INTRODUCTION

In 1956 Frederick H. Test and Harold Heatwole returned to the University of Michigan from Venezuela with a living specimen of a distinctive marsupial frog, genus *Gastrotheca*, which subsequently gave birth to young. These frogs, together with two others collected by Test in 1951, reposed in the late Charles F. Walker's office for more than two decades. With his characteristic caution and thoroughness he compared the specimens with the types of many other *Gastrotheca*, selected a type specimen, and wrote a draft of the description of the holotype. As a lasting tribute to Walker's long interest in marsupial frogs, it is appropriate to associate his name with the species that he recognized as distinct so many years ago.

*GASTROTHECA WALKERI* NEW SPECIES

**HOLOTYPE** — UMMZ 117177 (field number CD 2243), an adult female, collected between the Estación Biológica Rancho Grande and Paso Portachuelo, Estado Aragua, Venezuela, 1100 m, on 13 August 1956 by Harold Heatwole (preserved 2 September 1956).

*Museum of Natural History and Department of Systematics and Ecology, University of Kansas, Lawrence, Kansas 66045*
Paratypes — AMNH 70720, 70722, BMNH 1975.1314-15, EBRG 15, 64-65, KU 193390-91, 166765, UMMZ 113881-82, 117178 (21 young born to holotype) from Estación Biológica Rancho Grande, 1100 m; KU 166766, 167851 (skeleton) from km 26 on Maracay-Ocumare de la Costa Road, 770 m; KU 166767-69 from km 29 on Maracay-Ocumare de la Costa Road, 650 m, all in Estado Aragua, Venezuela.

Diagnosis — A moderately large Gastrotheca (♂♂ to 47.3 mm, ♀♀ to 70.1 mm) with long legs (ratio of tibia length to snout-vent length 54.8-63.7, $\bar{x} = 58.5$ percent), skin on dorsum smooth, fifth toe webbed to base of disc, small triangular calcar on heel, small triangular dermal process on margin of upper eyelid, and openings into brooding pouches directed anterolaterally from longitudinal external folds of pouch; dermis of head not co-ossified with skull; development direct without free-living larval stage.

Four other species of Gastrotheca have triangular dermal processes on the eyelids; of these, the processes are minute in G. longipes, whereas those in G. ceratophrys, G. cornuta, and G. humbertoi are much larger than the processes in G. walkeri. Furthermore, in those three species the snout is shorter and deeper than in G. walkeri. Gastrotheca ceratophrys also differs from G. walkeri by having transverse rows of small tubercles on the dorsum; G. cornuta differs by having the webbing extending only to a point midway between the distal subarticular tubercle and the disc on the fifth toe, and G. humbertoi has a blue tongue and buccal cavity, as compared with pale green in G. walkeri. Gastrotheca longipes is green, and G. humbertoi is mottled green and dark brown, whereas the other three species are brown. Females of the other four species have the opening of the brood pouch directed anteriorly from an inverted V- or U-shaped fold. The only other species having a brood pouch like that in G. walkeri is G. williamsoni, a smaller species (♀ 53.8 mm) with large calcars but no dermal processes on the eyelids. Amphignathodon guentheri also has dermal processes on the eyelids and calcars, but it differs from Gastrotheca by having teeth on the mandible.

Description of Holotype — Adult female with empty brood pouch; head slightly wider than long; snout truncate in dorsal view, rounded in profile with anteroventral inclination from nostrils; canthus rounded; loreal region barely concave; lips thin, rounded; nostrils nearly terminal, slightly protuberant; internarial region flat; interorbital area flat, slightly wider than eyelid; tympanum smooth with distinct annulus; upper edge of tympanum covered by moderately heavy
supratympanic fold. Body robust; upper arm slender; forearm robust, bearing ventrolateral row of low tubercles; palmar tubercle bifid; subarticular tubercles large, round; supernumerary tubercles small, present only proximally; discs large, round, width of that on third finger equal to size of tympanum; thumb barely shorter than second finger; webbing formula: II \(2^+ - 3 \) III \(3^- - 2^+\) IV. Hind limb long (tibia 60.9\% of snout-vent length), slender; heel bearing small triangular calcar; outer tarsal fold weak distally; inner metatarsal tubercle elliptical, visible from above; outer metatarsal tubercle absent; subarticular tubercles large, round; supernumerary tubercles small, present only on proximal segments; discs slightly smaller than those on fingers; webbing formula I \(1 - 2\) II \(1 - 2^+\) III \(1 - 1^+\) IV \(1^+ - V\). Skin on dorsum smooth with scattered small granules; transverse row of larger granules connecting small triangular dermal processes on margins of eyelids; narrow granular dorsolateral fold extending from posterior corner of eyelid above tympanum to point about midlength of body; skin on belly coarsely granular, that on throat weakly granular. Anal opening directed posteriorly at upper level of thighs, bordered above by short, transverse tuberculate ridge and below by two pairs of large tubercles. Dorsal pouch openings consisting of two slightly curved longitudinal slits about 8 mm in length with their anterior corners at level of posterior margins of sacral diapophyses and separated anteriorly by about 11 mm. Tongue cordiform; choanae large, ovoid; prevomerine teeth 8-9 on transverse processes between choanae.

Color (in preservative) of dorsum pale salmon red; broad creamy white suborbital bar; gray blotch on snout and four smaller spots on margin of upper lip; irregular narrow dark line along canthus; narrow dark interorbital line connecting dermal processes on eyelids; large middorsal brown quadrangular blotch behind head, continuous posterolaterally with pair of bars that curve obliquely into axillae; posterior to these a series of three chevrons — one in middle of dorsum anterior to pouch openings, one crossing anterior parts of pouch openings, one posterior to margin of pouch openings, laterally all becoming diffuse and tending to merge, forming zone of dark flecks on flanks. Limbs pale reddish tan with dusky flecks forming weakly defined transverse bars on thighs, shanks and feet; dusky flecks concentrated on fourth and fifth toes and connecting web; irregular dusky spots on posterior surfaces of thighs; venter dull yellowish white.

**Measurements of Holotype in mm.** — Snout-vent 60.3, tibia 36.7, foot 30.9, head width 23.3, head length 21.6, interorbital distance 6.8,
internarial distance 4.5, eyelid width 5.2, diameter of eye 6.3, diameter of tympanum 3.5.

Table 1. Measurements and proportions of Gastrotheca Walkeri.
(5 males, 6 females; range followed by mean).

<table>
<thead>
<tr>
<th>Character</th>
<th>Males</th>
<th>Females</th>
</tr>
</thead>
<tbody>
<tr>
<td>Snout-vent Length (SVL)</td>
<td>43.7-47.3 (45.6)</td>
<td>60.3-70.1 (65.1)</td>
</tr>
<tr>
<td>Tibia Length/SVL</td>
<td>0.568-0.611 (0.582)</td>
<td>0.561-0.609 (0.582)</td>
</tr>
<tr>
<td>Foot Length/SVL</td>
<td>0.413-0.485 (0.448)</td>
<td>0.449-0.512 (0.465)</td>
</tr>
<tr>
<td>Head Length/SVL</td>
<td>0.333-0.369 (0.352)</td>
<td>0.325-0.359 (0.347)</td>
</tr>
<tr>
<td>Head Width/SVL</td>
<td>0.348-0.397 (0.370)</td>
<td>0.364-0.390 (0.379)</td>
</tr>
<tr>
<td>Interorbital Distance/Head Width</td>
<td>0.244-0.291 (0.277)</td>
<td>0.283-0.321 (0.308)</td>
</tr>
<tr>
<td>Tympanum/Eye</td>
<td>0.429-0.553 (0.505)</td>
<td>0.484-0.615 (0.541)</td>
</tr>
<tr>
<td>Third Finger/Head Length</td>
<td>0.909-1.046 (0.955)</td>
<td>0.927-1.014 (0.960)</td>
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</table>

Variation. — Measurements and proportions are summarized in table 1. Structurally all of the adults are essentially the same as the holotype; in some individuals the dorsal granules are not so well developed as in the holotype. On the other hand, the coloration is highly variable, although the pattern in all individuals is generally like that of the holotype. In life the dorsal ground color is olive-tan to reddish brown with dark gray to brown chevrons on the back and flecks on the body and limbs (Fig. 1). In some individuals the flanks are col-

Fig. 1. Paratype of Gastrotheca Walkeri, KU 166768, ♀, 52.4 mm snout-vent length.
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ored like the dorsum and the lateral ends of the chevrons are diffuse; in others the flanks are cream to pale green, and the lateral ends of the chevrons are distinct. In some individuals a distinct enamel-white suborbital bar is present; in others the suborbital bar is barely evident. The anal stripe and heel stripes are white. The anterior and posterior surfaces of the thighs, ventral surfaces of limbs, upper arms and throat are pale green, and the belly is cream. The iris is reddish bronze with fine dark brown to black reticulations. The lining of the mouth and tongue are pale green.

**LIFE HISTORY AND ECOLOGY.** — One female having a snout-vent length of 60.3 mm (holotype) gave birth to 21 young on 1 September 1956; another having a snout-vent length of 55.0 mm gave birth to 13 young on 11 December 1975. A female (69.0 mm) collected on 3 August 1974 contained 31 ovarian eggs, and one (65.1 mm) collected on 10 October 1974 contained 17 developing young in the pouches. Another female (66.8 mm) has 14 young associated with it. Recently born young have snout-vent lengths of about 16 mm.

*Gastrotheca walkeri* inhabits premontane moist forest (Ewel et al., 1976) at elevations of more than 650 m on the northern (windward) slopes of the Cordillera de la Costa. At higher elevations (± 1000 m) the vegetation changes to cloud forest (premontane wet forest of Ewel et al., 1976), which is continuous through the Paso Portachuelo (1125 m) and down on the southern (leeward) slopes to about 1050 m. The Estación Biológica Rancho Grande is located at 1100 m on the leeward slopes of the cordillera. Presently all localities from which *G. walkeri* is known are along the front of the Cordillera de la Costa. All individuals have been collected at night; most were on branches of bushes and trees or on palm fronds 1-2 m above the ground, but two were on a cliff in the spray zone of a waterfall.

**REMARKS.** — Two other marsupial frogs occur sympatrically with *G. walkeri* at Rancho Grande. *Gastrotheca ovifera* is about the same size as *G. walkeri* and also has direct development. *Flectonotus pygmaeus* is much smaller (♂ to 28 mm, ♀ to 41 mm), lives in arboreal bromeliads and produces advanced tadpoles. *Gastrotheca ovifera* and *Flectonotus pygaeus* are widely distributed in cloud forest in the Cordillera de la Costa.

Two other species of *Gastrotheca* are herein reported from Venezuela for the first time; *G. helenae* has been collected on Cerro Tamá in the Cordillera Oriental of the Andes in extreme western Venezuela (KU 181070), and *G. nicefori* has been taken on the eastern slopes of
the Cordillera Oriental (KU 181071) and in the Mérida Andes (KU 133392). The former is known only from Cerro Tamá and the latter has an extensive distribution in the Andes in Colombia and the highlands in eastern Panamá. Gastrotheca williamsoni is known only from San Esteban, Estado Carabobo, on the Caribbean lowlands. The other species occur in the Cordillera de la Costa. The six Venezuelan species of marsupial frogs can be identified by the following key:

1. Skin on head co-ossified with skull ......................... 2
   Skin on head free from skull .............................. 3

2. Transverse occipital ridge smooth; dorsum uniform tan or gray; limbs not barred .................................G. nicefori
   Transverse occipital ridge bearing spinous elevations; dorsum tan or brown with bold darker markings; limbs barred with dark brown or black .................................G. ovifera

3. Triangular dermal calcar present on heel ...................... 4
   Calcar absent .............................................. 5

4. Triangular dermal process present on margin of eyelid. .G. walkeri
   Dermal process absent on eyelid ..............................G. williamsoni

5. Snout-vent length of adults more than 45 mm; skin on dorsum granular; venter dark with light flecks .........................G. helenae
   Snout-vent length less than 42 mm; skin on dorsum smooth; venter uniform pale ..............................F. pygmaeus

Studies on the phylogenetic relationships among the marsupial frogs are still in progress, but on the basis of osteological, external morphological and reproductive characteristics, G. walkeri seems to belong to a group of species including G. longipes (upper Amazon Basin), G. viridis (southeastern Brasil) and G. williamsoni (northern Venezuela). These species seem to be related to another group (G. angustifrons, ceratophrys and cornuta) in Panamá and the Chocoan lowlands of northwestern South America. All of these species are inhabitants of lower montane and tropical rainforests at elevations of less than 1200 m and all have direct development of eggs into froglets.
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LITERATURE CITED


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