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### A REVIEW OF THE CENTROLENID FROGS OF ECUADOR WITH DESCRIPTIONS OF NEW SPECIES

By

JOHN D. LYNCH<sup>1</sup> AND WILLIAM E. DUELLMAN<sup>2</sup>

Since the description of *Centrolene geckoideum* by Jiménez de la Espada (1872), there have been few contributions to our knowledge of Ecuadorian centrolenid frogs. Boulenger (1882, 1898, 1899) named three Ecuadorian species as *Hyla* or *Hylella*. Noble (1924) recorded another species. Goin (1961) named three new species, and Goodman and Goin (1970) commented on additional Ecuadorian specimens of *Centrolene geckoideum*.

The generic status of these frogs has been reviewed by Noble (1920), Taylor (1951), Goin (1964) and Savage (1967). Taylor (1951) perceived the distinctive features of the assemblage and proposed the recognition of the Centrolenidae, a family occurring from southern México to Perú and Surinam and with an additional proliferation of species in southeastern Brasil.

The Middle American species have been reviewed by Taylor (1949, 1952, 1958), Duellman and Tulecke (1960), Savage (1967), and Savage and Starrett (1967). Taylor and Cochran (1953) summarized the Brazilian species; Cochran and Goin (1970) accounted for the known Colombian species, and Rivero (1968) published on the Venezuelan centrolenids. Additional species have been named from Perú (Boulenger, 1918), Surinam (Goin, 1966), Brasil (Lutz and Kloss, 1952), and Guyana (Goin, 1968).

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Currently the Centrolenidae is composed of two genera—*Centrolene* Jiménez de la Espada, 1872, and *Centrolenella* Noble, 1920; approximately 50 species are recognized in the family. Eight species have been recorded from Ecuador: *Centrolene geckoideum* and *Centrolenella buckleyi*, *cochranae*, *fleischmanni*, *griffithsi*, *ocellifera*, *parabambae*, and *petersi*.

Field work in Ecuador from 1967 through 1972 has resulted in the accumulation of nearly 200 specimens, representing all of the previously known Ecuadorian species of *Centrolenella*, two species heretofore unknown from Ecuador, and eleven new species named herein. We have examined the type specimens of all Ecuadorian taxa. Our investigations show the presence of 19 species of centrolenids in Ecuador. We present data on all the *Centrolenella* but include *Centrolene geckoideum* only in the key. Additionally, we treat the Colombian *Centrolenella medemi*, although the species has yet to be found in Ecuador.

Most areas of Ecuador have been explored in the course of our field work. Duellman worked mostly in the Amazonian lowlands and slopes, whereas Lynch spent most of his time at high elevations in the Andes and on the Pacific slopes of the Andes. Both of us spent limited time on the mesic Pacific lowlands. Based on our experience, we have noted a high degree of endemism in the faunas on the Pacific and Amazonian slopes and in some semi-isolated mountain ranges in Ecuador. We suspect that the centrolenid fauna is much larger than the 19 species now known from Ecuador.<sup>3</sup> Accordingly, in this paper we examine the current state of our knowledge of Ecuadorian centrolenids.

#### Acknowledgments

For the loan of specimens or for provision of working space in their respective institutions, we are grateful to James R. Dixon, Alice G. C. Grandison, M. S. Hoogmoed, Konrad Klemmer, Charles W. Myers, Günther Peters, Douglas A. Rossman, Charles F. Walker, and George R. Zug. We are grateful to the following persons whose efforts in the field enhanced our collections of centrolenid frogs: Joseph T. Collins, Martha L. Crump, Stephen R. Edwards, Thomas H. Fritts, Marsha Lynch, Bruce MacBryde, John E. Simmons, Gerald R. Smith, Linda Trueb, and Charles F. Walker. Field work in Ecuador was partially supported by Watkins Museum of Natural

<sup>3</sup> Subsequent to the completion of this paper, we received a specimen of an apparently unnamed species of *Centrolenella*, obtained at the Estación Biológica Río Palenque, Provincia Los Ríos. The specimen would be identified in our key as *C. cochranae*.



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Abbreviations for collections used throughout the text are:

AMNH	American Museum of Natural History
BMNH	British Museum (Natural History)
CAS	California Academy of Sciences
KU	University of Kansas Museum of Natural History
LSU	Louisiana State University
RMNH	Rijksmuseum van Natuurlijke Historie
SMF	Senckenbergische Museum Frankfurt
TCWC	Texas Cooperative Wildlife Collection
UMMZ	University of Michigan Museum of Zoology
USNM	United States National Museum (National Museum of Natural History)
ZMB	Zoologisches Museum Berlin

### TAXONOMIC CHARACTERS

With the exception of *Centrolene geckoideum*, living centrolenids usually are small, slender-limbed, green frogs. Most preserved examples seem to offer a limited suite of characters useful in their classification. The apparent paucity of characters is in part illusory, for there has been a multiplicity of names applied to comparatively few species in some areas; furthermore, there has been a limited amount of well-preserved material with detailed records of coloration of living frogs. In the following paragraphs we discuss those taxonomic characters found to be useful by us and contemporary investigators (Savage, 1967; Savage and Starrett, 1967).

*Prevomerine teeth*.—Prevomerine teeth and dentigerous processes are absent in 9 species: *anomala*, *buckleyi*, *fleischmanni*, *griffithsi*, *megacheira*, *munozorum*, *pellucida*, *peristicta*, and *pipilata*. Judgment on the absence of teeth should be held in abeyance for *anomala* and *pellucida*, inasmuch as we have a single specimen of each. *Centrolenella pellucida* is a member of the *fleischmanni* group, and if it does have prevomerine teeth, it would be the only species of the group to have them. *Centrolenella anomala* seems to be allied most closely to *C. cochranæ*, some specimens of which lack prevomerine teeth. Prevomerine teeth usually are absent in *grandisonæ*. The teeth usually are present in *cochranæ*, *flavopunctata*, *ocellifera*, *prosolepon*, and *siren*, and are found in all ex-



amples examined of *audax* (4), *medemi* (1), *midas* (11), and *resplendens* (2).

*Color of bones.*—In living and recently preserved specimens of many centrolenids, the bones are green. The color is seen most easily on the ventral surface of the shank. We have seen living examples of all species discussed here except *medemi*. Color of the bones was recorded for most specimens after field work in 1967; our only material of two species was collected in 1967 (*ocellifera* and *resplendens*), and no notations of bone color were made.

Based on color notes of living frogs, the following taxa have green bones: *audax*, *buckleyi*, *cochranae*, *flavopunctata*, *grandisonae* (pale), *griffithsi* (pale), *megacheira*, *midas*, *peristicta* (pale), *pipilata*, *prosoblepon*, and *siren*; white bones were observed in *anomala*, *fleischmanni*, *munozorum*, and *pellucida*. Some specimens of green-boned species collected in 1967 still retain green bones. Dissection of preserved specimens of *medemi*, *ocellifera*, and *resplendens*, revealed no green pigment in the bones. We are tempted to argue that the bones of these species were white in life; however, we must point out that the pale green bones of *griffithsi* quickly fade to white in preservative.

*Humeral spines.*—On some centrolenids, a hook-like process extends anteriorly from the deltoid ridge of the humerus. This feature was used initially to distinguish *Centrolenella* and *Cochranella* but is no longer regarded as adequate grounds for generic distinction (Goin, 1964). Humeral spines usually are present only in males, and the spines appear to become more pronounced in larger, and presumably, older individuals. The spine is usually absent in females (Eaton, 1958, reported small spines in female *prosoblepon*). The spines are present in *audax*, *buckleyi*, *grandisonae*, *medemi* (small), *peristicta*, *pipilata*, and *prosoblepon*. Normally *griffithsi* lacks humeral spines, but one individual (KU 142649) has small humeral spines. The distal end of the humerus of males is provided with expanded lateral flanges in some of our examples of *grandisonae*, *peristicta*, and *pipilata*; sexual dimorphism of this sort is well-known in some *Eupsophus* and some *Leptodactylus* (Lynch, 1971).

*Snout shape.*—The shape of the snout in dorsal view (Fig. 1) varies from subacuminate (*fleischmanni*) to round (*audax*, *buckleyi*, *flavopunctata*, *grandisonae*, *munozorum*, *ocellifera*, *pellucida*, *peristicta*, *prosoblepon*, and *resplendens*) or truncate (*anomala*, *cochranae*, *griffithsi*, *medemi*, *megacheira*, *midas*, and *siren*). Truncate snouts (in dorsal view) result from the protuberant nostrils lending an angular appearance to the top of the snout. Protuberant nostrils



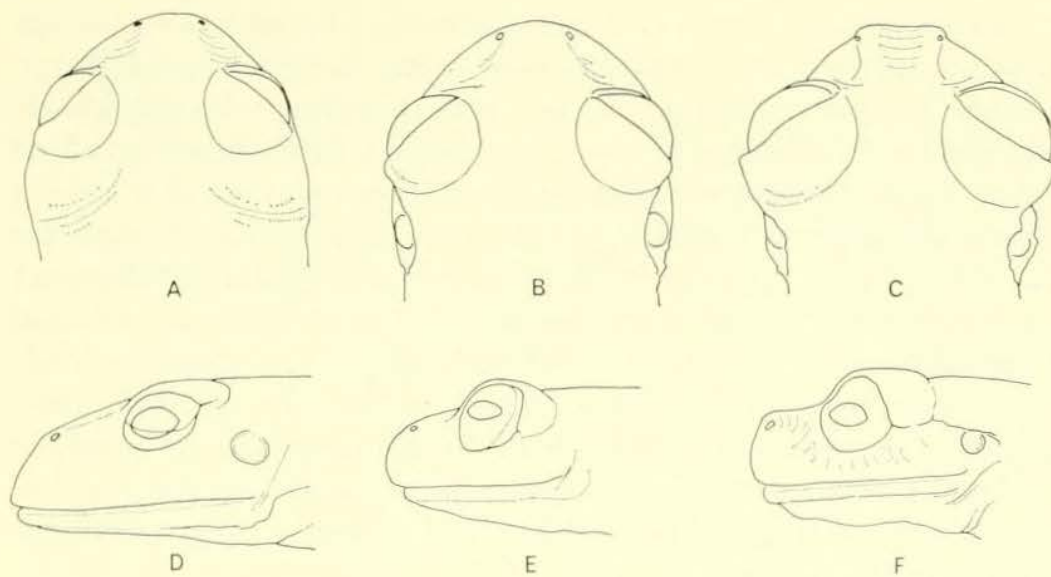


FIG. 1. Heads of *Centrolenella*: Dorsal views. A. *C. fleischmanni*, KU 146606. B. *C. audax*, KU 143290. C. *C. anomala*, KU 143299. Lateral views. D. *C. resplendens*, KU 118053. E. *C. munozorum*, KU 118054. F. *C. griffithsi*, KU 118040.

are also found among some of those species with round snouts (dorsal view) but the nostrils do not extend as far anteriorly.

In lateral view (Fig. 1), the snout profile varies from strongly sloping (*resplendens*) to a weakly sloping or rounded (*buckleyi*), to rounded *flavopunctata*, *grandisonae*, *munozorum*, *pellucida*, *peristicta*, and in some female *prosoblepon*, to truncate (*anomala*, *audax*, *cochranae*, weakly in *fleischmanni*, *griffithsi*, *medemi*, *megacheira*, *midas*, *ocellifera*, *pipilata*, most *prosoblepon*, and *siren*). The laterally truncate snouts again reflect the presence of protuberant nostrils (more so than any differences in shape of the underlying skeleton).

An additional feature of the snout is the angularity of the canthus and loreal region. The canthus rostralis is scarcely evident in *fleischmanni*, *munozorum*, and *pellucida*, whereas it is much more distinct in those frogs having more vertical loreal regions (all other species, except *grandisonae*, *peristicta*, and *pipilata*).

*Tympanum*.—Tympana are present in all centrolenids we examined. The tympana are concealed beneath the skin in *medemi*, *munozorum*, and *pellucida*, but at least partially visible in others (lower one-fourth visible in *buckleyi* to entirely visible in some *fleischmanni*, *peristicta*, and *pipilata*). The upper edge of the tympanum usually is obscured by a supratympanic fold or may be simply covered by a thickening of the skin in the absence of a distinct supratympanic fold. The extent of the exposed portion of the tympanum is probably not a reliable feature for species recognition.



The tympanic region is directed strongly dorsolaterally (as opposed to being nearly vertical in most frogs) in *fleischmanni*, *munozorum*, and *pellucida*; this feature, in combination with the weakly marked canthus, seems to give these frogs a flatter head than that seen in the other Ecuadorian species. These species also have a strong dorsolateral orientation to the tympanum. The tympana are strongly oriented laterally (little or no dorsal or posterior inflection) in *grandisonae*, *ocellifera*, and *peristicta*. The tympana are oriented posterolaterally with little or no dorsal inflection in *anomala*, *buckleyi*, *midas*, *pipilata*, and *siren*. The tympana are oriented dorsolaterally, but much less so than in *fleischmanni* and its allies, in *audax*, *cochranae*, *griffithsi*, *megacheira*, *prosoblepon*, and *resplendens*; in these frogs there may be little to moderate posterior inflection of the tympana.

*Skin texture*.—The skin of the venter is coarsely areolate in all species examined. The skin of the dorsal surfaces varies in texture and is useful in species recognition. The dorsal skin of *medemi* is smooth, unlike any other Ecuadorian centrolenid. Most species have finely shagreened skin on the dorsum without warts or spinules (*audax*, *flavopunctata*, *fleischmanni*, *grandisonae*, *griffithsi*, *midas*, *munozorum*, *ocellifera*, *peristicta*, *pellucida*, *prosoblepon*, and *siren*). Shagreened skin with scattered enameled<sup>4</sup> warts is found in *pipilata* and *resplendens*; *resplendens* has many more warts (Plate 2C). *Centrolenella cochranae* has scattered warts on a shagreened dorsum; *C. anomala* has a shagreened dorsum with more numerous warts, and *C. megacheira* has pustular skin on the dorsum. The skin on the dorsum of *buckleyi* is shagreened with spinules, which are most numerous laterally.

*Dermal ornamentation*.—Few species of the family have what Taylor and Cochran (1953) termed "decoration" or tarsal and ulnar folds. We find that many of the folds and tubercles are enameled and thus appear to be distinctive. *Centrolenella grandisonae* has low tubercles along the outer edge of the forearm and tarsus; the tubercles are present distally along the lateral edge of the hand and foot to the digital pads. A similar arrangement of more pronounced tubercles is found in *C. peristicta* (Fig. 3) and *C. pipilata*. *Centrolenella resplendens* has a scalloped fringe along the outer edge of the hand and arm (Fig. 3), and foot and tarsus (Fig. 4); the fringe continues around the heel. A thin fringe, without warts or scalloping, occurs along the hand and forearm and the foot and tarsus of *C. pellucida*.

<sup>4</sup> The term "enameled" is used throughout to denote the shiny white elevations found in the skin of some centrolenids.



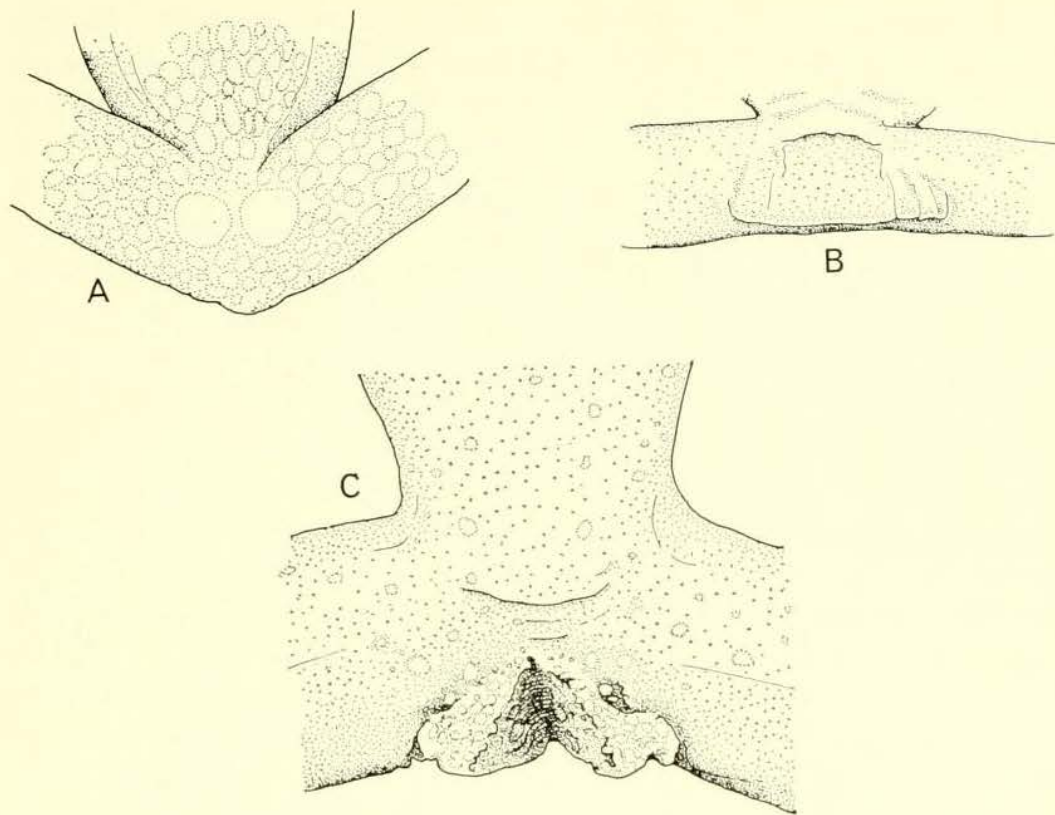


FIG. 2. Anal ornamentation in *Centrolenella*. A. Ventral view of posterior ventrum of *C. siren*, KU 146621. B. Posterior view of anal region of *C. pellucida*, KU 143298. C. Dorsal view of *C. resplendens*, KU 118053.

Most of the Ecuadorian frogs have two to four large, round subanal tubercles (Fig. 2). Five species have more extensive anal ornamentation. Six Ecuadorian species do not have subanal tubercles (*anomala*, *fleischmanni*, *medemi*, *munozorum*, *ocellifera*, and *pellucida*).

The small tubercles lateral and posteroventral to the vent in *grandisonae*, *peristicta*, and *pipilata* are enameled and seem to represent a rudimentary character-state for the "anal decoration" character-state reported by Taylor and Cochran (1953); none of these species has enlarged para- or postanal warts or folds. *Centrolenella pellucida* has a transverse fold below the vent (Fig. 2); the fold is enameled. The "anal decoration" is most extensive and unique in *C. resplendens* (Fig. 2). A similar feature appears to be present in Taylor and Cochran's (1953) *surda* of southeastern Brasil. In *resplendens*, a pair of thick folds extends laterally from the vent onto the posterior surface of the thighs; the folds are connected at their lateral extent by a semicircular fold extending medio-ventrally beneath the anus. These folds and the area between them are ornamented with enameled warts and short ridges.



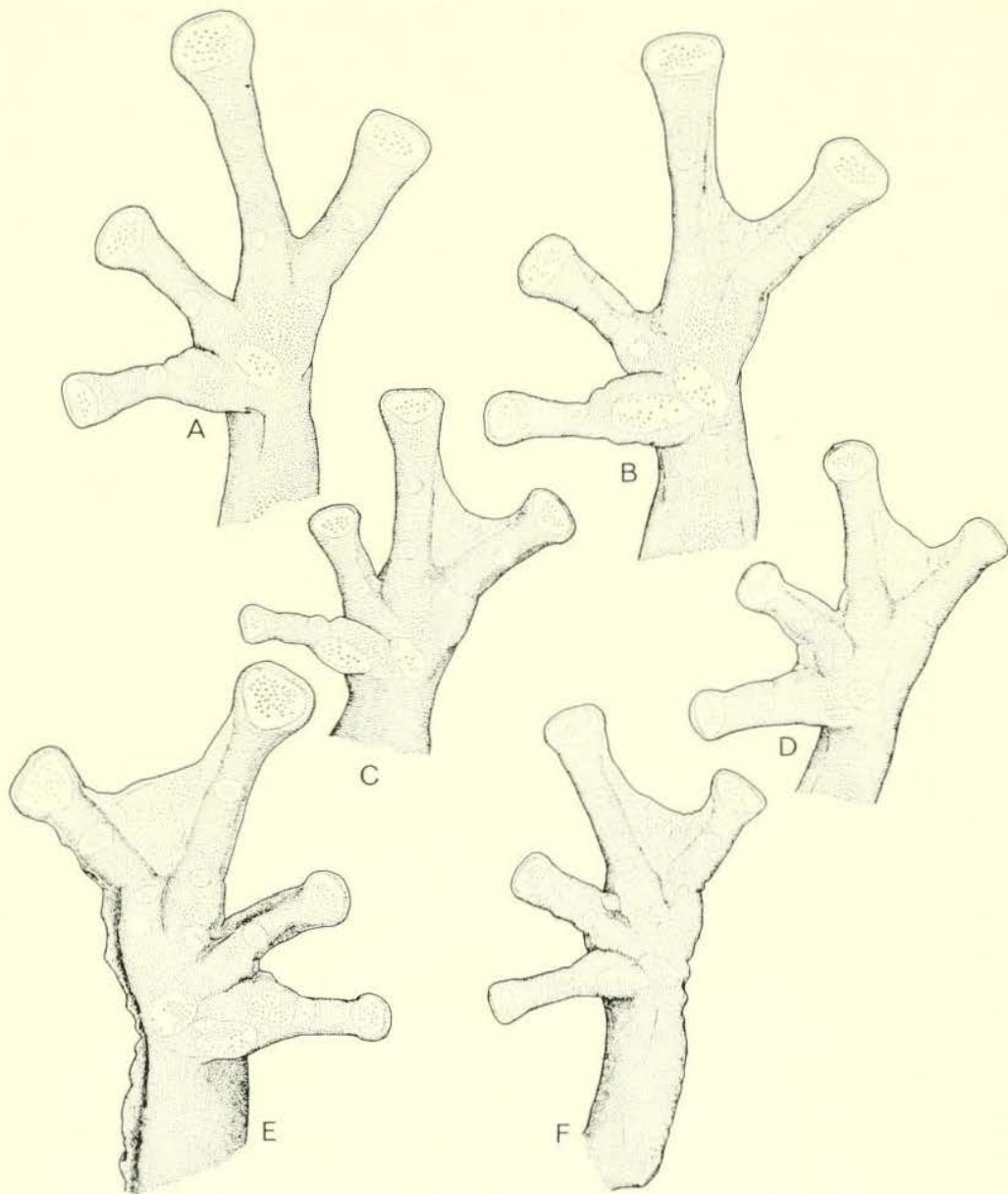


FIG. 3. Palmar views of hands of *Centrolenella*. A. *C. griffithsi*, KU 118040. B. *C. grandisonae*, KU 118047. C. *C. flavopunctata*, KU 121050. D. *C. munozorum*, KU 118054. E. *C. resplendens*, KU 118053. F. *C. peristicta*, KU 118051.

*Hands and feet.*—The first finger is as long as or longer than the second in all Ecuadorian centrolenids. In two Peruvian species we have examined, the first finger is shorter than the second. The palmar and subarticular tubercles are difficult to see on most preserved examples and are not accorded significance here. The fingers bear discs that are wider than long but vary between being more nearly round or truncate. The species with more rounded finger discs are *buckleyi*, *fleischmanni*, *griffithsi*, *munozorum*, *pellucida*, *pipilata*, *resplendens*; *megacheira* is intermediate between rounded and truncate discs include *anomala*, *audax*, *cochranae*, *flavopunctata*, *gran-*



*disonae*, *medemi*, *midas*, *ocellifera*, *peristicta*, *prosoblepon*, and *siren*. The finger discs are larger than those of the toes in all species examined, but in several species (*anomala*, *audax*, *fleischmanni*, *medemi*, *megacheira*, *munozorum*, *pellucida*, *pipilata*, *prosoblepon*, and *resplendens*) the discs are more nearly equal in size than in *cochranae*, *flavopunctata*, *grandisonae*, *griffithsi*, *midas*, *ocellifera*, *peristicta*, and *siren*. The fingers bear narrow lateral fringes in *anomala*, *audax*, *buckleyi*, *fleischmanni*, *grandisonae*, *megacheira*, *munozorum*, *pellucida*, *peristicta*, *pipilata*, *prosoblepon*, and *resplendens* but not in *cochranae*, *flavopunctata*, *griffithsi*, *medemi*, *midas*, *ocellifera*, or *siren*.

The extent of webbing of the hands and feet has been used commonly in order to distinguish species of centrolenids. In recording the extent of webbing we have followed Savage and Heyer (1967). The least finger webbing is seen in *anomala*, *cochranae*, *griffithsi*, *megacheira*, and *siren* (Fig. 3); *buckleyi*, *grandisonae*, and *pipilata* have only slightly greater webbing of the fingers (Fig. 3). In these eight taxa the webbing does not enclose the distal subarticular tubercle. The most extensive webbing seen in Ecuadorian *Centrolenella* was found in the holotype of *petersi* and an example referred to *fleischmanni* (KU 121052). In these specimens the web reaches the disc of the fourth finger and nearly to the disc of the third ( $\text{III}1\frac{1}{2}\text{-IV}$ ); the modal webbing for *fleischmanni* is  $\text{III}1\frac{1}{2}\text{-2IV}$ . The webbing completely encloses the distal subarticular tubercle of fingers III and IV in *flavopunctata*, *medemi*, *peristicta*, and *resplendens* (Fig. 3) and is only slightly less extensive in *fleischmanni*, *midas*, *ocellifera*, and *prosoblepon* (Fig. 3). The distal subarticular tubercle of IV, but not III, is free of webbing in *audax* and *pellucida*.

Most species studied have a small outer metatarsal tubercle; none was found in *audax*, *flavomaculata*, *fleischmanni*, *medemi*, *midas*, *munozorum*, *ocellifera*, *pellucida*, *resplendens*, or *siren*.

The extent of webbing on the feet parallels that of the fingers, but species group less well. The least webbing is seen in *cochranae*, *griffithsi*, and *siren*, and with only slightly more webbing in *anomala*, *buckleyi*, *megacheira*, and *pipilata* (Fig. 4). The webbing formulae for these seven species range from  $12\text{-}2\frac{1}{2}\text{III}1\frac{1}{2}\text{-}3\text{III}2\text{-}3\text{IV}3\text{-}2\text{V}$  of *cochranae* and *siren* to the comparatively well-webbed *pipilata* ( $11\text{-}2\text{III}1\text{-}2\frac{1}{2}\text{III}1\text{-}2\frac{1}{2}\text{IV}2\frac{1}{2}\text{-}1\text{V}$ ). Nine species have more webbing than *pipilata* but less than the extensive webbing of *medemi* and *resplendens* (*audax*, *flavopunctata*, *fleischmanni*, *grandisonae*, *midas*, *ocellifera*, *pellucida*, *peristicta*, and *prosoblepon*). Toe webbing is most extensive in *medemi* where the web reaches the discs on all but the fourth toe.



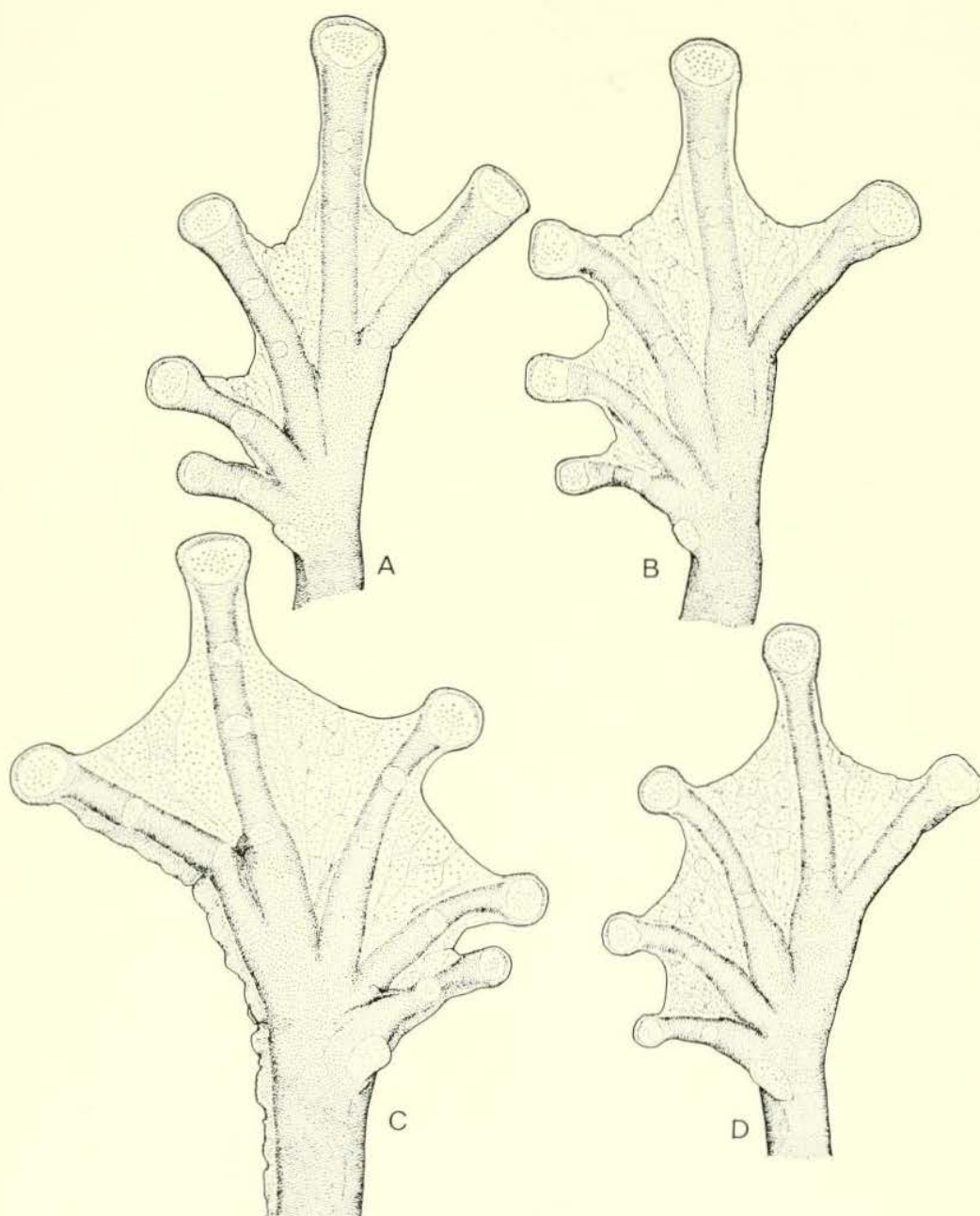


FIG. 4. Plantar views of feet of *Centrolenella*. A. *C. griffithsi*, KU 118040. B. *C. grandisonae*, KU 118047. C. *C. resplendens*, KU 1180653. D. *C. flavopunctata*, KU 121048.

*Peritoneal coloration.*—The parietal peritoneum is white (heart not visible in life) in all Ecuadorian *Centrolenella* except *fleischmanni*, *munozorum*, and *pellucida*; in these three species the heart is visible through the skin of the chest. The visceral peritoneum is white in *fleischmanni*, *munozorum*, *pellucida*, and *resplendens*. The latter is the only Ecuadorian species with both white parietal and visceral peritonea.

In living frogs, if the heart is visible, the parietal peritoneum is clear; if the heart is not visible, the parietal peritoneum is opaque



and white. The character-states of the visceral peritoneum are more difficult to observe in living frogs. If the intestine is dark (as seen through the skin of the venter), the visceral peritoneum is clear; if the intestine is yellow or white, the visceral peritoneum is opaque and white.

In preserved examples, inspection of peritoneal pigmentation is best made by cutting into the abdomen and recording whether the intestine is white or not (visceral peritoneum) and whether the inside of the belly beneath the liver is white or not (parietal peritoneum).

Three peritoneal pigmentation patterns are presently known: 1) clear parietal, white visceral (*fleischmanni* and *pulverata* groups and at least *C. albotunica*, *eurygnatha*, and *vanzolinii* of southeastern Brasil); 2) white parietal, clear visceral (*prosoblepon* group); and 3) white parietal, white visceral (*antioquiensis* and *resplendens*).

*Ground color in preservative.*—The ground color of preserved frogs is cream to creamy-white in *fleischmanni* (including the holotype of *petersi*), *munozorum*, and *pellucida*. The ground color of *anomala* is pale brown. The ground color of *flavopunctata*, *medemi*, and *pipilata* is gray to slate-gray. That of *grandisonae*, *griffithsi*, *ocellifera*, *peristicta*, and *resplendens* is pale to dull lavender and contrasts with the darker lavender ground color of *audax*, *buckleyi*, *cochranae*, *megacheira*, *midas*, *prosoblepon*, and *siren*.

*Color patterns.*—The most simple color patterns are those of *audax*, *flavopunctata*, *midas*, and *siren* (white flecks on ground color), *griffithsi* (lavender to black flecks on ground color), *buckleyi* (moderately distinct white labial stripe continuing onto flanks separating lavender or purple dorsum from cream venter), and *fleischmanni* and *munozorum* (faint peppered reticulation of dorsal surfaces). No color pattern is seen in *pellucida*.

The color pattern of *resplendens* consists of many small white spots (enameled warts) on a dull lavender ground color. *Centrotenella medemi* has a simple pattern of large cream spots on the dorsal surfaces, unlike the pattern of any other centrolenid.

The other centrolenids with non-ocellated color patterns include *grandisonae*, *peristicta*, and *pipilata* with small, diffuse black (or lavender) spots and equally diffuse white spots on the dorsal surfaces and *megacheira* and *prosoblepon* with discrete dark lavender spots on the dorsum and limbs (spotting reduced or absent in *prosoblepon*).

The other three species known from Ecuador (*anomala*, *cochranae*, and *ocellifera*) and the Peruvian *ocellata* have a dorsal pattern of ocelli. The ocelli are large in *ocellata* but small in the three



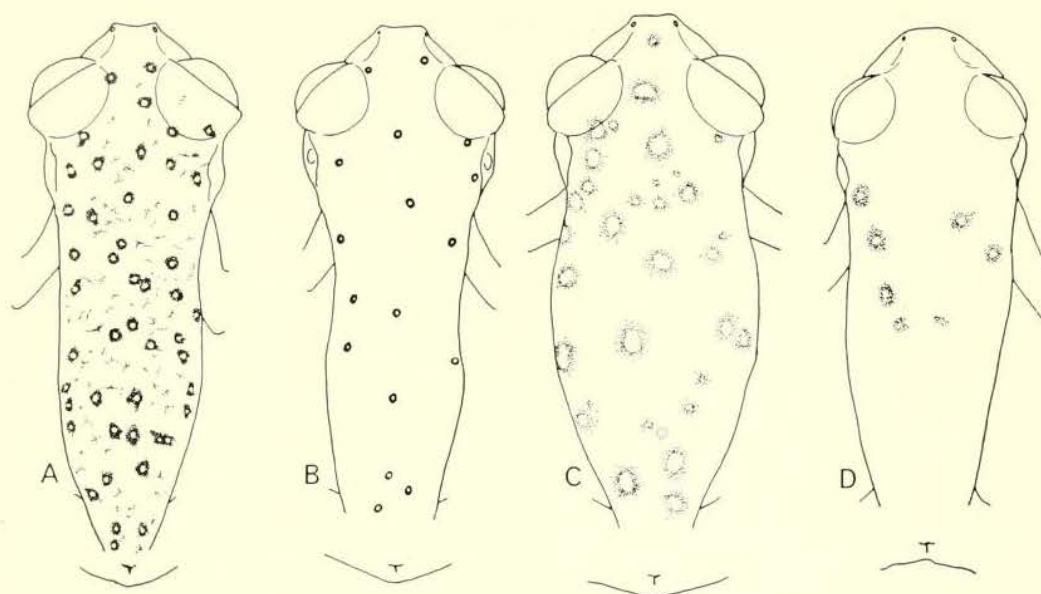


FIG. 5. Dorsal patterns of ocellated *Centrolenella*. A. *C. anomala*, KU 143299. B. *C. cochranæ*, KU 121035. C. *C. ocellata*, LSU 25990. D. *C. ocellifera*, KU 118046.

Ecuadorian ocellated *Centrolenella* (Fig. 5). The ocelli of *anomala* are black with white centers; those of *cochranæ* are deep lavender with white centers, and those of *ocellifera* faint lavender without white centers. The pattern of *ocellifera* also includes small non-ocellated white spots (Fig. 5).

#### KEY TO ECUADORIAN CENTROLENID FROGS

1. Discs on fingers as large as eye ..... *Centrolene geckoideum*  
 Discs on fingers less than half size of eye ..... 2
2. Dorsum tan with black ocelli enclosing cream (orange in life) spots ..... *Centrolenella anomala*  
 Dorsum white, cream, gray, or lavender (green in life) with or without spots or ocelli ..... 3
3. Heart visible in life; bones white; dorsum cream or white in preservative ocelli absent ..... 4  
 Heart not visible in life, bones green (unknown in *medemi*, *ocellifera*, and *resplendens*); dorsum lavender or slate gray in preservative; ocelli and spots present or absent ..... 6
4. Tympanum visible ..... *Centrolenella fleischmanni*  
 Tympanum concealed ..... 5
5. Forearm and tarsus each bearing a dermal fold on ventrolateral edge; transverse dermal fold below anus .....  
 ..... *Centrolenella pellucida*



- Forearm and tarsus lacking dermal folds; no transverse dermal fold below anus ..... *Centrolenella munozorum*
6. Webbing extending no more than midway between basal and distal subarticular tubercles on fourth finger ..... 7  
 Webbing extending at least to base of distal subarticular tubercle on fourth finger ..... 10
7. Dorsal skin pustular ..... *Centrolenella megacheira*  
 Dorsal skin shagreened ..... 8
8. Dorsum with distinct small black ocelli enclosing pale spots ..... *Centrolenella cochranæ*  
 Dorsum without ocelli ..... 9
9. Dorsum with white (yellow in life) flecks .... *Centrolenella siren*  
 Dorsum with or without diffuse black flecks ..... *Centrolenella griffithsi*
10. Broad, scalloped dermal fringe on ventrolateral edges of forearm and foot; U-shaped anal fold; snout sloping anteroventrally; dorsum with white warts ..... *Centrolenella resplendens*  
 Not nearly so fancy ..... 11
11. Dorsum of body and limbs slate gray with large cream spots; webbing extending to discs on all but fourth toe ..... *Centrolenella medemi*  
 Dorsum of body and limbs unicolor, ocellated, or flecked; webbing less extensive on feet ..... 12
12. Dorsum with dark ocelli ..... *Centrolenella ocellifera*  
 Dorsum without ocelli ..... 13
13. Webbing extending beyond distal subarticular tubercle of fourth finger ..... 14  
 Webbing not extending beyond distal subarticular tubercle of fourth finger ..... 16
14. Dorsum unicolor or with distinct dark flecks; no pale flecks ..... *Centrolenella prosoblepon*  
 Dorsum with pale flecks; diffuse dark flecks present or not .. 15
15. Dorsum of body slate gray (dark green in life) with white (yellow in life) flecks ..... *Centrolenella flavopunctata*  
 Dorsum of body pale lavender (pale green in life) with dark lavender spots and few white flecks .... *Centrolenella peristicta*
16. Dorsum with pale flecks, no dark flecks; prevomerine teeth present ..... 17

- Dorsum unicolor with dark and pale flecks; prevomerine teeth absent ..... 18
17. Humeral spine present in males; pale flecks numerous on dorsum ..... *Centrolenella audax*  
 Humeral spine absent in males; pale flecks few, principally laterally ..... *Centrolenella midas*
18. Dorsum unicolor ..... *Centrolenella buckleyi*  
 Dorsum with dark and pale flecks ..... 19
19. Snout truncate in dorsal and lateral profiles .....  
 ..... *Centrolenella pipilata*  
 Snout round in dorsal and lateral profiles. ....  
 ..... *Centrolenella grandisonae*

### ACCOUNTS OF SPECIES

In the following accounts we attempt to make comparable statements in the diagnoses and descriptions. In order to facilitate comparisons of primary character states among species, we have numbered what we consider to be the primary character in the diagnoses. The webbing formula in the diagnosis of each species is the modal formula; variation is given in the description. Measurements and proportions are for Ecuadorian specimens only, unless otherwise noted.

Specimens designated as paratypes and paratopotypes (in addition to holotypes) are those on which descriptions of new species were based. In some cases measurements of referred specimens have been incorporated into statements of ranges of variation.

Colored photographs of 15 species are reproduced on Plates 1 and 2 (following pages 16 and 26).

Taxonomic changes and their justifications, comments on type specimens and literature, and observations on behavior and ecology are given in the "Remarks" section of each account. All specimens examined are listed in a terminal section of the paper.

#### *Centrolenella anomala* new species Plate 2H

*Holotype*.—KU 143299, an adult male, 24.1 mm, from the Río Azuela, 1740 m, Quito-Lago Agrio road, Provincia Napo, Ecuador, obtained on 23 October 1971, by William E. Duellman.

*Diagnosis*.—1) prevomerine teeth absent; 2) bones white; 3) parietal peritoneum white; visceral peritoneum clear; 4) color in



life tan with black ocelli with orange-tan centers; in preservative, brown with black ocelli with white spots; 5) webbing between outer fingers  $\text{III}3^{+}\text{-}2\frac{2}{3}\text{IV}$ ; 6) webbing on foot  $\text{I}2\text{-}2\frac{1}{4}\text{II}1\text{-}2\frac{1}{4}\text{III}1\text{-}2^{+}\text{IV}2\frac{2}{3}\text{-}1\frac{1}{2}\text{V}$ ; 7) snout truncate in dorsal and lateral profiles; 8) dorsal skin shagreened with minute spicules and elevated warts corresponding to ocelli; 9) arms and legs lacking dermal fringes; 10) humeral spine absent in male; 11) lower two-thirds of tympanum visible, directed posterolaterally with dorsal inclination.

*Centrolenella anomala* differs from all other centrolenids by being tan instead of green; it further differs from other species having ocellated patterns (*cochranae*, *ocellata*, and *ocellifera*) by having more ocelli and scattered black flecks between ocelli. Moreover, *anomala* differs from *ocellifera* by having less webbing between the outer fingers, from *cochranae* by lacking prevomerine teeth, and from *ocellata* by having the snout truncate and lower two-thirds of the tympanum visible, whereas in *ocellata* the snout is round and the tympanum is concealed.

*Description*.—Adult male moderate-sized, 24.1 mm in snout-vent length; females not known. Head slightly wider than body; width of head 33.2 percent of snout-vent length; snout short, truncate in dorsal and lateral profiles (Fig. 1); canthus round; loreal region concave; lips not flared; nostrils nearly terminal on snout, protuberant, directed dorsolaterally; internarial area depressed. Eye large, protuberant, directed anterolaterally. Supratympanic fold very weak, barely covering upper edge of tympanum; tympanum directed posterolaterally with dorsal inclination. Prevomerine dentigerous processes and teeth absent; choanae small, ovoid, near margin of mouth; tongue not notched posteriorly, barely free behind; vocal slits extending from lateral base of tongue to angles of jaws.

Humeral spine absent; ulnar fold and tubercles absent; first finger longer than second; fourth finger nearly as long as third; lateral fringes present on fingers; webbing absent between first and second fingers, vestigial between second and third; webbing formula for outer fingers  $\text{III}3^{+}\text{-}2\frac{2}{3}\text{IV}$ ; discs broad, truncate; subarticular tubercles large, round, simple; supernumerary tubercles absent; palmar single, ovoid; nuptial excrescences absent. Hind limbs slender; length of tibia 54.4 percent of snout-vent length, tarsal folds and tubercles absent; inner metatarsal tubercle large, elongate; outer metatarsal tubercle small, round; subarticular tubercles large, round; supernumerary tubercles absent; feet about two-thirds webbed; webbing formula  $\text{I}2\text{-}2\frac{1}{4}\text{II}1\text{-}2\frac{1}{4}\text{III}1\text{-}2^{+}\text{IV}2\frac{2}{3}\text{-}1\frac{1}{2}\text{V}$ ; discs on toes slightly smaller and more nearly round than those on fingers.



Skin on dorsal surfaces of head, body, forearms, and shanks with many minute spicules and larger spicules corresponding to ocelli; skin of belly and ventral surfaces of thighs granular; other surfaces smooth; anal opening directed posteroventrally at midlevel of thighs; anal folds and tubercles absent.

Color in preservative: dorsal surfaces of head, body, forearms, fourth fingers, thighs, shanks, feet, and fourth and fifth toes brown with dark brown flecks and head, body, forearms, and shanks with black ocelli enclosing white spots (Fig. 5); other surfaces creamy tan.

Color in life: dorsum tan with small black ocelli enclosing orange-tan spots; chest white; heart not visible; throat, visceral peritoneum, and ventral surfaces of limbs lacking pigment; bones white; iris bronze with black reticulations.

*Distribution*.—This distinctive species is known only from the type locality, a rivulet flowing into the Río Azuela on the east slope of Volcán Reventador at an elevation of 1740 m (Fig. 6). The small stream is about 50 m north of the bridge over the Río Azuela on the Quito-Lago Agrio road. In this area there is a narrow relatively gentle slope between the steep slopes of Volcán Reventador to the west and the chasm of the Río Coca to the east.

*Remarks*.—The single specimen was kept alive for two days and two nights, during which time it was observed frequently. At no time did it take on any greenish color; it remained tan with no noticeable change in pigmentation. After 18 months in alcohol the dorsum has a faint lavender tint.

The holotype was on a mossy limb of a bush about 1.5 m above a cascading rivulet at night. *Hyla phyllognatha* and four other species of *Centrolenella* (*megacheira*, *pellucida*, *pipilata*, and *siren*) were found in the same stream and in other small streams nearby in the cloud forest, but no other individuals of *C. anomala* were observed.

*Etymology*.—The specific name is from the Greek *anomalos* meaning unusual, deviating from the general rule; the name is used in allusion to the distinctive tan color of this species.

#### ***Centrolenella audax* new species**

*Holotype*.—KU 146624, an adult male, 23.0 mm, from Salto de

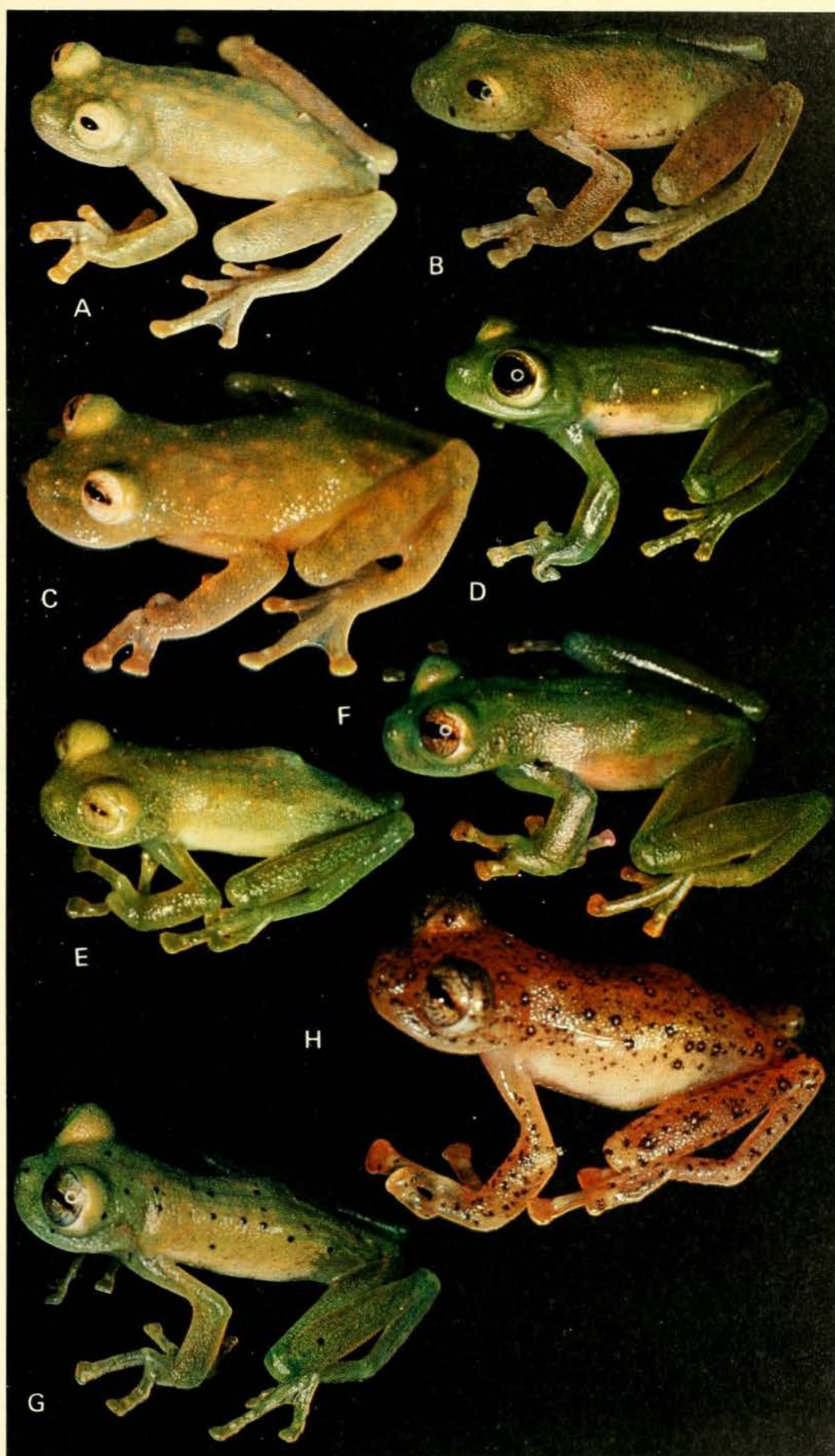
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PLATE I. A. *Centrolenella fleischmanni*, KU 146607; B. *C. munozorum*, KU 123225; C. *C. pellucida*, KU 143298 (holotype); D. *C. midas*, KU 123219 (holotype); E. *C. siren*, KU 143293; F. *C. flavopunctata*, KU 123224; G. *C. cochranæ*, KU 123216; H. *C. anomala*, KU 143299 (holotype). All  $\times 2$ .



PLATE 1







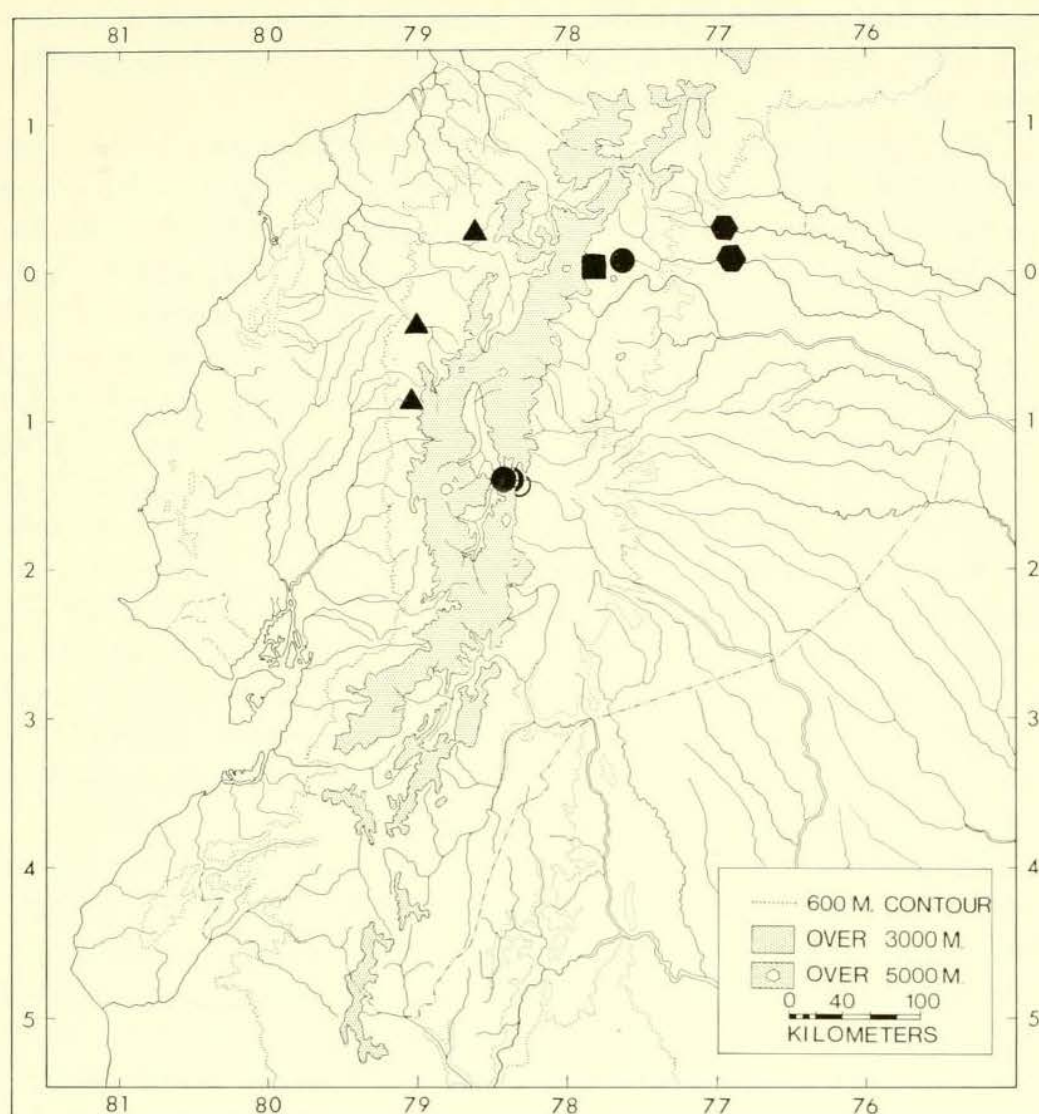


FIG. 6. Distribution of *Centrolenella anomala* (square), *C. cochranae* (circles), *C. ocellifera* (triangles), *C. resplendens* (hexagons).

Agua, 2.5 km NNE of Río Reventador on Quito-Lago Agrio road, 1660 m, Provincia Napo, Ecuador, obtained on 7 April 1972, by William E. Duellman.

*Paratypes*.—KU 143290 and 143292, adult males, from 16.5 km NNE of Santa Rosa on Quito-Lago Agrio road, 1700 m, Provincia Napo, Ecuador, obtained on 18 October 1971, by Joseph T. Collins and William E. Duellman.

*Diagnosis*.—1) prevomerine teeth 2-4; 2) bones green; 3) parietal peritoneum white; visceral peritoneum clear; 4) color in life pale green with small yellow flecks; in preservative, lavender with white flecks; 5) webbing between outer fingers III2<sup>+</sup>-2IV; 6) webbing on foot II-2-III1-2+III1-2+IV2<sup>+</sup>-1V; 7) snout round in dorsal view, truncate in lateral profile; 8) dorsal skin shagreened; 9) arms

and legs lacking dermal folds; 10) humeral spine present in males; 11) lower four-fifths of tympanum visible, directed dorsolaterally with slight posterior inclination.

The coloration of *audax* is like that of *flavopunctata*, *midas*, and *siren*, but the males of these species lack humeral spines. No other species having humeral spines has a green dorsum with yellow flecks.

*Description*.—Adult males moderate-sized, 23.0-23.6 mm ( $\bar{x}$ =23.3, N=3) in snout-vent length; females not known. Head much wider than body, width of head 34.8-43.5 percent ( $\bar{x}$ =37.8, N=3) of snout-vent length; snout short, round in dorsal view, truncate in lateral profile (Fig. 1); canthus round; loreal region barely concave; lips not flared; nostrils four-fifths distance from eyes to tip of snout, slightly protuberant dorsolaterally; internarial area depressed. Eye moderately large, directed anterolaterally. Supratympanic fold absent; lower four-fifths of tympanum visible, directed dorsolaterally with slight posterior inclination. Prevomerine dentigerous processes posteromedially inclined, narrowly separated medially, between longitudinally elliptical choanae, bearing 2-4 teeth; tongue nearly round, barely free behind; vocal slits extending from midlateral base of tongue to angles of jaws.

Humeral spine large, parallel to humerus; ulnar fold and tubercles absent; first finger longer than second; third finger slightly shorter than fourth; lateral fringes present on fingers; webbing absent between first and second fingers, vestigial between second and third; webbing formula for outer fingers III(2<sup>+</sup>-2<sup>½</sup>)-(2<sup>-</sup>-2<sup>+</sup>)IV; discs broad, truncate; subarticular tubercles small, round, simple; supernumerary tubercles absent; palmar tubercles rectangular, simple; nuptial excrescences absent. Hind limbs moderately slender; length of tibia 51.3-55.6 percent ( $\bar{x}$ =54.0, N=3) of snout-vent length; tarsal folds and tubercles absent; inner metatarsal tubercle small, elliptical, outer metatarsal tubercle absent; subarticular tubercles small, round; supernumerary tubercles absent; feet about two-thirds webbed; webbing formula II-(2<sup>-</sup>-2<sup>+</sup>)III1-(2<sup>+</sup>-2<sup>¼</sup>)III1-2<sup>+</sup>IV2<sup>+</sup>-IV; discs on toes slightly smaller than those on fingers.

Skin on dorsal surfaces shagreened; skin on belly and proximal ventral surfaces of thighs granular; other surfaces smooth; anal opening directed posteroventrally at upper level of thighs; pair of large tubercles ventral to anus.

Color in preservative: dorsal surfaces of head, body, forearms, thighs, and shanks lavender with small white dots; hands, feet, and ventral surfaces cream.

Color in life: dorsum green with gold flecks; fingers and toes pale yellow; chest white; heart not visible; visceral peritoneum and



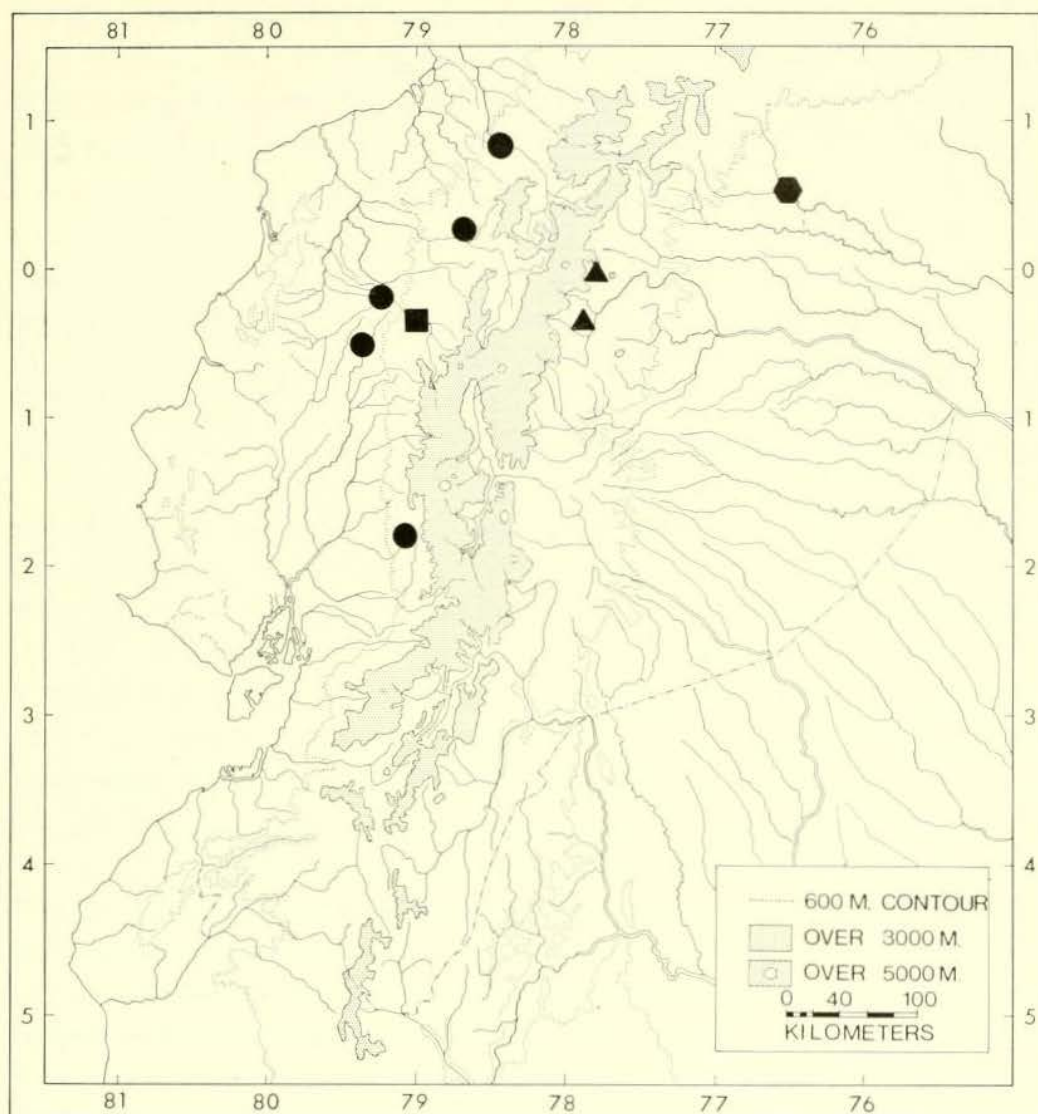


FIG. 7. Distribution of *Centrolenella audax* (triangles), *C. grandisonae* (square), *C. medemi* (hexagon), and *C. prosoblepon* (circles).

ventral surfaces of limbs unpigmented; bones green; iris pale bronze with black reticulations.

*Distribution.*—This species presently is known from only two localities at elevations of 1660 and 1700 m on the Amazonian slopes of the Cordillera Oriental of the Andes (Fig. 7). The type of locality is a deeply recessed waterfall in a nearly vertical cliff at a point 2.5 km north-northeast of the bridge over the Río Reventador on the Quito-Lago Agrio road.

*Remarks.*—The holotype was found in a bromeliad on a cliff below and in the spray zone of the waterfall. In another bromeliad a metamorphosing young having a snout-vent length of 13.5 mm and a tail 19.5 mm in length was found. Two individuals were found at night on vegetation over a stream 16.5 km north-northeast of Santa

Rosa; three other species of *Centrolenella* were found there—*mega-cheira*, *pipilata*, and *siren*.

*Etymology*.—The specific name is Latin, meaning daring, and is used in allusion to the precipitous regions inhabited by the species.

***Centrolenella buckleyi* (Boulenger)**

Plate 2E

*Hylella buckleyi* Boulenger, 1882:420 [Syntypes.—BMNH 78.1.25.16 from Intac, Provincia Imbabura Ecuador; BMNH 80.12.5.201 from "Paitanga" (=Pallatanga), Provincia Chimborazo, Ecuador].

*Hyla purpurea* Nieden, 1923:267 [Substitute name for *Hylella buckleyi* Boulenger].

*Cochranella buckleyi*—Taylor, 1951:35.

*Centrolenella buckleyi*—Goin, 1964:6.

*Diagnosis*.—1) prevomerine teeth absent; 2) bones green; 3) parietal peritoneum white; visceral peritoneum clear; 4) color in life dark green; in preservative, purple; 5) webbing between outer fingers  $\text{III}2\frac{1}{2}$ -2+IV; 6) webbing on foot  $\text{II}1\frac{1}{2}$ -2+ $\text{III}1\frac{1}{3}$ -2 $\frac{1}{4}$ IV3+-1 $\frac{1}{4}$ V; 7) snout round in dorsal view, in profile round above and slightly sloping anteriorly; 8) dorsal skin shagreened with minute spinules; 9) arms and legs lacking dermal folds; 10) humeral spine present in males; 11) lower one-fourth to one-half of tympanum visible, directed posterolaterally with slight dorsal inclination.

*Centrolenella buckleyi* is like many specimens of *griffithsi* and some *prosolepon* in being uniform lavender above in preservative, but it differs from both of these by having an inclined snout in lateral profile, spinules in the dorsal skin, and only the lower one-fourth to one-half of the tympanum visible. It further differs from *griffithsi* by having more webbing on the hand and humeral spines in males, and from *prosolepon* by having less webbing on the hand and lacking prevomerine teeth.

*Description*.—Adults large, snout-vent length 28.4-29.5 mm ( $\bar{x}$ =29.0, N=2) in males, 29.8-34.4 mm ( $\bar{x}$ =31.7, N=5) in females. Head not as wide as body; width of head 32.5-38.6 percent ( $\bar{x}$ =34.7, N=7) of snout-vent length; snout short, round in dorsal view, round above and slightly sloping anteriorly in profile; canthus round; loreal region concave; lips flared; nostrils two-thirds distance from eyes to tip of snout, barely protuberant laterally; internarial area flat. Eyes moderately large, directed anterolaterally. Supratympanic fold moderately heavy; lower one-fourth to one-half of tympanum visible, directed posterolaterally with slight dorsal inclination. Prevomerine dentigerous processes and teeth absent; choanae small, ovoid; tongue cordiform, shallowly notched behind; free posteriorly for about one-fourth of its length; vocal slits extending posterolaterally from midlateral base of tongue to angles of jaws.



Humeral spine short, pointed, nearly parallel to humerus; ulnar fold and tubercles absent; first finger equal in length to second; fourth finger slightly shorter than third; lateral fringes present on fingers; webbing absent between first, second, and third fingers; webbing formula for outer fingers  $\text{III}(2^+-2\frac{1}{4})-(2\frac{1}{4}-2\frac{3}{4})\text{IV}$ ; discs broadly rounded; subarticular tubercles moderately large, conical, simple; distal tubercle on fourth finger weakly bifid; supernumerary tubercles small, numerous on basal segments; palmar tubercle large, ovoid; nuptial excrescences absent. Hind limbs moderately robust; length of tibia 49.4-56.4 percent ( $\bar{x}=51.2$ ,  $N=7$ ) of snout-vent length; tarsal folds and tubercles absent; inner metatarsal tubercle large, ovoid; outer metatarsal tubercle small, round; subarticular small, round; supernumerary tubercles small, present basally; toes about three-fourths webbed; webbing formula  $\text{I}(1\frac{1}{3}-1\frac{2}{3})-(2-2^+)\text{II}(1-1^+)-2^+\text{III}(1-1\frac{2}{3})-(2^+-3^+)\text{IV}(2\frac{3}{4}-3^+)-(1\frac{1}{2}-2^+)\text{V}$ ; discs on toes slightly smaller than those on fingers.

Skin on dorsum shagreened with minute spinules; skin on belly and proximal posteroventral surfaces of thighs granular; other surfaces smooth; anal opening directed posteroventrally at midlevel of thighs; several small and four large tubercles below anus.

Color in preservative: dorsal surfaces, except fingers and toes, purple; other surfaces cream; narrow cream stripe on edge of upper lip in some specimens.

Color in life: dorsal surfaces bright to dark green, sharply demarcated laterally from white lower flanks; chin and most of venter pale green; parietal peritoneum yellow; heart not visible; edge of upper lip, outer edge of tarsus, and anal stripe white; bones green; iris pale copper flecked with black.

*Distribution.*—*Centrolenella buckleyi* occurs from the Mérida Andes in western Venezuela southward through the Andes and interandean valleys to southern Ecuador (Fig. 8). Although the species has been recorded at elevations as low as 1500 m, authenticated records in Colombia and Ecuador are all above 2000 m; we have found the species at elevations up to 3000 m.

*Remarks.*—We have found individuals in terrestrial bromeliads and in vegetation in *ciénegas*, the quaking meadows in many high Andean localities. Francisco León of the Universidad Católica in Quito collected two specimens from bromeliads in a *Eucalyptus* grove near Machachi. Thomas H. Fritts obtained one from a bromeliad on an island in Laguna Cuicocha. *Centrolenella buckleyi* may breed in the same situations as other centrolenids—rapid, mountain streams—but *buckleyi* frequents non-stream situations (Laguna Cuicocha, the bog-like *ciénegas*) where trees, if present,

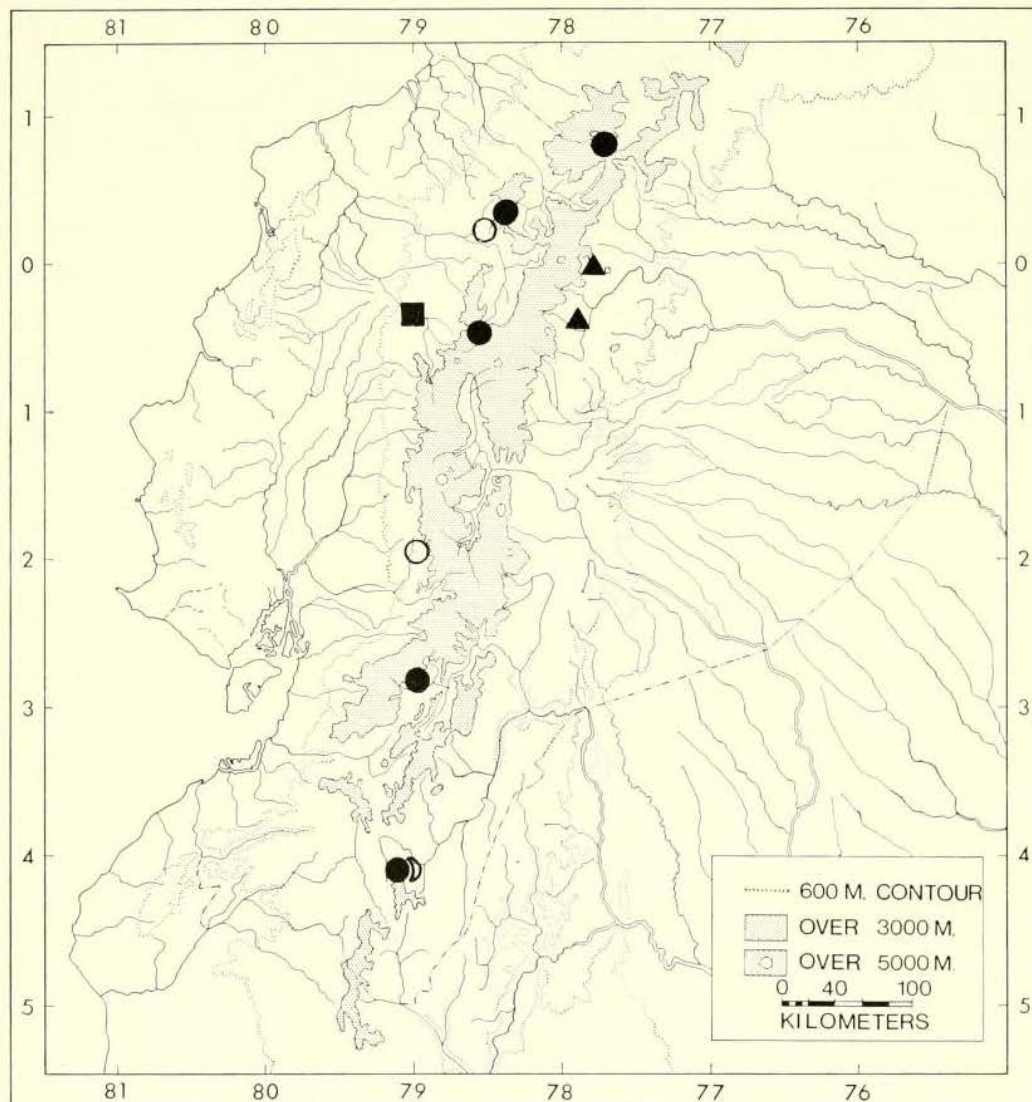


FIG. 8. Distribution of *Centrolenella buckleyi* (circles), *C. peristicta* (square), and *C. pipilata* (triangles); open symbols are literature records.

are small and rarely overhang water. Because of the absence of streams, we suspect that the tadpoles may develop in bromeliads or in *ciénegas*, a radical departure from the adaptive zone of centro-lenid frogs.

As noted by Goin (1961:101), one of the syntypes (BMNH 80.12.5.201) is now represented by disarticulated bones and the other (BMNH 78.1.25.16) is missing.

Rivero (1968) named *Centrolenella buckleyi venezuelensis* from the Mérida Andes of western Venezuela. We have not been concerned with northern populations which may or may not be conspecific with *buckleyi*; thus, we use the binomial for the populations in Ecuador.



**Centrolenella cochranae** (Goin)

## Plate 1G

*Cochranella cochranae* Goin, 1961:97 [Holotype.—BMNH 1912.11.1.68 from El Topo, Río Pastaza, Provincia Tungurahua, Ecuador].

*Centrolenella cochranae* Goin, 1964:6.

**Diagnosis.**—1) prevomerine teeth 0-3; 2) bones green; 3) parietal peritoneum white; visceral peritoneum clear; 4) color in life pale green with minute purple ocelli with red centers; in preservative, lavender with purple ocelli with white centers; 5) webbing between fingers III3-2 $\frac{1}{4}$ IV; 6) webbing on foot I2-2 $\frac{1}{4}$ II1 $\frac{1}{2}$ -2 $\frac{1}{2}$ III2-3IV3-1 $\frac{1}{4}$ V; 7) snout truncate in dorsal and lateral profiles; 8) dorsal skin shagreened with elevated warts corresponding to ocelli; 9) arms and legs lacking dermal folds; 10) humeral spine absent in males; 11) lower three-fourths of tympanum visible, directed dorsolaterally.

The first impression of the dorsal pattern of *cochranae* is of black flecks on a green ground color; however, upon closer inspection it is evident that the markings actually are small ocelli (Fig. 5). *Centrolenella cochranae* differs from other species having ocellated dorsal patterns (*anomala*, *ocellata*, and *ocellifera*) by having smaller ocelli and prevomerine teeth (absent in some *cochranae*). Furthermore, the species differs from *anomala* by having a green instead of brown dorsum, from *ocellifera* by having less webbing between the outer fingers, and from *ocellata* by having the snout truncate and the lower three-fourths of the tympanum visible, whereas in *ocellata* the snout is round and the tympanum concealed.

**Description.**—Adults moderately large; snout-vent length 23.8-26.7 mm ( $\bar{x}$ =25.0, N=6) in males, 30.0 mm in single female. Head noticeably wider than body; width of head 33.0-35.3 percent ( $\bar{x}$ =34.0, N=7) of snout-vent length; snout short, truncate in dorsal and lateral profiles; canthus round, loreal region concave; lips moderately flared; nostrils nearly terminal, directed anterolaterally; internarial area depressed. Eye large, protuberant, directed anterolaterally. Supratympanic fold absent; lower three-fourths of tympanum visible, directed dorsolaterally. Prevomerine dentigerous processes absent in one specimen, present in six; processes transverse between choanae, bearing 1-3 teeth; choanae small, ovoid, near edge of mouth; tongue cordiform, free posteriorly; vocal slits extending from midlateral base of tongue to angles of jaws.

Humeral spine absent; ulnar fold and tubercles absent; first finger longer than second; fourth finger slightly shorter than third; lateral fringes absent on fingers; webbing absent between first and second fingers, vestigial between second and third; webbing formula for outer fingers III(3-3 $^{+}$ )-(2 $\frac{1}{4}$ -3)IV; discs broader than deep,



rounded; subarticular tubercles small, round, simple; supernumerary tubercles absent; palmar tubercle large, elliptical; nuptial excrescences absent. Hind limbs slender; length of tibia 55.7-61.8 percent ( $\bar{x}$ =58.7, N=7) of snout-vent length; tarsal folds and tubercles absent; inner metatarsal tubercle large, flat, elongate; outer metatarsal tubercle small, conical; subarticular tubercles small, round; supernumerary tubercles absent; feet about two-thirds webbed; webbing formula  $I2-(2^+-2\frac{1}{2})II(1\frac{1}{2}-1\frac{3}{4})-(2^+-2\frac{3}{4})III2-(3^+-3^+)IV(3^+-3^+)-(2-2^-)V$ ; discs on toes smaller and more nearly round than those on fingers.

Skin on dorsal surfaces smooth with scattered spicules; skin on belly and ventral surfaces of thighs granular; other surfaces smooth; anal opening directed posteroventrally at midlevel of thighs; pair of large tubercles below anus.

Color in preservative: dorsal surfaces of head and body lavender with small black ocelli enclosing minute white dots or some solid black flecks; other dorsal surfaces creamy tan with black flecks on thighs and shanks of some specimens.

Color in life: pale green with black or purple ocelli enclosing pink or red dots; chest white; heart not visible; visceral peritoneum and ventral and concealed surfaces of limbs unpigmented; bones green; iris pale gray with black flecks.

*Distribution.*—Most localities from which *Centrolenella cochranae* is known are in the lower valley (1100-1300 m) of the Río Pastaza on the eastern face of the Andes (Fig. 6); additionally the species is known from an elevation of 1150 m in the Cordillera del Dué above the Río Coca ( $\pm$  180 km NNE of the Río Pastaza valley). On the basis of these few localities it seems that *cochranae*, along with *flavopunctata*, inhabits intermediate elevations between the ranges of the lowland species (*medemi*, *midas*, *munozorum*, and *resplendens*) and the numerous species in the higher cloud forests (*anomala*, *audax*, *megacheira*, *pellucida*, *pipilata*, and *siren*).

*Remarks.*—Goin (1961:97) described *cochranae* as lacking prevomerine teeth, but he (1964:2) noted the presence of teeth in six other specimens. Six of our seven specimens have prevomerine teeth, and one lacks not only teeth but dentigerous processes.

We compared two of our specimens (KU 121033, 123217) with the holotypes of *cochranae* (BMNH 1912.11.1.68) and *C. ocellata* (Boulenger, 1918) (BMNH 1912.11.1.19) from Huancabamba, Departamento Pasco, Perú. Our specimens compare favorably with the holotype of *cochranae* but are different from *ocellata* in several characters. *Centrolenella ocellata* differs from *C. cochranae* as follows: 1) prevomerine teeth absent; 2) ocelli much larger (Fig. 5); 3) snout truncate; 4) first finger shorter than second.



All of our specimens were obtained at night from vegetation overhanging small mountain streams. The call consists of a single, high-pitched note. Other than the calls, no evidence of reproduction was noted while we were collecting in the range of *cochrane* (April, June, July, August). Individuals seemed to be sparsely distributed in the habitat.

***Centrolenella flavopunctata* new species**

Plate 1F

*Holotype*.—KU 121048, an adult male, 21.6 mm, from Mera, Provincia Pastaza, Ecuador, obtained on 14 July 1968, by John D. Lynch.

*Paratopotypes*.—KU 121041, 28 June 1968, John D. Lynch; 121043-46, 2 July 1968, John D. Lynch and Gerald R. Smith; 121049, 14 July 1968, John D. Lynch; 121050-51, 24 July 1968, John D. Lynch.

*Diagnosis*.—1) prevomerine teeth 0-3 on low processes; 2) bones green; 3) parietal peritoneum white; visceral peritoneum clear; 4) color in life green with pale yellow flecks; in preservative, slate gray with white flecks; 5) webbing between outer fingers III<sub>2</sub>-1½IV; 6) webbing on foot I1-1½II0-2-III1-2-IV2-1V; 7) snout round in dorsal and lateral profiles; 8) dorsal skin shagreened; 9) arms and legs lacking dermal folds; 10) humeral spine absent in males; 11) lower three-fourths of tympanum visible, directed dorsolaterally with slight posterior inclination.

*Centrolenella flavopunctata* is like *midas* and *siren* in having a lavender dorsum with white flecks (in life, green with gold flecks) and no black flecks, but it differs from both species by having a rounded, instead of truncate, snout and slightly more webbing on the hands and feet. *Centrolenella siren* further differs from *flavopunctata* by having nearly the entire tympanum visible and strongly inclined posteriorly, whereas only about three-fourths of the tympanum is visible and directed dorsolaterally in *flavopunctata*.

*Description*.—Adults rather small; snout-vent length 20.6-23.2 mm ( $\bar{x}$ =21.6, N=7) in males, 24.1-25.7 mm ( $\bar{x}$ =24.9, N=3) in females. Head slightly wider than body; width of head 34.6-38.3 percent ( $\bar{x}$ =36.2, N=10) of snout-vent length; snout short, round in dorsal and lateral profiles; canthus round; loreal region barely concave; lips not flared; nostrils nearly terminal on snout, not protuberant, directed antero-dorsolaterally; internarial area barely depressed. Eye moderately large, directed anterolaterally. Supratympanic fold absent; lower three-fourths of tympanum visible, directed dorsolaterally with slight posterior inclination. Prevomerine denticerous processes



small, low, widely separated between longitudinally rectangular choanae, bearing 0-3 teeth; tongue broadly cordiform, barely free posteriorly; vocal slits extending from midlateral base of tongue to angles of jaws.

Humeral spine absent; ulnar fold and tubercles absent; first finger longer than second; fourth finger much shorter than third; fringes absent on fingers; webbing absent between first and second fingers; webbing formula for other fingers  $III(1\frac{2}{3}-2)-(1-1\frac{2}{3})IV$ ; discs truncate, subarticular tubercles small, round, simple; supernumerary tubercles absent; palmar tubercle large, elliptical; nuptial excrescences absent (Fig. 3). Hind limbs moderately robust; length of tibia 55.3-62.0 percent ( $\bar{x}=58.0$ ,  $N=10$ ) of snout-vent length; tarsal folds and tubercles absent; inner metatarsal tubercle small, flat, elliptical; outer metatarsal tubercle absent; subarticular tubercles small, round; supernumerary tubercles absent; feet about three-fourths webbed; webbing formula  $I(0-1)-(1-1\frac{1}{4})II(0-1)-(0-2)III(0-1)-(1\frac{1}{4}-2)IV(2-2+)-(0-1)V$ ; discs on toes smaller and more nearly round than those on fingers (Fig. 4).

Skin on dorsal surfaces shagreened; skin on belly and proximal posteroventral surfaces of thighs granular; other surfaces smooth; anal opening directed posteriorly at upper level of thighs; pair of large tubercles below anus.

Color in preservative: dorsal surfaces of head, body, and limbs lavender or slate gray with many minute white flecks; other surfaces dull creamy tan.

Color in life: dorsal surfaces of head, body, and limbs pale green with numerous minute yellow flecks on body and limbs; edge of upper lip pale yellow; fingers and toes yellow; chest white; visceral peritoneum unpigmented; throat pale bluish green; bones green; iris pale grayish white, with or without golden tint, with dark gray or brown flecks or fine reticulations.

*Distribution*.—Most specimens are from elevations of 1000-1800 m in the Pastaza Valley in the eastern slope of the Andes; the species is also known from an elevation of 720 m in the Serranía de Umbaqui, 200 km NNE of the former locality (Fig. 9). One faded specimen with no visible yellow flecks from San José Abajo, Provincia Napo (AMNH 22187) tentatively is referred to this species. The locality is between 700 and 1000 m on the eastern slope of Volcán Sumaco, about 130 km NE of the Pastaza Valley. *Centrolenella*

→

PLATE 2. A. *Centrolenella megacheira*, KU 143245 (holotype); B. *C. griffithsi*, KU 121039; C. *C. resplendens*, KU 118053 (holotype); D. *C. pipilata*, KU 143278 (holotype); E. *C. buckleyi*, KU 144131; F. *C. prosoblepon*, KU 146609; G. *C. peristicta*, KU 121053. All  $\times 2$ .



PLATE 2



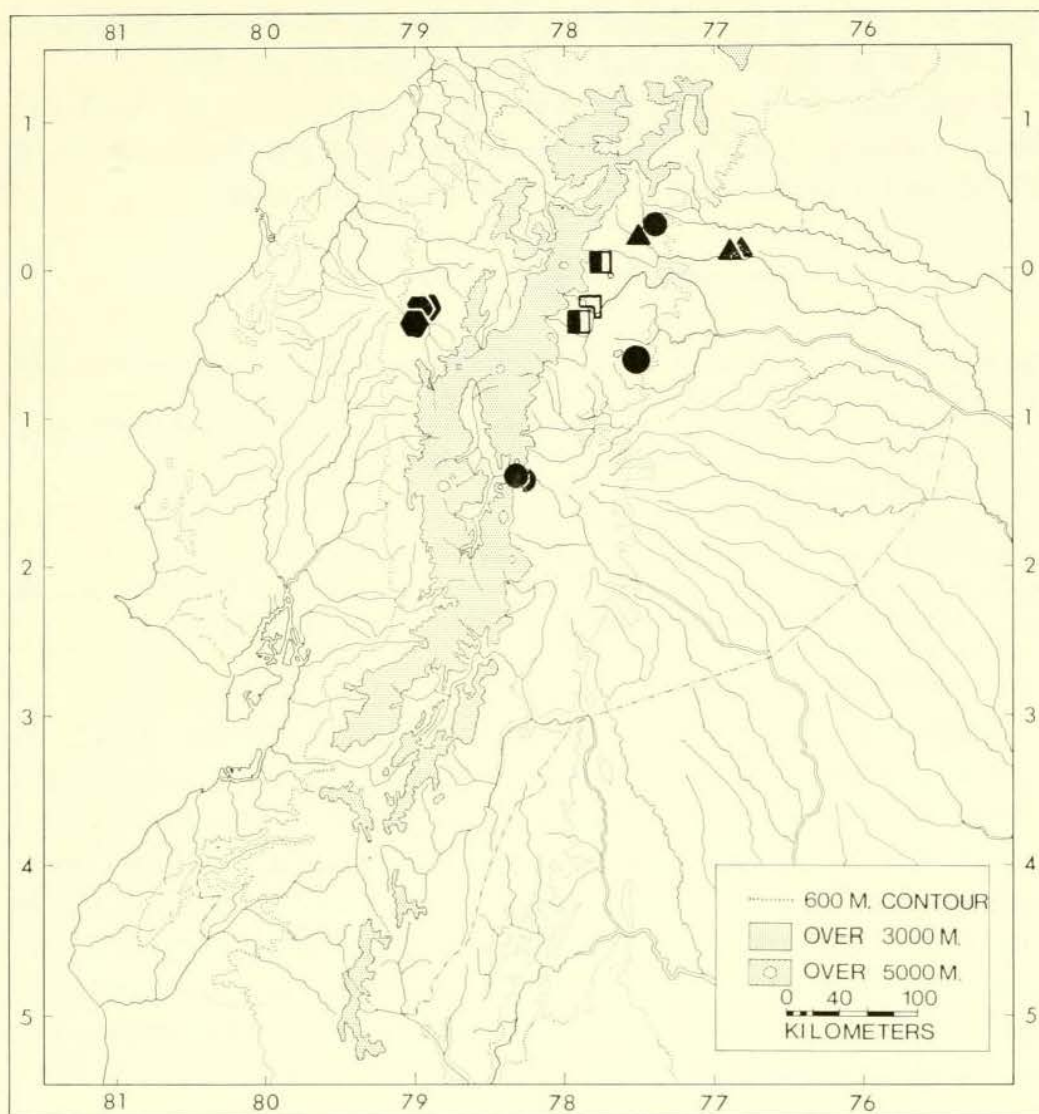


FIG. 9. Distribution of *Centrolenella flavopunctata* (circles), *C. griffithsi* (hexagons), *C. megacheira* (solid squares), *C. midas* (triangles), and *C. siren* (open squares); half closed squares are localities for both *C. megacheira* and *C. siren*.

*flavopunctata*, together with *C. cochranæ*, inhabits intermediate elevations between the ranges of the lowland species (*medemi*, *midas*, *munozorum*, and *resplendens*) and the cloud forest inhabitants at higher elevations (*anomala*, *audax*, *megacheira*, *pellucida*, *pipilata*, and *siren*). Although *cochranæ* and *flavopunctata* occur at about the same elevations on the eastern slopes of the Andes, the two species have not been found in sympatry.

*Remarks.*—One was found on a bush in forest by day; most were collected in a deep ravine. Males were perched on small herbs in the spray-zone of a small waterfall. No eggs were observed although one gravid female was found. At several small streams between Mera and the Río Alpayacu, males were calling on 2, 14, and 24 July



1968. Recently metamorphosed young having snout-vent lengths of 14.5 and 16.0 mm were found on 28 June and 6 July 1968.

*Etymology*.—The specific name is a combination of the Latin *flavus*, meaning golden yellow, and the Latin *punctatus*, meaning dotted, and is used in reference to the dorsal coloration.

### ***Centrolenella fleischmanni* (Boettger)**

#### Plate 1A

*Hylella fleischmanni* Boettger, 1893:251 [Holotype.—SMF 3760 from San José, Provincia San José, Costa Rica].

*Hylella cappellei* Lidth de Jeude, 1904:94 [Holotype.—RMNH 4463 from Saramacca, Surinam; synonymy *vide* Goin, 1964:1].

*Centrolenella fleischmanni*—Noble, 1924:67.

*Centrolenella cappellei*—Noble, 1926:18.

*Cochranella fleischmanni*—Taylor, 1951:34.

*Cochranella petersi* Goin, 1961:96 [Holotype.—BMNH 1902.5.27.24 from Río Durango, Provincia Esmeraldas, Ecuador]. New synonym.

*Centrolenella fleischmanni*—Goin, 1964:1.

*Centrolenella petersi*—Goin, 1964:6.

*Diagnosis*.—1) prevomerine teeth absent, 2) bones white; 3) parietal peritoneum clear; visceral peritoneum white; 4) color in life pale green with pale yellow spots; in preservative, cream with faint dark flecks; 5) webbing between outer fingers III2-1½IV; 6) webbing on foot II-2-II0-2III1-2+IV2+1V; 7) snout subacuminate in dorsal view, round in lateral profile; 8) dorsal skin shagreened; 9) arms and legs lacking dermal folds; 10) humeral spine absent in males; 11) tympanum almost entirely visible, directed dorsolaterally with slight posterior inclination.

*Centrolenella fleischmanni* differs from other Ecuadorian centro-lenids that have the heart visible in life and a white dorsum in preservative (*munozorum* and *pellucida*) by having the snout subacuminate in dorsal view and truncate in lateral profile, and the tympanum distinct. The other species have round snouts and the tympanum concealed. Furthermore, *pellucida* differs from *fleischmanni* by having ulnar, tarsal, and anal folds. *Centrolenella orcostalis* from Venezuela differs from *fleischmanni* by having minute enamel (yellow in life) flecks on the dorsum.

*Description*.—Adult males small; snout-vent length 19.2-21.2 mm ( $\bar{x}$ =20.4, N=5). Head wider than body; width of head 38.3-40.6 percent ( $\bar{x}$ =39.2, N=4) of snout-vent length; snout short, shallow, roundly subacuminate in dorsal view, round in lateral profile (Fig. 1); canthus round; loreal region shallowly concave; lips not flared; nostrils three-fourths distance from eye to tip of snout, barely protuberant, directed dorsolaterally; internarial area slightly depressed. Eye large, protuberant, strongly oriented anteriorly. Supratympanic

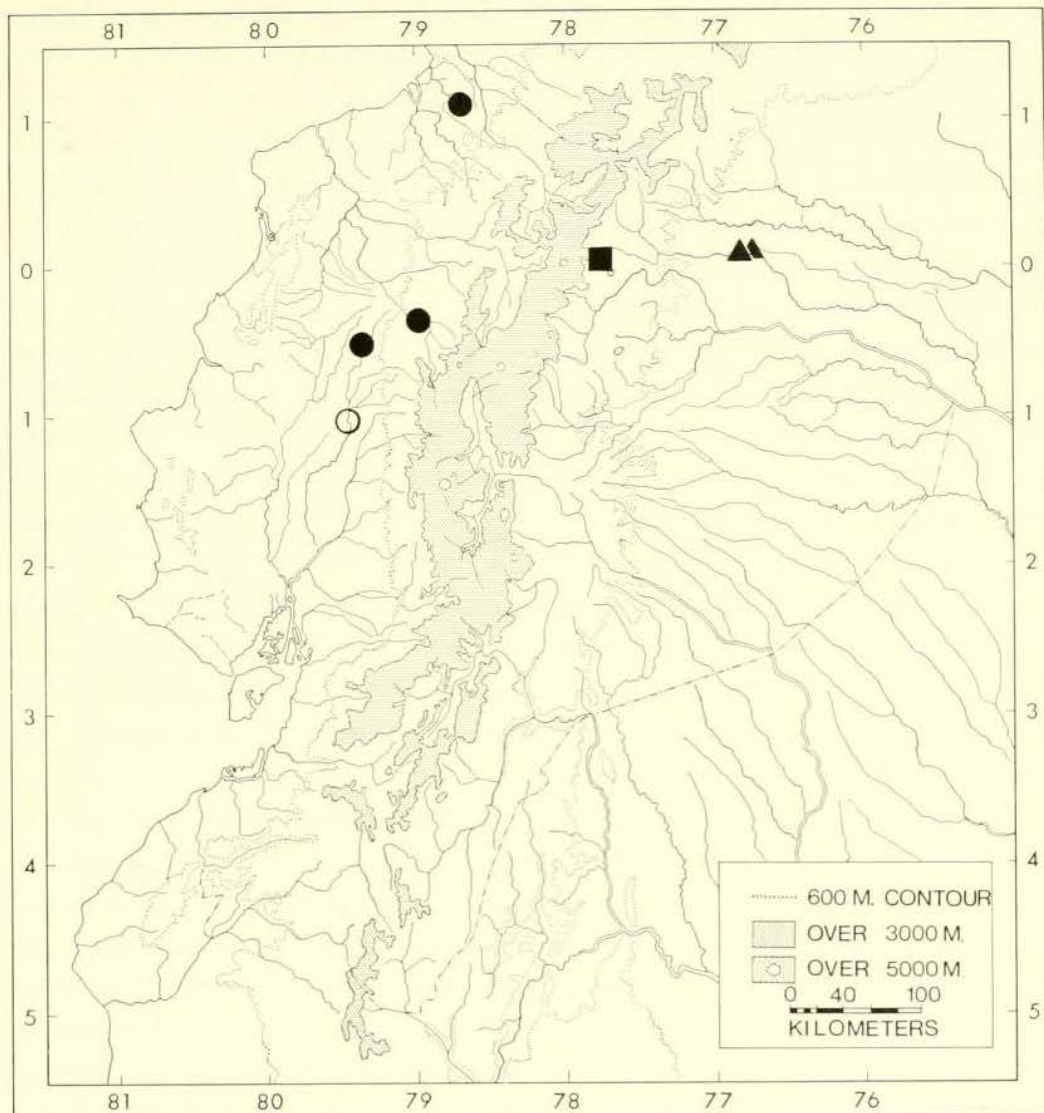


FIG. 10. Distribution of *Centrolenella fleischmanni* (circles), *C. munozorum* (triangles), and *C. pellucida* (square); open symbol is a literature record.

fold absent; tympanum small, about one-fourth diameter of eye, nearly entirely visible, directed dorsolaterally with slight posterior inclination. Prevomerine dentigerous processes and teeth absent; choanae small, round, near margin of mouth; tongue ovoid, free posteriorly for about one-fourth of its length; vocal slits extending from midlateral base of tongue to angles of jaws.

Humeral spine absent; ulnar folds and tubercles absent; first finger longer than second; fourth finger nearly as long as third; lateral fringes present on fingers; webbing vestigial between first and second and second and third fingers; webbing formula for outer fingers III(0-2)-(1 $\frac{3}{4}$ -1 $\frac{1}{2}$ )IV; discs moderate, rounded, subarticular tubercles small, round, simple; supernumerary tubercles absent; palmar tubercle small, ovoid; nuptial excrescences absent. Hind limbs slender;



length of tibia 51.9-57.3 percent ( $\bar{x}$ =55.1,  $N$ =4) of snout-vent length; tarsal folds and tubercles absent; inner metatarsal tubercle low, flat, elliptical; outer metatarsal tubercle absent; subarticular tubercles small, round; supranumerary tubercles absent; feet about three-fourths webbed; webbing formula I(0-1)-(1½-2)II(0-1)-(2-2<sup>+</sup>)III(1-2<sup>+</sup>)-(2-2<sup>+</sup>)IV(2-2<sup>+</sup>)-1V; discs of toes round, slightly smaller than those on fingers.

Skin on dorsal surfaces of head and body shagreened; skin on belly and ventral surfaces of thighs granular; other surfaces smooth; anal opening directed posteriorly at upper level of thighs; anal folds and tubercles absent.

Color in preservative: dorsum creamy white with scattered black flecks visible under microscope; eyelids and hepatic peritoneum white; skin elsewhere transparent.

Color in life: dorsum pale green with pale yellow or yellowish green spots, so large in some individuals so as to give appearance of a pale frog with darker green reticulations; heart visible; belly white; tips of digits yellow; other surfaces unpigmented; bones white; iris white to pale yellow.

*Distribution*.—This is the most widespread species of *Centrolenella*, ranging from Veracruz and Guerrero, México to Ecuador and Surinam (Goin, 1964; Savage, 1967). In Ecuador it occurs on the Pacific lowlands and to an elevation of 1460 m at Tandapi on the Pacific slopes of the Cordillera Occidental of the Andes (Fig. 10).

*Remarks*.—Numerous males were calling over small streams in April at the Estación Biológica Río Palenque north of Quevedo. The single specimen from Tandapi was on a leaf of an herb about 2 m above the ground at night.

Goin (1961:96) diagnosed *petersi* as differing from *fleischmanni* by having more extensive webbing on the hand. One specimen (KU 121052) is like the holotype in having a webbing formula for the outer fingers III0-1½IV, whereas other Ecuadorian specimens have III(1½-2)-1½IV. Examination of series of specimens from Costa Rica and Panamá reveals that most fall within the range of variation in the webbing of the hand as displayed by the three Ecuadorian specimens, but three have only one free digit on the third finger and about one and one-half digits free on the fourth finger. Due to the lateral fringes on the fingers, the determination of the point of departure of the web is highly subjective in some specimens. We have observed living *fleischmanni* in México, Guatemala, Costa Rica, and Panamá, as well as in Ecuador. Comparison of colored photographs of living individuals from throughout this range reveals that north-



ern frogs tend to be less distinctively marked than southern ones, but the reticulate pattern is evident in some Panamanian specimens.

Despite the wide geographic range of the species as outlined by Goin (1964:4), he was reluctant to accept the occurrence of *fleischmanni* in Ecuador; he stated: "I have examined the specimen (USNM 60520) that Noble (1924:67) recorded as *fleischmanni* from Guevedo [=Quevedo, 56 km south of a locality where we obtained four specimens], Ecuador, and agree with him that this individual looks like typical *fleischmanni* from along the north coast of South America. It seems improbable to me, however, that this species actually occurs in Ecuador."

We have examined the type specimens of all of the nominal species included in the foregoing synonymy and have compared our findings with data obtained from series of living and preserved frogs. We conclude that the holotype of *Cochranella petersi* and KU 121052 represent the extreme in variation of webbing in *Centrolenella fleischmanni* and that *Cochranella petersi* Goin, 1961, is a junior synonym of *Centrolenella fleischmanni* (Boettger, 1893).

#### *Centrolenella grandisonae* Cochran and Goin

*Centrolenella grandisonae* Cochran and Goin, 1970:513 [Holotype.—BMNH 1910.7.11.68 from Pueblo Rico, Departamento Caldas, Colombia].

*Diagnosis*.—1) prevomerine teeth usually absent; 2) bones pale green; 3) parietal peritoneum white; visceral peritoneum clear; 4) color in life green with minute yellow, white, and black flecks; in preservative, pale lavender with small gray spots and white flecks; 5) webbing between outer fingers III $2\frac{1}{2}$ -2+IV; 6) webbing on foot II-2-III1-2-III1-2IV2+1 $\frac{1}{2}$ V; 7) snout round in dorsal and lateral profiles; 8) dorsal skin shagreened; 9) row of low, indistinct tubercles on ventrolateral edges of forearm and tarsus; 10) humeral spine present in males; 11) tympanum entirely visible, directed laterally with posterodorsal inclination.

Two other Ecuadorian species are lavender (in preservative) with dark spots and white flecks. Of these, *pipilata* differs from *grandisonae* by having ulnar and tarsal folds, truncate snout, and incised webbing. *Centrolenella peristicta* is nearly identical to *grandisonae* in coloration and structural features, except that *peristicta* has more webbing on the hand (1 $\frac{1}{2}$  phalanges free on fourth finger; 2+ free in *grandisonae*) and is smaller (mean snout-vent length 19.7 mm; 24.8 in *grandisonae*).

*Description*.—Adults moderately large; snout-vent length in males 23.7-25.8 mm ( $\bar{x}$ =24.8, N=4); females not known. Head about as wide as body; width of head 24.6-33.3 percent ( $\bar{x}$ =31.1, N=4) of



snout-vent length; snout short, rounded in dorsal view, in lateral view inclined above, truncate below, giving a rounded appearance; canthus rounded; loreal region barely concave; lips not flared; nostrils nearly terminal on snout, slightly protuberant dorsolaterally; internarial area slightly depressed. Eye large, directed anterolaterally. Supratympanic fold weak; entire tympanum visible, directed laterally with posterodorsal inclination. Prevomerine dentigerous processes and teeth absent; choanae small, round; tongue cordiform, notched behind, free posteriorly for about one-fourth of its length; vocal slits extending from midlateral base of tongue to angles of jaws.

Humeral spine blunt, perpendicular to humerus; row of low tubercles on ventrolateral edge of forearm; first finger longer than second; fourth finger much shorter than third; lateral fringes present on fingers; webbing absent between first and second fingers, vestigial between second and third fingers; webbing formula for outer fingers  $\text{III}(2\frac{1}{4}\text{-}2\frac{2}{3})\text{-(}2\text{-}2^+\text{)IV}$ ; discs truncate; subarticular tubercles small, round, simple; supernumerary tubercles absent; palmar tubercle ovoid, simple; nuptial excrescences absent (Fig. 3). Hind limbs slender; length of tibia 54.9-57.3 percent ( $\bar{x}$ =55.8,  $N$ =4) of snout-vent length; row of low, indistinct tubercles on ventrolateral edge of tarsus; inner metatarsal tubercle small, elliptical; outer metatarsal tubercle small, ovoid; subarticular tubercles small, round; supernumerary tubercles absent; toes about two-thirds webbed; webbing formula  $\text{I}(0\text{-}1\frac{1}{2})\text{-}1\frac{1}{3}\text{-}2^+\text{)II}(0\text{-}1)\text{-(}1\frac{1}{2}\text{-}2^+\text{)III}(1\text{-}1\frac{1}{4})\text{-(}2\text{-}2^+\text{)IV}(2\text{-}2\frac{1}{4})\text{-(}1\text{-}1\frac{1}{2})\text{V}$ ; discs smaller and more nearly round than those on fingers (Fig. 4).

Skin on dorsal surfaces shagreened; skin on belly and proximal posteroventral surfaces of thighs granular, other surfaces smooth; anal opening directed posteriorly at upper level of thighs; pair of large tubercles below anus.

Color in preservative: dorsal surfaces lavender with large dark smudges and small white flecks; other surfaces cream.

Color in life: green with minute yellow and white flecks and dark green and black spots on body and limbs; tips of digits pale yellow; humeral spine bluish green, vocal sac green; chest white; heart not visible; visceral peritoneum transparent; bones green; iris pale golden bronze flecked with black.

*Distribution.*—*Centrolenella grandisonae* occurs at moderate elevations on the Pacific slopes of the Cordillera Occidental of the Andes from southwestern Colombia to northwestern Ecuador (Fig. 7). In Colombia it is known from Pueblo Rico, 1540 m and Santa



Leticia, 2000 m, Departamento Caldas, and in Ecuador from Tandapi, 1460 m, Provincia Pichincha.

*Remarks.*—Three calling males were found along the small stream in cloud forest at Tandapi in July 1967. With the exception of one metamorphosing young found along the Río Tandapi, *grandisonae* was observed only along the one stream, where males were calling from leaves of bushes and trees by a waterfall. None of the other four species of *Centrolenella* known from Tandapi was found along this stream. The metamorphosing young has a snout-vent length of 13.5 mm and a tail stub of 2 mm.

The holotype of *grandisonae* is the largest known specimen of the species (27.4 mm) and is the only one having prevomerine teeth.

### *Centrolenella griffithsi* (Goin)

#### Plate 2C

*Cochranella griffithsi* Goin, 1961:99 [Holotype.—BMNH 1940.2.20.4 from Río Saloya, Provincia Pichincha, Ecuador].

*Centrolenella griffithsi* Goin, 1964:6.

*Diagnosis.*—1) prevomerine teeth absent; 2) bones pale green; 3) parietal peritoneum clear; visceral peritoneum white; 4) color in life yellowish green with or without dark flecks; in preservative, dull lavender; 5) webbing between outer fingers III3-2 $\frac{3}{4}$ IV; 6) webbing on foot I2-2 $\frac{1}{4}$ III1-2 $\frac{1}{4}$ III1-2 $\frac{1}{2}$ IV2 $\frac{3}{4}$ -IV; 7) snout truncate in dorsal and lateral profiles; 8) dorsal skin shagreened; 9) arms and legs lacking dermal folds; 10) humeral spine absent in males; 11) lower three-fourths of tympanum visible, directed dorsolaterally with posterior inclination.

The diagnostic characters of *griffithsi* resemble those of three other *Centrolenella*—*buckleyi*, *megacheira*, and *prosolepon*. Of these, *megacheira* is much larger and has pustular dorsal skin. *Centrolenella buckleyi* and *prosolepon* have more webbing, and the males have humeral spines.

*Description.*—Adults moderately large; snout-vent length 19.7-26.1 mm ( $\bar{x}$ =24.1, N=14) in males, 21.6-24.8 ( $\bar{x}$ =23.4, N=3) in females. Head slightly wider than body; width of head 30.6-34.7 percent ( $\bar{x}$ =32.3, N=17) of snout-vent length; snout short, truncate in dorsal and lateral profiles (Fig. 1); canthus round; loreal region concave; lips not flared; nostrils nearly terminal on snout, slight protuberant dorsolaterally; internarial area barely depressed. Eye moderately large, directed anterolaterally. Supratympanic fold barely evident; lower three fourths of tympanum visible, directed dorsolaterally with posterior inclination. Prevomerine dentigerous processes and teeth absent; choanae large, quadrangular; tongue



cordiform, distinctly notched behind, barely free posteriorly; vocal slits extending from midlateral base of tongue to angles of jaws.

Humeral spine absent; ulnar fold and tubercles absent; first finger longer than second; fourth finger noticeably shorter than third; lateral fringes absent on fingers; webbing absent between first, second, and third fingers; webbing formula for outer fingers III3-2 $\frac{3}{4}$ IV; discs broad, rounded; subarticular tubercles small, round, simple; supernumerary tubercles absent; palmar tubercle large, elliptical, simple; nuptial excrescences absent (Fig. 3). Hind limbs slender; length of tibia 52.4-62.3 percent ( $\bar{x}$ =55.2, N=17) of snout-vent length; tarsal folds and tubercles absent; inner metatarsal tubercle small, ovoid; outer metatarsal tubercle absent; subarticular tubercles small, round; supernumerary tubercles absent; feet about one-half webbed; webbing formula I(2-2 $^{+}$ )-(2 $^{+}$ -2 $\frac{1}{4}$ )II(1 $^{+}$ -1 $\frac{1}{2}$ )-(2 $\frac{1}{2}$ -3 $^{-}$ )III1 $\frac{1}{2}$ -(2 $\frac{1}{3}$ -3 $^{-}$ )IV(2 $\frac{1}{3}$ -3 $^{-}$ )-2-V; discs on toes smaller and more nearly round than those on fingers (Fig. 4).

Skin on dorsal surfaces shagreened; skin on belly and postero-ventral surfaces of thighs granular; other surfaces smooth; anal opening directed posteriorly at upper level of thighs; pair of large tubercles below anus.

Color in preservative: dorsal surfaces of head, body, forearms, shanks, and feet dull lavender with or without minute black flecks; other surfaces cream.

Color in life: dorsal surfaces pale yellowish green with or without dark green flecks; tips of digits pale yellow; chest white; heart not visible; visceral peritoneum transparent; bones pale green; iris whitish bronze.

*Distribution.*—*Centrolenella griffithsi* occurs on the Pacific slopes of the Cordillera Occidental of the Andes from southwestern Columbia to northwestern Ecuador (Fig. 9); the species inhabits cloud forests at elevations of 1200-2170 m.

*Remarks.*—Most of our specimens were obtained from low vegetation in cloud forest at Tandapi. Males were calling from leaves of herbs and bushes over cascading streams. One was found in the axil of an elephant-ear plant by day. Calling males were observed by Lynch on each of his five trips to Tandapi (March 1968, June 1968, July 1967, 1968, and 1970). Sparsely distributed and sporadically calling males were heard every evening at Tandapi, but the breeding season clearly is in March, when most available sites were occupied by calling males, and vegetation overhanging streams was festooned with egg masses. Eggs were not observed in June or July.

In July 1968, while we were collecting astroblepoid catfishes in the gravel at the bottom of a small stream, two centrolenid tadpoles



were found. These may be the tadpoles of *griffithsi*, the most abundant of the five species of *Centrolenella* known from Tandapi; only *griffithsi* adults were found along the stream. Structurally identical tadpoles were collected at Pilaló, Provincia Cotopaxi, 2500 m.

Goin (1969:99) gave the type locality as "Río Saloya, Ecuador, 4000 feet." This locality probably is the point on the Río Saloya where it is crossed by the road from Chillogallo to Santo Domingo de los Colorados, the only road west from Quito in 1940, when the specimens were collected. The point where the road crosses the Río Saloya is about 1200 m. The species is abundant in the next valley south, that of the Río Pilatón.

### *Centrolenella medemi* Cochran and Goin

*Centrolenella medemi* Cochran and Goin [Holotype.—USNM 152277 from Puerto Asís, Comisaria Putumayo, Colombia].

*Diagnosis*.—1) prevomerine teeth 2-3; 2) bone color unknown; 3) heart apparently not visible; 4) color in life unknown; in preservative, dark gray with many cream spots; 5) webbing between outer fingers III2-1½IV; 6) webbing on foot I0-0II0-0III0-1IV1-0V; 7) snout truncate in dorsal and lateral profiles; 8) dorsal skin smooth; 9) arms and legs lacking dermal folds; 10) small humeral spine present in males; 11) tympanum concealed.

*Centrolenella medemi* is unique among known centrolenids by having a dark gray dorsum with many large, round spots on all dorsal surfaces. The only other Amazonian species having humeral spines, *audax* and *pipilata*, have distinct tympana, less webbing, and a pale green dorsum with small yellow flecks (*audax*) or dark green with black spots and yellow flecks (*pipilata*).

*Description*.—Adult male moderate in size, 25.3 mm in snout-vent length; head much wider than body; width of head 39.5 percent of snout-vent length; snout moderately short, truncate in dorsal and lateral profiles; canthus round; loreal region barely concave; lips not flared; nostrils nearly terminal, not protuberant, directed dorso-laterally; internarial area flat. Eye moderately large, directed antero-laterally. Supratympanic fold absent; tympanum concealed. Prevomerine dentigerous processes short, transverse between choanae, bearing 2-3 teeth; choanae small, ovoid, near margin of mouth; tongue ovoid, barely free posteriorly; vocal slits extending from midlateral base of tongue towards angles of jaws.

Humeral spine curved, not projecting; ulnar folds and tubercles absent; lateral fringes absent on fingers; webbing formula I2-2½II2-3+III2-1½IV; discs large, truncate; subarticular tubercles large, round, simple; supernumerary tubercles absent; palmar tubercle



large, simple, ovoid; nuptial excrescences absent. Hind limbs robust; length of tibia 68.8 percent of snout-vent length; tarsal folds and tubercles absent; inner metatarsal tubercle low, elongate; outer metatarsal absent; subarticular tubercles small, round; supernumerary tubercles absent; feet essentially fully webbed; webbing formula  $I0-0II0-0III0-1IV1-0V$ ; discs on toes slightly smaller and more nearly round than those on fingers.

Skin on belly granular; skin on other surfaces smooth; anal opening directed posteriorly at upper level of thighs; anal folds and tubercles absent.

Color in preservative: all dorsal surfaces slate gray with many round cream spots; ventral surfaces cream. Color in life unknown.

*Distribution*.—Known only from the type locality at an elevation of about 280 m on the Río Putumayo in Amazonian Colombia (Fig. 7).

*Remarks*.—This distinctive species is included here in the anticipation that it will be found in Ecuador; the type locality is only 20 km north of the Ecuadorian border.

### ***Centrolenella megacheira* new species**

#### Plate 2A

*Holotype*.—KU 143245, an adult male, 27.1 mm, from a stream 16.5 km NNE of Santa Rosa, 1700 m. on Quito-Lago Agrio road, Provincia Napo, Ecuador, one of a series obtained on 17 October 1971, by Joseph T. Collins and William E. Duellman.

*Paratopotypes*.—KU 143246-72, BMNH 1971.1854-55, CAS 135498-9, UMMZ 131668 (3) obtained on 17-19 October 1971, by Joseph T. Collins and William E. Duellman.

*Diagnosis*.—1) prevomerine teeth absent; 2) bones green; 3) parietal peritoneum white; visceral peritoneum clear; 4) color in life green with black spots; in preservative, lavender with black spots; 5) webbing between outer fingers  $III3-2\frac{1}{2}IV$ ; 6) webbing on foot  $I2-2+III1\frac{1}{2}-2\frac{1}{2}III1\frac{1}{2}-2\frac{1}{4}IV3-1\frac{1}{3}V$ ; 7) snout truncate in dorsal and lateral profiles; 8) dorsal skin pustular; 9) arms and legs lacking dermal folds; 10) humeral spine absent in males; 11) lower three-fourths of tympanum visible, directed dorsolaterally with slight posterior inclination.

*Centrolenella megacheira* is distinguished from all other Andean species by its large size, pustular dorsal skin, and small amount of webbing on the hands and feet. The presence of black flecks on the dorsum also is characteristic of *prosoblepon*, males of which have humeral spines.



*Descriptions.*—Adults large; snout-vent length 27.1-32.8 mm ( $\bar{x}$ =28.2, N=20) in males, 32.1-32.8 mm ( $\bar{x}$ =32.5, N=3) in females. Head much wider than body; width of head 32.8-37.4 percent ( $\bar{x}$ =34.3, N=23) of snout-vent length; snout short, truncate in dorsal and lateral profiles; canthus rounded; loreal region slightly concave; lips barely flared; nostrils four-fifths distance from eye to tip of snout, slightly protuberant dorsolaterally; internarial area depressed. Eye large, directed more anteriorly than laterally. Supratympanic fold weak; lower three-fourths of tympanum visible, directed dorso-laterally with slight posterior inclination. Prevomerine dentigerous processes and teeth absent; choanae small, ovoid; tongue cordiform, barely free posteriorly; vocal slits extending from midlateral base of tongue to angles of jaws.

Humeral spine absent; ulnar fold and tubercles absent; hand large; first finger equal in length to second; fourth finger slightly shorter than third; lateral fringes present on fingers; webbing absent between first and second fingers; webbing formula for other fingers II( $2^+-2\frac{1}{2}$ )-(3 $\frac{1}{2}$ -3 $\frac{3}{4}$ )III( $2\frac{1}{2}$ -3 $^-$ )-(2 $\frac{1}{2}$ -3)IV; discs broader than deep, rounded; subarticular tubercles large, ovoid, simple; supernumerary tubercles absent; palmar tubercle large, ovoid, simple; nuptial excrescences absent. Hind limbs slender; length of tibia 53.7-62.3 percent ( $\bar{x}$ =56.9, N=23) of snout-vent length; tarsal folds and tubercles absent; inner metatarsal tubercle large, elliptical; outer metatarsal tubercle small, ovoid; subarticular tubercles small, round; supernumerary tubercles absent; feet about one-half webbed; webbing formula I(2 $^-$ -2)-(2 $^+$ -2 $\frac{1}{2}$ )II(1-1 $\frac{2}{3}$ )-(2 $\frac{1}{2}$ -2 $\frac{2}{3}$ )III(1 $\frac{1}{3}$ -1 $\frac{3}{4}$ )-(2 $\frac{1}{2}$ -3 $^-$ )IV(2 $\frac{2}{3}$ -3-1)-(1 $\frac{1}{2}$ -2 $^-$ )V; discs on toes slightly smaller and more nearly round than those on fingers.

Skin on dorsal surfaces pustular; skin on belly and ventral surfaces of thighs granular; other surfaces smooth; anal opening directed posteriorly at upper level of thighs; pair of large tubercles below anus.

Color in preservative: dorsal surfaces of head, body, hind limbs, and forearms lavender with small, round, black dots; hands, feet, upper arms, and ventral surfaces cream.

Color in life: dorsum green with black dots; flanks cream; chest white; heart not visible; visceral peritoneum unpigmented; other ventral surfaces green; iris pale grayish bronze; bones green.

*Distribution.*—The species currently is known at two localities at elevations of 1700 and 1740 m on the Amazonian slopes of the Cordillera Oriental in Ecuador (Fig. 9). The type locality is a small stream which drains into a tributary of the Río Salado. This stream



is crossed by the Quito-Lago Agrio road at a point 16.5 km north-northeast of the village of Santa Rosa.

*Remarks.*—Individuals were found at night on leaves and stems of bushes and trees overhanging streams in cloud forest. Males were calling in October 1971. At the type locality, *audax*, *pipilata*, and *siren* were found with *megacheira*; at the Río Azuela, *anomala*, *pelucida*, *pipilata*, and *siren* occurred along the same streams with *megacheira*.

*Etymology.*—The specific name is from the Greek *megas*, meaning large, and the Greek *cheiros*, meaning hand; the name is used in reference to the exceedingly large hands of this species.

### ***Centrolenella midas* new species**

#### Plate 1D

*Holotype.*—KU 123219, an adult male, 19.2 mm, from Santa Cecilia, 340 m, Provincia Napo, Ecuador, obtained on 22 June 1968, by Linda Trueb.

*Paratypes.*—KU 107026, 23 November 1966, William E. Duellman; KU 146625, 2 April, Martha L. Crump; KU 150622, 25 June 1971, Philip S. Humphrey; KU 150623, 28 August 1971, Martha L. Crump, all from the type locality. KU 125334, 23 May 1969, Thomas H. Fritts, and UMMZ 129314, 6 May 1969; Charles F. Walker from Lago Agrio, 330 m, Provincia Napo, Ecuador.

*Diagnosis.*—1) prevomerine teeth 1-3; 2) bones green; 3) parietal peritoneum white; visceral peritoneum clear; 4) color in life dark green with yellow flecks; in preservative, lavender with white flecks; 5) webbing between outer fingers III2-2-IV; 6) webbing on foot I1-2III1-2III1-2+IV2+-IV; 7) snout truncate in dorsal and lateral profiles; 8) dorsal skin shagreened; 9) arms and legs lacking dermal folds; 10) humeral spine absent in males; 11) lower two-thirds of tympanum visible, directed dorsolaterally with strong posterior inclination.

*Centrolenella midas* is like *flavopunctata* and *siren* in having a lavender dorsum with white flecks (in life, green with gold flecks) and no black flecks; it differs from *flavopunctata* by having a truncate, instead of round snout and slightly less webbing on the hands and feet. *Centrolenella siren* differs from *midas* by having less webbing and a more prominent tympanum oriented posterolaterally, instead of dorsolaterally.

*Description.*—Adults small; snout-vent length 17.4-19.2 mm ( $\bar{x}$ =18.4, N=3) in males, 20.6-25.6 mm ( $\bar{x}$ =22.7, N=7) in females. Head wider than body; width of head 33.3-39.1 percent ( $\bar{x}$ =36.0, N=10) of snout-vent length; snout short, truncate in dorsal and lateral profiles;



canthus round; loreal region concave; lips rounded; nostrils nearly terminal on snout, slightly protuberant dorsolaterally; internarial area depressed. Eye moderately large, directed anterolaterally. Supratympanic fold absent; lower two-thirds of tympanum visible, directed dorsolaterally with strong posterior inclination. Dentigerous processes of prevomers small, low, widely separated between moderately large, round choanae, bearing 1-3 teeth; tongue broadly cordiform, barely free posteriorly; vocal slits extending from mid-lateral base of tongue to angles of jaws.

Humeral spine absent; ulnar fold and tubercles absent; first finger longer than second; fourth finger noticeably shorter than third; webbing vestigial between first and second fingers; webbing formula for other fingers  $II(2-2^+)-(3^+-3\frac{1}{2})III(2^--2^+)-(1\frac{1}{2}-2^+)IV$ ; discs truncate; subarticular tubercles small, round, simple; supernumerary tubercles absent; palmar tubercle large, elliptical; nuptial excrescences absent. Hind limbs moderately slender; length of tibia 53.1-62.0 percent ( $\bar{x}=57.7$ ,  $N=10$ ) of snout-vent length; tarsal folds and tubercles absent; inner metatarsal tubercle elongate, rounded in section; outer metatarsal tubercle absent; subarticular tubercles small, round; supernumerary tubercles absent; feet about two-thirds webbed; webbing formula  $I(0-1\frac{1}{3})-(2^--2^+)II(\frac{1}{2}-1)-(2-2^+)III1-(2-2\frac{1}{4})IV(2-2^+)-IV$ ; discs on toes more nearly round than those on fingers.

Skin on dorsal surfaces shagreened; skin on belly and proximal posteroventral surfaces of thighs granular; other surfaces smooth; anal opening directed posteriorly at upper level of thighs; pair of large tubercles below anus.

Color in preservative: dorsal surfaces of head, body, and limbs lavender with few small white flecks on body; other surfaces creamy white.

Color in life: dorsum of head, body, and limbs dark green with a few small yellow flecks dorsolaterally on body; hands and feet dull greenish yellow; chest white; heart not visible; visceral peritoneum unpigmented; iris silvery bronze with black reticulations; bones green.

*Distribution*.—This species is known from three localities at elevations of 330-570 m along the Río Aguarico in the upper Amazon Basin in Ecuador (Fig. 9). In this area it occurs in sympatry with *munozorum* and *resplendens*.

*Remarks*.—Individuals have been found throughout the year on leaves of herbs and trees along small rivulets in rainforest. The call consists of three short notes.

*Etymology*.—The specific name is that of a king in Greek mythology, at whose touch everything turned to gold. The name is



associated with this frog known along the Río Aguarico, meaning rich water, in reference to gold found in the river, and in allusion to the gold flecks on the frogs.

***Centrolenella munozorum* new species**

Plate 1B

*Holotype*.—KU 118054, an adult male, 20.2 mm, from Santa Cecilia, 340 m, Provincia Napo, Ecuador, obtained on 18 June 1967, by John D. Lynch.

*Paratypes*.—KU 105251, 13 July 1966, Charles M. Fugler; KU 123225, 13 July 1968, William E. Duellman; KU 150620, 13 August 1971, Martha L. Crump; KU 150621, 10 October 1971, Martha L. Crump, all from Santa Cecilia, and UMMZ 129313 from Lago Agrio, 330 m, 14 km E Santa Cecilia, Provincia Napo, Ecuador, 6 May 1969, Charles F. Walker.

*Diagnosis*.—1) prevomerine teeth absent; 2) bones white; 3) parietal peritoneum clear; visceral peritoneum white; 4) color in life pale green with pale greenish yellow spots; in preservative, creamy white with pale gray reticulations; 5) webbing between outer fingers III1½-1¼IV; 6) webbing on foot I0-III0-1½III1-2IV2-IV; 7) snout round in dorsal and lateral profiles; 8) dorsal skin shagreened; 9) arms and legs lacking dermal folds; 10) humeral spine absent in males; 11) tympanum concealed; strongly directed dorsolaterally.

Two other Ecuadorian species have the heart visible in life and a white dorsum in preservative. *Centrolenella pellucida* differs from *munozorum* by having ulnar, tarsal, and anal folds, and *fleischmanni* differs by having the snout subacuminate in dorsal view and truncate in lateral profile and the tympanum is distinct; in *munozorum* and *pellucida* the snout is round, and the tympanum is concealed. The Venezuelan *orocostalis* has enamel white (yellow in life) flecks on the dorsum.

*Description*.—Adults small; snout-vent length in males 18.8-20.5 mm ( $\bar{x}$ =19.7, N=5), in one female 20.7 mm. Head wider than body; width of head 37.7-40.7 percent ( $\bar{x}$ =38.4, N=6) of snout-vent length; snout short, shallow, round in dorsal and lateral profiles (Fig. 1); canthus round; loreal region shallowly concave; lips slightly flared; nostrils about four-fifths distance from eye to tip of snout, barely protuberant, directed dorsolaterally; internarial area slightly depressed. Eye moderately large, protuberant, directed anterolaterally. Supratympanic fold absent; tympanum concealed, strongly directed dorsolaterally. Prevomerine dentigerous processes and teeth absent; choanae small, ovoid, near margin of mouth; tongue ovoid, barely



free posteriorly; vocal slits extending from posterolateral base of tongue to angles of jaws.

Humeral spine absent; ulnar fold and tubercles absent; first finger longer than second; fourth finger nearly as long as third; lateral fringes present on fingers; webbing vestigial between first and second and second and third fingers; webbing formula for outer fingers III(1½-2⁻)-(1-1½)IV; discs small, rounded, subarticular tubercles small, round, simple; supernumerary tubercles present on proximal segments of first and second fingers; palmar tubercle small, round; nuptial excrescences absent (Fig. 3). Hind limbs slender; length of tibia 57.5-59.6 percent ( $\bar{x}$ =58.4, N=5) of snout-vent length in males, 54.1 percent in one female; tarsal folds and tubercles absent; inner metatarsal tubercle small, elongate; outer metatarsal tubercle absent; subarticular tubercles small, round; supernumerary tubercles absent; fringe on inner edge of first toe; toes about three-fourths webbed; webbing formula I0-(1-⅔)II(0-1)-(1½-2⁻)III(0-1)-(2⁻-2⁺)IV(2-2)-(0-1)V; discs on toes round, slightly smaller than those on fingers.

Skin on dorsal surfaces of head and body shagreened; skin on belly and proximal ventral surfaces of thighs weakly granular; other surfaces smooth; anal opening directed posteriorly at upper level of thighs; anal folds and tubercles absent.

Color in preservative: dorsal surfaces of head, body, forearms, thighs, and shanks creamy white with many minute black flecks giving appearance of gray with unpigmented spots; eyelid and hepatic peritoneum white; other surfaces unpigmented.

Color in life: dorsum pale green with pale yellow or yellowish green spots; limbs pale green, with slightly darker crossbars in one; thighs unpigmented; iris pale gold.

*Distribution.*—Currently this species is known from only two localities along the Río Aguarico in the Amazonian lowlands of Ecuador (Fig. 10).

*Remarks.*—All individuals were found in lowland rainforest. At Santa Cecilia the frogs were found on leaves of bushes and trees at night: one over a pond, one away from water in primary forest, one on a palm frond 2 m above a stream, and one on an herbaceous leaf more than 2 m above a stream. The specimen from Lago Agrio was obtained from the foliage of a large tree that was felled during the clearing of primary forest.

*Etymology.*—The specific name is a patronym for Ing. Ildefonso Muñoz B. and Sra. Blanca Muñoz, our congenial hosts at Santa Cecilia.



**Centrolenella ocellifera** (Boulenger)

*Hyla ocellifera* Boulenger, 1899:277 [Holotype.—BMNH 98.5.19.3 from Paramba, Provincia Imbabura, Ecuador].

*Cochranella ocellifera*—Taylor, 1951:35.

*Centrolenella ocellifera*—Goin, 1964:6.

*Diagnosis*.—1) prevomerine teeth absent; 2) bones white (?); 3) parietal peritoneum white; visceral peritoneum clear; 4) color in life green with yellow spots; in preservative, pale lavender with faint purple ocelli enclosing white spots; 5) webbing between outer fingers III2-1 $\frac{3}{4}$ IV; 6) webbing on foot I1-2III1-2III1-2IV2<sup>+</sup>-IV; 7) snout round in dorsal view, truncate in lateral profile; 8) skin shagreened; 9) arms and legs lacking dermal folds; 10) humeral spine absent in males; 11) lower two-thirds of tympanum visible, directed laterally with slight posterodorsal inclination.

*Centrolenella ocellifera* has shagreened skin and few large ocelli on the dorsum. Other species having ocellated dorsal patterns (*anomala*, *cochranae*, and *ocellata*) have minute spicules in the dorsal skin and less webbing between the outer fingers. Furthermore, *ocellifera* differs from *anomala* by having a green instead of brown dorsum, from *ocellata* by having the lower two-thirds of the tympanum visible (concealed in *ocellata*), and from *cochranae* by having larger ocelli, snout round in dorsal view, and prevomerine teeth absent (*cochranae* has small ocelli, snout truncate in dorsal view, and prevomerine teeth usually present).

*Description*.—Adults moderate-sized; snout-vent length 20.0 mm in male, 26.7 mm in female. Head as wide as body; width of head 32.9-37.0 percent ( $\bar{x}$ =35.0, N=2) of snout-vent length; snout short, round in dorsal view, truncate in lateral profiles; canthus round; loreal region concave; lips slightly flared; nostrils four-fifths distance from eye to tip of snout, not protuberant, directed laterally; internarial area flat. Eye large, protuberant, directed anterolaterally. Supratympanic fold not evident; lower two-thirds of tympanum visible, directed laterally with slight posterodorsal inclination. Prevomerine teeth absent in one male, 2-3 on transverse processes between choanae in one female; choanae small, rectangular; tongue ovoid, slightly free posteriorly.

Humeral spine absent; ulnar folds and tubercles absent; first finger larger than the second; fourth finger nearly as long as third; fingers extensively webbed; webbing formula I2 $\frac{3}{4}$ -2III2-3III2-(1 $\frac{1}{2}$ -1 $\frac{3}{4}$ )IV; fringe on outer edge of fourth finger; discs moderately broad, truncate; subarticular tubercles small, round, simple (distal tubercle on fourth fingers bifid in female); supernumerary tubercles absent; palmar tubercle single, ovoid; nuptial excrescences absent. Hind



limbs long, slender; tibia length 52.4-59.5 percent ( $\bar{x}$ =55.9, N=2) of snout-vent length; tarsal folds and tubercles absent; inner metatarsal tubercle moderately small, elliptical; outer metatarsal tubercle absent; subarticular tubercles small, round; supernumerary tubercles absent; feet about three-fourths webbed; webbing formula II-2III-2-III(1-1)-2IV2<sup>+</sup>-1V; fringe on inner edge of first toe; discs on toes smaller and more nearly round than those on fingers.

Skin on dorsal surfaces shagreened, that on belly and ventral surfaces of thighs weakly granular; other surfaces smooth; anal opening directed posteriorly at upper level of thighs; anal folds and tubercles absent.

Color in preservative: dorsal surfaces of head, body, and shanks pale lavender, scattered dark brown flecks; three or four thin purple ocelli with cream centers in scapular region (Fig. 5); chest and belly cream; other surfaces transparent.

Color in life: body green with pale yellow spots and dark green flecks on body; limbs paler green; chest white; heart not visible; visceral peritoneum transparent; iris gray-bronze.

*Distribution.*—*Centrolenella ocellifera* inhabits the Pacific slopes of the Andes (Fig. 6). In addition to the holotype from Paramba (777 m), we have a specimen from Tandapi (1460 m) and have seen a specimen in the Gustavo Orcés-V. collection in the United States National Museum from Pilaló (2320 m).

*Remarks.*—Our specimen was found at night on a fern in cloud forest. The fern was at the edge of a cliff about 10 m above the Río Pilatón.

### ***Centrolenella pellucida* new species**

#### Plate 1C

*Holotype.*—KU 143298, a gravid female, 22.0 mm from the Río Azuela, 1740 m, Quito-Lago Agrio road, Provincia Napo, Ecuador, obtained on 20 October 1971, by William E. Duellman.

*Diagnosis.*—1) prevomerine teeth absent; 2) bones white; 3) parietal peritoneum clear; visceral peritoneum white; 4) color in life pale green with diffuse yellow spots; in preservative, uniform cream; 5) webbing between outer fingers III2<sup>+</sup>-2IV; 6) webbing on foot II-2+III-1½III1-2+IV2<sup>+</sup>-1V; 7) snout round in dorsal and lateral profiles; 8) dorsal skin shagreened; 9) unscalloped dermal fold on outer edge of hand and forearm and on foot and tarsus; transverse dermal fold below anus; 10) humeral spine absent in males; 11) tympanum concealed.

Among the Ecuadorian species (*fleischmanni*, *pellucida*, and *munozorum*) having the heart visible in life and the dorsum white



in preservative, *C. pellucida* is unique in possessing ulnar, tarsal, and anal folds. Moreover, in *C. fleischmanni* the snout is subacuminate in dorsal view and truncate in lateral profile, and the tympanum is distinct; in *C. pellucida* and *C. munozorum* the snout is round, and the tympanum is concealed. The Venezuelan *orocostalis*, a member of the *fleischmanni* group, also lacks dermal folds.

*Description*.—Males unknown; adult female small, 22.0 mm in snout-vent length; head slightly wider than body; width of head 36.4 percent of snout-vent length; snout short, round in dorsal and lateral profiles; canthus round; loreal region barely concave; lips not flared; nostrils nearly terminal, directed laterally, not protuberant; internarial area flat. Eye large, protuberant, strongly oriented anteriorly. Supratympanic fold absent; tympanum concealed. Prevomerine dentigerous processes and teeth absent; choanae large, oval; tongue ovoid, barely free posteriorly.

Humeral spine absent; narrow, unscalloped dermal fold on ventrolateral edge of forearm and outer edge of hand; fringes absent on fingers; first finger longer than second; fourth finger slightly shorter than third; fingers extensively webbed; webbing formula  $I2-2+II2-3III2+2IV$ ; discs moderately large, rounded; subarticular tubercles small, low; supernumerary tubercles absent; palmar tubercle small, indistinct. Hind limbs slender; tibia length 56.4 percent of snout-vent length; narrow, unscalloped dermal fold along outer edge of tarsus and fifth toe; inner metatarsal tubercle small, ovoid; outer metatarsal tubercle absent; subarticular tubercles small, low; supernumerary tubercles absent; feet about three-fourths webbed; webbing formula  $II-2III1-1\frac{1}{2}III1-2+IV2+IV$ ; discs on toes round, slightly smaller than those on fingers.

Skin on dorsum of head and body shagreened; skin on other surfaces smooth; anal opening directed posteriorly at upper level of thighs; transverse dermal fold below anus at posteroventral edge of thighs (Fig. 2).

Color in preservative: dorsum creamy white with minute purple flecks visible under magnification; hepatic peritoneum white; skin on ventral surfaces transparent.

Color in life: dorsum pale green with diffuse yellow spots; venter and hidden surfaces of limbs lacking pigment; fingers and toes yellow; parietal peritoneum clear; heart visible; bones white; iris pale silvery bronze.

*Distribution*.—This small species is known only from the type locality on the east slope of Volcán Reventador on the Amazonian slopes of the Andes (Fig. 10).

*Remarks*.—The holotype was on the leaf of an herb over a small



stream at night. See the account of *anomala* for a detailed description of the type locality and comments on associated species.

*Etymology*.—The specific name is Latin meaning transparent and is applied to this species having a transparent parietal peritoneum.

***Centrolenella peristicta* new species**

Plate 2G

*Holotype*.—KU 118051, an adult male, 20.6 mm, from Tandapi, 1460 m, Provincia Pichincha, Ecuador, obtained on 23 July 1967, by John D. Lynch.

*Paratopotypes*.—KU 118052, 24 July 1967, Marsha Lynch; 121053, 28 July 1968, Gerald R. Smith.

*Diagnosis*.—1) prevomerine teeth absent; 2) bones pale green; 3) parietal peritoneum white; visceral peritoneum clear; 4) color in life pale green with minute yellow, white, and black flecks; in preservative, pale lavender with dark lavender spots and few white flecks; 5) webbing between outer fingers III<sub>2</sub>-1½IV; 6) webbing on foot I1-2 III1-2 III1-2+IV2-1V; 7) snout round in dorsal and lateral profiles; 8) dorsal skin shagreened; 9) row of low tubercles on ventrolateral edges of forearm and tarsus; 10) humeral spine present in males; 11) tympanum entirely visible, directed laterally with slight dorsal inclination.

Two other Ecuadorian species are lavender (in preservative) with dark spots and white flecks. Of these *pipilata* differs from *peristicta* by having ulnar and tarsal folds, truncate snout, and incised webbing. *Centrolenella grandisonae* is nearly identical to *peristicta* in coloration and structural features, except that *grandisonae* has less webbing on the hand (2+ phalanges free on fourth finger; 1½ free in *peristicta*) and is larger (mean snout-vent length 24.8 mm; 19.7 mm in *peristicta*).

*Description*.—Adults small; snout-vent length 18.7-20.6 mm ( $\bar{x}$ =19.7, N=2) in males, 20.5 mm in one female. Head no wider than body; width of head 32.5-32.7 percent ( $\bar{x}$ =32.6, N=3); snout short, round in dorsal and lateral profiles; canthus round; loreal region concave; lips rounded; nostrils nearly terminal on snout, slightly protuberant dorsolaterally; internarial area depressed. Eye moderate sized, directed more laterally than anteriorly. Supratympanic fold weak; tympanum entirely visible, directed laterally with slight dorsal inclination. Prevomerine dentigerous processes and teeth absent; choanae small, ovoid; tongue cordiform, shallowly notched behind, barely free posteriorly; vocal slits extending from midlateral base of tongue to angles of jaws.

Humeral spine curved, terminus parallel to humerus; row of low



tubercles on ventrolateral edge of forearm; first finger longer than second; fourth finger much shorter than third; lateral fringes present on fingers; webbing vestigial between first and second fingers; webbing formula for other fingers  $II(2-2\frac{1}{2})-3+III2-1\frac{1}{2}IV$ ; discs truncate; subarticular tubercles small, round; distal subarticular tubercle on fourth finger bifid; supernumerary tubercles small, round, present on proximal segments of digits 2-4; palmar tubercle large, ovoid; nuptial excrescences absent (Fig. 3). Hind limbs slender; length of tibia 52.2-58.8 percent ( $\bar{x}=54.8$ ,  $N=3$ ) of snout-vent length; row of low tubercles on ventrolateral edge of tarsus; inner metatarsal tubercle elliptical; outer metatarsal tubercle small, ovoid; subarticular tubercles small, round; supernumerary tubercles absent; feet about two-thirds webbed; webbing formula  $II-(1\frac{1}{2}-2)III-(2-2^+)III1-(2-2^+)IV(2-2^+)-1V$ ; discs smaller and more nearly round than those on fingers.

Skin on dorsum shagreened; skin on belly and proximal postero-ventral surfaces of thighs granular; other surfaces smooth; anal opening directed posteriorly at upper level of thighs; pair of large tubercles below anal opening.

Color in preservative: dorsal surfaces lavender with dark spots and scattered cream flecks; other surfaces cream.

Color in life: dorsal surfaces pale to medium green with dark green spots and white and yellow flecks; flanks yellow-green; belly yellow; vocal sac green; tips of digits pale yellow; heart not visible; bones green; iris grayish bronze with brown or copper ring around pupil.

*Distribution*.—This species is known only from Tandapi (formerly Cornejo Astorga), a village at the point where the Quito-Santo Domingo de los Colorados road crosses the Río Pilatón at an elevation of 1460 m on the Pacific slopes of the Cordillera Occidental of the Andes (Fig. 8).

*Remarks*.—All three individuals were obtained in July on vegetation in cloud forest at night. One was on an elephant-ear leaf; one was on a fern in the spray zone of a waterfall, and one was on a bush over a waterfall. None was calling.

*Etymology*.—The specific name is derived from the Greek *peristiktos*, meaning dappled, and refers to the spotted color pattern.

### ***Centrolenella pipilata* new species**

#### Plate 2D

*Holotype*.—KU 143278, an adult male, 22.9 mm, from a stream 16.5 km NNE of Santa Rosa, 1700 m, on Quito-Lago Agrio road,



Provincia Napo, Ecuador, obtained on 17 October 1971, by William E. Duellman.

*Paratopotypes*.—KU 143279-83, 17-18 October 1971, William E. Duellman and Joseph T. Collins.

*Diagnosis*.—1) prevomerine teeth absent; 2) bones green; 3) parietal peritoneum white; visceral peritoneum clear; 4) color in life dark green with diffuse black spots and pale yellow flecks; in preservative, gray with dark and pale flecks; 5) webbing between outer fingers  $\text{III}2\frac{1}{4}\text{--}2\frac{2}{3}\text{IV}$ ; 6) webbing on foot indented  $\text{II-}2\text{+III-}2\text{+III-}2\frac{1}{2}\text{IV}2\frac{2}{3}\text{--IV}$ ; 7) snout truncate in dorsal and lateral profiles; 8) dorsal skin shagreened with elevated warts corresponding to pale flecks; 9) unscalloped fringe on outer edge of hand, forearm, and foot; fringe with low scallops on tarsus; 10) humeral spine present in males; 11) tympanum entirely visible, directed posterolaterally with no dorsal inclination.

*Centrolenella pipilata* resembles two other Ecuadorian species in coloration, but both *grandisonae* and *peristicta* differ in having ulnar and tarsal tubercles instead of folds and in having round, instead of truncate, snouts. Two other Ecuadorian species have ulnar and tarsal folds; *pellucida* is white in preservative and in life lacks markings and a white peritoneum, whereas *resplendens* is a much larger, fringe-limbed frog. Males of both of those species lack humeral spines.

*Description*.—Adults moderately small; snout-vent length 19.5-22.9 mm ( $\bar{x}$ =21.5,  $N$ =10) in males, 21.8-22.1 mm ( $\bar{x}$ =21.9,  $N$ =2) in females. Head noticeably wider than body; width of head 32.9-38.9 percent ( $\bar{x}$ =35.2,  $N$ =12) of snout-vent length; snout extremely short, truncate in dorsal and lateral profiles; canthus round; loreal region barely concave; lips not flared; nostrils three-fourths distance from eye to tip of snout, protuberant anterodorsolaterally; internarial area slightly depressed. Eye large, protuberant, directed more anteriorly than laterally. Supratympanic fold weak; tympanum entirely visible, directed posterolaterally with no dorsal inclination. Prevomerine dentigerous processes and teeth absent; choanae small, ovoid; tongue cordiform, shallowly notched behind, barely free posteriorly; vocal slits extending from midlateral base of tongue to angles of jaws.

Humeral spine blunt, oriented at about  $30^\circ$  from humerus; unscalloped dermal fringe on ventrolateral edge of forearm and outer edge of hand; first finger longer than second; fourth finger noticeably shorter than third; lateral fringes on fingers; webbing absent between first, second, and third fingers; webbing formula for outer fingers  $\text{III}(2\text{+}2\frac{1}{2})\text{--}(2\text{+}2)\text{IV}$ ; webbing incised; discs broad, rounded; subarticular tubercles moderately large, subconical, simple; super-



numerary tubercles small, present on proximal segments of all digits; palmar tubercle large, ovoid; nuptial excrescences absent. Hind limbs moderately slender; length of tibia 55.7-61.9 percent ( $\bar{x}$ =59.7,  $N=12$ ) of snout-vent length; scalloped dermal fold on ventrolateral edge of tarsus; unscalloped dermal fold on outer edge of foot; inner metatarsal tubercle large, ovoid; outer metatarsal tubercle small, round; subarticular tubercles small, round; supernumerary tubercles minute, present on proximal segments of digits; toes about two-thirds webbed; webbing formula I(1-1½)-(2-2⁺)III-(2-2⅔)III(1-1¼)-(2⁺-2½)IV(2⅓-2½)-(1-1½)V; discs on toes slightly smaller than those on fingers.

Skin on dorsal surfaces shagreened with elevated warts corresponding to white spots; skin on belly and ventral surfaces of thighs granular; other surfaces smooth; anal opening directed posteroventrally at midlevel of thighs; many small and two large tubercles below anus.

Color in preservative: all dorsal surfaces lavender with dark spots and white dots; ventral surfaces cream.

Color in life: dorsum dark green with diffuse black flecks and pale yellow flecks; flecks on side of head silvery white; chest white; heart not visible; other ventral surfaces pale green; discs pale yellow; bones green; iris pale bronze with black reticulations.

*Distribution*.—In Ecuador, *C. pipilata* is known from two localities (1700 and 1740 m) on the Amazonian slopes of the Cordillera Oriental of the Andes (Fig. 8).

*Remarks*.—All individuals were found at night on vegetation along cascading mountain streams in cloud forest. Both females were in amplexus; one deposited a clutch of 18 eggs having clear jelly and pale green yolks. At the Río Azuela, *pipilata* was found in sympatry with *anomala*, *megacheira*, *pellucida*, and *siren*, and at 16.5 km north-northeast of Santa Rosa, it was found with *audax*, *megacheira*, and *siren*.

At first we thought our specimens might be *Centrolenella johnelsi* Cochran and Goin, but the much larger size of *johnelsi* (♂ 29.3 mm) and certain structural differences negated this assignment. Furthermore, *johnelsi* is known only from San Pedro, Departamento Antioquia, in northern Colombia.

See the account of *megacheira* for a description of the type locality.

*Etymology*.—The specific name is an adjectival derivative of the Latin verb *pipila*, meaning to peep, and refers to the characteristic call of this and many other centrolenid frogs.



**Centrolenella prosoblepon** (Boettger)

## Plate 2F

*Hyla prosoblepon* Boettger, 1892:45 [Syntypes.—SMF 3756 and ZMB 28019 from "Plantago Cairo" (La Junta), near Limón, Provincia Limón, Costa Rica].

*Hyella puncticrus* Boulenger, 1896:431 [Syntypes.—BHNH 96.10.8.70-71 from La Palma, Provincia San José, Costa Rica].

*Hyla parabambae* Boulenger, 1898:125 [Holotype.—BMNH 98.4.28.163 from Paramba, Provincia Imbabura, Ecuador]. New synonym.

*Centrolene prosoblepon*—Noble, 1924:66.

*Centrolene parambae* (emendation)—Dunn, 1933:73.

*Cochranella parambae*—Taylor, 1951:35.

*Cochranella parabambae*—Taylor, 1951:35.

*Centrolenella prosoblepon*—Goin, 1964:5.

*Centrolenella parabambae*—Goin, 1964:6.

**Diagnosis.**—1) prevomerine teeth 0-4; 2) bones green; 3) parietal peritoneum white; visceral peritoneum clear; 4) color in life green, usually with black dots; in preservative, lavender, usually with dark lavender dots; 5) webbing between outer fingers III2-1½IV; 6) webbing on foot I1-2III1-2+III1-2IV2+1V; 7) snout round in dorsal view, truncate in lateral profile; 8) dorsal skin shagreened; 9) arms and legs lacking dermal folds; 10) humeral spine present in males; 11) lower two-thirds of tympanum visible, directed dorso-laterally with posterior inclination.

This species most closely resembles *megacheira* and *griffithsi*, both of which have less webbing and lack humeral spines in males. *Centrolenella megacheira* further differs from *prosoblepon* by having much larger hands and pustular, instead of shagreened, skin on the dorsum. Unspotted *prosoblepon* are colored like *buckleyi*, which also has humeral spines in males, but *buckleyi* has less webbing, an inclined snout, and only the lower one-fourth of the tympanum visible.

**Description.**—Adults large, snout-vent length 21.7-25.6 mm ( $\bar{x}$ =24.1, N=5) in males, 25.4-27.2 mm ( $\bar{x}$ =26.4, N=3) in females. Head slightly wider than body; width of head 33.1-35.6 percent ( $\bar{x}$ =34.1, N=8) of snout-vent length; snout moderately short, round in dorsal view, truncate in lateral profile; canthus round; loreal region concave; lips slightly flared; nostrils three-fourths distance from eyes to tip of snout, slightly protuberant dorsolaterally; internarial area slightly depressed. Eye moderately large, directed anterolaterally. Supratympanic fold weak; lower two-thirds of tympanum visible, directed dorsolaterally with posterior inclination. Prevomerine dentigerous processes posteromedially inclined, narrowly separated medially between moderately large, ovoid choanae, bearing 0-4 teeth; tongue broadly cordiform, shallowly notched behind, barely



free posteriorly; vocal slits extending from posterolateral edges of tongue to angles of jaws.

Humeral spine pointed, oriented about  $30^\circ$  anterior to humerus; ulnar fold and tubercles absent; first finger longer than second; fourth finger slightly shorter than third; lateral fringes present on fingers; webbing absent between first and second fingers, vestigial between second and third; webbing formula for outer fingers III(2-2<sup>+</sup>)-(1-1½)IV; discs broad, truncate; subarticular tubercles small, round, simple; supernumerary tubercles absent; palmar tubercle large, ovoid, simple; nuptial excrescences absent. Hind limbs moderately slender; length of tibia 51.4-57.6 percent ( $\bar{x}$ =54.6, N=8) of snout-vent length; tarsal folds and tubercles absent; inner metatarsal tubercle small, flat, elliptical; outer metatarsal tubercle small, ovoid; subarticular tubercles small, round; supernumerary tubercles absent; feet about two-thirds webbed; webbing formula I(1-1½)-(2<sup>+</sup>-2<sup>+</sup>)III-(2-2<sup>+</sup>)III1-(2<sup>-</sup>-2<sup>+</sup>)IV(2-2<sup>+</sup>)-IV; discs truncate, slightly smaller than those on fingers.

Skin on dorsal surfaces of head, body, forearms, and shanks shagreened; skin on belly and posteroventral surfaces of thighs granular; other surfaces smooth; anal opening directed posteroventrally at upper level of thighs; pair of large tubercles below anus.

Color in preservative: dorsal surfaces, exclusive of two inner fingers and first three toes lavender, usually with numerous small dark lavender dots; other surfaces cream.

Color in life: dorsal surfaces green with or without black flecks; tips of digits pale yellow; chest white; heart not visible; throat green; bones green; iris grayish white to pale bronze with brown or gray flecks.

*Distribution*.—This species occurs to elevations of about 1200 m from lower Central America (Caribbean and Pacific slopes in Costa Rica and Panamá) southward on Pacific slopes and lowlands to western Ecuador, where it has been taken at elevations of 220 to 800 m (Fig. 7). We have examined two specimens from the Pacific versant of Colombia. Cochran and Goin (1970:508) listed *C. parabambae* from Medellín, Río Mecaya, and Serranía de Macarena, Colombia. The last two localities are east of the Andes, so it is doubtful if the specimens from there actually are *prosoblepon*.

*Remarks*.—The identity of *Centrolenella parabambae* has been greatly confused in the literature. As noted by Savage (1967:330): "Apparently the name [*C. parabambae*] has been applied to any population of small, uniformly lavender (in preservative) centrolenids with vomerine teeth from Panama, Colombia, and Ecuador." Savage noted that Panamanian frogs referred to "*parambae*" by



Dunn (1933) are *spinosa*. Two characteristics of *parabambae* (as given in the type description by Boulenger, 1898) are responsible for the confusion: 1) absence of a humeral spine; the holotype is a female; 2) uniformly lavender dorsum, except for dark flecks on hind limbs.

We compared a nearly uniformly lavender female (KU 121055) from Santo Domingo de los Colorados, Ecuador, with the holotype and noted that structurally the two frogs were identical; the holotype has small indefinite dark flecks on the thighs, shanks, and feet, whereas KU 121055 has one fleck on one shank and two and three flecks on the feet. Subsequent comparison of KU 121055 with two females and five males of *prosoblepon* from Ecuador revealed that the only differences were in the numbers and disposition of dark flecks on the dorsum. The numbers of flecks in the nine specimens are (average value for limbs; means in parentheses after ranges): head 0-38 (11.0), body 0-58 (23.1), forearm 0-11 (6.1), thigh 0-10 (5.2), shank 0-23 (9.4), foot 2-11 (5.1). In those specimens having many flecks on the body (49 and 58), the flecks are present over the entire dorsum; in those having fewer flecks (19, 21, 24, 32), the flecks are present only laterally. One individual has only five flecks (all laterally), and two lack flecks on the body. Two individuals have three and five small white flecks dorsally.

One specimen from Colombia has reduced flecking, whereas the other is normal. cursory examination of series of *prosoblepon* from Costa Rica and Panamá revealed considerable variation in the number of flecks on the dorsum, but no specimens lacked flecks. Taylor (1952:772) mentioned a specimen from Moravia, Costa Rica in which the spotting was "... sparse and confined largely to limbs and posterior part of dorsum." The apparent continuum of variation in dorsal pattern and the absence of structural features to distinguish flecked and plain individuals necessitates the placement of *Centrolenella parabambae* (Boulenger, 1898) in the synonymy of *Centrolenella prosoblepon* (Boettger, 1892).

Three of our specimens were found on low vegetation in forest; four others were calling from vegetation over a cascading mountain stream at Balzapamba in July 1970.

Tadpoles agreeing with the description of *prosoblepon* by Starrett (1960:12) were collected late at night as they swam on the bottom of silt-bottomed pools in streams at Balzapamba.

### ***Centrolenella resplendens* new species**

Plate 2C

*Holotype*.—KU 118053, an adult male, 27.3 mm, from Santa



Cecilia, 340 m, Provincia Napo, Ecuador, obtained on 14 June 1967, by John D. Lynch.

*Diagnosis.*—1) prevomerine teeth 2 on low processes; 2) bones white (?); 3) parietal and visceral peritonea white; 4) color in life dark green with white to bluish green flecks; in preservative, dull lavender with white flecks; 5) webbing between outer fingers III2-1IV; 6) webbing on foot I1-1½II0-2+III1-2IV2-0V; 7) snout round in dorsal view and gradually inclined anteroventrally in lateral view; 8) dorsal skin shagreened with elevated warts corresponding to white flecks; 9) scalloped dermal fold on outer edge of hand, forearm, and elbow, on heel, tarsus, and foot; U-shaped anal fold; 10) humeral spine absent in males; 11) lower four-fifths of tympanum visible, directed dorsolaterally.

*Centrolenella resplendens* is unlike any other *Centrolenella* known from South America; *euknemos* and *pulverata* from Central America are like *resplendens* in having scalloped dermal folds on the limbs. *Centrolenella pulverata* differs from the other two species by having the heart visible in life, dorsum white in preservative, snout short and slightly inclined anteroventrally, and dorsal skin uniformly granular. In contrast, in *euknemos* and *resplendens* the heart is not visible in life, the dorsum is lavender in preservative, the snout is long and gradually inclined anteroventrally, and the dorsal skin is shagreened with scattered elevations. *Centrolenella resplendens* differs from *euknemos* by having a deeper snout that is round instead of subacuminate in dorsal view, more extensive anal folds, and more extensive webbing. The modal webbing formulae in *euknemos* are: hand—I3-3II3-3¾III2-2IV, foot I1-1½II1-2½III1-2IV2-1V (Savage and Starrett (1967:606).

*Description.*—Adult male large, 27.3 mm in snout-vent length; females not known. Head slightly wider than body; width of head 34.8 percent of snout-vent length; snout long, round in dorsal view, gradually sloping from nostrils to tip in lateral profile (Fig. 1); canthus round; loreal region barely concave; lips slightly flared; nostrils about two-thirds distance from eyes to tip of snout, not protuberant, directed dorsolaterally; internarial area barely depressed. Eye large, directed more laterally than anteriorly. Supratympanic fold absent; tympanum directed dorsolaterally. Prevomerine denticulous processes low, short, transverse between choanae, each bearing two teeth; choanae large; longitudinally rectangular; tongue ovoid, barely free posteriorly; vocal slits extending from posterolateral base of tongue to angles of jaws.

Humeral spine absent; scalloped dermal fold around elbow, along ventrolateral edge of forearm and outer edge of fourth finger;



first finger longer than second; fourth finger slightly shorter than third; lateral fringes on fingers; webbing absent between first and second fingers, vestigial between second and third; webbing formula for outer fingers III2-IIV; discs large, nearly round; subarticular tubercles small, round, simple; supernumerary tubercles absent; palmar tubercle simple, large, ovoid; nuptial excrescences absent (Fig. 3). Hind limbs moderately robust; length of tibia 53.5 percent of snout-vent length; scalloped fold around heel, along ventrolateral edge of foot and outer edge of fifth toe; inner metatarsal tubercle large, triangular; outer metatarsal tubercle absent; subarticular tubercles small, round; supernumerary tubercles absent; feet nearly fully webbed; webbing formula II-1½II0-2+III1-2IV2-0V; discs on toes round, slightly smaller than those on fingers (Fig. 4).

Skin on dorsal surfaces of head, body, and limbs, and lateral surface of head and flanks shagreened with small tubercles corresponding to white spots; belly and proximal posteroventral surfaces of thighs granular; other surfaces smooth; anal opening directed posteriorly at upper level of thighs, bordered laterally and ventrally by fleshy tuberculate U-shaped fold; two conical tubercles below fold (Fig. 2).

Color in preservative: head, flanks, and dorsal surfaces of body and limbs (except thumb and toes 1-3) dull lavender with many small, white spots; venter and posterior surfaces of thighs cream.

Color in life: dorsum dark green with white to bluish green spots; fringes on forearm and foot and fold around anus white; venter yellow; iris gray.

*Distribution*.—Known only from the type locality and Santa María de Sucumbios, Colombia, about 40 km NNW of Santa Cecilia (Fig. 6).

*Remarks*.—The holotype was perched on a leaf of a bush about 30 cm above the ground during light rain at night in primary rainforest. Subsequent work at Santa Cecilia from 1967 through 1972 has resulted in the collection of thousands of frogs, but no additional specimens of *resplendens* have been found.

The Colombian specimen (AMNH 88083) is a juvenile having a snout-vent length of 16.5 mm. The white dermal folds and flecks are essentially the same as those in the holotype, but the webbing, as typical of juveniles, is less extensive.

*Etymology*.—The specific name is derived from the Latin verb *resplendo* meaning to glitter, and is used in allusion to the jewel-like appearance of the living frog.



**Centrolenella siren** new species

## Plate 1E

*Holotype*.—KU 146610, an adult male, 20.7 mm, from a small tributary of the Río Salado, about 1 km upstream from the Río Coca, 1410 m, Provincia Napo, Ecuador, one of a series obtained on 7 April 1972, by William E. Duellman and John E. Simmons.

*Paratopotypes*.—KU 146611-23, same date and collectors.

*Diagnosis*.—1) prevomerine teeth 0-2; 2) bones green; 3) parietal peritoneum white; visceral peritoneum clear; 4) color in life green with yellow flecks; in preservative, lavender with white flecks; 5) webbing between outer fingers  $\text{III}2\frac{2}{3}\text{-}2\frac{1}{2}\text{IV}$ ; 6) webbing on foot  $\text{I}2\text{-}2\frac{1}{4}\text{II}1\frac{1}{2}\text{-}2\frac{2}{3}\text{III}1\frac{1}{2}\text{-}3\text{IV}3\text{-}2\text{-V}$ ; 7) snout truncate in dorsal and lateral profiles; 8) dorsal skin shagreened; 9) arms and legs lacking dermal folds; 10) humeral spine absent in males; 11) lower four-fifths of tympanum visible, directed posterolaterally with slight dorsal inclination.

*Centrolenella siren* is like *flavopunctata* and *midas* in having a lavender dorsum with white flecks (in life, green with gold flecks) with no black flecks, but it differs from both of those species by having much less webbing on the hands and feet and a more prominent tympanum oriented posterolaterally, instead of dorsolaterally. *Centrolenella flavopunctata* further differs from *siren* by having a rounded, instead of truncate, snout.

*Description*.—Adults moderately small; snout-vent length 19.8-22.0 mm ( $\bar{x}$ =20.8, N=14) in males; females unknown. Head much wider than body; width of head 30.0-37.0 percent ( $\bar{x}$ =34.7, N=14) of snout-vent length; snout extremely short, truncate in dorsal and lateral views; canthus round; loreal region barely concave; lips not flared; nostrils nearly terminal on snout, not protuberant, directed laterally; internarial area flat. Eye moderately large, directed anterolaterally. Supratympanic fold absent; lower four-fifths of tympanum visible, directed posterolaterally with slight dorsal inclination. Prevomerine dentigerous processes small, low, widely separated, between small round choanae, bearing 0-2 teeth; tongue round, barely free posteriorly; vocal slits extending from midlateral base of tongue to angles of jaws.

Humeral spine absent; ulnar fold and tubercles absent; first finger about equal in length to second; fourth finger noticeably shorter than third; fringes absent on fingers; webbing absent between first and second fingers, vestigial between second and third; webbing formula for outer fingers  $\text{III}(2\frac{1}{2}\text{-}2\frac{2}{3})\text{-(}2\frac{1}{4}\text{-}2\frac{1}{2}\text{)IV}$ ; discs truncate; subarticular tubercles small, round, simple; supernumerary tubercles absent; palmar tubercle large, elliptical; nuptial excrescences absent.



Hind limbs slender; length of tibia 54.8-60.1 percent ( $\bar{x}$ =57.3, N=14) of snout-vent length; tarsal folds and tubercles absent; inner metatarsal tubercle small, ovoid; outer metatarsal tubercle absent; sub-articular tubercles small, round; supernumerary tubercles absent; feet about one-half webbed; webbing formula I2-(2<sup>+</sup>-2<sup>¼</sup>)II(1<sup>¼</sup>-1<sup>½</sup>)-(2<sup>½</sup>-2<sup>¾</sup>)III1<sup>½</sup>-(2<sup>¾</sup>-3)IV3-(1<sup>¾</sup>-2)V; discs on toes smaller and more nearly round than those on fingers.

Skin on dorsal surfaces shagreened; skin on belly and ventral surfaces of thighs granular; other surfaces smooth; anal opening directed posteriorly at upper level of thighs; pair of large tubercles below anus (Fig. 2).

Color in preservative: dorsum of head, body, and limbs lavender with many small, white flecks on head and body; other surfaces pale cream.

Color in life: dorsum green with gold flecks; fingers and toes pale yellow; chest white; heart not visible; other ventral surfaces pale dull green; bones green; iris pale bronze with fine black reticulations.

*Distribution*.—*Centrolenella siren* occurs in cloud forest on the Amazonian slopes of the Andes, where it is known from elevations of 1410-1740 m (Fig. 9). *Centrolenella siren* occurs in sympatry with *anomala*, *audax*, *megacheira*, *pellucida*, and *pipilata*.

*Remarks*.—All individuals were found at night on low vegetation along small mountain streams in cloud forest. The type locality is a small stream at the south edge of the Papallacta-Lago Agrio road about 300 m west of the bridge across the Río Salado and approximately 1 km up the Río Salado from its confluence with the Río Coca.

*Etymology*.—The specific name refers to the nymphs of Classical mythology, who by their sweet singing enticed seafarers to destruction; the name is used here in allusion to the fact that the call of these small frogs entices collectors to the nocturnal perils of streams.

## DISCUSSION

Savage (1967) recognized three species groups of *Centrolenella* in Central America. He characterized the *fleischmanni* group as having white bones in life, a colorless parietal peritoneum, a white visceral peritoneum, a white ground color in preservative, and in lacking prevomerine teeth and dentigerous processes. The *prosohlepon* group was characterized as having green bones in life, a white (opaque) parietal peritoneum, a colorless visceral peritoneum, lavender ground color in preservative, and prevomerine teeth and



dentigerous processes. He recognized a third group for the somewhat annectant *pulverata*.

Three Ecuadorian species (*fleischmanni*, *munozorum*, and *pellucida*) clearly fit into Savage's *fleischmanni* group. With the exceptions of *anomala*, *medemi*, *ocellifera*, and *resplendens*, the remaining Ecuadorian *Centrolenella* agree with Savage's definition of the *prosoblepon* group. The presence of prevomerine teeth and processes is variable in the Ecuadorian representatives of the *prosoblepon* group (*sensu* Savage) but is usually constant within species. However, a single specimen of *cochranae* and one of *prosoblepon* lack teeth and processes, whereas all other specimens of these species examined have them.

Except for the absence of prevomerine teeth and processes, *buckleyi*, *grandisonae*, *griffithsi*, *megacheira*, *peristicta*, and *pipilata* agree with the definition of the Central American *prosoblepon* group. However, the agreement is weakened by the pale-green (contrasted with green) bones of *grandisonae*, *griffithsi*, and *peristicta* (a character-state of the *pulverata* group). Savage characterized the *pulverata* group as having pale green bones, a colorless parietal peritoneum (heart visible), opaque visceral peritoneum, yellowish-white ground color in preservative, and prevomerine teeth and processes. On examining the holotype of *pulverata* (ZMB 7842) in 1969, Duellman noted the ground color was lavender. Aside from having pale green bones, *grandisonae*, *griffithsi*, and *peristicta* do not agree with the definition of the *pulverata* group. We know of no Ecuadorian *Centrolenella* assignable to the *pulverata* group. The Venezuelan *Centrolenella antisthenesi* may be allied with *pulverata*; *antisthenesi* has a clear parietal peritoneum, opaque visceral peritoneum, prevomerine teeth, lavender dorsum, green bones, and subanal tubercles and lacks a humeral spine.

Three Ecuadorian species (and possibly the Colombian *medemi*) depart from the *fleischmanni*-*prosoblepon* arrangement. *Centrolenella anomala* is *prosoblepon*-like, except in lacking prevomerine teeth, having white bones, and in lacking a lavender ground color. The opaque parietal peritoneum and brown ground color exclude it from the homogeneous *fleischmanni* group. *Centrolenella ocellifera* and *resplendens* presumably have white bones (green bones were not recorded in their color descriptions in life). Both have prevomerine teeth and low dentigerous processes, an opaque parietal peritoneum, and lavender ground color. *Centrolenella resplendens* differs further in having white visceral peritoneum (a character-state of the *fleischmanni* and *pulverata* groups). The combination



of characteristics cited above does not recommend them for any of Savage's (1967) groups.

We noted the absence of large subanal tubercles in *anomala*, *fleischmanni*, *medemi*, *munozorum*, *ocellifera*, and *pellucida*, and their presence in the remaining Ecuadorian *Centrolenella*. Subanal tubercles are absent in most Central American centrolenids; we found them in *ilex*, *prosoblepon*, and *pulverata* and in *antioquiensis* (Colombia) and *antisthenesi* (Venezuela). The absence of subanal tubercles in the frogs of the *fleischmanni* group and in *anomala*, *medemi*, and *ocellifera* (enigmatic in having white bones) thus may not be significant. Tubercles are present in *resplendens* (also enigmatic in presumably having white bones) but these may not be homologous to those in the frogs lacking the elaborate post- and para-anal ornamentation of *resplendens*.

Humeral spines are not known in any frog of the *fleischmanni* group. Goin's (1964) and Savage's (1967) conclusion that presence or absence of the spines cannot be used to support generic separation of *Centrolenella* and *Cochranella* is substantiated here in that an otherwise "normal" *griffithsi* has humeral spines. This specimen may prove to be distinct from *griffithsi* but at present no features other than the humeral spine support that argument. Accordingly, the presence of humeral spines possibly may be intraspecifically variable, at least in *griffithsi*. Small spines occur on the humeri of *medemi* but not in *anomala*, *ocellifera*, or *resplendens* (species with presumed or known white bones). The presence of humeral spines in *audax*, *buckleyi*, *grandisonae*, *medemi*, *peristicta*, *pipilata*, and *prosoblepon* does not suggest to us that these frogs are more closely related to one another than they may be to species lacking humeral spines. This assemblage seems to be heterogeneous: three have prevomerine teeth and processes, two have pale green as compared to green bones, and one lacks subanal tubercles.

*Centrolenella antioquiensis* and *resplendes* differ from all other known *Centrolenella* by having opaque parietal and visceral peritonea. Otherwise they share few characters; *antioquiensis* has a humeral spine and green bones (absent and white in *resplendens*) and lacks dermal ornamentation and prevomerine teeth (both present in *resplendens*).

The Ecuadorian *Centrolenella* thus far described do not readily fit into the arrangement of Central American forms proposed by Savage (1967). Inspection of Taylor and Cochran's (1953) account of southeastern Brazilian centrolenids reveals comparable lack of fit with Savage's three groups in Central America. Because we anticipate the discovery of many undescribed *Centrolenella* in north-



western South America, at this time we prefer not to alter Savage's groupings or define new species groups based on our study of Ecuadorian species. We offer only the following comments on putative relationships of the 19 species, as described below.

*Centrolenella fleischmanni*, *munozorum*, and *pellucida* constitute a well-circumscribed group of species having white bones and a colorless parietal peritoneum (heart visible) in life, a white visceral peritoneum, a white ground color in preservative, and in lacking distinct canthi, subanal tubercles, humeral spines, and prevomerine teeth and processes.

*Centrolenella audax*, *cochranae*, *flavopunctata*, *midas*, *prosoblepon*, and *siren* constitute a group having green bones and an opaque parietal peritoneum (heart not visible) in life, a clear visceral peritoneum, a very pale to dark lavender ground color in preservative, and in having distinct canthi, subanal tubercles, and prevomerine teeth and processes. Two of these (*audax* and *prosoblepon*) have humeral spines.

*Centrolenella buckleyi*, *grandisonae*, *griffithsi*, *megacheira*, *peristicta*, and *pipilata* fall into a somewhat heterogeneous group agreeing in most respects with that listed above, except in the uniform absence of prevomerine teeth and processes. The bones are pale green in *grandisonae*, *griffithsi*, and *peristicta*; *griffithsi* and *megacheira* lack humeral spines.

*Centrolenella anomala* differs markedly from all other centrolenids in the combination of white bones and an opaque parietal peritoneum in life, clear visceral peritoneum, a brown ground color in life and in preservative, distinct canthi, and in lacking prevomerine teeth and processes, subanal tubercles, and humeral spines. Its ocellated color pattern on a shagreened dorsum with warts and the reduced webbing of the fingers lend it a striking similarity to *cochranae*; the similarity is out-weighed by the numerous differences between the two species.

*Centrolenella ocellifera* also differs markedly from other centrolenids. The presumably white bones in life, opaque parietal peritoneum, clear visceral peritoneum, and absence of subanal tubercles, coupled with the pale lavender ground color in preservative, distinct canthi, prevomerine teeth and processes, ocellated color pattern, and the absence of humeral spines suggests some relationship with *anomala* or with the group of species listed above, which included *audax* and *cochranae*.

*Centrolenella resplendens* appears to be trenchantly different from other Ecuadorian *Centrolenella* chiefly because of its dermal ornamentation (scalloped limb fringes, para- and postanal ornamen-



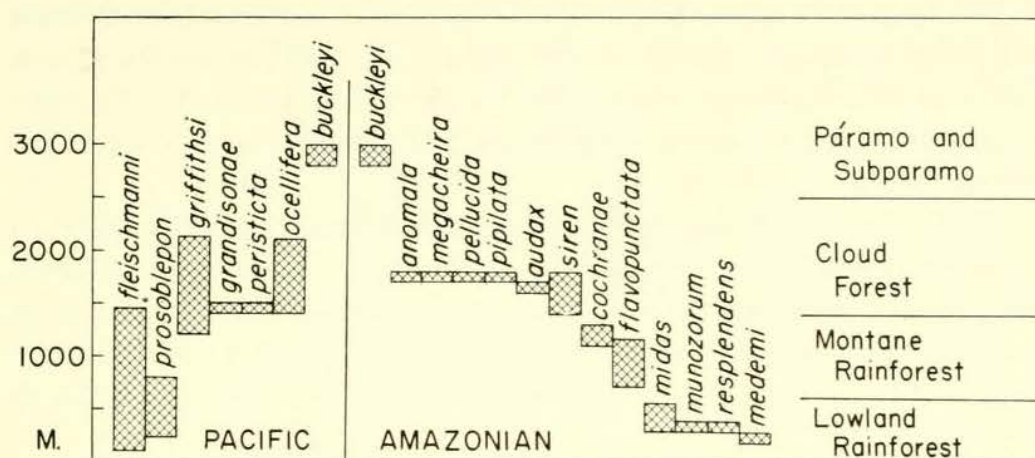


FIG. 11. Altitudinal distributions of *Centrolenella* in Ecuador; vertical line = continental divide.

tation, and enameled warts). Also it differs from other known centrolenids by the following combination of characters: white bones in life, opaque parietal peritoneum, white visceral peritoneum, lavender ground color in preservative, and prevomerine teeth.

*Centrolenella medemi* differs from all Ecuadorian centrolenids in having smooth skin on the dorsum and the decidedly non-centrolenid color pattern. We do not know the color of the bones in living individuals. Humeral spines are present, although small, and sub-anal tubercles are lacking. The fully-webbed digits, elongate hindlimbs, and completely concealed tympana, coupled with skin texture and color pattern suggested the possibility that the frog was not a centrolenid but a hylid of the *Cryptobatrachus* and *Stephania* group; however, dissection of the tarsus revealed that the tarsal bones are fused, as in all centrolenids but not in hylids.

Our knowledge of the distribution of *Centrolenella* in Ecuador is limited; even so, some patterns consistent with other groups of frogs (eleutherodactylines, dendrobatids, and hylids) are apparent. We can divide the Ecuadorian *Centrolenella* into six ecogeographic assemblages. Each is associated with definite vegetation formations and geographic regions (Fig. 11). These can be summarized as follows:

*Lowland Amazonian rainforest*.—Four species (*medemi*, *midas*, *munozorum*, and *resplendens*) occur only at elevations of less than 600 m in Amazonian rainforest, where they apparently are limited to breeding along small, sometimes intermittent, streams having a low gradient. The apparent restricted ranges of the species probably is a reflection of inadequate collecting; most likely the species will eventually be found in more distant areas in the upper Amazon Basin.



*Montane rainforest, Amazonian slopes.*—Two species (*cochranae* and *flavopunctata*) inhabit elevations of 700-1300 m on the lower eastern slopes of the Andes. In this area they live along streams with steep gradients. Warm temperatures and high amounts of rainfall prevail throughout the year.

*Cloud forest, Amazonian slopes.*—This is the richest area in Ecuador for centrolenids; six species (*anomala*, *audax*, *megacheira*, *pellucida*, *pipilata*, and *siren*) occur at elevations of 1400-1800 m on the Amazonian slopes of the Andes. This area of cool cloud forest daily bathed in mist has luxuriant vegetation and many cascading streams.

*Páramo and subparamo.*—This cool, windy region has been greatly disturbed by man. Some areas are noticeably drier than others. Throughout the páramo precipitation is lower than in cloud forests, but the low temperatures result in low rates of evaporation. A single species (*buckleyi*) occurs in wet meadows and terrestrial bromeliads in the interandean valleys and on high Amazonian and Pacific slopes between 2500 and 3000 m. Records from lower elevations on the Andean slopes are questionable.

*Cloud forest, Pacific slopes.*—Five species (*fleischmanni*, *grandisonae*, *griffithsi*, *ocellifera*, and *peristicta*) occur at elevations of 1400-2200 m on the Pacific slopes of the Andes, where the habitat is like that at similar elevations on the Amazonian slopes.

*Pacific lowlands.*—Two species (*fleischmanni* and *prosoblepon*) are known from mesic forests on the Pacific lowlands, where rainfall is far more seasonal than in the Amazon lowlands. *Centrolenella fleischmanni* occurs up to 1460 m, and *prosoblepon* goes up to at least 800 m.

Excluding the high Andean *buckleyi*, we find 12 species on the Amazonian slopes and lowlands and only six species on the Pacific slopes and lowlands. In addition to the fewer species on the Pacific slopes, there is a difference in altitudinal assemblages. The two species on the Pacific lowlands also inhabit the lower Andean slopes; in the Amazonian region, two distinctive assemblages occur within the same elevational range—one group in the lowlands, and one on the slopes. No species is known from both Pacific and Amazonian slopes or lowlands, except *buckleyi* which is at high elevations.

Greater species richness in cloud forest results in higher numbers of sympatric species there. At Tandapi at an elevation of 1460 m on the Pacific slopes, there are five species (*fleischmanni*, *grandisonae*, *griffithsi*, *ocellifera*, and *peristicta*). At the Río Azuela at an elevation of 1740 m on the Pacific slopes, five species (*anomala*, *megacheira*, *pellucida*, *pipilata*, and *siren*) were found along one



small rivulet. Three species (*midas*, *munozorum*, and *resplendens*) have been found at one locality, Santa Cecilia, at an elevation of 340 m in the Amazon Basin. Two species (*fleischmanni* and *prosoblepon*) occur in sympatry at the Río Palenque at an elevation of 220 m on the Pacific lowlands.

These limited data probably are only suggestive of the true ecological and altitudinal distributions of these small frogs. Hopefully this discussion will serve as a basis for future investigations and not be destined to be the only commentary on them before they and their habitat are eliminated by human activity.

### SUMMARY

Our collections from Ecuador contain many centrolenid frogs. Our taxonomic conclusions are based on the examination of holotypes of all of the Ecuadorian centrolenids, study of series of specimens, and observations of the frogs in the field.

We recognize 19 species in Ecuador; one of these, *Centrolene geckoideum*, is not treated in this paper. One Colombian species, *Centrolenella medemi*, is treated, because it probably occurs in eastern Ecuador. Eleven new species are named; seven (*Centrolenella anomala*, *audax*, *flavopunctata*, *megacheira*, *pellucida*, *pipilata*, and *siren*) are from the Amazonian slopes of the Andes; three (*Centrolenella midas*, *munozorum*, *resplendens*) are from the Amazon Basin, and one (*Centrolenella peristicta*) is from the Pacific slopes of the Andes. *Centrolenella parabambae* (Boulenger, 1898) and *Centrolenella petersi* (Goin, 1961) are placed in the synonymies of *Centrolenella prosoblepon* (Boettger, 1892) and *Centrolenella fleischmanni* (Boettger, 1893), respectively.

Savage (1967) placed the Central American species of *Centrolenella* in three groups: 1) *fleischmanni*, 2) *prosoblepon*, and 3) *pulverata*. The distinction of these three groups in Ecuador is not clear. Three species (*fleischmanni*, *munozorum*, *pellucida*) clearly belong to the *fleischmanni* group. *Centrolenella audax*, *buckleyi*, *cochranae*, *flavopunctata*, *grandisonae*, *griffithsi*, *megacheira*, *midas*, *peristicta*, *pipilata*, and *siren* can be placed in the *prosoblepon* group, redefined to include species with or without prevomerine teeth. *Centrolenella anomala*, *ocellifera*, and *resplendens* cannot be placed in any of the defined groups.

The maximum diversity of *Centrolenella* in Ecuador is in the cloud forests. Six species (five occur sympatrically) inhabit the cloud forests on the Amazonian slopes of the Andes. Five sympatric species occur in the cloud forests on the Pacific slopes of the Andes. In other regions there are fewer species: Amazonian lowlands (4),



lower Amazonian slopes of the Andes (2), Pacific lowlands (2). Only *Centrolenella buckleyi* occurs in the high Andes and inter-andean valleys.

We provide the first records of four species from Colombia: *Centrolenella griffithsi*, *ilex*, *prosoblepon*, and *resplendens*.

## RESUMEN

Nuestras colecciones del Ecuador contienen muchas ranas de la familia Centrolenidae. Nuestras conclusiones taxonómicas son basadas en el examen de los holotipos de todos los centrolenidos ecuatorianos, estudio de serie de ejemplares, y observaciones de las ranas en sus ambientes naturales.

Se reconocen 19 especies de centrolenidos en Ecuador; una, *Centrolene geckoideum*, no está tratado en esta publicación. Un especie colombiano, *Centrolenella medemi*, está tratado, porque probablemente se ocurren en el oriente del Ecuador. Once especies nuevas se nombran; siete (*Centrolenella anomala*, *audax*, *flavopunctata*, *megacheira*, *pellucida*, *pipilata*, *siren*) se encuentran en las laderas amazónicas de los Andes, tres (*Centrolenella midas*, *munozorum*, *resplendens*) son de la cuenca amazónica, y una (*Centrolenella peristicta*) es de las laderas de Pacífico de los Andes. *Centrolenella parabambae* (Boulenger, 1898) y *Centrolenella petersi* (Goin, 1961) son colocadas en las sinónimias de *Centrolenella prosoblepon* (Boettger, 1892) y *Centrolenella fleischmanni* (Boettger, 1893), respectivamente.

Savage (1967) puso las especies centroamericanas de *Centrolenella* en tres grupos: 1) *fleischmanni*, 2) *prosoblepon*, and 3) *pulverata*. La distinción de estos tres grupos en los centrolenidos ecuatorianos no está lucida. Tres especies (*fleischmanni*, *munozorum*, *pellucida*) claramente pertenecen al grupo *fleischmanni*. *Centrolenella audax*, *buckleyi*, *cochranae*, *flavopunctata*, *grandisonae*, *griffithsi*, *megacheira*, *midas*, *peristicta*, *pipilata*, *prosoblepon*, y *siren* se pueden colocar en un grupo *prosoblepon* redefinido para incluir especies con los dientes prevomerianos presentes o ausentes. *Centrolenella anomala*, *ocellifera*, y *resplendens* no se pueden colocar en los grupos definidos.

La diversidad máxima en *Centrolenella* en Ecuador está en el bosque neblino. Seis especies (cinco ocurren simpátricamente) habitan los bosques neblinos en las laderas amazónicas de los Andes. Cinco especies simpátricos ocurren en los bosques neblinos en las laderas de Pacífico de los Andes. En otras regiones hay menos especies: Tierras bajas amazónicas (4), laderas bajas amazónicas