

Observations on Body Size, Sympatry, and Niche Divergence in Softshell Turtles (Trionychidae)

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ABSTRACT. – The living softshell turtle species of the family Trionychidae, approximately 25 in number, show relatively low levels of sympatry, and the hypothesis is offered that, when gross sympatry does occur, direct competition between the species in question may be mitigated by possible character displacement manifested, *inter alia*, by divergence in adult size. Such divergence, when correlated with certain other changes, including development of exaggerated plastral callosities and other specializations for surviving drought conditions, as well as salinity tolerance, carapacial pankinesis, and feeding specializations ranging from piscivory to molluscivory, probably facilitates the utilization of different microhabitats and feeding niches by various trionychid species within the same general area. Examples of the resulting gross sympatry exist in North America (*Apalone spinifera* and *A. mutica*) and Africa (*Trionyx triunguis*, *Cyclanorbis elegans*, and *Cyclanorbis senegalensis*), but reach their greatest degree in Asia, where the small or medium *Lissemys*, the large *Aspideretes*, and the giant *Chitra* are grossly sympatric in much of the Indian subcontinent, and culminating in the *Amyda–Dogania–Chitra–Pelochelys* assemblage in a small area of western Thailand and in eastern Java. In that the data for maximum size of each of the extant softshell species in the last thorough review of the Trionychidae were presented very conservatively, these are re-evaluated in the light of new size records for many of the species. A breakdown into general categories of small, medium, large, and giant trionychid species is proposed, and cases of sympatry between members of these size categories are discussed. A detailed discussion of size, identity, and new specimens of the poorly-documented giant species *Rafetus swinhoei* is also offered.

KEY WORDS. – Reptilia; Testudines; Trionychidae; *Amyda*; *Apalone*; *Aspideretes*; *Chitra*; *Cyclanorbis*; *Cycloderma*; *Dogania*; *Lissemys*; *Pelochelys*; *Pelodiscus*; *Rafetus*; *Trionyx*; turtle; morphometrics; body size; sympatry; character displacement; Africa; North America; Asia

Several turtle families, including the Bataguridae and the Testudinidae, include species that encompass a remarkable range of adult body size, from dwarf forms (the batagurid *Geoemyda spengleri* or the testudinid *Homopus signatus*, each only ca. 100 mm in carapace length at maturity) to the 800 mm batagurid *Orlitia borneensis* and the 1200 mm testudinid *Geochelone nigra*. This order-of-magnitude range in linear dimensions corresponds to about three orders of magnitude in body mass, and clearly has enormous implications for a wide range of functions, including thermoregulation, crypsis, availability of protected retreats, feeding community associations, avoidance of direct competition with otherwise relatively closely related species, salinity tolerance, choice of nesting sites, depth of nests, and the food-chain role played by each species as predator or prey. Nonetheless, such size adaptation must take into account the fact that hatchlings and juveniles of all chelonian species are relatively small, the retreats and feeding niches of the juveniles and the predatory stresses upon them may be quite different from those of the adults, and generalizations about interactions between species of greatly different adult sizes must note that a direct encounter may frequently involve an adult of a small species and a juvenile or hatchling of a larger

one. Furthermore, while “smallness” may well be an important adaptive response of certain species to their environment, there is clearly a size below which a hatchling is unlikely to survive, especially among testudinids and terrestrial batagurids in which the carapace length of the hatchling may be as much as 30% of the adult carapace length, whereas it may be only about 5% in the case of very large cheloniids (e.g., *Caretta caretta*) or testudinids (e.g., *Geochelone nigra*).

The softshelled turtles of the family Trionychidae present a further case of notable size diversity within a single family. Indeed, size variation is by far the most externally conspicuous mode of morphological diversification shown by live softshells, to the extent that adult trionychids may be so externally nondescript that, if they cannot be differentiated by size category, identification to species may not be easy. Apart from size, the external characters distinguishing species lie principally in color patterns (most strikingly in juveniles), position of the eyes (very far forward in piscivorous forms such as *Chitra*, *Pelochelys*, and *Cycloderma frenatum*; in an intermediate position in species with generalized diets; far back in the durophagous *Trionyx triunguis* and even further in *Dogania subplana*), and the degree of

development of the callosities of the plastron. Other external features may include the texture of the carapacial surface (random pits, pits arranged in lines or curves, or shagreen-like asperity), and the presence or absence of warts or tubercles on the nuchal area of the carapace and/or adjacent parts of the neck. The scalation of the forelimbs may also be important, although sometimes difficult to describe simply or unambiguously when constructing identification keys.

The forms with the most complete secondary or epithelial bony plastra (e.g., *Lissemys punctata*, *L. scutata*, *Cyclanorbis senegalensis*, *Cycloderma aubryi*) appear to be adapted to resist dessication during prolonged droughts or dry seasons, and have other adaptations that may resist water loss, including development of semilunar valves concealing the retracted hind limbs and considerable reduction of the unossified portions of the carapace.

The factors that have shaped the development and evolution of these most improbable of all turtles have been discussed by Pritchard (1984) and Meylan (1987). To the layman, a softshell turtle seems virtually an oxymoron, a creature lacking the rigid shell that, to many, defines the very concept of a turtle; in short, an evolutionary mistake. The truth is very different. Trionychids may seem to be extraordinarily vulnerable, but in fact the flexible parts of the shell are very tough, their very flexibility precluding fracture through trauma, and the vital organs are rather well protected by the heavily ossified anterior and central parts of the carapace. Because the carapace takes the form of a shallow bowl or flat shield without significant plastral bracing to prevent distortion under vertical pressure, it is strengthened in most species by thickening of the neural and pleural elements (at least in mature animals), and by broadening of the ribs and rib heads, which are strongly sutured with the vertebral column.

The plastron may also be heavily armored with enlarged callosities (although this is not always the case). But it is significant that the plastral bones and callosities of softshells remain loosely juxtaposed or interdigitated rather than rigidly sutured, with the frequent exception of close sutural bonding or fusion of the hyoplastra to the hypoplastra, and sometimes also between the xiphiplastra in the midline. But the ability of a live trionychid to undergo extraordinary and instantaneous changes in overall body thickness by plastral kinesis as the neck and head are rapidly extended and retracted is never compromised.

The trionychids also show considerable variation in the ontogeny of development of the callosities of the plastron and the pleural bones of the carapace. For example, in *Apalone* the plastral callosities and pleural bones are feebly developed in young animals and do not reach their full expression until maturity is reached; in *Apalone ferox*, the fully ossified condition of the hyo-hypoplastral and xiphiplastral callosities is not reached until old age. On the other hand, the callosities and pleural bones of the giant taxa *Chitra* and *Pelochelys* reach mature expression even when the turtles are only 10–20% of mature dimensions.

The ability to accommodate dramatic visceral displacement in the course of neck and limb retraction and extension may be one of the principal advantages of the elimination of the peripheral bones and the loss of rigid external scutes in trionychids. But other advantages may be the facilitation of gas exchange through the highly vascular unossified ventral surface of the “shell,” and mechanical advantages afforded by the flexible carapace flap. The former is evidenced by the fine capillary networks visible externally in the superficial unpigmented areas of the plastron, and the tendency of the entire underside to “blush” pink or red when a trionychid is stressed, as by being turned on its back on land. The flexible carapace flap may facilitate very rapid swimming without the energy-extravagant shell rolling that occurs during vigorous swimming activity in many hard-shelled turtle species, and it certainly seems to facilitate rapid and effective shuffling of the animal into bottom substrates, from which many trionychid species practice a form of “ambush feeding” upon prey too fast to be caught by pursuit.

Many trionychids are rather large animals, yet curiously the existence, degree, and even direction of sexual size dimorphism had not been clarified for any species except the well-studied but unspecialized and limited North American forms of the genus *Apalone* when Meylan wrote his 1987 monograph. Furthermore, the actual maximum size reached by each of the extant species is often unclear, museum series of these elusive and large turtles often being highly inadequate. Yet knowledge of the potential size reached by the various trionychids constitutes essential raw data upon which to base a consideration of the role of absolute size and evaluation of character displacement involving size divergence between sympatric trionychid species as a possible means by which niche competition may be mitigated.

Partial partitioning of ecological niches by divergence in adult size is characteristic of several sympatric congeneric or confamilial turtle species assemblages. For example, in the llanos of Venezuela, three species of *Podocnemis* display gross sympatry — the very large *P. expansa*, the medium-sized *P. unifilis*, and the small *P. vogli* (Pritchard and Trebbau, 1984). In the Rio Negro, the small *P. vogli* is replaced by the small *P. erythrocephala*, and in the Rio Amazonas by the small *P. sextuberculata*. Species of different adult size within these groups select different nesting habitats, and the aquatic and terrestrial microhabitats available to or selected by each species also differ.

Among terrestrial chelonians, testudinid species show very limited sympatry. In the few cases where several species occur together (e.g., five species in Karoo National Park, South Africa), size divergence is very marked, with a very large species (*Geochelone pardalis*, carapace length up to 705 mm) the medium *Chersina angulata* (up to 267 mm) and the small *Psammobates tentorius* (up to 140 mm) grossly sympatric at low altitudes, the very small *Homopus boulengeri* at intermediate levels, and the small to medium *Homopus femoralis* alone occupying the high tablelands (Branch, 1990).

Rarely are two or more really large trionychid species found in microsympatry, although cases of gross sympatry between large and small species, or large, medium, and small species are not infrequent. Perhaps the most extreme example of generic sympatry in this family may be that prevailing at the eastern end of the island of Java, Indonesia, where four trionychid genera are found. The giant *Chitra* and the large *Amyda* are at least partially sympatric (although my experience at certain collecting sites suggests that, in many cases, only one form or the other occurs), the small *Dogania* occupies much smaller, rocky streams and intermediate to higher altitudes, and the giant *Pelochelys* may avoid competition with the similarly-sized *Chitra* by showing preference for estuarine environments.

Meylan (1987) was conservative in his stated maximum sizes for the various trionychid species. He quoted the length of the bony disc as his standard measurement rather than the much greater total leathery carapace length, and in most cases he utilized data from numbered museum specimens that he had personally measured, although he also cited records from presumably reliable literature (Annandale, 1912; Siebenrock, 1913; Deraniyagala, 1939) in some cases. However, specimens or records that have become available in the years subsequent to Meylan's publication exceed the size of his largest specimens in numerous cases, and such records are documented below.

METHODS

The decision was made to analyze primarily straight-line bony disc length (= BDL) measurements whenever possible, for several reasons. 1) These were the measurements used by Meylan (1987). 2) Such measurements can be obtained from practically all specimens, living, preserved, or skeletal; only on live hatchlings are they difficult. 3) They are the only measurements possible on skeletal or palaeontological specimens. 4) Absolute body mass, while conceivably a better index of size, is only rarely recorded, cannot be taken from preserved material, and is subject to widespread fluctuation in life, depending upon degree of nutrition and hydration of the animal. 5) The overall leathery carapace length (= LCL) is certainly easier to measure in live specimens and more reflective of total shell size of the animal, but the bony disc is often quite evident externally and measurable in live softshells, and in preserved material the leathery extension may be distorted, curled upwards or downwards, or otherwise difficult to measure. 6) It is a matter of preference whether the size of a softshell is best measured by the length of the bony disc or the leathery carapace — I would argue that the bony disc is the structure that fixes and defines the length of the ten dorsal vertebrae, the spacing between the shoulder and pelvic girdles, and other fundamental size parameters, and is thus the better index.

In all cases, my definition of BDL corresponds to the maximum straight-line length of the ossified, textured part of the carapace. In taxa such as *Chitra* and *Pelochelys*, with

significant incurving in the posterior margin of the bony disc, this is greater than the midline disc length. Length was not measured to the posterior tips of the eighth ribs even when these extended posteriorly to the bony disc itself.

RESULTS

Species are listed below alphabetically by genus and species. Maximum known sizes of bony disc length (BDL) and leathery carapace length (LCL) are also recorded in Table 1.

Amyda cartilaginea. — Meylan's (1987) largest specimen of this widespread southeast Asian species had a BDL of 316 mm. However, much larger specimens are known, although they occur primarily in protected or captive situations where they are not subject to early mortality for human consumption. Van Dijk (1992), in the most detailed field study of this species available, measured a BDL of 378 mm, with an estimated LCL in life of over 600 mm. He observed that live animals with estimated LCL of 600–750 mm were regularly seen in zoos and temple ponds in Bangkok. Cox et al. (1998) indicated that the species may reach a LCL of 830 mm, based upon a measured specimen living in captivity. The largest wild specimens to be found today appear to be from Sumatra; Shepherd (2000) indicated that specimens weighing 30–40 kg were sold regularly in North Sumatra.

The largest *A. cartilaginea* in the Pritchard collection, an adult male skeleton from Penang, Malaysia (PCHP 5043) has a BDL of 527 mm and had a LCL of 763 mm. However, a specimen in the collection of Chulalongkorn University, Bangkok, is larger at a BDL of 570 mm.

Apalone ferox. — The largest Florida softshell measured by Meylan (1987) was UF 45341, with BDL of 371 mm. Two decades ago (Pritchard, 1980), I reported a colossal living female *A. ferox* from Osceola County, Florida, weighing 73 pounds (33.2 kg) and with a LCL of 628 mm, but I did not report the BDL. In December 1998, I revisited this animal (Fig. 1), in captivity since April 1979, at Gatorland Zoo north of Kissimmee, Florida. It was in excellent and vigorous condition, not obese, and weighed 72 lbs (32.7 kg). The leathery carapace had grown by 10 mm in 19 years, to 638 mm, and the margins of the bony disc were quite clear and indicated a BDL of 442 mm.

Very recently, a still larger specimen has come to light. This turtle, a female from Lake Okeechobee, Florida, was caught alive by Henry Courson in the course of commercial fishing operations in August 2000, and was sold to a commercial reptile exhibit, where it soon died. The live weight was certified to be 91 pounds (41.4 kg) and curved leathery carapace length 29 inches (736 mm) (Cocking, 2000). The deceased specimen was donated to Chelonian Research Institute, where the LCL was found to be 673 mm. A skeleton was prepared, and the BDL was 387 mm. The turtle had a great deal of fat, and the bones of the carapace were completely ankylosed, with no sutures apparent. Furthermore, on each side of the plastron, the hyo-, hypo-, and xiphiplastron were ankylosed into a single massive bone. It

Table 1. General body size categories for softshell turtles (Trionychidae) arranged by increasing size of bony disc length. Maximum known bony disc length (BDL) and leathery carapace length (LCL) are given along with reference sources.

Category	Maximum Length		Sources
	BDL	LCL	
Small Species (Maximum BDL < 280 mm)			
<i>Apalone mutica</i>	180 mm	356 mm	Ernst et al., 1994; Present study
<i>Pelodiscus sinensis</i>	201 mm	—	Meylan, 1987
<i>Dogania subplana</i>	217 mm*	310 mm	Grossman and Grychta, 1998
<i>Lissemys scutata</i>	230 mm	—#	Webb, 1982
Medium Species (Maximum BDL 280–370 mm)			
<i>Apalone spinifera</i>	288 mm*	540 mm	Halk, 1986.
<i>Pelodiscus steindachneri</i>	300 mm*	500 mm	McKeown and Webb, 1982; Devaux, 1999
<i>Cyclanorbis senegalensis</i>	325 mm	350 mm	Meylan, 1987; Devaux, 1998
<i>Cycloderma aubryi</i>	365 mm	—#	Meylan, 1987
<i>Lissemys punctata</i>	370 mm	—#	Deraniyagala, 1939
Large Species (Maximum BDL 370–600 mm)			
<i>Aspideretes leithii</i>	380 mm	635 mm	Meylan, 1987; Das, 1991
<i>Trionyx triunguis</i>	410 mm	950 mm^	Meylan, 1987; Branch, 1988
<i>Aspideretes hurum</i>	416 mm	600 mm	Meylan, 1987; Das 1995
<i>Nilssonia formosa</i>	420 mm*	570 mm	P.P. van Dijk, <i>pers. comm.</i>
<i>Apalone ferox</i>	442 mm	673 mm	Present study
<i>Rafetus euphraticus</i>	450 mm*	680 mm	Taskavak, 1998
<i>Cyclanorbis elegans</i>	490 mm	600 mm	Present study
<i>Cycloderma frenatum</i>	535 mm	—#	Meylan, 1987
<i>Aspideretes nigricans</i>	550 mm*	910 mm	Das, 1991, 1995
<i>Amyda cartilaginea</i>	563 mm	763 mm	Present study
<i>Aspideretes gangeticus</i>	600 mm*	940 mm	Das, 1991
Giant Species (Maximum BDL > 600 mm)			
<i>Rafetus swinhoei</i>	635 mm	1041 mm	Present study
<i>Chitra indica</i>	724 mm*	1100 mm	Das, in press
<i>Pelochelys cantorii</i>	730 mm*	1000 mm	Rhodin et al., 1993
<i>Chitra chitra</i>	738 mm	1220 mm*	Present study
<i>Pelochelys bibroni</i>	745 mm*	1020 mm	Rhodin et al., 1993

*asterisk indicates estimated dimension

^this record suggests that the maximum BDL is underestimated

#for these cyclanorbine species, the posterior leathery flap is very short and the LCL and BDL are very similar.

is curious that this individual, considerably larger than the Gatorland specimen in both LCL and overall weight, had a smaller BDL, but it could have been that soft tissues (including the leathery disc) continued to grow long after the bony carapace had ankylosed, precluding further bony growth.

Apalone mutica. — Meylan (1987) cited UMMZ 128086, with BDL of 124 mm, as the largest recorded specimen of this species. However, PCHP 2746, with a BDL of 180 mm, greatly exceeds this figure. Ernst et al. (1994) reported a maximum LCL of 356 mm for females of this species. Maximum BDL was not stated, but I estimate that a LCL of 356 mm would correspond to a BDL of over 200 mm.

Apalone spinifera. — The largest specimen cited by Meylan (1987) was UF 37228, with a BDL of 186.5 mm. Halk (1986) described a huge female *A. spinifera* from Louisiana with a LCL of 540 mm and weight of 11.7 kg. Ratios of BDL to LCL are poorly documented even for this well-known species, but Stejneger (1944) observed that a very large male *Apalone spinifera aspera* (MCZ 1597) had a BDL of 240 mm and LCL of 450 mm. Applying this same ratio, the Louisiana specimen would have had an estimated BDL of 288 mm.

Aspideretes gangeticus. — Meylan (1987) cited Annandale's (1912) BDL record of 485 mm. However, Das (1991) gave dimensions of a gigantic individual with LCL of 940 mm and weight of 67.0 kg. Such a turtle probably had a BDL of over 600 mm.

Aspideretes hurum. — Meylan (1987) cited a specimen with BDL of 416 mm (from Annandale, 1912). Das (1995) indicated a LCL of 600 mm, this probably being an animal of about the same size as the one measured by Annandale.

Aspideretes leithii. — Meylan (1987) cited a specimen with BDL of 380 mm (EOM 2819). Das (1991) mentioned a live individual with LCL of 635 mm as well as a 610 mm, 29 kg male specimen. These were probably slightly larger than EOM 2819.

Aspideretes nigricans. — This species is confined to the tank at the Shrine of Bayazid Bostami in Chittagong, Bangladesh. Meylan (1987), citing Annandale (1912), gave the maximum BDL as 403 mm. Ahsan and Saeed (1989) reported a maximum LCL of 780 mm and weight of 54 kg. Das (1991) cited a maximum of 800 mm. Such specimens would considerably exceed a BDL of 403 mm, and were probably of the order of 500–550 mm. Das (1995) gave the maximum LCL as up to approximately 910 mm.

Chitra chitra. — This species was described in 1986 and thus was not included by Meylan (1987). It is usually thought to be confined to western Thailand (Ratburi and Kanchanaburi Provinces; Mae Klong, Khwae Yai, and Kwae Noi rivers; Nutaphand, 1990), but there are a scattering of records from the Malay Peninsula (e.g., Gunong Tahan; Smith, 1922), and reliable records from sites on the Solo and Pasuruan rivers of eastern Java (McCord and PCHP, unpubl. data). Nutaphand (1979) gave details of a Thai specimen



Figure 1. Gigantic living specimen of *Apalone ferox* from Florida, USA, with bony disc length (BDL) of 442 mm and leathery carapace length (LCL) of 638 mm.

measuring 1150 mm in LCL, and weighing 120 kg. The two largest carapaces of this species in the collection of Chulalongkorn University (Bangkok) each have a BDL of 610 mm.

While studying *C. chitra* in eastern Java in 1997, Linh Uong and I encountered an enigmatic specimen that far exceeds the size of any museum-preserved *Chitra* specimen. Having confirmed the contemporary presence of the species in several areas of the Solo drainage, we visited a small museum at the site where the cranium of the celebrated "Java Man" had been discovered a century ago. Outside this museum, various vendors were offering both modern human skulls and quite sophisticated fake fossils of various kinds for sale. Following our enquiry about turtle fossils, we were taken to a house and shown an ostensible fossil of a giant softshell turtle consisting of a virtually complete carapace with substantial very hard matrix material attached to the underside (Fig. 2). The specimen was offered for sale for 6 million rupiah (then about \$6000 US), and had reportedly been collected by a Mr. Harno two months before at a site about 10 km north of the museum.

The non-negotiable price precluded purchase, but we examined the specimen carefully. It appeared to be indistinguishable from a modern *Chitra* carapace, and the detail of the complex surface sculpturing was sufficiently perfect that we concluded that it had not been carved. Thus, if not a genuine fossil, the specimen was presumably either a cast of a Recent carapace or an actual modern specimen, tricked up to look like a fossil. Invasive tests were not permitted, and we concluded that the latter interpretation was the most probable. But even the alternative (i.e., that it was a cast) required that there had originally been a genuine specimen of the same size.

The dimensions of the specimen were as follows: maximum BDL, 738 mm; midline BDL, 702 mm, bony disc width, 677 mm (measurements did not include exposed ribtips). By comparison, an adult live specimen of *C. chitra* had a maximum BDL of 385 mm and a LCL of 570 mm (BDL 67.5% of LCL). Another Solo specimen had a BDL of 270 mm and LCL of 425 mm (63.5%), and a third had BDL

of 379 mm and LCL of 570 mm (66.5%). The mean BDL/LCL ratio of 65.8% indicates an estimated LCL of 1120 mm for the pseudo-fossil specimen.

I regard this as a credible length for two reasons: 1) anecdotes (e.g., Annandale and Shastri, 1914) have long indicated that *Chitra* may attain such sizes; 2) modern softshell turtles in southeast Asia definitely attain such a length (see discussion below under *Rafetus swinhoei*); indeed, Van Dijk (1992) reported that, in Thailand, only gigantic specimens of *C. chitra*, 70–90 kg in weight, were caught in or near the Srinagarind Reservoir, and observed that the maximum LCL was over 1200 mm with weight of over 150 kg; subsequently reported by Cox et al. (1998) to be up to 1220 mm in LCL.

Chitra indica. — A specimen of *C. indica*, MNHP 1880-182, with BDL of 550 mm was the largest trionychid specimen recorded by Meylan (1987). However, the species apparently gets much larger than this. Annandale and Shastri (1914) reported a total shell length of "at least six feet" (1830 mm) for the largest Indian specimens, but the possibility of this either being a total body length (including outstretched neck), or an exaggeration by a lay observer, makes it subject to question. The largest specimen examined by Annandale (1912) had a bony disc measuring 523 mm.

When Meylan was preparing his 1987 monograph, all specimens of *Chitra* were referred to *C. indica*. However, with the proposal of a new species name (*C. chitra* Nutaphand, 1986) for the southeast Asian form, some of the largest specimens of the genus would now be attributed to this species, and are discussed above.



Figure 2. Purported fossil carapace of record size, apparently manufactured from a gigantic contemporary specimen of *Chitra chitra* (BDL 738 mm), from the Solo River, Java, Indonesia. Human skull for scale.

The question then remains as to the maximum size reached by *C. indica* (in the contemporary sense as a species limited to the Indian subcontinent). Few would dispute the statement of Smith (1931) that this is the largest of the Indian trionychids, although the maximum LCL he mentioned was only 800 mm; this was repeated by Minton (1966). Daniel (1983) claimed that *C. indica* had a LCL exceeding 800 mm. Other authors have quoted higher figures (Gunther, 1864: 37 inches = 940 mm; Tikader and Sharma, 1985: 900 mm; Das, 1985: 1520 mm; Das, 1991: 1830 mm). Das (in press) quotes a maximum LCL of 1100 mm, and since this figure was provided in the most recent work of a very reliable authority who worked in the Indian subcontinent, I shall provisionally accept it. The BDL for this specimen may be estimated using the proportionality formula of 65.8% of leathery shell length established above for the related *C. chitra*, giving an estimated BDL of 724 mm.

Cyclanorbis elegans. — Meylan (1987) cited a BDL of 475 mm for this species (NMW 1437). In May 2000 I measured a live specimen (Fig. 3) with BDL of 490 mm and LCL of 600 mm in the collection of A Cupullata (Corsica).

Cyclanorbis senegalensis. — Meylan (1987) listed a BDL of 325 mm for this species (BMNH 1949.1.3.51). Devaux (1998) recorded a LCL of 350 mm.

Cycloderma aubryi. — Meylan (1987) cited a maximum BDL of 365 mm for this species (BMNH 61.7.29).

Cycloderma frenatum. — Meylan (1987) cited a BDL of 535 mm (BMNH, type of *Aspidochelys livingstonii*).

Dogania subplana. — Meylan (1987) noted that all of the bony discs of this species that he measured were less than 180 mm in length. However, he also observed that a very large skull (BMNH 81.10.10.12) that had been illustrated by Dalrymple (1977) may have corresponded to an individual with BDL of ca. 250 mm. Some individuals of *Dogania* are markedly macrocephalic, and experience with unrelated macrocephalic species (*Chinemys nigricans*, *Macrochelys temminckii*, *Caretta caretta*, *Platysternon megacephalum*) suggests that head width may not be linearly related to carapace length. Indeed, strongly macrocephalic individuals may not have longer carapaces than specimens without significant macrocephaly, although they may well be much older. However, the aforementioned large skull of this species is not only very wide, it is also unusually long. Macrocephaly typically increases the width rather than the length of a skull, and thus an unusually long skull may indeed have come from a particularly large individual. The basicranial length of BMNH 81.10.10.12 was given by Dalrymple (1977) as 106.9 mm. The two most macrocephalic specimens in the Pritchard collection (PCHP 2919 and 4674, respectively) have basicranial lengths of 76.2 and 76.8 mm, respectively (BDL of 175 and 193 mm, respectively). These figures give slightly different BDL estimates of 245 and 268 mm, respectively, for the giant specimen. Thus, Meylan's (1987) extrapolation of a possible BDL of 250 mm for BMNH 81.10.10.12 was probably correct.

These considerations do not address the question as to what is the maximum, typical, and minimum size at maturity



Figure 3. Record-sized adult female *Cyclanorbis elegans* (BDL 490 mm) at the A Cupullata facility, Corsica. Note the well-developed flexible flaps protecting the hind limbs and tail, and the single pair of plastral callosities.

of *D. subplana*. The smallest egg-bearing females are actually amazingly small. PCHP 5039 and 5044 (both adult females, prepared as skeletons) had BDL of only 97 and 102 mm, respectively. Each was found to contain three fully shelled eggs when prepared. The specimens had not yet developed pankinesis (Pritchard, 1993). Two adult males in the Pritchard collection (PCHP 4674 and 4898) had BDL of 185 and 193 mm, respectively, and LCL of 283 and 254 mm, respectively. These data suggest that sexual size dimorphism in this species may favor males.

The drawing in Meylan (1987:16) showing the bony disc and leathery carapace outlines of the holotype of *D. subplana* may not correspond to reality, in that the length of the bony disc, as drawn, is barely more than 50% of the indicated length of the overall leathery disc. The actual ratio is apparently variable. In PCHP 4898 the bony disc occupies 76% of the length of the leathery carapace, and in PCHP 4674 it occupies 65.4%. The largest *D. subplana* in the collection of Chulalongkorn University, Bangkok, measures 195 mm in maximum BDL, 191 mm in midline BDL, and 202 mm in bony disc width.

Grossmann and Grychta (1998) reported what appears to be a record-sized *D. subplana* (discounting BMNH 81.10.10.12, known only from a skull), although when measured this live individual had spent a decade in captivity. It had a LCL of 310 mm, width of 225 mm, and weight of 3.93 kg. These dimensions approach Nutaphand's (1979) report of a LCL of 350 mm for *D. subplana*, although the credibility of this record is compromised by his report of an unrealistic maximum weight of 15 kg. Grossmann and Grychta did not report the BDL of their specimen, although an estimate based upon the ratios in PCHP 4674 and 4898 (above) suggest that it might have been 70% of 310 mm, or 217 mm. These authors also reported an adult female specimen with LCL of 215 mm.

Lissemys punctata. — Meylan (1987) cited a BDL of 370 mm (from Deraniyagala, 1939).

Lissemys scutata. — This species, formerly considered a subspecies of *L. punctata*, was elevated to species status by Webb (1982), but was not listed by Meylan (1987). Webb reported that it was a smaller species than *L. punctata*, and estimated from a dry shell (BMNH 88.12.3.4) that it might reach 220–230 mm over curve. Theobald (1876) made the estimate “8 inches or more,” and Bourret (1941) mentioned a maximum size of 230 mm.

Nilssonina formosa. — The largest specimen cited by Meylan (1987) was a BDL of 274 mm previously recorded by Annandale (1912). Annandale and Shastri (1914) reported that some specimens at the Arrakan Pagoda in Mandalay were considerably larger than any specimens preserved in museums, and van Dijk (1993) observed that the specimens in temple ponds in Myanmar were mostly of large size. He saw a live one in the Yatanabon Zoo, Mandalay, measuring 490 mm in LCL, and reported specimens of over 30 kg seen in the Doke-tha-wady River. The largest in the Pritchard collection (PCHP 5035) measures 344 mm in BDL. It lacks precise locality data, having been obtained from a market in southern Yunnan specializing in turtles imported from Myanmar. A larger specimen recently measured by P.P. van Dijk (*pers. comm.*) in Guangzhou (China) had a LCL of 570 mm and weight of 20–25 kg. The bony disc was not measured, but the proportions of the turtle as recorded in a photograph suggested a BDL of 400–420 mm.

Pelochelys bibroni. — The concept of *P. bibroni*, formerly considered to occupy the entire generic range from New Guinea through Indonesia and Malaysia to China and India, has now been restricted to include only the population

of southern New Guinea (Rhodin et al., 1993; Webb, 1995). This distinctive animal has a bold carapacial pattern reminiscent of that of *C. chitra*, and indeed an early illustration of this taxon in Günther (1864) was considered to be an artist's error by Smith (1931), who dismissed it as “a *P. bibroni*, but with the markings of *Chitra indica*.” Webb (1995) mentioned several features of the shell and integument that separate *P. bibroni* from *P. cantorii*, and to these differences may be added the less specialized skull configuration of *P. bibroni*, that of *P. cantorii* being uniquely broad in the region of the snout and orbits.

Meylan's (1987) largest *P. bibroni* (including *P. cantorii*) had a BDL of 415 mm. However, the largest true *P. bibroni* reported by Rhodin et al. (1993) had a LCL of 1020 mm. The ratio between BDL and LCL in this species has not been adequately documented, but a large live specimen illustrated on the cover of Vol. 1 No. 1 of *Chelonian Conservation and Biology* (November 1993) is shown in directly vertical profile, and the outlines of the bony disc are clearly visible. The photographic image of the leathery shell measures 100 mm in length and that of the bony disc measures 73 mm, giving an estimate that the actual BDL of the 1020 mm LCL specimen would be 745 mm.

Pelochelys cantorii. — This species was not recognized by Meylan (1987), but any *Pelochelys* from outside southern New Guinea would currently be referred to this taxon. De Rooij (1915) cited a prodigious length of 1290 mm for an example of this species, although she did not furnish details, and this record has often been quoted since. A turtle this size would have a BDL of about 942 mm. Rhodin et al. (1993) reviewed records of body size for large *P. cantorii* (as *P. bibroni*), and apart from literature records of misidentified specimens of the Hoan Kiem turtle from Vietnam (now known to be *Rafetus swinhoei*; see discussion below), the “second tier” of gigantic animals includes specimens around 900–1000 mm in LCL. The latter records are fully credible, and indicate a BDL of about 730 mm. But de Rooij's (1915) record should be rejected in that the specimen was reported to have a width of only 740 mm (57% of length), whereas Webb (1995) made it clear that *Pelochelys* has a nearly circular carapace whose shape does not change markedly throughout life, and whose width/length ratio is in the range of 93–102%. This is very different from the leathery carapace proportions of *Chitra indica*, in which the width of young adults may be only about 83% of carapace length. Thus, the specimen reported by de Rooij was probably not seen by her, and the length reported was most likely the length of the entire animal with neck outstretched.

There is probably geographic variation in the maximum size reached by *P. cantorii*. In Thailand, typical adults measure about 600 mm in LCL, and few if any significantly greater than this have been recorded.

Pelodiscus sinensis. — Meylan (1987) cited a BDL of 201 mm (ZSM 429/1911), but see discussion below of the sizes of other potential species in the “*sinensis* complex,” specifically *Pelodiscus maackii*, *P. axenaria*, and *P. parviformis*.



Figure 4. Adult *Rafetus swinhoei*, in Hoan Kiem Lake, Hanoi, Vietnam, on 14 March 2000. Photo by Ha Dinh Duc.

Pelodiscus steindachneri. — This species was placed in the genus *Palea* by Meylan (1987), but at the skeletal level *P. sinensis* and *P. steindachneri* are very similar, as Pope (1935) pointed out, and the differences relate principally to the nuchal tubercles and carapacial wattles of *P. steindachneri*. Kordikova (1991) synonymized *Palea* with the genus *Pelodiscus*.

Meylan's (1987) largest specimen (MNHN unnumbered) had a BDL of 170 mm. Specimen C84 in the University of Hanoi collection is slightly longer (175 mm). The suprascapular fontanelles in this specimen are reduced to two small, circular openings. The largest individual measured by Rudolphi and Weser (1998) had a LCL measuring 295 mm, which would suggest a BDL of about 200 mm. Devaux (1999), having examined numerous adults in markets in China, reported that such specimens were generally 3–5 kg in weight, and had leathery carapaces up to 500 mm long. This estimate may not be sufficiently rigorous to constitute an actual record, but McKeown and Webb (1982) reported that a series of large adults from the introduced population in Hawaii (Oahu and Kauai) had LCL of 276–426 mm. The biggest in this series, subsequently cited by Ernst and Barbour (1989), probably had a BDL in excess of 300 mm. Two specimens each about 400 mm in LCL were recently observed by P.P. van Dijk (*pers. comm.*) in South Chinese markets.

Rafetus euphraticus. — The largest specimen reported by Meylan (1987) had a BDL of 282 mm, a record cited from Siebenrock (1913). A somewhat larger specimen in the Pritchard collection (PCHP 4062) measures 310 mm in BDL, and is a very old female from Iran. The suprascapular fontanelles are still open, as they were in Meylan's largest specimen examined (BDL 273 mm) — although they were not in a smaller individual measuring 217 mm. Gramentz (1991) mentioned a specimen of *R. euphraticus* with LCL of 560 mm. Taskavak (1998) reported a still larger one with

LCL of 680 mm; BDL was not stated but may have been about 450 mm.

Rafetus swinhoei. — This species from eastern China and northern Vietnam appears to be on the brink of extinction. Long known only from the Chinese holotype (Gray, 1873; Meylan and Webb, 1988), it is now known that there is also a northern Vietnam specimen (NMW 30911) in the Naturhistorisches Museum Wien (Farkas, 1992). These specimens, with respective LCL of 330 and 380 mm, suggest a species of only medium size, but it is now recognized (Meylan and Webb, 1988) that several very large softshell specimens from the lowlands inland from Shanghai, China, described by Heude (1880) under the generic name *Yuen* are in fact attributable to this species.

The specimens described by Heude include one of 66 kg and others of 52 and 67 kg, and Heude accepted fishermen's accounts of turtles of up to 180 kg. The stretched (head-extended) total body length of two individuals was 1400 and 1410 mm. Adults were reported to be very difficult and dangerous to catch, and they were generally encountered by chance rather than as a target of a directed fishery. The variability of the coloration of the available specimens was such that Heude described the single taxon under no fewer than five species names (*Yuen leprosus*, *Y. maculatus*, *Y. pallens*, *Y. elegans*, and *Y. viridis*), although only *Y. maculatus* was illustrated. The few recent Vietnamese specimens also appear to show great variability in the degree of spotting, the half-grown Vienna specimen from Hanoi, for example, showing significant maculation (Farkas, 1992), and this is intense in the holotype, while photographs of very large, old adults in Hoan Kiem Lake, Hanoi, appear to show completely plain specimens. A live adult in the Shanghai Zoo has a plain gray carapace, but some degree of marbling and maculation is visible on the head.

Calculations taken from Heude's illustrations were the basis for Meylan's estimate that *R. swinhoei* may reach a

BDL of 490 mm, making it the second largest trionychid species on his list. Heude's specimens can no longer be traced, if they were ever archived (Meylan and Webb, 1988), and recent information suggests that *R. swinhoei* no longer occurs in the Shanghai area, although a rather confusing paper by Zhao (1997) claimed that three juvenile specimens of *R. swinhoei* had been received by the Shanghai Natural History Museum in the past few years. Zhao assumed that these turtles had been brought from abroad, in view of the lack of any records of the species from China for 120 years, although Zhao and Adler (1993) illustrated a live adult specimen, caught at Gejiu, southeast Yunnan, China. This site is on the drainage of the Red River, which flows southeastward into northern Vietnam and through Hanoi. Recently, Farkas and Fritz (1998) examined the three juvenile specimens described by Zhao, and declared them all to be referable to *A. cartilaginea*. In December 1999, I examined two preserved juvenile softshells, nos. 4766 and 4767 in the Shanghai Natural History Museum, that may or may not have been from the series examined by Farkas and Fritz. Both were labeled *R. swinhoei* and had respective LCL of 140 and 178 mm. Plastral callosities were absent in these juvenile specimens, but the eighth pleurals were not reduced and the head markings and shell ridging were strongly suggestive of *A. cartilaginea*, and I believe this represents the correct identification.

Niekisch et al. (1997) reported upon a third confirmed museum specimen of *R. swinhoei* (ZMB 36437-38), formerly in the Berlin Zoo, of which only the soft parts and viscera had been preserved.

Undocumented Chinese specimens of *R. swinhoei* include two that I examined in the Shanghai Natural History Museum in December 1999. Both were labeled *P. bibroni*. The first specimen, a bony carapace only, had a BDL measuring 565 mm and bony disc width of 581 mm (648 mm across the widest span of the rib tips). Nuchal indentation was insignificant and there was no posterior indentation. Identification was based not only upon the large size but also the strongly reduced eighth costal bones. There were 7 neural bones, the seventh being isolated from the remainder of the series and costal pairs VI, VII, and VIII making median contact. The carapace was very flat and had a coarsely punctate pattern of random arrangement in the central portions but organized into longitudinal rows laterally. The second specimen was an entire, dry-mounted animal, somewhat distorted and stained with oily secretions. Maximum BDL was 486 mm, maximum bony disc width was 432 mm, and width across the widest span of the rib tips was 489 mm. The specimen was a male (tail extending about 120 mm beyond the rear margin of the leathery carapace), with a slightly bilobed carapace and spotted head. Maximum skull width was 111 mm and the orbital separation was 9.4 mm. The shell was smooth, with no nuchal tubercles, and the eighth pleurals were strongly reduced (maximum span across both eighth pleurals was 127 mm).

I also examined and photographed the single live specimen of *R. swinhoei* in the Shanghai Zoo, originally from

Gejiu, Yunnan, that had been illustrated by Zhao and Adler (1993). The animal is a male and is exceptionally large, with an autumn weight of 150 kg and a spring weight of 140 kg, and is in excellent condition. It has been in the Shanghai Zoo collection since 1972. I was able to obtain a reasonable approximation of the LCL at 1041 mm and the carapace width as 787 mm. It is probably the largest trionychid in captivity, except for a reported 1220 mm *C. chitra* in a private collection in Thailand (P.P. van Dijk, *pers. comm.*). I was advised that small numbers of live specimens, up to three or four at a time, continue to arrive in the markets of Nanning (Guangxi) and Gejiu (Yunnan) during the spring and summer months, although P.P. van Dijk (*pers. comm.*) warns that there is potential confusion with unusually large specimens of *N. formosa* imported from Myanmar.

My own field work in northern Vietnam suggests that the species still exists there, but is extremely rare. At most a few individuals live in Hoan Kiem Lake in downtown Hanoi (Fig. 4) (at the present time, it is possible that there is only one of these turtles left; Ha Dinh Duc, *pers. comm.*). Photographs of these few individuals show the kind of variability, especially in head shape and maculation, that prompted Heude (1880) to name five separate species. Available literature (e.g., Constable, 1982; Rudolphi and Weser, 1998) has previously identified the Hoan Kiem turtles as *P. bibroni*, but examination of available skeletal and mounted material and photographs of living specimens, as well as in-depth discussions with Ha Dinh Duc of the University of Hanoi, indicate that the turtles in question are definitely not *Pelochelys*, and are either *R. swinhoei* or a new species with close affinity to the latter. In fact, Ha Dinh Duc (2000) has recently described the Hoan Kiem turtle as a new species (*R. leloii*), but whether the new species is valid or not remains very much in question.



Figure 5. Skull of *Rafetus swinhoei* from northern Vietnam (left), with skull of *Pelochelys cantorii* for comparison (right).



Figure 6. Gigantic specimen of *Rafetus swinhoei* (BDL ca. 635 mm) on exhibit in Ngoc Son Temple, Hoan Kiem Lake, Vietnam.



Figure 7. Gigantic specimen of *Rafetus swinhoei* (BDL 633 mm) on exhibit in the municipal museum in Hoa Binh, Vietnam.

The head shape of Vietnamese specimens is completely different from that of *Pelochelys*, lacking the extreme flattening and widely separated orbits of the latter (Fig. 5); the eighth pleural bones are reduced as is typical of the genus *Rafetus* but no other extant Old World trionychids, including *A. cartilaginea*; and the xiphiplastral callosities are absent, although they are always present in large adult *A. cartilaginea* and are extensive throughout life in *Pelochelys*. As regards affinities with turtles further to the west, size alone, as well as the undivided first neural bone, would preclude allocation to *Aspideretes*. On the other hand, no characters are in hand to differentiate the few available Vietnam specimens from *R. swinhoei*, and, given the reduced status of populations of *R. swinhoei* anywhere, appropriate series for comparing Chinese with Vietnamese turtles may never be available.

One of the Hoan Kiem turtles died several years ago, and has been mounted on exhibit in a large glass case in Ngoc Son Temple on the larger of the two islands in the lake (Fig. 6). The accompanying label claims that the turtle, found in 1968, weighed 250 kg, with a length of 2100 mm and a width of 1200 mm, and was said to be 400–500 years old. I was prevented from making accurate confirmation of the dimensions by the sealed glass case surrounding the specimen, but by careful alignment of a measuring tape along the base and

the exterior glass, I was able to make measurements that were at least unbiased, and probably accurate within 30 or 40 mm at worst. Dimensions thus recorded were as follows: total length as mounted (head, neck, and carapace, tail not protruding beyond rim of shell), 1448 mm; width of leathery shell, 711 mm; LCL (possibly posteriorly reconstructed), 965 mm; BDL, 635 mm.

The skeleton of a second Hoan Kiem specimen, with some curious errors in placement of certain bones, is in the Hanoi Museum, in the care of Nguyen Duc Hong. The specimen was not available for me to measure but it appears to be an adult. Photographs indicate an estimated BDL of 600 mm.

The Hoan Kiem turtles are famous throughout Vietnam, but it is not generally realized that a softshelled turtle even larger than the mounted individual in Ngoc Son was found near Hoa Binh in 1993, and despite efforts to keep it alive in a converted hotel swimming pool, it died within a few days. Fortunately it was carefully mounted and placed on exhibit in the municipal museum in Hoa Binh, where it remains (Fig. 7). Newspaper accounts at the time of capture gave the carapace length as 1200 mm and the weight as 121 kg. However, the specimen was fully accessible and I was able to determine the maximum LCL (over the curve, but there was very little convexity) as 1095 mm, the maximum BDL as 633 mm, the maximum straight width as 740 mm, the straight head width as 170 mm, the total skull length as 250 mm, and the total length (as mounted, head and neck extended) as 1560 mm. It may be the largest softshell on exhibit in any museum. For the present purposes, I am inclined to discount the unsupported estimate of a LCL of about 1900 mm in a caption to a photograph of one of the Hoan Kiem turtles basking on the small island in the lake (Niekisch et al., 1997).

Few other specimens of *R. swinhoei* are available for measurement. However, specimen T91 in the University of Hanoi collection (Fig. 8), from the Ma Song River, has a BDL of 446 mm and width of 442 mm. Another specimen was confiscated from a passenger arriving from Vinh at Hanoi Railway Station in 1995. The turtle was freshly dead, and had a LCL of 620 mm, width of 570 mm, and weighed 29 kg (Ha Dinh Duc, pers. comm.). This must have been a subadult specimen, suggesting that some reproduction has occurred recently, somewhere.

Experienced Vietnamese fishermen have reported occasional additional specimens. Nguyen Hoy Son and his son Nguyen Duc Viet, captors of the Hoa Binh specimen, reported that individuals weighing 84 kg (from Hoa Binh) and 175 kg (from Thai Binh) had been caught in 1978. Nguyen Van Ao reported that he had captured two individuals in the Ao Chau Swamp — a 104 kg specimen in 1972 and a 68 kg specimen in 1978 or 1979. The swamp, 6 m deep with holes up to 20 m, and 160 ha in size during the dry season (200 ha during the wet season), is located northwest of Hanoi, near Phu Tho, Ha Hoa Phu Tho Province. Nguyen Van Ao was of the opinion that many such turtles remained in the swamp.

Interviews with veteran river fishermen in the Ao Chau area and north to the China border in November 2000

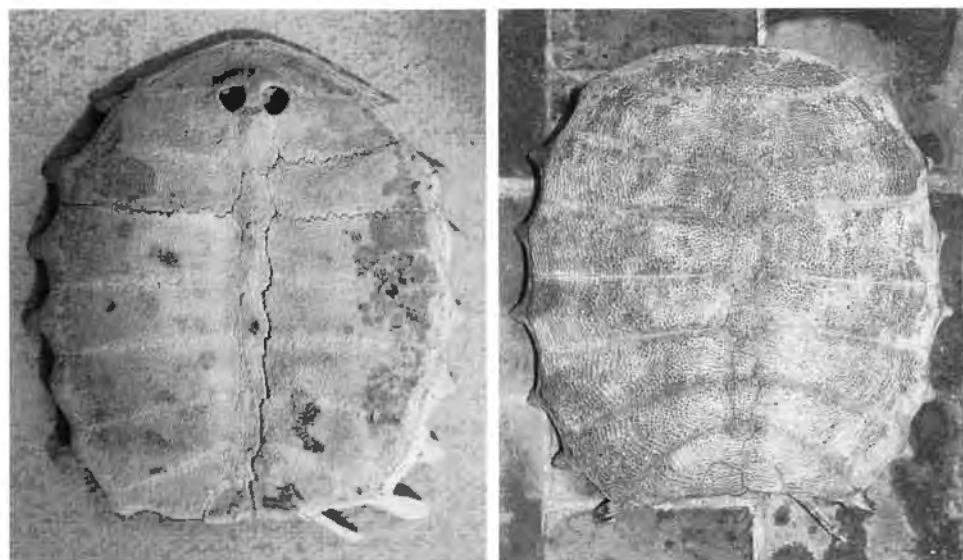


Figure 8. Comparison between bony carapaces of the two species of *Rafetus*: (left) *R. euphraticus* (PCHP 4062; BDL 310 mm), (right) *R. swinhoei* (Univ. of Hanoi T91; BDL 446 mm).

yielded extensive anecdotal natural history data about *R. swinhoei* that will be the subject of a future report. In two cases, the interviewees were able to produce nearly complete skeletons of *R. swinhoei* specimens that they had caught; these were being kept for Chinese medicines, but were purchased and incorporated into the collections of Chelonian Research Institute. One of these, caught in a pond at Dam Ben near Ha Hoa (Phu Tho Province) beside the Red River, was a juvenile with BDL of approximately 350 mm, that had been caught as recently as August 1999, indicating some recent successful reproduction. A somewhat larger skeleton (BDL 476 mm), lacking the skull, was obtained from a fisherman at Ao Chau Lake; it had been caught in 1982. In the smaller specimen the circular suprascapular fontanelles were open; in the larger they were closed. It is possible that the closure of these fontanelles is as unpredictable as in the congener *R. euphraticus*.

Trionyx triunguis. — Meylan (1987) cited a BDL of 410 mm (KNM-VP-ER-8123). Branch (1988) gave the maximum LCL as 950 mm and the maximum weight as 40 kg.

DISCUSSION

As Meylan (1987) observed, Recent trionychids are, for the most part, large turtles. Comparisons may perhaps best be made between the maximum known size of the various species, in that quoted values for mean adult dimensions data are often flawed by the inclusion of individuals of uncertain maturity in the sample sizes, and furthermore, since trionychids are widely utilized for food almost wherever they occur, opportunities for individuals to achieve their growth potential nowadays may be rare. Yet they presumably evolved in a milieu in which individual turtles became safer from predation and many other trials of life as they became larger. For almost any trionychid population today, demographic analysis is likely to show evidence of anthropogenic pressure, with depression of mean adult size and

rarity of individuals that have reached asymptotic size. Yet, in a truly intact population, individuals that would normally be considered unusually large are likely to constitute a significant, if not major, part of the population. This is illustrated by the very large size of many individuals in the unexploited captive population of *A. nigricans* in Chittagong, Bangladesh.

Using the maximum bony disc length (BDL) standard, living trionychids may be reasonably grouped into four general size categories; small (< 280 mm); medium (280–370 mm); large (370–600 mm); and giant (> 600 mm). Comparisons are somewhat complicated by the very different body masses of specimens of, say, the gracile *A. mutica* and the robust *L. punctata* with equal bony carapace length, or the fact that in the cyclanorbine genera *Lissemys* and *Cycloderma* the posterior leathery flap is of very modest development and the bony disc is thus very close to the length of the entire leathery carapace. Furthermore, the widespread South Asian species *L. punctata* may reach a BDL of 370 mm in Sri Lanka but is generally much smaller in India.

Whether a version of “Pritchard’s Rule” (Murphy and Henderson, 1997), which proposes a generally predictable relationship between the typical and the maximum length of snakes of a given species, also holds for turtles is unclear. Nevertheless, subjective substitution of “typical” sizes for “maximum” sizes for trionychid species, while obviously giving smaller numerical values, gives similar category allocations. The category assignments are given in Table 1.

Within-category examples of sympatry are rare. There are none among the small and medium species. Among large species, there is gross sympatry in Bangladesh between the widespread *A. hurum* and the extremely localized *A. nigricans*, and in Africa there is gross sympatry in some areas between *C. elegans* and *T. triunguis*. Among giant species, it is possible that the range of *P. cantorii* infringes

upon that of no fewer than three other members of the group, namely *R. swinhoei*, *C. chitra*, and *C. indica*, although there is substantial ecological separation. *Pelochelys cantorii* is frequently found in estuarine or even marine waters (Das, 1991, affirms that "all recent reports of the species are from marine/estuarine environments") whereas the other three have not been recorded in such habitats. Most typically, one finds that the medium-sized species live alone, and the small ones are likely to be grossly sympatric with much larger ones. Thus, *L. punctata* is sympatric with the much larger *A. hurum* and *A. gangeticus*, *D. subplana* is sympatric with the much larger *A. cartilaginea*, *P. sinensis* is sympatric with the much larger *R. swinhoei*, *C. senegalensis* is sympatric with the much larger *T. triunguis*, and so on. In all cases, sympatric implies grossly sympatric; the actual ecological situations may be much more complex, and some of the most interesting cases are discussed below.

Trionychids in China

The trionychid fauna of eastern China is inadequately understood, and any ecological interpretations made here will necessarily be tentative ones. Heude (1880) described more than twenty Chinese trionychid species, but the vast majority of these have long been synonymized with *P. sinensis*, with the few very large species synonymized with *R. swinhoei* as described above. In addition, the medium-sized species *P. steindachneri* is always considered valid, although the closeness of its relationship with *P. sinensis* is arguable (Meylan, 1987; Kordikova, 1991).

Beyond these species, there has been recent recognition of *Pelodiscus maackii* (Brandt, 1858) by Fritz and Obst (1999). This species, allied with *P. sinensis*, has a dorsal pattern of fine white spots; it is distributed in eastern Russia, Manchuria, and Korea. Furthermore, two very small species of *Pelodiscus* from China have also been described recently: *P. axenaria* (Zhou et al., 1991) and *P. parviformis* (Tang, 1997). The former, averaging only 97 mm in LCL and 100–300 g in weight, is described as a snail-eating form sympatric with *P. sinensis* in Hunan Province, whereas *P. parviformis*, from Guanxi and Hunan, is barely larger (110–120 mm), and has a characteristic conspicuous dark figure in the center of the carapace.

Much of southern China is mountainous and the coastal plain is narrow, but the small Chinese softshell *P. sinensis* is very widespread in the lowland areas, extending south to northern Vietnam as well as to Taiwan and Hainan. To the north it is replaced by *P. maackii*, a somewhat larger (LCL 353 mm; Stejneger, 1907) but related form. In the southern part of this range, there is the potential for range overlap with the medium-sized (LCL to 500 mm) species *P. steindachneri*. Few data are available on the details of this potential interaction, but P.P. van Dijk (*pers. comm.*) reports that *P. steindachneri* is considered to be an upland stream animal, whereas *P. sinensis* is a floodplain dweller, an altitudinal separation also reported by Pope (1935). Devaux (1999), on the other hand, reported that both *P. sinensis* and *P.*

steindachneri were found in flood-plain habitats that included rice fields.

Pope (1935) noted that *P. steindachneri* has a much less aggressive disposition than *P. sinensis*, and further observed that, on Hainan, the flesh of *P. steindachneri* sold for an enormously higher price than did that of *P. sinensis*, a difference in palatability that, Pope speculated, may well be reflected in the life histories of the two species. The differential price is also expressed in Vietnam today; Duc and Broad (1995) reported that, in Hue (Vietnam) in November 1993, *P. sinensis* meat sold for 20,000 dong per kilo, whereas that of *P. steindachneri* sold for 170,000 dong per kilo—about \$17 US, a figure high enough to reflect probable traditional medicine value in addition to protein content or taste.

Again, it must be emphasized that ecological knowledge of Chinese softshells is woefully incomplete. Nevertheless, a possible emergent pattern is one in which the small *P. sinensis* is widespread in lowland floodplains and other bodies of water, and is replaced by a slightly larger form (*P. maackii*) to the north, in an area where no other softshells are present. To the south, two very small forms, *P. axenaria* and *P. parviformis*, each significantly smaller than *P. sinensis*, exist sympatrically with it.

There may also be partial sympatry with the larger species *P. steindachneri* (although this is mitigated by some degree of altitudinal separation), as well as with the giant form *R. swinhoei* in both eastern China and northern Vietnam. In coastal and estuarine areas, substantially separated from other trionychids by its different habitat, is the giant species *P. cantorii*, although the detailed distribution of this species in China is very poorly documented. These interpretations all fall within our hypothesis that, where there is no actual habitat separation, trionychid species may co-exist and minimize competition by evolving (or having already evolved) divergent adult sizes and the different life styles and ecology that accompany such changes. Such an hypothesis does not preclude the various species being preadapted for successful coexistence by achieving divergent sizes before they became sympatric, although it is unlikely that the fossil record will ever be detailed enough to identify which happened first.

Adult size divergence will carry with it divergence in many ecological characteristics, and would be driven by one or more of them. These include habitat selection, salinity tolerance, drought resistance, nest depth, predators and prey, and others—thus achieving the classical non-overlapping N-dimensional hypervolumes identified by ecological theory as necessary for coexistence, while making only the genetic changes required to alter the age or size at which growth ceases or becomes asymptotic.

A partially parallel observation at an intraspecific rather than interspecific level would be the progressive size divergence of initially identical male and female hatchlings of certain dimorphic North American map turtle (*Graptemys*) species as they approach their dramatically different mature sizes. Various factors could be invoked (e.g., the need for rapid achievement of sexual maturity at a small size in males

versus large body size, correlated with high clutch biomass, and slow maturation in females) to provide the selective pressure for such divergence. At maturity, the diminutive males and large females of such species as *G. ernsti* are able to occupy drastically different microhabitats and feeding niches, and thus simultaneously achieve the efficiency advantages that come with specialization and the higher carrying capacity advantage that comes with the species as a whole occupying more than one microhabitat and feeding niche.

Calibrating the size differences in the genus *Pelodiscus* cannot yet be done accurately; indeed, the very validity of the two very small forms (*P. axenaria* and *P. parviformis*) has yet to be confirmed. The size relationship between *P. sinensis* and *P. steindachneri* is not as suggested by Meylan's (1987) data, which indicated that his largest specimen of *P. sinensis* had a BDL of 201 mm, whereas the largest *P. steindachneri* was only 170 mm. The figures given by Ernst and Barbour (1989) for maximum LCL — 250 and 426 mm, respectively, for *P. sinensis* and *P. steindachneri* — are more likely to reflect the actual direction and degree of difference.

Members of the *P. sinensis* complex also show size variation. Mao (1971) found that, on Taiwan, male *P. sinensis* averaged only 149 mm in LCL (range, 132–165 mm), and females were even smaller (135 mm on average). One might thus speculate that there could be localized size differential as an index to ecological separation of the two softshells in southern China and northern Vietnam, with the development of, or colonization by, truly large species (except for the estuarine/marine *P. cantorii*) prevented in much of southern China by the lack of suitable habitat (i.e., large areas of lowland terrain, drained by large, meandering river systems). Such areas exist in the Red River valley and in the area inland from the city of Shanghai, but in between, the lowland coastal plains are very narrow.

The reason for the small size of *P. sinensis* in Taiwan is not clear. However, in the absence of any other sympatric trionychid species in the habitat, one can assume that it is some general factor of insular ecology and habitat rather than details of relationships with other trionychids that has shaped this population.

Trionychids in North America

Only a single genus of softshells, *Apalone* (morphologically most closely related to the Old World *Rafetus*), has reached North America. There are currently no trionychids at all in South America, although Wood and Patterson (1973) described a trionychid plastral bone from the middle Pliocene of northern Venezuela. This species represents a turtle considerably larger than any living North American trionychid, but comparable in size with the late Paleocene *Paleotrionyx quinni* from Colorado. Thus, the contemporary pattern of North American trionychid zoogeography and interrelationships is much simpler than in Africa or Asia, with one large species (*A. ferox*), one medium species (*A.*

spinifera), and one small species (*A. mutica*) partially sympatric with both of the larger ones. However, there are hints that the pattern may have had greater complexity, including other large forms, in the past. There is only minor geographic overlap between *A. ferox* and *A. spinifera*, with *A. ferox* primarily in the Florida peninsula and *A. spinifera* occupying habitats throughout much of the remainder of the eastern and central United States, excluding the Florida peninsula. Habitats are somewhat different (Carr, 1952), *A. ferox* showing a strong tendency to occupy ponds and lakes, and even settling basins in phosphate mining areas, whereas *A. spinifera* is primarily fluvial.

The ecological relationship between *A. spinifera* and *A. mutica* is especially interesting, in that these two species are sympatric over a large area of the central United States, and they have been the subject of more field studies than any non-American species. As regards size, our criterion of maximum size places them in different categories, *A. mutica* being small and *A. spinifera* being medium. Vogt (1981) also observed that *A. mutica* is the smaller of the two species. This size relationship appears to be maintained throughout the area of gross sympatry of the species, although the specifics vary. For example, in Wisconsin, female *A. mutica* have a LCL of 170–340 mm and males 110–180 mm whereas female *A. spinifera* are 170–460 mm and males about 200 mm (Vogt, 1981). In Kansas, Collins (1974) reported that the largest female *A. mutica* had LCL of 244 mm, while the largest *A. spinifera* was 270 mm. In Louisiana, Dundee and Rossman (1996) reported maximum LCL of the two species to be 356 and 540 mm, respectively. In Illinois, the largest *A. mutica* measured 233 mm and the largest *A. spinifera* 282 mm (Smith, 1961). In Texas, *A. mutica* reaches 356 mm and *A. spinifera* 432 mm (Garrett and Barker, 1987). In Alabama, *A. mutica* reaches 355 mm (but *A. m. calvata* only 287 mm) and *A. spinifera* 430 mm (Mount, 1975).

The ecological differences reported for the two species are similarly variable. Detailed comparisons in Iowa by Williams and Christiansen (1981) reported that the two species were sympatric in much of Iowa, but different in details of microhabitat and in feeding strategies and diet. *Apalone mutica* occurred only in the larger sections of major rivers, basked almost entirely on mud banks or sandy beaches, was a water-column feeder subsisting mainly upon invertebrates (Diptera, Tricoptera, Coleoptera, and Hemiptera), and was associated with unobstructed sand-bottomed rivers. On the other hand, *A. spinifera* occurred throughout every major and minor stream examined and in many lentic situations; basked on rocks, floating logs, and other objects when mud banks and sandy beaches were not available; was primarily a bottom feeder subsisting upon carrion and crayfish as well as a surprising amount of plant material; and was usually found around piles of debris in addition to unobstructed areas. It appeared to have a competitive advantage over the more sedentary *A. mutica*.

Some of Anderson's (1965) observations in Missouri contrast strikingly with those of Williams and Christensen.

Anderson found that *A. mutica* could be found in nonstagnant ponds and even in Ozark streams with rocky bottoms, and fed upon fish, crayfish, frogs, tadpoles, and molluscs — a diet that would be considered typical of *A. spinifera* in Iowa.

Other authors have reported various observations on the ecological and behavioral differences between the two species. In Alabama, Mount (1975) reported that the optimal habitat of *A. spinifera* was a free-flowing creek or river with a sand-gravel substrate, whereas *A. mutica* seemed best adapted to streams or backwaters of streams having deposits of silt, or sand and silt, on the bottom and along the margins. Mount considered that the impoundment of the Tennessee River throughout its length in Alabama had apparently favored *A. mutica* and had been detrimental to *A. spinifera*. On the other hand, McCoy (1982) described a reverse situation in Pennsylvania, where *A. spinifera* had expanded its range into the eastern part of the state (Delaware Valley and vicinity of Philadelphia), probably by artificial introduction, whereas *A. mutica* had not been recorded anywhere in the state since 1901, and the character of the large rivers of the Ohio drainage had been so altered by pollution that *A. mutica* may have been extirpated from those streams.

Various authors (e.g., Collins, 1974; Vogt, 1981) have commented upon the different disposition of the two species when handled, *A. mutica* having "a timid and gentle disposition when handled, rarely attempting to bite," whereas *A. spinifera* had "an aggressive, nasty temper, and will bite if not handled carefully." Nevertheless, Anderson's (1965) experience with *A. mutica* in Missouri was quite different; he reported the species to be "pugnacious and difficult to handle. The long snakelike neck enables it to strike out with surprising speed, and the knifelike edges of the jaw can inflict a painful injury."

In most parts of the world where sympatric trionychid species occur, it would be premature to attempt a quantitative analysis of size divergence; adequate sample sizes of turtles of known origin and capture method are not available. However, preliminary analysis of the relationship between the two substantially sympatric North American trionychid species reveals that, although each of the two have surprisingly different body size, ecology, diet, and even dispositions from one part of their range to another, the size differential between the two species is maintained. *Apalone spinifera* is always the larger of the two — even though, in one habitat, the largest *A. mutica* may actually be larger than

the largest *A. spinifera* from another habitat. This phenomenon provides strong circumstantial evidence that size divergence, and the various ecological, trophic, and adaptive differences that are linked with size divergence, is a fundamental attribute of trionychid sympatry. The differences may be quantified and analyzed by introducing the concept of "size divergence ratio," namely the ratio between the body sizes (here using the maximum size of the larger sex as the selected index) of the sympatric populations. Data for various populations of *A. spinifera* and *A. mutica* are shown in Table 2.

Big softshells, in general, need big rivers or lakes, unless they are able to colonize the marine environment permanently. The question thus arises as to why trionychids of all kinds are absent from the Amazon, and why there are no large forms in the Mississippi. An explanation for the absence of trionychids from the Amazon may be either that the family never penetrated to this area (indeed, there is no fossil evidence of such), or that the well-established pelomedusids (and possibly chelids also) already occupied the "large turtle" niches in this river system. Indeed, Simpson (1945) went so far as to say that trionychids and chelids may be ecologically incompatible, the two continents where chelids occur (Australia and South America) being conspicuous by the absence of trionychids, found on all other continents. However, trionychids and chelids are sympatric on the island of New Guinea.

For the Mississippi, the contemporary absence of all really large aquatic turtles except for *Macrochelys* takes some explanation. Part of the answer may lie in the observation that, around the world, the archetypal "big river turtles" (*Dermatemys*, *Chitra*, *Callagur*, *Batagur*, *Podocnemis expansa*, etc.) are all tropical forms adapted to cycles of wet and dry seasons that generate seasonally exposed sandbanks on which the turtles nest. The Mississippi environment is profoundly different in that its water regimen and temperatures are controlled by a climate characterized by cold winters, with freezing temperatures for at least several weeks a year in the northern reaches, and occasional subzero conditions even in the south.

Nevertheless, North America once had a variety of very large trionychids. Hay (1908) outlined the geological distribution of trionychids in North America, reporting a good variety already present by the Upper Cretaceous in the western states. At this time there were also two species of trionychids in New Jersey. By the Middle Eocene, "Emydidae

Table 2. Size divergence ratios for various sympatric populations of *Apalone spinifera* and *A. mutica* in North America, using the maximum BDL and LCL of the largest sex (females). The mean size divergence ratio of the leathery shell for the five specific US localities is 1.28; this corresponds to a ratio of approximately 2.2 for body weight divergence, assuming the species have the same proportions.

Parameter	Location	<i>A. spinifera</i>	<i>A. mutica</i>	Size Divergence Ratio
Bony disc length (BDL)	USA (overall)	288 mm	180 mm	1.60
Leathery carapace length (LCL)	USA (overall)	540 mm	356 mm	1.52
	Wisconsin	460 mm	340 mm	1.35
	Kansas	270 mm	244 mm	1.11
	Louisiana	540 mm	356 mm	1.52
	Illinois	282 mm	233 mm	1.21
	Texas	430 mm	356 mm	1.21

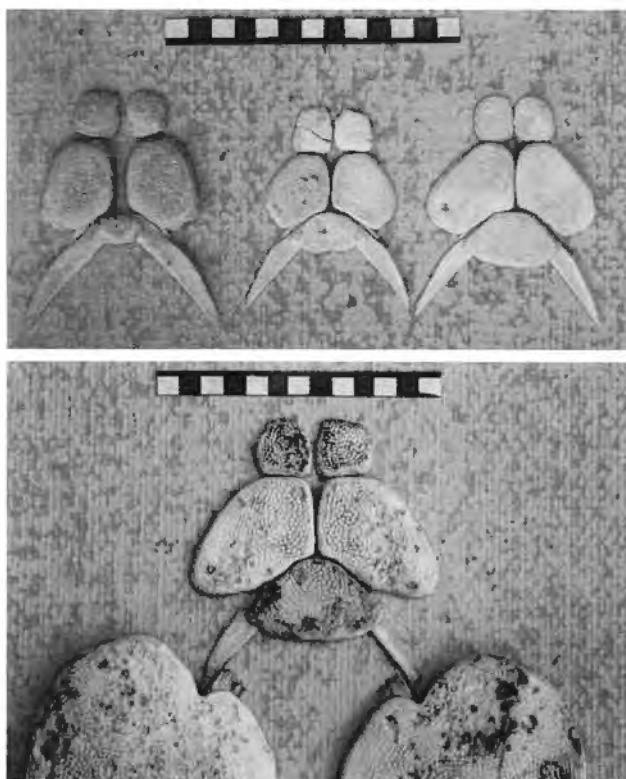


Figure 9. Anterior bony plastra of four specimens of *Cyclanorbis senegalensis* showing variation in size of entoplastral callosity.

abounded and Trionychidae ran riot" in the Bridger beds of Wyoming (Hay, 1908), although it is unclear how many of these, based in many cases on fragments only, are valid; Gaffney (1979) suggested that the source of the "riot" was not the turtles themselves but the paleontologists describing them. But what is clear is that some of the species were very large. *Amyda crassa* with a BDL of 475 mm, *Temnotrionyx manducans* at > 500 mm, and *Aspideretes splendidus* at 538 mm were substantial animals, the last nearly reaching my arbitrary giant category. Many other species described by Hay had bony disc lengths of 350–430 mm, i.e., were medium to large. However, the largest of all, and indeed the largest trionychid on record, was a 970 mm specimen (Univ. Wyoming No. 2382) collected from the Eocene Bridger Formation of Wyoming in 1965 and described by Gaffney (1979).

Trionychids in Africa

Among large species, the situation in Africa today is also simpler than it may have been in the past. The three large cyclanorbid species (*C. elegans*, *C. frenatum*, and *C. aubryi*) are now entirely allopatric. However, a fourth species, *C. senegalensis*, has a wide range that encompasses the entire distribution of its congener *C. elegans* (Loveridge and Williams, 1957; Iverson, 1992), and extends considerably further west (as far as Senegal).

These two congeners have developed morphological adaptations and size divergence that may constitute evidence of partitioning of microhabitats. *Cyclanorbis senegalensis* has extensive development of plastral callosi-

ties at maturity (Fig. 9). These have been reported to number "7 to 9 or more" in adults (Loveridge and Williams, 1957) or "9 or more" (Meylan, 1987). Ambiguity may derive from interpretation of the single huge callosity covering the hyoplastron and hypoplastron on each side, but counting each of these as one, a series of 15 specimens in the PCHP collection (BDL, 150–240 mm) were uniform in having 7 callosities. This contrasts sharply with the 2–4 plastral callosities in *C. elegans* (Loveridge and Williams, 1957).

Moreover, the disposition of the callosities in *C. senegalensis* is unique in that the anterior lobe of the plastron is extraordinarily armored, with entoplastral, paired epiplastral, and unique paired preplastral callosities well developed in adults, whereas the posterior lobe includes only a slender pair of flimsy xiphiplastra lacking callosities of any kind, except for some slight surface roughening in the largest adults. There is a degree of functional parallelism with the even more armored Asian *Lissemys*, although the actual details of the ventral armor are so different that it appears to have evolved independently in the two genera. In *Lissemys*, the anterior lobe is fortified by enlarged entoplastral and very large epiplastral callosities only (Figs. 10 and 11), and the hyo-hypoplastral callosities are so large that they curve upwards dorsolaterally so as to present a curved bony edge that replaces the "missing" peripheral bones above the bridge region in hard-shelled turtles. The xiphiplastra also bear extensive callosities, a prenuchal is present, and the very reduced posterior flap of the carapace is stiffened by a series of bony callosities of posteriorly diminishing size, independent of any deeper dermal bones, that mimic the function of peripheral bones in hard-shelled turtles. Meylan (1987) has presented the argument that these bones are primitive rather than derived. I disagree for the following reasons:

1. The trionychid shell has two layers of bones of very different texture and appearance, the deeper thecal layer (corresponding to the shell bones of hard-shelled turtles),



Figure 10. Bony plastron of *Lissemys punctata* showing contribution of entoplastral and epiplastral callosities to ossification of plastron.

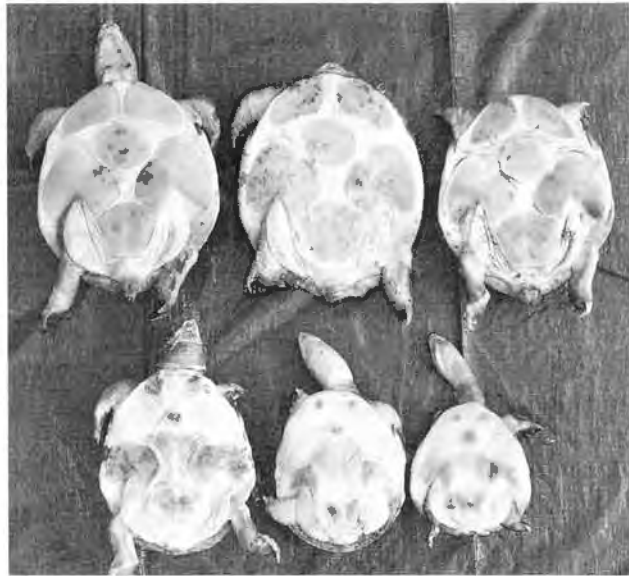


Figure 11. Bony plastra of six specimens of *Lissemys scutata* showing variation in relative size of entoplastral callosity.

and the more superficial epithecal bones, with their characteristic sculptured surface patterns and completely different arrangement (Zangerl, 1969). The bones in the posterior shell margin of *Lissemys* are fragments of epithecal bone, with no trace of an underlying thecal core; they may be considered as isolated bony callosities. In that the entire epithecal shell is neomorphic in trionychids, the bones in question must also be neomorphs — as must the prenuchal, unknown except in cyclanorbine trionychids.

2. The bones in the leathery shell margin of *Lissemys* have no one-to-one correspondence with the ribs, as true peripheral bones do.

3. The fossil record of trionychids is quite rich and diverse and extends back to the Cretaceous, but posterior marginal bones are only found in the modern and highly derived genus *Lissemys*, in which both carapace and plastron have become extensively ossified. Had there been persistent lineages of trionychids throughout the Tertiary that had never lost their ancestral peripheral bones, it is probable that some sporadic representatives of this lineage would be represented as fossils. Even as isolated fragments, they would be easily identifiable.

The extravagantly armored anterior part of the plastron in *C. senegalensis* is striking, especially in contrast with the absence of posterior callosities. A possible function of this, that would also rationalize the presence of a prenuchal (well separated from the anterior margin of the nuchal bone, in contrast to the situation in *Lissemys*), could be that, during times of drought, the turtle could thrust itself deep into viscous or yielding substrates by elevating the anterior lobe and using the limbs to generate the necessary force, the head and anterior parts of the shell being protected by the various bony elements mentioned above. Devaux (1998) confirmed that the habitat of this species in Senegal consists of shallow ponds, marshes, and oxbow lakes rather than deep or flowing water, and Das (1991) described such behavior in the

Asiatic cyclanorbine *L. punctata*: “when hunting for invertebrates, the turtle closes its shell anterior and ploughs through the mud with head partially retracted.”

The neural series of *C. senegalensis* is characterized by frequent interruptions in the series by contiguous pairs of pleurals; and a prenuchal bone is present whereas it is absent in *C. elegans*. The latter species may also have an interrupted neural bone series (Meylan, 1987), but less frequently, and in fewer places. *Cyclanorbis elegans* also has a shorter snout and much broader jaw surfaces, and a much shorter bridge than *C. senegalensis*, a feature normally interpreted as an adaptation for rapid and effective swimming, permitting longer strokes of the forelimbs. The two species differ strikingly in color at all ages (Loveridge and Williams, 1957). And, significantly for the present essay, *C. elegans* is quite a large turtle, with LCL reaching at least 600 mm and BDL up to 490 mm (Fig. 3), whereas the largest bony disc of *C. senegalensis* measured by Meylan (1987) had a BDL of only 325 mm. Devaux (1998) observed that a specimen of *C. senegalensis* from Senegal with a LCL of 350 mm was the largest recorded individual.

These multiple morphological differences may most easily be interpreted as adaptations to relatively arid conditions, including temporary waters, by *C. senegalensis*, and to large rivers and permanent waters by *C. elegans*. The former condition would seem to be the more primitive at least within the Cyclanorbinæ in that those forms adapted to life in open, permanent waters would appear to be derived from a smaller, more armored ancestral form, progressively mimicking some of the generalized or primitive features of species such as *T. triunguis* or the larger Asian softshells, but not directly derived from such species. If the reverse were the case, the presence (persistence?) of the semilunar plastral valves in *C. elegans* would be difficult to explain. Nonetheless, Loveridge and Williams (1957) have argued that *C. elegans* is the more primitive member of the genus, i.e., the one that reflects the presumed ancestral condition more closely. Reconstruction of cyclanorbine phylogeny is complicated by the lack of key fossil material, and must recognize that the morphological and contemporary ecological evidence strongly suggests that the cyclanorbine phylogeny was characterized by a series of reversals between aquatic specialization and adaptations for seasonal terrestrial survival.

Thus, chelonians as a group were surely originally terrestrial, universally laying cleidoic eggs, and with the primordial serpentine swimming undulation made impossible by the rigid shell and short tail. Nevertheless, it seems clear that the encarpaced body form with limbs that could be modified into webbed, swimming members exhibited remarkable preadaptation for a return to aquatic life, and the various shared trionychid features — loss of scutes, scales, and peripheral bones, extensively webbed extremities, tubular nostrils, etc. — indicate a fundamentally aquatic family. But the next stage of cyclanorbine evolution, the development of semilunar valves to conceal the retracted hindlimbs, suggests a modification associated with secondary terrestrial adaptation. This then became more extreme as the

versus large body size, correlated with high clutch biomass, and slow maturation in females) to provide the selective pressure for such divergence. At maturity, the diminutive males and large females of such species as *G. ernsti* are able to occupy drastically different microhabitats and feeding niches, and thus simultaneously achieve the efficiency advantages that come with specialization and the higher carrying capacity advantage that comes with the species as a whole occupying more than one microhabitat and feeding niche.

Calibrating the size differences in the genus *Pelodiscus* cannot yet be done accurately; indeed, the very validity of the two very small forms (*P. axenaria* and *P. parviformis*) has yet to be confirmed. The size relationship between *P. sinensis* and *P. steindachneri* is not as suggested by Meylan's (1987) data, which indicated that his largest specimen of *P. sinensis* had a BDL of 201 mm, whereas the largest *P. steindachneri* was only 170 mm. The figures given by Ernst and Barbour (1989) for maximum LCL — 250 and 426 mm, respectively, for *P. sinensis* and *P. steindachneri* — are more likely to reflect the actual direction and degree of difference.

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African and Asiatic lineages modified different components of their bony shells and developed armor in the divergent ways described above. The Asiatic group developed features unique in the group including a domed carapace with a rim stiffened by rigid dorso-lateral outgrowths of the hyohypoplastral callosities and neomorphic peripheral ossifications. Finally, certain species — the two large extant African cyclanorbine species and some extinct relatives — underwent a fourth reversal and became adapted for fully aquatic life.

One of the key characters used in characterizing cyclanorbine species has been the size of the entoplastral callosity — and this has also been used to differentiate the two Asiatic species *L. punctata* and *L. scutata*. Yet examination of ontogenetic series reveals not only a great deal of random variation even among specimens of comparable size (Fig. 11), but also very strong association of the size of this callosity with the degree of maturity of the specimen in question; indeed, Bhupathy (1989) found the entoplastral callosity to be completely absent in 34 of 740 *L. punctata* examined at Keoladeo, all but 8 of these being less than 130 mm LCL. Thus, *L. punctata* and *L. scutata* only seem to have entoplastral callosities of relatively different size when one compares individuals of similar absolute size (i.e., adult *L. scutata* and subadult *L. punctata*) rather than of comparable age or maturity. In a large adult *L. punctata*, the callosities are as developed as they are in a (smaller) adult *L. scutata*.

Superimposed upon this aggregation of allopatric large cyclanorbrates in Africa, with a medium-sized species substantially sympatric with one of them in the north-central and northwestern area, is the widespread occurrence of a more distantly related, very generalized trionychid. This is *T. triunguis*, widespread in the Nile Valley, south as far as Lake Turkana, west throughout rivers of sub-Saharan West Africa, and down the southwestern coast as far as northern Namibia. The species even inhabits the lower Gambia and Casamance rivers (Iverson, 1992; Devaux, 1998), both of which have substantially reversed flow especially during high tides, and are strongly saline for great distances inland. Villiers (1957) reported two specimens captured in the sea off Dakar. This species has high tolerance of salt and alkaline waters, and occurs in the eastern Mediterranean (as far north as Turkey and a single record for Greece) as well as in Atlantic waters of Angola (Carr and Carr, 1985), and this pre-adaptation may have facilitated colonization of the highly alkaline Lake Turkana (Meylan et al., 1990). The range of *T. triunguis* does not currently overlap that of *C. frenatum*, but a reasonable abundance of cyclanorbine fossil material from early Pliocene sediments of the Lake Turkana Basin (Meylan et al., 1990), referable not only to three living species (*C. frenatum*, *C. senegalensis*, and *C. elegans*) but also to two extinct species, *Cycloderma debroinae* and *Cyclanorbis turkanensis* suggests that softshells in this basin have a complex history indeed.

For some reason, the Lake Turkana assemblage was unstable — possibly because the water levels and salinity of the lake were themselves unstable. *Cycloderma frenatum*

retreated to the south and *C. senegalensis* and *C. elegans* to the northwest, and the other species became extinct. The only trionychid remaining in Lake Turkana today is *T. triunguis*. I hypothesize that *T. triunguis* invaded the Turkana Basin subsequent to the establishment of the cyclanorbrates there, and proceeded to displace them by being better adapted (or preadapted) to this habitat. Possibly, too, the Turkana Basin has become progressively more hyperalkaline, and has now reached the point where only the euryhaline-adapted *T. triunguis* could survive. Nonetheless, *Trionyx* is not particularly new to Lake Turkana, being known as a fossil from nearby Koobi Fora, from sediments between 1 and 2.5 million years old (Wood, 1979).

Today, *T. triunguis* is allopatric with *C. frenatum* and partially so with *C. aubryi*, a species confined to the Zaire River basin, where Iverson (1992) indicated only a single inland record of *T. triunguis*. Nevertheless, P.A. Meylan (*pers. comm.*) reports that both *C. aubryi* and *T. triunguis* occur in the lower, middle, and upper reaches of the Zaire, and that both also occur throughout much of Gabon. *Trionyx triunguis* also has substantial gross sympatry with the two *Cyclanorbis* species, both in the Upper Nile and in West Africa. The overlap with the range of the small *C. senegalensis*, apparently adapted for smaller or temporary bodies of water, presents no problems; but the sympatry with the relatively large *C. elegans* and *C. aubryi* over such a substantial area is very interesting. Without extensive field data it would be difficult to offer an ecological interpretation, but one hypothesis might be that *T. triunguis* had undergone relatively recent range expansion and was in the process of progressive displacement of these two cyclanorbine species throughout much of their range, as may have already happened in Lake Turkana.

Trionychids in Asia

In south, southeast, and eastern Asia, a series of almost completely allopatric large trionychids extends from the Indus River in Pakistan through India, Bangladesh, and Myanmar, Thailand, Laos, Cambodia, southern China, southern Vietnam, north to southeastern China, and south through Malaysia to Indonesia (as far east as western Bali). This series includes *A. gangeticus* in the Indus and the Upper and Middle Ganges; *A. hurum* in the lower Ganges; *A. nigricans* with a relictual distribution near Chittagong, Bangladesh; *A. leithii* in Peninsular India; *N. formosa* in Myanmar; and *A. cartilaginea* in Thailand, the Mekong drainage, and through Malaysia to Bali. The almost extinct *R. swinhoei*, a giant species, forms a logical terminal member of this series (ecologically if not taxonomically), with an original distribution in extreme eastern Asia, from the lowlands of northern Vietnam to the vicinity of Shanghai.

Some taxonomic ambiguity pervades this assemblage. For example, *A. nigricans* may simply represent a single, long-term captive population of *A. hurum*, including individuals of unusual age and size, some deformed through inbreeding and disease. Furthermore, *Nilssonina* may be a

synonym of *Amyda*, the structural differences between *formosa* in Myanmar and *cartilaginea* in Thailand being minimal (van Dijk, 1992). The wide-ranging *A. cartilaginea* may represent a complex of related taxa (van Dijk, 1992), and the congenericity of *R. swinhoei* and the much smaller *R. euphraticus* (Fig. 8), separated by the entire width of the Asian continent, may be an artifact of parallelism in two characters — the reduced eighth pleural bones (also shown by *Apalone*), and the very reduced plastral callosities (also shown by *Dogania*). But it is more probably a natural genus with a relictual distribution, there being a number of shared skull characters (Meylan, 1987). The two species may be considered terminal members of a temperate softshell group eliminated from Central Asia by Himalayan uplift. The Kazakhstan fossil genus *Ultrionyx*, which shares many morphological characters with *Rafetus* including great size, reduced eighth pleurals, and virtual absence of plastral ornamentation or callosities, may be a testimony to the once widespread nature of the *Rafetus* complex (Kordikova and Chkhikvadze, 1990). Furthermore, a gigantic (970 mm BDL) trionychid specimen from the Eocene Bridger Formation of Wyoming, USA, described by Gaffney (1979), has a number of *Rafetus*-like characters quite apart from its enormous size; these include reduction of the eighth pair of pleural bones, reduced carapacial surface ornamentation, and virtual absence of plastral callosities. Gaffney declined to name this species, which may be closely related to the also very large (BDL 700 mm) *Paleotriton* *quinni* from the Palaeocene of Colorado.

Nonetheless, whatever the taxonomic relationships, actual sympatry within this series of large trionychids is very scant, and consists primarily of some penetration of *A. hurum* into the middle Ganges (where it is much scarcer than *A. gangeticus*), and some complimentary penetration of *A. gangeticus* into the Ganges delta in Bangladesh, where it is greatly outnumbered by *A. hurum*. These species are easily distinguished by color pattern (large, complete carapacial ocelli and a prominent temporal light marking on each side in *A. hurum*; rudimentary, distorted ocelli only in juveniles of *A. gangeticus*, and a pattern of thin dark lines on the head), but their osteology is so similar that no features have been identified that can reliably distinguish bony shells. Detailed information on the distribution of *A. leithii*, the peninsular Indian representative of this series, is lacking, but Das (1991) quoted unsubstantiated reports to the effect that it may be sympatric with *A. gangeticus* in Gujarat, although its primary range is in Madhya Pradesh, Maharashtra, Karnataka, Andhra Pradesh, Orissa, and Tamil Nadu. Bhupathy and Ajith Kumar (1988), noting the first occurrence of *A. hurum* in Rajasthan, collected 20 specimens in the Keoladeo National Park, but elsewhere Bhupathy (in Vijayan, 1988) noted that a sample of the large trionychids observed to live in the Park included 112 *A. gangeticus* and only 6 *A. hurum*, which may be a rough index to the relative abundance of the two species in the Middle and Upper Ganges.

The modest degree of sympatry between *A. gangeticus* and *A. hurum* may simply represent inevitable mixing, in a

single large river system, of a delta and estuarine specialist (*A. hurum*) with an upriver specialist (*A. gangeticus*). Possibly partition of habitats was more defined in earlier times, when denser populations may have competed for limited food, nesting space, and other resources, and these relationships may have changed in recent times as populations of both species have been depleted by market hunting.

Within this series of large trionychids, smaller species are interposed here and there. In South Asia, the two *Lissemys* species (*L. punctata* and *L. scutata*) are locally very abundant in India, Bangladesh, and Myanmar, and although grossly sympatric with several larger trionychids, competition is avoided by their adaptation for a very different habitat. These species are scarce to absent in large rivers, but plentiful in seasonally flooded wetlands, where their small size, extensively armored shells, and completely retractile extremities (with semilunar valves closing over the hind limbs), allow them to withstand protracted periods of drought by estivation in dried mud (Auffenberg, 1981; Bhupathy and Vijayan, 1994). The density of estivating *L. punctata* may be extremely high at Keoladeo National Park — up to 950 per hectare (Bhupathy and Vijayan, 1994). When the other species of trionychids in the park (i.e., *A. gangeticus* and *A. hurum*) attempted to estivate, they either abandoned the estivation sites or died within a maximum of 49 days. *Lissemys*, by contrast, could survive estivation for as much as 160 days (Bhupathy and Vijayan, 1994).

In Sri Lanka large trionychids are absent, and it is interesting that the indigenous population of *Lissemys* is characterized by significantly larger adult size than on the continent. In Sri Lanka, the species frequently reaches a BDL of 370 mm or more (Deraniyagala, 1939), whereas on the continent, in conditions of gross sympatry with larger trionychids, the adult size tends to be distinctly smaller. Bhupathy (1989) reported that only 25 out of 740 specimens examined in Keoladeo National Park in India exceeded an over-the-curve LCL of 278 mm, the largest individual measuring 350 mm (probably a straight BDL of ca. 315 mm based on comparisons of other *L. punctata* shells from Keoladeo in the PCHP collection). In reality, the largest specimen was a striking and exceptionally large outlier within a sample size of many hundred turtles. By contrast, Deraniyagala found that, in Sri Lanka, 370 mm was frequently reached or exceeded. One such turtle, weighing 6.9 kg, would dwarf any *Lissemys* from India, where the largest of many hundreds of specimens examined by Bhupathy (1989) weighed 5.2 kg.

In southeast Asia, a second small trionychid species survives in a world dominated by larger species, utilizing a very different habitat from that occupied by *Lissemys*. This is *D. subplana*, a species showing some marked specializations of habitat, diet, and morphology. Its carapacial osteology is characterized by the unique morphological adaptation of pankinesis (Pritchard, 1993), a device that, in combination with small size, allows the animal to insert itself into irregular cracks beneath or between large boulders in the upland stream environments it inhabits.

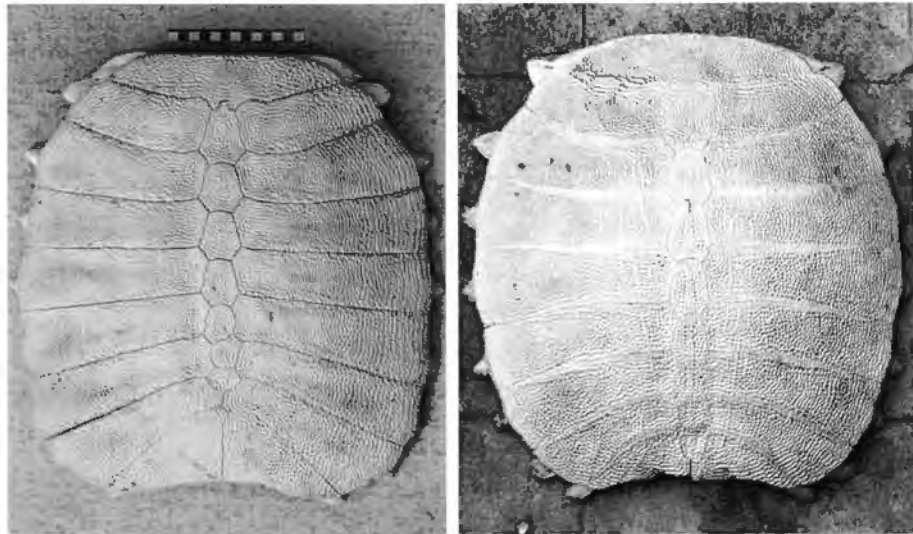


Figure 12. Comparison between bony carapaces of (left) *Chitra chitra* (PCHP 4995, BDL 421 mm) and (right) *Pelochelys cantorii* (PCHP 2921, BDL 398 mm).

Furthermore, it has a durophagous diet, manifested skeletally by macrocephaly, with closure of skull sutures, expansion of the tomial surfaces, and general robust form.

The giant species, five in number (two *Pelochelys*, two *Chitra*, and *R. swinhoei*), together with the almost-giant *A. gangeticus*, are primarily Asian, with some penetration of the two *Pelochelys* into the Australasian region (New Guinea plus some possible fossils in Australia). *Pelochelys* and *Chitra* share two noteworthy features — enormous size and both carapacial and plastral osteology that is so similar that skeletons without skulls (Fig. 12) are difficult to distinguish, a problem described by van Dijk (1994). Both, too, have invariable configurations of four plastral callosities (a hyohypoplastral and a xiphiplastral element on each side, with no trace of callosities on the anterior elements), an incurved posterior margin to the bony carapacial disc, and extreme development of the skull for capture of elusive prey, especially live fish. The significant differences lie almost entirely in the cephalic region, the skull of *Chitra* being extremely elongate and narrow, and with the orbits small and very anteriorly located. In *Pelochelys*, the head has a toad-like appearance, the skull being flattened and distinctly shorter and wider than that of *Chitra*, with bowed lateral margins and well-separated orbits. Furthermore, *Chitra* has a subtriangular flap of stiff cartilage that forms an anterior extension of the very foreshortened nuchal bone, which gives turtles of this genus an additional unique aspect in that the juncture between the neck and the anterior part of the carapace is difficult to detect. Traces of this are evident in *Pelochelys* also.

Direct comparisons of the bony shells of *C. chitra* and *P. cantorii* do reveal some subtle differences, but they are not meristic or clear-cut characters of the kind that could be included in an identification key. They include the following details of *Chitra* relative to *Pelochelys*: 1) thicker carapace, with more sinuous sutural lines and a significantly coarser

pattern of surface pitting, 2) rib tips in general broader and rounded (tapered in *Pelochelys*); posteriormost rib tips extending further, 3) carapace less flattened, 4) anterior margin of nuchal bone convexly curved (usually straight or slightly concave in *Pelochelys*), and 5) epithecal bone of carapace curving away from costiform processes of nuchal bone, leaving an open window between costiform process, first rib tip, and edge of epithecal carapace.

Both *Chitra* and *Pelochelys* spend much time buried within bottom substrates and are highly aquatic. Both are known to feed on live fish and other elusive prey by means of rapid strikes of the exceedingly long neck. Why the skulls should be so different is unclear, but *Chitra*, which generally occurs in freshwater riverine habitats, may typically strike from an almost entirely concealed position, only the small eyes and nostrils being exposed above the substrate, whereas the euryhaline *Pelochelys* may more often strike from within the water column. An alternative suggestion by P.P. van Dijk (*pers. comm.*) is that *Chitra* is a “buccal sucker,” and *Pelochelys* a “precision snapper.” In captivity, *Chitra* is certainly adept at ambush feeding upon live fish from a position of concealment under a bottom substrate of sand, striking forward with astonishing rapidity. Feeding of large *Pelochelys* can be even more alarming, the strike being so fast that details cannot be seen with the naked eye, but the sound of the explosive strike and the turbulence of water it generates are impressive indeed.

Both of these genera are poorly known, and may well include significantly more species than have already been named. *Chitra* is often considered to be restricted to the Indian subregion, but its distribution is actually much broader than this. *Chitra indica* is known primarily from northern India (with low-density but widespread occurrence in the south), Pakistan, Bangladesh, and Nepal, and *C. chitra* is reported from two very well separated areas — the Ratburi and Kanchanaburi region of western Thailand (Nutaphand, 1979) and the Solo and other rivers of eastern Java (Philippen,

1998; McCord and PCHP, unpubl. data). The genus also occurs in Burma (four specimens in PCHP collection), and the form there may well be an undescribed taxon. Furthermore, softshells generally similar to *C. chitra* have been reported from the Malay Peninsula (Smith, 1931; W. McCord, pers. comm.), although details are lacking.

These giant trionychids are broadly sympatric with members of the series of large species in Asia, the ecological separation apparently being manifested in the exclusively riverine habitat, size differences, and feeding specializations of *Chitra*. *Pelochelys* appears to be more tolerant of saline conditions than any other trionychid except for *Trionyx triunguis*, and this provides sufficient ecological separation for *Pelochelys* to occur in gross but probably not microsympatry with smaller trionychid species in a huge area extending from China and India through southeast Asia to the Philippines and southward through western Indonesia. *Dogania* and *Chitra* reach as far southeast as eastern Java, and *Amyda* extends across the straits to eastern Bali, but *Pelochelys* continues intermittently further east, to New Guinea. Yet it is rare almost everywhere and unrecorded from huge areas within this extensive range.

In southern New Guinea, a form recently distinguished as true *P. bibroni* occurs in both freshwater and marine situations, where it is the only trionychid (Rhodin et al., 1993; Webb, 1995). The carapacial markings of this species are amazingly similar to those of *C. chitra*, and the soft structures of the head (especially the fleshy "lips") appear very different from those of *P. cantorii*. The skull also, with its dorsolaterally-directed orbits and evenly tapered sides, is quite different from *P. cantorii*, in which the skull is very broad and flattened, with dorsally-directed orbits and strongly bowed sides, forming an even and almost continuous convexity in dorsal aspect, from the premaxillae to the squamosals (see e.g., Webb [1995, Fig. 4], for *P. bibroni*; Smith [1931, Fig. 36], for *P. cantorii* [labeled *P. bibroni*]). The sharing of such similar and striking carapace markings by these two species remains unexplained. Possible answers presumably lie either in the direction of convergence under similar although unknown selective forces, or in the direction of retention of a shared ancestral pattern. Meylan (1987) considered the pattern of bold carapacial ocelli seen in many Asiatic trionychids to be a primitive rather than a derived feature, although if the bold pattern showed by *C. chitra* and *P. bibroni* is primitive, it is noteworthy that it has been lost in *P. cantorii* and is substantially muted in the undescribed *Chitra* form in the Ayeyarwady River system in Myanmar.

Interestingly, Webb (1995) found that juvenile *P. bibroni* lacked the bold dorsal color pattern of adults, although the available specimens were too few to pinpoint the size range at which the pattern first appeared. I found that it was already present in a live specimen of about 150 mm LCL.

A little-recognized but important factor that shows sharp contrast between *Chitra* and *Pelochelys* is the clutch size. In *C. indica* clutch size is reported to be 118 (mean of 10 clutches; Das, 1991) and 65–178 (Whitaker and Andrews, 1997) and in *C. chitra* clutch size is 60–110 (Cox et al.,

1998), but *P. cantorii* has a clutch size of only 20–28 (Vijaya, 1982). Kar and Rao (1985) reported that *P. cantorii* in India (Brahmini and Baitarani rivers) migrates to sea beaches to nest, whereas *C. indica* in India generally nests on sandbanks far inland (e.g., in the Chambal Sanctuary in Central India). This phenomenon (i.e., of two related, morphologically similar, and geographically overlapping species having starkly contrasting nesting habitats, namely riverine sandbanks and sea beaches) is also shown by the batagurids *Batagur* and *Callagur* in Malaysia (Dunson and Moll, 1980). The former migrates upstream to nest on riverine sandbanks and the latter downstream, entering the sea and emerging to nest on maritime beaches. Interestingly, *P. bibroni*, living in southern New Guinea in an area far from the known range of *Chitra*, has not only developed a carapacial pattern similar to *Chitra* but may also nest in freshwater systems, e.g., in Lake Murray and the Upper Fly River (Rhodin et al., 1993). It is unclear where *P. cantorii* nests in northern New Guinea, where *Chitra* is also absent.

The adaptive interpretation of the vastly different clutch sizes of *Chitra* and *Pelochelys* may reflect that the former, nesting as it does on dry-season exposed sandbanks, may be constrained to produce only a single clutch per year, as does the giant pelomedusid *Podocnemis expansa*, that lays a single, very large clutch per season (Pritchard and Trebbau, 1984), and that nests on seasonally exposed sandbanks in Amazonia. On the other hand, maritime beaches and shores of intracoastal waterways or delta shorelines, while doubtless not being precisely equally conducive to successful incubation at all times of the year, are not seasonally inundated after a short dry season, and iteroparity is possible — as is universal among the marine turtles of the families Cheloniidae and Dermochelyidae. When it is possible, it may be more useful to lay multiple, relatively small clutches rather than a single huge one, in that a single predation or erosion event will no longer destroy the entire season's production.

Sexual Size Dimorphism

Data on sexual size dimorphism in trionychids have suggested that the largest individuals of *A. cartilaginea*, *D. subplana*, *R. swinhoei*, and *P. sinensis* appear to be males, contrasting with the female-biased dimorphism of *Apalone* (Meylan, 1987). Shrestha (1997) indicated that female *L. punctata* are much larger than males (275 versus 175 mm, respectively). Nearly all giant *C. chitra* known from Thailand have been females, but this may be partially an artifact of capture methods employed (P.P. van Dijk, pers. comm.). Rashid and Swingland (1997) reported that male *A. gangeticus* were larger than females, but their largest specimen was a female, and the numerical data presented were inconclusive (large males: 615–770 mm, mean 686.9 mm; large females: 560–780 mm, mean 662.4 mm). Data for *A. hurum* were a little more persuasive (males 390–455.4 mm, mean 411.5 mm; females 245–410 mm, mean 342 mm), but the lower cutoff point for selection of large individuals in each group appears to have been arbitrary.

The general trend of sexual size dimorphism appears to demonstrate a phenomenon also found in testudinids and kinosternids, namely "female size conservatism" (Pritchard and Trebbau, 1984), with females larger in the smaller species and males larger in the larger ones. The probable rationale is that, among species constrained by their environment to be small, females still have to attain an adequate shell volume to contain a clutch of adequate size and number of eggs. In large species, on the other hand, even moderate-size individual females may have adequate shell volume. Also, enormous size may be a disadvantage during nesting excursions, and sexual selection may favor the largest males, which are able to commandeer any female they may select by sheer size advantage. Exceptions exist, for example in the small *D. subplana* (males larger) or the very large cheloniid *Chelonia mydas* (females larger) and, apparently, *C. chitra* (females larger).

CONCLUSIONS

Living trionychid species, although mostly large to very large turtles, display a wide range of adult body sizes, and gross sympatry between the approximately 25 recognized extant species almost always involves size differences. In some cases these differences may reflect the different body sizes of the ancestral taxa that came together to produce a given sympatric assemblage, and in others they may reflect evolution of diverse sizes as a form of character displacement following sympatry and resulting niche competition. In general, however, it appears that the adult size of chelonians is easily modified either by genetic selection or by environmental conditions, and many widespread or archipelagic species (*Terrapene carolina*, *Melanochelys trijuga*, *Geochelone nigra*, *Pelusios sinuatus*) show profound geographic variation in adult size without having speciated, even in the absence of obvious competition from other turtle species with closely similar habitats and patterns of resource use. When potential competition is present, size divergence (and the suite of ecological differences it makes possible), is manifested in multi-species sympatric assemblages within various families of turtles, including the Testudinidae and Pelomedusidae as well as the Trionychidae.

In addition to size differences, specializations or adaptations that may also facilitate avoidance of competition between grossly sympatric trionychids include: 1) enlarged plastral and sometimes additional carapacial callosities, especially in smaller species, to possibly facilitate occupation of shallow or temporary water habitats and survival during drought periods by burial in dried mud; 2) tolerance of certain large and giant species for saline environments; 3) specializations, especially of the head and neck, for capture of elusive living prey; 4) adoption of completely different nesting environments; and 5) penetration of entirely new microhabitats by such morphological adaptations as pankinesis in adult turtles to facilitate concealment under boulders in hill streams.

The hypothesis that size divergence may represent a form of character displacement within trionychid species gains support from the observation that, among partially sympatric species, the smaller species is likely not only to have a wider range than the larger one, but also to reach a larger adult size where it is not in sympatry with a larger species. Examples of this phenomenon include the smaller *L. punctata* and the larger *A. leithii*, or the smaller *P. sinensis* and the larger *P. steindachneri*.

This contribution is rich in hypotheses but the very deficient state of our actual knowledge of the natural history of the softshell turtles of the world remains evident. I shall be well pleased if this paper assists in the design and direction of useful studies of trionychids by upcoming generations of chelonologists.

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