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Studies of morphological and molecular phylogenetic divergence in spiders (Araneae: *Homalonychus*) from the American southwest, including divergence along the Baja California Peninsula

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Abstract

Comparative phylogenetic and phylogeographic analyses have revealed a pervasive midpeninsular divergence in the mitochondrial genealogies of numerous vertebrate taxa distributed on the Baja California Peninsula. In this study, we extend the investigation of regional vicariance in Baja California to an arthropod taxon by examining patterns of phylogenetic and morphological divergence in the spider genus *Homalonychus* (Araneae, Homalonychidae). We analyzed data from two mtDNA genes (16S rRNA and NADH dehydrogenase subunit (1) and a nuclear gene (28S rRNA) using maximum parsimony and Bayesian phylogenetic analyses, and also conducted geometric morphometric analyses employing landmark data on male and female genitalia. Genes and morphology both reveal a deep split across the Colorado River and Gulf of California, separating *Homalonychus selenopoides* on the east side of river from its congener *Homalonychus theologus* on the west side of the river, including the Baja California Peninsula. Along the north–south axis of the Baja Peninsula, an apparently more recent midpeninsular phylogenetic break is evident within *H. theologus* in the mitochondrial genome and in female genitalia. However, there is no measurable divergence between northern and southern populations in either nuclear DNA or male genitalia. We suggest that this discordance between datasets reflects either a difference in rates of evolution between male versus female systems, or that male-based nuclear gene flow is obscuring a phylogenetic split that is fixed in the female-based systems. Our findings provide additional support for a midpeninsular Baja divergence event, although the timing and geological evidence for such an event remain elusive.

Keywords: Midpeninsular seaway; Regional biogeography; Gulf of California; Colorado River; Phylogeography; Geometric morphometrics; Sea of Cortez; Bayes factors; Bayesian molecular clock rooting

1. Introduction

The field of phylogeography has revolutionized studies of regional biogeography. Whereas, geographically widespread taxa were at one time considered uninformative in biogeographic analysis, these taxa are informative and sometimes sought after for phylogeographic analysis. Such phylogeographic studies have taught evolutionary biologists two general lessons. First, many species previously thought to represent single cohesive lineages (e.g., based on morphological homogeneity) have been found to actually represent cryptic lineage complexes. Such cryptic lineage divergence is common in both vertebrate (Joseph and Moritz, 1994; Riddle et al., 2000a,b; Zink et al., 2001) and invertebrate taxa (Bond et al., 2001; Bond and Sierwald, 2003; Hedin, 1997a; Hedin and Wood, 2002; Wilcox et al., 1997). Second, co-distributed taxa from the same geographic region often reveal similar patterns of phylogenetic

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and/or phylogeographic structuring (Avise and Ball, 1990), as in the southeastern United States (Avise et al., 1987; Avise and Nelson, 1989), northeastern Australia (Joseph and Moritz, 1994; Schneider et al., 1998) and the Baja California Peninsula (Lawlor et al., 2002; Murphy and Aguirre-Léon, 2002; Riddle et al., 2000a; Zink et al., 2001).

The Baja California Peninsula is one of the longest peninsulas in the world, a geographically isolated landmass that stretches over a thousand kilometers from southern California to Cabo San Lucas. The formation of the peninsula and subsequent opening of the gulf originated from continental rifting and crustal transfer between the North American and Pacific Plates followed by extensional faulting (Holt et al., 2000; Stock and Hodges, 1989; Umhoefer et al., 2002). The region is dominated by low elevation xeric habitats, including some of the driest desert regions in North America. Because of the peninsula's complex geological history, high taxonomic endemicity, large number of off-shore islands, and obvious geographic isolation, the region has long been a favorite of biogeographers (see Grismer, 2000; Hafner and Riddle, 1997). Recent biogeographic work using principles of comparative phylogeography has been particularly informative, revealing a mosaic biogeographic history that includes evidence for both old vicariant events (summarized in Murphy and Aguirre-Léon, 2002; Riddle et al., 2000a), as well as post-Pleistocene dispersal and range expansion (e.g., Alvarez-Castañeda and Patton, 2004; Hurtado et al., 2004; Nason et al., 2002; Whorley et al., 2004).

Although multiple vicariant events have likely impacted the Baja California Peninsula and surrounding deserts, we are particularly interested in two hypothesized vicariant events discussed in previous studies. The older of the two events concerns the separation of taxa at the northern end of the Gulf of California, where the Colorado River drains into the Gulf. This vicariance separates "continental" clades found predominately east of the Colorado River from the "peninsular" clades found west of the river (Fig. 1). This phylogenetic break is hypothesized to have resulted from a northern embayment of the Gulf of California during the Late Miocene–Pliocene (6.5–3 Ma) (Lamb et al., 1989; Metzger, 1968; Oskin and Stock, 2003; Shafiqullah et al., 1980), although earlier vicariance associated with the rifting of the peninsula and formation of the Gulf itself cannot be ruled out.

An hypothesized more recent and seemingly more prevalent event is the "midpeninsular event" of Riddle et al. (2000a). Midpeninsular vicariance is hypothesized to reflect the formation of a trans-peninsular seaway that separated terrestrial elements along a north/south axis sometime during the mid-Pleistocene (ca. 1 Ma; Upton and Murphy, 1997), although earlier dates are possible (see Section 4). Despite the lack of geological evidence for a midpeninsular seaway, the biological evidence for some type of barrier appears overwhelming. Riddle et al. (2000a), in summarizing available data and adding new data, suggest that there is evidence for midpeninsular vicariance in ten of twelve

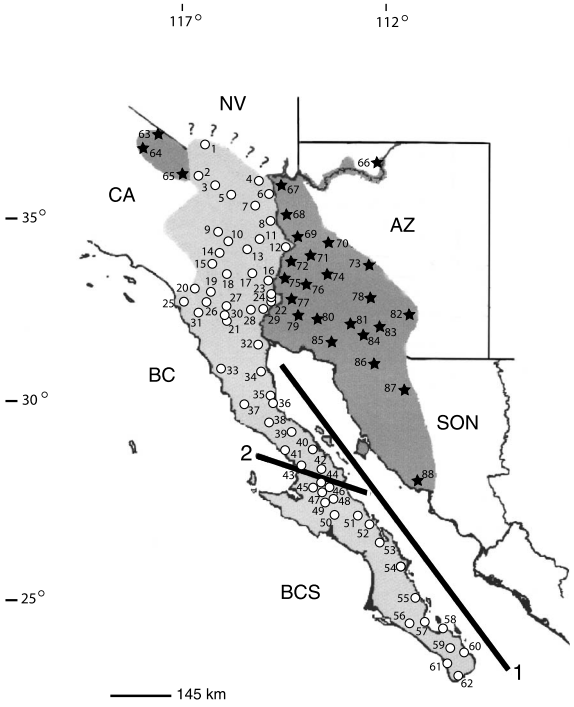

Fig. 1. Regional map, including distribution of *Homalonychus* and two hypothesized vicariant events. The distribution of *H. theologus* is indicated by light gray (sampled sites, white circles), whereas that of *H. selenopoides* is indicated by dark gray (sampled sites, black stars). Location numbers correspond to those found in Appendix A. Southwestern Nevada represents an area of distributional ambiguity—species occurrence in this region is uncertain. Hypothesized vicariant events (following Riddle et al., 2000a) include: (1) rifting of the peninsula away from the mainland and inundation of the basin by the Sea of Cortéz, and (2) transgression separating the northern portion of the peninsula from the southern portion. (NV, Nevada; CA, California; AZ, Arizona; BC, Baja California; BCS, Baja California Sur; Son, Sonora).

vertebrate taxa that have been subject to phylogeographic analyses (their Table 1). Many taxa show phylogeographic or phylogenetic breaks in the vicinity of the Vizcaíno Desert (28–30° N latitude), but the exact geographic location of the split appears to differ considerably across groups (see Riddle et al., 2000a). These differences are thought to reflect differences in post-vicariance dispersal, but might also represent artifacts of sparse geographic sampling in the region, or even multiple vicariant processes at different times.

A notable feature of midpeninsular vicariance is the apparent "cryptic" nature of this event within species. Whereas mtDNA evidence reveals a clear signature of divergence between north and south peninsular regions, other more noticeable features (e.g., morphology) show few differences. This lack of morphological divergence is potentially consistent with recent divergence (morphology evolving more slowly than molecules), but is also consistent with post-vicariance gene flow across northern and southern groups. In this regard, it is important to note that essentially all of the recent phylogeographic research has been based entirely on mitochondrial (female-based) evidence. Although these studies indicate a general lack of post-vicariance female gene flow (haplotypes from

Table 1
Number of unique haplotypes and sequence divergence values within and between clades for the combined 16S-ND1 data

	Unique haplotypes/ number of specimens	Genetic divergence within clades (uncorrected *p* distances) Avg (min–max)	Genetic divergence between clades (uncorrected *p* distances) Avg (min–max)
H. selenopoides	55/64	3% (0–6%)	*H. theologus* (CA + NV + BC)—13% (12–15%)
H. theologus (CA + NV + BC)	71/103	2% (0–4%)	*H. theologus* (BCS)—9% (8–10%)
H. theologus (BCS)	31/31	4% (0–7%)	*H. selenopoides* (AZ, DV, Sonora)—13% (12–15%)

different clades are rarely collected together; Riddle et al., 2000a; Zink et al., 2001), this does not preclude male-based gene flow in these systems.

Our study focuses on the spider genus *Homalonychus*. This genus is the sole member of the spider family Homalonychidae, and includes only two species (*H. theologus* Chamberlin and *H. selenopoides* Marx). The homalonychids are non-web-building spiders endemic to southwestern North America (Fig. 1). Members of both species are typically found under rocks, dead vegetation or other debris. We often find a series of incrementally larger exuviae under the same rock under which spiders are collected, suggesting that the spiders are relatively sedentary, although wandering adult males and juveniles have been collected at night (pers. obs.). The phenomenon of male and juvenile spiders being more vagile than females has been documented in several spider groups (Brady, 1964; Foelix, 1996; Robinson, 1982). From rearing these spiders in the lab, we know that they are relatively long-lived (e.g., taking over 3 years to reach adulthood) and that females may live as adults for at least two years. The two species of *Homalonychus* can be separated only upon close examination of either male or female genitalia (Roth, 1984). *Homalonychus theologus* has a shorter palpal embolus (male genitalia) and median lobe of the epigynum (female genitalia), while *H. selenopoides* has a longer, more curved embolus and a longer median lobe. Roth (1984) commented extensively on geographic genitalic variation in *H. selenopoides* females, but made no mention of female variation in the wide-ranging *H. theologus*, or variation in males of either species.

The circum-gulf distribution of *Homalonychus* is consistent with that of other taxa that show "continental" plus "peninsular" phylogenetic structuring (Riddle et al., 2000a). *Homalonychus selenopoides* is distributed mostly to the east of the Colorado River, occurring in Sonoran Desert habitats from central Sonora north to the Grand Canyon (Fig. 1). A few populations have also been found west of the river in the northern Mojave Desert (Roth, 1984), a distributional pattern very similar to "continental" *Peromyscus eremicus* (see Riddle et al., 2000b). Conversely, *H. theologus* occurs primarily in low elevation desert habitats west of the Colorado River, ranging from the central Mojave south to the tip of the Baja California Peninsula, including a distributional arm that reaches to southwestern California west of the Peninsular Ranges (Fig. 1). There are no confirmed records of these species occurring in sympatry, although Roth (1984) suggested the possibility of hybridization near Yuma, Arizona. The Colorado River appears to be a perfect geographic barrier separating the species, at least at the northern end of the Gulf of California.

The primary objective of this study is to examine the biogeographic history of *Homalonychus*, focusing particular attention on the two hypothesized vicariant events outlined above. These are the separation of the Baja California Peninsula from the mainland, and an event occurring along the peninsula. Although arthropod diversity and endemicity is high on the Baja Peninsula (e.g., Johnson and Ward, 2002; Truxal, 1960; Williams, 1980), our study is one of the first arthropod studies to address regional biogeographic questions using modern phylogeographic methods (see also Gantenbein et al., 2001). We present phylogenetic analyses of both nuclear and mitochondrial DNA sequence data from a geographically broad sample of *Homalonychus*, and combine these data with geometric morphometric analyses of male and female genitalia. The formal documentation of morphological divergence in addition to the consideration of phylogenetic divergence in both nuclear and mitochondrial genetic systems allows us to more fully explore the generality and biological significance of midpeninsular "cryptic" vicariance.

2. Methods

2.1. Specimen sampling

We collected a comprehensive sample of spiders over the geographic range of both species, spacing collection sites to prevent sampling gaps that could bias phylogenetic analyses (Fig. 1). In total, we sampled *H. theologus* at 62 sites and *H. selenopoides* at 26 sites, collecting three to five spiders per site. Attempts to collect adults were made so that their genitalia could be used in morphometric analyses. In some instances, juvenile spiders were brought back to the lab and reared to adulthood. One to two legs were removed from each spider, placed in 100% EtOH and stored in a −80 °C freezer. The rest of the spider was placed in 70–80% EtOH for morphological analyses and vouchering purposes. Voucher numbers, collecting locality information, and GenBank accession numbers are provided in Appendix A. The majority of specimens have been deposited in the National Museum of Natural History, though a few remain in the personal collections of the authors.

2.2. Molecular analyses

Genomic DNA was extracted from the femur of one leg of larger spiders (late instars or adults), or the entire leg(s)

of smaller spiders (spiderlings or early instars), using the CTAB protocol of Shahjahan et al. (1995) or a Qiagen DNEasy kit. Partial fragments of the mitochondrial 16S rRNA gene (~600 bp) were amplified from 205 individuals using the polymerase chain reaction (PCR). The 3′ end of the 16S gene was amplified using the primer LR-N-13398 (Simon et al., 1994) combined with N1-J-12534 (5′-GCGTCTCTGAAGGGTTGTAG-3′; this study), N1-J-12581HO (5′-CCTTTTCGAATTTGAATATA-3′; this study) or N1-J-12860 (5′-AGATAGAAACCAACCTGG-3′; this study). Partial fragments of the mitochondrial NADH dehydrogenase subunit 1 (ND1 hereafter) gene (372 bp) were also amplified from 198 of the same 205 individuals, using the primer LR-N-12945 (Hedin, 1997a), paired with either N1-J-12261 (Hedin, 1997b), SBAJAND1 (5′-GCTACTCTTCGAATACTCC-3′; this study), or N1-J-12228ish (5′-TTGAATTNGCTGATCAYCC-3′; this study).

A subset of individuals (20) was sampled for the nuclear 28S rRNA gene. This subset included representatives of populations that spanned the phylogenetic and geographic diversity represented in the mtDNA matrices. PCR was used to amplify 800 bp of 28S with 28S-O (Hedin and Maddison, 2001) and 28S-B (5′-TCGGAAGGAAC CAGCTACTA-3; this study). Previous studies in other spider groups suggest that these loci evolve at different rates, with ND1 evolving faster than 16S, which both evolve faster than 28S (Hedin and Maddison, 2001). This rate variation, coupled with differences in modes of inheritance of mtDNA vs. nDNA, should provide different levels of resolution and perhaps reflect differences in sex-biased demography or dispersal in *Homalonychus*. PCR products were purified using polyacrylamide gels (Sambrook et al., 1989) or Amicon Microcon microconcentrator purification columns, and sequenced using Big Dye Terminator 3.0 Ready Reactions on an ABI 377 automated sequencer. DNA sequences were edited and aligned by eye using SeqApp v1.9a169 (Gilbert, 1993) and MacClade 4.0 (Maddison and Maddison, 2001). The mtDNA alignment is available from the MPE website.

2.3. Phylogenetic analyses

Maximum parsimony was used as an optimality criterion to reconstruct gene trees using PAUP* v4.0b10 (Swofford, 2002). Parsimony analysis of the 28S data was conducted using the branch and bound algorithm. Standard heuristic parsimony searches of the combined 16S-ND1 dataset resulted in a large number of most parsimonious trees. In an attempt to maximize the number of tree islands examined, we conducted a heuristic search with 10,000 random addition sequence replicates, saving 100 trees per replicate by specifying to store up to 100 trees with a score greater than one. Non-parametric bootstrap (Felsenstein, 1985) was used to evaluate nodal support for the 28S (100,000 pseudoreplicates) and 16S-ND1 datasets (10,000 pseudoreplicates). Because of the computational time it would take to evaluate nodal support on the full mtDNA matrix, a genetically divergent subset of sequences (10 per clade) from each of three major recovered clades was sampled. At least one haplotype from subclades within each major clade was used, with additional haplotypes chosen to maximize the geographic spread represented in each major clade. The search strategy used per bootstrap pseudoreplicate included 10 random addition sequence replicates and TBR branch swapping, using the same strategy mentioned above for the full 16S-ND1 dataset.

MrBayes v3b4 (Huelsenbeck and Ronquist, 2001) was used to estimate topologies, model parameters, and posterior probabilities of inferred clades for both datasets, and to root trees using a Bayesian molecular clock method (Huelsenbeck et al., 2002; Jennings et al., 2003). Likelihood ratio tests (LRTs) were used as a model choice criterion (Modeltest: Posada and Crandall, 1998; MrModeltest: Nylander, 2002). Three replicate analyses were conducted for each dataset using random starting trees, default priors, and four heated chains at the default temperature. Average likelihood scores ($-\ln L$) were examined to ensure convergence of likelihood values across replicate analyses. If these values differed by more than a few tenths of a point, additional analyses were ran until we obtained three analyses which converged on nearly the same value. Although likelihoods are an important parameter to examine, a potentially more useful method to determine convergence is to establish whether the posterior probabilities of clades have converged. We used Converge v0.1 (Warren et al., 2003) to visualize posterior probabilities against chain length, allowing us to assess convergence and also determine the number of generations to eliminate as burn-in. If posterior probabilities had not converged after completion of analyses, chains decidedly were not long enough and more generations were run.

Homalonychids are morphologically unique spiders of uncertain phylogenetic placement (Roth, 1984). Although never considered in a modern or formal phylogenetic analysis, homalonychids have historically been hypothesized as relatives of several different spider groups. These include Pisauridae and Selenopidae (Marx, 1891), Zodariidae (Petrunkevitch, 1923), Ctenoidea (Mello-Leitão, 1941), and Pisauroidea (Lehtinen, 1967). Given the lack of understanding of family-level relationships within spiders (Coddington and Levi, 1991), we believe that a phylogenetic search for the sister group to *Homalonychus* would require an analysis of many (>30) taxa. Even if it were possible to pinpoint the sister group of *Homalonychus*, the morphological and biogeographical distinctiveness of these spiders suggests a long history of phylogenetic isolation. This would suggest a rooting problem in which a distant outgroup taxon is connected to a relatively close-knit ingroup (see Holland et al., 2003; Jennings et al., 2003; Steele et al., 2005; Wheeler, 1990). Under this condition, placement of the root along any of the ingroup branches is essentially equiprobable. As such, we used Bayesian midpoint rooting and Bayesian molecular clock methods to root *Homalonychus* trees. Posterior probabilities for root positions were

obtained for the 28S dataset using post_root, described in Salter (2004) and for the mtDNA dataset using a perl script written by A. Fabrikant (personal communication; available upon request from S. Crews).

We used Bayes factors (Jeffreys, 1961; Kass and Raftery, 1995), or posterior odds, to determine the appropriateness of assuming a molecular clock for each of the genes (Huelsenbeck et al., 2002). Bayes factors represent one's change in beliefs after viewing the data, and they do not have standard cutoff values like most test statistics; however, it is believed that they will give similar results to likelihood approaches, while they can also be used to test non-nested models (Nylander et al., 2004). We estimated Bayes factors as twice the difference of the log-transformed harmonic mean of the likelihoods of the alternative hypothesis (clock applied) minus the harmonic mean of the likelihoods of the null hypothesis (no clock) (Brandley et al., 2005; Kass and Raftery, 1995; Nylander et al., 2004; Schmitz et al., 2005). Likelihood harmonic means were obtained using the 'sump' command in MrBayes v3b4 (Huelsenbeck and Ronquist, 2001).

2.4. Morphometric analyses

Specimens (241 adult female and 92 adult males) were borrowed from the American Museum of Natural History (AMNH), the Essig Museum at the University of California (UC) Berkeley, UC Riverside, the California Academy of Sciences (CAS), or represent new collections. Digital images were acquired using a Nikon Coolpix 990 digital camera attached to an Olympus SZX12 dissecting microscope. One image each was captured for both the external and internal epigynum. Only personal specimens and a majority of CAS specimens were dissected, leaving 132 images of the internal epigyna. Epigyna were cleared in clove oil or lactic acid, and remaining tissues were dissected away using forceps and an insect pin. One image was captured of the left male palpus in dorsal view, one in the retrolateral view and one in lateral view. A number (SCC_001–SCC_296) was placed in each vial for vouchering purposes. Fine sand in a dish with ethanol was used to stabilize the genitalia and great care was taken to minimize tilting or distortion.

Morphometric analyses consisted of scoring landmarks (Bookstein, 1991); a Procrustes analysis (Rohlf and Slice, 1990); an affine, partial warp analysis based on the thin-plate spline (Rohlf et al., 1996); and a non-affine relative warp analysis (Rohlf, 1993). Using tpsUtil version 1.11 (Rohlf, 2002a), files of the images were constructed and imported into tpsDIG32 version 1.31 (Rohlf, 2002b) which was used to place landmarks on the images.

Files containing images with the chosen landmarks (Fig. 2) were imported into tpsRelw version 1.26 (Rohlf, 2002c). A tangent configuration of all the images from each analysis was computed using a generalized Procrustes analysis. The generalized Procrustes analysis in this program computes this tangent configuration based on a generalized least squares (GLS) procedure following Gower (1971), but modified as in Rohlf and Slice (1990). The Procrustes superimposition method has drawbacks, such as distributing differences localized at a few landmarks over all of the landmarks (see Section 3), but this is circumvented if shape change is not localized at any particular landmark(s) (Rohlf and Slice, 1990).

A relative warp analysis was then performed, which is equivalent to a principal components analysis of the partial-warp scores when $\alpha = 0$ and is used to describe within-group variation. Bookstein (1991) introduced α, a scaling parameter that can be applied when calculating the relative warp scores. An α of 0 gives equal weight to all partial warps such that large- and small-scale differences of shape change are equivalent. If one wishes to place more emphasis on large-scale changes (those with lower bending energies), or small-scale changes (those with higher bending energies), α can be set above or below zero, respectively (Bookstein, 1991; Rohlf, 1993).

The plot of the relative warp scores may allow one to distinguish morphological clusters. If morphological clusters were present, a Hotelling's T^2 test was performed to determine if there were statistically significant differences in shape between morphological groups that were defined a priori. When morphological clusters were not detected from the relative warp analysis with $\alpha = 0$, Hotelling's T^2 was used to assess differences in shape that may not be visually apparent in the warp analyses. Hotelling's T^2 tests were conducted using PAST v.1.06 (Hammer and Harper, 2003).

3. Results

3.1. Phylogenetic analyses

3.1.1. 16S-ND1

One hundred fifty seven unique haplotypes were found in our sample of 198 individuals—these unique haplotypes were used as terminals in phylogenetic analyses. Assuming a root placement along one of the long internal branches (see below) parsimony analyses of these data recovered three major geographic clades, corresponding to an 'eastern' clade (Sonora, Arizona and Death Valley), a northern Baja + California clade, and a southern Baja clade. The reduced-matrix bootstrapping indicates strong support for the three geographical clades (bootstrap proportions: 100, 100, 100). Sequence divergence values both within and between clades are summarized in Table 1.

Bayesian searches using a GTR + I + Γ model of nucleotide substitution were initially run for 10,000,000 generations. However, because Converge v0.1 (Warren et al., 2003) analyses indicated a lack of convergence, these analyses were repeated with 25,000,000 generations, sampling every 1000th tree. Bayesian trees also include three major clades, corresponding to those found in parsimony searches (posterior probabilities: 1.0, 1.0, 1.0, respectively). An unrooted 50% majority rule tree consensus phylogram from this analysis is shown in Fig. 3. The southern Baja

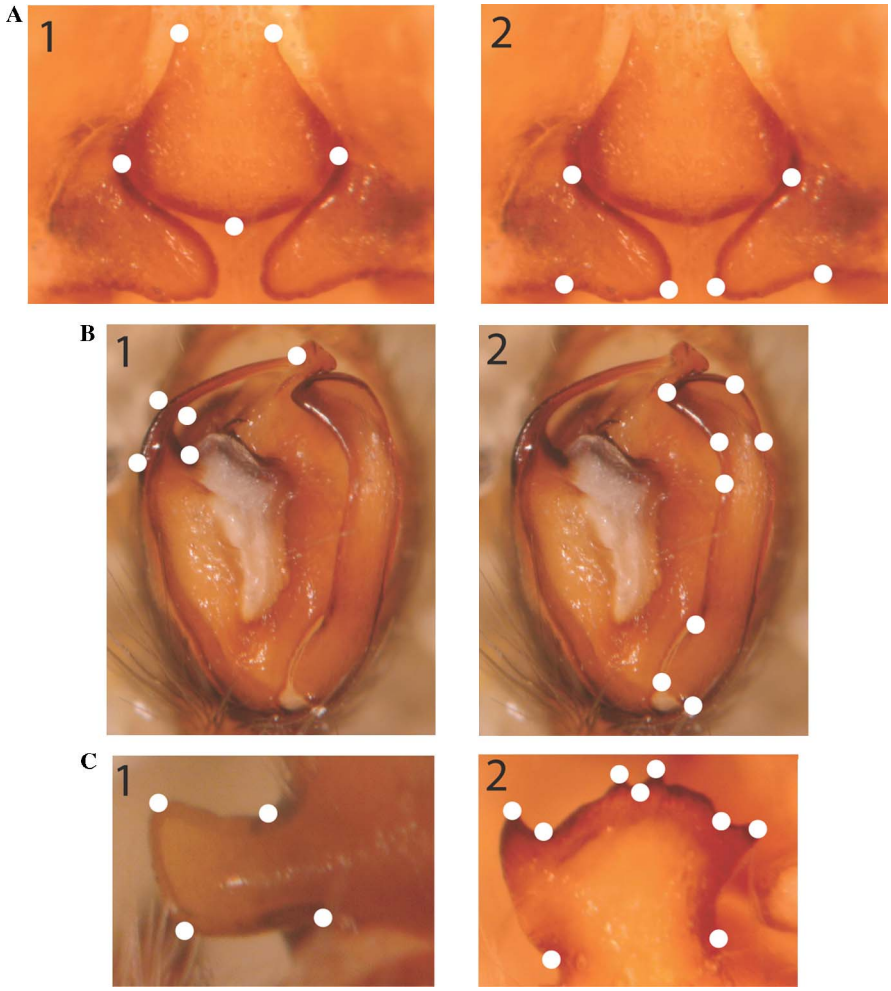

Fig. 2. Landmark configurations used in morphometric analyses on the median (A1) and lateral (A2) lobes of the external epigyna of the female and on the embolus (B1), median apophysis (B2), cymbial process (C1) and retrolateral tibial apophysis (C2) of the male palpus.

clade has the longest internal branches, while the Arizona and northern Baja + California have less internal divergence, respectively. There is considerable phylogenetic structure within regional clades, with many well-supported ($p > 0.95$) subclades. The majority of these subclades consist of haplotypes from the same locality or geographically proximate localities, indicating restricted female-based gene flow. An exception is the northern portion of northern Baja + California clade, where a few closely related haplotypes are shared over a large geographic area.

3.1.2. 28S

28S sequences were gathered from 20 individuals that spanned the phylogenetic and geographic diversity of the mtDNA sample (see Fig. 3). A single most parsimonious tree was inferred (Fig. 4), including two major clades corresponding to the eastern and western species, supported by high bootstrap support (100). There was no sequence variation found within the western clade and little variation in the eastern clade. Bayesian analyses, run for 500,000 generations sampling every 100th tree, yielded an identical topology.

3.1.3. Root placement

To root trees we used Bayesian methods enforcing a molecular clock and used the Bayes factor to determine whether or not the data were evolving in a clock-like manner. According to the Bayes factor, analyses with and without a clock enforced differ very strongly (Table 2), and are not consistent with molecular clock expectations. However, Huelsenbeck et al. (2002) found that clock rooting was relatively robust to rate heterogeneity, meaning that it is still possible to accurately root trees using a molecular clock, even when local clock deviations exist.

Phylogenetic analyses of taxa that have distributions similar to *Homalonychus* indicate a primary east to west (i.e., AZ + Sonora vs. CA + Baja) division (Riddle et al., 2000a). As such, we predicted a (eastern (western–northern + western–southern)) clade structure within *Homoalonychus*. The 28S data are clearly consistent with this prediction—in Bayesian midpoint rooting analyses, the east–west split has a posterior probability of 0.80. In the Bayesian molecular clock rooting analysis, the east–west split has a posterior probability of 0.73. Although these values may be statistically negligible, they are

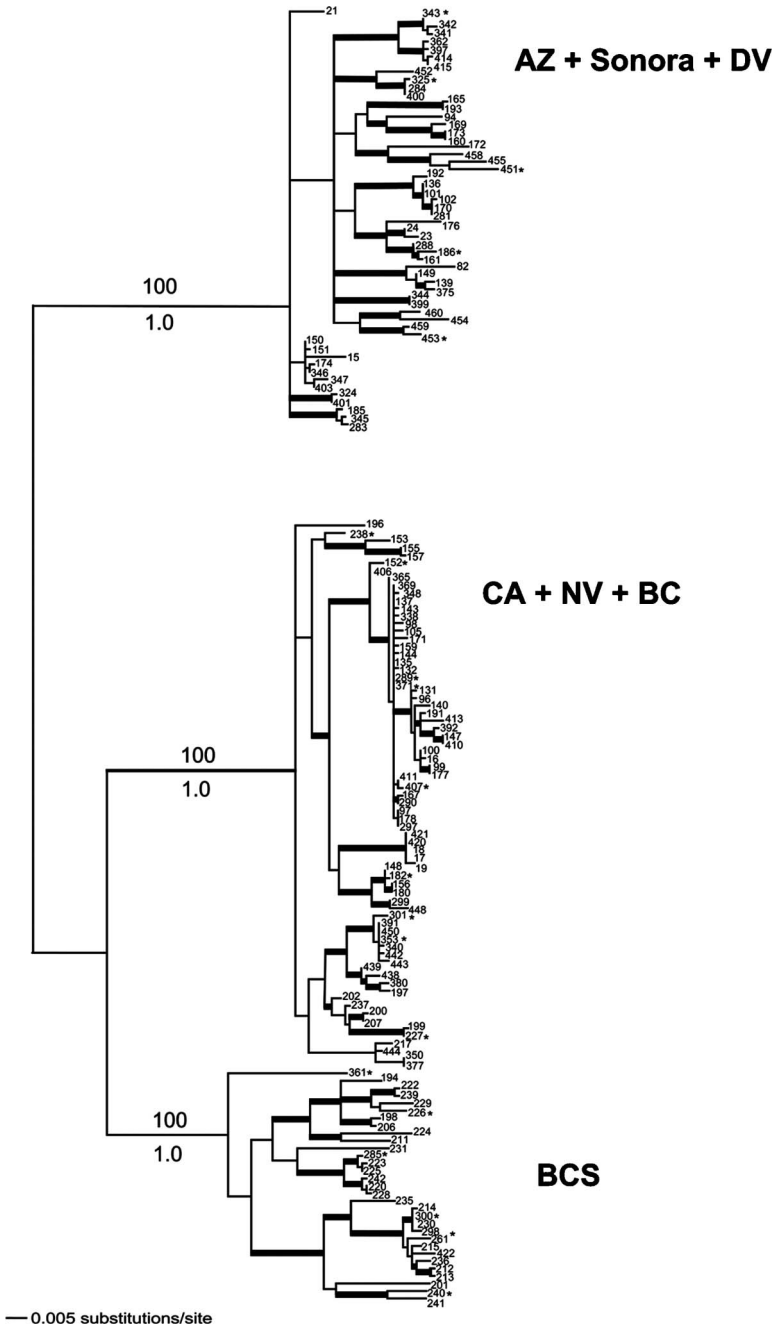

Fig. 3. 50% majority rule consensus phylogram of 30,000 trees sampled from the posterior distribution of the Bayesian analysis of 16S-ND1 data. Numbers represent non-parametric bootstrap and Bayesian posterior probability values, shown only for the three major clades. Branches supported by >95% Bayesian posterior probabilities are thickened. Asterisks designate haplotypes used in the 28S analysis (also see Appendix A). Haplotype numbers correspond to voucher numbers listed in Appendix A. (DV, Death Valley; AZ, Arizona; BC, Baja California; CA, California; BCS, Baja California Sur; NV, Nevada).

much higher than posterior probability values for alternative root placements. Three alternative root placements are most relevant for the mtDNA (e.g., the root falling on one of the long internal branches separating major clades). Posterior probabilities for these three alternatives are presented in Table 3, for both Bayesian midpoint and Bayesian molecular clock analyses. As for the 28S data, the mtDNA data are consistent with the deepest split in the tree separating eastern and western clades.

3.2. Morphometric analyses

Plots of relative warp 1 (RW1) against relative warp 2 (RW2) of the median lobes of the epigyna and the emboli of the palpi allowed the visualization of two morphological clusters (Fig. 5). These two clusters include an eastern group (including Death Valley) corresponding to *H. selenopoides*, and a western group corresponding to *H. theologus*. In the analysis of median epigynal lobes, RW1 and RW2 explain 90% of the variation in the data. In the

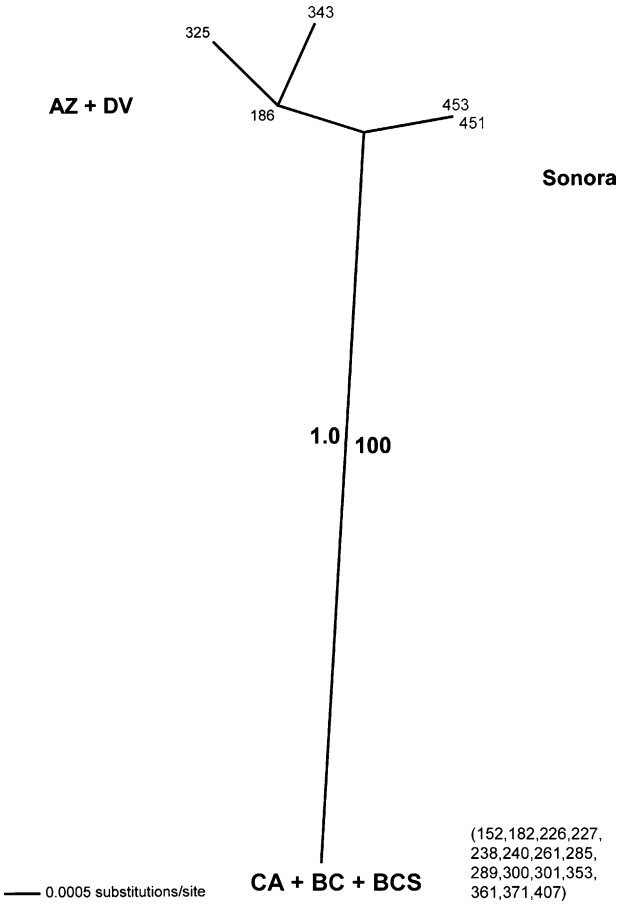

Fig. 4. Consensus phylogram of 51,000 trees sampled from the posterior distribution of the Bayesian analysis of 28S data. Numbers represent bootstrap and Bayesian values. Haplotype numbers correspond to voucher numbers listed in Appendix A.

analysis of male emboli, 82% of the variation was explained by RW1 and RW2. The shape differences between both sexes of the recognized species are statistically significant.

When a statistical test using Hotelling's T^2 was performed on *H. theologus* using northern and southern genetic clades as a priori groups, a significant difference was found in the median apophyses, cymbial processes and RTAs of the males ($p < 0.002$, $p < 0.015$, and $p < 0.006$, respectively), but not in the emboli. However, when this test was performed on the uniform components alone, in order to identify if the differences in shape were due to large- or small-scale changes, the results were not significant. Also, applying a Bonferroni correction procedure to the results of the Hotelling's T^2 test rendered the results of the test no longer significant. It is possible that a difference in sample size could also be responsible for the significant result, as only 18 males were from Baja California Sur, while 61 were from the northern clade.

Table 3
Posterior probabilities of three alternative root placements from the Bayesian midpoint analyses for 16S-ND1 (top) and for the Bayesian clock analysis (bottom)

Gene	E (WN, WS)	WN (E, WS)	WS (E, WN)
16S-ND1	0.9998	0.0001	0
16S-ND1	1.00	0	0

(E, east; WN, western–northern; WS, western–southern).

Significant results were also found in the median and lateral lobes of the epigyna of *H. theologus* females when Hotelling's T^2 was used ($p < 0.001$ and $p < 0.007$). Again, this test was performed on the uniform component alone, and the results were not significant ($p > 0.74$ and $p < 0.26$). Due to this finding, a relative warp analysis with $\alpha = 1$ (more weight placed on partial warps with lower bending energies; emphasis on large-scale changes) was performed with the assumption that in one of the plots some separation should be visible because of the extremely low p values. Although there is considerable overlap, two groups corresponding to the southern Baja clade and the northern Baja clade are apparent in the relative warp plot (Fig. 6). Relative warps 1 and 2 explained 74% and 14% of the variance, respectively. Slight differences are noticeable when the means from the landmarks of both groups were examined, although the largest difference was apparent in landmark 5. If there is a large deviation from the mean in one landmark, GLS superimposition distributes this difference over all the landmarks (Rohlf and Slice, 1990). Therefore, it is possible that one landmark could cause the apparent significant difference of all landmarks between groups. To ensure that this was not occurring, means from a resistant fit superimposition method, which distributes differences in a more uniform manner than Procrustes, were calculated and plotted along with the Procrustes means. This plot (results not shown) suggests that the significant differences observed in the shape of the median lobe are not due to the excessive deviation of one landmark.

4. Discussion

4.1. Continental versus peninsular vicariant events

All datasets reveal a deep phylogenetic split separating the *H. selenopoides* "continental" clade (found predominately east of the Colorado River), from *H. theologus* "peninsular" clades found west and south of the river (Figs. 1, 3 and 4). Similar patterns of phylogenetic divergence have

Table 2
Harmonic means of marginal likelihoods for each gene from Bayesian analyses with and without molecular clock enforced, used to calculate the Bayes factors

Gene	Without clock enforced	With clock enforced	$2 \log_e (B_{10})$	Evidence against H_0
16S-ND1	−7379.06	−7389.91	21.70	Very strong
28S	−1076.87	−1092.76	31.78	Very strong

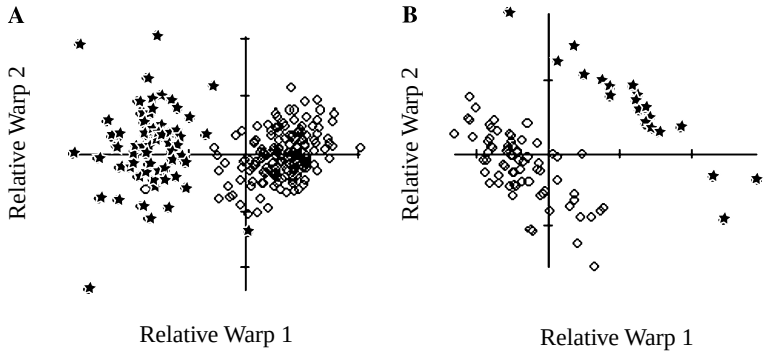

Fig. 5. Plots of the relative warp scores for (A) the median epigynal lobe of females and (B) emboli of the males. Black stars correspond to *H. selenopoides* and white diamonds correspond to *H. theologus*.

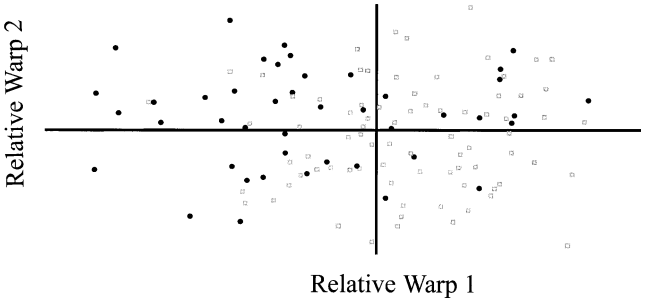

Fig. 6. Plot of relative warp scores of median epigynal lobes of *H. theologus* females with $\alpha = 1$. Filled symbols represent specimens from the northern Baja + California clade and open circles represent specimens from the southern Baja clade.

been observed in many other taxa that inhabit this region. For example, explicit phylogenetic evidence for continental/peninsular divergence has been found in a cactus (Nason et al., 2002), *Drosophila* (Hurtado et al., 2004) and in two rodent species (Riddle et al., 2000b,c). An east/west phylogenetic break across the Colorado River has also been found in the desert tortoise (Lamb et al., 1989), although this species does not extend south along the peninsula. The modern biogeographic influence of the Colorado River appears to vary across taxa. For example, gene flow in desert iguanas and chuckwallas is not impeded by the Colorado River, as identical mtDNA clonal assemblages are found on either side of the river (Lamb et al., 1992). This is in contrast to studies on pocket gophers, in which divergence occurs along a north–south axis paralleling the river, while east–west populations remain the same (Smith and Patton, 1980).

There are multiple events that may have caused east–west divergence in such a large array of taxa. This east–west divergence might correspond to separation of the Baja Peninsula from the mainland and subsequent marine incursion of the Gulf of California, hypothesized to have occurred 12–5 Ma (Gastil et al., 1975; Lonsdale, 1989; Oskin and Stock, 2003). Alternatively, this east–west divergence might reflect an inundation of the Gulf of California that extended north to at least San Gorgonio Pass in Riverside County (Allen, 1957; McDougall et al., 1999). Grismer (1994) and Riddle et al. (2000a) treat this as a single event that occurred 3 Ma, but there is evidence for multiple marine incursions in this region from 14 Ma to <5.2 Ma (Buising, 1990; Durham and Allison, 1960; McDougall, 1998; McDougall et al., 1999). A molecular clock has been used to date the east–west divergence in two groups—Riddle et al. (2000b) use a clock to date divergences in the *Peromyscus eremicus* group, stating that "separations…of East + West *eremicus*…are likely to have occurred within the late Neogene" (5.5–1.8 Ma, their Fig. 9). Lamb et al. (1989) date the east/west tortoise divergence to the middle or late Pliocene (ca. 2–3 Ma). It is not obvious whether these differences in clock estimates reflect variance in the estimates themselves, or alternatively, multiple events occurring at different times.

4.2. Midpeninsular vicariance

A well-supported phylogenetic split separating Baja populations of *H. theologus* is evident from analyses of the mitochondrial data. This division separates California + Baja California (BC) haplotypes from Baja California Sur (BCS) haplotypes. Our findings in *Homalonychus* represent the first conclusive evidence for deep mitochondrial divergence in midpeninsular Baja in an arthropod, and are concordant with findings from several vertebrate taxa. These include side-blotched lizards (Upton and Murphy, 1997), small mammals (Riddle et al., 2000a; Whorley et al., 2004), birds (Zink et al., 2001) and snakes (Rodríguez-Robles and De Jesús-Esco, 2000). It would appear that a major event in the past has caused coincident genetic divergence in many members of this regional fauna. Because this divergence occurs in so many disparate taxa (i.e., both vertebrates and invertebrates), it is perhaps best explained by a single vicariant event, or a series of temporally close events in the same general area. The geographic position, underlying causative factors, and possible timing of this event(s) are discussed below.

The phylogenetic splits seen in the vertebrate and *Homalonychus* mtDNA data occur in slightly different areas of the midpeninsular region, but are all in the vicinity

of the Vizcaíno Desert (28–30° N latitude). In Riddle et al. (2000a), northern haplotypes of some taxa are sometimes found within the range of mostly southern haplotypes, and vice versa, while in other taxa this does not occur. It is not obvious whether northern and southern haplotypes have ever been collected from the same site. Of course, a failure to collect northern and southern haplotypes from the same locality may also reflect within-site sampling insufficiencies. In this study, northern and southern haplotypes were never collected from the same locality. Also, southern haplotypes were never found within the known range of northern haplotypes, and vice versa. The closest sites having the divergent northern and southern haplotypes are from the San Javier Wash region south of Rosario and Calmallí, which are separated by 32 km.

There are several different hypotheses as to what event(s) explain midpeninsular vicariance, including midpeninsular transitions in weather patterns and climate, substrate, and/or a midpeninsular seaway (Grismer, 2000; Upton and Murphy, 1997). A change in substrate or weather patterns seems particularly unlikely to explain vicariance in *Homalonychus*. The distribution of *Homalonychus* spans multiple desert regions that are very different from one another. *Homalonychus* is found almost as far north as the Great Basin desert, throughout the Death Valley, the Colorado Desert, the Mojave Desert, the Peninsular Desert (sensu Riddle et al., 2000a) and the Sonoran Desert. The climatic regime in each of these regions is quite diverse, there are a variety of substrates, and the plant life also differs greatly (Polis, 1991). If weather patterns and/or habitat change were involved in the disruption of gene flow, these differences are certainly not obvious.

Most studies have interpreted phylogeographic breaks in the midpeninsular region as reflecting a midpeninsular seaway dated at approximately 1 Ma (i.e., Riddle et al., 2000a,b; Rodríguez-Robles and De Jesús-Esco, 2000,; Zink et al., 2001). This seaway hypothesis originates from Upton and Murphy (1997, p. 110) who state that "magnetic anomalies associated with the Delfin Basin suggest that the Gulf midriff islands broke away from the peninsula about 1 million years ago (Ma) as a consequence of seafloor spreading (Moore, 1973). Assuming that *Uta antiqua* was isolated on the midriff islands as they were formed (Murphy, 1983), and given its position on the cladogram relative to the peninsular north–south break, we date the formation of the midpeninsular seaway at about 1 Ma." However, more recently, Murphy and Aguirre-Léon (2002) have argued for a general lack of geological evidence supporting a seaway 1 Ma, suggesting that alternative mechanisms, perhaps at different times, may be responsible for midpeninsular vicariance.

Rocks of Pliocene to late Pleistocene age have been found in the midpeninsular regions, but these are thought to be of continental origin (i.e., lacustrine and fluvial conglomerates and sandstones; Barthelmy, 1975). Beal (1948) mentions the presence of shells and suggested this part of the peninsula was recently submerged. However, because of the isolated occurrences and scattering of shells, Barthelmy (1975) attributes their presence to floods from the campsite middens of early humans. It is worth mentioning that volcanism, which would certainly impact local biological components, has been widespread both geographically and temporally in Baja's geological history. For instance, there are more than 2500 km^2 of volcanic rocks in the midpeninsular region from the Sea of Cortéz to the Pacific Coast dated at ages of 10–6 Ma, and continuing in the Tres Vírgenes region until 700 kya (Sawlan and Smith, 1984). Barthelmy (1975) suggests that lava flows in the midpeninsular region resulted from faulting during the lower Pliocene.

Although geological evidence for a midpeninsular seaway at 1 Ma is lacking, this does not preclude the existence of such a seaway at an earlier date. Helenes and Carreño (1999) suggested a midpeninsular seaway during the Miocene, although this is disputed by Oskin and Stock (2003). Also, it has been suggested that a seaway existed from Santa Rosalía to the San Ignacio area 7–2 Ma (Upton and Murphy, 1997), and although Holt et al. (2000) have now found the age of the basin to be around 7 Ma, it clearly had a western margin only a few km west of Santa Rosalía (Wilson, 1948; Wilson and Rocha, 1955). Given this limited western extent, it is doubtful that it would have acted as complete barrier to gene flow. Evidence against a midpeninsular seaway in the past 2 million years comes from the Gulf Escarpment, a series of ranges along the eastern side of the peninsula. The escarpment is a few hundred to a few thousand meters high and probably began forming due to faulting around the initial formation of the gulf as a seaway 8.2–6.5 Ma (Oskin and Stock, 2003; Umhoefer et al., 2002).

An alternative to a single midpeninsular event might be multiple events. The combination global sea level data of Haq et al. (1988) suggests that around 2.75 Ma sea level rose slightly, but at 2.5–2.4 Ma there was a rather large regression (~100 m). Around 2 Ma a slight transgression began, followed by a rather large regression at 1.75 Ma. Once again around 1.5 Ma there was another slight transgression, followed by a very large decrease in sea level 1 Ma. While global sea level data has its merits as giving a general idea of worldwide sea level conditions, it may not provide much resolution on its own. For instance, transgressions and regressions occurring in a particular area may have more to do with local geology, such as uplift and subsidence rates, than eustatic controls alone. Glaciation data recovered from oceanic cores provides rather high resolution, as these cores provide stratigraphic, magnetic, percent $CaCO_3$, and δO^{18} data. Data from Raymo et al. (1989) suggest rather large (causing up to 80 m sea level change) onsets of glaciation at 2.48 Ma, 2.40–2.32 Ma and 2–1.95 Ma. The sea level data suggest that a seaway in central Baja 1 or 1.75 Ma would be less likely than one 2 or 1.5 Ma, although transgressions at this time were very slight. The glaciation data suggest a seaway would be particularly unlikely 2.5–2 Ma. These data suggest that sea level was much lower in the past, but it hasn't been much higher in the past 1–2 Ma than it is now.

In summary, it appears that the original date of a midpeninsular seaway was based on questionable interpretations of geological data combined with limited phylogenetic evidence. However, multiple phylogeographic studies have since accepted this temporal hypothesis at face value, often without critical analysis. We are not suggesting that a vicariance-based earth history hypothesis is necessarily incorrect, as the prevailing patterns seen in the phylogeographic history of so many different taxa probably requires this sort of explanation. However, the geological evidence for a seaway at any time remains elusive, and other geological evidence points to deeper vicariance, perhaps occurring at multiple times in the past. For these reasons, we caution against the unquestioned use of 1 Ma midpeninsular vicariant dates, particularly if extrapolating other dates from this date, and urge researchers to collect additional temporal and geological evidence on this problem.

4.3. Interpreting differences in patterns of divergence

Patterns of divergence and relationships inferred from different types of data (e.g., mtDNA versus nuclear DNA) can disagree, reflecting dissimilarities in modes of inheritance or relative rates of evolution. In *Homalonychus*, three major clades are inferred in analysis of the mtDNA data. These are an 'eastern' clade, a Baja California + California clade and a Baja California Sur clade (Fig. 3). However, analyses of the 28S nuclear DNA gene only reveal two clades, one corresponding to the 'eastern' clade and one consisting of both BC + CA and BCS. The morphological separation of different species seems clear (Fig. 5), but analyses focused on the northern and southern Baja genetic clades of *H. theologus* reveals a pattern of no separation in male genitalia, with some separation in female genitalia (Fig. 6).

Although there are many possible explanations for the different patterns of divergence seen in our data, we view two alternative hypotheses as the most relevant. The first hypothesis involves a midpeninsular barrier that has forced a permanent biological barrier between northern and southern populations. In effect, midpeninsular vicariance has caused speciation. Our ability to detect this speciation event in different data partitions depends upon rates of evolution of these partitions, and the absolute timing of the event. Depending upon the recency of the event, mitochondrial genes may be the only partition expected to reveal divergence. In general, mtDNA in animals evolves faster than nuclear DNA (see Avise, 2000, p. 16 and references therein), and this seems to be the case for the genes used in this study. And although animal genitalia sometimes evolve very rapidly (see Eberhard, 1985), there are numerous spider studies that have revealed deep mitochondrial divergence without coincident divergence in genitalia (e.g., Bond et al., 2001; Hedin, 1997a; Hendrixson and Bond, 2005). Under the permanent barrier hypothesis, the observed patterns in *Homalonychus* are most consistent with relatively recent divergence, as we would expect divergence to accumulate in all data partitions as the absolute timing of the event is pushed deeper in time.

An alternative hypothesis again involves a midpeninsular barrier, but in this case, the barrier has not forced a permanent separation of northern and southern populations. Here, differences in patterns of divergence between data partitions primarily reflect sexual differences in dispersal ability. In particular, if populations have been fragmented historically, and females are relatively sedentary, differences in mitochondrial genes (passed through females) and female genitalia are expected to accrue. General patterns of mtDNA structuring, plus the observation that no mtDNA haplotypes from northern or southern clades were ever collected together, suggest highly limited female dispersal. Also, adult female *Homalonychus* have never been observed wandering and are not known to balloon. On the other hand, if males are mobile relative to females, male-based gene flow may erase any north/south differences that have accrued in either nuclear genes or male genitalia. Male-based gene flow combined with gene conversion (Graur and Li, 2000) might further homogenize rRNA differences. Finally, we note that many adult males have been collected while wandering at night (pers. obs.). These types of biological differences between the sexes are the suspected cause of divergence discordance between allozyme and mtDNA data in the salamander genus *Batrachoseps* (Jockusch and Wake, 2002), where primarily male-mediated gene flow is occurring after primary divergence in allopatry.

Divergence patterns seen in co-distributed taxa may help distinguish the alternatives suggested above. For example, a point of evidence against an old, permanent barrier at the midpeninsula is the general lack of morphologically recognized species divergence seen in this region. Whereas mtDNA evidence reveals a clear signature of divergence between north and south peninsular regions in many taxa, other more noticeable features (e.g., morphology) show few differences. As suggested by Grismer (2000), "there are no species that unequivocally show this pattern of variation based on morphology alone." We note, however, that very few researchers have looked closely for such patterns of variation (for an exception see Riddle et al., 2000b for the *P. eremicus* group). Conversely, a general argument against impermanence is the lack of mitochondrial clade sympatry in other taxa. We do not expect females to be dispersal-limited in all taxa that have been studied. If females are moving and reproducing freely, we would expect mitochondrial clades to overlap and intermingle more often. The fact that we do not see this pattern suggests that more permanent biological barriers have arisen between northern and southern geographic groups. In combination, both a general lack of morphological divergence and mtDNA clade sympatry suggests that midpeninsular vicariance has been both recent and permanent. However, distinguishing whether recent corresponds to one million years ago, versus for example, three million years ago, is still perhaps not possible with these data.

5. Conclusions

The historical biogeography of the desert southwest, and the Baja Peninsula in particular, reflects a complex history of geological and climatic change. One or several such events have caused a pervasive mtDNA phylogeographic break at the midpeninsular region of Baja in a large number of taxa. At the very least, this midpeninsular vicariance has given rise to "evolutionarily significant areas" (see Moritz and Faith, 1998), a novel and significant finding from both a biogeographic and conservation perspective. However, understanding whether or not the reciprocally monophyletic mitochondrial clades recovered in a large number of taxa represent incipient species (recent, permanent barrier not yet reflected in most character systems) versus transient, sex-limited genetic units (impermanent barrier with male-based gene flow) requires additional data. Although we've argued above for a "recent and permanent" scenario, we certainly do not expect the midpeninsular barrier to have had the same biological impact across all taxa of the region. To help clarify this issue, we encourage more coincident or post-hoc analyses of morphological and nuclear DNA data in groups that show midpeninsular mtDNA molecular divergence. In addition, the absolute timing of and geological evidence for midpeninsular vicariance continues to remain elusive. Additional geological study, and application of well-calibrated molecular clocks, may help to resolve this ambiguity.

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Appendix A

Species identity, location number, location information, GenBank accession number and voucher number for all specimens used in the molecular aspect of this study. Location numbers correspond to those shown in Fig. 1.

Species	Location number	Locality	GenBank Accession Nos. 16S + ND1/28S
H. theologus	**1**	NV: Nye CO, 0.25 mi. N of Hwy 95, Specter Range N 36°35′003″ W 116°72′078″	AY955639 (g407), AY955640 (g408), AY959920 (g407—**28S**)
H. theologus	**2**	CA: Inyo CO, Nopah Range, 0.5 miles E of Hwy 178 N 36°08′220″ W 116°10′127″	AY955609 (g417), AY955610 (g418)
H. theologus	**3**	CA: Inyo CO, N of Kingston Range, Smith Talc Rd, 5.1 mi. to fork with Mesquite Valley Rd N 35°47′87″ W 115°59′131″	AY955592 (g80), AY955591 (g95), AY955593 (g371), AY959902 (g371—**28S**)
H. theologus	**4**	NV: Clark CO, 0.7 miles E of Hwy 161, 3.6 miles NE of Jean N 35°48′901″ W 115°22′487″	AY955638 (g365), AY955637 (g405), AY955636 (g406)
H. theologus	**5**	CA: San Bernardino CO, Kingston Road, E of Winter's Pass N 35°43′290″ W 115°41′206″	AY955594 (g81)
H. theologus	**6**	NV: Clark CO, SE of Hwy 95, E side of El Dorado Mountains N 35°47′159″ W 114°51′520″	AY955633 (g163), AY955634 (g164), AY955635 (g289), AY959910 (g289—**28S**)
H. theologus	**7**	CA: San Bernardino CO, East Mojave National Scenic Area, Von Trigger Hills N 35°04″ W 115°09″	AY955630 (g132)
H. theologus	**8**	CA: San Bernardino CO, Highway 95, 5.9 miles S of Needles @ 5 mile Station Rd N 34°41′089″ W 114°36′943″	AY955605 (g133), AY955604 (g134), AY955608 (g138), AY955606 (g159), AY955607 (g293)

(*continued on next page*)

Appendix A (*continued*)

Species	Location number	Locality	GenBank Accession Nos. 16S + ND1/28S
H. theologus	**9**	CA: San Bernardino CO, Rasor Road, off I-15 N 35°08′183″ W 116°02′529″	AY955623 (g97), AY955624 (g178), AY955625 (g297)
H. theologus	**10**	CA: San Bernardino CO, Pisgah Lava Flow, ~1 mi. down Pisgah Crater Rd N 34°45′919″ W 116°22′722″	AY955588 (g167), AY955590 (g290), AY955589 (g338)
H. theologus	**11**	CA: San Bernardino CO, Granite Mtns, 0.7 mi. off Kelbaker Rd N 34°44′158″ W 115°40′892″	AY955584 (g411), AY955585 (g412)
H. theologus	**12**	CA: San Bernardino CO, 1 mi. N of Earp, off Parker Dam Road N 34°10′924″ W 114°18′023″	AY955580 (g143), AY955582 (g146), AY955581 (g158), AY955583 (g110)
H. theologus	**13**	CA: San Bernardino CO, east Kelbaker Road N 34°42′392″ W 115°40′487″	AY955621 (g144), AY955620 (g179), AY955622 (g396)
H. theologus	**14**	CA: San Bernardino CO, S of 29 Palms, Rocky Road, W of Utah Street N 34°06′632″ W 116°02′529″	AY955629 (g135), AY955628 (g294), AY955627 (g295)
H. theologus	**15**	CA: Riverside CO, Whitewater Canyon N 33°56′455″ W 116°38′427″	AY955631 (g413)
H. theologus	**16**	CA: Imperial CO, Milpitas Wash Rd, 0.7 mi. W of Hwy 78 N 33°17′048″ W 114°47′536″	AY955595 (g98), AY955596 (g105), AY955597 (g171)
H. theologus	**17**	CA: Riverside CO, E side of Chuckwalla Mountains N 33°37′247″ W 115°18′405″	AY955579 (g137), AY955578 (g348), AY955577 (g369)
H. theologus	**18**	CA: Riverside CO, Cactus City, 11 miles W of Chiriaco Summit, off I-10 N 33°40′305″ W 115°54′955″	AY95557 (g96), AY955568 (g131), AY955569 (g140), AY955571 (g191)
H. theologus	**19**	CA: San Diego CO, Anza Borrego Desert SP, 1 mi. W jnct. Rockhouse and Butler Cyn N 33°23′641″ W 116°22′491″	AY955562 (g153), AY955563 (g154), AY955560 (g155), AY955561 (g157)
H. theologus	**20**	CA: San Diego CO, Hwy 76, 4.2 miles W of Nate Harrison Grade Rd N 33°21′590″ W 117°02′543″	AY955601 (g340), AY955602 (g394), AY955603 (g395)
H. theologus	**21**	CA: San Diego CO, Anza Borrego Desert State Park, NE of Hayden Springs N 32°42′670″ W 116°06′961″	AY955567 (g420), AY955566 (g421)
H. theologus	**22**	CA: Imperial CO, Picacho, 4.8 mi. N of All American Canal N 32°51′520″ W 114°38′483″	AY955617 (g148), AY955616 (g180), AY955618 (g188)
H. theologus	**23**	CA: Imperial CO, Picacho, 11.5 miles S of All American Canal N 32°57′016″ W 114°37′914″	AY955615 (g156)
H. theologus	**24**	CA: Imperial CO, Picacho, jnct. of Picacho Road and No Name Wash N 32°55′133″ W 114°38′542″	AY955619 (g182), AY959915 (g182—**28S**)
H. theologus	**25**	CA: San Diego CO, Mission Trails Regional Park, Kwaay Paay Peak N 32°49′732″ W 117°02′543″	AY955598 (g189), AY955599 (g287), AY955600 (g353), AY959909 (g353—**28S**)
H. theologus	**26**	CA: Imperial CO, Yaqui Pass N 33°15′ W 116°35′	AY955564 (g147), AY955565 (g392)
H. theologus	**27**	CA: San Diego CO, Anza Borrego Desert State Park, 1 mile N of Harper Canyon N 33°07′437″ W 116°15′029″	AY955632 (g410)
H. theologus	**28**	CA: Imperial CO, Sidewinder Road, 5 mi. N of I-8, below Pasadena Mountain N 32°47′255″ W 114°45′793″	AY955626 (g16)
H. theologus	**29**	CA: Imperial CO, W side Cargo Muchacho Mtns, Ogilby Road, 9.5 mi. N jnct. with I-8 N 32°54′394″ W 114°50′339″	AY955574 (g99), AY955572 (g100), AY955573 (g103), AY955575 (g177), AY955576 (g184)
H. theologus	**30**	CA: Imperial CO, Ocotillo, S S2 and Shell Canyon Rd N 32°46′547″ W 116°00′432″	AY955612 (g17), AY955611 (g18), AY955613 (g19), AY955614 (g152), AY959915 (g152—**28S**)
H. theologus	**31**	CA: San Diego CO, Jamul, Barrett Junction, N of Hwy 94 N 32°37′212″ W 116°43′650″	AY955586 (g391), AY955587 (g450)
H. theologus	**32**	Mex: BC: Mex Hwy 5, 6 mi. S of La Ventana N 31°42′627″ W 115°03′020″	AY955650 (g299), AY955651 (g448)
H. theologus	**33**	Mex: BC: 19 miles S of San Vicente on Mex Hwy 1 N 31°06′845″ W 116°09′260″	AY955657 (g378), AY959922 (g301), AY959916 (g301—**28S**)

Appendix A (*continued*)

Species	Location number	Locality	GenBank Accession Nos. 16S + ND1/28S
H. theologus	**34**	Mex: BC: Sierra San Felipe, W of Sierra Abandonada N 31°03′588″ W 114°57′352″	AY955662 (g440), AY959912 (g238—**28S**)
H. theologus	**35**	Mex: BC: 7 mi. S of Puertocitos N 30°15′24″ W 114°39′925″	AY955652 (g200), AY955655 (g202), AY955653 (g207)
H. theologus	**36**	Mex: BC: Hwy 1 road to San Judas N 30°01′852″ W 114°34′515″	AY955654 (g199), AY955656 (g227), AY959901 (g227—**28S**)
H. theologus	**37**	Mex: BC: 11.2 miles E of El Rosario N 30°03′404″ W 115°34′693″	AY955646 (g237), AY955647 (g379)
H. theologus	**38**	Mex: BC: 4 miles W of Cataviña N 29°46′317″ W 114°45′74″	AY955644 (g350), AY955645 (g377)
H. theologus	**39**	Mex: BC: Mex Hwy 1, 6 mi. S of Laguna Chapala N 29°19′872″ W 114°18′460″	AY955648 (g217), AY955649 (g444)
H. theologus	**40**	Mex: BC: Mex Hwy 1, 4.9 miles S of jnct with road to Bahia de Los Angeles N 28°58′687″ W 114°09′708″	AY955641 (g380), AY955642 (g438), AY955643 (g439)
H. theologus	**41**	Mex: BC: Mex Hwy 1, 0.5 miles S of jnct. of road to Santa Rosalillita N 28°43′355″ W 114°05′753″	AY955660 (g197), AY955659 (g442), AY955661 (g443)
H. theologus	**42**	Mex: BC: Rancho Esperanza N 28°14′ W 113°28′	AY955689 (g122)
H. theologus	**43**	Mex: BC: S of Rosarito, San Javier Wash N 28°33′ W 114°02′	AY955658 (g196)
H. theologus	**44**	Mex: BC: Mesa La Frutilla N 28°13′ W 113°31′	AY955681 (g212)
H. theologus	**45**	Mex: BC: Rancho Datilas exit N 28°11′ W 113°34′	AY955688 (g211), AY955686 (g213), AY955687 (g236)
H. theologus	**46**	Mex: BC: Rancho Mesquital N 28°17′00″ W 113°48′00″	AY955690 (g156)
H. theologus	**47**	Mex: BC: near Pozo Aleman N 28°03′ W 113°23′	AY955685 (g329)
H. theologus	**48**	Mex: BC: Calmallí N 28°07′ W 113°25′	AY955666 (g214), AY955667 (g215), AY959903 (g300), AY959903 (g300—**28S**)
H. theologus	**49**	Mex: BC: El Arco Road, 22.3 miles E of Mex Hwy 1 N 27°59′818″ W 113°27′079″	AY955669 (g230)
H. theologus	**50**	Mex: BCS: road to Sierra San Francisco N 27°29′397″ W 113°11′290″	AY959899 (g243), AY959900 (g261), AY959917 (g261—**28S**)
H. theologus	**51**	Mex: BCS: 11 miles W of Las Virgenes N 27°22′872″ W 112°40′721″	AY955674 (g235)
H. theologus	**52**	Mex: BCS: 5 mi. S of San Lucas, S of Santa Rosalia N 27°11′372″ W 112°12′312″	AY959897 (g219), AY959898 (g232)
H. theologus	**53**	Mex: BCS: Mex Hwy 1, 5 mi. N of Playa Armenta N 26°39′849″ W 111°52′956″	AY955684 (g201)
H. theologus	**54**	Mex: BCS: 6.5 miles N of Loreto N 26°04′834″ W 111°23′531″	AY955675 (g224), AY955676 (g240), AY955677 (g241), AY959911 (g240—**28S**)
H. theologus	**55**	Mex: BCS: N of Agua Verde N 25°33′247″ W 110°09′310″	AY955663 (g222), AY955664 (g239)
H. theologus	**56**	Mex: BCS: 11 miles E of Mex Hwy 1 on road to Mission San Luis Gonzaga N 24°57′800″ W 111°27′360″	AY955682 (g229)
H. theologus	**57**	Mex: BCS: 8 mi. N San Juan de la Costa, road to Bahia Coyote N 24°27′727″ W 110°47′032″	AY955691 (g226), AY959896 (g333), AY959913 (g226—**28S**)
H. theologus	**58**	Mex: BCS: 1 mile NE of Pichelingue N 24°17′426″ W 110°19′187″	AY955683 (g231)
H. theologus	**59**	Mex: BCS: 2 miles NW of El Triunfo N 23°47′062″ W 110°07′339″	AY955673 (g194), AY955671 (g223), AY955672 (g225), AY955670 (g285), AY959918 (g285—**28S**)
H. theologus	**60**	Mex: BCS: 2.5 miles N of Los Barriles N 23°43′613″ W 109°42′526″	AY955678 (g220), AY955680 (g228), AY955679 (g242)

(*continued on next page*)

Appendix A (*continued*)

Species	Location number	Locality	GenBank Accession Nos. 16S + ND1/28S
H. theologus	**61**	Mex: BCS: Mex Hwy 19, S of Todos Santos N 23°01′653″ W 110°04′893″	AY959894 (g198), AY959895 (g206)
H. theologus	**62**	Mex: BCS: 2 miles N of Mex Hwy 1, 10.7 miles E of Cabo San Lucas at Hwy 19 N 22°58′514″ W 109°50′011″	AY955665 (g361), AY959919 (g361—**28S**)
H. selenopoides	**63**	CA: Inyo CO, Death Valley NP, vic. Scotty's Castle N 37°01′998″ W 117°18′588″	AY955501 (g414), AY955502 (g415)
H. selenopoides	**64**	CA: Inyo CO, Death Valley NP, Saline Valley Rd, Grapevine Cyn, S end of Saline Valley N 36°33′844″ W 117°35′482″	AY955499 (g362), AY955500 (g397)
H. selenopoides	**65**	CA: Inyo CO, Death Valley NP, E of Salsberry Gap N 35°56′962″ W 116°24′798″	AY955498 (g341), AY955496 (g342), AY955497 (g343), AY959905 (g343—**28S**)
H. selenopoides	**66**	AZ: Coconino CO, Grand Canyon NP, above Whitmore Rapid - south beach N 36°52′00″ W 111°32′00″	AY955519 (g94)
H. selenopoides	**67**	AZ: Mohave CO, jnct of Hwy 93 and Willow Beach Road N 35°57′118″ W 114°38′990″	AY955550 (g160), AY955551 (g169), AY955549 (g173)
H. selenopoides	**68**	AZ: Mohave CO, 1 mile down Arroyo Vista, off Bullhead City Parkway, E of Hwy 95 N 35°02′993″ W 114°34′143″	AY955506 (g165), AY955507 (g193), AY955508 (g402)
H. selenopoides	**69**	AZ: Mohave CO, NE side of Mohave Mountains N 34°35′901″ W 114°11′171″	AY955534 (g22), AY955535 (g23), AY955533 (g24)
H. selenopoides	**70**	AZ: Mohave CO, S of Wickieup, 2.7 miles from Hwy 93, Burro Creek Crossing Rd N 34°36′449″ W 113°28′921″	AY955547 (g161), AY955546 (g186), AY955548 (g288) AY959906 (g186—**28S**)
H. selenopoides	**71**	AZ: La Paz CO, Hwy 72, 6.6 miles from junction with Hwy 95 N 33°59′632″ W 114°06′070″	AY955525 (g82)
H. selenopoides	**72**	AZ: La Paz CO, 9 miles S of Parker, W of Hwy 92, Bouse Wash N 34°00′627″ W 114°15′430″	AY955538 (g176)
H. selenopoides	**73**	AZ: Yavapai CO, Constellation N 34°00′261″ W 112°39′012″	AY955509 (g172)
H. selenopoides	**74**	AZ: La Paz CO, Eagletail Mountains, S of I-10, ~5 miles down Palomas-Harquahala Rd N 33°32′574″ W 113°33′698″	AY955516 (g174), AY955517 (g346), AY955518 (g359)
H. selenopoides	**75**	AZ: La Paz CO, W side of Dome Rock Mountains, 2.5 miles SE I-10 @ Tom Wells jnct N 33°36′775″ W 114°23′907″	AY955512 (g101), AY955511 (g102), AY955510 (g136), AY955514 (g166), AY955513 (g170), AY955515 (g281)
H. selenopoides	**76**	AZ: Yuma CO, Kofa NWR, road to Palm Canyon N 33°22′604″ W 114°11′038″	AY955528 (g149), AY955527 (g151), AY955526 (g192)
H. selenopoides	**77**	AZ: Yuma CO, 1 mile SE Hidden Shores RV Village, off Imperial Dam Road N 32°52′590″ W 114°27′139″	AY955522 (g139), AY955524 (g150), AY955523 (g375)
H. selenopoides	**78**	AZ: Maricopa CO, N side of Maricopa Mountains Wilderness, on Butterfield Trail N 33°01′575″ W 112°29′364″	AY955529 (g15), AY955531 (g141), AY955530 (g142), AY955532 (g190)
H. selenopoides	**79**	AZ: Yuma CO, I-8 @ Tacna exit, 0.25 mi. S on Tacna Rd N 32°41′307″ W 113°57′204″	AY955542 (g21)
H. selenopoides	**80**	AZ: Yuma CO, Mohawk Mountains, off I-8 @ Ave 52 E / Old Highway 80 N 32°42′826″ W 113°44′334″	AY955536 (g347), AY955537 (g403)
H. selenopoides	**81**	AZ: Pima CO, Growler Mountains, Charlie Bell Pass Rd N 32°23′682″ W 113°04′722″	AY955520 (g324), AY955521 (g401)
H. selenopoides	**82**	AZ: Pima CO, Tucson Mountains N 32°12′005″ W 111°07′003″	AY955544 (g168), AY955543 (g344), AY955545 (g399)
H. selenopoides	**83**	AZ: Pima CO, Organ Pipe Cactus NM, Alamo Canyon Cmpgrd N 32°04′304″ W 112°43′673″	AY955504 (g284), AY955503 (g325), AY955505 (g400), AY959904 (g325—**28S**)

Appendix A (*continued*)

Species	Location number	Locality	GenBank Accession Nos. 16S + ND1/28S
H. selenopoides	**84**	AZ: Pima CO, Organ Pipe Cactus NM, Quitobaquito Hills N 31°56′517″ W 113°00′832″	AY955539 (g185), AY955541 (g283), AY955540 (g345)
H. selenopoides	**85**	Mex: Sonora: 25 miles SW of Sonoita, on Mex Hwy 8 N 31°41′485″ W 113°15′811″	AY955554 (g452)
H. selenopoides	**86**	Mex: Sonora: 34.2 mi. N of Caborca on Mex Hwy 2 N 31°10′376″ W 112°27′445″	AY955553 (g454), AY955552 (g460)
H. selenopoides	**87**	Mex: Sonora: 19.7 mi. NW of Santa Ana on Mex Hwy 2 N 30°35′152″ W 111°27′810″	AY955556 (g453), AY955555 (g459), AY959908 (g453—**28S**)
H. selenopoides	**88**	Mex: Sonora: W of San Carlos N 27°59′990″ W 111°07′953″	AY955559 (g451), AY955558 (g455), AY955557 (g458), AY959907 (g451—**28S**)

Appendix B. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ympev.2005.11.010.

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