

Short Notes

Lamella and scansor numbers in *Thecadactylus rapicauda* (Gekkonidae): Patterns revealed through correlational analysis and implications for systematic and functional studies

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Many taxa of lizards bear transversely enlarged subdigital scales that are often a source of systematic characters. Among gekkonid and polychrotid lizards, elaborations of such scales, called lamellae and scansors, are employed in adhesive locomotion (Colette, 1961; Hiller, 1968; Russell, 1975). Subdigital lamellae and scansors are derivatives of scales, the form, shape and number of which are thought to reflect function (Russell, 1981) as well as indicate patterns of relationship (Couper et al., 1993; Raxworthy and Nussbaum, 1993; Grismer et al., 1994). While lamellae in the loose sense encompass all subdigital scales that are transversely enlarged, they can be divided into two subsets (fig. 1): scansors, the distal lamellae most closely involved in adhesion and therefore occurring on the hyperextensible portion of a digit (Russell, 1981, 1986); and basal lamellae, which differ morphologically from scansors (Russell, 1981), and are situated more proximally. Scale patterns in squamates are generally regarded as being genetically determined and discrete (Hecht, 1952). Counts of total lamellae feature in both systematic (Grismer et al., 1994, etc.) and functional (Hecht, 1952; Peterson, 1983a, b; Mayer in Losos, 1990; Glossip and Losos, 1997) studies.

Numbers of total lamellae vary both within and between digits and, as a consequence, most authors choose to count these structures on a smaller set of digits, on the assumption

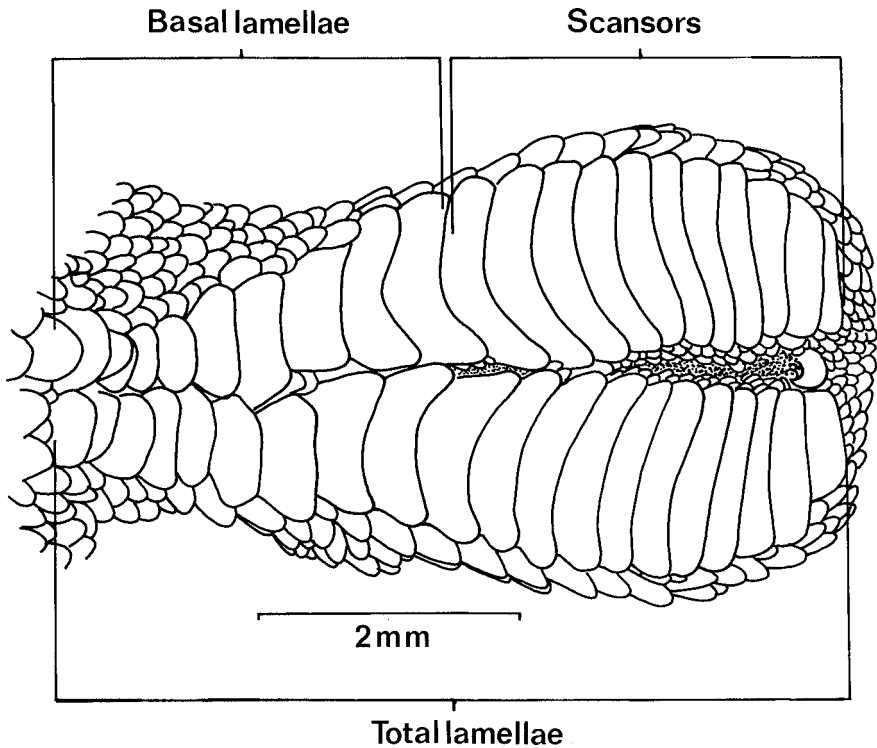


Figure 1. Ventral view of digit IV, left pes of *Thecadactylus rapicauda*, showing the location of the total lamella number and its subsets: scansors and basal lamellae, the former being positioned beneath the hyperextensible region of the digit.

that these digits will be representative or maximally informative (e.g. Digit IV: Broadley, 1977; King, 1962. Digits I, III, and IV: Ota et al., 1995). Although such selectivity is pragmatic and potentially justifiable, we are unaware of any studies that have formally addressed the questions of which digits are maximally informative, and which are the most appropriate for a particular taxon. As both the manus and pes of lizards generally exhibit asymmetry of digital length, digits three and four are often chosen for total lamella counts (Hecht, 1952; Colette, 1961). This has been justified because, being the largest, these digits are assumed to be most load-bearing (Hecht, 1952), and the easiest to distinguish and count (Colette, 1961). However, asymmetry of the length of digits varies markedly across taxa (Russell et al., 1997), even when phalangeal counts are identical. Given that discrepancy exists between the differential length of digits in different taxa, the question of how representative or informative selected total lamella counts are of a particular taxon remains, and should be assessed before a selection is made of which data to record and employ.

Herein we investigate the variation within and between total lamella, scansor, and basal lamella (fig. 1) counts on manual and pedal digits of the gekkonid *Thecadactylus rapicauda* as an exemplar. Stemming from this, we outline a method by which maximally informative data for systematic and functional studies might be selected. We examine the question of whether there are high levels of correlation between total lamella, scansor, and basal lamella counts on all digits of the manus and pes and explore ways to determine, on a smaller subsample, which of these counts are of most interest in the context of the question (systematic, functional, or both) at hand. We also address the question of whether correlational patterns exhibited by scansor and basal lamella counts mirror those of total lamella counts, or if these two component counts exhibit independent patterns.

By undertaking such a correlational study of these iterative homologues, we investigate whether different digits provide new or merely repeated information, and which, if any, digits are most representative (being most highly correlated) of the other digits on the limb in question. Both highly representative and poorly representative counts form valid characters for systematic studies and focal points for functional considerations. The inclusion of the former is justified as a proxy for the other digits, while the inclusion of the latter is justified as an indicator of the uniqueness of a particular digit, which may be of particular importance in functional studies.

Total lamella number (fig. 1) was recorded for all digits of the right manus and pes of 40 specimens of *Thecadactylus rapicauda* from across its broad range (see Appendix 1 for a list of specimens and their localities). A sample size of 40 was selected arbitrarily as a trade-off between time involved in data collection and a sufficient sample. We suggest that twenty would be a minimum sample size for this methodology. Additionally, the scansor number was recorded by counting those enlarged plates that occur only beneath the hyperextensible portion of each digit (Russell, 1981). This was achieved by reflecting the distal portion of each digit with an entomological pin to determine the point of inflection at which hyperextension occurs (Russell and Bels, 2001). Due to the intimate involvement of scansors in adhesion, they may be more constrained by selection than the more extensive total lamellar series (as counted by Hecht, 1952). Finally, basal lamella number was calculated by subtracting scansor number from the total lamella count (fig. 1). These two groups of 'subset' counts are included here as potentially useful, albeit neglected (but see Russell, 1981; Russell and Bels, 2001), characters for systematic and functional studies.

The resulting data (table 1 for summary) were tested for normality using the Kolmogorov-Smirnov test and were found to be highly non-normal for total lamella, scansor, and basal lamella counts. For this reason, and due to their discontinuous nature, Spearman correlations (Sokal and Rohlf, 1995) were used in the analysis. Six sets of correlations were conducted: one for each combination of total lamella, scansor, and basal lamella counts for the fore and hindlimb. For each digit in each set, Spearman correlation coefficients with the remaining four digits were averaged. This resulted in a single Average Spearman Correlation Coefficient for each digit. Although this does not represent a rigorous statistic, we believe that it does give a good idea of how representative a count is of other such counts, and is easier to interpret than a correlation of a particular digital count with the total respective count for the entire limb (which would eliminate the use of averages). These average Spearman's correlation coefficients were then used to determine how representative a particular count was of all other counts in a set (without accounting for differential digital lengths).

Average Spearman correlation coefficients for total lamella, scansor, and basal lamella counts of fore and hindlimbs follow several patterns (fig. 2). Similar general patterns are evident for both total lamella and scansor counts for the forelimb, with digit I being least representative of the others (see Russell and Bauer, 1990: 464-466 for possible reasons),

Table 1. Summary of statistics for counts of total lamellae, scansors, and basal lamellae on all digits of the manus and pes for 40 specimens of *Thecadactylus rapicauda*. All values are mean \pm standard deviation.

		Digit				
		I	II	III	IV	V
Manus	Total lamellae	15.7 \pm 2.0	18.6 \pm 1.6	20.1 \pm 1.7	20.6 \pm 1.6	18.8 \pm 2.2
	Scansors	8.3 \pm 1.3	11.0 \pm 1.1	11.5 \pm 1.0	11.8 \pm 0.9	10.9 \pm 0.9
	Basal lamellae	7.4 \pm 1.5	7.7 \pm 1.2	8.6 \pm 1.3	8.7 \pm 1.4	7.9 \pm 1.7
Pes	Total lamellae	17.6 \pm 2.0	19.7 \pm 1.9	21.1 \pm 1.9	21.6 \pm 1.8	20.3 \pm 1.4
	Scansors	9.5 \pm 1.3	11.6 \pm 0.8	12.1 \pm 1.1	12.3 \pm 0.9	11.5 \pm 0.9
	Basal lamellae	8.3 \pm 2.2	8.1 \pm 1.5	9.1 \pm 1.4	9.3 \pm 1.5	8.9 \pm 1.0

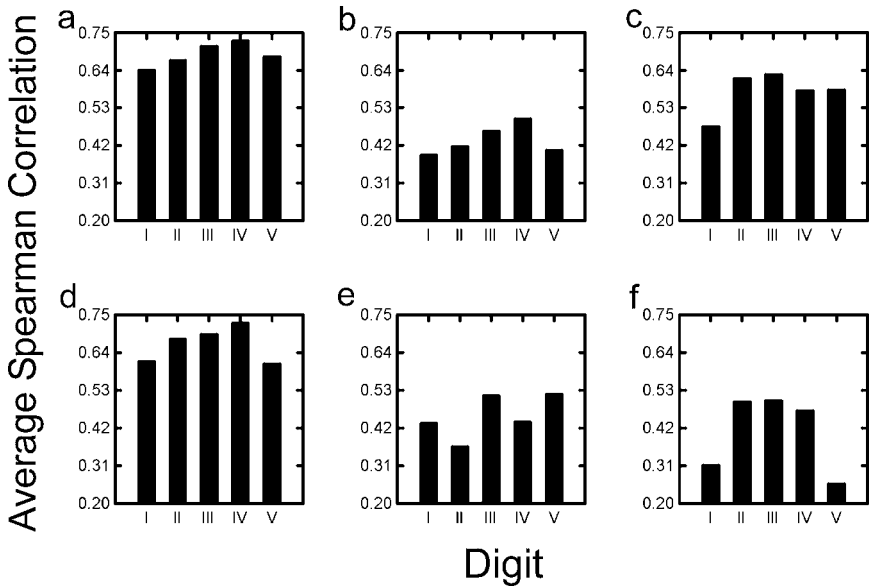


Figure 2. Average Spearman correlation coefficients for each digit with all other digits for total lamella (a, d), scansor (b, e), and basal lamella (c, f) counts for fore (a, b, c) and hindlimbs (d, e, f) for *Thecadactylus rapicauda* ($n = 40$).

digits II, III and IV being increasingly representative of the other digits, and digit V being less representative (fig. 2a, b). A similar pattern is revealed for the total lamella counts for the hindlimb (fig. 2d), except that digit V is the least representative. The pattern changes, however, when the scansor counts for the hindlimb and basal lamella counts for both limbs are considered (fig. 2e, c, f, respectively). For hindlimb scansor counts, digit II is the least representative while digit V is the most representative. When basal lamella counts are analyzed, digit III is most representative on both limbs (fig. 2c, f). The least representative digits for front and hindlimbs are I and V (fig. 2c, f), respectively, corresponding to the least representative digits for total lamella counts (fig. 2a, d).

These results suggest that for *Thecadactylus rapicauda*, a total lamella count for the forelimb would best be represented by digits I and IV, while for the hindlimb it would be best represented by digits IV and V. Representative scansor counts for the forelimb would mirror the situation for the total lamella counts of that limb, but the hindlimb would be most effectively represented by counts of scansors on digits II and V. Basal lamella counts would be best represented by digits I and III for the forelimb and by digits III and V for the hindlimb.

These findings also demonstrate that scansor and basal lamella counts contain different information from total lamella counts, validating their systematic utility. Since scansors are most closely involved with adhesion and their counts follow different patterns than those of basal lamellae, from a functional perspective they may be of greater interest than basal lamellae. Furthermore, since phalangeal length differs within digits (Russell and Bauer, 1990; Russell et al., 1997), it is not surprising that scansor and basal lamella counts also contain independent information.

The morphology and relative degree of development (large versus reduced) of digit I is highly variable amongst geckos in general (Russell and Bauer, 1990), which suggests that total lamella counts in general will be highly variable both within and between taxa. In certain taxa there may be major differences in patterns of expression of this digit between the fore and hindlimbs (even in the same species). Thus, any attempt to include total lamella, scansor or basal lamella counts of digit I in systematic analyses should take account of the high degree of variability of this digit across taxa.

Hecht (1952) and Colette (1961) both pointed out the generally held contention that digit IV is the longest and may therefore be representative of total lamella counts and patterns for the entire manus and pes. While this prediction holds true for total lamella counts and scansor counts of the manus of *Thecadactylus rapicauda*, and total lamella counts of the pes, it is not reflected in scansor counts of the pes or basal lamella counts of both the manus and pes. Pedal (vs. manual) geometry in geckos (Russell et al., 1997) might contribute to this discrepancy, with digit IV of the pes being generally shorter than digit III (Russell et al., 1997: fig. 2a, b). Proportions of the basal (non-scansor-bearing) to distal (scansor-bearing) portions of digit IV among geckos vary considerably (Russell et al., 1997: 784 — *Rhoptropus*) and may result in unexpected patterns of total lamella, scansor and basal lamella counts for that digit.

The data presented for *Thecadactylus rapicauda* and the comparative data available for pedal proportions and structure in geckos (Russell and Bauer, 1990; Russell et al., 1997) illustrate that the most appropriate characters for a particular taxon to be included in a systematic, functional or ecological study may not necessarily be the most intuitive. Such data further indicate that total lamella counts (which include all transversely widened subdigital scales), and scansor and basal lamella counts (which represent subsets of the total lamella count) do not necessarily exhibit similar patterns. Thus, the distinction between scansors and basal lamellae (which functionally are restricted to the basal part

of the digit in many taxa) is real, and each type of modified scale may be subjected to different selective pressures.

For both fore and hindlimbs, average correlation coefficients are greater overall for total lamella counts than for scansor counts or basal lamella counts. The range for all lamella counts is comparable between limbs. Autocorrelation does not appear to be a prevalent issue, given that the highest average correlation in the analysis is 0.727 (fig. 2d, digit IV; the lowest is 0.257 — fig. 2f, digit V). There is considerable inherent variation, and an appropriate choice of characters to investigate may well yield more discriminatory information than a default choice of a total lamella count for digit IV on manus and pes (for example).

Determining which morphological characters are most appropriate to include in a study can be time consuming, and data collection can be arduous and lengthy. Our correlational approach provides a potential avenue for exploring how to maximize the utility of the data collected by asking some initial questions about a smaller subset of the entire set of organisms available for examination. The initial effort involved in running the correlational analysis may well circumvent time spent in gathering data that provide no further discriminatory or explanatory power. This approach is applicable to an array of comparable variables where serially repeated counts are involved. Care should be taken in such correlational analysis to avoid or account for the potential confounding effects of ontogeny and selection. For example, Hecht (1952) noted that total lamella number was subject to selection in the gekkonid *Aristelliger*, with the count range differing between subadult and adult individuals. Unfortunately, Hecht (1952) did not distinguish between basal lamellae and scansors, so the subtleties of such differences cannot be dissected further.

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Appendix 1.

Museums, catalogue numbers, and collection localities for specimens used. Abbreviations follow Leviton et al. (1985), except Oklahoma Museum of Natural History.

CAS: 8767 — St. Croix; 13263 — Ecuador, Pichincha; 15816, 15817 — Ecuador, Napo-Pastaza.

FMNH: 45449, 109825 — Peru, Loreto; 49109, 49112, 49114 — Mexico, Yucatan; 168128, 228257 — Peru, Madre de Dios.

KU: 96489, 96490 — Panama, Bocas del Toro; 130197 — Brasil, Para; 194933, 204963, 204964, 204965, 207765, 215009, 220185, 220186 — Peru, Madre de Dios; 220485, 222360 — Peru, Loreto; 229881 — Dominica.

MCZ: 4744 — Brasil, Amazonas; 60816, 60818, 60819 — Dominica; 81220, 171650 — Guyana, Mazaruni-Potaro.

Oklahoma Museum of Natural History: 36427, 36434 — Ecuador, Sucumbios; 36753 — Brazil, Pará; 37333, 37334 — Brazil, Rondônia.

UMMZ: 80812, 80813, 83284 — Mexico, Yucatan; 83325 — Dominica.