

Functional Morphology of the Palato-Maxillary Apparatus in “Palatine Dragging” Snakes (Serpentes: Elapidae: *Acanthophis*, *Oxyuranus*)

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ABSTRACT Elapid snakes have previously been divided into two groups (palatine erectors and palatine draggers) based on the morphology and inferred movements of their palatine bone during prey transport (swallowing). We investigated the morphology and the functioning of the feeding apparatus of several palatine draggers (*Acanthophis antarcticus*, *Oxyuranus scutellatus*, *Pseudechis australis*) and compared them to published records of palatine erectors. We found that the palatine in draggers does not move as a straight extension of the pterygoid as originally proposed. The dragger palato-pterygoid joint flexes laterally with maxillary rotation when the mouth opens and the jaw apparatus is protracted and slightly ventrally during mouth closing. In contrast, in palatine erectors, the palato-pterygoid joint flexes ventrally during upper jaw protraction. In draggers, the anterior end of the palatine also projects rostrally during protraction, unlike the stability of the anterior end seen in erectors. Palatine draggers differ from palatine erectors in four structural features of the palatine and its relationships to surrounding elements. The function of the palato-pterygoid bar in both draggers and erectors can be explained by a typical colubroid muscle contraction pattern, which acts on a set of core characters shared among all derived snakes. Although palatine dragging elapids share a fundamental design of the palato-maxillary apparatus with all higher snakes, they provide yet another demonstration of minor structural modifications producing functional variants. *J. Morphol.* 271:73–85, 2010. © 2009 Wiley-Liss, Inc.

KEY WORDS: hydrophiinae; feeding mechanics; prey transport; jaw function; form-function integration

INTRODUCTION

Elapid snakes comprise 250–300 species in 62 genera of cobras and their relatives (Greene, 1997; Greer, 1997; Pough et al., 2004). A large portion of this diversity is concentrated in the Australasian region, which has 29 genera and >75 species of terrestrial elapids and six genera with about 70 species of marine elapids that are nested within the terrestrial clade (Greene, 1997; Sanders et al., 2008).

McDowell (1970) split elapid snakes into two major groups: palatine draggers including the terrestrial and marine Australasian species and

palatine erectors including all African and Asian species. The division was based on presumed consistent differences in the palatine bone and its associations with surrounding structures, from which McDowell (1970) deduced the functioning of the bone during prey transport (swallowing). The rostral palatines and caudal pterygoids are tooth-bearing elements that lie medial to the maxillae in the roof of the mouth. The palatine and pterygoid on each side form a palato-pterygoid bar that is independently mobile with respect to the braincase. The palato-pterygoid bars are used predominantly in prey transport by alternately ratcheting over the prey (Cundall, 1983), a behavior termed the “pterygoid walk” (Bolt and Ewer, 1964).

McDowell (1970) proposed that members of the palatine erectors erect the palatine along with the maxilla during maximum protraction of the palato-pterygoid bar. Palatine erection was described as an upward rotation of the anterior end of the palatine with respect to the pterygoid, which remains horizontal. This movement was presumed to be driven by maxillary rotation that is transmitted to the palatine via an anatomical linkage between the two bones. Rotation of the palatine was presumed to be facilitated by a simple palato-pterygoid joint and a well-developed choanal process, which serves as the fulcrum for rotation (Figs. 1A and 2A). Recent examination of the feeding mechanics of a number of proposed palatine erectors showed that palatine erection does indeed occur in those taxa but is not dependent on movements of the maxilla or the presence of a choanal process, as proposed by McDowell (1970). Instead, a muscle contraction pattern used during prey transport by other colubroids, together

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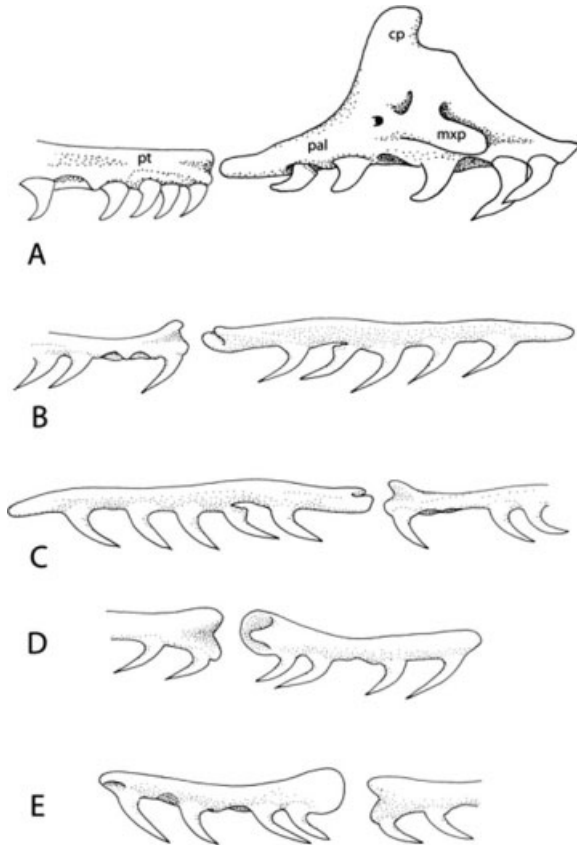


Fig. 1. Morphology of the palatine bone and the palato-pterygoid joint. The rostral ends of the pterygoids are shown disarticulated from the palatines to show the conformation of the joints. (A) Lateral view of the right palatine and the rostral end of the pterygoid of the palatine erector *Naja pallida* showing the choanal and maxillary processes of the palatine. (B) Medial view and (C) lateral view of the left palatine and the rostral end of the pterygoid of *Oxyuranus scutellatus*. (D) Medial view and (E) lateral view of the left palatine and the rostral end of the pterygoid of *Acanthophis antarcticus*. Both *Oxyuranus* and *Acanthophis* are palatine draggers. cp, choanal process; mxp, maxillary process; pal, palatine bone; pt, pterygoid bone.

with a moveable palato-pterygoid joint and anterior palatine attachment to the snout, is sufficient to produce palatine erection (Deufel and Cundall, 2003).

In members of the Australasian palatine draggers, McDowell (1970) proposed that the palatine moves as a direct, rostral extension of the pterygoid, remaining horizontal during protraction of the palato-pterygoid bar, even though the maxilla might be highly mobile (McDowell, 1970; Fig. 2B). Loss of a choanal process on the palatine was predicted to facilitate horizontal excursions of the bone, and the complexity of the palato-pterygoid joint was predicted to prevent any flexion. Additionally, the lack of a connection between palatine and maxilla was predicted to preclude participation of the palatine in maxillary rotation. However, not all palatine draggers lack a choanal process. There is variability in the size of the process when it is present, but in

most species, the process is almost vertical and does not roof the choanal passage (Scanlon, 2003) and thus would not impede rostral translation of the palatine as proposed by McDowell (1970).

McDowell (1970) thus used primarily a few characters of the palatine bone to predict the functioning of the bone and to propose a dichotomous taxonomy of elapid snakes. However, empirical studies reveal that complex structure–function relationships rarely conform to expected patterns (Gans, 1983; Lauder, 1995, 1996). Furthermore, the palatine characters suggested by McDowell (1970) to produce palatine erection in African and Asian elapids were actually not involved in producing the behavior (Deufel and Cundall, 2003), suggesting that the situation in proposed palatine draggers might also be more complex. In this study, we examine the function of the palato-maxillary apparatus in three presumed palatine draggers: *Acanthophis* sp. (death adder), *Oxyuranus scutellatus* (taipan), and *Pseudechis australis* (mulga or king brown snake). We then compared the function and morphology of the feeding apparatus of these presumed draggers to published records of palatine erectors.

MATERIALS AND METHODS

Function of the Palato-Maxillary Apparatus

We investigated the function of the palato-maxillary apparatus during intraoral prey transport in three presumed palatine

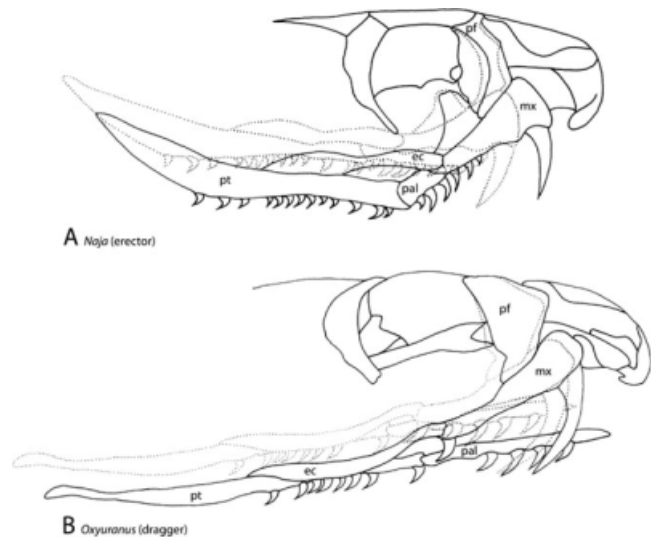


Fig. 2. Comparison of the palatine movements proposed by McDowell (1970). (A) Lateral view of the rostral portion of the skull of the palatine erector *Naja* with protracted palato-pterygoid bar showing "erected" palatine. (B) Lateral view of the rostral portion of the skull of the palatine dragger *Oxyuranus* with protracted palato-pterygoid bar showing "dragging" palatine. Solid outlines show the palato-maxillary apparatus in a protracted position; position at rest is shown with stippled outlines. ec, ectopterygoid; mx, maxilla; pal, palatine; pf, prefrontal; pt, pterygoid.

draggers, *Acanthophis* sp., *Oxyuranus scutellatus*, and *Pseudechis australis*. The systematics of the genus *Acanthophis* is currently in flux, with recognition of a variable number of species and subspecies based on genetic characters, biogeography, and scalation patterns (Wüster et al., 2005). A stable phylogeny for death adders has not yet been achieved. Thus, we are unclear which of the species of *Acanthophis* we used in our study, but based on appearance the snakes likely were *A. antarcticus*. *Acanthophis* is a stocky, broad-headed snake convergent on vipers in its body proportions and feeding ecology (Shine, 1980). *Oxyuranus* and *Pseudechis*, on the other hand, both have long, slender bodies, and a head not much wider than the anterior trunk (Cogger, 2000). Selection of species for investigation was constrained by the availability of live specimens in North American zoo collections.

We videotaped five adult *Acanthophis* sp. (probably *A. antarcticus*) while swallowing mice and, on two occasions, lizards (adult *Sceloporus merriami* and *Eublepharis macularius*). Three animals were recorded twice, one animal once, and one animal 10 times. Six adult *Oxyuranus scutellatus* were videotaped swallowing rats. One animal was recorded on four occasions, twice eating one rat, twice eating two. Two animals were recorded on one occasion and three animals on two occasions, each time eating one rat. One *Pseudechis australis* was videotaped on two occasions, each time eating one rat. All animals were videotaped at Zoo Atlanta, except for one *Acanthophis*, which was housed at Lehigh University. The zoo animals resided in their display cages during videotaping while the video camera and light source were placed ~1.5 m in front of the cage. The *Acanthophis* at Lehigh University was placed in a small filming arena for videotaping.

Prey transport in all animals was recorded with a Panasonic S-VHS AG-456 video camera and analyzed field-by-field (60 fields/sec) with a Panasonic AG-1970 S-VHS VCR. We took three measurements from the video records to determine possible associations among the movements of the palatine, the maxilla, and the snout: 1) In head-on views, we measured snout rotation around its long axis at maximum protraction of the jaws as the angle between a line along the inferior edge of the rostral scale and a line across the top of the braincase; 2) in lateral views, we measured maximum maxillary rotation at maximum jaw protraction as the angle between the long axis of the maxilla and the long axis of the braincase; 3) also in lateral views, we measured the angle between the long axis of the pterygoid and the long axis of the palatine (Fig. 3).

Because we had the opportunity to videotape only a single specimen of *Pseudechis australis* and on only two occasions, and because the resulting records showed no views of the inside of the mouth, we focused our analysis on *Acanthophis* and *Oxyuranus scutellatus*.

Morphology

In our delineation of the characters producing the behavior of the palatine bone, we focused mainly on the bones of the palato-maxillary apparatus, the dorsal constrictor muscles involved in protraction, elevation, and retraction of the elements of the upper jaw, and some of the jaw adductors. These structures are used in transporting prey through the oral cavity in snakes (Cundall and Greene, 2000; Cundall and Irish, 2008; McDowell, 2008). We also examined the joints between those bones, any processes on those bones, and any ligaments potentially constraining or guiding movements.

In the morphological analysis, we performed dissections on five *Acanthophis antarcticus* (South Australian Museum: SAM 44735, SAM 44736; California Academy of Science: CAS 113707, CAS 118896, CAS 109910) and four *Oxyuranus scutellatus* (Queensland Museum: QMJ 36906, QMJ 40261, QMJ 40271, QMJ 61838). We also examined the following skeletal material: *Acanthophis antarcticus* (American Museum of Natural History: AMNH 75086) and *Oxyuranus scutellatus* (American Museum of Natural History: AMNH 117809).

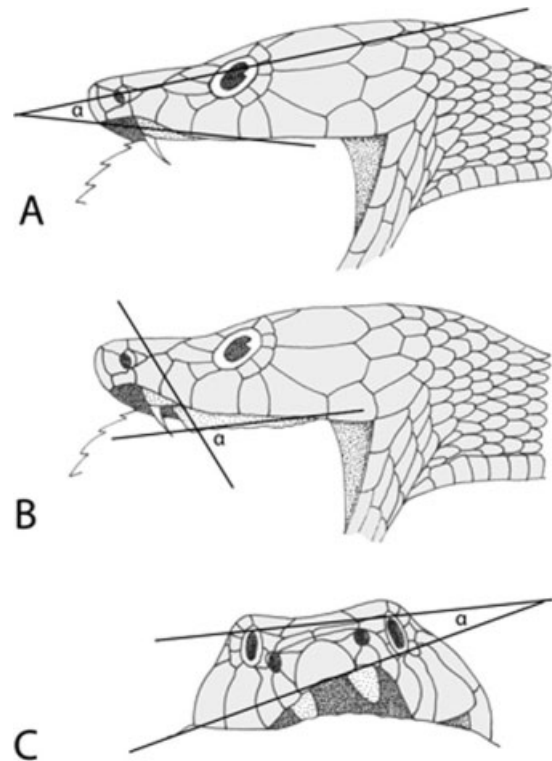


Fig. 3. Illustration of a generalized snake showing how angle measurements were taken from the video records of prey transport. (A) Maximum snout rotation, (B) maximum maxillary rotation, and (C) maximum angle between pterygoid and palatine.

To quantify variability between the morphologies of the species investigated, we measured anatomical structures on the dissected specimens. We included any structures that may be involved in the production of the palatine erection behavior. Measurements of bony elements were straight-line measurements and included 1) length of the braincase along the dorsal midline; 2) length of the pterygoid; 3) length of the pterygoid tooth row; 4) length of the palatine bone; 5) length of the palatine tooth row; 6) length of the ectopterygoid; 7) length of the maxilla; 8) location of the maxillo-prefrontal joint, measured from the rear end of the maxilla to the central (vertical) axis of the prefrontal; and 9) location of the ectopterygoid-ptyerygoid joint, measured from the rear end of the pterygoid to the posterior edge of the joint. Measurements of muscles were usually taken along the anterior and posterior boundaries of the muscle, following the fiber direction, to estimate the length of the longest and the shortest fibers in the muscle. Muscle measurements included 1) length of protractor pterygoideus muscle from the anteriormost point of origin to the anteriormost point of insertion on the pterygoid; 2) length of protractor pterygoideus muscle from the posteriormost point of origin to the posteriormost point of insertion on the pterygoid; 3) length of retractor pterygoideus muscle fibers along the posterior edge of the muscle; 4) length of retractor pterygoideus muscle fibers along the anterior edge of the muscle; 5) length of levator pterygoideus muscle fibers located in the middle of the muscle; 6) forward extent of the protractor pterygoideus muscle insertion on the pterygoid, measured from the posterior end of the bone; 7) length of the protractor quadratus muscle, including its tendon, measured along its posterior edge; and 8) length of the protractor quadratus muscle, including its tendon, measured along its anterior edge. All anatomical measurements were straight-line

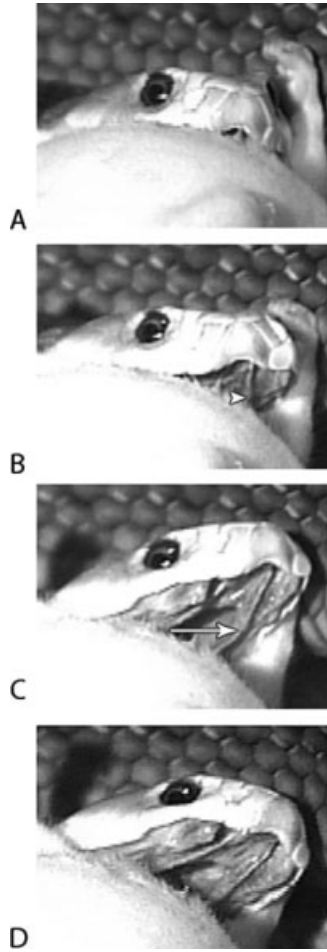


Fig. 4. Representative stages of a single palato-maxillary protraction/retraction cycle in *Oxyuranus scutellatus* (palatine dragger). (A) at rest; (B) at the end of mouth opening, showing the protracted maxilla and the laterally deflected palato-ptyergoid joint (arrowhead); (C) at the beginning of mouth closing, showing the depressed palato-ptyergoid joint (arrow); (D) beginning of protraction of contralateral side.

measures, scaled to the length of the braincase for statistical analysis.

To estimate the direction of excursion of the prefrontal bone during palato-maxillary protraction, we measured the angle formed between the prefrontal-frontal joint and the transverse axis of the head in dorsal view in both dissected and dry specimens.

Both functional data from video tapes and anatomical data from dissections were analyzed with SPSS for Windows (M. J. Norusis, Upper Saddle River, NJ). The data were first analyzed for homogeneity of variance using Levene's test. After homogeneity was ascertained, the data were analyzed with a one-way analysis of variance or the Mann-Whitney *U* test if variances proved unequal.

RESULTS

Function of the Palato-Maxillary Apparatus

Video records of prey transport show that *Acanthophis antarcticus* and *Oxyuranus scutellatus* share similar palato-maxillary kinematics.

Kinematics observed on the exterior of the head of *Pseudechis australis* match the behaviors of the other two species. The following description is for one generalized unilateral protraction/retraction cycle of the palato-maxillary apparatus.

Mouth opening begins by depression and slight protraction of the mandible. The distal end of the quadrate is slightly depressed and protracted, pushing the mandible rostrally. Protraction of the palato-ptyergoid bar and ectopterygoid begins, and the caudal end of the maxilla is depressed as the maxilla begins rotation around the prefrontal, swinging the fang tip slightly rostrally. As mouth

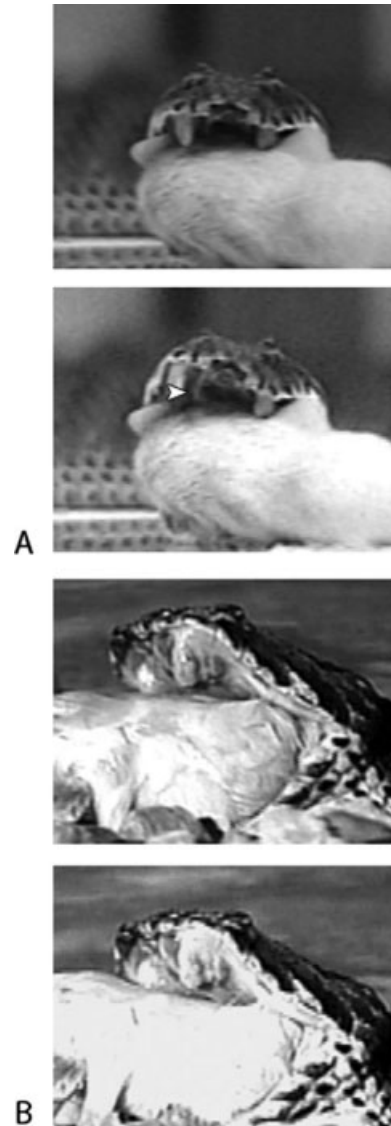


Fig. 5. Representative stages of a single palato-maxillary protraction/retraction cycle in two different individuals of *Acanthophis* (palatine dragger). (A) Anterior view showing the lateral deflection of the palato-ptyergoid joint (arrowhead) and the rotation of the snout during protraction of the right palato-ptyergoid bar; (B) oblique view of the protracting left palato-ptyergoid bar.

TABLE 1. Measurements from video records taken from four *Acanthophis antarcticus* and five *Oxyuranus scutellatus*.

	Snout rotation		Maxillary rotation		Joint flexion ^a		Prefrontal angle	
	N	Mean ± SD	N	Mean ± SD	N	Mean ± SD	N	Mean ± SD
<i>A. antarcticus</i>	11	10 ± 4	19	12 ± 3	16	32 ± 14	5	13 ± 3
<i>O. scutellatus</i>	21	10 ± 3	3	12 ± 4	9	32 ± 9	4	74 ± 8
<i>F</i>		0.000		0.003		<i>U</i> = 71		301.9
<i>P</i>		0.997		0.955		0.955		<0.01

Angles of the rotational axis of the prefrontal on the frontal from the transverse plane were measured on preserved specimens. Mean angles are rounded to the nearest degree and standard deviations to the nearest whole number.

^aUsing Mann-Whitney *U* test.

opening progresses, maxillary movement becomes more pronounced by the additional rotation of the prefrontal on the frontal when maxillary rotation on the prefrontal is at its maximum. Prefrontal movement has been noted in *Acanthophis* (Fairley, 1929; McDowell, 1969; McKay, 1889), but it also occurs in *Oxyuranus scutellatus* as evidenced by movement of the overlying preocular scale (Fig. 4D). Maxillary and prefrontal rotation carries the fang rostrolaterally (Fig. 5A,B). There is no significant difference between *Acanthophis antarcticus* and *Oxyuranus scutellatus* in degree of maxillary rotation ($F = 0.003$, $df = 31$, $P = 0.955$; Table 1). In both species, snout rotation around the long axis of the head matches maxillary rotation and moves the snout away from the rostral end of the protracting maxilla and palatine.

As the maxilla rotates, the rostral end of the protracted pterygoid and the caudal end of the palatine move slightly laterally. The joint remains displaced laterally and slightly rostrally at the end of mouth-opening (Figs. 4B and 5B). The anterior end of the palatine does not remain stationary with respect to the snout but projects rostrally ventral and lateral to the ventral snout elements (Fig. 4D).

The beginning of mouth closing is marked by depression of the palato-ptyergoid bar onto the prey. The flexed palato-ptyergoid joint moves slightly ventrally at this point (Figs. 4B and 5C; Table 1), in contrast to McDowell's (1970) prediction that the joint is inflexible. Mean palato-ptyergoid joint angles are 32° and do not differ significantly between *Acanthophis* and *Oxyuranus* (Mann-Whitney $U = 71$, $P = 0.955$; Table 1). Mean joint angles are less than those reported for the palatine erectors *Dendroaspis polylepis* (52°) and *Naja pallida* (43°) (Deufel and Cundall, 2003) indicating that palatine draggers flex the joint less.

Depression of the palato-ptyergoid bar brings the teeth of the pterygoid into contact with the surface of the prey where they anchor the head during the advance of the jaw apparatus on the contralateral side. Surprisingly, records of *Acanthophis antarcticus* feeding on lizards reveal that the palatine and its teeth do not contact the prey surface during any part of the transport cycle.

This has not been as obvious in snakes feeding on mice because the hair of mouse prey obscures views of the palato-ptyergoid teeth during transport. Lack of contact with the prey during transport suggests that the palatine may function only during prey capture.

Immediately after depression of the palato-ptyergoid bar, the mandible is adducted and the palato-maxillary apparatus is retracted, which at least for larger prey items usually means that the snake's braincase is protracted over the prey. The caudal end of the maxilla moves dorsally and the distal end of the prefrontal moves caudally as both bones return to their resting positions. As the mandible is adducted, the distal end of the quadrate swings caudally and dorsally. The fangs do not penetrate the prey during transport when the rostral end of the maxilla moves ventrally during retraction. After mouth-closing, the palato-maxillary elements of the contralateral side begin their advance over the prey and the two sides of the jaw apparatus alternately ratchet over the prey in typical "ptyergoid walk" fashion (Bolt and Ewer, 1964).

Morphology

Skull. The palatines of both *Acanthophis antarcticus* and *Oxyuranus scutellatus* lack choanal and maxillary processes (Fig. 1), as considered typical for palatine draggers by McDowell (1970). The caudal end of the palatine in both species has a finger-like medial and a flat, paddle-shaped lateral process that clasp the anterior end of the pterygoid, which has dorsal and ventral processes. Thus, the palato-ptyergoid joint can be considered a saddle joint. Although the joint has enough play to allow flexion in any direction during manipulation of dissected specimens, lateral flexion is most easily achieved, suggesting that protraction of the pterygoid would cause the palato-ptyergoid joint to preferentially move laterally. In the specimens of *O. scutellatus* that we examined, the dorsal process on the rostral end of the pterygoid is about the same length as the ventral process, contra the description by Covacevich et al. (1980), and does not prevent ventroflexion of the joint in dissected

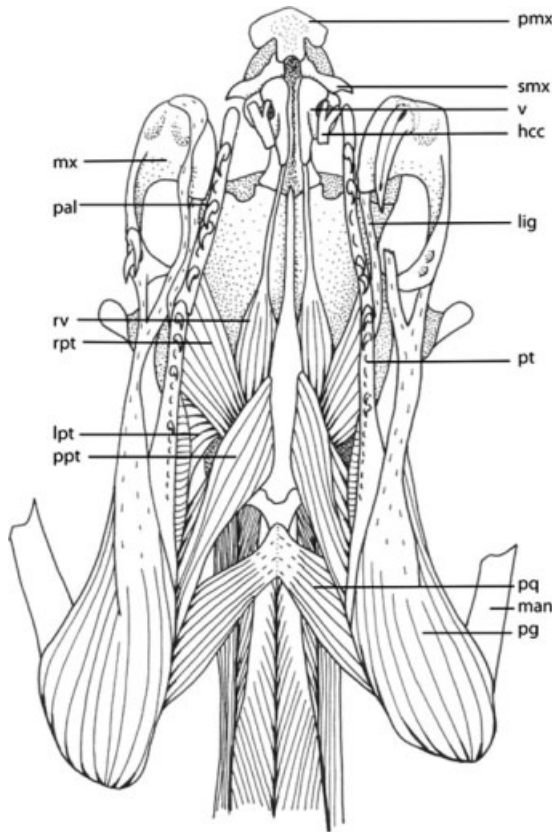


Fig. 6. Roof of the mouth of *Oxyuranus scutellatus* (palatine dragger) with the mucosa removed showing the musculo-skeletal elements involved in moving the palatamaxillary apparatus. hcc, hypochoanal cartilage; lig, ligament connecting rotromedial process of the maxilla to the lateral surface of the palatopterygoid joint; lpt, levator pterygoidei; man, mandible; mx, maxilla; pal, palatine; pg, pterygoideus; pmx, premaxilla; ppt, protractor pterygoidei; pt, pterygoid; rpt, retractor pterygoidei; rv, retractor vomeris; smx, septomaxilla; v, vomere.

specimens. In both species, the palatine reaches rostrally to the level of the rostral end of the maxilla (Figs. 6 and 7). The palatine is significantly longer in *O. scutellatus* than in *A. antarcticus* ($F = 8.7$, $df = 8$, $P = 0.021$; Table 2) but the lengths of the tooth rows do not differ. This is due to the fact that in *O. scutellatus*, the anterior end of the palatine is edentulous (Shea et al., 1993; Figs. 1 B,C and 5). The rostral end of the palatine in both *A. antarcticus* and *O. scutellatus* lacks the ligamentous connection to the hypochoanal cartilage of the snout found in those palatine erecting elapids that have been examined (*Naja pallida*, *Dendroaspis polylepis*, *Ophiophagus hannah*; Deufel and Cundall, 2003). This suggests that the rostral end of the palatine in draggers is able to move relatively freely with respect to the ventral snout elements.

The relative length of the pterygoid does not differ between the two species, but the tooth row is again shorter in *Oxyuranus scutellatus* ($F = 17.2$,

$df = 8$, $P \leq 0.01$; Table 2) because it does not extend as far caudally as in *Acanthophis*. The pterygoids also differ in that *A. antarcticus* possesses a lateral projection that underlies the rear end of the ectopterygoid instead of a gradually widening wing as in *Oxyuranus* (Figs. 6–9).

The ectopterygoid does not differ significantly in length in the two species but in *Acanthophis*, it bears a prominent, recurved, lateral projection that serves as the rostral attachment point of the pterygoideus muscle (Fairley, 1929; McKay, 1889; Fig. 7). A somewhat similar but smaller process has been described in the sea snake *Pelamis platurus* (McDowell, 1986).

The maxillae of *Acanthophis antarcticus* and *Oxyuranus scutellatus* do not differ in relative length and are similar in overall shape (Figs. 8 and 9). They consist of a thick, medially expanded, rostral part that bears two fang sockets and a slender caudal portion with a medial expansion at the rear that receives the anterior end of the

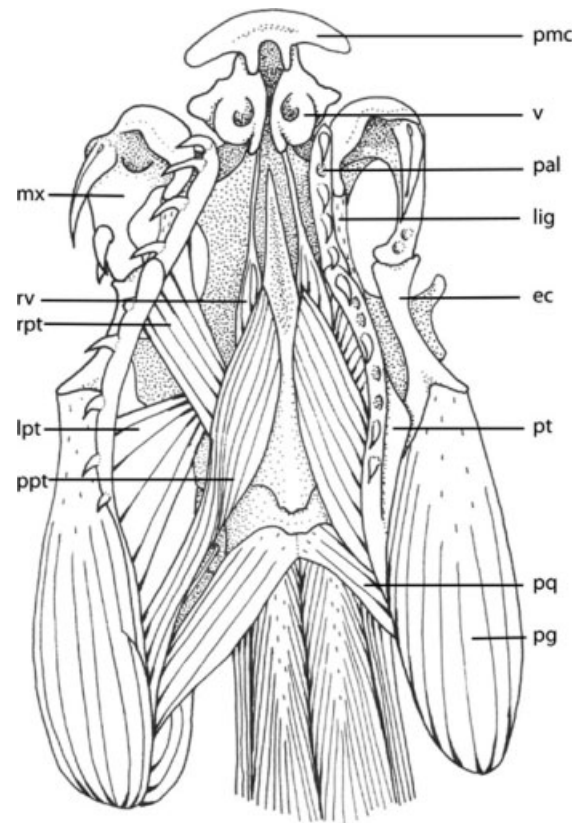


Fig. 7. Roof of the mouth of *Acanthophis antarcticus* (palatine dragger) with the mucosa removed showing the musculo-skeletal elements involved in moving the palatamaxillary apparatus. ec, ectopterygoid; lig, ligament connecting rotromedial process of the maxilla to the lateral surface of the palatopterygoid joint; lpt, levator pterygoidei; mx, maxilla; pal, palatine; pg, pterygoideus; pmx, premaxilla; ppt, protractor pterygoidei; pt, pterygoid; pq, protractor quadratus; rpt, retractor pterygoidei; rv, retractor vomeris; v, vomere.

TABLE 2. Morphological measurements given as ratios with respect to the length of the braincase

	<i>Acanthophis</i> (n = 5)		<i>Oxyuranus</i> (n = 4)		F	P
	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD		
Length of braincase along dorsal midline	18	2.85	24	1.33	17	<0.01
Length of pterygoid	1.11	0.11	1.00	0.05	3.99	0.09
Length of pterygoid tooth row	0.73	0.09	0.50	0.05	17	<0.05
Length of palatine	0.38	0.03	0.48	0.06	8.72	<0.05
Length of palatine tooth row	0.34	0.03	0.34	0.03	0.06	0.81
Length of ectopterygoid	0.42	0.04	0.43	0.03	0.05	0.83
Length of maxilla ^a	0.40	0.01	0.45	0.04	U = 2.5	0.061
Location of maxillo-prefrontal joint	0.33	0.03	0.33	0.02	0.00	0.98
Location of ectopterygoid-ptyergoid joint	0.73	0.07	0.68	0.06	1.48	0.26
Minimum length of protractor pterygoideus	0.90	0.08	0.60	0.03	51	<0.01
Maximum length of protractor pterygoideus	1.08	0.08	0.66	0.02	99	<0.01
Minimum length of retractor pterygoideus	0.35	0.05	0.29	0.07	2.46	0.16
Maximum length of retractor pterygoideus	0.39	0.03	0.37	0.06	0.33	0.59
Length of levator pterygoideus	0.38	0.05	0.27	0.06	11	<0.05
Rostral extent of protractor pterygoideus insertion	0.37	0.09	0.39	0.08	0.15	0.71
Length of protractor quadratus along posterior edge	0.67	0.07	0.60	0.05	3.02	0.13
Length of protractor quadratus along anterior edge	0.61	0.04	0.56	0.05	2.63	0.15

Means, standard deviations, *F*-values smaller than 10, and *P*-values are rounded to two decimal points. *F*-values larger than 10 are rounded to whole numbers.

^aUsing Mann-Whitney *U* test.

ectopterygoid. In both the species, the dorsal surface of the maxilla is sloped and faces slightly caudally, whereas the ventral surface is horizontal when the maxilla is at rest. Several posterior maxillary teeth are separated from the fangs by a diastema. The posterior maxillary teeth of *Oxyuranus scutellatus* bear grooves similar to those on the

fangs, and the rostral-most posterior maxillary tooth in AMNH 117809 even has a hollow base and a depression at the distal end of the groove

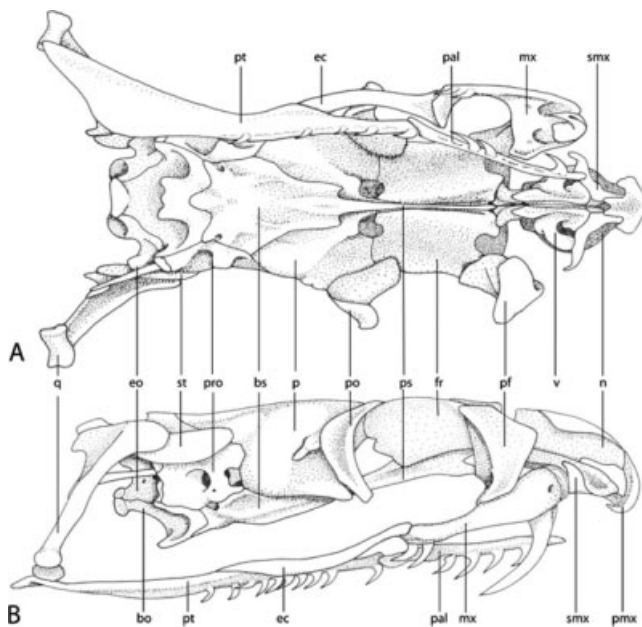


Fig. 8. Skull of *Oxyuranus scutellatus* (palatine dragger). (A) Ventral view; (B) lateral view. bo, basioccipital; bs, basisphenoid; ec, ectopterygoid; eo, exoccipital; fr, frontal; mx, maxilla; n, nasal; p, parietal; pal, palatine; pf, prefrontal; pmx, premaxilla; po, postorbital; ps, parasphenoid; pt, pterygoid; pro, prootic; q, quadrate; smx, septomaxilla; so, supraoccipital; st, supratemporal; v, vomer.

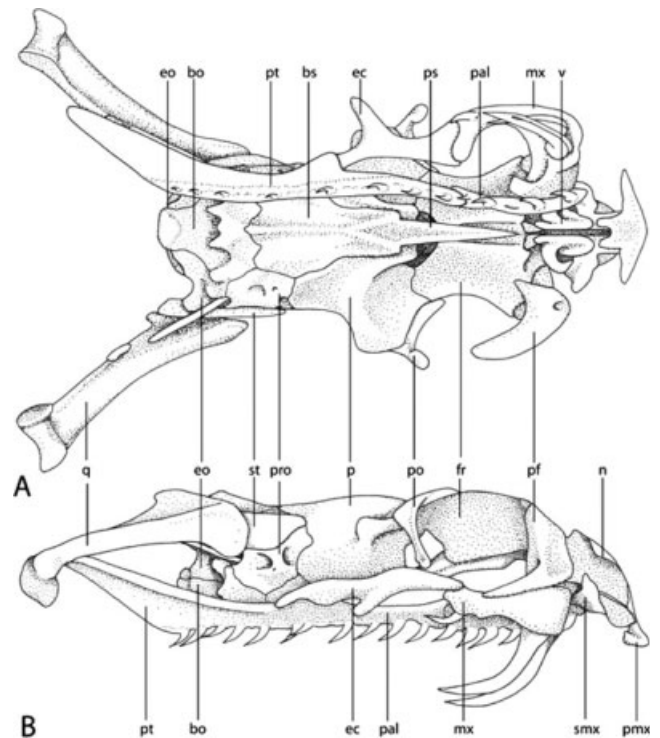


Fig. 9. Skull of *Acanthophis antarcticus* (palatine dragger). (A) Ventral view; (B) lateral view. bo, basioccipital; bs, basisphenoid; ec, ectopterygoid; eo, exoccipital; fr, frontal; mx, maxilla; n, nasal; p, parietal; pal, palatine; pf, prefrontal; pmx, premaxilla; po, postorbital; ps, parasphenoid; pt, pterygoid; pro, prootic; q, quadrate; smx, septomaxilla; so, supraoccipital; st, supratemporal; v, vomer.

where one would find a discharge orifice for the venom in functional fangs. This is inconsistent with the suggestion that the fangs in elapids develop from the posterior end of the upper jaw, being homologous with the fangs of rear-fanged snakes (Vonk et al., 2008). Covacevich et al. (1980) also found grooved posterior maxillary teeth in *O. scutellatus* and *O. microlepidotus*.

In both *Acanthophis antarcticus* and *Oxyuranus scutellatus*, the medial rostral maxilla bears a caudally directed process that serves as an attachment point for a ligament that is directed caudo-medially to attach to the lateral process of the caudal end of the palatine at the palato-ptyergoid joint (Figs. 6 and 7). Maxillary rotation will thus be transmitted directly to the palato-ptyergoid joint and pull the joint rostrally as the maxilla is rotating. This ligament is absent in palatine erecting elapids (Deufel and Cundall, 2003). The location of the maxillary-prefrontal joint does not differ significantly between *Acanthophis* and *Oxyuranus*, although in *O. scutellatus* the maxilla projects slightly beyond the rostral end of the prefrontal (Table 2; Fig. 8A). This places the fang in *O. scutellatus* slightly rostral to the center of maxillary rotation on the prefrontal. The maxillary-prefrontal joint is very simple. The distal end of the prefrontal is approximately oval, almost completely flat, with the exception of a slight ventral bend at the medial edge of the joint surface, and faces rostroventrally to articulate with the flat, sloping dorsal surface of the maxilla. The distal articular surface of the prefrontal differs in *Acanthophis* only in that it is tear-shaped, with a tapering process that runs posteroventrally (Fig. 9). The angle of the joint axis of the prefrontal on the frontal differs significantly between the two species ($F = 301.9$, $df = 8$, $P < 0.01$; Table 1). In *O. scutellatus*, the prefrontal-frontal joint axis is oriented strongly caudolaterally in dorsal view. Even though the prefrontal-frontal joint is more obliquely oriented in *O. scutellatus* than in *A. antarcticus*, the video records do not indicate a greater lateral excursion of prefrontal and maxilla in *Oxyuranus* (Figs. 4 and 5). This suggests that the superficial orientation of the prefrontal-frontal joint does not necessarily match its rotational axis.

Muscles. The muscles involved in alternately ratcheting the palato-ptyergoid bars over the surface of the prey during "ptyergoid walk" prey transport (Boltt and Ewer, 1964) are the dorsal constrictors and the ptyergoideus (Cundall, 1983; Cundall and Gans, 1979).

The dorsal constrictors in snakes are composed of five pairs of muscles extending from the floor of the braincase to the snout, the palato-ptyergoid bar, and the quadrate-mandibular region (Cundall, 1983; Haas, 1930, 1931a, 1931b). Protraction of the palato-maxillary apparatus is achieved by simultaneous contraction of the levator and pro-

tractor ptyergoidei muscles. The protractor quadrati muscle protracts the distal end of the quadrate and the quadrate-mandibular joint, thus protracting the mandible. Retraction of the palato-ptyergoid bar and the snout are achieved by contraction of the retractor ptyergoidei muscle and retractor vomeris muscle, respectively (Cundall, 1983).

The protractor quadrati is a thin strap of muscle that in *Oxyuranus* originates on the basioccipital along the midventral line opposite its partner (Fig. 7). In *Acanthophis*, it originates more broadly along the basioccipital-basisphenoid suture. It passes caudolaterally dorsal to the protractor ptyergoideus to insert medially on the distal half of the quadrate and on the connective tissue surrounding the jaw joint (Fig. 6). McKay (1889) stated that the muscle inserts only on the medial portion of the quadrate in *Acanthophis antarcticus*. The muscle does not differ significantly in relative length in *A. antarcticus* and *O. scutellatus* (Table 2).

The protractor ptyergoidei muscle originates on the basisphenoid approximately at the level of the rear edge of the orbit in both species (Figs. 6 and 7). The origin is relatively extensive, covering most of the parabasisphenoid medial to the origins of the m. retractor ptyergoidei and m. retractor vomeris. Protractor ptyergoidei muscle fibers extend caudally and insert on the entire rear one-third of the dorsal side of the ptyergoid, caudal to the insertion of the m. levator ptyergoidei (Fairley, 1929; McKay, 1889). There is no significant difference in the rostral extent of the insertion on the ptyergoid in the two species (Table 2). The protractor ptyergoidei muscle is much longer in *Acanthophis* than in *Oxyuranus* (Table 2) originating well rostral to the origin of the retractor ptyergoidei muscle. This condition of the m. protractor ptyergoidei converges on the condition of the muscle seen in many vipers (Cundall, 2002). Its contraction pulls the caudal end of the ptyergoid rostromedially, causing the rostral end of the ptyergoid to move slightly laterally, a displacement seen during the mouth-opening phase of prey transport. The longer m. protractor ptyergoidei in *A. antarcticus* suggests that it rotates the maxilla more extensively than *O. scutellatus*, even suggesting viper-like rotation capabilities of the maxilla. Although both McKay (1889) and Fairley (1929) mention that *Acanthophis* has the most extensive maxillary rotation of any Australian elapid, we did not find any significant difference between *Acanthophis* and *Oxyuranus* during prey transport (Table 1).

The m. levator ptyergoidei originates on the lateral parietal bone caudal to the postorbital bone. In *Acanthophis*, it originates with a strong, round tendon on a shelf-like process on the parietal, whereas in *Oxyuranus scutellatus*, the tendon is flatter and attaches to a much smaller, rounded process directly posterior to a strong "ligament"

attaching the anterior medial surface of the venom gland to the parietal bone (Figs. 8B and 9B). Fibers fan ventrally and caudally from the origin to insert on the entire middle third of the dorsal surface of the pterygoid, directly rostral to the insertion of the m. protractor pterygoideus. The insertion extends to cover the entire ectopterygoid-ptyerygoid joint without any fibers directly inserting on the ectopterygoid. Although the rostral fibers run caudally in *Acanthophis*, they run directly ventrally in *O. scutellatus*. Fibers of this muscle are significantly longer in *Acanthophis* (Table 2). The levator pulls the pterygoid rostrally and dorsally when it contracts.

The retractor pterygoidei muscle originates lateral and caudal to the origin of the protractor pterygoidei muscle on the parabasisphenoid and the parietal bone. It extends rostrally and ventrally to insert on the dorsal surface of the posterior quarter of the palatine and the anterior fifth of the pterygoid (McKay, 1889). Tendon fibers from the retractor pterygoidei to the vagina dentis run along laterally and partially merge with the ligament connecting the medial side of the rostral end of the maxilla to the lateral palato-ptyerygoid joint. In neither *Acanthophis* nor *Oxyuranus* are there any fibers extending to the dorsal surface of the caudal end of the maxilla as in *Naja pallida* (Deufel and Cundall, 2003). Depending on the relative position of the braincase and palatine, retractor contraction pulls the palato-ptyerygoid joint area either caudomedially or caudolaterally (or pulls the braincase anteromedially or anterolaterally if the pterygoid is fixed) and puts tension on the vagina dentis (Fairley, 1929; McKay, 1889). The length of this muscle does not differ significantly between *Acanthophis* and *Oxyuranus scutellatus* (Table 2).

The m. retractor vomeris originates rostralateral to the origin of the m. protractor pterygoidei and rostromedial to the origin of the m. retractor pterygoidei in a depression on the parabasisphenoid. Its fibers converge to form a small tendon that inserts on the dorsal caudal end of the vomer. The muscle is more robust in *Oxyuranus scutellatus* than in *Acanthophis antarcticus* (Figs. 6 and 7).

The m. pterygoideus and m. pterygoideus accessorius are part of the jaw adductor muscle group but also act on the palato-maxillary apparatus during the mouth-closing phase of the transport cycle (Cundall, 1983; Cundall and Gans, 1979). In *Acanthophis*, the pterygoideus muscle attaches to the caudal and dorsal surface of a lateral process in the middle of the ectopterygoid and to the posterodorsal surface of the ectopterygoid posterior to the process (Fig. 7). In *Oxyuranus scutellatus*, the pterygoideus muscle attaches to the entire ventrolateral ectopterygoid and extends tendons to the vagina dentis along both sides of the maxilla (Fig. 6). The pterygoideus muscle does not extend ten-

dons to the vagina dentis in *Acanthophis*. In neither *A. antarcticus* nor *O. scutellatus* does the pterygoideus muscle extend tendons to the capsule of the venom gland as seen in *Naja pallida* and *Dendroaspis polylepis* (Deufel and Cundall, 2003). The caudal end of the pterygoideus attaches to the ventral retroarticular process of the mandible. The pterygoideus muscle can act as an adductor of the mandible or as a retractor of the ectopterygoid and the maxilla (Cundall, 1983; Cundall and Gans, 1979). The pterygoideus accessorius muscle is difficult to separate from the pterygoideus muscle in both species, forming a thin sheet of muscle merging with the dorsomedial surface of the belly of the m. pterygoideus. This difficulty in distinguishing the two muscles has been remarked on by McKay (1889), who decided that the division into two separately named muscles was unnecessary. This is unlike the condition found in *Naja pallida*, *Dendroaspis polylepis*, and other palatine erecting elapids, in which the m. pterygoideus accessorius is a much more distinct muscle (Deufel and Cundall, 2003; Haas, 1930, 1931a, 1931b). Accessorius fibers extend caudolaterally from the ventral surface of the caudal half of the pterygoid to insert on the medial retroarticular process.

In summary, of the 16 morphological measurements taken, 11 showed no significant difference between the two species. Only five of the measurements differed significantly, including the lengths of the pterygoid tooth row, the palatine, the anterior and posterior fibers of the protractor pterygoideus, and the levator pterygoidei (Table 2; Fig. 10). Other, nonquantifiable, differences include the anterior attachment of the pterygoideus muscle to a lateral process of the ectopterygoid and the lack of pterygoideus tendons to the vagina dentis in *Acanthophis*.

DISCUSSION

The palatine bone of *Acanthophis antarcticus* and *Oxyuranus scutellatus* does not behave as a straight rostral extension of the pterygoid and does not remain horizontal during prey transport as proposed for palatine draggers (McDowell, 1970). The palatine of *Acanthophis* and *Oxyuranus* also functions differently from the palatine in palatine erecting elapids (Deufel and Cundall, 2003), showing less pronounced dorsal or ventral bending of the palato-ptyerygoid joint and additionally a strong lateral movement of the joint during protraction. The palatine bone of *Acanthophis* and *Oxyuranus* also undergoes more pronounced rostral translation during protraction than that of palatine erectors, as predicted by McDowell (1970).

The function of the palato-maxillary apparatus of the two species of palatine draggers examined can be explained by a number of characters in which they differ from palatine erecting (African

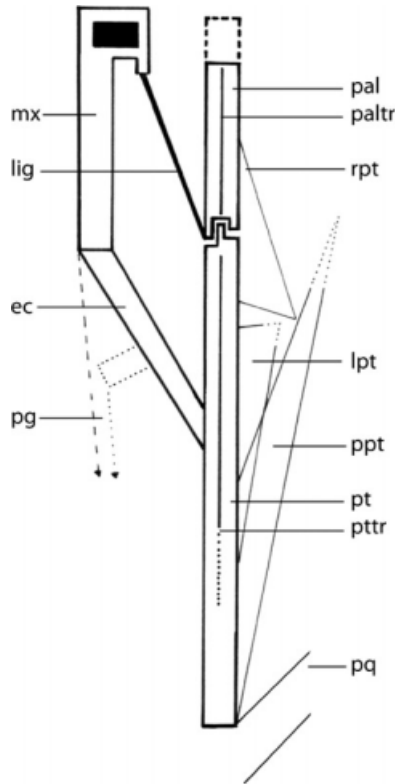


Fig. 10. Diagrammatic representation of one side of the palatomaxillary apparatus of *Acanthophis antarcticus* and *Oxyuranus scutellatus* (palatine draggers). Characters that differ significantly between the two species are indicated by dotted lines if the structure is only present or larger in *A. antarcticus* and by dashed lines if the structure is only present or larger in *O. scutellatus*. paltr, palatine tooth row; pttr, pterygoid tooth row, for other abbreviations see Figure 9.

and Asian) elapids (Fig. 11). The function of the palato-ptyergoid joint of *Acanthophis antarcticus* and *Oxyuranus scutellatus* is intimately tied to the movements of the maxilla by the sturdy ligament directly connecting the rostromedial maxilla to the lateral face of the caudal end of the palatine at the palato-ptyergoid joint. During protraction of the palato-maxillary apparatus by the protractor and levator pterygoidei muscles, any maxillary rotation that brings the fang into a more erect position puts tension on this ligament and pulls the palato-ptyergoid joint rostromedially (Fig. 12). This movement is seen during the mouth-opening phase of prey transport (Figs. 3B and 4B). In erectors, without this ligamentous connection between the maxilla and the palato-ptyergoid joint, the palato-ptyergoid joint moves dorsally at this stage in the transport cycle, caused only by the contraction of the levator and protractor pterygoidei muscles (Deufel and Cundall, 2003). The relatively limited ventral flexion of the palato-ptyergoid joint at the beginning of the mouth-closing phase of prey transport in *Acanthophis* and *Oxyuranus* compared with palatine erectors is likely due to the

fact that in draggers the retractor pterygoidei insertion spans the joint dorsally and the conformation of the joint itself facilitates lateral over dorsoventral flexion (Figs. 1, 6, 7, and 12). In contrast, in erectors, the retractor pterygoidei insertion remains rostral to the palato-ptyergoid joint, leaving the joint free to move (Deufel and Cundall, 2006). The lack of attachment of the rostral end of the palatine bone to the hypochoanal cartilage of the snout and the absence of a choanal process tying the palatine to the roof of the choanal passage both facilitate the pronounced rostral translation of the palatine during protraction of the palato-maxillary apparatus in draggers (Figs. 4, 5, and 12). Lack of attachment of the rostral end of the palatine to the snout also allows the rostral end of the palatine to move forward with respect to the snout instead of bracing against it, reducing forces leading to strong palato-ptyergoid joint flexion. In contrast, in palatine erectors, the rostral end of the palatine is attached to the snout and protraction of the palato-ptyergoid bar braces the palatine against the snout, resulting in

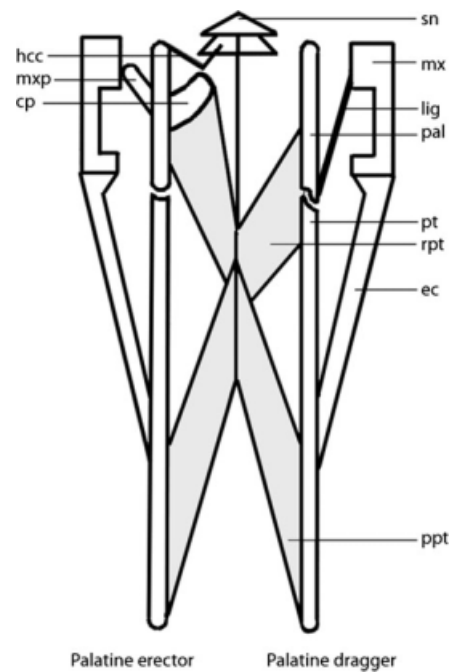


Fig. 11. Diagrammatic comparison of the palatomaxillary apparatus of palatine erectors and palatine draggers. Palatine erectors have a choanal process (cp) and a maxillary process (mp) on the palatine (pal), the rostral end of the palatine is connected to the hypochoanal cartilage (hcc), and the retractor pterygoidei (rpt) does not span the palato-ptyergoid joint. In contrast, palatine draggers generally lack a choanal process and a maxillary process, the rostral end of the palatine is not connected to the hypochoanal cartilage of the snout, the retractor pterygoidei spans the palato-ptyergoid joint, and a ligament (lig) connects the lateral surface of the palato-ptyergoid joint to the medial surface of the rostral end of the maxilla (mx). ec, ectopterygoid; ppt, protractor pterygoidei.

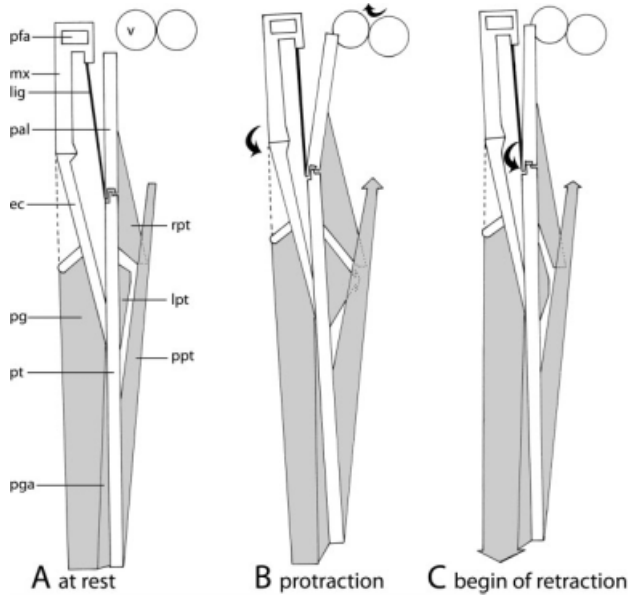


Fig. 12. Diagrammatic representation of the function of the palato-maxillary apparatus during prey transport in the palatine dragger *Acanthophis antarcticus* in ventral view. Elements are scaled using the means of the anatomical measurements. Contracting muscles are shown with arrowheads. (A) Palato-maxillary apparatus at rest. (B) Protracted palato-maxillary apparatus at the end of mouth opening with the rear end of the maxilla depressed (arrow), the palato-ptyergoid joint elevated and moved laterally, and the snout rotated (arrow). (C) Beginning of mouth closing depresses the palato-ptyergoid joint (arrow). ec, ectopterygoid; lig, ligament; lpt, levator pterygoidei; mx, maxilla; pal, palatine; pfa, level of prefrontal articulation; pg, pterygoideus; pga, pterygoideus accessorius; ppt, protractor pterygoidei; rpt, retractor pterygoidei. See text for more information.

pronounced flexion of the palato-ptyergoid joint with limited rostral translation of the palatine (Deufel and Cundall, 2006).

These few changes in the design of the palato-maxillary apparatus of the Australasian palatine draggers resulted in the absence of pronounced palatine rotation at the beginning of the mouth-closing phase of pterygoid walk prey transport that is seen in other elapids (Deufel and Cundall, 2003) and most other colubroids (Cundall, 1983; Cundall and Gans, 1979; Cundall and Greene, 2000; Dullemeijer, 1956; Kardong et al., 1986). Aside from the absence of pronounced, sharp flexion of the palato-ptyergoid joint, the pterygoid walk of palatine draggers is very similar to the pterygoid walk of other colubroids. The palato-ptyergoid bar is first elevated and protracted over the prey during mouth opening and then drops onto the surface of the prey at the beginning of mouth closing. The action of the palatine during prey transport seems to be only of minor importance because the palatine teeth rarely if ever make contact with the surface of the prey. It is mainly the pterygoid that walks the head of the

snake over its prey. For the pterygoid to ratchet forward and backward with respect of the braincase, its rostral end has to be able to move. This can be achieved either by extensive flexion of the palato-ptyergoid joint when the rostral end of the palatine is attached to the snout and thus limited in its movement (as in palatine erecting elapids), or by relatively limited ventral bending and additional lateral bending of the joint when the rostral end of the palatine is free from the snout and can translate rostrally during protraction (as in palatine dragging elapids). Thus, as in palatine erectors, the basic function of the palato-maxillary apparatus of palatine draggers is only another variation of the pterygoid walk prey transport mechanism of colubroid snakes.

Because the basic function of the palato-maxillary apparatus of palatine erectors and palatine draggers is fundamentally similar as well as being not exactly as predicted by McDowell (1970), we suggest abandoning the “erector” and “dragger” designations. If designations other than the clade names are desired, we prefer designations that are not based on function but on the distinct morphological differences of the two groups, although we do not see a need for adding to the plethora of awkward names already in the literature.

There is relatively little variation in the basic morphology of the components of the prey transport apparatus in the two species examined here (Fig. 10). The relatively long protractor pterygoideus muscle of *Acanthophis antarcticus* is convergent on some vipers, which have protractors that originate well rostral on the braincase (Bolt and Ewer, 1964; Cundall, 2002; Dullemeijer, 1956; Kardong, 1973), and suggests that *Acanthophis* is able to protract the palato-maxillary apparatus to a greater extent than *Oxyuranus scutellatus*. We could not detect a significant difference in maxillary rotation in the two species during prey transport. However, maxillary rotation in *Acanthophis* is larger during prey capture than during transport, even though rotation is not nearly as pronounced as in the viperid *Crotalus* (Cundall, 2002; Deufel and Cundall, 2006; Young et al., 2001). In those vipers that release prey, the full rotational capabilities of prefrontal and maxilla are only realized during release of the prey after the strike, not during the extension phase of the strike or prey transport (Cundall, 2002; Cundall and Beaupre, 2001). However, *Acanthophis* usually does not release its prey (Deufel and Cundall, 2006). Thus, the functional significance of the elongate protractor pterygoidei muscle in *Acanthophis* remains unclear. The same is true for the prominent lateral process of the ectopterygoid of *Acanthophis*. This process serves as the main point of origin of the pterygoideus, which, unlike in other elapids, does not send tendons to insert on the vagina dentis. Thus, *Acanthophis* appears to lack a mechanism to

pull the vagina dentis against the entrance orifice of the fang during the envenomating bite, potentially influencing the pressure with which venom can be introduced into a prey. A similar pronounced lateral process on the ectopterygoid has not been described for any other elapid. The longer palatine bone of *O. scutellatus* compared with *Acanthophis* is because of a rostral edentulous extension of the palatine whose functional significance remains a mystery. None of this variation suggests any significant functional pattern and does not appear to affect prey transport kinematics.

The observed morphological variation among the palatine draggers examined and between palatine draggers and palatine erectors could be carrying only a phylogenetic signal, or characters may have responded to selection pressures not obvious in this analysis. Differences may have been driven by the functional demands of prey envenomation, not transport. Prey envenomation involves structures that also participate in prey transport; there is extensive overlap in the characters that produce both behaviors. Both the maxilla used in envenomation and the palato-ptyergoid bar used in transport are driven by movements of the pterygoid bone caused by the dorsal constrictor muscles. The overlapping character suites of envenomation and transport are subject to stabilizing selection that maintains overall system function. We assume that characters vary only within certain thresholds or overall system function will be impaired and fitness will decrease. The evolution of individual characters of the palato-maxillary apparatus thus may be constrained by their functional interactions in producing several behaviors (Schwenk, 2001; Schwenk and Wagner, 2001; Wagner and Schwenk, 2000).

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