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26

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VANZOLINIUS, A NEW GENUS PROPOSED FOR *LEPTODACTYLUS DISCODACTYLUS* (AMPHIBIA, LEPTODACTYLIDAE)

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The relationships of *Leptodactylus discodactylus* Boulenger have been obscure. In the first analysis of the relationships of *discodactylus* since Boulenger's description, I (1970) placed this species in the Melanonotus group of the genus *Leptodactylus*, based primarily on external morphology. This relationship was questioned when certain life history data were gathered (Heyer and Bellin, 1973). In a recent analysis of the relationships of the genus *Adenomera* within the subfamily Leptodactylinae (Heyer, 1974), I concluded that *discodactylus* was most closely related to *Lithodytes lineatus*, and with a certain amount of hesitation redefined *Lithodytes* to include *discodactylus*. Since then, the karyotype has been determined for *discodactylus* (Heyer and Diment, in prep.) and I have been able to examine more material of *Lithodytes lineatus*, which has resulted in a change of one character state. With this additional information, I believe that there is now sufficient evidence to firmly establish the generic identity of *discodactylus*.

Previously (Heyer, 1974), primitive and derived states were defined for 50 taxonomic characters, and polarities of character states were inferred for members of the subfamily Leptodactylinae. Alternate phylogenies were constructed based on shared derived character states. One phylogeny was chosen that was thought to best represent the actual relationships within the subfamily. The analysis showed that *Adenomera*, *Leptodactylus*, *Lithodytes lineatus*, and *discodactylus* constitute a tight taxonomic cluster. It is the relationships among these taxa that need to be reevaluated; this study, therefore, is limited to examining the relationships among these four taxa.

Methods and Materials

The same methods and data are used as in Heyer (1974) with the following modifications: 1) If all four taxa share the same character state, that character is not used; 2) If a derived state is unique to one taxon, it is not used as it gives no information on common ancestry; 3) The units of comparison are different, necessitating a redescription of the character states (see below). In the previous study, the unit used in the analysis was the species. In this study, as generic relationships are the focus, the unit of comparison is the genus; 4) Four characters (pterygoid-parasphenoid overlap; iliacus externus muscle; adductor longus muscle; gluteus muscle), were shown to be suspect in the original determination of direction of change of states (Heyer, 1974), and as no additional evidence has been accumulated to resolve these characters, they are omitted in the present study.

Character state descriptions: External vocal sacs—Primitive state: No external vocal sac. State 1: No external vocal sac or indications of lateral vocal folds. State 2: No external vocal sac, indications of vocal folds, or well-developed lateral vocal sacs. The direction of change of character states is: P→1→2.

Male thumb—Primitive state: Nuptial adspersities present in form of pad. State 3: No nuptial adspersities. State 4: Either spines on thumb, or in case of Fuscus group, no adspersities (see Heyer, 1974). The directions of change of character states are: 3←P→4.

Body glands—Primitive state: No well-defined glands. State 5: No glands and/or dorsolateral folds.

Toe disks—The dorsal toe disks of *Lithodytes lineatus* have dorsal scutes, similar to those of *Hylodes* and distinct from the longitudinal grooves in the disks of *discodactylus*. Primitive state: No disks. State 6: No disks and/or disks lacking dorsal grooves or scutes. State 7: Toe disks with scutes on dorsal surface. State 8: Toe disks with longitudinal grooves on dorsal surface. The directions of change of character states are: P→6→7.
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Toe web—Primitive state: Toes fringed. State 9: Toes fringed or free. State 10: Toes free. The direction of change of character states is: P→9→10.

Egg pigment—Primitive state: Melanocytes present or absent. State 11: No melanocytes.

Geniohyoideus lateralis muscle—Primitive state: No lateral flare or slip. State 12: Lateral flare or slip present.

Sternohyoideus muscle origin—Primitive state: Single or double slip from sternum. State 13: Double slip from sternum.

Sternohyoideus muscle insertion—Primitive state: Lateral edge of hyoid plate. State 14: Some fibers near midline of hyoid plate.

Gracilis minor—Primitive state: Broad. State 15: Rudimentary.

Frontoparietal fontanelle—Primitive state: None. State 16: Small fontanelle present or absent.

Anterior articulation of vomer—Primitive state: Vomer articulating with maxilla or premaxilla or neither. State 17: Vomer articulating with maxilla or premaxilla.

Sphenethmoid-optic foramen relationship—Primitive state: Posterior extent of sphenethmoid far from optic foramen. State 18: Posterior extent of sphenethmoid far from to bordering optic foramen.

Anterior extent of sphenethmoid—Primitive state: To mid-vomer. State 19: To mid-vomer or more anteriad.

Terminal phalanges—Primitive state: Knobbed. State 20: T-shaped.

Karyotypes—Heyer and Diment (in prep.) argued that two aspects of karyotypes yield phylogenetic information on the genera *Adenomera* and *Leptodactylus*: diploid number and presence or absence of acrocentric chromosomes. The primitive karyotype was argued to have a diploid number of 26 with acrocentric chromosomes.

Diploid number—Primitive state: 2N = 26 or 24. State 21:

2N = 22. State 22: 2N = 18. The direction of change of states is: P→21→22.

Acrocentric chromosomes—Primitive state: Present. State 23: Present or absent. State 24: Absent. The direction of change of character states is: P→23→24.

Relationships

The four taxa have the following advanced states: *Adenomera*—1, 3, 6, 10, 11, 12, 14, 15, 16, 18, 19, 20; *Leptodactylus*—2, 4, 5, 9, 12, 16, 18, 19, 21, 23; *lineatus*—3, 5, 7, 10, 11, 13, 14, 17, 20, 22, 24; *discodactylus*—3, 8, 11, 13, 15, 17, 20, 21.

Two taxa pairs share the most derived character states (7): *Adenomera–lineatus* and *lineatus–discodactylus*. As *Leptodactylus* and *discodactylus* only share one derived state, the best phylogeny using the *Adenomera–lineatus* pair cluster is that shown in Fig. 1, A. Two alternate phylogenies are possible using the *lineatus–discodactylus* cluster (Fig. 1, B, C). *Adenomera* shares 6 states with *Leptodactylus* (Fig. 1, C) and 5 states with *discodactylus* (Fig. 1, C, D). The phylogenies figured (A–E) are all of the reasonable possibilities.

In evaluating which phylogenies are likely to give a truer reflection of the actual relationships among these taxa, three criteria may be applied to the phylogenies. The first criterion was used in constructing the phylogenies—maximizing the number of shared character states, or in Hennig's terms, seeking sister-groups. Using this criterion, the phylogenies of Fig. 1, A, B, C are preferred over those of Fig. 1, C and D. A second criterion is the number of convergences of character states required by each phylogeny. The fewer the number, the more likely that the phylogeny is correct. The number of convergences in each of the phylogenies pictured are: Fig. 1, A and B, 13 convergences; Fig. 1, C, 11 convergences; Fig. 1, D and E, 15 convergences. A third criterion is to evaluate the ancestral clusters in terms of non-convergent character states. That is, if a character state is already convergent in

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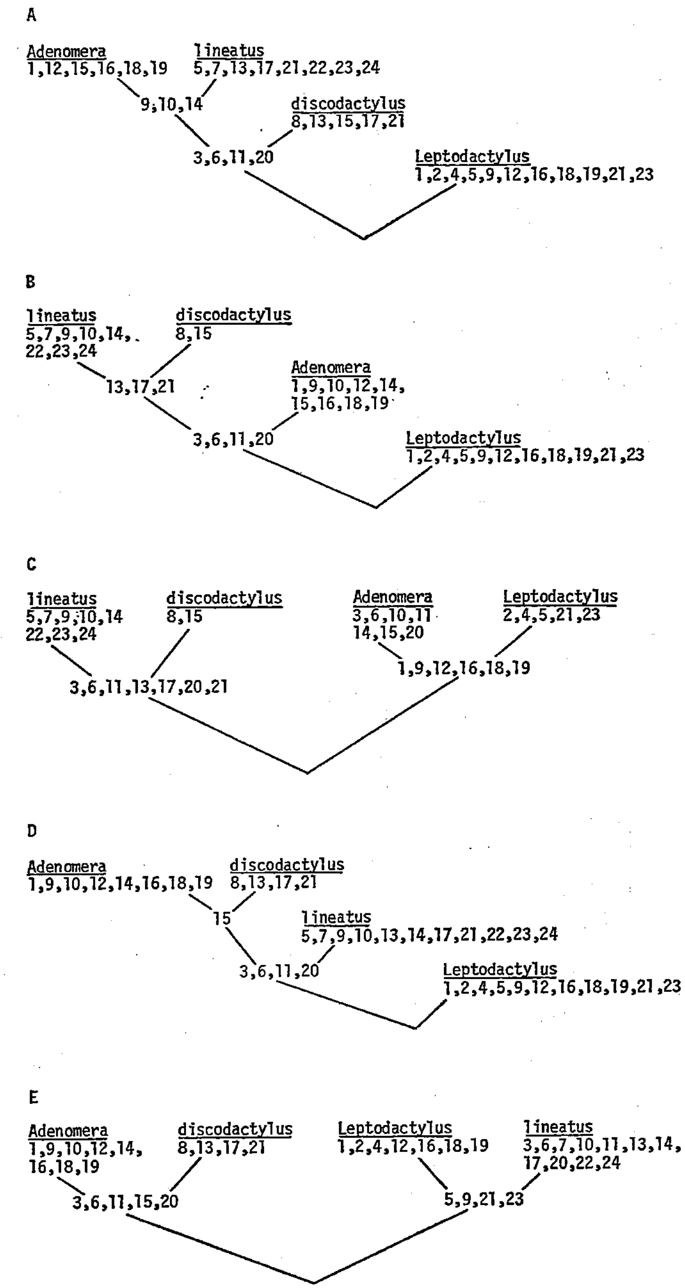
Fig. 1. Five possible phylogenies for *Adenomera*, *Leptodactylus*, *Lithodytes lineatus*, and *discodactylus*.



a given phylogeny, its phylogenetic information content is not as great as non-convergent character states. A set of four shared derived character states that are not convergent in the phylogeny is more robust than a set of four derived states that are convergent within the total phylogeny. The phylogenies of Fig. 1, A and B are strong, with six non-convergent states ancestral to either *Adenomera* and *lineatus* (Fig. 1, A) or *lineatus* and *discodactylus* (Fig. 1, B) and four non-convergent states ancestral to *Adenomera, lineatus,* and *discodactylus.* The phylogeny of Fig. 1, C is almost as strong as *Adenomera* and *Leptodactylus* share five non-convergent states; however, *lineatus* and *discodactylus* share but two non-convergent states. The phylogeny of Fig. 1, D has the same non-convergent states ancestral to *Adenomera, discodactylus,* and *lineatus* that are found in the phylogenies of Fig. 1, A and B. Within the cluster of these three taxa, the phylogeny of Fig. 1, D is weakest, as *Adenomera* and *discodactylus* only share one non-convergent state while each of these taxa shares two non-convergent states with *lineatus* (Fig. 1, A, B). The phylogeny of Fig. 1, E is weak, *Adenomera* and *discodactylus* sharing only one non-convergent state and *lineatus* and *Leptodactylus* sharing two non-convergent states.

The phylogenies of Fig. 1, A, B, and C are the most robust. All three have the maximum number of shared derived states for a species pair. The phylogenies of Fig. 1, A and B have the most shared non-convergent ancestral states, while that of Fig. 1, C has the least number of convergent states. The phylogenies of Fig. 1, D and E are much weaker in comparison and are not further considered.

It is necessary at this point to reiterate my concept of a genus: it should 1) be monophyletic, 2) be reasonable in size (number of species), and 3) represent a distinct adaptive complex if possible. Criterion 2 does not apply here, as *Adenomera, Leptodactylus* and *Lithodytes* combined have about 40 species. As developed elsewhere (Heyer, 1973, 1974), *Adenomera* is a wet forest genus, *Leptodactylus* is a savanna genus and each has evolved in response to the very different selective pressures associated with the two environments. The resolution of how many genera are represented among *Adenomera,*

Leptodactylus, discodactylus, and *lineatus* thus hinges on adaptive complexes, which information is not complete for *discodactylus* and *lineatus.* The available evidence is sufficient to determine the broad adaptive relationships of *lineatus* and *discodactylus,* however. No egg clutches have been found for either form, so it is not known whether either has a foam nest. In both, the eggs are non-pigmented (determined from advanced ovarian eggs), which strongly suggests that the eggs are hidden in some fashion. In the case of *lineatus,* the eggs are large and of the same size found in *Eleutherodactylus,* which has direct development. The eggs are small in *discodactylus* and are probably laid at the male calling sites, which are at the edge of seepage areas in naturally occurring enclosures formed by tree roots and leaves (Heyer and Bellin, 1973). The calling sites of *lineatus* are not known, but collections indicate that they are terrestrial and/or standing water breeders. With what is known, *discodactylus* can be categorized as having adaptive complexes distinct from both *Adenomera* and *Leptodactylus.* Briefly, *discodactylus* is adapted to the slow moving stream way of life, *Adenomera* is adapted to the terrestrial, wet-forest way of life, and *Leptodactylus* is adapted to xeric environments.

Combining this information with the phylogenies of Fig. 1, A, B, C, the following nomenclatural decisions are possible. If *Adenomera, Leptodactylus,* and *discodactylus* are generically distinct, then *lineatus* would have to be a distinct genus according to the phylogeny of Fig. 1, A, or it could be combined with *discodactylus* in a common genus in the phylogenies of Fig. 1, B and C. *Lithodytes lineatus* has a number of derived states in addition to those shared with *discodactylus,* however, including dorsolateral folds, free toes, and a derived karyotype. These unshared derived states, together with the probability that *lineatus* and *discodactylus* differ in mode and habitat of egg and larval development convince me that *lineatus* and *discodactylus* are generically distinct.

A comment might be helpful in explaining why I think this decision is the proper one to make. In the previous study (Heyer, 1974), the evidence then available dictated that *discodactylus* was certainly not a *Leptodactylus*. To remove *discodactylus* from the genus *Leptodactylus*, a decision had to be made to include the species in the genus *Lithodytes* or to name a new genus for it. I chose the former course because it was nomenclaturally conservative and I hoped that more information on life history and karyotypes would resolve the matter. Combining *lineatus* and *discodactylus* in a common genus was believed to be an unsatisfactory solution, however, as the two species appear very dissimilar. The karyotypic evidence further supports the generic differentiation of these two species. The relationships of *discodactylus* have been of concern because externally *discodactylus* looks like members of the Melanonotus group of the genus *Leptodactylus*, or if the toe fringe were removed, like members of the genus *Adenomera*. It is apparent that the similarities of *discodactylus* to certain species of *Leptodactylus* and *Adenomera* are based on shared primitive character states, however. The analysis of derived shared character states clearly demonstrates the divergent evolutionary pathways of these three taxonomic units.

Taxonomic Conclusions

Four genera are recognized in the *Leptodactylus*-complex: *Adenomera*, which contains five species, *Leptodactylus*, which contains about 35 species, *Lithodytes*, which contains one species, and a genus for *discodactylus*. Definitions of *Adenomera* and *Leptodactylus* may be found in Heyer (1974); a definition of *Lithodytes* may be found in Lynch (1971). As no generic name has been proposed for *discodactylus*, a new genus is described as follows:

Vanzolinius, new genus

Type species: *Leptodactylus discodactylus* Boulenger, 1883.

Diagnosis: *Vanzolinius* is unique among leptodactylid frogs in possessing a bony mesosternum and expanded toe disks with longitudinal grooves on the dorsal surfaces. All other genera with a bony mesosternum either do not have toe disks or, if disks are present, either do not have any dorsal modifications or have dermal scutes.

Definition: Pupil horizontal; tympanum distinct; vocal sac internal; male thumb without nuptial adspersities; body without well defined glands; toes disked with dorsal surfaces with 3–5 longitudinal grooves; tarsal fold present; metatarsal tubercles neither pronounced nor cornified; toes with lateral fringes; eggs lacking melanophores; large clutch size (> 1000 eggs); depressor mandibulae condition DFsq (large slip originating from dorsal fascia, small slip originating from squamosal area); geniohyoideus medialis continuous medially; geniohyoideus lateralis without lateral flare or slip; anterior petrohyoideus insertion on edge of hyoid; sternohyoideus origin with distinct slips from anterior mesosternum and another from posterior meso, and/or xiphisternum; sternohyoideus insertion near lateral edge of hyoid; omohyoideus insertion on hyoid plate and fascia between posterolateral and posteromedial processes of hyoid; tendon of semitendinosus confluent with posterior portion of sartorius insertion on knee and tendons of gracilis minor and major passing dorsad to tendon of semitendinosus; iliacus externus extending from ¾ to full length of iliac bone; tensor fasciae latae insertion posterior to iliacus externus on iliac bone; gracilis minor narrow; interior and exterior portions of the semitendinosus uniting in common tendon distally, exterior portion larger or equal to interior (smaller) portion; sartorius moderately developed; accessory head of adductor magnus without distinct tendon; adductor longus well developed; gluteus insertion on cruralis and knee; quadratojugal well developed, contacting maxilla; maxillary teeth present; nasals widely separated; no frontoparietal fontanelle; zygomatic ramus of squamosal just longer than, just shorter than, or equal to otic ramus; vomerine teeth present; vomers not in medial contact; vomer articulation with premaxilla and/or maxilla; posterior extent of sphenethmoid widely separated from optic foramen; sphenethmoid extending anteriorly to middle of vomers; occipital condyles widely separated; no anterior processes of hyale; alary process of hyoid somewhat narrow and stalked; posterolateral process of hyoid present; ilium with well developed dorsal crest; terminal phalanges T-shaped, expanded; mesosternum a bony style; xiphisternum entire, single; diploid chromosome number 22, one pair of acrocentric chromosomes.

Etymology: The genus, masculine in gender, is named for Dr. Paulo E. Vanzolini, in recognition of his work on the South American herpetofauna.

Content: Monotypic. For further details of morphology and distribution, see Heyer (1970).

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