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Phylogenetic relationships of Semaphore geckos (Squamata: Sphaerodactylidae: *Pristurus*) with an assessment of the taxonomy of *Pristurus rupestris*

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Abstract

A molecular phylogeny of the sphaerodactylid geckos of the genus *Pristurus* is inferred based on an alignment of 1845 base pairs (bp) of concatenated mitochondrial (*12S*) and nuclear (*acm4*, *cmos*, *rag1* and *rag2*) genes for 80 individuals, representing 18 of the 23–26 species, and the three subspecies of *P. rupestris*. The results indicate that *P. rupestris* is polyphyletic and includes two highly divergent clades: the eastern clade, found in coastal Iran and throughout the Hajar Mountain range in northern Oman and eastern UAE; and the western clade, distributed from central coastal Oman, through Yemen, Saudi Arabia and north to southern Jordan. Inferred haplotype networks for the four nuclear genes show that the eastern and western clades of “*P. rupestris*” are highly differentiated and do not share any alleles. Moreover, although the two clades are differentiated by a morphological multivariate analysis, no one character or set of characters was found to be diagnostic. Based on the molecular analysis of specimens from the type locality of *P. rupestris rupestris*, the name *P. rupestris* is applied to the eastern clade. The name that should apply to the western clade cannot be clarified until morphological and genetic data for “*P. rupestris*” is available from the vicinity of Bosaso, Somalia, and therefore we refer to it as *Pristurus* sp. 1. The phylogenetic tree of *Pristurus* supports the hypothesis that *P. celerrimus* is sister to all the other species in the analyses and that the Socotra Archipelago was independently colonized a minimum of two times.

Key words: gecko, Arabia, phylogeny, taxonomy, systematics, Socotra Archipelago, mitochondrial DNA, nuclear DNA.

Introduction

The sphaerodactylid geckos of the genus *Pristurus* Rüppell, 1835, also known as Semaphore geckos, comprise 23–26 species (Arnold 2009; Sindaco & Jeremčenko 2008; Uetz 2013), characterized by being mostly diurnal,

heliothermic and by signaling each other by waving their tails. These features are unusual among geckos, which are mainly nocturnal, active at comparatively low temperatures and communicate predominantly by vocalization or by chemical cues. In fact, some *Pristurus* species behave more like desert agamid lizards than typical geckos (Arnold 1993). Most of the species of the genus are found in northeast Africa (7 species, 4 endemic), the Arabian Peninsula (14 species, 12 endemic) and the Socotra Archipelago (7 species, all endemic), with a widely distributed species, *P. rupestris* Blanford, 1874, extending into coastal Iran. Unexpectedly, a new isolated species, *P. adrarensis* Geniez & Arnold, 2006, was recently described from a very small area in Mauritania, constituting a 4700 km range extension to the west.

At a morphological level, *Pristurus* species are characterized externally by having simple toes without expanded adhesive pads beneath, tail compressed laterally, dorsal scaling consisting of small granules without larger tubercles on the body, flanks often with longitudinal series of short dark or reddish streaks separated by pale spots, pupil round or vertically elliptical with complete (or notchless) borders, absence of preanal and femoral pores, cloacal tubercles and postcloacal sacs (Arnold 1977, 1982, 1986a, 2009). These main features, together with other morphological, behavioral and ecological characters were used by Arnold (2009) to infer a phylogenetic analysis and suggested that *Pristurus* is most closely related to *Quedenfeldtia* of Morocco and then successively to the American Sphaerodactylini and *Saurodactylus* from the Maghreb (Arnold 2009). A recent multilocus phylogenetic analysis including representatives of 107 of 118 recognized gecko genera (Gamble *et al.* 2012) indicates that *Pristurus* is sister to *Saurodactylus* and that *Quedenfeldtia* is sister to the South American *Aristelliger*, suggesting a high degree of homoplasy in morphology, ecology and behavior in *Pristurus* and *Quedenfeldtia*.

Despite the interest in *Pristurus* from a biogeographical, evolutionary, ecological and behavioral points of view, the genus has been relatively neglected, compared to other gecko groups from the same region like *Hemidactylus* and *Stenodactylus*, for which very robust phylogenetic hypotheses and an updated taxonomic knowledge exist (Carranza & Arnold 2012; Fujita & Papenfuss 2011; Gómez-Díaz *et al.* 2012; Metallinou & Carranza 2013; Metallinou & Crochet, 2013; Metallinou *et al.* 2012; Šmíd *et al.* 2013a,b). A recent phylogeny by Arnold (2009) based on 72 morphological characters of 20 species, supported earlier hypotheses, which suggested that *Pristurus celerrimus* Arnold, 1977 is sister to all other species (Arnold 1986a, 1993). It also recovered a monophyletic assemblage of nine species distinctive in their morphology, ecology and behavior that were considered by Arnold (2009) as members of the subgenus *Spatalura* Gray, 1863. Interestingly, only two (*P. insignis* Blanford, 1881 and *P. insignoides* Arnold, 1986a) of the five endemic species from the Socotra Archipelago included in Arnold's (2009) morphological phylogeny were recovered monophyletic. *Pristurus obsti* Rösler & Wranik, 1999 and *P. samhaensis* Rösler & Wranik, 1999 were not included in Arnold's (2009) phylogenetic analysis. Relationships among other members of the genus were not very well supported and therefore were left unresolved. The only previous molecular phylogeny of *Pristurus* included 11 species that were analyzed independently for one mitochondrial fragment (1457 bp of ND2 and adjoining tRNAs) and one nuclear locus (1381 bp of RAG1) (Papenfuss *et al.* 2009). The results of this molecular phylogeny were largely congruent with the morphological results of Arnold (2009) concurring on the position of *P. celerrimus* and the monophyly of the four members of the subgenus *Spatalura* included in the analyses. Regarding the Socotran species, results differed between the two markers used by Papenfuss *et al.* (2009), but in all analyses *P. abdelkuri* Arnold, 1986a, endemic to Abd al-Kuri Island, branched independently from the other three *Pristurus* species from Socotra Island included in the study (*P. obsti* and *P. samhaensis* were not in the analyses). Despite being a partial phylogeny, the molecular tree by Papenfuss *et al.* (2009) clearly showed that the level of genetic variability within *Pristurus* was very high, some of these diverging lineages including members of *P. rupestris*.

Pristurus rupestris is the most widely distributed species in the genus, being found in northeast Africa (Eritrea, Djibouti, north of Somalia and adjoining Ethiopia), the Arabian Peninsula (southern Jordan, Saudi Arabia, Yemen, Oman, UAE, Qatar, Bahrain and various other islands in the Gulf, including Khark island, one of the original type localities), and in coastal Iran, from Bushehr in the west to Sistan and Baluchistan province in the east (Arnold 1993, 2009; Sindaco & Jeremčenko 2008; Gholamifard *et al.* 2009). Three subspecies of *Pristurus rupestris* are currently recognized: *P. rupestris rupestris* Blanford, 1874 [type locality: "insulae Kharfvel Carrack" (=Khark Island) and Maskat (=Muscat), restricted to Muscat by Schmidt 1952]; *P. rupestris iranicus* Schmidt, 1952 [type locality: "insulae Kharfvel Carrack" (=Khark Island)]; and *P. rupestris guweirensis* Haas, 1943 [described as *P. flavipunctatus guweirensis*, type locality: "Nubian sandstone desert of Guweira (=Quweira), between Ma'an and

Guweira police station”, Jordan]. One species, *Pristurus migiurtinicus* Scortecci, 1933 [type locality “Bender Cassim” (= Bosaso), Somalia], was synonymized with *P. rupestris* by Loveridge (1947).

Pristurus rupestris is one of the smallest species, measuring usually less than 30 mm of snout-vent length. It is found from sea level up to 2330 m in the Jebel Akhdar, northern Oman, and to 3000 m in Yemen (pers. obs.). It is, by far, the most abundant reptile species in Oman and other areas of Arabia, where it occurs from quite mesic habitats to arid lowlands and mountains. This gecko is nearly always found on rocky or stony surfaces, mainly within a meter above the ground, but also on tree trunks and branches, especially in forested areas. Occasionally it occurs on sandy substrates but always in the vicinity of rocks. It can be abundant in villages, towns and even cities, preferring man-made walls, other constructions and planted trees. *Pristurus rupestris* is diurnal, heliothermic, and is a passive forager (“sit and wait”), spending long periods at feeding perches (Arnold 1980, 1993). The most usual refuges are rock crevices and the interstices between stones. The tail is approximately 1.5 times longer than the snout-vent length, flattened vertically, sometimes with a fringe on the upper mid-line and both sexes use it to produce a wide repertoire of signals, including curling it over the back (Arnold 1993; Ross 1990).

Here, we use molecular data to infer the phylogenetic relationships of the genus *Pristurus* and to revise the taxonomy of *Pristurus rupestris*. The results indicate that *P. rupestris* is polyphyletic and includes two highly differentiated clades: the eastern clade, distributed across northern Oman, UAE and Iran; and the western clade, which extends from coastal middle-southern Oman, to Yemen, western Saudi Arabia and up to southern Jordan (Fig. 1). The two clades are also differentiated from a morphological point of view. The name *Pristurus rupestris* is applied to the eastern clade and, until more data of “*P. rupestris*” from Somalia is available, we temporarily refer to the western clade as *Pristurus* sp. 1.

Material and methods

Molecular analyses. Molecular samples, DNA extraction and amplification. A total of 80 individuals of *Pristurus* including 18 of the 23–26 species were included in the phylogenetic analyses. Two members of the family Gekkonidae available from GenBank, *Gekko gekko* (Linnaeus, 1758), *Phelsuma modesta* Mertens, 1970, and one from the family Phyllodactylidae, *Tarentola mauritanica* (Linnaeus, 1758), were used to root the tree based on published evidence (Gamble *et al.* 2011, 2012). As a result of the uncertain phylogenetic position of *Pristurus* in the tree of Gekkota (Gamble *et al.* 2011, 2012), more distant outgroups were preferred over closer ones. A list of all *Pristurus* included in the molecular analyses with their taxonomic identification, sample code, voucher code, country, and corresponding geographical distribution data and GenBank accession numbers for all sequenced genes is presented in Appendix I. To select which samples of “*Pristurus rupestris*” should be included in the molecular phylogeny but especially to analyze the distribution ranges of the two lineages, a preliminary molecular analysis was carried out sequencing one mitochondrial fragment of the gene encoding the ribosomal 12S rRNA for 512 specimens of “*P. rupestris*” (data not shown). This included samples from across its distribution range in Arabian and one locality from Iran, including members of the three recognized subspecies (Fig. 1). The results of the preliminary analysis of the 12S data were used to set the boundaries between the eastern (384 specimens) and western (128 specimens) clades of “*P. rupestris*” (Fig. 1). As a result of the high level of genetic variability detected within the 384 specimens of the eastern clade of “*P. rupestris*” analyzed, seven specimens, four from the type locality of *P. r. rupestris* (Specimens IBES7680, IBES6038, IBES7709 and IBES6039; see Appendix I) and two others that could be confidently assigned to the same lineage than the samples from the type locality of *P. r. rupestris*, were selected together with one sample of *P. rupestris iranicus* for further multilocus phylogenetic analyses (locs. 15–20 in Fig. 1). The high level of genetic variability within the eastern clade of “*P. rupestris*” will be addressed somewhere else (work in progress). The 128 specimens belonging to the western clade of “*P. rupestris*” were genetically uniform and therefore the 15 specimens included in the multilocus analyses were selected covering the whole distribution range of the western clade in Arabia (locs. 1–14 in Fig. 1), including two samples of *P. r. guweirensis* from Jordan (loc. 1).

Genomic DNA was extracted from ethanol-preserved tissue samples using the Qiagen DNeasy Blood & Tissue Kit (Qiagen, Valencia, CA, USA) or the SpeedTools Tissue DNA Extraction kit (Biotools, Madrid, Spain). Five genetic markers were PCR-amplified and sequenced: one mitochondrial fragment of the gene encoding the ribosomal 12S rRNA (12S; primers 12Sa and 12Sb—Kocher *et al.* 1989), and four nuclear fragments of the genes

encoding the acetylcholinergic receptor M4 (*acm4*; primers tg-F and tg-R—Gamble *et al.* 2008), the oocyte maturation factor Mos (*cmos*; primers FUF and FUR—Gamble *et al.* 2008), a short fragment of the recombination-activating gene 1 (*rag1*; primers F700 and R700—Bauer *et al.* 2007), and the recombination-activating gene 2 (*rag2*; primers PyF1 and PyR—Gamble *et al.* 2008). PCR conditions used for the amplification of the 12S mitochondrial fragment as well as the nuclear genes *cmos*, *rag1* and *rag2* can be found in Šmíd *et al.* (2013a), and for the nuclear gene *acm4* in Barata *et al.* (2012).

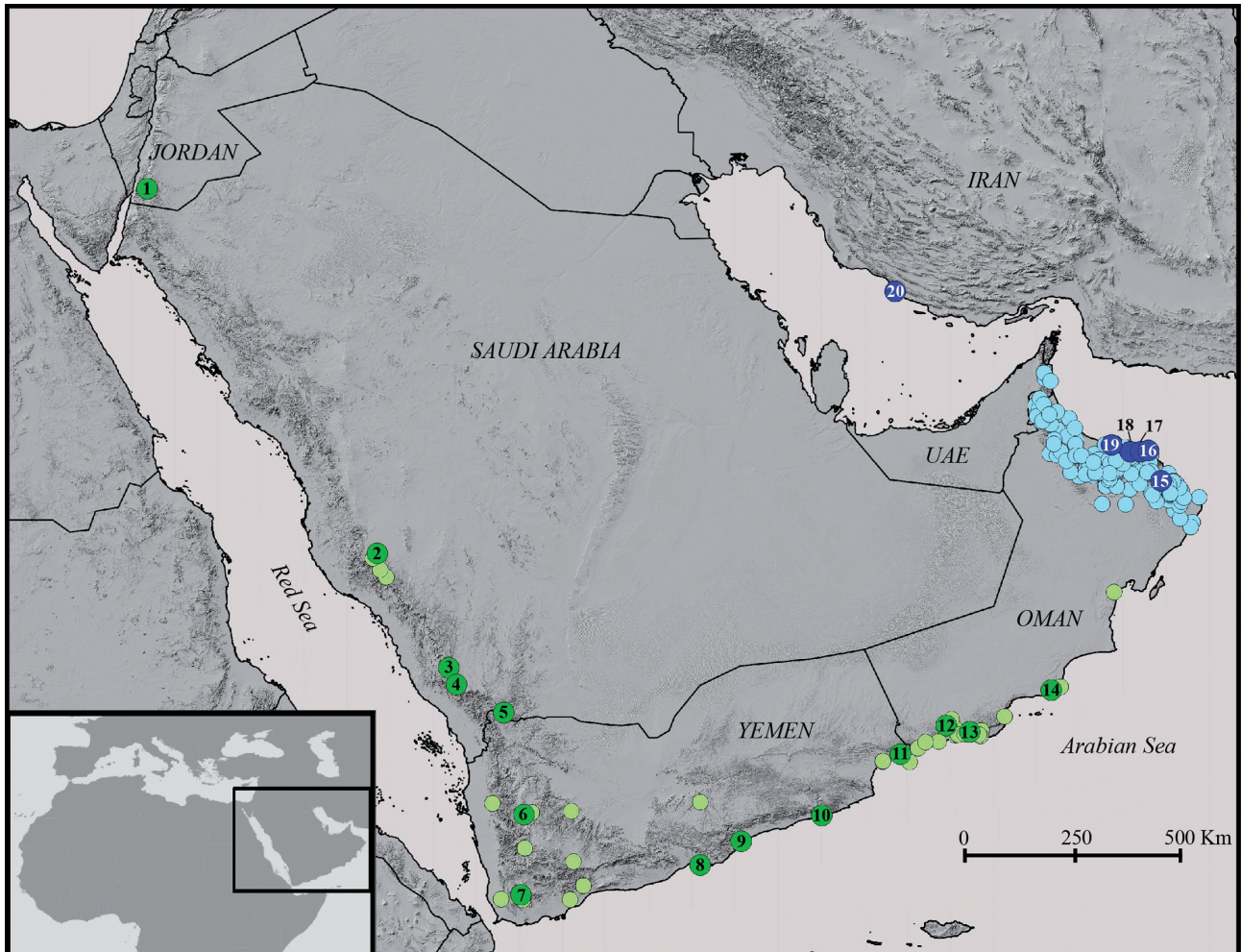


FIGURE 1. Map of localities of *Pristurus rupestris* and *Pristurus* sp. 1. Blue localities are specimens of “*P. rupestris*” referred to as the eastern clade. Dark blue corresponds to localities included in the genetic analyses (Figs. 2-3; Appendix I); light blue to specimens genotyped for the 12S gene to determine the distribution of *P. rupestris*. Green, localities refer to *Pristurus* sp. 1, the western clade of “*P. rupestris*”. Dark green corresponds to localities of specimens included in the genetic analyses (Figs. 2-3; Appendix I), and light green corresponds to specimens genotyped for the 12S gene only to indicate the distribution of *Pristurus* sp. 1.

Sequence analysis. Geneious v. R6 (Biomatters Ltd.) was used for assembling and editing the chromatographs. Heterozygous positions for the nuclear coding gene fragment were identified based on the presence of two peaks of approximately equal height at a single nucleotide site in both strands. The nuclear coding fragments were translated into amino acids and no stop codons were observed. DNA sequences were aligned using MAFFT v.6 (Kato & Toh 2008) applying parameters by default (Auto strategy, Gap opening penalty: 1.53, Offset value: 0.0). Phased sequences of the *acm4*, *cmos*, *rag1* and *rag2* genes were used for the network analyses and to infer independent phylogenies for each nuclear gene. SEQPHASE (Flot 2010) 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). Uncorrected mean genetic distances between and within groups for the mitochondrial gene fragment were calculated using MEGA 5 (Tamura *et al.* 2011), using the *p*-distance model.

Phylogenetic and network analyses. Best-fitting models were inferred for each gene independently using jModeltest v.0.1.1 (Posada 2008) under the Akaike information criterion (AIC) (Akaike 1973). Phylogenetic analyses were performed using Maximum Likelihood (ML) and Bayesian (BI) methods. Maximum Likelihood analyses were performed in RAxML v.7.0.3 (Stamatakis 2006). The dataset was partitioned by gene and a GTR+G model was used with parameters estimated independently for each partition. Independent ML trees were also produced for each nuclear gene (datasets phased). Reliability of the ML tree was assessed by bootstrap analysis (Felsenstein 1985) including 1000 replications. Bayesian analyses were performed with BEAST v.1.6.1 (Drummond & Rambaut 2007) using the same dataset used in the ML analysis but without the outgroups. Analyses were run three times for 5×10^7 generations with a sampling frequency of 10 000. Models and prior specifications applied were as follows (otherwise by default): model of sequence evolution for each independent partition as indicated in Table 1; coalescent constant size process of speciation; random starting tree; alpha Uniform (0, 10); fix mean rate of molecular clock model to 1. The xml file was manually modified to “Ambiguities=TRUE” for the *acm4*, *cmos*, *rag1* and *rag2* partitions to account for variability in the heterozygote positions, instead of treating them as missing data. Convergence was assessed by examining the posterior trace plots and by confirming sufficient effective sample sizes for all parameters in Tracer v1.5 (Rambaut & Drummond, 2007). The results of the individual runs were combined in LogCombiner discarding 10% of the samples and the ultrametric tree was produced with TreeAnnotator (both provided with the BEAST package). Nodes in the phylogenies were considered strongly supported if they received ML bootstrap values $\geq 70\%$ and posterior probability (pp) support values ≥ 0.95 (Huelsenbeck & Rannala 2004; Wilcox *et al.* 2002). The branch attachment frequency (BAF) algorithm implemented in the package Phyutility 2.2.4 (Smith & Dunn 2007) was used to explore how often in the 13 500 trees from the posterior of BEAST analysis (after “burnin”; see above) the eastern and western clades of the polyphyletic “*P. rupestris*” were joined in a single clade.

TABLE 1. Information on the length of all partitions used in the phylogenetic analyses, model of sequence evolution selected by jModelTest (model), and number of variable and parsimony-informative sites.

Gene	length (bp)	N	model	variable sites		parsimony-informative sites	
				with outgroup	without outgroup	with outgroup	without outgroup
12S	405	81	GTR+I+G	246	219	199	181
acm4	429	59	HKY+I+G	95	59	57	44
cmos	372	63	HKY+I+G	107	87	80	69
rag1	279	78	HKY+G	103	84	73	65
rag2	360	76	HKY	121	94	93	80

Genealogical relationships in the four nuclear genes between the eastern and western clades of “*P. rupestris*” were assessed with haplotype networks constructed using statistical parsimony as implemented in the program TCS v.1.21 (Clement *et al.* 2000). Phased sequences were used (see above) and a connection limit of 95% was applied.

Morphological analyses. Morphological samples, variables and museums acronyms. Eighty five alcohol-preserved adult specimens of “*Pristurus rupestris*” were included in the morphological analyses. Of these, 32 specimens belonged to the eastern clade and 53 specimens to the western clade of “*P. rupestris*”. Based on the 12S preliminary study (see above) all the specimens from the eastern clade of “*P. rupestris*” were selected from the genetic lineage that included the specimens from the type locality of *P. r. rupestris*. A list of all studied specimens with their GPS localities is presented in Appendix II. Specimens were obtained from the following institutions: Museo Civico di Storia Naturale di Carmagnola, Turin, Italy (MCCI); S. Carranza’s field series housed at the Institute of Evolutionary Biology (IBE), Barcelona, Spain; and Lukáš Kratochvíl’s field series from Yemen (JEM), housed at the Department of Ecology, Charles University in Prague, Czech Republic. Variables for the morphological analyses were selected based on previous taxonomic studies of *Pristurus* (Arnold 1977, 1982, 1986a, 1993, 2009), and on our own personal observations. One body size and 11 shape measurements were taken by the same person (A.B.) on the left side of each specimen. As a result of the diminutive size of the specimens, measurements were obtained from highly precise picture measurements using the software ImageJ (Abramoff *et al.* 2012). The snout-vent length (SVL), was measured from beneath as the distance from tip of snout to vent; shape

variables: head length (HL), measured laterally from tip of snout to base of the anterior ear border; head depth (HD), measured laterally from above the eyes to the commissure of mouth; maximum head width (HW), measured from beneath at its widest part, usually at the level of temporal region; transverse orbital diameter (OD); brachium length (BL), from elbow to the insertion of the forelimb on the anterior part of body; antebrachium length (AL), from wrist to elbow; thigh length (ThL), measured from knee to the insertion of the hind limb on the posterior side of body; crus length (CL), measured from ankle to knee; axilla-groin length (AGL), distance measured from beneath, between the fore and hind limb insertion points; scapular width (SW), distance measured from beneath, between the insertion of the left and right fore limbs; pelvic width (PW), distance measured from beneath, between the insertion of the left and right hind limbs.

Multivariate analyses. Statistical analyses were used to investigate differences in size and shape between the eastern and western clades of “*Pristurus rupestris*” identified by the molecular phylogenetic analyses. All measurements were \log_{10} -transformed to increase the homogeneity of variances. To remove the effect of body size on the shape variables, we computed the residuals of each morphometric variable regressed against SVL using ordinary least-squared regression. For shape variables we performed a principal components analysis (PCA) on the correlation matrix of the residuals to visualize the shape variation of both species in a reduced dimensional space. We tested for shape differences between both clades by means of a permutational MANOVA (PERMANOVA) on the PCA scores, using a Euclidean distance matrix with 10 000 permutations to assess significance. To assess the contribution of each shape variable at separating the two lineages, we performed a one-way ANOVA on each of the six principal components retained in the PCA analysis. Regarding body size, we tested for differences in SVL between groups using a one-way ANOVA. All analyses were performed in the R environment using the packages Stats (R development Core Team 2013) and vegan (Oksanen 2013).

Results

Molecular analyses

The dataset used for the multilocus phylogenetic analyses consisted of an alignment of 1845 base pairs (bp) of concatenated mitochondrial and unphased nuclear DNA for 80 *Pristurus*, including representatives of 18 of the 23–26 species, as well as the three subspecies of “*P. rupestris*”. The eight species that could not be included in our study were: *P. gasperetti* Arnold, 1986a (not recognized by Arnold 2009; considered a synonym of *P. flavipunctatus* Rüppell, 1835); *P. longipes* Peters, 1871 (not recognized by Arnold 2009; considered a synonym of *P. crucifer* (Valenciennes, 1861), but see Schatti & Gasperetti 1994; Loveridge 1947); *P. mazbah* Al-Safadi, 1989 (not recognized by Arnold 2009; considered a synonym of *P. saada* Arnold, 1986a); *Pristurus ornithocephalus* Arnold, 1986a; *P. phillipsii* Boulenger, 1895; *P. saada*; *P. simonettai* (Lanza & Sassi, 1968); and *P. schneideri* Rösler, Köhler & Böhme, 2008. All information related to each partition including alignment length, model selected, and the number of variable and parsimony-informative sites of the molecular dataset is presented in Table 1.

The results of the ML and BI analyses are presented in Fig. 2. The two trees were almost identical and show that “*Pristurus rupestris*” is polyphyletic and includes two highly divergent and very well supported clades: the eastern clade, which includes all seven specimens from localities 15–20 (Figs. 1 and 2; Appendix I); and the western clade, which includes all 15 specimens from localities 1–14 (Figs. 1 and 2; Appendix I). The uncorrected genetic distance (*p*-distance) for the *I2S* between the eastern and western clades is 13.3 ± 1.6 %. The level of genetic variability for the *I2S* within the western clade is 2.21 ± 0.4 % and within the eastern clade is 0.39 ± 0.14 %, although within this latter clade only specimens from the type locality of *P. r. rupestris* or from the same genetic lineage as specimens from the type locality were included. The results of the haplotype network analyses of all the specimen of “*P. rupestris*” selected are presented in Fig. 3 and clearly show that, despite the relatively large number of specimens analyzed, the eastern and western clades do not share a single haplotype in any of the four nuclear genes. Moreover, in the *cmos*, *rag1* and *rag2*, the two clades form unconnected parsimony networks under the stringent 95% threshold applied. The results of the ML analyses of the phased datasets of the four nuclear genes are presented in Appendix III and clearly show that the eastern and western clades of “*P. rupestris*” do not share nuclear gene haplotypes with any other *Pristurus* species included in the present analysis. In fact, with the only exception of *P. samhaensis* and *P. sokotranus*, which share one haplotype in the *cmos* and one in the *rag1* genes, all the other species of *Pristurus* included in the analyses present private haplotypes for all four nuclear genes (see

Appendix III). The results of the BAF analysis conducted over the 13500 trees of the BEAST posterior indicated that the eastern and western clades appear as sister clades at a very low frequency (2.11%).

Besides the polyphyly of “*P. rupestris*”, the phylogenetic tree from Fig. 2 also supports that *P. celerrimus* is sister to all other *Pristurus* included in the analyses. The six species from Socotra and the satellite island of Samha form a monophyletic group, although the bootstrap and pp support for this assemblage is very low. Within this island clade, the large (*P. insignis* and *P. insignoides*) and the small (*P. obsti*, *P. guichardi* Arnold 1986a, *P. samhaensis* and *P. sokotranus* Parker, 1938) species form two very well supported reciprocally monophyletic groups. *Pristurus obsti* and *P. guichardi* are closely related sister taxa with a genetic distance in the *12S* of 6.1 ± 1.1 %. According to our results, *Pristurus sokotranus* is paraphyletic, with one of the three sampled specimens from Socotra Island being more closely related to *P. samhaensis* from Samha Island than to the other two specimens of *P. sokotranus* included in the phylogenetic analyses. The clade formed by the species from Socotra and Samha Islands, is sister to a large and very well supported clade that includes 12 taxa comprising the western clade of “*P. rupestris*”, five species in the subgenus *Spatalura*, the eastern clade of “*P. rupestris*”, and five species distributed in Mauritania (*P. adrarensis*), Abd al Kuri Island (*P. abdelkuri*), Oman (*P. gallagheri* Arnold, 1986a), Saudia Arabia (*P. popovi* Arnold, 1982), and Yemen and eastern Africa (*P. flavipunctatus*). *Pristurus popovi* and *P. flavipunctatus* form a well supported clade, but other relationships within this group are weakly supported, like the phylogenetic position of the eastern and western clades of “*P. rupestris*”, or the sister taxa relationship between the endemic species from Abd al-Kuri (*P. abdelkuri*; Socotra Archipelago) and *P. gallagheri*.

Multivariate analyses of the morphological data

For the comparison of body shape between the eastern and western clades of “*P. rupestris*”, we retained the six first PCA components explaining 83.11% of variance (Table 2). The results of the PERMANOVA revealed significant shape differences between the two clades ($F_{1,83} = 11.268$, $P < 0.0001$). When each component was analyzed independently by means of ANOVAs, only the first and the second components produced significant differences between groups ($F_{1,83} = 15.41$, $P < 0.0001$ and $F_{1,83} = 27.26$, $P < 0.0001$, respectively) (Table 3; Fig. 4). These two components mostly correspond to limb and head dimensions (Table 2; Fig. 4) and accounted for approximately 50% of the total variance. Specimens from the western clade appear to have relatively wider and higher heads and shorter limbs. Regarding body size, the ANOVA revealed that there are significant size differences between the two clades ($F_{1,83} = 8.76$, $P < 0.0001$) (Fig. 4). Descriptive statistics for the 12 size and shape variables included in the morphological analysis are presented in Table 4.

TABLE 2. Loadings, eigenvalues, and variance explained by each of the first six components retained from the PCA performed on shape residuals.

Trait	PC1	PC2	PC3	PC4	PC5	PC6
HL	-0.26	-0.37	0.30	0.29	0.04	0.30
HD	-0.01	-0.49	0.15	-0.18	-0.52	0.44
HW	0.28	-0.45	-0.06	-0.26	-0.09	-0.18
OD	-0.06	-0.32	0.53	0.38	0.13	-0.58
BL	-0.34	-0.16	-0.36	-0.23	-0.24	-0.43
AL	-0.42	-0.06	-0.19	0.05	0.39	0.20
ThL	-0.43	-0.09	-0.09	-0.19	-0.12	-0.25
CL	-0.41	-0.21	-0.07	-0.21	0.35	0.12
AGL	-0.05	-0.12	-0.52	0.73	-0.23	0.07
SW	0.31	-0.34	-0.17	-0.06	0.55	0.11
PW	0.31	-0.32	-0.36	0.03	0.10	-0.18
Eigenvalue	3.34	2.16	1.37	0.93	0.79	0.56
Variance explained (in %)	30.32	19.63	12.43	8.47	7.15	5.10

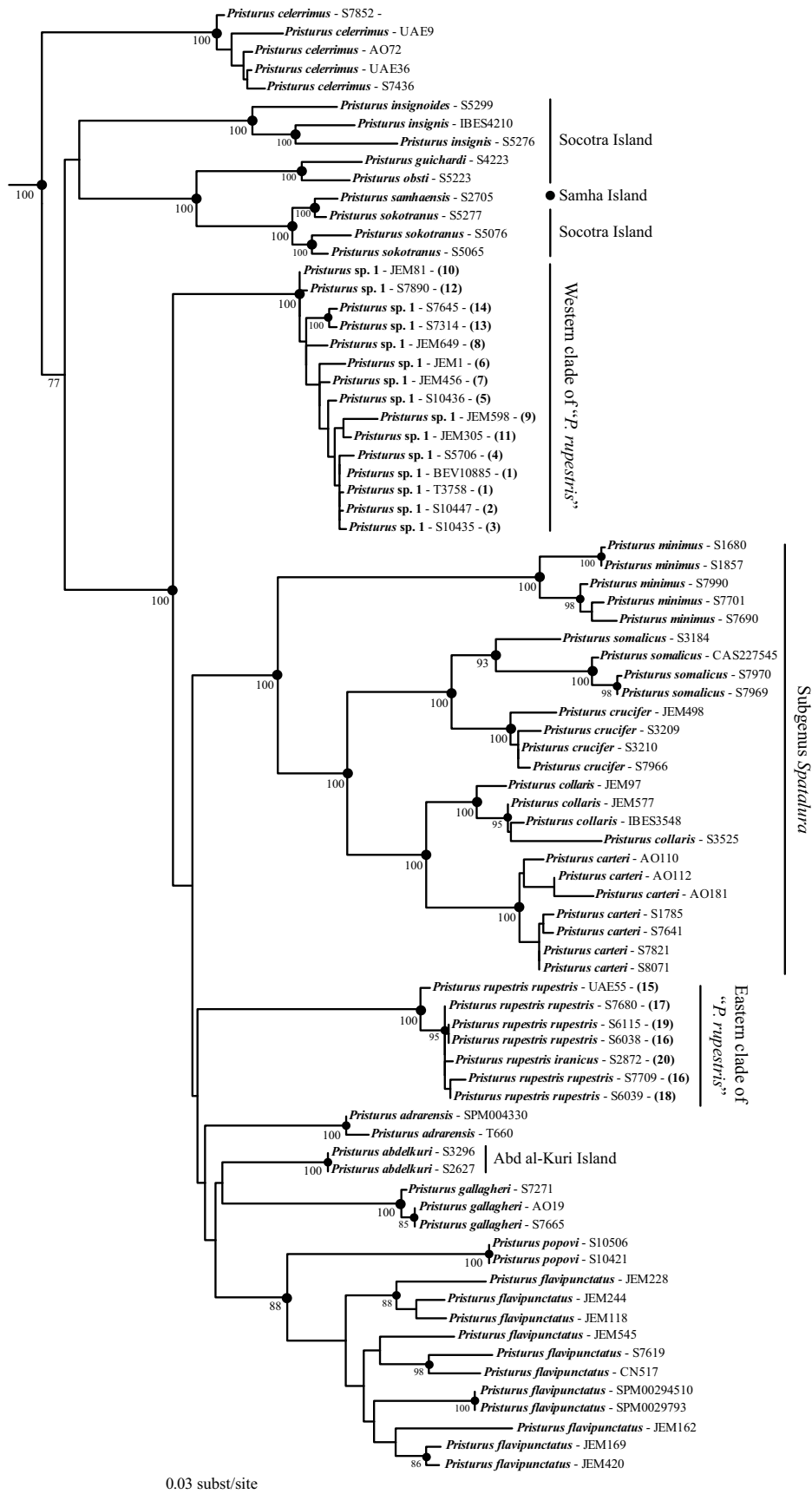


FIGURE 2. ML tree of *Pristurus* inferred using *12S* mtDNA, and *acm4*, *cmos*, *rag1*, *rag2* nuclear gene fragments. Bootstrap values $\geq 70\%$ are shown next to the nodes. Black circles on nodes indicate posterior probability values ≥ 0.95 . The tree was rooted using *Gekko gecko*, *Phelsuma modesta*, and *Tarentola mauritanica*. Information on the samples is given in Appendix I.

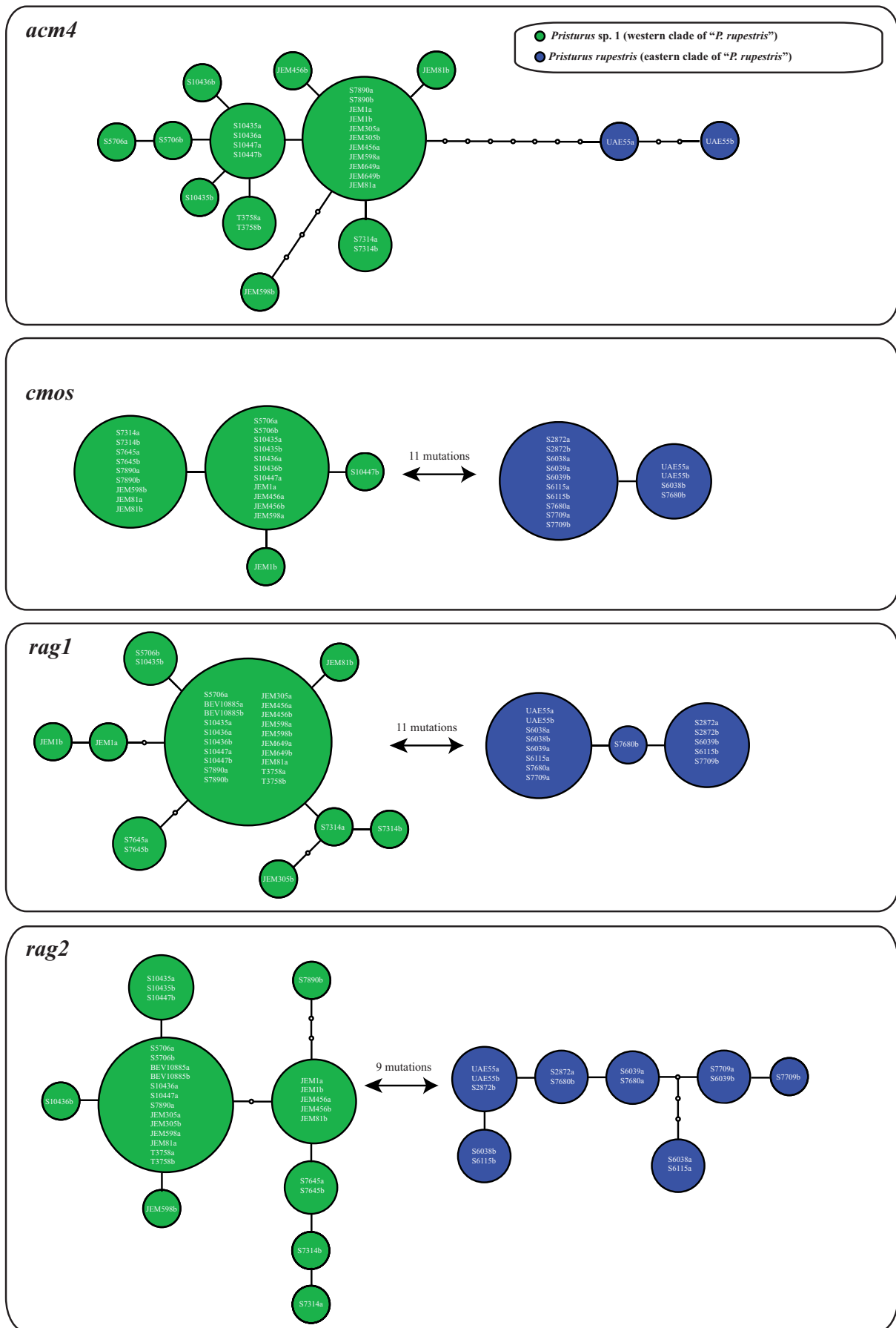


FIGURE 3. Haplotype networks of the phased sequences of nuclear markers *acm4*, *cmos*, *rag1* and *rag2*. Phase probabilities were set as ≥ 0.7 . Information on the samples is shown in Appendix I.

TABLE 3. Results of the ANOVAs performed on each of the six components retained from the PCA analysis. F values along with their associated *P*-values are given.

	PC1	PC2	PC3	PC4	PC5	PC6
F1,84	15.41	27.26	0.109	2.933	0.01	0.429
<i>P</i> -value	0.000178 ***	1.29e-06 ***	0.742	0.0905	0.922	0.515

TABLE 4. Descriptive statistics for the 12 continuous variables for *P. rupestris* and *P. sp. 1*. Mean ± Standard Error of the Mean (SE) and range are given.

Variable	<i>Pristurus sp. 1</i> (n=53)	<i>P. rupestris</i> (n=32)
	Mean±SE (Min–Max)	Mean±SE (Min–Max)
SVL	24.40 ± 0.33 (19.29–28.82)	25.87 ± 0.34 (22.05–30.06)
Head length (HL)	6.04 ± 0.07 (5.12–7.25)	6.28 ± 0.06 (5.34–6.84)
Head depth (HD)	2.57 ± 0.03 (2.07–3.17)	2.48 ± 0.04 (2.08–2.96)
Head width (HW)	5.28 ± 0.06 (4.23–6.50)	5.00 ± 0.07 (4.27–5.73)
Orbital diameter (OD)	1.54 ± 0.02 (1.30–1.84)	1.53 ± 0.02 (1.26–1.78)
Brachium length (BL)	2.71 ± 0.07 (1.86–3.93)	2.95 ± 0.06 (2.34–3.58)
Antebrachium length (AL)	3.50 ± 0.07 (1.81–4.57)	3.90 ± 0.07 (3.14–4.80)
Thigh length (ThL)	4.30 ± 0.10 (2.79–5.30)	4.88 ± 0.10 (3.89–6.21)
Crus length (CL)	4.96 ± 0.09 (3.68–6.06)	5.24 ± 0.08 (4.20–5.99)
Axilla-groin length (AGL)	9.69 ± 0.18 (7.38–12.32)	10.52 ± 0.22 (8.68–13.67)
Scapular width (SW)	4.89 ± 0.09 (3.46–6.55)	4.73 ± 0.10 (3.71–5.90)
Pelvic width (PW)	4.16 ± 0.08 (3.03–5.39)	4.00 ± 0.08 (3.32–5.19)

Taxonomic account

Based on the *I2S* genetic distances and the results of the phylogenetic and haplotype network analyses (Figs. 2 and 3; Appendix III), it is certain that the taxon “*Pristurus rupestris*” contains two genetically well differentiated species: namely the eastern clade of “*P. rupestris*”, inhabiting coastal Iran and the al Hajar Mountain range in northern Oman and eastern UAE; and the western clade of “*P. rupestris*”, distributed from coastal middle Oman, through Yemen, Saudi Arabia and up to southern Jordan (Fig. 1). Specimens IBES7680, IBES6038, IBES7709 and IBES6039, are all from the type locality of *P. r. rupestris* (Muscat) and genetic sample S2872 is a *P. r. iranicus* from Iran. Therefore, the molecular results confirm that the name *Pristurus rupestris* applies to the eastern clade (Fig. 1). As for the western clade, two possible names are available *Pristurus guweirensis* Haas, 1943 (= *P. r. guweirensis* elevated to species) and *Pristurus migiurtinicus* Scortecci, 1933 (synonymized with *P. rupestris* by Loveridge 1947). Specimen BEV10885 and sample T3758 originate from the type locality of *P. r. guweirensis*, in the sandstone desert of Guweira (=Quweira), 10 km south of the city of Quweira, Jordan. Unfortunately, no samples for genetic or morphological analysis of “*P. rupestris*” are available from or near the type locality of *Pristurus migiurtinicus* (“Bender Cassim” (=Bosaso), Somalia). Moreover, the holotype of *Pristurus migiurtinicus* Scortecci, 1933 housed at the Museo Civico di Storia Naturale di Milano under reference MSNM Re97 (formerly 1323), was sent on loan to the Natural History Museum, London back in 1980 and the type is apparently lost. As a result of the impossibility of studying morphologically and genetically any specimens of *Pristurus migiurtinicus*, it is not possible at present to know which of the two names, *P. guweirensis* (= *P. r. guweirensis* elevated to species) or *P. migiurtinicus*, applies to the western clade of “*P. rupestris*”. Therefore, until material of “*P. rupestris*” from Somalia is obtained and analyzed we prefer to refer to the western clade as *Pristurus sp. 1*.

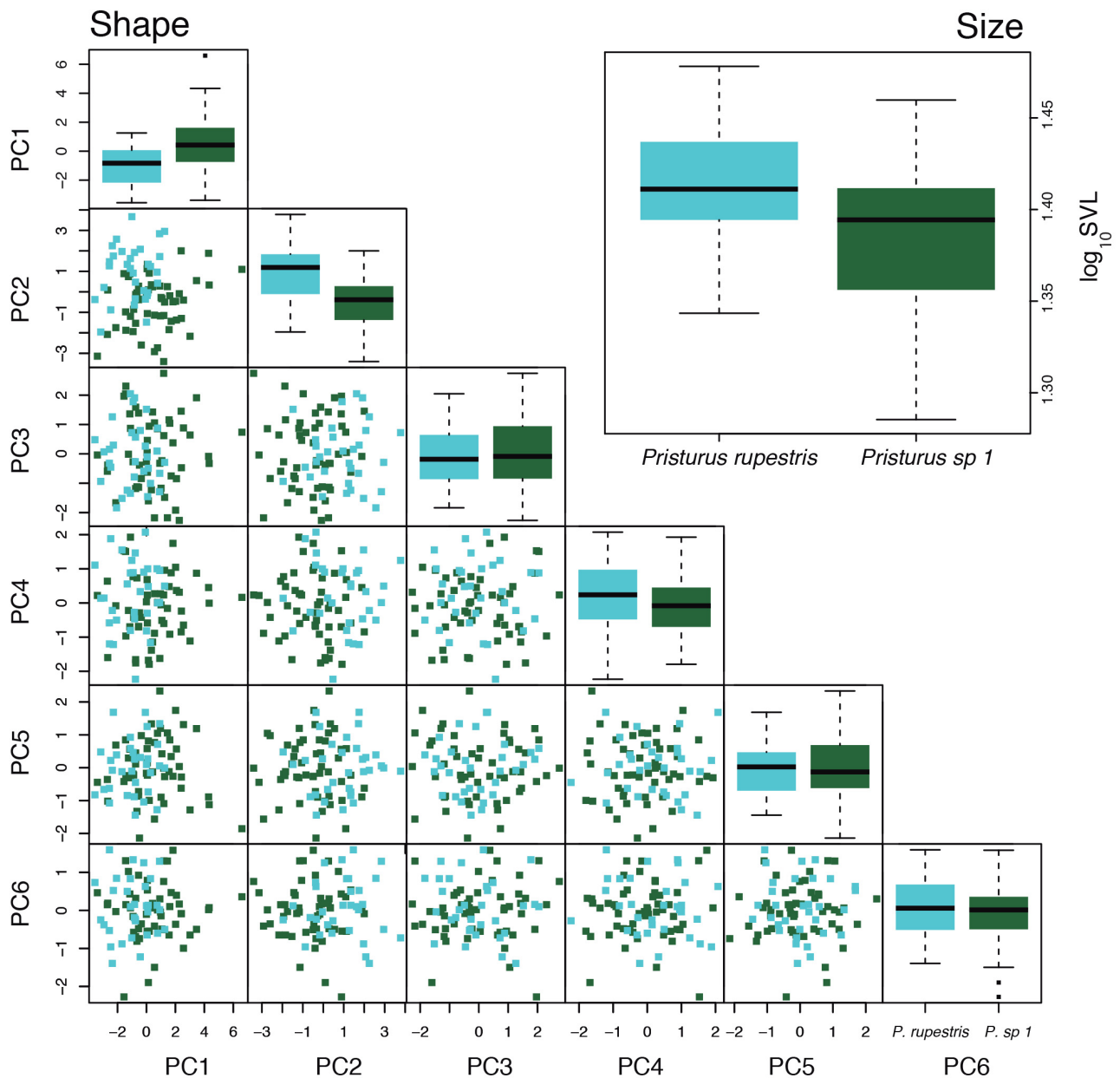


FIGURE 4. Charts presenting the size and shape variation existing between *Pristurus rupestris* (eastern clade of “*P. rupestris*”) in blue and *Pristurus sp. 1* (western clade of “*P. rupestris*”) in green. The upper-right chart shows size variation by means of a boxplot on the log-transformed SVL values. The lower-left chart shows the shape variation reflected in the six components retained from the PCA analysis (accounting for 83.11% of the total variance). All bivariate combinations are presented along with a boxplot comparing the variation of both species on each component.

Discussion

The phylogenetic analyses presented in Fig. 2 clearly show that what was previously regarded as *Pristurus rupestris* includes two different species: *P. rupestris* and *Pristurus sp. 1*. Within *P. rupestris* there are two subspecies described, *P. r. rupestris* (type locality Muscat, Oman) and *P. r. iranicus* (type locality Khark Island, Iran). Our results show that these two subspecies are not differentiated genetically, and that *P. r. iranicus* makes *P. r. rupestris* paraphyletic. This suggests that the distribution of *P. rupestris* in Iran is probably the result of a recent colonization from Arabia. However, until material from the type locality of *P. r. iranicus* is analyzed, we prefer not to speculate about the origin and taxonomic validity of the Iranian subspecies. As shown in Fig. 1, we could not include specimens from Qatar, Bahrain and other islands in the Gulf, as well as from coastal eastern Saudi Arabia.



FIGURE 5. Pictures of live *Pristurus* sp. 1. A–B, specimen from 25 km south of Quweira, Jordan (photo by R. Sindaco); C, typical specimen from moist habitats in Dhofar performing characteristic tail signaling (Wadi Dharbat, Dhofar, Oman) (photo by S. Carranza).

However, based on the geographic distribution of *P. rupestris* and *Pristurus* sp. 1, we can speculate that the populations distributed across the eastern coast of the Arabian Peninsula belong to *P. r. rupestris* (work in progress).

Pristurus sp. 1 (Fig. 5) is one of the most widely distributed species in the genus, occurring from southern Jordan to central Oman (Fig. 1). Although we could not incorporate samples from Africa in our analyses, probably the populations from Eritrea, Djibouti, northern Somalia and adjoining Ethiopia, previously assigned to “*P. rupestris*”, belong to *Pristurus* sp. 1, or to an undescribed taxon. Despite its large distribution range, the level of uncorrected genetic variability in the mitochondrial *12S* within *Pristurus* sp. 1 is very low ($2.21 \pm 0.4\%$), especially if compared with the level of intraspecific variability in other *Pristurus* species, like for instance *P. minimus* Arnold 1977 ($4.61 \pm 0.7\%$), *P. flavipunctatus* ($7.63 \pm 0.8\%$), *P. somalicus* Parker, 1932 ($5.78 \pm 1.0\%$) and *P. collaris* (Steindachner, 1867) ($3.64 \pm 0.6\%$). In fact, *Pristurus* sp. 1 has a similar level of intraspecific genetic variability to *P. carteri* (Gray, 1863) ($2.61 \pm 0.5\%$), *P. celerrimus* ($2.58 \pm 0.5\%$), and *P. crucifer* ($1.78 \pm 0.4\%$), all of which have much more restricted distribution ranges. The relatively low level of genetic variability within *Pristurus* sp. 1 contrasts with its rather high level of morphological variability. Over its range this diminutive gecko occupies many different habitats, from very arid open areas to moist subtropical forest, and from sea level up to 3000 m (pers. obs.). As a result of that, it exhibits marked variation, especially in coloring, size and behavior, and even neighboring populations may show some differences (Arnold 1980, 1993; pers. observ.). According to Arnold (1980) and our personal observations, in Dhofar, animals from moist habitats such as Wadi Sayq and Wadi Dharbat are relatively large, dark, with the underside of the tail opaque white and with very heavy markings on the throat. In contrast, drier habitats tend to be occupied by smaller, paler animals on which dark markings are reduced, although even here animals from dark backgrounds tend to be darker (Fig. 5). As with *P. carteri*, physiological color change is not the main cause of this variation.

A high level of morphological variability also occurs in *P. rupestris* and this seems linked to the diversity of habitats and altitudes occupied by this species, from very arid open areas to forested areas, and from sea level up to 2330 m. In fact, some of the morphs identified in *Pristurus* sp. 1 can be also identified in *P. rupestris*, which suggests a high level of phenotypic convergence between these two species (Arnold 1993; pers. obs.). Although no data are available, it is probable that both *P. rupestris* and *Pristurus* sp. 1, like other small lizards that are active by day in open places, are subject to heavy predation by visually oriented hunters, especially birds. Therefore, there must be a strong selective pressure for crypsis and camouflage, which explains the appearance of similar (convergent) morphs related to habitat in both species. This reason, together with the overall morphological similarity between *P. rupestris* and *Pristurus* sp. 1, may explain why, despite being the most abundant reptile species in Arabia, and having been collected intensively and included in some systematic revisions (Arnold 1977, 1980, 1982, 1986a,b; Leviton *et al.* 1992), their taxonomy has never been clarified. It is in cases like this, with high levels of morphological variability and convergence in very similar species, that molecular methods are more helpful (Gvoždík *et al.* 2008). Although our preliminary morphological analyses including several variables on a restricted sampling seem to suggest that the two species may be differentiated, more analyses including more variables (especially pholidotic) and many more samples will be needed in order to see the extent of morphological variability within and between both species and to try to find some clear diagnostic characters.

The phylogenetic tree presented in Fig. 2 coincides partially with Arnold's (2009) morphological tree and the molecular phylogeny by Papenfuss *et al.* (2009). All three phylogenies suggest that *P. celerrimus* is sister to the remaining *Pristurus* species. Our dataset is the first to include all seven endemic species of *Pristurus* from the Socotra Archipelago and indicates that this small radiation has a minimum of two independent origins, one for all six species from Socotra, and the satellite islands of Samha and Darsa, and another independent origin for *P. abdelkuri* from Abd al-Kuri Island. However, until a calibrated phylogeny for the genus *Pristurus* is produced (work in progress) it will not be possible to know if the deep split that separates the large (*P. insignis* and *P. insignoides*) and small (*P. sokotranus*, *P. obsti*, *P. guichardi*, and *P. samhaensis*) species endemic to the Socotra Archipelago occurred before or after the separation of Socotra from mainland Arabia. An independent origin for Abd al-Kuri reptile species has already been proposed for an endemic skink of the genus *Trachylepis* (Sindaco *et al.* 2012) and for the ancestor of the two endemic *Hemidactylus* geckos (Gómez-Díaz *et al.* 2012, Carranza & Arnold 2012, Šmíd *et al.* 2013a). These molecular studies indicate that despite being just 60 km to the west of Samha Island, at least four of the five endemic lizard species from Abd al-Kuri have had independent origins from

species of the same genus now present in Samha, Darsa and Socotra Islands (which were merged into a single island during the sea level fluctuations that occurred during the Pleistocene). This is very unusual and contrasts with what has been found in other archipelagoes. For instance, in the Canary and Cape Verde Islands, species usually colonized one of the islands of the archipelago and, from there, spread to neighboring islands (Arnold *et al.* 2008; Carranza & Arnold 2006; Carranza *et al.* 1999, 2000, 2001; Maca-Meyer *et al.* 2003; Miralles *et al.* 2011; Vasconcelos *et al.* 2010). According to Arnold (2009), *P. obsti* and *P. samhaensis* are very similar in their morphology to *P. guichardi* and *P. sokotranus*, respectively. Our molecular data indicates that the two arboreal Socotran endemics, *P. obsti* and *P. guichardi*, are genetically well differentiated. Razzetti *et al.* (2011), state that these two species segregate altitudinally within Socotra Island, with *P. obsti* being distributed at lower altitudes than *P. guichardi*. The taxonomy of *P. sokotranus* is more complicated. According to our molecular results, including three specimens from three different localities within Socotra Island, *P. samhaensis* is more closely related to one of the specimens, making *P. sokotranus* paraphyletic. Analyses with more samples from across the distribution range of *P. sokotranus* and *P. samhaensis*, including their type localities will be necessary to clarify the taxonomy of these two species (work in progress).

Relationships between members of the subgenus *Spatalura* are very similar to those recovered by Papenfuss *et al.* (2009). In both phylogenies, *P. minimus* is sister to all the other members of *Spatalura* and *P. somalicus* and *P. crucifer* are sister taxa. Moreover, like the morphological phylogeny by Arnold (2009), our results support the close relationship between *P. carteri* and *P. collaris*. The nested position of *P. adraensis* within the clade formed by the 12 species (Fig. 2), suggests that this 4700 km range extension occurred from east to west, after the first colonization of the Socotra Archipelago. However, until more samples are included in a calibrated phylogeny of the genus, we prefer not to hypothesize about the possible causes of the presence of this isolated species in Mauritania, or the biogeography and evolution of this interesting genus of diurnal geckos.

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References

- Abràmoff, M.D., Magalhaes, P.J. & Ram, S.J. (2004) Image Processing with ImageJ. *Biophotonics International*, 11, 36–42.
- Akaike, H. (1973) Information theory and an extension of the maximum likelihood principle. In: Petrov, B.N. & Csaki, F. (Eds.), *Information theory and an extension of the maximum likelihood principle*. Akademiai Kiado, Budapest, pp. 267–281.
- Al-Safadi, M.M. (1989) A new species of semaphore gecko (*Pristurus*: Gekkonidae) from Yemen Arab Republic. *Proceedings of the Egyptian Academy of Sciences*, 39, 9–15.
- Arnold, E.N. (1977) The scientific results of the Oman flora and fauna survey 1975. Little-known geckos (Reptilia: Gekkonidae) from Arabia with descriptions of two new species from the Sultanate of Oman. *Journal of Oman Studies Special Report*, 1, 81–110.

- Arnold, E.N. (1980) The scientific results of the Oman flora and fauna survey 1977 (Dhofar). The reptiles and amphibians of Dhofar, southern Arabia. *Journal of Oman Studies Special Report*, 2, 273–332.
- Arnold, E.N. (1982) A new semaphore gecko (*Pristurus*: Gekkonidae) and a new dwarf snake (*Eirenis*: Colubridae) from Southwestern Arabia. *Fauna of Saudi Arabia*, 4, 468–477.
- Arnold, E.N. (1986a) New species of semaphore gecko (*Pristurus*: Gekkonidae) from Arabia and Socotra. *Fauna of Saudi Arabia*, 8, 352–377
- Arnold, E.N. (1986b) A key and annotated checklist to the lizards and amphisbaenians of Arabia. *Fauna of Saudi Arabia*, 8, 385–435.
- Arnold, E.N. (1993) Historical changes in the ecology and behavior of semaphore geckos (*Pristurus*, Gekkonidae) and their relatives. *Journal of Zoology*, 229, 353–384.
<http://dx.doi.org/10.1111/j.1469-7998.1993.tb02642.x>
- Arnold, E.N. (2009) Relationships, evolution and biogeography of Semaphore geckos, *Pristurus* (Squamata, Sphaerodactylidae) based on morphology. *Zootaxa*, 2060, 1–21.
- Arnold, E.N., Vasconcelos, R., Harris, D.J., Mateo, J.A. & Carranza, S. (2008) Systematics, biogeography and evolution of the endemic *Hemidactylus* geckos (Reptilia, Squamata, Gekkonidae) of the Cape Verde Islands: based on morphology and mitochondrial and nuclear DNA sequences. *Zoologica Scripta*, 37, 619–636.
<http://dx.doi.org/10.1111/j.1463-6409.2008.00351.x>
- Barata, M., Carranza, S. & Harris, D.J. (2012) Extreme genetic diversity in the lizard *Atlantolacerta andreanskyi* (Werner, 1929): a montane cryptic species complex. *BMC Evolutionary Biology*, 12, 167.
<http://dx.doi.org/10.1186/1471-2148-12-167>
- Bauer, A.M., DeSilva, A., Greenbaum, E. & Jackman, T.R. (2007) A new species of day gecko from high elevation in Sri Lanka, with a preliminary phylogeny of Sri Lankan *Cnemaspis* (Reptilia: Squamata: Gekkonidae). *Mitteilungen aus dem Museum für Naturkunde in Berlin. Zoologische Reihe*, 83 (Supplement), 22–32.
- Blanford, W.T. (1874) Description of new lizards from Persia and Baluchistan. *Annals and Magazine of Natural History*, 13, 453–455.
- Blanford, W.T. (1881) Notes on the lizards collected in Socotra by Professor I. Bayley Balfour. *Proceedings of the Zoological Society of London*, 1881, 464–469.
- Boulenger, G.A. (1895) On the reptiles and batrachians obtained by Mr. E. Lort-Philips in Somaliland. *Annals and Magazine of Natural History*, 16, 165–169.
- Carranza, S. & Arnold, E.N. (2012) 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. *Zootaxa*, 3378, 1–95.
- Carranza, S. & Arnold, E.N. (2006) Systematics, biogeography, and evolution of *Hemidactylus* geckos (Reptilia: Gekkonidae) elucidated using mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution*, 38, 531–545.
<http://dx.doi.org/10.1016/j.ympev.2005.07.012>
- Carranza, S., Arnold, E.N., Mateo, J.A. & López-Jurado, L.F. (2000) Long-distance colonization and radiation in gekkonid lizards, *Tarentola* (Reptilia: Gekkonidae), revealed by mitochondrial DNA sequences. *Proceedings of the Royal Society of London, Series B*, 267, 637–649.
<http://dx.doi.org/10.1098/rspb.2000.1050>
- Carranza, S., Arnold, E.N., Mateo, J.A. & López-Jurado, L.F. (2001) Parallel gigantism and complex colonization patterns in the Cape Verde scincid lizards *Mabuya* and *Macroscoincus* (Reptilia: Scincidae) revealed by mitochondrial DNA sequences. *Proceedings of the Royal Society of London, Series B*, 268, 1595–1603.
<http://dx.doi.org/10.1098/rspb.2001.1699>
- Carranza, S., Arnold, E.N., Thomas, R.H., Mateo, J.A. & López-Jurado, L.F. (1999) Status of the extinct giant lacertid lizard *Gallotia simonyi simonyi* (Reptilia: Lacertidae) assessed using mtDNA sequences from museum specimens. *Herpetological Journal*, 9, 83–86.
- Clement, M., Posada, D. & Crandall, K.A. (2000) TCS: a computer program to estimate gene genealogies. *Molecular Ecology*, 9, 1657.
<http://dx.doi.org/10.1046/j.1365-294x.2000.01020.x>
- Drummond, A. & Rambaut, A. (2007) BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology*, 7, 214.
<http://dx.doi.org/10.1186/1471-2148-7-214>
- Felsenstein, J. (1985) Confidence-limits on phylogenies – an approach using the bootstrap. *Evolution*, 39, 783.
<http://dx.doi.org/10.2307/2408678>
- Flot, J.F. (2010) seqphase: a web tool for interconverting phase input/output files and fasta sequence alignments. *Molecular Ecology Resources*, 10, 162–166.
<http://dx.doi.org/10.1111/j.1755-0998.2009.02732.x>
- Fujita, M.K. & Papenfuss, T.J. (2011) Molecular systematics of *Stenodactylus* (Gekkonidae), an Afro-Arabian gecko species complex. *Molecular Phylogenetics and Evolution*, 58, 71–75.
<http://dx.doi.org/10.1016/j.ympev.2010.10.014>
- Gamble, T., Bauer, A.M., Greenbaum, E. & Jackman, T.R. (2008) Evidence of Gondwanan vicariance in an ancient clade of geckos. *Journal of Biogeography*, 35, 88–104

- Gamble, T., Bauer, A.M., Colli, G.R., Greenbaum, E., Jackman, T.R., Vitt, L.J. & Simons, A.M. (2011) Coming to America: multiple origins of New World geckos. *Journal of Evolutionary Biology*, 24, 231–244.
<http://dx.doi.org/10.1111/j.1420-9101.2010.02184.x>
- Gamble, T., Greenbaum, E., Jackman, T.R., Russell, A.P. & Bauer, A.M. (2012) Repeated origin and loss of adhesive toepads in geckos. *PLoS ONE*, 7, e39429.
<http://dx.doi.org/10.1371/journal.pone.0039429>
- Geniez, P. & Arnold, E.N. (2006) A new species of semaphore gecko *Pristurus* (Squamata: Gekkonidae) from Mauretania, represents a 4700km range extension for genus. *Zootaxa*, 1317, 57–68.
- Gómez-Díaz, E., Sindaco, R., Pupin, F., Fasola, M. & Carranza, S. (2012) Origin and in situ diversification in *Hemidactylus* geckos of the Socotra Archipelago. *Molecular Ecology*, 21, 4074–4092.
<http://dx.doi.org/10.1111/j.1365-294x.2012.05672.x>
- Gholamifard, A., Esmaeili, H.R. & Kami, H.G. (2009) First report of Blanford's semaphore gecko, *Pristurus rupestris* (Blanford 1874) (Sauria: Gekkonidae) in Fars Province, Iran. *Iranian Journal of Animal Biosystematics*, 5, 91–93.
- Gray, J.E. (1863) Description of new lizard obtained by Mr. Henry Carter on the south-east coast of Arabia. *Proceedings of the Zoological Society of London*, 1863, 236–237.
- Gvoždík, V., Moravec, J. & Kratochvíl, L. (2008) Geographic morphological variation in parapatric Western Palearctic tree frogs, *Hyla arborea* and *Hyla savignyi*: are related species similarly affected by climatic conditions? *Biological Journal of the Linnean Society*, 95, 539–556.
<http://dx.doi.org/10.1111/j.1095-8312.2008.01056.x>
- Haas, G. (1943) On a collection of reptiles from Palestine, Transjordan and Sinai. *Copeia*, 1943, 10–15.
<http://dx.doi.org/10.2307/1437872>
- Harrigan, R.J., Mazza, M.E. & Sorenson, M.D. (2008) Computation vs. cloning: evaluation of two methods for haplotype determination. *Molecular Ecology Resources*, 8, 1239–1248.
<http://dx.doi.org/10.1111/j.1755-0998.2008.02241.x>
- Huelsenbeck, J.P. & Rannala, B. (2004) Frequentist properties of Bayesian posterior probabilities of phylogenetic trees under simple and complex substitution models. *Systematic Biology*, 53, 904–913.
<http://dx.doi.org/10.1080/10635150490522629>
- Katoh, K. & Toh, H. (2008) Recent developments in the MAFFT multiple sequence alignment program. *Briefings in Bioinformatics*, 9, 286–298.
<http://dx.doi.org/10.1093/bib/bbn013>
- Kocher, T.D., Thomas, W.K., Meyer, A., Edwards, S.V., Paabo, S., Villablanca, F.X. & Wilson, A.C. (1989) Dynamics of mitochondrial DNA evolution in animals: amplification and sequencing with conserved primers. *Proceedings of the National Academy of Sciences USA*, 86, 6196–6200.
<http://dx.doi.org/10.1073/pnas.86.16.6196>
- Lanza, B. & Sassi, A.R. (1968) On a new genus and species of gekkonid lizard from Somalia. *Monitore Zoologico Italiano*, 2 (supplemento), 17–26.
- Leviton, A.E., Anderson, S.C., Adler, K. & Minton, S.A. (1992) *Handbook to Middle East amphibians and reptiles*. Society for the Study of Amphibians and Reptiles, Oxford, Ohio, 252 pp.
- Linnaeus, C. (1758) *Systema naturæ per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata. 10th Edition*. Laurentii Salvii, Holmiæ. 824 pp.
- Loveridge, A. (1947) Revision of the African lizards of the family Gekkonidae. *Bulletin of the Museum of Comparative Zoology at Harvard College*, 98, 3–469.
- Maca-Meyer, N., Carranza, S., Rando, J.C., Arnold, E.N. & Cabrera, V.M. (2003) Status and relationships of the extinct giant Canary Island *Gallotia goliath* (Reptilia: Lacertidae), assessed using ancient mtDNA from its mummified remains. *Biological Journal of the Linnean Society*, 80, 659–670.
<http://dx.doi.org/10.1111/j.1095-8312.2003.00265.x>
- Mertens, R. (1970) Neues über einige Taxa der Geckonengattung *Phelsuma. Senckenbergiana biologica*, 51, 1–13.
- Metallinou, M., Arnold, E.N., Crochet, P.-A., Geniez, P., Brito, J.C., Lymberakis, P., Baha El Din, S., Sindaco, R., Robinson, M. & Carranza, S. (2012) Conquering the Sahara and Arabian deserts: Systematics and biogeography of *Stenodactylus* geckos (Reptilia: Gekkonidae). *BMC Evolutionary Biology*, 12, 258.
<http://dx.doi.org/10.1186/1471-2148-12-258>
- Metallinou, M. & Carranza, S. (2013) New species of *Stenodactylus* (Squamata: Gekkonidae) from the Sharqiyah Sands in northeastern Oman. *Zootaxa*, 3745 (4), 449–468.
<http://dx.doi.org/10.11646/zootaxa.3745.4.3>
- Metallinou, M. & Crochet, P.-A. (2013) Nomenclature of African species of the genus *Stenodactylus* (Squamata: Gekkonidae). *Zootaxa*, 3691 (3), 365–376.
<http://dx.doi.org/10.11646/zootaxa.3691.3.5>
- Miralles, A., Vasconcelos, R., Perera, A., Harris, D.J. & Carranza, S. (2011) An integrative taxonomic revision of the Cape Verdean skinks (Squamata, Scincidae). *Zoologica Scripta*, 40, 16–44.

- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G. L., Solymos P., Stevens M.H.H. & Wagner H. (2013) *Vegan: Community Ecology Package*. R package version 2.0-7. Available from: <http://CRAN.R-project.org/package=vegan> (accessed 4 June 2014)
- Papenfuss, T.J., Jackman, T., Bauer, A., Stuart, B.L., Robinson, M.D., Parham, J.F. (2009) Phylogenetic relationships among species in the sphaerodactylid lizard genus *Pristurus*. *Proceedings of the California Academy of Sciences*, 60, 675–681.
- Parker, H.W. (1932) Two collection of amphibians and reptiles from British Somaliland. *Proceedings of the Zoological Society of London*, 1932, 335–367.
- Parker, H.W. (1938) A new gecko from Socotra. *Annals and Magazine of Natural History*, 1, 305–307.
- Peters, W. (1871) Über neue Reptilien aus Ostafrika und Sarawak (Borneo), vorzüglich aus der Sammlung des Hrn. Marquis J. Doria zu Genua. *Monatsberichte der Königlich Akademie der Wissenschaften zu Berlin*, 1871, 566–581.
- Posada, D. (2008) jModelTest: Phylogenetic model averaging. *Molecular Biology and Evolution*, 25, 1253–1256. <http://dx.doi.org/10.1093/molbev/msn083>
- R Core Team (2013) R: a language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria. Available from: <http://www.R-project.org/> (accessed 4 June 2014)
- Rambaut, A. & Drummond, A.J. (2007) Tracer v1. 4. Available from: <http://beast.bio.ed.ac.uk/> (accessed 1 July 2014)
- Razzetti, E., Sindaco, R., Grieco, C., Pella, F., Ziliani, U., Pupin, F., Riservato, E., Pellitteri-Rosa, D., Suleiman, A.S., Al-Aseily, B.A., Carugati, C., Boncompagni, E. & Fasola, M. (2011) Annotated checklist and distribution of the Socotran Archipelago Herpetofauna (Reptilia). *Zootaxa*, 2826, 1–44.
- Rösler, H., Köhler, J., Böhme, W. (2008) A new species of the diurnal gekkonid genus *Pristurus*, Rüppell, 1835 from the Red Sea island Hanish al-Kabir, Yemen. *Amphibia-Reptilia*, 29, 217–227. <http://dx.doi.org/10.1163/156853808784124983>
- Rösler, H. & Wranik, W. (1999) Beiträge zur Herpetologie der Republik Jemen. 5. Drei neue Gecko-Arten vom Sokotra-Archipel (Reptilia: Sauria: Gekkonidae). *Zoologische Abhandlungen Staatliches Museum für Tierkunde, Dresden*, 50, 249–265.
- Ross, W. (1990) Notes on the behaviour of *Pristurus rupestris* (Reptilia: Gekkonidae) with special reference to tail signaling. *Fauna of Saudi Arabia*, 11, 300–305.
- Rüppell, E. (1835) *Neue Wirbelthiere zu der Fauna von Abyssinien gehörig, entdeckt und beschrieben*. Amphibien. S. Schmerber, Frankfurt A. M., 148 pp.
- Schätti, B., & Gasperetti, J. (1994) A contribution to the herpetofauna of Southwest Arabia. *Fauna of Saudi Arabia*, 14, 348–423.
- Schmidt, K.P. (1852) Diagnoses of new amphibians and reptiles from Iran. *Natural History Miscellanea*, 93, 1–2.
- Sindaco, R. & Jeremčenko, V.K. (2008) *The reptiles of the Western Palearctic. Annotated checklist and distributional atlas of the turtles, crocodiles, amphisbaenians and lizards of Europe, North Africa, Middle East and Central Asia*. Monografie della Societas Herpetologica Italica – I, 579 pp.
- Sindaco, R., Metallinou, M., Pupin, F., Fasola, M. & Carranza, S. (2012) Forgotten in the ocean: systematics, biogeography and evolution of the *Trachylepis* skinks of the Socotra Archipelago. *Zoologica Scripta*, 41, 346–362. <http://dx.doi.org/10.1111/j.1463-6409.2012.00540.x>
- Šmíd, J., Carranza, S., Kratochvíl, L., Gvoždík, V., Karim Nasher, A. & Moravec, J. (2013a) Out of Arabia: A complex biogeographic history of multiple vicariance and dispersal events in the gecko genus *Hemidactylus* (Reptilia: Gekkonidae). *PLoS ONE*, 8, e64018. <http://dx.doi.org/10.1371/journal.pone.0064018>
- Šmíd, J., Moravec, J., Kratochvíl, L., Gvoždík, V., Karim Nasher, A., Busais, S.M., Wilms, T., Shobrak, M.Y. & Carranza, S. (2013b) Two newly recognized species of *Hemidactylus* (Squamata, Gekkonidae) from the Arabian Peninsula and Sinai, Egypt. *ZooKeys*, 355, 79–107. <http://dx.doi.org/10.3897/zookeys.355.6190>
- Smith, S.A. & Dunn, C.W. (2007) Phyutility: a phyloinformatics tool for trees, alignments and molecular data. *Bioinformatics*, 24, 715–716. <http://dx.doi.org/10.1093/bioinformatics/btm619>
- Stamatakis, A. (2006) RAXML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics*, 22, 2688–2690. <http://dx.doi.org/10.1093/bioinformatics/btl446>
- Steindachner, F. (1867) *Reise der Österreichischen Fregatte Novara um die Erde in den Jahren 1857, 1858, 1859 unter den Befehlen des Commodore B. von Wüllerstorff-Urbair (Zoologie)*. Vol. I. Part 3. Reptilien. K. Gerold's Sohn/Kaiserlich-Königl. Hof- und Staatsdruckerei, Wien, pp.1–98. [1869 on title page]
- Stephens, M., Smith, N.J. & Donnelly, P. (2001) A new statistical method for haplotype reconstruction from population data. *American Journal of Human Genetics*, 68, 978–989. <http://dx.doi.org/10.1086/319501>
- Tamura, K., Peterson, D., Peterson, N., Stecher, G., Nei, M. & Kumar, S. (2011) MEGA5: Molecular evolutionary genetics analysis using Maximum Likelihood, evolutionary distance, and Maximum Parsimony methods. *Molecular Biology and Evolution*, 28, 2731–2739. <http://dx.doi.org/10.1093/molbev/msr121>

- Uetz, P. (2013) The Reptile Database. Available from: <http://www.reptile-database.org> (accessed 4 December 2013)
- Valenciennes, A. (1861) Notes sur les animaux d'Abysinie rapportés par M. Courbon. *Compte Rendu des Séances de l'Académie des Sciences*, 52, 433–434. [Paris]
- Vasconcelos, R., Carranza, S. & Harris, D.J. (2010) Insight into an island radiation: the *Tarentola* geckos of the Cape Verde archipelago. *Journal of Biogeography*, 37, 1047–1060.
<http://dx.doi.org/10.1111/j.1365-2699.2009.02254.x>
- Wilcox, T.P., Zwickl, D.J., Heath, T.A. & Hillis, D.M. (2002) Phylogenetic relationships of the dwarf boas and a comparison of Bayesian and bootstrap measures of phylogenetic support. *Molecular Phylogenetics and Evolution*, 25, 361–371.
[http://dx.doi.org/10.1016/s1055-7903\(02\)00244-0](http://dx.doi.org/10.1016/s1055-7903(02)00244-0)

APPENDIX I. Information on the *Pristurus* specimens included in the phylogenetic analyses, with precise locality data and GenBank accession numbers. (Soc.) = Socotra Archipelago. IBE: Institute of Evolutionary Biology, Barcelona, Spain; MCCI: Museo Civico di Storia Naturale di Carmagnola, Turin, Italy; JEM: Department of Ecology, Charles University in Prague, Czech Republic; BEV: Laboratoire de Biogéographie et Ecologie des Vertébrés, Université de Montpellier II, France; CAS: California Academy of Sciences, California, San Francisco, USA; TMHC: Tomáš Mazuch Herpetological Collection, Czech Republic; SMB: Sherif M. Baha El Din Herpetological collection, El Cairo, Egypt.

Species	Sample code	Voucher code	Country	code	Latitude	Longitude	12S	acm4	cmos	rag1	rag2	Loc.
<i>P. abdelkuri</i>	S2627	MCCI-R1592-2	Yemen (Soc.)	-	12.18548	52.23756	KJ849839	KJ849917	KJ849973	KJ850033	KJ850108	
<i>P. abdelkuri</i>	S3296	MCCI-R1592-1	Yemen (Soc.)	-	12.69713	53.48669	KJ849840	KJ849918	KJ849974	KJ850034	KJ850109	
<i>P. adharensis</i>	SPM004330	BEV5916	Mauritania	-	-13.27	-13.27	KJ849841	-	-	-	-	
<i>P. adharensis</i>	T660	-	Mauritania	-	20.58	-13.27	KJ849842	KJ849919	KJ849975	KJ850035	KJ850110	
<i>P. carteri</i>	AO110	-	Oman	-	20.58	54.06917	KJ849843	KJ849920	KJ849976	KJ850036	KJ850111	
<i>P. carteri</i>	AO112	-	Oman	-	17.66028	53.90667	KJ849844	KJ849921	KJ849977	KJ850037	KJ850112	
<i>P. carteri</i>	AO181	-	Oman	-	17.24222	54.65806	KJ849845	KJ849922	KJ849978	KJ850038	KJ850113	
<i>P. carteri</i>	SI1785	-	Oman	-	17.02583	58.81975	KJ849846	KJ849923	-	KJ850039	KJ850114	
<i>P. carteri</i>	S7641	IBES7641	Oman	-	20.55547	59.6082	KJ849847	KJ849924	KJ849979	KJ850040	KJ850115	
<i>P. carteri</i>	S7821	-	Oman	-	21.95181	57.52845	KJ849848	KJ849925	KJ849980	KJ850041	KJ850116	
<i>P. carteri</i>	S8071	IBES8071	Oman	-	19.03103	57.52845	KJ849849	KJ849926	KJ849981	KJ850042	KJ850117	
<i>P. celerrimus</i>	AO72	-	Oman	-	19.03103	57.43194	KJ849850	KJ849927	-	KJ850043	KJ850118	
<i>P. celerrimus</i>	S7436	IBES7436	Oman	-	23.17333	56.36005	KJ849851	KJ849928	-	KJ850044	KJ850119	
<i>P. celerrimus</i>	S7852	IBES7852	Oman	-	23.54458	57.60424	KJ849852	KJ849929	KJ849982	KJ850045	KJ850120	
<i>P. celerrimus</i>	UAE36	-	UAE	-	23.07126	56.29833	KJ849853	KJ849930	KJ849983	KJ850046	KJ850121	
<i>P. celerrimus</i>	UAE9	-	Oman	-	25.45417	56.23472	KJ849854	KJ849931	KJ849984	KJ850047	KJ850122	
<i>P. collaris</i>	JEM577	JEM577	Yemen	-	25.96528	49.33	KJ849857	KJ849933	-	KJ850048	-	
<i>P. collaris</i>	JEM97	JEM97	Yemen	-	14.63	49.03	KJ849858	KJ849934	-	KJ850049	KJ850124	
<i>P. collaris</i>	S3525	-	Yemen	-	14.9	49.248253	KJ849855	-	-	-	-	
<i>P. collaris</i>	S3548	SMB11549	Yemen	-	14.592317	49.248253	KJ849856	KJ849932	KJ849985	-	KJ850123	
<i>P. crucifer</i>	JEM498	JEM498	Yemen	-	14.592317	43.25	KJ849862	KJ849938	-	KJ850053	-	
<i>P. crucifer</i>	S3209	-	Somalia	-	13.43	44.2239	KJ849859	KJ849935	KJ849986	KJ850050	KJ850125	
<i>P. crucifer</i>	S3210	-	Somalia	-	9.6366	44.2239	KJ849860	KJ849936	KJ849987	KJ850051	KJ850126	
<i>P. crucifer</i>	S7966	TMHC2013.12.450	Ethiopia	-	9.6366	41.83886	KJ849861	KJ849937	KJ849988	KJ850052	KJ850127	
<i>P. flavipunctatus</i>	CN517	IBECN517	Eritrea	-	9.57745	38.95722	KJ849863	-	KJ849989	KJ850054	KJ850128	
<i>P. flavipunctatus</i>	JEM118	JEM118	Yemen	-	15.6103	49.08	KJ849865	-	KJ849991	KJ850056	KJ850130	

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Species	Sample code	Voucher code	Country	code	Latitude	Longitude	I2S	acm4	cmos	rag1	rag2	Loc.
<i>P. abdelkuri</i>	S2627	MCCI-R1592-2	Yemen (Soc.)	-	12.18548	52.23756	KJ849839	KJ849917	KJ849973	KJ850033	KJ850108	
<i>P. abdelkuri</i>	S3296	MCCI-R1592-1	Yemen (Soc.)	-	12.69713	53.48669	KJ849840	KJ849918	KJ849974	KJ850034	KJ850109	
<i>P. adnarensis</i>	SPM004330	BEV5916	Mauritania	-	-13.27	-13.27	KJ849841	-	-	-	-	
<i>P. adnarensis</i>	T660	-	Mauritania	-	20.58	-13.27	KJ849842	KJ849919	KJ849975	KJ850035	KJ850110	
<i>P. carteri</i>	AO110	-	Oman	-	20.58	54.06917	KJ849843	KJ849920	KJ849976	KJ850036	KJ850111	
<i>P. carteri</i>	AO112	-	Oman	-	17.66028	53.90667	KJ849844	KJ849921	KJ849977	KJ850037	KJ850112	
<i>P. carteri</i>	AO181	-	Oman	-	17.24222	54.65806	KJ849845	KJ849922	KJ849978	KJ850038	KJ850113	
<i>P. carteri</i>	SI785	-	Oman	-	17.02583	58.81975	KJ849846	KJ849923	-	KJ850039	KJ850114	
<i>P. carteri</i>	S7641	IBES7641	Oman	-	20.55547	59.6082	KJ849847	KJ849924	KJ849979	KJ850040	KJ850115	
<i>P. carteri</i>	S7821	-	Oman	-	21.95181	57.52845	KJ849848	KJ849925	KJ849980	KJ850041	KJ850116	
<i>P. carteri</i>	S8071	IBES8071	Oman	-	19.03103	57.52845	KJ849849	KJ849926	KJ849981	KJ850042	KJ850117	
<i>P. celerrimus</i>	AO72	-	Oman	-	19.03103	57.43194	KJ849850	KJ849927	-	KJ850043	KJ850118	
<i>P. celerrimus</i>	S7436	IBES7436	Oman	-	23.17333	56.36005	KJ849851	KJ849928	-	KJ850044	KJ850119	
<i>P. celerrimus</i>	S7852	IBES7852	Oman	-	23.54458	57.60424	KJ849852	KJ849929	KJ849982	KJ850045	KJ850120	
<i>P. celerrimus</i>	UAE36	-	UAE	-	23.07126	56.29833	KJ849853	KJ849930	KJ849983	KJ850046	KJ850121	
<i>P. celerrimus</i>	UAE9	-	Oman	-	25.45417	56.23472	KJ849854	KJ849931	KJ849984	KJ850047	KJ850122	
<i>P. collaris</i>	JEM577	JEM577	Yemen	-	25.96528	49.33	KJ849857	KJ849933	-	KJ850048	-	
<i>P. collaris</i>	JEM97	JEM97	Yemen	-	14.63	49.03	KJ849858	KJ849934	-	KJ850049	KJ850124	
<i>P. collaris</i>	S3525	-	Yemen	-	14.9	49.248253	KJ849855	-	-	-	-	
<i>P. collaris</i>	S3548	SMB11549	Yemen	-	14.592317	49.248253	KJ849856	KJ849932	KJ849985	-	KJ850123	
<i>P. crueifer</i>	JEM498	JEM498	Yemen	-	14.592317	43.25	KJ849862	KJ849938	-	KJ850053	-	
<i>P. crueifer</i>	S3209	-	Somalia	-	13.43	44.2239	KJ849859	KJ849935	KJ849986	KJ850050	KJ850125	
<i>P. crueifer</i>	S3210	-	Somalia	-	9.6366	44.2239	KJ849860	KJ849936	KJ849987	KJ850051	KJ850126	
<i>P. crueifer</i>	S7966	TMHC2013.12.450	Ethiopia	-	9.6366	41.83886	KJ849861	KJ849937	KJ849988	KJ850052	KJ850127	
<i>P. flavipunctatus</i>	CN517	IBECN517	Eritrea	-	9.57745	38.95722	KJ849863	-	KJ849989	KJ850054	KJ850128	
<i>P. flavipunctatus</i>	JEM118	JEM118	Yemen	-	15.6103	49.08	KJ849865	-	KJ849991	KJ850056	KJ850130	

APPENDIX I. (Continued)

Species	Sample code	Voucher code	Country	Loc. code	Latitude	Longitude	I25	acm4	cmos	rag1	rag2
<i>P. flavipunctatus</i>	JEM162	JEM162	Yemen	-	14.65	44.2	KJ849866	-	-	KJ850057	-
<i>P. flavipunctatus</i>	JEM169	JEM169	Yemen	-	14.9	43.47	KJ849867	-	-	KJ850058	KJ850131
<i>P. flavipunctatus</i>	JEM228	JEM228	Yemen	-	13.52	43.95	KJ849868	-	KJ849992	KJ850059	KJ850132
<i>P. flavipunctatus</i>	JEM244	JEM244	Yemen	-	13.87	45.8	KJ849869	-	KJ849993	KJ850060	KJ850133
<i>P. flavipunctatus</i>	JEM420	JEM420	Yemen	-	13.02	44.55	KJ849870	-	-	KJ850061	KJ850134
<i>P. flavipunctatus</i>	JEM545	JEM545	Yemen	-	15.72	43.62	KJ849871	-	KJ849994	KJ850062	KJ850135
<i>P. flavipunctatus</i>	S7619	TMHC2013.12.449	Somalia	-	10.03335	45.15981	KJ849864	-	KJ849990	KJ850055	KJ850129
<i>P. flavipunctatus</i>	SPM00294510	-	Egypt	-	22.18	36.35	KJ849872	-	-	KJ850063	KJ850136
<i>P. flavipunctatus</i>	SPM0029793	-	Egypt	-	22.18	36.35	KJ849873	KJ849939	KJ849995	-	KJ850137
<i>P. gallagheri</i>	AO19	-	Oman	-	22.78667	57.59389	KJ849874	KJ849940	-	KJ850064	-
<i>P. gallagheri</i>	S7271	IBES7271	Oman	-	23.18292	57.41627	KJ849875	-	KJ849996	KJ850065	KJ850138
<i>P. gallagheri</i>	S7665	IBES7665	Oman	-	22.92395	57.68267	KJ849876	-	-	KJ850066	KJ850139
<i>P. guichardi</i>	S4223	-	Yemen (Soc.)	-	12.5636	54.0418	KJ849877	KJ849941	KJ849997	KJ850067	KJ850140
<i>P. insignis</i>	S4210	-	Yemen (Soc.)	-	12.5353	54.3752	KJ849878	KJ849942	KJ849998	KJ850068	KJ850141
<i>P. insignis</i>	S5276	-	Yemen (Soc.)	-	12.5132	53.4223	KJ849879	KJ849943	KJ849999	KJ850069	KJ850142
<i>P. insignoides</i>	S5299	-	Yemen (Soc.)	-	12.5727	54.0464	KJ849880	KJ849944	KJ850000	KJ850070	KJ850143
<i>P. minimus</i>	S1680	IBES1680	Oman	-	20.55547	58.81975	KJ849881	KJ849945	KJ850001	KJ850071	KJ850144
<i>P. minimus</i>	S1857	-	Oman	-	20.41939	58.81237	KJ849882	KJ849946	KJ850002	KJ850072	KJ850145
<i>P. minimus</i>	S7690	IBES7690	Oman	-	21.95181	59.6082	KJ849883	KJ849947	KJ850003	KJ850073	KJ850146
<i>P. minimus</i>	S7701	IBES7701	Oman	-	20.59722	58.26669	KJ849884	KJ849948	KJ850004	KJ850074	KJ850147
<i>P. minimus</i>	S7990	IBES7990	Oman	-	19.03103	57.52845	KJ849885	KJ849949	KJ850005	KJ850075	KJ850148
<i>P. obsti</i>	S5223	-	Yemen (Soc.)	-	12.5417	53.3734	KJ849886	KJ849950	KJ850006	KJ850076	KJ850149
<i>P. popovi</i>	S10421	IBES10421	Saudi Arabia	-	18.20716	42.41003	KJ849887	-	-	KJ850077	KJ850150
<i>P. popovi</i>	S10506	IBES10506	Saudi Arabia	-	18.26042	42.37877	KJ849888	-	-	KJ850078	KJ850151
<i>P. rupestris iranica</i>	S2872	-	Iran	20	27.306694	52.710806	KJ849903	-	KJ850018	KJ850094	KJ850166
<i>P. rupestris rupestris</i>	S6038	IBES6038	Oman	16	23.589399	58.166075	KJ849904	-	KJ850019	KJ850095	KJ850167
<i>P. rupestris rupestris</i>	S6115	IBES6115	Oman	19	23.74533	57.73245	KJ849906	-	KJ850021	KJ850097	KJ850169
<i>P. rupestris rupestris</i>	S7680	IBES7680	Oman	17	23.59032	58.4078	KJ849907	-	KJ850022	KJ850098	KJ850170
<i>P. rupestris rupestris</i>	UAE55	IBEUAE55	Oman	15	22.91639	58.87694	KJ849909	KJ849964	KJ850024	KJ850100	KJ850172

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APPENDIX 1. (Continued)

Species	Sample code	Voucher code	Country	code	Latitude	Longitude	I2S	acm4	cmos	rag1	rag2	Loc.
<i>P. rupestris rupestris</i>	S6039	IBES6039	Oman	18	23.589399	58.166075	KJ849905	-	KJ850020	KJ850096	KJ850168	
<i>P. rupestris rupestris</i>	S7709	IBES7709	Oman	16	23.61589	58.58542	KJ849908	-	KJ850023	KJ850099	KJ850171	
<i>P. samhaensis</i>	S2705	MCCI-R1596	Yemen (Soc.)	-	12.1731	53.0122	KJ849910	KJ849965	KJ850025	KJ850101	KJ850173	
<i>P. sokotranus</i>	S5065	-	Yemen (Soc.)	-	12.6091	54.1559	KJ849911	KJ849966	KJ850026	KJ850102	KJ850174	
<i>P. sokotranus</i>	S5076	-	Yemen (Soc.)	-	12.56356	54.04176	KJ849912	KJ849967	KJ850027	KJ850103	KJ850175	
<i>P. sokotranus</i>	S5277	-	Yemen (Soc.)	-	12.491	53.5623	KJ849913	KJ849968	KJ850028	KJ850104	KJ850176	
<i>P. somalicus</i>	CAS227545	CAS227545	Somalia	-	11.19416	49.2195	-	KJ849969	KJ850029	KJ850105	KJ850177	
<i>P. somalicus</i>	S3184	-	Somalia	-	8.966968	46.145403	KJ849914	KJ849970	KJ850030	-	KJ850178	
<i>P. somalicus</i>	S7969	TMHC2013.12.452	Somalia	-	10.03778	44.78831	KJ849915	KJ849971	KJ850031	KJ850106	KJ850179	
<i>P. somalicus</i>	S7970	TMHC2013.12.453	Somalia	-	9.73055	44.419383	KJ849916	KJ849972	KJ850032	KJ850107	KJ850180	
<i>P. sp. 1</i>	BEV10885	BEV10885	Jordan	1	29.69038	35.35802	-	-	-	KJ850079	KJ850152	
<i>P. sp. 1</i>	JEM1	JEM1	Yemen	6	15.28	44.2	KJ849896	KJ849957	KJ850014	KJ850087	KJ850160	
<i>P. sp. 1</i>	JEM305	JEM305	Yemen	11	16.63	53.01	KJ849897	KJ849958	-	KJ850088	KJ850161	
<i>P. sp. 1</i>	JEM456	JEM456	Yemen	7	13.52	44.05	KJ849898	KJ849959	KJ850015	KJ850089	KJ850162	
<i>P. sp. 1</i>	JEM598	JEM598	Yemen	9	14.77	49.6	KJ849899	KJ849960	KJ850016	KJ850090	KJ850163	
<i>P. sp. 1</i>	JEM649	JEM649	Yemen	8	14.01	48.32	KJ849900	KJ849961	-	KJ850091	-	
<i>P. sp. 1</i>	JEM81	-	Yemen	10	15.15	51.01	KJ849901	KJ849962	KJ850017	KJ850092	KJ850164	
<i>P. sp. 1</i>	S10435	IBES10435	Saudi Arabia	3	18.57702	42.35605	KJ849889	KJ849951	KJ850007	KJ850080	KJ850153	
<i>P. sp. 1</i>	S10436	IBES10436	Saudi Arabia	5	17.53827	43.6298	KJ849890	KJ849952	KJ850008	KJ850081	KJ850154	
<i>P. sp. 1</i>	S10447	IBES10447	Saudi Arabia	2	21.22914	40.69745	KJ849891	KJ849953	KJ850009	KJ850082	KJ850155	
<i>P. sp. 1</i>	S5706	IBES5706	Saudi Arabia	4	18.1873	42.5351	KJ849892	KJ849954	KJ850010	KJ850083	KJ850156	
<i>P. sp. 1</i>	S7314	IBES7314	Oman	13	17.08981	54.4428	KJ849893	KJ849955	KJ850011	KJ850084	KJ850157	
<i>P. sp. 1</i>	S7645	IBES7645	Oman	14	18.05712	56.33459	KJ849894	-	KJ850012	KJ850085	KJ850158	
<i>P. sp. 1</i>	S7890	-	Oman	12	17.2386	53.89913	KJ849895	KJ849956	KJ850013	KJ850086	KJ850159	
<i>P. sp. 1</i>	T3758	-	Jordan	1	29.69038	35.35802	KJ849902	KJ849963	-	KJ850093	KJ850165	

APPENDIX II. Information on the *Pristurus rupestris* (eastern clade of “*P. rupestris*”) and *P. sp. 1* (western clade of “*P. rupestris*”) included in the morphological analyses.

Species	Specimen Code	Country	Latitude	Longitude
<i>P. sp. 1</i>	IBEA0149	Oman	17.174440	54.094720
<i>P. sp. 1</i>	IBES10411	Saudi Arabia	21.225770	40.697860
<i>P. sp. 1</i>	IBES10431	Saudi Arabia	21.229140	40.697450
<i>P. sp. 1</i>	IBES10447	Saudi Arabia	21.229140	40.697450
<i>P. sp. 1</i>	IBES10455	Saudi Arabia	21.225770	40.697860
<i>P. sp. 1</i>	IBES10474	Saudi Arabia	21.227320	40.694220
<i>P. sp. 1</i>	IBES10487	Saudi Arabia	21.114850	40.599400
<i>P. sp. 1</i>	IBES7645	Oman	18.057120	56.334590
<i>P. sp. 1</i>	IBES7683	Oman	18.132160	56.551330
<i>P. sp. 1</i>	IBES7692	Oman	17.121420	54.714040
<i>P. sp. 1</i>	IBES7952	Oman	17.041300	54.326050
<i>P. sp. 1</i>	JEM1	Yemen	15.28	44.2
<i>P. sp. 1</i>	JEM171	Yemen	14.65	44.20
<i>P. sp. 1</i>	JEM172	Yemen	14.65	44.20
<i>P. sp. 1</i>	JEM193	Yemen	13.3	44.06
<i>P. sp. 1</i>	JEM2	Yemen	15.28	44.2
<i>P. sp. 1</i>	JEM20	Yemen	15.37	44.47
<i>P. sp. 1</i>	JEM217	Yemen	13.32	44.12
<i>P. sp. 1</i>	JEM243	Yemen	13.87	45.80
<i>P. sp. 1</i>	JEM245	Yemen	13.87	45.80
<i>P. sp. 1</i>	JEM249	Yemen	13.87	45.80
<i>P. sp. 1</i>	JEM250	Yemen	13.87	45.80
<i>P. sp. 1</i>	JEM3	Yemen	15.28	44.2
<i>P. sp. 1</i>	JEM300	Yemen	16.63	53.01
<i>P. sp. 1</i>	JEM305	Yemen	16.63	53.01
<i>P. sp. 1</i>	JEM306	Yemen	16.63	53.01
<i>P. sp. 1</i>	JEM458	Yemen	13.52	44.05
<i>P. sp. 1</i>	JEM546	Yemen	15.72	43.62
<i>P. sp. 1</i>	JEM547	Yemen	15.72	43.62
<i>P. sp. 1</i>	JEM598	Yemen	14.77	49.60
<i>P. sp. 1</i>	JEM6	Yemen	15.37	44.47
<i>P. sp. 1</i>	JEM649	Yemen	14.01	48.32
<i>P. sp. 1</i>	JEM7	Yemen	15.37	44.47
<i>P. sp. 1</i>	MCCI-R1417-1	Yemen	15.4104	44.1147
<i>P. sp. 1</i>	MCCI-R1417-2	Yemen	15.4104	44.1147
<i>P. sp. 1</i>	MCCI-R1417-3	Yemen	15.4104	44.1147
<i>P. sp. 1</i>	MCCI-R405	Jordan	29.5765	35.4197
<i>P. sp. 1</i>	MCCI-R595	Jordan	29.5765	35.4197
<i>P. sp. 1</i>	MCCI-R596	Jordan	29.5765	35.4197
<i>P. sp. 1</i>	MCCI-R896-2	Yemen	15.02	43.45
<i>P. sp. 1</i>	MCCI-R896-3	Yemen	15.02	43.45

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APPENDIX II. (Continued)

Species	Specimen Code	Country	Latitude	Longitude
<i>P. sp. 1</i>	MCCI-R897	Yemen	15.24	45.15
<i>P. sp. 1</i>	MCCI-R898-1	Yemen	15.01	43.44
<i>P. sp. 1</i>	MCCI-R898-2	Yemen	15.01	43.44
<i>P. sp. 1</i>	MCCI-R899-1	Yemen	15.54	48.47
<i>P. sp. 1</i>	MCCI-R899-2	Yemen	15.54	48.47
<i>P. sp. 1</i>	MCCI-R899-3	Yemen	15.54	48.47
<i>P. sp. 1</i>	MCCI-R899-4	Yemen	15.54	48.47
<i>P. sp. 1</i>	MCCI-R899-5	Yemen	15.54	48.47
<i>P. sp. 1</i>	MCCI-R900-1	Yemen	12.7747	45.0231
<i>P. sp. 1</i>	MCCI-R900-2	Yemen	12.7747	45.0231
<i>P. sp. 1</i>	MCCI-R900-3	Yemen	12.7747	45.0231
<i>P. sp. 1</i>	MCCI-R900-4	Yemen	12.7747	45.0231
<i>P. rupestris</i>	IBES6038	Oman	23.589399	58.165075
<i>P. rupestris</i>	IBES6039	Oman	23.589399	58.165075
<i>P. rupestris</i>	IBES6040	Oman	23.589399	58.165075
<i>P. rupestris</i>	IBES6131	Oman	23.589399	58.165075
<i>P. rupestris</i>	IBES6135	Oman	23.085750	59.046683
<i>P. rupestris</i>	IBES6140	Oman	23.589399	58.165075
<i>P. rupestris</i>	IBES7068	Oman	23.554560	58.187460
<i>P. rupestris</i>	IBES7398	Oman	23.293080	57.977470
<i>P. rupestris</i>	IBES7409	Oman	23.786010	57.795320
<i>P. rupestris</i>	IBES7416	Oman	23.786010	57.795320
<i>P. rupestris</i>	IBES7418	Oman	23.310270	57.995840
<i>P. rupestris</i>	IBES7422	Oman	23.513720	57.853400
<i>P. rupestris</i>	IBES7439	Oman	23.786010	57.795320
<i>P. rupestris</i>	IBES7446	Oman	23.786010	57.795320
<i>P. rupestris</i>	IBES7473	Oman	22.895140	59.137610
<i>P. rupestris</i>	IBES7525	Oman	23.164830	58.385300
<i>P. rupestris</i>	IBES7527	Oman	22.823740	59.007590
<i>P. rupestris</i>	IBES7534	Oman	23.131670	58.618890
<i>P. rupestris</i>	IBES7535	Oman	23.106030	58.644440
<i>P. rupestris</i>	IBES7553	Oman	23.131670	58.618890
<i>P. rupestris</i>	IBES7561	Oman	22.896280	59.160190
<i>P. rupestris</i>	IBES7675	Oman	23.589399	58.165075
<i>P. rupestris</i>	IBES7680	Oman	23.590320	58.407800
<i>P. rupestris</i>	IBES7709	Oman	23.615890	58.585420
<i>P. rupestris</i>	IBES7729	Oman	23.072330	58.186680
<i>P. rupestris</i>	IBES7738	Oman	23.452280	58.505340
<i>P. rupestris</i>	IBES7749	Oman	23.754680	57.581270
<i>P. rupestris</i>	IBES7864	Oman	23.690940	58.039380
<i>P. rupestris</i>	IBES7874	Oman	23.310270	57.995840
<i>P. rupestris</i>	IBES9018	Oman	22.833260	58.988210
<i>P. rupestris</i>	IBEUAE55	Oman	22.916390	58.876940
<i>P. rupestris</i>	IBEUAE58	Oman	23.108060	58.562500

