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A review of the geckos of the genus *Hemidactylus* (Squamata: Gekkonidae) from Oman based on morphology, mitochondrial and nuclear data, with descriptions of eight new species

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Abstract

The genus *Hemidactylus* is one of the most species-rich and widely distributed of all reptile genera, being found in the tropical and subtropical regions of the world and hundreds of continental and oceanic islands. Despite having already 111 species, the number of species described in recent years is very high. This has been facilitated, in part, by the use of molecular techniques, which in most cases have been employed to confirm the differentiation at the DNA level of some morphologically variable forms and to discover some cryptic lineages.

Preliminary analyses indicate that some *Hemidactylus* species from Oman are quite variable in their morphology and may include more than one species. In order to test this hypothesis we inferred a molecular phylogeny including 131 *Hemidactylus* (20 species) using 1385 base pairs of mitochondrial DNA (353 bp *12S*; 302 bp *cytb*; 588 bp *nd4* and 142 bp *tRNAs*) and 1481 bp of nuclear DNA (403 bp c-*mos*; 668 bp *mc1r* and 410 bp *rag2*) and analyzed 226 specimens (15 species) for several meristic and pholidotic characters of which we took 3103 photographs that have been deposited in MorphoBank (project 483). Our results indicate the presence of eight new species of *Hemidactylus* geckos in Arabia: *H. luqueorum* sp. nov. and *H. hajarensis* sp. nov. from North Oman; *H. masirahensis* sp. nov. from Masirah Island; *H. inexpectatus* sp. nov. from one locality on coastal Central Oman; *H. alkiyumii* sp. nov., *H. festivus* sp. nov. and *H. paucituberculatus* sp. nov. from Dhofar, Southern Oman; and finally *H. endophis* sp. nov. probably from North Oman and described on the basis of morphology alone. An identification key to the genus *Hemidactylus* from Oman is also presented. With these descriptions, the number of *Hemidactylus* species found in Oman increases from 7 to 13 and the number of endemic *Hemidactylus* from 0 to 6. The description of three new species endemic to the Hajar Mountains in North Oman highlights the importance of this mountain range as a biodiversity hotspot that, up to now, includes 12 reptile species that are found nowhere else in the World. Another hotspot of *Hemidactylus* biodiversity is the Dhofar Mountain range, in the extreme Southwestern corner of Oman and East Yemen. As a result of its particular geographic situation, orography and the effect of the Southwest Monsoons, this mountain range presents a diverse variety of habitats with different species of *Hemidactylus* adapted to them.

With the exception of *H. flaviviridis* and *H. leschenaultii*, which belong to the Tropical Asian clade of *Hemidactylus*, all Arabian *Hemidactylus* for which DNA sequence is available are members of the Arid clade of *Hemidactylus*. Relatively recent dispersal appears to have taken place within Arabia in the *H. turcicus* group, with the South Arabian *H. lemurinus* occurring far from other confirmed members of this assemblage. *Hemidactylus flaviviridis* and a clade of *H. robustus* are genetically uniform, widespread in Arabia and beyond and occur around human habitations, suggesting that much of their large distributions are anthropogenic, as appears to be so in several other *Hemidactylus* species outside Arabia.

The way in which species of Arabian *Hemidactylus* separate ecologically is surprisingly varied. They may occur at similar altitudes but replace each other geographically, or if they are sympatric there may be altitudinal separation. Humidity may also be an important factor, and when animals exist within a few meters of each other, structural niche may be significant. While four native species occur close together in Dhofar, most *Hemidactylus* communities in Arabia consist of only one or two species, although climbing geckos belonging to other genera, such as *Asaccus* and *Ptyodactylus*, may also be present.

Key words. *Hemidactylus*, Arabia, phylogeny, molecular clock, taxonomy, systematics, mtDNA, nDNA, MorphoBank

Abstract in Arabic

الوزغ نصفي الإصبع من أكثر أجناس السحالي انتشارًا وتنوعًا وينتمي هذا النوع إلى عائلة الوزغيات، ويرجع هذا الإنتشار إلى قدرتها على التكيف مع الظروف الطبيعية في المناطق الاستوائية وشبه الاستوائية من العالم، كما يمكن ملاحظتها أيضـًا في العديد من الجزر القارية والمحيطية على حد السواء.

وعلى الرغم من أن عدد هذه الأنواع يصل إلى (111) نوعـًا؛ فإن العديد منها تم اكتشافه في السنوات القليلة الماضية، ولقد ساهمت التقنيات المستخدمة في علم الأحياء الجزيئية بشكل جزئي في هذه الزيادة المطّردة، واستخدمت هذه التقنيات في معظم البحوث العلمية لتأكيد وجود التباين فى مستوى الحمض النووي (DNA) وهي المادة المسئولة عن نقل السمات الوراثية من جيل لآخر بين الأنواع المتشابهة والتي قد يلاحظ وجود بعض الفروق البسيطة في مظهرها الخارجي كما نتج عن استخدام هذه التقنيات أيضـًا إكتشاف روابط وقرابة وراثية غير ظاهرة بين أنواع أخرى من هذه الوزغيات.

كما أشارت التحاليل الأولية لعينات الوزغ نصفي الإصبع من سلطنة عمان إلى وجود تنوع واضح في المظهر الخارجي لها، ولتأكيد مدى صحة هذه الفرضية تم الاستدلال بتقنيات علم السلالات الجزيئية (Phylogeny) وذلك باستخدام: عدد (131) عينة وزغ نصفي الإصبع من (20) نوع مختلف من هذه السحالي، وتم استخدام نوعين من المؤشرات أو العلامات (marker) المستخرجة من الحمض النووي ؛ الأول من عضيات الميتوكوندوريا (mtDNA) وبطول (1385) قاعدة نيتروجينية مزدوجة[1] والآخر من أنوية الخلايا (nuclear DNA) وبطول (1481) قاعدة نيتروجينية مزدوجة [2].
وتم استخدام هذين المؤشرين في تحليل (228) عينة لعدد (15) نوع في بيانات تتعلق بمظهر بعض الأجزاء الخارجية لتلك السحالي، إضافة إلى عدد من تطبيقات صلات القرابة الوراثية (Meristic and Pholidotic characters) والتي قمنا بتوثيقها من خلال (3103) صورة فوتوغرافية والتي تم وضعها في ال مورفوبانك (MorphoBank) تحت مشروع رقم (483).
أشارت نتائج هذا البحث إلى وجود ثمانية أنواع جديدة من الوزغ نصفي الإصبع تضاف إلى الأنواع الموجودة مسبقـًا في شبه الجزيرة العربية، وتمت تسمية الأنواع الجديدة كالتالي:
(*H. luqueorum*) و (*H. hajarensis*) من جبال الحجر بشمال سلطنة عُمان، و (*H. masirahensis*) من جزيرة مصيرة، و (*H. inexpectatus*) من أحد المواقع بسواحل محافظة الوسطى، وثلاثة أنواع أخرى من محافظة ظفار (*H. alkiyumii*)، و (*H. festivus*) و (*H. paucituberculatus*)، و أخيرًا (*H. endophis*) من الاجزاء الشمالية للسلطنة أيضـًا علمـًا بأن هذا النوع لم يتم استخدام تقنيات علم الأحياء الجزيئية عليه وتم الاكتفاء بآلية الوصف المظهري، كما تم ارفاق مفتاح لتصنيف (identification key) الوزغ نصفي اللإصبع في سلطنة عمان.
ومن نتائج هذا البحث أن زاد مجموع أنواع الوزغ نصفي الإصبع في سلطنة عمان من سبعة أنواع إلى ثلاثة عشر نوعٍ، ومن منظور التنوع الوراثي لهذه السحالي فإن السلطنة تنفرد بعدد ستة أنواع جديدة ولم تكن الدراسات السابقة تشير إلى أي تنوعٍ خاص لهذا النوع بالسلطنة.
إن انفراد سلسلة جبال الحجر والواقعة شمال سلطنة عمان بثلاثة أنواع جديدة من الوزغ نصفي الإصبع يشير إلى الحساسية البيئية لهذه المنطقة؛ كمكن مهم للتنوع الأحيائي (Biodiversity hotspot) إضافـةً إلى (12) إثني عشر نوعـًا من الزواحف تستأثر به هذه المنطقة عن بقية العالم.
وتعتبرسلسلة جبال ظفار أيضـًا مكمنـًا آخر لتنوع الوزغ نصفي الإصبع وتحديدًا جهة الجنوب الغربي من السلطنة والتي تطل على المناطق القريبة من شرقي اليمن؛ ويرجع الفضل في ذلك التنوع إلى الطبيعة الجبلية وتأثرها بالرياح الموسمية الجنوب غربية، مما أدى إلى ظهور بيئات متنوعة لعدد من أنواع الوزغ نصفي الإصبع والتي بدورها تأقلمت بشكل جيد معها.
وباستثناء نوعين من الأنواع التي تمثل الوزغ نصفية الإصبع وهما: (*H. flaviviridis*) و (*H. leschenaultii*) واللتان تنتميان إلى عائلة الوزغ نصفية الإصبع الآسيوية الإستوائية، فإن جميع الانواع الاخرى في شبه الجزيرة العربية والتي تتوفر لها بيانات عن الحمض النووي (DNA) تنتمي الى عائلة الوزغ نصفية الإصبع المنتشرة في المناطق الجافة.
لقد ظهر تشتت حديث نسبيا(تم استنتاج ذلك باستخدام تقنيات علم السلالات الجزيئية) لمجموعة *H. turcicus* فى شبه الجزيرة العربية مع مجموعة أخرى تواجدت في جنوب شبه الجزيرة العربية وهي (*H. lemurinus*) وأدى ذلك إلى تكيف هذين النوعين بعيدًا عن التكتل الأصلي للوزغ نصفي الاصبع بشبه الجزيرة.
إن (*Hemidactylus flaviviridis*) و مجموعة من (*H. robustus*) تحملان تماثلا واضحا على المستوى الوراثي، وينتشران في شبه الجزيرة العربية وخارجها وتحديدا عند التجمعات البشرية مما يوحي أن العوامل التي أدت إلى انتشارها في الأغلب عوامل بشرية، ويظهر ذلك جليـًا في أنواع أخرى للوزغ نصفي الإصبع في العالم.
ان الظروف البيئية التي ساهمت في الفصل بين انواع الوزغ نصفي الاصبع في شبه الجزيرة العربية (سلطنة عمان)، كانت وعلى غير المتوقع متنوعة، فمن الممكن تواجد هذه الوزغيات على ارتفاعات متشابهة ولكن تفترق في انتشارها الجغرافي، أو يكون الحائل بارزًا كالارتفاع عن سطح البحر مثلاً.
كما يحتمل أن يكون للرطوبة النسبية دور مهم في تكوين هذا التنوع، ولكن عندما يكون فارق الارتفاع بضع مترات فقط ومن البديهي أن الرطوبة النسبية غير ذات تأثير فإن تضاريس الموقع تلعب الدور الأهم في درجة التأثير على التنوع.
بينما تتواجد أربعة أنواع من الوزغيات نصفية الإصبع قريبة من بعضها في ظفار نرى أن معظم تجمعات هذه الوزغيات في شبه الجزيرة العربية لا تتشكل سوى من نوع واحد أو نوعين كحد أقصى، كما يمكن مشاهدة أنواع أخرى من الوزغيات المتسلقة أيضـًا في نفس المكان تنتمي لاجناس مختلفة أخرى كالوزغ مروحي الأصبع أو البرص *Asaccus* and *Ptyodactylus* .

INTRODUCTION

The gecko genus *Hemidactylus* Oken, 1817 is widely distributed in the warmer parts of the world and is one of the largest in the Gekkota, comprising approximately 111 recognized species (Uetz 2012), with more than 23 new species having being described within the last 10 years and some species belonging to other genera having been transferred to *Hemidactylus* (Arnold *et al.* 2008; Busais & Joger 2011a; Carranza & Arnold 2006; Giri 2008; Giri & Bauer 2008; Giri *et al.* 2009; Mahony 2009; Moravec *et al.* 2011; Sindaco *et al.* 2007, 2009; Torki *et al.* 2011; Ullenbruch *et al.* 2010; among others). Recent investigations using mitochondrial DNA phylogenies (Carranza & Arnold 2006) show that, although morphologically fairly uniform, *Hemidactylus* is quite diverse genetically with several main groups, some of which are geographically constrained. Many recognized species also show high levels of internal diversity and are better regarded as species complexes.

A region that has been recently investigated comprises the Arabian Peninsula and its hinterland, which extends as far North as the Sinai, Jordan, Iraq and Iran and is known to contain at least 16 recognized taxa of *Hemidactylus*: *H. dawudazraqi* Moravec, Kratochvíl, Amr, Jandzik, Smid and Gvozdik, 2011; *H. flaviviridis* Rüppell, 1835; *H. homoeolepis* Blanford, 1881; *H. jumailiae* Busais and Joger, 2011; *H. lavadeserticus* Moravec and Böhme, 1997; *H. lemurinus* Arnold, 1980; *H. leschenaultii* Duméril and Bibron, 1836; *H. mindiae* Baha el Din, 2005; *H. persicus* Anderson, 1872; *H. robustus* Heyden, 1827; *H. romeshkanicus* Torki, Manthey and Mirko, 2011; *H. saba* Busais and Joger, 2011; *H. shihraensis* Busais and Joger, 2011a; *H. sinaitus* Boulenger, 1885; *H. turcicus* (Linnaeus, 1758); *H. yerburyii* Anderson 1895. Some individuals of these forms were included in the molecular study on the phylogenetic relationships of *Hemidactylus* using mtDNA by Carranza and Arnold (2006) and several others have also been included in recent mtDNA phylogenies by Busais and Joger (2011a,b) and Moravec *et al.* (2011). However, *H. homoeolepis*, *H. persicus* and *H. yerburii* as presently understood are all quite variable in their morphology (Arnold 1977, 1980, 1986; Arnold & Gallagher 1977) and may consist of more than one species. Several of these morphologically variable forms occur in the Sultante of Oman and neighboring Eastern Yemen.

With approximately 100 species of reptiles, Oman harbors around 50% of the total number of reptile species in the Arabian Peninsula. Within Oman, two biodiversity rich areas with high levels of endemicity are recognized: the Hajar Mountains in the North and the Dhofar Mountains in the South of Oman and East Yemen (Fig. 1). Although the Hajar Mountains have a complex geological history that dates back to approximately 300 mya, their history of uplift into a mountain range probably began some 30 mya, as a result of the opening of the Gulf of Aden (Bosworth *et al.* 2005; Glennie 2006; Laughton 1966). In fact, it has been suggested that they probably rose into a high range only in the last 4–6 my or even less, during the latest phase of plate tectonics that affected Oman (Glennie 2006). The Hajar Mountains run for about 650 km, from Ruus al Jibal (Musandam Peninsula) in Northwest Oman to the Jebel Qahwan in Northeast Oman (Fig. 1). Most of this region is within Oman but a small section, just South of Ruus al Jibal, is included in the United Arab Emirates. The mountains reach 2087 m above sea level (asl) at Ruus al Jibal and 2980 m at Jebel Akhdar. They are thus high enough to influence local climate significantly, the rainfall being considerably higher than that of the arid lowland regions to the West and South. Many of the mountain wadis have some surface water, at least intermittently, and they often support areas of quite luxuriant vegetation. It is in such wadis that much of the mountain herpetofauna is found. The Hajar Mountains are home to a relatively high number of reptile species that are endemic to this region, like the two lacertid species of the genus *Omanosaura* (*O. jayakari* (Boulenger, 1887) and *O. cyanura* (Arnold, 1972)), four species of geckos of the genus *Asaccus* (*A. montanus* Gardner, 1994, *A. gallagheri* Arnold, 1972, *A. caudivolvulus* Arnold and Gardner, 1994, and *A. platyrhynchus* Arnold and Gardner, 1994), two *Pristurus* (*P. celerrimus* Arnold, 1977 and *P. gallagheri* Arnold, 1986), and a viper of the genus *Echis* (*E. omanensis* Babocsay, 2004). Moreover, preliminary analyses also indicate that the Hajar Mountain populations of the geckos *Ptyodactylus hasselquistii* (Donndorf, 1798) and *Pristurus rupestris* Blanford, 1874 may also represent new species (work in progress). *Hemidactylus* geckos assigned to *H. persicus* occur in isolation in the Jebel Akhdar region in North Oman (Arnold 1977, 1986; Arnold & Gallagher 1977) and have recently been found in the adjoining mountains of the Eastern Hajars, as far south as the Jebel Qahwan.

The Dhofar Mountain range is situated within the Southern Province of Oman. It lies approximately between 16º 30’ and 17º 45’ N and 52º45’ and 55º 30’ E. It is bounded to the North by the Rub al Khali (also known as the Empty Quarter), the largest desert in Arabia, to the South by the Arabian Sea and is separated from the rest of Oman in the Northeast by a desert steppe (Sale 1980) (Fig. 1). The Dhofar Mountain range was uplifted as a result

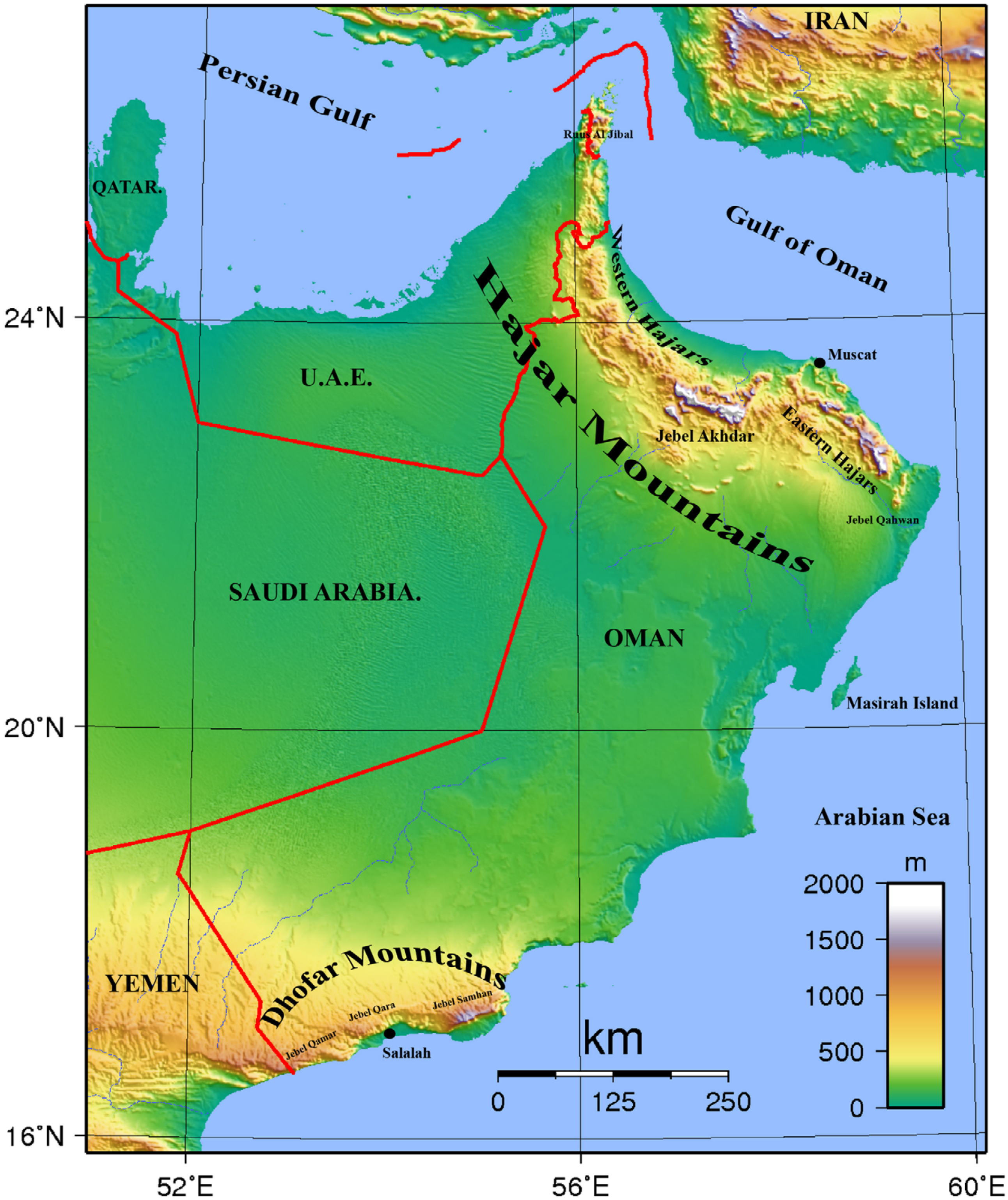

FIGURE 1. Schematic map of the study region showing the position of the Northern and Southern Oman mountains with the name of some relevant massifs.

of the opening of the Gulf of Aden and the formation of the Red Sea by plate separation (Bosworth *et al.* 2005; Glennie 2006; Laughton 1966). The top of the mountain range constitutes a relatively flat plateau, for the most part between 700 and 900 m above sea level and some 10–25 km wide that runs for about 150 km, from the Jebel Qamar in the West, through the Jebel Qara in the central part, to the Jebel Samhan in the East (Fig. 1), the highest point reaching over 2000 m in this latter massif (Sale 1980). The Dhofar Mountains lie within the monsoon belt and most rain falls as drizzle during the summer Southwest Monsoon in July and August and is responsible for the unique green vegetation on the Southward (sea) side of this mountain range, where the clouds form a variable belt along the coast from the Jebel Qamar to the Jebel Samhan that press against the mountain ridges. While the clouds only occasionally spill over the top of Jebel Qamar, on the much lower Jebel Qara they ride up to the summit (Sale 1980). However, the Northern slopes across the whole mountain range are in rain shadow. As a result of that, the Northward (land) side of the Dhofar Mountains is much drier and less vegetated than the lush Southward side. These climatic differences have played and important role in shaping the flora and fauna of this interesting biodiversity rich region (Arnold 1980; Buttiker & Gallagher 1980; Gallagher & Rogers 1980; Greathead 1980; Harrison 1980; Hoogstraal 1980; Larsen 1980; Waterston 1980; Wiltshire 1980).

As mentioned above, some species of *Hemidactylus* inhabiting the Hajar and Dhofar mountains as well as Masirah Island and some intervening areas in Oman have been found to be morphologically highly variable (Arnold 1977, 1980, 1986; Arnold & Gallagher 1977). To investigate this further and explore the relationships and history of Arabian *Hemidactylus*, in the present work we have used morphology and phylogenies inferred with both mitochondrial and nuclear markers including many representatives of these conflictive species and also a good representation of Arabian *Hemidactylus* as well as other members of the Arid clade (Carranza & Arnold 2006). The results of our morphological and molecular investigations have revealed the existence of eight new species of *Hemidactylus* that are described herein, six of them endemic to Oman.

MATERIAL AND METHODS

Morphological analysis

A total of 226 specimens were analyzed, including representatives of each one of the eight new species described herein plus other related Arabian and African taxa from the Arid clade (Carranza & Arnold 2006). Most of the specimens compared were from material in the extensive collection of the Natural History Museum, London (BMNH), S. Carranza's field series housed at the Institute of Evolutionary Biology (IBE), Spain and some specimens from the Oman Natural History Museum, Muscat (ONHM). The following measurements were taken by the same person (S.C.) using a digital caliper with accuracy to the nearest 0.1 mm and were expressed in millimeters: snout-vent length (SVL), measured from tip of snout to vent; trunk length (TRL), measured from posterior edge of forelimb insertion to anterior edge of hindlimb insertion; tail length (TL), from vent to tip of tail; head length (HL), distance between retroarticular process of jaw and tip of snout; head width (HW), measured at its widest part, usually at the level of temporal region; head height (HH), maximum height of head, measured from occiput to underside of jaws; orbital diameter (OD), considered as the greatest diameter of orbit; nares to eye distance (NE), distance between tip of snout and anteriormost point of eye; internarial distance (IN), distance between nares; anterior interorbital distance (IO1), distance between left and right supracilary scale rows at anteriormost point of eyes; posterior interorbital distance (IO2), distance between left and right supracilary scale rows at posteriormost point of eyes. It is important to take into account that preservation often puts limits on taking some formal measurements and ratios. Those involving limb lengths are frequently difficult to obtain because museum specimens are often stiff. The depth of the head and its lateral appearance also varies very substantially with the position of the kinetic skull when the animal concerned was preserved, which makes ratios involving head depth, and its length or width, highly variable. Kinetic movements of the skull may also change the shape of the external opening of the ear. Allometric change in proportions is another potentially confounding factor, thus within a species of *Hemidactylus* head size tends to fall with growth, while the relative breadth of the adhesive pads on the digits usually increases markedly; these trends are also often apparent when similar species of different sizes are compared. In addition to the metric dimension measured, the following pholidotic (meristic) characters were also collected by the same person (S.C.) using a dissecting microscope: longitudinal tubercle rows (TB), counted across dorsum at mid-body; number of preanal pores (PAP); number of supralabial (SL) and infralabial (IL) scales; lamellae under the first and fourth toes of pes (LP 1st and LP 4th).

The morphological characteristics of the 226 specimens studied belonging to 15 different taxa were carefully photographed using a Nikon 300 camera with a 60 mm macro, in order to build up a database of comparative material of Arabian *Hemidactylus* and to make all the data available to the scientific community. The complete

TABLE 1.- 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 an asterisk (*) indicate specimens for which only the *12S* gene was sequenced. Individuals with the specimen code highlighted with a hatch symbol (#) were included in the BEAST analysis (see materials and methods). Individuals with the specimen code highlighted with a superscript "H" are Holotypes, and with a superscript "P" are Paratypes. Specimens with identical sequences have the same GenBank accession number. *Hemidactylus* sp.1 corresponds to the same unnamed taxon reported by Moravec *et al*. (2011).

SPECIES	CODE	VOUCHER	LOCALITY	COUNTRY	12S	Cytb	ND4+tRNAs	C-*mos*	*Mc1r*	*RAG-2*
H. alkiyumii sp. nov.	S3337		Wadi Hasik	Oman	JQ957039	JQ957170	-	JQ957123	JQ957239	JQ957401
H. alkiyumii sp. nov.	S3472[#]		Wadi Hasik	Oman	JQ957040	JQ957171	JQ957310	JQ957123	JQ957240	JQ957403
H. alkiyumii sp. nov.	S7789		7.5 km S Hasik	Oman	JQ957043	JQ957175	JQ957315	JQ957123	JQ957240	JQ957404
H. alkiyumii sp. nov.	S7441	IBES7441	3.5 km NE Sadah	Oman	JQ957041	JQ957172	JQ957311	JQ957123	JQ957240	JQ957404
H. alkiyumii sp. nov.	S7666	IBES7666	3.5 km NE Sadah	Oman	JQ957041	JQ957172	JQ957313	JQ957123	JQ957242	JQ957401
H. alkiyumii sp. nov.	S7858	IBES7858	3 km NW of Hasik	Oman	JQ957040	JQ957177	JQ957317	JQ957123	JQ957245	JQ957404
H. alkiyumii sp. nov.	S7453	IBES7453	3 km NW of Hasik	Oman	JQ957040	JQ957173	JQ957312	JQ957123	JQ957241	JQ957405
H. alkiyumii sp. nov.	CAS227519	CAS227519	"11 km SE of Bosasso" (wrong locality)	"Somalia"	DQ120343	DQ120172	JQ957309	-	JQ957238	JQ957402
H. alkiyumii sp. nov.	AO129	BMNH2005.1662[H]	Tawi Atair	Oman	JQ957038	JQ957169	-	JQ957122	JQ957237	JQ957401
H. alkiyumii sp. nov.	AO128[#]	BMNH2005.1663[P]	Tawi Atair	Oman	JQ957038	JQ957168	-	JQ957121	JQ957236	JQ957401
H. alkiyumii sp. nov.	S7837	IBES7837	Dalkut	Oman	JQ957044	JQ957176	JQ957316	JQ957123	JQ957244	JQ957401
H. alkiyumii sp. nov.	S7740[#]	IBES7740	Dalkut	Oman	JQ957042	JQ957174	JQ957314	JQ957123	JQ957243	JQ957401
H. alkiyumii sp. nov.	S7888	IBES7888	Dalkut	Oman	JQ957042	JQ957178	JQ957318	JQ957123	JQ957246	JQ957401
H. alkiyumii sp. nov.	S7891	IBES7891	Dalkut	Oman	JQ957045	-	JQ957319	JQ957123	JQ957246	JQ957401
H. alkiyumii sp. nov.	JS2*		3 km E of Hauf	Yemen	JQ957090					
H. alkiyumii sp. nov.	JS3*		3 km E of Hauf	Yemen	JQ957091					
H. alkiyumii sp. nov.	JS4*		3 km E of Hauf	Yemen	JQ957090					
H. alkiyumii sp. nov.	JS7*		Damqawt	Yemen	JQ957094					
H. alkiyumii sp. nov.	JS62*		Salalah City	Oman	JQ957092					
H. alkiyumii sp. nov.	JS63*		Salalah City	Oman	JQ957092					
H. alkiyumii sp. nov.	JS64*		Salalah City	Oman	JQ957093					
H. alkiyumii sp. nov.	JS77*		2 km NW of Dalkut	Oman	JQ957090					
H. alkiyumii sp. nov.	JS78*		2 km NW of Dalkut	Oman	JQ957090					
H. alkiyumii sp. nov.	JS79*		2 km NW of Dalkut	Oman	JQ957090					
H. alkiyumii sp. nov.	JS80*		2 km NW of Dalkut	Oman	JQ957090					
H. alkiyumii sp. nov.	JS87*		8 km N. Salalah Airport	Oman	JQ957092					
H. alkiyumii sp. nov.	JS88*		8 km N. Salalah Airport	Oman	JQ957092					
H. alkiyumii sp. nov.	JS89*		8 km N. Salalah Airport	Oman	JQ957092					
H. alkiyumii sp. nov.	JS90*		3 km E Ain Hamran	Oman	JQ957092					
H. alkiyumii sp. nov.	JS91*		3 km E Ain Hamran	Oman	JQ957092					
H. alkiyumii sp. nov.	JS92*		Mirbat	Oman	JQ957093					
H. alkiyumii sp. nov.	JS93*		Close to Tawi Atair	Oman	JQ957092					
H. alkiyumii sp. nov.	JS94*		Taiq Cave	Oman	JQ957092					
H. alkiyumii sp. nov.	JS95*		Taiq Cave	Oman	JQ957095					
H. alkiyumii sp. nov.	JS96*		Taiq Cave	Oman	JQ957092					
H. alkiyumii sp. nov.	JS97*		Taiq Cave	Oman	JQ957092					
H. alkiyumii sp. nov.	S7192*	IBES7192	3.5 km NE from Sadah	Oman	JQ957089					
H. alkiyumii sp. nov.	S7053*	IBES7053	3.5 km NE from Sadah	Oman	JQ957088					
H. alkiyumii sp. nov.	S7101*	IBES7101	9 km SW of Hadbin	Oman	JQ957089					
H. alkiyumii sp. nov.	S7194*		9 km SW of Hadbin	Oman	JQ957089					
H. citernii	CAS227534[#]	CAS227534	Bari Region	Somalia	DQ120383	DQ120212	JQ957320	JQ957124	JQ957247	JQ957406
H. citernii	CAS227535	CAS227535	Bari Region	Somalia	DQ120384	DQ120213	JQ957321	JQ957124	JQ957248	JQ957407
H. dawudazraqi	J12404[#]		Wadi al Burbeyath	Jordan	DQ120335	DQ120164	JQ957397	JQ957161	JQ957299	JQ957442
H. dawudazraqi	J0504[#]		Dair al Khaf	Jordan	DQ120336	DQ120165	JQ957396	JQ957161	JQ957300	JQ957441
H. dawudazraqi	J0404		Dair al Khaf	Jordan	JQ957082	JQ957230	JQ957395	JQ957161	JQ957299	JQ957440
H. festivus sp. nov.	S7419[#]	IBES7419[P]	20 km S of Thumrait	Oman	JQ957047	JQ957181	JQ957324	JQ957125	JQ957252	JQ957410
H. festivus sp. nov.	AO126		3 km SE of Haluf	Oman	JQ957047	JQ957181	-	-	-	-
H. festivus sp. nov.	AO82		3 km SE of Haluf	Oman	JQ957047	JQ957181	JQ957323	JQ957125	JQ957251	JQ957410
H. festivus sp. nov.	AO122		Wadi Ayoun	Oman	JQ957047	JQ957179	JQ957322	JQ957125	-	JQ957409

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TABLE 1.(Continued)

SPECIES	CODE	VOUCHER	LOCALITY	COUNTRY	12S	Cytb	ND4+tRNAs	C-mos	Mc1r	RAG-2
H. festivus sp. nov.	AO120		Wadi Ayoun	Oman	JQ957047	JQ957179	JQ957322	JQ957125	JQ957249	JQ957408
H. festivus sp. nov.	AO154		Close to Mughsayl	Oman	JQ957047	JQ957182	JQ957322	JQ957125	JQ957250	JQ957409
H. festivus sp. nov.	AO121		Wadi Ayoun	Oman	JQ957046	JQ957180	JQ957322	JQ957125	JQ957250	JQ957409
H. festivus sp. nov.	JS1*		Wadi Hadramaut	Yemen	JQ957096					
H. festivus sp. nov.	JS12*		Damqawt	Yemen	JQ957097					
H. festivus sp. nov.	JS15*		Damqawt	Yemen	JQ957097					
H. festivus sp. nov.	JS70*		Mughsayl	Oman	JQ957098					
H. festivus sp. nov.	JS71*		Mughsayl	Oman	JQ957098					
H. festivus sp. nov.	JS72*		Mughsayl	Oman	JQ957098					
H. festivus sp. nov.	JS73*		Mughsayl	Oman	JQ957098					
H. festivus sp. nov.	JS85*		Mudayy	Oman	JQ957098					
H. festivus sp. nov.	JS86*		Mughsayl	Oman	JQ957098					
H. flaviviridis	AO23		E of Nizwa	Oman	JQ957048	JQ957183	JQ957325	JQ957126	JQ957253	JQ957411
H. flaviviridis	AO93[#]		East Khor	Oman	JQ957049	JQ957184	JQ957326	JQ957126	JQ957253	JQ957412
H. flaviviridis	Hflav*		Fajurah	UAE	JQ957116					
H. flaviviridis	JS117*		Nakhl	Oman	JQ957119					
H. flaviviridis	UAE62*		Ibra	Oman	JQ957118					
H. flaviviridis	JS119*		Jalan Bani Bu Hasan	Oman	JQ957119					
H. flaviviridis	AO92*		East Khor	Oman	JQ957117					
H. flaviviridis	JS118*		Salalah	Oman	JQ957120					
H. foudaii	SPM001825[#]		Jebel Elba	Egypt	DQ120385	DQ120214	JQ957327	JQ957127	-	JQ957413
H. hajarensis sp. nov.	CAS227612	CAS227612	4.5 km N of Tanuf	Oman	DQ120337	DQ120166	JQ957328	JQ957128	JQ957254	JQ957414
H. hajarensis sp. nov.	CAS227614	CAS227614	4.5 km N of Tanuf	Oman	DQ120338	DQ120167	JQ957329	JQ957128	JQ957255	JQ957415
H. hajarensis sp. nov.	S1969	BMNH2008.701	Wadi Mayh	Oman	JQ957055	JQ957189	JQ957335	JQ957128	JQ957260	JQ957415
H. hajarensis sp. nov.	S2136	BMNH2008.702	Wadi Mayh	Oman	JQ957050	JQ957185	JQ957337	-	JQ957260	JQ957415
H. hajarensis sp. nov.	S1660[#]	BMNH2008.703	Jebel Abu Daud	Oman	JQ957050	JQ957185	JQ957330	JQ957128	JQ957256	JQ957415
H. hajarensis sp. nov.	S2064	BMNH2008.709	Wadi Hebaheba, Jebel Qawan	Oman	JQ957053	JQ957188	JQ957336	JQ957128	-	-
H. hajarensis sp. nov.	S1777	IBES1777	Wadi Hebaheba, Jebel Qawan	Oman	JQ957053	JQ957188	JQ957333	JQ957130	JQ957258	JQ957418
H. hajarensis sp. nov.	S1772	BMNH2008.706	Wadi Hebaheba, Jebel Qawan	Oman	JQ957052	JQ957187	JQ957332	JQ957129	-	JQ957417
H. hajarensis sp. nov.	S1880	BMNH2008.707	Wadi Hebaheba, Jebel Qawan	Oman	JQ957052	JQ957187	JQ957332	JQ957128	JQ957259	JQ957420
H. hajarensis sp. nov.	S2139	BMNH2008.708	Wadi Hebaheba, Jebel Qawan	Oman	JQ957052	JQ957187	JQ957338	JQ957128	JQ957261	JQ957421
H. hajarensis sp. nov.	S1693[#]	BMNH2008.704	Wadi Tiwi	Oman	JQ957051	JQ957186	JQ957331	JQ957128	JQ957257	JQ957416
H. hajarensis sp. nov.	S1782	BMNH2008.705	Wadi Tiwi	Oman	JQ957054	JQ957187	JQ957334	JQ957128	-	JQ957419
H. hajarensis sp. nov.	JS65*		Wadi N of Qurayyat	Oman	JQ957105					
H. hajarensis sp. nov.	JS81*		Wadi Bani Awf	Oman	JQ957099					
H. hajarensis sp. nov.	JS98*		Muqal	Oman	JQ957101					
H. hajarensis sp. nov.	JS99*		Muqal	Oman	JQ957106					
H. hajarensis sp. nov.	S7076*	BMNH2005.1664	Wadi Tanuf	Oman	JQ957100					
H. hajarensis sp. nov.	S8064*	IBES8064	Wadi Tanuf	Oman	JQ957102					
H. hajarensis sp. nov.	S7151*	IBES7151	Wadi Tanuf	Oman	JQ957102					
H. hajarensis sp. nov.	S7124*	ONHM3706[P]	Wadi Bani Khalid	Oman	JQ957101					
H. hajarensis sp. nov.	S7336*	IBES7336[P]	Wadi Bani Khalid	Oman	JQ957104					
H. hajarensis sp. nov.	S7335*	IBES7335[P]	Wadi Bani Khalid	Oman	JQ957101					
H. hajarensis sp. nov.	S7170*	BMNH2008.714[H]	Wadi Bani Khalid	Oman	JQ957101					
H. hajarensis sp. nov.	S7184*	IBES7184	9 km N Al Chayan	Oman	JQ957103					
H. hajarensis sp. nov.	S7587*	IBES7587	9 km N Al Chayan	Oman	JQ957103					
H. hajarensis sp. nov.	S7154*	IBES7154	9 km N Al Chayan	Oman	JQ957103					
H. hajarensis sp. nov.	S7321*		9 km N Al Chayan	Oman	JQ957103					
H. hajarensis sp. nov.	S6061*		9 km N Al Chayan	Oman	JQ957099					
H. homoeolepis	S4209[#]		Wadi Ayhaft, Socotra Island	Yemen	JQ957059	JQ957194	JQ957342	JQ957132	JQ957264	JQ957422
H. homoeolepis	S3399		Hadibo, Socotra Island	Yemen	JQ957059	JQ957193	JQ957341	JQ957132	JQ957263	JQ957422
H. homoeolepis	S7929	IBES7929	14.5 km NE of Sharbthat	Oman	JQ957057	JQ957198	JQ957349	JQ957131	JQ957262	JQ957422

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TABLE 1.(Continued)

SPECIES	CODE	VOUCHER	LOCALITY	COUNTRY	12S	Cytb	ND4+tRNAs	C-mos	Mc1r	RAG-2
H. homoeolepis	S7676	IBES7676	Asylah	Oman	JQ957057	-	JQ957345	JQ957133	JQ957262	JQ957422
H. homoeolepis	S7657[#]	IBES7657	Asylah	Oman	JQ957057	JQ957195	JQ957343	JQ957133	JQ957262	JQ957422
H. homoeolepis	S7673	IBES7673	Asylah	Oman	JQ957057	-	JQ957344	JQ957133	JQ957262	JQ957422
H. homoeolepis	S7664	IBES7664	Asylah	Oman	JQ957057	JQ957195	JQ957344	JQ957133	JQ957262	JQ957422
H. homoeolepis	S7668	IBES7668	Asylah	Oman	JQ957057	JQ957195	JQ957344	JQ957133	JQ957262	JQ957422
H. homoeolepis	S7966	IBES7966	14.5 km NE of Sharbthat	Oman	JQ957057	JQ957197	JQ957350	JQ957136	JQ957262	JQ957422
H. homoeolepis	S7924	IBES7924	14.5 km NE of Sharbthat	Oman	JQ957057	JQ957197	JQ957348	JQ957135	JQ957262	JQ957422
H. homoeolepis	S7871		5 km W of Mughsayl	Oman	JQ957057	JQ957196	JQ957346	JQ957134	JQ957265	JQ957422
H. homoeolepis	AO81	IBEAO81	3 km SE of Haluf	Oman	JQ957057	JQ957191	JQ957340	JQ957131	JQ957262	JQ957422
H. homoeolepis	S7909	IBES7909	Wadi Ayoun	Oman	JQ957057	JQ957196	JQ957340	JQ957131	JQ957262	JQ957422
H. homoeolepis	AO85	IBEAO85	N of Wadi Ayoun	Oman	JQ957058	JQ957192	JQ957340	JQ957131	-	JQ957422
H. homoeolepis	AO119	IBEAO119	Wadi Ayoun	Oman	JQ957056	JQ957190	JQ957339	JQ957131	JQ957262	JQ957422
H. homoeolepis	S7893	IBES7893	5 km W of Mughsayl	Oman	JQ957060	JQ957196	JQ957347	-	JQ957266	JQ957422
H. homoeolepis	S7091*		Wadi Ayoun	Oman	JQ957110					
H. homoeolepis	JS5*		3 km E Hauf	Yemen	JQ957111					
H. homoeolepis	JS6*		3 km E Hauf	Yemen	JQ957108					
H. homoeolepis	JS8*		Damqawt	Yemen	JQ957109					
H. homoeolepis	JS75*		Mughsayl	Oman	JQ957112					
H. inexpectatus sp. nov.	S1892	BMNH2008.712[P]	2.5 km SE Ar Rumayliyah	Oman	JQ957066	JQ957206	JQ957364	JQ957141	JQ957274	JQ957427
H. inexpectatus sp. nov.	S7700	IBES7700[P]	2.5 km SE Ar Rumayliyah	Oman	JQ957066	JQ957209	JQ957367	JQ957140	JQ957277	JQ957426
H. inexpectatus sp. nov.	S2166	BMNH2008.711[H]	2.5 km SE Ar Rumayliyah	Oman	JQ957067	JQ957207	JQ957365	JQ957140	JQ957275	JQ957426
H. inexpectatus sp. nov.	S7735	IBES7735[P]	2.5 km SE Ar Rumayliyah	Oman	JQ957067	JQ957210	JQ957368	JQ957140	JQ957273	JQ957426
H. inexpectatus sp. nov.	S1798	IBES1798[P]	2.5 km SE Ar Rumayliyah	Oman	JQ957065	JQ957205	JQ957363	JQ957140	JQ957273	JQ957426
H. inexpectatus sp. nov.	S7722	IBES7722[P]	2.5 km SE Ar Rumayliyah	Oman	JQ957068	-	JQ957366	JQ957140	JQ957274	JQ957426
H. inexpectatus sp. nov.	S7674[#]	ONHM3711[P]	2.5 km SE Ar Rumayliyah	Oman	JQ957067	JQ957208	JQ957366	JQ957140	JQ957276	JQ957426
H. lemurinus	AO117		Wadi Ayoun	Oman	JQ957062	JQ957200	JQ957352	JQ957137	JQ957268	JQ957423
H. lemurinus	AO123		Wadi Ayoun	Oman	JQ957062	JQ957200	JQ957354	JQ957137	-	JQ957423
H. lemurinus	AO116[#]		Wadi Ayoun	Oman	JQ957061	JQ957199	JQ957351	JQ957137	JQ957267	-
H. lemurinus	AO118		Wadi Ayoun	Oman	JQ957061	JQ957201	JQ957353	JQ957137	JQ957269	JQ957423
H. lemurinus	AO124		Wadi Ayoun	Oman	JQ957061	JQ957201	JQ957355	JQ957137	-	JQ957423
H. lemurinus	JS9*		Damqawt	Yemen	JQ957113					
H. lemurinus	JS10*		Damqawt	Yemen	JQ957114					
H. lemurinus	JS11*		Damqawt	Yemen	JQ957113					
H. luqueorum sp. nov.	S2152	ONHM3705[P]	Wadi Bani Habib, Jebel Akhdar	Oman	JQ957070	JQ957214	JQ957372	JQ957146	JQ957278	JQ957431
H. luqueorum sp. nov.	AO46	BMNH2005.1660[H]	Sayq, Jebel Akhdar	Oman	JQ957069	JQ957212	JQ957370	JQ957143	JQ957279	JQ957429
H. luqueorum sp. nov.	AO155[#]	BMNH2005.1661[P]	Sayq, Jebel Akhdar	Oman	JQ957069	JQ957211	JQ957369	JQ957142	JQ957278	JQ957428
H. luqueorum sp. nov.	AO59	BMNH2005.1658[P]	Wadi Bani Habib, Jebel Akhdar	Oman	JQ957069	JQ957212	JQ957371	JQ957144	JQ957280	JQ957430
H. luqueorum sp. nov.	S8068	IBES8068[P]	Wadi al Khahafa, Jebel Akhdar	Oman	JQ957069	JQ957215	JQ957373	JQ957147	JQ957281	JQ957430
H. luqueorum sp. nov.	S1756	BMNH2008.710	Wadi al Khahafa, Jebel Akhdar	Oman	JQ957069	JQ957213	-	JQ957145	JQ957281	JQ957430
H. luqueorum sp. nov.	S7771*	IBES7771[P]	1 km E from Hat, Jebel Akhdar	Oman	JQ957107					
H. luqueorum sp. nov.	S6056*	IBES6056	1 km E from Hat, Jebel Akhdar	Oman	JQ957107					
H. luqueorum sp. nov.	S7155*	IBES7155	1 km E from Hat, Jebel Akhdar	Oman	JQ957107					
H. luqueorum sp. nov.	S6085*	IBES6085[P]	1 km E from Hat, Jebel Akhdar	Oman	JQ957107					
H. luqueorum sp. nov.	S6080*		1 km E from Hat, Jebel Akhdar	Oman	JQ957107					
H. luqueorum sp. nov.	S7843*		1 km E from Hat, Jebel Akhdar	Oman	JQ957107					
H. macropholis	CAS227511[#]	CAS227511	11 km SE of Bosasso	Somalia	DQ120379	DQ120208	JQ957356	JQ957138	JQ957270	JQ957424
H. masirahensis sp. nov.	S3412		Wadi Harf, Masirah island	Oman	JQ957063	JQ957202	JQ957359	JQ957139	JQ957272	JQ957425
H. masirahensis sp. nov.	S7707	IBES7707	Wadi Maahdi, Masirah island	Oman	JQ957063	JQ957202	JQ957361	JQ957139	JQ957272	JQ957425
H. masirahensis sp. nov.	S1878	BMNH2008.713	Wadi Haql. Masirah island	Oman	JQ957063	JQ957202	JQ957357	JQ957139	-	JQ957425
H. masirahensis sp. nov.	S7661	IBES7661	Wadi Maahdi, Masirah island	Oman	JQ957063	JQ957202	-	JQ957139	JQ957272	JQ957425
H. masirahensis sp. nov.	S2044	IBES2044	Wadi Haql, Masirah island	Oman	JQ957064	JQ957203	JQ957358	JQ957139	JQ957271	JQ957425
H. masirahensis sp. nov.	S7651[#]	ONHM3710[P]	Wadi Maahdi, Masirah island	Oman	JQ957063	JQ957204	JQ957360	JQ957139	JQ957272	JQ957425
H. masirahensis sp. nov.	S7710	IBES7710[P]	Wadi Maahdi, Masirah island	Oman	JQ957063	JQ957204	JQ957362	JQ957139	JQ957272	JQ957425

……*continued on next page*

TABLE 1.(Continued)

SPECIES	CODE	VOUCHER	LOCALITY	COUNTRY	12S	Cytb	ND4+tRNAs	C-mos	Mc1r	RAG-2
H. modestus	CAS198934[#]	CAS198934	Kijiado District, Rift Valley Province	Kenya	DQ120386	DQ120215	-	JQ957149	JQ957283	JQ957432
H. paucituberculatus sp. nov.	S7988	IBES7988	Khor Sawli	Oman	JQ957072	-	JQ957383	JQ957150	JQ957291	JQ957425
H. paucituberculatus sp. nov.	AO104	IBEAO104	East Khor	Oman	JQ957072	JQ957217	JQ957375	JQ957150	JQ957284	JQ957425
H. paucituberculatus sp. nov.	AO162		Khor Sawli	Oman	JQ957072	JQ957217	JQ957376	JQ957151	JQ957285	JQ957425
H. paucituberculatus sp. nov.	S3261		Wadi Darbat	Oman	JQ957072	JQ957217	JQ957379	JQ957150	JQ957284	-
H. paucituberculatus sp. nov.	S7921	ONHM3709[P]	Khor Sawli	Oman	JQ957072	JQ957217	JQ957376	JQ957150	JQ957289	-
H. paucituberculatus sp. nov.	S7646	IBES7646[P]	Khor Sawli	Oman	JQ957072	JQ957217	JQ957380	JQ957150	JQ957287	JQ957425
H. paucituberculatus sp. nov.	S7910[#]	IBES7910	East Khor	Oman	JQ957072	JQ957217	JQ957377	JQ957150	JQ957286	JQ957425
H. paucituberculatus sp. nov.	AO91	IBEAO91	East Khor	Oman	JQ957072	JQ957217	JQ957377	JQ957151	-	JQ957425
H. paucituberculatus sp. nov.	S7994	IBES7994	Wadi Darbat	Oman	JQ957072	JQ957221	JQ957384	JQ957151	JQ957292	JQ957425
H. paucituberculatus sp. nov.	S3235		Wadi Darbat	Oman	JQ957072	JQ957218	JQ957378	JQ957150	JQ957286	-
H. paucituberculatus sp. nov.	S8004	IBES8004	3.5 km NE Sadah	Oman	JQ957072	JQ957222	JQ957385	JQ957150	JQ957287	JQ957425
H. paucituberculatus sp. nov.	S7930	IBES7930	Wadi Hasik	Oman	JQ957073	JQ957220	JQ957382	JQ957150	JQ957290	JQ957433
H. paucituberculatus sp. nov.	S7902	IBES7902	3 km NW of Hasik	Oman	JQ957073	JQ957219	-	JQ957150	JQ957288	JQ957425
H. paucituberculatus sp. nov.	S7812		Wadi Hasik	Oman	JQ957073	JQ957219	JQ957381	JQ957150	JQ957288	-
H. paucituberculatus sp. nov.	S7492*	IBES7492	9 km SW of Hadbin	Oman	JQ957073					
H. paucituberculatus sp. nov.	S7201*		Wadi Darbat	Oman	JQ957115					
H. paucituberculatus sp. nov.	S7364*	IBES7364	Khor Sawli	Oman	JQ957072					
H. paucituberculatus sp. nov.	S7663*	IBES7663	Khor Sawli	Oman	JQ957072					
H. paucituberculatus sp. nov.	S7183*	IBES7183	Khor Sawli	Oman	JQ957072					
H. persicus	FTHM005100[#]	FTHM005100	Bushehr	Iran	JQ957076	JQ957224	-	JQ957152	-	-
H. persicus	MVZ234385[#]	MVZ Herps 234385	Lipar Village, Sistan and Baluchistan	Iran	JQ957077	JQ957225	JQ957386	JQ957152	JQ957293	JQ957435
H. persicus	FTHM005000	FTHM005000	Mahshar	Iran	JQ957074	JQ957223	-	JQ957152	-	JQ957434
H. persicus	FTHM005001	FTHM005001	Mahshar	Iran	JQ957075	JQ957223	-	JQ957152	-	-
H. robustus	S2151		8 km W Shannah	Oman	JQ957081	JQ957228	JQ957389	JQ957158	JQ957294	JQ957409
H. robustus	S1677		1 km W airport, Masirah Island	Oman	JQ957080	JQ957228	JQ957389	JQ957153	-	JQ957409
H. robustus	S1905		1 km W airport, Masirah Island	Oman	JQ957080	JQ957228	JQ957389	JQ957158	JQ957294	JQ957438
H. robustus	S1962		1 km W airport, Masirah Island	Oman	JQ957080	JQ957228	JQ957389	JQ957154	JQ957294	JQ957409
H. robustus	S1788[#]		1 km W airport, Masirah Island	Oman	JQ957080	JQ957228	JQ957389	JQ957154	JQ957294	JQ957436
H. robustus	S2150		1 km W airport, Masirah Island	Oman	JQ957080	JQ957228	JQ957391	JQ957159	-	JQ957409
H. robustus	SPM001859[#]		Safaga	Egypt	DQ120347	DQ120176	JQ957394	JQ957160	JQ957298	JQ957439
H. robustus	AO164b		East Khor	Oman	JQ957078	JQ957226	JQ957387	JQ957153	JQ957294	JQ957436
H. robustus	AO165[#]		East Khor	Oman	JQ957078	JQ957226	JQ957387	JQ957154	JQ957295	JQ957437
H. robustus	AO4		Al Azaiba	Oman	JQ957079	JQ957227	-	-	-	-
H. robustus	UAE25		Wadi Tayybiyah	UAE	JQ957079	JQ957227	-	-	-	-
H. robustus	AO3		Al Azaiba	Oman	JQ957079	JQ957227	JQ957388	JQ957155	JQ957294	JQ957409
H. robustus	Hturc2		Dhafra Beach, near Ruwais	UAE	AF186117	AF184989	-	JQ957156	-	JQ957409
H. robustus	SPM001501		Dhafra Beach, near Ruwais	UAE	AF186117	JQ957227	-	-	-	-
H. robustus	R1415		Mukalla Airport	Yemen	AF186117	JQ957229	JQ957392	JQ957154	JQ957297	JQ957436
H. robustus	S1688		8 km W Shannah	Oman	AF186117	JQ957226	JQ957390	JQ957157	JQ957296	JQ957409
H. robustus	SPM001503		Abu Dhabi	UAE	AF186117	JQ957226	JQ957393	-	-	-
H. sinaitus	JS150[#]		15 km SE of Atbara	Sudan	JQ957083	JQ957232	-	JQ957164	JQ957303	JQ957446
H. sinaitus	JS147		Wad Ben Naga	Sudan	JQ957084	JQ957231	-	JQ957164	JQ957302	JQ957446
H. sinaitus	JS146		Wad Ben Naga	Sudan	JQ957083	JQ957231	-	JQ957164	-	JQ957446
H. sp. 1	Sher10660[#]	Sher10660	Ayoun Musa	Egypt	JQ957071	JQ957216	JQ957374	JQ957148	JQ957282	JQ957409
H. turcicus	SPM000788		Erzin	Turkey	DQ120334	DQ120163	JQ957398	JQ957162	-	JQ957443
H. turcicus	SPM001629[#]		Torregorda	Spain	DQ120311	DQ120140	JQ957399	JQ957162	JQ957301	JQ957444
H. turcicus	SPM002086		Barcelona	Spain	DQ120313	DQ120142	JQ957400	JQ957163	JQ957301	JQ957445
H. yerburii	JS40[#]		3 km S of Najd an Nashamah	Yemen	JQ957086	JQ957235	-	JQ957167	JQ957306	JQ957447
H. yerburii	JS44		Al Hababi	Yemen	JQ957086	JQ957235	-	JQ957166	JQ957307	JQ957448
H. yerburii	JS60#		6 km N Al Hisn	Yemen	JQ957087	JQ957234	-	JQ957166	JQ957308	JQ957447
H. yerburii	JS29		8 km N of Lahij	Yemen	JQ957085	JQ957233	-	JQ957165	JQ957304	JQ957447
H. yerburii	JS30		8 km N of Lahij	Yemen	JQ957085	JQ957234	-	JQ957166	JQ957305	JQ957447

collection of 3103 high-resolution photographs has been deposited in MorphoBank (Project 483; http://www.morphobank.org/). Sexual differences on body size and shape were tested using a one-way ANOVA in the program JMP v. 5.5.1. Summary statistics (mean, maximum, minimum and Standard Error) were calculated for each character of all the species included in the present study. If a character was not dimorphic, summary statistics for all the specimens and for males and females independently were presented. If the character was dimorphic, only summary statistics for males and females were presented.

A list of all studied specimens with their corresponding Museum accession numbers, locality data, metric and meristic information and MorphoBank accession numbers is presented in Appendix I.

Molecular analyses

Molecular samples, DNA extraction and amplification

A total of 222 individuals were included in the molecular study. Sampling was more intense in Oman but relevant samples of the Arid clade from other places in the Middle East and Africa were also included. The ribosomal 12S rRNA and cytochrome *b* genes for 15 specimens were from Carranza and Arnold (2006) and therefore were downloaded from GenBank and the same individuals were sequenced for the remaining genes. The ribosomal 12S rRNA of 15 specimens from Yemen (Busais & Joger 2011a) including representatives of the three new species and one new subspecies described therein, were kindly donated by U. Joger for comparison with the new species described in the present study. A list of 207 individuals included in the molecular analyses (samples from Busais & Joger 2011a not included) with their codes, voucher references, corresponding localities and GenBank accession numbers for all genes sequenced is presented in Table 1. As shown in Table 1, a total of 131 specimens were sequenced for up to seven genes (see below) and 76 individuals were sequenced for the 12S rRNA only. The latter include six specimens of *H. flaviviridis*, three of *H. lemurinus*, five of *H. homoeolepis* and 62 individuals belonging to seven new species described herein. The 12S rRNA sequences of these 76 specimens were used as a "Barcode" to crosscheck their morphological identification with molecular data and, in the case of samples belonging to the new species, they were also used to infer the level of genetic variability. The reasons for not amplifying all seven genes for these 76 specimens where the following: 1.—samples starting with code JS (Table 1) belong to another study on the molecular relationships of Arabian *Hemidactylus* (were not collected by us) and, therefore, data on the full set of mtDNA and nDNA genes will be presented elsewhere (work in progress); and/or 2.—morphological and molecular analyses were fully congruent in the taxonomic identification of the specimens and the new DNA samples did not represent any new lineage in the phylogeny of Arabian *Hemidactylus*.

Maps indicating the geographical distribution of all Omani *Hemidactylus* are shown in Figs. 2–4. For seven out of the eight new species described herein plus *H. homoeolepis* the distribution maps include both specimens used for the molecular analyses and bibliographic/museum records, so represent complete distribution ranges of the species. One of the new species described herein could not be mapped as a result of lack of precise locality of the single specimen available (see below). For the widely distributed *H. robustus* and the Tropical Asian (and most probably introduced) *H. flaviviridis*, only the geographic origin of the samples included in the molecular analyses is presented. For *H. leschenaultii*, the other Tropical Asian species and likely introduced, we show the single locality where it has been found (Gardner 1992).

Genomic DNA was extracted from ethanol-preserved tissue samples using the Qiagen DNeasy Blood & Tissue Kit. One hundred and thirty-one specimens were sequenced for up to four mitochondrial genes encoding the ribosomal 12S rRNA (*12S*), cytochrome *b* (*cytb*), NADH deshidrogenase 4 (*nd4*) and the adjacent tRNA region (*tRNAs*; including the complete sequences of *tRNA-His* and *tRNA-Ser* and the first eight nucleotides of *tRNA-Leu*) and three nuclear markers encoding the oocyte maturation factor MOS (c-*mos*), the melano-cortin 1 receptor (*mc1r*) and the recombination activating gene 2 (*rag2*). Primers, PCR conditions and source references for the amplification of all mitochondrial and nuclear markers are listed in Table 2.

TABLE 2. Amplification conditions and information on markers used in this study.

Locus	Fragment length (bp)	Primer sequence (5’ to 3’)	Primer orientation	Tª annealing	Reference
12S	~390	12Sa AAACTGGGATTAGATACCCCACTAT 12Sb GAGGGTGACGGGCGGTGTGT	Forward Reverse	48º	Kocher et al. 1989
cyb	~300	cb1 CCATCCAACATCTCAGCATGATGAAA cb2 CCCTCAGAATGATATTTGTCCTCA	Forward Reverse	45º	Kocher et al. 1989
nd4+tRNAs	~800	ND4 CACCTATGACTACCAAAAGCTCATGTAGAAGC Leu CATTACTTTTACTTGGATTTGCACCA	Forward Reverse	52º	Arévalo et al. 1994
c-mos	~400	FUF TTTGGTTCKGTCTACAAGGCTAC FUR AGGGAACATCCAAAGTCTCCAAT	Forward Reverse	55º	Gamble et al. 2008
mc1r	~670	MC1R-F AGGCNGCCATYGTCAAGAACCGGAACC MC1R-R ACTCCGRAAGGCRTAAATGATGGGGTCCAC	Forward Reverse	52º	Pinho et al. 2009
Rag2	~410	RAG2-PY1-F CCCTGAGTTTGGATGCTGTACTT RAG2-PY1-R AACTGCCTRTTGTCCCCTGGTAT	Forward Reverse	65º	Gamble et al. 2008

The PCR conditions were as follows: 95°C for 2 min, 35 cycles of denaturation at 92°C for 30 sec, annealing (see table) for 45 sec, and extension at 72º for 1min, and a final extension step at 72º for 5 min.

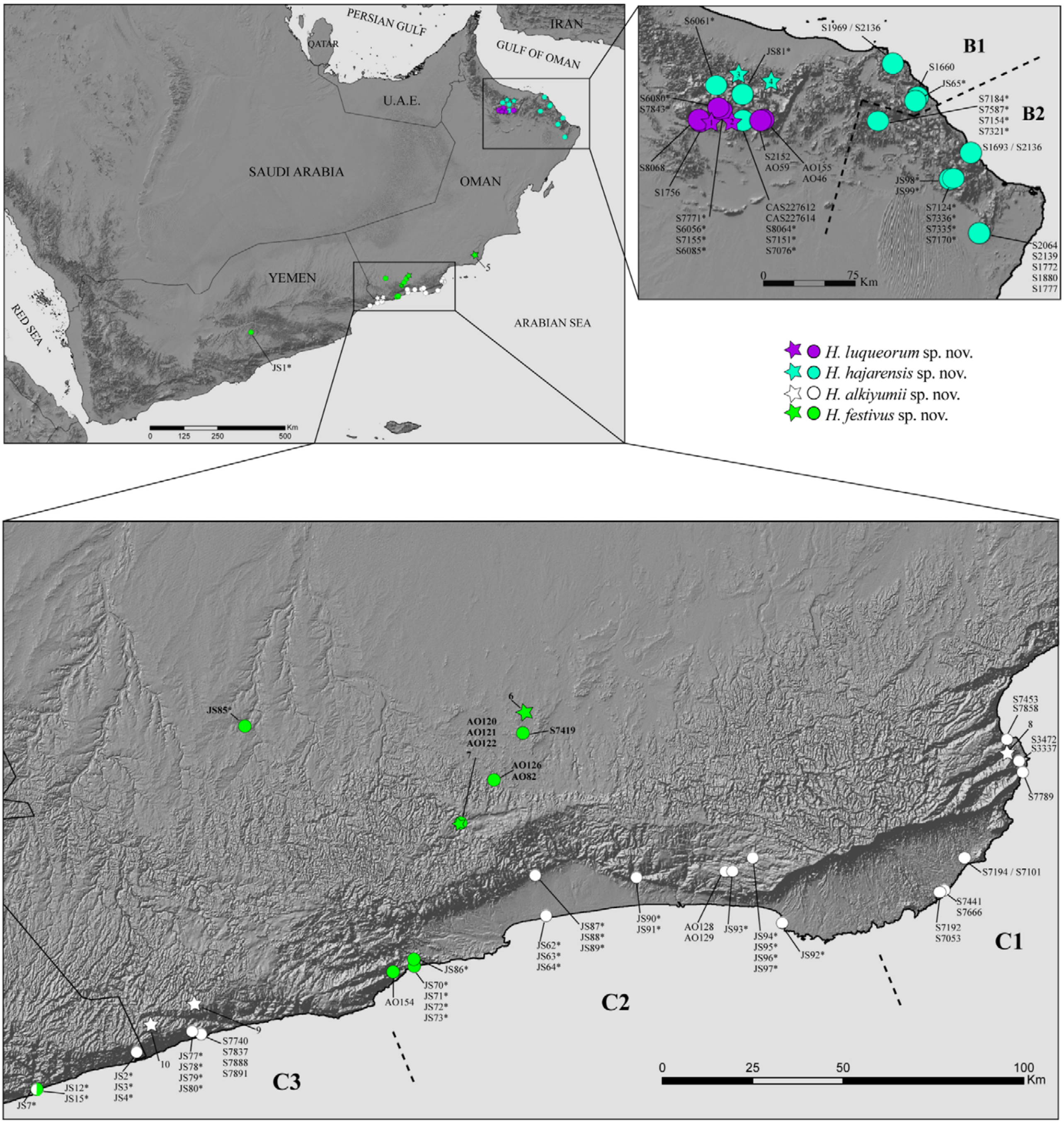

FIGURE 2. Distribution map of *Hemidactylus luqueorum* sp. nov., *H. hajarensis* sp. nov., *H. alkiyumii* sp. nov. and *H. festivus* sp. nov. Color dots indicate specimens included in the molecular analyses and listed in Table 1. Stars indicate Museum specimens included in the morphological analyses only and listed in Appendix I: 1) BMNH1975.916; 2) BMNH1975.41, BMNH1980.558; 3) BMNH1976.1404; 4) BMNH1977.35; 5) BMNH1983.706; 6) BMNH1977.975; 7) BMNH1977.976–981; 8) BMNH1977.963–966; 9) BMNH1977.956–959; 10) BMNH1977.972–973 and BMNH1976.1409. Dashed lines delimit the different genetic lineages found within *H. hajarensis* (B1 and B2) and *H. alkiyumii* (C1, C2 and C3) and shown in Fig. 5 and Appendix III.

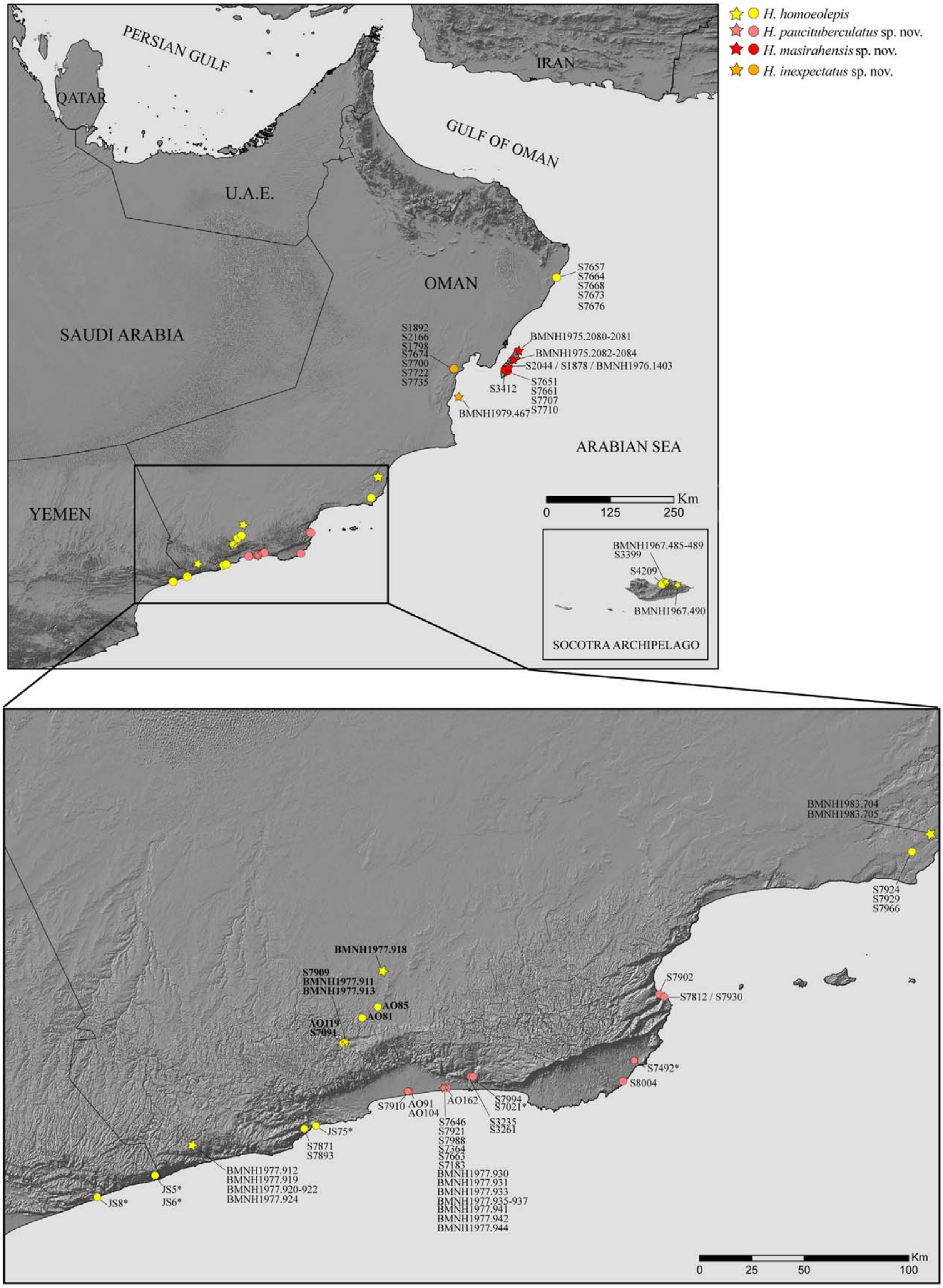

FIGURE 3. Distribution map of *H. homoeolepis*, *H. paucituberculatus* sp. nov., *H. masirahensis* sp. nov. and *H. inexpectatus* sp. nov. Color dots indicate specimens included in the molecular analyses and listed in Table 1. Stars indicate Museum specimens included in the morphological analyses only and listed in Appendix I. Specimen of *H. homoeolepis* BMNH1953.1.6.99 from Shaqra (Yemen; location: 13.35 N – 45.70 E) is not shown in the map.

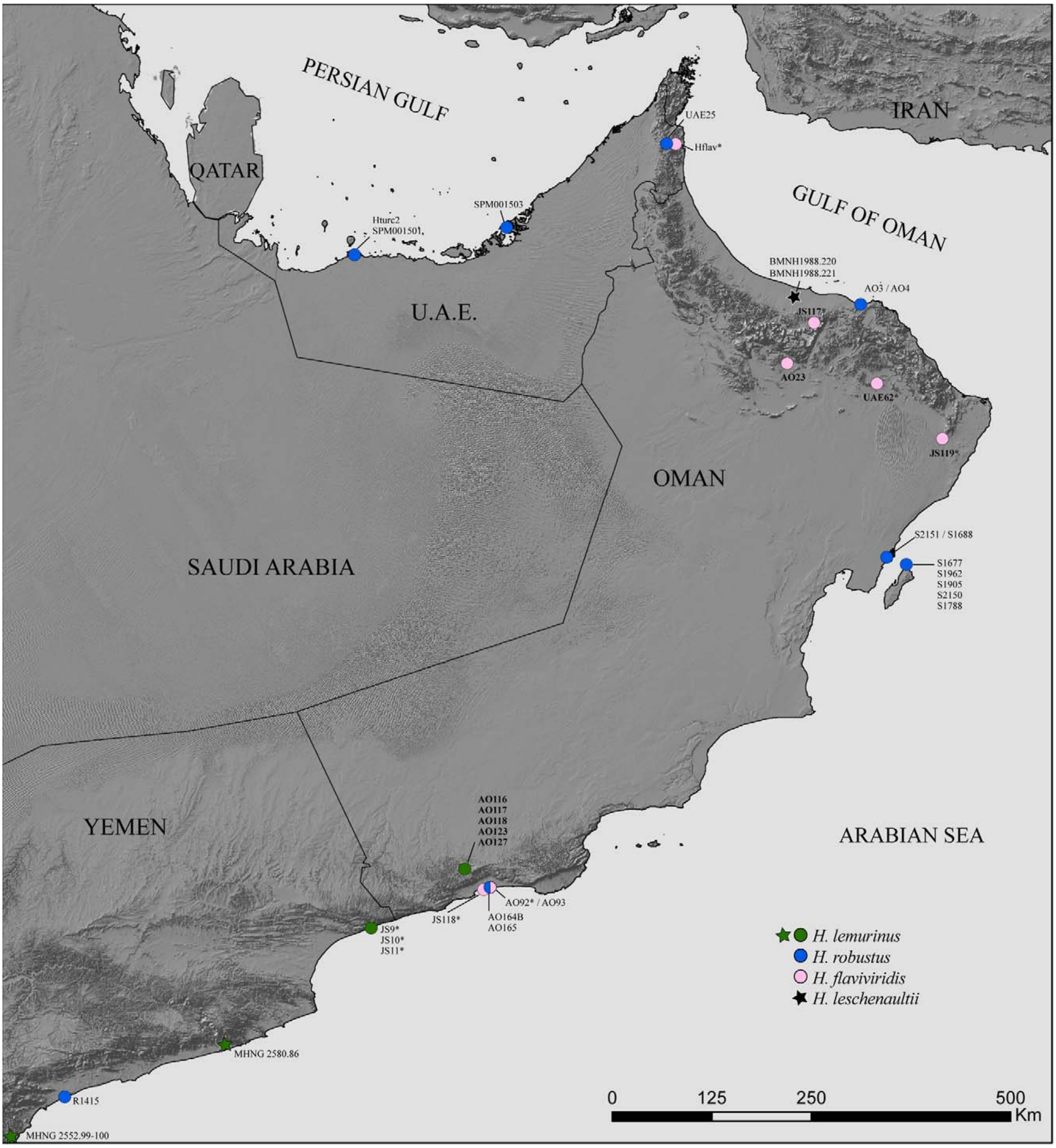

FIGURE 4. Distribution map with all known localities of *H. lemurinus*, the localities of *H. flaviviridis* and *H. robustus* specimens included in the molecular analyses and the only locality of *H. leschenaultii* in Oman. Color dots indicate specimens included in the molecular analyses and listed in Table 1. Stars indicate Museum specimens not included in the molecular analyses. The acronym MHNG refers to the Muséum d'Histoire Naturelle de la Ville de Genève.

Sequence analysis

Chromatographs were checked manually, assembled and edited using Geneious v. 5.3.6 (Biomatters Ltd.). DNA sequences were aligned using MAFFT v.6 (Katoh & Toh 2008) with the options maxiterate 1000 and localpair. Poorly aligned positions of the two non-transcribed mtDNA regions (*12S* and *tRNAs*) were eliminated with G-blocks (Castresana 2000) using low stringency options (Talavera & Castresana 2007). Coding mtDNA and nDNA gene fragments were translated into amino acids and no stop codons were observed. For nuclear loci, c-*mos*, *mc1r* and *rag2*, heterozygous individuals were identified based on the presence of two peaks of approximately equal height at a single nucleotide site. SEQPHASE (Flot 2010) (http://www.mnhn.fr/jfflot/seqphase/) was used to convert the input files, and the software PHASE v. 2.1.1 to resolve phased haplotypes (Stephens *et al.* 2001). Default settings of PHASE were used except for phase probabilities that were set as ≥ 0.7 (see Harrigan *et al.* 2008). All polymorphic sites with a probability of < 0.7 were coded in both alleles with the appropriate IUPAC ambiguity code. Phased nuclear sequences were used for the network analyses and the unphased sequences for the phylogenetic analyses (see below). Uncorrected genetic distances were calculated using MEGA 5 (Tamura *et al.* 2011)

Phylogenetic and network analyses

Three datasets were assembled for the phylogenetic analyses of *Hemidactylus*. Dataset 1 consisted of an alignment of 2866 base pairs (bp) of concatenated mitochondrial and unphased nuclear DNA for 131 *Hemidactylus*, of which 129 were representatives of the Arid clade (see Table 1). The 2866 bp of aligned sequence included 1385 bp of mtDNA (353 bp *12S*; 302 bp *cytb*; 588 bp *nd4* and 142 bp *tRNAs*) and 1481 bp of nDNA (403 bp c-*mos*; 668 bp *mc1r* and 410 bp *rag2*).

Dataset 2 included a selection of 30 specimens from Dataset 1 (including a complete set of seven genes) and was used to infer the dates of the speciation events (see below). The alignment of Dataset 2 was exactly the same as Dataset 1 and therefore also included 2866 bp.

Dataset 3 consisted of an alignment of 350 bp of the *12S* mitochondrial gene only for 188 individuals. It included representatives of the three new species and one subspecies described from Yemen by Busais & Joger (2011a), representatives of seven out of the eight new species described herein (no DNA is available for the eighth species) and individuals belonging to *H. y. yerburii* (this study and Busais & Joger 2011a,b), *H. robustus* (this study and Busais & Joger 2011a,b), *H. sinaitus* (Busais & Joger 2011a,b), and *H. homoeolepis* (this study). Dataset 3 was assembled with two objectives: 1.- to show the genetic differentiation between the four new *Hemidactylus* taxa recently described from Yemen (Busais & Joger 2011a,b) and the seven new Arabian species described herein for which DNA was available; and 2.- to show the level of genetic variability within the seven new species described herein for which DNA was available, including all the samples listed in Table 1. This explains why specimens not relevant for objectives 1 and 2 that were already included in Datasets 1 and 2 like *H. modestus* (Günther, 1894), *H. citernii* Boulenger, 1912, *H. foundaii* Baha el Din, 2003, *H. macropholis* Boulenger, 1896, *H. turcicus*, *H. dawudazraqi* and *H.* sp. 1 were excluded from Dataset 3 (the highly divergent sequences of some of these specimens affected the phylogenetic analyses using the short *12S* mitochondrial fragment). A thorough analysis of the phylogenetic relationships of Arabian *Hemidactylus* using both mtDNA and nDNA data and including all taxa known to date from both mainland Arabia and the Socotra Archipelago plus several new undescribed lineages from Yemen and Saudi Arabia is in progress (data not shown).

Phylogenetic analyses of Datasets 1 and 3 were performed using Maximum Likelihood (ML) and Bayesian (BI) methods. Separate ML and BI analyses were also performed on all seven independent partitions (*12S*, *cytb*, *ND4*, *tRNAs*, c-*mos*, *mc1r* and *rag2*) of Dataset 1 to test for conflicting signal among genes (data not shown). Best-fitting nucleotide substitution models were selected for each partition under the Akaike information criterion (Akaike 1973) using jModelTest v.0.1.1 (Posada 2008). The GTR+I+G model was independently estimated for Dataset 3 (*12S*) and for each of the *cytb*, *nd4*, *tRNAs*, *mc1r* and *rag2* partitions of Dataset 1. The GTR+G and the HKY+G were selected for the *12S* and c-*mos* partitions of Dataset 1, respectively. Alignment gaps were treated as missing data and the nuclear gene sequences were not phased. *Hemidactylus flaviviridis* was used to root the tree, based on published evidence (Carranza & Arnold 2006).

Bayesian analyses of both Datasets 1 and 3 were performed with MrBayes 3.1.2 (Huelsenbeck & Ronquist

2001; Ronquist & Huelsenbeck 2003) and, in the concatenated Dataset 1, with best fitting models applied to each partition (gene) and all parameters unlinked across partitions. Analyses were run for $2x10^7$ generations, with sampling intervals of 1000 generations, producing 20000 trees. Convergence and appropriate sampling of the BI analyses were confirmed examining the standard deviation of the split frequencies between the two simultaneous runs and the Potential Scale Reduction Factor (PSRF) diagnostic. Burn-in was performed discarding the first 5000 trees of each run for both Datasets 1 and 3 and a majority-rule consensus tree was generated from the remaining trees.

Maximum Likeliohood analyses of both Datasets 1 and 3 were performed in RAxML v.7.0.3 (Stamatakis 2006). A GTR+I+G model was used and, in Dataset 1, parameters were estimated independently for each partition. Reliability of the ML tree was assessed by bootstrap analysis (Felsenstein 1985) including 1000 replications. Nodes were considered strongly supported if they received ML bootstrap values ≥ 70% and posterior probability (pp) support values ≥ 0.95 (Huelsenbeck & Rannala 2004; Wilcox *et al.* 2002)

Haplotype networks were constructed for the three nuclear markers: c-*mos*, *mc1r* and *rag2* using phased haplotypes (see above) with TCS v.1.21 (Clement *et al.* 2000), applying default settings (probability of parsimony cut-off: 95%).

Estimation of divergence times

The lack of internal calibration points in *Hemidactylus* precluded the direct estimation of the time of the cladogenetic events in our phylogeny. Alternatively, the substitution rate of the same mitochondrial region calculated for other lizard groups could be used for this purpose. Mean substitution rates and their standard errors for the same *12S* and *cytb* gene regions used in the present study were extracted from fully-calibrated phylogenies of various lizard groups from the Canary islands: *Tarentola* sp. (Gekkonidae) (Carranza *et al.* 2000, 2002), *Gallotia* sp. (Lacertidae) (Cox *et al.* 2010), and *Chalcides* sp. (Scincidae) (Brown & Pestano 1998; Brown & Yang 2010; Carranza *et al.* 2008a).

As explained in (Cox *et al.* 2010), the Canary Islands are excellent to calibrate phylogenies as their geological history and island ages are very well known. All seven major islands have independent origins and tend to be older in the East and relatively recent in the West (Appendix II). The oldest islands are Fuerteventura and Lanzarote, with the origin of subaerial rocks being dated at 20.4–20.6 million years ago (mya) (Carracedo *et al.* 1998; Coello *et al.* 1992). The central island of Gran Canaria appeared 14.5 mya (Carracedo *et al.* 1998). In the West, some parts of Tenerife emerged approximately 11.6 mya (Ancochea *et al.* 1990; Guillou *et al.* 2004) and the island of La Gomera about 10.5 mya (Ancochea *et al.* 2006). Other parts of currently Tenerife appeared 6.5 mya (Anaga) and 7.4 mya (Teno) (Guillou *et al.* 2004). The two most recently emerged islands are in the Western extreme of the archipelago. La Palma appeared 1.77 mya (Guillou *et al.* 2001) while the oldest subaerial rocks on El Hierro have been dated at 1.12 mya (Guillou *et al.* 1996). Previous phylogenies all suggest a general East–West pattern of colonization as might be predicted from these ages. El Hierro was the last islands to be colonized by *Gallotia* and other lizards (Brown & Pestano 1998; Carranza *et al.* 2002) and bats (Pestano *et al.* 2003) also appear to have colonized El Hierro soon after its appearance.

To infer the evolutionary rates of lacertid lizards, apart from the Canary Islands endemic *Gallotia*, we used other taxa and a second biogeographical event. This was the end of the Messinian Salinity Crisis (MSC) that occurred 5.3 mya. Approximately 5.59 mya, tectonic uplift of more than 1000 m along the African and Iberian continental margins formed the Gibraltar arch producing a land bridge. This closed the two marine gateways between the Atlantic Ocean and the Mediterranean Sea that existed in the Miocene (Duggen *et al.* 2003) and isolated the Mediterranean. Without input from the Atlantic Ocean, its surface level dropped by over 1000 m, perhaps in less than 1000 years (Blondel & Aronson 1999; Hsü *et al.* 1977, 1973; Krijgsman *et al.* 1999). The fall desiccated large areas of the Mediterranean Sea bed, which were subsequently partly covered with freshwater sediments brought in by rivers. The end of the MSC at 5.3 mya was caused by the collapse of the Gibraltar arch, which opened the Strait of Gibraltar. This allowed the entire Mediterranean basin to fill again in less than 100 years (Blondel & Aronson 1999; Hsü *et al.* 1977, 1973; Krijgsman *et al.* 1999) and broke the land connection, which had existed for nearly 300000 years. This event is very well known and has been associated with speciation in several other reptile and amphibian groups (Carranza *et al.* 2008b; Carranza & Wade 2004; Escoriza *et al.* 2006; see

Pleguezuelos *et al.* 2008 for a review). According to Brown *et al.* (2008); the opening of the Gibraltar Strait acted as a vicariant event, giving rise to the two endemic lizards of the Balearic Islands: *Podarcis lilfordii* in the Gymnesic Islands (Mallorca, Menorca and surrounding islets) and *P. pityusensis* in the Pityusic Islands (Ibiza, Formentera and surrounding islets).

Comprehensive mtDNA datasets were assembled for each one of the three non-introduced reptile groups present in the Canary Islands (with the lacertids including also *P. lilfordii* and *P. pityusensis* from the Balearic Islands). Evolutionary rates for exactly the same *12S* and *cytb* mtDNA regions used in the present work were calculated with BEAST v.1.6.1 (Drummond & Rambaut 2007). All analyses used calibrations from the biogeographical events described above (island ages and/or the end of the MSC; see Appendix II). Island ages represent times of earliest possible colonization of the islands and so were specified as maximal node age constraints (Cox *et al.* 2010). To implement this in BEAST, we used uniform priors from 0 to the time of emergence of the island. A minimal node age of 1 mya was also used to constrain the "El Hierro-La Gomera" node. A previous study indicate that reptiles have been present on El Hierro for substantial proportions of their post-emergence periods (Thorpe *et al.* 1994). Application of this rather arbitrary minimal constraint therefore avoided proposal states with unrealistically recent node ages (Brown & Yang 2010; Cox *et al.* 2010). The split between *P. lilfordii* and *P. pityusensis* as a result of the end of the MSC 5.3 mya was implemented in BEAST using a Normal prior: mean 5.25; Standard Deviation 0.03.

These values were used as informative priors in the three independent calibration analyses of *Gallotia, Tarentola* and *Chalcides* (Appendix II). From the results of these analyses we extracted the meanRate posterior (mean and standard error) for each mtDNA partition and for each one of the tree reptile taxa using Tracer v. 1.5 (Rambaut & Drummond 2007). The values of the meanRate posteriors of all three reptile taxa were combined resulting in a single value for the *12S*: 0.00755 ± 0.00247 and *cytb*: 0.0228 ± 0.00806 mtDNA regions (see Appendix II).

The combined values of the meanRate posteriors were used to calibrate our *Hemidactylus* phylogeny. 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 and standard error) (0.00755 ± 0.00247 for the *12S* and 0.0228 ± 0.00806 for the *cytb*). We used BEAST to estimate dates of the cladogenetic events from the concatenated dataset. The dataset comprised sequences from all seven partitions (the nuclear genes c-*mos*, *mc1r* and *rag2* unphased) but, 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 (30 specimens in total; see Table 1). This method excludes closely related terminal taxa because the Yule tree prior (see below) does not include a model of coalescence, which can complicate rate estimation for closely related sequences (Ho *et al.* 2005). Analyses were run four times for $5x10^7$ generations with a sampling frequency of 10000. Models and prior specifications applied were as follows (otherwise by default): GTR+I+G (*12S*, *cytb*), TrN+I+G (*nd4*, *mc1r*), TrN+I (*tRNAs*), TrN+G (c-*mos*), GTR+G (*rag2*); Relaxed Uncorrelated Lognormal Clock (estimate); 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).

RESULTS AND DISCUSSION

The results of the molecular (Figs. 5–8; Appendix III; see also Table 1) and morphological (Appendix I) analyses confirm the presence of seven new species of *Hemidactylus* geckos in Arabia. One more species is recognized on the basis of morphology alone.

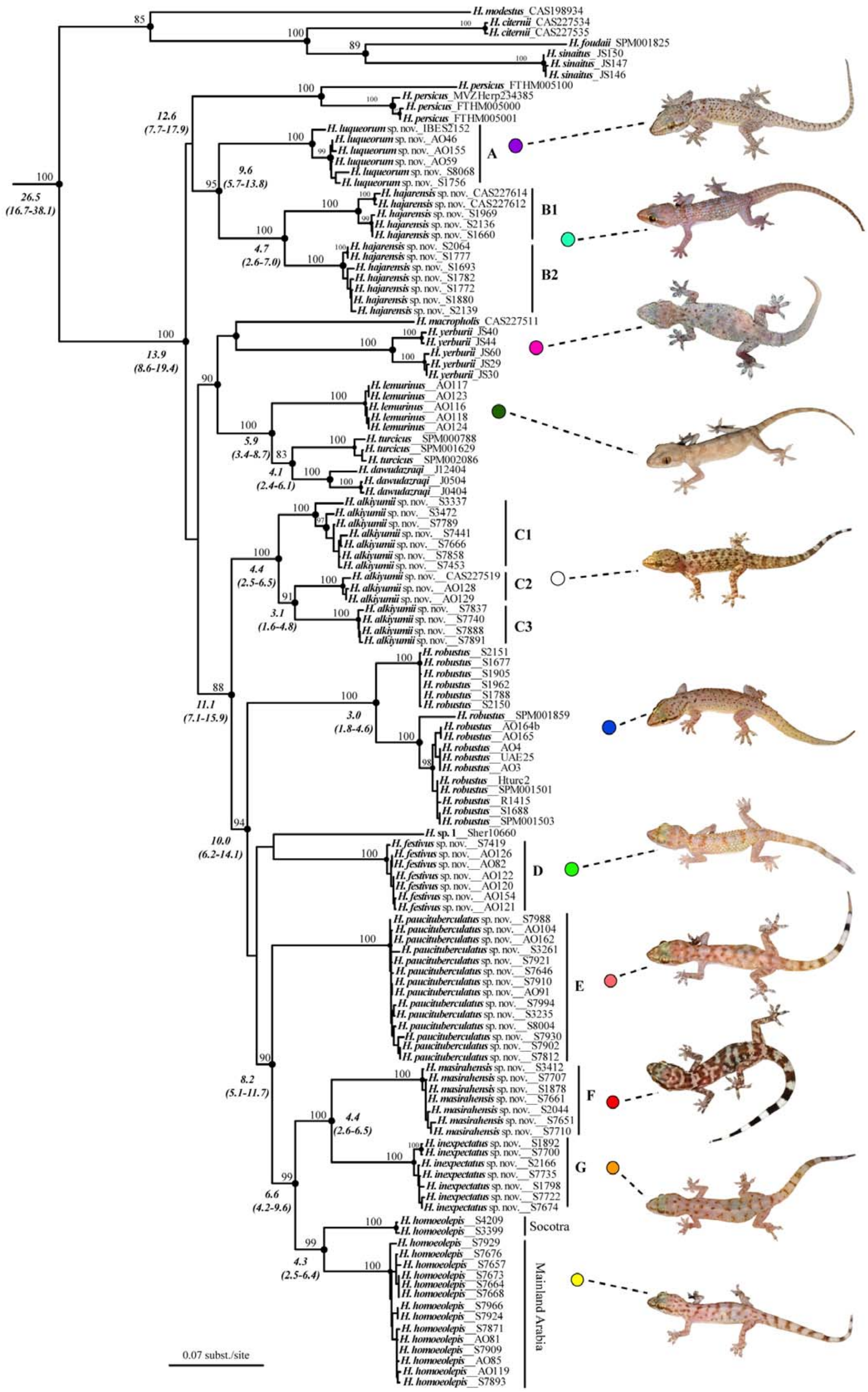

FIGURE 5. Maximum likelihood (ML) phylogenetic tree of 131 *Hemidactylus* specimens of the Arid clade (Carranza & Arnold, 2006) based on 2866 bp of concatenated sequences of four mitochondrial (*12S*, *cyb*, *nd4* and *tRNAs*) and three nuclear (c-*mos*, *mc1r* and *rag2*) genes. Two specimens of *H. flaviviridis* were used to root the tree and have not been included in the figure. Tree topology and branch lengths are for the sampled tree with the highest likelihood by RaxML (100 searches, log likelihood = -20540.526926). Each sequence is labeled with the specimen code and taxa name (see Table 1). Maximum-likelihood bootstrap support values above 70% are indicated above branches and black dots by the nodes indicate a posterior probability value ≥ 0.95 in the Bayesian analysis. Age estimates inferred with BEAST are indicated in italics below some relevant nodes and include the mean and, between brackets, the HPD 95% confidence interval. Silhouettes of *Hemidactylus* taxa are not size-scaled.

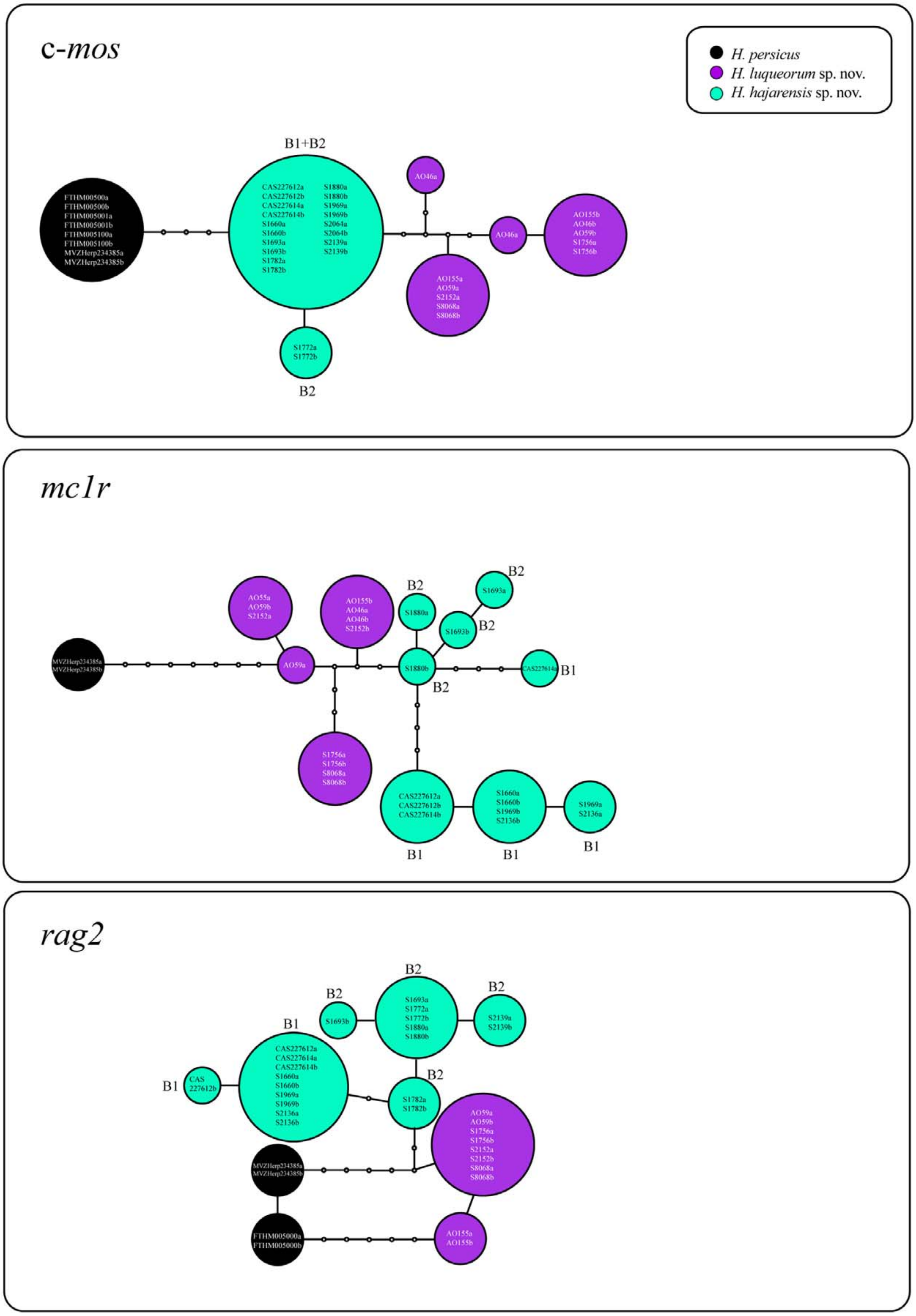

FIGURE 6. Statistical parsimony nuclear allele networks of c-*mos*, *mc1r* and *rag2* loci with colors corresponding to species *H. persicus*, *H. luqueorum* sp. nov. and *H. hajarensis* sp. nov.. Circle sizes are proportional to the number of alleles. White circles represent mutational steps. B1 and B2 refer to the different genetic lineages found within *H. hajarensis* (see Fig. 5 and Appendix III).

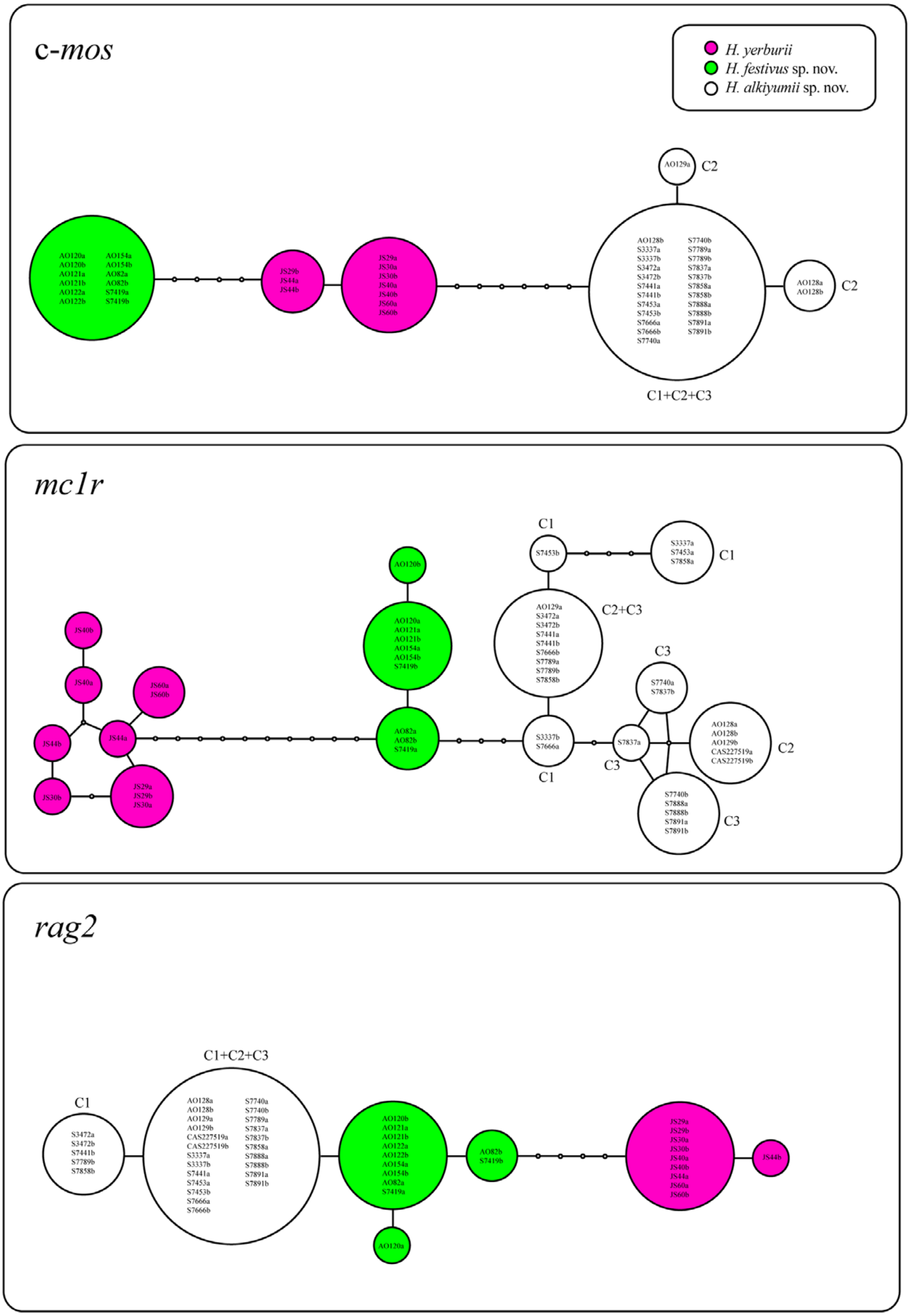

FIGURE 7. Statistical parsimony nuclear allele networks of c-*mos*, *mc1r* and *rag2* loci with colors corresponding to species *H. yerburii*, *H. festivus* sp. nov. and *H. alkiyumii* sp. nov.. Circle sizes are proportional to the number of alleles. White circles represent mutational steps. C1, C2 and C3 refer to the different genetic lineages found within *H. alkiyumii* (see Fig. 5 and Appendix III).

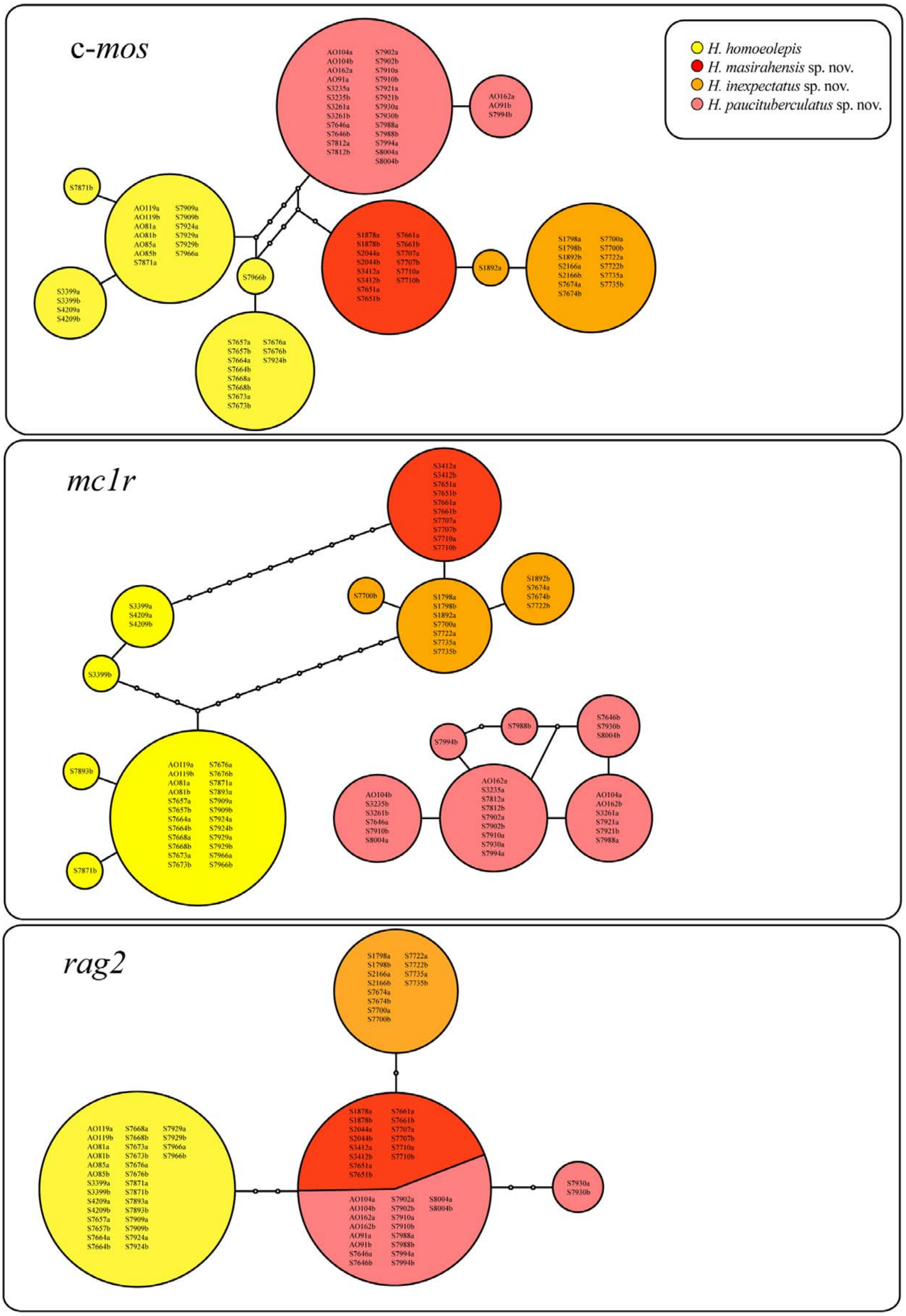

FIGURE 8. Statistical parsimony nuclear allele networks of c-*mos*, *mc1r* and *rag2* loci with colors corresponding to species *H. homoeolepis*, *H. masirahensis* sp. nov., *H. inexpectatus* sp. nov. and *H. paucituberculatus* sp. nov.. Circle sizes are proportional to the number of alleles.

Systematics

Family **Gekkonidae** Oppel, 1811

Genus ***Hemidactylus*** Oken, 1817

Hemidactylus persicus and similar species

The type locality of *Hemidactylus persicus* was restricted to Shiraz, Persia (=Iran) by Smith (1935). Morphologically typical animals occur in Northeast Saudi Arabia (as far South as AI-Hufof and perhaps ar-Riyadh), in Bahrain, Kuwait, and lowland Iraq, Southern Iran, Pakistan and Gujarat (India) (Anderson 1999; Leviton *et al.* 1992; Minton 1966; Sindaco & Jeremcenko 2008; Smith 1935; Vyas *et al.* 2006). They are characterized by relatively small size (up to 67 mm SVL), a low number of lamellae under the 1st toe of pes (mean 8.8, 8–9) and relatively numerous preanal pores in males (mean 9.2, 8–11) arranged in a V-shaped line in front of the vent (Appendix I). Other animals that have been assigned to *H. persicus* occur in isolation in the Jebel Akhdar region of North Oman (Arnold 1977, 1986; Arnold & Gallagher 1977; see Figs. 1 and 2) and have recently been found in the adjoining mountains of the Eastern Hajars as far South as Jebel Qahwan. Morphology (Appendix I; Figs. 9–10, and 12), phylogenetic analysis of Dataset 1 (Fig. 5) and Dataset 3 (*12S* only; Appendix III) nuclear networks of three independent loci (*c-mos*, *mc1r* and *rag2*) (Fig. 6) indicate that there are two new species endemic to the Hajar Mountains in North Oman. These two new species are distinct both from each other and from typical *H. persicus*, and occur within 10–15 km of each other on the Jebel Akhdar. One is especially large and confined to the Jebel Akhdar area, while the other occurs here and in the Eastern Hajars, populations in the two areas of its distribution exhibiting marked genetic divergence (Fig. 5B1 and B2; Appendix IIIB1 and B2). These species are described below.

Hemidactylus luqueorum sp. nov.

(Figs. 2, 5A, 6, 9–11; Table 1; Appendix I; Appendix IIIA)
MorphoBank M94288–M94372 M94378–M94393 M100049–M100093

Hemidactylus persicus Arnold and Gallagher, 1977: 65; Arnold, 1977: 102; Arnold, 1986: 419; Leviton, Anderson, Adler and Minton, 1992: 38 (part.); van der Kooij, 2000: 112 (part.); Sindaco and Jeremcenko, 2008: 115 (part.).

Holotype

BMNH2005.1660, male from Sayq, 1961 m, Jebel Akhdar (North Oman), 23.07639'N 57.62861'E WGS84, collected in October 2005 by S. Carranza, E.N. Arnold and D. Donaire (MorphoBank M94288–M94303). **Paratypes**: BMNH1971.41, female from Wadi Sayq, 1900 m, Jebel Akhdar (North Oman), collected by M.D. Gallagher (MorphoBank M94304–M94312); BMNH1980.558, male from Wadi Sayq, 1900 m, Jebel Akhdar (North Oman), collected by M.D. Gallagher (MorphoBank M94313–M94350); BMNH1975.916, female from Birkat Sahfan, Jebel Akhdar (Oman), collected by D.L. Harrison (MorphoBank M94378–M94384). BMNH2005.1661, juvenile from Sayq, 1961 m, Jebel Akhdar (North Oman), 23.07639'N 57.62861'E WGS84, collected in October 2005 by S. Carranza, E.N. Arnold and D. Donaire; BMNH2005.1658, female from Wadi Bani Habib, 2200 m, Jebel Akhdar (North Oman), 23.0711'N 57.60417'E WGS84, collected in October 2005 by S. Carranza, E.N. Arnold and D. Donaire (MorphoBank M94363–M94372); BMNH2005.1659, female from Wadi Bani Habib, 2200 m, Jebel Akhdar (North Oman), 23.0711'N 57.60417'E WGS84, collected in October 2005 by S. Carranza, E.N. Arnold and D. Donaire (MorphoBank M94363–M94372); IBES8068, female from Wadi al Khahafa, 492 m, Jebel Akhdar (North Oman), 23.07419'N 57.12208'E WGS84, collected on the 10th of October 2010 by S. Carranza and F. Amat (MorphoBank M100056–M100064); IBES7771, female from 1 km East of Hat, 1124 m, Jebel Akhdar (North Oman), 23.18292'N 57.41627'E WGS84, collected by S. Carranza, E. Gómez-Díaz and F. Amat on the 9th of May 2011 (MorphoBank M100065–M100073); IBES6085, female, same collecting data as IBES7771 (MorphoBank M100083–M00093); ONHM3705, female from Wadi Bani Habib, 2200 m, Jebel

Akhdar (North Oman), 23.0711’N 57.60417’E WGS84, collected in October 2005 by S. Carranza, E.N. Arnold and D. Donaire (MorphoBank M94363–M94372).

Other material examined

Two vouchers listed in Appendix I under *H. luqueorum* sp. nov. and not mentioned above. Two unvouchered specimens (tissue codes S6080 and S7843) included in the molecular analyses only (Table 1).

Diagnosis

A large-sized *Hemidactylus* with a maximum recorded SVL of 88 mm; with a mean of 14.2 (13–15) longitudinal rows of enlarged dorsal tubercles at mid-body; adhesive pads broad, in adults maximum width of pad on fourth toe of the pes more than half its length; lamellae under the 1st toe of pes mean 10.3 (10–11); lamellae under the 4th toe of pes mean 13.6 (13–14); preanal pores mean 5.3 (5–6); expanded subcaudal scales extending proximally as far as the second whorl after the vent and starting just after the hemipenial bulge in males; dorsum grey–buff with irregular small spots; a dark stripe from the nostril, through the eye, on to cheek above ear and often on to neck; tail with small irregular dark blotches basally and numerous transverse dark bands more distally, the total number being around 17. Underside of tail pale but large subcaudals suffused with grey formed by dark chromatophores that increase in intensity distally; underside of toe pads also grey.

Hemidactylus luqueorum is generally similar to *H. persicus* in number of its moderately-sized dorsal tubercles across mid-body, and large adhesive pads on toes but differs from it in its much larger size (SVL mean 76.8 mm, max. 88 mm, compared with mean. 56.4 mm, max. 67 mm), reduced number of preanal pores in males (mean 5.3, 5–6, compared with mean 9.2, 8–11), and presence of more lamellae under the first toe of pes (mean 10.3, 10–11, compared with mean 8.8, 8–9). For differences from the second North Oman species of *Hemidactylus* see below.

Etymology

The species epithet "*luqueorum*" is a collective genitive plural Latin noun to honour Salvador Carranza’s wife, Maria Teresa Luque, and her family for all their love and support. Without their encouragement and help it would have been impossible to accomplish this work.

Genetic and phylogeographic remarks

Hemidactylus luqueorum is monophyletic in the phylogenetic analyses of Dataset 1 (Fig. 5A) and Dataset 3 (Appendix IIIA). In both phylogenetic trees it forms a clade together with *H. persicus* and the second North Oman species of *Hemidactylus* described below, although the bootstrap support and pp values are very low (see Fig. 5 and Appendix III). According to the results of the dating analysis inferred with Dataset 2, these three species split about 12.6 mya (95% HPD: 7.7–17.9). According to Fig. 5 and Appendix III, *Hemidactylus luqueorum* is more closely related to the second North Oman species of *Hemidacytlus* described below (Fig. 5B, Appendix IIIB), from which it split approximately 9.6 mya (95% HPD: 5.7–13.8). The level of genetic variability within *H. luqueorum* is 2% in the *cytb* and 0.2% in the *12S*. The uncorrected genetic distances between *H. luqueorum* and the second North Oman species of *Hemidactylus* described below are 15.6% in the *cytb* and 6.9% in the *12S*; and between *H. luqueorum* and *H. persicus* are 14.6% in the *cytb* and 9.8% in the *12S*. The results of the nuclear networks presented in Fig 6 and a network analysis including all specimens from Dataset 1 (data not shown) indicate that all alleles of *H. luqueorum* for all three independent loci analyzed (*c-mos*, *mc1r* and *rag2*) are private (not shared with any other species included in the present analyses).

Distribution

Despite intensive surveys across the Hajar Mountain range and especially the Eastern Hajars, *H. luqueorum* has only been found in the Jebel Akhdar, the largest structural domain of the Western Hajar Mountains in North Oman (Figs. 1 and 2). It has been recorded from 492 m altitude (Wadi Al Khahafa) up to 2200 m (Wadi Bani Habib).

Habits

The species occurs on rocky sides of wadis and on buildings and occasionally on gravely wadi floors. Mainly nocturnal, several specimens were active during the day in a narrow wadi 1 km East of Hat (Fig. 11A). According to Arnold and Gallagher (1977), specimens BMNH1971.41 and BMNH1975.916 were caught during the day, one

FIGURE 9. A) male, Holotype of *H. luqueorum* sp. nov. from Sayq, Jebel Akhdar (BMNH2005.1660); B) left: male of *H. luqueorum* Wadi Sayq, Jebel Akhdar (BMNH1980.558); right: female of *H. hajarensis* sp. nov. from Wadi Sabt, Jebel Akhdar (BMNH1977.35); C) above, *H. hajarensis* (BMNH1977.35); below *H. luqueorum* (BMNH1980.558); D) underside of right hind feet; left: *H. luqueorum* (BMNH1980.558), right: *H. hajarensis* (BMNH1977.35).

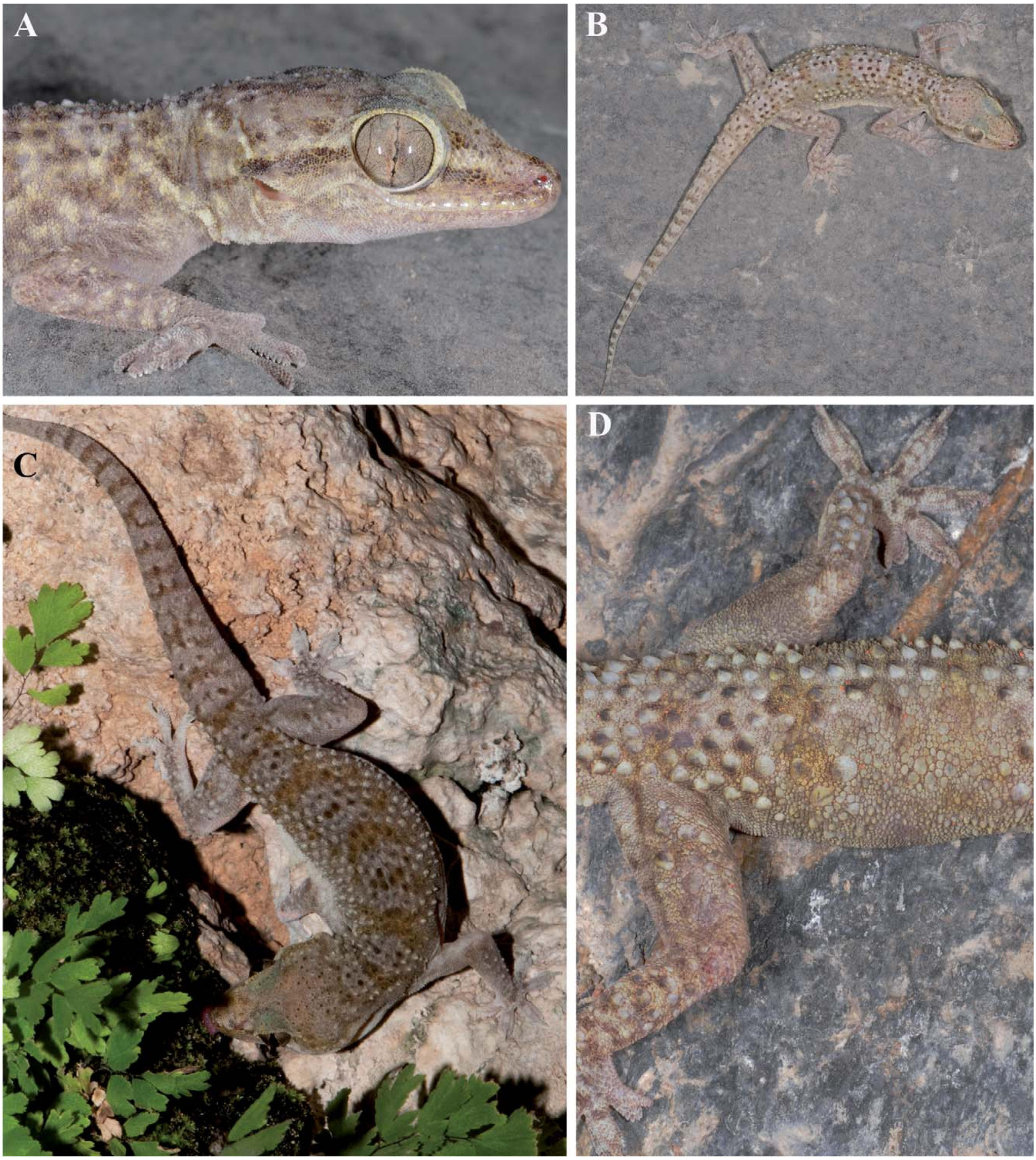

FIGURE 10. Live specimens of *H. luqueorum* sp. nov. A) and B) male from Wadi al Khahafa, Jebel Akhdar (IBES8068); C) unvouchered specimen photographed in its natural habitat in a cave at approximately 1 km E of Hat, Jebel Akhdar (photograph by Felix Amat); D) detail of an area of regenerated skin on the back of an unvouchered specimen, probably as a results of fights with conspecifics or attacks from predators.

on an overhanging rock-face and the other in a shallow cave. It can be locally abundant inside large caves and share habitat with *Asaccus platyrhynchus*. In Wadi Bani Habib, at 2000 m, it has been found together with *Asaccus montanus* and at Wadi al Kahafa, at much lower altitude, it shares habitat with both *A. platyrhynchus* and *Ptyodactylus hasselquistii*. It moves relatively slowly and is quite confident, sometimes allowing one to approach quite closely to take pictures. It losses the skin very easily when being handled and sometimes specimens have large scars of regenerated skin on the back, probably as a results of fights with conspecifics or attacks from predators (Fig. 10D).

Description

Head and body markedly depressed; head broad, especially posteriorly and neck well defined. Head length about 24–28% of SVL (mean males 25%, mean females 26%), head width 70–78% of head length (mean males 75%, mean females 74%), and head height 36–51% of head length (mean males 46%, mean females 44%). Adhesive pads broad; in adults maximum width of pad on fourth hind toe more than half its length.

Nostril between rostral, supranasal and two superposed postnasals, with the first supralabial scale usually also entering narrowly into its border. One, occasionally 2 scales separating supranasals on midline. About 14–19 scales in a straight line from postnasal to edge of orbit. Small conical tubercles scattered in orbital area, crown of head and temporal area above the level of ear opening and immediately in front of the upper part of this. Ear opening with its longest axis running upwards and backwards, smooth-edged, usually half or more of eye diameter. Supralabial scales mean 11.8 (10–14), infralabials mean 9.1 (8–10). Mental scale broadly triangular posteriorly bordered by two large postmentals making contact behind it, a second pair of more lateral postmentals also present, all four with a smooth transverse posterior border, the postmentals contacting the first and second supralabials; second and more posterior infralabials bordered by more irregular and smaller enlarged scales. Gulars fine.

Enlarged tubercles present on back, arranged in 14.2 (mean) (13–15) longitudinal rows at mid-body, which also form backwardly directed oblique rows from near midline to flank, 12–16 across mid-body, and 16–18 in a paravertebral row from the level of the axilla to that of the groin, where they are separated by spaces of about their own length. Enlarged tubercles keeled and trihedral but becoming smaller and more pointed on flanks. Ventrals small, but larger than dorsals and more imbricate, about 48–50 in a transverse row at mid body between lateral folds. Males with 5–6 preanal pores (mean 5.3) separated by one or two scales giving a formula of 2+3, 3+2 or 3+3. Scales on upper forelimb small and imbricate, interspersed with enlarged tubercles on distal section. Scales on front of thigh and beneath about same size as belly scales and imbricate, rather larger under tibia, enlarged tubercles present on upper surface of both femur and tibia and also on posterior edge of foot. Lamellae under the toes of pes: 1st toe mean 10.3 (10–11); 4th toe mean 13.6 (13–14).

Tail relatively slender, although sometimes thickened proximally; six enlarged, keeled and pointed tubercles on each whorl proximally, dropping to four around whorl 8 or 10. Tubercles about one third the length of basal whorls, becoming smaller and placed more posteriorly on whorls distally. About 10–11 small scales in longitudinal row on fourth whorl after vent, around seven small scales between tubercles on fourth and fifth whorls. Subcaudal scales enlarged and broad, extending proximally as far as the second whorl after the vent and starting just after the hemipenial bulge in males.

In spirit pale grey-buff; a dark stripe from the nostril, through the eye, on to cheek above ear and often on to neck; body with irregular small spots; some tubercles on forebody and vertebral area have opaque white coloring on one side and dark coloring on the other. Belly pale but there may be a slight stipple at the sides, the dark punctate spots being smaller than the scales. Tail with small irregular dark blotches basally and numerous transverse dark bands more distally, initially on every other whorl and then on each one, the total number being around 17. Underside of tail pale but large subcaudals suffused with grey formed by dark chromatophores that increase in intensity distally. Underside of toe pads also grey.

Distinctive features of Holotype

Male, 80.4 mm SVL; tail truncated, 59 mm long. Supralabial scales 13/12; infralabials 9/9; 15 rows of enlarged tubercles at mid-back; 6 (3+3) preanal pores; lamellae under the 1st toe of pes 10/11, 4th toe of pes 14/13.

FIGURE 11. Different localities where *H. luqueorum* sp. nov. has been found A) 1 km E of Hat, Jebel Akhdar. In this locality *H. luqueorum* was found out during the day close to crevices and in small caves on the large boulders at the sides of the narrow Wadi; B) Wadi Bani Habib, Jebel Akhdar. In this locality *H. luqueorum* was found at night in man made constructions and on boulders; C) Wadi al Khahafa, Jebel Akhdar, where two specimens of *H. luqueorum* have been found at just 492 m altitude on the rocky sides of the wadi.

***Hemidactylus hajarensis* sp. nov.**

(Figs. 2, 5B, 6, 9B–D, 12–13; Table 1; Appendix I; Appendix IIIB)

MorphoBank M94393–M94415 M94459–M94465 M94515–M94542 M94558–M94586 M94630–M94643 M94649–M94664 M94666–M94684 M94700–M94721 M99874–M99917 M99921–M99937 M99954–M99993

Hemidactylus persicus Arnold, 1986: 419; Leviton, Anderson, Adler and Minton, 1992: 38 (part.); van der Kooij, 2000: 112 (part.); Carranza and Arnold, 2006: 536; Sindaco and Jeremcenko, 2008: 115 (part.).

Holotype

BMNH2008.714, male from Wadi Bani Khalid, 647 m, Eastern Hajar (North Oman), 22.61609'N 59.09371'E WGS84, collected in May 2011 by S. Carranza, E. Gómez-Díaz and F. Amat (MorphoBank M99903–M99917; Fig. 12D). **Paratypes**: ONHM3706, male, same collecting data as Holotype (MorphoBank M99885–M99893); IBES7335, male, same collecting data as Holotype (MorphoBank M99894–M99902; Fig. 11D); IBES7336, female, same collecting data as Holotype (MorphoBank M99969–M99976).

Other material examined

Eighteen vouchers listed in Appendix I under *H. hajarensis* sp. nov. and not mentioned above. Specimens CAS227612, CAS227614, BMNH2008.705 (juvenile) and samples JS65, JS81, JS98 JS99, S7321, and S6061 were included in the molecular analyses only (Table 1).

Diagnosis

A medium-sized *Hemidactylus* with a maximum recorded SVL of 66.9 mm; with a mean of 14.2 (13–15) longitudinal rows of enlarged dorsal tubercles at mid-body; adhesive pads fairly broad, in adults maximum width of pad on the fourth toe about 0.4–0.5 of its length; lamellae under the 1st toe of pes mean 8.0 (7–9); lamellae under the 4th toe of pes mean 12.1 (11–14); preanal pores mean 5.5 (4–6); expanded subcaudal scales extending proximally as far as the second or third whorl after the vent and starting just after the hemipenial bulge in males; dorsum grey-buff with irregular small spots; a dark stripe from the nostril, through the eye, on to cheek above ear and often on to neck; tail with small irregular dark blotches basally and numerous transverse dark bands more distally, the total number being around 17. Underside of tail pale but large subcaudals may be suffused with grey formed by dark chromatophores that increase in intensity distally; underside of toe pads also grey.

Hemidactylus hajarensis is generally similar to *H. persicus* in the number of its moderately-sized dorsal tubercles across mid-body, and large adhesive pads on toes but differs from it in its reduced number of preanal pores in males (mean 5.5, 4–6, compared with mean 9.2, 8–11). *Hemidactylus hajarensis* differs from *H. luqueorum* sp. nov. in its smaller size (SVL mean 54 mm, max. 66.9 mm, compared with mean. 76.8 mm, max. 88 mm), and in having fewer lamellae under the 1st toe of pes (mean 8.0, 7–9, compared with mean 10.3, 10–11), and under the 4th toe of pes (mean 12.1, 11–14, compared with mean 13.6, 13–14)

Etymology

The species epithet "*hajarensis*" is an adjective that refers to the mountain range where the species is found, the Hajar Mountains.

Genetic and phylogeographic remarks

Hemidactylus hajarensis is monophyletic in the phylogenetic analyses of Dataset 1 (Fig. 5B) and Dataset 3 (Appendix IIIB). In both phylogenetic trees it forms a clade together with *H. persicus* and *H. luqueorum* sp. nov., although bootstrap support and pp values are very low (see Fig. 5 and Appendix III). According to the results of the dating analysis inferred with Dataset 2, these three species split about 12.6 mya (95% HPD: 7.7–17.9). According to Fig. 5 and Appendix III, *H. hajarensis* is more closely related to *H. luqueorum* (Fig. 5B, Appendix IIIB), from which it split approximately 9.6 mya (95% HPD: 5.7–13.8). The level of genetic variability within *H. hajarensis* is very high, 6.1% in the *cytb* and 2.6% in the *12S*. As shown in Fig. 5B and Appendix IIIB, *H. hajarensis* consists of two very well differentiated and well-supported clades, B1 and B2. The uncorrected genetic distances between these two clades are 10.5% in the *cytb* and 5% in the *12S*. As shown in Fig. 2, the geographical limits between clades B1 and B2 are not very clear, being clade B1 present in the Jebel Akhdar and in the coastal areas close to

FIGURE 12. Live specimens of *H. hajarensis* sp. nov. A) male from Wadi Tanuf (IBES7151); B) male from Wadi Bani Khalid (IBES7335); C) female from Wadi Tanuf (IBES8064); D) male, Holotype, from Wadi Bani Khalid (BMNH2008.714); E) same specimen as in B.

Muscat (Wadi Mayh, Jebel Abu Daud and a wadi North of Qurayyat), while clade B2 seems restricted to the Eastern Hajars. According to the calibrations, clades B1 and B2 split approximately 4.7 mya (95% HPD: 2.6–7.0). The uncorrected genetic distances between *H. hajarensis* and *H. luqueorum* are 15.6% in the *cytb* and 6.9% in the *12S*; and between *H. hajarensis* and *H. persicus* 15.1% in the *cytb* and 10.7% in the *12S*. The results of the nuclear networks presented in Fig 6 and a network analysis including all specimens from Dataset 1 (data not shown) indicate that all alleles of *H. hajarensis* for all three independent loci analyzed (c-*mos*, *mc1r* and *rag2*) are private (not shared with any other species included in the present analyses). It is also interesting to notice that, although clades B1 and B2 share alleles of the c-*mos* gene, specimens of these two clades do not share a single allele of the *mc1r* and *rag2* nuclear genes. The high genetic differentiation between clades B1 and B2 of *H. hajarensis* suggests long separation of the two units. However, the absence of clear morphological differences between these two clades and the relatively low number of available vouchers to carry out a thorough morphological analysis prevents us from taking any taxonomic decisions at present. Future studies should clarify the taxonomic status of these two clades (work in progress).

Distribution

The species is widespread in the mountains of North Oman from the Jebel Akhdar to the East. Despite intensive surveys across the Hajar Mountain range, it has never been found to the West of the Jebel Akhdar, in the Western Hajars or in the Musandam Peninsula. Several localities exist for the coastal wadis near Muscat and the Eastern Hajars, from Jebel Al Abyad in the West to Jebel Qahwan in the extreme East. Across its distribution range it has been recorded from almost sea level (22 m in Wadi Mayh) up to 1683 m in a locality 9 km North of Al Chayan (Table 1).

Habits

Hemidactylus hajarensis has been found at sides of wadis low on rocks that were interspersed and sometimes partly overhung with vegetation. The species was also sometimes seen on gravel floors of wadis (Fig. 13). Strictly nocturnal, it has never been recorded during the day. *H. hajarensis* moves quickly and is very agile, fleeing to a nearby refuge seconds after being spotted. In Wadi Tiwi and Wadi Hebaheba, *H. hajarensis* occurs also low on rocks. As *H. luqueorum*, it losses the skin very easily when being handled and sometimes specimens have scars of regenerated skin on the back, probably as a results of fights with conspecifics or attacks from predators (Fig. 12D). This species has never been found in sympatry with *H. luqueorum*, however, it shares habitat with *Asaccus platyrhynchus* and *Ptyodactylus hasselquistii*.

Description

Head and body markedly depressed. Head breadth variable and neck well defined. Head length about 24–31% of SVL (mean males 28%, mean females 27%), head width 65–85% of head length (mean males 71%, mean females 72%), and head height 36–55% of head length (mean males and females 42%). Adhesive pads fairly broad; in adults maximum width of pad on fourth hind toe about 0.4–0.5 of its length.

Nostril between rostral, supranasal and two superposed postnasals, with the first supralabial scale usually also entering narrowly into its border. Usually one scale separating supranasals on midline. About 14–18 scales in a straight line from postnasal to edge of orbit. Small conical tubercles scattered in orbital area, crown of head and temporal area above the level of ear opening and immediately in front of the upper part of this. Ear opening with its longest axis running upwards and backwards, smooth-edged, usually about half or more of eye diameter. Supralabial scales mean 10.7 (9–12), infralabials mean 8.8 (7–10). Mental scale broadly triangular posteriorly bordered by two large postmentals making contact behind it, a second pair of more lateral postmentals also present, the postmentals contacting the first and second supralabials; second and more posterior lower labials bordered by more irregular and smaller enlarged scales. Gulars fine.

Enlarged tubercles present on back, arranged in 14.2 (mean) (13–15) longitudinal rows at mid-body, which also form backwardly directed oblique rows from near midline to flank, and 16–18 in a paravertebral row from the level of the axilla to that of the groin, where they are separated by spaces of about their own length. Enlarged tubercles strongly keeled and trihedral but becoming smaller and more conical on flanks. Ventrals small, but larger than dorsals and more imbricate, about 34–43 in a transverse row at mid body between lateral folds. Males with 4–6 preanal pores (mean 5.5) separated by one or two scales giving a formula of 2+2 or 3+3. Scales on upper forelimb

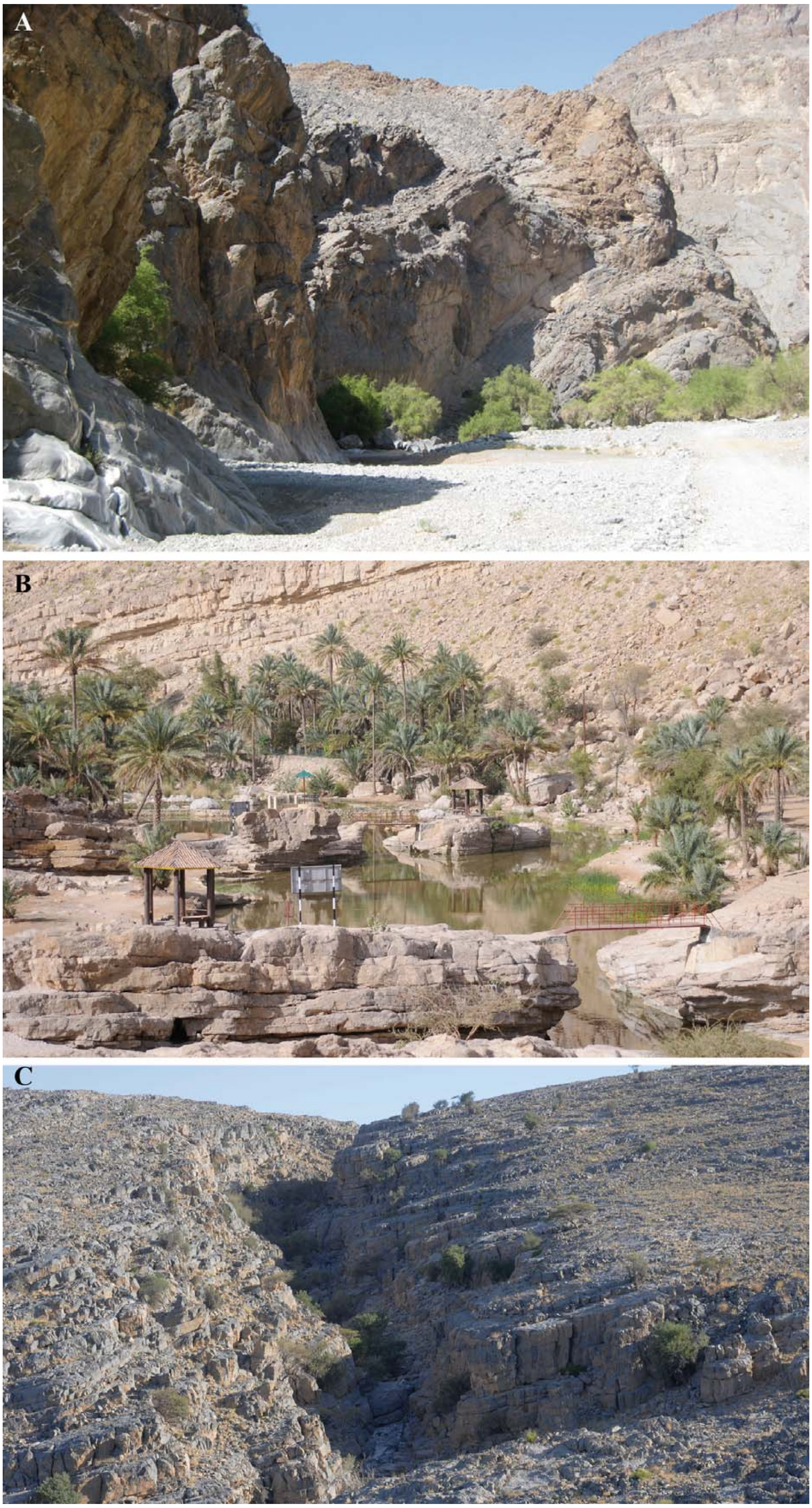

FIGURE 13. Different localities where *H. hajarensis* sp. nov. has been found A) Wadi Tanuf, Jebel Akhdar. In this locality *H. hajarensis* has been found in several occasion during the night on the rocky sides of the wadi; B) Wadi Bani Khalid, Eastern Hajar Mountains, where *H. hajarensis* was found at night on the ground and on boulders; D) 9 km N of Al Chayan, in the Eastern Hajar Mountains, where *H. hajarensis* was relatively abundant and several specimens were found on the rocky substrate and on boulders and rocky sides of the small wadis.

small and imbricate, interspersed with enlarged tubercles on distal section. Scales on front of thigh and beneath hind leg about same size as belly scales and imbricate, enlarged tubercles present on upper surface of both femur and tibia. Lamellae under the toes of pes: 1st toe mean 8.0 (7–9), 4th toe mean 12.1 (11–14).

Tail relatively slender; between eight and six enlarged, keeled and pointed tubercles on each whorl on tail base, dropping to four from about 4–10th whorl after vent. Tubercles about one third the length of basal whorls, becoming smaller and placed more posteriorly on whorls distally. Subcaudal scales enlarged and broad, extending proximally as far as the second or third whorl after the vent and the starting just after the hemipenial bulge in males.

In spirit pale grey-buff; a dark stripe from the nostril, through the eye, on to cheek above ear and often on to neck; body with irregular small spots; some tubercles on forebody and vertebral area have opaque white coloring on one side and dark coloring on the other. Belly pale but there may be a very fine slight stipple at the sides, the dark punctuate spots being much smaller than the scales. Tail with small irregular dark blotches basally and numerous irregular dark bands more distally, the total number being around 17. Underside of tail pale but large subcaudals may be suffused in some places with grey formed by dark chromatophores that increase in intensity distally. Underside of toe pads also grey. In life, animals from many localities have dark blotches or bars on the upper surface that are suffused yellow-orange.

Distinctive features of Holotype

Male, 59.8 mm SVL; tail missing from the base. Supralabial scales 10/10; infralabials 9/9; 14 rows of enlarged tubercles at mid-back; 6 (3+3) preanal pores; lamellae under the 1st toe of pes 8/8, 4th toe of pes 12/12.

Hemidactylus yerburii **and similar species**

According to Anderson, 1895: 636, the types of *Hemidactylus yerburii* come from “Haithalhim and Laheh” although the types were registered at the British Museum as from Haithalhim (BMNH95.5.23.9) and Aden (BMNH95.5.23.8) (Appendix I). Specimens from the type localities or near the type localities are characterized by relatively small size (SVL mean 63.6 mm, max. 67.6 mm), high number of enlarged tubercles present on back, arranged in 16.7 (mean) (16–17) longitudinal rows at mid-body, a high number of preanal pores in males (mean 12.8, 10–15) in a V-shaped line in front of the vent and the enlarged laterally expanded subcaudal scales often do not begin until 3–6 (average 4.5) tail whorls after the vent.

According to Arnold (1980, 1986), there is a very marked geographical variation among specimens assigned to *H. yerburii*. For instance, the Northernmost populations assigned to *H. yerburyii*, which come from around an-Namas and Sabt Al Alaya in the Northern Asir Mountains (Saudi Arabia) are like Southern Asir animals in having fewer femoral pores (9–11) than typical *H. yerburyii* and in the expanded subcadual scales beginning closer to the vent, being separated from it by 2–4 whorls (average 2.5), (pers. observ.). However, they are distinctive from typical *H. yerburii* in being large (up to 72 mm from snout to vent), and in having dorsal tubercles that are reduced in size and not obviously trihedral, at least on the mid-back. These animals may also sometimes have more dark transverse bars on the intact tail than typical *H. yerburyii*. The taxonomic status of these distinct Saudi Arabian populations of *H. yerburii* is under study.

Morphological variation of Yemeni populations formerly assigned to *H. yerburii* has been recently assessed using both morphological and molecular data by Busais and Joger (2011a,b). The results of these investigations led to the description of one new species: *H. jumailiae*, and one subspecies: *H. yerburii montanus*, endemic to the mountains of Southwest Yemen. Two other species of *Hemidactylus* that externally resemble *H. yerburii* but that are phylogenetically unrelated to it have also been described in the same work: *H. shihraensis* and *H. saba*. Before the studies by Busais and Joger (2011a,b), the only specimen of *H. yerburii* that had been included in a molecular phylogeny was a specimen from Najran, Saudi Arabia (Carranza & Arnold 2006). According to the analysis by Carranza and Arnold (2006), *H. yerburii* branched outside the Arid clade, sister to *H. mabouia*. A closer examination of the mtDNA sequences revealed that the *12S* mtDNA of *H. yerburii* was, in fact, from *H. mabouia*. The *cytb* sequence of *H. yerburii* from Carranza and Arnold (2006) was correct and it has been used in other studies (Moravec *et al.* 2011).

Medium-sized *Hemidactylus* with numerous enlarged dorsal tubercles that occur in the Dhofar area of Southern Oman and neighboring East Yemen have been previously assigned to *H. yerburyii*. However, considerable geographic variation in the populations placed in this species has been noted including differences within Dhofar itself (Arnold 1980, 1986). Morphology (Appendix I; Figs. 14–15, 17–18), phylogenetic analyses of Dataset 1 (Fig. 5) and Dataset 3 (*12S* only; Appendix III), and nuclear networks of three independent loci (c-*mos*, *mc1r* and *rag2*) (Fig. 7) indicate that two species are present in the Dhofar region in Southern Oman and neighboring East Yemen. Although they have been found in sympatry in one locality in East Yemen (Fig. 2), these two species usually differ in habitat.

Hemidactylus alkiyumii **sp. nov.**

(Figs. 2, 5C, 7, 14–16, Table 1; Appendix I; Appendix IIIC)
MorphoBank M95099–M95289 M99609–M99718

Hemidactylus yerburii Arnold, 1977: 101 (part.); Arnold, 1986: 283 (part.); Arnold, 1986: 420 (part.); Schätti and Desvoignes, 1999: 52 (part.); van der Kooij, 2000: 113 (part.); Sindaco and Jeremcenko, 2008: 117 (part.).

Holotype

BMNH2005.1662, male from Tawi Atair, 610 m, Dhofar region (South Oman), 17.11639'N 54.54861'E WGS84, collected in October 2005 by S. Carranza, E.N. Arnold and D. Donaire (MorphoBank M95264–M95275; Fig. 13A). **Paratypes**: ONHM3707, male, same collecting data as Holotype (MorphoBank M95290–M95304); BMNH2005.1663, female, same collecting data as Holotype (MorphoBank M95276–M95289); IBES8078, female from Tawi Atair, 610 m, Dhofar region (South Oman) 17.11639'N 54.54861'E WGS84, collected in October 2010 by S. Carranza and F. Amat (MorphoBank M99654–M99660); IBES8079, female, same collecting data as IBES8078 (MorphoBank M99661–M99667); IBES8080, female, same collecting data as IBES8078 (MorphoBank M99668–M99674).

Other material examined

Twenty-three vouchers listed in Appendix I under *H. alkiyumii* sp. nov. and not mentioned above. Specimen CAS227519, IBES7666, IBES7740 and samples S3337, S3472, S7789, JS2, JS3, JS4, JS7, JS62, JS63, JS64, JS77, JS78, JS79, JS80, JS87, JS88, JS89, JS90, JS91, JS92, JS93, JS94, JS95, JS96, JS97, and S7194 were included in the molecular analyses only (Table 1).

Diagnosis

A medium-sized *Hemidactylus* with a maximum recorded SVL of 74.5 mm; with a mean of 12.9 (11–14) longitudinal rows of dorsal tubercles at mid-body; adhesive pads medium-sized; lamellae under the 1st toe of pes mean 7.0 (6–9); lamellae under the 4th toe of pes mean 10.8 (10–12); preanal pores mean 7.3 (6–10); expanded subcaudal scales usually beginning 1–4 verticils behind vent (average about 2); dorsum somber, sometimes with a pattern of irregular spots or dark transverse crosses with approximately one on neck, three on body and one or two on anterior sacrum (Fig. 15A), not diffused with yellow in life; tubercles on body sometimes with opaque white pigment, which may be on medial side of tubercles while lateral sides are dark; tail not light distally, with pattern of 11–14 dark bands that are not especially widely separated and only extend ventrally towards the tail tip where they are not very conspicuous.

Hemidactylus alkiyumii differs from *H. yerburii* in its larger size (SVL max.74.5 mm, compared with max. 67.6 mm), in having fewer longitudinal rows of dorsal tubercles at mid-body (mean 12.9, 11–14, compared with mean 16.7, 16–17), fewer preanal pores in males (mean 7.3, 6–10, compared with mean 12.8, 10–15), and in having enlarged tubercles on tail that are not spinose. It differs from *H. yerburii montanus*, endemic to the highlands of Yemen, in its larger size (SVL max. 74.5 mm, compared with max. 68 mm), in having higher number of lamellae under the 1st toe of pes (mean. 7.0, 6–9, compared with mean 6.2 in both males and females, 5–7), in having fewer longitudinal rows of dorsal tubercles at mid-body (mean 12.9, 11–14, compared with mean 15.1 in males and 15.4 in females, 14–16), and in having fewer preanal pores in males (mean 7.3, 6–10, compared with mean 10.1). It differs from *H. jumailiae* from Yemen (formerly *H. yerburii*) in its larger size (SVL max. 74.5 mm, compared with max. 47 mm), in having higher number of lamellae under the 1st toe of pes (mean. 7.0, 6–9, compared with mean 6.3, 6–7), and in having large trihedral tubercles present on back (small cycloid tubercles in

H. jumailiae). It differs from *H. shihraensis* from Yemen in its larger size (SVL max. 74.5 mm, compared with max. 48.2 mm), in having higher number of lamellae under the 1st toe of pes (mean 7.0, 6–9, compared with 6), and more preanal pores in males (mean 7.3, 6–10, compared with 6). It differs from *H. saba* in its larger size (SVL max. 74.5 mm, compared with max. 59 mm), in having more preanal pores in males (mean 7.3, 6–10, compared with 6), and more supralabials (mean 10.0, 9–12, compared with 8–9). For differences from the second species of Dhofar *Hemidactylus* see below.

Etymology

The species epithet "*alkiyumii*" is a genitive Latin noun to honor Ali bin Amer Al Kiyumi, Director General of Nature Conservation of the Sultanate of Oman, for his knowledge and interest in the preservation of the biodiversity of Oman and for his help and support towards our ongoing studies on the reptile fauna of Oman.

Genetic and phylogeographic remarks

Hemidactylus alkiyumii is monophyletic in the phylogenetic analyses of Dataset 1 (Fig. 5C) and Dataset 3 (Appendix IIIC). In both trees it is not closely related to any specific taxa. According to Fig. 5, it is sister to a well-

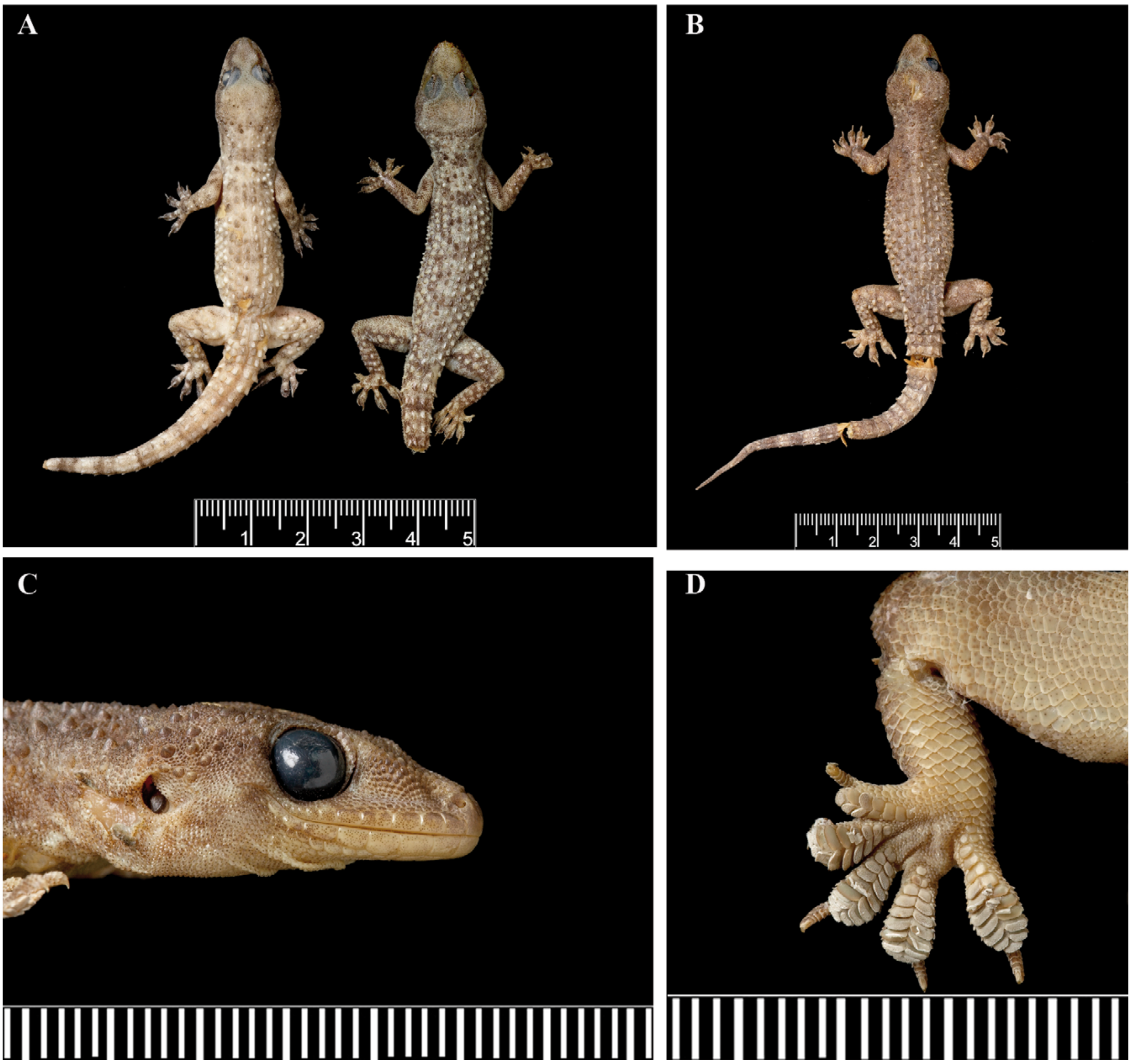

FIGURE 14. Preserved specimens of *H. alkiyumii* sp. nov. A) left: male, Holotype from Tawi Atair, Dhofar (BMNH2005.1662); right: male from Wadi Rubkat, Dhofar (BMNH1977.964); B) male from the Khadrafi Plateau, Dhofar (BMNH1977.972); C) detail of the head of the same specimen as in B; D) detail of the right hind foot of the same specimen as in B.

supported clade formed by *H. robustus*, *H.* sp. 1, lineages D, E, F, G and *H. homoeolepis*. In Appendix III it is also sister to a similar assemblage but in this latter case the sister clade of *H. alkiyumii* includes also *H.* sp. (OTU 7 in Busais & Joger 2011a), *H. shihraensis* and *H. saba*; specimens for which only the *12S* gene was available. Based on this molecular evidence, it is clear from Fig. 5 and Appendix III that *H. alkiyumii* is not phylogenetically closely related to *H. y. yerburii*, *H. y. montanus*, or to former members of *H. yerburii*: *H. jumailiae* and the other Dhofar *Hemidactylus* described below (Fig. 5D) or the two new species of *Hemidactylus* similar to *H. yerburii* described from Yemen by Busais and Joger (2011a) (*H. shihraensis* and *H. saba*). According to the results of the dating analysis inferred with Dataset 2, *H. alkiyumii* split from its sister clade about 11.1 mya (95% HPD: 7.1–15.9). Uncorrected genetic distances between *H. alkiyumii* and *H. y. yerburii* are 19.4% in the *cytb* and 9.7% in the *12S*; between *H. alkiyumii* and *H. y. montanus* 9.3% in the *12S*; between *H. alkiyumii* and *H. jumailiae* 9.3% in the *12S*; between *H. alkiyumii* and the other Dhofar *Hemidactylus* described below (Fig. 5D) 14.1% in the *cytb* and 6.5% in the *12S*; between *H. alkiyumii* and *H. shihraensis* 7.3% in the *12S*; and between *H. alkiyumii* and *H. saba* 9.5% in the *12S*.

The level of genetic variability within *H. alkiyumii* is very high: 8.8% in the *cytb* and 2.5% in the *12S*. As shown in Fig. 5C and Appendix IIIC, *H. alkiyumii* consists of three very well differentiated and well-supported clades, C1, C2 and C3; being in all the analyses C1 sister to a clade formed by C2 and C3. The uncorrected genetic distances between these three clades are 10.6%, 13.5% and 11% in the *cytb* (C1 *vs.* C2, C1 *vs.* C3 and C2 *vs.* C3, respectively) and 4.3%, 4.2% and 4.2% in the *12S* (C1 *vs.* C2, C1 *vs.* C3 and C2 *vs.* C3, respectively). As shown in Fig. 2, clades C1, C2 and C3 are clearly delimited geographically from East to West. According to the calibrations, clade C1 split from the ancestor of C2 and C3 approximately 4.4 mya (95% HPD: 2.5–6.5), while clades C2 and C3 split about 3.1 mya (95% HPD: 1.6–4.8) (see Fig. 5C). The results of the nuclear networks presented in Fig 7 and a network analysis including all specimens from Dataset 1 (data not shown) indicate that all alleles of *H. alkiyumii* for all three independent loci analyzed (c-*mos*, *mc1r* and *rag2*) are private (not shared with any other species included in the present analyses). It is also interesting to notice that, although clades C1, C2 and C3 share alleles of the c-*mos* and *rag2* genes, specimens of clade C1 do not share alleles of *mc1r* with C2 and C3 and the latter two clades only share a single allele (AO129a) of the *mc1r* gene. Despite the genetic differentiation between clades C1, C2 and C3 of *H. alkiyumii*, which suggests long separation of these three units, the absence of clear morphological differences between these three clades and the relatively low number of available vouchers to carry out a thorough morphological analysis (Appendix I), prevents us from reaching any taxonomic conclusions at present. Future studies should clarify the taxonomic status of clades C1, C2 and C3 of *H. alkiyumii* (work in progress).

As shown in Fig. 5C, Appendix IIIC and Fig. 7, the mitochondrial and nuclear DNA of specimens AO128 and AO129 turn out to be virtually identical with that of a specimen originally identified as *H. macropholis* from 11 km NW of Bargal, Bari region, Somalia (CAS227519) that was included in the phylogeny by Carranza and Arnold (2006; Fig. 1). This makes the original determination of the Bargal individual doubtful, especially as a second specimen of *H. macropholis*, from the Bari region, 11 km SE of Bosasso (CAS227511) also included in Carranza and Arnold (2006) and in the present study (Table 1; specimen CAS227511), has quite different mitochondrial and nuclear DNA with a genetic divergence from *H. alkiyumii* of 19% in *cytb* and 9% in *12S*. As a result of that, and that the collector of the two specimens was the same and visited Tawi Atair (South Oman) and Somalia within the same trip, we consider specimen CAS227511 most probably from Tawi Atair (South Oman) and belonging to *H. alkiyumii*

Distribution

This species inhabits the forested seaward face of the mountains of Dhofar and Eastern Yemen, from Damqawt (Yemen) in the West to North of Wadi Hasik in the East (Fig. 2). Across its distribution range it has been recorded from sea level (8 m in Salalah City, South Oman) up to 800 m in Taiq Cave (South Oman) (Table 1).

Habits

Often in relatively mesic forested areas, though also in more open wadis in East Dhofar and in the gardens within Salalah City (South Oman). Found on rock faces, in shallow caves and on buildings. Mainly nocturnal, several specimens were out during the day in the shadow in densely forested areas in Dalkut (South Oman) and hiding in the caves in Tawi Atair (South Oman) (Fig. 16). It can be locally abundant inside large caves. It is relatively quick and losses its skin when handled. Therefore, sometimes specimens have scars of regenerated skin

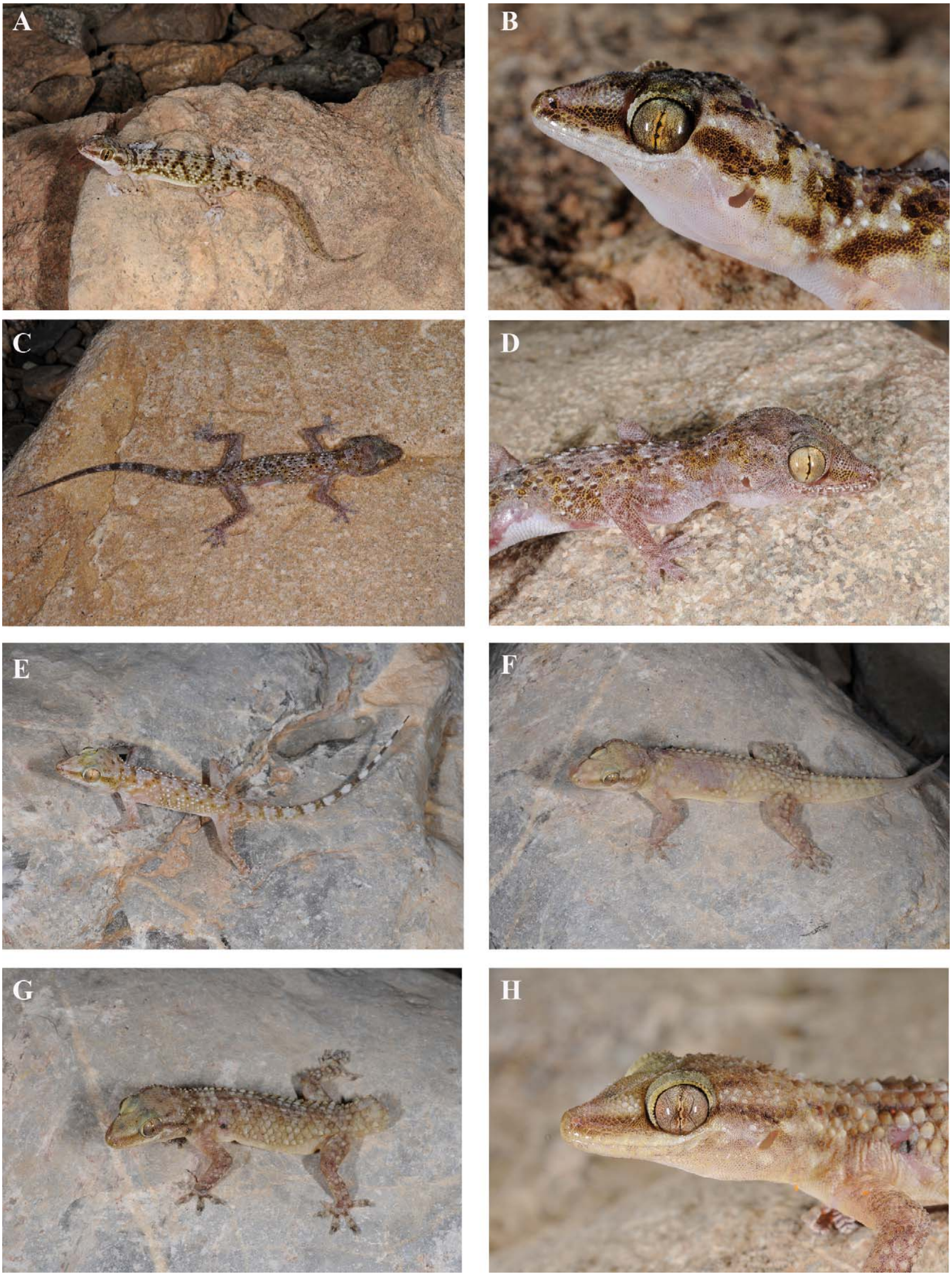

FIGURE 15. Live specimens of *H. alkiyumii* sp. nov. A) and B) female from 3.5 km NE of Sadah (IBES7441); C) and D) female from 3 km NW of Hasik (IBES7858); E) male from 3 km NW of Hasik (IBES7453); F) male from Dalkut (IBES7888); G) and H) female from Dalkut (IBES7891).

on the back, probably as a result of fights with conspecifics or attacks from predators (Fig. 15F). *Hemidactylus alkiyumii* shares habitat with *Ptyodactylus hasselquistii* and small *Hemidactylus* of the *H. homoeolepis* group, although the latter *Hemidactylus* are mainly ground-dwelling, while *H. alkiyumii* is rock-dwelling.

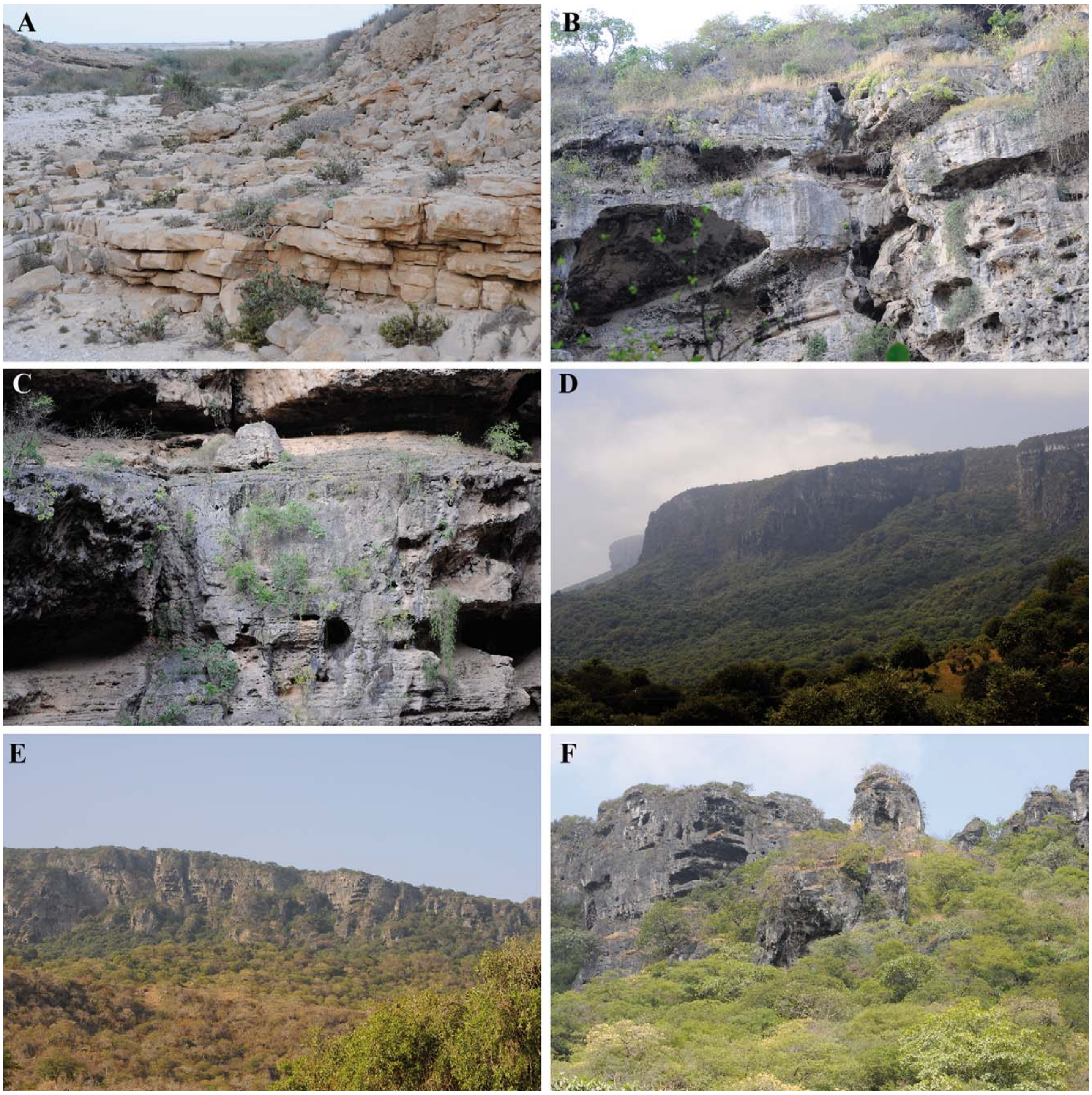

FIGURE 16. Different localities where *H. alkiyumii* sp. nov. has been found. A) 3 km N of Hasik, where the species has been found on the floor and on the rocky sides of the wadi; B) and C) Tawi Atair sink hole, type locality of *H. alkiyumii*; D) and E) Jebel al Qamar in SW Oman; F) Dalkut, in the Jebel Al Qamar, a locality where many specimens of *H. alkiyumii* were found during the day in caves and large crevices in boulders and cliffs (see Appendix I and Table 1).

Description

Males up to 74 mm SVL. Head and body markedly depressed (but less so than in *H. luqueorum*, *H. hajarensis* and *H. persicus* and head less broad than in these species). Head length about 25–29% of SVL (mean males and females 27%), head width 68–85% of head length (mean males 78%, mean females 75%), head height 39–53% of length (mean males 47%, mean females 46%). Adhesive pads on digits quite broad; in adults maximum width of pad on fourth hind toe about half its length.

Nostril between rostral, supranasal and two superposed postnasals, with the first supralabial scale usually also entering narrowly into its border. Usually one scale separating the supranasals on midline. About 10–15 scales in a straight line from postnasal to edge of orbit. Small conical tubercles scattered on orbital area, on crown of head and larger on temporal area above the level of ear opening and immediately in front the upper part of this. Ear opening often elongated, its longest axis running upwards and backwards, smooth-edged, about half or more of eye diameter. Supralabial scales mean 10.0 (9–12), infralabials mean 7.9 (7–9). Mental scale broadly triangular, posteriorly bordered by two large postmentals making contact behind it, a second pair of more lateral postmentals also present, all four with a fairly smooth common transverse posterior border, which may be concave posteriorly, the postmentals contacting the first and second supralabials. Second and more posterior infralabials bordered by more irregular and smaller enlarged scales. Gulars fine.

Enlarged tubercles present on back, arranged in obliquely diagonal rows from near midline to flank, mean 12.9 (11–14) across mid-body and 13–15 in a paraventral row from the level of the axilla to that of the groin, where they are separated by spaces usually less than their own length. Tubercles strongly keeled, trihedral and striated, largest on the upper flanks but becoming smaller and more projecting and rounded lower down. Ventrals small, but larger than dorsals and imbricate, about 44–48 in a transverse row at mid-body between lateral folds (when these are discernible). Males with 6–10 preanal pores (mean 7.3), sometimes separated by one or two scales giving a formula of 3+3, 4+3, 4+4, or 5+5. Scales on upper forelimb small and imbricate, interspersed with enlarged tubercles on distal section that are smaller in the East. Scales beneath hind leg about same size as belly scales and imbricate, rather larger on front surface of thigh, enlarged tubercles present on upper surface of both femur and tibia where may be in contact, but smaller in East; also on posterior edge of foot. Lamellae under the toes of pes: 1st toe mean 7.0 (6–9), 4th toe mean 10.8 (10–12).

Tail relatively slender, although sometimes clearly swollen at base; six enlarged, keeled and pointed tubercles on each whorl proximally, dropping to four around whorl 9–12. Tubercles about one half the length of basal whorls, becoming smaller and placed more posteriorly on whorls distally. Small dorsal scales on tail may be muticarinate, 8–9 in longitudinal row on fourth whorl after vent, around 2–5 small scales between tubercles on fourth and fifth whorls. Subcaudal scales enlarged and broad, extending proximally as far as whorls 1–4 after the vent (average 2), and starting just after the hemipenial bulge in males.

Color varying from brown-grey in the West to pale buff in the East; sometimes a dark stripe from the nostril, through the eye, on to the cheek above ear and often on to neck; body sometimes with irregular spots; occasionally dark transverse crosses on mid-back (one on neck, three on body and one or two on anterior sacrum; Fig. 15A). Some opaque white pigment on tubercles in the East, where it may occur on one side of tubercles while the other is dark. Belly pale. Tail with numerous transverse dark bands more distally, initially on every other whorl and then on each one, the total number being around 11–14. Underside of tail pale but large subcaudals grey, the color increasing in intensity distally and made up of dark chromatophores. Underside of toe pads also grayish.

Distinctive features of Holotype

Half grown male; 56.4 mm SVL; tail 48 mm long with tip missing; some skin missing from mid-belly. Supralabial scales 11/12, infralabials 8/7; about 13 rows of enlarged tubercles at mid-back; 8 (4+4) preanal pores; lamellae under the 1st toe of pes 8/8, 4th toe of pes 12/12.

***Hemidactylus festivus* sp. nov.**

(Figs. 2, 5D, 7, 17–19, Table 1; Appendix I; Appendix IIID)
MorphoBank M95305–M95421 M99719–M99810

Hemidactylus yerburii Arnold, 1977: 101 (part.); Arnold, 1986: 283 (part.); Arnold, 1986: 420 (part.); Schätti and Desvoignes, 1999: 52 (part.); van der Kooij, 2000: 113 (part.); Sindaco and Jeremcenko, 2008: 117 (part.).

Holotype

BMNH1977.977, female from Wadi Ayoun, 670 m, Dhofar region (South Oman) 17.24671'N 53.88774'E WGS84, collected in October 1977 by E.N. Arnold (MorphoBank M95339–M95353). Paratypes: BMNH1977.978, female, same collecting data as Holotype (MorphoBank M95354–M95367); BMNH1977.976, female, same collecting data as Holotype (MorphoBank M95323–M95338); BMNH1977.979, female, same collecting data as Holotype (MorphoBank M95368–M95379); BMNH1977.980, female, same collecting data as Holotype (MorphoBank M95380–M95392); BMNH1977.981, female, same collecting data as Holotype (MorphoBank M95393–M95407); IBES7419, female from 20 km South of Thumrait, 586 m, Dhofar region (South Oman) 17.4596'N 54.0446'E, collected in October 2010 by S. Carranza and F. Amat (MorphoBank M99801–M99810); IBES7159, male from Wadi Ayoun, 670 m, Dhofar region (South Oman) 17.24671'N 53.88774'E WGS84, collected in May 2011 by S. Carranza, E. Gómez-Díaz and F. Amat (MorphoBank M99733–M99743); ONHM3708, male, same collecting data as IBES7159 (MorphoBank M99744–M99753); IBES7605, male, same collecting data as IBES7159 (MorphoBank M99754–M99763); IBES8062, male from Wadi Ayoun, 670 m, Dhofar region (South Oman) 17.24671'N 53.88774'E WGS84, collected in October 2010 by S. Carranza and F. Amat (MorphoBank M99764–M99773).

Other material examined

Five vouchers listed in Appendix I under *H. festivus* sp. nov. and not mentioned above. Samples AO126, AO82, AO122, AO120, AO154, AO121, JS1, JS12, JS15, JS70, JS71, JS72, JS73, JS85, and JS86 were included in the molecular analyses only (Table 1).

Diagnosis

A medium-sized *Hemidactylus* with a maximum recorded SVL of 53.6 mm; with a mean of 13.3 (12–15) longitudinal rows of enlarged dorsal tubercles at mid-body; adhesive pads on toes medium-sized; lamellae under the 1st toe of pes mean 6.9 (6–7); lamellae under the 4th toe mean 11.3 (10–12); preanal pores 6; expanded subcaudals usually beginning 1–8 verticils behind vent (average about 4). Distinctive pattern of narrow dark bands – one on neck, three on body and one on anterior sacrum, often suffused with yellow in life; tubercles on body often with opaque white pigment, sometimes on medial side of tubercles, while lateral sides are dark. Tail very light distally with pattern of 7–9 widely separated dark bands, the more distal of which extend to the ventral surface.

Distinguished from *H. alkiyumii* by its smaller adult size (SVL max. 53.6 mm, compared with max. 74.5 mm), fewer preanal pores in males (6, compared with mean 7.3, 6–10), more slender habitus and distinctive coloring of the tail and body. *Hemidactylus festivus* differs from *H. yerburii* in its smaller adult size (SVL max. 53.6 mm, compared with max. 67.6 mm in *H. yerburii*), in having fewer longitudinal rows of dorsal tubercles at mid-body (mean 13.3, 12–15, compared with mean 16.7, 16–17), fewer preanal pores in males (6, compared with mean 12.8, 10–15), and in having enlarged tubercles on tail that are not spinose. It differs from *H. yerburii montanus*, endemic to the highlands of Yemen, in its smaller adult size (SVL max. 53.6 mm, compared with max. 68 mm in *H. y. montanus*), in having fewer longitudinal rows of dorsal tubercles at mid-body (mean 13.3, 12–15, compared with mean 15.1 in males and 15.47 in females, 14–16), and in having fewer preanal pores in males (6, compared with mean 10.2). It differs from *H. jumailiae* from Yemen (formerly *H. yerburii*) in having large trihedral tubercles present on back (small cycloid tubercles in *H. jumailiae*), more slender habitus and distinctive coloring. It differs from *H. shihraensis* in having higher number of lamellae under the 1st toe of pes (mean 6.9, 6–7, compared with 6), higher number of lamellae under the 4th toe of pes (mean 11.3, 10–12, compared with 10). It differs from *H. saba* in having lower number of lamellae under the 1st toe of pes (mean 6.9, 6–7 compared with 8), a higher number of ventral scales (about 45 in a transverse row at mid-body between lateral folds where these are discernible, compared with an average of 31 in males and 30 in females in *H. saba*).

Etymology

The species epithet "*festivus*" is an adjective that refers to the "happy" aspect of this species, with its bright coloring in the dorsal pattern of living animals and with the juveniles moving around leaping with the tail raised to show its conspicuous black and white coloring.

Genetic and phylogeographic remark

Hemidactylus festivus is monophyletic in the phylogenetic analyses of Dataset 1 (Fig. 5D) and Dataset 3 (Appendix IIID). The phylogenetic relationships of *H. festivus* are different in Fig. 5 and Appendix III, as a result of the different taxa included in Datasets 1 and 3. According to Fig. 5, *H. festivus* is sister to *H.* sp. 1, although

FIGURE 17. Preserved specimens of *H. festivus* sp. nov. A) left: female from Wadi Ayoun (BMNH1977.976); right: female, Holotype, from Wadi Ayoun (BMNH1977.977); B) detail of the head of the Holotype (BMNH1977.977); C) detail of the left hind foot of the Holotype (BMNH1977.977).

bootstrap and pp support values are very low. However, the phylogenetic tree from Appendix III suggest that *H. festivus* is sister to *H. shihraensis*, a species recently described from the Hadramaut, Eastern Yemen (Busais & Joger 2011a) and also closely related to *H. saba* from Northwest Yemen and to an undescribed *Hemidactylus* (*Hemidactylus* sp.) from Western Yemen (Busais & Joger 2011a). Both phylogenetic trees (Fig. 5 and Appendix III) support the position of *H. festivus* between *H. robustus* and the small *Hemidactylus* of the *H. homoeolepis* group (*H. homoeolepis* plus the three new species described below belonging to clades E, F and G). The support for this clade in Fig. 5 is very high. The absence of the sister taxa of *H. festivus*, *H. shihraensis*, and also of *H. saba* and *H.* sp. from Dataset 2 (the dataset used for calibrations), prevents us from commenting on the dates of the possible origin of *H. festivus*. Uncorrected genetic distances between *H. festivus* and *H. alkiyumii* are 14.1% in the *cytb* and 6.5% in the *12S;* between *H. festivus* and *H. y. yerburii* 19.4% in the *cytb* and 10% in the *12S*; between *H. festivus* and *H. y. montanus* 9.5% in the *12S*; between *H. festivus* and *H. jumailiae* 10.3% in the *12S*; between *H. festivus* and *H. shihraensis* 5.3% in the *12S*; and between *H. festivus* and *H. saba* 8% in the *12S*. An individual of *H. festivus* from the Hadramaut (JS1; see Fig. 1), just 110 km North of the type locality of *H. shihraensis* (Ghayl Ba Wazir in Google Earth – Ghail Bawazeer in Busais & Joger 2011a), is genetically very similar to the other individuals of *H. festivus* situated between 430 and 600 km further East and maintains its genetic distinctiveness with the geographically closer *H. shihraensis*. Despite the relatively large area occupied by *H. festivus* (more than 850 km in a straight line between specimens JS1 and BMNH1983.706), the level of genetic variability is rather low: 0.4% in the *cytb* and 0.1% in the *12S*, suggesting that *H. festivus* probably has a continuous distribution between the Hadramaut area in Yemen and Oman. Alternatively, the specimens from Wadi Hadramaut may be the result of a human-meditaed introduction, although we consider this hypothesis very unlikely.

The results of the nuclear networks presented in Fig 7 and a network analysis including all specimens from Dataset 1 (data not shown) indicate that all alleles of *H. festivus* for all three independent loci analyzed (c-*mos*, *mc1r* and *rag2*) are private (not shared with any other species included in the analyses).

Distribution

Hemidactylus festivus is distributed across 850 km, from the Hadramaut area in Southeastern Yemen to Southern Dhofar province in Oman, as far East as Sawqirah (Fig. 2). Although it can be found geographically very close to *H. alkiyumii* (even in sympatry at one locality; see Fig. 2 specimens JS7, JS12 and JS15), *H. festivus* mainly occupies the dry landward (Northern) side of the mountains, on the other side of the Dhofar Mountains and, in general, much dryer habitats than *H. alkiyumii*. Interestingly, *Hemidactylus festivus* is also found in Wadi Mughsayl on the Salalah coast, an area between clades C2 and C3 of *H. alkiyumii* in which this latter species has never been recorded.

Habits

The species occurs on rock pavements and low down on large boulders. At the type locality, *H. festivus* is replaced further from the ground by *Hemidactylus lemurinus* and *Ptyodactylus* (Arnold 1980) and newborns and juveniles share the ground with the much smaller *H. homoeolepis*. Although it occurs in drier habitats than *H. alkiyumii*, it is not found in really arid situations (Fig. 19). This species is particularly agile and subadults especially progress in a series of leaps when pursued, with the tail raised to show its conspicuous black and white coloring. Specimens from Wadi Ayoun collected in June were gravid but none had eggs in early October (Arnold 1980). According to our observations, *H. festivus* seems a strictly nocturnal gecko, as it has never been observed active during the day.

Description

Up to 53.6 mm SVL. Head and body markedly depressed; head broad, especially posteriorly and neck well defined. Head length about 26–30% of SVL (mean males 28, mean females 27%), head width 63–81% of head length (mean males 71%, mean females 72%), and head height 38–54% of length (mean males 45%, mean females 44%). Adhesive pads quite narrow; in adults the maximum width of pad on fourth hind toe a third to a half its length.

Nostril between rostral, supranasal and two superposed postnasals, with the first supralabial scale usually also entering narrowly into its border. Usually one scale separating supranasals on midline. About 13–15 scales in a straight line from postnasal to edge of orbit. Small conical tubercles scattered in orbital area and on crown of head

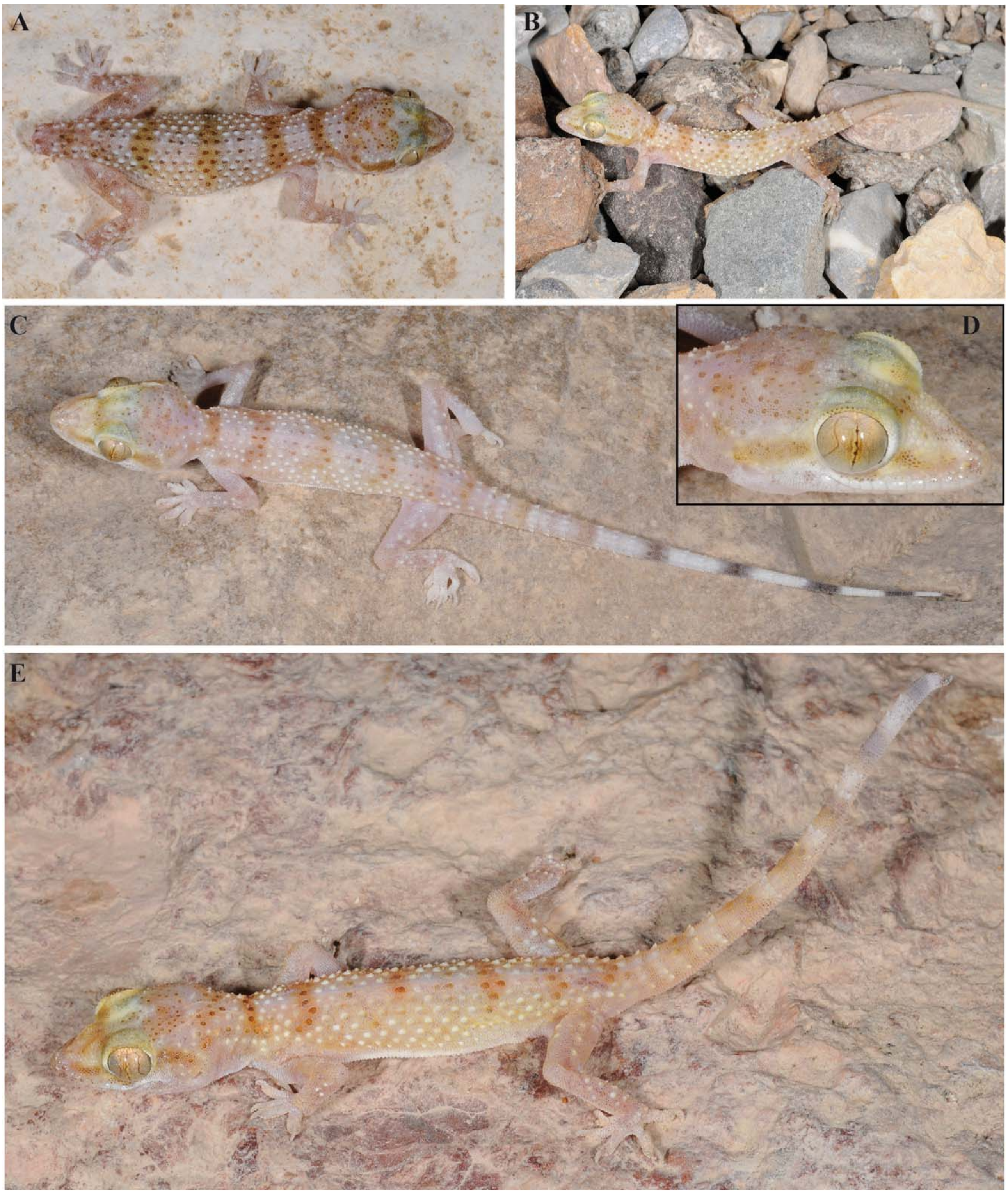

FIGURE 18. Live specimens of *H. festivus* sp. nov. A) female from Wadi Ayoun (IBES7616); B) male from Wadi Mughsayl (IBES7899); C) and D) complete body and detail of the head of an unvouchered specimen from Wadi Ayoun; E) female from 20 km S of Thumrait in typical posture with the tail raised (IBES7419).

and often larger on temporal area above the level of ear opening, and immediately in front of the upper part of this. Ear opening often broad inverted comma shape with its longest axis running upwards and backwards, smooth-edged, usually less than one third of eye diameter. Supralabial scales mean 9.8 (9–11), infralabials mean 8.4 (7–10). Mental scale broadly triangular, posteriorly bordered by two large postmentals making contact behind it, a second

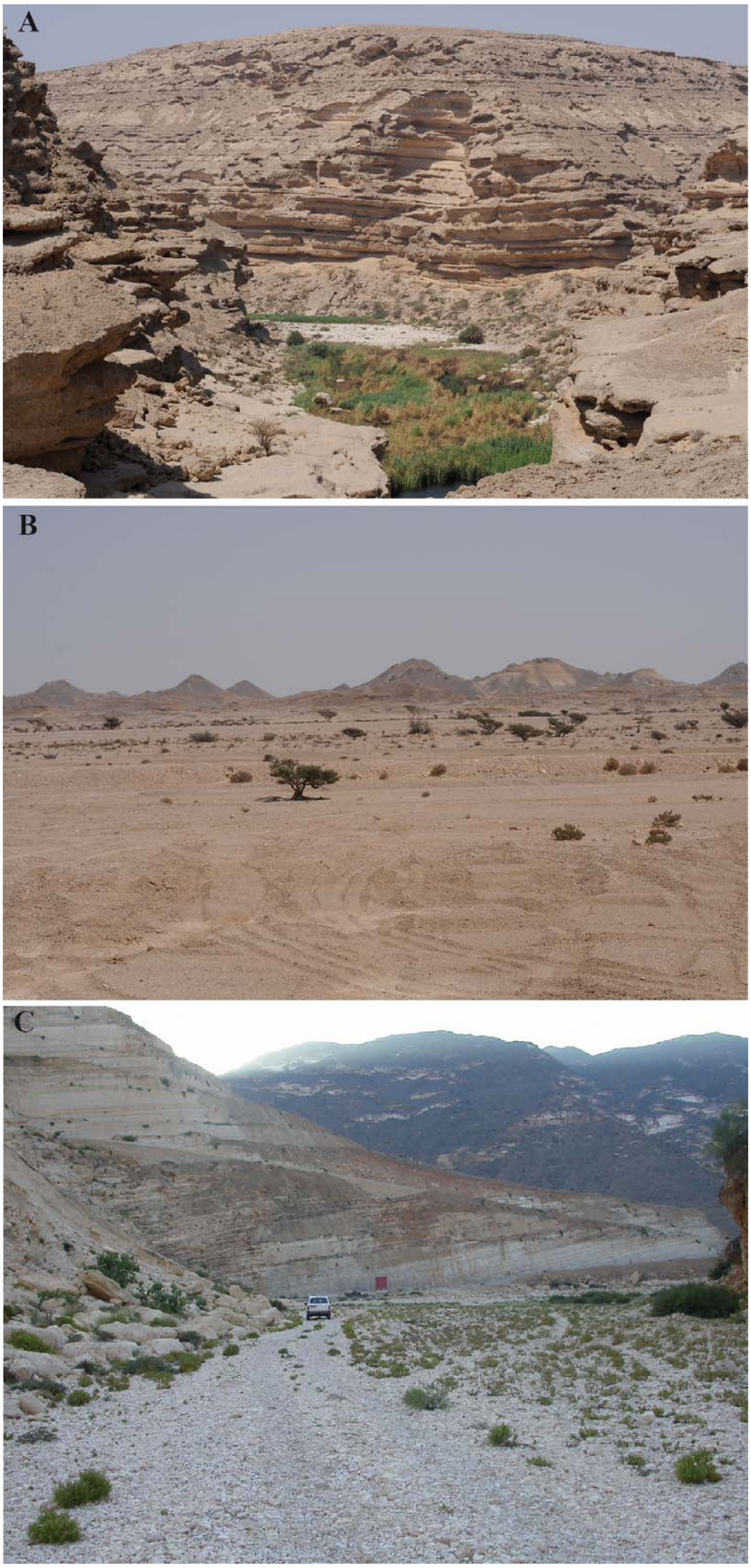

FIGURE 19. Different localities where *H. festivus* sp. nov. and *H. homoeolepis* have been found. A) Wadi Ayoun, type locality of *H. festivus* where *H. festivus* occurs on the ground and low down on large boulders and *H. homoeolepis* occurs exclusively on the ground; B) 20 km S of Thumrait, where *H. festivus* and *H. homoeolepis* have been found mainly moving around on the rocky substrate; C) Wadi Mughsayl, W of Salalah. As in Wadi Ayoun, at this locality *H. festivus* occurs on the ground and low down on the rocky sides of the wadi, while *H. homoeolepis* occurs exclusively on the ground.

pair of more lateral postmentals also present, all four with a smooth common transverse posterior border; second postmentals contacting the first and second upper labials; third and more posterior lower labials bordered by more irregular and smaller enlarged scales. Gulars fine, rounded with little overlap.

Enlarged tubercles present on back, arranged in obliquely diagonal rows from near midline to flank, mean 13.3 (12–15) across mid-body, and 15–17 in a paravertebral row from the level of the axilla to that of the groin, and largest on upper flank, where they are separated by spaces of about their own length or less. Tubercles keeled, striated and trihedral but becoming smaller and more rounded on lower flanks. Ventral scales small, and flat, but larger than dorsals and imbricate, about 45 in a transverse row at mid body between lateral folds where these are discernible. Males with 6 preanal pores, sometimes separated by one or two scales giving a formula of 3+3. Scales on upper forelimb small and imbricate, interspersed with enlarged tubercles of different sizes on distal section. Scales on front of thigh and beneath about same size as belly scales and imbricate, rather larger under tibia, enlarged tubercles present on upper surface of both femur and tibia and also on posterior edge of foot. Lamellae under the toes of pes: 1st toe mean 6.9 (6–7), 4th toe mean 11.3 (10–12).

Tail relatively slender; 6 enlarged, keeled and pointed tubercles on each whorl proximally, dropping to 4 around whorl 8 or 10. Tubercles about half the length of basal whorls, becoming smaller and placed more posteriorly on whorls distally. About 9–10 small scales in longitudinal row on fourth whorl after vent, around five small scales between tubercles on fourth and fifth whorls. Subcaudal scales enlarged and broad, extending proximally as far as whorls 1–7 after the vent (average 4).

In alcohol, often warm pale buff; sometimes a vague darker stripe from the nostril, through the eye and on to cheek above ear; neck and body with narrow darker bands that are convex posteriorly – one on neck, three on body and one on anterior sacrum, bars do not extend on to flanks and may be suffused with yellow in life. Tubercles away from midline with dense white pigment, often the medial surface white and the lateral one darker than background, where scattered dark chromatophores can be seen. Tubercles on limbs and basal tail also white. Belly white, throat limbs and tail pale buff beneath. Underside of adhesive pads on toes pale. Tail becoming much lighter towards tip, with 7–9 widely separated dark bars above, beginning around verticil 8 or 9, each about a whorl long and separated by one or two whorls from the next; bars much shorter than intervening areas; more posterior bars extend to ventral surface. Juveniles like adults but distal tail colouring more contrasting and intense.

Distinctive features of Holotype

Adult female, 49 mm SVL; tail intact 58 mm long; a longitudinal incision present on left side of belly. Supralabial scales 9/10, infralabials 9/9; 14 rows of enlarged tubercles at mid-back; lamellae under the 1st toe of pes 7/7, 4th toe of pes 11/11.

The *Hemidactylus homoeolepis* group

Until 1977, *Hemidactylus homoeolepis* was regarded as endemic to Socotra Island, but the revision of Arabian geckos by Arnold (1977) reported it from the Arabian mainland. This work suggested that it might have an extensive if interrupted distribution along the Southeastern seaboard of the peninsula. On Socotra, *H. homoeolepis* is relatively large and robust with small, sometimes slightly imbricate, dorsal scales and ventrals that occasionally show a slight serration at their edges. Socotran *H. homoeolepis* have SVL up to 42 mm, a low number of lamellae under the 1st toe of pes 4–5 and under the 4th toe of pes 7–8; preanal pores in males 3–6, arranged in a V-shaped line in front of the vent (Appendix I and pers. observ.). Morphological differences between Arabian mainland populations of *H. homoeolepis* were investigated in depth by Arnold (1977, 1980), who concluded that the differences between some of the known populations are greater than those between some recognized species of *Hemidactylus*. Morphology (Appendix I; Figs. 20–22, 24–25, 27–28), phylogenetic analyses of Dataset 1 (Fig. 5) and Dataset 3 (*12S* only; Appendix III), and nuclear networks of three independent loci (c-*mos*, *mc1r* and *rag2*) (Fig. 8) indicate that there are three new species of the *H. homoeolepis* group, all endemic to Oman (Fig. 3). These three new species are distinct both from each other and from typical *H. homoeolepis* and, as a result of that, are described below.

Hemidactylus homoeolepis Blanford, 1881

(Figs. 3, 5, 8, 19–21, Table 1; Appendix I; Appendix III)
MorphoBank M95683–M95823 M100000–M100038 M102031–M102145

Hemidactylus (Liurus) homoeolepis Blanford, 1881: 464. (Syntypes: BMNH1946.9.6.99 male, and 1946.9.7.1 female; Socotra Island, Yemen; collected by I.B. Balfour)

Hemidactylus homoeolepis: Arnold, 1977: 103 (part.); Arnold, 1980: 279 (part.); Arnold, 1986: 419 (part.); Schätti and Desvoignes, 1999: 50 (part.); van der Kooij, 2000: 111 (part.); Carranza and Arnold, 2006: 536; Sindaco and Jeremcenko, 2008: 115 (part.).

Material examined

Twenty-seven vouchers listed in Appendix I under the name *H. homoeolepis*. Juvenile specimens AO81, AO85, AO119 and samples S4209, S3399, S7091, JS5, JS6, JS8, JS75 were included in the molecular analyses only (Table 1).

Diagnosis

A small member of the *H. homeolepis* group with a maximum recorded SVL of 42 mm. Undepressed head; scaling fine without tubercles with the exception of specimen BMNH1953.1.6.9 from Shaqara, Southwest Yemen, which presents large tubercles on the hind back, tail base and hind limbs. Lamellae under the 1st toe of pes mean 4.7 (4–5); lamellae under the 4th toe mean 8.4 (7–10); preanal pores mean 5.5 (3–6); expanded subcaudal scales beginning some way from tail base; dorsal pattern spotted. For differences from the three new species described herein formerly part of *H. homoeolepis* (clades E–G in Fig. 5 and Appendix III) see below.

Genetic and phylogeographic remarks

Hemidactylus homoeolepis is monophyletic in the phylogenetic analyses of Dataset 1 (Fig. 5) and Dataset 3 (Appendix III). According to both Fig. 5 and Apendix III, *H. homoeolepis* is sister to a clade formed by two of the new species described below (clades F and G). This topology is very well supported and is maintained even if the two endemic *Hemidactylus* from the island of Abd Al Kuri (Socotra Archipelago), *H. oxyrhinus* Boulenger, 1899 and *H. forbesii* Boulenger, 1899 are included in the analyses (Gómez-Díaz *et al.* in press). According to the analyses by Gómez-Díaz *et al.* (In press), the two endemics from Abd Al Kuri are sister taxa and branch within the "*H. homoeolepis* group", in a position between the new species from clade E (described below) and a monophyletic assemblage formed by clades F, G and *H. homoeolepis*. According to the results of the analysis of Dataset 2 (dates inserted in Fig. 5), *H. homoeolepis* split from its sister clade approximately 6.6 mya (95% HPD: 4.2–9.6) and the species colonized the Socotra Archipelago about 4.3 mya (95% HPD: 2.5–6.4). Since at that time Socotra was already close to its actual position (Bosworth *et al.* 2005; Laughton 1966; Samuel *et al*. 1997), our data suggests that, similar to the skinks of the genus *Trachylepis* and the ancestor of the two endemic *Hemidactylus* from Abd Al Kuri, *H. homoeolepis* arrived to the archipelago by transmarine dispersal from Southeast Arabia (Gómez-Díaz *et al.* in press; Sindaco *et al.* in press.). The dates of origin of *H. homoeolepis* and colonization of the Socotra Archipelago by *H. homoeolepis* do not differ much from the inferred dates of these two events by Gómez-Díaz *et al.* (In press) using the same methods and calibrations but including *H. oxyrhinus* and *H. forbesii* (5.9 mya [95% HPD: 3.6–8.6] and 4.3 [95% HPD: 2.5–6.4], respectively).

Uncorrected genetic distances between *H. homoeolepis* and the other three members of the "*H. homoeolepis* group" (described as new species below) are very high: *H. homoeolepis vs.* the new species from clade G (Fig. 5, Appendix III) 13% in the *cytb* and 8.4% in the *12S*; *H. homoeolepis vs.* the new species from clade F (Fig. 5, Appendix III) 11.2% in the *cytb* and 8.8% in the *12S*; *H. homoeolepis vs.* the new species from clade E (Fig. 5, Appendix III) 11% in the *cytb* and 8.5% in the *12S.* The results of the nuclear networks presented in Fig. 8 and a network analysis including all members of Dataset 1 (data not shown) clearly show that all alleles of *H. homoeolepis* for all three independent loci analyzed (c-*mos*, *mc1r* and *rag2*) are private (not shared with any other species included in the analyses).

The level of genetic variability within *H. homoeolepis* is rather high: 3.2% in the *cytb* and 1.3% in the *12S*, and is the result of the relatively high level of genetic differentiation between mainland Arabia and Socotra Island populations of *H. homoeolepis* (uncorrected genetic distances of 10.4% in the *cytb* and 5.7% in the *12S*). This

FIGURE 20. A) left: female of *H. homoeolepis* from Wadi Sayq (BMNH1977.919); right: male, Holotype, of *H. paucituberculatus* sp. nov. from Khor Sawli (BMNH1977.935); B) detail of the underside of the tail, left: *H. homoeolepis* (BMNH1977.919); right: *H. paucituberculatus* (BMNH1977.935); C) detail of the head of the Holotype of *H. paucituberculatus* (BMNH1977.935).

FIGURE 21. Live specimens of *H. homoeolepis*. A) unvouchered specimen from Wadi Ayoun (photograph by Roberto Sindaco); B) male from Asylah (IBES7676); C) detail of the underside of the tail of the same specimen as in B; D) unvouchered specimen from Socotra Island, Yemen (photograph by Fabio Pupin).

genetic differentiation at the mtDNA level is also supported by differentiation at the nuclear level and by morphological differences in size, tuberculation, number of lamellae under the toes of pes, which suggests that Arabian mainland populations may, in fact, represent a new species (data not shown; work in progress). Although most specimens of *H. homoeolepis* across its distribution range in mainland Arabia are morphologically very uniform, one single isolated specimen from the coastal city of Shaqra (13.35'N 45.70'E; Southwest Yemen, 850 km to the West of the main distribution range of the species; BMNH1953.1.6.9; see Appendix I; MorphoBank: M102031–M102050) presents several differences from Eastern *H. homoeolepis*. The main differences are: dorsal scales flatter and slightly more imbricate; ventrals markedly larger with distinct serrated edges; presence of numerous enlarged unkeeled tubercles on the hind parts, just in front of the pelvic region that increase in size and frequency posteriorly. These are much bigger than the intermediate scales and are irregularly arranged although they tend to form transverse rows on tail base (rest of the tail is missing). Similar large scales occur on the tibia. Although no material is available for genetic comparisons, all these differences suggest that the specimen from Shaqra, Yemen may be part of yet another undescribed species of the *H. homoeolepis* group.

Distribution

Hemidacytlus homoeolepis is found in Socotra, Samha and Darsa Islands (Socotra Archipelago), Shaqra in Southwest Yemen, extreme Eastern Yemen, Dhofar region in South Oman and adjoining Central Oman and North Oman (Asylah) (Fig. 3). Across its distribution range it has been recorded from sea level (4 m in Wadi Mughsayl) up to 670 m in Wadi Ayoun (Table 1).

Habits

Hemidactylus homoeolepis is a small and strictly nocturnal gecko found in usually dry places on rock surfaces near the ground and on sandy and stony substrates close by. At Wadi Ayoun it occupies stony ground and sloping rock pavements and at Thumrait was found on screes of small stones (Fig. 19B). According to Arnold (1980), at these localities 62% of sixty-four animals checked were first sighted on the ground and all but one of the others were lower than 60 cm from it. At Wadi Ayoun *H. homoeolepis* is sympatric with three other nocturnal geckos: *H. lemurinus*, *H. festivus* and *Ptyodactylus*; although only newborns and juveniles of *H. festivus* are found in the same microhabitat (stony ground). *Hemidacytlus homoeolepis* is very agile, often proceeding in a series of leaps when pursued.

***Hemidactylus paucituberculatus* sp. nov.**

(Figs. 3, 5, 8, 20, 22–23, Table 1; Appendix I; Appendix III)
MorphoBank M100347–M100537

Hemidactylus homoeolepis: Arnold, 1977: 103 (part.); Arnold, 1980: 279 (part.); Arnold, 1986: 419 (part.); Schätti and Desvoignes, 1999: 50 (part.); van der Kooij, 2000: 111 (part.); Sindaco and Jeremcenko, 2008: 115 (part.).

Holotype

BMNH1977.935, male from Khor Sawli, Salalah plain, Dhofar (South Oman), 17.04'N 54.32'E WGS84, collected in October 1977 by E.N. Arnold (MorphoBank M100347–M100363). **Paratypes**: BMNH1977.930, male, same collecting data as Holotype (MorphoBank M100364–M100380); BMNH1977.937, male, same collecting data as Holotype (MorphoBank M100381–M100397); BMNH1977.931, female, same collecting data as Holotype (MorphoBank M100416–M100431); BMNH1977.936, female, same collecting data as Holotype (MorphoBank M100432–M100447); BMNH1977.933, female, same collecting data as Holotype (MorphoBank M100448–M100464); BMNH1977.944, female, same collecting data as Holotype (MorphoBank M100465–M100479); BMNH1977.941, female, same collecting data as Holotype (MorphoBank M100480–M100496); BMNH1977.942, female, same collecting data as Holotype (MorphoBank M100497–M100501); ONHM3709, female from Khor Sawli, Salalah plain, Dhofar (South Oman), collected in October 2010 by S. Carranza and F. Amat (MorphoBank M100502–M100515); IBES7646, female, same collecting data as ONHM3709 (MorphoBank M100530–M100537);

Other material examined

Five vouchers listed in Appendix I under *H. paucituberculatus* sp. nov. and not mentioned above. Juvenile specimens IBES7988, IBEAO104 IBES7364, IBES7336, IBES7183 IBEAO91, IBES7492 and samples AO162, S3261, S3235, S7812, S7201 were included in the molecular analyses only (Table 1).

Diagnosis

A small, moderately depressed *Hemidactylus* with a maximum recorded SVL of 38.4 mm. Usually with flat enlarged tubercles on sides of dorsum as far forwards as mid-body that are also present on sides of dorsal tail base and on the hind legs where they are raised, and may also occur on the lower forelimb; lamellae under the 1st finger of pes mean 4.9 (4–5); lamellae under the 4th toe mean 8.3 (7–9); preanal pores 6 in all males analyzed (Appendix I); expanded subcaudal scales usually extend almost to tail base. Dorsum with a pattern of irregular dark spots and streaks; tail with around 8–9 dark bands that increase in intensity distally and contrast strongly with smaller pale interstices.

Hemidactylus paucituberculatus differs from neighboring populations of *H. homoeolepis* from South Oman in its rather larger adult size (SVL mean 32.2 mm, max. 38.4, compared with mean 30.1 mm, max. 33.4 mm), presence of enlarged tubercles and expanded subcaudal scales usually extending almost to tail base (expanded subcaudal scales beginning some way from tail base in *H. homoeolepis*). Not distinguished in its maximum adult body size from populations of *H. homoeolepis* from the Socotra Archipelago (SVL max. 39.7 mm) or from the single specimen from Shaqra (SVL 36.4 mm). For differences from the other two new species described herein formerly part of *H. homoeolepis* (clades F–G in Fig. 5 and Appendix III) see below.

Etymology

The species epithet "*paucituberculatus*" is an adjective derived from Latin that refers to the presence of few tubercles on sides of dorsum as far forward as mid-body that are also present on sides of dorsal tail base and on the hind legs.

Genetic and phylogeographic remarks

Hemidactylus paucituberculatus is monophyletic in the phylogenetic analyses of Dataset 1 (Fig. 5E) and Dataset 3 (Appendix IIIE). According to Fig. 5 and Appendix III, *H. paucituberculatus* is sister to a monophyletic group formed by *H. homoeolepis* and the two new species described below (clades F and G). However, this topology is altered when the two endemic *Hemidactylus* from the island of Abd Al Kuri (Socotra Archipelago), *H. oxyrhinus* and *H. forbesii*, are included in the analyses (Gómez-Díaz *et al.* in press). According to Gómez-Díaz *et al.* in press), the two endemic *Hemidactylus* from Abd Al Kuri form a clade that branches between *H. paucituberculatus* and the monophyletic assemblage formed by clades F, G and *H. homoeolepis.* According to the results of the analysis of Dataset 2 (dates inserted in Fig. 5), *H. paucituberculatus* split from its sister clade approximately 8.2 mya (95% HPD: 5.1–11.7). This date of origin of *H. paucituberculatus* does not differ much from the inferred date by (Gómez-Díaz *et al.* in press) using the same methods and calibrations and including *H. oxyrhinus* and *H. forbesii* (7.4 mya; 95% HPD: 4.6–10.8).

Uncorrected genetic distances between *H. paucituberculatus* and the other members of the "*H. homoeolepis* group" (two of them described as new species below) are very high: *H. paucituberculatus vs. H. homoeolepis* 11% in the *cytb* and 8.5% in the *12S*; *H. paucituberculatus vs.* the new species from clade F (Fig. 5, Appendix III) 12.9% in the *cytb* and 9.2% in the *12S*; *H. paucituberculatus vs.* the new species from clade G (Fig. 5, Appendix III) 13.5% in the *cytb* and 8.9% in the *12S.*

The results of the nuclear networks presented in Fig. 8 are very interesting and, while all alleles of *H. paucituberculatus* for the nuclear genes c-*mos* and *mc1r* are private (not shared with its closermost taxa (Fig. 8) or with any other species of *Hemidactylus* from Dataset 1 or the two endemics from Abd Al Kuri (data not shown)), 18 alleles of *H. paucituberculatus* out of a total of 20 alleles for the nuclear gene *rag2* are shared with the new species of clade G described below (Figs. 5 and 8). Given the fact that there is complete lineage sorting for the mtDNA (Appendix III) and in the nuclear networks of c-*mos* and *mc1r* (*H. paucituberculatus* even forms an independent network not connected to the other three species in *mc1r*; see Fig. 8), and that no hybrids have been detected, all evidence at hand points towards ancestral polymorphism rather than ongoing interspecific gene flow. The level of genetic variability within *H. paucituberculatus* is very low: 0.6% in the *cytb* and 0.2% in the *12S,* and coincides with the high level of morphological homogeneity of this species (Appendix I).

FIGURE 22. Live specimens of *H. paucituberculatus* sp. nov. A) unvouchered specimen from Wadi Darbat (photograph by Roberto Sindaco); B) detail of the underside of the tail of the same specimen as in A; C) and D) detail of the head and underside of the tail of a female from Wadi Hasik (IBES7930); E) male from Wadi Darbat photographed from the underside (IBES7994); F), G) and H) different pictures including a detail of the head of a male from 3.5 km NE of Sadah (IBES8004); I) newborn from Khor Sawli (IBES7364).

The morphological investigation of a juvenile *Hemidactylus* (BMNH1974.4051) from Al-Hasikiyah island (spelling from Google Earth), Dhofar (South Oman), suggests that it may belong to *H. paucituberculatus* (data not shown). Although it would make sense biogeographically, the juvenile specimen is not very well preserved and therefore it cannot be indentified with confidence. Future exploration of Al-Hasikiyah Island and the nearby islands of Al-Sawda, Al-Hallaniyah, and Al-Qibliyah should clarify the taxonomic status of the populations of *Hemidactylus* inhabiting this interesting archipelago.

Distribution

Hemidacytlus paucituberculatus is endemic to South Oman and is found in Central Dhofar (Salalah plain), from Salalah to Hasik (Fig. 3). Like *H. alkiyumii* sp. nov., it inhabits the forested seaward (Southern) face of the Dhofar Mountains (Fig. 1) but in this case it is restricted to the area East of Salalah. Across its distribution range it has been recorded from sea level (9 m in Khor Sawli) up to 211 m in Wadi Darbat (Table 1)

Habits

A small and strictly nocturnal gecko found in usually dry places on rock surfaces near the ground and on the beach on sandy substrates with some rocks present (Fig. 23). In several places *H. paucituberculatus* is sympatric with *H. alkiyumii* and *Ptyodactylus*; although neither of these two gecko species occupy the same microhabitat (stony ground). *Hemidacytlus paucituberculatus* is very agile, often proceeding in a series of leaps when pursued.

Description

Up to 38.4 mm SVL. Head and body strongly depressed; head not especially broad posteriorly and neck well defined. In adults head length about 24–29% of SVL (mean males and females 25%), head width 60–78% of head length (mean males 70%, mean females 71%), and head height 38–49% of head length (mean males 39%, mean females 41%). Adhesive pads moderate; in adults maximum width of pad on fourth hind toe around a third its length.

Nostril between rostral, supranasal and two superposed postnasals, with the first supralabial scale usually also entering narrowly into its border. One scale separating supranasals on midline. About 10–13 scales in a straight line from postnasal to edge of orbit. No enlarged scales or tubercles on head (occasionally very few weakly enlarged scales); ear opening with its longest axis running upwards and backwards, smooth-edged, usually half of eye diameter or less. Supralabial scales mean 8.9 (8–10), infralabial scales mean 7.4 (6–9). Mental scale broadly triangular posteriorly bordered by two large postmentals making contact behind it, a second pair of more lateral postmentals also present, the large postmentals contacting the first, or first and second, supralabials; second and more posterior infralabials bordered by more irregular and smaller enlarged scales. Gulars fine, imbricate posteriorly

Weakly enlarged flat smooth scales scattered on sides of mid-and posterior dorsum of body, becoming larger on sacral region and tail base, and on hind limbs where they are conical. Ventral scales small, but larger than dorsals and imbricate**,** about 32 in a transverse row at mid body between lateral folds (often not very apparent). All males analyzed have 6 preanal pores (Appendix I); usually 2 cloacal tubercles on each side. Scales on upper forelimb small and imbricate, often some enlarged tubercles on lower limb; scattered enlarged raised tubercles present on upper surface of both femur and tibia; scales on front of thigh and beneath about same size as belly scales or rather smaller; scales rather larger and more imbricate under tibia. Lamellae under the toes of pes: 1st toe mean 4.9 (4–5); 4th toe mean 8.3 (7–9).

Tail relatively slender with no tubercles after whorl 6. About 7 small scales in longitudinal row on fourth whorl after vent. Subcaudal scales enlarged and broad, extending proximally almost to tail base and starting soon after the hemipenial bulge in males.

In alcohol pale grey-buff or buff; a broad dark stripe from the nostril, through the eye, on to cheek above ear and often on to neck; body with irregular dark spots and streaks that are often stronger anteriorly; belly pale. Tail with six or more dark bands each covering two or more whorls, being rather broader than pale intervening areas and increasing in intensity distally; ventral surface of tail pale and often irregularly blotched or stippled, the most distal four or so dorsal bands extending on to it.

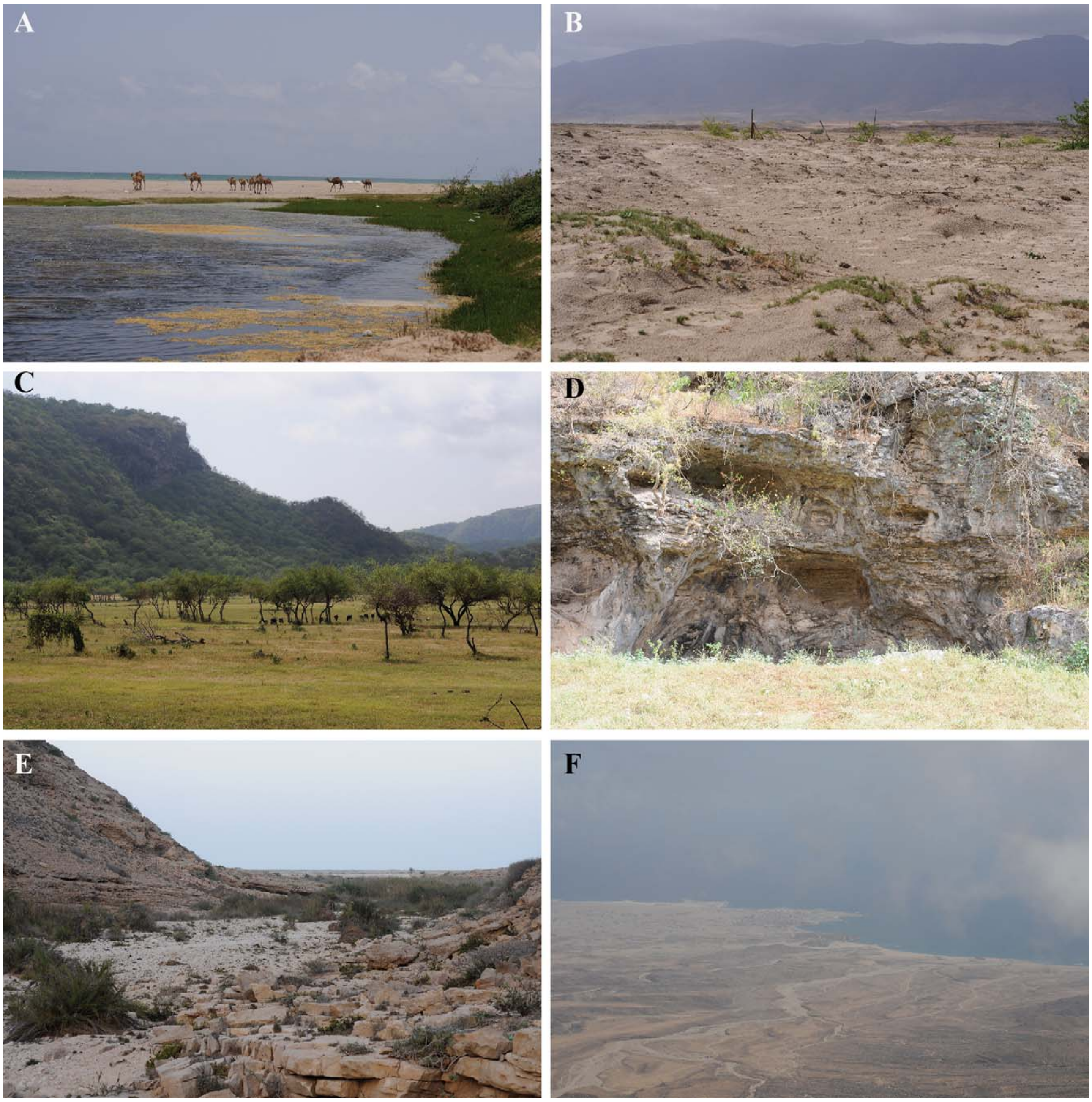

FIGURE 23.-Different localities where *H. paucituberculatus* sp. nov. has been found. A) and B) Khor Sawli, where specimens were found under rocks during the day or moving around on the ground at night; C) and D) Wadi Darbat; E) 3 km N of Wadi Hasik, where *H. paucituberculatus* has been found in sympatry with *H. alkiyumii*; F) image of the Salalah plain, main habitat of *H. paucituberculatus*, taken from the summit of Jebel Samhan.

Distinctive features of Holotype

Adult male 33.5 mm SVL, tail 39 mm long, broken about half way along its length with a regenerated tip. Supralabial scales 10/9, infralabials 7/7; 6 preanal pores; lamellae under the 1st toe of pes 4/4, under the 4th toe of pes 7/7.

***Hemidactylus masirahensis* sp. nov.**
(Figs. 3, 5, 8, 24–26, Table 1; Appendix I; Appendix III)
MorphoBank M10094–M100230

Hemidactylus homoeolepis: Arnold, 1977: 103 (part.); Arnold, 1980: 279 (part.); Arnold, 1986: 419 (part.); Schätti and Desvoignes, 1999: 50 (part.); van der Kooij, 2000: 111 (part.); Sindaco and Jeremcenko, 2008: 115 (part.).

Holotype

BMNH1975.2080, male from East of R.A.F. camp, North end of Masirah Island (Oman), collected by T.D. Rogers (MorphoBank M10094–M100115). **Paratypes**: BMNH1975.2081, female, same collecting data as Holotype; BMNH1975.2082, male from Wadi dhu Mayhi, Masirah Island (Oman), 700 m, collected by T.D. Rogers (MorphoBank M100116–M100137); BMNH1975.2084, female, same data as BMNH1975.2082 (MorphoBank M100158–M100175); BMNH1975.2083, female, same data as BMNH1975.2082 (MorphoBank M100176–M100196); IBES7710, female from Wadi Maahdi, Masirah Island (Oman), collected in October 2010 by S. Carranza and F. Amat (MorphoBank M100220–M100226); ONHM3710, female, same collecting data as IBES7710 (MorphoBank M100227–M100230).

Other material examined

One voucher listed in Appendix I under *H. masirahensis* sp. nov. and not mentioned above. Juveniles or badly preserved specimens IBES7707, BMNH2008.713, IBES7661, IBES2004 and one sample (S3412) were included in the molecular analysis only (Table 1).

Diagnosis

A small, slender, depressed *Hemidactylus* with a maximum recorded SVL of 42 mm. Usually with scattered weakly enlarged scales on sides of dorsum of body that become larger posteriorly especially on sacral region, tail base, and hind legs where they are raised and tuberculate; adhesive pads narrow; lamellae under the 1st toe of pes 6; lamellae under the 4th toe mean 10.0 (10–11); preanal pores 4 in the two males analyzed (Appendix I); expanded subcaudal scales usually extend almost to tail base. Dorsum with a pattern of irregular dark spots and streaks; tail with 8–9 dark bands that increase in intensity distally contrasting with smaller pale interstices, more distal 4–6 bands extend to ventral surface, each covering two or more whorls distally and being rather broader than interstices.

Hemidactylus masirahensis differs from *H. homoeolepis* in its larger adult size (SVL mean 32.2 mm, max. 45 mm, compared with mean 31.8 mm, max. 39.7 mm), greater depression of the head and body, more usual presence of dorsal tubercles on the body, lower number of preanal pores in males (4 compared with mean 5.5, 3–6), higher number of lamellae under the 1st toe of pes (6 compared with mean 4.7, 4–5), and under the 4th toe of pes (mean 10.0, 10–11, compared with mean 8.4, 7–11), presence of enlarged tubercles and expanded subcaudal scales usually extend almost to tail base (expanded subcaudal scales beginning some way from tail base in *H. homoeolepis*), different coloring (dark bands of the tail more conspicuous and marked in *H. masirahensis*, especially on the underside of tail). Distinguished from *H. paucituberculatus* by its larger adult size (SVL mean 32.2 mm, max. 45 mm, compared with mean 32.2 mm, max. 38.4 mm), greater depression of head and body, more usual presence of dorsal tubercles on body, lower number of preanal pores in males (4 compared with 6), higher number of lamellae under the 1st toe of pes (6 compared with mean 4.9, 4–5), and under the 4th toe of pes (mean 10.0, 10–11, compared with mean 8.3, 7–9), different coloring (dark bands of the tail more conspicuous and marked in *H. masirahensis*, especially on the underside of tail).

Etymology

The species epithet "*masirahensis*" is an adjective that refers to the place where the species is found, Masirah Island off the coast of Central Oman.

Genetic and phylogenetic remarks

Hemidactylus masirahensis is monophyletic in the phylogenetic analyses of Dataset 1 (Fig. 5F) and Dataset 3 (Appendix IIIF). According to Fig. 5 and Appendix III, it is sister to a new species described below (clade G). This topology is very well supported and is maintained even if the two endemic *Hemidactylus* from the island of Abd Al

FIGURE 24. Preserved specimens of *H. masirahensis* sp. nov. from Masirah Island A) male, Holotype, from E of R.A.F. camp (BMNH1975.2080); B) detail of the head of the Holotype; C) and D) female, from Wadi Maahdi (IBES7710); E) from left to right: female (BMNH1975.2081), female (BMNH1975.2083), male (BMNH1975.2082), female (BMNH1975.2084).

Kuri (Socotra Archipelago), *H. oxyrhinus* and *H. forbesii*, are included in the analyses (Gómez-Díaz *et al.* in press). According to the analyses by Gómez-Díaz *et al.* (In press), the two endemics from Abd Al Kuri are sister taxa and branch within the "*H. homoeolepis* group", in a position between *H. paucituberculatus* and a monophyletic assemblage formed by *H. masirahensis*, clade G and *H. homoeolepis*. According to the results of the analysis of Dataset 2 (dates inserted in Fig. 5), *H. masirahensis* split from its sister taxa approximately 4.4 mya (95% HPD: 2.6–6.5). This date of origin of *H. masirahensis* does not differ much from the inferred date by Gómez-Díaz *et al.* (In press) using the same methods and calibrations and including *H. oxyrhinus* and *H. forbesii* (4.2 mya; 95% HPD: 2.4–6.3).

Uncorrected genetic distances between *H. masirahensis* and the other members of the "*H. homoeolepis* group" (one of them described as new species below) are very high: *H. masirahensis vs. H. homoeolepis* 11.2% in the *cytb* and 8.8% in the *12S*; *H. masirahensis vs. H. paucituberculatus* 12.9% in the *cytb* and 9.2% in the *12S*; *H. masirahensis vs.* the new species from clade G (Fig. 5, Appendix III) 14.8% in the *cytb* and 6% in the *12S*.

The results of the nuclear networks presented in Fig. 8 are very interesting and, while all alleles of *H. masirahensis* for the nuclear genes c-*mos* and *mc1r* are private (not shared with its closermost taxa (Fig. 8) or with any other species of *Hemidactylus* from Dataset 1 or the two endemics from Abd Al Kuri (data not shown)), all 14 alleles of *H. masirahensis* of the nuclear gene *rag2* are shared with *H. paucituberculatus*. Given the fact that there is complete lineage sorting for the mtDNA (Appendix III) and in the nuclear genes c-*mos* and *mc1r*, and that no hybrids have been detected, all evidence at hand points towards ancestral polymorphism rather than ongoing interspecific gene flow.

The level of genetic variability within *H. masirahensis* is very low: 0.3% in the *cytb* and 0.1% in the *12S*, and coincides with the high level of morphological homogeneity of this species (Appendix I).

Distribution

Hemidactylus masirahensis is endemic to Masirah Island, Central Oman (Fig. 3). It has been found in very arid terrain of igneous rocks like basalt, serpentine, pyroclastics and some radiolarite almost completely devoid of vegetation (Fig. 26). Specimens for whom data is available indicate that it has been found between 40–52 m altitude.

Habits

Hemidactylus masirahensis is a small and strictly nocturnal gecko found in dry places on rock surfaces near the ground. *Hemidactylus masirahensis* is sympatric with *Bunopus spatalurus hajarensis* Arnold, 1980, with whom it shares the same spatial niche. Like all the other members of the "*H. homoeolepis* group" it is very agile, often proceeding in a series of leaps when pursued.

Description

Up to 45 mm SVL. Head and body strongly depressed; head not especially broad posteriorly and neck well defined. In adults head length about 24–28% of SVL (mean males and females 26%), head width 64–73% of head length (mean males 68%, mean females 69%), and head height 35–49% of head length (mean males 39%, mean females 42%). Adhesive pads moderate; in adults maximum width of pad on fourth hind toe less than a third of its length.

Nostril between rostral, supranasal and two superposed postnasals, with the first upper labial scale usually also entering narrowly into its border or not. One scale separating supranasals on midline. About 11–13 scales in a straight line from postnasal to edge of orbit. No more than a few slightly enlarged scales on dorsum of head. Ear opening with its longest axis running upwards and backwards, smooth-edged, usually half of eye diameter or less. Supralabial scales mean 9.0 (8–10), infralabials mean 7.3 (7–8). Mental scale broadly triangular posteriorly, bordered by two large postmentals making contact behind it, a second pair of more lateral postmentals also present, the large postmentals contacting the first or first and second upper labials; second and more posterior lower labials bordered by more irregular and smaller enlarged scales. Gulars fine, imbricate posteriorly

Weakly enlarged flat smooth scales scattered on sides of mid-and posterior dorsum of body, becoming larger and tuberculate on sacral region and tail base, and on hind limbs where conical. Ventral scales small, but larger than dorsals and imbricate, about 30–34 in a transverse row at mid body between lateral folds (often not very apparent). The only two males available have 4 preanal pores; 2–3 cloacal tubercles on each side. Scales on upper forelimb small and imbricate, with no enlarged tubercles. Scales on front of thigh and beneath about same size as belly scales or rather smaller, larger and imbricate under tibia; scattered enlarged raised tubercles present on upper surface of both femur and tibia. Lamellae under the toes of pes: 1st toe mean 6.0 (6), 4th toe mean 10.0 (10–11).

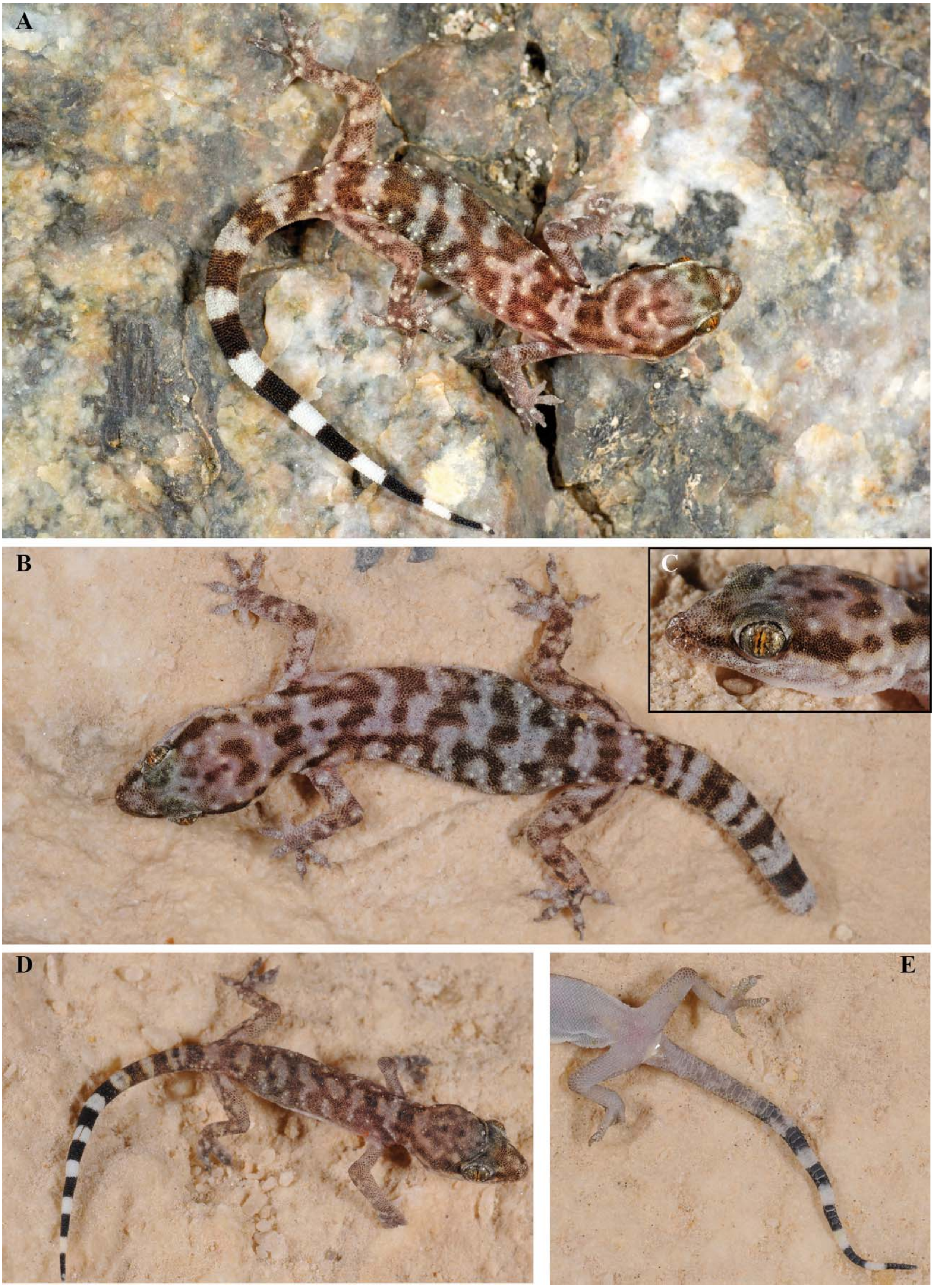

FIGURE 25. Live specimens of *H. masirahensis* sp. nov. from Masirah Island A) unvouchered specimen from Wadi Harf (photograph by Roberto Sindaco); B) female from Wadi Maahdi (IBES7710); C) detail of the head of the same specimen as in B. D) juvenile from Wadi Maahdi (IBES7707); E) underside of the tail of the same specimen as in D.

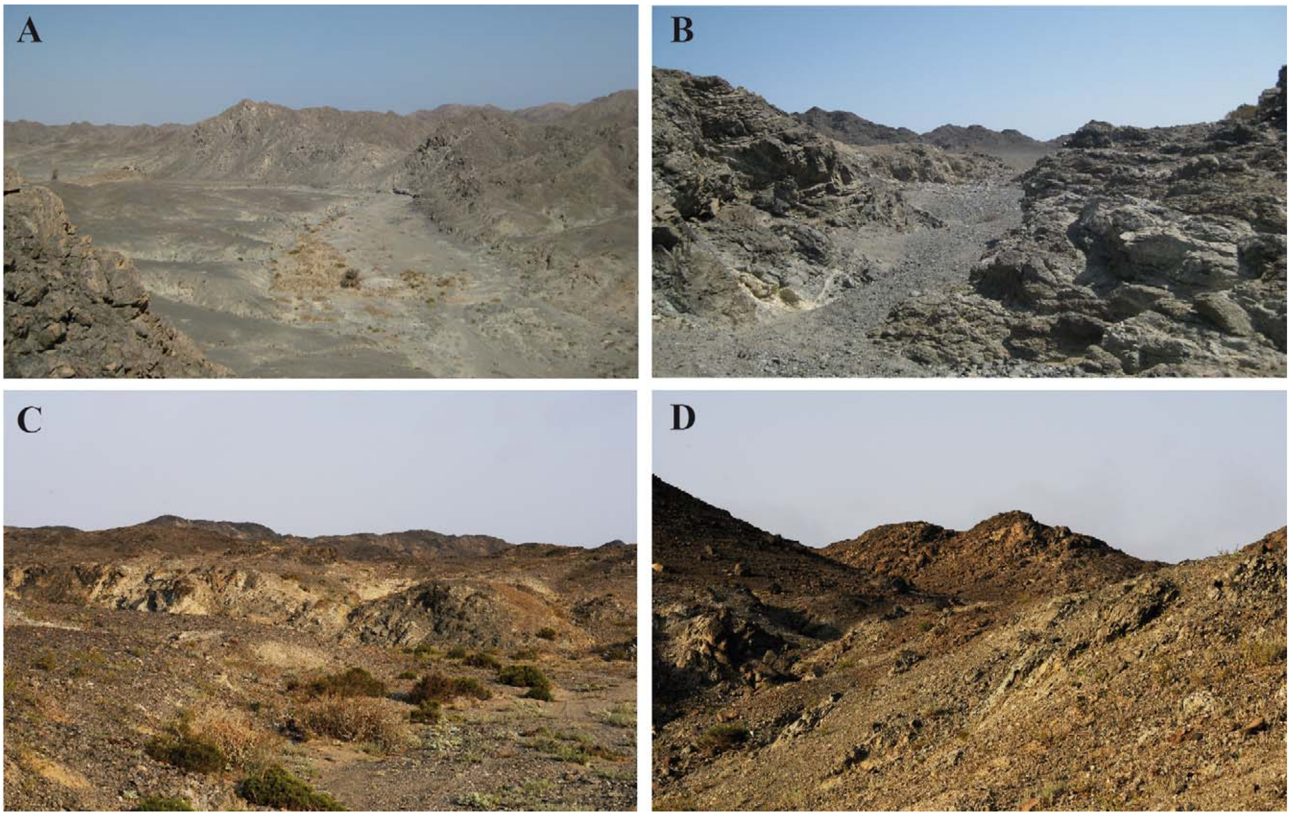

FIGURE 26. Different localities in Masirah Island where *H. masirahensis* sp. nov. has been found. In all these localities *H. masirahensis* occurred on the ground and the rocky sides of the wadis A) and B) Wadi Haql; C) and D) Wadi Maahdi.

Tail relatively slender with no tubercles away from base. About 7–10 small scales in longitudinal row on fourth whorl after vent. Subcaudal scales enlarged and broad, extending proximally as far as about the second whorl after the vent and starting soon after the hemipenial bulge in males.

In alcohol pale grey-buff or buff; a broad dark stripe from the nostril, through the eye, on to cheek above ear and often on to neck, where narrower and more medial; body with irregular dark spots and streaks that may form a coarse irregular reticulation; Belly pale. Tail with 8–9 dark bands that increase in intensity and contrast with pale ground color distally; more distal 4–6 bands extend to ventral surface, each covering two or more whorls distally and being rather broader than interstices. Pale areas on underside of tail may be irregularly blotched or stippled.

Distinctive features of Holotype

Adult male 42.1 mm SVL; tail complete, 50 mm long; supralabial scales 9/8, infralabials 7/8; 4 preanal pores; lamellae under the 1st toe of pes 6/6, under the 4th toe of pes 10/10.

***Hemidactylus inexpectatus* sp. nov.**

(Figs. 3, 5, 8, 27–29, Table 1; Appendix I; Appendix III)

MorphoBank M100233–M100346

Holotype

BMNH2008.711, male from 2.5 km Southeast of Ar Rumayliyah, 20.3319’N 57.78989’E, collected on the 29th of October 2008 by S. Carranza, E.N. Arnold and S. Alrabiei (MorphoBank M100257–M100280). **Paratypes**: BMNH2008.712, male, same collecting data as Holotype (MorphoBank M100233–M100256); IBES1798, male, same collecting data as Holotype (MorphoBank M100281–M100301); IBES7722, male from the same locality as the Holotype, collected on the 11th of October 2010 by S. Carranza and F. Amat (MorphoBank M100302–M100310); IBES7700, female, same collecting data as IBES7722 (MorphoBank M100311–M100315); IBES7735, female, same collecting data as IBES7722 (MorphoBank M100316–M100320); ONHM3711, female, same collecting data as IBES7722 (MorphoBank M100321–M100328).

Other material examined

Specimen BMNH1979.467 from Hamar-an-Nafur Island, Oman (see Appendix I).

Diagnosis

A small, slender, depressed *Hemidactylus* growing up to 44.1 mm SVL. Low conical or weakly keeled tubercles on back and neck, arranged in 14 regular rows at mid-body, largest on lateral dorsum compared with mid-back and flank; larger tubercles present on hind limbs and tail; adhesive pads narrow, lamellae under the 1st toe of pes 6, lamellae under toe 4th toe mean 10.5 (10–11); preanal pores 4; expanded subcaudal scales extend to about 2–4 whorls from tail base. Dorsum with a pattern of irregular dark spots and streaks; tail with 8–9 dark bands that increase in intensity distally contrasting with pale interstices, the final 5–6 extending to the ventral surface.

Hemidactylus inexpectatus differs from *H. homoeolepis* by its larger adult size (SVL mean 37.5 mm, max. 44.1 mm, compared with mean 31.8 mm, max. 39.7 mm), presence of conical or weakly keeled and extensive tubercles on the body, nape hind legs and tail (generally absence of tubercles in *H. homoeolepis*), lower number of preanal pores in males (4 compared with mean 5.5, 3–6), higher number of lamellae under the 1st toe of pes (6 compared with mean 4.7, 4–5), and under the 4th toe of pes (mean 10.5, 10–11, compared with mean 8.4, 7–11). Distinguished from *H. paucituberculatus* by its larger adult size (SVL mean 37.5 mm, max. 44.1 mm, compared with mean 32.2 mm, max. 38.4 mm), larger conical or weakly keeled and more extensive tubercles on the body, nape, hind legs and tail, lower number of preanal pores in males (4 compared with 6), higher number of lamellae under the 1st toe of pes (6 compared with mean 4.9, 4–5), and under the 4th toe of pes (mean 10.5, 10–11, compared with mean 8.3, 7–9). Distinguished from *H. masirahensis* by having a less depressed head and body, larger conical or weakly keeled and more extensive tubercles on the body, nape, hind legs and tail, different coloring (dark bands of the tail less conspicuous and marked in *H. inexpectatus*, especially on adults and in the underside of the tail).

Etymology

The species epithet "*inexpectatus*" refers to the unexpected finding of this distinct new species of *Hemidactylus* in this area of Central Oman.

Genetic and phylogenetic remarks

Hemidactylus inexpectatus is monophyletic in the phylogenetic analyses of Dataset 1 (Fig. 5G) and Dataset 3 (Appendix IIIG). According to Fig. 5 and Appendix III, it is sister to *H. masirahensis* sp. nov. This topology is very well supported and is maintained even if the two endemic *Hemidactylus* from the island of Abd Al Kuri (Socotra Archipelago), *H. oxyrhinus* and *H. forbesii*, are included in the analyses (Gómez-Díaz *et al.* in press). According to the analyses by Gómez-Díaz *et al.* (In press), the two endemics from Abd Al Kuri are sister taxa and branch within the "*H. homoeolepis* group", in a position between *H. paucituberculatus* and a monophyletic assemblage formed by *H. masirahensis*, *H. inexpectatus* and *H. homoeolepis*. According to the results of the analysis of Dataset 2 (dates inserted in Fig. 5), *H. inexpectatus* and *H. masirahensis* split approximately 4.4 mya (95% HPD: 2.6–6.5). This date does not differ much from the inferred date of the same split by Gómez-Díaz *et al.* (In press) using the same methods and calibrations and including *H. oxyrhinus* and *H. forbesii* (4.2 mya; 95% HPD: 2.4–6.6).

Uncorrected genetic distances between *H. inexpectatus* and the other members of the "*H. homoeolepis* group" are very high: *H. inexpectatus vs. H. homoeolepis* 13% in the *cytb* and 8.4% in the *12S*; *H. inexpectatus vs. H. paucituberculatus* 13.5% in the *cytb* and 8.9% in the *12S*; *H. inexpectatus vs. H. masirahensis* 14.8% in the *cytb* and 6% in the *12S.*

The results of the nuclear networks presented in Fig. 8 and networks including all the specimens from Dataset 1 (data now shown) indicate that all alleles of *H. inexpectatus* for all three independent loci analyzed (c-*mos, mc1r* and *rag2*) are private (not shared with any other species included in the analyses).

The level of genetic variability within *H. inexpectatus* is relatively high: 1.4% in the *cytb* and 0.5% in the *12S*, especially if one considers that all the specimens have been collected within an area of less than 0.1 km^2.

The assignation of specimen BMNH1979.467 from the offshore island of Hammar-an-Nafur to *H. inexpectatus* is based exclusively on morphological grounds. It will be very important to compare fresh material from this small island with the mainland specimens of *H. inexpectatus* (work in progress).

FIGURE 27. Preserved specimens of *H. inexpectatus* sp. nov. A–E) male, Holotype, from the type locality, 2.5 km SE of Ar Rumayliyah (BMNH2008.711); F) juvenile from Hamar-an-Nafur Island (BMNH1979.467).

Distribution

Known only from a single locality in Mainland Arabia (on the coast of the Gulf of Masirah, West of Barr al Hikman, Central Oman) and from the offshore island of Hammar-an-Nafur, situated 58 km Southeast of the type locality (Fig. 3). The altitude at the type locality is 65 m above sea level.

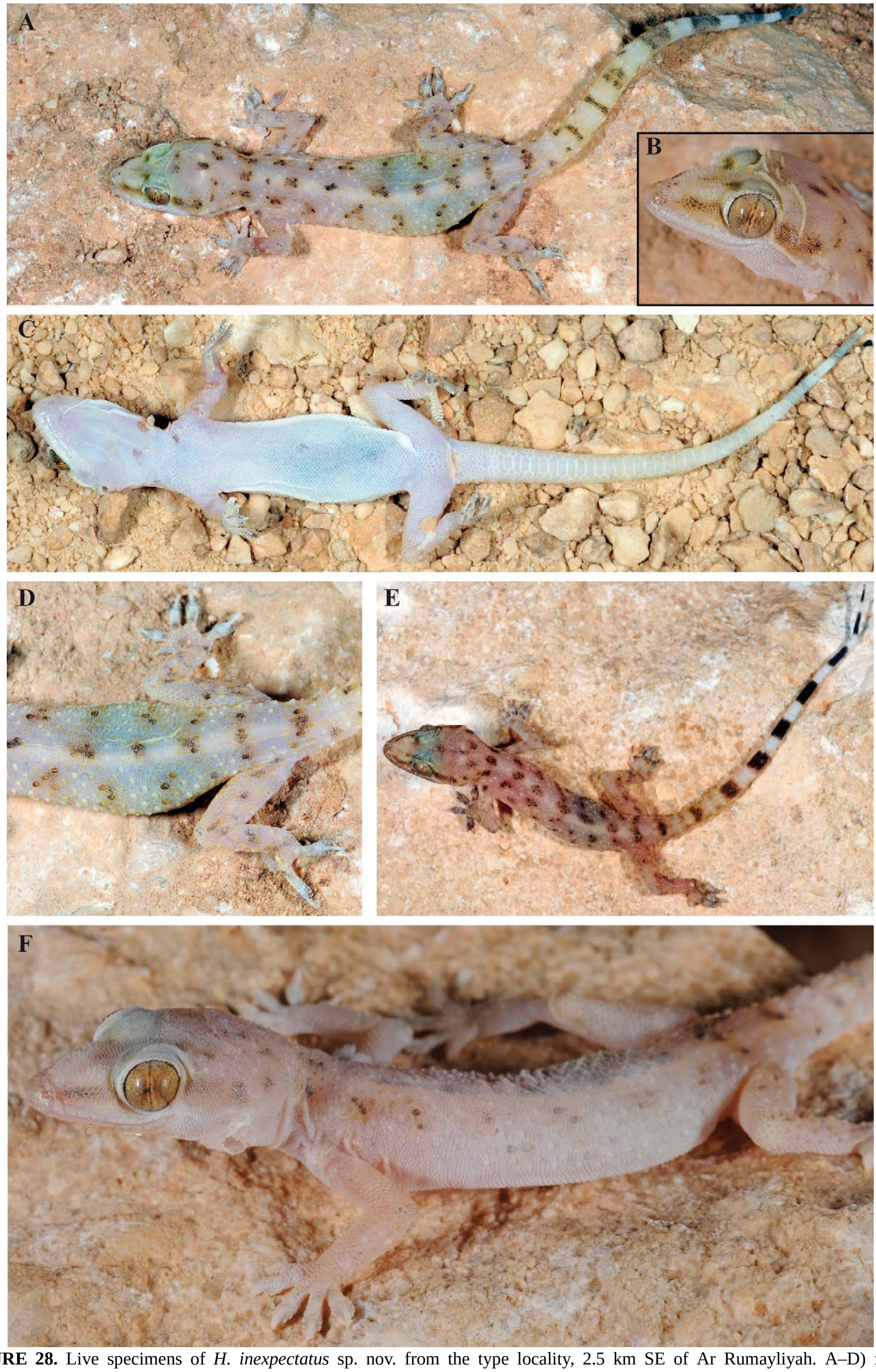

FIGURE 28. Live specimens of *H. inexpectatus* sp. nov. from the type locality, 2.5 km SE of Ar Rumayliyah. A–D) female (IBES7700); E) female (IBES7735); F) female (IBES7674).

FIGURE 29. View of the type locality of *H. inexpectatus* sp. nov., 2.5 km SE of Ar Rumayliyah. In this rather vegetated locality by the water, the species was found on rocky substrate like the one seen at the background of picture A.

Habits

Very little is known about this species of *Hemidactylus.* On the mainland, it is active after dark on low bare rock outcrops with very little or no vegetation. The only mainland locality known for this species is in a wadi and specimens were quite close to water (Fig. 29). Like all the other members of the "*H. homoeolepis* group" it is very agile, often proceeding in a series of leaps when pursued.

Description

Up to 44.1 mm SVL. Head and body depressed; head not especially broad posteriorly and neck well defined. In adults head length about 26–29% of SVL (mean males 26% mean females 27%), head width 63–70% of head length (mean males 67%, mean females 68%), and head height 34–41% of head length (mean males 35%, mean females 40%). Adhesive pads moderate; in adults maximum width of pad on fourth hind toe less than a third of its length.

Nostril between rostral, supranasal and two superposed postnasals, with the first upper labial scale usually also entering narrowly into its border. One scale separating supranasals on midline. About 13–14 scales in a straight line from postnasal to edge of orbit. No more than a few slightly enlarged scales or tubercles on dorsum of head. Ear opening with its longest axis running upwards and backwards, smooth-edged, usually half of eye diameter or less. Supralabial scales mean 10.4 (9–11), infralabials scales mean 8.2 (7–9). Mental scale broadly triangular posteriorly, bordered by two large postmentals making contact behind it, a second pair of more lateral postmentals also present, the large postmentals contacting the first or first and second upper labials; second and more posterior lower labials bordered by more irregular and smaller enlarged scales. Gulars fine, imbricate posteriorly

Low conical or weakly keeled tubercles on back and neck, arranged in 14 regular rows at mid-body, largest on lateral back compared with mid-back and flank; larger tubercles present on hind limbs. Ventral scales small, but larger than dorsals and imbricate, about 35–42 in a transverse row at mid body between lateral folds (often not very apparent). Preanal pores in males 4; 2–3 cloacal tubercles on each side. Scales on upper forelimb small and imbricate, with a few enlarged tubercles or not. Scales on front of thigh and beneath about same size as belly scales (or rather smaller), rather larger and imbricate under tibia; enlarged raised tubercles present on upper surface of both femur and tibia. Lamellae under the toes of pes: 1st toe mean 6.0 (6), 4th toe mean 10.5 (10–11).

Tail relatively slender with 8 to 6 tubercles at the base, the number dropping to 4 and then to 2 about half way to tip and being absent distally. About 10–11 small scales in a longitudinal row on fourth whorl after vent. Subcaudal scales enlarged and broad, extending proximally as far as whorl 2–4 after the vent.

In alcohol pale grey; a broad dark stripe from the nostril, through the eye, on to cheek above ear; body with irregular dark spots and streaks. Belly pale. Tail with 8–9 dark bands that increase in intensity and contrast with pale ground color distally; more distal 5–6 bands extend to ventral surface, each covering the equivalent of two or more whorls distally and being equal or rather broader than interstices. Pale areas on underside of tail may be irregularly blotched or stippled.

Distinctive features of Holotype

Adult male, 44.1 mm SVL; tail intact 50 mm long; 14 rows of enlarged tubercles at mid-back; supralabial scales 10/10, infralabials 8/7; 4 preanal pores; lamellae under the 1st toe of pes 6/6, 4th toe of pes 11/11.

An enigmatic North Oman *Hemidactylus* from the stomach of a preserved snake

In 1976, a distinctive male *Hemidactylus* was found in the stomach of a snake, *Platyceps rhodorachis* (Jan, 1865) (BMNH85.11.7.16), sent to the Natural History Museum, London by Colonel Atmaram Sadashiv G. Jayakar in 1885 with the locality 'Muscat' (Arnold 1986; Arnold & Gallagher 1977) (Fig. 30). Colonel A.S.G. Jayakar (1844–1911) was sent to Oman by the Indian Medical Service in 1878 and during his 30 years in the Muscat area he studied the local wildlife and collected many specimens that he donated to the British Museum of Natural History, having several species named after him (some examples include the Arabian sand boa *Eryx jayakari* Boulenger, 1888, the lacertid *Omanosaura jayakari*, the seahorse *Hippocampus jayakari* Boulenger, 1900, the fish *Lestidiops jayakari* Boulenger 1889, and the endangered mountain goat *Hemitragus jayakari* Thomas, 1894). Although no similar *Hemidactylus* have been encountered since, it is unlikely that the specimen came from a locality very far from Muscat itself, as all the other reptile and amphibian species in Jayakar's substantial collections have subsequently been found quite close to this town. Jayakar may, however, have obtained some of his material outside the immediate vicinity of Muscat. A possible indication of where this might be involves the type material of the lacertid *Omanosaura jayakari,* which Jayakar obtained. These specimens have higher average dorsal and other scale counts than those from other areas of North Oman where the species is known to occur, namely the Jebel Akhdar region, the Eastern United Arab Emirates, and the Musandam Peninsula (Arnold 1986; Arnold & Gallagher 1977). Recently, specimens with such high counts have been found south of Muscat (in the Eastern Hajars at Wadi Tiwi and Wadi Bani Khalid), raising the possibility that Jayakar's *Hemidactylus* also came from there. However, careful searches south of Muscat, specifically in Wadi Mayh near Quryat, and at Wadi Tiwi, Wadi Bani Khalid, and Jebal Qahwan, only produced *Hemidactylus hajarensis* sp. nov. It is possible that the enigmatic *Hemidactylus* may not live in the rocky situations typical of other Arabian species of the genus, and may have a distinctive habitat of its own, for example trees or bushes. Such situations should be explored in further searches for this form. Meanwhile, as Jayakar's specimen is different from all other known Arabian *Hemidactylus*, it is described below as a new species.

Another enigmatic male *Hemidactylus* (BMNH1996.394) was also found in the stomach of a snake identified as *Pseudocerastes persicus* by M.D. Gallagher at Jebel Qahwan, above Wadi Hebaheba, near Sur (22.10N 59.20E, 808m) in Northeast Oman. Most of this gecko had been digested and only the posterior body, hind-limbs and tail remain, but these show a combination of features that, when compared with other *Hemidactylus* from Wadi Habaheba and other parts of the Eastern Hajars, allowed us to confidently identify it as *H. hajarensis* sp. nov.

Hemidactylus endophis **sp. nov.**

(Fig. 30, Appendix I)
MorphoBank M101997–M102030

Hemidactylus sp: Arnold, 1977: 102; Arnold, 1980: 279 (part.); Arnold, 1986: 420; van der Kooij, 2000: 110.

Holotype

BMNH1976.1323, male, lodged in the gullet of a *Platyceps rhodorachis* (BMNH85.11.7.16) labeled as "Muscat", collected by A.S.G. Jayakar (MorphoBank M101997–M102030).

Diagnosis

Hemidactylus endophis can be distinguished from all currently described Arabian members of *Hemidactylus* based on the following combination of characters: A medium-sized *Hemidactylus* (only known specimen 59 mm SVL); large tubercles on dorsum relatively weakly keeled, arranged in 16 regular rows at mid-body, largest on lower flanks; scaling on belly coarse (about 26–28 in transverse row at mid-belly), coarse bluntly pointed and imbricate scales in front of vent similar to those on belly; adhesive pads on digits not especially broad, about half as wide as long on 4th toe of pes; lamellae under the 1st toe of pes 6, lamellae under the 4th toe 9; 7 femoral pores under each thigh (14 in total), broadly separated medially by 6 scales.

Etymology

From the classical Greek prefix *endŏ-* meaning inside, and *ŏphis*, a snake.

Distribution

Presumably the Muscat region of North Oman.

Habits

Unknown.

Description of Holotype

Fifty-nine mm SVL. Head and body apparently not very markedly depressed; head not especially broad or neck well defined. Head length about 24% of SVL, head width 68% of head length, and head height 46% of head

FIGURE 30. Pictures showing different details of the Holotype of *H. endophis* sp. nov. (BMNH1976.1323).

length. Adhesive pads on digits not especially broad, maximum width of pad on fourth hind toe about a third of its length.

Nostril between rostral, supranasal and two superposed postnasals, with the first upper labial scale usually also entering narrowly into its border. One scale separating supranasals on midline. About 12–13 scales in a straight line from postnasal to edge of orbit. Small rounded and slightly keeled tubercles scattered in posterior interorbital, crown of head and temporal area above the level of ear opening and immediately in front of the upper part of this. The anterior part of the palpebral fold with very coarse scales. Ear opening with its smooth-edged, fairly rounded, longest axis less than half diameter of eye. Supralabial scales 9/11, infralabials 9/10. Mental broadly triangular posteriorly, bordered by two large postmentals making contact behind this, a second pair of more lateral postmentals also present, their hind borders rounded and extending posterior of those of the larger more medial postmentals which contact the first and second supralabials; second and more posterior infralabials bordered by more irregular and smaller enlarged scales. Gulars small and imbricate.

Enlarged tubercles present on back, arranged in obliquely diagonal rows running from near midline posteriorly to flank, 16 across mid-body, and 19 in a paravertebral row from the level of the axilla to that of the groin, where they are separated by spaces of about their own length. Tubercles weakly keeled. The largest and most backwardly pointed on posterior flanks where tubercles finely striated and spaces between them smaller than tubercles themselves. Belly scales much larger than dorsals and flat and imbricate, about 26–28 in a transverse row at mid-body between lateral folds. Femoral pores 7 under each thigh (14 in total), broadly separated medially by 6 scales. Scales on upper forelimb flat and imbricate above and largest distally, where there are a few enlarged tubercles posteriorly. Seven large tubercles on dorsal surface of femur and eleven on tibia. Underside of hindlimb with flat overlapping scales more or less like those on belly. Lamellae under the 1st toe of pes 6, under the 4th toe of pes 9. Tail missing

In alcohol beige grey above and paler below. No pattern discernible, probably because of partial digestion.

The *Hemidactylus turcicus* group

(Figs. 4, 5, 31, Table 1; Appendix I; Appendix III)

Hemidactylus turcicus turcicus (Linnaeus, 1758) has a mainly circum-Mediterranean distribution including many islands and with populations extending to the South along the Nile River up to the border with Sudan (Sindaco & Jeremcenko 2008). They have also been introduced recently in the Canary Islands, Mexico, Cuba, Florida, and in other areas of the United States (Kraus 2009). According to a recent phylogenetic study from Carranza and Arnold (2006), *H. turcicus* may have originated in the Middle East from where it moved Westwards across the whole Mediterranean, eventually reaching the Atlantic Ocean. In this same study, the authors obtained two distinct mtDNA lineages of *H. turcicus* with little genetic divergence between them, suggesting that the phylogeographic pattern obtained was the result of a very rapid and recent spread. Results obtained for the European populations of another gecko, *Tarentola mauritanica* had, until recently, been interpreted to support the same scenario. However, Rato *et al.* (2010, 2011) have shown that the phylogeographic pattern of both *T. mauritanica* and *H. turcicus* are not solely the result of a recent colonization but represent two unprecedented cases of selective sweeps taking place in the same geographic area (Rato *et al.* 2010, 2011). While the circum-Mediterranean populations of *H. turcicus* represent two closely related lineages, the dark-colored *H. lavadeserticus* was described from the black Syrian basal desert, *H. mindiae* was reported from Southern Jordan (Amr *et al.* 2007) and a new morphologically and genetically distinct species, *H. dawudazraqi*, was recently described from a wide area ranging from Southern Syria to Southwestern Jordan (Moravec *et al.* 2011). Some inland North Arabian *Hemidactylus* may also form part of the *H. turcicus* assemblage, including ones from (spelling copied from the BMNH records) Qunfidah, Saudi Arabia (BMNH1992.170–171); 150 km south of Taymah, Saudi Arabia (BMNH1992.169); Hali, Saudi Arabia (18º 44’N 41º 24’E; BMNH1992.200–2001); 20 km East of Hail (BMNH1988.209) and Riyadh (BMNH1986.215). An animal from Hail is illustrated by Leviton *et al.* (1992; plate 5).

Interestingly, *H. lemurinus* described from Wadi Ayoun in Central Dhofar, South Oman (Figs. 4 and 31) turns out to be part of the *H. turcicus* group (Fig. 5; Appendix III), closely related to a clade formed by *H. turcicus* and *H. dawudazraqi*. According to the results of the dating analysis inferred with Dataset 2, *H. lemurinus* and the ancestor of *H. turcicus* and *H. dawudazraqi* split about 5.9 mya (95% HPD: 3.4–8.7). Uncorrected genetic distances between *H. lemurinus* and *H. turcicus* are 14% in the *cytb* and 4.6% in the *12S*; between *H. lemurinus* and *H. dawudazraqi* 13.8% in the *cytb* and 4.4% in the *12S*. As shown in Fig. 31, superficially *H. lemurinus* is unlike other members of the group, differing by its relatively large size, big head, slender limbs and tail, absence of enlarged tubercles on the dorsum, and in its pallid coloration. Since *H. lemurinus* was described, it has been recorded from near Mughsayl in Western Dhofar, South Oman (A.S. Gardner, pers. comm.; not shown in Fig. 4 as no specimens are available and its presence could not be confirmed in any of our trips), and close to the Southern coast of Yemen at Sayhut and Wadi Hajr (Schatti & Desvoignes 1999). The latter record is about 650 km west of the type locality.

FIGURE 31. Pictures of live specimens and typical habitat of *H. lemurinus.* A–C) two unvouchered specimens (A and C are the same specimen) of *H. lemurinus* photographed in Wadi Ayoun, the type locality of the species. D) and E) detail of the big smooth white boulders at Wadi Ayoun, where *H. lemurinus* is found at night running with great agility, side by side with *Ptyodactylus hasselquistii*.

Hemidactylus robustus

(Figs. 4, 5, 32, Table 1; Appendix I; Appendix III)

The distribution of *H. robustus* is difficult to predict with certainty due to the confusion with *H. turcicus* and other similar taxa (Sindaco & Jeremcenko 2008; Bauer *et al*. in press). In Arabia it is widely distributed, with populations on the Western coast starting from at least 22º N Southwards to the Aden region. It is also present in Socotra Island, the Hadramaut and occurs in Oman in coastal Dhofar, on Masirah Island and the neighboring mainland, around the Sharqiya Sands (formerly Wahiba Sands) and Northwards to the Eastern United Arab Emirates. *Hemidactylus robustus* also occurs in costal Iran, Pakistan, in Gurajat (India), along the African Red Sea coast of Southern Egypt and Sudan, in Eritrea, East Ethiopia, Djibuti, Somalia and extreme Northeast Kenya.

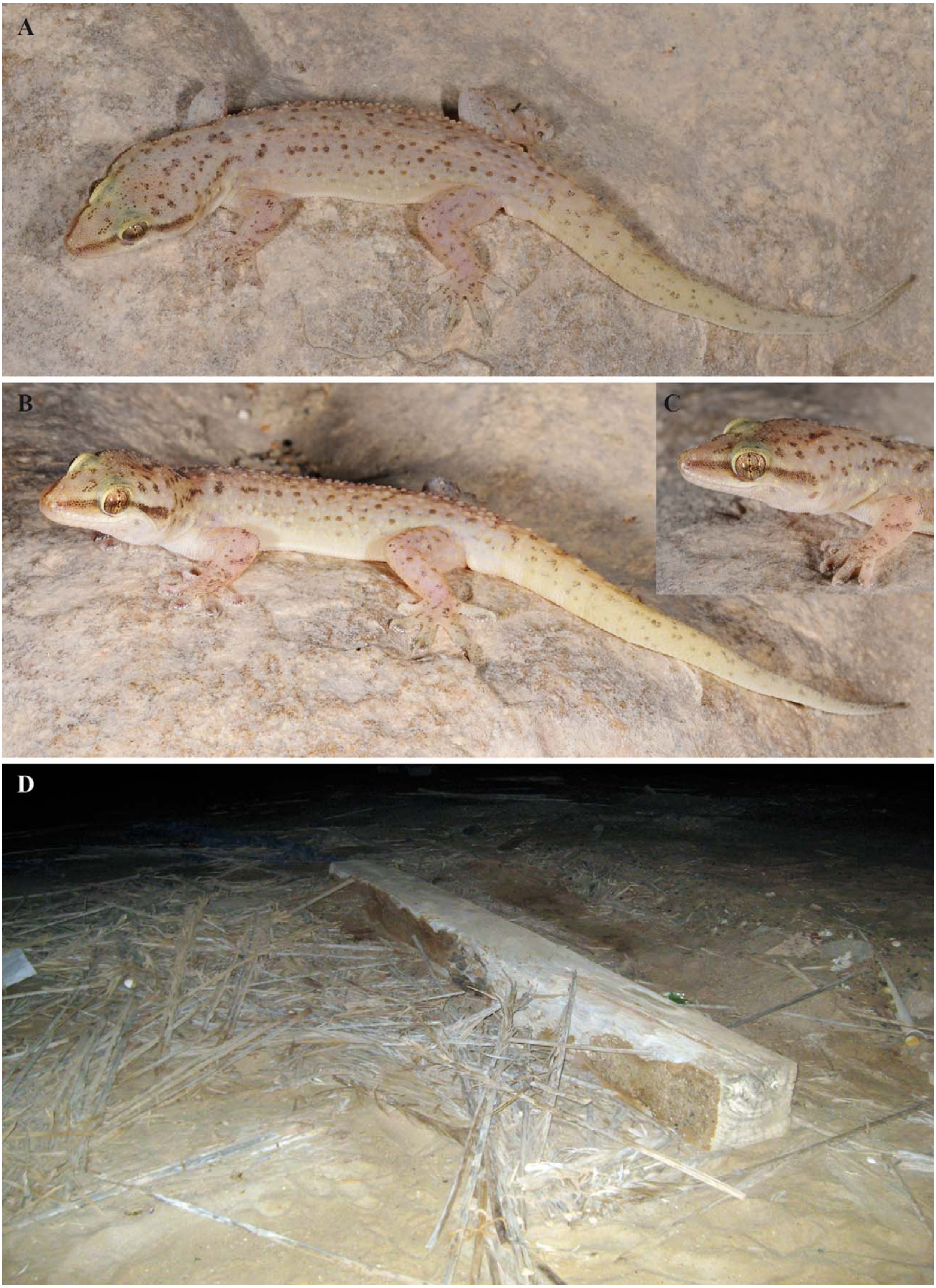

FIGURE 32. Pictures of a live specimen and one locality of *H. robustus*. A–C) unvouchered specimen from East Khor, Dhofar; D) picture of the locality 8 km W of Shannah, where representatives of the two divergent phylogenetic lineages of *H. robustus* have been found in sympatry (see main text, Fig. 5 and Appendix III).

Available material from widely separated localities (Fig. 4) in the United Arab Emirates, Al Azaiba in North Oman, 8 km W of Shannah (opposite Masirah), Dhofar (South Oman) and Yemen form a clade (Fig. 5) and are all genetically very similar, showing a low divergence from a specimen from Safaga, Egypt. In contrast, animals from Masirah Island and one from Shannah, on the nearby mainland, form a separate clade that differs by 8.7% in the *cytb* and 3.6% in the *12S*. According to the results of the dating analysis inferred with Dataset 2, the two clades of *H. robustus* split approximately 3.0 mya (95% HPD: 1.8–4.6).

Such divergence and restricted known coexistence at Shannah suggests that the two clades may represent separate species but, as yet, they are not associated with known morphological differences. The presence of two distinct mtDNA clades in Arabia suggests that *H. robustus* originated there. The genetic uniformity of the geographically widespread clade of *H. robustus* may indicate that it has spread over its very large range only quite recently. The frequent occurrence of this form in anthropogenic situations suggests that such dispersal may have been by inadvertent transport with people.

Members of the Tropical Asian clade of *Hemidactylus*

(Figs. 4, 33, Table 1)

Two species found in Arabia belong to the Tropical Asian clade (Carranza & Arnold 2006). *Hemidactylus flaviviridis* extends from Northern India, Westwards around the coastal areas of the Arabian Peninsula, to the coast of Egypt, Sudan, Eritrea, Djibuti and Northern Somalia. According to Largen and Spawls (2010), its presence in Africa is believed to be the result of accidental introduction along with baggage or cargo carried by trading vessels. Specimens from Oman are not obviously different in morphology from animals elsewhere, including specimens from the species' main range in Northern India. Mitochondrial DNA is similar at widely separated localities in Iran, United Arab Emirates and Oman and also on Socotra (Carranza & Arnold 2006), indicating relatively recent, perhaps anthropogenic spread, as with *H. robustus* (see above). A second member of the Tropical Asian clade, *Hemidactylus leschenaultii* of India and Sri Lanka, occurs in a locality on the Batinah coast of North Oman (Gardner 1992). According to van der Kooij (2000), it is a nocturnal arboreal gecko that is found exclusively on old *Acacia* trees with many hiding places. When present, it displaces *H. robustus* from this habitat. As for *H. flaviviridis*, populations in Oman show no obvious morphological differentiation suggesting that this species may also be the result of an introduction. Unfortunately, we could not visit the localities of *H. leschenaultii* in any of our expeditions to Oman and, as a result of that, this species was not included in the phylogenetic analyses.

Biogeography of Arabian *Hemidactylus*

Endemic species of *Hemidactylus* in Arabia and its northern hinterland for which DNA is available belong to the Arid clade of that genus. The ancestor of the assemblage is likely to have originated in adjoining Northeast Africa, as more basal members of the Arid clade are found there and on neighboring Socotra island (Carranza & Arnold 2006; Gómez-Díaz *et al.* in press), and three of the four other main clades of *Hemidactylus* are primarily African (Carranza & Arnold 2006).

It is likely that vicariance was the main driver of early divergence in Arabian *Hemidactylus*. Some of this was probably related to geological events. For example, disjunctions in many clades suggest that Northern Oman has been intermittently separated from the rest of Arabia, something that may have been caused by marine incursions (Arnold 2009; Glennie 2006). Climatic change, particularly aridification, may also have interrupted the ranges of *Hemidactylus* taxa, which are essentially fairly mesic in their requirements.

As with North Oman, other disjunctions in *Hemidactylus* elsewhere in Arabia are sometimes repeated in other taxa. For instance, in Southern Arabia, the separation of the Dhofar endemics, *H. alkiyumii* and *H. festivus* from the more Western *H. yerburyii* complex, is repeated in several other taxa including *Uromastyx* and *Echis* (Arnold *et al.* 2009; Wilms & Schmitz 2007). Smaller-scale separations occur in the Dhofar region where endemics may occur in East Dhofar with related taxa being present to the West, and sometimes the North and further East as well. This pattern is found in *H. paucituberculatus* and *H. homoeolepis*, in *H. alkiyumii* and *H. festivus,* and among other geckos in the *Pristurus rupestris* and *P. carteri* complexes, and probably in *Tropiocolotes* as well (Arnold 1977, 1980, 2009).

FIGURE 33. Pictures of live specimens of the two representatives of *Hemidactylus* of the Tropical Asian clade (Carranza & Arnold, 2006) present in Arabia (probably introduced). A) unvouchered *H. flaviviridis* from Socotra Island, Yemen (photograph by Fabio Pupin); B) *H. leschenaultii* from Sri Lanka (photograph by R. Alexander Pyron).

Although most genetic and morphological diversity in Arabian *Hemidactylus* is found in the South of the peninsula, the occurrence of some units in North Arabia and beyond may be long standing. For example, this is suggested in *H. persicus* by its strong divergence from other Arabian members of the Arid clade and by its genetic diversity within Iran (see above).

Wide, fragmented ranges that overlap other taxa indicate that some subclades of *Hemidactylus* that separated in Arabia later dispersed and then differentiated. More striking cases include the *H. homoeolepis* group with its four allopatric species in Southern Arabia, and the members of the *H. turcicus* group in the Levant (*H. turcicus*, *H. lavadeserticus* and *H. dawudazraqi*) and 2000 km away in Dhofar (*H. lemurinus*). It is important to notice that, although none of the seven non-introduced species of *Hemidactylus* from the Socotra Archipelago have been included in the present work, a thorough phylogenetic and phylogeographic analysis of Socotran *Hemidactylus* has been carried out by Gómez-Díaz *et al.* (in press) and the results indicate that the two endemic species from Abd Al Kuri (*H. forbesii* and *H. oxyrhinus*) and the morphologically and genetically distinct *H. homoeolepis* from Socotra, Samha and Darsa have independently colonized the Socotra Archipelago from the Dhofar region in South Oman within the last 6.8 my. These results highlight the importance of Dhofar as a center of diversification in *Hemidactylus*.

As already noted, one clade of *H. robustus* and the studied populations of *H. flaviviridis*, which is a member of the Tropical Asian clade of *Hemidactylus*, are distinctive in their genetic uniformity and wide ranges in Arabia and outside it. These characteristics may result from recent spread with people, especially as the species are often found in and around human habitations. Similar and more marked cases are known in such *Hemidactylus* species as *H. turcicus* in the Mediterranean area and North America (although see Rato *et al.* 2011), *H. mabouia* in the Neotropics, *H. frenatus* in the Indian and Pacific Oceans, and *H. garnotii* in the Pacific Ocean (Carranza & Arnold 2006). The disjunct presence of *H. leschenaultii*, another member of the Tropical Asian clade, on the Batinah plain in North Oman may also be anthropogenic. Given the diversity of *Hemidactylus* in Northeast Africa and Arabia, it is remarkable that the genus is not naturally more widespread in North Africa. The presence of *Tarentola* geckos throughout this region suggests that this species and *Hemidactylus* might exclude each other, especially as *Tarentola* itself does not penetrate into Arabia or Northeast Africa where so many *Hemidactylus* are found

Ecological separation

The way in which species of Arabian *Hemidactylus* separate ecologically is surprisingly varied. They may occur at similar altitudes but replace each other geographically, as in the *H. homoeolepis* group. Or if they are sympatric there may be altitudinal separation, such as that between *H. hajarensis* and *H. luqueorum* on the Jebel Akhdar in North Oman where these two species have never been recorded in the same locality. Humidity may also be an important factor, as in the separation of the relatively mesic *H. alkiyumii* and more xeric *H. festivus* in Dhofar. When animals exist within a few meters of each other, structural niche may be significant, as at Wadi Ayoun in Dhofar where *H. festivus* occurs on rocks closer to the ground than *H. lemurinus*, and *H. homoeolepis* lower still and on the ground (Arnold 1980). While four native species occur close together in Dhofar, most *Hemidactylus* communities in Arabia consist of only one or two species, although climbing geckos belonging to other genera, such as *Asaccus* and *Ptyodactylus*, may also be present. In Oman at least, *Ptyodactylus* tends to occur further from the ground than *Hemidactylus* species. Occurrence of *Hemidactylus* together with *Asaccus* in North Oman is very frequent and, for instance, *H. luqueorum* and *A. platyrhynchus* were found sharing the same microhabitat inside a cave close to Hat, Jebel Akhdar, and *H. hajarensis* and *A. platyrhynchus* have been found on the same rocks in Wadi Tanuf, Jebel Akhdar (pers. observ.). *Hemidactylus luqueorum* has also been seen found in syntopy with the small *A. montanus* but their size differences suggest that there are corresponding differences in the size of the prey taken. It is interesting to notice that *H. luqueorum* and *H. hajarensis* are not known to occur in the mountains running north from Jebel Akhdar to the Musandam Peninsula, where *Ptyodactylus*, *Asaccus*, *H. robustus* and *H. flaviviridis* have been recorded. The reasons for that interesting biogeographic pattern are unknown but the phylogenetic analyses presented here indicate that both species *H. luqueorum* and *H. hajarensis* have been present in the Hajar Mountains for the last 8 my, so its absence in the Western Hajar Mountains and Musandam Peninsula cannot be explained by lack of time to disperse to these areas further North. Ecological niche modelling of these two *Hemidactylus* species should indicate if this absence can be explained by environmental variables alone or if it is the result of other ecological factors. A similar case occurs with *P. rupestris*, very abundant across the Hajar Mountain range but absent from the Musandam Peninsula (Arnold 2009).

Key to the genus *Hemidactylus* from Oman

1a - No enlarged tubercles on upper surface of body, hind legs and tail or, if present, tubercles on body few and weak 2

1b - Numerous enlarged tubercles, which are usually raised and keeled, on the upper surface of the body, limbs and tail; those on the body usually arranged in regular longitudinal rows 8

2a - Adults up to about 45 mm from snout to vent; 3–6 preanal pores in males only; lamellae under the 1st toe of pes 4–6; 4th toe of pes 7–11. 3

2b - Adults over 50 mm from snout to vent, often considerably so; lamellae under the 1st toe of pes 6–10; 4th toe of pes 9–14 6

3a - Adults from Oman up to 34 mm from snout to vent; scaling fine, without any tubercles; expanded subcaudal scales beginning some way from tail base, dorsal pattern spotted . . . . *H. homoeolepis*

3b - Adults larger than 34 mm (up to 45 mm) from snout to vent; tubercles present on the body, nape, and hind legs; expanded subcaudal scales usually extend almost to tail base 4

4a - Adults larger than 39 mm (up to 45 mm) from snout to vent; presence of enlarged tubercles beyond mid-body; 4 preanal pores in males; lamellae under the 1st finger of pes 6; lamellae under the 4th toe of pes 10–11 5

4b - Adults up to 39 mm from snout to vent; usually with flat enlarged tubercles on sides of dorsum as far forwards as mid-body that are also present on sides of dorsal tail base and on the hind legs, and may also occur on the lower forelimb; 6 preanal pores in males; lamellae under the 1st finger of pes 4–5; lamellae under the 4th toe of pes 7–9 . . . . *H. paucituberculatus sp. nov.*

5a - Low conical or weakly keeled tubercles on back and neck, arranged in 14 regular rows at mid-body, largest on lateral dorsum compared with mid-back and flank; larger tubercles present on hind limbs and tail; adhesive pads narrow; 4 preanal pores in males, lamellae under the 1st toe of pes 6; lamellae under the 4th toe of pes 10–11 . . . . *H. inexpectatus* sp. nov.

5b - Presence of flat enlarged tubercles mainly on the sides of the body and hind limbs; very contrasting tail with black bands with pale interstices, even in adults, that extend to the ventral surface; 4 preanal pores in males; lamellae under the 1st toe of pes 6; lamellae under the 4th toe of pes 10–11; Masirah Island . . . . *H. masirahensis* sp. nov.

6a – Enlarged tubercles present on sides of tail; tail depressed; males with a series of femoral pores interrupted on the preanal region, 4–16 pores on the underside of each thigh… 7

6b - No enlarged tubercles on the sides of the tail; tail round (not depressed); 3–8 pores present in front of vent in both sexes . . . . *H. lemurinus*

7a - Adults up to 95 mm from snout to vent; tubercles never present on back; tail with clear regular segments; 4–14 femoral pores on the underside of each thigh; lamellae under the 1st toe of pes 7–10; dorsal coloration yellowish-gray, pale yellow or yellowish-green, unmarked or with rather feeble dark wavy transverse bands; underside pale to bright yellow . . . . *H. flaviviridis*

7b - Adults up to 80 mm from snout to vent; upper surface of body covered with small granules, uniform or intermixed with more or less numerous scattered round tubercles; 10–20 femoral pores on the underside of each thigh; lamellae under the 1st toe of pes 6–7, under the 4th toe 9–12; dorsal coloration grey, with darker markings, forming undulating cross bars, rhomboidal spots on the middle of the back, or regular longitudinal bands; a dark stripe form the eye tothe shoulder; lower surface white… . . . . *H. leschenaultii*

8a - Femoral pores present, at least in males, 7 under each thigh, broadly separated medially by 6 scales; tubercles on the back large, strongly keeled and striate; lamellae under the 1st toe of pes 6; 4th toe of pes 9 . . . . *H. endophis* sp. nov.

8b - Preanal pores 4–10 in males, either in a continuous row or separated by one or two scales but never extend on to thighs 9

9a - Adults up to 55 mm from snout to vent; adhesive pads not strongly expanded, not much wider than toe; claws short; tubercles on back rather small and not clearly striated; lamellae under the 1st toe of pes 5–7; 4th toe of pes 9–11; a very distinctive black streak running from the nostril through the eye to the ear opening . . . . *H. robustus*

9b - Adults up to 88 mm from snout to vent, although one species does not exceed 53 mm; adhesive pads on digits strongly expanded, much wider than toe; tubercles on back of moderate to large size and striated; lamellae under the 1st toe of pes 6–11; 4th toe of pes 10–14 10

10a - Lamellae under the 1st toe of pes 7–11; 4th toe of pes 11–14; endemic to the Hajar Mountains, North Oman 11

10b - Lamellae under the 1st toe of pes 6–8; 4th toe of pes 10–12; South Oman 12

11a - Adults up to 67 mm from snout to vent; lamellae under the 1st toe of pes 7–9. . . . . *H. hajarensis* sp. nov.
11b - Adults up to 88 mm from snout to vent; lamellae under the 1st toe of pes 10–11. *H. luqueorum* sp. nov.

12a - Adults up to 53.6 mm from snout to vent; preanal pores 6; slender habitus; distinctive pattern of narrow dark bands—one on neck, three on body and one on anterior sacrum, often suffused with yellow in life; tail very light distally with a pattern of 7–9 widely separated dark bands, the more distal of which extend to the ventral surface . . . . *H. festivus* sp. nov.
12b - Adults up to 74.5 mm from snout to vent; preanal pores 6–10; more robust habitus; tail not light distally, with pattern of 11–14 dark bands that are not especially widely separated and only extend ventrally towards the tail tip where they are not very conspicuous. . . . . *H. alkiyumii* sp. nov.

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Appendix I: Measurements and scale counts of the specimens of Hemidactylus (all measurements in mm). Catalogue: BMNH = British Museum, IBE = Institute of Evolutionary Biology; Locality: OM = Oman, SA = Saudi Arabia, SO = Somalia, YE = Yemen, IQ = Iraq, BA = Bahrain, PA = Pakistan, UAE = United Arab Emirates, ER = Eritrea, IN = India, ETH = Ethiopia, SU = Sudan, EG = Egypt; SVL: snout-vent length; TRL: trunk length; TL: tail length; HL: head length; HW: head width; HH: head height; OD: orbital diameter; NE: nares to eye distance; IN: internarial distance; IO1: anterior interorbital distance; IO2: posterior interorbital distance; TB: longitudinal tubercle rows; PAP: number of preanal pores; SL: number of supralabial scales; IL: number of infralabial scales; LP 1st: number of lamellae under the first finger of the pes; LP 4th: number of lamellae under the fourth finger of the pes; MorphoBank: MorphoBank codes (project P483) for the pictures of all specimens included in the morphological analysis. Individuals with the specimen code highlighted with a superscript "H" are Holotypes and with a superscript "P" are Paratypes.

Species	Catalogue	Locality	Sex	SVL	TRL	TL	HL	HW	HH	ratio HL/SVL	ratio HW/HL	ratio HH/HL	OD	NE	IN	IO1	IO2	TB	PAP	SL (L/R)	IL (L/R)	LP 1st (L/R)	LP 4rth (L/R)	Morphobank
H. persicus	**BMNH1932.10.1.12**	SA, Ruins of Hedjaz	M	67	29.2	75	15.5	13.1	7.6	0.23	0.85	0.49	3.9	5.9	2.4	5.7	8.4		9	13/13	9/9	?/?	14/?	M94802-M94817
H. persicus	**BMNH1906.8.10.10**	PA, Sind	M	64	25	68	14.9	13.6	8.2	0.23	0.91	0.55	4.2	6	2.1	5.8	8.1	14	10	?/11	?/8	?/?	?/?	M94769-M94777
H. persicus	**BMNH76.10.28.8**	PA, Near Rohri, Sind	M	66.1	26.5	77	16.1	14.4	9.6	0.24	0.89	0.60	4.1	6.6	1.3	6.5	8.7	15	8	11/10	9/9	9/9	?/13	M94741-M94754
H. persicus	**BMNH85.7.11.2**	PA, Hydrab, Sind	M	58	23.1		15	11.5	7.5	0.26	0.77	0.50	3.7	5.5	1.9	5.6	7.3	15	8	13/12	10/9	9/9	11/11	M94755-M94768
H. persicus	**BMNH1921.3.29.1**	IQ, Amara	M	63.5	28.2	72	16	12.5	7.6	0.25	0.78	0.48	4.5	5.6	2.2	5.7	8.2	14	10	12/10	8/9	9/9	14/14	M94778-M94789
H. persicus	**BMNH1971.1383**	BA, Ras Salba	M	61.2	28.2		14	12.5	7.6	0.23	0.89	0.54	3.9	5.2	2.2	5	8	15	9	?/12	8/9	9/9	13/13	M94930-M94943
H. persicus	**BMNH1971.1384**	BA, Ras Salba	M	49.7	21.7	60	11	9.4	5.8	0.22	0.85	0.53	3.3	4.7	1.7	4.7	5.9	?	10	12/12	10/10	9/9	13/13	M94944-M94956
H. persicus	**BMNH1975.977**	BA, Howar Island, Persian Gulf	M	57.4	22.5		13.5	10.6	6.4	0.24	0.79	0.47	3.7	5.1	1.7	5.3	6.8	14	4+4	11/11	10/11	9/9	13/13	M94971-M94984
H. persicus	**BMNH1983.1439**	SA, Hofuf	M	50.1	23		12.7	9.43	5.65	0.25	0.74	0.44	3.3	4.1	1.8	4.7	6	16	10	12/12	9/9	9/9	11/13	M94885-M94997
H. persicus	**BMNH1983.1440**	SA, Hofuf	M	47.4	19.1		13.4	9.1	5.8	0.28	0.68	0.43	3	4.3	1.4	4.3	5.9	14	11	12/11	9/9	8/8	13/13	M94998-M95012
H. persicus	**BMNH1971.1141**	BA, Quanats	M	58.8	25.3		16	?	?	0.27			?	?	?	?	?	14	9	?/?	?/?	9/9	12/14	M94905-M94916
H. persicus	**BMNH1971.26**	BA, Jesra, Jebel al Dukhan	M	63.9	22.5		16.8	13.7	8.3	0.26	0.82	0.49	4.1	5.8	2.4	6.2	8	15	9	13/12	10/9	9/?	13/13	M94864-M94877
H. persicus	**BMNH1971.31**	BA, Jesra, Jebel al Dukhan	M	60.6	26.3	72	15.1	11.9	6.9	0.25	0.79	0.46	4	5.9	1.6	5.6	7.5	16	9	11/11	9/10	8/9	13/13	M94878-M94891
H. persicus	**BMNH85.7.11.3**	PA, Hydrab, Sind	F	57.1	23.4		12	11	6.6	0.21	0.92	0.55	3.6	4.9	1.7	5.3	7.4	15		12/10	9/8	9/8	13/13	M95086-M95099
H. persicus	**BMNH1921.3.30.4**	IQ, Baghdad	F	57.6	23.1		14.4	11.2	6.8	0.25	0.78	0.47	4.2	5.5	1.9	5.1	6.7	15		11/10	10/10	?/?	?/?	M94790-M94801
H. persicus	**BMNH1971.1140**	BA, Quanats	F	64.7	30.6		16.3	11	6.8	0.25	0.67	0.42	3.9	5.4	2.3	5.8	6.8	15		13/11	11/11	9/0	13/13	M94892-M94904
H. persicus	**BMNH1971.1142**	BA, Quanats	F	55.2	23.6		12.9	10.5	6.7	0.23	0.81	0.52	3.3	5.3	1.8	4.6	6.5	15		12/9	11/10	9/9	13/13	M94917-M94929
H. persicus	**BMNH1971.1386**	BA, Jebel al Dukhan	F	52.5	24	55	13.2	10.3	5.7	0.25	0.78	0.43	3.9	4.3	1.5	4.2	5.7	14		10/11	10/10	?/9	13/13	M94958-M94970
H. persicus	**BMNH1961.1504**	IQ, Khalis	F	36.9	16		9.2	7.2	4.9	0.25	0.78	0.53	2.3	3.2	1.6	3.6	4.7	15		10/10	10/11	9/?	13/13	M94818-M94836
H. persicus	**BMNH1961.1505**	IQ, Khalis	F	36.4	14.8		9.1	7.1	4.9	0.25	0.78	0.54	2.7	3.6	1.4	3.9	4.4	16		11/12	10/10	9/9	14/14	M94851-M94863
		Statistical tests																						
		Number of individuals (M/F)		13/7	13/7		13/7	12/7	12/7	13/7	12/7	12/7	12/7	12/7	12/7	12/7	12/7	11/7		12/7	12/7	11/6	12/6	
		One-way ANOVA *F* value		3.930	1.766		5.275	5.650	5.261	0.478	0.554	0.028	2.363	4.240	0.813	5.447	7.418	0.622		5.171	6.927	0.130	0.516	
		Degrees of freedom		18	18		18	17	17	18	17	17	17	17	17	17	17	16		17	17	15	16	
		Probability (*P*)		0.062	0.200		0.033*	0.029*	0.034*	0.497	0.466	0.869	0.142	0.055	0.379	0.032*	0.014*	0.441		0.036*	0.017*	0.722	0.482	
		Summary Statistics (Total)																						
		Number of Individuals (N)		20	20	7				20	19	19	19	19	19			18	13			17	18	
		Mean		56.4	23.8	68.4				0.24	0.80	0.49	3.6	5.1	1.8			14.8	9.2			8.8	13	
		Maximum		67	30.6	77				0.28	0.92	0.60	4.5	6.6	2.4			16	11			9	14	
		Minimum		36.4	14.8	55				0.21	0.67	0.42	2.3	3.2	1.3			14	8			8	13	
		Standard Error Mean		1.95	0.89	3.06				0.003	0.01	0.01	0.12	0.20	0.07			0.16	0.25			0.06	0.16	
		Summary Statistics (Males)																						
		Number of Individuals (N)		13	13	6	13	12	12	13	12	12	12	12	12	12	12	11	13	12	12	11	12	
		Mean		59	24.6	70.6	14.6	11.8	7.2	0.24	0.81	0.49	3.8	5.3	1.9	5.4	7.4	14.2	9.2	11.6	9.1	8.8	12.9	
		Maximum		67	29.2	77	16.8	14.4	9.6	0.28	0.91	0.60	4.5	6.6	2.4	6.5	8.7	16	11	13	10.5	9	14	
		Minimum		47	19.1	60	11	9.1	5.6	0.22	0.68	0.43	3	4.1	1.3	4.3	5.9	14	8	10.5	8	8	11	
		Standard Error Mean		1.78	0.82	2.47	0.45	0.52	0.34	0.004	0.019	0.014	0.12	0.21	0.10	0.18	0.29	0.23	0.25	0.22	0.19	0.09	0.22	
		Summary Statistics (Females)																						
		Number of Individuals (N)		7	7	1	7	7	7	7	7	7	7	7	7	7	7	7		7	7	6	6	
		Mean		51.4	22.2	55	12.4	9.7	6	0.24	0.78	0.49	3.4	4.6	1.7	4.6	6	15		10.8	10	8.9	13.1	
		Maximum		64.7	30.6	55	16.3	11.2	6.8	0.25	0.92	0.55	4.2	5.5	2.3	5.8	7.4	16		12	11	9	14	
		Minimum		36.4	14.8	55	9.1	7.1	4.9	0.21	0.67	0.42	2.3	3.2	1.4	3.6	4.4	14		10	8.5	8.5	13	
		Standard Error Mean		4	2	-	0.99	0.68	0.33	0.005	0.02	0.02	0.26	0.34	0.11	0.30	0.42	0.21		0.26	0.29	0.08	0.16	

……*continued on next page*

Appendix I. (Continued)

Species	Catalogue	Locality	Sex	SVL	TRL	TL	HL	HW	HH	ratio HL/SVL	ratio HW/HL	ratio HH/HL	OD	NE	IN	IO1	IO2	TB	PAP	SL (L/R)	IL (L/R)	LP 1st (L/R)	LP 4rth (L/R)	Morphobank
H. luqueorum sp. nov.	**BMNH2005.1660**[H]	OM, Sayq, Jebel Akhdar	M	80.4	35.8		21.3	15.9	9.9	0.26	0.75	0.46	5	7.4	2.2	6.2	9	15	3+3	13/12	9/9	10/11	14/13	M94288-M94303
H. luqueorum sp. nov.	**BMNH1980.558**[P]	OM, Wadi Sayq, Jebel Akhdar	M	88	38	95	23	18	10.9	0.26	0.78	0.47	5.8	8.4	2.6	7.4	10.4	15	2+3	13/12	9/9	10/10	13/13	M94313-M94350
H. luqueorum sp. nov.	**BMNH2008.710**	OM, Wadi al Khahafa, Jebel Akhdar	M	73	30.7		18.5	13.6	8.4	0.25	0.74	0.45	5.6	6.2	2.6	6.1	8.7	13		11/11	9/8	10/10	14/14	M94385-M94393
H. luqueorum sp. nov.	**IBES7155**	OM, 1 km E of Hat, Jebel Akhdar	M	82.1	34.6		21.7	16.5	10.2	0.26	0.76	0.47	5.6	8.3	2.7	7.3	10.5	14	3+2	10/11	10/10	10/10	13/13	M100049-M100055
H. luqueorum sp. nov.	**IBES8068**[P]	OM, Wadi al Khahafa, Jebel Akhdar	F	76.5	28.9	78	19.2	14	9.1	0.25	0.73	0.47	5.4	6.9	2.4	6.9	10	15		10/11	9/9	10/10	14/14	M100056-M100064
H. luqueorum sp. nov.	**IBES7771**[P]	OM, 1 km E of Hat, Jebel Akhdar	F	76.4	36.4		19.8	14.8	8.2	0.26	0.75	0.41	5.1	7.1	1.9	6.3	8.6	14		12/13	10/10	10/10	13/13	M100065-M100073
H. luqueorum sp. nov.	**IBES6056**	OM, 1 km E of Hat, Jebel Akhdar	F	59	28.3		15.9	11.4	5.8	0.27	0.72	0.36	4.3	5.7	1.8	5.3	7.3			13/13	9/10	10/10	14/14	M100074-M100082
H. luqueorum sp. nov.	**IBES6085**[P]	OM, 1 km E of Hat, Jebel Akhdar	F	83.4	43.1		20.3	15.1	8.5	0.24	0.74	0.42	5.3	7.4	2.3	7.9	10.9			11/10	9/8	11/11	14/14	M100083-M100093
H. luqueorum sp. nov.	**BMNH1971.41**[P]	OM, Wadi Sayq, Jebel Akhdar	F	69	25.8		19.4	13.5	9.1	0.28	0.70	0.47	5	7	2.1	6	8.1	14		14/13	9/9	10/10	14/14	M94304-M94312
H. luqueorum sp. nov.	**BMNH2005.1658**[P]	OM, Wadi Bani Habib, Jebel Akhdar	F	84.7	35.4		21.2	16.3	10.3	0.25	0.77	0.49	5.9	7.8	2.4	6.4	9	14		13/13	10/10	11/11	14/14	M94351-M94356
H. luqueorum sp. nov.	**BMNH2005.1659**[P]	OM, Wadi Bani Habib, Jebel Akhdar	F	75	30		20	15	8.5	0.27	0.75	0.43	5	7.6	2.4	6.6	9	14		12/12	9/9	11/11	13/14	M94357-M94362
H. luqueorum sp. nov.	**ONHM3705**[P]	OM, Wadi Bani Habib, Jebel Akhdar	F	85	35.3		21.3	16.7	10	0.25	0.78	0.47	6.1	6.8	2.4	7.2	10.2	14		11/10	9/9	10/11	14/13	M94363-M94372
H. luqueorum sp. nov.	**BMNH1975.916**[P]	OM, Birkat Sahfan, Jebel Akhdar	F	67	28.7		18.4	14.2	9.4	0.27	0.77	0.51	5.2	6.5	2.3	5.7	9			13/11	8/9	10/11	14/14	M94378-M94384
		Sexual dimorphism																						
		Number of individuals (M/F)		4/9	4/9		4/9	4/9	4/9	4/9	4/9	4/9	4/9	4/9	4/9	4/9	4/9	4/6		4/9	4/9	4/9	4/9	
		One-way ANOVA *F* value		1.369	0.623		2.502	2.138	2.091	0.129	0.690	0.374	0.704	1.729	4.789	0.350	0.685	0.037		0.215	0.014	1.627	2.835	
		Degrees of freedom		11	11		11	11	11	11	11	11	11	11	11	11	11	8		11	11	11	11	
		Probability (*P*)		0.266	0.446		0.142	0.171	0.176	0.726	0.423	0.553	0.419	0.215	0.051	0.566	0.425	0.851		0.651	0.906	0.228	0.120	
		Summary Statistics (Total)																						
		Number of Individuals (N)		13	13	2	13	13	13	13	13	13	13	13	13	13	13	10	3	13	13	13	13	
		Mean		76.88	33.15	86.5	20	15	9.1	0.25	0.74	0.45	5.3	7.1	2.3	6.5	9.2	14.2	5.3	11.8	9.1	10.3	13.6	
		Maximum		88	43.1	95	23	18	10.9	0.28	0.78	0.51	6.1	8.4	2.7	7.9	10.9	15	6	13.5	10	11	14	
		Minimum		59	25.8	78	15.9	11.4	5.8	0.24	0.70	0.36	4.3	5.7	1.8	5.3	7.3	13	5	10.5	8.5	10	13	
		Standard Error Mean		2.30	1.34	8.5	0.50	0.477	0.36	0.003	0.006	0.01	0.13	0.21	0.07	0.20	0.29	0.2	0.33	0.3	0.15	0.11	0.11	
		Summary Statistics (Males)																						
		Number of Individuals (N)		4	4	1	4	4	4	4	4	4	4	4	4	4	4	4	3	4	4	4	4	
		Mean		80.8	34.7	95	21.1	16	9.8	0.25	0.75	0.46	5.5	7.5	2.5	6.7	9.6	14.2	5.3	11.6	9.1	10.1	13.3	
		Maximum		88	38	95	23	18	10.9	0.26	0.78	0.47	5.8	8.4	2.7	7.4	10.5	15	6	12.5	10	10.5	14	
		Minimum		73	30.7	95	18.5	13.6	8.4	0.25	0.74	0.45	5	6.2	2.2	6.1	8.7	13	5	10.5	8.5	10	13	
		Standard Error Mean		3	1.5	-	0.94	0.91	0.52	0.002	0.008	0.004	0.17	0.51	0.11	0.34	0.46	0.47	0.33	0.51	0.31	0.12	0.23	
		Summary Statistics (Females)																						
		Number of Individuals (N)		9	9	1	9	9	9	9	9	9	9	9	9	9	9	6		9	9	9	9	
		Mean		75.1	32.4	78	19.5	14.5	8.7	0.26	0.74	0.44	5.2	6.9	2.2	6.4	9.1	14.1		11.9	9.1	10.4	13.7	
		Maximum		85	43.1	78	21.3	16.7	10.3	0.28	0.78	0.51	6.1	7.8	2.4	7.9	10.9	15		13.5	10	11	14	
		Minimum		59	25.8	78	15.9	11.4	5.8	0.24	0.70	0.36	4.3	5.7	1.8	5.3	7.3	14		10.5	8.5	10	13	
		Standard Error Mean		2.94	1.82	-	0.54	0.52	0.43	0.004	0.008	0.015	0.17	0.20	0.07	0.26	0.36	0.16		0.39	0.18	0.15	0.12	

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Appendix I. (Continued)

Species	Catalogue	Locality	Sex	SVL	TRL	TL	HL	HW	HH	ratio HL/SVL	ratio HW/HL	ratio HH/HL	OD	NE	IN	IO1	IO2	TB	PAP	SL (L/R)	IL (L/R)	LP 1st (L/R)	LP 4rth (L/R)	Morphobank
H. hajarensis sp. nov.	**BMNH2008.703**	OM, Jebel Abu Daud	M	59.7	28.3		17.1	11.2	8	0.29	0.65	0.47	4.8	6.1	2.1	6	6.9	14	2+2	?/11	?/9	?/9	12/13	M94544-M94557
H. hajarensis sp. nov.	**BMNH2008.706**	OM, Wadi Hebaheba, Jebel Qahwan	M	48.7	18.7		14.2	9.9	5.8	0.29	0.70	0.41	4	5.3	1.8	4.4	6.9	15	3+3	11/11	7/8	8/?	12/?	M94572-M94586
H. hajarensis sp. nov.	**IBES1777**	OM, Wadi Hebaheba, Jebel Qahwan	M	46.2	19.6		13.6	9	5.4	0.29	0.66	0.40	3.8	4	1.8	3.9	5.8	14	2+2	12/11	9/10	8/8	11/11	M94666-M94684
H. hajarensis sp. nov.	**BMNH2008.708**	OM, Wadi Hebaheba, Jebel Qahwan	M	40	15.8		12.2	8.2	5.3	0.31	0.67	0.43	3.3	3.8	1.3	3.6	5.2		3+3	11/10	10/9	8/8	12/12	M94700-M94721
H. hajarensis sp. nov.	**IBES7151**	OM, Wadi Tanuf	M	56.7	23.5		15.6	12.2	5.6	0.28	0.78	0.36	3.8	5.6	2	5.6	6.8	14	3+3	11/11	10/9	9/8	13/12	M99874-M99884
H. hajarensis sp. nov.	**ONHM3706**[P]	OM, Wadi Bani Khalid	M	52.8	21.6		15.2	10.6	6.1	0.29	0.70	0.40	4.4	5.4	1.9	5.2	7.4	14	3+3	10/10	8/9	8/8	12/12	M99885-M99893
H. hajarensis sp. nov.	**IBES7335**[P]	OM, Wadi Bani Khalid	M	47.1	18.4		13.7	9.3	5.6	0.29	0.68	0.41	3.7	5	1.5	4.6	6.8	14	3+3	10/10	9/9	7/7	12/12	M99894-M99902
H. hajarensis sp. nov.	**BMNH2008.714**[H]	OM, Wadi Bani Khalid	M	59.8	23.7		15.5	12.7	7.4	0.26	0.82	0.48	4.5	6.3	1.7	5.8	8.5	14	3+3	10/10	9/9	8/8	12/12	M99903-M99917
H. hajarensis sp. nov.	**IBES7154**	OM, 9 km N Al Chayan	M	62.7	28		17	12.9	7.2	0.27	0.76	0.42	4.3	6.3	1.8	5.5	8.2	14	3+3	11/10	8/8	8/8	12/12	M99921-M99937
H. hajarensis sp. nov.	**BMNH2005.1664**	OM, Wadi Tanuf	F	56	23.8		16	11.5	7.1	0.29	0.72	0.44	4.1	5.1	1.9	5.6	7.1	15		11/11	9/10	8/8	13/13	M94393-M94404
H. hajarensis sp. nov.	**BMNH1976.1404**	OM, Ar Rustaq	F	50	21.7		13.2	9.7	6.1	0.26	0.73	0.46	3.3	4	2	4.1	6.3	15		11/11	10/9	9/9	14/14	M94405-M94415
H. hajarensis sp. nov.	**BMNH1977.35**	OM, Wadi Sabt, Jebel Akhdar	F	57.4	25.8	70	13.7	11.7	7.6	0.24	0.85	0.55	4.1	5.4	1.7	6	7.4	14		11/11	9/9	8/8	13/13	M94459-M94465
H. hajarensis sp. nov.	**BMNH2008.702**	OM, Wadi Mayh	F	61	26.2		17.1	11.4	6.4	0.28	0.67	0.37	4.4	5.8	1.9	4.8	7	15		?/11	8/9	8/8	12/13	M94515-M94529
H. hajarensis sp. nov.	**BMNH2008.701**	OM, Wadi Mayh	F	52	22.7		14.4	10.6	6.2	0.28	0.74	0.43	3.9	5.4	2.1	4.8	6.5	14		11/12	9/9	9/9	12/12	M94530-M94542
H. hajarensis sp. nov.	**BMNH2008.704**	OM, Wadi Tiwi	F	54.6	22.2		15.7	10.2	7.2	0.29	0.65	0.46	4	5.5	1.8	4.9	6.7	14		12/12	10/8	8/8	11/?	M94558-M94571
H. hajarensis sp. nov.	**BMNH2008.709**	OM, Wadi Hebaheba, Jebel Qahwan	F	60	26		16.7	12.2	7.1	0.28	0.73	0.43	4.3	5.4	1.8	5.2	7.6	15		12/12	8/9	8/8	12/12	M94630-M94643
H. hajarensis sp. nov.	**BMNH2008.707**	OM, Wadi Hebaheba, Jebel Qahwan	F	44.3	18.2		13.7	9.5	5.2	0.31	0.69	0.38	4	4.3	1.4	4.7	6.1	14		11/11	9/8	7/8	12/12	M94649-M94664
H. hajarensis sp. nov.	**IBES8064**	OM, Wadi Tanuf	F	47.8	20.1	63	13.5	10	6	0.28	0.74	0.44	2.9	5	1.4	4.8	6.2			9/10	9/9	8/8	12/12	M99954-M99961
H. hajarensis sp. nov.	**IBES7076**	OM, Wadi Tanuf	F	60.4	27.4		16.6	11.6	6.8	0.27	0.70	0.41	4.5	6	2.2	5.9	7.2			10/9	8/9	8/8	12/12	M99962-M99968
H. hajarensis sp. nov.	**IBES7336**[P]	OM, Wadi Bani Khalid	F	46.7	19.3		13.8	9.6	6	0.30	0.70	0.43	3.5	4.6	1.8	4.7	6.5	13		10/10	9/9	7/7	12/12	M99969-M99976
H. hajarensis sp. nov.	**IBES7184**	OM, 9 km N Al Chayan	F	57.5	24.5		15.5	11.4	5.8	0.27	0.74	0.37	4.3	5.3	1.7	4.5	7.1	15		10/10	9/9	8/8	12/12	M99977-M99986
H. hajarensis sp. nov.	**IBES7587**	OM, 9 km N Al Chayan	F	66.9	29.1		18.5	13.3	7.3	0.28	0.72	0.39	4.1	6.7	1.9	5.7	7.7	14		12/11	9/9	8/8	12/13	M99987-M99993
		Sexual dimorphism																						
		Number of individuals (M/F)		9/13	9/13		9/13	9/13	9/13	9/13	9/13	9/13	9/13	9/13	9/13	9/13	9/13	9/13		9/13	9/13	9/13	9/13	
		One-way ANOVA *F* value		0.592	1.053		0.254	0.121	0.497	0.800	0.128	0.162	0.313	0.014	0.222	0.102	0.040	0.827		0.530	0.158	0.005	1.296	
		Degrees of freedom		20	20		20	20	20	20	20	20	20	20	20	20	20	17		20	20	20	20	
		Probability (*P*)		0.450	0.317		0.619	0.731	0.488	0.723	0.584	0.691	0.581	0.905	0.642	0.751	0.842	0.375		0.474	0.695	0.940	0.268	
		Summary Statistics (Total)																						
		Number of Individuals (N)		22	22	2	22	22	22	22	22	22	22	22	22	22	22	19	9	22	22	22	22	
		Mean		54	22.9	66.5	15.1	10.8	6.4	0.28	0.71	0.42	4	5.2	1.79	5	6.9	14.2	5.5	10.7	8.8	8	12.1	
		Maximum		66.9	29.1	70	18.5	13.3	8	0.31	0.85	0.55	4.8	6.7	2.2	6	8.5	15	6	12	9.5	9	14	
		Minimum		40	15.8	63	12.2	8.2	5.2	0.24	0.65	0.36	2.9	3.8	1.3	3.6	5.2	13	4	9.5	7.5	7	11	
		Standard Error Mean		1.47	0.79	3.5	0.34	0.29	0.17	0.003	0.01	0.009	0.09	0.16	0.04	0.14	0.16	0.12	0.29	0.15	0.10	0.10	0.13	
		Summary Statistics (Males)																						
		Number of Individuals (N)		9	9		9	9	9	9	9	9	9	9	9	9	9	8	9	9	9	9	9	
		Mean		52.6	21.9		14.9	10.6	6.2	0.28	0.71	0.42	4	5.3	1.7	4.9	6.9	14.1	5.5	10.6	8.8	8	12	
		Maximum		62.7	28.3		17.1	12.9	8	0.31	0.82	0.48	4.8	6.3	2.1	6	8.5	15	6	11.5	9.5	9	12.5	
		Minimum		40	15.8		12.2	8.2	5.3	0.26	0.65	0.36	3.3	3.8	1.3	3.6	5.2	14	4	10	7.5	7	11	
		Standard Error Mean		2.54	1.43		0.54	0.56	0.33	0.004	0.019	0.012	0.15	0.30	0.08	0.28	0.34	0.12	0.29	0.18	0.23	0.17	0.14	
		Summary Statistics (Females)																						
		Number of Individuals (N)		13	13	2	13	13	13	13	13	13	13	13	13	13	13	11		13	13	13	13	
		Mean		54.9	23.6	66.5	15.2	10.9	6.5	0.27	0.72	0.42	3.9	5.2	1.8	5	6.8	14.3		10.8	8.9	8	12.3	
		Maximum		66.9	29.1	70	18.5	13.3	7.6	0.31	0.85	0.55	4.5	6.7	2.12	6	7.7	15		12	9.5	9	14	
		Minimum		44.3	18.2	63	13.2	9.5	5.2	0.24	0.65	0.37	2.9	4	1.4	4.1	6.1	13		9.5	8.5	7	11	
		Standard Error Mean		1.81	0.9	3.5	0.46	0.31	0.19	0.004	0.013	0.013	0.12	0.19	0.06	0.16	0.14	0.2		0.23	0.09	0.14	0.2	

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Appendix I. (Continued)

Species	Catalogue	Locality	Sex	SVL	TRL	TL	HL	HW	HH	ratio HL/SVL	ratio HW/HL	ratio HH/HL	OD	NE	IN	IO1	IO2	TB	PAP	SL (L/R)	IL (L/R)	LP 1st (L/R)	LP 4rth (L/R)	Morphobank
H. yerburii TYPE	**BMNH95.5.23.9**	YE, Haithalhim, near Aden	M	67.6	28.1		15.4	14.6	9.1	0.23	0.95	0.59	4.6	6.4	1.7			17	6+6	?/11	?/8	7/7	10/10	M95614-M95629
H. yerburii TYPE	**BMNH95.5.23.8**	YE, Aden	M	61.5	24.8		16.4	12.4	8.3	0.27	0.76	0.51	4	5.9	1.7	6.2	7.7	17	6+4	10/10	8/8	7/7	10/10	M95597-M95613
H. yerburii	**BMNH95.11.27.3**	YE, Aden	M	63.6	25	72	17	13.1	7.9	0.27	0.77	0.46	4.4	6.4	1.7	6.2	8.1	16	15	11/11	10/8	7/7	10/10	M95630-M95647
H. yerburii	**BMNH1987.846**	YE, Al Hudaydah	M	62.7	25.1		16.3	12.1	8	0.26	0.74	0.49	4.4	6.2	1.8			17	12	11/10	8/8	7/?	11	M95659-M95672
H. yerburii	**BMNH1987.847**	YE, Al Hudaydah	M	63	24		16.4	13	7.4	0.26	0.79	0.45	4.5	6.2	1.8	6.1	8		15	11/10	9/8			M95673-M95682
H. yerburii	**BMNH1945.12.18.12**	YE, Jebel Shansan, Aden	F	54	21.6	58	14.5	10.8	7	0.27	0.74	0.48	3.9	5.3	1.7	5.3	7.1	16		11/11	8/8	7/7	9/9	M95648-M95658
		Summary Statistics (Males)																						
		Number of Individuals (N)		5	5	1	5	5	5	5	5	5	5	5	5	3	3	4	5	5	5	4	4	
		Mean		63.6	25.4	72	16.3	13	8.1	0.25	0.82	0.5	4.3	6.2	1.7	6.1	7.9	16.7	12.8	10.6	8.3	7	10.2	
		Maximum		67.6	28.1		17	14.6	9.1	0.27	0.95	0.59	4.6	6.4	1.8	6.2	8.1	17	15	11	9	7	11	
		Minimum		61.5	24		15.4	12.1	7.4	0.23	0.74	0.45	4	5.9	1.7	6.1	7.7	16	10	10	8	7	10	
		Standard Error Mean		1.03	0.70		0.25	0.43	0.28	0.007	0.03	0.02	0.10	0.09	0.02	0.03	0.12	0.25	0.96	0.18	0.2	0	0.25	
		Standard Deviation		2.32	1.57		0.57	0.96	0.62	0.016	0.08	0.05	0.22	0.20	0.05	0.05	0.20	0.5	2.16	0.41	0.44	0	0.5	
		Upper 95% Mean		66.56	27.34		17.01	14.23	8.91	0.27	0.90	0.56	4.66	6.47	1.80	6.31	8.45	17.54	15.49	11.11	8.85	7	11.04	
		Lower 95% Mean		60.79	23.45		15.58	11.84	7.36	0.23	0.69	0.43	4.09	5.96	1.67	6.02	7.41	15.95	10.10	10.08	7.74	7	9.45	

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Appendix I. (Continued)

Species	Catalogue	Locality	Sex	SVL	TRL	TL	HL	HW	HH	ratio HL/SVL	ratio HW/HL	ratio HH/HL	OD	NE	IN	IO1	IO2	TB	PAP	SL (L/R)	IL (L/R)	LP 1st (L/R)	LP 4rth (L/R)	Morphobank
H. alkiyumii sp. nov.	**BMNH2005.1662[H]**	OM, Tawi Atair	M	56.4	22.5		15.4	11.5	7.5	0.27	0.75	0.49	3.8	5.4	2	5	6.3	13	4+4	11/12	8/7	8/8	12/12	M95264-M95275
H. alkiyumii sp. nov.	**ONHM3707[P]**	OM, Tawi Atair	M	49.5	20.2		14.1	10.6	6.6	0.28	0.75	0.47	3.5	4.7	1.9	4.8	6.7	12	4+4	9/9	7/7	8/8	12/12	M95290-M95304
H. alkiyumii sp. nov.	**BMNH1977.972**	OM, Khadrafi Plateau	M	74.5	31.5		18.4	15.6	9.3	0.25	0.85	0.51	5	6.6	2.8	5.8	9	14	5+5	9/9	7/7	7/7	10/10	M95233-M95248
H. alkiyumii sp. nov.	**BMNH1977.964**	OM, Wadi Rubkat	M	58.6	24.4		15.5	12.7	7.4	0.26	0.82	0.48	4.5	6	1.6	5.5	7.4	14	3+3	11/11	8/8	7/7	11/11	M95187-M95202
H. alkiyumii sp. nov.	**BMNH1977.963**	OM, Wadi Rubkat	M	65.5	27.7		16.7	13.7	8.9	0.25	0.82	0.53	4	5.8	1.8	5.2	7.2	12	3+3	10/10	8/9	7/7	11/11	M95171-M95186
H. alkiyumii sp. nov.	**BMNH1977.957**	OM, Wadi Sayq	M	61	25		17.2	13.1	8	0.28	0.76	0.47	4.3	5.5	2.3	6.1	8.8	13	4+3	11/9	7/7	6/6	10/10	M95132-M95144
H. alkiyumii sp. nov.	**BMNH1977.959**	OM, Wadi Sayq	M	53.3	24.4		14.8	11	5.8	0.28	0.74	0.39	3.5	5	2.2	5.3	6.8	13	4+4	10/10	7/7	?/8	?/11	M95160-M95170
H. alkiyumii sp. nov.	**IBES7453**	OM, 3 km NW of Hasik	M	53	20.6	58.2	14.7	10.8	6.3	0.28	0.73	0.43	3.8	5.2	1.85	5.5	8	13	3+3	11/11	9/9	7/7	11/11	M99609-M99615
H. alkiyumii sp. nov.	**IBES7837**	OM, Dalkut	M	67.5	25.3		17.7	14.7	8.9	0.26	0.83	0.50	4.4	6.6	2	6.4	9.6	12	4+3	9/10	8/7	7/7	10/10	M99616-M99622
H. alkiyumii sp. nov.	**IBES7888**	OM, Dalkut	M	62.5	27.7		16.8	13.3	7.8	0.27	0.79	0.46	4.1	6.1	2.3	6.2	8.7	11	10	11/10	8/8	6/6	11/11	M99623-M99629
H. alkiyumii sp. nov.	**IBES7397**	OM, Dalkut	M	66.1	27.1		18.1	14.6	9.1	0.27	0.81	0.50	4.5	6.7	2.1	6.2	8.4	13	8	9/10	8/8	7/7	11/11	M99630-M99637
H. alkiyumii sp. nov.	**IBES7053**	OM, 3.5 km NE from Sadah	M	55	22.6		15.2	11.6	7.1	0.28	0.76	0.47	4.1	6	2	5.5	8.2	13	3+3	10/11	8/8	8/8	12/12	M99638-M99644
H. alkiyumii sp. nov.	**IBES7101**	OM, 9 km SW of Hadbin	M	62.4	25		17.3	12.8	7.9	0.28	0.74	0.46	4.8	5.9	2.1	6.1	8.9		3+3	10/10	9/8	7/7	11/10	M99645-M99653
H. alkiyumii sp. nov.	**BMNH2005.1663[P]**	OM, Tawi Atair	F	68.6	25.1		18.7	14.5	9.3	0.27	0.78	0.50	4.3	6.7	2.2	6.2	9.6	14		11/11	8/9	9/9	12/12	M95276-M95289
H. alkiyumii sp. nov.	**IBES8078[P]**	OM, Tawi Atair	F	62.3	28.8		17.3	13.2	8.3	0.28	0.76	0.48	4.3	6.2	2.7	5.9	7.8	14		9/9	9/8	7/7	12/12	M99654-M99660
H. alkiyumii sp. nov.	**IBES8079[P]**	OM, Tawi Atair	F	58	23.4		15.7	12.1	6.7	0.27	0.77	0.43	4.3	6.1	1.9	5.3	7.7	12		9/9	8/7	7/7	11/11	M99661-M99667
H. alkiyumii sp. nov.	**IBES8080[P]**	OM, Tawi Atair	F	53.2	23.1		15.3	11	6.7	0.29	0.72	0.44	3.7	5.6	1.9	4.8	7.3	13		9/11	8/8	8/8	12/11	M99668-M99674
H. alkiyumii sp. nov.	**BMNH1977.973**	OM, Khadrafi Plateau	F	46.7	20.4	56	12.6	10.3	6.5	0.27	0.82	0.52	3.4	4.2	2	4.1	5.8	12		11/10	8/8	6/6	10/10	M95249-M95263
H. alkiyumii sp. nov.	**BMNH1977.965**	OM, Wadi Rubkat	F	55	23.1		14.7	11.8	6.9	0.27	0.80	0.47	4.4	5.3	2.1	5.3	7.3	14		11/11	8/9	7/7	11/10	M95203-M95216
H. alkiyumii sp. nov.	**BMNH1977.966**	OM, Wadi Rubkat	F	53.3	22.3		15.4	11.6	6.6	0.29	0.75	0.43	4.7	5.2	2.1	5.4	7.4	14		10/9	8/9	7/7	11/10	M95217-M95231
H. alkiyumii sp. nov.	**BMNH1977.958**	OM, Wadi Sayq	F	61.6	27.1	65	15.1	11.9	7.8	0.25	0.79	0.52	4.3	5.6	1.9	5.9	6.8	13		10/9	7/8	6/6	10/10	M95145-M95159
H. alkiyumii sp. nov.	**BMNH1977.956**	OM, Wadi Sayq	F	60.1	27		16.6	12.3	8	0.28	0.74	0.48	4.6	5.4	1.9	6.1	7.1	14		10/10	8/9	7/7	10/10	M95117-M95131
H. alkiyumii sp. nov.	**BMNH1976.1409**	OM, Khadrafi Plateau	F	64.2	28.8		17	13.5	8.7	0.26	0.79	0.51	4.5	6	2.5	6.3	8.1	13		10/9	8/8	7/7	11/11	M95099-M95116
H. alkiyumii sp. nov.	**IBES7441**	OM, 3.5 km NE Sadah	F	57.3	27.1		16.1	12.1	8.3	0.28	0.75	0.52	4	5.4	2.2	5.6	7.8	14		9/9	8/8	7/7	11/11	M99675-M99681
H. alkiyumii sp. nov.	**IBES7858**	OM, 3 km NW of Hasik	F	57	25.1		16	11.1	7	0.28	0.69	0.44	4.8	5.1	2.3	5.4	7	13		10/10	9/9	7/7	11/11	M99682-M99688
H. alkiyumii sp. nov.	**IBES7891**	OM, Dalkut	F	56.8	24.7		15.4	11.5	7	0.27	0.75	0.45	4	5.5	1.8	5.6	7.2	12		11/10	7/8	7/7	10/10	M99689-M99696
H. alkiyumii sp. nov.	**IBES7879**	OM, Dalkut	F	62.5	24.7		17	13.2	7.8	0.27	0.78	0.46	4.3	6.6	1.9	5.3	7.7			10/9	7/8	6/6	10/10	M99705-M99711
H. alkiyumii sp. nov.	**IBES7897**	OM, Dalkut	F	55.3	24		15	11.5	5.9	0.27	0.77	0.39	3.9	5.2	1.7	5.3	7.3	12		11/10	8/9	6/6	10/10	M99697-M99704
H. alkiyumii sp. nov.	**IBES7192**	OM, 3.5 km NE from Sadah	F	46.5	20.1		13.7	9.3	5.6	0.29	0.68	0.41	4	5.1	1.5	4.4	6.3			11/11	8/8	7/6	11/11	M99712-M99718
		Sexual dimorphism																						
		Number of individuals (M/F)		13/16	13/16		13/16	13/16	13/16	13/16	13/16	13/16	13/16	13/16	13/16	13/16	13/16	12/14		13/16	13/16	13/16	13/16	
		One-way ANOVA *F* value		1.572	0.054		1.114	2.465	1.108	1.092	2.264	0.320	0.073	0.983	0.103	1.177	3.159	1.332		0.281	2.864	0.802	0.832	
		Degrees of freedom		27	27		27	27	27	27	27	27	27	27	27	27	27	24		27	27	27	27	
		Probability (*P*)		0.220	0.817		0.294	0.128	0.301	0.305	0.144	0.576	0.788	0.330	0.750	0.287	0.086	0.259		0.600	0.102	0.378	0.369	
		Summary Statistics (Total)																						
		Number of Individuals (N)		29	29	3	29	29	29	29	29	29	29	29	29	29	29	26	13	29	29	29	29	
		Mean		58.7	24.7	59.7	15.9	12.3	7.5	0.27	0.76	0.46	4.2	5.6	2	5.5	7.6	12.9	7.3	10	7.9	7	10.8	
		Maximum		74.5	31.5	65	18.7	15.6	9.3	0.29	0.85	0.53	5	6.7	2.8	6.4	9.6	14	10	11.5	9	9	12	
		Minimum		46.5	20.1	56	12.6	9.3	5.6	0.25	0.68	0.39	3.4	4.2	1.5	4.1	5.8	11	6	9	7	6	10	
		Standard Error Mean		1.20	0.52	2.70	0.26	0.27	0.19	0.002	0.007	0.007	0.07	0.11	0.05	0.10	0.17	0.17	0.40	0.13	0.10	0.13	0.13	
		Summary Statistics (Males)																						
		Number of Individuals (N)		13	13	1	13	13	13	13	13	13	13	13	13	13	13	12	13	13	13	13	13	
		Mean		60.4	24.9	58.2	16.3	12.7	7.7	0.27	0.78	0.47	4.1	5.8	2	5.6	8	12.7	7.3	10.1	7.7	7.1	10.9	
		Maximum		74.5	31.5	-	18.4	15.6	9.3	0.28	0.85	0.53	5	6.7	2.8	6.4	9.6	14	10	11.5	9	8	12	
		Minimum		49.5	20.2	-	14.1	10.6	5.8	0.25	0.73	0.39	3.5	4.7	1.6	4.8	6.3	11	6	9	7	6	10	
		Standard Error Mean		1.94	0.86	-	0.39	0.44	0.3	0.003	0.011	0.009	0.12	0.17	0.08	0.14	0.28	0.25	0.40	0.21	0.18	0.19	0.19	
		Summary Statistics (Females)																						
		Number of Individuals (N)		16	16	2	16	16	16	16	16	16	16	16	16	16	16	14		16	16	16	16	
		Mean		57.4	24.6	60.5	15.7	11.9	7.3	0.27	0.75	0.46	4.2	5.5	2	5.4	7.3	13.1		9.9	8.1	6.9	10.7	
		Maximum		68.6	28.8	65	18.7	14.5	9.3	0.29	0.82	0.52	4.8	6.7	2.7	6.3	9.6	14		11	9	9	12	
		Minimum		46.5	20.1	56	12.6	9.3	5.6	0.25	0.68	0.39	3.4	4.2	1.5	4.1	5.8	12		9	7.5	6	10	
		Standard Error Mean		1.47	0.65	4.5	0.36	0.31	0.25	0.002	0.009	0.01	0.09	0.15	0.074	0.15	0.20	0.23		0.17	0.11	0.19	0.17	

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Appendix I. (Continued)

Species	Catalogue	Locality	Sex	SVL	TRL	TL	HL	HW	HH	ratio HL/SVL	ratio HW/HL	ratio HH/HL	OD	NE	IN	IO1	IO2	TB	PAP	SL (L/R)	IL (L/R)	LP 1st (L/R)	LP 4rth (L/R)	Morphobank
H. festivus sp. nov.	**BMNH1983.706**	OM, 3 Km NW of Sawqirah	M	51.4	20.5	50	13.5	10.9	7.3	0.26	0.81	0.54	4.2	4.5	1.5	5.7	7.8	15	6	10/11	8/8	7/7	11/11	M95408-M95421
H. festivus sp. nov.	**IBES7159**[P]	OM, Wadi Ayoun	M	52.5	22.3		14.7	10.4	6.7	0.28	0.71	0.46	3.7	5.1	1.7	5.3	7.2	13	3+3	11/11	9/9	7/7	12/12	M99733-M99743
H. festivus sp. nov.	**ONHM3708**[P]	OM, Wadi Ayoun	M	50.1	22.9		14.4	9.6	5.6	0.29	0.67	0.39	3.7	4.7	1.8	4.7	6.1	12	3+3	10/10	8/8	?/7	12/12	M99744-M99753
H. festivus sp. nov.	**IBES7605**[P]	OM, Wadi Ayoun	M	53.6	23.9		15.8	10.5	6.2	0.29	0.66	0.39	4.3	5	2.1	4.9	7.4	12	3+3	10/9	10/9	7/7	11/11	M99754-M99763
H. festivus sp. nov.	**IBES8062**[P]	OM, Wadi Ayoun	M	51.5	22.4		14.5	10.5	6.9	0.28	0.72	0.48	4.5	5.1	1.4	5.8	7.6	13	3+3	10/9	8/8	7/7	12/12	M99764-M99773
H. festivus sp. nov.	**IBES7899**	OM, Wadi Mughsayl	M	52.6	24		14.6	10.2	6.7	0.28	0.70	0.46	4.1	5.1	2	5.8	7.5	13	3+3	10/9	8/8	7/7	11/11	M99774-M99780
H. festivus sp. nov.	**BMNH1977.977**[H]	OM, Wadi Ayoun	F	49	20	58	13.1	10	6.9	0.27	0.76	0.53	3.5	4.7	1.9	4.5	6.2	14		9/10	9/9	7/7	11/11	M95339-M95353
H. festivus sp. nov.	**BMNH1977.975**	OM, 16 Km S of Thumrait	F	49	21.7		13.3	9.9	6.2	0.27	0.74	0.47	3.5	4.6	1.9	5.4	6.6	14		10/10	9/9	7/7	10/10	M95305-M95322
H. festivus sp. nov.	**BMNH1977.978**[P]	OM, Wadi Ayoun	F	48.7	22	56	13	9.6	5.9	0.27	0.74	0.45	4	4.8	1.6	4.7	5.8	14		10/10	8/10	7/7	11/11	M95354-M95367
H. festivus sp. nov.	**BMNH1977.976**[P]	OM, Wadi Ayoun	F	53.3	23.7		14	10.2	6.1	0.26	0.73	0.44	4.4	4.5	1.7	4.6	6.1	14		10/9	9/8	7/7	11/11	M95323-M95338
H. festivus sp. nov.	**BMNH1977.979**[P]	OM, Wadi Ayoun	F	43.7	18		11.8	8.9	5.3	0.27	0.75	0.45	3.3	4.1	1.8	3.9	5.3	14		9/9	8/9	7/7	12/11	M95368-M95379
H. festivus sp. nov.	**BMNH1977.980**[P]	OM, Wadi Ayoun	F	38	14.9		10.6	7.8	4.9	0.28	0.74	0.46	2.9	3.7	1.4	3.2	5.1	13		10/9	8/7	?/7	?/?	M95380-M95392
H. festivus sp. nov.	**BMNH1977.981**[P]	OM, Wadi Ayoun	F	36	15.6		10.3	7.1	4.4	0.29	0.69	0.43	2.8	3	1.5	3.7	4.8	14		11/9	8/8	7/7	11/11	M95393-M95407
H. festivus sp. nov.	**IBES7616**	OM, Wadi Ayoun	F	53.1	26.6		14.5	9.2	6.1	0.27	0.63	0.42	4	5.1	1.8	5	7.3	13		10/10	8/9	7/7	12/?	M99781-M99790
H. festivus sp. nov.	**IBES8063**	OM, Wadi Ayoun	F	43.1	18.7	53.1	12.8	9	4.8	0.30	0.70	0.38	3.8	4.4	1.6	5	6.2	12		11/10	9/8	7/7	12/12	M99791-M99800
H. festivus sp. nov.	**IBES7419**[P]	OM, 20 Km S of Thumrait	F	40.6	18.3		11.6	8.3	4.9	0.29	0.72	0.42	3.5	4.2	1.2	4.3	5.5	13		9/9	9/8	6/6	10/11	M99801-M99810
		Sexual dimorphism																						
		Number of individuals (M/F)		6/10	6/10		6/10	6/10	6/10	6/10	6/10	6/10	6/10	6/10	6/10	6/10	6/10	6/10		6/10	6/10	6/10	6/9	
		One-way ANOVA *F* value		6.19	2.00		10.91	8.98	7.52	0.276	0.165	0.176	5.59	6.52	0.564	9.489	10.69	0.693		1.355	0.074	0.686	2.288	
		Degrees of freedom		15	16		15	15	15	15	15	15	15	15	15	15	15	15		15	15	15	14	
		Probability (*P*)		0.025*	0.177		0.004*	0.009*	0.015*	0.606	0.690	0.680	0.031*	0.022*	0.464	0.007*	0.005*	0.418		0.262	0.788	0.420	0.152	
		Summary Statistics (Total)																						
		Number of Individuals (N)			16	4				16	16	16			16			16	6	16	16	16	15	
		Mean			20.8	54.2				0.27	0.71	0.44			1.6			13.3	6	9.8	8.4	6.94	11.3	
		Maximum			26.6	58				0.30	0.81	0.54			2.1			15	6	11	9.5	7	12	
		Minimum			14.9	50				0.26	0.63	0.38			1.2			12	6	9	7.5	6	10	
		Standard Error Mean			0.76	1.74				0.002	0.01	0.01			0.05			0.20	-	0.12	0.12	0.05	0.15	
		Summary Statistics (Males)																						
		Number of Individuals (N)		6	6	1	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	
		Mean		51.4	22	50	14.4	10.2	6.5	0.28	0.71	0.45	4	4.92	1.7	5.3	7	13.1	6	10	8.4	7	11.5	
		Maximum		53.6	24	-	15.8	10.9	7.3	0.29	0.81	0.54	4.5	5.1	2.1	5.8	7.8	15	6	11	9.5	7	12	
		Minimum		50.1	22.3	-	13.5	9.6	5.6	0.26	0.66	0.39	3.7	4.5	1.4	4.7	6.1	12	6	9.5	8	7	11	
		Standard Error Mean		0.69	0.73	-	0.29	0.18	0.21	0.003	0.01	0.019	0.11	0.08	0.09	0.17	0.27	0.4	-	0.21	0.22	-	0.2	
		Summary Statistics (Females)																						
		Number of Individuals (N)		10	10	3	10	10	10	10	10	10	10	10	10	10	10	10		10	10	10	9	
		Mean		45.4	19.9	55.7	12.5	9	5.5	0.27	0.72	0.44	3.5	4.3	1.6	4.4	5.8	13.5		9.7	8.5	6.9	11.1	
		Maximum		53.3	26.6	58	14.5	10.2	6.9	0.30	0.76	0.53	4.4	5.1	1.9	5.4	7.3	14		10.5	9	7	12	
		Minimum		36	14.9	53.1	10.3	7.1	4.4	0.26	0.63	0.38	2.8	3	1.2	3.2	4.8	12		9	7.5	6	10	
		Standard Error Mean		1.92	1.14	1.4	0.43	0.31	0.25	0.003	0.012	0.012	0.15	0.19	0.07	0.21	0.23	0.22		0.15	0.14	0.1	0.21	

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Appendix I. (Continued)

Species	Catalogue	Locality	Sex	SVL	TRL	TL	HL	HW	HH	ratio HL/SVL	ratio HW/HL	ratio HH/HL	OD	NE	IN	IO1	IO2	TB	PAP	SL (L/R)	IL (L/R)	LP 1st (L/R)	LP 4rth (L/R)	Morphobank
H. homoeolepis	**BMHN1977.920**	OM, Wadi Sayq	M	31.8	14.3		8.2	5.4	3.4	0.26	0.66	0.41	1.8	2.5	1.1	2.5	3		6	9/9	7/7	5/5	8/7	M95763-M95768
H. homoeolepis	**BMHN1977.922**	OM, Wadi Sayq	M	30.9	13.6		7.7	5.4	3	0.25	0.70	0.39	1.7	2.3	1.3	2.7	3.4		6	10/9	8/7	5/4	7/8	M95783-M95795
H. homoeolepis	**BMHN1977.912**	OM, Wadi Sayq	M	29.3	13		7.3	5.3	3.1	0.25	0.73	0.42	1.8	2.4	1.2	2.6	3.5		6	10/8	7/7	?/5	8/8	M95698-M95714
H. homoeolepis	**BMHN1977.911**	OM, Wadi Ayoun	M	32.4	13.7		8.4	5.9	3.7	0.26	0.70	0.44	2	2.6	1.7	3.5	4		6	?/9	7/7	?/5	8/8	M95683-M95697
H. homoeolepis	**BMHN1983.705**	OM, 3 Km NW of Sawqirah	M	28.1	10.6		7.1	4.6	2.8	0.25	0.65	0.39	1.6	2.2	1.1	2.1	3.4		5	9/10	8/8	?/?	?/8	M95824-M95838
H. homoeolepis	**BMHN1977.918**	OM, 16Km S of Thumrait	M	31.7	14.7		7	5.4	3.2	0.22	0.77	0.46	1.8	?	?	2.6	3.7		2+2	10/8	7/7	4/?	8/?	M95730-M95747
H. homoeolepis	**IBES7676**	OM, Asylah	M	32.8	14.1	36	8.2	6.3	3.4	0.25	0.77	0.41	2.1	2.9	1.2	2.7	4.2		6	9/9	8/8	5/5	8/8	M999494-M9999
H. homoeolepis	**IBES7668**	OM, Asylah	M	30.3	11.9		8.5	6.1	3.3	0.28	0.72	0.39	2.2	2.6	1.2	2.8	3.9		6	10/10	8/8	5/5	8/8	M100000-M100007
H. homoeolepis	**IBES7657**	OM, Asylah	M	29.4	11.7		7.3	4.7	2.9	0.25	0.64	0.40	2.2	2.4	1.1	2	2.8		6	10/10	8/8	5/5	8/8	M100008-M100011
H. homoeolepis	**IBES7673**	OM, Asylah	M	33.4	14.3		8.5	5.7	3.5	0.25	0.67	0.41	2.2	2.6	1.2	3.1	3.9		6	9/10	7/8	5/5	9/9	M100012-M100017
H. homoeolepis	**IBES7929**	OM, 14.5 km NE of Sharbthat	M	25.6	9.9		6.8	4.5	3.1	0.27	0.66	0.46	1.9	2	1.1	2.6	2.8		6	9/9	7/8	5/5	?/8	M100018-M100022
H. homoeolepis	**IBES7924**	OM, 14.5 km NE of Sharbthat	M	29.6	12.9		7.6	5.2	3	0.26	0.68	0.39	1.9	2.3	1.2	2.1	3.4		6	10/10	6/7	4/5	8/8	M100023-M100027
H. homoeolepis	**IBES7909**	OM, Wadi Ayoun	M	29.7	12.5		7.8	5.1	2.9	0.26	0.65	0.37	1.9	2.3	1.3	2.4	3.4		6	9/9	7/8	4/4	8/8	M100028-M100033
H. homoeolepis	**IBES7893**	OM, Wadi Mughsayl	M	29.6	12.4		7.6	5.1	3.1	0.26	0.67	0.41	2	2	1.1	2.7	3.7		6	9/8	6/8	4/4	8/8	M100034-M100038
H. homoeolepis	**BMHN1967.486**	YE, Hadiboh plain, Socotra	M	39.1	16.2		9.1	7.6	4.9	0.23	0.84	0.54	2.7	3.6	1.5	4	5.3		5	8/9	8/7	5/5	10/10	M102095-M102108
H. homoeolepis	**BMHN1967.487**	YE, Hadiboh plain, Socotra	M	39.5	17.2		8.7	7	4.4	0.22	0.80	0.51	2.2	3.6	1.7	3.9	4.9		3	8/8	8/8	5/5	9/9	M102109-M102130
H. homoeolepis	**BMHN1967.488**	YE, Hadiboh plain, Socotra	M	35.8	14.6		7.8	6.4	4.2	0.22	0.82	0.54	2.4	3.5	1	3.3	4.2		6	10/9	9/8	5/5	?/10	M102131-M102145
H. homoeolepis	**BMHN1977.919**	OM, Wadi Sayq	F	29.9	13		7.4	5.1	2.6	0.25	0.69	0.35	1.6	?	?	2.6	3.3			9/8	7/8	?/5	8/8	M95748-M95762
H. homoeolepis	**BMHN1977.921**	OM, Wadi Sayq	F	28.9	12.9	26	7.2	4.9	2.8	0.25	0.68	0.39	1.8	2.2	1.1	2.3	3.3			10/10	8/8	5/4	8/8	M95769-M95782
H. homoeolepis	**BMHN1977.924**	OM, Wadi Sayq	F	32.1	14.9		7.7	5	2.9	0.24	0.65	0.38	1.6	2.6	1.4	2.5	3.5			10/8	7/7	5/?	8/?	M95796-M95808
H. homoeolepis	**BMHN1977.913**	OM, Wadi Ayoun	F	26.5	11.2	25	6.7	4.8	2.7	0.25	0.72	0.40	1.7	2.3	1.1	2.5	3.8			8/9	8/7	5/4	8/8	M95715-M95729
H. homoeolepis	**BMHN1983.704**	OM, 3 Km NW of Sawqirah	F	30.1	12.6		7.1	5.1	3.7	0.24	0.72	0.52	1.9	2.4	1	2.2	3.7			8/8	8/7	5/4	8/8	M95809-M95823
H. homoeolepis	**IBES7664**	OM, Asylah	F	28.9	12.1	25.3	7.6	4.8	3	0.26	0.63	0.39	1.8	2.5	?	2.9	3.5			10/10	8/9	5/5	8/8	M100039-M100043
H. homoeolepis	**IBES7966**	OM, 14.5 km NE of Sharbthat	F	31.8	14		7.7	5.5	3.6	0.24	0.71	0.47	2.3	2.7	1.3	3.2	3.8			9/9	7/7	4/4	8/8	M100044-M100048
H. homoeolepis	**BMHN1953.1.6.99**	YE, Shugra/Shaqra/Shuqrah	F	36.4	18.2		7.8	5.9	3.9	0.21	0.75	0.5	1.9	2.6	1.1	2.9	3.1			8/8	6/7	4/4	8/8	M102031-M102050
H. homoeolepis	**BMHN1967.485**	YE, Hadiboh plain, Socotra	F	39.1	18		8.7	7.6	4.4	0.22	0.87	0.51	2.2			3.8	5			9/9	9/9	5/5	10/11	M102051-M102065
H. homoeolepis	**BMHN1967.489**	YE, Hadiboh plain, Socotra	F	30.5	12.1		7.9	5.5	3.6	0.26	0.70	0.46	1.7	2.8	1.1	3.1	3.4			10/10	7/8	5/5	10/10	M102066-M102079
H. homoeolepis	**BMHN1967.490**	YE, Hammadera, Socotra	F	39.7	17.5		9	6.5	4.4	0.23	0.72	0.49	2.5	3.1	1.5	3.7	4.6			11/10	8/8	5/5	10/10	M102080-M102094
		Sexual dimorphism																						
		Number of individuals (M/F)		17/11	17/11		17/11	17/11	17/11	17/11	17/11	17/11	17/11	16/9	16/8	17/11	17/11			17/11	17/11	16/11	17/11	
		One-way ANOVA *F* value		0.094	1.014		0.345	0.114	0.002	1.699	0.001	0.214	1.083	0.033	0.333	0.139	0.001			0.022	0.338	0.183	0.786	
		Degrees of freedom		26	26		26	26	26	26	26	26	26	23	22	26	26			26	26	26	26	
		Probability (*P*)		0.761	0.323		0.561	0.738	0.959	0.203	0.974	0.647	0.307	0.855	0.569	0.711	0.974			0.882	0.565	0.672	0.383	
		Summary Statistics (Total)																						
		Number of Individuals (N)		28	28	4	28	28	28	28	28	28	28	25	24	28	28		17	28	28	27	28	
		Mean		31.8	13.7	28	7.8	5.5	3.4	0.24	0.71	0.43	1.9	2.6	1.2	2.8	3.7		5.5	9.1	7.5	4.7	8.4	
		Maximum		39.7	18.2	36	9.1	7.6	4.9	0.28	0.87	0.54	2.7	3.6	1.7	4	5.3		6	10.5	9	5	10.5	
		Minimum		25.6	9.9	25	6.7	4.5	2.6	0.21	0.63	0.35	1.6	2	1	2	2.8		3	8	6.5	4	7.5	
		Standard Error Mean		0.73	0.40	2.64	0.12	0.15	0.11	0.003	0.011	0.01	0.05	0.08	0.04	0.1	0.11		0.21	0.12	0.11	0.07	0.16	
		Summary Statistics (Males)																						
		Number of Individuals (N)		17	17	1	17	17	17	17	17	17	17	16	16	17	17		17	17	17	16	17	
		Mean		31.7	13.3	36	7.8	5.6	3.4	0.24	0.71	0.43	2	2.6	1.25	2.8	3.7		5.5	9.1	7.5	4.7	8.2	
		Maximum		39.5	17.2	36	9.1	7.6	4.9	0.28	0.84	0.54	2.7	3.6	1.7	4	5.3		6	10	8.5	5	10	
		Minimum		25.6	9.9	36	6.8	4.5	2.8	0.22	0.64	0.37	1.6	2	1	2	2.8		3	8	6.5	4	7.5	
		Standard Error Mean		0.88	0.45	-	0.15	0.2	0.14	0.004	0.015	0.012	0.06	0.13	0.05	0.14	0.16		0.21	0.13	0.12	0.1	0.18	
		Summary Statistics (Females)																						
		Number of Individuals (N)		11	11	3	11	11	11	11	11	11	11	9	8	11	11			11	11	11	11	
		Mean		32.1	14.2	25.4	7.7	5.5	3.4	0.24	0.71	0.44	1.9	2.5	1.2	2.8	3.7			9.1	7.6	4.6	8.5	
		Maximum		39.7	18.2	26	9	7.6	4.4	0.26	0.87	0.52	2.5	3.1	1.5	3.8	5			10.5	9	5	10.5	
		Minimum		26.5	11.2	25	6.7	4.8	2.6	0.21	0.63	0.35	1.6	2.2	1	2.2	3.1			8	6.5	4	8	
		Standard Error Mean		1.3	0.77	0.29	0.2	0.26	0.19	0.004	0.01	0.01	0.08	0.09	0.06	0.16	0.17			0.26	0.21	0.12	0.30	

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Appendix I. (Continued)

Species	Catalogue	Locality	Sex	SVL	TRL	TL	HL	HW	HH	ratio HL/SVL	ratio HW/HL	ratio HH/HL	OD	NE	IN	IO1	IO2	TB	PAP	SL (L/R)	IL (L/R)	LP 1st (L/R)	LP 4rth (L/R)	Morphobank
H. paucituberculatus sp. nov.	**BMNH1977.935**[H]	OM, Khor Sawli	M	33.5	14.2		8.5	6.1	3.6	0.25	0.72	0.42	2.2	2.8	1.4	3.1	3.9		6	10/9	7/7	4/4	7/7	M100347-M100363
H. paucituberculatus sp. nov.	**BMNH1977.930**[P]	OM, Khor Sawli	M	38.4	17.4		9.4	7	3.9	0.24	0.74	0.41	2.1	2.9	1.4	3	4.5		6	9/10	7/6	5/?	9/8	M100364-M100380
H. paucituberculatus sp. nov.	**BMNHNH1977.937**[P]	OM, Khor Sawli	M	33.5	14.2		9	6.4	3.4	0.27	0.71	0.38	2.2	2.9	1.4	2.8	3.6		6	10/9	6/7	5/5	8/8	M100381-M100397
H. paucituberculatus sp. nov.	**IBES7910**	OM, East Khor	M	31.8	12.6		8.2	5.6	3.2	0.26	0.68	0.39	2.3	2.8	1.1	2.9	3.8		6	8/9	7/7	5/?	?/?	M100398-M100405
H. paucituberculatus sp. nov.	**IBES8004**	OM, 3.5 km NE Sadah	M	35.4	13.9		8.9	5.9	3.5	0.25	0.66	0.39	2.2	3.1	1.2	3.3	4.4		6	9/9	8/8	5/5	9/9	M100406-M100409
H. paucituberculatus sp. nov.	**IBES7994**	OM, Wadi Darbat	M	25.9	10.6	26.9	7	5	2.8	0.27	0.71	0.40	1.9	2.2	1.1	2.7	3.3		6	9/8	7/7	5/5	9/9	M100410-M100415
H. paucituberculatus sp. nov.	**BMNH1977.931**[P]	OM, Khor Sawli	F	33.6	14.5		8.4	6.1	4.1	0.25	0.73	0.49	2.2	2.5	1.4	3.4	4.2			8/8	7/7	5/5	8/8	M100416-M100431
H. paucituberculatus sp. nov.	**BMNH1977.936**[P]	OM, Khor Sawli	F	36.5	16.7		9.1	6.2	3.6	0.25	0.68	0.40	2.2	2.9	1.7	2.8	3.9			9/8	7/7	5/5	8/8	M100432-M100447
H. paucituberculatus sp. nov.	**BMNH1977.933**[P]	OM, Khor Sawli	F	34.1	16.4	25.3	8.1	6.2	3.7	0.24	0.77	0.46	2	2.5	1.1	2.8	3.5			9/8	8/8	?/?	8/8	M100448-M100464
H. paucituberculatus sp. nov.	**BMNH1977.944**[P]	OM, Khor Sawli	F	30.1	13		7.8	5.3	3	0.26	0.68	0.38	1.6	2.5	1.2	2.7	3.3			10/10	8/8	?/5	8/8	M100465-M100479
H. paucituberculatus sp. nov.	**BMNH1977.941**[P]	OM, Khor Sawli	F	32	14.3		8	5.6	3.1	0.25	0.70	0.39	1.7	2.7	1.2	2.6	3.3			10/9	8/7	?/?	?/8	M100480-M100496
H. paucituberculatus sp. nov.	**BMNH1977.942**[P]	OM, Khor Sawli	F	29.9	14.4		7.7	5.4	2.9	0.26	0.70	0.38	1.7	2.3	?	2.7	3.3			10/9	7/7	5/5	8/8	M100497-M100501
H. paucituberculatus sp. nov.	**ONHM3709**[P]	OM, Khor Sawli	F	32.8	14.3	38.8	8.2	5.7	3.4	0.25	0.70	0.41	2.1	2.9	1.5	2.9	3.6			9/10	7/8	5/5	9/9	M100502-M100515
H. paucituberculatus sp. nov.	**IBES7930**	OM, Wadi Hasik	F	33.8	13.5	36.7	8.2	6.4	3.3	0.24	0.78	0.40	2.2	2.7	1.4	3.1	4.5			8/8	8/8	5/5	9/9	M100516-M100524
H. paucituberculatus sp. nov.	**IBES7902**	OM, 3 km NW of Hasik	F	34.3	14		8.2	6.2	3.4	0.24	0.76	0.41	2.2	2.8	1.1	3	4.1			8/8	8/7	5/5	9/9	M100525-M100529
H. paucituberculatus sp. nov.	**IBES7646**[P]	OM, Khor Sawli	F	21	7.8		6	3.6	2.7	0.29	0.60	0.45	1.2	1.7		2.3	2.8			10/9	?/9	5/5	9/8	M100530-M100537
		Sexual dimorphism																						
		Number of individuals (M/F)		6/10	6/10		6/10	6/10	6/10	6/10	6/10	6/10	6/10	6/10	6/8	6/10	6/10			6/10	6/10	6/8	5/10	
		One-way ANOVA *F* value		0.337	0.003		1.606	0.680	0.148	0.257	0.078	1.355	2.597	1.771	0.326	0.948	1.074			0.267	4.414	1.371	0.022	
		Degrees of freedom		14	14		14	14	14	14	14	14	14	14	12	14	14			14	14	12	13	
		Probability (*P*)		0.570	0.952		0.225	0.423	0.705	0.619	0.783	0.263	0.129	0.204	0.578	0.346	0.317			0.613	0.054	0.264	0.883	
		Summary Statistics (Total)																						
		Number of Individuals (N)		16	16	4	16	16	16	16	16	16	16	16	14	16	16		6	16	16	14	15	
		Mean		32.2	13.8	31.9	8.1	5.7	3.3	0.25	0.70	0.41	2	2.6	1.3	2.8	3.7		6	8.9	7.4	4.9	8.3	
		Maximum		38.4	17.4	38.8	9.4	7	4.1	0.29	0.78	0.49	2.3	3.1	1.7	3.4	4.5		6	10	9	5	9	
		Minimum		21	7.8	25.3	6	3.6	2.7	0.24	0.60	0.38	1.2	1.7	1.1	2.3	2.8		6	8	6.5	4	7	
		Standard Error Mean		1.03	0.57	3.4	0.20	0.19	0.09	0.003	0.01	0.007	0.07	0.08	0.04	0.06	0.12		0	0.16	0.16	0.07	0.15	
		Summary Statistics (Males)																						
		Number of Individuals (N)		6	6	1	6	6	6	6	6	6	6	6	6	6	6		6	6	6	6	5	
		Mean		33	13.8	26.9	8.5	6	3.4	0.25	0.70	0.39	2.1	2.7	1.2	2.9	3.9		6	9	7	4.8	8.3	
		Maximum		38.4	17.4	26.9	9.4	7	3.9	0.27	0.74	0.42	2.3	3.1	1.4	3.3	4.5		6	9.5	8	5	9	
		Minimum		25.9	10.6	26.9	7	5	2.8	0.24	0.66	0.38	1.9	2.2	1.1	2.7	3.3		6	8.5	6.5	4	7	
		Standard Error Mean		1.7	0.91	-	0.34	0.27	0.15	0.004	0.01	0.006	0.05	0.12	0.06	0.08	0.18		-	0.2	0.22	0.16	0.37	
		Summary Statistics (Females)																						
		Number of Individuals (N)		10	10	3	10	10	10	10	10	10	10	10	8	10	10			10	10	8	10	
		Mean		31.8	13.8	33.6	7.9	5.6	3.3	0.25	0.71	0.41	1.9	2.5	1.3	2.8	3.6			8.9	7.6	5	8.3	
		Maximum		36.5	16.7	38.8	9.1	6.4	4.1	0.29	0.78	0.49	2.2	2.9	1.7	3.4	4.5			10	9	5	9	
		Minimum		21	7.8	25.3	6	3.6	2.7	0.24	0.6	0.38	1.2	1.7	1.1	2.3	2.8			8	7	5	8	
		Standard Error Mean		1.35	0.76	4.19	0.24	0.25	0.13	0.004	0.01	0.01	0.10	0.11	0.07	0.09	0.16			0.24	0.19	-	0.15	

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Appendix I. (Continued)

Species	Catalogue	Locality	Sex	SVL	TRL	TL	HL	HW	HH	ratio HL/SVL	ratio HW/HL	ratio HH/HL	OD	NE	IN	IO1	IO2	TB	PAP	SL (L/R)	IL (L/R)	LP 1st (L/R)	LP 4rth (L/R)	Morphobank
H. masirahensis sp. nov.	**BMNH1975.2080**[H]	OM, E. of R.A.F. camp, Masriah Is.	M	42.1	18.1	50	10.8	7.9	4.7	0.26	0.73	0.44	2.8	3.8	1.6	3.4	5		4	9/8	7/8	6/6	10/10	M10094-M100115
H. masirahensis sp. nov.	**BMNH1975.2082**[P]	OM, Wadi dhu Mayhi, Masriah Is.	M	37.2	16.1	40	9.9	6.3	3.5	0.27	0.64	0.35	2.4	3.4	1.5	3.2	3.7		4	10/9	8/7	6/6	10/10	M100116-M100137
H. masirahensis sp. nov.	**BMNH1975.2081**[P]	OM, E. of R.A.F. camp, Masriah Is.	F	45	20	41	10.7	7.6	4.7	0.24	0.71	0.44	2.3	3.6	1.7	3.6	3.9			10/9	8/7	6/6	10/11	M100138-M100157
H. masirahensis sp. nov.	**BMNH1975.2084**[P]	OM, Wadi dhu Mayhi, Masriah Is.	F	37.6	17.6		9.5	6.9	3.9	0.25	0.73	0.41	2.1	3.2	1.3	3	4			9/9	?/7	6/6	10/10	M100158-M100175
H. masirahensis sp. nov.	**BMNH1975.2083**[P]	OM, Wadi dhu Mayhi, Masriah Is.	F	34.3	13.9		9.2	6.3	3.6	0.27	0.68	0.39	2.4	3.3	1.5	3.3	3.9			9/10	7/8	6/6	10/10	M100176-M100196
H. masirahensis sp. nov.	**BMNH1976.1403**	OM, Wadi Haql, Masriah Is.	F	26.9	11.4		7.2	5	3.1	0.27	0.69	0.43	1.8	2.4	1	3	3.5			10/9	8/7	?/?	?/?	M100197-M100219
H. masirahensis sp. nov.	**IBES7710**[P]	OM, Wadi Maahdi, Masriah Is.	F	33.5	14.8		8.3	6.1	4.1	0.25	0.73	0.49	2	2.5	1.3	3.5	4.5			8/8	7/8	6/6	10/10	M100220-M100226
H. masirahensis sp. nov.	**ONHM3710**[P]	OM, Wadi Maahdi, Masriah Is.	F	25.7	10.1	29.6	7.3	4.7	3	0.28	0.64	0.41	1.9	2.3	1.1	2.4	3.3			9/9	7/7	6/6	10/10	M100227-M100230
		Summary Statistics (Total)																						
		Number of Individuals (N)		8	8	4	8	8	8	8	8	8	8	8	8	8	8		2	8	8	7	7	
		Mean		32.2	15.25	40.1	9.1	6.3	3.8	0.26	0.69	0.42	2.2	3	1.3	3.1	3.9		4	9	7.3	6	10.01	
		Maximum		45	20	50	10.8	7.9	4.7	0.28	0.73	0.49	2.8	3.8	1.7	3.6	5		4	9.5	7.5	6	10.5	
		Minimum		25.7	10.1	29.6	7.2	4.7	3	0.24	0.64	0.35	1.8	2.3	1	2.4	3.3		4	8	7	6	10	
		Standard Error Mean		2.37	1.19	4.17	0.49	0.39	0.23	0.004	0.013	0.014	0.11	0.20	0.08	0.13	0.19		0	0.19	0.08	0	0.07	
		Summary Statistics (Males)																						
		Number of Individuals (N)		2	2	2	2	2	2	2	2	2	2	2	2	2	2		2	2	2	2	2	
		Mean		39.6	17.1	45	10.3	7.1	4.1	0.26	0.68	0.39	2.6	3.6	1.5	3.3	4.3		4	9	7.5	6	10	
		Maximum		42.1	18.1	50	10.8	7.9	4.7	0.27	0.73	0.44	2.8	3.8	1.6	3.4	5		4	9.5	7.5	6	10	
		Minimum		37.2	16.1	40	9.9	7.1	3.5	0.26	0.64	0.35	2.4	3.4	1.5	3.2	3.7		4	8.5	7.5	6	10	
		Standard Error Mean		2.45	1	5	0.45	0.8	0.6	0.005	0.045	0.045	0.2	0.2	0.005	0.1	0.65		-	0.5	-	-	-	
		Summary Statistics (Females)																						
		Number of Individuals (N)		6	6	6	6	6	6	6	6	6	6	6	6	6	6			6	6	5	5	
		Mean		33.8	14.6	35.3	8.7	6.1	3.7	0.26	0.69	0.42	2	2.8	1.3	3.1	3.8			9	7.3	6	10.1	
		Maximum		45	20	41	10.7	7.6	4.7	0.28	0.73	0.49	2.4	3.6	1.7	3.6	4.5			9.5	7.5	6	10.5	
		Minimum		25.7	10	29.6	7.2	4.7	3	0.24	0.64	0.39	1.8	2.3	1	2.4	3.3			8	7	6	10	
		Standard Error Mean		2.9	1.51	5.7	0.55	0.45	0.26	0.006	0.01	0.01	0.09	0.22	0.1	0.17	0.17			0.23	0.1	-	0.1	
H. inexpectatus sp. nov.	**BMNH2008.712**[P]	OM, 2.5 Km SE Ar Rumayliyah	M	41	16.9	45	10.8	7.4	3.7	0.26	0.69	0.34	2.5	3.7	1.5	3	4.9	14	4	11/10	8/8	6/6	10/10	M100233-M100256
H. inexpectatus sp. nov.	**BMNH2008.711**[H]	OM, 2.5 Km SE Ar Rumayliyah	M	44.1	18.1	50	11.5	7.8	4	0.26	0.68	0.35	2.4	3.6	1.6	4	5.5	14	4	10/10	8/7	6/6	11/11	M100257-M100280
H. inexpectatus sp. nov.	**IBES1798**[P]	OM, 2.5 Km SE Ar Rumayliyah	M	39.3	16.6		10.2	6.4	3.8	0.26	0.63	0.37	2.2	3.7	1.5	3.5	4.7	14	4	11/11	8/8	6/6	11/11	M100281-M100301
H. inexpectatus sp. nov.	**IBES7722**[P]	OM, 2.5 Km SE Ar Rumayliyah	M	32.3	12.6	38.5	9.1	6.3	3.3	0.28	0.69	0.36	2.2	2.9	1.2	2.8	3.9	14	4	11/11	8/8	?/?	?/?	M100302-M100310
H. inexpectatus sp. nov.	**IBES7700**[P]	OM, 2.5 Km SE Ar Rumayliyah	F	39.9	17		10.3	7.1	3.9	0.26	0.69	0.38	2.5	3.5	1.4	3.7	5.1	14		10/11	8/9	6/6	11/11	M100311-M100315
H. inexpectatus sp. nov.	**IBES7735**[P]	OM, 2.5 Km SE Ar Rumayliyah	F	30.1	13.4	34	8.7	5.7	3.6	0.29	0.66	0.41	2.3	2.7	1.3	3	4	14		10/9	8/9	6/6	10/10	M100316-M100320
H. inexpectatus sp. nov.	**ONHM3711**[P]	OM, 2.5 Km SE Ar Rumayliyah	F	36.4	16.1		9.6	6.7	3.9	0.26	0.70	0.41	2.4	3.5	1.1	3.4	4.6	14		10/11	9/9	6/6	10/10	M100321-M100328
H. inexpectatus sp. nov.	**BMNH1979.467**	OM, Hamar-an-Nafur island	J	24.4	10.5	27	7.1	4.7	2.5	0.29	0.66	0.35	1.8	2.1	0.9	2.2	3	14		11/11	8/8	7/6	11/11	M100329-M100346
		Summary Statistics (Total)																						
		Number of Individuals (N)		7	7	4	7	7	7	7	7	7	7	7	7	7	7	7	4	7	7	6	6	
		Mean		37.5	15.8	41.8	10	6.7	3.7	0.26	0.67	0.37	2.3	3.3	1.3	3.3	4.6	14	4	10.4	8.2	6	10.5	
		Maximum		44.1	18.1	50	11.5	7.8	4	0.29	0.70	0.41	2.5	3.7	1.6	4	5.5	14	4	11	9	6	11	
		Minimum		30.1	12.6	34	8.7	5.7	3.3	0.26	0.63	0.34	2.2	2.7	1.1	2.8	3.9	14	4	9.5	7.5	6	10	
		Standard Error Mean		1.87	0.76	3.52	0.36	0.27	0.08	0.004	0.009	0.01	0.04	0.15	0.06	0.16	0.21	0	0	0.20	0.18	0	0.22	
		Summary Statistics (Males)																						
		Number of Individuals (N)		4	4	3	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	3	3	
		Mean		39.1	16	44.5	10.4	6.9	3.7	0.26	0.67	0.35	2.3	3.4	1.4	3.3	4.7	14	4	10.6	7.8	6	10.6	
		Maximum		44.1	18.1	50	11.5	7.8	4	0.28	0.69	0.37	2.5	3.7	1.6	4	5.5	14	4	11	8	6	11	
		Minimum		32.3	12.6	38.5	9.1	6.3	3.3	0.26	0.63	0.34	2.2	2.9	1.2	2.8	3.9	14	4	10	7.5	6	10	
		Standard Error Mean		2.49	1.19	3.32	0.5	0.37	0.14	0.005	0.014	0.006	0.07	0.19	0.08	0.26	0.33	-	-	0.23	0.12	-	0.33	
		Summary Statistics (Females)																						
		Number of Individuals (N)		3	3	1	3	3	3	3	3	3	3	3	3	3	3	3		3	3	3	3	
		Mean		35.4	15.5	34	9.5	6.5	3.8	0.27	0.68	0.4	2.4	3.2	1.2	3.3	4.5	14		10.1	8.6	6	10.3	
		Maximum		39.9	17	34	10.3	7.1	3.9	0.29	0.7	0.41	2.5	3.5	1.4	3.7	5.1	14		10.5	9	6	11	
		Minimum		30.1	13.4	34	8.7	5.7	3.6	0.26	0.66	0.38	2.3	2.7	1.1	3	4	14		9.5	8.5	6	10	
		Standard Error Mean		2.86	1.08	-	0.46	0.41	0.1	0.001	0.012	0.001	0.05	0.26	0.08	0.20	0.31	-		0.33	0.16	-	0.33	
H. endophis	**BMNH1976.1323**[H]	OM, "Muscat"	M	59	25.1		14.2	9.7	6.6	0.24	0.68	0.46	3	5.9	1.7	5	5.9	16	7+7	9/11	9/10	6/6	9/9	M101997-M102030
H. lemurinus	**IBES8058**	OM, Wadi Ayoun	M	63.6	26.3		16.8	12.8	7.9	0.26	0.76	0.47	5	6.1	2.1	6.7	10.1		3+3	10/9	8/8	7/7	11/11	M100787-M100799
H. lemurinus	**IBES8059**	OM, Wadi Ayoun	F	46.6	18.1		13.9	11.1	6.8	0.30	0.80	0.49	4.3	5.1	1.7	6	7.8		3+3	10/10	8/8	?/7	11/11	M100800-M100809

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Appendix I. (Continued)

Species	Catalogue	Locality	Sex	SVL	TRL	TL	HL	HW	HH	ratio HL/SVL	ratio HW/HL	ratio HH/HL	OD	NE	IN	IO1	IO2	TB	PAP	SL (L/R)	IL (L/R)	LP 1st (L/R)	LP 4rth (L/R)	Morphobank
H. robustus	**BMNHNH1934.11.8.10**	SA, Jeddah	M	46.2	21.1		10.4	8.9	5	0.23	0.86	0.48	2.6	3.7	1.3	4.1	5.3	16	6	9/8	9/8	6/6	?/10	M96106-M96123
H. robustus	**BMNHNH1973.1842**	UAE, S of Khor Jakkan	M	40.9	17.8		10.3	8	5.6	0.25	0.78	0.54	2.5	3.6	1.5	3.7	4.8	14	6	9/8	7/7	5/5	10/10	M96499-M96517
H. robustus	**BMNH1982.258**	UAE, Sharjah	M	45.7	21.2		10.8	8.9	5.7	0.24	0.82	0.53	2.6	3.5	1.3	3.9	5.2	14	6	8/9	8/8	5/5	9/9	M96738-M96754
H. robustus	**BMNH1975.831**	UAE, outskirts of Dubai	M	39.4	17.9		9.2	7.8		0.23	0.85		2.4	3.4	1.5	3.5	4.7	14	6	8/9	7/8	6/6	?/10	M96551-M96568
H. robustus	**BMNH1976.1408**	OM, Juzayrah, off Masirah Island	M	39.2	17.2	39	9.6	7.9	4.9	0.24	0.82	0.51	2.2	3.2	1.3	3.6	4.5	15	6	9/9	8/9	6/?	?/?	M96597-M96615
H. robustus	**BMNH1985.564**	OM, Salalah	M	44.3	22.6		12	8.1	5.5	0.27	0.68	0.46	2.3	4	1.3	3.9	5	16	3+3	9/9	8/8	6/?	?/10	M96755-M96773
H. robustus	**BMNH1992.201**	SA, Kiyat	M	44.4	19.3		11.4	9	5.3	0.26	0.79	0.46	3	3.6	1.2			15	6	10/9	8/9	6/?	10/?	M96791-M96805
H. robustus	**BMNH1971.1143**	UAE, 2 Km E of Sharjah	M	46.4	22.2		11.7	9	5.4	0.25	0.77	0.46	2.4	4.1	1.7	4	5.2	14	7	9/9	8/8	6/6	9/9	M96382-M96395
H. robustus	**BMNH1971.1145**	UAE, Sharjah Creek	M	33.4	14.5	30	8	6.4	4.1	0.24	0.80	0.51	1.8	2.9	1.6	3.1	4.4	14	6	10/9	8/8	6/6	9/9	M96413-M96429
H. robustus	**BMNH1963.672**	YE, near Al Hudaydah	M	45.7	21.6	35.1	10.6	8.9	5.7	0.23	0.84	0.54	2.6	4	1.5	4.5	5.6	15	3+3	10/8	7/7	6/6	?/10	M96321-M96336
H. robustus	**BMNH1975.1032**	OM, R.A.F camp, Marisah Island	M	42	18.6	39	10.1	7.7	4.8	0.24	0.76	0.48	3.3	3.5	1.7	3.7	4.4	14	3+3	9/9	8/7	6/6	9/9	M96569-M96588
H. robustus	**BMNH1959.1.5.11**	ER, Alet	M	46.5	20.4	40	11	9.2	5.7	0.24	0.84	0.52	2.5	4.3	1.6	5.1	6	15	7	9/9	7/7	6/6	9/9	M96303-M96319
H. robustus	**BMNH1973.440**	PA, university campus, Karachi	M	38.9	17.9		9.5	7.2	4.3	0.24	0.76	0.45	2.6	2.9	1.4	3.7	5.1	15	6	9/9	8/8	6/6	9/9	M96464-M96481
H. robustus	**BMNH1973.438**	PA, university campus, Karachi	M	39.5	19.3	42	9.2	7.9	4.4	0.23	0.86	0.48	2.5	3.3	1.5	4.2	5.4	14	7	9/9	9/8	6/6	10/?	M96430-M96446
H. robustus	**BMNH1973.439**	PA, university campus, Karachi	M	36.2	17.8		8.7	6.9	4.2	0.24	0.79	0.48	2.1	2.8	1.4	3.6	4.7	14	6	9/9	8/9	6/6	10/10	M96447-M96463
H. robustus	**BMNH83.3.26.5**	PA, Karachi	M	44.8	20	52	10.6	8.1	5.1	0.24	0.76	0.48	2.4	3.9	1.2	3.8	4.5	16	6	10/10	7/8	7/7	10/11	M95840-M95855
H. robustus	**BMNH84.7.25.6**	IN, Sind	M	44.9	20.3		11.3	8.3	5.1	0.25	0.73	0.45	2.5	3.8	1.6	5	6	14	3+3	9/9	7/7	6/6	10/10	M95886-M95900
H. robustus	**BMNH84.7.25.7**	IN, Sind	M	43.6	18.6	38	10.5	8	4.9	0.24	0.76	0.47	2.7	3.8	1.5	3.8	5.2	17	3+3	11/10	9/8	7/7	10/10	M95872-M95885
H. robustus	**BMNH1937.12.5.270**	SO, Bonama district, 41º50'; 10º10'	M	45.7	20		11.8	9.3	5.5	0.26	0.79	0.47	3	3.7	1.5	4	5.6	15	6	8/10	7/7	6/6	9/9	M96056-M96072
H. robustus	**BMNH1937.12.5.271**	SO, Bonama district, 41º50'; 10º10'	M	41.7	17.9		10.7	8.6	5	0.26	0.80	0.47	2.8	3.8	1.8	3.7	5.3	15	3+3	9/9	7/7	5/5	9/9	M96073-M96088
H. robustus	**BMNH1937.12.5.272**	SO, Bonama district, 41º50'; 10º10'	M	42.8	20.1		10.9	8.6	5.1	0.25	0.79	0.47	3	3.9	1.6	4.1	5.6	15	5	10/10	8/8	6/6	9/9	M96089-M96105
H. robustus	**BMNH1956.1.6.67**	YE, Wadi Hatash, Hadramaut	M	54.6	26.8	48	13.4	9.9	6.1	0.25	0.74	0.46	3.2	4.4	1.7	4.2	5.9	15	6	7/8	7/7	7/7	11/11	M96245-M96263
H. robustus	**BMNH1934.11.8.11**	SA, Jeddah	F	42.6	19.4		10	7.5	5.1	0.23	0.75	0.51	2.5	2.8	1.6	3.7	5.1	14		8/9	7/7	6/6	10/10	M96124-M96137
H. robustus	**BMNH1934.11.8.12**	SA, Jeddah	F	38	16.3		10	6.7	4.5	0.26	0.67	0.45	2.5	3.6	1.2	3.5	4.4	14		9/9	8/8	6/6	10/10	M96138-M96151
H. robustus	**BMNH1978.2031**	SA, Jeddah	F	46.1	20.2	50	11.2	8.6	4.9	0.24	0.77	0.44	2.5	3.5	1.3	4.1	6	15		9/8	7/8	6/6	10/10	M96720-M96737
H. robustus	**BMNH1978.910**	SA, Jeddah	F	50.8	22.3		11.5	9.2	6.1	0.23	0.80	0.53	2.8	3.8	1.7	4.1	5.7	15		9/9	7/7	6/7	10/10	M96706-M96719
H. robustus	**BMNH1970.1547**	UAE, Sharjah	F	49.6	21.6	47	11	8.2	5.4	0.22	0.75	0.49	3.4	3.8		4.4	5.9	14		9/9	8/8	?/?	10/10	M96368-M96381
H. robustus	**BMNH1977.36**	OM, Wattayeh, near Muscat	F	42.4	21.3	45	10.5	7.5	5.2	0.25	0.71	0.50	2.3	3.3	1.6	3.9	4.9	15		8/9	8/8	7/7	10/10	M96671-M96684
H. robustus	**BMNH1977.37**	OM, Wattayeh, near Muscat	F	31.2	15.3	32	7.9	6.2	3.9	0.25	0.78	0.49	1.8	2.7	1.1	2.9	3.8	15		10/10	7/8	7/6	11/11	M96685-M96701
H. robustus	**BMNH1973.1844**	UAE, Ras Ghanada	F	39.2	16.7		10	7.4	4.7	0.26	0.74	0.47	2.5	3.2	1.5	3.2	4.2	16		10/9	7/7	6/6	10/10	M96535-M96550
H. robustus	**BMNH1973.1843**	UAE, S of Khor Jakkan	F	40.8	19.3		9.7	7	4.7	0.24	0.72	0.48	2.4	3.2	1.6	3.3	4.1	15		10/9	8/8	6/5	?/?	M96518-M96534
H. robustus	**BMNH1953.1.7.88**	YE, Hadiboh, Socotra	F	47.1	22.7		10.3	8.4	5.7	0.22	0.82	0.55	2.2	3.7	5.1	4	5.1	16		9/9	7/8	?/7	?/11	M96152-M96167
H. robustus	**BMNH1953.1.7.89**	YE, Hadiboh, Socotra	F	47.4	22.6		10	8.6	5.56	0.21	0.86	0.56	2.7	3.6	1.3	4	5.1	16		9/9	7/8	6/6	10/10	M96230-M96244
H. robustus	**BMNH1965.1448**	YE, Socotra	F	36	15.8		9.7	7	4.3	0.27	0.72	0.44	2.6	3.3	1.3	3	4	15		11/9	8/8	6/6	10/10	M96354-M96367
H. robustus	**BMNH1973.1841**	UAE, Ras al Kaymah	F	48.5	22.6		10.5	8.2	5.6	0.22	0.78	0.53	2.7	3.7	1.6	3.5	5	16		9/9	8/8	6/6	10/9	M96482-M96498
H. robustus	**BMNH1992.200**	SA, Kiyat	F	45.5	22		11.2	7.6	5.2	0.25	0.68	0.46	2.7	3.7	1.2	4	4.7	16		8/8	7/7	5/5	?/10	M96774-M96790
H. robustus	**BMNH1971.1144**	UAE, Sharjah Creek	F	45.4	22	50	10.6	8.1	5.2	0.23	0.76	0.49	2.5	3.6	1.6	4	5.2	14		9/10	8/8	6/6	9/9	M96396-M96412
H. robustus	**BMNH1963.673**	YE, near ABS	F	39	16.1		9.6	6.7	4.1	0.25	0.70	0.43	2.3	3.2	1.3	3.3	4.4	15		9/9	7/8	6/6	10/?	M96337-M96353
H. robustus	**BMNH83.3.26.6**	PA, Karachi	F	44	20.8	40	9.4	7.9	4.8	0.21	0.84	0.51	2.4	3.6	1.6	3	5	14		10/10	8/8	6/?	10/10	M95856-M95871
H. robustus	**BMNH1937.12.5.267**	SO, Bonama district, 41º50'; 10º10'	F	42.4	19.5		10.8	7.4	4.5	0.25	0.69	0.42	2.5	3.4	1.6	3.5	4.5	15		9/9	7/7	6/6	9/9	M96023-M96055
H. robustus	**BMNH1956.1.6.68**	YE, Wadi Hatash, Hadramaut	F	49.1	22.5	55	12.2	8.5	5.3	0.25	0.70	0.43	3	4.4	1.6	3.9	5.1	14		10/9	7/7	7/7	10/10	M96266-M96285
H. robustus	**BMNH1956.1.6.69**	YE, Wadi Hatash, Hadramaut	F	34.2	16.1		8.9	6	3.7	0.26	0.67	0.42						14		8/8	7/7	7/7	10/11	M96286-M96302
H. robustus	**BMNH97.11.31**	YE, Hadramaut	F	51.3	22.5		12.2	9.5	6.2	0.24	0.78	0.51	2.8	4.4	1.7	4.3	5.9	14		9/10	8/7	7/7	10/10	M95929-M95946
H. robustus	**BMNH97.11.32**	YE, Hadramaut	F	44.7	20.3		10.9	8	5.1	0.24	0.73	0.47	2.9	4	1.6	4	5.5	14		8/9	7/7	7/7	10/10	M95947-M95961
H. robustus	**BMNH97.11.33**	YE, Hadramaut	F	42.6	20.6		9.8	6.9	4.6	0.23	0.70	0.47	2.7	3.6	1.4	4.3	5.1	14		9/8	8/7	7/7	10/10	M95962-M95976
		Sexual dimorphism																						
		Number of individuals (M/F)		22/23	22/23	9/7	22/23	22/23	21/23	22/23	22/23	21/23	22/22	22/22	22/21	21/22	21/22	22/23		22/23	22/23	22/22	21/22	
		One-way ANOVA *F* value		0.057	0.108	2.193	0.326	5.332	0.613	1.387	9.746	0.128	0.017	0.504	0.780	2.887	1.583	0.021		0.0001	2.544	3.143	4.654	
		Degrees of freedom		43	43	14	43	43	42	43	43	42	42	42	41	41	41	43		43	43	42	41	
		Probability (*P*)		0.811	0.743	0.160	0.570	0.025*	0.437	0.245	0.003*	0.721	0.894	0.481	0.382	0.096	0.215	0.885		0.001	0.118	0.083	0.036*	
		Summary Statistics																						
		Number of Individuals (N)		45	45	16	45		44	45		44	44	44	43	43	43	45	22	45	45	44		
		Mean		43.2	19.8	42.6	10.4		5	0.24		0.48	2.5	3.5	1.5	3.8	5	14.8	6	9	7.6	6.1		
		Maximum		54.6	26.8	55	13.4		6.2	0.27		0.56	3.4	4.4	5.1	5.1	6	17	7	10.5	8.5	7		
		Minimum		31.2	14.5	30	7.9		3.7	0.21		0.42	1.8	2.7	1.1	2.9	3.8	14	5	7.5	7	5		
		Standard Error Mean		0.72	0.37	1.81	0.163		0.09	0.002		0.005	0.05	0.006	0.088	0.07	0.08	0.12	0.09	0.08	0.07	0.08		
		Summary Statistics (Males)																						
		Number of Individuals (N)		22	22	9	22	22	21	22	22	21	22	22	22	21	21	22	22	22	22	22	21	
		Mean		43	19.6	40.3	10.5	8.3	5.1	0.24	0.79	0.48	2.5	3.6	1.4	3.9	5.1	14.8	6	9	7.7	6	9.6	
		Maximum		54.6	26.8	52	13.4	9.9	6.1	0.27	0.86	0.54	3.3	4.4	1.8	5.1	6	17	7	10.5	8.5	7	11	
		Minimum		33.4	14.5	30	8	6.4	4.1	0.23	0.68	0.45	1.8	2.8	1.2	3.1	4	14	5	7.5	7	5	9	
		Standard Error Mean		0.93	0.52	2.1	0.25	0.17	0.11	0.002	0.009	0.006	0.07	0.09	0.03	0.1	0.11	0.18	0.09	0.13	0.13	0.11	0.13	
		Summary Statistics (Females)																						
		Number of Individuals (N)		23	23	7	23	23	23	23	23	23	22	22	21	22	22	23		23	23	22	22	
		Mean		43.3	19.9	45.5	10.3	7.7	4.9	0.23	0.74	0.48	2.5	3.5	1.6	3.7	4.9	14.7		9	7.5	6.2	10	
		Maximum		51.3	22.7	55	12.2	9.5	6.2	0.27	0.86	0.56	3.4	4.4	5.1	4.4	6	16		10	8	7	11	
		Minimum		31.2	15.3	32	7.9	6	3.7	0.21	0.67	0.42	1.8	2.7	1.1	2.9	3.8	14		8	7	5	9	
		Standard Error Mean		1.11	0.54	2.86	0.2	0.18	0.13	0.003	0.011	0.008	0.006	0.08	0.17	0.09	0.13	0.16		0.12	0.08	0.12	0.09	

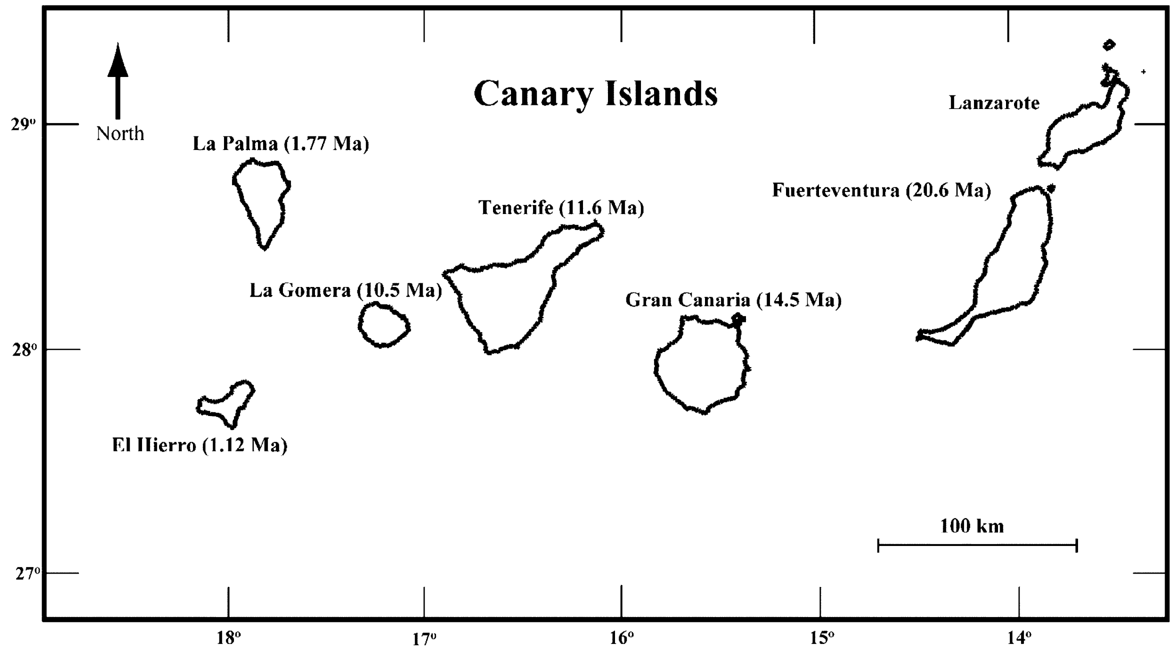
……*continued on next page*

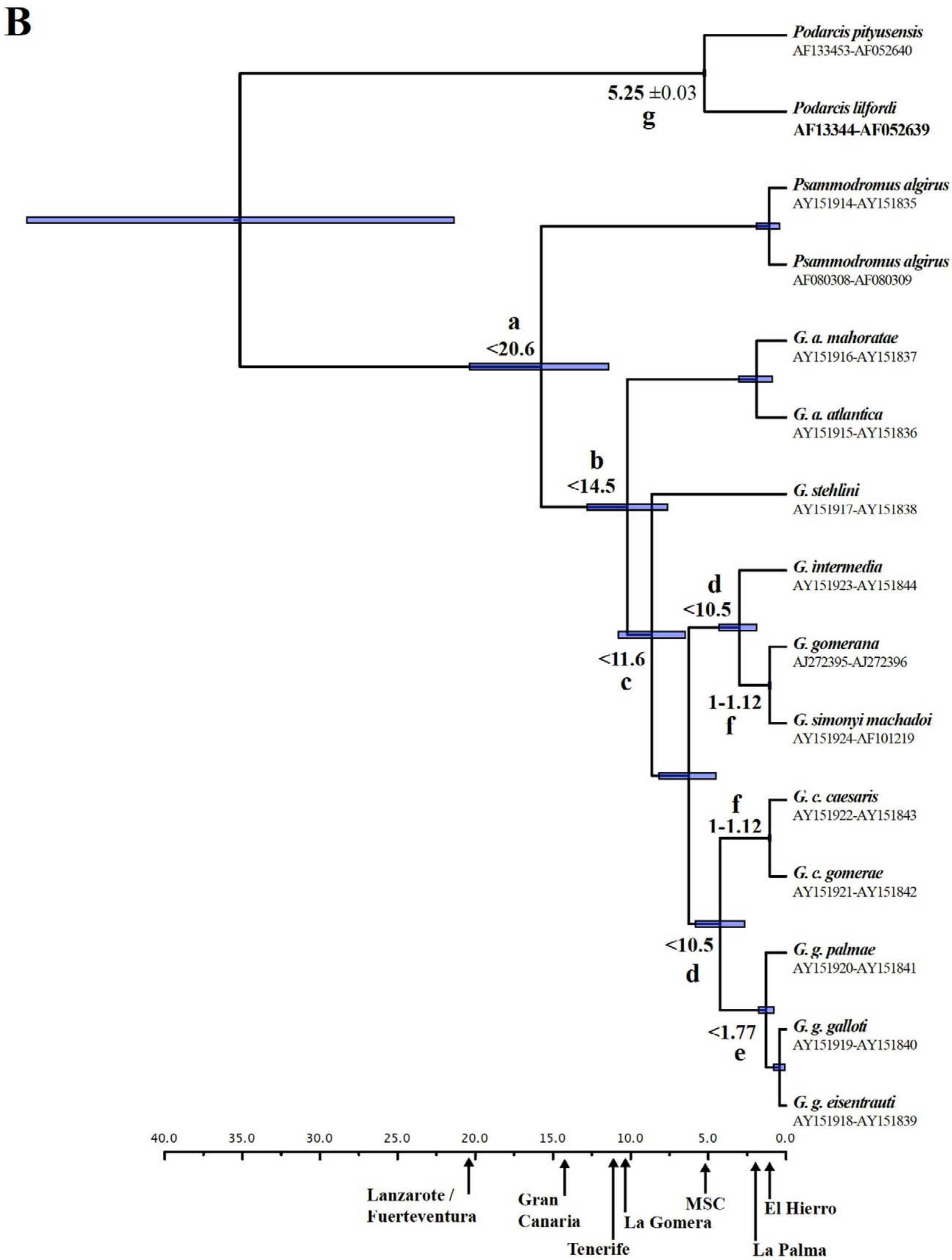
Appendix I. (Continued)

Species	Catalogue	Locality	Sex	SVL	TRL	TL	HL	HW	HH	ratio HL/SVL	ratio HW/HL	ratio HH/HL	OD	NE	IN	IO1	IO2	TB	PAP	SL (L/R)	IL (L/R)	LP 1st (L/R)	LP 4rth (L/R)	Morphobank
H. sinaitus HOLOTYPE	**BMNH82.8.16.27**	EG, Mount Sinai (prob. from Sudan)	M	41.2	17.5	43	8.4	6.9	4.6	0.20	0.82	0.55	2.5	3.4	1.2	3.8	5.2	15	4	9/9	8/8	5/5	9/9	M100538-M100557
H. sinaitus	**BMNH97.10.28.85**	SU, Durrur, N of Suakin	M	40.4	20.7		9.8	7.1	4.8	0.24	0.72	0.49	2.7	3.3	1.5	3.6	4.8	15	5	7/8	7/7	5/5	10/10	M100558-M100577
H. sinaitus	**BMNH97.10.28.84**	SU, Durrur, N of Suakin	M	45	22.5		10.7	8.2	5.2	0.24	0.77	0.49	2.8	3.7	1.8	4.5	5.8	15	4	8/8	7/6	5/5	9/9	M100578-M100595
H. sinaitus	**BMNH97.10.28.87**	SU, Wadi Haifa	M	40.3	18.1	44	9.1	7.3	4.7	0.23	0.80	0.52	2.3	3.6	1.3	3.9	5	14	8	9/9	7/7	7/7	10/10	M100596-M100615
H. sinaitus	**BMNH1974.3931**	ETH, Mule River, Danakil	M	39	19.1		9.8	7.3	4.5	0.25	0.74	0.46	2.7	3.1	1.7	3.4	4.7	16	4	8/8	8/6	?/?	9/9	M100622-M100638
H. sinaitus	**BMNH1937.12.5.293**	SO, Borama district, 43° 15' /10° 30'	M	40.4	17.7	35	10.9	7.9	4.8	0.27	0.72	0.44	2.6	3.4	1.5	3.6	5.2	15	6	8/8	7/7	?/6	?/10	M100639-M100657
H. sinaitus	**BMNH1937.12.5.294**	SO, Borama district, 43° 15' /10° 30'	M	30.7	13.2	31	8.3	5.2	4.2	0.27	0.63	0.51	2.1	2.7	1.3	2.8	3.8	?	6	9/9	6/6	5/?	10/?	M100658-M100674
H. sinaitus	**BMNH97.10.28.83**	SU, Durrur, N of Suakin	F	47	23		10.4	8.4	5.5	0.22	0.81	0.53	2.9	4	1.4	4.9	5.7	14		10/9	8/7	5/5	10/10	M100675-M100691
H. sinaitus	**BMNH95.5.23.7**	YE, Sheikh Osman, near Aden	F	51.2	26	54	11.8	8.1	5.1	0.23	0.69	0.43	3.2	5	1.6	4.3	6.1	15		10/11	9/10	4/5	10/10	M100692-M100710
H. sinaitus	**BMNH1945.12.12.14**	YE, Bir Fadhl, Aden	F	38.7	15.9		9.8	6.9	5.3	0.25	0.70	0.54	2.5	3.1	1.2	4.1	5.7	15		9/9	9/9	5/5	10/10	M100711-M100739
		Summary Statistics (Total)																						
		Number of Individuals (N)		10	10	5	10	10	10	10	10	10	10	10	10	10	10	9	7	10	10	9	10	
		Mean		41.3	19.3	41.4	9.9	7.3	4.8	0.24	0.74	0.49	2.6	3.5	1.45	3.9	5.2	14.8	5.2	8.7	7.4	5.2	9.7	
		Maximum		51.2	26	54	11.8	8.4	5.5	0.27	0.82	0.55	3.2	5	1.8	4.9	6.1	16	8	10.5	9.5	7	10	
		Minimum		30.7	13.2	31	8.3	5.2	4.2	0.20	0.63	0.43	2.1	2.7	1.2	2.8	3.8	14	4	7.5	6	4.5	9	
		Standard Error Mean		1.73	1.18	3.98	0.34	0.29	0.12	0.006	0.019	0.013	0.09	0.19	0.06	0.18	0.21	0.20	0.56	0.28	0.34	0.21	0.15	
		Summary Statistics (Males)																						
		Number of Individuals (N)		7	7	4	7	7	7	7	7	7	7	7	7	7	7	6	7	7	7	6	7	
		Mean		39.5	18.4	38.2	9.5	7.1	4.6	0.24	0.74	0.49	2.5	3.3	1.4	3.6	4.9	15	5.2	8.3	6.9	5.5	9.5	
		Maximum		45	22.5	44	10.9	8.2	5.2	0.27	0.82	0.55	2.8	3.7	1.8	4.5	5.8	16	8	9	8	7	10	
		Minimum		30.7	13.2	31	8.3	5.2	4.2	0.20	0.63	0.44	2.1	2.7	1.2	2.8	3.8	14	4	7.5	6	5	9	
		Standard Error Mean		1.64	1.1	3.1	0.38	0.36	0.11	0.009	0.023	0.013	0.09	0.12	0.08	0.19	0.23	0.25	0.56	0.23	0.22	0.34	0.20	
		Summary Statistics (Females)																						
		Number of Individuals (N)		3	3	1	3	3	3	3	3	3	3	3	3	3	3	3		3	3	3	3	
		Mean		45.6	21.6	54	10.6	7.8	5.3	0.23	0.73	0.5	2.8	4	1.4	4.4	5.8	14.6		9.6	8.6	4.8	10	
		Maximum		51.2	26	54	11.8	8.4	5.5	0.25	0.81	0.54	3.2	5	1.6	4.9	6.1	15		10.5	9.5	5	10	
		Minimum		38.7	15.9	54	9.8	6.9	5.1	0.22	0.69	0.43	2.5	3.1	1.2	4.1	5.7	14		9	7.5	4.5	10	
		Standard Error Mean		3.6	2.99	-	0.59	0.45	0.11	0.008	0.038	0.035	0.20	0.54	0.11	0.20	0.13	0.33		0.44	0.6	0.16	-	
H. shugraensis TYPE	**BMNH1953.1.6.97**	YE, near Shugra, W of Aden	M	43.6	19.6	47	10.8	7.7	4.9	0.25	0.71	0.45	3.1	3.4	?	4.4	5.5	14	5	10/9	10/9	5/5	10/10	M100740-M100766
H. shugraensis TYPE	**BMNH1953.1.6.98**	YE, near Shugra, W of Aden	M	41.5	19.8		9.9	7.9	5.2	0.24	0.80	0.53	3.1	4	1.4	4.2	6	14	5	9/10	9/9	5/5	9/9	M100767-M100786

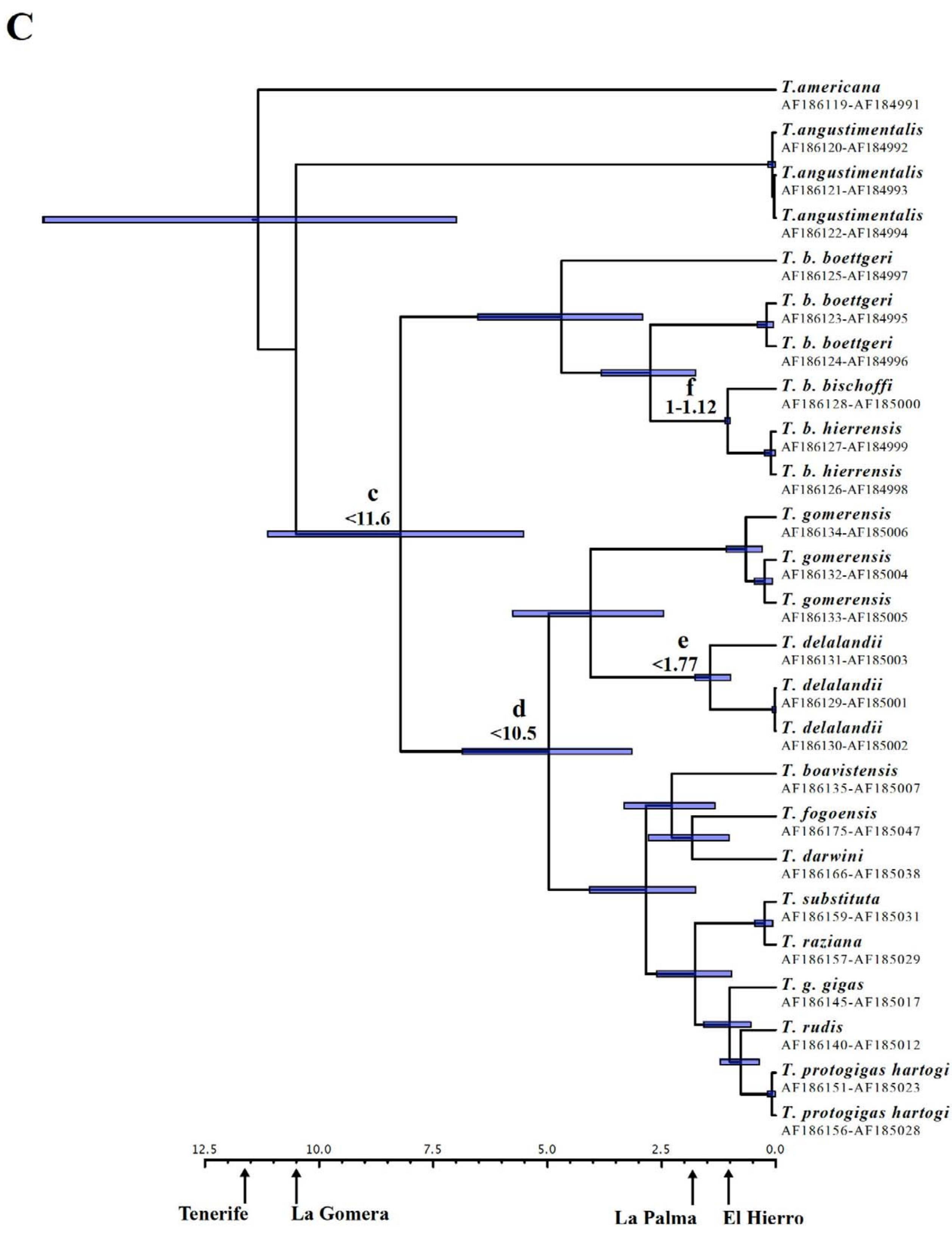
Appendix II: Calculation of independent and combined mean rates (μ) and Standard Deviations (σ) for the mtDNA genes *12S* and *cytb* based on the analysis of mtDNA phylogenies of the Canary Islands reptile genera *Gallotia*, *Tarentola* and *Chalcides*, using island ages and the Messinian Salinity Crisis as calibration points. A.- Canary Islands ages; B.- Result of the BEAST analysis of *Gallotia*. Nodes a-g, calibration points: a, age of the oldest islands Fuerteventura and Lanzarote (Uniform prior: 0-20.6); b, age of Gran Canaria (Uniform prior: 0-14.5); c, age of the oldest emerged part of Tenerife (Roque del Conde) (Uniform prior: 0-11.6); d, age of La Gomera (Uniform prior: 0-10.5); e, age of La Palma (Uniform prior: 0-1.77); f, age of El Hierro assuming that it was colonized soon after its appearance (see materials and methods) (Uniform prior: 1-1.12); g, end of the Messinian Salinity Crisis, a vicariant event that is assumed to have caused the split between the two endemic *Podarcis* from the Balearic Islands, *P. lilfordii* and *P. pityusensis* (see materials and methods) (Normal prior: mean 5.25, standard Deviation 0.03). C.- Result of the BEAST analysis of *Tarentola*. Nodes c-f calibration points, same priors as in *Gallotia* (B). D.- Result of the BEAST analysis of *Chalcides*. Nodes c, d and f calibration points, same priors as in *Gallotia* (B).

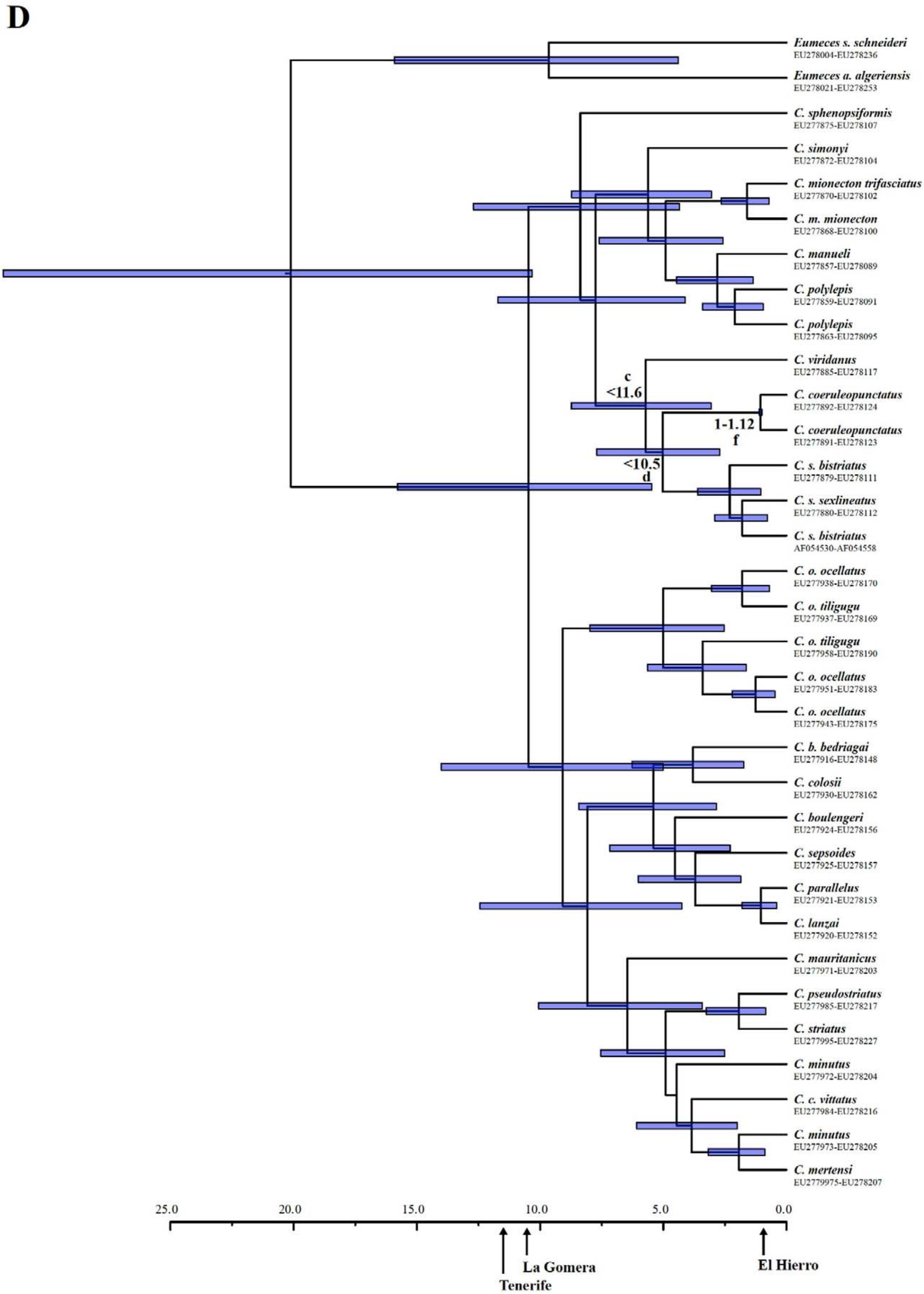
A





B
Podarcis pityusensis
AF133453-AF052640
5.25 ±0.03
g
Podarcis lilfordi
AF13344-AF052639
Psammodromus algirus
AY151914-AY151835
Psammodromus algirus
AF080308-AF080309
a
<20.6
G. a. mahoratae
AY151916-AY151837
G. a. atlantica
AY151915-AY151836
b
<14.5
G. stehlini
AY151917-AY151838
G. intermedia
AY151923-AY151844
d
<10.5
G. gomerana
AJ272395-AJ272396
<11.6
c
1-1.12
f
G. simonyi machadoi
AY151924-AF101219
f
1-1.12
G. c. caesaris
AY151922-AY151843
G. c. gomerae
AY151921-AY151842
<10.5
d
G. g. palmae
AY151920-AY151841
<1.77
e
G. g. galloti
AY151919-AY151840
G. g. eisentrauti
AY151918-AY151839
40.0 35.0 30.0 25.0 20.0 15.0 10.0 5.0 0.0
Lanzarote / Fuerteventura
Gran Canaria
Tenerife
La Gomera
MSC
El Hierro
La Palma


C
T.americana
AF186119-AF184991
T.angustimentalis
AF186120-AF184992
T.angustimentalis
AF186121-AF184993
T.angustimentalis
AF186122-AF184994
T. b. boettgeri
AF186125-AF184997
T. b. boettgeri
AF186123-AF184995
T. b. boettgeri
AF186124-AF184996
f
1-1.12
T. b. bischoffi
AF186128-AF185000
T. b. hierrensis
AF186127-AF184999
T. b. hierrensis
AF186126-AF184998
c
<11.6
T. gomerensis
AF186134-AF185006
T. gomerensis
AF186132-AF185004
T. gomerensis
AF186133-AF185005
e
<1.77
T. delalandii
AF186131-AF185003
T. delalandii
AF186129-AF185001
d
<10.5
T. delalandii
AF186130-AF185002
T. boavistensis
AF186135-AF185007
T. fogoensis
AF186175-AF185047
T. darwini
AF186166-AF185038
T. substituta
AF186159-AF185031
T. raziana
AF186157-AF185029
T. g. gigas
AF186145-AF185017
T. rudis
AF186140-AF185012
T. protogigas hartogi
AF186151-AF185023
T. protogigas hartogi
AF186156-AF185028
12.5
10.0
7.5
5.0
2.5
0.0
Tenerife
La Gomera
La Palma
El Hierro


D
Eumeces s. schneideri
EU278004-EU278236
Eumeces a. algeriensis
EU278021-EU278253
C. sphenopsiformis
EU277875-EU278107
C. simonyi
EU277872-EU278104
C. mionecton trifasciatus
EU277870-EU278102
C. m. mionecton
EU277868-EU278100
C. manueli
EU277857-EU278089
C. polylepis
EU277859-EU278091
C. polylepis
EU277863-EU278095
C. viridanus
EU277885-EU278117
c
<11.6
C. coeruleopunctatus
EU277892-EU278124
1-1.12
f
C. coeruleopunctatus
EU277891-EU278123
<10.5
d
C. s. bistriatus
EU277879-EU278111
C. s. sexlineatus
EU277880-EU278112
C. s. bistriatus
AF054530-AF054558
C. o. ocellatus
EU277938-EU278170
C. o. tiligugu
EU277937-EU278169
C. o. tiligugu
EU277958-EU278190
C. o. ocellatus
EU277951-EU278183
C. o. ocellatus
EU277943-EU278175
C. b. bedriagai
EU277916-EU278148
C. colosii
EU277930-EU278162
C. boulengeri
EU277924-EU278156
C. sepsoides
EU277925-EU278157
C. parallelus
EU277921-EU278153
C. lanzai
EU277920-EU278152
C. mauritanicus
EU277971-EU278203
C. pseudostriatus
EU277985-EU278217
C. striatus
EU277995-EU278227
C. minutus
EU277972-EU278204
C. c. vittatus
EU277984-EU278216
C. minutus
EU277973-EU278205
C. mertensi
EU2779975-EU278207
25.0
20.0
15.0
10.0
5.0
0.0
La Gomera
Tenerife
El Hierro

Independent and combined values of the mean rate and Standard Deviations obtained from each independent analysis of all three reptile taxa shown above (B-D).

The combined value of the mean rate (μ) was the average of the tree values calculated with the following simple formula:

$$\mu_X = \frac{\sum_i N_{X_i}\mu_{X_i}}{\sum_i N_{X_i}}$$

N (sample size) is equal in all three independent analyses on BEAST (B-C).

The combined value of the Standard Deviation was based on the following formula:

$$\sigma_X = \sqrt{\frac{\sum_i N_{X_i}(\sigma_{X_i}^2 + \mu_{X_i}^2)}{\sum_i N_{X_i}} - \mu_X^2} = \sqrt{\frac{\sum_i N_{X_i}\sigma_{X_i}^2}{\sum_i N_{X_i}} + \frac{\sum_{i<j} N_{X_i}N_{X_j}(\mu_{X_i} - \mu_{X_j})^2}{\left(\sum_i N_{X_i}\right)^2}}$$

Std. Dev. (σ) = SE/$\sqrt{N_{ESS}}$

SE = Standard Error of the mean

N_{ESS}= Effective Sampling Size of the meanRate posterior after burnin.

Results:

12S	*Chalcides*	*Tarentola*	*Gallotia*	Combined
Mean rate (μ)	0.00890	0.0102	0.00553	0.00755
Std. Dev. (σ)	0.00240	0.00207	0.00128	0.00247

cytb	*Chalcides*	*Tarentola*	*Gallotia*	Combined
Mean rate (μ)	0.0253	0.0334	0.0164	0.0228
Std. Dev. (σ)	0.00699	0.00680	0.00317	0.00806

Appendix III: Maximum-likelihood tree inferred using Dataset 3 (350 bp of the *12S* gene). *Hemidactylus flaviviridis* was used to root the tree (not shown). Specimens labelled as OTU 1, 3, 5, 6 and 7 refer to specimens from Busais & Joger (2011a). Filled circles by the nodes indicate bootstrap support in the ML analysis ≥ 70% and posterior probability values in the Bayesian analysis ≥ 0.95.