

COUNTING VENTRAL SCALES IN ASIAN ANILIOID SNAKES

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The anteroventral scalation patterns of 48 specimens (24 species) of Asian anilioid snakes (Anomochilidae, Cyliodrophiidae, Uropeltidae) were examined. Scales were pinned and X-rayed to allow the position of the neck joint to be determined. Asian anilioids have a pattern of anteroventral scalation that prevents application of the standard Dowling system for identifying the first (anteriormost) ventral scale. No repeated pattern is found between anteroventral scalation and the position of the neck joint. Between four and eight post-mentum midventral scales lie anterior to the neck joint, with intraspecific variation occurring by up to two scales. Variation in the position of the neck joint is probably caused by variation in scalation and preservation, and perhaps ontogeny, with fewer midventral scales anterior to the neck joint in larger specimens. We recommend that counts of Asian anilioid ventral scales for taxonomic purposes include all midventral scales between the mental and anal scales. For precise comparisons of preloacal vertebral numbers among Asian anilioids and other snakes, dissections or X-rays are required.

Key words: methodology, morphology, Serpentes, scalation, Uropeltidae

INTRODUCTION

In a highly influential and widely cited paper, Dowling (1951) proposed a standard system for identifying the anteriormost ventral scale in snakes. As Dowling recognised, the posteriormost ventral is readily identified as the scale adjacent to the anal scale(s), but the anteriormost ventral is not so obvious (see also Peters, 1964: 378). In the majority of alethinophidians, enlarged anterior chin shields are separated from wider scales by a number of small gular scales that are often irregular and not present in a single midventral line. Dowling's system identified the first ventral as the anteriormost wider midline scale that is directly in contact with the first row of dorsal scales. Wide scales lying between this first ventral and smaller gulars were termed "preventrals" by Rasmussen & Howell (1982; see also Largen & Rasmussen, 1993: 317). As well as being consistent and repeatable across different workers, the first ventral was described by Dowling as corresponding to the first vertebra behind the neck joint of the axial skeleton, at least in ten colubrid genera. Thus, given that the vast majority of alethinophidians have a 1:1 correspondence between vertebrae and ventral scales (Alexander & Gans, 1966), the numbers of ventral scales counted using Dowling's system equals the number of preloacal vertebrae.

In some groups of snakes, the anteroventral pattern of scalation does not correspond to that described by Dowling, and Dowling's system cannot clearly be applied. In this paper, we examine the anterior ventral scales of one of these groups, the anilioids, comprising the South American Aniliidae, and the Asian Anomochilidae, Cyliodrophiidae and Uropeltidae (*sensu* McDiarmid *et al.*, 1999). Anilioid monophyly is not well supported, but all but one species (the sole aniliid,

Anilius scytale) are included in the more probably monophyletic (Gower *et al.*, 2005) "Asian anilioids", which are the focus of this study.

PREVIOUS STUDIES

A precise methodology is generally not presented in even the more significant of previous studies reporting ventral counts in Asian anilioids (e.g. Boulenger, 1890; Wall, 1921; Smith, 1943; Constable, 1949; Rajendran, 1985). Beddome (1886) did not describe a method for counting, but did describe ventral scales as occurring right up to the mental scale or immediately behind the first infralabials (if these meet behind the mental) in several genera of Uropeltidae. Bachman (1985) employed the same method in presenting ventral counts for *Cyliodrophis maculatus*. In some cases, new counts made (by DJG) of individual specimens allow us to infer that previously reported ventral counts have included all midventral scales between the mental and anal scales (e.g. at least some of the counts presented by Günther, 1864). However, there are some discrepancies between counts given by other previous workers (without an explicit method) and counts made by one of us (DJG) that include all midventral scales between the mental and anal scales. For example, the type specimen of *Rhinophis fergusonianus* was originally described as having 184 ventrals (Boulenger, 1896) but we count 196, and *Silybura shortii* was originally described as having 134 ventrals (Beddome, 1863) but the four syntypes (McDiarmid *et al.*, 1999) have 137-147. Other possible systems for identifying the anteriormost ventral in Asian anilioids where this has not been clearly described include the first scale that is wider than long (e.g. see Schmidt & Davis, 1941) or the first midventral scale that is the same width as other undoubted (more posterior) ventrals (e.g. see Thompson, 1914). It might be noted that very few taxonomic studies of Asian anilioids have been

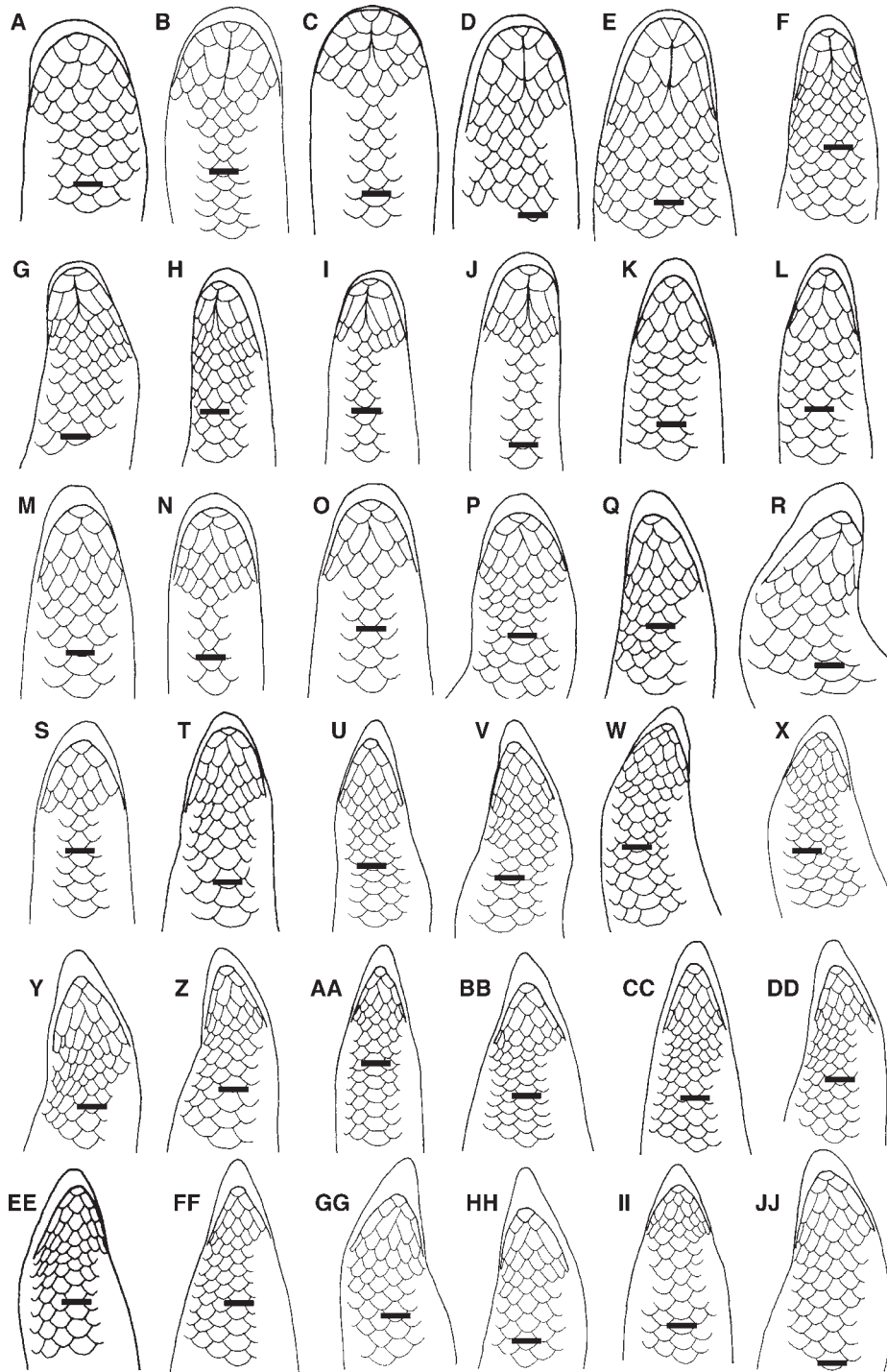


FIG. 1. Outline figures (from camera lucida drawings) of the anteroventral scalation patterns in a range of Asian aniloid snakes. Black bars indicate the position of the occipito-vertebral (neck) joint, as determined by pinning scales and X-raying specimens. The following taxa and specimen numbers (see Appendix 1 for further details) are illustrated, with total length of each specimen reported in parentheses: A. *Anomochilus leonardi* BMNH 1946.1.17.4 (274 mm); B. *Cylindrophis lineolatus* BMNH 1901.5.17.1 (665 mm); C. *C. ruffus* BMNH 87.2.7.1 (415 mm); D & E. *C. maculatus* DNM MW 1762 & 1797 (369 & 407 mm); F. *Melanophidium wynaudense* BMNH field tag MW 2542 (426 mm); G & H. *M. punctatum* BMNH field tags MW 2691 & 2479 (282 & 461 mm); I & J. *M. bilineatum* BMNH 74.4.29.698 & 699 (355 & 175 mm); K & L. *Brachyophidium rhodogaster* BMNH 1923.10.13.33 & 36 (116 & 184 mm); M. *Teretrurus sanguineus* 74.4.29.76 (215 mm); N & O. *Platyplectrurus trilineatus* BMNH 88.1.27.38 & 39 (328 & 395 mm); P. *P. madurensis* BMNH 1923.10.13.29-31 (361 mm); Q & R. *Plectrurus aureus* BMNH 89.7.6.7 & 8 (350 & 215 mm); S. *P. canaricus* BMNH 79.7.4.6-14 (379 mm); T. *Uropeltis macrolepis* BMNH 97.7.19.6 (257 mm); U & V. *U. dindigalensis* BMNH 83.1.12.6 & 7 (358 & 231 mm); W & X. *U. nitida* BMNH 78.1.11.2 & 1 (290 & 295 mm); Y. *U. ocellatus* BMNH 74.4.29.96 (300 mm); Z & AA. *Rhinophis travancoricus* BMNH field tag MW 219 & 221 (183 & 113 mm); BB, CC & DD. *U. phillipsi* DNM MW1759; 1761 & 1757 (294; 184 & 318 mm); EE. *U. melanogaster* BMNH 1905.3.25.66 (176 mm); FF. *R. philippinus* DNM MW 1739 (246 mm); GG & HH. *R. oxyrhynchus* BMNH 95.6.22.1; 233+5 (440 & 419 mm); II & JJ. *Pseudotyphlops philippinus* BMNH1955.1.9.61 & 60 (385 & 203 mm).

published since Dowling's (1951) system was proposed.

METHODS

Forty-eight ethanol preserved specimens representing all genera and a total of 23 species of anomochilids (one species), cylindrophids (three species) and uropeltids (19 species) were examined (see Appendix 1). Between four and eight fine entomological pins were inserted perpendicular to the long axis of the body, into anterior midventral scales in the estimated region of the neck joint, with adjacent pins generally spaced by one midventral scale. Pinned specimens were subsequently X-rayed, and camera lucida drawings were made of anterior midventral scalation patterns. The radiographs allowed the position of the neck (occipito-vertebral) joint to be related to external scalation. A total of 48 specimens were pinned and X-rayed. Generally, two or three different sized specimens of each included species were examined.

RESULTS

Unlike in most colubroids and other non-anilioid alethinophidians, Asian anilioids do not have intervening scales obviously lying between the anterior scales of the midventral row and adjacent dorsal scale row (Fig. 1). Additionally, Asian anilioids generally have fairly narrow ventral scales, less than twice as wide as adjacent dorsal scale rows, which gradually narrow anteriorly onto the underside of the head. These midventral scales extend far anteriorly, up to the chin where they contact the mental scale or are separated from it by only a single pair of paramedian chin scales and/or the anteriormost infralabials. Thus, Dowling's system cannot be applied.

There seems to be no readily implemented way of recognising the position of the occipito-vertebral joint from external scalation in Asian anilioids. In our sample, the number of midventral scales lying anterior to the occipito-vertebral joint varied from four (some *Cylindrophis*, *Melanophidium*, *Rhinophis*) to eight (only *Pseudotyphlops*). Intraspecific variation was never more than two in our small samples. Variation probably correlates, in part, with variation in the presence (*Cylindrophis*, *Melanophidium*) or absence (other Asian anilioids) of a mental groove, intraspecific variation in whether the anteriormost midventral scale contacts the mental or infralabials (Fig. 1K, II) or is separated from them by at least one paramedian pair of scales (Fig. 1L, HH, JJ), and variation in the length of the stalk of the occipital condyle, which is markedly elongated in many uropeltids (e.g. Rieppel & Zaher, 2002).

For Asian anilioids, attempts to identify the first ventral as the anteriormost midventral scale that is wider than long or the width of typical (further posterior) ventral scales are both problematic because generally the midventral scales narrow anteriorly in a very gradual manner (Fig. 1), and the exposed width of ventral scales

varies as specimens are manipulated because of mobile scale imbrication.

In all cases where two or more specimens of substantial different lengths were examined (e.g. Fig. 1D & E, G & H, I & J, N & O, U & V, Z & AA, CC & DD, GG & HH, II & JJ), the larger specimens had fewer midventral scales lying anterior to the occipito-vertebral joint.

DISCUSSION

In the vast majority of extant snakes, there is a 1:1 correspondence between vertebrae and ventral scales, in agreement with knowledge of dermis-vertebral relations during ontogeny (Alexander & Gans, 1966). Thus, establishing standard methods for identifying the anteriormost ventral scale and making repeatable counts of ventral scales is important for two kinds of comparisons that can be made: (1) among conspecifics and closely related species, and (2) among different major lineages of snakes. The former is important in assessments of variation for species- and population-level systematics, while the latter informs broader studies of snake phylogeny and evolution.

We detected some ontogenetic variation in the alignment of the occipito-vertebral joint and anterior midventral scales (see Fig. 1), but it is unclear whether this reflects ontogenetic reduction in relative head length, or is simply a result of preservational differences or is even an artefact of our small sample size.

Asian anilioids have a 1:1 correspondence between vertebrae and ventral scales (Alexander & Gans, 1966 - contra Bellairs & Underwood, 1951), so that a secure method for allowing the position of the occipito-vertebral joint to be determined from external scalation would allow precise comparisons of vertebral numbers with most other lineages of snakes without recourse to X-ray or internal examination. However, based on our results, there seems to be no repeatable system for identifying the anteriormost midventral scale that corresponds with the occipito-vertebral joint in Asian anilioids. In light of this, we make two recommendations: (1) for comparisons at lower levels (especially at or below the genus), ventral counts include all midventral scales between the mental and anal scales; (2) where workers choose not to follow our recommended system, the method should be described. Further, we make three additional observations: (1) individuals of the same species with the same number of precloacal vertebrae might vary in ventral scale counts made using this method because of small amounts of intraspecific variation in precise scalation patterns; (2) for comparisons of numbers of body segments among genera of Asian anilioids, and among anilioids and other snakes, it must be borne in mind that ventral counts for anilioids made in the recommended manner will be (up to eight) higher than the number of precloacal vertebrae; (3) for precise comparisons of vertebral numbers among anilioids and other snakes, specimens must be dissected or X-rayed. Comparisons among major lineages of snakes of numbers of

precloacal vertebrae based on a proxy of ventral scales counted using different methods will be biased in a relatively trivial (though directional, in at least some cases) manner.

Our recommended solution of not excluding any midventral scales between the mental and anal is consistent with some other studies that report ventral scale counts for Asian anilioids, whether described clearly (e.g. Bachman, 1985) or not (e.g. Günther's, 1864 count for the holotype of *Uropeltis bicatenata*). Intraspecific variation in ventral scale counts made using our recommended system for Asian anilioids might not correlate precisely with variation in precloacal vertebrae. This is largely because of intraspecific variation in exact scalation patterns immediately behind the mentum. In addition, variation in the preservation of individuals is likely to cause some differences in how midventral scales align with the occipito-vertebral joint. This might be exacerbated for uropeltids, at least some of which have notably free movement of the anterior end of the vertebral column within the 'integumentary envelope', in association with a particular mode of burrowing (Gans *et al.*, 1978). Thus, small variations in pre-vertebral midventral scale counts for Asian anilioids are probably not of wider relevance.

Some snakes do not have a 1:1 correspondence between vertebrae and ventral scales, for example acrochordids, some marine elapids, typhlopids and anomalepidids (Alexander & Gans, 1966). Some of these and some additional taxa that do have a 1:1 correspondence (e.g. *Anilius*, leptotyphlopids) are superficially similar to Asian anilioids in having anteroventral scalation patterns that do not permit the implementation of Dowling's (1951) system. Novel approaches to counting ventral scales were taken in some studies of these groups, for example Smith (1926: xvi) counted ventral scales in sea snakes "from the first enlarged (bituberculated) scale that can be found upon the neck". In other cases, ventral counts are not regularly recorded, for example middorsal scale counts are often the main or only longitudinal scalation count reported for scolecophidians (e.g. Gower *et al.*, 2004).

Almost all non-anilioid, non-colubroid alethinophidians (pythons, boas and close relatives, possibly not a clade) have a scalation pattern that allows Dowling's (1951) system to be applied, although we are not aware of how consistently this relates to the position of the occipito-vertebral joint. The Xenopeltidae resemble Asian anilioids in not having any obviously intervening gular scales between the anterior midventral scales and the first dorsal scale row (personal observation of *Xenopeltis unicolor*). *Xenophidion*, ungaliophiids and tropidophiids also have scalation patterns amenable to the application of Dowling's system. The latter, along with the monotypic *Anilius* (which has a pattern of anteroventral scalation superficially similar to Asian anilioids), might be the only extant alethinophidians to lie outside of a clade comprising Asian anilioids and all other alethinophidians (e.g.

Slowinski & Lawson, 2002; Wilcox *et al.*, 2002; Vidal & Hedges, 2004). Thus the most recent molecular phylogenetic hypotheses for the major lineages of snakes suggest that scalation patterns for which Dowling's system can and cannot be applied are homoplastic.

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APPENDIX 1

MATERIAL OF ASIAN ANILIOIDS PINNED, X-RAYED, AND EXAMINED

BMNH – The Natural History Museum, London; DNM – Department of National Museums, Colombo, Sri Lanka. Taxonomy follows McDiarmid *et al.* (1999). For those BMNH specimens renumbered after 1946, the more recent number is given.

Anomochilus leonardi (BMNH 1952.1.2.63; 1946.1.17.4), *Cylindrophis lineolatus* (BMNH 1901.5.17.1), *C. maculatus* (DNM MW 1762 & 1797), *C. ruffus* (BMNH IV.23.2.b; 87.2.7.1; 1980.909), *Melanophidium bilineatum* (BMNH 74.4.29.698 & 699), *M. punctatum* (BMNH field tag MW 2479 & 2691), *M. wynaudense* (BMNH field tag MW 2542), *Brachyophidium rhodogaster* (BMNH 1923.10.13.33 & 36; 1936.6.11.3), *Teretrurus sanguineus* (two of BMNH 1946.1.16.57–62), *Plectrurus aureus* (BMNH 89.7.6.7 & 8), *P. canaricus* (two of BMNH 79.7.4.6–14), *Platyplectrurus madurensis* (two of BMNH 1923.10.13.29–31), *P. trilineatus* (BMNH 88.1.27.38 & 39), *Pseudotyphlops philippinus* (BMNH 1955.1.9.60 & 61), *Rhinophis oxyrhynchus* (BMNH 233+5; 95.6.22.1), *R. philippinus* (DNM MW 1739, 1754 & 1756), *R. travancoricus* (BMNH field tag MW 219 & 221), *Uropeltis dindigalensis* (two of BMNH 1946.1.16.2–4), *U. macrolepis* (BMNH 97.7.19.6; 1958.14.62), *U. melanogaster* (BMNH 61.6.11.1–5; 1905.3.25.66–72), *U. nitida* (BMNH 1946.1.16.30 & 31), *U. ocellatus* (BMNH 74.4.29.95 & 96), *U. phillipsi* (DNM MW 1757; 1759 & 1761).

