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MACROEVOLUTIONARY PATTERNS IN RHYNCHOCEPHALIA: IS THE TUATARA (*SPHENODON PUNCTATUS*) A LIVING FOSSIL?

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Abstract: The tuatara, *Sphenodon punctatus*, known from 32 small islands around New Zealand, has often been noted as a classic ‘living fossil’ because of its apparently close resemblance to its Mesozoic forebears and because of a long, low-diversity history. This designation has been disputed because of the wide diversity of Mesozoic forms and because of derived adaptations in living *Sphenodon*. We provide a testable definition for ‘living fossils’ based on a slow rate of lineage evolution and a morphology close to the centroid of clade morphospace. We show that through their history

since the Triassic, rhynchocephalians had heterogeneous rates of morphological evolution and occupied wide morphospaces during the Triassic and Jurassic, and these then declined in the Cretaceous. In particular, we demonstrate that the extant tuatara underwent unusually slow lineage evolution, and is morphologically conservative, being located near the centre of the morphospace for all Rhynchocephalia.

Key words: Rhynchocephalia, Sphenodontia, rates of evolution, living fossils, morphospace.

THE Rhynchocephalia is an ancient group of reptiles that emerged during the Early or Middle Triassic (Jones *et al.* 2013). They are unusual among the 10 000 species of living reptiles, being ranked at times as an order equivalent to the Crocodylia, Squamata and Testudines (Pough *et al.* 2012), but represented today by a single species, *Sphenodon punctatus* (Hay *et al.* 2010; Jones & Cree 2012; Cree 2014). This species is geographically restricted to the islands of New Zealand, and it is best known by its vernacular name ‘tuatara’. *S. punctatus* was first described by J. E. Gray in 1831, but he misidentified it as an agamid lizard (Sharell 1966; Robb 1977; Cree 2014). A few years later, Günther (1867) noted its similarities with some fossil forms, and in consequence erected the Order Rhynchocephalia, which has long been identified as sister to Squamata, the much larger clade comprising lizards and snakes.

Sphenodon punctatus has often been identified as a ‘living fossil’ (Fraser 1993; Sues *et al.* 1994; Jones 2008; Jones *et al.* 2009; Meloro & Jones 2012; Cree 2014) for a variety of reasons: (1) the living form, superficially, seems little different from its distant Mesozoic ancestors; (2) the clade has had a very long duration, but with low diversity and possibly long-lived species and genera; (3) it is the solitary sister clade to the equally ancient Squamata, comprising over 9000 species; (4) there is a long gap in

geological time between the modern form and the youngest fossil forms, in the Miocene, Paleocene and Cretaceous; and (5) it shows supposedly ‘primitive’ anatomical features such as the closed lower temporal bar.

This view has been disputed because, during the last three decades, many fossil species of rhynchocephalians have been described, so partially rejecting reason (2) above. Several of these newly described species show a wide variety of ecological adaptations, either to terrestrial or marine environments (e.g. *Pamizinsaurus*, *Pleurosaurus*), as well as a diverse array of dietary preferences (Jones 2008, 2009; Meloro & Jones 2012; Rauhut *et al.* 2012; Martínez *et al.* 2013). These observations contradict the common view of the Rhynchocephalia as a morphologically unchanged group, reason (1) above, and suggest that it had high diversity and morphological disparity through time (Sues *et al.* 1994; Reynoso 1997, 2000, 2005; Evans *et al.* 2001; Jones 2008; Jones *et al.* 2009; Apesteguía & Jones 2012; Cree 2014). Also, recent work on the extant *Sphenodon* indicates that it is not as conservative as was previously believed (Jones 2008; Meloro & Jones 2012; Cree 2014), with a presumably secondarily fused lower temporal bar (Whiteside 1986), thus rejecting reason (5) above. However, the traditional view of the Rhynchocephalia as an unchanged group through time

still dominates in textbooks and other sources (e.g. Sharell 1966; Robb 1977; Mitchell *et al.* 2008) despite the lack of clarity over the definition of what a ‘living fossil’ is. Researchers may agree on which taxa are ‘living fossils’ (e.g. Schopf 1984; Casane & Laurenti 2013), but there is no testable definition.

The concept of ‘living fossils’ has been problematic since the term was coined by Charles Darwin (1859), as there is no such identifiable class of organisms, but oft-cited examples do share some or all of the noted features. Note that the phrase ‘relict species’ encapsulates some characteristics of ‘living fossils’, referring to a species or a group of species that remains from a large group that is mainly extinct (Grandcolas *et al.* 2014).

Here, we propose a hypothesis that can be tested by computational morphometric and phylogenetic comparative methods (PCM): ‘a living fossil should show both statistically significantly slow rates of morphological evolution and it should be morphologically conservative.’ The first measure is assessed with respect to sister taxa and sister clades, and using standard PCM approaches for assessing the statistical significance of evolutionary rates. The second measure of morphological conservatism can be assessed by determining whether the taxon lies close to the early, or geologically earliest, members of its clade or close to the centroid of the hyperdimensional morphospace. The distance of each species from the centroid can be measured, but there is no agreed statistical test to

distinguish classes of morphological conservatism, just that the taxon in question is closer to the centroid than other taxa are; perhaps closer to the centroid than the majority of taxa, including fossil forms.

We explore here the morphological disparity of all the Rhynchocephalia, and where the extant *Sphenodon* fits within the clade. Based on a phylogenetic analysis of the whole clade, we identify rates of morphological evolution and changes in morphospace using geometric morphometrics of the lower jaw, and find evidence that *Sphenodon* evolved slowly, and is morphologically conservative when compared to extinct rhynchocephalians, especially the earliest forms.

METHOD

Phylogeny of Rhynchocephalia

To construct a phylogeny for Rhynchocephalia and explore evolutionary rates, we used the recently published data matrix of 74 discrete morphological characters from Apesteguía *et al.* (2014). We ran a maximum parsimony analysis with TNT v. 1.1 (Goloboff *et al.* 2008) following the settings of Apesteguía *et al.* (2014), and as a result we recovered the same 22 MPTs of 218 steps as they did. All MPTs were reduced to a time-scaled strict consensus tree (Fig. 1). The discrete morphological character data matrix

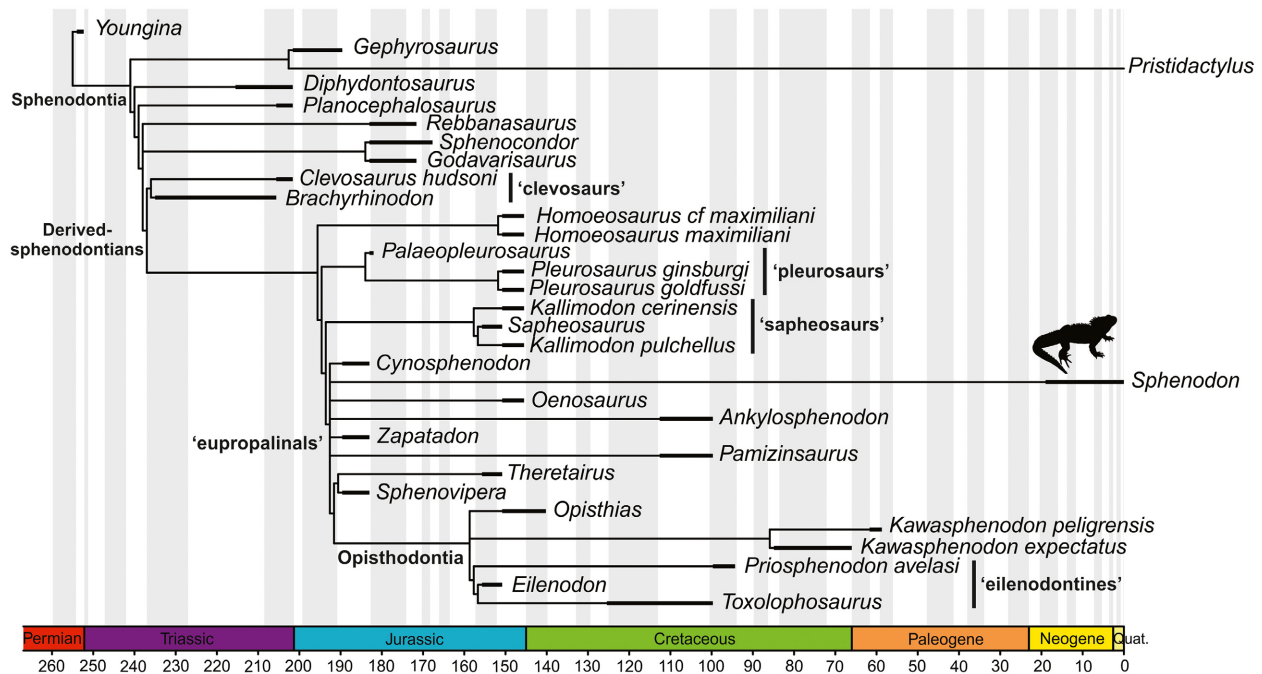


FIG. 1. Time-scaled phylogeny of Rhynchocephalia, based on a strict consensus tree of 22 most parsimonious trees (details in Herrera-Flores *et al.* 2017). Note that *Youngina* and extant *Pristidactylus* are outgroups to Rhynchocephalia. Abbreviation: Quat., Quaternary. Colour online.

and 22 MPTs were used later for evolutionary rates analyses using the methods described below.

Evolutionary rates

Rates of morphological evolution were investigated using maximum-likelihood methods, following the protocols of Lloyd *et al.* (2012), Brusatte *et al.* (2014) and Wang & Lloyd (2016). We first time-scaled our MPTs, establishing ages for terminal taxa by compiling ages (FAD, first appearance date and LAD, last appearance date) for each taxon using the Paleobiology Database and the literature, to determine the latest consensus view on the ages of relevant geological formations (<https://paleobiodb.org>). Following the work of Brusatte *et al.* (2014) and Wang & Lloyd (2016), we used two current available methods for determining the dates of nodes and branch durations, the ‘equal’ and ‘minimum branch length’ (mbl) methods. For both methods, we used the settings recommended by Brusatte *et al.* (2014) and Wang & Lloyd (2016), with a fixed duration of 1 myr for the ‘minimum branch length’ method and 2 myr for a root-length of the ‘equal’ method. When dating the trees we used a randomization approach, and performed 100 replicates to incorporate potential uncertainty arising from sampling each terminal taxon’s age randomly from between their first and last appearance dates. This generated 100 time-scaled phylogenies for each of the 22 MPTs, and for both the ‘equal’ and ‘mbl’ methods. Before running the rates analyses we excluded the extant squamate *Pristidactylus*. Using all the time-scaled phylogenies and the discrete morphological character data, we assessed whether rates of morphological evolution were homogeneous, or if particular branches or clades have significantly low or high rates relative to the remainder of the tree (Lloyd *et al.* 2012). Comparative rates were assessed using likelihood ratio tests (LRTs) between single rate models (homogenous rates) and two rate models (particular branch has different rates to the rest of the tree). An alpha threshold of 0.01 was used to evaluate significance, with Benjamini–Hochberg false discovery rate correction. Sensitivity tests were performed with *Sphenodon* removed from the tree and character data, to ensure that the long terminal branch associated with *Sphenodon* was not biasing the rates results. All analyses were performed in R (R Core Team 2015), using the packages `paleotree` (Bapst 2012) and `Claddis` (Lloyd 2016), and with a modified version of the script of Wang & Lloyd (2016).

To illustrate the evolutionary rates results, we figure one MPT for both the ‘equal’ (MPT 1) and ‘mbl’ (MPT 6) analyses (Fig. 2). Pie charts are used to indicate the proportion of significantly high and significantly low per-branch rates results, based on the 100 dating replications.

These trees were selected because they accurately reflect most of the results recovered across all 22 MPTs, and we highlight branches that consistently show the same high/low rates in other MPTs. All MPTs are individually figured in Herrera-Flores *et al.* (2017).

Morphospace and disparity analysis

To investigate macroevolutionary trends in Rhynchocephalia, we analysed changes in morphospace occupation through time, based on variations in dentary shape. We chose to focus on morphological variation in the dentary because it is commonly the best preserved part in fossil rhynchocephalians, which can retain more than 80% of the shape of the complete mandible. Also it has been shown in studies of a broad array of vertebrates that mandibular shape captures information about dietary preferences and so can discriminate major ecomorphological groupings (e.g. Kammerer *et al.* 2006; Anderson *et al.* 2011, 2013; Stubbs *et al.* 2013). Further, mandible shape variation may be measured readily from two-dimensional images. We compiled images of dentaries for 30 fossil rhynchocephalians from the literature, plus pictures from 14 museum specimens of the extant *Sphenodon* to assess variation within this single taxon, and to determine where it falls in comparison with Mesozoic taxa. We performed a separate geometric morphometric analysis of all samples of *Sphenodon* to identify the specimen that best represents the average shape of its dentary. All images were uniformly oriented to the same side (right). Seven landmarks and 26 semi-landmarks were set on the dentary images (see Herrera-Flores *et al.* 2017), using the program `tpsDig` (Rohlf 2006).

After Procrustes superposition to correct for variable sizes of the mandibles and variable orientations of images, the corrected coordinate data from the landmarks were subjected to principal components analysis (PCA) in R (R Core Team 2015), employing the package `geomorph` (Adams & Otárola-Castillo 2013). Three plots were produced, one to show morphospace occupation through the Mesozoic, one to observe macroevolutionary trends according to different feeding strategies of rhynchocephalians, and another to explore the phylogenetic branching patterns within the morphospace (a phylomorphospace). For the feeding strategies plot, we used the dietary preferences proposed by Jones (2006a, 2009), Rauhut *et al.* (2012) and Martínez *et al.* (2013) based on rhynchocephalian tooth shape. The phylomorphospace was produced using the R package `phytools` (Revell 2012). We randomly selected one dated MPT and cropped the tips that lacked PC coordinate data. This pruned phylogeny was used to reconstruct ancestral PC coordinate data with maximum likelihood estimation, and the branching

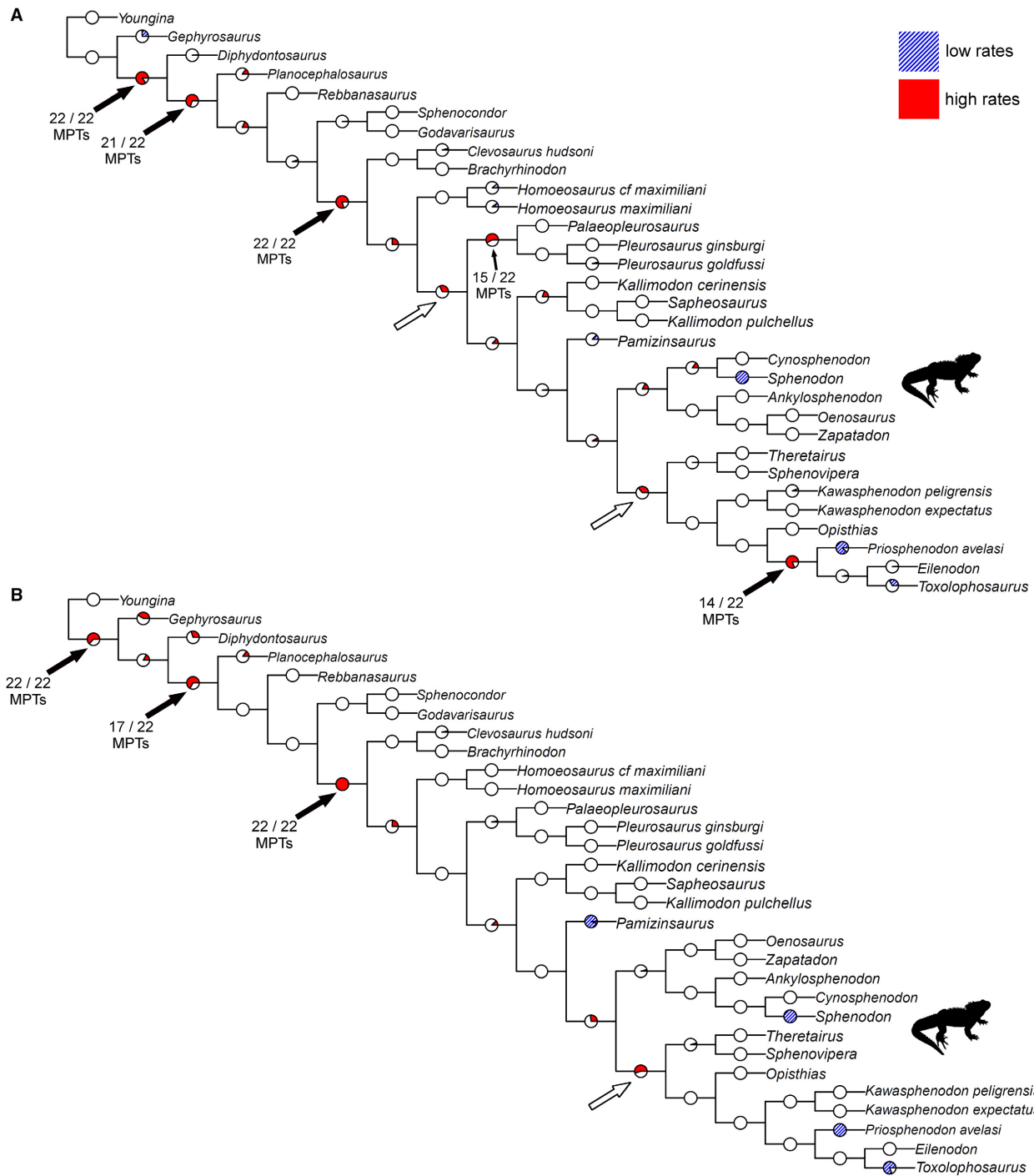


FIG. 2. Evolutionary rates analyses of Rhynchocephalia, illustrating results from per-branch likelihood tests using the ‘equal’ (A) and the ‘mbl’ (B) dating methods. One of the 22 most parsimonious trees (MPTs) is illustrated for each analysis. Pie charts on the branches are used to indicate the proportion of significantly high, significantly low and non-significant (white) rates results, based on 100 dating replications. Arrows denote branches that are consistently found to have significant rates in most MPTs (black arrows) or some MPTs (white arrows). For complete results for all MPT trees, see Herrera-Flores *et al.* (2017). *Sphenodon* illustration by Steven Traver. Colour online.

pattern was superimposed within the morphospace. As previously mentioned, we included a sample of the extant *Sphenodon* in all plots for comparative purposes. To

explore the extent to which *Sphenodon* represents a conservative, or ‘average’, morphology, we examined Procrustes distances (describing the magnitude of the shape

deviation) between each sampled dentary and the Procrustes mean shape of the entire sample (in *morphologika*; O'Higgins & Jones 1998, 2006).

To test for statistically significant overlaps in morphospace occupancy between groups of taxa sorted by geological period and by feeding mode, we used our PC coordinate data and performed a one-way NPMANOVA test in PAST (Hammer *et al.* 2001) using Euclidean distances, 10 000 permutations and Bonferroni-corrected p-values. Additionally, morphological disparity for temporal and feeding groups was quantified with the sum of variances metric, calculated using PC coordinate data from the first ten ordination axes (subsuming 91% of overall variation). Confidence intervals associated with calculated disparity values were generated by bootstrapping with 10 000 replications. Disparity calculations were performed in R (R Core Team 2015).

RESULTS

Evolutionary rates

Rates analyses using both the 'equal' and 'mbl' methods show similar results overall, with heterogeneous rates found throughout the phylogeny (Fig. 2). Both analyses show significantly high rates of character change on basal branches along the 'backbone' of the phylogeny, and on the branch leading to 'derived rhynchocephalians'. These high-rate branches are recovered consistently in most dating replicates, and in most MPTs. Significantly high rates are frequently found on the branch subtending a derived clade formed by *Sphenovipera*, *Theretairus* and the Opisthodontia, although this is not recovered as consistently across dating replicates and in all MPTs (Fig. 2). For the extant *Sphenodon*, both methods demonstrated that it has significantly low rates of morphological evolution, which contrasts with the occasionally high and, more often, non-significant rates shown by the branches preceding it, and with its closest relatives, such as the Early Jurassic *Cynospheodon* (Fig. 2). Within the derived rhynchocephalians, the 'equal' dated trees also showed higher rates on the internal branches subtending pleurosaurs and eilenodontines (Fig. 2A), although these high rates are not seen in the more conservative 'mbl' approach (Fig. 2B). Another difference between both methods is that for taxa near the base of the tree (*Gephyrosaurus*, *Diphydontosaurus*, *Planocephalosaurus*), the 'mbl' method found high rates on these terminal branches (Fig. 2B), while the 'equal' method showed low or non-significant rates (Fig. 2A). One interesting case is one of the morphologically specialized species *Pamizinsaurus*, from the Early Cretaceous, which showed low rates of morphological evolution in the 'mbl' analyses (Fig. 2B).

Importantly, all these rates results for extinct taxa are consistent in the sensitivity analyses, when *Sphenodon* is removed (see supplementary results in Herrera-Flores *et al.* 2017).

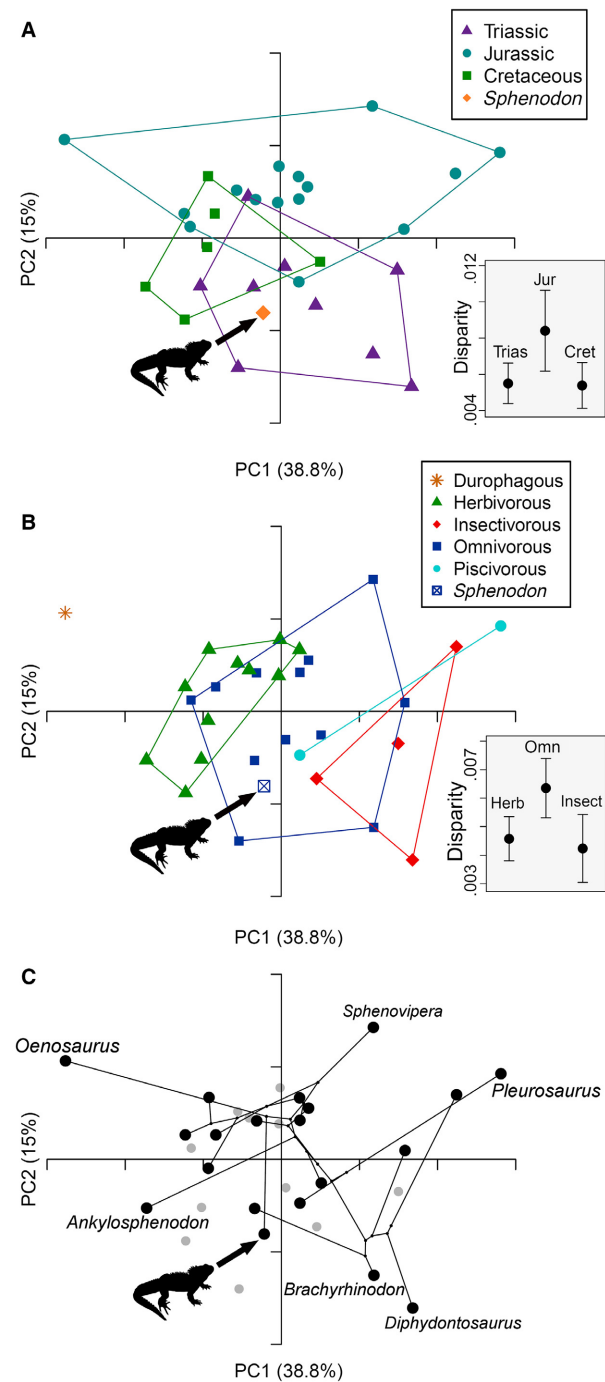
Morphospace analysis

The morphospace analysis demonstrates that rhynchocephalians experienced important changes in morphospace occupation through time (Fig. 3A). Their morphospace in the Triassic was reasonably large, which suggests that the group had an initial burst of high morphological disparity after its origin in the Early or Middle Triassic. On the other hand, Jurassic rhynchocephalians considerably increased their morphospace occupation compared to the Triassic, but also moved into a different morphospace. The PC1–PC2 morphospace plot (Fig. 3A) shows that in the Cretaceous, rhynchocephalians experienced a considerable decrease in morphospace occupation, to about half of the area occupied in the Triassic and a third of that occupied in the Jurassic. The sum of variances disparity metric confirms that Jurassic taxa had the highest disparity, while disparity of Triassic and Cretaceous taxa was subequal and considerably lower (Fig. 3A). Results of the NPMANOVA test only found significant differences in morphospaces between the Triassic and Cretaceous ($p = 0.035$), and non-significant differences between Triassic and Jurassic taxa (Herrera-Flores *et al.* 2017, table S1). The living *Sphenodon* lies close to the centroid within the morphospace of Triassic taxa and near the zone where morphospaces of Mesozoic taxa overlap.

As expected, the mandibular landmarks provide good discrimination of feeding strategies among rhynchocephalians (Fig. 3B). Herbivorous taxa form a tight cluster with a high diversity of species, while insectivorous forms also occupy a relatively tight cluster but with considerably fewer species. The only known durophagous taxon (*Oenosaurus*) occupies a completely different morphospace region to other rhynchocephalians. In the case of omnivorous taxa (which also include carnivores), they show the greatest morphospace occupation, and this slightly overlaps with the herbivorous, insectivorous, and piscivorous morphospaces. For the piscivorous taxa, one of them (*Palaeopleurosaurus*) overlaps with omnivorous taxa, while the other piscivorous taxon (*Pleurosaurus*) occupies distinct morphospace. *Sphenodon*, identified as an omnivore (Sharell 1966; Robb 1977; Cree 2014), falls near the centre of the feeding morphospace plot (Fig. 3B). Disparity analyses show that omnivorous taxa had high disparity, while herbivorous and insectivorous had lower disparity. When comparing morphospace occupation through one-way NPMANOVA, only samples of

herbivorous–insectivorous ($p = 0.005$) and herbivorous–omnivorous ($p = 0.046$) forms were significantly different from each other, while other feeding modes did not show any significant differences among the samples (Herrera-Flores *et al.* 2017, table S2).

The phylomorphospace (Fig. 3C) reveals that the shape of the dentary in *Sphenodon* differs from that of its closest relatives. The branch leading to *Sphenodon* traverses PC2



and originates from a cluster of internal nodes and terminal tips also located centrally along PC1. The shape of the dentary in *Sphenodon* is convergent with that in basal forms, such as the ‘clevosaurus’. Some taxa closely related to *Sphenodon* can also trace their branches back to this central cluster from outlying positions in morphospace, such as *Oenosaurus* and *Ankylosphenodon*.

When comparing Procrustes distances between each sampled taxon and the Procrustes mean landmark configuration for all specimens, *Sphenodon* deviates little from the average shape. Of the 31 taxa, *Sphenodon* is the seventh most similar to the average shape. The other forms most similar to the average shape are (in order) *Clevo-saurus*, *Opisthias*, *Kallimodon* and *Palaeopleurosaurus*. The most divergent forms are (in order) *Oenosaurus*, *Pleurosaurus*, *Brachyrhinodon*, *Gephyrosaurus* and *Diphydontosaurus* (see full list in Herrera-Flores *et al.* 2017).

DISCUSSION

Frequently, the recognition of an extant species as a ‘living fossil’ is historical, a consequence of the discovery of fossil relatives before the living species, as in the case of the coelacanth *Latimeria* (Casane & Laurenti 2013). In the case of the tuatara, this species was noted as a living fossil because of its ‘almost identical structure’ to the Late Jurassic *Homoeosaurus* (Robb 1977). However, recent studies on *Sphenodon* and some of its fossil relatives have disputed the assumed long-term morphological and molecular stasis of the group (Hay *et al.* 2008; Jones 2008; Meloro & Jones 2012). In Victorian times, only the living form was known, and it was recognized as sister to the highly diverse Squamata (lizards, amphisbaenians and snakes). With increasing knowledge of the fossil record of rhynchocephalians, the morphological similarity between *Sphenodon* and some fossil forms became clear.

These claims became easier to assess with substantial increases in knowledge of fossil rhynchocephalians in the past 30 years (Jones 2008), and the application of

FIG. 3. Rhynchocephalian morphospace occupation, based on a geometric morphometric analysis of the dentary. Plots show temporal (A) and dietary (B) groupings, and a phylomorphospace (C). Note that the modern *Sphenodon* lies close to the centre of the morphospace plots. Morphological disparity (sum of variances) plots are included for the temporal (A) and dietary (B) groups. In the phylomorphospace (C), key taxa are named, and only major phylogenetic relationships are shown. Taxa within the morphospace that were not included in the phylogeny are denoted by grey circles. Error bars are 95% confidence intervals based on 10 000 replications. *Sphenodon* illustration by Steven Traver. For names of taxa in the plots see Herrera-Flores *et al.* (2017). Colour online.

cladistic methodology, following the first phylogenetic analysis of the group (Fraser & Benton 1989). Recent geometric morphometric works (Jones 2008; Meloro & Jones 2012) have refuted the morphological stasis of the Rhynchocephalia by reference to the disparity of skull and tooth shape. Our study agrees with Jones (2008) and Meloro & Jones (2012), by showing that the Rhynchocephalia was a diverse group with wide morphological disparity, and not an unchanging group through time, as previously believed. However, we dispute the suggestion by Jones (2008) and Meloro & Jones (2012) that the tuatara is a non-conservative species. Our results provide a wider perspective on the position of *Sphenodon* among fossil taxa following a considerable increase in the number of fossil taxa, by using morphological information from the lower jaw and novel macroevolutionary methods to explore rates of morphological evolution over time.

In terms of a numerically testable hypothesis, we suggested earlier that 'a living fossil should show both statistically significantly slow rates of morphological evolution and it should be morphologically conservative.' Our study confirms that *Sphenodon* fits both of these criteria and so is a 'living fossil'.

First, we found statistically significantly slow rates of morphological evolution in *Sphenodon* (Fig. 2). Overall, rates of morphological evolution in rhynchocephalians were heterogeneous (Fig. 2A, B), which suggests that the group has had a complex evolutionary history. Our study hints that much of the morphological diversity seen in the clade originated through a small number of evolutionary 'bursts', with a mix of high rates on basal and derived branches in the tree (Fig. 2). It is unexpected to see 'average' rates of morphological evolution for some highly specialized taxa, such as *Oenosaurus* and *Ankylosphenodon*, as well as low rates for the bizarre *Pamizinsaurus*. This finding is apparently contradicted by evidence that *Sphenodon* is an advanced taxon based on the presence of derived morphological features (Gorniak *et al.* 1982; Jones 2008; Curtis *et al.* 2010, 2011; Jones *et al.* 2012). However, recent work (Reynoso 1996, 2000, 2003; Reynoso & Clark 1998; Apesteguía & Novas 2003) shows that the most closely related species to *Sphenodon* is the Early Jurassic *Cynosphenodon*, a species that showed average rates of morphological change compared to the low rates in *Sphenodon*, according to our analysis. This may indicate that the Sphenodontinae, the clade that comprises *Sphenodon* and *Cynosphenodon*, experienced long-term morphological stasis after the Early Jurassic.

The fact that *Sphenodon* has the highest rate of molecular evolution among living vertebrates (Hay *et al.* 2008; Subramanian *et al.* 2009) confirms that rates of molecular and morphological evolution are decoupled (Subramanian *et al.* 2009). In such comparisons, of course, we cannot comment on rates of change in non-preserved

morphology. A problem with our study is that there is such a long time gap between living *Sphenodon* and its Early Jurassic sister taxon, so rates cannot be compared with confidence. Likewise, phylogenomic studies can only compare living *Sphenodon* with extant squamates, separated by some 2×240 myr of independent history. The long *Sphenodon* branch is problematic also because it cannot be broken up by intervening branching events, and so any rate calculation is averaged, and probably underestimated.

Second, in terms of morphology, *Sphenodon* passes the test to be called a 'living fossil' because of its conservative position in morphospace (Fig. 3). Our geometric morphometric study confirms the expanded morphospace of rhynchocephalians in the Triassic and Jurassic, and a decrease in the Cretaceous. The fact that Jurassic rhynchocephalians occupied an almost entirely different morphospace from their Triassic precursors might be a consequence of the Triassic–Jurassic extinction, and dramatic changes in the biota and the ecological position of rhynchocephalians in their ecosystems. The dramatic decrease in morphospace occupied by Cretaceous rhynchocephalians has usually been related to the radiation of squamates (Apesteguía & Novas 2003; Jones 2006b; Jones *et al.* 2009; Meloro & Jones 2012), but this cannot be confirmed here.

In focusing on lower jaw morphology, we have reduced the sample of morphological characters when compared to studies based on the skull (e.g. Jones, 2008), but we have increased the sample of taxa, and the lower jaw encompasses key information about feeding adaptation (Kammerer *et al.* 2006; Anderson *et al.* 2011, 2013; Stubbs *et al.* 2013). Our results differ from those of Jones (2008), who found tight ecomorphological clusters relating to phylogenetic position, such as a cluster of basal taxa (e.g. *Diphydontosaurus*, *Gephyrosaurus*, *Planocephalosaurus*) as well as some derived groups such as clevosaurids. Our results show that morphological differences cross-cut phylogeny, with high morphological diversity among basal rhynchocephalians and within the derived genus *Clevosaurus* (Fig. 3). Meloro & Jones (2012) suggested that the possible ancestor of *Clevosaurus* must have been 'Sphenodon-like'. Our results show that *Sphenodon* converges with the Triassic species of *Clevosaurus* (*C. hudsoni* and *C. sectumsemper*) close to the centroid of morphospace, and both *Sphenodon* and *Clevosaurus* possess two of the most average mandibular morphologies of all rhynchocephalians. This indicates that the morphology of the modern tuatara is conservative and it is also an 'average rhynchocephalian'.

Tooth shape is also very important for the evolution of feeding modes in rhynchocephalians (Jones 2009; Meloro & Jones 2012; Rauhut *et al.* 2012; Martínez *et al.* 2013). The most basal taxa (*Gephyrosaurus*, *Diphydontosaurus*,

Planocephalosaurus) are identified as insectivorous because of their piercing teeth, but later species evolved many different tooth shapes reflecting their wide variety of dietary preferences, such as the carnivorous or omnivorous cleveosaurs, the omnivorous sphenodontines, the piscivorous pleurosaurs, and the specialized herbivorous eilenodontids (Throckmorton *et al.* 1981; Rasmussen & Callison 1981; Jones 2008, 2009; Meloro & Jones 2012; Rauhut *et al.* 2012; Martínez *et al.* 2013). One special case of feeding adaptation among rhynchocephalians is the Late Jurassic *Oenosaurus muehlheimensis*, which had a complex crushing dentition for a durophagous diet of molluscs or crabs (Rauhut *et al.* 2012). Another interesting case of dietary adaptation is the Early Cretaceous *Ankylosphenodon pachyostosis*, which developed continuously growing teeth ankylized into the lower jaw for an herbivorous diet (Reynoso 2000).

Throughout their evolutionary history, rhynchocephalians evolved dental and cranial modifications for different ecological niches (Jones 2008). Current research suggests that rhynchocephalians had at least five dietary preferences (Jones 2006a, 2009; Rauhut *et al.* 2012; Martínez *et al.* 2013). The morphospaces occupied by rhynchocephalians with these five dietary preferences (Fig. 3B) were generally small, except for those with an omnivorous or carnivorous diet, which occupied a wide morphospace area. Evidence of the success of the omnivorous diet is provided by the oldest known survivor of the K–Pg extinction, the early Paleocene *Kawasphenodon peligrensis*, which has been regarded as an omnivore (Apesteguía *et al.* 2014), as is the extant tuatara (Curtis *et al.* 2011; Jones *et al.* 2012; Cree 2014).

Aspects of the biology of the living tuatara have been noted recently as evidence that it cannot be regarded as a ‘living fossil’. For example, many authors have noted the complexity of the feeding mechanism of *Sphenodon* (Gorniak *et al.* 1982; Jones 2008; Curtis *et al.* 2010, 2011; Jones *et al.* 2012), and the propalinal movement of the lower jaw has been marked as unique among living amniotes (Gorniak *et al.* 1982; Jones 2008; Curtis *et al.* 2010, 2011; Jones *et al.* 2012). Another important feature of the tuatara is the presence of a complete lower temporal bar in the skull, which is a derived condition when compared with other fossil rhynchocephalians (Whiteside 1986; Jones 2008; Curtis *et al.* 2011; Jones *et al.* 2012). Furthermore, studies on the biology of the tuatara have demonstrated that its physiology is quite advanced, because, in contrast to many other living reptiles, the tuatara is well adapted to cold environments (Cree 2014). Also, the tuatara shows complex behaviour, especially in its interspecific relationship with seabirds (Corkery 2012; Cree 2014). In addition, a recent molecular study of the hypervariable regions of mitochondrial DNA of subfossil and extant specimens of the tuatara demonstrated that

this species has very high rates of molecular evolution (Hay *et al.* 2008; Subramanian *et al.* 2009).

Notwithstanding these observations of the uniqueness of *Sphenodon*, our analysis of evolutionary rates and geometric morphometrics shows not only that the tuatara is generally morphologically conservative, resembling some of its Mesozoic forebears, but that it actually occupies a position close to the centroid of the hyperdimensional morphospace, as well as in the morphospace bounded by axes PC1 vs PC2 (Fig. 3). Also, *Sphenodon* is recovered as possessing the seventh ‘most average’ morphology out of the 31 taxa used in this study. Even if it fails some of the definitions of ‘living fossil’, *Sphenodon* is part of a lineage that has been long-enduring and existed at low diversity through hundreds of millions of years, it follows a long time gap with few fossils, and it is a relict, being the survivor of a once more diverse clade and now lone sister to the biodiverse Squamata. We provide a new definition of ‘living fossil’ here, in terms of both a statistically significantly slow rate of morphological evolution and morphological conservatism. *Sphenodon* shows both characteristics, a slow rate of evolution when compared to the mean for all rhynchocephalians, and a position close to the centroid in the overall morphospace defined by the extinct members of the clade.

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DATA ARCHIVING STATEMENT

Data for this study are available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.568jh>

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