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VOLUME 10 ISSUE 1 JUNE 2023

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Jordan Journal of Natural History

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It is a pleasure to present issue 8 of Jordan Journal of Natural History (JJNH), a journal published by the Conservation Monitoring Centre, The Royal Society for the Conservation of Nature (RSCN). The Jordan Journal of Natural History (JJNH) is an open access international scientific journal publishing original research and reviews in nature history in its broadest sense. This is taken to include conservation biology, botany, geology, paleontology, zoology, and ecology, including a broad range of systematics papers encompassing traditional taxonomic revisions and descriptions, cladistics analyses and molecular phylogenetic. The editorial policy of JJNH will follow the lines of most international journals. All manuscripts received by the editor will be examined by referees, who will be instructed to judge the papers by the significance and novelty of the results reported and to favour briefness of presentation.

The editorial board will make every effort to ensure prompt processing of the manuscripts received and to widen the circulation of the journal as far as possible. A group of distinguished scholars have agreed to serve on the editorial board. Without the service and dedication of these eminent scholars, JJNH would have never existed. Now, the editorial board is encouraged by the continuous growth of the journal and its formation into a true multidisciplinary publication. We are also honored to have the privilege of working with all members of the international advisory board served by a team of highly reputable researchers from different countries across the globe. We are also delighted with our team of national and international reviewers who are actively involved in research in different natural history fields and who provide authors with high quality reviews and helpful comments to improve their manuscripts.

We would like to reaffirm that the success of the journal depends on the quality of reviewing and, equally, the quality of the research papers published. In addition to being a hard-copy journal, JJNH is an open access journal which means that all contents are freely available for the users and their institutions free of charge. Users are allowed to read, download, copy, distribute, print, search, or link to the full texts of the articles in this journal without asking for prior permission from the publisher or the author. This is in accordance with the BOAI definition of open access.

At the end of this preface, would like to thank our readers and authors for their continuing interest in JJNH, and each member of our editorial and review boards for their continued hard work, support and dedication, which made it possible to bring another new issue of JJNH to the multidisciplinary international audience. We very much appreciate your support as we strive to make JJNH one of the most leading and authoritative journals in the field of Natural History Sciences.

June, 2022

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Hamidan, NA, Geiger, MF and Freyhof, J. 2014. *Garra jordanica*, a new species from the Dead Sea basin with remarks on the relationship of *G. ghorensis, G. tibanica* and *G. rufa* (Teleostei: Cyprinidae). *Ichthyological Exploration of Freshwaters*, 25(3): 223-236.

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A Brief Overview of the Origin of the Land Mammals of Costa Rica

Lucía Isabel López[1] and José Manuel Mora[2*]

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Abstract: Despite its small size (51.000 km^2), there is approximately 5% of the world's known mammal species (over 260) in Costa Rica alone. This rich biodiversity is due, at least in part, to its geographical position along the bridge that connects North and South America and separates the Atlantic from the Pacific Ocean. To understand whence, when, and how mammals settled in Costa Rica, it is necessary to take into account the geological, climatic, and ecological processes that occurred in Central America during the Cenozoic. The origin of Costa Rica follows from a series of complex geological events ensuing from the interaction of three tectonic plates, a microplate, and several exotic tectonic fragments from different plates. Central American vertebrate fossils mainly are from the late Cenozoic and represent all the major taxonomic groups. However, the history of Central American mammals lacks further direct fossil evidence. Known vertebrate fossils date not only to before and after the closure of the Isthmus of Panama, but they also constitute the direct fossil record documenting what clearly was a dispersal route between North and South America. The mixture began with the exchange that took place over the islands making up the current Central American region, and increased when the Central American isthmus was closed and became dry land, because it allowed a greater traffic of mammals. Within this framework of global and local abiotic patterns of change, the Great American Biotic Interchange (GABI) stands out because it constitutes one of the most significant biogeographical events worldwide. Central American mammal fossils help provide an understanding of the GABI after the closure of the Panamanian isthmus. This work analyzes these facts and summarizes some of the more recent pertinent findings to provide a brief overview of mammalian history in Costa Rica.

Key words: Central America, dispersal routes, faunal interchanges, geological history, Great American Biotic Interchange, marsupials, tectonic.

Introduction

Costa Rica is a small country: with an area of 51,100 km^2 covering only 0.034% of the land surface of the Earth (Mora *et al*., 2021). Despite its small area, the country has a rich biodiversity, due, at least in part, to its geographical position along the bridge that connects North and South America and has allowed for the movement of species from the north to the south and vice versa. In addition, Costa Rica occupies an interoceanic position at the narrow Central American isthmus, which separates the Atlantic from the Pacific Ocean (Alvarado and Cárdenes, 2016). There are over 260 mammal species documented from Costa Rica , that is approximately 5% of the world's known mammal species (SINAC, 2014). This represents almost a 150-fold difference between the proportion of area covered and the proportion of mammalian biodiversity present. Ecological conditions for this high diversity have been discussed widely (Burger, 1981; Gómez, 1986; Pillay *et al*., 2022), and a large amount of information has been generated regarding the history of the origin and arrival of the mammals of Costa Rica. The present work summarizes some of the more recent pertinent findings to provide a brief overview of mammalian history in Costa Rica.

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Major mammalian dispersals occurred at times of low sea levels, resulting in loss of endemism on continents that originally were isolated, such as South America and Africa, along with changes in the composition of the Holarctic fauna (Janis, 1993). Historical invasions have been through exchange routes working as bridges that could become filters: some taxa are able to pass but others are not. The Central American isthmus has been such a corridor for many species of mammals, but also acted as a filter for other species (Alvarado, 1994; Alvarado and Cárdenes, 2016). Deserts, mountains, xeric vegetation, and rainforests, are strong filters for many species of mammals (Simpson, 1977).

To understand whence, when, and how mammals settled in Costa Rica, it is necessary to take into account the geological, climatic, and ecological processes that occurred in Central America during the Cenozoic; the same processes underway in South and North America similarly had important influences. However, the geological history of the Central American region—and that of Costa Rica in particular—is of fundamental importance. “Distant” aspects of these processes had important local biological influences here including the uplift and formation of the Andes Mountain range and the formation of Amazonian forests (Antonelli *et al*., 2009; Hoorn *et al*., 2010; Antoine *et al*., 2016; Pelegrin *et al*., 2018). At the same time, “local” aspects are also critical, such as the formation of open savannah-type habitats associated with the cyclical Quaternary glaciations, the establishment of a terrestrial connection between South and North America and its impact on oceanic and atmospheric currents, and therefore on global climate in general (Bacon *et al*., 2015; Carrillo *et al*., 2015; Montes *et al*., 2015). Within this framework of global abiotic patterns of change, the Great American Biotic Interchange (GABI) stands out because it constitutes one of the most significant biogeographical events worldwide (Webb, 2006; Lucas and Alvarado, 2016; Pelegrin *et al*., 2018). The GABI had an enormous influence on the development of mammal communities in the Americas (Pelegrin *et al*., 2018). This context was the framework for key evolutionary events to understand the establishment of the mammal fauna in Central America and of the fauna in the Neotropics in general and the mammals of Costa Rica in particular (Bacon *et al*., 2015; Carrillo *et al*., 2015; Erkens, 2015; Chávez, 2016).

Geology of Costa Rica

The origin of Costa Rica follows from a series of complex geological events ensuing from the interaction of three tectonic plates: Caribbean, Cocos, and Nazca, as well as the Panama microplate, and several exotic megablocks, tectonic fragments from different plates (Alvarado and Cárdenes, 2016) (Figure 1). The oldest rocks of Costa Rica date to about 200 Ma and developed many km southwest of the actual position (Table 1). The geological history of Costa Rica can be separated into several stages, some of which occurred simultaneously (Table 1). The territory of the country is part of the bridge connecting North and South America and occupying the Central American seaway (Figure 2). The active subduction of the Cocos plate beneath the Caribbean plate, volcanism, and several other tectonic phenomena, are examples of Costa Rican geological history that continues today.

Mammals of the Neotropics

The Americas comprise two zoogeographic regions (Figure 3): The Nearctic includes almost all of North America while the Neotropical begins in northeastern Mexico and includes Central and South America (Cox, 2001). The Neotropical region is considered as the most biodiverse globally, in particular insofar as mammals are concerned, with about 25% (about 1145 spp.) of the global diversity of the group residing in this region (Patterson, 2000; Rull, 2008, Pelegrin *et al*., 2018). The region includes rainforests, temperate forests, deserts, savannahs, paramos, and steppes, associated

Table 1. Principal geological events related to the development of Costa Rica according to the division of the geological time scale (GTS) and its age (Ma = million years ago)

Division GTS	**Ma**	**Events**	**Observations**
Jurassic	200	Oldest rocks in Costa Rica	At Santa Elena, Nicoya Peninsula, others. Formed to the southwest of the current position.
Late Cretaceous	80 – 66	Loma Chumico Formation (Nicoya) Volcano-sedimentary unit	Product of accumulation of organic matter in anoxic and deep environments High global °T No ocean currents
Cretaceous	> 66	No landmasses with terrestrial faunas	There is no record of continental fossil vertebrates in South Central America for the Paleogene, nor prior to the late Oligocene
		Proto-Antilles bridge	Exchange of biota between North and South America Territories moving east – northeast
End of the Cretaceous	66	Shallow seas “nearby” Island Arc	Some biological interchanges
Paleocene – Lower Eocene	66 – 49	Tectonic activity Cerro Turrubares was an active volcano	Cerro Turrubares is part of the Herradura promontory (an island that went from Cerro Turrubares to Jacó)
		“Territory” acquired current position	Current Costa Rican location occupied by islands and promontories Establishment of tectonic features similar to the current ones Developing of carbonate platforms (Basin of Tempisque River)
		Subduction is established in the Mesoamerican Trench	Tectonic activity increases.
Upper Eocene	41 – 34	Regional uplifting	Basins with shallow water marine sedimentation (< 200 m) Promotes sedimentation of carbonate platforms
		Interruption of volcanic activity	
		Formation of the La Candelaria basin begins.	Basin accumulated several km thick sediments. Continued into the Miocene
Oligocene	34 – 24	Decrease of the sea level in the Central American seaway	Separation of basins Local reef development Decreases the depth of sedimentary basins Biota exchange by island hopping and swimming
		Submarine volcanism in back basins of Talamanca (among others).	In the Térraba River area, very thick marine sediments are deposited on the continental slope.
		Northern part of Costa Rica emerges Continuous sedimentation in the southern part.	Northern part of Costa Rica subjected to erosion
	27 – 25	Farallon Plate broke up into the Cocos and Nazca plates High volcanic activity all over Costa Rica	Modern tectonic configuration of Costa Rica begins

Miocene	24 – 5	Shallow marine deposition all over the country Sedimentation in independent basins Growth of Talamanca Intense erosion on both slopes High volcanic activity continues (to 8 Ma)	Biological exchange island hopping or swimming islands in what is now Central America
		Reorganization of tectonic plates Consolidation of volcanic activity	Ignimbrite and other pyroclastic deposits Witnesses: Cordilleras of Aguacate, Tilarán and Cutris – Sarapiquí
		High tectonic activity Uplift associated with the collision of the Cocos Ridge with the Mesoamerican trench (5.4 Ma)	Exhumation of Talamanca characterized by a sudden increase in uplift rates between 5.5 and 3.5 Ma Tectonics and intense seismicity off Quepos and Osa Extinction of volcanism in Talamanca Decrease in the depth of the Mesoamerican trench in the collision zone Existence of underwater landslides Coastal uplift Talamanca uprising accelerates
		Since 8 Ma the inner arc has been parallel to the modern volcanic front,	It progressively retreated towards the northeast of the country
Pliocene	5 – 1.8	High volcanic activity Clogging of sedimentary basins	Closure of the Central America bridge (Isthmus of Panama) Biological exchange (GABI)
		Melting of glaciers and snowcaps of higher mountains	Together with volcanic activity in a tropical environment contributed to generate very thick lahars and alluvial deposits.
Quaternary	1.8 – present	Establishment of current volcanic mountain ranges	Central Valley depression forms This highland basin filled with a thick accumulation (> 1 km) of volcanic products (andesitic to dacitic lavas, pyroclastic rocks, lahar, and debris avalanche deposits)

with a wide latitudinal range and a highly complex topography (Tews et al., 2004). It is the second most diversified region in terms of the number of mammal families (after tropical Africa), with at least fifty-six families (compared to fifty-eight families in Africa; Vaughan *et al*., 2015). However, Africa has twenty endemic families whereas in the Neotropics, twenty-eight are endemic. South America was separated from North America by the Central American Seaway more than 150 million years ago (Dartnell, 2019). The separation of these two continental masses began 190 – 180 Ma with the breakup of Pangea (Figure 4) through the rift that separated Laurasia from Gondwana (Veevers, 2004; Dartnell, 2019). South America and Africa began their separation with the subsequent formation of the South Atlantic Ocean 100 –110 Ma (Ezcurra and Agnolín, 2012). Although linked to other landmasses for several million years after this separation between them, the biota of North and South America evolved independently, with successful radiations and extinctions, and with some exchanges between the continents (Simpson, 1950). There is also evidence that the Neotropical mammalian biodiversity was higher in the past than it is today, partly because many species have gone extinct owing to the effects of climate change, habitat fragmentation, disease, and more recently, human impact (MacFadden, 2005).

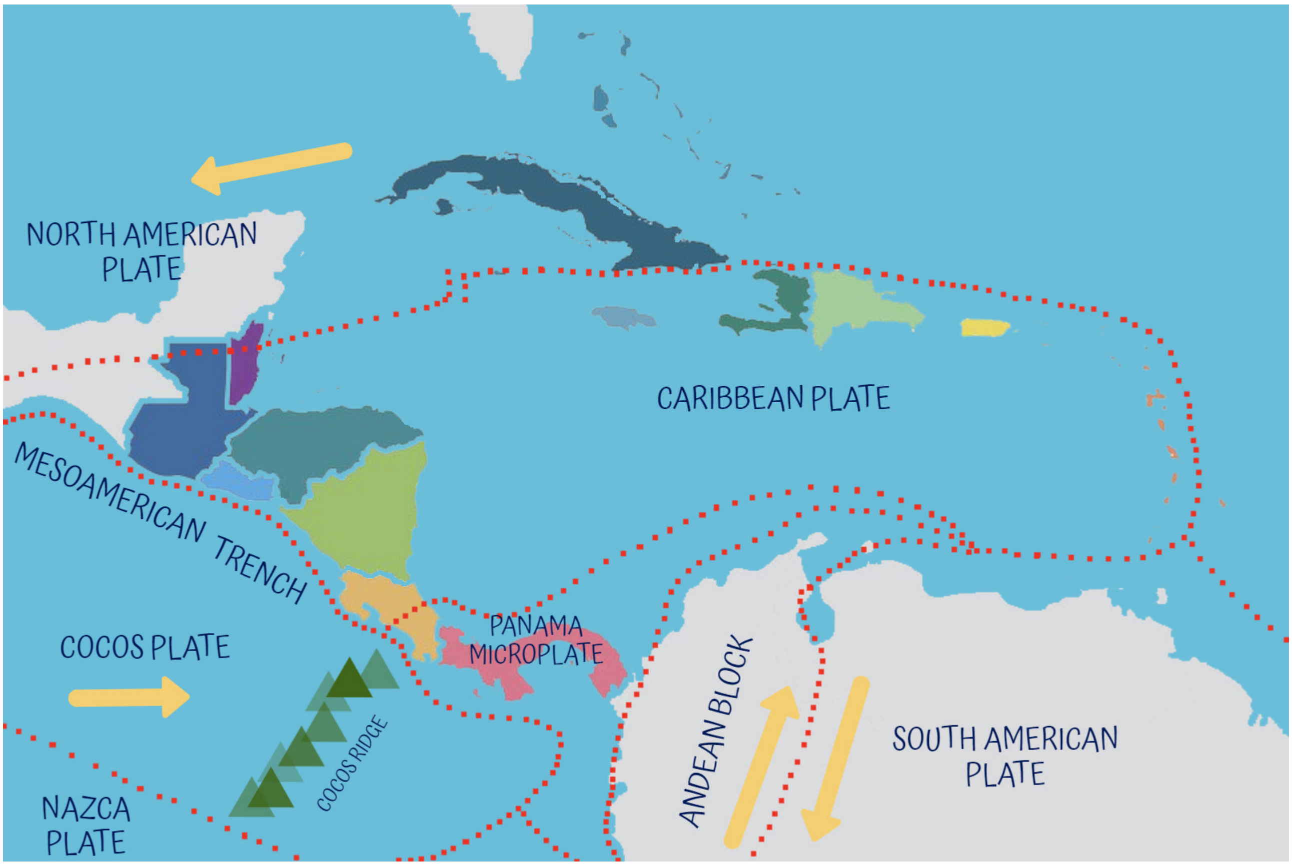

Figure 1. Location and relationship of Central America, including Costa Rica, with the tectonic plates that have determined the geological history of the country. Figure by Lucía I. López.

The magnitude of the faunal exchanges before the land connection between North and South America through the Isthmus of Panama about 3 – 4 Ma is still under debate (MacFadden, 2005; Agnolin *et al*., 2019). A wide variety of tetrapod, including mammals such as camels, peccaries, horses, monkeys, procyonids, mustelids, and ground sloths, among others, are known to have crossed the passage between North and South America long before of the establishment of the bridge (Cione *et al*., 2015; Pelegrin *et al*., 2018; Agnolin *et al*., 2019). Taxa that successfully crossed between continents prior to the establishment (i.e., established themselves) have been designated "herald" taxa (Webb, 1985). Similarly, the age of the connection is still under debate, as some authors argue that it occurred several million years ago, 3 Ma (Coates and Stallard, 2013; Montes *et al*., 2015; Erkens, 2015). In that respect, Iturralde-Vinent and MacPhee (1999) proposed the presence of a precursor steppingstone connection along the Greater Antilles and Aves Ridge landspan, termed GAARlandia, permanently subsiding <32 Ma. Taxa transgressing in either direction prior to 32 Ma (e.g., Dasypodidae, Pampatheriidae, Megalonychidae, Mylodontidae, Caviomorpha, and Platyrrhini) may have taken that sweepstakes route initially, with recent taxa instead using the Panama land bridge or its precursor stepping stone island systems.

In any case, during the time that North and South America were separated, camels and horses, for example, evolved in the former, but later became extinct from this continent (Webb and Stehli, 1995; Honey *et al*., 1998). However, before their extinction they passed from North America to Eurasia. Camelids originated in North America, and some authors consider them indicators of the GABI that began with the closure of the Isthmus of Panama (Webb and Stehli, 1995).

However, there is evidence that camels colonized South America before the existence of the Central American land bridge (Reguero *et al*., 2007), potentially

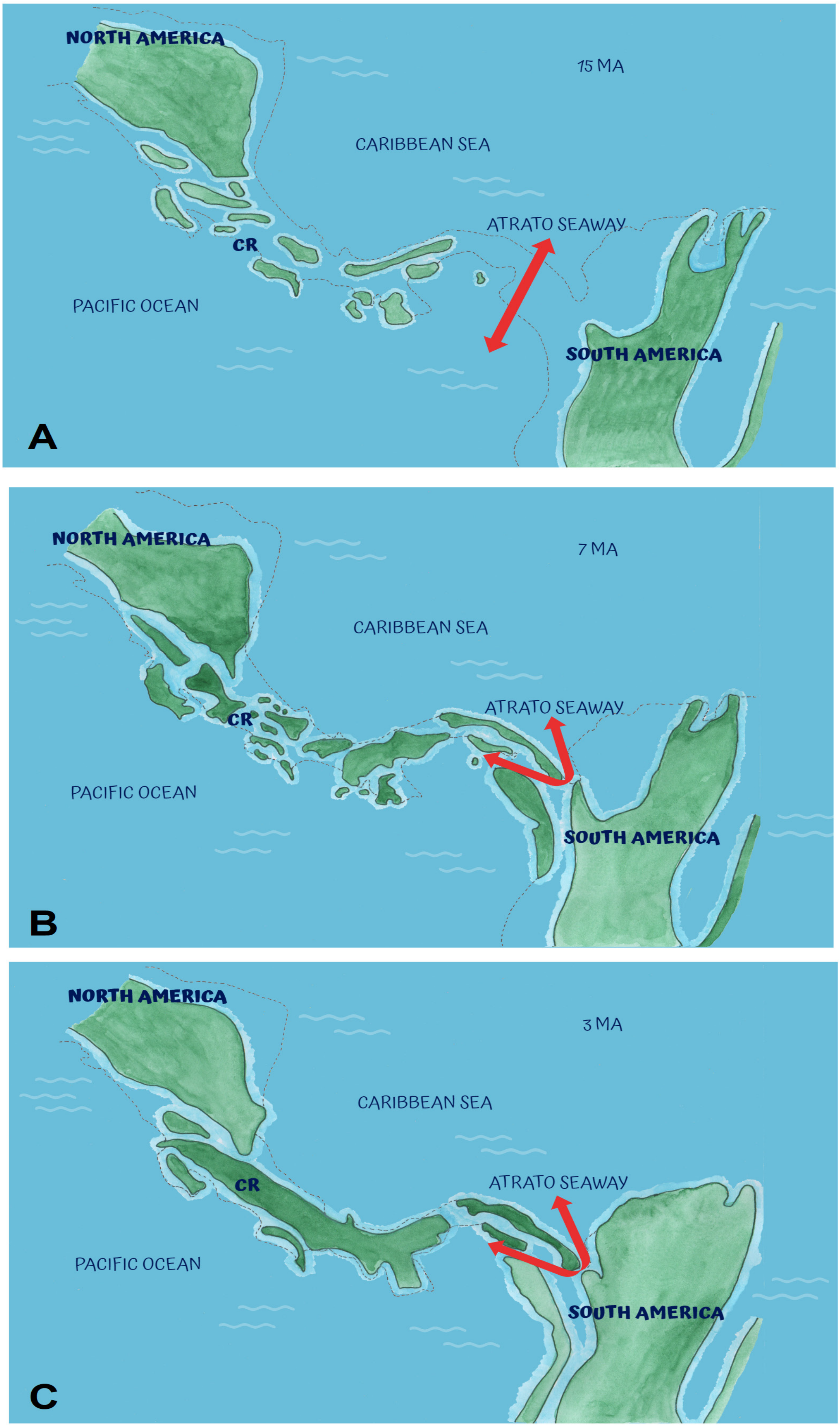

Figure 2. Three phases of the geological history of Costa Rica (CR): A) 15 Ma during the Miocene, B) 7 Ma also during the Miocene, and C) 3 Ma during the Pliocene. Figure by Lucia I. López.

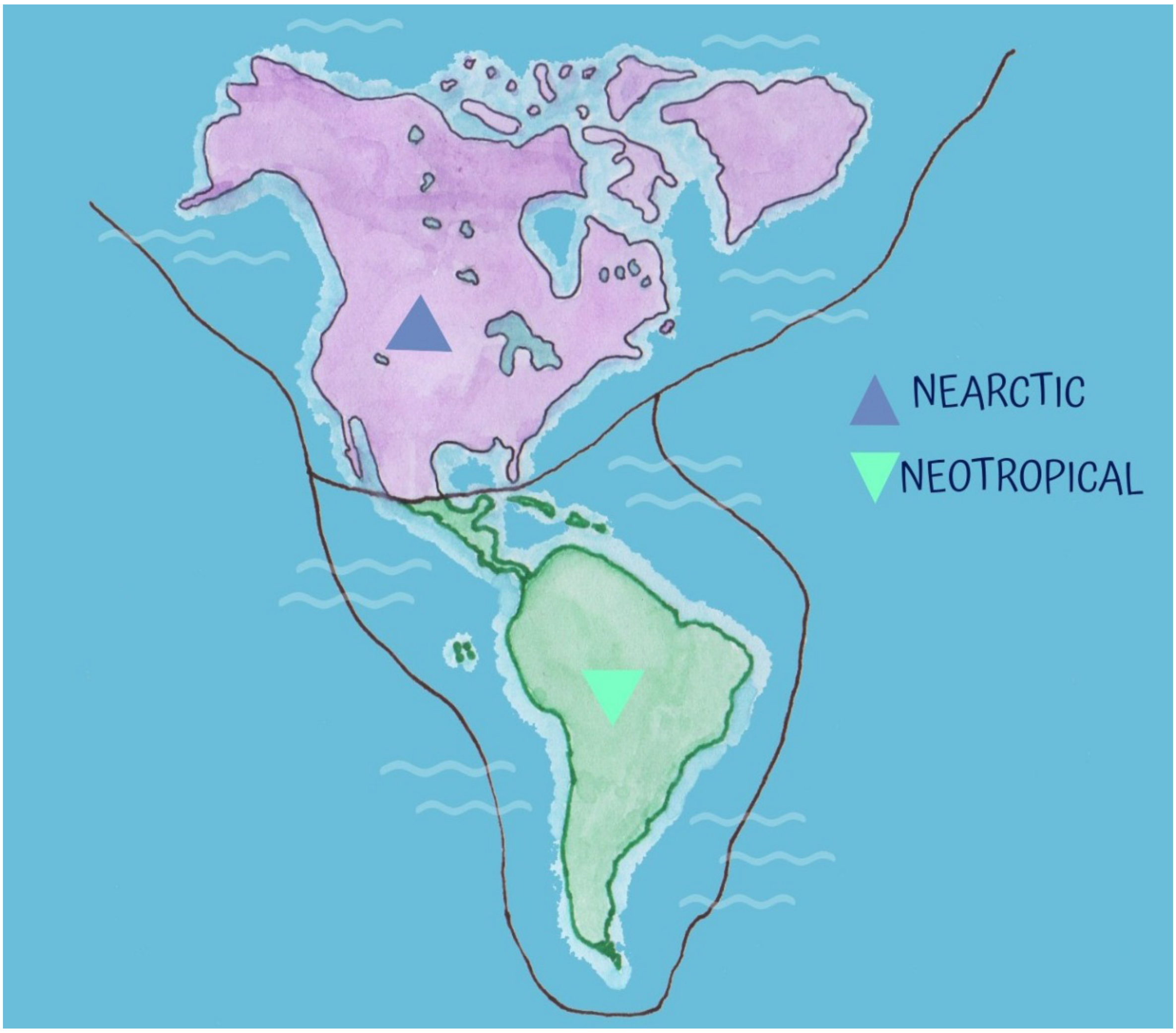

Figure 3. The Neartic and Neotropical zoogeographic regions occupy the territory of the Americas. Figure by Lucía I. López.

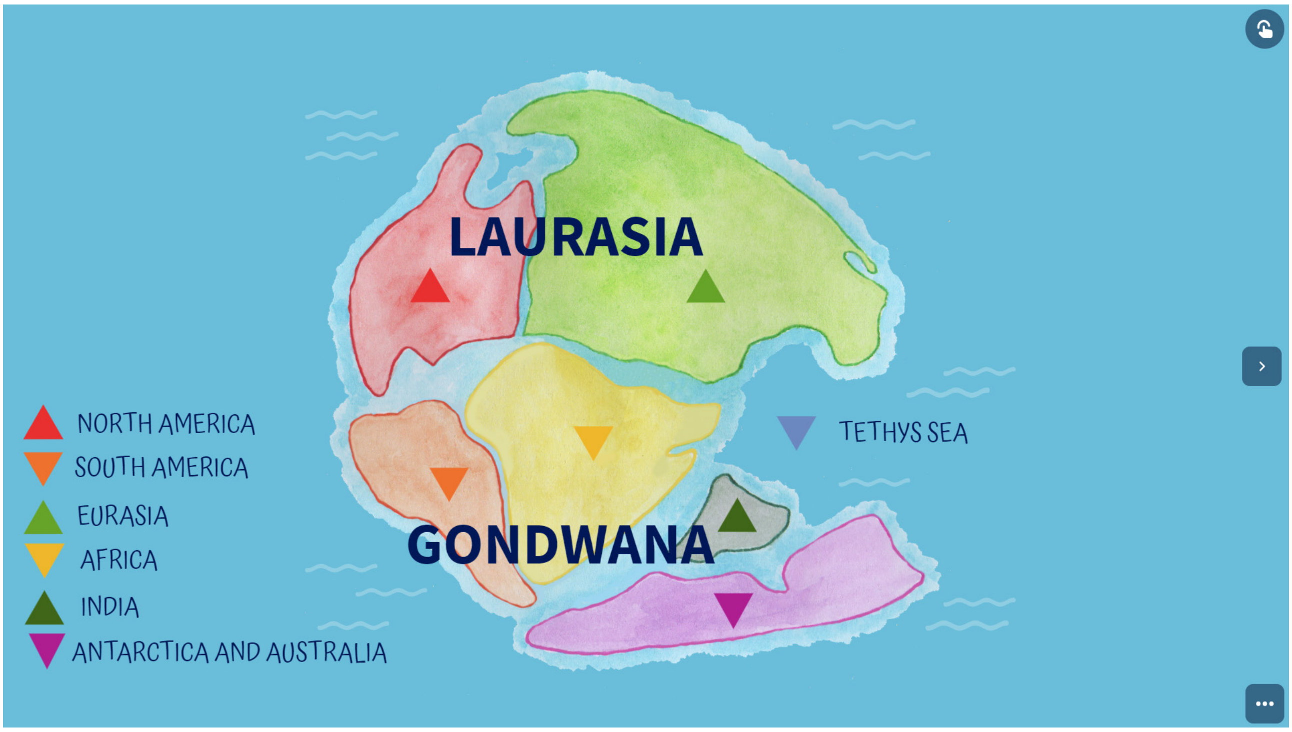

Figure 4. Land masses of the Earth at the end of the Triassic 190 Million years ago. Figure by Lucía I. López.

supporting the GAARlandia hypothesis. In South America, in turn, there was a great radiation of large edentate mammals such as the giant armadillos and the giant ground sloths (Simpson, 1950); similarly, some taxa among which were successful at establishing themselves in North America.

The Neotropics does not constitute all of South America but does include Central America and portions of Mexico (part of North America). However, to contextualize the origin of Costa Rican mammals more fully, it is convenient first to analyze the history of South American mammals separately. At this level, it is key first to review the biogeographical isolation of South America and subsequently the impact and consequences of the GABI, both in North and South America, and in Central America in general and Costa Rica in particular. However, it is clear that the taxa of North American mammals have had a great influence on the species and community composition of the mammal fauna of Central and South America, and therefore, the origin of these mammals is also relevant. With the exception of the southernmost part of the Florida peninsula and Greenland, the Nearctic Biogeographical Region includes nearly all of North America north of the tropical sections of Mexico. The Cenozoic history of North America mammals is examined in detail in Woodburne (2004). It is generally accepted that South America remained isolated from the rest of the continental masses around 80 Ma, until the establishment of the Isthmus of Panama 3 – 4 Ma, which connected it with North America (MacFadden, 2006; Agnolin *et al*., 2019). However, more recent interpretations suggest that South America retained a connection to Antarctica until the Oligocene (30 Ma; McLoughlin, 2001). This connection allowed faunal exchanges between South America and Australia according to recent evidence based on marsupials. This information proposes a dispersal of marsupials from their origin in North America to Australia via South America and Antarctica (Woodburne and Case, 1996; Luo *et al*., 2003; Meredith *et al*., 2008). In addition, it is possible that after the separation of South America from Africa at the end of the Cretaceous (75 Ma), the formation of a volcanic arc of islands began in the Caribbean that allowed faunal exchanges from North America (Horne, 1994; Iturralde-Vinent and MacPhee, 1999). As a result, the splendid isolation of South America was neither as large nor as long as previously thought (Erkens, 2015; Hoorn and Flantua, 2015; Agnolin *et al*., 2019). The isolation of South America varies between 80 Ma, as traditionally assumed, (Simpson, 1980; Flynn and Wyss, 1998) and 50 Ma according to the most recent paleontological evidence (Ezcurra and Agnolín, 2012; Bacon *et al*., 2015). This difference is key when considering the evolution of South American mammals.

The mammals of South America have four components, with marsupials as ancient colonizers being the first to arrive. Marsupials arrived from their area of origin in North America to South America in the Late Cretaceous and diversified into groups such as current didelphids (Wilson *et al*., 2016). The first records of various lineages of placental mammals date back to the Paleocene and Eocene (de Oliveira and Goin, 2011; Herrera *et al*., 2012). Among these groups are xenarthrans and various lineages of ungulates (de Oliveira and Goin, 2011; Herrera *et al*., 2012). Xenarthra is the taxon that is currently hypothesized to contain the orders Pilosa (sloths and anteaters) and Cingulata (armadillos). Although one species of armadillo has invaded North America, as have in the recent past some species of ground sloths, they otherwise are an exclusively South American group (Simpson, 1980; dos Reis *et al*., 2014). Based on fossil data, these mammals appeared in the Upper Paleocene (Riochican of Argentina [Chubut], 55.8 – 57.0 Ma, for Dasypodidae [Simpson, 1935]) and diversified during the Oligocene (Vizcaíno, 2009, see dos Reis *et al*., 2014). For their part, ungulates developed during the Paleocene from North American ancestors and diversified into groups such as litopterns, notoungulates, pyrotherians, xenungulates, and astrapotherians (Billet, 2011; Cione *et al*., 2015). Recent evidence suggests that *Macrauchenia* (litopterns) and *Toxodon* (Notoungulata) constitute a sister group to the extant perissodactyls (Buckley, 2015; Westbury *et al*., 2017). This suggests that the ancestors of these groups came from North America and radiated extensively, resulting in substantial species diversity during the Oligocene and Miocene. Marsupials, xenarthrans, and ungulates make up the first autochthonous faunal component of South America (Pelegrin, 2018); they are the members of the first stratum of Simpson (1950).

The second component is the arrival of the ancestors of South American primates and rodents (de Oliveira *et al*., 2009) that make up the second stratum of Simpson (1950) occurring from the end of the Lower Eocene to the upper one when conditions for dispersal from Africa were present (Springer *et al*., 2011; Ezcurra and Agnolín, 2012). This process could have been possible by physical means such as the formation of potential island arcs between the continents and the directionality of the oceanic currents in the Atlantic, which was just being formed and therefore at a shorter distance between the two continents. These currents may have carried rafts of vegetation from the large river basins of Central and West Africa (Antoine *et al*., 2011; Bond *et al*., 2015).

Some faunal interchanges between North and South America were facilitated by a hypothetical Antillean arc that connected the southeastern USA to Venezuela, the tongue of land called GAARlandia, (Lucas and Alvarado, 1994). This hypothesis explains the brevity of the Caribbean – Mainland exchanges between the Eocene and the Oligocene. The possible existence of GAARlandia has key implications for understanding the early phases of biotic exchange between North and South America before the Pliocene (Agnolin *et al*., 2019). However, there is no geological evidence for this hypothesis. On the contrary, colonization was apparently heavily filtered and assembled in a piecemeal fashion consistent with over-water dispersal (Ali and Hedges, 2021). Recent evidence suggests that Central America played little or no part in these two oldest components: Late Cretaceous/Paleocene and Eocene/Oligocene (Lucas and Alvarado, 2016). During those dispersal times, Central America was either nonexistent (in part), or was isolated as an island arc, so the most likely north–south pathway for land vertebrate would be across GAARlandia (Lucas, 1986; Alvarado, 1994; Lucas and Alvarado, 2016), but see Ali and Hedges (2021).

Current evidence suggests that island chains existed between North and South America during the Paleogene (e.g. Dávalos, 2004; Pindell and Kennan, 2009; Agnolin *et al*., 2019). These islands could be related to the proto-Antilles or to the Panamanian tectonic microplate and the igneous complexes derived from the Galapagos hotspot (Montes *et al*., 2012b). Regardless of origin, the island chains enabled faunal exchange between North and South America at various times. This phase has been called Pre-GABI or Proto-GABI (Wroe *et al*., 2004; Cione *et al*., 2015) and has been supported by the recent increase in fossil finds in North, Central, and South America. At the Oligocene-Miocene boundary, a new phase of exchanges began that preceded the GABI itself (Bacon *et al*., 2015). These exchanges lasted throughout the Neogene until the first stage of the GABI with the formation of the connection between North and South America (Woodbourne, 2010). These were very complex geological processes that have found support in molecular phylogenetic studies. Already during the Neogene, the degree of connection between the two continents increased (Prothero *et al*., 2014; Carrillo *et al*., 2015).

During the ProtoGABI, several mammal taxa participated in the exchanges, based on evidence from molecular data. Also, there is fossil evidence of *Panamacebus* from the Lower Miocene of Panama (Arikareean Ar4 faunal zone, ca. 21 Ma), which is not only the first platyrrhine fossil primate found outside of South America, but also the earliest fossil evidence of mammalian exchange from South America to North America (Bloch *et al*., 2016). Added to this exchange, are the oldest records of sloths in the Greater Antilles from the Oligocene and Early Miocene of Puerto Rico and Cuba (White and MacPhee, 2001; MacPhee, 2005). The Oligocene glaciations could have caused a sea level drop, thus allowing the passage of mammals due to low sea levels, and the connection between northwestern South America and the island arc between Costa Rica and Panama (Coates *et al*., 2004).

Later, continental drift and plate tectonics caused the formation of a bridge mainly by means of the uplift of the earth's crust and volcanism, which created a geological corridor between North and South America (Alvarado, 1994; Laurito and Valerio, 2012b; Alvarado and Cárdenes, 2016). This corridor allowed the passage of fauna from South America to North America and vice versa, including the GABI as a highly relevant biological event. The Mesoamerican bridge has also acted as a filter in both directions, but particularly from South America to North America, because climatic conditions in North America are less favorable for tropical taxa (Alvarado, 1994; Pelegrin *et al*., 2018). During the Miocene (23.8 Ma – 5.3 Ma), climatic regimes generally were less seasonal than those of comparable regions of today, and many forested biomes were replaced with more open-country woodlands or grasslands (MacFadden, 2006).

The mammals of Costa Rica within the context of Central America

The mammals that inhabit Central America derive from four sources: The North Americans, the old South Americans, the young South Americans, and the Mesoamerican unit (Simpson 1950; Rich and Rich, 1983; MacFadden, 2006; Woodbourne, 2010). The North Americans dispersed to the southern limit of nuclear Central America (Nicaragua). During the GABI, they also managed, to some extent, prior to that event, to disperse southward as far as South America (Simpson, 1950). The old South Americans are the American marsupials, the xenarthrans, and some bats. Before the GABI, these taxa arrived in Central America, most likely by drifting over water or, in the case of bats, by flying; most likely wind aided during storms (Simpson, 1950). Young South Americans include primates and rodents (Simpson, 1950). Before the GABI, these mammals arrived in Central America possibly as "waif dispersers" by means of sweepstakes routes through the Central American seaway (Coates *et al*., 2004). The Mesoamerican unit evolved in this region, whence they spread to other areas (Rich and Rich, 1983). This unit is questioned by some on the basis that there is no convincing evidence that this region was the center of origin for mammals before the GABI (Webb, 1985). Following this reasoning, Central America acted as a filter to dispersal during the GABI, as well as a center of mammalian evolution, although there is no evidence of something similar occurring during the Pleistocene (Alvarado, 1994; Alvarado and Cárdenes, 2016).

Central American vertebrate fossils are mainly from the late Cenozoic and represent all the major taxonomic groups of vertebrates (Lucas and Alvarado, 2016). This vertebrate fossil record is concentrated in Miocene and Pleistocene sedimentary strata (Lucas and Alvarado, 2016). However, the history of Central American mammals lacks further direct fossil evidence. There are basically no fossils from the Mesozoic (> 66 Ma) and there are very few fossils prior to the Miocene (beginning 23 Ma; Rich and Rich, 1983). That results in the fact that perhaps only 25% or less of the mammalian history of Central America is known, and virtually all of that known history in each case is documented by few fossils (Rich and Rich, 1983). Several fossil sites have been found in all Central American countries, but with little information (Rich and Rich, 1983; Cisneros, 2005). The most diverse group of mammals known from Central American fossils are armadillos, glyptodonts and several other taxa now in the orders Cingulata and Pilosa;

all are of South American origin (Lucas and Alvarado, 2016). These include giant ground sloths of the families Megalonychidae and Megatheriidae (Lucas and Alvarado, 2016). The group also contain small ground sloths (Mylodontidae), including two taxa endemic to Central America from the Pleistocene of Barranca del Sisimico (El Salvador; Webb and Perrigo, 1985). On the other hand, all fossil carnivore taxa, including cats, sabertoothed cats, dogs, bears, and raccoons are of North American origin (Lucas and Alvarado, 2016). Fossil remains of these latter are from Miocene and Pleistocene faunas generally of low diversity and are uncommon (Webb and Perrigo, 1984; Cisneros, 2005, 2011). The southernmost Pleistocene record of the coyote *Canis latrans* is from Costa Rica (Lucas *et al*., 1997). Most Central America ungulates are of North American origin: proboscideans, perissodactyls, including *Tapirus* sp. cf *terrestris*, and artiodactyls, including a Camelidae (*Palaeolama mirifica*) from lacustrine deposits (Pérez, 2013). The only ungulates of South American origin are the notoungulates, and mostly pertain to a *Mixotoxodon*, apparently endemic to northern South and Central America (Laurito, 1993; Lucas and Alvarado, 2016).

In Costa Rica, fossil mammals are known from more than forty-five Pleistocene localities (Alvarado and Cárdenes, 2016). Most of these are proboscideans such as *Cuvieronius hyodon* (Gomphotheriidae), and the mammoth *Mammuthus columbi* (Mammutidae), the southernmost record of mammoths in Central America (Alvarado and Cárdenes, 2016). These localities contain only one or a few large mammalian taxa, but small mammals have been poorly studied (Alvarado and Cárdenes, 2016). This suggests a likely bias towards the preservation of high energy fluvial, alluvial, ignimbrite, and lahar deposits, as well as a bias towards the collection or preservation of large-sized fossils (Alvarado and Cárdenes, 2016). Rodents are basically absent, excluding capybaras (Hydrochoerinae, Caviidae) that are large; rabbit (Lagomorpha) records are scarce, and only few fossil bats have been reported (Webb and Perrigo, 1984; Czaplewski *et al*., 2003; Lucas and Alvarado, 2016). However, a rodent fossil fauna was described by Laurito (2003) from La Palmera locality at San Carlos county in Alajuela province likely of the Upper Pleistocene age and including four species: *Tylomys watsoni*, *Reithrodontomys mexicanus* (which should be reexamined in light of taxonomic changes), *Sigmodon hispidus* (now *S. hirsutus*), and *Proechimys semispinosus*.

Other documented fossil groups include horses, tapirs, camels, and proboscideans, that represent three distinct orders of North American origin (Lucas and Alvarado, 2010a, b). The proboscidean gomphotheres (*Gomphotherium*) first arrived in Central America about 10 Ma. *Cuvieronius* arrived in Central America about 3 Ma and continued expanding their range to southern South America (Lucas, 2013). Finally, there is record of a Pleistocene arrival in Honduras based on a single record of the American mastodon, *Mammut americanum* (Lucas and Alvarado, 1991; Lucas and Alvarado, 2016). A frequent problem is that many fossiliferous sites have not been reported or adequately safeguarded. They also have not been assessed due to the lack of institutional support for investigations as well as other factors (Lucas and Alvarado, 2016). Due to the sparse knowledge generated and the general lack of mammalian fossil remains in Central America, the faunal exchanges of the Paleogene and Neogene ("Tertiary", between 66 and 2.5 Ma), remain unclear, a situation aggravated by the fact that the exact positions of some parts of Central America, and even of its mere existence, are also unknown, both in broad strokes as well as in many other details (Rich and Rich, 1983). It is possible that these regions could have contributed to the exchange of mammals, but it is not known how much. For example, the only dinosaur fossil reported from Central America is a femur discovered in 1971, possibly from a hadrosaur (Lucas and Alvarado, 2016). This fossil comes from the Cretaceous of Valle de Angeles

(Honduras), a locality interpreted as part of a possible terrane that was attached—or at least was close to—southwestern Mexico during the Cretaceous (Lucas and Alvarado, 2016), arriving there in a “Viking funeral ship” as defined by McKenna (1973). After the Neogene, about 2.5 Ma, the situation is better known, for example, as noted above for Costa Rica.

The fossil faunas of the Central American Quaternary reflect a mixture of elements from North and South America that began with the terrestrial connection between these two continental masses 5 – 1 Ma, particularly by means of the GABI (Rich and Rich, 1983). North American mammal families from the Pleistocene of Central America include Leporidae, Felidae, Canidae, Gomphotheriidae, Mammutidae, Elephantidae, Tapiridae, Equidae, Tayassuidae, Camelidae, Cervidae, and Bovidae (Alvarado and Cárdenes, 2016). Families of South American origin include: Dasypodidae, Glyptodontidae, Megalonychidae, Megatheriidae, Mylodontidae, Caviidae (Hydrochoerinae) and Toxodontidae (Alvarado and Cárdenes, 2016).

An important case to note across the history of Central American mammals is that of the Guanajuato Fauna, from the Eocene – Oligocene transition (ca. 34 Ma), being one of the oldest in the region (Rich and Rich, 1983). The Guanajuato Fauna includes two genera of rodents and contrasts with previously mentioned sites in two senses, first, practically all the other sites contain fossils of species of medium or large body sizes, and date to later than the Miocene (< 23 Ma; Rich and Rich, 1983). One of these genera, *Guanajuatomys*, is of clear phylogenetic affinity with the caviomorphs of South America (Black and Stephens, 1973). Perhaps the high affinity of Central American mammals with those of North America can be attributed to the fact that the fossils found belong to the largest mammals (Rich and Rich, 1983). The Guanajuato fauna could be the evidence of a second component of the “tertiary” fauna of Mesoamerica, those smaller endemic mammals (Rich and Rich, 1983). Three genera of rodents from Texas (USA) of approximately the same date as the Guanajuato fauna, as well as a didelphid from the middle Miocene, support the previous idea. One of the Texas rodent genera, *Prolapsus*, also has evolutionary affinities with the caviomorphs of South America (Slaughter, 1978; Wood, 1980). These data have led to speculations on the possible evolutionary role of mammals originating in Mesoamerica that could have resulted in the American caviomorph fauna without the need for an exchange across the Atlantic (Rich and Rich, 1983; but see de Oliveira *et al*., 2009).

Molecular evidence suggests a genetic divergence about 43 Ma between the South American caviomorphs (Parvorder: Caviomorpha) and its sister group, the African parvorder Phiomorpha (Antoine *et al*., 2011). The oldest records of caviomorphs date to the Peruvian Middle Eocene (Antoine *et al*., 2011). Subsequently, caviomorph rodents diversified widely during the Oligocene (Bertrand *et al*., 2012; Boivin *et al*., 2016) and created several lineages adapted to different ecological conditions; some of them even acquired considerable sizes, for example *Josephoartigasia monesi* (Dinomyidae) being of around 1000 kg (Pelegrin *et al*., 2018; Rinderknecht and Blanco, 2008). Based on these two aspects, the pacaranas (Dinomyidae), agoutis (Dasyproctidae), pacas (Cuniculidae), maras, capybaras and guinea pigs (Caviidae), tuco-tucos (Ctenomyidae), and spiny rats and hutias (Echimyidae), among others, were consolidated.

The African origin of South American rodents is supported by the arrival of primates also from Africa (de Oliveira, *et al.,* 2009; Defler, 2019). These constituted the origin of the new world primates whose oldest known representative is *Perupithecus* from the Peruvian Eocene (Divisaderan) (Figure 5). This primate has phylogenetic affinity with African taxa such as its approximate contemporary *Talahpithecus parvus* (Bond, *et al.,* 2015; Kay, 2015), which is considered the closest relative of the platyrrhines, the modern ‘New World’ monkeys. The parvorder Platyrrhini includes marmosets

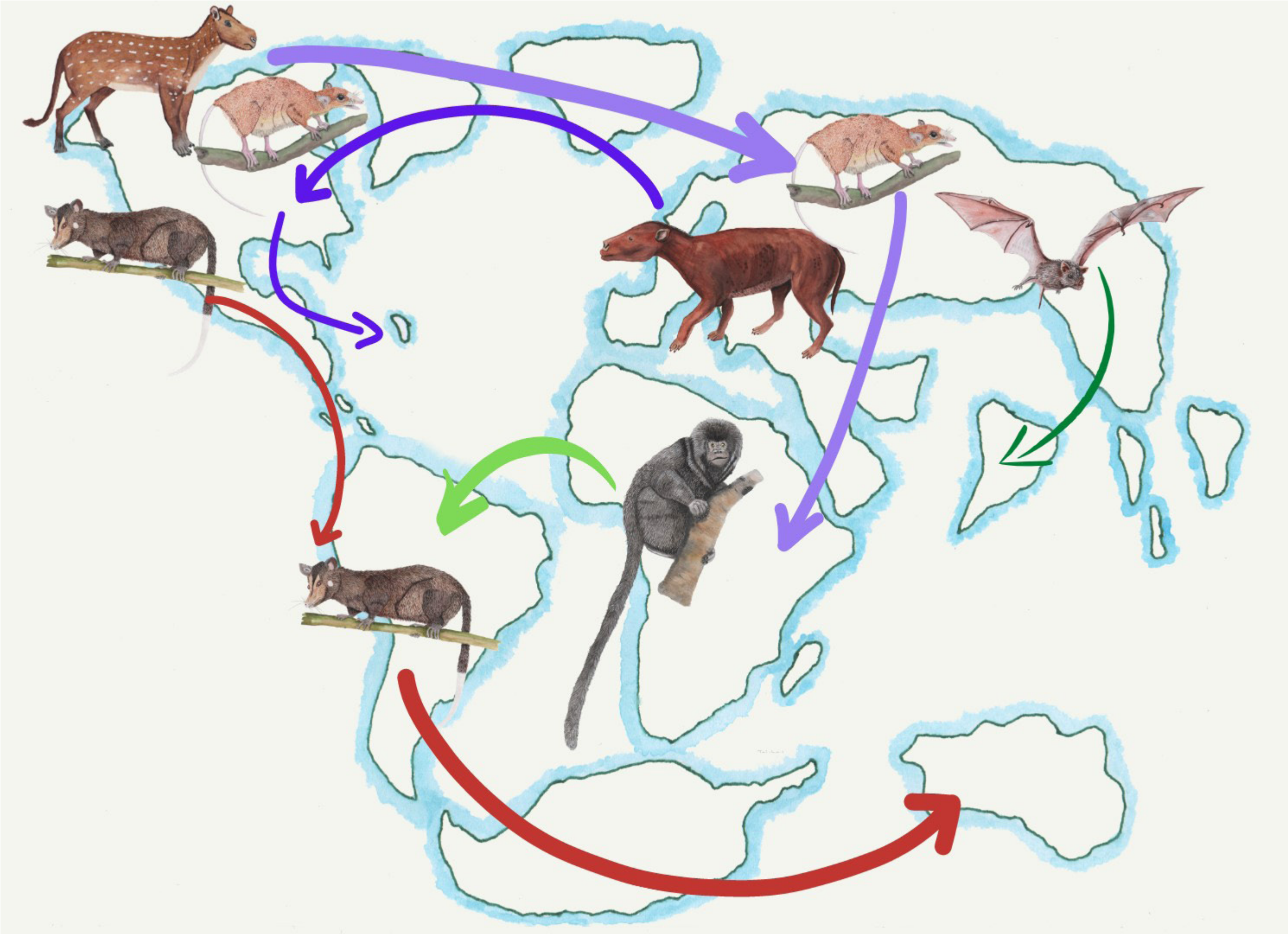

Figure 5. Some examples of mammalian dispersals during the Eocene including the arrival of *Perupithecus* ancestors in South America from Africa (green arrow). Also, the dispersal of marsupials from North to South America and then to Australia via Antarctica (red arrows). Figure by Lucía I. López.

and tamarins (Callitrichidae), capuchins (Cebidae), night monkeys (Aotidae), sakis and uakaris (Pitheciidae), and spider and howler monkeys (Atelidae; Rylands and Mittermeier, 2009). *Branisella* from the Upper Oligocene of Bolivia is the oldest fossil record of the group; it therefore is assumed that they diversified at the beginning shortly prior to that time (Pelegrin *et al*., 2018).

The similarity between hystricomorph rodents from Africa and South America may be attributed to exchanges across the Atlantic Ocean during the late Eocene (Lavocat, 1980). This was possible because the distance between these two continents at the end of the Eocene was smaller, thereby allowing for taxa to raft across the Atlantic in less than fifteen days (Houle, 1999).

Fossils of large mammals such as artiodactyls are relatively well-known from Central American and include anthracotheres, camels, deer, gelocids, oreodonts, peccaries and even bison. These fossils are from generally dispersed localities in the Miocene and Pleistocene (Webb and Perrigo, 1984; Lucas *et al*., 1997, 2008; Cisneros, 2005, 2008; Rincon *et al*., 2013; Lucas, 2014). Perissodactyls are represented by a few records of tapirs and rhinoceroses, as well as many horses. *Aceratherium* rhinoceros are known from the Miocene of Honduras and Panama. The horses include hipparionine records from the Miocene and *Equus* records from the Pleistocene, including some interesting horse assemblages from the late Miocene of Costa Rica (Laurito and Valerio, 2010b). Another example from these times, which is endemic to Central America, is *Pliohippus hondurensis* from Honduras (Lucas and Alvarado, 2016). Fossils and knowledge of marine mammals in the region are scarce. Recently recovered fossils include true whales and other cetaceans and sirenians from the Pliocene and the Miocene of Costa Rica, Nicaragua, and Panama (Lucas *et al*., 2009; Laurito *et al*., 2011; Uhen *et al*., 2011; Lucas and Alvarado, 2016). The locality of San Gerardo de Limoncito is the only one in Costa Rica containing both aquatic and terrestrial mammals (Laurito and Valerio, 2012b). With respect to aquatic mammals, this locality has yielded freshwater cetaceans such as the Iniidae *Goniodelphis* sp., and marine forms such as *Hadrodelphis* sp., *Orycterocetus* sp., and *Eurhinodelphis* sp., jointly denoting paleocaribbean epicontinental affinities with the Florida peninsula, North Atlantic, and the Mediterranean Sea (Valerio and Laurito, 2012; Alvarado and Cárdenes, 2016).

It has been claimed that all the pre-Pleistocene mammalian faunas from Central America to Panama had no affinities with those of South America (Ferrusquia-Villafranca, 2003). Even the Miocene Panama Canal Cucaracha (Gaillard Cut) Fauna (15 Ma) only contained congeners of North American faunas (MacFadden, 2005). The variety of the Cucaracha Fauna is large, including horses, rhinoceros, and artiodactyls, as well as carnivores and even rodents (Rich and Rich, 1983); it is considered as having the oldest vertebrate records in Central America (Laurito and Valerio, 2012b). However, it is surprising that all these fossils are of North American origin despite their proximity to South America, suggesting overland dispersal into southern Central America just west of the Central American seaway (MacFadden, 2005). A Miocene fauna from Colombia, 400 km to the east of the Bolívar Trench, contained only South American genera (Rich and Rich, 1983). In contrast, Late Miocene mammal localities from Honduras, El Salvador, and Mexico produced fossils similar to those found in North America (MacFadden, 2005). These faunas date back to 20 – 8 Ma and include a canid, cat, proboscidean, horse, peccary, camel, and a horned artiodactyl (MacFadden, 2005).

Thus, the general pattern appears to indicate that all Central American "Tertiary" faunas were related to North American faunas, with some rare exceptions. In the last three decades, data have been generated and further illuminated the pre-Pleistocene faunas of Central America, in particular in Costa Rica. For example, the Fauna of San Gerardo de Limoncito in the Coto Brus Valley, dating back to about 8.5 – 6.5 Ma (Miocene), is characterized by a mixture of vertebrates of Palearctic, Nearctic, and Neotropical origins, and contains representatives of the first South Americans mammals that arrived in southern Central America (Laurito and Valerio, 2012b). These investigations have concluded that the arrival of South American mammals to the land connection over the Isthmus of Panama can be attributed to the shortening of the ocean passages among the islands due to normal subduction processes and the rapid uplift that southern Central America experienced because of the tectonic activity in the region (Laurito and Valerio, 2012b). Added to this are the climatic elements prevailing at that time, which favored the predominance of humid and warm basal forests both in northwestern Colombia and in southern Central America (Laurito and Valerio, 2012b). These conditions allowed xenarthrans, which are considered to be good swimmers and island jumpers, to migrate north. In contrast, they seem to have limited the southward migration of North American mammals (Laurito and Valerio, 2012b). The latter managed to cross into South America later, when the climate became drier and after a continuous land corridor was established (Laurito and Valerio, 2012b). Early Pleistocene or Late Pliocene fossil records from Bajo Barrantes (Costa Rica) of *Mixotoxodon larensis* (Notoungulata: Toxodontidae), may predate the arrival in Costa Rica of North American immigrants (Laurito, 1993; Lucas *et al*., 1997).

The first fossil record of megatheriine sloths (Megatheriidae) in Central America was obtained from the Fauna of San Gerardo de Limoncito, which also represents the earliest record of this subfamily outside South America, dating back to 5.8 Ma, i.e., before the closure of the isthmus of Panama (Rincón *et al*., 2020). The first fossil record of

Tayassuidae from the Cenozoic of Costa Rica also was obtained from this fauna, including the first confirmed record for the Northern Hemisphere of two species being distributed sympatrically (Valerio and Laurito, 2020). In addition, the fauna includes the first Costa Rican and Central American record of the camel *Hemiauchenia vera*, a finding that also constitutes the southernmost record of this species in the Northern Hemisphere (Laurito and Valerio, 2016).

In the late Miocene, the exchange of fauna increased by island hopping across the Bolívar Trench (MacFadden, 2006). Fossils of two genera of ground sloths from the Miocene of South America that are also found in North America similarly should have been found in Central America. However, they do not appear in the Gracias Fauna of Honduras, the only Central American paleofauna with temporal correspondence (Rich and Rich, 1983). This highlights the lack of information regarding the fossil history of Central American mammals. It has been postulated that perhaps these two genera passed from South America to North America by island hopping using Caribbean islands. However, had that been the case, these genera would have dispersed rapidly back south (Rich and Rich, 1983). This can be attributed to the fact that the exchange of the Miocene was not one way as evidenced by procyonids which arrived in South America from North America over 7.0 – 7.5 Ma (Patterson and Pascual, 1972) probably via the isthmus of Panama (Laurito and Valerio, 2012b).

Faunal exchanges between both continents increased in the Upper Miocene (Smith and Klicka, 2010; Bacon *et al*., 2015). These exchanges allowed tapirs, peccaries, and ruminants, of North American origin to transgress the Bolívar Trench and be recorded from the Amazon basin about 9.5 Ma (Campbell *et al*., 2010; Prothero *et al*., 2014). Other North American mammals found in South America support these periodic incursions, including gomphotheres in Peru (Campbell *et al*., 2000), the first South American procyonids (*Cyonasua*), about 9 Ma (Forasiepi *et al*., 2014), and sigmodontine rodents, whose first remains have been recorded in South America by the end of the Upper Miocene, about 5.8 Ma (Pelegrin *et al*., 2018). The colonization of mammals from South America in North America includes sloths of the genus *Pliometanastes* (Megalonychidae), recorded in sediments from the Upper Miocene (8.5 – 6.5 Ma) in Costa Rica (Laurito and Valerio, 2012a). The earliest records of peccaries (Tayassuidae) in Costa Rica date back to the Late Miocene (5.8 Ma), from the locality of San Gerardo de Limoncito. This record constitutes the southernmost locality for *Protherohyus brachydontus*, and the only one from Central America (Valerio and Laurito, 2020). Moreover, for the first time for the Northern Hemisphere, this finding confirmed the distribution of this species being sympatric with that of *Prosthennops serus* (Valerio and Laurito, 2020).

The classical view is that the South American mammals' splendid isolation was negatively affected by the invasion of somehow more advanced North American mammals, which resulted in the competitive exclusion of well-established groups such as marsupials and in particular sparassodonts (e.g., Piper, 2009). For example, the arrival into South America of some of the aforementioned groups coincided with the decline of the South American carnivorous Marsupialiformes of the family Borhyaenidae (Wilson *et al*., 2016). The first interpretations of the dichotomy in species diversity resulting from the intercontinental faunal interchange explained the lower diversification of the autochthonous faunas of South America as having resulted from this fauna's lower competitive capacity in relation to the immigrant taxa from North America (e.g., Piper, 2009). However, ecological pressures were derived from the dramatic tectonic, climatic, and biogeographical changes in the region associated with both the formation of the Central American bridge and that of the Andes in addition to the development of the Pleistocene glaciations. Interspecific competition, therefore, was unlikely to have been a highly relevant factor at a macroevolutionary scale (Antonelli *et al*., 2009; Prevosti *et al*., 2013; Bacon *et al*., 2016).

Most of the exchanges included groups that inhabited forests, for which reason the existence of a forested corridor was necessary, and therefore also that of a continuous tongue of land between North and South America. The first candidate for this union is the Baudó land bridge that existed about 10 Ma, which allowed for the connection of northwestern South America with the central area of Panama through the San Blas-Darién and Baudó mountains (Campbell *et al*., 2000). By this means, one closure of the Central American seaway may have occurred around 10 Ma (Montes *et al*., 2012a, 2015). Faunal exchanges would depend on fluctuations in sea level, because when sea levels rose, passage by land was severely limited (Prothero *et al*., 2014).

When the bridge was complete, exchanges became more feasible, but would have depended on the biology of the species involved. For example, the cold climate of the Pleistocene allowed for the exchange of savanna-adapted forms due to the existence of a nearly continuous belt of savanna between North and South America through Central America (e.g., MacFadden, 2006). Mammoths arrived in Central America at the beginning of the Pleistocene and are found throughout most of the region, which demonstrates the presence of savannahs and grasslands in the rain shadow areas of Pleistocene volcanoes and ignimbrite plateaus (Cisneros, 2005; Lucas *et al*., 2008; Lucas and Alvarado 2010a; Lucas and Alvarado, 2016). The savannahs and thorny shrub habitats of the Pliocene and Early Pleistocene (5 – 2 Ma) were fit for the exchange of more xeric adapted fauna and grazing animals, as well as other taxa adapted to the savannah such as glyptodonts, horses, ground sloths, and camels (Rich and Rich, 1983). Fossils from these epochs show that 22 of 31 mammalian genera involved in the exchange between the Americas were adapted to savannah habitats (Rich and Rich, 1983). Grasses—and the corresponding mammalian grazers—evolved in South America (ca. 25 Ma) earlier than they did in North America (ca. 15 Ma) based on fossil evidence (MacFadden, 1997, 2006). From the end of the Pleistocene (ca. 12 Ka) to the present, there was an extension of the tropical humid forest in Central America from South America that cut into the savannah corridor, which led to a decrease in the exchange of grassland taxa through the isthmus. During that time, only the taxa adapted to humid forests and savannahs were able to advance from South America to North America and vice versa. The fauna of the tropical forests of northern South America passed to Central America at a time when the fauna of the isthmus took on its modern Neotropical character (Rich and Rich, 1983).

Costa Rica and the GABI

For the GABI to have taken place, the existence of Costa Rica is essential because its territory is one of the principal components of the geological and terrestrial bridge that connects North America with South America. It is clear that to form the bridge, the closure or consolidation of the Isthmus of Panama has also been essential: a complete land union through the Bolivar Trench to South America (Montes *et al*., 2015). The GABI has been divided into four phases based on analysis of the fossil fauna of South American mammals (Simpson, 1980). The first two phases are not part of the GABI per se (Simpson, 1950), but the third and fourth are. As already noted, during the first stratum of the Cretaceous-Paleocene, the entry of autochthonous components occurred, represented by early migrants from North America. The second stratum is constituted by the transatlantic colonization from Africa in the Eocene by the ancestors of Neotropical rodents and primates (Boivin *et al*., 2016). The third stratum groups all exchanges undertaken during the formation of the Central American land bridge in the Pliocene (Marshall, 1988; Webb, 1991).

It should be emphasized that recent conclusions indicate that the GABI was much more complex and gradual than had been supposed, which is why it has been suggested to abandon the simplistic vision of a singular migratory event (Bacon *et al*., 2015, Winston *et al*., 2016). The GABI had distinct intervals of active exchange (Woodburne, 2010; Table 2).

This implies complex scenarios of exchanges where—as already noted above—the groups of mammals involved experienced strong selective pressures derived from tectonic, climatic, and biogeographical changes in the region. The GABI was a dynamic exchange that included bidirectional migrations, consisting of phases throughout the Pliocene and Pleistocene, with each of the phases including different waves of lineage colonization between the two continents (Table 2). The core of the GABI was composed of a series of large migratory waves that began about 3 Ma and persisted throughout the Pleistocene (Woodburne,

Table 2. Some examples of the main groups of mammals participating in the faunal interchange between North and South America during each of the four events of the GABI* after Woodburne (2010).

* GABI = Great American Biotic Interchange. Table prepared based on data from Woodburne (2010).

Event	Age Ma	From NA	From SA
GABI 1	3 - 2.4	Grisons: *Galictis*-Mustelidae Foxes: "*Dusicyon*"-Canidae Horses: Hippidion, Equidae Gomphotheres: *Stegomastodon* = *Notiomastodon*- Gomphotheridae.	Large herbivorous armadillos: *Holmesina*-Pampateridae Insectivorous armadillos: *Dasypus*-Dasypodidae Giant sloths: *Eremotherium*-Megatheriidae Arboreal porcupines: *Erethizon*-Erethizontidae
GABI-2	1.8	Bears: Arctotherium-Ursidae Cats: *Felis*, *Puma*, *Panthera*, *Smilodon*-Felidae Skunks: *Conepatus*-Mephitidae Otters: *Lontra*-Mustelidae Peccaries: *Catagonus*-Tayassuidae Deer: *Epyuriceros*, *Antifer*-Cervidae Camelids: *Hemiauchenia*-Camelidae Tapirs: *Tapirus*- Tapiridae Gomphotheres: *Cuvieronius*-Gomphotheriidae Horses: *Equus*-Equidae	Anteaters (*Myrmecophaga*)
GABI-3	0.8 - 0.7	Pampas cat: *Leopardus*-Felidae Peccaries: *Tayassu*-Tayassuidae Deer: *Paraceros*, *Hippocamelus*-Cervidae	Opossums (*Didelphis*)
GABI-4	last 0.125	Coati: *Nasua*-Procyonidae Giant otter: *Pteronura*- Mustelidae Dogs: *Canis*-Canidae Cats: *Herpailurus*-Felidae Glyptodont: Glyptothorium-Chlamyphoridae Rabbits: *Sylvilagus*-Leporidae The human species	

2010). This great exchange is explained by the appearance of the Central American bridge and the consequent closure of the isthmus of Panama (Woodburne, 2010). However, there were dispersals—albeit more limited—before that time, of which perhaps the oldest is represented by the sloths *Thinobadites* and *Pliometanastes*, derived from South American mylodontid and megalonychid ancestors respectively (Woodburne, 2010). These faunas are about 8.5 – 9 Ma (Woodburne, 2010).

Today representatives of these groups include the three-tod sloth (*Bradypus variegatus*: Bradypodidae) found in Costa Rica from sea level to highlands (Figure 6). Woodburne (2010) divided the GABI into four events. GABI-1 event lasted from about 3 to 2.4 Ma and included several North American lineages as well as some from South America (Table 2). Procyonids were the first placental carnivores that arrived in South America after the closing of the Central American seaway (Woodburne *et al*., 2006; Soibelzon, 2011). Today representatives of this family in Costa Rica includes the Cacomistle (*Bassariscus sumichrasti*) found at low and middle elevations (Figure 7). South American lineages include Erethizontidae although there is evidence that the arrival of these rodents into North America dates to the Upper Miocene (Upham and Patterson, 2012). The interchange during the GABI-2 event (1.8 Ma) was biased in favor of North American families, with only anteaters (Myrmecophaga) entering North America (Woodburne, 2010; Prevosti *et al*., 2013; Cione *et al*., 2015).

The North American continent included the prominent presence of carnivorous lineages (Table 2). Opossums (*Didelphis*) colonized North America during the GABI-3 event (0.8

Figure 6. A female three-toed sloth (*Bradypus variegatus*), a member of Bradypodidae, a typical South American family. The green color is due to algae growing on the sloth hair. Photo by José M. Mora.

Figure 7. The cacomistle (*Bassariscus sumichrasti*) a member of Procyonidae, a family of North American origin. Photo by José M. Mora.

– 0.7 Ma), a time when a number of North American taxa arrived in South America. The last event, GABI-4 is hypothesized to have taken place in the last 0.125 Ma time, when several North American carnivores and herbivores entered South America (Table 2). This event also includes the arrival of the human species to South America during the Late Pleistocene, probably between 18,000 and at least 15,000 years ago (Pérez *et al*., 2016). This is a key component of the GABI-4 event due to the negative impact that humans had on the environment provoking the extinction of many species during the Pleistocene-Holocene (Goebel *et al*., 2008; Cione *et al*., 2009; Barnosky and Lindsey, 2010).

Fossils of Central American vertebrates date not only to before and after the closure of the Isthmus of Panama, but they also constitute the direct fossil record documenting what clearly was a dispersal route between North and South America. The mixture began with the exchange that took place over the islands making up the current Central American region and increased when the Central American isthmus was closed and became dry land because it allowed for a greater traffic of mammals. About twenty families of mammals that inhabit Costa Rica are of South American origin, but a similar number are of North American origin. Because these interpretations are based entirely on the study of fossils, and because fossils are not common in the region, there remain many limitations regarding a more complete understanding of the chronology of the GABI (Rich and Rich, 1983). There are also still many unknowns regarding the physical conditions and dates of the mammal exchanges between the Americas, and the role of the Caribbean and Central American islands in these exchanges.

Conclusions

Central American mammal fossils are primarily of the late Cenozoic age and help provide an understanding of the GABI after the closure of the Panamanian isthmus (Lucas and Alvarado, 2016). Late Pleistocene mammals have been collected from several localities extending from Panama to Mexico, most of which are similar to those from rain forest habitats, with the addition of the white-tailed deer (*Odocoileus virginianus*) of a North American origin (MacFadden, 2006). However, several taxa occupied more open grassland habitats, such as *Toxodon*, mammoths (*Mammut*), horses (*Equus*), and even pronghorns and the 'Old-World' migrant bison (*Bison*). The region and its mammal fossils record the northern limit of toxodonts and the southern limit of bison and white-tailed deer. This classic interchange fauna combines extant genera with North and South American megafauna that subsequently became extinct during the late Pleistocene (MacFadden, 2006).

The land connection between North and South America provided a way for mammals from both landmasses to move between them. The most important of those exchanges was the so-called GABI. However, it is known now that the GABI was not a singular event, but was divided into different phases that have been dated and documented with greater precision as fossil records have increased (Pelegrin., 2018). The novel concept of a compound GABI was a very complex process with a network of biotic interactions conditioned mainly by changing abiotic factors that occurred during the process of paleoenvironmental configuration of the entire American continent.

Central America is the bridge that allowed both the GABI and other faunal exchanges between North and South America. However, Central America could have been the center of origin for mammals before the Paleocene (> 66 Ma). From this epoch until the Eocene (~55 Ma), there was a shift towards more tropical conditions in North America that could imply a northward shift of the mammalian fauna originating in Central America, as documented by fossils in North America (Rich and Rich, 1983). There is evidence to support this hypothesis based on the finding of fossils of ancestral groups of South American and southern North

American affinities in more northern areas of North America. Because of this, the existence of tropical mammals in Mesoamerica has been postulated during the Paleocene, with extensive documentation only of the faunas of the United States from the beginning of the Eocene, when they already had arrived from the south due to more favorable climatic conditions (Rich and Rich, 1983).

In any case, Central America served as a route of biological exchange between North and South America, but it also could have been an important center of origin for mammals. Likewise, and being of no less importance , is the fact that at the same time, the Isthmus of Panama interrupted the connection between the Atlantic and Pacific oceans, which led to the independent evolution of their biota, and allowed for an increase of marine biodiversity in the region (Haug and Tiedemann, 1998). In addition, this barrier caused changes in ocean currents that impacted the planet's climate, including the drier climate in Africa. This new climate may have influenced changes from forested to more open habitats. This, in turn, has impacted some primates to become terrestrial and bipedal, initiating perhaps the evolutionary process that eventually ended with what came to be *Homo sapiens*.

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Revision of the Genus *Nebo* (Simon, 1878) in Saudi Arabia with a Description of a New Species from the Jazan Province (Scorpiones: Diplocentridae)

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Abstract: The genus *Nebo* Simon, 1878 in Saudi Arabia is revised based on morphometric and morphological characters for adult specimens. The presence of *Nebo hierichonticus* (Simon, 1872) has been justified for the first time from Saudi Arabia and compared with materials collected from Jordan. More specimens of *Nebo yemenensis* Francke, 1980 including adult males and females were collected and recorded in this study. *Nebo jazanensis* sp. n. is described and fully illustrated based on adult males and females collected from Jazan Province and compared with other species of the genus *Nebo* known from the Arabian Peninsula and Jordan. Notes on its habitats are provided.

Key words: Scorpions, *Nebo jazanensis*, Jazan province, Arabian Peninsula.

Introduction

The genus *Nebo* has been established by Simon in 1878 by transferring *Hemiscorpio hierichonticus* (Simon, 1872) to the new genus. His description was based on two specimens collected from Jericho, the Jordan Valley. This genus includes nine species all of which occurring in the Arabian Peninsula and the Middle East; *Nebo poggesii* Sissom, 1994, *Nebo flavipes* Simon, 1882, *Nebo grandis* Francke, 1980 and *Nebo yemenensis* Francke, 1980 in Yemen, *Nebo omanensis* Francke, 1980, *Nebo franckei* Vachon, 1980 and *Nebo whitei* Vachon, 1980 in Oman, *Nebo henjamicus* Francke, 1980 in the island of Henjam, Arabian Gulf, and *Nebo hierichonticus* Simon, 1872 in Jordan, Palestine and Sinai (Francke, 1980). Over the decades, the taxonomy of this genus remained unclear and problematic (Birula, 1910,1917; Vachon, 1965, 1980). Francke (1980) made the most comprehensive revision of the genus providing specific morphometric ratios as a reliable and consistent method to resolve the problem of morphological homogeneity of this genus exhibited across its wide geographical ranges. These ratios were used to recognize *Nebo hierichonticus* and *Nebo flavipes* as valid species, and to describe four more new species of *Nebo* from southern Arabian Peninsula.

Vachon (1980) described two more species of *Nebo* from Oman; *Nebo whitei* Vachon, 1980 and *Nebo franckei* Vachon, 1980, from immature specimens, depending on morphological characteristics and variations on trichobothrial arrangements on external surface of pedipalp patella.

Kinzelbach (1985) and Vachon & Kinzelbach (1987) argued that all *Nebo* species should be regarded as subspecies of *N. hierichonticus* Simon, 1872 without providing proper justification. Hendrixon (2006) depicted a map showing the distribution of *Nebo* sp. in the Arabian Peninsula, however, he was cautious not to assign it to a specific level. Similarly, Francke (1980) did not assign *Nebo* in Saudi Arabia to a specific taxon. The following authors Al-Asmari *et al.* (2007, 2009, 2013), Alqahtani *et al.* (2019) and Alqahtani and Badry (2021) considered all *Nebo* specimens collected from various regions in Saudi Arabia as *Nebo hierichonticus* without providing morphological diagnosis or morphometric measurements. Alqahtani (2022) recorded

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Nebo yemenensis from southern Saudi Arabia for the first time.

Meanwhile, morphometric ratios provided by Francke (1980) were adopted by Sissom (1994) as valid and reliable characters to distinguish species of this genus, since other morphological characters previously used to separate species within other diplocentrine genera (e.g., trichobothrial patterns, pectinal tooth counts, tarsomere II spine-formulas and carination) were proved to be with limited significance in distinguishing *Nebo* species. Sissom (1994) also provided important amendments and expanded on the morphometric ratios stated by Francke (1980) as a result of the examination of new specimens and added on the morphology of male hemispermatophore as a distinguishing character that supports Francke (1980) described species diagnosed solely on morphometric ratios, Hemispermatophore character was more recently found to be variable by Hendrixon (2006) when he examined more specimens from Saudi Arabia.

Other recent studies reported on the scorpions of Saudi Arabia (Alqahtani *et al.,* 2019; Aloufi *et al*., 2022; Alqahtani & Badry, 2021).

In this study, we adopted morphometric ratios to prove the validity of the presence of both *Nebo hierichonticus* and *Nebo yemenensis* in Saudi Arabia. Also, we described a new species *Nebo jazanensis* sp. n. based on specimens collected from Jazan province.

Materials and Methods

Twenty males and nineteen females were collected from five localities in Saudi Arabia (Table 1). One male and one female collected from two localities in Jordan were used in the comparative study.

Illustrations and measurements were made with the aid of stereoscopic microscope with a camera and an ocular micrometer (efix). Measurements follow Sissom (1990) and are given in mm. Carinal terminology is after Francke (1977). Trichobothrial notations follow Vachon (1974, 1975) and morphological terminology mostly follows Vachon (1952), Stahnke (1970) and Hjelle (1990). Specimens were collected by ultraviolet detection at night and preserved in 80% alcohol. Many collected subadult and juvenile specimens were excluded from this study because morphometric characteristics work only for adults (Francke,1980), sexual maturity was assumed by a combination of characteristics; in males by the presence of fully developed paraxial organs and the presence of prominent scallops on the pedipalp chela fingers, in females on the basis of size and on examining reproductive system in certain cases. Holotype male and other paratypes of the new species, and all other examined material in this study will be deposited in the Department of Biology, the University of Jordan, Amman, Jordan (JUST).

Seven morphometric ratios were established by Francke (1980): **1**= carapace length / metasomal segment II length; **2**= pedipalp

Table 1. Localities from which scorpions were collected.

Locality	Governorate / Country	No. of specimens ♂	♀	N	E
Al Bahah	Al Bahah / Saudi Arabia	0	2	20° 01’ 20.12”	41° 28’ 18.11”
Al Boqa’a	Jazan / Saudi Arabia	15	15	17° 20’ 29.04”	43° 09’ 43.90”
Al Fegrah	Al Madinah / Saudi Arabia	1	0	24° 21’ 44.34”	38° 57’ 44.75”
Wadi Al Muataf	Jazan / Saudi Arabia	2	2	17° 19’ 19.50”	43° 08’ 40.50”
Wadi Awed	Jazan / Saudi Arabia	1	0	17° 20’ 53.81”	43° 10’ 16.68”
Alqan	Tabuk / Saudi Arabia	1	0	29° 05’ 33.20”	35° 22’ 50.20”
Al Mujeb	Amman / Jordan	1	0	31° 24’ 36.60”	35° 53’ 55.30”
Kufranjeh Dam	Ajloun / Jordan	0	1	32° 16’ 10.70”	35° 39’ 01.40”

femur length / width; **3**= metasomal segment V length / pedipalp chela movable finger length; **4**= metasomal segment V length / carapace length; **5**= metasomal segment V length / metasomal segment II width; **6**= pedipalp chela length / depth; **7**= pedipalp femur length / pedipalp chela depth. Specimens were measured, then the seven ratios were calculated. Table (2) shows the codes, sex, species, and localities of studied specimens.

Table 2. Codes, sex, species, and localities of studied specimens.

Code	Sex	Species	Locality	Date	Code.	Sex	Species	Locality	Date
1 H	♂	*N. hierichonticus*	Al Boqa’a	4. 5.2022	22 h	♀	*N. hierichonticus*	Al Bahah	5.2005
2 H	♂	*N. hierichonticus*	Al Wadi Muataf	5.5.2022	23 h	♀	*N. hierichonticus*	Al Bahah	5.2005
3 H	♂	*N. hierichonticus*	Al Boqa’a	9.7.2022	24 Y	♂	*N. yemenensis*	Wadi Al Muataf	5.5.2022
4 H	♂	*N. hierichonticus*	Al Boqa’a	9.7.2022	25 Y	♂	*N. yemenensis*	Al Boqa’a	19.7.2022
5 H	♂	*N. hierichonticus*	Al Boqa’a	9.7.2022	26 y	♀	*N. yemenensis*	Al Boqa’a	4.5.2022
6 H	♂	*N. hierichonticus*	Al Boqa’a	9.7.2022	27 y	♀	*N. yemenensis*	Al Boqa’a	4.5.2022
7 H	♂	*N. hierichonticus*	Al Boqa’a	9.7.2022	28 y	♀	*N. yemenensis*	Wadi Al Muataf	5.52022
8 H	♂	*N. hierichonticus*	Al Boqa’a	9.7.2022	29 y	♀	*N. yemenensis*	Wadi Al Muataf	5.5.2022
9 H	♂	*N. hierichonticus*	Al Boqa’a	20.7.2022	30 y	♀	*N. yemenensis*	Al Boqa’a	9.7.2022
10 H	♂	*N. hierichonticus*	Al Boqa’a	20.7.2022	31 y	♀	*N. yemenensis*	Al Boqa’a	9.7.2022
11 H	♂	*N. hierichonticus*	Al Fegrah	28 .8.2022	32 J	♂	*N. jazanensis*	Al Boqa’a	9.7.2022
12 H	♂	*N. hierichonticus*	Alqan	26.6.2012	33 J	♂	*N. jazanensis*	Al Boqa’a	20.7.2022
13 H	♂	*N. hierichonticus*	Wadi Al-Mujeb\ Jordan	8.5.2020	34 J	♂	*N. jazanensis*	Al Boqa’a	20.7.2022
14 h	♀	*N. hierichonticus*	Al Boqa’a	4.5.2022	35 J	♂	*N. jazanensis*	Al Boqa’a	20.7.2022
15 h	♀	*N. hierichonticus*	Al Boqa’a	9.7.2022	36 J	♂	*N. jazanensis*	Al Boqa’a	28.8.2022
16 h	♀	*N. hierichonticus*	Al Boqa’a	9.7.2022	37 j	♀	*N. jazanensis*	Al Boqa’a	9.7.2022
17 h	♀	*N. hierichonticus*	Al Boqa’a	20.7.2022	38 j	♀	*N. jazanensis*	Al Boqa’a	9.7.2022
18 h	♀	*N. hierichonticus*	Al Boqa’a	20.7.2022	39 j	♀	*N. jazanensis*	Al Boqa’a	9.7.2022
19 h	♀	*N. hierichonticus*	Al Boqa’a	20.7.2022	40 j	♀	*N. jazanensis*	Al Boqa’a	20.7.2022
20 h	♀	*N. hierichonticus*	Al Boqa’a	20.7.2022	41 j	♀	*N. jazanensis*	Al Boqa’a	20.7.2022
21 h	♀	*N.hierichonticus*	Kufranjeh Dam\ Jordan	3.5.2020					

Results

Systematics

Family **Diplocentridae** Karsch, 1880
Genus ***Nebo*** Simon, 1878
Nebo hierichonticus (Simon, 1872)
Figs. 1,4, Tab. 2-7, 12

Type locality and type depository: Jericho in the Jordan Valley, and was placed in the genus *Hemiscorpio* Peters, 1861 Family Scorpionidae (Genus *Hemiscorpius*. Now in Family Hemiscorpiidae). Simon (1878) established the genus *Nebo* for this species. Holotype is at Muséum national d’Histoire naturelle, Paris, France (MNHN).

Material examined: **Saudi Arabia**, Jazan Province, Al Boqa’a, Al-Dayer Governorate , 937 m a. s. l., 1 ♂, 1♀, 04May 2022, *leg*. A. Aloufi; Jazan Province, Wadi Al Muataf, Al-Dayer Governorate, 785 m a. s. l., 1 ♂, 05 May 2022, *leg*. A. Aloufi; Jazan Province, Al Boqa'a, Al-Dayer Governorate, 937 m a. s. l., 6 ♂♂, 2♀♀, 09 July 2022, *leg*. A. Aloufi; Al Boqa'a, Jazan Province, Al-Dayer Governorate, 937 m a. s. l., 2 ♂♂, 4♀♀, 20 July 2022, *leg*. A. Aloufi; Al Madinah Al Monawwarah Province, Al Fegrah, 1549 m a. s. l., 1♂, 28 August 2022, *leg*. A. Aloufi; Tabuk Province, Alqan, 1209 m a. s. l., 1♂, 26 June 2012, *leg*. A. Aloufi; Al Bahah Province, 2170 m a. s. l., 2 ♀♀, May 2005, *leg*. M. El-Hawagry. **Jordan**, Amman Governorate, Al-Mujeb, 661 m a. s. l., 1♂, 8 May 2020, *leg*. B. Abu Afifeh; Ajloun Governorate, Kufranjeh Dam, 83 m a. s. l., 1♀, 3 May 2020, *leg*. B. Abu Afifeh.

Diagnosis of examined material: Adult males 90.85-123.45 mm long (Table 4), females 91.50 – 140.60 mm long (Table 6). Pectinal tooth count 16–19 in males, 13–16 in females. Carapace length to metasomal segment II length ratio (#1) 1.31-1.43 in males, 1.44-1.61 in females; pedipalp femur length to width ratio (#2) 2.70-3.33 in males, 2.65-2.82 in females; metasomal segment V length to pedipalp chela movable finger length ratio (#3) 0.90-1.16 in males, 0.95-1.06 in females; metasomal segment V length to carapace length ratio (#4) 1.12-1.24 in males, 1.04-1.12 in females; metasomal segment V length to metasomal segment II width ratio (#5) 2.57-3.16 in males, 2.57-2.96 in females; pedipalp chela length to depth ratio (#6) 2.66-2.94 in males, 2.40-2.67 in females; pedipalp femur length to pedipalp chela depth ratio (#7) 1.30-1.66 in males, 1.16-1.29 in females.

Remarks: The material examined in this study from Saudi Arabia, compared with male and female from Jordan, has morphometric ratios given in Tables (5 and 7), found to be compatible with the ratios established by (Francke, 1980) (Table 3), with exceptions of small deviations in ratios #1, #2, and #4; for females; so the morphometric ratios given by (Francke, 1980, Table 3, p. 40) for females *Nebo hierichonticus* has been modified and expanded as follows: ratio #1 ≤ 1.61 instead of < 1.60; ratio #2 ≥ 2.65 instead of >2.65; and ratio # 4 ≥ 1.04 instead of >1.10. Adult males of *Nebo hierichonticus* have the unique feature of the presence of undulations and a noticeable gap between pedipalp chela fingers when they are totally closed. (Fig. 4C), this character did not exist

Table 3: Morphometric characterization of adult *Nebo* species, based on ratios established by Francke (1980), and Sissom (1994), Characters represent morphometric ratios as follows: **1**= carapace length to metasomal segment II length; **2**= pedipalp femur length to width; **3**= metasomal segment V length to pedipalp chela movable finger length; **4**= metasomal segment V length to carapace length; **5**= metasomal segment V length to metasomal segment II width; **6**= pedipalp chela length to depth; **7**= pedipalp femur length to pedipalp chela depth.

Species	Sex	Morphometric Ratios						
		#1	#2	#3	#4	#5	#6	#7
*Nebo hierichonticu*s	♂	< 1.45	>2.65	> 0.90	> 1.10	> 2.55	> 2.65	> 1.25
	♀	≤ 1.61	≥2.65	> 0.90	≥ 1.04	>2.55	>2.30	> 1.15
Nebo flavipes	♀	1.73 -1.79	2.20- 2.39	0.77– 0.89	0.83- 0.92	1.87- 2.22	2.10- 2.18	0.96- 1.00
Nebo henjamicus	♂	< 1.20	>3.00	> 1.20	> 1.25	> 3.10	< 2.60	> 1.25
Nebo grandis	♂	1.42	3.00	0.92	1.14	2.81	2.59	1.34
	♀	< 1.60	≥ 2.40	0.84- 1.00	0.96- 1.10	> 2.60	< 2.30	< 1.15
Nebo poggesii	♂	1.27	3.56	1.04	1.26	3.22	2.91	1.61
	♀	1.51- 1.56	2.54- 2.72	0.88- 1.04	1.04- 1.10	2.67- 3.11	2.42- 2.52	1.19- 1.25
Nebo omanensis	♂	1.25- 1.70	2.75- 3.00	1.10- 1.20	1.10- 1.20	2.60- 3.10	2.35- 2.50	1.20- 1.30
	♀	1.25- 1.70	2.30- 2.60	1.00- 1.10	0.95- 1.10	2.50- 3.00	2.20- 2.30	1.05- 1.15
Nebo yemenensis	♂	1.50- 1.60	2.30- 2.60	0.90- 1.00	1.00- 1.10	2.30- 2.55	2.45- 2.55	1.20- 1.30
	♀	1.54- 1.70	2.30- 2.66	0.90- 1.07	0.90- 1.03	2.27- 2.56	2.27- 2.55	1.14- 1.23
Nebo jazanensis sp. n.	♂	1.66- 1.78	2.38- 2.65	0.85- 0.99	0.86- 0.96	2.08- 2.38	2.64- 2.87	1.28- 1.33
	♀	1.71- 1.75	2.30- 2.50	0.88- 0.98	0.91- 0.95	2.16- 2.33	2.45- 2.71	1.10- 1.28

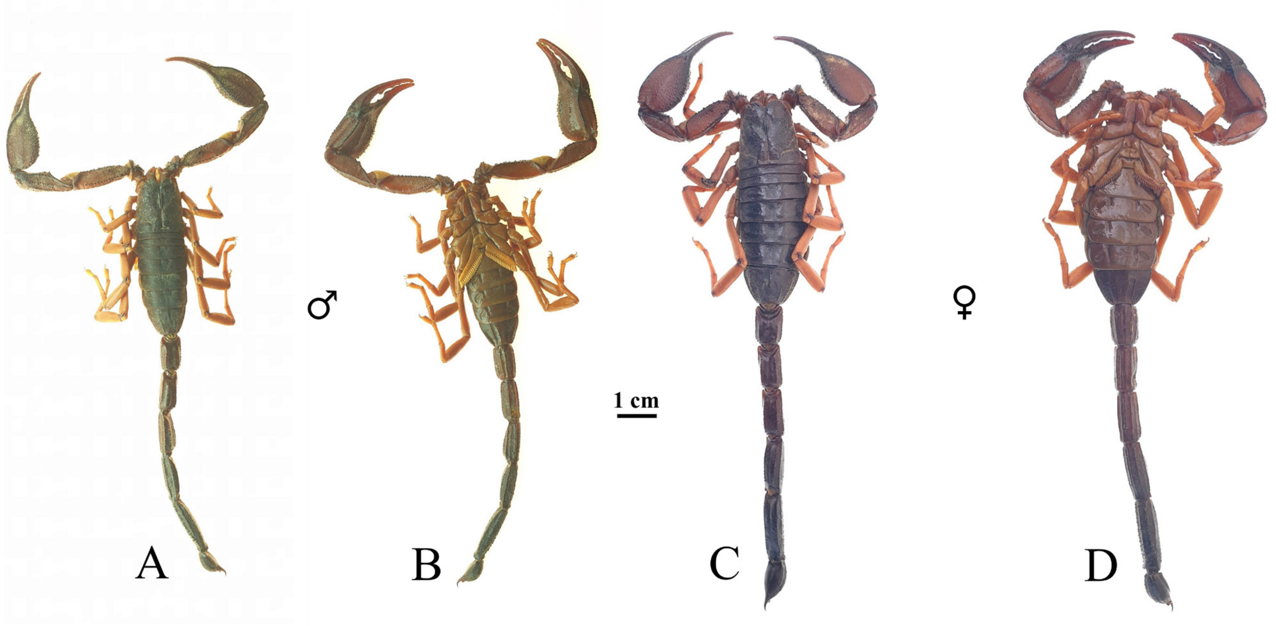

Figure 1. Male and female *Nebo hierichonticus* from Al Boqa'a, Jazan Province, Saudi Arabia. Scale bar: 1 cm.

in males of *Nebo yemenensis* (Fig. 4B), nor in *Nebo jazanensis* sp. n. (Fig. 4A).

Distribution: Palestine, Jordan, Egypt, and Saudi Arabia.

Nebo yemenensis Francke, 1980

Figs. 2, 4, Tab. 2-3, 8-9, 12

Type locality and type depository: Holotype adult female, from Yemen Arab Republic, 15 miles NW Sana, under stones at top of El Kaber Pass between Hugga and Haz (ca. 9200 ft.), 2 February 1938 (E. B. Britton; British Museum Expedition to SW Arabia); British Museum of Natural History (BMNH).

Material examined: **Saudi Arabia**, Jazan Province, Al Boqa'a, Al-Dayer Governorate, 937 m a. s. l., 2♀♀, 04 May 2022, *leg*. A. Aloufi; Jazan Province, Wadi Al Muataf, Al-Dayer Governorate, 785 m a. s. l., 2 ♀♀, 05 May 2022, *leg*. A. Aloufi; Jazan Province, Al Boqa'a, Al-Dayer Governorate, 937 m a. s. l., 1 ♂, 2♀♀, 09 July 2022, *leg*. A. Aloufi; Jazan Province, Al Boqa'a, Al-Dayer Governorate, 937 m a. s. l., 1 ♂, 19 July 2022, *leg*. A. Aloufi.

Diagnosis of examined material: Adult males 92.05 -94.50 mm long, females 87.10 – 105.45 mm long (Table 8). Pectinal tooth counts 16–19 in males, 14–15 in females. Carapace length to metasomal segment II length ratio (#1) 1.56-1.58 in males, 1.60-1.70 in females; pedipalp femur length to width ratio (#2) 2.51-2.57 in males, 2.36-2.63 in females; metasomal segment V length to pedipalp chela movable finger length ratio (#3) 0.91-0.94 in males, 0.90-0.95 in females; metasomal segment V length to carapace length ratio (#4) 1.00 in males, 0.93-1.00 in females; metasomal segment V length to metasomal segment II width ratio (#5) 2.39-2.43 in males, 2.27-2.50 in females; pedipalp chela length to depth ratio (#6) 2.54-2.55 in males, 2.32-2.55 in females; pedipalp femur length to pedipalp chela depth ratio (#7) 1.24-1.26 in males, 1.14-1.23 in females.

Remarks. *Nebo yemenensis* has been recorded in Saudi Arabia from Jazan by Alqahtani (2022). The newly examined material has morphometric ratios given in Table (9) which is compatible with those calculated by Francke (1980) and later expanded by Sissom (1990) (Table 3).

Distribution: Yemen, and Saudi Arabia.

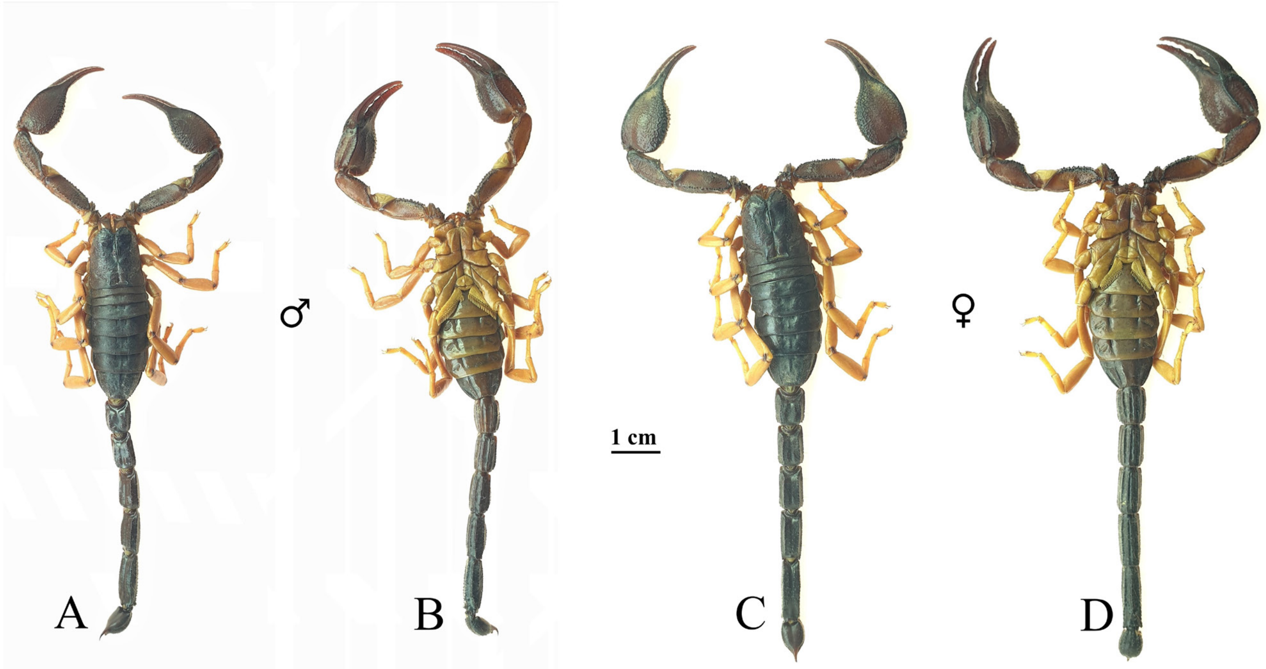

Figure 2. Male and female *Nebo yemenensis* from Al Boqa'a, Jazan Province, Saudi Arabia. Scale bar: 1 cm.

Nebo jazanensis sp. n.

Figs. 3-6, Tab. 2-3, 10-12

Type locality and type depository: **Saudi Arabia**, Al Boqa'a, Al-Dayer Governorate, Jazan Province, 937 m a. s. l., 17° 20' 29.04"N, 43° 09' 43.90"E, Department of Biology, the University of Jordan, Amman, Jordan (JUST).

Type material examined: **Saudi Arabia**, Al Boqa'a, Al-Dayer Governorate, Jazan Province, 937 m a. s. l., 1♂, 2♀♀, 09 July 2022, *leg*. A. Aloufi; Al Boqa'a, Al-Dayer Governorate, Jazan Province, 937 m a. s. l., 3 ♂♂, 3♀♀, 19 July 2022, *leg*. A. Aloufi; Wadi Awed, Al-Dayer Governorate, Jazan Province, 839 m a. s. l., 1♂, 23 May 2022, *leg*. A. Aloufi.

Etymology: The specific name refers to Jazan; the province from which the new species was collected.

Diagnosis: Adult males 77.20-98.20 mm long, females 85.20–104.55 mm long (Table 10). Pectinal tooth count 16–19 in males, 12–15 in females. Carapace length to metasomal segment II length ratio (#1) 1.66-1.78 in males, 1.71-1.75 in females; pedipalp femur length to width ratio (#2) 2.38-2.65 in males, 2.30-2.50 in females; metasomal segment V length to pedipalp chela movable finger length ratio (#3) 0.85-0.99 in males, 0.88-0.98 in females; metasomal segment V length to carapace length ratio (#4) 0.86-0.96 in males, 0.91-0.95 in females; metasomal segment V length to metasomal segment II width ratio (#5) 2.08-2.38 in males, 2.16-2.33 in females; pedipalp chela length to depth ratio (#6) 2.64-2.87 in males, 2.45-2.71 in females; pedipalp femur length to pedipalp chela depth ratio (#7) 1.28-1.33 in males, 1.10-1.28 in females.

Comparison: Adult *Nebo jazanensis* sp. n. can be separated from adult *N. hierichonticus* by ratios #1, #2, #4, and #5; from adult *N. yemenensis* by ratios #1, #4, and #6 in males, (and for females only #1); from adult *N. omanensis* Francke, 1980 by ratios #2, #3, #4, #5 and #6 in males, and by ratios #1,#2,#3,#5 and #6 in females; from adult females *N. flavipes* Simon, 1882 by ratios #6 and #7; from adult females *N. poggesii* Sissom, 1994 by ratios #1,#2, #4 and #5; and from adult females *N. grandis* Francke, 1980 by ratios#1, #4, #5, and #6. (Tables 3 and 12).

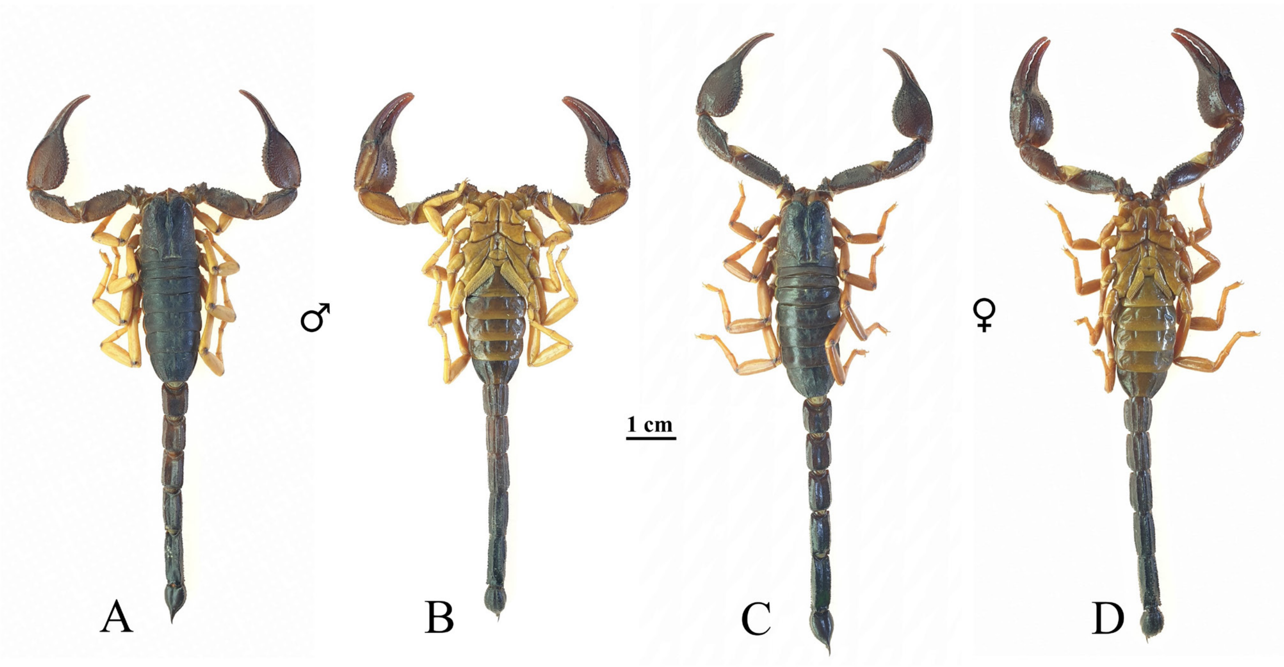

Figure 3. Male holotype and female paratype *Nebo jazanensis* sp. n. from Al Boqa'a, Jazan Province, Saudi Arabia. Scale bar: 1 cm.

Description: Based on male holotype (unless otherwise specified). Measurements are in Table (10).

Coloration: Carapace is reddish brown. Mesosoma: Tergites dark reddish brown. Sternites olive-brown. Coxae, coxapophyses, sternum, genital operculum, and pectines yellowish-olive. Pedipalp: femur, patella, and chela manus light reddish-brown dorsally, and olive-brown ventrally, carinae of femur, patella, and chela manus dark reddish-brown, chela fingers and granules dark reddish-brown. Internal surface of chela manus reddish-brown; light reddish brown to olive-brown around the joint with patella. Finger denticles and movable finger condyles black. Metasoma: metasomal segments I-II reddish brown; III reddish brown anteriorly and dark brown to black posteriorly, IV-V dark brown to black. Granules on dorsolateral, ventrolateral, and ventral submedian carinae light reddish brown. Telson dark reddish brown to black. Walking legs: yellowish olive, spines and condyles red or reddish-brown. Chelicerae: chelicera manus reddish-brown with dark-brown reticulations, fingers reddish-brown, teeth dark reddish-brown.

Chelicerae: dorsal surface of manus smooth, convex; prolateral and ventral surfaces densely setose; cheliceral fingers with normal diplocentrid dentition (Vachon, 1963); fixed finger dorsal and ventral surfaces densely setose, dorsal margin bears 4 teeth: distal, subdistal, median, and basal; ventral margin without teeth; movable finger dorsal surface smooth; ventral surface densely setose; dorsal margin bears 4 teeth: external distal, subdistal, median, and basal; ventral margin with internal distal teeth. The movable finger always ends in two distal teeth, one external and one internal, between which is inserted the distal tooth of the fixed finger.

Prosoma: Carapace anterior margin strongly bilobed; anteriomedian longitudinal carapacial furrow suturiform. Carapace acarinate, only posterior lateral carina visible, carapacial surface granular with small to medium granules; posterior lateral surfaces shagreened with fine granules. Posterior lateral furrows distinct; a deep transverse posterior median furrow passing along posterior margin and joining median furrow in the middle which extends towards the median eyes. Anterior margin with a few medium setae and distinct depression. Median ocular tubercle distinct and situated anterior to the middle. A pair of median eyes separated from each other by more than their diameter; and three pairs of lateral eyes arranged in a slight curve; anterior eyes slightly larger and closer to each other than to smaller posterior eyes. A few moderate setae on surface of carapace; two setae situated behind median eyes.

Mesosoma: Tergites I-VI acarinate, matt covered with fine granules completely in males; glossy and smooth, at most slightly shagreened laterally in females. Tergite VII with four distinct carinae in posterior half of segment, densely shagreened in males, usually only slightly shagreened, mainly near carinae, in females, posterior margin of tergites with microsetae and a long seta on seventh tergite at posterior third of each lateral carina. Sternites smooth and shining, only sternite VII slightly shagreened laterally in males with four smooth carinae which are sometimes only slightly indicated; sternites with setae. Genital operculum subtriangular in males, subovoid in females, wider than long and distinctly shorter than the subpentagonal sternum in both sexes. Pectines of male relatively long; reaching well beyond coxa-trochanter articulation of leg IV; not reaching this articulation in the female.

Metasoma: (Figure. 6). Segments I-III with 10, segment IV with 8, and segment V with 7 carinae. Dorsolateral and lateral supramedian carinae moderate, crenulate on I-III, serrate on IV. Lateral inframedian carinae on segments I-III moderate, granular; on I with complete carinae; on II-III present on posterior three-fourth; on IV represented by a faint line of small granules; on V present on anterior two-thirds of segment. Ventral submedian and ventrolateral carinae moderate, smooth on I-III; moderate, crenulate on IV. Intercarinal surfaces on segments I-V sparsely to moderately granular. Segment V: dorsolateral carinae moderate, irregularly serrate; lateromedian carinae present on anterior two-thirds of segment, strong, irregularly serrate; ventromedian and ventrolateral carinae very strong, serrate. Dorsal and lateral intercarinal surfaces moderately, coarsely granular; ventral intercarinal surfaces with large, spiniod denticles distally. All segments with moderate red setae.

Telson: (Figure. 6). Vesicle flat and smooth dorsally, globular and granulated ventrally and laterally; ventral aspect with numerous small, spinoid granules, vesicle with many red macrosetae even on the base of aculeus. Aculeus strongly curved and very short; vesicle 5 times longer than aculeus. Subaculear tubercle present, strong, subconical; surface of the subaculear tubercle with tiny granules and many red setae.

Pedipalp: Femur: dorsointernal, ventrointernal, and dorsoexternal carinae strong, granulose; ventroexternal carina weak, granular. Dorsal, ventral, and inner surfaces densely granulate (Figure 5A). Patella: dorsointernal, ventrointernal, external, and ventroexternal carinae strong, granulose; dorsoexternal carinae moderate, with rather fused granules; dorsomedian carina weak to moderate. Dorsal surface densely granulated with fine to moderate rounded granules, internal surface with fine to moderate, rather pointed granules, ventral surface rather smooth except several granules mainly around indistinct and irregular ventromedian carina (Figures 5B-D). Chela with dorsal marginal carina strong, granulose; dorsointernal carina strong, serrate; digital carina strong, smooth; external secondary carina weak, granular; ventroexternal carina weak, coarsely crenulate basally, smooth to granular distally; ventromedian carina weak, smooth; ventrointernal carina strong, smooth; inner accessory carina with six to eight medium-sized granules. Dorsal surface with moderate reticulation; external face reticulate or densely, coarsely granular; inner surface densely, coarsely granular (Figures 5E-H).

Chela fingers are relatively long. Fixed and movable fingers with 7 strong accessory denticles. Trichobothriotaxy of type C; orthobothriotaxic (Vachon, 1974); femur of pedipalp with 3 (1 internal, 1 dorsal, 1 external, and 0 ventral) trichobothria; patella of pedipalp with 19 (1 internal, 2 dorsal, 13 external, and 3 ventral) trichobothria; chela of pedipalp with 26 trichobothria; of them 16 on the hand (0 internal, 2 dorsal, 10 external, and 4 ventral) trichobothria; and 10 on the fixed finger (2 internal, 4 dorsal, 4 external, and 0 ventral) trichobothria (Figure. 5).

Legs: tibial spurs lacking; tarsi with prolateral pedal spurs only; basitarsus of all legs with 4-6 spines near spur ventrally on outer side and another spine more proximally, tarsi of right legs I to IV with 7/9 - 8/9 - 8/9 - 9/9 internal and external spines arranged in two rows extending to narrow latero-apical lobes near claws; tarsi with a small dorsal finger-like process apically between claws.

Sexual dimorphism: Males differed from females as follows: (**a**) tergites I-VI matt, completely covered by fine granules in males, but glossy and smooth, at most slightly shagreened laterally in females, tergite VII densely shagreened in males, usually only slightly shagreened, mainly near carinae, in females. Sternite VII slightly shagreened laterally in males and almost smooth in females; (**b**) genital operculum subtriangular in males, subovoid in females; (**c**) dentate margin length of pecten to pecten length is longer in males than in females; 0.92-0.94 in males (n=5), and 0.77-0.79 in females (n=5); (**d**) pectinal tooth count 16-19 in males (of 10 combs from n=5 males: 1 comb with 16 teeth, 2 with 17, 6 with 18, 1 with 19); the average pectinal tooth count per pecten in males is 17.7, 12-15 in females (of 9 combs from n=5 females, 1 is damaged: 1 comb with 12 teeth, 4 with 14, 4 with 15); the average pectinal tooth count per pecten in females is 14.2.

Distribution: Jazan Province, Saudi Arabia.

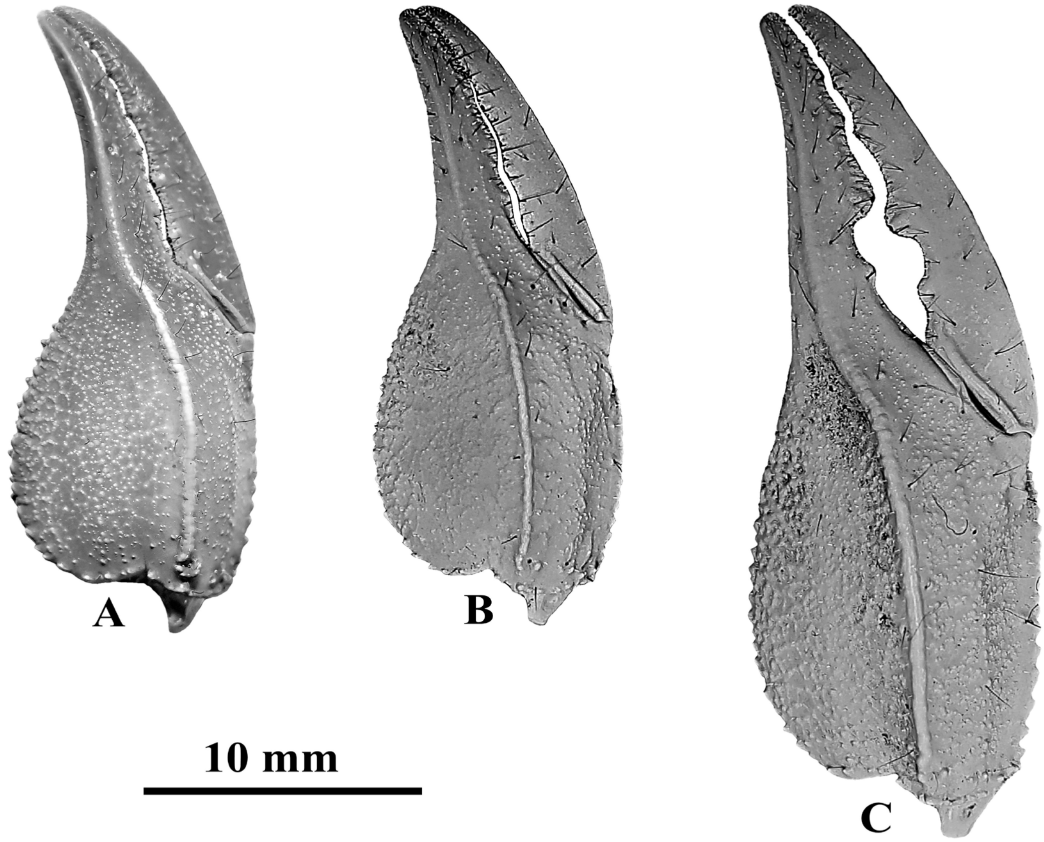

Figure 4. Dextral pedipalp chelae of males. **A**. *Nebo jazanensis* sp. n., **B**. *Nebo yemenensis.* **C**. *Nebo hierichonticus*. Scale bar: 10 mm.

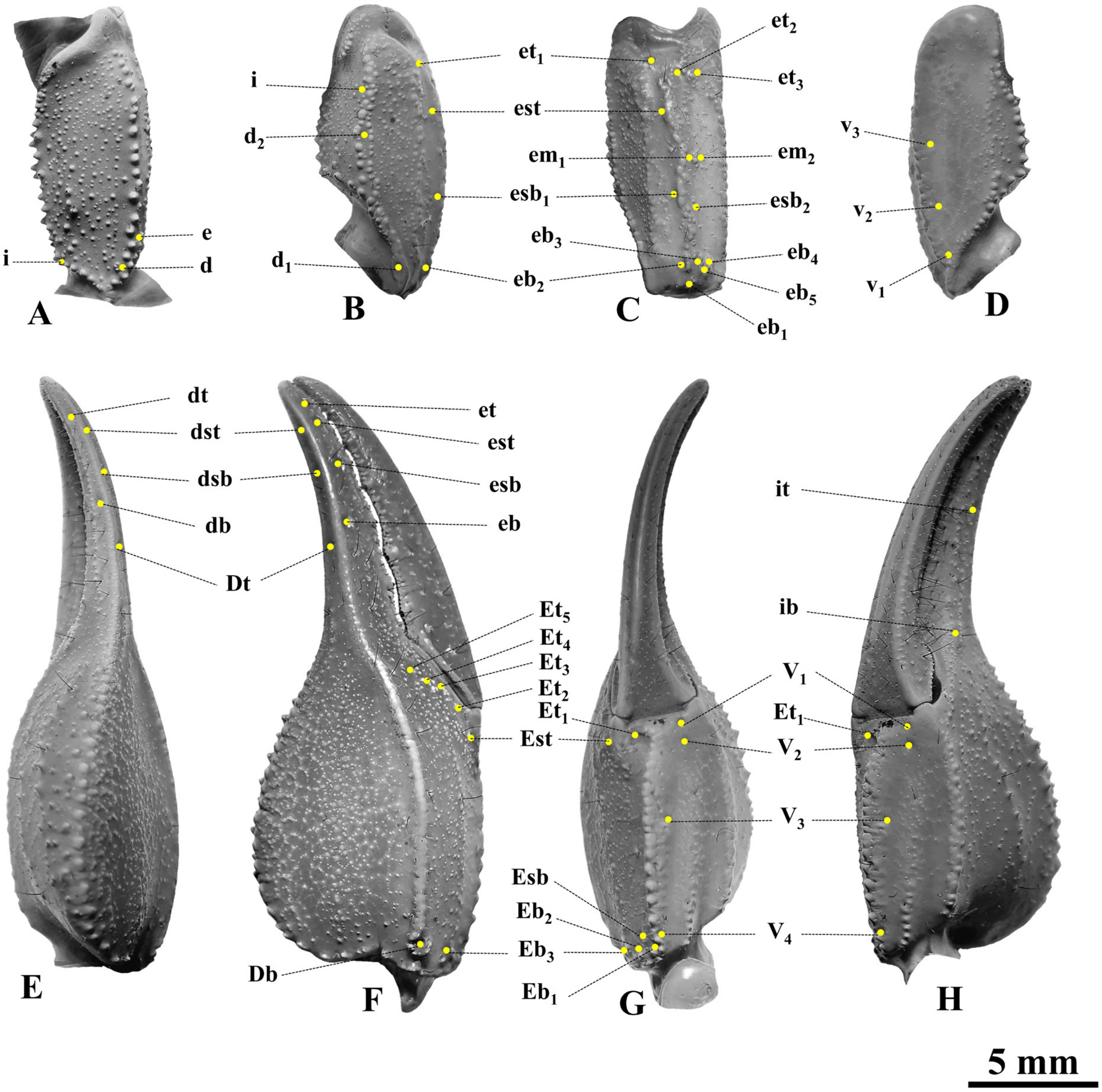

Figure 5. Dextral pedipalp of *Nebo jazanensis* **sp. n.**, male holotype. **A**. Femur, dorsal aspect. **B**. Patella, dorsal aspect. **C**. Patella, external aspect, **D**. Patella, ventral aspect. **E**. Chela, dorsal aspect. **F**. Chela, external aspect. **G**. Chela, ventral aspect. **H**. Chela, ventrointernal aspect. Abbreviations for trichobothria: On the femur, patella and fingers, the trichobothria are denoted by small letters as **d**: dorsal, **v**: ventral, **e**: external, **i**: internal. On the hand, they are denoted by capital letters: **D**, **V**, and **E**. The dorsal ones on fixed finger can be dorsal basal **db**; dorsal suprabasal **dsb**; dorsal subterminal **dst**; dorsal terminal **dt**, but on the hand, dorsal basal **Db**; dorsal terminal **Dt**. The external ones can be basal **b**, suprabasal **sb**, median **m**, subterminal **st**, terminal **t**. Thus, a trichobothrium on external surface of fixed finger or patella symbolized by **eb**: external basal; **esb**: external suprabasal; **em**: external median;**est**: external subterminal; **et**: external terminal. Whereas on external surface of the hand symbolized by **Eb**: external basal; **Esb**: external suprabasal; **Est**: external subterminal; **Et**: external terminal. Scale bar: 5 mm.

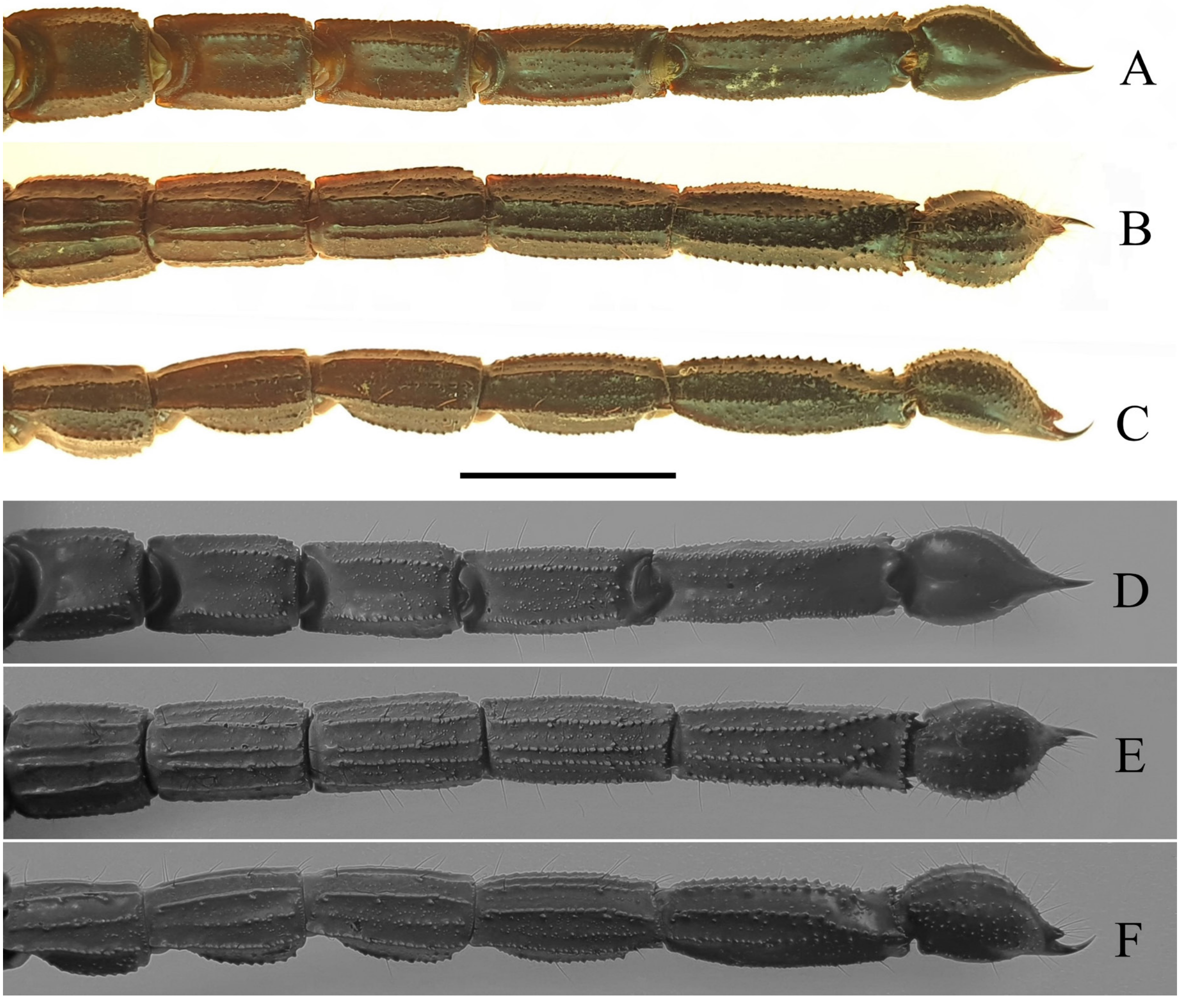

Figure 6. *Nebo jazanensis* **sp**. **n**., male holotype, metasoma and telson in dorsal (**A**, **D**), ventral (**B**, **E**) and lateral (**C**, **F**) aspects. **A-C**. Under white light. **D-F**. Under UV light. Scale bar: 10 mm.

Table 4: Measurements for adult males of *Nebo hierichonticus*. Measurements and morphometrics are in mm.

	1 H	2 H	3 H	4 H	5 H	6 H	7 H	8 H	9 H	10 H	11 H	12 H	13 H
Total length	117.35	11.45	117.6	123.45	118.35	113.4	105.7	108.1	112.7	117.5	110.4	94.60	90.85
Carapace Length	13.80	13.32	14.15	14.45	14.40	14.10	12.65	13.15	13.56	14.17	12.85	10.96	10.15
Metasoma II Length	10.20	9.84	10.15	11.00	10.60	10.35	9.55	10.10	9.72	10.68	9.48	7.62	7.10
Metasoma II Width	5.64	5.28	5.55	5.55	5.75	5.40	5.45	5.30	5.28	5.64	5.16	4.44	4.43
Metasoma V Length	16.81	16.33	15.90	17.55	17.30	16.85	14.90	15.85	15.85	16.81	15.97	12.36	11.50
Pedipalp Femur length	15.00	14.65	15.55	17.30	16.80	15.45	13.90	14.55	14.89	15.97	13.69	10.68	10.20
Pedipalp Femur width	4.80	4.68	5.25	5.20	5.35	5.10	4.95	4.70	4.68	5.16	4.56	3.96	3.80
Pedipalp Chela length	29.70	29.00	29.25	30.45	30.50	29.05	26.25	29.40	29.29	31.93	26.29	22.17	22.35
Pedipalp Chela depth	10.20	9.85	10.80	10.40	10.75	10.55	9.72	10.30	10.20	11.16	9.90	8.20	7.80
Movable finger Length	18.60	16.80	16.80	17.05	17.75	16.85	14.70	15.60	15.60	17.41	13.81	12.00	12.10

Table 5: Morphometrical ratios for adult males of *Nebo hierichonticus*.

	Ratios \ Specimen code	1 H	2 H	3 H	4 H	5 H	6 H	7 H	8 H	9 H	10 H	11 H	12 H	13 H
1	Carapace length / Metasoma II length	1.35	1.35	1.39	1.31	1.36	1.36	1.32	1.30	1.40	1.33	1.36	1.44	1.43
2	Pedipalp Femur length / Width	3.13	3.13	2.96	3.33	3.14	3.03	2.81	3.10	3.19	3.09	3.00	2.70	2.68
3	Metasoma V length / Movable finger length	0.90	0.97	0.95	1.03	0.97	1.00	1.01	1.02	1.02	0.97	1.16	1.03	0.95
4	Metasoma V length / Carapace length	1.22	1.23	1.12	1.21	1.20	1.20	1.18	1.21	1.17	1.19	1.24	1.13	1.13
5	Metasoma V length / Metasoma II Width	2.98	3.09	2.86	3.16	3.01	3.12	2.73	2.99	3.00	2.98	3.09	2.78	2.78
6	Pedipalp Chela length / Chela depth	2.91	2.94	2.71	2.93	2.84	2.75	2.70	2.85	2.87	2.86	2.66	2.70	2.70
7	Femur length / chela depth	1.47	1.49	1.44	1.66	1.56	1.46	1.43	1.41	1.46	1.43	1.38	1.30	1.31

Table 6: Measurements for adult females of *Nebo hierichonticus*. Measurements and morphometrics are in mm.

	14 h	15 h	16 h	17 h	18 h	19 h	20 h	21 h	22 h	23 h
Total length	114.85	116.95	122.50	129.20	125.40	109.10	112.80	91.50	140.60	115.30
Carapace Length	15.00	14.60	16.05	16.21	15.61	14.17	15.36	10.20	16.81	15.01
Metasoma II Length	9.48	9.05	10.35	10.80	10.44	9.00	9.84	7.08	11.40	9.60
Metasoma II Width	5.80	5.25	5.90	6.00	6.12	5.64	5.64	4.44	6.48	5.76
Metasoma V Length	15.60	15.15	16.95	17.77	16.81	15.01	16.57	11.40	18.61	16.00
Pedipalp Femur length	13.55	12.90	14.55	15.49	14.89	12.73	14.05	9.85	15.73	13.81
Pedipalp Femur width	5.04	4.85	5.45	5.52	5.28	4.80	5.16	3.66	5.88	5.20
Pedipalp Chela length	27.50	26.70	30.10	31.93	30.75	27.49	29.65	22.45	33.61	31.21
Pedipalp Chela depth	10.50	10.92	12.55	12.00	11.52	10.80	11.64	8.40	12.85	11.76
Movable finger Length	14.65	15.30	17.90	17.89	17.05	14.41	16.21	12.00	19.45	16.56

Table 7: Morphometrical ratios for adult females of *Nebo hierichonticus*.

	Ratios \ Specimen code	14 h	15 h	16 h	17 h	18 h	19 h	20 h	21 h	22 h	23 h
1	Carapace length / Metasoma II length	1.58	1.61	1.55	1.50	1.50	1.57	1.56	1.44	1.47	1.56
2	Pedipalp Femur length / Width	2.69	2.66	2.67	2.81	2.82	2.65	2.72	2.69	2.68	2.66
3	Metasoma V length / Movable finger length	1.06	0.99	0.95	0.99	0.99	1.04	1.02	0.95	0.96	0.97
4	Metasoma V length / Carapace length	1.04	1.04	1.06	1.10	1.08	1.06	1.08	1.12	1.11	1.07
5	Metasoma V length / Metasoma II Width	2.69	2.74	2.87	2.96	2.75	2.66	2.94	2.57	2.87	2.78
6	Pedipalp Chela length / Chela depth	2.62	2.45	2.40	2.66	2.67	2.55	2.55	2.67	2.62	2.65
7	Femur length /chela depth	1.29	1.28	1.16	1.29	1.29	1.18	1.21	1.17	1.22	1.17

Table 8: Measurements for adult males and females of *Nebo yemenensis*. Measurements and morphometrics are in mm.

	24 Y	25 Y	26 y	27 y	28 y	29 y	30 y	31 y
Total length	92.05	94.50	101.65	87.10	96.05	93.55	105.45	101.50
Carapace Length	11.90	12.14	13.80	12.00	13.09	12.61	14.15	13.80
Metasoma II Length	7.55	7.80	8.40	7.75	7.92	7.56	8.82	8.55
Metasoma II Width	4.90	5.10	5.52	4.90	5.16	5.04	5.64	5.50
Metasoma V Length	11.95	12.20	13.81	11.12	12.24	11.88	13.95	13.60
Pedipalp Femur length	10.80	11.28	12.24	10.20	11.40	11.04	12.48	12.30
Pedipalp Femur width	4.20	4.50	4.80	4.32	4.56	4.32	4.90	4.85
Pedipalp Chela length	22.10	22.80	24.80	21.85	23.53	22.25	25.93	25.55
Pedipalp Chela depth	8.70	8.95	10.68	8.64	9.24	9.00	10.80	10.80
Movable finger Length	13.05	12.97	14.65	12.35	13.60	12.48	14.89	14.60

Table 9: Morphometrical ratios for adult males and females of *Nebo yemenensis.*

	Ratios \ Specimen code	24 Y	25 Y	26 y	27 y	28 y	29 y	30 y	31 y
1	Carapace length / Metasoma II length	1.58	1.56	1.64	1.70	1.65	1.67	1.60	1.61
2	Pedipalp Femur length / Width	2.57	2.51	2.55	2.36	2.50	2.56	2.60	2.63
3	Metasoma V length / Movable finger length	0.91	0.94	0.94	0.90	0.90	0.95	0.94	0.93
4	Metasoma V length /Carapace length	1.00	1.00	1.00	0.93	0.94	0.94	0.99	0.99
5	Metasoma V length / Metasoma II Width	2.43	2.39	2.50	2.27	2.37	2.36	2.47	2.47
6	Pedipalp Chela length / Chela depth	2.54	2.55	2.32	2.53	2.55	2.47	2.40	2.37
7	Femur length /chela depth	1.24	1.26	1.15	1.18	1.23	1.23	1.16	1.14

Table 10: Measurements for adult males and females of *Nebo jazanensis* sp. n. Measurements and morphometrics are in mm.

	32 J	33 J	34 J	35 J	36 J	37 j	38 j	39 j	40 j	41 j
Total length	89.10	78.40	77.30	77.20	98.20	94.45	86.25	104.55	100.10	85.20
Carapace Length	12.35	10.44	10.68	9.60	12.97	12.80	12.00	13.33	13.35	11.04
Metasoma II Length	7.40	5.88	6.24	5.76	7.80	7.45	6.95	7.80	7.80	6.30
Metasoma II Width	4.80	4.32	4.32	4.08	5.28	5.40	4.95	5.40	5.40	4.44
Metasoma V Length	11.40	9.00	9.84	8.76	12.48	11.65	11.40	12.36	12.60	10.08
Pedipalp Femur length	11.15	9.00	9.48	8.64	11.76	10.95	10.45	11.52	11.05	9.24
Pedipalp Femur width	4.40	3.78	3.84	3.48	4.44	4.45	4.20	4.60	4.56	4.02
Pedipalp Chela length	23.00	19.69	20.29	18.61	23.41	22.95	22.20	24.37	24.97	20.19
Pedipalp Chela depth	8.70	6.96	7.56	6.48	8.88	9.35	8.40	9.00	10.08	7.68
Movable finger Length	13.10	10.56	10.92	9.60	12.61	13.20	12.85	13.05	13.45	10.32

Table 11: Morphometrical ratios for adult males and females of *Nebo jazanensis* sp. n.

	Ratios \ Specimen code	32 J	33 J	34 J	35 J	36 J	37 j	38 j	39 j	40 j	41 j
1	Carapace length / Metasoma II length	1.67	1.78	1.71	1.67	1.66	1.72	1.73	1.71	1.71	1.75
2	Pedipalp Femur length / Width	2.53	2.38	2.56	2.48	2.65	2.46	2.49	2.50	2.42	2.30
3	Metasoma V length / Movable finger length	0.87	0.85	0.90	0.91	0.99	0.88	0.89	0.95	0.94	0.98
4	Metasoma V length / Carapace length	0.92	0.86	0.92	0.91	0.96	0.91	0.95	0.93	0.94	0.91
5	Metasoma V length / Metasoma II Width	2.38	2.08	2.28	2.15	2.36	2.16	2.30	2.29	2.33	2.27
6	Pedipalp Chela length / Chela depth	2.64	2.83	2.68	2.87	2.64	2.45	2.64	2.71	2.48	2.63
7	Femur length /chela depth	1.28	1.29	1.30	1.33	1.32	1.17	1.24	1.28	1.10	1.20

Table 12: Identification aid matrix for three *Nebo* species (adult males and females). The numbers in the matrix refer to the ratios given in Table 3.

Males Females	*Nebo hierichonticus*	*Nebo yemenensis*	*Nebo jazanensis* sp. n.
Nebo hierichonticus		2, 4, 5, 6	1, 2, 4, 5
Nebo yemenensis	2, 4, 5		1, 4, 6
Nebo jazanensis sp. n.	1, 2, 4, 5	1	

Ecology

The collection site is located in the village of Al Boqa'a (1061 m asl), located in the southwestern heights of the Sarawat Mountains, Al-Dayer Governorate, to the east of Jazan region. The terrain consists of rocky slopes below that embrace deep valleys (Figure 7). It is intensively used as a farmland growing millet, coffee, and quince. Other wild flora includes *Ficus vasta*, *Tamarindus indica*, *Acacia asak*, and *Ficus cordata* ssp. *salicifolia*, in addition to *Cissus rotundifolius* covers the valley with many aromatic plants such as *Ocimum tenuiflorum* and *Artemisia judaica.* Other scorpions that were found in the same area include *Compsobuthus manzonii, Hottentotta scaber, N. yemenensis* and *N. hierichonticus* and *Parabuthus liosoma*.

Discussion

The present study described a new species to the genus *Nebo*, increasing the number of species for this genus to 10. Morphometric ratios of the new species show that it is clearly different from both syntropic species, *N. yemenensis* and *N. hierichonticus* (Table 12). Within the same study area, Al Boqa'a, Al-Dayer Governorate, three species of *Nebo* occur. Similar observation of presence of sympatric species of the genus *Nebo* was documented by Francke (1980), whereas *N. flavipes*, *N. grandis* and *N. yemenensis* were reported in close proximity from each others in Yemen. The distance between *N. grandis* and *N. yemenensis* is about 110 km, and that between *N. flavipes* and *N. yemenensis* is about 66 km. In Oman, the distance between *N. franckei* and *N. whitei* is about 112 km (Vachon, 1980).

It seems that *N. hierichonticus* distribution range extends from Jordan, Sinai, and Palestine (Francke, 1980, Amr and Al-Oran, 1994, Qumsiyeh *et al.,* 2014) further south into Saudi Arabia in around Tabuk in the north to Al Madinah Al Monawwarah provinces and, further south to Al Bahah reaching Jazan close to Yemen borders these records reduce the geographical discontinuity between the previously known northern distribution of the genus from Egypt and Jordan and the densely speciated southern distribution in Yemen and Oman. Francke (1980) stated that specimens collected from north of Jiddah and Qunfidan (= Qunfidah) are morphometrically closer to *N. hierichonticus* on some ratios, while closer to *N. yemenensis* in others. It seems that Yemen is the source of speciation for the four species of this genus in southwestern Arabia.

Similar sympatric species that occur within confined geographic areas were reported in Wadi Araba. Both *Buthacus arava* Cain, Gefen & Prendini, 2021 and *Buthacus yotvatensis* Levy, Amitai & Shulov, 1973 were collected from the same locality in Wadi Khanzeerah, Karak Governorate, Jordan (Cain *et al.,* 2021).

Our study included a large collection of adult *Nebo* specimens from Saudi Arabia and comparative materials from Jordan confirms the significance of morphometric ratios as a valid tool to distinguish species

Figure 7. Al Boqa'a, Jazan Province, the locality from which Nebo jazanensis sp. n. was collected.

of this enigmatic genus as suggested by Francke (1980). The recent molecular work of Alqahtani *et al.* (2023) predicted the presence of interspecific and intraspecific variations among or within *Nebo hierichonticus* and *Nebo yemenensis* that may indicate the presence of other distinct species. This finding supports our newly described species.

Finding three sympatric species within the same area requires further scrutiny by means of molecular tools to reveal their identity and phylogenetic relationship.

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First record of the African powder post beetle, *Lyctus africanus* Lesne 1907 (Insecta: Coleoptera: Bostrichidae: Lyctinae), from Jordan

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Abstract: The African powder post beetle, *Lyctus africanus* Lesne 1907 is recorded from Jordan for the first time. Specimens were collected from infested wood in Jordan Valley near the Dead Sea. The distribution and available data about this beetle are given.

Keywords: New records, wood packing, wood inspection, *Lyctus africanus*.

Introduction

Beetles of the family Bostrichidae are about 570 species in 90 genera often named as powder post beetles because of their ability to reduce wood or bamboo to a thin external shell covering the frass produced by the boring activities of the adults and larvae (Beaver *et al*, 2011, Zhang 2011). Records of the bostrichid fauna of the Middle East are rare, only Iran (Damoiseau 1969; Liu *et al*., 2016) and Palestine (Halperin & Damoiseau 1980; Halperin & Geis 1999; Chikatunov *et al*., 2006) have been well studied. The subfamily Lyctinae (previously treated as family Lyctidae) have about 70 species in 12 genera worldwide. The powder post beetles are slender and uniformly colored brown to black, and 2-7 mm long. The head is prominent from above, and the antennae have a two-segmented club. (Norman and Triplehorn 2005) The genus *Lyctus* Fabricius, 1792 is the largest of the subfamily with 25 species worldwide (Borowski 2007). *Lyctus* species may completely destroy wooden furniture, beams, tool handles, and hardwood floors. They live beneath the surface for months, and timbers from which the adults have emerged appear with tiny holes. Painted or varnished wood is not attacked (Norman and Triplehorn 2005).

Lyctus africanus was first described by Lesne in 1907 from Africa. Gerberg (1957) revised the New World Lyctidae, provided an illustrated and detailed description of *L. africanus,* and listed two synonyms of *L. africanus: L. politus* Kraus, 1911, and *L. spinifrons* Stebb, 1914. *Lyctus africanus* was previously recorded from Palestine, Pakistan, Turkey; India, Nepal (Liu & Beaver 2018), Papua New Guinea (Liu 2010), and Thailand (Beaver *et al*., 2011). *Lyctus africanus* is considered a pan-tropical species expected to become a cosmopolitan species, including, Madagascar, USA, and Northern Territory in Australia (Gerberg 1957). Gardner (1933) recovered *L. africanus* and described its larva from bamboo, *Bambosa* sp. (Poaceae). More than 85 hosts were listed from India (Beeson & Bhatia 1937). It was recorded from Liquorice (*Glycyrrhiza glabra*) (Leguminosae) and other dry roots (Gerberg 1957 and Cymorek 1961). Iwata (1982) recorded this species from *Morus alba* (Moraceae) in Japan.

Halperin & Geis (1999) recorded seven species of Lyctinae (including *L. africanus*) from Palestine and Sinai and discussed their damage and prevention. Only one species from Lyctinae was previously recorded from Jordan, *Acantholyctus cornifrons* (Lesne) (Liu and Geis 2019).

The objectives of this paper are to officially record *L. africanus* from Jordan for the first time, and to provide available data about its biology and distribution.

Materials and Methods

The powder post beetles were collected by the second author from a hotel east of the Dead Sea in the Jordan Valley. The hotel had

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many wooden structures and decorations from which woody powder was falling down on many places causing annoyance to the hotel staff and visitors. The wood was badly affected and turned into powder (Figure 1A). Powder post beetles and pieces of damaged wood were taken to the University of Jordan for Identification by the first author. The beetles were identified using the key of Liu and Geis (2019), and then the identification was confirmed by checking the original description of Lesne (1907), the detailed description of Gerberg (1957), and by comparing our specimens to the paratype color photos of *L. africanus* provided by the Types Virtual Collections, in the Royal Belgian Institute of Natural Sciences. Digital images were taken by a 65

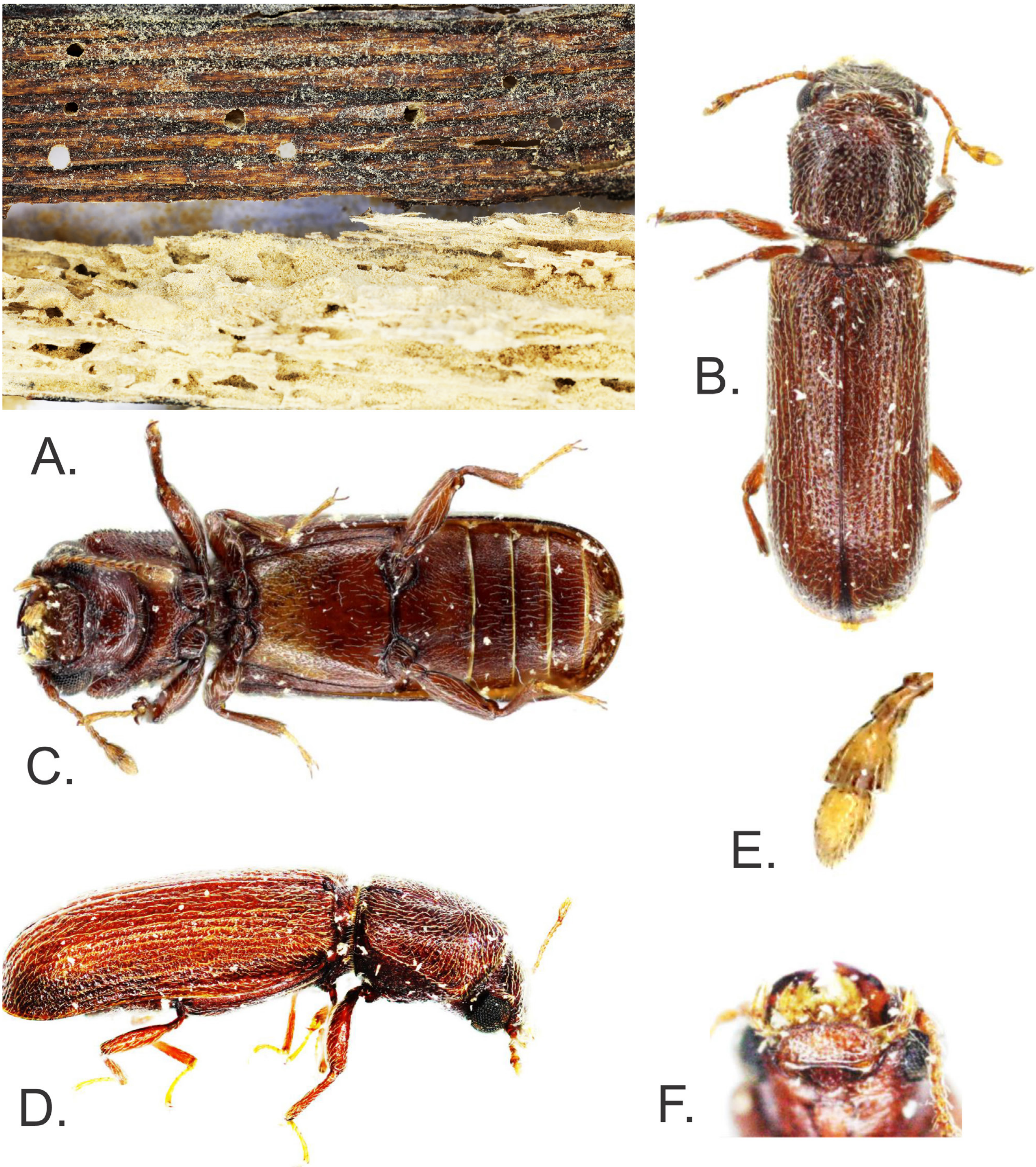

Figure 1. A. Symptoms of infested wood (above, outside symptoms; below, inside symptoms). **B.** Dorsal view of *Lyctus africanus***. C.** Ventral view**. D.** lateral view. **E.** Antennal club. **F.** Head and mandibles.

mm macro lens mounted on a Canon (Tokyo, Japan) 5D Mark IV camera with continuous LED ring light. Several images were taken at different focusing distances, and then they were stacked using Helicon Focus software and processed by Adobe Photoshop as needed. Voucher specimens of the collected samples were preserved in the University of Jordan Insect Museum.

Results and Discussion

Lyctus africanus Lesne 1907 is recoded from Jordan for the first time. This species most probably entered Jordan in wood imported from India. The hotel administration mentioned that infested wooden structures at the hotel were imported from India in which the species is well known to occur. However, another possibility, but less likely, is that the pest could have come from Palestine. Halperin & Geis (1999) recorded the following seven species of Lyctinae from Palestine and Sinai and discussed their damage and prevention: *Lyctus linearis* (Goeze) and *L. planicollis* Le Conte *L. africanus* Lesne; *L. brunneus* (Stephens); *L. parallelocollis* Blackburn; *Minthea rugicollis* Walker; *Trogoxylon impression* (Comolli); and *Acantholyctus comifrons* Lesne. Two of these species are found in both countries (*L. africanus* and *Acantholyctus comifrons*). The other five species may eventually be found in Jordan.

L. africanus (Figures 1B-F) resembles *brunneus* (Steph.), from which it is differentiated by the contiguous, continuous, unelevated lateral lobes of the postclypeus and frontal lobes. The female can be distinguished by the heavy fringe of hairs on the distal margin of the fourth sternite, which is lacking in the latter species. *L. africanas* is smaller than *brunneus*.

Fourteen species of *Lyctus* have Eurasian distribution. *Lyctus brunneus* is cosmopolitan and *L. africanus* is pan-tropical. The origin of the Eurasian species is difficult to determine because their original distribution was greatly changed by international trade (Liu and Geis 2019).

Powder post beetles are frequently intercepted in wood packaging. Several species are highly polyphagous (Booth *et al.,* 1990). Many powder post beetles can attack treated wood such as wooden packing materials after treatment. Therefore, their presence does not necessarily indicate that the treatment was not effective (Haack *et al.,* 2014). Powder post beetles are among the major pests of wooden packing materials shipped to the EU mainly from India and china. *Lyctus* species are considered the most abundant invasive pests in the Bostrichidae. Interceptions of species of Lyctinae have increased rapidly in the EU since 2009 (Eyre *et al.*, 2018). As wooden packing materials continue to be used in international trade and as long as the global warming continues, increasing changes in the powder post beetle's fauna of the subfamily Lyctinae are expected in the Eurasian area (Liu and Geis 2019).

Conclusion

After recording *L. africanus* Lesne 1907 from Jordan for the first time, only two species of Lyctinae are known to occur in Jordan so far. This proves that species of subfamily Lyctinae as well as the family Bostrichidae need investigation in Jordan. Plant protection authorities in Jordan should pay special attention to Lyctine species that may enter the country and should alert workers at trade ports to carefully inspect wooden packaging materials used in shipments entering Jordan.

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Notes on the aquatic macroinvertebrates of the Mujib River Basin and Azraq Wetland Reserve in Jordan for use in biomonitoring

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Abstract: Freshwater is in crisis globally. Arid countries such as Jordan are particularly challenged regarding freshwater, especially considering growing demand and increasing pollution pressure. Water resource monitoring is essential to combat the threats to freshwater and ensure effective and sustainable management of scarce freshwater resources. Biomonitoring using aquatic macroinvertebrates provides a practical, cost-effective, and holistic approach to assessing water quality and freshwater ecosystem health. We surveyed the aquatic macroinvertebrates at four sites in Jordan, three sites in the Mujib River basin and at one site in the Azraq Wetland Reserve, using biomonitoring survey methods employed and accredited in South Africa. The surveys present a first dedicated aquatic macroinvertebrate survey of the Azraq Wetland Reserve, and a first survey of the Mujib River basin using standard biomonitoring techniques, rather than exhaustive sampling. We report the taxa sampled at each site, identified in-field to family-level where possible. We recorded 20 different taxa at the Azraq Wetland Reserve, and 28 different taxa within the Mujib River basin. The diversity of taxa sampled using standard biomonitoring techniques supported previous work by Alhejoj, Bandel and Salameh (2014) demonstrating that aquatic macroinvertebrates present a useful tool for biomonitoring of water resources in Jordan. However, we suggest that follow-up research is done to build on and refine the ‘Jordan Biomonitor System for Watercourses (JBSW)’ developed by Alhejoj, Bandel and Salameh (2014). The JBSW should be modified to become an integrated index based on the community, identified to family-level, of aquatic macroinvertebrates present to make it easy and practical to use in-field, comparable to indices developed and validated elsewhere in the world. If this is done, biomonitoring using aquatic macroinvertebrates could become a powerful tool to help assess and manage the precious freshwater resources in Jordan as they come under ever increasing pressure from overexploitation, pollution, and growing demand.

Key words: water scarcity, water quality, Jordan, aquatic macroinvertebrates, biomonitoring

Introduction

The Hashemite Kingdom of Jordan (hereafter Jordan) is a critically water scarce country (Jaber *et al.*, 1997; Schyns *et al.*, 2015). The importance and rarity of precious freshwater resources grows daily as unsustainable extraction practices diminish surface and groundwater reserves in an attempt to meet growing demand from rapid population growth and increasing urbanization (Hadadin *et al.*, 2010; Hellegers *et al.*, 2022). Unsustainable use and diversion of freshwater supplies have already led to degradation of freshwater systems, even resulting in local extinctions (Amr *et al.*, 2011) and ecological or social disasters (Procházka *et al.*, 2008; Mir and Hamidan, 2012; Whitman, 2019). For example, the Azraq Oasis within the Azraq Wetland Reserve is now considered an ecological

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disaster area after the springs which supplied it began drying in the 1980s. In 1992 the oasis was completely desiccated due to exploitation of the fresh water supply to support the cities of Azraq and Amman (Disi *et al.*, 2014). The current day oasis represents approximately 5-10% of its size prior to the 1980s, after restoration efforts by the Royal Society for the Conservation of Nature (RSCN; Whitman, 2019). Degradation, or outright loss, of freshwater ecosystems presents a major problem worldwide, but especially in water scarce regions such as Jordan. Freshwater ecosystems provide a range of goods and services that both humans and biodiversity are completely reliant on, such as water treatment, clean drinking water, disaster mitigation, fish, fibre, recreational and cultural importance, and intrinsic 'quality of life' value (Díaz *et al.*, 2018; Dudgeon, 2019; Albert *et al.*, 2021; Lynch *et al.*, 2023). Considering the critical importance of freshwater resource preservation in Jordan, it has become vital to design and implement water quality monitoring programs, and to establish which humans and biodiversity are reliant on which freshwater resources.

Aquatic macroinvertebrates represent a highly useful group for assessing and monitoring water quality and river or lake health. This is because different taxa have unique habitat preferences in terms of water quality parameters and physical habitat characteristics, as well as unique tolerance levels for pollution (Johnson *et al.*, 1993; Muralidharan *et al.*, 2010; Arias-Real *et al.*, 2022). Through determining what aquatic macroinvertebrates are present or absent from a system, in addition to their tolerance levels for pollution and disturbance, one can infer information about the water quality and ecological health of a system (Alhejoj *et al.*, 2014b). For example, Alhejoj et al. (2017) point out that the *Planorbis*, *Gyraulus* and *Ancylus* genera have been nearly completely excluded from Jordan freshwater systems because of increasing pollution. In this study, we sampled sites within the Mujib River basin, as well as a site within the Azraq Wetland Reserve, in Jordan to determine what macroinvertebrate taxa were present. To the best of our knowledge, this presents a first dedicated assessment of the aquatic macroinvertebrates present at the Azraq Wetland Reserve. The Mujib basin has been previously sampled, either for specific groups of invertebrates, or for all aquatic macroinvertebrates (Amr *et al.*, 2013; Haddad *et al.*, 2013; Ramadan and Katbeh-Bader, 2018). However, in this assessment, we sampled using the techniques outlined in the South African Scoring System (SASS) version 5 (Dickens and Graham, 2002) to test the efficacy and feasibility of implementing a similar aquatic macroinvertebrate biomonitoring technique at these locations. These locations were chosen because of the importance of the freshwater in the Mujib River basin and Azraq Wetland Reserve for biodiversity, as signalled by the establishment of the Mujib Biosphere Reserve in 1987 (Haddad *et al.*, 2013), and the recognition of the Azraq Wetland Reserve (Disi *et al.*, 2004) as a Ramsar site (https://rsis.ramsar.org/ris/135), an Important Bird Area (BirdLife International, 2023), and a International Union for the Conservation of Nature (IUCN) Green List site (IUCN, 2023). The freshwater supplied by the Mujib River basin is also essential for human use (e.g., abstractions for agriculture, domestic water supply, and ecotourism), especially for supplying Jordan's capital city, Amman (Hamidan, 2014). The Azraq Wetland Reserve is also a highly valued cultural, historical, and tourism site (Disi *et al.*, 2004; Maher *et al.*, 2021; Boyd *et al.*, 2022). Therefore, it is crucial to establish what biodiversity is present in the basin, and to assess the plausibility of biomonitoring for determining the water quality and health of the system to enable sustainable management. We aimed 1) to gather a first assessment of the aquatic macroinvertebrates present at the Azraq Wetland Reserve, and a first assessment of aquatic macroinvertebrates in the Mujib River basin using standard biomonitoring sampling techniques, and 2) based on these sampling efforts, to form recommendations on using macroinvertebrates for biomonitoring water quality and aquatic ecosystem health within these systems to follow up on initial work done to develop the 'Jordan Biomonitor System for Watercourses (JBSW)' developed by Alhejoj, Bandel and Salameh (2014a).

Materials and Methods

Study sites: The Mujib basin contains two major sub-catchments, the Wadi Mujib (~4500 km^2) and the Wadi Wala (or Haidan; ~2100 km^2) catchments, and ranges from an elevation of ~950 meters above sea level in the east, to ~430 meters below sea level in the west (Hamidan, 2014). Rainfall in the catchment falls largely over the Boreal Winter and Spring, falling in a gradient from ~50 mm per year in the east to ~300 mm per year in the west (El-Naqa, 1993; Al-Harahsheh and Al-Amoush, 2010). There are two large impoundments in the catchment, the Wala Dam (on the Haidan River) and the Mujib Dam (on the Mujib River). These are associated with abstraction partly for domestic and industrial use within the settlements in the catchment, and primarily for irrigation for numerous small to medium-scale rangeland practices. Perennial flow in the Mujib River is maintained by surfacing groundwater (Ijam and Al-Mahamid, 2012; Farhan and Al-Shaikh, 2017). Little water from the Mujib River actually reaches the Dead Sea, since it is diverted to a water treatment plant and siphoned off for human use just before it eventually empties (Hamidan, 2014). Approximately 40-50 of aquatic macroinvertebrate species have been recorded in the Mujib River sub-catchment, representing 27 families and five different orders (Haddad *et al.*, 2013). Approximately 75 insect species from 33 families within seven orders were recently recorded through exhaustive sampling within the Haidan sub-catchment (Ramadan and Katbeh-Bader, 2018). River flow is measured at gauging stations on the dams and at a weir located just upstream from where the water is diverted or flows into the Dead Sea. Water quality and biomonitoring data are not regularly collected in the basin.

The Azraq Wetland Reserve is within the Azraq basin, 500 meters above sea level (Disi *et al.*, 2004). The reserve falls in within the hyper arid north-eastern part of Jordan, with a mean annual rainfall of only ~70 mm per year. The wetland dried up completely in 1980 following overexploitation of the surface and surrounding groundwater. Restoration efforts by the RSCN are ongoing, with water resupplied to the reserve via groundwater extraction. The current area of the reserve is maintained at approximately 10% of its former size. However, it is still recognised as a wetland of international significance by the Ramsar Convention (https://rsis.ramsar.org/ris/135), as an Important Bird Area by Birdlife International (BirdLife International, 2023), and was added to the IUCN Green List in 2018 based on the fact that it hosts a range of fish (including the critically endangered and endemic Azraq killifish or toothcarp *Aphanius sirhani*), birds, mammals, reptiles, and macroinvertebrates (IUCN, 2023). The only assessment of macroinvertebrates in the Azraq Wetland Reserve we are aware of was a survey of the terrestrial arthropods (Amr *et al.*, 1996), we can find no published data on previous assessment of the aquatic macroinvertebrates. For more information on the Azraq Wetland Reserve biodiversity and status, see Disi *et al.* (2004).

Aquatic macroinvertebrate surveys were conducted between 22 – 24 October 2022 at three sites (Haidan Bridge, Al Banna, and Malagi) within the Mujib basin and one site within the Azraq Wetland Reserve (Figure 1, Table 1). The Haidan Bridge site was ~7.5 km upstream of the Mujib Biosphere Reserve boundary, downstream of the Wala dam. The Al Banna site was on the eastern border of the Mujib Biosphere Reserve, downstream of the Mujib dam. The Malagi site was within the Mujib Biosphere Reserve, upstream of the Mujib River waterfall within the Mujib gorge, but downstream of the confluence of the Mujib and Haidan Rivers (Figure 1).

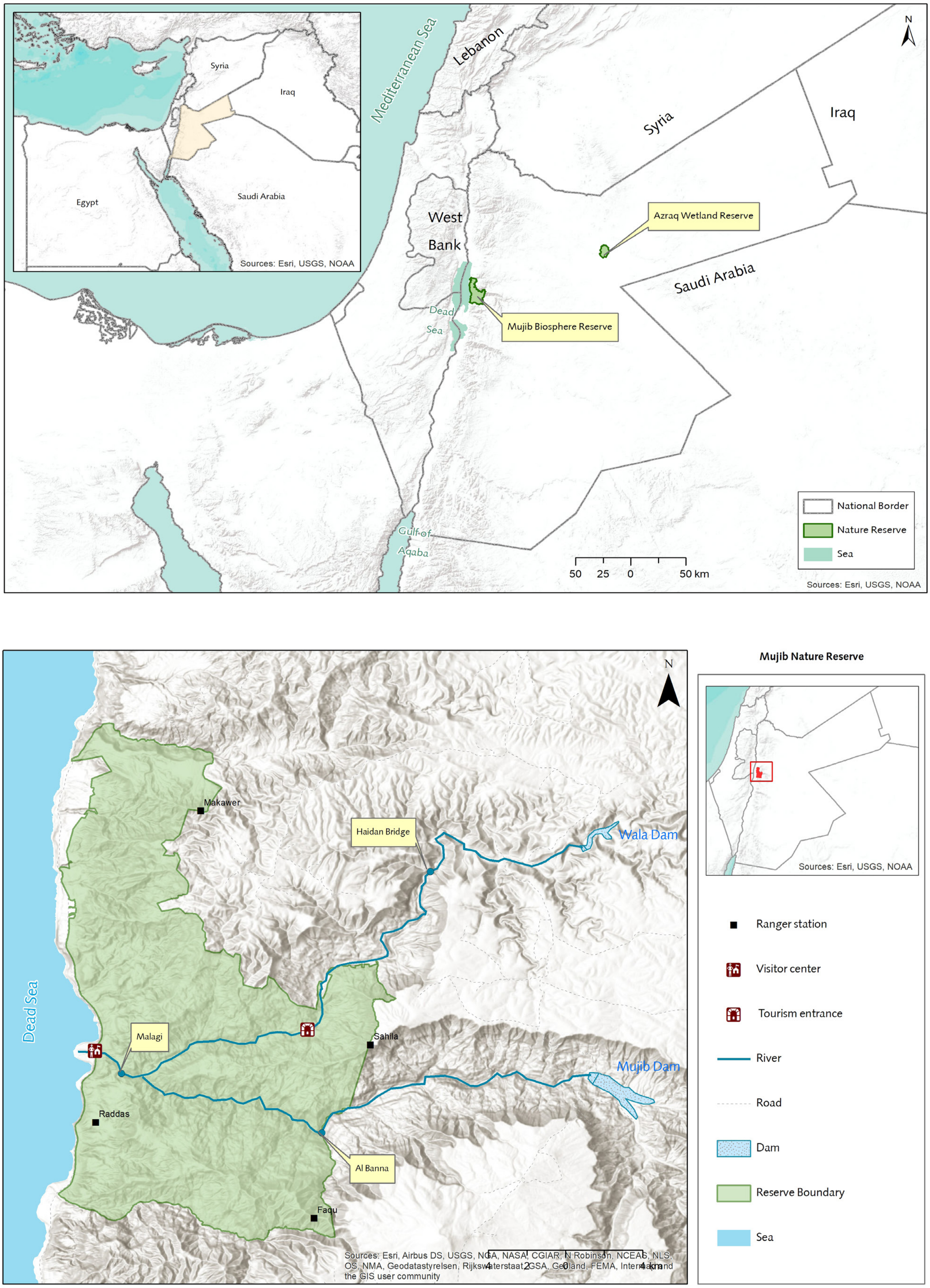

Figure 1. Map showing A) the position of the Azraq Wetland Reserve and the Mujib basin within Jordan, and B) the specific location of the aquatic macroinvertebrate survey sites within the Mujib basin, along with the location of the large Mujib and Wala impoundments, as well as the boundaries of the Mujib Biosphere Reserve. The Mujib basin drains into the Dead Sea in the west. Note the different scales.

Table 1. Details on the survey sites, showing the assigned site name, the date of sample, the river the site was on (not applicable for the Azraq Wetland Reserve), and GPS coordinates.

Site	Date sampled	River	Latitude (°N)	Longitude (°E)
Malagi	22/10/2022	Mujib	31.456317	35.585585
Al Banna	23/10/2022	Mujib	31.440868	35.692322
Hidan Bridge	23/10/2022	Haidan	31.529216	35.726725
Azraq Wetland Reserve	24/10/2022		31.501160	36.49150

Data collection: Aquatic macroinvertebrates surveys were conducted at each site using the sampling method described in the South Africa Scoring System version 5 (SASS5; for full details see Dickens and Graham, 2002). Briefly, the SASS5 method uses a standardised rapid kick-sampling protocol to thoroughly sample aquatic macroinvertebrates in streams or rivers across habitat biotopes. Sampling covers three river components; stones (in and out of current), vegetation (instream and at the river edge), and sediments (gravel, sand, and mud). Samples are collected with a 30x30 centimetre frame net with a pore size of one millimetre^2. For each component, the sample is diluted in a white tray so that the sampler can spend 15 minutes identifying each macroinvertebrate sampled. The sampler also notes taxa anecdotally that they can manually catch or see with visual observations (see Dickens and Graham, 2002). The method is accredited to ISO 17025 standards. Sampling was conducted by a South African Department of Water and Sanitation (DWS) accredited SASS5 practitioner. The method was modified in-field to effectively gather a representative sample the site at the Azraq Wetland Reserve; no stones components were available for sampling, so only the sediments and vegetation were sampled, along with anecdotal observations. Four different sites were sampled at the Azraq Wetland Reserve, one at each of the main pans, with the samples pooled for identification and reporting. The macroinvertebrates sampled were identified to family level where possible on-site. Flow velocity data were also collected at each site (with the exception of the Azraq Wetland Reserve) using a transparent velocity head rod (hereafter 'velocity plank'; Fonstad *et al.*, 2005; WRC, 2016; Graham and Taylor, 2018).

Results

Site status

The sites (Figure 2) varied in terms of the human and livestock impact, flow, and availability of instream habitat for macroinvertebrates. The Haidan Bridge site appeared popular for public visitation, leading to a build of waste pollution. Livestock were observed in the area feeding on marginal vegetation. There were a variety of pools and water depths, increasing instream flow- and depth-related habitat heterogeneity. The Al Banna site showed some evidence of use by locals and livestock, with some waste pollution present. Instream aquatic macroinvertebrate structural habitat was the most varied, though there was little variation in flow depth or velocity. The Malagi site showed minimal human or livestock impact. The instream habitat was limited by the fact that the stones were mostly embedded or armoured by mineralization. Average flow velocity at the sites were 0.036 $m^3.second^{-1}$, 0.126 $m^3.second^{-1}$, and 0.729 $m^3.second^{-1}$ at the Haidan Bridge, Al Banna, and Malagi sites, respectively.

Macroinvertebrates

The Azraq Wetland Reserve site had the highest number of taxa, with 20 different family level taxa identified from 10 orders or clades (Table 2). The Haidan Bridge site had 18 family level taxa from nine orders or clades, the Al Banna site 15 family level taxa from eight orders or clades, and the Malagi site 13 family level taxa from eight orders or clades (Table 2).

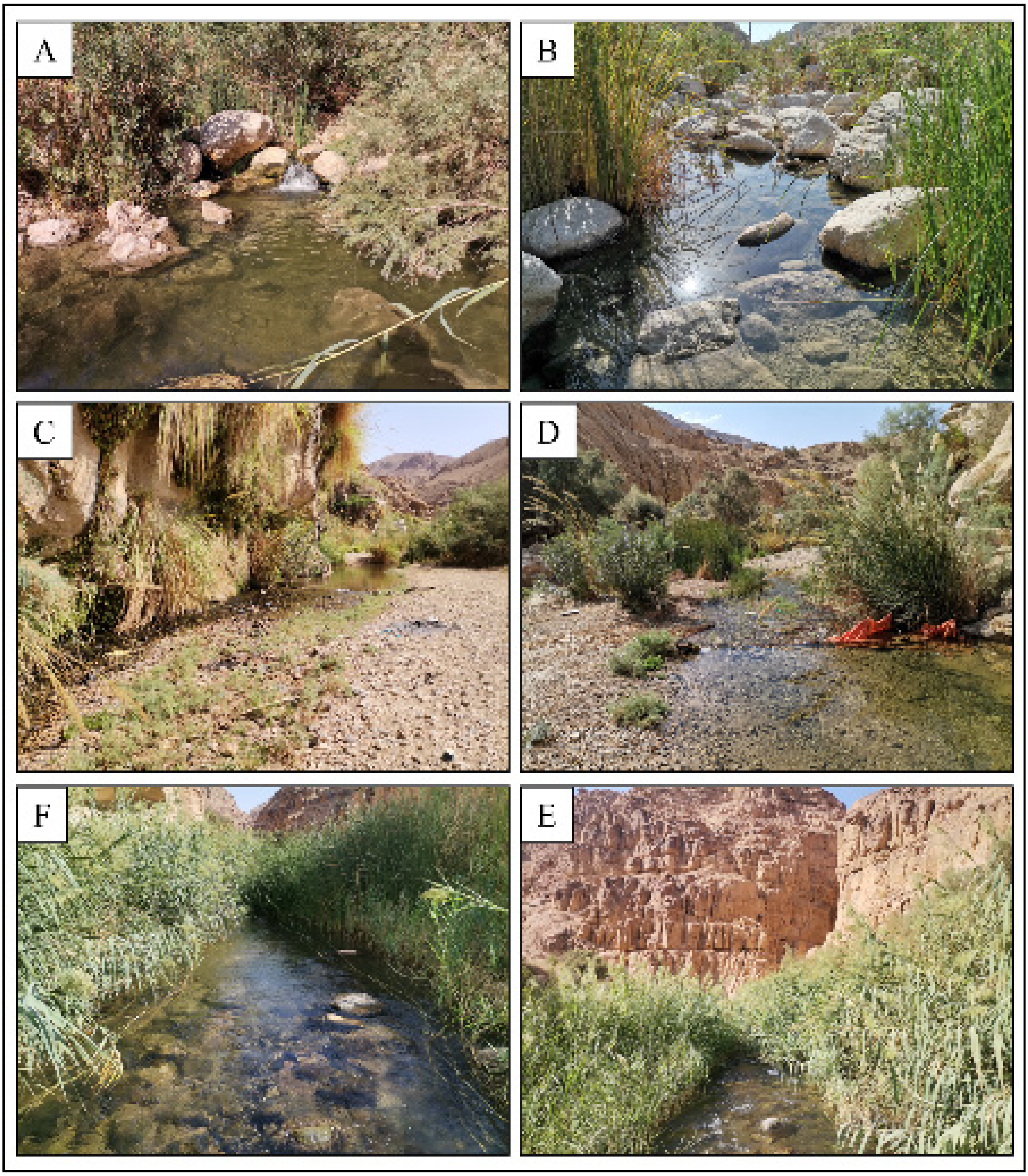

Figure 2. Upstream (left column) and downstream (right column) images of the Haidan Bridge (A and B), Al Banna (C and D), and Malagi (E and F) aquatic macroinvertebrate survey sites.

Table 2. Aquatic macroinvertebrate taxa sampled at each survey site; x denotes presence.

Order level grouping[*]	Family level grouping[*]	Site and presence of taxon			
		Malagi	Al Banna	Haidan Bridge	Azraq Wetland Reserve
Amphipoda	Amphipoda[e]				x
Caenogastropoda[a]	Melanopsidae	x	x	x	x
	Thiaridae	x	x		x
Coleoptera	Dytiscidae				x
Cycloneritida	Neritidae		x		x
Decapoda	Potamonautidae	x	x	x	
Diptera	Chironomidae	x	x	x	x
	Culicidae			x	x
	Dolichopodidae		x		
	Simuliidae	x			
	Tabanidae		x		x
	Tipulidae	x			
Ephemeroptera	Baetidae 1 sp	x			x
	Baetidae 2 sp			x	
	Caenidae	x		x	
	Leptophlebiidae			x	
Hemiptera	Corixidae		x	x	
	Gerridae			x	x
	Naucoridae			x	
	Nepidae				x
	Notonectidae			x	x
	Pleidae				x
	Veliidae	x	x	x	x
Hirudinea[b]	Hirudinea[a]			x	
Hygrophila[c]	Lymnaeidae				x
	Physidae				x
Odonata	Aeshnidae			x	x
	Coenagrionidae	x	x	x	x
	Euphaeidae		x	x	
	Gomphidae	x	x		
	Libellulidae		x		x
Oligochaeta[d]	Oligochaeta[d]	x	x	x	
Trichoptera	Hydropsychidae	x	x		
Trombidiformes	Hydracarina[f]			x	x
	No. Order level taxa	8	8	9	10
	No. Family level taxa	13	15	18	20

Notes: * Taxa were grouped to the nearest taxonomic level as possible based on existing taxonomic classes or what is possible with in-field identification. [a] Subclass Caenogastropoda; [b] Subclass Hirudinea; [c] Superorder Hygrophila; [d] Subclass Oligochaeta; [e] Order Amphipoda; [f] Unranked grouping for many families of aquatic mites.

Discussion

Freshwater scarcity is a pressing global issue (Gleick and Cooley, 2021). Jordan faces especially severe freshwater scarcity due to its arid climate, unsustainable reliance on limited water resources, and increasing population (Jaber *et al.*, 1997; Al-Assa'd and Abdulla, 2010; Schyns *et al.*, 2015; Clemens *et al.*, 2020; Dombrowsky *et al.*, 2022; Oberhauser *et al.*, 2023). As demand surpasses supply, Jordan faces significant challenges in maintaining adequate water quantity and quality for domestic, agricultural, and industrial purposes (Whitman, 2019). As a result, it is essential to monitor the rare and precious freshwater resources in Jordan to ensure sustainable management, use, and preservation of freshwater for both humans and biodiversity alike. This study presents, as far as we are aware, a first directed survey of the aquatic macroinvertebrates in the Azraq Wetland Reserve, as well as a first survey of the aquatic macroinvertebrates using standard biomonitoring techniques in the Mujib basin, in Jordan (Disi *et al.*, 2004; Haddad *et al.*, 2013; Alhejoj *et al.*, 2014b, 2014a, 2017; Ramadan and Katbeh-Bader, 2018). A good variety of taxa across a range of suspected pollution and water quality tolerances were present in the Azraq Wetland Reserve and the Mujib River basin. As a result, following the earlier work of Alhejoj, Bandel and Salameh (2014a), we recommend that biomonitoring via surveying the aquatic macroinvertebrates in these locations could provide a powerful tool to assess the health and the quality of the water resources. However, this suggestion is subject to the provision that family-level aquatic macroinvertebrate tolerances and sensitivities are validated for Jordan to develop an integrated index for rapid, in-field assessment of water resource water quality and ecological health, as employed elsewhere in the world (e.g., Dickens and Graham, 2002; Morse *et al.*, 2007; Paisley *et al.*, 2014; Odountan *et al.*, 2019; Ndatimana *et al.*, 2023).

Notes on aquatic macroinvertebrates of the Azraq Wetland Reserve and Mujib River basin

This study provides a first dedicated survey of the aquatic macroinvertebrates at a site in the Azraq Wetland Reserve, to the best of our knowledge. We identified specimens from 20 families within 10 orders or clades. The Amphipoda (malacostracan crustaceans, Class Amphipoda), Dytiscidae (predatory diving beetles, Order Coleoptera), Lymnaeidae (pond snails, Superorder Hygrophila), Nepidae (water scorpions, Order Hemiptera), Physidae (bladder snails, Superorder Hygrophila), and Pleidae (pygmy backswimmers, Order Hemiptera) were recorded in the Wetland Reserve and not in the Mujib River basin, likely reflecting geographic and habitat variation (i.e., wetland *versus* river). More thorough sampling at regular time intervals and at more locations across the Wetland Reserve may yield additional insights into the diversity and abundance of the different taxa present. A total of 28 families of macroinvertebrate were identified in the Mujib basin, similar to the number reported in previous more exhaustive assessments (Haddad *et al.*, 2013; Ramadan and Katbeh-Bader, 2018), supporting the effectiveness of sampling using SASS5 methods for an efficient and thorough sampling of aquatic macroinvertebrates. Variations in the taxa present at each site likely reflected the variations in human impacts, flow, and habitat availability (Dickens and Graham, 2002). For example, the Haidan Bridge site had low flow rates and water in standing pools at various depths, creating heterogenous habitat for different species with different habitat-flow-depth preferences. In contrast, the Malagi site showed minimal human impact, but was more uniform in instream habitat, flow velocities, and flow depths, limiting habitat for a variety of taxa.

The potential use of aquatic macroinvertebrates for biomonitoring in Jordan

Water resource monitoring involves the regular assessment of physical, chemical, and biological parameters to evaluate the health and safety of water resources (Altenburger *et al.*, 2015; Behmel *et al.*, 2016). Monitoring helps identify patterns of use, identify potential contaminants, track pollution sources, and implement appropriate mitigation measures. Essentially, monitoring provides the core data for making informed decisions regarding water resource management, protection, and restoration (Chapman, 1996; Lovett *et al.*, 2007). Among the various monitoring methods, biomonitoring stands out as an effective, practical, and holistic approach for assessing the health of freshwater bodies (Friberg *et al.*, 2011). Aquatic macroinvertebrates present an especially useful biomonitoring tool, given they 1) are easy to sample and identify, so monitoring does not require sophisticated equipment or complex laboratory analyses, making it cost-effective method, 2) play a critical role in freshwater ecosystems, 3) are found in abundance and variety in freshwater systems around the globe, and 4) are highly responsive to changes in water quality, with taxon-specific sensitivities and tolerances (Dickens and Graham, 2002; Bonada *et al.*, 2006). Essentially, surveying aquatic macroinvertebrates provide an affordable, rapid, integrated assessment of the impacts of various stressors, including pollution, habitat degradation, and changes in water flow, providing a holistic view of water quality and ecological health of aquatic systems. Though freshwater systems are scarce in Jordan, this study supported previous work by Alhejoj, Bandel and Salameh (2014a) demonstrating that they still contain a rich biodiversity of aquatic macroinvertebrates suitable for biomonitoring purposes. However, the classifications listed in the 'Jordanian Biomonitor System for Watercourses (JBSW)' proposed by Alhejoj, Bandel and Salameh (2014a) are loosely based on the presence or absence of key taxa at various taxonomic hierarchies with known pollution tolerances, rather than an integrated index based on the ecology and sensitivity of the entire community present at a similar, easily identifiable, taxonomic hierarchy (Alhejoj *et al.*, 2014a). As a result, the JBSW largely inhibits the rapid field assessment possible using family-level taxonomic identification. For example, our results suggested that each of the sample sites could show anywhere from moderate to high water quality according to the JBSW depending on the genus or species of Neritidae (nerites, Order Cycloneritida), Melanopsidae (melanopsids, Superfamily Cerithioidea), Caenidae (small squaregill mayflies, Order Ephemeroptera), or Chironomidae (chironomids, Order Diptera) specimens at each site. Genus or species-level resolution identifications of aquatic macroinvertebrates are seldom possible without laboratory analysis by taxonomic experts. Therefore, for the JBSW to be practical in-field to develop rapid assessments, it may be necessary to refine evaluation to easily identifiable family-level taxonomic requirements. Overall, we recommend that dedicated research is done to follow up on the excellent ground work done by Alhejoj, Bandel and Salameh (2014a) to develop a reworked, thorough aquatic macroinvertebrate biomonitoring tool based on taxonomic classifications rapidly identifiable in-field, similar to those developed and employed for other nations (e.g., Dickens and Graham, 2002; Palmer and Taylor, 2004; Morse *et al.*, 2007).

Conclusions

Water quality monitoring is essential in water-scarce regions like Jordan to ensure sustainable water resource management and protect the health of ecosystems and communities. Among the various monitoring methods, biomonitoring using aquatic macroinvertebrate offers a practical and effective approach to generate a holistic view of water quality and water body health. The cost-effectiveness, ease of sampling, and standardized protocols make it particularly suitable for resource-limited regions such as Jordan. We recommend that a scoring system to calculate an aquatic macroinvertebrate biomonitoring index similar to those used elsewhere in the world (Dickens and Graham, 1998; Morse *et al.*, 2007; Paisley *et al.*, 2014; Odountan *et al.*, 2019) be developed and validated for the taxa at family level in Jordan to follow up on initial work done by Alhejoj, Bandel and Salameh (2014a). Thereafter, efficient and effective biomonitoring can be integrated into water quality monitoring programs to enhance Jordan's ability to address water scarcity challenges and promote the sustainable use of its limited water resources.

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Short Communication

Beak Abnormality in Indian Rock Dove (*Columba livia*) in Nilgiris, India

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Beak abnormalities have been reported across a wide range of avian species (Pomeroy, 1962; Craves 1994). Beak deformities are typically rare (<1%) in wild bird populations (Pomeroy, 1962; Tweit et al. 1983; Nogales et al. 1990; Rockwell et al. 2003), and most reports relate to single individuals (Craves, 1994). Recently, however, epizootics of beak deformities have occurred in resident species in Alaska (Handel et al. 2010) and in other regions of North America (Van Hemert and Handel, 2010; Van Hemert, *et al.,* 2012). In this note, the researchers present one record of a deformed bill in a rock dove (*Columba livia*) in Nilgiris, Tamil Nadu, India.

On 10/3/2023, the researchers observed a beak deformity in a rock dove from Ooty, from a human habitation of the Upper Nilgiris (11.399209, 76.704345). The deformation was observed in the upper mandible of this bird which was found to be oversized (Figure 1). In India, very little information is available on beak deformities in birds namely common myna (*Acridotheres tristis*), Indian Jungle Crow (*Corvus culminatus*), Indian House Crow (*Corvus spledens*), Indian Rock Pigeon (*Columba livia*), Indian Eagle Owls (*Bubo bengalensis*), and Ashy-crowned Sparrow-lark (*Eremospterix griseus*) (Pandey, *et al.,* 2018; Siva, *et al.*; 2021; Anurag and Yadav 2021; Chouhan, *et al.;* 2022; Samal, *et al.;* 2023). Van Hemert and Hallen (2010) reported that the handling of the food by birds with bill deformities may cause a functional limitation. Bill deformities may also prevent the bird from having a defence against ectoparasites (Clayton, *et al.;* 2005), which is likely to produce a decrease in its health conditions. Functional limitations and the decreasing health conditions can affect survival, which may be the reason why bill abnormalities are uncommon in wild birds, with a frequency estimate of less than 0.5%

Figure 1. We observed a deformation in the upper mandible of this bird which was found to be oversized.

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(Pomeroy, 1962). The records of the Rock Dove show it is was very healthy even though it has been affected by bill deformities. Thus, the researchers believe that this abnormality has not significantly affected the feeding abilities of this Rock Dove because the bird has apparently survived and remained healthy to the age recorded. This state contrasts with that of other birds where the abnormality of the bill may have increased the mortality rate and led to the death of the bird (Marti, *et al*.; 2008).

The causes of the bill abnormality in this individual are unknown, but the current record increases knowledge on the presence of development deformities in birds. This is important for future monitoring because an increase in the incidence of abnormal bills in birds could indicate environmental toxicological problems in resident areas.

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Short Communication

Further Records of the Long-eared Hedgehog, *Hemiechinus auritus* (Gmelin, 1770), in Saudi Arabia

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Abstract: The present note provides additional records for long-eared hedgehog, *Hemiechinus auritus* from Saudi Arabia, increasing its current known distribution range further to the west.

Three species of hedgehogs have been recorded from Saudi Arabia, namely: Brandt's hedgehog, *Paraechinus hypomelas* (Brandt, 1836), distributed in southwest of the country (Nader, 1991), the desert hedgehog, *Paraechinus aethiopicus* (Ehrenberg, 1832), known to occur in most deserts of Saudi Arabia (Harrison and Bates, 1991), and the long-eared hedgehog, *Hemiechinus auritus* (Gmelin, 1770) with very few records from localities along the Eastern Province (Pitcher, 1976; Kock and Nader, 1996).

The long-eared hedgehog, *Hemiechinus auritus* (Gmelin, 1770), is distributed throughout the Eastern Mediterranean region, north of Egypt and Jabal Al Akhadr in Libya to southwest Asia to southwestern Pakistan, eastern Ukraine through Mongolia to China (Wilson and Reeder, 2005). In the Arabian Peninsula, its distribution extends from Kuwait reaching as far Bahrain (Al-Khalili, 1990; Abu Baker *et al*., 2022).

Very little is known about the distribution of this species in Saudi Arabia. Its presence in Saudi Arabia is based on four localities along the Eastern Province: Abu Hadriyah, Dharan, Safaniyah (Pitcher, 1976), and Ras al Abkhara (Kock and Nader, 1996). Since then, no further records were reported.

On the May 2nd, 2023, the researchers visited Al Majma'h area after receiving a video showing a citizen rescuing a long-eared hedgehog that fell in a well. Al Majma'h (25° 54' 18.49" N 45° 19' 55.92" E) is a small agricultural town located about 170 NW km of Riyadh (Figure 1). The area is an agricultural land cultivated with watermelons, tomatoes, berries and palm trees. Wells are abundant and are used for irrigating the crops and trees. The soil is hard and compacted with abundance of the Egyptian Spiny-tailed Lizard, *Uromastyx aegyptia*, and burrows. Other mammals observed include the desert hedgehog, *Paraechinus aethiopicus*.

A total of ten Sherman traps (10X12X38 cm) baited with peanut butter and oat meals were placed on the farm at noon time and were checked at sunset and in the following morning. One adult female was trapped after sunset. On the next day, one subadult was caught in the field and photographed. One further specimen was seen in Al Mulhem (25° 11' 24.41" N 46° 21' 35.11" E) at the edge of a semi-arid region with abundance of desert shrubs.

Hemiechinus auritus is the smallest species of hedgehogs in Saudi Arabia (Figure 2). It is characterized by the presence of very long and pointed ears as a distinctive feature for this hedgehog. Tips of dorsal spines are white. Base of the scapular spines is black. A gap in the forehead spines is lacking. Face is covered by white hair and little brown hair around the eyes, but without a facial mask. The muzzle has a grey tint. Belly is buff white. 4-5 pairs of mammae are present in the female. Skull is small and delicate . Large tympanic bullae. First upper incisors are pointed forward. Elevated crown of lower second premolar biscuspid (Amr, 2012).

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Figure 1. Habitat of the long-eared hedgehog at Al Majma'h area.

Figure 2. The long-eared hedgehog, *Hemiechinus auratus.* A. and B. Subadult. C. Female.

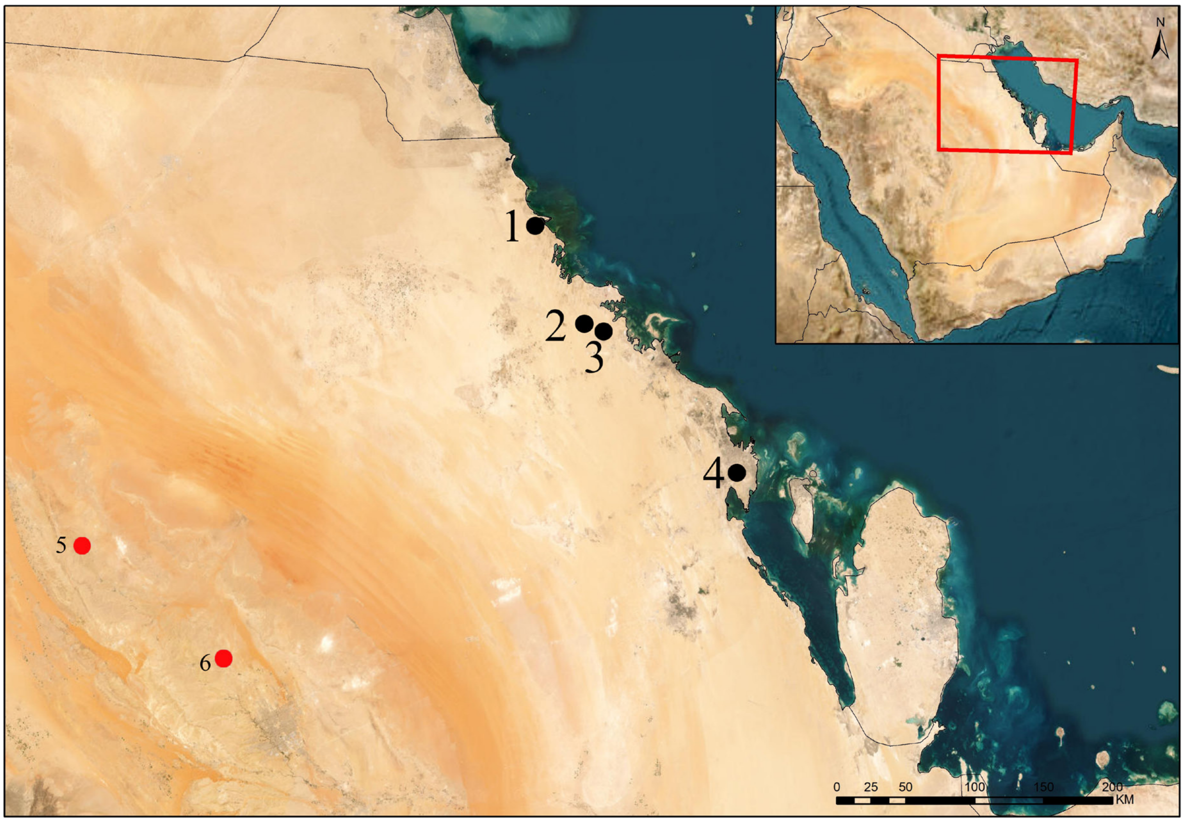

Figure 3. Localities from which *H. auritus* was reported. 1. Abu Hadriyah. 2. Safaniyah. 3. Ras al Abkhara 4. Dharan. 5. Al Majma'h. 6. Al Mulhem.

The present record expands the range of the long-eared hedgehog deep into central Saudi Arabia, about 400 km to the east from the coastal eastern province, suggesting its occurrence along the eastern part of the country between the Arabian Gulf and the Arabian Shield mountains (Figure 3). This record confirms the presence of a viable population almost fifty years after it was recorded by Pitcher (1976). It avoids sand deserts and extreme desertic conditions, contrary to the desert hedgehog, *P. aethiopicus*.

It feeds on various insects, centipedes, and land snails (Schoenfeld and Yom-Tov, 1985). This species digs its burrows or seeks refuge in depressions. In Saudi Arabia, Pitcher (1976) reported that the young are born in March. Remains of a long-eared hedgehog were recovered from owl pellets near al Jubial (Kock and Nader, 1996).

Initial assessment in the national Red List for the mammals of Saudi Arabia classified *H. auritus* as data- deficient, since it was reported from few localities more than fifty years ago. This suggests that further field studies should be conducted to add additional localities along the Arabian Shield mountains and the eastern part of Saudi Arabia to validate its conservation status. This animal is liked by farmers since it is known to feed on scorpions and other pests such as locusts and land snails in agricultural areas, hence, it should be naturally protected.

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Short Communication

First Record of the Eastern Black-Winged Kite *Elanus caeruleus vociferus* in Syria

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Abstract: The present note provides a first documented record of the Eastern Black-winged Kite *Elanus caeruleus* from Syria. An updated map of its current distribution across Syria is provided.

Keywords: Syria, Black-winged Kite, birds of prey.

The Black-winged Kite (Figure 1) is widespread in the countries of the Middle East; around Syria, Iraq (Salim, 2002), Turkey (Karakaş and Biricik, 2017), Lebanon (Ramadan-Jaradi; *et al.,* 2020) and Jordan (Khoury; *et al.,* 2017). This species was not listed in the checklist of the Syrian birds (Murdoch and Betton 2008) or in other publications on the birds of Syria covering Deir ez-Zor, Palmyra, and the lower reaches of the Euphrates (Aidek, 2010; Murdoch, 2010; Murdoch and Aidek, 2012).

Field observations were recorded over the past 14 years from several sites in Syria (Table 1, Figure 2). A total of 22 observations were documented since 2009-2023 for the Eastern Black-winged Kite along the coast region and the Orontes basin, the lower Euphrates and the most southwestern region of the country (Figure 2). Due to security constraints, the possibility to conduct field work became impossible. Locals and hunters have posted photos of this bird on social media platforms (i.e. Facebook) inquiring about the nature of this species that was rare and infrequently observed. It seems that the Black-winged Kite spread across Syria from three directions, Iraq from the east, Turkey from the north and Jordan from the south (Figure 2). It also appears from dates of observations that this bird is a winter visitor, as the dates indicates (September to February) with two observations in March. Despite that it is considered as a breeding bird in Turkey (Karakaş and Biricik, 2017), Iraq (Salim, 2002), and Jordan (Khoury; *et al.,* 2017), its breeding status has not been confirmed yet in Syria.

In Syria, the Black-winged Kite is under the pressure of hunting or capturing as most other birds of prey. Locals believe that this species can be sold at high prices as other raptors. Capturing birds of prey in Syria increased tremendously over the past years due to economic pressure among the most of the Syrian society sectors.

Public awareness is urgently needed to protect this species in Syria, and further studies are required to better understand its biology, habitat preference and breeding status in Syria.

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Table 1: Sites, geographic coordinator, and dates of recorded of Black-winged Kite.

Regions	Sites	Geographic Coordinator	Date		
Lower Euphrates	Abu Kamal	34.4589724, 40.9180437	Nov. 2009	Sep. 2018	
	Hajeen	34.6865759, 40.8570163	Oct. 2020		
	Abu Hamam	34.8522053, 40.7305936	Oct. 2020		
Coast region and Orontes basin	Jabla	35.3614549, 35.9327176	Feb. 2020	Nov. 2022	
	Banias	35.1783723, 35.9464267	Nov. 2020		
	Mesiaf	35.0654766, 36.3514943	Sep. 2021	Mar. 2022	Oct. 2022
	Safita	34.8204211, 36.1224387	Dec. 2021	Oct. 2021	
	Latakia	35.5357735, 35.8430024	Oct. 2022		
	Al-Sqeilbiyeh	35.3638303, 36.3962891	Nov. 2021		
	Mhardeh	35.2501077,36.5803132	Jan. 2023		
	Homs	34.723876, 36.7223178	Feb. 2021		
	Tell Al-Darah	35.0310412, 36.9438673	Nov. 2021	Dec. 2021	
Southwest region	Sweida	32.7081434, 36.5622998	Feb. 2012	Mar. 2020	
	Daraa	32.6242823, 36.1144943	Dec. 2022		
	Tseil	32.8341612, 35.99134	Feb. 2023		

Figure 1. Black-winged Kite from Tell Al-Darah, Syria (Photo by Ehab Jbr).

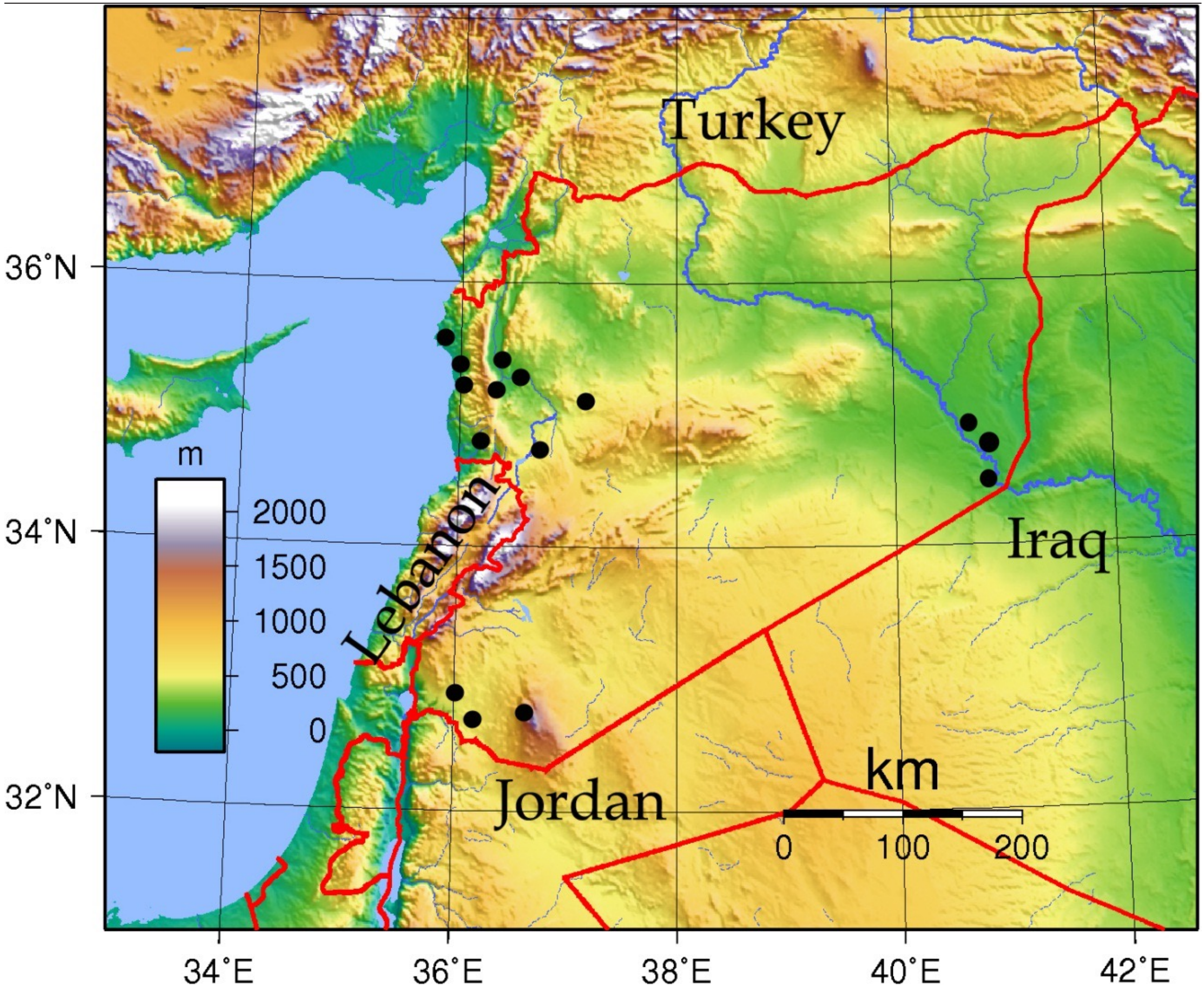

Figure 2. Distribution of Eastern Black-winged Kite in Syria.

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Short Communication

A New Record of the Honey Badger *Mellivora capensis* from Burqu Nature Reserve in the Eastern Desert, Jordan

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Keywords: Mesocarnivores, Distribution range, Citizen science, Eurasian badger

Abstract: The present note provides additional records for the Honey Badger *Mellivora capensis* from Jordan, increasing its current known distribution range further to the north east.

The honey badger *Mellivora capensis* (Schreber 1776) is a widely distributed species ranging through the Savanna and steppe from Nepal, east India, and Tukmenistan westwards to Lebanon, and south of the Mediterranean to South Africa. It is the only species in the genus Mellivora, distributed in Africa, Southwest Asia, and the Indian peninsula (Do Linh San, *et al*., 2016). The honey badger is a Least-Concern (LC) species according to the IUCN Red List and is known by its wide-range distribution and occurrence in a variety of habitats (Do Linh San, *et al*., 2016). It is one the least studied mesocarnivores within its distribution range (Sharifi, *et al*., 2020).

In Jordan, the species status is unknown, with no information available on the threats to its habitat and population. This species is recorded in Azraq, Al–Lujoon, near the southern part of the Jordan River, Jordan Valley and Mursa' (Eid, *et al*., 2020). The honey badger is considered a very rare species and is expected to exist at a very low density in Jordan (Eid, *et al.,* 2020).

On the 2nd of July, 2022, a local guide in Burqu Nature Reserve in eastern Jordan managed to video film the honey badger northwest of the Burqu Dam. The honey badger was spotted running at 09:30 pm and was immediately filmed for approximately thirty seconds. The exact coordination is N 32.669095, E 37.835977. Several photos were extracted from the video proving the presence of the honey badger in the area (Fig. 1).

This record expands the species' distribution range to the east. However, the scarcity in ecological data mainly on habitat selection due to the wide distribution range and the nature of the honey badger being a low-density population species (Begg, *et al*., 2005) hinders the exact prediction of its distribution pattern in Jordan. Topography and land cover types were found to be positively correlated with the honey badger presence, while distance to road and villages were negatively correlated with the occurrence of the species (Gupta, *et al.*, 2012). Vegetation cover and productivity play an important role in the habitat selection of the honey badger (Kheswa, *et al.*, 2018). The preference of honey badgers for denser vegetation may be a predictor of resources availability (Pettorelli, *et al.*, 2011). In Burqu, the area is covered with scarce scrub vegetation, and there are few spots with Tamarisk trees surrounding artificial water ponds, which can serve as preferable habitats for the honey badger. One the other hand, the dense vegetation found in the Azraq wetland reserve can make a preferable habitat for the honey badger. Even though the wetland had several records of the Eurasian badger (*Meles meles*) [Hraishah: pers. Comm], the area around the wetland is populated and extended which posed challenges for the record of the honey badger in 1997 (Qatrameez and Nassar, 1997) resulting in a misidentification , especially that the record was based on foot print signs. In addition, no data are available in the reviewed literature on the existence of the honey badger and the

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Figure 1. Photos of the honey badger extracted from the video showing the clear contrast between the white hair across the dorsal surface and the black hair across the ventral surface.

Eurasian badger in the same location, and the potential competition that may result.

In conclusion, it is recommended to equip this honey badger in Burqu with Satellite tracking to better understand the life-history traits of this species within the range of arid lands with scarce vegetation. Expanding research on other possible distribution ranges is also recommended. This record has proved the great usefulness of citizen science if supported with integrated management of protected areas for the benefit of local communities.

Acknowledgment

I would like to extend my thanks to Mr. Eid Salameh Za'al for his interest and enthusiasm while documenting this important record, and to Mr. Matar Al Masaeed, who followed up the record, identified the exact location, and prepared the record for documentation.

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The Royal Society for the Conservation of Nature

Is a national organization devoted to the conservation of Jordan's wildlife. It was founded in 1966 under the patronage of His Majesty the late King Hussein and has been given responsibility by the government to establish and manage protected areas and enforce environmental laws. As such, it is one of the few non-governmental organizations in the Middle East to be granted such a public service mandate.

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