Prey processing in *Leurognathus marmoratus* and the evolution of form and function in desmognathine salamanders (Plethodontidae)

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Function and biological role of morphological specialization in desmognathine salamanders are analysed in the light of studies of feeding in *Leurognathus marmoratus*. Nine morphological features uniquely characterize the Desmognathinae as compared to its sister group, the Plethodontinae, and other salamanders: (1) heavily ossified and strongly articulated skull and mandible; (2) flat, wedgelike head profile; (3) stalked occipital condyles; (4) modified atlas; (5) modified anterior trunk vertebrae; (6) atlanto-mandibular ligaments; (7) enlarged dorsal spinal muscles; (8) enlarged quadrato-pectoralis muscles; and (9) hind limbs relatively larger than forelimbs. Dorsoventral head mobility is increased at the atlanto-occipital joint by the stalked occipital condyles which simultaneously increase the mechanical advantage of the hypertrophied axial muscles that cross the joint. During head depression the atlanto-mandibular ligaments are placed in tension. Force generated by the quadrato-pectoralis muscles is transmitted directly to the mandible, creating a powerful bite with the jaws in full occlusion. Desmognathines use an efficient static pressure system for subduing and/or killing prey items held in the jaws, not a kinetic-inertial mechanism, as previously suggested. *Leurognathus* exhibits a behaviour ('head-tucking') unique to desmognathines that is consistent with the static-pressure hypothesis. Several desmognathine features (1, 2, 5, 7, 9) are not explicable as adaptations for feeding; these function as locomotory specializations for burrowing, especially for wedging under rocks within and alongside streams. Desmognathines use head-tucking during such wedging and burrowing movements, thus locomotory specializations act in concert with the feeding specializations. We suggest that origin of the atlanto-mandibular ligaments can be considered a 'key innovation' in that it allowed the secondary invasion of stream habitats by adults of ancestral desmognathines.

ADDITIONAL KEY WORDS:—Urodela – Desmognathinae – feeding – locomotion – burrowing – morphology – evolution.

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INTRODUCTION

The Desmognathinae comprises three genera of unusual plethodontid salamanders. *Desmognathus* Baird, 1880, *Leurognathus* Moore, 1899 and *Phaeognathus* Highton, 1961. The distinctiveness of this subfamily was emphasized historically by its elevation to familial status (e.g. Cope, 1869, 1889; Smith & Taylor, 1948; Soler, 1950), but current consensus includes it within Plethodontidae (e.g. Dunn, 1926; Wake, 1966; Regal, 1966; Lombard & Wake, 1986; Duellman & Trueb, 1986). This disagreement has remained purely taxonomic; no worker has doubted the monophyly of Desmognathinae nor its sister relationship with the plethodontine plethodontids.

The principal basis for both the taxonomic disagreement noted above and the strong confidence evinced in desmognathine monophyly is the shared presence in this group of a uniquely derived suite of morphological characters. These include the following: (1) heavily ossified and strongly articulated skull and mandible; (2) streamlined, flat, wedgelike head profile; (3) stalked (pedunculate) occipital condyles; (4) modified atlas; (5) modified anterior trunk vertebrae; (6) atlanto-mandibular ligaments; (7) hypertrophied dorsal spinal muscles; (8) hypertrophied quadrato-pectoralis (gularis) muscles; and (9) hind limbs relatively larger than forelimbs.

The morphological manifestations of these characters have been dealt with by a number of workers (see below), most comprehensively by Wake (1966). These authors are remarkably uniform in their accounts. In contrast, the functional significance of the characters remains uncertain and is the source of some contention. In particular, recent functional analyses of salamander feeding have challenged earlier conclusions based on morphological inference (Eaton, 1957; Larsen & Guthrie, 1975; Dockx & de Vree, 1986; Dalrymple, Juterbock & La Valley, 1985; Larsen & Beneski, 1988). Furthermore, most workers have dealt with a limited subset of salient characters, while other have assumed *a piori* that all are functionally related and, therefore, shaped by a single cause. Lastly, there has been general confusion regarding the *function* of a feature versus its *biological role* (Bock & von Wahlert, 1965). Consequently, some disagreements in the literature reflect differing conclusions about biological role (e.g. feeding vs

burrowing) based on essentially similar functional conclusions (e.g. increased cranial dorsoflexion).

In this paper we review the morphology of the characters in question and the history of ideas regarding their functional and biological interpretation. We present new functional data on feeding in *Leurognathus marmoratus* that bear directly on these issues, and we analyse these data in light of previously published hypotheses.

MORPHOLOGICAL CHARACTERS

Heavily ossified and strongly articulated skull and mandible

Soler (1950), Wake (1966), Hinderstein (1971). The skull and particularly the mandible is heavier and more solid than in plethodontine species. In general, skull bones are thicker and more closely articulated. The suspensoria are ossified much more extensively in desmognathines than in plethodontines and bony articulations are broader and firmer. For example, left and right parietal bones interlock by means of numerous finger-like projections along their articulating surfaces. The parietal and squamosal articulate tightly by means of a tongue-and-groove joint. These types of articulations are unusual among salamanders. The premaxillae are particularly massive; their frontal processes are fused, leaving only a small internasal fontanelle which is lost entirely in some old individuals. The processes are broad and only slightly narrower than the premaxillary tooth row, and the palatal shelves are broader and better developed than in any plethodontine. The parasphenoids are uniquely hypertrophied in desmognathines. They are broad posteriorly, with large posterolateral processes that extend to an articulate with the quadrates. This morphology is diagnostic of the Desmognathinae. The prefrontals are absent as discrete elements, allowing for a broad and solid articulation between the maxilla and frontal. The frontal has a large, bony process that extends into the antorbital region and apparently strengthens the skull in the region between the vomer and the frontal-maxilla. Cope (1869) found the ossified antorbital to be so striking that he used it as a diagnostic character for his Desmognathidae. The dentaries are large, massive, and broad ventrally. The Meckelian grooves are nearly closed and the dentary encases the prearticulars.

Flat, wedgelike head profile

Soler (1950), Wake (1966). In lateral view the head of desmognathines is flat and wedgelike. The dorsal surface of the skull is flat, smooth and devoid of muscles, which have shifted their origins lateroventrally relative to plethodontines. Some parts of the adductor musculature (e.g. the adductor mandibulae anterior) lie in a deep groove or trough. The dorsolateral margins of the skull are ridgelike. Vomerine vaulting is absent or reduced.

Stalked occipital condyles

Dunn (1926), Noble (1927, 1931), Soler (1950), Wake (1966), Hinderstein (1971). The occipital condyles of all non-desmognathine salamanders are 'sessile', i.e.

not particularly prominent and attached to the occiput by a relatively broad base. In contrast, desmognathine condyles are 'stalked', or 'pedunculate'. They protrude from the occiput on relatively lengthy processes, thereby increasing the distance between the skull and the atlas.

Modified atlas

Dunn (1926), Noble (1927, 1931), Soler (1950), Wake (1966), Hinderstein (1971).
The desmognathine atlas is modified in several ways. It is raised above the level of the trunk vertebrae and its centrum lies at a small angle relative to the longitudinal axis. The atlas has a large, raised, transverse ridge across the posterior end of the neural arch that receives the atlanto-mandibular ligaments (see below) on its anterior aspect. The condylar facets are enlarged and the odontoid processes greatly reduced. These do not fit into the foramen magnum as in other salamanders.

Modified anterior trunk vertebrae

Soler (1950), Wake (1966), Worthington & Wake (1972), Hinderstein (1971). The anterior trunk vertebrae in desmognathines differ in two ways relative to other plethodontids. The first three trunk vertebrae are especially robust (at least in *Desmognathus*), having greater mass and width than more posterior vertebrae. Second, the first three to ten trunk vertebrae have accessory processes (pterygapophyses) arising from the dorsal surfaces of the postzygapophyses.

Atlanto-mandibular ligaments

Dunn (1926), Noble (1927; 1931), Soler (1950), Wake (1966), Hinderstein (1971), Dalrymple et al. *(1985), Larsen & Beneski (1988).* The most often described peculiarity of desmognathine cranial anatomy is the presence of stout ligaments that run from the posterodorsal transverse ridges of the atlas (see above), across the atlanto-occipital joint, to the coronoid processes of the mandible. The ligaments lie in deeply concave, longitudinal troughs in the parietal and otic bones. These parietal-otic troughs are also unique to desmognathines. They form a distinct posterolateral aspect of the parietal that is separated from the flat, smooth anterior portion by a ridge.

The atlanto-mandibular ligament is associated with the superficial portion of the adductor mandibulae anterior (the temporal muscle of earlier workers). The precise nature of this association has never been described, to our knowledge. Dunn (1926: 45) noted only that 'the atlas slip of the temporalis is tendinous in *Desmognathus* and *Leurognathus*', a description reiterated by Noble (1927: 6). Soler (1950: 469) wrote that fibres of the adductor 'encircle' the ligament, whereas Hinderstein (1971: 471) reported the ligament 'enclosed' by the muscle. It is probable that ancestrally the ligament was directly associated with the adductor muscle and was, in fact, its tendon, lacking any connection to the atlas. Such an incipient condition is retained in some non-desmognathine salamanders (Dubecq, 1925; Francis, 1934; Baird, 1951; Wake, 1966; Caroll & Holmes, 1980). The brief descriptions noted above suggest that the atlanto-mandibular ligaments are anatomically and therefore, functionally, independent of any

surrounding musculature (see fig. 9 in Wake, 1966, and fig. 8 in Larsen & Beneski, 1988).

The ligament is histologically typical of most tendons and ligaments in comprising collagen fibres almost entirely with no evidence of elastin (Dalrymple *et al.*, 1985).

Enlarged dorsal spinal muscles

Wake (1966), Hinderstein (1971), Worthington & Wake (1972). Particularly well-developed dorsal spinal muscles characterize desmognathine salamanders. These originate from the dorsal surfaces of the anterior trunk vertebrae, notably including the pterygapophyses described above. Insertion is on the back of the skull extending from the otic crests posteriorly to the parietal bone anterior to the parietal-otic trough.

Enlarged quadrato-pectoralis muscles

Piatt (1935), Soler (1950), Eaton (1937, 1957), Wake (1966), Hinderstein (1971). Worthington & Wake (1972). This muscle [called the gularis by Eaton (1937, 1957) and some others] originates on the pectoral fascia and skin of the gular fold. It inserts onto the quadrate and articular bones, and fascia of the depressor mandibulae and adductor musculature. In the resting animal, the bulge of this muscle on the ventrolateral aspect of the head and neck is so apparent that it creates what Piatt (1935: 222) referred to as 'the characteristic *Desmognathus* "profile" '. The muscle is so-enlarged in all desmognathines.

Hind limbs relatively larger than forelimbs

Wake (1966). In all three desmognathine genera there is a disparity in size between the forelimbs and the hind limbs. This size disparity, reflected in limb length and to a lesser extent, limb robustness, is pronounced in *Desmognathus* and *Leurognathus*. In *Phaeognathus*, all four limbs are secondarily reduced, but the hind limbs remain larger than the forelimbs. The developmental basis of this disparity is complex; forelimb size is smaller than expected, but it is not certain that hind limb size is larger than expected (Wake, unpublished data).

REVIEW OF PUTATIVE FUNCTION AND BIOLOGICAL ROLE

An historical review of ideas relating to desmognathine cranial and cervical function and biological role is presented in Table 1. Note that the distinction between 'function' and 'biological role' is our own, none of the studies cited here differentiated between them explicitly. Hinderstein (1971) and Larsen & Beneski (1988) distinguished between purely functional hypotheses and presumed 'selective forces'. The distinction is worth making because conclusions regarding biological role of anatomical features in the absence of experimental and/or natural history data are subjective, and as such, difficult to falsify. In contrast, purely functional conclusions regarding mechanical attributes of the system are more easily tested, either experimentally or theoretically. As a consequence, disagreements have arisen regarding the adaptive significance of desmognathine

TABLE 1. An historical review of hypotheses relating to the function and biological role of desmognathine salamander specializations. Distinctions between function and biological role are mostly our own. Character numbers refer to the morphological characters listed at the bottom of the Table and discussed in the text

Source	Characters	Proposed functions(s)	Proposed biological role
Dunn (1926)	3, 4, 6	1. Mandibular depression prevented 2. Skull raised to open mouth 3. Downward bending of head prevented 4. Anterior body stiffened	Burrowing
Noble (1927, 1931)	3, 4, 6	1. Mandibular depression limited 2. Skull raised to open mouth fully 3. Head strengthened	Burrowing
Eaton (1957)	3, 4, 6–8	Increase in head-raising muscle leverage	None specified
Wake (1966)	1–9	1. Mandibular depression limited 2. Skull raised to open mouth 3. Cranio-atlantal flexibility increased for skull elevation 4. Anterior body stiffened	1. Burrowing 2. Locomotion (streamlining)
Brodie (1978) Brodie et al. (1989)	None specified	Increased bite force	Predator repulsion
Hinderstein (1971)	1, 3–7	1. Mandibular depression limited 2. Skull raised to open mouth fully 3. Cranio-atlantal flexibility increased 4. Mandible held against quadrate 5. Increased head weight	1. Feeding 2. Burrowing
Worthington & Wake (1972)	3–8	1. Mandibular depression limited 2. Head used as wedge 3. Head dorsoflexion for substrate pushing	Burrowing
Dalrymple et al. (1985)	1, 2, 6, 8	1. Increased bite force by means of elastic energy storage and increased cranial inertia 2. Increased bite force and jaw-locking through cranial depression 3. Jaws held firmly closed 4. Head used as wedge 5. Head dorsoflexion for substrate pushing	1. Feeding 2. Burrowing
Larsen & Beneski (1988)	6	1. Mandibular depression limited 2. Increased bite force	1. Feeding (2. Burrowing) (3. Predator repulsion) (4. Courtship)

Characters:
1. Robust skull and mandible
2. Flat, wedgelike head profile
3. Stalked occipital condyles
4. Modified atlas
5. Modified anterior trunk vertebrae

6. Atlanto-mandibular ligaments
7. Enlarged dorsal spinal muscles
8. Enlarged quadrato-pectoralis muscles
9. Relatively larger hind limbs

specialization even in the light of identical functional conclusions. For example, nearly every study has concluded that mandibular depression is to some extent limited in desmognathines, but these studies are almost equally divided between burrowing and feeding as the biological role of choice for such a mechanism.

Cope (1889) called attention to several desmognathine cranial specializations, noting the 'peculiar' morphology of the adductor musculture and its tendons, the occipital condyles, and the strengthened skull bones. He believed that these features enabled *Desmognathus* 'to burrow among stones and in earth more readily than the species of other genera' (p. 196).

Dunn (1926) noted the presence of the atlanto-mandibular ligaments, modified atlas and stalked condyles, and considered them diagnostic of Desmognathinae. He regarded them as a cohesive suite of characters and was the first to relate them to a specific functional hypothesis, as well as a biological role: 'Thus the lower jaw is immovably attached to the atlas, and the mouth is opened by raising the skull. The function of this arrangement, with which is connected the stalked condyles, and collared atlas of these forms, is to prevent the downward bending of the head, and to stiffen the anterior part of the body' (p. 45), 'so that it can be forced under things' (p. 59). Noble (1927, 1931) agreed with Dunn (1926) except that he found that some mandibular depression was possible.

In contrast, Eaton (1957) rather vigorously disagreed with both Dunn and Noble. He dissected a single *Desmognathus quadramaculatus* and found that the adductor muscle was only 'partly tendinous', though his description suggests that his specimen might have been a juvenile. In any case, Eaton's (1957) electrical stimulation of the superficial muscles in an anaesthetized individual led him to dismiss Dunn's (1926) hypothesis of an immobile mandible; he further concluded that the mechanism of head elevation was identical in non-desmognathine salamanders and believed that desmognathines differed from other species in certain attributes only in degree. To these differences he ascribed no particular function or biological role other than an increase in leverage for head-elevating muscles.

Wake (1966) reviewed the morphology of the Desmognathinae and other plethodontids and described all of the putative spcializations noted in this paper. For the most part Wake (1966: 47) agreed with Dunn (1926) in characterizing desmognathines as a group of salamanders with 'a unique mouth opening mechansism by means of which the mandibles are held relatively rigid and the skulls proper are raised [as well as having] extensive skeletal and muscular modifications related to functional changes in mouth opening mechanics'. However, Wake (1966: 57) also accepted Noble's (1927, 1931) findings in emphazing that, 'The mandibles are far from immobile in desmognathines'. He further agreed that the anterior part of the body would be stiffened, but that the atlanto-occipital joint is more flexible than in plethodontines. Wake (1966) did not attribute the mechanics of mouth opening to any particular biological role; however, he regarded the wedge-shaped, robust desmognathine skull and mandible, hypertrophied dorsal spinal muscles, and relatively larger hind limbs as adaptations for burrowing.

Hinderstein (1971) more or less reiterated Wake's (1966) functional conclusions, although he stated explicitly several hypotheses regarding the function of the atlanto-mandibular ligaments (Table 1). He departed from

Wake's (1966) views, however, in concluding that the unique desmognathine
mechanism is an adaptation for feeding. Specifically, he envisioned these
salamanders feeding on the bottoms of fast-moving streams, anchored there by
their massive crania. Resting with their mandibles on the stream bottom would
then necessitate mouth opening by cranial elevation. He ascribed a secondary
role for this mechanism to burrowing.

Worthington & Wake (1972: 275–276) succinctly described a specific
mechanism whereby the desmognathine morphology might be used in
burrowing: 'A stout ligament extends from the atlas to the mandible, restricting
the downward motion of the mandible. Strong throat muscles pull the head
down to the point at which the temporal [atlanto-mandibular] ligament
becomes taut, and the head, bent sharply downward, is used as a wedge by the
organisms, to allow them to squeeze under rocks and into burrows. In order to
function effectively, the head must be raised, and this task is accomplished
mainly by the dorsal spinal muscles, which are greatly hypertrophied in
desmognathine salamanders'. These conclusions were based on observations of
living desmognathines.

Two recent studies have examined experimentally the role of the atlanto-
mandibular ligaments. Dalrymple et al. (1985) and Larsen & Beneski (1988)
both studied feeding in *Desmognathus*. Dalrymple et al. (1985) discovered that
immediately after lingual ingestion, the salamander often assumed a so-called
'head-tuck' posture in which the entire head was ventroflexed with the mouth
shut. Occurrence of this behaviour was significantly correlated with the size of
the prey item and its position in the mouth after ingestion. Salamanders were
more likely to head-tuck if prey protruded from the jaws after ingestion.
Electromyographic recordings showed the quadrato-pectoralis muscles to be
active during head-tucking. They found that the head was elevated during
mouth opening by the dorsal spinal muscles and presented circumstantial
evidence suggesting a large bite force in *Desmognathus*. They concluded that the
desmognathine jaw mechanism is specialized as a kinetic-inertial mechanism,
sensu Olson (1961), arguing that such a mechanism would confer a more
powerful bite owing to two factors: (1) the atlanto-mandibular ligaments,
stretched during jaw opening, would store elastic strain energy; this energy
would be released during jaw closure by elastic recoil of the ligaments;
(2) increased mass of the skull and mandible. By increasing mass and
acceleration of the jaws relative to other salamanders, bite force would be
increased $(F = ma)$. A secondary conclusion was that the atlanto-mandibular
ligaments would also be stretched during head-tucking and that these would
help to keep the jaws closed while applying static pressure to large or active prey.
These functional conclusions led Dalrymple et al. (1985) to propose that
desmognathines are adapted to eat relatively larger prey, but they noted
anecdotally that head-tucking, followed by skull dorsoflexion, also occurs during
burrowing. Therefore, they did not rule out burrowing as a factor in the
evolution of this mechanism.

Larsen & Beneski's (1988) high-speed cine analysis of feeding in *Desmognathus*
showed that mandibular depression is restricted, but not stopped, by the atlanto-
mandibular ligaments. They also showed that cranial elevation contributes
significantly to gape during mouth opening, but pointed out that this is true in
other, non-desmognathine salamanders as well. They concluded that cranial

dorsoflexion during mouth opening is 'independent of any peculiar morphological adaptations' (p. 1309) and concurred with the principal conclusions of Dalrymple *et al.* (1985). Larsen & Beneski (1988) suggested that functional aspects of desmognathine head and neck mechanics differ only in degree, and possibly efficiency, from other salamanders, agreeing in this sense with Eaton (1957). They went on to note that no consensus had emerged regarding the biological role of the desmognathine specializations, but suggested four possibilities: feeding, burrowing, predator repulsion and courting. They concluded that the primary selective force shaping this structural complex was that it allowed an increase in bite force without a concomitant increase in head and body size. 'Improvements' in the other biological roles were viewed by these authors as secondary to that of feeding.

PREY PROCESSING IN *LEUROGNATHUS MARMORATUS*

Background and methods

The genus *Leurognathus* comprises a single species, *L. marmoratus*. It is a fully aquatic salamander inhabiting sandy and rocky bottom pools of Appalachian Mountain streams in the south-eastern United States (Pope, 1924, 1928; Dunn, 1926; Pope & Hairston, 1947; Hairston, 1949; Martof, 1962). It feeds primarily on aquatic insects and the aquatic larvae of terrestrial insects (Martof & Scott, 1957).

Remarkably, *Leurognathus marmoratus* utilizes a fundamentally terrestrial feeding mechanism (tongue projection) when feeding under water (Schwenk & Wake, 1988, and in preparation). We observed feeding in 22 captive specimens over a period of several months. Specimens fed readily on waxmoth larvae (*Galleria mellonella*) dropped into the water and less readily on earthworm segments. Two specimens were induced to feed in a small, plexiglass filming chamber filled with water. These were filmed at 50 frames per second (measured) with a Bolex 16 mm cine camera and synchronized stroboscopic illumination (Helmuth-Chadwick). Nineteen feeding sequences were filmed. Of these, seven sequences were complete, including ingestion, intra-oral transport, and deglutition [see Bramble & Wake (1985) and Schwenk & Throckmorton (1989) for discussions of vertebrate feeding stages]. Ten additional sequences included ingestion and at least the first part of intraoral transport, and the remaining two sequences included lingual ingestion only. Films were analysed frame by frame on a Vanguard motion analyser. Still 35 mm photographs were produced from individual 16 mm cine frames (Fig. 1); tracings and measurements were made directly from the motion analyser screen.

Prey processing in Leurognathus

Lingual projection and prey capture (ingestion) in *Leurognathus* is similar to that reported for *Desmognathus* Larsen & Beneski, 1988) with the exception that the entire feeding sequence occurs under water (Schwenk & Wake, 1988). Importantly, the feeding cycles of *Leurognathus* and *Desmognathus* are similar in most essentials to feeding in a variety of other lingual-feeding salamanders (e.g. Larsen *et al.*, 1989; Reilly & Lauder, 1989, 1990; Miller & Larsen, 1990).
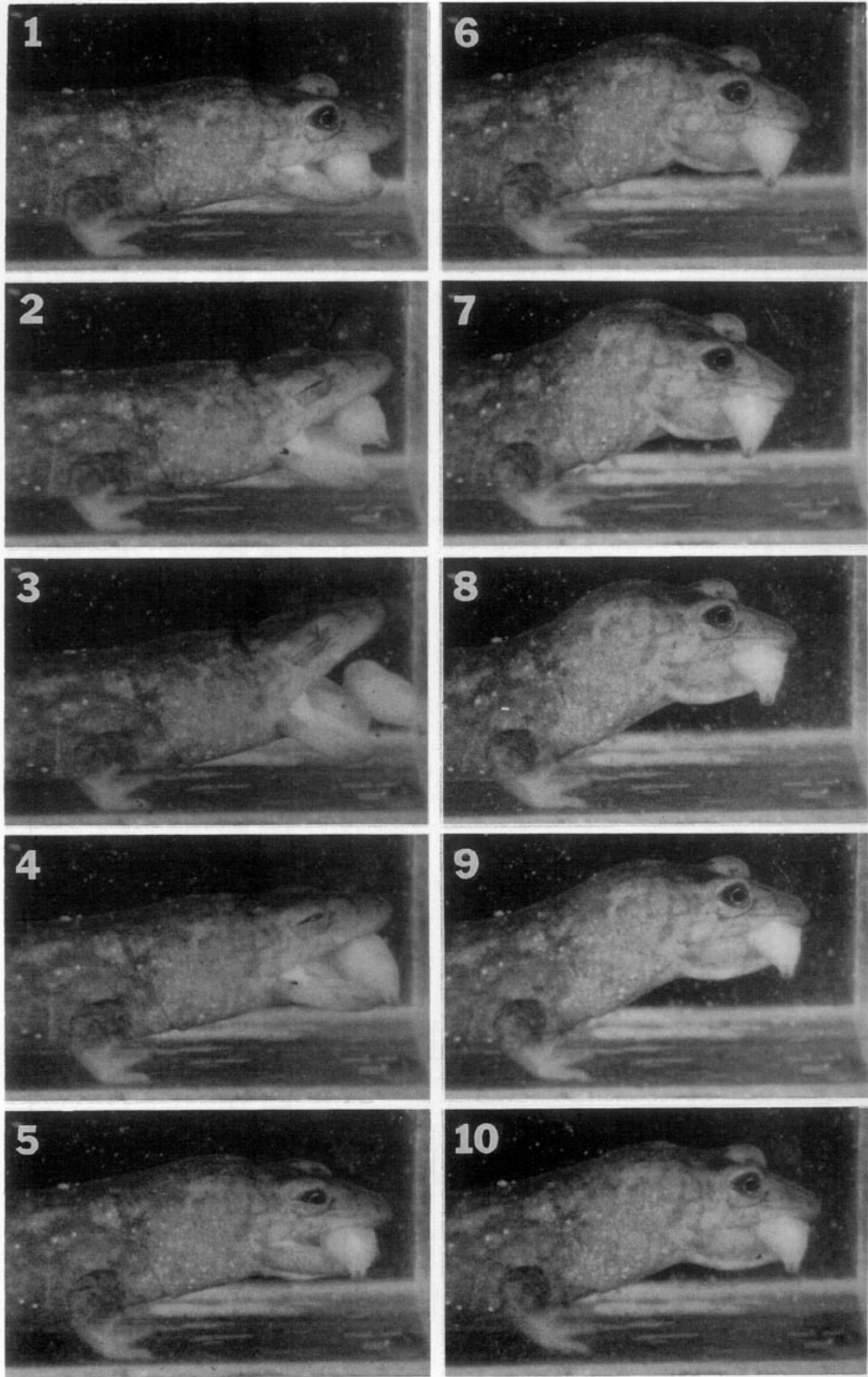
However, one conspicuous difference was found in the feeding cycle of *Leurognathus* as compared with other salamanders: the occurrence of sharp, rapid cranial ventroflexion(s) immediately following ingestion (Figs 1, 2). This behaviour appears to be identical to that reported in *Desmognathus* by Dalrymple *et al.* (1985) and called by them 'head-tucking' (see above). The behaviour involves strong ventroflexion of the cranium at the atlanto-occipital joint anywhere from one to 13 times after prey capture, but always preceding intra-oral transport proper. In most cases the mouth is opened wide before the head tuck, principally by cranial elevation. The head tuck is then initiated as the jaws close in a rapid bite. In some cases, a bite does not precede the head-tuck (e.g. Fig. 2). In these instances, the jaws are only slightly parted at the start of the head-tuck owing to the presence of the prey item between the upper and lower tooth rows (see below). As the head-tuck progresses, gape is decreased until full jaw closure is achieved at maximum cranial ventroflexion. The head is then elevated and as this occurs the jaws part again, seemingly from elastic recoil of the body of the prey item. The head-tucking sequence, with or without a bite, is then usually repeated.

Head-tucking occurred in nine of 16 analysable feeding sequences and was significantly correlated with the presence of the prey item between the teeth ($\chi^2 = 8.96$; $P < 0.003$; df $= 1$); indeed, in only one case did a salamander fail to head-tuck when the prey item came to be held between the teeth after ingestion. In that sequence the waxworm was transported and swallowed immediately following capture. In two cases, the waxworm was initially held within the mouth but was promptly transferred by the tongue to a position between upper and lower anterior tooth rows. Only then was head-tucking initiated. In six other cases the waxworm was brought wholly within the mouth after prehension and transported for swallowing directly, without further manipulation and without head-tucking. Following head-tucking, a series of hyolingual transport movements is initiated [never inertial transport as stated by Dalrymple *et al.* (1985); see also Larsen & Beneski (1988)] and the prey is swallowed.

DISCUSSION

We believe that most studies have been hindered in their functional analyses to a greater or lesser extent because they have assumed, *a priori*, that all

Figure 1. *Leurognathus marmoratus*, a desmognathine plethodontid salamander, exhibiting a bite and single head-tuck following ingestion of a waxmoth larva. Photos from consecutive frames of a 16 mm cine film shot at a measured rate of 50 fps. Sequence filmed with the salamander completely submerged in water. The salamander is motionless at the start of the sequence (frame 1). Note that the larva is held between the tooth rows and that the jaws are held apart by the thickness of its body. Also note the nearly flat resting angle between the cervical and cranial axes, indicating that the head is only slightly bent at the atlanto-occiptal (A-O) joint). During the bite, maximum gape is achieved by elevation of the cranium and depression of the mandible while the worm remains adherent to the tongue (frames 2 and 3). Jaw closure occurs in frames 4 and 5. At the moment of upper jaw contact with the prey item (frame 5), cranial ventroflexion (VF) is initiated at the A-O joint. As VF proceeds, the A-O angle is further decreased by dorsal bending of the cervical vertebral axis until maximum cranial VF (minimum A-O) angle is achieved by frame 7. Subsequently (frames 8–10 and beyond), VF slowly decreased until the resting position is again attained. Note that at the beginning of the head-tuck sequence (frame 6), upper and lower tooth rows are in contact and the worm is effectively crushed. Additional VF serves to increase the force of this bite, a static-pressure system (see text). Head-tucks are usually repeated, with or without a preceding bite.
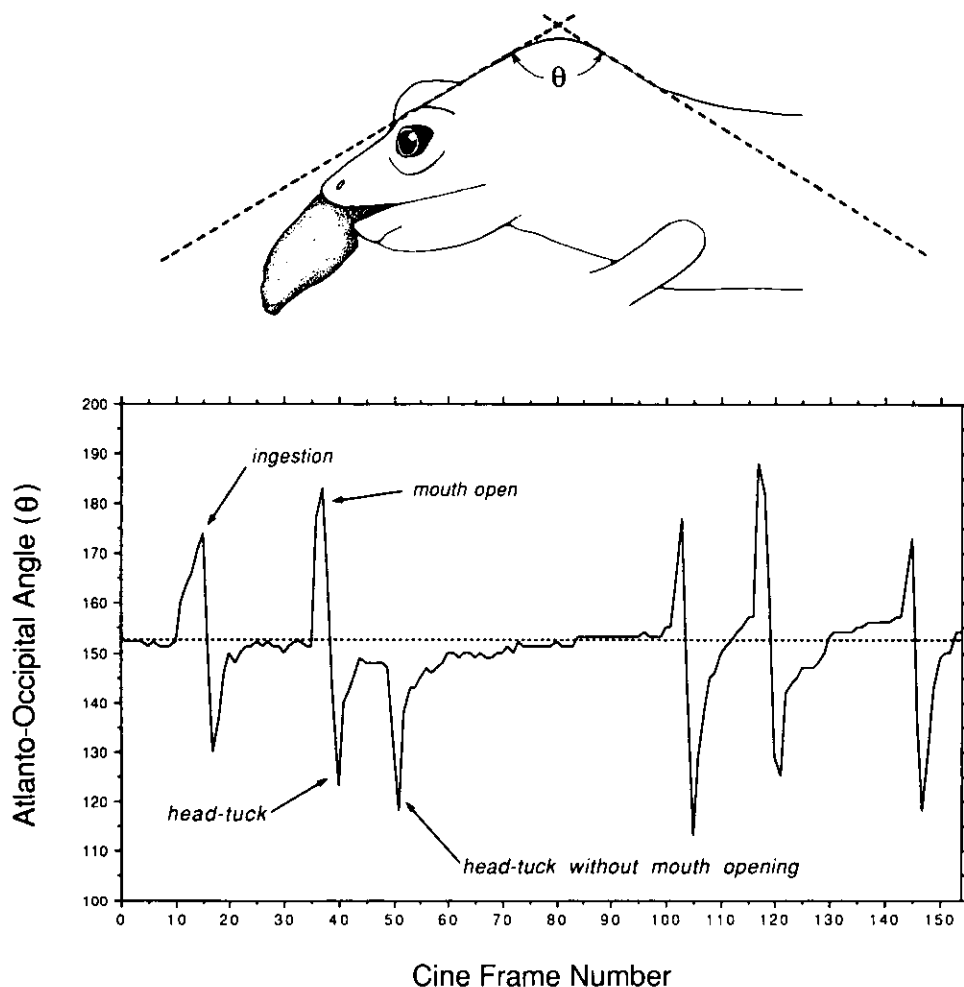
Figure 2. Plot illustrating changes in the angle between the vertebral axis and the cranium (atlanto-occiptal angle, θ, illustrated above the plot) for an ingestion (prey capture) sequence and six subsequent head-tucks in *Leurognathus marmoratus* feeding underwater. A-O angle was measured manually from tracings made on a motion analyser screen from 16 mm cine film. Frame rate measured at 50 fps. A decrease in θ represents cranial ventroflexion, or head-tucking. Note the rapidity of the head tucks (c. 40 ms duration) and the relatively slower decay to the rest position. It is likely that return to the rest position is caused by elastic recoil of the atlanto-mandibular ligaments, and not muscular action, although we have no direct evidence of this. Also note that head tucks occur in the absence of inital jaw opening, with the upper and lower jaws already in contact. In these instances a kinetic-inertial mechanism cannot possibly be operating (see text). Slight deviations evident in θ undoubtedly reflect measurement error, which was determined to be $c. \pm 1°$.

desmognathine morphological modifications are functionally related in some way. We suggest that there are at least two forces shaping desmognathine head and neck morphology. Thus we believe that four characters must be considered independent of the others in a purely functional sense: stalked occipital condyles; modified atlas; atlanto-mandibular ligaments; and hypertrophied quadrato-pectoralis musculture. These characters can be explained as a functional complex operating in the context of feeding. The remaining five characters [robust (massive) skull and mandible; flat, wedgelike head profile;

hypertrophied dorsal spinal muscles; modified anterior trunk vertebrae; and relatively larger hind limbs] probably act in concert with this functional complex, but in the context of head-first burrowing.

Desmognathine specialization and feeding

Early hypotheses of mandibular fixation or significant restriction in desmognathines (Table 1) have been falsified by recent cinegraphic studies (Larsen & Beneski, 1988; Larsen *et al.*, 1989; this study). Dunn's (1926) suggestion that downward bending of the head would be prevented by the atlanto-mandibular ligaments has been rejected. Indeed, cranial ventroflexion is a striking feature of the desmognathine feeding mechanism (see below). In contrast to previous suggestions, several studies have now shown that cranial elevation during mouth opening is ubiquitous among salamanders, not unique to desmognathines and, therefore, cannot be associated with desmognathine specialization (Larsen & Guthrie, 1975; Roth, 1976; Lombard & Wake, 1977; Dockx & de Vree, 1986; Larsen *et al.* 1989).

A number of workers have suggested adaptation for increased bite force in desmognathines relative to other salamanders, but evidence is circumstantial: (1) the jaws produce an audible 'snap' when closed (Brodie, 1978); (2) the jaws are used defensively against formidable vertebrate predators such as shrews and snakes, and seem to 'lock' shut (Brodie, 1978; Brodie, Dowdey & Anthony, 1989); (3) earthworm prey are often cut in half when captured (Dalrymple *et al.*, 1985). There are no direct measurements of bite force in desmognathines or any other salamander as far as we know, therefore conclusions regarding *relative* bite force among species are highly speculative.

Dalrymple *et al.* (1985) proposed a kinetic–inertial (K–I) model to account for this putatively larger bite force (see Review, above). Their model is based on the discussion of Olson (1961: 209) who characterized K–I mechanisms in the following way: 'The effective action of the jaw and teeth depends primarily upon forces developed by rapid motion of the lower jaws relative to the upper. Once motion has been initiated, it is the velocity and mass of the jaws that are effective. *The jaws at rest tend to exert little force and in or near occlusal position the forces serve to do little more than hold position*' [italics added]. Support for the K–I model is weak, however. For example, in the discussion of bite force above, only point one is consistent with a K–I mechanism. Point two and probably point three, relate to bite force generated *after* occlusion. Comparative and biomechanical considerations further undermine the case for a K–I system being especially well-developed in desmognathines. Many generalized, non-desmognathine salamanders possess a jaw mechanism that should function as well or better in elastic energy storage during jaw opening. In these species the mandible and atlas are connected by the levator (adductor) mandibulae anterior (superficial portion) and its associated tendon (Baird, 1951; Hinderstein, 1971). This is the muscle *through* which the atlanto-mandibular ligament runs in desmognathines and the tendon from which, presumably, the ligament arose ancestrally. For example, in the plethodontine genus *Pseudoeurycea*, the muscle is 'a heavy, cordlike bundle of fibers, [originating] from a short heavy tendon attached to the neural spine of the atlas' (Baird, 1951: 243). Typically, vertebrate mechanisms using elastic energy storage are just such muscle-tendon systems that exploit the

mechanical properties of both tissues, including the important series elastic component of muscle (e.g. Cavagna, 1970; Cavagna & Citterio, 1974; Cavagna, Heglund & Taylor, 1977). Therefore, isolation of the tendon from the muscle, as apparently occurred in the evolution of the atlanto-mandibular ligament, would confer no advantage to the elastic strain energy storage mechanism already present ancestrally and may, in fact, have limited it. Such isolation would eliminate the elastic muscle component from the atlanto-mandibular linkage, leaving only the highly inelastic ligament. The stiffness of ligament, resulting from the high elastic (Young's) modulus of collagenous tissue (Wainwright *et al.*, 1976), suits it to its usual role in force transmission or movement restriction. We do not disallow the possibility of the desmognathine mechanism functioning in elastic energy storage. Indeed, the inelastic nature of the atlanto-mandibular ligaments might enable them to store energy more efficiently over very small excursion distances and there is no denying the important role of tendon elasticity in vertebrate locomotion (e.g. Alexander, 1984; Dimery, Alexander & Ker, 1986). However, we point out the unusual nature of an isolated, collagenous ligament acting in elastic strain energy storage and emphasize the role of the atlanto-mandibular ligaments in *transmitting force* to the mandible, as it is this function that seems to characterize uniquely the desmognathine salamanders (discussed below).

Our study of *Leurognathus*, as well as observations of Dalrymple *et al.* (1985) on *Desmognathus*, indicate that the one unique behavioural trait characteristic of desmognathine feeding is that of cranial ventroflexion, or head-tucking. It is therefore reasonable to conclude that it is this behaviour that is associated with at least some of the head and neck specializations exhibited by desmognathines. If one accepts that cranial ventroflexion with the mouth closed is the salient feature of desmognathine behaviour, and not cranial dorsoflexion in order to open the mouth (as previously supposed), then the first four morphological characters noted above are easily interpreted: stalked condyles increase the degree of cranial ventroflexion possible at the atlanto-occipial joint by allowing the skull to swing through a greater arc. The force for this ventroflexion is provided by the massive quadrato-pectoralis musculature (Dalrymple *et al.*, 1985). The hypertrophy of these muscles relative to plethodontines reflects their potentially greater force production. Greater force production is also enhanced by the stalked condyles which increase the quadrato-pectoralis moment arm (i.e. its mechanical advantage (Fig. 3). As the skull is ventroflexed at the atlanto-occipital joint the atlanto-mandibular ligaments become taut. The atlas is modified to receive the stout ligaments and to resist the potentially large reaction forces generated at the atlanto-occipital joint. Most importantly, however, the force required to tense the ligaments is provided by the powerful quadrato-pectoralis musculature and not the relatively feeble depressor mandibulae muscles. Recruitment of these large axial muscles would provide much more power to act on the ligaments than would be possible through mandibular depression (or cranial elevation with mandibular stabilization). During cranial ventroflexion, the mandible would be pulled into occlusion with the upper jaw. Thus jaw closure would be accomplished by active depression of the cranium and passive elevation (relative to the cranium) of the mandible through tension in the ligaments. Once the cranium is depressed beyond the rest position, the ligaments must become increasingly taut, even with the tooth rows of upper and
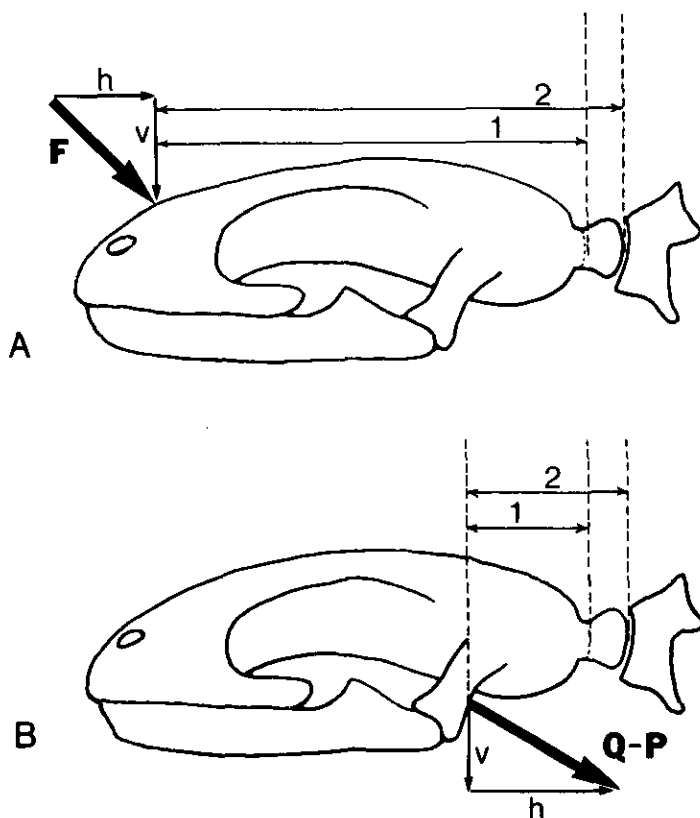
Figure 3. Schematic illustration of a desmognathine salamander skull (lateral view) showing changes in mechanical advantage obtaining from the evolution of pedunculate occipital condyles. A, Pedunculate condyles would increase the mechanical advantage of reaction forces (F) operating against the skull during burrowing. Such forces are divisible into horizontal (h) and vertical (v) components. The vertical component of the force would tend to bend the salamander's head away from the axis, an action highly disadvantageous during burrowing. Its lever arm (2) is greater than would be present with plesiomorphic, sessile condyles (1). Hence pedunculate condyles tend to increase atlanto-occipital flexibility. B, In contrast, a similar increase in the length of the lever arm for the vertical component of the quadrato-pectoralis muscle (Q-P) (2 vs 1) increases the efficacy of this muscle in causing cranial ventroflexion during head-tucking, resulting in increased bite force after jaw closure and the promotion of an effective static-pressure system. Mechanical advantage of the dorsal spinal muscles is similarly improved (see text).

lower jaws in full occlusion. The collagenous ligaments are ideally suited to transmit the full force of the quadrato-pectoralis musculature to the mandible. In this way, an extremely powerful bite force can be generated by recruitment of hypertrophied axial muscles as opposed to the relatively smaller and weaker adductor mandibulae musculature.

Our conclusions differ from those of Dalrymple *et al.* (1985) and Larsen & Beneski (1988) mostly in emphasis; these workers stressed the role of the desmognathine jaw mechanism in producing an effective kinetic–inertial system. While a kinetic–inertial jaw mechanism is to some extent present in the Desmognathinae as in most tetrapods (see above), we do not believe that its development is significantly greater than in plethodontines or other salamanders and, therefore, cannot account for the unusual morphological attributes of the desmognathines. Rather, we believe that this system is an extreme expression of

the alternate mechanism in Olson's (1961: 209) dichotomy, a static-pressure system, in which, 'The primary action results from pressures exerted by the jaws *when nearly closed and initially not in motion*' [italics added]. It is the development of powerful occlusal forces once the jaws are closed and no longer moving relative to one another that uniquely characterizes the remarkable desmognathine mechanism. Indeed, head-tucking in *Leurognathus* sometimes occurs in the absence of mouth opening (Fig. 2). Dalrymple *et al.* (1985) noted this function of head-tucking, but considered it secondary to the K–I system.

Dalrymple *et al.* (1985) and this study have established that desmognathines are unique in the way that they handle prey once captured, immobilizing and possibly killing their prey with a specialized static-pressure jaw mechanism utilizing cranial ventroflexion. There is a precise form-function correlation between the observed behaviour and unique attributes of desmognathine anatomy and mechanical analysis suggests that they are functionally linked. Therefore, we conclude that feeding has been a significant determinant of cranial and cervical specialization in desmognathine salamanders.

Desmognathine specialization and burrowing

While cranial ventroflexion and a powerful static-pressure jaw mechanism account for four desmognathine characters, five others remain unexplained: heavily ossified skull and mandible; flat, wedgelike head profile; hypertrophied dorsal spinal muscles; modified anterior trunk vertebrae; and relatively larger hind limbs. Below, we discuss the biomechanics of head-first burrowing, consider desmognathine morphology in light of this discussion, and note the observational and ecological evidence in support of burrowing as a factor in desmognathine evolution.

Gans (1960, 1974) described three components of head-first burrowing: substrate entry, tunnel extension and tunnel widening. Animals might exhibit all, none, or a subset of these. For example, salamanders might exploit existing crevices and holes in the ground without creating their own. However, existing crevices that are too narrow to permit entry might be widened and possibly extended, or a salamander might create a wholly new tunnel. Exploitation of existing crevices requires no particular specialization, but active burrowing is likely to require some form of morphological and functional modification. Differences among species might reflect differences in the manner and extent to which each activity is performed.

Crevice widening requires the ability to move the substrate to the sides, compacting it and enlarging the opening. Amphisbaenians accomplish this by forcefully moving the snout and head dorsad (spade-snouted forms) or side-to-side (keel-snouted forms; Gans, 1974). In most cases they generate powerful flexion of the head through use of segmental axial muscles acting on the cranium through a tendon.

Tunnel extension and initial substrate entry entail the creation of an opening in solid substrate. In amphisbaenians and other head-first burrowers this is usually accomplished by ramming. Ramming pushes the anterior end of the cranium into the substrate, either displacing it to the sides or compacting it anteriorly. Compaction would be detrimental to subsequent penetrations, hence a skull form that maximizes displacement is advantageous. Gans (1974) noted that a long, slender, pointed cone would be maximally efficient for substrate

penetration, but would be likely to fail; shaping the snout like a wedge is one strategy for strengthening the snout while retaining most of the advantages of a cone. This is the strategy adopted by most amphisbaenians.

Ramming and pushing the substrate must also place significant stress on the skull. Head-first burrowers generally exhibit robust skulls characterized by increased ossification and greater suture complexity. This is true in gymnophione amphibians (Wake & Hanken, 1982; Wake, 1993), amphisbaenians (Gans, 1960, 1974), uropeltid snakes (Gans, 1973), and some burrowing mammals (Hildebrand, 1985; Wake, 1993).

Gans (1960) pointed out that the force required for a given degree of tunnel penetration is proportional to the cross-sectional area of the burrower. Amphisbaenians reduce head and body diameter while maintaining forceful cranial movement by recruiting muscle fibres distributed over several body segments.

Finally, Gans (1974) noted that many amphisbaenians assume a snout-depressed posture when penetrating the substrate. He pointed out that this functionally countersinks the lower jaw so that it cannot be forced open by shear from the substrate. It also serves to concentrate reaction forces to the dorsal surface of the snout which, in amphisbaenians, is variously modified to resist such forces. Furthermore, in such forms further snout depression, resulting from these reaction forces, is resisted by a nuchal tendon joining the dorsal axial skeleton to the cranium.

Burrowing is a compelling explanation for the evolution of desmognathine form because it plausibly relates and explains the remaining five features noted at the outset of this section. The heavily ossified skull and mandible, with their strongly articulated sutures, resist stresses caused by ramming or pushing into crevices. The flat, wedgelike head profile displaces the substrate, minimizing its anterior compaction while maintaining skull strength. The hypertrophied dorsal spinal musculature acts in conjunction with the hypertrophied quadrato-pectoralis muscles to provide powerful dorsoventral flexion of the head for substrate compaction during crevice widening. We note that this behaviour exploits the stalked occipital condyles, which increase the mechanical advantage of these muscles (Fig. 3). The condyles also increase the mechanical advantage of substrate reaction forces, but these could be resisted by the hypertrophied, antagonistic cervical musculature and by assumption of a snout-depressed posture. This posture would serve to accentuate the wedgelike head profile, placing the atlanto-mandibular ligaments in tension and concentrating bending forces onto the top of the snout. Further snout depression would be resisted by the tensed ligaments which would also 'lock' the mandible closed and prevent mouth opening from substrate shear. Furthermore, use of posteriorly placed axial musculature distributed over more than one body segment not only provides more force through recruitment or more fibres, but serves to minimize head diameter and, therefore, the energy necessary for substrate penetration. Finally, the relatively larger hind limbs of desmognathines provide greater thrust for initial ramming, wedging or crevice widening while the smaller forelimbs maintain a reduced cross-sectional area anteriorly. Thrust might also be increased by rapidly straightening an initially flexed, elongate body.

Observational evidence supports our proposed mechanism of head-first burrowing in desmognathines. A number of early workers, including Cope (1889) and Dunn (1926) knew the propensity of *Desmognathus* species to wedge

themselves under objects such as stones. Worthington & Wake (1972: 275–276) observed that *Desmognathus* used head-tucking 'to allow them to squeeze under rocks and into burrows' and noted that this is followed by head elevation. Similarly, Dalrymple *et al.* (1985: 257) commented that desmognathines used head-tucking to 'push substrate with their heavy, flattened skulls in burrowing . . . and then the entire head is dorsoflexed as a wedge for pushing aside substrate'. Brandon (1965: 70) performed simple experiments with *Phaeognathus* and found that, when attempting to penetrate dense soil, his specimens 'repeatedly lifted the posterior part of the head and pushed against the soil with the snout', a clear description of head-tucking. These observations indicate that desmognathines are, indeed, burrowers that utilize head-tucking and dorso-ventral cranial flexion, as outlined above.

Unlike feeding specialization, which seems to be consistent among all desmognathine species, burrowing ability is likely to vary. This variability probably relates to differences in habitat use among genera. For example, *Leurognathus marmoratus* is a fully aquatic species whose burrowing behaviour is restricted to wedging itself under stream-bottom rocks. Martof (1962) noted that *Leurognathus* prefers rocky to sandy stream bottoms. In contrast, *Phaeognathus hubrichti* is fully terrestrial and is known to burrow actively in soil (Brandon, 1965; Wake, unpublished data). Species of *Desmognathus* are intermediate in habitat use, but are most often described as 'wedgers', like *Leurognathus* (Dunn, 1926; Noble, 1927; Wake, 1966; Worthington & Wake, 1972).

Because the mechanical requirements of wedging under rocks are probably somewhat different from tunnelling through soil, we might expect intergeneric differences among desmognathines in the degree and nature of specializations relating to burrowing. The preliminary observations noted above suggest that all genera are subjected to ramming forces resulting from wedging (*Leurognathus, Desmognathus*) or substrate entry (*Phaeognathus, Desmognathus?*). Brandon's (1965) observations confirm that, given the right conditions (loose enough soil or an initial starting crevice), *Phaeognathus* is capable of creating its own tunnel. Indeed, *Phaeognathus* is associated with burrows in the field (e.g. Valentine, 1963; Huheey, 1964; Dodd, 1988) and there is morphological evidence suggesting that it is particularly specialized for burrowing (Wake & Schwenk, unpublished).

While feeding and burrowing seem to be the principal biological roles for desmognathine specializations, other, secondary roles are possible. The static-pressure jaw mechanism, for example, benefits the animal in any situation in which a powerful bite would be of use, as in defence against predators (Brodie, 1978; Brodie *et al.*, 1989). The fact that more generalized salamanders lacking such specialization have also evolved powerful bites used in antipredator behaviour (e.g. Noble, 1931; Stebbins, 1951; Wake, 1963; Nussbaum, 1976; Brodie, 1977; Feder & Arnold, 1982) suggests that this was not a significant factor in the origin of this mechanism. One can imagine other scenarios in which the desmognathine jaw mechanism might be useful (intraspecific courtship and agonistic behaviour, for example; see Arnold & Houck, 1982, for discussion of the former), but there is presently no evidence for these.

Evolutionary conclusions

Desmognathines share a suite of uniquely derived characters that are explicable as adaptations serving the complementary roles of feeding and head-

first burrowing. In order to discern evolutionary patterns among these characters it is necessary to consider them in light of a phylogenetic hypothesis. However, salamander relationships have long been controversial (Hecht & Edwards, 1977; Duellman & Trueb, 1986), and new molecular evidence (Larson, 1991) fails to corroborate hypotheses based on morphology, in particular the generally accepted view that Ambystomatidae is the sister group of Plethodontidae. Nor is a robust hypothesis of desmognathine species relationships available at this time. Therefore, interpretation of desmognathine synapomorphies in an historical context is difficult. Nonetheless, some generalizations can be made.

Plethodontine plethodontids are morphologically more similar to any potential outgroups, including ambystomatids, than are desmognathines. Use of the head for crevice-widening and burrowing in soil is widespread among plethodontines and ambystomatids (Heatwole, 1960, and references therein), and is therefore likely to be plesiomorphic. However, the desmognathines appear to be far more proficient in these functions than other taxa and they are particularly effective in wedging head-first into the bottoms and sides of rocky streams. The morphological features enabling these behaviours, however, also contribute directly to the unique desmognathine mechanism of immobilizing and processing prey, once captured. Central to both roles is the presence of the atlanto-mandibular ligaments, which may be viewed as a key innovation in desmognathine evolution. However, in the absence of a robust phylogenetic hypothesis and any intermediate form, we are unable to argue convincingly for the primacy of either feeding or burrowing in the adaptive evolution of desmognathine salamanders.

By 'key innovation' we mean a trait that allowed desmognathines to exploit a new adaptive zone relative to their ancestors (*sensu* Baum & Larson, 1991). Although Wake (1966) argued that desmognathines retained the ancestral adaptive zone, new evidence, including use of the tongue in feeding underwater (Schwenk & Wake, 1988) and the several ways in which head mobility has been exapted during desmognathine phylogenesis (this paper), argues for a secondary 'invasion' of stream habitats by adult desmognathines. Beachy & Bruce (1992) argued convincingly that lunglessness evolved as a rheotropic adaptation in stream larvae. In order to test this hypothesis it will be necessary to use a comparative, phylogenetic methodology, such as that advocated by Baum & Larson (1991). The morphological specializations we have described are variably expressed among desmognathine species; mapping these features onto a cladogram might elucidate the historical sequence of character transformations that have led to the highly specialized feeding and locomotor systems of desmognathine salamanders. Such an analysis awaits a well-corroborated phylogeny of Desmognathinae.

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