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Feeding Behavior and the Saddleback Shell of *Dipsochelys arnoldi*

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The term saddleback has been applied to giant tortoises with flattened carapaces with raised apertures. Galapagos giant tortoises (*Chelonoidis nigra*) with this morphology were first described by Porter (1815): “the form of the shell... is elongated, turning up forwards in the manner of a Spanish saddle.” Porter’s observations were based on the extreme saddleback forms from Charles (Floreana) and Hood (Española) islands. The unusual form of the carapace in these taxa was observed by Günther (1877) to be associated with the ability to extend their necks vertically. He also noted the unusual flexibility of the atlas articulation but did not propose any functional explanation for these features. The standard contemporary interpretation of the saddleback morphotype is that it is an adaptation to facilitate browsing (Snow, 1964; Pritchard, 1979; Arnold, 1979; Bour, 1983; Fritts, 1984). It is suggested that the high aperture of the shell enables the tortoise to stretch its long neck upwards to reach leaves on shrubs and trees, combined with a reduced plastron to allow a general increase in agility (Arnold, 1979). This browsing action is reputed to be particularly important in dry habitats where grasses are sparse and shrubs form an important part of the diet (Arnold, 1979). This explanation has also been used to account for the historical presence of saddlebacked forms on Rodrigues Island in the Mascarenes (*Cylindraspis vosmaeri*) (Arnold, 1979). There have also been suggestions that the ability of Galapagos saddlebacks to stretch the neck high may be an advantage in agonistic male rivalry (Fritts, 1984). Observations of aggressive behavior involving the use of the extended neck and head were first recorded by Delano (1817). How these adaptations have manifested themselves behaviorally in Indian Ocean giant tortoises (*Dipsochelys* spp.) have been speculative (Bour, 1984) as saddleback forms there are either extinct or only recently discovered (*D. arnoldi* Bour, 1982).

Giant tortoises of the genus *Dipsochelys* are typically domed animals but do include flattened forms or morphotypes. Bour (1983) observed that Günther intended to describe a specimen of *Dipsochelys arnoldi* as “*Testudo sellaris*” in reference to the resemblance of its carapace to a saddle (*sella*). He further noted that there were close comparisons between the Galapagos and Indian Ocean forms with “*Testudo daudinii*” (*D. arnoldi* and *D. daudinii*) being equivalent to the saddlebacked Galapagos “*T. ephippium*” [= *Chelonoidis nigra abingdonii*]. This point was also noted by Rothschild (1915). The morphology of the saddlebacked

Dipsochelys has been reviewed by Bour (1983, 1984) who concluded that *D. daudinii* should be classed as an “elongated” form and that only *D. arnoldi* is fully saddlebacked.

The discovery in 1997 of 18 living captive Seychelles saddlebacked tortoises, *D. arnoldi* (Gerlach and Canning, 1997, 1998), raised the possibility of investigating the feeding and social behaviors of these animals in order to determine whether the saddlebacked condition is of functional significance in *Dipsochelys*. In a review of *Dipsochelys* (Gerlach and Canning, 1998) a number of skeletal autapomorphies were detected in *D. arnoldi*. These were postulated to be specializations associated with a browsing mode of feeding. The present paper re-examines these characters in the light of new behavioral observations.

There is currently no consensus on the use of generic, subgeneric, and specific names in most giant tortoise taxa. For practical purposes I have considered the three recognizable groups of recent giant tortoises to be distinct genera: *Chelonoidis* (Galapagos), *Cylindraspis* (Mascarenes), and *Dipsochelys* (Seychelles, Aldabra, Madagascar), although all can be considered subgenera of *Geochelone*. Specific names follow Pritchard (1996) for *Chelonoidis*, Bour (1984) for *Cylindraspis*, and Gerlach and Canning (1998) for *Dipsochelys* (including the use of *D. dussumieri* for the Aldabran species rather than the more frequent *D. elephantina* or *Geochelone gigantea*).

Materials and Methods. — This paper follows the anatomical systematic study of all *Dipsochelys* species (Gerlach and Canning, 1998), interpretations of the osteology and musculature follow Walker (1973) and original dissections of *Testudo kleinmanni* and *Geochelone elegans*. Interpretations of muscular actions are based on manipulation of dissected specimens of the above species and supported by observations of feeding and locomotion in captive *D. arnoldi* in Seychelles.

A comparison of feeding and movement in the living *Dipsochelys* species was made by observation of captive *D. arnoldi* ($n = 17$), *D. hololissa* ($n = 8$), and *D. dussumieri* ($n = 20$). All tortoises studied were long-term captives or captive-bred in Seychelles; for most original histories are not known. Although captive conditions varied the distinct morphologies were easily recognizable and any effect of dietary distortion appears to be minimal.

In order to determine whether the saddlebacked *D. arnoldi* is able to reach higher vegetation than the domed *D. hololissa* and *D. dussumieri*, individuals of various sizes were encouraged to stretch upwards to reach fruit. Browsing abilities in the different species were investigated by observing tortoises presented with creepers (*Pueraria phaseoloides* and *Canavalia cathartica*) draped over a 1 m high fence. In addition, 25 randomly timed feeding observations were made on 4 individuals of each species. Each observation was for 1 minute, during which it was noted whether the animal was grazing or browsing.

For each tortoise a series of measurements were made. Initially tortoises were measured at rest, when the following measurements were taken: straight carapace length and

Table 1. Specimens examined in anatomical and behavioral studies. Abbreviations: BM(NH) (P), British Museum (Natural History) (Palaeontology); BM(NH) (Z), British Museum (Natural History) (Zoology); MNHN, Muséum National d'Histoire Naturelle; NPTS, Nature Protection Trust of Seychelles; OUM, Oxford University Museum; UMZ, University Museum of Zoology, Cambridge. CL = straight carapace length.

Species	n	CL (cm)	Specimen numbers or location
Anatomical			
<i>D. dussumieri</i>	20	55-123	BM(NH)(Z) 74.2.62, 1949.1.4.53, 1949.1.4.61-2, 1949.1.4.64, 1949.1.4.65, 1949.1.4.83, 1949.1.5.5, W1/1/R4; MNHN DD61; NPTS 1995.1, 1996.1, 1998.2-4; OUM 1951a-b, 19668-9, 19657, 19642; UMZ R3814, R3812-3
<i>D. hololissa</i>	6	95-138	BM(NH) (Z) 1949.1.4.45, W1-1A/R4/52/B16/334, Tring 184; MNHN 1944.269, 1907.71; UMZ R3796
<i>D. arnoldi</i>	3	73-87.5	BM(NH) (P) R3231; (Z) 74.2.6.6; MNHN 7872
Behavioral			
<i>D. dussumieri</i>	20	25.5-110	Seychelles captives
<i>D. hololissa</i>	8	62-127	Seychelles captives
<i>D. arnoldi</i>	17	59-102	Seychelles captives

aperture height (distance from the ground to the lowest part of the nuchal scute, with the plastron resting flat on the ground). Tortoises encouraged to stretch upwards to reach fruit were measured as follows: height of plastron off the ground during high standing (distance from the ground to the underside of the gulars), height of top of aperture during high standing (distance from the ground to the lowest part of the nuchal), and maximum head height (maximum vertical distance between ground and top of head). All measurements were recorded to the nearest 5 mm. The sizes of the tortoises examined are given in Table 1.

Results. — Osteological specializations of *D. arnoldi* apparently associated with feeding behavior can be found in the skull, forelimb, and carapace. The skull differs from all other *Dipsochelys* in the possession of a raised dorsal surface of the prootic and opisthotic. This results in an inflated otic chamber, a condition otherwise known only from *Gopherus* species (Bramble, 1982). In *Gopherus* the inflated otic chamber is associated with the presence of an otolith (Bramble, 1982), although no such structure has been detected in *D. arnoldi*. The raised dorsal surfaces of the prootic and opisthotic provide enlarged attachment sites for the origin of a branch of the adductor mandibularis muscle (Fig. 1). This muscle inserts on the angular and provides for adduction and retraction of the dentary. The retractive action of this muscle is supported by the geniohyoideus muscle which originates on the hyoid, with a branch from the postero-ventral part of the processus articularis of the quadrate. This muscle has a well-developed insertion on the dentary symphysis where there is a strong, ossified lingual bar (*D. arnoldi* appears to be unique in possessing this character). The combination of the lingual bar and the raised prootic and opisthotic support a strong dentary retraction action of the geniohyoideus. Protraction of the dentary is

provided by the pterygoideus which originates on a ridge on the descending parietal process and inserts on the angular. All these muscles provide a propalinal bite which is used in chelonians to give a grinding action to the jaws. Normally this is a weak action and is only effective in moving food particles deeper into the gape. In *D. arnoldi* the extreme development of the geniohyoideus and pterygoideus provides for very strong propalinal action, resulting in a clean, shearing bite. Comparisons of the biting action of *D. arnoldi* and the grazing congeners *D. hololissa* and *D. dussumieri* reveals that the grazing tortoises are able to pull up grasses with a cropping action but tear leaves by repeatedly biting and shredding off irregular strips of leaf. In contrast, *D. arnoldi* is able to produce a clean bite, enabling large pieces of leaf to be sheared off with a single bite. Thus, *D. arnoldi* is a highly efficient consumer of shrub and tree leaves, rather than primarily a grazer.

The forelimb of *D. arnoldi* is distinctive in having a pronounced curvature to the humerus (Fig. 2a). This provides an enlarged surface area for the attachment of the triceps brachii which originates on the scapula and the dorsal face of the humerus and inserts on the olecranon process of the ulna (Fig. 2c). The action of this muscle is primarily as an extensor of the lower part of the forelimb. It also acts to protract and abduct the humerus across the shoulder joint. The forelimb rotates slightly during abduction and this action is supported by the latissimus dorsi muscle. The latissimus dorsi originates from the inside of the carapace, at a point near the suture of the first and second costal scutes. In *D. arnoldi* there is a characteristic depression at this point,

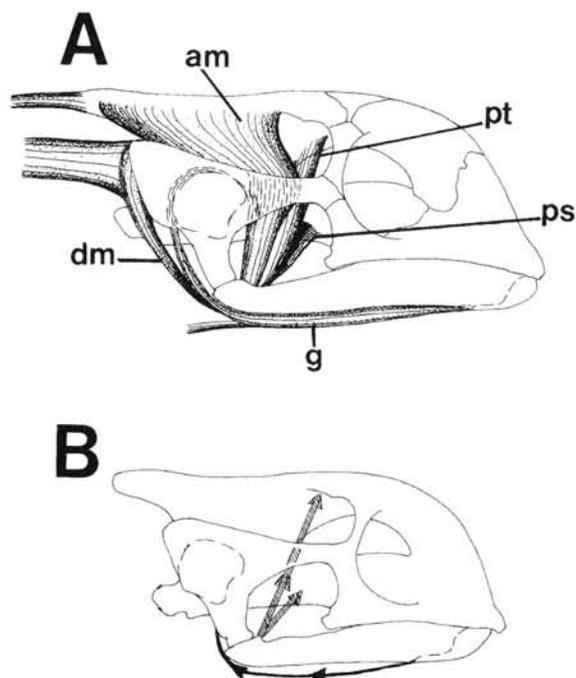


Figure 1. Deep jaw musculature of *D. arnoldi*. **A.** Deep cranial musculature. Key: am = adductor mandibularis; dm = depressor mandibularis; g = geniohyoideus; ps = pseudotemporalis; pt = pterygoideus. **B.** Main jaw forces in the propalinal bite.

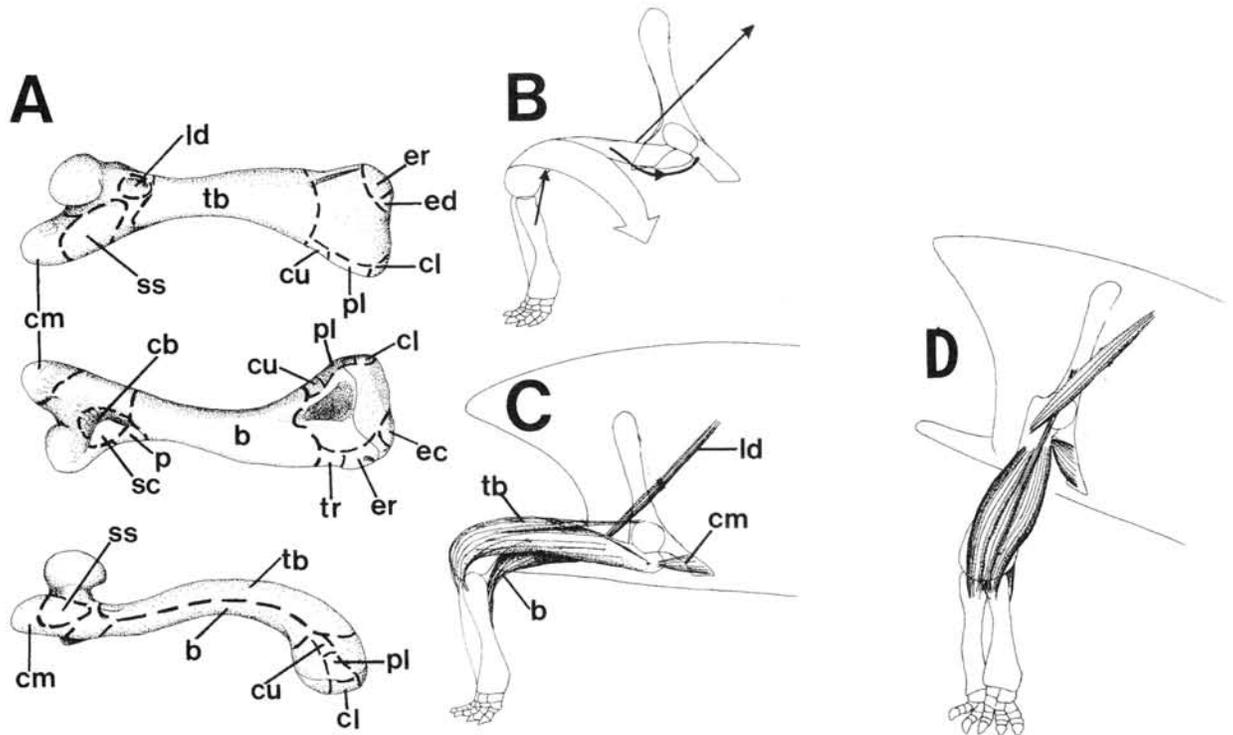


Figure 2. Forelimb action in *D. arnoldi*. **A.** Muscle attachment sites on right humerus: dorsal, ventral, and lateral views. **B.** Main forces in humeral adduction. **C.** Standing forelimb posture, showing main humeral musculature. **D.** Extended forelimb posture. Key: b = brachialis inferior; cb = coracobrachialis brevis; cl = flexor carpi ulnaris; cm = coracobrachialis magnus; cu = flexor carpi radialis; ec = extensor carpi ulnaris; ed = extensor digitorum; er = extensor radialis; ld = latissimus dorsi; p = pectoralis; pl = palmaris longus; sc = supracoracoideus; ss = subscapularis; tb = triceps brachii; tr = tractor radii.

corresponding to an internal bony projection supporting the latissimus dorsi. The insertion of this muscle is on the dorsal surface of the humerus, shortly distal to the humeral head; in *D. arnoldi* there is a distinct pit providing for its insertion (Fig. 2a).

The expanded triceps brachii and latissimus dorsi cause a strong abduction and rotation of the humerus and extension of the lower limb (Fig. 2b), enabling the extended leg to be brought under the body and held straight as the front of the shell is raised during browsing (Fig. 2d). This action results in a high reach which can be sustained for long periods of time.

Observations of the captive animals confirm that *D. arnoldi* is able to browse leaves off high vegetation. During browsing the primary action to reach high vegetation is the raising of the front part of the shell off the ground and the sustained high reaching stance. From a normal standing position with the plastron held horizontally the forelimb is rotated and abducted by the combined action of the triceps brachii and latissimus dorsi (Fig. 2b). This extends and straightens the normally sprawling forelimb and brings it towards the center of the body. The effect of this is to raise the front of the shell and bring the plastron to an angle of 20° from the ground. Instead of stretching the neck upwards to reach leaves it is held at a horizontal level and projected directly forwards (Fig. 3). Once a bite has been taken the propalinal shearing action is accompanied by retraction of

the neck to tear leaves off the plant. At no point is the neck stretched upwards.

In contrast, browsing by the captive dome-shaped tortoises (*D. hololissa* and *D. dussumieri*) was attempted from a resting position, with the neck stretched upwards. The weak propalinal bite combines with the inefficient angle of neck retraction to produce a pulling action. If the vegetation being browsed is a loosely attached creeper this may be sufficient to pull a mass of vegetation to the ground. Branches of shrubs or trees and firmly attached creepers are only



Figure 3. Browsing posture in *D. arnoldi*.

Table 2. Regression statistics.

Variable	Species	Regression	t	d.f.	p	r ²
Aperture height	<i>dussumieri</i>	$y=0.158x+5.600$	6.733	18	<0.001	0.715
	<i>hololissa</i>	$y=0.138x+8.076$	3.727	6	<0.01	0.767
	<i>arnoldi</i>	$y=0.153x+16.054$	14.183	15	<0.001	0.927
Leg length	<i>dussumieri</i>	$y=0.249x-2.789$	12.493	18	<0.001	0.897
	<i>hololissa</i>	$y=0.210x-0.179$	2.636	6	<0.05	0.814
	<i>arnoldi</i>	$y=0.330x+5.077$	3.781	15	<0.002	0.472
Raised aperture	<i>dussumieri</i>	$y=0.332x+8.545$	5.376	18	<0.001	0.616
	<i>hololissa</i>	$y=0.306x+12.206$	4.425	6	<0.01	0.766
	<i>arnoldi</i>	$y=0.128x+44.759$	2.394	15	<0.05	0.108
Head height	<i>dussumieri</i>	$y=0.388x+25.018$	4.191	18	<0.001	0.417
	<i>hololissa</i>	$y=0.533x+13.943$	3.531	6	<0.02	0.148
	<i>arnoldi</i>	$y=0.307x+40.526$	3.528	15	<0.01	0.447

shredded by this action. Wild *D. dussumieri* on Curieuse Island may also browse from a standing position, stretching upwards. This is followed by a downwards pull and neck retraction; effectively the same shredding action as achieved from a resting position (*pers. obs.*).

Comparisons of the measurements of the three taxa demonstrates predictable significant relationships between all measured variables and carapace length (Table 2). T-tests of the regressions found no significant differences between *D. dussumieri* and *D. hololissa* ($p > 0.05$ for both slope and elevation). *Dipsochelys arnoldi* differs from both other species in the elevations of all regressions ($t > 5.02, p < 0.001$ for all cases) but not in slope ($p > 0.05$ for all cases). Compared to the other two species, *D. arnoldi* has a higher aperture (Fig. 4A) ($60 \pm 12\%$ higher than *D. hololissa*, $59 \pm 7\%$ higher than *D. dussumieri*) and is able to raise the

aperture higher (Fig. 4C) ($46 \pm 19\%$ higher than *D. hololissa*, $46 \pm 11\%$ higher than *D. dussumieri*). This is largely a result of the greater leg length when at full stretch (Fig. 4B) ($51 \pm 47\%$ longer than *D. hololissa*, $59 \pm 13\%$ longer than *D. dussumieri*). The fully raised head height is not significantly different (Fig. 4D) (3% on average) as vertical neck extension is not a normal part of feeding in *D. arnoldi*, but does occur in the other two species.

Dipsochelys arnoldi is a highly efficient browser due primarily to its ability to reach the same height as the grazing species, but with its raised aperture allowing retention of strong horizontal neck retraction rather than having to raise the head and neck. It is a browser by preference with all feeding observations being of browsing. For the other species browsing formed only $50 \pm 18\%$ in *D. hololissa* and $22 \pm 17\%$ in *D. dussumieri*.

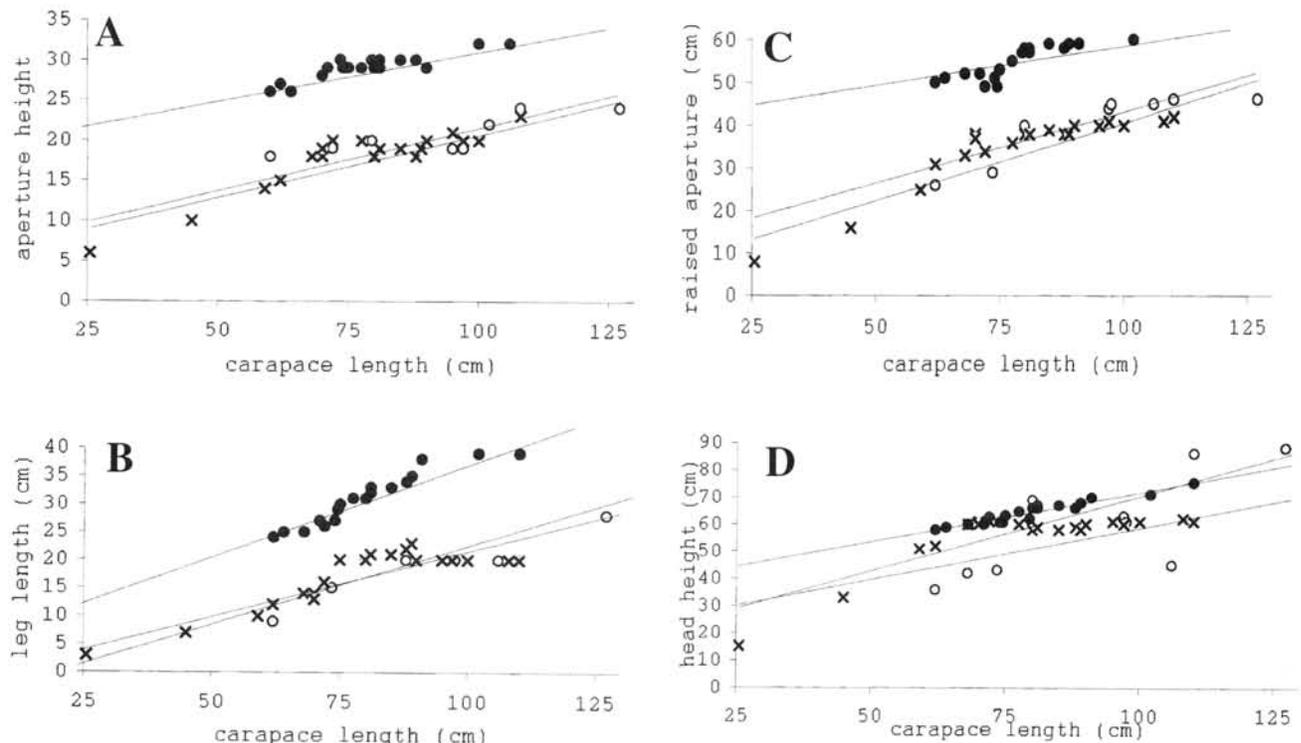


Figure 4. Comparison of heights reached by *Dipsochelys* spp. A. Height of shell aperture. B. Height of plastron off ground during high standing. C. Height of top of aperture during high standing. D. Maximum height of head. Key: ● = *D. arnoldi*; x = *D. dussumieri*; o = *D. hololissa*.

Discussion.—From the observations of feeding behavior in captive *Dipsoschelys* it is apparent that there are significant ecological differences between the saddlebacked *D. arnoldi* and the more domed *D. hololissa* and *D. dussumieri*. The observations support suggestions that saddlebacked morphology facilitates browsing. In *D. arnoldi* efficient browsing is possible as a result of the high shell aperture and the use of the triceps brachii and latissimus dorsi muscles to extend the front limb and raise the front of the shell. Vertical extension of the neck, suggested to be a primary driving force behind the evolution of saddlebacked shells in some Galapagos tortoises, is not used in *D. arnoldi*. This species is further specialized for feeding on large, thick leaves by the elaboration of the propalinal bite resulting from the development of the geniohyoideus and pterygoideus musculature and attachment sites.

Dipsoschelys arnoldi differs from saddlebacked Galapagos and Mascarene tortoises in its osteological specializations. Some degree of humeral curvature is seen in sub-fossil remains believed to be referable to saddlebacked *Cylindraspis triserrata* (Günther, 1877) but this is not as pronounced as in *D. arnoldi*. The skulls of *Chelonoidis* and *Cylindraspis* do not show any evidence of unusually developed musculature associated with specialized jaw action except in *Cylindraspis triserrata*. This species is unique in having three dentary alveolar ridges instead of the usual two (Günther, 1877; Arnold, 1979; Bour, 1984). The functional significance of these ridges is presumed to be a feeding specialization (Arnold, 1979). As with the specialized dentary of *D. arnoldi*, these ridges would only be effective feeding structures for a propalinal bite, when they would rub against the median ridges of the palate. Unlike in *D. arnoldi* there is no ossified lingual bar, although the point of insertion of the geniohyoideus on the dentary symphysis is unusually broad. There are no detectable specializations of the geniohyoideus attachment on the cranium. In all *Cylindraspis* the pterygoideus supporting ridge on the descending parietal process is highly developed. These data indicate that the saddlebacked *C. triserrata* was also a browsing species, although it may not have been able to sustain the upright feeding posture used by *D. arnoldi*.

In *Chelonoidis* the saddlebacked condition may have evolved initially as an adaptation to facilitate browsing but the vertical enlargement of the aperture, elongation of the neck, and the flexibility of the atlas articulation appear to be driven by sexual selection. These characters are used by male saddlebacks in agonistic encounters where dominance is determined by the height to which the contestants can reach, as recorded by Fritts (1984): "the competing tortoises attempt to achieve dominance by raising the head as high as possible and, if necessary, by gaping and biting each other on the head or upper jaw." The intimidatory nature of the display is further exaggerated by the pale color of the head and neck in these forms (Fritts, 1984).

Speculation that saddleback forms of giant tortoises evolved in the Seychelles, Mascarene, and Galapagos is-

lands as adaptations for a browsing diet seem to be well founded. It is possible that the extreme forms seen in the Galapagos are an exaggeration of the basic saddleback morphology due to further sexual selection. Of the living tortoises *D. arnoldi* is the most specialized browsing form and its feeding specializations account for most of the notable morphological differences between it and the grazing *Dipsoschelys* species.

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