The Systematic Relationships of *Dravidogecko anamallensis* (Günther 1875)

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Abstract. -The relationships of the monotypic gekkonine genus *Dravidogecko* are assessed by comparative evaluation of its external and internal morphology. A suite of shared-derived features is possessed by *Hemidactylus* and a variety of satellite genera, including *Dravidogecko*. These similarities are advocated as being so compelling, and the ostensible defining features of *Dravidogecko* to be so weak that the latter is subsumed as a junior synonym of *Hemidactylus*. The biogeographic consequences of this taxonomic shift are considered.

Key words: Dravidogecko, Hemidactylus, Teratolepis, digits, scansors, phalanges, paraphalangeal elements, muscles, biogeography, India.

Introduction

Dravidogecko is a monotypic genus of gekkonid lizards endemic to south India. The single species, *D. anamallensis,* was originally described as a member of the genus *Hoplodactylus* (Günther, 1875; Strauch, 1887), but following the work of Smith (1933), it was assigned to a new genus, primarily on the basis of differences in the distal scansors and in preanal pore arrangement. Subsequently it has been demonstrated that *Dravidogecko* is a gekkonine gecko, whereas *Hoplodactylus sensu stricto* is a diplodactyline (Underwood, 1954; Kluge, 1967). The relationships of *Dravidogecko* have remained obscure, and the systematic status of the species has never been investigated adequately. It is known from only a few specimens from the Anaimalais, Palnis and Tirunelveli Hills (Satyamurti, 1962; Murthy, 1985) but is reportedly widely distributed throughout forested areas of southern peninsular India (Daniel, 1983).

Russell (1972) considered *Dravidogecko* to belong, on morpho-functional grounds, in the *Hemidactylus* group, along with *Hemidactylus*, *Briba, Teratolepis* and *Cosymbotus*. Kluge (1983) placed it, along with the other gekkonine genera previously mentioned, in the tribe Gekkonini on the basis of the absence of the second ceratobranchial arch. Russell (1976: 238; Fig. 14) suggested that *Dravidogecko* had a digital structure that was most closely approached by that of *Hemidactylus* and its close allies. While external form of the digits is particularly sensitive to functional demands and thus prone to exhibiting convergence and parallelism (Russell, 1979), details of the internal anatomy are much more helpful at indicating true homology and, therefore, affinity (Russell, 1976, 1979; Russell and Bauer, 1990). We herein present the results of a comparative survey of both the external and internal anatomy of the feet and digits in *Hemidactylus* (and its close relatives) and use these to demonstrate both the wide range of variation present and the shared derived features that circumscribe this cluster and help clarify the relationships of the enigmatic *Dravidogecko*. We further relegate the generic name *Dravidogecko* into the synonymy of *Hemidactylus* as there are no derived features of *Dravidogecko* that are not also shared by at least some *Hemidactylus*. It is probable that *H. anamallensis* is a primitive hemidactyl.

Materials and Methods

Specimens of *Dravidogecko* were examined or borrowed from the collections of The Natural History Museum, London (BMNH) and the Institute Royal des Sciences Naturelles de Belgique, Brussels

(IRSNB). Comparative material of other gekkonines, especially *Hemidactylus*, were borrowed from the BMNH and the California Academy of Sciences, San Francisco (CAS). Observations on toe structure were made using a Nikon SMZ-10 microscope. The specimens examined are listed below. All numbers refer to BMNH specimens unless otherwise identified.

Dravidogecko anamallensis 82.5.22.79-84; IRSNB 1194.
Briba brasiliana 1971.1045.
Cosymbotus craspedotus 1926.12.7.7, 1930.10.9.2
C. platyurus xxi.36a, 97.6.21.4, 97.12.28.10, CAS 18565, CAS 18567
Hemidactylus albopunctatus 1946.8.22.75; *H. ansorgii* 1901.1.28.22; 1966.337; *H. barodanus* 1905.11.7.1-6; 1937.12.5.215-216; 1958.1.6.29; 1970.1437-38; *H. bouvieri* 66.4.12.3; 75.4.26.10; *H. bowringii* 1929.12.1.7-10; 1940.4.26.2-3; 1956.1.11.15-16; *H. brookii* 1918.11.12.2-10; 1930.10.6.6; 1931.12.10.6-7; 1970.2196-98; 1971.242; *H. citernii* 1931.7.20.114-119 and 128-130; 1937.12.5.202-204; *H. curlei* 1946.8.25.41; *H. depressus* 52.2.19.21; 61.2.21.5; 1948.1.7.35; *H. echinus* 89.7.6.1; 1903.7.28.1-2; *H. fasciatus* 1919.8.16.48; 1956.1.11.37-40; 1971.253; *H. flaviviridis* 1931.7.20.153-155; 1971.1378-1382; *H. forbesii* 1946.8.25.43-47; *H. frenatus* 1938.10.2.1; 1952.1.4.30-31; 1970.1879-1895; *H. garnotii* 95.11.7.1; 1903.2.21.1-2; 1940.6.3.24-29; *H. giganteus* 1908.12.28.27; 1969.828-829; *H. gracilis* 74.4.29.1388; 80.11.10.47; *H. granti* 1957.1.9.52-66; *H. greeffii* 93.12.7.1; 98.3.30.21-22; *H. homeolepis* 99.12.5.38; 1953.1.7.84-85; 1967.485-489; *H. isolepis* 1952.1.7.79-80; *H. jubensis* 1946.8.23.66; *H. karenorum* 68.4.3.88-89; 91.11.26.13-14; *H. laevis* 1946.8.25.42; *H. leschenaulti* 70.5.18.70-71; 74.4.29.233-236 (six specimens); *H. longicephalus* 1936.8.1.287-305; *H. mabouia* 1923.11.9.46-50; 1964.1429-35; 1970.2209-15; *H. macropholis* 1931.7.20.109; 1937.12.5.250-258; *H. maculatus* 69.8.25.15; 1956.1.11.44; *H. megalops* 1946.8.25.67; *H. mercatorius* 1930.7.1.84-90; 1938.8.3.11-15; *H. muriceus* 1926.9.24.13; 1966.283; *H. modestus* 1946.8.25.37; *H. ophiolepis* 1937.12.5.324-325; *H. oxyrhinus* 99.12.5.170-175; 1967.491-494; *H. persicus* 1970.250; 1972.716; *H. prashadi* 1946.8.14.66-69; *H. pumilio* 1946.8.20.1; 1946.8.25.58-61; *H. reticulatus* 1901.3.8.1-3; *H. richardsoni* 1916.5.29.1; 1919.8.16.49; *H. ruspolii* 1937.12.5.228-229; 1937.12.5.239-246; *H. sinaitus* 97.10.28.83-86; 1937.2.5.293; 1953.1.6.97-98; *H. smithi* 1931.7.20.85-89; 1972.745; *H. somalicus* 1946.8.25.77-78; *H. squamulatus* 98.1.8.2-3; 1902.5.26.2; 1923.10.9.2; 1923.10.9.14-15; *H. subtriedrus* 74.11.11.1; *H. taylori* 1946.8.23.48; *H. triedrus* xxi.19a-b; *H. tropidolepis* 1937.12.5.322-323; *H. turcicus* 1934.11.8.10- 14; 1971.1143-45; *H. yerburii* 99.12.13.43-44; 1903.6.26.3-4; 1945.12.18.12.
Teratolepis fasciata 69.8.28.32; 1933.7.8.37; 1963.1019; 1964.930-931; *T. albofasciatus* 1963.613-621

Results

A considerable range of variation in digital form and subdigital scansor design exists among members of the genus *Hemidactylus* (Fig. 1). This variation is evident in such aspects as the number of divided scansors (lamellae), the extent of their division, the extent of the undivided lamellar series at the base of the digits, and the length, form and degree of separation of the free, distal, claw-bearing segment of the digits. Figure 2 illustrates the general form of the ventral aspect of the right pes of *Dravidogecko* and provides comparison with the ventral aspects of the fourth pedal digit of *Hemidactylus reticulatus* and *Teratolepis fasciata.* While some species of *Hemidactylus*, such as *H. garnotii* and *H. smithii* (Fig. 1), have digits with a large number of completely divided scansors, and an elongate, free distal, claw-bearing portion, this is not so for other species, such as *Teratolepis albofasciatus* (see Grandison and Soman, 1963), *Hemidactylus somalicus* and *H. bouvieri* (Fig. 1). In the latter three cases the number of scansors is small, only the distal most ones are notched, and the distal, free, claw-bearing portion of the digit

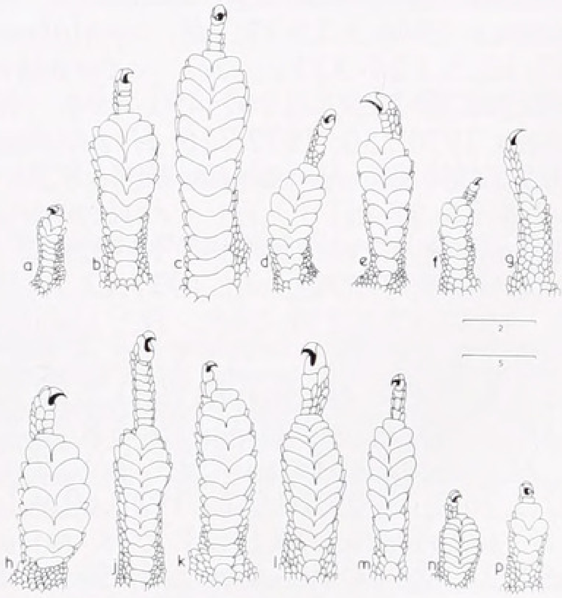

FIG. 1. The array of digital form in the genera *Hemidactylus* and *Teratolepis*. All illustrations are of the fourth digit of the pes; a-e, j are of the right pes, f-h, k-p are of the left pes. The 2 mm scale bar refers to all specimens except n, to which the 5 mm scale bar applies. All catalogue numbers refer to the Natural History Museum, London (BMNH). a. *Teratolepis albofasciatus* 1963.617; b. *Hemidactylus bowringii* 1929.12.1.6; c. *H. garnotii* 95.11.7.1; d. *H. barodanus* 1970.1438; e. *H. turcicus* 1971.1144; f. *H. somalicus* 1946.8.25.77; g. *H. ophiolepis* 1937.12.5.324; h. *H. mabouia* 1964.1431; j. *H. forbesii* 1946.8.25.47; k. *H. smithii* 1931.7.20.85; l. *H. fasciatus* 1919.8.16.48; m. *H. ansorgii* 1901.1.28.22; n. *H. richardsonii* 1916.5.29.1; p. *H. bouvieri* 66.4.12.3.

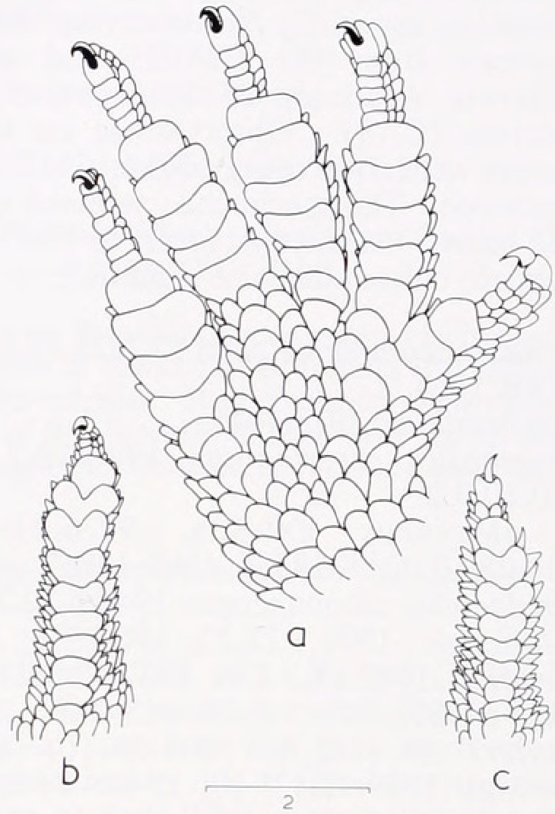

FIG. 2. a. Ventral aspect of the right pes of *Dravidogecko anamallensis*, BMNH 82.5.22.79. b. Ventral aspect of the fourth digit, right pes of *Hemidactylus reticulatus*, BMNH 1901.3.8.1. c. Ventral aspect of the fourth digit, left pes of *Teratolepis fasciata*, BMNH 1933.7.8.37. Scale bar in millimeters.

is relatively short. This situation is also seen in *Hemidactylus reticulatus* and *Teratolepis fasciata* (Fig. 2, b, c). The almost continuous range of variation in external digital characters, especially among the west Asian and Somali species of the *Hemidactylus* group of geckos has long been recognized, and has resulted in the establishment of several different, largely arbitrary, generic arrangements (see Parker, 1942 for a discussion). Thus, while division of the scansors is generally characteristic of the genus *Hemidactylus*, there are many species that express this trait only marginally.

Russell (1976: Fig. 14) indicated this potential continuity in scansor form, from undivided to completely divided, by comparing *Dravidogecko* with *Cyrtodactylus brevipalmatus*, *Hemidactylus reticulatus* and *H. barodanus*. While this was simply a depiction of change of form assembled as a morphotypic series, it was also implied that there may be deeper underlying anatomical clues that are indicative of the closeness of relationship of *Dravidogecko* to *Hemidactylus*. The superficial comparisons of the digits(Figs. 1, 2; see above) provide some idea of the potential range of variation, but should be treated with caution when being implicated in arguments about relationship because of the extreme plasticity of external digital form. [Such aspects are well exemplified by the taxonomic history of the taxon that is the subject of this contribution.] Detailed examination of the internal anatomy of the digits provides more convincing evidence about the affinities of *Dravidogecko*.

Russell (1976) presented a mechanistic diagram of the main features of digital design in *Hemidactylus*. The chief aspects of note here are the unusual form and relationships of the antepenultimate phalanx of digits III-V of the pes (Russell, 1977), the distal extent of the dorsal interossei muscles along the digit, and the means of tendinous insertion of these muscles onto the scansors. The pattern of digital characteristics of *Hemidactylus* is essentially repeated in *Dravidogecko* and is restricted to only a few other genera *(Briba, Cosymbotus* and *Teratolepis*). This suite of shared-derived digital features of these taxa (the short, erect nature of the antepenultimate phalanx of pedal digits III-V, the distal extension of the dorsal interossei muscles as far as the distal end of the antepenultimate phalanx, and the tendinous insertion of the dorsal interossei muscles onto the distal margin of each scansor in turn) unites them as a distinctive evolutionary unit. Apart from *Hemidactylus*, all of the other genera in this cluster are either monotypic *(Briba* and *Dravidogecko*) or include only two species *(Cosymbotus* and *Teratolepis)*.

Dissection of the digits of *Dravidogecko* reveals that the dorsal interossei muscles are well-developed and robust and extend as fleshy bellies as far distally as the digital inflection (the point of emplacement of the reduced, erect antepenultimate phalanx onmanual digits III and IV and pedal digits III-V). The dorsal interossei muscles send individual tendons to the distal borders of the scansors as they do in *Hemidactylus* (see Russell, 1976) and *Cosymbotus*. This situation also pertains in *Teratolepis* and *Briba* (Russell, 1972). *Dravidogecko* also shares with *Hemidactylus, Briba* and *Cosymbotus* the particular morphology and placement of paraphalangeal elements (Russell and Bauer, 1988).

The above comparisons indicate that *Dravidogecko* shares with other members of the *Hemidactylus* radiation (*Hemidactylus, Briba, Cosymbotus, Teratolepis*) all of the derived digital features that distinguish these taxa from all other geckos. However, apomorphic features characteristic of many *Hemidactylus* species, such as those associated with the complete division of the scansors, are lacking in *Dravidogecko*. It is therefore likely that *D. anamallensis* is a relatively plesiomorphic member of this radiation. As such, it is probable that the recognition of *Dravidogecko* renders *Hemidactylus* as presently construed paraphyletic. In order to maintain monophyletic generic units we hereby place *Dravidogecko* into the synonymy of *Hemidactylus* Gray, 1825. The correct designation for the single known species formerly referred to this genus thus becomes *Hemidactylus anamallensis* (Günther 1875), new combination.

Discussion

Many lizard families include monotypic genera. Although in some cases these represent independently evolving lineages, in most they are relatively primitive or highly derived members of other lineages, and their recognition renders the latter groups paraphyletic. *Hemidactylus* is the most specious genus in the Gekkonidae, with 75 species currently recognized (Kluge, 1991). Relationships within the genus are very poorly understood (Parker, 1942; Loveridge, 1947; Kluge, 1969; Bastinck, 1981) and a general uniformity among most forms (Russell, 1976) has rendered casual attempts at investigating its phylogeny unsuccessful. The placement of *Dravidogecko anamallensis* into this morass, of course, does nothing to aid this confusion. It does, however, ensure that *Hemidactylus anamallensis* is taken into account if and when a generic revision of all *Hemidactylus* is accomplished.

It is not only in the interest of maintaining monophyletic groups that the revaluation of monotypic genera is undertaken. Current nomenclatural usage has implications for non-systematists. As an endemic Indian subcontinent form, *Dravidogecko* might be used to support arguments about the uniqueness and antiquity of the Indian biota. The use by biogeographers of classification schemes that do not adequately reflect phylogenetic patterns has been shown to lead to the erection of demonstrably false hypotheses

(Bauer, 1989). Clearly, biogeographic interpretations must be based upon the phylogenetic relationships of the organisms considered. Some other *Hemidactylus* group geckos sharing with *H. anamallensis* at least partially undivided scansors are also Indian forms (e.g., *Teratolepis albofasciatus* from the Ratnagiri District, Maharashtra, *Hemidactylus gracilis* from the Madhya Pradesh, Maharashtra and Andhra Pradesh (Smith, 1935;Murthy, 1985), and *H. reticulatus* from Tamil Nadu, Andhra Pradesh and Karnataka (Smith, 1935; Murthy, 1985)). *Teratolepi fasciata* is also from the Indian subcontinent (Anderson, 1964; Minton, 1966) and it appears likely that the hemidactyls, as a group, have undergone a long period of evolution and diversification within the region.

Although the geographic ranges of some forms of *Hemidactylus* are indicative of relatively recent expansions (Kluge, 1967, 1969), most Indian species are moderately to highly circumscribed in their distribution and hold the promise of contributing substantially to biogeographic hypotheses of area relationships within peninsular India. However, both biogeographic analyses and meaningful studies of the evolution of the pedal characteristics that have made *Hemidactylus sensu lato* so successful in India (and elsewhere) must await the ultimate resolution of phylogenetic relationships within the genus. In subsuming *Dravidogecko* within *Hemidactylus* we concur with the sentiments expressed by Loveridge (1947: 97) in discussing the African members of this radiation, "Any arrangement that would break up so unwieldy a genus as *Hemidactylus* is worthy of careful attention . . ." Such an arrangement must be phylogenetically based, and at present insufficient data are at hand to attempt this. However, we regard the identification of all members belonging to the *Hemidactylus* clade as a necessary first step in the process.

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