REVIEW ARTICLE   **Open access**

On the historical biogeography of the subfamily Uromastycinae: how did *Saara* achieve its eastern range

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Abstract
Here, we challenge the origin center of the subfamily Uromastycinae, i.e., eastern or southern Asia, and east to west dispersal toward the Middle East and Africa and suggest that Afro-Arabia is a more probable candidate as the center. The uromastycine clade diverged in Afro-Arabia during the Oligocene, forming the *Uromastyx* and *Saara* roots; the *Saara* root diverged into a northern clade and an eastern clade during Middle Miocene. The northern clade either dispersed towards the Gomphotherium landbridge; the populations that did not cross the landbridge evolved into *S. loricata*, and the passed ones dispersed eastwards and evolved into *S. asmussi*; or it extended towards central Iran during the intermittent Tethys seaway connections and/or permanent Tethys seaway closure, and the vicariant Zagros orogeny caused the evolution of *S. loricata* in the western Zagros and *S. asmussi* in the eastern Zagros and central Iran. The eastern clade, *S. hardwickii*, followed a path that formed through the contact of the Indian and Arabian Peninsula continental shelves, amplified by the sea level regression during the Middle Miocene glaciation.

Keywords: Acrodont, Africa, Agamid, dispersal, *Uromastyx*, vicariance.

INTRODUCTION

The subfamily Uromastycinae Theobald, 1868 is a basal taxon of Agamidae distributed in the desert belt of the Old World, and is phylogenetically a sister taxon to other agamid taxa (Townsend et al. 2011; Pyron et al. 2013; Takesh et al. 2020). It is composed of two genera (Wilms et al. 2009): *Uromastyx* Merrem, 1820 (Saharo-Arabian genus with 15 species distributed from the Atlantic coast of north-west Africa to Iran and across the Arabian Peninsula) and *Saara* Gray, 1845 (Irano-Turanian genus with three species distributed in Iraq, Iran, Afghanistan, Pakistan, and India). It is estimated that the divergence of the group began during the Oligocene, ca. 30–25 million years ago (Ma) (Joger 1986; Amer and Kumazawa 2005a; Tamar et al. 2018), and it is hypothesized that an initial stage of radiation probably occurred in the eastern Middle East, prior to the connection between Africa and Eurasia approximately 18 Ma (i.e., the Gomphotherium landbridge; Rögl, 1998). Amer and Kumazawa (2005a) suggested that the ancestor of *Uromastyx* sensu stricto (s.s.) most likely derived from this region. *Uromastyx* s.s. divided into two clades around 18.1–16.3 Ma: one clade led to *U. thomasi*, and the other formed the common ancestor of all the remaining species which diverged into two main clades around 15.5–15 Ma. One of

these latter clades forms the common ancestor of *U. aegyptia* and *U. ocellata* group, which diverged from each other about 14.3 Ma. The other group formed the common ancestor of the *U. princeps* group and the *U. acanthinura* group which diverged from each other at about 12.4 Ma. The mode of this cladogenesis has been suggested by other studies (e.g., Joger 1986; Amer and Kumazawa 2005a; and Wilms et al. 2009). The distribution ranges of *Uromastyx* s.s. and its species are depicted in figures 1A and 2A–O. *Saara* is divided into two clades that split around 18.6–16.6 Ma: one clade led to *S. hardwickii*. The other forms the common ancestor of *S. loricata* and *S. asmussi*, which diverged from each other around 6 Ma. The distribution range of *Saara* and its species are presented in figures 1B, 2P–R.
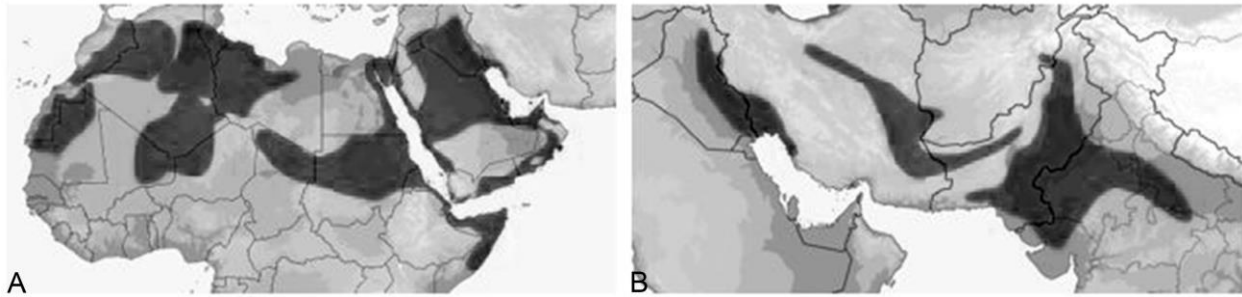

FIGURE 1. Distribution ranges of the genus *Uromastyx* (A), and the genus *Saara* (B) (Adopted from http://www.repfocus.dk).

By now, biogeographical studies have tried to determine the divergence time and the mode of cladogenesis in the subfamily Uromastycinae (e.g., Amer & Kumazawa 2005a; Tamar et al. 2018; Šmíd et al. 2021), but inferences on the origin and dispersal route are confined to some speculations, including southern or eastern Asia as the origin, and east to west dispersal and passing across the Gomphotherium landbridge (Amer & Kumazawa 2005a; Tamar et al. 2018). In the present paper, we reviewed previous studies on paleontology, geology and phylogeny to form a plausible scenario on the biogeography of the subfamily.

PALEONTOLOGICAL EVIDENCES
Vullo et al. (2023) showed that the fragmentary specimen including a dentary fragment bearing five teeth was anatomically misinterpreted as *Jeddaherdan aleadonta* (sensu Apesteguía et al. 2016), and it does not originate from Cretaceous beds but comes from Quaternary in age, and must be considered as an indeterminate species of *Uromastyx*. Čerňanský et al. (2021) reported a fossil *Uromastyx* from Gujarat, India, based on an incomplete mandible, which dates back to the Middle Miocene (ca. 14 Ma). *Uromastyx*, as well, was reported from the Neogene of southern Italy by Schleich et al. (1996), but Delfino et al. (2008) regarded its identification as poorly substantiated. Another fossil belongs to the extinct *Uromastyx europaeus* Moody 1980, and was recorded from the Phosphorites du Quercy in France, which dates back to the Oligocene (ca. 33.9–28.4 Ma) (Rage and Augé 2015). Holmes et al. (2010) described several jaws with attached teeth of a Uromastycine fossil from the lower Oligocene (ca. 33 Ma) deposits of the Jebel Qatrani Formation in the Fayum Depression, Egypt. *Barbaturex morrisoni* is a giant fossil acrodontan lizard recorded from the Middle Eocene (ca. 40 Ma) Pondaung Formation of Myanmar and has been proposed to be the sister taxon to Uromastycinae. Morphological (based on an incomplete mandible) and molecular analyses confirmed the monophyly of *Barbaturex* and Uromastycinae (Head et al. 2013). Averianov and Danilov (1996) described mandible fragments belonging to Uromastycinae from the Early Eocene (ca. 56–47 Ma) Alay beds at the Andarak two locality in Kyrgyzstan.
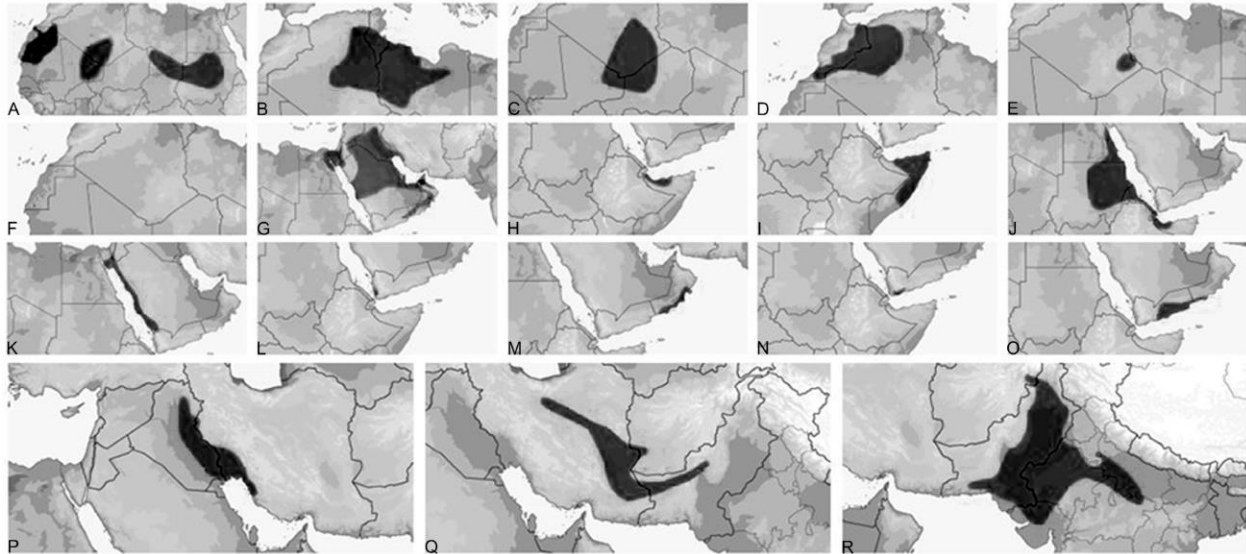
FIGURE 2. Distribution ranges of the species of the subfamily Uromastycinae: A) *U.dispar* [left = *U. d. flavifasciata*; middle = *U. d. maliensis*; right = *U. d. dispar*]; B) *U. acanthinura*; C) *U. geyri*; D) *U. nigriventris*; E) *U. alfredschmidti*; F) *U. occidentalis*; G) *U. aegyptia* [left = *U. a. aegyptia*; middle = *U. a. microlepis*; right = *U. a. leptieni*]; H) *U. macfadyeni*; I) *U. princeps*; J) *U. ocellata*; K) *U. ornata*; L) *U. shobraki*; M) *U. thomasi*; N) *U. yemenesis*; O) *U. benti*; P) *S. loricata*; Q) *S. asmussi*; R) *S. hardwickii* (adopted from http://www.repfocus.dk).

THE OLD WORLD DURING THE CENOZOIC

During the Cenozoic, tectonic compression and numerous microplate fusions between Europe and Africa impacted the Mediterranean area, and Eurasia moved northwards (Kuhlemann 2003). Simultaneously, a complex pattern of changing seaways and landbridges influenced the Eurasian ecosystems and landscapes (e.g. Rögl 1998; Popov et al. 2004). This was amplified by the following climatic changes: a) as the Cretaceous, the warm climate continued during the Late Paleocene and Early Eocene; b) next the temperature gradually decreased during the Late Eocene, and an abrupt steep global cooling and a big drop of the eustatic sea level occurred around Eocene/Oligocene boundary as per the formation of the first ice-sheets in Antarctica (Zachos et al. 2001). Simultaneously, the Alpine orogeny formed the multiple mountain ranges along the southern rim of Eurasia. The combination of these events resulted in a large sea regression, and a barrier was formed between the Tethys and Paratethys oceans. Additionally, the India-Asia collision began around the Eocene/Oligocene boundary (ca. 34 Ma). During the Late Oligocene, the temperature re-increased and the warming trend continued towards the Middle Miocene. The first incidence of the Arabian plate breakage from Afro-Arabia continent dates back to ca. 25 Ma in the Oligocene (Brown 1972). The Zagros fold and thrust belt was mainly formed by the collision of the Eurasian Plate and the Arabian Plate and appeared during the Miocene (ca. 25–5 Ma) (Mouthereau et al. 2012). Since the Late Cretaceous to the Early Miocene (100–18 Ma), Afro-Arabia was isolated from Eurasia (Rögl, 1998). The Early Miocene (ca. 20 Ma) was the time of marine transgression, during which the Paratethys reconnected with the Mediterranean Sea. By ca. 18 Ma, Arabia collided with Eurasia through plate tectonic activities, and the Eastern Mediterranean seaway was closed (Rögl 1998; Harzhauser et al. 2002). The closure of the Tethyan Seaway was a diachronous process; in the high Zagros, the seawater retreat was earlier at ca. 20–18.5 Ma (Pirouz et al. 2017; Sun et al. 2021) facilitated terrestrial faunal exchanges through the Gomphotherium landbridge. Despite temporal discontinuities, the landbridge has persisted continuously from ca. 15 Ma (Harzhauser et al. 2007; Pook et al. 2009; Šmíd et al. 2013). In the Early Miocene the Arabian Peninsula further completely separated from Africa as a tectonic consequence of the Afar mantle plume leading to the formation of the Red Sea, the Gulf of Aden, and the East African Rift Valley. This accompanied considerable uplifting of some mountain systems

along the plate boundaries (Girdler 1991; Schandelmeier et al. 1997). Since ca. 16 Ma, major global cooling occurred during two intervals: the Middle Miocene (∼14–13 Ma) and the Late Miocene (∼7–6 Ma). Around 14.2 Ma, the commencement of the Middle Miocene climatic cooling is characterized by the expansion of the East-Antarctic ice-sheet (Shevenell et al. 2004) causing a sea level regression. In the Middle Miocene (ca. 15–12.8 Ma), marine transgressions and regressions affected the Tethyan Seaway leading to its intermittent closure (intermittent Tethys seaway connections), but the permanent closure of the Tethyan Seaway in its northwestern segment at ca. 12.8 Ma was related to the long-term sea level decrease caused by the permanent growth of the East Antarctica Ice Sheet. In the western Zagros foreland, the last seawater retreat was defined at 12.8 Ma. (Hamon et al. 2013; Sun et al. 2021). The glaciation in the Northern Hemisphere was initiated at ∼7–6 Ma (He et al. 2021). The continental shelf of the Indian Plate juxtaposed that of Arabian Peninsula at around 15–12 Ma (Aitchison et al. 2007). The seawater retreated from the northwestern Zagros foreland permanently interrupted the connections between the Indian Ocean and the proto-Mediterranean Sea after 12.8 Ma (Sun et al. 2021). During the Early Pliocene, the climatic warming trend reversal is reflected by a gentle warming until 3.2 Ma (Zachos et al. 2001), when the onset of permanent Arctic glaciation heralded the Pleistocene ice-ages.

PHYLOGENETIC RECONSTRUCTIONS AND DIVERGENCE TIME

Several phylogenic reconstructions have tried to unravel the divergence time of the subfamily Uromastycinae. Amer and Kumazawa (2005a) suggested the Middle Eocene (ca. 50–40 Ma) as the divergence time of the *Uromatyx* clade from its sister taxon. Looking at the south Asian distribution and the stem position of *S. hardwickii*, Amer and Kumazawa (2005a) suggested that *Uromastyx* originated in central–south Asia and migrated westward. According to Tejero-Cicuéndez et al. (2022), *Saara* diverged from *Uromastyx* at about 40 Ma (the Eocene), whereas the Oligocene (ca. 30–25 Ma) is generally attributed to this divergence (Amer and Kumazawa 2005a; Tamar et al. 2018). An initial radiation might have occurred in the eastern Middle East much earlier than the Gomphotherium landbridge, and the predecessors of *Uromastyx* s.s. might be derived from one of the initial lineages (Amer and Kumazawa 2005a). Tejero-Cicuéndez et al. (2022) estimated that *Uromastyx* s.s. began to diverge during the Oligocene (ca. 27 Ma), whereas the Middle Miocene was considered as the divergence time in other analyses (e.g., Amer and Kumazawa 2005a: 15–11 Ma; Tamar et al. 2018; 16 [20.9–12.8] Ma).

Based on the different phylogenetic analyses (e.g., Wilms et al. 2009; Tamar et al. 2018), *Uromastyx* taxa have been divided into five groups: in the Arabian clade (sensu Amer and Kumazawa 2005a), the *U. aegyptia* group (distributed in the Arabian Peninsula and northern Egypt) and the *U. ocellata* group (including *U. benti*, *U. shobraki*, *U. yemenensis*, *U. ocellata*, and *U. ornat*a; distributed in the Arabian Peninsula and west to the Red Sea) are sister to one another, and in the African clade (sensu Amer and Kumazawa 2005a) the *U. princeps* group (including *U. princeps* and *U. macfadyeni*; distributed in the Horn of Africa and west to the Red Sea) and the *U. acanthinura* group (including *U. geyri*, *U. alfredschmidti*, *U. acanthinura*, *U. nigriventris*, and *U. dispar*; distributed from the center towards north, west, northwestern of Africa) are sister to each other. The *U. thomasi* group is sister to all the previous groups (sensu Tamar et al. 2018) and is distributed across the southwestern of Arabian Peninsula.

The divergence time between the *U. aegyptia* group and the *U. ocellata* group dates back to the Oligocene (ca. 23–21 Ma) based on Tejero-Cicuéndez et al. (2022). The Middle Miocene was, however, suggested in other analyses (e.g., Amer and Kumazawa 2005a: 14–12 Ma; Tamar et al. 2018: 14.3 [18.2–11] Ma). The most probable explanations for speciation in the *U. ocellata* group are the Yemen Plateau uplifting (basal dichotomy in the group during the Late Miocene [ca. 10.5–9.5 Ma]), habitat fragmentation due to the Red Sea expansion and the tectonic instability around the Red Sea, southern dispersal on both sides of the Red Sea, and reopening of the Bab-el-Mandeb strait as a vicariant event at around 5 Ma (divergence between *U. ocellata* and *U. ornata* during the Early Miocene [ca. 7.7–5.8 Ma]) (Girdler 1984, 1991; Schandelmeier et al. 1997; Geoffroy et al. 1998; Wilms 2001; Amer and Kumazawa 2005a; Bosworth et al. 2005).

According to Tejero-Cicuéndez et al. (2022), the African clade diverged during Oligocene (ca. 24–22 Ma), forming the *U. princeps* and *U. acanthinura* groups. The other analyses estimated that this divergence occurred much later during the Middle Miocene due to terrestrial barriers and habitat fragmentation following the tectonic and geological activities of the Afar mantle plume (e.g., volcanism, the formation of the East African Rift Valley, and the uplifting of mountain ridges) (e.g., Girdler 1991; Bosworth et al. 2005; Amer and Kumazawa 2005a: 12.5–10 Ma; Tamar et al. 2018: 12.4 [16.2–9.3] Ma). The most plausible explanations for speciation in the *U. acanthinura* group are habitat fragmentation and isolation of local populations due to climatic impacts (e.g., cooling and drying) that led to a major expansion of grassland and desert environments (basal dichotomy in the group during the Pliocene [ca. 5.4–2.4 Ma]) and the East African Rift Valley and associated mountains as terrestrial barriers (divergence in *U. princeps* group during the Miocene [12–10 Ma]) (Girdler 1991; McClanahan and Young 1996; Agusti et al. 1999; deMenocal and Brown, 1999; MacDonald 2003; Amer and Kumazawa 2005a).

CHALLENGING REASONS AGAINST THE PROPOSED HYPOTHESIS
Some molecular studies (Joger 1986, Honda et al. 2000; Amer and Kumazawa, 2005a, 2005b) are consistent with a view that extant Agamidae originated from Asia and that some descendant lineages (e.g., Uromastycinae) dispersed to Africa during the Cenozoic, when they were geographically connected to or in close proximity to Eurasia. According to Amer and Kumazawa (2005a), the Uromastycine clade originated in central or southern Asia in the Late Cretaceous (ca. 80 Ma). The current scenario suggests that the Uromastycine clade dispersed westwards into south-western Asia, Arabia and North Africa, most likely during the Eocene–Oligocene onwards and then started diverging during the Oligocene (ca. 30–25 Ma), so that an initial radiation probably occurred in the eastern Middle East, prior to the Gomphotherium landbridge. This does not, however, agree with 1) Rage and Augé (2015) who reported *Uromastyx europaeus* from the Oligocene deposit of the Phosphorites du Quercy in France (ca. 33.9–28.4 Ma), and 2) Holmes et al. (2010), who reported a Uromastycine fossil from the lower Oligocene deposits of the Jebel Qatrani Formation in the Fayum Depression, Egypt (ca. 33 Ma).

Afro-Arabia was isolated from other continents between the Late Cretaceous and the Early Miocene (100–18 Ma) (Rögl 1998; Calviño et al. 2016). If Uromastycinae originated in central or southern Asia, the presence of fossils (i.e., Holmes et al. 2010) in Africa becomes untenable. If, indeed, central or southern Asia is the center of origin of *Uromastyx* s.l., and the divergence between *Saara* and *Uromastyx* occurred by the Gomphotherium landbridge, it would be more reasonable wether *S. loricata*, or, at least *S. asmussi*, which are closer to northern Africa and the Red Sea (i.e., the diversification center of *Uromastyx* s.s.) than *S. hardwickii*, would be the sister taxon of *Uromastyx* sensu stricto.

PLAUSIBLE ALTERNATIVE SCENARIO ON THE CURRENT BIOGEOGRAPHY OF *SAARA*
Since Africa was isolated from Eurasia between the Late Cretaceous and the Early Miocene (Rögl 1998; Calviño et al. 2016), recording a Uromastycine in Kyrgyzstan (Averianov and Danilov 1996) during the Early Eocene (ca. 56–47 Ma) raised a hypothesis: it might be that uromastycines dispersed in the Eurasian part of Laurasia before its separation from Afro-Arabia. Such hypothesis can also be suggested for the presence of *U. europaeus* in France. Noteworthy is the fact that the glaciation in the Eocene/Oligocene boundary might have caused the Mediterranean Sea level regression (Rögl 1999) so that intercontinental non-avian faunal exchanges between Afro-Arabia, and Eurasia might have been facilitated. Accordingly, *U. europaeus* might have dispersed from Afro-Arabia to Europe at the Eocene/Oligocene boundary.

Fossils from Egypt (Holmes et al. 2010) demonstrate that uromastycines certainly existed in Afro-Arabia from the Late Cretaceous to the Early Oligocene. The clade then diverged in the Early Oligocene (ca. 30–29 Ma) in Afro-Arabia, forming the root of *Saara* and the root of *Uromastyx* sensu stricto. Because the Late Oligocene to the Early Miocene (ca. 28–17 Ma) was the time of marine transgression caused by temperature increasing (Ebril et al. 2021), it is unlikely that *Saara* was able to leave Afro-Arabia. The defenders of the Gomphotherium landbridge theory advocate that the uromastycine clade found its way towards west through this landbridge (e.g., Amer and Kumazawa 2005a; Wilms et al. 2009). In response to the discordance between the Early Oligocene divergence and

the early Gomphotherium landbridge, they suggest that an initial stage of radiation probably occurred in the eastern Middle East, prior to the establishment of the Gomphotherium landbridge, and that the ancestor of *Uromastyx* most likely derived from this region. However, no convincing evidence is presented. Nonetheless, another scenario might explain how *Saara* dispersed eastward. The *Saara* root diverged during the Early Miocene (Tamar et al. 2018) and formed two clades:

1) a northern clade (*S. loricata-S. asmussi* clade). Two scenarios may explain how the northern clade dispersed and then speciated: in the first scenario, the clade might disperse northward, passed across Gomphotherium landbridge, and then dispersed eastward (Fig 3A). The population that did not cross the landbridge evolved into *S. loricata*, and the population passed across the landbridge evolved into *S. asmussi* by a peripatric speciation. The divergence of the two species dates back to the Late Miocene (ca. 6 Ma). In the second scenario, the northern clade might have extended its range towards central Iran during the intermittent Tethys seaway connections and/or permanent Tethys seaway closure (Fig 3B). Then the Zagros orogeny might have split the parental population into two parts: one evolved into *S. loricata* distributed in the western Zagros regions, and the another evolved into *S. asmussi* distributed in the eastern Zagros and central Iran. This represents an interesting hypothesis on the role of the Zagros uplifting in allopatric speciation forming two new and distinct species.

2) an eastern clade (evolved into *S. hardwickii*), which passed across a path that formed through the contact of the Indian and Arabian Peninsula continental shelves (Fig. 4) (Aitchison et al. 2007), strengthened by the sea level regression of the Persian Gulf and the Oman Sea owing to the Middle Miocene glaciation (Lambeck 1996). The Middle Miocene fossil in Gujarat, India (Čerňanský et al. 2021) is a valuable trace that provides support for this hypothesis on the biogeography of *S. hardwickii* and is supported by the chronology of paleontological events including the Late Cretaceous (Apesteguía et al. 2016), the Early Oligocene (Holmes et al. 2010), and the Middle Miocene (Čerňanský et al. 2021). The currently accepted hypothesis cannot explain the chronology, however suggesting that alternative hypotheses are called for.
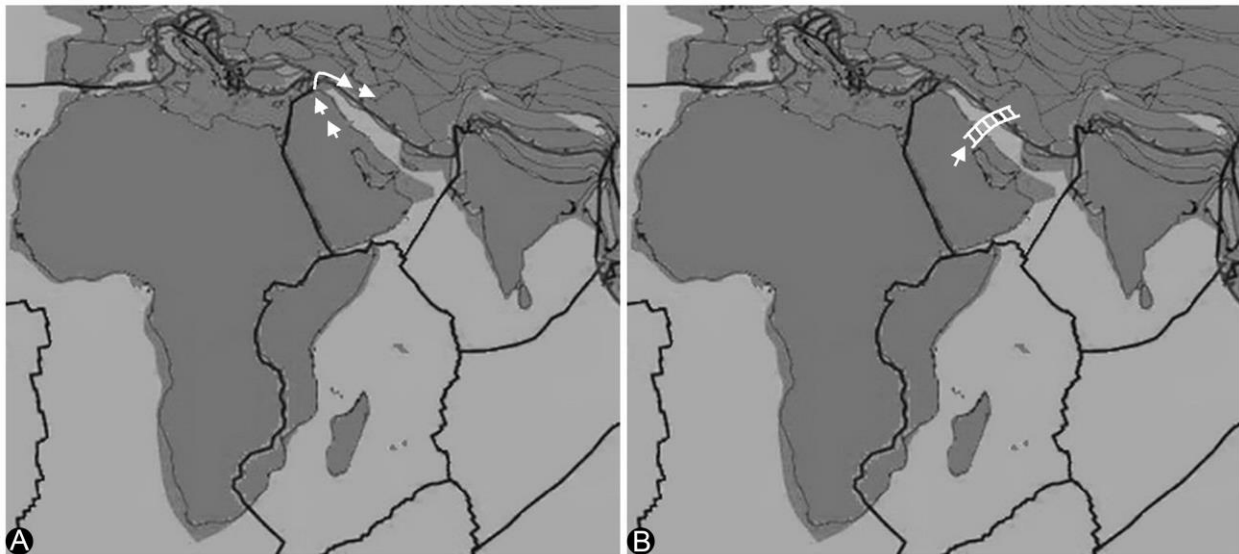

FIGURE 3. Two new hypotheses for the dispersal route of the *Saara*'s northern clade in the Middle Miocene. A) dispersal through Gomphotherium landbridge, B) dispersal through the intermittent Tethys seaway connections and/or permanent Tethys seaway closure.
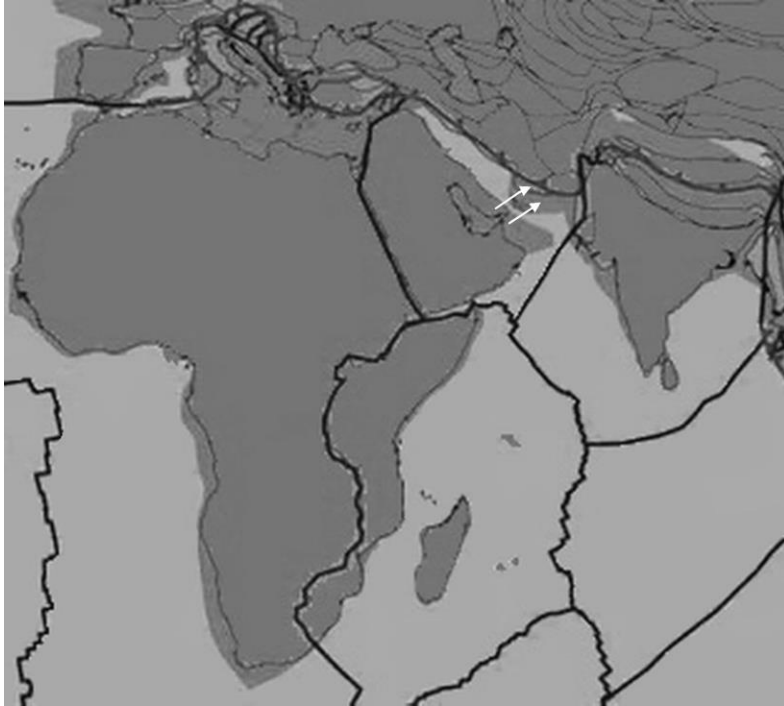
FIGURE 4. The hypothesis of the Indian and Arabian Peninsula continental shelves' contact for the dispersal route of the *Saara*'s eastern clade in the Middle Miocene.
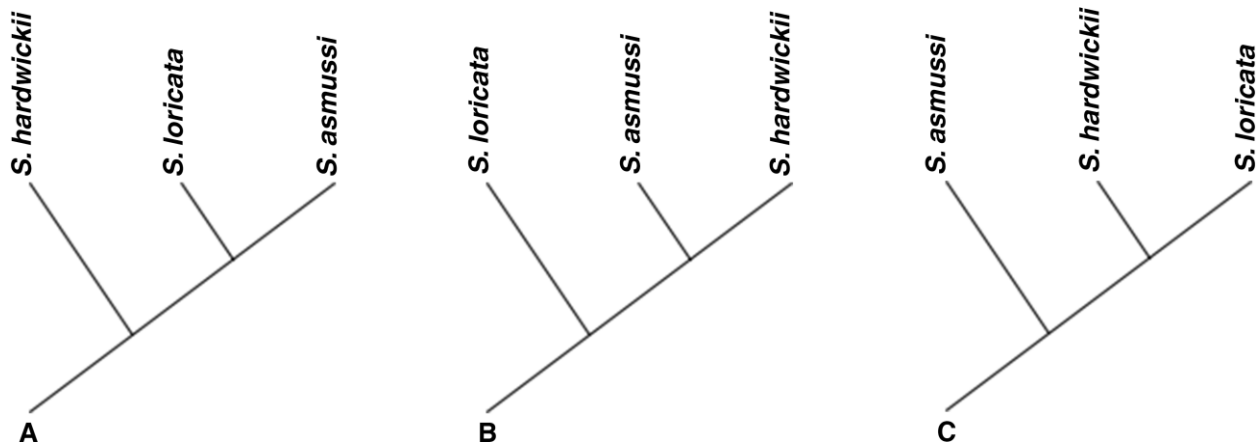

FIGURE 5. Three phylogenetic trees for the species of the genus *Saara*.

DISCUSSION

Acrodont lizards mainly inhabit the following Gondwanan plates adjacent to or part of Asia: Afro-Arabia, which connected with Asia ca. 18 Ma; India, which connected with Asia ca. 50 Ma; and Southeast Asia, which connected with Asia through the Indochinese blocks ca. 120 Ma or earlier, small terranes to the south of Indochina ca. 65 Ma, and small island terranes as far north as Sulawesi ca. 10 Ma (Macey et al. 2000; Okajima and Kumazawa 2010; Grismer 2016). Taxa associated with a particular Gondwanan plate are expected to have deep divergences (endemic clade or basal paraphyletic group) or, at least, a sister-group relationship with taxa in adjacent regions of Asia. According to this logic and assuming the gondwanian origin of Acrodonta (Macey et al. 2000; Holmes et al. 2010), Uromastycinae, which is suggested to be the first offshoot of Agamidae (e.g., Okajima and Kumazawa, 2010), can present a sister-group relationship between *Uromastyx* in Africa and *Saara* in the Middle East. Two lines of evidence support our hypothesis: 1) as per paleontological studies (e.g., Holmes et al. 2010; Čerňanský et al. 2021) the uromastycine clade has existed in Afro-Arabia before the basal dichotomy, forming *Saara* and

Uromastyx during the Oligocene; 2) by considering the current biogeographical scenario, which is based on molecular phylogeny (e.g., Wilms et al. 2009; Pyron et al. 2013; Tamar et al. 2018), *S. loricata*, or, at least, *S. asmussi*, should have been the sister taxon of *Uromastyx* sensu stricto, whereas it is not.

The Gomphotherium landbridge is a well-known candidate for facilitating a great faunal exchange between Afro-Arabia and Asia (Rögl 1998, 1999; Mirzaie Ataabadi 2010; Göhlich 2020) and has persisted continuously since ca. 15 Ma (Harzhauser et al. 2007; Pook et al. 2009; Šmíd et al. 2013). Two other candidates, however, can be nominated for such a faunal exchange: 1) intermittent Tethys seaway connections and/or permanent Tethys seaway closure followed by Zagros orogeny, and 2) the Indian and Arabian Peninsula continental shelf contact followed by subsequent glacial Persian Gulf and the Oman Sea regression. Noteworthy, however, is the fact that by considering the Gomphotherium landbridge as the only biogeographical candidate for uromastycine dispersal route, and based on the universal distribution of *Saara* species (Fig 1B, 2P–R), the dispersal route and plausible speciation centers of the clade passed from west Zagros (*S. loricata*), the Gomphotherium landbridge, Central Iran, west Pakistan (both for *S. asmussi*), east Pakistan, and India (*S. hardwickii*). Consequently, of three phylogenetic trees (Fig 5), the tree number B better represents the phylogenetic relationships corresponding to the Gomphotherium landbridge hypothesis. In this situation, the clade that led to *S. hardwickii* should have diverged after the clade leading to *S. loricata.* The molecular studies, however, depict a different phylogenetic tree (Fig. 5A); they suggest that the clade led to *S. hardwickii* diverged from the *loricata-asmussi* clade in the Middle Miocene ca. 18–16 Ma (Wilms et al. 2009; Tamar et al. 2018), and its trace has been discovered in India (Gujarat) by 14 Ma (Čerňanský et al. 2021). They further determined that *S. loricata* and *S. asmussi* are sister taxa diverged from each other at ca. 6–5 Ma (Pyron et al. 2013; Tamar et al. 2018). Therefore, here we rule out the Gomphotherium landbridge scenario for the eastern clade (i.e., *S. hardwickii*). Looking at the paleogeography and paleoclimatology of the old world (see section 3), we suggest that the eastern clade passed across a corridor that formed through the contact of Indian and Arabian Peninsula continental shelves amplified by subsequent glacial Persian Gulf and the Oman Sea regression. This scenario is concordant with the phylogenetic biogeography of the genus *Saara*.

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