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#### A taxonomic reassessment of *Piramys auffenbergi*, a neglected turtle from the late Miocene of Piram Island, Gujarat, India

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**Background.** *Piramys auffenbergi* was described as an emydine turtle based on a well-preserved skull retrieved from late Miocene deposits exposed on Piram Island, India. The description and figures provided in the original publication are vague and do not support assignment to Emydinae. This taxon has mostly been ignored by subsequent authors.

**Material & Methods.** We reexamine the holotype specimen and provide an extensive description and diagnosis for *Piramys auffenbergi* and included this taxon in a global character-taxon matrix for Pleurodira.

**Results.** The presence of a processus trochlearis pterygoidei and the absence of nasals conclusively show pleurodiran affinities. Inclusion of *Piramys auffenbergi* in a phylogenetic analysis retrieves this taxon within Stereogenyini and as sister to the Asian taxa *Shweboemys pilgrimi* and *Brontochelys gaffneyi*.

**Discussion.** Our reexamination of the holotype of *Piramys auffenbergi* confidently rejects the original assessment of this taxon as an emydine testudinoid and conclusively shows affinities with the pleurodiran clade Stereogenyini instead. Even though most taxa from this lineage are thought to be coastal turtles, all Asian stereogenyines were collected from continental deposits, suggesting a more diverse paleoecology for the group.

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13	
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31

#### 32 INTRODUCTION

33 *Piramys auffenbergi* was described by Prasad (1974) based on a single skull (GSI 18133)

34 retrieved from Neogene sediments exposed on the small island of Piram, Gujarat State, India

35 (Fig. 1). Prasad (1974) identified the taxon as an emydine, but the diagnosis and the description

36 are general and do not reveal any emydine affinities. Today, only cryptodiran cheloniids,

37 geoemydids (formerly part of Emydidae), testudinids, and trionychids occur in India (TTWG,

38 2017), but stereogenyine pleurodires inhabited the area as recently as the Plio/Pleistocene

39 (Gaffney et al., 2011).

Here we provide an extensive description and diagnosis of *Piramys auffenbergi* based on a
reexamination of the holotype specimen. Phylogenetic analysis concludes that this taxon is a
representative of Stereogenyini, a clade that includes other South Asian forms, namely the
Plio/Pleistocene *Shweboemys pilgrimi* Swinton, 1939 from Myanmar, and the late Oligocene *Brontochelys gaffneyi* (Wood, 1970) from Pakistan. We also provide an updated account of the
paleoecology and biogeography of the group, concluding that, although they were most likely

- 46 adapted (or at least highly tolerant) to salty waters, stereogenyines were still restricted
- 47 geographically and not as widespread as modern sea turtles.
- 48 Institutional abbreviations.— GSI, Geological Survey of India, Kolkata, India.
- 49

50 SYSTEMATIC PALEONTOLOGY

- 51 PLEURODIRA Cope, 1865
- 52 PELOMEDUSOIDES Broin, 1988
- 53 PODOCNEMIDIDAE Cope, 1868
- 54 STEREOGENYINI Gaffney et al., 2011
- 55 STEREOGENYITA Gaffney et al., 2011
- 56 Piramys auffenbergi Prasad, 1974
- 57 Holotype.— GSI 18133, a partial skull (Prasad, 1974, figs. 2–4, pl. 3.1; Figure 2).
- 58 Type locality and horizon.— Piram Island (Fig. 1), Gulf of Khambhat (formerly Gulf of
- 59 Cambay), Gujarat, India; conglomerate beds, middle Siwaliks (Prasad, 1974), Dhok Pathan age,
- 60 late Miocene (Nanda, Sehgal & Chauhan, 2017).
- 61 Referred material.— No specimens have been referred to date.
- 62 Diagnosis.—*Piramys auffenbergi* can be diagnosed as a representative of Pleurodira by the
- 63 presence of the processus trochlearis pterygoidei and of Pelomedusoides by the absence of nasal
- 64 bones. *Piramys auffenbergi* can be diagnosed as a representative of Stereogenyini by the small
- entrance to the antrum postoticum, the condylus mandibularis projecting ventrally from the
- 66 cavum tympani, and the posteriorly broad skull. Piramys auffenbergi is distinguished from the
- other members of Stereogenyini by the following combination of characters: a pinched snout
- 68 (not present in Latentemys plowdeni Gaffney et al., 2011, Bairdemys venezuelensis [Wood &

Díaz de Gamero, 1971], and *B. sanchezi* Gaffney et al., 2008), a deep interorbital groove on the
prefrontal and frontal (otherwise present in *Cordichelys antiqua* [Andrews, 1903]), foramen
nervi trigemini located above the level of the sulcus palatinopterygoideus (in contrast to the more
ventrally displaced foramen nervi trigemini in *Shweboemys pilgrimi* and *Brontochelys gaffneyi*),
the lower temporal emargination rising above the ventral level of the orbit (shallower in *C. antiqua* and unknown for other Stereogenyita), and the foramen stapedio-temporale placed
anteriorly (autapomorphic character).

76

77 DESCRIPTION

Preservations.—The skull was likely buried intact but suffered much weathering damage 78 more recently. The bone is nevertheless of good quality and sutures are well preserved. The 79 palate and ventral aspects of the basicranium are still obscured by matrix, but the 80 dermatocranium and the dorsal parts of the basicranium are exposed (Fig. 2). The margins of the 81 external nares and the median portions of the labial margins are damaged, but the remaining 82 margins likely approximate their original outlines. The temporal roofing, by contrast, is 83 massively eroded and the extent of the upper temporal emarginations can therefore not be 84 85 assessed anymore. Much of the postorbitals, parietals, quadratojugals, squamosals, and the supraoccipital are missing. Faint scute sulci are apparent on the postorbitals and parietals (Fig. 86 87 2A).

Prefrontal.—The prefrontals are relatively small, paired elements that form the anterodorsal aspects of the orbit and the anterior third of the narrow interorbital space. The anterior margins are damaged, but the prefrontals likely formed the dorsal roof of the external nares, as nasals were likely absent. The prefrontals contact the frontals posteriorly along a straight, transverse

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suture, the maxillae ventrally along a straight, horizontal suture, and one another along a straight,
median suture. The descending branch of the prefrontal contacts the frontal posteriorly and the
maxilla ventrally, but potential, more-distal contacts with the vomer and palatine are obscured by
matrix (Fig. 2C). The prefrontals jointly form a deep, median grove on the dorsal skull surface
(Fig. 2A).

97 Frontal.—The frontals are the only bones that are undamaged. The dorsal plate of the frontals forms the posterior two thirds of the interorbital space and posterodorsal margins of the 98 anterolaterally facing orbits. The frontals contact the prefrontals anteriorly along a straight, 99 100 transverse suture, the postorbitals laterally along parasagittal sutures of uneven length, the parietals posteriorly along straight, transverse sutures, and one another along a straight, median 101 suture. Within the orbits, the frontals contact the prefrontals anteriorly and the postorbitals 102 laterally. The median groove formed by the prefrontals continues posteriorly onto the frontals 103 (Fig. 2A), but fades to oblivion towards the posterior margins of these elements. 104 Parietal.—Symmetric damage to the dorsal plate of the parietal creates the illusion that the 105 parietals are relatively small elements that define the margins of well-developed upper temporal 106 emarginations, but all margins show signs of damage and the extent of this emargination cannot 107 be assessed with any confidence. It is therefore only clear that the dorsal plates of the parietals 108 contact the frontals anteriorly along straight, transverse sutures and the postorbitals along 109 oblique, anterolateral sutures. Together with the postorbitals, the parietals form a pair of sulci 110 111 that converge towards the posterior and that likely trace the outline of a large internarial scute (scute ii of Ferreira et al., 2015) that covered the prefrontals, frontals, and the medial portions of 112 the postorbitals and parietals. The descending process of the parietals contacts the pterygoid 113 114 anterior to the foramen nervi trigemini, forms the dorsal margin of this foramen, and contacts the

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prootic and supraoccipital posterior to it (Fig. 2A). The foramen nervi trigemini is located above 115 the level of the sulcus palatinopterygoideus and is well separated from the foramen stapedio-116 temporale by the prootic (Fig. 2C). More anterior contacts, if present, are obscured by matrix. 117 Postorbital.—The posterior margins of the postorbitals show signs of damage and it is 118 therefore not possible to assess if they originally contributed to the upper temporal 119 120 emarginations, although the thickness of their damaged margins makes this implausible. However, as the intact posterior margins converge, it is unlikely that they were significantly 121 larger than preserved. The dorsal plates of the postorbitals at least contact the frontals medially, 122 the parietals posteromedially, the jugals ventrally, and the quadratojugals posterolaterally. The 123 descending process of the postorbital forms much of the posterior wall of the orbit, but its distal 124 contacts are obscured by matrix. We are not able to discern a dorsal pocket within the upper 125 limits of the posterior wall of the orbit. 126

Jugal.—The jugals are relatively large elements that form the posteroventral aspects of the 127 orbit. Although the posteroventral aspects are damaged on both sides, enough is preserved to 128 indicate that a well-developed lower temporal emargination is developed that rises to the level of 129 the lower third of the orbit and that is anterodorsally framed by the jugals (Fig. 2B). The jugals 130 contact the postorbitals dorsally along horizontal sutures, the quadratojugal posteriorly along a 131 transverse suture, and the maxillae anteroventrally along a slightly oblique suture. The jugals 132 133 contact the maxilla anteriorly and the postorbitals laterally on the surface of the skull, but matrix 134 obscures possible contacts within the orbit.

Quadratojugal.—Only a fragment of the quadratojugal remains on the right side of the skull
(Fig. 2B). It is therefore unclear if the quadratojugal contributes to the upper or lower temporal
emarginations, although a contribution to the lower temporal emargination appears highly likely.

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Only a short, anteromedial contact is preserved with the postorbital, an elongate anterior contact
with the jugal, and remnants of the posterior contact of the quadrate anterior to the cavum
tympani.

Squamosal.—A fragment of the right squamosal is available at the back of the skull (Fig. 2A). 141 This fragment contacts the quadrate anterolaterally and the opisthotic anteromedially within the 142 upper temporal fossa. A likely contribution of the squamosal to the region posterior to the cavum 143 tympani cannot be discerned from that of the quadrate. However, the massive nature of the 144 damaged quadrates suggests that the squamosal did not contribute to the antrum postoticum. 145 Premaxilla.—The anterior tip of the skull is damaged, but the median, cleft like notch appears 146 to be genuine, as much of the left labial margin is intact (Fig. 2D). We are unable to discern the 147 contacts, or even the presence, of premaxillae. 148

Maxilla.—The maxillae can only be observed in anterior and lateral views, as the palate is hidden by matrix. On the skull surface, the high maxillae contact the jugals below the orbit along transverse sutures and the prefrontals dorsally along horizontal suture. These contacts can partially be traced within the orbits, but matrix obscures their full extent. It is unclear if an anterior contact is developed with the premaxillae. Likely contacts with the palatines are obscured by matrix. The maxillae otherwise form the labial margins of the jaw, the anteroventral margins of the orbit, and the lateral margin of the broad external nares.

Prootic.—Only the left prootic can be observed in dorsal view and its sutures are obscured by localized damage to the surface of the skull. The left prootic clearly contacts the descending process of the parietal anteromedially and the quadrate laterally. Contacts are certainly present with the supraoccipital posteromedially and the opisthotic posteriorly, but their orientation and size cannot be estimated with confidence. The left prootic partially roofs the foramen nervi

trigemini and together with the left quadrate forms the foramen stapedio-temporale, which is 161 situated at the anterior margin of the otic capsule and oriented anteriorly (Fig. 2A). 162 Opisthotic.—Only the external aspects of the opisthotics can be observed. Within the upper 163 temporal fossa, the opisthotics contact the supraoccipital anteromedially, the quadrate 164 anterolaterally, the squamosal posterolaterally, and the exoccipital posteromedially. 165 166 Quadrate.—Much of the quadrates remains on both sides of the skull, but most surfaces are damaged, making it difficult to discern its original shapes and contacts. At the very least, the 167 quadrate contacts the quadratojugal anterodorsally and the squamosal posteriorly along the skull 168 surface. Within the upper temporal fossa, the quadrate contacts the squamosal posteriorly, the 169 opisthotic posteromedially, and the prootic anteromedially. Although damage to the middle ear is 170 significant, it is apparent that the quadrates fully enclosed the incisura columella auris and 171 Eustachian tube and that the quadrates fully formed the highly reduced antrum postoticum. 172 However, matrix obscures the presence of a possible precolumellar fossa. In lateral view (Fig. 173 2C), the mandibular condule of the quadrate projects ventrally, beyond the ventral outline of the 174 cavum tympani. 175 Supraoccipital.—The supraoccipital is heavily eroded and some of its contacts are obscured 176 by damage. It is therefore not possible to assess its possible contribution to the dorsal skull roof 177 or the length of the supraoccipital crest. Within the upper temporal fossa, the supraoccipital 178 certainly contacts the parietal anteromedially, the prootic anterolaterally, the opisthotic 179

- 180 posterolaterally, and the exoccipital posteriorly. In posterior view, the supraoccipital roofs the
- 181 foramen magnum and contacts the exoccipitals ventrally.

Exoccipital.—The exoccipitals are both present, but their ventral portions are obscured by
matrix. These bones form the lateral margins of the foramen magnum, contact the supraoccipital

dorsally, the opisthotic anterolaterally, but their likely ventral contacts with the basioccipital are

obscured. Although the occipital condyle is heavily damaged, the sulcus left by the contact

between the exoccipitals laterally and the basioccipital ventrally are still visible (Fig. 2E).

187

188 MATERIAL & METHODS

#### 189 Matrix & Phylogenetic Analysis

We integrated the holotype of *Piramys auffenbergi* into the phylogenetic matrix of Ferreira et al. 190 (2018) to assess its relationships to other pleurodires. The matrix was modified through the 191 addition of a new character (ch. 245: PM, median notch on upper jaw; see Supplementary Files) 192 and by updating the scorings of some taxa (see Supplementary Files for full list of changes). As 193 in the original analysis (Ferreira et al., 2018), twelve characters (14, 18, 19, 71, 95, 96, 99, 101, 194 119, 129, 174, 175) were interpreted as forming morphoclines and were ordered in the analysis. 195 The resulting matrix was analyzed in TNT v. 1.5 (Goloboff & Catalano, 2016) using a traditional 196 search with 2000 replicates of Wagner trees, random seed set to 0, branch-swapping algorithm 197 Tree Bisection Reconnection (TBR), hold = 0, and collapsing zero-length branches according to 198 rule '1'. The most parsimonious trees (MPTs) were subject to a second round of TBR and a strict 199 consensus was obtained from the resulting MPTs. Consistency (CI) and Retention (RI) indexes, 200 Bremer support, and resampling values (bootstrap and jackknife, using 1000 resamples for 201 calculating absolute and difference of frequencies; Goloboff et al., 2003) were retrieved using 202 203 implemented functions in TNT.

204

205 RESULTS

The search yielded 270 MPTs with 1134 steps (CI=0.288; RI=0.748). The strict consensus (see

207 Supplementary Files) differs slightly from the results of Ferreira et al. (2018) by yielding a

208 polytomy in the clade that includes the extant Erymnochelys madagascariensis (Grandidier

209 1867) and Peltocephalus dumerilianus (Schweigger 1812). Piramys auffenbergi is retrieved with

relatively high support (Bremer support = 2; see Supplementary Files) inside Stereogenyini in a

211 polytomy with Stereogenys cromeri Andrews, 1901 and Shweboemys pilgrimi (Fig. 3).

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#### 213 DISCUSSION & CONCLUSION

#### 214 Alpha taxonomy and phylogenetic relationships

Prasad (1974) documented in the original description and figures of the holotype of *Piramys* 215 *auffenbergi* the presence of large nasals, elongate prefrontals, small frontals that do not 216 contribute to the orbits, and deep upper temporal emarginations. Prasad (1974) unfortunately did 217 not explain why he felt Piramys auffenbergi to be an emydine, but we note that the presence of 218 nasals is neither consistent with an assignment to Emydinae in particular, nor Testudinoidea 219 more generally, as testudinoids universally lack nasal bones. Our re-examination of the type 220 specimen allows us to better evaluate the cranial morphology and taxonomic affinities of this 221 222 taxon and to present a more detailed list of diagnostic characters.

The most apparent differences in our interpretation of the skull is that nasals are absent, that the prefrontals are situated at the front of the orbits, that the frontals broadly contribute to the orbits, that the margin of the upper temporal emargination is not preserved, and that a trochlear process is present on the pterygoid. The presence of a trochlear process of the pterygoid and the absence of nasals clearly hint at pleurodiran and pelomedusoids affinities for *Piramys auffenbergi*, respectively (Gaffney, Tong & Meylan, 2006). The trochlear process is almost

completely embedded in matrix, but its lateral tip can be seen anterior to the otic capsule (Fig.230 2C).

The posteriorly broadened skull, small anterior opening of the antrum postoticum, and a 231 mandibular condyle projecting ventrally from the cavum tympani in lateral view (Fig. 2) suggest 232 stereogenvine affinities (Gaffney et al., 2011; Ferreira et al., 2015). The results of our 233 234 phylogenetic analysis (Fig. 3) support this initial hypothesis, even though *Piramys auffenbergi* is scored as "unknown" for several characters that support the monophyly of Stereogenvini. The 235 majority of characters that resolve relationships within Stereogenvini, e.g., presence of a 236 secondary palate with a midline cleft (Gaffney et al., 2011; Ferreira et al., 2015), refer to features 237 in the ventral region of the skull. Unfortunately, this region is covered by matrix in GSI 18133, 238 hampering a more detailed account of its taxonomic affinities. Nevertheless, the pinched snout 239 (ch. 41, state 1), premaxillae protruding anteriorly beyond the dorsal edge of the apertura narium 240 externa (ch. 43, state 1), the small opening of the antrum postoticum (ch. 86, state 2), the ventral 241 projection of the mandibular condyle (ch. 90, state 1), and the median notch in the upper jaw (ch. 242 246, state 2) supports *Piramys auffenbergi* as a Stereogenvini with close affinities to *Stereogenys* 243 cromeri and Shweboemvs pilgrimi (Fig. 3). 244

Comparisons of *Piramys auffenbergi* with other Asian stereogenyines reveal osteological and
chronological distinctness. The Bugti Hills in Pakistan, the type locality of *Brontochelys gaffneyi*, are now considered to be late Oligocene in age (Welcome et al., 2001; see discussion in
the next section) whereas the Irrawaddy Beds in Myanmar, the type locality of *Shweboemys pilgrimi*, are thought to be Pliocene/Pleistocene age (Thein, Nu & Pyone, 2012). The sediments
exposed on Piram Island are dated as late Miocene (Nanda, Sehgal & Chauhan, 2017) and *Piramys auffenbergi* therefore is temporally distinct. *Piramys auffenbergi* differs from

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Brontochelvs gaffnevi by the presence of a pinched snout, anterodorsally facing orbits, and a 252 median notch in the upper jaw. On the other hand, Piramys auffenbergi differs from Shweboemys 253 *pilgrimi* by the presence of an interorbital space that is narrower than the diameter of the orbits 254 and the straight prefrontal-frontal suture. Furthermore, Piramys auffenbergi can be distinguished 255 from both other Asian stereogenvines by the presence of a narrow interorbital groove, the more 256 257 posterodorsally located foramen nervi trigemini, and the anterior, instead of dorsal, opening of the foramen stapedio-temporale. We are therefore able to confirm the validity of Piramys 258 auffenbergi, though not as a testudinoid cryptodire, but rather as a podocnemidid pleurodire. 259

260

#### 261 Paleoecology and biogeography

Members of Stereogenvini are currently thought to be durophagous, because they have broad and 262 flat triturating surfaces combined with a secondary palate (Ferreira et al., 2015), features that are 263 prevalent among extant turtles with durophagous dietary preferences (Foth, Rabi & Joyce, 2017). 264 The palate is not exposed in the holotype of *Piramys auffenbergi* and we are therefore not able to 265 assess the diet of this taxon with confidence. However, the high maxillae, anterodorsally oriented 266 orbits, and posteriorly broadened skull with space for well-developed adductor muscles (Fig. 3) 267 are features consistent with this life style. Considering the placement of Piramys auffenbergi 268 within Stereogenyini we therefore predict the presence of durophagous features in this taxon as 269 well. 270

Members of Stereogenyini are furthermore though to have had a marine, or at least coastal, lifestyle based on limb morphology (Weems & Knight, 2013), shell morphology (Pérez-García, 2017), and depositional environments (Ferreira et al., 2015). Although most stereogenyine taxa have indeed been recovered from sediments that represent coastal or open sea depositional

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environments (Ferreira et al., 2015), we here note that all known Asian stereogenyines were 275 collected from continental deposits, at least as indicated by the prevalence of terrestrial mammals 276 in combination with fresh water aquatic fish and reptiles. In particular, the type of *Brontochelvs* 277 gaffnevi was collected from late Oligocene (not Miocene as reported Wood, 1970; Gaffnev et al., 278 2011) continental sediments exposed in the region of Dera Bugti, Pakistan (Marivaux et al., 279 1999; Welcome et al., 2001), Shweboemys pilgrimi from the continental Plio/Pleistocene 280 Irrawaddy Beds of Myanmar (Thein, Nu & Pyone, 2012), and, as demonstrated herein, Piramys 281 auffenbergi from the continental late Miocene middle Siwaliks of India (Nanda, Sehgal & 282 Chauhan, 2017). Given that all Asian taxa also form a clade (Fig. 3), it appears that the more 283 continental clade Stereogenyita is nested within the more marine adapted clade Stereogenyini 284 (Fig. 3), indicating a certain amount of ecological fluidity within the group. However, as deltaic 285 and marine sediments often interfinger finely and as estuarine and coastal turtles are expected to 286 be found in numerous coastal facies, we suggest that the available data is not sufficient to 287 establish a rigorous pattern for the moment. Nevertheless, the fact that our phylogenetic analysis 288 retrieves two geographically separated clades, the Afro-Asian Stereogenyita and the South 289 American Bairdemydita, suggests that the even more salt tolerant forms were not highly marine, 290 as greater amounts of dispersal and less endemism were otherwise to be expected. 291 Despite the broad geographic distribution of stereogenyines across North and South America, 292 Africa, and India, they did not achieve the degree of cosmopolitanism seen in modern sea turtles 293 294 (Chelonoidae; TTWG 2017). Instead, it appears that they were restricted to equatorial and subtropical regions of the northern hemisphere (Fig. 4). This hints at the possibility that their 295 distribution was limited by cooler temperatures outside of the tropics. 296

297

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382

#### 383 Figure 1: The type locality of *Piramys auffenbergi*.

(A) A simplified map of India. Gujarat State is highlighted in purple, all other states in various
shades of grey. (B) Detailed view of the Gulf of Khambhat. Piram Island is highlighted in purple.

Figure 2: GSI 18133, *Piramys auffenbergi*, holotype, late Miocene of Piram Island, Gujarat,
India.

#### Manuscript to be reviewed

389 Photographs and illustrations of specimen in (A) dorsal, (B) right lateral, (C) left lateral, (D)

anterior, and (E) posterior views. Abbreviations: *fnt*, foramen nervi trigemini; *fr*, frontal; *fst*,

foramen stapedio-temporale; *ju*, jugal; *mx*, maxilla; *op*, opisthotic; *pa*, parietal; *pf*, prefrontal; *po*,

postorbital; *pr*, prootic; *ptp*, processus trochlearis pterygoidei; *qj*, quadratojugal; *qu*, quadrate; *so*,

393 supraoccipital; *sq*, squamosal.

394

#### 395 Figure 3: Phylogenetic hypothesis of Stereogenyina.

396 A time-calibrated cladogram depicting a portion of the strict consensus topology of 270 MPTs

397 with 1134 steps retrieved from the phylogenetic analysis using ordered characters. Dark lines

398 highlight the known temporal distribution of a taxon and the colored continent symbols highlight

their known spatial distribution. The full tree is provided in the Supplementary File S2.

400

#### 401 Figure 4: Geographic distribution of stereogenyines.

402 Section of world map indicating localities of extinct taxa assigned to Stereogenyini. Red circles

403 indicate Stereogenyita, green circles Bairdemydita, and blue circles non-Stereogenyita and non-

404 Bairdemydita steregeonyines. 1, Bairdemys venezuelensis; 2, B. thalassica Ferreira et al., 2015;

405 3, B. sanchezi; 4, B. winklerae Gaffney et al., 2008; 5, B. hartsteini Gaffney & Wood, 2002; 6,

406 "B." healeyorum Weems & Knight, 2013; 7, Mogharemys blanckenhorni (Dacqué, 1912); 8,

407 Cordichelys antiqua; 9, Latentemys plowdeni; 10, Stereogenys cromeri; 11, Lemurchelys

408 diasphax Gaffney et al., 2011; 12, Brontochelys gaffneyi; 13, Shweboemys pilgrimi; 14, Piramys

409 auffenbergi. Abbreviations: EG, Egypt, MM, Myanmar, PK, Pakistan, PR, Puerto Rico, US,

410 United States of America, VE, Venezuela.

411

- 412 Supplemental File S1: Character taxon matrix used in phylogenetic analysis, including full
- 413 character list and character state definitions.

414

- 415 Supplemental File S2: List of changes to Ferreira et al. (2018)'s matrix, strict consensus
- tree retrieved from the phylogenetic analysis, bootstrap, jackknife and Bremer support
- 417 values, and list of common synapomorphies for Stereogenyina.

418

419

# Figure 1

The type locality of *Piramys auffenbergi*.

(A) A simplified map of India. Gujarat State is highlighted in purple, all other states in various shades of grey. (B) Detailed view of the Gulf of Khambhat. Piram Island is highlighted in purple.



# Figure 2

GSI 18133, Piramys auffenbergi, holotype, late Miocene of Piram Island, Gujarat, India.

Photographs and illustrations of specimen in (A) dorsal, (B) right lateral, (C) left lateral, (D) anterior, and (E) posterior views. Abbreviations: *fnt*, foramen nervi trigemini; *fr*, frontal; *fst*, foramen stapedio-temporale; *ju*, jugal; *mx*, maxilla; *op*, opisthotic; *pa*, parietal; *pf*, prefrontal; *po*, postorbital; *pr*, prootic; *ptp*, processus trochlearis pterygoidei; *qj*, quadratojugal; *qu*, quadrate; *so*, supraoccipital; *sq*, squamosal.

#### Manuscript to be reviewed



# Figure 3

Phylogenetic hypothesis of Stereogenyina.

A time-calibrated cladogram depicting a portion of the strict consensus topology of 270 MPTs with 1134 steps retrieved from the phylogenetic analysis using ordered characters. Dark lines highlight the known temporal distribution of a taxon and the colored continent symbols highlight their known spatial distribution. The full tree is provided in the Supplementary File S2.

		Stereogenyita					Bairdemydita								
		s auffenbergi 🕌	veboemys pilgrimi 🤙				mys venezuelensis 🔫	issica 🔶	mys winklerae <	steini <	mys sanchezi <		7		Jorni
Pleistocene		y my	Shi		key		rdei	nala	rdei	arts	rdei		ine		ent
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	Messinian			*	s di	-		lme		lme		ш	olq	-	ld s
	Tortonian			imeri <	rchely.	affneyi		Bairde		Bairde		aleyon	temys	iqua	aremy
	Serravallian			cro	nm	s gê						hei	ten	ant	hgo
Miocene	Langhian			shu	e Le	elys						"SA	La	)ys	Mo
	Burdigalian			reoger		ontoch						airdem		rdichel	
	Aquitanian			Ste		Bro						"Bá		S	
Oligocene	Chattian														
Oligocelle	Rupelian				-					St	ereog	enyina Stereo	ogeny	ini	

## Figure 4

Geographic distribution of stereogenyines.

Section of world map indicating localities of extinct taxa assigned to Stereogenyini. Red circles indicate Stereogenyita, green circles Bairdemydita, and blue circles non-Stereogenyita and non-Bairdemydita steregeonyines. 1, *Bairdemys venezuelensis*; 2, *B. thalassica* Ferreira et al., 2015; 3, *B. sanchezi*; 4, *B. winklerae* Gaffney et al., 2008; 5, *B. hartsteini* Gaffney & Wood, 2002; 6, "*B." healeyorum* Weems & Knight, 2013; 7, *Mogharemys blanckenhorni* (Dacqué, 1912); 8, *Cordichelys antiqua*; 9, *Latentemys plowdeni*; 10, *Stereogenys cromeri*; 11, *Lemurchelys diasphax* Gaffney et al., 2011; 12, *Brontochelys gaffneyi*; 13, *Shweboemys pilgrimi*; 14, *Piramys auffenbergi*. Abbreviations: EG, Egypt, MM, Myanmar, PK, Pakistan, PR, Puerto Rico, US, United States of America, VE, Venezuela.

