THE PATTERN OF DERMAL-VERTEBRAL CORRELATION IN SNAKES AND AMPHISBAENIANS

by

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INTRODUCTION

It has long been known that the arrangement of external scales retains a constant relation to the primary pattern of mesodermal segmentation. The ratio of the number of dermal scale rows or annuli to the number of vertebrae has, therefore, been considered to be of fundamental importance in squamate classification (Stehli, 1910; Camp, 1923). Yet the difficulty of determining it has fostered the presentation of hypotheses based on relatively few total counts; some such hypotheses have relied upon comparisons made by dissection along limited portions of the trunk. The general implication communicated by the many statements in the literature has been that the ratios are constant at the generic or familial level, that the ratios ordinarily represent simple, whole number relations (i.e. 1 : 1, 1 : 2, 2 : 1), and that the scale-vertebra relation is constant along the length of the body.

Authors have disagreed regarding the presumed evolution of these regularities; thus Stehli (1910) argued that the 1 : 1 ratio was primitive, while Camp (1923) considered it to be most highly advanced. The most "primitive" snakes (Bellairs & Underwood, 1951) were generally stated to have a 2 : 1 and the "advanced" forms a 1 : 1 ratio. In contrast, the presumably most primitive amphisbaenid (Smalian, 1884) has generally been stated to have a 1 : 1 and all other, and presumably more advanced, forms, a 2 : 1 ratio.

A recent report (Gans & Taub, 1965) showed a simple method of determining these ratios, emphasized that the ratios varied markedly at the species

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level, and also showed that the relationship of scales to vertebrae within the Typhlopidae was not a simple, whole number ratio. This suggested the desirability of checking the actual values on which the various rules had been established.

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METHODS

The arrangement and numbers of scale rows, or annuli, on the dorsal and ventral surface of trunk and tail, and the numbers of trunk and caudal vertebrae were determined for some 220 specimens. Similar determinations were accomplished on 130 specimens of *Blanus*. Additionally, determinations on some 100 other specimens recorded by Gans & Taub (1965), Gans & Laurent (1965), and by List (1956, unpublished thesis) were also used in the analysis. The ranges of observed values are shown by species in table 1 for the amphisbaenids, and in table 2 for the "primitive" snakes and a few advanced snakes.

The forms sampled include the 23 recognized genera of amphisbaenids, fifteen genera of primitive snakes, and various advanced snakes. The various ratios observed in each family or other grouping are shown in table 3.

The numbers and proportions of vertebrae were determined fom X-rays taken with an unfiltered 60 KVP dental unit at 3.5 ma on Kodak Type AA

industrial film; the target to film distance was 50 inches. All determinations were made under a dissecting microscope. Measurement of proportions obviously had to be restricted to those vertebrae X-rayed while lying with their long axis in parallel to the film. Hypaque and fine steel pins were used to indicate the position of dermal segments relative to skeletal structures.

Checks indicated that the counts of dermal and vertebral elements along the trunk were repeatable with less than 1% error. Caudal structures, particularly in short-tailed forms, are markedly reduced in size and the vertebrae are often partially fused. The differences between repeated counts here approached 10%. Correlation of caudal dermal and vertebral elements also poses a problem, particularly in the typhlopids. Here the tail is short, sharply curved, and composed of smaller vertebral elements. Additionally the X-rays suggest that the soft tissues may shift (possibly post-mortem) so that the cloacal slit may, in a given species, fall anywhere from the third caudal to the fourth from last trunk vertebra. It may be that this accounts for some of the apparently aberrant ratios; otherwise it may be that species differences are being dealt with.

RESULTS

Serpentes

Trunk proportions. — Neither the length of the dermal segments nor of the vertebrae remains constant throughout the trunk region. The changes are gradual, but quite evident when comparisons are made between regions.

Both scales and vertebrae of the nuchal-pectoral and precloacal regions are generally of equivalent length, and definitely shorter than those of the midthoracic region. The lengths of the scales and vertebrae generally change in parallel, maintaining a constant relationship along the trunk, and giving rise to the described simple, whole number ratios (i.e. 1 : 1, 2 : 1, etc.). This is in accord with the expected basic embryological relationships of the dermal and vertebral elements. In a few forms, the constancy of the relationship is disrupted by (seemingly secondary) changes in the dermal elements, changes that result in deviant ratios.

Richmond (in litt.) commented on the marked regional differences in scale size seen in certain typhlopids. Yet the vertebral column of these forms shows the same regional proportions described above for other snakes, except perhaps for a shorter precloacal region, and a sharp change in the length of vertebrae between the thoracic and precloacal zones. The dermal elements also increase in length along the trunk, but seemingly with no corresponding decrease in the short precloacal region. The degree of increase appears to be species specific.

The hydrophiid *Laticauda laticaudata* shows the "normal" dermal and vertebral proportions. The two specimens of *Lapemis hardwicki*, which differ so drastically that there is some doubt whether they are indeed conspecific, show variation in dermal, but not vertebral proportions. One specimen (MCZ 23755) shows an increase in dermal length between the nuchal-pectoral and midthoracic regions, that is followed by a decrease posteriorly in the region leading to the relatively small precloacal and caudal scales. The other specimen (MCZ 20647), however, shows little change of length of the dermal elements throughout the trunk region; the elements of the nuchal-pectoral are equal to or even slightly greater than those of the midthoracic zone.

Trunk ratios. — Bellairs & Underwood (1951) stated that various modified burrowing snakes of the families Typhlopidae, Leptotyphlopidae, and Uropeltidae always have a ratio of transverse ventral rows to vertebrae of 2 : 1, and that these thus differ from all other snakes which always have a ratio of 1 : 1. This statement led Williams (1959) to the conclusion that the uropeltids had not been directly derived from *Cylindrophis* (Aniliidae) or its immediate relatives, despite much evidence demonstrated by him to the contrary.

Comparison of the data given in table 3 shows clearly that snakes, except for members of the genera *Typhlops, Helminthophis, Anomalepis,* and *Liotyphlops,* always have a 1 : 1 ratio between the number of enlarged ventral shields and of vertebrae. The literature statements regarding the departure from this ratio by members of the Leptotyphlopidae and Uropeltidae are thus in error.

In the Typhlopidae (sensu lato) the ratios vary from 1.5 : 1 to 2.3 : 1. However, as already pointed out by Gans & Taub (1965) and suggested in List's unpublished thesis the values (1) ordinarily do not represent simple, whole number ratios, (2) generally depart significantly from 2 : 1, and (3) are species specific.

The comparison of dermal and vertebral proportions for three of the typhlopid species (*T. congestus, T. reticulatus,* and *T.* sp., a yet unidentified, large African form) indicates that within the nuchal-pectoral region the dermal-vertebral ratio is constant at 2 : 1. Thus the overall deviation from this ratio for the species (1.75 to 1.9 : 1; 1.5 to 1.75 : 1, 2.1 : 1, respectively) is due to differences primarily in the midthoracic, but also in the precloacal region.

A different situation exists in boid snakes. It has long been known (cf. de Witte, 1962; Gans & Laurent, 1965) that some of these have dorsal scales that are much smaller and hence shorter (when measured along the snake's axis) than the widened ventral shields. This implies that there must be more

dorsal than ventral scales along the length of the trunk. The present ob-
servations confirm this and also show that there are "additional" scales in-
volved, since the correlation between the number of ventral shields and that
of vertebrae is more regular. A similar case may exist within the colubrids,
as a figure of the nuchal region of a specimen of *Spalerosophis cliffordi*
(Barash & Hoofien, 1956) shows multiple dorsal scales corresponding to
the enlarged ventrals.

On the other hand, Parker (1940) reported that within the colubrid genus
Thrasops, T. flavigularis is unique in possessing dorsal scales whose length
is nearly twice that of the ventrals. The two specimens of that species viewed
here show dorsal scale to vertebrae ratios of 0.59 : 1 and 0.78 : 1. The ventral
scale ratios are 1 : 1, as are both the dorsal and ventral ratios in the other
species of *Thrasops*.

Only four boid genera, among them the peculiar *Tropidophis,* do not show
the size reduction and numerical increase of dorsal scales. *Casarea,* recently
(Parker, 1965) placed in the Bolyeridae, shows the more typical boid pattern.

The snakes of the family Acrochordidae have the body covered by nume-
rous small scales, most projecting into a pointed, posteriorly curving hook.
The ratios are constant along the body and along the tail, though the number
of scales is much larger than that of the vertebrae.

Within the hydrophiids, the specimen of *Laticauda laticaudata* has 1 : 1
ratios both dorsally and ventrally. The two specimens of *Lapemis hardwicki,*
however, show both dorsal and ventral scale patterns and ratios which are
quite irregular, and which vary considerably between the two specimens. In
one the dorsal and ventral ratios are ~1.3 : 1 and 1.1 : 1, respectively, while
those of the other specimen are ~1.8 : 1 and 1.4 : 1. The tail ratios, 1.1 : 1
and 1.2 : 1, in the two specimens are quite similar.

Caudal region. — With two exceptions all forms show a 1 : 1 ratio of
dermal segments to vertebrae along the tail. One exception is formed by the
two species of the genus *Helminthophis,* the other by some species of
Typhlops. The occurrence in the latter has been commented upon. In the
specimen of *Boa,* the number of dorsal, but not of ventral segments is larger
than the number of vertebrae. Here again, supplementary dorsal segments
are being dealt with.

Amphisbaenia

Trunk proportions. — The majority of the amphisbaenids examined show
a regional variation of vertebral length that is similar to that found in most
snakes. In general, there also occur changes in the lengths of the dermal

elements corresponding to those in the vertebrae, resulting in simple, whole number dermal-vertebral ratios.

In a few forms deviations from the normal pattern do exist; such deviations occur most often in the nuchal-pectoral region. The most extensive deviations occur in four genera where the nuchal-pectoral vertebrae are significantly longer than those of the midthoracic region. The differences vary from approximately 5% in *Leposternon* to 15 to 20% in *Monopeltis, Tomuropeltis,* and *Mesobaena.* Although corresponding changes in the length of the dermal elements seem to occur in *Mesobaena,* there are no such changes in the other three genera.

Representatives of three other genera, *Ancylocranium, Bronia,* and *Rhineura,* show similar, but less extensive modifications. Here, the length of the nuchal-pectoral vertebrae is equal to that of the vertebrae of the mid-thoracic region. These forms show corresponding changes in the dermal elements. A fourth form, *Cadea palirostrata,* shows the same general pattern of vertebral lengths, but while the dermal elements of the ventral surface concur with this, those of the dorsal surface vary further. This variation occurs within the midthoracic region where there seems to be a decrease in the length of the annular segments.

The second, and presumably more primitive species of the genus, *Cadea blanoides,* shows "normal" proportions of vertebrae and dermal elements of the dorsal surface. Ventrally the dermal proportions change, with the most marked changes concentrated in the precloacal region.

All other amphisbaenids show "normal" vertebral and dermal proportions.

Trunk ratios. — In the Amphisbaenia the skin is subdivided into so-called dermal annuli that are separated by inter-annular grooves that ring the body. In most species there are clearly defined lateral sulci which divide the annuli into subequal dorsal and ventral half-annuli. Correlation of number of dermal annuli with that of vertebrae is complicated since a certain number of anterior body annuli extend over the posterior aspect of the skull. It is thus not the first, but for instance the sixth to eighth annulus in *Blanus,* that corresponds to the position of the atlas.

Allowing for this, there are some four groups of ratios between number of ventral half-annuli and vertebrae. (1) The two species of the genus *Blanus* always show a ratio of 1 : 1 between the number of body annuli and that of vertebrae. (2) The species of the presumably primitive (Vanzolini, 1951) genera *Bipes* and *Cadea* show values between 1.2 and 2 : 1. (3) Members of the "advanced" rhineurine genera *Leposternon, Monopeltis,* and *Tomuropeltis* (but not of the genus *Rhineura*) show a ratio equal to sig-

nificantly greater than 2 : 1. (4) All other species, including the bulk of the members of this group, have a simple ratio of 2 : 1.

Most amphisbaenids have the same number of dorsal and of ventral half-annuli. Where intercalated half-annuli occur, they are almost always dorsal. Their number is generally low along the trunk, though many species have one or more over the back of the skull or in the cloacal region. The frequency of dorsal intercalated half-annuli is generally less than 2%, only in a few populations of *Amphisbaena innocens* have values up to 10% been reported (Gans & Alexander, 1962).

The two species of *Bipes* and the two specimens of *Cadea* are then unique in possession of a significantly greater number of dorsal half-annuli than ventral. In *Bipes,* the ratio of dorsal half-annuli to vertebrae is 2 : 1, suggesting that the ratio of ventral to vertebrae may represent secondary reduction. In *Cadea* the dorsal ratio is slightly less than 2 : 1 for the least specialized, and somewhat more than 2 : 1 for the most specialized species. *Cadea* is the only amphisbaenid genus with very poorly expressed lateral sulci. The contact region between dorsal and ventral half-annuli is characterized by multiple and irregular interdigitations, yielding a confusing pattern, and making correlations difficult.

Caudal region. — The vast majority of species have a ratio of 1 :1 between the number of caudal annuli and vertebrae. Exceptions to this are found only in one of the species of *Cadea* and both species of *Bipes.*

In *Cadea palirostrata,* the departure from 1 : 1 is restricted to the dorsal surface of the tail, where it ranges from 1.3 to 1.6 : 1. It is clearly due to the intercalation of additional dorsal half-annuli. In *Bipes* the departure from a 1 : 1 ratio occurs both dorsally and ventrally, though the dorsal ratio is again larger in one of the two species.

DISCUSSION

The present survey provides evidence that the regional changes in the lengths of the dermal and vertebral elements are correlated within certain groups of squamates. The correlation is of two kinds. First, there are the dermal-vertebral ratios, which appear fixed on various taxonomic levels. Secondly, there is a general regularity in the relative length of dermal and of vertebral elements in different groups; departures from this regularity appear to occur primarily for immediate functional causes.

The dermal-vertebral ratios have traditionally been used in denoting higher categories of squamates. Certain assumptions concerning these are here shown to be wrong. The additional evidence simplifies certain aspects of the taxonomic pattern; it also presents some new problems. It is now possible to

generalize regarding the pattern to be expected in these several families, and to differentiate between basic trends and limited departures from these. The assumption is that such departures have quite probably been forced by selective pressures established by secondary adaptive factors.

The pattern exhibited by the serpentes permits a simplification of their presumptive phylogeny since it suggests that the group is relatively homogenous as far as this characteristic is concerned. Most species show a 1 : 1 ratio both dorsally and ventrally on both trunk and tail. The clarification of this point is useful since it permits pursuit of the hypothesis that uropeltids and aniliids are closely related (cf. Williams, 1959).

The modification of the dorsal skin (ventral, rarely) by variation in the size and number of scales in certain boids, colubrids and hydrophiids obviously represents secondary departures from the basic pattern.

As interesting as the general constancy is the departure from this observed in the four genera generally combined under the heading Typhlopidae. Their specialization in this characteristic provides additional evidence for McDowell & Bogert's (1954) suggestion that the typhlopids are more distinct from the remainder of the snakes than are the leptotyphlopids. In spite of publication of the hypothesis that these genera are "lizards", it remains most plausible to follow the view of List (1956) who states that "these groups have diverged from each other at an early date, but are derived from a common ancestor".

The pattern in the amphisbaenids is similarly suggestive. Most of the species have a 2 : 1 ratio, both ventrally and dorsally, on the trunk and a 1 : 1 ratio on the tail. A 1 : 1 ratio on both trunk and tail is found only in the two species of the genus *Blanus*. There are numerous other characters which suggest that this genus is one of the most primitive in the group.

Vanzolini (1951) and Gans (1960) have suggested that the genera *Cadea* and *Bipes* are the next most primitive pleurodont species, while the genus *Trogonophis* is clearly the acrodont form retaining the most generalized character pattern. Other authors have argued that *Bipes* represents a distinct line to be distinguished on the family level.

The primitive status of *Cadea* and *Bipes* may explain their distinct patterns. *Bipes* is certainly different in that the ventral ratios of both trunk and tail depart significantly from 2 : 1, and 1 : 1, respectively. *Cadea* is less modified in that the ventral caudal ratios are regular. *Mesobaena*, a genus at least superficially similar to *Cadea,* has the ratios common to most amphisbaenids. This, and the finding of the 2 : 1 ratio along the dorsal surface of both species of *Bipes,* and one of *Cadea,* and on the ventral surface of the other species of *Cadea,* offers at least the presumption that the condition seen in these genera

is not an intermediate or different condition but a secondary modification. It is highly interesting that the acrodont genus *Trogonophis,* shown in some characters to be more generalized than *Blanus,* has the standard 2 : 1 trunk and 1 : 1 tail ratios noted in other members of that family.

The increase in the number of dorsal and ventral body half-annuli in the three rhineurine genera, *Monopeltis, Tomuropeltis,* and *Leposternon,* can be shown to occur in the modified nuchal-pectoral region. Here the vertebrae are significantly longer than those of the trunk region, whereas the pattern in the vast majority of species is one in which the nuchal are significantly shorter than the trunk vertebrae. As the relative length of the dermal annuli in the nuchal-pectoral region does not undergo a correlated change, the dermal-vertebral ratio approaches 3 : 1, thus yielding an overall increase beyond the common 2 : 1 ratio. The increased ratios are thus a secondary result of the specialized excavating mechanism. Of interest here are the normal ratios of the genera *Aulura* and *Rhineura.* The former is unspecialized, while the latter evidences a level of specialization approaching that of the other forms. The results then support other evidence that the grouping may be artificial.

While the present study has simplified the patterns observed within the snakes and amphisbaenids, it does not provide a clear indication regarding the evolutionary sequence. In snakes, the two groupings are each sufficiently old to support the contention that either pattern may have been primitive. In amphisbaenids, *Blanus* may or may not retain an "ancestral" condition, although the finding of a 1 : 1 caudal ratio consistently throughout the amphisbaenids suggests that this may be the case.

If the evidence for this 1 : 1 to 2 : 1 sequence be accepted, it would support Stehli's (1910) contention that the squamate integumentary patterns are primitively 1 : 1, and upset Camp's (1923) argument in the opposite direction. There is, however, no reason to suppose that the trend need always go in the same direction in the various squamate groups.

TABLE I

Numbers of segments and vertebrae in Amphisbaenia.

Species	Number of specimens	Ventral annuli (Dorsal) [1]			Vertebrae		
		Body	Lateral	Caudal	Body	Lateral	Caudal
Amphisbaenidae							
Amphisbaena alba	2	204–212	2–3	?11–16	102–107	2	15–16
A. angustifrons	1	190	3	13	93	2?	14?
A. camura	1	203	3	6(Autot)	102	2	5
A. carvalhoi	2	237–245	3	20–21	119–122?	3	21
A. darwini heterozonata	2	198	3–4	16	97–98	2–3	16
A. dubia	2	216–226(215–226)	2–3	14–16	107–112	2	15–17
A. fenestrata	1	236	2	14	117?	2?	16?
A. fuliginosa	2	205–215(208–215)	4	25	104–108	2–4	25–26
A. leeseri	2	223–227	3	16(+ 1 Autot)	111–113	2–3	18
A. manni	2	225–235	2–4	(Autot)	?112–117?	–	(Autot)
A. mitchelli	1	215(213)	3	27(28)	108	2	28
A. munoai	2	208–212	2–3	20	104–106	1–2	20
A. o. occidentalis	1	264	3/4	23	131	2	26
A. ridleyi	1	172	2	17(18)	87	1	20
A. silvestrii	1	180(178)	3	21	89	3	20
A. vermicularis	1	229	4	26	114	2	28
Ancylocranium s. somalicum	1	197	5	6	97	3	8
Anops kingi	2	229–232(230–232)	3–4	18	113–114	2	19
Aulura anomala	1	184	5/4	14	92	3	14
Baikia africana	1	250(251)	3	21	126	2	21
Bipes biporus	2	?154–161?(259–260)	4	21(25?)	129–130	1–2	16–18
B. canaliculatus	1	165(210)	5	30	104	1	22
Blanus cinereus	11	119–133	1–3	17–22	115–127	2–4	18–21
B. strauchi	119	98–128	1–4	15–20	92–122	1–4	14–20
Bronia brasiliana	2	225–227	3	13	111	3	14
Cadea blanoides	4	185–196(200–211)	2–3	10–12	105–107	2	12
C. palirostrata	9	272–294(306–336)	3–4(3–5)	13–15(16–19)	136–145	2–3	12–13

Species	Number of specimens	Ventral annuli (Dorsal)[1]			Vertebrae		
		Body	Lateral	Caudal	Body	Lateral	Caudal
Chirindia e. ewerbecki	3	260-265	3	23-26(24-26)	131-135	2-3	23-25
Cynisca leucura	1	220	3	7	110	2	6
Geocalamus acutus	1	216	3	22	107	2	21
Leposternon[2] affine	2	243-285(256-292)	5(3-4)	10-12(10-14)	100-106?	3-4	8-11
L. boulengeri	2	273-286(284)	4-5(3-5)	11(11-12)	99-102	2	9-12
L. crassum	2	214-225(228-256)	5-6	9?(11-12)	98-99	3-4	10-12
L. phocaena	2	206-222(227-238)	5	?8-10(10-11)	84-100	3-4	?7-11
L. polystegum	2	286-353(285-357)	4-6(3-6)	11-14(12-16)	125-134	3	11
L. scutigerum	2	270-307(282-303)	6-7(6)	11-13(12-14)	120-121	3-4	11-12
L. wuchereri	2	264-277(270-283)	4	10-13(10-14?)	119-122	3	11-13
Loveridgea ionidesii	2	250-254	4	24(+ 1 Autot)	123-126	2-3	26
Mesobaena huebneri	1	269	3	17	134	2	19
Monopeltis c. capensis	2	188-200(188-199)	3	7-8	87-90	1-2	7-8
M. guentheri	2	242-258(244-258)	3-4	25	?123-127	2-3	23
Rhineura floridana	2	246-247(246)	2-3	16	122	2-3	15-16
Tomuropeltis pistillum	1	287(290)	2	19	134?	2	20
Zygaspis capensis	1	223	5	9	111	3	7
Z. quadrifrons	2	209-211(208-209)	4	8	106	2-3	6
Trogonophidae							
Agamodon a. anguliceps	2	128-129	3-4	16-17	64-66	2-4	15
A. compressus	2	146-152	4	21-22	73	3	20-21
Diplometopon zarudnyi	1	176(177)	3	17	89	1	16
Pachycalamus brevis	2	169-172(170-172)	3(3-4)	16-18	86-88	2	14-15
Trogonophis wiegmanni elegans	2	145-151	3-4	11-12	74-77?	2-3	11

1) Dorsal data presented only if different from ventral.
2) Genus presently under revision by Gans.
Autot. indicates autotomized tail.

TABLE 2

Number of scales and vertebrae in Serpentes.

Species	Number of specimens	Scale rows Body		Scale rows Caudal		Vertebrae	
		Ventral	Dorsal	Ventral	Dorsal	Body	Caudal
Typhlopidae							
Anomalepis aspinosus [1]	1	—	328	—	—	173	—
Helminthophis albirostris	2	?388-430?	382-428	12-22	14-22	205-233	7-15
H. ternetzii	1	469	468	11	13	242	11
H. sp.	1	468	467	27	27	230	17
Liotyphlops albirostris [2]	3	—	—	—	—	234-252	8-10
L. albirostris [3]	2	—	344-353	15-16	—	207-208	16
Typhlops aluensis	4	?335-358	344-356	17-20	18-19	?175-181	?11-15
T. ataeniatus [4]	5	—	457-476(B + C)	—	—	297-307(B + C)	
T. bituberculatus	2	435-592	439-589	16-23	16-23	219-300	13-15
T. braminus [3]	6	—	282-312	11-12	—	174-182	10-11
T. blandfordi [3]	1	—	435	10	—	237	11
T. boettgeri [3]	1	—	377	8	—	200	7
T. congestus	3	?320-343?	314-334	9-11	7-11	180-182	7-12
T. c. cuneirostris [4]	5	—	215-248(B + C)	—	—	115-126(B + C)	
T. cuneirostris calabresii [4]	34	—	257-302(B + C)	—	—	130-143(B + C)	
T. infralabialis	1	503	503	15	16	289	13
T. lumbricalis [3]	1	—	279	10	11	169	10
T. luzonensis	1	349	346	11	—	208	10
T. platycephalus [3]	1	—	371	11	—	222	11
T. polygrammicus [3]	3	—	392-409	16-19	—	193-206	14-16
T. proximus	3	321-343	321-343	10-13	10-13	160-173	7-12
T. pusillus [3]	1	—	290	12	—	158	12
T. reticulatus [3]	1	—	213	10	—	143	9
T. reticulatus	9	214-251	215-261	?7-11?	?7-10?	137-155	6-10
T. richardi [3]	1	—	331	13	—	204	13
T. rostellatus [3]	1	—	320	14	—	183	10

Species	Number of specimens	Scale rows Body Ventral	Scale rows Body Dorsal	Scale rows Caudal Ventral	Scale rows Caudal Dorsal	Vertebrae Body	Vertebrae Caudal
T. schlegeli [3]	2	—	407–456	7–8	—	189–202	8–9
T. scorteccii [4]	10	352–390 (B+C)				?226–255(B+C)	
T. solomonis	3	371–393	373–390	17–21	18–22	219–222	13–16
T. torresianus	2	393–398	388–397	10–21	11–21	196	10–16
T. unitaeniatus [4]	12	—	496–536(B+C)			315–334(B+C)	
T. vermicularis [3]	1	—	346	13	—	193	12
Leptotyphlopidae							
Leptotyphlops conjuncta	4	?196–226?	200–230	?21–26?	?21–26?	191–223	?21–26
L. emini [3]	1	—	242	21	—	224	25
L. longicauda	4	206–222	208–232	?30–33?	?30–33?	208–215	?25–32?
L. magnamaculata [3]	1	—	222	19	—	231	19
L. maximus [3]	1	—	199	14	—	202	17
L. nigricans [3]	1	—	207	28	—	198	29
L. phillipsi	3	334–343	334–344	?41–48?	?41–48?	335–343	?41–49?
Uropeltidae							
Brachyophidium rhodogaster	4	139–145	140–146	6–11?	6–11?	138–143	9–12
Melanophidium wynaudense	1 [5]	169	171	14+	15+	168	14+
Platyplectrurus madurensis	2	166–168	167–168	13+	13–14+	166–167	?12–14+
Plectrurus perroteti	1	156	158	11+	13+	154	12+
Rhinophis blythi	4	154–156	154–156	5–10	5–10	152–157	7–11
R. philippinus	5	151–168	151–166	4–5	4–5	150–166	5–9
Uropeltis ocellatus	2	191–195	188–192	10–11	10–11	191–198?	14–15
U. pulneyensis	2	166–173	168–174	8	8	167–173	9
U. rubrolineatus	10	136–169	139–170	7–13	7–13	136–169	8–11
U. woodmasoni	4	167–180	167–175	7–14	7–14	166–179	8–15
Aniliidae							
Anilius scytale	1	218	220	16+	16+	217	16+
Cylindrophis maculatus	5	195–210	198–213	6–9	6–9	195–209	8–9?
C. rufus	1	187	191	6	7?	186	7

Species	Number of specimens	Scale rows		Caudal		Vertebrae	
		Ventral	Body Dorsal	Ventral	Dorsal	Body	Caudal
Xenopeltidae							
Xenopeltis unicolor	2	184–188	184–185	26–30?	26–32	187–190	26–30?
Boidae							
Acranthophis							
madagascariensis	1	237	460	34+	51+	?246±10	34+
Aspidiotes melanocephalus	1	294	470	48+	56+	293	48+
Boa canina	1	198	488	68?	79	203	73
B. enydris	1	260	340	111	111	261	112
Bothrochilus boa	1	264	385	54+	57+	266	57±1
Calabaria reinhardti	1	231	256	27+	27+	236	26+
Charina bottae	1	211	312	40+	47+	215	44
Chondropython viridis	1	236	590	82	91	240±2	83±6
Corallus (Boa) annulatus	1	265	415	86	89+	268	86+
Emygrus asper	1	139	186±3	21±	19+	144	21+
Epicrates angulifer	1	286	413±10	82	88	290	~79+2
E. striatus	2	287–295	433–466	92–93+	92–97+	291–296	91–92
Eryx colubrinus	2	?182–184?	270–277	?26–28?	?26–28?	187–190	28–29
E. conicus	1	188	265	19+	20+	190	18+
E. jaculus	2	?168–182?	254–278	18?	18?	174–185	19
Eunectes notaeus	1	230	316	59	66	238	65+
Liasis amethystinus	2	315–321	290–318±10	113–116+	111–114+	318–322±5	118–119±1
L. childreni	1	281	348	46+	48+	275	48+
L. fuscus	1	273	421	74+	75+	282	76±
Lichanura roseofusca	1	235	245	48+	52+	235±2	52+
Python (Morelia) argus	1	268	359	79+	81+	276	86
P. sebae	1	278	606	78+	109+	283	75+
Sanzinia madagascariensis	1	206	274	40+	42+	208	42+
Trachyboa boulengeri	2	132–135	128–132	24–25+	23–25+	131–134	24
Tropidophis melanurus	2	193–199	199–202	40–41+	41–43+	196–198±1	41
T. semicincta	1	204	210	39+	39+	211	37+

Species	Number of specimens	Scale rows				Vertebrae	
		Body		Caudal		Body	Caudal
		Ventral	Dorsal	Ventral	Dorsal		
Bolyeridae							
Casarea dussumieri	1[5]	226	414	129+	206+	225	126
Acrochordidae							
Acrochordus granulatus	2	959–996	680–709	188–224	226–280	201–205	48–50±1
Colubridae							
Ahaetulla mycterizans	1	191	200	139	139	194	140
Dasypeltis scabra	1	217	218	66	69	217	69
Duberria lutrix	1	134	141	20	19	134	22
Elachistodon westermanni	2	201–211	212–218	60	60	210–215	59–60
Malpolon monspessulanus	1	172	180	89	91	175	92
Psammophylax tritaeniatus	1	172	177	59	59	175	63
Thrasops flavigularis	2	204–210	124–159	143–148	143–147	205–209	145–150
T. j. jacksoni	2	188–203	184–196	135–145	135–146	195–205	137–149
T. schmidti	1	174	178	144	142	174	149
T. occidentalis	2	180–188	177–189	125–127	123–126	182–189	126–129
Hydrophiidae							
Lapemis hardwicki	2	?113–204	159–250	34	32–33	127–143	29–30
Laticauda laticaudata	1	250	249	43	42	252	47
Elapidae							
Micrurus sp.	1	229	236	23	22	232	25
Viperidae							
Crotalus terrificus	1	178	174	25?	25?	176	28

1) Data from Dunn (1941) in List (1956).
2) Data from Dunn & Tihen (1944) in List (1956).
3) Data from List (1956).
4) Data from Gans & Laurent (1965) and Gans & Taub (1965).

5) Skull plus a few anterior vertebrae missing.

— data not available.

(B + C) = total of body plus caudal.

TABLE 3

Dermal-vertebral ratios.

	Number of species	Body		Caudal	
		Ventral	Dorsal	Ventral	Dorsal
Serpentes					
Typhlopidae					
Anomalepis [1])	1	—	1.9 : 1	—	—
Helminthophis	3	1.8–2.0 : 1	1.8–2.0 : 1	1.0–1.7 : 1	1.0–1.7 : 1
Liotyphlops [2])	1	—	1.7–2.0 : 1	1 : 1	—
Typhlops [3])	25	1.5–2.3 : 1	1.5–2.3 : 1	1.0–1.5 : 1	1.0–1.5 : 1
Leptotyphlopidae					
Leptotyphlops [4])	7	1 : 1	1 : 1	1 : 1	1 : 1
Uropeltidae					
Brachyophidium	1	1 : 1	1 : 1	1 : 1	1 : 1
Melanophidium	1	1 : 1	1 : 1	1 : 1	1 : 1
Platyplectrurus	1	1 : 1	1 : 1	1 : 1	1 : 1
Plectrurus	1	1 : 1	1 : 1	1 : 1	1 : 1
Rhinophis	2	1 : 1	1 : 1	1 : 1	1 : 1
Uropeltis	4	1 : 1	1 : 1	1 : 1	1 : 1
Aniliidae					
Anilius	1	1 : 1	1 : 1	1 : 1	1 : 1
Cylindrophis	2	1 : 1	1 : 1	1 : 1	1 : 1
Xenopeltidae					
Xenopeltis	1	1 : 1	1 : 1	1 : 1	1 : 1
Boidae					
Acrantophis	1	1 : 1	1.9 : 1	1 : 1	1.5 : 1
Aspidiotes	1	1 : 1	1.6 : 1	1 : 1	1.2 : 1
Boa	2	1 : 1	1.3–2.5 : 1	1 : 1	1 : 1
Bothrochilus	1	1 : 1	1.5 : 1	1 : 1	1 : 1
Calabaria	1	1 : 1	1.1 : 1	1 : 1	1 : 1
Charina	1	1 : 1	1.5 : 1	1 : 1	1.1 : 1
Chondropython	1	1 : 1	2.5 : 1	1 : 1	1 : 1
Corallus	1	1 : 1	1.6 : 1	1 : 1	1 : 1
Enygrus	1	1 : 1	1.3 : 1	1 : 1	0.9 : 1
Epicrates	2	1 : 1	1.4–1.5 : 1	1 : 1	1.0–1.1 : 1
Eryx	3	1 : 1	1.4 : 1	1 : 1	1.0–1.1 : 1
Eunectes	1	1 : 1	1.3 : 1	0.9 : 1	1 : 1
Liasis	3	1 : 1	9.0–1.5 : 1	1 : 1	1 : 1
Lichanura	1	1 : 1	1 : 1	0.9 : 1	1 : 1
Python	2	1 : 1	1.3–2.1 : 1	0.9–1.0 : 1	0.9–1.5 : 1
Sanzinia	1	1 : 1	1.3 : 1	1 : 1	1 : 1
Trachyboa	1	1 : 1	1 : 1	1 : 1	1 : 1
Tropidophis	2	1 : 1	1 : 1	1 : 1	1 : 1

	Number of species	Body		Caudal	
		Ventral	Dorsal	Ventral	Dorsal
Bolyeridae					
Casarea	1	1 : 1	1.8 : 1	1 : 1	1.6 : 1
Acrochordidae					
Acrochordus	1	4.7–5.0 : 1	3.4–3.5 : 1	3.9–4.5 : 1	4.7–5.6 : 1
Colubridae					
Ahaetulla	1	1 : 1	1 : 1	1 : 1	1 : 1
Dasypeltis	1	1 : 1	1 : 1	1 : 1	1 : 1
Duberria	1	1 : 1	1 : 1	1 : 1	1 : 1
Elachistodon	1	1 : 1	1 : 1	1 : 1	1 : 1
Malpolon	1	1 : 1	1 : 1	1 : 1	1 : 1
Psammophylax	1	1 : 1	1 : 1	1 : 1	1 : 1
Thrasops	3	1 : 1	0.6–1 : 1	1 : 1	1 : 1
Hydrophiidae					
Lapemis	1	?1.1–1.4 : 1	1.2–1.8 : 1	1.1 : 1	1.1 : 1
Laticauda	1	1 : 1	1 : 1	1 : 1	1 : 1
Elapidae					
Micrurus	1	1 : 1	1 : 1	1 : 1	1 : 1
Viperidae					
Crotalus	1	1 : 1	1 : 1	1 : 1	1 : 1
Amphisbaenia					
Amphisbaenidae					
Amphisbaena	16	2 : 1	2 : 1	1 : 1	1 : 1
Ancylocranium	1	2 : 1	2 : 1	1 : 1	1 : 1
Anops	1	2 : 1	2 : 1	1 : 1	1 : 1
Aulura	1	2 : 1	2 : 1	1 : 1	1 : 1
Baikia	1	2 : 1	2 : 1	1 : 1	1 : 1
Bipes biporus		~1.2 : 1	2 : 1	1.2–1.3 : 1	1.4–1.6 : 1
Bipes canaliculatus		~1.6 : 1	2 : 1	~1.4 : 1	~1.4 : 1
Blanus	2	1 : 1	1 : 1	1 : 1	1 : 1
Bronia	1	2 : 1	2 : 1	1 : 1	1 : 1
Cadea blanoides		~1.8 : 1	1.9–2.0 : 1	1 : 1	1 : 1
Cadea palirostrata		2 : 1	2.2–2.4 : 1	1 : 1	~1.3–1.6 : 1
Chirindia	1	2 : 1	2 : 1	1 : 1	1 : 1
Cynisca	1	2 : 1	2 : 1	1 : 1	1 : 1
Geocalamus	1	2 : 1	2 : 1	1 : 1	1 : 1
Leposternon	7	2.2–2.9 : 1	2.2–2.9 : 1	1.0–1.3 : 1	1.0–1.5 : 1
Loveridgea	1	2 : 1	2 : 1	1 : 1	1 : 1
Mesobaena	1	2 : 1	2 : 1	1 : 1	1 : 1
Monopeltis	2	2.0–2.2 : 1	2.0–2.2 : 1	1 : 1	1 : 1
Rhineura	1	2 : 1	2 : 1	1 : 1	1 : 1
Tomuropeltis	1	~2.2 : 1	~2.2 : 1	1 : 1	1 : 1
Zygaspis	2	2 : 1	2 : 1	1 : 1	1 : 1

	Number of species	Body		Caudal	
		Ventral	Dorsal	Ventral	Dorsal
Trogonophidae					
Agamodon	2	2 : 1	2 : 1	1 : 1	1 : 1
Diplometopon	1	2 : 1	2 : 1	1 : 1	1 : 1
Pachycalamus	1	2 : 1	2 : 1	1 : 1	1 : 1
Trogonophis	1	2 : 1	2 : 1	1 : 1	1 : 1

[1]) Data from Dunn (1941) in List (1956).

[2]) Data from Dunn & Tihen (1944) in List (1956).

[3]) Includes data from Gans & Laurent (1965), Gans & Taub (1965), and List (1956).

[4]) Includes data from List (1956).

— data not available.

LIST OF SPECIMENS USED

Serpentes

Typhlopidae. — *Helminthophis albirostris* (Peters): MCZ 25232, 25234. *H. ternetzii* Boulenger: CG 1594. *H.* sp.: MCZ 67933. *Typhlops aluensis* Boulenger: MCZ 73767, 73768, 73769, 73770. *T. bituberculatus* (Peters): MCZ 32810, 51890. *T. congestus* (Duméril & Bibron): CM 8043, 15213, 15217. *T. infralabialis* Waite: MCZ 65990. *T. luzonensis* Taylor: MCZ 79698. *T. proximus* Waite: MCZ 10278, 72081, 72082. *T. reticulatus* (Linné): IB 7207, 8964, 14752, 14758, 14762, 16245; UMMZ 55853, 60655, 63235. *T. solomonis* Parker: MCZ 72083, 72085, 72086. *T. torresianus* Boulenger: MCZ 53752, 53753. *T.* sp.: IB 14029, 14030.

Leptotyphlopidae. — *Leptotyphlops conjuncta* (Jan): MCZ 52628, 52629, 52630, 52631. *L. longicauda* (Peters): MCZ 40093, 40094, 40095, 40096. *L. phillipsi* Barbour: MCZ 9642, 9643, 9644.

Uropeltidae — *Brachyophidium rhodogaster* Wall: CG 1699, 1700, 1801, 1802, 1804, 1806. *Melanophidium wynaudense* (Beddome): MCZ 24739. *Platyplectrurus madurensis* Beddome: MCZ 18044, 18045. *Plectrurus perroteti* Duméril & Bibron: MCZ 4178. *Rhinophis blythi* Kelaart: MCZ 1319A, 1319B, 34887, 34888, 39816. *R. philippinus* (Cuvier): MCZ 18034, 18035, 18037, 18038, 48947, plus one unnumbered specimen. *Uropeltis ocellatus* (Beddome): MCZ 3873, 3884, 47288, 47389. *U. pulneyensis* (Beddome): MCZ 1335, 47042, 47043. *U. rubrolineatus* (Günther): MCZ 3850, 3880, 3881, 3911, 47035, 47036, 47037, 47038, 47039, 47040. *U. woodmasoni* (Theobald): CG 1693, 1695, 1696, 1697.

Aniliidae. — *Anilius scytale* (Linné): MCZ 2950. *Cylindrophis maculatus* (Linné): MCZ 57192, 57193, 57194, 57195, 34886. *C. rufus* (Laurenti): CG 2518.

Xenopeltidae. — *Xenopeltis unicolor* Boie: CG 2713, 2954.

Boidae. — *Acrantophis madagascariensis* (Duméril & Bibron): MCZ 51848. *Aspidiotes melanocephalus* Krefft: MCZ 32808. *Boa canina* Linné: CG 2696. *B. enydris* Linné: MCZ 80858. *Bothrochilus boa* (Schlegel): MCZ 26940. *Calabaria reinhardti* (Schlegel): MCZ 9237. *Charina bottae* (Blainville): MCZ 63601. *Chondropython viridis* (Schlegel): MCZ 84010. *Corallus* (*Boa*) *annulatus* (Cope): MCZ 76678. *Enygrus asper* (Günther): MCZ 84012. *Epicrates angulifer* Bibron: MCZ 46465. *E. striatus* (Fischer): MCZ

68573, 68574. *Eryx colubrinus* (Linné): MCZ 39008, 39010. *E. conicus* (Schneider):
MCZ 3885. *E. jaculus* (Linné): MCZ 32798, 34050. *Eunectes notaeus* Cope: MCZ 2795.
Liasis amethystinus (Schneider): MCZ 59124, 84013. *L. childreni* Gray: MCZ 4215.
L. fuscus Peters: MCZ 59125. *Lichanura roseofusca* Cope: MCZ 29339. *Python argus*
(Duméril & Bibron): MCZ 59045. *P. sebae* (Gmelin): MCZ 40302. *Sanzinia madagas-
cariensis* (Duméril & Bibron): MCZ 11811. *Trachyboa boulengeri* Peracca: MCZ
29249, 29250. *Tropidophis melanurus* (Schlegel): MCZ 44862, 44864. *T. semicincta*
(Gundlach): MCZ 18122.

Bolyeridae. — *Casarea dussumieri* (Schlegel): MCZ 49135.

Acrochordidae. — *Acrochordus granulatus* (Schneider): MCZ 25607, 65573.

Colubridae. — *Ahaetulla mycterizans* (Linné): CG 2777. *Dasypeltis scabra* (Linné):
CG 0518. *Duberria lutrix* (Linné): CG 2275. *Elachistodon westermanni* Reinhardt:
CNHM 152140; KM R6401. *Malpolon monspessulanus* (Hermann): CG 2486. *Psammo-
phylax tritaeniatus* (Günther): CG 2522. *Thrasops flavigularis* (Hallowell): MCZ
8776, 51909. *T. jacksoni* Günther: MCZ 9276, 40551, 48342. *T. occidentalis* Parker:
MCZ 49686, 55232.

Hydrophiidae. — *Lapemis hardwicki* Gray: MCZ 20647, 23755. *Laticauda laticaudata*
(Linné): CG 3080.

Elapidae. — *Micrurus* sp.: CG 3273.

Viperidae. — *Crotalus terrificus* (Laurenti): CG 3272.

Amphisbaenia

Amphisbaenidae. — *Amphisbaena alba* Linné: CG 1331, 3329. *A. angustifrons* Cope:
CG 3321. *A. camura* Cope: CG 3322. *A. carvalhoi* Gans: CG 2833, 2834. *A. darwini
heterozonata* Burmeister: CG 1341, 2800. *A. dubia* Müller: CG 2092, 2093. *A. fene-
strata* (Cope): UMMZ 73847. *A. fuliginosa* Linné: CG 2802, 3086. *A. leeseri* Gans:
CG 2803, 2804. *A. manni* Barbour: AMNH 41051, 41078. *A. mitchelli* Proctor: CG
2764. *A. munoai* Klappenbach: CG 2768, 2769. *A. o. occidentalis* Cope: CG 1660. *A.
ridleyi* Boulenger: CG 2501. *A. silvestrii* Boulenger: CG 2718. *A. vermicularis* Wagler:
USNM 6035. *Ancylocranium s. somalicum* (Scortecci): CG 3035. *Anops kingi* Bell:
CG 3324, 3325. *Aulura anomala* Barbour: CG 2766. *Baikia africana* Gray: BM 1964.253.
Bipes biporus (Cope): CG 2538, 2539. *B. canaliculatus* Bonnaterre: CM 4321. *Blanus
cinereus* (Valisnieri): (Alexander, 1966). *B. strauchi* (Bedriaga): (Alexander, 1966).
Bronia brasiliana Gray: VM 12346-861, 12346-? *Cadea blanoides* Stejneger: MCZ
13571, 13572, 13573, 13574. *C. palirostrata* Dickerson: MCZ 12331, 12332, 12333, 12448,
12449, 12450, 12452, 12453, 12454. *Chirindia e. ewerbecki* Werner: CG 3326, 3327, 3328.
Cynisca leucura (Duméril & Bibron): CG 2301. *Geocalamus acutus* Sternfeld: MCZ
41120. *Leposternon affine* (Boettger): VM 12374; ZMU 26267. *L. boulengeri* (Boett-
ger): BM 1956.1.3.27, 1956.1.3.28. *L. crassum* (Strauch): VM 12370:3, 12370:4. *L.
phocaena* (Duméril & Bibron): UMMZ 60518; ZMU 9388. *L. polystegum* (Duméril):
NHMB 68D; ZMU 9808. *L. scutigerum* (Hemprich): BM 1904.2.2.2; ZMU 1398.
L. wuchereri (Peters): VM 12373; ZMU 9389. *Loveridgea ionidesii* (Battersby): CG
1830, 1831. *Mesobaena huebneri* Mertens: CNHM 130987. *Monopeltis c. capensis* Smith:
CG 1589, 1591. *M. guentheri* Boulenger: CG 3308, 3309. *Rhineura floridana* (Baird):
CG 2995, 2996. *Tomuropeltis pistillum* (Boettger): CG 1588. *Zygaspis capensis* (Peters):
CG 1587. *Zygaspis quadrifrons* (Thominot): CG 1824, 1826.

Trogonophidae. — *Agamodon a. anguliceps* Peters: CG 361-20, 361-29. *A. compressus*
Mocquard: CG 3330, 10149. *Diplometopon zarudnyi* Nikolski: CG 1688. *Pachycalamus
brevis* Günther: CG 2511, 2512. *Trogonophis wiegmanni elegans* (Gervais): CG 1897,
1899.

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