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The Golfo Dulce yellow sea snake (Elapidae: *Hydrophis platurus xanthos*) from morphological vs molecular perspectives

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ABSTRACT

The yellow sea snake *Hydrophis platurus xanthos* is found only in Costa Rica's south-Pacific embayment of Golfo Dulce, confined to a <215-m deep inner basin. This endemic population is geographically separated from the pelagic sea snake *H. platurus platurus* by >20 km and has distinctive morphological characters suggesting potential phylogenetic divergence. Our study confirms morphological diagnosability of the Golfo Dulce population using coloration (predominantly yellow versus dorsally black) and consistently small body size (<60 cm in total length). Several significant differences in cephalic and caudal scale counts are also documented. Seven preserved yellow specimens collected outside Golfo Dulce in the 1970s are morphologically consistent *H. p. xanthos* suggesting they originated from inside the gulf. Despite this, when we use reduced representation sequencing to examine single-nucleotide polymorphisms, targeted squamate conserved loci, and mined mitochondrial DNA, our molecular analyses provide no evidence that *H. p. xanthos* and *H. p. platurus* are separately evolving lineages. Indeed, we find near-complete lack of structure both within and between these populations. The absence of genetic differentiation, which suggests regular gene flow despite contrary morphological and biogeographic factors, creates an intriguing paradox. Recent separation and/or high selection pressure may be in effect.

Keywords: Central America; Costa Rica; DArTseq; marine reptile; mtDNA; morphology; phylogeography; SqCL; xanthic coloration

INTRODUCTION

The Golfo Dulce yellow sea snake *Hydrophis platurus xanthos* Bessesen & Galbreath 2017 (hereafter the yellow sea snake) has been described as a subspecies of the widely distributed pelagic sea snake *H. platurus* (Fig 1A; hereafter the pelagic sea snake). We use recognized trinomials for the purpose of comparing these morphologically distinct geographical populations but note that some authors here do not recognize subspecies as a valid taxonomic rank (see Burbrink *et al.* 2022). The yellow sea snake inhabits the narrow inlet of Golfo Dulce on the south-Pacific side of Costa Rica (Solórzano 2011, Bessesen 2012; Fig. 1B). Golfo Dulce is considered a 'tropical fjord' because its mesopelagic inner basin has limited exchange with the coastal masses (Wolff *et al.* 1996), and the yellow sea snake is confined to that inner basin (Bessesen 2012, 2015, 2022, Solórzano & Sasa 2024, Lillywhite 2025) where a calm, estuarian circulation pattern prevails (Svendsen *et al.* 2006). Inhabiting a single area of occupancy <260 km^2 (Bessesen *et al.* 2023; Fig. 1C), this endemic population is estimated at <30,000 individuals (Bessesen *et al.* 2022). Importantly, it is geographically separated from the pelagic sea snake population by a greater than 20-km spatial gap (Bessesen 2012, 2022) characterized by shallow waters (≤30 m) and a complicated current structure (Svendsen *et al.* 2006, Morales-Ramírez *et al.* 2015).

Habitat partitioning suggests allopatric distribution, and the yellow sea snake is distinct in both appearance and ecology (Lillywhite *et al.* 2015, Bessesen & Galbreath 2017, Bessesen & Gonzalez-Suarez 2022, Bessesen *et al.* 2023). In addition to its xanthic coloration (predominantly yellow, lacking a solid black dorsum), a significant reduction in body size has been documented; notably, no yellow sea snake was found to reach the sexually mature length of the pelagic sea snake (Bessesen & Galbreath 2017) reported as ≥60 cm (Kropach 1975, Vallarino & Weldon 1996). Environmental conditions may have contributed to these phenotypic changes, as water temperatures in Golfo Dulce are 2–4 °C higher than in the open ocean (Rincon-Alejos & Ballestero-Sakson 2015, Bessesen *et al.* 2023). Pale integument has been proposed to help the yellow sea snake reduce overheating at the water surface (Solórzano 2011, Bessesen 2012), and smaller body size would allow the serpent to shed heat more readily (Bessesen & Galbreath 2017). Lighter coloring, however, could also lead to photosensitivity. The yellow sea snake evinces a nocturnal diel pattern, which is in direct contrast to the diurnal pattern of the pelagic sea snake (Bessesen & González-Suárez 2022). Feeding at night seems to require a higher tolerance for evening wave activity, and while the pelagic sea snake actively avoids rough waters (Rubinoff *et al.* 1986, Cook & Brischoux 2014), the yellow sea snake is commonly found in turbulent conditions (Beaufort wind force 3–4), assuming a unique sinusoidal ambush posture that appears to have a stabilizing effect in the waves (Bessesen & Galbreath 2017). It also shows no association with drift lines (Lillywhite *et al.* 2015, Bessesen 2022), which are commonly used by pelagic sea snakes for transport, feeding, and possibly reproduction (Kropach 1973, 1975). Visual cues are thought to play a role in drift line detection among pelagic sea snakes (Brischoux & Lillywhite 2011). Hence, the yellow sea snake's disassociation with drift lines may relate to its nocturnal feeding strategy as visibility is naturally inhibited at night (Bessesen 2022).

Given the conspicuous differences in morphology and ecology between the yellow and pelagic sea snakes, we considered the possibility that they could be separate species (Mayr 1942, De Queiroz 2007). The present paper addresses this by examining evidence of divergence through morphological and molecular approaches. First, we examined both live and vouchered museum specimens to compare morphology. We further sought to determine the geographic origin of yellow sea snakes recorded off the coast of Central America. Voris *et al.* (1970) and Kropach (1971) were the first to report yellow sea snakes; the latter found 3% of the snakes collected outside the mouth of Golfo Dulce to be yellow. Additional researchers documented yellow sea snakes in the Pacific waters off Central America, though frequencies dropped precipitously the farther from Golfo Dulce they worked. For example, in northern Costa Rica, Tu (1976) collected 3077 sea snakes and found only four (0.1%) yellows, while farther to the south Kropach (1971) spotted one yellow snake among the tens of thousands of pelagic sea snakes recorded in Panama Bay. When the Golfo Dulce population was identified, it was hypothesized that yellow specimens seen in the open Pacific (hereafter '1970s specimens') may have been swept out from the embayment (Bessesen 2015).

We also undertook comparative molecular analyses of contemporary specimens using nuclear and mitochondrial DNA (mtDNA) to test for structure between populations. Within the rapidly radiating *Hydrophis* clade, low variability of molecular markers can make gene trees challenging to resolve (Lukoschek & Keogh 2006, Rasmussen 2011, Sanders *et al.* 2013), but when examining allele frequencies across spatial gradients, a pattern of isolation-by-distance is often expected to emerge, whereby genetic similarity decreases as spatial distance increases (Wright 1943). Given our study species' enormous east-west range from the east coast of Africa to the west coast of the Americas (Hecht *et al.* 1974, Lillywhite *et al.* 2018), we anticipated finding shallow geographical variation across its oceanic distribution but with more genetic changes attributed to the Golfo Dulce endemic, *H. p. xanthos*, possibly supporting a species designation.

METHODS & MATERIALS

Morphological analyses

From 2017 to 2024, we conducted physical examinations of 124 yellow sea snakes from the inner basin of Golfo Dulce, including 93 free-ranging individuals briefly captured by net from a boat, and 31 preserved specimens at the Zoological Museum of University of Costa Rica (UCR 20612, 20614–16, 20618–19, 20648–49, 20677, 20691, 20817–18, 20836–37, 20840, 21575, 21577, 21881, 21883, 21886, 21889, 21970, 21975–76, 21978, and six yet-uncatalogued specimens). Following Bessesen and Galbreath (2017), we recorded measurements of weight (WT), girth (circumference at thickest point), total length (TL; using the string technique), tail length (against a measuring stick) and paddle height (using calipers). We removed six particularly small (<38 cm TL) specimens from analyses of weight, girth, length and tail dimensions to avoid possible age-related statistical bias. Because formalin and ethanol are known to cause dehydration in preserved squamate specimens (Vervust *et al.* 2009), we focused only on live weights for analysis. For cephalic scale counts (preoculars, postoculars, anterior temporals, supralabials, and infralabials), we followed Smith (1926). We counted ventral scales (atlas-axis to cloaca, excluding vent shield) and subcaudal scales (vent to tip) per Dowling (1951). Following Rasmussen *et al.* (2014), scale rows (not including ventral scales) were counted ≤4 times around the neck (narrowest point), around the midbody (thickest point), and vertically across the flattened mid-paddle (unilaterally). On live snakes, scales were counted using high-resolution photography and employing a system of red marks arranged on the skin in situ.

For comparison, we examined a total of 229 pelagic sea snakes from outside Golfo Dulce. Of those, 25 were live snakes captured and released following measurements of weight and TL. The remaining pelagic specimens came from institutional collections, including the Field Museum of Natural History (FMNH 9774–75, 16736, 16923–26, 41590, 69768, 79982–85, 97693, 105089, 140155, 140157, 142966, 154857, 154862, 154864–65, 154869, 154872–73, 154886–87, 163200, 163213, 165284, 171579–87, 171589–602, 171604–09, 171611–12, 171614–27, 171629–41, 171643–49, 171651–64, 171666–73, 171675–87, 171689–704, 213669); Australian Museum (AMS 314, 1604, 3154, 3187, 3291, 3791, 3828, 4164, 4283, 6750, 7032, 8944, 8979, 9270, 9316, 10502, 13139, 13766, 13811, 15028, 16862, 19101, 44530, 45813, 92314, 107164, 178108, 178305, 188315–20, 202225–30, 202301, 202878, and one uncatalogued specimen); University of Colorado Museum of Natural History (UCM 58903–58907, 58909); Natural History Museum of Denmark (ZMK R66143); Arizona State University Natural History Collections (ASUHEC 2617, 29264); and two uncatalogued specimens preserved at Osa Conservation's Piro Research Station in Costa

Rica. A majority of pelagic specimens (n=135) were collected in Costa Rica; of those, 67% (n=90) were found near the mouth of Golfo Dulce, making them proximate neighbors to *H. p. xanthos*. As with the yellow sea snakes, specimens <38 cm TL (n=39) were removed from size-related analyses.

Finally, we examined seven 1970s specimens, all exhibiting xanthic coloration, from FMNH (171603), UCM (58900-58902, 58907), American Museum of Natural History (AMNH 106682), and United States National Museum of Natural History (USNM 192279). On a few of the 1970s specimens (n=4) and pelagic sea snakes (n=4) we examined rib/vertebrae counts and heart placement using radiographic techniques (Rasmussen 1989). All excepting one 1970s specimen had a metal pin marking the location of the heart, which allowed counts from atlas-to-heart to determine heart placement along the vertebral column; we also counted caudal vertebrae.

Descriptive statistics were generated in R version 4.2.1 (R Core Team 2022). We compared continuous variables between populations using Welch Two Sample t-tests (t.test function in base R), and frequencies of categorical variables (i.e., having one or more supralabials in contact with the ocular orbit) using Pearson's Chi-squared tests (chisq.test function in base R) with a Yates’ continuity correction. To control the increased familywise error rate caused by multiple comparisons we applied a False Discovery Rate (FDR) correction (Benjamini & Hochberg 1995, Pike 2011).

Molecular analyses

In 2023, we collected tissue samples (tail biopsies) from 50 yellow sea snakes and 25 pelagic sea snakes briefly captured from adjacent populations in the inner basin and immediately outside Golfo Dulce, respectively. Collection of yellow sea snakes was limited to the densest 34-km^2 portion of their range, while pelagic sea snake collection occurred within 79 km^2;

there was a spatial gap of 33 km between collection areas. Samples were stored in 95% ethanol. We extracted DNA following the DNeasy Blood and Tissue Kit (Qiagen) protocol and quantified the extracts using a Quantus fluorometer to obtain >500 ng of DNA at concentrations of 50 ng/ml. Samples were concentrated using a Centrivap DNA concentrator, if required, and checked for quality using gel electrophoresis. The DNA extractions for each of the two sequencing processes described below were done separately but with identical protocols.

For Diversity Arrays Technology sequencing (DArTseq), we aggregated genetic samples for 27 yellow and 21 pelagic sea snakes from Costa Rica with 15 additional pelagic specimens obtained at various locations across the Indo-West Pacific (IWP, which ranges from Sri Lanka to the East Coast of Australia) and the United Arab Emirates (UAE; see Supplementary Material, Table S1). The samples were sent to Diversity Arrays Technology Pty Ltd (Canberra, Australia) where SNP genotyping was conducted using a proprietary genome complexity reduction pipeline with a pair of restriction enzymes (PstI and HpaII; Kilian *et al.* 2012, Georges *et al.* 2018). After initial digestion/ligation reactions and amplification, samples were sequenced on an Illumina HiSeq 2500. A third of samples were sequenced a second time for use as technical replicates. We obtained raw demultiplexed reads from DArTseq, which we checked for quality using FastQC (Andrews 2010), then filtered out adaptors and quality trimmed the reads using BBduk (Bushnell 2014). We filtered out potential microbial and human contamination using Kraken2 (Lu *et al.* 2022). We then assembled loci and called SNPs using iPYRAD v.0.9.85 (Eaton & Overcast 2020) run on the University of Adelaide Phoenix HPC. Filtered and demultiplexed reads were assembled de novo, setting the cluster threshold to 0.90, mindepth (statistical and majority rule) to 5 and maxdepth to 10000. We retained 1 SNP per RAD locus to reduce the effects of linkage, using the --thin command in vcftools (Danecek *et al.* 2011).

We used two datasets for SNP population genetic analyses: Dataset 1 included 54 samples from across the full range of the study species *H. platurus* with no missing loci (n = 498), while Dataset 2 included 43 samples from the adjacent Costa Rican populations with 614 unlinked loci. We generated Principal Component Analysis (PCA) plots using the SNP data for each grouping separately. Using the Hierfstat package (Goudet 2005) in R, we estimated observed (Ho) and expected (He) heterozygosity and F-statistics (F_{IS}: inbreeding coefficient; F_{ST}: the proportion of differentiation due to genetic structure).

For target sequence capture, samples for 15 yellow and nine pelagic sea snakes from Costa Rica (Table S1) underwent library preparation for sequence capture at Daicel Arbor Biosciences (Ann Arbor, MI, USA). Samples were optimized for capture using the SqCL v2 probe set (Singhal *et al.* 2017), which targets ultra conserved elements (UCE; Faircloth *et al.* 2012), Anchored Hybrid Enrichment (AHE; Lemmon *et al.* 2012), and other traditional squamate loci (Singhal *et al.* 2017). Sequencing was conducted on an Illumina Hi-Seq platform. For outgroups, we downloaded raw SqCL sequences from the National Center for Biological Information (NCBI) Sequence Read Archive (dataset: Hills & Singhal 2023) via the SRA toolkit v. 3.1.0: *Hydrophis kingii* (SRR23022445), *Hydrophis macdowelli* (SRR23022444), *Aipysurus duboisii* (SRR23022465), *Emydocephalus annulatus* (SRR230224499) and *Laticauda colubrina* (SRR23022443). After raw reads were cleaned using illumiprocessor (Faircloth 2013) and trimmed with trimmomatic (Bolger *et al.* 2014), contigs were assembled using SPades (Prjibelski *et al.* 2020) with default parameters. We then matched our contigs to the SqCL v2 probe set (Singhal *et al.* 2017) and aligned them using MAFFT v. 1.5.0 (Katoh *et al.* 2002). We processed all the data in PHYLUCE v. 1.7.3 (Faircloth 2016) run on the Field Museum Grainger Bioinformatics Center Phoebe HPC. A concatenated file with the data matrix at 95% completeness was used to estimate a gene tree in IQ-TREE v.2 (Minh *et al.* 2020). The pipeline was then rerun with only Costa Rica's adjacent populations to make a species-specific network in SplitsTree4 v. 4.19.2 (Huson & Bryant 2006).

To mine mtDNA, we used Geneious Prime v.2024.0.3 (https://www.geneious.com) with default settings. We imported raw paired (forward and reverse) fastq target-capture reads and trimmed those reads using BBduk v. 38.84 (Bushnell 2014). We then imported our raw trimmed DArTseq reads, including technical replicates. From the National Center for Biological Information (NCBI) GenBank database, we downloaded a complete mitogenome for *H. platurus* (MK775530 from S. Korea, 18,101 bp; Kim *et al.* 2020), and setting it as the reference genome in the Map to Reference tool in Geneious, we independently mapped each sample. For any snake that was sequenced for both DArTseq and target capture and/or had replicate DArTseq sequences, we aligned those and generated an individual consensus sequence (with the 'Highest Quality' setting). Four mapped sequences were removed from further analysis due to insufficient data, resulting in a final mtDNA dataset of 33 yellow and 20 pelagic sea snakes (Table S1). Using MAFFT in the Multiple Align tool (default settings), the mapped sequences were then aligned with the reference genome, as well as several other complete sea snake mitochondrial genomes downloaded from NCBI GenBank to serve as outgroups: *H. curtus* (MT712129; Zhang & Yan 2020), *H. melanocephalus* (MK775532; Yi *et al.* 2020), *H. ornatus* (NC_066233; Xiaokaiti *et al.* 2022), *Aipysurus eydouxii* (NC_062614; NCBI Genome Project), *Emydocephalus ijimae* (MK775531, Yi *et al.* 2019) and *Laticauda colubrina* (NC_036054; NCBI Genome Project). A gene tree was generated using RAxML v. 8 (Stamatakis 2014; default settings) and rooted with *Laticauda colubrina* (Fig. 5).

RESULTS

Morphology

All 124 yellow sea snakes from the inner basin of Golfo Dulce are predominantly yellow. Signs of melanin are not entirely absent though, as most have one or more tiny black dots or specks located on the body or head, often near the supraocular and/or parietal scales (Fig. 2A). Only seventeen (14%) have marks >1 cm on the body, including some with narrow dorsal dashes (Fig. 2B) and one with a thin mottled stripe. None has a solid black dorsum or black bands across the tail paddle. Irises are consistently light in color, usually pale grey green (Fig. 2C). Descriptive measurements of the yellow sea snake (Table 1) are recorded as live WT: 22–90 g (mean=45.5); girth: 4–6.5 cm (mean=5.2); TL: 39–59.3 cm (mean=49.5), SVL as TL minus tail: 34.25–53.3 cm (mean=44.1); tail length: 4.25–7 cm (mean=5.5); and paddle height: 0.8–1.4 cm (mean=0.98). Cephalic scales (Fig. 2E–F) are represented by two nasal shields (touching; no internasals); two prefrontals (no loreals); one frontal; two parietals; unilaterally, preoculars: 0–2 (mode=1); postoculars 1–3 (mode=2); anterior temporals: 2–3 (rarely 4); supralabials: 7–10 (mode=8); infralabials: 10–13 (mode=11, with the first five larger in size); and two anterior sublinguals (separated by small scales). In 73% of specimens, a supralabial (usually the fourth, occasionally the fifth, and rarely both) touched the ocular orbit. For body scales, we counted around the neck: 36–47 (mean=42.7); around the midbody: 45–59 (mean=52.1); vertical paddle: 11–13 (mode=12); ventrals: 245–383 (mean=314.4); and subcaudals: 38–53 (mean=45.1).

The pale integument and light iris of the yellow sea snake contrasts with the solid black dorsum and dark eye of the pelagic sea snake (Fig 2D). Yellow sea snakes also consistently lack the black spots or bands on the lateral tail paddle that are seen in pelagic sea snakes. Even taking a conservative approach for multiple comparison tests by applying an FDR correction, several morphological characters significantly differ between the two groups (Table 1). Overall, yellow sea snakes are smaller than pelagic sea snakes, as demonstrated by reductions in live weight, TL, tail length, and paddle height. Paddle aspect ratio (as tail height/length) indicates the tail of the yellow sea snake is narrower, and we also find fewer paddle scale row counts. Cephalic scalation shows additional significant differences: yellow sea snakes are less likely than pelagic sea snakes to have one preocular scale rather than two and exhibit a higher frequency of labial-to-orbit contact (Fig. 2E).

Comparisons between contemporary yellow sea snakes and the 1970s specimens captured off-shore show near-perfect alignment (Table 1). After FDR-correction, the only character out of sync is girth. All the 1970s specimens are within the recorded size range for the yellow sea snake, and an even higher percentage (86%) show at least one labial scale in contact with an eye.

We did not obtain rib counts for any yellow sea snakes; however, radiographs of four 1970s specimens and four pelagic sea snakes allowed counts of body ribs (1970s =146–152, pelagic=139–155), caudal vertebrae (1970s =32–34, pelagic=29–33) total counts (body-caudal; 1970s=180–185, pelagic=168–185), and atlas-to-heart counts (1970s =44–47, pelagic=39–47). Although minimum counts are consistently lower in the pelagic specimens, larger sample sizes are needed to clarify whether genuine variations in rib/vertebrae counts can be linked with color. Half (n=2) of our radiographed pelagic sea snakes were gravid, which may have influenced heart position. One (ZMK R66143) carried six embryotic offspring. The other (FMNH 165213) shows two fetuses no longer in well-formed embryonic sacs with one positioned more elongate, head pointed toward the caudal end of the mother’s body suggesting it may have been moving through the oviduct; if so, it is possible that additional neonates were released prior to capture or conservation.

Genetics

Despite the morphological differences reported above, our molecular analyses do not support the hypothesis of separate species. For both DArTseq Dataset 1 (samples from across the full range of the study species) and Dataset 2 (adjacent populations in Costa Rica), PCAs fail to show clustering between geographic regions or between the yellow and pelagic populations (Fig. 3A-B). Regional groups show similar patterns of within-population variation (Ho, He, F_{IS}; Tables 2–3), and F_{ST} (genetic variation within an individual relative to its subpopulation) is close to zero across the species range (Table 4) and within the adjacent Costa Rican populations (-0.0006459).

When examining the SqCL sequence data, we find no evidence of genetic structure between the adjacent but geographically separated yellow and pelagic sea snakes (Fig. 3C–D); SplitsTree generates a starburst pattern of near-equal distance between all specimens. Our analysis of the mined mtDNA returns similar results (Fig. 3E). We note that the amount of mtDNA mapped from our DArTseq and SqCL sequences to the *H. platurus* reference mitogenome was limited based on visual inspection and the Geneious statistics comparing the sequences within our final alignment (Pairwise Identity=13.7%; Identical Sites=4.4%).

DISCUSSION

We compared morphological and molecular markers of the yellow sea snake (*Hydrophis platurus xanthos*) residing inside Golfo Dulce against the pelagic sea snake (*H. p. platurus*) ranging across the Indo-Pacific Ocean. Comparative morphology illuminated multiple differences between populations: not only does the yellow sea snake exhibit xanthic coloration with light irises and a reduction in all body size measurements, including live weight, it shows statistically significant shifts in tail morphology (paddle shape as aspect ratio and paddle scale count), preocular count, and frequency of labial scales touching an eye. Despite these morphological differences, comparative molecular analyses using SNPs, target-capture loci, and mined mtDNA did not reveal genetic differentiation between populations.

On the simplest level, our results suggest intense selection for certain morphological features inside Golfo Dulce and/or an evolutionary split too recent to identify.

A morphological perspective

Bessesen and Galbreath (2017) and Solórzano and Sasa (2024) suggest elevated sea surface temperatures in Golfo Dulce may promote lighter coloration and smaller body size in yellow sea snakes relative to pelagic sea snakes. As a species, *H. platurus* is known to be polymorphic. Smith (1926) published seven color forms, all versions of dark above and light below (see Supplementary Material, Fig. S1). In and near the Persian Gulf, some specimens appear whitish yellow with a light brown dorsum and pale paddle markings (iNaturalist 2024, J. Crowe-Riddell, pers. comm.). However, unlike the mixed phenotypes seen elsewhere, the yellow sea snakes have 100% conformity in xanthic coloration. They are also consistently smaller across various measurements: girth, TL, tail length, and paddle height. Because such traits are linked by allometry, we consider them to represent a unified shift in body size. Our expanded dataset only slightly increases the yellow sea snake's max length to 59.3 cm (from 59 cm: Bessesen & Galbreath 2017), and still no specimens reach the reported minimum length for a gravid pelagic sea snake (≥60 cm; Kropach 1975, Vallarino & Weldon 1996). While individual snake weights can vary due to age, prey consumption, sexual dimorphism, breeding condition, health, and ecology (Feldman & Meiri 2013), the yellow sea snake weighs on averages 40% less than the pelagic sea snake. The difference in tail shape is also of interest. Not only is the tail of the yellow sea snake naturally smaller, but the aspect ratio of height/length suggests it is narrower and has fewer scale rows. Perhaps bound to the relatively calm subsurface waters of the inner basin, the snakes in Golfo Dulce do not require as much paddle power as those diving the open ocean. Furthermore, the yellow sea snakes are significantly more likely than their pelagic counterparts to have one prefrontal scale versus two. Tu (1976) mentioned a trait shared among four yellow specimens collected off Costa Rica: at least one supralabial in contact with the ocular orbit. We found nearly three-quarters of yellow sea snakes exhibited that trait compared with approximately 50% of pelagic sea snakes. Scale count variability and clinal changes between geographical areas are common in squamates (Dohm & Garland 1993), and it is unknown whether the prefrontal and labial-to-orbit traits have been increasing through selection due to reduced space on a smaller animal, or whether they are simply phenotypic variance derived through genetic drift. Either way these characters may be moving toward fixation in the yellow population.

When considering the establishment of the yellow population, it is noteworthy that the inner basin of Golfo Dulce may have been fully cut off from the Pacific Ocean during some period of its geological history (T. Garner pers. comm.). Published geological models indicate that during the late Pleistocene the Osa region was submerged apart from three small islands (the highest peaks of the modern day Osa Peninsula; Gardner *et al.* 2013). Any pelagic sea snakes in the region at that time could have navigated around the islands and used waters adjacent to their coasts. By 125 kya, the Osa landmass was being uplifted by subduction, forming an unbroken peninsula (Gardner *et al.* 2013) and potentially capturing a group of pelagic sea snakes within the boundaries of Golfo Dulce. During the last glacial maximum, nominal eustatic curves suggest sea levels dropped <130 m (Lambeck *et al.* 2014). Seeing as present-day Golfo Dulce has a sill at 60 m depth and outer basin generally less than 30 m deep (the shallow zone that today separates the yellow from the pelagic sea snake*;* Bessesen 2022) it is conceivable that low sea levels isolated the deep inner basin of Golfo Dulce for tens of thousands of years (T. Gardner, pers. comm.). The enclosed basin, essentially a brackish lake, would have offered a considerably different habitat than the adjacent Pacific, with the potential to accelerate differentiation. An alternative hypothesis provides for a weather event or anomalous wave having swept tens to thousands of pelagic sea snakes into the inner basin.

Owing to the bathymetry of Golfo Dulce and its fiord-like characteristics (Svendsen *et al.* 2006), the potential for frequent contact between Costa Rica's adjacent yellow and pelagic sea snake populations is low. They appear separated by a >20-km spatial gap centered over shallow waters (mostly 10–30 m deep; Bessesen 2022) with a complicated current structure (Svendsen *et al.* 2006, Morales-Ramírez *et al.* 2015). Among nearly 900 recorded observations of Golfo Dulce yellow sea snakes over a 15-year period, only one occurred in that shallow zone (Bessesen 2015). That these snakes are weak swimmers that spend their time diving and floating without active horizontal movements (Kropach 1973, Graham *et al.* 1987, Rubinoff *et al.* 1988) further reduces the likelihood of crossing such a sizable space. We know yellow sea snakes are sometimes swept out of the embayment (Bessesen 2015, 2022), and pelagic sea snakes may occasionally wash in (Bessesen & Galbreath 2017, Solórzano & Sasa 2024). However, the latter do not appear to survive long term as evinced by an absence of typical black-and-yellow individuals in the inner basin (Solórzano 2011, Bessesen 2015, Lillywhite et al 2015, Bessesen 2022) coinciding with reported effects of elevated thermal conditions. Surface temperatures in Golfo Dulce reach at least 32.5 °C (Rincon-Alejos & Ballestero-Sakson 2015, Bessesen *et al.* 2023). In lab experiments, every pelagic sea snake held in water heated to 32 °C stayed at the bottom of the tank (Graham *et al.* 1971), and in waters ≥33 °C, none survived longer than two days (Dunson & Ehlert 1971). Solórzano and Sasa (2024) published a photo of an interbreeding event in the inner basin of Golfo Dulce, but because the coupling is reported to be a male yellow sea snake and female pelagic, reproductive success is unlikely given the improbable odds that she could withstand the environment to parturition. Successful interbreeding within the distribution area of the yellow sea snake where thermal conditions and other hydrological characteristics appear unsuitable to ‘outsiders’ (Bessesen 2022, Bessesen *et al.* 2023) likely requires a male pelagic sea snake carried in on a rogue wave or current to mate with a female yellow sea snake adapted to survive there for her 6- to 8-month gestation period (Savage 2002).

Our morphological data provided evidence that the 1970s specimens captured off Central America were likely to have originated from inside Golfo Dulce, as they aligned closely with the yellow sea snake. This finding is further supported by mapping the collection sites of Kropach (1971), Bolaños *et al.* (1974) and Tu (1976) and comparing the percentage of yellow snake encounters from their studies which show higher percentages nearer the embayment. One of the 1970s specimens was found >500 km from Golfo Dulce in the Gulf of Panama (Kropach 1971) but no yellow sea snakes have been reported beyond Central America. The survival rate of yellow sea snakes that transition to open ocean, where waters are colder and contain higher salt content is unknown. Though our sample size was small, a reduction in average girth among our 1970s specimens may suggest weight loss (McCue *et al.* 2012), possibly due to reduced feeding in an unfamiliar environment.

A molecular perspective

Population structure has been studied in sea snakes (Lukoschek & Shine 2012, Sheehy *et al.* 2012, Bech *et al.* 2016, Nitschke *et al*. 2018, Ludington & Sanders 2021). Notably, the *Aipysurus-Emydocephalus* clade showed defined geographical genetic patterns, including intraspecific splits, while the *Hydrophis* clade showed weak population differentiation, suggesting that rapid distribution and speciation may have reduced phylogenetic signal across their range (Nitschke *et al.* 2018). The DArTseq methods used in our study have nevertheless detected population structure in more than a dozen other *Hydrophis* species, even over small geographic distances (JH, pers. comm.). So, it is curious that we failed to find any clear structure across the near-global pelagic sea snake. The species reportedly diverged 5–7 mya, spreading across oceans from its Indo-Australian origins (Lee *et al.* 2016). While it seems to have reached the Americas after the formation of the Isthmus of Panama obstructed access to the Atlantic Ocean (Lillywhite *et al.* 2018), as recently as 2.8 mya (O'Dea *et al.* 2016), a much more recent arrival would help explain the low genetic variation between eastern and western sides of the Pacific, with some level of continued gene flow across oceans. Population structure can be reduced or lacking in marine fauna that live a pelagic lifestyle (Pfaller *et al.* 2018) and/or form exceedingly large and far-ranging populations (Palumbi 1994, Anderson *et al.* 2020). Still, panmixia across oceans should be interpreted with caution, as samples rarely cover the full range of the taxa, making subtle genetic differentiation challenging to detect, especially within recently diverging populations (Grosberg & Cunningham 2001). Yellowfin tuna (*Thunnus albacares*), once thought to be globally panmictic, showed discrete populations once migratory patterns were factored in (Pecoraro *et al.* 2018). Increased sampling of the pelagic sea snake from across its expansive range will be needed to gain a clearer understanding of its global population structure.

In accord with a mitochondrial-based phylogeography study by Sheehy *et al.* (2012), we found limited evidence of differentiation between the yellow and pelagic populations. We did not capture mtDNA directly from tissue samples but instead mined it from raw nuclear sequences (e.g., Stobie *et al.* 2018). While our resulting mtDNA sequences were incomplete, results derived from those data were mirrored by more robust SNP and SqCL data. Limited within-population structure across the narrow range of the yellow sea snake could be expected due to the small collection area. However, because reduced gene flow is often associated with geographic barriers (Gruber *et al.* 2013), and there is a sizeable shallow zone separating the yellow and pelagic sea snake populations (Bessesen 2022), the dearth of structure between those groups was unexpected. If the yellow sea snake population formed through vicariance due to tectonic subduction coinciding with the last glacial stand, promoting divergence (see A Morphological Perspective), perhaps when sea levels rose, allowing for sporadic interbreeding events, a recombination of genes removed evidence of an earlier, more complete separation, though even with admixture and recombination we would expect some sign of population structure. If the population formed by some number of individuals more recently washed in, founder effect should have produced a genetic signature of rapid population growth typically following a range expansion.

Uncovering no evidence of genetic divergence in the geographically isolated and morphologically and ecologically distinct yellow sea snake creates a paradox. Though undetected in our analyses, a modest number of nuclear genes related to color, size, tail shape and/or scalation may have changed (Dohm & Garland 1993, Karsenty & Wagner 2002, Aubret 2015, Ullate-Agote *et al.* 2020). While a snake's color can be determined by a single gene mutation (Ullate-Agote *et al.* 2020), body size is more complex, generally driven by multiple genes as well as gene regulators and phenotypic plasticity associated with feeding and/or environmental factors (Karsenty & Wagner 2002, Aubret 2015). The anatomy and physiology of the yellow sea snake could be further influenced by feeding at night (Bessesen & González-Suárez) and inhabiting waters with elevated temperatures, lower salinity and limited dissolved oxygen compared with the open Pacific Ocean (Bessesen *et al.* 2023). Epigenetic gene regulation is known to influence body plan diversification in reptiles (Martín-del-Campo *et al.* 2019), and snakes are well known for their phenotypic plasticity (Aubret *et al.* 2004). The New Caledonia sea krait (*Laticauda saintgironsi*) presents clinal phenotypic variation across known colonies with differing habitats but with no apparent genetic variation (Bech *et al.* 2016). Similarly, Shine *et al.* (2012) found considerable phenotypic differences between two colonies of turtle-headed sea snakes (*Emydocephalus annulatus*) inhabiting adjacent bays. Forsman (2015) argues that irreversible developmental plasticity should be considered within the framework of quantitative genetics as it is fundamentally similar to gene expression and includes genetic components. Having demonstrated developmental plasticity in sea snakes, Bonnett *et al.* (2021) made the point that genetic homogeneity between spatially defined phenotypes does not negate the possibility of speciation but rather supports the idea of plasticity as a mechanism to facilitate speciation through the establishment of distinct, environmentally influenced subpopulations.

CONCLUSIONS

To better elucidate the genetic underpinnings of differences seen between the yellow and pelagic sea snakes, whole-genomic based work may prove useful (Nater *et al.* 2015, Streicher & Ruane 2018; Card *et al.* 2023), as well as the examination of particular genes for which selection may be strong in Golfo Dulce. In addition to explaining the morphological changes reported here, future research has potential to offer insight into the genetic and/or epigenetic mechanisms of: thermal tolerance (the yellow sea snake inhabits waters that may exceed the reported thermal maximum for the pelagic sea snake); visual acuity (nocturnality in the yellow sea snake may have led to improved night-vision or reduced reliance on vision); osmoregulation (the yellow sea snake inhabits low-saline waters which could reduce its ability to shield or excrete salts from the body); and/or blood-oxygen carrying capacity (the yellow sea snake inhabits waters with reduced dissolved oxygen).

Our study raises important questions about the complexities of the evolutionary process. From a morphological perspective the yellow sea snake is distinct, with unambiguous xanthic coloration and multiple changes to body size, weight, tail shape and scalation. Those changes also coincide with considerable ecological shifts (SM Table 3), including sequestration due to a geographical barrier (Bessesen 2012, 2022, Solórzano & Sasa 2024, Lillywhite 2025), divergent habitat suitability metrics (Bessesen *et al.* 2023), and adaptive behaviors, such as its disassociation with drift lines (Lillywhite *et al.* 2015, Bessesen

2022), nocturnal activity cycle (Bessesen & González-Suárez 2022 and unusual feeding behavior (Bessesen & Galbreath 2017). Such findings suggest the yellow sea snake is on a unique trajectory, and yet our genetic work offers no clear sign of evolutionary divergence. Genetic relationships among sea snakes may be difficult to resolve, especially for rapidly radiating hydrophiids, which present inadequate molecular resolution (Lukoschek & Keogh 2006, Rasmussen *et al.* 2011, Sanders *et al.* 2013), and to complicate matters, snakes exhibit high levels of developmental plasticity that may not always or entirely be linked to genetics (Burbrink *et al.* 2020). Still, fine-scale structure within a single snake species can usually be detected across relatively short distances even without morphological differentiation (Marshall *et al.* 2009, Pernetta *et al.* 2011, Meister *et al.* 2012). The complete lack of population structure between our two study populations is both unexpected and difficult to reconcile. We have done our best to consider potential causes and leave it to our readers and future researchers to interpret the implications of this work. Perhaps the yellow sea snake was once fully isolated but has been hybridizing with pelagic sea snake since the end of the last glacial maxima. Perhaps it became more recently isolated and is in the early stages of speciation, its evolutionary trail yet undefined.

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CRediT STATEMENT

Brooke Bessesen (study conception and design, data collection, lab preparation, data analysis, manuscript writing and revision), Manuela González-Suárez (funding, study design, data analysis), Guido Saborío-R. (permit acquisition, data collection), Edward Myers (data analysis), Balázs Buzás (data collection), Csaba Géczy (data collection), Arne Rasmussen (study design, data collection), Kate Sanders (funding, study design), Sara Ruane (funding, lab preparation), and James Nankivell (study design, data collection, lab preparation, data analysis). All authors, except B. Buzás and C. Géczy, contributed to the interpretation of results, and all authors reviewed this manuscript.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT: Upon acceptance of this manuscript, the data underlying this study will be made available via the NCBI database (raw SqCL sequences and demultiplexed DArTseq reads; BioProject ID: TBD) and/or Figshare (.vcf files and embargoed morphological data; private link available on reasonable request).

SUPPLEMENTARY MATERIALS

Table S1 All genetic samples used in this study identifying specific analyses (SNPs = single nucleotide polymorphisms, SqCL = squamate conserved loci, and/or mined mtDNA); for mined mtDNA we include the method of sequencing used for the derivative source.

Table S2 Additional sources of morphological data for the pelagic sea snake *Hydrophis platurus.*

Table S3 Ecological differences between *H. p. xanthos* and *H. p. platurus*

Figure S1 Photo of seven specimens held at the Natural History Museum, London, showing Smith´s (1926) color variations.

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TABLES

Table 1. Morphological characters for *Hydrophis platurus xanthos* and test results of comparisons with the 1970s specimens (yellow sea snakes collected from the Eastern Tropical Pacific Ocean) and *H. p. platurus*; results of the False Discovery Rate correction (Benjamini & Hochberg 1995, Pike 2010) presented as FDR-adjusted p-values (q-values). Xanthic coloration=predominantly yellow, lacking a solid black dorsum; *=0.04995; additional sources of morphological data for *H. p. platurus* can be found in Supplementary Material (Table S2).

			COMPARED WITH									
	H. p. xanthos		*1970s specimens*					*H. p. platurus*				
Character	**# specimens**	**mean+/-sd**	**#**	**mean +/-sd**	**t-value**	**p-value**	**q-value**	**#**	**mean +/-sd**	**t-value**	**p-value**	**q-value**
Live weight (g)	91	45.3+/-13.1	NA	NA	NA	NA	NA	24	75.7+/-29.7	-4.9	**<0.001**	**<0.001**
Girth (cm)	51	5.2+/-0.8	5	4.1+/-0.4	5.2	**0.001**	**0.021**	87	8.7+/-2.5	-12.5	**<0.001**	**<0.001**
Snout-Vent length	117	44.1+/-3.9	5	41.9+/-7.2	0.7	0.547	0.744	107	62.2+/-17.2	-10.7	**<0.001**	**<0.001**
Total length (TL, cm)	118	49.5+/-4.3	5	46.8+/-7.9	0.8	0.476	0.744	188	63.8+/-17.1	-10.9	**<0.001**	**<0.001**
Tail length (cm)	117	5.4+/-0.6	5	4.9+/-0.8	1.4	0.169	0.608	107	7.2+/-1.8	-9.8	**<0.001**	**<0.001**
Tail/TL ratio	117	0.11+/-0.01	5	0.10+/-0.01	0.8	0.296	0.707	107	0.11+/-0.09	-0.4	0.701	0.791
Paddle height (cm)	62	0.98+/-0.1	5	0.92+/-0.1	1.2	0.300	0.707	109	1.6+/-1.8	-12.4	**<0.001**	**<0.001**

Paddle aspect ratio	62	0.18+/-0.02	5	0.19+/-0.05	-0.6	0.579	0.744	106	0.23+/-0.19	-2.9	**0.004**	**0.008**
Preoculars	49	1.0+/-0.1	6	1.0+/-0.0	0.6	0.569	0.744	97	1.2+/-0.4	-3.9	**<0.001**	**<0.001**
Postoculars	48	1.9+/-0.3	6	2+/-0.0	-1.5	0.128	0.608	96	1.9+/-0.3	-0.4	0.712	0.791
Anterior temporals	50	2.6+/-0.5	6	2.9+/-0.5	-1.7	0.142	0.608	78	2.6+/-0.4	-0.8	0.418	0.597
Supralabials	49	8.4+/-0.6	6	8.3+/-0.8	0.2	0.858	0.858	94	8.4+/-1.4	-0.3	0.769	0.809
Infralabials	48	11.0+/-0.6	6	10.8+/-0.5	1.1	0.314	0.707	97	11.0+/-0.7	-0.5	0.605	0.756
Neck scale rows	43	42.7+/-3.0	7	38.4+/-2.9	3.6	**0.007**	0.061	38	42.4+/-3.1	-0.7	0.479	0.639
Midbody scale rows	42	52.1+/-3.3	7	51.1+/-5.1	0.5	0.634	0.761	36	54.0+/-4.6	-2.0	0.053	0.082
Paddle scales	17	12.4+/-0.5	7	12.1+/-0.7	0.7	0.483	0.744	76	13.4+/-1.0	-6.2	**<0.001**	**<0.001**
Ventrals	27	314.4+/-29.2	7	310.4+/-40	0.2	0.813	0.858	27	314.6+/-57.6	-0.0	0.988	0.988
Subcaudals	26	45.1+/-3.4	7	46.7+/-5.3	-0.8	0.475	0.744	67	46.8+/-4.2	-2.0	**0.050***	0.082
Xanthic coloration	124	100%	7	100%	NA	NA	NA	229	0%	χ2=348.6	**< 0.001**	**< 0.001**
Labial touches orbit	57	73%	7	86%	χ2=0.5	0.675	0.858	194	51%	χ2=5.5	**0.004**	**0.008**

Table 2. Population genetic metrics (Ho=heterozygosity; He=expected heterozygosity; F_{IS}=inbreeding coefficient) for samples (number in parentheses) with no missing loci from across the full range of the species, including *H. p. platurus* from Costa Rica (CR), Indo-West Pacific (IWP), United Arab Emirates (UAE), and *H. p. xanthos* (xanthos) from inside Golfo Dulce.

Population	**Ho**	**He**	**F_{IS}**
CR (18)	0.0497	0.0582	0.0835
IWP (8)	0.059	0.0624	0.035
UAE (7)	0.0476	0.0567	0.0875
xanthos (21)	0.0517	0.0574	0.0636

Table 3. Population genetic metrics (Ho=heterozygosity; He=expected heterozygosity; F_{IS}=inbreeding coefficient) for samples from the Costa Rican population of *H. p. platurus* (CR) and *H. p. xanthos* (xanthos) from inside Golfo Dulce.

Population	**Ho**	**He**	**F_{IS}**
CR (20)	0.0614	0.0736	0.062
xanthos (23)	0.0621	0.0688	0.0979

Table 4. The F-statistic F_{ST} (allele variation within relative to between subpopulations) for samples with no missing loci from across the full range of the species, including *H. p. platurus* from Costa Rica (CR), Indo-West Pacific (IWP), United Arab Emirates (UAE), and *H. p. xanthos* (xanthos) from inside Golfo Dulce.

	CR	**IWP**	**UAE**
IWP	0.006698		
UAE	0.010871	0.004178	

xanthos	0.000715	0.012546	0.011157

FIGURES

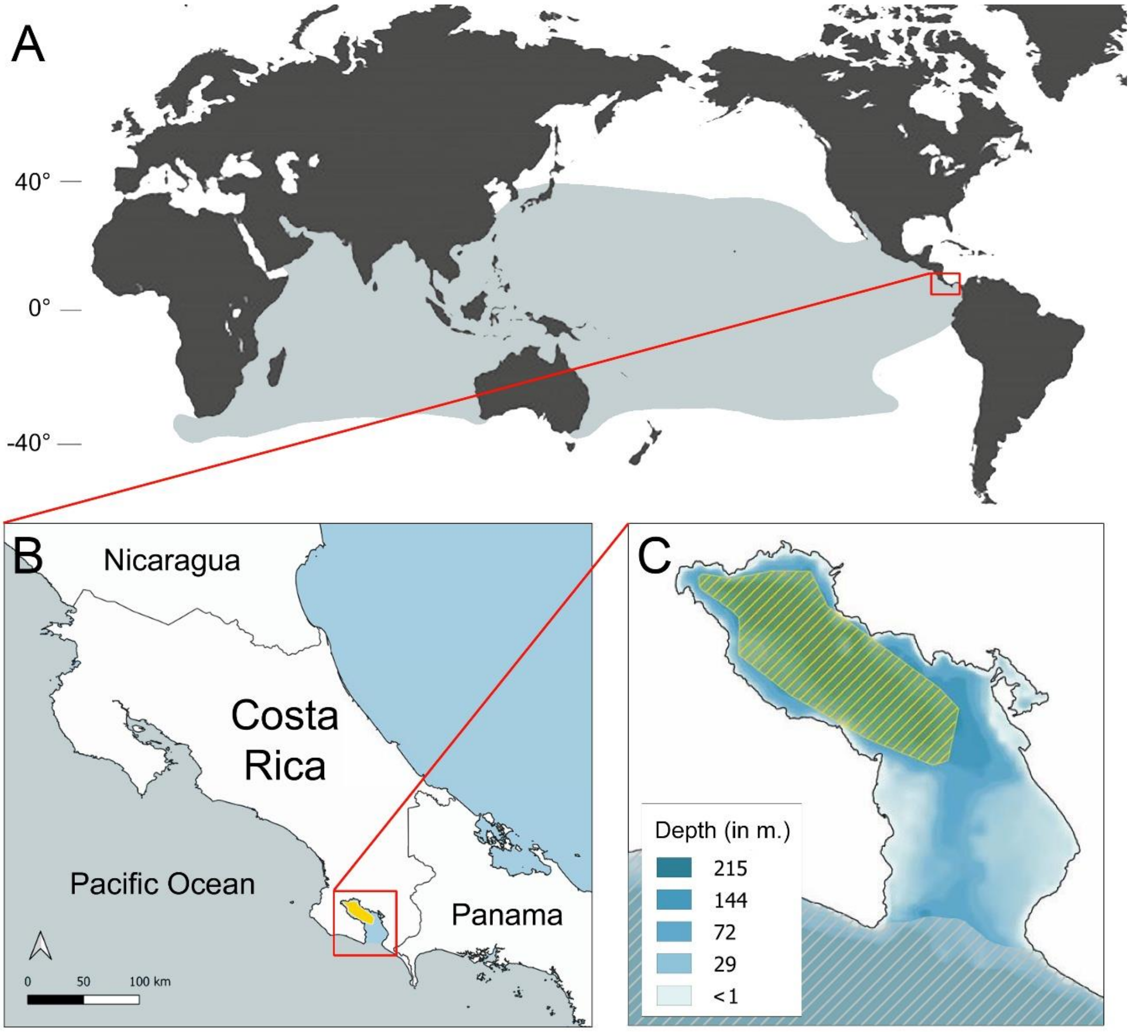

Figure 1. Distribution of the study species: A, *Hydrophis platurus platurus* ranging across the Indo-Pacific Ocean (grey; based on Brischoux *et al.* 2016); B, *H. p. xanthos* inside Golfo Dulce in south-Pacific Costa Rica (yellow shading; based on Bessesen et al. 2024); C, a spatial gap between the two populations is marked by shallow waters with a complicated current structure.

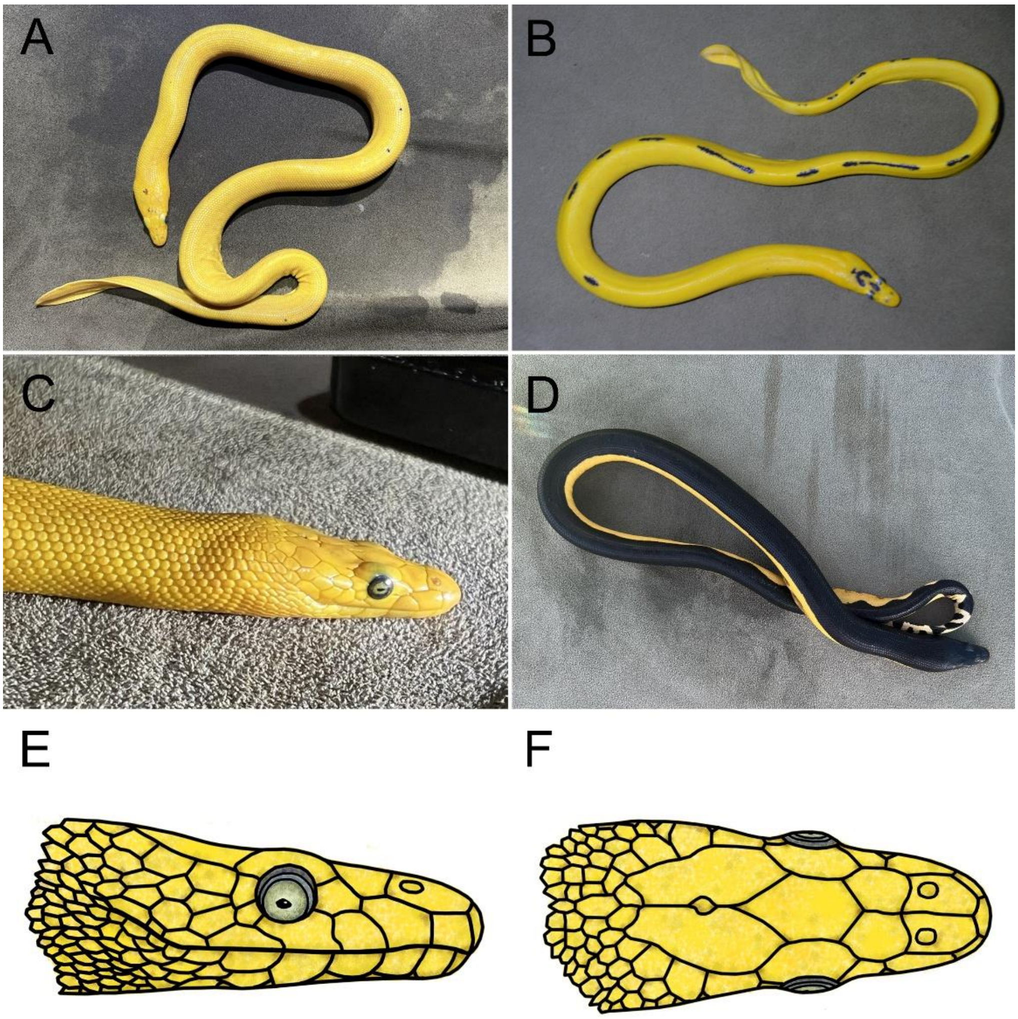

Figure 2. A-B, Diagnosable xanthic coloration of *Hydrophis platurus xanthos* (predominantly yellow with a few black dots; more rarely with dashed dorsal lines or thin strip) and (C) light iris, as compared with (D) typical coloration of *H. p. platurus* with solid black dorsum and lateral tail markings; illustrated cephalic scalation of *H. p. xanthos*: E, lateral view (note lack of subocular scale creates labial-to-orbit contact); and F) dorsal view. Photos and illustrations: B. Bessesen

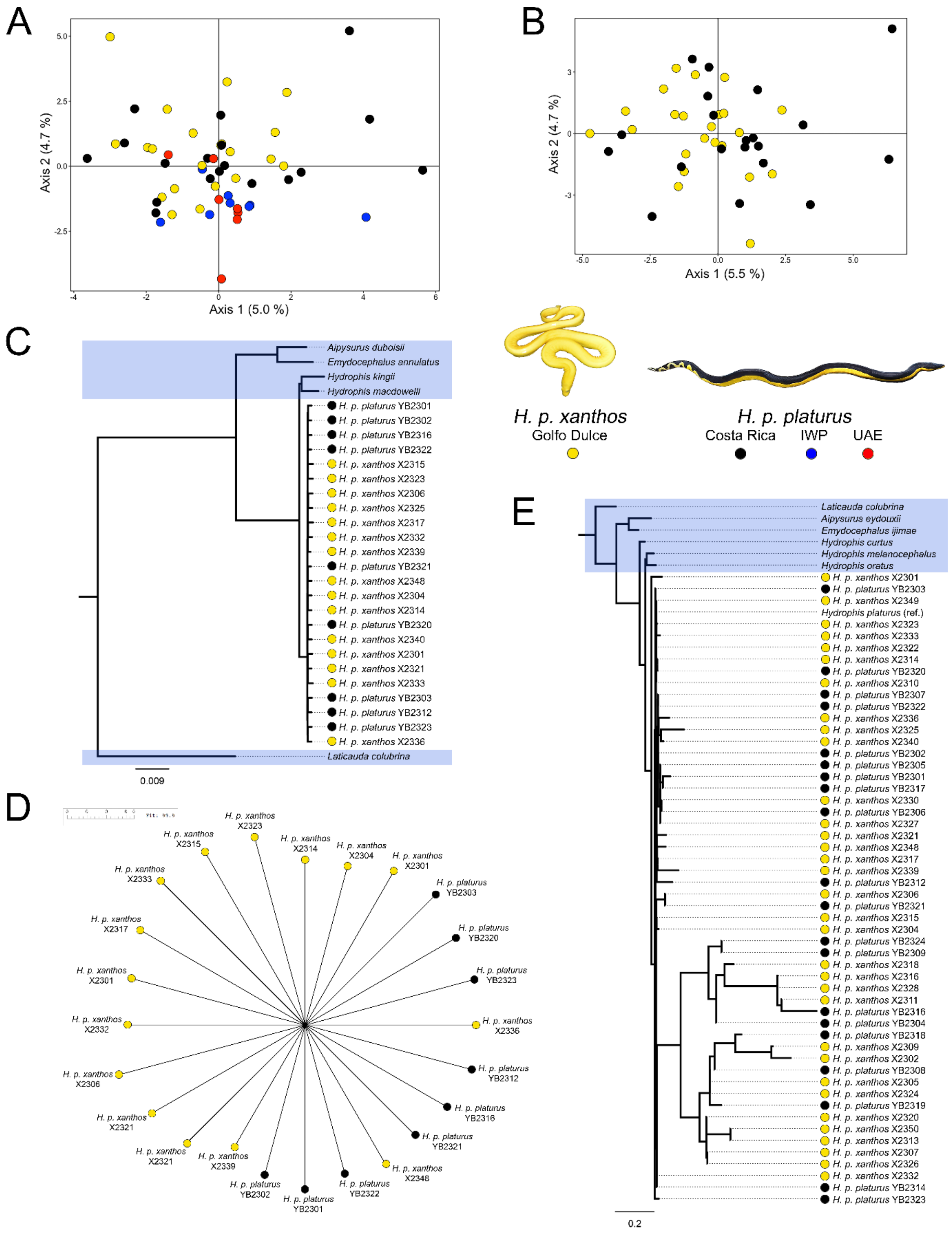

Figure 3. Genetic analyses comparing *Hydrophis platurus xanthos* and *H. p. platurus*: A, Principal Component Analysis (PCA) for single-nucleotide polymorphism (SNP) samples

from across the full range of the species (no missing loci) divided as *H. p. platurus* from Costa Rica, Indo-West Pacific (IWP), United Arab Emirates (UAE) and *H. p. xanthos* (Golfo Dulce); B, PCA of Costa Rican SNP samples; C, IQ-Tree of SqCL sequences, including outgroups (shaded in blue), at a 95% matrix; D, SplitsTree network of SqCL sequences from Costa Rican samples of *H. p. xanthos* (n=15), *H. p. platurus* (n=9) at a 95% matrix; and E) RAxML tree of mapped mitogenomes of *H. p. xanthos* (n=33) and *H. p. platurus* (n=20), plus the reference *H. platurus* and outgroups (shaded in blue

SUPPLEMENTARY MATERIAL

Table S1. Samples used for genetic analysis by taxa (*L.=Laticauda; A.=Aipysurus; E.=Emydocephalus; H.=Hydrophis*), denoting their use (x) in the three analyses (SNPs = single nucleotide polymorphisms; SqCL = squamate conserved loci; and mitogenome = mtDNA); for mined mtDNA we include the method of sequencing used for the derivative source (rad = DArTseq; radx2=w technical replicate; tar=target capture).

Taxon	**Location**	**Source**	**studyID**	**SNPs**	**SqCL**	**mtDNA**	**mined as**
L. colubrina	Not reported	SRA	SRR23022443		x		
L. colubrina	Not reported	GenBank	NC_036054			x	
A. duboisii	Not reported	SRA	SRR23022465		x		
A. eydouxii	Not reported	GenBank	NC_062614			x	
E. annulatus	Not reported	SRA	SRR23022449		x		
E. ijimae	Okinawa, Japan	GenBank	MK775531			x	
H. curtus	Hainan Province, China	GenBank	MT712129			x	
H. kingii	Not reported	SRA	SRR23022445		x		
H. macdowelli	Not reported	SRA	SRR23022444		x		
H. melanocephalus	Okinawa, Japan	GenBank	MK775532			x	
H. ornatus	Not reported	GenBank	NC_066233			x	
H. platurus	Sri Lanka	KLS	KLS0095	x			
H. platurus	Gulf of Carpentaria, AU	KLS	KLS0786	x			
H. platurus	Gulf of Carpentaria, AU	KLS	KLS0787	x			
H. platurus	Gulf of Carpentaria, AU	KLS	KLS0788	x			
H. platurus	Gulf of Carpentaria, AU	KLS	KLS0789	x			
H. platurus	Gulf of Carpentaria, AU	KLS	KLS0790	x			
H. platurus	Gulf of Carpentaria, AU	MAGNT	MAGNT R36633	x			
H. platurus	Floreat Beach, W AU	WAM/ABCT	WAM R101240	x			

H. platurus	Gulf of Oman, UAE	UAE/Balazs	ss_UAE368	x			
H. platurus	Gulf of Oman, UAE	UAE/Balazs	ss_UAE618	x			
H. platurus	Gulf of Oman, UAE	UAE/Balazs	ss_UAE621	x			
H. platurus	Gulf of Oman, UAE	UAE/Balazs	ss_UAE633	x			
H. platurus	Gulf of Oman, UAE	UAE/Balazs	ss_UAE634	x			
H. platurus	Gulf of Oman, UAE	UAE/Balazs	ss_UAE647	x			
H. platurus	Gulf of Oman, UAE	UAE/Balazs	ss_UAE652	x			
H. platurus	South Korea	GenBank	MK775530			x	reference
H. p. platurus	Costa Rica	GenBank	YB2301	x	x	x	radtar
H. p. platurus	Costa Rica	GenBank	YB2302	x	x	x	radtar
H. p. platurus	Costa Rica	GenBank	YB2303		x	x	tar
H. p. platurus	Costa Rica	GenBank	YB2304	x		x	radx2
H. p. platurus	Costa Rica	GenBank	YB2305	x		x	rad
H. p. platurus	Costa Rica	GenBank	YB2306	x		x	rad
H. p. platurus	Costa Rica	GenBank	YB2307	x		x	rad
H. p. platurus	Costa Rica	GenBank	YB2308	x		x	rad
H. p. platurus	Costa Rica	GenBank	YB2309	x		x	rad
H. p. platurus	Costa Rica	GenBank	YB2310	x		removed	rad
H. p. platurus	Costa Rica	GenBank	YB2312	x	x	x	radtar
H. p. platurus	Costa Rica	GenBank	YB2313	x		removed	rad
H. p. platurus	Costa Rica	GenBank	YB2314	x		x	rad
H. p. platurus	Costa Rica	GenBank	YB2316	x	x	x	radtar
H. p. platurus	Costa Rica	GenBank	YB2317	x		x	rad
H. p. platurus	Costa Rica	GenBank	YB2318	x		x	rad
H. p. platurus	Costa Rica	GenBank	YB2319	x		x	rad
H. p. platurus	Costa Rica	GenBank	YB2320	x	x	x	radtar
H. p. platurus	Costa Rica	GenBank	YB2321	x	x	x	radtar
H. p. platurus	Costa Rica	GenBank	YB2322	x		x	radtar
H. p. platurus	Costa Rica	GenBank	YB2323	x	x	x	radtar

H. p. platurus	Costa Rica	GenBank	YB2324	x		x	rad
H. p. xanthos	Golfo Dulce	GenBank	X2301	x	x	x	radtar
H. p. xanthos	Golfo Dulce	GenBank	X2302	x		x	radx2
H. p. xanthos	Golfo Dulce	GenBank	X2304		x	x	tar
H. p. xanthos	Golfo Dulce	GenBank	X2305	x		x	rad
H. p. xanthos	Golfo Dulce	GenBank	X2306	x	x	x	radtar
H. p. xanthos	Golfo Dulce	GenBank	X2307	x		x	radx2
H. p. xanthos	Golfo Dulce	GenBank	X2309	x		x	rad
H. p. xanthos	Golfo Dulce	GenBank	X2310	x		x	rad
H. p. xanthos	Golfo Dulce	GenBank	X2311	x		x	rad
H. p. xanthos	Golfo Dulce	GenBank	X2313	x		x	radx2
H. p. xanthos	Golfo Dulce	GenBank	X2314	x	x	x	radtar
H. p. xanthos	Golfo Dulce	GenBank	X2315	x	x	x	radtar
H. p. xanthos	Golfo Dulce	GenBank	X2316	x		x	rad
H. p. xanthos	Golfo Dulce	GenBank	X2317		x	x	tar
H. p. xanthos	Golfo Dulce	GenBank	X2318	x		x	radx2
H. p. xanthos	Golfo Dulce	GenBank	X2319	x		removed	rad
H. p. xanthos	Golfo Dulce	GenBank	X2320	x		x	rad
H. p. xanthos	Golfo Dulce	GenBank	X2321		x	x	tar
H. p. xanthos	Golfo Dulce	GenBank	X2322	x		x	rad
H. p. xanthos	Golfo Dulce	GenBank	X2323	x	x	x	radtar
H. p. xanthos	Golfo Dulce	GenBank	X2324	x		x	rad
H. p. xanthos	Golfo Dulce	GenBank	X2325		x	x	tar
H. p. xanthos	Golfo Dulce	GenBank	X2326	x		x	rad
H. p. xanthos	Golfo Dulce	GenBank	X2327	x		x	rad
H. p. xanthos	Golfo Dulce	GenBank	X2328	x		x	radx2
H. p. xanthos	Golfo Dulce	GenBank	X2329	x		removed	rad
H. p. xanthos	Golfo Dulce	GenBank	X2330	x		x	rad
H. p. xanthos	Golfo Dulce	GenBank	X2332	x	x	x	radtar

H. p. xanthos	Golfo Dulce	GenBank	X2333	x	x	x	radx2tar
H. p. xanthos	Golfo Dulce	GenBank	X2336		x	x	tar
H. p. xanthos	Golfo Dulce	GenBank	X2339		x	x	tar
H. p. xanthos	Golfo Dulce	GenBank	X2340		x	x	tar
H. p. xanthos	Golfo Dulce	GenBank	X2348		x	x	tar
H. p. xanthos	Golfo Dulce	GenBank	X2349	x		x	rad
H. p. xanthos	Golfo Dulce	GenBank	X2350	x		x	rad

Table S2. Additional sources of morphological data for the pelagic sea snake *Hydrophis platurus* (snout-vent length=SNV)*;* reference list below.

Character	**Reported results (study reference)**			
Live weight (g)	≤150 (Graham et al. 1971)	≤195 (Rubinoff et al. 1986)	≤110.5 (Kim et al. 2020)	≤154 (Buzas et al. 2018)
Girth (cm)	--	--	--	--
SVL (cm)	≤61.8 (Kim et al. 2020)	--	--	--
Total length (TL, cm)	~88 female (Smith 1926)	≤74 (Graham et al. 1971)	≤79 (Tu 1976)	≤113 Pickwell & Culotta (1980)
Tail length (cm)	8–9 (Smith 1926)	≤8.2 (Tu 1976)	≤8.1 (Kim et al. 2020)	--
Tail/TL ratio	~0.112 (Cook & Brischoux 2014)	--	--	--
Paddle height (cm)	--	--	--	--

Paddle aspect ratio	--	--	--	--
Preoculars	1–2 (Smith 1926)	1–2 (Kropach 1973)	1 (Kim et al. 2020)	--
Postoculars	2–3 (Smith 1926)	2–4 (Kropach 1973)	2 (Kim et al. 2020)	--
Anterior temporals	2–3 (Smith 1926)	2–4 (Kropach 1973)	2–3 (Kim et al. 2020)	--
Supralabials	7–8 (Smith 1926)	6–10 (Kropach 1973)	7–9 (Kim et al. 2020)	--
Infralabials	10–11 (Smith 1926)	9–14 (Kropach 1973)	10–11 (Kim et al. 2020)	--
Neck scale rows	36–54 (Tu 1976)	41–54 (Kim et al. 2020)	--	--
Midbody scale rows	49–67 (Smith 1926)	44–61 (Tu 1976)	53–65 (Kim et al. 2020)	49–67 (Buzas et al. 2018)
Paddle scales	--	--	--	--
Ventrals	264–406 (Smith 1926)	274–382 (Voris 1975)	266–289 (Kim et al. 2020)	264–440 (Buzas et al. 2018)

Subcaudals	39–62 (Tu 1976)	42 (Kim et al. 2020)		--
Xanthic coloration	3% (Kropach 1971)	0.1% (Bolaños et al. 1974)	0.1% (Tu 1976)	--
Labial touches orbit	40% (Minton 1966	49% (Kropach 1973)	17% (Tu 1976)	--

TABLE S2 REFERENCES

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Table S3. Differences in conservation status and ecological factors between *Hydrophis platurus xanthos* and *H. p. platurus*; reference list below.

	H. p. xanthos	*H. p. platurus*
IUCN Red List conservation status	Endangered (EN)[1]	Least Concern (LC)[2]
Global abundance	~30,000[3,4]	>1,000,000[5,6]
Range	Golfo Dulce, inner basin[3,7]	Indo-Pacific Oceans[8]
Extent of occurrence (km2)	<300[1,3,7]	>2,500,000[6]
Suitable depth (m)	>100[3,7]	≥10[5]
Average SST (°C)	30[3,7]	26-28[9,10,11]
Average salinity (ppt)	<31[3,7]	35[12]
Average DO (mg/ L)	6.5[3,7]	7.0-8.0[13]
Feeding posture	sinusoidal[14]	elongate[5]
Diel pattern	nocturnal[9,15]	Diurnal[16,17]
Drift line use	no[3,9]	yes[5,9]
Wave tolerance	<1.2 m[3,14]	<0.1 m[5,9,16]

TABLE S3 REFERENCES

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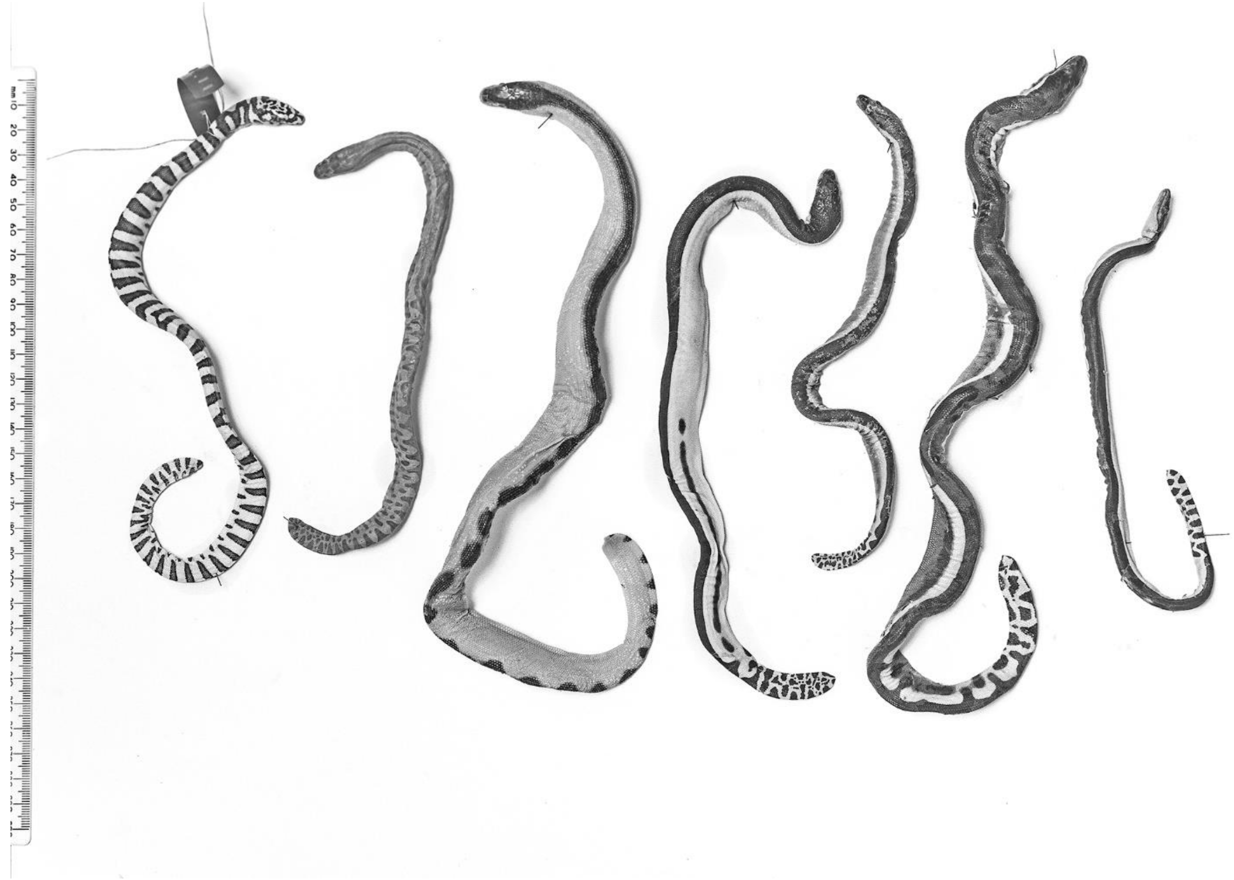

Figure S1. Specimens held at the Natural History Museum, London, demonstrate Smith´s (1926) seven color variations. Photo: G. Brovad, modified by M. Scharff.