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ARTICLES

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A Neotype for the Aldabra Tortoise, *Testudo gigantea* Schweigger, 1812

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Statement of the problem: nomenclatural instability and confusion

Ever since their discovery by Europeans, giant tortoises of the western Indian Ocean have been at the center of taxonomic debates (Chambers 2004; Crumly 1988). Two clades are now recognized from this region (Arnold 1979): *Cylindraspis* spp., the extinct Mascarene tortoises, and *Aldabrachelys* from the Seychelles-Aldabra-Madagascar region (SAM). During nearly two centuries, no fewer than five generic names, and 13 epithets have been applied to the giant tortoises of SAM, with nearly 30 binomial combinations. Yet, recent genetic research indicates that despite this plethora of names there are but three distinguishable congeneric species in SAM: two fossil forms from Madagascar, and one living taxon, the Aldabra Tortoise (Austin et al. 2003; Karanth et al. 2005; Le et al. 2006; Palkovacs et al. 2002, 2003).

In the eye of this taxonomic tempest is the Aldabra Tortoise. Over the past two decades there has been growing confusion about which scientific name to apply to the giant tortoise that lives on Aldabra Atoll. During this period at least four generic names (*Aldabrachelys*, “*Dipsochelys*,” *Geochelone*, and *Testudo*) and three epithets (“*dussumieri*,” *elephantina*, and *gigantea*) have been used for this tortoise, with no fewer than six binomial combinations. This nomenclatural uncertainty affects not only the two fossil species on Madagascar, but also ongoing debates about giant tortoises from other islands in the Comores and Republic of Seychelles.

The contemporary surfeit of names for the Aldabra Tortoise stems from three issues: evolving opinions on the intergeneric relationships of land tortoises (Testudinidae), enhanced understanding of the taxonomic relationships of the nominal species that lives on Aldabra and Seychelles, and varying interpretations of how to deal with Schweigger’s (1812) description of *Testudo gigantea*, for which there is no known type specimen.

With regard to the question of intergeneric relationships, ever since Loveridge and Williams’ (1957:220 ff.) seminal study, the Linnean genus *Testudo* has generally been restricted to certain Old World, non-gigantic species, although as late as 1996 *Testudo gigantea* was still in use (e.g., Blaszkiewicz 1996). Loveridge and Williams (p. 225) proposed the subgenus *Aldabrachelys* for grouping the Aldabra tortoise and other closely related species within *Geochelone* Fitzinger, 1835. “*Dipsochelys*” was coined by Bour (1982) to replace *Aldabrachelys* (see below) as the genus for the Aldabra tortoise and its close relatives. Today the use of

Aldabrachelys (or “*Dipsochelys*”) as a full generic name, instead of *Geochelone*, comes from the generally accepted conclusion that *Geochelone* (*s. lat.*) is not monophyletic but that its subgenera are monophyletic, although there are divergent views (see Austin et al. 2003:1415; Caccone et al. 1999:6; Crumly 1982:232; 1985:117; Crumly and Sánchez-Villagra 2004; Gaffney and Meylan 1988:210; Le et al. 2006; Meylan and Auffenberg 1987:74; Meylan and Sterrer 2000:68; Palkovacs et al. 2002:224).

From no later than 1877 until at least 1915 more than one species of giant tortoise was thought to live on Aldabra Atoll. Some of the better known works that reported various species to be sympatric on Aldabra, are Günther (1877:10): *elephantina*, *daudinii*, *hololissa*, and *ponderosa*; Boulenger (1889:167–169): *elephantina*, *daudinii*, *hololissa*, and *gigantea* (with *ponderosa* regarded as a junior synonym to *elephantina*); Rothschild (1897): *gigantea* and *daudini* [*sic*] (with *elephantina*, *hololissa*, and *ponderosa* regarded as junior synonyms of *gigantea*); and Rothschild (1915:425–427): *daudinii* and *elephantina* (with *gigantea* on some other island in Seychelles, and *hololissa* regarded as a junior synonym of *gigantea*, and *ponderosa* regarded as a hybrid of *elephantina* and *gigantea*).

Since 1950 most workers have agreed that just one species of giant tortoise, *gigantea*, lives on Aldabra and the Seychelles (e.g., Mertens and Wermuth 1955:377–378; Wermuth and Mertens 1961:204, 1977:84; Williams 1950:520, 551; 1952:557). However, in the last two decades there have been renewed claims that as many as four species of giant tortoise are living, or have lived, on Aldabra and Seychelles islands (e.g., Bour 1985a:54 ff, 1985b:60 ff., 1988:403; Gerlach 2004); these assertions have been contradicted by recent molecular genetic work (Austin et al. 2003; Karanth et al. 2005; Le et al. 2006; Palkovacs et al. 2002, 2003). Questions about intergeneric relationships and multiple species on Aldabra and Seychelles are beyond the scope of this paper. Here I evaluate only the nomenclatural status of Schweigger’s (1812) name, *Testudo gigantea*.

Origin and early use of *Testudo gigantea* Schweigger

In 1812 *Testudo gigantea* was described by Schweigger in two places (page 327 and pages 362–363) in a monograph that was republished partially two years later (1814) (see Bour 1984a:162; Loveridge and Williams 1957:533). According to Schweigger (1812:327), the specimen upon which his description was based, from the royal collection of Lisbon, was examined in a museum in Paris (although not specifically stated, it was later assumed that this specimen was in the Muséum National d’Histoire Naturelle, Paris; see Bour 1984a:162; Crumly 1986:238; Pritchard 1986:522). It has been questioned if Schweigger “specially indicated” a type (Pritchard 1986:522; Rothschild 1915:430), for it was not customary at that time to do so. Nonetheless, the single specimen that Schweigger described is *ipso facto* the holotype, and it has been lost since at least the beginning of the 20th Century (Bour 1984a:162; Crumly 1986:238–239; Rothschild 1915:430). The “habitat” of *T. gigantea* was listed by Schweigger (1812) as “Brasilia.” Certain other species described by Schweigger (1812), with erroneous localities, are recognized today (Crumly 1988:2; Pritchard 1986:531).

Between 1831 and 1881 numerous authors referred to *T. gigantea* in varying ways showing that there was considerable confusion about the taxonomy and zoogeography of giant tortoises, and this

species in particular. *T. gigantea* was placed within the complex synonymy of *Testudo indica*, a species regarded by Gray (1831a:3, 1831b:9) as highly variable and found in many parts of the tropical world. Later, Gray (1844:5–6, 1855:5–6) placed *T. gigantea* within the synonymy of *Testudo indica*, but simultaneously listed it as “*T. gigantea* Schweig.?” (or “*T. gigantea* Schweigger?”) in the synonymy of *Testudo tabulata*. Duméril and Bibron (1835:114, 120, 121, 123) and Duméril and Duméril (1851:5) recognized *T. gigantea* Schweigger as a separate species, of unknown “*patria*,” but noted that it resembled closely *T. elephantina*, a species known from the region of the Mozambique Channel, including Aldabra and other islands. Gray (1869:171, 1870:7) made cautionary remarks about the risks of “determining species without the examination of all the parts of the animal, the skull as well as the thorax” raising the possibility that *gigantea*, as well as eight other nominal species of giant tortoise, might not be distinct species. Günther (1877:22 fn.) commented that *T. gigantea* may be the same species as *T. elephantina*, the latter known to live on Aldabra. Other interpretations during this fifty-year period include listing *Testudo gigantea* Schweigger under *Testudo tabulata* (Temminck and Schlegel 1835:69), a synonym of *Geochelone* (*Chelonoidis*) *denticulata* Linnaeus 1766, from South America; and using the name *Scapia gigantea* Schweigger (Gray 1872:3, 8) as a new combination based upon a specimen of *Manouria emys* Schlegel and Müller, 1844, a species known from Southeast Asia.

Establishment of *Testudo gigantea* Schweigger as the Aldabra Tortoise

Hubrecht (1881:43) was the earliest author known to explicitly list the locality of *T. gigantea* Schweigger as Aldabra, “the chief dwelling place of the closely allied *Testudo elephantina*.” He raised the question if these are distinct species, or “merely varieties of the same species.” Boulenger, in his seminal catalogue (1889:168) listed the locality of *T. gigantea* Schweigger as Aldabra, along with *elephantina* and two other nominal species. He later (1894:305) referred to “the true *Testudo gigantea* of Schweigger” having earlier indicated that a fossil form from Madagascar is “most nearly allied to *Testudo gigantea* of the Aldabra Islands” (1893:581).

From 1881 until present, *T. gigantea* has been applied to the Aldabra Tortoise, with varying opinions on the number of other giant tortoise species on this atoll and elsewhere in the Seychelles islands. As many as seven different species have been recognized at one time from the Aldabra and Seychelles area (Rothschild 1915), and as many as four species were thought to occur on Aldabra by Günther (1877:10) and Boulenger (1889:167–169).

Rothschild (1897:407) recognized *T. gigantea* Schweigger as the oldest name for the Aldabra Tortoise, and established *elephantina* and *ponderosa* as subspecies, or “casual aberrations of *T. gigantea*,” he also recognized *T. daudini*. By 1950 *T. gigantea* was the only species of Indian Ocean giant tortoise mentioned in Williams’ comparative study (1950:520, 536, 552), and later Williams (1952:557 fn.) drew attention to the fact that “*T. gigantea* is the oldest name” for the Aldabra Tortoise. In 1957 Loveridge and Williams (1957:225) designated *T. gigantea* Schweigger, as the type species of their new subgenus *Aldabrachelys*. Apart from the Aldabra Tortoise and the extinct Madagascar *grandidieri*, the only other species that they specifically included in their new subgenus

was *T. sumeiri* [sic], a name applied to a gigantic specimen of confused origin but generally thought to come from the Seychelles. Mertens and Wermuth (1955:377–378) and Wermuth and Mertens (1961:204) listed only one species from the Aldabra and Seychelles area: *Testudo gigantea* Schweigger, 1812, with three subspecies: *T. g. gigantea* from Mahé, *T. g. daudinii* from Aldabra's south island, and *T. g. elephantina* from Aldabra's north island. Other major taxonomic studies of testudines that continued to recognize *T. gigantea* as the only species from Aldabra include Auffenberg (1974:142) and Wermuth and Mertens (1977:84). Moreover, scores of authors in more than a hundred papers in a wide variety of scientific publications have also referred to the species of the Aldabra tortoise as *gigantea* (Gerlach 2001:23 tab. 1; Stimson, in Pritchard 1986:522).

Varying opinions on the established nomenclatural system

In 1982 Bour stated that Schweigger's type description of *T. gigantea* applied "incontestablement" [unquestionably] to an extinct Mascarene tortoise, now known as *Cylindraspis indica* (Schneider, 1783). Though acknowledging that *gigantea* had been used for decades, including by himself (e.g., Bour 1979:1225, 1980:543, 544, 1981:120), Bour concluded that the name could not be applied to the Aldabra Tortoise and decided it was a junior synonym of *T. indica* Schneider, 1783. He then revived Duméril and Bibron's (1835) name, *T. elephantina* for the Aldabra Tortoise. Bour further concluded that *Aldabrachelys* (Loveridge and Williams 1957: 225 "Type species: *Testudo gigantea* Schweigger") was not available for the Aldabra Tortoise, but a junior synonym of *Cylindraspis* Fitzinger, 1835. On the basis of these decisions, Bour erected a new genus "*Dipsochelys*" for the giant tortoises of the Seychelles-Aldabra-Madagascar region. He later published more extensive arguments along these same lines (Bour 1984a, b); in all cases his evidence was based solely on Schweigger's (1812) description.

Pritchard (1986) agreed with Bour that Schweigger had not described an Aldabra Tortoise. However, he concluded that the 1812 description applied to the South American *Geochelone* (*Chelonoidis*) *denticulata*. Like Bour, Pritchard developed intricate arguments for reinterpreting the original description. His strongest point was an assertion that "there is persuasive circumstantial evidence that the specimen indeed came from Brazil" (1986:528). While his reinterpretation is compelling, a careful reading of Pritchard's arguments reveals that they are replete with qualifiers and caveats (for example in regard to the reliability of type localities from that era, Schweigger's two recognizable descriptions of *denticulata* listed the species as native to Virginia [Crumly 1988:2; Pritchard 1986:531]; see Rasmussen and Prys-Jones [2003] for a detailed discussion on the complexities of interpreting locality data from 19th Century ornithological specimens). Moreover, Pritchard stated that Schweigger did not designate type specimens, indicating that no type specimen for *T. gigantea* will ever be located. While Pritchard agreed with Bour that *gigantea* should be replaced by *elephantina*, he argued that *Aldabrachelys* should be maintained as per his interpretation of the rules and recommendations of the International Commission of Zoological Nomenclature (ICZN). He admitted that "invalidation of the familiar epithet *gigantea* represents a rather profound upheaval," reporting that this name was well established during the past fifty years of publications

(1986:522, 531).

Crumly (1986) adopted a conservative approach to these nomenclatural dilemmas, explaining that Schweigger's (1812) description was not easy to interpret, and observing that *gigantea* was the established name for the Aldabra Tortoise. Given that the priority of the ICZN is to maintain stability and universality, he saw no reason to cause instability in a system that was established and widely used by a diversity of researchers and publications, and he reasoned that both *gigantea* and *Aldabrachelys* are valid and should be retained.

In their taxonomic review published for the Association of Systematics Collections, King and Burke (1989:70) decided to follow Pritchard (1986), as did Broadley and Howell (1991:8) in their checklist and synoptic keys. However, numerous specialists in chelonian systematics have continued to use *gigantea* for the Aldabra Tortoise, employing either *Geochelone* or *Aldabrachelys* as the generic name (e.g., Austin and Arnold 2001:2515; Austin et al. 2002:281, 2003:1417; Crumly 1988:2; Crumly and Sánchez-Villagra 2004:136, tab. 2; Ernst and Barbour 1989:250; Iverson 1992:249; Meylan and Auffenberg 1986:303, 1987:76; Meylan and Sterrer 2000:52; Zug et al. 2001:44 ff.).

A major proponent of name change for the Aldabra Tortoise and rejection of the established nomenclatural system has been Gerlach (e.g., Gerlach 1997, 2001, 2004; Gerlach and Canning 1995; see Frazier 2006 for details), who argued for the use of "*Dipsochelys dussumieri*" for the Aldabra Tortoise, thereby rejecting Bour (1984a:171 fn. 1, 1984b:282) and Pritchard's (1986:532) arguments that Gray's (1831) *T. dussumieri* is a *nomen oblitum*. In fact, Gray (1831a:3, 1831b:9, 1844:5, 1855:6), as well as Temminck and Schlegel (1835:75), clearly used "*Test. dussumieri*" only as a synonym for *Testudo indica* Schneider, 1783; hence, *T. dussumieri* is an unavailable name (ICZN Art. 11.6; Frazier, *in prep.*). Gerlach (2001:23 tab. 1) has presented a summary of names used in tortoise publications that clearly shows that *gigantea* is the established name for the Aldabra Tortoise.

Bour, in proposing the invalidation of *gigantea*, admitted to being "embarrassed to run counter to an apparently satisfying system" (1984b:281), but it is unclear what name he now prefers for the Aldabra Tortoise. Recently he has coauthored publications that have used *Aldabrachelys gigantea* (Austin et al. 2002, 2003). Yet, he has also been a coauthor of a paper in which "*Dipsochelys dussumieri*" was used for the Aldabra Tortoise (Gerlach and Bour 2003). In his review of Gerlach's (2004) popular book, Bour (2004) wrote: "[t]he author [Gerlach] has chosen to use a generic name, *Dipsochelys*, and a specific name, *dussumieri*, which are not absolutely unequivocal."

Possible disadvantages from the continued use of *Testudo gigantea* Schweigger

The only possible problem that has been mentioned for the continued use of *gigantea* for the Aldabra Tortoise is Pritchard's remark (1986:532) that the same species name was used by Grandidier (1868a, b) for an extinct giant tortoise from Madagascar, *Emys gigantea*. However, this junior homonym of *T. gigantea* Schweigger was purposely replaced by Vaillant (1885:876) with *T. grandidieri* (see also Boulenger 1894:305). Hence, *Emys gigantea* has long since been supplanted by *T. grandidieri*, with widespread and continuous use, including by Pritchard himself

(Pritchard and Trebbau 1984:198). The only way that this homonym could cause a problem would be to invalidate Vaillant's established designation and try to supplant it with Grandidier's long disused name—a proposition that would only cause more chaos and instability and contravene ICZN Article 59.1 (1999).

Summary of the contemporary situation regarding *Testudo gigantea* Schweigger

The above discussion clearly shows that there is not only general instability and chaos regarding the valid name of the Aldabra Tortoise, but the major proponents (Bour 1982, 1984a, b; Gerlach 2001; Pritchard 1986) for “invalidating” *gigantea* have admitted that this action causes upheaval in an established nomenclatural system, thereby negating the ICZN objectives of stability, priority, and universality. Other specialists of chelonian taxonomy and systematics have chosen to reject the claim that Schweigger's (1812) *T. gigantea* is not valid (see above). As mentioned earlier, Rothschild (1915) and Bour (1982) reported that the type specimen is lost. Although other workers (e.g., Arnold, Gerlach, Pritchard) have examined type material of giant tortoises in the Muséum National d'Histoire Naturelle, Paris, with special attention to old types, there is no evidence that Schweigger's (1812) type is extant. Consequently, while scholars may continue to reinterpret Schweigger's (1812) description, there can be no unequivocal determination, for this type specimen is lost.

Designation of the neotype for *Testudo gigantea* Schweigger, 1812

To clarify the situation and stabilize the name for the Aldabra Tortoise, I designate USNM 269962, an adult male from Dune Patates, South Island, Aldabra Atoll, Republic of Seychelles, as the neotype of *Testudo gigantea* Schweigger, 1812. This specimen at the National Museum of Natural History, Smithsonian Institution, consists of a skull, mandible, articulated carapace and plastron, scutes (most of which are attached to the shell), postcranial skeleton, and fragments of skin. Skull measurements (mm) are: basicranial length = 110; maximum length = 123; maximum width = 82.9. Shell measurements (cm) are: straight carapace length = 82.4, curved carapace length = 116.2; straight width of 3rd vertebral = 28.0, curved width of 3rd vertebral = 30.1; and plastron length = 65.0 (see Grubb [1971:330] for a description of methods for measuring Aldabra Tortoise shells). There is a conspicuous nuchal scute; and the fourth vertebral has an epoxy-filled circle where a titanium disk was once attached (see Gaymer 1973). This neotype is a specimen of the nominal species *Testudo gigantea* Schweigger, which has recently been defined and diagnosed thoroughly as *Aldabrachelys gigantea* by Arnold (1979:138), as *Geochelone gigantea* by Crumly (1982:218 ff., 1985:124) and Crumly and Sánchez-Villagra (2004:Table 2. ff.), and as “*Dipsochelys elephantina*” by Bour (1994:19–25, 93 ff.). As Loveridge and Williams (1957:225) noted when erecting the subgenus *Aldabrachelys*, this taxon is characterized by having the external naris higher than wide.

The status of *Aldabrachelys* Loveridge and Williams, 1957

As summarized above, Bour (1982:117, 1984a:170, 1984b:282) stated that Loveridge and Williams' (1957:225) subgeneric name *Aldabrachelys* is a junior synonym for *Cylindraspis* Fitzinger,

1835, and is thus not valid for the Aldabra Tortoise. Nonetheless, various authors have reasoned that without a ruling by the ICZN, *Aldabrachelys* continues to be available for the Aldabra Tortoise (Crumly 1986:240; King and Burke 1989:70; Meylan and Auffenberg 1987:74; Pritchard 1986:532). Bour (1994:136–137) contended that these authors were in error, and he stated that he will continue to use “*Dipsochelys*” for the generic name of the Aldabra Tortoise until a “hypothetical decision” is taken by the Commission. It is unclear if he ever submitted a proposal to the Commission, and as Bour (1994:137) admitted, the Commission has not offered an opinion on the status of the purported misidentified type specimen of *Aldabrachelys*. Hence, Loveridge and Williams' (1957) name continues to be available for the Aldabra Tortoise and closely allied species. In any case, *Dipsochelys* Bour, 1982, is a subjective junior synonym and not a valid name for the Aldabra Tortoise. Moreover, the designation of a neotype for the type species (*Testudo gigantea* Schweigger) of the genus *Aldabrachelys* Loveridge and Williams (1957) removes the nomenclatural confusion associated with the generic name of the Aldabra Tortoise. *Aldabrachelys* stands as the valid generic name for *Aldabrachelys gigantea* and other closely allied species (*A. abrupta*, *A. grandidieri*, and *A. laetoliensis*) whenever these species are regarded as generically distinct from other taxa of giant tortoises.

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Histology and Histochemistry of Caudal Courtship Glands in Three Arkansas Plethodontid Salamanders

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Breeding behavior in plethodontid salamanders is comprised of several stages that employ tactile, chemical, and possibly visual stimulation (Verrell 1997). Certain integumentary glands called caudal courtship glands, located at the dorsal base of the tail in some male plethodontid salamanders, presumably produce pheromones and are of special interest concerning courtship and mating behavior (Sever 1989). Caudal courtship glands were first reported and histologically described in plethodontids by Noble (1929), who called them “hedonic” glands. Arnold (1977) later renamed them “courtship” glands and suggested these glands be referred to by their anatomical position (hence the name “caudal” courtship glands; Staub and Paladin 1997). Courtship glands may play a pivotal role in reproduction by pheromonally influencing female receptivity during mating (Sever 2003), and thereby influencing individual mating success.

Caudal courtship glands produce secretions during the breeding season (Sever 1989, 2003). During the mating season some male plethodontids (e.g., *Plethodon jacksoni* = *Plethodon wehrlei*—Newman 1954; *Eurycea multiplicata*—Noble 1929) exhibit an elevated ridge or protuberance at the dorsal base of the tail within which caudal courtship glands have been found (Hamlett et al. 1998; Sever 1989; Trauth et al. 1993). The secretions produced by these glands are thought to aid in eliciting the “tail-straddling walk,” which is a courtship component unique to plethodontids (Arnold 1977). During this walk the female places her snout directly above the glands on the tail base of the male. Her nasolabial grooves are believed to transfer chemicals from these glands to her vomeronasal organs (Houck and Sever 1994) where pheromonal stimulation presumably maintains the female’s interest while the male deposits a spermatophore on the substrate. The female then may pick up the spermatophore with her cloacal lips, essentially completing the tail-straddling walk. Since spermatophore deposition is dependent upon the female being in the tail-straddling position (Houck and Reagan 1990) and because pheromonal secretions from the caudal courtship glands presumably increase the likelihood that the female will remain in this position, these glands would increase success in male insemination of a female. Although sexual dimorphism and hypertrophy during the breeding season provide compelling evidence of a courtship function for these glands (Sever 2003), functional tests have not been performed.

Caudal courtship glands are known in *Desmognathus*, *Eurycea*, and *Plethodon* (Sever 2003). Histological evidence also exists for several species of *Eurycea* (Hamlett et al. 1998; Noble 1929; Sever

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