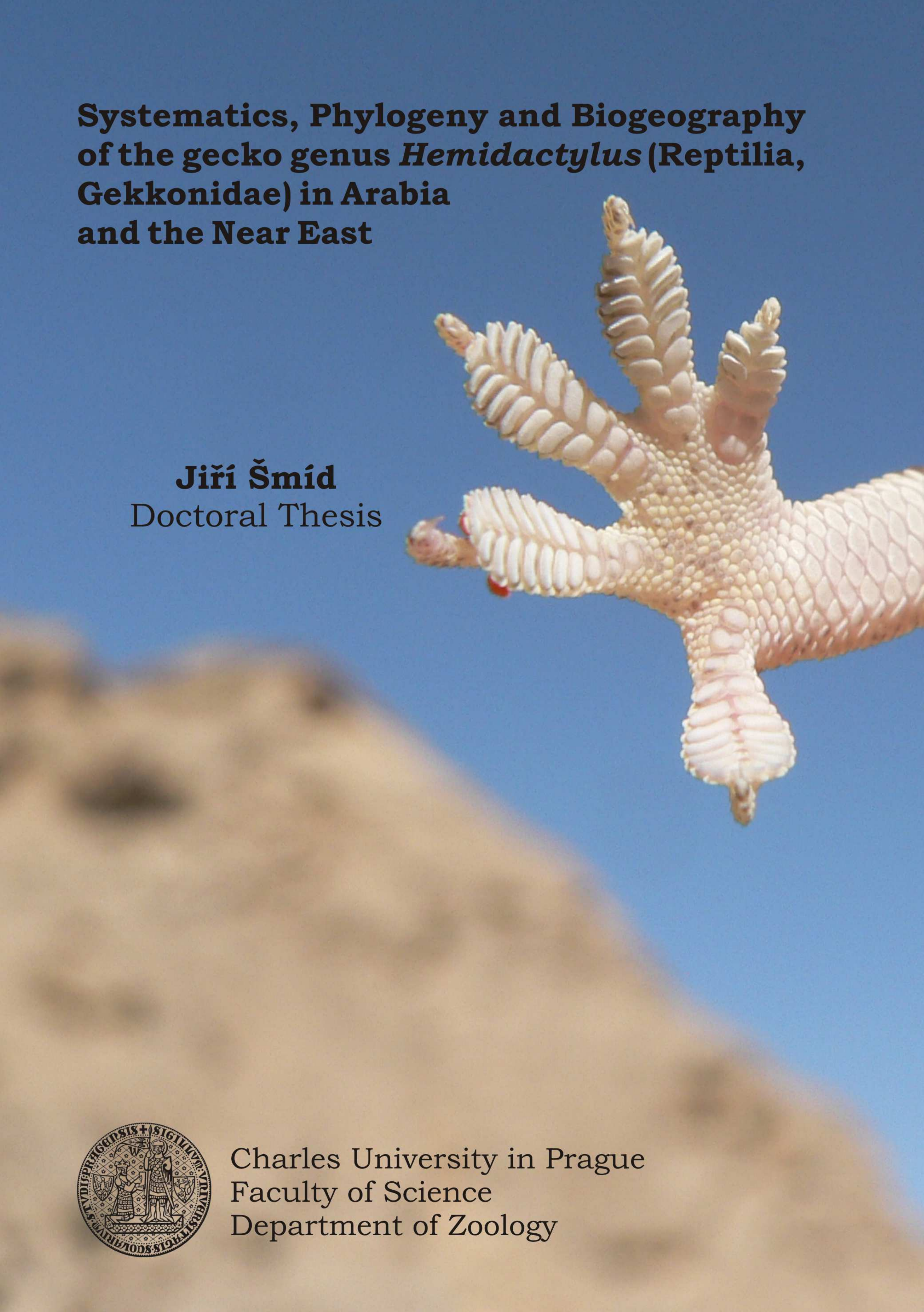
Systematics, Phylogeny and Biogeography of the gecko genus *Hemidactylus* (Reptilia, Gekkonidae) in Arabia and the Near East



Jiří Šmíd

Doctoral Thesis

Charles University in Prague
Faculty of Science
Department of Zoology

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Doctoral Thesis
Supervised by RNDr. Jiří Moravec, CSc.
National museum in Prague

Prague
2015

DECLARATION

I hereby declare that this thesis is the result of my own work and effort. It has not been presented, nor is being presented, either wholly or in part, for any other degree.

In Prague

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Jiří Šmíd

DISCLAIMER

New species names are proposed and taxonomic changes are introduced in this thesis. If not published yet, the usage of these names is provisional and must not be regarded as publication in the sense of Article 8 of the International Code of Zoological Nomenclature (hereafter the Code). In accordance with Articles 8.2 and 8.3 of the Code, in the event that this thesis is made available - as it will -, I hereby disclaim that it has been issued for public and permanent scientific record or for purposes of zoological nomenclature, and is therefore not published within the meaning of the Code.

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I did not go to the Arabian desert to collect plants nor to make a map; such things were incidental... I went there to find peace in the hardship of desert travel and the company of desert peoples.

Wilfred Thesiger (1959): Arabian sands

ABSTRACT (in English)

Until relatively recently, the gecko genus *Hemidactylus* was considered to contain only several hard-to-distinguish species in the eastern Mediterranean and the Arabian Peninsula. This was mostly given by the apparent morphological uniformity of the geckos in combination with their often synanthropic lifestyle, which facilitated the dispersal of some of the species over large ranges. However, our understanding of the diversity of the genus was about to change with the onset of molecular phylogenetic methods that became extensively available and routinely applied to tackle the questions of systematics and phylogeny of all kinds of organisms. This thesis focuses on resolving the phylogeny, systematics, and biogeography of the Arabian *Hemidactylus*. Using an unprecedented sampling of over 500 samples of more than 40 *Hemidactylus* species from the eastern Mediterranean, Arabian Peninsula, Socotra, North and East Africa and Iran and sequencing up to six genes (two mitochondrial – 12S rRNA, cyt *b*; four nuclear – *cmos*, *mc1r*, *rag1*, *rag2*) I reconstructed the time-calibrated phylogeny of the arid clade of *Hemidactylus*, inferred its complex biogeographical history in the region, and detected seven potentially new species. The results of the biogeographic analyses indicate that the current distribution of the genus has been shaped by both vicariant and dispersal events in its history. The vicariant events were most probably caused by the geological processes in the area coincident with the separation and drifting of landmasses in the Early Miocene. Since its separation from Africa, southern Arabia has been an important centre of diversification for *Hemidactylus* from where it repeatedly dispersed to all the neighbouring areas. The discovery of the unexpectedly high genetic diversity of the Arabian *Hemidactylus* with several lineages potentially representing yet unknown species led to more detailed examination of the genetic data and also the morphological characters in order to resolve the taxonomy of these candidate species. As a result of that, one species was resurrected from the synonymy of *H. turcicus* and four new species were (are being) described. Most of the new species were found in the mountains of southwestern Arabia, stressing the importance of this poorly studied region as one of the richest parts of Arabia in terms of reptile diversity and endemicity.

ABSTRAKT (in Czech)

Donedávna byli gekoni rodu *Hemidactylus* vyskytující se v oblasti východního Mediteránu a na Arabském poloostrově považováni za relativně nediverzifikovanou skupinu. Jednak to bylo způsobeno jejich výraznou morfologickou uniformitou a zároveň jejich často synantropním způsobem života, díky kterému byly některé druhy rozšířeny na velké vzdálenosti. Nicméně s nástupem molekulárně-fylogenetických metod jakožto běžné techniky rutinně používané k odhalování fylogenetických vztahů mezi organismy se naše poznání diverzity tohoto rodu radikálně změnilo. Cílem této práce bylo odhalit fylogenetické a biogeografické vztahy a systematiku arabských zástupců rodu *Hemidactylus*. Analýzou přes 500 jedinců více než 40 druhů pocházejících z východního Mediteránu, Arabského poloostrova, Sokotry, severní a východní Afriky a Íránu a sekvencí šesti genů (dva mitochondriální - 12S rRNA, cyt *b*; čtyři jaderné – *cmos*, *mc1r*, *rag1*, *rag2*) se podařilo rekonstruovat kalibrovanou fylogenezi tzv. aridního kladu rodu *Hemidactylus*, odvodit jeho komplexní biogeografickou historii a odhalit sedm potenciálně nových druhů. Výsledky biogeografické analýzy naznačují, že současné rozšíření rodu bylo formováno jak vikariančními tak disperzními událostmi. Vikarianční události je možné dát do souvislosti s kontinentálním rozpadem v časném miocénu. Arábie byla po svém osamostatnění od africké kontinentální masy důležitým diversifikačním centrem rodu *Hemidactylus*, ze kterého docházelo k opakovaným kolonizacím do všech okolních oblastí. Objev nečekané diverzity arabských gekonů rodu *Hemidactylus* vedl k detailnější analýze genetických dat a k analýze morfologických znaků, jejichž cílem bylo vyřešení taxonomie nově objevených linií. Jeden druh dříve synonymizovaný s druhem *H. turcicus* byl rozpoznán jako samostatný a čtyři další druhy byly nově popsány. Většina nových druhů pochází z málo probádaných horských oblastí jihozápadní Arábie a zdůrazňuje tak důležitost tohoto regionu coby centra mimořádné diverzity a endemismu plazů v kontextu Arabského poloostrova.

CONTENTS

1. INTRODUCTION

Understanding the Earth's biological diversity is one of the main aims of science. Ever since Alfred Russell Wallace came with the 'Law' of new species creation (Wallace 1855) and later on Charles Darwin with the 'Origin of species' (Darwin 1859), both of whom understood recent life forms as terminal offshoots diverging from a single common ancestor, biologists have been trying to identify and untangle these branches of the tree of life. Despite the long-term effort, the knowledge of the evolutionary relationships of many groups remains, however, far from complete. With the currently ongoing biodiversity crisis when species are going extinct faster than we are classifying them (Costello *et al.* 2013) and species populations are declining drastically (WWF 2014), understanding the world biodiversity has become an even more eminent issue. Central pillars of systematic biology are reconstructions of phylogenetic histories, species boundaries delimitations, and species classification (i.e. taxonomy; Wiens & Penkrot 2002; De Queiroz 2007; Steele & Pires 2011). Since the species is a fundamental unit in biology (Hull 1977), its proper delineation and description are therefore essential for reliable estimates of evolutionary history of higher taxa as well as for biodiversity conservation efforts (Sites & Crandall 1997).

Recognition of new species has traditionally relied on characters from several methodical approaches such as morphology, ethology, ecology, karyology, or genetics. With the increasing availability of genetic data for most organisms, new standards are being proposed with the DNA data being given a central role in taxonomy (Tautz *et al.* 2002, 2003). Single mitochondrial (mtDNA) gene phylogenies that prevailed in the last decade are now being replaced by multilocus approaches which can not only detect genetic diversification between species/populations, but also account for uncertainties associated with mtDNA tree estimations (such as maternal inheritance, increased mutation rate, undetected hybridization, etc.). Although there have been numerous methods of DNA-based species delimitations developed to provide a reliable measure of species diversification that can serve as stand-alone evidence for taxonomic results (Pons *et al.* 2006; Yang & Rannala 2010; Ence & Carstens 2011; Zhang *et al.* 2013), it is strongly advocated against such single-line evidence to be used as a new species diagnosis without also defining the species on the basis of intrinsic characters (Bauer *et al.* 2010a). Instead, genetic data are meant to become a coherent part of the current system. As a result of that, combining multiple complementary data sources (genetics, morphology, ethology, etc.), proposed under the framework of integrative taxonomy (Dayrat 2005), has become a need for obtaining credible taxonomic information. Such an approach is particularly useful in cases of morphologically conservative groups where cryptic species have probably been overlooked. The Arabian representatives of the gecko genus *Hemidactylus* represent one such group.

1.1 STUDY AREA: THE ARABIAN PENINSULA, ITS GEOGRAPHY AND GEOLOGICAL HISTORY

The Arabian Peninsula is the south-westernmost extension of the continent of Asia. The Mesopotamian lowlands and the Levant provide broad land connection with the mainland Asia in the north, while other parts of the peninsula are surrounded by seas and thus isolated from other landmasses: by the Red Sea from the west, the Gulf of Aden and Indian Ocean from the south, and the Persian (Arabian) Gulf and Gulf of Oman from the east (Fig. 1). The only recent land bridge connecting Arabia with Africa is the isthmus of Sinai. Arabia is rimmed from the west by the Hijaz and Asir Mountain ranges that stretch along the whole Red Sea coasts and reach up to over 3000 m of elevation in their southern parts in the area of Yemeni/Saudi borders. The mountains rise up abruptly from the Tihamah Desert, a lowland belt of a narrow coastal plain not wider than 60 km in its widest part and typical for its high temperatures and low rainfall throughout the year (El-Demerdash *et al.* 1994). The mountains continue along the southern Arabian shores of Yemen as the Hadhramaut Plateau up to the Dhofar Mountains in southernmost Oman. The inland Arabia east of the Hijaz and Asir Mountains descends gradually towards the Persian Gulf. In the eastern corner of the Arabian Peninsula, in northern Oman and partially also in the UAE, is situated another mountain system, the Hajar Mountains. They run for about 650 km along the shoreline of the Gulf of Oman and tower up to almost 3000 m and are thus able to influence the climate in the area significantly (Carranza & Arnold 2012). The Hajar Mountains are isolated from the Dhofar Mountains by 700 km of gravel or sand flat deserts, a distance insurmountable for many species not adapted for life in harsh desert conditions. This results not only in geographic, but also biological isolation of the Hajars (see below section 1.2). In southeastern part of the mainland Arabia mostly in Saudi Arabia, but marginally also in Oman and the UAE, extends the Rub' al Khali desert, also termed the Empty Quarter, a vast system of wave-shaped sand dunes, the largest desert in Arabia and the largest sand desert in the world (Edgell 2006). Gravel plains of central Oman separate the Rub' al Khali from a much smaller sand desert, the Sharqiyah Sands, situated in eastern Oman.

The Arabian lithospheric plate has been moving northward since the breakup of Gondwana about 160 million years ago (Ma; Jokat *et al.* 2003). The pre-Arabian landmass was connected to Africa until the emergence and subsequent expansion of the Red Sea rift in the Oligocene (~30–24 Ma) which is believed to have started in the southern Red Sea region as a result of increased tectonic activity (Courtillot 1980; Bosworth *et al.* 2005; Chorowicz 2005) (Fig. 2). Once the Red Sea trench was established, the sea completely separated Arabia from Africa. The Arabian Plate's counterclockwise rotation and its continuous movement northward caused its collision with Eurasia and the establishment of a temporal land bridge, termed the *Gomphotherium* land bridge, in the early Miocene (~19–17 Ma; Rögl 1998). This bridge allowed Eurasian and Afro-Arabian faunal exchanges over a short period of time (Harzhauser *et al.* 2007). The collision with Eurasia significantly slowed down the movement of the Arabian Plate. It resulted in the creation of a continuous orogenic belt formed by the Anatolian plateau in Turkey and stretching east to the Zagros, Alborz, and Kopet Dagh in Iran (Dercourt *et al.* 1986). Coincident with the *Gomphotherium* land bridge connection was the separation of Socotra from what is nowadays known as Dhofar (Oman) coasts about 17.6 Ma and the onset of its rifting southwards to its current position, about 250 km east-northeast from the cape of the Horn of Africa (Laughton 1966; Autin *et al.* 2010). The phase of temporal Asian-Arabian

Fig. 1. Physical map of the area of study with names of countries indicated in italics, water bodies in blue, and topographical elements in bold.

land bridge connection was followed by a permanent land bridge established ~14 Ma and closing the Proto-Persian Gulf from the northwest (Bosworth *et al.* 2005) (Fig. 2).

As indicated by increased salinity of the Red Sea and massive halite depositions throughout its basin, Arabia was temporarily reconnected with Africa via a closed Bab-el-Mandeb strait in the Late Miocene (~10–5.3 Ma; Redfield *et al.* 2003; Bosworth *et al.* 2005). After the reopening of the Bab-el-Mandeb strait 5.3 Ma Arabia became finally and permanently separated from Africa. Neither subsequent shifts of tectonic plates nor later glacial-interglacial sea-level fluctuations are believed to result in another land bridge between Arabia and Africa after the Miocene (Fernandes *et al.* 2006). On the other hand, broader connection with the mainland Asia has been established repeatedly when the Persian Gulf was waterless or at most formed by a series of freshwater lakes during the Pleistocene sea-level lowstands (Lambeck 1996; Uchupi *et al.* 1999). The Arabian Plate continues moving in a north-northwest direction relative to Eurasia, which causes frequent earthquakes in the tectonically instable contact zone in the Zagros range in Iran (Berberian 1981; Reilinger *et al.* 1997).

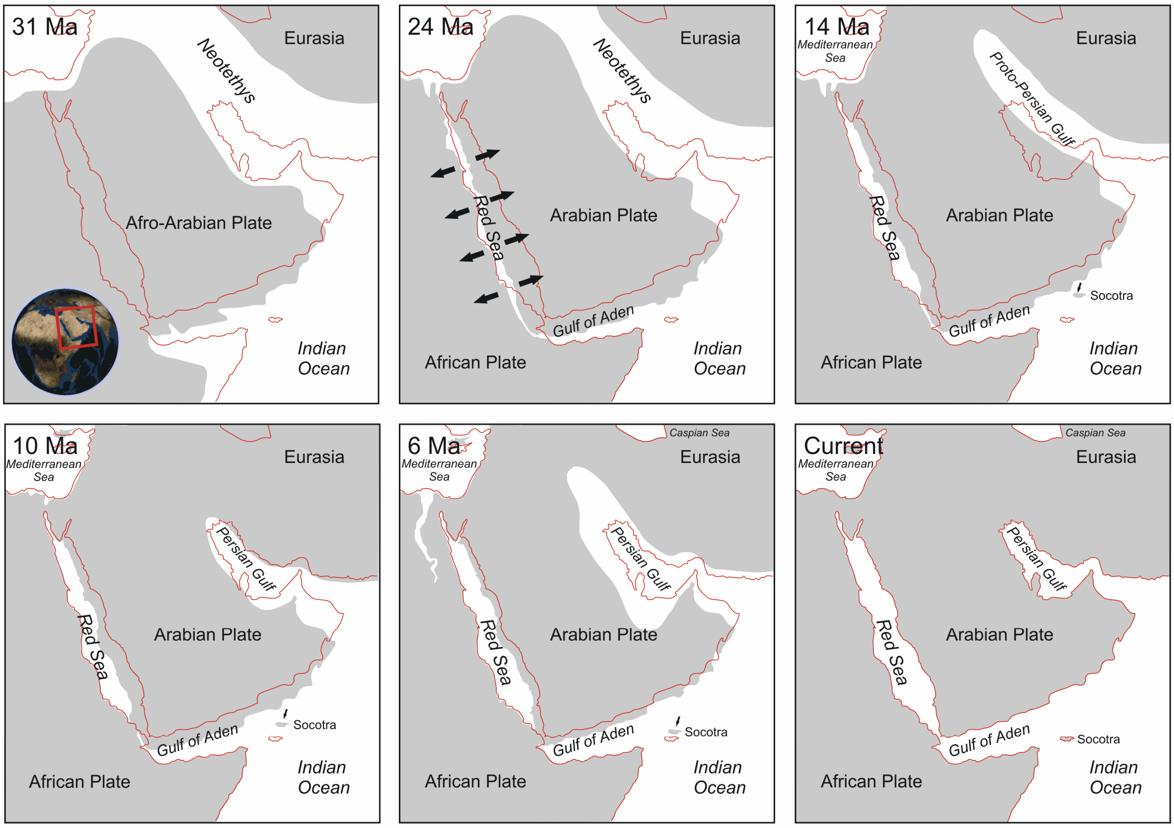

Fig. 2. Geological history of the Arabian Peninsula from the Oligocene to present. Red line outlines the current shape of continents, black arrows mark continental movements. Modified after Rögl (1998) and Bosworth *et al.* (2005).

The history of the formation of the mountain massifs on the Arabian Peninsula is closely linked to the geological history of the subcontinent itself. The central and southern parts of Arabia were emergent during the Eocene and early Oligocene and the origin of the high elevation areas around the Red Sea, including the Hijaz and Asir Mountains, can be explained by uplift since the middle Miocene (~15 Ma; Bohannon *et al.* 1989). Their emergence was therefore subsequent to the continental breakup. On the contrary, the uplift of the Hajar Mountains in the north of Oman began probably in the Early Oligocene (~30 Ma) as a result of the opening of the Gulf of Aden (Glennie 2007), and was pronounced during the Oligocene–Miocene (Kusky *et al.* 2005). Detailed descriptions of all geological processes responsible for and associated with the Afro-Arabian separation are not the scope of this work; they are described in great details in the geological literature cited throughout the text above.

Very little is known about the climate evolution in Arabia since it departed from Africa. There is evidence of the establishment of arid conditions in the Arabian Peninsula during the Late Miocene (~10–5.5 Ma; Huang *et al.* 2007). At about the same time, the monsoonal climate of coastal Dhofar observed today that brings the annual precipitation in a short season of intense rain developed between 8 and 4.6 Ma (Griffin 2002). Other data are usually limited and focused on rather short-term climatic fluctuations during the eras of the latest Pleistocene and Holocene when climate fluctuations affected the monsoonal pattern in southern Arabia and resulted in repeated episodes of contractions and expansions of rain-dependent habitats (McClure 1978; Goudie *et al.* 2000; Glennie & Singhvi 2002; Jung *et al.* 2004; Parker *et al.* 2004).

1.2 BIODIVERSITY AND BIOGEOGRAPHY OF ARABIAN REPTILES

Already the early explorers recognized Arabia's key intermediate position between three vast biogeographic realms – the Afrotropic, Palearctic, and Oriental, and noticed certain patterns in the distribution of species across the peninsula (Bent & Bent 1900). The mountainous areas along the Red Sea were recognized as bearing significant resemblance in species composition with the eastern Mediterranean (Scott 1942), the fauna of the Hajars resembled that of the Iranian highlands. However, until recently when detailed analyses of biogeographical history have been combined with the data from geological surveys, the knowledge of the distribution patterns among Arabian animals remained merely speculative.

Within Arabia, the most obvious division is between taxa living in the arid areas that occupy most of the peninsula and the forms confined to more mesic areas in the mountains (Arnold 1987). While major part of the peninsula is covered by deserts of various types and is relatively poor in terms of species numbers, the mountains on its margins host rich diversity of habitats and species.

There are four main areas with increased biodiversity in Arabia: i) the deserts of Jordan, ii) the Hijaz and Asir Mountains and their immediate vicinity along the Saudi and Yemeni shores, iii) the Dhofar Mountains in southeastern Oman, and iv) the Hajar Mountains. The first three have been identified by the Conservation International initiative as the Biodiversity Hotspots, biogeographic regions with a significant reservoir of global biodiversity (Mittermeier *et al.* 1999, 2004; Myers *et al.* 2000). Eastern parts of Jordan belong to the Mediterranean Basin Hotspot; the highlands of Yemen and Saudi Arabia are a disjunct extension of the Eastern Afromontane Hotspot; lower areas of the Hijaz and Asir ranges together with southern coasts of Yemen and Oman are part of the Horn of Africa Hotspot (Fig. 3) (Mittermeier *et al.* 2004). The latter two hotspots have their larger parts in Africa and their presence in Arabia thus points out the historical connectivity of the two continents. The hotspots are crucial most importantly for the diversity of vertebrates, among which they host the highest total number of species and the highest number of endemics of the peninsular fauna. For a comparison, from a total numbers of species endemic to Arabia, 50% of mammals, 100% of birds, 90% of snakes, 74% of lizards, 100% of amphibians, and 74% of freshwater fish occur within the combined area of the Arabian parts of the Horn of Africa and Eastern Afromontane Hotspots (Mallon 2011) (although the number of lizard species has increased significantly since Mallon's calculations and the proportion of endemics may therefore be even higher today).

The southeastern part of the Mediterranean Hotspot represented by the Syrian Desert (Badia) and Wadi Araba ecozones in Jordan also hosts numerous endemic lizard and snake taxa (e.g. *Acanthodactylus orientalis*, *A. robustus* [Lacertidae], *Stenodactylus grandiceps* [Gekkonidae], *Laudakia stellio picea* [Agamidae]) (Disi *et al.* 1999, 2001; Amr & Disi 2011; Disi 2011). Although it is only a marginal part of the otherwise large Mediterranean Hotspot it provides important connection and suitable habitats for species shared between Arabia and the Mediterranean.

The Hajars in the north of Oman are an important hotspot for many endemic reptile taxa. The mountain belt has been recognized as one of the centres of endemism for Arabian reptiles (Arnold 1987), however, it has not been given the official Hotspot status which it truly deserves, at least from the perspective of reptile diversity. A number of narrow-range species restricted in their distribution to the Hajars or their foothills can be found among reptiles (e.g. four species of the genus *Asaccus* [Phyllodactylidae], three species of *Hemidactylus* [Gekkonidae], two species of *Pristurus* [Sphaerodactylidae], or a completely distinct genus *Omanosaura* [Lacertidae] separated from other lacertid genera for about 40 million years (Hipsley *et al.* 2009; Gardner 2013)).

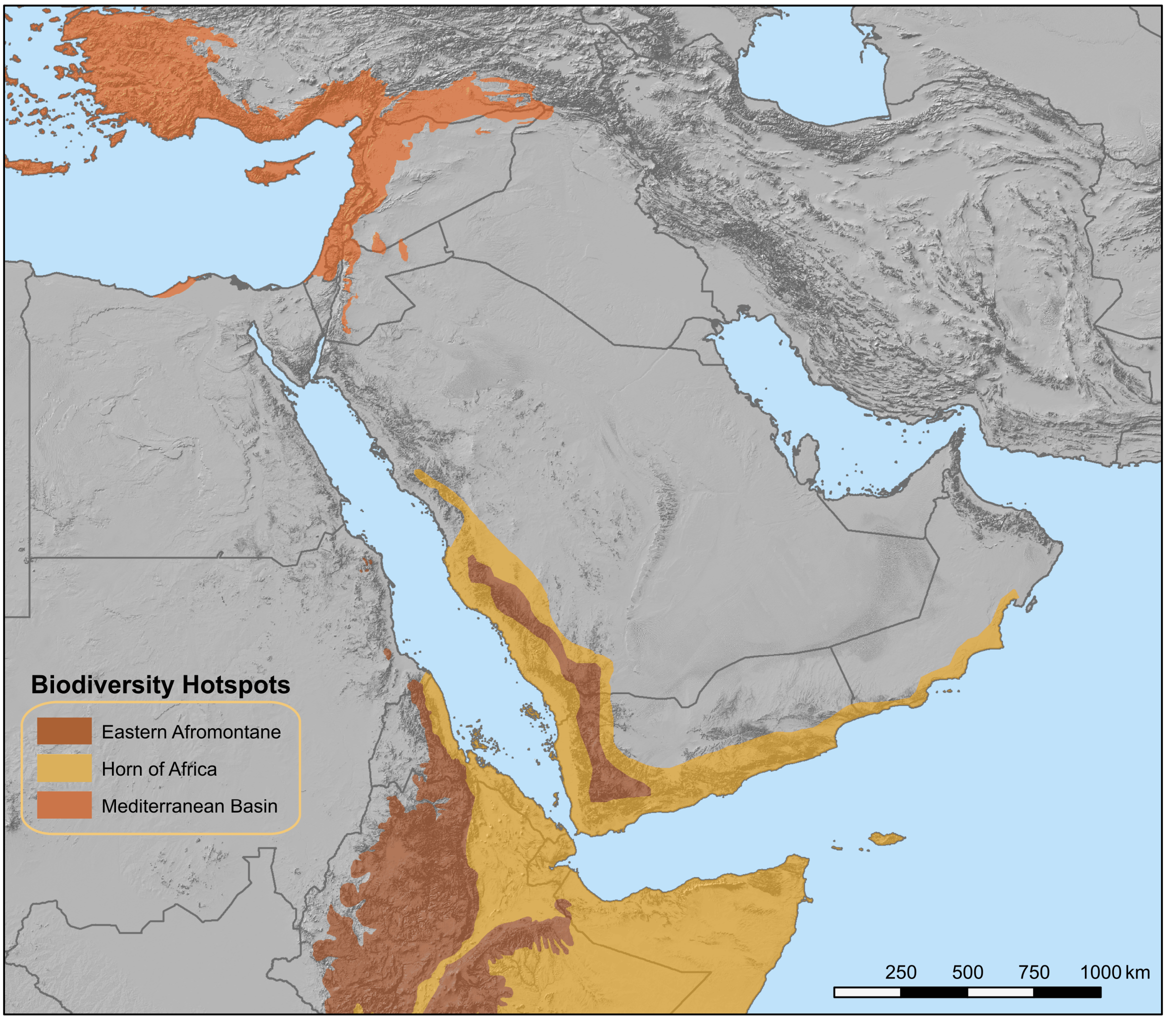

Fig. 3. Biodiversity hotspots in the Arabian Peninsula.

The Dhofar Mountains represent the easternmost protrusion of the Horn of Africa Hotspot and its deeply-carved wadis serve as enclaves for many typically African genera (e.g. *Acanthocercus* [Agamidae], *Bitis* [Viperidae], *Atractaspis* [Lamprophiidae], or a non-reptile example, the rock hyrax *Procavia* [Procaviidae]). The faunal dissimilarity of the south and north Oman has been obvious for long and underscored the fact that both regions belonged to different biogeographic regions, the north being part of the Arabian zone, the south of the Arabian-Afrotropical transition zone (Sindaco & Jeremčenko 2008). Latest research stresses the biogeographic independence of Dhofar by finding surprising genetic differentiation between the northern and southern Omani populations in previously thought widespread taxa or by discovering several new species endemic to Dhofar only. The restricted ranges of the Dhofar endemics (e.g. *Mesalina ayunensis* [Lacertidae], *Platyceps thomasi* [Colubridae], *Hemidactylus lemurinus* [Gekkonidae], *Uromastyx benti* [Uromastycidae]) can be, however, attributed to the poor knowledge of the fauna of Yemen caused by the difficult accessibility of the country. It is hence likely that more intense field research in the Hadhramaut Plateau of Yemen would bring new distribution records of these now geographically limited taxa.

Contrary to the mountain ranges teeming with reptiles, the isolated lowland deserts in the Arabian periphery, such as the Tihamah Desert or Sharqiyah Sands, are relatively poor in terms of biodiversity. Nevertheless, even these harsh regions harbour unique herpetofauna with endemic species present (e.g. *Scincus hemprichii* [Scincidae], *Duttaphrynus scorteccii* [Bufonidae] in the Tihamah; *Stenodactylus sharqiyahensis* [Gekkonidae] in the Sharqiyah) (Arnold & Leviton 1977; Metallinou & Carranza 2013).

1.3 HISTORICAL BIOGEOGRAPHY OF ARABIAN REPTILES

Geological history of Arabia has been unequivocally one of the key factors contributing to the current composition of local fauna. The complex geological and climatic history has shaped the species composition and their distributions. The diversity of landscapes across the peninsula provides a rich diversity of habitats, which, in turn, can host a wide variety of species. Common Gondwanan origin of Arabia and Africa is reflected in the relatedness of their faunas and the Oligocene continental breakup was apparently the first important factor shaping the diversity of both regions. Extensive phylogenetic research carried out on the Afro-Arabian reptiles has provided numerous examples of taxa distributed on both sides of the Red Sea that became geographically separated most likely by means of vicariance caused by the emergence of the sea. The segregations of the African and Arabian clades within the Saharo-Sindian genera *Stenodactylus*, *Mesalina*, and *Echis* (Viperidae) have been linked with the Red Sea formation by molecular dating analyses, the estimations of the divergence events being 21.8 Ma, 19.4 Ma, and 17–16 Ma, respectively (although the dates of the splits seem to be younger than the geological dating of the Red Sea emergence, they have been put in connection with this event by the authors (Arnold *et al.* 2009; Pook *et al.* 2009; Metallinou *et al.* 2012; Kapli *et al.* 2014)). Concordantly, the split within the genus *Chamaeleo* (Chamaeleonidae) between the clade containing the south Arabian *C. arabicus* and *C. calyptratus* from its sister clade containing mostly African species also coincides with the formation of the Red Sea (Macey *et al.* 2008). Subsequent gradual movement of Arabia north-eastward resulting in its further isolation from Africa separated the lineages on both sides of the sea. From then on the dispersal was possible only by overcoming the sea most likely by rafting or by using the temporal land bridge that closed the Bab-el-Mandeb strait in the Late Miocene (see above).

There are several studies that support the ongoing faunal connectivity between Africa and Arabia by reconstructing phylogenetic relationships with molecular clock analyses implemented. While the main direction of Afro-Arabian dispersal events has been from Africa to Arabia, opposite direction of immigration has been also reported. For instance, the origin of the Arabian cobra (*Naja arabica*; Elapidae) and its isolation from its closely related African species is believed to be relatively recent, most likely dating back to the Late Pliocene/Early Pleistocene (Trape *et al.* 2009). Similarly, the divergence of *Varanus yemenensis* (Varanidae) from its African relatives is estimated to take place ~6.9 Ma (Portik & Papenfuss 2012), and although the highest posterior density interval of confidence is relatively wide (~12.5–2.1 Ma) the authors believed that the dispersal occurred via the Bab-el-Mandeb land bridge. At the level of intraspecific diversity is treated the divergence within *Bitis arietans* (Viperidae) with the Arabian populations having departed from their African conspecifics around 4 Ma (Barlow *et al.* 2013). Two independent studies of the position and divergence dating of the Arabian populations of the African helmeted terrapins (*Pelomedusa* complex, Pelomedusidae) brought results roughly corresponding with each other and also coincident in time with those for *Naja* and *Varanus*. According to the estimates made by Wong *et al.* (2010), the Arabian clade (currently recognized as *P. barbata* (Petzold *et al.* 2014)) diverged and dispersed to southern Arabia ~14.1–2.4 Ma. Their results predate those by Vargas-Ramírez *et al.* (2010), who put the split between the Early and Late Pliocene. While Vargas-Ramírez *et al.* (2010) underline the importance of the existence of the land bridge in the area and its possible role in the dispersal, Wong *et al.* (2010) argue that a natural over-water dispersal cannot be ruled out in the case of turtles, as at least some freshwater turtle species have been shown to be salt tolerant. Nevertheless, until more precise dating is available, both scenarios should be considered equally plausible.

The opposite direction, i.e. from Arabia to Africa, has not been recorded in reptiles as many times as that from Africa to Arabia. One of the rare examples is the genus *Mesalina* (Lacertidae). *Mesalina* has a complex biogeographic history closely tied to geological processes that have taken place within its distribution range (Kapli *et al.* 2008, 2014; Šmíd & Frynta 2012). The phylogenetic and biogeographic analyses of 12 out of 14 species of the genus support a scenario of twofold independent colonization of Africa from Arabia (Kapli *et al.* 2014). The ancestor of *M. rubropunctata* dispersed to Africa about 14 Ma and was followed by the *M. guttulata* complex ~11.3–10.4 Ma. The dispersal events are explained as having taken place either through the southern Bab-el Mandeb land bridge or by the northern route via the Sinai Peninsula (Kapli *et al.* 2014).

The lack, or rather, complete absence of reptile fossil record in certain Arabian reptile groups (e.g. geckos, lacertids; Estes 1983) limits the biogeographic reconstructions to the application of the molecular dating approach. On the other hand, for a comparison, studies tracking the bilateral Afro-Arabian colonization history of mammals, i.e. a well studied group with well known and rich fossils, rely more on fossil evidence (Winkler 2002; Gheerbrant & Rage 2006; Abbate *et al.* 2013), although results based on molecular clock calibration are also appearing (Lecompte *et al.* 2008; Fernandes 2011; Kopp *et al.* 2014). It has been shown that the migration from one continent to another is also a recurrent phenomenon in mammals. Murines (Muridae) apparently dispersed from Asia to Africa around 11.8 Ma (Jacobs *et al.* 1989), a species of *Myomyscus* (Muridae) evidently spread to the Arabic region at about 5.1 ± 0.6 Ma (Lecompte *et al.* 2008), *Megapedetes* (Pedetidae) dispersed from East Africa to Saudi Arabia in the late Early

Miocene (Winkler 2002), and the first ancestor of the Arabian baboon (*Papio hamadryas*; Cercopithecidae) probably left Africa in the Middle Pleistocene (Wildman *et al.* 2004), a result contradicting previous hypothesis about baboons being introduced into Arabia by humans (Thomas 1900; Kopp *et al.* 2014). Since Arabian mammals are not the topic of this study I refer the reader to the study by Delany (1989) for more details on their zoogeography.

Apart from the southern colonization route to (or from) Arabia over the Red Sea, a northern route from the Middle East has also been proposed for several taxa. The genus *Uromastyx* (Uromastycidae) is of Central Asian origin and colonized Arabia and Africa about 15–12 Ma (Amer & Kumazawa 2005). Also the genus *Scincus* (Scincidae) appears to have spread into and diversified in Arabia around 6 Ma (Carranza *et al.* 2008). The continuous Hijaz and Asir Mountains have apparently worked as migration corridors and enabled species with Mediterranean affinities to spread from the Levant southward to the highlands of Yemen. Such cases have been reported in *Chamaeleo* (Chamaeleonidae; Macey *et al.* 2008) or *Hyla* (Hylidae; Gvoždík *et al.* 2010).

The repeated and relatively recent episodes of the Persian Gulf desiccation during the Pleistocene glacial cycles resulted in the presence of closely related or even similar taxa in the Hajar Mountains in northern Oman and the Zagros in southern Iran. Both mountain systems can be considered the centres of radiation of the genus *Asaccus* with four species being present in Oman and the UAE and another ten species in Iran (Gardner 2013; Šmíd *et al.* 2014). A preliminary phylogeny of the genus showed that the Arabian and Iranian species do not form reciprocally monophyletic groups (Papenfuss *et al.* 2010) indicating more complex biogeographic pattern of the genus rather than two independent *in situ* radiations, one in Oman and one in Iran. The close affinity of the Hajar Mountains with the mainland Asia is supported by the presence of species widespread in Iran or Pakistan and also present in the Hajars, but otherwise absent from the Arabian Peninsula. Two viper species (*Echis carinatus*, *Pseudocerastes persicus*) have disjunct populations in the Hajar Mountains. The Omani and UAE populations of *Echis carinatus* have been confirmed to be genetically almost identical with specimens from India and Pakistan (Pook *et al.* 2009) or even from Turkmenistan (Arnold *et al.* 2009) suggesting recent gene flow between these populations. The position of the Arabian populations of *P. persicus* remains unknown even after the first attempt of the genus phylogeny has been made (Fathinia *et al.* 2014). The position of the northern Omani populations of many reptile taxa with respect to their Asian and southern Oman relatives should be investigated in more details to better assess their biogeographic affinities.

The most recent and perhaps the most intense period of faunal interchange in the history of sea-surrounded Arabia has been taking place in the last centuries due to increasing vessel traffic that have resulted in numerous unintentional introductions among reptiles. Genetic uniformity across large distribution areas that suggests very recent range expansions has been confirmed for two lizard species, *Hemidactylus flaviviridis* (Carranza & Arnold 2012) and *Chalcides ocellatus* (Lavin & Papenfuss 2012). However, the majority of introduced species is known to be successful intruders on the basis of historical records documenting their dispersal and establishment (e.g. *Calotes versicolor* [Agamidae], *Ramphotyphlops braminus* [Typhlopidae], *Trachemys scripta* [Emydidae]; Gasperetti 1988; Gasperetti *et al.* 1993; Gardner 2013).

Worth mentioning is the Socotra Archipelago and its unique herpetofauna. All native reptile species of Socotra are endemic to the archipelago and have a close link to the reptile fauna of southern Arabia (Razzetti *et al.* 2011; Vasconcelos & Carranza 2014). This is produced both by vicariance being a result of the Middle Miocene detachment of Socotra form southern Arabia and its subsequent southward drifting, and by oversea dispersals. The vicariant origin has been reported in the endemic snake genera *Hemerophis* (Colubridae) and *Ditypophis* (Lamprophiidae; Nagy *et al.* 2003), and in the genera *Pristurus* (Papenfuss *et al.* 2009), *Chamaeleo* (Macey *et al.* 2008), *Xerotyphlops* (Typhlopidae; Kornilios *et al.* 2013). Dispersals from the Arabian mainland are known to have occurred in the genera *Trachylepis* (Scincidae; Sindaco *et al.* 2012), *Mesalina* (Kapli *et al.* 2014), and *Hemidactylus* (Gómez-Díaz *et al.* 2012; Vasconcelos & Carranza 2014). The Socotra Archipelago is thus one of the best studied island systems in terms of its biogeographic history, despite its remoteness and poor accessibility.

1.4 STUDY GROUP: THE GENUS *HEMIDACTYLUS*

The genus *Hemidactylus* currently contains 132 species (Uetz 2014) and ranks among the top ten species-rich reptile genera and the second richest genus within Gekkonidae (Pincheira-Donoso *et al.* 2013). Several genera considered in the past closely related to *Hemidactylus*, such as *Briba*, *Cosymbotus*, *Dravidogecko*, or *Teratolepis* (Kluge 1983), have been synonymized with it on the basis of genetic evidence (Carranza & Arnold 2006; Bauer *et al.* 2008). All recent large-scale molecular phylogenetic studies agree in that *Hemidactylus* is a sister genus to the world's richest gecko genus *Cyrtodactylus* (Gamble *et al.* 2011, 2012; Pyron *et al.* 2013), a relationship already foretold to some degree by Kluge (1967) based on morphological evidence. The combined number of species in the *Hemidactylus* + *Cyrtodactylus* clade thus forms almost one third of the total diversity of Gekkonidae, emphasizing the extent of speciation in these genera.

Hemidactylus has a global circumtropical distribution, which is a result of its ancient repeated transmarine colonizations to different parts of the world (Kluge 1969; Vences *et al.* 2004; Carranza & Arnold 2006; Gamble *et al.* 2011). Nevertheless, recent human-aided translocations have also contributed significantly to the current range of the genus (e.g. Jadin *et al.* 2009; Das *et al.* 2011; Torres-Carvajal & Tapia 2011; Mori & Plebani 2012).

First comprehensive phylogeny of the genus was published by Carranza & Arnold (2006), who divided *Hemidactylus* into five main clades. Additional studies detected that one of the five clades originated in an error (Bansal & Karanth 2010; Bauer *et al.* 2010b) and adjusted the number of clades to four. These are: 1) Tropical Asian clade, 2) *H. angulatus* clade. 3) arid clade and 4) African-Atlantic clade (Fig. 4). The clades are nearly geographically exclusive despite the relatively rich colonization history of the genus.

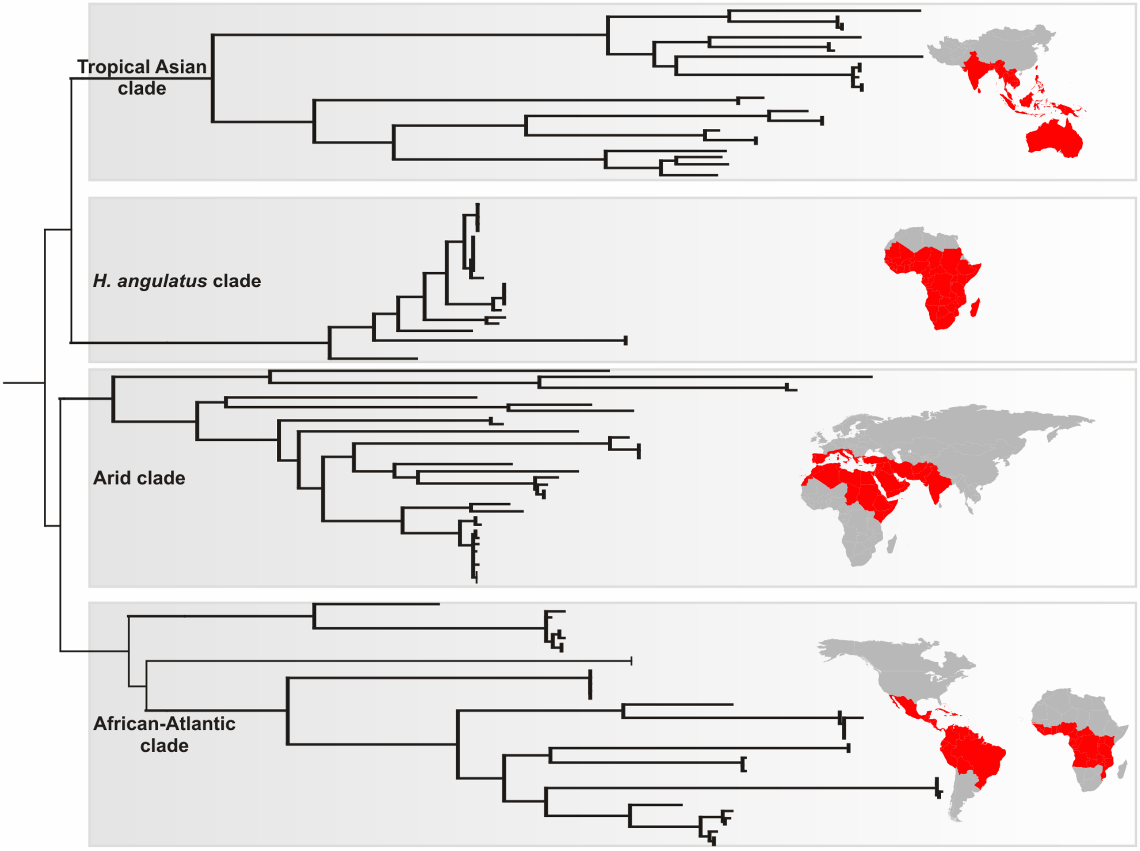

Fig. 4. Phylogeny of the genus *Hemidactylus* with the four main clades and their approximate distribution indicated (modified after Carranza & Arnold 2006).

The New World *Hemidactylus* species dispersed to their current ranges by at least five independent colonizations. *Hemidactylus brasilianus* and *H. palaichthus* have been dated to colonize South America from Africa 9–21 Ma, respectively 16–30 Ma (Gable *et al.* 2011). Contrary to these ancient colonizations, *H. mabouia* and *H. angulatus* (formerly H. *haitianus*) and *H. turcicus* have been introduced by anthropogenic dispersals from Africa (the former two; Weiss & Hedges 2007; Gamble *et al.* 2011) or from the Mediterranean (*H. turcicus;* Carranza & Arnold 2006). The recent dispersal of *H. mabouia* to the South America can also be evidenced by its presence in mostly anthropogenous habitats (Kluge 1969; Moravec pers. com.). Similar results supporting human-mediated translocations of this species were brought by Jesus *et al.* (2005) from the Gulf of Guinea islands. Independent of the New World colonizations has been that from Africa to the Cape Verde archipelago. The three species endemic to Cape Verde (*H. boavistensis*, *H. bouvieri*, *H. lopezjuradoi*) have probably reached the archipelago between

10.2 and 17.6 Ma (Arnold *et al.* 2008) and were followed recently by *H. angulatus* that has been introduced by humans (Carranza & Arnold 2006).

On the other side of Africa, in the Indian Ocean, similar complex biogeographic patterns have been recorded for *Hemidactylus*. There is strong genetic evidence for natural Pleistocene colonizations of Madagascar by *H. mercatorius* and the Comoros by *H. platycephalus*, whereas some other populations of *Hemidactylus* in the Malagasy area (*H. mercatorius* and *H. brooki* on the Comoros) were most probably introduced by humans (Vences *et al.* 2004). Gómez-Díaz *et al.* (2012), who studied the history of the Socotran species discovered that their origin have probably involved a vicariant event coincident with the breakup of Socotra and mainland Arabia in the Early Miocene, and two independent Pliocene dispersals. One of the most widespread *Hemidactylus* species, *H. frenatus*, with a range that stretches from the East African shores over most of the Indian Ocean coasts and islands through Southeast Asia and further across the Pacific to the South American western coasts, has also most probably been introduced to many parts of its vast range due to human-aided recent colonizations from some as yet uninvestigated source region in Southeast Asia (Carranza & Arnold 2006). Such 'weedy' commensal species, as *H. angulatus*, *H. frenatus*, *H. mabouia*, or *H. turcicus* have contributed to the current large and almost circumtropical distribution of the genus.

The arid clade of *Hemidactylus* is the most species-rich of the four clades. Carranza and Arnold (2006) had at the time of their analyses 14 species of this clade included and expected another 27 species unsampled by them to be part of it. Since then the number has risen, being a result of taxonomic studies from Oman and Yemen. Busais and Joger (2011a) uncovered high diversification of *Hemidactylus* in Yemen, particularly in its south-western mountainous part, and later (Busais & Joger 2011b) described three new species and one subspecies from the area. Carranza and Arnold (2012) contributed significantly to the knowledge of the Arabian *Hemidactylus* systematics by describing eight new species from Oman.

Yet, the knowledge of the species richness of *Hemidactylus* is far from complete and the number of new species being described every year is not slowing down (Fig. 5). Since 2010 alone there have been in total 23 new species described, most of them from the arid clade (some as a result of the studies presented in this thesis).

Due to its extreme species richness and difficult accessibility of the region, complex studies of the Arabian and East African *Hemidactylus* have been lacking. All previous works focused on rather narrow geographic areas (Yemen, Oman, Socotra) without providing direct comparison from other regions. Moreover, the extreme morphological uniformity of the Arabian and African *Hemidactylus* species has led to repeated descriptions of already known taxa (Loveridge 1936; Haas & Battersby 1959; Sharma 1981) what made the taxonomy of the genus very convoluted. For instance, there are at least 30 *Hemidactylus* species in the Horn of Africa, one of the richest *Hemidactylus* global hotspots, that putatively belong to the arid clade and a large part of which is known only from the type material or several additional specimens (e.g. Boulenger 1895, 1901; Calabresi 1927; Parker 1932, 1942; Scortecci 1948; Lanza 1978). Most of these species have never been included in any phylogenetic study. Material from such hard-to-access places (Somalia, eastern Ethiopia) is very rare and any recently collected specimens are very valuable.

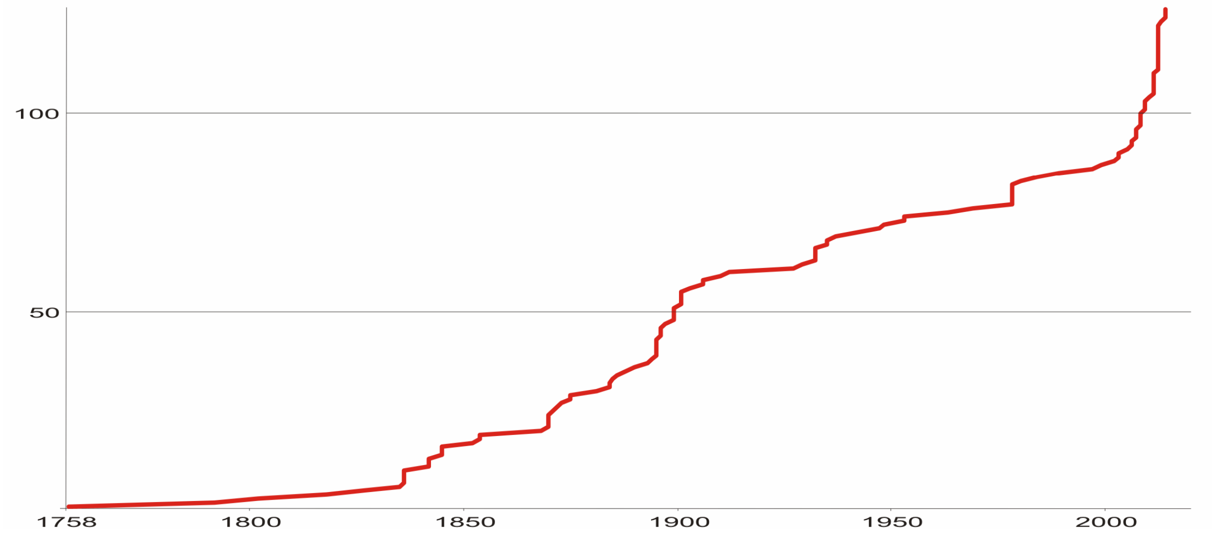

Fig. 5. Cumulative number of described *Hemidactylus* species. Note the rapid increase in species descriptions after 2000.

However, not only little known and only once collected species can be poorly understood from a taxonomic point of view. Probably the best-known of all *Hemidactylus* species, *H. turcicus*, the only European *Hemidactylus* and a species also present in the North and Central America (e.g. Schwaner *et al.* 2008) was until recently difficult to define. For its similarity with *H. robustus* these two species were for long considered conspecific, until Lanza (1990) and later Moravec and Böhme (1997) recognized them as distinct. Several subspecies of *H. turcicus* have been described – *H. t. lavadeserticus* from Syria, *H. t. parkeri* from Tanzania, *H. t. spinalis* from Menorca – but their validity or phylogenetic relationships remained unknown. Despite the omnipresence of *H. turcicus* throughout literally the whole coastal Mediterranean only a few studies addressed its taxonomy and delimitation from other *Hemidactylus* species. Its coastal character of distribution together with genetic uniformity throughout the range indicated recent and rapid dispersal (Carranza & Arnold 2006). However, the source region of its colonization remained unknown.

The extreme species richness of the arid clade of *Hemidactylus* together with the pronounced morphological uniformity of the clade, cryptic genetic diversity within many species, complex biogeographic history of the genus, and often high affinity to anthropogenic habitats make this group an excellent example for studying the evolution, phylogeny, systematics, and biogeography in the still poorly known part of the world.

2. AIMS OF THE STUDY

This thesis focuses on the phylogeny, systematics and biogeography of the arid clade of the genus *Hemidactylus* using an integrative combination of genetic and morphological approaches. After reconstructing the relationships within the arid clade I aimed to resolve the taxonomy of the species studied. Specific aims of the thesis were:

1) The first aim of this thesis was to assess genetic differentiation within *Hemidactylus turcicus* and its phylogenetic position in the arid clade with special emphasis on the eastern Mediterranean *Hemidactylus* species. Using genetic and morphological data we aimed to identify the source region from where *H. turcicus* colonized the Mediterranean, assess the magnitude of the Levantine radiation, and evaluate the validity and taxonomic status of the two subspecies, *H. t. lavadeserticus* and *H. turcicus spinalis.*

2) The second aim of this thesis was to assemble all data available from previous studies on the Arabian *Hemidactylus* phylogeny and combine them into a single data set. These data were completed with material newly collected in areas from where samples were not available (Iran, Oman, Ethiopia, Somalia) to cover the whole of the Arabian Peninsula and the adjoining regions to be able to produce a reliable phylogeny of *Hemidactylus* with as many species as possible included.

3) With the material available from all the key regions I sequenced up to six genes (both mitochondrial and nuclear) to infer a robust phylogeny of the *Hemidactylus* arid clade and to identify potentially new species. Additionally, I intended to reconstruct the historical biogeography of the group in the region by employing molecular clock calibration and reconstruction of ancestral nodes distribution and assessed the influence of the geological history of the region on the evolution of the genus.

4) The fourth aim was to provide a revision of the taxonomy and nomenclature of the members of the arid clade of *Hemidactylus* based on an integrative approach of combined multilocus genetic and morphological data. While genetic data were employed as first measures to estimate the differentiation within *Hemidactylus*, morphological data were used to proper species delimitation and as an evidence to assess phenotypic variability of the candidate species detected in the genetic analyses.

3. SUMMARY OF PUBLICATIONS

I. Moravec, J., Kratochvíl, L. Amr, Z.S., Jandzik, D., Šmíd, J., Gvoždík, V. (2011) High genetic differentiation within the *Hemidactylus turcicus* complex (Reptilia: Gekkonidae) in the Levant, with comments on the phylogeny and systematics of the genus. *Zootaxa*, 2894, 21–38.

Hemidactylus turcicus is a species widespread in the Mediterranean. Its current distribution is believed to be a result of human-mediated dispersal within the last millennia, yet its biogeographic affinities remained unknown. Using complete cytochrome *b* sequences, this paper focuses on the diversification within *H. turcicus* and its phylogenetic position among other *Hemidactylus* species. Special attention is paid especially to other eastern Mediterranean species, including the subspecies *H. t. lavadeserticus*. Genetic data reveal high diversification of *Hemidactylus* in the Levant with a new species present in Jordan. This species is described in this work as *H. dawudazraqi*. The data also support the species status for *H. t. lavadeserticus*. Very shallow genetic structuring within *H. turcicus* supports the hypothesis of recent dispersal. Two main clades of *H. turcicus* correspond approximately to the northern and southern part of its Mediterranean range. The high diversification of *Hemidactylus* in the Levant and the presence of the basal clade of *H. turcicus* there suggest that this region has been an important radiation centre from where *H. turcicus* probably expanded to its current range.

II. Šmíd, J., Moravec, J., Zawadzki, M., van den Berg, M. (2015) One subspecies less for the European herpetofauna: the taxonomic and nomenclatural status of *Hemidactylus turcicus spinalis* (Reptilia: Gekkonidae). *Zootaxa*, 3911, 443–446.

Hemidactylus turcicus has very shallow genetic structure and low degree of morphological variability across its range. Following the results of the first paper we here focused on another enigmatic subspecies, *H. t. spinalis*. The subspecies was described by Buchholz in 1954 from a small islet off the coast of Menorca on the basis of its different colour pattern. It has been considered a younger synonym of *H. turcicus* by most authors, but sufficient evidence to undertake official synonymization was still lacking. We conducted a field work in order to sample new material from the type locality that could be used for direct comparison with other *H. turcicus* populations and clarify the status of the little known subspecies. Morphological examination and sequences of two mitochondrial and three nuclear genes allowed us to assess the validity of this subspecies. The topotypes (and also morphotypes) of *H. t. spinalis* share identical haplotypes with other Mediterranean *H. turcicus* samples in all studied genes and morphological characters also overlap. Therefore we reject the subspecies status of this island population and synonymize *H. t. spinalis* with *H. turcicus*.

III. Šmíd, J., Mazuch, T., Sindaco, R. (2014) An additional record of the little known gecko *Hemidactylus granchii* Lanza, 1978 (Reptilia: Gekkonidae) from Somalia. Scripta Herpetologica. Studies on Amphibians and Reptiles in honour of Benedetto Lanza, 165–169 pp.

The Horn of Africa is one of the richest regions of the world in terms of reptiles. The inaccessibility of the area hampers the research of local herpetofauna and any material from here is very valuable for science. The reptile fauna of Somalia is very poorly known, the last compendia were published almost 40 years ago. Moreover, many species are known only from the type material. In this paper we report the first finding of *Hemidactylus granchii* known until today only from the holotype and two paratypes. We provide morphological comparison of all known existing specimens and with other *Hemidactylus* species in the area. The new record extends the distribution of this endemic species more than 450 km north-westwards.

IV. Šmíd, J., Carranza, S., Kratochvíl, L., Gvoždík, V., Nasher, A.K., Moravec, J. (2013) Out of Arabia: A Complex Biogeographic History of Multiple Vicariance and Dispersal Events in the Gecko Genus *Hemidactylus* (Reptilia: Gekkonidae). *Plos ONE*, 8, e64018.

This paper focuses on a large-scale phylogeny of the arid clade of *Hemidactylus* on the Arabian Peninsula and its surroundings. By analyzing up to three mitochondrial (12S rRNA, ND4, cyt *b*) and four nuclear gene fragments (cmos, mc1r, rag1, rag2) with a data set consisting of 358 samples we were able to reconstruct robust phylogeny of the Arabian *Hemidactylus*. The time-calibrated analysis unveiled an unexpectedly high genetic diversity within this clade with at least seven undescribed species identified. Furthermore, by reconstructing the biogeographic history of the genus we were able to link its evolutionary history with major geological events that occurred in the area within the last 30 million years. Two basal divergences correspond with the break-ups of the Arabian and African landmasses and the separation of Socotra from the Arabian mainland, respectively, segregating the genus by means of vicariance. The formation of the Red Sea led to isolation of the Arabian Peninsula where *Hemidactylus* underwent massive radiation in the Miocene and from where it dispersed repeatedly to Africa, Socotra, Iran, and the Levant. Therefore, as we show in this paper, the evolutionary history of *Hemidactylus* in Arabia and its surroundings has a complex pattern of several vicariant and multiple dispersal events. The Arabian Peninsula represents the source region for *Hemidactylus* dispersal.

V. Šmíd, J., Moravec, J., Kratochvíl, L., Gvoždík, V., Nasher, A. K., Busais, S. M., Wilms, T., Shobrak, M. Y., Carranza, S. (2013) Two newly recognized species of *Hemidactylus* (Squamata, Gekkonidae) from the Arabian Peninsula and Sinai, Egypt. *ZooKeys*, 355, 79–107.

As a follow-up of the previous study, here we present a detailed view on one of the monophyletic species groups identified in the large-scale phylogenetic analysis of *Hemidactylus*. The group contains three species (*H. saba* and two until now unrecognized species) and is therefore termed the *Hemidactylus saba* species group. We provide a taxonomic revision of this species group using genetic and morphological data and new material from new regions. All three species are well supported by both morphological and genetic evidence. One of the species is described as new (*H. ulii*). The second species was identified as *H. granosus*, a species superficially described by Heyden in 1827 and later placed in the synonymy of *H. turcicus*. Since this older name was available, but its original description was not sufficient for today's standards in taxonomy, we provided a redescription and re-diagnosis of *H. granosus*.

VI. Šmíd, J., Moravec, J., Kratochvíl, L., Nasher, A.K., Mazuch, T., Gvoždík, V., Carranza, S. Multilocus phylogeny and taxonomic revision of the *Hemidactylus robustus* species group (Reptilia, Gekkonidae) with descriptions of three new species from Yemen and Ethiopia. Accepted for publication in Systematics and Biodiversity.

Until relatively recently, *H. robustus* was considered conspecific with *H. turcicus* for their morphological similarity. However, genetic data revealed that these two taxa are not even closely related. Instead, *H. robustus* belongs to a group of four species of which the other three are undescribed. We here aim at this species group, employing multilocus phylogenetic analysis (six genes) and also species-tree analysis together with multidimensional analyses of morphological characters (PCA, DFA). All available data support the existence of all these putative species and despite they cannot be distinguished on the basis of metric characters (body shape), meristic characters prove to be useful for their determination. Our results presented in this paper highlight the importance of the southwest Arabia and the Ethiopian highlands as one of the world's hotspots unique for its endemic and extremely rich reptile fauna.

4. PUBLICATIONS

Paper I

Moravec, J., Kratochvíl, L. Amr, Z.S., Jandzik, D., **Šmíd, J.**, Gvoždík, V. (2011): High genetic differentiation within the *Hemidactylus turcicus* complex (Reptilia: Gekkonidae) in the Levant, with comments on the phylogeny and systematics of the genus. *Zootaxa*, 2894: 21–38.
IF 2011 = 0.927

Author contribution:
I hereby declare that Jiří Šmíd contributed to the publication with:

- JŠ measured specimens for morphological analyses, performed descriptive statistics and morphological comparison of the species studied, and contributed to the manuscript editing

In Prague Jiří Moravec

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High genetic differentiation within the *Hemidactylus turcicus* complex (Reptilia: Gekkonidae) in the Levant, with comments on the phylogeny and systematics of the genus

JIŘÍ MORAVEC[1,7], LUKÁŠ KRATOCHVÍL[2], ZUAIR S. AMR[3],
DAVID JANDZIK[4], JIŘÍ ŠMÍD[1,5] & VÁCLAV GVOŽDÍK[1,6]

[1] *Department of Zoology, National Museum, 19300 Prague, Czech Republic. E-mail: jiri.moravec@nm.cz*

[2] *Department of Ecology, Faculty of Science, Charles University in Prague, Viničná 7, Prague, Czech Republic. E-mail: lukkrat@email.cz*

[3] *Department of Biology, Faculty of Sciences, Jordan University for Science and Technology, Irbid, Jordan. E-mail: amrz@just.edu.jo*

[4] *Department of Zoology, Faculty of Natural Sciences, Comenius University in Bratislava, Mlynska dolina B-1, SK-84215 Bratislava, Slovakia. E-mail: jandzik@fns.uniba.sk*

[5] *Department of Zoology, Faculty of Science, Charles University in Prague, Viničná 7, Prague, Czech Republic. E-mail: jirismd@gmail.com*

[6] *Department of Vertebrate Evolutionary Biology and Genetics, Institute of Animal Physiology and Genetics, Academy of Sciences of the Czech Republic, 277 21 Liběchov, Czech Republic. E-mail: vgvozdik@email.cz*

[7] *Corresponding author*

Abstract

The molecular phylogeny of *Hemidactylus turcicus* (sensu lato) and related Levantine taxa of *Hemidactylus* geckos were studied using mitochondrial DNA sequence data. Five main phylogenetic lineages were detected within the distribution area of *H. turcicus*: (1) *H. turcicus* (sensu stricto) from the Mediterranean region comprising two widely distributed haplotype groups divergent by 2.1%; (2) *H.* cf. *turcicus* from north-eastern Israel forming a divergent (7.2%) sister lineage to *H. turcicus* s.s.; (3) *H. turcicus lavadeserticus* from the black Syrian basalt desert; (4) *H. mindiae* from southern Jordan; and (5) a highly supported lineage representing an unnamed species of *Hemidactylus* distributed in southern Syria and Jordan. On the basis of the obtained phylogenies, genetic divergences and morphological comparisons, the subspecies *H. turcicus lavadeserticus* is elevated to full species level and the unnamed *Hemidactylus* clade is described as a new species, *H. dawudazraqi* **sp. n.** In addition, an unnamed lineage of *Hemidactylus* from southern Sinai and exceptional genetic differentiation within "*H. turcicus*-like" forms from Yemen are reported, the type locality of *H. turcicus* is discussed and also comments are provided on the phylogeny and systematics of the genus *Hemidactylus*.

Key words: Reptilia, Gekkonidae, *Hemidactylus*, Molecular Phylogeny, Near East, Jordan, Syria, *Hemidactylus lavadeserticus*, *H. dawudazraqi* **sp. n.**, Endemism

Introduction

The wide range of the Mediterranean house gecko *Hemidactylus turcicus* (Linnaeus) extends from the Western Mediterranean, including Canary Islands, to the Near East (beside introductions to the New World). Whereas the circum-Mediterranean populations represent only two closely related evolutionary lineages (Rato *et al.* 2011), two samples from northern and western Jordan have been found to form a divergent clade considered a sister taxon to the Mediterranean form (Carranza and Arnold 2006). The morphologically well-differentiated subspecies *Hemidactylus turcicus lavadeserticus* Moravec & Böhme was described from the area of the black basalt desert in southern Syria (Moravec and Böhme 1997) and the presence of the recently described *Hemidactylus mindiae* Baha El Din has been proven in the Wadi Ramm sandstone massifs of southern Jordan (Amr *et al.* 2007). These facts suggest that proper taxonomic assignment of the Jordanian and other Levantine populations usually assigned to *Hemi-*

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dactylus turcicus could be more complicated and the need for investigation of their taxonomy by methods of molecular phylogenetics becomes eligible.

In the present paper we focused on evaluation of genetic variation of *Hemidactylus* geckos from the distribution area of *H. turcicus* with special emphasis on the Levantine *Hemidactylus* populations using mitochondrial DNA sequence data with the aim to elucidate phylogenetic relationships and taxonomic position of the Syrian and Jordanian forms.

Material and methods

Original data for molecular phylogeny. For the purpose of molecular phylogenetic analysis, we sequenced the mitochondrial (mtDNA) cytochrome *b* gene (*Cytb*) in *Hemidactylus* geckos from the distribution area of *H. turcicus* (sensu Sindaco and Jeremčenko 2008), geckos morphologically resembling *H. turcicus* from Yemen (*Hemidactylus* sp. 2–8: Hd 59 and Hd83–90 = "*H. turcicus*-like") and *H.* cf. *yerburii* Anderson (Hd60) from Yemen (for localities see Table 1).

Briefly, total genomic DNA was extracted from tissue samples of the museum voucher specimens or from samples obtained by biopsy from individuals collected in the field using the Genomed JetQuick Tissue DNA Spin Kit (Löhne, Germany) following the manufacturer's instructions. Complete sequences of the *Cytb* gene (1137 bp) was targeted and amplified by the primers L14910 and H16064 (Burbrink *et al.* 2000). In samples with degraded DNA, we obtained a short fragment (307 bp) of the *Cytb* gene using the conserved primers L14841 and H15149 (Kocher *et al.* 1989). PCR conditions followed the original protocol in the case of the complete *Cytb* (Burbrink *et al.* 2000). The following protocol was applied for amplifications of the short fragment: initial denaturation step at 94 °C for 7 min, 35 subsequent cycles of 94 °C for 30 s, 45 °C for 45 s and 72 °C for 1 min, and final extension step of 72 °C for 10 min. Sequencing was carried out by Macrogen Inc. (Seoul, Korea, http://www.macrogen.com) using the PCR primers (short fragment) or with a combination of the PCR primers and the newly developed *H. turcicus*-specific internal primers HdcbLinT (5'–ACCAACCTAATATCAGC–3') and HdcbHinT (5'–ATCGCTGTTGGTGTTTA–3') in sequencing the complete *Cytb*.

Complete or almost complete *Cytb* sequences were obtained in all studied specimens except for two samples (Hd22, Hd41) in which we were able to obtain only 307 bp fragment due to low quality of the source DNA. All these sequences were deposited to GenBank (Acc. Nos. HQ833711–HQ833764).

Molecular phylogenetic analyses. With the aim to detect phylogenetic position and species identity of all our samples from the distribution area of *Hemidactylus turcicus* and morphologically similar representatives from surrounding territories, we performed a taxon-wide dataset analysis first. Beside our original data, it also encompassed 303 bp-long *Cytb* sequences from Carranza and Arnold (2006) homologous to our 307 bp fragment (GenBank Acc. Nos. DQ120127–DQ120297) and partial *Cytb* sequences of *H. imbricatus* Bauer, Giri, Greenbaum, Jackman, Dharne & Shouche (formerly *Teratolepis fasciata* (Blyth)); GenBank Acc. Nos. EU268385–EU268386; Bauer *et al.* 2008). This dataset (further assigned as "short *Cytb*" dataset) contained 110 sequences of 35 valid and several probably undescribed taxa of *Hemidactylus* and allowed nesting our samples within the phylogeny of the genus (Fig. 1). Only the distinct haplotypes, selected using the Collapse 1.2 software (Posada 2006), were included in the analysis. Three diverse gekkotan species (*Coleonyx variegatus* (Baird), Eublepharidae, Acc. No. AB114446, Kumazawa 2007; *Tarentola mauritanica* (Linnaeus), Phyllodactylidae, Acc. No. AF364327, Carranza *et al.* 2002; *Sphaerodactylus vincenti* Boulenger, Sphaerodactylidae, Acc. No. FJ404649; Y. Surget-Groba & R. S. Thorpe., unpubl.) were used as outgroups in this case.

A taxonomically more restricted dataset was used for a particular analysis of our samples from the distribution area of *H. turcicus*, including the Levantine samples. It consisted of 47 complete *Cytb* sequences from the distribution area of *H. turcicus* together with seven distinctive haplotypes of the 303 bp-long sequences of *H. turcicus* from Carranza and Arnold (2006) and one our 307 bp-long sequence of *H. mindiae* (Hd 22) from southern Jordan (further assigned as "complete *Cytb*" dataset). The other, non-distinctive haplotypes of *H. turcicus* from Carranza and Arnold (2006), were only assigned to the particular subclades of *H. turcicus* based on their similarities to the complete *Cytb* haplotypes, because they might not be entirely identical with the individual haplotypes as some short fragments could fit to more than one sequence. As outgroups, we used *Cytb* sequences of *H.* cf. *angulatus* Hallowell (sample No. HdC1; Limbe, Cameroon), *H.* cf. *fasciatus* Gray (Hd30; Bakingili, Mt. Cameroon, Cameroon), *Hemidactylus* sp. 2–3 (Hd59, Hd90), *H.* cf. *yerburii* (Hd60). Their outgroup phylogenetic postitions in respect to our *Hemidactylus* samples from the distribution area of *H. turcicus* were verified by inference of the previous taxon-wide phylogeny.

TABLE 1. Samples from the distribution area of *H. turcicus* s.l. and outgroup taxa included in the molecular phylogenetic analysis of the complete *Cytb* dataset (holotype of *H. dawudazraqi* **sp. n.** in bold).

Taxon	Group	Individual	Locality	Country	Voucher	GenBank
H. turcicus	A	Hd55	Ardenica	Albania	not collected	HQ833711
H. turcicus	A	Hd56	Himarë	Albania	not collected	HQ833712
H. turcicus	A	Hd65	Brač Is.	Croatia	not collected	HQ833713
H. turcicus	A	Hd66	Brač Is.	Croatia	not collected	HQ833714
H. turcicus	A	Hd69	Cavtat	Croatia	not collected	HQ833715
H. turcicus	A	Hd01	Gecitköy, N. Cyprus	Cyprus	NMP6V 72103	HQ833716
H. turcicus	B	Hd34	Sharm el-Sheikh, Sinai	Egypt	not collected	HQ833717
H. turcicus	B	Hd37	El Arish, Sinai	Egypt	NMP6V 72081	HQ833718
H. turcicus	B	Hd93	Dahab, Sinai	Egypt	not collected	HQ833719
H. turcicus	A	Hd26	Stomio, Larissa	Greece	not collected	HQ833720
H. turcicus	A	Hd27	Stomio, Larissa	Greece	not collected	HQ833721
H. turcicus	A	Hd42	Perivoli, Korfu Is.	Greece	NMP6V 72073	HQ833722
H. turcicus	A	Hd77	Kavros, Crete	Greece	NMP6V 74050	HQ833723
H. turcicus	A	Hd78	Kavros, Crete	Greece	NMP6V 74167	HQ833724
H. turcicus	A	Hd91	Stoupa, Peloponnese	Greece	not collected	HQ833725
H. turcicus	A	Hd92	Gialova, Peloponnese	Greece	not collected	HQ833726
H. turcicus	B		Kato Gatzea, Volos	Greece	see Carranza & Arnold (2006)	DQ120139
H. turcicus	A	Hdit1	Riomaggiore	Italy	not collected	HQ833727
H. turcicus	B		Qariat Arkmane	Morocco	see Carranza & Arnold (2006)	DQ120141
H. turcicus	B	Hd03	Cabo de Gata	Spain	not collected	HQ833728
H. turcicus	B	Hd04	Cabo de Gata	Spain	not collected	HQ833729
H. turcicus	B		Torregorda, Cadiz	Spain	see Carranza & Arnold (2006)	DQ120140
H. turcicus	A	Hd32	Cyrrhus	Syria	NMP6V 74046/1	HQ833730
H. turcicus	A	Hd33	Cyrrhus	Syria	NMP6V 74046/2	HQ833731
H. turcicus	A	Hd36	Qualat al Marquab	Syria	NMP6V 72497	HQ833732
H. turcicus	B	Hd94	Palmyra	Syria	NMP6V 74131/1	HQ833733
H. turcicus	B	Hd95	Palmyra	Syria	NMP6V 74131/2	HQ833734
H. turcicus	B		Jendouba	Tunisia	see Carranza & Arnold (2006)	DQ120145
H. turcicus	B		Gafsa	Tunisia	see Carranza & Arnold (2006)	DQ120157
H. turcicus	B	Hd05	Adana	Turkey	not collected	HQ833735
H. turcicus	A	Hd62	Finike	Turkey	NMP6V 73626/1	HQ833736
H. turcicus	A	Hd63	Finike	Turkey	NMP6V 73626/2	HQ833737
H. turcicus	B	Hd72	Antakya	Turkey	not collected	HQ833738
H. turcicus	B	Hd75	Antakya	Turkey	NMP6V 74047/1	HQ833739
H. turcicus	A	Hd76	Antakya	Turkey	NMP6V 74047/2	HQ833740
H. cf. turcicus		Hd02	Karkom	Israel	not collected	HQ833741
H. lavadeserticus		Hd31	Ar´Raqiyeh	Syria	NMP6V 74049/1	HQ833742
H. lavadeserticus		Hd70	Ar´Raqiyeh	Syria	NMP6V 74049/2	HQ833743
H. lavadeserticus		Hd71	Ar´Raqiyeh	Syria	NMP6V 74049/3	HQ833744

continued next page

TABLE 1. (continued)

Taxon	Group	Individual	Locality	Country	Voucher	GenBank
H. lavadeserticus		Hd73	Ar´Raqiyeh	Syria	NMP6V 74049/4	HQ833745
H. lavadeserticus		Hd74	Ar´Raqiyeh	Syria	NMP6V 74049/5	HQ833746
H. mindiae		Hd22	Jabal Ghazali	Jordan	NMP6V 72323/2	HQ833747
H. mindiae		Hd23	Wadi Ramm	Jordan	NMP6V 72739/1	HQ833748
H. dawudazraqi **sp. n.**	N	Hd16	Rashiedeh	Syria	NMP6V 70457	HQ833749
H. dawudazraqi **sp. n.**	N	Hd24	Jawa	Jordan	NMP6V 72740/1	HQ833750
H. dawudazraqi **sp. n.**	N	Hd25	Jawa	Jordan	NMP6V 72740/2	HQ833751
H. dawudazraqi **sp. n.**	N	Hd51	Azraq	Jordan	NMP6V 74134/2	HQ833752
H. dawudazraqi **sp. n.**	**N**	**Hd52**	**Azraq**	**Jordan**	**NMP6V 74134/1**	**HQ833753**
H. dawudazraqi **sp. n.**	N		Dair al Khaf	Jordan	NMP6V 72130	DQ120165
H. dawudazraqi **sp. n.**	W1	Hd43	Wadi Mujib	Jordan	NMP6V 74135/6	HQ833754
H. dawudazraqi **sp. n.**	W1	Hd44	Wadi Mujib	Jordan	NMP6V 74135/7	HQ833755
H. dawudazraqi **sp. n.**	W2		Wadi al Burbeyath	Jordan	not collected	DQ120164
H. dawudazraqi **sp. n.**	S	Hd47	Little Petra	Jordan	NMP6V 74136/1	HQ833756
H. dawudazraqi **sp. n.**	S	Hd48	Little Petra	Jordan	NMP6V 74136/7	HQ833757
H. dawudazraqi **sp. n.**	S	Hd50	Petra	Jordan	NMP6V 74137	HQ833758
Hemidactylus sp. 1		Hd41	Sharm el-Sheikh, Sinai	Egypt	NMP6V 70163/2	HQ833759
Hemidactylus sp. 2		Hd90	Ghoyal Ba-Wazir	Yemen	NMP6V 74169	HQ833760
Hemidactylus sp. 3		Hd59	Damuawt (Dangut)	Yemen	NMP6V 74170	HQ833761
H. cf. *yerburii*		Hd60	Taizz	Yemen	NMP6V 74168	HQ833762
H. cf. *fasciatus*		Hd30	Bakingili, Mt. Cameroon	Cameroon	NMP6V 73366	HQ833763
H. haitianus (former *H.* cf. *angulatus*)		HdC1	Limbe	Cameroon	NMP6V 73365/3	HQ833764

The analyzed *Cytb* sequences contained no indels or stop codons (checked in DnaSP 5.10 software; Librado and Rozas 2009). The best-fit models of sequence evolution were selected under the Akaike information criterion (AIC) using jModelTest 0.1.1 (Posada 2008) for the maximum likelihood (ML) calculations and MrModeltest 2.3 (Nylander 2004) for the Bayesian analyses (BA). The ML analyses were performed in PhyML 3.0 (Guindon and Gascuel 2003) by the approach of the best of the nearest neighbor interchange and the subtree pruning and regrafting algorithms of branch swapping to maximize tree likelihood, and using the best-fit substitution model for each dataset [(1) short *Cytb*: TVM+I+G, substitution rate matrix AC = 0.29, AG = CT = 4.49, AT = 0.50, CG = 0.33, GT = 1.00, proportion of invariable sites *Pinv* = 0.339, gamma shape rate variation among sites α = 0.554, base frequencies A = 0.35, C = 0.42, G = 0.08, T = 0.15; (2) complete *Cytb*: TIM1+I+G, AC = GT = 1.00, AG = 7.93, AT = CG = 0.35, CT = 3.50, *Pinv* = 0.422, α = 0.893, A = 0.34, C = 0.34, G = 0.10, T = 0.22]. Bootstrap values based on 1000 resampled datasets were calculated to assess the branch supports. Bayesian analyses were performed in MrBayes 3.2 (Huelsenbeck and Ronquist 2001, Ronquist and Huelsenbeck 2003). The analyses were set with partitions for the codon positions and likelihood settings corresponded to the best-fit models of sequence evolution for each codon position with parameters optimized during the runs [(1) short *Cytb* pos1/pos2/pos3: SYM+I+G/GTR+G/GTR+G; (2) complete *Cytb* pos1/pos2/pos3: GTR+G/GTR+I+G/GTR+I+G]. The analyses were performed with two runs and four chains for each run for six million generations, and sampling every 100th tree. First 1/10 of samples were discarded as a burn-in (log-likelihood scores of sampled trees plotted against the generation time showed that stationarity was achieved after the first 100,000 generations in both datasets and runs). A 50% majority-rule consensus tree was subsequently produced from the remaining trees after discarding the burn-in trees, and the posterior probabilities (BPP) as branch supports were calculated as the frequency of samples recovering any particular clade (Huelsenbeck and Ronquist 2001). Each BA analysis was repeated four times with random starting trees and the results were examined to compare split frequencies between the separate analyses in order to ensure that the BA analyses reached convergence. Average genetic uncorrected *p*-distances were calculated in DnaSP 5.10 (Librado and Rozas 2009) based on the complete *Cytb* dataset.

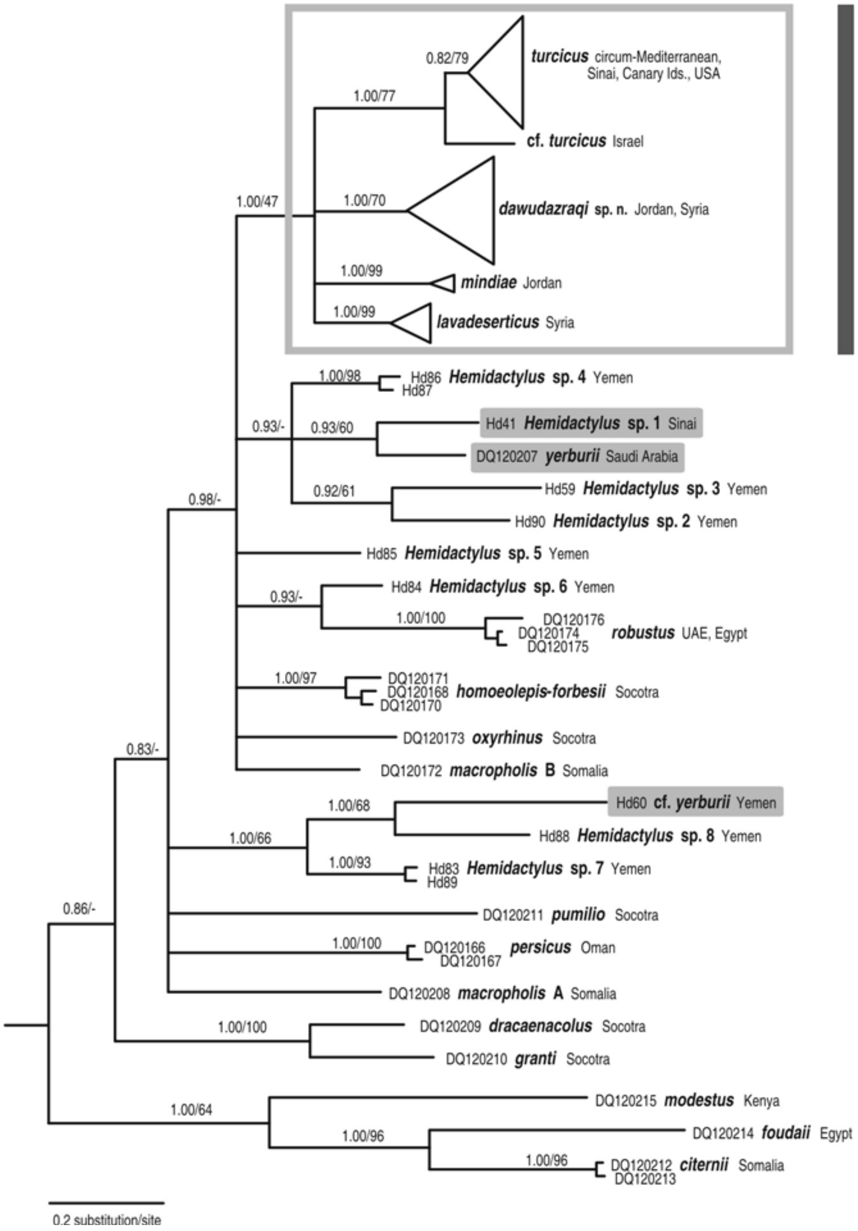

FIGURE 1. Section of the majority-rule consensus tree of the Bayesian phylogeny of *Hemidactylus* geckos focused on the species from the Arid species group (sensu Carranza and Arnold 2006). The section is a part of the taxon-wide phylogeny of the genus based on distinct haplotypes of a 303 bp-long fragment of *Cytb* and was used to locate several problematic *Hemidactylus* forms within the generic phylogeny. The phylogenetic positions of *H. yerburii* from Arabia and *Hemidactylus* sp. 1 (southern Sinai, Egypt) are highlighted (see text for details). Numbers above branches are Bayesian posterior probabilities and ML bootstrap values, if above 50 %. Branches with node support below 0.50 BPP were collapsed as were the individual clades within the frame, which indicates the *H. turcicus* clade. This clade was subjected to a further phylogenetic analysis based on complete *Cytb* (Fig. 2).

Morphological comparison. To obtain comparative morphological data, 94 voucher specimens of *Hemidactylus* from the Eastern Mediterranean and Levant were examined (for localities see the text and appendix 1; museum abbreviations are as follow: NMP6V—National Museum Prague, ZFMK—Zoologisches Forschungsmuseum A. Koenig, Bonn).

The following metric characters were taken using a digital calliper and a dissecting microscope: snout-vent length (SVL)—distance from the snout tip to cloaca; head length (HL)—distance from the snout tip to the anterior edge of the ear; head width (HW)—greatest width of the head; head depth (HD)—greatest depth of the head; tail length (TL)—from cloaca to the tail tip, if original. All examined characters were taken to the nearest 0.1 mm. Meristic and qualitative pholidotic characters were counted and evaluated as follows: number of upper labials—from the rostral to the mouth corner, last labial defined by its considerably larger size comparing with posteriorly adjacent scales; number of lower labials—from mental to the mouth corner; number of lamellae under the first toe—including unpaired proximal ones; number of lamellae under the fourth toe—including unpaired proximal ones; number of preanal pores; number of the anterior tail segments bearing at least six tail tubercles; contact of postmental scales with the second lower labial; contact of the medial nasals; size and shape of the dorsal tubercles. Notes on the colouration in life were taken from the field notes and photographs.

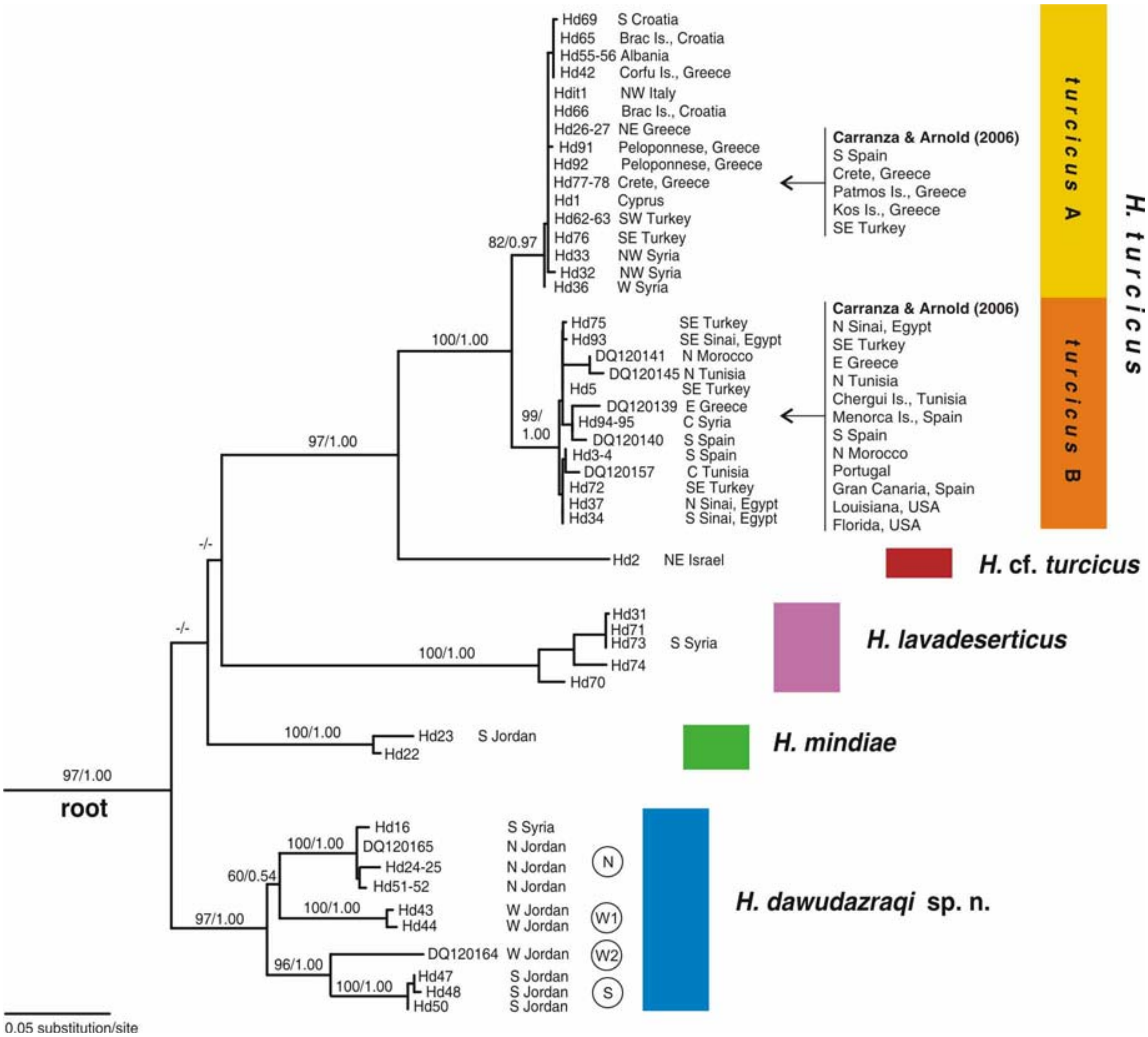

FIGURE 2. Maximum likelihood tree of *H. turcicus* and the Levantine taxa of *Hemidactylus* based on the complete mitochondrial *Cytb* (1137 bp) and 303 bp-long sequences from Carranza and Arnold (2006). Short sequences which did not possess unique haplotypes were only allocated into one of the two sublineages of *H. turcicus*. Letters in circles correspond to the geographic origin of the sublineages of *H. dawudazraqi* **sp. n.** Numbers above branches are ML bootstrap values and Bayesian posterior probabilities, if above 50 %. The tree was rooted by *H. haitianus* (HdC1), *H.* cf. *fasciatus* (Hd30), *H.* cf. *yerburii* (Hd60), *Hemidactylus* sp. 2 (Hd90) and *Hemidactylus* sp. 3 (Hd59).

Results

Molecular phylogeny. The initial taxon-wide phylogenetic analyses of the genus *Hemidactylus* yielded similar trees in ML [log likelihood (ln*L*) = -8314.8] and BA [mean ln*L* = -8314.5] (not shown; partial results in Fig. 1), which were in general concordance with the phylogeny published by Carranza and Arnold (2006). None of our samples from the distribution area of *H. turcicus*, "*H. turcicus*-like" or *H.* cf. *yerburii* were positioned outside the species from the Arid species group from Northeast Africa, Southwest Asia and the Mediterranean (sensu Carranza and Arnold 2006), and therefore, could not represent an introduced non-native species from the outside of the Arid species group. This is particularly important to note as some *Hemidactylus* species are frequently transported by humans (Rödder *et al.* 2008). The samples from the distribution area of *H. turcicus* formed a terminal clade (*H. turcicus* clade) within the Arid group with high support in BA (1.00). The individual Hd41 (*Hemidactylus* sp. 1) from southern Sinai, Egypt appeared as an outlier in this respect, because it turned out to be a close relative of *H. yerburii* from Saudi Arabia (DQ120207; 9.7% uncorrected *p*-distance), positioned outside the *turcicus* clade. Similarly, *Hemidactylus* sp. 2–8 from Yemen ("*H. turcicus*-like") were also all nested outside the *turcicus* clade, moreover scattered in different lineages across the Arid group (Fig. 1).

The complete *Cytb* dataset provided a detailed view of the relationships among *Hemidactylus* geckos from the distribution area of *H. turcicus*, which all were determined as *H. turcicus* sensu lato (s.l.) except for specimens from the Wadi Ramm massif, southern Jordan, diagnosed as *H. mindiae* (Amr *et al.* 2007). Both computational approaches provided essentially the same phylograms [Fig. 2; ML: ln$L$ = -6727.9; BA: mean ln$L$ =-6564.2] regarding partitioning into the five main lineages (although without significantly supported resolution of their mutual relationships in most cases): (1) *H. turcicus* sensu stricto (s.s.; type locality Turkey; see discussion) from the Mediterranean region (and introduced to America) comprising two widely distributed haplotype groups—*turcicus* A and *turcicus* B (see also Rato *et al.* 2011), with average between-group genetic uncorrected *p*-distance of 2.1% (Table 2); (2) a single sample from north-eastern Israel, which we provisionally name *H.* cf. *turcicus*, forming a sister (1.00/97), but divergent (7.2%) lineage to *H. turcicus* s.s.; (3) *H. turcicus lavadeserticus* from the black lava desert in southern Syria; (4) *H. mindiae* from southern Jordan showing genetic distance to other lineages 8.4–10.4 %; (5) a highly supported (1.00/97) lineage representing an unnamed species of *Hemidactylus* distributed in southern Syria and Jordan. The last lineage possesses surprisingly high intraspecific genetic differentiation forming four further sublineages, which we name in accordance with their geographical distribution: northern (N), western 1 (W1), western 2 (W2), and southern (S).

Genetic distances between all main lineages and sublineages as well as outgroup Yemeni taxa *Hemidactylus* sp. 2, *Hemidactylus* sp. 3, and *H.* cf. *yerburii* are in Table 2.

TABLE 2. Genetic average uncorrected *p*-distances between the Levant and circum-Mediterranean taxa and populations of *Hemidactylus* and some outgroup species from Yemen based on complete *Cytb* (1137bp) in percentage. Within group average genetic distances in bold on the diagonal.

		1	1a	1b	2	3	4	5	5a	5b	5c	6	7	8
1	*H. turcicus*	**1.0**												
1a	*H. turcicus* A	-	**0.1**											
1b	*H. turcicus* B	-	2.1	**0.2**										
2	*H.* cf. *turcicus*	7.2	-	-	-									
3	*H. lavadeserticus*	11.4	-	-	11.9	**1.2**								
4	*H. mindiae*	9.8	-	-	9.7	10.4	-							
5	*H. dawudazraqi* **sp. n.**	10.0	-	-	9.9	11.1	8.4	**3.5**						
5a	N	-	-	-	-	-	-	-	**0.5**					
5b	W1	-	-	-	-	-	-	-	5.0	**0.2**				
5c	S	-	-	-	-	-	-	-	5.3	6.2	**0.2**			
6	*Hemidactylus* sp. 2	15.4	-	-	15.8	16.3	15.7	15.7	-	-	-	-		
7	*Hemidactylus* sp. 3	15.8	-	-	16.7	17.5	16.0	16.4	-	-	-	10.9	-	
8	*H.* cf. *yerburii*	18.7	-	-	17.8	19.5	19.0	19.2	-	-	-	18.2	17.9	-

Taxonomy

On the basis of the obtained phylogenies and together with morphological comparisons and distinct geographic distributions (see below), and in concordance with the genetic species concept (Baker and Bradley 2006), two main taxonomic implications are adopted. First, the subspecies *H. turcicus lavadeserticus* is elevated to the full species level. Secondly, an unnamed *Hemidactylus* clade from southern Syria and Jordan is described here as a new species.

Hemidactylus lavadeserticus **Moravec & Böhme, 1997 (new status)**

Figs. 5 (C–D)

Hemidactylus turcicus lavadeserticus—Moravec and Böhme (1997), Disi *et al.* (2001), Moravec (2002), Baha El Din (2005), Amr *et al.* (2007), Sindaco and Jeremčenko (2008).

Holotype. NMP6V 35540/1. Type locality: Ar'Raqiyeh, 32°48'N, 37°05'E, Muhafazat of Sweida, Syria.

Paratypes. NMP6V 34831/1, NMP6V 35540/2–4, ZFMK 64409, the same locality as holotype.

Note. At present, *H. lavadeserticus* is known only from its type locality in the basalt desert of southern Syria. However, its occurrence in the basalt fields of northeastern Jordan and northern Saudi Arabia is expected.

Hemidactylus dawudazraqi **sp. n.**

Figs. 3 (A–B), 4 (A–E), 5 (D)

Hemidactylus turcica—Flower (1933). Incorrect subsequent spelling.

Hemidactylus turcicus turcicus—Werner (1971), Disi (1996, 2002), Moravec and Böhme (1997), Disi and Amr (1998), Disi *et al.* (1999, 2001, 2004), Carranza and Arnold (2006), Amr *et al.* (2007).

Hemidactylus turcicus lavadeserticus—Carranza and Arnold (2006).

Holotype. NMP6V 74134/1, adult male, Azraq, 31°49.770'N, 36°48.433'E, ca. 515 m a.s.l., Jordan, collected on 1–2 July 2006 by L. Kratochvíl, GenBank Acc. No. HQ833753 (*Cytb*).

Paratypes. NMP6V 74134/2–17, six adult males and ten adult females, the same locality and collecting data as the holotype; NMP6V 35541, subadult male, Azraq, 31°50'N, 36°49'E, ca. 510 m a.s.l., Jordan, collected on 16 May 1996 by J. Moravec; NMP6V 72130/1–3, Dair al Khaf, 32°19'N, 36°53'E, ca. 1120 m a.s.l., one adult male and two adult females, Jordan, collected on 3 June 2004 by D. Modrý; NMP6V72131, subadult specimen, Jawa, 32°20'N, 37°02'E, ca. 935 m a.s.l., Jordan, collected on 4 June 2004 by D. Modrý; NMP6V 72740/1–2, two adult females, Jawa, 32°20'N, 37°02'E, ca. 935 m a.s.l., Jordan, collected on 27 June 2005 by M. Abu Baker and D. Modrý; NMP6V 70457, subadult specimen, Rashiedeh, 32°40'N, 36°50'E, ca. 1425 m a.s.l., Muhafazat of Sweida, Syria, collected on 14 May 1999 by J. Moravec

Referred material. NMP6V 70616, adult female, Azraq, 31°50'N, 36°49'E, ca. 510 m a.s.l., Jordan, collected on May 1997 by D. Modrý; NMP6V 74138/1–6, two adult females, four subadult specimens, Azraq, 31°49.770'N, 36°48.433'E, ca. 515 m a.s.l., Jordan, collected on 1–2 July 2006 by L. Kratochvíl; NMP6V 74135/1–7, five adult females and two subadult specimens, Wadi Mujib 31°26.023'N, 35°47.489'E, ca. 795 m a.s.l., Jordan, collected on 21–22 June 2006 by L. Kratochvíl; NMP6V 74136/1–7, five adult females and two subadult specimens, Little Petra 30°22'N, 35°27'E, ca. 1081 m a.s.l., Jordan, collected on 27 June 2006 by L. Kratochvíl; NMP6V 74137, adult male, Petra 30°19.318'N, 35°27.968'E, ca. 1013 m a.s.l., Jordan, collected on 28 June 2006 by L. Kratochvíl.

Diagnosis. A species of the Arid species group of *Hemidactylus* as revealed from mtDNA analyses, which can be distinguished by the following molecular and morphological characters: (1) diagnostic nucleotide substitutions in *Cytb*, from all other Levantine taxa in positions 28 A (adenine) → G (guanine), 29 T (thymine) → C (cytosine), 175 A → G, 176 C → A, 246 T → C, 426 C → A, 531 C → T, 564 T → C, 663 A → C, 792 C → A, 985 G → T (GenBank Acc. Nos. HQ833749–HQ833758); (2) small size, SVL 40.1–47.8 mm in males, 41.4–49.9 mm in females; (3) robust head, head depth 44.9–56.4 % of head length, head width 74.3–90.7 % of head length; (4) long tail, tail length 119.8–140.9 % of SVL; (5) nasals separated by a small scale in 92 % of individuals; (6) large anterior postmentals in contact with 1st and less frequently also with the 2nd lower labials, both postmentals in contact with the 2nd lower labials in 8 %; (7) 8–11 upper labials; (8) 6-8 lower labials ; (9) 12–15 rows of large, round, conical, slightly keeled, dorsal tubercles; (10) 6–7 lamellae under the 1st toe and 9–12 lamellae under the 4th toe; (11) 5–8 tail segments bearing 6 tubercles; (12) 6–8 preanal pores in males; (13) in life, dorsum pinkish or yellowish white to yellowish orange with a pattern of irregular light brown to orange brown crossbars, head with dark longitudinal streak in loreal and postocular area, tail with a conspicuous pattern of 9–11 dark brown to black transverse bands on yellowish white to white background.

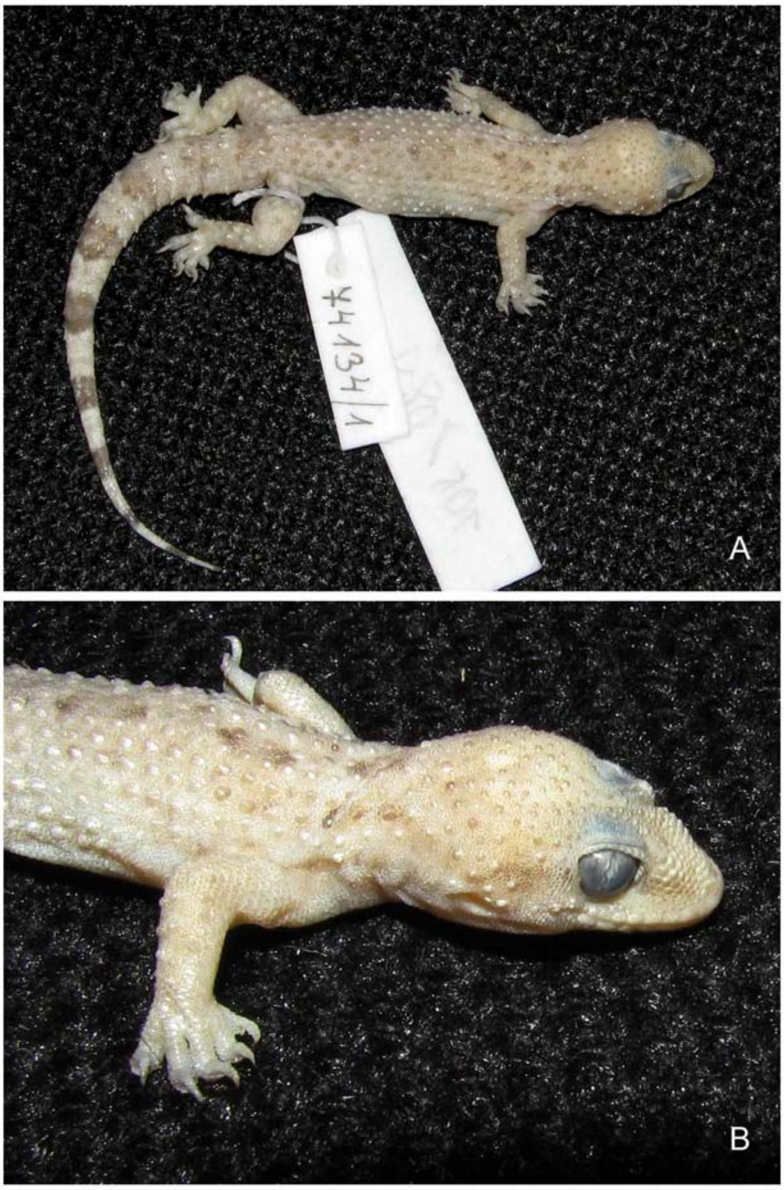

FIGURE 3. Holotype of *Hemidactylus dawudazraqi* **sp. n.** (NMP6V 74134/1), (A) dorsal view, and (B) detail of the head.

Comparisons. The new species can be distinguished from other Levantine species of the Arid species group of *Hemidactylus* by following combination of characters (see also Table 3): from *H. turcicus* by smaller size (maximal size 47.8 mm vs. 54.1 mm in males and 49.9 mm vs. 56.2 mm in females), significantly longer tail relatively to SVL (TL 119.9–140,9 vs. 103.0–121.4 % of SVL) (ANCOVA, tail length as dependent variable, SVL as a covariate, species as factor; species: F (1, 17) = 14.456, p = 0.0014), higher number of lamellae under the 4th toe (9–12 vs. 8–11), and genetic divergence of 10.0 % in *Cytb* (uncorrected *p*-distances); from *H. lavadeserticus* by robust head and body (head depth 44.9–56.4 % vs. 35.0–47.0 % of head length), larger relative tail length (119.8–140.9 % vs. 114.1–117.4 % of SVL), low frequency of contact of both postmentals with the 2nd lower labials (8 % vs. 100 %), lower average number of lamellae under the 1st toe (6–7 vs. 7–8), larger and more prominent dorsal tubercles, higher number of tail segments bearing 6 tubercles (5-8 vs. 2–6), and genetic divergence of 11.1 % in *Cytb*; from *H. mindiae* by robust head and body (head depth 44.9–56.4 % vs. 33.9–47.3 % of head length), lower number of upper labials (8–11 vs. 10–13), low frequency of contact of both postmentals with the 2nd lower labials (8 % vs. 80 %), higher number of preanal pores in males (6–8 vs. 4–6), and genetic divergence of 8.4 % in *Cytb*.

Description of the holotype. Adult male (Figs. 3 A–B), SVL 46.4 mm, head length 10.9 mm, head width 9.5 mm, head depth 6 mm, tail length 60.6 mm. Upper labials (left/right) 9/9, rows of dorsal tubercles 14, lamellae under the 1st toe 7/7, lamellae under the 4th toe 11/11, tail segments bearing six tubercles. Nostril surrounded by rostral, three subequal nasals and the 1st upper labial. Uppermost nasals separated by one smaller scale. Mental large, pentagonal and deeply impacted between anterior postmentals. Anterior postmentals large, nearly as long as wide, shorter than mental, in punctual contact behind the symphysial, in contact with the 1st lower labial (left) and the 1st and 2nd (punctually) lower labials (right). Posterior postmentals smaller, in contact with the 1st and 2nd lower labials (left) and the 2nd lower labial (right). Digits moderately dilated. Dorsal tubercles round, prominent, feebly keeled, in 14 longitudinal rows. Tail tubercles on the anterior six tail segments slightly larger and obviously keeled. Scales on underside of tail enlarged and imbricate. In alcohol, whitish gray dorsally, with five inconspicuous dark crossbars on the neck and body, and with nine dark transverse bands on tail.

Variation. As mentioned in the part on molecular phylogeny of *H. turcicus* (s. l.), the new species shows relatively high intraspecific genetic differentiation, forming at least four sublineages (N, W1, W2, and S; Fig. 2.). In comparison with the population from southern Syria and northern Jordan (sublineage N), the animals from Wadi Mujib (sublineage W1) and Petra and Little Petra (sublineage S) have less robust head and body, relatively larger eyes and smaller and narrower dorsal and especially tail tubercles. The tendency towards depressed head and body and smaller dorsal and tail tubercles appears to be higher in sublineage S (comparative voucher specimens of sublineage W2 were not at our disposal). This variation could reflect differences in habitats of the individual *H. dawudazraqi* sublineages. Whereas the representatives of sublineage N were collected predominantly on the ground in open areas with stony or loamy-sandy substrates, populations belonging to sublineage W1 and especially sublineage S were associated with rocky areas, caves and rock crevices. Similarly, the new species displays a colour variation corresponding to the substrate character. Individuals from basalt areas (Jawa and Dair al Khaf; Fig. 4 C–D) have yellowish orange to orange brown colouration in contrast to the light pinkish to yellowish white ground colour of the specimens inhabiting light substrata (Fig. 4 E).

Distribution and ecology. The known range of *H. dawudazraqi* reaches from southern Syria to southwestern Jordan (Fig. 6). The northernmost locality lies ca. 20 km W of the type locality of *H. lavadeserticus* and the southernmost locality is situated ca 75 km N of the known Jordanian occurrence of *H. mindiae*. We can expect that the range of the new species probably covers wider areas of southern Syria and northern and central Jordan.

The type locality lies at the edge of the oasis Azraq, which is situated at the border between basalt lava areas of northern Jordan and stony to loamy-sandy desert of central Jordan. At this place, *H. dawudazraqi* was collected predominantly in open desert habitat characterised by light loamy-sandy substrate and scattered herbaceous and bush vegetation (Fig. 4 F). Here, the adult and subadult specimens were frequently encountered on open ground by night. This terrestrial mode of life corresponds well with the find of a multiple egg clutch containing nine eggs of *H. dawudazraqi* deposited under a flat stone lying on the ground in an open arid area (L. Kratochvíl, pers. com., own obs.) and with the reports that the geckos were observed in deep horizontal burrows in association with termites of the family Hodotermitidae in the Azraq Nature Reserve (Disi and Amr 1998, Disi *et al.* 1999). Rarely, the individual specimens of *H. dawudazraqi* were also collected on the walls of small houses at the periphery of the town of Azraq (a synantropic mode of life was also observed at the Syrian locality of Rashiedeh). Other reptiles found in sympatry with *H. dawudazraqi* included *Mesalina brevirostris* Blanford, *M. guttulata* (Lichtenstein), *Trachylepis vittata* (Olivier), *Trapelus pallidus agnetae* (Werner), *Pseudotrapelus sinaitus werneri* Moravec, *Chamaeleo chamaeleon* (Linneaus), *Spalerosophis diadema* (Schlegel), and three other species of geckos (*Bunopus tuberculatus* Blanford; *Cyrtopodion scabrum* (Heyden) and *Stenodactylus grandiceps* Haas) were observed near Azraq (J. Moravec, L. Kratochvíl, V. Gvoždík, pers. obs.).

TABLE 3. Morphological comparison of *H. dawudazraqi* **sp. n.** with other Levantine *Hemidactylus* species (mean ± standard deviation and ranges are given).

n Mean±SD Min – Max		***H. dawudazraqi* sp. n.**		***H. turcicus***		***H. lavadeserticus***		***H. minidae* (Jordan)**		***H. mindiae* (Baha El Din 2005)**
Supralabials	25	9.2 ± 0.53 8 – 11	31	8.3 ± 0.50 7 – 10	11	9.4 ± 0.39 8 – 10	5	10.8 ± 0.76 10 – 12	12	12.0 ± 0.60 11 – 13
Infralabials	25	6.9 ± 0.41 6 – 8	31	6.8 ± 0.40 6 – 8	11	7.1 ± 0.38 6 – 8	5	8.1 ± 0.42 7 – 9	12	8.5 ± 0.50 8 – 9
Rows of dorsal tubercles	25	13.9 ± 0.64 12 – 15	31	13.9 ± 0.67 12 – 16	11	14.0 ± 0.00 14 – 14	5	12.4 ± 0.89 12 – 14	12	14.6 ± 0.80 14 – 16
Lamellae under 1st toe	25	6.6 ± 0.47 6 – 7	31	6.6 ± 0.45 6 –7	11	7.4 ± 0.49 7 – 8	5	6.2 ± 0.27 6 – 7	12	7.0 ± 0.40 6 – 8
Lamellae under 4th toe	25	10.9 ± 0.48 9 – 12	31	9.7 ± 0.62 8 – 11	11	11.4 ± 0.39 11 – 12	5	10 ± 0.00 10 – 10	12	10.8 ± 0.50 10 – 11
Tail segments bearing 6 tubercles	13	6.5 ± 1.05 5 – 8	18	5.4 ± 1.56 2 – 8	9	3.3 ± 1.41 2 – 6	5	5.0 ± 1.22 4 – 7	9	8.0 ± 2.00 4 – 10
Preanal pores (males)	10	6.5 ± 0.70 6 – 8	15	7.2 ± 1.47 6 – 10	5	6.0 ± 0.00 6 – 6	1	4	4	6.0 ± 0.00 6 – 6
HD*100/HL	20	49.1 ± 3.70 44.9 – 56.4	28	46.0 ± 3.93 38,8 – 56.5	7	41.8 ± 4.50 35.0 – 47.0	3	44.3 ± 2.60 42.8 – 47.3	12	37.0 ± 2.30 33.9 – 40.8
HW*100/HL	20	81.3 ± 4.60 74.3 – 90.7	28	77.7 ± 5.00 68.1 – 88.8	7	74.0 ± 5.50 64.2 – 80.2	3	79.7 ± 4.50 74.6 – 83.1	12	73.3 ± 3.70 67.7 – 80.0
SVL (males)	6	44.7 ± 2.70 40.1 – 47.8	14	46.3 ± 5.69 37.3 – 54.1	3	46.6 ± 0.72 45.8 – 47.2	1	49.3	12	55*
SVL (females)	14	46.1 ± 2.28 41.4 – 49.9	14	49.1 ± 5.252 36.7 – 56.2	5	46.4 ± 2.72 42.2 – 49.6	3	49.8 ± 11.02 37.1 – 56.6	–	–
TL*100/SVL	5	126.8 ± 8.97 119.8 – 140.9	7	112.8 ± 5.86 103.0 – 121.4	2	115.7 ± 2.35 114.1 – 117.4	3	119.3 ± 4.71 114.1 – 123.4	–	–
Nasals in contact (%)	25	8.0	31	13.3	11	0.0	5	0.0	–	–
Both postmentals in contact with 2nd lower labials (%)	25	8.0	31	12.9	11	100	5	80.0	–	–

* Baha El Din (2005) does not distinguish sexes.

As mentioned in the chapter about variation, geckos from Wadi Mujib, Little Petra and Petra were predominantly rock dwellers looking for shelters in rock crevices and caves.

Etymology. The specific name is a patronym for our colleague and friend David Modrý in recognition of his important contributions to the knowledge of the Jordanian herpetofauna. The name is used in its Arabic form as a compound of Arabic *Dawud* (David) and *Azraq* (the name of the type locality meaning “Blue” in English and “Modrý” in Czech).

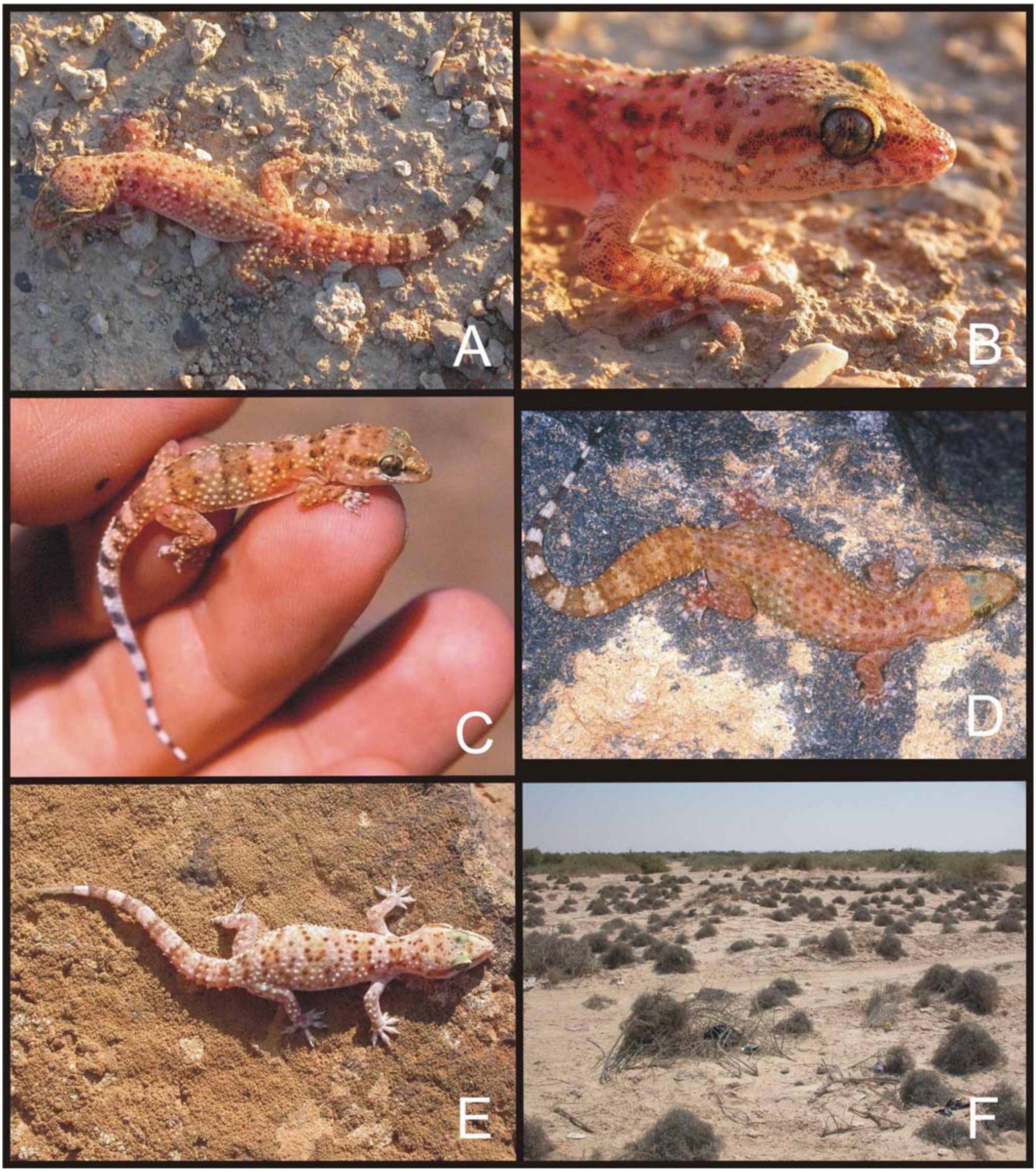

FIGURE 4. *Hemidactylus dawudazraqi* **sp. n.**, (A) adult male from the type locality (uncollected), (B) detail of the head of the same specimen. (C) Subadult paratype of *Hemidactylus dawudazraqi* **sp. n.** (NMP6V 70457) from Rashiedeh (Syria). (D), adult female paratype of *Hemidactylus dawudazraqi* **sp. n.** (NMP6V 7213/2) from Dair al Khaf (Jordan). (E) Adult female of *Hemidactylus dawudazraqi* **sp. n.** from Wadi Mujib (Jordan) (uncollected). (F) Type locality of *Hemidactylus dawudazraqi* **sp. n.,** Azraq (Jordan).

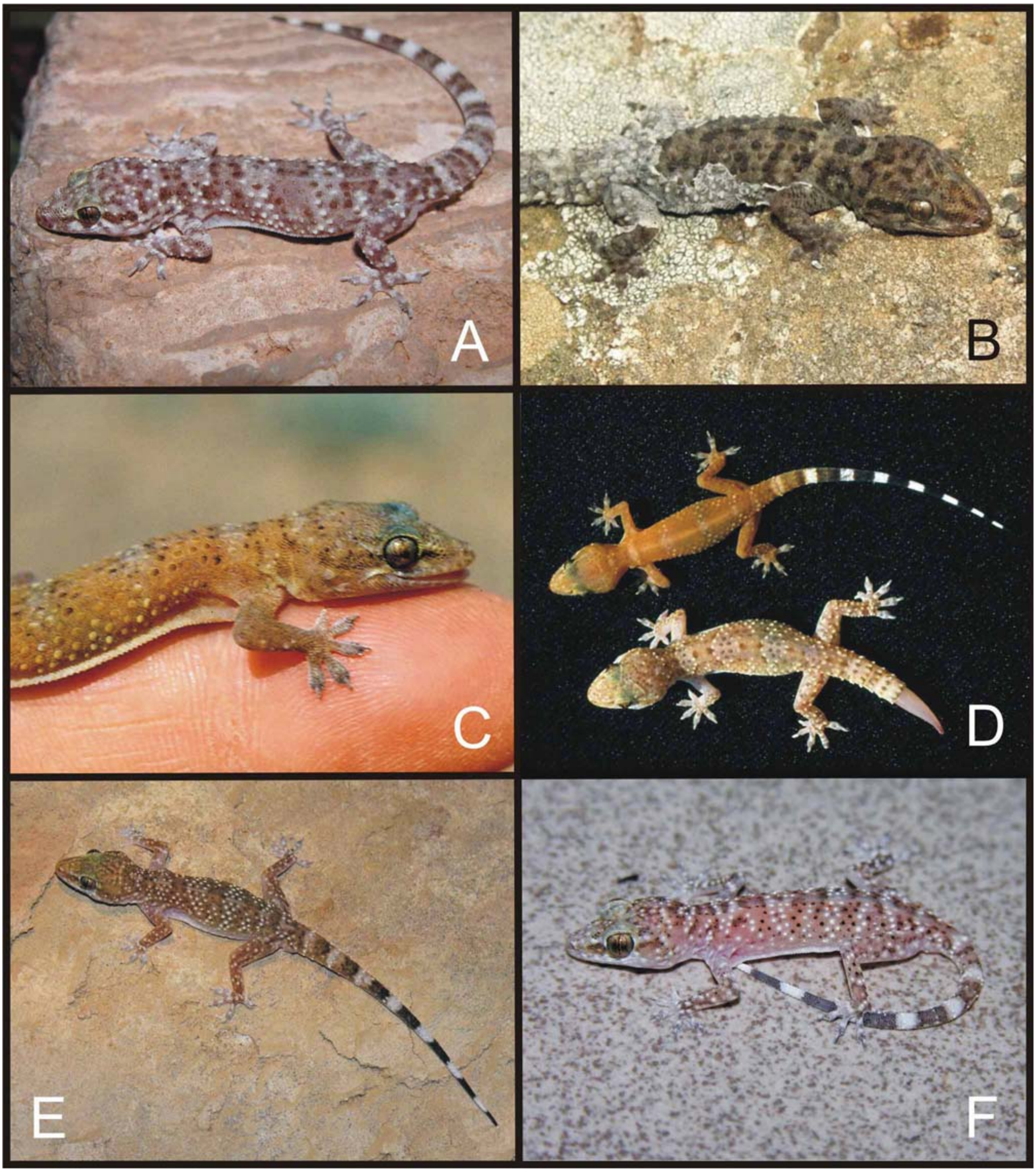

FIGURE 5. (A) Adult female of *Hemidactylus turcicus* (NMP6V 74131/1) from Palmyra (Syria). (B) Adult specimen of *Hemidactylus* cf. *turcicus* from NE Israel. (C) Male paratype of *Hemidactylus lavadeserticus* (NMP6V 35540/3). (D) Subadult male paratype of *Hemidactylus dawudazraqi* **sp. n.** (NMP6V 35541) from the type locality (lower individual) compared with subadult male paratype of *Hemidactylus lavadeserticus* (ZFMK 64409). (E) Adult male of *Hemidactylus mindiae* (NMP6V 72739/2) from Wadi Ramm (Jordan). (F) Subadult specimen of *Hemidactylus mindiae* (NMP6V 72739/3) from Wadi Ramm (Jordan).

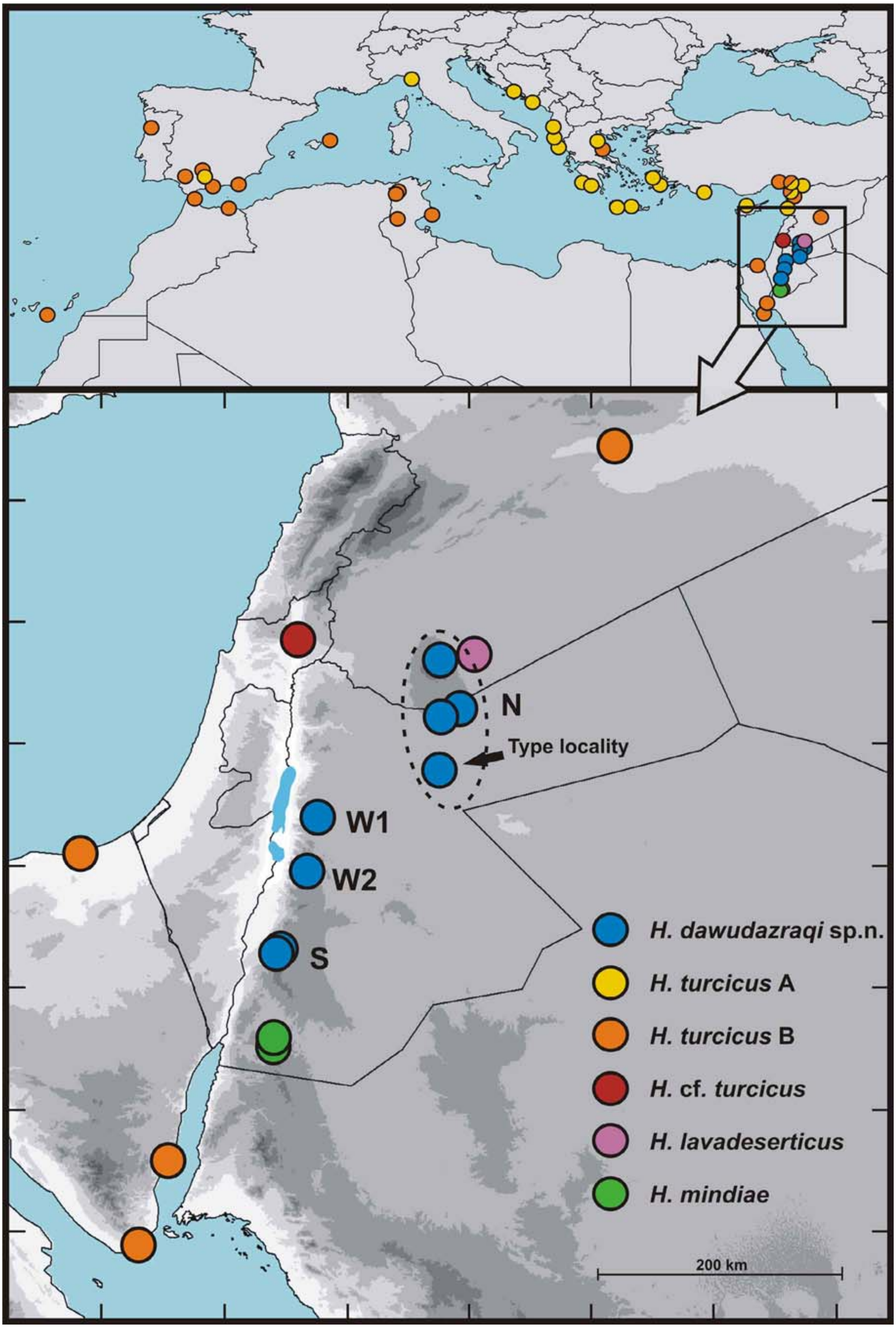

FIGURE 6. Schematic map showing distributions of individual *Hemidactylus* species and their forms in the Mediterranean and Levant as inferred from the molecular analyses (see also Figs. 1 and 2).

Discussion

Differentiation among *Hemidactylus* populations in the Levant. Molecular phylogeny of *Hemidactylus* geckos from the distribution area of *H. turcicus* s.l. showed high genetic differentiation in the Levant. Beside the previously described *H. mindiae* from southern Jordan (Amr *et al.* 2007), the phylogeny resulted in the recognition of one additional new species, *H. dawudazraqi*, one subspecies elevated to the full-species rank, *H. lavadeserticus* (Note: the *H. turcicus lavadeserticus* of Carranza and Arnold 2006 is *H. dawudazraqi*), and one taxon with uncertain taxonomic position tentatively referred to as *H.* cf. *turcicus*. On the other hand, all other specimens from around the Mediterranean as well as the introduced populations from North America formed one clade consisting of two subclades, *turcicus* A and *turcicus* B, separated by a moderate divergence of 2.1%. Considering this distribution pattern, it is evident that the Levant is a region supporting an endemic radiation of *H. turcicus*-complex taxa. According to current knowledge, *H. mindiae*, *H. dawudazraqi*, *H. lavadeserticus* and *H.* cf. *turcicus* are predominantly taxa inhabiting rocks and large stones (*H. mindiae*, *H. dawudazraqi*, and *H.* cf. *turcicus*), or sometimes open ground (*H. dawudazraqi*, *H. lavadeserticus*) in natural habitats, whereras *H. turcicus* s.s. is mostly known as a synantropic species, usually inhabiting walls and buildings. In addition, the known distribution of *H. dawudazraqi* (Fig. 6) may point to the possible importance of the Dead Sea Rift as a historical barrier playing a role in the speciation of various Levantine taxa (see also Gvoždík *et al.* 2010).

From the overall phylogenetic pattern it is probable that *H. turcicus* s.s. also originated from the Levantine region as both haplotype groups *turcicus* A and *turcicus* B are present there, even within single localities, like their sister taxon *H.* cf. *turcicus* from rocky habitats in north-eastern Israel. It is evident that both haplotype groups of *H. turcicus* were spread around the Mediterranean, *turcicus* A in a northwestern direction into Asia Minor and southeastern Europe and *turcicus* B in a southwestern direction into Sinai, North Africa as far as Iberia (see also Rato *et al.* 2011). It is not properly explained what could be the importance of human-mediated dispersal in the initial phase of distributional expansions. However, based on the low genetic variation it seems that the dispersal events occurred quite rapidly, at least in the *turcicus* A haplogroup. Alternatively, the low level of mtDNA genetic diversity and structure in the eastern European populations of *H. turcicus* could also be explained as a possible result of the genetic hitch-hiking process leading to a mitochondrial selective sweep (Rato *et al.* 2011). Nevertheless, the human-mediated dispersal apparently played an important role in intermixing both haplogroups (see Fig. 6 and Rato *et al.* 2011) in historical times as well as in the long-distance colonisation events, like in the case of colonisations of the Canary Islands or America (both by *turcicus* B). In concordance with this hypothesis, Locey and Stone (2006) suggested multiple jump dispersal events as the likeliest mode of expansion in introduced North American populations of *H. turcicus*. Similar human-mediated dispersal was also suggested in another Mediterranean reptile species, the ocellated skink *Chalcides ocellatus* (Forskal) (Kornilios *et al.* 2010), or in a small mammal species, the lesser white-toothed shrews from the *Crocidura suaveolens* group (Dubey *et al.* 2007). Further research focused on demographic analyses based on fast-evolving genetic markers is necessary for a better understanding of evolutionary history and distributional expansions of *H. turcicus*.

Taxonomy and type locality of *H. turcicus*. From the taxonomic point of view, subspecific epithets could be applied for the haplotype groups *turcicus* A and *turcicus* B. However, we rather refrain from taxonomic differentiation of the two haplogroups as no consistent morphological differences are currently known between them, no differentiation was uncovered by Rato *et al.* (2011) in two studied nuclear genes (*ACM4* and *RAG2*), and the two groups have probably been intermixed by human sea transport in the recent times (see also the map in Rato *et al.* 2011). Moreover, the type locality of *H. turcicus* remains ambiguous and complicates eventual intraspecific taxonomy. The type locality was originally stated as "Oriente" by Linnaeus (1758) and later assigned to be Turkey according to the scientific name (Mertens and Müller 1928, 1940). However, Smith and Taylor (1950a,b) restricted the type locality to Cairo, Egypt, without providing any explanation. Such an action was unwarranted as subsequently pointed by Neill (1951) and corrected back to Turkey. In this respect Schmidt (1953) specified the type locality as "Asiatic Turkey", and this act was followed by Mertens and Wermuth (1960). Nevertheless, Salvador (1981) considered Smith and Taylor's (1950a,b) restriction as valid and revived Cairo, Egypt again as the type locality of *H. turcicus*. We do not agree with Salvador (1981) and follow the view of Neill (1951) and the majority of later authors (e.g., Mertens and Wermuth 1960, Baha El Din 2005). In conformity with the International Code of Zoological Nomenclature (ICZN 1999), Recommendation 76A.2. ("A statement of a type locality that is found to be erroneous should be corrected.") we formally propose "Asiatic Turkey" as the type locality of *H. turcicus*.

The narrow-ranging and generally neglected subspecies *H. turcicus spinalis* Buchholz (type locality Isla Addaya Grande on the north coast of Menorca) probably falls within the haplogroup B in concordance with the sample from Menorca. Nevertheless, specimens from the type locality itself should be tested first by molecular markers before any final taxonomic assignment.

Comments on the phylogeny and systematics of *Hemidactylus*. Our initial taxon-wide phylogenetic analysis of *Hemidactylus* also contributed to the knowledge of the phylogeny of some *Hemidactylus* taxa occurring out of the distribution area of *H. turcicus*. In comparison to the *Hemidactylus* phylogeny of Carranza and Arnold (2006) we did not uncover the *H. mabouia* clade (content: *H. mabouia* (Moreau de Jonnès), *H. yerburii*). Tropical *H. mabouia* was placed within the African-Atlantic clade with a high support (BPP/ML bootstrap: 1.00/77), and *H. yerburii* clearly among the Arid species. Moreover, we found *H. yerburii* (and *H.* cf. *yerburii*) positioned in two different lineages within the Arid species group (Fig. 1). It appears that the *H. mabouia* clade sensu Carranza and Arnold (2006) originated by an error. *Hemidactylus mabouia* is apparently a part of the African-Atlantic clade (a similar result was recently obtained by Bauer *et al.* 2010), while *H. yerburii* is a member of the Arid species group as would be expected from its morphology (e.g., Sindaco and Jeremčenko 2008). The artificial "*H. mabouia* clade" emerged from the concatenated dataset (*Cytb* and *12S rRNA*), where the *12S rRNA* sequence (DQ120378) of "*H. yerburii*" is in fact the sequence of *H. mabouia*. This error was probably caused by contamination of the *12S* PCR amplicon of the supposed *H. yerburii* sample by the *H. mabouia* sample (S. Carranza, pers. comm., 2010).

Within the Arid species group (sensu Carranza and Arnold 2006), the ambiguous position of *H. yerburii* also deserves special attention. Our sample from Yemen, *H.* cf. *yerburii*, is 17.5 % distant (uncorrected *p*-distance; not shown) from Saudi Arabian *H. yerburii* (from Carranza and Arnold 2006). Another striking fact is that *H. yerburii* from southwestern Saudi Arabia is a close relative of an enigmatic sample (Hd41; *Hemidactylus* sp. 1) from southern Sinai, Egypt, which we assumed to be *H. turcicus* according to its morphology at the beginning of our study. In the same region (vicinity of Sharm el-Sheikh) we confirmed *H. turcicus* s.s. (Hd34) as well, the expected species in the region. Thus, it seems that at least two different "*H. turcicus*-like" species occur in the region of the coastal southern Sinai. According to Baha El Din (2006) and Sindaco and Jeremčenko (2008), only three species occur in Sinai: *H. turcicus*, *H. mindiae* and the introduced *H. flaviviridis* Rüppell. *Hemidactylus robustus* Heyden might be present too as it is known from the nearby localities on the continental Egyptian Red Sea coast (Baha El Din 2006). However, all these species were included in our analyses and are nested in different clades from that of *Hemidactylus* sp. 1. As the locality Sharm el-Sheikh is situated on the coast, it is highly feasible that our individual of *Hemidactylus* sp. 1 could represent a non-native species, or introgressed mtDNA from a species introduced to Sinai from the neighbouring Arabian Peninsula by a ship transport. Therefore, for the time being, *Hemidactylus* sp. 1 remains an unnamed taxon and will be subjected to the future research as well as the different *H. yerburii* forms. A similar unclear situation was found in the case of seven "*H. turcicus*-like" forms from Yemen (*Hemidactylus* sp. 2–8), which were scattered in different and unique positions across the Arid species group. They document an unusually high diversity of the Yemeni representatives of the Arid group and will be investigated in more details in future studies.

In our complete *Cytb* dataset we used an individual of *H.* cf. *angulatus* from coastal Cameroon (HdC1) as a distant outgroup. This sample also turned out to be interesting for the biogeographic and taxonomic interpretations as it belonged to the same haplotype as the sample from Bioko Island, Equatorial Guinea (DQ120218; Carranza and Arnold 2006) and clustered together with *H. haitianus* Meerwarth from the Caribbean (uncorrected p-distances 2%; details not shown). This result demonstrates that the recently revalidated *H. haitianus* (Bauer *et al.* 2010) is present in Cameroon too, at least in the coastal region.

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APPENDIX 1. Additional specimens examined morphologically.

Hemidactylus lavadeserticus: SYRIA: Muhafazat of Sweida: Ar'Raqiyeh, NMP6V 74049/1–5.

Hemidactylus mindiae: JORDAN: Jabal Ghazali, NMP6V 72323/1–2; Wadi Ramm, Nughra-Raddet Salem, NMP6V 72739/1–3.

Hemidactylus turcicus: CYPRUS: Famagusta, NMP6V 71587/1–3; Yali 71592/1–2. GREECE: Crete, Kavros, NMP6V 74050, 74167; Kastellorizo Islands, St. Georges, NMP6V 70667–70668; Korfu, Perivoli, NMP6V 72073. ITALY: Gagliari, NMP6V 70629. SYRIA: Banias, NMP6V 34747; Busra ash Sham, 34830/1–2, 35542/2–4; Cyrrhus, NMP6V 74046/1–2; Palmyra, NMP6V 34748/1–3, 74131/1–3; Qualat al Marquab, NMP6V 72497. TURKEY: Finike, 73626/1–3; Kaş, NMP6V 70648/1–2.

Paper II

Šmíd, J., Moravec, J., Zawadzki, M., van den Berg, M. (2015): One subspecies less for the European herpetofauna: the taxonomic and nomenclatural status of *Hemidactylus turcicus spinalis* (Reptilia: Gekkonidae). *Zootaxa*, 3911: 443–446.
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- JŠ performed the fieldwork, laboratory work and the phylogenetic analyses, and wrote the paper

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One subspecies less for the European herpetofauna: the taxonomic and nomenclatural status of *Hemidactylus turcicus spinalis* (Reptilia: Gekkonidae)

JIŘÍ ŠMÍD[1, 2], JIŘÍ MORAVEC [1,5], MIKE ZAWADZKI[3] & MARTEN VAN DEN BERG[4]
[1]*Department of Zoology, National Museum, Cirkusová 1740, Prague, Czech Republic*
[2]*Department of Zoology, Faculty of Science, Charles University in Prague, Viničná 7, Prague, Czech Republic*
[3]*Am Rissener Bahnhof 16 c, 22559 Hamburg, Germany*
[4]*Purmerenderweg 141, 1461DH Zuidoostbeemster, The Netherlands*
[5]*Corresponding author. E-mail: jiri_moravec@nm.cz*

Reptile systematics is currently primarily supported by genetic evidence, which has brought numbers of cases of taxonomic reconsiderations within the last years. Genetic studies have resulted in taxonomic changes at the subspecific level with many subspecies being synonymized with species, lumped together, or elevated to a species status (see Torstrom *et al.* 2014 for a review). The reptile fauna of Europe ranks among the best studied in the world in terms of taxonomy, yet it still includes taxa whose original descriptions were based on insufficient morphological diagnoses and the status of which should be reassessed by integrating genetic methods. One such case is provided here.

Hemidactylus turcicus (Linnaeus) is a species distributed throughout the whole Mediterranean, most probably due to human-aided dispersal. Previous studies identified two widely distributed haplotype groups of *H. turcicus*—clade A and clade B (Moravec *et al.* 2011; Rato *et al.* 2011) with almost parapatric distribution ranges, roughly corresponding to northeastern and southwestern Mediterranean, respectively. The diversification between the clades A and B is nevertheless very shallow compared to genetic structure detected in other *Hemidactylus* species (Carranza & Arnold 2012; Šmíd *et al.* 2013). Regarding the taxonomy and nomenclature of *H. turcicus* we (Moravec *et al.* 2011) speculated about the phylogenetic position and taxonomic validity of the narrow-range and generally neglected subspecies *H. turcicus spinalis* Buchholz (type locality Isla Addaya Grande [Illa Gran d'Addaia] off the north coast of Menorca) and concluded that genetic examination of specimens from its type locality should precede any taxonomic decisions.

Buchholz (1954) based the description of *H. t. spinalis* on the distinct, longitudinally striped dorsal pattern of five specimens from Illa Gran d'Addaia (Fig. 1). Other morphological characters examined by him did not differ from those in other populations of *H. turcicus*. The subspecies was accepted in the influential compendium by Mertens & Wermuth (1960). Later on, despite the claim by Martínez-Rica (1974) that Buchholz's diagnostic characters were vague and unsatisfactory for a subspecies description, the taxon was considered valid by Salvador (1981), listed in the 1992 Red Book of Spanish Vertebrates as Rare (R) (Blanco *et al.* 1992) and in its updated 2002 version as Least Concern (LC) (Geniez 2002), and some authors continued to speculate on its validity (Salvador & Pleguezuelos 2002; Sindaco & Jeremčenko 2008; Rivera *et al.* 2011). Recently, van den Berg *et al.* (2013) pointed out that the dorsal colour pattern was not consistent among all specimens of *H. t. spinalis* on Illa Gran d'Addaia. The authors suggested rejecting the validity of this subspecies by arguing that the description was based on a limited number of specimens that may have been closely related and thus shared the unique morphological trait. Nevertheless, genetic data supporting this rejection were until now missing.

Here we provide the first genetic data of the *spinalis* morphotype from the type locality of *H. t. spinalis* and compare them with published sequences of *H. turcicus* from throughout its range (including Asiatic Turkey, its proposed type locality [Moravec *et al.* 2011]) to finally settle the debate concerning the validity of *H. t. spinalis*.

New material examined comprised four specimens of *Hemidactylus turcicus* from Illa Gran d'Addaia including the animal reported by van den Berg (2013; sample code JS323) and three voucher specimens from the collection of the National Museum, Prague (NMP6V 74986/1–3, sample codes M16–M18), some with very markedly developed dark dorsal stripe typical for the *spinalis* morphotype. Additionally, three individuals from the adjoining Menorcan city of Port d'Addaia (NMP6V 74984 [sample M05], NMP6V 74985/1–2 [M06–M07]) were examined. Photographs of all specimens together with all sequence alignments were deposited in MorphoBank (http://www.morphobank.org, Project 1236).

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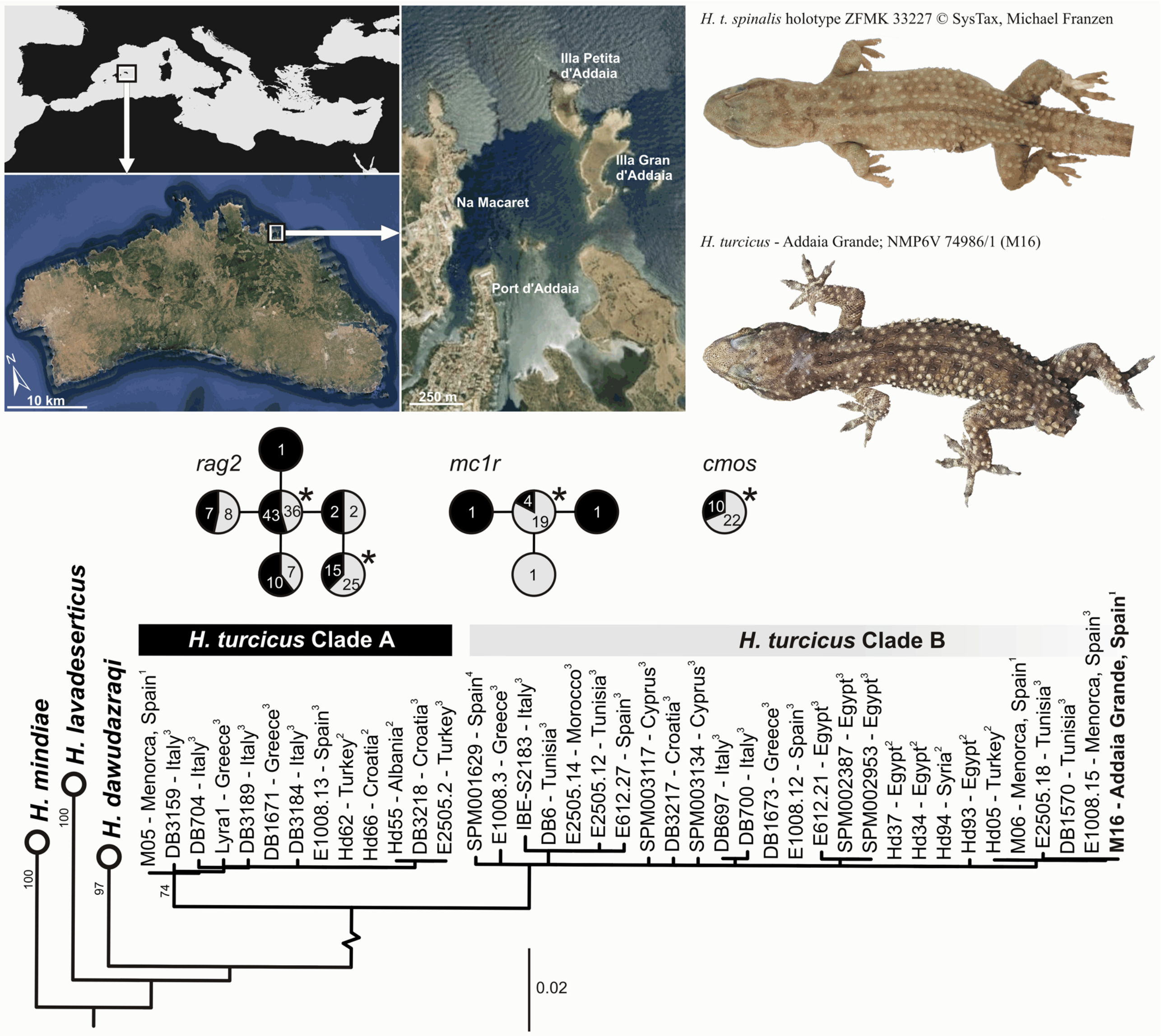

FIGURE 1. Upper left: map of the Mediterranean, Menorca, and Illa Gran d'Addaia, the type locality of *H. t. spinalis* (from www.google.com/earth). Upper right: comparison of the holotype of *H. t. spinalis* (ZFMK 33227) with a specimen NMP6V 74986/1 (sample no. M16) from the same locality; note the dark vertebral stripe, a character typical for the subspecies. Specimens are not to scale. Middle: median joining nuclear allele networks of the three sequenced nDNA gene fragments. Circle sizes are not proportional to the number of alleles, these are given as the numbers within each circle or circular sector. Colours correspond to *H. turcicus* clades A and B as defined by Moravec *et al.* (2011) and Rato *et al*. (2011). Alleles marked with asterisks include specimens of *H. t. spinalis*. Below: Maximum likelihood phylogenetic tree of *H. turcicus* and its closest relatives based on concatenated mtDNA sequences (*12S* and *cytb*); *H. flaviviridis* (outgroup) and *H. lemurinus* not shown; specimens of *H. dawudazraqi*, *H. lavadeserticus*, and *H. mindiae* are collapsed into circles; samples of *H. turcicus* are labelled as in the original source which is given by the upper index number (1–new material; 2—Moravec *et al.* (2011); 3—Rato *et al*. (2011); 4—Šmíd *et al.* (2013)). Specimen in bold represents *H. t. spinalis*.

Genomic DNA was extracted and two mitochondrial (12S rRNA (*12S*)—ca. 400 bp, *cytb*—315 bp) and three nuclear gene fragments (*cmos*—402 bp, *mc1r*—666 bp, *rag2*—408 bp) were amplified using primers and following conditions described elsewhere (Šmíd *et al.* 2013). Only the *cytb* was amplified using a different pair of primers (CB1—CCATCCAACATCTCAGCATGA and CB2—CCCTCAGAATGATATTTGTCC; modified after Kocher *et al.* (1989)) producing a fragment of 315 bp overlapping completely with that produced in the aforementioned study. New sequences were combined with those of *H. turcicus* and related species (*H. dawudazraqi*, *H. lavadeserticus*, *H. lemurinus*, *H. mindiae*) published in previous studies (Carranza & Arnold 2006; Gamble *et al.* 2011; Moravec *et al.* 2011; Rato *et al.* 2011; Šmíd *et al.* 2013) into a single dataset. Two specimens of *H. flaviviridis* were used as outgroup (samples JS111 and JS119 from Šmíd *et al.* 2013). Assembly of contigs, sequence alignment, substitution model selection, and maximum likelihood (ML) analysis of the two mtDNA gene fragments concatenated were performed as described in details by Šmíd *et al.* (2013). The best nucleotide substitution models were as follows: *12S*, *cytb*—GTR + G; *cmos*, *rag2*—JC; *mc1r*—HKY. Only unique haplotypes were included in the ML analysis. Haplotype identification was done in DnaSP 5.1 (Rozas *et al.* 2003), which recognized 68 unique haplotypes. To infer genealogical relationships within *H. turcicus* for each nuclear gene we phased the alignments and reconstructed haplotype networks following Rato *et al.* (2011), with the only difference that the *p* threshold was set to 0.7. Because Rato *et al.* (2011) and Šmíd *et al.* (2013) sequenced different *rag2* fragments that overlap only partially (334 bp) the alignment was trimmed to include only this overlapping region.

All samples of *H. t. spinalis* shared identical haplotypes in all genes but *rag2* in which the sample JS323 differed in two nucleotide positions along the 334 bp long alignment. All phylogenetic analyses were congruent in that *H. t. spinalis* is nested within the *H. turcicus* clade B (Fig. 1). Sequences of all gene fragments were identical to those of *H. turcicus* already deposited in GenBank: *12S*—KC818741, DQ120299–300 shared with samples from Turkey, Cyprus, Jordan, Greece, Croatia, Italy, France, Tunisia, Spain, Morocco, Portugal, and USA; *cytb*—DQ120146–47, HQ675989, HQ676016, HQ833728–29 shared with samples from Tunisia, Spain, and Morocco; *cmos*—JQ957162 shared with samples from Turkey, Lebanon, Egypt, Albania, and Spain; *mc1r* - JQ957301 shared with samples from Egypt and Spain; *rag2*—e.g. HQ676055–56 (M16–M18) and JQ957423, JQ957440–42 (JS323) shared with samples of *H. turcicus* from Turkey, Israel, Egypt, and Spain and even with other *Hemidactylus* species (*H. dawudazraqi*, *H. lemurinus*, *H. mindiae*). Because all these genes have identical haplotypes deposited in Genbank we do not submit the data there.

The three NMP specimens from Illa Gran d'Addaia have the following morphological characters: supralabials 8–9; infralabials 6–8; rows of dorsal tubercles 12–14; lamellae under 1st toe 6–7; lamellae under 4th toe 10; preanal pores 6–7; SVL 42.6–52.4 mm. All morphological characters of the specimens from Illa Gran d'Addaia, including the type series of *H. t. spinalis*, fall within the known range of *H. turcicus* intraspecific variability (Moravec *et al*. 2011) (although from the numbers of lamellae under fingers given by Buchholz (1954) we assume he probably confused the 1st and 5th finger). Examination of the dorsal pattern of seven specimens of *H. turcicus* from Illa Gran d'Addaia (van den Berg *et al.* 2013, NMP collection) revealed a wide variation in the dorsal pattern ranging continuously from spotted to striped forms (Fig. 1).

Therefore, as there are no consistent morphological characters delimiting the Illa Gran d'Addaia population of *H. turcicus* from other Mediterranean populations and all the specimens from Illa Gran d'Addaia are in all examined molecular markers indistinguishable from other *H. turcicus* samples from the Mediterranean (including its designated type locality in Asiatic Turkey), we definitively reject the subspecific status of this population and synonymize the name *Hemidactylus turcicus spinalis* Buchholz, 1954 with the name *Hemidactylus turcicus* (Linnaeus, 1758).

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Paper III

Šmíd, J., Mazuch, T., Sindaco, R. (2014): An additional record of the little known gecko *Hemidactylus granchii* Lanza, 1978 (Reptilia: Gekkonidae) from Somalia. *Scripta Herpetologica. Studies on Amphibians and Reptiles in honour of Benedetto Lanza*: 165–169.

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- JŠ acquired morphological data and wrote the paper

An additional record of the little known gecko *Hemidactylus granchii* Lanza, 1978 (Reptilia: Gekkonidae) from Somalia

Jiří Šmíd [1,2]*, Tomáš Mazuch [3], Roberto Sindaco [4]

[1] *Department of Zoology, National Museum - Cirkusová 1740, 193 00, Prague, Czech Republic*
[2] *Department of Zoology, Faculty of Science, Charles University - Viničná 7*
128 44 Prague, Czech Republic
[3] *Dříteč 65, 53305, Czech Republic*
[4] *c/o Museo Civico di Storia Naturale - Via S. Francesco di Sales 88, 10022 Carmagnola (TO), Italy*
* *Corresponding author:* jirismd@gmail.com

Abstract. We report a new locality of *Hemidactylus granchii* from northern Somalia. Until now, the gecko was known only from the type series from three localities in southern and central Somalia. This record extends the known range more than 450 km north-westwards. A comparison with morphologically similar species is provided.

Keywords. Gekkonidae, Somalia, distribution, new record.

Gecko fauna of Somalia comprises more than 50 species in nine genera (*Hemidactylus*, *Hemitheconyx, Holodactylus, Homopholis*, *Lygodactylus*, *Pristurus, Ptyodactylus, Tarentola* and *Tropiocolotes*). Among them, the genus *Hemidactylus* represents an overwhelming majority with 30 described taxa (Lanza, 1990; Uetz, 2013; Šmíd et al. 2013). Lanza (1978) contributed significantly to the knowledge of Somali herpetofauna by publishing an overview of East African amphibians and reptiles with, among others, descriptions of four new species and one subspecies of *Hemidactylus* (*H. arnoldi* Lanza, 1978, *H. bavazzanoi* Lanza, 1978, *H. funaiolii* Lanza, 1978, *H. granchii* Lanza, 1978, *H. yerburii pauciporosus* Lanza, 1978). Although these taxa remain valid to date, they are rather enigmatic. Virtually nothing is known about their biology, distribution or systematic affinities and they are very scarcely represented in museum collections. Here we provide an additional record of *H. granchii*, known so far from the type series only.

The type material of *H. granchii* is deposited in the zoological collection of the Museum of Natural History 'La Specola', University of Firenze, Italy. The holotype (MZUF 21188), an adult male, was collected "circa 80 km a N di Obbia (Somalia centrale), M. Bianchi, XI.1930" [about 80 km N of Obbia, about 06°00'N 48°30'E; eastern central Somalia (Lanza, 1978)], according to the original museum label. The two paratypes, both adult females, were collected at different localities and are equipped with the following labels: 1) MZUF 21114 - "Uarscek (zona di) (Somalia centrale), C. Koch leg. et don., X. 1957" [Uarscek area, about 02°20'N

45°40'E; southern central Somalia (Lanza, 1978)] and 2) MZUF 21189 - "30 km a S di Galcaio, tra Galcaio e Uargalo (Somali centrale), M. Bianchi, XI.1930" [between Uargalo and Galcaio, 30 km S of Galcaio, about 06°30'N 47°25'E; central Somalia (Lanza, 1978)] (Fig. 1).

One adult female was collected by one of us (TM) on November 29th, 2010 by the road from Hargeisa to Berbera, ca. 45 km NE of Hargeisa, Somaliland (9°43'49.98"N, 44°25'9.78"E, 1110 m a.s.l.) and is temporarily deposited in the private collection of Tomáš Mazuch (TMHC 2012.07.088). The animal was caught during the daytime by an entrance to a sewer drain under the road. Surrounding habitat was a stony plain with scattered and mostly shrubby vegetation (Fig. 2). Other reptile species observed in the locality were *Agama rueppelli* Vaillant, 1882, *Xenagama taylori* (Parker, 1935), *Pristurus crucifer* (Valenciennes, 1861), *Pseuderemias mucronata* (Blanford, 1870), and *Hemidactylus albopunctatus* Loveridge, 1947.

This specimen corresponds in morphology with the original description of

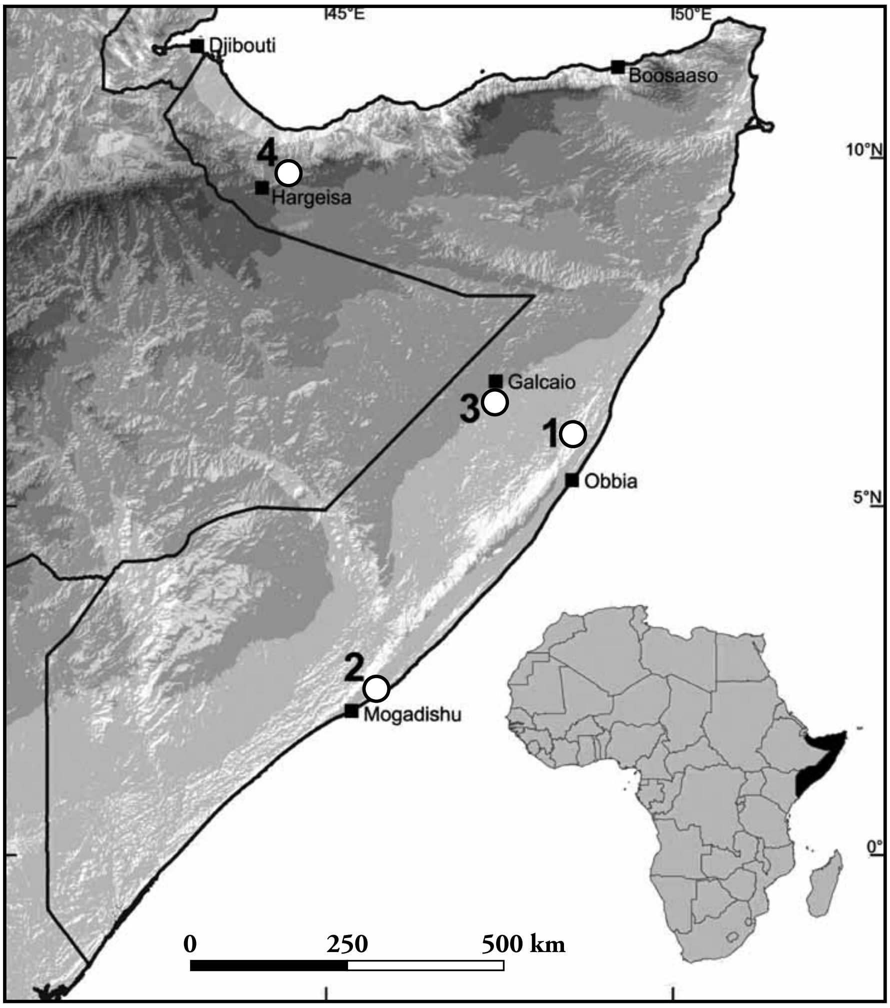

Figure 1. Map of known distribution of *Hemidactylus granchii*. 1. Type locality; 2. Locality of the paratype MZUF 21114; 3. Locality of the paratype MZUF 21189; 4. New record.

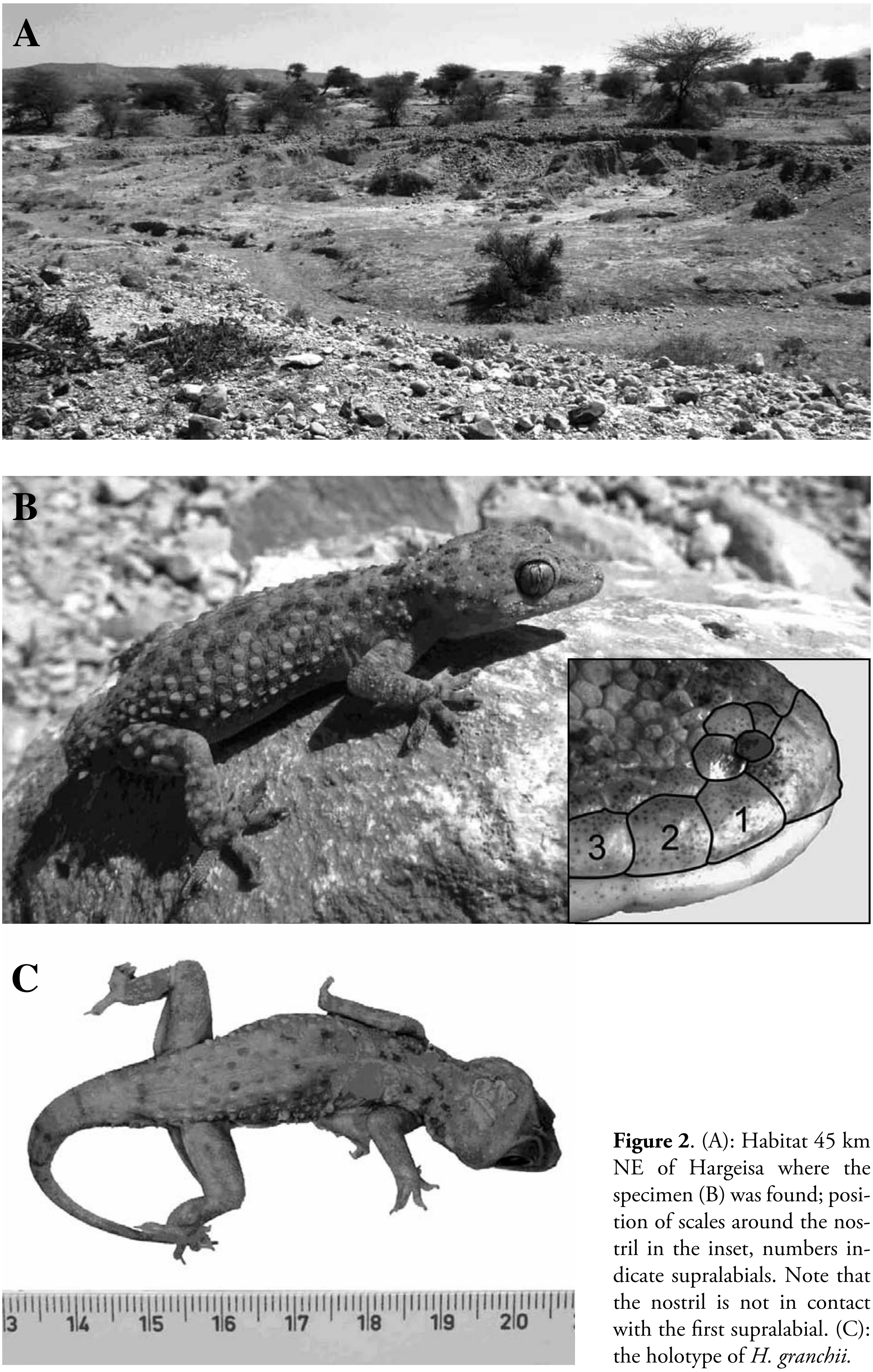

Figure 2. (A): Habitat 45 km NE of Hargeisa where the specimen (B) was found; position of scales around the nostril in the inset, numbers indicate supralabials. Note that the nostril is not in contact with the first supralabial. (C): the holotype of *H. granchii*.

H. granchii in being rather stout, medium-sized *Hemidactylus* (SVL = 50.03 mm; Head length = 13.34 mm; Axilla to groin = 21.86 mm). Nostrils are separated from first supralabials and are bordered by the rostral and three nasals. Dorsum is covered with large keeled tubercles forming 14 longitudinal rows; 20 tubercles in a paravertebral row from axilla to groin. More meristic characters are summarized in Table 1. Dorsal colour pattern is inconspicuous and consists of randomly distributed dark brown spots usually restricted to dorsal tubercles and not extending onto smaller granules. Dark spots on the neck and behind forelimbs tend to form transverse bands.

High-resolution pictures of all four existing specimens of *H. granchii* have been deposited in Morphobank (Project 1069; holotype: M309540-575; paratype MZUF 21114: M309576-599; paratype MZUF 21189: M309600-625; TMHC 2012.07.088: M309626-672; http://www.morphobank.org).

H. granchii can be distinguished from the following species, that can be found or are expected to occur in this region and that all share the appearance of robust geckos with large dorsal subtrihedral tubercles:

Table 1. Comparison of meristic characters of all known individuals of *H. granchii*.

		MZUF 21188 Holotype ♂	**MZUF 21114** Paratype ♀	**MZUF 21189** Paratype ♀	**TMHC 2012.07.088** ♀
Finger lamellae	1st	8	7	7	6
	2nd	8	7	8	7
	3rd	8	8/7	8	8
	4th	8	8	8/9	8
	5th	9	9	9	9
Toe lamellae	1st	7	7	7	6
	2nd	9	8	8/9	8/9
	3rd	10	9	9	8
	4th	11	10	10	10/9
	5th	11	10	10	9/10
Number of infralabials in contact with first postmental		2	1/2	2	1/2
Tail with basal constriction		No	Tail missing	No	Tail missing
Rows of dorsal tubercles		14	15-16	15-16	14
1st upper labial touching nostril		No	No	No	No
Supralabials		9/9	9/9	10/10	10/10
Infralabials		6/7	6/7	7/7	7/7
Preanal pores		5	-	-	-

- *H. arnoldi* has a conspicuous dorsal colour pattern of broad, dark, transverse bands. Between the base of the 1st and 5th toe there is a marked roundish smooth enlarged scale surrounded by small granular scales (Lanza, 1978).
- *H. barodanus* Boulenger, 1901 differs from *H. granchii* in having more infralabial scales (8 vs. 7 in *H. granchii*) and relatively flat dorsal tubercles without distinct keels.
- *H. macropholis* Boulenger, 1896 differs in the arrangement of the scales around the nostril. First supralabial in *H. macropholis* is in contact with the nostril unlike in *H. granchii,* where rostral is touching the outermost nasal and separates the nostril from the first supralabial. *H. macropholis* has also lower number of infralabials (8 vs. 6-7 in *H. granchii*).
- *H. taylori* Parker, 1932 has a higher number of lamellae under the 2nd finger (9 vs. 7-8 in *H. granchii*) and under the 1st toe (8 vs. 7 in *H. granchii*). It also has more dilated digits than *H. granchii* (see Lanza 1978, Fig. 19 on p. 262) and anterior chin shields in contact only with the first infralabial (1st and 2nd infralabials in *H. granchii*, at least on one side). The most remarkable difference, which unfortunately can not be compared in the newly reported specimen, is the shape of unregenerated tail. The tail of *H. taylori* has a basal constriction and is considerably wide in comparison with that of *H. granchii*.
- *H. yerburii pauciporosus* has more supralabials than *H. granchii* (11 vs. 9-10) and the nostril is in contact with the first supralabial.

This new record brings the only additional specimen of *H. granchii* after 35 years from its description and extends its known distribution more than 450 km north-westwards. Despite the new locality lies within Somalia and the species thus remains endemic to this country, its distribution is expected to span across the Ethiopian region of Ogaden as well. However, this remains to be confirmed. More research in this region is essential to provide better knowledge of the distribution of local rare and mostly endemic reptile fauna.

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Paper IV

Šmíd, J., Carranza, S., Kratochvíl, L., Gvoždík, V., Nasher, A.K., Moravec, J. (2013): Out of Arabia: a complex biogeographic history of multiple vicariance and dispersal events in the gecko genus *Hemidactylus* (Reptilia: Gekkonidae). *Plos ONE* 8(5): e64018. doi:10.1371/journal.pone.0064018.
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Author contribution:
- JŠ acquired and the data, conceived and designed the experiment, performed the laboratory work, performed the phylogenetic analyses, and wrote the paper

Out of Arabia: A Complex Biogeographic History of Multiple Vicariance and Dispersal Events in the Gecko Genus *Hemidactylus* (Reptilia: Gekkonidae)

Jiří Šmíd[1,2]*, Salvador Carranza[3], Lukáš Kratochvíl[4], Václav Gvoždík[1,5], Abdul Karim Nasher[6], Jiří Moravec[1]

1 Department of Zoology, National Museum, Prague, Czech Republic, **2** Department of Zoology, Faculty of Science, Charles University in Prague, Prague, Czech Republic, **3** Institute of Evolutionary Biology (CSIC-UPF), Barcelona, Spain, **4** Department of Ecology, Faculty of Science, Charles University in Prague, Prague, Czech Republic, **5** Department of Environmental Sciences, Biogeography, University of Basel, Basel, Switzerland, **6** Faculty of Science, University of Sana'a, Sana'a, Yemen

Abstract

The geological history of the Arabian Peninsula has played a crucial role in shaping current diversity and distribution patterns of many Arabian and African faunal elements. The gecko genus *Hemidactylus* is not an exception. In this study, we provide an insight into the phylogeny and systematics of 45 recognized species of the so-called Arid clade of the genus *Hemidactylus* from Arabia, the Horn of Africa, the Levant and Iran. The material comprises 358 specimens sequenced for up to two mitochondrial (12S rRNA, cytochrome *b*) and four nuclear (*mc1r*, *cmos*, *rag1*, *rag2*) genes with 4766 bp of the concatenated alignment length. A robust calibrated phylogeny and reconstruction of historical biogeography are inferred. We link the history of this genus with major geological events that occurred in the region within the last 30 million years. Two basal divergences correspond with the break-ups of the Arabian and African landmasses and subsequent separation of Socotra from the Arabian mainland, respectively, segregating the genus by means of vicariance. Formation of the Red Sea led to isolation and subsequent radiation in the Arabian Peninsula, which was followed by multiple independent expansions: 13.1 Ma to Iran; 9.8 Ma to NE Africa; 8.2 to Socotra Archipelago; 7–7.3 Ma two colonizations to the Near East; 5.9 Ma to NE Africa; and 4.1 to Socotra. Moreover, using multiple genetic markers we detected cryptic diversity within the genus, particularly in south-western Arabia and the Ethiopian highlands, and confirmed the existence of at least seven new species in the area. These findings highlight the role of Arabia and the Horn of Africa as an important *Hemidactylus* diversity hotspot.

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* E-mail: jirismd@gmail.com

Introduction

With 122 currently valid species, the genus *Hemidactylus* is the second most speciose gecko genus (after *Cyrtodactylus*) and ranks among the top ten species-rich genera of reptiles [1]. *Hemidactylus* geckos are widely distributed across all tropical and subtropical continental landmasses and hundreds of intervening continental and oceanic islands, from Southeast Asia westwards over Africa to the New World [2,3]. As already shown by many authors [4–10], the current distribution of the genus has been highly affected by repeated transmarine colonizations caused either by human activity or by spontaneous rafting, which have contributed significantly to the unusually wide distribution range of the genus [4,6]. For instance, the transatlantic colonization of Central and South America by African species has occurred independently at least four times [10]. The most species-rich areas include the tropics and subtropics of the Old World, with the highest species richness being achieved in the Horn of Africa (Somalia and adjacent countries), which, based on the current taxonomy of the genus, is known to be inhabited by 38 species [1,11–13].

As a result of its wide distribution and high species richness, the genus *Hemidactylus* represents an excellent model for testing biogeographic, ecological and evolutionary hypotheses, and has therefore become a centre of attention of molecular phylogenetic studies [5–7,14–26]. The first comprehensive phylogeny covering about one third of all *Hemidactylus* species was published by Carranza and Arnold [6]. Taking into account additional adjustments [19,23], this work resulted in the division of the genus into four phylogenetic lineages: (i) Tropical Asian clade, (ii) *H. angulatus* clade, (iii) Arid clade, and (iv) African – Atlantic clade. All Arabian *Hemidactylus* species belong to the Arid clade with only two exceptions: *H. flaviviridis* and *H. leschenaulti,* which are part of the Tropical Asian clade and have most probably been introduced into Arabia by human-mediated transportation [7]. Mainland Arabian *Hemidactylus* have witnessed a substantial increase of described taxa, from 9 to 21 within the last two years [7,21,23]. Moreover, recent works from the Levant [23] and the Socotra Archipelago [26] reported the occurrence of several unnamed (or putative) species in the Sinai, Yemen mainland and Socotra, suggesting that the real diversity of the Arabian members of the Arid clade of *Hemidactylus* is still largely underestimated. In contrast to the relatively high number of recent studies on Arabian *Hemidactylus*, virtually nothing is known about Northeast African *Hemidactylus* from a phylogenetic point of view. Preliminary analyses including up to 9 *Hemidactylus* species [6,7] suggest that these belong to the Arid clade, the *H. angulatus* clade or the African-Atlantic clade. The main reason of the poor knowledge of Northeast African *Hemidactylus* is the difficult accessibility of the region, which has made it almost impossible to perform any systematic zoological research for the last two decades.

Looking at the region from a geological perspective, the process of separation of the Arabian Peninsula from the African landmass took place from the mid-Oligocene to the Early Miocene (31–23 Ma) as a consequence of the East African Rift system faulting, which resulted in the formation of the Red Sea and the Gulf of Aden [27–29]. This continental break-up propagated from East to West, splitting the oceanic crust and triggering the separation of the Socotra Archipelago from the Dhofar region in Oman approximately 24 Ma [29–31]. Africa and Arabia became reconnected in a period between 10–5.3 Ma when massive halite deposits formed a land bridge in the Bab-el-Mandeb strait [29,32]; for general map with geographic names used in the text see Fig. S1. The long-term connectivity between Africa and Arabia and the subsequent geological events have had a crucial impact on the regional biogeography and explain the close biogeographic affinities between NE African and SW Arabian faunas [33,34]. It has been suggested that the diversity and distribution of current Afro-Arabian herpetofauna was influenced mainly by the three following factors: 1) the formation of the Red Sea in the Oligocene (27–24 Ma), which resulted in a vicariance event separating African and Arabian fauna [35,36]; 2) temporary reconnection of Africa and Arabia 10–5.3 Ma [29] and the geographic proximity of these landmasses, particularly in the narrowest point (Bab-el-Mandeb strait), which was only 5 km wide during the driest periods within the last 0.5 million years [37] and may have facilitated faunal exchange by means of dispersal [32,34]; and 3) the penetration of some Afrotropical and Mediterranean elements to SW Arabia from the north along the Hijaz and Asir mountain ranges, which provide suitable conditions for more temperate species than the otherwise arid desert environment of the Arabian Peninsula [35,38,39]. All these factors may have affected speciation and current distribution of *Hemidactylus* geckos.

In the present study, we provide new molecular data for *Hemidactylus* geckos from Arabia and the Horn of Africa and produce the most complete phylogeny to date of *Hemidactylus* from the Arid clade with the intention to: (1) evaluate the phylogenetic relationships among individual *Hemidactylus* populations and assess their systematics, (2) increment our knowledge on the *Hemidactylus* species from Arabia and the Horn of Africa and assess their mutual affinities, (3) reanalyze recent patterns of geographic distribution and reconstruct potential ways of historical dispersal routes or vicariance events, and (4) find possible correspondences between the geological history of the region with evolutionary splits of ancestral lineages in *Hemidactylus*.

Methods

Ethic Statement

Most of the investigated material comes from museum voucher specimens (BMNH London, CAS San Francisco, IBE Barcelona, NMP Prague; see Table S1). Vouchers and tissue samples were kindly accessed as loans by the appropriate curators with their permission to use the samples for DNA analyses (B. Clarke and E. N. Arnold – BMNH; J. Vindum – CAS; S. Carranza – IBE; J. Moravec – NMP). Remaining samples were obtained in the field with appropriate collecting permits (Oman: issued by Ali Alkiyumii, Ministry of Environment and Climate Affairs of the Sultanate of Oman: Refs 08/2005, 16/2008, 38/2010, 12/2011; Yemen: issued by Omer Baeshen, Environment Protection Agency, Sana'a, Republic of Yemen: Ref 10/2007; Kenya: issued by National Council for Science and Technology (NCST), Nairobi, Kenya). No endangered or protected species was collected and no samples from protected or private areas were used for this study. Research was conducted with the approval of Central Commission for Animal Welfare, the Czech Republic, accreditation no. 1090/2012–MZE–17214. All efforts were made to minimize animal suffering.

Table 1. Summary of DNA partitions.

Gene	Length (bp)	Model	Var	Pars. inf.	LRT
cytb	295–1137	GTR+G	615	550	not rejected ($P<0.47086$)
nd4	588	GTR+I+G	314	252	rejected ($P<0.00037$)
tRNAs	146	GTR+G	75	58	rejected ($P<0.00424$)
12S	317–396	GTR+I+G	200	167	rejected ($P<5.05957E-9$)
cmos	402	TPM1+I+G	59	36	not rejected ($P<0.15766$)
mc1r	666	GTR+I+G	99	73	not rejected ($P<0.08567$)
rag1	280, 1023	GTR+G	138	75	not rejected ($P<0.52772$)
rag2	408	TrN+I+G	60	39	rejected ($P<0.00475$)

Information on the length of all partitions used in the phylogenetic analyses, model of sequence evolution selected by jModelTest [44] (Model), number of variable (Var) and parsimony-informative (Pars. inf.) sites calculated for the ingroup only, and the results of the test of rate homogeneity (LRT) run in MEGA [52] using only the subset of 58 sequences selected for the BEAST analysis (see Methods).

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Tissue Samples, DNA Extraction and PCR Amplification

In total, sequences of 358 *Hemidactylus* specimens were used in this study. Additionally, 15 sequences of the 12S rRNA (*12S*) mitochondrial gene of three taxa recently described from Yemen [21], which were kindly donated by U. Joger, were included into the analysis. Ten specimens of *H. flaviviridis* were used as outgroups [7]. Localities, specimen codes and GenBank accession numbers of all genes included in the phylogenetic analyses are shown in Table S1.

Total genomic DNA was extracted using Geneaid Extraction Kit and DNeasy Tissue Kit (Qiagen) following the protocols therein. Two mtDNA genes (partial sequence of *12S*, and cytochrome *b* - *cytb*) and four nDNA genes encoding the proto-oncogene *mos* (*cmos*), the melano-cortin 1 receptor (*mc1r*) and the recombination activating genes 1 and 2 (*rag1* and *rag2*, respectively) were amplified. Two sets of primers were used for the *cytb*: one set for the complete 1137 bp of the *cytb* gene and, when this long fragment failed to amplify, a second set that amplifies a shorter region of 307 bp was employed [6,7]. Also for *rag1*, two pairs of primers were used: one for a region of over 1000 bp and, when as a result of poor DNA quality this long fragment could not be amplified, a second pair of primers amplifying 280 bp was employed. A complete list of all primers used, their sequences,

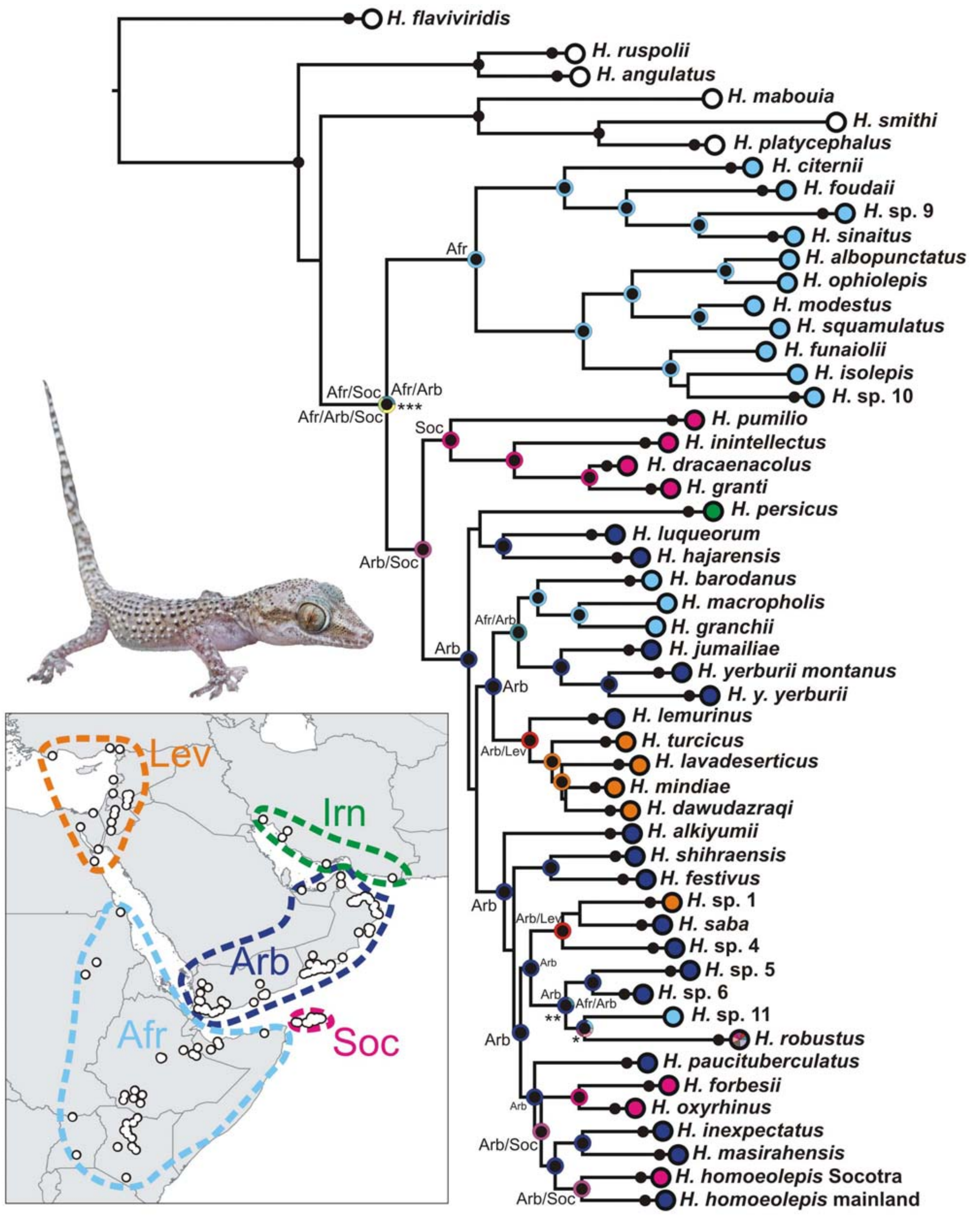

Figure 1. Maximum likelihood phylogenetic tree of the Arid clade of the genus *Hemidactylus*. Individuals of one species are collapsed into one terminal branch. Black dots on the nodes and on the terminal lineages indicate ML bootstrap values ≥70 and BI posterior probabilities ≥0.95. Species are coloured according to their geographic origin marked on the inset map where the sampling is also depicted. Colours and abbreviations in the nodes indicate reconstruction of ancestral distribution. The probability of the ancestral area reconstruction of the node marked with * is: Afr 19%, Afr/Arb 33.3%, Afr/Arb/Lev 19%, Afr/Arb/Irn 19%, Afr/Arb/Lev/Irn 9.5%; of the node **: Arb 80.5%, Afr/Arb 19.5%; of the node ***: Afr/Arb 33.3%, Afr/

Soc 33.3%, Afr/Arb/Soc 33.3%; for all other nodes 100% for the area depicted. Undescribed species are labelled in accordance with previous works [7.23].
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length of amplified region, PCR conditions and source is given in Table S2.

Sequence Alignment

Apart from the genes amplified for the present study (see above), the final alignment included also the mitochondrial NADH dehydrogenase 4 (*nd4*) coding gene and the adjacent tRNA region (*tRNAs*; including the complete sequences of tRNA-His and tRNA-Ser and the first eight nucleotides of tRNA-Leu) from [7]. Chromatograms of all sequences newly produced for this study were checked by eye and assembled using the software Geneious v. 5.3.6 [40]. DNA sequences were aligned using MAFFT v.6 [41] with the options maxiterate 1000 and localpair. Poorly aligned positions of some mtDNA regions (*12S* and *tRNAs*) were eliminated with G-blocks [42] using low stringency options [43]. No stop codons were detected after translation of the protein-coding genes with standard genetic code for nuclear genes and the vertebrate mitochondrial code for the *cytb* and *nd4* genes into amino acids, suggesting that all genes are functional and no pseudogenes were amplified. Occasional heterozygous positions in the nuclear genes were coded according to the IUPAC ambiguity codes.

Phylogenetic Analyses

The final alignment of all concatenated genes included 4766 bp (2267 bp of mtDNA and 2499 bp of nDNA). The best-fitting model of nucleotide substitution was assessed for each gene independently using jModelTest v.0.1.1 [44] under the Akaike information criterion (AIC). All information related to each partition including alignment length, model selected, and the number of variable and parsimony-informative sites are presented in Table 1.

Maximum Likelihood (ML) and Bayesian Inference (BI) analyses were performed to infer the phylogenetic relationships among the taxa included in the present study (Tab. S1). ML analyses were performed in RAxML v 7.0.3 [45] with a GTR+I+G model of evolution with 100 random addition replicates and partition branch lengths and parameters estimated independently for each partition. Nodal support of the ML tree was assessed by 1000 bootstrap pseudoreplications [46]. Bayesian analyses were performed in MrBayes 3.1.2 [47] with appropriate best fitting models applied to all partitions (Tab. 1) and all parameters unlinked across partitions. Analyses were run for 10^7 generations with sampling frequency of 1000 generations. After assurance that the log-likelihood achieved stationarity (as plotted

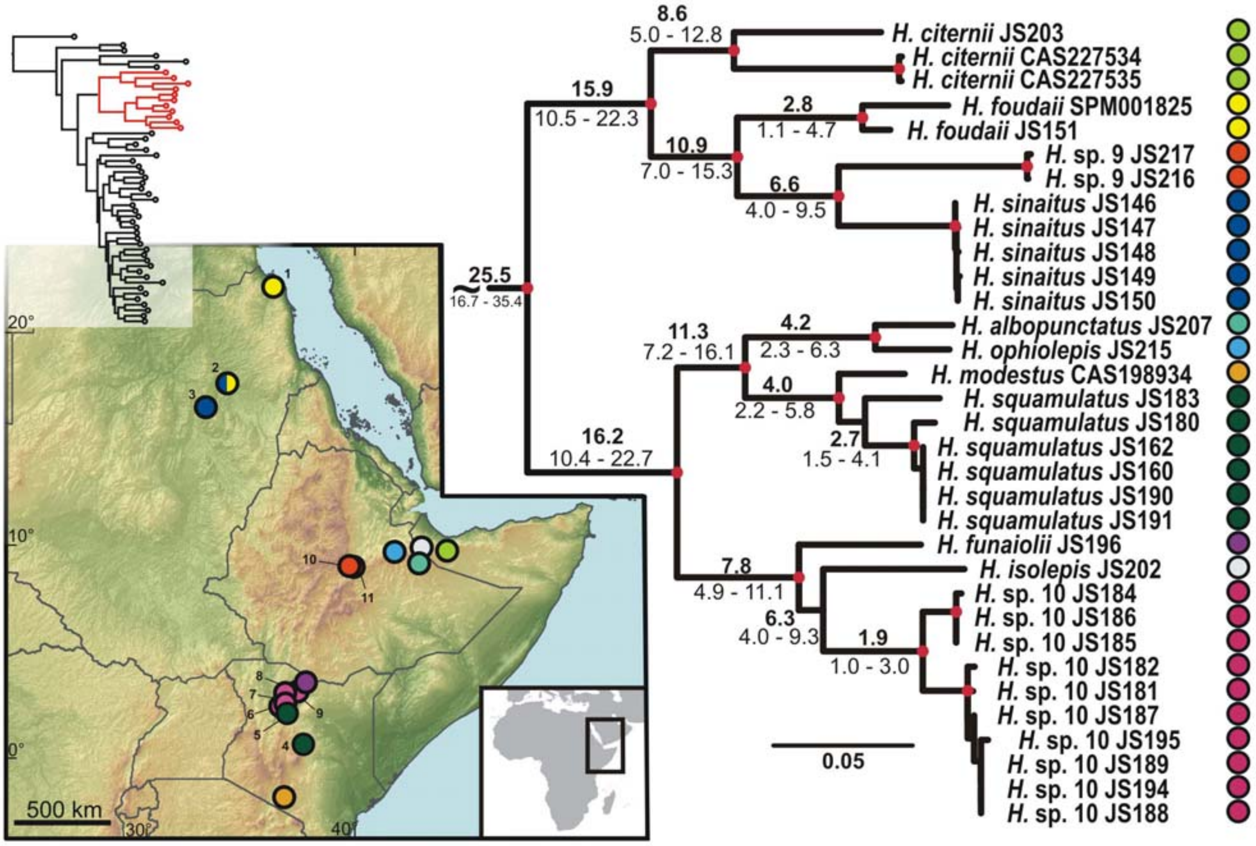

Figure 2. Detail of the phylogenetic tree of the Arid clade *Hemidactylus*: African subclade. Red dots in the nodes indicate ML bootstrap values ≥70 and BI pp≥0.95. Numbers after species names refer to sample codes; numbers on the right correspond with the localities numbers in the map. Ages of the nodes estimated with BEAST dating analysis are indicated by the nodes, mean above in bold, 95% HPD interval in plain below.
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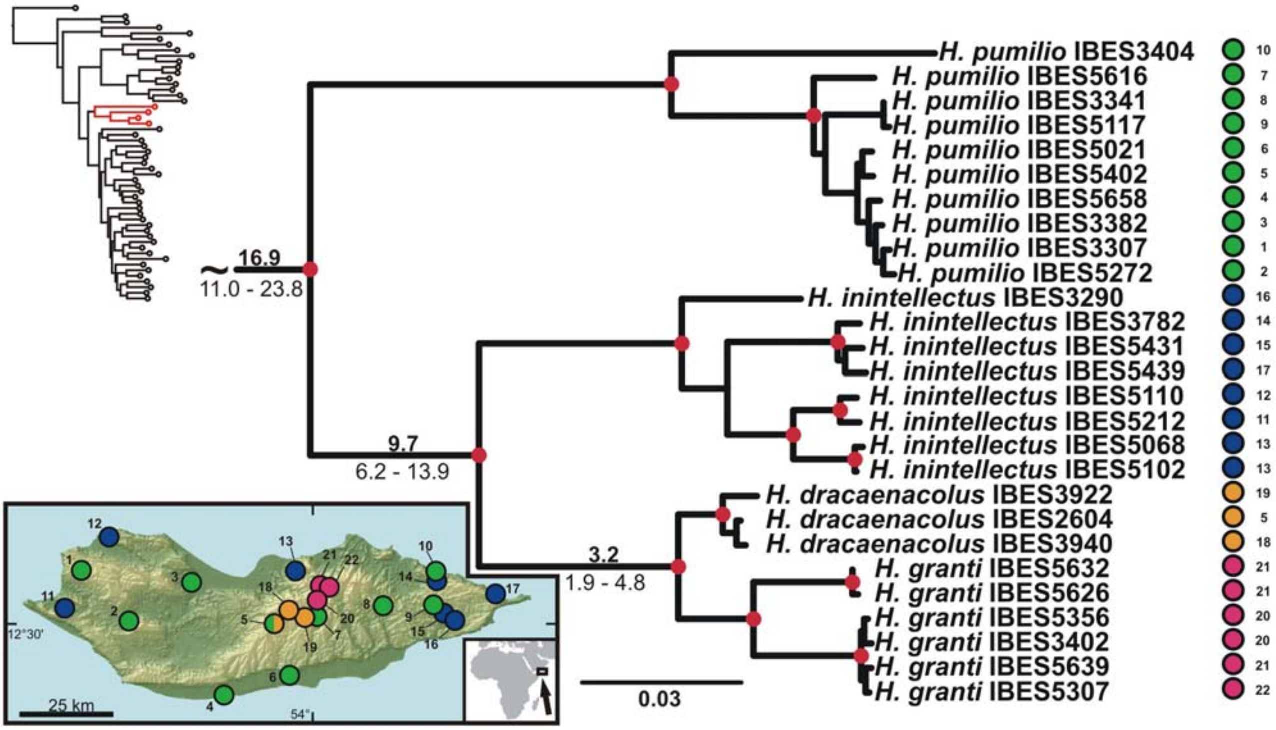

Figure 3. Detail of the phylogenetic tree of the Arid clade *Hemidactylus*: Socotran subclade. Red dots in the nodes indicate ML bootstrap values ≥70 and BI pp≥0.95. Numbers after species names refer to sample codes; numbers on the right correspond with the localities numbers in the map. Ages of the nodes estimated with BEAST dating analysis are indicated by the nodes, mean above in bold, 95% HPD interval in plain below.
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against generations), the first 20% of obtained trees were discarded as a burn-in and a 50% majority rule consensus tree was produced from the posterior distribution of the trees and posterior probabilities calculated as the percentage of a sampled tree recovering any particular clade [48]. Nodes that received ML bootstrap support values ≥70% and posterior probability (pp) values ≥0.95 were considered strongly supported [48,49]. To filter out the potentially strong bias of mtDNA on the resulting phylogeny, another dataset containing nuclear genes (unphased) only was assembled and used for the same phylogenetic analyses (ML, BI) with the same settings as described above and the results were compared with that of mtDNA+nDNA analyses.

Molecular Dating Analysis

As already highlighted [7], the lack of internal calibration points in *Hemidactylus* precludes the direct estimation of the time of the cladogenetic events in our phylogeny. Therefore, the mean substitution rate of the same *cytb* and *12S* mitochondrial regions calculated for other lizard groups [7] was used for this purpose. Specifically, we set a normal distribution prior for the ucld.mean parameter of the *12S* and *cytb* partitions based on the combined meanRate posteriors (mean ± standard error) (0.00755±0.00247 for *12S* and 0.0228±0.00806 for *cytb*). The dataset for molecular dating analysis comprised sequences from all eight partitions (see Tab. 1; all nuclear genes unphased) from which the substitution rates of the *12S* and *cytb* partitions were used to estimate dates of the cladogenetic events. The analysis was performed in BEAST v. 1.6.1 [50]. As is customary for such analyses, we used a phylogeny pruned arbitrarily to include one representative from each of the major lineages uncovered with the concatenated analysis (58 specimens in total; see Tab. S1). This method excludes closely related terminal taxa because the Yule tree prior does not include a model of coalescence, which can complicate rate estimation for closely related sequences [51]. A likelihood-ratio test implemented in MEGA 5 [52] was used to test if the different partitions included in the dating analysis were evolving clock-like (see Tab. 1). This information was used to choose between the strict-clock and the relaxed uncorrelated lognormal clock priors implemented in BEAST [53]. Analyses were run four times for $5x10^7$ generations with a sampling frequency of 10 000. Models and prior specifications applied were as follows (otherwise by default): GTR+I+G, strict clock (*mc1r*, *cmos*); GTR+G, strict clock (*rag1*, *cytb*); GTR+I+G, relaxed uncorrelated lognormal clock (*nd4*, *12S*), GTR+G, relaxed uncorrelated lognormal clock (*tRNAs*); TrN+I+G, relaxed uncorrelated lognormal clock (*rag2*); Yule process of speciation; random starting tree; alpha Uniform (0, 10); yule.birthRate (0, 1000); ucld.mean of *12S* Normal (initial value: 0.00755, mean: 0.00755, Stdev: 0.00247); ucld.mean of *cytb* Normal (initial value: 0.0228, mean: 0.0228, Stdev: 0.00806).

Biogeographic Analysis

To reconstruct the biogeographic history of the Arid clade *Hemidactylus* species included in our phylogenetic analyses we used S-DIVA 1.9b [54], a statistical extension of the dispersal-vicariance analysis DIVA [55]. S-DIVA employs all sampled trees, not only the final consensus phylogeny, to reconstruct ancestral states and weights the ancestral distribution reconstruction at each node by the frequency of the given node. The same dataset used for the molecular dating analysis, containing 58 specimens, was employed for the biogeographic analysis. A BI analysis with the same settings as was used to infer the BI tree of the complete dataset was run (see above). The resulting 10 000

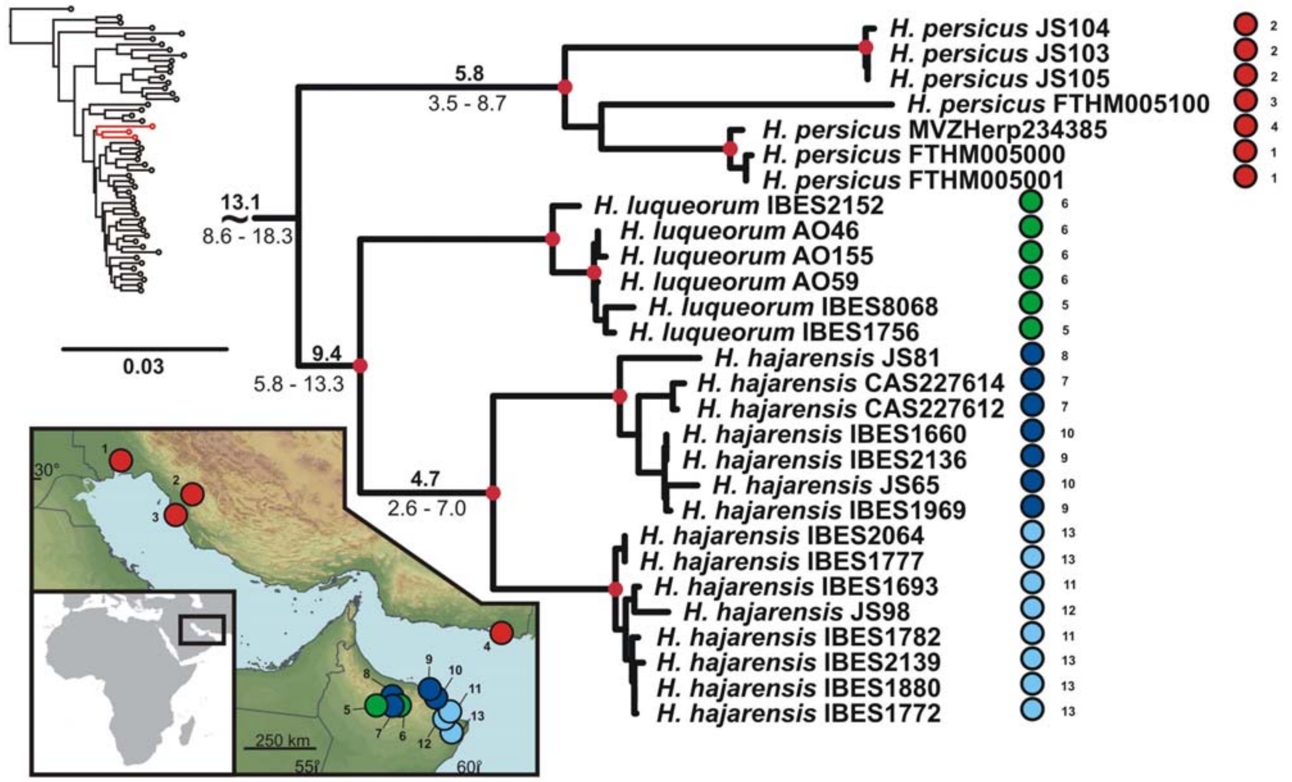

Figure 4. Detail of the phylogenetic tree of the Arid clade *Hemidactylus*: The Persian Gulf. Red dots in the nodes indicate ML bootstrap values ≥70 and BI pp≥0.95. Numbers after species names refer to sample codes; numbers on the right correspond with the localities numbers in the map. Ages of the nodes estimated with BEAST dating analysis are indicated by the nodes, mean above in bold, 95% HPD interval in plain below.
doi:10.1371/journal.pone.0064018.g004

trees were imported into S-DIVA and the burn-in was performed therein. Species were assigned to five separated and well-defined geographic areas (Fig. 1): 1) Horn of Africa, including parts of NE Sudan; 2) South Arabia, consisting of Yemen, Oman, and United Arab Emirates; 3) Socotra Archipelago; 4) Levant and Sinai; and 5) Iran. In the widely distributed *H. robustus*, multiple geographic areas were defined according to the origin of our samples. The outgroup species were not evaluated in this analysis. The maximum number of unit areas allowed in the ancestral distribution ("Max areas") was constrained to 4 and the "Allow reconstruction" option was activated. All other settings were left by default.

Results

The results of the phylogenetic analyses of the complete *Hemidactylus* dataset using ML and BI methods had the same topology at higher nodes and differed only slightly at the intraspecific level (Figs. S2, S3). As a result of that, only the ML tree with the bootstrap and pp support for both methods is presented with species clades drawn as collapsed (Fig. 1). All relevant information for the main groups of the Arid clade are depicted in details in Figs. 2, 3, 4, 5, 6, 7, 8, 9. Exactly the same subclades and species were also recovered from the analyses of the nDNA dataset only (Fig. S4). Variation in nuclear genes is an important indicator of species separation and an evidence of complete lineage sorting, suggesting existence of isolated species. The result of the estimates of the divergence dates has been incorporated in Figs. 2, 3, 4, 5, 6, 7, 8, 9 and the original result of the BEAST analysis is provided in Fig. S5.

Hemidactylus ruspolii and *H. angulatus* form a clade corresponding to the *H. angulatus* clade [6]. *Hemidactylus mabouia* and *H. platycephalus* cluster together as part of the African-Atlantic clade [6,19,23] together with *H. smithi*, incorporated into a phylogeny for the first time here, and thus confirmed to be a part of this clade. According to our analyses, all other *Hemidactylus* taxa, 29 Arabian species and 15 species from Northeast Africa analyzed in the present study, form a well supported monophyletic group (ML bootstrap = 100/Bayesian pp = 1) - the Arid clade. According to the phylogenetic hypotheses presented in Figs. 1, 2, 3, 4, 5, 6, 7, 8, 9, the Arid clade is formed by three phylogenetically and biogeographically clearly separated subclades. Basal dichotomy in the Arid clade separated 29.1 Ma (95% highest posterior density interval [HPD] 19.2–40.3; Figs 2, S5) a monophyletic group (100/1) of eleven strictly African species (*H. albopunctatus*, *H. citernii*, *H. foudaii*, *H. funaiolii*, *H. isolepis*, *H. modestus*, *H. ophiolepis*, *H. sinaitus*, *H. squamulatus*, *H.* sp. 9, *H.* sp. 10) from the rest. The second clade (99/1) that branches off consists of four Socotran species (*H. pumilio, H. inintellectus, H. dracaenacolus, H. granti*), which separated 20 Ma (HPD 13.3–27.9) and is sister to all the other, mostly mainland Arabian, species (Figs. 3, S5). Mutual relationships of subclades within the mainly Arabian radiation were not resolved with certainty in any of the analyses performed. Species in this Arabian radiation form four well supported individual clades which started to radiate 15 Ma (HPD 9.9–20.8) and formed: 1) a lineage of *H. persicus* samples from Iran; 2), a clade (100/1) consisting of *H. luqueorum* and *H. hajarensis*, which separated 13.1 Ma (HPD 8.6–18.3) from *H. persicus*, although the sister relationship between *H. persicus* and the latter two species does

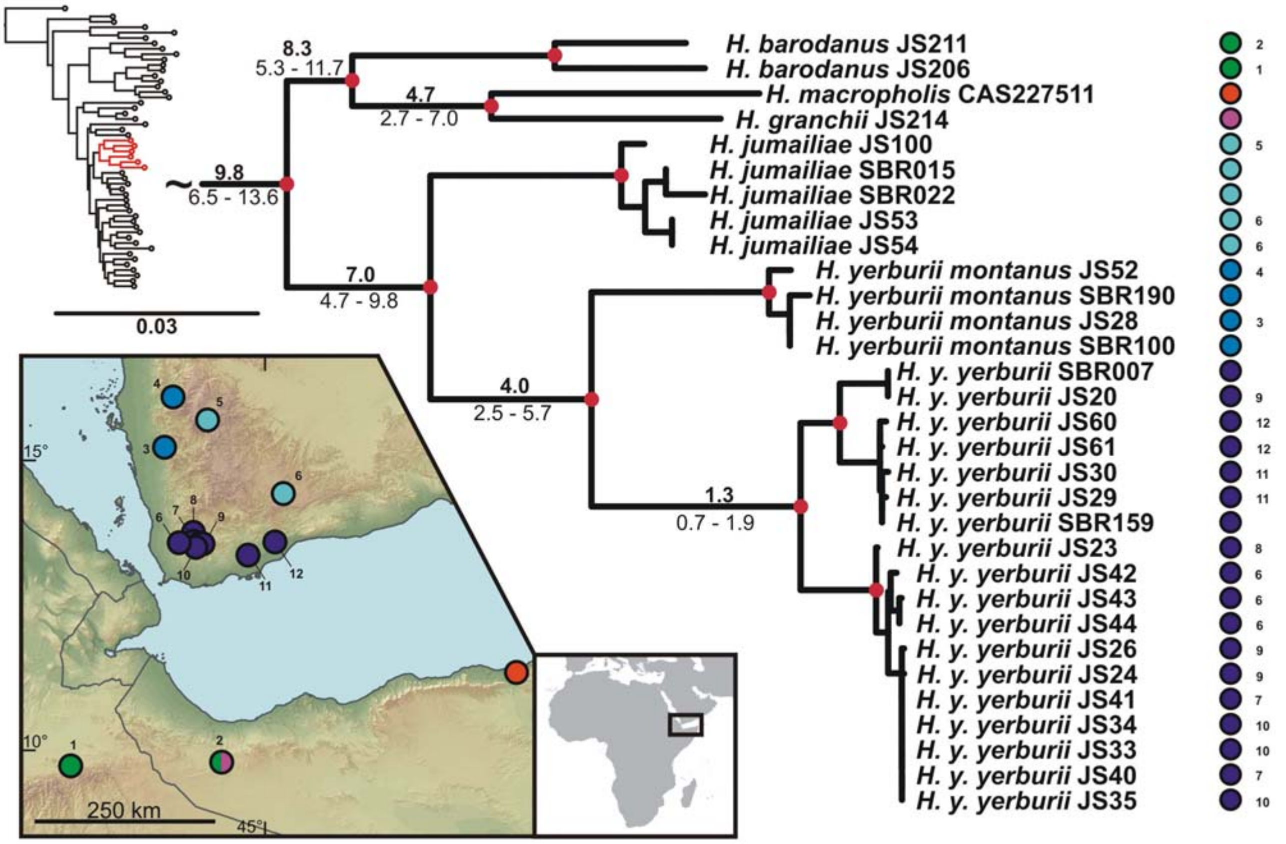

Figure 5. Detail of the phylogenetic tree of the Arid clade *Hemidactylus*: The Gulf of Aden. Red dots in the nodes indicate ML bootstrap values ≥70 and BI pp≥0.95. Numbers after species names refer to sample codes; numbers on the right correspond with the localities numbers in the map. Ages of the nodes estimated with BEAST dating analysis are indicated by the nodes, mean above in bold, 95% HPD interval in plain below.
doi:10.1371/journal.pone.0064018.g005

not have convincing support (38/0.87) (Fig. 4); 3) a clade (94/1) containing three African (*H. barodanus*, *H. granchii*, *H. macropholis*), four South Arabian (*H. jumailiae*, *H. lemurinus*, *H. y. yerburii*, *H. yerburii montanus*) and four Levantine (*H. dawudazraqi*, *H. lavadeserticus*, *H. mindiae*, *H. turcicus*) taxa, which diverged 11.3 Ma (HPD 7.5–15.6) (Figs. 5, 6, S5); and 4) a clade (99/1) that radiated 11.9 Ma (HPD 8–16.6, Fig. S5) containing eleven South Arabian species (*H. alkiyumii*, *H. festivus*, *H. homoeolepis*, *H. inexpectatus*, *H. masirahensis*, *H. paucituberculatus*, *H. shihraensis*, *H. saba*, *H.* sp. 4, *H.* sp. 5, *H.* sp. 6; species numbers 1–8 correspond to those in [23]), three Socotran species (*H. forbesii*, *H. homoeolepis*, *H. oxyrhinus*), the widespread *H. robustus* and two yet undescribed species, one from the Sinai (*H.* sp. 1) and another one from central Ethiopia (*H.* sp. 11) (Figs. 7, 8, 9).

In the reconstruction of the ancestral geographic distribution, the importance of changing the max areas in S-DIVA was explored (down to two, data not shown). We also tried to split the geographic origin assignments into more units (up to nine, data not shown) in order to obtain more detailed resolution. However, neither decreasing the number of max areas nor increasing the number of geographic units altered significantly the probabilities of ancestral ranges or changed the patterns of historical distribution of the ancestors. Therefore, the number of max areas was set to 4 and the area of interest was divided into the five regions described above (see Methods). The maximal S-DIVA value determining support for ancestral range reconstruction was 5309.02. The final results of the S-DIVA analysis are incorporated in the tree from Fig. 1.

Discussion

The results of our analyses confirm the monophyly of the Arid clade of *Hemidactylus* as previously suggested [6]. Originally this clade consisted of only 13 species from Arabia, Socotra, East Africa and the Mediterranean. Additional 24 taxa were added to this clade in later studies [7,19–21,23,26]. With the new species revealed in previous [19,23] and this study, the Arid clade of *Hemidactylus* accounts for 35.4% out of a total of 130 recognized *Hemidactylus* species. Taking into account 16 species and subspecies from East Africa, some of which are likely to be a part of the Arid clade but are still pending to be included in any phylogenetic analysis (*H. arnoldi*, *H. barbierii*, *H. bavazzanoi*, *H. curlei*, *H. fragilis*, *H. jubensis*, *H. klauberi*, *H. laevis*, *H. laticaudatus*, *H. megalops*, *H. ophiolepoides*, *H. puccionii*, *H. somalicus*, *H. taylori*, *H. tropidolepis*, *H. yerburii pauciporosus*) and that there are some regions in Arabia like Saudi Arabia, which are still largely unexplored, we can conclude that the Arid clade can be regarded as the most speciose of all *Hemidactylus* clades [6].

African – Arabian Vicariance and African Radiation

The basal dichotomy within the Arid clade separates a monophyletic group of eleven species (see Fig. 1) of strictly African origin. Because all the members of this African subclade

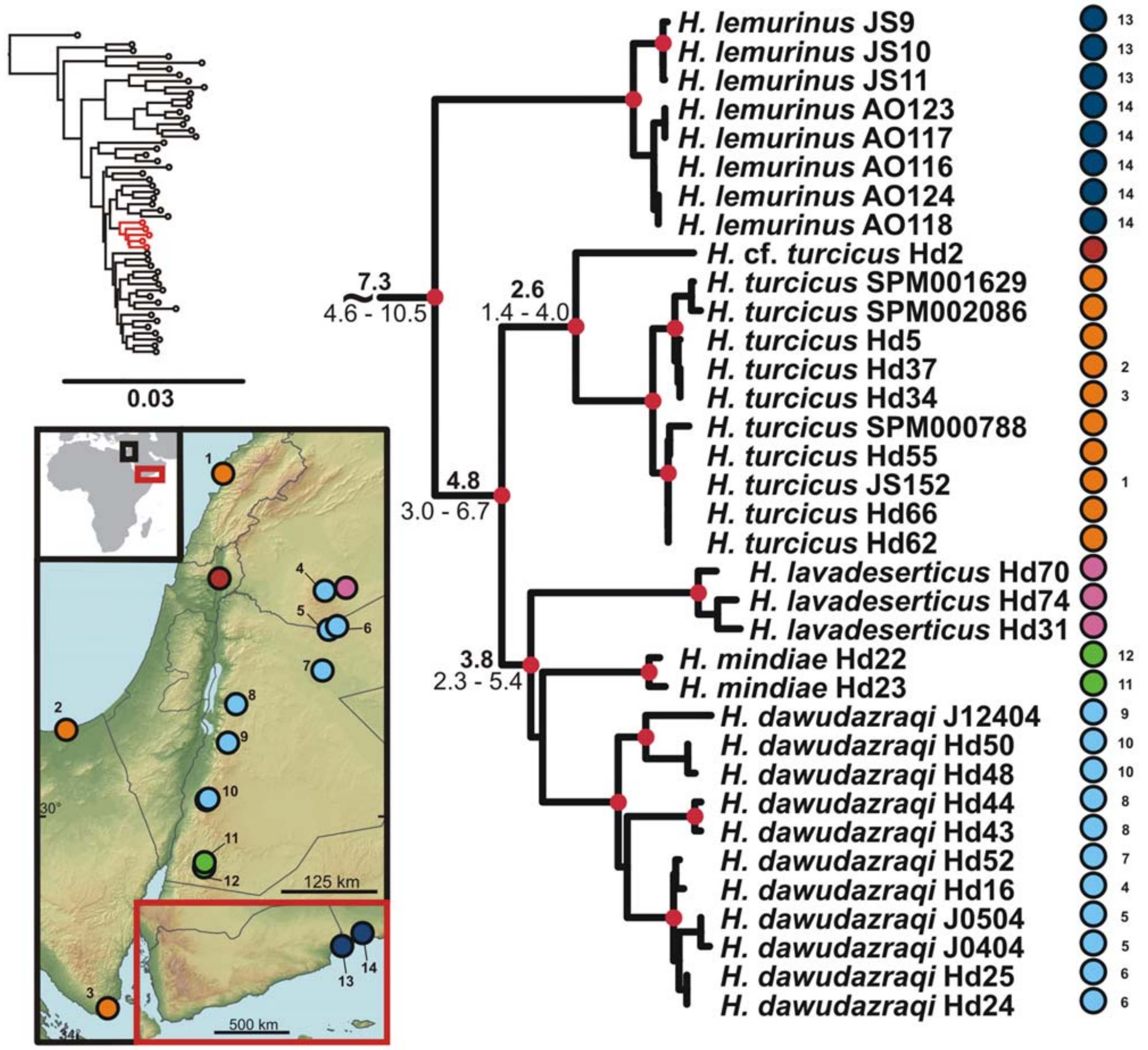

Figure 6. Detail of the phylogenetic tree of the Arid clade *Hemidactylus*: The Levant. Red dots in the nodes indicate ML bootstrap values ≥70 and BI pp≥0.95. Numbers after species names refer to sample codes; numbers on the right correspond with the localities numbers in the map. Ages of the nodes estimated with BEAST dating analysis are indicated by the nodes, mean above in bold, 95% HPD interval in plain below.
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inhabit Northeast Africa, their ancestor was presumably of the same origin (Fig. 2). Apart from the nine known species forming this subclade there are other two clearly separated lineages that, according to preliminary morphological analyses, deserve species status (work in progress). These two lineages are provisionally named *H.* sp. 9 (*Hemidactylus* sp. from central Ethiopia) and *H.* sp. 10 (*Hemidactylus* sp. from northern Kenya). According to the age estimates, this basal split took place 29.1 Ma (HPD 19.2–40.3 Ma, Figs. 2, S5). This date matches very well the geological estimates of the break-up of the Afro-Arabian continent and the consequent formation of the Red Sea and the Gulf of Aden [28,29] and is supported by the same vicariant split from other studies [35,36]. Therefore, the break-up of the African and Arabian tectonic plates seems to be responsible for the vicariant separation of the ancestors of these endemic African species from the rest of the Arid clade. The African subclade is formed by two well-supported and morphologically differentiated lineages: 1) species with distinctly enlarged dorsal tubercles and with bristly appearance (*H. citernii*, *H. foudaii*, *H. sinaitus*, *H.* sp. 9) and 2) smooth-looking species without conical dorsal tubercles (*H. albopunctatus*, *H. funaiolii*, *H. isolepis*, *H. modestus*, *H. ophiolepis*, *H. squamulatus*, *H.* sp. 10). These two groups are distributed NW and SE of the Great Rift Valley (see Fig. 2), respectively with a minor overlap in the Ahmar Mountains in Ethiopia and Somalia and separated from each other 25.5 Ma (HPD 16.7–35.4). Of all taxa belonging to the African subclade, *H. sinaitus* from Sudan is particularly interesting from a taxonomic point of view. Until now, the only individuals of "*H. sinaitus*" that have been sequenced are from Yemen [20,21; unpublished sequences provided by U. Joger]. The type locality of *H. sinaitus* was reassessed from the original Mount Sinai to the

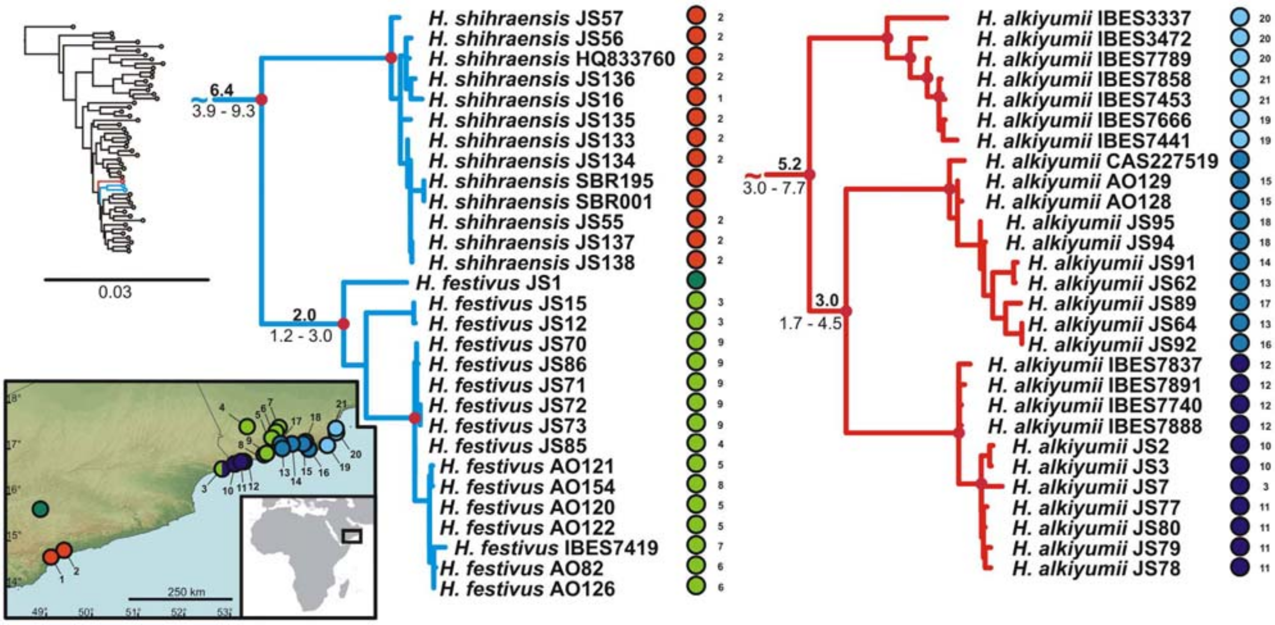

Figure 7. Detail of the phylogenetic tree of the Arid clade *Hemidactylus*: Hadhramaut and Dhofar. Red dots in the nodes indicate ML bootstrap values ≥70 and BI pp≥0.95. Numbers after species names refer to sample codes; numbers on the right correspond with the localities numbers in the map. Ages of the nodes estimated with BEAST dating analysis are indicated by the nodes, mean above in bold, 95% HPD interval in plain below.
doi:10.1371/journal.pone.0064018.g007

Sudanese shores of the Red Sea in the region of Suakin and Durrur [N of Suakin] [56,57]. According to the phylogeny presented in Fig. 1, and after morphological examination of the specimens of "*H. sinaitus*" from Yemen included elsewhere [20,21] (data not shown), we conclude that the name *Hemidactylus sinaitus* applies to the populations from NE Africa only, and that the "*H. sinaitus*" from Yemen represents a new species (provisionally referred here as *Hemidactylus* sp. 6). To reveal more details about this African *Hemidactylus* subclade and to have a better idea of their biogeography, systematics and evolution, a much larger sampling, including more species from these difficult to access regions, will be essential (Tab. S3; work in progress).

Arabian – Socotran Vicariance

After the separation of the African subclade, a subsequent split within the Arid clade of *Hemidactylus* segregated the ancestor of a group of four Socotran species (*H. dracaenacolus*, *H. granti*, *H. inintellectus*, and *H. pumilio*; Figs. 1, 3, S5). Our inferred dates suggest that this Socotran subclade split approximately 16.9 Ma (HPD 11.0–23.8). As already suggested [26], this split most probably represents another vicariant event in the history of the genus *Hemidactylus*, produced by the initial continental break-up about 24 Ma and subsequent oceanic spreading occurring 17.5 Ma in the eastern part of the Gulf of Aden, which triggered the drifting of the Socotra Archipelago from the Arabian mainland [29]. These dates fit the HPD estimate of the segregation of this subclade. As shown in Fig. 3, the level of intraspecific variation of these Socotran species is very high. According to the results of the BPP (Bayesian Phylogenetics and Phylogeography [58]) species delimitation method applied by Gómez-Díaz et al. [26], the four endemic Socotran species in fact consist of 13 putative species, and suggest that the diversity of *Hemidactylus* on the relatively small island of Socotra is very high and has probably been favoured by ecological diversification and morphological separation of evolutionary independent lineages [26,59,60].

All the remaining species after the separation of the African and Socotran subclades form a well supported monophyletic group of mostly Arabian species. Eighteen out of 31 species within this subclade are distributed in South Arabia, four in Africa, five in the Levant and Sinai, three in the Socotra Archipelago, one in Iran, and one is widespread in coastal areas of all these regions (Tab. S3). The results of our phylogenetic and biogeographic analyses, together with the divergence time estimates, indicate that multiple independent dispersal events from Arabia have taken place in the history of *Hemidactylus* alongside the vicariant events described above.

Dispersal to Iran

The oldest reported dispersal from Arabia occurred 13.1 Ma (HPD 8.6–18.3; Figs. 4, S5) when the ancestor of *H. persicus* colonized Iran. Since the closest relatives of *H. persicus* are found in northern Oman, the dispersal occurred most probably via the *Gomphotherium* land bridge [61] connecting the Arabian and Anatolian plates 18 Ma. After a temporary period of disconnection the bridge was continuously present since the mid-Miocene about 15 Ma ago and allowed faunal exchanges between Eurasia and Afro-Arabia [35,36,61,62]. Alternatively, the colonization of Iran could take place across the Proto-Arabian Gulf after the *Gomphotherium* bridge disappeared. A recent colonization of Iran by *H. persicus* can be ruled out alone by the deep level of intraspecific differentiation within the Iranian populations, indicating its long presence in the area (Fig. 4). Animals morphologically assignable to this species also occur in NE Saudi Arabia, Iraq, Kuwait and Bahrain [3], however, samples from none of these countries were available for this study. Until some specimens of *H. persicus* from NE Arabia and also of another Iranian species, *H. romeshkanicus*, which resembles morphologically other *Hemi-*

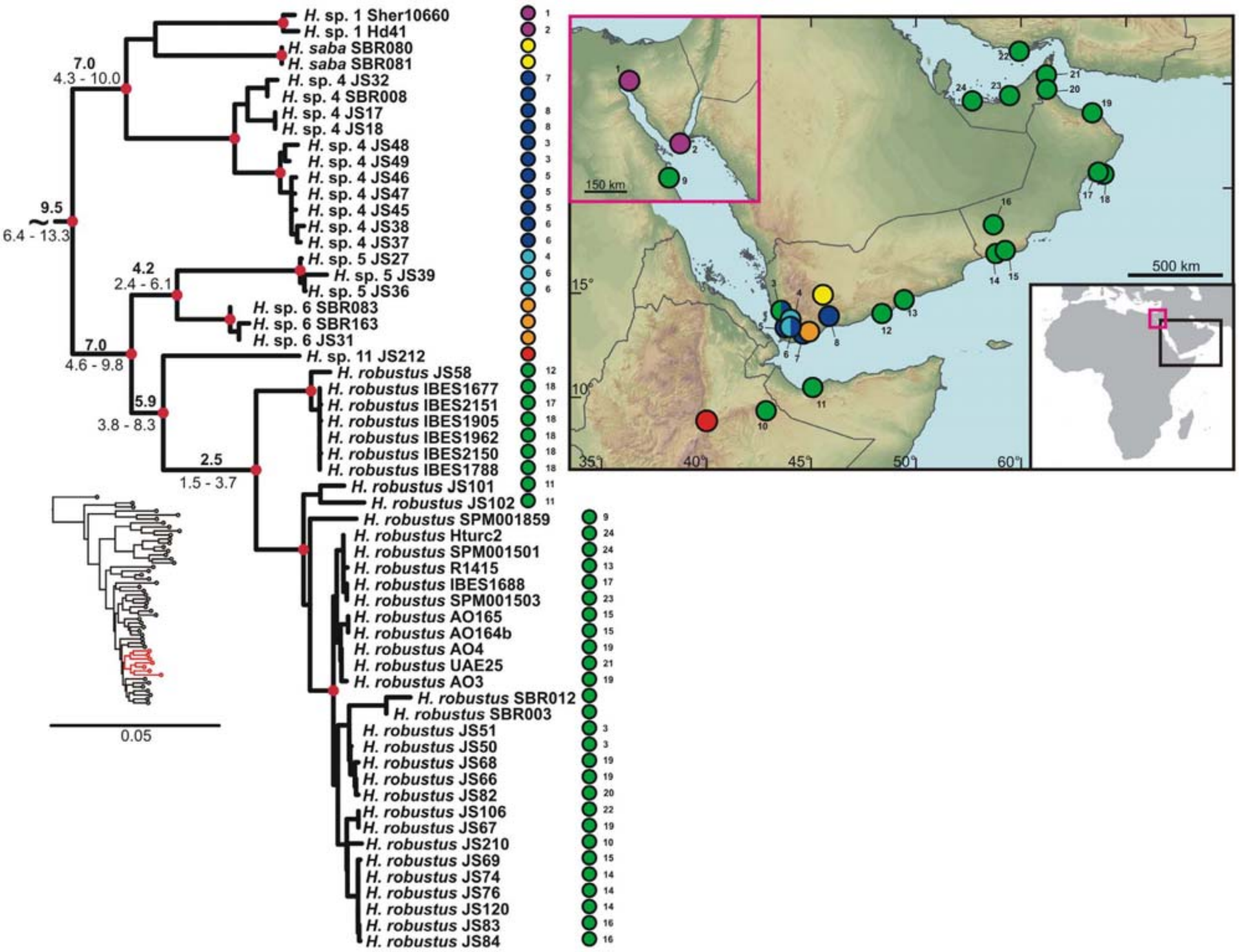

Figure 8. Detail of the phylogenetic tree of the Arid clade *Hemidactylus*: *H. robustus* and related species. Red dots in the nodes indicate ML bootstrap values ≥70 and BI pp≥0.95. Numbers after species names refer to sample codes; numbers on the right correspond with the localities numbers in the map. Ages of the nodes estimated with BEAST dating analysis are indicated by the nodes, mean above in bold, 95% HPD interval in plain below.
doi:10.1371/journal.pone.0064018.g008

dactylus representatives from the Arid clade [63], are analyzed and included in the biogeographic context of the Persian Gulf surroundings, a closer insight into the zoogeographic history of *H. persicus* remains unclear.

Dispersals to Africa

According to our findings, apart from the African subclade, a remnant from the vicariant split between Africa and Arabia (Fig. 2), Africa has been colonized at least twice independently from Arabia in the history of the *Hemidactylus* Arid clade (Fig. 1). One dispersal event, a jump with subsequent radiation in Africa, occurred 9.8 Ma (HPD 6.5–13.6; Figs. 1, 5, S5). At that time, Africa and Arabia were temporarily connected by a land bridge of halite deposits [29]. Therefore, the ancestor of the three species (*H. barodanus*, *H. granchii*, *H. macropholis*) representing the African branch may have used this bridge for crossing to Africa. Their sister group is restricted to the mountain areas and their foothills in SW Yemen (Fig. 5) which have undergone a continuous uplift since the Late Miocene up to the Holocene [27], producing an important vertical structuring of the region and probably triggering speciation in this relatively small area.

The younger from the two detected dispersals from Arabia to Africa has a divergence time estimate of 5.9 Ma (HPD 1.5–8.3; Figs. 1, 8, S5). HPD interval indicates that this dispersal event could be facilitated by the presence of a land bridge or, after re-opening of the Bab-el-Mandeb strait and final separation of Africa from Southwest Arabia 5.3 Ma [29], happed as an over-water transfer. As in the first dispersal to Africa, the closest relatives of the colonizer (*Hemidactylus* sp. 11) inhabit south-western Yemen. Apparently, the Red Sea after its opening in the mid-Oligocene to the Early Miocene (31–23 Ma) did not form an insurmountable barrier and enabled faunal exchanges, that may have been facilitated by the temporary land bridge connection (10–5.3 Ma), from one side to the other [32,34,35,64].

It is worth noting that the successful transcontinental colonizations of *Hemidactylus* between Africa and Arabia took place only in one direction, from Arabia to Africa. Despite there is evidence that the opposite direction of the same route has been used multiple times after the Red Sea opening [32,34,35,64] and that the African subclade also experienced an important radiation (see above), none of its members was able to penetrate to Arabia. The genus *Hemidactylus* thus represents a unique example of animals

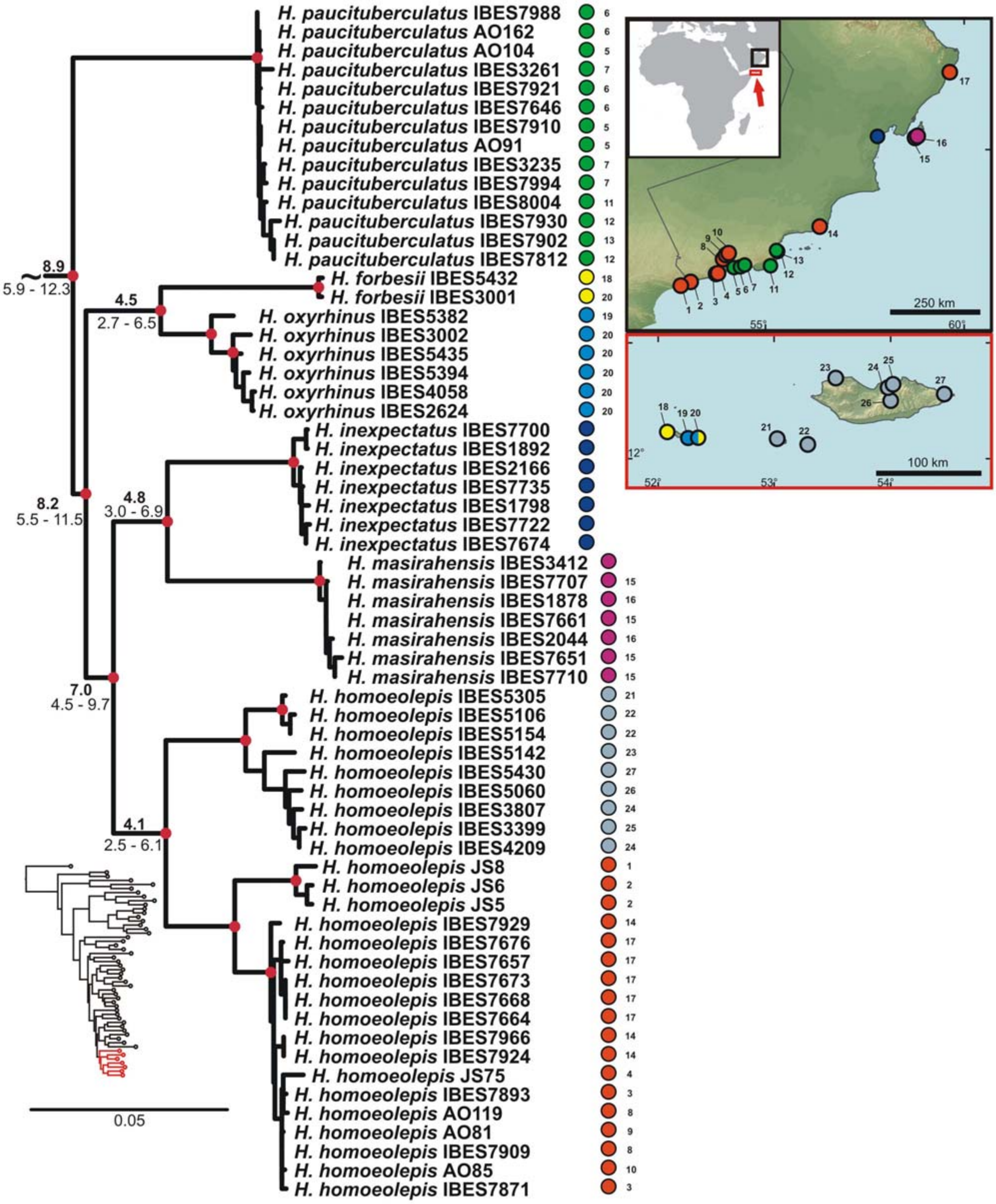

Figure 9. Detail of the phylogenetic tree of the Arid clade *Hemidactylus*: Oman and Socotra Archipelago. Red dots in the nodes indicate ML bootstrap values ≥70 and BI pp≥0.95. Numbers after species names refer to sample codes; numbers on the right correspond with the localities numbers in the map. Ages of the nodes estimated with BEAST dating analysis are indicated by the nodes, mean above in bold, 95% HPD interval in plain below.

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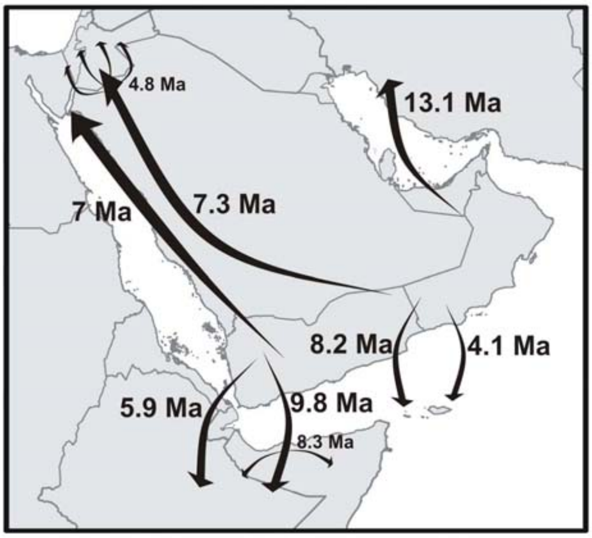

Figure 10. Summary of historical dispersal events of *Hemidactylus* geckos from Arabia. Dates by arrows indicate mean time estimates of the events. *In situ* radiation of some lineages following their dispersal is indicated as a radiation of arrows.
doi:10.1371/journal.pone.0064018.g010

with the main direction of dispersals from Arabia towards Africa, unlike in most other reported cases where the direction was the opposite [32–36,64].

Dispersals to the Socotra Archipelago

Identically to the African pattern, the Socotra Archipelago experienced one vicariant event followed by two colonizations [26]. After its separation from the Arabian landmass with ancestors of the four species described above carried on, the islands were colonized by two subsequent independent overseas dispersals. First, the ancestor of *H. forbesii* and *H. oxyrhinus* colonized the Abd al Kuri Island (the westernmost islands of the Socotra Archipelago), approximately 8.2 Ma (HPD 5.5–11.5; Figs. 1, 9, S5). This colonization was followed by an *in situ* intraisland speciation 4.5 Ma (HPD 2.7–6.5) [26].

An additional colonization event took place 4.1 Ma (HPD 2.5–6.1; Figs. 9, S5), when the ancestor of *H. homoeolepis* dispersed from South Arabia to Socotra, Darsa and Samha Islands [26]. High genetic differences between Socotran and mainland populations of *H. homoeolepis*, together with a high level of morphological differentiation of some populations of mainland Arabia suggest that *H. homoeolepis* includes in fact several undescribed species (work in progress).

Dispersals to the Levant and Sinai

In accordance with the pattern of two dispersals to each Africa and Socotra, there have been two independent dispersal events from South Arabia to the Levant and Sinai occurring approximately at the same time, ca 7 Ma. In one case, the ancestor of four Levantine species (*H. dawudazraqi*, *H. lavadeserticus*, *H. mindiae*, *H. turcicus*) dispersed from South Arabia. The cluster of these four species is sister to the geographically distant *H. lemurinus* from South Arabia. The isolation from *H. lemurinus* dates back to 7.3 Ma (HPD 4.6–10.5) and subsequent radiation in the Levant took place 4.8 Ma (HPD 3.0–6.7; Figs. 1, 6, S5). All these four species are endemic to the Levant and Sinai except *H. turcicus*, which, most probably, has spread across most Mediterranean coastal areas by human-mediated dispersal [6,23]. Close phylogenetic relationship of south Arabian *H. lemurinus* with the Levantine taxa is even more enigmatic when morphology and ecology is taken into account. Whereas all the Levantine taxa possess distinct dorsal tubercles and are rock or ground dwelling [23], *H. lemurinus* is entirely smooth without any enlarged scales on the dorsum and restricted to large pale water-smoothed boulders [65,66]. It seems to occupy the same ecological niche as sympatric *Ptyodactylus* to which it superficially resembles. For better understanding of the polarization and speed of morphological evolution within this subclade, more detailed research on the pace of phenotypic changes and evolution of habitat use is required.

Hemidactylus sp. 1, the second colonizer of the north Arabia, diverged from its sister species 7.0 Ma (HPD 4.3–10.0) and subsequently colonized Sinai. Its sister species, *H. saba*, and *H.* sp. 4, are distributed in the mountains of western Yemen [23] (Fig. 8). Whether its occurrence in coastal Sinai is caused artificially by human-mediated (probably ship) transport or if its range stretches along the Hijaz and Asir Mountains in Saudi Arabia, an important colonization route [39,67,68], remains unknown and requires additional sampling from the eastern Red Sea coast.

Human-mediated Dispersal of *H. robustus*

Although there is a certain genetic structure within *H. robustus* with a deep historical pre-Pleistocene origin of radiation (2.5 Ma; HPD 1.5–3.7; Fig. 8), it is not reflected in the geographical structuring of its populations. *Hemidactylus robustus* has been distributed all over the area of our study recently, most probably by human-mediated dispersal [7,57,69] similarly to *H. flaviviridis* (this study, data not shown) and *Chalcides ocellatus* [70,71]. Even though some geographical pattern of *H. robustus* populations might have evolved historically, it was probably blurred by the recent dispersal of individual lineages. It is interesting to notice that, even though we hypothesize that such mixture of populations has been a recurrent phenomenon in recent times, the original genetic pattern has not disappeared entirely yet.

Concluding Remarks

As is obvious from the presented phylogeny, divergence time estimates and historical biogeographic reconstructions, evolutionary history of the genus *Hemidactylus* in Arabia and its surroundings has a complex pattern of several vicariant events connected to major continental break-ups in the geological history of the region followed by multiple subsequent dispersal events from Arabia to other surrounding regions (Fig. 10). It thus forms a unique laboratory of evolutionary and biogeographic processes where the geological history of the area has played a crucial role in forming the phylogenetic pattern of *Hemidactylus* found today and contributed significantly to local diversity of the genus. Discovered cryptic diversity of *Hemidactylus* in the mountains of Yemen and Ethiopia emphasizes the importance of these highland areas as a part of the Eastern Afromontane biodiversity hotspot [72,73]. Comparing overall reptile species richness in South Arabia and the Horn of Africa with how little is known about it we can assume that future studies may reveal more cryptic species (see also [74]) in various reptile groups with unforeseen phylogenetic and biogeographic relationships.

Supporting Information

Figure S1 Physical map of the region of the study with geographic names of important features and countries that appear in the text. Country names are in italics.
(TIF)

Figure S2 Original ML phylogenetic tree with all individuals analyzed. ML bootstrap support values ≥70 shown.
(TIF)

Figure S3 Original BI phylogenetic tree with all individuals analyzed. BI posterior probabilities ≥0.95 shown.
(TIF)

Figure S4 ML tree as a result of an analysis of four nDNA genes. ML bootstrap support/BI pp drawn by the nodes. Only bootstrap values ≥70 (ML) and BI pp≥0.95 shown.
(TIF)

Figure S5 Chronogram showing the results from BEAST. Mean node estimates in bold, 95% HPD intervals in brackets and as the blue node bar.
(TIF)

Table S1 Complete list of material used for this study. Information on the specimens included in the phylogenetic analyses are listed in alphabetical order, with the corresponding GenBank accession numbers. Individuals with the specimen code highlighted with a hatch symbol (#) were included in the BEAST and S-DIVA analyses (see Methods).
(PDF)

Table S2 Molecular markers, primers, primer sequences, amplification conditions and original primer sources used in this study.
(PDF)

Table S3 List of all *Hemidactylus* species from Arabia, the Horn of Africa, the Levant and Iran. Black dots indicate known distribution records for each country, the rightmost column shows species included in this study.
(PDF)

Acknowledgments

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Author Contributions

Conceived and designed the experiments: JS SC LK VG JM. Performed the experiments: JS SC. Analyzed the data: JS SC. Wrote the paper: JS SC. Gathered data: JS SC LK VG AKN JM.

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Table S1. Complete list of material used for this study. Information on the specimens included in the phylogenetic analyses listed in alphabetical order, with the corresponding GenBank accession numbers. Individuals with the specimen code highlighted with a hatch symbol (#) were included in the BEAST and S-DIVA analyses (see Materials and methods).

SPECIES	CODE	VOUCHER	COUNTRY	LOCALITY	*12S*	*cytb*	*nd4 + tRNAs*	*cmos*	*mc1r*	*rag2*	*rag1*
H. albopunctatus	JS207#		Ethiopia	42 km SE of Jijiga	KC818657	KC818794	-	KC818745	KC818901	KC819017	KC818952
H. alkiyumii	S3337		Oman	Wadi Hasik	JQ957039	JQ957170	-	JQ957123	JQ957239	JQ957401	-
H. alkiyumii	S3472#		Oman	Wadi Hasik	JQ957040	JQ957171	JQ957310	JQ957123	JQ957240	JQ957403	-
H. alkiyumii	S7789		Oman	7.5 km S Hasik	JQ957043	JQ957175	JQ957315	JQ957123	JQ957240	JQ957404	-
H. alkiyumii	S7441	IBES7441	Oman	3.5 km NE Sadah	JQ957041	JQ957172	JQ957311	JQ957123	JQ957240	JQ957404	-
H. alkiyumii	S7666	IBES7666	Oman	3.5 km NE Sadah	JQ957041	JQ957172	JQ957313	JQ957123	JQ957242	JQ957401	-
H. alkiyumii	S7858	IBES7858	Oman	3 km NW of Hasik	JQ957040	JQ957177	JQ957317	JQ957123	JQ957245	JQ957404	-
H. alkiyumii	S7453	IBES7453	Oman	3 km NW of Hasik	JQ957040	JQ957173	JQ957312	JQ957123	JQ957241	JQ957405	-
H. alkiyumii	CAS227519	CAS227519	“Somalia”	“11 km SE of Bosasso” (wrong locality)	DQ120343	DQ120172	JQ957309	-	JQ957238	JQ957402	-
H. alkiyumii	AO129	BM2005.1662	Oman	Tawi Atair	JQ957038	JQ957169	-	JQ957122	JQ957237	JQ957401	-
H. alkiyumii	AO128	BM2005.1663	Oman	Tawi Atair	JQ957038	JQ957168	-	JQ957121	JQ957236	JQ957401	-
H. alkiyumii	S7837	IBES7837	Oman	Dalkut	JQ957044	JQ957176	JQ957316	JQ957123	JQ957244	JQ957401	-
H. alkiyumii	S7740	IBES7740	Oman	Dalkut	JQ957042	JQ957174	JQ957314	JQ957123	JQ957243	JQ957401	-
H. alkiyumii	S7888	IBES7888	Oman	Dalkut	JQ957042	JQ957178	JQ957318	JQ957123	JQ957246	JQ957401	-
H. alkiyumii	S7891	IBES7891	Oman	Dalkut	JQ957045	-	JQ957319	JQ957123	JQ957246	JQ957401	-
H. alkiyumii	JS2#	NMP6V 74799/1	Yemen	3 km E Hauf	JQ957090	KC818795	-	JQ957123	JQ957244	JQ957401	KC818953
H. alkiyumii	JS3	NMP6V 74799/9	Yemen	3 km E Hauf	JQ957091	KC818795	-	JQ957123	JQ957246	JQ957401	KC818954
H. alkiyumii	JS7	NMP6V 74800	Yemen	Damqawt	JQ957094	KC818796	-	-	-	-	-
H. alkiyumii	JS62#	NMP6V 74839/1	Oman	Salalah city	JQ957092	KC818802	-	KC818746	KC818902	JQ957401	KC818955
H. alkiyumii	JS64	NMP6V 74839/3	Oman	Salalah city	JQ957093	KC818803	-	-	-	-	-
H. alkiyumii	JS77	NMP6V 74838/1	Oman	2 km NW of Dalkut	JQ957090	KC818797	-	-	-	-	-
H. alkiyumii	JS78	NMP6V 74838/2	Oman	2 km NW of Dalkut	JQ957090	KC818798	-	-	-	-	-
H. alkiyumii	JS79	NMP6V 74838/3	Oman	2 km NW of Dalkut	JQ957090	KC818799	-	-	-	-	-
H. alkiyumii	JS80	NMP6V 74838/4	Oman	2 km NW of Dalkut	JQ957090	KC818800	-	-	-	-	-
H. alkiyumii	JS89	NMP6V 74840/3	Oman	8 km N. Salalah airport	JQ957092	KC818801	-	-	-	-	-
H. alkiyumii	JS91	NMP6V 74842/2	Oman	3 km E. Ain Hamran	JQ957092	KC818802	-	-	-	-	-
H. alkiyumii	JS92	NMP6V 74843	Oman	Mirbat	JQ957093	KC818803	-	-	-	-	-
H. alkiyumii	JS94	NMP6V 74844/1	Oman	Taiq Cave	JQ957092	KC818804	-	-	-	-	-
H. alkiyumii	JS95	NMP6V 74844/2	Oman	Taiq Cave	JQ957095	KC818805	-	-	-	-	-
H. angulatus	JS121	NMP6V 74847	Ethiopia	Agere Maryam	KC818658	KC818806	-	-	-	-	-
H. angulatus	JS122	NMP6V 74845/1	Ethiopia	Arba Minch	KC818659	KC818807	-	-	-	-	-
H. angulatus	JS123	NMP6V 74845/2	Ethiopia	Arba Minch	KC818659	KC818807	-	KC818747	KC818903	KC819018	KC818956
H. angulatus	JS124	NMP6V 74846	Ethiopia	Konso	KC818658	KC818808	-	-	-	-	-
H. angulatus	JS125	NMP6V 74848	Ethiopia	Yabello	KC818658	KC818809	-	-	-	-	-
H. angulatus	JS126	NMP6V 74852	Ethiopia	Jinka	KC818660	KC818810	-	-	-	-	-
H. angulatus	JS127	NMP6V 74853	Ethiopia	Arba Minch	KC818659	KC818811	-	-	-	-	-
H. angulatus	JS129	NMP6V 74851/2	Ethiopia	Hammar	KC818658	KC818812	-	-	-	-	-
H. angulatus	JS153	NMP6V 74814/1	Kenya	South Horr	KC818661	-	-	KC818748	KC818904	KC819019	-
H. angulatus	JS154	NMP6V 74814/2	Kenya	South Horr	KC818662	-	-	-	-	-	-
H. angulatus	JS155	NMP6V 74814/3	Kenya	South Horr	KC818662	-	-	-	-	-	-
H. angulatus	JS156	NMP6V 74814/4	Kenya	South Horr	KC818661	-	-	-	-	-	-
H. angulatus	JS157	NMP6V 74814/5	Kenya	South Horr	KC818663	-	-	-	-	-	-
H. angulatus	JS163	NMP6V 74813/1	Kenya	Nginyang	KC818664	-	-	-	-	-	-
H. angulatus	JS164	NMP6V 74813/2	Kenya	Nginyang	KC818665	-	-	-	-	-	-
H. angulatus	JS165	NMP6V 74813/3	Kenya	Nginyang	KC818664	-	-	-	-	-	-
H. angulatus	JS166	NMP6V 74813/4	Kenya	Nginyang	KC818665	-	-	-	-	-	-
H. angulatus	JS167	NMP6V 74813/5	Kenya	Nginyang	KC818665	-	-	KC818749	-	-	-
H. angulatus	JS174	NMP6V 74815/3	Uganda	Ubbi, Otzi Forest	KC818666	KC818813	-	KC818749	KC818905	KC819020	-
H. angulatus	JS175	NMP6V 74815/2	Kenya	Ubbi, Otzi Forest	KC818667	-	-	-	-	-	-
H. angulatus	JS176	NMP6V 74815/1	Kenya	Ubbi, Otzi Forest	KC818667	-	-	-	-	-	-
H. angulatus	JS179	NMP6V 74849/2	Kenya	South Horr	KC818662	-	-	-	-	-	-
H. barodanus	JS206#		Ethiopia	15 km NE of Dire Dawa	KC818668	-	-	KC818750	KC818906	KC819021	KC818957
H. barodanus	JS211		Somalia	Laas Geel	KC818669	KC818814	-	-	-	-	-
H. citernii	CAS227534	CAS227534	Somalia	Bari Region	DQ120383	DQ120212	JQ957320	JQ957124	JQ957247	JQ957406	-
H. citernii	CAS227535#	CAS227535	Somalia	Bari Region	DQ120384	DQ120213	JQ957321	JQ957124	JQ957248	JQ957407	-
H. citernii	JS203#		Somalia	Laas Geel	KC818670	KC818815	-	KC818751	KC818907	KC819022	KC818958
H. dawudazraqi	J12404		Jordan	Wadi al Burbeyath	DQ120335	DQ120164	JQ957397	JQ957161	JQ957299	JQ957442	-
H. dawudazraqi	J0504		Jordan	Dair al Khaf	DQ120336	DQ120165	JQ957396	JQ957161	JQ957300	JQ957441	-
H. dawudazraqi	J0404		Jordan	Dair al Khaf	JQ957082	JQ957230	JQ957395	JQ957161	JQ957299	JQ957440	-
H. dawudazraqi	Hd16	NMP6V 70457	Syria	Rashiedeh	KC818671	HQ833749	-	-	-	-	-
H. dawudazraqi	Hd24	NMP6V 72740/1	Jordan	Jawa	KC818672	HQ833750	-	-	-	-	-
H. dawudazraqi	Hd25	NMP6V 72740/2	Jordan	Jawa	KC818672	HQ833751	-	-	-	-	-
H. dawudazraqi	Hd43	NMP6V 74135/6	Jordan	Wadi Mujib	KC818673	HQ833754	-	-	-	-	-
H. dawudazraqi	Hd44	NMP6V 74135/7	Jordan	Wadi Mujib	KC818674	HQ833755	-	-	-	-	-
H. dawudazraqi	Hd48	NMP6V 74136/7	Jordan	Little Petra	KC818675	HQ833757	-	JQ957161	KC818908	JQ957423	KC818959
H. dawudazraqi	Hd50	NMP6V 74137	Jordan	Petra	KC818675	HQ833758	-	-	-	-	-
H. dawudazraqi	Hd52#	NMP6V 74134/1	Jordan	Azraq	KC818671	HQ833753	-	JQ957161	JQ957299	JQ957423	KC818960
H. dracaenacolus	IBES3922		Yemen	Wadi Zeriq, Socotra Island	JQ982783	JQ982890	JQ982704	KC818753	JQ982642	KC819023	-
H. dracaenacolus	IBES3940		Yemen	Bivio Diksam, Socotra Island	JQ982784	JQ982891	JQ982705	KC818752	JQ982644	KC819023	-
H. dracaenacolus	IBES2604#		Yemen	Tahr Diksam, Socotra Island	JQ982781	JQ982889	JQ982702	KC818752	JQ982643	KC819023	-
H. festivus	S7419	IBES7419	Oman	20 km S of Tumrait	JQ957047	JQ957181	JQ957324	JQ957125	JQ957252	JQ957410	-
H. festivus	AO126		Oman	3 km SE of Haluf	JQ957047	JQ957181	-	-	-	-	-
H. festivus	AO82		Oman	3 km SE of Haluf	JQ957047	JQ957181	JQ957323	JQ957125	JQ957251	JQ957410	-
H. festivus	AO122		Oman	Wadi Ayoun	JQ957047	JQ957179	JQ957322	JQ957125	-	JQ957409	-
H. festivus	AO120		Oman	Wadi Ayoun	JQ957047	JQ957179	JQ957322	JQ957125	JQ957249	JQ957408	-
H. festivus	AO154		Oman	Close to Mughsayl	JQ957047	JQ957182	JQ957322	JQ957125	JQ957250	JQ957409	-
H. festivus	AO121		Oman	Wadi Ayoun	JQ957046	JQ957180	JQ957322	JQ957125	JQ957250	JQ957409	-
H. festivus	JS1#	NMP6V 74812	Yemen	Wadi Hadramauth	JQ957096	KC818816	-	JQ957125	KC818909	JQ957409	KC818961
H. festivus	JS12#		Yemen	Damqawt	JQ957097	HQ833761	-	JQ957125	KC818910	KC819024	KC818962
H. festivus	JS15	NMP6V 74170	Yemen	Damqawt	JQ957097	HQ833761	-	-	-	-	-
H. festivus	JS70	NMP6V 74854/1	Oman	Mughsayl	JQ957098	KC818817	-	-	-	-	-
H. festivus	JS71#	NMP6V 74854/2	Oman	Mughsayl	JQ957098	KC818817	-	JQ957125	JQ957250	JQ957408	KC818963
H. festivus	JS72	NMP6V 74854/3	Oman	Mughsayl	JQ957098	KC818818	-	-	-	-	-
H. festivus	JS73	NMP6V 74854/4	Oman	Mughsayl	JQ957098	KC818819	-	JQ957125	JQ957250	KC819025	KC818964
H. festivus	JS85		Oman	Mudayy	JQ957098	KC818820	-	-	-	-	-
H. festivus	JS86	NMP6V 74855	Oman	Mughsayl	JQ957098	KC818821	-	-	-	-	-
H. flaviviridis	AO23		Oman	E. of Nizwa	JQ957048	JQ957183	JQ957325	JQ957126	JQ957253	JQ957411	-
H. flaviviridis	AO93		Oman	East Khor	JQ957049	JQ957184	JQ957326	JQ957126	JQ957253	JQ957412	-
H. flaviviridis	JS111		Pakistan	Okara	KC818676	KC818822	-	JQ957126	JQ957253	KC819026	KC818965
H. flaviviridis	JS113		India	Haridwar	KC818676	KC818823	-	JQ957126	JQ957253	KC819027	KC818966
H. flaviviridis	JS115		Yemen	14 km N of Mocha	JQ957119	KC818824	-	-	-	-	-
H. flaviviridis	JS116		Yemen	Zabid	JQ957119	JQ957183	-	-	-	-	-
H. flaviviridis	JS117		Oman	Nakhl	JQ957119	KC818825	-	-	-	-	-
H. flaviviridis	JS118		Oman	Salalah	JQ957120	JQ957184	-	-	-	-	-

SPECIES	CODE	VOUCHER	COUNTRY	LOCALITY	*12S*	*cytb*	ND4 + tRNAs	c*mos*	*mc1r*	*rag2*	*rag1*
H. flaviviridis	JS119		Oman	Jalan Bani Bu Hasan	JQ957119	JQ957183	-	KC818754	KC818911	KC819028	KC818967
H. flaviviridis	JS213		Ethiopia	Metahara	KC818676	KC818826	-	-	-	-	-
H. forbesii	IBE3001$^{\#}$		Yemen	Bir Al Aguz, Abd al Kuri Island	JQ982785	JQ982893	JQ982707	KC818755	JQ982645	JQ957425	-
H. forbesii	IBE5432		Yemen	Al Alyah, Abd al Kuri Island	JQ982786	JQ982894	JQ982711	KC818756	JQ982647	JQ957425	-
H. foudaii	SPM001825$^{\#}$		Egypt	Jebel Elba	DQ120385	DQ120214	JQ957327	JQ957127	-	JQ957413	-
H. foudaii	JS151$^{\#}$	NMP6V 74808	Sudan	15 km SE of Atbara	KC818677	-	-	KC818757	KC818912	KC819029	KC818968
H. funaiolii	JS196$^{\#}$		Kenya	Hurri Hills	KC818678	KC818827	-	KC818758	KC818913	KC819030	KC818969
H. granchii	JS214$^{\#}$		Somalia	40 km NE of Hargeisa	KC818679	KC818828	-	JQ957138	KC818914	KC819031	KC818970
H. granti	IBES3402$^{\#}$		Yemen		JQ982787	JQ982897	JQ982712	KC818752	JQ982651	KC819023	-
H. granti	IBES5356		Yemen		JQ982789	JQ982896	JQ982712	KC818752	JQ982652	KC819032	-
H. granti	IBES5307		Yemen	Adho Dimellus, Socotra Island	JQ982788	JQ982902	JQ982716	KC818759	JQ982652	KC819023	-
H. granti	IBES5626		Yemen	Scant, Socotra Island	JQ982790	JQ982903	JQ982718	KC818752	JQ982655	KC819023	-
H. granti	IBES5632		Yemen	Scant, Socotra Island	JQ982790	JQ982903	JQ982719	KC818760	JQ982655	KC819023	-
H. granti	IBES5639		Yemen	Scant, Socotra Island	JQ982787	JQ982902	JQ982720	KC818752	JQ982652	KC819033	-
H. hajarensis	CAS227612	CAS227612	Oman	4.5 km. N of Tanuf	DQ120337	DQ120166	JQ957328	JQ957128	JQ957254	JQ957414	-
H. hajarensis	CAS227614	CAS227614	Oman	4.5 km N. of Tanuf	DQ120338	DQ120167	JQ957329	JQ957128	JQ957255	JQ957415	-
H. hajarensis	S1969	BM2008.701	Oman	Wadi Mayh	JQ957055	JQ957189	JQ957335	JQ957128	JQ957260	JQ957415	-
H. hajarensis	S2136	BM2008.702	Oman	Wadi Mayh	JQ957050	JQ957185	JQ957337	-	JQ957260	JQ957415	-
H. hajarensis	S1660$^{\#}$	BM2008.703	Oman	Jebel Abu Daud	JQ957050	JQ957185	JQ957330	JQ957128	JQ957256	JQ957415	-
H. hajarensis	S2064	BM2008.709	Oman	Wadi Hebaheba, Jebel Qawan	JQ957053	JQ957188	JQ957336	JQ957128	-	-	-
H. hajarensis	S1777	S1777	Oman	Wadi Hebaheba, Jebel Qawan	JQ957053	JQ957188	JQ957333	JQ957130	JQ957258	JQ957418	-
H. hajarensis	S1772	BM2008.706	Oman	Wadi Hebaheba, Jebel Qawan	JQ957052	JQ957187	JQ957332	JQ957129	-	JQ957417	-
H. hajarensis	S1880	BM2008.707	Oman	Wadi Hebaheba, Jebel Qawan	JQ957052	JQ957187	JQ957332	JQ957128	JQ957259	JQ957420	-
H. hajarensis	S2139	BM2008.708	Oman	Wadi Hebaheba, Jebel Qawan	JQ957052	JQ957187	JQ957338	JQ957128	JQ957261	JQ957421	-
H. hajarensis	S1693	BM2008.704	Oman	Wadi Tiwi	JQ957051	JQ957186	JQ957331	JQ957128	JQ957257	JQ957416	-
H. hajarensis	S1782	BM2008.705	Oman	Wadi Tiwi	JQ957054	JQ957187	JQ957334	JQ957128	-	JQ957419	-
H. hajarensis	JS65	NMP6V 74862	Oman	Wadi N of Qurayyat	JQ957105	KC818829	-	-	-	-	-
H. hajarensis	JS81	NMP6V 74861	Oman	Wadi Bani Awf	JQ957099	KC818830	-	JQ957128	-	JQ957415	KC818971
H. hajarensis	JS98$^{\#}$	NMP6V 74860/1	Oman	Muqal	JQ957101	KC818831	-	JQ957128	KC818915	JQ957419	KC818972
H. homoeolepis	S4209		Yemen	Wadi Ayhaft, Socotra Island	JQ957059	JQ957194	JQ957342	JQ957132	JQ957264	JQ957422	-
H. homoeolepis	S3399		Yemen	Hadibo, Socotra Island	JQ957059	JQ957193	JQ957341	JQ957132	JQ957263	JQ957422	-
H. homoeolepis	S7929$^{\#}$	IBES7929	Oman	14.5 km NE of Sharbthat	JQ957057	JQ957198	JQ957349	JQ957131	JQ957262	JQ957422	-
H. homoeolepis	S7676	IBES7676	Oman	Asylah	JQ957057	-	JQ957345	JQ957133	JQ957262	JQ957422	-
H. homoeolepis	S7657	IBES7657	Oman	Asylah	JQ957057	JQ957195	JQ957343	JQ957133	JQ957262	JQ957422	-
H. homoeolepis	S7673	IBES7673	Oman	Asylah	JQ957057	-	JQ957344	JQ957133	JQ957262	JQ957422	-
H. homoeolepis	S7664	IBES7664	Oman	Asylah	JQ957057	JQ957195	JQ957344	JQ957133	JQ957262	JQ957422	-
H. homoeolepis	S7668	IBES7668	Oman	Asylah	JQ957057	JQ957195	JQ957344	JQ957133	JQ957262	JQ957422	-
H. homoeolepis	S7966	IBES7966	Oman	14.5 km NE of Sharbthat	JQ957057	JQ957197	JQ957350	JQ957136	JQ957262	JQ957422	-
H. homoeolepis	S7924	IBES7924	Oman	14.5 km NE of Sharbthat	JQ957057	JQ957197	JQ957348	JQ957135	JQ957262	JQ957422	-
H. homoeolepis	S7871		Oman	5 km W of Mughsayl	JQ957057	JQ957196	JQ957346	JQ957134	JQ957265	JQ957422	-
H. homoeolepis	AO81	IBEAO81	Oman	3 km SE of Haluf	JQ957057	JQ957191	JQ957340	JQ957131	JQ957262	JQ957422	-
H. homoeolepis	S7909	IBES7909	Oman	Wadi Ayoun	JQ957057	JQ957196	JQ957340	JQ957131	JQ957262	JQ957422	-
H. homoeolepis	AO85	IBEAO85	Oman	N of Wadi Ayoun	JQ957058	JQ957192	JQ957340	JQ957131	-	JQ957422	-
H. homoeolepis	AO119	IBEAO119	Oman	Wadi Ayoun	JQ957056	JQ957190	JQ957339	JQ957131	JQ957262	JQ957422	-
H. homoeolepis	S7893	IBES7893	Oman	5 km W of Mughsayl	JQ957060	JQ957196	JQ957347	-	JQ957266	JQ957422	-
H. homoeolepis	JS5	NMP6V 74805/1	Yemen	3 km E. Hauf	JQ957111	KC818832	-	-	-	-	-
H. homoeolepis	JS6	NMP6V 74805/2	Yemen	3 km E. Hauf	JQ957108	KC818832	-	KC818761	KC818916	JQ957422	KC818973
H. homoeolepis	JS8	NMP6V 74806	Yemen	Damqawt	JQ957109	KC818834	-	-	-	-	-
H. homoeolepis	JS75	NMP6V 74863	Oman	Mughsayl	JQ957112	KC818833	-	-	-	-	-
H. homoeolepis	IBES3807		Yemen	Wadi Ayahft, Socotra Island	JQ982793	JQ982908	JQ982725	KC818762	JQ982658	JQ957422	-
H. homoeolepis	IBES5142		Yemen	Cave Close Qualansia, Socotra Island	JQ982796	JQ982913	JQ982730	JQ957132	JQ982656	KC819034	-
H. homoeolepis	IBES5060		Yemen	Type Loc of H. dracaenacolus, Socotra	JQ982794	JQ982910	-	JQ957132	JQ982659	JQ957422	-
H. homoeolepis	IBES5154		Yemen	Darsa Island	JQ982795	JQ982914	JQ982729	JQ957132	JQ982656	JQ957422	-
H. homoeolepis	IBES5305		Yemen	Khaysat, Samhah Island	JQ982797	JQ982904	JQ982721	JQ957132	JQ982656	JQ957422	-
H. homoeolepis	IBES5106$^{\#}$		Yemen	Darsa Island	JQ982795	JQ982912	JQ982729	KC818763	JQ982656	JQ957422	-
H. homoeolepis	IBES5430		Yemen	W of Fikhah, Socotra Island	JQ982798	JQ982919	JQ982735	KC818764	JQ982656	JQ957422	-
H. inexpectatus	S1892	BM2008.712	Oman	2.5 km SE Ar Rumayliyah	JQ957066	JQ957206	JQ957364	JQ957141	JQ957274	JQ957427	-
H. inexpectatus	S7700	IBES7700	Oman	2.5 km SE Ar Rumayliyah	JQ957066	JQ957209	JQ957367	JQ957140	JQ957277	JQ957426	-
H. inexpectatus	S2166	BM2008.711	Oman	2.5 km SE Ar Rumayliyah	JQ957067	JQ957207	JQ957365	JQ957140	JQ957275	JQ957426	-
H. inexpectatus	S7735	IBES7735	Oman	2.5 km SE Ar Rumayliyah	JQ957067	JQ957210	JQ957368	JQ957140	JQ957273	JQ957426	-
H. inexpectatus	S1798$^{\#}$	S1798	Oman	2.5 km SE Ar Rumayliyah	JQ957065	JQ957205	JQ957363	JQ957140	JQ957273	JQ957426	-
H. inexpectatus	S7722	IBES7722	Oman	2.5 km SE Ar Rumayliyah	JQ957068	-	JQ957366	JQ957140	JQ957274	JQ957426	-
H. inexpectatus	S7674	IBES7674	Oman	2.5 km SE Ar Rumayliyah	JQ957067	JQ957208	JQ957366	JQ957140	JQ957276	JQ957426	-
H. inintellectus	IBES3290		Yemen	Wadi Kilisan S of Afafes Momi plateau,	JQ982799	JQ982924	JQ982738	-	JQ982666	-	-
H. inintellectus	IBES5212		Yemen	Close To Shuab, Socotra Island	JQ982804	JQ982925	JQ982750	KC818767	JQ982668	KC819035	-
H. inintellectus	IBES5068		Yemen	Wadi Ayahft, Socotra Island	JQ982802	JQ982922	JQ982748	KC818766	JQ982673	KC819035	-
H. inintellectus	IBES5102		Yemen	Wadi Ayahft, Socotra Island	JQ982802	JQ982929	JQ982737	KC818767	JQ982668	KC819035	-
H. inintellectus	IBES5110$^{\#}$		Yemen	Cave Close Qualansia, Socotra Island	JQ982803	JQ982930	JQ982742	KC818768	JQ982668	KC819035	-
H. inintellectus	IBE5439		Yemen	W of Fikhah, Socotra Island	JQ982806	JQ982931	JQ982749	KC818765	JQ982671	KC819035	-
H. inintellectus	IBE5431		Yemen	Lingohur Momi plateau, Socotra Island	JQ982805	JQ982932	JQ982751	KC818765	JQ982666	KC819035	-
H. inintellectus	IBE3782		Yemen	Homhil, Socotra Island	JQ982800	JQ982921	JQ982736	KC818765	JQ982671	KC819035	-
H. isolepis	JS202$^{\#}$		Somalia	8 km S of Borama	KC818680	KC818835	-	KC818769	KC818917	KC819036	KC818974
H. jumailiae	JS100	NMP6V 74819	Yemen	Sana´a	KC818681	KC818836	-	-	-	KC819037	-
H. jumailiae	JS53$^{\#}$	NMP6V 74818/1	Yemen	25 km NW of Al Bayda	KC818682	KC818837	-	KC818770	KC818918	KC819038	KC818975
H. jumailiae	JS54	NMP6V 74818/2	Yemen	25 km NW of Al Bayda	KC818682	KC818838	-	-	-	-	-
H. lavadeserticus	Hd31	NMP6V 74049/1	Syria	Ar´Raqiyeh	KC818684	HQ833742	-	-	-	-	-
H. lavadeserticus	Hd70$^{\#}$	NMP6V 74049/2	Syria	Ar´Raqiyeh	KC818683	HQ833743	-	JQ957161	KC818919	KC819039	KC818976
H. lavadeserticus	Hd74	NMP6V 74049/5	Syria	Ar´Raqiyeh	KC818684	HQ833746	-	-	-	-	-
H. lemurinus	AO117		Oman	Wadi Ayoun	JQ957062	JQ957200	JQ957352	JQ957137	JQ957268	JQ957423	-
H. lemurinus	AO123		Oman	Wadi Ayoun	JQ957062	JQ957200	JQ957354	JQ957137	-	JQ957423	-
H. lemurinus	AO116		Oman	Wadi Ayoun	JQ957061	JQ957199	JQ957351	JQ957137	JQ957267	-	-
H. lemurinus	AO118		Oman	Wadi Ayoun	JQ957061	JQ957201	JQ957353	JQ957137	JQ957269	JQ957423	-
H. lemurinus	AO124		Oman	Wadi Ayoun	JQ957061	JQ957201	JQ957355	JQ957137	-	JQ957423	-
H. lemurinus	JS9$^{\#}$		Yemen	Damqawt	JQ957113	KC818839	-	JQ957137	KC818921	JQ957423	KC818978
H. lemurinus	JS10	NMP6V 74801/1	Yemen	Damqawt	JQ957114	-	-	-	-	-	-
H. lemurinus	JS11	NMP6V 74801/2	Yemen	Damqawt	JQ957113	KC818839	-	JQ957137	KC818920	JQ957423	KC818977
H. luqueorum	S2152$^{\#}$	BM2005.1659	Oman	Wadi Bani Habib, Jebel Akhdar	JQ957070	JQ957214	JQ957372	JQ957146	JQ957278	JQ957431	-
H. luqueorum	AO46	BM2005.1660	Oman	Sayq, Jebel Akhdar	JQ957069	JQ957212	JQ957370	JQ957143	JQ957279	JQ957429	-
H. luqueorum	AO155	BM2005.1661	Oman	Sayq, Jebel Akhdar	JQ957069	JQ957211	JQ957369	JQ957142	JQ957278	JQ957428	-
H. luqueorum	AO59	BM2005.1658	Oman	Wadi Bani Habib, Jebel Akhdar	JQ957069	JQ957212	JQ957371	JQ957144	JQ957280	JQ957430	-
H. luqueorum	S8068	IBES8068	Oman	Wadi al Khahafa, Jebel Akhdar	JQ957069	JQ957215	JQ957373	JQ957147	JQ957281	JQ957430	-
H. luqueorum	S1756	BM2008.710	Oman	Wadi al Khahafa, Jebel Akhdar	JQ957069	JQ957213	-	JQ957145	JQ957281	JQ957430	-
H. mabouia	JS173	NMP6V 74804	Uganda	Mpanga forest	KC818685	KC818840	-	KC818771	KC818922	KC819040	KC818979
H. macropholis	CAS227511$^{\#}$	CAS227511	Somalia	11 km SE of Bosasso	DQ120379	DQ120208	JQ957356	JQ957138	JQ957270	JQ957424	-
H. masirahensis	S3412		Oman	Wadi Harf, Masirah island	JQ957063	JQ957202	JQ957359	JQ957139	JQ957272	JQ957425	-
H. masirahensis	S7707	IBES7707	Oman	Wadi Maahdi, Masirah island	JQ957063	JQ957202	JQ957361	JQ957139	JQ957272	JQ957425	-
H. masirahensis	S1878	BM2008.713	Oman	Wadi Haql. Masirah island	JQ957063	JQ957202	JQ957357	JQ957139	-	JQ957425	-
H. masirahensis	S7661	IBES7661	Oman	Wadi Maahdi, Masirah island	JQ957063	JQ957202	-	JQ957139	JQ957272	JQ957425	-
H. masirahensis	S2044$^{\#}$	S2044	Oman	Wadi Haql, Masirah island	JQ957064	JQ957203	JQ957358	JQ957139	JQ957271	JQ957425	-
H. masirahensis	S7651	IBES7651	Oman	Wadi Maahdi, Masirah island	JQ957063	JQ957204	JQ957360	JQ957139	JQ957272	JQ957425	-
H. masirahensis	S7710	IBES7710	Oman	Wadi Maahdi, Masirah island	JQ957063	JQ957204	JQ957362	JQ957139	JQ957272	JQ957425	-
H. mindiae	Hd22$^{\#}$	NMP6V 72323/2	Jordan	Jabal Ghazali	KC818686	HQ833747	-	JQ957128	-	JQ957423	KC818980
H. mindiae	Hd23	NMP6V 72739/1	Jordan	Wadi Ramm Nughra	KC818686	HQ833748	-	JQ957128	-	KC819041	KC818981
H. modestus	CAS198934$^{\#}$	CAS198934	Kenya	Kijiado District, Rift Valley Province	DQ120386	DQ120215	-	JQ957149	JQ957283	JQ957432	-
H. ophiolepis	JS215$^{\#}$		Ethiopia	15 km NE of Dire Dawa	KC818689	KC818841	-	KC818772	KC818923	KC819042	KC818982
H. oxyrhinus	IBE2624$^{\#}$		Yemen	Bir Al Aguz ,Abd al Kuri Island	JQ982807	JQ982936	JQ982754	KC818773	JQ982676	JQ957425	-
H. oxyrhinus	IBE5394		Yemen	Bir Al Aguz ,Abd al Kuri Island	JQ982810	JQ982935	JQ982757	KC818773	JQ982677	JQ957425	-
H. oxyrhinus	IBE3002		Yemen	Bir Al Aguz ,Abd al Kuri Island	JQ982808	JQ982937	JQ982755	KC818774	JQ982678	KC819043	-
H. oxyrhinus	IBE5435		Yemen	Bir Al Aguz ,Abd al Kuri Island	JQ982811	JQ982941	JQ982760	KC818774	JQ982677	JQ957425	-

SPECIES	CODE	VOUCHER	COUNTRY	LOCALITY	*12S*	*cytb*	ND4 + tRNAs	c*mos*	*mc1r*	*rag2*	*rag1*
H. oxyrhinus	IBE4058		Yemen	Bir Al Aguz ,Abd al Kuri Island	JQ982807	JQ982940	JQ982759	KC818773	JQ982676	JQ957425	-
H. oxyrhinus	IBE5382		Yemen	Khaysat Salih ,Abd al Kuri Island	JQ982809	JQ982942	JQ982764	KC818774	JQ982675	JQ957425	-
H. paucituberculatus	S7988	IBES7988	Oman	Khor Sauli	JQ957072	-	JQ957383	JQ957150	JQ957291	JQ957425	-
H. paucituberculatus	AO104[#]	IBEAO104	Oman	East Khor	JQ957072	JQ957217	JQ957375	JQ957150	JQ957284	JQ957425	-
H. paucituberculatus	AO162		Oman	Khor Sauli	JQ957072	JQ957217	JQ957376	JQ957151	JQ957285	JQ957425	-
H. paucituberculatus	S3261		Oman	Wadi Darbat	JQ957072	JQ957217	JQ957379	JQ957150	JQ957284	-	-
H. paucituberculatus	S7921	IBES7921	Oman	Khor Sauli	JQ957072	JQ957217	JQ957376	JQ957150	JQ957289	-	-
H. paucituberculatus	S7646	IBES7646	Oman	Khor Sauli	JQ957072	JQ957217	JQ957380	JQ957150	JQ957287	JQ957425	-
H. paucituberculatus	S7910	IBES7910	Oman	East Khor	JQ957072	JQ957217	JQ957377	JQ957150	JQ957286	JQ957425	-
H. paucituberculatus	AO91	IBEAO91	Oman	East Khor	JQ957072	JQ957217	JQ957377	JQ957151	-	JQ957425	-
H. paucituberculatus	S7994	IBES7994	Oman	Wadi Darbat	JQ957072	JQ957221	JQ957384	JQ957151	JQ957292	JQ957425	-
H. paucituberculatus	S3235		Oman	Wadi Darbat	JQ957072	JQ957218	JQ957378	JQ957150	JQ957286	-	-
H. paucituberculatus	S8004	IBES8004	Oman	3.5 km NE Sadah	JQ957072	JQ957222	JQ957385	JQ957150	JQ957287	JQ957425	-
H. paucituberculatus	S7930	IBES7930	Oman	Wadi Hasik	JQ957073	JQ957220	JQ957382	JQ957150	JQ957290	JQ957433	-
H. paucituberculatus	S7902	IBES7902	Oman	3 km NW of Hasik	JQ957073	JQ957219	-	JQ957150	JQ957288	JQ957425	-
H. paucituberculatus	S7812		Oman	Wadi Hasik	JQ957073	JQ957219	JQ957381	JQ957150	JQ957288	-	-
H. persicus	FTHM005100	FTHM005100	Iran	Bushehr	JQ957076	JQ957224	-	JQ957152	-	-	-
H. persicus	MVZ234385[#]	MVZ Herps	Iran	Lipar Village, Sistan and Baluchistan	JQ957077	JQ957225	JQ957386	JQ957152	JQ957293	JQ957435	-
H. persicus	FTHM005000	FTHM005000	Iran	Mahshar	JQ957074	JQ957223	-	JQ957152	-	JQ957434	-
H. persicus	FTHM005001	FTHM005001	Iran	Mahshar	JQ957075	JQ957223	-	JQ957152	-	-	-
H. persicus	JS103[#]	NMP6V 74807/1	Iran	Booreki	KC818691	KC818842	-	KC818775	KC818924	KC819044	KC818983
H. persicus	JS104	NMP6V 74807/2	Iran	Booreki	KC818690	KC818843	-	KC818775	KC818925	JQ957434	KC818984
H. persicus	JS105	NMP6V 74807/3	Iran	Booreki	KC818691	KC818844	-	-	-	-	-
H. platycephalus	JS168	NMP6V 74864/1	Kenya	Ngurunit	KC818692	-	-	-	-	-	-
H. platycephalus	JS169	NMP6V 74864/2	Kenya	Ngurunit	KC818693	KC818845	-	KC818776	KC818926	KC819045	KC818985
H. platycephalus	JS171	NMP6V 74865/1	Kenya	Wamba	KC818694	KC818846	-	KC818776	KC818926	KC819046	KC818986
H. platycephalus	JS172	NMP6V 74865/2	Kenya	Wamba	KC818695	-	-	-	-	-	-
H. pumilio	IBES3307		Yemen	Near Qedami, Socotra Island	JQ982813	JQ982946	JQ982769	KC818777	JQ982685	KC819047	-
H. pumilio	IBES3382		Yemen	Damir Wadi Luntir, Socotra Island	JQ982815	JQ982951	JQ982774	-	JQ982689	-	-
H. pumilio	IBES3404		Yemen	Ghubbat Timbar, Socotra Island	JQ982816	JQ982952	JQ982770	KC818777	JQ982690	KC819048	-
H. pumilio	IBES3341		Yemen	Between Jooh and Di Ishal, Socotra Island	JQ982814	JQ982949	JQ982772	-	JQ982683	-	-
H. pumilio	IBES5272		Yemen	Socotra Island	JQ982813	JQ982955	JQ982777	KC818777	JQ982694	KC819049	-
H. pumilio	IBES5117[#]		Yemen	Ridah, Socotra Island	JQ982818	JQ982954	JQ982776	KC818777	JQ982683	KC819047	-
H. pumilio	IBES5021		Yemen	Steroh, Socotra Island	JQ982817	JQ982948	JQ982771	KC818777	JQ982693	KC819047	-
H. pumilio	IBES5616		Yemen	Firmin, Socotra Island	JQ982820	JQ982957	JQ982779	KC818777	JQ982699	KC819050	-
H. pumilio	IBES5658		Yemen	South, Socotra Island	JQ982822	JQ982961	JQ982780	KC818777	JQ982683	KC819047	-
H. pumilio	IBES5402		Yemen	Tahr Diksam, Socotra Island	JQ982819	JQ982956	JQ982778	KC818777	JQ982697	KC819047	-
H. robustus	S2151		Oman	8 km W Shannah	JQ957081	JQ957228	JQ957389	JQ957158	JQ957294	JQ957409	-
H. robustus	S1677		Oman	1 km W airport, Masirah Island	JQ957080	JQ957228	JQ957389	JQ957153	-	JQ957409	-
H. robustus	S1905		Oman	1 km W airport, Masirah Island	JQ957080	JQ957228	JQ957389	JQ957158	JQ957294	JQ957438	-
H. robustus	S1962		Oman	1 km W airport, Masirah Island	JQ957080	JQ957228	JQ957389	JQ957154	JQ957294	JQ957409	-
H. robustus	S1788		Oman	1 km W airport, Masirah Island	JQ957080	JQ957228	JQ957389	JQ957154	JQ957294	JQ957436	-
H. robustus	S2150		Oman	1 km W airport, Masirah Island	JQ957080	JQ957228	JQ957391	JQ957159	-	JQ957409	-
H. robustus	SPM001859		Egypt	Safaga	DQ120347	DQ120176	JQ957394	JQ957160	JQ957298	JQ957439	-
H. robustus	AO164b		Oman	East Khor	JQ957078	JQ957226	JQ957387	JQ957153	JQ957294	JQ957436	-
H. robustus	AO165		Oman	East Khor	JQ957078	JQ957226	JQ957387	JQ957154	JQ957295	JQ957437	-
H. robustus	AO4		Oman	Al Azaiba	JQ957079	JQ957227	-	-	-	-	-
H. robustus	UAE25		UAE	Wadi Tayybiyah	JQ957079	JQ957227	-	-	-	-	-
H. robustus	AO3		Oman	Al Azaiba	JQ957079	JQ957227	JQ957388	JQ957155	JQ957294	JQ957409	-
H. robustus	Hturc2		UAE	Dhafra Beach, near Ruwais	AF186117	AF184989	-	JQ957156	-	JQ957409	-
H. robustus	SPM001501		UAE	Dhafra Beach, near Ruwais	AF186117	JQ957227	-	-	-	-	-
H. robustus	R1415		Yemen	Mukalla Airport	AF186117	JQ957229	JQ957392	JQ957154	JQ957297	JQ957436	-
H. robustus	S1688		Oman	8 km W Shannah	AF186117	JQ957226	JQ957390	JQ957157	JQ957296	JQ957409	-
H. robustus	SPM001503		UAE	Abu Dhabi	AF186117	JQ957226	JQ957393	-	-	-	-
H. robustus	JS50[#]	NMP6V 74821/1	Yemen	Wadi Zabid	KC818701	KC818852	-	KC818779	KC818928	JQ957409	KC818987
H. robustus	JS51	NMP6V 74821/2	Yemen	Wadi Zabid	KC818701	KC818853	-	-	-	-	-
H. robustus	JS58[#]	NMP6V 74829	Yemen	Bir Ali	KC818702	KC818854	-	KC818780	KC818929	KC819051	KC818988
H. robustus	JS66	NMP6V 74867/1	Oman	Muscat Airport	KC818701	KC818855	-	-	-	-	-
H. robustus	JS67	NMP6V 74867/2	Oman	Muscat Airport	KC818703	KC818849	-	KC818781	KC818930	JQ957409	KC818989
H. robustus	JS68	NMP6V 74867/3	Oman	Muscat Airport	KC818701	KC818856	-	-	-	-	-
H. robustus	JS69	NMP6V 74868	Oman	Salalah	KC818699	KC818857	-	-	-	-	-
H. robustus	JS74	NMP6V 74869/1	Oman	Mughsayl	KC818699	KC818850	-	-	-	-	-
H. robustus	JS76	NMP6V 74869/2	Oman	Mughsayl	KC818699	KC818850	-	-	-	-	-
H. robustus	JS82		Oman	Al Qarbi	KC818701	KC818858	-	-	-	-	-
H. robustus	JS83	NMP6V 74870/1	Oman	Shisr	KC818704	KC818859	-	-	-	-	-
H. robustus	JS84	NMP6V 74870/2	Oman	Shisr	KC818705	KC818859	-	-	-	-	-
H. robustus	JS101		Somalia	Berbera	KC818696	KC818847	-	KC818778	KC818927	JQ957409	KC818987
H. robustus	JS102		Somalia	Berbera	KC818697	KC818848	-	-	-	-	-
H. robustus	JS106	NMP6V 74820	Iran	Bandar-e Lengeh	KC818698	KC818849	-	-	-	-	-
H. robustus	JS120	NMP6V 74869/3	Oman	Mughsayl	KC818699	KC818850	-	-	-	-	-
H. robustus	JS210		Ethiopia	Jijiga	KC818700	KC818851	-	-	-	-	-
H. ruspolii	JS177	NMP6V 74871/3	Kenya	Kalacha	KC818706	KC818860	-	KC818782	KC818931	KC819052	-
H. ruspolii	JS192	NMP6V 74871/1	Kenya	Kalacha	KC818706	-	-	-	-	-	-
H. ruspolii	JS193	NMP6V 74871/2	Kenya	Kalacha	KC818706	-	-	KC818782	-	-	-
H. shihraensis	JS16[#]	NMP6V 74816	Yemen	11 km N of Mukalla	KC818710	-	-	KC818783	KC818932	KC819053	KC818990
H. shihraensis	JS55	NMP6V 74817/1	Yemen	Ghayl Ba Wazir	KC818707	KC818862	-	-	-	-	-
H. shihraensis	JS56	NMP6V 74817/2	Yemen	Ghayl Ba Wazir	KC818711	KC818864	-	KC818784	KC818933	KC819054	KC818991
H. shihraensis	JS57	NMP6V 74817/3	Yemen	Ghayl Ba Wazir	KC818707	KC818865	-	KC818783	KC818934	JQ957410	KC818992
H. shihraensis	JS133	NMP6V 74817/4	Yemen	Ghayl Ba Wazir	KC818707	KC818861	-	-	-	-	-
H. shihraensis	JS134	NMP6V 74817/5	Yemen	Ghayl Ba Wazir	KC818707	KC818862	-	-	-	-	-
H. shihraensis	JS135	NMP6V 74817/6	Yemen	Ghayl Ba Wazir	KC818708	-	-	-	-	-	-
H. shihraensis	JS136	NMP6V 74817/7	Yemen	Ghayl Ba Wazir	KC818709	KC818863	-	-	-	-	-
H. shihraensis	JS137	NMP6V 74817/8	Yemen	Ghayl Ba Wazir	KC818707	KC818862	-	-	-	-	-
H. shihraensis	JS138	NMP6V 74817/9	Yemen	Ghayl Ba Wazir	KC818707	KC818862	-	-	-	-	-
H. shihraensis	Hd90	NMP6V 74169	Yemen	Ghayl Ba Wazir	-	HQ833760	-	-	-	-	-
H. sinaitus	JS146	NMP6V 74809/1	Sudan	Wad Ben Naga	KC818712	KC818866	-	JQ957164	KC818935	JQ957446	KC818993
H. sinaitus	JS147	NMP6V 74809/2	Sudan	Wad Ben Naga	KC818713	KC818867	-	JQ957164	JQ957302	JQ957446	KC818994
H. sinaitus	JS148	NMP6V 74809/3	Sudan	Wad Ben Naga	KC818712	KC818868	-	-	-	-	-
H. sinaitus	JS149	NMP6V 74809/4	Sudan	Wad Ben Naga	KC818714	KC818869	-	-	-	-	-
H. sinaitus	JS150[#]	NMP6V 74810	Sudan	15 km SE of Atbara	KC818712	KC818869	-	JQ957164	JQ957303	JQ957446	KC818995
H. smithi	JS208		Somalia	30 km N of Shiikh	KC818715	KC818870	-	KC818785	KC818936	KC819055	KC818996
H. squamulatus	JS160	NMP6V 74872/2	Kenya	South Horr	KC818737	-	-	-	-	-	-
H. squamulatus	JS162	NMP6V 74872/4	Kenya	South Horr	KC818737	-	-	-	-	-	-
H. squamulatus	JS180		Kenya	South Horr	KC818738	-	-	-	-	-	-
H. squamulatus	JS183[#]		Kenya	Isiolo	KC818739	-	-	JQ957149	KC818946	KC819065	KC819005
H. squamulatus	JS190	NMP6V 74872/5	Kenya	South Horr	KC818737	-	-	-	-	-	-
H. squamulatus	JS191[#]	NMP6V 74872/6	Kenya	South Horr	KC818737	KC818888	-	JQ957149	KC818947	KC819066	KC819006
H. turcicus	SPM000788		Turkey	Erzin	DQ120334	DQ120163	JQ957398	JQ957162	-	JQ957443	-
H. turcicus	SPM001629		Spain	Torregorda, Cádiz	DQ120311	DQ120140	JQ957399	JQ957162	JQ957301	JQ957444	-
H. turcicus	SPM002086		Spain	Barcelona	DQ120313	DQ120142	JQ957400	JQ957163	JQ957301	JQ957445	-
H. turcicus	Hd55		Albania	Ardenica	KC818742	HQ833711	-	JQ957162	KC818949	KC819068	KC819009
H. turcicus	Hd62	NMP6V 73626/1	Turkey	Finike	KC818743	HQ833736	-	-	-	-	-
H. turcicus	Hd66		Croatia	Sumartin	KC818742	HQ833714	-	-	-	-	-
H. turcicus	JS152	NMP6V 74215	Lebanon	Aamchit	KC818742	HQ833714	-	JQ957162	KC818950	KC819069	KC819010
H. turcicus	Hd2[#]		Israel	Almagor	KC818740	HQ833741	-	KC818793	KC818948	JQ957423	KC819007
H. turcicus	Hd5		Turkey	Adana	KC818741	HQ833735	-	JQ957162	-	JQ957423	-
H. turcicus	Hd34[#]		Egypt	Sharn All Shiekh	KC818741	HQ833717	-	JQ957162	JQ957301	KC819067	KC819008
H. turcicus	Hd37	NMP6V 72081	Egypt	El Arish	KC818741	HQ833718	-	-	-	-	-
H. yerburii yerburii	JS40[#]	NMP6V 74824/1	Yemen	3 km S of Najd an Nashamah	JQ957086	KC818894	-	JQ957167	JQ957306	JQ957447	KC819013

SPECIES	**CODE**	**VOUCHER**	**COUNTRY**	**LOCALITY**	*12S*	*cytb*	**ND4 + tRNAs**	**c**_mos_	*mc1r*	*rag2*	*rag1*
H. yerburii yerburii	JS44	NMP6V 74828/2	Yemen	Al Hababi	JQ957086	KC818897	-	JQ957166	JQ957307	JQ957448	KC819014
H. yerburii yerburii	JS60	NMP6V 74822/2	Yemen	6 km N of Al Hisn	JQ957087	KC818893	-	JQ957166	JQ957308	JQ957447	KC819015
H. yerburii yerburii	JS29[#]	NMP6V 74826	Yemen	8 km N of Lahij	JQ957085	KC818892	-	JQ957165	JQ957304	JQ957447	KC819011
H. yerburii yerburii	JS30	-	Yemen	8 km N of Lahij	JQ957085	KC818893	-	JQ957166	JQ957305	JQ957447	KC819012
H. yerburii yerburii	JS20	NMP6V 74168	Yemen	27 km S of Taizz	KC818744	HQ833762	-	-	-	-	-
H. yerburii yerburii	JS23	NMP6V 74827/2	Yemen	Jabel Habeshi	JQ957086	KC818889	-	-	-	-	-
H. yerburii yerburii	JS24	NMP6V 74825/1	Yemen	At Turbah	JQ957086	KC818890	-	-	-	-	-
H. yerburii yerburii	JS26	NMP6V 74825/2	Yemen	At Turbah	JQ957086	KC818891	-	-	-	-	-
H. yerburii yerburii	JS33	NMP6V 74823/1	Yemen	14 km NW of At Turbah	JQ957086	KC818894	-	-	-	-	-
H. yerburii yerburii	JS34	NMP6V 74823/2	Yemen	14 km NW of At Turbah	JQ957086	KC818894	-	-	-	-	-
H. yerburii yerburii	JS35	NMP6V 74823/3	Yemen	14 km NW of At Turbah	JQ957086	KC818894	-	-	-	-	-
H. yerburii yerburii	JS41	NMP6V 74824/2	Yemen	3 km S of Najd an Nashamah	JQ957086	KC818894	-	-	-	-	-
H. yerburii yerburii	JS42	NMP6V 74828/1	Yemen	Al Hababi	JQ957086	KC818895	-	-	-	-	-
H. yerburii yerburii	JS43	-	Yemen	Al Hababi	JQ957086	KC818896	-	-	-	-	-
H. yerburii yerburii	JS61	NMP6V 74822/3	Yemen	6 km N of Al Hisn	JQ957087	KC818898	-	-	-	-	-
H. yerburii montanus	JS28	NMP6V 74802	Yemen	Jabal Bura	KC818687	KC818899	-	-	-	-	-
H. yerburii montanus	JS52[#]	NMP6V 74803	Yemen	5 km NE of Hajjah	KC818688	KC818900	-	KC818750	KC818951	KC819070	KC819016
H. sp. 1	Hd41	NMP6V70163/2	Egypt	Sharm All Shiekh	KC818724	HQ833759	-	-	-	-	KC818981
H. sp. 1	Sher10660[#]	Sher10660	Egypt	Ayoun Musa	JQ957071	JQ957216	JQ957374	JQ957148	JQ957282	JQ957409	-
H. sp. 4	JS17[#]	NMP6V 74831/1	Yemen	Al Hadr	KC818725	KC818874	-	KC818787	KC818940	KC819059	KC818999
H. sp. 4	JS18	NMP6V 74831/2	Yemen	Al Hadr	KC818725	-	-	-	-	-	-
H. sp. 4	JS32	NMP6V 74835	Yemen	35 km W of Lahij	KC818726	KC818875	-	KC818788	KC818941	KC819060	KC819000
H. sp. 4	JS37	NMP6V 74832/1	Yemen	3 km S of Najd an Nashamah	KC818727	KC818876	-	-	-	-	-
H. sp. 4	JS38	NMP6V 74832/2	Yemen	3 km S of Najd an Nashamah	KC818727	KC818877	-	-	-	-	-
H. sp. 4	JS45		Yemen	Al Hababi	KC818728	KC818878	-	-	-	-	-
H. sp. 4	JS46	NMP6V 74833/1	Yemen	Al Hababi	KC818728	KC818879	-	-	-	-	-
H. sp. 4	JS47	NMP6V 74833/2	Yemen	Al Hababi	KC818729	KC818880	-	KC818789	KC818942	KC819061	KC819001
H. sp. 4	JS48	NMP6V 74834/1	Yemen	Wadi Zabid	KC818730	KC818881	-	KC818789	KC818943	KC819062	KC819001
H. sp. 4	JS49	NMP6V 74834/2	Yemen	Wadi Zabid	KC818731	KC818882	-	-	-	-	-
H. sp. 5	JS27		Yemen	Jabal Sabir	KC818732	KC818883	-	-	-	-	-
H. sp. 5	JS36[#]	NMP6V 74836/1	Yemen	3 km S of Najd an Nashamah	KC818734	KC818884	-	KC818790	-	JQ957409	KC819002
H. sp. 5	JS39	NMP6V 74836/2	Yemen	3 km S of Najd an Nashamah	KC818733	KC818885	-	-	-	-	-
H. sp. 6	JS31[#]	NMP6V 74837	Yemen	8 km N of Lahij	KC818735	KC818886	-	KC818791	KC818944	KC819063	KC819003
H. sp. 9	JS216[#]		Ethiopia	10 km E of Yidi	KC818736	KC818887	-	KC818792	KC818945	KC819064	KC819004
H. sp. 9	JS217		Ethiopia	Awash	KC818736	KC818887	-	-	-	-	-
H. sp. 10	JS181[#]		Kenya	Gus	KC818716	KC818871	-	KC818769	KC818937	KC819056	KC818997
H. sp. 10	JS182		Kenya		KC818717	-	-	-	-	-	-
H. sp. 10	JS184[#]		Kenya	Kalacha	KC818718	KC818872	-	KC818769	KC818938	KC819057	-
H. sp. 10	JS185		Kenya	Kalacha	KC818719	-	-	-	-	-	-
H. sp. 10	JS186		Kenya	Kalacha	KC818719	-	-	-	-	-	-
H. sp. 10	JS187		Kenya		KC818720	-	-	KC818769	-	-	-
H. sp. 10	JS188		Kenya		KC818721	-	-	-	-	-	-
H. sp. 10	JS189		Kenya		KC818721	-	-	-	-	-	-
H. sp. 10	JS194		Kenya	Korante plain	KC818721	-	-	-	-	-	-
H. sp. 10	JS195		Kenya	Korante plain	KC818722	-	-	-	-	-	-
H. sp. 11	JS212[#]		Ethiopia	2 km N of Metehara	KC818723	KC818873	-	KC818786	KC818939	KC819058	KC818998

Table S2. Molecular markers, primers, primer sequences, amplification conditions and original primer sources used in this study

Gene	Primer name	Primer sequence (5´- 3´)	Analyzed fragment length (bp)	T^{a} annealing	Primer source
12S rRNA	12Sa	AAACTGGGATTAGATACCCCACTAT	381 - 396	48º	Kocher et al. 1989
	12Sb	TGAGGAGGGTGACGGGCGGT			
cytb short	Cytb1	CCATCCAACATCTCAGCATGATGAAA	307	46º	Kocher et al. 1989 (shortened)
	Cytb2	CCCTCAGAATGATATTTGTCCTCA			
cytb long	L14910	GACCTGTGATMTGAAAACCAYCGTTGT	1137	46º	Burbrink et al. 2000
	H16064	CTTTGGTTTACAAGAACAATGCTTTA			
cmos	FUF	TTTGGTTCKGTCTACAAGGCTAC	403	53º	Gamble et al. 2008
	FUR	AGGGAACATCCAAAGTCTCCAAT			
mc1r	MC1RF	AGGCNGCCATYGTCAAGAACCGGAACC	668	56°	Pinho et al. 2009
	MC1RR	CTCCGRAAGGCRTAAATGATGGGGTCCAC			
rag1 short	F700	GGAGACATGGACACAATCCATCCTAC	280	53º	Bauer et al. 2007
	R700	TTTGTACTGAGATGGATCTTTTTGCA			
rag1 long	R13	TCTGAATGGAAATTCAAGCTGTT	1023	58°	Groth and Barrowclough 1999
	R18	GATGCTGCCTCGGTCGGCCACCTTT			
rag2	Py1F	CCCTGAGTTTGGATGCTGTACTT	410	53º	Gamble et al. 2008
	Py1R	AACTGCCTRTTGTCCCCTGGTAT			

References to Table S2.

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Groth JG, Barrowclough GF (1999) Basal Divergences in Birds and the Phylogenetic Utility of the Nuclear RAG-1 Gene. Mol Phylogenet Evol 12(2): 115-123.

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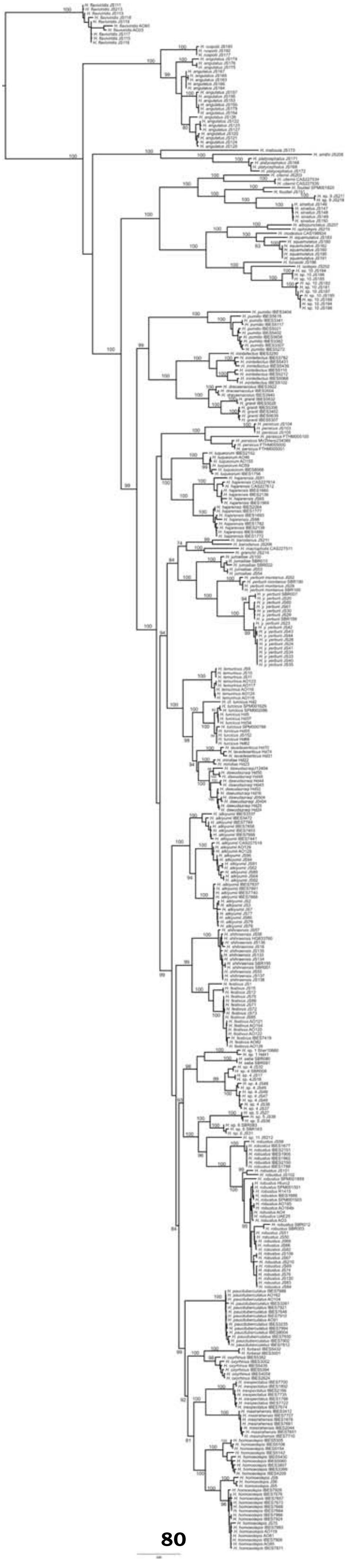
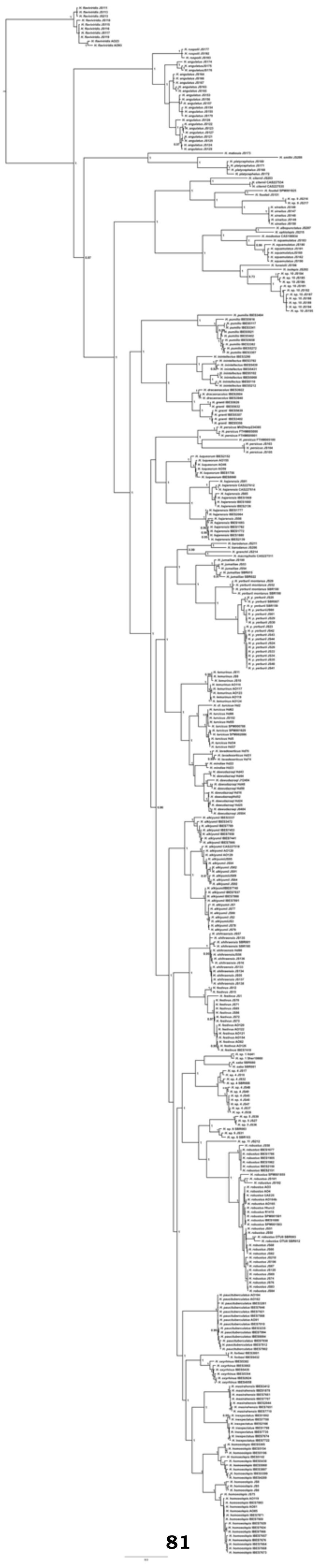
Table S3. List of all *Hemidactylus* species from Arabia, the Horn of Africa, the Levant and Iran. Black dots indicate known distribution records for each country, the rightmost column shows species included in this study.

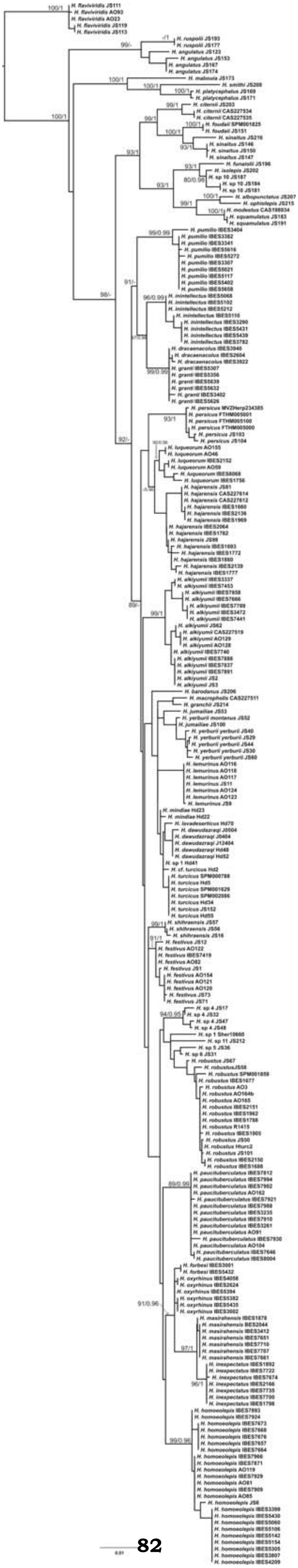
	Arabia					Iran	Africa							The Levant				Used in this study
	Oman	Saudi Arabia	UAE	Yemen	Socotra Archipel.		Djibouti	Egypt	Eritrea	Ethiopia	Kenya	Somalia	Sudan	Israel	Jordan	Syria	Lebanon	
H. albopunctatus										●		●						●
H. alkiyumii	●			●														●
H. angulatus									●	●	●		●					●
H. arnoldi							●					●						
H. barbierii											●							
H. barodanus									●	●		●						●
H. bavazzanoi										●	●	●						
H. citernii												●						●
H. curlei							?			●		●						
H. dawudazraqi															●	●		●
H. dracaenacolus					●													●
H. endophis	●																	
H. festivus	●			●														●
H. flaviviridis	●	●	●	●	●	●	●	●	●	●		●	●					●
H. forbesii					●													●
H. foudaii								●					●					●
H. frenatus							●				●	●						
H. funaiolii											●	●						●
H. granchii												●						●
H. granti					●													●
H. hajarensis	●																	●
H. homoeolepis	●	●		●	●													●
H. inexpectatus	●																	●
H. inintellectus					●													●
H. isolepis										●	●	●						●
H. jubensis										●								
H. jumailiae				●														●
H. klauberi												●						
H. laevis												●						
H. laticaudatus									●	●								
H. lavadeserticus																●		●

H. lemurinus	●			●														●
H. leschenaultii	●																	
H. luqueorum	●																	●
H. mabouia									●	●	●	●	●					●
H. macropholis									?	●	●	●						●
H. masirahensis	●																	●
H. megalops												●						
H. mercatorius											●	●						
H. mindiae								●							●			●
H. modestus											●	●						●
H. ophiolepis										●								●
H. ophiolepoides										●		●						
H. oxyrhinus					●													●
H. paucituberculatus	●																	●
H. persicus	?	●	●			●												●
H. platycephalus										●	●	●						●
H. puccionii												●						
H. pumilio					●													●
H. robustus	●	●	●	●	●	●	●	●	●	●	●	●	●					●
H. romeshkanicus						●												
H. ruspolii										●	●	●						●
H. saba				●														●
H. shihraensis				●														●
H. sinaitus									●	●		●	●					●
H. smithi										●		●						●
H. somalicus										●		●						
H. squamulatus										●	●	●						●
H. taylori												●						
H. tropidolepis										●	●	●						
H. turcicus								●					●	●	●	●	●	●
H. yerburii yerburii				●														●
H. yerburii montanus				●														●
H. yerburii pauciporosus												●						


Mediterranean Sea
Levant
Iraq
Iran
Sinai
Kuwait
Persian Gulf
Saudi Arabia
Egypt
Hijaz Mts
Arabian Peninsula
Red Sea
UAE
Asir Mts
Oman
Sudan
Dhofar
Hadhramaut
Eritrea
Yemen
Bab-el-Mandeb strait
Gulf of Aden
Socotra Archipelago
Ahmar Mts
Somalia
Ethiopia
South Sudan
Horn of Africa
100 m
250 m
500 m
1000 m
2000 m
3000 m
4000 m
0
125
250
500
750
1,000 Kilometers



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H. flaviviridis JS113
99/-
-/1
H. ruspolii JS193
H. ruspolii JS177
H. angulatus JS123
H. angulatus JS153
H. angulatus JS167
H. angulatus JS174
100/1
H. mabouia JS173
100/1
H. smithi JS208
100/1
H. platycephalus JS169
H. platycephalus JS171
100/1
99/1
H. citernii JS203
H. citernii CAS227534
H. citernii CAS227535
99/1
100/1
H. foudaii SPM001825
H. foudaii JS151
100/1
H. sinaitus JS216
93/1
H. sinaitus JS146
H. sinaitus JS150
H. sinaitus JS147
93/1
93/1
H. funaiolii JS196
H. isolepis JS202
80/0.98
H. sp 10 JS187
H. sp 10 JS184
H. sp 10 JS181
93/1
100/1
H. albopunctatus JS207
H. ophiolepis JS215
99/1
100/1
H. modestus CAS198934
H. squamulatus JS183
H. squamulatus JS191
99/0.99
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H. pumilio IBES3382
H. pumilio IBES3341
H. pumilio IBES5616
H. pumilio IBES5272
H. pumilio IBES3307
H. pumilio IBES5021
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H. pumilio IBES5402
H. pumilio IBES5658
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98/-
96/0.99
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H. inintellectus IBES5212
H. inintellectus IBES5110
H. inintellectus IBES3290
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H. inintellectus IBES5439
H. inintellectus IBES3782
H. dracaenacolus IBES3940
H. dracaenacolus IBES2604
H. dracaenacolus IBES3922
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H. granti IBES5356
H. granti IBES5639
H. granti IBES5632
H. granti IBES3402
H. granti IBES5626
H. persicus MVZHerp234385
93/1
H. persicus FTHM005001
H. persicus FTHM005100
H. persicus FTHM005000
H. persicus JS103
H. persicus JS104
92/-
90/0.98
H. luqueorum AO155
H. luqueorum AO46
H. luqueorum IBES2152
H. luqueorum AO59
H. luqueorum IBES8068
H. luqueorum IBES1756
-/0.98
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H. hajarensis IBES1969
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H. alkiyumii IBES7858
H. alkiyumii IBES7666
89/-
H. alkiyumii IBES7789
H. alkiyumii IBES3472
99/1
H. alkiyumii IBES7441
H. alkiyumii JS62
H. alkiyumii CAS227519
H. alkiyumii AO129
H. alkiyumii AO128
H. alkiyumii IBES7740
H. alkiyumii IBES7586
H. alkiyumii IBES7837
H. alkiyumii IBES7891
H. alkiyumii JS2
H. alkiyumii JS3
H. barodanus JS206
H. macropholis CAS227511
H. granchii JS214
H. jumailiae JS53
H. yerburii montanus JS52
H. jumailiae JS100
H. yerburii yerburii JS40
H. yerburii yerburii JS29
H. yerburii yerburii JS44
H. yerburii yerburii JS30
H. yerburii yerburii JS60
H. lemurinus AO116
H. lemurinus AO118
H. lemurinus AO117
H. lemurinus JS11
H. lemurinus AO124
H. lemurinus AO123
H. lemurinus JS9
H. mindiae Hd23
H. mindiae Hd22
H. lavadeserticus Hd70
H. dawudazraqi J0504
H. dawudazraqi J0404
H. dawudazraqi J12404
H. dawudazraqi Hd48
H. dawudazraqi Hd52
H. sp 1 Hd41
H. cf. turcicus Hd2
H. turcicus SPM000788
H. turcicus Hd5
H. turcicus SPM001629
H. turcicus SPM002086
H. turcicus Hd34
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H. turcicus Hd55
99/1
H. shihraensis JS57
H. shihraensis JS56
H. shihraensis JS16
91/1
H. festivus JS12
H. festivus AO122
H. festivus IBES7419
H. festivus AO82
H. festivus JS1
H. festivus AO154
H. festivus AO121
H. festivus AO120
H. festivus JS73
H. festivus JS71
94/0.95
H. sp 4 JS17
H. sp 4 JS32
H. sp 4 JS47
H. sp 4 JS48
H. sp 1 Sher10660
H. sp 11 JS212
H. sp 5 JS36
H. sp 6 JS31
H. robustus JS67
H. robustusJS58
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H. robustus IBES1677
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H. robustus AO164b
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89/0.99
H. paucituberculatus IBES7902
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91/0.96
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97/1
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96/1
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99/0.96
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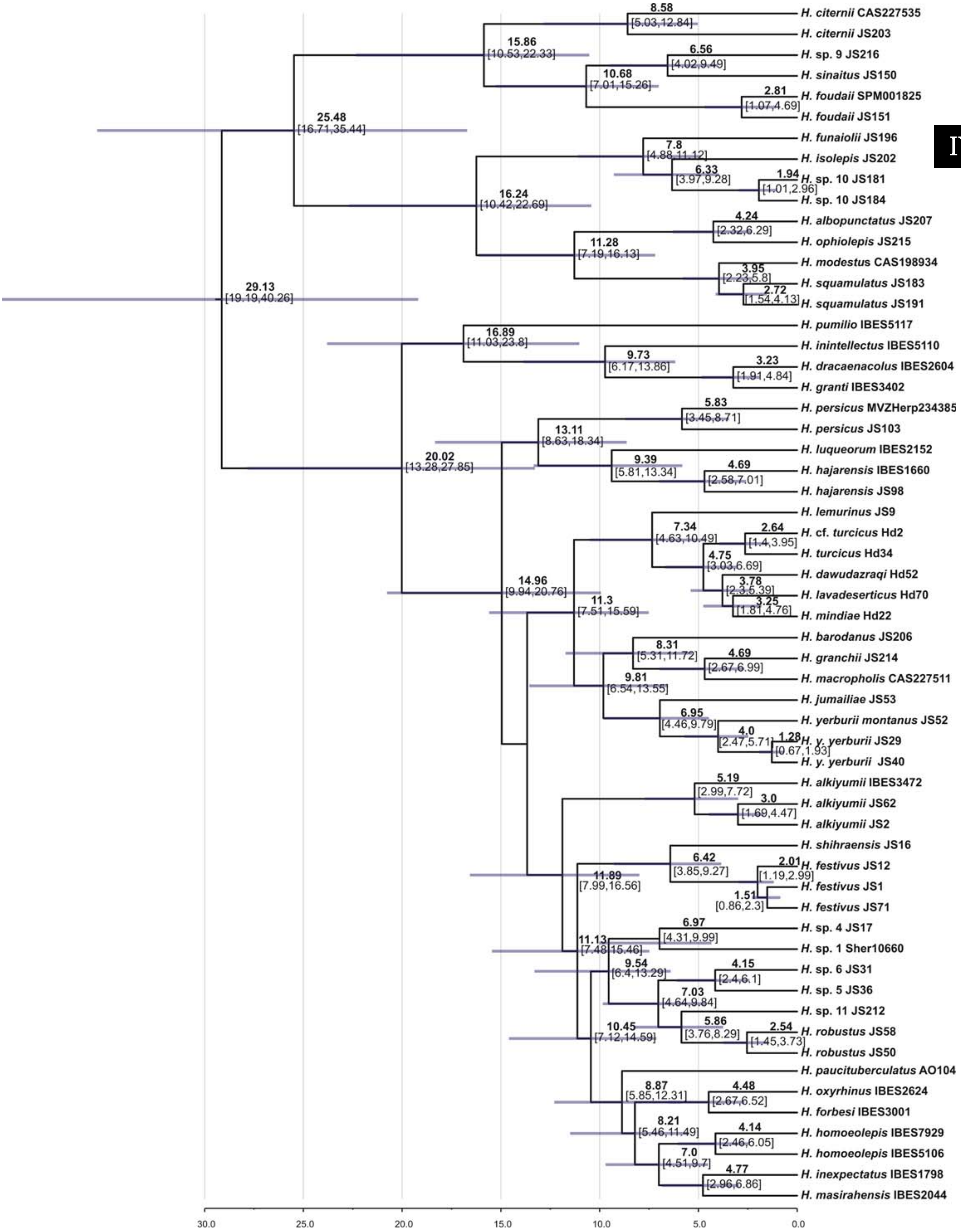
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H. inintellectus IBES5110
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3.23
H. dracaenacolus IBES2604
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H. granti IBES3402
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H. persicus MVZHerp234385
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9.39
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4.69
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H. lemurinus JS9
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H. turcicus Hd34
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3.78
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H. mindiae Hd22
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H. sp. 5 JS36
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H. sp. 11 JS212
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H. masirahensis IBES2044
30.0
25.0
20.0
15.0
10.0
5.0
0.0

Paper V

Šmíd, J., Moravec, J., Kratochvíl, L., Gvoždík, V., Nasher, A. K., Busais, S. M., Wilms, T., Shobrak, M. Y., Carranza, S. (2013): Two newly recognized species of *Hemidactylus* (Squamata, Gekkonidae) from the Arabian Peninsula and Sinai, Egypt. *ZooKeys* 355: 79–107. doi: 10.3897/zookeys.355.6190.
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Author contribution:
- JŠ acquired and the genetic and morphological data, performed the phylogenetic analyses and analyses of morphological characters, and wrote the paper

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RESEARCH ARTICLE

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Two newly recognized species of *Hemidactylus* (Squamata, Gekkonidae) from the Arabian Peninsula and Sinai, Egypt

Jiří Šmíd[1,2,†], Jiří Moravec[1,‡], Lukáš Kratochvíl[3,§], Václav Gvoždík[1,|],
Abdul Karim Nasher[4,¶], Salem M. Busais[5,6,#], Thomas Wilms[7,††],
Mohammed Y. Shobrak[8,‡‡], Salvador Carranza[9,§§]

1 *Department of Zoology, National Museum, Cirkusová 1740, Prague, Czech Republic* **2** *Department of Zoology, Faculty of Science, Charles University in Prague, Viničná 7, Prague, Czech Republic* **3** *Department of Ecology, Faculty of Science, Charles University in Prague, Viničná 7, Prague, Czech Republic* **4** *Faculty of Science, University of Sana'a, Sana'a, Yemen* **5** *Biology Department, Faculty of Education, University of Aden, Aden, Yemen* **6** *Faculty of Sciences, University of Hail, Hail, Saudi Arabia* **7** *Zoologischer Garten Frankfurt, Bernhard-Grzimek-Allee 1, Frankfurt am Main, Germany* **8** *Biology department, Faculty of Science, Taif University 888, Taif, Saudi Arabia* **9** *Institute of Evolutionary Biology (CSIC-Universitat Pompeu Fabra), Passeig Marítim de la Barceloneta 37–49, Barcelona, Spain*

† *http://zoobank.org/A1094092-6B76-4A14-AC6E-6D4EF2E49BC8*
‡ *http://zoobank.org/860D3E6B-8AC6-48A5-A94E-47F2F0CFFB72*
† *http://zoobank.org/BCF502BE-88CB-4CEF-B015-1975DB8A8920*
| *http://zoobank.org/BF30E84D-46C5-45EE-9140-E7E2154D9A66*
¶ *http://zoobank.org/D6D37DD5-AC94-4747-8C49-C043831FA591*
# *http://zoobank.org/71D11914-B33C-416A-B38F-C4E52989D29F*
†† *http://zoobank.org/582AA795-9E86-4608-9D10-353D47E610F2*
‡‡ *http://zoobank.org/7D466342-7FF7-4A35-B257-1D92459D390E*
§§ *http://zoobank.org/6CBAB265-9ECB-42EF-81F4-84E5ACC0342E*

Corresponding author: *Jiří Moravec* (jiri.moravec@nm.cz)

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Abstract

A recent molecular phylogeny of the Arid clade of the genus *Hemidactylus* revealed that the recently described *H. saba* and two unnamed *Hemidactylus* species from Sinai, Saudi Arabia and Yemen form a well-supported monophyletic group within the Arabian radiation of the genus. The name '*Hemidactylus saba* species group' is suggested for this clade. According to the results of morphological comparisons and the molecular analyses using two mitochondrial (*12S* and *cytb*) and four nuclear (*cmos*, *mc1r*, *rag1*, *rag2*) genes, the name *Hemidactylus granosus* Heyden, 1827 is resurrected from the synonymy of *H. turcicus* for the Sinai and Saudi Arabian species. The third species of this group from Yemen is described formally as a new species *H. ulii* **sp. n**. The phylogenetic relationships of the members of '*Hemidactylus saba* species group' are evaluated and the distribution and ecology of individual species are discussed.

Keywords

Reptilia, Gekkonidae, molecular phylogeny, Arabia, Red Sea, *Hemidactylus saba* species group, *Hemidactylus granosus* Heyden, 1827, *Hemidactylus ulii* sp. n.

Introduction

The genus *Hemidactylus* Oken, 1817, the second most species-rich genus of Gekkonidae (122 currently valid species; Uetz 2013), has been witnessing a species-description boom within the last decade. Eighteen species have been described within the last two years, most of them from the Arabian Peninsula and surroundings areas where 13 new species and a new subspecies have been discovered (Busais and Joger 2011a; Moravec et al. 2011; Torki et al. 2011; Carranza and Arnold 2012). Despite the large number of taxa added recently to the Arid clade of *Hemidactylus* [*sensu* Carranza and Arnold (2006)], it has been shown that the real diversity of *Hemidactylus* in Arabia and northeast Africa is still underestimated, with at least seven species remaining to be described (Busais and Joger 2011b; Moravec et al. 2011; Šmíd et al. 2013). A recent study (Šmíd et al. 2013) revealed that two of these newly recognized but still unnamed species, one from Sinai [labelled in accordance to previous works (Moravec et al. 2011; Šmíd et al. 2013) as *Hemidactylus* sp. 1] and one from Yemen (*Hemidactylus* sp. 4), clustered with the recently described Yemeni endemic *H. saba* Busais & Joger, 2011. They form a very well supported clade within the Arabian radiation of the genus (Fig. 1). Although the phylogenetic relationships among these three species were not resolved satisfactorily, it was inferred that they began to diversify approximately 7 million years ago (95% highest posterior density interval 4.3–10), what was followed by a subsequent dispersal of the Sinai species from southern Arabia to the north (Šmíd et al. 2013).

The discovery of a monophyletic species group consisting of one recently described and two newly recognized species calls upon a more thorough study of the nomenclatural status, evolutionary relationships, taxonomy and distribution of its members based on further genetic and morphological data. The present study focuses on this task.

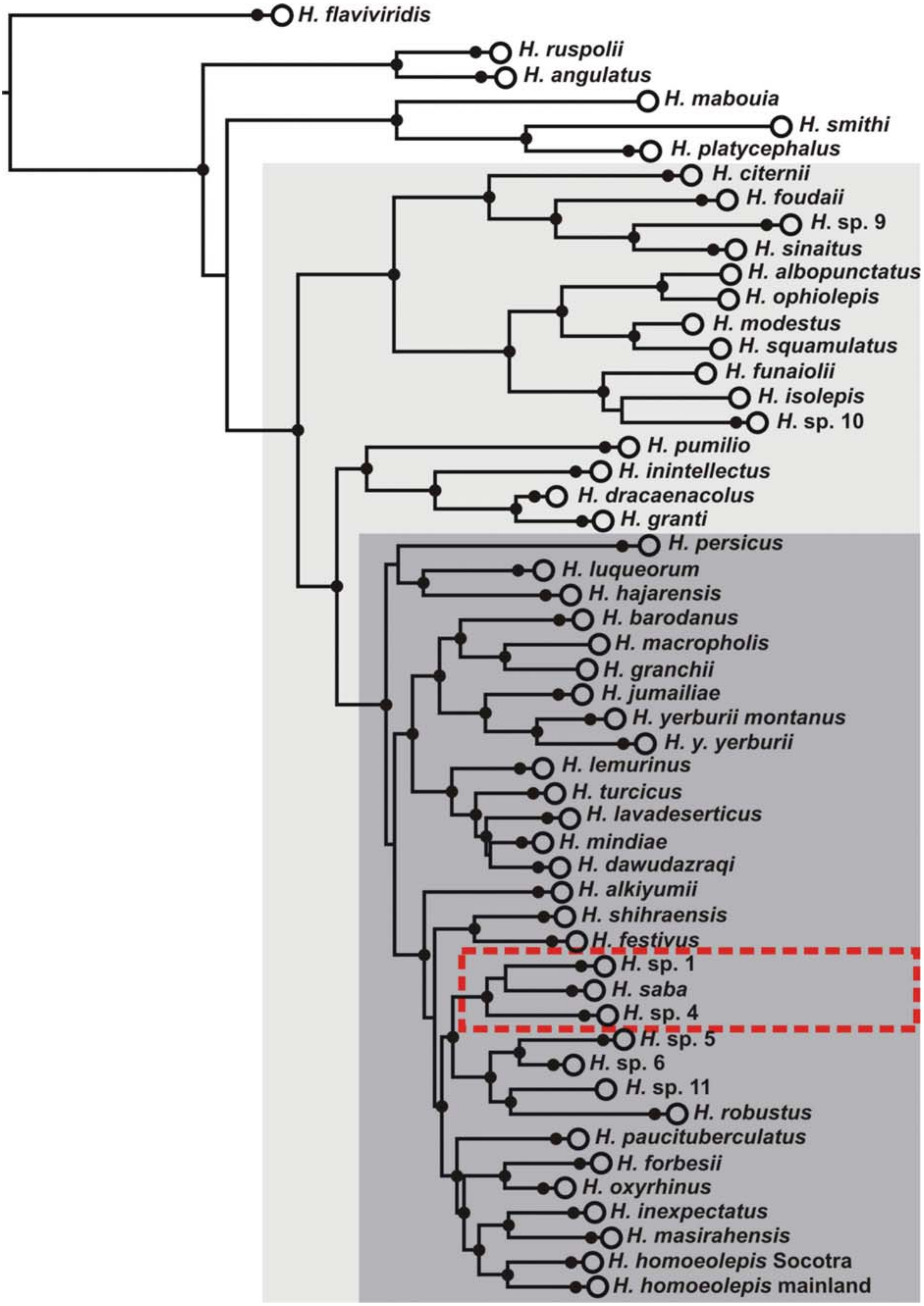

Figure 1. Phylogeny of the *Hemidactylus* Arid clade (light grey rectangle) modified after Šmíd et al. (2013). Dark grey rectangle highlights the Arabian radiation of this clade, dashed red line delimits the '*H. saba* species group' dealt with in this study. Black dots indicate ML bootstrap values ≥ 70 and BI posterior probabilities ≥ 0.95.

Material and methods

Material for phylogenetic analyses

In order to resolve the phylogenetic relationships between the two newly recognized *Hemidactylus* species and *H. saba* based on genetic data, a dataset containing only representatives of these three species was assembled. Apart from the data used by Šmíd et al. (2013), additional sequences of the following specimens were produced (Table 1): the holotype and two paratypes of *H. saba* (the only known existing material), 21 individuals from Sinai and Saudi Arabia belonging to *H.* sp. 1 (Šmíd et al. 2013), and five individuals of the undescribed species from Yemen (*H.* sp. 4; Šmíd et al. 2013), one of which was included in the study by Busais and Joger (2011a) (labelled as 'OTU 7' therein). Total genomic DNA was extracted using DNeasy Blood & Tissue Kit (Qiagen). Subsequently, sequences for up to two mitochondrial (12SrRNA [*12S*] – ca. 400 bp and cytochrome *b* [*cytb*] – 307 bp) and four nuclear (*cmos* – 402 bp, *mc1r* – 666 bp, *rag1* – 1023 bp, *rag2* – 408 bp) were produced using primers and PCR conditions described in details elsewhere (Šmíd et al. 2013). Chromatograms of all newly obtained sequences were checked by eye and assembled in Geneious 5.6.5 (Biomatters, http://www.geneious.com/). All genes were aligned individually using MAFFT (Katoh and Toh 2008) with the iterative refinement algorithm with 1000 iterations. Poorly aligned positions in the alignment of *12S* were eliminated with Gblocks (Castresana 2000) under low stringency options (Talavera and Castresana 2007), producing a final *12S* alignment of 386 bp. Alignments of all coding genes were trimmed so that all started by the first codon position and no stop codons were revealed when translated into amino acids with the appropriate genetic codes.

Phylogenetic analyses and haplotype networks construction

The final dataset consisted of 36 ingroup individuals. Specimen numbers, localities, and GenBank accession numbers of all genes sequenced are presented in Table 1. The alignment of all concatenated genes was 4012 bp long. The software jModelTest 2.1.1 (Guindon and Gascuel 2003; Darriba et al. 2012) was used to assess the best-fitting model of nucleotide substitution for each gene separately under the Akaike information criterion [AIC, Akaike (1973)]. The best-fitting models were selected as follows: *12S* – GTR+G; *cytb* – GTR+I+G; *cmos* – HKY+I; *mc1r* – TIM2+I; *rag1* – HKY+I; *rag2* – TrN+I). Phylogenetic analyses were performed using maximum likelihood (ML) and Bayesian inference (BI) methods. In order to detect the potential effect of the nuclear genes on the tree topology and nodal support, independent analyses were run on two datasets: (1) a dataset containing mtDNA genes only (*12S*, *cytb*), and (2) a concatenated dataset of all mtDNA and nDNA genes. Sequences of nuclear genes were not phased; heterozygous positions were coded according to the IUPAC ambiguity codes. Gaps were treated as missing data. Three specimens of *H. flaviviridis* and one of *H. angulatus*, representatives of two different clades of *Hemidactylus* (Carranza and Arnold 2006), were used to root the trees. Uncorrected genetic distances (*p* distances) were calculated in MEGA 5 (Tamura et al. 2011). Almost complete *cytb* sequences (1127 bp) of the new species from Yemen deposited in GenBank (Šmíd et al. 2013) were used to calculate *p* distances within this species, whereas an alignment of 307 bp was used to obtain intraspecific *p* distances within *H. saba* and the new species from Saudi Arabia and Sinai, and also interspecific *p* distances between these three species.

Maximum likelihood analyses of both datasets were performed in RAxML 7.0.3 (Stamatakis 2006) using raxmlGUI (Silvestro and Michalak 2012) graphical extension with parameters estimated independently for each partition, GTR+I+G model of nucleotide evolution and a heuristic search with 100 random addition replicates. Support of the tree nodes was assessed by bootstrap analysis with 1000 pseudoreplications (Felsenstein 1985).

The BI analyses were run in MrBayes 3.2.1 (Ronquist et al. 2012). Appropriate equivalents of the best-fitting models were specified to each partition (gene) and all parameters were unlinked across partitions. Analyses were performed with two runs and four chains for each run for 10^7 generations, with sampling interval of 1000 generations. Appropriate sampling was confirmed by examining the stationarity of log likelihood (ln*L*) values and the value of average standard deviations of the split frequencies. Convergence between two simultaneous runs was confirmed by the PSRF (potential scale reduction factor) value. From 10^4 sampled trees, 25% were discarded as a burn-in and a majority-rule consensus tree was produced from the remaining ones, with posterior probabilities (pp) of each clade embedded. Nodes with ML bootstrap values ≥ 70% and pp values ≥ 0.95 were considered highly supported (Huelsenbeck and Rannala 2004).

Heterozygous positions in nuclear genes were identified based on the presence of double peaks in chromatograms and using the Heterozygote Plugin in Geneious. For the purpose of haplotype network construction, haplotypes from sequences with more than one heterozygous position were resolved in PHASE 2.1.1 (Stephens et al. 2001). Input data for PHASE were prepared in SeqPHASE (Flot 2010). In order to include as much data as possible, sequences of all *Hemidactylus* species from the Arid clade used in our previous study (Šmíd et al. 2013) were combined with the newly produced sequences and phased together (data not shown). In the case of *rag1*, the original alignment was trimmed to 846 bp, the length at which sequences of all individuals did not contain any N ends that would give misleading results in the allele reconstruction (Joly et al. 2007). PHASE was run under default settings except the probability threshold, which was set to 0.7. Haplotype networks of the four nuclear markers (*cmos*, *mc1r*, *rag1*, *rag2*) were drawn using TCS 1.21 (Clement et al. 2000) with 95% connection limit.

Material for morphological analyses

Material for morphological comparison included 225 specimens of 8 *Hemidactylus* species and one subspecies (Appendix) and was obtained from the following collec-

Table 1. List of material used for the phylogenetic analyses. Holotype of *Hemidactylus ulii* sp. n. and *H. saba* are in bold. The column 'Loc. Nº' refers to the locality number as shown in Fig. 6.

Species	Code	Museum number	Country	Locality	Loc. Nº	Lat	Long	*12S*	*cytb*	*cmos*	*mc1r*	*rag1*	*rag2*
H. granosus	Sher10660	SMB 10660	Egypt	Ayoun Musa	1	29.875	32.649	JQ957071	JQ957216	JQ957148	JQ957282	-	JQ957409
H. granosus	Hd41	NMP6V70163/2	Egypt	Sharm el Sheik; Sinai	2	27.885	34.317	KC818724	HQ833759	JQ957148	-	KC818981	KF647606
H. granosus	Hd96	NMP6V70163/1	Egypt	Sharm el Sheik; Sinai	2	27.885	34.317	KC818724	HQ833759	-	-	-	KF647607
H. granosus	Hd97	NMP6V70163/3	Egypt	Sharm el Sheik; Sinai	2	27.885	34.317	KC818724	HQ833759	-	-	-	KF647608
H. granosus	HSA63	ZFMK 94084	Saudi Arabia	Al Wajh	3	26.208	36.4976	KC818724	HQ833759	KF647576	KF647589	KF647596	KF647610
H. granosus	HSA64	ZFMK 94085	Saudi Arabia	Al Wajh	3	26.208	36.4976	KF647571	-	-	-	-	-
H. granosus	HSA65	ZFMK 94086	Saudi Arabia	15 km S of Al Wajh	4	26.123	36.5689	KF647570	KF647581	KF647574	KF647590	KF647601	KF647610
H. granosus	HSA66	ZFMK 94087	Saudi Arabia	15 km S of Al Wajh	4	26.123	36.5689	KC818724	-	-	-	-	-
H. granosus	HSA67	ZFMK 94088	Saudi Arabia	15 km S of Al Wajh	4	26.123	36.5689	KF647569	-	-	-	-	-
H. granosus	HSA68	TUZC-R8	Saudi Arabia	15 km S of Al Wajh	4	26.123	36.5689	KF647570	-	-	-	-	-
H. granosus	HSA69	ZFMK 94089	Saudi Arabia	15 km S of Al Wajh	4	26.123	36.5689	KF647570	-	-	-	-	-
H. granosus	HSA70	TUZC-R9	Saudi Arabia	72 km N of Umluj	5	25.614	36.9867	KF647569	KF647582	JQ957148	KF647591	KF647600	KF647609
H. granosus	HSA62	TUZC-R10	Saudi Arabia	180 km W of Hail	6	26.883	40.0874	KF647569	KF647585	JQ957148	KF647588	KF647602	KF647609
H. granosus	HSA61	IBES10001	Saudi Arabia	Al Ghat	7	26.054	45.0003	KF647569	KF647585	JQ957148	KF647588	KF647599	KF647610
H. granosus	HSA57	IBES10183	Saudi Arabia	30 km NE of Alhawiyah	8	21.624	40.7094	KF647568	KF647580	-	-	KF647597	KF647610
H. granosus	HSA58	ZFMK 94090	Saudi Arabia	30 km NE of Alhawiyah	8	21.624	40.7094	KF647569	-	-	-	-	-
H. granosus	HSA59	TUZC-R11	Saudi Arabia	30 km NE of Alhawiyah	8	21.624	40.7094	KF647569	-	-	-	-	-
H. granosus	HSA60	IBES10344	Saudi Arabia	30 km NE of Alhawiyah	8	21.624	40.7094	KF647569	KF647583	-	-	KF647598	KF647610
H. granosus	HSA54	IBES10150	Saudi Arabia	20 km S of Ashayrah	9	21.602	40.6911	KF647568	KF647584	KF647576	KF647588	KF647595	KF647609
H. granosus	HSA55	ZFMK 94091	Saudi Arabia	20 km S of Ashayrah	9	21.602	40.6911	KF647569	KF647584	KF647575	KF647588	KF647596	KF647610
H. granosus	HSA56	IBES10363	Saudi Arabia	20 km S of Ashayrah	9	21.602	40.6911	KF647569	-	-	-	-	-
H. granosus	ZFMK 87236	ZFMK 87236	Saudi Arabia	Taif National Wildlife Research Center	10	21.25	40.96	KF647569	-	-	-	-	-
H. saba	BJ27	NHM-BS N41914	Yemen	Marib	17	14.9	45.5	KF647567	-	KF647573	-	-	KF647605
H. saba	BJ28	NHM-BS N41913	Yemen	Marib	17	14.9	45.5	KF647567	KF647579	KF647573	KF647586	-	KF647605
H. saba	**BJ29**	**NHM-BS N41912**	**Yemen**	**Marib**	17	14.9	45.5	KF647567	-	KF647573	KF647587	KF647594	KF647605
H. ulii sp. n.	JS48	NMP6V 74834/1	Yemen	Wadi Zabid	11	14.147	43.517	KC818730	KC818881	KC818789	KC818943	KC819001	KC819062

Species	Code	Museum number	Country	Locality	Loc. Nº	Lat	Long	*12S*	*cytb*	*cmos*	*mc1r*	*rag1*	*rag2*
H. ulii sp. n.	JS49	NMP6V 74834/2	Yemen	Wadi Zabid	11	14.147	43.517	KC818731	KC818882	KC818789	-	KF647603	KF647614
H. ulii sp. n.	JS45	not collected	Yemen	Al Hababi	12	13.333	43.722	KC818728	KC818878	-	-	-	KF647612
H. ulii sp. n.	JS46	NMP6V 74833/1	Yemen	Al Hababi	12	13.333	43.722	KC818728	KC818879	KC818789	-	-	KF647613
***H. ulii* sp. n.**	**JS47**	**NMP6V 74833/2**	**Yemen**	**Al Hababi**	12	13.333	43.722	KC818729	KC818880	KC818789	KC818942	KC819001	KC819061
H. ulii sp. n.	JS37	NMP6V 74832/1	Yemen	3 km S of Najd an Nashamah	13	13.358	43.957	KC818727	KC818876	KF647578	KC818943	-	KF647611
H. ulii sp. n.	JS38	NMP6V 74832/2	Yemen	3 km S of Najd an Nashamah	13	13.358	43.957	KC818727	KC818877	KC818789	KF647593	-	KF647614
H. ulii sp. n.	JS32	NMP6V 74835	Yemen	35 km W of Lahij	14	13.032	44.558	KC818726	KC818875	KC818788	KC818941	KC819000	KC819060
H. ulii sp. n.	BJ09	NHM-BS N41916	Yemen	Radman	15	14.1	45.283	KF647572	-	KF647577	KF647592	-	KC819059
H. ulii sp. n.	JS17	NMP6V 74831/1	Yemen	Al Hadr	16	13.877	45.8	KC818725	KC818874	KC818787	KC818940	KC818999	KC819059
H. ulii sp. n.	JS18	NMP6V 74831/2	Yemen	Al Hadr	16	13.877	45.8	KC818725	-	KC818789	-	KF647604	KC819059
H. angulatus	JS123	NMP6V 74845/2	Ethiopia	Arba Minch	-	6.034	37.564	KC818659	KC818807	KC818747	KC818903	KC818956	KC819018
H. flaviviridis	JS111	not collected	Pakistan	Okara	-	30.811	73.457	KC818676	KC818822	JQ957126	JQ957253	KC818965	KC819026
H. flaviviridis	JS113	not collected	India	Haridwar	-	29.964	78.201	KC818676	KC818823	JQ957126	JQ957253	KC818966	KC819027
H. flaviviridis	JS119	not collected	Oman	Jalan Bani Bu Hassan	-	22.089	59.278	JQ957119	JQ957183	KC818754	KC818911	KC818967	KC819028

tions: National Museum Prague, Czech Republic (NMP); Natural History Museum in Braunschweig, Germany (NHM-BS); Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt, Germany (SMF); Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany (ZFMK); Museo Civico di Storia Naturale "Giacomo Doria", Genova, Italy (MSNG); Museo Civico di Storia Naturale di Milano, Milano, Italy (MSNM); Museo Civico di Storia Naturale, Carmagnola, Italy (MCCI); Università di Firenze, Museo Zoologico "La Specola", Firenze, Italy (MZUF); British Museum of Natural History, London, UK (BMNH); California Academy of Sciences, San Francisco, USA (CAS); Taif University Zoological Collection, Taif, Saudi Arabia (TUZC); Institute of Evolutionary Biology Collection, Barcelona, Spain (IBES); Tomas Mazuch private collection, Dříteč, Czech Republic (TMHC); L. Kratochvíl collection (JEM); J. Šmíd collection (JS); Sherif Baha El Din private collection, Cairo, Egypt (SMB). Names of localities and governorates are spelled according to Google Earth (http://www.google.com/earth/). All coordinates are in WGS84 geographic coordinate system. Table of localities in a CSV text format and high-resolution photographs of all individuals analyzed in this study (397 pictures in total) have been deposited in MorphoBank (Project 1006; http://www.morphobank.org).

Morphological characters

The following measurements were taken with Powerfix digital calliper to the nearest 0.1 mm: snout-vent length (SVL), measured from tip of snout to vent; head length (HL), measured from tip of snout to retroarticular process of jaw; head width (HW), taken at the widest part of the head; head depth (HD), maximum depth of head; left eye diameter (E), measured horizontally; axilla-groin distance (AG), measured from posterior end of front limb insertion to anterior end of hind limb insertion; tail length (TL), measured from vent to tip of original tail. In addition to these metric characters, the following meristic characters were examined using a dissecting microscope: number of upper and lower labials (left/right); contact of nasals; number of infralabials in contact with first postmentals; mutual position of first postmentals; number of longitudinal rows of enlarged dorsal tubercles; number of lamellae under the first and fourth toe including unpaired proximal ones; and number of preanal pores in males. Terminology and diagnostic characters follow Moravec and Böhme (1997) and Moravec et al. (2011).

Results

Phylogenetic analyses of both datasets resulted in trees presented in Fig. 2. Tree topology remains congruent with that showed in Šmíd et al. (2013). The three species form a well-supported monophyletic group (mtDNA: ML bootstrap 85/ Bayesian pp 1; mtDNA + nDNA: 100/1) to which we will refer to as the '*Hemidactylus saba* species group'

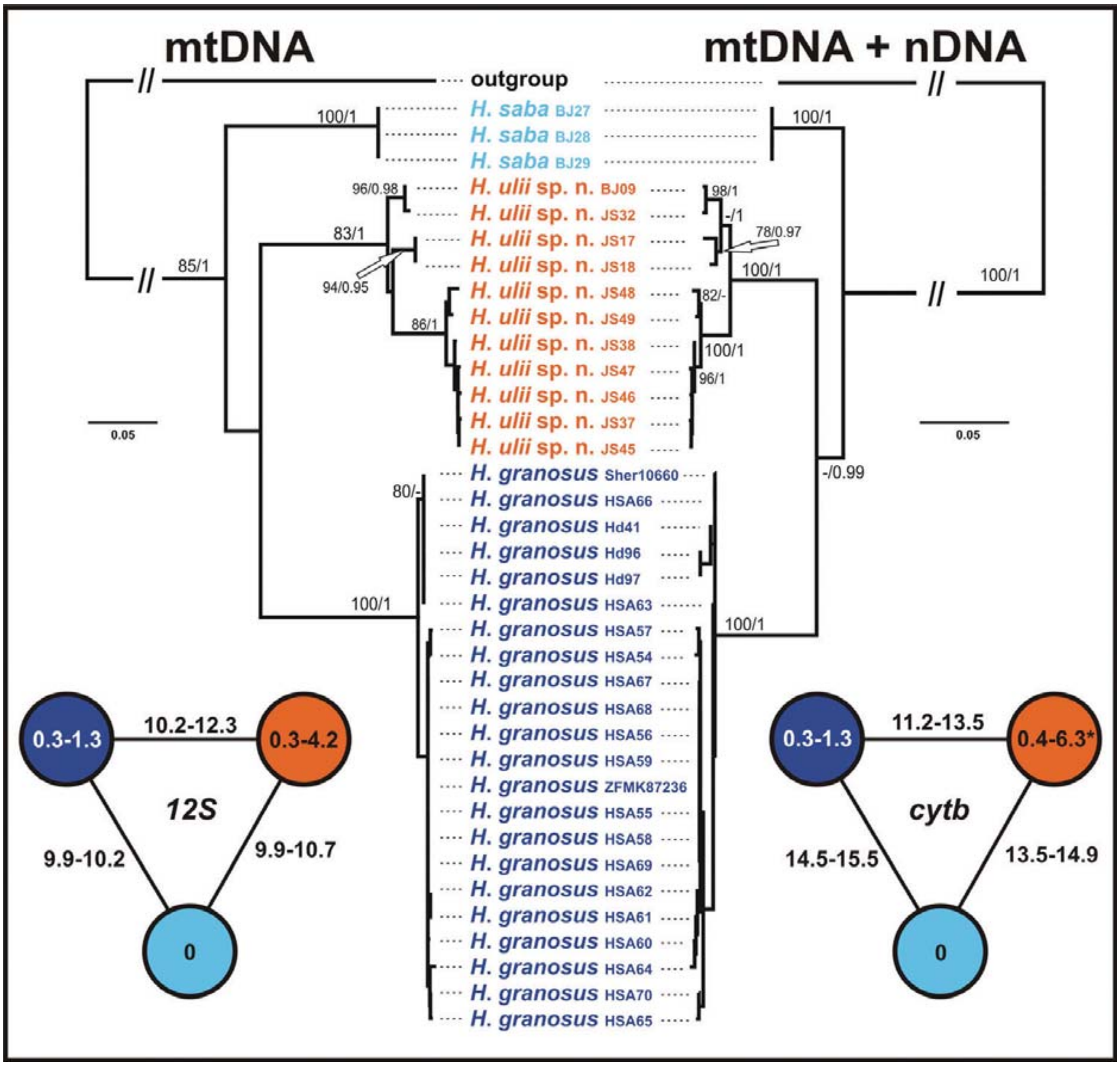

Figure 2. Maximum likelihood trees of mtDNA and mtDNA + nDNA datasets of the '*Hemidactylus saba* species group'. ML bootstrap values/Bayesian posterior probabilities are indicated by the nodes. *Hemidactylus flaviviridis* and *H. angulatus* were used as outgroups. At the sides, schematic networks showing intra- and interspecific uncorrected *p* distances (in %) in the sequences of *12S* and *cytb*. * intraspecific distances within *H. ulii* sp. n. are based on an alignment of 1127 bp, all other values for *cytb* are calculated for an alignment of 307 bp.

[support of individual species: *H. saba* (100/1; 100/1), *Hemidactylus* sp. 1 from Sinai and Saudi Arabia (100/1; 100/1), *Hemidactylus* sp. 4 from Yemen (83/1; 100/1)]. The performed analyses did not resolve the topology within this species group despite the inclusion of more individuals and additional genetic data in comparison with previous works (Moravec et al. 2011; Šmíd et al. 2013). Therefore, with the current knowledge, this group remains polytomic. There is no genetic variability within *H. saba* (all three specimens analyzed originate from the same locality) in both of the studied mtDNA genes and a very little variability in nDNA (*mc1r* and *rag1* only) (Fig. 3). The species from Sinai and Saudi Arabia also shows very little variation in mtDNA (intraspecific *p*

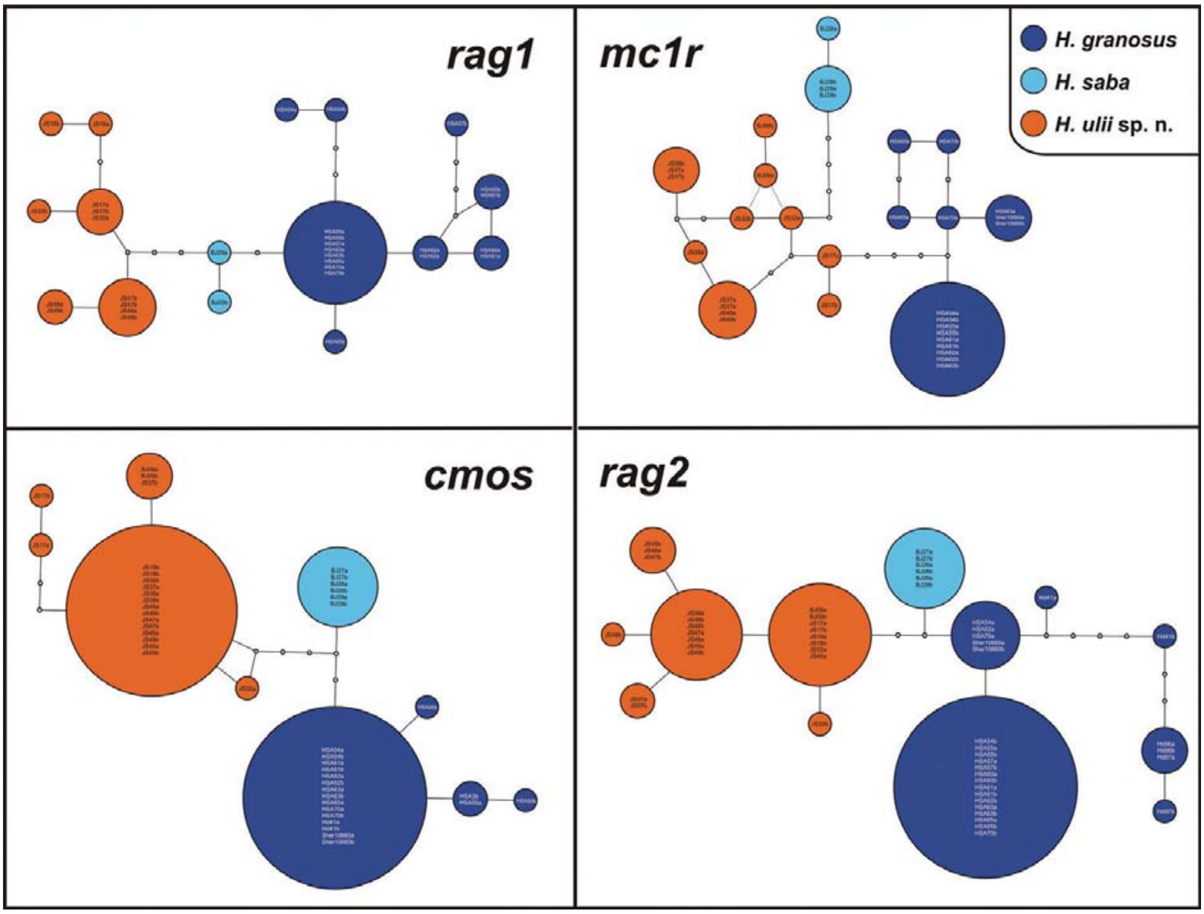

Figure 3. Nuclear allele networks of the four loci analyzed (*cmos*, *mc1r*, *rag1*, *rag2*). Circle sizes are proportional to the number of alleles. Small white circles represent mutational steps. Position of alleles BJ09a and BJ09b in the *mc1r* network is indicated by dashed lines because the sequence of the sample BJ09 (voucher NHM-BS N41916) was 108 bp shorter than the rest of the alignment and haplotype network reconstructions based on both 666 bp and 558 bp alignments linked these alleles to JS32b and JS32a, respectively.

distance max. 1.3% in both *12S* and *cytb*), but it varies in sequences of all the nDNA genes studied (Fig. 3). On the other hand, the unnamed *Hemidactylus* from Yemen exhibits relatively deep intraspecific differentiation into three well supported lineages. Uncorrected genetic distances between these lineages are up to 6.3% in *cytb* and up to 4.2% in *12S* (Fig. 2). Moreover, the nDNA genes show a high level of genetic differentiation (Fig. 3). Intra- and interspecific genetic distances in both mtDNA genes analyzed between all three species are shown in Fig. 2. The results of the nuclear networks indicate that all alleles for all four independent loci are specific for each species.

The results of the molecular analyses, together with a unique combination of morphological features (see below) confirm the earlier conclusion that the newly recognized *Hemidactylus* sp. 1 and *Hemidactylus* sp. 4 represent two separate species, whose taxonomy and nomenclature need to be resolved.

Systematics

Redescription of *Hemidactylus granosus* Heyden, 1827

http://species-id.net/wiki/Hemidactylus_granosus

Figs 4, 5

Hemidactylus granosus Heyden, 1827: p. 17; Tab. 5, Fig. 1. Lectotype SMF 8723 designated by Mertens (1967); collected by E. Rüppell 1827.

Hemidactylus turcicus (Linnaeus, 1758) – Boettger (1893: 29; part.); Anderson (1898: 80; part.); Salvador (1981: 84; part.); Baha El Din (2006: 66; part.).

Hemidactylus turcicus turcicus (Linnaeus, 1758) – Loveridge (1947: 143; part.); Mertens and Wermuth (1960: 79; part.); Baha El Din (2005: 19; part.); Mertens (1967: 55).

Hemidactylus verrucosus (Cuvier, 1829 [*corr. H. verrucosus* Gray, 1831]) – Rüppell (1845: 300; part.).

Hemidactylus sp. 1 – Moravec et al. (2011: 24); Carranza and Arnold (2012: 17); Šmíd et al. (2013: 3).

Terra typica (Heyden 1827): “Egypten, Arabien, und Abyssinien”.

Terra typica restricta [by lectotype designation by Mertens (1967)]: “Arabia petraea” = Sinai, Egypt.

Material examined. SMF 8723 (lectotype, adult male), Petr. Arabica [Arabia petraea], collected by E. Rüppell in 1827 (MorphoBank M305565–M305594); NMP6V 70163/1 (adult female, MorphoBank M305520–M305528), NMP6V 70163/2 (adult male, MorphoBank M305529–M305542), NMP6V 70163/3–4 (adult females, MorphoBank M305543–M305554, M305555–M305564), Egypt, South Sinai governorate, Sharm el-Sheikh (27.885°N, 34.317°E), ca. 30 m a.s.l., collected by R. Kovář and R. Víta in 1996; ZFMK 94084, ZFMK 94085 (adult females, MorphoBank M305744–M305760, M305761–M305775), Saudi Arabia, Tabuk province, Al Wajh (26.2076°N, 36.4976°E), 5 m a.s.l., 31. V. 2012; ZFMK 94086 (adult female, MorphoBank M305778–M305791), ZFMK 94088, ZFMK 94089 (adult males, M305793–M305799, M305807, M305822–M305827, M305828–M305841), Saudi Arabia, Tabuk province, 15 km S of Al Wajh (26.1226°N, 36.5689°E), 25 m a.s.l., 31. V. 2012; TUZC-R10 (adult female, MorphoBank M305728–M305743), Saudi Arabia, Hail province, 180 km N of Hail (26.8831°N, 40.0874°E), 1020 m a.s.l., 30. V. 2012; IBES10183, TUZC-R11 (adult males, MorphoBank M305656–M305671, M305688–M305701), ZFMK 94090,IBES10344 (adult females, MorphoBank M305672–M305687, M305702–M305717), Saudi Arabia, Makkah province, 30 km NE of Alhawiyah (21.6244°N, 40.7094°E), 1295 m a.s.l., 28. V. 2012; IBES10150, IBES10363 (adult males, MorphoBank M305615–M305628, M305643–M305655), ZFMK 94091 (adult female, MorphoBank M305629–M305642), Saudi Arabia, Makkah province, 20 km S of

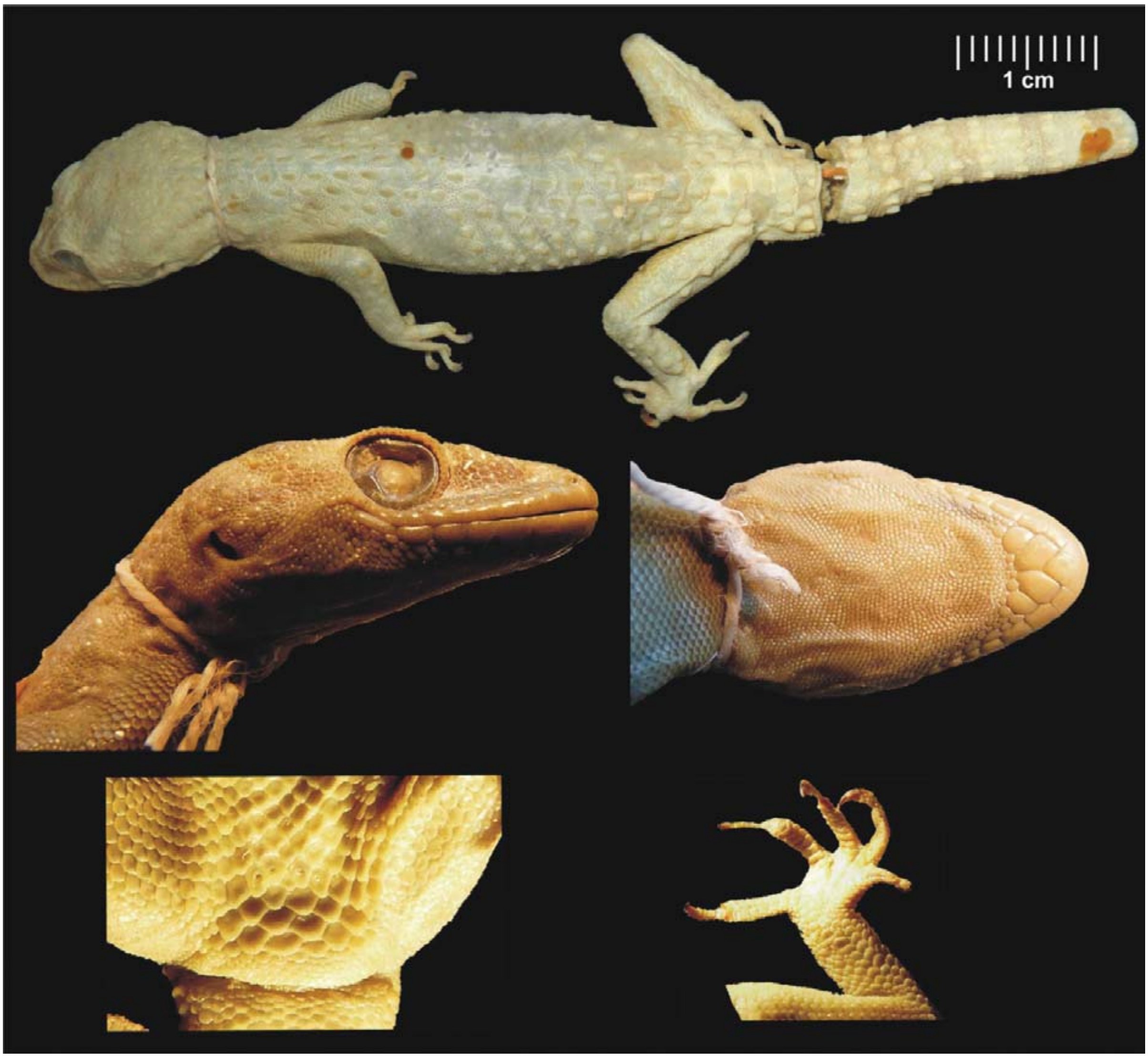

Figure 4. Male lectotype of *Hemidactylus granosus* (SMF 8723) from Sinai, Egypt. General habitus, lateral and ventral view of the head, precloacal region with preanal pores, right hind leg. Scale refers to the uppermost picture only.

Ashayrah (21.6022°N, 40.6911°E), 1316 m a.s.l. , 28. V. 2012. All Saudi specimens were collected by M. Shobrak, S. Carranza and T. Wilms.

Referred material. SMB 10660, Egypt, Suez governorate, Ayoun Musa (29.875°N, 32.649°E), ca. 12 m a.s.l., collected by S. Baha El Din, date unknown; TUZC-R9, Saudi Arabia, Tabuk province, 72 km N of Umluj (25.614°N, 36.9867°E), 19 m a.s.l., 31. V. 2012; IBES10001, Saudi Arabia, Riyadh province, Al Ghat (26.0545°N, 45.0003°E), 776 m a.s.l., 29. V. 2012; ZFMK 94087, TUZC-R8, Saudi Arabia, Tabuk province, 15 km S of Al Wajh (26.1226°N, 36.5689°E), 25 m a.s.l., 31. V. 2012; ZFMK 87236, Saudi Arabia, Makkah province, Taif National Wildlife Research Center (21.25°N, 40.96°E), 25. VI. 2007 by T. Wilms. These specimens were used for the molecular analyses only.

Status and nomenclature. Heyden (1827) described *Hemidactylus granosus* as a new species occurring in Egypt, Arabia and Abyssinia (Ethiopia and Eritrea). Although not explicitly mentioned by the author, the description was apparently based on four specimens collected by Rüppell currently deposited in the Senckenberg Naturmuseum Frankfurt (collection numbers SMF 8723–8726). Heyden did not diagnose the new species against *H. turcicus* (Linnaeus, 1758) and in respect to our today's knowledge on the morphological variation in *Hemidactylus* the description of *H. granosus* is very general. Traditionally, *H. turcicus* has been considered a common species widely distributed across the Mediterranean and the Middle East. As the general diagnostic characters of *H. granosus* given by Heyden (1827) were also applicable to *H. turcicus* at that time, the name *Hemidactylus granosus* Heyden, 1827 was considered its junior synonym (e.g. Boulenger 1885, Loveridge 1947, Mertens and Wermuth 1960, Mertens 1967, Salvador 1981, Baha El Din 2006).

Recent examination (by JŠ) of four specimens collected by Rüppell (SMF 8723–8726) has shown that one of them [SMF 8723 designated by Mertens (1967) as lectotype of *H. granosus*; for description see below] corresponds morphologically to *Hemidactylus* sp. 1 from Sinai. The other three specimens from this series morphologically correspond to *H. robustus* Heyden, 1827 (SMF 8725, 8726) and *H.* cf. *granosus* (SMF 8724), an animal superficially resembling *H. granosus* but differing from the members of the '*H. saba* species group' in several important characters (see below). These findings lead to the conclusion that *Hemidactylus granosus* Heyden, 1827 is a valid taxon and needs to be resurrected from the synonymy of *H. turcicus*. In the light of current knowledge, the range of *H. turcicus* does not include a large part of Egypt, being restricted mostly to northern Egypt including Sinai and its Red Sea coast. The species is also missing in Arabia (sensu lato) and Ethiopia (Carranza and Arnold 2006; Moravec et al. 2011; Rato et al. 2011; Šmíd et al. 2013).

Diagnosis. *Hemidactylus granosus* is a member of the '*Hemidactylus saba* species group' within the Arabian radiation of the Arid clade as evidenced by the mtDNA and nDNA analyses. The species has the following combination of molecular and morphological characters: (1) Uncorrected genetic distance from *H. saba*: 9.9–10.2% in *12S*, 14.5–15.5% in *cytb*; from *Hemidactylus* sp. 4: 10.2–12.3% in *12S*, 11.2–13.5% in *cytb*; (2) small size, SVL 39.0–53.2 mm in males, 40.6–53.3 mm in females; (3) rather elongated head, head length 24–28% of SVL, head width 68–86% of head length, head depth 33–47% of head length; (4) tail length 107–130% of SVL; (5) uppermost nasals separated by a small shield in 89% of specimens; (6) large anterior postmentals in wide mutual contact, and always in contact with the 1st and 2nd lower labial; (7) 9–11 upper labials; (8) 7–9 lower labials; (9) 14–15 longitudinal rows of enlarged, subtriangular, distinctly keeled dorsal tubercles; (10) 7–8 lamellae under the 1st toe and 10–13 under the 4th toe; (11) ca. 6–8 tail segments bearing 6 pointed tubercles; (12) 4–7 preanal pores in males forming a continuous row on the left and right side; (13) subcaudals enlarged; (14) in life, dorsum pale buff with dark brown spots tending to form transverse bands or X-shaped markings, dark horizontal stripe in prefrontal and temporal region, tail with ca. 10–13 dark brown transverse bands, venter white.

Description of the lectotype. SMF 8723, adult male [erroneously determined as female by Mertens (1967)]. Head and body moderately depressed (Fig. 4). Upper labials (10/10), lower labials (8/7). Nostril between rostral, three subequal nasals and in punctual contact with first upper labial. Uppermost nasals separated by a small inserted scale. Mental triangular, as long as wide. Anterior postmentals long, in a broad contact

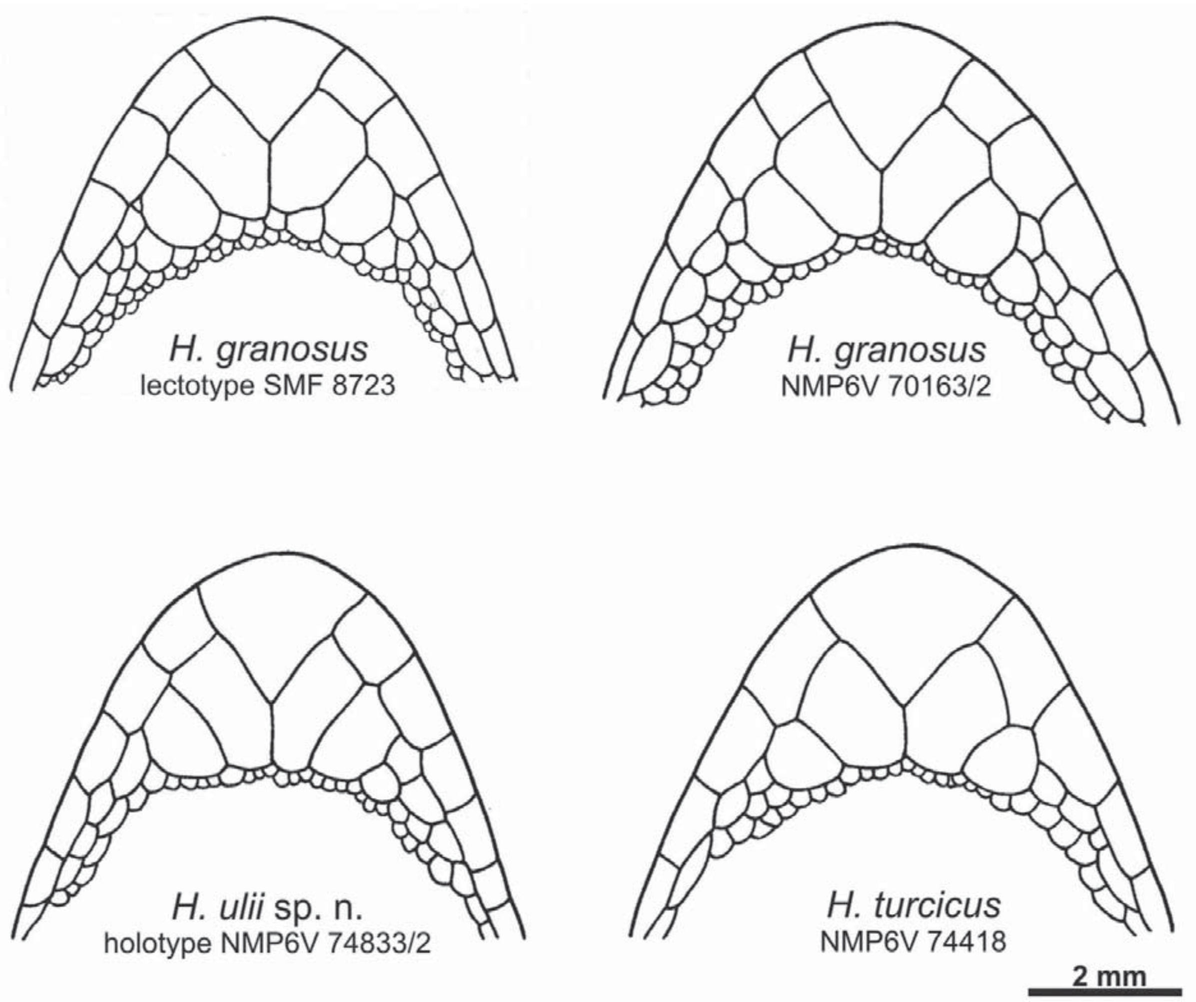

Figure 5. Schematic drawing of the chin region of the lectotype and a new specimen from Sinai of *Hemidactylus granosus*, the holotype of *H. ulii* sp. n., and *H. turcicus* from Sinai.

with each other, both in contact with the 1st and 2nd lower labial reaching in about one fourth of the width of the 2nd labial. Second postmentals almost round, touching only the 2nd lower labial (Fig. 5). Two enlarged scales behind each second postmental, the lateral ones in contact with the 3rd lower labial. Eye moderate (E/HL=0.26). Head long, distinctly separated from body by a slender neck. Crescent-shaped ear opening. Interorbital region, crown of head and temporal area above the level of ear opening covered by round smooth tubercles. Dorsal region of the specimen is slightly scarred so it is not possible to count the enlarged tubercles on both sides precisely, but there are seven longitudinal rows of large, keeled and caudally pointed tubercles on the left side from which we infer there were originally 14 rows on both sides together. Lower arms, thighs and lower legs with prominent tubercles without keels. Tail original with 6 segments bearing 6 pointed tubercles, broken into three pieces, subcaudals enlarged from just after the hemipenial bulges. Lamellae under the 1st toe 7/7, lamellae under the 4th toe 11/11. Four preanal pores in a continuous row. No femoral pores or enlarged femoral scales. Colour (in alcohol) faded due to long fixation.

Measurements (in mm): SVL 51.5, HL 12.9, HW 9.8, HD 6.0, E 3.3, AG 23.7.

Paralectotype SMF 8724 differs from other individuals of *H. granosus* in having relatively high head (HD 50% of HL), lower number of lower labials (6), uppermost nasals in wide contact, first postmentals in contact with 1st lower labials, and 2 preanal pores.

Comparison. *Hemidactylus granosus* can be distinguished from other member of the '*Hemidactylus saba* species group' and from other congeners distributed in Sinai and the Red Sea coast by the following set of characters (see also Table 2).

From *H. saba* by having distinctly keeled dorsal tubercles (smooth in *H. saba*), and lower number of lamellae under the 1st toe (7–8 vs. 8–9).

From *Hemidactylus* sp. 4 (described below) by its larger size (max. SVL 53.2 mm vs. 40.4 mm in males, 53.3 mm vs. 40.7 mm in females), in having more frequently separated uppermost nasals (100% vs. 60% of specimens), lower number of preanal pores in males (4–7 vs. 8), and higher number of lamellae under the 1st (7–8 vs. 5–6) and 4th (10–13 vs. 8–9) toe.

From *H. flaviviridis* by its smaller size (max. SVL 53.2 mm in males and 53.3 mm in females vs. up to 90 mm [Anderson (1999); sexes not distinguished]), by the presence of enlarged dorsal tubercles, and the absence of femoral pores in males.

From *H. mindiae* by the lower number of supralabials (9–11 vs. 10–12), by having anterior postmentals in wide contact (punctual in *H. mindiae*) and keeled dorsal tubercles (smooth in *H. mindiae*).

From *H. robustus* by the larger size of males (max. SVL 53.2 mm vs. 43.7 mm), longer tail (tail length 53.0–64.8 mm vs. 40.9–48.7 mm), and lower number of preanal pores in males (4–7 vs. 5–8).

From *H. turcicus* by its higher number of upper labials (9–11 vs. 7–10), in having anterior postmentals more frequently in contact with 2nd lower labial (100% vs. 12.1%), in having anterior postmentals in wide mutual contact behind the mental scale (contact punctual in 67% specimens of *H. turcicus*), and by the lower number of preanal pores in males (4–7 vs. 6–10).

Variation. Specimens with intact tail vary in number of tail segments bearing 6 pointed tubercles (7–8). The original portion of the tail of the female NMP6V 70163/4 is very wide at the base, separated from cloacal region by a basal constriction. One specimen (IBES10212) is the only animal with 15 longitudinal rows of enlarged tubercles. Another one (IBES10284) has uppermost nasals in wide contact. Most striking is the variation in the number of preanal pores in males. Whereas the lectotype and the only male from Sinai (NMP6V 70163/2) have both 4 pores, all males from Saudi Arabia have 6–7 pores. There seems to be clinal variability in this character, males from NW of the known range (Fig. 6) possess only 4 preanal pores, all animals from the eastern Red Sea coast in Saudi Arabia have 6 pores and a single individual from the southern limit of the range has 7 pores.

Coloration (in life) pale buff dorsally (Fig. 7). Conspicuous dark brown horizontal stripe in loreal and temporal area, terminated at the level of ear from where it continues in a series of dark patches on the neck. Four barely visible X-shaped markings on dorsum formed mainly by dark brown enlarged tubercles (first on nape, second across scapulae, third in lumbal region, and fourth just in front of the anterior insertion of hind limbs). Isolated dark brown stripe runs across body in the place of posterior insertion of hind

Table 2. Morphological comparison among members of the '*Hemidactylus saba* species group' and with other *Hemidactylus* species from Sinai and SW Yemen. The values are given as follows: sample size, mean ± standard deviation above, min. – max. value below.

Species / Character	***H. saba* species group**						***H. robustus***		***H. turcicus***		***H. mindiae***		***H. jumailiae***		***H. y. yerburii***		***H. y. montanus***	
	H. granosus		***H. saba***		***H. ulii* sp. n.**													
Upper labials	18	9.4 ± 0.5	3	9.3 ± 0.8	10	9.3 ± 0.8	27	9.4 ± 0.7	33	8.2 ± 0.5	5	10.8 ± 0.8	18	9.8 ± 0.7	51	10.3 ± 0.7	57	10.2 ± 0.7
		9–11		8–10		8–10		8–11		7 - 10		10 - 12		8–12		9–12		8–12
Lower labials	18	7.4 ± 0.4	3	7.7 ± 0.6	10	8.0 ± 0.6	27	7.7 ± 0.6	33	6.7 ± 0.5	5	8.1 ± 0.4	18	8.2 ± 0.6	51	7.9 ± 0.5	57	7.8 ± 0.6
		7–9		7–8		7–9		6–9		6–8		7–9		7–10		6–9		6–10
Nasals in contact (%)	18	11	3	33.3	10	40	27	22.2	33	21.2	5	0	18	5.5	51	7.8	57	5.3
1st postmental in contact with 2nd lower labial (%)	18	100	3	33.3	10	100	27	70.3	33	12.1	5	80	18	83.3	51	98	57	89.5
Rows of dorsal tubercles	18	14.1 ± 0.2	3	14 ± 0.0	10	14.1 ± 1.0	27	14.8 ± 1.2	33	13.8 ± 0.7	5	12.4 ± 0.9	15	14 ± 1.4	46	15.3 ± 1.1	53	15.2 ± 1.2
		14–15		14–14		12–16		13–18		12–16		12–14		12–16		13–18		12–18
Pores	8	5.6 ± 1.1	1	6	2	8 ± 0.0	9	6.1 ± 0.8	13	7.2 ± 1.4	1	4	9	7.2 ± 1.1	23	13.7 ± 2.2	27	11.2 ± 1.1
		4–7				8 - 8		5–8		6–10				6–9		10–18		9–13
Lamellae under 1st toe	18	7.4 ± 0.5	3	8.2 ± 0.3	10	5.4 ± 0.5	27	6.1 ± 0.5	32	6.5 ± 0.5	5	6.2 ± 0.3	18	6.9 ± 0.7	51	6.7 ± 0.4	57	6.3 ± 0.4
		7–8		8–9		5–6		5–8		6–7		6–7		6–8		6–8		5–7
Lamellae under 4th toe	18	11.5 ± 0.7	3	11.2 ± 0.3	10	8.6 ± 0.5	27	10.1 ± 0.7	32	9.7 ± 0.6	5	10 ± 0.0	18	10.9 ± 0.8	51	10.4 ± 0.6	57	10.2 ± 0.5
		10 - 13		11–12		8–9		8–12		8–11		10–10		9–12		9–12		9–11
SVL (males)	8	46.8 ± 5.9	1	58.3	2	38.6 ± 2.6	8	41.8 ± 2.3	13	46.0 ± 5.8	1	49.3	8	48.4 ± 4.1	23	58.5 ± 7.1	25	56.5 ± 5.7
		39.0–53.2				36.8–40.4		37.0–43.7		37.3–54.1				40.0–54.2		43.6–74.9		45.2–65.3
SVL (females)	10	49.0 ± 3.5	2	53.5 ± 7.9	2	40.1 ± 0.9	16	43.6 ± 4.7	18	49.2 ± 5.1	4	46.2 ± 11.4	8	48.6 ± 3.3	23	55.7 ± 5.3	30	52.6 ± 5.1
		40.6–53.3		47.9–59.1		39.4–40.7		32.7–50.1		39.4–56.2		35.6–56.6		43.1–54.0		43.6–62.1		42.4–64.1

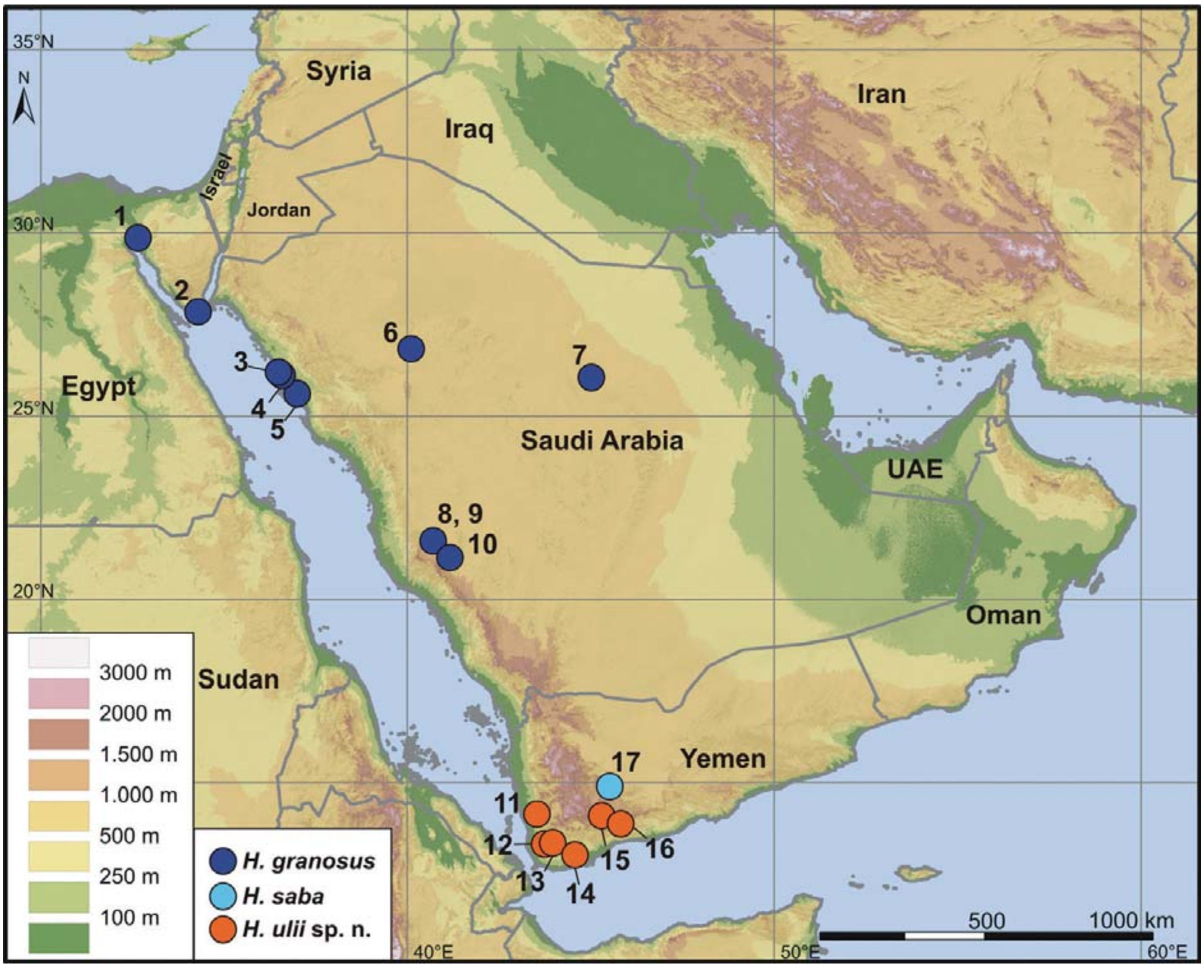

Figure 6. Distribution map of *Hemidactylus granosus*, *H. saba* and *H. ulii* sp. n. For the list of locality names and their corresponding numbers in the map see Table 1.

limbs. Regenerated tails are uniformly buff from above. Dorsum, sides of chin, underside of front and hind limbs and underside of tail with faint stipple visible under magnification. Belly white. Tips of fingers and toes black behind insertion of terminal phalanges. Coloration is consistent among all specimens and varies only in distinctness of the markings.

There is a very low variation in mtDNA between specimens from Sinai and Saudi Arabia (max. 1.3% in both *12S* and *cytb*). All animals from Sinai share the same haplotypes in *12S* and also *cytb* gene. All four nuclear loci studied show some degree of intraspecific variation (Fig. 3).

Distribution and ecology. Eduard Rüppell collected the original series in 1827 when he began his marine biological studies of the Red Sea and travelled from Egypt to Eritrea. There is no specific information that he went to Arabia as well (Rüppell 1826–1828; Klausewitz 2002; Wagner 2008); therefore the original distribution of *H. granosus* described as "Egypt, Arabia, and Abyssinia [Ethiopia and Eritrea]" by Heyden (1827) was probably too general and incorrect. Because there were no other specimens assignable with certainty to *H. granosus* apart from the four individuals collected in Sinai (SMF 8723–8726, for their current status see 'Status and nomenclature' section) (Boettger 1893), one of which became the lectotype after Mertens' (1967) designation, Sinai could

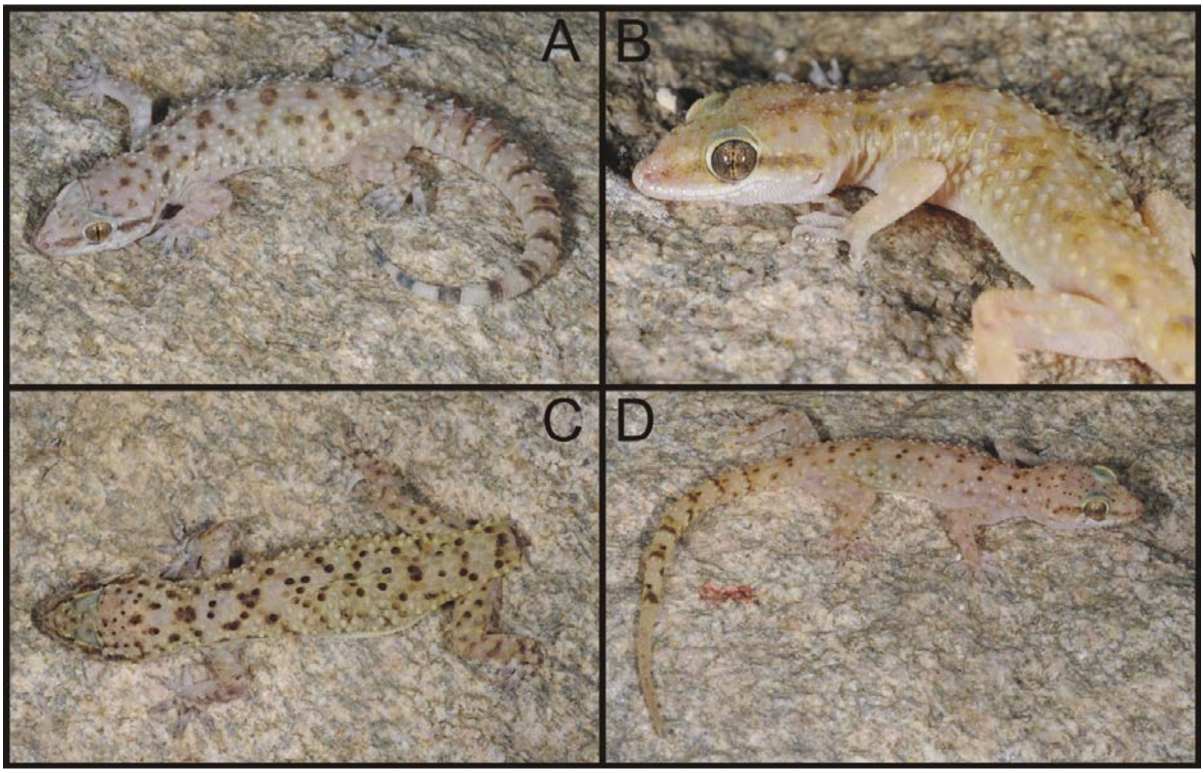

Figure 7. Live specimens of *H. granosus* from Saudi Arabia. **A** IBES10344, 30 km NE of Alhawiyah (loc. number 8) **B** TUZC-R10, 180 km W of Hail (6) **C** ZFMK 94091, 20 km S of Ashayrah (9) **D** ZFMK 94086, 15 km S of Al Wajh (4).

be considered the only reliable locality for *H. granosus*. Here, *H. granosus* is also confirmed from two coastal localities in south and west Sinai and from coastal and inland regions in western and central Saudi Arabia (Fig. 6). Nevertheless, a wider distribution of the species along the Red Sea coast can be expected. According to Baha El Din (2005), *Hemidactylus* geckos inhabiting the interior lowland of Sinai and the Eastern Desert in Egypt stand out in having notably coarse scalation. Interestingly, the areas with occurrence of animals with coarse scalation correspond with the presence of individuals with low numbers of preanal pores (Baha El Din 2005), which is typical for the Sinai populations of *H. granosus*.

In 1996, when the NMP specimens were collected, the locality in Sharm el-Sheikh was formed by a crop field supplied with drain water from nearby habitations. Geckos were found during the day under unused empty barrels and also inside buildings. Other species syntopic with *H. granosus* in Sharm el-Sheikh were: *Hemidactylus turcicus*, *Chalcides ocellatus* (Forskål, 1775), *Stenodactylus sthenodactylus* (Lichtenstein, 1823), and *Ptyodactylus hasselquistii* (Donndorff, 1798) (R. Víta in litt, 2013). However, when visited again in 2010, the locality had changed dramatically (R. Víta in litt, 2013). The whole area was under heavy development and the irrigation channels had disappeared. The current conditions at the place are unknown to us. In 2011 JM surveyed a neighbouring urban area east of this locality. It was covered by a mosaic of tourist resorts and abandoned ruderal plots. In dry anthropogenic habitats (e.g. rubbish dumps, road ditches, old walls and buildings, abandoned construction sites, natural but heavily disturbed open areas, etc.) dominated two very abundant gecko species. *Ptyodactylus* *hasselquistii* occupied primarily various vertical surfaces whereas *Cyrtopodion scabrum* (Heyden, 1827) prevailed on the ground. *Tropiocolotes nattereri* Steindachner, 1901 was found in dry and relatively well-preserved natural places. *Hemidactylus turcicus* was occasionally encountered in more humid artificial habitats in parks and hotel gardens. Specimens from Saudi Arabia were mostly collected during the day inside concrete tunnels under roads. In some of the tunnels they were syntopic with *Ptyodactylus hasselquistii*. One specimen was also collected on the walls of the Taif National Wildlife Research Centre, where it was also syntopic with *Ptyodactylus hasselquistii*.

***Hemidactylus ulii* sp. n.**

http://zoobank.org/8E15D1BC-5D4D-4A55-AFEB-2E20FAD40112
http://species-id.net/wiki/Hemidactylus_ulii
Figs 5, 7, 8

Hemidactylus turcicus – Rösler and Wranik (1998: 120; part.).
Hemidactylus sp. 'OTU7' – Busais and Joger (2011a: 27); Busais and Joger (2011b: 268); Carranza and Arnold (2012: 95).
Hemidactylus sp. 4 – Moravec et al. (2011: 25); Šmíd et al. (2013: 3).

Holotype. NMP6V 74833/2, adult male (MorphoBank M305892–M305902), Yemen, Ta'izz governorate, Al Hababi (13.333°N, 43.722°E), 463 m a.s.l.; collected by L. Kratochvíl, 28. X. 2007.

Paratypes. NMP6V 74833/1 (adult male, MorphoBank M305884–M305891), same collecting data as holotype; NMP6V 74831/1–2 (one adult and one subadult female, MorphoBank M305854–M305863, M305864–M305870), Yemen, Abyan governorate, Al Hadr (13.877°N, 45.8°E), 1151 m a.s.l., collected by L. Kratochvíl on 22. X. 2005; NMP6V 74832/1–2 (two subadult females, MorphoBank M305871–M305875, M305876–M305883), Yemen, Ta'izz governorate, ca. 3 km S of Najd an Nashamah by road (13.358°N, 43.957°E), 1182 m a.s.l., collected by L. Kratochvíl on 26. X. 2007; NMP6V 74834/1–2 (one adult and one subadult female, MorphoBank M305903–M305911), Yemen, Dhamar governorate, Wadi Zabid (14.147°N, 43.517°E), 292 m a.s.l., collected by L. Kratochvíl on 29. X. 2007; NHM-BS N41916 (juvenile, MorphoBank M305842–M305852), Yemen, Al Bayda' governorate, Radman (14.1°N, 45.283°E), collected by W. Mustafa on 13. XI. 2007.

Referred material. NMP6V 74835 (juvenile), Yemen, Lahij governorate, wadi 35 km W of Lahij (13.032°N, 44.558°E), 297 m a.s.l., collected by L. Kratochvíl on 25. X. 2007; JEM476 (juvenile), same collecting data as holotype; All juvenile specimens were used for comparison of meristic characters and included in the molecular analyses.

Diagnosis. A small species of the '*Hemidactylus saba* species group' within the Arabian radiation of the Arid clade of *Hemidactylus*, as evidenced by the mtDNA and nDNA analyses. The new species is characterized by the following combination of molecular and morphological characters: (1) Uncorrected genetic distances from *H. saba*:

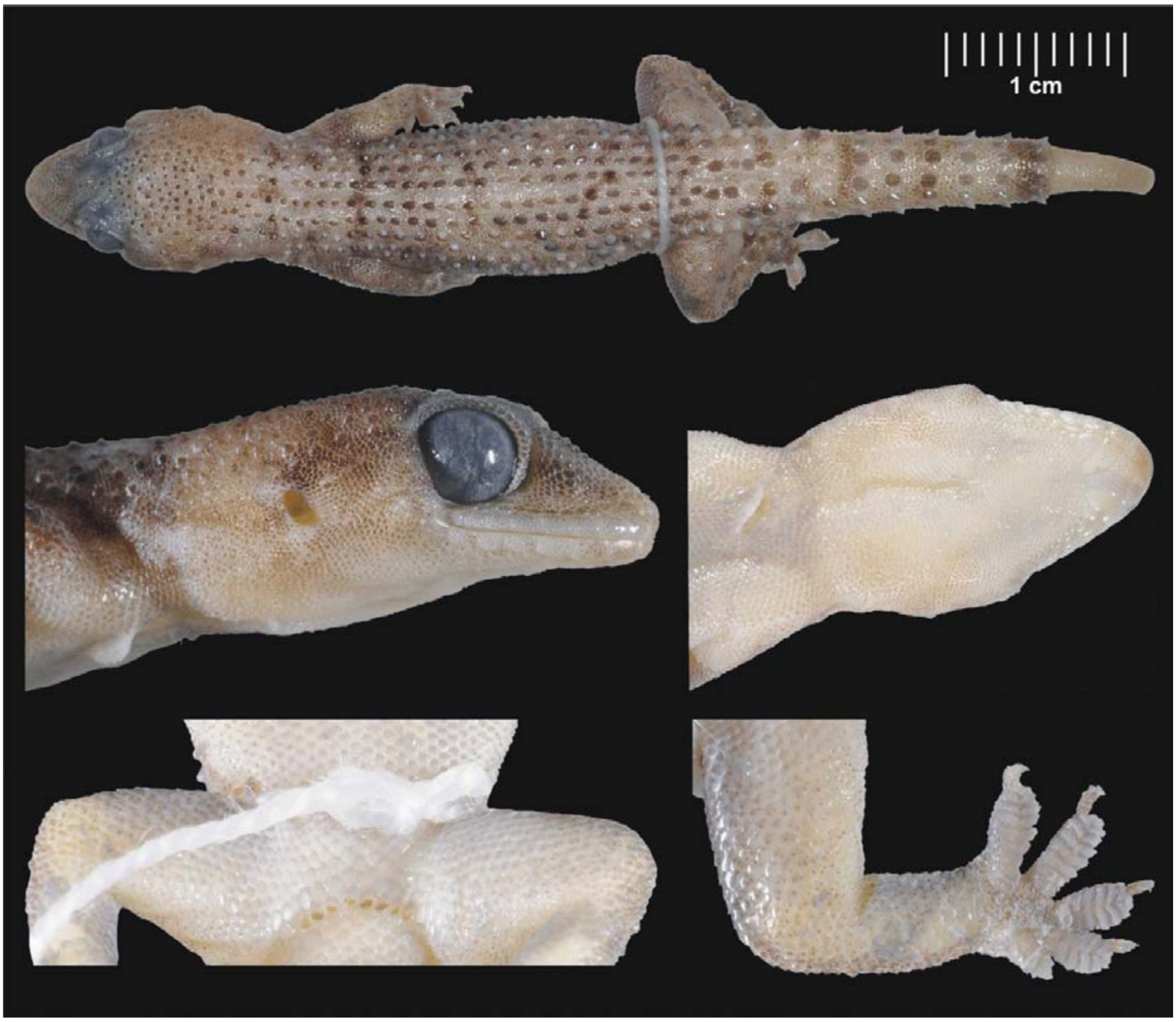

Figure 8. Holotype of *Hemidactylus ulii* sp. n. (NMP6V 74833/2, male) from Al Hababi, Yemen. General habitus, lateral and ventral view of the head, precloacal region with preanal pores, right hind leg. Scale refers to the uppermost picture only.

9.9–10.7% in *12S*, 13.5–14.9% in *cytb*; from *H. granosus*: 10.2–12.3% in *12S*, 11.2–13.5% in *cytb*; (2) small size with a maximum recorded SVL 40.7 mm (36.8–40.4 mm in males, 39.4–40.7 mm in females); (3) moderately robust head, head length 28–30% of SVL, head width 70–75% of head length, head depth 37–46% of head length; (4) tail length 116% of SVL (only 1 specimen with intact tail); (5) uppermost nasals separated by a small shield (60% specimens) or in wide contact (40%); (6) large anterior postmentals in wide mutual contact in 90% of individuals, and in contact with the 1st and 2nd lower labial (scarcely and unilaterally with the 1st lower labial only); (7) 8–10 upper labials; (8) 7–9 lower labials; (9) dorsum with 12-16 longitudinal rows of enlarged, slightly keeled, conical tubercles; (10) 5–6 lamellae under the 1st toe and 8–9 lamellae under the 4th toe; (11) ca. 6–8 tail segments bearing 6 tubercles; (12) 8 preanal pores in one continuous row in males; (13) subcaudals enlarged; (14) in alcohol dorsum brownish grey with a pattern of more or less conspicuous dark transverse bands starting on the nape, tail with 9 dark brown transverse bands.

Comparison. *Hemidactylus ulii* sp. n. can be distinguished from the other members of the '*Hemidactylus saba* species group' and from all other congeners distributed in the region by the following combination of characters (see also Table 2):

From *H. granosus* by its smaller size (max. SVL 40.4 mm vs. 53.2 mm in males, 40.7 mm vs. 53.3 mm in females), by having less frequently separated uppermost nasals (60% vs. 89% of specimens), higher number of preanal pores in males (8 vs. 4–7), and lower number of lamellae under the 1st (5–6 vs. 7–8) and 4th (8–9 vs. 10–13) toe.

From *H. saba* by its smaller size (max. SVL 40.4 mm vs. 58.3 mm in males, 40.7 mm vs. 59.1 mm in females), higher number of preanal pores in males (8 vs. 6), and lower number of lamellae under the 1st (5–6 vs. 8–9) and 4th (8–9 vs. 11–12) toe.

From *H. flaviviridis* by its smaller size (maximum SVL 40.4 mm in males, 40.7 mm in females vs. up to 90 mm [Anderson (1999); sexes not distinguished]), the presence of enlarged dorsal tubercles, and the absence of femoral pores in males.

From *H. jumailiae* by its smaller size (max. SVL 40.4 mm vs. 54.2 mm in males, 40.7 mm vs. 54.0 mm in females), lower frequency of separated uppermost nasals (60% vs. 95%), in having conical and at least slightly keeled dorsal tubercles (vs. non-protruding and smooth tubercles), and lower number of lamellae under the 1st (5–6 vs. 6–8) and 4th (8–9 vs. 9–12) toe.

From *H. robustus* by its smaller size (max. SVL 40.4 mm vs. 43.7 mm in males, 40.7 mm vs. 50.1 mm in females), and lower number of lamellae under the 4th toe (8–9 vs. 8–12).

From *H. sinaitus* by the presence of enlarged tile-like subcaudals and in having separated uppermost nasals (60% vs. 9% of specimens).

From *H. yerburii montanus* by its smaller size (maximum SVL 40.4 mm vs. 65.3 mm in males, 40.7 mm vs. 64.1 mm in females), lower number of preanal pores in males (8 vs. 9–13), and lower number of lamellae under the 4th toe (8–9 vs. 9–11).

From *H. yerburii yerburii* by its smaller size (maximum SVL 40.4 mm vs. 74.9 mm in males, 40.7 mm vs. 62.1 mm in females), lower number of supralabials (8–10 vs. 9–12), lower frequency of having separated uppermost nasals (60% vs. 92%), lower number of preanal pores in males (8 vs. 10–18), and lower number of lamellae under the 1st (5–6 vs. 6–8) and 4th (8–9 vs. 9–12) toe.

Description of holotype. NMP6V 74833/2, adult male. Body slightly depressed to cylindrical (Fig. 8). Upper labials 8/8, lower labials 7/7. Nostril between rostral, three nasals and in punctual contact with the first upper labial. Uppermost nasals separated by a small inserted shield. Mental almost triangular. Anterior postmentals large and very long, in wide mutual contact behind mental, in contact with the 1st lower labial (left) and the 1st and 2nd lower labials (right) (Fig. 5). Posterior postmentals smaller, in contact with the 1st and 2nd (left) and the 2nd (right) lower labial. Eye moderate (E/HL=0.24). Supraciliar granules with prominent projections, which form a comb-like structure above the eyes. Parietal and temporal region covered with round pointed regularly distributed tubercles. Ear opening oval. Dorsum with 14 longitudinal rows of enlarged, prominent, caudally pointed tubercles bearing distinct longitudinal keels. Thighs and lower legs with scattered enlarged tubercles. Tail partially regenerated from about half of its original

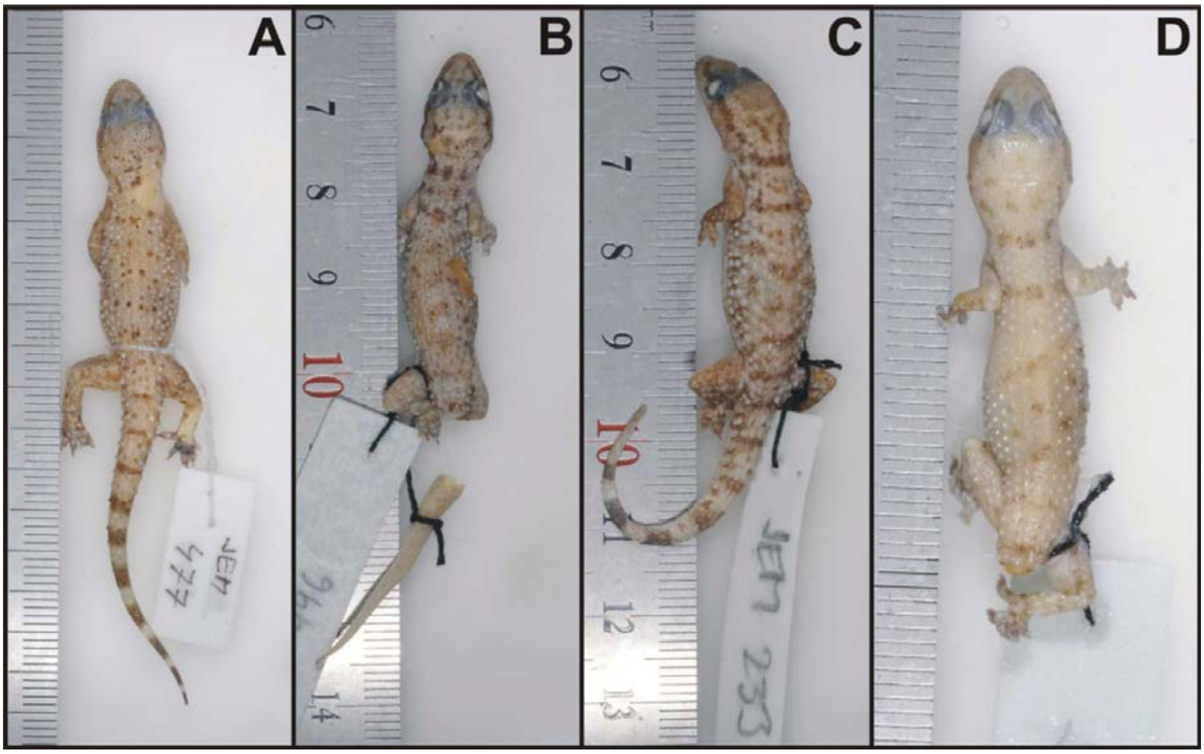

Figure 9. Four (out of eight) paratypes of *Hemidactylus ulii* sp. n. **A** NMP6V 74833/1, male **B** NMP6V 74834/1, female **C** NMP6V 74831/1, female **D** NMP6V 74832/1, subadult female.

length (estimate), original part relatively thick without basal constriction. Conical and keeled tail tubercles on tail segments forming regular whorls. Each whorl separated from the next one by four small scales. Subcaudals enlarged, tile-like. Regenerated part of the tail with small uniform scales without tubercles. Lamellae under the 1st toe 6/6, lamellae under the 4th toe 8/8. Eight preanal pores, no femoral pores or enlarged femoral scales.

Measurements (in mm): SVL 40.4, HL 11.5, HW 8.6, HD 5.2, E 2.8, AG 16.2.

Coloration of holotype in preservative. Overall dorsal coloration brownish grey. An indistinct dark horizontal stripe in loreal and temporal area. Seven dark brown transverse bands across the nape and body, the one in scapular region being the most conspicuous. Dark brown bands also on the original part of the tail. Belly whitish.

Variation. The paratypes (Fig. 9) differ from the holotype in the following features: number of upper labials 8–10; number of lower labials 7–9; four paratypes (NMP6V 74831/1, NMP6V 74832/1–2, NMP6V 748333/1) have uppermost nasals in wide contact; anterior postmentals in contact with 2nd lower labials on both sides (except of NMP6V 74832/1 where the arrangement is the same as in the holotype); longitudinal rows of enlarged tubercles 12–16; lamellae under the 1st toe 5–6, lamellae under the 4th toe 8–9. The intact tail of the paratype NMP6V 74833/1 has 7 segments bearing at least six enlarged spine-like tubercles and 9 dark brown transverse bands widening towards the tail tip.

Measurements of paratypes (in mm): NMP6V 74831/1: SVL 40.7, HL 11.5, HW 8.2, HD 4.9, E 3.0, AG 19.0; NMP6V 74831/2: SVL 32.0, HL 9.3, HW 6.6, HD 3.7, E 2.1, AG 12.7; NMP6V 74832/1: SVL 32.7, HL 9.7, HW 7.0, HD 3.4, E 2.3, AG 14.3; NMP6V 74832/2: SVL 32.9, HL 9.3, HW 6.7, HD 3.6, E 2.4, AG 13.5;

NMP6V 74833/1: SVL 36.8, HL 10.7, HW 8.0, HD 4.5, E 2.4, AG 14.1, TL 42.5; NMP6V 74834/1: SVL 39.4, HL 11.1, HW 8.1, HD 4.4, E 2.7, AG 16.7; NMP6V 74834/2: SVL 32.0, HL 9.5, HW 6.7, HD 3.9, E 2.5, AG 13.8; NHM-BS N41916: juvenile, not measured.

As already mentioned (Results), the level of genetic variability within *H. ulii* sp. n. is very high. The species is divided into three well supported sublineages which reflect the geographic origin of the samples. Although there is a certain geographic separation corresponding with these sublineages, the exact limits are not distinct and also morphological variation among paratypes is not congruent with geography.

Etymology. The species epithet "*ulii*" is a patronym for Prof. Ulrich Joger, a German herpetologist known as Uli among friends, in recognition of his important contribution to the knowledge of the herpetofauna of the Western Palearctic.

Distribution and ecology. *Hemidactylus ulii* sp. n. is known from inland mid-altitude areas (292–1182 m) of southwestern Yemen (Fig. 6). Most specimens were collected in open dry wadis with scattered rocks and boulders, in stony deserts and also in the vicinity of villages in gardens and irrigated cropland fields.

The following reptile species were found to occur in sympatry with *H. ulii*: *Bunopus spatalurus* Anderson, 1901; *Hemidactylus y. yerburii* Anderson, 1895; *Pristurus crucifer* (Valenciennes, 1861); *P. flavipunctatus* Rüppell, 1835; *P. rupestris* Blanford, 1874; *Ptyodactylus* sp.; *Tropiocolotes scorteccii* Cherchi and Spano, 1963; *Acanthodactylus* sp.; *Chamaeleo arabicus* Matschie, 1893; *Pseudotrapelus sinaitus* (Heyden, 1827); *Trapelus flavimaculatus* Rüppell, 1835; and *Pelomedusa subrufa* (Bonnaterre, 1789).

Discussion

Previous phylogenetic studies of the Arid clade of *Hemidactylus* disclosed an extraordinarily rich diversity within this genus in the Arabian Peninsula (Moravec et al. 2011; Carranza and Arnold 2012; Šmíd et al. 2013). The latter work, besides of showing the phylogenetic relationships among individual species of the Arid clade, highlighted the high level of genetic differentiation and existence of several yet undescribed taxa within this genus. The '*Hemidactylus saba* species group' as defined herein represents one of the monophyletic groups within the Arabian radiation. All three species forming this group – *H. granosus*, *H. saba*, and *H. ulii* sp. n. – are well defined and distinguishable both genetically and morphologically from each other, as well as from other *Hemidactylus* species that occur in the same area. Geographically, *H. saba* and *H. ulii* sp. n. are confined to the foothills and submontane areas of southwestern Yemen, where they occupy mid-altitude elevations (292–1182 m in *H. ulii* sp. n., 1180 m in *H. saba*). In comparison, *H. granosus* has a much wider distribution, spanning from northeastern Egypt to central Saudi Arabia. It was found from the sea-level up to almost 1600 m in the Asir Mountains, which stretch along the eastern Red Sea coast of the Arabian Peninsula. Its occurrence in eastern Egypt is also likely based on observations of Baha El Din (2005, 2006), who reported morphologically variable populations of *H. turcicus* (sensu lato) in these regions attributable to *H. granosus* (see Distribution and ecology). The distribution of *H. granosus* in the coastal Sinai and Saudi Arabia near important marine junctions together with the genetic uniformity of this species indicates extensive gene flow between these populations. It may be the result of recent colonization event(s), their inadvertent human-mediated transportation or perpetual contact of populations in a continuous range. The continuous range of *H. granosus* along the Hijaz and Asir Mountains in western Arabia confirms that these mountain ranges can serve as a corridor providing connection between the eastern Mediterranean and southern Arabia (Scott 1942; Gvoždík et al. 2010).

The highlands of southwestern Saudi Arabia and Yemen are known to host a high number of endemic taxa (Balletto et al. 1985; Arnold 1986; Gasperetti 1988; Harrison and Bates 1991; Gasperetti et al. 1993). The genus *Hemidactylus* also shows a high rate of speciation and endemicity in the area. Currently, there are eight species and one subspecies known from the Yemen highlands, which makes *Hemidactylus* one of the most specious reptile genera in the area (Fritz and Schütte 1987; Busais and Joger 2011b; Šmíd et al. 2013; Uetz 2013). As new genetic and morphological data are becoming available from Arabia even more new species are to be expected (Moravec et al. 2011; Šmíd et al. 2013), thus fulfilling the prognosis of Baha El Din (2005) and the models of Ficetola et al. (2013) which suggested that the Red Sea region is likely to contribute significantly to the diversity of *Hemidactylus*.

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Appendix

Specimens examined

H. flaviviridis (8 individuals) - NMP6V 74858 (Oman, Jalan Bani Bu Hasan); NMP6V 74859/1–5 (Pakistan, Multan); NMP6V 74856 (Pakistan, Rakhni); NMP6V 74857 (Pakistan, Sukkur)

H. jumailiae (18 individuals) - NMP6V 74818/1 (Yemen, near Al Bayda [At Dageeg]); NMP6V 74819 (Yemen, Sana'a); NHM-BS N41788, NHM-BS N41890 (paratype), NHM-BS N41891, NHM-BS N41893 (holotype), NHM-BS N41894 (paratype), NHM-BS N41897 (paratype) (Yemen, Ibb); NHM-BS N41898 (paratype, the same number as one of *H. y. montanus* paratypes, Busais and Joger 2011b), NHM-BS N41899 (paratype) (Yemen, Thamar); BMNH1982.1143–44 (Yemen, Al Nabi Shuaib, 30 Km W. of Sana'a); BMNH1982.1145 (Yemen, Sana'a); BMNH1982.1146 (Yemen, Wadi Ahger, 45 Km. W. of Sana'a); BMNH1952.1.3.52 (Yemen, Sana'a); MSNG-YEM02, MSNG-YEM03 (Yemen, El Menghil); MCCI-R814 (Yemen, Hababah)

H. mindiae (5 individuals) - NMP6V 71323/1–2 (Jordan, Jabal Ghazali); NMP6V 72739/1–3 (Jordan, Wadi Ramm Nughra Radet Salem)

H. robustus (27 individuals) - SMF 8720 (lectotype), SMF 8721 ("Abyssinia" [Ethiopia and Eritrea]); SMF 8725–8726 – redetermined from *H. granosus* (Egypt, Sinai); JS210, TMHC2012.07.092, TMHC2012.07.100 (Ethiopia, Jijiga), CAS130512 – redetermined from *H. macropholis* as it is in the CAS catalogue (Kenya, vicinity of Mandera); NMP6V 74820 (Iran, Bandar Lengeh); NMP6V 74821/1–2 (Yemen, Wadi Zabid); NMP6V 74829 (Yemen, Bir Ali); JS144 (Kenya, Garissa); NMP6V 74867/1–3 (Oman, Muscat); NMP6V 74868 (Oman, Salalah); NMP6V 74869/1–7 (Oman, Mughsayl); NMP6V 74870/1–2 (Oman, Shisr); MCCI–R815 (Yemen, Zabid)

H. saba (3 individuals) - NHM-BS N41912 (holotype, MorphoBank M305478–M305492), NHM-BS N41913 (paratype, MorphoBank M305493–M305504), NHM-BS N41914 (paratype, MorphoBank M305505–M305519) (Yemen, Marib)

H. sinaitus (23 individuals) - BMNH82.8.16.27 (holotype, probably from Suakin, Sudan); BMNH97.10.28.83–85 (Sudan, Durrur, N of Suakin); BMNH97.10.28.87 (Sudan, Wadi Haifa); BMNH1974.3931 (Ethiopia, Mule River?, Danakil); BMNH1937.12.5.293–294 (Somalia, Borama district); BMNH95.5.23.7 (Yemen, Sheikh Osman, near Aden); BMNH1945.12.12.14 (Yemen, Bir Fadhl, Aden); NMP6V 74809/1–4 (Sudan, Wad Ben Naga); NMP6V 74810 (Sudan, 15 km SE Atbara); MZUF28645–646 (Yemen, Moka); MZUF10914, MSNM521 (Eritrea, Isola [island] Sheik-Said); MSNM523–524 (Eritrea, Ailet); CAS174021–022 (Sudan, Assalaya)

H. turcicus (33 individuals) - NMP6V 34747 (Syria, Baniyas); NMP6V 34748/1–3 (Syria, Palmyra); NMP6V 34749 (Syria, Salkhad); NMP6V 70648/1–4 (Turkey, Kaş); NMP6V 70668 (Greece, Kastellorizo, St. Georgies); NMP6V 71056

(Egypt, Bahariya); NMP6V 71587/1–3 (Cyprus, Famagusta); NMP6V 71592/1–2 (Cyprus, Yali); NMP6V 72497 (Syria); NMP6V 74046/1–2 (Syria, Cyrrhus); NMP6V 74047/1–2 (Turkey, Antakya); NMP6V 74050 (Greece, Crete, Kavros); NMP6V 74131/1–3 (Syria, Palmyra); NMP6V 73626/1–3 (Turkey, Finike); NMP6V 70269 (Italy, Sardinia, Cagliari); NMP6V 72073 (Greece, Korfu, Nicos); NMP6V 74167 (Greece, Crete, Kavros); NMP6V 70667 (Greece, Kastellorizo); NMP6V 70163/5 (Egypt, Sharm el-Sheikh)

H. yerburii yerburii (51 individuals) - NMP6V 74827/1–4 (Yemen, Jabel Habeshi); NMP6V 74825/1–2 (Yemen, Al Turbah); NMP6V 74826 (Yemen, N of Lahij, Wadi Tuban); NMP6V 74823/1–3 (Yemen, 14 km NW of Al Turbah); NMP6V 74824/1–2 (Yemen, 3 km S of Najd an Nashamah); NMP6V 74828/1–3 (Yemen, Al Hababi); NMP6V 74822/1–5 (Yemen, near Zinjubar); MSNG-YEM01 (Yemen, Ta'izz); MSNG-YEM05, MSNG-YEM06 (Yemen, Vahren); NHM-BS N41856–59, NHM-BS N41861–64, NHM-BS N41866, NHM-BS N41868–69, NHM-BS N41888 (Yemen, Tour Albaha); NHM-BS N41860 (Yemen, Lahij); NHM-BS N41871–72 (Yemen, Radfan); NHM-BS N41873 (Yemen, Shihr); NHM-BS N41875 (Yemen, Ariab); NHM-BS N41876–77, NHM-BS N41879–86 (Yemen, Lowder); NHM-BS N41887 (Yemen, Aden)

H. yerburii montanus (57 individuals) - NMP6V 74802 (Yemen, Jabal Bura); NHM-BS N41751–52 (paratypes), NHM-BS N41758 (paratype), NHM-BS N41762–63, NHM-BS N41765–66, NHM-BS N41768–69, NHM-BS N41770 (paratype), NHM-BS N41772–74, NHM-BS N41779, NHM-BS N41783 (paratype), NHM-BS N41785 (paratype), NHM-BS N41791 (paratype), NHM-BS N41793 (paratype), NHM-BS N41797–800 (paratypes), NHM-BS N41802–06 (paratypes), NHM-BS N41807 (paratype), NHM-BS N41809 (paratype), NHM-BS N41811–15 (paratypes), NHM-BS N41818 (paratype), NHM-BS N41821 (paratype), NHM-BS N41823 (paratype), NHM-BS N41836 (holotype), NHM-BS N41839, NHM-BS N41840 (paratype), NHM-BS N41842 (paratype), NHM-BS N41843, NHM-BS N41844 (paratype), NHM-BS N41846, NHM-BS N41848, NHM-BS N41851–52, NHM-BS N41867 (paratype) (Yemen, Ibb); NHM-BS N41771 (paratype) (Yemen, Yareem); NHM-BS N41789–90 (Yemen, Thamar); NHM-BS N41833–34 (paratypes) (Yemen, Wadah); NHM-BS N41853–55 (paratypes) (Yemen, Sana'a).

Paper VI

Šmíd, J., Moravec, J., Kratochvíl, L., Nasher, A.K., Mazuch, T., Gvoždík, V., Carranza, S.: Multilocus phylogeny and taxonomic revision of the *Hemidactylus robustus* species group (Reptilia, Gekkonidae) with descriptions of three new species from Yemen and Ethiopia. Accepted for publication in *Systematics and Biodiversity*.

Author contribution:

- JŠ performed the laboratory work and the phylogenetic analyses, the analyses of morphological data, and wrote the paper

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VI

Research Article

Multilocus phylogeny and taxonomic revision of the *Hemidactylus robustus* species group (Reptilia, Gekkonidae) with descriptions of three new species from Yemen and Ethiopia

JIŘÍ ŠMÍD[1,2], JIŘÍ MORAVEC[3], LUKÁŠ KRATOCHVÍL[4], ABDUL K. NASHER[5], TOMÁŠ MAZUCH[6], VÁCLAV GVOŽDÍK[3] & SALVADOR CARRANZA[7]

[1]Department of Zoology, National Museum, Cirkusová 1740, Prague, Czech Republic
[2]Department of Zoology, Faculty of Science, Charles University in Prague, Viničná 7, Prague, Czech Republic
[3]Department of Zoology, National Museum, Cirkusová 1740, Prague, Czech Republic
[4]Department of Ecology, Faculty of Science, Charles University in Prague, Viničná 7, Prague, Czech Republic
[5]Faculty of Science, University of Sana‘a, Sana’a, Yemen
[6]Dříteč 65, 53305, Czech Republic
[7]Institute of Evolutionary Biology (CSIC-Universitat Pompeu Fabra), Passeig Marítim de la Barceloneta 37–49, Barcelona, Spain

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The gecko genus *Hemidactylus*, with its 132 currently recognized species, ranks among the most species-rich reptile genera. Recent phylogenetic studies disclosed unexpectedly high genetic variability and complex biogeographic history within its arid clade distributed in the Mediterranean, Northeast Africa, Middle East and the Indian subcontinent. Particularly, the species from the Arabian Peninsula have been lately the subject of many taxonomic revisions that have resulted in the descriptions of 16 new taxa. Yet not all detected cryptic lineages have been treated taxonomically and thoroughly investigated morphologically. Based on phylogenetic analyses of two mtDNA (*12S*, *cytb*) and four nDNA (*cmos*, *mc1r*, *rag1*, *rag2*) gene fragments of a total length of 4015 bp in combination with analysis of morphological characters, we reinvestigate the systematics of the *H. robustus* species group consisting of the widespread *H. robustus* and three undescribed species, two of which occur in Southwest Yemen and one in central Ethiopia. By comparing two phylogenetic inference methods, concatenated gene trees and species-tree estimation, we reconstruct the phylogeny of the *H. robustus* species group. The coalescent-based species-tree estimation resulted in different tree topology than the concatenation approach, being probably a result of incomplete lineage sorting of ancestral polymorphism, suggesting that the *H. robustus* species group is in a stage of incipient speciation. The degree of differentiation of the characters examined within the *H. robustus* species group allowed us to provide a redescription of *H. robustus* and formally describe three new species of *Hemidactylus* – *H. adensis* sp. nov. and *H. mandebensis* sp. nov. from Yemen and *H. awashensis* sp. nov. from Ethiopia.

Key words: Arabia, biogeography, diversity, geckos, Horn of Africa, incipient speciation, radiation, species tree

Introduction

Knowledge of the herpetofauna of the Afro-Arabian contact zone has increased rapidly over the past years. Closely related taxa from various reptile groups occur on both sides of the Red Sea and Gulf of Aden and provide excellent examples for studying the biogeographic history of the area. Several possible scenarios, not mutually exclusive, have been proposed to explain and reconstruct the distribution patterns of the reptile fauna. They range from ancient vicariant splits resulting from the Oligocene separation of the Arabian Peninsula from Africa (e.g. Macey et al., 2008; Metallinou et al., 2012) through Miocene dispersals either across the Red Sea and Gulf of Aden or via a land bridge that closed the Bab-el-Mandeb strait *c.* 11–5 Ma (e.g. Portik & Papenfuss, 2012; Trape, Chirio, Broadley, & Wüster, 2009) to recent human-mediated dispersals of mostly synanthropic species (e.g. Lavin & Papenfuss, 2012).

The geckos of the genus *Hemidactylus* rank among the best-studied reptile groups in the area and represent an excellent example of a lineage in which the current distribution in the area was formed by episodes conforming to

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Correspondence to: Jiří Šmíd. E-mail: jirismd@gmail.com

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all the above-mentioned biogeographic scenarios (Šmíd et al., 2013a). The current global circumtropical distribution of the genus is a result of repeated natural transmarine colonizations (Carranza & Arnold, 2006; Gamble et al., 2011; Kluge, 1969; Vences et al., 2004). Phylogenetic studies indicate that the genus is divided into four divergent clades: (1) African−Atlantic clade; (2) *H. angulatus* clade; (3) tropical Asian clade; and (4) arid clade (Bansal & Karanth, 2010; Bauer, Jackman, Greenbaum, Giri, & de Silva, 2010; Carranza & Arnold, 2006; Moravec et al., 2011). The arid clade is the most species-rich and encompasses the majority of the Arabian and East African species. It is formed by three main geographically exclusive radiations, the African, Socotran and Arabian, corresponding to continental and island break-ups in the region. After their separation, the members of the Arabian radiation underwent multiple dispersals from Arabia to the surrounding regions including human-aided translocations (Carranza & Arnold, 2012; Gómez-Díaz, Sindaco, Pupin, Fasola, & Carranza, 2012; Šmíd et al., 2013a). The genus and particularly its Arabian radiation has been the subject of several recent taxonomic revisions, which have resulted in the descriptions of 16 new taxa (Busais & Joger, 2011b; Carranza & Arnold, 2012; Moravec et al., 2011; Šmíd et al., 2013b, Vasconcelos & Carranza, 2014). Despite these taxonomic revisions, a recent multilocus phylogeny by Šmíd et al. (2013a) uncovered a high level of undescribed diversity in the arid clade of *Hemidactylus*, including several lineages closely related to *H. robustus*.

Hemidactylus robustus Heyden is a widespread species inhabiting coastal areas along the Red Sea, Arabian Sea and Persian Gulf and occurring also in the hinterland of the Horn of Africa and Arabia (Sindaco & Jeremčenko, 2008). The character of its distribution, which follows important ship routes, and life in close association with humans indicate that some parts of the large range of *H. robustus* may be the result of recent dispersal most likely mediated by humans (Bauer, Jackman, Greenbaum, & Papenfuss, 2006; Bauer, Vyas, Jackman, Lajmi, & Giri, 2012; Šmíd et al., 2013a). *Hemidactylus robustus* was long considered a junior synonym of *H. turcicus* (Linnaeus), a species widespread in the Mediterranean (e.g. Arnold, 1980, 1986; Fritz & Schütte, 1987; Kluge, 1993; Lanza, 1978; Mertens, 1922; Schätti, 1989; Schätti & Gasperetti, 1994). This was the result of their overall morphological similarity and the lack of a thorough taxonomic revision of both species. Although some authors have treated *H. robustus* as a separate species (Baha El Din, 2003, 2005, 2006; Lanza, 1990; Moravec & Böhme, 1997), its recognition as a separate taxon was fully confirmed only by analysis of genetic data (Carranza & Arnold, 2006) and further elaborated by other studies (Carranza & Arnold, 2012; Moravec et al., 2011; Šmíd et al., 2013a).

The absence of a detailed morphological description of *H. robustus* and the existence of three candidate *Hemidactylus* species closely related to it (*H.* sp. 5, *H.* sp. 6, *H.* sp. 11; Šmíd et al., 2013a) call for a thorough systematic and integrative taxonomic assessment of this clade, herein defined as *H. robustus* species group. Here, we address this issue by using morphological data and sequences of mitochondrial (mtDNA) and nuclear (nDNA) markers.

Materials and methods

Material for phylogenetic analyses

For the genetic analyses, we assembled a dataset including 60 *Hemidactylus* samples. Of these, 33 specimens belong to the *H. robustus* species group and 23 to its sister clade, the *H. saba* species group as defined by Šmíd et al. (2013b). Three samples of *H. flaviviridis* and one of *H. angulatus*, representing two distinct clades of *Hemidactylus* were used as outgroups. All samples from the *H. saba* species group and the outgroup taxa were taken from our previous studies (Šmíd et al., 2013a, 2013b). We added new sequences of the specimens of the *H. robustus* group used by Šmíd et al. (2013a) to complete the dataset. We also added 12 new specimens of the African species described herein (*H.* sp. 11) and six new specimens of one of the two new species from Yemen (*H.* sp. 6). Additional *12S* and *cytb* sequences for 23 *H. robustus* individuals published by Šmíd et al. (2013a) were used to assess the intraspecific variability within this species and to calculate genetic distances between *H. robustus* and other *Hemidactylus* species. For a complete list of the material used in the genetic analyses including museum acronyms, sample codes, locality data and corresponding GenBank accession numbers see Table 1.

DNA extraction and sequencing

Genomic DNA was extracted using commercial kits. We sequenced up to two mtDNA and four nDNA gene fragments. The targeted genes were 12S rRNA (*12S* – *c.* 400 bp) and cytochrome *b* (*cytb* – *c.* 1137 bp, or 307 bp when the long fragment failed to amplify) for mtDNA and the proto-oncogene mos (*cmos* – 402 bp), the melanocortin 1 receptor (*mc1r* – 666 bp) and the recombination activating genes 1 and 2 (*rag1* – 1023 bp and *rag2* – 408 bp) for nDNA. Primers and PCR conditions were identical to those described in detail by Šmíd et al. (2013a). Chromatograms were checked by eye and complementary sequences assembled and edited using Geneious 5.6.5 (Biomatters Ltd). All genes were aligned individually using MAFFT (Katoh & Toh, 2008) as implemented in Geneious with 1000 iterations of the iterative refinement algorithm. Poorly aligned regions in the *12S* alignment were eliminated with Gblocks (Castresana,

Table 1. Material used for the genetic analyses. Specimens marked with asterisks were used in the *BEAST analysis, holotypes of the new species described here are in bold, Loc. No refers to the locality numbers shown in Fig. 2.

Species	Species designation in Šmíd et al. (2013a)	Code	Museum number	Country	Locality	Loc. No	Lat	Long	*12S*	*cytb*	*cmos*	*mc1r*	*rag1*	*rag2*	MorphoBank
H. mandebensis sp. nov.	*H.* sp. 5	JS27*	NMP6V 74970	Yemen	Jabal Sabir	1	13.528	43.952	KC818732	KC818883	KC818790	TBA	TBA	JQ957409	Project 1172, M329407-M329416
H. mandebensis sp. nov.	*H.* sp. 5	JS36*	NMP6V 74836/1	Yemen	3 km S of Najd an Nashamah	2	13.358	43.957	KC818734	KC818884	KC818790	TBA	KC819002	JQ957409	Project 1172, M329505-M329516
H. mandebensis sp. nov.	*H.* sp. 5	JS39*	NMP6V 74836/2	Yemen	3 km S of Najd an Nashamah	2	13.358	43.957	KC818733	KC818885	KC818790	-	TBA	JQ957409	Project 1172, M329385-M329406
H. adensis sp. nov.	*H.* sp. 6	JS31*	NMP6V 74837	Yemen	N of Lahij - Wadi Tuban	3	13.13	44.85	KC818735	KC818886	KC818735	KC818886	KC819003	KC819063	Project 1172, M329190-M329206
H. adensis sp. nov.	*H.* sp. 6	BJ10*	NHM-BS N41907	Yemen	Sheikh Othman	5	12.9167	44.9833	TBA	TBA	TBA	TBA	TBA	TBA	Project 1172, M329181-M329189
H. adensis sp. nov.	*H.* sp. 6	BJ11*	NHM-BS N41906	Yemen	Sheikh Othman	5	12.9167	44.9833	TBA	TBA	TBA	TBA	TBA	TBA	Project 1172, M329173-M329180
H. adensis sp. nov.	*H.* sp. 6	BJ12	NHM-BS N41905	Yemen	Sheikh Othman	5	12.9167	44.9833	TBA	-	TBA	TBA	-	TBA	Project 1172, M329165-M329172
H. adensis sp. nov.	*H.* sp. 6	BJ13*	NHM-BS N41902	Yemen	Lahij	4	13.0546	44.878	TBA	TBA	TBA	TBA	TBA	TBA	Project 1172, M329131-M329140
H. adensis sp. nov.	*H.* sp. 6	BJ14*	NHM-BS N41903	Yemen	Lahij	4	13.0546	44.878	TBA	TBA	TBA	TBA	TBA	TBA	Project 1172, M329141-M329153
H. adensis sp. nov.	*H.* sp. 6	BJ15*	NHM-BS N41904	Yemen	Sheikh Othman	5	12.9167	44.9833	TBA	TBA	TBA	TBA	TBA	KC819063	Project 1172, M329154-M329164
H. awashensis sp. nov.	*H.* sp. 11	JS204*	-	Ethiopia	Metehara	11	8.9207	39.9031	TBA	TBA	KC818786	KC818939	TBA	KC819058	-
H. awashensis sp. nov.	*H.* sp. 11	JS212	NMP6V 74977	Ethiopia	Metehara	11	8.9207	39.9031	KC818723	KC818873	KC818786	KC818939	KC818998	KC819058	Project 1172, M328897- M328937
H. awashensis sp. nov.	*H.* sp. 11	JS242*	-	Ethiopia	Metehara	11	8.908	39.9122	KC818723	TBA	KC818786	KC818939	-	KC819058	-
H. awashensis sp. nov.	*H.* sp. 11	JS243*	-	Ethiopia	Metehara	11	8.908	39.9122	KC818723	TBA	KC818786	KC818939	-	TBA	-
H. awashensis sp. nov.	*H.* sp. 11	JS244*	NMP6V 74978/1	Ethiopia	Metehara	11	8.908	39.9122	TBA	TBA	KC818786	KC818939	-	KC819058	Project 1172, M328942-M328968
H. awashensis sp. nov.	*H.* sp. 11	JS245*	NMP6V 74978/2	Ethiopia	Metehara	11	8.908	39.9122	KC818723	TBA	KC818786	KC818939	-	KC819058	Project 1172, M328969-M329004
H. awashensis sp. nov.	*H.* sp. 11	JS246	-	Ethiopia	Metehara	11	8.908	39.9122	KC818723	TBA	KC818786	-	-	TBA	-
H. awashensis sp. nov.	*H.* sp. 11	JS247*	NMP6V 74978/3	Ethiopia	Metehara	11	8.908	39.9122	KC818723	TBA	KC818786	KC818939	-	TBA	Project 1172, M329005-M329042
H. awashensis sp. nov.	*H.* sp. 11	JS248*	-	Ethiopia	Metehara	11	8.9234	39.9051	TBA	TBA	KC818786	KC818939	-	KC819058	-
H. awashensis sp. nov.	*H.* sp. 11	JS249*	NMP6V 74979	Ethiopia	Metehara	11	8.9215	39.912	KC818723	TBA	KC818786	KC818939	-	KC819058	Project 1172, M329043-M329085
H. awashensis sp. nov.	*H.* sp. 11	JS250*	NMP6V 74980	Ethiopia	Metehara	11	8.9306	39.9048	TBA	TBA	KC818786	KC818939	-	KC819058	Project 1172, M329086-M329118
H. awashensis sp. nov.	*H.* sp. 11	JS321	NMP6V 74981	Ethiopia	Metehara	11	8.908	39.9122	KC818723	-	-	-	-	-	Project 1172, M329119-M329130
H. awashensis sp. nov.	*H.* sp. 11	JS322	-	Ethiopia	Metehara	11	8.908	39.9122	KC818723	-	-	-	-	-	-
H. robustus	*H. robustus*	JS50*	NMP6V 74821/1	Yemen	Wadi Zabid	6	14.16	43.492	KC818701	KC818852	KC818779	KC818928	KC818987	JQ957409	Project 1172, M329207-M329215
H. robustus	*H. robustus*	JS58*	NMP6V 74829	Yemen	Bir Ali	7	14.006	48.322	KC818702	KC818854	KC818780	KC818929	KC818988	KC819051	Project 1172, M329225-M329246
H. robustus	*H. robustus*	JS101*	-	Somalia	Berbera	10	10.464	45.032	KC818696	KC818847	KC818778	KC818927	KC818987	JQ957409	-
H. robustus	*H. robustus*	JS106*	NMP6V 74820	Iran	Bandar-e-Lengeh	-	26.541	54.869	KC818698	KC818849	TBA	TBA	TBA	JQ957409	-
H. robustus	*H. robustus*	AO164b*	-	Oman	East Khor	9	17.0267	54.1747	JQ957078	JQ957226	JQ957153	JQ957294	TBA	JQ957436	-
H. robustus	*H. robustus*	AO165*	-	Oman	East Khor	9	17.0267	54.1747	JQ957078	JQ957226	JQ957154	JQ957295	TBA	JQ957437	-
H. robustus	*H. robustus*	SPM001859*	SPM001859	Egypt	Safaga	-	26.7577	33.925	DQ120347	DQ120176	JQ957160	JQ957298	TBA	JQ957439	-
H. robustus	*H. robustus*	S1788*	-	Oman	1 km W airport, Masirah Island	-	20.6675	58.8743	JQ957080	JQ957228	JQ957154	JQ957294	TBA	JQ957436	-
H. robustus	*H. robustus*	S2151*	-	Oman	8 km W Shannah	-	20.7529	58.6532	JQ957081	JQ957228	JQ957158	JQ957294	TBA	JQ957409	-
H. robustus	*H. robustus*	R1415	MCCI R1415	Yemen	Mukalla Airport	8	14.665	49.3734	AF186117	JQ957229	JQ957154	JQ957297	-	JQ957436	-
H. granosus	*H.* sp. 1	Sher10660	SMB 10660	Egypt	Ayoun Musa, Sinai	-	29.8751	32.6489	JQ957071	JQ957216	JQ957148	JQ957282	-	JQ957409	-
H. granosus	*H.* sp. 1	HSA54*	IBES 10150	Saudi Arabia	20 km S of Ashayrah	-	21.6022	40.6911	KF647568	KF647584	KF647576	KF647588	KF647595	KF647609	Project 1006, M305615−M305628
H. granosus	*H.* sp. 1	HSA55*	ZFMK 94091	Saudi Arabia	20 km S of Ashayrah	-	21.6022	40.6911	KF647569	KF647584	KF647575	KF647588	KF647596	KF647610	Project 1006, M305629−M305642
H. granosus	*H.* sp. 1	HSA57	IBES 10183	Saudi Arabia	30 km NE of Alhawiyah	-	21.6244	40.7094	KF647568	KF647580	-	-	KF647597	KF647610	Project 1006, M305656−M305671
H. granosus	*H.* sp. 1	HSA60	IBES 10344	Saudi Arabia	30 km NE of Alhawiyah	-	21.6244	40.7094	KF647569	KF647583	-	-	KF647598	KF647610	Project 1006, M305702−M305717
H. granosus	*H.* sp. 1	HSA61*	IBES 10001	Saudi Arabia	Al Ghat	-	26.0545	45.0003	KF647569	KF647585	JQ957148	KF647588	KF647599	KF647610	-
H. granosus	*H.* sp. 1	HSA62*	TUZC-R10	Saudi Arabia	180 km W of Hail	-	26.8831	40.0874	KF647569	KF647585	JQ957148	KF647588	KF647602	KF647609	Project 1006, M305728−M305743
H. granosus	*H.* sp. 1	HSA63*	ZFMK 94084	Saudi Arabia	Al Wajh	-	26.2076	36.4976	KC818724	HQ833759	KF647576	KF647589	KF647596	KF647610	Project 1006, M305744−M305760
H. granosus	*H.* sp. 1	HSA65*	ZFMK 94086	Saudi Arabia	15 km S of Al Wajh	-	26.1226	36.5689	KF647570	KF647581	KF647574	KF647590	KF647601	KF647610	Project 1006, M305778−M305791
H. granosus	*H.* sp. 1	HSA70*	TUZC-R9	Saudi Arabia	72 km N of Umluj	-	25.614	36.9867	KF647569	KF647582	JQ957148	KF647591	KF647600	KF647609	-

(*continued*)

Table 1. (*Continued*)

Species	Species designation in Šmíd et al. (2013a)	Code	Museum number	Country	Locality	Loc. No	Lat	Long	*12S*	*cytb*	*cmos*	*mc1r*	*rag1*	*rag2*	MorphoBank
H. saba	*H. saba*	BJ27	NHM-BS N41914	Yemen	Marib	-	14.9	45.5	KF647567	-	KF647573	-	-	KF647605	Project 1006, M305505–M305519
H. saba	*H. saba*	BJ28*	NHM-BS N41913	Yemen	Marib	-	14.9	45.5	KF647567	KF647579	KF647573	KF647586	-	KF647605	Project 1006, M305493–M305504
H. saba	*H. saba*	BJ29*	NHM-BS N41912	Yemen	Marib	-	14.9	45.5	KF647567	-	KF647573	KF647587	KF647594	KF647605	Project 1006, M305478–M305492
H. ulii	*H.* sp. 4	JS17*	NMP6V 74831/1	Yemen	Al Hadr	-	13.877	45.8	KC818725	KC818874	KC818787	KC818940	KC818999	KC819059	Project 1006, M305854–M305863
H. ulii	*H.* sp. 4	JS18	NMP6V 74831/2	Yemen	Al Hadr	-	13.877	45.8	KC818725	-	KC818789	-	KF647604	KC819059	Project 1006, M305864–M305870
H. ulii	*H.* sp. 4	JS37*	NMP6V 74832/1	Yemen	3 km S of Najd an Nashamah	-	13.358	43.957	KC818727	KC818876	KF647578	KC818943	-	KF647611	Project 1006, M305871–M305875
H. ulii	*H.* sp. 4	JS38*	NMP6V 74832/2	Yemen	3 km S of Najd an Nashamah	-	13.358	43.957	KC818727	KC818877	KC818789	KF647593	-	KF647614	Project 1006, M305876–M305883
H. ulii	*H.* sp. 4	JS46	NMP6V 74833/1	Yemen	Al Hababi	-	13.333	43.722	KC818728	KC818879	KC818789	-	-	KF647613	Project 1006, M305884–M305891
H. ulii	*H.* sp. 4	JS47*	NMP6V 74833/2	Yemen	Al Hababi	-	13.333	43.722	KC818729	KC818880	KC818789	KC818942	KC819001	KC819061	Project 1006, M305892–M305902
H. ulii	*H.* sp. 4	JS48*	NMP6V 74834/1	Yemen	Wadi Zabid	-	14.147	43.517	KC818730	KC818881	KC818789	KC818943	KC819001	KC819062	Project 1006, M305903–M305911
H. ulii	*H.* sp. 4	JS49*	NMP6V 74834/2	Yemen	Wadi Zabid	-	14.147	43.517	KC818731	KC818882	KC818789	-	KF647603	KF647614	-
H. ulii	*H.* sp. 4	JS32*	NMP6V 74835	Yemen	village wadi near Al Turbah	-	13.032	44.558	KC818726	KC818875	KC818788	KC818941	KC819000	KC819060	-
H. ulii	*H.* sp. 4	BJ09	NHM-BS N41916	Yemen	Radman	-	14.1	45.2833	KF647572	-	KF647577	KF647592	-	KC819059	Project 1006, M305842–M305852
H. angulatus	*H. angulatus*	JS123	NMP6V 74845/2	Ethiopia	Arba Minch	-	6.034	37.564	KC818659	KC818807	KC818747	KC818903	KC818956	KC819018	-
H. flaviviridis	*H. flaviviridis*	JS111	-	Pakistan	Okara	-	30.811	73.457	KC818676	KC818822	JQ957126	JQ957253	KC818965	KC819026	-
H. flaviviridis	*H. flaviviridis*	JS113	-	India	Haridwar	-	29.964	78.201	KC818676	KC818823	JQ957126	JQ957253	KC818966	KC819027	-
H. flaviviridis	*H. flaviviridis*	JS119	-	Oman	Jalan Bani Bu Hasan	-	22.089	59.278	JQ957119	JQ957183	KC818754	KC818911	KC818967	KC819028	-

2000) under low stringency options (Talavera & Castresana, 2007), resulting in an alignment of 387 bp. Alignments of all protein-coding genes were trimmed to start on the first codon position; no stop codons were detected when translated into amino acids with the appropriate genetic codes.

Phylogenetic analyses and haplotype network construction

The best-fit models of nucleotide evolution were assessed using PartitionFinder (Lanfear, Calcott, Ho, & Guindon, 2012), which allows reduction of the number of necessary models by merging predefined partitions and thus facilitates the process of computation. Because a trial analysis with all protein-coding genes partitioned by codon position yielded similar results to those presented below (data not shown), and in order to avoid overparameterization of the analyses, we partitioned the dataset by genes with the only exception of *cytb*, which was partitioned by codon position. The greedy search mode of the program was run under the following settings: branch lengths linked, only models of evolution available in BEAST evaluated, AIC model selection criterion applied. All partitions were recognized as evolving according to individual models, the only exception being *cmos*, *rag1* and *rag2*, which were suggested to be merged under one model. The best-fit models of evolution according to the best scheme were: *12S*−GTR+G; *cytb*_pos1−GTR+G; *cytb*_pos2−GTR+I; *cytb*_pos3−GTR+I; *cmos* + *rag1* + *rag2*−HKY+I; *mc1r*−HKY+I+G.

We performed phylogenetic analyses using Maximum likelihood (ML) and Bayesian Inference (BI) methods. All gene alignments were concatenated into a single alignment with final length of 4015 bp. Sequences of nuclear genes were not phased; heterozygous positions were coded according to the IUPAC ambiguity codes. Gaps were treated as missing data. Uncorrected genetic distances (*p* distances) were calculated in MEGA 5 (Tamura et al., 2011). Due to incomplete ends of some of the sequences, the final *cytb* alignment for computation of genetic distance was 1073 bp long. Only sequences with an almost complete *cytb* gene fragment amplified were used to calculate intra- and interspecific genetic distances for this marker.

Maximum likelihood analyses were performed in RAxML 7.0.3 (Stamatakis, 2006) using raxmlGUI 1.2 interface (Silvestro & Michalak, 2012) with partitions inferred by PartitionFinder (see above) and the GTR+G+I model of sequence evolution. Heuristic search included 100 random addition replicates with parameters estimated independently for each partition. Nodal support was assessed by bootstrap analysis with 1000 pseudoreplications (Felsenstein, 1985).

Bayesian analyses were performed with MrBayes 3.2.1 (Ronquist et al., 2012). Appropriate equivalents of the best-fit model were specified for each partition supported by PartitionFinder (see above), all parameters were unlinked across partitions and ploidy of the mtDNA genes was set to haploid. The analyses were run for 10^7 generations with sampling frequency every 10^3 generations. Numbers of runs and chains were left as default, two and four, respectively. Sufficient number of generations was confirmed by examining the stationarity of the log likelihood (ln*L*) values of the sampled trees and the value of average standard deviations of the split frequencies being lower than 0.01. Convergence of the two runs was confirmed by the values of PSRF (potential scale reduction factor) reaching 1.00. The burn-in fraction was left as default at 25% of sampled trees, thus from the 10^4 produced trees, 2500 were discarded. A majority-rule consensus tree was produced from the remaining 7500 trees with posterior probability (pp) values embedded. Branches with ML bootstrap values $\geq$ 70% and pp values $\geq$ 0.95 were considered highly supported (Huelsenbeck & Rannala, 2004).

Both ML and BI analyses with the same settings as described above were also performed for mtDNA alone and for each nuclear gene (unphased) independently. Only in the BI analysis of the *mc1r* the number of runs was set to 4 and number of chains to 8 because the independent runs did not reach convergence (PSRF of some parameters > 1.00) with the default settings (i.e. 2 runs, 4 chains).

The genealogical relationships between the species were also assessed with allele networks of phased nuclear markers. Heterozygous positions were detected using the Heterozygote Plugin of Geneious and by checking the sequences by eye. Only representatives of the *H. robustus* species group were phased. Our observations indicate that including distant taxa can strongly affect the results of phasing and distort the real picture of the network (data not shown). All alignments were trimmed to the length of the shortest sequence to avoid misleading results in the allele reconstruction (Joly, Stevens, & van Vuuren, 2007). SeqPHASE (Flot, 2010) was used to convert the input files, PHASE 2.1.1 (Stephens, Smith, & Donnelly, 2001) was used to reconstruct the gametic phases. The probability threshold of PHASE was set to 0.7. Allele networks were constructed using statistical parsimony (Templeton, Crandall, & Sing, 1992) implemented in TCS 1.21 (Clement, Posada, & Crandall, 2000) with 95% connection limit.

Species tree estimation

Alongside the analyses of the concatenated dataset we analysed the data using a multigene coalescent-based species-tree method implemented in *BEAST (Heled & Drummond, 2010). To attain maximum accuracy of the analysis (following Camargo, Avila, Morando, & Sites, 2012), each species was represented by as many individuals as available ideally with all the targeted genes sequenced. Individuals with more than two genes missing were excluded (see Table 1). Alignments of both mtDNA and all four nDNA genes were imported independently into BEAUTI 1.7.5. Nuclear genes were phased prior to the analysis following the steps described above. Appropriate substitution models followed the results of PartitionFinder (see above). Because BEAST assumes no recombination within loci (Heled & Drummond, 2010), we tested for the presence of recombination within all nuclear loci analysed using RDP4 (Martin et al., 2010). Site, clock, and tree models were unlinked across partitions except the site model for *cmos*, *rag1* and *rag2*, which were merged into one partition according to PartitionFinder. The *cytb* alignment was partitioned into three codon positions with all respective parameters unlinked. Base frequencies of all genes were set to empirical and the ploidy type of the mtDNA genes was set to mitochondrial. We enforced a strict molecular clock model with uniform prior on the clock distribution and estimated the rate with mean fixed at 1. We used UPGMA starting trees for all genes and uniform (0, 1000) Yule species tree prior. Other prior settings applied were as follows (otherwise by default): alpha Uniform (0, 10), initial=0.5; relative rates of substitution in the GTR model Uniform (0, 100), initial=1 and Uniform (0, 10) for the second codon position of *cytb*; relative rate parameter (*.mu) Uniform (0, 1.0E100), initial=1. Because the nuclear alignments still contained some unresolved heterozygous positions after being phased we included these ambiguous positions in the analysis by removing the operator on the transition-transversion parameter of the HKY model (kappa), giving it an initial value of 0.5 and changing the 'useAmbiguities' parameter of all nDNA genes in the produced xml file to 'true'. Outgroup taxa were not included in the *BEAST analysis. Three independent runs each of 10^9 MCMC generations with parameter log every 10^5 generations were run in BEAST 1.7.5 (Drummond & Rambaut, 2007; Drummond, Suchard, Xie, & Rambaut, 2012). The resulting parameters were checked for stationarity, convergence and effective sample sizes (ESS) in Tracer 1.5. The resulting tree files were combined in LogCombiner 1.7.5 with first 10% of each run discarded as burn-in. A maximum clade credibility tree from the sampled trees was produced using TreeAnnotator 1.7.5. A species-tree analysis with identical settings as described above was conducted with the phased nDNA genes alone in order to test the influence of the mtDNA on the topology. Apart from producing a maximum clade credibility tree of the full dataset (mtDNA + nDNA), we visualized all post burn-in sampled trees from all three runs (27 000 trees) using DensiTree 2.1.11 (Bouckaert, 2010), which allows superimposing all the sampled trees and thus assessing the prevailing topology by the density of branch lines.

Material for morphological analyses

Analyses of morphological characters were performed on a series of 44 individuals of the *H. robustus* species group (27 individuals of *H. robustus*, three of *H.* sp. 5, seven of *H.* sp. 6 and seven of *H.* sp. 11) and additional 525 voucher specimens representing 40 *Hemidactylus* species and subspecies for comparison. A complete list of examined specimens is given in Appendix S1 (see online supplemental material, which is available from the article's Taylor & Francis Online page at http://dx.doi.org/10.1080/14772000.2014.996264). Morphological data for species not available to us (*H. arnoldi*, *H. bavazzanoi*, *H. puccionii*, *H. romeshkanicus* and *H. tropidolepis*) were taken from original descriptions and other relevant sources (Calabresi, 1923, 1927; Lanza, 1978; Torki, Manthey, & Barts, 2011). The material was assembled from the following collections: Natural History Museum, London, UK (NHMUK); California Academy of Sciences, San Francisco, USA (CAS); Institute of Evolutionary Biology Collection, Barcelona, Spain (IBES); Museo Civico di Storia Naturale, Carmagnola, Italy (MCCI); Museo Civico di Storia Naturale 'Giacomo Doria', Genova, Italy (MSNG); Museo Civico di Storia Naturale di Milano, Milano, Italy (MSNM); University di Firenze, Museo Zoologico 'La Specola', Firenze (Florence), Italy (MZUF); Natural History Museum in Braunschweig, Germany (NHM-BS); National Museum Prague, Czech Republic (NMP); Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt, Germany (SMF); Tomas Mazuch herpetological collection (private), Dříteč, Czech Republic (TMHC); Taif University Zoological Collection, Taif, Saudi Arabia (TUZC); Zoologisches Forschung Institut und Museum Alexander Koenig Bonn, Germany (ZFMK). High-resolution photographs of all studied specimens of the *H. robustus* species group have been deposited and are available for download at MorphoBank (Project 1172; http://www.morphobank.org). Spelling of locality names is according to Google Earth (http://www.google.com/earth/).

Morphological characters examined

Following previous morphological studies of the arid clade of *Hemidactylus* (Carranza & Arnold, 2012; Moravec & Böhme, 1997; Moravec et al., 2011; Šmíd et al., 2013b), we measured the following metric and meristic characters using a Powerfix digital calliper (rounding to nearest 0.1 mm) and a dissecting microscope: snout-vent length (SVL), measured from tip of snout to vent; head length (HL), measured from tip of snout to retroarticular process of jaw; head width (HW), measured at the widest part of the head; head depth (HD), maximum depth of head; left eye diameter (E), measured horizontally; axilla-groin distance (AG), measured from posterior end of front limb insertion to anterior end of hind limb insertion; tail length (TL), measured from vent to tip of original tail; number of supra- and infralabials (left/right); contact of uppermost nasals; number of infralabials in contact with anterior postmentals; mutual position of anterior postmentals; number of longitudinal rows of enlarged dorsal tubercles; number of lamellae under the 1st and 4th toe of hind leg including unpaired proximal ones; and number of preanal pores in males.

Morphological analyses

To assess morphological variation of the metric variables within the *H. robustus* species group without including *a priori* assumptions about grouping, a principal component analysis (PCA) was performed in Statistica 8.0 (StatSoft Ltd). We accounted for body size effect by regressing log-transformed metric variables against log-transformed SVL and calculating residuals, which were used as PCA input data. A broken-stick model (Frontier, 1976) was used to determine the number of significant, and therefore interpretable, PCA components. Components identified as significant were tested by one-way ANOVA to determine the significance of between-species differences and the allocation of species into homogeneous groups with unequal sample size *post-hoc* tests (Significant differences and Homogeneous groups). Meristic characters important for distinguishing the species were determined by discriminant function analysis (DFA). Most of the meristic variables significantly deviated from normality (Anderson-Darling test, $P < 0.05$) and although DFA assumes normal distribution of variables, it has been shown that the resultant significance tests are still reliable if normality assumption is violated (Tabachnick & Fidell, 1996). Juveniles were included only in interspecific comparisons of meristic characters. As a result of the absence of sexual size dimorphism in the arid clade of *Hemidactylus* (Carranza & Arnold, 2012), both sexes were analysed together.

Results

No evidence of recombination was detected within the nuclear loci. All three independent *BEAST runs converged, ESS values of all parameters of all runs exceeded 200, a critical value suggested by the BEAST manual and indicating adequate mixing of the MCMC analyses. The ESS of the likelihoods was > 4700. The *H. robustus* group was recovered as highly supported in the *BEAST analysis (Fig. 1, pp = 1.00). Contrary to Šmíd et al. (2013a), the *BEAST analysis reconstructed the new

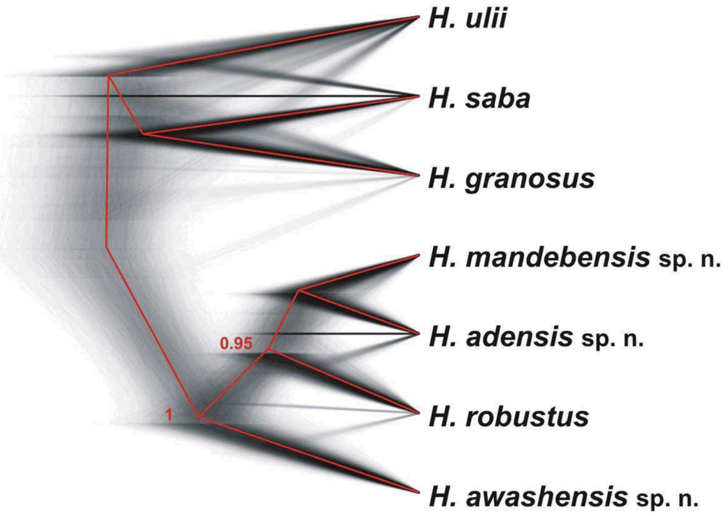

Fig. 1. Species-tree cloudogram of the *H. robustus* and *H. saba* species groups based on 27 000 post-burn-in trees resulting from 3 runs of *BEAST, each producing 10 000 trees from which 10% was discarded as burn-in. This analysis was based on 2 mtDNA and 4 nDNA fragments. Higher colour densities represent higher levels of certainty. Maximum clade credibility tree is superimposed upon the cloudogram in red with posterior probability values ≥ 0.95 embedded.

species from Ethiopia as sister to a clade composed of *H. robustus* and the two new species from Yemen (pp = 0.95). The species-tree estimated from nDNA alone also recovered the latter clade as the only well-supported clade (pp = 1.00; Appendix S2, see supplemental material online). According to the phylogenetic analyses of the concatenated mtDNA + nDNA dataset (Fig. 2) and mtDNA alone (Appendix S3, see supplemental material online), the two new species from Yemen form a well-supported monophyletic group (mtDNA + nDNA: 100/

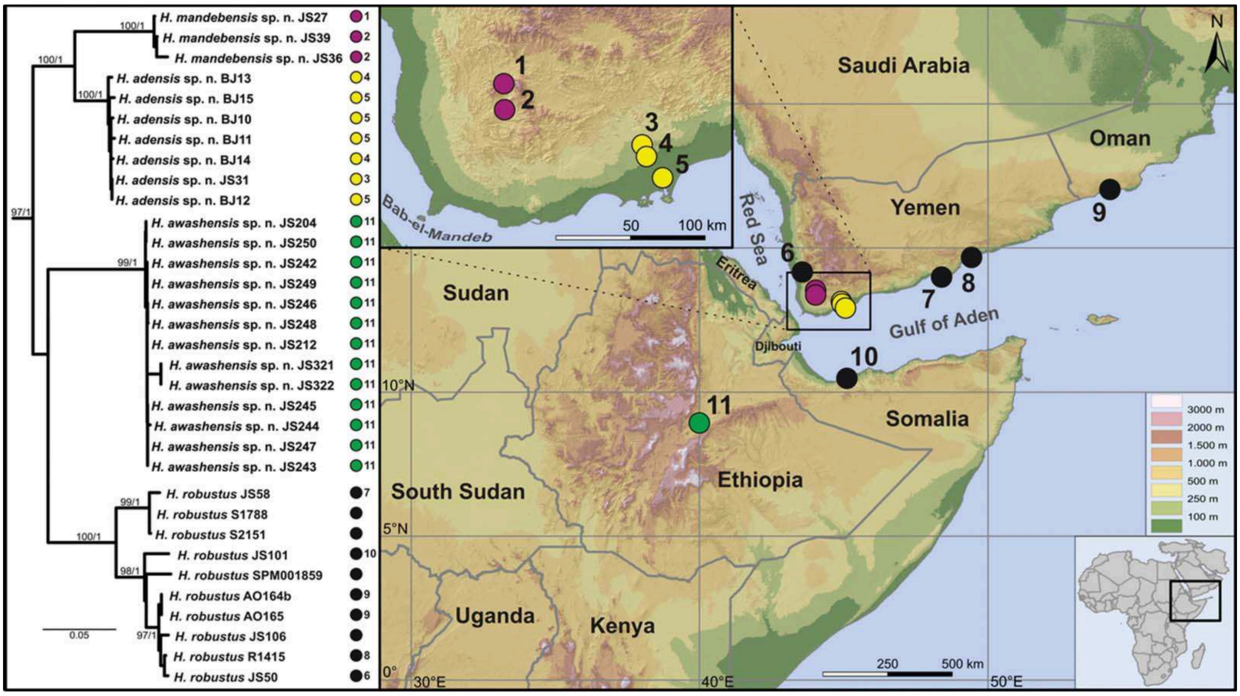

Fig. 2. Maximum likelihood tree of the *Hemidactylus robustus* species group and map of sample locations. The tree is based on a concatenated dataset of all mtDNA and nDNA genes analysed (see Table 1). The outgroup and the *H. saba* species group were included in the analysis but are not shown. Node labels indicate ML bootstrap values (≥ 70%)/ Bayesian posterior probabilities (≥ 0.95). Numbers next to colour marks in the tree correspond to locality numbers in the map (also listed in Table 1). Symbols without numbers are from outside the map range.

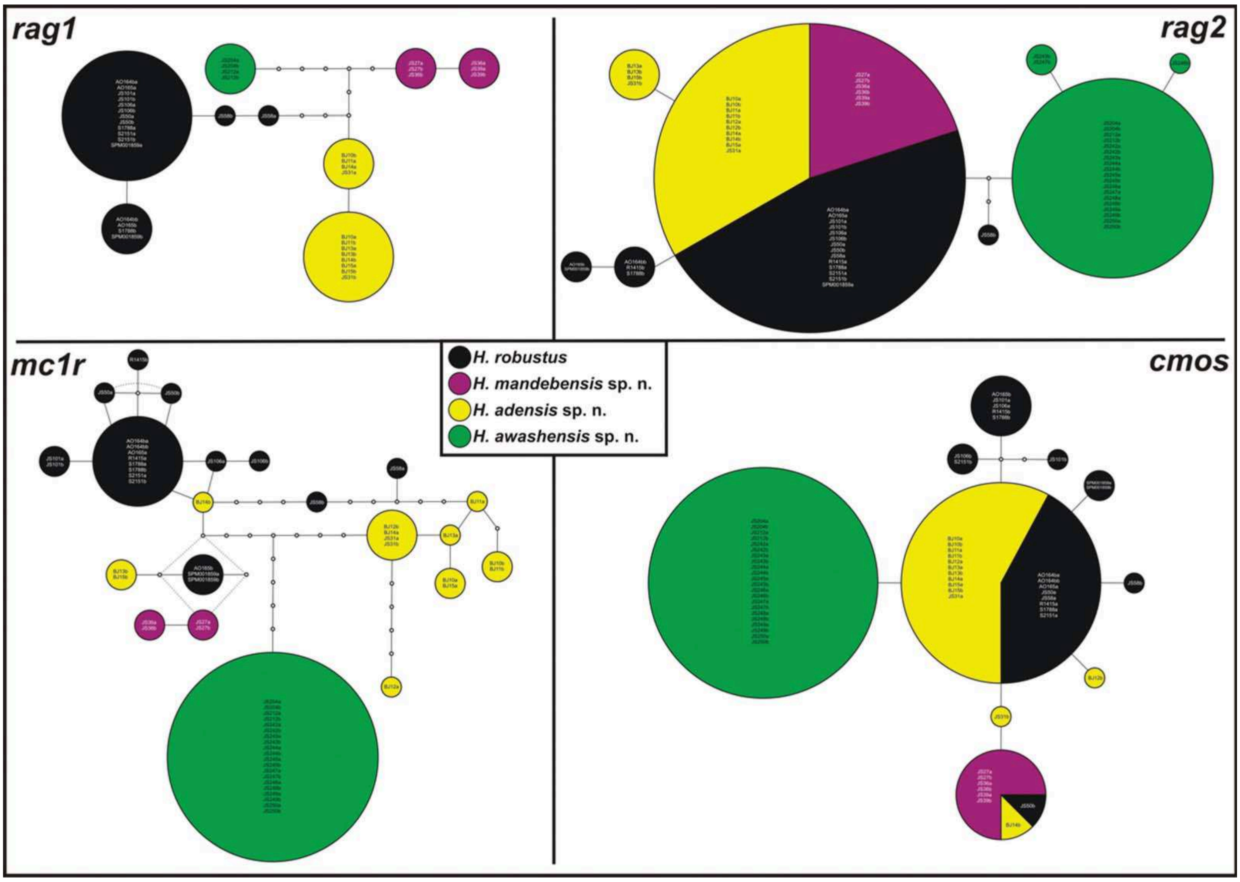

Fig. 3. Nuclear allele networks of the four analysed nuclear loci. Circle sizes are proportional to the number of alleles, empty circles represent mutational steps. Dashed lines in the *mc1r* network are of the same length as the full lines (i.e. one mutational step) and are drawn longer only for the graphical purposes.

1.00; mtDNA: 99/1.00). Phylogenetic analyses of individual unphased nDNA genes produced poorly resolved trees, probably due to the low variability and numerous heterozygous positions present (Appendix S4, see supplemental material online). On the other hand, allele networks produced with phased datasets provided higher resolution of the inter- and intraspecific genetic differentiation at the nDNA level (Fig. 3). The results indicate that alleles of *mc1r* and *rag1* are unique for each species; alleles of *cmos* and *rag2* are specific only for the Ethiopian species. The two new species from Yemen and *H. robustus* share two identical alleles in *cmos* and one in *rag2*. Two (out of three) of these shared alleles were identified as ancestral and placed in central position in the networks. Their presence can be therefore attributed to incomplete lineage sorting of ancestral polymorphism.

Intraspecific variability within the three new species described herein was very low at the mtDNA level (Appendix S3, see supplemental material online), being probably a result of restricted geographic distribution of the sampled material. The new species from Ethiopia and one of the two new species from Yemen (*H*. sp. 5) are characterized by very low variability in all nDNA genes. On the contrary, *H. robustus* and the second new species from Yemen (*H*. sp. 6) are more variable, particularly in some of the genes (*mc1r*, *cmos*; Fig. 3), owing to the high proportion of heterozygous positions.

Only the first PCA component was identified as interpretable by the broken-stick model. It accounted for 58.7% of variability and was influenced mostly by HL and HW residuals. Although it was significant for the species differentiation (ANOVA, $P < 0.005$), the species formed largely overlapping clouds in the PCA space and the *post-hoc* significant difference and homogeneous groups tests distinguished only *H*. sp. 11 from *H. robustus* and *H*. sp. 6 (Appendix S5, see supplemental material online). On the contrary, DFA conducted using meristic variables only resulted in a highly correct classification of individuals (95.35%). The best meristic characters for species delimitation were the number of lamellae under the 1st and 4th toes and number of infralabials in contact with anterior postmentals. Characters differentiating species of the *H. robustus* group are summarized in Appendix S6 (see supplemental material online).

The recognition of three unnamed *Hemidactylus* species closely related to *H. robustus*, with which they form the *Hemidactylus robustus* species group is supported by the results of the phylogenetic analyses and the degree of morphological differentiation. Formal species diagnoses and descriptions of the unnamed species as well as a redescription of *H. robustus* follows.

Status and nomenclature of *Hemidactylus robustus*

The original description of *Hemidactylus robustus* (the species epithet published erroneously as '*robustns*' due to a typographical error) provided by Heyden (1827: 19) is very short and has a form of a brief marginal note to the description of *H. granosus* Heyden, 1827. Although not explicitly mentioned by the author, the description was apparently based on three specimens collected by Rüppell (Boettger, 1893), which are currently deposited in the SMF collection. One of the specimens was probably lost because there are now only two specimens in the SMF collection under collection numbers SMF 8720 and SMF 8721. Moreover, there are two tails but only one voucher in the SMF 8721 jar indicating that the third specimen must have existed. Specimen SMF 8720 was designated as lectotype by Mertens (1967).

Family Gekkonidae

Genus *Hemidactylus* Oken, 1817

Hemidactylus robustus Heyden, 1827

Synonymy. *Hemidactylus karachiensis* in: Murray (1884); *Hemidactylus parkeri* in: Loveridge (1936); *Hemidactylus porbandarensis* in: Sharma (1981).

Lectotype. SMF 8720, adult female (MorphoBank M329277-M329312), 'Abyssinien' [= Ethiopia and Eritrea], collected 1826 by E. Rüppell (1828 according to the SMF catalogue, but this date is impossible given the year of the description), designated by Mertens (1967).

Paralectotype. SMF 8721, adult female (MorphoBank M329313-M329344), same data as lectotype.

Type locality. Originally 'Abyssinien' as given by Heyden (1827). The type material was collected by Eduard Rüppell, who travelled in 1826 along the Red Sea coast from Suez, Egypt south to Massawa, Eritrea during his vessel-based explorations of marine fauna and, to our knowledge, did not penetrate into the African inland (Klausewitz, 2002; Wagner, 2008). Considering that Rüppell spent most of his 1826 journey on the Red Sea coast of Eritrea (Klausewitz, 2002), we specify here the type locality as 'the Red Sea coast of the State of Eritrea'.

Diagnosis. *Hemidactylus robustus* is a member of the *Hemidactylus robustus* species group within the Arabian radiation of the arid clade of *Hemidactylus* as evident from mtDNA and nDNA analyses. The species has the following combination of molecular and morphological characters: (1) medium size with maximum recorded SVL 54.6 mm for males and 51.3 mm for females (Carranza & Arnold, 2012); (2) 6–9 infralabials and 8–11 supralabials; (3) snout forming a convex line between eye and nostril from lateral view; (4) infraorbital, parietal and temporal region covered with numerous regularly spaced round unkeeled tubercles; (5) anterior postmentals in wide medial contact; (6) dorsum with 13–18 longitudinal rows of round, weakly keeled and posteriorly pointed tubercles; (7) 5–8 preanal pores in males; (8) 5–8 lamellae under the 1st toe; (9) 8–12 lamellae under the 4th toe; (10) enlarged subcaudals; (11) tail with weakly distinct whorls of tubercles that do not stand out from the tail outline from dorsal view; (12) in life with distinct dark bands from nostrils across eyes to ear openings from where they continue as interrupted lines to shoulder region; the bands form a distinct dark head outline from a dorsal view; dorsum with irregular dark markings sometimes forming indistinct X-shaped marks at midbody, sometimes fusing and forming vertebral stripe on scapulae; tail with widely spaced dark transverse bars restricted to dorsal or dorsolateral part, never extending to ventral part of tail.

Description of the lectotype. Adult female (Figs 4–9). Measurements (in mm): SVL 44.1, HL 10.7, HW 8.9, HD 5.9, E 2.9, AG 19.6. Head and body stout, head robust and wide (HW = 84% HL, HD = 55% HL), eyes moderate (E = 27% HL). Nostril bordered by large rostral, three subequal nasals and first supralabial. Uppermost nasals separated by an inserted scale. Supralabials 8/9, infralabials 7/8. Mental large, as wide as long, forming right-angled isosceles triangle. Anterior postmentals in wide medial contact behind mental and in contact with the 1st infralabial. Posterior postmentals large and in contact with the 1st and 2nd infralabials. Ear opening tear-shaped with the tip pointing anteroventrally. Interorbital, parietal and temporal head region covered by small imbricate scales intermixed with larger round regularly spaced tubercles that continue onto body dorsum and form 16 rows of keeled and posteriorly pointed tubercles. The keeling is most prominent on the vertebral and paravertebral lines and diminishes in magnitude towards flanks. Gulars and ventrals small, imbricate. Posterior side of forearms, thighs and lower legs covered by small juxtaposed scales intermixed with large round tubercles.

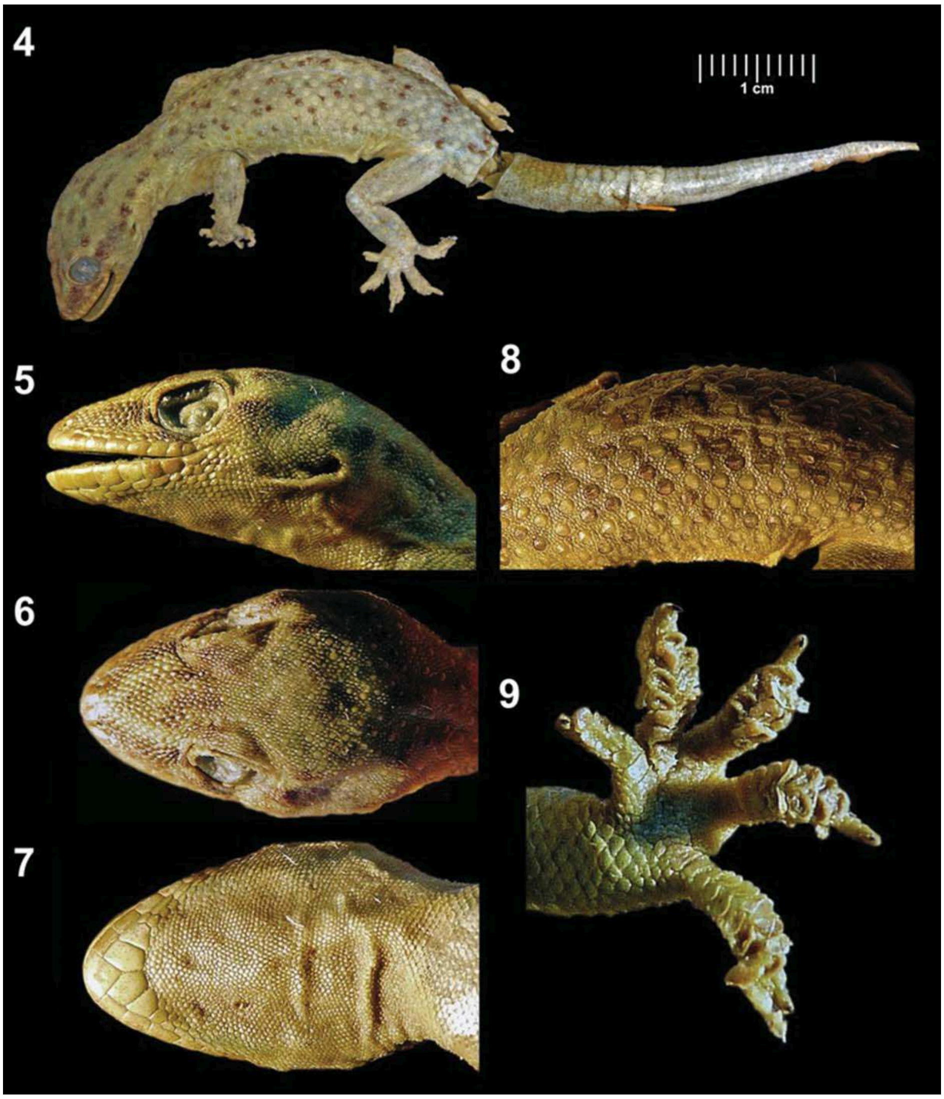

Fig. 4−9. Lectotype of *Hemidactylus robustus* (SMF 8720, adult female) showing **4,** general body habitus; **5,** lateral; **6,** dorsal and **7,** ventral view of the head; **8,** detail of the arrangement of dorsal tubercles; and **9.** lamellae under the toes of left hind foot. Scale refers to the uppermost picture only.

Anterior thigh surface with smooth imbricate scales. Lamellae under the 1st toe 6/6, under the 4th toe 10/9. Tail regenerated from its base, detached from body. Dorsal tail scales uniform, ventrals enlarged and tile-like. Belly cut open medially with an approximately 1 cm long incision.

Colouration in preservative. Base colour greenish grey caused by a long fixation with a copper wire attaching the tail to body. Dark markings on head and body still present; dark brown band runs from snout tip to eye and continues from posterior eye margin above ear up to shoulder region. Dorsum of head with several, mostly longitudinally oriented, irregular dark spots. Body dorsum with small dark spots restricted to enlarged tubercles and not forming any regular markings. The whole dorsal body surface covered with faint stipple visible under magnification. Venter uniformly pale greyish (tone affected by the copper wire). For colouration of *H. robustus* in life see Fig. 16.

Variation. Paralectotype SMF 8721 differs from the lectotype by having a lower number of infralabials on the right side (6) and a higher number of supralabials (10/10). Anterior postmentals are unilaterally in contact with the 1st and 2nd infralabials. Among other examined specimens, maximum SVL was recorded 50.1 mm (female), which is concordant with data published by other authors (Baha El Din, 2005, 2006; Carranza & Arnold, 2012); number of infralabials varies from 6 to 9 (mean 7.7 ± 0.7); number of supralabials varies from 8 to 11 (9.4 ± 0.8). Four of the 27 examined specimens (15%) have the uppermost nasals in point contact, 7% (2 specimens) in wide medial contact. Position of anterior postmentals with respect to infralabials is variable. In 30% of the examined individuals in contact with the 1st infralabial only, while in 41% with the 1st and 2nd. Number of rows of dorsal tubercles varies from 13 to 18 (15 ± 1.2). Number of lamellae under the 1st toe varies between 5–8 (6 ± 0.5), under the 4th toe between 8–12 (10 ± 0.8). The eight examined males had from 5 to 8 preanal pores (6.1 ± 0.8). Our data correspond to those published by Baha El Din (2005) for the Egyptian Red Sea populations (n = 19) and the Middle East and East African populations (n = 11) of *H. robustus* including the holotype of *H. parkeri*.

There is a certain degree of genetic differentiation within *H. robustus* that, however, does not correspond to any geographic structuring. The basal split within the species was dated to 2.5 (1.5–3.7) Ma (Šmíd et al., 2013a) and separated two main clades that overlap geographically. Average *p* distances calculated on a sample of 34 individuals used in our previous study (Šmíd et al. 2013a) and covering the whole range of the species (each haplotype included once) reach 1.9 ± 1.2% with a maximum of 4.4% in *12S* and 4.6 ± 4.0 with a maximum of 9.9% in *cytb*. The intraspecific variability is also reflected in the nDNA. All four nuclear genes studied form complex structures mostly resembling a star-like pattern with one most frequent central haplotype within *H. robustus* (Fig. 3).

Distribution and ecology. The range of *H. robustus* encompasses extensive areas along the shores of the Red Sea, Gulf of Aden, Arabian Sea, Gulf of Oman and Persian Gulf; it also penetrates inland in the Arabian Peninsula and Horn of Africa, although in the light of recent taxonomic changes (Šmíd et al., 2013b), records from inland Arabia are doubtful and should be reassessed. The western Red Sea range extends from Sinai, where it overlaps with the distributions of *H. turcicus* and *H. granosus*, through Sudan, Eritrea and Djibouti. Thus, with the current knowledge, the ranges of *H. robustus* and *H. turcicus* are parapatric with a minor overlap in northern and eastern Egypt. The distribution of *H. robustus* stretches eastwards to coastal Iran, Pakistan and Gujarat (India) (Bauer et al., 2006, 2012; Šmíd et al., 2014). In Africa, the range extends south to Somalia and Kenya. Evidence points toward an introduction to the Socotra Archipelago and Zanzibar (Lanza, 1990; Razzetti et al., 2011). Based on the presence of all known main divergent genetic lineages of *H. robustus* in Arabia, the species is supposed to have originated there (Carranza & Arnold, 2012). Its broad recent distribution is attributed to human-aided translocations (Šmíd et al., 2013a). This assumption is supported by its character of distribution, often restricted to important port cities, indicative of the synanthropic nature of the species. *Hemidactylus robustus* is usually found in association with human habitations throughout its range. It can be found under debris, amongst rocks or fallen logs, climbing on walls of abandoned or inhabited buildings or even inside houses. According to Baha El Din (2006) and our own observations (Oman, Al Kamil), it can also inhabit sandy substrates and littoral sand dunes. It does not extend to high altitudes; the highest records available to us (Ethiopia, Jijiga) are situated at 1650 m, the elevation limit in Somalia is 1400 m (Largen & Spawls, 2010).

Hemidactylus mandebensis sp. nov.

Synonymy. *Hemidactylus* sp. 5 in: Moravec et al. (2011), Šmíd et al. (2013a, 2013b.).

Holotype. NMP6V 74836/2, adult male (MorphoBank M329385-M329406), Yemen, Ta'izz governorate, 3 km S of Najd an Nashamah, 13.358°N, 43.957°E, 1182 m a.s.l., 26. X. 2007, collected by L. Kratochvíl.

Paratypes. NMP6V 74836/1, adult female (MorphoBank M329505-M329516), same data as holotype; NMP6V 74970, subadult female (MorphoBank M329407-M329416), Yemen, Ta'izz governorate, Jabal Sabir, 13.528°N, 43.952°E, 1253 m a.s.l., 26. X. 2005, collected by L. Kratochvíl.

Etymology. The species epithet is an adjective that refers to the Bab-el-Mandeb strait, the southern gate to the Red Sea in the vicinity of which the species occurs.

Diagnosis. A small-sized species of the *H. robustus* species group within the arid clade of *Hemidactylus* characterized by: (1) small size with maximum recorded SVL 41.5 mm in the only known male and 39.1 mm in females; (2) 7–8 infralabials and 9 supralabials; (3) infraorbital, parietal and temporal region covered with numerous round unkeeled tubercles; (4) large anterior postmentals in wide mutual contact; (5) dorsum with 12–14 longitudinal rows of round, enlarged, keeled, and posteriorly slightly pointed tubercles; (6) 6 preanal pores in males (only one male known); (7) 5–6 lamellae under the 1st toe; (8) 8–9 lamellae under the 4th toe; (9) enlarged subcaudals; (10) in life having dark brown irregular pattern on greyish body colour, two prominent dark stripes from eye to the shoulder region and bright white dorsal tubercles.

Description of the holotype. Adult male (Figs 10–15). Measurements (in mm): SVL 41.5, HL 10.6, HW 8.5, HD 5.1, E 2.7, AG 17.5. Head distinctly separated from body by a narrower neck; head wide (HW = 80% HL) and relatively high (HD = 48% HL); snout oblong from lateral view, slightly pointed from dorsal view. Rostral large with indistinct medial groove; nostrils surrounded by

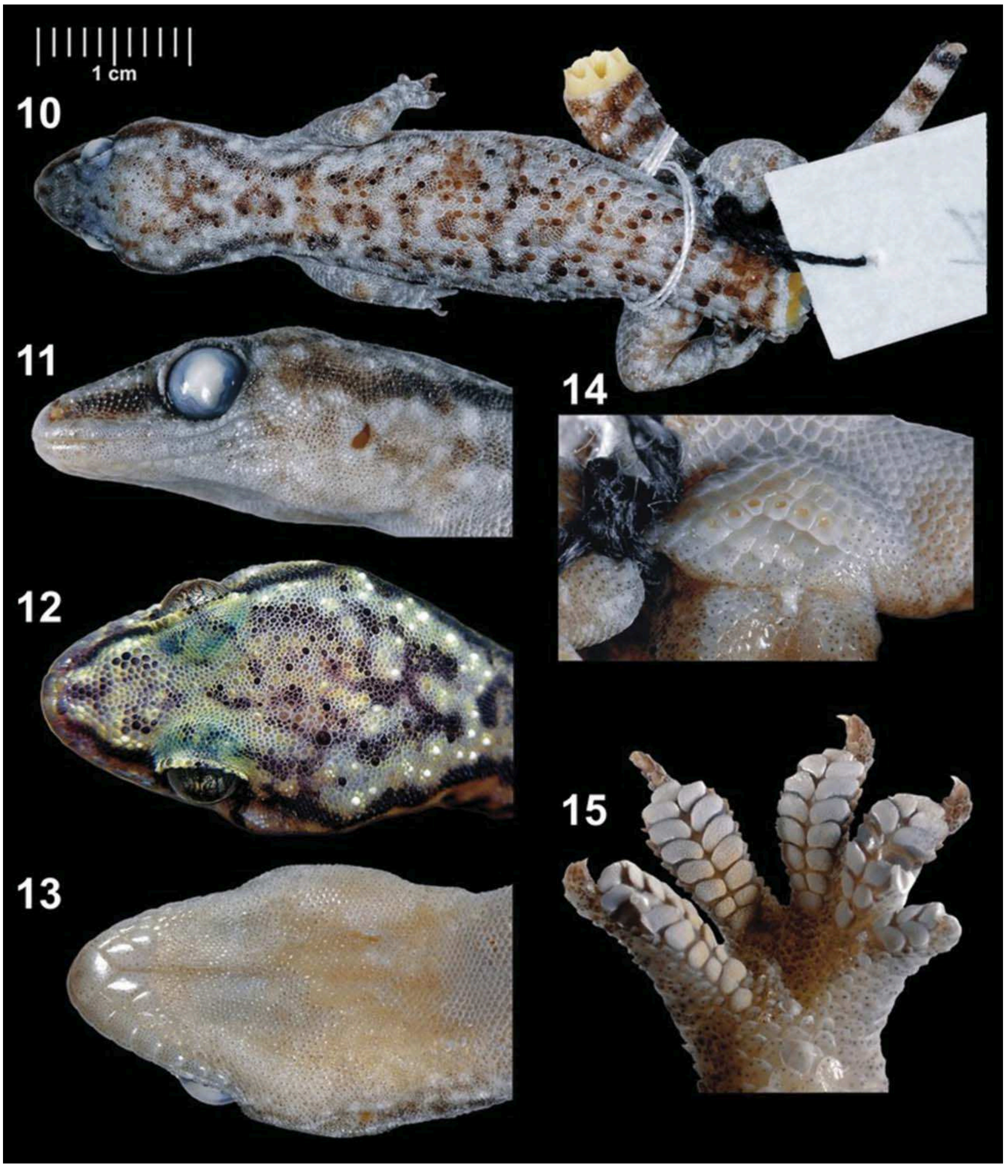

Fig. 10−15. Holotype of *H. mandebensis* sp. nov. (NMP6V 74836/2, adult male) showing **10**, general body habitus; **11**, lateral; **12**, dorsal; and **13**, ventral view of the head; **14**, precloacal region with preanal pores visible; and **15**, lamellae under the toes of right hind foot. Scale refers to the uppermost picture only.

rostral, three nasals and 1st supralabial; uppermost nasals being the largest and in wide mutual medial contact. Mental triangular; large trapezoid-shaped anterior postmentals in wide contact behind mental and in contact with 1st (left) and 1st and partially 2nd (right) infralabials; posterior postmentals about half size of the anterior ones and in contact with 1st and 2nd (left) and 2nd (right) infralabials. Supralabials 9/9, infralabials 8/8. Ear opening ovoid. Dorsal surface of head from the interorbital level posteriorly covered by numerous juxtaposed scales intermixed with larger isolated round scales; one large unpaired round scale in the left parietal area. Enlarged head tubercles continue on neck and body forming 14 longitudinal rows in the widest body part. Dorsal tubercles in paravertebral line keeled and slightly prominent posteriorly, the keels and pointy shape disappear towards flanks where the tubercles are smaller, smooth and flat. Enlarged unkeeled tubercles present also on dorsal parts of arms and legs, those on legs prominently pointed. Body oval in cross section. Ventral scales imbricate, small in gular area and on flanks and increasing in size towards mid-belly. Lamellae under the 1st toe 6/6, under the 4th toe 9/9. Six preanal pores forming an open U-shaped continuous row. Prominent hemipenial bulges. Tail detached from body, original with partially regenerated tip. Five whorls containing at least six enlarged scales, lateral scales of the whorls not

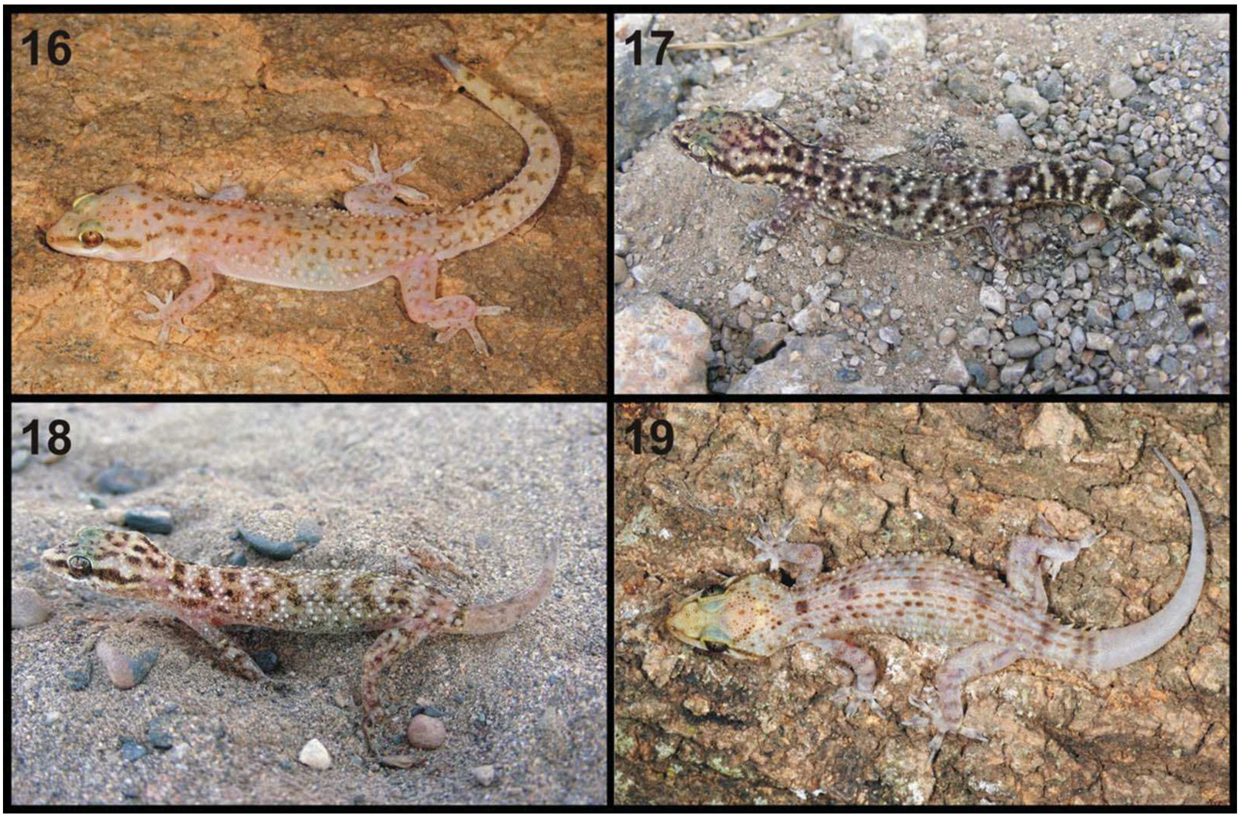

Fig. 16–19. Live specimens. **16**, *H. robustus* (TMHC 2012.02.048) from Shalatein, Egypt; **17**, holotype of *H. mandebensis* sp. nov. (NMP6V 74386/2) from 3 km S of Najd an Nashamah, Yemen; **18**, paratype of *H. adensis* sp. nov. (NMP6V 74837) from Wadi Tuban, Yemen; **19**, paratype of *H. awashensis* sp. nov. (NMP6V 74978/2) from Awash, Ethiopia.

standing out from the dorsal outline of the tail. Subcaudals enlarged, unpaired. A small wound about 2 mm long on left side of ventrum, probably caused post mortem. Tongue removed for genetic analyses.

Colouration in life (Fig. 17). Dorsal colour grey with numerous irregular dark-brown to black blotches on body and tail. Dark brown stripe from nostril to eye just above supralabials and continuing from posterior eye margin above ear opening onto neck and along body up to the shoulder area, where it gets interrupted into isolated dark spots. Distinct W-shaped dark blotch in the middle of nape, followed posteriorly by an interrupted dark vertebral line going up to pelvic area. Some of the tubercles on body dorsum bright white contrasting strongly with the otherwise dark colour. Tail with irregularly shaped dark transverse bands, underside white. Venter creamy white with dark stipple most clearly developed in lower chin and throat area. The vivid dorsal colour pattern faded after fixation.

Variation. The two paratypes differ from the holotype in several characters. SVL of the adult female NMP6V 74836/1 = 39.1 mm. Number of infralabials varies between 7–8. Unlike the holotype, both paratypes have uppermost nasals separated by a row of inserted scales. Anterior postmentals always in contact with only the 1st infralabial. Specimen NMP6V 74970 has only 12 longitudinal rows of enlarged dorsal tubercles. Number of lamellae under the 1st and 4th toes are lower in both paratypes, 5/5 and 8/8 respectively. There is no specimen with original tail preserved. Colour pattern of both paratypes is faded due to fixation. Nevertheless, the dark stripes on head continuing as interrupted paravertebral lines are still evident and the dark 'W' on the nape is also visible. Ranges of values of morphological characters are summarized in Table 2.

Intraspecific genetic *p* distances within *H. mandebensis* sp. nov. range between 0.3–1.1% in *12S* and 0.5–2% in *cytb*. Even the two specimens from the same locality (NMP6V 74836/1–2) do not share haplotypes in any of the mtDNA genes studied. From the nuclear genes analysed, the alleles of *cmos* and *rag2* are shared across the species while *mc1r* and *rag1* express some degree of differentiation (Fig. 3).

Distribution and ecology. *Hemidactylus mandebensis* sp. nov. is for now known only from two localities in the mountainous SW Yemen at elevations of 1182 m and

Table 2. Morphological comparison of the *Hemidactylus robustus* species group members. The values are given as follows: sample size, mean ± standard deviation above, min.–max. below.

	H. robustus	*H. mandebensis* sp. nov.	*H. adensis* sp. nov.	*H. awashensis* sp. nov.
SVL (males)	8, 41.8 ± 2.3 37.0–43.7	1, 41.5	2, 34.0 ± 5.5 30.1–37.9	4, 51.3 ± 4.4 45.3–54.8
SVL (females)	16, 43.6 ± 4.7 32.7–50.1	2, 35.0 ± 5.8 30.9–39.1	4, 36.7 ± 5.6 29.9–41.8	2, 49.5 ± 4.1 46.7–52.4
Head length	24, 10.7 ± 0.9 8.7–12.8	3, 9.4 ± 1.2 8.2–10.6	6, 9.3 ± 1.1 8.0–10.3	7, 13.3 ± 1.7 10.5–15.6
Head width	24, 8.2 ± 0.8 6.3–9.4	3, 7.4 ± 1.2 6.1–8.5	6, 6.9 ± 0.9 5.9–7.8	7, 10.4 ± 1.4 7.8–12.2
Head depth	24, 4.7 ± 0.6 3.7–5.9	3, 4.3 ± 0.7 3.6–5.1	6, 3.8 ± 0.5 3.2–4.3	7, 5.8 ± 0.6 4.9–6.9
Supralabials	27, 9.4 ± 0.7 8–11	3, 9 ± 0.0 9–9	6, 8.8 ± 0.7 8–10	7, 9.1 ± 0.7 8–11
Infralabials	27, 7.7 ± 0.6 6–9	3, 7.5 ± 0.5 7–8	6, 6.9 ± 0.6 6–8	7, 7.4 ± 0.6 6–8
Nasals in contact (%)	27, 22	3, 33	7, 0	7, 0
1st postmental in contact with 2nd lower labial (%)	27, 70	3, 17	7, 93	7, 86
Rows of dorsal tubercles	27, 14.8 ± 1.2 13–18	3, 13.3 ± 1.2 12–14	6, 14 ± 0.0 14–14	7, 14 ± 0.0 14–14
Preanal pores	9, 6.1 ± 0.8 5–8	1, 6	2, 6.5 ± 0.7 6–7	2, 4.5 ± 0.7 4–5
Lamellae under 1st toe	27, 6.1 ± 0.5 5–8	3, 5.3 ± 0.6 5–6	6, 5.3 ± 0.4 5–6	7, 8 ± 0.0 8–8
Lamellae under 4th toe	27, 10.1 ± 0.7 8–12	3, 8.3 ± 0.6 8–9	6, 9.3 ± 0.4 9–10	7, 11.4 ± 0.5 11–12

1253 m a.s.l. situated about 20 km from each other (Fig. 2). The specimens were found at night climbing rock faces on the edge of irrigated fields. Interestingly, only gecko species (Gekkota) were found to live in sympatry with *H. mandebensis* sp. nov. The species were: *Hemidactylus ulii*, *H. y. yerburii*, *Ptyodactylus* sp., *Pristurus flavipunctatus*, *Pristurus* sp. 1 (sensu Badiane et al., 2014).

Hemidactylus adensis sp. nov.

Synonymy. *Hemidactylus* sp. 6 in: Moravec et al. (2011); Šmíd et al. (2013a, 2013b); *Hemidactylus sinaitus* in: Busais & Joger (2011a, 2011b).

Holotype. NHM-BS N41904, adult male (MorphoBank M329154-M329164), Yemen, Lahij governorate, Sheikh Othman, 13.917°N, 44.983°E, 22 m a.s.l., 22. III. 2009, collected by S. M. Busais.

Paratypes. NHM-BS N41905–907, subadult male (NHM-BS N41905, MorphoBank M329165-M329172), juvenile (NHM-BS N41906, MorphoBank M329173-M329180), subadult female (NHM-BS N41907, MorphoBank M329181-M329189), same data as holotype; NHM-BS N41902–903, adult females (MorphoBank M329131-M329140, M329141-M329153, respectively), Yemen, Lahij governorate, Lahij, 13.055°N, 44.878°E, 136 m a.s. l., 18. I. 2008, collected by S. M. Busais; NMP6V 74837, adult female (MorphoBank M329190-M329206), Yemen, Wadi Tuban (N of Lahij), 13.13°N, 44.85°E, 200 m a.s.l., 25. X. 2007, collected by L. Kratochvíl.

Etymology. The species epithet *adensis* is an adjective referring to the area where the species is found, lowlands in the vicinity of the city of Aden.

Diagnosis. A small-sized *Hemidactylus*, member of the *H. robustus* species group as part of the Arabian radiation of the *Hemidactylus* arid clade characterized by: (1) small size with maximum SVL 37.9 mm for males and 41.8 mm for females; (2) pointy and relatively long and flat head (HL = 24–27% SVL; HD = 40–42% HL); (3) 6–7 infralabials and 8–10 supralabials; (4) uppermost nasals divided by intervening row of inserted scales; (5) 14 rows of enlarged mostly flat and indistinctly keeled dorsal tubercles; (6) 6–7 preanal pores in males; (7) 5–6 lamellae under the 1st toe; (8) 9–10 lamellae under the 4th toe; (9) enlarged subcaudals; (10) indistinct tail whorls not

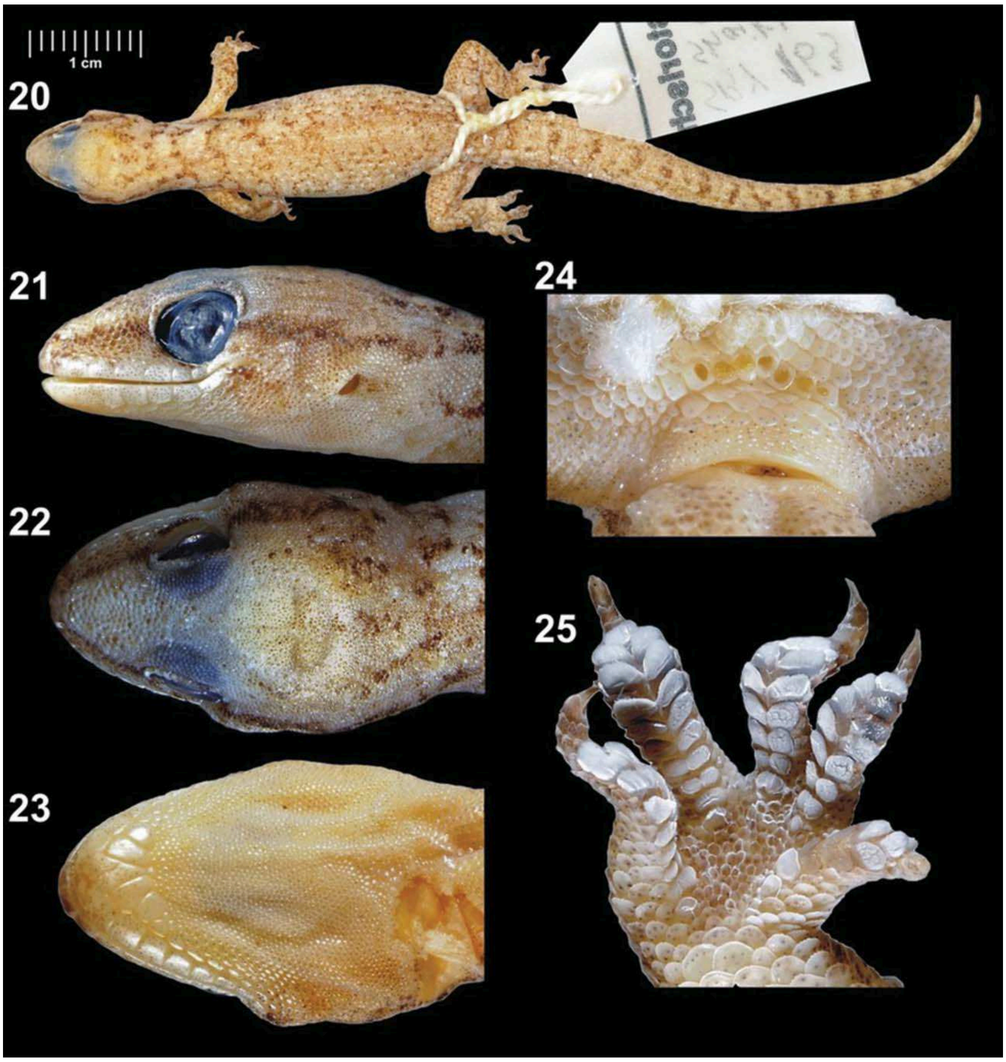

Fig. 20–25. Holotype of *H. adensis* sp. nov. (NHM-BS N41904, adult male) showing **20**, general body habitus; **21**, lateral, **22**, dorsal and **23**, ventral view of the head; **24**, precloacal region with preanal pores visible; and **25**, lamellae under the toes of right hind foot. Scale refers to the uppermost picture only.

disrupting the tail outline when viewed from above; (11) contrasting dark brown stripes on the otherwise greyish body running from nostrils over eye and temporal area up to scapular region where they are connected by two to three transverse bars.

Description of the holotype. Adult male (Figs 20–25). Measurements (in mm): SVL 37.9, HL 10.3, HW 7.8, HD 4.3, E 2.1, AG 16.7. Head and body slightly depressed, head concave with oblong snout, eyes not protruding from lateral head outline (in the fixed specimen). Supralabials 8/8, infralabials 6/7. Nostril bordered by wide rostral, three subequal nasals and 1st supralabial; uppermost nasals separated by one inserted scale about twice as long as wide. Mental clearly triangular and very long, reaching up to posterior margin of anterior postmentals and separating them from each other; anterior postmentals long and in contact with 1st and 2nd infralabials; posterior postmentals semicircular, in contact with 2nd infralabial. Dorsal head and body surface covered with small juxtaposed scales intermixed with enlarged, smooth and non-protruding tubercles arranged in 14 longitudinal rows; equally shaped tubercles present also on dorsal parts of arms and legs. Vertebral and paravertebral tubercles run continuously onto tail where they form regular whorls. Two whorls with six enlarged scales, lateral scales of the whorls do not stand out from the dorsal outline of the tail. Ventrals imbricate, smallest in gular region, scales on body flanks and venter of almost equal size. Lamellae under the 1st toe 5/6, under the 4th toe 10/10. Seven preanal pores in a continuous row. Distinct hemipenial bulges. Tail original, longer than SVL; subcaudal scales enlarged from just after the hemipenial bulges, unpaired. A small patch of skin on right side of throat missing, chest opened by irregular X-shaped cut, heart and part of lungs removed; tongue removed for genetic analyses.

Colouration in preservative. Base colour uniformly creamy to beige brown with irregular light brown markings all over the body. Light brown stripe running on both sides from uppermost nasals to eye and continuing from posterior eye margin above ear onto nape and shoulders, where they are connected by two darker transverse bars. Head dorsally uniformly beige with faint stipple of light brown spots and several darker tubercles. Mouth corners with light brown blotches, faint spot also behind ear opening. Indistinct W-shaped marking on the nape. Dorsum stained with light brown markings not forming any regular pattern, darker spots usually restricted to one or only a few dorsal scales. Scales on posterior side of thighs divided into light anterior and dark posterior half. Tail with indicated dark transverse markings. Head and body venter creamy white, tail creamy brownish with darker longitudinal stripe in medial line. Chin tip, gular and belly margins with black stipple that gets weaker towards mid-gular and mid-belly (visible under magnification).

Variation. The largest female among the paratypes (NMP6V 74837; Fig. 18) is of equal size as the holotype (SVL 41.8 mm). The holotype is the only specimen with intact original tail. Number of supralabials varies from 8 to 10. Number of infralabials is consistently 6–7, specimen NMP6V 74837 being the only exception with 8 infralabials. Specimen NHM-BS N41905 is the only paratype with unilateral contact of anterior postmental with only the 1st infralabial, all other specimens have the condition found in the holotype, i.e. contact with the 1st and 2nd infralabials. However, the holotype is the only specimen with anterior postmentals not touching each other and being separated by a very long mental shield. In all paratypes the mental scale is long and triangular but anterior postmentals are in wide contact behind it. The only other male in the series, a subadult male NHM-BS N41905, has 6 preanal pores in the same arrangement as the holotype. All paratypes have 9 lamellae under the 4th toe (only NMP6V 74837 has 9/10) (see also Table 2).

There is no obvious difference in the colour pattern among the fixed material; however in NHM-BS N41903 the magnitude of the dark markings on the head and nape is well developed. Dorsal pattern of specimens NHM-BS N41902 and NMP6V 74837 constituted by more or less prominent dark transverse bands regularly spaced between scapulae and tail base, the two bands at mid-body cross each other and form a clear X. NMP6V 74837 is the only specimen whose life colouration is known from pictures. It is consistent with that described above for the holotype, differing only in that the contours are more prominent than in the fixed material, the dark 'W' on the nape being clearly visible as well as several dark spots on head dorsum (remained after fixation).

Genetic variability within *H. adensis* sp. nov. is very low (Fig. 2). Maximum divergence within the species reaches 0.9% in *12S* and 1.4% in *cytb* and separates individuals found at the same locality. The variation in the nDNA varies strongly among genes (Fig. 3). While there are only two very close alleles in *rag1* and *rag2*, *cmos* presents a higher level of variation caused by the presence of three heterozygotes. The most variable is the *mc1r* gene where all but one individuals of *H. adensis* sp. nov. have multiple heterozygous positions throughout the alignment.

Distribution and ecology. All three known localities from where *H. adensis* sp. nov. is known lie along the road from Aden to Lahij and further north-westward (Fig. 2) at altitudes from 12 to 200 m a.s.l. Specimens were collected in habitats influenced by humans – gardens around towns and field margins. Some specimens were collected during the day on neem trees (*Azadirachta indica*, Meliaceae) or under them on the ground hidden under fallen leaves (Busais, 2011). One specimen was collected on the edge of a dried-out wadi also neighbouring cultivated fields. Other reptile species found syntopically with *H. adensis* sp. nov. at the locality Wadi Tuban north of Lahij were: *Hemidactylus flaviviridis*, *H. y. yerburii*, *Stenodactylus yemenensis*, *Acanthodactylus* sp.

Hemidactylus awashensis sp. nov.

Synonymy. *Hemidactylus macropholis* in: Lanza (1972, 1978 [partim]), Largen and Spawls (2006 [partim], 2010 [partim]; *Hemidactylus* aff. *macropholis* in: Mazuch (2013); *Hemidactylus* sp. 11 in: Šmíd et al. (2013a, 2013b).

Holotype. NMP6V 74979, adult male (MorphoBank M329043-M329085), Ethiopia, Oromia Region, Metehara, 8.922°N, 39.912°E, 981 m a.s.l., 19. XI. 2010, collected by T. Mazuch.

Paratypes. All paratypes were collected in the vicinity of Metehara by T. Mazuch, P. Novák, V. Trailin. NMP6V 74980, adult male (MorphoBank M329086-M329118), 8.931°N, 39.905° E, 1020 m a.s.l.; NMP6V 74977, adult female (MorphoBank M328897–M328937), 8.921°N, 39.903°E, 990 m a.s.l., both collected 19. XI. 2010; NMP6V 74978/1–3, subadult female (NMP6V 74978/1, MorphoBank M328942–M328968), adult female (NMP6V 74978/2, MorphoBank M328969–M329004), adult male (NMP6V 74978/3, MorphoBank M329005–M329042), 8.908°N, 39.912°E, 964 m a.s.l., 22. VII. 2011.

Other material. NMP6V 74981, juvenile (MorphoBank M329119-M329130), JS242–243, JS246, JS322, 8.908°N, 39.912°E, 964 m a.s.l., 22. VII. 2011; JS204, 8.921°N, 39.903°E, 990 m a.s.l., 19. XI. 2010; JS248, 8.923°N, 39.905°E, 990 m a.s.l., 19. XI. 2010, all collected in the vicinity of Metehara by T. Mazuch, P. Novák, V. Trailin. MZUF 22202, adult male (MorphoBank M328886-M328896), Awash National Park (Shoa, Ethiopia), unknown date and collector. The JS codes refer to material available as tissue samples only. The juvenile specimen was used for genetic analyses only; the MZUF specimen was used only for analyses of morphological characters.

Etymology. The species epithet is an adjective referring to the region where all known material has been collected – the surroundings of the Awash National Park in central Ethiopia.

Diagnosis. A medium-sized species of the *H. robustus* species group within the arid clade of *Hemidactylus* characterized by: (1) medium size with maximum recorded SVL 54.8 mm (45.3–54.8 mm in males, 38.5–52.4 mm in females); (2) large and robust head (HL 13.3 ± 1.7 mm, HD 5.8 ± 0.6 mm, HL = 26–28% of SVL, HD = 41–46% of HL); (3) relatively large horizontal eye diameter (24–29% of HL); (4) uppermost nasals always separated by a small shield; (5) large anterior postmentals in wide mutual contact; (6) dorsum with 14 longitudinal rows of enlarged, strongly keeled, conical tubercles; (7) low number of preanal pores in males (4–5); (8) 8 lamellae under the 1st toe; (9) 11–12 lamellae under the 4th toe; (10) enlarged subcaudals; (11) brownish grey colouration with a row of dark brown vertebral blotches starting on the nape and continuing as transverse bars (12–13) onto tail, smaller isolated dark patches also on flanks, dark horizontal stripe in prefrontal and temporal region.

Description of the holotype. Adult male (Figs 26–33). Measurements (in mm): SVL 51.1, HL 13.8, HW 10.6, HD 6.0, E 3.8, AG 19.5. Head and body slightly depressed; head pointy, relatively wide (HW = 76% HL) separated by a distinctly narrowed neck; eyes large (horizontal eye diameter = 28% HL). Rostral large with a distinct medial groove; nostrils bordered by rostral, first supralabial and three nasals of equal size. Uppermost nasals separated by an inserted scale. Mental almost triangular; anterior postmentals long and in wide mutual contact behind mental and in contact with 1st and partially also 2nd infralabials. Postmentals roundish on posterior margin and in contact with 2nd infralabial. Supralabials 10/10, infralabials 8/8. Ear opening bean-shaped. Dorsal head surface covered with small round scales intermixed with larger, round, unkeeled tubercles in the temporal and parietal area. Body dorsum covered with large, prominent, triangular, posteriorly pointed tubercles with distinct medial keels in 14 longitudinal rows. Posterior side of forearms with small unkeeled pointy tubercles; thighs and lower legs with numerous large unkeeled tubercles. Ventral scales roughly hexagonal, imbricate. Lamellae under the 1st toe 8/8, under the 4th toe 11/11. Relatively long terminal (without lamellae) phalanges. Five preanal pores (3/2) arranged in a V-shaped line, separated in the medial line by a row of ventrals. Terminal part of the tail regenerated (original part 48.6 mm, regenerate 7.2 mm), tail with 7 whorls bearing more than 6 enlarged scales. Lateral scales of the whorls stand out from the dorsal tail outline. Subcaudals enlarged, unpaired starting from the first whorl and covering the whole width of the tail underside towards the tip. A small patch of dorsal skin missing on the vertebral region just behind the scapulae. Tongue removed for genetic analyses.

Colouration in life. Base colour of dorsal parts beige-brownish to grey with distinct scattered vertebral and paravertebral longitudinally oriented dark blotches starting on the nape and not forming any regular pattern. Dark markings on head more regular. Dark brown stripe from nostril to anterior margin of eye continues from posterior eye margin to the ear; additional stripe from the upper posterior eye margin runs in temporal-parietal region. Both terminate at the level of ear. Mouth corners with dark circular markings. Dorsal side of head bears dark brown markings, four patches in front of eyes forming corners of a rhomboid and four in parietal region with the same arrangement. Upper sides of lower arms and lower legs with indistinct dark stripes. Venter creamy whitish with faint stipple increasing in magnitude on lower side of limbs. The stipple also on enlarged dorsal tubercles (visible under magnification). The colour pattern has remained consistent after 4 years of fixation.

Variation. There is no significant difference in the colouration only that the 4 preocular dark blotches prominent in the holotype are indistinct in all the paratypes (Fig. 19). The size (SVL) of adult specimens varies between 45.3–54.8 mm in males and 46.7–52.4 mm in females. In the only two specimens with original intact tails (NMP6V 74977, NMP6V 74978/1) the tail represents 133 and 131% of SVL, respectively. Number of supralabials from 8 to 10 (9.1 ± 0.7), number of infralabials varies from 6 to 8 (7.4 ± 0.6). One paratype (NMP6V 74978/3) has anterior postmentals in contact with 1st infralabial only. Specimen MZUF22202 has 4 preanal pores in a continuous row. The number of preanal pores could not be counted precisely in the other two male paratypes (NMP6V 74978/3, NMP6V 74980) because their precloacal region is damaged. The less damaged specimen NMP6V 74980 has apparently 4–5 preanal pores forming a continuous row. The lamellae under the 1st toe are

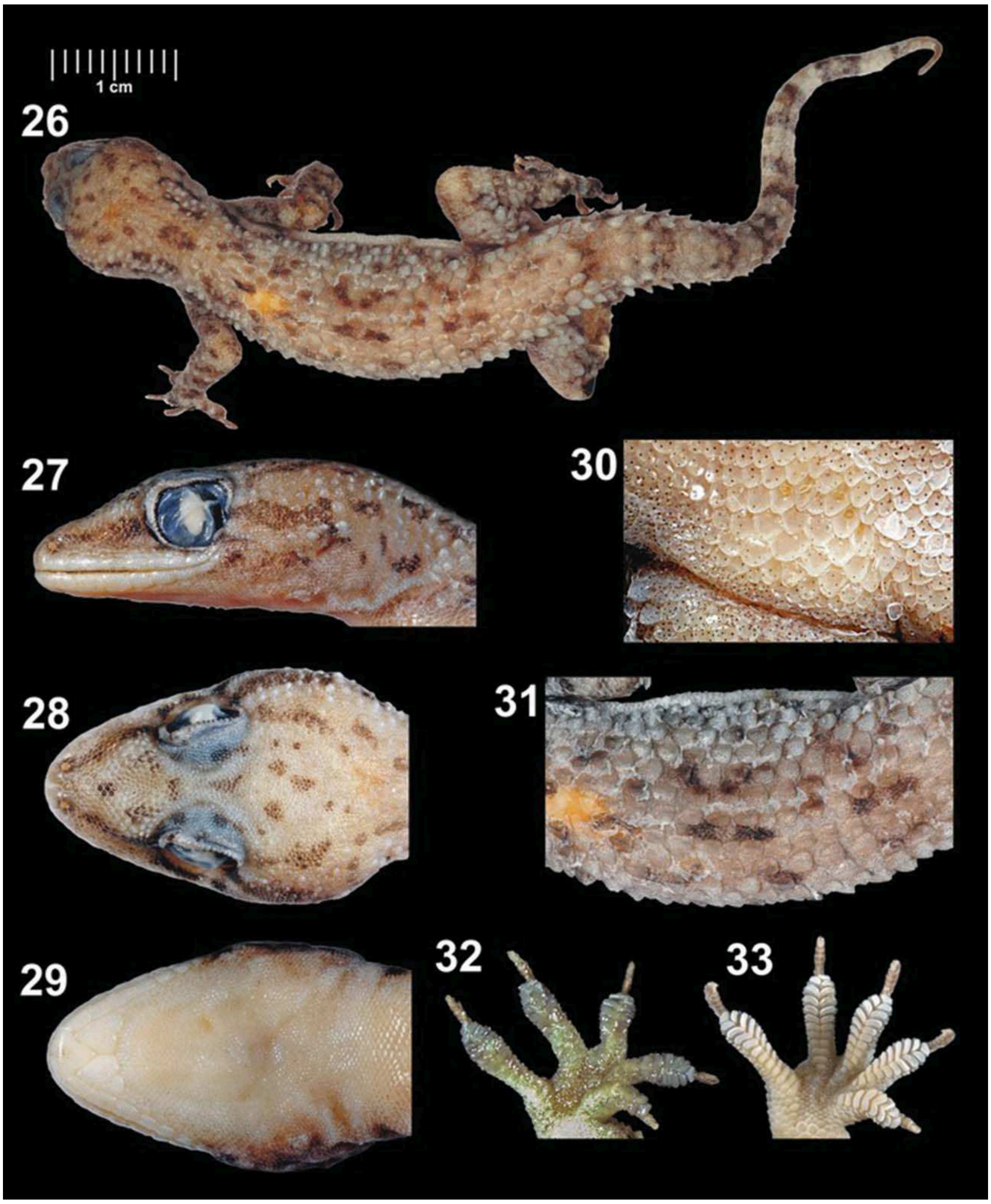

Fig. 26–33. Holotype of *H. awashensis* sp. nov. (NMP6V 74979, adult male) showing **26**, general body habitus; **27**, lateral, **28**, dorsal and **29**, ventral view of the head; **30**, precloacal region with preanal pores visible; **31**, detail of the arrangement of dorsal tubercles; and **32**, lamellae under the toes of right hind foot. **33**, Lamellae under the toes of paratype NMP6V 74978/3. Scale refers to the uppermost picture only.

invariably 8, while under the 4th toe vary between 11 and 12 (see also Table 2).

Given the small area of origin of all samples of *H. awashensis* sp. nov. there is almost no genetic variability within this species (Fig. 2). The range of intraspecific mtDNA *p* distances is 0.3–0.9% in *12S* and 0.1–0.2% in *cytb*. Among the sequenced nuclear genes there is also almost no variability, all animals share identical alleles in *cmos*, *mc1r* and *rag1* and three specimens were heterozygous in three nucleotide positions in *rag2* (Fig. 3).

Distribution and ecology. All known specimens of *H. awashensis* sp. nov. have been collected northwest of the town of Metehara, between the Fantale volcano and the town within a radius of *c.* 3 km. The region around the volcano is characterized by extensive fields with lava boulders protruding from grassy pastures with scattered acacia trees. Specimens were captured or observed at night on these ragged stones with numerous cracks and caves that serve as day shelters for the geckos. Several young individuals were observed also on house walls in

Metehara where, however, the introduced *H. flaviviridis* dominates. Other reptile species found syntopic with *H. awashensis* sp. nov. were: *Hemidactylus flaviviridis*, *H. sinaitus*, *Tarentola annularis*, *Agama spinosa*, *Latastia doriai*, *Philochortus phillipsi*, *P. spinalis*, *Platyceps taylori*, *Stigmochelys pardalis*, *Trachylepis brevicollis*, *T. quinquetaeniata*.

Discussion

As shown in previous large-scale phylogenetic studies (Carranza & Arnold, 2012; Gómez-Díaz et al., 2012; Šmíd et al., 2013a), the arid clade of the genus *Hemidactylus* has undergone a substantial radiation in the Arabian Peninsula and surrounding regions within the last 15 Ma. Not only have these studies outlined the phylogenetic relationships among the already recognized species, but they have also provided evidence of high genetic differentiation of *Hemidactylus* with at least 11 cryptic species detected. As a follow-up of these published phylogenies, and as part of the taxonomic and nomenclatural studies in the arid clade of *Hemidactylus* (Busais & Joger, 2011b; Carranza & Arnold, 2012; Moravec et al., 2011; Šmíd et al., 2013b, Vasconcelos & Carranza, 2014), we herein formally establish the *H. robustus* species group, redescribe the widely distributed and until now insufficiently diagnosed *H. robustus*, describe three new *Hemidactylus* species from Yemen and Ethiopia and provide further data on the phylogeny of the *H. robustus* species group.

Interestingly, by narrowing the focus to representatives of the *H. robustus* and *H. saba* species groups compared with the broader sampling used in our previous study (Šmíd et al., 2013a) and adding a new material of *H. awashensis* and *H. adensis*, the compelling support of the within-group relationships has diminished. The phylogenetic tree based on a concatenated alignment of all mtDNA and nDNA sequences supports the sister-species relationship between *H. mandebensis* and *H. adensis*, while the positions of *H. robustus* and *H. awashensis* remain unresolved (Fig. 2). This contrasts with the first published phylogeny of this group (Šmíd et al., 2013a), in which, also based on a concatenated dataset using the same combination of genes, the latter two species were recovered as a well-supported clade. This topological inconsistency led us to employ the coalescent species-tree estimation. Multilocus species-tree approaches have been suggested to have better estimation accuracy for inferring true evolutionary relationships among species than concatenations (Heled & Drummond, 2010; Liu & Edwards, 2009). Phylogenetic reconstructions of concatenated datasets do not account for individual gene histories and potential discordance between gene trees and can therefore result in misleading or even erroneous, highly supported topologies (Edwards, Liu, & Pearl, 2007; Kubatko & Degnan, 2007). Moreover, analyses of different subsamples of the same dataset have been shown to sometimes produce strongly divergent topologies (e.g. Song, Liu, Edwards, & Wu, 2012). By contrast, coalescent-based species-tree inference has been shown to be more accurate in species delimitation, while accounting for uncertainties associated with gene tree estimations (such as incomplete lineage sorting or discordance among loci) (Heled & Drummond, 2010; Knowles & Carstens, 2007).

The species-tree analysis of the *H. robustus* and *H. saba* species groups recovered the *H. robustus* species group as monophyletic and highly supported (pp = 1.00), with *H. awashensis* representing the sister lineage to a clade of *H. robustus* + *H. mandebensis* + *H. adensis* (pp = 0.95) (Fig. 1). In contrast to the tree based on concatenated data, *H. mandebensis* and *H. adensis* were not sufficiently supported as sister taxa in the species-tree estimation. Therefore, with the current knowledge, we consider the *H. robustus* group strongly supported with largely unresolved phylogenetic relationships between its members, with *H. awashensis* being both morphologically and genetically the most divergent. It is possible that there are still some species belonging to this group which are missing in the analyses and the absence of which hampers the correct reconstruction of the phylogenetic relationships, because, as has been shown, phylogenetic analyses with incomplete taxon sampling can sometimes decrease accuracy or result in different tree topologies (Heath, Zwickl, Kim, & Hillis, 2008; Huelsenbeck & Lander, 2003; Ruane, Bryson, Pyron, & Burbrink, 2014). If this is the case, we presume such species to occur in the herpetologically poorly explored Horn of Africa (Mazuch, 2013; Wagner, Leaché, Mazuch, & Böhme, 2013a; Wagner, Mazuch, & Bauer, 2013b; unpublished data).

The degree of diversification within the *H. robustus* species group at the level of nuclear DNA is apparent from the nuclear networks (Fig. 3). *Hemidactylus awashensis* has unique alleles in all the studied genes and all species are well differentiated in the networks of *mc1r* and *rag1*. On the other hand, *H. robustus*, *H. mandebensis* and *H. adensis* share a common haplotype in *cmos* and *rag2*. This clearly demonstrates very shallow structuring in the *cmos* and *rag2* networks (see also Appendix S4, see supplemental material online) within this group of *Hemidactylus* being probably a result of shared ancestral polymorphism and incomplete lineage sorting rather than ongoing gene flow. If the latter was the case, one would expect to also see some degree of allele sharing in other genes. Moreover, the same *rag2* allele is even shared with *H. granosus*, a representative of another species group (Appendix S4, see supplemental material online). Both *cmos* and *rag2* can thus be considered of low ‘informativeness’ (see Camargo et al., 2012) for phylogenetic analyses of closely related *Hemidactylus* species. Because only a relatively small number of loci were used in our analyses, having two of them poorly informative could bias the whole phylogenetic reconstruction which then resulted in a less resolved tree. Identical pattern was recovered by Vasconcelos and Carranza (2014) in other closely related and recently diverging *Hemidactylus* taxa (*H. homoeolepis* and *H. minutus*), where also allele sharing in *cmos* on one hand and good separation in *mc1r* and *rag1* on the other was detected. The *H. robustus* species group is apparently in a stage of incipient speciation. Incomplete lineage sorting, ubiquitous at the initial stages of species divergence, complicates inference of shallow phylogenetic structure within this group.

Due to the above described topological discrepancies, the timing of the African colonization by this group needs to be reconsidered. The basal split within the *H. robustus* species group occurred 7 (4.6−9.8) Ma and was supposed to be followed by the separation of *H. awashensis* and *H. robustus* 5.9 (3.8−8.3) Ma (Šmíd et al., 2013a). However, with the unresolved topology, only the basal split remains trustworthy and the colonization of Africa by the ancestral *H. awashensis* might have happened earlier than previously estimated. Nevertheless, even if this shift of the colonization estimation is taken into consideration, the time window of the event still overlaps with the reconnection of Africa and Arabia by a land bridge in the Bab-el-Mandeb area *c*. 11−5 Ma (Redfield, Wheeler, & Often, 2003) by which the Afro-Arabian faunal exchange must have been significantly facilitated. After this period, south Arabia and the Horn of Africa never got in direct contact again (Fernandes, Rohling, & Siddall, 2006).

A large number of new *Hemidactylus* species described during the last years including all the three described herein were discovered in Yemen and Ethiopia. Both these areas are parts of the Eastern Afromontane and the Horn of Africa biodiversity hotspots, places with a high number and a high proportion of endemic reptile species (Mittermeier et al., 2004) and, as can be seen here, also places where biodiversity is still probably underestimated. Both regions are characterized by a complex geomorphology, high altitudinal zonation and wide variety of natural habitats, factors supporting rich species assemblages on relatively small geographic areas. With nine species in SW Yemen and at least eleven in NE Ethiopia (Šmíd et al., 2013a; unpubl. data), and considering the knowledge on other reptile taxa, *Hemidactylus* represents the most species-rich reptile genus in the area. What mechanisms, whether morphological or behavioural differentiation, niche utilization, climatic adaptation, or a combination of several of them are responsible for this diversity is still unknown.

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Supporting information

Appendix S1. List of specimens examined for morphological comparisons.

Appendix S2. Species-tree (maximum clade credibility tree) of the *H. robustus* and *H. saba* species groups based on the four studied nuclear genes only (*cmos*, *mc1r*, *rag1*, *rag2*). Posterior probabilities ≥ 0.95 shown.

Appendix S3. Maximum likelihood tree of the *H. robustus* and *H. saba* species groups based on concatenated alignment of the mtDNA genes only (*12S* and *cytb*). Node labels indicate ML bootstrap values (≥ 70%)/Bayesian posterior probabilities (≥ 0.95).

Appendix S4. Maximum likelihood trees of the *H. robustus* and *H. saba* species groups based on independent alignments of *cmos*, *mc1r*, *rag1*, and *rag2*. Node labels indicate ML bootstrap values (≥ 70%)/Bayesian posterior probabilities (≥ 0.95).

Appendix S5. Results of Unequal N HSD (honest significant difference) *post-hoc* tests for one-way ANOVA. Significance of differences between species and statistically homogeneous groups are given. Numbers in bold indicate significant differences between species.

Appendix S6. Morphological and genetic comparisons of the species within the *Hemidactylus robustus* species group members and with other *Hemidactylus* taxa occurring within their distribution ranges.

Appendix S7. Mean uncorrected *p* distances (complete deletion) between members of the Arabian radiation of *Hemidactylus* based on fragments of *12S* gene (below the diagonal) and *cytb* (above the diagonal). Values for the *H. robustus* species group are in bold. Material for comparison from Šmíd et al. (2013a).

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Supporting information

Appendix S1. List of specimens examined for morphological comparisons.

H. albopunctatus (1 individual) – TMHC 2012.07.087 (Ethiopia, Kebri Beyah).

H. angulatus (29 individuals) – NMP6V 74847 (Ethiopia, Hagere Maryam); NMP6V 74845/1–5, NMP6V 74853 (Ethiopia, Arba Minch); NMP6V 74846 (Ethiopia, Konso); NMP6V 74848 (Ethiopia, Yebelo); NMP6V 74852 (Ethiopia, Jinka); NMP6V 74851/1–2 (Ethiopia, Hammar); NMP6V 74814/1–5, NMP6V 74849/1–2, TMHC 2014.05.471 (Kenya, South Horr); NMP6V 74815/1–3 (Uganda, Ubbi); NMP6V 74813/1–5 (Kenya, Kinyang); NMP6V 74850 (Kenya, road to Lokichar).

H. alkiyumii (32 individuals) – NMP6V 74800 (Yemen, Damqawt); NMP6V 74799/1–11 (Yemen, Hawf); NMP6V 74838/1–4 (Oman, Hafouf); NMP6V 74839/1–4 (Oman, Salalah); NMP6V 74843 (Oman, Mirbat); NMP6V 74842/1–2 (Oman, Ain Tabruq); NMP6V 74840/1–3 (Oman, Ain Jarziz); NMP6V 74844/1–4 (Oman, Taiq Cave); NMP6V 74841, CAS227519 (Oman, Tawi Atayr).

H. barodanus (5 individuals) – TMHC2012.07.082–83 (Ethiopia, 20 km NE of Dire Dawa); TMHC2012.07.085 (Ethiopia, Dire Dawa); TMHC 2012.07.081 (Ethiopia, Hidenu); TMHC 2012.07.091 (Somalia, Laas Geel).

H. citernii (5 individuals) – TMHC2012.07.096–97, TMHC2012.07.099 (Somalia, Laaleys); TMHC2012.07.098 (Somalia, 10 km SE of Berbera); TMHC 2012.07.095 (Somalia, Laas Geel).

H. dracaenacolus (4 individuals) – MCCI R1578-1–2, MCCI R1502-1–2 (Yemen, Socotra).

H. festivus (8 individuals) – NMP6V 74812 (Yemen, Wadi Hadramawt); NMP6V 74811/1–2 (Yemen, Damqawt); NMP6V 74854/1–4, NMP6V 74855 (Oman, Mughsayl).

H. flaviviridis (8 individuals) – NMP6V 74858 (Oman, Jalan Bani Bu Hasan); NMP6V 74859/1–5 (Pakistan, Multan); NMP6V 74856 (Pakistan, Rakhni); NMP6V 74857 (Pakistan, Sukkur).

H. forbesii (8 individuals) – MCCI R1579a, b (8 ex.) (Yemen, Abd al Kuri).

H. foudaii (1 individual) – NMP6V 74808 (Sudan, 15 km SE of Atbara).

H. funaiolii (1 individual) – NMP6V 74452 (Kenya, Hurri Hills).

H. granchii (4 individuals) – MZUF 21188 (holotype) (Somalia, ca. 80 km N of Obbia); MZUF 21114 (paratype) (Somalia, Uarscek area); MZUF 21189 (paratype) (Somalia, 30 km S of Galcaio); TMHC 2012.07.088 (Somalia, ca. 45 km NE of Hargeisa).

H. granosus (18 individuals) – SMF 8723 (lectotype) (Egypt, Sinai); NMP6V 70163/1–4 (Egypt, Sharm el-Sheikh); ZFMK 94084–85 (Saudi Arabia, Al Wajh); ZFMK 94086, ZFMK 94088–89 (Saudi Arabia, 15 km S of Al Wajh); TUZC-R10 (Saudi Arabia, 180 km N of Hail); IBES 10183, TUZC-R11, ZFMK 94090, IBES 10344 (Saudi Arabia, 30 km NE of Alhawiyah); IBES 10150, IBES 10363, ZFMK 94091 (Saudi Arabia, 20 km S of Ashayrah).

H. granti (4 individuals) – MCCI R1606-1–2, MCCI R1501-2008, MCCI R1501-2009 (Yemen, Socotra).

H. hajarensis (3 individuals) – NMP6V 74861 (Oman, Wadi Bani Awf); NMP6V 74862 (Oman, Quriyat); NMP6V 74860/2 (Oman, Muqal).

H. homoeolepis (42 individuals) – BMNH 81.7.22.6–7 (Yemen, Socotra); IBES 10573–7, IBES 10578–79 (Yemen, Socotra, Ras Shuab); IBES 10630–31 (Yemen, Socotra, Damaram); IBES 10687, IBES 5326, IBES 10745, IBES 3314 (Yemen, Socotra, Hadibo city); IBES 3281, IBES 10629 (Yemen, Socotra, wadi S of Wadi Shoab); IBES 5305, IBES 5189 , IBES 3562 (Yemen, Samha Is., Inland of Khaysat village); IBES 5353, IBES 5306, IBES 5154 (Yemen, Darsa Is.); BMHN 1967.485–89, BMNH 1953.1.7.83, BMNH 1953.1.7.87, BMNH 99.12.5.38 (Yemen, Socotra, Hadiboh Plain); BMHN 1967.490 (Yemen, Socotra, Hammadera); BMNH 99.12.5..40–41 (Yemen, Socotra, Dahmis); BMNH 99.12.5.43 (Yemen, Socotra, Adho dimelus); BMNH 1953.1.7.86 (Yemen, Socotra, Qualanya); IBES 3419 (Yemen, Socotra, Dixam Plateau); IBES 3289 (Yemen, Socotra, E of Hadibo); BMNH 99.12.5.42 (Yemen, Socotra, Homhil); IBES 1173 (Yemen, Socotra, Shuab area); IBES 1054 (Yemen, Socotra, Wadi Ayhaft); IBES 1169 (Yemen, Socotra, Sirahon).

H. inintellectus (4 individuals) – MCCI R1441 (paratype) (Yemen, Socotra, Temedeh area); MCCI R1469 (paratype) (Yemen, Socotra, 6 km SW of Qalansiyah); MCCI R1437 (paratype) (Yemen, Socotra, between Hadibo and Qadub); MCCI R1471 (paratype) (Yemen, Socotra, Wadi Kilisan south of Afafes).

H. isolepis (1 individual) – NMP6V 74447 (Somalia, 8 km S of Borama).

H. jumailiae (18 individuals) – NMP6V 74818/1 (Yemen, near Al Bayda [At Dageeg]); NMP6V 74819 (Yemen, Sana'a); NHM-BS N41788, NHM-BS N41890 (paratype), NHM-BS N41891, NHM-BS N41893 (holotype), NHM-BS N41894 (paratype), NHM-BS N41897 (paratype) (Yemen, Ibb); NHM-BS N41898 (paratype, the same accession number as one of *H. y. montanus* paratypes, Busais and Joger 2011b), NHM-BS N41899 (paratype) (Yemen, Thamar); BMNH1982.1143–44 (Yemen, Al Nabi Shuaib, 30 Km W. of Sana'a); BMNH1982.1145 (Yemen, Sana'a); BMNH1982.1146 (Yemen, Wadi Ahger, 45 Km. W. of Sana'a); BMNH1952.1.3.52 (Yemen, Sana'a); MSNG-YEM02, MSNG-YEM03 (Yemen, El Menghil); MCCI-R814 (Yemen, Hababah).

H. laticaudatus (4 individuals) – MSNM 959 (Eritrea, Fiume Caha); MSNM 858–859 (Ethiopa, Gondar); MSNM 626 (holotype of *H. l. fossatii*) (Eritrea, Saganeiti).

H. mabouia (1 individual) – NMP6V 74804 (Uganda, Mpanga Forest).

H. macropholis (90 individuals) – MSNG 28883 (syntype, Ethiopia/Somalia boundary, Dolo); CAS 122233–34, CAS 122330 (Kenya, Laisamis); CAS 130000, CAS 130094 (Kenya, vicinity of Buna); CAS 130231–2, CAS 130234–5 (Kenya, Rhamu); CAS 130513–17 (Kenya, vicinity of Mandera); CAS 130538–40 (Kenya, ca. 1 mi NE Mandera); CAS 140284–88 (Kenya, 30 mi E of Wajir at Wajir Bor); CAS 146969–70 (Kenya, Wajir); CAS 148344–49, CAS 151126, CAS 152938, CAS 153459, CAS 158935 (Somalia, Lower Juba River, near Mareri); MSNG 28567 (3 ex.), MSNG 29102 (4 ex.) (Somalia, Lugh); MSNG 29201 (Somalia, Bardera); MSNM 193–94, MSNM 198, MZUF 10812–13, MZUF 10824–25, MZUF 10827 (Somalia, Gardo [Qardho]); MSNM 335–37 (Somalia, Garoe [Garowe]); MSNM 344 (Somalia, Belet Uen [Beledweyne]); MSNM 345, MZUF 2429 (Somalia, El Bur [Ceelbuur]); MSNM 347 (Somalia, Meregh); MZUF 1592, MZUF 1631, MZUF 1727, MZUF 24656–59 (Somalia, Dinsor [Dinsoor]); MZUF 21090, MZUF 21092 (Somalia, Odweina [Oodweyne]); MZUF 21091 (Somalia, 47 km E of Burao); MZUF 24463–71 (Somalia, Baidoa); MZUF26364 (Somalia, Burtinle); MZUF 2986–89 (Somalia, Genale [Janale]); MZUF 2999 (Somalia, Oddur [Xuddur]]; MZUF 3028 (Somalia, Gelib [Jilib]); MZUF 5236–37, MZUF 5242 (Somalia, Bud Bud); MZUF 697 (Somalia, Uegit [Wajid]); MCCI R1224 (2 ex.) (Kenya, Illaut).

H. mindiae (5 individuals) – NMP6V 72323/1–2 (Jordan, Jabal Ghazali); NMP6V 72739/1–3 (Jordan, Wadi Ramm).

H. oxyrhinus (9 individuals) – MCCI R1587 (9 ex.) (Yemen, Abd al Kuri).

H. ophiolepis (1 individual) – TMHC 2012.07.094 (Ethiopia, 15 km NE of Dire Dawa).

H. persicus (4 individuals) – NMP6V 74807/1–4 (Iran, Booreki).

H. platycephalus (5 individuals) – NMP6V 74866 (Kenya, South Horr); NMP6V 74864/1–2 (Kenya, Ngurunit); NMP6V 74865/1 (Kenya, Wamba).

H. pumilio (7 individuals) – MCCI R1484-1–2 (Yemen, Socotra, Wadi Sirahon); MCCI R1513 (Yemen, Socotra, Plateau N. Of Shuab); MCCI R1443 (Yemen, Socotra, 400m E of Mahfer); MCCI R1512-1–2 (Yemen, Socotra, Mala area); MCCI R1514 (Yemen, Socotra, Qedami).

H. robustus (27 individuals) – SMF 8725 (MorphoBank M329345-M329365), SMF 8726 (MorphoBank M329366-M329384) ("Petraeisches Arabien" [Egypt, Sinai]); TMHC2012.07.092–93, TMHC2012.07.100 (Ethiopia, Jijiga); CAS130512 (Kenya, vicinity of Mandera); NMP6V 74820 (Iran, Bandar Lengeh); NMP6V 74821/1–2 (MorphoBank [NMP6V 74821/2] M329216-M329224) (Yemen, Wadi Zabid); NMP6V 74829 (Yemen, Bir Ali); TMHC 2012.06.068 (Kenya, Garissa); NMP6V 74867/1–3 (Oman, Muscat); NMP6V 74868 (Oman, Salalah); NMP6V 74869/1–7 (Oman, Mughsayl); NMP6V 74870/1–2 (Oman, Shisr); MCCI–R815 (MorphoBank M329247-M329276) (Yemen, Zabid).

H. ruspolii (4 individuals) – NMP6V 74871/1–3 (Kenya, Kalacha); MSNM 608 (Ethiopia, Galadi).

H. saba (3 individuals) – NHM-BS N41912 (holotype), NHM-BS N41913 (paratype), NHM-BS N41914 (paratype) (Yemen, Marib).

H. shihraensis (10 individuals) – NMP6V 74816 (Yemen, Al Mukalla); NMP6V 74817/1–9 (Yemen, Ghayl Ba-Wazir).

H. sinaitus (23 individuals) - BMNH82.8.16.27 (holotype, probably from Suakin, Sudan); BMNH97.10.28.83–85 (Sudan, Durrur, N of Suakin); BMNH97.10.28.87 (Sudan, Wadi Haifa); BMNH1974.3931 (Ethiopia, Mule River?, Danakil); BMNH1937.12.5.293–294 (Somalia, Borama district); BMNH95.5.23.7 (Yemen, Sheikh Osman, near Aden); BMNH1945.12.12.14 (Yemen, Bir Fadhl, Aden); NMP6V 74809/1–4 (Sudan, Wad Ben Naga); NMP6V 74810 (Sudan, 15 km SE Atbara); MZUF28645–646 (Yemen, Moka); MZUF10914, MSNM521 (Eritrea, Isola [island] Sheik-Said); MSNM523–524 (Eritrea, Ailet); CAS174021–022 (Sudan, Assalaya).

H. smithi (1 individual) – TMHC 2012.07.086 (Somalia, ca. 30 km N of Shiikh).

H. squamulatus (9 individuals) – NMP6V 74872/1–6, NMP6V 74971, TMHC 2013.10.447 (Kenya, South Horr); NMP6V 74972 (Kenya, Isiolo).

H. taylori (1 individual) – MSNM 195 (Somalia, Heibogan, near Gardo).

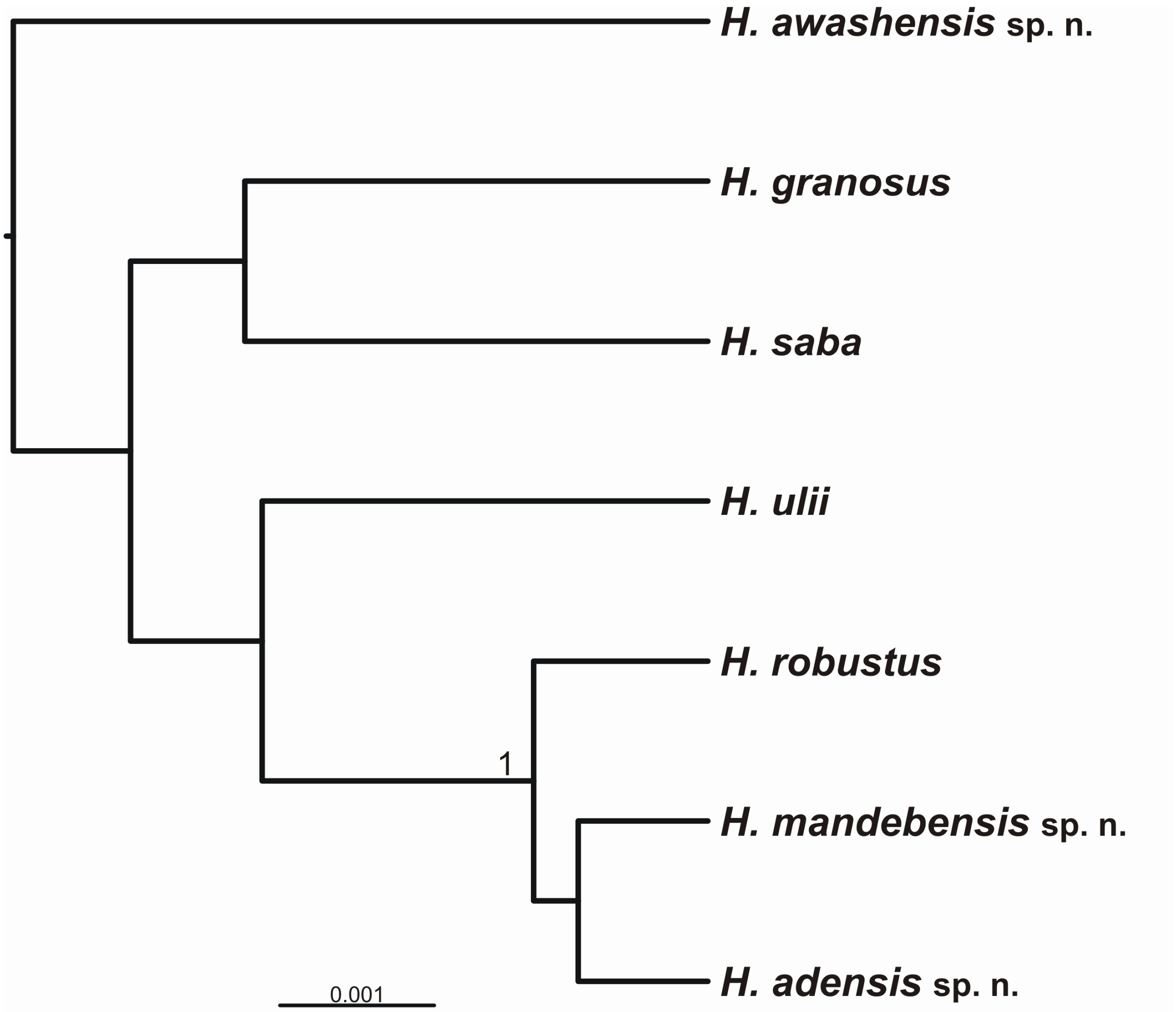
H. turcicus (33 individuals) – NMP6V 34747 (Syria, Baniyas); NMP6V 34748/1–3 (Syria, Palmyra); NMP6V 34749 (Syria, Salkhad); NMP6V 70648/1–4 (Turkey, Kaş); NMP6V 70667–668 (Greece, Kastellorizo, St. Georgies); NMP6V 71056 (Egypt, Bahariya); NMP6V 71587/1–3 (Cyprus, Famagusta); NMP6V 71592/1–2 (Cyprus, Yali); NMP6V 72497 (Syria, Qualat al Marquab); NMP6V 74046/1–2 (Syria, Cyrrhus); NMP6V 74047/1–2 (Turkey, Antakya); NMP6V 74050 (Greece, Crete, Kavros); NMP6V 74131/1–3 (Syria, Palmyra); NMP6V 73626/1–3 (Turkey, Finike); NMP6V 70269 (Italy, Sardinia, Cagliari); NMP6V 72073 (Greece, Korfu, Nicos); NMP6V 74167 (Greece, Crete, Kavros); NMP6V 70163/5 (Egypt, Sharm el-Sheikh).

H. ulii (8 individuals) – NMP6V 74831/1–2 (paratypes) (Yemen, Al Hadr); NMP6V 74835 (Yemen, village wadi near Al Turbah); NMP6V 74832/1–2 (paratypes) (Yemen, 3 km S of Najd an Nashamah); NMP6V 74833/1 (paratype), NMP6V 74833/2 (holotype) (Yemen, Al Hababi); NMP6V 74834/1 (paratype) (Yemen, Wadi Zabid).

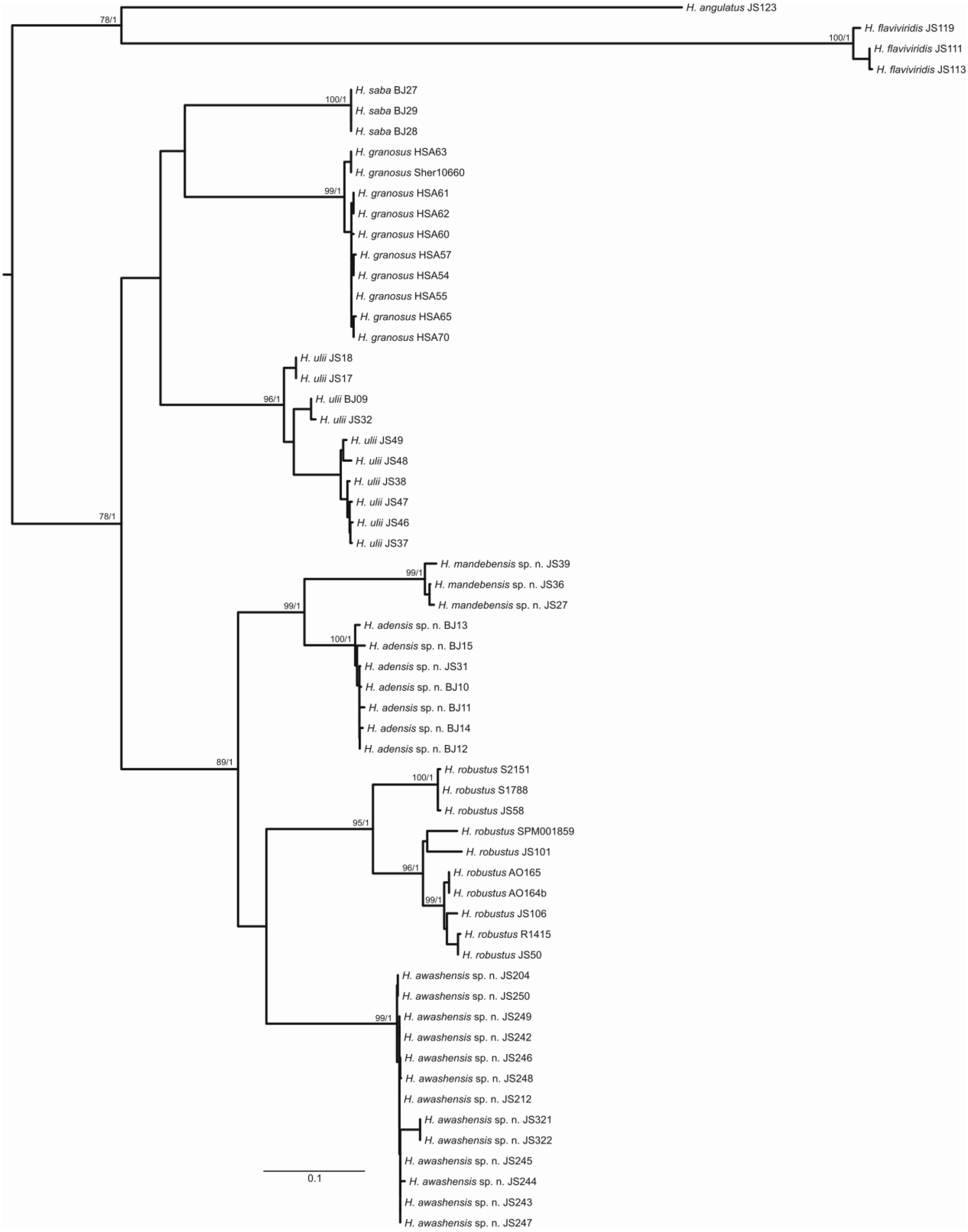
H. yerburii yerburii (51 individuals) – NMP6V 74827/1–4 (Yemen, Jabel Habeshi); NMP6V 74825/1–2 (Yemen, Al Turbah); NMP6V 74826 (Yemen, N of Lahij, Wadi Tuban); NMP6V 74823/1–3 (Yemen, 14 km NW of Al Turbah); NMP6V 74824/1–2 (Yemen, 3 km S of Najd an Nashamah); NMP6V 74828/1–3 (Yemen, Al Hababi); NMP6V 74822/1–5 (Yemen, near Zinjubar); MSNG-YEM01 (Yemen, Ta'izz); MSNG-YEM05, MSNG-YEM06 (Yemen, Vahren); NHM-BS N41856–59, NHM-BS N41861–64, NHM-BS N41866, NHM-BS N41868–69, NHM-BS N41888 (Yemen, Tour Albaha); NHM-BS N41860 (Yemen, Lahij); NHM-BS N41871–72 (Yemen, Radfan); NHM-BS N41873 (Yemen, Shihr); NHM-BS N41875 (Yemen, Ariab); NHM-BS N41876–77, NHM-BS N41879–86 (Yemen, Lowder); NHM-BS N41887 (Yemen, Aden).

H. yerburii montanus (57 individuals) – NMP6V 74802 (Yemen, Jabal Bura); NHM-BS N41751–52 (paratypes), NHM-BS N41758 (paratype), NHM-BS N41762–63, NHM-BS N41765–66, NHM-BS N41768–69, NHM-BS N41770 (paratype), NHM-BS N41772–74, NHM-BS N41779, NHM-BS N41783 (paratype), NHM-BS N41785 (paratype), NHM-BS N41791 (paratype), NHM-BS N41793 (paratype), NHM-BS N41797–800 (paratypes), NHM-BS N41802–06 (paratypes), NHM-BS N41807 (paratype), NHM-BS N41809 (paratype), NHM-BS N41811–15 (paratypes), NHM-BS N41818 (paratype), NHM-BS N41821 (paratype), NHM-BS N41823 (paratype), NHM-BS N41836 (holotype), NHM-BS N41839, NHM-BS N41840 (paratype), NHM-BS N41842 (paratype), NHM-BS N41843, NHM-BS N41844 (paratype), NHM-BS N41846, NHM-BS N41848, NHM-BS N41851–52, NHM-BS N41867 (paratype) (Yemen, Ibb); NHM-BS N41771 (paratype) (Yemen, Yareem); NHM-BS N41789–90 (Yemen, Thamar); NHM-BS N41833–34 (paratypes) (Yemen, Wadah); NHM-BS N41853–55 (paratypes) (Yemen, Sana'a).

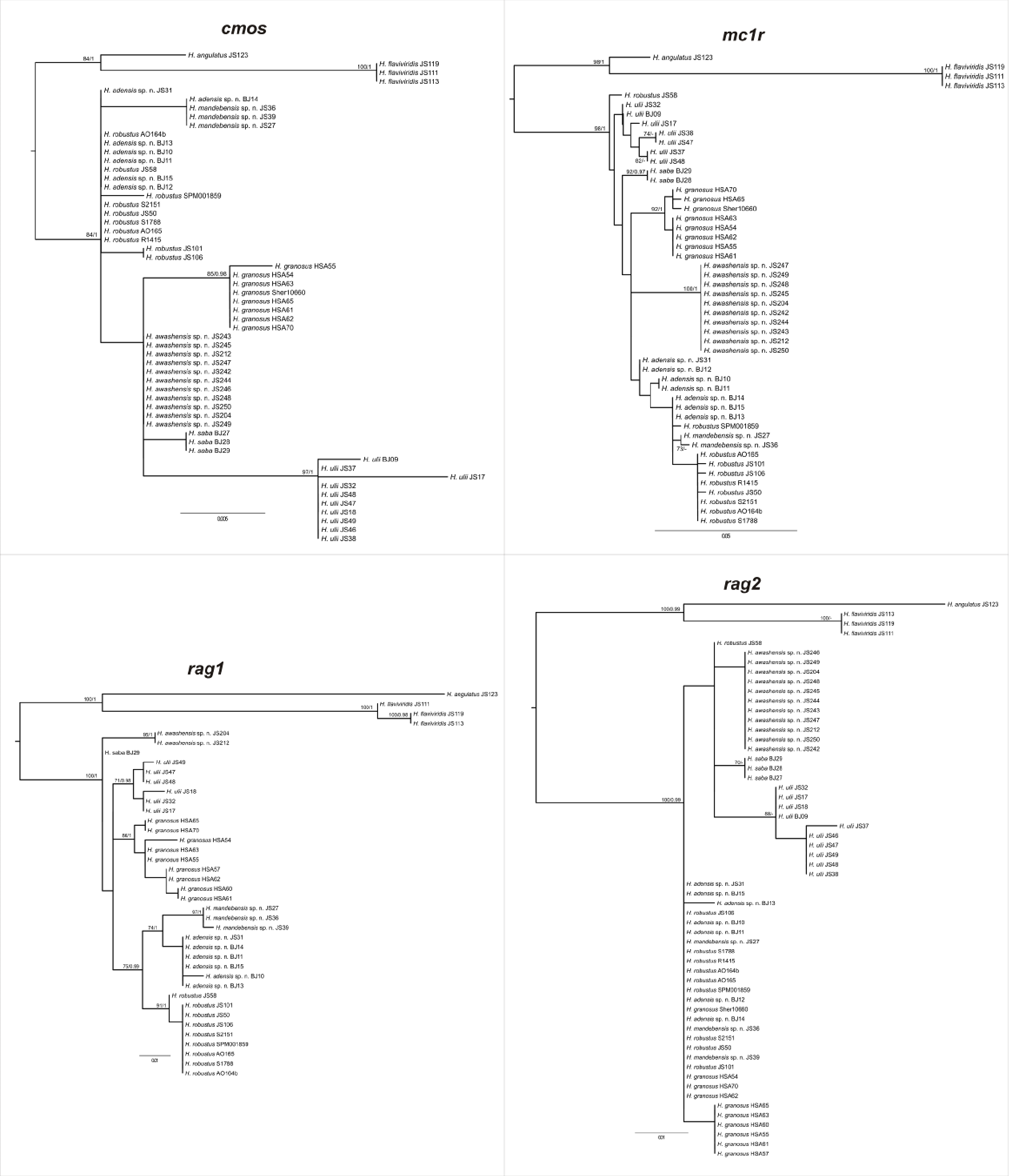
H. yerburii pauciporosus (3 individuals) – MZUF 6245 (holotype, Somalia, Galgalo); CAS 227510–11 (Somalia, 11 km SE (by road) of Bosaso)



Appendix S2. Species-tree (maximum clade credibility tree) of the *H. robustus* and *H. saba* species groups based on the four studied nuclear genes only (*cmos*, *mc1r*, *rag1*, *rag2*). Posterior probabilities ≥ 0.95 shown.



Appendix S3. Maximum likelihood tree of the *H. robustus* and *H. saba* species groups based on concatenated alignment of the mtDNA genes only (*12S* and *cytb*). Node labels indicate ML bootstrap values (≥ 70%)/ Bayesian posterior probabilities (≥ 0.95).



Appendix S4. Maximum likelihood trees of the *H. robustus* and *H. saba* species groups based on independent alignments of *cmos*, *mc1r*, *rag1*, and *rag2*. Node labels indicate ML bootstrap values (≥ 70%)/ Bayesian posterior probabilities (≥ 0.95).

Appendix S5. Results of Unequal N HSD (honest significant difference) *post-hoc* tests for one-way ANOVA. Significance of differences between species and statistically homogenous groups are given. Numbers in bold indicate significant differences between species for a given component.

Significant difference				**Homogeneous groups**
	robustus	sp11	sp5	
robustus				A
sp11	**0.000247**			B
sp5	0.591128	0.214295		AB
sp6	0.817197	**0.003801**	0.916751	A

Appendix S6. Morphological and genetic comparisons of the species within the *Hemidactylus robustus* species group members and with other *Hemidactylus* taxa occurring within their distribution ranges.

Hemidactylus robustus can be distinguished from other members of the *Hemidactylus robustus* species group by the following genetic distances: from *H.* sp. 5 by 9.7 ± 0.4% in *12S* and 15.9 ± 0.2% in *cytb*; from *H.* sp. 6 by 8.7 ± 0.7% in *12S* and 14.2 ± 0.3% in *cytb*; from *H.* sp. 11 by 6.2 ± 0.5% in *12S* and 14.1 ± 0.2% in *cytb* (for *p* distances from other *Hemidactylus* species from the Arabian radiation see Appendix S7). Moreover, *H. robustus* can be differentiated from the species above by the following combination of morphological characters: From *H.* sp. 5 by a higher number of lamellae under the 4th toe (9–12 vs. 8–9). From *H.* sp. 6 by its larger size (max. SVL 51.3 mm vs. 41.8 mm in females), generally larger head proportions (HL 10.5 ± 1.2 mm vs. 9.3 ± 1.1 mm; HW 8.0 ± 0.9 mm vs. 6.9 ± 0.9 mm; HD 4.6 ± 0.6 mm vs. 3.8 ± 0.5 mm). From *H.* sp. 11 by smaller head proportions (HL 10.5 ± 1.2 mm vs. 13.3 ± 1.7 mm; HW 8.0 ± 0.9 mm vs. 10.4 ± 1.4 mm; HD 4.6 ± 0.6 mm vs. 5.8 ± 0.6 mm), higher number of preanal pores in males (5–8 vs. 4–5), and lower number of lamellae under the 1st (5–8 vs. 8) and 4th (8–12 vs. 11–12) toes.

As a result of the large distribution of *H. robustus*, we have divided the following comparisons according to geographic origin of the species (species present in more areas are listed only once).

Arabian species: *Hemidactylus robustus* differs from *H. flaviviridis*, *H. inexpectatus*, *H. lemurinus*, *H. leschenaultii*, *H. masirahensis*, *H. minutus*, and *H. paucituberculatus* by the presence of well developed dorsal tubercles with at least the medial lines prominently keeled. From *H. alkiyumii*, *H. hajarensis*, *H. luqueorum*, *H. yerburii yerburii*, *H. yerburii montanus* by its smaller size with SVL not exceeding 55 mm. From *H. endophis* by the absence of femoral pores. From *H. festivus* and *H. shihraensis* by more stout habitus, head not so distinctly separated from body by slender neck, distinct colour pattern not composed of yellowish transverse bands (one on neck, three on body and one on anterior sacrum), and by absence of wide dark brown to black transverse bars on tail. From *H. granosus* by its shorter tail (40.9–48.7 mm vs. 53.0–64.8 mm) and higher number of preanal pores (5–8 vs. 4–7). From *H. jumailiae* by its different tail morphology (tail not swollen at the base in adults, tail whorls less developed), and in colour pattern not forming a mosaic of interconnected dark patches (see Busais & Joger 2011b, Fig. 4). From *H. mindiae* by a lower number of supralabials (8–11 vs.11–13), higher number of preanal pores in males (5–8 vs. 4–6), and different colour pattern on tail not consisting of dark bands being broader than the inserted white ones (see Amr, Modrý, Baker, Al Zaidanyen & Moravec 2007, Fig. 1; Baha el Din 2005). From *H. saba* by less developed tail whorls and lower number of lamellae under the 1st (5–8 vs. 8–9) and 4th (8–12 vs. 11–12) toes. From *H. sinaitus* by the presence of enlarged tile-like subcaudals. From *H. turcicus* by less developed tail whorls and a higher proportion of animals with anterior postmentals at least in unilateral contact with 1st and 2nd infralabials (70 % vs. 12 %). From *H. ulii* by its larger size (max SVL 54.6 mm vs. 40.4 mm in males, 51.3 mm vs. 43.7 mm in females (Šmíd et al. 2013b)) and higher number of lamellae under the 4th toe (8–12 vs. 8–9).

Iranian species: *Hemidactylus robustus* differs from *H. persicus* by its smaller size (max SVL 54.6 mm vs. 67 in males, 51.3 mm vs. 63.2 mm in females), and in having a lower number of preanal pores in males (5–8 vs. 8–11) (male data from Carranza & Arnold 2012). From *H. romeshkanicus* by its smaller size (max SVL 54.6 vs. 70.0 in males [single specimen known]), lower number of preanal pores in males (5–8 vs. 12), and lower number of supralabials (8–11 vs. 15) (Torki et al. 2011).

African species: *Hemidactylus robustus* differs from *H. albopunctatus*, *H. barbouri*, *H. curlei*, *H. fragilis*, *H. frenatus*, *H. funaiolii*, *H. isolepis*, *H. klauberi*, *H. laevis*, *H. laticaudatus*, *H. megalops*, *H. modestus*, *H. ophiolepis*, *H. ophiolepoides*, and *H. somalicus* by the presence of enlarged dorsal body tubercles forming regular longitudinal rows and at least the medial lines being prominently keeled (Largen & Spawls 2010; Loveridge 1947). From *H. arnoldi* by the absence of round smooth enlarged scale on feet situated between the base of 1st and 5th toes. From *H. barodanus* by its smaller size (51.3 mm vs. 62.6 mm in females), different colour pattern in life formed by isolated dark blotches encompassing several tubercles (see Mazuch 2013, p. 51), and less developed tail whorls. From *H. bavazzanoi*, *H. citernii*, and *H. puccionii* by different colour pattern not consisting of wide (*H. bavazzanoi*) or narrow (*H. citernii*, *H. puccionii*) regular dark transverse bands on body dorsum (Lanza 1978). From *H. foudaii* by having uppermost nasals separated (in 78 % specimens vs. 0 %), lower number of preanal pores in males (5–8 vs. 9), and less developed and protuberant dorsal and particularly tail tubercles (see Baha El Din 2003, Fig. 3). From *H. granchii* by having the first supralabial in contact with nostril (vs. separated in *H. granchii*; see Šmíd, Mazuch & Sindaco 2014). From *H. mabouia*, *H. mercatorius*, *H. platycephalus*, and *H. smithi* by having larger oval and posteriorly prominent dorsal tubercles with central keel, at least in the vertebral line (vs. smooth, round and not prominent in the other species). From *H. macropholis* by its smaller size (max SVL 54.6 mm vs. 81.3 mm in males, 51.3 mm vs. 82.2 mm in females), lower number of preanal pores in males (5–8 vs. 6–13), and by having less developed and protuberant dorsal and tail tubercles (see Mazuch 2013, p. 76). From *H. mrimaensis* by its different body habitus, larger dorsal tubercles, and by not having pointy snout (see Malonza & Bauer 2014, Fig. 4). From *H. ruspolii* by the absence of femoral pores in males, less developed dorsal and tail tubercles, tail not swollen at the base, and by different colour pattern in life, formed by isolated longitudinal dark blotches encompassing several tubercles (see Largen & Spawls 2010, Fig. 203). From *H. squamulatus* by its larger size (max SVL 54.6 mm vs. 43.2 mm in males, 51.3 mm vs. 44.6 mm in females), presence of granular dorsal scales intermixed with enlarged, oval and posteriorly prominent dorsal tubercles with central keel, at least in the vertebral line (vs. imbricate and smooth dorsal scales), and by having the uppermost nasals separated (in 78 % specimens vs. 0 %). From *H. taylori* by its smaller size (max SVL 51.3 mm vs. 74.7 mm in females) and tail not swollen at the base. From *H. tropidolepis* by its different scalation; *H. tropidolepis* having large and strongly keeled overlapping scales of unequal size. From *H. yerburii pauciporosus* by its smaller size (max SVL

54.6 mm vs. 61 mm in males, 51.3 mm vs. 57.1 mm in females) and lower number of supralabials (8–11 vs. 11–12).

Socotran Archipelago species: *Hemidactylus robustus* differs from *H. dracaenacolus* by its smaller size (max SVL 54.6 mm vs. 69.2 mm in males, 51.3 mm vs. 64.9 mm in females), the presence of posteriorly prominent dorsal tubercles with central keel, at least in the vertebral line and different colour pattern (longitudinal dark lines in *H. dracaenacolus*; see Razzetti et al. 2011, Fig. 6a). From *H. forbesii* by its much smaller size (max SVL 54.6 mm vs. 92.2 mm in males, 51.3 mm vs. 85.4 mm in females), lower number of lamellae under the 1st (5–8 vs. 10) and 4th (8–12 vs. 14) toes, and the presence of posteriorly prominent dorsal tubercles with central keel, at least in the vertebral line. From H. *granti* by the presence of posteriorly prominent dorsal tubercles with central keel, at least in the vertebral line and by its smaller size (max SVL 54.6 mm vs. 60 mm in males, 51.3 mm vs. 70.1 mm in females). From *H. homoeolepis* by the presence of posteriorly prominent dorsal tubercles with central keel, at least in the vertebral line, and its larger size (max SVL 54.6 mm vs. 46.8 mm in males, 51.3 mm vs. 43.7 mm in females). From *H. inintellectus* by the arrangement of preanal pores forming a single series of 5–8 pores vs. two rows separated by 2–3 scales in *H. inintellectus*, different colour pattern forming small scattered spots (vs. more or less well defined transverse bands on trunk in *H. inintellectus*; see Sindaco, Ziliani, Razzetti, Carugati, Grieco, Pupin, ... Fasola 2009, Fig. 3), strongly evident dark band across the eye, and the absence of wide dark and light bands on tail. From *H. oxyrhinus* by the presence of preanal pores in males (absent in *H. oxyrhinus*), and small granular scales among the dorsal enlarged tubercles (back with large tubercles only in *H. oxyrhinus*). From *H. pumilio* by the presence of posteriorly prominent dorsal tubercles with central keel, at least in the vertebral line, and its larger size (max SVL 54.6 mm vs. 26.4 mm in males, 51.3 mm vs. 30.1 mm in females).

Hemidactylus mandebensis sp. n. differs from other members of the *H. robustus* group genetically as follows: *p* distances from *H.* sp. 6: 6.1 ± 0.2% in *12S* and 10.8 ± 0.2% in *cytb*; from *H.* sp. 11: 7.1 ± 0.3% in *12S* and 15.4 ± 0.1% in *cytb* (for comparison with *H. robustus* see above, with other *Hemidactylus* species see Appendix S7). *Hemidactylus mandebensis* sp. n. can be differentiated morphologically by the following combination of characters: From *H.* sp. 6 by having anterior postmentals usually in contact with the 1st infralabial only (NMP6V 74836/2 unilaterally also with the 2nd) vs. in contact with the 1st and the 2nd in *H.* sp. 6 (unilaterally with the 1st infralabial only in NHM-BS N41905) and lower number of lamellae under the 4th toe (8–9 vs. 9–10). From *H.* sp. 11 by its smaller body size (max SVL 41.5 mm vs. 54.8 mm in males, 39.1 mm vs. 52.4 mm in females) and head proportions (HL 9.4 ± 1.0 mm vs. 13.3 ± 1.7 mm; HW 7.4 ± 1.0 mm vs. 10.4 ± 1.4 mm; HD 4.3 ± 0.6 vs. 5.8 ± 0.6 mm), by having anterior postmentals usually in contact with the 1st infralabial only vs. with the 1st and 2nd infralabials, higher number of preanal pores in males (6 vs. 4–5), and lower number of lamellae under the 1st (5–6 vs. 8) and 4th (8–9 vs. 11–12) toes. It can be distinguished from other *Hemidactylus* species as follows: From *H. flaviviridis* by its smaller size (max. SVL 41.5 mm vs. up to 90 mm; Anderson 1999), the presence of enlarged dorsal tubercles, and the absence of femoral pores in males. From *H. jumailiae* by its smaller size (max. SVL 41.5 mm vs. 54.2 mm in males, 39.1 mm vs. 54.0 mm in females), lower number of lamellae under the 1st (5–6 vs. 6–8) and 4th (8–9 vs. 9–12) toes, and by having at least slightly keeled dorsal tubercles in vertebral line (vs. smooth tubercles in *H. jumailiae*). From *H. saba* by its smaller size (max. SVL 41.5 mm vs. 58.3 mm in males, 39.1 mm vs. 59.1 mm in females), by having at least slightly keeled dorsal tubercles in vertebral line (vs. smooth tubercles in *H. saba*), and lower number of lamellae under the 1st (5–6 vs. 8–9) and 4th (8–9 vs. 11–12) toe. From *H. sinaitus* by the presence of enlarged tile-like subcaudals. From *H. ulii* by having smaller caudal whorls not disrupting the tail outline from dorsal view, anterior postmentals in contact with the 1st infralabial only (NMP6V 74836/2 unilaterally also with the 2nd) vs. with the 1st and 2nd infralabials in 80 % specimens of *H. ulii*, and a lower number of preanal pores in males (6 vs. 8). From *H. yerburii montanus* by its smaller size (max. SVL 41.5 mm vs. 65.3 mm in males, 39.1 mm vs. 64.1 mm in females) and lower number of preanal pores in males (6 vs. 9–13). *H. yerburii yerburii* by its smaller size (max. SVL 41.5 mm vs. 74.9 mm in males, 39.1 mm vs. 62.1 mm in females) and lower number of preanal pores in males (6 vs. 10–18).

Hemidactylus adensis sp. n. can be distinguished from other *H. robustus* species group members on the basis of genetic differentiation. From *H. robustus* and *H. mandebensis* sp. n. as described above, *p* distances separating it from *H.* sp. 11: 5.6 ± 0.2% in *12S* and 12.3 ± 0.2% in *cytb* (for *p* distances from other *Hemidactylus* species from the Arabian radiation see Appendix S7). Morphologically, *H. adensis* sp. n. differs from *H.* sp. 11 by its smaller body and head proportions (SVL 34.0 ± 5.5 mm vs. 51.3 ± 4.4 mm; HL 9.3 ± 1.1 mm vs. 13.3 ± 1.7 mm; HW 6.9 ± 0.9 mm vs. 10.4 ± 1.4 mm; HD 3.8 ± 0.5 mm vs. 5.8 ± 0.6 mm), high number of preanal pores in males (6–7 vs. 4–5), and lower number of lamellae under the 1st (5–6 vs. 8) and 4th (9–10 vs. 11–12) toes. *Hemidactylus adensis* sp. n. differs from other *Hemidactylus* species from south-western Yemen as follows: From *H. flaviviridis* by its smaller size (max. SVL 41.8 mm vs. up to 90 mm; Anderson 1999), presence of enlarged dorsal tubercles, and absence of femoral pores in males. From *H. jumailiae* by its smaller size (max. SVL 37.9 mm vs. 54.2 mm in males, 41.8 mm vs. 54.0 mm in females), tail base not swollen, and by its different colour pattern not composed by wide dark transverse dorsal bands. From *H. saba* by its smaller size (max. SVL 37.9 mm vs. 58.3 mm in males, 41.8 mm vs. 59.1 mm in females), less developed tail whorls (only two with at least 6 tubercles vs. at least 6), and lower number of lamellae under the 1st (5–6 vs. 8–9) and 4th (9–10 vs. 11–12) toes. From *H. sinaitus* by the presence of enlarged tile-like subcaudals and by having uppermost nasals invariably separated by an inserted scale (vs. in contact in *H. sinaitus*). From *H. ulii* by having smaller and less whorls on tail which do not disturb the tail outline from above, lower number of preanal pores in males (6–7 vs. 8), and by having unkeeled and not distinctly posteriorly protruding dorsal tubercles. From *H. yerburii montanus* by its smaller size (max. SVL 37.9 mm vs. 65.3 mm in males, 41.8 mm vs. 64.1 mm in females), by having unkeeled and less prominent dorsal tubercles, and lower number of preanal pores in males (6–7 vs. 9–13). From *H. yerburii*

yerburii by its smaller size (max. SVL 37.9 mm vs. 74.9 mm in males, 41.8 mm vs. 62.1 mm in females), by having almost smooth dorsal tubercles without prominent keels, and lower number of preanal pores in males (6–7 vs. 10–18).

Hemidactylus awashensis sp. n. can be distinguished from other members of the *H. robustus* group as described above, from other congeners distributed in central Ethiopia (Largen & Spawls 2010) on the basis of genetic differentiation (for *p* distances see above and Appendix S7) and by the following combination of morphological characters: From *H. albopunctatus*, *H. curlei*, *H. flaviviridis*, *H. isolepis*, *H. jubensis*, *H. laevis*, *H. laticaudatus* (including *H. fossatii*), *H. ophiolepis*, *H. ophiolepoides*, *H. platycephalus*, *H. puccionii*, *H. squamulatus*, *H. somalicus*, *H. tropidolepis* by large, keeled and posteriorly pointed dorsal subtrihedral tubercles. From *H. angulatus* by the absence of femoral pores in males and by having dorsal tubercles arranged in regular rows (not so in *H. angulatus*). From *H. arnoldi* by the absence of round enlarged scale on the base of the 1st and 5th toe surrounded by small granular scales (Lanza, 1978). From *H. barodanus* by its smaller size (max. SVL in females 52.4 mm vs. 62.6 mm), prominently pointed and distinctly keeled dorsal tubercles (vs. flat and almost smooth in *H. barodanus*), and by different colour pattern (see Mazuch 2013, p. 51). From *H. bavazzanoi* by a very distinct colour pattern characterized by dark banding in *H. bavazzanoi*, larger size (max. SVL 54.8 mm vs. 40 mm in males), lower number of preanal pores in males (4–5 vs. 7), and higher number of lamellae under the 1st (8 vs. 6) and 4th (11–12 vs. 10) toes (Lanza 1978). From *H. macropholis* by its smaller size (max. SVL 54.8 mm vs. 95 mm in males, 52.4 mm vs. 89 mm in females), lower number of preanal pores in males (4–5 vs. 6–13; Lanza 1978), anterior postmentals usually in contact with 2nd infralabial (vs. with only 1st in *H. macropholis*), distinct dark stripe from nostril to ear opening, and by general difference in coloration (greyish vs. reddish in life). From *H. ruspolii* by the absence of femoral pores in males, higher number of lamellae under the 1st (8 vs. 5–6) and 4th (11–12 vs. 8–9) toes, and by lacking the overall prickly appearance caused by the numerous pointy tubercles particularly in temporal region and on tail base. From *H. sinaitus* by the presence of enlarged tile-like subcaudals, higher number of lamellae under the 1st (8 vs. 4–7) and 4th (11–12 vs. 9–11) toes, and by having uppermost nasals separated by an inserted scale. From *H. smithi* by the absence of femoral pores, lower number of infralabials (6–8 vs. 9), large keeled tubercles (vs. small smooth in *H. smithi*), and by different colour pattern (dark longitudinal stripes on body in *H. smithi*). From *H. yerburii pauciporosus* by higher number of lamellae under the 1st toe (8 vs. 5–7).

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Appendix S7. Mean uncorrected *p* distances (complete deletion) between members of the Arabian radiation of *Hemidactylus* based on fragments of *12S* gene (below the diagonal) and *cytb* (above the diagonal). Values for the *H. robustus* species group are in bold. Material for comparison taken from from Šmíd et al. (2013a).

		1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**
1	*H. alkiyumii*		0.165	0.15	0.145	0.162	0.18	0.144	0.175	0.129	0.137	0.151	0.157	0.165	0.162	0.179	0.178	0.147	0.174	0.144	0.129	0.166	0.174	0.142	0.156	0.136	0.217	0.195	0.196	**0.168**	**0.139**	**0.13**	**0.152**
2	*H. barodanus*	0.076		0.179	0.159	0.179	0.154	0.161	0.173	0.168	0.183	0.187	0.153	0.182	0.177	0.146	0.148	0.174	0.19	0.148	0.148	0.16	0.185	0.159	0.17	0.183	0.19	0.15	0.194	**0.188**	**0.156**	**0.167**	**0.159**
3	*H. dawudazraqi*	0.08	0.076		0.148	0.167	0.188	0.154	0.17	0.149	0.133	0.157	0.151	0.111	0.142	0.161	0.167	0.159	0.113	0.17	0.127	0.17	0.166	0.151	0.102	0.145	0.167	0.188	0.186	**0.153**	**0.124**	**0.112**	**0.151**
4	*H. festivus*	0.065	0.084	0.088		0.149	0.178	0.124	0.18	0.123	0.13	0.139	0.163	0.159	0.158	0.157	0.16	0.125	0.141	0.135	0.121	0.145	0.158	0.12	0.151	0.126	0.196	0.187	0.188	**0.153**	**0.129**	**0.143**	**0.134**
5	*H. forbesii*	0.081	0.099	0.104	0.074		0.183	0.171	0.196	0.148	0.135	0.14	0.156	0.198	0.167	0.162	0.188	0.141	0.171	0.091	0.123	0.168	0.163	0.14	0.163	0.145	0.173	0.194	0.193	**0.17**	**0.153**	**0.141**	**0.16**
6	*H. granchii*	0.074	0.053	0.074	0.096	0.113		0.172	0.189	0.192	0.193	0.212	0.169	0.188	0.181	0.149	0.162	0.186	0.179	0.185	0.167	0.169	0.188	0.177	0.19	0.196	0.188	0.146	0.216	**0.177**	**0.173**	**0.165**	**0.172**
7	*H. granosus*	0.086	0.107	0.097	0.074	0.09	0.114		0.181	0.152	0.152	0.166	0.176	0.155	0.177	0.163	0.171	0.136	0.166	0.14	0.121	0.144	0.148	0.137	0.137	0.12	0.179	0.193	0.194	**0.139**	**0.127**	**0.136**	**0.155**
8	*H. hajarensis*	0.081	0.082	0.077	0.086	0.106	0.082	0.11		0.174	0.171	0.196	0.166	0.174	0.167	0.157	0.175	0.184	0.176	0.171	0.142	0.172	0.183	0.185	0.167	0.175	0.178	0.188	0.195	**0.184**	**0.175**	**0.164**	**0.198**
9	*H. homoeolepis*	0.078	0.103	0.106	0.076	0.04	0.117	0.098	0.101		0.119	0.14	0.164	0.172	0.15	0.165	0.172	0.147	0.162	0.136	0.117	0.164	0.17	0.154	0.145	0.151	0.206	0.182	0.2	**0.164**	**0.128**	**0.138**	**0.15**
10	*H. minutus*	0.086	0.106	0.114	0.071	0.053	0.11	0.092	0.114	0.048		0.141	0.156	0.162	0.146	0.171	0.166	0.124	0.161	0.115	0.081	0.166	0.164	0.135	0.14	0.131	0.183	0.182	0.21	**0.158**	**0.124**	**0.13**	**0.149**
11	*H. inexpectatus*	0.088	0.102	0.113	0.096	0.058	0.124	0.096	0.113	0.046	0.072		0.17	0.189	0.172	0.171	0.204	0.156	0.157	0.147	0.142	0.175	0.173	0.158	0.153	0.141	0.204	0.215	0.206	**0.175**	**0.147**	**0.154**	**0.174**
12	*H. jumailiae*	0.074	0.063	0.074	0.081	0.103	0.071	0.095	0.083	0.097	0.107	0.101		0.186	0.172	0.141	0.183	0.167	0.178	0.161	0.139	0.175	0.176	0.163	0.169	0.18	0.135	0.194	0.17	**0.181**	**0.178**	**0.162**	**0.194**
13	*H. lavadeserticus*	0.071	0.071	0.042	0.077	0.09	0.08	0.091	0.08	0.094	0.109	0.102	0.07		0.149	0.167	0.165	0.193	0.112	0.19	0.137	0.181	0.178	0.163	0.117	0.141	0.205	0.182	0.199	**0.136**	**0.124**	**0.128**	**0.162**
14	*H. lemurinus*	0.06	0.072	0.04	0.07	0.084	0.067	0.094	0.07	0.087	0.096	0.095	0.067	0.033		0.176	0.162	0.181	0.144	0.158	0.125	0.186	0.191	0.167	0.148	0.159	0.201	0.196	0.204	**0.184**	**0.152**	**0.131**	**0.185**
15	*H. luqueorum*	0.073	0.072	0.072	0.078	0.081	0.077	0.098	0.075	0.08	0.087	0.1	0.083	0.072	0.057		0.172	0.174	0.19	0.165	0.133	0.164	0.183	0.172	0.162	0.163	0.176	0.185	0.17	**0.164**	**0.145**	**0.157**	**0.176**
16	*H. macropholis*	0.083	0.065	0.078	0.097	0.108	0.072	0.118	0.086	0.108	0.106	0.107	0.07	0.085	0.072	0.07		0.181	0.179	0.172	0.133	0.17	0.19	0.159	0.169	0.167	0.216	0.15	0.208	**0.176**	**0.151**	**0.162**	**0.183**
17	*H. masirahensis*	0.076	0.099	0.098	0.078	0.068	0.107	0.097	0.103	0.057	0.069	0.048	0.093	0.084	0.076	0.092	0.103		0.152	0.143	0.123	0.158	0.192	0.136	0.16	0.138	0.177	0.175	0.186	**0.164**	**0.162**	**0.147**	**0.167**
18	*H. mindiae*	0.08	0.072	0.037	0.076	0.102	0.074	0.091	0.078	0.106	0.1	0.113	0.078	0.03	0.035	0.067	0.09	0.089		0.174	0.149	0.161	0.183	0.18	0.119	0.146	0.185	0.187	0.215	**0.152**	**0.137**	**0.129**	**0.156**
19	*H. oxyrhinus*	0.075	0.092	0.082	0.074	0.034	0.099	0.094	0.106	0.05	0.061	0.057	0.098	0.076	0.063	0.079	0.096	0.066	0.088		0.095	0.162	0.167	0.132	0.153	0.141	0.197	0.193	0.201	**0.164**	**0.145**	**0.117**	**0.149**
20	*H. paucituberculatus*	0.069	0.092	0.088	0.064	0.06	0.106	0.082	0.11	0.053	0.067	0.062	0.089	0.08	0.077	0.088	0.101	0.064	0.081	0.051		0.151	0.154	0.124	0.121	0.112	0.168	0.161	0.178	**0.139**	**0.117**	**0.114**	**0.142**
21	*H. persicus*	0.087	0.097	0.091	0.075	0.109	0.093	0.108	0.09	0.096	0.11	0.107	0.09	0.094	0.076	0.083	0.109	0.097	0.092	0.097	0.091		0.169	0.161	0.17	0.148	0.206	0.194	0.209	**0.156**	**0.162**	**0.156**	**0.177**
22	*H. saba*	0.085	0.106	0.101	0.075	0.088	0.113	0.065	0.1	0.088	0.091	0.104	0.093	0.094	0.084	0.088	0.11	0.078	0.099	0.088	0.092	0.103		0.148	0.166	0.15	0.19	0.204	0.205	**0.185**	**0.135**	**0.146**	**0.174**
23	*H. shihraensis*	0.059	0.081	0.086	0.048	0.074	0.093	0.076	0.078	0.073	0.077	0.074	0.079	0.074	0.072	0.076	0.099	0.076	0.079	0.077	0.072	0.086	0.083		0.166	0.131	0.198	0.195	0.187	**0.168**	**0.153**	**0.133**	**0.178**
24	*H. turcicus*	0.068	0.066	0.05	0.071	0.085	0.078	0.092	0.078	0.092	0.099	0.093	0.072	0.038	0.039	0.064	0.073	0.082	0.043	0.078	0.078	0.082	0.099	0.076		0.13	0.178	0.178	0.185	**0.16**	**0.128**	**0.129**	**0.161**
25	*H. ulii*	0.093	0.113	0.102	0.084	0.088	0.121	0.071	0.113	0.089	0.103	0.083	0.097	0.101	0.092	0.084	0.115	0.083	0.104	0.081	0.069	0.103	0.076	0.08	0.099		0.195	0.159	0.187	**0.153**	**0.128**	**0.13**	**0.148**
26	*H. y. montanus*	0.096	0.069	0.092	0.093	0.106	0.078	0.114	0.094	0.117	0.124	0.122	0.061	0.087	0.077	0.085	0.097	0.114	0.088	0.112	0.113	0.104	0.117	0.093	0.085	0.111		0.204	0.159	**0.212**	**0.195**	**0.192**	**0.225**
27	*H. y. pauciporosus*	0.078	0.053	0.072	0.09	0.099	0.046	0.104	0.084	0.104	0.098	0.103	0.068	0.076	0.063	0.063	0.051	0.099	0.078	0.085	0.092	0.094	0.106	0.093	0.075	0.111	0.085		0.221	**0.191**	**0.181**	**0.178**	**0.185**
28	*H. y. yerburii*	0.1	0.077	0.091	0.101	0.125	0.092	0.107	0.105	0.118	0.124	0.115	0.05	0.09	0.091	0.103	0.092	0.115	0.097	0.119	0.103	0.116	0.12	0.098	0.092	0.112	0.047	0.085		**0.196**	**0.187**	**0.197**	**0.234**
29	***H. robustus***	**0.099**	**0.125**	**0.106**	**0.105**	**0.102**	**0.124**	**0.091**	**0.11**	**0.105**	**0.11**	**0.103**	**0.102**	**0.105**	**0.097**	**0.104**	**0.118**	**0.085**	**0.114**	**0.108**	**0.108**	**0.11**	**0.099**	**0.098**	**0.108**	**0.101**	**0.105**	**0.116**	**0.109**		**0.159**	**0.142**	**0.141**
30	***H. mandebensis* sp. n.**	**0.072**	**0.082**	**0.077**	**0.067**	**0.086**	**0.087**	**0.079**	**0.082**	**0.073**	**0.09**	**0.083**	**0.072**	**0.067**	**0.064**	**0.081**	**0.091**	**0.077**	**0.075**	**0.077**	**0.072**	**0.077**	**0.091**	**0.07**	**0.076**	**0.083**	**0.094**	**0.081**	**0.085**	**0.097**		**0.108**	**0.154**
31	***H. adensis* sp. n.**	**0.064**	**0.087**	**0.088**	**0.076**	**0.078**	**0.091**	**0.084**	**0.094**	**0.074**	**0.074**	**0.075**	**0.082**	**0.076**	**0.07**	**0.079**	**0.088**	**0.072**	**0.081**	**0.078**	**0.064**	**0.093**	**0.099**	**0.065**	**0.078**	**0.079**	**0.102**	**0.077**	**0.099**	**0.087**	**0.061**		**0.123**
32	***H. awashensis* sp. n.**	**0.08**	**0.104**	**0.088**	**0.077**	**0.095**	**0.106**	**0.089**	**0.109**	**0.081**	**0.088**	**0.089**	**0.089**	**0.09**	**0.08**	**0.097**	**0.102**	**0.074**	**0.099**	**0.088**	**0.088**	**0.097**	**0.086**	**0.08**	**0.092**	**0.089**	**0.095**	**0.099**	**0.089**	**0.062**	**0.071**	**0.056**	

5. GENERAL SUMMARY

In the publications included in this thesis we have explored the evolutionary history, systematics, and taxonomy of the gecko genus *Hemidactylus* in Arabia and East Africa. *Hemidactylus* is a morphologically uniform group of geckos for which the application of genetic data is essential to resolve its phylogeny. As the studies clearly show, the diversity of *Hemidactylus* was greatly underestimated in the past. My colleagues and I have revealed the pronounced genetic differentiation that resulted in the discovery of many yet unknown species in Arabia and Africa (Paper IV), some of which turned out to be microendemics with very limited ranges (Papers III, V). On the other hand, several species widespread in the area of study, such as *H. flaviviridis*, *H. robustus*, or *H. turcicus*, that are often associated with humans were confirmed to be recently introduced over large areas (Papers I, II, VI). Moreover, our robust and time-calibrated phylogeny allowed us to infer the biogeographic history of the genus (Paper IV) and put it in the context of the history of the area. With this information available we were able to directly compare the history of *Hemidactylus* with other reptile taxa (see chapter 1.3). As it turned out, *Hemidactylus* is unique among other reptiles for its repeated dispersals from Arabia to Africa, while the opposite direction of colonizations prevailed in other reptile groups. At least seven independent dispersal events from Arabia have been recorded - two to Africa, two to Socotra Archipelago, two to the Levant, and one to Iran. Since some of the dispersals took place relatively deep in the past, the ancestors had enough time to speciate into more species in their new ranges. Such was the case of the species pair *H. forbesii*–*H. oxyrhinus* in the Abd al Kuri island (part of the Socotra Archipelago), which represents one the most extreme examples of intraisland speciation ever reported (Gómez-Díaz *et al.* 2012). The pronounced and unexpected diversification of *Hemidactylus* corresponds to some degree with that of other gecko genera (work in progress) and points to South Arabia as to an important reptile biodiversity hotspots that undoubtedly deserves more attention of systematic herpetologists.

Another important outcome of this study is, I believe, classification of *Hemidactylus* into monophyletic groups without taxonomic rank. It facilitates the orientation in its diverse phylogeny. The four main clades established by Carranza & Arnold (2006; see chapter 1.4 herein) became widely accepted. We could therefore focus on the arid clade of *Hemidactylus* in Paper IV and then further zoom down only to its Arabian radiation in Papers V and VI, in which we defined the *Hemidactylus saba* species group and *H. robustus* species group. These species groups contain 3–4 species and represent excellent and meaningful units for taxonomic revisions. Without establishing them one would be overwhelmed by the number of species that can occur within the same range of the taxa in question. Although this subdivision is strictly informal and used to facilitate the work of taxonomists, I believe such categorization can also help non-specialists when handling large phylogenies of extremely rich genera. Similar approach has been established for other diversified reptile genera (e.g. *Acanthodactylus*, *Cyrtopodion*; Salvador 1982; Anderson 1999)

The number of *Hemidactylus* species has more than doubled in Arabia within the last decade. Taking into account that material from large parts of the Arabian interior was missing in the analyses we can still expect some new species to be discovered. Further research should focus on the poorly explored areas of the Arabian Peninsula such as the Hijaz and Asir Mountains of Saudi Arabia, which can host still undetected species. Another very important area of next study is the Horn of Africa from where we have discovered three new species (Paper IV, VI), however, our unpublished data indicate the presence of many more (the non-specificity is deliberate). The Paper III shows that basically any material from this region is very valuable and can represent significant contribution for larger comparative studies.

This systematic and taxonomic work contributed to the knowledge of the diversity of the Arabian and African gecko fauna. The descriptions of the new species are a crucial basis for further research of the reptile species richness, assessments of conservation statuses, analyses of endemicity etc. And since species is the fundamental unit in biology it should be treated as such and, if possible, it should be given a name.

6. SUMMARY OF RESULTS

- The *Hemidactylus turcicus* complex forms a genetically diversified clade with at least 5–6 species present in the Levant.

- A new species, *H. dawudazraqi*, was described from Jordan and Syria.

- The subspecies *H. turcicus lavadeserticus* was elevated to a species.

- Genetic data support that *H. turcicus* is divided into two clades which correspond geographically to the northern and southern Mediterranean.

- The shallow genetic structure within *H. turcicus* supports the assumption about its recent dispersal mediated by human activity most likely from the source area in the Levant.

- There are no genetic or morphological differences between the subspecies *H. turcicus spinalis* and other Mediterranean populations of *H. turcicus*.

- *Hemidactylus turcicus spinalis* was synonymized with *H. turcicus*.

- A new specimen of *H. granchii*, a species known until now only from the type material, was recorded from Somalia. This record extended the known distribution of this Somali endemic by more than 450 km north-westwards.

- The arid clade of *Hemidactylus* is formed by the African, Socotran, and Arabian radiations.

- South Arabia and the Horn of Africa represent major speciation centres of the *Hemidactylus* arid clade with at least seven undescribed species present.

- Biogeographic history of the arid clade is closely connected with the geological history of the African-Arabian contact zone. The basal division of the arid clade into the three main radiations – African, Socotran, Arabian – is a result of vicariance and coincides with continental break-ups and the isolation of Arabia from Africa and Socotra archipelago from Arabia in the Middle Oligocene and Middle Miocene, respectively.

- South Arabia served as a source region for *Hemidactylus* dispersals into all neighbouring areas after the current position of landmasses was established. Seven independent colonizations out of Arabia were recorded since the Middle Miocene - two to Africa (9.8 and 5.9 Ma), two to the Socotra archipelago (8.2 and 4.1 Ma), two to the Levant (7.3 and 7 Ma, and one to Iran (13.1 Ma).

- The *H. saba* species group that contains *H. saba* and two other species (unrecognized at the time) and is part of the Arabian radiation was defined and subjected to further genetic and morphological analyses.

- One of the unrecognized species of the *H. saba* group distributed in Saudi Arabia and Egypt was on the basis of morphological characters found to be conspecific with *H. granosus*, a name formerly considered a junior synonym of *H. turcicus*. Therefore, the name *H. granosus* was resurrected and the species was redescribed.

- The other unrecognized species of the *H. saba* group distributed in southwestern Yemen was described as *H. ulii*.

- The *H. robustus* species group that contains *H. robustus* and three other species (unrecognized at the time) and is part of the Arabian radiation was defined and subjected to further and more elaborate morphological and genetic analyses, including the coalescent-based species-tree estimation.

- *Hemidactylus robustus* was redescribed.

- *Hemidactylus mandebensis* was described from the mountainous part of southwestern Yemen.

- *Hemidactylus adensis* was described from the Aden lowland, Yemen.

- *Hemidactylus awashensis* was described from the surroundings of the Awash National Park in central Ethiopia.

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8. ANNEX

Other papers published during this PhD

Metallinou, M., Vasconcelos, R., **Šmíd, J.**, Sindaco, R., Carranza, S. (2014) Filling in the gap: two new records and an updated distribution map for the Gulf Sand gecko *Pseudoceramodactylus khobarensis* Haas, 1957. *Biodiversity Data Journal*, 2, e4011
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Taxonomic paper

Filling in the gap: two new records and an updated distribution map for the Gulf Sand gecko *Pseudoceramodactylus khobarensis* Haas, 1957

Margarita Metallinou[†], Raquel Vasconcelos[‡,†], Jiří Šmíd[§,|], Roberto Sindaco[¶], Salvador Carranza[†]

† Institute of Evolutionary Biology (CSIC-Universitat Pompeu Fabra), Barcelona, Spain
‡ CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Universidade do Porto, Vairão, Portugal
§ Department of Zoology, National Museum, Prague, Czech Republic
| Department of Zoology, Faculty of Science, Charles University in Prague, Prague, Czech Republic
¶ Museo Civico di Storia Naturale, Carmagnola (TO), Italy

Corresponding author: Margarita Metallinou (margarita.metallinou@ibe.upf-csic.es)

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Keywords

Reptilia, Gekkonidae, DNA, 12S, distribution range, Arabia, sabkha

Introduction

The genus *Pseudoceramodactylus* Haas, 1957 comprises a single species, the Gulf Sand gecko *P. khobarensis*, described from eastern Saudi Arabia (Haas 1957) and is known to be distributed across parts of the Arabian Gulf, including Kuwait, Bahrain, Qatar and the United Arab Emirates (U.A.E.) (Sindaco and Jeremčenko 2008, Valdeón et al. 2013). It has also been reported from Qeshm Island, Iran (Dakhteh et al. 2007, Sharifi et al. 2012) and a few localities are known from coastal eastern Oman (Fujita and Papenfuss 2011, Gardner 2013, Metallinou et al. 2012). *Pseudoceramodactylus khobarensis* are nocturnal geckos, found on moist, salt-impregnated to solid, salt-encrusted flats (sabkhas) (Fig. 1a, b, c) and are often the sole reptile dweller of such extreme environments (Arnold 1977, Gardner

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Annotated checklist and distribution of the lizards of Iran

JIŘÍ ŠMÍD[1, 2, *], JIŘÍ MORAVEC[1], PETR KODYM[3], LUKÁŠ KRATOCHVÍL[4], SEYYED SAEED HOSSEINIAN YOUSEFKHANI[5], ESKANDAR RASTEGAR-POUYANI[6] & DANIEL FRYNTA[2]
[1] *Department of Zoology, National Museum, Cirkusová 1740, Prague, Czech Republic.*
[2] *Department of Zoology, Faculty of Science, Charles University in Prague, Viničná 7, Prague, Czech Republic.*
[3] *National Institute of Public Health, Šrobárova 48, Prague, Czech Republic*
[4] *Department of Ecology, Faculty of Science, Charles University, Viničná 7, Prague, Czech Republic.*
[5] *Department of Biology, Faculty of Science, Ferdowsi University of Mashhad, Mashhad, Iran.*
[6] *Department of Biology, Faculty of Science, Hakim Sabzevari University, Sabzevar, Iran.*
[*] *Corresponding author. E-mail: jirismd@gmail.com.*

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First records of the soft-shelled turtle, *Pelodiscus sinensis* (WIEGMANN, 1834), in the Balkans

The Chinese Soft-Shelled Turtle, *Pelodiscus sinensis* (WIEGMANN, 1834), a member of the family Trionychidae, is a highly aquatic species. *Pelodiscus sinensis* is native to the Amur and Ussuri river basins in northern China and far east Russian Federation, through Korea, central and south China, Hainan and Taiwan, and to Vietnam in the south, whereas Japan is treated as a non-native area of occurence (e.g., OTA et al. 2004; FRITZ et al. 2010). This species is formed by four distinct phylogenetic lineages (FRITZ et al. 2010). In Asia these turtles are traditionally farmed in large quantities as a source of food (CHEUNG & DUDGEON 2006; HAITAO et al. 2008). Economically, *Pelodiscus sinensis* is the most important turtle in the world, alongside *Trachemys scripta* (THUNBERG in SCHOEPFF, 1792) (TELECKY 2001; HAITAO et al. 2008). Chinese Soft-Shelled Turtles were systematically introduced, mainly as a food source, into the wild of many Asian countries and the United States including the Hawaii Islands (MCKEON & WEBB 1982; OTA et al. 2004; SY et al. 2004; DAS & YAAKOB 2007; KRAUS 2009a). Recently, there have been reports of occasional introductions in Europe, namely from the Iberian Peninsula (MALKMUS 2006; EGAÑA-CALLEJO 2007; GARCÍA-BERTHOU et al. 2007) and Latvia (PUPINS & PUPINA 2011) as a side-effect of pet trade. There are also records of *P. sinensis* from Central Europe where several observation are known from Vienna, Austria (R. GEMEL, pers. comm.) and one adult specimen (CL 325 mm) was caught near Diessen, Bavaria, Germany in 1946 which is assumed to be a survivor from a fish-hatchery where 20 juveniles were kept in 1913 (GERLACH 1960). In this study we present the first records of introduction of *P. sinensis* into the Balkans.

The study area covers Slovenia, Croatia and Bosnia and Herzegovina. Turtles were either caught by netting or just observed without capture. The map was created using ArcGIS 9.3 software (ESRI Redlands, CA: Environmental Systems Research Institute) and WGS84 coordinate system. In total, eight *P. sinensis* specimens were caught or observed in four localities (Fig. 1).

The locality in Bosnia and Herzegovina lies in the karst area of Mostarsko Blato, between the villages Provo and Donji Gradac (43.384346 N / 17.653113 E), municipality of Široki Brijeg, near the River Neretva at Mostar (Fig. 1, A). Two individuals were observed in August 2010. One female was caught (Fig. 1; body mass 482 g, straight carapax length of 146 mm), the larger specimen escaped. The pond (surface approx. 0.8 ha, max. depth 8 m, average depth 4-5 m), where the turtles were observed, developed from a brick clay quarry flooded in the 1980s. The pond was bordered by steep muddy banks with rocky outcrops in the southern shore. The aquatic vegetation consisted of representatives of the genera *Typha*, *Phragmites*, *Juncus* and *Elodea*. The surrounding area was mostly grasses with isolated trees. In winter, the pond surface freezes. There are no native freshwater turtle species reported from Mostarsko Blato.

In Croatia, the locality 'Park Maksimir' is situated at the center of Zagreb city near the Sava River (Fig. 1, B). There are two records of *P. sinensis* from the ponds at this location in the database of the Zagreb Zoo. The first is from summer 2008 when an adult male (200 mm straight carapax length) was caught in the pond 'Treće Jezero' (2 ha, depth 1-4 m, 45.825283 N, 16.018536 E). The animal was in good condition and is still living in the Zagreb Zoo. The second, a fully grown male, was caught in late summer of 2010 in another pond in the park ('Prvo Jezero', 1.5 ha, depth 0.6-3.3 m, 45.821831 N, 16.021044 E). The animal was entrusted to private care. Another two animals were recorded in this park; a male caught in August 2009 ('Treće Jezero'), and a specimen observed also in 2009 ('Četvrto Jezero', 1.1 ha, depth 0.5-1 m, 45.830611 N, 16.027506 E; B. LAUŠ, Zagreb, Croatian Herpetological Society, pers. obs.). In 2010, *P. sinensis* was reported again from 'Četvrto Jezero' by Lana MALOVIČ, Zagreb, public institution 'Maksimir', probably the same animal as in 2009. Aquatic vegetation of the ponds consisted mostly of plants of the genera *Carex* and

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Modelling the potential distribution of *Mesalina watsonana* (Stoliczka, 1872) (Reptilia: Lacertidae) on the Iranian Plateau

Seyyed Saeed Hosseinian Yousefkhani[1*], Eskandar Rastegar-Pouyani[2],
Nasrullah Rastegar-Pouyani[1,3], Rafaqat Masroor[4], and Jiří Šmíd[5,6]

[1]*Iranian Plateau Herpetology Research Group (IPHRG), Faculty of Science, Razi University, Kermanshah, Iran.* [2]*Department of Biology, Faculty of Science, Hakim Sabzevari University, Sabzevar, Iran.* [3]*Department of Biology, Faculty of Science, Razi University, Kermanshah, Iran.* [4]*Zoological Sciences Division, Pakistan Museum of Natural History, Shakarparian, Islamabad, Pakistan.* [5]*Department of Zoology, National Museum, Prague, Czech Republic.* [6]*Department of Zoology, Faculty of Science, Charles University, Prague, Czech Republic.*

The Persian Long-tailed Desert Lizard, *Mesalina watsonana*, is one of the most common and most widely distributed lizards on the Iranian Plateau extending from Iran to Pakistan and Afghanistan. The species is frequently encountered in various types of habitats. We collected over 600 distributional records from available literature, museum collections, and our own field work and used bioclimatic and land cover characteristics to develop a model of potential distribution for *M. watsonana*. According to the model, the most important factors limiting the distribution of *M. watsonana* are: precipitation in wettest quarter exceeding 250–300 mm, precipitation in coldest quarter lower than 40 mm and exceeding 250 mm, altitudes above 2500 m and slopes steeper than 10.5°. The model suggests that most of the Iranian Plateau is suitable for the species except for some isolated areas such as the Dasht-e Kavir and Dasht-e Lut deserts in Iran, Helmand basin in Afghanistan, the Karakum Desert in Turkmenistan, the western Chagai-Kharan deserts of Pakistani Balochistan, and Thar and Cholistan deserts in eastern Pakistan. The most important factor in these regions appears to be the extremely low rainfall during coldest quarter of the year. The outer boundary of the distribution of *M. watsonana* follows important biogeographic barriers that are also clearly delimited by climatic conditions.

Keywords: Middle East, Iran, Afghanistan, Pakistan, Maxent, habitat suitability, potential distribution.

Introduction

Mesalina Gray, 1838 is a widespread lacertid genus distributed throughout the Saharo-Sindian desert belt from Morocco in the west to westernmost India in the east. The genus currently contains 14 species, most of which are found in Africa (Schleich, Kästle, & Kabisch, 1996; Sindaco & Jeremčenko, 2008). The Persian Long-tailed Desert Lizard, *Mesalina watsonana* (Stoliczka, 1872), is widely distributed in most of Iran, Pakistan, Afghanistan and westernmost parts of the Indian Thar Desert (Anderson, 1999; Khan, Baig, Masroor, & Arshad, 2008; Sindaco & Jeremčenko, 2008). Marginally it also occurs in Turkmenistan, where it is restricted to clay and crushed stone substrate in the Karakum Desert and northern Kopet Dagh piedmont (Shammakov, 1981; Schammakov, Ataev, & Rustamov, 1993). The range in Afghanistan is limited to the western and southern lowlands (Leviton & Anderson 1963; Clark, Clark, Anderson, &

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[*] Corresponding author. Email: Mesalina.watsonana@gmail.com

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Genetic variability of *Mesalina watsonana* (Reptilia: Lacertidae) on the Iranian plateau and its phylogenetic and biogeographic affinities as inferred from mtDNA sequences

Jiří Šmíd[1,2,*], Daniel Frynta[1]

[1] *Department of Zoology, Faculty of Science, Charles University in Prague, Viničná 7, 128 44, Prague 2, Czech Republic. *Corresponding author.* E-mail: jirismd@gmail.com
[2] *Department of Zoology, National Museum, Cirkusová 1740, 193 00 Prague, Czech Republic.*

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Abstract. The lacertid lizard *Mesalina watsonana* is widely distributed on the Iranian plateau where it is one of the most common lizards. However, the intraspecific variability and the phylogenetic position of this species within the genus still remain unknown. We sequenced a 715bp long fragment of the mtDNA cytochrome *b* gene from lizards sampled in 10 localities covering the Iranian distribution range of the species. We identified four distinct and geographically isolated clades with an average genetic divergence between them ranging from 9.8 to 13.1% (p-distance) which is comparable to the values of genetic distance commonly reported between Lacertidae species. Analyses combining data from recently published phylogeny of the genus *Mesalina* with our dataset confirmed the monophyly of *M. watsonana*. The isolation of this species from the rest of the genus points out the important role of the Zagros Mountains uplift during the Miocene. It is possible that this geological event participated on the isolation of the ancestor of *M. watsonana* from the rest of the *Mesalina* lizards and together with the upheaval of the whole Iranian plateau provided suitable environmental conditions for rapid diversification of this species.

Keywords. *Mesalina watsonana*, Lacertidae, Iran, Zagros, mtDNA, phylogeny.

INTRODUCTION

The upland area of the Iranian plateau represents a unique biogeographical element in the Middle East, isolated from the neighboring territories (Anderson, 1968, 1999; Fisher, 1968; Coad, 1998). It encompasses most of the territory of Iran, reaching Afghanistan and Pakistan in the east. The geographical delimitation of the Iranian plateau is determined by high mountain ranges of the Zagros in the west, Elborz and Kopet Dagh in the north, lofty peaks of Hindu Kush in Afghanistan in the east and Makran and Sulaiman moun-

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Greenhouse netting as an effective trap for lizards in the Gran Canaria Island

Jiří Šmíd[1]*

The Canary Islands reptile fauna consists of endemic species only, most of them restricted to individual islands. The island of Gran Canaria hosts only three autochthonous (*Gallotia stehlini*, *Chalcides sexlineatus* and *Tarentola boettgeri*) and two introduced lizard species (*G. atlantica* and *Hemidactylus turcicus*) (Salvador and Pleguezuelos, 2002). During a field trip to Gran Canaria in April 2010 I found an alarming number of mummified lizards being trapped between two layers of a greenhouse netting (Fig. 1). These enclosed plantations (mostly tomatoes and bananas) are widespread around almost every village all over the coast, especially in the northern and souteastern part of the island. In a 2 m long section of the fence there were imprisoned five adult *G. stehlini*, one *C. sexlineatus* and one *T. boettgeri*. This number can be biased, since bigger animals were easier to find whereas smaller geckos or skinks may have escaped my attention. Although all lizards of Gran Canaria are treated as of „Least Concern“ (LC) according to the IUCN criteria (Miras et al., 2009a, 2009b; Sá-Sousa et al., 2009) and trapping in the fence can be hardly considered devastating for lizard populations, together with other threats (Machado et al., 1985), this accidental trapping could decrease abundances of these species. Therefore, if there is any chance to use another alternative material to this multi-layer netting it should be preferred in the greenhouse constructions. Thus the risk these endemic species are exposed to would be highly reduced.

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Figure 1. Two *G. stehlini* and one *T. boettgeri* trapped in the netting (above); lizards gathered from 2 m length of the fence (bellow). Blue arrows indicate *T. boettgeri*, red *C. sexlineatus*.

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[1] Department of Zoology, Faculty of Science, Charles University, Viničná 7, 128 44 Prague, Czech Republic

* corresponding author: e-mail: jirismd@gmail.com

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New remarkable snake records from Oman

Jiří Šmíd[1,2]

The herpetofauna of the southeastern horn of the Arabian Peninsula, comprising the Sultanate of Oman and the United Arab Emirates (UAE), is very diverse and consists of ca 58 species of lizards, 21 species of terrestrial snakes and one amphisbaenid (Gardner 2009). Its geographic position between the Asiatic continental landmass in the northeast, vast deserts of Saudi Arabia in the northwest and proximity of the African horn in the southwest indicates different origin of individual taxonomic elements. Most of the reptiles from UAE and the northeast mountain region of Oman show affinities to Iranian taxa (e.g. *Asaccus, Cyrtopodion scabrum, Hemidactylus persicus, Echis carinatus sochureki, Pseudocerastes persicus* etc (see Arnold, 1972)), whereas the herpetofauna of southern Oman and neighboring Yemen consists of large number of African elements (e.g. *Acanthocercus, Chamaeleo, Trachylepis brevicollis, Bitis* (Anderson 1896)). Even after long-term field studies (Arnold, 1980; Gallagher and Arnold, 1988; Gardner, 2009; Gasperetti, 1988; Kooij, 2000) many species remain almost unknown. The snake species *Lytorhynchus diadema, Platyceps thomasi* and *P. variabilis* belong to this group of scarcely encountered or even rare animals. Therefore, it was surprising to find all these three species during a two-week survey period. All the animals were found during a herpetological excursion into the Sultanate of Oman in April 2010. The record of *P. variabilis* is the first for Oman and the first out of Yemen at all, and thus increases the number of terrestrial Omani snake species reported to date.

Species accounts

Lytorhynchus diadema (Duméril, Bibron & Duméril, 1854)

Locality: 3 km W of Asaylah (21.95329 N, 59.61119 E, alt. 30 m, No. 1 in Fig. 1), 13.IV.2010, 9:00 pm

Locality description: Sandy hills with scattered rocks and sparse vegetation.

The nocturnal leaf-nosed snake inhabits dry and mostly sandy areas. Its upper lip overlaps the lower which is an adaptation for life in loose substrates (the same as we can see in the genus *Eryx*) . Its distribution spans from Morocco in the west across northern Africa and onto the Arabian Peninsula reaching SW Iran. The locality mentioned herein could represent the easternmost point of the species distribution (see maps in Gasperetti, 1988 and Egan, 2007). The snake was very calm and did not attempt to bite during handling at night. However, after spending the night in a cloth bag it became very vigorous and repeatedly tried to bite. While being photographed, the snake coiled into a double coil (one

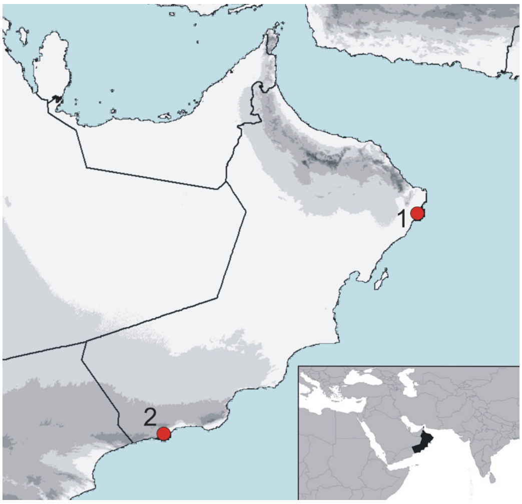

Figure 1. Map of Oman showing localities described in the text. Number 1 marks locality of *L. diadema*, number 2 of *P. thomasi* and *P. variabilis.*

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1 Department of Zoology, National Museum, Cirkusova 1740, 193 00, Prague, Czech Republic;
2 Department of Zoology, Faculty of Science, Charles University, Viničná 7, 128 44 Prague, Czech Republic;
e-mail: jirismd@gmail.com