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THE STATUS OF THE GENERA ECPLEOPUS, ARTHROSEPS AND ASPIDOLAEMUS (SAURIA, TETRAURIDAE)

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POSTILLA

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THE STATUS OF THE GENERA ECPLEOPUS, ARTHROSEPS, AND ASPIDOLAEMUS (SAURIA, TEIIDAE)

THOMAS UZZELL
Department of Biology and Peabody Museum of Natural History, Yale University

ABSTRACT

The genus *Ecpleopus* is diagnosed within Group II of the Teiidae by the elongate, keeled dorsal scales arranged in diagonal and transverse rows, smooth ventral scales in diagonal and transverse rows, first superciliary elongate, first supraocular in contact with the frontonasal and loreal, and superciliary series incomplete so that only first and fourth supraoculars are separated from the palpebrals.

The usual presence of plicae on the anterior part of the tongue suggests relationships with *Ptychoglossus* and *Alopoglossus*, which are distinctive within Group II because they have completely plicate tongues. *Leposoma* and *Arthrosaura* also appear to be related to *Ecpleopus*. The diagnostic characters of *Ecpleopus*, however, suggest that its relationships to these four genera are not especially close.

I consider *Arthroseps* a synonym of *Ecpleopus*. The genus is apparently monotypic. *Arthroseps werneri*, *A. fluminensis*, and *Alopoglossus gracilis* are junior synonyms of *Ecpleopus gaudichaudi*. *Aspidolaemus*, with *Ecpleopus (Aspidolaemus) affinis* as the only species, is recognized as a separate genus related to *Prionodactylus* and *Pholidobolus*.

*Ecpleopus gaudichaudi* is known from altitudes of less than 1000 m above sea level in eastern Brazil from Goyas south to Santa Catarina.

*E. gaudichaudi*, in contrast to most members of Group II, may mature only a single egg at a time.
INTRODUCTION

One of the most poorly understood genera of Group II (Boulenger, 1885b) of the family Teiidae is Ecpleopus, described by Duméril and Bibron (1839) for their species Ecpleopus gaudichaudi. Peters (1862) enlarged the scope of Ecpleopus, including in it as subgenera Ecpleopus for E. gaudichaudi, Aspidolaemus for E. affinis, as well as Pholidobolus, Oreosaurus, Euspondylus, Argalia, Xestosaurus, and Proctoporus. Boulenger (1885b) modified Peters' concept of Ecpleopus by removing from it all the subgenera except Ecpleopus and Aspidolaemus. Since Ecpleopus affinis is a common species in museum collections, its characteristics, rather than those of the rarely collected E. gaudichaudi, have been the basis of most workers' concept of the genus Ecpleopus.

Recently I undertook to examine as many specimens as possible of Ecpleopus gaudichaudi. I now know 12 specimens that I consider to be this species; I have examined 10 of them; 2 have apparently been destroyed. Several specimens reported under this name were misidentified. Included in these 12 specimens are 4 holotypes, of which I have seen 3. Examination of these specimens bears out my conviction (Uzzell, 1959) that Ecpleopus gaudichaudi is very dissimilar to Ecpleopus affinis. It also indicates that the genus Arthroseps is a synonym of Ecpleopus. Ecpleopus has features that suggest affinities with Arthrosaura, with Ptychoglossus and Alopoglossus, and with Leposoma.

Abbreviations used:

BMNH — British Museum (Natural History), London
DZSP — Departamento de Zoologia, Secretaria da Agricultura, São Paulo
MNHN — Muséum National d'Histoire Naturelle, Paris
NHMB — Naturhistorisches Museum, Basel
NHMW — Naturhistorisches Museum, Wien
SMF — Senckenberg Museum, Frankfurt
UKMNH — University of Kansas, Museum of Natural History
UMMZ — University of Michigan, Museum of Zoology
ZSM — Zoologische Staatssammlung, Munich
Ecpleopus Duméril and Bibron

Ecpleopus Duméril and Bibron, 1839: 434.  
Arthroseps Boulenger, 1898: 920. New synonymy.

DEFINITION. Tongue with imbricate scalelike papillae on middle and, sometimes, on posterior part; anteriorly usually with oblique folds\(^1\). Snout short, blunt. Head scales without striations and rugosities; single frontonasal, frontal, and interparietal; median occipital variable; paired prefrontals, frontoparietals, parietals and occipitals. Four supraoculars on each side, the second and third in contact with palpebrals. First superciliary elongate, not expanded onto dorsal surface of head. First supraocular elongate, narrowly in contact with loreal, relatively broadly in contact with frontonasal. Prefrontals and first supraocular subequal in length. Nasals not in contact; nostril in middle of nasal; a short suture posteriorly from nostril to hind margin of nasal. Loreal present, diagonally placed, separated from supralabial scales by contact between nasal and frenoocular. Eyelids developed, lower with relatively large translucent disc divided into two pieces by a vertical groove. Ear opening moderately large; tympanum only slightly recessed, not overhung by scales. One unpaired and three paired chinshields, the last pair not touching at midline; all chinshields in contact with labials. Gular crease weak; collar fold not well marked. Posterior median gular and collar scales shaped like ventrals.

Dorsal scales elongate, hexagonal, long pointed, strongly keeled, imbricate, the points overlapping the sutures between scales of next posterior row. Lateral scales similar. Ventral scales long, hexagonal, smooth, less sharply pointed than dorsals and laterals, imbricate, the points overlapping the sutures between scales of next posterior row. Scales mainly in complete rings around body, but dorsals somewhat shorter than ventrals. Caudal scales resembling body scales, keeled above and on sides, smooth below. A single series, usually with three scales, of elongate, smooth, preanal.

Limbs pentadactyl; digits clawed. Forefoot with enlarged plate-like scales along inner margin of palm between thumb and wrist,

\(^1\) The holotype of Ecpleopus gaudichaudi has papillae rather than plicae anteriorly.
the edges not produced. Upper tibial scales keeled. Underside of third and fourth digits of hind foot with paired scales proximally, the inner scale of each pair not tuberculate.

Usually one preanal pore on each side in both sexes; pore surrounded by a single scale.

Tail rounded in cross section.

Clear yellow below, brown above, with two light dorsolateral lines that approach each other on the neck.

_Ecpleopus_ is readily recognized by the following suite of characters: dorsals keeled, forming diagonal and transverse rows; ventrals smooth, forming diagonal and transverse rows; first supraocular touching both loreal and undivided frontonasal; superciliary series incomplete, so that second and third supraoculares touch the palpebrals; tongue usually with plicae at anterior end.

**REMARKS.** Folds, or plicae, occur (as Ruibal, 1952, pointed out) on the posterior, notched part of the tongue of many teiid lizards. Folds on the middle and anterior parts of the tongue, however, are unusual. They have been observed in _Ptychoglossus_ and _Alopoglossus_, in which the entire surface of the tongue is plicate. The arrangement in _Ecpleopus_ therefore appears to be structurally intermediate between the generally papillate condition and the completely plicate condition. Folds on the tongue have been reported in non-teiid genera. The tongue of _Takydromus_ (Lacertidae) is completely plicate (Boulenger, 1885a). The pattern (de Rooij, 1915: fig. 1-5) strongly resembles that seen in _Alopoglossus_ and _Ptychoglossus_. The lateral margin of the tongue of _Lacerta viridis_, as well as the posterior, notched part, has folds rather than plicae (Seiller, 1892).

Plicae similar to those in _Alopoglossus_, _Ptychoglossus_, and _Takydromus_ apparently occur in _Tetradoactylus_, one of the six genera of the Gerrhosauridae (Boulenger, 1885a).

Xantusiids and dibamids also have plicae on the posterior part of the tongue. The apices are directed forward in the xantusiids, but in _Dibamus_ the plicae, instead of forming chevrons, form curves, with the convex side forward (de Rooij, 1915: fig. 1-7).

Although the figure of the tongue of _Heloderma_ and of _Lanthodonotus_ given by McDowell and Bogert (1954: figs. 29D, E)
suggests that there are plicae on the anterior part of the tongue in these two genera, plicae are absent on the tongues of the individual of each genus that I have examined. Plicae thus appear to be confined to the families placed by Camp (1923) in the Scincomorpha, although very similar arrangements of folds are restricted to the Lacertoidea.

Regardless of the phylogeny of the Lacertilia that is accepted, plicate tongues have been developed or lost repeatedly within the Scincomorpha.

_Ecpleopus gaudichaudi_ Duméril and Bibron (Fig. 1)

_Ecpleopus gaudichaudi_ Duméril and Bibron, 1839: 436.

_Arthroseps werneri_ Boulenger, 1898: 921, _New synonymy._

_Alopoglossus gracilis_ Werner, 1913: 13. _New synonymy._

_Arthroseps fluminensis_ Amaral, 1932: 67. _New synonymy._

The characteristics of _E. gaudichaudi_ are the same as those of the genus. Four features, the structure of the tongue, the nature of the feet, the hemipenis, and the coloration, merit additional comment.

**TONGUE.** The tongue of _E. gaudichaudi_ is moderately long, with two relatively long smooth points anteriorly and a notch behind, giving the tongue an arrowheaded shape. The anterior part, just behind the smooth anterior points, and sometimes the posterior part around the notch are covered on the dorsal part with folds, or plicae, which form chevrons, the apex on the midline and anterior. On the middle and sometimes the posterior part, the tongue is covered dorsally by imbricate, rhomboidal, scalelike papillae. These can be viewed as formed by two sets of chevron-shaped divisions, one set with the apices forward, the other with the apices posteriorly directed. It is easy to imagine the transformation between papillae and plicae by the loss of the chevrons with posteriorly directed apices.

The presence of papillae on the middle and sometimes the posterior part of the tongue of all specimens of _E. gaudichaudi_ examined and the usual presence of plicae at the anterior tip perhaps makes the absence of plicae at the anterior tip of the
FIG. 1. Lateral view of the head of *Ecpleopus gaudichaudi* (SMF 11757) showing the contact between the palpebral series and the second and third supraoculars and the contact between the first superciliary and the loreal. ×14.

holotype of *E. gaudichaudi* more understandable. If subdivision of the folds to form papillae (or fusion of papillae to form plicae) is under genetic control such that it occurs in part of the tongue but not all, only a slight shift in timing or of developmental field would be required to produce a tongue with papillae at the anterior end as well as at the middle. The alternative arrangement, a completely plicate tongue, may also occur in some individuals of
E. gaudichaudi. Because of the rather generally papillate condition, I suspect that plicae represent the derived condition. I view their occurrence within Group II of the Teiidae as a single occurrence indicating affinity between Ecpleopus on the one hand and Alopoglossus and Ptychoglossus on the other.

FEET. The toes of E. gaudichaudi are short and slightly depressed (Fig. 2). On the ventral surface, the lamellae are divided. The digits of both feet appear to be joined together at the bases so that the palmar region seems to extend beyond the metapodial region of the foot. The claws are weak and curved. Although on the palm the thenar scales are moderately large, the medial edge is not produced into a free ridge. The inner member of each pair of subdigital lamellae at the base of the third and fourth toes is not swollen to produce a marked tubercle. Many of these features
of the feet vary among members of Group II of the Teiidae but their adaptive significance has not been investigated.

HEMIPENIS. I have examined the left hemipenis of UMMZ 79948 and UMMZ 115639. Each hemipenis was washed in distilled water, slit along the sulcus spermaticus, stained overnight in a dilute solution of alizarin red S in 0.5 percent KOH, and destained in distilled water.

Neither of the hemipenes examined shows any evidence of the calcareous spinules that occur in the hemipenes of many species of the genera of Group II of the Teiidae. The flounces in which the calcareous spinules are usually located are also absent. Description of the organ is therefore difficult; some features can be seen in Figure 3. The prominent fleshy fold in the middle of the organ is the median welt. It appears to extend into each of the lobes of the bilobate organ. The lobes themselves have the fleshy folds usually found in hemipenes of members of Group II.

FIG. 3. Structure of the left hemipenis of Ecpleopus gaudichaudi (UMMZ 115639). The inverted organ has been slit along the sulcus spermaticus. $\times$ 18.
COLORATION. Specimens of *Ecpleopus gaudichaudi* are generally brown above and clear yellow below. There are a pair of light dorsolateral lines 1-2 scales wide and dark bordered, on the posterior part of the head, on the shoulders and on the sacral regions. These light lines are usually broken on the head. There may thus be light patches on the outer edge of each parietal, a rounded light patch covering the posterolateral corner of each paramedian occipital scale as well as adjacent parts of adjacent scales, and a light crescent on the posterior part of the interparietal. Since the light spots on the paramedian occipital scales are closer to midline than the light spots on the parietals or dorsal scales, the pattern appears to consist of two dorsolateral light lines running from the head onto the shoulders, but pinched together at the neck.

The scales beneath the feet and hands are peppered with dark pigment. The labials are dark brown but light bordered. The tympanum is clear.

**Specimens of Ecpleopus gaudichaudi**

Since so few specimens of *Ecpleopus gaudichaudi* are known and since several of these are lost or have no locality other than Brazil, I have tabulated the characteristics for each individual (Table 1). Invariant characters are included in the generic diagnosis.

1. Little need be added to the description of the holotype of *Ecpleopus gaudichaudi* (Duméril and Bibron 1839). The specimen (MNHN 7047) is an adult female with a single preanal pore on each side. The type locality is Brazil. Peters (1862) reported that the posterior maxillary teeth are bicuspid, but the second (posterior) cusp must be very small because I did not see it.

2. I have examined the holotype (BMNH 98.1.17.1, reregistered as 1946.8.2.4) of *Arthroseps werneri* Boulenger (1898). The specimen is a female collected by Franz Werner at Blumenau, Santa Catarina, Brazil (map). Except for the presence of plicae at the anterior tip of the tongue and the absence of a median occipital, the holotype of *A. werneri* agrees with the holotype of *E. gaudichaudi* in all characters that I consider taxonomically important. I therefore place *Arthroseps* in the synonymy of *Ecpleopus* (new synonymy), and *A. werneri* in the synonymy of *E. gaudichaudi* (new synonymy).
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\(^1\) Holotype of *Arthroseps fluminensis*.

\(^2\) Holotype of *Arthroseps werneri*.

\(^3\) Holotype of *Alopoglossus gracilis*; data from Werner (1913).

\(^4\) To cloacal opening.

\(^5\) Holotype of *Ecpleopus gaudichaudi*. 
Southeastern Brazil from Goyas south to Santa Catarina, showing localities for *Ecleopopus gaudichaudi*. The open symbol represents the type locality for *Alopoglossus gracilis* Werner; solid symbols show localities for specimens examined when the localities were definite.
3. The holotype of *Alopoglossus gracilis* Werner (1913) was collected in the valley of the Rio Humboldt, a tributary of the Rio Itapocu in Santa Catarina, Brazil. It was apparently lost during World War II. Werner's generic placement of his species indicates that the tongue had conspicuous plicae. Characters in Table 1 show that *Alopoglossus gracilis* belongs with the other specimens referred to *Ecpleopus gaudichaudi*. Ruibal (1952) recorded specimens of *Alopoglossus* from the Pacific slopes of Ecuador and from the edges of the Amazonian basin from southern Peru north and east to British Guiana; these localities are enormously distant from the type locality of *Alopoglossus gracilis*. Since there seems little reason to expect members of the genus *Alopoglossus* in Santa Catarina, and since the morphological features of *A. gracilis* are so similar to those of *Ecpleopus gaudichaudi*, I consider *A. gracilis* a junior synonym of *E. gaudichaudi* (new synonymy).

4. Although Amaral (1932) stated that the holotype of *Arthroseps fluminensis* does not fit Boulenger's description of *A. werneri* in important features, he did not specify the differences. I have examined the holotype of *A. fluminensis* (DZSP 800), an adult female from the Serra de Macaé in Rio de Janeiro. I am unable to detect any important differences between it and the other specimens referred to *E. gaudichaudi*. I therefore consider *A. fluminensis* a junior synonym of *E. gaudichaudi* (new synonymy).

5. Localities and museum numbers for seven other specimens of *E. gaudichaudi* are given in the list of specimens examined. Specific localities are indicated on the map.

6. Tschudi's (1847) specimen from Brazil was soon lost (Peters, 1862). It adds nothing to our knowledge of this species.

**Biology of Ecpleopus gaudichaudi**

Virtually nothing is known about the ecology of *Ecpleopus gaudichaudi*. Its general similarity to *Leposoma* in body form and size suggest similarities in ecology. Specimens of *Leposoma* have been collected in damp leaves, under logs, in grassy marshes, under dead leaves along dried stream beds, and on leaves of forest floor (Ruibal, 1952). Both *Ecpleopus* and *Leposoma* are lowland animals, *Leposoma* occurring at altitudes of less than 600 m above
sea level (Ruibal, 1952) and *Ecpleopus* at altitudes of up to perhaps 1000 m.

The holotype of *E. gaudichaudi* contains one egg with a wrinkled leathery shell. I estimated the egg to be 7 mm long and about 5 mm in diameter. The holotype of *A. fluminensis* contains a single enlarged ovum. Perhaps the normal clutch size for these small lizards is one rather than the two generally observed in species of Group II (Uzzell 1959, 1965, 1966; Fouquette 1968).

**RANGE.** The known range of *Ecpleopus gaudichaudi* is from Goyas on the north to Santa Catarina on the south (map). Most of the localities are in the immediate coastal drainages of southeastern Brazil, but the Goyas locality suggests that this genus, like *Placosoma* (Uzzell 1959, 1962) may have populations extending well to the north and west, perhaps being limited by the rainforest areas of the Amazon basin.

**Specimens Examined**

Brazil (no state given): MNHN 7047 (holotype of *Ecpleopus gaudichaudi*), MNHN 2828, NHMW 19160.


" Goyas: UMMZ 79948.


" " Serra de Macaé: DZSP 800 (holotype of *Arthroseps fluminensis*).

" Santa Catarina: Blumenau: BMNH 98.1.17.1, recatalogued as 1946.8.2.4 (holotype of *Arthroseps werneri*).

" " Joinville: SMF 11757.


**Relationships of Ecpleopus**

I first realized that *Ecpleopus* is related to *Alopoglossus* and *Ptychoglossus* when I discovered plicae on the anterior part of the tongue of two specimens (UMMZ 79948 and 115639). It was
surprising not to find plicae at the tip of the tongue of the holotype of *E. gaudichaudi*. Nevertheless, the large number of features that these two specimens share with the holotype of *E. gaudichaudi* convinces me that they are conspecific with the holotype.

*Ecpleopus* also shares many features with *Leposoma*, which, as Ruibal (1952) observed, is very similar to *Alopoglossus*. These genera are also similar to *Arthrosaura*. The characters that the five genera share are few. Nevertheless, combinations of characters do offer support for the few distinctive characters of the group (Table 2).

In all five genera, the first supraocular is elongate. The long first superciliary is not expanded onto the dorsal surface of the head, but forms a suture with the first supraocular at the canthus rostralis. The loreal is separated from the labials in *Leposoma*, *Alopoglossus* and *Ecpleopus*. More importantly, except in *Arthrosaura*, the loreal is a relatively narrow, diagonally placed scale, with the upper end anterior to the lower. There is usually a single row of elongate preanal scales, although in some forms of two genera (*Leposoma*, *Arthrosaura*) the middle scale may be divided into anterior and posterior parts, and in *Arthrosaura*, all the preanal scales are relatively short.

There are usually three pairs of chinshields; the anterior pairs are in contact on the midline. The last chinshield is separated from the labials by small scales in some forms of all genera except *Arthrosaura* and *Ecpleopus*. Usually, the gular, collar, and ventral scales are shaped alike. *Arthrosaura* and one species of *Alopoglossus* have widened median gular scales. Some species of both *Arthrosaura* and *PsychoGLOSSUS* have 3-3 supraoculars, but other species and the three other genera have 4-4 supraoculars.

I examined 28 characters that I believe are taxonomically significant to determine the overall similarity of the five genera considered. For 13 of the 28 characters, one state (marked by asterisks in Table 2) could be postulated to be primitive on the basis of nearly uniform distribution in other members of Group II (or, occasionally, in other groups) of the Teiidae. The remaining characters have states all of which can be found in genera of Group II other than the five considered here.

Five tabulations of shared character states are presented in Table 3. For phenetic comparisons, a genus with more than one character state was considered to share a state with each genus
### TABLE 2. Characteristics of five genera of Group II.

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<th>Characteristic</th>
<th>Arthrosaura</th>
<th>Ecpleopus</th>
<th>Leposoma</th>
<th>Alopoglossus</th>
<th>Ptychoglossus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Superciliary Series</td>
<td>complete*</td>
<td>broken[^4]</td>
<td>complete*</td>
<td>complete*</td>
<td>complete*</td>
</tr>
<tr>
<td>Supraoccurlars</td>
<td>3 or 4[^5]</td>
<td>4</td>
<td>4</td>
<td>4</td>
<td>3 or 4[^6]</td>
</tr>
<tr>
<td>Length of Parietal and Interparietal</td>
<td>equal</td>
<td>parietals shorter[^*7]</td>
<td>equal</td>
<td>equal</td>
<td></td>
</tr>
<tr>
<td>Interparietal Width</td>
<td>narrow[^*]</td>
<td>narrow[^*]</td>
<td>broad or narrow[^*8]</td>
<td>narrow[^*]</td>
<td>narrow[^*]</td>
</tr>
<tr>
<td>Occipitals</td>
<td>absent</td>
<td>present</td>
<td>absent</td>
<td>absent</td>
<td>absent</td>
</tr>
<tr>
<td>Frontonasal-First Supraocular</td>
<td>separated[^*]</td>
<td>in contact</td>
<td>separated[^*]</td>
<td>separated[^*]</td>
<td>separated[^*]</td>
</tr>
<tr>
<td>Loreal and labials</td>
<td>in contact</td>
<td>separated</td>
<td>separated</td>
<td>usually in contact[^6]</td>
<td></td>
</tr>
</tbody>
</table>

[^1]: Postulated primitive state (see text).
[^2]: Da Cunha (1967) reported striae on the head scales of *A. kockii*; they are absent on specimens I have examined (UKMNH 69812-14); the temporal scales are keeled in *A. kockii*.
[^3]: Absent on anterior head scales of some *L. rugiceps*; Ruibal 1952.
[^4]: Present on posterior head scales of *A. buckleyi*; Ruibal 1952.
[^5]: Second and third supraoculars touch palpebrals.
[^6]: Species identifications in this genus are uncertain.
[^7]: Parietals and interparietal of equal length in *L. scincoides*; Ruibal 1952.
[^8]: Narrow in *L. scincoides*; Ruibal 1952.
<table>
<thead>
<tr>
<th>Last Chinshields</th>
<th>Arthrosaura</th>
<th>Ecleopus</th>
<th>Leposoma</th>
<th>Alopoglossus</th>
<th>Ptychoglossus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Labials touching chinshields in</td>
<td>touching labials</td>
<td>touching labials</td>
<td>touching labials or not</td>
<td>separated from or barely touching labials</td>
<td>separated from or barely touching labials</td>
</tr>
<tr>
<td>Gulars</td>
<td>smooth*</td>
<td>smooth*</td>
<td>keeled</td>
<td>keeled</td>
<td>smooth*</td>
</tr>
<tr>
<td>two widened rows</td>
<td>no widened rows</td>
<td>no widened rows</td>
<td>two or no widened rows</td>
<td>no widened rows</td>
<td></td>
</tr>
<tr>
<td>Dorsals</td>
<td>keeled</td>
<td>keeled</td>
<td>leaf shaped or parallel-sided</td>
<td>keeled</td>
<td>convex or keeled parallel-sided</td>
</tr>
<tr>
<td>parallel-sided</td>
<td>parallel-sided</td>
<td>leaf shaped</td>
<td>leaf shaped</td>
<td></td>
<td></td>
</tr>
<tr>
<td>long pointed</td>
<td>long pointed</td>
<td>mucronate</td>
<td>mucronate</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ventral</td>
<td>smooth*</td>
<td>smooth*</td>
<td>keeled or smooth*</td>
<td>keeled or smooth*</td>
<td>smooth*</td>
</tr>
<tr>
<td>longitudinal rows*</td>
<td>diagonal rows</td>
<td>longitudinal*</td>
<td>longitudinal*</td>
<td>Longitudinal rows*</td>
<td></td>
</tr>
<tr>
<td>rounded posteriorly</td>
<td>long pointed</td>
<td>truncate, rounded</td>
<td>truncate, rounded or pointed</td>
<td>truncate rounded or pointed</td>
<td>rectangular*</td>
</tr>
</tbody>
</table>

9 Labials touching chinshields in L. scincoides; Ruibal 1952.
10 Widened in A. buckleyi; Ruibal 1952.
11 Parallel-sided in L. annectans and L. scincoides; Ruibal 1952.
12 Keeled or smooth in L. rugiceps; Ruibal 1952.
13 Smooth in A. festae and A. andeanus; Ruibal 1952.
14 In diagonal rows in L. scincoides and L. annectens; Ruibal 1952.
15 Long pointed in L. scincoides; Peters 1862.
16 Pointed in A. copii and A. carinicaudatus; rounded in A. andeanus; truncated in A. festae; pointed, rounded, or truncated in A. buckleyi; Ruibal 1952.
<table>
<thead>
<tr>
<th>Preanal Scales</th>
<th>middle divided or not smooth*</th>
<th>middle not divided smooth*</th>
<th>middle divided or not\textsuperscript{17} smooth* or keeled</th>
<th>middle not divided smooth*</th>
<th>middle not divided smooth*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Forelimbs</td>
<td>keeled</td>
<td>smooth</td>
<td>keeled</td>
<td>keeled</td>
<td>smooth</td>
</tr>
<tr>
<td>Thenar Scales</td>
<td>inner edge free</td>
<td>no free edge</td>
<td>inner edge free</td>
<td>inner edge free</td>
<td>inner edge free</td>
</tr>
<tr>
<td>Inner Lamellae under 4th Toe</td>
<td>swollen</td>
<td>not swollen</td>
<td>swollen</td>
<td>swollen</td>
<td>swollen</td>
</tr>
<tr>
<td>Preanal Pores</td>
<td>males</td>
<td>both sexes\textsuperscript{19}</td>
<td>both sexes</td>
<td>males</td>
<td>males</td>
</tr>
<tr>
<td>Femoral Pores</td>
<td>males</td>
<td>absent</td>
<td>males</td>
<td>males</td>
<td>males</td>
</tr>
<tr>
<td>Tongue</td>
<td>papillate*</td>
<td>papillate*\textsuperscript{20} or plicate anteriorly</td>
<td>papillate*</td>
<td>plicate</td>
<td>plicate</td>
</tr>
<tr>
<td>Maxillary Teeth</td>
<td>mostly tricuspid*</td>
<td>mostly unicuspid\textsuperscript{21}</td>
<td>mostly tricuspid*</td>
<td>mostly bicuspid\textsuperscript{22}</td>
<td>mostly bicuspid\textsuperscript{22}</td>
</tr>
<tr>
<td>Tympanum</td>
<td>deeply recessed</td>
<td>moderately recessed</td>
<td>moderately recessed</td>
<td>deeply recessed</td>
<td>moderately or deeply recessed\textsuperscript{6}</td>
</tr>
<tr>
<td>Hemipenis</td>
<td>numerous spinules in each flounce*</td>
<td>spines absent</td>
<td>two spines per flounce</td>
<td>spines absent</td>
<td>spines absent</td>
</tr>
</tbody>
</table>

\textsuperscript{17} Not divided in \emph{L. guianense}; Ruibal 1952.
\textsuperscript{18} Weakly keeled in \emph{A. carinicaudatum}; Ruibal 1952.
\textsuperscript{19} Absent in some females.
\textsuperscript{20} Papillate anteriorly in holotype of \emph{E. gaudichaudi}.
\textsuperscript{21} Hind cusp present but reduced (Peters 1862) or absent; anterior cusp absent.
\textsuperscript{22} Hind cusp essentially lost.
TABLE 3. Numbers of characters for which pairs of genera share states.

<table>
<thead>
<tr>
<th>GENUS PAIR</th>
<th>PHENETIC COMPARISONS</th>
<th>PHYLLETIC ANALYSIS</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>All characters</td>
<td>Scored characters</td>
</tr>
<tr>
<td>Ecpleopus — Leposoma</td>
<td>14</td>
<td>6</td>
</tr>
<tr>
<td>&quot; — Ptychoglossus</td>
<td>16</td>
<td>6</td>
</tr>
<tr>
<td>&quot; — Arthrosaura</td>
<td>12</td>
<td>6</td>
</tr>
<tr>
<td>&quot; — Alopoglossus</td>
<td>11</td>
<td>6</td>
</tr>
<tr>
<td>Leposoma — Ptychoglossus</td>
<td>17</td>
<td>6</td>
</tr>
<tr>
<td>&quot; — Arthrosaura</td>
<td>18</td>
<td>9</td>
</tr>
<tr>
<td>&quot; — Alopoglossus</td>
<td>23</td>
<td>10</td>
</tr>
<tr>
<td>Ptychoglossus — Arthrosaura</td>
<td>19</td>
<td>9</td>
</tr>
<tr>
<td>&quot; — Alopoglossus</td>
<td>23</td>
<td>10</td>
</tr>
<tr>
<td>Arthrosaura — Alopoglossus</td>
<td>20</td>
<td>9</td>
</tr>
</tbody>
</table>

Data derived from Table 2. For phenetic comparisons, variable characters could be shared in each state observed; for phyletic analysis, only characters for which derived states were shared were counted.

that had at least one of those states; for phyletic analysis, only derived states were counted.

Using all 28 characters, Ptychoglossus and Alopoglossus, which share 23 states and Alopoglossus and Leposoma, which also share 23 states, are most alike. Arthrosaura shares 18 to 20 characters with these three genera.

When the number of primitive states retained by each genus is tabulated, Arthrosaura has 11 out of 13 and Ptychoglossus 9, Leposoma may show the primitive state for 8 characters, although interspecific variation may result in derived states for 4 of these; Alopoglossus, with between 7 and 4 primitive states, and Ecpleopus, with 7 or 6, appear to be more highly derived.

Phyletic comparisons based on derived character states presumably give better evidence of common descent than comparisons based on primitive characters, which may be retained in many independent phyletic lines. In such comparisons, Leposoma and Alopoglossus share the highest number (6 of 13) of derived states, followed by Ptychoglossus and Alopoglossus (4).

Since many of the derived character states occur variably within one or more of the genera compared, it is possible (if the genera themselves are valid)\(^3\) that the ancestral stock that gave rise to them was heterozygous for many of the factors controlling the

\(^3\) The number of features in which *Leposoma scincoides* differs from other *Leposoma* and resembles *Ecpleopus* is remarkable.
production of these states. Throckmorton (1962) presented careful arguments for such heterozygous inheritance in *Drosophila*. The presence of individuals or species with derived states for these intragenerically variable characters suggests descent from stocks that were heterozygous for controlling factors, but not common descent from derived stocks.

If variable characters are removed from consideration, only *Ptychoglossus* and *Alopoglossus* share any number of derived states (4); *Arthrosaura* shares one characteristic (short interparietal) with each of these two; *Ecpleopus* shares another (absence of hemipenial spines). In addition, *Alopoglossus* and *Ptychoglossus* share the completely plicate tongue and generally bicuspid teeth.

Although phenetically *Ecpleopus* seems almost equally close to all four other genera, sharing states for about half the characters with each, it shares the highest number of derived character states (2) with *Alopoglossus* and *Leposoma*. *Ecpleopus* is particularly close to *Leposoma scincoides*. On the other hand, the complete absence of hemipenial spines, the usually unicuspid teeth, and presence of plicae on the anterior part of the tongue of most individuals ally *Ecpleopus* most closely with *Ptychoglossus* and *Alopoglossus*.

The exact phylogenetic position of *Ecpleopus* remains unclear, but it is set off from its relatives by a series of features that are distinctive within the group.

**Specimens Misidentified as E. Gaudichaudii**

I have examined MNHN 7048, supposedly the specimen reported by Guichenot (1855) as *Ecpleopus gaudichaudi*. The specimen is a female, 46 mm snout to vent. Scales have been rubbed off the top of the head except for the supraorbital region, the shoulders, and the tail. It is difficult to determine the identity of this specimen; clearly, however, it is not *Ecpleopus gaudichaudi*.

The dorsal body scales are quadrangular and only slightly imbricate: no keeling is perceivable, but perhaps the scales were weakly keeled at some time. The dorsal scales form transverse series only; laterally, the scales have the same shape, but there is a wide zone of intercalation of additional rows between the
dorsal rows, which become narrower on the sides. The lateral scales adjacent to the ventral scales are very small and irregular, forming a fold along the sides of the body. The ventrals are square, in 12 longitudinal and 24 transverse rows. There are 41 scales around the midbody region. The anterior row of preanals has two scales; there are four elongate scales and two lateral slivers in the posterior row.

Few of the head scales can be described. There appear to be two moderately large supraoculars on each side; possibly (there is no evidence) a third small scale was present anterior to the two that can be seen. Contact with the palpebrals cannot be determined. The lower eyelid is too badly damaged to see a translucent disc if one was present. The nostril is present in the middle of a large nasal; there is no loreal, and the nasal extends in a point to the eye opening. There are five supralabials to and including the small supralabial under the posterior corner of the eye.

There are four pairs of chinshields, the anterior two of which are in contact across the midline; all are in contact with the labials. The gular crease is well developed, and the pregulars are rectangular and arranged in transverse rows; enlarged pregular scales are absent. The posterior gulars are rectangular and in seven transverse rows; the collar scales are elongate rectangles.

The subdigital lamellae on the third and fourth toes are divided proximally, but the inner scale of each pair is not tuberculate; the lamellae number about 20 under the fourth toe. Under the fourth finger, the lamellae are not divided, and number 12.

The tympanum is deeply recessed, and overhung by scales of the external opening.

There are no femoral pores.

The tongue is papillate throughout.

There are numerous characters that distinguish this specimen from Ecpleopus gaudichaudi, and, in fact, from all small teiids known from Patrocinio, Minas Geraes (map) or adjacent areas of Brazil, whence Guichenot’s specimen supposedly came. Certain features, such as the arrangement of the nasal and absence of the loreal, suggest that this specimen belongs to some species of Proctoporus but I am unwilling to commit myself to this position. No member of the genus Proctoporus is known from any area of Brazil.

Other reports of Ecpleopus gaudichaudi, all from Ecuador, are
based on misidentifications. Günther (1859) reported specimens of *Aspidolaemus affinis* as *Cercosaura gaudichaudi*; Boulenger (1885b) provided the correct specific name for these individuals. Boulenger (1882) reported specimens of *Pholidobolus montium* as *Cercosaura gaudichaudi*, but later (1885b) corrected the identification. Müller (1882) also reported a specimen (NHMB 3768) from Ecuador as *Ecpleopus gaudichaudi*. I have examined this specimen, and it is clearly referable to *Aspidolaemus affinis*.

**Relationships of Aspidolaemus affinis**

The second of the two species that Boulenger (1885) left in the genus *Ecpleopus* is only distantly related to *E. gaudichaudi*. The subgeneric name *Aspidolaemus* Peters, 1862, is available for this species.

*Aspidolaemus affinis* (Peters)

*Ecpleopus (Aspidolaemus) affinis* Peters, 1862: 199.

The relationships of this species are closer to *Pantodactylus, Prionodactylus*, and especially *Pholidobolus* than to *Ecpleopus gaudichaudi* (Uzzell, 1959). Among the many characters of this species that distinguish it from *Ecpleopus gaudichaudi* are the expanded first superciliary, the pigmented disc in the lower eyelid, the deeply recessed tympanum, the quadrangular to subhexagonal dorsal scales, the longitudinal rows of quadrangular ventral scales, and the calcareous spines in the hemipenis.

The relationships of *Aspidolaemus* with *Prionodactylus, Pantodactylus* and *Pholidobolus* are suggested by the two widened rows of gular scales, the longitudinal rows of ventral scales; the expanded first superciliary, and the relative shortness of the posterior preanals. The exact relationships of *Aspidolaemus* to these genera is not clear; it can be distinguished from all three by the complete absence of femoral pores and by the opaqueness of the disc in the lower eyelid. It can be distinguished from *Pholidobolus* (except for the curious *Pholidobolus anomalus* Müller, 1923) by the presence of prefrontals. It can be distinguished from *Prionodactylus* and *Pantodactylus* by the weakness of the keeling of the dorsal scales, which have several ridges.
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