0.9 0.75 ? ? 2.9 1.16 0.45-0.55 ? ? 0.69-1.0 ? 1.1 0.77 2.3 0.46 ? 0.43 0.24-0.39 8.49 0.96 0.74 0.83 Chalcides ocellatus 193 7.0 6.0 1.0 12.0-13.0 17.0-18.0 40.0 ? 6.0 ? 4.0 1.5 0.436332 0.16 0.44 0.63 1.16 0.66 ? ? 1.66 1.08 ? ? ? 1.0 1.08 1.2 0.8 1.5 0.5 3.3 0.36 ? 11.44 1.08 0.92 0.57 Salvator merianae cmgr 10.0 5.0 ? 12.0-13.0 16.0 ? ? ? ? ? 2.5 Tupinambis teguixin amnh r155248 8.0-11.0 7.0-10.0 ? 3.0-15.0 13.0-33.0 24.0-26.0?? 2.07.0-10.01.11-3.9? 0.2-0.4? 0.4-1.0?? 0.41-0.53? 1.8-3.01.21-2.27 0.42-0.56?? 0.69-1.0? 1.2-1.3 0.71-0.89 1.41-2.3 0.5-0.7 2.5-3.5 0.39-0.53 0.24-0.39 8.13-9.9 1.06-1.39? 0.7-0.89 Tupinambis teguixin ZMH R12172 9.0 4.0-5.0 3.0 11.0 14.0-15.0 ????? 1.98? 0.29 0.25-0.49 0.62 1.06-1.92 0.34-0.99 ? ? 2.64 1.43 0.56 ? ? ? 1.01-1.6 ? ? ? ? ? ? ? ? ? ? ? ? ? ? Anguis veronensis 102 9.0 4.0 1.0 ? 10.0 24.0 ? 6.0 ? 9.0-10.0 0.7 0.977384 0.13 0.24 0.7 0.82 0.63 ? ? 1.5 1.1 ? 2.0 0.43 1.0 0.86 0.62 0.72 0.73 0.54 3.11 0.42 ? ???? Pseudopus apodus 214 7.0 5.0 1.0 13.0 14.0-16.0 52.0 3.0-4.0 6.0?7.0-10.0 1.8 0.959931 0.38?????1.35??1.25 0.7?0.98 0.81 0.85 1.38 0.52 3.16???? ?? ? 9.0-10.0 2.0 18.0 20.0-21.0 28.0 ? ? ? 6.0 1.2 Broadleysaurus major 164

0.942478 0.17 0.21 0.6 1.41 0.56 0.37 ? 1.7 1.14 ? 2.0 0.3 0.69-1.0 0.98 0.87 0.94 1.86 0.5 3.0 0.45 1.1 11.0 1.17 0.9 0.59

Blanus strauchi 287

 Ablepharus_kitaibelli_239
 ? ? 1.0 13.0-14.0 18.0 33.0 ? ? ? ? 3.9

 1.134464 0.33 ? 0.65 ? 0.48 ? ? 2.8 1.4 ? ? ? ? 1.13 ? ? ? ? ? ? ? ? ? ? ? ?

Blanus_rufus_156 1.33 1.09 ? ? 1.44 ? ? ? ? ? ? ? ? ? 2.1 ? ? ? ? ? ? ? ?

7.0 2.0 1.0 4.0 8.0 ? ? ? ? ? 2.0

? 2.0 1.0 3.0 ? ? ? ? ? ? ? ? ? ? 1.0 0.48

0.872665 0.33 ? 0.57 1.06-1.92 ? ? ? 1.7 1.05 ? ? ? ? ? ? ? 2.3 0.43 ? ? ? ? ? ? ?

 Gallotia_simonyi_nhmw849
 9.0 8.0-9.0 5.0 20.0 23.0-24.0 25.0 7.0 6.0 2.0

 6.0 1.27 0.855211 ? ? 0.58 ? ? 0.36 ? 1.85 1.08 0.32 0.81 0.46 1.2 1.07 ? ? ? ? ? ? 0.25-0.35 11.25

 0.93 0.95 0.72

 Psammodromus_algirus_amnh_r59605
 8.0-11.0 2.0-6.0 3.0 16.0-31.0 13.0-33.0 ? ? ? ?

 ? 1.11-3.9 ? 0.2-0.4 ? ? ? ? ? 1.8-3.0 ? 0.2-0.41 1.06-4.7 0.09-0.39 1.1-1.97 ? ? ? ? ? ? ? ? ? ? ? ? ?

 Psammodromus_algirus_amnh_r92976
 8.0-11.0 ? 3.0 16.0-31.0 13.0-33.0 ? ? 5.0-6.0 ?

 5.0 1.11-3.9 ? 0.2-0.4 ? ? ? ? ? 1.8-3.0 ? ? ? 0.09-0.39 0.69-1.0 ? ? ? ? ? ? 0.21-0.38 ? ? ? ? ?

 Psammodromus_algirus_nhmw788
 11.0 4.0-5.0 2.0 19.0 22.0-23.0 26.0 6.0 6.0

 2.0 5.0 1.0 0.802851-0.925025 0.37 ? 0.38-0.39 1.0 ? 0.34 ? 2.62-2.64 1.27-1.32 0.39 ? 0.34-0.35

 0.92 ? ? ? ? ? ? ? 15.0 0.95 0.83 0.72

 Psammodromus_algirus_uamr_ps_9
 9.0 4.0-5.0 3.0 19.0 23.0-25.0 ? ? ? ? 5.0 1.8

 0.698132-0.872665 ? ? 0.38 ? ? 0.34 ? 2.45 1.36 ? 1.81 0.39 1.2 ? 1.3 0.8 0.9 0.6 3.4 0.45 ? 14.14

 0.96 0.86 ?

Acanthodactylus_boskianus_276 8.0 5.0 ? 20.0 25.0 26.0 ? ? ? 6.0 0.97 0.663225 0.56 0.41 0.45 1.33 0.57 0.38 ? 4.27-4.37 ? 0.48 1.0 ? 0.8 1.25 1.1 0.93 1.1 0.56 3.85 0.33 0.56 ? ? 0.84 ?

Acanthodactylus_erythrurus_uamr_acvii ? 4.0 ? ? 23.0 ? ? ? ? 6.0 1.27 0.436332-0.870919 ? ? ? ? 0.44 ? 4.0 2.0 0.52 ? ? ? ? 0.92 1.12 0.5 3.21 0.31 0.47 13.55 0.93 0.88 0.8

 Eremias_velox_nhmw822
 7.0 4.0-6.0 2.0 18.0-19.0 22.0-24.0

 26.0 8.0 5.0-6.0 2.0 7.0 1.0 0.453786 0.3 ? 0.46 1.06-1.92 ? 0.37 ? 3.6 2.08-2.13 0.54 ? ? 0.91-0.92

 1.16 ? ? ? ? ? ? ? 14.9 0.91 0.88 0.89

 Mesalina_guttulata_272
 ? ? 2.0 24.0 26.0-28.0 ? ? ? ? 5.0 1.0

 0.715585 0.4 ? 0.41 1.06-1.92 0.59 0.36 ? 3.2-3.21 1.6 0.56 1.55 0.29 1.0 1.14 0.8 0.9 0.94 0.48

 3.86 0.37 ? ? ? ? 0.79

 Ophisops_elegans_281
 7.0 5.0-6.0 3.0 20.0-21.0 26.0-27.0

 24.0 ? ? ? 6.0 1.5 ? 0.5 0.42 0.31 1.4 0.5 0.4 ? 3.78-3.83 1.78 ? ? 0.22 0.8 1.57 ? 0.74 0.64 ? ? 0.48 ?

 ? ? 0.93 0.89

 Ophisops_elegans_282
 7.0 5.0-6.0 ? 17.0-18.0 22.0 24.0 ? ? ?

 6.0 1.16 0.645772 0.45 ? ? ? 0.46 ? ? 3.4 1.78 0.39 ? ? 0.69 1.3 1.12 0.87 ? 0.37 3.35 0.39 ? ? ? ?

 0.86

Ophisops_elegans_amnh_r43265

Ophisops elegans amnh r90235

8.0-11.0 ? 3.0 16.0-31.0 13.0-33.0 ? ? ? ? ? ? ? ?

? 2.0-6.0 3.0 16.0-31.0 13.0-33.0 ? ? ? ? ? ? ? ?

 Algyroides_fitzingeri_351
 ? 5.0 ? 18.0-19.0 23.0 ? ? ? ? ? 1.5 0.7766715

 0.33 ? ? ? ? ? ? ? ? ? 1.56 0.24 1.11 1.16 1.1 0.9 ? ? ? 0.32 ? ? ? ? 0.73

 Algyroides_nigropunctatus_nhmw797
 ? ? 2.0 19.0-20.0 23.0 26.0 6.0 6.0 2.0 5.0 1.0

 0.575959 0.39 ? 0.43-0.47 1.06-1.92 ? 0.37 ? 2.13-2.28 1.36-1.42 0.34-0.41 1.26-1.33 0.34-0.36 0.9

 ? ? ? ? ? ? 0.6-0.8 8.75 1.24 0.75 0.85

 Anatololacerta_danfordi_283
 9.0 5.0-6.0 2.0 19.0-20.0 24.0 ? ? ? ? 6.0 1.0 ?

 0.41 0.4 ? 1.4 0.55 0.37-0.39 ? 2.78-3.0 1.68 ? ? 0.33 ? 1.25 ? 1.0 ? ? 3.9 0.32 0.36 ? ? ? ?

A_danfordi_284 9.0 6.0 2.0 18.0-19.0 24.0 27.0 ? ? ? 5.0 1.3 0.802851 0.42 0.4 ? 1.0 0.56 0.38 ? 2.94 1.65 ? ? 0.24 1.2 ? 1.0 1.0 1.2 0.4 3.3 0.25 ? ? ? ? 0.78

 Archaeolacerta_bedriagae_167
 8.0 6.0 3.0 18.0-19.0 25.0 26.0 ? ? ? 4.0 1.16 ?

 0.46 0.34 0.47 1.57 0.6 0.35-0.39 ? 2.47-2.76 1.61 ? ? 0.29 1.12 1.11 1.0 ? 0.88 0.5 4.0 0.21 0.27

 15.52 0.88 ? 0.76

Appendix 9

Archaeolacerta_bedriagae_srk00_120	8.0 5.0-6.0 2.0 16.0 ? ? ? ? ? ? 0.9 0.872665-
1.22173 ? ? ? ? ? 0.37 ? 2.29 1.52 0.43 2.73 0.3 1.12	.??????????????
Iberolacerta_cyreni_uamr_lm4	9.0 ? 3.0 ? 23.0 27.0 ? ? ? 5.0 0.88 0.872665-
1.22173 ? ? ? ? ? 0.39 ? 2.08-2.5 1.6 ? 1.79 0.19-0.2	5 1.0-1.4 ? 1.07 0.99 1.0 0.59 3.3 0.26 0.42 11.9
0.9 0.84 0.7	
I_monticola_uamr_lm77	8.0???????5.02.080.872665-
1.22173 ? ? 0.43 ? ? 0.36 ? 1.98-2.14 1.43 0.43 2.36	0.29 1.2 ? 1.37 1.0 ? 0.39 3.53 0.33 0.35 ? ?
0.88 0.71-0.73	
Iberolacerta_monticola_uamr_lm92 ?? 3.0	17.0-18.0????????????????0.37?2.18
1.21-2.27 ? ? 0.32 1.2 ? ? 0.99 ? ? 3.7 0.26 ? ? 0.9 0.	8 0.68
Phoenicolacerta_troodica_318	9.0 5.0 3.0 16.0 22.0-23.0 ? ? ? ? 5.0 1.0 ? 0.27
0.44 ? 1.0 0.56 0.38 ? 2.69 1.56 ? ? 0.46 1.16 ? 1.1 0	0.8 0.7 0.5 4.5 0.4 0.48 ? ? ? ? ?
P_troodica_319	9.0 4.0-6.0 2.0 16.0-17.0 20.0
27.0????1.33?0.43??1.40.55??2.361.5??	0.45 1.0 1.57 1.1 0.9 1.0 0.5 4.8 0.38 0.52 ? ? ? ?
Podarcis_hispanicus_uamr_h30	7.0 5.0 2.0 17.0 22.0 26.0 ? ? ? 5.0 1.3
0.872665-1.22173 ? ? 0.48 ? ? 0.38 ? 2.77 1.77 0.3	1.19 0.41 1.14 ? 0.9 0.9 1.2 0.4 4.3 0.28 0.44
14.68 0.91 0.97 0.75	
Podarcis_muralis_311	7.0 5.0-6.0 3.0 19.0 24.0 ? ? ? ? 6.0 1.3 ? 0.26
0.31 ? 1.05 0.45 0.37 ? 2.25 1.56 ? ? 0.43 1.2-1.5 1.	14 1.3 0.9 ? 0.6 3.0 0.36 0.43 ? ? ? 0.77
Podarcis_muralis_312	7.0 6.0-7.0 2.0 17.0 22.0 ? ? ? ? 5.0 1.2
0.977384 0.33 0.33 0.39 1.42 0.47 0.35 ? 2.38 1.56	? 1.54 0.32 1.0 1.18 ? ? ? ? ? ? ? ? ? ? 0.93 0.79
Podarcis_muralis_313	? 6.0 3.0 18.0 23.0 ? ? ? ? ? ? ? ? 0.29 ? 1.36 ?
? ? 2.67 1.53 0.43 ? 0.28 1.1 1.26 1.0 0.8 0.8 0.6 3.1	? 0.48 14.02 ? 0.98 ?
Podarcis_muralis_nhmuk1920.1.20.801	7.0 6.0 3.0 17.0 22.0-23.0 ? 6.0 6.0 2.0 6.0 ? ?
0.43????????????????????????????????????	
Podarcis_siculus_25	7.0 4.0-5.0 3.0 16.0 ? 28.0 ? 6.0 ? ? 2.0
1.01229 0.46 0.32 0.44 1.88 0.63 0.38 ? 2.33 1.33 0	.41 1.64 0.33 1.0 1.22 1.2 ? 1.2 ? 3.8 0.4 ? ?
1.03 0.91 0.78	

Appendix 9

 Podarcis_siculus_125
 7.0 4.0-6.0 3.0 18.0-19.0 23.0 26.0 ? ? ? 4.0

 1.6 ? 0.39 0.37 ? 1.47 0.42 0.42 ? 2.23 1.64 ? ? 0.26 1.4 1.2 ? 0.8 0.9 0.52 3.8 0.41 0.44 ? ? ? 0.77

 Podarcis_siculus_amnh_r110436
 5.0-7.0 2.0-6.0 3.0 16.0-31.0 13.0-33.0 27.0

 52.0 ? 5.0-6.0 ? ? ? ? ? ? 0.4-1.0 ? ? 0.41-0.53 ? 1.8-3.0 ? ? 1.06-4.7 0.09-0.39 1.1-1.97 ? ? ? ? ? ? ?

 ? ? ? ? ? ?

 Podarcis_tiliguerta_153
 7.0 6.0 3.0 19.0 24.0 ? ? ? ? 5.0 0.8

 0.907571 0.28 0.3 0.47 1.47 0.49 0.35 ? 2.59 2.0 ? 1.62 ? ? 1.18 1.1 0.8 1.4 0.4 3.7 0.47 0.44 13.96

 1.0 0.87 0.75

 Podarcis_tiliguerta_154
 7.0 ? ? 17.0-18.0 ? 25.0 ? ? ? 4.0 1.2 ?

 0.26 0.38 ? 1.5 0.64 0.37 ? 2.22 1.44 ? ? 0.48 1.3 1.1 1.0 0.9 1.1 0.4 4.0 0.38 0.53 13.19 0.95 0.91

 0.78

 Podarcis_waglerianus_390
 7.0 6.0 2.0 17.0 22.0-23.0 27.0 ? ? ? 6.0 1.5

 0.959931 0.37 0.38 0.45 1.47 0.55 0.38 ? 2.27 1.5 ? 1.71 0.24 1.4 1.22 1.3 0.8 1.7 0.5 3.4 0.45 0.49

 13.78 0.98 0.87 0.78

 Takydromus_sp_151
 9.0 6.0-7.0 3.0 30.0 29.0-33.0 27.0 ? ?

 ? 5.0 ? ? ? 0.38 0.6 1.4 0.54 0.31 0.1-37.9 2.6 1.18 ? ? ? 1.2 ? 1.0 0.86 1.1 0.43 3.8 0.4 0.58 ? ? ?

 0.75

Zootoca_vivipara_179 1.18682 0.27 0.33 0.42 1.6 0.51 0.46 ? 2.35 1.35 ? 1.89 0.24 ? 1.33 1.1 0.9 0.7 0.6 ? 0.3-0.34 0.45-1.1 12.71 ? 0.92 0.7

 Timon_pater_nhmuk1920.1.20.2722
 9.0 ? 3.0 14.0-16.0 21.0-22.0 27.0 7.0 ? 2.0 5.0

 ? ? 0.31 ? ? ? ? 0.53 ? 1.54 1.0-1.2 ? ? 0.6 1.1-1.97 ? ? ? ? ? ? ? ? ? ? 13.3 ? ? ?

 Timon_pater_gmz_d.36_x.171
 9.0 7.0-8.0 3.0 20.0-23.0 27.0-28.0 ? ?

 ? ? ? ? ? 0.36 ? ? ? ? 0.48 ? 1.82 1.36 ? 0.82 0.79 0.69-1.0 ? ? ? ? ? ? ? ? ? ? ? ? ?

 Timon_princeps_nhmw32881
 9.0 5.0-7.0 3.0 ? 24.0-26.0 ? ? ? ? ? 1.0

 0.699877-0.837758 0.39 ? 0.52-0.54 1.06-1.92 ? 0.37 ? 1.54-1.64 1.03-1.2 0.39-0.4 1.08 0.5 1.23

 0.89 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?

?? 3.0?? 27.0??? 5.0???????????

 Timon_lepidus_216
 ? 8.0 3.0 19.0-20.0 ? 28.0 ? ? ? 5.0 0.9

 0.890118 0.29 0.46 0.57 1.41 0.57 0.45 ? 1.8 1.49 0.38 0.93 0.68 1.09 1.3 1.1 0.7 1.5 0.44 ? 0.35

 0.49 11.36 0.98 0.83 0.74

Timon_lepidus_amnh_r577708.0-11.0 2.0-6.0 3.0 16.0-31.0 13.0-33.0 ? 7.0-8.0 5.0-6.0 2.0 6.0 ? ? 0.2-0.4 ? ? ? ? 0.41-0.53 ? 1.8-3.0 1.21-2.27 0.42-0.56 ? 0.4-0.61.1-1.97 ? ? ? ? ? ? 0.39-0.53 0.24-0.39 10.0-15.52 0.78-0.94 0.82-1.11 0.7-0.89

 T_lepidus_mncn41021
 9.0 7.0 3.0 22.0 27.0-28.0 ? ? ?

 ? ? 0.9-1.1 ? ? ? ? ? ? ? ? 1.8-3.0 ? ? ? 0.61-0.79 1.1-1.97 ? ? ? 1.87 0.59 ? 0.37 ? ? ? ? ?

 T_lepidus_mnhn1887_545
 8.0 ? ? 21.0-22.0 28.0 27.0 ? ? 2.0 6.0

 1.0 ? ? ? ? ? ? 0.4-0.43 ? 1.8-3.0 1.0-1.2 ? ? 0.61-0.79 ? ? ? 0.7 1.7 0.6 2.6 0.45 0.43 ? ? ? ?

 T_lepidus_mrac3390
 9.0 6.0 ? 23.0-24.0 ? 27.0 7.0 ? 2.0 ?

 1.2 0.872665-1.22173 ? ? 0.54 1.06-1.92 ? 0.44 ? 1.53 ? 0.2-0.41 0.7 0.68 1.97 0.81 ? ? ? ? ? ? ? ? ?

 ? ?

 T_lepidus_mrac92_050_r_1
 9.0 6.0-7.0 3.0 22.0 ? 27.0 ? ? ? 5.0 1.1

 0.872665-1.22173 ? ? 0.51 ? ? 0.45 ? 1.96 1.31 0.34 1.02 0.5 1.65 ? 1.3 ? 2.0 0.6 ? 0.38 0.34 11.65

 0.97 0.83 0.71

 T_lepidus_nhmw699
 9.0 5.0-7.0 3.0 21.0 28.0 27.0 ? ? ? ?

 1.0 0.959931-1.134464 0.31-0.35 ? ? ? ? 0.48 ? 1.76 1.5 0.34 0.78 0.81 1.3 ? 1.25 0.78 1.67 0.47 ?

 0.4 0.38 ? ? ? ?

 T_lepidus_pimuz_a_iii0965
 8.0-11.0 7.0 ? 16.0-17.0 24.0-25.0 ? ? 8.0 2.0 ?

 0.9-1.1 ? ? ? ? ? ? ? ? 1.8-3.0 1.0-1.2 ? ? 0.61-0.79 ? 0.99 ? 0.7 ? 0.52 2.2 ? ? ? ? ?

 Lacerta_agilis_cipa1550
 9.0 5.0 2.0 16.0 20.0-21.0 28.0 ? ? ?

 4.0 1.38 0.977384 0.18 ? 0.48 ? ? 0.37 ? 2.0 1.04 ? 2.03 0.29 1.02 ? 0.73 0.66 1.28 0.5 3.07 0.39

 0.74 12.86 0.9 0.71 0.71

Lacerta_agilis_176 7.0 4.0-5.0 3.0 15.0-16.0 20.0-21.0 29.0 ? ? ? 4.0 1.81 0.959931 0.3 0.46 0.47 1.59 0.51 0.42-0.47 ? 1.85-2.15 1.2 ? 3.2 0.32 0.98 1.25 ? 0.8 1.0 0.53 3.2 0.36 0.45 10.17 0.96 0.77 0.7

Lacerta_agilis_mdhc_177 ? 5.0-6.0 2.0 15.0 20.0 28.0 ? ? ? 5.0 1.3 1.047198 0.33 0.47 0.45 1.47 0.55 0.42 ? 1.8 1.33 0.46 2.75 0.37 1.04 1.14 1.1 0.8 1.1 0.61 3.3 ? 0.56 12.7 1.09 0.83 0.73

 Lacerta_agilis_mdhc_178
 9.0 ? 2.0 16.0-17.0 18.0-20.0 27.0 ? ? ?

 ? 1.4 1.204277 0.33 0.34 0.54 1.32 0.62 0.41 ? 2.0 1.12 ? 2.62 0.3 1.2 1.05 ? 0.8 1.3 0.61 3.1 0.41

 0.5 11.29 0.88 0.85 0.72

 Lacerta_agilis_230
 9.0 6.0-8.0 ? 16.0-17.0 22.0 28.0 ? ? ?

 4.0 1.5 1.22173 0.29 0.43 0.47 1.21 0.54 0.33 ? 2.18 1.23 ? ? 0.36 1.0 1.18 1.1 ? 0.6 0.5 3.4 ? 0.66

 11.69 0.78 0.87 0.67

 Lacerta_agilis_mdhc_231
 9.0 ? 3.0 17.0 19.0 28.0 ? ? ? 4.0 1.2

 1.256637 0.24 0.46 0.48 1.0 0.54 0.39 ? 1.92 1.2 0.45 3.4 0.3 0.96 1.15 1.3 0.7 ? ? 3.3 0.42 0.68

 13.67 1.13 ? 0.68

Lacerta_agilis_mncn15979 9.0 ? 2.0 ? 18.0-19.0 ? ? ? ? 6.0 1.11-3.9 ? ? ? ? ? ? ? ? ? ? ? .1 ? ? ? 0.9 0.55 ? 0.39 ? ? ? ? ?

Lacerta_agilis_mnhn1963_49 9.0 4.0-6.0 3.0 15.0-16.0 19.0-21.0 28.0 7.0 ? 2.0 4.0 ? ? ? ? ? ? 0.29 ? ? ? ? ? 1.0 ? ? ? ? ? ? 0.35 ? ? ? ? ?

Lacerta_agilis_nhmw802 9.0 ? ? 17.0-18.0 21.0-22.0 28.0 ? 6.0 3.0 4.0 1.33 0.7801622-0.785398 ? ? 0.49-0.56 1.06-1.92 ? 0.29 ? 1.93-2.01 1.32 ? ? 0.25-0.29 ? 1.18 ? ? ? ? ? ? ? 11.0 1.03 0.88 0.68

 Lacerta_agilis_pimuz_a_iii0902
 7.0 2.0-6.0 3.0 ? 20.0 ? ? ? ? ? ? ? ? ? 0.53 ? ?

 0.29-0.4 ? 1.74 1.18 0.36 ? 0.25 0.9 1.1 ? ? ? ? ? ? ? ? ? ? ? ? ? ?

Lacerta_agilis_ZMH_R12174 7.0 4.0 2.0 16.0-17.0 20.0-22.0 ? 7.0 5.0-6.0 2.0 4.0 ? ? 0.23 ? ? ? 0.34-0.99 0.37 ? 1.53 1.4 ? 3.1 0.27 0.69-1.0 1.01-1.6 ? ? ? ? ? ? ? ? ? 0.95-1.05 ? 0.71

Lacerta_bilineata_15 11.0 5.0 3.0 19.0 24.0-25.0 25.0 ? 6.0 2.0 6.0 1.29 0.994838 0.29 0.43 0.44 1.6 0.58 0.37 ? 1.81 1.13 ? 1.8 0.28 1.28 1.07 1.3 0.7 1.2 0.6 3.2 0.48 0.5 13.99 0.89 0.96 ?

Lacerta_bilineata_48 ? 5.0-6.0 2.0 14.0-15.0 18.0-21.0 ? ? ? ? ? 0.9-1.1 ? ? ? ? ? ? ? 1.8-3.0 ? ? ? ? 1.1-1.97 1.25 ? 1.1 0.7 0.52 2.6 0.44 ? ? ? ? ?

 Lacerta_bilineata_73
 8.0-9.0 6.0-7.0 2.0 15.0 21.0-22.0 ? ? ? ? 5.0

 1.0 ? 0.25 ? ? ? 0.52 ? ? 2.2 1.21 ? ? ? 1.0 1.2 ? ? ? ? 2.8 ? ? ? ? ? ?

Lacerta_bilineata_77 11.0 5.0-7.0 ? 19.0 24.0-25.0 27.0 ? ? ? 6.0 1.0 1.047198 0.26 0.39 0.45 1.63 0.52 0.31 ? 1.81 1.06 ? 2.25 0.23 1.3 1.12 ? 0.8 0.9 0.55 ? 0.41 ? 13.56 1.06 ? 0.8

 Lacerta_bilineata_84
 ? 5.0-6.0 3.0 17.0-18.0 23.0 27.0 ? ? ? 6.0 1.0 ?

 0.28 0.38 0.54 1.5 0.34 0.37 ? 1.9 1.17 ? ? 0.23 1.26 1.15 1.3 0.8 1.5 0.54 3.4 ? 0.53 8.13 1.1 0.75

 0.76

 Lacerta_bilineata_381
 10.0-11.0 ? 2.0 ? 26.0 ? ? ? ? ? 1.0 1.186824

 0.3 0.4 0.51 1.38 0.56 0.36 ? 1.82 1.15 ? 1.91 0.32 1.4 1.09 ? ? ? ? ? ? ? ? ? ? ? ? ?

 Lacerta_bilineata_420
 11.0 5.0-6.0 ? 21.0 ? 27.0 ? ? ? 6.0 ? ? ? ? ? ?

 0.58 ? ? 1.68 1.14 ? ? 0.29 1.25 ? 1.3 0.8 1.2 0.64 3.5 ? ? 11.8 0.97 ? 0.77

Lacerta_bilineata_amnh_r1148 8.0-11.0 2.0-6.0 1.0-2.0 16.0-31.0 13.0-33.0 ? ? ? ? 0.7-0.89 ? 0.2-0.4 ? ? ? ? 0.41-0.53 ? 1.3-1.79 1.21-2.27 ? 0.95-1.05 0.09-0.39 1.1-1.97 ? ? ? ? ? ? ? ? ? ? ? ? ? ?

 Lacerta_bilineata_mncn16505
 9.0 5.0-6.0 ? 17.0-18.0 19.0-22.0 28.0 ?

 ? ? ? 0.9-1.1 ? ? ? ? ? ? ? ? ? 1.0-1.2 ? ? ? 1.27 ? 1.3 ? 1.0 0.6 2.8 0.43 ? ? ? ? 0.75

Lacerta_bilineata_pimuz_a_iii1276 ? 7.0-8.0 3.0 17.0 21.0-22.0 ? ? ? ? ? 0.9-1.1 ? ? ? ? ? ? ? ? ? ? 1.85 1.0-1.2 ? ? 0.3 1.73 1.16 1.4 0.8 1.7 0.52 2.0 ? ? ? ? ? ? ?

Lacerta_bilineata_uam_q21 ? 6.0-7.0 3.0 16.0 21.0-22.0 ? ? 6.0 2.0 5.0 1.52 0.872665-1.22173 ? ? 0.48 ? ? 0.39 ? 1.85 ? 0.32 1.87 0.2 1.12 ? 1.2 0.9 ? 0.7 3.2 0.48 ? ? 1.0 0.62 0.7 Lacerta media nhmw34809 9.0 6.0 ? 22.0 27.0 ? ? ? ? ? 0.9-1.1 0.809833-0.855211??0.41-0.51??0.25-0.35?2.09??1.55-1.6?1.31.04??????????????????? Lacerta media huj ost z 299 ? 2.0-6.0 3.0 ? 13.0-33.0 27.0 ? ? ? 5.0 Lacerta media huj ost z 396 9.0 2.0-6.0 ? 16.0-31.0 13.0-33.0 ? ? ? Lacerta schreiberi cipa778 9.0 ? 3.0 18.0-19.0 21.0-23.0 27.0 ? ? ? 5.0 1.39 1.047198 0.27 ? 0.47 ? ? 0.43 ? 1.69 1.05 ? 1.3 0.46 ? ? ? ? ? ? ? ? 0.39 11.71 ? 0.9 0.72 Lacerta_schreiberi cipa1256 9.0 6.0 ? ? ? 28.0 ? ? ? ? 1.11-3.9 ? ? ? ? ? ? ? ? 9.0 5.0-6.0 3.0 16.0-18.0 23.0-24.0 ? ? ? ? ? ? ? Lacerta schreiberi cipa1511 Lacerta schreiberi cipa1517 9.0???21.0-22.027.0???5.01.11-3.9??? Lacerta schreiberi nhmuk1906.10.30.14 ? 6.0 3.0 18.0 23.0-24.0 28.0 7.0 7.0 2.0 ? ? ? ? ? ? ? ? ? 0.45 ? 1.95 1.0-1.2 ? ? 0.2 1.3 ? ? ? ? ? ? 0.45 0.31 ? ? ? 0.72 Lacerta schreiberi uam s 6 8.0 5.0-6.0 3.0 17.0-18.0 21.0-22.0 27.0 ? ? 2.0 5.0 1.29 0.872665-1.22173 ? ? 0.43 ? ? 0.41 ? 1.68-1.81 1.13 0.4 1.14 0.52 ? ? 1.5 0.8 0.91 0.5 3.0 0.43?14.01 0.84 0.85 0.72 Lacerta strigata 304 7.0 4.0 2.0 16.0-17.0 20.0-21.0 27.0 ? ? ? 5.0 0.9 1.15192 0.38 0.44 0.47 ? 0.61 0.39 ? 2.13 1.33 ? 1.75 0.4 1.2 1.25 1.3 0.8 1.3 0.53 2.9 0.45 0.57 14.92 0.88 0.92 0.83 Lacerta strigata nhmw10918 ? 6.0-7.0 2.0 17.0-18.0 ? ? ? ? ? ? 1.0 0.942478 Lacerta trilineata 240 11.0? 2.0 20.0-21.0 26.0??????? 0.907571 ? 0.41 ? 1.68 0.67 ? ? 1.3-1.79 1.0-1.2 ? ? ? 1.1-1.97 1.19 1.4 0.8 1.3 ? 3.1 0.44 ? ? ? ? ? 11.0 6.0 3.0 ? 27.0 25.0 ? ? ? ? ? Lacerta trilineata 241 0.942478 0.25 0.33 0.5 1.92 0.47 0.37 ? 1.74 1.6 ? 1.14 0.44 1.43 1.1 1.4 0.8 1.4 0.58 3.3 0.52 0.63 14.89 1.11 0.78 0.79

Lacerta_trilineata_295 ? 5.0 3.0 ? 23.0-24.0 ? ? ? ? 1.33

 Lacerta_trilineata_356
 12.0 5.0-6.0 2.0 ? 27.0 27.0 ? ? ? ? 1.2

 1.064651 0.23 0.31 0.6 1.6 0.52 0.46 ? 1.75 1.38 ? 1.38 0.4 ? ? 1.4 0.8 1.3 0.6 3.1 0.48 ? 12.31 1.07

 0.9 0.77

Lacerta_trilineata_mrac95_050_r_0001 ? 6.0 3.0 23.0 26.0-27.0 27.0 ? ? ? 6.0 1.2 1.223476-1.570796 ? ? 0.52 ? ? 0.44 ? 1.6 1.36 0.45 1.34 0.29 1.48 ? ? 0.7 ? ? 3.1 0.47 0.57 12.02 0.87 0.81 0.79

L_trilineata_mrac95_050_r_0002 9.0 6.0 3.0 20.0-21.0 26.0-27.0 27.0 ? ? ? 6.0 1.0 1.223476-1.570796 ? ? 0.47 ? ? 0.46 ? 1.61 1.16 0.32 1.42 0.26 1.57 ? 1.3 0.8 1.8 0.6 3.2 ? 0.56 13.77 ? 0.91 0.73

L_trilineata_nhmuk1914.1.12.1 ? 6.0 1.0-2.0 21.0 27.0 27.0 6.0 7.0 2.0 6.0 ? ? 0.3 ? ? ? ? 0.43 ? 1.7 1.0-1.2 ? ? 0.33 1.1-1.97 ? ? ? ? ? ? 0.5 0.42 ? ? ? 0.71

 Lacerta_trilineata_zzsid_r_235_76
 ? 6.0 2.0 18.0-20.0 23.0-24.0 ? ? ? ? ? 1.0 1.223476

 1.570796 ? ? ? ? ? 0.46 ? 1.9 1.39 0.4 2.73 ? 1.43 ? 1.3 0.8 1.4 0.6 ? 0.44 0.63 12.08 ? 0.88 0.74

Lacerta_viridis_mnhn1888_139 ? 5.0-6.0 3.0 19.0-20.0 24.0-25.0 27.0 8.0 ? 2.0 ? ? ? ? ? ? ? 0.38 ? ? ? 0.2-0.3 ? 0.09-0.39 1.4 ? ? ? ? ? ? 0.5 0.46 ? ? ? ?

 Lacerta_viridis_mnhn1887_813
 9.0 3.0-4.0 3.0 14.0-16.0 19.0-20.0 27.0 ? ? 3.0

 ? ? ? ? ? ? ? 0.34 ? ? 1.0-1.2 0.25-0.35 ? ? 1.3 ? ? ? ? ? ? 0.41 ? ? ? ? ?

Lacerta_viridis_mrac91_077_r_76 8.0 5.0 2.0 19.0-20.0 24.0 27.0 ? ? ? 5.0 1.64 1.223476-1.570796 ? ? 0.52 ? ? 0.39 ? 1.69 1.22 0.43 1.88 0.32 1.33 ? ? 0.8 1.3 ? 3.2 0.47 0.56 12.82 ? ? 0.7 Lacerta_viridis_nhmw887 11.0 6.0 2.0 20.0-21.0 27.0-28.0 28.0 6.0 7.0 ? 6.0 1.0 0.907571-0.994838 0.3 ? 0.52-0.53 1.06-1.92 ? 0.42-0.46 ? 1.73 1.26 ? 1.56-1.61 ? 1.1 1.08 ? ? ? ? ? ? 0.58 11.2 0.88 0.82 ?

Lacerta_viridis_nhmw906 11.0 5.0-6.0 2.0 21.0 29.0 28.0 6.0 7.0 2.0 6.0 1.04 0.8779006 0.3 ? 0.52 ? ? 0.41 ? 1.59 1.25 ? 1.32 0.38 1.15 1.07 ? ? ? ? ? ? ? 11.8 1.04 1.11 0.75

 Lacerta_viridis_nhmw32879_3
 11.0 5.0-6.0 3.0 18.0 24.0 ? ? ? ? ? 1.0

 0.977384 0.29 ? 0.57 ? ? 0.39 ? 1.46-1.52 1.0 ? 1.11 ? 1.08 1.09 ? ? ? ? ? ? ? ? ? ? ? ?

Lacerta_viridis_zzsid_r_287_80 9.0 4.0 2.0 17.0 22.0 28.0 ? ? 2.0 6.0 1.61 1.223476-1.570796 ? ? ? ? ? 0.37 ? 1.7 1.07 0.46 2.19 0.28 1.26 ? 1.3 0.8 1.1 0.5 ? 0.4 0.47 12.49 0.97 0.84 ?

 Lacerta_viridis_zzsid_r_463_87
 9.0 5.0-6.0 ? 17.0 21.0-22.0 28.0 ? 8.0 ? 6.0

 1.33 1.223476-1.570796 ? ? 0.54 ? ? 0.38 ? 1.83 1.14 0.42 3.45 0.34 1.37 ? 1.4 0.8 ? ? 3.1 0.44 ?

 12.34 1.0 0.86 0.66

&[num]

Gekko gecko 112

?110??01?1?1?0?01010??0101?-1?1??0-?001???00000110010????1000?-00?11?1??10??0??1?11?0-?-?100?1?0?-?1?0101?0??0?????000?1-100110000000?10?0??1200101??111??0110??10?-

?????10??????????????????????000???100?????000

Varanus_exanthematicus_335

10?1001-??0101000000?000000-

0011?10?0011011100001101?-10?0010??10-

?101010?11001????10???01?0?0????0?111?00???01001?0?0?1?1?101100010100?001?????100??1 ?100022001110?01?1?1??1011??100100001??1?1000?10--001110-??00?000

Chalcides_ocellatus_193

01???00?0???0010?0?1?000110-

0011?0-?0110?0?0?1001111?-

1111?010?00?1???0?1?110011??111000?11?10100?01?00??0?0?01?00?01???-

1?111101010001210??1011001???110??2000110?1????0101?10011?0111101?1100000?0111000 00????01?110 Salvator_merianae_cmgr

Tupinambis_teguixin_amnh_r155248101?011-0?1?0??1???100?01?1110100-0?001??01?1??0000??1?1???1-???101????10????010??0?0???01?0?-0?00???1????001-1?1?1100000??131?00??0-?10?0110-0?[12]2001110-010?1011??1?00?0?0?0[01]110100001001011111?1111110011

Anguis_veronensis_102

Pseudopus_apodus_214

1110?01-??01?-1??001?001110-

Broadleysaurus_major_164

Ablepharus_kitaibelli_239

Blanus_rufus_156

Blanus_strauchi_287

101111??1111?1?0101??001001?10??-

?1?00?00001?10?110?0-0?---?-???00110????1?1??20?11??-?00?01?10????1-0?????0000?-?1101110010011????01110101??11?100??[01]0?-

Gallotia_caesaris_srk00_346

Gallotia_simonyi_nhmw849

??00?1000???100?00??1?1?0?10?0011??1010?1?11?0?0?0?10??01?0?100?21030?00??1101?????1 ??0?11010110001001?001011?10[01]011010?0011

Gallotia_stehlini_mncn22226

??10?1???100?01??1?1?01?0????0?????10?11???03???3??01101??001???1??101101?1?????11? 011?????01??????0?

Psammodromus_algirus_amnh_r92976

 Psammodromus_algirus_nhmw788
 11??00?00000???0001?000010?0?01110

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 00?101?01010?0?01?0100?0???001??100?210?0-??

00001010??1?00?1101010101000010110100011010?1000

Acanthodactylus_boskianus_276

Acanthodactylus_erythrurus_uamr_acvii

1010?1011001011???10?001???01?1?00??1?1001???0?110??0-

Mesalina_guttulata_272

Ophisops_elegans_281

111000?0??0?01100011?000?01?11?100??1011?101000?000??-10010011-??-

1?110??11001?1?0110110?1?011?0??01?0001000??10?1?10?11-

11100101000001?00000001110??111?112?010-00-

???00??1?00110010011100??000000?1?????000????10?000

Ophisops_elegans_282

Algyroides_nigropunctatus_nhmw797

?1???00[01]??00????0011000?11?0101100?1??11??0?1??110?0110?0?0110?1?001?1?1??1 0?011?1??1?1?00-???0??00101?00??000?1?1???1?1-011?110100??0?20??0000101010110-01210??-00-01000011??0??0?0010110010000001100-0101011010?1001

Anatololacerta_danfordi_283

01??0??11?1??00101?1?001???101?110??-

0???00001?1?01?0000??011?0110?0?1011010000012?0000?11110??11?00?2101100?-11001010?0?010100?111?0?1??000?111101?000????0?1011

A_danfordi_284

111000000??0?1100011???0010?1011111?1?1????1?0100??000?0?00011?????100???[01]1 1001???10??110??01?1000001111??0?0001?011??11?-

?1101101000??1??0??0?11?10??1?10?1?1?1110?????01?10?010101??11?1?0?1??00001?0111?00 ?????1??011

Archaeolacerta_bedriagae_167

 Archaeolacerta_bedriagae_srk00_120
 ?11??0????000?????0100[01]00?10?1?10

 ????10????1?01???110?01??1?2??0????1011101????1??11??0?01100?0?111????0000?0?????1?

Iberolacerta_cyreni_uamr_lm4

 $1110?0?0?0??111???10?????????????101???1?0?100?000??10??0110????110001\\??111?121???0110?0???10??1???0?1101?1???1-1???01?110000??1?00????1101?1????2?010-00-?0101010?000?00010110?11?0000111?01?010????00?011$

I_monticola_uamr_lm77

111??10010?1?11????0???????????????101???1?01?1?100?1???110??01101???1?001? ??111?121?0-?1?00?-?11???1001?0?0?1?1101?-

 Iberolacerta_monticola_uamr_lm92
 ????????????????????00010?10?1?10

 ?1?110??????010111?0?1???1???011????11?00????0?1?1?1??-0110?1-?11???1?01??000??1??1?

 1???01?100??10??100??1?1?????021??211111???10010?0001?1110?01?0?1??100011?0

 1?010????0??011

 Phoenicolacerta_troodica_318
 111000000001100010?0000110?01??0

 ?101111??0?10???0?-0?010111??1??1010?00?0001??10?1110?0-?0?000?011?0????

 ?10??1??1?1

 00100101000???201000010?101?11100121??110???????100??0?001?01?0????000?1?00

 1?010????1??001

P_troodica_319

Podarcis_hispanicus_uamr_h30

Podarcis_muralis_311

Podarcis_muralis_312

Podarcis_muralis_313

Podarcis_muralis_nhmuk1920.1.20.801

Podarcis_siculus_25

0?1?11010000??3000????1?10??11?00??1110-

?0?0010?0?1?0000?1?0010110???000000??11110?????10?011

Podarcis_siculus_125

111001?00101?11?0110?01?101011?1111?1?101?111?1?1001??1000111?11110010??1?0 ??1??1011111?0-

10??00?0??0?01????01?0??1?100????11?01000011??0101?111?00?111??1210?1?0?????01011?1? 0?1?11101?1?0??10000111?1??10????1??001

Podarcis_siculus_amnh_r110436

Podarcis_tiliguerta_153

Podarcis_tiliguerta_154

Podarcis_waglerianus_390

?11?00?00001???0001??010?010111?11??10101?1111?010?011?10001[01]?211001??0??1 10?00???011111?0-00?0?100110101?1?001?0??1??0?-

1010110100011130?00?01?0?01?111?01210?0?01100?011111110?0?1111111?10?110??11111?0 00????11?000

Takydromus_sp_151

Zootoca_vivipara_179

10?0??0000?1111?0011?00???0?1??11?-

?1??11??00100110111100?00???01010?0??10???101?00?0111?1?0110??001110?1001-1000-10000

?10?11?0??1-0?1011010???01210???110?100?11100??1?2?110-

Timon_pater_nhmuk1920.1.20.2722
T_pater_nhmuk1920.1.20.1259

Timon_pater_gmz_d.36_x.171

Timon_kurdistanicus_nhmw18545

Timon_princeps_nhmw32881

111000??0?000??0011??0??1?11?11110???10??10?11?10?1?00100?1????1?01??1110001 ?11?1?111?010-

Timon_lepidus_cipa761

Timon_lepidus_216

Timon_lepidus_amnh_r57770

T_lepidus_mncn41021

T_lepidus_mnhn1887_545

T_lepidus_mrac3390

??10?11-

T_lepidus_mrac92_050_r_1

T_lepidus_nhmw699

110???000?????0??10?1101?01?111110?0?0110???1?0?011110?00?????10?00?1?10001 001?0?11121?0-

T_lepidus_pimuz_a_iii0965

Timon_lepidus_gmz_vd36.x1246

Lacerta_agilis_amnh_r76854

Lacerta_agilis_cipa1550

Lacerta_agilis_176

Lacerta_agilis_mdhc_177

Lacerta_agilis_mdhc_178

 $11?0?1?00101?110001??01010??101?11??1?1?110111?10001??10001100110?0001??1?0\\11????1?11?0?0?100?00?1?00?000???10?110100?001111?10010112??0011?0110??11?00?1101\\0-01001?01?10?01000011?101?1?0??100?01110??010???10?011$

Lacerta_agilis_230

11?0010?011?101?0011?000?0001??1112?101010???11010??1?01000?1101???00?0?1110 11????0?111???-

Lacerta_agilis_mdhc_231

Lacerta_agilis_mncn15979

Lacerta_agilis_mnhn1963_49

Lacerta_agilis_nhmw802

Lacerta_agilis_pimuz_a_iii0902

Lacerta_agilis_ZMH_R12174

Lacerta_bilineata_15

Lacerta_bilineata_48

101?110?000?1131?1?100?110??1???012?01??0111?1?101??0?1000???101?1????00?011?????010 ??????011

Lacerta_bilineata_73

11100?0?0?0?0?0?010?10??00??011111?001?????1001?100-

Lacerta_bilineata_77

Lacerta_bilineata_84

Lacerta_bilineata_381

Lacerta_bilineata_420

Lacerta_bilineata_amnh_r1148

Lacerta_bilineata_amnh_r109472

Lacerta_bilineata_mncn16505

1110?10?010?0?1?0?1??1????101?112????111??????1?1?????0????0??1??0?1????1?0?? ???01?????0-

00????0??1???1?0??01??????0???1?01?1000?[01]1?1??????1???1???112?011011?011010101 0?1???11?101?1????110101?0-1??00??????011

Lacerta_bilineata_pimuz_a_iii1276

Lacerta_bilineata_uam_q21

1111?100?10?00????10?000101?1?1?111?001?0????1?01????-

0?0?0?1????00101???11??0???101?11???-

Lacerta_media_nhmw34809

Lacerta_media_huj_ost_z_299

Lacerta_media_huj_ost_z_396

Lacerta_schreiberi_cipa778

Lacerta_schreiberi_cipa1256

1?1??1?????001???1??0?1??10??1?10-

?????????01001??0??0??00??????100?10????01???1?0-

Lacerta_schreiberi_cipa1511

Lacerta_schreiberi_nhmuk1906.10.30.14

Lacerta_schreiberi_uam_s_6

11?0??00?011011???10?0111??1????111??01?????1?10[01]1100??0??0?0?101001??[01] 1000?????01?111?0-

?0?0?1????0?0?[01]0?10?10111?010?00??11?10000?1?11?0????11???0???0?0???10?0-0???000010????[01]110?1111????110?011101?010111?101011

Lacerta_strigata_304

Lacerta_strigata_nhmw10918

Lacerta_trilineata_240

Lacerta_trilineata_241

1110??[01]??????00?11?0111?????1?11?0010?0111?101100110??001??111001????11? 11001??011121?0?0??01?000????010???110?1???000001111010000013?11010111?00???1?01210 1110?[01]?1?0111?0011??1???101?1????1111??????000????00??11

Lacerta_trilineata_295

1110010?0??0111000?1??10?0001??11?1??000??11?1?011001?010??1?0?1100?000??110? 0?1?00?1121?0-

Lacerta_trilineata_356

Lacerta_trilineata_mrac95_050_r_0001

1110?1??????11???100?11111?????1?2??01001???0?0??1?110?010?1?1?1?0001?1100001 1??101?120?0-

L_trilineata_mrac95_050_r_0002

L_trilineata_nhmuk1914.1.12.1

Lacerta_trilineata_zzsid_r_235_76

1111?11??0?0?01???10?1101?10??1?112??01?????1?010?0?-

Lacerta_viridis_amnh_r154761

Lacerta_viridis_amnh_r154762

0?001??01?01?11?0?0?????0000?0?1??100000?013?1[01]0??1???0?111100121??1000-001?1?01??1??1?1111?1?1010001000111011000????100001

Lacerta_viridis_mncn16504

Lacerta_viridis_mnhn1888_139

Lacerta_viridis_mnhn1887_813

Lacerta_viridis_mrac91_077_r_76

?110?100???1110????0??10101?1?112?101110???1?011011?0?0???11??1000?1??10?0? 00??101??21?0-

0?10?00?010????001?1101100??0100??11?100101??1000??[01]10101?????012?111011111101?0 1?0??00001110111?0[01]011010?10-11000????00?011

Lacerta_viridis_nhmw887

?1?00?0001??0??0011?0110?10?111?1?21?011??111?1011?11101000?1101101001?10110 1????0???1211???0?0??000100110?00?11?1?1?0????01??101000?1?31010101???01111????210?1 000-011011?????01?111??11100?011010??0-1100011010?0011

Lacerta_viridis_nhmw906

1?100????0?0???0011?01?01010111???11?01????11?011??110100011?01??100?1??110? 00??0?111?1?0-

Lacerta_viridis_nhmw32879_3

Lacerta viridis zzsid r 287 80

Lacerta_viridis_zzsid_r_463_87

1110?1?1?0111?????11?01[01]1???1?1?11?1?0?????1???0?1??0-

0?000???0?1?010???[01]11??????0??11?10-

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proc/;

65-fossil-cd matrix xread	
252 120	
&[cont]	
Gekko_gecko_112 0.16 0.42 0.58 0.7 0.45 ? ? ? 2.2 ? ? ? ? ? ? ? ?	11.0 9.0 ? ? 30.0 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? . 48 ? ? ? 0.8 ?
Varanus_exanthematicus_335 0.733038 ? ? ? 0.9 0.75 ? ? 2.9 ? 0.45-0.55 ? ?	9.0 ? 1.0 9.0 10.0-11.0 ? ? ? ? ? ? ? 0.69-1.0 ? 1.1 ? ? ? 4.4 0.43 ? ? ? ? 0.83
Chalcides_ocellatus_193	7.0 6.0 1.0 12.0-13.0 ? ? ? 6.0 ? 4.0 1.5
0.436332 ? ? 0.63 1.16 0.66 ? ? 1.66 ? ? ? ? ? ?	? 1.2 0.8 ? 0.5 ? ? 0.96 ? ? 0.92 0.57
Salvator_merianae_cmgr	?? 1.0??????2.5 0.872665-
1.22173 0.34 ? 0.4-1.0 ? ? ? ? 2.0 ? 0.51 ? ? ? *	???????????????
Tupinambis_teguixin_amnh_r155248 1.11-3.9 ? ? ? ? ? ? 0.41-0.53 ? 1.8-3.0 ? ? ? ? ? 1.39 0.82-1.11 0.7-0.89	8.0-11.0 7.0-10.0 3.0 ? 13.0-33.0 ? ? ? ? ? ? ? ? ? ? 1.41-2.3 ? ? 0.39-0.53 0.24-0.39 8.13-9.9 1.06-
Tupinambis_teguixin_ZMH_R12172	9.0 4.0-5.0 ? ? 14.0-15.0 ? ? ? ? ? 1.98 ? ?
0.25-0.49 0.62 1.06-1.92 0.34-0.99 ? ? ? 1.43	0.56 ? ? ? 1.01-1.6 ? ? ? ? ? ? ? ? ? ? ? ?
Anguis_veronensis_102	9.0 ? ? ? ? 24.0 2.0 6.0 ? ? 0.7
0.977384 ? 0.24 0.7 0.82 0.63 ? ? ? ? ? 2.0 0.4	3 1.0 ? 0.62 ? 0.73 0.54 3.11 ? ? ? ? ? ? ?
Pseudopus_apodus_214	7.0 5.0 1.0 13.0 ? ? 3.0-4.0 6.0 ? 7.0-
10.0 ? 0.959931 0.38 ? ? ? ? ? ? ? 1.35 ? ? 1.25 ?	? 1.1-1.97 0.98 ? ? ? 0.52 ? ? ? ? ? ? ? ? ?
Broadleysaurus_major_164	7.0 ? 2.0 18.0 ? 28.0 ? 7.0 ? 6.0 1.2 0.942478
0.17 ? 0.6 ? 0.56 0.37 ? ? 1.14 ? ? ? ? ? ? ? ? ? ?	3.0 ? 1.1 11.0 1.17 0.9 ?
Ablepharus_kitaibelli_239	8.0-10.0 3.0-4.0 ? 13.0-14.0 18.0 33.0 ? ? ? ?
3.9 1.134464 0.33 ? 0.65 ? 0.48 ? ? 2.8 ? ? ? ?	? 1.13 ? ? ? ? ? ? ? ? ? ? ? ?
Blanus_rufus_156 1.09??1.44???????????????????????	? 2.0 1.0 3.0 ? ? ? ? ? ? ? ? ? 1.0 ? ?
Blanus_strauchi_287	7.0 2.0 1.0 4.0 8.0 ? ? ? ? ? 2.0
0.872665 0.33 ? ? 1.06-1.92 ? ? ? 1.7 ? ? ? ? ?	? ? ? 2.3 0.43 ? ? ? ? ? ? ?

Gallotia caesaris srk00 346 7.0 6.0 3.0 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 1.21-Gallotia simonyi nhmw849 9.0 ? 5.0 20.0 ? 25.0 ? ? ? 6.0 ? 0.855211 ? ? 0.58??0.36?1.851.08??0.461.2??????????0.950.72 Gallotia stehlini mncn22226 ?? 4.0-5.0? 20.0-21.0???? 5.0??????????? ?? 1.21-2.27?????????????..34?????? Psammodromus_algirus_amnh_r59605 ???????????.1.11-3.9?0.2-0.4???????? 8.0-11.0???13.0-33.0??5.0-6.0??????? Psammodromus algirus amnh r92976 Psammodromus algirus nhmw788 ? 4.0-5.0 ? 19.0 ? 26.0 6.0 6.0 ? 5.0 1.0 0.802851-0.925025?????0.34????1.53-2.04?????????????????0.83? Psammodromus algirus uamr ps 9 9.0???23.0-25.0?????1.8???0.38?? 0.34 ? 2.45 ? ? 1.81 ? ? ? 1.3 ? 0.9 ? ? ? ? 14.14 0.96 ? 0.73 ? 5.0 2.0 20.0 ? 26.0 ? ? ? ? 0.97 0.663225 ? ? Acanthodactylus boskianus 276 ? ? 0.57 0.38 ? 4.27-4.37 2.27 0.48 1.0 0.55 ? 1.25 ? ? 1.1 ? 3.85 0.33 0.56 ? ? ? 0.82 Acanthodactylus erythrurus uamr acvii 7.0 4.0 ? 18.0-19.0 ? ? ? ? ? 6.0 ? 0.436332-0.870919 ?????????2.0?????0.921.12???0.47?0.930.88? Eremias velox nhmw822 ? 4.0-6.0 2.0 18.0-19.0 ? 26.0 ? 5.0-6.0 2.0? 1.0 0.453786?? 0.46?? 0.37? 3.6 2.08-2.13 0.54?? 0.91-0.92??????????? 14.9 0.91 0.88 ? Mesalina guttulata 272 ?? 2.0 24.0 26.0-28.0 27.0??? 5.0 1.0 0.715585 0.4 ? 0.41 1.06-1.92 ? 0.36 ? 3.2-3.21 1.6 ? 1.55 ? 1.0 1.14 0.8 ? ? 0.48 3.86 ? ? ? ? 0.93 ? Ophisops elegans 281 7.0 5.0-6.0 3.0 20.0-21.0 ? 24.0 ? ? ? 6.0??0.5?0.31??0.4??1.78????1.57??0.64?3.880.480.6???0.89 Ophisops elegans 282 7.0 5.0-6.0 ? 17.0-18.0 ? ? ? ? ? ? ? ? ? 0.45???0.46??3.4????0.69?1.120.870.630.373.350.39????0.86 ? 2.0-6.0 ? 16.0-31.0 13.0-33.0 ? ? ? ? ? ? ? ? ? ? Ophisops elegans amnh r43265

Ophisops elegans amnh r90235 8.0-11.0 2.0-6.0 ? ? 13.0-33.0 ? ? ? ? ? ? ? ? ? ? ? Algyroides fitzingeri 351 10.0 ? 2.0 ? ? ? ? ? ? ? 1.5 ? 0.33 ? ? ? ? ? ? ? ? ? ???1.11?1.1??3.60.32???0.840.73 Algyroides nigropunctatus nhmw797 ? 7.0 ? ? 23.0 26.0 6.0 6.0 2.0 5.0 ? ? 0.39 ? 0.43-0.47 1.06-1.92 ? 0.37 ? 2.13-2.28 ? 0.34-0.41 ? 0.34-0.36 0.9 ? ? ? ? ? ? ? 0.6-0.8 8.75 1.24 ? ? Anatololacerta danfordi 283 ? 5.0-6.0 ? 19.0-20.0 ? ? ? ? ? ? 1.0 ? ? ? ? 1.4 ? 0.37-0.39 ? ? 1.68 ? ? 0.33 ? ? ? 1.0 ? 0.56 ? ? 0.36 ? ? ? ? A danfordi 284 9.0 6.0 ? 18.0-19.0 ? ? ? ? ? 5.0 1.3 0.802851 0.42 ? ? 1.0 0.56 0.38 ? 2.94 1.65 ? ? 0.24 ? ? 1.0 ? ? ? ? ? ? ? ? ? ? ? ? Archaeolacerta bedriagae 167 ? 6.0 3.0 18.0-19.0 25.0 ? ? ? ? 4.0 1.16 ? 0.46 ? 0.47 ? 0.6 0.35-0.39 ? 2.47-2.76 1.61 ? ? ? ? ? 1.0 0.93 0.88 0.5 ? ? 0.27 15.52 0.88 ? 0.76 Archaeolacerta bedriagae srk00 120 8.0 5.0-6.0 ? ? 20.0-22.0 ? ? ? ? ? 0.9 9.0 ? 3.0 ? ? ? ? ? ? ? 0.88 ? ? ? ? ? ? 0.39 ? Iberolacerta cyreni uamr lm4 2.08-2.5 1.6 ? ? ? ? ? ? ? ? 0.59 ? 0.26 ? ? 0.9 0.84 ? I monticola uamr lm77 8.0????27.0????2.08?????? 0.36 ? 1.98-2.14 1.43 0.43 ? 0.29 1.2 ? ? 1.0 1.0 ? 3.53 ? ? ? ? ? 0.71-0.73 Iberolacerta monticola uamr 1m92 ? 5.0-6.0 3.0 ? 21.0-22.0 ? ? ? ? ? ? ? ? ? ? ? ? ? 0.37 ? ? ????1.2?1.0?0.75?????0.9?0.68 Phoenicolacerta_troodica_318 9.0 5.0 3.0 16.0 ? ? ? ? ? ? 1.0 ? ? ? ? 1.0 0.56 0.38 ? 2.69 1.56 ? ? ? 1.16 1.2 1.1 ? ? 0.5 ? ? 0.48 ? ? ? 0.78 P troodica 319 ?? 2.0 16.0-17.0? 27.0????? ? 0.43 ? ? 1.4 0.55 ? ? 2.36 1.5 ? ? 0.45 ? ? ? ? ? ? ? ? 0.52 ? ? ? ? ? 5.0 ? ? ? ? ? ? ? 5.0 1.3 ? ? ? ? ? ? 0.38 ? 2.77 Podarcis_hispanicus_uamr_h30 ???0.41 1.14 ? 0.9 0.9 ? 0.4 4.3 ? 0.44 ? ? 0.97 ? Podarcis muralis 311 7.0????????6.0??0.260.31?1.05? 0.37 ? 2.25 1.56 ? ? 0.43 1.2-1.5 1.14 ? 0.9 ? 0.6 3.0 ? 0.43 ? ? ? 0.77

Podarcis muralis 312 7.0 6.0-7.0 2.0 17.0 ? ? ? ? ? 5.0 ? 0.977384 ? ? 0.39 1.42 0.47 ? ? 2.38 1.56 ? ? 0.32 ? 1.18 ? ? ? ? ? 0.42 ? ? ? ? 0.79 Podarcis muralis 313 ? 6.0 3.0 ? ? ? ? ? ? ? ? ? ? 0.29 ? 1.36 ? ? ? ? 1.53 0.43 ? 0.28 ? 1.26 ? ? 0.8 ? ? ? 0.48 14.02 ? ? ? Podarcis muralis nhmuk1920.1.20.801 ? 6.0 3.0 17.0 22.0-23.0 27.0 6.0 6.0 2.0 ? ? ? Podarcis siculus 25 7.0???20.0-21.0??6.0?5.0? 1.01229 0.46 0.32 ? 1.88 ? 0.38 ? ? 1.33 ? ? 0.33 ? 1.22 1.2 ? ? 0.5 3.8 0.4 ? ? 1.03 ? ? Podarcis siculus 125 7.0??18.0-19.0?????1.6?????0.42 ? 2.23 ? ? ? ? 1.4 ? ? 0.8 ? 0.52 ? ? 0.44 ? ? ? 0.77 Podarcis siculus amnh r110436 ? 2.0-6.0 ? 16.0-31.0 13.0-33.0 27.0-52.0 ? Podarcis tiliguerta 153 7.0 6.0 3.0 19.0 ? ? ? ? ? ? 0.8 0.907571 0.28 0.3 ? 1.47 0.49 0.35 ? 2.59 2.0 ? ? 0.48 1.3 1.18 1.1 0.8 1.4 ? 3.7 ? ? 13.96 1.0 0.87 ? ? 6.0-7.0 ? 17.0-18.0 ? ? ? ? ? 4.0 1.2 ? Podarcis tiliguerta 154 ? ? ? 1.5 0.64 0.37 ? 2.22 ? ? ? ? ? 1.1 1.0 ? 1.1 ? ? 0.38 ? ? ? 0.91 0.78 Podarcis waglerianus 390 7.0 ? 2.0 ? 22.0-23.0 ? ? ? ? 6.0 ? 0.959931 0.37 0.38 0.45 1.47 ? ? ? 2.27 ? ? 1.71 0.24 1.4 1.22 1.3 0.8 1.7 ? ? ? ? ? 0.98 0.87 0.78 Takydromus sp 151 ? 6.0-7.0 3.0 ? ? 27.0 ? ? ? ? ? ? ? 0.38 0.6????2.61.18????1.34??1.10.43?????0.75 7.0 5.0 3.0 19.0-20.0 22.0 28.0 ? ? ? ? Zootoca vivipara 179 1.3 ? 0.27 0.33 ? 1.6 ? 0.46 ? ? 1.35 ? ? 0.24 ? ? 1.1 0.9 ? ? 3.5 0.3-0.34 ? 12.71 1.13 ? 0.7 Timon pater nhmuk1920.1.20.2722 9.0 5.0-7.0 ? 14.0-16.0 21.0-22.0 27.0 ? 6.0 ? T_pater_nhmuk1920.1.20.1259 ?? 3.0?? 27.0-28.0?? 2.0 5.0-6.0?? 0.35?????????????????????0.24???0.8 Timon pater gmz d.36 x.171 9.0 7.0-8.0 3.0 ? 27.0-28.0 ? ? ? ? ? ? ?

? 7.0 3.0 ? 22.0-23.0 ? ? ? ? ? 0.98 0.907571 ? Timon kurdistanicus nhmw18545 Timon princeps nhmw32881 9.0 5.0-7.0 ? 18.0 24.0-26.0 ? ? ? ? ? 1.0 ? 0.39 ? 0.52-0.54 1.06-1.92 ? ? ? 1.54-1.64 ? 0.39-0.4 ? 0.5 1.23 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? Timon lepidus cipa761 ? 7.0-9.0 ? 22.0 ? ? ? ? ? 5.0 ? ? ? ? ? ? Timon lepidus 216 ???19.0-20.0?28.0???5.0??? 0.46 0.57 1.41 ? 0.45 ? 1.8 ? ? 0.93 0.68 ? 1.3 1.1 0.7 1.5 0.44 ? 0.35 ? ? ? 0.83 0.74 Timon lepidus amnh r57770 ? 2.0-6.0 3.0 16.0-31.0 13.0-33.0 ? ? ? 2.0???0.2-0.4????0.41-0.53??1.21-2.270.42-0.560.7-0.90.4-0.61.1-1.97?????????????? 0.78-0.94 ? 0.7-0.89 T lepidus mncn41021 9.0 7.0 ? ? ? ? ? ? ? 5.0 ? ? ? ? ? ?????1.0-1.2??0.61-0.79????1.87??0.37????? ?? 3.0? 28.0??? 2.0 6.0 1.0?????? T lepidus mnhn1887 545 ? 0.4-0.43 ? 1.8-3.0 1.0-1.2 ? ? 0.61-0.79 1.8 ? 1.4 0.7 ? ? 2.6 0.45 0.43 ? ? ? ? T lepidus mrac3390 9.0???30.0-31.027.07.0?2.0?1.2 0.872665-1.22173???1.06-1.92?0.44???0.2-0.410.70.681.970.81??????????????????????? T_lepidus_mrac92_050_r_1 ? 6.0-7.0 ? 22.0 30.0 27.0 ? ? ? 5.0 ? 0.872665-1.22173??0.51??0.45??1.310.341.02????0.72.0?????0.97?? T lepidus nhmw699 9.0???28.0????????0.31-0.35?? ????????.0.78?1.31.0?0.781.670.47?0.4????0.7 T lepidus pimuz a iii0965 8.0-11.0 7.0 ? 16.0-17.0 ? ? ? 8.0 2.0 ? 0.9-1.1 Timon lepidus gmz vd36.x1246 9.0??20.0-21.026.0?6.0?????0.33??? Lacerta agilis amnh r76854 8.0-11.0 2.0-6.0 ? 16.0-31.0 13.0-33.0 27.0-9.0 5.0 ? 16.0 20.0-21.0 28.0 ? ? ? ? Lacerta agilis cipa1550

1.38??????0.37?2.01.04???1.02?0.730.661.28?????0.9?0.71

Lacerta agilis 176 ??? 15.0-16.0? 29.0????? 1.81? 0.3 0.46 0.47 1.59 ? ? ? 1.85-2.15 1.2 ? 3.2 0.32 0.98 ? ? ? ? 0.53 ? ? ? 10.17 0.96 0.77 ? Lacerta agilis mdhc 177 7.0 5.0-6.0 2.0 15.0 ? 28.0 ? ? ? 5.0 1.3 ? ? 0.47 ? 1.47 ? ? ? ? ? 0.46 ? ? 1.04 ? ? 0.8 ? ? ? ? 0.56 ? 1.09 0.83 0.73 Lacerta agilis mdhc 178 ?? 2.0? 18.0-20.0 27.0???? 1.4? 0.33 0.34 0.54 ? 0.62 0.41 ? 2.0 ? ? 2.62 0.3 1.2 1.05 ? 0.8 1.3 ? 3.1 ? ? ? 0.88 0.85 ? Lacerta agilis 230 9.0 ? 3.0 16.0-17.0 22.0 ? ? ? ? 4.0 1.5 ? 0.29 ? 0.47 ? 0.54 ? ? ? ? ? 4.7 ? ? ? ? 0.8 0.6 ? ? ? 0.66 ? 0.78 ? ? Lacerta agilis mdhc 231 9.0 5.0-6.0 3.0 ????????? 1.2 ???? 1.0 0.54 0.39 ? ? 1.2 ? 3.4 0.3 0.96 1.15 1.3 ? 0.9 0.5 ? ? ? 13.67 ? 0.81 0.68 Lacerta agilis mncn15979 ????18.0-19.027.0????1.11-3.9???? Lacerta agilis mnhn1963 49 ? 4.0-6.0 ? 15.0-16.0 ? ? 7.0 ? ? 4.0 ? ? ? ? ? ? ????????1.0??????0.35?????? Lacerta agilis nhmw802 9.0 5.0-6.0 2.0 ? ? 28.0 ? 6.0 ? 4.0 1.33 ????1.06-1.92?0.29?1.93-2.011.320.29-0.35???1.18??????11.01.03?0.68 Lacerta agilis pimuz a iii0902 7.0 2.0-6.0 3.0 ? ? ? ? ? ? ? ? ? ? ? 0.53 ? ? ? ? Lacerta agilis ZMH R12174 ???16.0-17.020.0-22.0?7.0??4.0? ? 0.23 ? ? ? 0.34-0.99 ? ? 1.53 1.4 ? ? ? ? 1.01-1.6 ? ? ? ? ? ? 11.66 0.95-1.05 ? ? Lacerta bilineata 15 11.0 ? 3.0 19.0 24.0-25.0 25.0 ? 6.0 ? ? 1.29 ? 0.29 0.43 0.44 1.6 ? 0.37 ? 1.81 1.13 ? 1.8 0.28 ? 1.07 ? 0.7 1.2 ? ? 0.48 ? 13.99 0.89 0.96 ? Lacerta bilineata 48 ? 5.0-6.0 2.0 ? 18.0-21.0 ? ? ? ? ? 0.9-1.1 ? ? ? Lacerta_bilineata_73 8.0-9.0 6.0-7.0 2.0 15.0 21.0-22.0 ? ? ? ? 5.0 ? ? 0.25 ? ? ? 0.52 ? ? 2.2 1.21 ? ? ? 1.0 1.2 ? ? ? ? 2.8 ? ? ? ? ? Lacerta bilineata 77 ? 5.0-7.0 3.0 19.0 ? 27.0 ? ? ? 6.0 ? 1.047198 0.26 0.39 ? 1.63 ? ? ? 1.81 ? ? 2.25 0.23 ? 1.12 ? 0.8 0.9 ? 3.3 0.41 ? 13.56 1.06 0.67 ?

Lacerta bilineata 84 ? 5.0-6.0 ? ? ? 27.0 ? ? ? 6.0 1.0 ? ? 0.38 0.54 1.5 ? 0.37 ? ? 1.17 ? ? 0.23 1.26 ? 1.3 0.8 1.5 0.54 3.4 ? 0.53 ? ? 0.75 0.76 Lacerta bilineata 381 ? 5.0-6.0 2.0 20.0-22.0 ? ? ? ? ? ? ? 1.186824 ? Lacerta bilineata 420 ? 5.0-6.0 3.0 21.0 26.0-27.0 ? ? ? ? 6.0 ? ? ? ? ? ? 0.58 ? ? 1.68 ? 0.36 ? 0.29 1.25 ? ? ? 1.2 ? 3.5 ? ? 11.8 ? ? ? Lacerta bilineata amnh r1148 ? 2.0-6.0 ? ? ? ? ? ? ? ? ? 0.7-0.89 ? 0.2-0.4 ? ? ? 5.0-7.0 7.0-10.0 1.0-2.0 16.0-31.0 ? ? ? ? ? ? ? Lacerta bilineata amnh r109472 Lacerta bilineata mncn16505 ????19.0-22.0 28.0????0.9-1.1?? ????????1.0-1.2???1.27???1.0?2.80.43????0.75 1.85???0.31.731.16??1.7???????? 9.0 6.0-7.0 3.0 16.0 ? 26.0 ? 6.0 2.0 5.0 ? ? ? ? Lacerta bilineata uam q21 0.48??????0.321.870.2??1.2??0.73.20.48???0.62? Lacerta media nhmw34809 ? 6.0 2.0 ? ? ? ? ? ? ? ? 0.9-1.1 0.809833-0.855211??0.41-0.51????2.09???0.42-0.46?1.04?????????????????? Lacerta media huj ost z 299 ???16.0-31.013.0-33.0????5.0?? Lacerta_media_huj_ost_z_396 9.0 ? 3.0 16.0-31.0 ? ? ? ? ? ? 1.11-3.9 Lacerta schreiberi cipa778 ? 5.0-6.0 ? 18.0-19.0 21.0-23.0 27.0 ? ? ? ? 1.39 ? 0.27 ? 0.47 ? ? 0.43 ? 1.69 1.05 ? 1.3 0.46 ? ? ? ? ? ? ? ? 0.39 11.71 ? 0.9 ? 9.0 6.0 ? ? ? ? ? ? 5.0 ? ? ? ? ? ? ? ? ? 1.0-Lacerta_schreiberi_cipa1256 Lacerta schreiberi cipa1511 9.0 ? 3.0 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 1.3-1.79

Lacerta_schreiberi_cipa1517 ? 1.8-3.0 1.0-1.2 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?	??1.0-2.0?21.0-22.0????5.0??????????
Lacerta_schreiberi_nhmuk1906.10.30.14 1.95????????????????????????????????????	? 6.0 ? ? 23.0-24.0 28.0 ? ? 2.0 ? ? ? ? ? ? ? ? 0.45 ?
Lacerta_schreiberi_uam_s_6	8.0 5.0-6.0 ? 17.0-18.0 21.0-22.0 ? ? ? 2.0 5.0
1.29 0.872665-1.22173 ? ? 0.43 ? ? ? ? 1.68-	1.81 ? ? ? ? 1.34 ? ? ? 0.91 0.5 ? 0.43 ? 14.01 0.84 ? ?
Lacerta_strigata_304 1.15192 0.38 0.44 0.47 ? 0.61 0.39 ? 2.13 ? ?	7.0 ? 2.0 16.0-17.0 20.0-21.0 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?
Lacerta_strigata_nhmw10918 0.48 ? ? 0.33 ? 1.88 ? ? 2.14 ? 1.12 ? ? ? ? ? ?	?? 2.0 17.0-18.0 22.0-24.0 ????????????????????????????????????
Lacerta_trilineata_240 0.907571???????1.3-1.79 1.0-1.2????	11.0 ? 2.0 20.0-21.0 26.0 28.0 ? ? ? ? ? ? ? ? ? ? 0.8 1.3 0.56 ? ? ? ? ? ? ?
Lacerta_trilineata_241	? 6.0 ? 20.0-21.0 ? 25.0 ? ? ? ? ?
0.942478 ? 0.33 ? ? 0.47 0.37 ? 1.74 1.6 ? ? ?	? 1.43 1.1 1.4 0.8 1.4 ? ? 0.52 0.63 14.89 1.11 0.78 0.79
Lacerta_trilineata_295 1.33 1.308997 0.26 ? ? 1.67 0.6 ? ? 1.87 1.5	?? 3.0 18.0-19.0 23.0-24.0?????? 0.33?? 1.52 1.03? 0.7? 0.58?????????
Lacerta_trilineata_356	?? 2.0? 27.0 27.0??????? 0.23? 0.6
? 0.52 0.46 ? 1.75 ? ? 1.38 0.4 ? ? ? 0.8 1.3 0	.6 3.1?? 12.31 1.07??
Lacerta_trilineata_mrac95_050_r_0001	14.0 6.0 ? 23.0 26.0-27.0 27.0 ? ? ? ? 1.2 1.223476-
1.570796???????1.6??1.340.29??1.	4 ? 1.6 0.6 ? 0.47 ? ? ? 0.81 ?
L_trilineata_mrac95_050_r_0002	9.0 ? ? 20.0-21.0 26.0-27.0 27.0 ? ? ? 6.0 1.0 ?
? ? 0.47 ? ? 0.46 ? 1.61 1.16 ? ? 0.26 ? ? ? ? 1	1.8 0.6 ? 0.53 ? ? ? 0.91 0.73
Lacerta_trilineata_nhmuk1914.1.12.1	? 6.0 ? 21.0 27.0 ? 6.0 ? 2.0 6.0 ? ? 0.3 ? ? ? ?
0.43 ? ? 1.0-1.2 ? ? 0.33 ? ? ? ? ? ? ? ? ? 0.42 ?	? ? 0.71
Lacerta_trilineata_zzsid_r_235_76	8.0 6.0 2.0 ? 23.0-24.0 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 0.4
2.73?????1.4 0.6 3.2 0.44 0.63 12.08 0.96	6 0.88 ?
Lacerta_viridis_amnh_r154761	8.0-11.0 2.0-6.0 3.0 16.0-31.0 ? 27.0-52.0 7.0-
8.0 5.0-6.0 2.0 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?	? ? ? ? ? ? ? ? ? ? ? ?

Lacerta viridis amnh r154762 ? 2.0-6.0 3.0 ? 13.0-33.0 27.0-52.0 ? ? ? 5.0 ? ? Lacerta viridis mncn16504 ???????0.41????? Lacerta viridis mnhn1888 139 9.0???24.0-25.027.08.0?????????????? ???0.2-0.3??????????0.46???? Lacerta viridis mnhn1887 813 9.0 3.0-4.0 ? 14.0-16.0 19.0-20.0 27.0 ? ? 3.0 Lacerta viridis mrac91 077 r 76 ???? 24.0 27.0??? 5.0 1.64 1.223476-1.570796??0.52????1.220.431.880.32??1.4?1.3?3.20.470.56???? ? 6.0 2.0 ? 27.0-28.0 28.0 6.0 ? ? 6.0 Lacerta viridis nhmw887 1.0 0.907571-0.994838 0.3 ? 0.52-0.53 ? ? 0.42-0.46 ? 1.73 1.26 ? 1.56-1.61 0.44-0.46 ? ? ? ? ? ? ? ? ? 0.58 11.2 ? ? ? Lacerta viridis nhmw906 11.0? 2.0 21.0 29.0 28.0 6.0?? 6.0 1.04 0.8779006 0.3 ? ? ? ? 0.41 ? ? ? ? 1.32 ? 1.15 1.07 ? ? ? ? ? ? ? 11.8 ? ? 0.75 ? 5.0-6.0 3.0 18.0 ? ? ? ? ? ? ? 0.977384 Lacerta viridis nhmw32879 3 0.29 ? 0.57 ? ? ? ? ? 1.0 ? 1.11 0.25-0.3 1.08 1.09 ? ? ? ? ? ? ? ? ? ? ? ? ? ? 4.0 ? 17.0 ? 28.0 ? ? 2.0 6.0 1.61 ? ? ? ? ? ? Lacerta viridis zzsid r 287 80 0.37??1.070.462.190.281.26???1.10.52.9?0.4712.49??? ? 5.0-6.0 3.0 17.0 21.0-22.0 ? ? 8.0 ? 6.0 1.33 Lacerta viridis zzsid r 463 87 1.223476-1.570796??0.54????1.831.14?3.45?1.37?1.4??0.53.10.44?12.341.0?? &[num] Gekko gecko 112 ?1??00??0?11????10?0?0?10?0-1??100??001???0?00???00???1??10?0?-00?????0??0??0?1?????0-

Varanus_exanthematicus_335

1??10??-

0??????0000???00???0??101??00??0?11??0??1???-

10?00?0????1?01?1????0?1?111000??100?0?0?001??1?0?1?0?0?110?0?1-

??10??00?101?0????02001?0???01?0??200?11?-

??110????01???1?0?000?????0????1?????1?0?????0?0

Chalcides_ocellatus_193

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?01??0-????010101??0??????111?0?0-0?-

?1??001??1001???1?1??0??1?10??0???1?0?10?0???1??00??01-

Salvator_merianae_cmgr

Anguis_veronensis_102

Broadleysaurus_major_164

Blanus_rufus_156

Blanus_strauchi_287

1?11?10??11?01?01011????0??11?0?-

Gallotia_caesaris_srk00_346

Gallotia_simonyi_nhmw849

Gallotia_stehlini_mncn22226

Psammodromus_algirus_amnh_r59605

Psammodromus_algirus_nhmw788 ?10?0???00????00?1??0?0101?10???0-???00???010??10?011??0????12??0?????1???00??1?1??1??0?????00???11???1000 ??1?01?1000?0???100?00??1???11??01210?0?0-00??10????1?00?110?0101011??1???1??10?001101??1000

Psammodromus algirus uamr ps 9

Acanthodactylus_boskianus_276

0?1?00?00???100??0?1?-00-?000?1111??1?1??00???10??1???0?101?1?0?0????0?001

Acanthodactylus_erythrurus_uamr_acvii 10???1??100101????10?0???0????1?0?-

??11?0????????0?0?-

Eremias_velox_nhmw822

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Mesalina_guttulata_272

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Ophisops_elegans_281

Ophisops_elegans_282

Anatololacerta_danfordi_283

A_danfordi_284

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Archaeolacerta_bedriagae_167

Iberolacerta_cyreni_uamr_lm4

I_monticola_uamr_lm77

Phoenicolacerta_troodica_318

P_troodica_319

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Podarcis_hispanicus_uamr_h30

Podarcis_muralis_311

Podarcis_muralis_312

Podarcis_muralis_313

Podarcis_muralis_nhmuk1920.1.20.801

Podarcis_siculus_25

Podarcis_siculus_125

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Podarcis_siculus_amnh_r110436

Podarcis_tiliguerta_153

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Podarcis_tiliguerta_154

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Podarcis_waglerianus_390

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Takydromus_sp_151

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 Zootoca_vivipara_179
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Timon_pater_nhmuk1920.1.20.2722

T_pater_nhmuk1920.1.20.1259

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Timon_kurdistanicus_nhmw18545

Timon_princeps_nhmw32881

Timon_lepidus_cipa761

Timon_lepidus_216

Timon_lepidus_amnh_r57770

T_lepidus_mncn41021

T_lepidus_mnhn1887_545

T_lepidus_mrac3390

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$T_lepidus_mrac92_050_r_1$

T_lepidus_nhmw699

T_lepidus_pimuz_a_iii0965

Timon_lepidus_gmz_vd36.x1246

Lacerta_agilis_amnh_r76854

Lacerta_agilis_cipa1550

Lacerta_agilis_176

Lacerta_agilis_mdhc_177

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Lacerta_agilis_mdhc_178

Lacerta_agilis_230

Lacerta_agilis_mdhc_231

Lacerta_agilis_mncn15979

Lacerta_agilis_mnhn1963_49

Lacerta_agilis_nhmw802

Lacerta_agilis_pimuz_a_iii0902

Lacerta_agilis_ZMH_R12174

Lacerta_bilineata_15

Lacerta_bilineata_48

Lacerta_bilineata_73

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Lacerta_bilineata_381

Lacerta_bilineata_420

Lacerta_bilineata_amnh_r1148

Lacerta_bilineata_amnh_r109472

Lacerta_bilineata_mncn16505

Lacerta_bilineata_pimuz_a_iii1276

Lacerta_bilineata_uam_q21

Lacerta_media_nhmw34809

Lacerta_media_huj_ost_z_299

$Lacerta_media_huj_ost_z_396$

Lacerta_schreiberi_cipa778

Lacerta_schreiberi_cipa1256

Lacerta_schreiberi_cipa1511

Lacerta_schreiberi_cipa1517

Lacerta_schreiberi_nhmuk1906.10.30.14

Lacerta_schreiberi_uam_s_6

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Lacerta_strigata_304

Lacerta_strigata_nhmw10918

Lacerta_trilineata_240

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Lacerta_trilineata_241

Lacerta_trilineata_295

Lacerta_trilineata_356

Lacerta_trilineata_mrac95_050_r_0001

L_trilineata_mrac95_050_r_0002

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Lacerta_trilineata_nhmuk1914.1.12.1

Lacerta_trilineata_zzsid_r_235_76

Lacerta_viridis_amnh_r154761

Lacerta_viridis_amnh_r154762

Lacerta_viridis_mncn16504

Lacerta_viridis_mnhn1888_139

Lacerta_viridis_mnhn1887_813

Lacerta_viridis_mrac91_077_r_76

Lacerta_viridis_nhmw887

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Lacerta_viridis_nhmw906

Lacerta_viridis_nhmw32879_3

Lacerta_viridis_zzsid_r_287_80

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Lacerta_viridis_zzsid_r_463_87

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proc/;
Appendix 10

(Available also at https://figshare.com/s/c4f60604a2a013f6a86d)

Absolute (not normalised) scores of the six accuracy measurements per matrix. **Abbreviations**: RF, Robinson-Foulds distances; DC, Distortion-Coefficients; sr, symmetric resampling; jk, jackknife; cld, clade delimitation; otr, overall tree resolution.

Main matrix

	RF	DC	sr	jk	cld	otr
ew	17.79233	31.25278	12	12.3	1.584221	3.5
K=5, iw	23.83475	27.97796	8.2	8.7	0.672911	5
K=5, 25%	23.19916	29.50167	8.8	9.6	0.851358	5
K=5, 50%	24.05504	29.8744	9	9.8	1.023317	5
K=5, 75%	23.8093	29.99414	8.9	9.8	1.119154	5
K=5, 100%	24.86862	29.68398	8.8	9.7	1.146536	5
K=10, iw	20.95338	29.72909	10.5	11.4	0.974464	5
K=10, 25%	19.61436	30.9775	11	12	0.913794	5
K=10, 50%	25.35165	28.11525	11.2	12.2	0.367847	3
K=10, 75%	18.7076	31.38176	11.3	12.3	0.945075	5
K=10, 100%	20.79228	30.26674	11.3	12.2	0.802274	3.5
K=20, iw	18.86015	31.4889	11.7	12.5	1.165106	5
K=20, 25%	16.64832	31.77308	12.1	12.9	0.942538	3.5
K=20, 50%	16.55507	31.73121	12.3	13.1	1.206656	5
K=20, 75%	17.08898	31.66406	12.3	13.2	1.206656	5
K=20, 100%	18.55508	31.62868	12.4	13.3	1.0429	5
K=50, iw	16.91103	31.58706	12.2	12.8	1.420395	5
K=50, 25%	17.53809	31.65293	12.4	13	1.365632	5
K=50, 50%	18.93644	31.57334	12.5	13.1	1.493054	5
K=50, 75%	17.87712	31.37788	12.6	13.2	1.21091	5
K=50, 100%	17.81776	31.58129	12.6	13.3	1.079354	5
K=100, iw	18.04658	31.23817	12.2	12.7	0.940229	5
K=100, 25%	17.52114	31.44997	12.4	12.9	1.21091	5
K=100, 50%	20.15677	29.29052	12.5	13	1.471256	5
K=100, 75%	19.60592	31.43006	12.5	13.1	1.471273	5
K=100, 100%	18.32627	30.8437	12.6	13.1	1.581509	5
K=150, iw	18.3771	30.63963	12.2	12.7	1.303714	5
K=150, 25%	20.20762	31.25205	12.3	12.9	1.360174	5
K=150, 50%	18.49577	31.09399	12.4	13	1.916911	5
K=150, 75%	17.95338	30.82725	12.5	13	1.59864	5
K=150, 100%	19.2161	30.22388	12.5	13.1	2	5
K=200, iw	18.89829	31.36466	12.3	12.7	1.568137	5
K=200, 25%	17.5297	31.06447	12.3	12.9	1.568137	5
K=200, 50%	19.58048	30.53948	12.5	13	1.933723	5
K=200, 75%	18.12288	31.09435	12.5	13	1.505542	5
K=200, 100%	17.48728	30.955	12.5	13	1.63069	5

45-fossil matrix

	RF	DC	sr	jk	cld	otr
ew	20.24154	29.2612	5.2	5.2	1.603782	4
K=5, iw	27.51268	25.76098	4.7	5	0.524165	5
K=5, 25%	27.16527	26.28609	5.1	5.4	1	4
K=5, 50%	27.16527	27.1318	5.1	5.5	0.839725	4.5
K=5, 75%	28.29235	26.06161	5.1	5.4	0.271245	5
K=5, 100%	27.58895	25.91081	5	5.3	0.317593	4
K=10, iw	23.29237	29.02227	5.1	5.4	1.084682	4.5
K=10, 25%	22.5466	29.63447	5.8	5.5	1.125998	5
K=10, 50%	24.46188	29.1233	5.7	6	1.042874	4.5
K=10, 75%	24.32632	28.62177	5.8	6.1	1.117777	3.5
K=10, 100%	26.32629	26.88305	5.8	6	0.828415	4
K=20, iw	20.79238	29.84238	5.5	5.9	1.231545	4
K=20, 25%	20.41097	30.27617	5.7	6.1	1.219154	4
K=20, 50%	22.34322	29.65352	5.9	6.2	0.943486	5
K=20, 75%	23.56353	29.01705	6	6.3	0.907077	5
K=20, 100%	22.53813	30.0016	6	6.4	1.608448	5
K=50, iw	20.43644	29.95837	5.8	6.1	1.605209	5
K=50, 25%	19.27541	30.15223	5.9	6.3	1.484785	5
K=50, 50%	19.35169	30.30906	5.9	6.3	1.591205	5
K=50, 75%	21.67373	30.21973	6	6.3	1.471916	4.5
K=50, 100%	19.4449	31.07445	6.1	6.4	1.293616	3
K=100, iw	21.46184	29.83329	5.8	6	1.071475	5
K=100, 25%	19.4619	29.31482	5.9	6.2	1.106144	5
K=100, 50%	20.65677	29.24211	5.9	6.3	1.155392	5
K=100, 75%	17.06358	31.33202	5.9	6.3	1.352638	3.5
K=100, 100%	21.16525	30.70288	6	6.4	1.775654	5
K=150, iw	20.03816	29.40812	5.7	6	0.909537	5
K=150, 25%	18.36867	30.91699	5.8	6.2	1.644742	5
K=150, 50%	20.17372	30.1251	5.9	6.2	1.732055	5
K=150, 75%	19.20763	30.44606	5.9	6.3	1.826786	5
K=150, 100%	18.37712	30.77521	5.9	6.3	1.844991	5
K=200, iw	19.02121	30.47935	5.8	6	1.618277	5
K=200, 25%	19.32626	30.63259	5.8	6.2	1.389881	5
K=200, 50%	18.4873	30.69415	5.9	6.2	1.808582	5
K=200, 75%	20.84321	30.30083	5.9	6.3	1.574351	5
K=200, 100%	18.1822	30.78866	5.9	6.3	1.844991	5

65-fossil matrix

	RF	DC	sr	jk	cld	otr
ew	15.58475	25.50205	1.6	1.5	0.725978	0.5
K=5, iw	16.4407	27.69343	1.5	1.6	0.732339	1.5
K=5, 25%	16.72881	24.92079	1.6	1.6	1.038473	1.5
K=5, 50%	17.33051	25.92209	1.6	1.6	1.000722	1.5
K=5, 75%	18.88136	24.19804	1.6	1.6	1.552517	2
K=5, 100%	18.81358	22.52081	1.6	1.6	0.134935	2
K=10, iw	16.80508	27.04147	1.7	1.7	0.686167	2
K=10, 25%	17.78815	25.54637	1.7	1.8	0.753759	2.5
K=10, 50%	15.60168	24.23541	1.7	1.7	0.416726	1.5
K=10, 75%	16.49151	26.91009	1.7	1.8	0.969308	1.5
K=10, 100%	16.22036	26.83784	1.7	1.8	0.802036	1.5
K=20, iw	15.48308	28.22482	1.7	1.8	0.476819	1.5
K=20, 25%	16.05088	28.15267	1.8	1.8	1.565095	2.5
K=20, 50%	15.62713	27.31088	1.8	1.8	0.607373	2
K=20, 75%	15.33048	27.64329	1.8	1.8	1.194296	2.5
K=20, 100%	16.27966	26.88283	1.8	1.8	0.524651	1.5
K=50, iw	16.00847	26.10518	1.7	1.8	0.390857	1.5
K=50, 25%	14.62713	26.10309	1.7	1.8	0.390937	1.5
K=50, 50%	15.54239	27.26213	1.8	1.8	1.560424	2.5
K=50, 75%	15.71188	26.33333	1.8	1.8	0.837478	1.5
K=50, 100%	14.33897	26.04632	1.8	1.9	0.311042	1.5
K=100, iw	16.38137	26.44816	1.7	1.8	0.796432	2.5
K=100, 25%	14.55086	24.76488	1.7	1.8	0.58955	1.5
K=100, 50%	16.66951	26.89837	1.8	1.8	1.212581	2.5
K=100, 75%	16.82204	28.14006	1.8	1.8	0.544564	2.5
K=100, 100%	16.31357	26.21387	1.8	1.8	1.021977	2.5
K=150, iw	14.64409	26.72703	1.7	1.8	0.305836	1.5
K=150, 25%	15.74578	28.74314	1.7	1.8	0.723199	2.5
K=150, 50%	16.67797	26.81082	1.8	1.8	0.569689	2
K=150, 75%	16.04237	27.38827	1.8	1.8	1.164301	2
K=150, 100%	15.67799	27.44375	1.8	1.8	0.802801	2
K=200, iw	16.73726	26.72124	1.7	1.8	0.983272	2.5
K=200, 25%	16.69494	26.97422	1.7	1.8	0.838772	2.5
K=200, 50%	15.8305	28.32687	1.8	1.8	1.237902	2.5
K=200, 75%	15.59322	27.79678	1.8	1.8	1.555058	2.5
K=200, 100%	15.81357	23.36341	1.8	1.8	0.821853	1.5

Cd matrix

	RF	DC	sr	jk	cld	otr
ew	23.72031	27.1003	12.7	13.3	0.3531	5
K=5, iw	22.39828	29.84336	9.2	9.6	0.80915	5
K=5, 25%	22.92375	29.96018	9.8	10.6	0.420036	5
K=5, 50%	21.72035	31.07986	9.8	11	1.065908	5
K=5, 75%	20.90679	30.66308	9.8	10.9	0.82438	5
K=5, 100%	20.89827	30.60257	9.7	10.7	1.050554	5
K=10, iw	18.6271	31.7498	11.4	12	0.902774	5
K=10, 25%	20.15251	30.08911	12	12.8	0.747773	5
K=10, 50%	17.5	32.13877	12.1	13.1	1.269354	5
K=10, 75%	18.51694	31.98176	12.1	13.1	1.198959	5
K=10, 100%	18.51694	31.98176	12.1	13	0.999412	5
K=20, iw	18.47458	31.76119	12.4	13.1	1.048242	5
K=20, 25%	18.90679	31.59878	12.7	13.6	0.939322	5
K=20, 50%	19.55931	31.62521	13	13.9	1.101731	5
K=20, 75%	18.71185	31.51391	13.1	14	0.852366	5
K=20, 100%	19.21185	31.57257	13.1	14	1.209521	5
K=50, iw	20.40676	31.53508	12.7	13.4	0.991565	5
K=50, 25%	18.04237	31.42016	12.8	13.6	1.145243	5
K=50, 50%	20.89824	30.43836	13.1	13.8	1.013571	5
K=50, 75%	20.8983	31.09441	13.2	14	1.033223	5
K=50, 100%	20.99147	30.67053	13.3	14.1	1.293387	5
K=100, iw	18.37285	30.9411	12.1	12.8	1.849067	5
K=100, 25%	19.15255	30.55751	12.2	12.9	1.492819	5
K=100, 50%	17.94916	31.55803	12.4	13	1.158351	5
K=100, 75%	16.66103	31.78979	12.4	13.1	1.379191	5
K=100, 100%	16.72033	31.77236	12.5	13.1	1.844799	5
K=150, iw	18.68644	30.83275	11.8	12.3	1.492819	5
K=150, 25%	21.0254	30.20799	11.9	12.4	1.822755	5
K=150, 50%	16.50849	31.85091	12	12.6	1.379191	5
K=150, 75%	17.74576	31.53675	12	12.6	1.208238	5
K=150, 100%	18.32204	30.94189	12.1	12.7	1.883074	5
K=200, iw	20.45766	29.87266	11.8	12.4	0.470899	5
K=200, 25%	19.90677	30.10372	11.8	12.4	1.319986	5
K=200, 50%	18.4915	30.90384	12	12.5	1.932961	5
K=200, 75%	20.24575	29.83734	11.9	12.6	1.319986	5
K=200, 100%	20.09322	30.19031	12	12.6	1.247037	5

45-fossil-cd matrix

	RF	DC	sr	jk	cld	otr
ew	24.84321	29.23301	8.7	9.1	1.27886	4.5
K=5, iw	26.74151	28.90378	5.6	5.9	0.608595	5
K=5, 25%	24.26694	29.2131	5.8	6	1.025733	5
K=5, 50%	24.60591	28.81429	5.7	5.9	0.804591	5
K=5, 75%	24.91099	28.18883	5.5	5.7	0.728227	5
K=5, 100%	25.17375	28.27702	5.4	5.6	0.610792	5
K=10, iw	24.69912	29.92534	6.6	7.1	0.838586	4
K=10, 25%	23.24152	29.26832	6.8	7.3	0.848362	4.5
K=10, 50%	23.27545	29.69518	6.9	7.3	0.968357	5
K=10, 75%	23.24153	29.95351	6.9	7.3	1.618215	5
K=10, 100%	23.64832	29.48694	6.8	7.2	1.249522	5
K=20, iw	23.41949	28.92269	7.1	7.5	0.719039	4.5
K=20, 25%	24.44493	29.16775	7.3	7.8	0.988152	5
K=20, 50%	25.26696	29.85524	7.5	8	0.94998	5
K=20, 75%	24.00425	29.57657	7.6	8	0.902757	4.5
K=20, 100%	21.6822	29.72587	7.6	8	0.779538	3.5
K=50, iw	22.99574	29.04527	7.1	7.5	1.000204	4.5
K=50, 25%	23.67373	29.07232	7.4	7.7	0.712478	4.5
K=50, 50%	24.34321	29.67837	7.5	7.9	0.388083	5
K=50, 75%	23.91105	28.80637	7.7	8	0.274251	5
K=50, 100%	24.62288	29.98158	7.8	8.2	1.482375	5
K=100, iw	22.92793	29.63539	7.7	8.2	0.927815	5
K=100, 25%	23.88561	28.41013	7.8	8.3	0.764281	5
K=100, 50%	21.63137	29.3485	7.8	8.3	0.726809	5
K=100, 75%	23.23303	29.00833	7.9	8.4	0.689982	4.5
K=100, 100%	22.97032	29.30681	7.9	8.4	0.689431	5
K=150, iw	24.03816	29.41718	8	8.5	0.966443	5
K=150, 25%	23.11439	28.69143	8.1	8.6	0.704864	5
K=150, 50%	22.69911	29.56964	8.1	8.7	0.646147	5
K=150, 75%	22.14831	28.1115	8.2	8.8	0.704313	5
K=150, 100%	23.44488	29.70314	8.2	8.7	0.689384	5
K=200, iw	23.81779	28.74472	8.2	8.7	0.788483	5
K=200, 25%	22.25848	29.21789	8.3	8.7	0.726809	5
K=200, 50%	23.75846	29.78046	8.3	8.8	0.69224	5
K=200, 75%	22.05508	29.50607	8.3	8.9	0.669193	5
K=200, 100%	21.63985	29.28755	8.4	8.9	0.634624	5

65-fossil-cd matrix

	RF	DC	sr	jk	cld	otr
ew	25.45763	26.82445	2.6	2.7	0.994907	4
K=5, iw	28.41526	25.43758	1.4	1.3	1.196487	4.5
K=5, 25%	26.27964	24.28466	1.4	1.3	1.046036	3.5
K=5, 50%	27.73728	24.0197	1.3	1.3	1.076377	4.5
K=5, 75%	29.27965	20.48551	1.3	1.2	0.129555	4.5
K=5, 100%	29.94915	20.07409	1.2	1.2	0.6035	4.5
K=10, iw	24.99999	27.31241	1.6	1.6	1.519525	3.5
K=10, 25%	26.28812	27.27805	1.6	1.7	0.668539	4.5
K=10, 50%	28.18642	25.55273	1.6	1.6	1.113817	5
K=10, 75%	27.77117	24.59153	1.5	1.6	0.894867	4.5
K=10, 100%	25.88134	26.95594	1.5	1.5	1.069152	4
K=20, iw	24.65253	27.68245	1.9	2	1.053938	4
K=20, 25%	25.88983	26.18924	1.9	2	1.392713	4
K=20, 50%	24.77117	28.03124	1.9	2	0.742197	4.5
K=20, 75%	25.29661	27.95508	1.8	1.9	1.030038	4
K=20, 100%	22.97457	26.40497	1.8	1.9	0.869662	3.5
K=50, iw	25.37289	27.61543	2.3	2.4	0.898263	4.5
K=50, 25%	25.34747	28.41648	2.3	2.3	0.785556	4.5
K=50, 50%	24.92372	27.68897	2.3	2.3	0.833877	4.5
K=50, 75%	24.97457	26.36373	2.2	2.3	0.850725	5
K=50, 100%	23.68643	28.13582	2.2	2.3	0.81912	4.5
K=100, iw	24.1949	25.66351	2.5	2.6	0.79731	4.5
K=100, 25%	23.58475	27.65549	2.5	2.6	0.831266	4.5
K=100, 50%	23.7627	27.95273	2.5	2.6	0.645488	3.5
K=100, 75%	22.99154	28.07961	2.5	2.6	0.965874	3.5
K=100, 100%	23.32201	27.70988	2.5	2.5	0.684733	4.5
K=150, iw	23.05086	27.1264	2.6	2.6	0.783923	4
K=150, 25%	24.35592	26.83268	2.6	2.6	0.736124	5
K=150, 50%	25.51695	25.01356	2.6	2.7	0.732532	5
K=150, 75%	24.40677	27.89975	2.6	2.6	0.520765	4.5
K=150, 100%	24.10171	27.89662	2.6	2.6	0.619956	4.5
K=200, iw	26.27116	25.52209	2.6	2.7	0.890427	5
K=200, 25%	25.88134	24.79308	2.6	2.7	0.795285	4.5
K=200, 50%	24.57628	25.52032	2.6	2.7	0.86816	4.5
K=200, 75%	24.96609	27.85806	2.6	2.7	0.935353	4.5
K=200, 100%	24.49152	28.16958	2.6	2.7	0.777067	5

Appendix 11

(Available also at https://figshare.com/s/c4f60604a2a013f6a86d)

Phylogenetic trees (single MPT or strict consensus) resulting from analysing the six character matrices using 36 different weighting strategies each.

1. Main matrix





1.2. K-value of 5, implied weights



1.3. K-value of 5, extended implied weights, assumed homoplasy for missing entries: 25%



1.4. K-value of 5, extended implied weights, assumed homoplasy for missing entries: 50%



1.5. K-value of 5, extended implied weights, assumed homoplasy for missing entries: 75%



1.6. K-value of 5, extended implied weights, assumed homoplasy for missing entries: 100%



1.7. K-value of 10, implied weights



1.8. K-value of 10, extended implied weights, assumed homoplasy for missing entries: 25%



1.9. K-value of 10, extended implied weights, assumed homoplasy for missing entries: 50% (strict

consensus)



1.10. K-value of 10, extended implied weights, assumed homoplasy for missing entries: 75%



1.11. K-value of 10, extended implied weights, assumed homoplasy for missing entries: 100%

(strict consensus)



1.12. K-value of 20, implied weights



1.13. K-value of 20, extended implied weights, assumed homoplasy for missing entries: 25% (strict

consensus)



1.14. K-value of 20, extended implied weights, assumed homoplasy for missing entries: 50%



1.15. K-value of 20, extended implied weights, assumed homoplasy for missing entries: 75%



1.16. K-value of 20, extended implied weights, assumed homoplasy for missing entries: 100%



1.17. K-value of 50, implied weights



1.18. K-value of 50, extended implied weights, assumed homoplasy for missing entries: 25%



1.19. K-value of 50, extended implied weights, assumed homoplasy for missing entries: 50%



1.20. K-value of 50, extended implied weights, assumed homoplasy for missing entries: 75%



1.21. K-value of 50, extended implied weights, assumed homoplasy for missing entries: 100%



1.22. K-value of 100, implied weights



1.23. K-value of 100, extended implied weights, assumed homoplasy for missing entries: 25%



1.24. K-value of 100, extended implied weights, assumed homoplasy for missing entries: 50%



1.25. K-value of 100, extended implied weights, assumed homoplasy for missing entries: 75%



1.26. K-value of 100, extended implied weights, assumed homoplasy for missing entries: 100%



1.27. K-value of 150, implied weights



1.28. K-value of 150, extended implied weights, assumed homoplasy for missing entries: 25%



1.29. K-value of 150, extended implied weights, assumed homoplasy for missing entries: 50%



1.30. K-value of 150, extended implied weights, assumed homoplasy for missing entries: 75%




1.32. K-value of 200, implied weights



1.33. K-value of 200, extended implied weights, assumed homoplasy for missing entries: 25%



1.34. K-value of 200, extended implied weights, assumed homoplasy for missing entries: 50%



1.35. K-value of 200, extended implied weights, assumed homoplasy for missing entries: 75%



1.36. K-value of 200, extended implied weights, assumed homoplasy for missing entries: 100%



2. 45-fossil matrix

2.1. Equal weights (strict consensus)



2.2. K-value of 5, implied weights



2.3. K-value of 5, extended implied weights, assumed homoplasy for missing entries: 25% (strict

consensus)



2.4. K-value of 5, extended implied weights, assumed homoplasy for missing entries: 50%

strict consensus



2.5. K-value of 5, extended implied weights, assumed homoplasy for missing entries: 75%



2.6. K-value of 5, extended implied weights, assumed homoplasy for missing entries: 100% (strict

consensus)



2.7. K-value of 10, implied weights (strict consensus)



2.8. K-value of 10, extended implied weights, assumed homoplasy for missing entries: 25%



2.9. K-value of 10, extended implied weights, assumed homoplasy for missing entries: 50% (strict

consensus)



2.10. K-value of 10, extended implied weights, assumed homoplasy for missing entries: 75% (strict

consensus)



2.11. K-value of 10, extended implied weights, assumed homoplasy for missing entries: 100% (strict consensus)



2.12. K-value of 20, implied weights (strict consensus)



2.13. K-value of 20, extended implied weights, assumed homoplasy for missing entries: 25% (strict

consensus)



2.14. K-value of 20, extended implied weights, assumed homoplasy for missing entries: 50%



2.15. K-value of 20, extended implied weights, assumed homoplasy for missing entries: 75%



2.16. K-value of 20, extended implied weights, assumed homoplasy for missing entries: 100%



2.17. K-value of 50, implied weights



2.18. K-value of 50, extended implied weights, assumed homoplasy for missing entries: 25%



2.19. K-value of 50, extended implied weights, assumed homoplasy for missing entries: 50%



2.20. K-value of 50, extended implied weights, assumed homoplasy for missing entries: 75% (strict

consensus)



2.21. K-value of 50, extended implied weights, assumed homoplasy for missing entries: 100%

(strict consensus)



2.22. K-value of 100, implied weights



2.23. K-value of 100, extended implied weights, assumed homoplasy for missing entries: 25%



2.24. K-value of 100, extended implied weights, assumed homoplasy for missing entries: 50%



2.25. K-value of 100, extended implied weights, assumed homoplasy for missing entries: 75%

(strict consensus)



2.26. K-value of 100, extended implied weights, assumed homoplasy for missing entries: 100%



2.27. K-value of 150, implied weights



2.28. K-value of 150, extended implied weights, assumed homoplasy for missing entries: 25%



2.29. K-value of 150, extended implied weights, assumed homoplasy for missing entries: 50%



2.30. K-value of 150, extended implied weights, assumed homoplasy for missing entries: 75%


2.31. K-value of 150, extended implied weights, assumed homoplasy for missing entries: 100%



2.32. K-value of 200, implied weights



2.33. K-value of 200, extended implied weights, assumed homoplasy for missing entries: 25%



2.34. K-value of 200, extended implied weights, assumed homoplasy for missing entries: 50%



2.35. K-value of 200, extended implied weights, assumed homoplasy for missing entries: 75%



2.36. K-value of 200, extended implied weights, assumed homoplasy for missing entries: 100%



3. 65-fossil matrix

3.1. Equal weights (strict consensus)



3.2. K-value of 5, implied weights (strict consensus)



3.3. K-value of 5, extended implied weights, assumed homoplasy for missing entries: 25% (strict



3.4. K-value of 5, extended implied weights, assumed homoplasy for missing entries: 50% (strict



3.5. K-value of 5, extended implied weights, assumed homoplasy for missing entries: 75% (strict



3.6. K-value of 5, extended implied weights, assumed homoplasy for missing entries: 100% (strict



3.7. K-value of 10, implied weights (strict consensus)



3.8. K-value of 10, extended implied weights, assumed homoplasy for missing entries: 25% (strict



3.9. K-value of 10, extended implied weights, assumed homoplasy for missing entries: 50% (strict



3.10. K-value of 10, extended implied weights, assumed homoplasy for missing entries: 75% (strict



3.11. K-value of 10, extended implied weights, assumed homoplasy for missing entries: 100%



3.12. K-value of 20, implied weights (strict consensus)



3.13. K-value of 20, extended implied weights, assumed homoplasy for missing entries: 25% (strict



3.14. K-value of 20, extended implied weights, assumed homoplasy for missing entries: 50% (strict



3.15. K-value of 20, extended implied weights, assumed homoplasy for missing entries: 75% (strict



3.16. K-value of 20, extended implied weights, assumed homoplasy for missing entries: 100%



3.17. K-value of 50, implied weights (strict consensus)



3.18. K-value of 50, extended implied weights, assumed homoplasy for missing entries: 25% (strict



3.19. K-value of 50, extended implied weights, assumed homoplasy for missing entries: 50% (strict



3.20. K-value of 50, extended implied weights, assumed homoplasy for missing entries: 75% (strict



3.21. K-value of 50, extended implied weights, assumed homoplasy for missing entries: 100%



3.22. K-value of 100, implied weights (strict consensus)



3.23. K-value of 100, extended implied weights, assumed homoplasy for missing entries: 25%



3.24. K-value of 100, extended implied weights, assumed homoplasy for missing entries: 50%



3.25. K-value of 100, extended implied weights, assumed homoplasy for missing entries: 75%



3.26. K-value of 100, extended implied weights, assumed homoplasy for missing entries: 100%



3.27. K-value of 150, implied weights (strict consensus)



3.28. K-value of 150, extended implied weights, assumed homoplasy for missing entries: 25%



3.29. K-value of 150, extended implied weights, assumed homoplasy for missing entries: 50%



3.30. K-value of 150, extended implied weights, assumed homoplasy for missing entries: 75%


3.31. K-value of 150, extended implied weights, assumed homoplasy for missing entries: 100%



3.32. K-value of 200, implied weights (strict consensus)



3.33. K-value of 200, extended implied weights, assumed homoplasy for missing entries: 25%



3.34. K-value of 200, extended implied weights, assumed homoplasy for missing entries: 50%



3.35. K-value of 200, extended implied weights, assumed homoplasy for missing entries: 75%



3.36. K-value of 200, extended implied weights, assumed homoplasy for missing entries: 100%



4. Cd matrix

4.1. Equal weights



4.2. K-value of 5, implied weights



4.3. K-value of 5, extended implied weights, assumed homoplasy for missing entries: 25%



4.4. K-value of 5, extended implied weights, assumed homoplasy for missing entries: 50%



4.5. K-value of 5, extended implied weights, assumed homoplasy for missing entries: 75%



4.6. K-value of 5, extended implied weights, assumed homoplasy for missing entries: 100%



4.7. K-value of 10, implied weights



4.8. K-value of 10, extended implied weights, assumed homoplasy for missing entries: 25%



4.9. K-value of 10, extended implied weights, assumed homoplasy for missing entries: 50%



4.10. K-value of 10, extended implied weights, assumed homoplasy for missing entries: 75%



4.11. K-value of 10, extended implied weights, assumed homoplasy for missing entries: 100%



4.12. K-value of 20, implied weights



4.13. K-value of 20, extended implied weights, assumed homoplasy for missing entries: 25%



4.14. K-value of 20, extended implied weights, assumed homoplasy for missing entries: 50%



4.15. K-value of 20, extended implied weights, assumed homoplasy for missing entries: 75%



4.16. K-value of 20, extended implied weights, assumed homoplasy for missing entries: 100%



4.17. K-value of 50, implied weights



4.18. K-value of 50, extended implied weights, assumed homoplasy for missing entries: 25%



4.19. K-value of 50, extended implied weights, assumed homoplasy for missing entries: 50%



4.20. K-value of 50, extended implied weights, assumed homoplasy for missing entries: 75%



4.21. K-value of 50, extended implied weights, assumed homoplasy for missing entries: 100%



4.22. K-value of 100, implied weights



4.23. K-value of 100, extended implied weights, assumed homoplasy for missing entries: 25%



4.24. K-value of 100, extended implied weights, assumed homoplasy for missing entries: 50%



4.25. K-value of 100, extended implied weights, assumed homoplasy for missing entries: 75%



4.26. K-value of 100, extended implied weights, assumed homoplasy for missing entries: 100%



4.27. K-value of 150, implied weights



4.28. K-value of 150, extended implied weights, assumed homoplasy for missing entries: 25%



4.29. K-value of 150, extended implied weights, assumed homoplasy for missing entries: 50%



4.30. K-value of 150, extended implied weights, assumed homoplasy for missing entries: 75%


4.31. K-value of 150, extended implied weights, assumed homoplasy for missing entries: 100%





4.33. K-value of 200, extended implied weights, assumed homoplasy for missing entries: 25%



4.34. K-value of 200, extended implied weights, assumed homoplasy for missing entries: 50%



4.35. K-value of 200, extended implied weights, assumed homoplasy for missing entries: 75%



4.36. K-value of 200, extended implied weights, assumed homoplasy for missing entries: 100%



5. 45-fossil-cd matrix

5.1. Equal weights (strict consensus)



5.2. K-value of 5, implied weights



5.3. K-value of 5, extended implied weights, assumed homoplasy for missing entries: 25%



5.4. K-value of 5, extended implied weights, assumed homoplasy for missing entries: 50%



5.5. K-value of 5, extended implied weights, assumed homoplasy for missing entries: 75%



5.6. K-value of 5, extended implied weights, assumed homoplasy for missing entries: 100%



5.7. K-value of 10, implied weights (strict consensus)



5.8. K-value of 10, extended implied weights, assumed homoplasy for missing entries: 25% (strict

consensus)



5.9. K-value of 10, extended implied weights, assumed homoplasy for missing entries: 50%



5.10. K-value of 10, extended implied weights, assumed homoplasy for missing entries: 75%



5.11. K-value of 10, extended implied weights, assumed homoplasy for missing entries: 100%



5.12. K-value of 20, implied weights (strict consensus)



5.13. K-value of 20, extended implied weights, assumed homoplasy for missing entries: 25%



5.14. K-value of 20, extended implied weights, assumed homoplasy for missing entries: 50%



5.15. K-value of 20, extended implied weights, assumed homoplasy for missing entries: 75%

strict consensus



5.16. K-value of 20, extended implied weights, assumed homoplasy for missing entries: 100%

strict consensus



5.17. K-value of 50, implied weights

strict consensus



5.18. K-value of 50, extended implied weights, assumed homoplasy for missing entries: 25%



5.19. K-value of 50, extended implied weights, assumed homoplasy for missing entries: 50%



5.20. K-value of 50, extended implied weights, assumed homoplasy for missing entries: 75% (strict

consensus)



5.21. K-value of 50, extended implied weights, assumed homoplasy for missing entries: 100%





5.23. K-value of 100, extended implied weights, assumed homoplasy for missing entries: 25%

(strict consensus)





5.25. K-value of 100, extended implied weights, assumed homoplasy for missing entries: 75%

(strict consensus)



5.26. K-value of 100, extended implied weights, assumed homoplasy for missing entries: 100%



5.27. K-value of 150, implied weights



5.28. K-value of 150, extended implied weights, assumed homoplasy for missing entries: 25%

(strict consensus)



5.29. K-value of 150, extended implied weights, assumed homoplasy for missing entries: 50%



5.30. K-value of 150, extended implied weights, assumed homoplasy for missing entries: 75%


5.31. K-value of 150, extended implied weights, assumed homoplasy for missing entries: 100%



5.32. K-value of 200, implied weights





5.34. K-value of 200, extended implied weights, assumed homoplasy for missing entries: 50%



5.35. K-value of 200, extended implied weights, assumed homoplasy for missing entries: 75%



5.36. K-value of 200, extended implied weights, assumed homoplasy for missing entries: 100%



6. 65-fossil-cd matrix

6.1. Equal weights (strict consensus)



6.2. K-value of 5, implied weights (strict consensus)



6.3. K-value of 5, extended implied weights, assumed homoplasy for missing entries: 25% (strict

consensus) Tree 0: 112 no 112 bbis_teguixin_amnh_r15524 .anus strauchi 287 .anus rufus 156 .lepharus kitaibelli 239 Tupinambi Bla Abl pus MH_R12172 ola uamr 1m9 M _r43265 amnh_r90235 _282 12 1nh r110436 1nhmw822 alis_nhmuk1920.1.20 zingeri_351 ta_bedriagae_167 siculus_25 ordi 284 danfordi dica 318 tatus nhmw7 lm77 ani_uamr_lm4 nicus uamr h30 a_bedriagae_srk00-jralis_312 bilineata uam q21 cis muralis 313 ccis muralis_313 ccis muralis_311 iridis zzsid~r 463 87 iridis mnhn1887 813 'iridis mnhn1887 813 'iridis mnhn1887 813 difis tatus and tatus fordi 284 olacerta_danfordi_283 eerta troodica 318 nigropunctatus_nhmw7 ola uamr 1m77 Phoen Algyr laces Ib Podar Lacerta Lacerta Lacerta Lacerta Lacerta Рc squiis amnh r76854 s_tiliguerta_153 ardilis mdhc_231 amodromus_algirus_amnh r9297 Lacerta aquiis mncn15979 Psammodromus_algirus nhmw788 certa viridis mnhn1888 139 Lacerta schreiberi cipa1256 — Psammodromus algirus_amnh_r5960 bilineata 381 agglis pimuz_a_iii0902 ta strigata La erta ata 381 pimuz_a_iii0902 gata nhmw10918 eiberi nhmuk1906.10 a nhmw34809 peata amph w100470 mnhn19 is_cipa1550 c 287 80 pimuz_a_iii12 77 Lacert nhmw906 huj ost huj ost huj ost eata mnc La a a medi 14.1 _zzsid_r_235_ mrac91 077 r_76 beri_cipa778 idis_amnh_r154762 idis_amnh_r154761 eata amnh_r1148 eata 84 ius amnh_r57770 ius_216 050 a c 92 cn41021 mnhn1887 545 epidus cipa761 a_caesaris_srk ~ vd36.x1246 mncn41 dus k00 346 imon lepid... imon kurdistanicus ... T lepidus pimuz a ii1050. T pater_nhmuk1920.1.20.1259 Timon_princeps_nhmuk1920.1.20.2722 T lepidus mrac3390 T imon pater qmz d.36 x.171 Timon т

6.4. K-value of 5, extended implied weights, assumed homoplasy for missing entries: 50% (strict

consensus)



6.5. K-value of 5, extended implied weights, assumed homoplasy for missing entries: 75% (strict

consensus)



6.6. K-value of 5, extended implied weights, assumed homoplasy for missing entries: 100% (strict



6.7. K-value of 10, implied weights (strict consensus)



6.8. K-value of 10, extended implied weights, assumed homoplasy for missing entries: 25% (strict

consensus) Tree 0: amnh r90235 amnh_r43265 282 291 ae_167 danfordi 283 uamr 1m9 318 h30 1887_813 6854 r9297 uz a iii12 d r 287_80 s 6 1550 a1550 hi mncn22226 i_nhmw849 hmw10918 nhmuk1906.10 34809 amnh_r109472 r154762 mrac91 077_r_76 463 8 z 299 r1148 14 050 r 8545 0.2722 h_r57770 on lebidus amnh_r57770 on lepidus 216 on pater gmz d.36 x.171 lepidus pimuz a iii0965 pater nhmuk1920.1.20.1259

6.9. K-value of 10, extended implied weights, assumed homoplasy for missing entries: 50%



6.10. K-value of 10, extended implied weights, assumed homoplasy for missing entries: 75% (strict



6.11. K-value of 10, extended implied weights, assumed homoplasy for missing entries: 100%



6.12. K-value of 20, implied weights (strict consensus)



6.13. K-value of 20, extended implied weights, assumed homoplasy for missing entries: 25% (strict

consensus)



6.14. K-value of 20, extended implied weights, assumed homoplasy for missing entries: 50% (strict



6.15. K-value of 20, extended implied weights, assumed homoplasy for missing entries: 75% (strict

consensus)



6.16. K-value of 20, extended implied weights, assumed homoplasy for missing entries: 100%



6.17. K-value of 50, implied weights (strict consensus)



6.18. K-value of 50, extended implied weights, assumed homoplasy for missing entries: 25% (strict

consensus)



6.19. K-value of 50, extended implied weights, assumed homoplasy for missing entries: 50% (strict



6.20. K-value of 50, extended implied weights, assumed homoplasy for missing entries: 75%



6.21. K-value of 50, extended implied weights, assumed homoplasy for missing entries: 100%



6.22. K-value of 100, implied weights (strict consensus)



6.23. K-value of 100, extended implied weights, assumed homoplasy for missing entries: 25%



6.24. K-value of 100, extended implied weights, assumed homoplasy for missing entries: 50%



6.25. K-value of 100, extended implied weights, assumed homoplasy for missing entries: 75%



6.26. K-value of 100, extended implied weights, assumed homoplasy for missing entries: 100%



6.27. K-value of 150, implied weights (strict consensus)



6.28. K-value of 150, extended implied weights, assumed homoplasy for missing entries: 25%



6.29. K-value of 150, extended implied weights, assumed homoplasy for missing entries: 50%



6.30. K-value of 150, extended implied weights, assumed homoplasy for missing entries: 75%


6.31. K-value of 150, extended implied weights, assumed homoplasy for missing entries: 100%



6.32. K-value of 200, implied weights



6.33. K-value of 200, extended implied weights, assumed homoplasy for missing entries: 25%



6.34. K-value of 200, extended implied weights, assumed homoplasy for missing entries: 50%



6.35. K-value of 200, extended implied weights, assumed homoplasy for missing entries: 75%



6.36. K-value of 200, extended implied weights, assumed homoplasy for missing entries: 100%

