

Taxonomy of Indian Ocean Giant Tortoises (*Dipsochelys*)

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ABSTRACT. – The genus *Dipsochelys* comprises giant tortoises from Aldabra, Seychelles, and Madagascar. This paper reviews the taxonomy of the genus, recognizing and redescribing six species: *D. dussumieri* (Aldabra), *D. daudinii* (Seychelles?), *D. hololissa* (Seychelles), *D. arnoldi* (Seychelles), *D. abrupta* (Madagascar), and *D. grandidieri* (Madagascar). The species are reliably distinguished by their osteology, their external features being variable. The nomenclature of the Aldabran species is confused; this paper recommends a strict application of the rules of nomenclature and the resurrection of *D. dussumieri* (Gray, 1831) in preference to the invalid *Geochelone gigantea* (Schweigger, 1812) or the junior synonym *D. elephantina* (Duméril and Bibron, 1835). Phylogenetic relationships supported by a cladistic analysis of osteological features suggest that the Malagasy species share a common ancestry with two of the Seychelles forms (*D. arnoldi* and *D. hololissa*), with the Aldabran *D. dussumieri* and the presumed Seychelles species *D. daudinii* forming a separate clade. This may support suggestions that the Aldabran population is descended from an undescribed extinct population from the Comoros rather than from Madagascar. Of the six species redescribed only three remain extant (*D. dussumieri*, *D. hololissa*, and *D. arnoldi*).

KEY WORDS. – Reptilia; Testudines; Testudinidae; *Dipsochelys*; tortoise; morphology; taxonomy; systematics; phylogeny; Aldabra; Seychelles; Madagascar; Indian Ocean

In recent times giant tortoises inhabited many of the islands of the western Indian Ocean with species of the genus *Dipsochelys* being recorded from Madagascar, the Comoros, Glorieuse, Aldabra, Assumption, Astove, Cosmoledo, Providence, the granitic Seychelles islands, and the coralline island of Denis (Fig. 1) (Stoddart and Peake, 1979). Exploitation by human settlers in the region led to the extinction of all wild populations by 1840, with the exception of a remnant group on Aldabra, *D. dussumieri* (previously referred to as *Geochelone gigantea* or *D. elephantina*). Our knowledge of the extinct populations is extremely fragmentary with only a small number of museum specimens and subfossils being recorded (Bour, 1984b) and historical records being very sparse and imprecise (Stoddart and Peake, 1979). Subfossil material is relatively abundant for the Malagasy and Aldabran populations (Bour, 1994), the latter has been used to demonstrate that Aldabra was colonized by giant tortoises on three separate occasions over the last 140,000 years, following sea level rises and inundations (Taylor et al., 1979). Each colonization event appears to have been by a form almost identical to the living species (Arnold, 1979). This fact has been used to suggest that Aldabra was colonized from nearby Madagascar and that the Malagasy, Aldabra, and Seychelles forms represent a single highly polymorphic species (Arnold, 1979), despite the very superficial resemblance of the Malagasy and Aldabran forms. Subsequent discovery of fragmentary subfossil remains on the Comoros (Bour, 1994) suggest that an alternative view of their biogeography may be possible and that the still unidentifiable

Comoros population could have been the source of the Aldabran tortoises. Under this scenario the Aldabran population would have been genetically isolated from both the Malagasy and granitic Seychelles populations for an extended period of time (Gerlach and Canning, 1996b). This scenario would have Aldabra colonized from its closest high island source (360 km to the Comoros) rather than alternative, more distant sources (Madagascar, 420 km; granitic Seychelles, 1150 km), in accordance with the predominant marine currents.

Although it has generally been believed that the giant tortoises of the central granitic Seychelles islands became extinct in the 1840s, with *D. dussumieri* surviving only on the outlying coralline atoll of Aldabra, there have been reports of individuals of possible Seychelles origin within captive herds of Aldabra tortoises (Bour, 1982, 1984a). In all cases it has been concluded that these were no more than unusual growth forms of a single, variable species.

In January 1995 three tortoises (two living and one dead) in a hotel garden in Seychelles were brought to our attention with the suggestion that they might belong to one of the original granitic Seychelles species. While the shells appeared to resemble those described for granitic Seychelles species (Günther, 1877; Bour, 1982), they could not be positively identified on the basis of external morphology due to the known influences of dietary imbalances in captivity (Highfield, 1990).

The taxonomy of the Aldabra-Seychelles-Madagascar giant tortoises has long been an area of great confusion (Rothschild, 1915; Arnold, 1979; Bour, 1984a) due to the captive origin of many specimens, the paucity of reliable

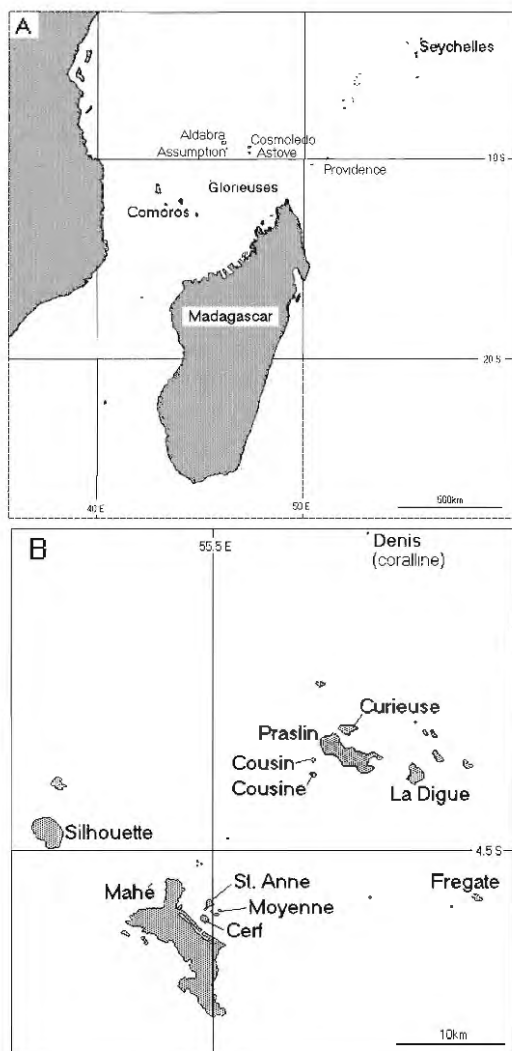


Figure 1. Islands of the western Indian Ocean (A) and the granitic Seychelles islands (B), showing islands and island groups mentioned in the text.

provenance data, and the frequent loss of specimen labels and numbers. Attempts at revision have varied from the recognition of a wide range of poorly defined species (Rothschild, 1915) to the conclusion that all forms belong to a single, variable taxon (Arnold, 1979). Some of this confusion has been cleared in recent years through careful study of the Malagasy fossil taxa (Bour, 1994), but the Aldabra-Seychelles group remains confused.

In order to help resolve these identification problems we undertook a revision of all *Dipsochelys* giant tortoises, the results of which are presented in this study. Our results rely largely on osteological and morphological data, all of which were collected during this study, with the exception of the Malagasy subfossil data, taken from Bour (1994), and data from wild tortoises on Aldabra, taken from a variety of cited sources.

METHODS AND MATERIALS

Specimens Examined. — A total of 84 specimens of *Dipsochelys* was examined. The osteological study exam-

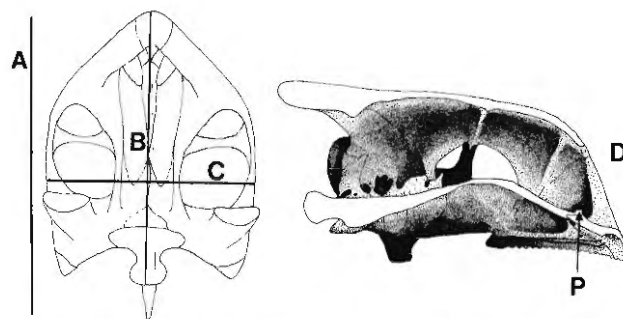


Figure 2. *Dipsochelys dussumieri* skull in ventral and lateral cross-section views showing recorded measurements and the position of the processus vomerinus dorsalis (P). A) premaxilla – supraoccipital crest, B) premaxilla – occipital condyle, C) skull width, D) skull height.

ined 49 specimens in the collections of the British Museum (Natural History), the University Museum of Zoology (Cambridge), the Oxford University Museum, the Muséum National d'Histoire Naturelle (Paris), the Seychelles Natural History Museum, the Nature Protection Trust of Seychelles, and in private collections. Of these, only 13 were of known origin (12 from Aldabra, 1 from Madagascar). Shells and stuffed mounts of a further 35 specimens were examined. Type materials of all described species were examined, with the exception of *D. hololissa* (Günther, 1877), the type material of this species having been destroyed (Bour, 1984b). All specimens examined are listed in the Appendix.

The starting point for this revision was the diagnosis of the extant Aldabran species *D. dussumieri* using skeletal material of known Aldabran origin ($n = 12$). Characters found to be variable within this group were assumed to be of no systematic value and were subsequently excluded from the taxon diagnosis. Museum specimens were then referred to this taxon on the basis of the presence of the characters uniting the Aldabran specimens. This allowed the Aldabran species to be defined on the basis of osteological characters and the variation of shell morphology; this taxon accounts for 64 of the specimens examined, leaving 20 which fall outside the range of variation. These remaining specimens fall into 6 discrete groups representing 6 separate taxa. In the descriptions below all taxa are compared to the relatively well known Aldabran species. All morphometric data were analyzed by principal component analysis, which supported the groupings proposed by examination of individual characters.

Terminology. — Cranial anatomy terminology follows Gaffney (1972) with the addition of the processus frontalis circumolfactorius of Bour (1994) (the ventral process of the frontals, marking the division between the nasal cavity and the braincase) and of a new structure autapomorphic for *Dipsochelys*. This structure, the processus vomerinus dorsalis, is positioned on the dorsum of the vomer between the foramina praepalatina and anterior to the sulcus vomerinus (Fig. 2). In life it supports an enlarged medial nasal gland (equivalent to the vomeronasal organ; Parsons, 1970) (Fig. 2 in Arnold, 1979). Terminology for post-cranial anatomy follows Walker (1973).

Taxonomy. — The generic status of the taxon *Dipsochelys* has been the subject of dispute. We have

Table 1. Morphometrics of *Dipsochelys* adults (measurements in cm, summarized with means \pm standard deviations and ranges). Data for wild *D. dussumieri* from Honegger (1967), *D. abrupta* and *D. grandidieri* from Bour (1994).

Species	Sex (provenance)	<i>n</i>	Carapace Length (Straight)	Carapace Length (Curved)	Carapace Width (Straight)	Carapace Height	Plastron Length
<i>D. dussumieri</i>	males (museum)	21	103.9 \pm 14.9 (76-123)	137.2 \pm 17.8 (119-160)	69.8 \pm 10.5 (47-87)	54.9 \pm 10.2 (41-64)	81.7 \pm 10.3 (70-95)
	females (museum)	18	76.8 \pm 10.8 (52-88)	101 \pm 15.0 (67-122)	54 \pm 7.1 (38-68)	41 \pm 6.9 (30-52)	63.3 \pm 7.5 (48-74)
	males (wild)	12	79.6 \pm 9.4 (65-96)	106.7 \pm 13.8 (79-132)	49.3 \pm 6.7 (39-61)	41.6 \pm 3.3 (39-46)	-
	females (wild)	19	61.9 \pm 5.6 (47-70)	85.7 \pm 7.8 (66-99)	40.2 \pm 3.2 (32-46)	35.6 \pm 4.0 (28-44)	-
<i>D. daudinii</i>	male	1	83	98	49	34	62
<i>D. hololissa</i>	males (museum)	7	123.4 \pm 11.0 (97-138)	143.2 \pm 16.4 (123-175)	79.9 \pm 9.1 (69-97)	58.5 \pm 4.9 (52-69)	89.6 \pm 12.4 (78-125)
	female (museum)	1	95	128	79	52	71
	males (live)	5	110.1 \pm 12.4 (98-127)	143.3 \pm 3.5 (138-145)	78.9 \pm 8.8 (72-95)	55.2 \pm 6.4 (48-65)	84.5 \pm 9.9 (74-101)
	females (live)	3	68.4 \pm 6.2 (62-80)	92 \pm 8.3 (75-103)	58.6 \pm 12.1 (50-68)	38.6 \pm 9.9 (28-45)	56.3 \pm 8.5 (52-62)
<i>D. abrupta</i>	males	2	115	145	79	55	92
<i>D. grandidieri</i>	males	4	86.0 \pm 50.6 (94-125)	138.8 \pm 12.4 (120-150)	89.3 \pm 12.9 (75-104)	46.3 \pm 0.9 (45-47)	86.7 \pm 5.2 (82-94)
	females	2	(97-116)	(129-148)	(74-87)	(40-48)	(79-91)
<i>D. arnoldi</i>	males (museum)	3	76.2 \pm 11.0 (61-96)	112.5 \pm 6.4 (106-124)	56.1 \pm 3.2 (51-63)	43.1 \pm 6.6 (39-49)	66.7 \pm 4.3 (61-79)
	females (museum)	1	85	105	55	46	65
	males (live)	14	78.8 \pm 9.0 (62-91)	100.6 \pm 12.8 (81-123)	47.3 \pm 6.6 (38-60)	39.2 \pm 7.1 (31-56)	58.0 \pm 6.3 (44-65)
	females (live)	4	70.0 \pm 11.3 (59-85)	88.0 \pm 13.7 (77-108)	52.0 \pm 6.1 (45-56)	36.5 \pm 6.6 (31-46)	54.8 \pm 10.7 (43-69)

followed Bour (1982; 1984a, 1994) in recognizing it at full generic rank and we use it in preference to *Aldabrachelys* (Loveridge and Williams, 1957) because the type specimen of *Testudo gigantea* Schweigger, 1812, the type species of *Aldabrachelys*, was not an Aldabran tortoise (Bour, 1984b) but a specimen of the South American *Chelonoidis denticulata* (Linnaeus, 1766) (Pritchard, 1986).

The taxa we distinguished are separated from one another by an average of 7 cranial characters. This is similar to the 9 characters separating *Astrochelys radiata* (Shaw, 1802) and *A. yniphora* (Vaillant, 1885), the 8 characters separating the *Gopherus* species and 8 separating the *Cylindraspis* species, but is much higher than the 2 characters separating the Galapagos *Chelonoidis* taxa (*pers. obs.*). Consequently, we have recognized the taxa in this revision as full species.

Cladistic analysis of osteological features was performed using Hennig86 (Farris, 1988). No character weighting was used and all characters were scored non-additively. *Astrochelys radiata* was used as the outgroup in accordance with recent phylogenetic proposals (Bour, 1984b).

Abbreviations. — Institutional abbreviations are as follows: AM, Académie Malgache; BMNH-P, British Museum (Natural History) (Palaeontology); BMNH-Z, British Museum (Natural History) (Zoology); MGM, Madras Government Museum; MNHN-AC, Muséum National d'Histoire Naturelle (Anatomie Comparative); MNHN-R, Muséum National d'Histoire Naturelle (Reptiles); NPTS, Nature Protection Trust of Seychelles; OUM, Oxford University Museum; RCS, Royal College of Surgeons, London; RMNH,

Rijkmuseum van Natuurlijke Historie, Leiden; SNHM, Seychelles Natural History Museum; UMZ, University Museum of Zoology, Cambridge.

RESULTS

Shell measurements and proportions of all six species of *Dipsochelys* are summarized in Table 1. The skull measurements used are shown in Fig. 2. Measurements of all type specimens are given in Table 2 and systematically important character states of the shell and skeleton of all six species are given in Table 3.

Principal component analysis of morphometric data from all museum and living specimens demonstrated clear morphological separation of most taxa (Fig. 3). The only exceptions to this are *D. daudinii* and *D. abrupta* which are each represented by a single adult individual. The clustering of wild tortoises at the center of the *D. dussumieri* Aldabran grouping highlights the difference between wild and captive morphologies, giving an indication of the variability of this taxon in captivity. It should be noted that the other taxa are not centered on this wild group, indicating that their morphology is not simply a consequence of carapace distortion in captivity as has been suggested previously (e.g., Arnold, 1979).

Dipsochelys Bour, 1982

Diagnosis. — Giant tortoises defined by modifications of the nasal aperture associated with an ability to draw water up through the nasal passages. These comprise an enlarged

Table 2. Measurements of *Dipsoschelys* type specimens (RCS 1020–1 from Günther, 1877).

Species	Specimen	Carapace (cm)				Plastron (cm)	Skull (mm)				Mandible (mm)
		Length (Straight)	Length (Curved)	Width	Height	Length	Premax.-condyle	Premax.-crest	Width	Height	Length
<i>D. dussumieri</i>	RMNH 3231	18	22	13	10	16	-	-	-	-	-
<i>D. daudinii</i>	MNHN-AC 11819	83	98	49	34	62	-	-	-	-	-
<i>D. hololissa</i>	RCS 1020	61	76	37	29	45	-	-	-	-	-
	RCS 1021	95	126	58	42	68	-	-	-	-	-
	UMZ R3796	114	128	76	62	82	130	141	103	68	90
<i>D. abrupta</i>	MNHN-P MAD3500	>92	-	70	-	>72	-	-	-	-	-
<i>D. grandidieri</i>	MNHN-P MAD3501	124	150	104	47	94	-	-	-	-	-
<i>D. arnoldi</i>	MNHN-R 7872	73	91	47	33	53	100	107	71	49	66
	MNHN-R 9564	61	75	34	26	45	-	-	-	-	-
	BMNH-Z 74.2.6.5-6	89	100	56	44	55	-	-	-	-	-

external narial opening, which is higher than wide and reaches the labial border of the maxillae and a bony support to the median nasal gland, the processus vomerinus dorsalis. The premaxilla is ventrally elongated and participates in the formation of the palate. The nasal chamber is exceptionally long and high and anteriorly bordered by a flap of cavernous tissue which probably functions as a valve (Arnold, 1979). The epipubis is fully ossified.

***Dipsoschelys dussumieri* (Gray, 1831)**
(Figs. 4, 5, and 14)

Testudo indica Schneider, 1783 (*ex errore*), Dekay in Harlan, 1827:292

Testudo dussumieri Gray, 1831:1

Testudo elephantina Duméril and Bibron, 1835:110

Testudo gigantea Schweigger, 1812 (*ex errore*), Duméril and Bibron, 1835:120

Testudo ponderosa Günther, 1877:35

Testudo hololissa Günther, 1877:39 (*partim*)

Testudo sumeirei Sauzier, 1892:396

Testudo gouffei Rothschild, 1906:753

Testudo daudinii Duméril and Bibron, 1835 (*ex errore*), Sauzier, 1895:2

Aldabrachelys gigantea (Schweigger, 1812), Loveridge and Williams, 1957:259

Dipsoschelys elephantina (Duméril and Bibron, 1835), Bour, 1982:117

Distribution and Status. — Naturally restricted to Aldabra Atoll. In historical times it was probably also present on nearby islands. Extinct throughout much of the presumed historic range; some 150,000 survive on Aldabra (Bourn and Coe, 1978). Wild populations were introduced to the granitic Seychelles islands of Curieuse and Fregate. Small free-range groups exist on Cerf, Moyenne, Silhouette, Consin, Cousine, Bird, and Denis in the central Seychelles, on several of the Amirantes, and on Changu Island near Zanzibar.

Holotype. — RMNH 3231, juvenile in alcohol, collected by J.J. Dussumier on "Insula Aldebra" (= Aldabra), date unknown, probably about 1830.

Diagnosis. — A giant tortoise distinguished from all other *Dipsoschelys* by: 1) deep anal notch; 2) abdomino-

femoral suture curved; 3) top of nasal aperture lower than top of orbits; 4) foramen orbito-nasale small or absent; 5) no posterior tympanic projection on quadrate; 6) processus frontalis circumolfactorius small, irregular; 7) dentary alveolar ridges weakly dentate; 8) scapula-acromion angle 130°.

External Morphology

Shell. — The shell is domed and its posterior width is slightly greater than the anterior (mean $114.8 \pm 5.4\%$; 104–123%). The vertebrals usually have raised centers. The second or third vertebral is the highest point of the shell, with no more than an 8% difference between them; vertebral 4 is 8–14% (mean $11.8 \pm 2.0\%$) lower than the highest point. Vertebrals 1 and 5 slope downwards very steeply. Vertebrals 2 to 4 are approximately equal in length. Costal 1 is approximately equal to costal 2 in anterior-posterior length. The carapace is evenly domed; the height to the top of the costal at the middle of vertebral 3 is 73–85% of the shell height and the tops of the costals are angled at approximately 40° to the horizontal. The anterior and posterior marginals are flared outwards in 4% of specimens. The costo-marginal suture is almost straight, usually curving upwards above the sixth marginal. The scutes are concentrically ridged, usually be-

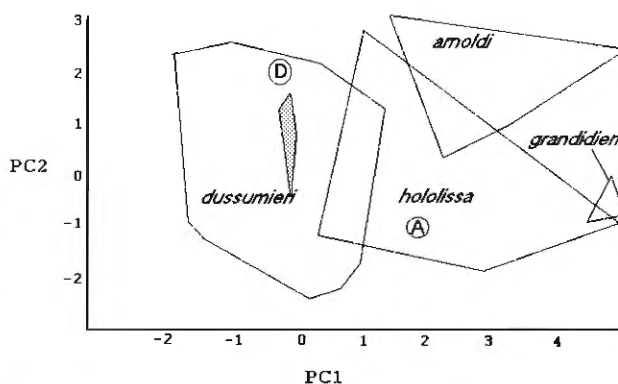


Figure 3. Principal component analysis of *Dipsoschelys* taxa. *D. daudinii* (D) and *D. abrupta* (A) are represented by single complete specimens. The range of wild *D. dussumieri* is shaded. Factor loadings (eigenvalues of PC1; PC2): anal notch (-0.29; -0.87); costal 1 (0.01; 0.33); costal 2 (-0.07; -0.07); costal height (0.63; -0.40); anal notch (-0.87; 0.01); vertebral 2 (0.57; -0.49); vertebral 3 (-0.51; -0.03); vertebral 4 (-0.82; -0.32).

Table 3. Character states of *Dipsochelys* species (means \pm standard deviations and ranges are given for all meristic characters). Characters marked with an asterisk were used in the phylogenetic analysis (Fig. 15).

	<i>dussumieri</i>	<i>daudinii</i>	<i>hololissa</i>	<i>abrupta</i>	<i>grandidieri</i>	<i>arnoldi</i>
	<i>n</i> = 42	<i>n</i> = 2	<i>n</i> = 12	<i>n</i> = 6	<i>n</i> = 6	<i>n</i> = 22
Shell						
Shape	domed	saddle	domed	domed	flat	saddle
Posterior/anterior width (%)	114.8 \pm 5.4 (104-123)	115	109.1 \pm 3.5 (103-112)	109.2 \pm 0.5 (108-110)	101.2 \pm 0.1 (100-103)	130.3 \pm 7.9 (120-140)
2nd/3rd vertebral height (%)	83.5 \pm 6.4 (79-107)	100	96.7 \pm 1.6 (92-103)	ca. 95	99.0 \pm 0.5 (98-100)	99.1 \pm 0.5 (98-100)
4th/3rd vertebral height (%)	88.2 \pm 2.0 (83-114)	100	63.8 \pm 2.1 (80-100)	ca. 85	99.0 \pm 0.5 (98-100)	96.4 \pm 1.4 (94-100)
1st/2nd costal length (%)	96.2 \pm 5.1 (85-114)	93	97.8 \pm 5.2 (73-109)	110	110.3 \pm 0.8 (104-114)	142.3 \pm 16.0 (120-157)
Costal height/3rd vertebral height	0.78 \pm 0.04 (0.73-0.85)	0.82	0.88 \pm 0.01 (0.86-0.89)	ca. 0.80	0.95 \pm 0.01 (0.93-1.00)	0.88 \pm 0.01 (0.85-0.89)
2nd/3rd vertebral length (%)	95.2 \pm 4.1 (91-110)	86	101.8 \pm 0.9 (100-105)	105	105.2 \pm 3.0 (100-109)	115.2 \pm 7.5 (104-124)
3rd/4th vertebral length (%)	84.6 \pm 5.2 (78-125)	93	83.4 \pm 3.3 (78-133)	116	88.2 \pm 2.5 (81-97)	66.1 \pm 11.8 (50-78)
Pit on suture of costal 1 and 2	0	0	0	0	0	1
Costo-marginal suture straight	1	1	1	0	0	1
Caudal recurved	1	1	0-1	1	1	0
Plastron length (% carapace)	85.4 \pm 7.9 (75-94)	75	83.4 \pm 6.2 (71-91)	80	86.5 \pm 0.5 (76-87)	78.4 \pm 2.6 (61-82)
Abdomino-femoral suture angled	0	1	1	1	1	1
Humero-pectoral suture angle	0	0	140-150°	90°	90°	150°
Anal notch (% length of anals)	22.3 \pm 6.4 (14-32)	15	2.3 \pm 1.8 (0-16)	20.5 \pm 7.5 (13-28)	0	3.8 \pm 2.5 (0-15)
Skeleton	<i>n</i> = 27	<i>n</i> = 1	<i>n</i> = 6	<i>n</i> = 1	<i>n</i> = 2	<i>n</i> = 1
Premax.-condyle length (mm)	98.6 \pm 5.6 (61-153)	?	108 \pm 6.2 (102-153)	143	153 (103-202)	100
Articular truncated *	0	0	1	?	1	0
Symphysial dentary ridge	0	0	0	0	0	1
Dentary curved	0	1	0	0	0	0
Dentary inflated *	0	0	0	1	1	0
Postorbital angle to skull roof	20-45°	30°	5-10°	?	15°	45°
Proc. frontalis circumolfactorius *	small	?	large	?	large	small
Proc. trochlearis oticum large *	0	0	1	1	1	1
Quadrates tympanic projection *	0	0	1	1	1	1
Squamosal with dorsal process	0	1	0	0	0	0
Inflated tympanic chamber	0	0	0	0	0	1
Quadrates diverging	0	0	0	0	1	0
Flange on ridge from quadrate to foramen nervi trigemini	0	0	0	0	0	1
Depression on basisphenoid *	0	0	1	1	1	0
Depression on basioccipital	0	0	0	1	0	0
Basioccipital with ventral ridge *	0	0	1 (83%)	1	1	1
Proc. vomerinus dorsalis	large	?	small	?	large	large
4th cervical biconvex	0	0	0	1	0	0
8th/7th dorsal vertebra	0.4	0.5	0.63-0.81	?	?	?
Dorsals 8 and 9 clearly separated	0	0	1	?	?	?
Lateral concavity on scapula	1	1	0	1	1	1
Acromion - scapula angle (approx.)	130°	115°	100-115°	115-120°	125°	120°
Humerus curved	0	0	0	0	0	1
Intertubercular fossa contacts humerus head	1	1	1	1	0	1
Humeral processes parallel	0	0	0	1	0	0
Coronoid fossa *	oval	oval	rounded	triangular	rounded	triangular
Ulna curved *	1	1	0	1	1	0
Large olecranon process	1	1	0	1	1	1
Pelvis fused *	1	1	0	1	0	1
Tapered femur *	0	0	0	1	1	0
Grooved tibia *	1	1	0	1	1	0

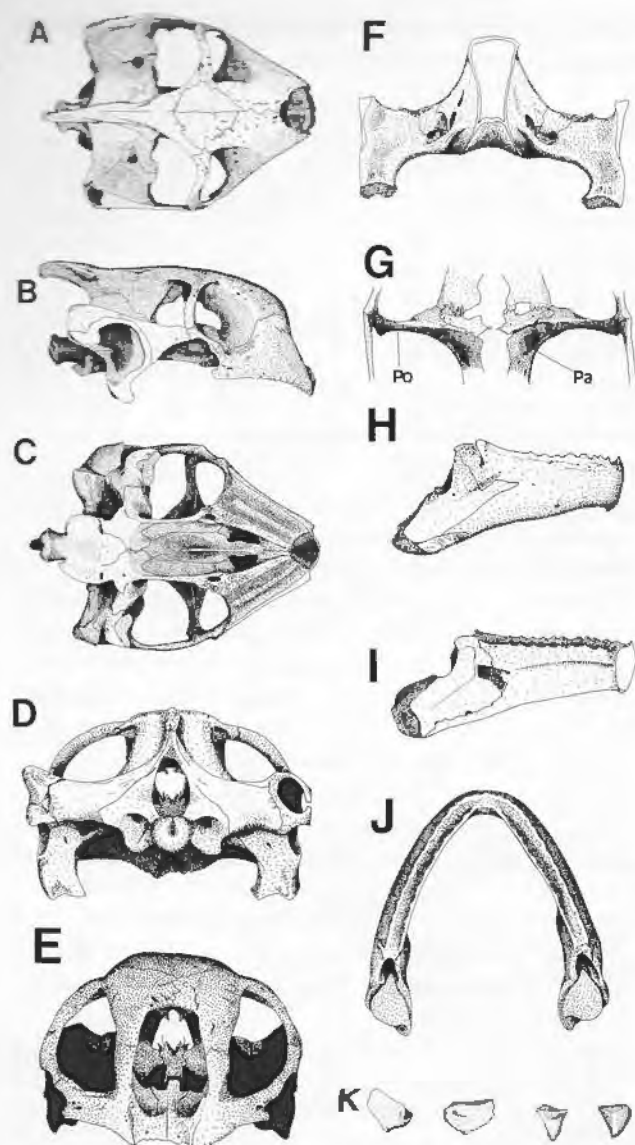


Figure 4. *Dipsochelys dussumieri* (UMZ 3814) skull (A–G) and mandible (H–K). A) dorsal, B) lateral, C) ventral, D) posterior, E) anterior, F) anterior view of section through skull (across line C in Fig. 2), G) ventral view (palate removed) of processus frontalis circumolfactorius (F), Po – postorbitals, Pa – parietals, H) labial, I) lingual, J) dorsal, K) right articular in lateral, medial, posterior, and anterior views.

coming smooth with age and are dark blackish-brown to black. As is normal for all *Dipsochelys* there are 5 vertebral scutes, 8 costals, and 22 marginals. A nuchal is present in 98.7% of wild specimens ($n = 223$; Gaymer, 1968) and the caudal may be either single or double (single in 46.8% of 223 wild specimens; Gaymer, 1968). The caudal is flat or slightly reverted. The plastron length is 75–90% of the straight carapace length in males, the bridge length forming 48–62% of the plastron. In females the proportions are 86–94% and 47–55%, respectively. In wild populations these proportions change isometrically with growth and the plastron is on average 82 and 93% of carapace length in adult males and females, respectively (Grubb, 1971). The gulars are as long as they are wide. The humero-pectoral and abdomino-



Figure 5. Living *Dipsochelys dussumieri*, Curieuse Island, Seychelles.

femoral sutures are straight or slightly curved, but never angled. The anal scutes are notched, the notch occupying 14–25% (mean $21.7 \pm 4.6\%$) of the length of the anal scutes in males and 21–32% (mean $23.5 \pm 8.3\%$) in females (data from museum specimens).

Body. — There are no notable diagnostic external characters on the head, neck, or limbs. The head bears a small frontal scale, two large prefrontals, and a large, undivided temporal. The tail of males is very long with 13–20 (mean 15.9) scales between the cloaca and the tip of the tail; the terminal scale is slightly enlarged (reaching a maximum length of 50 mm in males over 78 cm straight carapace length) and is always at least twice as long as wide. In females the tail is much shorter, with only 8–11 (mean 8.9) scales and no enlargement of the terminal scale.

Osteology

Skull. — The back of the supraoccipital crest is raised slightly above the parietals and extends beyond the occipital condyle. The postorbitals are narrow, becoming broader with age; they slope downwards sharply, this angle is more acute in large males but is always at least 10° from the horizontal. They contact the skull roof at an angle of $20\text{--}45^\circ$ (mean $24.1 \pm 9.9^\circ$) from the horizontal, descending to $30\text{--}50^\circ$ (mean $45.3 \pm 6.1^\circ$) at their midpoint. The processus frontalis circumolfactorius is small and irregular in shape. A ridge runs along the ventral surface of the postorbitals, crossing the posterior part of the processus frontalis circumolfactorius. The nasal aperture is high as in all *Dipsochelys* species. The foramen orbito-nasale is usually absent, if present it is very small. The quadrate has no process on the upper posterior margin of the tympanic aperture. There is no ornament on the squamosal. The incisura columella auris is usually enclosed by the quadrate (in 96% of specimens). The stapes is long and thin with a slender, perforate footplate. The processus trochlearis oticum is poorly developed. In 4% of specimens there is a vertical ridge on the descending process of the parietals, medial to the trigeminal nerve foramina. The foramen nervi trigemini is clearly divided in 80% of specimens. The anterior foramen of the canalis cavernosus is small and surrounded by the parietals. There is a moderately

large processus vomerinus dorsalis. The alveolar ridges on the maxillae are weakly developed and do not extend onto the premaxillae. The palate is deeply concave with a ventral midline ridge running the full length of the vomers. The choanae are large and clearly visible in ventral view. The basisphenoid is flat. The tuberculum basioccipitale is poorly developed and the occipital condyle has no ventral ridge. The degree of separation of the foramen chorda tympani inferius from the fenestra postotica is variable.

The dentary has weakly developed toothed alveolar ridges. The articulars are not truncated anteriorly except in very small skulls (truncated in one specimen with premaxilla-occipital condyle length of 61 mm), as is normal in testudinids where ossification of Meckel's cartilage is incomplete. The length:width ratio of the articulars is 1:1.8–2 (excluding the incompletely ossified juvenile).

Hyoid. — Only the cornu branchiale is ossified.

Vertebrae. — The third cervical vertebra is biconvex. The first seven dorsal vertebrae are uniform, the eighth onwards distinctly shortened. This shortening is abrupt, with the eighth and all subsequent vertebrae being 35–40% of the length of the seventh. The eighth and ninth dorsals are fused. There are 25 caudal vertebrae, the last 5–7 being fused.

Pectoral Girdle and Forelimbs. — Fusion of the scapula and coracoid is variable. There is a lateral concavity on the scapula. The angle between the main shaft of the scapula and the acromion process is 130° in lateral view and 160° in ventral view. The medial process of the humerus is angled to the shaft of the humerus and its full extent is visible in dorsal view. The intertubercular fossa contacts the head of the humerus. The antero-dorsal surface of the humerus is smooth. The coronoid fossa is oval in outline. The curved ulna bears a distinct olecranon process. The radius is 0–10% shorter than the ulna. Fusion of the bones in the carpus is variable and may include the radial, proximal central, and medial 3. There are five digits.

Pelvis and Hindlimbs. — The pubes, ilia, and ischia are all fused. There is a short iliac sacral process, a short lateral process on the posterior margin of the ischium, and a long antero-ventrally directed process on the pubis. Sexual dimorphism is apparent in the pelvis: in males the ilium is 10% shorter than the ischium and the pelvis is 15% wider than high; the pubes are directed forwards, the anterior part of their symphysis forming an angle of 90°. In females the ilium is 5–10% longer than the ischium, the height of the pelvis approximately equals the width, the pubes are directed forwards into a long anterior process with a symphyseal angle of 40° due to ossification of the epipubis, and there are dorsal and ventral ridges along the symphysis. In females the metischial processes are also more pronounced. These differences are largely associated with an enlarged pelvic attachment for the pubischiofemoralis muscle in females. The femur does not taper, its proximal end is no more than 1.5 times the width of the distal end. The trochanters may be separated by a groove or fused together. There is a groove on the posterior distal surface of the tibia. The astragalus and

calcaneum are fused, the other bones of the pes remain separate. There are five digits.

Synonyms

Testudo gigantea Schweigger, 1812. — The type specimen of *Testudo gigantea* has been identified as the South American *Chelonoidis denticulata* (Pritchard, 1986) and the various combinations of *T. gigantea*, *Geochelone gigantea*, and *Aldabrachelys gigantea* cannot be applied to the Indian Ocean giant tortoises.

Testudo elephantina Duméril and Bibron, 1835. — This name was used to refer to eight specimens from "Anjouan, Aldebra, les Comores." The type series includes one specimen referred to *D. daudinii* (Bour, 1985), however, the lectotype (MNHN-R 7874) and the six other specimens (MNHN-R A1942, 7873, 7875, 9314, 9565, and DD61) are conspecific and indistinguishable from the Aldabran species for which the name *elephantina* has frequently been used. Although it is a junior synonym of *dussumieri*, *elephantina* is preferred by some authors due to the designation of *dussumieri* as a *nomen oblitum* by Bour (1985) on the grounds of nomenclatural stability and its lack of use between 1831 and 1984. However, since 1973 *nomina oblita* could be designated only by application to the ICZN (International Commission on Zoological Nomenclature, 1985) and the name *dussumieri* therefore remains available. The argument of nomenclatural stability is invalid since *gigantea* and *elephantina* were both used with equal frequency until 1957, after which, following Loveridge and Williams (1957), *gigantea* was used exclusively until 1982 (Bour, 1982). Since Bour's rejection of *gigantea*, the name *elephantina* has been sporadically used, but the majority of authors continue to use *gigantea*. Thus *elephantina* has only been used intermittently since 1982 and has no nomenclatural stability. Resurrecting the senior synonym *dussumieri* would thus not threaten nomenclatural stability and would also avoid potential confusion between the junior synonym *elephantina* and the superficially similar name *Geochelone (Chelonoidis) elephantopus* (Harlan, 1827) (Crumly, 1986; Bour, 1994), historically used for Galapagos tortoises. However, even that name has valid senior synonyms, and Galapagos tortoises have now been referred to *Geochelone (Chelonoidis) nigra* (Quoy and Gaimard, 1824) (Pritchard, 1996).

Testudo ponderosa Günther, 1877. — This name was applied to a female skeleton (BMNH-Z 64.12.20.27) and an isolated pelvis (BMNH-Z 76.1.4.1) on the basis of a number of cranial characters and the shape of the pelvis. The cranial characters all lie within the range of variation of *D. dussumieri*. The pelvis of the two specimens cannot be separated from those of typical female *D. dussumieri*, therefore this taxon should be regarded as a synonym of *D. dussumieri*.

Testudo sumeirei Sauzier, 1892. — The holotype (BMNH-Z 1929.12.27.1) differs from typical *D. dussumieri* in the more gradually sloping 4th and 5th vertebrae and the

absence of a nuchal. These characters fall within the range of variation of wild Aldabran *D. dussumieri*. The relatively high frequency of nuchal absence in museum collections (10.4%, $n = 77$; Arnold, 1979) compared to wild Aldabran tortoises (1.3%, $n = 223$; Gaymer, 1968) may indicate that the frequency of nuchal absence may have been higher in some island populations. The skull of the holotype cannot be located but was reported to have the quadrate unfused surrounding the incisura columella auris (Loveridge and Williams, 1957). This condition is also found in BMNH-Z 1949.1.4.65 but not in BMNH-Z 1969.1.5.10. The variability of this character in other Testudinidae (*pers. obs.*) makes it of limited taxonomic value. These characters are insufficient to allow *T. sumeirei* to be recognized as a distinct taxon.

Testudo gouffei Rothschild, 1906. — This name was applied to a large male from Thérèse Island (BMNH-Z 1949.1.4.66) on the basis of cranial characters, brown carapace, and raised scales on the limbs and head. The skull is identifiable as that of a large *D. dussumieri*. It is exceptionally heavily fused and rugose, suggesting either dietary problems or some form of metabolic abnormality.

***Dipsochelys daudinii* (Duméril and Bibron, 1835)**
(Figs. 6 and 14)

Testudo indica Schneider, 1783 (*ex errore*), Cuvier, 1824:209
Testudo daudinii Duméril and Bibron, 1835:125

Distribution and Status. — The natural distribution of this species is not known. Only two known specimens are referred to this species: the holotype (lacking collection data) and a juvenile in alcohol (MNHN-R 1942; Bour, 1984a). The latter was collected by J.J. Dussumier on one of the granitic islands of Seychelles around 1830 (precise date and locality unknown) and it is not known whether it was wild-collected or imported from another island. A granitic island origin is also generally assumed for the holotype (Bour, 1984a). The species is presumed to be extinct.

Holotype. — MNHN-AC 11819, adult male skeleton, and MNHN-R 7640, separately mounted scutes of same animal, from "Indes Orientales," collector unknown.

Diagnosis. — A giant tortoise distinguished from all other *Dipsochelys* by: 1) vertebral 2 shorter than vertebral 3; 2) anterior marginals flared forwards; 3) squamosal with dorsal process; 4) large foramen orbito-nasale; 5) dentary curved upwards anteriorly.

External Morphology

Shell. — The single adult shell differs from *D. dussumieri* in its narrow, low, saddle-backed outline. The posterior width of the carapace is distinctly greater than the anterior (115%). The vertebrals have slightly raised centers, vertebrals 1–4 are of equal height. Vertebral 5 slopes downwards very steeply. Vertebral 2 is 14% shorter than vertebral 3; in other species it is the same length or longer. The height to the top

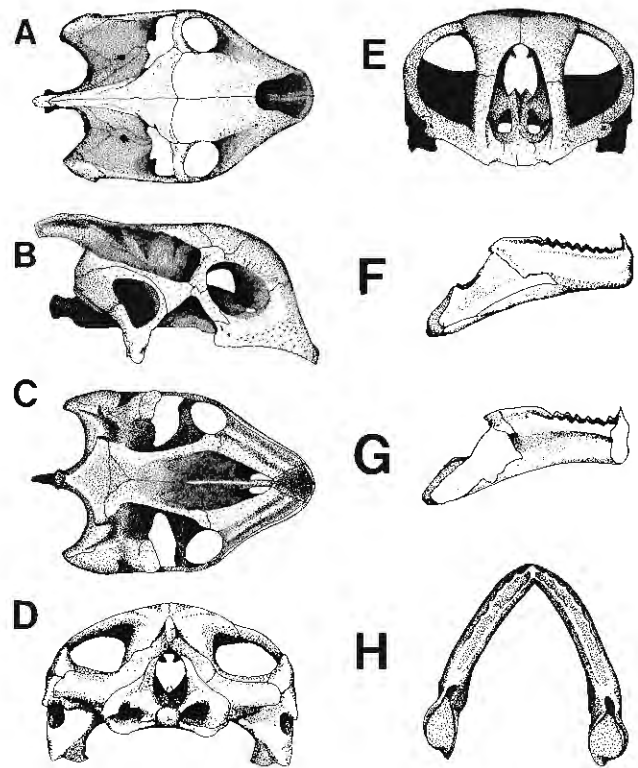


Figure 6. *Dipsochelys daudinii* (after Cuvier, 1824) skull (A–E) and mandible (F–H). A) dorsal, B) lateral, C) ventral, D) posterior, E) anterior, F) labial, G) lingual, H) dorsal.

of the costal at the middle of vertebral 3 is 80% of the shell height and the tops of the costals are angled at approximately 35° to the horizontal. The anterior marginals project forwards and the posterior marginals are flared outwards; deep notches between anterior and posterior marginals give a scalloped effect. The scutes are smooth and dark brown. A nuchal is present but is almost concealed in anterior and dorsal views by the projecting first marginals. The caudal is single and reverted. The plastron is 75% of the straight carapace length, of which the bridge forms 52%. The gulars are 1.5 times wider than long. The abdomino-femoral suture is angled. The anal scutes are slightly notched (15% of their length).

The juvenile specimen referred to the species (Bour, 1984a) has a more exposed nuchal, deeper anal notch (33%), and lighter brown coloration.

Body. — The skin of the juvenile in alcohol is light brown and its head scales are highly fractured. The skin of the holotype is not preserved.

Osteology

Skull. — The skull of the holotype is not preserved but was described and figured by Cuvier (1824); that illustration is used as the basis of the following description. The skull resembles that of *D. dussumieri* but the postorbitals slope downwards gradually, contacting the skull roof at an angle of 30° from the horizontal and descending to 35° at their midpoint. The top of the nasal aperture is level with the top of the orbits. The squamosal extends posteriorly in a dorsal

process. The quadrate bears a well developed anteriorly directed process on the upper posterior margin of the tympanic aperture. The foramen orbito-nasale is large. The processus frontalis circumolfactorius, foramen nervi trigemini, anterior foramen of the canalis cavernosum, processus vomerinus dorsalis, and the degree of separation of the foramen chorda tympani inferius from the fenestra postotica are not illustrated. The curvature of the premaxillae and the small exposure of the prootic noted by Bour (1984a) are sometimes seen in *D. dussumieri*.

The dentary has well developed toothed alveolar ridges and is distinctly curved in lateral view. The articulars do not appear to have been truncated anteriorly (length:width approximately 2:1).

The characteristic squamosal projection provides an enlarged surface for the attachment of the pars superficialis of the adductor mandibulae externus muscle on its medial surface and the depressor mandibulae muscle on its lateral surface. These features result in a strong and slightly propalinal bite, which is also found in a number of other tortoise taxa and especially pronounced in the Galapagos *Chelonoidis* taxa. The well developed musculature may be associated with a saddle-backed carapace to facilitate head and neck extension for browsing and feeding on coarse shrubby vegetation.

Post-Cranial Skeleton. — The skeleton is preserved and all characters are indistinguishable from *D. dussumieri* except for the scapula-acromion angle which is 115°.

***Dipsochelys hololissa* (Günther, 1877)**

(Figs. 7, 8, 9, and 14)

Testudo hololissa Günther, 1875:296 (*nomen nudum*)

Testudo elephantina Duméril and Bibron, 1835 (*ex errore*),
Günther, 1877:21

Testudo hololissa Günther, 1877:39 (*partim*)

Testudo gigantea Schweigger, 1812 (*ex errore*), Rothschild,
1897:407

Testudo daudinii Duméril and Bibron, 1835 (*ex errore*),
Rothschild, 1915:433

Dipsochelys elephantina (Duméril and Bibron, 1835) (*ex errore*), Bour, 1994:85

Distribution and Status. — The natural distribution of this species is not definitely known. Although believed by Günther (1877) to have been of Aldabran origin it has been demonstrated by Sauzier (1899) that the lectotype was probably from one of the granitic Seychelles islands.

The neotype was kept in captivity at the Casuarina Beach Hotel in Seychelles where it was recently discovered and recognized as representing this previously presumed extinct species (Gerlach and Canning, 1996a, 1997). Prior to purchase by the hotel it had been privately kept in the mountains of Mahé, reputedly for at least 100 years. Its presence in a relatively inaccessible part of the island before 1895 raises the possibility that it may have been collected from the wild population of giant tortoises that survived on Mahé until about 1840 (Sauzier, 1899). The current popula-

tion of the species is 8 individuals living in captivity in Seychelles.

All museum specimens of the species lack firm provenance data. Three were captives of unknown origin (MNHN-AC 1907.71, BMNH-ZW 1-1A/R4/52/B 16/334, and BMNH-Z 1949.1.4.45) and one had been living free-range on Cerf (SNHM un-numbered). BMNH-Z 'Tring 184' was kept on Egmont Atoll, Chagos, from 1800 to 1897. Its precise origin is not recorded but can be determined with some confidence. It was present on Egmont before the atoll's settlement in 1800–05 (Rothschild, 1915); the presence of tortoises is not recorded in earlier historical documents relating to the atoll and it can be concluded that this tortoise was released on the island by one of the exploratory vessels before 1800. Only four ships visited the atoll before 1800, of which only the *Heure du Berger* came by way of islands supporting tortoises and this is therefore the only vessel that could have transported 'Tring 184.' The ship was in Seychelles in 1771, visiting St. Anne first and then Praslin before sailing directly to the Chagos group. Visits were also made by launch to Mahé, Silhouette, and La Digue (McAteer, 1991). It is probable that 'Tring 184' was collected from one of these islands. As the islands had then only been settled for six months it is unlikely that there had been much movement of

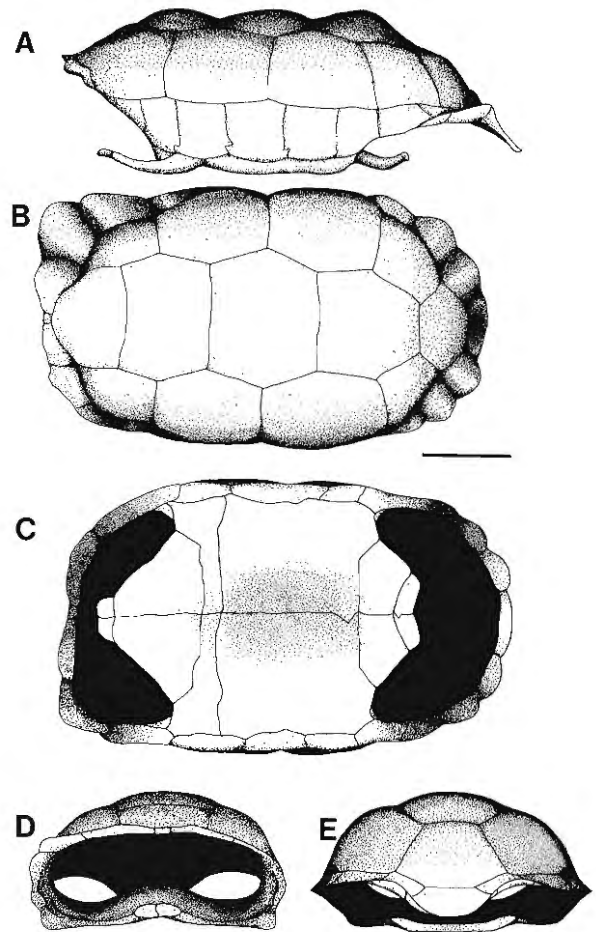


Figure 7. Shell of *Dipsochelys hololissa* Neotype (UMZ R3796) in A) lateral, B) dorsal, C) ventral, D) anterior, and E) posterior views. Scale bar = 20 cm.

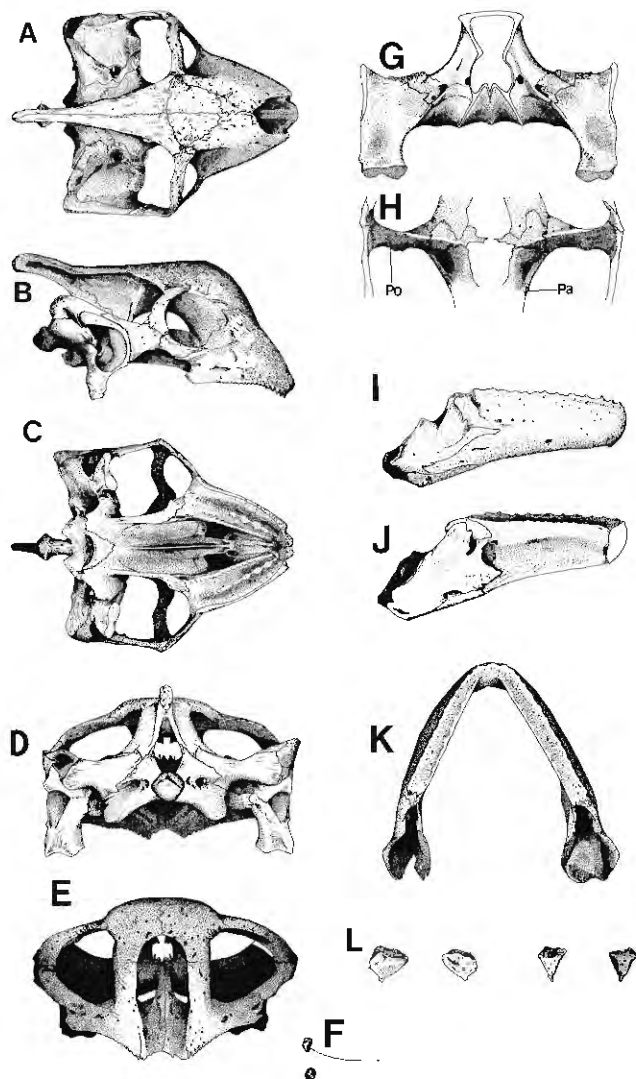


Figure 8. *Dipsochelys hololissa* Neotype (UMZ R3796) skull (A–H) and mandible (I–L). A) dorsal, B) lateral, C) ventral, D) posterior, E) anterior, F) stapes, G) anterior view of section through skull, H) ventral view (palate removed) of processus frontalis circumolfactorius (F), Po – postorbitals, Pa – parietals, I) labial, J) lingual, K) dorsal (left articular removed), L) left articular in lateral, medial, posterior, and anterior views.

tortoises between the islands. From the historical evidence relating to 'Tring 184' it can be concluded that *D. hololissa* originated on the central, granitic Seychelles islands.

Lectotype. — RCS 1021, adult male carapace, collected from "Seychelle Islands," believed to be granitic islands of the group (Sauzier, 1899), collector unknown, date of collection believed to be 1808 (Sauzier, 1899). Lectotype designation by Rothschild (1915). Lost during the Second World War.

Paralectotype. — RCS 1020, young male carapace, origin unknown, catalogued in 1810. Lost during the Second World War.

Neotype. — UMZ R3796, skeleton and scutes, adult male, carapace length 114 cm. Kept in captivity at the Casuarina Beach Hotel, Mahé, Seychelles, until its death in December 1994. Original provenance unknown. This specimen is hereby referred to *D. hololissa* and designated as the



Figure 9. Living *Dipsochelys hololissa*, Silhouette Island, Seychelles.

Neotype on the basis of the combination of the characteristically high costals, flared marginals, and the sharply angled humero-pectoral suture (145°).

Other Specimens. — The female referred to this species by Günther (1877) (BMNH-Z 88.3.20.1) does not resemble the description of *D. hololissa* and was originally identified solely on the basis of its smooth scutes; it is indistinguishable from *D. dussumieri* and should be removed from the type series of *D. hololissa*.

Diagnosis. — A giant tortoise distinguished from all other *Dipsochelys* by the following characters: 1) humero-pectoral suture angled at $140\text{--}145^\circ$; 2) extreme truncation of the articulars; 3) postorbitals bowed posteriorly throughout length; 4) processus frontalis circumolfactorius large and regular in shape; 5) acromion process at $100\text{--}115^\circ$ to scapula; 6) no olecranon process; 7) reduced fusion of skeletal elements.

External Morphology

Shell. — The shell is domed, its posterior width is slightly greater than the anterior (mean $109 \pm 3.5\%$; $103\text{--}112\%$). The vertebrals have raised centers, vertebral 3 is the highest point of the shell but is only $1\text{--}5\%$ (mean $2.3 \pm 1.6\%$) higher than vertebral 2 and $4\text{--}9\%$ (mean $6.2 \pm 2.1\%$) higher than vertebral 4. Vertebrals 1 and 5 slope downwards steeply. The carapace is broad and dorsally flattened; the height to the top of the costal at the middle of vertebral 3 is $86\text{--}89\%$ of the shell height and the tops of the costals are angled at less than 10° to the horizontal. The scutes are usually smooth and dark brown. A nuchal is present, the caudal is either flat or curved under the carapace and is usually single (divided in the lectotype according to Rothschild, 1915). The anterior and posterior marginals are flared outwards and deeply notched, producing a scalloped effect. The male plastron is $71\text{--}91\%$ of the straight carapace length, of which $42\text{--}57\%$ is the bridge. Female plastron is $75\text{--}85\%$ of the straight carapace length, of which $52\text{--}55\%$ is the bridge. The width of each gular is $1.5\text{--}1.7$ times the length. The lateral quarter of the humero-pectoral suture is angled forwards at $140\text{--}145^\circ$ to its main section. The abdomino-femoral suture is angled. The anals are not notched, or notched to only $4\text{--}16\%$ of their length. The xiphiplastral margin is thickened.

Body. — Squamation of the head is similar to that of *D. dussumieri*. Males have the terminal caudal scale expanded into a broad, flat claw up to 50 mm long, the width of which is always equal to the length; this is also present in *D. arnoldi* and in large *D. dussumieri*.

Osteology

Skull. — The postorbitals are broader than in *D. dussumieri* and slope downwards gradually. They are almost horizontal at their contact with the skull roof (5–10° from the horizontal, mean $8.3 \pm 2.4^\circ$), descending to 10–30° (mean $25.0 \pm 7.1^\circ$) at their midpoint, resulting in a highly characteristic forward-looking appearance that is not found in any other species of the genus. The foramen orbito-nasale is present, but small. The processus frontalis circumolfactorius is large and is constricted at the mid-point of its length (this distinguishes it from *D. grandidieri* in which it is very large and irregular). The top of the nasal aperture is level with the top of the orbits. The quadrate bears a well-developed anteriorly directed process on the upper posterior margin of the tympanic aperture. The processus trochlearis oticum is well developed and broad. The processus vomerinus dorsalis is very small or absent; this process is significantly larger in all other *Dipsochelys* species. The alveolar ridges on the maxillae are pronounced and continue onto the lateral margins of the premaxillae. There is a deep pit on the basisphenoid which continues onto the basioccipital (also found in *D. abrupta*). The tuberculum basioccipitale is well developed and there is a ventral ridge on the occipital condyle (also found in *D. abrupta* and *D. arnoldi*). The supraoccipital crest is always well developed (even in juvenile specimens).

The dentary is deep with toothed alveolar ridges, it is slightly inflated labially. The articulars are truncated anteriorly with ossification remaining incomplete in all specimens of *D. hololissa* with the exception of BMNH-Z 'Tring 184' in which the entire articular region is fused into a single bone. There are also other features of abnormally heavy ossification associated with great size and age in this specimen; the fusion of the articular region has not been found in any other *Dipsochelys* specimen and is clearly aberrant. The articulars of all other *D. hololissa* specimens are characteristically short (length/width = 1.1 rather than the 1.6–2.0 of other *Dipsochelys* species; this difference is statistically significant: $t = 10.11$, $p < 0.001$).

Vertebrae. — As in *D. dussumieri*, except that the shortening of the dorsals is gradual with the eighth being 80% of the length of the seventh and the ninth 40% of the seventh.

Pectoral Girdle and Forelimbs. — The angle between the main shaft of the scapula and the acromion process is 100–115° instead of the 115–130° found in other *Dipsochelys* species. The coronoid fossa on the humerus is rounded, unlike the oval outline of *D. dussumieri*. There is no distinct olecranon process on the ulna, unlike the other species.

Pelvis and Hindlimbs. — Indistinguishable from *D. dussumieri* except in usually remaining incompletely fused. Unlike in *D. dussumieri*, there is no groove on the tibia.

Dipsochelys abrupta (Grandidier, 1868)

(Figs. 10 and 14)

Testudo abrupta Grandidier, 1868:377

Geochelone abrupta (Grandidier, 1868), Pritchard, 1967:172

Astrochelys (?) *abrupta* (Grandidier, 1868), Bour, 1980:544

Dipsochelys abrupta (Grandidier, 1868), Bour, 1982:118

Distribution and Status. — Known only from subfossil material from west (Andrahomana-Amparihindro) and central (Ampasambazimba) Madagascar. Material of this species has been dated to 750–2850 years before present (Bour, 1994).

Lectotype. — MNHN-P MAD3500, incomplete fossil male carapace, estimated length 100 cm (Bour, 1994), collected by A. Grandidier in 1868 at Ambolisatra, Madagascar. Lectotype designation by Bour (1994).

Paralectotypes. — Plastral fragments and six other bones referred by Vaillant (1885) but now lost (Bour, 1994).

Diagnosis. — A giant tortoise distinguished from all other *Dipsochelys* by: 1) gulars longer than wide; 2) wide vomer; 3) depression on basioccipital; 4) fourth cervical vertebra biconvex.

External Morphology

Shell. — The shell is domed, its posterior width is slightly greater (109%) than the anterior. The vertebrae have almost flat centers, vertebral 3 is the highest (5% higher than vertebral 2 and 15% higher than vertebral 4). Vertebrae 1 and 5 slope downwards steeply. The carapace is evenly domed; the height to the top of the costal at the middle of vertebral 3 is 80% of the shell height and the tops of the costals are angled at approximately 45° to the horizontal. The anterior and posterior marginals are not flared outwards or notched. The costo-marginal suture is sinuous. A small nuchal is present and the unreverted caudal is single. The plastron is 80% of the straight carapace length in the one complete example, of which the bridge forms 43%. The gulars are longer than wide. The pectorals are short, the lateral quarter of the humero-pectoral suture is angled forwards at 90° to its main section. The abdomino-femoral suture is angled. The anal scutes are notched to 13–28% of their length.

Body. — Unknown.

Osteology

Skull. — Only a single poorly preserved cranium and a fragmentary dentary are known. These differ from *D.*

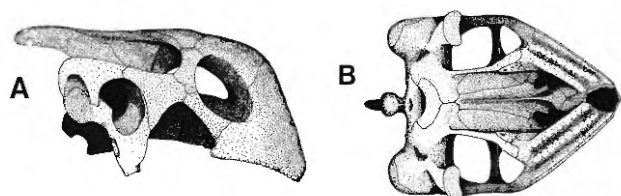


Figure 10. *Dipsochelys abrupta* skull (reconstruction of AM 'Ampasambazimba 1909'). A) lateral, B) ventral.

dussumieri in that the quadrate bears a well-developed anteriorly directed process on the upper posterior margin of the tympanic aperture. The foramen orbito-nasal is present, but small. The processus trochlearis oticum is well developed and broad. The alveolar ridges on the maxillae are well developed, their anterior extent is not known. The anterior portion of the vomer is unusually wide. There is a depression on the ventral surface of the basisphenoid extending onto the anterior margin of the basioccipital, a similar depression in the middle of the basioccipital, and a ventral ridge on the occipital condyle.

The dentary is deep with strongly toothed alveolar ridges. The posterior half of the dentary is inflated labially. The articular region is not preserved.

Vertebrae. — The atlas is not preserved. The fourth cervical vertebra is biconvex, instead of the third as in all other *Dipsosaurus* species. No dorsal vertebrae are preserved. No complete caudal series is preserved.

Pectoral Girdle and Forelimbs. — The angle between the main shaft of the scapula and the acromion process is 115–120° in lateral view and 165° in ventral view. Both medial and lateral processes of the humerus are parallel with the shaft, so that the former is obscured in dorsal view. The antero-dorsal surface of the humerus bears a distinct ridge between the lateral process and the humeral head. The coronoid fossa is triangular in outline. The ulna is straight. The manus is not preserved.

Pelvis and Hindlimbs. — The pelvis is fused, the pelves of both sexes are similar to those of *D. dussumieri*. The femur tapers distally in anterior view as in *D. grandidieri*, the proximal end being at least 1.6 times wider than the distal end. There is no groove on the lateral surface of the tibia. The pes is not preserved.

***Dipsosaurus grandidieri* (Vaillant, 1885)**

(Figs. 11 and 14)

Emys gigantea Grandidier, 1868:378

Testudo grandidieri Vaillant, 1885:876

Testudo madagascariensis Rothschild, 1915:pl. xxxiv, fig. 3-4

Geochelone grandidieri (Vaillant, 1885), Loveridge and Williams, 1957:224

Aldabrachelys grandidieri (Vaillant, 1885), Bour, 1980:544

Dipsosaurus grandidieri (Vaillant, 1885), Bour, 1982:118

Distribution and Status. — Known only from subfossil material from southwest (Beloha-Ambato) Madagascar. Material of this species has been dated to 1250–2290 years before present (Bour, 1994).

Lectotype. — MNHN-P MAD3501, fossil male carapace, length 124 cm, collected by A. Grandidier in 1867 at Etseré, Madagascar. Lectotype designation by Bour (1985).

Paralectotype. — MNHN-P MAD3502, fossil carapace, estimated length 125 cm (Bour, 1994), collected by A. Grandidier in 1867 at Etseré, Madagascar.

Diagnosis. — A giant tortoise distinguished from all other *Dipsosaurus* by: 1) flattened carapace; 2) sides of carapace bulging; 3) short gulars; 4) top of nasal aperture

higher than top of orbits; 5) diverging quadrates; 6) broad postorbitals; 7) very large processus vomerinus dorsalis.

External Morphology

Shell. — The shell is dorsally flattened, its anterior and posterior widths are equal. The sides of the shell bulge outwards characteristically at the midpoint of the carapace. The vertebral scutes have very slightly raised centers, vertebrals 2, 3, and 4 are the same height. The first and fifth vertebrals slope downwards very gradually. The carapace is broad and dorsally flattened; the height to the top of the costal at the middle of vertebral 3 is 93–100% of the shell height and the tops of the costals are angled at approximately 5° to the horizontal. The anterior and posterior marginals are flared outwards slightly, only the front marginals are notched. The costo-marginal suture is sinuous. The nuchal is very small. The caudal is not reverted. The plastron is 76–87% of the straight carapace length of which the bridge forms 47–51%. The gulars are short, 1.3 times wider than long. The pectorals are small and the lateral quarter of the humero-pectoral suture is angled forwards at 90° to its main section. The abdomino-femoral suture is angled. The anal scutes are not notched and in males are thickened along the posterior xiphiplastral margin.

Body. — Unknown.

Osteology

Skull. — The skull differs from that of *D. dussumieri* in that the postorbitals are broad and slope downwards gradually. They are almost horizontal at their contact with the skull roof, descending to 40° from the horizontal at their midpoint. The foramen orbito-nasale is present, but small. The processus frontalis circumolfactorius is very large and irregular in outline with a distinct ridge along the midline. The nasal aperture is higher than in any other *Dipsosaurus* species, extending above the upper margin of the orbits. The quadrate bears a well developed anteriorly directed process on the upper posterior margin of the tympanic aperture. There is a low ridge running up from the antero-medial face of the base of the quadrate onto the descending process of the parietals and onto the postorbitals, anterior to the foramen nervi trigemini. The quadrates diverge. The stapes is not preserved. The processus trochlearis oticum is well developed and broad. The foramen nervi trigemini is not divided. The processus vomerinus dorsalis is much larger than in any other *Dipsosaurus* species. The alveolar ridges on the maxillae are well developed but not strongly dentate and continue onto the premaxillae. There is a depression on the ventral surface of the basisphenoid extending onto the anterior margin of the basioccipital. The tuberculum basioccipitale is absent and the occipital condyle bears a ventral ridge.

The dentary is deep with strongly toothed alveolar ridges and is inflated labially. The alveolar ridges do not extend onto the symphysis. The articulars are truncated anteriorly (length/width = 1.6), which is a significant char-

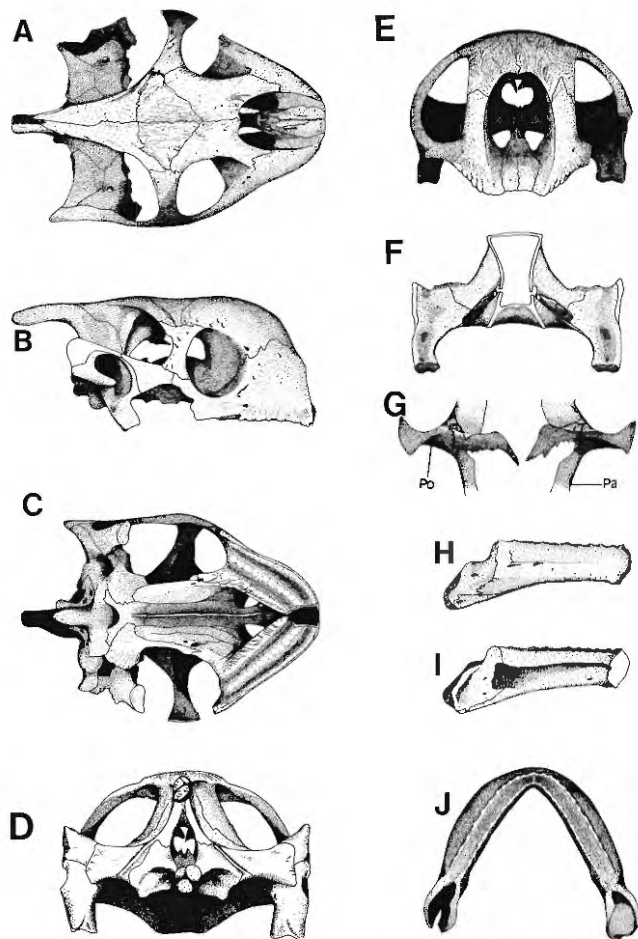


Figure 11. *Dipsochelys grandidieri* (BMNH-P 1974, right side reconstructed) skull (A–G) and mandible (H–J). A) dorsal, B) lateral, C) ventral, D) posterior, E) anterior, F) anterior view of section through skull, G) ventral view (palate removed) of processus frontalis circumolfactorius (F), Po – postorbitals, Pa – parietals, H) labial, I) lingual, J) dorsal (left articular removed).

acteristic of *D. grandidieri* and *D. hololissa*; it is not found in the adults of any other species, although small juveniles of *D. dussumieri* and *Astrochelys radiata* have truncated articulars where ossification of Meckel's cartilage is incomplete.

Vertebrae. — Cervicals are similar to those of *D. dussumieri*. No dorsals are preserved. No complete series of caudals are preserved, the terminal caudals are not fused.

Pectoral Girdle and Forelimbs. — The angle between the main shaft of the scapula and the acromion process is 125° in lateral view and 150° in ventral view. The intertubercular fossa is separated from the head of the humerus by a depression. The coronoid fossa is rounded in outline. The manus is not preserved.

Pelvis and Hindlimbs. — The pelvis is often unfused, a character otherwise found only in *D. hololissa*. The only detectable difference from *D. dussumieri* is the more pronounced curvature of the ilia. The femur tapers distally in anterior view, as in *D. abrupta*, the proximal end being at least 1.6 times wider than the distal end. There is no groove on the lateral surface of the tibia. No diagnostic characters are apparent on the pes.

Dipsochelys arnoldi Bour, 1982

(Figs. 12, 13, and 14)

Testudo elephantina Duméril and Bibron, 1835 (*ex errore*), Duméril 1854:197

Testudo indica Schneider, 1783 (*ex errore*), Gray, 1855:6

Testudo vosmaeri Fitzinger, 1826 (*ex errore*), Gray, 1855:6

Testudo daudinii Duméril and Bibron, 1835 (*ex errore*), Günther, 1877:33

Distribution and Status. — There are no reliable provenance data associated with any of the specimens referred to this species. As at least two specimens referred to the species date from before 1796, when the granitic islands of the Seychelles group were frequently visited but the outer coralline islands only rarely; a granitic Seychelles origin is therefore likely, as suggested by Bour (1982, 1984a). Subfossil material from Mahé may be referable to this species (see below).

Two living individuals in Mauritius were referred to this species in 1982 (Bour, 1982) but have since been suggested to be abnormal *D. dussumieri* (Bour, 1984a). The current population of this species is 18 individuals kept in captivity in Seychelles (Gerlach and Canning, 1997; *pers. obs.*), their origins are unknown.

Holotype. — MNHN-AC 9564, stuffed adult male, carapace length 60.5 cm, collected by Delamarre in 1844, locality "Bourbon."

Paratypes. — BMNH-Z 74.2.6.5–6, stuffed adult male with partial skeleton, carapace length 87.5 cm, collected by Lord Derby, locality "India?"; MNHN-R 7872, stuffed adult male, skeleton extracted (MNHN-R 1988.67.89), carapace length 72.5 cm, collected by Descossas, origin and date unknown.

Diagnosis. — A giant tortoise distinguished from all other *Dipsochelys* by the following characters: 1) vertebral 3 shorter than 2; 2) costal 1 longer than 2; 3) depression on suture of costals 1 and 2 usually present; 4) inflated tympanic chamber; 5) lingual dentary ridge; 6) antero-medial flange on quadrate.

External Morphology

Shell. — The shell is elongate and low, saddle-backed in outline, its posterior width is significantly greater (mean $130 \pm 7.9\%$; 120–140%) than the anterior. The vertebrae have slightly raised centers. Vertebrae 2–4 are all at the same height, vertebrae 1 and 5 slope downwards gradually. Vertebral 3 is slightly shorter than vertebral 2 (mean $14.7 \pm 8.5\%$; 4–31%) and significantly shorter than vertebral 4 (mean $33 \pm 11.8\%$; 10–50%). Costal 1 is elongated, being 110–157% longer than costal 2 (mean $142 \pm 16.0\%$). These proportions differ from those in other species, where vertebral 3 is at least as long as vertebral 2 and approximately equal to vertebral 4, and the first two costals are approximately equal in length. There is a depression on the suture of costals 1 and 2. This

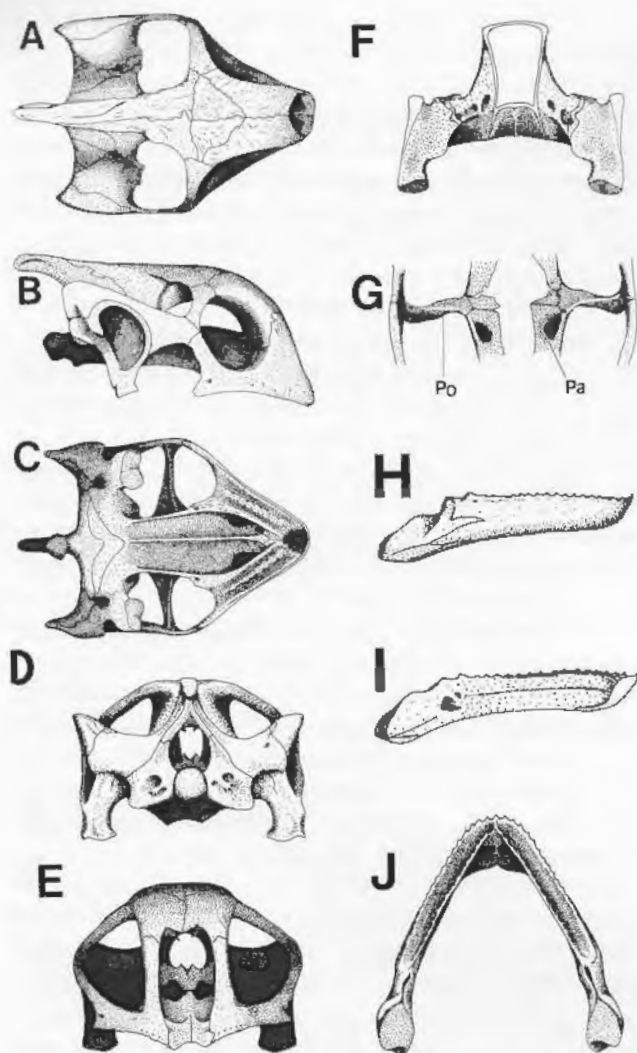


Figure 12. *Dipsochelys arnoldi* (MNHN-R 7872) skull (A-G) and mandible (H-J). A) dorsal, B) lateral, C) ventral, D) posterior, E) anterior, F) anterior view of section through skull, G) ventral view (palate removed) of processus frontalis circumolfactorius (F), Po - postorbitals, Pa - parietals, H) labial, I) lingual, J) dorsal.

is usually a single pit 0.5–1 cm deep, with extremes of development of 0.1–3 cm. In some specimens an irregular series of pits are present instead of a single depression. The carapace is broad and dorsally flattened; the height to the top of the costal at the middle of vertebral 3 is 85–89% of the shell height and the tops of the costals are angled at less than 10° to the horizontal. The anterior marginals are flared forwards slightly, the posterior marginals are flared outwards, both are only slightly notched; in BMNH-Z 74.2.6.5 the anterior and posterior marginals are curved upwards. The scutes are smooth and dark blackish-brown to black. A large nuchal is present and the caudal may be either single or double. The caudal is not reverted and is either flat or curved slightly under the carapace. In males the plastron length is 61–87% of the carapace length, of which the bridge forms 45–52%; in females it is 67–89%, of which the bridge is 62–65%. The length of each gular is equal to its

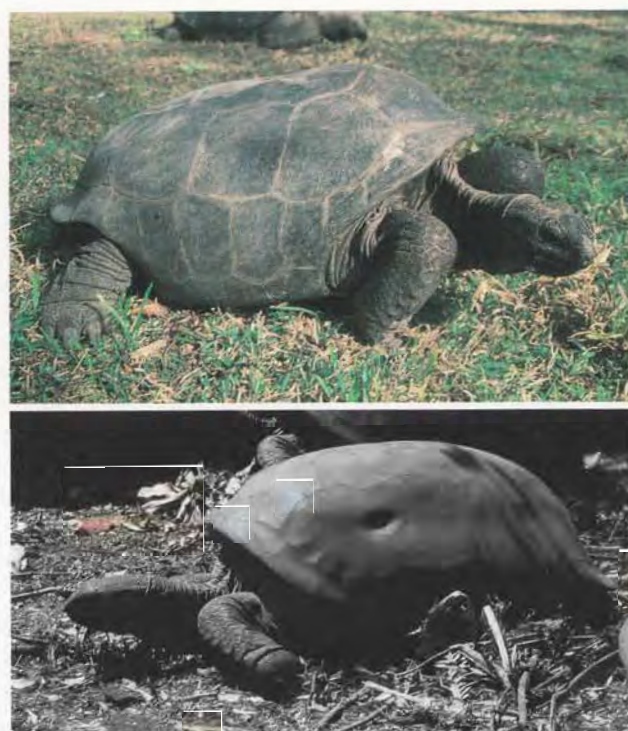


Figure 13. Living *Dipsochelys arnoldi*. A. Top) Silhouette Island, Seychelles. B. Bottom) Mahé Island, Seychelles; note extreme development of the depression on the suture of costals 1 and 2.

width. The lateral quarter of the humero-pectoral suture is angled forwards at 150° to its main section. The abdomino-femoral suture is angled. Notching of the anal scutes is restricted to 0–15% (mean $3.8 \pm 2.5\%$) of their length.

Body. — Squamation of the head is similar to that of *D. dussumieri*. The normally undivided temporal is fractured into three equal sized scales in BMNH-Z 74.2.6.5. The tails of males usually bear a well developed large terminal scale, 35 mm long and approximately equal in width; in females the terminal scale is not enlarged.

Osteology

Skull. — The skull differs from that of *D. dussumieri* in that the postorbitals slope downwards steeply and evenly at an angle of 45° throughout their length. The processus frontalis circumolfactorius is small and irregular in outline. The foramen orbito-nasale is moderately large. The top of the nasal aperture is level with the top of the orbits. The quadrate bears a well developed anteriorly directed process on the upper posterior margin of the tympanic aperture and an antero-medially directed flange on the quadrate above the articular surface. A vertical ridge runs down the descending process of the parietal medial to the foramen nervi trigemini. The stapes is not preserved. The tympanic cavity is inflated, resulting in a raising of the dorsal surface of the prootic. The processus trochlearis oticum is well developed and broad. The foramen nervi trigemini is divided externally. There is a ventral ridge on the occipital condyle. The foramen chorda tympani inferius is confluent with the fenestra postotica.

The dentary is deep with toothed alveolar ridges. There is a well developed horizontal flange on the ventral margin of the lingual symphyseal surface for the insertion of the geniohyoideus muscle. The articulars are not truncated (length/width = 1.8).

Vertebrae. — Indistinguishable from *D. dussumieri*.

Pectoral Girdle and Forelimbs. — All characters are as found in *D. dussumieri* except for the scapula-acromion angle of 120°, the strong curvature of the humerus with its triangular coronoid fossa, and the straight ulna.

The curvature of the humerus provides an enlarged surface for the attachment of the triceps brachii and brachialis inferior muscles; these are used in retraction and rotation of the forelimb. This character is found to a lesser degree in other giant tortoise taxa, including *Cylindraspis vosmaeri* (Fitzinger, 1826) and several of the Galapagos *Chelonoidis* taxa, all saddle-backed forms. Further powerful forelimb abduction is provided by the strong carapace attachment site for the latissimus dorsi muscle as represented by the depression on the suture of costals 1 and 2. It is probable that the powerful forelimb movement combines with the saddle-backed carapace to allow relatively high level browsing, as is suggested by observation of living animals. Adaptation to high browsing may also account for the labial dentary ridge in *D. arnoldi* which would allow for a stronger contraction of the geniohyoideus muscle, used in the propalinal movement of the lower jaw which could be advantageous in browsing. Living specimens demonstrate a strong shearing propalinal action resulting in a stronger, sharper bite than in other species.

Pelvis and Hindlimbs. — The pelvis is indistinguishable from *D. dussumieri*. Hind limbs as *D. dussumieri* except that there is no groove on the lateral surface of the tibia.

Hybrid Taxa

Hybrids between different taxa of Seychelles and Aldabra *Dipsochelys* have been reported since 1915 (Rothschild, 1915). Preliminary genetic analysis has suggested that living captive groups in Seychelles may include

hybrids between *D. dussumieri* and *D. hololissa* (L. Noble, pers. comm.). These tortoises have domed carapaces but are more elongate and the marginals are usually more flattened than in typical *D. dussumieri*. They differ from *D. hololissa* in having relatively high shells with the height to the top of the costals at the third vertebral being less than 85% of the carapace height. These characteristics are also found in several museum specimens. The skeletons of 4 hybrids in the BMNH (listed in the Appendix) were indistinguishable from *D. dussumieri* except for the presence of a quadrate tympanic projection, large processus trochlearis oticum, basisphenoid depression, large processus frontalis circumolfactorius, bowed postorbital, and truncated articular.

Subfossil Specimens

Seychelles. — There is little subfossil material from the central granitic Seychelles available for examination. There are three partial carapaces from La Digue (Bour, 1988) which are too fragmentary to identify beyond noting the flaring of the marginals reminiscent of *D. daudinii* or *D. arnoldi*. Two carapaces without associated data (BMNH-P 4682, 9373) are more complete. These were probably collected by the Percy Sladen Memorial Expedition under J. Stanley Gardiner in 1905–9 (Gardiner, 1936; Arnold, 1979), possibly in association with the subfossil right humerus (BMNH-P 3231) and eighth cervical vertebra (BMNH-P 3232) collected in 1905 by L. Tonnet at Anse Royale, Mahé, and brought to England by that expedition. The carapaces are both incomplete but are sufficiently well preserved for several important characters to be recognizable. The general outline is saddle-backed with little height difference in the first four vertebrals; the nuchal is moderately large and the anterior marginals flare outwards; vertebral 2 is 2–50% longer than vertebral 3, which is only 70% the length of vertebral 4 and costal 1 is 25% longer than costal 2, all characteristics of *D. arnoldi*. The subfossil vertebra (BMNH-P 3232) has no diagnostic characters but is associated with the humerus (BMNH-P 3231), which is highly distinctive.

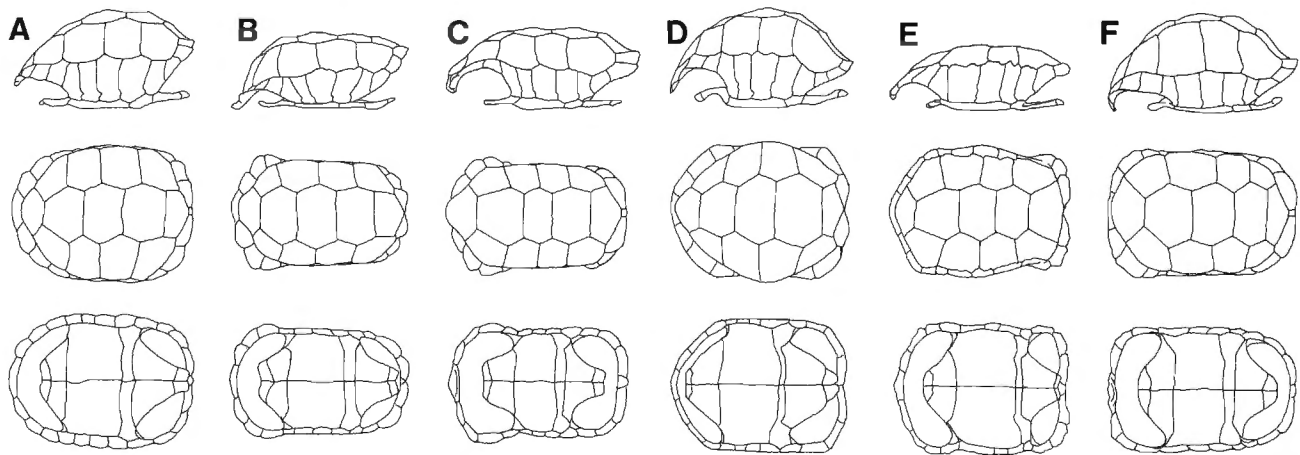


Figure 14. Shells of adult male *Dipsochelys* in lateral, dorsal, and ventral views. **A)** *D. dussumieri* (MNHN-R 7874); **B)** *D. daudinii* (after Cuvier, 1824); **C)** *D. arnoldi* (MNHN-R 7872); **D)** *D. abrupta* (BMNH-P R5890); **E)** *D. grandidieri* (BMNH-P R1972); **F)** *D. hololissa* (RCS 1021, after Günther, 1877).

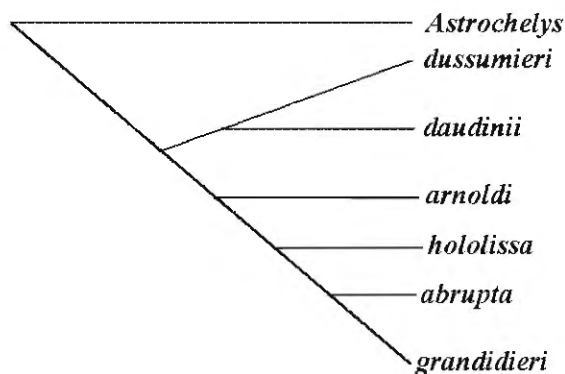


Figure 15. Proposed phylogeny of *Dipsochelys* species based on selected osteological characters from Table 3.

Its posterior face is very strongly curved, the medial process is parallel to the curved surface, and the coronoid fossa is triangular. These features are characteristic of *D. arnoldi*.

Aldabra. — The Aldabran subfossil material (BMNH-PR3783–5, R6790, R8762, R11438–9) contains a variety of skeletal elements and shell fragments. Of this material scapular fragments (R8762) show a scapula-acromion angle of 130° and a lateral concavity on the scapula. Humeri (R8762) have angled humeral processes and oval coronoid fossae. An incomplete skull (R11438) lacks a basisphenoid depression, condylar ridge, and squamosal ornament. This combination of characters is found only in *D. dussumieri*.

PHYLOGENY

The cladistic analysis, based on selected osteological characters (Table 3) produced a single tree, shown in Fig. 15, with a consistency index of 0.76 and a retention index of 0.77. This suggests that the monophyletic clade of Malagasy *Dipsochelys* (*D. abrupta* and *D. grandidieri*) shares a common ancestry with the Seychelles species (*D. hololissa* and *D. arnoldi*). The Aldabran *D. dussumieri* forms a separate clade with *D. daudinii*, which is of uncertain provenance. The close relationship between these latter two taxa may suggest that *D. daudinii* originated from one of the coralline islands of the Seychelles group. The phylogeny can be taken to suggest that the Seychelles islands provided the colonizing source for the Aldabran and Malagasy forms as has been suggested previously (Bour, 1984b). It has been assumed that Aldabra was repeatedly colonized by animals drifting from Madagascar (Arnold, 1979). The proposed relationships indicate that this is unlikely. Restriction of the analysis to cranial characters produces the same phylogeny, but with retention and consistency indices of 1.0, indicating that cranial characters are less susceptible to convergence than post-cranial morphology.

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APPENDIX

Specimens of *Dipsochelys* examined. *D. dussumieri*: BMNH-P 'Frazer Coll. No 38'; BMNH-Z 88.3.20.1, 1874.2.6.2 (= 74.2.6.2), 1947.3.4.1 (= 1929.12.27.1), 1949.1.4.53 (= Tring 139), 1949.1.4.54, 1949.1.4.60 (= Tring 143), 1949.1.4.64 (= Tring 148), 1949.1.4.65 (= Tring 145), 1949.1.4.66 (= Tring 144), 1949.1.4.86 (= Tring 173), 1949.1.5.5 (= Tring 166), 1969.1.5.10, 1978.772, RR1947.3.4.89 (= 1864.12.20.27, 64.12.20.27), Tring 147, 'Wandsworth /1/1/R4/52/B15'; MGM '*Testudo emys*'; MNHN-R 1884.268, 1909-221, 1986.755 (= 86.755), 7640, 7873-5, 9562, 9565, A1942, DD61; NPTS 1995.1, 1996.1; OUM 19642, 19651a-b, 19657, 19668-9; RMNH 3231; UMZ R3812-4; additional specimens in private collections (B. Beckett, R. Bour, S. Tolan, and R. Woodroffe). *D. cf. dussumieri* (Aldabra subfossil material): BMNH-P R3783-5, R6790, R8762, R11438-9. *D. daudini*: MNHN-R 1942, 7640; MNHN-AC A.11819 (skeleton of 7640). *D. hololissa*: BMNH-Z 1877.5.15.1-2 (= 77.5.15.1-2), 1949.1.4.45 (= Tring 115), Wandsworth 1-1A/R4/52/B16/334, Tring 184; MNHN-AC 1944.269, 1907.71; SNHM un-numbered '*D. arnoldi*'; UMZ R3796. *D. abrupta* (identified by Bour, 1994): AM 'Ampasambazimba 1909', 'Amparihingidro 1964'; BMNH-P R1124-8, R2017-8, R2020-4, R2207-8, R5890, R11249, R11255-64, R11431-7; MNHN-P MAD480, MAD503-4, MAD507, MAD514, MAD520, MAD526-7, MAD599-604, MAD909, MAD1057, MAD1271, MAD3503-8, MAD3509-10, MAD3516. *D. grandidieri* (identified by Bour, 1994): AM 'Beloha 1932', 'Tsirave 1930'; BMNH-Z 1984.1282, 94.6.5.1; BMNH-P R210, R1972, R1974-5, R1983, R11251, R20164; MNHN-P MAD593-4, MAD597, MAD607, MAD1701, MAD3511-4, MAD3517-9, MAD3520-1. *D. arnoldi*: BMNH-Z 74.2.6.5-6, 1897.10.16.1; MNHN-R 7872, 1988.6789 (mount of 7872), 9564. *D. cf. arnoldi* (Seychelles subfossil material): BMNH-PR3231-2, R4682, R9373. *D. dussumieri* x *hololissa*: BMNH-Z 1949.1.4.61-2 (= Tring 140), 1949.1.4.83 (= Tring 172), '790', '84'.

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