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Nocturnality in Synapsids Predates the Origin of Mammals by Over 100 Million Years

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The distribution of scleral ossicles in nonmammalian synapsids

Scleral ossicles, and particularly more or less complete scleral rings, are rarely preserved in nonmammalian synapsid specimens. To give some sense of this, the great majority of specimens that we included in this analysis (31 of 38) are from the Karoo Basin of South Africa. Thousands of synapsid fossils have been collected from the Karoo [1, 2], but our sample includes nearly all of the specimens from that basin that possess sufficiently complete and prepared scleral rings to allow measurement. The infrequency of preservation of scleral ossicles stems in part from their small size and fragility. However, their rarity in museum collections, particularly in older specimens, also is related to changing preparation tools and techniques. Of the South African specimens we included, the majority were collected in the past two to three decades (i.e., when more delicate and precise preparation tools have been available).

There is no single compilation in the literature of synapsid specimens and/or taxa that possess disarticulated scleral ossicles or articulated scleral rings, although reports of individual taxa possessing scleral elements are not uncommon [3-11]. Sidor's [12] skull simplification dataset is the most comprehensive single resource for the distribution of scleral elements among synapsids, and he notes their presence in members of eight major synapsid clades (Varanopidae, Ophiacodontidae, Biarmosuchia, Dinocephalia, Anomodontia, Gorgonopsia, Therocephalia, Cynodontia). Most individual references in the literature concern specimens belonging to one of these clades [13], although a few help to establish the presence of scleral ossicles in other taxa [4, 11, 14, 15], most importantly Sphenacodontidae. Together, these sources show that scleral elements were present in nearly all nonmammalian synapsid lineages, although their potential absence in Caseasauria (i.e., Eothyrididae and Caseidae), Edaphosauridae, and Probainognathia require some further discussion.

Traditionally, [16, 17], Caseasauria has been hypothesized to be the most basal synapsid clade, although a recent phylogenetic analysis [18] has placed the group in a somewhat more crownward position on the phylogeny. Eothyridid caseasaurs are small carnivores known from very limited material [19, 20], whereas caseids are medium to large herbivores [17, 21], including taxa that were likely among the largest tetrapods of their time. We are unaware of any reports in the literature of scleral elements preserved in any caseasaur, nor do we know of any specimens in which they are preserved.

Edaphosauridae is another basal synapsid clade comprised predominantly of herbivores [17, 21], although basal members of the group likely were at least omnivorous if not faunivorous [22]. The clade's position as the sister taxon of Sphenacodontia within Eupelycosauria has been relatively stable in recent phylogenetic analyses (including [18]), and it includes the iconic Permian herbivore *Edaphosaurus*, which is characterized by a sail on its back formed by elongate neural spines ornamented with transverse tubercles [23]. As with caseasaurs, we are unaware of any reports in the literature of scleral elements preserved in any edaphosaurid, nor do we know of unpublished specimens in which they are preserved.

If the apparent absence of scleral elements in Caseasauria and Edaphosauridae is a real feature (i.e., it is not an artifact of the delicate scleral plates not being preserved in any known specimen), it almost certainly represents a secondary loss even if caseasaurs are the most basal synapsid clade. Given the broad distribution of scleral plates within vertebrates in general [24] and among basal synapsids (Fig. S1), it is highly unlikely that scleral ossicles were lost in the earliest synapsids and then re-expressed within various synapsid subclades.

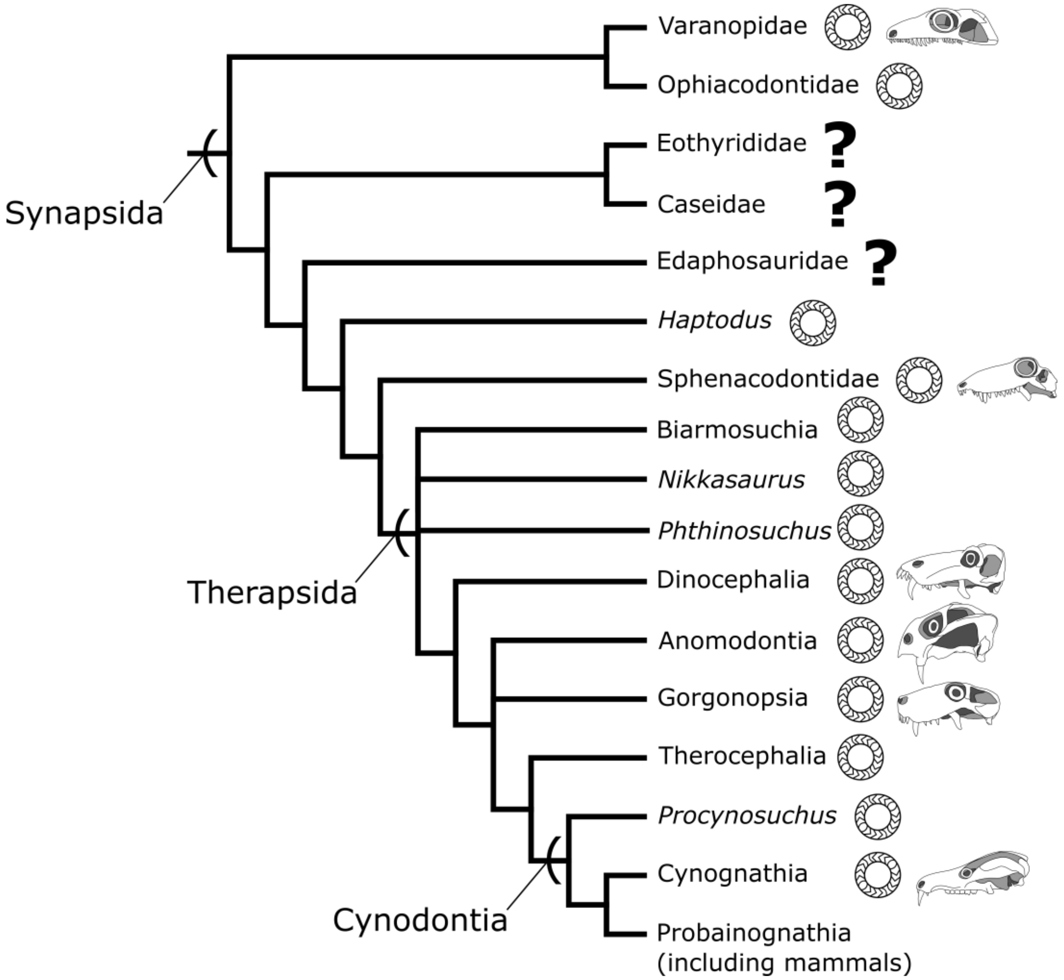

Fig. S1. Simplified cladogram showing the relationships of the main clades of Synapsida, and the distribution of scleral ossicles within the group. Taxa with a scleral ring next to their names include at least one member that is known to preserve scleral ossicles. Taxa with "?" next to their names have no known members that preserve scleral ossicles, but for which this absence may be a taphonomic artifact. Distribution of scleral ossicles is primarily based on [12] and our observations during the course of this study. The presence of scleral ossicles in *Haptodus* is based on [14], the presence of scleral ossicles in *Nikkasaurus* is based on [25], and the presence of scleral ossicles in *Phthinosuchus* is based on [26]. Tree topology for non-therapsid synapsids is based on [18]. Tree topology for Therapsida is based on [16, 27, 28]. The placement of *Tritylodon* within Cynognathia follows [27], but note that other analyses reconstruct tritylodontids as probainognathians (e.g., see reviews in [29, 30], and more recent analyses such as [31, 32]). The phylogenetic placement of *Nikkasaurus* is uncertain, but it has generally been regarded to be a basal therapsid [19]. *Phthinosuchus* has been variously suggested to be a basal therapsid or related to biarmosuchians or gorgonopsians [33-40].

Scleral ossicles are extremely rare in cynodonts; they have been reported only in the basal cynodont *Procynosuchus* and the tritylodontid *Tritylodon* [12]. In addition to a small number of basal taxa such as *Procynosuchus* and *Thrinaxodon*, Cynodontia consists of two main clades, Cynognathia and Probainognathia [30]. Cynognathia primarily includes omnivorous or herbivorous species and was most diverse during the Triassic; Probainognathia mostly includes small carnivores in its early history and is represented by mammals in the extant biota (see reviews in [30, 34]. Assuming that *Tritylodon* is a member of Cynognathia (see below), we are unaware of any reports of preserved scleral elements in any probainognathian specimens. However, the rarity of scleral ossicles in nonmammalian cynodont specimens makes it difficult to assess whether the absence of ossicles in mammals is a probainognathian synapomorphy or if it evolved at a later point within the clade. It also would not be surprising if the loss of scleral ossicles in the ancestors of mammals was only one of multiple losses in Cynodontia. For example, the basal cynodont *Thrinaxodon liorhinus* is known from a large number of specimens (over 100 are present in major museum collections in South Africa alone; [2], many of which are extremely well preserved and prepared, yet none preserve evidence of scleral ossicles. The absence of scleral ossicles in so many specimens of *T. liorhinus* is very suggestive of the species truly lacking them, but their presence in *Tritylodon* indicates that at least some advanced cynodonts retained them, a pattern consistent with multiple losses

Potential significance of the loss of scleral rings in synapsids

The scleral ring of amniotes is found near the corneal-scleral junction, the eye sulcus, and is considered to provide mechanical stability in response to forces generated by the muscles involved in accommodation [41-43]. Accommodation involves a dynamic change in the overall refractive power of the eye [43], which enables focusing on objects at various depths in the visual field. The need for accommodation is particularly high for large eyes with large pupils, which reduces the depth of field, i.e. the distance over which objects appear sharp (84). Conversely, small eyes with small pupils have a large depth of field with little need for accommodation.

There are several mechanisms for accommodation within amniotes [43], but all of them involve changes in the radius of curvature of refractive surfaces. The modification of the curvatures of these refractive surfaces is achieved by the action of ciliary muscles, which originate at the sclera beneath the scleral ossicles. Mammals differ from birds and lizards in nearly exclusively relying on lens accommodation, with corneal accommodation being absent.

It has been suggested that the absence of scleral rings in mammals is associated with the absence of corneal accommodation [43]. Early mammals were small [29] and therefore would have had small eyes in terms of absolute dimensions. As noted above, small eyes with small pupils increase the depth of field, rendering large accommodative amplitudes unnecessary. The need for accommodation would be further reduced if early mammals were active in mesopic or scotopic conditions because focusing over large distances may be less important under low light levels. As such, the absence of scleral ossicles in mammals, and their reliance on lens accommodation, would be a by-product of the miniaturization that occurred in basal mammals and their immediate ancestors, but further testing of this hypothesis is necessary.

Because the members of Caseasauria and Edaphosauridae are predominantly herbivorous, it is also tempting to speculate that the potential loss of scleral elements in the clades may have been correlated with the evolution of herbivory. However, the absence of scleral ossicles in the carnivorous eothyridid caseasaurs, as well as the fact that scleral ossicles are known to occur in several members of Anomodontia (the most diverse clade of herbivorous nonmammalian synapsids) make such a correlation seem unlikely.

The phylogenetic placement of *Tritylodon longaevus* and its implications for the ancestral activity pattern of mammals

Tritylodontidae is a clade of derived nonmammalian cynodonts known from near the Triassic-Jurassic boundary to the Early Cretaceous [45-47]. Members of the clade are noteworthy for their superficially rodent-like enlarged incisors and very mammal-like skulls and postcranial skeletons. The relationship of tritylodontids to other cynodonts has been a source of uncertainty for some time, with two major hypotheses being advanced. The first of these posits that tritylodontids are highly derived cynognathians, specifically a subclade of traversodontids [16, 33, 48-57]. The alternative hypothesis places tritylodontids among advanced probainognathians, usually very close to basal mammals [29, 31, 32, 37, 58-63]. Because *Tritylodon longaevus* is the only nonmammalian cynodont included in our analysis, the question of whether it is a cynognathian or probainognathian does not directly affect our specific results regarding its diel activity pattern. However, both hypotheses have important implications for both the distribution of scleral elements among cynodonts and the ancestral diel activity pattern of mammals.

When discussing the distribution of scleral elements in Synapsida (above), we assumed that *Tritylodon* (and by extension Tritylodontidae) is part of Cynognathia. If this is the case, then *Tritylodon* has only limited relevance to the specific problem of the diel activity patterns of basal mammals because Cynognathia is a completely extinct clade with no living descendants. At best, it would demonstrate that at least some Jurassic cynodonts with superficially mammalian morphologies were capable of nocturnal activity, raising the possibility that this behavior pattern was widespread among cynodonts. Similarly, although *Tritylodon* would show that scleral elements may have been present in the common ancestor of Eucynodontia (i.e., Cynognathia + Probainognathia), it would not speak to whether the loss of scleral elements was a probainognathian synapomorphy or something that occurred after the divergence of the probainognathian lineage.

The implications are more interesting if *Tritylodon* and other tritylodontids are members of Probainognathia. Analyses that have recovered Tritylodontidae within Probainognathia typically place it very close to Mammalia [28]. The presence of scleral ossicles in a member of such a crownward clade would suggest that they were not lost until late in probainognathian history, perhaps at or near the origin of mammals. It would also raise the probability of finding scleral rings in other probainognathian taxa, which would be significant because it would allow assessment of the diel activity patterns of other taxa close to the ancestors of mammals. More importantly, if tritylodontids were nocturnal and are closely related to mammals, it would suggest that nocturnality was well established in derived probainognathians, and that the common ancestor of mammals likely inherited this activity pattern from its own ancestors. In turn, this would imply that many of the distinctive features of mammals (e.g. relatively large brain, distinctive organization of the circadian system, unusual properties of the eye) did not evolve because of a shift to nocturnal activity in basal mammals. Instead, if they are related to nocturnality, they would represent refined adaptations to this temporal niche in animals whose ancestors had already occupied it.

Ancestral state reconstruction of diel activity patterns in nonmammalian synapsids

A long term goal of our project is to reconstruct the evolution of diel activity patterns in synapsids. The current dataset contains information on probabilistic estimates of diel activity in

24 species. This is a small sample, but it represents the majority of major clades within the assemblage of non-mammalian synapsids. Thus, we began to explore the potential macroevolutionary implications of the distribution of diel activity patterns, well aware that such an analysis is preliminary. Nevertheless it may help in testing existing hypotheses and stimulating new research.

We estimated the ancestral state for diel activity patterns in nonmammalian synapsids with maximum likelihood and Bayesian techniques. First, we evaluated the trait distribution across the tree (see Figure 4 in the main manuscript) in the light of transition rates and found that a model with all transition rates different (ARD) does not explain the current data better than a model with all rates equal (ER). The likelihood ratio test of the log-likelihoods for ER and ARD models obtained with the ace() function of the ‘ape’ package [64] for R [65] suggests that the ER model cannot be rejected (P=0.32). These calculations were performed with the original coding, meaning that trait reconstructions did not reflect uncertainty in optimal lambda used in phylogenetic flexible discriminant analysis or ambiguity in species averages. In the original coding *Tiarajudens eccentricus* was scored as scotopic, *Titanophoneus potens* as mesopic, and *Cyonosaurus* spp. as photopic. Alternate coding of the traits (*Tiarajudens eccentricus* mesopic, *Titanophoneus potens* and *Cyonosaurus* spp. scotopic) resulted in P=0.09, suggesting that different rates may not be fully excluded. The likelihood ratio test performed on log-likelihoods from BayesTraits [66]; software is available from www.evolution.rdg.ac.uk) with multistate traits for the three ambiguous taxa also indicates that the ER model may fit the current data better (P=0.22). Therefore, we performed maximum likelihood reconstructions under this model.

Reconstructions of the ancestral nodes indicate a nocturnal ancestry of synapsids. Maximum likelihood estimates obtained from ace() show support for scotopic ocular image formation

(86.12% with original coding and 81.1% with alternate coding). BayesTraits (maximum likelihood) supported scotopic ocular image formation with original, alternate, and multistate coding (93.33%, 86.6%, and 89.9% respectively). Ace() also yielded support for scotopic ocular image formation at the therapsid node with original and alternate coding (70.2% and 45.6%, respectively), yet BayesTraits yielded conflicting results. With original and multistate coding, BayesTraits yielded support for a scotopic therapsid node (91.6% and 69.6% respectively) but supported a mesopic ancestral state with the alternate coding (62.4%). Figure S2 illustrates the reconstructed ancestral states across nonmammalian synapsids calculated with ace() performed with the original coding.

We can also present Bayesian support for a nocturnal origin of synapsids, but it is important to note that this result depends on the choice of parameter settings. First, we assumed equal transition rates between different states, as suggested by the maximum likelihood results, and applied a uniform prior with 0 and 0.4 as lower and upper bounds (note that maximum likelihood results suggested a transition rate of 0.25 for the ER model; in the ARD model the six transition rates varied from 0-0.32). Setting the deviation rate to 1.5 yielded an appropriate acceptance rate. On the basis of a run with 1000000 generations and burn-in removal (25% of generations were removed) we found that nocturnality at the base of synapsids is currently the favored trait (~59-69%, depending on choice of coding). This result is similar to the maximum likelihood result, which may not be surprising given the narrow prior bounds. Support for this reconstruction is weakened when the upper bound of the prior is increased or a hyperprior is applied. This demonstrates that ancestral state reconstructions of diel activity patterns require further investigation and more detailed taxon sampling, even though current data point towards nocturnality being the ancestral character state for synapsids.

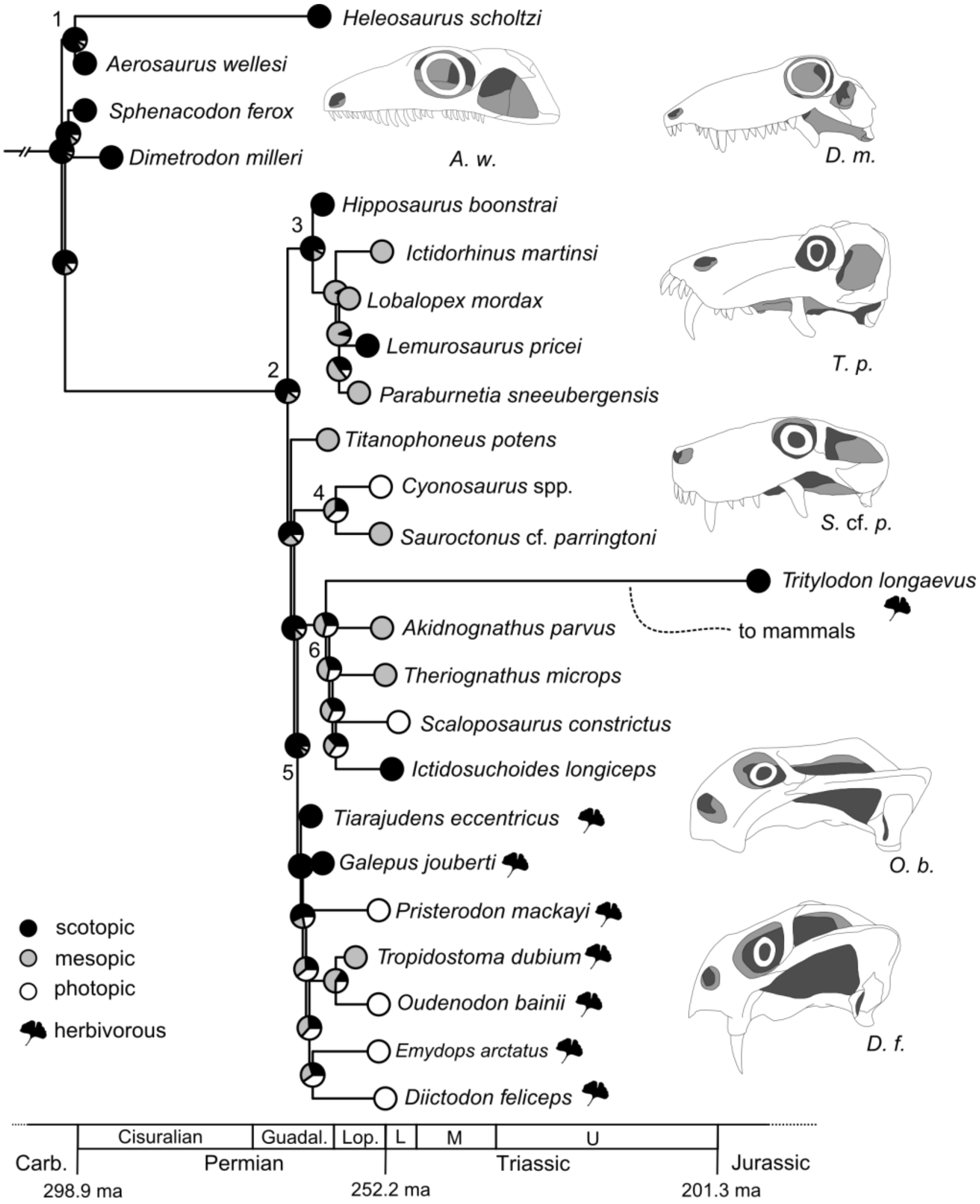

Fig. S2. Maximum likelihood reconstructions of ocular image formation in nonmammalian synapsids, obtained from the ace() function in the ‘ape’ package for R [64, 65] with original coding of traits (see text for further explanation). Preliminary results from maximum likelihood and Bayesian methods cannot exclude nocturnality as the ancestral character state for synapsids, but further studies are needed to better characterize the evolution of diel activity patterns in the clade. 1 = Varanopidae, 2 = Sphenacodontidae, 3 = Biarmosuchia, 4 = Gorgonopsia, 5 = Anomodontia, 6 = Therocephalia. *Titanophoneus potens* is a member of Dinocephalia, and *Tritylodon longaevus* is a member of Cynodontia.

Background on the methodological approach for inferring diel activity patterns in the fossil record and a discussion of previous criticism

The inference of ecology and behavior on the basis of morphology is a very challenging undertaking [67]. Requirements for a reliable inference include a solid understanding of the links between form, function, performance, and ecology, along with statistical control of phylogenetic covariance. It is an advantage to study morphological systems that can be analyzed from a physical perspective, and the most promising results seem to be achieved when general predictions of ecology and behavior are sought [68]. The vertebrate eye fits these criteria well and provides a rich system for quantitative, physics-based inferences. With that in mind, Schmitz and Motani [69] made a first attempt to explore the possible activity patterns of Mesozoic archosaurs and found strong indications that an unexpectedly large proportion of taxa had scleral ring and eye socket morphologies that were consistent with activity in scotopic conditions. In a subsequent comment-response exchange [70, 71] many additional details of the approach and underlying assumptions were explained, and we continue this exposition here in more depth. Specifically, we address major points of previous comments that targeted the correlation between osteological dimensions and soft-tissue structures of the eye, the use and calibration of prior probabilities, and the interpretation of fossils that are outside the range of living species. In brief, the concerns that were previously raised are unwarranted because the correlation of hard- and soft-tissues of the eyes is well understood, the priors are well-calibrated and their use biologically justified, and the interpretation of fossils outside the extant discriminant space range is functionally and methodologically acceptable. Nevertheless, all three points are central to the general approach to and the difficulties of inferring ecology and behavior in the fossil record. We think that this section will be a useful resource for other functional studies, including those addressing questions outside the system of the vertebrate eye. We outline further details of the approach and indicate possible pathways for future studies that would likely improve the current method.

The fossil record largely lacks soft tissue structures. Many functions are performed by non-mineralized tissues and therefore it is important to identify osteological proxies that can be used in lieu of soft-tissues. In general, the correlation between skeletal and non-mineralized tissue of the amniote eye is well-explored. The linkages between optical parameters such as aperture or focal length and morphological structures of the eyes are well documented, for both soft-tissue and skeletal traits [43, 72-75], even though more data are desirable.

Available data suggest strong correlations between two of the main optical parameters of eyes, posterior nodal distance and aperture [76], and two linear dimensions of eyeballs, axial length and lens diameter. Axial length is a proxy for posterior nodal distance and lens diameter is a proxy for the maximum aperture [43]. Both posterior nodal distance and aperture are important for estimating the light sensitivity of the optical system of the eye. The correlations were tested with data from species spanning nearly all major groups of vertebrates (mammals, birds, lizards and one amphibian and teleost each), indicating that the identified correlations potentially may be generalizable. Cornea diameter is another possible proxy for the size of the aperture, but thorough investigations of the correlation between these two structures are currently unavailable in the literature. It would be beneficial to have data for a much greater number of species in order to better understand possible phylogenetic differences, which will help to establish more accurate model parameters. Although proxies for posterior nodal distance and aperture are available, another optically relevant trait, the total number of photoreceptors in the eye, needs more attention. So far eye diameter and retinal area have simply been assumed to be good proxies [77].

Even though a tight correlation between eye diameter, retinal area, and the total number of photoreceptors seems intuitive, the field is lacking a thorough, quantitative analysis of this correlation.

Concerning the utility of skeletal features for estimating soft tissue parameters, the scleral ring and the bony eye socket itself provide good starting points. Orbit length and orbit height provide estimates of the equatorial eye diameter as studies on birds [43, 74] and lizards [75] have shown. Data from Schultz [72] strongly suggest a tight correlation between eye socket and eyeball volume in primates (Figure S3), and the same pattern was corroborated by linear dimensions of the eye and the orbit in primates [73]. Published data on teleosts, amphibians, non-primate mammals, and crocodylians are unavailable. Axial length of the eye, i.e., the distance from the cornea to the posterior pole, or the back of the eye can be estimated by the outer diameter of the scleral ring [43]. At first glance this may seem counterintuitive, especially given that these two dimensions are perpendicular to each other. However, eye ellipticity, the ratio of equatorial diameter to axial length, has low variability, hence the tight correlation between outer scleral ring diameter and axial length is not surprising [43]. Orbit depth may be another proxy for the axial length of the eye [43, 74-76, 79] yet data on birds indicate a fairly high degree of variability [43]. This variability is possibly tied to variance in the degree of ossification of the braincase and interorbital septum; influences from variable cross-sectional diameters of eye and jaw muscles cannot be excluded either. The orbital rim and eye socket are subject to influences from functional systems other than vision. Further data are needed to better understand how orbit shape may be influenced by the size of jaw muscles, or by the presence of supraorbital salt glands in diving birds. The scleral ring, a skeletal structure that is present within the eye, may be less prone to external, non-visual influences. In addition to eye axial length the external diameter of the scleral ring is also correlated with the equatorial eye diameter [43, 74, 75]. The internal diameter of the ring is linked with the equatorial lens diameter and aperture size, as indicated by data on birds [43]. Despite some shortcomings, the current data suggest strong correlations between eye socket, scleral ring, and eyeball dimensions. It should also be noted that possible phylogenetic differences in eye shape in terms of soft- and hard-tissue correlation, for example between birds and lizards, are at least partially accounted for in the discriminant analysis because the approach developed by Motani and Schmitz [80] incorporates phylogenetic covariance during the classification process.

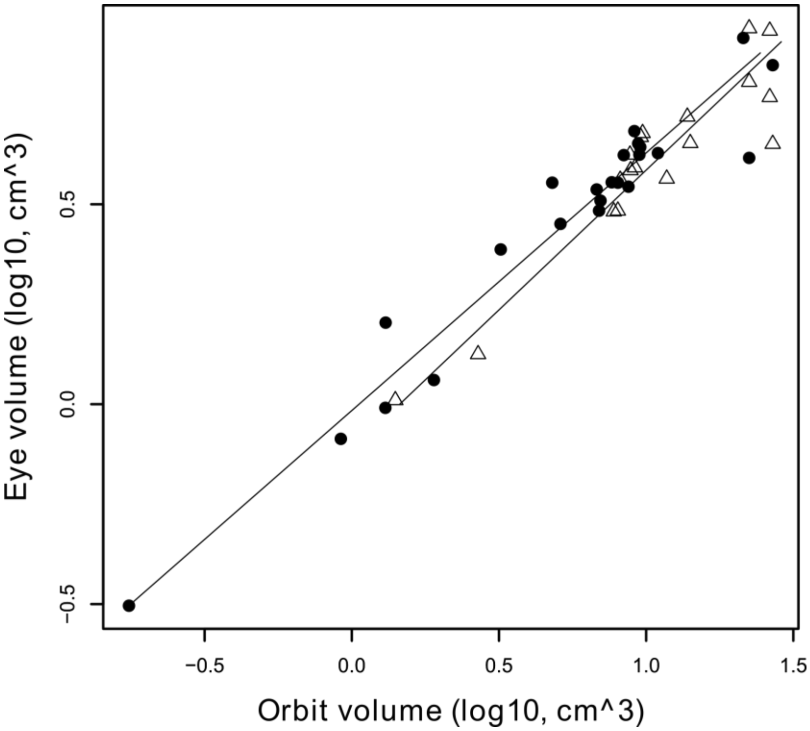

Fig. S3. A plot of eye volume against eye socket volume demonstrating the correlation between skeletal features and eyeball soft tissues in primates. Circles represent species averages of adult females, triangles are adult males, derived from data in [72]. Both slopes display negative allometry (males: 0.70, females: 0.65), but differences in slope as well as the intercepts (-0.11 and -0.02, respectively) are not significant. Lines were fitted using the standardized major axis technique [81]. Note the high R-squared values for both fitted lines (males: 0.87, females: 0.94).

The availability of optically relevant skeletal features makes it possible to quantitatively investigate the possible optical function of the eyes of extinct vertebrates. A traditional and widely used statistical method, discriminant analysis, was recently applied for the first time to this system [69, 71, 78, 80, 82]. Discriminant analysis provides probabilistic inferences as opposed to the frequently used visual inspection of the pattern of morphospace occupation. Inferences of a discriminant analysis should not be mistaken as definitive. In contrast, the model-based, probabilistic inference with clearly articulated assumptions is an advantage of this approach, because it allows for continued testing of results and refining of model parameters in future studies. The uncertainty of the classification results is directly accessible because the probabilities of alternate states for the character of diel activity patterns can be explicitly reported. Phylogenetic flexible discriminant analysis relies on several components and assumptions.

The discrimination rules of the discriminant analysis are established on the basis of a discriminant space, which is based on morphological and ecological traits. The scleral ring and orbit measurements used in this study represent 164 extant saurians from a broad phylogenetic sample. The diel activity patterns of the species in the data set are generally well-known and they are documented with references to the primary literature and well-resourced guide books [82]. Data on diel activity patterns are often anecdotal; quantitative data are virtually absent. It will be important to continuously update the dataset as new data become available. An important characteristic of the dataset is that it only includes terrestrial species. Aquatic species that use vision under water have different optics and experience an alternative selective regime that competes with the physical characteristics of the nocturnal/diurnal light environment. Therefore, they are not directly comparable. Future studies should aim to increase the sample of terrestrial taxa used to construct the discriminant space. Although the major characteristics of the discriminant space are not expected to change, additional data may be helpful for correctly classifying unknown samples that plot close to the current delineations between different categories. The addition of more species should go hand-in-hand with a continuous revision of the underlying phylogenetic framework. These extensions are a large undertaking that will take several years, and thus are beyond the scope of this contribution.

When classifying fossils or unknown samples the application of prior probabilities requires special attention, because priors influence the classification result. If not specified, equal priors are assumed and accordingly the discriminant analysis aims to classify unknown samples into equal proportions of inferred nocturnal, diurnal, and cathemeral species. Available data suggest that the proportions of different activity patterns are not equally distributed in the extant biosphere [69] and there is no reason to doubt that this ecological property of the living world did not exist in the past. While the data for estimating the proportions of activity patterns (n=1401 species) are not from the primary literature (Animal Diversity Web, ADW; animaldiversity.ummz.umich.edu/), they seem to agree well with other datasets that are fully referenced and peer-reviewed [71]. For example, the mammal data used for calibrating the prior correspond to the PanTHERIA [83] database once differences in the categories used in the classifications of diel activity patterns are accounted for. The proportion of nocturnal mammals is estimated at 45.7% (ADW) and 46.8% (PanTHERIA), diurnal mammals comprise 26.8 and 23.1%, respectively, whereas the cathemeral proportion is estimated at 27.5 and 30.1%. Hence, criticisms of this approach focused on the sources of diel activity data are not well-justified. However, we do recognize the need for additional quantitative data on diel activity patterns: morphological data can be collected for a large number of species in existing museum collections, but the ecologies of poorly known species frequently are a limiting factor. It is surprising that there are very few basic natural history data available even for many well-known species.

The fossil record provides the means to enrich our knowledge of the total morphospace occupied through the history of life. We explored the scleral ring and orbit length morphospace in Figs. 2a-c, showing that morphologically synapsids are very similar to lizards and birds, even if slightly larger. However, Fig 2d does not represent a morphospace; instead it is a phylogenetic discriminant space, informed by shape, size, and phylogenetic covariance among the sampled species. It is not surprising that many fossil taxa plot outside the range determined by extant species in the scleral ring and orbit discriminant space and we disagree with the notion to categorically exclude these taxa from any inferential analysis [70]. In this specific case the major reason for synapsids to plot in novel areas of discriminant space is the underlying phylogeny. The phylogenetic flexible discriminant analysis is performed at low lambda-values (0.08), meaning the tree is rescaled with short internal branches and long terminals. Given that the fossil synapsids are the most basal clade in this study and do not extend to the present time, their terminal branches are much shorter than the terminals leading to extant birds and lizards. This ultimately leads to absolutely larger discriminant scores for fossil synapsids. The other source for occupation of novel discriminant space can be traced back to absolute eye size, which has important functional consequences for visual performance [71]. Large eye size benefits both acuity and light sensitivity, performance measures that are needed by species active during the day as well as by those active at night. Functional equivalence would no longer be a given if there is reason to assume that there are fundamental differences in the correlations between hard- and soft-tissue structures of the eye, but there is currently no evidence to suggest this is the case.

However, we do agree that fossils presenting morphologies outside the range of the living world, which does not apply in the case of the synapsid scleral rings and orbits (see above), need very careful investigations. If there is clear evidence that a functional equivalence to extant species is no longer given, an interpretation of the ecological implications of a specific morphology may no longer be warranted.

Overall, the current approach yields a correct classification of unknown samples of approximately 80%, which means that on average 1 in 5 inferences of diel activity pattern of fossils is unreliable. The misclassification rate was determined by taking the extant species that were used to establish the discriminant functions, treating them as taxa with unknown category, calculating posterior classifications and comparing the results with the true category. Most misclassifications (~70%) are the erroneous inference of diurnal activity patterns, i.e., species that are in fact nocturnal or cathemeral are identified as diurnal. This misclassification bias, combined with the prior favoring of diurnality, make inferences of non-diurnal activity patterns in the fossil record less likely. In other words, the rejection of the null hypothesis (non-mammalian synapsids, or, in a previous study, Mesozoic archosaurs were diurnal) is penalized. Consequently, if nocturnality is inferred for unknown samples the morphological signals must be strong. We acknowledge problems of correctly identifying small cathemeral/crepuscular species, which are often grouped with diurnal species but remain optimistic that the method can be improved in the future.

The assumptions underlying this approach to infer ecology and behavior should be refined and improved continuously, as is the case with any analytical technique. Nevertheless, the methods have already provided important new insights and hypotheses that can be further tested as additional data and/or new analytical approaches become available. The synthesis of complementary data from the extant and fossil biota with modern phylogenetic comparative methods will serve to enrich our understanding of morphological evolution and its possible consequence for functional and ecological diversity including diel activity patterns over the history of life.

Does ontogenetic status bias our estimates of eye light sensitivity?

It is well known that eyes and associated osteological correlates such as bony orbits generally display negative allometry across ontogeny in tetrapods. Because of this, and the fact that our calculations include information on the size of osteological correlates of eye dimensions relative to the overall size of the skull, an important question to consider is whether our results are likely to be biased by the inclusion of juvenile or subadult specimens in our dataset. Here we present estimates of the ontogenetic status of all specimens included in our dataset. We will then consider the implications of these estimates for the issue of potential bias.

Aerosaurus wellesi (Varanopidae): *Aerosaurus wellesi* is represented by one specimen in our dataset, UCMP V2814/40096. This specimen is preserved as a partially articulated skeleton in one of a series of six blocks of sediment collected from UCMP locality V2814 (Camp Quarry). Langston and Reisz [84] (please also see [85]) noted that UCMP 40096 showed signs of skeletal immaturity, and that a second, more fragmentary specimen (UCMP 40097) preserved in the blocks represented an individual that was about twice as large in linear dimensions. Langston and Reisz [84] considered UCMP 40097 to be an adult; therefore we assume that UCMP 40096 had reached approximately 50% of maximum size.

Heleosaurus scholtzi (Varanopidae): *Heleosaurus scholtzi* is represented by one specimen in our data set, SAM-PK-K8305. SAM-PK-K8305 consists of an aggregation of *H. scholtzi* individuals of varying sizes [9], but only one individual includes a skull and scleral ring that is sufficiently complete to allow measurement. A complete adult skull is not known for *H. scholtzi*. However, the largest available specimens (SAM-PK-1070, see [86]; and the largest individual of SAM-PK-K8035) suggest basal skull lengths of over 50mm, and probably in the range of 60mm-65mm. We used the latter values as a conservative estimate of maximum size for *H. scholtzi* (i.e., one that would bias us towards finding an earlier ontogenetic stage for the included individual), which suggests that the individual in our dataset is 61%-66% of maximum size. The largest specimen of SAM-PK-8035 does not preserve a complete snout. However, the ratio of orbit length to the length from the nasofrontal suture to the posterior edge of the skull roof in that specimen is 0.75, whereas it is 0.78 in the specimen included in the dataset. This implies that the eyes of the included individual were likely very close in relative size to those of an adult individual.

Dimetrodon milleri (Sphenacodontidae): *Dimetrodon milleri* is represented by one specimen in our dataset, MCZ 2028. Very limited cranial remains are available for *D. milleri* [17, 87, 88], and MCZ 2028 is by far the most complete skull. Brink and Reisz [87] described a braincase of a second, somewhat larger specimen (MCZ 1365) of *D. milleri*, and they included a figure of the specimen in ventral view that shows that it extends from about the posterior edge of the lateral pterygoid flanges to the anterior end of the vomer. Assuming the palate of *D. milleri* had proportions similar to the skull of *D. limbatus* figured in Plate 13 of [87], we estimate that the basal skull length of MCZ 1365 was approximately 249mm. We used this length to estimate that MCZ 2028 was approximately 72% of maximum size.

Sphenacodon ferox (Sphenacodontidae): *Sphenaocodon ferox* is represented by one specimen in our dataset, NMMNH P-55367. There are few complete or nearly complete skulls of

Sphenacodon ferox (see review in [11]). The largest specimens they report are FMNH UC 35 and NMMNH P-55367, and these are of nearly the same size. Therefore, we estimate that NMMNH P-55367 is about 100% of maximum size.

Hipposaurus boonstrai (Biarmosuchia): *Hipposaurus boonstrai* is represented by one specimen in our dataset, SAM-PK-9081. Sidor [89] listed three specimens of *Hipposaurus*, of which SAM-PK-9081 is the largest. Therefore we consider the specimen to be approximately 100% of maximum size.

Ictidorhinus martinsi (Biarmosuchia): *Ictidorhinus martinsi* is represented by one specimen in our dataset, AMMH FARB 5226. This is the only known specimen of *I. martinsi*, making its ontogenetic stage uncertain. Sigogneau-Russell [38] suggested that the specimen might be a sub-adult based on the incomplete ossification of the anterior braincase. Therefore, we tentatively consider AMNH FARB 5226 to represent a sub-adult, although we do not know what fraction of maximum size it had attained.

Lemurosaurus pricei (Biarmosuchia): *Lemurosaurus pricei* is represented by one specimen in our dataset, NMQR 1702. NMQR 1702 is one of two known specimens of *L. pricei,* and Sidor and Welmann [90] state that it is the larger of the two (~150% the size of the other specimen). Therefore, we consider NMQR 1702 to be approximately 100% of maximum size.

Lobalopex mordax (Biarmosuchia): *Lobalopex mordax* is represented by one specimen in our dataset, CGP/1/61, which is the only known specimen of the species. This fact makes an exact estimate of its ontogenetic stage difficult. The relatively large size of the specimen and its proportions (e.g., see reconstruction in [91] lead us to conclude that it is unlikely to be a very young juvenile. Therefore, we tentatively consider CGP/1/61 to represent an adult.

Paraburnetia sneeubergensis (Biarmosuchia): *Paraburnetia sneeubergensis* is represented by one specimen in our dataset, SAM-PK-K10037. This is the only known specimen of the species, making an estimate of its ontogenetic stage uncertain. The skull is highly ornamented [92], which would be unexpected for a very young individual. Therefore, we tentatively consider SAM-PK-K10037 to represent an adult.

Titanophoneus potens (Dinocephalia): *Titanophoneus potens* is represented by one specimen in our dataset, PIN 157/1. Two well preserved skulls of *T. potens* are known, PIN 157/1 and PIN 157/3 [5, 93], of which PIN 157/1 is the smaller. Based on figures in [5], PIN 157/3 appears to have a basal skull length of about 500mm, and we used this value as a maximum size in the calculation of the ontogenetic stage of PIN 157/1. We estimate that PIN 157/1 is 78% of maximum size.

Cyonosaurus spp. (Gorgonopsia): We refer four specimens in our dataset to the genus *Cyonosaurus*, BP/1/2598, SAM-PK-K7594, SAM-PK-8790, and SAM-PK-K10033. Various measurements exist in the literature for *Cyonosaurus* specimens. None of the specimens that have skull length measures in [94] exceeds 200mm, and the largest specimen in [89] is 207mm long. Sigogneau [95] lists measurements for several *Cyonosaurus* specimens, the largest of which (BP/1/397) is 226mm. Because of the taxonomic uncertainty that continues to surround gorgonopsians, we used this as the maximum size value in the calculations for all of our specimens. We conclude that BP/1/2598 is 61% of adult size, SAM-PK-K7594 is 46% of maximum size, SAM-PK-8790 is 73% of maximum size , and SAM-PK-K10033 94% of maximum size.

Sauroctonus cf. *parringtoni* (Gorgonopsia): We refer two specimens in our dataset to *Sauroctonus* cf. *parringtoni*, SAM-PK-K10034 and SAM-PK-K10035. Gebauer [94, 96] notes specimens in the genus *Sauroctonus* that have skull lengths in the range of 225mm-250mm.

Likewise, her character state codings for *Sauroctonus* in her phylogenetic analysis [94] imply lengths up to 300mm. We used 250mm and 300mm to calculate an estimated range of ontogenetic stages for each specimen. We conclude that SAM-PK-K10034 is 49% to 59% of maximum size, and SAM-PK-K10035 is 64% to 77% of maximum size.

Diictodon feliceps (Anomodontia): There are three *Diictodon feliceps* specimens in our dataset, CGP/1/1582, CGP W 12, and SAM-PK-K10703. In our observations, large specimens of *Diictodon* typically reach basal skull lengths of about 12cm (e.g., SAM-PK-K7019 117mm; SAM-PK-K6929 118mm; SAM-PK-K6818 120mm; UCMP V3691/41757 123mm), and we used 123mm as the maximum size in our calculations of ontogenetic stage. We conclude that CGP/1/1582 is 58% of maximum size, CGP W 12 is 45% of maximum size, and SAM-PK-K10703 is 60% of maximum size.

Emydops arctatus (Anomodontia): One specimen in our dataset (SAM-PK-10703) represents *Emydops arctatus*. In our observations, large specimens of *E. arctatus* reach basal skull lengths of 6cm-7cm (e.g., BP/1/262 61mm; SAM-PK-708 61mm; NHMUK PV R4951 67mm; CGP CM86-600 66mm; MMK 4165 72.5mm), and we used 72.5mm as the maximum size in our calculations of ontogenetic stage. Therefore, we consider SAM-PK-K10703 to be 65% of maximum size.

Galepus jouberti (Anomodontia): Only one specimen of the basal anomodont *Galepus jouberti* is known [7, 97], AMNH FARB 5241. The specimen is preserved as a natural mold, and it does not show obvious characters that assist in assessing its ontogenetic stage. Botha-Brink and Angielczyk [98] showed that a specimen of the similar basal anomodont *Galeops* (SAM-PK-12261) with a skull length about 30% greater than AMNH FARB 5241 had multiple annuli preserved in its postcranial skeleton. Based on this observation, we infer that AMNH FARB 5241 is unlikely to be a very young juvenile, although we cannot state its ontogenetic stage with certainty.

Oudenodon bainii (Anomodontia): Three specimens in our dataset, BP/1/6974, SAM-PK-6045, and SAM-PK-K10124 can be referred with certainty to *Oudenodon bainii*, and a fourth (CGP JW 23) likely is part of this species as well. Large specimens of *Oudenodon bainii* reach basal skull lengths of 250mm-270mm (e.g.; BP/1/730 254mm; SAM-PK-K7493 270mm; NHCC LB353 255mm; [99] reported 272mm for BP/1/732), with rare specimens exceeding this size (e.g., TM 262 and NMNH 24625 both have basal lengths of about 300mm). We used 300mm as the maximum size in our calculations of ontogenetic stage. We estimate that BP/1/6974 is 48% of maximum size, SAM-PK-6045 is 31% of maximum size, SAM-PK-K10124is 32% of maximum size, and CGP JW 23 is about 32% of maximum size. SAM-PK-6045 and SAM-PK-K10124 are noteworthy among the anomodonts we sampled in having a “juvenile” appearance, with relatively large orbits for their size compared to larger specimens of *O. bainii*.

Pristerodon mackayi (Anomodontia): *Pristerodon mackayi* is represented by one specimen in our dataset, SAM-PK-K10997. Most of the specimens of *Pristerodon* that we have personally examined have basal skull lengths of less than 80mm. Keyser [100] reported some specimens that exceed 90mm, and we have used the largest of these (CGP M 467, 98mm) for the maximum size in our calculations. We estimate that SAM-PK-K10997 is 49% of adult size.

Tiarajudens eccentricus (Anomodontia): Only one specimen of *Tiarajudens eccentricus* is known, UFRGS PV393P, making it difficult to establish its precise ontogenetic stage. However, the specimen shows some characters that would be unexpected in a very young juvenile, such as heavily worn teeth and erupting replacement teeth [27]. Likewise, if the large sabre-like canines were display structures [27], they would be unexpected to be so strongly developed in a young juvenile. Therefore, we conclude that UFRGS PV393P most likely represents an adult individual.

Tropidostoma dubium (Anomodontia): *Tropidostoma dubium* is represented by two specimens in our dataset, CGP/1/2173 and SAM-PK-K8654. Most specimens of *Tropidostoma* are less than 200mm long [101], but a few specimens exceed 200mm (e.g., SAM-PK-2359 229mm; SAM-PK-K9960 209mm; CGP RS 327 227mm; CGP RMS 183 204mm). We used 229mm as a maximum size value in our calculations of ontogenetic stage. We conclude that CGP/1/2173 is 51% of maximum size and SAM-PK-K8654 is 41% of maximum size.

Akidnognathus parvus (Therocephalia): *Akidnognathus parvus* is represented by one specimen in our dataset, SAM-PK-4021. Huttenlocker [102] lists 150mm as the maximum skull length for this species, and we used this value in our calculations of ontogenetic stage. We estimate that SAM-PK-4021 is 69% of maximum size.

Ictidosuchoides longiceps (Therocephalia): *Ictidosuchoides longiceps* is represented by two specimens in our dataset, BP/1/218 and BP/1/223. Huttenlocker [102] lists 146mm as the maximum skull length for this species, and we used this value in our calculations of ontogenetic stage. We estimate that BP/1/218 is 69% of maximum size and BP/1/223 is 55% of maximum size.

Scaloposaurus constrictus (Therocephalia). *Scaloposaurus constrictus* is represented by two specimens in our dataset, BP/1/5220 and SAM-PK-K10980. Huttenlocker [102] lists 67mm as the maximum skull length for this species, and we used this value in our calculations of ontogenetic stage. We estimate that BP/1/5220 is 81% of maximum size and SAM-PK-K10980 is 83% of maximum size.

Theriognathus microps (Therocephalia): *Theriognathus microps* is represented by two specimens in our dataset, AMNH FARB 8226 and BP/1/717. Huttenlocker [102] lists 336mm as the maximum skull length for this species, and we used this value in our calculations of ontogenetic stage. We estimate that AMNH FARB 8226 is 40% of maximum size and BP/1/717 is 72% of maximum size.

Tritylodon longaevus (Cynodontia): *Tritylodon longaevus* is represented by one specimen in our dataset, BP/1/5109. We surveyed the literature to estimate the maximum size for the species. The largest value we found was a specimen described by Fourie [103] that has a maximum skull length of 250mm. Fourie [103] did not give a basal skull length for this specimen, but given the shape of the skull of *T. longaevus* the maximum skull length should be only slightly longer. Likewise, it should be conservative in the current context because it will cause us to underestimate the ontogenetic stage of BP/1/5109. Using this value for maximum size, we conclude that BP/1/5109 is 24% of maximum size.

Because scleral rings are rarely preserved in fossil synapsids, it is difficult to gain a clear picture of their patterns of intraspecific allometry. However, six species are represented by multiple individuals in our dataset, and these provide an opportunity to examine whether ontogenetic stage appears to be biasing our results. Juvenile tetrapods tend to have relatively larger eyes (and associated dimensions of osteological correlates) than adults, so it would be particularly worrisome if smaller individuals are reconstructed as nocturnal and larger individuals are reconstructed as diurnal. Consistent results across ontogenetic stages or no relationship between ontogenetic stage and reconstructed diel activity pattern would provide some confidence that we are unlikely to incorrectly estimate a nocturnal activity pattern simply because we happened to sample a small individual.

Three anomodont species are represented by multiple specimens in the dataset, *Diictodon feliceps*, *Tropidostoma dubium*, and *Oudenodon bainii*. Using average values for the species, we reconstructed *D. feliceps* as diurnal. We estimated that the three *D. feliceps* individuals in our dataset range from about 45% to 60% of maximum size. When considered individually, the two larger specimens are reconstructed as diurnal, whereas the smallest individual is reconstructed as nocturnal. This could indicate a bias for recovering a nocturnal activity pattern for young individuals. However, we do not think this is a problem for the specific case of *D. feliceps* because the larger two specimens and the species average data suggest diurnal habits, which is a conservative conclusion because our null hypothesis is that basal synapsids were diurnal.

Tropidostoma dubium is represented by two specimens in the dataset, which we estimate to be 41% to 51% of maximum size. The average species data for *T. dubium* suggested a cathemeral activity pattern, as did the data for the two individual specimens. At least within the size range we were able to sample, *T. dubium* has a stable reconstructed diel activity pattern regardless of size.

Oudenodon bainii is represented by three definite specimens in the dataset, as well as a fourth specimen that most likely is part of this species. The specimens range from 31% to 48% of maximum size. When average data for the species are used, *O. bainii* is reconstructed as diurnal. The three specimens that definitely represent *O. bainii*, including the two smallest specimens, all are reconstructed as diurnal as well. The fourth, less certain specimen (CGP JW 23) is reconstructed as cathemeral. However, this snout of this specimen is somewhat damaged. Therefore, the basal skull length we used is likely an underestimate, making the orbit and scleral ring dimensions seem artificially larger. Based on these results, we consider well preserved specimens of *O. bainii*, including those with “juvenile” skull proportions, to not be biased towards incorrectly suggesting a nocturnal activity pattern.

Three therocephalians are represented by multiple specimens in our dataset, *Theriognathus* *microps*, *Scaloposaurus constrictus*, and *Ictidosuchoides longiceps*. We estimated that the two specimens of *T. microps* are 40% and 72% of adult size, and when species average data are used, the taxon is reconstructed as cathemeral. Interestingly, when data for the individual specimens are analyzed, the smaller of these specimens (AMNH FARB 8226) is reconstructed as diurnal and the larger specimen is reconstructed as cathemeral, a pattern opposite of what would be expected if we were biased towards finding nocturnal habits for smaller individuals. This pattern may be a result of the absolute size of orbit and scleral rings: larger overall eye size may lead to cathemeral classification.

Scaloposaurus constrictus is represented by two specimens in our dataset. We estimated these specimens to be 81% and 83% of maximum size, and the species was consistently reconstructed as diurnal regardless of whether we used species average data or the measurements for the individual specimens. Although the two specimens are both close to maximum size, it is important to note that *S. constrictus* is a relatively small species, and thus might be expected to have relatively large eyes that could bias it towards being reconstructed as nocturnal.

Ictidosuchoides longiceps also is represented by two specimens in our dataset, which we estimated to be 55% and 69% of maximum size. When species average data are used, the species is reconstructed as being nocturnal. However, when the individual specimens are analyzed, one (the smaller) is estimated to be diurnal and the other nocturnal. We suspect that discrepancy is the result of preservation. As preserved, the scleral ring of BP/1/218 (the larger, putatively nocturnal specimen) is broken into multiple sections, and the ring itself is narrow with a wide aperture. In contrast, the scleral ring of BP/1/223 (the smaller, putatively diurnal specimen) is more complete, and the ring itself is wide, with a smaller aperture. We conclude that BP/1/223 more accurately preserves the original morphology of *Ictidosuchoides longiceps*, so there is a good chance that our classification of this species as nocturnal in our main results is in error. However, this error stems from taphonomy, not a bias towards reconstructing younger specimens as nocturnal.

Two gorgonopsians are represented by multiple specimens in our dataset, *Cyonosaurus* spp. and *Sauroctonus* cf. *parringtoni,* and they are the most problematic taxa in our analysis. *Sauroctonus* cf. *parringtoni* is represented by two individuals, one of which are reconstructed as diurnal and one of which is reconstructed as cathemeral (the species is reconstructed as cathemeral when average data are used). The larger of the two specimens (SAM-PK-K10035; 64% to 77% of adult size) is the one reconstructed as cathemeral, so the inconsistency for this taxon does not seem to stem from a bias for classifying younger individuals as nocturnal. SAM-PK-K10034 preserves both the left and right scleral rings. The right one is especially well preserved, and the ring itself is wide with a fairly small aperture. The right scleral ring of SAM-PK-K10035 also is nearly complete, but the ring has a relatively larger aperture and is relatively narrower on average than that of SAM-PK-K10034. Gorgonopsian taxonomy is somewhat confused, so the possibility exists that this is a real difference and that we inadvertently lumped together individuals of two different species characterized by different diel activity patterns. The specimens are similar enough that we think this is unlikely, however, and we strongly suspect that they represent a single taxon. An alternative hypothesis is that the difference stems from preservation. This hypothesis is supported by the fact that the width of the ring is more variable in SAM-PK-K10035 than in SAM-PK-K10034. Therefore, the situation here seems to be very similar to that for *I. longiceps,* and we think there is a good chance that our classification of this species as cathemeral in our main results is in error.

Cyonosaurus is represented by four individuals that may belong to at least two species. We estimate that these specimens range from 46% to 94% of maximum size. Two of the specimens are classified as diurnal, one as nocturnal, and one as cathemeral, and when average data are used *Cyonosaurus* is classified as diurnal. There does not seem to be an obvious bias towards reconstructing younger specimens as nocturnal because both the largest and smallest specimens were classified as diurnal. As with *Sauroctonus* and *Ictidosuchoides*, we suspect the discrepancies for *Cyonosaurus* likely stem from preservation. Looking across the four specimens, the preserved scleral rings range from a relatively narrow shape with a wide aperture (BP/1/2598) to seemingly wider with a small aperture (SAM-PK-K10333). They also vary in their quality of preservation, from the very complete ring of BP/1/2598 to the poorly preserved ring of SAM-PK8790. Based on our observations of the specimens, we posit that SAM-PK-K10333 and SAM-PK-K7594 most accurately preserve the morphology of the scleral ring. Both of these specimens are classsified as diurnal, as is the case when average data are used, so we conclude that *Cyonosaurus* is correctly classified in our primary results. Moreover, SAM-PK-K7594 is the smallest of the four specimens, so there does not seem to be an undue bias towards reconstructing younger specimens as nocturnal.

Taken together, our estimates of ontogenetic stage for all of our included specimens and our examination of the results in cases where species are represented by multiple specimens indicate that our nocturnal classifications for some synapsid taxa are not artifacts of examining juvenile specimens. The estimates of percentage of maximum size show that very few of the specimens in our dataset are very young individuals. Similarly, when we have multiple specimens available for a species, we seem to be able to classify them consistently across body sizes as long as they are well preserved. Preservation can have an effect on our results, but these cases seem to be easy to identify when comparative material is available.

Is the sail of *Dimetrodon* incompatible with nocturnal activity patterns?

Arguably the most distinctive structures evolved by any nonmammalian synapsids are the dorsal sails found in sphenacodontids and edaphosaurids, which are formed by hyperelongated neural spines of the dorsal vertebrae. There is a long history of speculation about the function and appearance of the sail in life [104-107]. In general, hypotheses about the function of the sail fall into five main categories: 1) biomechanics [87, 108, 109]; 2) thermoregulation [110-119]; 3) display [120, 121]; 4) defense [111, 122], and 5) fat storage [112]. Given that the proposed thermoregulatory function of the sail usually has been couched in terms of activity during the day (i.e., the sail as a means for attaining optimum temperatures more quickly or as a means to dump excess heat to the environment), an important question to consider is whether there is compelling evidence that the presence of the sail would preclude a nocturnal activity pattern for *Dimetrodon*. Here we review the debates over the function of the sail in the context of diel activity patterns. Because defensive and fat storage functions have only been proposed in the recent literature for the sails of edaphosaurids, we focus on the thermoregulation, display, and biomechanical hypotheses.

Romer [110] was the first to suggest a thermoregulatory function for the sail of *Dimetrodon*, although he and Rodbard [111] described this function in strictly qualitative terms. The sail was seen as a structure that would greatly increase the surface area of the animal relative to its volume, improving its ability to absorb heat. Moreover, the structure was thought to be well vascularized, with large blood vessels situated in the grooves that extend along most of the anterior and posterior surfaces of the neural spines that comprise the sail [108, 114]. Romer [110] also noted that the sail displayed positive allometry (also see [87, 112], which would allow it to maintain its function as body mass increased in larger individuals and larger species.

Subsequently, a number of authors used modeling approaches with varying assumptions to quantitatively test the effectiveness of the sails of *Dimetrodon* and *Edaphosaurus* as heat exchangers [113, 115-119]. Despite the ubiquity of idea that the sail functioned in thermoregulation, the results of these quantitative studies vary widely. Bramwell and Fellgett [113] concluded that the sail of *Dimetrodon* would have been an efficient heat exchanger both for warming and cooling the animal. Tracy et al. [116] largely agreed, but noted that the sail might have been most important in maintaining a stable body temperature, with the relative significance of its heating and cooling functions varying in relation to the size of the animal in question. Haack [115] suggested that the sail was likely most useful in its warming function and for maintaining a stable body temperature, not cooling, but also concluded that the effect was not as great as previously hypothesized. Florides et al. [118, 119] favored a heating function, but noted that the importance of this function would vary depending on environmental conditions (specifically, they hypothesized that the sail provided the most benefit under cooler conditions and could be a liability under hot conditions). Bennet's [117] study focused on the sail of *Edaphosaurus*, which differs in the details of its anatomy and allometric patterns from that of *Dimetrodon* [87, 112]. He concluded that if the sail was used for thermoregualtion in *Edaphosaurus*, it most likely functioned in cooling.

The lingering uncertainty about the manner in which the sail would have functioned in heat exchange and its effectiveness in that role indicates that a thermoregulatory function is not as definite as often portrayed. In addition, other aspects of a thermoregulatory function for the sail are problematic. For example, Huttenlocker et al.'s [23] examination of the internal structure of the neural spines of *Edaphosaurus* at both macroscopic and microscopic scales suggested that Ricqlès' [114] model of the circulatory organization in the sail of that taxon was not possible.

Similar problems apply to *Dimetrodon.* Huttenlocker et al. [123] noted that the highly vascularized bone tissue of the neural spines of *Dimetrodon* likely was associated with their rapid growth and need not reflect a thermoregulatory function. Rega et al. [109] stated that the lack of vascular canals in the anterior and posterior grooves of the spines called the presence of blood vessels in the grooves into question. Moreover, the presence of two to three large, vertical blood vessels at each vertebral segment in the sails of *Dimetrodon* and *Edaphosaurus* also would have made the sails very vulnerable to injury and would have greatly increased resistance to blood flow [23]. If the blood supply of the sail was instead associated with the superficial skin covering, it would have been much less efficient at raising or lowering the core body temperature of the animal [115].

The evolutionary history of the dorsal sail in edaphosaurids and sphenacodontids also argues against a thermoregulatory function. Huttenlocker et al. [123] noted that some neural spine features associated with the sail in *Dimetrodon*, such as the presence of anterior and posterior grooves and differentiation of the neural spine into a more proximal section that was embedded within the axial musculature and a distal section that extended past the musculature, can be found in other sphenacodontids like *Sphenacodon* that lack hyperelongate neural spines. Given that these taxa fall in a more basal position in sphenacodontid phylogeny [124], the implication is that a more subtle dorsal crest evolved earlier in sphenacodontid history, before it took on the extreme morphology seen in *Dimetrodon*. Tomkins et al. [121] also noted that the extreme dorsal sail morphology in sphenacodontids and edaphosaurids initially evolved in animals with relatively small body sizes (e.g., *Dimetrodon milleri* and *Ianthasaurus hardestiorum*), an observation confirmed by recent phylogenies of the groups [22, 124]. Citing previous modeling experiments, Tomkins et al. [121] raised the issue that the small size of these species would have conferred a low thermal inertia regardless of the presence of dorsal sail, reducing the need for an elaborate heat exchange system. Moreover, the sail could have made them liable to overheating if it was a highly vascularized heat exchanger [121].

We assert that the variable modeling results, problems with the proposed blood supply to the sail, and incompatible evolutionary scenarios call into question the thermoregulatory function of the sail of *Dimetrodon*. If that is the case, then the presence of the sail in *Dimetrodon milleri* need not preclude it being active under scotopic conditions. Furthermore, even if the sail was used for thermoregulation, this fact would presumably have no influence on the diel activity patterns of the other basal synapsids in our dataset because they either lack sails (*Aerosaurus*, *Heleosaurus*) or have only a rudimentary dorsal crest *(Sphenacodon*).

A hypothesized biomechanical function for the sail of *Dimetrodon* predates the thermoregulatory hypothesis. Romer [108] posited that the elongation of the neural spines in basal synapsids formed part of a system for strengthening an otherwise relatively weak vertebral column in animals with long, slender bodies. Romer and Price [87] reiterated this hypothesis, but both Romer [108, 110] and Romer and Price [87] were at a loss as to why such a trend was taken to the extreme observed in *Dimetrodon* and *Edaphosaurus*. When the thermoregulatory hypothesis for the function of the sail came to prominence, the previous suggestions of a biomechanical function for the sail largely fell by the wayside. Recently, however, Huttenlocker et al. [23, 123] and Rega et al. [109] noted a number of problems with the thermoregulatory hypothesis (see above), and have begun to reassess a possible biomechanical role for the sail. In particular, Rega et al. [109] used finite element analysis and data on bone remodeling associated with a microfracture that occurred in a neural spine of the large species *Dimetrodon giganhomogenes* to posit that the dumbbell cross-sectional shape of the neural spines (resulting from the anterior and posterior grooves) was strongly indicative of their being specialized for resisting lateral bending stresses. They also noted that similar morphologies can be found in the dorsal sail of the yellowfin tuna. In that animal the spines are embedded in a dense web of collagen that may function in resisting dorsoventral bending and increasing the efficiency of lateral undulation, and Rega et al. [109] hypothesized that the sail of *Dimetrodon* would have been similar in structure and function. If this is the case, it closely matches Romer's [108] original conception of the construction and function of the sail. Furthermore, a biomechanical function for the sail would be agnostic in the context of diel activity patterns: presumably the sail would function equally well in this role regardless of whether *Dimetrodon* was active during the day or night.

A third function that has been proposed for the sails of basal synapsids is intraspecific display [120, 121]. The information presented in support of this hypothesis largely consists of anecdotal comparisons to various living animals (e.g., Bakker's comparison to the display function of the dorsal crest of *Bos gaurus*; see [125] for more information on this display behavior), although Tomkins et al. [121] noted that the scaling exponent of the sail of *Dimetrodon* was similar to that of antler length relative to shoulder height in cervids. If a display function for the sail of *Dimetrodon* is assumed for the sake of argument, the important question it raises in terms of diel activity patterns is whether such a visual display function would be useful in a low-light setting. Although we cannot directly test the effectiveness of the dorsal sail as a display structure in scotopic conditions, we can ask whether extant nocturnal tetrapods use visual displays for communication. If the answer to the latter question is yes, then we cannot rule out a display function for the sail even if *Dimetrodon* was nocturnal.

There are a number of reports in the literature of visual signaling in extant nocturnal species.

This signaling can be mediated by behavior, aspects of body morphology or coloring, or by combinations of morphology and behavior. Visual signaling and communication by nocturnal frogs [126-132] and birds [133-140] have received significant recent attention, but examples exist for reptiles [141-143] and mammals [144-147] as well. Because of the precedent of the use of visual displays by living nocturnal tetrapods, there is no reason to think that the sail of *Dimetrodon* only would have been useful for that function if the animal was diurnal. Indeed, given the likely lack of an impedance-matching ear in pelycosaur-grade synapsids and the long-standing uncertainty about their sensitivity to airborne sounds [34, 37, 87, 148-156], a system for effective visual display and communication might have been a particularly valuable component of a nocturnal lifestyle.

In summary, even though hypotheses about the function of the dorsal sail in *Dimetrodon* usually have been framed with the implicit assumption that the animal was diurnal, we do not think that the sail is incompatible with a nocturnal activity pattern. We consider the available evidence for a thermoregulatory function of the sail to be inconclusive at best. The fact that various living nocturnal tetrapods use visual signaling means that the sail of *Dimetrodon* could have been employed in a similar fashion, and the sail could function in a biomechanical capacity regardless of ambient light levels.

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Dataset S1

Newick tree file

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Table S1. Fossil data used in the phylogenetic flexible discriminant function analysis. Species means are given in cases where a species is represented by more than one specimen. See below for the list of specimens used in the analysis.

Higher Taxon	**Species**	**Orbit Length (mm)**	**External Ring Diameter (mm)**	**Internal Ring Diameter (mm)**	**Basal Skull length (mm)**	**Sample Size**
Varanopidae	*Aerosaurus wellesi*	26.93	18.45	13.45	80.31	1
Varanopidae	*Heleosaurus scholtzi*	11.58	10.82	5.85	39.58	1
Sphenacodontidae	*Dimetrodon milleri*	38.34	37.44	24.62	180.00	1
Sphenacodontidae	*Sphenacodon ferox*	49.00	47.00	25.00	266.94	1
Biarmosuchia	*Hipposaurus boonstrai*	47.30	37.24	23.42	195.08	1
Biarmosuchia	*Ictidorhinus martinsi*	40.38	25.73	15.47	84.6	1
Biarmosuchia	*Lemurosaurus pricei*	37.34	33.70	18.38	117.52	1
Biarmosuchia	*Lobalopex mordax*	41.18	22.08	13.00	141.78	1
Biarmosuchia	*Paraburnetia sneeubergensis*	37.21	23.86	16.97	171.06	1
Dinocephalia	*Titanophoneus potens*	77.57	56.76	37.84	391.78	1
Gorgonopsia	*Sauroctonus* cf. *parringtoni*	38.05	25.96	13.94	169.49	2
Gorgonopsia	*Cyonosaurus* spp.	29.30	20.50	11.32	158.83	4
Anomodontia	*Diictodon feliceps*	20.49	12.05	6.94	66.84	3
Anomodontia	*Emydops arctatus*	15.13	8.80	6.30	47.38	1
Anomodontia	*Galepus jouberti*	19.52	17.55	13.87	40.02	1
Anomodontia	*Oudenodon bainii*	31.72	16.50	8.91	106.71	4
Anomodontia	*Pristerodon mackayi*	11.85	7.02	4.46	48.34	1
Anomodontia	*Tiarajudens eccentricus*	45.60	34.50	20.00	220	1
Anomodontia	*Tropidostoma dubium*	27.61	14.56	9.57	104.75	2
Therocephalia	*Akidnognathus parvus*	23.14	14.01	10.80	103.58	1
Therocephalia	*Ictidosuchoides longiceps*	17.65	13.52	9.08	90.5	2
Therocephalia	*Scaloposaurus constrictus*	14.53	7.80	4.72	55.19	2
Therocephalia	*Theriognathus microps*	30.25	17.23	10.66	187.35	2
Cynodontia	*Tritylodon longaevus*	12.30	10.60	7.26	60.64	1

Table S2. Maximum paleolatitude data for analyzed fossil synapsids. Abbreviation: PBDB, Paleobiology Database, www.paleodb.org.

Higher Taxon	Species	Maximum Paleolatitude	Source/comment
Varanopidae	*Aerosaurus wellesi*	3.5° N	PBDB
Varanopidae	*Heleosaurus scholtzi*	60.2° S	PBDB
Sphenacodontidae	*Dimetrodon milleri*	1.4° S	PBDB
Sphenacodontidae	*Sphenacodon ferox*	4.4° N	PBDB
Biarmosuchia	*Hipposaurus boonstrai*	~60° S	Taxon is known from the Karoo Basin and thus should have a paleolatitude similar to other Karoo species
Biarmosuchia	*Ictidorhinus martinsi*	~60° S	Same as above
Biarmosuchia	*Lemurosaurus pricei*	~60° S	Same as above
Biarmosuchia	*Lobalopex mordax*	59.7° S	PBDB
Biarmosuchia	*Paraburnetia sneeubergensis*	~60° S	Taxon is known from the Karoo Basin and thus should have a paleolatitude similar to other Karoo species
Dinocephalia	*Titanophonues potens*	~45-55° N	Taxon is from the Fore-Ural region of Russia, mid-to-high latutitude in the Permian
Gorgonopsia	*Sauroctonus* cf. *parringtoni*	~60° S	Taxon is known from the Karoo Basin and thus should have a paleolatitude similar to other Karoo species
Gorgonopsia	*Cyonosaurus* spp.	~60° S	Same as above
Anomodontia	*Diictodon feliceps*	61.1° S (for genus)	PBDB
Anomodontia	*Emydops arctatus*	59.2° S	PBDB
Anomodontia	*Galepus jouberti*	~60° S	Taxon is known from the Karoo Basin and thus should have a paleolatitude similar to other Karoo species
Anomodontia	*Oudenodon bainii*	59.2° S	PBDB
Anomodontia	*Pristerodon mackayi*	61.0° S	PBDB
Anomodontia	*Tiarajudens eccentricus*	46.6° S	PBDB
Anomodontia	*Tropidostoma dubium*	59.2° S	PBDB
Therocephalia	*Akidnognathus parvus*	~60° S	Taxon is known from the Karoo Basin and thus should have a paleolatitude similar to other Karoo species
Therocephalia	*Ictidosuchoides longiceps*	59.2° S	PBDB
Therocephalia	*Scaloposaurus constrictus*	66.1° S	PBDB
Therocephalia	*Theriognathus microps*	55.0° S	PBDB
Cynodontia	*Tritylodon longaevus*	43.5° S	PBDB

Table S3. The museum specimens of nonmammalian synapsids analyzed in this study (reference specimens). Institutional abbreviations are provided at the end of this list.

Reference Specimens

Varanopidae

Aerosaurus wellesi: UCMP V2814/40096

Heleosaurus scholtzi: SAM-PK-K8305

Sphenacodontidae

Dimetrodon milleri: MCZ 2028

Sphenacodon ferox: NMMNH P-55367 (measurements based on figures in 63)

Biarmosuchia

Hipposaurus boonstrai: SAM-PK-9081

Ictidorhinus martinsi: AMNH FARB 5226

Lemurosaurus pricei: NMQR 1702

Lobalopex mordax: CGP/1/61

Paraburnetia sneeubergensis: SAM-PK-K10037

Dinocephalia

Titanophoneus potens: PIN 157/1 (measurements based on figures in 57)

Gorgonopsia

Sauroctonus cf. *parringtoni*: SAM-PK-K10034 (left and right rings), SAM-PK-K10035

Cyonosaurus spp.: BP/1/2598, SAM-PK-K7594, SAM-PK-K8790, SAM-PK-K10033

Anomodontia

Diictodon feliceps: CGP/1/1582, CGP W12, SAM-PK-K5189 (left and right rings)

Emydops arctatus: SAM-PK-K10703

Galepus jouberti: AMNH FARB 5241

Oudenodon bainii: BP/1/6974, CGP JW23(?), SAM-PK-6045, SAM-PK-K10124

Pristerodon mackayi: SAM-PK-K10997

Tiarajudens eccentricus: UFRGS PV339P

Tropidostoma dubium: CGP/1/2173, SAM-PK-K8654

Therocephalia

Akidnognathus parvus: SAM-PK-4021

Ictidosuchoides longiceps: BP/1/2118, BP/1/223

Scaloposaurus constrictus: BP/1/5220, SAM-PK-K10980

Theriognathus microps: AMNH FARB 8226, BP/1/717

Cynodontia

Tritylodon longaevus: BP/1/5109

Institutional Abbreviations

AMNH: American Museum of Natural History, New York City, USA.

BP: Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, South Africa.

CGP: Council for Geosciences, Pretoria, South Africa.

MCZ: Museum of Comparative Zoology, Cambridge, USA.

NHCC: National Heritage Conservation Commission, Lusaka, Zambia.

NMMNH: New Mexico Museum of Natural History and Science, Albuquerque, USA.

NMQR: National Museum, Bloemfontein, South Africa.

PIN: Paleontological Institute, Moscow, Russia.

ROM: Royal Ontario Museum, Toronto, Canada.

SAM: Iziko South African Museum, Cape Town, South Africa.

UCMP: University of California Museum of Paleontology, Berkeley, USA.

UFRGS: Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil.