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# Systematic Studies of the North American Microhylid Genus *Gastrophryne*

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*ABSTRACT.*—The affinities of *Gastrophryne*, based on osteology, adaptations for myrmecophagy, secondary sexual characteristics, tadpole morphology, mating call, and karyotype, lie with *Hypopachus*, and not with *Microhyla. Gastrophryne* contains 5 species: *G. usta, G. elegans, G. pictiventris, G. carolinensis,* and *G. olivacea.* Although the latter 2 species occasionally hybridize, consistent differences in morphology and premating isolating mechanisms (especially call) are maintained in sympatric populations. The species are similar in diet, (predominantly ants), adult and larval feeding specializations, and body size. Details of anatomy, call, and terrestrial chorusing set *G. usta* apart. Foot morphology suggests that *G. elegans* and *G. pictiventris* are more closely related to each other than to *G. carolinensis* and *G. olivacea.*

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This paper includes studies of several aspects of the systematics of the genus *Gastrophryne. Gastrophryne* accounts for the ASIH Catalogue of American Amphibians and Reptiles include synonomies, distribution maps, audiospectograms, literature reviews, and etymologies. The abbreviations used for museums and collections are explained in Appendix I.

## GENERIC STATUS

All of the species of *Gastrophryne* were originally described as *Engystoma.* Stejneger (1910) reviewed the reasons for replacing *Engystoma* with *Gastrophryne.* Parker (1934), following a suggestion by Noble (1931), united *Gastrophryne* with the Asiatic genus *Microhyla.* Carvalho (1954) distributed the New World species that Parker had placed in *Microhyla* into 4 genera, including in *Gastrophryne* only the North American species, and suggested that *Gastrophryne* is closest to *Hypopachus,* another exclusively North American genus. Since Carvalho's paper, both *Microhyla* and *Gastrophryne* have been widely used for the species Carvalho placed in *Gastrophryne.* The use of *Microhyla* implies that the American species so treated are evolutionarily closer to the Asiatic species of *Microhyla* than they are to other microhylines. Reciprocally, the use of *Gastrophryne* is appropriate if its species are more different from Asiatic *Microhyla* than from some other genera. My thesis is that *Gastrophryne* and *Hypopachus* are much closer to each other than either is to Asiatic *Microhyla.*

*Osteology.—Gastrophryne* differ from *Microhyla* in having the quadratojugal in contact with the maxillary, the corocoids broader and shorter, terminal phalanges simple, toes more elongated and without disks (Carvalho, 1954). *Hypopachus* and *Gastrophryne* agree in all recorded osteological characters except the absence in *Gastrophryne* of a precoracoid clavicle bar in the pectoral girdle. Unfortunately, the more diagnostic osteological features all change convergently in several distinct lines of microhylids (Parker, 1928, 1934; Carvalho, 1954). Consequently, any conclusions of affinity based only on osteology are disputable.

*Myrmecophagous Habitus.*—Some of the characteristics of *Gastrophryne* are explicable as adaptations to myrmecophagy in combination with cryptozoic habits. The habitus of *Gastrophryne* is characterized by a relatively small head, short limbs, and a large abdomen. The small head may reflect the small size of ants (Dickerson, 1906). However, some nonburrowing frogs

which feed on ants do not have narrow heads. Perhaps myrmecophogy reduces the selective value of a large mouth and cryptozoic or burrowing habits favor a narrow pointed head. Several burrowing frogs with varied diets do not have narrow heads. Many frogs jump considerable distances to catch their prey—this (and the leg length required for it) is unnecessary for feeding on ants. *Microhyla pulcha* can jump 6 ft in one bound (Pope, 1931) but *G. carolinensis* can jump only 11 or 12 in (Anderson, 1954). Similarly, cryptozoic habits remove or reduce the dependence on long jumps for predator avoidance. The skin of *Gastrophryne* is leathery (Kellogg, 1932; Stebbins, 1966). Ant mandibles may be imbedded in the skin of *Gastrophryne* causing no apparent harm (Fitch, 1956a). *Gastrophryne* have a transverse dermal groove immediately behind the eyes which can be covered from behind by a fold of skin. In frogs that have not been molested the fold is usually small or absent. A disturbance frequently elicits a marked increase in the extent of the fold. I pricked a *G. carolinensis* near the eye with a needle whereupon the frog twisted his head sideways and increased the fold until it extended forward beyond the eye. The groove and fold of skin behind the head in *Gastrophryne* and various other microhylids may have evolved to protect the eyes from the ant stings. *G. carolinensis* has a sticky dermal secretion which protects it from ants (Anderson, 1954). These features are less developed in most *Microhyla*. Parker (1934) reported an occipital fold as present in all American *Microhyla* and *Hypopachus* species except *M. pictiventris* and *M. aequatorialis*. In contrast, Parker noted the absence of a fold for 10 Asiatic *Microhyla* and listed it as sometimes present or a trace in the other 6. Many Asiatic *Microhyla* have an *Acris* like habitus manifesting neither short legs nor a narrow head; their skin is not appreciably thickened. At least some Asiatic *Microhyla* eat ants, (Berry, 1965) but their habitus is apparently less modified for the combination of myrmecophagy with cryptozoic habits.

*Sexual Dimorphism.*—Adult male *Gastrophryne* usually have a dark throat and a vocal pouch and average smaller than females. Breeding males often have small pustules on the chin and front fingers (Anderson, 1954, for *G. carolinensis*; Mittleman, 1950, and Stebbins, 1951, for *G. olivacea*; Parker, 1934, UI 57896-98, and TN 31847 for *G. usta*; Taylor and Smith, 1945, for *G. elegans*; SC CRE 2970B for *G. pictiventris*). Breeding females frequently have pustules in the perianal region (Taylor, 1940, and KU 88026 for *G. olivacea*; FS 736-23, 736-24, and DU A5252 for *G. carolinensis*; UI 50895, 62728, 7836, KU 73921, UM 121194 for *G. usta*; KU 65322 for *G. elegans*; SC CRE 2970A for *G. pictiventris*). Particularly pustulose males may have perianal spicules but in such cases they are usually much less developed than those on the chin. Breeding males have a nuptial adhesive gland covering the thorax and inner surfaces of the arms (Fitch, 1956a, for *G. olivacea*; Conaway and Metter, 1967, for *G. carolinensis*; Sumichrast, 1880, for *G. usta*; KU 65321 for *G. elegans*; SC CRE 2970B for *G. pictiventris*). This gland is most often evident from thickened and yellowed skin. The glands may keep a pair united during intrusions or prevent displacement of a clasping male by a rival (Fitch, 1956a; Awbrey, 1965). The function of spicules is unknown.

This same complex of secondary sexual characteristics is known for some other New World microhylines including *Hypopachus* (Nelson, 1966). I find no mention of a nuptial gland in Asiatic *Microhyla*. Parker (1934) noted spicules or sexual dimorphism in pustularity for 5 of 10 American *Microhyla* species but listed neither for any Asiatic *Microhyla*. In secondary sexual characteristics, *Gastrophryne* thus agrees with *Hypopachus* and apparently differs from Asiatic *Microhyla.*

*Tadpole.*—Noble (1931) suggested that similar larvae of *Microhyla* and *Gastrophryne* indicate close affinity whereas Carvalho (1954) stressed that they are distinguished by different larvae. Descriptions of tadpoles for *G. carolinensis* and *G. olivacea* include Orton (1946), Wright and Wright (1949), Stebbins (1951) and Altig (1970). Nelson and Altig (ms.) describe the tadpoles of *G. elegans* and *G. usta.* The tadpole of *G. pictiventris* is unknown. *Gastrophryne* tadpoles agree in the following characteristics: coloration, body shape, upper lip with a pair of generally smooth edged flaps, flaps separated medially by a U-shaped notch; lower lip unornamented, spiracle adjacent to anus at base of tail fin; dorsal and ventral tail fins subequal in height; and no terminal flagellum on tail.

The tadpoles of various populations of *Hypopachus* are described by Stuart (1954), Taylor (1942), Wright and Wright (1949), Orton (1952), and others. They agree with those of *Gastrophryne* in the features cited (including coloration) except that the labial flaps of *Hypopachus* are longer, have scalloped or papillate margins, and have convergent or overlapping medial edges.

Parker (1934) summarizes earlier descriptions of the tadpoles of Asiatic Microhylinae. The more extensive subsequent descriptions are Bourret (1942), Bhaduri and Daniel (1956), and Inger (1966). Asiatic *Microhyla* tadpoles do not have flaps on the upper lip, several have ornamented lower lips, only *M. butleri* has the spiracle near the anus, all except *M. berdmorei* have a terminal flagellum on the tail and have the lower tail membrane about twice as wide as the upper, and none resemble *Gastrophryne* and *Hypopachus* in coloration. Moreover, none of the tadpoles described for any other Asiatic microhyline combines the morphological features which unite the tadpoles of *Gastrophryne* and *Hypopachus* although various species show some of these features. In addition, tadpoles of *Gastrophryne* and *Hypopachus* both manifest a median lamella which functionally bisects the oesophagous longitudinally (Nelson and Cuellar, 1968). This lamella is absent in 4 Asiatic *Microhyla* (Peter Hartz and Craig E. Nelson, current research). *Gastrophryne* tadpoles thus resemble those of *Hypopachus* and differ from those of *Microhyla.*

*Mating Call.*—The characteristics of the calls of *G. olivacea*, *G. carolinensis, G. usta* and *G. elegans* are summarized in Table 1. The call of *G. pictiventris* has not been recorded; Dr. Norman Scott (personal communication) reports this species has a prolonged *baa* similar to

TABLE 1. Range of variation in 3 features of *Gastrophryne* mating calls.

| Species | Duration (Seconds) | Fundamental (Hertz) | Dominant (Hertz) |
|---|---|---|---|
| *G. carolinensis* | 0.4-2.3 | 165-240 | 2400-3900 |
| *G. elegans* | 4.0-5.0 | 200 | 2900-3300 |
| *G. olivacea* | 0.9-3.7 | 170-280 | 2750-4600 |
| *G. usta* | 0.5-6.4 | 70-110 | 3500-3900 |

other *Gastrophryne.* Details of the data are in Table 2 (for *G. olivacea* and *G. carolinensis*) and Table 3 (for *G. usta*). The description for *G. elegans* is based on calls recorded from a chorus 8.2 mi S of Sebol, Alta Verapaz, Guatemala, at an air temperature of 25 C. Originals or copies of all tapes are deposited with The University of Texas Bioacoustical Library. Calls were analyzed with a sound spectrograph ("Sona-Graph", Kay Electric Co.). The fundamental is the distance between 2 adjacent harmonics. The dominant at any particular point in time is the loudest harmonic, determined either as the longest line in a section or, at appropriate amplification, as the darkest line in "narrow-band" audiospectrogram. Times of less than 2.2 sec were measured from the audiospectrogram; longer times were measured with a stop watch. The close similarity of the calls of *G. elegans, G. carolinensis,* and *G. olivacea* (Table 1) is unusual. The fundamental of *G. usta* is distinctly lower than that of the other 3 species.

The calls of *Hypopachus* are similar and consist of a single, untrilled (0.8-8.2 sec) note with fundamentals varying from about 100 to 220 Hz, and dominants usually between 1600 and 3200 Hz (Nelson, 1966). Heyer (in press) describes the calls of 6 Asiatic *Microhyla* species; all of these have pulsed calls and either do not have a harmonic structure or have a shifting pattern of emphasis. The mating call of *Gastrophryne* thus allies it with *Hypopachus* and distinguishes it from *Microhyla.*

*Karyotype.*—The diploid chromosome number in *G. carolinensis* is 22 (Morescalchi, 1968); the same number occurs in *Hypopachus* (Dr. James P. Bogart, per. comm.). Bai (1956) reported 26 for *Microhyla rubra.* Other Old World microhylid genera have 24, 26, and 28 (Cole and

TABLE 2. Mating calls of *G. carolinensis* and *G. olivacea*.

| Locality | Temperature Air C / Water C | Number of Calls | Duration (seconds) Range / Mean ± Std. Dev. | Fundamental (Hertz) Range / Mean ± Std. Dev. | Dominant (Hertz) Range / Mean ± Std. Dev. |
|---|---|---|---|---|---|
| *G. carolinensis* | | | | | |
| Florida Key Largo | 24.5/25.0 | 7 | 0.7 - 1.3<br>1.06 ± 0.22 | 160 - 200<br>181 ± 16 | 2400 - 3600<br>3146 ± 355 |
| *Florida, Welaka | 25/23 | 62 | 0.7 - 1.6<br>1.25 ± 0.20 | 205 - 240<br>218 ± 7 | 3000 - 3900<br>3435 ± 146 |
| Florida, Everglades Natl. Park | 25/26 | 9 | 1.1 - 1.5<br>1.26 ± 0.12 | 200 - 220<br>206 ± 10 | 2800 - 3600<br>3131 ± 240 |
| Florida, Key Largo | 25.5/26 | 17 | 1.3 - 2.3<br>1.80 ± 0.26 | 180 - 200<br>190 ± 10 | 2700 - 3500<br>3114 ± 185 |
| Florida, 1 mi S Homestead | -/- | 17 | .6 - 1.8<br>1.28 ± 0.24 | 200 - 250<br>223 ± 13 | 2775 - 3700<br>3313 ± 262 |
| Florida, Marion and Highland Cos. | -/- | 12 | 1.1 - 1.5<br>1.32 ± 0.15 | 200 - 220<br>202 ± 6 | 3000 - 3900<br>3430 ± 241 |
| S. Carolina, Marion Natl. Forest | 22/23.5 | 4 | 0.8 - 1.9<br>1.27 ± -- | 180 - 200<br>202 ± -- | 2950 - 3750<br>3353 ± --- |
| Virginia, Morattico | -/23.4 | 6 | 0.4 - 1.4<br>1.13 ± 0.33 | 180 - 200<br>197 ± 6 | 2800 - 3600<br>3245 ± 174 |
| *Oklahoma and Texas – Allopatric | -/20-30 | 82 | 0.5 - 2.4<br>1.31 ± 0.4 | 200 - 236<br>215 ± 3 | 3100 - 3700<br>3400 ± 120 |
| *Oklahoma and Texas – Sympatric | -/20-32 | 108 | 0.6 - 1.6<br>1.14 ± 0.3 | 165 - 211<br>190 ± 5 | 2400 - 3400<br>2920 ± 130 |
| *G. olivacea* | | | | | |
| *Oklahoma and Texas – Sympatric | -/19-32 | 114 | 1.1 - 3.0<br>2.15 ± 0.37 | 200 - 260<br>238 ± 10 | 3700 - 4600<br>4420 ± 120 |
| *Oklahoma and Texas – Allopatric | -/19-32 | 40 | 0.9 - 3.7<br>2.45 ± 0.57 | 170 - 238<br>210 ± 7 | 3700 - 5000<br>4200 ± 130 |
| Texas, Presidio Co. Sierra Vieja Mountains | 23/22 | 13 | 2.0 - 2.3<br>2.51 ± 0.33 | 155 - 166<br>158 ± 3 | 2750 - 4300<br>3410 ± 367 |
| Kansas, 1-3 mi S Mankato | 23/23 | 23 | 1.1 - 2.5<br>1.82 ± 0.38 | 160 - 200<br>179 ± 11 | 2600 - 3800<br>3254 ± 271 |
| Sonora, 3.8 mi W Alamos | 22.5/24.8 | 21 | 1.7 - 2.8<br>2.20 ± 0.34 | 213 - 215<br>237 ± 13 | 3600 - 4500<br>3953 ± 355 |
| *Arizona, Peña Blanca Springs | 27/26 | 14 | 1.4 - 1.5<br>1.45 ± -- | 240 - 260<br>250 ± 6 | 3400 - 3900<br>3571 ± 150 |
| Tamaulipas, 12 mi S Ciudad Mante | 26/27.5 | 6 | 1.4 - 2.0<br>1.81 ± -- | 250 - 260<br>256 ± -- | 4600 - 4700<br>4050 ± --- |
| Sonora, near Alamos and Hermosillo | -/- | 17 | 0.9 - 2.2<br>1.52 ± 0.14 | 240 - 280<br>257 ± 16 | 3800 - 4700<br>4423 ± 264 |

*Temperature and length taken from Blair (1955b), fundamental and dominant from Awbrey (1965).

Zweifel, 1971). *Gastrophryne* and *Hypopachus* thus differ from Old World forms.

*Other Evidence.*—Using vertical starch-gel electrophoresis Nelson (1966) reported 9 plasma proteins in *Gastrophryne* of which 7 have analogues in *Hypopachus.* This suggests close affinity but provides no direct comparison with Asiatic *Microhyla. Hypopachus* X *Gastrophryne* hybrids metamorphose at a rate intermediate to those of the homospecific controls (Wilks and Laughlin,

TABLE 3. Mating Calls of *Gastrophryne usta.*

| Locality | Temperature Air C / Water C | Number of Calls | Duration (seconds) Range / Mean ± Std. Dev. | Fundamental (Hertz) Range / Mean ± Std. Dev. | Dominant (Hertz) Range / Mean ± Std. Dev. |
|---|---|---|---|---|---|
| El Salvador, 9.2 mi W Cojutepeque | 22/23 | 2 | 1.2 – 4.0<br>– – – | 70 – 75<br>– – – | 3500 – 3700<br>– – – – – |
| El Salvador, 5-15 km SSE Candelaria | 23/26 | 16 | 1.3 – 4.9<br>3.03 ± 0.97 | 70 – 120<br>91 ± 12 | 3500 – 3900<br>3723 ± 116 |
| Veracruz, 11 mi SW Conejos | 24/24 | 13 | 0.5 – 2.2<br>1.47 ± 0.49 | 70 – 110<br>93 ± 15 | 3500 – 3800<br>3595 ± 149 |
| Oaxaca, Juchitán | 25/– | 15 | 0.5 – 1.4<br>0.76 ± 0.91 | 95 – 100<br>99 ± 2 | 3400 – 4100<br>3856 ± 385 |
| Oaxaca, 8.5 and 14.2 mi W Zanatepec | 25.5/– | 21 | 0.68 – 3.7<br>1.05 ± 0.73 | 90 – 120<br>99 ± 10 | 3400 – 4750[1]<br>3997 ± 341 |
| Oaxaca, 1 mi W Tehuantepec | 26/27 | 4 | 0.4 – 0.7<br>0.55 ± – | 100 – 130<br>116 ± – | 3600 – 4400<br>3950 ± – |
| Veracruz, 0.2 mi SW Coatzocoalcos | 26/28 | 23 | 1.1 – 3.3<br>1.93 ± 0.65 | 100 – 120<br>101 ± 6 | 4000 – 4600<br>4240 ± 342 |
| Oaxaca, 9 mi E. La Venta | 27/– | 21 | 0.4 – 1.7<br>0.94 ± 0.35 | 90 – 100<br>96 ± 4 | 4100 – 4450<br>4218 ± 262 |
| Oaxaca, 5.6 km E. Zanatepec | 28/29 | 5 | 1.8 – 2.6<br>2.15 ± 0.34 | 100 – 120<br>115 ± 11 | 3700 – 4500<br>4255 ± 225 |
| Colima, 9 mi E Colima | –/– | 16 | 0.7 – 6.0<br>4.19 ± 1.39 | 80 – 100<br>98 ± 6 | 3100 – 3700[1]<br>3510 ± 361 |
| Colima, 20 mi E Manzanillo | –/– | 2 | 4.0 – 4.6<br>– – – – | 100<br>– – – | 3800 – 3900<br>– – – – – |
| Guatemala, 3 km E Escuintla | –/– | 5 | 4.1 – 8.2<br>5.31 ± 1.54 | 90 – 130<br>101 ± 4 | 4100 – 4600<br>4350 ± 152 |

[1]Dominant occasionally descends to 2300 – 2550 Hertz.

1962). This indicates a close relationship but provides no comparison with Asiatic *Microhyla.* The vocal cords of *G. olivacea* are distinct from those of several Old World microhylids (including 3 *Microhyla* species) (Trewavas, 1933) but no other comparisons are available.

*Conclusion.—Gastrophryne* agrees with Asiatic *Microhyla* in only 1 character in which it differs from *Hypopachus*: the absence of clavicle-procoracoid arch, a character known to have originated (by degeneration) several times in microhylid evolution. It agrees with *Hypopachus* and differs from *Microhyla* in several features of osteology, in internal and external morphology of the tadpoles, in extent of adaptations to myrmecophogy, in secondary sexual characters, in mating call, and in number of chromosomes. Data from serum protein analysis and hybridization are compatible with a close relationship between *Gastrophryne* and *Hypopachus.* Thus, the hypothesis that *Gastrophryne* is more closely related to Asiatic *Microhyla* than to other microhylines must be rejected and *Gastrophryne* (rather than *Microhyla*) is the appropriate generic name.

## SPECIES RECOGNIZED

There are 5 species: *G. usta, G. elegans, G. pictiventris, G. carolinensis,* and *G. olivacea. G. usta* has paired metatarsal tubercles; the other species have single metatarsal tubercles. *G. elegans* and *G. pictiventris* have dilated toe tips and a rudimentary web; the other species have simple toe tips and no webs.

Gaige (in Stuart, 1934) suggests that *G. elegans* differs from *G. pictiventris* in having an inguinal spot, a dark brown dorsal band, an occipital fold, and longer legs. Present specimens validate only the use of the inguinal spot and (usually) of the dorsal dark wedge. An occipital groove or fold is present on all *Gastrophryne*. The ratio of leg length to body length is: *G. elegans* (6 males) .815-.962, mean .881; *G. elegans* (3 females) .758, .827, and .863; *G. pictiventris* (17 males) .787-.943, mean .852; *G. pictiventris* (8 females) .777-947, mean .852. In addition, the ventral coloration of *G. elegans* consists of irregular white blotches separated by a narrow darker reticulum (the width of the dark areas much less than the width of the light areas) whereas that of *G. pictiventris* consists of smooth edged white blotches separated by dark areas which are usually broader than the minimum width of the white blotches. The 2 species are allopatric. The Honduranian *G. elegans* (Appendix I) is typical in these features.

*G. carolinensis* and *G. olivacea* (under its synonym *G. texensis*) were generally regarded as distinct prior to Hecht and Matalas' review (1946). These authors discuss series including intermediates from Latimer Co., Oklahoma and Victoria Co., Texas. In independently identifying the Victoria Co. material (US), I found 13 per cent intermediates where they had found 75 per cent. They examined Latimer Co. material (UM) which is a small sample (10 specimens) from larger series obtained by Bragg (UO, 43 additional specimens). Whereas, they specified 60 per cent hybrids, I find 12 per cent in the larger series (notes with the UO specimens indicate that Bragg regarded 18 per cent of them as hybrids). The discrepancies reflect my broader interpretation of the amount of ventral mottling in "pure" *G. olivacea*. Specimens with "mottling on the throat and sides of the abdomen" (Hecht and Matalas' criterion of intermediacy) are common throughout the southern third of the range and not infrequent in wooded NE Kansas (see intraspecific variation). Hecht and Matalas note large white areas on the abdomen in some Florida *G. carolinensis* (which restricts mottling to the sides as in their characterization of *G. olivacea*). Similar specimens occur in other areas (Marion County, Alabama, UA-uncatalogued; Athens, Clarke Co., Georgia, UG-625-part). Thus occasional specimens which are intermediate by Hecht and Matalas' criteria occur hundreds of miles from the zone of sympatry. My intermediates have strong mottling over at least the anterior portion of the abdomen (as well as the throat and sides of the abdomen) and lack the middorsal wedge and dorsolateral stripes often found in *G. carolinensis*. This reduces, but does not eliminate, overlap with patterns found outside the zone of sympatry.

I also noted intermediates from: Beavers Bend State Park, McCurtain County, Oklahoma (SL 1835, with 1 *G. carolinensis*); north of Sand Springs (UM 73209, 2 intermediates with 3 *G. olivacea*) Osage County, Oklahoma; Tulsa, Tulsa County, Oklahoma (UM 97294-97, 5 intermediates with 1 *G. olivacea*); 5 mi NE Fannin, Goliad County, Texas (US 83381); between Houston and South Houston, Harris County, Texas (TU 4679); and 13 mi W Cold Springs, San Jacinto County, Texas (TN 19455-56, with 1 *G. olivacea*).

Blair (1950) reports reciprocal laboratory hybrid tadpoles; and metamorphosed laboratory hybrids have been produced (Blair, 1955b). The fertility of hybrids has not been determined. Blair (1955b) analyzes calls from some intermediate wild individuals. These data, and the wild-caught intermediates, demonstrate that these species can and do hybridize occasionally. It is now accepted (Mayr, 1964) that occasional hybrids are not necessarily indicative of conspecifity. Indeed several lines of evidence indicate that *G. olivacea* and *G. carolinensis* are full biological species.

Sympatric or nearly sympatric (but morphologically distinct) populations of these species are discussed by Strecker (1908b,c), Bragg (1946, 1955), Smith (1947a), Blair (1950, 1952), Brown (1950), Peterson (1950), Blair (1951, 1955a,b), Smith and Saunders (1952), Lindsay (1954), Blair and Laughlin (1955), Raun (1960) and Awbrey (1965). Most of these authors comment on sympatric differences in morphology, habitat, call, or breeding season. In the zone of overlap, *G. carolinensis* is more restricted ecologically and typically occurs on forested floodplains; *G. olivacea* sometimes extends into the forest and occurs in choruses with *G. carolinensis* (Blair, 1955b). The zone of sympatry in Texas exceeds 150 mi in width but throughout this zone the species are easily distinguishable and apparent hybrids are rare.

Intrapopulational and geographic variation in mating calls is summarized in Table 2. Calls of sympatric populations differ in call length and emphasized frequency (Bragg, 1950a; Blair, 1955b). There is partial separation of both fundamental and call length for sympatric populations with no overlap in dominant frequencies (Awbrey, 1965) which confirms Blair's (1955b) demonstration that sympatric differences exceed adjacent allopatric differences (reinforcement). Typically, calls of *G. olivacea* have and those of *G. carolinensis* lack an initial "peep" (Blair, 1955b). Females respond to the call (Bogert, 1958) and discriminate between calls of different pitch (Awbrey, 1965).

Hecht and Matalas (1946) concluded there was no difference in average size of *G. olivacea* and *G. carolinensis* using samples combining specimens from throughout the ranges. However, there is considerable geographic variation in size in both species (Table 4) and in accord with observations by Blair (1950) and Blair (1955a), average differences of 1-4 mm separate the species in sympatry. In laboratory matings *G. olivacea* males clasp *G. carolinensis* females but some males of *G. carolinensis* are reluctant to clasp the smaller females of *G. olivacea* (Blair, 1950). Distinct differences occur in body length between adjacent adult year classes (Anderson, 1954; Fitch, 1956a). A preference of males for larger females within each species might be explained by the larger numbers of eggs in larger females (Anderson, 1954; Henderson, 1961), and by the presumably greater average fitness of the larger (and older) females.

Prolonged and heavy rainfall initiates breeding (Anderson, 1954). In eastern Oklahoma *G. carolinensis* is less dependent on rainfall for initiation of breeding than *G. olivacea* (Blair, 1950; Bragg, 1950a). This difference provides only partial isolation as mixed choruses form after heavy rains (Blair, 1955b).

Thus, although *G. carolinensis* and *G. olivacea* occasionally hybridize, distinct differences in color, average size, and isolating mechanisms (especially call) occur throughout a broad zone of sympatry. Consequently the two are distinct biological species.

## DISTRIBUTION

Locality records are summarized in Appendix I. *G. carolinensis* is known from Maryland south to Key West, Florida, and west to Texas and Kansas; noteworthy new records (Appendix I) are from Texas (Cameron and Kerr Cos.) and Missouri (Miller Co.). *G. elegans* is known from Veracruz south to Honduras; the Honduras record (Appendix I) extends the known range past major physiographic barriers. *G. olivacea* occurs from southern Nebraska and western Missouri south through the Great Plains and southern Arizona to San Luis Potosí and Nayarit; the Arkansas and east Texas localities (Cass, Chambers, Morris, Polk, and Nacogdoches Cos.) redefine the eastern limit. *G. pictiventris* is known from Nicaragua and Costa Rica. *G. usta* is known from coastal areas on the Pacific versant from Sinaloa south to El Salvador, and from the Gulf versant of Veracruz and Oaxaca.

There are two possible records of *Gastrophryne* from Morelos. A *G. olivacea* (FM 104398) catalogued as from 8 mi E of Cuernavaca on the road to Yautepec [Morelos, Mexico] corresponds to a "*Microhyla*" in E. H. Taylor's field catalogue for 1938 (H. Marx, per. comm.), not cited in Taylor and Smith (1945) or Smith and Taylor (1948). It is separated by a few hundred km from other records for this species. The situation is complicated by Taylor's (1942) description as *Hypopachus* of tadpoles from "kilometer 133 near Huajintlán, Morelos" which, if accurately portrayed, must belong to *Gastrophryne*. The tadpoles are apparently no longer extant; the description of them matches either *G. olivacea* or *G. usta* (known from approximately 100 km S of Huajintlán).

*G. usta* has hitherto been regarded as occurring at several inland localities which are either doubtful or demonstrably wrong. Two *G. usta* which Kellogg (1932) listed from inland Jalisco (US 46963 from Atemajac and AM 12113 from Oblatos) are *Hypopachus.* The *G. usta* from Agua Delgada, Guadalajara, cited by Günther (1900) is apparently assigned to *Hypopachus* by Parker (1934). Tanner and Robison (1960) listed a *G. usta* from 7.5 mi N of Magdalena,

TABLE 4. Geographic variation in snout-vent length (mm) of *G. olivacea* and *G. carolinensis*.

| Population | Males | | | | | | Females | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Lowland | | | Upland | | | Lowland | | | Upland | | |
| | No. | Mean | Std. Dev. | No. | Mean | Std. Dev. | No. | Mean | Std. Dev. | No. | Mean | Std. Dev. |
| *G. carolinensis* | | | | | | | | | | | | |
| Maryland | 5 | 27.42) | 2.70 | -- | --- | -- | -- | --- | -- | -- | --- | -- |
| Virginia | 25 | 26.23 | 1.90 | -- | --- | -- | 3 | 28.60 | -- | -- | --- | -- |
| North Carolina | 117 | 26.99 | 3.12 | -- | --- | -- | 53 | 27.59 | 2.94 | -- | --- | -- |
| Georgia | 35 | 24.51 | 2.04 | 40 | 28.20 | 1.59 | 39 | 26.73 | 2.51 | 21 | 30.40 | 2.13 |
| Florida-Alachua Co. | 64 | 22.79 | 1.65 | -- | --- | -- | 24 | 24.15 | 2.72 | -- | --- | -- |
| Florida–Other | 134 | 23.88 | 0.85 | -- | --- | -- | 141 | 24.07 | 2.91 | -- | --- | -- |
| Florida–Other* | 16 | 23.44 | 0.80 | -- | --- | -- | 11 | 25.91 | 1.92 | -- | --- | -- |
| Alabama-Tuscaloosca Co. | -- | --- | -- | 85 | 27.50 | 5.18 | -- | --- | -- | 15 | 32.26 | 4.21 |
| Alabama–Other | 31 | 24.88 | 1.63 | 57 | 28.47 | 1.29 | 16 | 26.35 | 2.35 | 32 | 32.49 | 5.81 |
| Tennessee | -- | --- | -- | 15 | 27.80 | 2.65 | -- | --- | -- | 9 | 28.14 | 4.02 |
| Kentucky | -- | --- | -- | 1 | (28.1) | -- | -- | --- | -- | 1 | (29.5) | -- |
| Mississippi | 34 | 24.62 | 1.39 | 26 | 27.85 | 1.84 | 30 | 26.77 | 2.36 | 38 | 30.18 | 2.57 |
| Louisiana | 311 | 25.58 | 1.86 | -- | --- | -- | 323 | 27.40 | 3.67 | -- | --- | -- |
| Arkansas | -- | --- | -- | 24 | 29.82 | 1.83 | -- | --- | -- | 29 | 32.24 | 2.91 |
| Missouri | -- | --- | -- | 11 | 29.65 | 1.70 | -- | --- | -- | 27 | 31.66 | 3.11 |
| Kansas | -- | --- | -- | 1 | (29.4) | -- | -- | --- | -- | 1 | (34.1) | -- |
| Texas–Montgomery Co.* | 14 | 26.21 | 1.12 | -- | --- | -- | -- | --- | -- | -- | --- | -- |
| Texas–Nacogdoches Co.* | 26 | 26.65 | 2.14 | -- | --- | -- | -- | --- | -- | -- | --- | -- |
| Texas–Additional | 32 | 25.52 | 1.85 | -- | --- | -- | 25 | 27.63 | 2.39 | -- | --- | -- |
| Oklahoma | -- | --- | -- | 32 | 29.49 | 1.45 | -- | --- | -- | 9 | 31.21 | 2.41 |
| *G. olivacea* | | | | | | | | | | | | |
| Missouri | -- | --- | -- | 9 | 29.32 | 2.60 | -- | --- | -- | 11 | 30.25 | 3.16 |
| Kansas | -- | --- | -- | 77 | 29.97 | 2.22 | -- | --- | -- | 61 | 31.61 | 3.20 |
| Arkansas | -- | --- | -- | 6 | 27.53 | 2.02 | -- | --- | -- | 3 | (27.2 - 31.6) | |
| Oklahoma–Eastern** | -- | --- | -- | 17 | 28.21 | 1.70 | -- | --- | -- | 10 | 32.76 | 2.80 |
| Oklahoma–Western** | -- | --- | -- | 6 | 27.98 | 1.60 | -- | --- | -- | 3 | (26.9 - 31.2) | |
| Oklahoma–Bryan Co.** | -- | --- | -- | 14 | 25.31 | 1.14 | -- | --- | -- | -- | --- | -- |
| Texas–Presidio Co.* | -- | --- | -- | 16 | 26.81 | 1.52 | -- | --- | -- | -- | --- | -- |
| Texas–Other | 70 | 24.45 | 2.04 | 17 | 25.96 | 1.64 | 54 | 26.65 | 2.56 | 14 | 26.99 | 2.45 |
| Texas–Other* | 193 | 23.30 | 1.53 | 105 | 25.01 | 1.42 | -- | --- | -- | -- | --- | -- |
| Tamaulipas | 17 | 23.68 | 1.81 | -- | --- | -- | 2 | (24.0 - 24.1) | | -- | --- | -- |
| San Luis Potosi | 1 | (23.5) | | -- | --- | -- | -- | --- | -- | -- | --- | -- |
| Nuevo Leon | 8 | 24.60 | 1.49 | -- | --- | -- | 1 | (27.6) | | -- | --- | -- |
| Coahuila | -- | --- | -- | 18 | 26.17 | 0.61 | -- | --- | -- | 3 | (27.7 - 34.1) | |
| Chihuahua | -- | --- | -- | -- | --- | -- | -- | --- | -- | 1 | (34.4) | -- |
| Durango | -- | --- | -- | 7 | 28.76 | 1.81 | -- | --- | -- | 1 | (30.6) | -- |
| Arizona–Pima Co. | -- | --- | -- | 18 | 27.28 | 1.56 | -- | --- | -- | 2 | (28.1 - 32.3) | |
| Arizona–Santa Cruz Co. | -- | --- | -- | 62 | 26.67 | 1.92 | -- | --- | -- | 15 | 29.72 | 1.62 |
| Sonora | 50 | 25.92 | 2.12 | -- | --- | -- | 14 | 31.33 | 2.73 | -- | --- | -- |
| Sinaloa | 56 | 24.62 | 1.62 | -- | --- | -- | 20 | 29.31 | 2.44 | -- | --- | -- |
| Nayarit | -- | --- | -- | -- | --- | -- | 1 | (23.6) | -- | -- | --- | -- |

*Data from Blair (1955a).

**Oklahoma divided: East and west of a line from Bartlesville to Dallas, Texas, with Osage Co. counted as east. Bryan Co., on the Red River lowlands, most closely resembles coastal Texas populations and is tabulated separately.

Jalisco, (Brigham Young Univ. 14049); this is a juvenile *Hypopachus*. Kellogg (1932) listed a *G. usta* from Valles, San Luis Potosí (US 46919); this is a juvenile *Hypopachus* (Taylor and Smith, 1945). Reese and Firschein (1950) listed *G. usta* from 6 mi NE Tihuatlán, Veracruz; this is a *G. elegans* (Reese, 1953). Gadow (1905) listed *Engystoma ustum* from Presidio and Motzorongo, Veracruz (both at 1500 ft). Parker (1934) assigned Gadow's use of *E. ustum* to the synonomy of *G. elegans* and listed specimens from Presidio; the British Museum has no microhylids from Motzorongo (Miss A. G. C. Grandison, per. comm.).

Dugés (1869) mentioned "*Engystoma sp. nov*?" from the states of Guadalajara (now Jalisco) and Guanajuato. *Hypopachus* was named by Keferstein (1867) and was first reported from Mexico by Boulenger (1883). In listing the fauna of Guanajuato and Michoacan Dugés (1895, 1896) listed *H. variolosus* but not *Engystoma.* Günther (1900) listed *H. variolosus* from Guadalajara collected by Dugés. Dugés clearly associated his "*Engystoma*" with *Hypopachus* when the latter was described. Presumably the records of Günther (1900) for *G. usta* from Guanajuato (collected by Dugés) and of Smith and Taylor (1948) from Buenavista, Guanjuato, both derive from Dugés. (*Hypopachus* does occur in Guanajuato: Nelson, 1966).

A *G. usta* (AM 13909) catalogued as from "2 mi W of Xochimilco, D. F., Mexico" (at about 2200 m) was collected by P. Ruthling. The validity of this locality is questionable (George Foley, per. comm.). No microhylids are otherwise known from the *Districto Federal*. This record is some 1000 m higher than any valid record of *G. usta.*

*Engystoma mexicanum*, a synonym of *Gastrophryne usta*, was described (Peters, 1870) from "the warmer regions of Mexico (Matamoros and other sites)." Although the title states that the collector was in Puebla and the specimens were from Mexico, the specimens have usually been listed as from Puebla (Kellogg, 1932; Parker, 1934; Smith and Taylor, 1948). Smith and Taylor (1950) fixed the type locality of *E. mexicanum* at [Izucar de] Matamoros, Puebla; this action is premature in the absence of any other records from Puebla or, indeed from the Balsas-Tepaltepec Basin which drains the Matamoros region.

Kellogg (1932) reported a *G. usta* from Minatitlan, Veracruz (US 47530). Smith and Taylor (1950) noted that the specimen is tagged as from Pinabete, Chiapas (at 8500 ft) and apparently corresponds to a field entry from Pinabete and that the elevation is "almost unbelievable," that all other Chiapas records are from the lowlands, and concluded confirmation is required. The specimen is *G. usta* but the locality certainly requires confirmation.

The type of *G. usta* (US 24965) was part of a collection which Cope listed as from Guadalajara, Jalisco. Most of the collection apparently came from coastal or foothills regions in western Mexico and 8 of the other 9 new species which Cope described from the collection do not occur there (Zweifel, 1959). The type now consists of a few disarticulated bones and bits of tissue, and I could not directly ascertain its identity. Cope's (1866) statement that the type has no webs is sufficient to associate the type with what is now called *G. usta* (and exclude the possibility that it is a juvenile *Hypopachus*).

*G. usta* thus seems to be reliably known only from coastal lowlands and foothills. It is apparently absent from the interior basins of the Lerma-Chapala system, and from other areas above 1000 m. As the original type locality of *G. usta* is apparently erroneous, I hereby propose an emended type locality of Tecoman, Colima (at 80 m elevation), a locality where it does occur (Oliver, 1937).

## GEOGRAPHIC VARIATION AND INFRASPECIFIC TAXA

*G. elegans* and *G. pictiventris* are known from too few specimens to justify a discussion of geographic variation. Tables 2-5 summarize variation in call and length for *G. carolinensis, G. olivacea* and *G. usta* and in coloration for the latter species. *G. carolinensis* and *G. olivacea* were separated into lowland and upland samples: coastal states were divided county by county on the basis of the 100 m contour line, except Texas was divided at the Balcones escarpment; non-coastal states and Coahuila, Chihuahua and Durango were considered upland; the remainder of the range in Mexico was considered lowland.

Average body length in coastal *G. carolinensis* populations increases from Florida to Maryland. Inland averages are uniformly larger than adjacent coastal samples. Western populations both on the lowlands and uplands average about 1 mm larger than corresponding eastern populations. Calls from Florida are higher pitched than those from Texas and Oklahoma (Blair, 1955b), but subsequent analysis does not agree (Table 2; Awbrey, 1965).

Variation in body length in *G. olivacea* parallels *G. carolinensis*: lowland populations are shorter than adjacent upland populations and northwardly increasing clines are evident in Pacific Coast populations and in upland populations from Texas to Kansas (Table 4). The

TABLE 5. Geographic variation of *Gastrophryne usta*.

| Locality | Sex | Snout-vent Length (mm.) No. | Range | Mean | Std. Dev. | Hair-fine Middorsal Stripe Present | Hair-fine Leg Stripe Present | Abdominal Reticulatulum Moderate to Dark | Abdominal Reticulations Visible | Dorsal Dark Wedge |
|---|---|---|---|---|---|---|---|---|---|---|
| Sinaloa | males | 13[1] | 21.0-25.6 | 23.0 | 1.83 | 6/10[2] | 0/2[2] | 5/12[2] | 11/12[2] | 2/2[2] |
| Nayarit | male | 1 | (21.5) | ---- | ---- | 0/1 | --- | 0/1 | 1/1 | --- |
| Colima | males | 26 | 20.4-27.8 | 24.2 | 1.71 | 0/25 | 0/16 | 4/12 | 7/12 | 3/16 |
| Guerrero | males | 39 | 19.5-24.9 | 22.9 | 1.41 | 2/38 | 1/29 | 7/38 | 27/38 | 17/29 |
| Sinaloa-Guerrero | females | 13 | 23.0-29.0 | 26.8 | 2.01 | 0/8 | 0/6 | 0/12 | 0/12 | 4/6 |
| Oaxaca (All) | males | 58 | 19.6-28.6 | 22.8 | 1.70 | --- | --- | --- | --- | --- |
| | females | 14 | 24.7-30.4 | 26.8 | 1.80 | --- | --- | --- | --- | --- |
| Oaxaca (Guerrero Border) | males | 2 | -------- | ---- | ---- | 0/2 | 0/2 | 0/2 | 2/2 | 2/2 |
| Oaxaca (S side of Isthmus) | males | 27 | -------- | ---- | ---- | 27/27 | 18/18 | 18/25 | 25/25 | 13/19 |
| | females | 10 | -------- | ---- | ---- | 7/9 | 4/6 | 0/8 | 6/8 | 6/6 |
| Oaxaca (N side of Isthmus) | males | 29 | -------- | ---- | ---- | 22/29 | 0/9 | 9/9 | 9/9 | --- |
| | females | 4 | -------- | ---- | ---- | 4/4 | 1/1 | 4/4 | 4/4 | 1/1 |
| Veracruz: Potrejo Viejo | males | 138 | 22.0-26.3 | 23.9 | 2.35 | 73/123 | 0/123 | 91/123 | 122/123 | 46/123 |
| Veracruz: Other | males | 51 | 20.6-26.1 | 23.5 | 1.49 | 38/66 | 5/51 | 37/52 | 46/52 | 23/54 |
| Veracruz: All | females | 24 | 23.1-29.1 | 25.5 | 2.12 | 19/23 | 0/27 | 15/26 | 22/26 | 12/20 |
| Chiapas | males | 24 | 18.8-24.6 | 21.5 | 1.42 | 43/45 | 21/23 | 14/26 | 17/26 | 7/9 |
| | females | 14 | 20.2-26.0 | 23.7 | 2.03 | 14/15 | 9/10 | 8/10 | 9/10 | 8/10 |
| Guatemala—El Salvador | males | 12 | 19.6-22.3 | 20.9 | 0.76 | 14/16 | 15/16 | 11/13 | 13/13 | 15/16 |
| | females | 6 | 23.1-25.3 | 24.6 | 0.81 | 6/7 | 6/7 | 4/7 | 5/7 | 4/6 |

[1]Number for snout-vent only.
[2]Number showing character over total number examined for this character. Some specimens were not examined for some characters or characters could not be adequately determined (due, for example, to bleaching).

available calls (Table 2) show appreciable geographic variation. Calls from Arizona, western Texas and Kansas have similar dominant frequencies. Frogs from these areas average appreciably larger than those from other areas for which calls are available (Table 4). Geographic variation in dominant frequency matches the pattern that would prevail if dominant frequency were inversely proportional to size (unfortunately few of the calls can be related to a specimen and this hypothesis cannot be tested directly). In fundamental frequency, the Arizona calls are most similar to those from Tamaulipas and Sonora and very different from those from Kansas and western Texas, but the temperatures for the Arizona recordings are appreciably higher than in Kansas and western Texas but approximately equivalent to those in Tamaulipas (and to what might be expected in Sonora). These relationships would be reasonable if the fundamental were primarily a function of temperature (as it is in *G. usta*, Table 3; dominant frequency in *G. usta* is also a function of temperature but geographic variation in size is much less than in *G. olivacea*).

In Arizona, Lowe (1964) recognizes *G. carolinensis* from the Parjarito and Patagonia Mountains in oak-woodland and oak-grass habitats and *G. olivacea* in Pima Co. from desert habitats and in relictual mesquite-grass habitats. He cites no data supporting these hypotheses. However, Blair (1955b) had proposed that calls from the Santa Cruz Mountains (Peña Blanca Springs) more closely resembled those of *G. carolinensis* than of *G. olivacea* and (Blair, 1955a) attributed this to interspecific clinal variation. As noted above, the Arizona (Peña Blanca Springs) calls resemble those of other large bodied populations in dominant and those of populations recorded at similar temperatures in fundamental. Moreover, the call of this population, like those of other *G. olivacea* but unlike those of *G. carolinensis* typically begins with a "peep" (Stebbins, 1951; Blair, 1955b). Wright and Wright (1949) cite the egg jelly of *G. carolinensis* as truncate and that of *G. olivacea* as not truncate; jellies from the Peña Blanca are truncate (Stebbins, 1951, 1954). However, Salthe (1963; per. comm.) had eggs of *G. olivacea*

from Oklahoma and Texas in which the jelly is truncate. *G. carolinensis* tadpoles usually have a distinct light stripe on the side of the tail; this stripe is usually obscure in *G. olivacea* (Wright and Wright, 1949). The stripe is obscure in a sample from Peña Blanca (US 49480). Thus call, egg truncation, and tadpole coloration all fail to support Lowe's (1964) hypotheses.

However, modal adult coloration in montane and desert samples from Arizona does differ. Frogs of both areas usually have leg bands and usually have dark spots indicating an occiput-to-groin stripe. A dorsolateral row of dark spots is more frequent in montane (30 of 55 specimens for which I have color notes) than in desert flat frogs (4 of 19). Most montane (40 of 55) but few (2 of 19) of desert flat frogs have mottling on the back of the throat (almost all have mottling on the chin and sides). However the range of coloration in both groups is similar and they agree in the features (legbands, ventral mottling, dorsal markings) in which they differ from geographically distant populations. Consequently adult coloration provides no obvious basis for separation of the Arizona populations into 2 species nor for suggesting affinities of the montane populations with *G. carolinensis* but further study might support subspecific distinctions.

*G. mazatlanensis* (Taylor, 1943) is based on specimens from Sinaloa and has been applied with species (Smith and Taylor, 1948; Wake, 1961; and others) or subspecies (Hecht and Matalas, 1946; Hardy and McDiarmid, 1969) rank to the populations of *G. olivacea*-like frogs on the Pacific lowlands of northwestern Mexico. In comparison with *G. olivacea, G. mazatlanensis* is characterized as smaller, with a narrower head, the snout more projecting, flattened above and rounding at the tip; eye proportionally smaller, smaller choanae; toes and fingers more rounded with no lateral ridge; foot slenderer; and with a trace of a black stripe or row of spots from behind eye to a point on the side (Taylor, 1943; Smith and Taylor, 1948). Body size will not separate these forms (Table 4). The relative head breadth and foot length of Sinaloan specimens is encompassed by the variation in 4 haphazardly selected Texas specimens (Nelson, 1966). Taylor (1940) includes a Coahuilan specimen having a smaller eye (than *G. mazatlanensis*) both absolutely and proportionally. Hecht and Matalas (1946) state that smaller specimens have more acute snouts and smaller heads. Neither Taylor (1940, 1943) nor Smith and Taylor (1948) give any measurements of width of foot or length of toes and no differences are apparent. In a series, (TN 16610-15), from Peña Blanca Springs, one (16612) has no black dots on the side; another (16614) has elongate spots separated by no more than their length beginning on the eyelid and reaching 2/3 of the distance to the groin on the right side. This trace of a stripe is more discontinuous on the left side but reaches nearly to the groin. The remaining 4 specimens are intermediate. Similar variation is shown by another series from Santa Cruz Co. (UA: R. L. Bezy 1154-1165). Thus, no data are known which justify the use of any of the diagnostic or key characters presented by Taylor (1943; Smith and Taylor, 1948) for either specific or subspecific distinctions.

Hecht and Matalas treat *mazatlanensis* as a subspecies distinguished by a blotch or spot on the femur and tibia which form a bar or continuous line when the limb is folded; dorsum with dark spots, as contrasted to *olivacea*, in which spots rarely present on the femur and tibia; if present usually not forming a distinct bar when the limb is folded; dorsum tan and generally without markings. They figure *G. olivacea* from Kansas, Nebraska, and Coahuila that have distinct dorsal markings and leg markings that form a distinct bar. Chrapliwy, Williams and Smith (1961) note for specimens from Chihuahua: a variation from a few black spots on the anterior 1/3 of the tan dorsum to numerous scattered black spots over the entire dorsum continuing posteriorly onto the femur; leg-bars variously developed; in some the leg-bars are inconspicuous or poorly defined, while in others broad and well developed, similar to the figure of *mazatlanensis*. A broad range of variation in development of leg bands also occurs in both montane and desert populations in Arizona. Leg bands thus provide, at best, an average separation.

The type series of *mazatlanensis* has the sides slightly mottled with lighter and darker (Taylor, 1943). Hecht and Matalas (1946) also contrast *olivacea* and *mazatlanensis* with respect to ventral coloration. Hardy and McDiarmid (1969) contrast the ventral coloration of Sinaloan,

Sonoran, and Texan *G. olivacea.* Hecht and Matalas (1946) and Wake (1961) report mottling for Arizonan and Sonoran specimens. Chrapliwy, Williams, and Smith (1961) report that in specimens from Chihuahua the ventrum is either immaculate or has a few scattered melanophores. Taylor (1940) and Webb (1960) discuss specimens from Durango which have pigment on the chest and sides of the body. Martin (1958) notes ventral mottling in specimens from Tamaulipas. Ventral mottling is thus frequent throughout Arizona and Mexico. Occasional specimens with partially mottled venters also occur elsewhere in the range of *G. olivacea* (e.g. Breahan Co., Mo, FM 123936-39; Jackson Co. Mo., KU 91001-03; Bourboun Co., Kansas, U.S. 73641; Douglas Co., Kansas, KU 88026-27; Taylor Co., Texas, AL, 54288).

In summary, none of the morphological characters proposed for separating *mazatlanensis* are valid. The features of coloration characteristic of Pacific lowland populations are common throughout Mexico and occur occasionally throughout the range. There is no present indication of an abrupt shift in the frequency of these features. In the absence of such a shift, the recognition of subspecies does not accurately reflect the pattern of geographic variation.

Variation in *G. usta* is summarized in Table 5. Frogs from Central America and Chiapas average slightly smaller than more northern populations. Frogs from the more SE regions typically have a hair-fine middorsal stripe, a similar stripe on the posterior surface of the leg, a dorsal dark wedge, and moderate to dark abdominal reticulations. Frogs from coastal Mexico between Guerrero and Sinaloa typically have neither hair-fine light stripe, have the abdomen only faintly reticulated, and often lack the dorsal wedge. Populations from geographically intermediate areas (northern Oaxaca and Veracruz) are more variable in all of these characters.

Taylor and Smith (1945) recognize 2 subspecies of *G. usta. G. usta gadovi* is smaller and has hair-fine middorsal and leg stripes whereas *G. usta usta* lacks these lines and is larger; the range of *G. u. usta* is Sinaloa and central Veracruz southward to near the Isthmus of Tehuantepec, *G. u. gadovi* occurs in Oaxaca and Chiapas (Smith and Taylor, 1948). The size distinction is invalid (Table 5). Duellman (1960) and Fouquette and Rossman (1963) discuss coloration and conclude that a redefinition is needed. Lynch (1965) regards the populations from Veracruz, northern Oaxaca, and the Pacific coast of Chiapas, Guatemala, and Central America as distinct from the Pacific Coast populations north of Tehuantepec. He characterizes the former as having a reticulated venter, smaller size, and the frequent presence of a hair-fine line on the dorsum and legs. He further observes that the types of *gadovi* are from a narrow zone of intergradation where the diagnostic features of the two races show some variation, and concludes that the only unequivocable solution seems to be to regard *gadovi* as synonymous with *usta*, and, consequently, names the Veracruz-El Salvador population *Gastrophryne usta retifera* with a type locality in Veracruz. In Veracruz, *G. usta* are relatively large (not small), the leg line is almost as uniformly absent as in the northwest, the middorsal stripe is less uniformly present than in Chiapas and Central America, and the ventral reticulations seem no more uniformly dark than around Tehuantepec and further southeast (Table 5). (Ventral coloration is tabulated two ways in Table 5 to reduce the possibility of misinterpreting Lynch's criterion of a reticulated venter.) Thus, *G. usta retifera* applies to an intermediate population and is unavailable for subspecies designation (following Lynch's own criteria). Furthermore, *E. mexicanum* Peters was not allocated to either subspecies by Lynch and, depending on the type locality assigned to it, might be a senior synonym of *retifera.* The Tehuantepec population, and consequently the name *Euphemphix gadovi* Boulenger, can be regarded as representative of the southeastern populations or as intermediate depending on the amount of emphasis placed on ventral coloration. Recognition of subspecies seems unwarranted, however, when one considers the mosiac distribution of some characters and realizes that the area occupied by intermediate populations is large relative to that occupied by more distinctive southeastern populations.

## HABITAT AND DIET

*Habitat.—Gastrophryne carolinensis* inhabits most low elevation vegetative formations in the southeastern United States (Wright and Wright, 1949; Duellman and Schwartz, 1958). At the western edge of its distribution, isolated populations occur in corridor forests and isolated patches of

forest (Blair and Laughlin, 1955; Blair, 1955b). The northern records are a series of isolated populations associated with features that provide special protection from climatic vagaries: coastal marshes (in Maryland, Conant, 1958) regions of sinkholes, caves and springs (in southwestern Virginia, Fowler and Hoffman, 1951; Tennessee, Bailey, 1936; Kentucky, Hirschfield and Collins, 1963; Missouri, Hurter, 1897; and Kansas, Smith, 1947a), and river bluffs (in Illinois, Smith, 1957; Missouri, Hurter, 1897; and Iowa, W. D. Klimstra, per. comm.). This suggests that along its northern margin *G. carolinensis* is restricted to sites where it can penetrate sufficiently deep into litter and loose debris to avoid freezing.

*G. olivacea* inhabits deciduous forest, prairie and river flood plains in eastern Kansas (Fitch, 1956a). Throughout the remainder of its range, the usual habitat is prairie or open woodland (Bragg, 1941; Lowe, 1964; Hardy and McDiarmid, 1969). *G. olivacea* has higher minimum developmental, activity, and breeding temperature requirements than other frogs with which it occurs (Fitch, 1956b; Hubbs and Armstrong, 1961; Ballinger and McKinney, 1966). Perhaps minimum temperatures during the breeding and tadpole seasons are limiting at the northern margin of its range. Bogert and Oliver (1945) suggest *G. olivacea* is excluded from southern California by desert conditions. The head and body in *G. olivacea* is more depressed than in the other species (Wright and Wright, 1949). This may reflect a habit of escaping drought and/or freezing by forcing its way under rocks and into crevices, situations where it is commonly encountered (Fitch, 1956a; Smith, 1956).

*Gastrophryne usta* typically occurs in open tropical deciduous forest formations (Duellman, 1960; Hardy and McDiarmid, 1969, per. obs.), marshes (Oliver, 1937), and savannas (Duellman, 1960). Duellman (1960) indicates exclusively evergreen forest for only 3 Oaxacan localities; at one of these *G. usta* was taken from a clearing (Fugler and Webb, 1957). I collected calling *G. usta* near El Treinta, Guerrero, from under leaves in a wooded gully bordering an extensive area of grass. The paired metatarsal tubercles characteristic of *G. usta* presumably are an adaptation for burrowing to escape the seasonal drought characteristic of open tropical deciduous forests.

*G. elegans* is known from humid evergreen tropical forests (Gadow, 1905; Stuart, 1958; Duellman, 1965). I collected 2 series in Alta Verapaz from shallow backwater pools along flooding rivers. In both instances males were calling from flooded patches of grass over 2 ft high. Forest occurs at the edge of both flood plains.

*G. pictiventris* is known from regions of evergreen tropical and subtropical forest (Holdridge, 1962). Dr. Norman Scott (per. comm.) reports a chorus of *G. pictiventris* from a temporary pool in primary forest at Puerto Viejo, Costa Rica.

*Diet.*—The tadpoles are restricted to filter feeding (Nelson and Cuellar, 1968). They feed largely on small plants and animals that accumulate at the surface of the water (Stebbins, 1954); Bragg (1947) notes that they float quietly near the surface. Ants and termites are the principle foods of *G. carolinensis* both by number and volume but many invertebrates are eaten (Anderson, 1954). Ants are predominant in the diet of *G. olivacea*, but small beetles are also eaten (Fitch, 1956a). Smith (1947b) reported a *G. usta* contains a large number of ants. Stomach contents from 2 other *G. usta* consist mainly of ants, but each includes part of a beetle (specimens from 9.8 mi W Pinotepa Nacional, Oaxaca, and 0.3 mi E Jaltipan, Veracruz). Stomach contents from 3 *G. elegans* (Guatemala: Tikal and 5 mi S Piedras Negras; Honduras: 15 km E La Ceiba) and 2 *G. pictiventris* (Nicaragua: 20 mi above Bluefields; Costa Rica: Puerto Viejo de Sarapiqui) consist exclusively of ants.

## ISOLATING MECHANISMS

Hybridization of *G. olivacea* with *G. carolinensis* (Blair, 1950; Blair, 1955b) demonstrates that premating isolating mechanisms are important in separating sympatric species. Most species are allopatric. Those known to occur in close proximity are *G. usta* and *G. elegans, G. usta* and *G. olivacea,* and *G. olivacea* and *G. carolinensis.* Partial habitat separation occurs in these 3 cases. *G. elegans* occurs mainly in evergreen tropical forests and *G. usta* occurs mainly in open

deciduous woodland. However, Parker (1934) lists both species from Salle's collections at Cordoba. Hardy and McDiarmid (1969) report that where the ranges of *G. usta* and *G. olivacea* overlap they behave as ecological replacements (with *G. olivacea* in more mesic situations) and have not been collected together. *G. olivacea* and *G. carolinensis* frequently occur together (see species recognized), but, *G. carolinensis* is usually found only in the more mesic, forested portions of the zone of sympatry.

The call of *G. usta* has a lower fundamental than those of *G. elegans* and *G. olivacea* (Table 1). (I cannot account for Hardy and McDiarmid's (1969) impression that pitch of *G. usta* calls is higher than *G. olivacea.*) The call of *G. olivacea* is unique in usually having an initial "peep" (see species recognized). The calls of *G. olivacea* and *G. carolinensis* overlap partially in all parameters if variation throughout the geographic ranges are considered but are distinct in the zone of sympatry (Table 2; Awbrey, 1965). Awbrey (1965) confirms Blair's (1955b) hypothesis of reinforcement of call differences in the zone of sympatry. Bogert (1958) notes that 2 series of *G. olivacea* calls from Sonora differ much more markedly in average length than the interspecific differences between *G. olivacea* and *G. carolinensis* in the zone of overlap. I believe, but am unable to demonstrate quantitatively, that differences in call length between *Gastrophryne* choruses are due to variation in the level of excitement of the males and that rainfall, temperatures, size of chorus, dispersion, noise of other species, and disturbance affect excitement. For *Hypopachus variolosus*, I found (Nelson, 1966) differences as great as 2.2 sec (between averages of 5 calls) for males in the same chorus.

Male *G. usta* almost invariably call from concealment under leaves, grass, trash, etc. either at the waters edge or as much as 10 m away; they have never been observed to call while actually in the water (per. obs.; Hardy and McDiarmid, 1969). This contrasts with *G. olivacea* (e.g. Stebbins, 1951; Fitch, 1956a), *G. carolinensis* (Wright, 1932; Anderson, 1954), *G. elegans* (per. obs.), and *G. pictiventris* (Dr. Norman Scott, per. comm.). The four latter species typically call with the body floating free but submerged from the axillae back, the forefeet resting on a stem or other object and the back strongly arched. Wright (1932) provides a photograph of this pose. In large choruses, *G. olivacea* may float free (Stebbins, 1951; per. obs.). However, *G. olivacea* sometimes call from land as a chorus forms (Dr. Robert Martin, per. comm.).

Blair (1950) suggests that differences in body size may act as a partial isolating mechanism in *G. olivacea* and *G. carolinensis* (see species recognized). Comparison of these 2 species (Table 4) with *G. usta* (Table 5), *G. elegans* (7 males range 21.3-25.9 mm, mean 23.6 mm; 4 females at 26.2, 27.0, 27.1, and 28.9 mm), and *G. pictiventris* (17 males range 25.1-30.8 mm, mean 26.8 mm, 8 females 27.3-37.2 mm, mean 32.6 mm) suggest that interspecies differences in average size are less than intraspecific ontogenetic and geographical variation in adult size. Most sympatric or nearly sympatric populations of different species differ by 3 mm or less in mean body length.

Bragg (1950a, c) and Blair (1955b) discuss the possibility that minor differences in breeding season, propensity to breed without rain, and propensity for daytime chorusing may act as "weak" partial isolating mechanisms separating *G. carolinensis* and *G. olivacea.* Fitch (1956a) notes daytime calling in *G. olivacea*, a feature Bragg (1950a) and Blair (1955b) list only for *G. carolinensis. G. usta, G. elegans,* and *G. pictiventris* do call at night after rains.

The principle premating isolating mechanisms appear to be habitat differences, calls, and the unique terrestrial calling behavior of *G. usta.*

## INTERSPECIFIC RELATIONSHIPS

Some evidence is available on intrageneric affinities. The species are similar in both larval and adult feeding adaptations, diets, size, and are essentially allopatric or parapatric. The general picture corresponds to that expected for a group of closely related species.

*G. usta* is set off by having 2 metatarsal tubercles, by the most distinctive call, and by chorusing on land. The first feature is presumably a modification for xeric habitats. The 2 other features might be the result of displacement by interactions with *Hypopachus. G. usta* and

*Hypopachus* are broadly sympatric and commonly chorus together. (Chorusing behavior in *Hypopachus* is similar to the other *Gastrophryne* species; per. obs.).

The remaining divide into 2 pairs of allied species. *G. elegans* and *G. pictiventris* are alike and differ from the other species in the genus in having dilated terminal phalanges on the outer toes and a trace of web and in coloration. Dilated terminal phalanges occur in other frogs that live in tropical forest litter. *G. carolinensis* and *G. olivacea* differ from the latter 2 in having simple terminal phalanges and in lacking webs. The juvenile coloration of *G. olivacea* is reminiscent of that of *G. carolinensis* (Fitch, 1956a). *G. elegans* resembles *G. usta* in having a pigmented abdominal shield (Willem, 1941; Nelson, 1966), but *G. olivacea* and *G. carolinensis* resemble *G. usta* in having simple phalanges and no traces of webs.

*Gastrophryne* existed in North America by the Miocene (Auffenberg, 1956; Holman, 1961). The 3 groups of *Gastrophryne* may have differentiated with the late Tertiary segregation of modern vegetational types or with Pleistocene shifts. Blair (1955b, 1965) suggested *G. olivacea* and *G. carolinensis* might have differentiated in southern refugia during the Pleistocene or, alternatively, as peripheral isolates. Until the Honduranean *G. elegans* was found, *G. elegans* and *G. pictiventris* obviously represented differentiation in 2 similar regions separated by an impassible barrier (the Motagua Valley).

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## APPENDIX I – LOCALITY RECORDS

In order to summarize the records as concisely as possible several conventions are used. Listings in a state (USA) are by county, in other countries by state or department. No punctuation is used within any 1 locality; localities in 1 county from 1 collection are separated by commas; localities in different collections are separated by semicolons. If 1 collection contains several records in 1 county based on the same town, only 1 is listed unless the distance between extremes approximates or exceeds 10 miles. Except for some marginal areas, no additional records are cited for counties for which a locality record has already been published. In citing published records preference is given respectively to summary papers, to exact over county only records, and to the earliest records. The following abbreviations are used for collections: AL—University of Alabama, AM—American Museum of Natural History, AP—Academy of Natural Sciences of Philadelphia, AS—Arizona State University, AU—Auburn University, AZ—University of Arizona, BC—Bryce C. Brown collection, CA—California Academy of Sciences, CZ—Museum of Comparative Zoology of Harvard University, DU—Duke University, EL—Ernest A. Liner collection, FM—Field Museum of Natural History, FS—Florida State University, JM—John S. Mecham collection, JV—Jaime Villa collection, KU—University of Kansas Museum of Natural History, LA—Los Angeles County Museum, LS—Louisiana State University, MS—Mississippi State University, RA—Ronald Altig collection, SC—University of Southern California, SD—Stanford University, SM—University of Southern Mississippi, ST—Strecker Museum of Baylor University, TA—Texas Cooperative Wildlife Collection of Texas Agricultural and Mechanical University, TN—Texas Natural History Collection of the University of Texas, TU—Tulane University, UC—University of California Museum of Vertebrate Zoology, UF—University of Florida, UG—University of Georgia, UI—University of Illinois Natural History Collection, UM—University of Michigan Museum of Zoology, UO—University of Oklahoma, US—United States National Museum, and UU—University of Utah. Dr. Bryce C. Brown kindly provided the records from BC and ST as well as certain other Texas citations (indicated as BB); Mr. Jeffrey Black checked the UO collection; with these exceptions, I have examined most of the specimens listed from all collections except TA, TN, and some groups from KU and UM. A small number of records could not be assigned to a county and were omitted.

### *Gastrophryne carolinensis* (Holbrook)

*ALABAMA.* Löding (1922) records by name only 7 counties of which Cherokee, Etowah, and Saint Clair are not represented by exact records. Brown (1956) cites by name only 21 counties of which Elmore is

not otherwise represented. Additional records: Baldwin (5 mi NE Fairhope, AU; Point Clear, 5 mi S Spanish Fort, AL), Calhoun (Fort McClellan, AM), Chambers (13 mi NNE Auburn, Lafayette, AL), Choctaw (2.5 mi S Butler, AL), Clark (6 mi S Jackson, UM; near Thomasville, AL), Clay (3.5 mi NW Ashland, UM), Coffee (.5 mi W Choctawatchee River, AL), Conecuh (2 mi E Evergreen, MS), Cullman (Burt, 1938b), Escambia (1.5 mi NW Brewton, 8 mi SW Brewton, AL), Geneva (Geneva, AL), Houston (6.5 mi S Columbia, just S Gordon, AU; near Dothan, Pansey, AL), Jackson (6 mi SW Bridgeport, Stevenson, AM; 2 mi S Scottsboro, AL), Jefferson (Holman, 1961), Lawrence (Imboden, US), Lee (Auburn, US; 9 mi W Auburn, 7 to 10 mi S Auburn, AU), Macon (Wright, 1932), Marengo (5 mi N Linden, Hackelburg, AL), Montgomery (Holt, 1924), Mobile (Strecker, 1909), Shelby (Holt, 1924), Talladega (Talladega, Horne's Pond, Howell's Cove, UM), Tuscaloosa (1 mi E Holt, UM; Tuskaloosa, AL, UF), and Walker (Pumpkin Center, AL).

*ARKANSAS.* Black and Dellinger (1938) cite localities for 10 counties (Clay, Garland, Green, Lafayette, Lawrence, Montgomery, Monroe, Prairie, Pulaski, and White). Burt (1936) cites localities in 5 more (Craighead, Dallas, Grant, Nevada, and Washington). Dowling (1957) adds county only records for 4 others (Chicot, Franklin, Jefferson and Madison). To these add: Arkansas (5 mi S Crockett's Bluff, TA), Clark (Arkadelphia, US; 11 mi NW Arkadelphia, UM), Conaway (Morrilton, UO), Crawford (Bragg, 1946), Drew (Montecello, FM), Fulton (near Mammoth Springs, FM), Howard (Ortenburger, 1929), Lonoke (25 mi E Little Rock, Black and Dellinger, 1938, as Pulaski Co.), Pike (Delight, FM), and Scott (15 mi W Waldron, UF).

*FLORIDA.* Carr (1940) provides an exact locality for Hernando and county only records for 26 others; of these, no exact record is available for Okaloosa. Duellman and Schwartz (1958) cite exact records for 4 counties in southern Florida (Broward, Collier, Dade, and Monroe). Additional records: Alachua (Strecker, 1909), Bay (near Callaway, UM), Brevard (Canaveral, AM), Calhoun (8.2 mi W Blountstown, UM; ¼ mi S ¼ mi E Kinard, UF), Charlotte (Bogert, 1958), Citrus (2 mi N Crystal River, 17.6 mi S Crystal River, TU; 1 mi E Invernis, UM), Dixie (2 mi N Suwannee, UF), Duval (Deckert, 1914), Escambia (Parker, 1934), Franklin (3.5 mi E Carrabelle, UF), Gadsden (Chattahoochee, AM, UF), Glades (Moore Haven, AM; mouth Apilachicola River, UM), Gulf (1 mi WNW Port Saint Joe, UF), Hamilton (4 mi NE White Springs, UM), Highlands (Bogert, 1954), Hillsboro (Bokermann, 1952), Holmes (2.5 mi E Ponce de Leon, UF; 2 mi WNW Ponce de Leon, TA), Indian River (Sebastian, CZ), Jackson (Butler's Landing, UF; 5 mi S Grand Ridge, TU; 7 mi S Marianna, TU; 3 mi SE Marianna, UF; 1.5 mi W Cambelton, AU; Florida Caverns State Park, FS; 3 mi NW Sneads, UF), Jefferson (6.5 mi W Monticello, UM), Lafayette (Mayo, AM), Lake (Alexander's Spring Creek, UF), Lee (Fort Myers, UM, US; 10 mi W Fort Myers, AM), Leon (6 mi W Normangee, 2.5 mi N .5 mi W Woodville, UF; Ochlochee River, AM; 2 mi E Tallahassee, TN), Levy (Cedar Key, TN), Liberty (.5 mi W Bristol, 13 mi S 5 mi W Bristol, 5 mi N 8 mi W Sumatra, Torreya State Park, UF; near Lake Mistic, 5 mi SW Rock Bluff, UM), Madison (Suwannee River NW of Falmouth, UM), Marion (Bogert, 1958), Nassau (near Anderson, UM), Osceola (E of Deer Park, Macoa Island, CZ), Okeechobee (Okeechobee, AM; mouth of Kissimmee River, TN), Orange (Dickerson, 1906), Palm Beach (Jupiter, 4 mi N 2 mi W of West Palm Beach, UF; Palm Beach, AP), Pinellas (Brimley, 1910), Polk (Telford, 1952), Putnam (Blair, 1955b), Saint Lucie (Fort Pierce, UM), Santa Rosa and Sarasota and Seminole (all 3, Strecker, 1909), Sumter (3 mi NW Panasoffkee, TN), Suwannee (Branford, KU), Taylor (Perry, UM; 4.5 mi W Perry, UF), Union (near Duke, UF), Volusia (15 mi W Daytona Beach, LS; N Ormind Beach, AL), Enterprise, AP), Walton (16 mi W Sweet Gum Head, UF), and Wakulla (Goose Creek, AM; Natural Bridge, Sopchoppy, FS; Saint Marks National Wildlife Refuge, TA), and Washington (Caryville, TA).

*GEORGIA.* Baker (2 mi S Baker, 1 mi W Newton, 3 mi W Newton, UG; 1 mi E Emory Field Station, near mouth of Ichawaynochaway Creek, UM), Bartow (near Emerson, US), Benhill (2 mi SW Fitzgerald, DU), Bleckley (Co. only, Brandt, 1953; Cochran, DU), Brantley (near Hoboken, near Lulaton, US; 1 mi E Waynesville, UM), Bryan (near Way's Station, UM), Burke (Mittleman, 1950), Calhoun (2.5 mi W Leary, UM), Camden (.5 mi S White Oak, UF), Charlton (Wright, 1932), Chatham (Savannah, AL; Tybee Island, AM), Chattahoochee (Co. only, Carter, 1934; 10 mi SE Columbus, MS; Fort Benning, US), Cherokee (5 mi W Canton, UG), Clarke (Athens, Kirota, Whitehall, UG), Clay (5 mi N Fort Gaines, AU), Decatur (Lake Decatur, US; 3 mi N US 90 on Ga 97, UF), Dooly (near Vienna, US), Early (6.5 mi W Blakely, UM), Echols (Howell, AM), Emanuel (1.5 mi S Midville, UC; McKinney's pond near Midville, UC, UG), Floyd (near Rome, US), Fulton (Carter, 1934), Glynn (Co. only, Carter, 1934; near Brunswick, US; 5 mi S Darien, UG), Green (Watson Springs, UG), Harris (Hamilton, UG), Irwin (6 mi NW Ocilla, and near Osierfield, UG), Jeff Davis (Hazelhurst, CA; 1 mi S Hazelhurst, TA; 1.5 mi W Hazelhurst, KU), Jenkins (Miller National Fish Hatchery, TA), Liberty (Strecker, 1909), Lincoln (near Lincolnton, US), Lowndes (near Valdesta, US), McIntosh (near Eulonia, US; Sapelo Island, KU, UG), Miller (1.5 mi S Baker Co. line, UM; 3 mi E Colquit, UF), Muscogee (Strecker, 1909), Richmond (Augusta, UG), Seminole (Sealy Spring, UF), Stephens (Ayersville, UG), Taylor (Mauk, UG), Telfair (3.5 mi E Jacksonville), Thomas (Thomasville, AM; 10 mi SE Thomasville, UG), Ware (Wright, 1932), Wayne (Wright, 1932), and Wilcox (2 mi SE Bowen thus probably in Ben Hill Co., TU).

*ILLINOIS.* Smith (1948, 1961) cites localities in Monroe and Randolph (also TA).

*IOWA.* Klimstra's record (1950a,b) for Davis remains unique.

*KANSAS.* Smith (1947a) reports one specimen from Cherokee (also KU).

*KENTUCKY.* Breckenridge (Hirschfield and Collins, 1963), Edmundson (KU), Pulaski and Warren (Barbour, 1946).

*LOUISIANA.* Burt (1936) cites localities in 7 parishes (Calcasieu, Concordia, Lafourche, Lincoln, St. Charles, St. Mary, and West Feliciana). Additional records: Allen (1 mi W Kinder, TA; 2 mi W Oakdale, UF; 4 mi W Oberlin, 3 mi E Oberlin, TU), Arcadia (near Evangeline, UF), Ascension (20 mi SSE Baton Rouge, 0.5 mi ENE Hope Villa, LS), Assumption (5 mi W Paincourtville, TU), Beauregard (De Ridder Airport, LS; 4.4 mi W Merryville, TU), Bossier (Ninock, TU), Caddo (4 mi SW Rodessa, 3 mi N Vivian, TU), Caldwell (4 mi N Columbia, 2.5 mi S Columbia, TU), Cameron (Neil, 1959), Catahoula (4 mi N Harrisonburg, TU), Claiborne (Carney Lake near Summerfield, TU), De Soto (Frierson, US), East Baton Rouge (Baton Rouge, AM, LS; 12 mi N Baton Rouge, 3 mi NW Grenwell Springs, 3 mi N Zachary, LS), East Feliciana (20 mi N Baton Rouge, 6 mi S Clinton, LS), Evangeline (Chilcot State Park, near Pine Prairie, TU; 3 mi N Eunice, UF), Grant (Fishville, Pollock, TU), Iberia (Avery Island, CA), Iberville (20 mi S Baton Rouge, LS; Rosdale, TU), Jackson (Walker, 1963), Jefferson (Bohon, Grand Isle, Lafitte, 1 mi N Metaire Pumping Station, TU; vicinity of Westwego, UC), Lafayette (Liner, 1956), Livingston (3.4 mi NE Port Vincent, SM), Madison (Delta, TU), Morehouse (5 mi E Bastrop, 8 mi E Mer Rouge, TU), Natchitoches (Kisatchie, TU), Orleans (Wright, 1932), Ouachita (Monroe, TA, TU), Plaquemines (3 mi SE Irontown, UM; Delta Wildlife Refuge, Lake Hermitage, TU), Pointe Coupee (Jacoby, 4.4 mi S Jacoby, New Roads, TU), Rapides (near Alexandria and Red River city limit, UF; about 7 mi SE Pineville, LS), Richland (Alto, TU), St. Bernard (Chalmette, TN; Shell Beach, TU), St. James (Gramercy, UM; Lutcher, TU), St. Landry (Fouquette, 1966), St. Martin (Henderson Leevee, Lake Martin, UF), St. Tammany (Strecker, 1909), Tangipahoa (1 mi E Amite, 8.9 mi N Flaker, TU; 1 mi NW Ponchatoula, UM), Terrebone (Liner, 1954, parish only; Chauvin, 9 mi SE Dulas, 3 mi SE Houma, TU), Union (Marion, Oakland, TU), Vermilion (Univ. Southern La. Field Station, UF), Vernon (4 mi SE Essa, TU; 15 mi S Evans, KU; 4.5 mi N Cravens, 5 mi S Leander, 7.6 mi E of South Fort Polk, TA), and Washington (Angie, TU; Bogalusa, UF, TU).

*MARYLAND.* Dorchester (Conant, 1958), Calvert (Noble and Hassler, 1936), and Saint Mary's (Fowler and Stine, 1953).

*MISSISSIPPI.* Smith and List (1955) cite locations in 4 counties (Jackson, Pearl River, Stone, and Tallahatchie). Additional records: Attala (about 15 mi N Koscinko, MS), Carroll (.5 mi N Teoc, MS), Chickasaw (1 mi W Houston, US), Choctaw (1 mi E Weir, MS), Coahoma (6 mi N Clarksdale, UM), Copiah (Hazlehurst, LS; 4 mi E Hazlehurst, SM), Forrest (6 mi N Hattiesburg, LS; 2 mi N Hattiesburg, 12 mi S Hattiesburg, 3 mi SE Petal, SM), George (10 mi W Lucedale, TU), Greene (16 mi NW Lucedale, TU), Hancock (Brimley, 1910), Harrison (Corrington, 1927), Hinds (Jackson, MS), Itawamba (6 mi NE Mantachie, MS; near Tremont, US), Jasper (7 mi SW Bay Springs, Louin, SM), Jones (about 8 mi N Laurel, MS), Lafayette (Potter, 1920), Lamar (6.5 mi NW Hattiesburg, 8 mi W Hattiesburg, 3 mi SW Hattiesburg, 12 mi W Purvis, SM), Lauderdale (2 mi E Meridian, 5 mi S Meridian, MS; 8 mi W Meridian, UM, US), Lee (Co. only, AM), Marion (1.5 mi E Cheraw, TU), Neshoba (6 mi N Philadelphia, US), Newton (about 1 mi SE Decatur, MS; 1 mi N Doolittle, US), Noxubee (Brooksville, CA, CZ, UM; Buff Lake, Green Timber Reservation No. 1, MS), Oktibbeha (Starkville, MS, US; 18 mi S Starkville, 1,100 yds N Buff Lake Spillway, MS), Perry (3 mi E New Agusta, 1 mi S Richton, SM), Pontotoc (7 mi N Gershorn, US), Rankin (4 mi NW Florence, 2 mi S Florence, SM), Tishomingo (Iuka, UM), Warren (Vicksburg, US), Washington (Co. only, US), Webster (3 mi SW Tommolen, US), and Yazoo (near Holly Bluff, UM).

*MISSOURI.* Barry (Co. only, Hecht and Matalas, 1946; 4 mi W Exeter, UM), Butler (Co. only Hurter, 1897; 7 mi W Poplar Bluff, KU), Dunklin (3 mi NW Campbell, KU), Green (6 mi NW Springfield, KU), New Madrid (Co. only, Hurter (1897); 12 mi NE Portageville, KU), Oregon (Calm, KU), Miller (Wright Cave at 2.2 mi W Brimley, KU), Ripley (Doniphan, KU), Saint Louis (Cliff Cave, Hurter, 1893; Saint Louis, CZ), Stone (near Fairy Cave; KU), Wayne (Co. only, Smith, 1961), Webster (12 mi E Springfield, KU), and Wright (SE Mansfield at private airfield, KU).

*NORTH CAROLINA.* Brimley (1939) cites 13 counties by name only; exact records are available for all except Beaufort, Cumberland, Hyde, and Polk. Other records: Bladen (3 mi N Bladenboro, 1 mi NW Council, 3.6 mi W Elizabethtown, White Lake, DU), Brunswick (1 mi W Bolivia; 3 mi S Supply, DU; Smith Island, Southport, AP), Camden (2 mi S of South Mills; AM), Carteret (Robertson and Tyson, 1950), Chatham (9 mi S Pittsboro, DU), Chowan (1 mi S St. Johns, DU; Edenton, US), Columbus (3-8 mi S Hallsboro, ¼ mi N Lake Waccamaw, DU; Lake Waccamaw, AP, US), Craven (4 mi E Dover, US), Dare (Nemuras, 1967), Durham (Durham, DU; New Hope Creek, US), Gaston (2 mi SE Stanley, DU), Gates (Carr and Goin, 1955), Halifax (Ryder, 1891), Hyde (vicinity of New Holland, UM), Johnson (2.5 mi E Angier, DU), Moore (Gosner and Black, 1956), Nash (2.3 mi S Spring Hope, DU), New Hanover, (Myers, 1924), Onslow (Fort Davis, UM; .5 mi NE Holly Ridge, about 9 mi N Holly Ridge, 3 mi WSW Verona, DU), Orange (6 mi SE Hillsboro, DU), Pamlico (Bayboro, Stonewall, US), Pender (5 mi SW Onslow Co. line, DU; 5-7 mi SW Onslow Co. line on US 117, FM), Perquiman (Delight-Nexon crossroads, AP), Pitt (Robertson and Tyson,

1950), Robeson (Maxton, AM, US), Scotland (3 mi S Hoffman, UG), Wake (Brimley, 1896), Washington (5 mi NW Cresswell, north shore Phelps Lake, DU), and Wayne (Goldsboro, CZ).

*OKLAHOMA.* Adair (Bragg and Dundee, 1950), Cherokee (Blair, 1950), Delaware (Ortenberger, 1929), Latimer (6 mi S Wilburton, near Talihina, UO), Le Flore (Bragg, 1950d; Cavanal Mountain at 2300 feet, Blair, per. comm.), Mayes (Blair, 1952), McCurtain (Burger, Smith and Smith, 1949), Okmulgee (Co. only, UM), Osage (N of Sand Spring, UM), Ottawa (2.5 mi S Peoria, KU; 3 mi S Wyandotte, AM), Pushmataha (2 mi W Albion, 7 mi SE Clayton, 2 mi W Kiamichi, TN), Rogers (Co. only, AM), Sequoyah (5 mi W Sallisaw, AM), Tulsa (Force, 1930), and Wagoner (Blair and Laughlin, 1955).

*SOUTH CAROLINA.* Aiken (2 mi S Beech Island, Jackson; UG), Barnwell (near Ellenton, UG), Beaufort (near Hardeeville, US), Berkley (16 to 18 mi NNE Charleston, UM), Charleston (type locality), Claredon (4 mi NE Santee on E shore Lake Marion, UF), Dorchester (23 mi NW Charleston, UM; 6 mi SW Somerville, DU; Beveris Backwater, UM), Georgetown (Arcadia Plantation, DU; Brookgreen Gardens at 3.5 mi SW Murrell's Inlet, UM), Horry (Obrecht, 1946), Jasper (Mittleman, 1950), Lee (6 mi SW Bishopville, UF), Lexington (Leesville, US), Richland (Corrington, 1929), and Saluda (Murray Lake, US).

*TENNESSEE.* Gentry (1955) lists 13 counties by name only; of these, no exact record is available for Benton, Campbell, Caroll, Coffee, Davidson, Dickson, Hardman, Henderson, and Humphreys. Other records: Anderson (Noris; UM), Blount (Wood, 1948), Chester (Endsley, 1954), Decatur (Co. only, KU), Henry (Blancard, 1922), Hamilton (Rhodes, 1896), Meigs (13 mi at 11° W of N from Decatur at 800 ft, UF), Marion (8 mi NW of South Pittsburg, AM), McMinn (Harper, 1935), Shelby (Rhodes, 1896), Sullivan (Bailey, 1936), and county unspecified (Tennessee side of Great Smokies National Park, Brimley, 1939).

*TEXAS.* Brown (1950) cites localities in 15 counties (Austin, Bowie, Brazos, Galveston, Harris, Hardin, Houston, Jefferson, Lamar, Leon, Liberty, Matagordo, Montgomery, Polk, Victoria) and a county only record for Walker. Smith and Saunders (1952) add records for Cass, Henderson, Orange, Refugio, and Tyler. Additional records: Anderson (10 mi SE Palestine, ST; Engling Wildlife Management Area, TA), Angelina (Hanks Creek Marina on Sam Rayborn Reservoir, 8 mi NW Lufkin, BB), Bastrop (2 mi SW Smithville, TA), Brazoria (Daneigen, 4 mi W Rosharon, BC; Lost Lake near Lake Jackson, UM; 2 mi N of West Columbia, TA), Burleson (4.9 mi SE junction farm roads 50 and 60, TN), Calhoun (Indianola, 2 mi E Port Comfort, ST; 11 mi SW Port Lavaca, TN; 14 mi W Port Lavaca, KU), Cameron (Brownsville, AM), Chambers (between Hankamer and Monroe City, 8 mi NE Wallisville, BC), Cherokee (Reklaw, TN), Colorado (SW of Eagle Lake, TA), Cook (2 mi S Bulcher City, TA), Dallas (Blair, 1955b), Falls (Co. only, Strecker, 1909; 1.5 mi N Durango, TA), Freestone (20 mi E Dew, 8 mi E Teague, ST), Gonzales (Blair, 1955b), Gregg (creek on A. Jackson farm, LA; 1 mi N junction Kilgore hwy and farm to market 1252, TA), Harrison (Caddo Lake, ST; Caddo Lake State Park near Karnak, TN; 15 mi N Marshall, BC), Jackson (7 mi S Ganado, TN; 1.5 mi E Lolita, TA; 4 mi S Lolita, BC), Jasper (E of Angelina River on hwy 63, 12 mi WSW Jasper, TA), Kerr (Kerr Wildlife Area, TA); McLennon (Strecker, 1908c), Madison (9.7 mi S Midway, TN; Normangee Lake, TA), Morris (1 mi N Douglasville, ST), Newton (15 mi NE Buna, TN; 1 mi E Burr Ferry, ST), Red River (6 mi S Boxelder; 5 mi S Lydia, ST), Refugio (Strecker, 1908a), Robertson (9.3 mi SSE New Baden at Southworth Bog, TA), Sabine (12 mi S Hemphill, ST), San Jacinto (3 mi S Cold Springs, 0.1 mi S Sheppard, ST; 3 mi N Evergreen, 10 mi E New Waverly, TA), Shelby (Burt, 1938), Tarrant (Lake Worth, Lake Tyler Dam, BB), Upshur (6 mi NW Harleton, BC; 3 mi SW Pritchett, ST), Walker (10 mi NW Huntsville, 11 mi NW New Waverly, TN; 15 mi WSW Huntsville, 10 mi E Huntsville, TA), Washington (8 mi E Brenham, TA), Wharton (5.8 mi SE Wharton, TN), Williamson (Roundrock, BB), and Wood (4.8 mi SE Quitman, TA).

*VIRGINIA.* Appomattox (Pamplin, US), Caroline (Dunn, 1918), Hanover (Wright, 1932), Chesterfield (Wright, 1932), Isle of Wright (6 mi NE Walters, 3 mi SW Windsor, US), Lancaster (Morattico, AM), Lee (Fowler and Hoffman, 1951), Nasemond (near Cypress Chapel, US), Nelson (Midway Mills, AP), Northhampton (Dickerson, 1906; 2 mi W Eastville, LA), Princess Anne (Co. only, Neil (1959), voice at Norfolk, LeConte (1856); Virginia Beach, between Sigma and Sand Bridge, US), and York (Yorktown, US).

*Gastrophryne elegans* (Boulenger)

*MEXICO.* VERACRUZ: Cordoba at 924 m (type locality), Motzorongo at 1500 ft (Gadow, 1905), Presidio at 1500 ft (Gadow, 1905; Parker, 1934), 6 mi E Tihuatlan (Reese, 1953), and CAMPECHE: Becan (Smith, 1938), Tres Brazos (Smith, 1938), 20 km N Xpujil (KU, Duellman, 1965, as Xpujil). A tadpole which may be of this species is from 2.6 mi E Tolome, Veracruz (Nelson and Altig, in press).

*GUATEMALA.* EL PETEN: 5 mi S Piedras Negras (Taylor and Smith, 1945), Tikal (Stuart, 1958), near Yaxha (UM), 12 mi E Yaxha (Stuart, 1934) and ALTA VERAPAZ: 28.3 km NE Campur at 260 m (Duellman, 1963), 8.2 mi S Sebol (TN).

*HONDURAS.* ATLANTIDA: about 15 km E La Ceiba at Corozal (LA).

*Gastrophryne pictiventirs* (Cope)

*NICARAGUA.* "Nicaragua" (type locality, Cope, 1886), and ZELAYA: 50 mi above Bluefields on Rio Escondido (Dunn, Trapido, and Evans, 1948).

*COSTA RICA.* LIMÓN: Cariari (LS) and Tortuguero (UF), and HEREDIA: the Río Reventazón (Dunn, Trapido and Evans, 1948), Puerto Viejo de Sarapiquí at about 100 m (JV, UM), and 1.5 mi S Puerto Viejo at Finca La Selva (SC).

*Gastrophryne olivacea* (Hallowell)

*ARIZONA.* Wake (1961) summarizes records for Santa Cruz and reports 2 localities in Pima County. Additional records are Pima (near Robles, 30 mi W Tucson, near Tracy's Trading Post, AZ) and Pinal (24.4 mi S Casa Grande, UC).

*ARKANSAS.* Bragg's (1946, 1950a) citation of *G. olivacea* from Fort Smith, Sebastian Co., is the only previous record for Arkansas. New records are: Montgomery (6 mi NW Langley, KU) and Sebastian (Van Buren, UO). (I have not examined the KU specimen as it is momentarily misplaced, but have examined the UO series).

*KANSAS.* Smith (1956) includes a map with records plotted for 27 counties (Anderson, Barber, Bourbon as Co. only, Chatauqua, Chase, Cherokee, Clark, Cowley, Doniphan, Douglas, Ellis, Ellsworth, Geary, Greenwood, Harper, Jefferson, Jewell, Leavenworth, Lyon, Meade, Montgomery, Pottawatomie as Co. only, Riley, Rush, Saline, Washington, and Wilson); he also (1934, 1950, 1956) gives exact localities in many of these. Additional records: Labbette (12 mi N Oswego, KU; Labbette, US), Marshall (2 mi S Irving, KU), Pottawatomie (6.5 mi S 3 mi E Garrison, 2.5 mi E and 13 mi S Olsburg, 1.5 mi N Tuttle Creek Dam, KU; near Rocky Ford Power Plant, US), Shawnee (5 mi E Topeka (KU), Wayandotte (Clark, 1956), and Woodson (Toronto, UM).

*MISSOURI.* Anderson (1942) reports localities in Cass, Jackson and Platt counties. Additional records: Bates (Amsterdam, KU), Boone (Metter, Morris, and Kangas, 1970), Buchanan (¼ mi E Saint Joseph city limits, FM), Clinton (Lilly, KU), Johnson (35 mi SW Blue Spring, KU), and additional localities (KU) in Jackson and Platt.

*NEBRASKA.* Loomis (1945, Gage Co.) is the only record.

*OKLAHOMA.* Published records for *Gastrophryne* are mostly by the late Dr. Arthur N. Bragg. His early papers reflect uncertainty as to the forms present; he assigned all Oklahoma records to *G. olivacea* (Bragg, 1943), but clearly differentiated 2 species (Bragg, 1946). A comparison of his recent papers (1946, 1950b, d) with the earlier ones allows the assignment of his records (1941, 1943, 1946, 1950b, 1951; Bragg and Dundee, 1950, 1951; Bragg and Hudson, 1951) as follows: *G. carolinensis* alone from 3 eastern counties (Delaware, Le Flore, McCurtain), both species from 3 counties (Adair, Cherokee, and Latimer), and *G. olivacea* alone by exact localities in Cleveland Co. and county only records for 33 other counties of which 9 are not otherwise represented: Adair, Atoka, Canadian (voice), Kiowa, Harper, Lincoln, Major, and Okmulgee. Additional records: Blaine (2.4 mi S Greenfield, FM, UO), Beckham (0.1 mi N jct US 238 with US 66, UO), Bryan (¼ mi N Colbert, TN), Caddo (old Fort Cobb, US), Carter (6 mi N Ardmore, KU), Cherokee (Bragg 1950b), Choctaw (11 mi W Fort Towson, 2¼ mi W Soper, UO), Coal (2 mi E Centrahoma, UO), Commanchee (Lawton, UO), Cotton (1 mi W Temple City Lake, UO), Creek (extreme NE corner of county, UO), Delaware (6 mi NW Grove, UO), Hughes (5 mi E McAlester, UO; 10 mi E Wetmore), Kay (Burt, 1936), Jackson (Duke, UO; 7 mi E El Dorado, UO), Jefferson (Mud Creek, SW of Waurika, 10.7 mi N Ringling, UO), Johnson (4 mi W Bromide, UO), Harper (Doby Springs, UM), Lattimer (near Wilburton, UO), LeFlore (Wistar Reservoir, UO), Logan (NW part of county, UO), Love (3 mi N Marietta, FM), Marshall (Carpenter, 1956), Mayes (Blair, 1950), McClain (near Payne Center, UM; S of Purcell, UO), Murray (5.5 mi NE Beswyn, 2 mi S Hennepin, near Prince's Falls, 8 mi S Sulfur, UO), Muskogee (1 mi N Braggs, AM), Oklahoma (Oklahoma City, SD), Osage (15 mi W Pawhuska, NW edge Tulsa, UO; N Sand Spring, UM; 5 mi W Turkey, AM), Payne (Cimarron River, FM; Lake Blackwell, UO), Pittsburg (McAlester, 10 mi W McAlester, UO), Pontotec (Carter and Cox, 1968, Co. only; Byrd's Mill W of Fittstown, 8 mi E Stratford, UO), Pottawatomie (24 mi E Norman, UO), Rogers (Garnett, UM; 2 mi N Tiawah, AM), Stephens (¼ mi S Duncan, UO), Tillman (7 mi S Snyder, 1 to 2 mi N jct Okla 5 and Okla 36, UO), Tulsa (vicinity of Dawson, 2 mi N Garnett, TN; Mingo Creek, UM; Parthenia, FM, UM; Tulsa, UM; 5 mi SW Tulsa, AM; 9 mi SE Tulsa, UO), Waggoner (4 mi S Catoosa, KU) and Washington (Bartlesville, KU).

*TEXAS.* Brown (1950) cites localities in 36 counties (Atascosa, Austin, Bee, Bexar, Bosque, Brazos, Burnet, Cameron, Colorado, Comal, Dallas, Denton, Duval, Frio, Gillespie, Goliad, Gonzales, Hays, Hidalgo, LaSalle, Leone, Live Oak, McLennon, Matagordo, Milam, Nueces, Palo Pinto, Starr, Tarrant, Tom Green,

Travis, Webb, Wharton, Welbarger, Williamson, and Zapata) and inexact citations for Medina, Val Verde, and Victoria. Smith and Sanders (1952) add citations for Coleman (as Brown), Fayette, Grimes, Hamilton, Mason and McCulloch. Additional records are: Anderson (2 mi W Cayuga, ST; Engling Wildlife Management Area, TA), Aransas (Aransas Refuge, TA; Rockport, UM), Archer (9 mi N Archer City, 3 mi N Windhurst, BB), Bandera (8 mi W Medina, KU), Bastrop (Burt, 1938), Bell (7 mi S Kileen, TN; 13 SW Kileen, 1.5 mi N Troy, ST; 6 mi E Temple, TA), Brewster (Axtell, 1959; Minton, 1960), Burleson (10 mi SE Bryan, 4.9 mi N Clay Station, 2.3 mi NE Lyons, TN; 2 mi NW Birch, Caldwell, 12 mi E Caldwell, 3 mi E Lyons, TA), Caldwell (Henderson, 1961), Calhoun (Indianola, Magnolia Beach, BC), Callahan (Cross Plains, BB), Cass (3 mi S Douglasville, BB), Chambers (beach highway 87, BB), Clay (2 mi S Vashti, UM), Coke (12 mi N jct 208 and 2105, BB), Coleman (Burt, 1938), Concho (6 mi E Eola, KU), Cooke (13.5 mi N Muenster, TA), Coryell (Jones Ranch, ST), Cottle (9 mi N Paducah, TA), Crosby (3 mi NW Kalgary, below White River Lake Dam, BB), Dawson (10 mi E Lamesa, TA), Dewitt (16.4 mi SE Cuero, TN; 5 mi S Yoakum, TA), Dimmit (8.7 mi NE Catarina, 2.3 mi SW Valley Wells, TN), Eastland (3 mi N Ranger, TA), Erath (Burt, 1938), Falls (Strecker, 1909), Fisher (14 mi S Hamlin, BB), Fort Bend (1 mi W Julitt, ST), Franklin (2 mi W Mt. Vernon, 9.3 mi N Mt. Vernon, UO), Freestone (9 mi W Teague, ST), Garza (Tinkle and Knopf, 1964), Harris (1 mi S Addicks, TN; ¼ mi N Almeda Plain, TA; 5.5 mi E Huesmith, BC; Simmons Bayou in Houston, ST), Hill (Lake Whitney near Whitney, UM), Houston (2.7 mi S Kennard, ST), Hunt (2 mi SW Greenville, UO), Irion (10 mi W Mertzon, BB), Jackson (7 mi S Ganado, TN; Lolita, TA; 18 mi NE Victoria, TN), Jim Wells (Alice, UO; 5 mi N Premont, 2 mi SE Sandia, TN), Jeff Davis (Hecht and Matalas, 1946), Karnes (3 mi S Gillett, TN), Kaufman (18 mi SSE Dallas, BB), Kenedy (3 mi S Mifflin, 2 mi S Sarita, BB), Kerr (Kerr Wildlife Area at 15 mi W Hunt, 2 mi W Kerrville, TA), Kimble (Paint Creek Ranch, ST), Kleburg (Kingsville, ST), Lamar (19 mi NW Detroit, ST), Lampassas (12 mi SW Lampassas, ST), Lavaca (8 mi S Halletsville, BC), Limestone (3 mi E Mart, ST), Lubbock (Tinkle and Knopf, 1964), Llano (W. J. Williams Ranch, TA), Madison (Furgerson crossing, TA; 3 mi S Midway, 9 mi N Midway, TN), Medina (2 mi N D'Hanis, 12 mi NNW D'Hanis, UC), Menard (Fort McKavett, KU), Mills (2.3 mi S Goldthwaite, 6 mi W Priddy, ST), Mitchell (7 mi NW Silver, TN), Montague (8 mi S St. Jo, BB), Montgomery (3.9 mi E Montgomery, TN), Morris (1 mi N Douglasville, BC), Nacogdoches (13 mi S Nacogdoches, TA), Navarro (3 mi W Kernes, BC), Parker (0.5 mi W Aledo High School, TA; 4 mi NE Springton, ST; Tin Top, UM; 2½ SW Tin Top, BC), Pecos (10.2 mi down Hovey road from US 67, TA), Polk (4 mi E Livingston, BB), Presidio (.5 mi SE Presidio, 11 mi W Valentine, TN), Red River (8 mi SW Boxelder, 5 mi S Lydia, ST; 4.5 mi N Clarksville, TN), Refugio (.5 mi N Woodsboro, TA; Woodshore, CA), Reeves (29 mi N Pecos, TN), Robertson (Burt, 1938), Runnels (1 mi S Winters, UO), San Jacinto (13 mi W Coldsprings, TN), San Patricio (Mathis, TN; 9 mi NE Sinton, Welder Wildlife Refuge near Sinton, TA), San Saba (3 mi W Bend, BB), Shakleford (17 mi NE Al Grey, BC; Matthews Ranch, BC, TN), Taylor (Abilene, AL; 11 mi S Abilene, BC), Terrell (Milstead, Mecham and McClintlock, 1950, as northern part of Co.; 13 mi S Sheffield, TN), Throckmorton (19 mi NW Albany, KU; Matthews Ranch, ST; 20 mi SW Throckmorton, TN), Trinity (2 mi SW Trinity, TA), Tyler (4 mi E Livingston, TA), Uvalde (New Concan, ST; 3 mi N Sabinal, Uvalde, TN), Victoria (Burt, 1938), Walker (10 mi NE Huntsville, TN, AS), Waller (1 mi W Waller, 15 mi W Waller, TA), Washington (US 290, Burton, JM; 3 mi SW Burton, 7 mi NW Burton, TA; 16 mi NE Brenham, TN), Wichita (Wichita Falls, KU; 5 mi NE Wichita Falls, KU), Willacy (Raymondville, UM), Wilson (Floresville, SD), Young (9.1 mi W New Castle, BB), and Zavala (4 mi S Batesville, 6 mi N Batesville, and 6 mi S La Pryor, TN).

*MÉXICO.* TAMAULIPAS: 5 mi E Ciudad Victoria (KU); 4 km W San Gerado (Martin, 1958); 2 mi NE Xicoténcatl (Martin, 1958); 3.6 mi W Xicoténcatl (UM); 2 mi E Villa Juárez (now Ciudad Mante) (Chrapliwy, Williams, and Smith, 1961); 3 mi E jct Mex 80 and Mex 85 (near Ciudad Mante) (TN); Magicatzin (TA); Río Guayalejo, 20 mi E Ciudad Mante (KU); 30 mi ESE Ciudad Mante (JM); 12 mi S Ciudad Mante (TN); 2.6 mi NW Altamira (EL); and 6.1 mi NW Tampico (EL); SAN LUIS POTOSÍ: 1 km E El Naranjo (EL); near Río Naranjo (Martin, 1958); and N Ciudad Valle (Chrapliwy, 1956); NUEVO LEON: 2 mi SE Sabinas Hidalgo (AM); near Sabinas Hidalgo (FM); near Monterey (FM); El Ayancual near Monterey (Maldonado-Koerdell, 1949); and 8 mi S Monterey (AM); COAHUILA: 26 mi S Allende (Chrapliwy, 1956); near Musquiz (Schmidt and Owens, 1944); 2-3 mi E Torreón (Taylor, 1940); and Las Margaritas at 2900 ft (KU); CHIHUAHUA: Chrapliwy, Williams, and Smith (1961) report 5 localities, other records: Río Santa Maria near Progresso (Taylor and Smith, 1945); Río Conchos near Beneficio (Smith, Williams and Moll, 1963); and Chihuahua (city; Firschein, 1950); DURANGO: to the 3 localities Webb (1960) summarizes add: Río Nazas 10 mi NNW Rodeo (UU); SONORA: to the 9 localities Wake (1961) summarizes, add: 2.3 mi S Magdalena (AZ); 9.4 mi E Huasabas (AZ); 15 mi N Hermosillo (AM); Río Sonora at 1st crossing by Hwy 15 S of Hermosillo (AZ); 17 mi W Hermosillo (Bogert, 1962); 20 mi W Hermosillo (AZ); 28 mi E Hermosillo (AM); 20 to 50 km E Kino (Hardy and McDiarmid, 1969); 25 mi E Mazatan (AM); San Carlos Bay at 9 mi W Guymas (AZ); 5 mi E Navojoa (UC, KU); La Aduana (AZ); and about 15 mi W Jct Mex 15 and Mex 16 (AZ). SINALOA: Hardy and McDiarmid (1969) lists specimens from 16 localities and cite reports of 5 additional localities, all below 250 m, to these add: 41 mi S Navojoa (AZ); 18.4 mi W Los Mochis jct (AZ); 7.9 mi NW Los Mochis jct (AZ); Rancho de Los Pocitos at 14.2 mi WNW Pericos jct at 50 ft (AZ); 14.9 mi N Mazatlan (AZ); and 7 mi W Concordia (CA); NAYARIT: Stebbin's (1966) citation of the range as extending into Nayarit is presumably based on a specimen from 3.7 mi E junction Yago Road and Mex 15 (CA); MORELOS: See text for discussion of two possible records; and YUCATÁN: A citation by Nelson (1966) was based on erroneous transcription of data by another party.

*Gastrophryne usta* (Cope)

*MÉXICO.* SINALOA: 9 localities cited by Hardy and McDiarmid (1969) plus 9 mi N Mazatlán at 100 ft (UC) and 11 mi SE Villa Unión (LA); NAYARIT: between San Blas and Mex 15 on Mex 54 (UI), 2.9 to 3.8 mi E San Blas (CA), 7 mi SE Tuxpan (Altig, 1964); COLIMA: 3 localities cited by Oliver (1937) plus 1 mi E Colima (AZ), 9 mi E Colima (Fouquette and Rossman, 1963), Periquillo (UM), Quesería (Smith and Taylor, 1948), Río Armería (UM), and near Tonila (AM); GUERRERO; 5 localities cited by Davis and Dixon (1965) plus 9.9 km N Acapulco (TN), 6 mi NW Acapulco (UF), 3 km N Agua del Obispo at 980 m (KU), 10 km S Agua del Obispo (TN), near Buena Vista (UI), El Treinta (Bokermann, 1952), El Limoncita near La Venta (FM, UI), 2.9 km N El Treinta (TN), 19.7 km N El Treinta (TN), 1 mi S El Treinta (FM), Laguna Coyuca (AM), 3.4 mi N Ocotito at 2200 ft (KU), 1 mi N Organos (Smith and Taylor, 1948), 10 mi W Pie de la Cuesta (UM), 9.8 mi E Tecpan (UM), Tierra Colorado (Taylor and Smith, 1945), 2 mi N Xaltinanguis (UI, Taylor and Smith, 1945, as Xaltinanguis); OAXACA: 7 localities cited by Duellman (1960) plus between isthmus road and La Venta on Mex 190 (UI), 10 km W Juchitán (UM), 9 mi E jct 185 and 190 at 20 ft (TN), 9.8 mi W Pinotepa Nacional (EL), 16¼ mi W Pinotepa Nacional (Holman, 1964), 2.5 mi W Tapanatepec (UM), 6.7 km W Tapanatepec (TN), 1 mi W Tehuantepec (KU), Tuxtepec at 32 m (UI), .5 mi S Tuxtepec (UI), 2 km S Valle Nacional at 100 m (KU), 1 mi S Valle Nacional (UI), 22.9 mi W Zanatepec (TN), 8.5 mi W Zanatepec (Fouquette and Rossman, 1963), 14.2 mi W Zanatepec (Fouquette and Rossman, 1963), 8 mi N Zanatepec (Lynch, 1965), and 5.6 mi E Zanatepec at 235 ft (TN); VERACRUZ: 4 localities cited by Duellman (1960) plus 9.6 mi W Alvarado (UM), 18 mi SE Alvarado (UM), near Canada (Smith and Taylor, 1948), 2 mi NE Catemaco at 1100 ft (LS), 4.4 mi N Ciudad Zerde (UA), Coatzocoalcos (Günther, 1900), 0.2 mi SW Coatzocoalcos (Fouquette and Rossman, 1963), 10 mi SW Conejos (TN), 11 mi SW Conejos (TN), Cordoba (Parker, 1934), 3.5 mi E Cordoba (AM), 11 mi E Cordoba (RA), Cuatlapan (TN), 4 mi E Encero (Smith and Taylor, 1948), 7 mi S Catemaco at Encinal at 120 ft (Pyburn, 1963), 1 mi ENE Encinal (UM), Escamilla (Smith and Taylor, 1948), 2.3 mi SE Jalapa (RA), 7.6 mi S Jalapa (RA), 0.3 mi E Jaltipan (EL), 20.5 mi E Jaltipan (EL), Palma Sola (Taylor and Smith, 1945), 5 mi W Paso de Ovejas (FM), Potrero Viejo (KU, ST, UM, US), Río Seco Potrero (UM), Rodriquez Clara (Smith and Taylor, 1948), near San Andres Tuxtla (Lynch, 1965), 2 km S Santiago Tuxtla (UM), Sauzal (UM), 0.5 km N Sauzal (UM), Tierra Colorado (FM), 30.5 km N Tierra Blanca (TN), 2.6 mi E Tolome (RA), 0.3 mi SE Tula (UM), Veracruz (Günther, 1900), and 4 to 5 mi S Veracruz (Lynch, 1965); CHIAPAS: 7 localities listed by Taylor and Smith (1945) plus 2 km W Acacoyagua (UM), vicinity of Escuintla (UM), 6 km NE Escuintla (UM), Huixtla (Lynch, 1965), La Grada (UM), and 7 mi NE Tapachula (KU).

*GUATEMALA.* SAN MARCOS: 2 km SW Pajapita (TN), ESCUINTLA: 3 km E Escuintla at El Salto (KU), 2.9 mi NW jct CA 2 and Santa Lucia Road at 1650 ft (TN), 32 km SE Mazatenango Tiquisate (UM), JUTIALPA: Finca La Trinidad (UM), RETALHULEU: Hacienda Casa Blanca (UM), and SUCHITIPEQUEZ: Finca El Horizonte near Mazatenango (LS).

*EL SALVADOR.* LA LIBERTAD: 10 mi NW Santa Tecla at about 2000 ft (Legler, 1964); SANTA ANA: 5-15 km ESE Candelaria (KU); and CUSCATLÁN: 7.2 km WNW Cojutepeque (Nelson and Cuellar, 1968).

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