

# *Pituophis deppei* (Duméril, Bibron & Duméril, 1854) or a reassessment of Mexican bullsnakes (Reptilia: Squamata: Colubridae)

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## Abstract

We investigated the morphology and distribution of *Pituophis deppei* (Duméril, Bibron & Duméril, 1854), Mexican populations of *P. catenifer* (Blainville, 1835), and *P. lineaticollis* (Cope, 1861) from west of the Isthmus of Tehuantepec, examined the relevant and traceable type series of Mexican nominal taxa belonging to this species group, and appraised so far unattended contemporaneous documents related to the collector Ferdinand Deppe. *Pituophis deppei* and *lineaticollis* virtually coexist along the central Transvolcanic Belt and in the Puebla-Oaxaca-Veracruz border triangle (first state records for *lineaticollis* in Veracruz). The allegedly diagnostic neck pattern does not reliably distinguish *deppei* from *lineaticollis* in, for instance, Michoacán. Deppe's bullsnake and the northern *catenifer* show largely parapatric ranges and are morphologically distinct. Supposed hybrids (*catenifer* × *deppei*) occur in a narrow sector across the Northern Plateau, and bullsnakes with in-between combinations of character states predominate along the Chihuahua-Sonora border north of the Sierra Tarahumara. Phenotypically intermediate specimens encompass part of the type series of *P. mexicanus* Duméril, Bibron & Duméril, 1854 (lectotype designation), a composite and long disused taxon including at least one original voucher akin to *catenifer* and one presumably from N Hidalgo (Huasteca). We recovered three syntypes of *Elaphis pleurostictus* Duméril, Bibron & Duméril, 1854 (syn. *P. deppei*) and unearthed a formerly neglected name-bearer of *P. deppei pholidostictus* Jan, 1863 (syn. *P. lineaticollis*). The study clarifies the origin of a limited number of Mexican amphibians and reptiles received from F. Deppe, re-establishes the type localities of *E. [Pituophis] deppei*, its simultaneous synonym *E. pleurostictus* D. B. & D., as well as the phrynosomatid lizard *Sceloporus grammicus* Wiegmann, 1828, and highlights resulting taxonomical complications. Also, it elucidates the origin of further zoological type material collected by this naturalist and addresses issues of nomenclatural relevance in the context of scientific names related to Deppe specimens.

## Resumen

Investigamos la morfología y la distribución de *Pituophis deppei* (Duméril, Bibron & Duméril, 1854), poblaciones mexicanas de *P. catenifer* (Blainville, 1835) y *P. lineaticollis* (Cope, 1861) al oeste del Istmo de Tehuantepec, examinamos el material de especímenes tipo relevantes y localizables de taxones nominales mexicanos que pertenecen a este grupo de especies, y analizamos documentos contemporáneos, y desatendidos hasta el momento, que se relacionan con el coleccionista Ferdinand Deppe. *Pituophis deppei* y *lineaticollis* prácticamente coexisten a lo largo del centro del Eje Neovolcánico y en el triángulo limítrofe Puebla-Oaxaca-Veracruz (primeros registros estatales para *lineaticollis* en Veracruz). El patrón del cuello, supuestamente de importancia diagnóstica, no permite distinguir de manera confiable entre *deppei* y *lineaticollis* en áreas de contacto, como por ejemplo en Michoacán. El Cincuate de Deppe y su congénérico norteño *catenifer* muestran áreas de distribución básicamente parapatrásicas y son morfológicamente distintos. Supuestos híbridos (*catenifer* × *deppei*) se encuentran en un sector estrecho a través de la Meseta del Norte y ejemplares intermedios predominan en la zona fronteriza de Chihuahua con Sonora, al norte de la Sierra Tarahumara. Especímenes fenotípicamente intermedios abarcan parte de la serie original de *P. mexicanus* Duméril, Bibron & Duméril, 1854 (designamos el lectotipo), taxón compuesto y en desuso desde hace mucho que incluye al menos un ejemplar tipo semejante a *catenifer* y uno presumiblemente del norte de Hidalgo (Huasteca). Encontramos tres syntypes de *Elaphis pleurostictus* Duméril, Bibron & Duméril, 1854 (sinónimo de *P. deppei*) y localizamos un portanombre anteriormente desconocido de *P. deppei pholidostictus* Jan, 1863 (sin. *P. lineaticollis*). El estudio clarifica el origen de algunos anfibios y reptiles mexicanos recibidos de F. Deppe, establece las localidades tipo de *E. [Pituophis] deppei* y de su sinónimo simultáneo *E. pleurostictus* D. B. & D., así como de la lagartija *Sceloporus grammicus* Wiegmann, 1828 (Phrynosomatidae), y señala las resultantes complicaciones taxonómicas. Además, esclarece la

procedencia de otros tipos zoológicos recolectados por este naturalista y aclara temas de relevancia nomenclatural en el contexto de nombres científicos relacionados con especímenes recolectados por Deppe.

## Zusammenfassung

Wir untersuchten die Morphologie und Verbreitung von *Pituophis deppei* (Duméril, Bibron & Duméril, 1854), mexikanische Populationen von *P. catenifer* (Blainville, 1835) sowie *P. lineaticollis* (Cope, 1861) von westlich des Isthmus von Tehuantepec, prüften relevante und auffindbares Typenmaterial von nominellen mexikanischen Taxa dieser Artengruppe und werteten bislang unbeachtete zeitgenössische Dokumente aus, die den Sammler Ferdinand Deppe betreffen. *Pituophis deppei* und *lineaticollis* leben entlang des zentralen transmexikanischen Vulkangürtels sowie im Puebla-Oaxaca-Veracruz Grenzdreieck praktisch nebeneinander (Erstnachweise für *lineaticollis* aus dem Bundesstaat Veracruz). In Kontaktzonen wie bspw. in Michoacán vermag das vermeintlich diagnostische Halsmuster *deppei* und *lineaticollis* nicht zuverlässig zu trennen. Deppes Bullennäther und der nördliche *catenifer* weisen weitgehend parapatrische Verbreitungsgebiete auf und sind morphologisch unterscheidbar. Vermutliche Hybride (*catenifer* × *deppei*) kommen in einem schmalen über das Nördliche Plateau verlaufenden Sektor vor, und Bullennäther mit intermediären Merkmalszuständen überwiegen im Grenzbereich zwischen Chihuahua und Sonora nördlich der Sierra Tarahumara. Phänotypisch intermediäre Exemplare finden sich auch innerhalb der Typenserie von *P. mexicanus* Duméril, Bibron & Duméril, 1854 (Festlegung des Lectotypus), ein heterogenes und lange unberücksichtigtes Taxon; sie beinhaltet zumindest ein *catenifer* ähnliches Exemplar sowie eines, das wohl aus Nord-Hidalgo (Huasteca) stammt. Wir fanden drei Syntypen von *Elaphis pleurostictus* Duméril, Bibron & Duméril, 1854 (Syn. *P. deppei*) und entdeckten einen zuvor unerkannten Namensträger von *P. deppei* *pholidostictus* Jan, 1863 (Syn. *P. lineaticollis*). Unsere Untersuchung klärt die Herkunft einiger von F. Deppe stammenden mexikanischen Amphibien und Reptilien, legt die Typuslokalitäten von *E. [Pituophis] deppei* und des simultanen Synonyms *E. pleurostictus* D. B. & D. sowie der Echse *Sceloporus grammicus* Wiegmann, 1828 (Phrynosomatidae) fest und erläutert resultierende taxonomische Konflikte. Der Ursprung weiteren durch diesen Naturalisten gesammelten zoologischen Typenmaterials wird erhellt und nomenklatorisch relevante Aspekte zu wissenschaftlichen Namen mit Bezug auf Deppes Exemplare werden behandelt.

## Key words

Distribution, Ferdinand Deppe, morphology, *Pituophis* spp. (*catenifer*, *deppei*, *lineaticollis*), *Sceloporus grammicus*, species boundaries, systematics, type localities, type material.

## Introduction

Our interest in Mexican bullsnares, and in the first place *Pituophis deppei* (Duméril, Bibron & Duméril, 1854), arose from the type series of *P. mexicanus* Duméril, Bibron & Duméril, 1854 that presents a confusing array of morphological peculiarities (SCHÄTTI *et al.*, 2018; SCHÄTTI & KUCHARZEWSKI, 2018).

STULL's (1932, 1940) revision of the Nearctic and northwestern Mesoamerican colubrid genus *Pituophis* Holbrook, 1842b identified the southern representatives *P. deppei* and *P. lineaticollis* (Cope, 1861b) as "a natural group characterized by the presence of two prefrontals [...] and the entrance of two supralabials into the orbit" instead of four prefrontals and a single supralabial in contact with the eye in the remaining taxa of the genus including *P. catenifer* (Blainville, 1835) and *P. sayi* (Schlegel, 1837) auct. DUELLMAN's (1960) reconsideration of the endemic northern Mexican *P. deppei*, a study basically limited to an analysis of ventral and subcaudal scale counts as well as dorsal colour pattern variation, reaffirmed species status for *P. lineaticollis* from SW Michoacán to Guatemala. This author ranked *P. deppei brevilineatus* Schmidt & Shannon, 1947 from Michoacán as a junior subjective synonym of *P. lineaticollis* (nominotypical ssp.), and he recognized *P. deppei gibsoni* Stuart, 1954 described from Chimaltenango in Guatemala to be a subspecies of the Central Mesoamerican "pinesnake" (*P. lineaticollis gibsoni*).

KLAUBER (1947) expressed certain qualms concerning the specific distinctiveness of *Pituophis catenifer* and *P. deppei*, and DIXON *et al.* (1962) reasoned upon the

examination of bullsnares with intermediate morphological character states from San Luis Potosí that "[t]he taxonomic position" of *deppei* "is somewhat in doubt". MORAFKA (1977) treated *Coluber catenifer* Blainville and *Elaphis deppei* Duméril, Bibron & Duméril as conspecific with *Coluber [Pituophis] melanoleucus* Daudin, 1803. McCRNIE & WILSON (2001) averred that *P. catenifer* and *P. deppei* "do show signs of intergradation in areas where their respective ranges come into contact" and concluded that the systematics of these species "[c]learly [...] are in need of a thorough analysis." Molecular data suggest genetic introgression across the Northern Plateau (BRYSON *et al.*, 2011).

This study investigates the distribution and morphology of *Pituophis deppei* as well as the variation of supposedly diagnostic head and body scale characters within Mexican *P. catenifer* and taxa of the *deppei* group sensu STULL (1940) or DUELLMAN (1960) including populations of the southeastern *P. lineaticollis* from west of the Isthmus of Tehuantepec, and appraises the disused *Pituophis mexicanus* Duméril, Bibron & Duméril.

## Material and Terms

Morphological data presented herein basically derive from 353 Mexican bullsnares deposited in institutional collections, viz. 94 *Pituophis catenifer*, 185 *P. deppei*,

22 unassigned (intermediate) or anomalous (2) specimens, 49 *P. lineaticollis*, one *P. cf. lineaticollis* and two syntypes of *P. mexicanus* Duméril, Bibron & Duméril (Appendix 1). These figures include 150 photo-determined vouchers, reliable counts for 8 *catenifer*, 19 *deppeli*, and 4 *lineaticollis* from STULL (1940) as well as data for 46 bullsnakes published by other students (see Note 1). Apart from *P. mexicanus* D. B. & D., we examined most name-bearers of the *deppeli* species group auct. (incl. *P. lineaticollis*) that could be located (see Types and Deppe and Note 4 for holotype of *Elaphis deppeli* D. B. & D.) except the holotypes of *Arizona jani* Cope and *A. lineaticollis* Cope (see Notes 14, 25), namely *Elaphis pleurostictus* D. B. & D. (4 syntypes), *Pituophis deppeli brevilineatus* Schmidt & Shannon (holotype, 4 paratypes), and *P. deppeli pholidostictus* D. B. & D. (3 syntypes). Miscellaneous data available for additional specimens (limited number of characters, not in Appendix 1, e.g., Notes 32, 43) encompass the number of dorsal marks or, for example, ventral counts for a *lineaticollis* from Oaxaca (DUELLMAN, 1960) and three unspecified *deppeli* mentioned by the same author (see Note 25).

Characters evaluated for the purpose of the present contribution are the following head and body scutes as well as dorsal colour pattern features: number of pre-frontals, supralabials, circumoculars (preocular, postocular, and subocular scales), ventrals, subcaudals (paired), and midbody rows (short for longitudinal rows of dorsal scales at midbody, maximum count), condition of the supralabials in relation to the eye (scales in contact), parietal size, and number of distinct dark median dorsal blotches down the trunk and on the tail. We distinguish postsubocular scales from postoculars auct. by their position, viz. situated below a line along the body axis passing through the lower edge of the eye. Some weight is attached to certain scale features (e.g., rostral shape, sublabials and inframaxillaries, keeling of dorsals) and the number of teeth on the maxillary and other dentigerous bones (small sample size). A dash separates right and left side counts (lateral head scales or teeth). [Note 1]

The geographic scope covers the area from the Mexico-US border and the Pacific versant of the northwestern Sierra Madre Occidental (or Pacific Cordillera) east of roughly 109° W longitude in Sonora to the Gulf littoral and the Isthmus of Tehuantepec (Fig. 1). The Lower Huasteca comprises areas below 750 m in this ethnic region. Geodetic positions in sexagesimal format (rounded to next minute) originate from geonames.org and elevations are in metres above sea level. ‘Highway’ refers to Mexican federal roads.

In certain cases, we consulted 1:50'000 topographic maps issued by the Instituto Nacional de Estadística y Geografía (INEGI) for the accurate location of places and determination of altitudes. The distribution pattern of vegetation communities (Figs 1, 7, 10, 14) is redrawn from the graphic available at the link indicated in the first map and we use the equivalents cloud forest (bosque mesófilo de montaña) as well as deciduous (selva baja caducifolia), evergreen (selva alta perennifolia), pine-

oak (bosque de pino-encino), semi-deciduous (selva mediana subcaducifolia), and thorn forest (selva baja espinosa). To be in line with literature (e.g., BRYSON *et al.*, 2011), we arbitrarily delimit the northwestern extent of the microphyllous and rosette-leaved scrublands of the Chihuahuan Desert along the Sonora state line (Fig. 1, see, e.g., RORABAUGH, 2008: Fig. 1 for different view).

In order to prevent ambiguities, Mexico and the independent federal state Mexico City (Ciudad de México, CDMX) are in English (without diacritic mark), as are capitals of homonymous entities (e.g., Aguascalientes, Chihuahua, Durango, Puebla, San Luis Potosí, Veracruz) which are anglicized by the epithet ‘City’, but the Estado de México (México State) as well as locality names, general terms such as protected areas (e.g., Parque Nacional, P. N.), and geomorphological features including waterbodies except the ‘Gulf’ (short for Gulf of Mexico) and Gulf of California (or Sea of Cortes) are spelt in Spanish. In the case of Tarahumara place names, we use Huicorichi (or Güicorichi, Chínipas Municipality) or Samachique (instead of Samachic, Guachochi Mun.) but prefer c-endings over alternative local pronunciation, for example Areponapuchic, Maguarichic, Mojárac hic, Temósachic, Tomochic (“Tomichi”), and Yepachic.

Except in taxonomic sections or where deemed to be opportune, scientific names are usually quoted with the full authorship (incl. year) only upon their first mention in most parts of the study. Our chresonymy of *Pituophis deppeli* is far from complete and essentially includes early synonyms or entries on relevant topics, and it harbours, for reasons of expediency and the necessity of presentation, literature records of intermediate bullsnakes. This operational term denotes unassigned specimens that show a combination of scale conditions in-between *P. catenifer* and *P. deppeli* (see Discussion).

Contrary to MORAFKA (1977) or SWEET & PARKER (1990), *Pituophis catenifer* (Blainville, 1835) is considered to be specifically different from *P. melanoleucus* (Daudin, 1803), the type species of the monophyletic *Pituophis* Holbrook, 1842b that inhabits the southeastern United States (e.g., RODRÍGUEZ-ROBLES & DE JESÚS-ESCOBAR, 2000; PYRON & BURBRINK, 2009; WALLACH *et al.*, 2014). Mexican populations from east of the Sierra Madre Occidental are commonly referred to *P. catenifer sayi* (Schlegel, 1837), a taxon including *Pityophis* [sic] *affinis* Hallowell, 1852 (e.g., BRYSON *et al.*, 2011; see Note 35). *Pituophis vertebralis* (Blainville, 1835), an endemic of Baja California, is extralimital to our study area. We do not address the status of the insular endemic *P. catenifer insulanus* Klauber, 1946 from Isla Cedros, which is inferred to be “closely related to populations on the adjacent mainland” (RODRÍGUEZ-ROBLES & DE JESÚS-ESCOBAR, 2000: 47) or regarded as “the sister species” of *P. vertebralis* (GRISMER, 2002: 298).

CONABIO and UNAM stand for Comisión Nacional para el Conocimiento y Uso de la Biodiversidad and Universidad Nacional Autónoma de México, respectively, in Mexico City. MABA is short for the Madrean Archipelago Biodiversity Assessment database (Tucson, Arizona)



**Fig. 1.** Localities, geomorphological features, and vegetation communities mentioned in this study.

accessible via madreandiscovery.org (inactive, visited July 31, 2019). We did not receive a reply to our request for photographs of bullsnakes including MSUM 4018, 7244, and 7909 deposited in the Michigan State University Museum (East Lansing) and repeated demands to the department and senior curators of the Royal Ontario Museum (Toronto) for disclosure of certain locality data of Northern Plateau *Pituophis* spp. and details regarding an

incomplete skeleton of a "*Pituophis deppei*" (ROM 861) from Veracruz remained unanswered.

Most standard codes of institutional collections used in this article are found in SABAJ (2019). Instead of CIB, OS, and INIRENA, respectively, we prefer CIBUAH (Centro de Investigaciones Biológicas, Universidad Autónoma de Hidalgo, Pachuca), OSU (Oregon State University, Department of Integrative Biology, Corvallis), and

UMSNH (Universidad Michoacana de San Nicolás Hidalgo, Instituto de Investigaciones sobre los Recursos Naturales [Colección Herpetológica (CHUM)], Morelia). Additional acronyms are EHT-HMS (Edward H. Taylor and Hobart M. Smith Mexican collection, incorporated into FMNH and UIMNH holdings), FC-UNAM (Facultad de Ciencias, UNAM, Mexico City), HMS (Hobart M. Smith personal collection), KLW (Kenneth L. Williams personal collection), PSC (Peter S. Chrapliwy personal collection), and WLF (William L. Farr personal collection, Houston).

## Results

### *Pituophis deppei* (Duméril, Bibron & Duméril, 1854) — Deppe's bullsna

*E.[aphis] Deppei* [sic]. — DUMÉRIL (1853: 57, nomen nudum, see Taxonomy).

*E.[aphis] pleurostictus* “nobis”. — DUMÉRIL (1853: 57, “de Montevideo”, nomen nudum, see Taxonomy).

*Elaphis Deppei* [sic] Duméril, Bibron & Duméril, 1854: 268 — “Mexique” (restricted to Teotihuacán [San Juan T.], México State, by SMITH & TAYLOR, 1950a: 334; re-established in the vicinity of Zimapán, Hidalgo, *hoc loco*). Holotype unlocated, leg. Ferdinand Deppe June 1825 (Table 1, see Taxonomy, Types and Deppe, Note 4, Implications).

*Elaphis pleurostictus* Duméril, Bibron & Duméril, 1854: 244 — “Montevideo” (“Amérique du Sud”, restricted to Teotihuacán [San Juan T.], México State, by SMITH & TAYLOR, 1950a: 334). Syntypes MNHN 6616 and ZMB 1733–35, leg. F. Deppe (Figs 2A–B, Table 1, see Types and Deppe, Implications).

*Coronella [...] Sayi* [sic] “Dekai” [partim]. — LICHTENSTEIN & VON MARTENS (1856: 25): “Mexico” (ZMB 1733–35, see Types and Deppe, Note 5).

*Arizona jani* Cope, 1861a: 369 — “Buena Vista, Mexico”, Coahuila. Holotype USNM 1522, coll. Darius N. Couch 1853 (see Notes 14, 16).

*A.[rizona] pleurosticta* [“Cope”]. — COPE (1861a: 370): “Uruguay” [sic] (see Types and Deppe, Note 7).

*A.[rizona] deppei*. — COPE (1861b: 301).

*A.[rizona] pleurostictus* [sic]. — COPE (1861b: 301).

*Pituophis Deppei* [sic] (“Mus. Berol.”). — JAN & SORDELLI (1867: Pl. II.2): no locality given (“Patrie incertaine”, “Collection Westphal-Castelnau, à Montpellier”).

*Pityophis* [sic] *sayi mexicanus* (Duméril, Bibron & Duméril, 1854) [“Dum. et Bibr.”] [partim]. — COPE (1887: 72): “Colima” (coll. János Xántus).

*Spilotes deppei*. — COPE (1887: 72).

*Pituophis pleurostictus* [ssp.]. — BOUCOURT (1888: 666, Pl. 42.2): incl. “type” of nominotypical taxon auct. from “Montevideo” (see Types and Deppe, Descriptions, and Taxonomy for *P. pleurostictus deppei* auct.).

*Pityophis* [sic] *Deppei* [sic]. — DUGÈS (1888: 125, Pl. XIII.15).

*Epiglottophis* [gen. nov.] Cope, 1891: 157 (type species “*S.[pilotes] deppei* D. and B.”).

*Pityophis* [sic] *pleurostictus*. — MÜLLER (1892: 203): “Mexiko”.

*Coluber deppii* [sic]. — BOULENGER (1894: 66, incl. BMNH 1868.4.7.38, 1871.2.7.35, 1892.2.8.52, 1894.4.26.7, see Appendix 1).

? *Coluber melanoleucus* Daudin, 1803 [partim, intermedius]. — BOULENGER (1894: 70): “Mexico” (BMNH 1845.2.21.95, see Note 29).

*Pituophis deppei* [sic]. — GÜNTHER (1895: 124 incl. footnote).

*Epiglottophis pleurostictus*. — COPE (1900: 861); WERNER (1929: 82, 88).

? *Pituophis pleurostictus* (“Duméril et Bibron”). — MERTENS (1930: 159): “St. Catharina, Berge bei Mexiko” (Santa Catarina is a frequent place name in that area and *P. lineaticollis* (Cope) cannot be ruled out).

*Pituophis d. deppei* [comb. nov.]. — STULL (1932: 1).

*Pituophis deppei jani* [comb. nov.]. — STULL (1932: 2, see Variation, Note 14).

*Pituophis d. deppei* [partim]. — TAYLOR (1939: 463): excl. FMNH 117000 (no. “5558”), “near Sabinas Hidalgo, Nuevo León” (Fig. 17A, see Discussion incl. Fig. 14 or DUNKLE & SMITH, 1937: *P. “sayi”*); STULL (1940: 25, Table 2, see Implications, Notes 16, 40).

*Pituophis catenifer affinis* Hallowell, 1852 [partim, intermedius]. — SMITH (1943: 458, Table 27): “21 miles north of Saltillo”, Coahuila (USNM 105302, see Discussion incl. Table 5).

*Pituophis sayi affinis* [partim, intermedius]. — TAYLOR (1952: 813): “2 kilometers east of Illescas, 7000 ft.”, San Luis Potosí (LSUMZ 2426, Fig. 15B, see Discussion incl. Table 5).

*Pituophis catenifer affinis*. — TAYLOR (1953: 1606): “6 mi. E of El Huisache” (El Huisache), San Luis Potosí (LSUMZ 4369).

*Pituophis d. deppei* [partim]. — DUELLMAN (1960: 605–606): excl. UMMZ 113634, “Llano Grande” (see Note 28) and USNM 110892, “Pájaro [Pájaro] Verde, Veracruz” (Fig. 11B, see Discussion incl. Fig. 10C: Table, Note 26, or SMITH, 1943: 460).

*Pituophis d. deppei* [partim, intermedius]. — DUELLMAN (1960: 605, Fig. 1 [map]): “Semachique”, Chihuahua (FMNH [“CNHM”] 11825, Fig. 15A, see Discussion incl. Table 5).

*Pituophis l. lineaticollis* (Cope, 1861b) [partim]. — DUELLMAN (1960: 608, Fig. 1 [map]): “40 km. N of Ciudad México” (Mexico City), México State (UIMNH 36223, see Discussion).

“*Pituophis deppei deppei* X *deppei jani*” [partim, intermedii]. — DIXON *et al.* (1962: 95): “between Matehuala and Villa Hidalgo”, San Luis Potosí (KU 67706 [CONANT, 1965] and unspecified specimens of KU 67694–711 series, see Note 9, Fig. 16).

*Pituophis d. deppei* [partim, intermedius]. — CONANT (1965: 22–23): “25 miles south of Matehuala” (vic. San Gabriel), San Luis Potosí (KU 67706, see Note 9, Discussion incl. Fig. 16).

*Pituophis melanoleucus affinis* [partim, intermediii]. — CONANT (1965: 19): “Río Florida”, Zacatecas (AMNH 85251) and “Guatimapé”, Durango (AMNH 88822, see Discussion incl. Table 5).

*Pituophis lineaticollis* [partim]. — DUELLMAN (1965: Table 8): “Sierra Ajusco”, Mexico City (see Discussion).

*Pituophis melanoleucus* [partim, intermediii]. — MORAFKA (1977: 76, Map 114): unspecified vouchers from Northern Plateau incl. vic. “Dr. Arroyo”, Nuevo León (see Discussion incl. Fig. 16, Note 29).

*Pituophis melanoleucus* “Hallowell” [partim]. — VAN DEVENDER & LOWE (1977: 46): “the Yepómera vicinity” (UAZ 34883, see Discussion, Note 40).

*Pituophis d. deppei* [partim]. — FLORES-VILLELA *et al.* (1991: 192): excl. “Río Florida, 26 Km S Puente de Canutillo”, Durango (MZFC 3488, see Note 16).

*Pituophis melanoleucus affinis* [partim]. — LEMOS-ESPINAL *et al.* (1994: 169, Table 1): “8.3 mi NW Ojo Caliente”, Zacatecas (PSC 1367).

*Pituophis catenifer affinis* [partim, intermedius]. — LEMOS-ESPINAL *et al.* (2004c: 209): (“Arenapanuchi” [Areponapuchic], UBIPRO 11678 [UCM 65738], see Discussion incl. Table 5 or LEMOS-ESPINAL & SMITH, 2007a: 609, Mapa 96).

*Pituophis deppei* [intermedius]. — LEMOS-ESPINAL *et al.* (2004a: 81): “Guicorichi, near Chinipas” or “Huicorichi”, Chihuahua (UBIPRO 11857 [UCM 65821], see Discussion incl. Table 5, Notes 16, 29: photos).

*Pituophis deppei* [partim]. — CANSECO-MÁRQUEZ & GUTIÉRREZ-MAYÉN (2010: 227): excl. CNAR 150, “cerca de [Near] Tehuacán”, Puebla (see Discussion incl. Fig. 10C: Table).

*Pituophis deppei* [partim, intermedius]. – RORABAUGH & LEMOS-ESPINAL (2016: 477, dorsal head view photo): “Culiacan, Sinaloa” (UAZ 25815, see Discussion incl. Table 5, Note 30).  
*Pituophis catenifer* [affinis] [partim]. – LEMOS-ESPINAL et al. (2018: 364, Map 71): “between La Soledad and Dr. Arroyo”, Nuevo León (UAZ 45528, see Note 28).

## Taxonomy

Conventionally, two subspecies of Deppe’s bullsnake are recognized, namely *Pituophis d. deppei* (Duméril, Bibron & Duméril, 1854) from the Sierra Madre Occidental across the Plateau to the Orizaba Range and *P. deppei jani* (Cope, 1861a) auct. in the Sierra Madre Oriental south to Hidalgo and Querétaro (e.g., STULL, 1932, 1940; DUELLMAN, 1960; HEIMES, 2016; see Variation, Distribution).

Bullsnake and other names published in the ‘Prodrome [...]’ including *E.[laphis] Deppei* [sic] Duméril, 1853, the authorship used by various later to recent herpetologists (e.g., DUELLMAN, 1960; LEMOS-ESPINAL et al., 2004a; LEMOS-ESPINAL & SMITH, 2007a–b; CANSECO-MÁRQUEZ & GUTIÉRREZ-MAYÉN, 2010; LEMOS-ESPINAL & DIXON, 2013, 2016; ENDERSON et al., 2014; LOC-BARRAGÁN & AHUMADA-CARRILLO, 2016; RORABAUGH & LEMOS-ESPINAL, 2016; LEMOS-ESPINAL et al., 2018, 2019), are nomina nuda (see chresonymy of *Pituophis mexicanus* D. B. & D.).

BOCCOURT (1888: 669) doubted whether *Elaphis deppei* and *E. pleurostictus* Duméril, Bibron & Duméril, 1854 were systematically distinct, noting difficulty to separate these varieties (“Il est difficile de bien distinguer cette variété [*deppei*] du *Pituophis pleurostictus*”) on the basis of reputedly unimportant (“très-peu importantes”) discrepancies in head scales and colour pattern (see Descriptions and Note 8). The illustrated *P. “pleurostictus, var. Deppei”* (sic, l.c.: Pl. 42.3, MNHN ?) is a *P. lineaticollis gibsoni* Stuart, 1954.

Possibly respecting page priority, BOULENGER (1894) listed *Elaphis pleurostictus* as the top-ranked available binomen under *Pituophis deppei* (“*Coluber deppei*”), but he considered the collector’s patronym to be the correct specific name (see Note 8). Almost simultaneously, GÜNTHER (1895) fixed the precedence of “*deppii*” because of “the difficulty of recognizing” *E. pleurostictus* that was “unduly increased” by its supposedly South American origin (“Monte Video”, see next section). Nevertheless, COPE (1900), and WERNER (1929) or MERTENS (1930) preferred the species-group name *pleurostictus* to “*deppii*” or *deppei*, respectively.

In a taxonomic round-up encompassing *Pituophis mexicanus* D. B. & D. (see following taxon), SMITH & TAYLOR (1950a) restricted the type localities of *Elaphis deppei* D. B. & D. as well as *E. pleurostictus* D. B. & D. and the putative junior synonym *P. deppei pholidostictus* Jan to Teotihuacán in NE México State (Fig. 1, see next section, Implications, Discussion, and Note 22).

JAN (1863: 59) had introduced *P.[ituophis] Deppei* (sic) var. *pholidostictus* upon specimens deposited in

the Berlin and Leiden collections (“Mus. Berol.” and “Leida”). STULL (1940) and SMITH & TAYLOR (1945) listed Jan’s taxon under *P. deppei* (nominotypical subspecies), an opinion accepted until today (e.g., DUELLMAN, 1960; WALLACH et al., 2014). Based on the Berlin syntypes (ZMB 1737–38, “leg. Deppe”, see next section), HALLERMANN (2007) clarified the identity of *P. “deppi* [sic] *pholidostictus* Jan”, 1863, viz. a junior subjective synonym of the Central Mesoamerican *P. lineaticollis* (Cope, 1861b). [Note 2]

The syntype status of RMNH 402 (“Mus. Berlin”, no further data, see next section and Note 4) and ZMB 1737–38 is not affected by DUELLMAN’s (1960: 604) inadvertent quotation of ZMB 1738 as the “[t]ype” of *Pituophis deppei pholidostictus* Jan because this does not meet the conditions of Art. 74.5 (ICZN, 1999). At the same time, we agree with SAVAGE & McDIARMID (2017: 14, 46, 76) that the single character state in the description of *P. d. pholidostictus*, namely six sublabials in contact with the inframaxillaries (“6 Sottolabiali a contatto degl’ inframaxillari”, JAN, 1863), does not sufficiently differentiate the taxon from “*P. pleurostictus (Elaphis — Dum. e Bibr.)*” with “5” scales along the chin shields (see Notes 2, 10). Though, indications in the ‘Elenco [...]’ (place of custody, origin) allow to track down the syntype series of *pholidostictus* Jan, 1863 and the lack of diagnostically relevant morphological features does not qualify for a nomen nudum. [Note 3]

## Types and Deppe

Originally, all later type material of *Elaphis deppei* (holotype, see Note 4), *E. pleurostictus*, and *Pituophis deppei pholidostictus* (syn. *P. lineaticollis*) had been deposited in Berlin (ZMB). One among the *E. pleurostictus* series (today MNHN 6616) was moved to Paris by initiative of “M. le professeur Valenciennes” (DUMÉRIL et al., 1854: 246), perhaps as a result of his visits paid to the Prussian Academy in 1826, accompanying Alexander Humboldt back to Germany, and 1829 (see below and Note 7: *Chirostoma* spp.). In 1843, RMNH 355 and, probably, a later syntype of *P. d. pholidostictus* (RMNH 402) from “Mexique” were registered at the Leiden Museum without mention of a collector. After these exchanges, five Mexican *Pituophis* spp. received from Ferdinand Deppe (1794–1861) continued in the ZMB collections. [Note 4]

Lamentably little information exists about most herpetological specimens collected by F. Deppe. All zoological material including “a quantity of reptiles” from his first Mexican mission between mid-December 1824 and January 1827 “was bought by the Zoological Museum of Berlin” (STRESEMANN, 1954), but only a portion of, for example, bird and fish samples procured during the explorations with Wilhelm Schiede in 1828 and 1829 “had been acquired by the museums of Berlin and Vienna”. They encompass those specimens collected prior to Deppe’s departure from Xalapa to Mexico City at the beginning

of May 1829 (l.c.; PAEPKE *et al.*, 2014). A questionable paratype of the anguid *Gerrhonotus tæniatus* Wiegmann, 1828 (*Abronia tæniata*, NMW 23470, GEMEL *et al.*, 2019; see Note 15) from the first expedition was registered in 1834, and we believe that at least a *Pituophis lineaticollis* from “Mexico” (NMW 26649.1, “1829”, without further data, see Note 22) was obtained from the naturalist’s brother Wilhelm Deppe, a temporary ZMB auditor (see Note 5).

Neither explicit evidence nor any hint pertaining to *Pituophis* spp. can be found in published accounts of Deppe’s travels (LICHENSTEIN, 1826a–b; SCHIEDE, 1829a–c, 1830) or in his correspondence archived in the MNF, the sales catalogue printed and distributed by W. DEPPE (1830), LICHENSTEIN’s (1836) auction prospectus listing additional samples, and in ZMB registers prior to 1855 (see Note 4). At first glance perplexing is the ostensible absence of Mexican bullsnakes in the ‘Nomenclator [...]’ (LICHENSTEIN & VON MARTENS, 1856) that compiles the ZMB amphibians and reptiles present in the mid-fifties of the 19<sup>th</sup> century. Thus, we are convinced that five “*Coronella [...]* Sayi Dekai. (*Ophibolus [...]* B. G. [Baird & Girard] Mexico)” (l.c.: 25) in fact refer to three “*Elaphis pleurostictus* Mus. Ber.” (ZMB 1733–35, “Deppe”) and two “*Elaphis pholidostictus* Wieg.” (ZMB 1737–38, “Deppe”) documented in the simultaneously instigated herpetological ‘Inventarkatalog’ (ZMB 1736 is a Palaeoarctic racer, *Coluber [Hemorrhois] ravergeri* Ménétriés, 1832). The ZMB 1737–38 entries were later underlined with red (indicates type status) and an asterisk, part of a brief comment added by Günther Peters in the 1960’s relying on an old label (“auf dem Etikett: *Pituophis deppei pholidostictus \*JAN\**”), additionally connotes ZMB 1737 as type material. ZMB 1733–35 are so far neglected syntypes of *E. pleurostictus* Duméril, Bibron & Duméril (see next section, Note 8, and Implications). [Note 5]

Hinrich Lichtenstein’s undated compilation of herpetological items among the last two shipments obtained from Deppe (“Verzeichniss der Amphibien des Hr. F. Deppe aus den beiden letzten Sendungen”, Appendix 2, see Note 4) mentions four “*Coluber pholidostictus* N.[obis]” without locality data. The minute cannot be linked to any of the collector’s shipments, and neither the binomen nor the specific epithet appear in the sighted documents related to Deppe. However, the catalogue entry for RMNH 355 (see Note 4) received from the Berlin Museum in 1843 nourishes our impression that Lichtenstein applied “*pholidostictus*” to at least one bullsnake specimen different from *Arizona lineaticollis* Cope, viz. Jan’s taxon and the one that Arend Friedrich August Wiegmann had in mind. Reversely, the original record of RMNH 402 (syntype of *P. deppei pholidostictus*, syn *P. lineaticollis*) in the Leiden collection says “*Coluber Deppei*” (sic). [Note 6]

“Montevideo”, the reputedly South American (“Amérique du Sud”) type locality of *Elaphis pleurostictus* Duméril, Bibron & Duméril, 1854 established by original indication upon MNHN 6616 (lacks further information incl. entry date), is the only reported locality data other

than “Mexico” for any bullsnake gathered by Deppe. It is true that no explicit evidence links this syntype to any collector but the site name hardly leaves qualms about the issue. LICHENSTEIN & VON MARTENS (1856: 13) enumerated a teiid lizard (“*Cnemidophorus [...]* Sackii [sic] Wieg.”, immature holotype) from “Montevideo”, and at least two lower vertebrate species among Deppe’s third shipment realized in winter 1825/26 (Lichtenstein’s “Verzeichniss [...] seiner dritten Sendung aus Mexico”, Appendix 2) originate from that place. These animals and plants, which arrived in Berlin on March 20, 1826, comprise three freshwater fishes (“*Atherina gigantea* N.[obis]”, n° 1–3) and all five syntypes of *Sceloporus grammicus* Wiegmann, 1828 (n° 11–15, “*A.[gama] grammica* N.[obis]”). [Note 7]

The freshwater silverside genus *Chirostoma* Swainson, 1839 (Atherinopsidae) is largely confined to the Central Plateau, and the type species *Ch. humboldtianum* (Valenciennes in Cuvier & Valenciennes, 1835) is recorded from, for example, former “Lago de Texcoco” (BARBOUR, 1973: 109). This proximity and the absence of other sites called Montevideo in the area under consideration argue for the assumption that the type locality of this atherinopsid, *Elaphis pleurostictus* D. B. & D., and *Sceloporus grammicus* Wiegmann possibly refers to the former hacienda at today’s Colonia Montevideo in Alcaldía Gustavo Adolfo Madero (G. A. M. Borough), Mexico City, and is certainly situated between the metropolis and Texcoco Municipality in México State (see Implications).

## Descriptions

Apart from irrelevant scale data, DUMÉRIL *et al.* (1854: 268) reported two supralabials entering the eye (4<sup>th</sup>–5<sup>th</sup>, total number not indicated), 233 ventrals, 67 paired subcaudals, 27 midbody rows, and an overall length of 1'658 mm (“du bout du museum à l’extrémité de la queue”, tail “0<sup>m</sup>23”) in the unidentified holotype of *Elaphis deppei* Duméril, Bibron & Duméril (see Note 4). Oddly enough, the account describes the dorsal colour pattern in terms of characters that are not present, viz. the lack of black lines on the pileus or absence of a temporal streak and in particular no longitudinal bands on the nape (“Point de lignes noires sur la tête, ni de bandes longitudinales sur la nuque, ni de raie allant de l’œil à l’angle de la bouche”).

The French authors had not seen the holotype of *Elaphis deppei* as evidenced by an earlier remark (“du musée de Berlin, en communication”, DUMÉRIL, 1853) or the indication of the original place of custody (“Musée de Berlin”, DUMÉRIL *et al.*, 1854) and a note (“Observations”) that the description of the species relies on data for a “*Coluber Deppei*” (sic) provided by Hermann Schlegel in Leiden (see Notes 4, 6). When penning the lines to his Paris colleagues, the informant might have had in mind a comparison with RMNH 402 (a later syntype of *Pituophis deppei pholidostictus* Jan) featuring pronounced longitudinal neck marks (see Taxonomy,

**Table 1.** Morphological data in type specimens of *Elaphis deppei* and *E. pleurostictus* Duméril, Bibron & Duméril (leg. Ferdinand Deppe). Acronym and accession code, number of prefrontals (prf), supralabials (spl) and scales in eye contact (lower figures), number of ventrals (ven, incl. preventrals), subcaudals (sbc), midbody scale rows (msr), and dorsal blotches (dbl) along trunk (above) and tail as well as pertinent details (gender, status, illustrations). Number of midbody rows in MNHN 6616 fide Ivan Ineich.

Specimen	prf	spl	ven	sbc	msr	dbl	remarks
(RMNH ?)	—	— 4–5	(? +) 233	67	27	— —	unidentified holotype of <i>Elaphis deppei</i> (data fide DUMÉRIL <i>et al.</i> , 1854), see Note 4
MNHN 6616	2	8 4	2 + 219	53	29	29 9	♀ syntype of <i>Elaphis pleurostictus</i> , see Note 8 Fig. 2A
ZMB 1733	2	8 4–5	3 + 211	61	29	35 14	♂ syntype of <i>E. pleurostictus</i>
ZMB 1734	2	7 3–4	2 + 227	58	29	38 11	♀ syntype of <i>E. pleurostictus</i> Fig. 2B
ZMB 1735	2	8 4–5	3 + 212	54	27	35 10	♂ syntype of <i>E. pleurostictus</i> observed co-minimum for total body scales (266)



**Fig. 2.** Dorsal and right lateral head views of two syntypes of *Elaphis pleurostictus* Duméril, Bibron & Duméril, MNHN 6616 (A, skull removed) and ZMB 1734 (B). Not to scale. Courtesy of Ivan Ineich (A).

Note 3, and preceding section) followed by dark-edged, oblong ovals down to midbody. These circumstances explain the limited data presented for *E. deppei* (e.g., lack of most head scale details, dentition) or virtually identical wording concerning the dorsal colour pattern as in the diagnosis of *E. pleurostictus* Duméril, Bibron & Duméril.

The description of *Elaphis pleurostictus* is based on various specimens and the specific epithet alluding to the dark lateral dotting was adopted from the catalogue name used for the Berlin specimens (ZMB 1733–35, see preceding section and Note 6) as mentioned in the synonymy (“*Coluber pleurostictus*. Musée de Berlin”)

and elsewhere (“la dénomination que nous empruntons au Musée de Berlin”, DUMÉRIL *et al.*, 1854: 244–245). The diagnosis (“Caractères”) mentions two supralabials (4<sup>th</sup>–5<sup>th</sup>) entering the eye but the descriptive text says one out of eight in MNHN 6616 from “Montevideo” (“l’individu de notre collection”, Fig. 2A). Except for the eponymous black-dotted flanks (“flancs piquetés de noir”), the general dorsal colour pattern is identical with the one of *E. deppei* (“Point [...] ni de raie s’étendant depuis l’œil jusqu’à l’angle de la bouche”, see above). Dentition counts based on the Paris syntype are 17/20 (maxillary), 10 (palatinum), and 13 (pterygoid, l.c.: 245). [Note 8]

**Table 2.** Geographic variation of the number of body scales and dorsal marks in *Pituophis deppei* males (top), females (middle line), and juveniles or specimens of unknown gender (bottom; range, sample size, mean, standard deviation). See Fig. 7 and Appendix 1 for groups and Figs 10B–C as to individual counts of Michoacán specimens (except TNHC 25426, UTA 6047–48, group J, partim) and southeastern corner (K, partim), and Note 40 for UAZ 34883 (Chihuahua, not tabulated).

Area	ventrals	subcaudals	ventrals + subcaudals	midbody scale rows	body blotches
A	217–224 (5, 220.4±2.7)	58–64 (3, 61.7±3.2)	280–287 (3, 283.3±3.5)	29–30 (5, 29.2±0.4)	30–42 (5, 37.2±4.4)
	218–221 (2, 219.5±2.1)	65–67 (2, 66.0±1.4)	283–288 (2, 285.5±3.5)	29 (2, 29.0±0.0)	34–43 (2, 38.5±6.4)
	—	—	—	—	31 (1, 31.0±0.0)
B	229–239 (3, 233.3±5.1)	60–66 (4, 62.5±2.5)	294–301 (3, 296.7±3.8)	27–29 (3, 27.7±1.2)	30–33 (3, 32.0±1.7)
	224–228 (2, 226.0±2.8)	62–66 (2, 64.0±2.8)	290 (2, 290.0±0.0)	—	—
C	225–235 (5, 229.2±4.5)	56–69 (5, 62.4±5.4)	285–296 (5, 291.6±4.2)	28–29 (4, 28.8±0.5)	23–30 (5, 26.2±2.8)
	223–234 (6, 227.7±4.0)	53–66 (6, 58.2±4.3)	280–292 (6, 285.8±5.0)	27–31 (6, 29.7±1.6)	23–32 (6, 28.2±3.2)
	226–232 (3, 228.7±3.1)	53–55 (3, 54.0±1.0)	281–286 (3, 282.7±2.9)	29–30 (4, 29.3±0.5)	26–28 (3, 27.0±1.0)
D	225–235 (6, 229.0±4.0)	61–66 (6, 64.2±1.9)	288–301 (6, 293.2±5.6)	29–31 (6, 29.3±0.8)	21–25 (6, 23.2±1.3)
	228 (1, 228.0±0.0)	—	—	31 (1, 31.0±0.0)	23 (1, 23.0±0.0)
	—	—	—	—	—
E	223–225 (5, 224.4±0.9)	57–64 (4, 61.0±3.6)	280–289 (4, 285.3±4.1)	29–31 (5, 29.4±0.9)	30–36 (6, 32.2±2.3)
	220–227 (4, 222.8±3.4)	59–60 (3, 59.3±0.6)	279–287 (3, 283.0±4.0)	29–31 (4, 30.0±1.2)	28–35 (5, 31.0±2.9)
	218–232 (6, 225.5±5.5)	58–63 (5, 60.4±2.1)	278–294 (5, 285.8±7.5)	29–31 (5, 30.2±1.1)	24–38 (10, 30.5±3.9)
F	216–226 (7, 222.0±4.0)	55–65 (7, 60.7±3.6)	271–291 (7, 280.7±7.0)	27–31 (7, 29.6±1.6)	35–50 (7, 41.0±4.9)
	212–225 (6, 219.7±5.8)	57–66 (5, 61.4±3.8)	275–286 (5, 280.8±4.3)	29–31 (6, 29.3±0.8)	33–44 (5, 39.6±4.4)
	212–222 (7, 215.9±3.8)	55–68 (8, 61.6±4.3)	273–284 (7, 278.4±4.4)	29 (3, 29.0±0.0)	36–45 (8, 39.5±3.0)
G	219–232 (9, 224.2±3.9)	60–67 (9, 63.2±2.7)	282–292 (9, 287.4±3.8)	29–31 (9, 29.4±0.9)	31–43 (9, 37.0±4.5)
	217–231 (9, 225.2±4.9)	57–62 (5, 59.0±2.3)	280–292 (5, 286.6±5.0)	29–30 (7, 29.3±0.5)	29–41 (7, 34.0±4.4)
	219–232 (2, 225.5±9.2)	56–64 (2, 60.0±5.7)	283 (1, 283.0±0.0)	29 (2, 29.0±0.0)	41 (1, 41.0±0.0)
H	—	—	—	—	—
	220–223 (2, 221.5±2.1)	53–63 (2, 58.0±7.1)	276–283 (2, 279.5±4.9)	29–31 (2, 30.0±1.4)	38–39 (2, 38.5±0.7)
	229 (2, 229.0±0.0)	52 (1, 52.0±0.0)	281 (1, 281.0±0.0)	27 (1, 27.0±0.0)	30 (1, 30.0±0.0)
I	222–232 (6, 226.8±4.3)	55–68 (5, 61.8±5.3)	278–295 (5, 289.2±7.0)	27–31 (6, 27.7±1.6)	28–39 (6, 33.5±4.2)
	225–235 (4, 228.5±4.4)	56–62 (2, 59.0±4.2)	283–289 (2, 286.0±4.2)	27–30 (3, 28.7±1.5)	27–38 (4, 31.8±4.6)
	225–230 (2, 227.5±3.5)	56–61 (3, 58.0±2.6)	282–291 (2, 286.5±6.4)	29–31 (3, 29.7±1.2)	31–42 (5, 36.4±3.9)
J	209–228 (31, 216.8±4.8)	50–66 (29, 59.3±3.8)	268–285 (28, 276.4±4.0)	27–31 (30, 28.6±1.1)	30–48 (28, 36.6±4.6)
	213–227 (9, 218.2±4.8)	46–58 (7, 52.3±4.0)	260–285 (7, 270.0±7.7)	28–29 (11, 28.7±0.5)	29–44 (9, 37.9±4.8)
	213–227 (3, 218.0±7.8)	56–63 (4, 59.5±2.9)	272–283 (3, 276.3±5.9)	27–31 (3, 28.3±2.3)	29–44 (5, 36.4±5.3)
K	212–226 (9, 218.8±4.5)	57–68 (9, 62.8±3.6)	269–292 (7, 281.6±7.1)	27–29 (9, 28.2±0.8)	26–36 (8, 32.8±3.6)
	216–225 (8, 220.9±3.1)	56–65 (8, 60.3±3.3)	274–288 (8, 281.1±4.5)	27–30 (8, 28.0±1.2)	28–38 (7, 32.6±3.8)
	217–229 (5, 223.0±5.2)	61–65 (3, 62.7±2.1)	279–289 (3, 284.7±5.1)	29–31 (4, 29.8±1.0)	32–40 (6, 36.3±3.1)

## Diagnosis

Two prefrontals (exceptionally 3, once 1 and  $\geq 4$  scales), usually two (4<sup>th</sup>–5<sup>th</sup>) out of eight supralabials (rarely 7, occasionally 9) in contact with eye, parietal mostly large (undivided), dorsals with two apical pits and keeled mid-dorsal series, in 27–31 rows at midbody, 209–239 ventrals ( $\delta\delta$  209–239,  $\varphi\varphi$  212–235), anal plate entire, 46–69 paired subcaudals (50–69, 46–67, resp.), total body scales 260–301 (266–301, 260–292), and 23–45 (21–50) dark mid-dorsal blotches on trunk (Tables 1–2, see Note 11 for potentially higher northwest body scale

counts as well as preceding and next section and Note 40 as to UAZ 34884 and UCM 67211).

## Variation

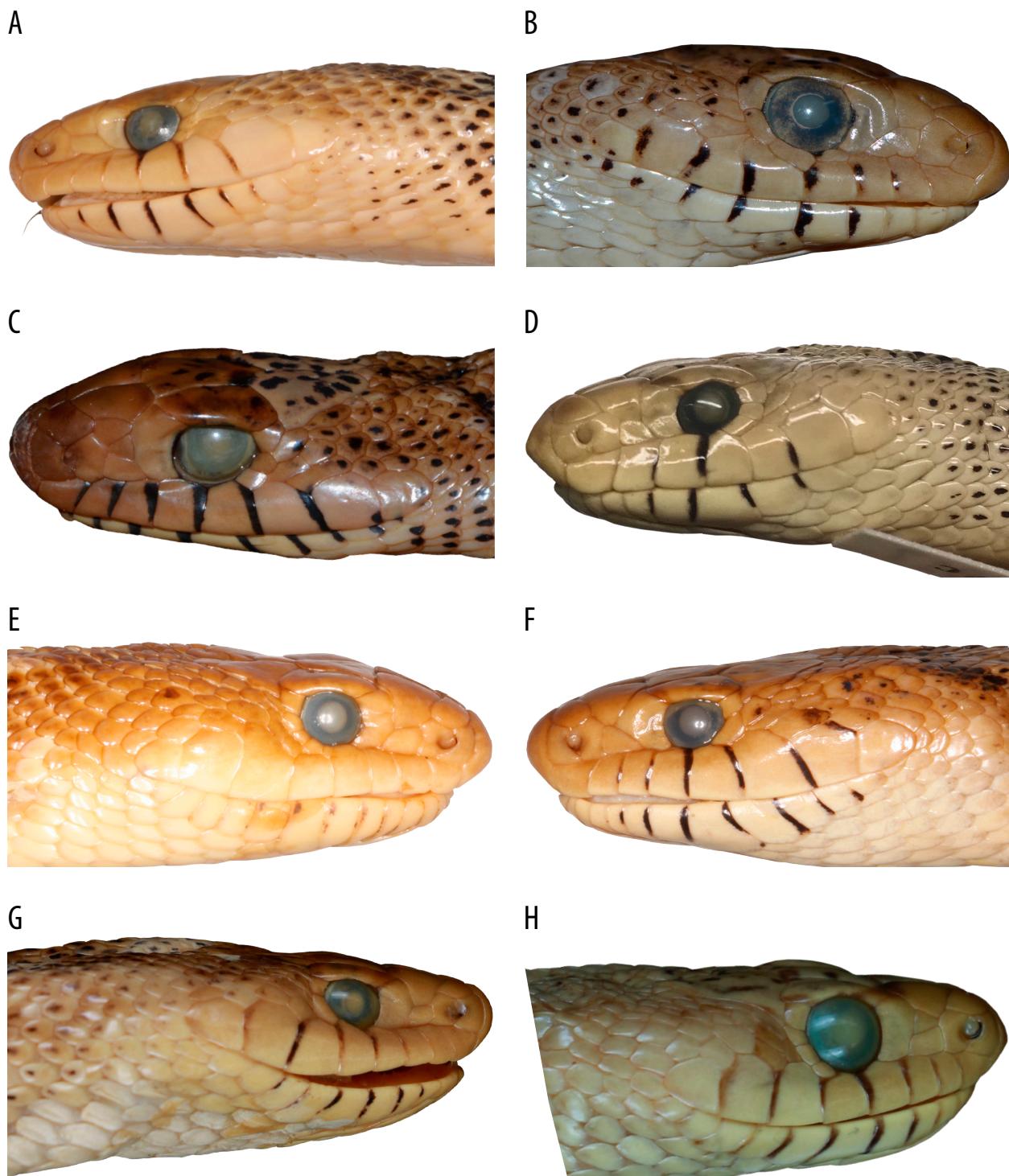
Pileus in studied material (Appendix 1) shows nine shields except in specimens with irregular prefrontals (Fig. 16, see Note 9) or parietals, viz. FMNH 33565 and 105481 (Figs 3E–F, antero-median portion of right shield separated in each, posterior tip of both fragmented in FMNH 33565, FMNH 105481 with partially divided frontal),



**Fig. 3.** Dorsal and right lateral (A–C) head views of *Pituophis deppei* AMNH 147886 (A, see Notes 9, 27), FMNH 106079 (B, see text and Note 9), MCZ 80910 (C, see Notes 9–10, 29), AMNH 4382 (D), FMNH 33565 (E), FMNH 105481 (F), and USNM 238337 (G). Not to scale. Courtesy of Joshua Mata (B), Joseph Martinez (C), Lauren Vonnahme (D), Aaron Mercer (E–F), and James Poindexter (G).

SDSNH 42711 (right parietal and posterior edge of left broken up), TNHC 29901 (left broken up), and TNHC 89287 (antero-median portion of right detached), or AMNH 4382 with semi-divided shields (Fig. 3D, deep

curved suture through both posteriorly, lateral edge of left apart). Smaller than usual parietals are found in, for example, AMNH 4383 (broken up posteriorly) or CNAR 15654 and UTA 5994 (both larger shields incompletely

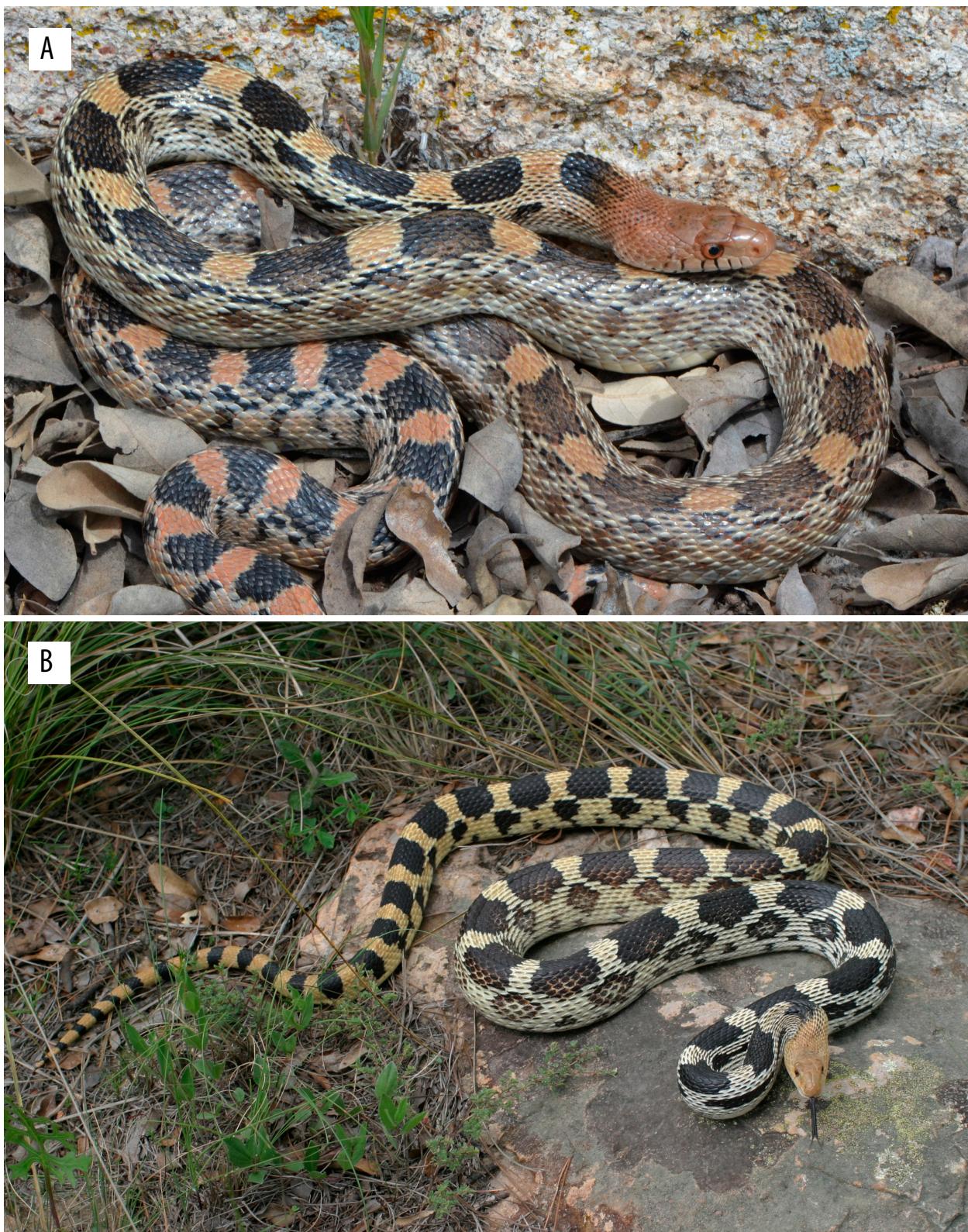


**Fig. 4.** Lateral head views of *Pituophis deppei* AMNH 110415 (A, shows standard scale configurations except narrow eye contact of 4<sup>th</sup> supralabial), CNAR 10939 (B), MZFC 621 (C), TCWC 54817 (D), UTA 4552 (E), UTA 6047 (F, standard configurations), and UTEP 4343–44 (G–H). Not to scale. Courtesy of Toby J. Hibbitts (D) and Muriel Norman & John Wakefield (G–H).

partitioned), and a syntype of *Elaphis pleurostictus* Duméril, Bibron & Duméril (ZMB 1735) with large parietals features a horseshoe-shaped suture that separates the antero-median portion of both plates to some degree (similarly running but less distinct suture in AMNH 93428). [Note 9]

The size and shape of the loreal and preocular (large in, e.g., AMNH 127904, FMNH 106079 [Fig. 3B], UTA

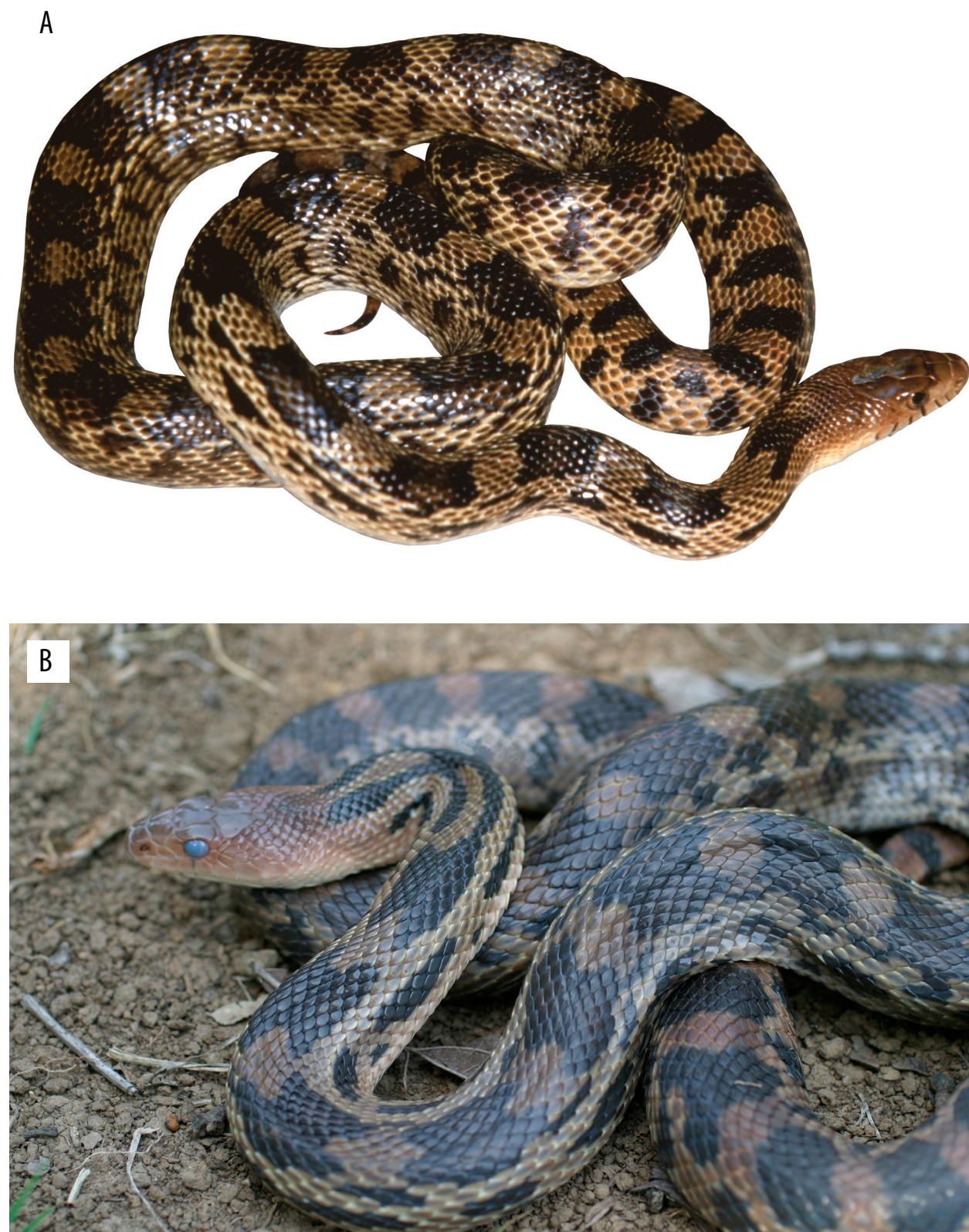
57619) are variable. Two loreals are found in AMNH 19849 and 19852 (see Note 9 incl. remark to MZFC 621) and the scale is absent on both sides in UTA 57619. Usually two or three postoculars are present, four in AMNH 92738 (only left side data) and UTEP 4344 (Fig. 4H). The supralabials total eight (occasionally 9, rarely 7) and the fourth and fifth normally enter the orbit (5<sup>th</sup>–6<sup>th</sup> or 3<sup>rd</sup>–4<sup>th</sup>, resp.). The extent of the eye contact of both in-



**Fig. 5.** *Pituophis deppei* from the Mesa Las Preñas (Tableland, 2'425 m) in El Llano Municipality (Aguascalientes, A) and “near highway 40 in Durango just east of the border with Sinaloa” (B, courtesy of Ian Recchio).

volved supralabials is variable and may actually occupy the width of merely one regular infraorbital scale (TCWC 54817, UTEP 4343, Figs 4D, 4G), as is the case with a syntype of *Elaphis pleurostictus* (ZMB 1733). Another name-bearer (MNHN 6616, Fig. 2A) shows a single (4<sup>th</sup>) supralabial in eye contact, and this condition is unilat-

erally present in AMNH 85247, MCZ 80910 (Fig. 3C), and UTA 4552 (Fig. 4E). Both latter specimens have two postsuboculars on the right side (large and small scute in MCZ 80910). In SMF 95022, a slender elongated scale excludes the fifth right supralabial from the orbit. A single supralabial (4<sup>th</sup>, unilateral data) entering the eye



**Fig. 6.** *Pituophis deppei* UMMZ 114596 (A, see DUELLMAN, 1960: Pl. 45.1) and *P. cf. deppei* (B, see Note 12) from near Cumbres de Acultzingo, Veracruz. Courtesy of Jonathan A. Campbell (A) and Ian Recchio (B).

and a large left postsubocular occur in LACM 114124. This configuration is also present on the right side in AMNH 68361 (left unknown) with fused fifth and sixth supralabials. Moreover, a large postsubocular is observed in CAS 96075 (only left count), CNAR 706 (right, left smaller), and FMNH 33564 (right, narrow contact of 5<sup>th</sup>

supralabial with orbit on both sides), and a smaller scute is found in various specimens from virtually throughout the distributional range. In CNAR 10939 (Fig. 4B) from México State, the anterior and posterior suboculars (one scale each) form a complete row of scales that excludes any supralabial from the eye on both sides. [Note 10]

Our maximum number of ventrals (239, Table 2) is from FMNH 106079 (♂). Two additional males (LSUMZ 4369, MCZ 19546) and a female (TNHC 82481) have 235 plates and SDSNH 57003 (♀) shows 234. The minimum of 209 is based on AMNH 4382 (♂, plus 2 pre-ventrals, “211” fide STULL, 1940: Table 2) from SE Zacatecas (see next section), CNAR 25285 (♂, plus 3 scales) from the Hidalgo-Querétaro border, and UMSNH 1890 (♂, plus 3) from Morelia, Michoacán. The highest number of subcaudals (69) relies on TCWC 54238, 68 paired scutes occur in UMSNH 73 and USNM 110891 (♂♂), and the maximum in females (67) is from MCZ 80910. As few as 46 subcaudals are observed in CNAR 10939 and we found counts lower than “52” (STULL, 1940: USNM 16442; DUELLMAN, 1960) in another female (49, UMSNH 1829, Fig. 10B: Table) and UMNH 21488 (♂, 50, ibid.; Table 2: group J). The maximum for ventrals and subcaudals (301) derives from FMNH 106079 and MCZ 19546 (♂♂, ♀♀ 292 or fewer scales), and by far the lowest sum (260) is found in CNAR 10939 (♀, see above). UMSNH 1829 (♀, Fig. 10B: Table) and ZMB 1735 (♂, Table 1, see next section for origin) have 266 scutes, 268 are present in AMNH 127904 (♀) and UMSNH 1890 (♂, Fig. 10B: Table), and all specimens belong to group J. SMF 95083 from adjacent Puebla has 269 (212 ventrals, Table 2). The dorsal scales are keeled except on the paraventral and lower lateral rows and arranged in 27–31 series at mid-body. No gender-related dimorphism is discernible in any evaluated scale character. [Note 11]

The maximum total length of “1800 mm” is from LSUMZ 4369 (TAYLOR, 1953: “*Pituophis catenifer affinis*”) and STULL (1940: 27, unspecified specimen) virtually recorded the same size (“1,790” mm). Both “very large males” (USNM 110890–91, SMITH, 1943, 1944) from Hidalgo (near Querétaro state line) merely measure ca. 1’380 mm snout-vent length (Steve Gorte in litt. October 2018). The largest dimension documented in literature (“6-ft, 6-in (2m)”, KARDON, 1995) relies on an individual in captivity.

Our limited dentition data yield 16–20 teeth on the maxillary (n=18), 8–10 on the palatinum (n=6), and 17–21 on the mandibular (n=12). STULL (1940: Table 1, pp. 27, 43) found slightly more on the palatinum (11) and mandibular (22) and recorded 8–14 teeth on the pterygoid. The “Montevideo” syntype of *Elaphis pleurostictus* (MNHN 6616, skull removed) has 17/20 teeth on the maxillaries and 13 on both pterygoids (DUMÉRIL *et al.*, 1854).

The head is unicoloured and without distinct pattern in most adults, or with a dark bar usually between the anterior tip of the supraoculars, erratic spots on the posterior pileus, and the supralabials (in particular infraorbital and posterior scales) narrowly dark-edged. The colouration of the head and nape may be dissimilar from the body (Fig. 5) and, occasionally, the head and neck strikingly differ from the trunk (e.g., BRYSON *et al.*, 2011: Fig. 5, LVT 10639). The dorsum is light grey to stramineous or brownish, with dark longitudinal (rectangular or anvil-shaped), squarish, oval, or round blotches that may convert into narrow transverse bars posteriorly

and do so on the tail (see below for ontogenetic darkening). The hue of the mid-dorsal segment between the dark blotches is often different from the flanks (Fig. 5A). A series of spots and/or highly variable dark marks including longitudinal or transverse streaks extend along the lateral and paraventral portions. The gorge and venter are usually cream to yellowish, uniform throughout to heavily patterned with black all over, and the posterior belly and underside of the tail may turn reddish in adults. [Note 12]

The normal range of dorsal body blotches is 23–45. Fifty are present in UAZ 46785 from Aguascalientes (versus 33–45 blotches in remaining 19 specimens of group F, Fig. 7, Table 2) with tightly compact and laterally connected marks reducing the lighter interspaces on the anterior two thirds of the trunk to small circles (transverse bars posteriorly), which gives the specimen a spotted appearance. UTA 57574 has 48 versus 44 or fewer in 41 *Pituophis deppei* of group J (see Discussion for Michoacán data). Comparatively few blotches occur from Coahuila south to San Luis Potosí (Table 2, see Note 40 as to Chihuahua). The Miquihuana series from the periphery in Tamaulipas (group D, MCZ 19545–50) shows constantly low counts (21–25). The tail bears seven to 17 dark transverse dorsal marks. [Note 13]

*Pituophis deppei jani* (Cope, 1861a) from Coahuila and Tamaulipas to Hidalgo and Querétaro (DUELLMAN, 1960) “is characterized by solid body-blotches that are black anteriorly and brown posteriorly” (instead of “black” throughout in adult *P. d. deppei* auct., “brown” on second half of trunk in juveniles), the “anterior dorsal interspaces six or more scales in length” (against “less than five scales”), “and the absence of dark stripes or rows of spots on the anterior part of the body” (implicitly present in *d. deppei* auct., l.c.: 604, 606). Supposed intraspecific differences in the dorsal colour pattern are refuted by live adults from Tamaulipas (e.g., LEMOS-ESPINAL & DIXON, 2013: 209, upper photo) or Nayarit (LOC-BARRAGÁN & AHUMADA-CARRILLO, 2016: Fig. 1), the reportedly lower number of dorsal body blotches in *P. d. jani* auct. (21–31 versus 27–49 in *d. deppei* auct., DUELLMAN, 1960) does not stand up to scrutiny (Table 2: groups B, E, I), and the subspecies *jani* auct. is poorly defined (e.g., DIXON *et al.*, 1962; see BRYSON *et al.*, 2011: 1577, Fig. 3; see next section for type locality of *P. deppei* sensu stricto). [Note 14]

## Implications

Regional disparity in certain meristic data (Table 2) allow to draw conclusions about the probable provenance of Ferdinand Deppe’s type material. The high number of ventrals (233) and total body scales (300, possibly including preventrals) in the unlocated name-bearer of *Elaphis* [*Pituophis*] *deppei* Duméril, Bibron & Duméril (Table 1, see Note 4) argues against Teotihuacán in NE México State as its potential origin, and the restricted type locality of this taxon (SMITH & TAYLOR, 1950a) seems to be incorrect (see chresonymy, Taxonomy). Rather, the

elevated figures including one of the highest body scale aggregate for the species precisely in the name-bearer clearly position the unidentified holotype within the Hidalgo cluster (Fig. 7, Table 2: group I). Based on all available evidence, we herewith determine the re-established type locality of *E. deppei* D. B. & D. near Zimapán (ca. 20°44' N 99°23' W) in NW Hidalgo close to the border with Querétaro. [Note 15]

Scale counts for the female “Montevideo” syntype of *Elaphis pleurostictus* Duméril, Bibron & Duméril (MNHN 6616, 219 ventrals, 272 total body scale, see Types and Deppe) match data of *Pituophis deppei* AMNH 19850 (♀, 217, 271, resp.) from the metropolitan area. This may also be the origin of the second female syntype of this taxon (ZMB 1734: 227, 285), one of only two *P. deppei* in our study sample with seven bilateral supralabials (see Note 10). Both male syntypes of *E. pleurostictus* D. B. & D. (ZMB 1733 and 1735: 211–212, 266–272, Table 1) show lower counts (incl. co-minimum for sum) and best conform to data for eleven male *deppei* from Michoacán and bordering Guanajuato (209–224, 268–285, Fig. 10B: Table, 266 in ♀ UMSNH 1829). These name-bearers may have been obtained between the México State-Michoacán border region and Mexico City in summer 1825 during the excursion that procured the holotype of *E. [Pituophis] deppei* D. B. & D.

Another series of bullsnakes with unclear origin comprises AMNH 3520–22 and 4382–83 from the “Gulf of California” (STULL, 1940). All five were received from Léon Diguet between 1899 and 1901, and AMNH 3522 is registered from “Real de Pinos, Gulf of California” (KLAUBER, 1941). This is the former name of Pinos, a mining town in SE Zacatecas near the San Luis Potosí state line (Fig. 1), and the pertinent morphological data for AMNH 3520–22 (220–224 ventrals, 279 total body scales, 33–35 dorsal body blotches) fit this group (Table 2: E). The collector visited the Pinos area as well as “Jalisco, Colima y las playas del Golfo de California” (shores of the Gulf of California) during his 1899–1900 mission sponsored by the French Ministry of Public Education (JAUREGUI, 1992). AMNH 4382–83 (♂♂) are remarkable for low ventral counts (209–217, incl. co-minimum), few total body scales (274–281), and unusual characters states within *Pituophis deppei* such as a narrow eye contact of the fifth supralabial and irregular parietals (Fig. 3D, see preceding section). Most likely, these males were obtained in 1901 between the federal capital (209–228 ventrals and sum 271–283 in 16 ♂♂ from the vicinity of Mexico City, see Note 22) and Puebla City (see Variation, SMF 95083) when Diguet travelled to the latter destination (l.c.).

## Distribution

*Pituophis deppei* inhabits the region delimited by the Sierra Madre Occidental, the Transvolcanic Belt and Orizaba Range including contiguous areas as far as the

Tehuacán Valley (Southern Plateau), the Sierra Madre Oriental north to central Nuevo León and S Coahuila, a deeply convex bulge (apex south of the Río Aguanaval drainage) through Zacatecas to near 25° N latitude on the Northern Plateau in central Durango, and the Pacific Cordillera. Probably, *P. deppei* occurs in NW Durango and over a good part of the Sierra Tarahumara. In deed and truth, however, we are not aware of published or otherwise documented locality data for any *Pituophis* spp. from the borderlands of Sinaloa, Chihuahua, and Durango, a huge inaccessible and poorly explored territory of the Sierra Madre Occidental and its foothill areas (Fig. 16, see Notes 28, 30). Deppe’s bullsnake is on record for the Oteros Valley (Maguarichic, Mojáracich; LEMOS-ESPINAL *et al.*, 2004d: Photos 115–116; BRYSON *et al.*, 2011; see Note 17) in Chihuahua, ca. 400 km air-line distance northwest from the confirmed main range, and in the municipalities of Moris (Mesa del Agua), Temósachic (vic. “Arroyo Hondo”, Yepachic) north to at least 29° N latitude (Yepómera), probably in-between Ocampo, and in the Yécora Valley, Sonora (Fig. 7, see end of Discussion and Notes 40–42). [Note 16]

Within its main range, *Pituophis deppei* occupies Chihuahuan Desert associations in S Coahuila and SW Nuevo León across NE Zacatecas and most of San Luis Potosí (see Note 16 and below) as well as mesquite grassland, cactus-thornscrub coppice, oak forest and the pine-oak zone, or cultivated land on the Mexican Plateau between the western limit of the cloud forest (Sierra Madre Oriental south to Sierra Negra) and the Sierra Madre Occidental including the oak belt along the Pacific versant. In places, Deppe’s bullsnake is common; MICHEL-PARRA *et al.* (2014) registered thirty observations within a year of field work (2013) at Laguna Zapotlán in Jalisco.

Remarkable is the absence of records from pine-oak forest (Fig. 1) in Nuevo León and SW Tamaulipas where *Pituophis deppei* is known only from the vicinities of Miquihuana and Bustamante south to the Tula Depression and from east of the Sierra Los Quemados in the semi-arid Jaumave Valley (e.g., AMNH 107292), Palmillas Municipality, that empties into the Gulf draining Río Chihue (Upper Tamesi). Deppe’s bullsnake avoids the deciduous forest zone or areas farther east in Tamaulipas and SE San Luis Potosí where it is not on record beyond the Sierra Alaquines. Actually, there seem to exist no documented collecting nor observation sites for the triangle from the vicinity of Ciudad del Maíz in the northern portion of this mountain range south to the Sierra Gorda (NE Querétaro, incl. Extoraz Valley) into NE Guanajuato, and west to the larger San Luis Potosí City area (Fig. 7).

Published locality data for Querétaro (e.g., DUELLMAN, 1960; DIXON *et al.*, 1972; BRYSON *et al.*, 2011) exist to east of Pinal de Amoles (ca. 99°30' W longitude, DIXON & LEMOS-ESPINAL, 2010: TCWC 37716). TNHC 82481 and further specimens of that series from the periphery in Hidalgo (vic. Zacualtipán, incl. TNHC 82482–86, see Note 36) were collected next to the northernmost known occurrence in Veracruz at Huayacocota (20°32' N 98°29' W, BRYSON *et al.*, 2011: LVT 10655). *Pituophis*

*deppei* lives in N Puebla and at short distance beyond the border west of Perote (Edgar A. Bello-Sánchez in litt. January 2019) in Veracruz including Frijol Colorado (19°35' N 97°21' W). The species is likely to occur in the Cerro Cofre de Perote (Mt.) area (HEIMES, 2016: Map 54, see Fig. 7) but two locality records from Veracruz listed in PÉREZ-HIGAREDA & SMITH (1991), namely San José Acateno in the littoral and the state capital Xalapa, rely on old references and are most certainly erroneous (see Note 16 for further doubtful Veracruz records).

The presence of Deppe's bullsnake in "southern Veracruz" as reported by DUELLMAN (1960) is based on seven specimens including a *Pituophis* cf. *lineaticollis* (USNM 110892, Fig. 11B, see Discussion and Note 26) and possibly all (incl. UMMZ 89358–59, see next) originate from the southern Orizaba Range (contrary to map of potential distribution in OCHOA-OCHOA *et al.*, 2006). There, *P. deppei* is documented for the vicinity of Acultzingo (incl. "Nueva Escocia", i.e., Puerto de Aire; PÉREZ-HIGAREDA & SMITH, 1991; BRYSON *et al.*, 2011: LVT 10677) and sight records exist for Palo Verde at ca. 1'800 m and Acultzinapa (18°41' N 97°11' W) above 2'300 m in the Orizaba Valley (Miguel Á. de la Torre-Loranca in litt. January 2019, Fig. 10C). The presence at the eastern perimeter of Ciudad Mendoza (El Encinar, l.c., ca. 1'300 m) needs verification. The origin of UMMZ 89358–59 ("questionably from Potrero Viejo", DUELLMAN, 1960) close to 600 m (P. V. in Amatlán de Los Reyes Mun., 18°53' N 96°51' W) is "incorrect" (PÉREZ-HIGAREDA & SMITH, 1991).

CANSECO-MÁRQUEZ & GUTIÉRREZ-MAYÉN (2010: incl. Mapa 87) drew the distributional limit in the Tehuacán Valley of Puebla ("solamente [...] Valle de Tehuacán"). The southernmost verified record of *Pituophis deppei* (UAZ 27042) is from 21 road miles (33.8 km) northwest of Teotitlán del Camino (T. de Flores Magón, Oaxaca), ca. 2 km south of San Sebastián Zinacatepec (18°20' N 97°15' W) along highway 131/135 in Puebla (Fig. 10C), and mentions of Deppe's bullsnake from beyond the state line are based on vague evidence. The implicit indication from N Oaxaca in WOOLRICH-PÍÑA *et al.* (2017: Table 19, "Tehuacán-Cuicatlán" Biosphere Reserve) requires confirmation and potential further reports of *P. deppei* from central Oaxaca ("Valles centrales", CASAS-ANDREU *et al.*, 2004; see OCHOA-OCHOA *et al.*, 2006: map; MATA-SILVA *et al.*, 2015: Table 4) most probably rely on confusion with *P. lineaticollis* (see Discussion). A record from the Pacific side of the Isthmus ("Tehuantepec", coll. François Sumichrast; BOULENGER, 1894; GÜNTHER, 1895: BMNH 1871.2.7.35) "seem[s] definitely in error" (SMITH & TAYLOR, 1945).

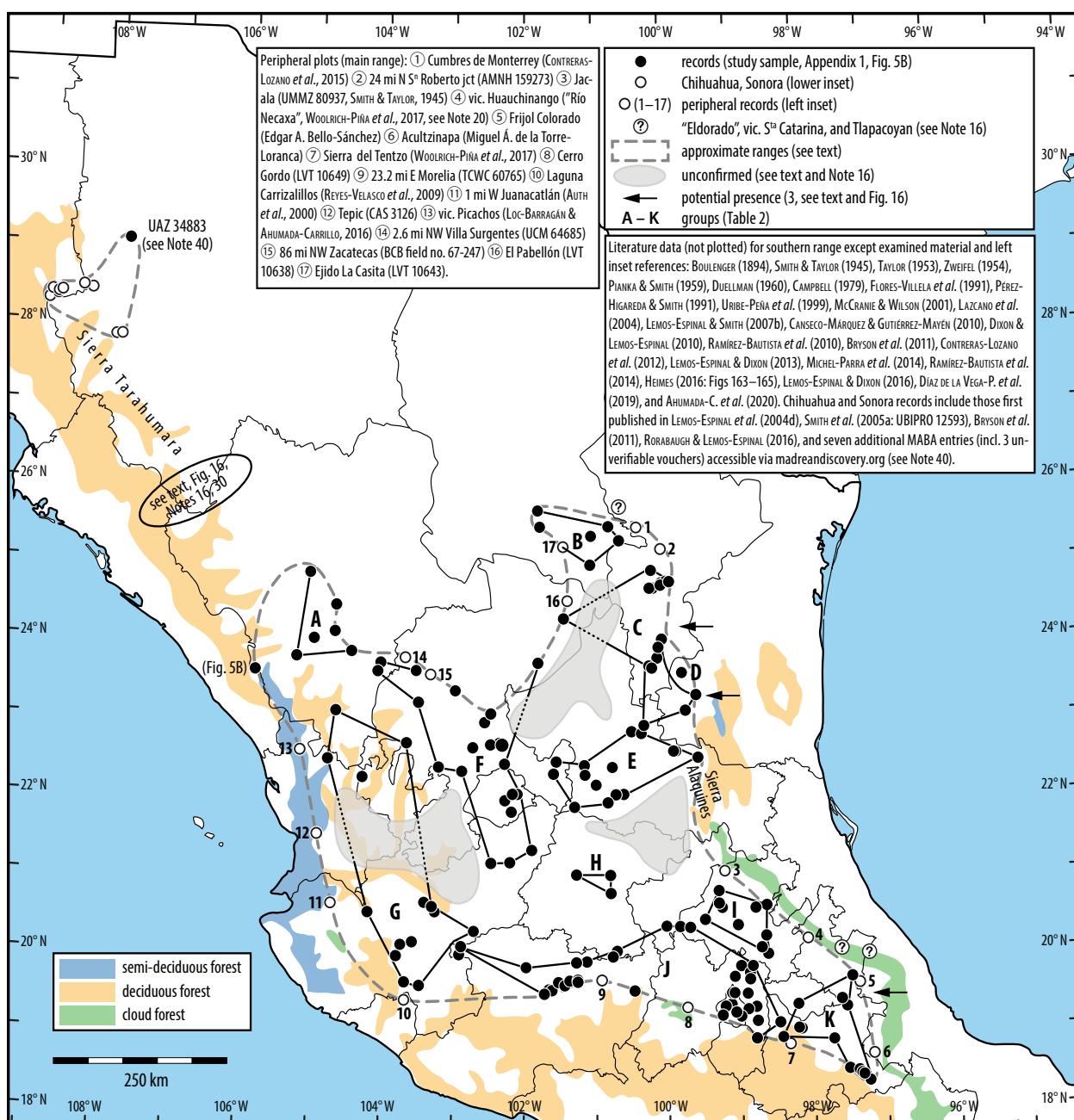
The course of the southern distributional limit in central W Puebla and W México State is poorly documented (no list of EBUAP holdings received, see Note 26). Bullsnakes from Morelos exclusively referred to *Pituophis deppei* (CASTRO-FRANCO & BUSTOS-ZAGAL, 1994) belong to *P. lineaticollis* (Cope) as evidenced by TAYLOR's (1939) account (see Discussion, Fig. 11A). Though, *P. deppei* TNHC 29666 from "85 km W Puebla" may have been

collected at the base of the Popocatépetl in extreme NE Morelos (vic. Ocuituco, ca. 18°53' N 98°47' W).

The presence of Deppe's bullsnake in the deciduous forest area of SW Jalisco remains unclear, the assumed distribution over most of Colima as shown in HAMMERMANN *et al.* (2007: map) is drawn in the absence of published data or evidence of other nature except COPE's (1887) vague indication (see chresonymy), and no verified records exist for the Pacific foothills in southern Sinaloa. The possible occurrence along the inland state line as mapped in, for instance, OCHOA-OCHOA *et al.* (2006) is only substantiated by WEBB's (1984) *Pituophis* "deppei deppei" from east of Loberas (ca. 23°30' N 105°50' W, ca. 1'950 m) on highway 40, viz. an unassigned specimen (AMNH 107040, see Discussion incl. Table 5). A live individual (Fig. 5B) from the same general area, only a few kilometres apart in immediately adjacent Durango west of the Sierra Madre Occidental watershed, corroborates genuine *P. deppei* for that zone. However, this does not imperatively entail its presence along the Pacific versant farther north in Durango and contiguous Sinaloa (Figs 7, 16, see Note 30).

In the northern Sierra Madre Occidental, *Pituophis deppei* is "found in oak-pine forests and transition zones between tropical deciduous forests and conifers" of Chihuahua (LEMOS-ESPINAL & SMITH, 2007a). In Sonora, the species is "known only from oak, pine-oak and pine forests in the mountains" from "west of Yécora along Highway 16 to east of Maycoba" (RORABAUGH & LEMOS-ESPINAL, 2016). Apart from the Oteros Valley (see above), Chihuahuan records of Deppe's bullsnake come from the Upper Mayo (Moris Mun.) that runs southwest towards the Gulf of California and from the Aros drainage (Yaqui hydrological system) where the species is documented for the headwaters of the Mulatos (Temósachic, Yécora) and the Río Sirupa (see end of Discussion and Notes 40–42). *Pituophis deppei* is expected to follow this river downstream of the confluence with the Papigochi (Yepómera area) and it possibly populates further tributaries of the Aros.

The usual lower limit of the elevational range is close to 1'000 m. The "Tepic" (21°31' N 104°54', ca. 930 m, Fig. 7: plot 12), Nayarit, record based on CAS 3126 (coll. Gustav Eisen & Frank Vaslit November 1894, lost in the 1906 earthquake and fire, Erica J. Ely in litt. November 2019) may corroborate the presence of *Pituophis deppei* slightly below 1'000 m. Laguna Carrizalillos in the "ecotone between tropical thorn scrub and oak forest" along the western periphery in Colima (REYES-VELASCO *et al.*, 2009; Fig. 7: plot 10) is situated at ca. 1'500 m. The species is confirmed up to ca. 1'700 m in Sonora (vic. Yécora, MABA 258608, see Note 41 for "Horqueta" record), above 2'000 m in Michoacán, Nayarit, or Tamaulipas (La Peña–Aserradero road, BRYSON *et al.*, 2011: LVT 10639), ca. 2'200 m or slightly higher in Chihuahua, Coahuila, Jalisco, Nuevo León, or San Luis Potosí, above 2'400 m in Veracruz (Frijol Colorado or in the Orizaba Range), 2'500 m in Aguascalientes and Durango, 2'800 m in N Puebla (Los Humeros, UMSNH



**Fig. 7.** Locality records and approximate distribution of *Pituophis deppei*. Solid (empty) symbols connote evaluated (literature) specimens. See caption to Fig. 10B–C for additional unexamined specimens from Michoacán, SE Puebla, and Veracruz (Orizaba Range).

72–73, 1571), and near 3'000 m at Bosque Quemado in Hidalgo (RAMÍREZ-BAUTISTA *et al.*, 2010). [Note 17]

### *Pituophis mexicanus* Duméril, Bibron & Duméril, 1854

*R.[hinechis] mexicanus* "nobilis". — DUMÉRIL (1853: 57, nomen nudum, see Taxonomy under *Pituophis deppei*).

*Pituophis mexicanus* Duméril, Bibron & Duméril, 1854: 236, Pl. 62 — "Mexique" (restricted to Sabinas Hidalgo, Nuevo León, by SMITH & TAYLOR, 1950a: 337). Types series: MNHN specimens incl. today's USNM 1415 (lectotype; Figs 8–9, Table 3, see Discussion, Note 36).

*Pituophis mexicanus* ["Dum. & Bibr."]. — GÜNTHER (1858a: 87).

*P.[ituophis] mexicanus* ["Dum. e Bibr."]. — JAN (1863: 59): "Messi-

co" (see Note 18); JAN & SORDELLI (1867: Pl. II.1) ["Dum. Bibr."]; "Mexique" ("Musée de Milan", *ibid.*)

*Pityophis* [sic] *sayi* [...] *mexicanus* ["Duméril et Bibron"]. — COPE (1875: 39); YARROW (1875: 539); COPE (1880: 23).

*Pityophis* [sic] *catenifer mexicanus*. — GARMAN (1884: 52).

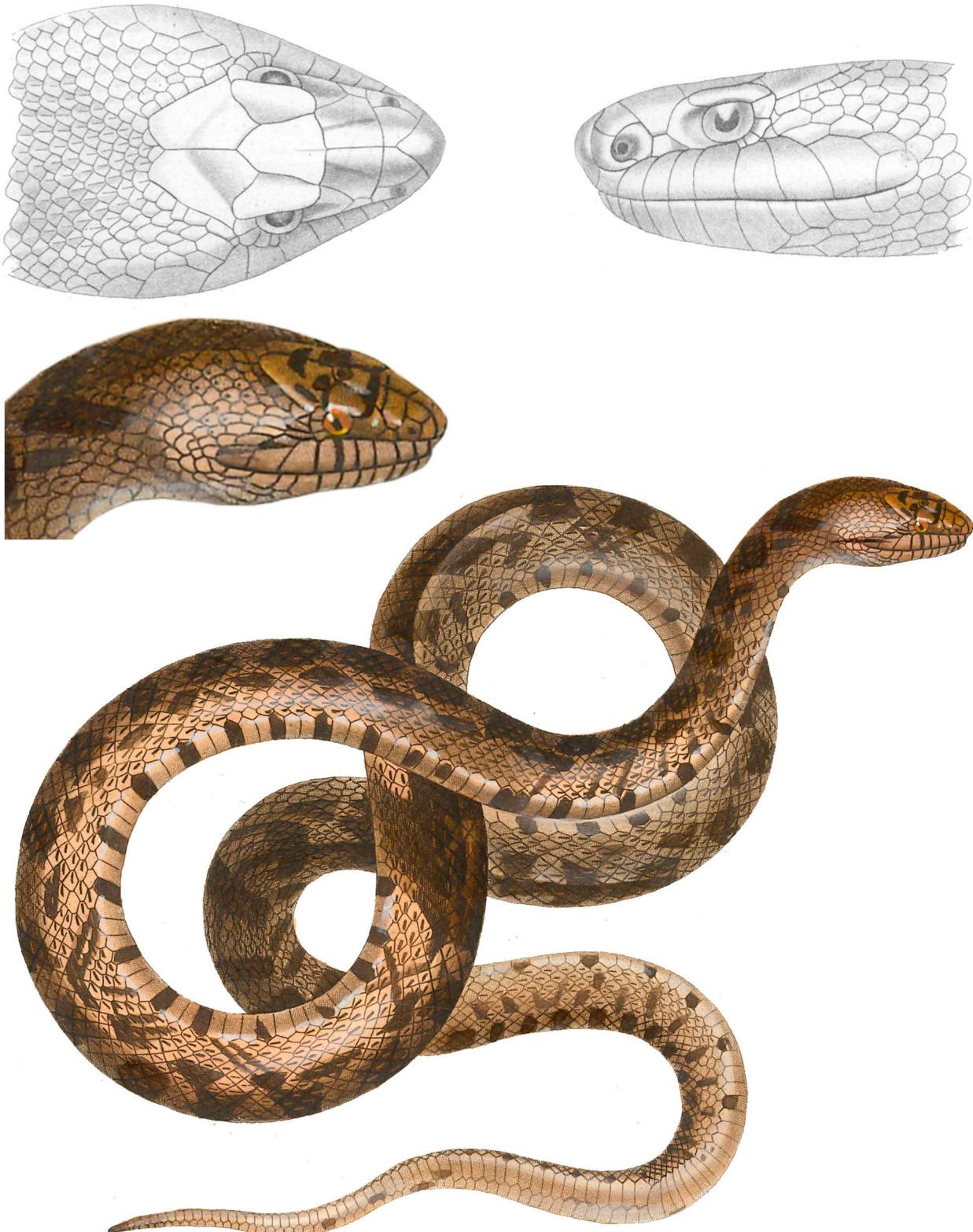
*Pityophis* [sic] *sayi mexicanus* ["Dum. et Bibr."] [partim]. — COPE (1887: 72, see *P. deppei*).

*Pituophis mexicanus* ["Duméril et Bibron"]. — BOCOURT (1888: 674, Pl. 42.4, see text incl. Table 3, Note 19).

*Pityophis* [sic] *mexicanus* ["D. B."]. — BOETTGER (1893: XXVIII).

*Pituophis mexicanus* [syn. *P. melanoleucus* (Daudin, 1803) ssp. *auct.*, see BOULENGER, 1894]. — SWEET & PARKER (1990: 2 ["Holotype"], see SCHÄTTI & KUCHARZEWSKI, 2018: Note 6).

*Pituophis mexicanus* [disused synonym of *Coluber catenifer* Blainville, 1835]. — SCHÄTTI *et al.* (2018: 71–72, Nota 13); SCHÄTTI & KUCHARZEWSKI (2018: 90–92, 95–97, Notes 6–7, Table 1; see Notes 28, 36).



**Fig. 8.** Rearranged reproduction of Plate 62 in DUMÉRIL et al. (1854) illustrating unlocated *Pituophis mexicanus* Duméril, Bibron & Duméril (type series). Not to scale. Hand-coloured copy formerly in Edoardo de Betta's library. Courtesy of Kraig Adler.

To the best of our knowledge, *Pituophis mexicanus* Duméril, Bibron & Duméril, 1854 was last used as valid in 1893 and finally has fallen into oblivion. WERNER (1929), to cite an example, did not mention the binomen at all. The present account sets forth the history of this

“nomen oblitum” (see Note 36) and gives a summary of available morphological data for the taxon.

BOULENGER (1894: 69) regarded *Pituophis mexicanus* “Dum. & Bibr.” as a younger name for *Coluber* [*Pituophis*] *melanoleucus* Daudin, 1803, but *P. mexicanus*



**Fig. 9.** Dorsal and right lateral head views of two male *Pituophis mexicanus* Duméril, Bibron & Duméril (type series), MNHN 3188 (A) and USNM 1415 (B, lectotype, see Discussion). Not to scale. Courtesy of Ivan Ineich (A) and Addison Wynn (B).

“non D. & B., Jan” ranks within the synonymy of *Elaphis deppei* Duméril, Bibron & Duméril, 1854. This refers to the allocation of a bullsnake reproduced in the ‘Iconographie générale [...]’ (JAN & SORDELLI, 1867). The absence of quotations of *P. mexicanus* “Jan” or “Jan & Sordelli” in synonymies or chresonymies published after STULL’s (1940) generic revision (e.g., DUELLMAN, 1960; WALLACH *et al.*, 2014) implies that this taxonomic authorship was no longer treated as systematically different from *mexicanus* D. B. & D., viz. is considered to be a junior subjective synonym of *Coluber [Pituophis] catenifer* Blainville, 1835 (see Discussion and Note 36). **[Note 18]**

Following COPE (1900), STULL (1940) classified *Pituophis mexicanus* “Duméril and Bibron” under *P. s. sayi* (Schlegel) auct. (see Material and Terms), and SMITH & TAYLOR (1945) referred Schlegel’s taxon to *P. catenifer* (Blainville). In accordance with this premise, viz. a junior subjective synonym of *P. catenifer sayi*, SMITH & TAYLOR (1950a) restricted the type locality of *P. mexicanus* to Sabinas Hidalgo in northern Nuevo León (Fig. 1, see Discussion).

The description of *Pituophis mexicanus* indicates a preocular and normally a small anterior subocular (absent in illustrated voucher, Fig. 8, Table 3), usually four but sometimes (“parfois”) two and once three or five prefrontals, nine supralabials (5<sup>th</sup> in eye contact, see Note 34), two postsuboculars (“quatre [4] post-oculaires”) excluding sixth supralabial from entering orbit (see Material and Terms, Note 19), 229–239 ventrals, 57–65 paired subcaudals, and 33–35 midbody rows (“rangées longitu-

dinales au tronc”). Above, the specimens are light to reddish tawny (“fauve”, in particular the head) but the hand-coloured plate rather shows a tan individual (Fig. 8). A black interocular band is present and an oblique brown streak bordered with black runs from the posterior edge of the eye to the angle of the mouth. The dorsal colour pattern basically consists of 50–56 rectangular or squarish brown or black median blotches on the trunk (see next paragraph) and 10–15 on the tail (“de cinquante à cinquante-six dans sa portion dorsale, de dix à quinze dans sa portion sus-caudale”, see Note 19 for ventral marking). The maximum total length is slightly over two metres (“Un sujet qui a 2<sup>m</sup>.064 de long”). Dentition counts are 17–20 (maxillary), 12 (palatinum), and 12–13 (pterygoid) teeth (DUMÉRIL *et al.*, 1854: 236–238).

The illustrated possibly male *Pituophis mexicanus* (DUMÉRIL *et al.*, 1854: Pl. 62) has two prefrontals (Fig. 8, Table 3) as well as a seemingly lower number of subcaudals (ca. 54) and more dorsal body blotches (ca. 59) than reported in the original description. Two examined males either show three prefrontals (MNHN 3188, right divided, left with deep groove at exterior border; “un exemplaire remarquable”, l.c.: 237) or there are paired prefrontals accompanied by two small symmetrical median shields anteriorly (USNM 1415, Fig. 9B). Both have a granular scale between the internasals. An unlocated specimen of the type series features a small azygous (fifth) scale between the frontal and the median prefrontals that are much shorter than the lateral ones (“une cinquième petite plaque médiane [...] en arrière des deux préfrontales médianes beaucoup plus courtes alors que

**Table 3.** Morphological data in type series (partim) of *Pituophis mexicanus* Duméril, Bibron & Duméril including unlocated MNHN specimen of uncertain status (see text). Data for unlocated paralectotype fide DUMÉRIL *et al.* (1854: 237 [msr], Pl. 62, see Fig. 8). Acronym and accession code (if available), number of prefrontals (prf), supralabials (spl) and scale in eye contact (lower figure), number of ventrals (ven, incl. preventrals), subcaudals (sbc), midbody scale rows (msr), and dorsal blotches (dbl) along trunk (above) and tail as well as pertinent details (gender, status, illustrations, explanations) including preocular condition. Number of midbody rows in MNHN 3811 (at 120<sup>th</sup> ventral) and USNM 1415 (117<sup>th</sup>) fide Ivan Ineich and Addison Wynn, respectively.

Specimen	prf	spl	ven	sbc	msr	dbl	remarks
MNHN ?	2	9 5*)	—	ca. 54	33 or 35	ca. 59 —	unlocated paralectotype (possibly ♂), Fig. 8 1 preocular, anterior subocular absent *) supralabial-eye contact see Note 19
MNHN 3188	3*)	9 5	2 + 241	58	33	58 12	♂ paralectotype, Fig. 9A 2 preoculars, small left anterior subocular present *) left prefrontal with deep lateral groove
USNM 1415	2 + 2*)	9 5	1 + 234	64	35	ca. 54 12	♂ lectotype (see Discussion), Fig. 9B 2/1 preoculars, small bilateral anterior subocular *) 2 smaller medio-anterior prefrontals
MNHN ?	4	9*) 5*)	—	—	—	—	unlocated potential paralectotype (BOCOURT, 1888: Pl. 42.4) 1 preocular and anterior subocular present on right side *) only left head scale conditions discernible

les externes”, l.c.). The anterior right lateral tip of the frontal is separated in MNHN 3188 and the anterior half longitudinally divided by a deep groove along the midline in USNM 1415 (Figs 9A–B). The latter presents a broken up left parietal and the fragmentation of the posterior pileus is even further advanced in MNHN 3188. That large voucher (2'001 [1'780 + 221] mm total length, see preceding paragraph) has an elevated number of ventrals (241 plus two preventrals, data Ivan Ineich), exceeding the indicated maximum count (239, l.c.), and certain disparity between this type specimen and the original description also exists in the number of dorsal blotches on the trunk (58, Table 3). [Note 19]

The type series of *Pituophis mexicanus* encompasses five or more specimens (see next paragraph) from unspecified places in “Mexique” and the only collector mentioned by DUMÉRIL *et al.* (1854) is Auguste Ghiesbrecht. Based on circumstantial evidence, SCHÄTTI *et al.* (2018) associated his specimen obtained in 1841 or early 1842 with MNHN 3188 (see Note 36). No other type specimen could be located in the Paris Museum (Ivan Ineich in litt. October 2017). BOCOURT’s (1888: Pl. 42.4) *P. mexicanus* is of uncertain taxonomic status and cannot be individually identified among MNHN bullsnakes catalogued before 1854. USNM 1415 was received in exchange (COCHRAN, 1961: “Jardin des Plantes”, JPP) and is devoid of collecting data (Addison Wynn in litt. October 2017).

STULL (1940: “type in Paris Museum”) or SMITH & TAYLOR (1945: “type in Mus. Hist. Nat. Paris”) conjectured the existence of a single name-bearer of *Pituophis mexicanus*. However, DUMÉRIL *et al.* (1854) had access to at least five original specimens as evidenced by their detailed description of variation in the number and configuration of prefrontals (see above). The assumption that STULL (1940) and/or SMITH & TAYLOR (1945) may have inadvertently opted for the illustrated *P. mexicanus*

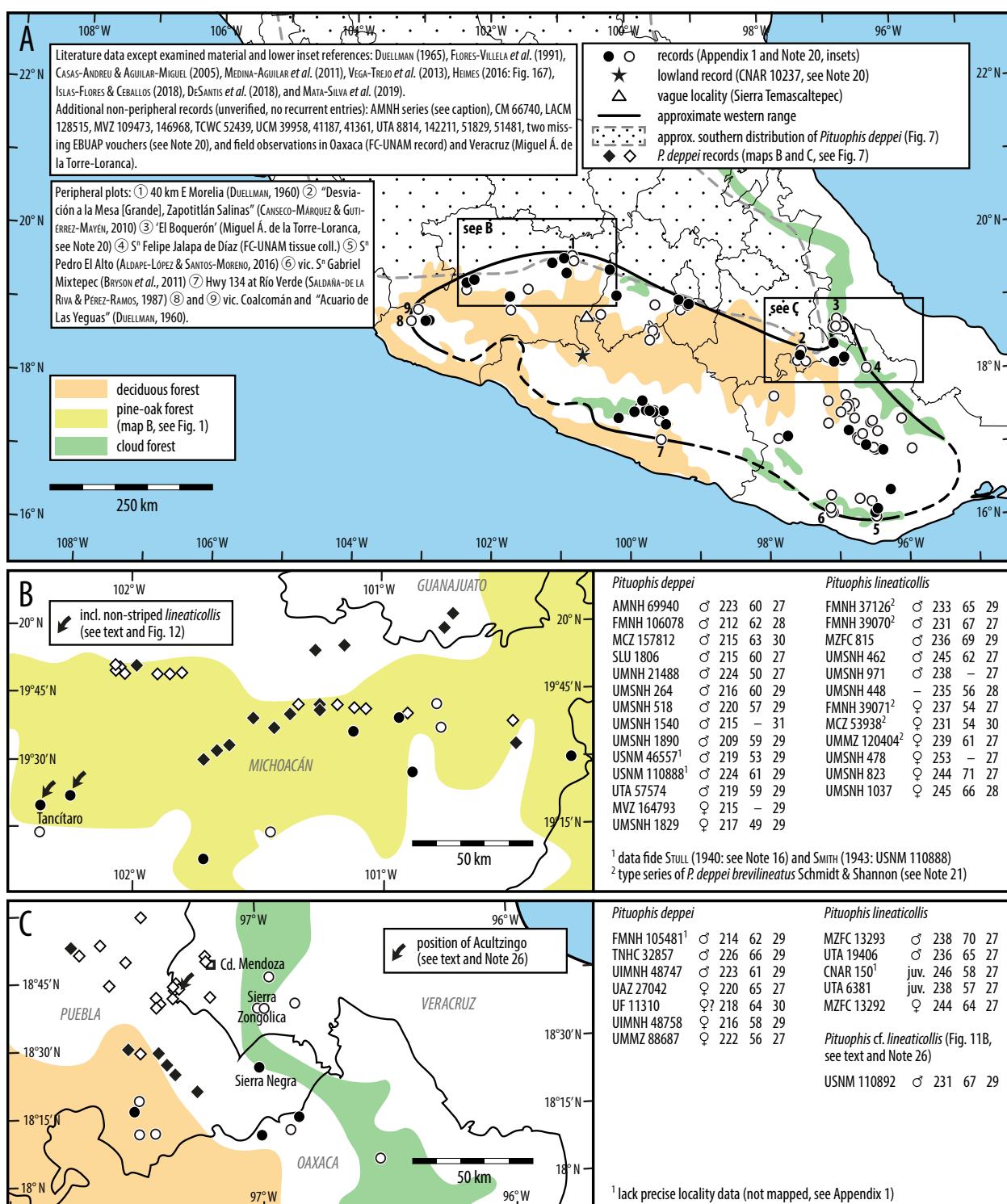
(Fig. 8) would conflict with the diagnostic features or contest their identifications, viz. *P. sayi* (Schlegel) and *P. catenifer* (Blainville) auct., respectively.

## Discussion

To conclude from literature records (e.g., TAYLOR, 1939; SMITH, 1943; SMITH & TAYLOR, 1950a; DUELLMAN, 1960; CANSECO-MÁRQUEZ & GUTIÉRREZ-MAYÉN, 2010; WOOLRICH-PIÑA *et al.*, 2005, 2017) and institutional holdings, *Pituophis deppei* (Duméril, Bibron & Duméril, 1854) and *P. lineaticollis* (Cope, 1861b) meet in central Michoacán, extreme SE Puebla, and in-between areas (Fig. 10), and they are purportedly sympatric at, for instance, Teotihuacán in México State as mapped by DUELLMAN (1960: Fig. 1, see below). [Note 20]

STULL (1940) or SMITH & TAYLOR (1945) and all later herpetologists working on the subject distinguished *Pituophis deppei* from *P. lineaticollis* for their dorsal colour pattern, and in the first place the absence or presence, respectively, of a longitudinally striped neck (e.g., HEIMES, 2016). Moreover, *lineaticollis* reportedly differs from Deppe’s bullsnake in elevated ventral counts (229–258 against 209–235, resp.) and a stable low (27) instead of an often higher number of dorsal scales (27–31) in *deppei* (STULL, 1940; DUELLMAN, 1960). We recorded 229–256 ventrals (♂♂ 229–245, ♀♀ 229–256) and 25–30 midbody rows in *lineaticollis* (Appendix 1). The range for subcaudals is 54–71 (60–71, 54–71, resp.) and there are 285–317 (291–312, 285–317) total body scales (Table 4 and data for specimens of unknown origin, 22 ♂♂, 20 ♀♀, 7 unsexed specimens). [Note 21]

The reputed presence of *Pituophis lineaticollis* near Teotihuacán in NE México State relies on UIMNH



**Fig. 10.** Locality records and approximate distribution of *Pituophis lineaticollis* west of the Isthmus of Tehuantepec (see Notes 20, 26) as well as number of ventrals, subcaudals, and midbody rows in *P. deppei* (except TNHC 25426, UTA 6047–48) and *P. lineaticollis* (except UTA 4478, 6049) from Michoacán including the vicinity of Acámbaro (FMNH 106078, USNM 46557) in Guanajuato (B) and the Oaxaca-Puebla-Veracruz borderlands (C, see Appendix 1 for data source and localities). Solid (empty) symbols connote evaluated (literature and/or institutional) specimens. The map includes data for ten unexamined *lineaticollis* from Oaxaca (AMNH 89584, 89586, 91079–80, 92879, 93231, 100886, 102980, 115634, 159275). *Pituophis deppei* records (◇) in maps B–C encompass those first published in TAYLOR (1939), DUELLMAN (1960), PÉREZ-HIGAREDA & SMITH (1991), CANSECO-MÁRQUEZ & GUTIÉRREZ-MAYÉN (2010), and HEIMES (2016: Fig. 165) as well as AMNH 110416 and 159265, EBUAP 776, MSUM 7244, OSU 10263, TCWC 33848 and 60765, UCM 12968, UMSNH 355, 604, 714 and 727 (all in B, unverified, no recurrent entries), LSUMZ 11013 and TCWC 68752 (both in C, ibid.), two Puebla photo vouchers (© Adam G. Clause, see Note 26 for link), and field observations in Veracruz (Miguel Á. de la Torre-Loranca, see Distribution).

**Table 4.** Geographic variation of body scales in *Pituophis lineaticollis* males (top), females (middle line), and juveniles or specimens of unknown gender (bottom; range, sample size, mean, standard deviation). See text including Note 21 for certain extremes and Figs 10B–C as to individual data from Michoacán (except UTA 4478, 6049) and the Oaxaca-Puebla border.

Area	ventrals	subcaudals	ventrals + subcaudals
Michoacán	231–245 (6, 236.8 ± 4.9)	62–69 (5, 65.6 ± 2.6)	298–307 (5, 302.2 ± 4.1)
	231–253 (7, 242.0 ± 7.0)	54–71 (6, 60.8 ± 6.7)	285–315 (6, 301.0 ± 11.5)
	235 (1, 235.0 ± 0.0)	56 (1, 56.0 ± 0.0)	291 (1, 291.0 ± 0.0)
Guerrero	232–241 (6, 237.2 ± 3.1)	62–69 (5, 65.2 ± 2.5)	294–307 (5, 302.0 ± 5.1)
	247–256 (6, 250.7 ± 3.6)	60–62 (5, 61.0 ± 0.7)	308–317 (5, 311.8 ± 4.4)
	240 (1, 240.0 +0.0)	61 (1, 61.0 +0.0)	301 (1, 301.0 +0.0)
Morelos	235–238 (2, 236.5 ± 1.4)	60–65 (2, 62.5 ± 1.4)	295–303 (2, 299.0 ± 1.4)
	—	—	—
	—	—	—
Oaxaca, Puebla	229–241 (5, 234.8 ± 5.2)	62–70 (5, 65.0 ± 3.3)	291–308 (5, 299.8 ± 6.5)
	229–246 (4, 241.0 ± 8.0)	54–67 (4, 61.8 ± 5.6)	296–308 (3, 303.7 ± 6.7)
	238–246 (3, 241.7 ± 4.0)	57–58 (2, 57.5 ± 0.7)	295–304 (2, 299.5 ± 6.4)

36223 “from 40 kilometers north of Ciudad México” (Mexico City) with “rather shorter neck-stripes” than usual (DUELLMAN, 1960: 608). This male has 30 dorsal blotches along the trunk with 222 ventrals and belongs to *P. deppei*. The indication of *lineaticollis* in SW Mexico City (“Sierra Ajusco”, l.c., 1965: Table 8) is not supported by evidence; MZFC 621 and 624 as well as a juvenile from this area (HEIMES, 2016: Fig. 164, see Note 17) are typical *deppei* except for the unique prefrontal-loreal configuration of MZFC 621 (see Note 9). URIBE-PEÑA *et al.* (1999) noted 211–226 ventrals (mean 219) for *deppei* from México State and Mexico City as opposed to 235–238 ventrals in two examined male *lineaticollis* from immediately adjacent Morelos (Table 4). Our data confirm much lower counts in *deppei* from the vicinity of Mexico City (16 ♂♂ 209–228,  $\bar{x}$  217.2, 3 ♀♀ 214–219,  $\bar{x}$  216.7). [Note 22]

As in the México-Morelos border region, *Pituophis deppei* and *P. lineaticollis* from Michoacán differ in ventral counts (Fig. 10B: Table). Regarding the dorsal colour pattern, various *lineaticollis* show stripes that extend over six or more head lengths down the neck, whereas these marks are “partially fragmented into rows of spots” in, for instance, UMMZ 119567 from Dos Aguas (Sierra de Coalcomán, DUELLMAN, 1960: Pl. 45.2), shorter than usual in “several” specimens “from the vicinity of Tancítaro” (l.c., type series of *P. deppei brevilineatus* Schmidt & Shannon, Fig. 10B) including UMSNH 448, and basically absent in two female paratypes of *P. d. brevilineatus* (FMNH 39071, MCZ 53938, Figs 12A–B) with 34–39 dorsal body blotches and UMSNH 478 collected between Tancítaro ( $19^{\circ}20'N$   $102^{\circ}22'W$ ) and Nuevo San Juan Parangaricutiro ( $19^{\circ}25'N$   $102^{\circ}08'W$ ). This female with 253 ventrals and 39 mostly rectangular mid-dorsal marks on the trunk essentially fits the dorsal colour pattern of *deppei* and in particular Michoacán specimens including TNHC 25426 (43) and UTA 6047–48 with 44 and 41 blotches, respectively (♂♂ 30–48, ♀♀ 36–43, see Variation for maximum). [Note 23]

The type series of *Pituophis deppei brevilineatus* Schmidt & Shannon (syn. *Arizona lineaticollis* Cope fide

DUELLMAN, 1960) embraces five specimens from the vicinity of Tancítaro, differs from *P. lineaticollis* auct. in a “lower number of ventrals” (“233–241” fide diagnosis, ignoring male paratype with “231”), and “[t]here is no actual overlap of characters” compared to *P. d. deppei* auct. (SCHMIDT & SHANNON, 1947). Our data for *P. d. brevilineatus* (2 ♂♂ 231–233 ventrals, 3 ♀♀ 231–239) including the number of subcaudals and midbody rows (Fig. 10B: Table) slightly diverge from the original description. UMSNH 478 from the vicinity of the type locality (see preceding paragraph) refutes a discrepancy with *lineaticollis* auct. in ventral counts. On the other hand, a female paratype of *brevilineatus* (MCZ 53938) with by far the lowest sum of ventrals and subcaudals (285, Table 4, s=11.5, 291 in FMNH 39071) differs from Michoacán *P. deppei* only in a higher number of ventrals (231 versus 215–225, resp., in 4 ♀♀ incl. TNHC 25426, UTA 6048). Notably, MCZ 53938 also approaches *deppei* in dorsal colour pattern (Fig. 12B) and has 30 midbody rows (verified by Joseph Martinez). The holotype of *brevilineatus* (FMNH 37126) shows 29 (SCHMIDT & SHANNON, 1947), contrary to the reputedly invariable number of midbody rows (27) throughout the whole range of *lineaticollis* (e.g., STULL, 1940; HEIMES, 2016; see Note 21).

Bullsnakes with ventral counts above 245, and thus clearly referable to *Pituophis lineaticollis*, but conforming to the characteristic dorsal colour pattern of *P. deppei* also occur in the Oaxaca-Puebla-Veracruz border region (CNAR 150). There again, the number of ventrals separate the taxa (Fig. 10C: Table). Though, SMITH (1943) surmised that “intergradation between these two is very strongly indicated” by USNM 110892 (“*deppei lineaticollis*”) from “near Acultzingo, Veracruz” (ca.  $18^{\circ}43'N$   $97^{\circ}18'W$ , 1'600–1'700 m) along the Puebla state line. DUELLMAN (1960) considered its dorsal pattern “more nearly like that of *deppei*.” However, this male features distinct neck stripes (Fig. 11B) and presents 231 ventrals, 67 subcaudals, and an elevated number of midbody rows (29). Given the vague origin of USNM 110892 and substantial variation observed in *lineaticollis* from



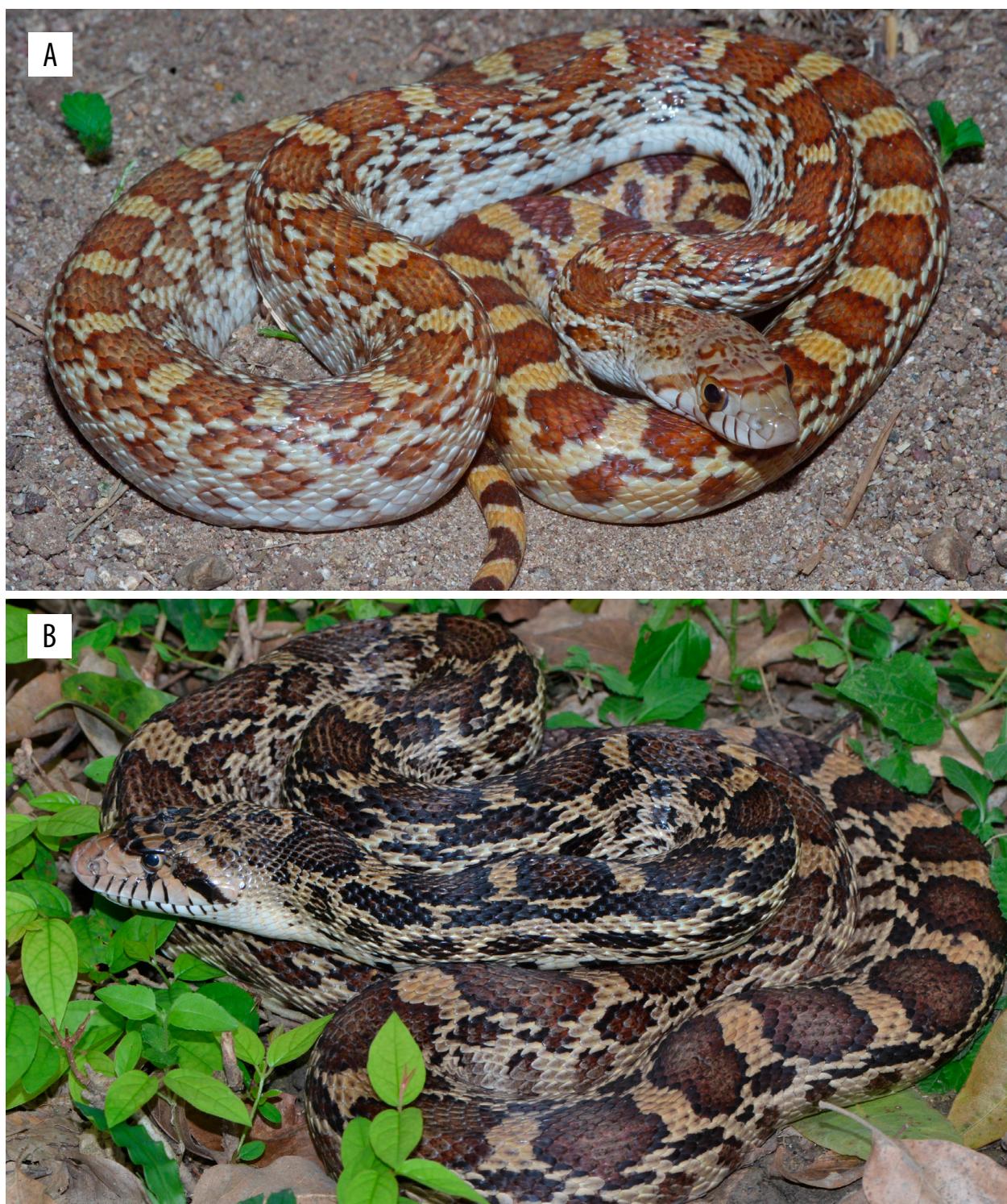
**Fig. 11.** *Pituophis lineaticollis* from San Juan Tlacotenco (2'300 m, Morelos, A) and dorsal view of *P. cf. lineaticollis* USNM 110892 from the Upper Orizaba Valley (B, courtesy of Esther Langan, see text incl. Fig. 10C, Note 26).

a comparatively small area of the Transvolcanic Belt in Michoacán (see above) as well as the “*deppei*” pattern of CNAR 150 from the vicinity of Tehuacán, we perceive no *a priori* reason to discard SMITH’s (1943) hypothesis

(see below and Note 26), the more so as the sum of ventrals and subcaudals in USNM 110892 (298) exceeds the maximum aggregate for *deppei* in Puebla (292, Table 2: group K, TNHC 32857). [Note 24]



**Fig. 12.** Dorsal colour pattern and lateral head scales in two paratypes of *Pituophis deppei brevilineatus* Schmidt & Shannon, FMNH 39071 (A) and MCZ 53938 (B). Not to scale. Courtesy of Joshua Mata (A) and Joseph Martinez (B).

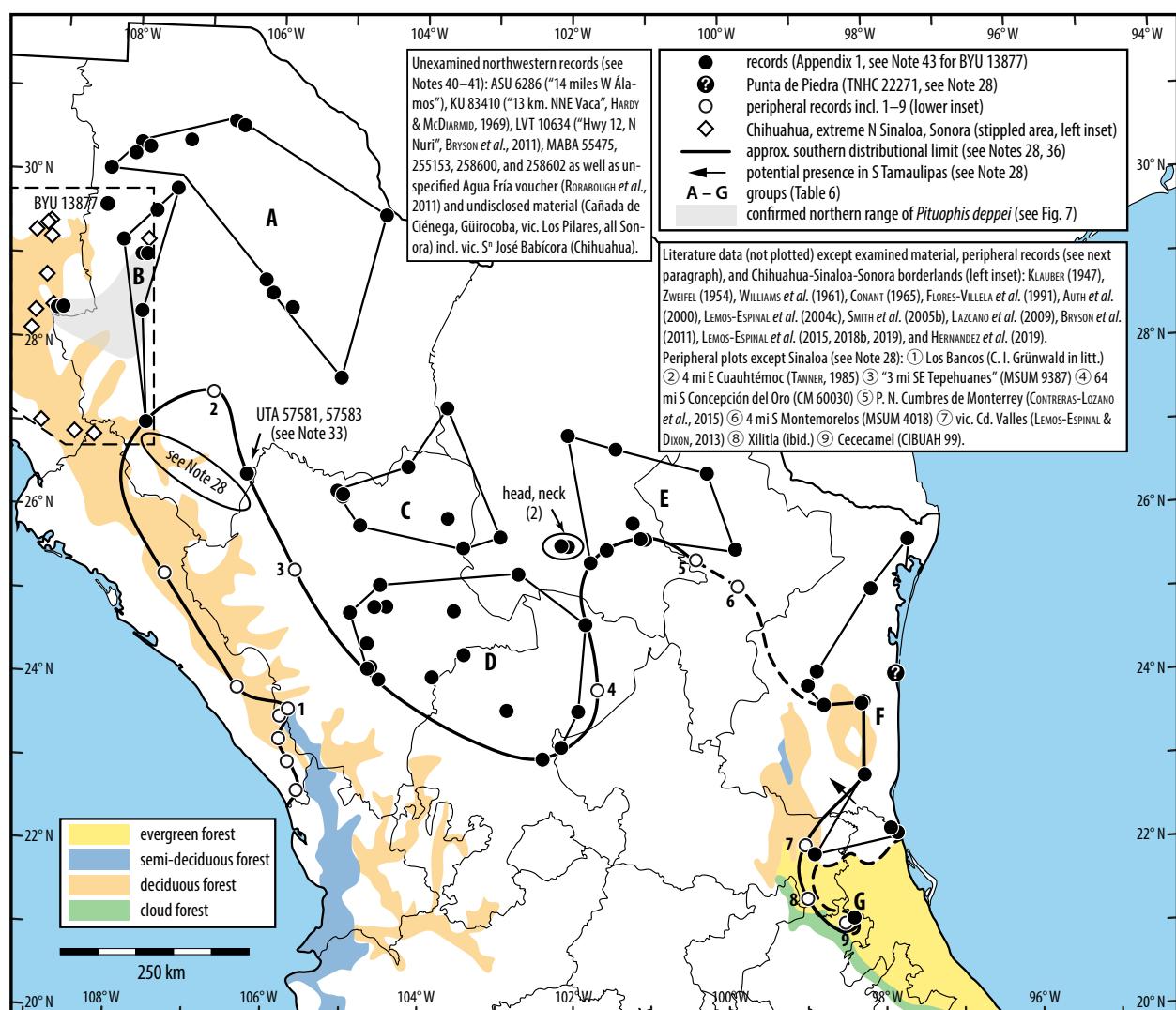


**Fig. 13.** *Pituophis catenifer* from Álamos (Sonora, A, courtesy of Matthew Cage) and the vicinity of Chalahuiyapa (ITAH compound, ca. 140 m, Hidalgo, B).

Based on DUELLMAN's (1960) data, the female "neotype" of *Arizona lineaticollis* Cope (UMMZ 114668) collected "24 km. NW of Oaxaca" de Juárez near Hacienda Vieja (or Zompantle, 17°14' N 96°49' W, ca. 1'660 m) on highway 190 with "long black neck-stripes followed posteriorly by 23 light-centered dorsal body-blotches" has an identical number of ventrals (229, l.c.: 605) as found in an unspecified *Pituophis deppei* from the Orizaba

Range less than 200 km airline distance farther northwest. The putative name-bearer shows by far the lowest ventral count recorded for female *lineaticollis* outside Michoacán (244–246 in three Oaxaca ♀♀, Table 4), which leads to the observed increased standard deviation. [Note 25]

In summary, we are not aware of any confirmed sympatric occurrence of *Pituophis deppei* and *P. lineaticol-*

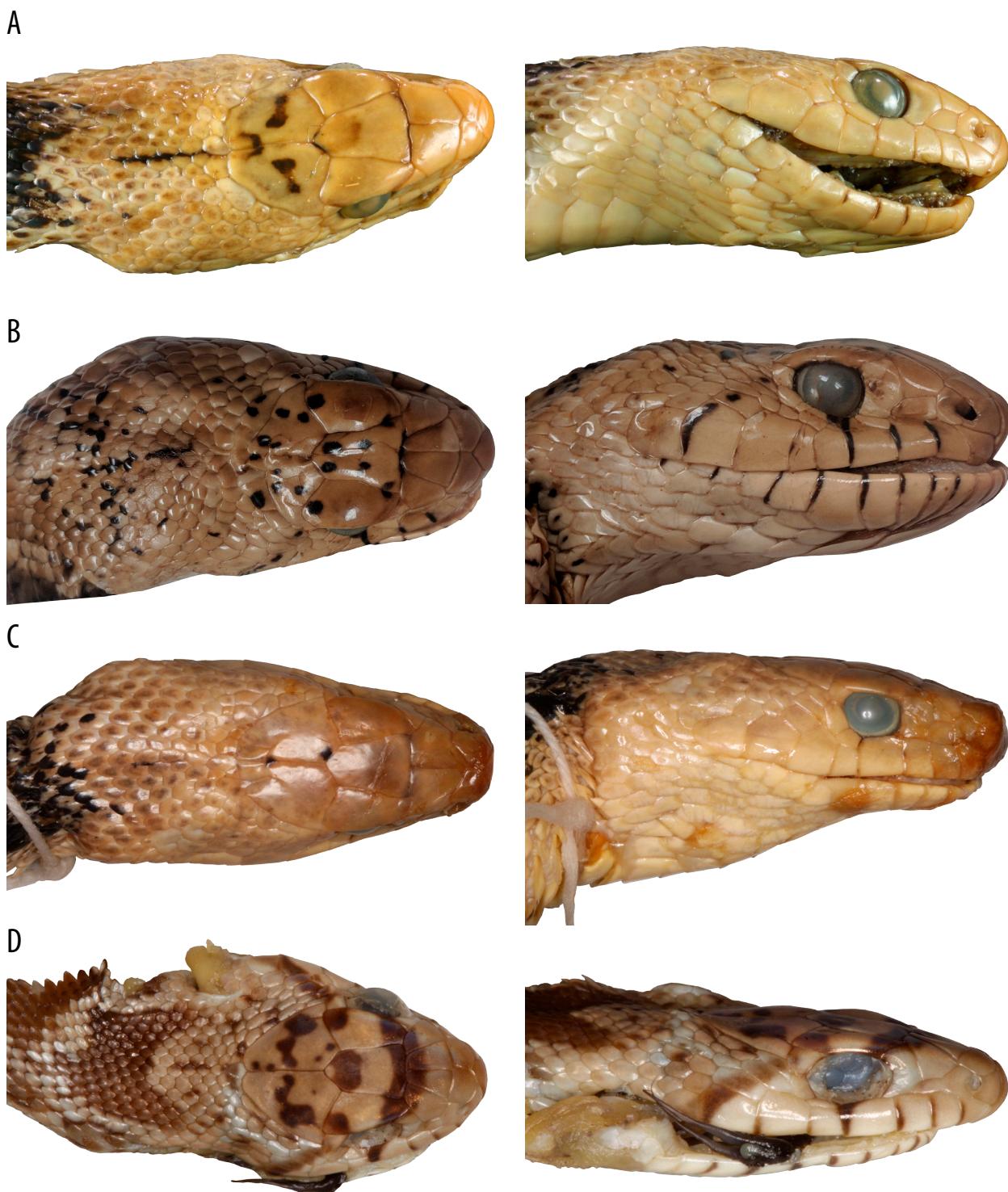


**Fig. 14.** Locality records and approximate distribution of *Pituophis catenifer* in Mexico except most of Sonora and the Baja California Peninsula. Solid (empty) symbols connote evaluated (literature) specimens. Locality records in DUNKLE & SMITH (1937), STULL (1940), SMITH (1943), FUGLER & WEBB, (1956), and FOUCETTE & ROSSMAN (1963) are represented by map entries (Appendix 1). See Note 28 for details and explanations.

lis although their ranges are in contact in, for example, Michoacán (Fig. 10B). There at least, two supposedly diagnostic characters (number of midbody rows, neck pattern) fail to reliably discriminate *deppei* from *lineaticollis*. The systematic allocation of USNM 110892, possibly from Veracruz, remains unresolved (Figs 10C: Table and 11B, Appendix 1). It needs to be noted that the “inferred [...] sister species” relationship between *deppei* and *lineaticollis* (BRYSON et al., 2011: 1575) shows weak backup (66% Bayesian posterior probability, 53% bootstraps). PYRON & BURBRINK’s (2009: Fig. 1) large multilocus data set and “strong [...] support” (100%) for “the same sister relationship between these two montane species” (BRYSON et al., 2011) is based on two *P. catenifer* from Arizona and Kansas, a single sequenced pet trade voucher of *deppei* (AF 141096, see RODRÍGUEZ-ROBLES & DE JESÚS-ESCOBAR, 2000: Table 1), and one *lineaticollis gibsoni* Stuart from “Guatemala” (PYRON & BURBRINK, 2009: Appendix S1). [Note 26]

*Pituophis deppei* (Duméril, Bibron & Duméril, 1854) and its alleged sister species *P. lineaticollis* (Cope, 1861b) differ from the northern *P. catenifer* (Blainville, 1835) in scale counts (see below) and, purportedly, qualitative morphological features such as the dorsal colour pattern and shape of the rostral (see Note 37). *Pituophis catenifer* is a polytypic wide-ranging Nearctic (incl. SW Canada) colubrine extending to Baja California, down the Mexican Pacific coast (Sinaloa), and across the Northern Plateau to the Gulf littoral (e.g., WALLACH et al., 2014; HEIMES, 2016). This species and *P. deppei* have largely parapatric ranges but occur together in a narrow sector probably all along their highland distributional limits (Figs 14, 16). [Notes 27–28]

According to literature (e.g., STULL, 1932, 1940; SMITH & TAYLOR, 1945; HEIMES, 2016), *Pituophis catenifer* and *P. deppei* differ in the number of prefrontals, four versus two shields, and a single instead of two supralabials with eye contact, respectively (see Diagnosis, Variation



**Fig. 15.** Dorsal and right lateral head views of three intermediate bullsnakes (FMNH 11825, LSUMZ 2426, UCM 66385, A–C) and an anomalous specimen from NW Durango (UTA 57616, D, see Note 30). Not to scale. Courtesy of Aaron Mercer (A) and Jackson Roberts (B).

incl. Figs 2–4, Notes 9–10, and Fig. 16). Though, DIXON *et al.* (1962) found four prefrontals in several among 18 *P. deppei deppei X deppei jani* from N San Luis Potosí (KU 67694–711). CONANT (1965) examined that series (see Note 9), reported peculiar combinations of supposedly diagnostic head scale conditions in bullsnakes from Durango (AMNH 68361, 88822) and Zacatecas (AMNH

85247, 85251), and concluded that “[t]he number of upper labials entering the eye, long used as a key character” to separate *P. catenifer* from *P. deppei*, “is subject to some variation”. Following MORAFKA (1977), specimens defying a proper identification are “especially clustered around” Doctor Arroyo in S Nuevo León and “about 30%” out “[o]f approximately forty *Pituophis*” from Tor-

**Table 5.** Morphological data in Mexican bullsnakes with head scale character states in-between *Pituophis catenifer* and *P. deppei* including UTA 57616 (Fig. 16). Acronym and accession code (grouped by federal state, incl. gender), number of prefrontals (prf), supralabials (spl, right/left side) and scales in eye contact (lower figures, *ibid.*), particular head scute conditions including precular (preoc, AMNH 118009), postocular (poc, MCZ 80225), and postisubocular (pos) scales as well as parietals (par, see Note 32), number of ventrals (ven), subcaudals (sbc), midbody scale rows (msr), dorsal body blotches (dbl), and number on tail in bracket), and comments. See chresonymy of *P. deppei* for verbatim taxonomic allocations and detailed locality data, and Appendix 1 for origin of material and msr counts.

Origin (state) specimen	prf	spl	head scale peculiarities	ven sbc	msr dbl	reference, illustrations, remarks
Chihuahua FMNH 11825 (♀)	2	8	large pos, large par	228	29	DUELLMAN (1960)
Chihuahua LACM 74031 (♀)	2	8	both prf notched anteriorly, medium-sized pos, multi-divided par	65	36 (10)	Fig. 15A
Chihuahua MCZ 80225 (♂)	2	4	left 5 <sup>th</sup> spl excluded from eye by large lower poc (fused with pos), large right pos, large par	229	29	only left side lateral head scale data available
Chihuahua NCSM 85998 (—)	5	8	small azygous prf behind internasal suture, pos absent (par condition unknown)	73	25 (10)	
Chihuahua UCM 65738 (♂?)	4	8	small pos, small par	211	—	few body scales
Chihuahua UCM 65748 (juv.)	4	4–5	(no notable details discernible on available photos) large par	64	37 (12)	
Chihuahua UCM 65821 (♂)	2	9/8 5/4	both prf notched anteriorly, large pos, large par	220	—	LEMOS-ESPINAL <i>et al.</i> (2004c: UBI PRO 11678)
Chihuahua UCM 66385 (♀)	2	8/7 4	5 <sup>th</sup> right spl narrow (below pos), left 4 <sup>th</sup> –5 <sup>th</sup> fused (wide eye contact), large par (notched posteriorly)	60	36 (—)	
Coahuila USNM 105302 (♀)	5	8/9 4–5/5–6	small left pos, short medio-posterior sutures on par	232	—	only left side lateral head scale data available
Durango AMNH 88822 (♂)	4	8 4–5	5 <sup>th</sup> spl enters eye “very narrowly”, small pos, large par	61	—	
Durango UTA 57616 (juv. ♂)	4	8 (4)	large left pos, wide eye contact of 4 <sup>th</sup> right spl and unusual exclusion of 5 <sup>th</sup> from orbit, large par	231	29	LEMOS-ESPINAL <i>et al.</i> (2004a: [“UBP”] 11857)
Durango UTEP 9370 (juv.)	4	8 4–5	large par	72	28 (11)	photos see Note 29
Nuevo León TCWC 54239 (♀)	2	8	large pos, large par	234	30/31	repeated changes in number of msr
Nuevo León UTA 3050 (♂)	2	4	medium-sized pos, large par	>61	35 (10)	Fig. 15C, see Note 40
Nuevo León UTA 38561 (subad.)	4	8 4–5	small right pos, large par	228	31	numerical body scale and pattern data fide SMITH (1943)
San Luis Potosí LSUMZ 2426 (—)	4	9/8 4–5	only posterior tip of 4 <sup>th</sup> spl enters eye (right upper anterior edge apart), large pos, par nonexistent	71	26 (12)	numerical data fide TAYLOR (1952): “not agreeing in all detail with [...] typical <i>affinis</i> ”, Fig. 15B

Table 5 continued.

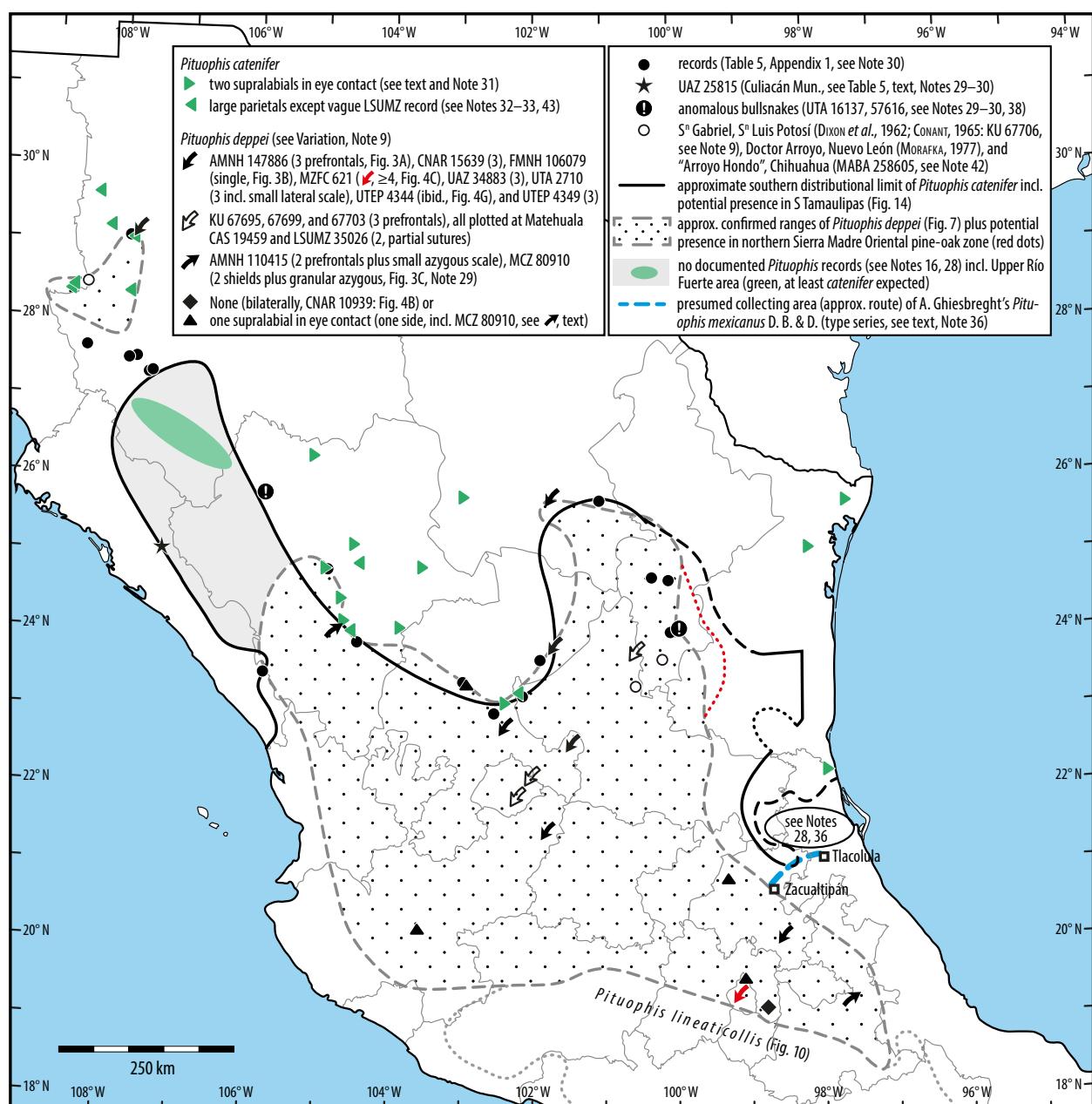
Origin (state) specimen	prf	spl	head scale peculiarities	ven sbc	msr dbl	reference, illustrations, remarks
Sinaloa AMNH 107040 (♀)	2	8	large pos, large par	227 67	31 40 (14)	WEBB (1984: “AMNH”): 1 <sup>st</sup> state record of “ <i>d. deppei</i> ” teeth on maxillary 18, palatinum 8, mandibular 21
Sinaloa UAZ 25815 (♂)	2	8	2 small pos, large par	225 62	29 39 (12)	RORABAUGH & LEMOS-ESPINAL (2016: dorsal head view photo), see Notes 29–30
Zacatecas AMNH 85251 (♀)	4	8	5 <sup>th</sup> right spl enters eye “only very narrowly” (no further published data)	218 49	31 33 (8)	data fide CONANT (1965)
Zacatecas AMNH 118009 (juv.)	4	8	5 <sup>th</sup> right spl in wide eye contact, 2/1 preoc, postero-lateral par edges apart	227 62	29 45 (13)	teeth on maxillary 19, palatinum 10, mandibular 21
Zacatecas UTEP 86337 (♀)	5	8	lower portion of right lateral par apart, small left pos, multi- divided par	223 60	33 36 (11)	“potential hybrid due to its coloration” (Carl Lieb in litt. via Vicky Zhuang, October 2018)

reón and Saltillo south to the cities of Zacatecas and San Luis Potosí (incl. CM 60007–40) “were very much intermediate in pattern and squamation”. “These intergrades are unstable in head and neck markings, often with two prefrontal scales, and one supralabial in contact with orbit, or the reverse, and are in some case [sic] asymmetrical (i.e., two prefrontals on one side, one on the other).” Twenty bullsnakes (incl. 2 AMNH specimens, see above) from at least 18 different localities (see Note 16 for Huicorichi records) in Chihuahua, Coahuila, Durango, Nuevo León, Sinaloa, and Zacatecas including immediately adjacent San Luis Potosí corroborate these findings (Figs 15–16, Table 5, Appendix 1, see chresonymy of *P. deppei* and end of chapter for northern Sierra Madre Occidental). [Note 29]

Bullsnakes inconsistent with the customary diagnoses of *Pituophis catenifer* and/or *P. deppei* auct. are common along their distributional limits across the Northern Plateau and documented from west of the Sierra Madre Occidental watershed to the vicinity of Doctor Arroyo in S Nuevo León (Fig. 16, Table 5). This scenario considers UAZ 25815 from the inland periphery of the known range of *catenifer* in central Sinaloa but far from any *deppei* records (see Distribution, Note 28). Undefinable specimens collected in the Matehuala–Villa Hidalgo sector (KU 67706, vic. San Gabriel, see Note 9) in San Luis Potosí (DIXON *et al.*, 1962; CONANT, 1965) come from clearly beyond the confirmed geographic limit of *catenifer*, a taxon apparently absent in Chihuahuan Desert associations of S Nuevo León (Figs 14, 16, see Note 28). Pleistocene range expansions across the northern Sierra Madre Oriental, allowing temporary reproductive interaction between incipient species, seem to account for the observed situation (see BRYSON *et al.*, 2011). Repeated shifts of ecological barriers coupled with alterations to habitats due to climatic fluctuations until the end of the last glacial episode (Wisconsinian, see below) and subsequent spatial segregation determined the genetic structure of bullsnakes not only along the current range limits of *catenifer* and *deppei* but resulted in phenotypical expression deep into today’s heartlands of both taxa. [Note 30]

Although generally considered uncommon, “two labials in contact with the orbit” as present in CM S-9511 from near Tampico (KLAUBER, 1947: 12, see below) occur in further Tamaulipan bullsnakes (UANL 6447, UTA 3346: Fig. 17C) and LSUMZ 258 (see Note 33) as well as in AMNH 147883 (right side), MZFC 3488 (only head and neck, 5 prefrontals, single small parietal), UMMZ 113634 (see Note 28), UTA 4859, 57617–18, and UTEP 4112 from Durango, UTEP 8636 (left) collected near the San Luis Potosí state line in Zacatecas, or in CM 60040 (unilateral data) from Coahuila close to the Durango border (Fig. 16), all of which are, apart from their supralabial-eye condition, flawless *Pituophis catenifer* (see Note 29). In *P. deppei*, this character is subject to random variation ranging from the degree of eye contact of both involved scales to the presence of postsuboculars and the exclusion of the fifth or any supralabial (bilateral in CNAR 10939, Fig. 4B) from the orbit (Figs 2, 3A–C, 4, see Variation). Consequently, we distinguish Deppe’s bullsnake from *catenifer* strictly by the number of prefrontals, viz. two (1–3, once  $\geq 4$  along southern distributional limit) as opposed to four or more shields (up to at least 8) in the latter species. [Note 31]

Small, fragmented, or nonexistent parietals exhibited by certain intermediate bullsnakes (Table 5) are characteristic of *Pituophis catenifer* (Fig. 17), but are essentially absent in *P. deppei* (see Variation and Note 9). Regarding the preocular, a single examined *catenifer*, LACM 59153 from Tamaulipas, shows a divided left scale (right side condition unknown). In two lowland Gulf *catenifer*, a suture runs along the anterior midline of the frontal (UANL 6531) and this shield is divided into five scutes, or there are six frontals and seven prefrontals instead (UMNH 10859, Fig. 17F, see Note 31). [Note 32]

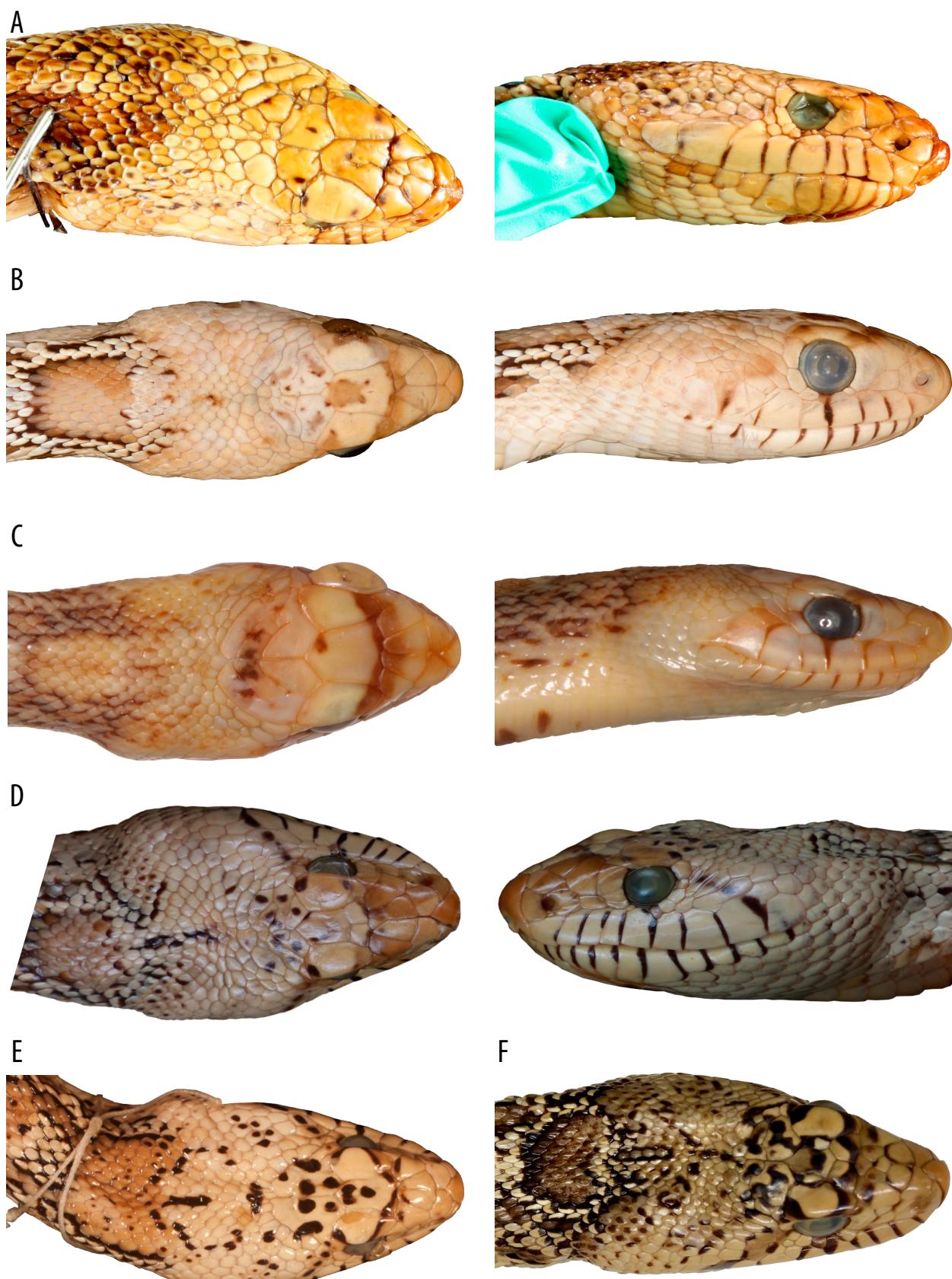


**Fig. 16.** Locality records of intermediate bullsnakes as well as UTA 16137 and 57616 (Fig. 15D), summary distribution data for Mexican *Pituophis* spp., probable origin of at least one *P. mexicanus* Duméril, Bibron & Duméril, 1854 (type series), and geographic repartition of unusual head scale states in *P. catenifer* (supralabial-eye contact, size of parietals) and *P. deppei* (number and/or condition of prefrontals, supralabial-eye contact). Solid (empty) symbols connote evaluated (literature) specimens.

With regard to body scales in Mexican *Pituophis catenifer*, we found 211–241 ventrals ( $\delta\delta$  211–236,  $\varphi\varphi$  217–237, unknown 211–241), 45–74 subcaudals (45–74, 48–59, and 46–66, resp.), and 273–306 (274–306, 273–296, 274–297) total body scales (Table 6, see Notes 39–40 for extremes). UCM 66158 from Sonora (vic. Yécora) and USNM 224451 (verified by Steve Gotte and Esther Langan) from near the Chihuahua border in NE Durango have a maximum of 29 midbody rows, and 31–35 occur in the rest of the study sample (Appendix 1) except MCZ 15923 from Chihuahua with “29” rows (STULL, 1940: Table 11; see below and Note 33 for FMNH 117000 and LSUMZ 258, resp.). TANNER

(1985) noted “29 to 33” dorsals at midbody for this state (see Note 43, BYU 13877).

The number of dorsal body blotches in our Mexican *Pituophis catenifer* series is highly variable (Table 6, see Notes 27 and 39 or, e.g., CONANT, 1965). The minimum (26) relies on BYU 13877 (Chihuahua) and low counts (30) occur in CM 60028 from the distributional limit in SE Coahuila with short paravertebral nape stripes and UCM 67211 (Yécora, Sonora). The highest count (60, TNHC 22271, see Note 28) comes from the Gulf Plain. In Chihuahua, the normal range is 34 (MCZ 15699) to 52 (USNM 105291) but as few as 26 are observed (see above) and as many as 59 marks along the trunk are



**Fig. 17.** Dorsal and lateral head views of *Pituophis catenifer* FMNH 117000 (A), USNM 105301 (B), UTA 3346 (C), UTEP 8632 (D), MCZ 80222 (E, see Notes 31–32), and UMNH 10859 (F). Not to scale. Courtesy of Aaron Mercer (A), James Poindexter (B), Muriel Norman & John Wakefield (D), Joseph Martinez (E), and Shannen L. Robson (F).

**Table 6.** Geographic variation of the number of body scales and dorsal marks in *Pituophis catenifer* males (top), females (middle line), and juveniles or specimens of unknown gender (bottom, sample size, mean, standard deviation). The number of body blotches in group G encompasses approximate count for CIBUAH 99 (juv., see Note 28). Only unilateral anterior subocular data available for specimens preceded by an asterisk (see Note 31 as to size of scale). See Fig. 14 and Appendix 1 for groups, Note 33 regarding dorsal blotches in photo vouchers (Chihuahua, Sonora), and Note 40 for Sonora (UCM 66158 and 67211, not tabulated).

Area	ventrals	subcaudals	ventrals + subcaudals	body blotches	anterior subocular
A	220–235 (11, 224.2 ±4.7)	56–66 (11, 60.5 ±2.9)	276–299 (10, 284.3 ±6.3)	38–52 (12, 43.2 ±4.7)	
	225–237 (8, 230.6 ±4.3)	52–59 (8, 55.9 ±2.6)	279–296 (8, 286.5 ±6.3)	34–59 (8, 45.4 ±8.0)	—
	224–241 (3, 231.0 ±8.9)	49–62 (3, 54.3 ±6.8)	277–293 (3, 285.3 ±8.0)	48–52 (3, 50.3 ±2.1)	
B	214–220 (6, 217.0 ±1.9)	60–71 (6, 65.2 ±4.1)	274–288 (6, 282.2 ±5.3)	36–44 (5, 39.2 ±4.0)	*UCM 65726 (complete subocular row on left side), USNM 46381 (see Note 32)
	230 (1, 230.0 ±0.0)	58 (1, 58.0 ±0.0)	288 (1, 288.0 ±0.0)	38 (1, 38.0 ±0.0)	
	—	65 (1, 65.0 ±0.0)	—	34–36 (2, 35.0 ±1.4)	
C	220–224 (5, 221.0 ±1.7)	57–60 (4, 58.8 ±1.3)	279–281 (4, 280.0 ±0.8)	32–47 (4, 40.5 ±6.9)	
	227–229 (2, 229.7 ±1.4)	52 (1, 52.0 ±0.0)	279 (1, 279.0 ±0.0)	40 (1, 40.0 ±0.0)	—
	226–233 (3, 230.0 ±3.5)	53–59 (3, 56.3 ±3.1)	283–290 (3, 286.0 ±3.6)	40–46 (3, 42.3 ±3.2)	
D	211–226 (5, 222.4 ±6.3)	57–66 (4, 60.8 ±4.1)	274–291 (4, 283.5 ±7.0)	35–44 (5, 39.2 ±4.0)	MCZ 80222 (Fig. 17E, right), UTEP 8632 (Fig. 17D, left), no data for UTA 57617–18
	217–236 (5, 227.2 ±6.9)	49–55 (4, 53.0 ±2.7)	276–291 (4, 282.8 ±6.4)	38–49 (5, 42.8 ±4.3)	
	211–235 (4, 220.8 ±10.5)	53–66 (4, 59.5 ±6.0)	274–291 (3, 282.0 ±8.5)	35–45 (4, 39.5 ±4.2)	
E	227–236 (3, 231.0 ±4.6)	45–60 (3, 51.3 ±7.7)	275–287 (3, 282.3 ±6.4)	39 (1, 39.0 ±0.0)	AMNH 107293, CM 60028, CNAR 27692, FMNH 117000 (Fig. 17A, see text), USNM 105301 (Fig. 17B)
	224–236 (5, 228.2 ±4.9)	49–55 (5, 51.8 ±2.6)	273–286 (5, 280.0 ±5.4)	38–50 (4, 43.3 ±5.7)	
	230–238 (2, 234.0 ±5.7)	[49 and ≥63, n=2]	[287 and ≥293, n=2]	30 (1, 30.0 ±0.0)	
F	227–230 (2, 228.5 ±2.1)	57–63 (2, 60.0 ±4.2)	287–290 (2, 288.5 ±2.1)	43–60 (2, 51.5 ±12.0)	*LACM 59153, *LACM 66938, MCZ 46323, *TNHC 22271, *UANL 6455, *UANL 6459, *UMNH 10859 (distinct, Fig. 17F)
	234–236 (3, 235.0 ±1.0)	48–52 (3, 50.0 ±2.0)	283–286 (3, 285.0 ±1.7)	47–57 (3, 52.0 ±5.0)	
	229–240 (6, 233.7 ±4.7)	46–62 (7, 54.6 ±5.7)	275–297 (6, 288.2 ±7.2)	43–50 (7, 45.0 ±2.6)	
G	234 (1, 234.0 ±0.0)	—	—	42 (1, 42.0 ±0.0)	bilaterally present in all five examined specimens
	232–238 (4, 234.8 ±2.5)	44–47 (4, 45.3 ±1.3)	277–282 (4, 280.0 ±2.1)	39–49 (4, 43.0 ±4.9)	(ITAH ♂, ♀, see Note 35)
	—	—	—	≥52, n=1]	

recorded beyond 30°30' N latitude (FMNH 986, STULL, 1940: Table 11, as “Field No. 938”), and fewer than 30 dorsal blotches are reported. [Note 33]

Bullsnakes from north of approximately 25°45' N latitude in Coahuila and Nuevo León are typical *Pituophis catenifer*. This is also true for most specimens from slightly farther south as exemplified by MCZ 157810 collected along highway 57 north of Saltillo (Higo area) with four prefrontals, a large postocular, undersized parietals, and 33 midbody rows. USNM 105301 (Fig. 17B, Appendix 1) gathered in the same general area or FMNH 117000 (Fig. 17A) from N Nuevo León show five or six prefrontals (only 2 larger lateral shields) and broken apart or small parietals, respectively. The latter specimen, with nine supralabials, has the fifth excluded from contact with the orbit by a complete row of five granular scales on the right side (left anterior subocular), the first supralabial divided and the preocular portion along the orbit detached on the left, and a deep groove at the anterior border of the frontal. Contrary to the indication in SMITH & DUNKLE (1937) regarding a *P. “s. sayi”* (no. “5448”, “scales in 29–27 rows”), FMNH 117000 (*P. “d. deppei”* fide TAYLOR, 1939) has 31 midbody rows (verified by Alan E. Resetar). This and another *catenifer* obtained roughly 30 km air-line distance farther northeast (km 83 on highway 85, BRYSON *et al.*, 2011: LVT 10666) come from the vicinity of the restricted type locality of the long disused *P. mexicanus* Duméril, Bibron & Duméril, 1854 established by SMITH & TAYLOR (1950a), Sabinas Hidalgo (Fig. 1).

The type series of *Pituophis mexicanus* D. B. & D. strikingly diverges in the number of dorsal body blotches (ca. 54–59, Table 3) compared to *P. catenifer* from Nuevo León (e.g., Sabinas Hidalgo) or Coahuila (30–46, 50 in AMNH 107293) and most Mexican populations evaluated for the purpose of this study (Table 6). The large paired prefrontals present in the illustrated *P. mexicanus* (DUMÉRIL *et al.*, 1854: Pl. 62, see Fig. 8) rule out its determination as *catenifer*

and would, if anything, allocate this missing voucher to Deppe's bullsnake. Nevertheless, the high number of ca. 59 dorsal trunk marks excludes that identification as well (Table 2). Both examined specimens (MNHN 3188, USNM 1415) are referable to *catenifer* on the basis of a single (5<sup>th</sup>) supralabial in eye contact, the break-up or complete fragmentation of their parietals and, partially, the frontal, 33–35 midbody rows, or two preoculars (unilateral in USNM 1415) and a tiny anterior subocular (unilateral in MNHN 3188). However, their prefrontal configurations (Figs 9A–B, Table 3) not unreservedly conform to what is observed in genuine Mexican *catenifer* as expounded to some depth in this chapter. [Note 34]

Both male *Pituophis mexicanus* (type series) show body scale counts (Table 3) in the upper range reported for ventrals in male *P. catenifer* from San Luis Potosí (220–245, mean 234) and are in line with their number of subcaudals (56–71,  $\bar{x}=65$ , LEMOS-ESPINAL & DIXON, 2013). Moreover, systematically verified bullsnakes other than certain Chihuahuan *catenifer* (and more western populations extralimital to this study, see Fig. 13A) matching the densely marked dorsal colour pattern displayed by the type series of *mexicanus*, viz. more than fifty median blotches down the trunk, are recorded only from Hidalgo (CIBUAH 99, photo voucher, no further data available), Tamaulipas, and adjacent Veracruz (Table 6: groups F–G, see above and Note 33). [Note 35]

The salient variation of head scutes in the type series of *Pituophis mexicanus* (Table 3) attests to composite nature, viz. is evidence of various involved taxa. The observed character states, and in particular the prefrontal versus supralabial-eye configurations, are incompatible with the conditions found in typical *P. catenifer* and *P. deppei* but emblematic of Northern Plateau bullsnakes clearly in-between these species as elaborated in this study (Table 5). However, Gulf *catenifer* and Central Highlands *deppei* are separated by natural barriers along the Sierra Madre Oriental (Fig. 16). The possibly Huastecan origin of two *mexicanus* (type series) as suggested by morphology (see preceding paragraph) perhaps indicates molecular phenomena related to “the influence of [...] Pleistocene climate change in shaping genetic diversity” (BRYSON *et al.*, 2011: 1570). Plausible is a scenario of reproductive interaction between *catenifer* and *deppei* (or incipient stages) in the central Sierra Madre Oriental during colder Quaternary periods and especially since the beginning of the Wisconsin glaciation (ca. 75'000 ybp). In places and at reasonable altitudes, contact between these taxa due to the decrease of currently inaccessible vegetation communities, in particular tropical forest above 750 m and the montane cloud zone, may have been possible until about 25'000 years ago (last glacial maximum). [Note 36]

Doubts regarding the identity of *Pituophis mexicanus* (see Results) have their origin in the evidently heterogeneous nature of the type series, and the binomen cannot be clearly assigned to any valid Mexican *Pituophis* spp. Therefore, we deem desirable to introduce a standard of application for the species-group name *mexicanus* D. B.

& D. by the fixation of a single name-bearer. In line with current views (e.g., WALLACH *et al.*, 2014; [reptile-database.org](#)), we designate USNM 1415 as the lectotype of *Pituophis mexicanus* Duméril, Bibron & Duméril, 1854 (Fig. 9B, Table 3). The selection of this extant male from “Mexique” (DUMÉRIL *et al.*, 1854) received from an unknown collector, possibly Auguste Ghiesbreght (see Note 36), prevents the collapse of long-standing and approved morphological species boundaries (number of prefrontals) and renders *mexicanus* D. B. & D., 1854 a junior subjective synonym of *catenifer* Blainville, 1835.

The supralabial-eye configuration of CM S-9511, a Tamaulipan *Pituophis catenifer* with two scales in eye contact as is characteristic of *P. deppei* (see above and Note 31), resulted in KLAUBER's (1947: 12) brief comment concerning potential conspecificity of *catenifer* (c. “sayi”) and *deppei* (“not impossible that intergradation may eventually be shown to exist”). “The several anomalies” of dorsal colour pattern and head scale features in bullsnakes from San Luis Potosí (DIXON *et al.*, 1962) and Durango or Zacatecas (see above and Note 27) “suggest that intergradation, convergence, or perhaps introgression may eventually be demonstrated between what virtually all herpetologists currently assume to be two well-defined species” (CONANT, 1965). “Nowhere are *Pituophis deppei* and *melanoleucus* [*catenifer*] known to occur sympatrically in the absence of intergrades” on the Northern Plateau (MORAFKA, 1977), “no clear habitat segregation between these two strikingly similar snakes (both occur in the desert proper and the peripheral mesquite grassland)” can be discerned, and there is “no evidence supporting the maintenance of *deppei* as a species” (l.c.). Though, existing differences between *catenifer* and *deppei* paired with a narrow sector of phenotypically intermediate bullsnakes favour the hypothesis of hybridization across the Northern Plateau over subspecies status for *deppei*. [Note 37]

Ranking the irregularities present immediately above the loreal in two *Pituophis deppei* from Jalisco (2 scales bilaterally, see Variation and Notes 9–10) as what they actually are, our differentiation criterion for *P. catenifer* and *P. deppei* employed throughout this study (4 or more prefrontals instead of 2, sporadically 1 or 3) generates a clean spatial separation of the taxa on the Northern Plateau, and the geographic pattern of the number of supralabials in eye contact or the condition of the parietal produce by and large identical demarcations (Fig. 16, see Diagnosis, Variation, text above, and Note 31, and below for northwestern montane bullsnakes). [Note 38]

The geographic limits of *Pituophis catenifer* and *P. deppei* (Figs 7, 14) on the Northern Plateau coincide with the repartition of large parietals (*deppei*, see Variation concerning 3 specimens from Guanajuato and San Luis Potosí or AMNH 4382 with semi-divided parietals, Fig. 3D) against divided to completely fragmented shields (*catenifer*, Fig. 16, see Note 32). The southern boundary of *catenifer* also defines the extent of erratic scale features and in particular the presence of an anterior subocular (see Notes 31–32; among *deppei* only in CNAR

10939, Fig. 4B) and the southwestern corner formed by 26° N latitude and 104° W longitude delimits the distribution of bullsnakes with 33 or more midbody rows. Generally speaking, a cline towards fewer dorsal scales in Mexican congeners including *P. lineaticollis* runs from the US border to the Isthmus of Tehuantepec (see Note 21).

Resorting to KLAUBER's (1947) analysis of ventral and subcaudal data, CONANT (1965) concluded that counts for Durango *Pituophis catenifer* (*P. "melanoleucus affinis"*) "are low in comparison with [...] more northern localities." Our data set for certain areas on the Northern Plateau (Table 6) is too small to prove or reject an overall north–south decrease of body scale numbers and come to a sound conclusions about morphological divergence from *P. deppei* or detect, for instance, possible character displacement. At any rate, certain populations from the northern Sierra Madre Occidental show as few as 214–218 ventrals in males (n=5, see Note 43). [Note 39]

More than a decade later, and despite recently published data on the subject (e.g., RORABAUGH *et al.*, 2011; ENDERSON *et al.*, 2014; LEMOS-ESPINAL *et al.*, 2015; RORABAUGH & LEMOS-ESPINAL, 2016; VAN DEVENDER & FERGUSON, 2019), RORABAUGH'S (2008: Table 1) assertion that the "[d]istribution of the two *Pituophis* [spp.] needs further investigation in eastern Sonora" has lost hardly any relevance. Various photo vouchers of Deppe's bullsnake from the northern Sierra Madre Occidental in Chihuahua (e.g., entries no. 59769, 258603) and Sonora (258606, 259025, 295431) appear in the MABA database but a single (UAZ 34883) out of nine examined northwestern montane bullsnakes (all from Chihuahua) with pertinent morphological data available other than regular *P. catenifer* (Appendix 1, Table 6: group B plus small Sonora sample) reveals to be a *P. deppei* as understood in this study (see end of chapter). [Note 40]

As far as we can detect, amazingly few detailed distribution records exist for *Pituophis catenifer* from the Chihuahua-Sonora border region inland of Álamos between ca. 26°45' and 29°45' N latitude and ca. 107°45'–109°30' W longitude (Fig. 14). The relative scarcity of preserved specimens combined with the lack of published pertinent scale data demand caution in drawing conclusion, not least on account of the shortage of verifiable or reliable identifications. Though, we see no reason to question the systematic allocation of two or three different lowland *P. catenifer* (LVT 10634, MABA 258602, 264837, see Fig. 14: left inset) from Rosario Municipality (Nuri, 28°07' N 109°20' W, ca. 375 m) and thornscrub habitat in SW Yécora (Curea, 28°19' N 109°17' W, ca. 490 m), the more so as a tissue sample was sequenced (LVT 10634, mtDNA data, BRYSON *et al.*, 2011: Appendix S2, see Note 35). Confirmed data indicate sympatry between this species and *P. deppei* for the Mulatos catchment area where *catenifer* extends east at least to Yécora (town, UCM 67211) and perhaps Maycoba (MABA 258607, see below), and *deppei* is substantiated from as far west as Mesa del Agua (ca. 109°00' W longitude) in

Chihuahua and the inland escarpment of the Mesa del Campanero in Sonora (MABA 295431, see Note 40). Moreover, both taxa coexist roughly 125 km airline distance northeast in the Río Sirupa drainage (Yepómera, Figs 1, 14). [Note 41]

The partially blurry ventral view photo of MABA 59769 from "2.2 km west of Yepachic" (Temósachic Mun., Chihuahua, see Notes 40–41), with head scale conditions perfectly fitting *Pituophis deppei* as understood in this study, does only allow a guess about the accurate number of scales but the sum of ventrals (ca. 235) and subcaudals (probably >70) appears to exceed 300 scutes. MABA 258605 (*P. "deppei"*), a yellow-headed adult with ca. 30 piceous dorsal blotches and an orange hue on the posterior trunk that becomes intense on the tail, has large parietals (except anterior lateral edges, see Note 43), eight supralabials of which only one (4<sup>th</sup>) contacts eye on right side (large postsubocular, left configuration unknown), and three prefrontals (large median scute bears faint incomplete groove), and thus qualifies as an intermediate specimen under the criteria established for that arbitrary operational grouping (see above). [Note 42]

MABA 258607 from "0.9 km E of Maycoba" ("1558 m" elev.) shows ca. 26 + 10 dorsal blotches (body and tail, marks onto midbody dark brown with black border, uniformly pitch black posteriorly) on a generally fawn-coloured anterior trunk (head light brown) followed by a reddish-brown dorsum to the tail tip, and a yellowish hue runs from the supralabials along the paraventral scale rows and possibly over the whole venter. The specimen (photo Thomas R. Van Devender, "son-trv 5150") seems to have four large prefrontals and its identification as *Pituophis "deppei"* appears to be incorrect but a proper appraisal on the basis of the uploaded image is problematical. [Note 43]

The number of prefrontals, our key character employed throughout this study to distinguish *Pituophis catenifer* from *P. deppei*, results in a definite separation of their ranges and parapatry with a hybridization zone across the Northern Plateau (Fig. 16). The size of the parietals (at least partially divided or small versus large, resp.) is in line and the supralabial condition (number of scales in eye contact) of most highland bullsnakes concurs with this geographic pattern. Twenty northwestern pine-oak zone specimens comprising MABA 59769 consist of ten male *catenifer* (Appendix 1, see Note 43), two *deppei* including the debatable UAZ 34883 with three prefrontals (see Note 40), and eight morphologically intermediate bullsnakes from Chihuahua (Table 5). Perhaps even more astonishing than the mere numerical ratio is the high frequency of comparatively large parietals (Fig. 16) and low dorsal scale maxima at midbody (29) in otherwise authentic *catenifer*, the in-between prefrontal configuration of UAZ 34883, ventral counts higher than 230 and over 300 total body scales in a flawless *deppei* (MABA 59769, see above) and a *catenifer* (UCM 66158) from the Yécora Valley, a basically identical dorsal colour pattern in the involved taxa (see Note 43), or the ab-

sence of females in our NW montane *catenifer* sample. These results call into question the distinctiveness of northern *deppei* from Sierra Madre Occidental *catenifer* and concerns regarding the veritable nature of these *Pituophis* populations are further fuelled by molecular data from the area under consideration suggesting “introgression, and possibly mtDNA capture” (BRYSON *et al.*, 2011: 1580). Bullsnakes that phenotypically match *deppei* are “nested within [...] *catenifer*” (l.c.: e.g., Figs 4–5), viz. share haplotypes with the Sonoran Desert phylogroup (see Note 35), and the taxa “are indistinguishable” (l.c.: 1575, 1578).

Dense sampling with rigorous identifications of specimens in the Sierra Madre Occidental south to Nayarit including the Pacific foothill area (Sinaloa), the northern Sierra Madre Oriental and inland Lower Huasteca, or along the western Transvolcanic Belt and in the Orizaba Range can elucidate the molecular processes underlying the variation observed in certain morphological characters and/or regions. Sequencing of nuclear DNA would definitely help to better understand the evolutionary history of Mexican bullsnakes, fully appraise the affinities and genetic make-up of montane populations from the northern Pacific Cordillera and the peripheral range of *Pituophis deppei* in the Sierra Madre Oriental, assess the systematic relationship of, for instance, *P. deppei brevilineatus* Schmidt & Shannon (Michoacán) or the status of *P. catenifer* from the Gulf evergreen forest, and perhaps reconsider the as yet enigmatic “*Pituophis mexicanus*”.

## Conclusions

*Pituophis deppei* (Duméril, Bibron & Duméril, 1854) is a variable bullsnake regarding head and body pholidosis and colouration characters. The northwestern range is poorly defined. The confirmed southern distributional limit argues for parapatry with *P. lineaticollis* (Cope, 1861b). In Michoacán there is no clear-cut geographic separation but *deppei* and *lineaticollis* differ in the number of ventrals, though not necessarily so in their dorsal colour pattern (shape of neck marks) or the number of midbody scale rows as exemplified by paratypes of *P. deppei brevilineatus* Schmidt & Shannon, 1947, which renders debatable the coherence of, and species status for, *lineaticollis* as defined today.

The Nearctic *Pituophis catenifer* (Blainville, 1835) extends to central Zacatecas and northernmost Veracruz (Tamaulipas border, first genuine state record: UMNH 10859, Fig. 17F), and penetrates into tropical lowland areas from San Luis Potosí to as far south as extreme NE Hidalgo and in adjacent Veracruz (vic. Huejutla de Reyes). Morphologically, a hiatus separates these Gulf (Huasteca) populations from southern inland *P. catenifer*. This species and *P. deppei* meet and hybridize in a narrow contact zone along the limits of their basically

parapatric ranges across the Northern Plateau. Typical *catenifer* and *deppei* can reliably be diagnosed through the number of prefrontal scales. Their geographic distribution largely concurs with further scale conditions (e.g., number of supralabials in eye contact, parietal size) that normally separate these species. Bullsnake populations from the northern Pacific Cordillera, in particular the Sierra Tarahumara and the Aros drainage, deserve special attention regarding their systematics and involved evolutionary events.

Specimens showing head scales configurations discordant with flawless *Pituophis catenifer* or *P. deppei* are observed on the Northern Plateau. Supposed Pleistocene range expansions underlie possibly genetic introgression across, for instance, the central and northern Sierra Madre Oriental. The type series of *P. mexicanus* Duméril, Bibron & Duméril, 1854 encompasses at least one specimen most probably collected in NE Hidalgo and exhibits a perplexing diversity of head and body scales including combinations characteristic of phenotypical hybrids between *catenifer* and *deppei*. The restriction of the type locality of the disused specific name *mexicanus* to Sabinas Hidalgo in N Nuevo León (SMITH & TAYLOR, 1950a) collides with morphological data for *catenifer* (presumed senior synonym) from this area. The declaration of a lectotype for *P. mexicanus* D. B. & D. preserves nomenclatural stability.

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## Appendix 1

Evaluated Mexican bullsnakes. Indicated are gender, data source (literature reference or person[s] who ascertained the number of midbody rows and, in certain cases, verified the gender; see following list of abbreviations, Note 1), and origin (a dagger [†] marks two unidentified localities, homonymous place names). The provider and field number (if available) are given if relevant (see text). An asterisk (\*) denotes photo vouchers. Specimens preceded by a black (●) or white circle (○) are devoid of ventral and subcaudal counts or all body scale data (incl. midbody rows), respectively.

**Abbreviations:** AW (A. Wynn, USNM), AWh (A. Whiting, BYU), BB (BANTA, 1962), BH (B. Hollingsworth, SDNHM: SDSNH series), BS (B. Stuart, NCSM), DD (DAVIS & DIXON, 1959), DJM (D. J. Morafka, coll.) DK (D. Kizirian, AMNH), DL (D. Lazcano, UANL), DS (DUNKLE & SMITH, 1937), DW (D. Wylie, INHS incl. UIMNH series), EC (COPE, 1861a–b), EE (E. J. Ely, CAS), EL (E. Langan, USNM), EPR (E. Pérez-Ramos, MZFC), ET (TAYLOR, 1939, 1949, 1952, 1953), FR (FOUQUETTE & ROSSMAN, 1963), FW (FUGLER & WEBB, 1956), GB (BOULENGER, 1894), GG (G. Gassner, NMW), GP (G. G. Pandelis), GS (G. Schneider, UMMZ), HS (SMITH, 1943, 1944), II (I. Ineich, MNHN-RA), JLE (J. A. Lemos-Espinal, coll.), JM (J. Martinez, MCZ), LCS (LEMOS-ESPINAL *et al.*, 1994), LK (KLAUBER, 1947), LSC (LEMOS-ESPINAL *et al.*, 2004a), LZ (C. Lieb and V. Zhuang, UTEP), MB (M. Bucci, UAZ), MD (McDIARMID, 1963), MK (M. Kaplan: MSUM), MR (J. Mata and A. E. Resetar, FMNH), NC (N. Camacho, LACM), OS (STULL, 1940: Tables 2–4, 10–11), PC (K. Piller and B. Crother, SLU), RC (CONANT, 1965), RM (A. E. Resetar and A. Mercer, FMNH), CS (Carol Spencer, MVZ), SD (C. Sheehy and M. Domohowski, UF), SG (S. Gotte, USNM), SLR (S. L. Robson, UMNH), SR (S. Rogers, CM), SS (SCHMIDT & SHANNON, 1947), TH (T. J. Hibbitts, TCWC), TL (T. LaDuc, TNHC), WCS (WILLIAMS *et al.*, 1961), and WD (DUELLMAN, 1960).

*Pituophis catenifer* (Blainville, 1835) (Fig. 14, Table 6). CHIHUAHUA: AMNH 3563, ♂, OS (San Diego, Casas Grandes Mun.); \*BYU 13877 (see Note 43), ♂, AWh (1 mi W Chihuichupa); FMNH 986 (“Field No. 938”), ♀, OS (“Ahumada”); HMS 36274,

♂, LCS (3 km S San Buenaventura); KLW 541, ?, LCS (2.8 mi S Camargo); \*MABA 315183, ♂ (2.4 air km S Ignacio Allende); MCZ 15699, ♀, OS (Pacheco); \*MCZ 15923 [dorsal head view photo], ♂, OS (Madera); \*○MCZ 80223 (wet skin, skull removed) and \*80224, ♂ (3 km W Yepómera); PSC 834, ?, LCS (4.2 mi N Chihuahua City); \*UAZ 34884, ♂ (Yepómera); UCM 20458, ♂, LCS (“nr Cd.” Chihuahua); UCM 21060, ♂, LCS (14.4 km S Nuevo Casas Grandes); UCM 46081, ♀, LCS (22.2 mi S Chihuahua City); \*UCM 65726, ♂ (vic. Tomochic, JLE, see Note 28); USNM 1542, ?, OS (“Presidio del Norte”, i.e., Ojinaga); USNM 14222a–b (♂♀) and 14293a–b (♂♀), OS (Chihuahua City); USNM 46372, ♂, OS (Casas Grandes); \*USNM 46381 (see Note 32), ♀, [OS] (Batopilas); USNM 104678, ♂, HS 1943 (9 mi W El Carrizal); USNM 104681 (♂), 104682 (♀), 104683 (♂), 104684 (♀), and 104685–86 (♂♂), HS 1943 (Río Santa María near Progreso); USNM 105291, ♂, HS 1943 (†39 mi E “Carmen”, see Note 31); USNM 110894, ♀, HS 1943 (Río Santa María near Progreso); \*\*UTA 57581 (♂) and 57583 (♀, not tabulated, see Note 33), GP (hwy 24 btw. Hidalgo del Parral [“Parral de Hidalgo”] and Guadalupe de Calvo, mapped ca. halfway at El Vergel). COAHUILA: \*CM 60028, ?, SR (48 mi N Saltillo, hwy 57, DJM); \*○CM 60029 (head, neck; jct. hwy 40 with COA 35 N Parras de La Fuente, DJM); \*CM 60040, ? (1 mi SE San Pedro de Las Colonias, DJM 1506); \*○FMNH 47085 (head; Cuatro Ciénelas); ○KU 39561 (head, neck), FW (4 mi E Paila); KU 39565, ♂, FW (“Sierra Mojada”); \*MCZ 157810, ♂, JM (44 km N Saltillo); \*○MZFC 3488 (head, neck; 26 km S Puente [Bridge] at Canutillo); PSC 1005 (“834”), ?, LCS (40.4 mi E Paila); UF 11309, ♀, FR (4.3 mi S Castaños); USNM 1539a–b, ♂♀, OS (Castañuela); \*USNM 105301 [head view photos] (Fig. 17B), ♀, HS 1943 (21 mi N Saltillo, Higo area); \*UTEP 9158, ♂, LZ (7.5 mi SE Viesca). DURANGO: \*AMNH 85252, juv., [RC] DK (6 mi E Durango City, “near the Río del Tunal”); AMNH 147883, ♂ (35 mi NE Durango City); \*MCZ 80222 (Fig. 17E, see Notes 31–32), ♀, JM (24 mi S Rodeo); UCM 20459, ♀, LCS (12 mi S Torreón de Canas); UCM 21059, ♂, LCS (7 mi N La Zarca); UCM 21637, ♂, LCS (14 mi N Durango City); \*UIMNH 48522 (ex KLW 741), ♀, WCS · DW (34.3 mi S Tlahualilo); \*UIMNH 48526 (ex PSC 969), ♂, WCS · DW (6.9 mi NW Bermejillo); \*UMMZ 113634, ♂, GS (east of Cuencamé, see Note 28); \*USNM 224451, ♂, EL (6.2 mi N Ceballos); UTA 4859, ♀ (1 mi S Rodeo); UTA 57617–18, ? and juv. (hwy 23 Durango–Santiago Papasquiaro at 24°49.88' N 104°57.34' W and 24°10.39' N 104°41.85' W, resp., coll. Jonathan A. Campbell); \*UTEP 4112 (see Note 29), ♀, LZ (5 mi NE Luis Moya); \*\*UTEP 6666–67, juvs, LZ (58 km N La Zarca, hwy 45); \*UTEP 9379, juv., LZ (1.3 road mi S Francisco Primo de Verdad). HIDALGO: ITAH ♂ (1) and ♀♀ (4, incl. 2 live individuals, see Note 35) without accession numbers (vic. Chalahuiyapa, Huejutla de Reyes). NUEVO LEÓN: AMNH 107293, ♀ (8.6 mi E Cadereyta); BMNH 1889.7.3.42 (see Note 39), ♂, GB [“*Coluber melanoleucus*” specimen ‘i’] (“Nuevo Leon”); \*FMNH 117000 (ex EHT-HMS 5448, Fig. 17A), ♀, DS · ET 1939 · RM (3 mi W Sabinas Hidalgo). SAN LUIS POTOSÍ: \*LACM 66938, juv., NC (5 mi E jct.

hwy 110 with 85 on Tampico road); \*LSUMZ 2427 [head view photos], ?, ET 1952 (vic. Illescas). SONORA (see Note 40): UCM 66158 (ex UBIPRO 12593), ♂ (“Los Parajes”, km 269.5 on hwy 16); UCM 67211 (ex UBIPRO 14453), ♂ (juv., Yécora). TAMAULIPAS: \*CM S-9511, ♀, LK · SR (“ $\frac{3}{4}$  mi. inland from Tamesi River”); \*LACM 59153, ♂, NC (8 mi NE Padilla); \*MCZ 46323, ♀, JM (jct. hwy 101 with Río Corona road); \*TNHC 22271, ♂, TL (Punta de Piedra, see Note 28); \*UANL 6447 [head view photos], ?, DL (vic. La Atravesada); \*UANL 6455 [ibid.], ?, DL (6 km SW Soto La Marina); \*UANL 6459 [ibid.], ?, DL (4.5 km SW Soto La M.); \*UANL 6531 [ibid.], ?, DL (22 km SW Aldama); \*○UANL 6599 [ibid.], ? (Casas); UTA 3346 (Fig. 17C), juv. (75 mi S Reynosa). VERACRUZ (first genuine state record): \*UMNH 10859 (Fig. 17F), ♀, SLR (8 mi S Tampico). ZACATECAS: \*○CM 60031 (head, neck; 72 mi S Concepción del Oro, DJM 681); \*CM 60037, ♂, SR (5 mi W Cedros, hwy 114, DJM 963); CNAR 15560, ♀ (9 mi SE Valparaíso); \*UTEP 8632 (Fig. 17D), ♀, LZ (3.2 mi NW Juan Aldama); \*UTEP 8634, ♀, LZ (6 km SE Tetillas); \*UTEP 8636 (see Notes 29, 31), ♂, LZ (12 mi NE Villa de Cos). ORIGIN UNCLEAR (Huasteca, see Note 33): \*LSUMZ 258 [head view photos], ?, ET 1949 (“region near Ciudad Maiz”).

Intermediate bullsnakes (morphologically in-between *Pituophis catenifer* and *P. deppei*, Fig. 16, Table 5) including UTA 16137 and 57616. CHIHUAHUA: \*FMNH 11825 (Fig. 15A), ♀, RM (Sarmachique); \*LACM 74031, ♀, NC (43 mi S Creel); \*MCZ 80225, ♂ (3 km W Yepómera); \*●NCSM 85998 (wet skin), ?, BS (“Barranca del Cobre”); \*UCM 65738 (ex UBIPRO 11678), ♂? (Areponapuchic, JLE 2003); \*UCM 65748, juv. (“Huicorichi”, JLE, see Note 16); \*UCM 65821 (ex UBIPRO 11857, see Note 29), ♂ (?), LSC ([“Rancho”] Huicorichi, JLE, see Note 16); UCM 66385 (Fig. 15C), ♀ (“Huicorichi”, ibid.). COAHUILA: \*USNM 105302 [head view photos], ♀, HS 1943 (21 mi N Saltillo, Higo area). DURANGO: \*AMNH 88822, ♂, [RC] DK (Guatimapé); UTA 57616 (Fig. 15D, see Note 30), ♂ (hwy 23 btw. Santa Catarina de Tepuehuanes and Guanacevi, coll. J. A. Campbell); \*UTEP 9370, juv., LZ (28 km S Durango City). NUEVO LEÓN: \*TCWC 54239, ♀, TH (16.1 mi E San Roberto jct.); UTA 3050, ♂ (“near San Roberto”); UTA 16137 (see Notes 29, 38), ♂ (51.3 km NE Doctor Arroyo, coll. Steve Hammack and company); UTA 38561, subad. (17–26 mi N Doctor Arroyo, “MX Hwy 6”, i.e., NL state road 61, arbitrarily mapped at  $24^{\circ}00' 100^{\circ}00'$ ). SAN LUIS POTOSÍ: \*LSUMZ 2426 [head view photos] (Fig. 15B), ?, ET 1952 (2 km E Illescas). SINALOA: AMNH 107040, ♀ (4 km E Loberas, hwy 40); \*UAZ 25815, ♂, MB (21.1 mi N Culiacán, see Note 30). ZACATECAS: AMNH 85251, ♀, RC (Río Florida, 15 mi NW Fresnillo); AMNH 118009, juv. (10 mi NE Morelos); \*UTEP 8637, ♀, LZ (38 mi NE Villa de Cos).

*Pituophis deppei* (Duméril, Bibron & Duméril) (Fig. 7, Tables 1–2). AGUASCALIENTES: CAS 87401, juv., BB (1 mi SW Presa del Llaveiro); CAS 87405, juv., BB (3 mi WSW “Cañada Honda”), EHT-HMS 5379, ?, DS (10 mi E Aguascalientes City); \*UAZ 46785, ♂, MB (Esteban San Castorena). CHIHUAHUA: \*UAZ 34883 (see Note 40), ♂ (Yepómera). COAHUILA: CNAR 27692, juv. (3 km E Arteaga); MCZ 407, juv., OS (Castañuela); \*FMNH 106079 (ex EHT-HMS 5374, Fig. 3B), ♂, MR (30 mi W La Rosa); \*TCWC 54237, ♂, TH (2.2 mi SW Guadalupe Victoria); \*TCWC 54817 (Fig. 4D), ♂, TH (4.9 mi W San Antonio Alazanas); USNM 1522, ♂ holotype of *Arizona janii* Cope (damaged, no ventral count, see Note 14), EC 1861a · OS (Buena Vista, Fig. 1, see Note 16). DURANGO: \*AMNH 68361, ♂, [RC] DK (10 mi E El Salto); CNAR 15617, ♂ (vic. San Miguel de La Michílita); CNAR 15620, ♂ (San Francisco Javier); \*\*MCZ 80909–10 (incl. Fig. 3C, see Notes 9–10 and 29 as to 80910), ♀♀, JM (7 mi N Durango City); \*○MSUM 3173, ? (22 mi N Morelillo); USNM 46365, ♂, OS (Hacienda Magdalena, see Note 16); \*UTEP 4346, ♂, LZ (15 mi SSE Durango City); \*UTEP 4348, ♀, LZ (“ca. 5 km E Teneraca”); \*UTEP 8630, ♂, LZ (4 mi SW Río Chico). GUANAJUATO: \*FMNH 106078 (Fig. 10B: Table), ♂, MR (4 mi S Acámbaro); \*SDSNH 42711, ♀, BH (12 mi S San Miguel de Allende); USNM 16442, ?,

OS (“Guanajuato”); USNM 46557 (Fig. 10B: Table), ♂, OS (Acámbaro, see Note 16); UTA 57619, ♂ (hwy 40 Durango–Gómez Palacio, not mapped); \*UTEP 4343 (Fig. 4G), ♀, LZ (6.5 mi NW San Miguel de Allende). HIDALGO: AMNH 75563 (see Note 15), ♂ (4 mi E Jonacapa); AMNH 93428, ♀ (5 mi W San José Atlán); AMNH 96650 (see Note 15), juv. (15 mi NW Ixmiquilpan); AMNH 127904, ♀ (“N of Tizayuca”); AMNH 159266, ♂ (0.7 mi N Lagunilla or 2.8 mi SE Yolotepec); AMNH 160913, juv. (4.3 mi E Pachuca); CNAR 15639, juv. (Santa Mónica, Epazoyucan); CNAR 15654 (see Note 15), ♂ (Vaquerías, Metztitlán Mun.); CNAR 25285 (ibid.), ♂ (Taguia); CNAR 29695, ♀ (Rancho ‘El Manzanal’, Metztitlán); \*LACM 114124, ♀, NC (“Trancas”, i.e., Morelos); \*TNHC 82481 (see Note 36), ♀, TL (7 km S Zacualtipán); \*UF 49522, ♂, SD (36 km from hwy “139” to P. N. El Chico); USNM 110890–91 (wet skins, head and tail intact), ♂♂, HS 1944 · SG [size] (Ixmiquilpan). JALISCO: AMNH 19848 (♂), \*19849 [dorsal and left head view photos] (♂), 19851 (♂), and \*19852 [ibid.] (juv.), OS (Jamay); AMNH 94870, juv. (10 mi SE San Juan de Los Lagos); AMNH 147886 (Fig. 3A), juv. (5.5 mi SE Lagos de Moreno); BMNH 1892.2.8.52, ♀, GB [specimen ‘b’] (Hacienda Vieja del Castillo); \*CAS 169852, ♂, EE (17 mi NW Ameca); CNAR 15569, ♀ (Jamay); LACM 1823, ♀, MD (Santa Clara); \*MSUM 3675, ? (vic. Jalostotitlán); \*●UF 42378, ♀, SD (“ca. 23 km N” Jocotepec turnoff, hwy 15 near Guadalajara); USNM 24969, ♂, OS (Guadalajara); USNM 46385, ♂, OS (Atemajac); UTA 4552 (Fig. 4D), ♀ (40 mi NW Cd. Guzmán); UTA 5994–95, ♂♂ (2.4 km NW Tapalpa); UTA 53368 (head and neck missing), ? (Atequique–Cd. Guzmán); UTA 57572–73, ♂♀ (Copala–Cd. Guzmán “north of Nevado de Colima”). MEXICO CITY: AMNH 19850, ♀ [OS] (vic. Atzacoalco, Gustavo A. Madero); BMNH 1868.4.7.38, ♂, GB [specimen ‘a’] (“City of Mexico”); CNAR 706–707, ? and ♂ (Nativitas, Xochimilco); CNAR 737–738, juv., ♂ (“Pedregal de San Ángel”, i.e., Jardines del Pedregal); \*○MVZ 62078, ♀, CS (vic. San Francisco Tecospa, Milpa Alta); MZFC 621 (Fig. 4C, see Note 9) and 624, ♂♂ (Sierra Ajusco); SMF 18539, ♂ (“Mexico”). MEXICO CITY AREA (see Implications): \*\*AMNH 4382–83 (incl. Fig. 3D), ♂♂, [OS] (“Gulf of California”); \*MHNH 6616 (Fig. 2A, Table 1), ♀ syntype of *Elaphis pleurostictus* Duméril, Bibron & Duméril (skull removed), II [incl. size] (“Montevideo”, see Types and Deppe). MÉXICO STATE: CNAR 1683, ♂ (Chapingo, Texcoco); CNAR 10939 (Fig. 4B), ♀ (Amecameca); MCZ 16051, ♂, OS (Teotihuacán); \*MVZ 57252, ♂, CS (“18 mi ESE Mexico City”); \*MVZ 164796, ♂, CS (turnoff hwy “150” [132] to San Martín de Las Pirámides); UCM 64476, ♂ (San Juan Teotihuacán); \*UIMNH 36223, ♂, DW (“40 km N Mexico City”, i.e., vic. Teotihuacán); USNM 110889, ♂, HS 1943 (“near Chalco”, Mexico City border). MICHOACÁN (Fig. 10B: Table, except TNHC 25426, UMSNH 1146, UTA 6047–48): \*AMNH 69940, ♂, DK (6 km E Carapán); \*MCZ 157812 (skull removed), ♂, JM (btw. hwy 43 and Tararameo, “ca. turnoff to San Juan”); \*MVZ 164793, ♀ (juv.), CS (Urupán–Pátzcuaro road btw. jct. hwy 120 and 6 mi W); \*SLU 1806, ♂, PC (1 mi S Quiroga); \*TNHC 25426, ♀, SLR (Pátzcuaro–Lagunillas, 1.1 mi S hwy 15 jct.); UMSNH 264, ♂ (San Juanito Itzicuaro, INIRENA site); UMSNH 518, ♂ (hwy 126 btw. Ajuno and Jujucato); ○UMSNH 1146, live ♂ (Ichán); UMSNH 1540, ♂ (Santa Rita de Casia); UMSNH 1829, ♀ (“La Catarina”, i.e., Santa Catarina, Tuxpan); UMSNH 1890, ♂ (Morelia, Fracc. Alameda); USNM 110888, ♂, HS 1943 (Tacícuaro); UTA 6047–48 (incl. Fig. 4F), ? and ♀ (12 mi W Jiquilpan); UTA 57574, ♂ (“Lago de Patzcuaro”). MORELOS (?): \*TNHC 29666, ♂, TL (“85 km W Puebla City”, see Distribution). NAYARIT: \*CAS 169661, ♀, EE (“W Santa Teresa”). NUEVO LEÓN: \*●CAS 115861, ?, EE (3 mi S Galeana); \*\*FMNH 33564–65 (incl. Fig. 3E), ♂♀, HS 1944 · RM (Ojo de Agua [La Fábrica]); \*NCSM 85997, ♂, BS (9 mi SE Galeana); \*SDSNH 57003, ♀, BH (4 km S Galeana); \*SDSNH 60481, ♀, BH (6 km W Doctor Arroyo); \*TCWC 54238, ♂, TH (9.2 mi E San Roberto jct.); \*TCWC 54240, ♀, TH (16.4 mi W Galeana jct.); \*TCWC 94148, ♂, TH (“nr. Dr. Arroyo”, coll. S. Hammack); \*○UAZ 41758, ? (1 mi SW “Punta de Reyna”, i.e., Puerto Reina); \*○UAZ 45528, ? (vic. La

Soledad, see Note 28); UTA 16136, ♀ (48 km S La Ascención); UTA 38560, ♀ (17–26 mi N Doctor Arroyo, “MX Hwy 6”, i.e., NL state road 61). PUEBLA (Fig. 10C: Table, partim): AMNH 19856, ♀ [OS] (“S.E. of Puebla” City); AMNH 110415 (Fig. 4A), ♀ (2 mi N Záratepec); BMNH 1894.4.26.7, ♂, GB [specimen ‘h’] (“S. Mexico”); ○CNAR 31578–79, juvs (Laguna de San Luis Atexcac); \*FMNH 105481 (ex EHT-HMS 27928, Fig. 3F), ♂, RM (“near Tehuacán”); \*FMNH 106007 and \*106009, juvs, MR (“near Tecamachalco”, coll. ET); SMF 84791, ♂ (“near Oriental”); SMF 95022, juv. (San Andrés Calpan); SMF 95083 and 95897, ♂♀ (San Andrés Cholula); \*TNHC 32857, ♂, TL (2 mi W jct. hwy 150 and Tehuacán turnoff); \*UAZ 27042, ♀, MB (21 mi NW Teotitlán del Camino, Oaxaca); \*UF 11310, ♀, SD (8 mi SE Tehuacán); \*UIMNH 48747 and \*48758, ♂♀, DW (San Diego Chalma); \*UMMZ 88687, ♀, GS (Tehuacán); UMSNH 72 (juv.), 73 (♂), and 1571 (juv., Los Humeros); USNM 46433, ♂, OS (Atlixco). QUERÉTARO: \*UTEP 9115, ♂, LZ (1.6 mi N San Juan del Rio). SAN LUIS POTOSÍ: LSUMZ 2425, ?, ET 1952 (15 km NW San Luis Potosí); LSUMZ 2603, juv., ET 1952 (15 mi NE San Luis Potosí); \*LSUMZ 4369 [head view photos], ♂, ET 1953 (6 mi E El Huisache); LSUMZ 4876, ?, ET 1953 (Amoles); \*SDSNH 49534, juv., BH (Ahualulco); \*SDSNH 57024, juv., BH (30 km S “Glorieta [Benito] Juárez”); \*TNHC 29901, ♂, TL (8 mi E Villa de Arriaga); \*TNHC 89287, ♂, TL (15 km E Cd. del Maíz); USNM 46554, ♂, OS (†“Jesús María”); UTA 4820, juv. (vic. Alvarez); UTA 58370, ♂ (22 mi W Cd. del Maíz, hwy 80); UTA 58371, ♀ (24.3 mi W Cd. del Maíz, hwy 80); \*UTEP 6352, juv., LZ (11 km S Huizache jct.). TAMAULIPAS: AMNH 107292, subad. (47.3 mi NE jct. hwy 101 with 80); \*LACM 114056, juv., NC (79 mi S Cd. Victoria, hwy 101); MCZ 19544 (♀) and 19545–50 (6 ♂♂), OS (Miquihuana). TLAXCALA: USNM 110887, ♂, HS 1943 (30 km N Puebla City). ZACATECAS: \*\*AMNH 3520–21, ♀♀, [OS] (“Real de Pinos”, see Implications); AMNH 85247 (see Note 29), ♂, RC (Río Florida, 15 mi NW Fresnillo); \*AMNH 92738, ♂, [RC] DK (6 mi E Sombrerete); \*\*CAS 96075–76, ♂♀, EE (Laguna Valderrama); \*CAS 169828, ♀, EE (5 km NNE Huejucar, Jalisco); PSC 1367, ?, LCS [*P. melanoleucus*] ssp.] (8.3 mi NW Ojo Caliente); \*UF 24753, ♀, SD (10.1 mi NE entronque Morelos, i.e., M. turnoff on hwy 54); \*UF 24784, juv., SD (17.1 mi NE Morelos turnoff, hwy 54); \*USNM 238336, ♀, SG (2 mi S Villanueva); \*USNM 238337 (Fig. 3G), ♀, SG (vic. “El Carmen” near jct. hwy 45 with 49); \*USNM 238339, ♀, SG (El Fuerte); \*USNM 346647, ?, EL · SG (20.8 km NE San Tiburcio); UTA 2710, ♀ (hwy 49 at “10.5 mi E. [= W] San Luis Potosí border”); \*UTEP 4344 (Fig. 4H), ♂, LZ (5.5 mi NW Sarteneja); \*○UTEP 4349 (head, neck; 4.4 mi SE Guadalupe). ORIGIN UNCLEAR (see Note 40): USNM 8321a–b, ♀♀, OS (“Chihuahua”). ORIGIN INCORRECT OR UNKNOWN: BMNH 1871.2.7.35, ♀, GB [specimen ‘c’] (“Tehuantepec”); ●RMNH 355, ♀ (leg. F. Deppe, see Note 4); ZMB 1733–35 (Fig. 2B, Table 1, see Implications), ♂♀♂, resp., syntypes of *Elaphis pleurostictus* Duméril, Bibron & Duméril (“Mexico”).

*Pituophis cf. lineaticollis*. VERACRUZ (?): \*USNM 110892 (Figs 10C: Table and 11B), ♂, HS 1943 (“near Acultzingo”, see Note 26).

*Pituophis lineaticollis* (Cope) (Fig. 10, Table 4). GUERRERO: CNAR 6453, ? (cruero de Carrizal de Bravo [intersection]); CNAR 10237, ? (Cd. Altamirano); CNAR 24251, ♀ (juv., Los Morros); FMNH 38356 (♀), 38357 (♂), and 38358–59 (♀♀), RM (Chilpancingo); MZFC 2945, ♂ (vic. Omiltemi); MZFC 16448, ♂ (Nueva Dehli–La Guitarra road); SMF 93847, ♀ (Xocomanatlán); TCWC 7465 and 9519, ♂♂, DD (Acahuizotla); USNM 46462, ♀, OS (Omiltemi); USNM 46537, ♂, OS (Acahuizotla). MICHOACÁN (Fig. 10B: Table, except UMSNH 274, UTA 4478, 6049): \*FMNH 37126, ♂ holotype of *Pituophis deppei brevilineatus* Schmidt & Shannon (see Note 21), SS · MR (Tancítaro); \*\*FMNH 39070–71 (incl. Fig. 12A), ♂♀ paratypes of *P. d. brevilineatus*, MR · RM (ibid.); \*MCZ 53938 (ex FMNH 39069, Fig. 12B), ♀ paratype of *P. d. brevilineatus*, JM (ibid.); \*MZFC 815, ♂, EPR (10 km NE Zitácuaro); \*UMMZ 120404 (ex FMNH 39072), ♀ paratype of *P. d. brevilineatus*, SS · GS (Tancítaro); ○UMSNH 274, live ♂ (Zoromutaro); UMSNH 448, juv. (Tancítaro, Col. San Miguel); UMSNH 462, ♂ (Las Trojes); UMSNH 478, ♀ (btw. Tancítaro and “San Juan Nuevo”, i.e., Nuevo S. J. Parangaricutiro); UMSNH 823, ♀ (Agua Zarca); UMSNH 971, ♂ (Plan de Víboras); UMSNH 1037, ♀ (“Mesa de Tzitzio”); UTA 4478, ♂ (Dos Aguas, Rancho ‘De los Pobres’); UTA 6049, ♀ (1.5 mi W Dos Aguas, Rancho ‘La Pastilla’). MORELOS: MZFC 572, ♂ (vic. Tepoztlán); UIMNH 35001 (ex EHT-HMS 15360), ♂, ET 1939 · DW (Tres Marias, near Tres Cumbres). OAXACA: \*INHS 9594, ♂, DW (“10 mi SE [Santa María] El Tule”); \*MVZ 164795, ♀, CS (ca. 5 mi NE San Pablo Villa de Mitla); MZFC 13292 (Fig. 10C: Table), ♀ (Puente de Fierro); MZFC 13293 (ibid.), ♂ (Puerto de La Soledad); UCM 41361, ♂ (37 mi NNE Putla Villa de Guerrero); UIMNH 6210 (see Note 25), ? (25 km N La Soledad); UMMZ 114668, ♀ “neotype” of *Arizona lineaticollis* Cope (see Discussion and Note 25), WD (24 km NW Oaxaca de Juárez); USNM 110893, ♀, HS 1943 (San Pedro Mártir Quiechapa); ZMB 83219, ♀ (San Mateo Río Hondo). N OAXACA OR PUEBLA (see Note 22): \*NMW 26649.1, ♂, GG (“Mexico”). PUEBLA (Fig. 10C: Table): CNAR 150 (ex EHT-HMS 3343), juv. (“cerca de [Near] Tehuacán”); UTA 6381, juv. (7 km NE Acatepec, hwy 125); UTA 19406, ♂ (5.6 km SSW Zapotitlán Salinas). ORIGIN UNKNOWN: RMNH 402, ♂ syntype of *Pituophis deppei pholidostictus* Jan (“Mexico”, see Note 22); USNM 30506, ♂, OS (“Mexican Plateau”); USNM 32220 (see Note 21), ♂, OS (“Mexico”); ZMB 1737–38, ♀♀ syntypes of *P. d. pholidostictus* (“Mexico”, see Note 22).

*Pituophis mexicanus* Duméril, Bibron & Duméril (Table 3). “MEXIQUE” (type material, see Note 36): \*MNHN 3188 (Fig. 9A), ♂ paralectotype (hoc loco), II (see Results for alien data); \*USNM 1415 (Fig. 9B), ♂ lectotype (hoc loco), AW (ex MNHN specimen).

## Appendix 2

Unpublished documents in the ‘Historische Arbeitsstelle’ of the Museum für Naturkunde, Berlin, catalogued under the header “Zool. Mus., Sign. S I”, and consulted ZMB registers.

Cuvier, G. u. Valenciennes, A., Paris.  
Deppe, Ferdinand u. Graf v. Sack., I/1, “Reiseunternehmen” Mexico.  
Deppe, Ferdinand, II, “Acta enthaltend die Eingangs Verzeichnisse von den Naturalien Sammlungen des Reisenden Hr. F. Deppe 1825–???” (compiled by M. Lichtenstein).  
Jan, Georg, Prof. Dr., Mailand, Briefe an Lichtenstein, 1854–1861, “Antw.-skizzen”.

Eingangskatalog des Zoologischen Museums 1816–1828 (updated by M. Lichtenstein).

Eingangsjournal über den Zugang von Naturalien des Königlichen Zoologischen Museums zu Berlin von 1816 bis 1857 (2 vols), Band 1: 1816–1840 (updated by M. Lichtenstein and J. Illicher).

## Appendix 3

Locality data for two hylid frogs (*Dryophytes* and *Rheohyla* spp.) and twelve type specimens of herpetological taxa described in WIEGMANN (1828–1834, coll. Ferdinand Deppe) as registered in the ZMB ‘Inventarkatalog’.

*Dryophytes euphorbiaceus* (Günther, 1858b) (Hylidae) ZMB 3162, “Jalapa”.

*Heloderma horridum* (Helodermatidae) ZMB 483 [“exsiccatum”] (holotype of *Trachyderma horridum* Wiegmann, 1829a: col. 421; see WIEGMANN, 1834: Table [Pl.] I), “Tehuantepec” (see Note 4).

*Incilius cristatus* (Bufonidae) ZMB 3523 (paralectotype) and 3524 (lectotype of *Bufo cristatus* Wiegmann, 1833: col. 660, “Umgegend von Jalapa”), [vic.] Xalapa (see PETERS, 1863: 81). Lectotype designation by FIRSCHEIN (1950: 83, footnote 2).

*Incilius marmoreus* (Bufonidae) ZMB 3529–31 (syntypes of *Bufo marmoreus* Wiegmann, 1833: col. 661), “Vera Cruz” (KELLOGG, 1932: 58, Table).

*Incilius valliceps* (Bufonidae) ZMB 3532 (paralectotype of *Bufo valliceps* Wiegmann, 1833: col. 657), “Vera Cruz” (KELLOGG, 1932: 70, Table). One of originally two syntypes registered under ZMB 3532 missing. Lectotype (ZMB 3527, ♂, “Mexico”) designated by MCCRANIE & KÖHLER (2000: 72, Fig. 2).

*Plestiodon lynxe* (Scincidae) ZMB 1271 (syntype of *Euprepes Lynxe* [sic] Wiegmann, 1834: 36, “prope Chico”), [Mineral del] “Chico” (see Note 15). Former juvenile syntype missing.

*Rheohyla miotympanum* (Cope, 1863) (Hylidae) ZMB 3163, “Jalapa”.

*Rhinella horribilis* (Bufonidae) ZMB 3479, 3481 (paralectotypes of *Bufo horribilis* Wiegmann, 1833: col. 654, “Umgegend von Vera Cruze” [sic]), “Misantla” (ZMB 3479; KELLOGG, 1932: 55, Table, as *Bufo [Rhinella] marinus* Linnaeus, 1758) and vicinity of “Veracruz” (ZMB 3481 [l.c.] and 62729). Lectotype (ZMB 3480, ♀, “Mexico”) designated by FOUCETTE & DUBOIS (2014: 320). Two paralectotypes, ZMB 3493 (PETERS, 1863: 81) and 62729 (originally registered under ZMB 3481), catalogued from “Mexico”.

*Staurotypus triporcatus* (Staurotypidae) ZMB 127 (holotype of *Terrapene triporcata* Wiegmann, 1828: col. 364, “im Rio Alvarado”), “Rio alvocado”.

## Notes

**Note 1.** The inclusion of certain alien data (see first paragraph in Material and Terms) would be a matter of guess-work because of methodological constraints (e.g., terminology for circumocular scales), and some incorporated ventral counts may encompass preventrals (usually 2 or 3). We rigorously discarded, for instance, subcaudal data relying on obviously, or most probably, incomplete tails (see Note 39), exercised particular care in the handling of midbody scale row counts (see Notes 11, 33) because of considerable variation (frequent reductions and additions of rows), and treated with reservations some communicated data accompanying photo vouchers. Precise dimensions for these specimens rely on informants, and in a few cases the verification of the gender is theirs. The number and configuration of head scales of various photo-examined bullsnakes are only documented for one side.

**Note 2.** It remains mysterious how Giorgio Jan managed to obtain data, such as the labio-inframaxillary condition, for the syntypes of *Pituophis deppei pholidostictus* Jan (4 or 5 sublabials in contact with anterior chin shields, see Note 10). His correspondence with Martin Hinrich Lichtenstein and the Berlin Museum’s Board between March 1854 and August 1856 (three letters, Appendix 2) resulted in one documented shipment of ZMB herpetological specimens to Milan towards the end of 1856, but no *Pituophis* spp. appear. PETERS (1861) explained why G. Jan did not receive snakes for examination and illustration in the ‘Iconographie générale [...]’.

**Note 3.** Alluding to multiple taxa in species group sections of the ‘Elenco [...]’ (JAN, 1863), SAVAGE & McDI-

ARMID (2017: 14) resorted to “BOULENGER [1893–1896] in regarding any new names in such lists as nomina nuda because they do not meet the requirements of Art. 12.1 of the Code that they be accompanied by a description or a definition. However, many of the synopses fully discriminate new species from congeners and stand as original descriptions.” Probably, that was precisely what BOULENGER (1893: 386, as *Zamenis oaxacae*) reasoned without a standard at hand when he credited the ‘Elenco [...]’ regarding, for example, *Coryphodon oaxaca* Jan, 1863 (*Coluber constrictor oaxaca*, see SCHÄTTI & KUCHARZEWSKI, 2018: 97, Table 1) even though the taxon was established upon character states identical with those for the allied Oriental “*C. [Ptyas] korros* (Reinw.)” (Schlegel, 1837). To be available, new species-group names published before 1931 do not need to comply with criteria such as, for instance, “a summary of the characters that differentiate the new nominal taxon from related or similar taxa” as advised for names introduced after 1930 (ICZN, 1999: Recommendation 13A). Among the few genera the present authors are well versed in, some of the “nomina nuda” spotted by SAVAGE & McDIARMID (2017: 74–78) meet the provisions of Art. 12.1 (ICZN, 1999) and we do not concur with their overall relegation of names based on arbitrary and, to a certain extent, inconsistent argumentation advocated without the consideration or a debate of evidence on specific topics presented in more recent publications. In the case of *Coryphodon oaxaca* Jan (see above), SAVAGE & McDIARMID (2017: 76) argued that the binomen was “made available by BOUCOURT” (1890: 697, 701–702 incl. footnote, Pl. 48.2) as *Bascanion oaxaca*, the Palaearctic racer *Z.[amenis] rho-*

*dorachis* Jan, 1863 (*Platyceps rhodorachis*) becomes Z. “*rhodorhachis* [sic] in De Filippi, 1865” (l.c.: 73), and another unjustified emendation (“*schirazianus* [sic] (JAN, 1865)”, l.c.: 64, 67) involves *P.[eriops] parallelus* [var.] *schirasiana* Jan, 1863 (*Spalerosophis diadema schirasianus*). SAVAGE & McDIARMID (2017: 66, 76) themselves reproduced the accurate orthography of *rhodorachis* elsewhere, and their original spelling of *schirasianus* in the ‘Elenco [...]’ (l.c.: 76, as “*schiraziana*”) is incorrect. Had they not been published in this work, no taxonomist would challenge, and much less categorically reject, new species-group names (*schirasianus*, *rhodorachis*) introduced for a diadem snake from the vicinity of Shiraz (Iran) with more than four prefrontals, twelve supralabials, and none of them in eye contact, or for a racer species from the same general area with 19 midbody rows, nine supralabials, and the eponymous red vertebral stripe (SCHÄTTI *et al.*, 2010: 650, 2014: 319–320). SAVAGE and McDIARMID (2017: 69) documented that the Mexican natricid *Tropidonotus mesomelanus* Jan, 1863 (“Messico”) was sufficiently diagnosed in the ‘Elenco [...]’, and that this senior subjective synonym of *Thamnophis melanogaster* (Peters, 1864) “could be considered a nomen oblitum as it apparently has not been used as a valid name after 1899 (Art. 23.9.1.1 of the Code)” (SAVAGE & McDIARMID, 2017: 70). The purpose of the Principle of Priority “is not [...] to upset a long-accepted name in its accustomed meaning” (Art. 23.2, ICZN, 1999), and Art. 23.9.2 (Reversal of precedence) provides the correct modus operandi to preserve taxonomic stability. It suggests that authors “should cite the two names together and state explicitly that the younger name is valid, and that the action is taken in accordance with this Article”. Instead of declaring *melanogaster* Peters a nomen protectum (“this has not been demonstrated by the criteria for such action”), SAVAGE & McDIARMID (2017) opted to resurrect *mesomelanus* Jan at the expense of (“in preference to”) the long-standing and exclusively applied scientific name of the Mexican black-bellied gartersnake (SCHÄTTI & KUCHARZEWSKI, 2018: 90, Note 3).

SMITH (1971) attributed the authorship of *Tropidonotus (Coluber) melanogaster* to Wilhelm DEPPE (1830) who used that name in the sales list of specimens collected by his brother Ferdinand (item no. 167, see Types and Deppe). Neither this trinomen nor LICHENSTEIN’s (1836) “[*Tropidonotus*] *melanogaster* Wieg.” (item no. 169 in auction catalogue of F. Deppe’s material) provide themselves an indication in the meaning of the Code (ICZN, 1999: Art. 12.2) and they are nomina nuda (see Note 5).

**Note 4.** The ZMB ‘Eingangskatalog’ (1816–1828, Appendix 2) and the ledger in use from 1816–1840 (‘Eingangsjournal [...]’, *ibid.*) usually lack locality records and field dates, and no general herpetological index was kept from 1829 until roughly 1855 (see last paragraph). Regarding the herpetological collection, only LICHENSTEIN’s (1823) inventory and his handwritten update of amphibians and reptiles (“Inventarium der Amphibien”, ca. 1822–1823) are conserved. Documents in the MfN

archives could not shed any light on the described exchanges of bullsnakes, and in particular failed to retrieve information from shipping lists or correspondence with, for instance, Achille Valenciennes (MNHN) and Hermann Schlegel (RMNH). At any rate, Hinrich Lichtenstein’s notes on Deppe’s shipments (Appendix 2) allow, for example, to exclude a number of potential bullsnake candidates from further consideration. These memoranda are comprised of preliminary short descriptions of new taxa that were elaborated for the never finished ‘Prodromus Faunæ mexicanæ’ (see, e.g., notice in W. DEPPE, 1830; WIEGMANN, 1828: 364, as Lichtenstein’s “Fauna Mexicos”).

No authority after Hermann Schlegel seems to ever have identified the holotype of *Elaphis deppei* D. B. & D. (“type in Leiden Museum”, STULL, 1940: 25; “Leiden, No. ???”, DUELLMAN, 1960: 604). Based on all information accessible then, SCHÄTTI & KUCHARZEWSKI (2018: Note 6) concluded that RMNH 355 “acquired [...] 1843” and registered as “*Lycodon pholidostictus*” (Esther Donderop in litt. September 2017) was the name-bearer of *E. deppei*. However, this incomplete and partly putrefied female with a truncated tail does not coincide at all with the original description. The only other traceable RMNH bullsnake received in those days from the Berlin Museum is the syntype of *Pituophis deppei pholidostictus* Jan (syn *P. lineaticollis*), RMNH 402, which lacks a precise registration date.

Deppe specimens “transferred to [the] Leyden Museum” (STREEMANN, 1954: 89) include, for instance, a presumed syntype of the mottled owl *Ciccaba virgata squamulata* (Bonaparte, 1850) collected on September 1, 1825, at “Los Cues” in “Puebla” (see Note 15) or “Las Cues” in the Province of Oaxaca (LICHENSTEIN, 1826b: 850, “Provinz”), viz. San Juan de Los Cués (18°03' N 97°03' W) in N Oaxaca. Populations of this raptor from the Tehuacán Valley south into Central America (Panama) are usually assigned to *C. virgata centralis* Griscom, 1929 described from the Isthmus of Tehuantepec (holotype MCZ 238212 from Chivela, ca. 16°43' N 95°00' W, Oaxaca) instead of Bonaparte’s subspecies reportedly inhabiting W Mexico south to Guerrero and Morelos (e.g., DEL HOYO & COLLAR, 2014).

The first volume of the herpetological ‘Inventarkatalog’ (ZMB 1–11331) encompasses the period from 1855 until 1893. Hereby, we act on the assumption that at least the entries up to ZMB 2745 were commissioned by Lichtenstein for the preparation of his ‘Nomenclator [...]’ (LICHENSTEIN & VON MARTEENS, 1856). Deppe material was registered until ca. 1860 (ZMB 3763, *Sibon nebulata* [Linnaeus, 1758]) and 14 Mexican amphibians and reptiles received from this collector including twelve type specimens of seven valid species were recorded with specific localities (Appendix 3: 4 toads, 1 turtle, and 2 lizards, incl. 2 hylid frogs without type status). Contrary to WIEGMANN (1834: 46, Table [Pl.] IV) who described *Læmanctus longipes* from Xalapa (“prope Jalapam”), the ‘Inventarkatalog’ reports ZMB 494 (holotype) from “Mexico”. The holotype of *Trachyderma* [*Heloderma*]

*horridum* Wiegmann, 1829a (ZMB 483, WERMUTH, 1958), a desiccated skin, arrived in Berlin at the beginning of 1828 (WIEGMANN, 1834: 25, “Ferdinando Deppe, ineunte anno 1828”) and was catalogued as from “Tehuantepēc” (TAYLOR, 1969). SMITH & TAYLOR (1950a) restricted the type locality to “Huajintlán (at Morelos border)” in Guerrero (18°37' N 99°25' W). Based on WIEGMANN’s (1829b) quotation of RECCHI’s account in HERNÁNDEZ (1651: 315, see Note 5, References), who reported the “Acaltetepon” from Cuernavaca (“in Quauhnahuacensibus agris”), BOGERT & MARTÍN DEL CAMPO (1956) re-restricted the type locality of *H. horridum* to the capital of Morelos.

**Note 5.** When HOLBROOK (1842a: 99, 101) proposed the binomen *Coronella sayi*, he considered “*Coluber Sayi* [sic] Schlegel” to be an older name for his kingsnake taxon (*Lampropeltis* Fitzinger, 1843). BAIRD & GIRARD (1853: 84) rectified this lapsus (“non Schl.”) and they listed “*Coluber Sayi*, Dekay” under *Ophibolus* [syn. *Lampropeltis*] *sayi*. DE KAY’s (1842) “*Coluber*” potpourri includes, for instance, species belonging to the genera *Coluber* Linnæus, 1758, *Diadophis* Baird & Girard, 1853, *Drymarchon* Fitzinger, 1843, *Storeria* Baird & Girard, 1853, *Opheodrys* Fitzinger, 1843, and *Pantherophis* Fitzinger, 1843, but no *Pituophis* spp. at all. Most probably, LICHTENSTEIN & VON MARTENS (1856: 25) were utterly embroiled in confusion over the authorship and generic allocation of *sayi* Schlegel, 1837 (see Material and Terms). STEINEGER (1902: 152, footnote 4) introduced the replacement name (nomen novum) *Lampropeltis holbrookii* for the secondary homonym *Coronella sayi* Holbrook, 1842a, a Nearctic species from central S Canada to NE Mexico.

Wilhelm DEPPE’s (1830) sales list of Mexican zoological items collected by his brother with W. Schiede was reprinted under a condensed misleading title (“Lichtenstein’s Preis-Verzeichniss mexicanischer Vögel” etc.) by Jean L. Cabanis in 1863 (see References). Though, the text is only closely reproduced (“dem Originale annähernd ähnlich”) and in then correct orthography. SMITH (1971) dealt with the status of four scientific names for reptiles introduced by W. DEPPE (1830), which are nomina nuda except in the case of *Chamaeleopsis* [*Corytophanes*] *Hernandesii* (sic). McCARANIE *et al.* (2004) dissented from this view advocating the disputable argument that the brochure with this binomen did not serve “the purpose of providing a public and permanent scientific record” (ICZN, 1999: Art. 8.1.1) and, thus, failed to meet the criteria of a published work. At any rate, W. DEPPE’s (1830) short text (see next) complies with the requirements for that objective within the meaning of the Code (ICZN, 1999: incl. Art. 8.4) and in particular it was “produced in an edition containing simultaneously obtainable copies” (Art. 8.1.3). Definitely, the “nomen nudum” (McCARANIE *et al.*, 2004) *Ch. hernandesii* Deppe conforms to Art. 12 (availability of names) since it was introduced with an indication (“*Chamaeleo Mexicanus* [sic] Hern.”) of the description and illustration of the “Cuapapalcatl” in one of Nardo Antonio Recchi’s (ca. 1540–1594, AN-

DRETTA, 2016; “Reccho” fide DEL POZO, 1977) compendia (“Aliorum Novae Hispaniae animalium [...]”: 721) of Francisco Hernández’s (1517–1587) chronicle, posthumously printed under the auspices of the Accademia dei Lincei in the ‘Rerum medicarum Novae Hispaniae’ or ‘Thesaurus [...]’ (HERNÁNDEZ, 1651). This reference to a pre-Linnæan author meets the provisions of Art. 12.2.1 (ICZN, 1999) for descriptions published before 1758 and *Corytophanes hernandesii* (W. Deppe, 1830) is the correct authorship for this helmeted basilisk. Apart from a shortened 1651 version (464 pp.), three editions of the ‘Rerum [...]’ bear dates between 1648 and 1651 and slightly differ in content (SMITH, 1969, 1999; DEL POZO, 1977; FLORES-VILLELA *et al.*, 2004).

Francisco Hernández’s original narrative (“Historiæ animalium et mineralium Novae Hispaniae”, 90 [+ 5] pp.) appears at the very end of the first comprehensive treatise of the Mexican flora and fauna covering more than a thousand pages (HERNÁNDEZ, 1651). In particular the third “tractatus” dealing with herpetology (“De Historia reptilium Novae Hispaniae”, pp. 58–70, see References), which heralds *Pituophis deppei* (Cap. XV, “Cencoatl”, DUGÈS, 1889), does not contain Latin binominals in the sense of modern species-group names. The credit to “Hern. mex. 327. 328. *Lacertus orbicularis*” in the description of *Lacerta orbicularis* [*Phrynosoma orbiculare*] Gmelin, 1789 actually refers to the “*lacerto orbiculari*” or “*Tapayaxin*” in N. A. Recchi’s revised version preceding F. Hernández’s (“Francisco Fernandez [sic] Philippi Secundi primario Medico authore”) primal text, viz. in the ninth part or book (“*Liber Nonus* [...]”, see References). Two engravings by Johannes Faber (1574–1629) showing the ventral and dorsal aspects of this phrynosomatid complete the account.

**Note 6.** To conclude from the ‘Inventarkatalog’ (“*Elaphis pholidostictus* Wieg.”), the in-house name “*Coluber pholidostictus*” for the later ZMB 1737–38 was coined by the curatorial member Arend F. A. Wiegmann, and this certainly applies to “*Coluber pleurostictus*” as well. “*Coluber Deppei*” (sic) might have been first overtly used by Hermann Schlegel (in litt.) as set forth in the original description (DUMÉRIL *et al.*, 1854; see Descriptions). Wiegmann also introduced new binomina in other zoological fields such as ichthyology (see Note 7) or malacology (e.g., VON MARTENS, 1865: 3, 31 etc.) including, for example, the nomen nudum “*Planorbis fragilis* Wieg.” (LICHENSTEIN, 1836: n° 198 etc.).

**Note 7.** Only few localities situated between Temascaltepec in SW México State, its capital Toluca, and Mexico City (incl. Chapultepec) appear in Lichtenstein’s “Verzeichniss [...]”, and Deppe’s letter dated May 18, 1825, accompanying the third shipment, does not reveal additional visited sites. The collector’s compilation mentions, for example, “15” unspecified lizards and snakes from the vicinities of Temascaltepec and Lerma de Villada near Toluca (“aus der Gegend von Lerma”, ca. 19°17' N 99°31' W) or the microendemic salamander *Ambystoma*

*mexicanum* (Shaw & Nodder, 1798) from one of the former Mexico City lakes (“Axelotes” in “Lagunen”), viz. Lago Chalco, Texcoco, or Xochimilco. “Montevideo”, however, does not occur (incl. LICHENSTEIN, 1826a–b) nor does this place name appear in other archived documents, the narratives of the second Mexican mission (SCHIEDE, 1829a–c, 1830), WIEGMANN’s (1828–1834) contributions on Deppe’s herpetological material with emphasis on new turtles and lizards, or in the review of his amphibian type specimens (PETERS, 1863). LICHENSTEIN & VON MARTENS (1856: 13, 17, 29) listed four reptile taxa from “Montevideo”, and it is noteworthy that a South American teiid with this origin (*Teius teyou* [Daudin, 1802], ZMB 885, coll. “Taubner”, see PETERS, 1869: 63; TAYLOR, 1969) immediately follows the holotype of *Cnemidophorus [Aspidoscelis] sackii* Wiegmann, 1834 (ZMB 884) in the herpetological ‘Inventarkatalog’ (see Note 4). The concurrence of these Deppe specimens and “Montevideo” may be due to a mix-up of data and the omission of one of them in the ‘Nomenclator [...]’ (l.c.), or a former label accompanying ZMB 884 indeed attested that the holotype of *C. sackii* Wiegmann (terra typica restricta “Cuernavaca, Morelos” fide SMITH, 1949; rescinded by DUELLMAN & ZWEIFEL, 1962: re-restriction to “Oaxaca [de Juárez], Oaxaca”) came from “Montevideo”.

As all new lizard species described in the ‘Beyträge zur Amphibienkunde’ or the ‘Herpetologia Mexicana’ (WIEGMANN, 1828, 1834) except *Euprepes [Plestiodon] lynxe* (Appendix 3, see Note 15) and *Læmanctus longipes* (see Note 4), *Sceloporus grammicus* lacks precise locality data. “Montevideo”, the veritable origin of the syntypes of *S. grammicus* Wiegmann (ZMB 641–643 and 69134–35 formerly catalogued under ZMB 643) registered from “Mexico” (“v. Sack & D.[eppe]” mission), invalidates the restriction of the type locality to “Chilpancingo” in Guerrero (SMITH & TAYLOR, 1950a; see ICBN, 1999: Art. 76.1) and upsets the widely accepted subspecific concept of *S. grammicus* auct. (*S. g. microlepidotus* Wiegmann, 1828, see SCHÄTTI & KUCHARZEWSKI, 2018: Note 2). “*Atherina gigantea*” is an informal name proposed for type material of the shortfin silverside *Chirostoma humboldtianum* (Valenciennes in Cuvier & Valenciennes, 1835) among the ZMB 1884–1888 series (6 specimens) including the holotypes of *Atherina humboldtiana* (ZMB 1885, coll. Deppe) and its simultaneous synonym *A. vomerina* Valenciennes, 1835 (ZMB 1888).

**Note 8.** Contrary to DUMÉRIL *et al.* (1854: “51”), the Paris syntype of *Elaphis pleurostictus* (MNHN 6616, Table 1, Fig. 2A) has 53 paired subcaudals and measures 1'222 mm in total length (Ivan Ineich in litt. April 2018) against 1'188 mm as reported. The aberrant supralabial-eye condition, namely only the fourth scale (“la quatrième seulement”) in contact with the orbit (5<sup>th</sup> separated by postsuboculars), body and tail scale counts, as well as dentition data (skull removed) equally rely on MNHN 6616. Though, the type series of *E. pleurostictus* D. B.

& D. “consists of all the specimens included [...] in the new nominal taxon” and “any evidence, published or unpublished, may be taken into account to determine what specimens constitute the type series” (ICZN, 1999: Art. 72.4.1 incl. cifra 1). Apart from the number of supralabials entering the eye, variation (2–3) is observed in the number of postoculars (“tantôt deux, tantôt trois post-oculaires”, DUMÉRIL *et al.*, 1854: 244), thus corroborating various specimens at hand (none of the four syntypes matches the reported dimensions). We refrain from the designation of a lectotype for *E. pleurostictus*, a simultaneous synonym of *Pituophis deppei*.

BOCOURT’s (1888: 667–668, caption to Pl. 42.2) postulation of the “Montevideo” specimen (MNHN 6616) as the holotype (“le type”) of “*Pituophis pleurostictus*” does not comply with the requirements for the fixation of a lectotype by inference (ICZN, 1999: Art. 74.6) because the taxon was based on more than one name-bearer. The Frenchman recorded usually eight supralabials, the fourth and fifth in eye contact (“Huit supéro-labiales ordinairement, dont la quatrième et la cinquième sont en rapport avec l’œil”) as shown in the illustration, which excludes MNHN 6616 from being the reproduced voucher. Discrepancy to our data can also be discerned in, for instance, the total length (“1<sup>m</sup>.24” m, l.c.: 668, see preceding paragraph). As a whole, BOCOURT’s (1888) œuvre and in particular the systematic concept of *Pituophis* Holbrook is difficult to understand and the identity of the “*Pituophis pleurostictus*” (l.c.: Pl. 42.2) engraved by Marie Firmin Bocourt himself or his father (FLORES-VILLELA *et al.*, 2016: Table 5) remains inscrutable. Paired with the “type” muddle, conflicting diagnostic data in the original description (supralabial-eye configuration) may have prompted BOULENGER (1894) to treat the specific name *pleurostictus* D. B. & D. with caution (see Taxonomy).

**Note 9.** FMNH 106079 (Fig. 3B, Coahuila) has a single prefrontal that presents a median groove anteriorly (Fig. 16: left inset). Three prefrontals (incl. median scale) occur in the northernmost confirmed record (UAZ 34883, see Note 40). The right prefrontal is divided in CNAR 15639 (Hidalgo, left scale with short anterior notch) or the lateral part is separated on the right side of AMNH 147886 (Fig. 3A, Jalisco) and in three specimens from Zacatecas (UTA 2710, UTEP 4344, 4349, see next). AMNH 110415 (central E Puebla) has a small azygous scale at the anterior prefrontal suture. MCZ 80910 shows an odd granular scute between the internasals and prefrontals (Fig. 3C). STULL (1940: Table 2) noted two “azygos” prefrontals in AMNH 19849 and 19852 from Jalisco. At least on the left side (only unilateral counts available), both have the postero-lateral portion of the prefrontal detached, which could be interpreted as two loreals (the condition is described as “a small azygos present on each side between prefrontal and preocular”, l.c.: 27). UTA 2710 and UTEP 4344 (Fig. 4H) from Zacatecas show a similar right side configuration but the upper “loreal” is larger and ranked as a small lateral prefrontal. MZFC 621 from the Sierra Ajusco (Mexico City)

exhibits bilaterally aberrant prefrontal-loreal conditions, i.e., the lateral portion of each prefrontal is separated and divided into two scales (Fig. 4C), of which the lower one could be termed an upper loreal (see above, Jalisco vouchers). DIXON *et al.* (1962) reported four prefrontals in four out of 18 “*Pituophis deppei deppei X deppei jani*” (KU 67694–711) collected “between Matehuala and Villa Hidalgo” in San Luis Potosí. According to CONANT (1965), these vouchers are KU 67706 from “25 miles south of Matehuala” (San Gabriel area, ca. 23°17' N 100°34' W, intermediate specimen, see chresonymy, Discussion incl. Fig. 16) with four prefrontals (“lateral ones are cut off from the frontal [...] by the preocular scale”) as well as KU 67695, 67699, and 67703 with basically three scutes and “incomplete sutures penetrating for short distances into the large prefrontal” in two among them. Two additional KU specimens (unspecified) from the same area show “short sutures [that] penetrate slightly into what otherwise are two large prefrontals” (l.c.). Up to four shields in *P. deppei* as noted by LEMOS-ESPINAL & DIXON (2013, 2016: “2–4 (usually two)” prefrontals) or LEMOS-ESPINAL *et al.* (2015, 2018, 2019) rely on these KU vouchers and UCM 67211 (SMITH *et al.*, 2005b), which belongs to *P. catenifer* (see Note 40). CAS 19459 and LSUMZ 35026 from the northern edge of the Central Plateau (S Aguascalientes, see Distribution, Fig. 16) have “sutures partially dividing the paired prefrontals into four scales” (MCCRANIE & WILSON, 2001).

The reader is referred to STULL (1940: Fig. 1) concerning the usual size and shape of the parietals. Various specimens exhibit slight aberrations from this illustrative example such as a distinct scale between the postero-median edges of the parietals (e.g., MCZ 80910, Fig. 3C), detached posterior tips (e.g., TCWC 94148), or deep grooves (e.g., UMSNH 518, left shield).

**Note 10.** STULL (1940: 27, Table 2) recorded a “loreal present in about 50 percent of the specimens” and its absence in ten AMNH *Pituophis deppei*. Seven of them in reality possess that scale (AMNH 3520–21, 4382–83 [incl. Fig. 3D], 19856) or have two loreals (AMNH 19849, 19852, see Note 9), and we suppose that three unexamined vouchers from Zacatecas (AMNH 3522, see Implications) and Jalisco (AMNH 19848, 19851) agree with one of the described conditions. Reversely, FISCHER (1882) reported a “*Pityophis* [sic] *deppeii*” of unknown origin (MTD 359, destroyed in World War II) with the loreal and prefrontal coalesced on both sides. In a live individual from near Otinapa in central Durango (photo Christoph I. Grünwald), the right loreal is absent (large preocular). The lower tip of the preocular is separated in AMNH 68361 (distinct small scale, only right side data) and STULL (1940: Table 2, see Note 32 for *catenifer*) reported two scales in USNM 8321a (see Note 40). Her mention of four “postoculars” in AMNH 3522 (left side) and 19851 (right), MCZ 19548 (ibid.: Table 3), and USNM 46365 (Durango, see Note 16) requires verification.

Seven supralabials (3<sup>rd</sup>–4<sup>th</sup> in eye contact) are present on both sides in a syntype of *Elaphis pleurostictus*

(ZMB 1734, Fig. 2B) as well as AMNH 19850 (Mexico City, “8” scales fide Stull, 1940: Table 2) and unilaterally in AMNH 19856 (Puebla), 68361 (Durango, only right side counts, CONANT, 1965), and 75563 (Hidalgo), and four northeastern *Pituophis deppei*. Nine supralabials are observed in UMMZ 88687 and USNM 46433 from Puebla, at least unilaterally in four specimens from Zacatecas and two from Nuevo León including SDSNH 57003 with three supralabials entering the eye (4<sup>th</sup>–6<sup>th</sup>, right side data) as well as on one side in AMNH 4383 and 19851, CNAR 706, FMNH 106078, MCZ 19544, 19546, 19548, 80909, and 157812, and possibly in the holotype of *Arizona jani* Cope (see Note 14). Usually, the posterior supralabial-eye contact is wide, may extend over the whole length of the scale (e.g., CNAR 15569, TCWC 54238, UIMNH 36223, UMMZ 88687, UTA 58370, UTEP 9115) as shown in JAN & SORDELLI (1867: Pl. II.2), or is confined to the anterior tip as exemplified by AMNH 4382 (Fig. 3D), 4383, and 69940, CNAR 706, TCWC 54817 (Fig. 4D), and UTEP 8630 from the Central and Northern Plateaus. A small postsubocular is bilaterally present in CNAR 15620, 15654, and 25285, FMNH 106078, and in TCWC 94148, possibly on both sides (only unilateral counts available) in CAS 169852, LACM 114056, USNM 346647, and TNHC 89287 as well as in MCZ 157812 (right), SMF 95897 (left), and UMSNH 1540 (left), a photographed individual (Fig. 6B), and an unspecified voucher (CANSECO-MÁRQUEZ & GUTIÉRREZ-MAYÉN, 2010: Fig. 146, right head view drawing).

Photos in KARDON (1995: 19, left upper and middle row pictures) substantiate two loreals (vertically divided scale, left head view) or the presence of a large postsubocular (right side) in *Pituophis deppei* “*jani*” (see paragraph following place marker for this Note), probably from Nuevo León. HIRSCHKORN & SKUBOWIUS (2011: 142, left bottom photo) show a *P. “d. deppei”* with two small postsuboculars and the fourth supralabial only in narrow eye contact (right side). Aberrant head scale conditions in breeders’ specimens should be treated with certain caution because they do not necessarily represent what is found in the great outdoors.

*Pituophis deppei* shows undirected variation in the size of the anterior and in particular posterior pair of inframaxillaries. Without exception, sublabial contact of the latter, if any, is limited to the anterior portion and the scutes are distinctly separated at least posteriorly. Usually, the posterior chin shields are distinctly smaller and more slender than the anterior pair. They are sometimes nonexistent (e.g., FMNH 106009 and UMSNH 73 from Puebla with four longitudinal rows of gular scales) but comparatively large in, for instance, two syntypes of *P. deppei pholidostictus* Jan (syn. *P. lineaticollis*, ZMB 1737–38) or as long as the anterior pair in various *P. deppei* from the Mexico City area to Tamaulipas (e.g., CNAR 706 and LACM 114056 or unilaterally in MZFC 621 and TNHC 29901).

**Note 11.** The maximum number of “249” ventrals reported for females by LEMOS-ESPINAL & DIXON (2013,

2016) or LEMOS-ESPINAL *et al.* (2015, 2016, 2018, 2019) most certainly stems from data for *Pituophis lineaticollis* (STULL, 1940; DUELLMAN, 1960; HEIMES, 2016; Table 4). DUELLMAN (1960: Table 1, ♀♀) indicated the same minimum number for ventrals (209) as determined herein and, inexplicably, this figure earlier appeared in BOULENGER (1894: 30 [Table II], 67), despite 212 being the lowest enumerated individual count for a BMNH female from “Mexico” (specimen ‘f’, total body scales 267). His upper and lower extremes for ventrals (233) and subcaudals (51) rely on the data for the holotype of *Elaphis* [*Pituophis*] *deppei* and the Paris syntype of *E. pleurostictus* (see Note 8 and Implications), respectively (DUMÉRIL *et al.*, 1854). As many as “79” subcaudals (STULL, 1940: 27, Table 2) in AMNH 32398 is due to a confusion of genera (see Note 16). Body scale counts higher than observed in the study sample (Appendix 1) may occur in the northern Sierra Madre Occidental (e.g., in MABA 59769, see end of Discussion and Notes 40–42). The anterior subcaudals of AMNH 4383 (1–4) and 159266 (1–8) are entire. FMNH 33564–65 from near the northeastern distributional limit have 29 midbody rows (verified by Aaron Mercer and Alan E. Reseter) and not 31 (“27–31–23”) as indicated for the female (FMNH 33565, SMITH, 1944). The scale row formulas for EHT-HMS 1108 and 5379 (“27–25–23”, DUNKLE & SMITH, 1937) as well as LSUMZ 4369 (“29, 25, 22”, TAYLOR, 1953) are undefined concerning the trunk level of the published figures. As few as “21” midbody rows (e.g., LEMOS-ESPINAL & DIXON, 2013, 2016; LEMOS-ESPINAL *et al.*, 2015, 2019) is in error. Near midbody, the lateral keeling of the dorsals may be absent below rows 10 (AMNH 94870, 96650, 127904, SMF 84791, UTA 6047, 58370) to 11 (AMNH 19856) or keels occur as far down as to row 5–6 (UTA 5994–95, 38560, 57573–74) and reach row 4 in SMF 95083.

**Note 12.** Individuals with reddish-brown head, nape, and posterior trunk contrasting with the general body colouration are recorded from, for example, Durango (MCCRANIE & WILSON, 2001: Pl. 14F) and Nayarit (LOC-BARRAGÁN & AHUMADA-CARRILLO, 2016: Fig. 1). Two live *Pituophis deppei* from central Durango (Otinapa, see Note 10) and Sonora (RORABAUGH & LEMOS-ESPINAL, 2016: photo p. 480) show a reddish-brown posterior body and tail as in UTA 57574 from Michoacán (venter yellowish) and frequently observed in the northwestern range (see Note 40), and these portions are coral red in an individual from the northern Sierra Tarahumara, Chihuahua (LEMODS-ESPINAL *et al.*, 2004d: Photos 115–116). The nape may be devoid of any marking and the neck pattern is subject to considerable variation in Central Highlands and S Puebla specimens as exemplified by an adult from Tlalnepantla (19°32' N 99°12' W, México State) with uniformly tawny head, neck, and anterior body (HEIMES, 2016: Fig. 163). Further photos of live individuals with locality data can be found in, for instance, DUELLMAN (1960: Veracruz), CONANT (1965: Zacatecas), CANSECO-MÁRQUEZ & GUTIÉRREZ-MAYÉN (2010: Puebla), RAMÍREZ-BAUTISTA *et al.* (2010: Hidalgo), LEMOS-ESPINAL & DIXON

(2013: San Luis Potosí, Tamaulipas), RAMÍREZ-BAUTISTA *et al.* (2014: Hidalgo), HEIMES (2016: Mexico City, México State, Querétaro), or LEMOS-ESPINAL & DIXON (2016: Jalisco, San Luis Potosí). The reader is referred to Notes 29 and 40 regarding pictures of additional specimens (unassigned vouchers and *P. deppei*, resp.) from Chihuahua and Sonora.

A bullsnake from Cumbres de Acultzingo (18°43' N 97°19' W, ca. 1'800 m) near the Puebla state line in Veracruz shows short but distinct paravertebral stripes immediately behind the head (Fig. 6B). *Pituophis deppei* is documented for this locality (e.g., Fig. 6A) but the nape pattern of the photographed individual (© Ian Recchio) is suggestive of *P. lineaticollis*, a taxon recorded from the Orizaba Valley (Upper Río Blanco) at roughly 30 km airline distance (first state records for Veracruz, see Discussion and Notes 20, 26), and it possibly occurs at much closer sites (Figs 10C, 11B). The lack of body scale data coupled with the observed variation of dorsal colour pattern in *lineaticollis*, in particular on the nape (see Notes 23–24), as well as the unresolved spatial separation along the respective ranges of these taxa near the southeastern distributional limit of Deppe’s bullsnake (Figs 7, 10C, see Distribution) make a specific allocation of the illustrated voucher (Fig. 6B) impossible. For the sake of expediency, we refer to this specimen with a medium-sized left postsubocular (right side unknown) as *Pituophis cf. deppei*.

**Note 13.** AMNH 107292 from the Jaumave Valley in Tamaulipas (see Distribution) has 26 dorsal body blotches and clusters with group C (228 ventrals, 53 subcaudals). Populations from Nuevo León, Tamaulipas, and the border triangle with San Luis Potosí (LSUMZ 4369) have low maxima (Table 2). “20–33” reported in DIXON *et al.* (1962: 96) is a lapsus (“25–30”, l.c.: 95). Instead of “a noticeable difference” in the “average number of dorsal body-blotches” between *Pituophis deppei* from Puebla and contiguous Veracruz (“southernmost sample”, n=12) vis-à-vis more northern populations of *P. d. deppei* auct. (34.6 versus 36.6–38.4, DUELLMAN, 1960), our data do not corroborate a perceptible difference between samples from Hidalgo and Puebla (Table 2: groups I, K). As few as 26 blotches occur in SMF 95083 (group K). UF 11310 from S Puebla has a total number of 36 (28 + 8) marks on the trunk and tail against 42–53 in eight specimens from that area.

**Note 14.** The holotype of *Arizona jani* Cope (USNM 1522) from Coahuila (Buena Vista, see Note 16) is “mutilated”, published data such as the number of supralabials (“eight” according to original description versus “9/8” fide STULL, 1940), subcaudals (“58” vs. “60”, resp., we accept the latter count), and midbody scales (“in twenty-seven or nine rows” vs. unrecorded) are disputed, and the numbers of ventrals and body blotches are unknown. Based on the length of the lighter segments between the anterior dorsal marks, STULL (1932, 1940: 23 [Key], 42, Table 3) assigned USNM 1522 and MCZ 19545–50 (see

paragraph containing place marker for this Note) from Miquihuana in Tamaulipas to the revalidated *Pituophis deppei jani* (Cope). SMITH (1944) classified four bull-snakes from Nuevo León (FMNH 33564–65) and NW Hidalgo (USNM 110890–91) under *P. d. jani* auct., averring that the “length of the anterior interspaces” and the degree of darkening of the posterior blotches are “more diagnostic [...] than [the] number of spots” (21–31 vs. 30–44 in *d. deppei* auct.). SMITH & TAYLOR (1945: 108) gave the distributional range of *jani* as “Northern Hidalgo [incl. Jacala, Fig. 7: plot 3] to southeastern Coahuila, on the interior arid slopes of the Sierra Madre Oriental” (e.g., “Galeana, Nuevo León”, see Distribution). FMNH 106079 from the periphery in Coahuila (l.c.), roughly 90 km west-northwest of the type locality of *A. jani* Cope, shows 35 + 10 dorsal blotches on the body and tail (38 + 11 in MCZ 407, see Appendix 1).

**Note 15.** During his first Mexican expedition (1824–1827, field activity from last days of December 1824 until end of 1826), Ferdinand Deppe explored the Central Highlands from Hidalgo to NE Michoacán, SW México State, and Morelos (STRESEMANN, 1954), and also traversed the distributional range of *Pituophis deppei* (see Distribution) beyond Xalapa en route to Mexico City or from the capital to Tehuacán when heading for Tehuantepec in company of William Bullock, Jr., at the end of August 1825. The naturalist collected along the eastern edge of the Mexican Plateau between Perote and the Pico de Orizaba (Mt.) in September 1828 with Wilhelm Schiede (SCHIEDE, 1829b) and, again, in the surroundings of Mexico City from May 1829 until the conclusion of the second mission. Late that same summer, Deppe abandoned natural history collecting and left for Acapulco and Monterey, the capital of ‘New California’ (i.e., California, United States, then Mexico). To earn a living, he worked as a commission agent for Henry Virmond between Acapulco, Mazatlán, and California until spring 1837 (e.g., LICHENSTEIN, 1839; STRESEMANN, 1954).

With regard to snakes, Ferdinand Deppe merely mentions unspecified “Schlangen” from the Zimapán area in NW Hidalgo offered for sale by natives in June 1825 (LICHENSTEIN, 1826a: 303) and rattlesnakes (“Klapperschlangen”) procured between Oaxaca de Juárez and San Ildefonso Villa Alta (17°20' N 96°09' W) in early autumn of that year (l.c.: 315). Natural history remarks in SCHIEDE’s (1829a–c, 1830) accounts of the second Mexican mission almost exclusively deal with botanical aspects. Three *Pituophis deppei* from NW Hidalgo (AMNH 75563, 96650, CNAR 15654) with 230 ventrals in all (58–65 subcaudals, max. in CNAR 15654) match data for the holotype. UTA 58365 and 58367 from the same general area (ca. 20°40–42' N 99°32–38' W) could not be located at this moment (Gregory G. Pandelis in litt. January 2020). CNAR 25285 (♂) collected less than 50 km airline distance southwest from Zimapán close to the border with Querétaro contrasts with its co-minimum for ventral counts (209, see Variation).

SMITH & TAYLOR (1950a) restricted the type locality of the anguid *Gerrhonotus tenuiatus* Wiegmann, 1828 (i.e., *Abrovia tenuiata*, coll. Deppe) to “El Chico” (Mineral del Chico, 20°13' N 98°44' W) north of Pachuca in Hidalgo (see SMITH & TAYLOR, 1950b). Following an erroneous interpretation (“in the nearby state of México”) of a quote in STRESEMANN (1954: 87) concerning “Chico” by TAYLOR (1969), GOOD *et al.* (1993) stated that “there is no definite record of Deppe collecting in Hidalgo”, which conflicts with the naturalist’s narrative (LICHENSTEIN, 1826a) and the type locality (“prope Chico”) of *Euprepes [Plestiodon] lynxe* Wiegmann, 1834. Both new lizard species were gathered during Deppe’s first Mexican mission and the collector produced a hand-coloured drawing after a live “*Lynxe* in Chico” (BANKMANN, 2002: illustr.), probably the extant syntype ZMB 1271 (Appendix 3). This is the only zoological illustration from Deppe’s hand kept in the MfN.

**Note 16.** KLAUBER (1941) clarified the origin of STULL’s (1932, 1940) “*Pituophis deppei*” from north of the Mexico-US border including a confusion with *Pantherophis obsoletus* (Say in James, 1823), or perhaps *P. emoryi* (Baird & Girard, 1853), communicated by Charles M. Bogert (AMNH 32397–98, San Marcos, Hays Cty, Texas). The documented distributional range of *P. deppei* in the Yécora area is delimited by ca. 28°27' N latitude (Chihuahua, 1 km E Arroyo Hondo, MABA 258604) along highway 16 (ENDERSON *et al.*, 2014: Table 2) between Mesa del Agua (ca. 109°00' W, MABA 258603) and west of Yepachic (ca. 28°25' N 108°23' W) in Chihuahua (MABA 59769, see Notes 41–42). The presence in the Chínipas Valley and along the Río Urique (W Chihuahua) is plausible as specimens morphologically in-between Deppe’s bullsnake and *P. catenifer* (see Discussion, Appendix 1) are on record for Huicorichi (or Güicorichi, UCM 65821, possibly incl. UCM 65748 and 66385: Fig. 15C), a ranch in Chínipas at roughly 1'500 m (27°38'6.5" N 108°28'19.0" W, LEMOS-ESPINAL *et al.*, 2004c; not “1900” m, ibid., 2004a; Julio A. Lemos-Espinal in litt. July 2018), and the vicinity of Samachique (FMNH 11825) at ca. 2'150 m (DUELLMAN, 1960; LEMOS-ESPINAL & SMITH, 2007a: 609). DUELLMAN (1960: Fig. 1) mapped *deppei* at approximately 27°30' N latitude and 106° W longitude roughly halfway between Chihuahua City and Hidalgo del Parral, which is not substantiated. Also, the ostensible occurrence of the species all over W Chihuahua north beyond 30°N latitude (HAMMERSON *et al.*, 2007: map) or in the Sierra Tarahumara as well as in NE Durango (e.g., OCHOA-OCHOA *et al.*, 2006: map) is not corroborated by specimens. A locality plotted in far NW Durango (LEMOS-ESPINAL *et al.*, 2019: 411, Map 42) relies on MZFC 3488 (FLORES-VILLELA *et al.*, 1991), which belongs to *catenifer* (Appendix 1). The northernmost incorporated *deppei* is USNM 46365 from ca. 24°52' N 105°04' W (Fig. 7).

In the absence of an entry for the type locality of *Arizona jani* Cope, 1861a, we have no doubt that the isolated “Buenavista” record in NW Coahuila’s Ocam-

po Municipality (LEMOS-ESPINAL & SMITH, 2007b: 547, Map 86; LEMOS-ESPINAL *et al.*, 2015: 660, Map 95) derives from a confusion of place names. The holotype of *A. jani* Cope (USNM 1522, see Note 14) obtained during Lieut. D. N. Couch's 1853 nostalgic veteran mission (CONANT, 1968) hailed from the Mexican War battlefield area at Buena Vista (Fig. 1) north of Rancho La Angostura, which today is within Saltillo's southern city boundary. WEBB (1960) clarified that a "uniformly brown" colubrid (KU 39564) from the vicinity of Ocampo, which FUGLER & WEBB (1956) had allocated to *Pituophis deppei* on "geographical grounds", is a *Pantherophis bairdi* (Yarrow in Cope, 1880) rather than "an undescribed species in the *deppei* group" (DUELLMAN, 1960: 605). Populations of Deppe's bullsnake as far north as ca. 26°30' N latitude in E Coahuila (OCHOA-OCHOA *et al.*, 2006: map) are most probably nonexistent. The northernmost Nuevo León plot in LEMOS-ESPINAL *et al.* (2018: 364, Map 69, unspecified voucher) from "12 mi W Santa Catarina" (west of Carvajal, ca. 25°42' N 100°34' W) near the Coahuila state line requires verification. The "Sabinas Hidalgo" record (l.c., see Discussion) is not mapped.

The identifications ("*Pituophis deppei*") of MSUM 7909 (missing, Moises Kaplan in litt. September 2019) from "Eldorado" in the immediate vicinity of Zoquipan (20°01' N 97°36' W, ca. 1'059 m) in the Gulf versant cloud forest zone of Puebla (Veracruz border, Río Tecolutla area) and of an incomplete skeleton (ROM 861, see Material and Terms) from Tlapacoyan (19°58' N 97°13' W, Veracruz) below 500 m in evergreen forest along the Puebla state line are utterly questionable. A "*Rhinechis deppei* Duméril et Bocourt" (fide "COPE, Ms.", No. 303, FERRARI-PÉREZ, 1886) obtained by the Comisión Geográfico-Exploradora at "S. José, Acatino" (San José Acateno, ca. 100 m) in central Veracruz close to the Puebla border is considered to rely on a misidentification, possibly in confusion with *Pseudelaphe flavirufa* (Cope, 1867). The "Jalapa" (Xalapa, ca. 1'400 m) record in PÉREZ-HIGAREDA & SMITH (1991) refers to the categorically incorrect origin of the holotype of *Arizona lineaticollis* Cope, 1861b (see Note 25) submitted almost forty years after the description of the taxon (COPE, 1900) and accepted by, for instance, SMITH & TAYLOR (1945, 1950a). *Pituophis deppei* USNM 46557 (coll. Edward W. Nelson & Edward A. Goldman), supposedly from "Tacámbaro" (STULL, 1940: Table 2; DUELLMAN, 1960: incl. Fig. 1 [map]) in Michoacán (19°14' N 101°27' W), in reality came from Acámbaro (SMITH, 1943) in Guanajuato (Figs 1, 10B). The absence of published or otherwise documented locality data for the southern Jalisco-Zacatecas borderlands into E Nayarit, large areas in W San Luis Potosí and peripheral Zacatecas, and for SE San Luis Potosí and limitrophe regions (Fig. 7, see paragraph following place marker for this Note) is presumably due to a lack of collecting. The presence of Deppe's bullsnake in, for instance, central Guerrero (OCHOA-OCHOA *et al.*, 2006: map) relies on *P. lineaticollis* (see Discussion).

**Note 17.** The maximum elevation of "3500 m" given by LEMOS-ESPINAL *et al.* (2015) appears implausible. *Pituophis deppei* attains at least 2'740 m in Mexico City (Sierra Ajusco, pers. observ. PH) and dwells above 2'600 m in semi-arid lava fields near Ciudad Serdán, Puebla (HEIMES, 2016: Fig. 165). The upper limit at "1500" m in Chihuahua (LEMOS-ESPINAL & SMITH, 2007a) collides with other published data (see Note 16) including the Mojára-chic voucher (BRYSON *et al.*, 2011: LVT 10681, 27°52' N 107°56' W, Maguarichic Mun.) from near 2'200 m, and the occurrence at "1100" m (incl. LEMOS-ESPINAL *et al.*, 2015) lacks specification. The lowest confirmed elevations in Chihuahua and Sonora are ca. 1'500 and 1'470 m, respectively (MABA 258604 and 259025, resp., see Notes 41–42). USNM 105302, morphologically in-between *P. catenifer* and *deppei* (see Discussion, Appendix 1), was obtained at ca. 1'100 m in SE Coahuila. Populations of Deppe's bullsnake below 1'300 m may exist in, for example, the vicinity of Ciudad del Maíz (ca. 1'250 m), San Luis Potosí, and ca. 1'060 m are documented near Ciudad Tula, Tamaulipas (William L. Farr in litt. April 2018, WLF 183). Elevations below 1'000 m occur along the Zacatecas-Jalisco border (Lower Río Juchipila) and the Río Grande de Santiago in Jalisco (ca. 700 m) but no specimens are reported (see Note 16 and Fig. 7 concerning large unexplored corner in this state). TCWC 33846 from Tequila (20°53' N 103°50' W) may come from ca. 1'200 m. The lower limit of "1900" m for *deppei* in Michoacán (DUELLMAN, 1961, 1965: Table 2) is too high in view of specimens from around the Lago de Chapala (ca. 1'525 m) including AMNH 82031, which swam ca. 100 m from the shoreline. The origin of a "d. *deppei*" from "2 mi. E Villa Hermosa" in Michoacán (AUTH *et al.*, 2000: BCBC field no. 67-657) is tricky to pinpoint. A locality of that name (Villahermosa, 18°52' N 102°03' W, ca. 200 m) exists in La Huacana Municipality, some way off principal roads near the Río Marqués in the Presa Infierillo [Dam] area, far beyond the verified limit of distribution, and roughly 800 m below the confirmed vertical minimum for the species. Rather, the "Villa Hermosa" specimen came from a neighbourhood quarter of Morelia (Colonia Villa Hermosa, San José de Las Torres) or Uruapan, and this BCBC record is not mapped (Fig. 7).

**Note 18.** *Coluber melanoleucus* Daudin sensu BOULENGER (1894) encompasses *C. sayi* Schlegel (COPE, 1900: 869), viz. *Pituophis catenifer* (Blainville), and the BMNH series is possibly more heterogeneous (see chresonymy of *P. deppei*, Note 29). STULL (1940: 25) agreed with BOULENGER (1894) that *P. "mexicanus* (not of Duméril and Bibron)" was a junior synonym of *deppei* but quoted the 'Elenco [...]' (JAN, 1863) as reference for her interpretation (see Note 3). There, "*P. mexicanus* Dum. e Bibr." is diagnosed through two prefrontals ("Due prefrontali") and 31–37 midbody rows, which obviously represents a composite taxon (see Discussion for character variation and intermediate bullsnakes). Besides head scale configurations, the destroyed possibly male MSNM specimen (accession number unknown, SCALI, 1995) from "Mex-

ique” depicted in JAN & SORDELLI (1867: Pl. II.1) exhibits details of the head and dorsal body colour pattern virtually identical with the illustrated *mexicanus* (Fig. 8). We recommend a search in the MNHN archives to confirm or discard the possibility that JAN & SORDELLI’s (1867) *mexicanus* might have been received or purchased from the Paris museum, as Giorgio Jan did with other institutions (see Note 2), and that the lost Milan voucher may in fact correspond to the unlocated MNHN type specimen (DUMÉRIL *et al.*, 1854: Pl. 62, see Note 19).

**Note 19.** The reproduction of *Pituophis mexicanus* in DUMÉRIL *et al.* (1854: Pl. 62) is partly inconsistent with the description regarding the number of postocular (incl. postsubocular) scales (4), the right supralabial-eye contact in the entire (coloured) individual refutes the text and both enlarged (black and white) head views, and the illustration does not show the intermittent black spots present on the posterior belly and underside of the tail (“Les lames sous-caudales sont irrégulièrement tachetées de noir”, l.c.: 238). Irregular parietal conditions as reported in the paragraph containing the place marker for this Note are also documented by a potential *P. mexicanus* paralectotype (see Discussion) reproduced in BOCOURT (1888: Pl. 42.4, see paragraph following Note marker) with undersized shields and fragmented posterior margins (“Pariétales [...] à contours indistincts, à cause des subdivisions anormales”, l.c.: 675).

**Note 20.** *Pituophis lineaticollis* extends from SW Michoacán southeast through the Mexican Highlands into Guatemala. West of the Isthmus of Tehuantepec, this bull-snake inhabits the Sierra Madre del Sur to the Sierra de Coalcomán, attains the northern distributional limit in E Michoacán (“Plateau in Michoacán”, DUELLMAN, 1961: 105), and it probably ranges across SW México State (incl. vic. Avándaro, pers. observ. PH), Morelos (e.g., San Juan Tlacotenco, 19°01' N 99°06' W, Fig. 11A), and southern Puebla to central Oaxaca (Fig. 10). In Veracruz, *lineaticollis* is documented from the border area with Oaxaca and Puebla, viz. Tezonapa Municipality ('Villa Unión', 18°38'35.64" N 96°50.45.21" W, place name not on INEGI sheet E14B67, ed. 2014), the immediate vicinity of Zongolica (Acontla, La Compañía), and at 'El Boquerón' along the Río Popocatl farther north (first state records, Miguel Á. de la Torre-Loranca in litt. January 2019, see Note 26). There are no published records for east of 96° W longitude (Zempoaltepec Range). Three EBUAP *lineaticollis* from Oaxaca (“cerca de [Near] Cerro Agua Tinta [Mt.]” at “8 km NE de Atlatlahuca” and “desviación y camino hacia” [turnoff and trail towards] Arroyo El Chorro [Creek] near San Juan Bautista Atlatlahuca) and Puebla (Atecoxco, Caltepec Mun., CANSECO-MÁRQUEZ & GUTIÉRREZ-MAYÉN, 2010) accessible via idigbio.org (without collection numbers) cannot be located (Carlos A. Hernández-Jiménez in litt. November 2019). The occurrence in N Puebla’s Gulf draining Necaxa Valley (WOOLRICH-PÍÑA *et al.*, 2017: Table 19; see Figs 1, 7: plot 4) is erroneous. Indications from “Colima” and

“Jalisco” in WALLACH *et al.* (2014) rely on COPE’s (1887) “*Pityophis* [sic] *sayi mexicanus*” (*P. deppei*, see chresonymy or GÜNTHER, 1895) and PONCE-CAMPOS & USTACH (2004), respectively. Their voucher (UTA 25959), a typical *lineaticollis* featuring long neck stripes, has no locality data (REYES-VELASCO *et al.*, 2012). The Sierra Temascaltepec (DUELLMAN, 1965: Table 8) is arbitrarily placed in the Guerrero-México-Michoacán border triangle, and the “Sierra de los Tarascos” in Michoacán is mapped at Volcán El Jorullo (Fig. 10).

Elevations of collecting sites are usually situated between about 1'500 m (e.g., BRYSON *et al.*, 2011) and 2'300 m in Michoacán (DUELLMAN, 1961, 1965) or Puebla (2'315 m, CANSECO-MÁRQUEZ & GUTIÉRREZ-MAYÉN, 2010), 2'410 m in Guerrero (SALDAÑA-DE LA RIVA & PÉREZ-RAMOS, 1987), at least 2'650 m in the Sierra Madre del Sur of Oaxaca (San José del Pacífico–San Mateo Río Hondo road, pers. observ. BS), and above 2'700 m (“9,000–10,000 feet”, TAYLOR, 1939: UIMNH 35001) along the Morelos-Mexico City border near Tres Cumbres. In Veracruz, *Pituophis lineaticollis* is recorded from between ca. 1'000–1'300 m (see above). DAVIS & DIXON (1959) found this bullsnaake below 1'000 m (“2800 ft.”) in “Tropical Deciduous Forest” near Acahuizotla (17°22' N 99°28' W), central Guerrero. CNAR 10237 from Ciudad Altamirano was collected at ca. 250 m in the Balsas Valley of Guerrero.

**Note 21.** DUELLMAN (1960: 607) found the highest ventral counts in Guerrero (234–258, mean 245.8, n=7, see below in this paragraph and Note 25). Four specimens from the Sierra de Coalcomán (Michoacán) have 236–246 ventrals ( $\bar{x}$  242.2) and 231–243 ( $\bar{x}$  237.1, l.c.) occur in “seven” *Pituophis lineaticollis* from the “Mexican Plateau in the state of Michoacán” when only “CNHM” (FMNH) 37126 and 39069–72 (type series of *P. deppei brevilineata* [sic] Schmidt & Shannon, 1947, see last paragraph or Appendix 1, text following place marker for this Note, and Note 23 for details) as well as UMMZ 101932 came from there. Our lower extreme for the number of ventrals (229) relies on INHS 9594 (♂) and UMMZ 114668 (♀ “neotype”, DUELLMAN, 1960, see text following Note marker, Note 25), respectively, and the former shows the minimum sum of ventrals and subcaudals (291) for males. The maximum of 71 subcaudals is based on a Michoacán female (UMSNH 823, Fig. 10B: Table) and USNM 32220 from “Mexico” (♂, sum 312, data fide STULL, 1940: Table 4). FMNH 38356 (♀, Guerrero) has the highest recorded sum of body scales (317) and the lowest verified aggregate (285) is from MCZ 53938 (Fig. 10B: Table, see text following Note marker, Note 23). The maximum for ventrals in Oaxaca females (246) relies on MVZ 164795 with the tip of the tail missing (subcaudals >64) and more total scales (>310) than indicated in Table 4. Females present higher upper extremes for ventral and total counts and we doubt some of DUELLMAN’s (1960: Table 1) gender determinations (e.g., ♂♂ with as much as 258 ventrals). Our Michoacán sample encompasses midbody scale row counts above the regular number (27, Fig. 10B: Table) for

*lineaticollis*, 29 rows occur in MZFC 572 from Morelos and USNM 110892 (Fig. 11C: Table, see Discussion), and maxima of 25 rows can be discerned in certain specimens from the Sierra Madre del Sur from Guerrero to S Oaxaca (ZMB 83219).

With respect to head scutes, deviations from the normal conditions are observed in MVZ 164795 (Oaxaca, azygous internasal or detached posterior tip of rostral, resp.), INHS 9594 (lateral portions of right prefrontal fused with preocular and loreal), NMW 26649.1 (triangular scale between lower borders of 5<sup>th</sup> and 6<sup>th</sup> left supralabial), UIMNH 35001 (9 supralabials, 4<sup>th</sup>–6<sup>th</sup> enter eye on right side, only 4<sup>th</sup> on left, with a postsubocular “segmented from the fifth or sixth labial”, TAYLOR, 1939), and in two paratypes of *Pituophis d. brevilineatus* Schmidt & Shannon from Michoacán, namely FMNH 39071 (2 small postsuboculars, only 4<sup>th</sup> supralabial enters eye, irregular scale between 5<sup>th</sup> and 6<sup>th</sup> right supralabial, Fig. 12A) and UMMZ 120404 with the posterior lower tip of the right preocular separated, which could be interpreted as an anterior subocular. A syntype of *P. deppei pholidostictus* Jan (RMNH 402) shows a huge preocular, and this scute is divided on the right side in MZFC 2945. Our poor dentition data for *P. lineaticollis* derive from five specimens from Guerrero (SMF 93847), Michoacán (UTA 4478, 6049), Oaxaca (UCM 41361), and Puebla (UTA 19406) with 16–19 maxillary teeth, 11 on the palatinum (n=1), and 21–23 on the mandibular (n=2). STULL (1940: Table 1, p. 48, n=4) recorded invariably 18 teeth on the maxillary, found considerable numerical variation on the palatine (9–12), and reported mandibular (20–22) and pterygoid (15) counts. Except for the latter figure and the maximum on the palatine (12), teeth numbers for *lineaticollis* are within the ranges observed in Deppe's bullsnake (see Variation).

In accordance with the masculine Greek noun *οφίζ* (ophis, i.e., snake) in the compound generic name, the subspecific epithet must be *brevilineatus* (ICZN, 1999: Art. 30.1.1) instead of the original or subsequent spelling (*Pituophis deppei “brevilineata”*, e.g., DUELLMAN, 1960).

**Note 22.** Probably, DUELLMAN (1960) was swayed by SMITH & TAYLOR's (1950a) restrictions of type localities within *Pituophis deppei* auct. (incl. *Elaphis pleurostictus* Duméril, Bibron & Duméril) to Teotihuacán, encompassing the putative junior synonym *P. deppei pholidostictus* Jan (syn. *Arizona lineaticollis* Cope). Apparently, these actions were taken without the examination of any type material (see Taxonomy, Types and Deppe, Descriptions) or access to veritable *P. lineaticollis* from that area (see, e.g., TAYLOR, 1939). Consequently, we deem the presence of this bullsnake in Mexico City and north of the capital to be incorrect, which invalidates the proposed terra typica restricta of *P. d. pholidostictus* Jan.

The ‘vicinity of Mexico City’ sample of *Pituophis deppei* consists of 19 bullsnakes (Appendix 1, 16 ♂♂, 3 ♀♀) from within a radius of 55 km centering around 19°20' N 99°00' W in the metropolis area north to Teotihuacán and including a supposed Morelos record (TNHC

29666). Michoacán specimens (11:4) corroborate the unbalanced gender ratio in group J (Table 2). A single female occurs among seven *P. deppei* from the vicinity of Miquihuana (group D).

Morphological data, above all the number of ventrals, subcaudals, and midbody rows, do not allow to delimit the origin of the syntypes of *Pituophis deppei pholidostictus* Jan (RMNH 402, ZMB 1737–38, no pertinent data for holotype of *Arizona lineaticollis* Cope). Ferdinand Deppe collected the type series of this taxon either along the Sierra Madre del Sur (Oaxaca) en route to the Isthmus of Tehuantepec in autumn 1825 (LICHENSTEIN, 1826a, see Note 15), between the Oaxacan capital and the Sierra de Juárez when heading for “Valle Real” (Valle Nacional, Fig. 1) in the Papaloapan Basin (early December 1825, LICHENSTEIN, 1826b), or south of Mexico City (N Morelos) including SW México State (1825–1826, 1828, incl. SCHIEDE, 1830). NMW 26649.1 (see Types and Deppe) with the second lowest ventral count (230) observed in male *P. lineaticollis* probably came from central Oaxaca (Table 4, see Note 21 for INHS 9594).

**Note 23.** In Michoacán, Deppe's bullsnake shows generally fewer subcaudals than *Pituophis lineaticollis* but considerably lower than usual counts (54–56, Fig. 10B: Table) are observed in three specimens including two female paratypes of *P. deppei brevilineatus* (FMNH 39071, MCZ 53938, UMSNH 448). UMSNH 971 displays neck stripes extending over seven head lengths (i.e., distance from tip of snout to postcranial constriction) and paravertebral streaks run to midbody in UMSNH 274 (alive, not tabulated). UMSNH 1037 with moderately long stripes is devoid of any nape pattern and exhibits obliquely transverse dark-bordered midbody marks. UTA 4478 from the Sierra Coalcomán has neck stripes beyond the 40<sup>th</sup> ventral followed by paravertebral rows of prominent dark-edged, oblong ovals. In CNAR 24251 from Guerrero, this pattern reaches all along the anterior trunk, similar to what is found in a *lineaticollis* from nearby Omiltemi (BRYSON et al., 2011: Fig. 5) or in RMNH 402 (see Descriptions). ISLAS-FLORES & CEBALLOS (2018: Fig. 4) depict a live juvenile from México State with neck streaks longer than six head lengths, and they stretch beyond eight times that measure in SMF 93847 from Guerrero. Extreme striping (six or more head lengths) is widespread in Guerrero (e.g., MZFC 2945), Morelos (MZFC 572), and Oaxaca (e.g., CANSECO-MÁRQUEZ & GUTIÉRREZ-MAYÉN, 2010: Foto 153; see Note 24) where the eponymous dorsal marking extends over at least seven head lengths down the trunk in, for instance, a juvenile from the Southern Plateau (Santiago Tenango Mun., photo Jonathan A. Campbell) or Sierra Madre del Sur individuals (pers. observ. BS).

**Note 24.** Details regarding the dorsal colour pattern of *Pituophis deppei* in S Puebla are provided in Notes 12–13. UMMZ 114596 (Fig. 6A, not examined) from adjacent Veracruz (Orizaba Range, Cumbres de Aculzingo) shows an anvil-shaped nape blotch (also present in, e.g., UAZ 27042, the southernmost known record) and

indication of narrow longitudinal lateral streaks on the neck (DUELLMAN, 1960: Pl. 45.1). A photographed *P. cf. deppei* from the same locality exhibits short paravertebral nape stripes (Fig. 6B). WOOLRICH-PIÑA *et al.* (2017: 845) depict a typical *P. lineaticollis* collected “near Tehuacán”. However, a *lineaticollis* in WOOLRICH-PIÑA *et al.* (2005: Foto 38) is from the Sierra Alquitrán (El Tejocote, 17°26' N 99°33' W) in Guerrero (HEIMES, 2016: Fig. 167), and not the Zapotitlán Salinas Valley (Puebla) close to the Oaxaca state line. UTA 19406 from this area displays neck stripes that extend over ca. six head lengths.

**Note 25.** Apart from the fact that it seems an unfortunate choice, DUELLMAN’S (1960) designation of a neotype (UMMZ 114668, coll. William E. Duellman) for *Arizona lineaticollis* Cope, 1861b is invalid (ICZN, 1999: Arts 75.3 or, e.g., 75.8) because the fixation was taken on the premise that “[N]o type specimen is known” (see SMITH & TAYLOR, 1945: 108), which ignores the existence of the holotype (ANSP 3548, MALNATE, 1971). Also, the reader wonders about the absence of a reference to COPE (1900) and the certainly incorrect type locality of *A. lineaticollis* Cope (holotype reportedly from “Jalapa”, see Note 16) or the poor description of UMMZ 114668 (lacks, e.g., head scutes, dorsal scale row counts, or size). DUELLMAN’S (1960) analysis merely involved two body scale features (ventral and subcaudal data), the number of dorsal blotches, and variation of the neck pattern in *Pituophis lineaticollis*. The study is largely devoid of individual pholidotic data, certain extreme figures (e.g., max. ventral count of 258 in Guerrero *lineaticollis*, see Note 21) are not further explained, systematically relevant characters such as the number of midbody rows are not considered, or a *Pantherophis bairdi* (Yarrow) is allocated to the *P. “deppei group”* and bullsnake species are confounded (see chresonymy of *P. deppei*, Notes 16, 28). The “Veracruz” *deppei* (l.c.: 605) refers to an unspecified specimen from the vicinity of Acultzingo with “229” ventrals, and two additional “high” counts from “Jalisco” and “Guanajuato” (“232”, “229”, resp.) remain unassigned and lack indication of gender. Given the range and average for three Oaxacan *lineaticollis* encompassing the female “neotype” and USNM 110893 (♀, data fide SMITH, 1943) from San Pedro Mártir Quiechapa (16°25' N 96°15' W) results in 241 ventrals for UIMNH 6210 from the Pacific versant of the Sierra Madre del Sur (“25 km. N of El [La] Soledad”, ca. 16°04' N 96°29' W on highway 175). STULL (1940: Tables 2–4, see Appendix 1) provides morphological data for a good number of bullsnakes incorporated in DUELLMAN (1960).

**Note 26.** Generally speaking, *Pituophis deppei* prefers open country (e.g., agricultural areas), whereas *P. lineaticollis* occupies wooded habitats including “thorny lower montane moist forest” near 1'800 m in the Mixteca (MATA-SILVA *et al.*, 2019) or cloud forest in Guerrero and Oaxaca (Fig. 10). Nevertheless, two *deppei* from Michoacán are from oak forest (UMSNH 1146, alive, not in Fig. 10B: Table) or registered from pine-oak forest (UM-

SNH 518), and the reputed limitation of *deppei* to “mesquite grassland and oak-bunch grass associations” (DUELLMAN, 1961) is incorrect (Fig. 10B). Putative sympatry near Tacámbaro is due to a confusion of localities (see Note 16) and only *lineaticollis* occurs (MEDINA-AGUILAR *et al.*, 2011: Apéndice 1). There, it lives in pine-oak forest (l.c.), as is the case farther east (e.g., UMSNH 462, 823, 971, 1037).

USNM 110892 (Fig. 11B) from the Puebla-Veracruz border area was supposedly dragged “by a rope held by men on a truck direct toward Orizaba, from Tehuacán” and found “cast away on bushes” along the wayside (SMITH, 1943). “In all probability the snake was killed in the vicinity of Pájaro Verde (near the crest of the pass)” and at “certainly [...] no greater distance than Tehuacán (some 35 km.)”. We cannot conceive of how it was possible to determine with certitude the detailed course and direction of the reported vehicle, and the specimen’s Puebla origin (vic. Pájaro Verde, 18°40' N 97°22' W, ca. 2'050 m) is conjectural. Nothing excludes that USNM 110892 met its fate southeast of the local watershed in Veracruz. There, *Pituophis deppei* is documented for the montane Valleys of Acatla and Xoxocotla (Acultzingo and Acultzinapa, resp., see Note 12) entering the Río Blanco and as far downstream as the vicinity of Ciudad Mendoza (Fig. 10C, see Distribution). At least one bullsnake from Cumbres de Acultzingo (18°43' N 97°18' W, Fig. 6A) belongs to *P. deppei* (see also Note 25), and this is also the case with two specimens encountered in the closer vicinity of Pájaro Verde, viz. EBUAP 776 collected near Azumbilla (CANSECO-MÁRQUEZ & GUTIÉRREZ-MAYÉN, 2010; requests for useful pictures were in vain) and a photographed juvenile (© Adam G. Clause, accessible via calphotos.berkeley.edu/cgi/img\_query?seq\_num=620620&one=T) from the same general area (vic. Azumbilla, ca. 18°39' N 97°24' W, ca. 2'040 m) in Nicolás Bravo (“Chapulco”) Municipality, Puebla.

*Pituophis lineaticollis* lives in the Sierra Zongolica farther east, the northernmost of a series of mountain ranges that form the Sierra Madre de Oaxaca and extend to extreme SE Puebla (Sierra Negra or S. Axuxco) and contiguous Veracruz (Fig. 10C, see Note 20). The Orizaba Valley (Río Blanco) versant and canyons of the Sierra Zongolica probably define the northeastern distributional limit of *P. lineaticollis*, as is the case with other snake species such as *Dendrophidion vinitor* (Smith, 1941), *Oxyrhopus petolarius* (Linnaeus, 1758), *Stenorrhina degenhardtii* (Berthold, 1845), or *Xenodon rabdocephalus* (Wied-Neuwied, 1824).

**Note 27.** Our analysis of colouration characters in mainland Mexican bullsnakes is limited to the number of median dorsal marks and the neck pattern. By and large, “mostly solid-colored dorsal body blotches [...] define” *Pituophis deppei* (MCCRANIE & WILSON, 2001) instead of “blotches with pale centers and outlined with black or dark brown”, viz. a generally “less boldly marked” dorsum in adult *P. catenifer* auct. (RORABAUGH & LEMOS-ESPINAL, 2016; e.g., Fig. 13A). Numerous authors described

the degree of darkening of these blotches, head pattern variation, or aspects associated with intermediate specimens (e.g., TAYLOR, 1952, 1953; CONANT, 1965; MORAFKA, 1977). An aberrant *catenifer* from “SE of Álamos” in S Sonora exhibits longitudinal stripes and elongate lateral marks on the neck and anterior trunk (RORABAUGH & LEMOS-ESPINAL, 2016: 479, left photo). “Reddish tones are strongly evident in [...] two live snakes” (AMNH 99152, 101373) from Durango (CONANT, 1965: incl. Fig. 8, see Note 12 for central Durango *P. deppei*).

Another character not thoroughly evaluated in this study is the shape of the rostral and/or the degree of penetration between the internasals, which in the first place is a diagnostic feature within *Pituophis catenifer* ssp. auct., in particular for the distinction of the western *affinis* Hallowell from *sayi* Schlegel auct. (e.g., BOUCOURT, 1888: Pls 42, 47; STULL, 1932; FUGLER & WEBB, 1956; FOUCQUETTE & ROSSMAN, 1963; CONANT, 1965). STULL (1940: 24 [Key]) noted discrepancies in rostral length between *sayi affinis* and *s. sayi* auct. (“only slightly longer than broad” against “nearly twice as long as broad”, different wording in l.c.: Table 1). According to KLAUBER (1947: 69, 71), the rostral is “wide” (“Snout blunter”) in *affinis* instead of “narrow” (“Snout sharper”) in *sayi*. The latter condition is found in *P. catenifer* from Tamaulipas (e.g., LACM 59153, TNHC 22271, posterior edge nearly contacts prefrontals). *Pituophis deppei* shows variation of the shape and its dorsal (internasal) extent (e.g., MCCRANIE & WILSON, 2001), and the rostral reaches “as far as in many [...] *affinis*” in AMNH 68361 (CONANT, 1965). In AMNH 147886, the posterior tip almost touches the prefrontals (Fig. 3A).

Noteworthy, the shape of the snout (rostral) was a key character used by DUMÉRIL *et al.* (1854) to diagnose “Isodontiens” snake genera. *Pituophis melanoleucus* (Daudin, 1803), *P. mexicanus* Duméril, Bibron & Duméril, 1854, and *P. vertebralis* (Blainville, 1835) formed a subgenus of *Rhinechis* auct. and were considered to differ from, for example, *Elaphis* Duméril, Bibron & Duméril, 1854 sensu stricto (“*Élaphe* [sic] proprement dit”) in a pointed versus blunt snout (“pointu” vs. “mousse”, l.c.: 192, Table), respectively. In reality, *Elaphis* auct. encompasses three nominal species belonging to *Pituophis* Holbrook, 1842b, namely *P. catenifer* (as *E. reticulatus* D. B. & D.), *P. deppei*, and its synonym *E. pleurostictus* (see chresonymy, Taxonomy). The remaining eleven taxa within “*Elaphis*” are today classified under ten valid species that fall under four different ratsnake genera, i.e., the Nearctic *Pantherophis* Fitzinger, 1843 (4), the Palaearctic *Elaphe* Fitzinger, 1833 (4) and *Zamenis* Wagler, 1830 (1) as well as the insular Far East Palaearctic and NE Oriental (Chinese) *Euprepiophis* Fitzinger, 1843 (1). The second subgenus of “*Élaphe*” sensu DUMÉRIL *et al.* (1854), viz. *Compsosoma* “Nobis” (preoccupied by *Compsosoma* Lacordaire, 1830: Coleoptera, Cerambycidae), includes the insular Far East Palaearctic *Elaphe quadrivirgata* (Boie, 1826) and three Oriental species of *Coelognathus* Fitzinger, 1843. COPE’s (1861a) diagnosis of *Arizona* Kennicott in Baird, 1859 avers that

the “form” of “the rostral plate is intermediate between those of “*Coluber*” [sensu GÜNTHER, 1858a] and *Pityophis* [sic]” auct.

**Note 28.** A comprehensive study of locality data for verified *Pituophis catenifer* and *P. deppei* (Figs 7, 14) shows a situation slightly different from “the fact that the ranges of *affinis* [*catenifer*] and *deppei*, in the classic sense, are known to overlap widely” on the Northern Plateau (CONANT, 1965). Sympatry is documented for the northern Sierra Madre Occidental (Fig. 16, see end of Discussion), the Durango-Sinaloa border along highway 40 (see third paragraph, Fig. 5B), a narrow intersection of the species’ ranges from central Durango to NE Zacatecas, as well as from S Coahuila (Paila-Castañuela area) to the P. N. Cumbres de Monterrey (CONTRERAS-LOZANO *et al.*, 2015) and, reputedly, around Doctor Arroyo in S Nuevo León (MORAFKA, 1977; see Note 29).

In southern Chihuahua, *Pituophis catenifer* is on record for the Sierra Madre Occidental between roughly 650 m in the vicinity of Batopilas (STULL, 1940) to above 2'000 m in the Urique Valley, for instance in the upper course near Samachique (LEMOS-ESPINAL & SMITH, 2007a: 609, Mapa 96, undisclosed voucher), and we are optimistic that *P. catenifer* dwells in the San Miguel Valley (Río Fuerte drainage, Figs 1, 14). No published records nor any documented reliable distribution data appear to exist for most of the southern Sierra Tarahumara (S Chihuahua), entire NW Durango, or adjacent Sinaloa, and the presence of *catenifer* in SW Chihuahua (e.g., MYERS *et al.*, 2019: Fig. 3h [map]) is conjectural (Fig. 16). The peripheral record of USNM 46381 from “near Batopilas” (STULL, 1940: Table 11), also notified by SMITH (1943: 458) and actually the only authentic *catenifer* documented for the southern Sierra Tarahumara (Fig. 14), does not appear in LEMOS-ESPINAL & SMITH (2007a: 609–609, Map 96) nor LEMOS-ESPINAL *et al.* (2015: 659–660, Map 95).

Our Pacific inland distributional limit in Sinaloa (Fig. 14) basically relies on HARDY & McDIARMID (1969), includes a locality record near the Durango state line along highway 40 (El Palmito, 23°34' N 105°50' W, Christoph I. Grünwald in litt. March 2018), and the southernmost site is from BEZY *et al.* (2017: CAS SU-24021). The range extent along the Pacific versant of the Sierra Madre Occidental seems to be determined by the limits of the semi-deciduous forest belt (see last paragraph), and the presence of *Pituophis catenifer* in peripheral NW Nayarit is pending corroboration. UMMZ 113634 (coll. Richard Parker August 1, 1955), reportedly a *P. deppei* from Llano Grande in Durango (23°52' N 105°12' W, DUELLMAN, 1960), belongs to *P. catenifer* (e.g., ≥6 prefrontals and divided parietals [injured], see paragraph following place marker for this Note). According to the collector’s field notes, this large roadkill (1'425 mm total length) was found in the plain (“llano”) of Cuencamé Municipality between Los Coyotes and the Río Mimbre (Greg Schneider in litt. November 2019). The presence of *catenifer* in S Zacatecas (e.g., LEMOS-ESPINAL *et al.*, 1994: PSC 1367, see chresonymy of *deppei*; BRYSON *et al.*, 2011: Fig. 2,

upper right map) and its distribution over nearly half of Aguascalientes (VÁZQUEZ-DÍAZ & QUINTERO-DÍAZ, 2005: map; CARBAJAL-MÁRQUEZ & QUINTERO-DÍAZ, 2016: 12, Table 3, “rare”) are unsubstantiated (e.g., BANTA, 1962; McCRAE & WILSON, 2001; MYERS *et al.*, 2019: Fig. 3h [map]). A *P. melanoleucus affinis*” from deciduous forest near sea level in Michoacán (23 km NW Punta San Telmo, ÁLVAREZ & DÍAZ-PARDO, 1983) cannot be located among ENCB *Pituophis* holdings and the determination was probably in confusion with another snake genus (Juan C. López-Vidal in litt. February 2020).

The distributional limit of *Pituophis catenifer* in S Nuevo León and contiguous Tamaulipas is unclear (Fig. 14, see also last paragraph). An entry at ca. 24°15' N 100°15' W (“4 km N La Escondida, on hwy. 2”, Aramberri Mun.) in LEMOS-ESPINAL *et al.* (2018: 364, Map 71) derives from UAZ 46777 collected about 200 km roughly north in Agualegas Municipality (“2.5 mi (rd) N” La E. fide ledger entry, ca. 26°17' N 99°47' W) and the dot “on MX hwy. 68, between La Soledad and Dr. Arroyo” (l.c., NL state road 61, ca. 23°50' N 100°05' W) is from UAZ 45528, viz. a *P. deppei* (Appendix 1). The extrapolated limit of *catenifer* in Nuevo León relies on MSUM 4018 from ca. 25°09' N 99°44' W (Fig. 14: plot 6, see LAZCANO *et al.*, 2009: Table 3) and one or several unspecified roadkills from the vicinity of Linares (l.c., ca. 24°51' N 99°34'30" W). Any attempt to establish the course of the range beyond highway 85 is guess work and the subject requires further investigation.

“Punta de Piedras” (P. de Piedra, TNHC 22271, Fig. 14) in Tamaulipas is mapped at 24°04' N 97°46' W in Soto La Marina Municipality, and not near 24°30' N 97°45' W (place and point in San Fernando Mun.). In the Gulf Plain, *Pituophis catenifer* is on record to as far south as the extreme N Veracruz thorn forest (UMNH 10859). Populations in the vicinity of Veracruz City (e.g., KU 39703, vic. Boca del Río) are introduced (PÉREZ-HIGARDEA, 1981). Accumulating evidence makes us believe that the reputed presence of *P. catenifer* (*P. melanoleucus sayi*) near ca. 21°20' N latitude (Amatlán and Cervantes Mun.) in the humid coastal belt of N Veracruz, resulting from an anthropological thesis (SORIANO-ARISTA, 2007: Table 1; see SCHÄTTI & KUCHARZEWSKI, 2018: 92), perhaps relies on confusion with *Pseudelaphe flavirufa* (Cope, 1867). More inland, *catenifer* is known from the western edge of the Lower Huasteca in San Luis Potosí (LEMOS-ESPINAL & DIXON, 2013; see next paragraph) and extreme NE Hidalgo (see Note 35), for example at Chalahuiyapa (21°09' N 98°22' W, BRYSON *et al.*, 2011: LVT 10659–60, see next) or Ceecamel (CIBUAH 99, Fig. 14: plot 9), Tepeolol, Valle Verde, and Zacayahual below ca. 250 m in the same municipality (Huejutla de Reyes, Leonardo Fernández-Badillo in litt. April 2018).

*Pituophis catenifer* prefers desert and semi-arid regions including “riparian woodland”, for instance along El Tunal River east of Durango City (AMNH 85252, CONANT, 1965). VAN DEVENDER & LOWE (1977) reported the species from “plains grassland, oak woodland and pine forest” in Chihuahua (see Note 40, sympatry with *P. dep-*

*pei*). Along both main cordilleras, it apparently enters at least peripheral deciduous forest areas. In the Gulf Plain, *P. catenifer* is deemed likely to live in thorn forest southeast of Gómez Farías, Tamaulipas (Fig. 14). Contrary to the situation in limitrophe Hidalgo and San Luis Potosí (see preceding paragraph), *catenifer* is not recorded from evergreen forest in N Veracruz except, most certainly, along the Hidalgo border near Huejutla de Reyes (Chalahuiyapa, Fig. 13B) where only remnants of the original tropical vegetation exist today. The species seems to be absent in semi-deciduous forest, avoids the Huastecan cloud forest, and its presence in “Montane Moist Forest” above 2'700 m (WILSON & JOHNSON, 2010: Table 1) is improbable. Eastern populations appear to be confined to low elevations, “the highest [...] in Tamaulipas is only 142 m” (William L. Farr in litt. April 2018), and *catenifer* possibly attains altitudes above 600 m near Xilitla in San Luis Potosí (see Note 35). UBIPRO 10556 from a maize field (“cornfield”) at “2148 m” in the Lago Los Mexicanos area (ca. 28°08' N 106°55' W) “was taken at a surprisingly high altitude for the species” (LEMOS-ESPINAL *et al.*, 2004b) and another Chihuahuan “*affinis*” (ibid., 2004c: UBIPRO 11664, i.e., UCM 65726) originates from roughly 150 m above that mark (“2310 m”, see also Notes 41, 43). In Durango, *catenifer* is encountered at ca. 2'400 m around Los Bancos (Fig. 14: plot 1) and it may attain elevations close to 2'500 m elsewhere in northern Mexico. The maximum of 2'800 m indicated in recent works (e.g., HEIMES, 2016; LEMOS-ESPINAL *et al.*, 2015, 2018, 2019) stems from MOSAUER’s (1932) report of a *P. sayi sayi* [...] found at over 9,000 feet” in the southern Guadalupe Mountains (New Mexico-Texas border) later quoted by STULL (1940: 131, “*sayi affinis*”). A similar upper limit (“about 9,000 ft.”) in Colorado is recorded by ELLIS & HENDERSON (1915: 261). The maximum elevation of “2895 m” for *catenifer* in WALLACH *et al.* (2014) may equally derive from US populations, while we doubt the species’ presence “up to 3650 m” in “Arizona” (RORABAUGH & LEMOS-ESPINAL, 2016).

**Note 29.** Besides UTA 16137 (S Nuevo León, see next paragraph) and UTA 57616 (see Note 30) as well as MABA 258605 and 258607 from Chihuahua and Sonora, respectively (see end of Discussion and Notes 40, 42–43), the number of intermediate specimens (Table 5, Appendix 1) does not encompass MCZ 80222 (Fig. 17E, see Notes 31–32) from N Durango nor five bullsnakes from along the limits of the essentially parapatric ranges of *Pituophis catenifer* and *P. deppei* in Durango and Zacatecas (San Luis Potosí border, Fig. 16). These are UTEP 4112 (4 prefrontals, 4<sup>th</sup>–5<sup>th</sup> supralabial enter orbit on left side, right configuration unknown) assigned to *catenifer* and four specimens showing unilaterally irregular supralabial-eye conditions (1 or 2 scales contact orbit) incompatible with their number of prefrontals (2 or 4–6, resp.), namely AMNH 85247 and MCZ 80910 (Fig. 3C, see Note 9) referred to *deppei* and, respectively, AMNH 147883 (*catenifer*) and UTEP 8636 (ibid., see Note 31). Data for a “*Coluber melanoleucus*” from

“Mexico” (BMNH 1845.2.21.95) in BOULENGER (1894: 29–30 [Table II], 69–70, specimen ‘m’) and details verified by Barry Hughes (in litt. July 2019) render this male a potential intermediate candidate due to only “one pair” of large prefrontals (plus two small anterior scales “not reaching nasal nor midline”), a single (4<sup>th</sup>) out of eight supralabials with eye contact, 29 midbody rows, as few as 267 body scales (211 ventrals, 56 subcaudals), and merely 23–25 dorsal body blotches. However, the specimen’s vague origin, the lack of a collector, and its registration at a time (1845) when Mexican territories included the southern US border states turn any further reasoning into speculation.

UTA 16137 with possibly two prefrontals and as many supralabials entering the orbit on the right side (left condition unknown, head severely damaged) conforms to *Pituophis deppei*. However, this male from Nuevo León state road 61 near La Escondida (ca. 24°04' N 99°56' W) has exceedingly few ventrals (215) and total body scales (275) compared to data for male *P. deppei* from S Nuevo León (Table 2: group C, ≥ 225 and ≥ 285, resp.). UTA 16137 collected at the very fringes of the distributional range confirmed for Deppe’s bullsnake (Figs 7, 16) features parietals of reduced size (see Variation, text following Note marker, Note 32) and is morphologically deviant (see Note 38, incl. dorsal blotch number) in the absence of documented sympatric or geographically close populations of *P. catenifer* (Fig. 14, see Note 28), and in particular around Doctor Arroyo (MORAFKA, 1977).

Intermediate bullsnakes illustrated in literature are UAZ 25815 (dorsal head view, RORABAUGH & LEMOS-ESPINAL, 2016: 477, upper photo) from low elevation in Sinaloa (see Note 30), UCM 65821 from Chihuahua (dorsal view, LEMOS-ESPINAL & SMITH, 2007a–b: Photos 184 and 213, resp.; LEMOS-ESPINAL *et al.*, 2015: Photo 508; HEIMES, 2016: Fig. 162), and possibly two additional northwestern montane vouchers (dorsal views of MABA 258605 and 258607, see Notes 40, 42–43).

**Note 30.** The pileus of UAZ 25815 conforms to typical *Pituophis deppei* (two prefrontals and, e.g., large parietals, RORABAUGH & LEMOS-ESPINAL, 2016: 477, upper photo) but a single supralabial contacts the eye (Table 5). The catalogue entry (“21.1 mi (rd) N Culican” [sic], coll. Charles H. Lowe 1957) would position the collecting site near 25°02' N 107°15'30” W on La Laguna road below Quebrada del Limoncito near the Arroyo El Cuate (Creek, ca. 215 m, Culiacán Municipality) and implies the presence of *P. deppei* in the Sinaloan foothills of the Sierra Madre Occidental (Fig. 16), far beyond the approved range (Fig. 7) and at a much lower elevation than recorded (see Distribution and Notes 16–17).

UTA 57616 from NW Durango has four prefrontals and a single (4<sup>th</sup>) out of eight supralabials in eye contact (Table 5) as characteristic of *Pituophis catenifer*. At least on the right side, however, the fourth supralabial occupies the width of two regular scales (i.e., 4<sup>th</sup>–5<sup>th</sup> coalesced) and the separation of the fifth from the orbit is unusual (slender elongated scute along whole upper

edge, Fig. 15D). The collecting site in Guanacevi Municipality (ca. 25°47' N 105°48' W, see Appendix 1) is situated roughly 125 km airline distance from the closest confirmed record of *P. deppei* (USNM 46365, see Note 16) but this heavily injured juvenile male shows head and body scale conditions such as large parietals and few midbody rows (29) as in Deppe’s bullsnake (see text following Note marker and Notes 31–32 for character states in *catenifer*). Moreover, the sum of body scales in UTA 57616 (267, 218 ventrals) is below counts for any incorporated genuine Mexican *catenifer* (min. 273, Table 6, see Note 39). No comparative data is available for sympatric *catenifer* but low ventral (214) or subcaudal (53) counts are observed in S Chihuahua (see Note 33) and as few as 214 ventrals occur farther northwest (Table 6: group B, Note 43). Pending further studies, UTA 57616 is ranked as anomalous (Fig. 16).

**Note 31.** Our *Pituophis catenifer* from Tamaulipas with two supralabials in eye contact (CM S-9511, UANL 6447, UTA 3346) were collected at least 170 km east of the closest verified records of *P. deppei* from Nuevo León to the Ciudad del Maíz area (Fig. 7). CM 60040 from SW Coahuila (4<sup>th</sup>–5<sup>th</sup> supralabial enter orbit on right side, left configuration unknown) was gathered more than 100 km west of the nearest known occurrence of *deppei* (FMNH 106079, MCZ 407) in the vicinity of Castañuela (see Note 28), and MZFC 3488 was obtained roughly 150 km north from the confirmed main range in Durango (Fig. 16). These bullsnakes clearly belong to *catenifer* (4–5 prefrontals, small or multi-divided parietals [see paragraph following place marker for Note], with symmetrical lunar-shaped sutures in UTA 3346 [Fig. 17C], 33–35 midbody rows, and 40–57 dorsal body blotches) as do two unspecified specimens out of nine Chihuahuan USNM “*catenifer affinis*” with two supralabials entering the orbit (SMITH, 1943: 459). Eight of them (USNM 104678, 104681–86, 110894) are from the northwestern part (vic. Carrizal and “Río Santa María near Progreso”) and the origin of USNM 105291 (“39 miles east of Carmen” or perhaps El Carmen, both frequent place names) is unclear.

Without taking account of UTEP 8636 (scale absent on left side), only three *Pituophis catenifer* among our sample and with data available (CM 60029, UTA 3346 [Fig. 17C], 4859) lack a postsubocular (1–2 scales). Supposedly, at least some counts for eight specimens from Chihuahua (6) and Coahuila (USNM 1539a–b) with four (bilateral) or five (one side, 4 on other) postoculars auct. (STULL, 1940: Tables 10–11; SMITH, 1943: Table 27, USNM 104684) include one or two postsuboculars. An anterior subocular is present in 23 evaluated *P. catenifer* encompassing UTA 57581 and 57583 (see Note 33, incl. unilateral data, scale tiny in AMNH 107293, CNAR 27692, LACM 59153, USNM 105301, UTEP 8632) from Chihuahua, Coahuila, Durango, Hidalgo, Nuevo León, San Luis Potosí, Tamaulipas, Veracruz, and Zacatecas (Figs 13B, 17A–B, D, F, Table 6, see Note 32).

Three prefrontals are the exception in *Pituophis deppei* and at least four scales occur in MZFC 621 from the

southern edge of the Central Plateau, over 200 km airline distance from transmontane *P. catenifer* (Huasteca) and more than 500 km from the closest known populations on the Mexican Plateau (Zacatecas, Fig. 16, see Variation and Note 9). Within *catenifer*, the median prefrontals are incompletely divided in MCZ 80222 (Fig. 17E) from Durango, at least six scales (subject to terminology for loreal region) occur in six specimens with data available from Coahuila (CM 60029, FMNH 47085, MCZ 15699), Nuevo León (FMNH 117000), Tamaulipas (UANL 6459), and Zacatecas (UTEP 8636), 7 or 8 (depending on frontal count, see paragraph following Note marker) are present in UMNH 10859 (Fig. 17F) from northernmost Veracruz with only two larger (lateral) prefrontals, and the maximum number (8 or 10 depending on terminology) relies on a Hidalgo specimen (ITAH no. 5).

**Note 32.** *Pituophis catenifer* usually has divided, small, or completely fragmented parietals. Apart from MCZ 80222 with short sutures (Fig. 17E), large parietals (Fig. 16) are present in Chihuahua and Sonora (see Note 43), Durango (AMNH 85252 or in MSUM 3172 [photo Moises Kaplan], not in Appendix 1), and the western San Luis Potosí-Zacatecas border (LSUMZ 2427) as well as in LSUMZ 258 (see Note 33) and at least four intermediate bullsnakes with four or more prefrontals from Chihuahua (UCM 65748), Durango (AMNH 88822, UTEP 9370), and Nuevo León (UTA 38561; condition unknown for AMNH 85251 and NCSM 85998, Table 5). The drawing voucher of a “*Pituophis catenifer* (Daudin, 1803)” (sic) with small subtriangular parietals in VÁZQUEZ-DÍAZ & QUINTERO-DÍAZ (2005: 204) does not show an Aguascalientes specimen (see Note 28). The configuration is reminiscent of, for example, UAZ 26055 from near the US border in Sonora (“62 km W of Sonoyta”, RORABAUGH & LEMOS-ESPINAL, 2016: 477, lower photo).

According to STULL (1940: Tables 10–11), two preoculars occur in six *Pituophis catenifer* from Chihuahua (AMNH 3563, MCZ 15699, USNM 1542, 14222b, 46381, unilateral in FMNH 986). In reality, the count for USNM 46381 includes an anterior subocular, as is the case with “2–2” reputed preoculars noted for USNM 105301 (SMITH, 1943: Table 27) from Coahuila (Fig. 17B, Table 6, see Note 31). Head scale terminology may equally modify preocular data reported by other authors, for instance two shields in ten specimens (unilateral in 3) from Chihuahua ( $n=26$ , TANNER, 1985), four Sinaloan *catenifer* ( $n=7$ , HARDY & McDIARMID, 1969), or in KU 39561 from S Coahuila (FUGLER & WEBB, 1956).

The variation of inframaxillary scales (dimensions, proportions) in *Pituophis catenifer* is similar to the divergence observed in *P. deppei* (see Note 10). Large anterior chin shields are found in, for example, TNHC 22271 or USNM 46381, and UTEP 4112 or 8636 show relatively large posterior inframaxillaries.

**Note 33.** The number of body blotches in group F (Table 6) does not include published data for LSUMZ 258 (“31”, TAYLOR, 1949: “region near Ciudad Maiz”,

coll. Charles R. Shaw) from a vague Huasteca locality probably in Tamaulipas (not mapped in Fig. 14). This putatively first record of *Pituophis “deppei jani* (Duméril)” (sic) from “San Luis Potosí” belongs to *P. catenifer* (5 prefrontals incl. “a small azygos scale just behind the internasal suture”, 4<sup>th</sup>–5<sup>th</sup> supralabial contact eye, see Note 32 for parietals). It shows 235 ventrals and 62 subcaudals but we doubt the midbody count (“27” rows) and number of trunk marks of LSUMZ 258, which “is anomalous in certain respects” (l.c., no dorsal view photo received).

Our results cast doubt on the statement that “[t]he number of spots appears to increase in general from south to north” in *Pituophis “sayi affinis”* (STULL, 1940: 128). TANNER (1985) recorded 26 dorsal body blotches in a *P. “melanoleucus affinis”* (BYU 13877) from the vicinity of Chihuahua (Fig. 1) as opposed to 32–56 trunk marks (mean 42.7) in 28 examined Chihuahuan *P. catenifer*. Counts range from 34–37 in MCZ 80223–24 from Yépómera, 36–48 in MABA 315183, MCZ 15923, and USNM 46381 (Appendix 1, Table 6) or in MABA 296333 and two vouchers from adjacent Sonora (MABA 255153, 258600) against as few as 30–33 in UCM 66158 and 67211 from the vicinity of Yécora (Appendix 1) and 30–32 in MABA 688194 and 689275 from farther north (see Note 40).

In terms of dorsal colouration, UTA 57581 and 57583 from S Chihuahua (♂♀, not tabulated) with 35–38 body blotches conform to western *Pituophis catenifer* (Table 6). Both show five prefrontals including a median anterior scute, present an anterior subocular (only on left side in UTA 57581), and their body scale figures, in particular subcaudal counts (♂ 63, ♀ 53, ventrals 214 and 225, sum 277 and 288, resp.), are in-between our data for geographically close samples (groups B–C).

**Note 34.** The type series of *Pituophis mexicanus* as well as BOCOURT’s (1888: Pl. 42.4) potential paralectotype (see text following place marker for this Note) have nine supralabials (Table 3), the key distinctive feature for this taxon according to the diagnosis (“Caractères”, DUMÉRIL *et al.*, 1854). Nine supralabials prevail in Gulf populations from Tamaulipas to Hidalgo (see Note 35), while eight scales seem to be more abundant in Chihuahua (TANNER, 1985) or, possibly, Sinaloa ( $n=7$ , HARDY & McDIARMID, 1969).

**Note 35.** Five ITAH *Pituophis catenifer* from the Hidalgo-Veracruz border near Huejutla de Reyes (Fig. 13B, Table 6: group G) have 9–10 (once 8 unilaterally) supralabials, a large left and 2 smaller right postoculars are present in a live individual, the parietals are vastly fragmented or nonexistent, and there are 33–37 midbody rows. These specimens diverge from the Tamaulipas sample (F) in fewer subcaudals, lower extremes for dorsal markings in four females (tip of tail missing in single ♂), and a strong tendency to exclude any supralabial from eye contact (slight to extremely narrow). Lower Huastecan *P. catenifer* (“*sayi*” auct.) exhibit differences in various

morphological characters such as the number of ventrals, constantly high midbody row counts (35–37, rarely 33), up to eight or more prefrontals (see Note 31), and an anterior subocular present in most specimens (or more dorsal body blotches in case of group F) versus, for instance, highland populations (“*affinis*” auct.) from along the San Luis Potosí-Zacatecas border as exemplified by LSUMZ 2427 with as few as 215 ventrals (TAYLOR, 1952: “*sayi affinis*”), 31 midbody rows, four prefrontals, large parietals, and the anterior subocular absent. This raises the question whether ventral and subcaudal counts in LEMOS-ESPINAL & DIXON (2013) for *P. catenifer* from San Luis Potosí (♂♂ 220–245, mean 234, and 56–71,  $\bar{x}$  65, resp., ♀♀ 226–251,  $\bar{x}$  239, and 50–64,  $\bar{x}$  58) entirely rely on specimens from the vicinity of Ciudad Valles and Xilitla (Fig. 14: plots 7–8), the only recorded localities (l.c.: 299, Map 83). It should be noted that these figures, which may indeed have been compiled for San Luis Potosí bullsnakes initially, are identical to data for *catenifer* in later contributions to NW Mexico or Coahuila, Durango, and Nuevo León (LEMOS-ESPINAL *et al.*, 2015, 2018, 2019).

Gulf *Pituophis catenifer* belong to the ‘Eastern’ phylogroup, which is defined by BRYSON *et al.* (2011: incl. Fig. 5, upper right map) as far south as the “Tamaulipan thornscrub” (l.c.: 1575), though two tissue samples from NE Hidalgo (Fig. 14) were sequenced (see Note 28 and l.c.: Fig. 2). This cluster extends north to the Great Plains and from the Lower Mississippi River west to the foothills of the Rocky Mountains, and basically corresponds to *P. catenifer* “*sayi*” sensu KLAUBER (1947). This author considered Sonoran *catenifer* “*affinis*” to be morphologically similar to, and systematically identical with, the Chihuahuan Desert phylogroup but BRYSON *et al.* (2011) found the former populations and those north to the Rocky Mountains to differ genetically compared to *catenifer* from west of ca. 109° W longitude (see text following place marker for this Note as to northern Sierra Madre Occidental). The Sonoran Desert phylogroup (l.c.) is represented by a single voucher (LVT 10634, see Fig. 14: left inset) and tissue samples of three *P. “d. deppei”* were sequenced, viz. LVT 10632 (possibly UCM 66158, 66385, or 67211, i.e., *catenifer* and an in-between; requests for specifications unanswered), 10637 (see Note 41), and 10681 (Mojárac hic, l.c.: Appendix S2).

**Note 36.** The presence of *Pituophis catenifer* in N Veracruz south to the vicinity of Tlacolula (ca. 150 m, SCHÄTTI & KUCHARZEWSKI, 2018: incl. Fig. 1) was conjectured on the basis of possibly erroneous indications from that area (see Note 28). Given the activity range of Auguste Ghiesbreght, the only recorded collector of any *Pituophis mexicanus* (type series, DUMÉRIL *et al.*, 1854), his specimen is likely to have been obtained between the Zacualtipán-Río Atlapexco sector in NE Hidalgo and Tlacolula, Veracruz (Fig. 16). At the end of the day, pondering over all available evidence including the existence of an exchanged former syntype of *P. mexicanus*, USNM 1415 competes with MNHN 3188 for approved provenance (coll. Au-

guste Ghiesbreght, see Results). Interestingly, a *P. deppei* from the vicinity of Zacualtipán (TNHC 82481, ♀, Table 2: group I) with 235 ventrals (tail incomplete, 29 midbody rows) shows the highest female count for the species (Tables 1–2, see Diagnosis, Variation) but has as few as 30 dorsal body blotches versus ca. 54 or more in *mexicanus* (type series, Table 3).

*Pituophis mexicanus* D. B. & D. does not challenge the priority of any valid, or potentially so, species-group name proposed for Mexican bullsnakes including *Coluber [Pituophis] vertebralis* Blainville. Technically, *mexicanus* D. B. & D. is a “nomen oblitum” (SCHÄTTI & KUCHARZEWSKI, 2018: 91) for not having been used as valid after 1899. However, nothing prevents this name to reappear for taxonomic purposes under the provisions of the Code (ICZN, 1999) including the conditions ruling on subjective senior synonyms after the explicit declaration of a younger nomen protectum (Reversal of precedence, Art. 23.9.2). If the necessity might arise for the recognition of ecologically different peripheral Lower Huasteca bullsnake populations (Fig. 14) as systematically distinct from the ‘Eastern’ phylogroup of *Pituophis catenifer* (see Note 35), *mexicanus* D. B. & D. needs to be taken into consideration.

**Note 37.** Based on head scale data conforming to *Pituophis deppei* as opposed to a dorsal colour pattern or “the rostral penetrating between the internasals ca. one-half of their length (*P. melanoleucus* characters)” as in *P. catenifer* auct., MCCRANIE & WILSON (2001) speculated that USNM 346647 from the “area of overlap [...]” appears to substantiate MORAFKA’s [1977] view” (see Note 27, Appendix 1), viz. subspecific rank for *deppei* auct. HIRSCHKORN & SKUBOWIUS (2011: 142) published excerpts from the summary of a manuscript by Craig Stanford (USC, “Stanford (in Vorb.) [...] lag uns nur als Zusammenfassung vor”) reporting extensive hybridization between *catenifer* “*affinis*” and *deppei* in an unspecified larger area of the Central (sic) Plateau (“Hybridisierungszone [...] in einem größeren Gebiet des zentralmexikanischen Plateaus”) but the indicated elevational range (“300–2440 m”) relies on localities in eastern Mexico (“erfassten Fundorte im östlichen Mexiko”).

**Note 38.** UTA 16137 (see Note 29, next paragraph) could be an exception to our diagnostic character (number of prefrontals) and, at any rate, corroborates the presence of anomalous specimens along the periphery of the distributional range confirmed for Deppe’s bullsnake (Fig. 7, see Fig. 16). Depending on the character state(s) deemed to define *Pituophis catenifer* and *P. deppei* auct., various examined specimens from along their respective distributional limits across the Northern Plateau and referred to the latter species could pass as unassigned bullsnakes or be classified differently (see penultimate paragraph of Discussion and Note 43 for parietal condition in northern Sierra Madre Occidental).

Leaving aside UTA 57616 (see Note 30), intermediate bullsnakes largely conform to scale and dorsal colour

pattern data of sympatric genuine *Pituophis catenifer* and *P. deppei* (Tables 2, 5–6). Compared to the latter, AMNH 85251 (Zacatecas) shows discrepancies in the number of subcaudals (49, exceedingly low count). USNM 105302 (♀) differs from Coahuila *deppei* (Table 2: group B, no data for ♀♀) in fewer subcaudals (53) and total body scales (281). Besides slight deviations from the usual number of dorsal blotches on the trunk vis-à-vis Durango and Zacatecas *catenifer* (AMNH 85251, 88822, UTEP 9370), UTA 3050 and 38561 from S Nuevo León with 26 marks have a far lower count than in any published Northern Plateau *catenifer* (see Note 33; 26 blotches also occur in UTA 16137, Note 29). Two intermediate specimens from the Barranca del Cobre (Copper Canyon) and Oteros Valley (Río Chínipas-Fuerte drainage) in the Sierra Tarahumara (LACM 74031, UCM 65821) present few blotches (Table 5: 25–28, resp.).

**Note 39.** KLAUBER's (1947: Table 5) “probable normal ranges” of 220–251 ventrals ( $\delta\delta$  220–241, ♀♀ 226–251) and 50–71 subcaudals (56–71, 50–64, resp.) in *Pituophis catenifer* “*affinis*” mostly stem from US material (l.c.: Fig. 1 [map]) but include data for a few Mexican border state specimens east to S Coahuila. A larger *P. catenifer* sample from Chihuahua (n=29, TANNER, 1985: “*melanoleucus affinis*”) with 213–238 ventrals ( $\delta\delta$  213–232, mean 225.1, ♀♀ 223–238,  $\bar{x}$  228.7) and 52–69 subcaudals (62–69,  $\bar{x}$  64.7, and 52–61,  $\bar{x}$  55.3, resp.) better suits to suggest “a general shortening of the body” in CONANT's (1965) Durango series (7  $\delta\delta$ , 3 ♀♀, incl. intermediate specimen AMNH 88822) with 213–230 ventrals (213–224 and 222–230, resp.) and 49–61 subcaudals (53–61, 49–52). According to STULL (1940: 127–128), “there is more or less tendency toward an increase from Mexico north” in, for instance, the number of ventrals and midbody rows (“dorsal scale formula”).

Our maximum number for ventrals in *Pituophis catenifer* (241, Table 6) is based on USNM 1542 (STULL, 1940: Table 10) from close to the Chihuahua-Texas border and the minima (211) rely on AMNH 85252 and UTEP 9158 from Durango and SW Coahuila, respectively, which lie below TANNER's (1985) lowest Chihuahua count for an unspecified male (213, see Note 29 for BMNH 1845.2.21.95). The maximum for subcaudals (74) is observed in UCM 66158 ( $\delta$ ) from Sonora (see Note 40, 71 in UCM 65726 and 67211) and the minimum (45) is after BOULENGER's (1894) Nuevo León specimen (BMNH 1889.7.3.42). Our results point towards a gender-related dimorphism in the subcaudal number of southern highland *P. catenifer* (4  $\delta\delta$  57–66, 4 ♀♀ 49–55, Table 6: group D, 49 in UTA 4859) and the small Gulf sample (group F, n=2 and 3, resp.). Data in TANNER (1985) and CONANT (1965) indicate a clear-cut difference (fewer subcaudals in ♀♀, see preceding paragraph) in Chihuahua and Durango populations, respectively. Our figures suggest fewer subcaudals in females of all analysed groups with data for both genders available except the Coahuila-Nuevo León cluster (Table 6: group E). At

the same time, females show largely identical total body scale counts as males and seem to possess more scutes in Chihuahua (at least in group A, 296 in MCZ 15699 and USNM 104684). AMNH 3563 has a sum of 299 ( $\delta$ , STULL, 1940: Table 11) and the maximum (306) is from Sonora (UCM 66158, see Note 40). As few as 273 ventrals plus subcaudals occur in UF 11309 (♀, FOUCETTE & ROSSMAN, 1963) from central Coahuila. “49” subcaudals in UIMNH 48522 (ex KLW 741, ♀, WILLIAMS et al., 1961; LEMOS-ESPINAL et al., 1994: 169, Table 1) from Durango is based on an incomplete tail tip and the total body blotch count (“48” instead of ca. 45) is slightly too high.

Noteworthy, the number of dorsal body blotches in Gulf lowland *Pituophis catenifer* (43–60, Table 6: group F, see Note 33) strikingly diverges from counts for the geographically closest populations of *P. deppei* in Tamaulipas (21–25, Table 2: group D and AMNH 107292, see Note 13). However, the dorsal colour pattern does not discriminate, for example, Coahuila *catenifer* (30–46 marks) from two *deppei* (FMNH 106079, MCZ 407, 35–38, see Note 14) collected along the distributional limit in the south of this state. Though, FMNH 106079 is the only examined *deppei* with a single prefrontal (Fig. 3B) and shows one of the co-maxima for total body scales (301), compared to fewer than 300 in any Mexican *catenifer* from east of the Sierra Madre Occidental and in particular the E Coahuila cluster (Table 6: E).

**Note 40.** *Pituophis* “*melanoleucus*” UAZ 34883 (VAN DEVENDER & LOWE, 1977) from Yepómera in Chihuahua with three prefrontals, the fourth and fifth out of eight supralabials in eye contact, and moderately large parietals ( $\delta$ , ca. 221 ventrals, 61 subcaudals, number of midbody rows unknown, 39 body blotches) meets the standards established for Deppe's bullsnake (see Diagnosis). Reversely, “*Pituophis d. deppei*” UCM 66158 and 67211 (“aberrant”) from the vicinity of Yécora (SMITH et al., 2005a–b, as UBIPRO 12593 and 14453, resp.) with four prefrontals and a single supralabial bordering the eye are *P. catenifer*. UCM 66158 ( $\delta$ ) from a “rocky mountain-side [...] 6.7 km (by air) WSW of Yécora” (MABA entry no. 264838, see Note 41) at ‘Los Parajes’, a restaurant in the Mesa del Campanero along the Hermosillo–Ciudad Chihuahua highway 16 (l. c., 2005a), with the maximum subcaudal (74) and total body scale count (306) in examined *catenifer*, has 29 dorsals at midbody, large parietals, and 33 body blotches (18 teeth on maxillary, 19 on mandibular). UCM 67211 ( $\delta$ ) has 224 ventrals, 71 subcaudals, 31 midbody rows, and large parietals. This juvenile male from pine forest (“Bosque de coníferas”, MABA entry no. 222646) in Yécora (town area, 28°22'04.0” N 108°55'32.6” W fide l.c., 2005b) shows as few as 30 body blotches. Reportedly, “the pattern is typical” but the centres of the anterior dorsal marks are brown instead of “a uniform shade head to tail”, and the overall dorsal aspect is clearly reminiscent of *catenifer* (see Note 27).

Five out of eight bullsnake records from Chihuahua (MABA 59769, 258603–05) and Sonora (Yécora Valley, MABA 258606, 258608, 259025, 295431 [ident.

294920]) plus MABA 258607 (see paragraph and further text following place marker for this Note) catalogued under *Pituophis deppei* in this database are documented by photographs showing the dorsal colour pattern (259025) as well as the prefrontal condition (2 scales, e.g., 258606, 295431) and additional head scale features in two individuals (MABA 59769, 258605, see text following Note marker, Note 42). Apart from MABA 315183 (Chihuahua, Appendix 1), five *P. catenifer* are accompanied by dorsal view photos, namely MABA 258600 (vic. Valle de Tacupero) and 255153 (Rancho ‘El Babisal’) from Sonora and three (MABA 296333, vic. San Buenaventura, Chihuahua; MABA 688194 and 689275, Mesa Tres Ríos, Bavispe Valley) from slightly north of the area indicated in our map (Fig. 14).

MABA 59769 with a brownish head is yellowish grey down to midbody and light brown posteriorly, has ca. 33 black dorsal blotches down the trunk (VAN DEVENDER & FERGUSON, 2019: photo, see Note 42), and conforms to *Pituophis deppei* in head scales (2 prefrontals, 2 supralabials enter eye on visible side, large parietals, see text following Note marker as to origin and body scale data). MABA 295431 from west-southwest of Yécora (“6.7 mi E of Restaurant Puerto de La Cruz”) shows dark red dorsal blotches on the central trunk. In this specimen and *P. deppei* MABA 258606 (“6.9 mi E of Yécora”) the posterior portion of the body and in particular the tail are orange red (see Note 12).

*Pituophis deppei* USNM 8321a–b from “Chihuahua” (STULL, 1940: Table 2) “bear the data «between Chihuahua and Mexico»” (SMITH, 1943: 460). This clue stems from an old label in the jar that states “Mexico-Chihua” (coll. “Potts”). Material received from this collector (John Potts, USNM 8311 etc. and earlier series) includes records from the “Valley of Mexico” (e.g., KELLOGG, 1932: 6, 22) and as far south as “Mexico City, 40 leagues S of” (Steve Gorte in litt. November 2019). USNM 8321a–b (♀♀) with a reportedly aberrant preocular condition (2 scales) show few ventral (215–221) and total body scales (273–275 fide STULL, 1940; see both paragraphs preceding Note marker and Note 43 for UAZ 34883 and MABA 59769, resp.).

**Note 41.** For reasons of presentation (density of symbols), some of our map entries (Fig. 14, stippled area) stand for several records from virtually identical locations. This applies to the immediate vicinity of Madera (Chihuahua, UAZ 34336, 3.2 km SE M., VAN DEVENDER & LOWE, 1977: *P. “melanoleucus affinis”*; mapped is USNM 15923, Appendix 1) and unrevealed vouchers in LEMOS-ESPINAL *et al.* (2015) from the Nuri area (Sonora, 1 km N N., 640 m N N. jct.; Fig. 14 shows LVT 10634, “Hwy 12, N Nuri”, BRYSON *et al.*, 2011; perhaps identical with MABA 264837 from “near Nuri”) and at “22.9 km S intersection to Nuri” (plotted is MABA 258602 from Curea) as well as near Yepómera (Chihuahua, 4.8 km W Y., 4.8 km S Y., 5 km N Y., 7 km E Y., embodied by MCZ 80223–24 and UAZ 34884). The indication “6.2 km N Tacupeto” on highway “16” in “Yécora” Municipality

(LEMOS-ESPINAL *et al.*, 2015) is inconclusive and either refers to a place along state road 117 close to Curea (28°18' N 109°16' W) or in the northern outskirts of Valle de Tacupero (or Tacupeto, 28°52' N 109°11' W) in Sahuaripa near the Arivechi border. We incorporated undisclosed *catenifer* records in LEMOS-ESPINAL & SMITH (2007a) and LEMOS-ESPINAL *et al.* (2015) from the vicinity of San José Babícora (or Bavícora, 29°15' N 107°45' W, Chihuahua) and Sonora, viz. Güirocoba (26°54' N 108°42' W), “16 km N [Los] Pilares” (ca. 29°16' N 109°20' W, unnamed road, location questionable), and “28.2 km SE” of the junction to San Nicolás on highway 16 (ca. 28°23' N 109°03' W, l.c., 2015). The latter record is from ca. 1'800 m in the uppermost Cañada La Ciénga (La C. Ravine) between La Palmita and the turnoff to Mesa de Encinas (El Llano) west of the Mesa del Campanero watershed, roughly 5 km airline distance from the collecting site of UCM 66158 (see Note 40) in the Mulatos drainage.

*Pituophis deppei* MABA 59769 is registered from “1395 m” elevation but the terrain west of Yepachic is situated at ca. 1'850 m. A tissue voucher (LVT 10637, BRYSON *et al.*, 2011) from “Horquetudo, S Yécora” perhaps originates from below 1'800 m in the lower course of one of two homonymous rivers or from between ca. 1'750 m in the ravine (Cañada El H.) to above 2'000 m on Cerro El Horquetudo (Mt.). The indicated lower limit of 1'470 m relies on MABA 259025 collected “SSE of Rancho Las Víboras” (Sonora) in a rocky canyon in “oak woodland”. A juvenile *P. deppei* from Mesa del Agua (MABA 258603, ca. 1'975 m) in Chihuahua was found “near barn under wood”. Except USNM 46381 from Batopilas (see Note 28), Chihuahuan *P. catenifer* in our study sample with reliable data available including MABA 315183 (“Grassland; agricultural fields”) were obtained between ca. 1'850 m and above 2'100 m (see Notes 28, 43). Elevations near 2'200 m are attained around San José Babícora. Specimens from the Mesa Tres Ríos area (MABA 688194, 689275) are from a rocky gorge in “pine-oak forest” at 1'600–1'700 m and MABA 296333 was observed in “grassland” at ca. 1'700 m (none mapped, see Note 40). Further Sonora entries accessible via this database (see Material and Terms) are from slightly above 700 m in “[r]iparian” environment along Arroyo Babisal (Creek, MABA 55475, RORABAUGH *et al.*, 2011) of the Lower Áros Valley (Rancho ‘El Babisal’, incl. MABA 255153) and from elevations close to or below 500 m in a variety of habitats including “pasture” in the rain shadow “tropical deciduous forest-foothills thornscrub transition” zone at Curea (MABA 258602, “inside of log”, incl. entry no. 539454). The unspecified “Rancho El Agua Fría” record (RORABAUGH *et al.*, 2011) is from “thornscrub” below 700 m (Lower Áros).

**Note 42.** We do not have better ventral view pictures than those accessible via madreandiscovery.org or low-resolved copies of MABA 59769 and 258605 (4 and 2, resp.) received from Thomas R. Van Devender in March 2019. The dorsal view photo of MABA 59769 is reproduced in VAN DEVENDER & FERGUSON (2019). The identity

of another illustrated “*Pituophis melanoleucus*” in this online report on the Yécora area remains unclear. The database associates MABA 59769 with “uaz-psv-102”. The ‘psv’ label, in combination with the catalogue number, indicates photo vouchers but UAZ 102 is a lizard specimen (Melanie Bucci in litt. January 2020). MABA 258605 was “climbing 2 m above ground in an oak” at “Arroyo Hondo, 46.1 mi E of Yécora” on highway 16 in Chihuahua (i.e., vic. hamlet Las Gallinas, ca. 28°26' N 108°29' W, ca. 1'500 m; “1459 m” according to MABA record, min. elevation indicated in RORABAUGH & LEMOS-ESPINAL, 2016). It was found at a short distance from MABA 258604 (*P. deppei*), no morphological data, “1 km E of Arroyo Hondo”, i.e., Arroyo Hondo Dos or neighbouring El Arroyo Hondo, ca. 1'500 m).

**Note 43.** The photo of MABA 258607 at hand does not allow to determine the number of supralabials nor the eye contact and the presence or absence of subocular scales (request for higher resolved picture unanswered), and this unclassified record is not mapped.

Apparently, MABA 258607 possesses large parietals as present in both examined montane *Pituophis catenifer* from Sonora (UCM 66158, 67211) as well as in BYU 13877 (see below), MCZ 15923, UAZ 34884, and UCM 65726 (Chihuahua, Fig. 16). Comparatively large shields also occur in at least one out of three Chihuahuan intermediate bullsnakes with four prefrontals (UCM 65748, Table 5). BYU 13877 (verified by Alison Whiting), MCZ 15923 (STULL, 1940: Table 11), and UCM 66158 (vic. Yécora) have maxima of 29 midbody rows. The latter

specimen exhibits black blotches throughout as typical for adult *P. deppei* (see Variation and Notes 27, 40). Near Yepómera both taxa are “dark, contrastingly-patterned” (VAN DEVENDER & LOWE, 1977; see Note 40).

BYU 13877, a *Pituophis catenifer* from Chuuhichupa (ca. 2'150 m) about 85 km roughly northwest from Yepómera, has an extremely low number (26) of “spots [that] are large, round, and without the usual convexity so common in most specimens” of *P. melanoleucus affinis*” (TANNER, 1985; see Note 33). The approximately same low count occurs in an unclassified photo voucher from Maycoba (MABA 258607, see Note 42), 30–33 are observed in Yécora *catenifer* (UCM 66158, 67211) as well as in *P. deppei* (MABA 59769) and an intermediate specimen (MABA 258605) from contiguous Chihuahua. Five *catenifer* from Yepómera and Madera (34–37, incl. data for UAZ 46909, not in Appendix 1) as well as UAZ 34883 (*deppei*, 39) and an in-between (MCZ 80225, 37) from Yepómera show more dorsal body blotches.

BYU 13877 (♂, 218 ventrals, 285 ventrals and sub-caudals), four male *Pituophis catenifer* from Tomochic (UCM 65726) north to Yepómera (MCZ 80224, UAZ 34884) and Madera (MCZ 15923) as well as one *P. deppei* (♂, UAZ 34883, see Note 40) and MCZ 80225 (♂, Table 5) from Yepómera show 211–221 ventrals (max. in UAZ 34883, min. in MCZ 80225, see also Table 6) and a sum of 274–288 (274–285 except in UCM 65726 with 71 subcaudals) versus much higher counts in the Yécora Valley, i.e., 224 ventrals (sum 295) and 232 (306) in two male *catenifer* (UCM 67211, 66158, resp.) and ca. 235 (> 300) in *deppei* (MABA 59769).

## Zoobank Registration

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