Festschrift for Marian Mlynarski

Max K. Hecht, Thomas C. LaDuke

Bolyerine vertebral variation: A problem for paleoherpetology

[With 2 text-figs]

Zmienność kręgowa u *Bolyerinae*: Problem dla paleoherpetologii

Abstract. The vertebrae of bolyerine snakes are described and compared. The range of morphological variation within this monophyletic group can be used as indicator of expected variation within clades at this level.

I. INTRODUCTION

The preservation of snakes in the fossil record is more frequent than generally acknowledged. Despite the abundance of snake vertebrae identification is difficult because of the scarcity of associated complete or partially complete cranial elements and intact vertebral columns. Snake vertebrae are solidly constructed and metamerically repeated so that they are often preserved in great numbers. They are usually preserved in the fossil record as disarticulated isolated elements and rarely as complete vertebral columns. For the paleontologists it would be indeed useful if the comparative morphology of snake vertebrae were more completely described (both qualitatively and quantitatively) so as to enable more successful identification of a single vertebra. Such an accomplishment would increase our knowledge of the history of the diversity of snakes and increase their importance and reliability in stratigraphy and paleoecology.

In any single species of snake the vertebrae gradually change along the vertebral axis in a gradient and within the ontogeny of any individual. Furthermore across taxa, as species and higher categories, there is great variation so that it is necessary to know to which region of the body a single vertebra belongs to before proper identification can be made. As a result isolated vertebrae have not been used as systematic characters in the recognition of most snake higher

taxa, although features of the entire vertebral column have been used by several students of the problem (HOFFSTETTER, 1946, 1960, 1968; UNDERWOOD, 1967). In paleophidiology overall similarity or the "gestalt" method is the primary method of identification of isolated vertebrae. It has been successful for herpetofaunas of the Pleistocene and Pliocene where similarity with the local living fauna is assumed. The problem becomes more difficult in the Miocene and earlier periods. The characterization of the vertebrae of higher categories is made more difficult because of the small samples in museum collections and the representation of taxa by a few middorsal elements of the vertebral column, generally from the middle of the trunk.

As stated above, the greatest difficulties in the identification of snake vertebrae are gradational variation within the column, ontogenetic variation and intertaxa variation. Intertaxa variation is more important in the identification of early Tertiary and Mesozoic faunas, than in later faunas. Another difficulty in the utilization of vertebrae as systematic characters is the relatively unsettled state of the classification of the henophidian and caenophilian snakes on the subfamily and family level of classification.

It is particularly informative to recognize the variation within monophyletic subfamilial groups. The living snakes of the island of Mauritius are useful in demonstrating some of the variation at this level.

The two genera *Bolyeria* and *Casarea* are both monospecific and are generally placed in a single taxon at the tribal or familial level. UNDERWOOD (1967) placed the two genera in the family *Boidae*, subfamily *Boinae* and the tribe *Bolyerini*. DOWLING and DUELLMAN (1978) placed the two genera is their own family. RAGE (1984) placed them in the subfamily *Bolyerinae*.

The island of Mauritius as indicated by subfossils (ARNOLD, 1980) was inhabited by this endemic subfamily. Both of these genera are now confined to Round Island, a small island off the coast of Mauritius. *Bolyeria* is known only from a half dozen specimens, whereas *Casarea* is known from a few more preserved specimens, some living examples and as a subfossil (ARNOLD, 1980). These two genera are characterized by a unique ophidian skull distinguished by the presence of a maxilla divided into two separate elements (ANTHONY and GUIBÉ, 1952). This condition is unique among the *Tetrapoda* and is one of the many features indicating the monophyly of the two genera.

It is for this reason we have chosen to compare the only available isolated vertebrae of these two genera in order to exemplify the degree of variation of what are apparently two closely related forms. The material is in the collection of the British Museum (Natural History). The first species *Bolyeria multicarinata* is BMNH no. 70. 11. 30. 4A and represents two vertebrae extracted between the region of 132—139 ventral scute segment of a total of 196 ventral scutes. The specimens of *Casarea dussumieri* (BMNH no. 70. 11. 30. 4D) are three vertebrae which were extracted from the region of ventral scales 143—146 of a total of 229 ventral scutes. These data indicate that the vertebrae of *Casarea* are slightly more posterior in the midtrunk vertebral series

than those of *Bolyeria*, although they are both from the middle of the body as a whole.

Morphological description of snake vertebrae is at best difficult because most of the similarities and differences are difficult to measure and more readily described qualitatively. The morphological terminology used here follows particularly the classic work of AUFFENBERG (1963). This basic terminology has been accepted by MEYLAN (1982), SZYNDLAR (1984), RAGE (1984) and LaDUKE (in press).

The following morphological description of these vertebrae will enable us to compare the degree of difference within a single subfamily of what is obviously a monophyletic group.

II. DESCRIPTION

Bolyeria multicarinata (BOIE)

One of two sequential midtrunk vertebrae from the level of 132—139 ventral scutes.

Ventral view (Fig. 1A): The centrum is relatively short with moderately strong subcentral ridges which diverge anteriorly with a slight prominence about halfway between the parapophyses and centrum. The haemal keel is broad and rounded anteriorly and is produced into a strong hypapophysis posteriorly. The hypapophysis is blade-like, posterio-ventrally directed with a strongly sinuous anterio-ventral surface created by an angular prominence. This prominence produces a subquadratic shape in lateral view giving the hypapophysis a blunt pointed distal tip which does not project beyond the condyle. Subcentral lymphatic fossae are weak, centered on the subcentral foramina. The anterior lymphatic notches are strong and rounded. A well developed process for a costal ligament projects from the ventro-lateral lip of the cotyle.

Anterior view (Fig. 1B): The cotyle is rounded. Its ventral edge is sharply recessed between the costal ligaments, but there is no emargination due to the anterior lymphatic notches. The paracotylar foramina are recessed in modest fossae. The prezygapophyseal buttress is very strong, its lateral edge is confluent with the anterior border of the paradiapophyseal facet. The neural canal is medium sized and subtriangular with its dorsal edge about half the width of its ventral edge. Within the neural canal, prominent ridges run anterio-posteriorly along the internal wall of the neural arch pedicel approximately two
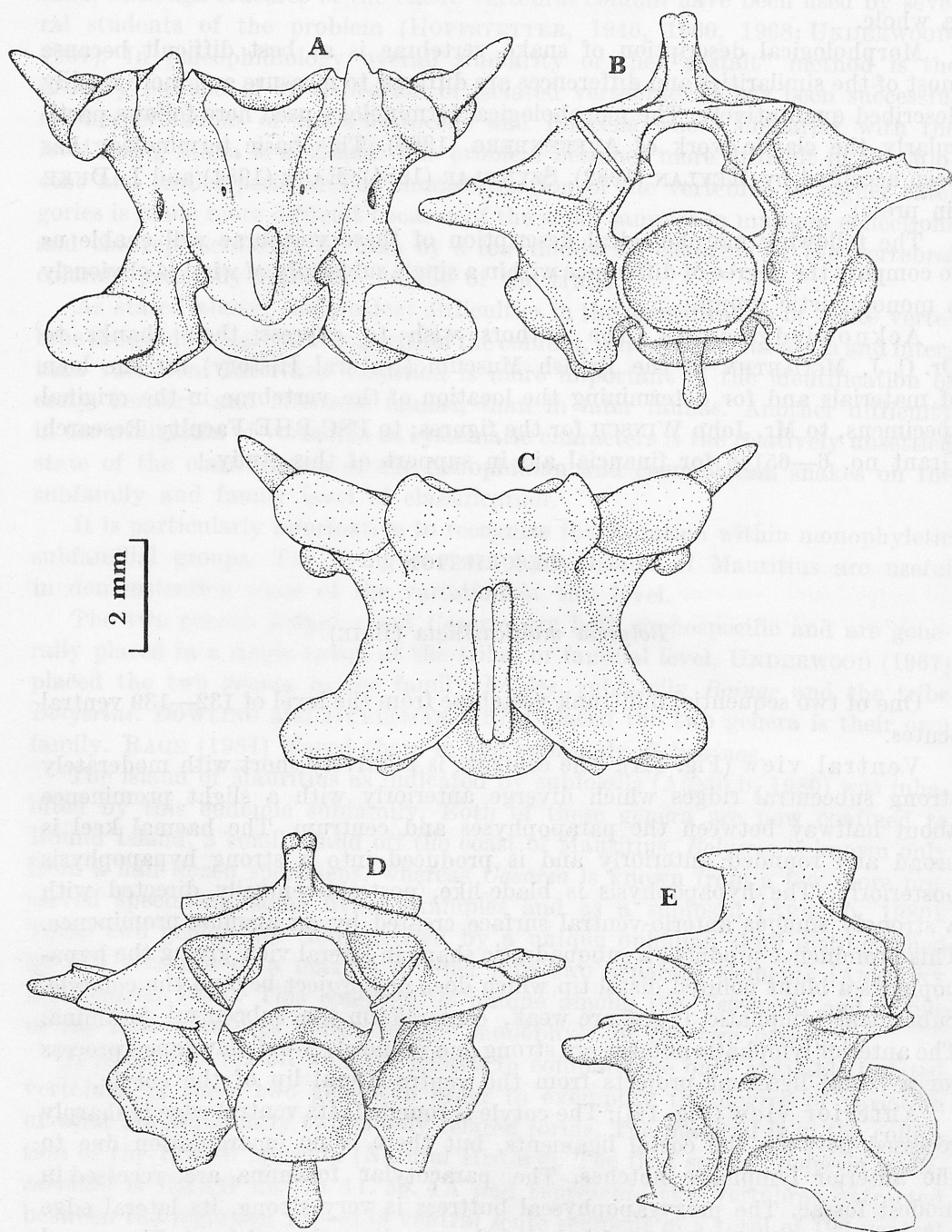
Fig. 1. Midtrunk vertebra of *Bolyeria multicarinata*. A — ventral, B — anterior, C — dorsal,
D — posterior, E — lateral views

thirds the distance up from the floor of the neural canal. The internal wall of the pedicel is excavated laterally below these ridges. This pocket in the pedicel shall henceforth be referred to as the Internal Neural Arch Pocket (INAP). A sharp subneural process projects directly caudad from the dorsal lip of the cotyle above the floor of the neural canal, which is also excavated ventrally.

The zygosphenal facets are mounted on thick, triangular blocks of bone, but the anterior edge of the zygosphene is quite thin and barely convex upward between these blocks. From above, the zygosphene is moderately broad with rounded lateral edges and a weakly notched crenate anterior border.

Dorsal view (Fig. 1C): Zygapophyses are moderately produced laterally. The prezygapophyses are subrectangular, with their long axis laterally directed and slightly less than twice the length of the short axis. The postzygapophyses are laterally directed elongate ovals. The prezygapophyseal processes (accessory processes of AUFFENBERG, 1963) are moderately elongate thin, acutely pointed distally and anterio-laterally directed. The posterior neural arch notch is broad, obtuse, and deeply incised. The neural spine projects caudally beyond the apex of the notch. The neural spine is of medium height, thickened dorsally, and has a very strong anterior overhang and weaker posterior overhang. The thickened dorsal edge is creased by a midsagittal sulcus and its anterior and posterior ends bifurcate slightly.

Posterior view (Fig. 1D): In posterior view the neural arch is depressed. The neural arch laminae are convex. The zygantral facets project slightly caudally beyond the neural arch laminae. No foramina are present posteriorly on the postzygapophyses between the zygantral and postzygapophyseal facets. There are no epizygapophyseal spines. The condyle is large and round, facing almost directly caudad.

Lateral view (Fig. 1E): Laterally the interzygapophyseal ridge is fairly prominent, but the edge is rounded. The synapophysis (paradiapophysis) consists of a small poorly developed parapophyseal portion and a prominent oval diapophysis projecting laterally from a point dorsad and slighty posterior to the parapophysis. A deeply incised sulcus for the costal ligament borders the diapophysis anteriorly. Parapophyseal processes are very small but sharply pointed.

Measurements of these vertebrae are given in Table I.

Casarea dussumieri (SCHLEGEL)

One of three sequential midtrunk vertebrae from the level of 143—146 ventral scutes.

Ventral view (Fig. 2A): The centrum is moderately elongate with very weak subcentral ridges. The haemal keel is rounded ventrally on its anterior half and is produced into a blade-like hypapophysis posteriorly. The hypapophysis is posteriorly directed, rounded distally and sinuous ventrally; its
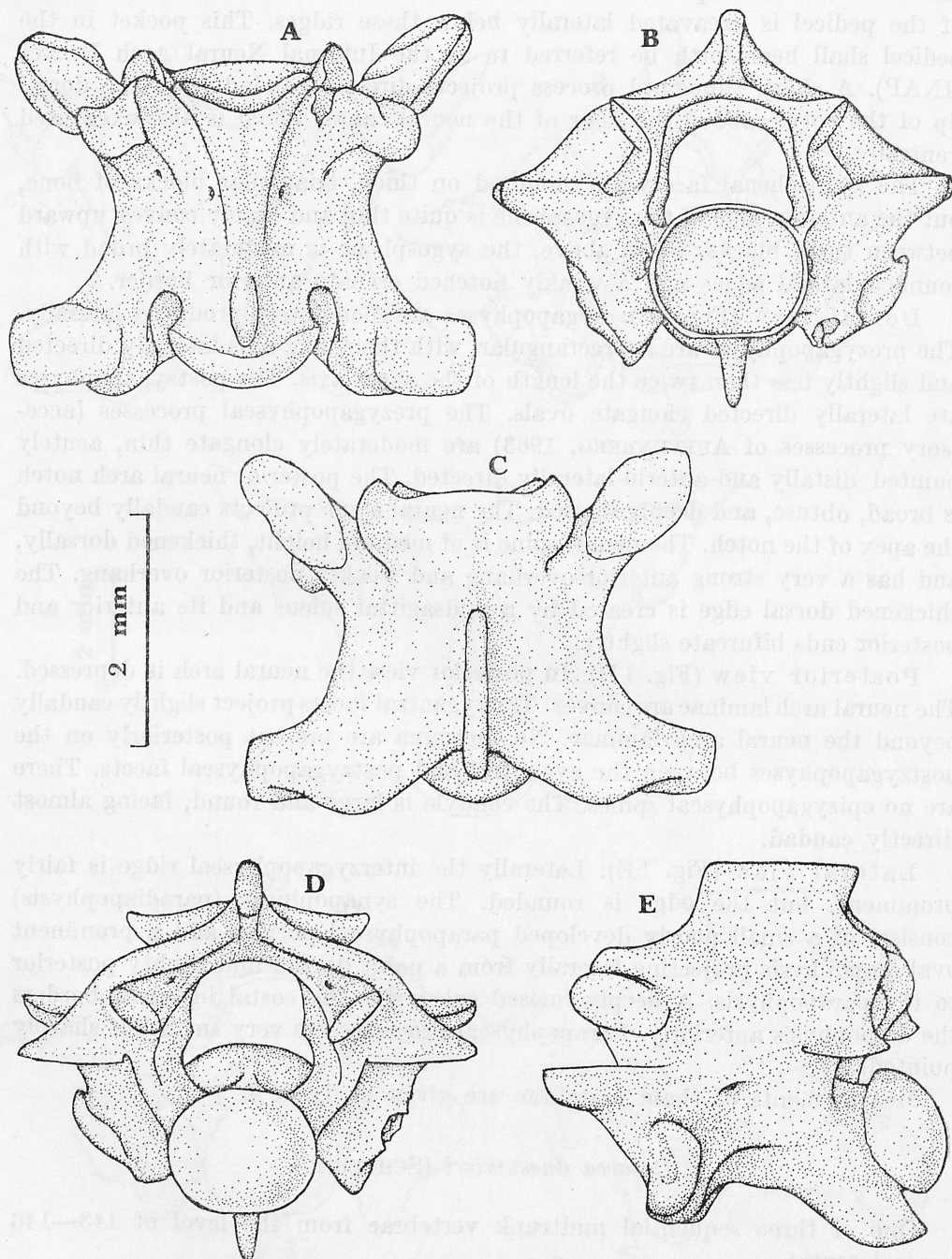
Fig. 2. Midtrunk vertebra of *Casarea dussumieri*. A — ventral, B — anterior, C — dorsal, D — posterior, E — lateral views

tip does not project caudally beyond the condyle. Subcentral lymphatic fossae are absent although subcentral foramina are present (unilaterally on two vertebrae, bilaterally on the third). Anterior lymphatic notches are very weak. Very small prominences are present on the ventrolateral lip of the cotyle for the attachment of the costal ligament.

Anterior view (Fig. 2B): The cotyle is depressed with a slightly recessed ventral lip. Paracotylar foramina are deeply recessed in fossae. The prezygapophyseal buttress is strong, but the paradiapophyseal facet is removed posteriorly from its lateral edge. The neural canal is very large, surpassing the cotyle in diameter. It is subquadratic, only slightly narrower dorsally than ventrally. Within the neural canal, ridges are only faintly developed on the medial side of the neural arch pedicel. These walls are not excavated below the ridges (INAP is lacking). The subneural process is strongly developed, bridging the ventrally excavated floor of the neural canal, but interrupted in the middle. The zygosphene is thin dorso-ventrally and slightly convex dorsally.

Dorsal view (Fig. 2C): From above, the zygosphene is broad, rounded laterally, and convex cranially. The zygapophyses are only weakly produced laterally. The prezygapophyses are elongate ovals, their long axes are directed more cranially than those of *Bolyeria*. In two of three vertebrae, the prezygapophyses are assymetrical, those on the right being broader than those on the left. Postzygapophyses are rectangular with the long axis directed laterally. Prezygapophyseal processes are obsolete. The neural arch notch is obtuse, but shallow. The neural spine projects posteriorly beyond the apex of this

Table I

Measurements (in mm) of vertebrae of bolyerine nakes⁴

Vertebra	Bolyeria		Casarea		
	1	2	1	2	3
CML	4.50	4.52	2.47	2.41	2.45
PRP	5.39	5.36	3.09	3.04	3.10
POW	8.02	7.93	3.94	3.87	3.92
PRW	8.05	8.04	3.97	3.98	3.94
PP	1.14	0.93	0.00	0.00	0.00
COH	2.47	2.34	1.16	1.17	1.19
CNH	2.11	2.14	1.06	1.04	1.03
NSH	1.84	1.86	0.71	0.69	0.72
NAW	4.66	4.59	1.09	1.09	0.94

Abbreviations: CML = centrum length; PRP = length from the anterior edge of the prezygapophysis to the posterior edge of the postzygapophysis; POW = width across the postzygapophyses; PRW = width across the prezygapophyses; PP = prezygapophyseal process length; COH = cotyle height; CNH = condyle height; NSH = neural spine height; NAW = neural arch width taken at waist.

notch. The neural arch laminae project caudally beyond the posterior edges of the postzygapophyses, concealing the zygantral facets from view above. The neural spine is low, and short anterio-posteriorly. It has no anterior overhang and only a slight posterior overhang. It is not thickened dorsally and bears no medial sulcus.

Posterior view (Fig. 2D): The neural arch is depressed as viewed posteriorly. The neural arch laminae are strongly convex. The zygantral facets project slightly caudad. No foramina are present posteriorly on the postzygapophyses. There are no epizygapophyseal spines. The condyle is medium sized, slightly depressed, and faces directly caudad.

Lateral view (Fig. 2E): The interzygapophyseal ridge is weak and rounded laterally. The synapophysis consists of a vertical parapophyseal facet and a laterally projecting oval diapophysis. A small depression is present for the reception of the costal ligament. The parapophyseal process is vestigial.

Measurements of these specimens are given in Table I.

III. DISCUSSION

Comparison of the vertebrae of these two genera reveals two fundamentally different types of vertebrae within a single subfamily in which the morphological differences are as great as between any two subfamilies of the *Colubridae* (DOWLING and DUELLMAN, 1978). In general conformation the wider shorter vertebrae of *Bolyeria* resemble the booid form whereas the longer vertebrae of *Casarea* resemble more closely some colubroid forms (Table I). On the other hand the development of the prezygapophyseal process bears great similarity to the colubroid level of development in *Bolyeria* whereas it is lacking or underdeveloped in *Casarea* as in many booids.

JOHNSON (1955) pointed out that many aspects of snake vertebral diversity were often associated with apparent phylogenetic relationships. His study was weakened by his reliance on X-ray photographs rather than detailed morphological studies. Yet, there are general features of vertebrae of burrowing or leaf litter forms such as reduction of the neural spine and prezygapophyseal process. Similarly there are morphological features of snake vertebrae that are generally associated with aquatic or arboreal habit. VINSON (1965) discusses the habits of the two genera describing *Bolyeria* as burrowing and *Casarea* as arboreal. The general features of *Bolyeria's* vertebrae do not indicate any specialization for burrowing habits. For example they have a relatively high neural spine and well developed prezygapophyseal processes. The general features of *Casarea* do not indicate any vertebral specialization for arboreal life. Thus it appears that the habits observed by VINSON (1965) are not directly reflected in the morphology of the isolated vertebrae.

As GASC (1974, 1976) has pointed out vertebral form is highly correlated

with biomechanical functions and therefore some features may have a recent adaptational features overlying phylogenetic characters. Of probable biomechanical and phylogenetic significance is the presence of hypapophyses throughout the bolyerine vertebral column which is also present in *Tropidophidae, Acrochordidae, Candoia*, some groups of *Colubridae* and other caenophidians.

There are many minor features which emphasize the distinctness of the two forms such as the presence of the Internal Neural Arch Pocket (INAP) and prezygapophyseal process in *Bolyeria*. Many other shape differences mentioned may be due to allometric patterns.

The distinctness of the two forms perhaps indicate an ancient separation of two generic lineages. The Mascarene islands are minicontinents supposedly derived from the Indian plate by the early Tertiary. If so, these snakes are autochthonous faunal elements, and they are part of an ancient fauna which has since been reduced to these islands. Another less likely alternative is that they are overwater waifs which have diversified on the islands.

IV. CONCLUSIONS

Midtrunk vertebrae of the two genera of *Bolyerinae* are divergent types implying that the allocation of extinct forms to family or subfamily based on isolated vertebrae may be questionable. Vertebral form in snakes, which evolve in response to biomechanical requirements of locomotion, sometimes obfuscate phylogenetic interpretations.

Department of Biology
Queens College of the City University of New York
Flushing, NY 11367, U.S.A.

REFERENCES

ANTHONY J., GUIBÉ J. 1952. Les affinités anatomiques de *Bolyeria* et de *Casarea* (Boïdés). Mém. Inst. Sci. Madagascar, sér. A, **7** (2): 189—201.

ARNOLD E. N. 1980. Recently extinct reptile populations from Mauritius and Reunion, Indian Ocean. J. Zool. London, **191**: 33—47.

AUFFENBERG W. 1963. The fossil snakes of Florida. Tulane Stud. Zool., New Orleans, **10** (3): 131—216.

DOWLING H. G., DUELLMAN W. E. 1978. Systematic herpetology: A synopsis of families and higher categories. HISS Publ., New York.

GASC J. P. 1974. L'interprétation fonctionelle de l'appareil musculo-squelettique de l'axe vertébral chez les Serpents (*Reptilia*). Mém. Mus. Natn. Hist. Nat., Ser. A, Paris, **83**: 1—182.

GASC J. P. 1976. Snake vertebrae — a mechanism or merely a taxonomist's toy? In: A. d'A. BELLAIRS, C. B. COX (eds): Morphology and biology of reptiles. Linn. Soc. Symp. Ser., London, **3**: 177—190.

HOFFSTETTER R. 1946. Remarques sur la classification des Ophidiens et particulierement des *Boidae* des Mascareignes (*Bolyerinae* subfam. nov.). Bull. Mus. Natn. Hist. Nat., Paris, (2), **18** (1): 132—135.

HOFFSTETTER R. 1960. Sur la classification des Boidés de Madagascar et des Mascareignes. Bull. Mus. Natn. Hist. Nat., Paris, (2), **32** (2): 131—138.

HOFFSTETTER R. 1968. (Review of) A Contribution to the classification of snakes (by G. UNDERWOOD). Copeia, Ann Arbor, 1968 (1): 201—213.

JOHNSON R. G. 1955. The adaptive and phylogenetic significance of vertebral form in snakes. Evolution, Lancaster **9** (4): 367—388.

LADUKE T. C. (in press) The ophidian paleofauna from Pit 91,1 Rancho La Brea.

MEYLAN P. A. 1982. The squamate reptiles of the Inglis 1A fauna (Irvingtonian: Citrus County, Florida). Bull. Florida State Mus., Biol. Sci., Gainesville, **27** (3): 1—85.

RAGE J. C. 1984. *Serpentes*. Encyclopedia of Paleoherpetology, Part 11. Gustav Fischer, Stuttgart, 80 pp.

SZYNDLAR Z. 1984. Fossil snakes from Poland. Acta zool. cracov., Kraków, **28** (1): 1—156.

UNDERWOOD G. 1967. A contribution to the classification of snakes. Brit. Mus. (Nat. Hist.), London, Publ. no. 653, x + 179 pp.

VINSON J. 1965. Sur la disposition progressive de la flore et de la faune de l'ile Ronde. Proc. Roy. Soc. Arts Sci. Mauritius, Port Louis, **2** (3): 263—268.

STRESZCZENIE

Kręgi tułowiowe dwóch rodzajów węży, *Bolyeria* i *Casarea*, należących do podrodziny *Bolyerinae*, wykazują znaczne różnice morfologiczne. Sugeruje to, iż właściwe oznaczenie przynależności rodzinnej i podrodzinnej kopalnych węży na podstawie pojedynczych kręgów może być wątpliwe.

Edited by Dr. Z. Szyndlar