amboinensis, *Cyclemys dentata*, and *Heosemys leytensis*. Casto De Elera (1895) listed many more turtle species from the Philippines that are totally undocumented: *Platysternon megacephalum*, *Callagur borneoensis*, *Ocadia sinensis*, *Chinemys reevesii*, *Siebenrockiella crassicollis*, *Geoemyda spengleri*, *Cuora trifasciata*, *Cuora flavomarginata*, *Pelodiscus sinensis*, and *Chitra indica*. Although most of these are surely in error, being far out of their known geographical ranges as compiled by Iverson (1992), field work is urgently needed in the face of massive deforestation in these islands (Hyman, 1984; Myers, 1988) to inventory the turtle fauna, which may also result in the discovery of species hitherto both new to the archipelago and unknown to science, as suspected by Taylor (1920), as well as clearing up "mystery" species such as *Heosemys leytensis* and *Pelochelys cumingii*.

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Literature Cited

ALCALA, A.C. 1986. Guide to Philippine Flora and Fauna. Vol. X. Amphibians and Reptiles. Manila: Natural Resources Management Centre, Ministry of Natural Resources and University of the Philippines, 195 pp.

BEMMELEN, R.W. VAN. 1949. The Geology of Indonesia. Vol. 1A. General geology of Indonesia and adjacent archipelagoes. The Hague: Martinus Nijhoff.

BOULENGER, G.A. 1894. On the herpetological fauna of Palawan and Balabac. Ann. Mag. Nat. Hist. (6)14:81-90.

BROWN, W.C., AND ALCALA, A.C. 1970. The zoogeography of the herpetofauna of the Philippines Islands, a fringing archipelago. Proc. Calif. Acad. Sci. (4)38:105-130.

CASTO DE ELERA, R.P.F. 1895. Catalogo sistematico de toda la fauna de Filipinas conocido hasta el presente. Vol. I. Vertebrados. Manila: Colegio de Santo Tomas, 701 pp.

EVERETT, A.H. 1889. Remarks on the zoo-geographical relationships of the island of Palawan and some adjacent islands. Proc. Zool. Soc. London 1889:219-228.

GAULKE, M. 1991. Systematic relationships of the Philippine water monitors as compared with *Varanus s. salvator*, with a discussion of dispersal routes. Mertensiella 2:154-167.

GAULKE, M. 1994. Contribution to the snake fauna of the Sulu Archipelago, with the description of a new subspecies of *Dendrelaphis caudolineatus* (Gray, 1834). Herpetol. J. 4:136-144.

HEANEY, L.R. 1985. Zoogeographic evidence for Middle and Late Pleistocene land bridges to the Philippine Islands. Modern Quaternary Res. SE Asia 9:127-143.

HEANEY, L.R. 1991. A synopsis of climatic and vegetational change in Southeast Asia. Climatic Change 19:53-61.

HYMAN, E. 1984. Forestry administration and policies in the Philippines. Environ. Mgmt. 7:511-524.

INGER, R.F. 1954. Systematics and zoogeography of Philippine Amphibia. Fieldiana Zool. 34:389-424.

INGER, R.F. 1966. The systematics and zoogeography of the Amphibia of Borneo. Fieldiana Zool. 52:1-402.

IVERSON, J.B. 1992. A Revised Checklist with Distribution Maps of the Turtles of the World. Richmond, Indiana: Privately printed, 363 pp.

LOVICH, J.E. 1994. Biodiversity and zoogeography of non-marine turtles in south-east Asia. In: Majumdar, S.K., Brenner, F.J., Lovich, J.E., Schalles, J.F., and Miller, E.W. (Eds.). Biological Diversity: Problems and Challenges. Easton: Pennsylvania Academy of Science, pp. 380-391.

MYERS, N. 1988. Environmental degradation and some economic consequences in the Philippines. Environ. Consv. 15:205-214.

OLLIER, C.D. 1985. The geological background to prehistory in island Southeast Asia. Modern Quaternary Res. in SE Asia 9:25-42.

PRITCHARD, P.C.H. 1979. Encyclopedia of Turtles. Neptune, NJ: T.F.H. Publications, 895 pp.

SMITH, M.A. 1931. The fauna of British India, including Ceylon and Burma. Reptilia and Amphibia. Vol. I.- Loricata, Testudines. London: Taylor and Francis, 185 pp.

TAYLOR, E.H. 1920. Philippine turtles. Phil. J. Sci. 16:111-144.

TAYLOR, E.H. 1921. Amphibians and turtles of the Philippines. Phil. J. Sci. 15:1-193.

WANG, L., AND WANG, P. 1990. Late Quaternary paleoceanography of the South China Sea: glacial-interglacial contrasts on an enclosed basin. Paleoceanography 5:77-90.

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Neural Bones in Australian Chelid Turtles

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Neural bones are median elements of the turtle carapace overlying the dorsal vertebrae. The ancestral condition is thought to be a series of eight relatively narrow, hexagonal neural bones with short sides anteriorly placed, forming a continuous series from the nuchal bone anteriorly to the first suprapygal posteriorly (Pritchard, 1988). This condition is retained in many extant species of the Bataguridae, Emydidae, and Cheloniidae, but frequently modified, for example, by elimination of elements at the ends of the series, formation of one or more octagonal elements, or alteration to a series of hexagons with short sides posteriorly.

Neural bones are probably structurally important for resisting downward pressure in high-domed species, but may be a disadvantage where lateral forces in flatter forms cause torsion among carapacial elements (Pritchard, 1988). Hence, strong swimmers that move by alternating thrusts of the rear limbs, and marine turtles that alternate strokes on land, tend to have reduced neural series with areas of median contiguity between opposing pleural bones (Pritchard, 1988). Neurals are often seemingly absent in Chelidae, where a fixed pelvic girdle and extensive plastral buttressing provide alternative structural resistances to downward pressure and lateral torsion caused by the sideways action of neck extension and withdrawal.

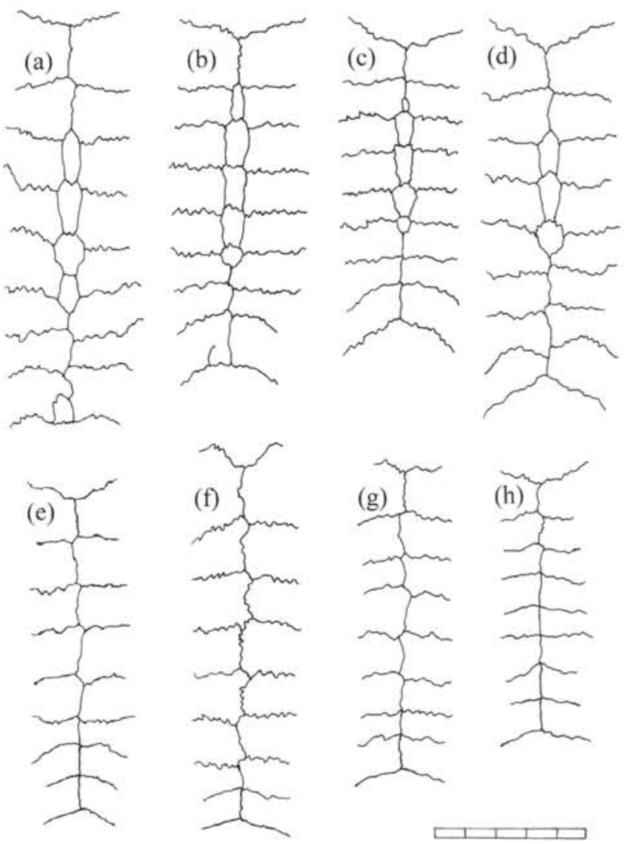

Figure 1. Comparison of the neural region of the dorsal carapace of the sibling species pair *Elseya* sp. aff. *latisternum* (Manning) **(upper row, a to d)** and *Elseya* sp. aff. *latisternum* (Bellinger) **(lower row, e to h)**. Scale = 5 cm. (a) AM 123042, (b) QM 59290, (c) QM 59289, (d) AM 123040, (e) AM 138387, (f) AM 138388, (g) UM 02016, (h) UM 02017.

Absence of neural bones was thought to be characteristic of all Australian chelid turtles (Boulenger, 1889; Waite, 1929; Williams, 1953; Zangerl, 1969) until neurals were reported as a consistent feature of *Chelodina oblonga* from Australia's southwest (Burbidge et al., 1974). Subsequently, neurals were also reported as inconsistent variations in five other Australian species (*Chelodina novaeguineae*, *C. siebenrocki*, *C. longicollis*, *Elseya latisternum*, and *Elseya* sp.) (Rhodin and Mittermeier, 1977). In most cases, however, these neurals were few, small, and rudimentary, not forming a contiguous series.

In this note, we report a second Australian chelid characterized by the consistent presence of well developed neurals. This feature incidentally provides a morphological basis for separating what was previously a cryptic species pair (Georges and Adams, 1992). We also argue, on examination of sections through the vertebral region, that all chelids possess neural bone elements, but that in those species traditionally regarded as lacking neurals, these elements are so reduced as to be submerged beneath the dorsal medially contiguous pleurals.

Materials and Methods. — Specimens were obtained from various collections, skeletonized, and the scutes removed to reveal the arrangement of bony elements. Longitudinal and transverse sections of shell vertebrae and associated neurals and pleurals were prepared with a diamond saw for the chelid turtles *Chelodina longicollis*, *C. oblonga*, *Emydura* sp. aff. *krefftii* (Fraser Island), *Emydura* sp. aff. *subglobosa* (Sleisbeck), and *Elseya dentata*, as well as for the trionychid *Aspideretes hurum*. Where exposed neurals were present, sections were arranged to transect one or more of them. Sections were examined under a microscope to ascertain the presence of sutures between the various elements.

Specimens Examined. — All unregistered specimens that remained intact following examination were lodged with the Queensland Museum. The sectioned specimens remain in the collection of the University of Canberra. Names given to undescribed species follow those of Georges and Adams (1992). Abbreviations: AM, Australian Museum; QM, Queensland Museum; NTM, Museums and Art Galleries of the Northern Territory; UM, University of Michigan field series; UC, University of Canberra; PCHP, Peter C.H. Pritchard personal collection.

Chelodina longicollis: QM 59266-68, 59274, 59281-82, UC 0164, 0166, 0174; *Chelodina oblonga*: QM 59272-74, UC 0161-63; *Chelodina expansa*: QM 59284; *Chelodina rugosa*: QM 59264; *Elseya dentata* (Daly River, N.T.): NTM 13319, 13521, 16330, QM 59277-80, UC 0179; *Elseya* sp. aff. *dentata* (South Alligator River, N.T.): AM 128002, 128004, QM 59285-88; *Elseya latisternum*: AM 123037, 123039, 125474-75, QM 48054-55; *Elseya* sp. aff. *latisternum* (Manning River, N.S.W.): AM 123040, 123042, QM 59289-90; *Elseya* sp. aff. *latisternum* (Bellinger River, N.S.W.): AM 138387-88, UM 02016-17; *Elseya novaeguineae* (Sepik River, New Guinea): AM 42662, 125038; *Emydura* sp. aff. *krefftii* (Fraser Island, Qld.): QM 59275-76; *Emydura* sp. aff. *subglobosa* (Sleisbeck, Katherine River, N.T.): NTM 13428, 13433, UC 0171-72, 0177; *Aspideretes hurum* (no data): UC 0167; *Chelus fimbriatus* (Venezuela): PCHP 3985; *Pelomedusa subrufa* (no data): UC 0221; *Phrynops gibbus* (no data): UC 0222.

Results. — Well developed neural bones forming a contiguous series were observed in specimens of *Aspideretes hurum* (*n* = 1, pleural pair VIII was in medial contact), *Pelomedusa subrufa* (*n* = 1, pleural pair VIII was in medial contact), *Chelus fimbriatus* (*n* = 1, pleural pair VIII was in medial contact), *Phrynops gibbus* (*n* = 1, pleural pair I and V to VIII were in medial contact), *Chelodina oblonga* (*n* = 6, pleural pairs I and VIII were in medial contact in all specimens with considerable variation for other pleural pairs), and *Elseya* sp. aff. *latisternum* (Manning River) (*n* = 4, pleural pairs I and VI to VIII were in contact in all specimens and pleural pair V in one specimen and II in two specimens) (Fig. 1). Neural bones were most developed in *Chelus*, being expanded both horizontally and vertically, yielding much enlarged canals for the longissimus dorsi muscles. Rudimentary exposed neurals, small and isolated, were evident as individual variants in *Chelodina longicollis* (1 of 9, UC 0166), *Elseya novaeguineae* (1 of 2, AM 42662), and *Elseya* sp. aff. *dentata* (South Alligator

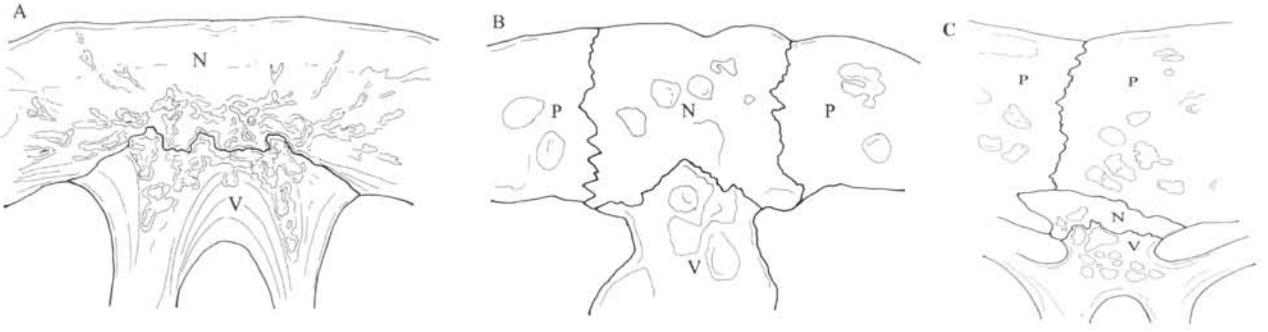

Figure 2. A. Transverse section through the first neural of *Aspideretes hurum* (UC 0167) showing the suture between the wide neural bone (N) and the vertebral neural arch (V). **B.** Transverse section through carapace of *Chelodina longicollis* (UC 0166) at pleural IV showing a narrow midline neural bone, lateral pleurals (P) and underlying vertebral neural arch. **C.** Transverse section through *Emydura* sp aff. *subglobosa* (UC 0177) at pleural IV showing location of a rudimentary neural bone underneath medially contiguous pleurals.

River, N.T.) (1 of 6, QM 59285). Table 1 shows the neural formulae for all these specimens, following the conventions of Pritchard (1988).

No exposed neurals were evident in any of the specimens of *Elseya latisternum* ($n = 6$), *Emydura* sp. aff. *krefftii* ($n = 2$), *Em.* sp. aff. *subglobosa* (Sleisbeck) ($n = 5$), *Elseya* sp. aff. *latisternum* (Bellinger) ($n = 4$) (Fig. 1), *Elseya dentata* ($n = 8$), *Chelodina expansa* ($n = 1$), or *Chelodina rugosa* ($n = 1$).

The presence of well developed exposed neurals in all four specimens of the undescribed species from the Manning drainage of New South Wales and their absence in all four individuals of its sister taxon (Georges and Adams, 1992) from the Bellinger River was a substantial and significant difference between these sibling taxa (Fisher Exact Test, $P < 0.05$).

A transverse section through the vertebral region of *Aspideretes hurum* revealed a suture between the neural bone and the underlying vertebral neural arch (Fig. 2A). Corresponding sections of a specimen of *Chelodina longicollis* with three exposed neurals revealed sutures similar to those observed in *A. hurum* (Fig. 2B), as did sections of *C. longicollis*, *Elseya dentata*, and *Em.* sp. aff. *subglobosa* (Sleisbeck) (Fig. 2C) in the absence of exposed neural bones.

Discussion. — This study establishes the undescribed *Elseya* from the Manning drainage of New South Wales as the second Australian chelid with well developed neural bones. The presence of neurals in this species and their absence in its sister taxon from the Bellinger River is a major discrete morphological difference in what was formerly a cryptic species pair (Georges and Adams, 1992). This species pair shows fixed differences at 20% of electrophoretic loci, despite little if any external morphological difference. This provides an important example of where surveys based on molecular techniques can serve to focus attention on morphological features that might otherwise have gone undetected.

The Manning River *Elseya* has a rather short series of 3 to 5 neurals, a condition similar to that found in *Phrynops gibbus* (Chelidae). There is no obvious lateral expansion of the rib heads to accommodate enlarged longissimus dorsi muscles and in fact the ribs fit quite closely to the sides of the neural arches. This combination is also seen in *Pelomedusa subrufa* (Pelomedusidae) and is therefore considered to be the primitive condition.

If the function of well developed neurals is to add stability to shells particularly subject to lateral torsion (Pritchard, 1988) and this function is supplanted in chelids by the presence of a fixed pelvic girdle and extensive buttressing, then we would expect to see a correlation between the presence of neurals in chelid turtles and the lack of development of plastral buttresses. Indeed, anterior plastral buttressing is poorly developed in *Chelodina oblonga*, compared to other species of similar body form and habits in the *Chelodina expansa* group, and *Chelodina oblonga* has well developed neurals. Similarly, among the short-necked chelid turtles of Australia (excluding *Pseudemydura*), the Manning River form of *Elseya* which has well developed neurals, has the least developed anterior bridge buttresses.

On the basis of the bone sections, we suggest that there are three neural character states:

1. Neural bones small, rudimentary, not visible in dorsal view, being obscured entirely by the pleurals which meet medially for the full length of their common midline suture.
2. Neural bones small, rudimentary, but exposed as small bony elements along the carapace midline. They do not form a contiguous series and pleural to pleural sutures make the predominant contribution to the midline suture.
3. Neural bones well developed and dorsally exposed, forming a contiguous midline series of two or more discrete elements. Pritchard (1988) has further subdivided this character state, based on a study of a greater range of specimens than examined here.

The demonstration of subsurface neural elements suturally separated from the neural arches of the dorsal vertebrae, with the possibility that neurals of some form may be present in all chelids, requires us to rethink our character definitions. The character state "neurals absent" should be instead "exposed neurals absent" and "neurals present" should become "neurals exposed". Also it will be necessary to appreciate that secondary development of exposed neurals may not imply reacquisition of a structure once lost but rather expansion of a persistent but rudimentary element.

Whether the subsurface neural elements are vestigial (that is, lacking function) is not clear. The possibility exists

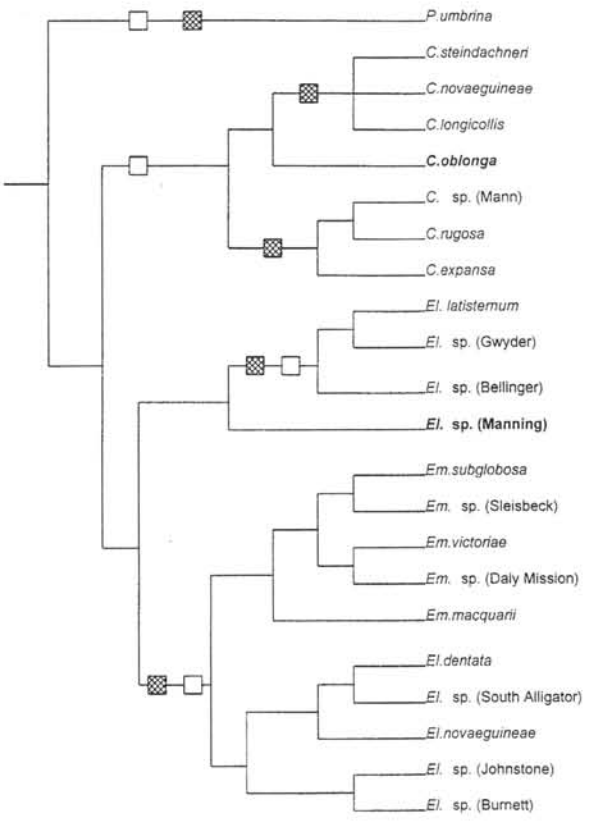

Figure 3. Occurrence of loss of exposed neurals mapped on the currently hypothesized phylogeny of Australian chelids (Georges and Adams, 1992). Open squares assume that in the Manning River *Elseya* neurals are ancestral and in *C. oblonga* they are secondarily derived. Hatched squares assume that both *C. oblonga* and *Elseya* sp. (Manning) retain ancestral neurals. Note: *Elusor macrurus* and *Rheodytes leukops* have been left out of this phylogeny for two reasons, 1) they were inadequately resolved (forming a trichotomy with the *Elseya dentata – Emydura* groups) and 2) they will have no effect on the neural character state, both species lacking exposed neurals.

that by spanning the midline carapace suture from below, they reinforce it and relieve lateral pressure that would otherwise come to bear on the neural arches should the shell be subjected to downward force. Such a function would explain their retention.

Matching the distribution of well developed neurals among chelid turtles with current phylogenetic hypotheses is problematic (Gaffney, 1977). Neurals are well developed in the South American *Chelus fimbriatus*, *Hydromedusa* spp., and the *Phrynops geoffroanus* complex (Rhodin and Mittermeier, 1983; Pritchard, 1988), and in the Australian *Chelodina oblonga* (Burbidge et al., 1974), and *Elseya* sp. aff. *latisternum* (Manning) (present study). The character also shows great individual variability in *Phrynops nasutus* and *P. gibbus* (Pritchard, 1988). Clearly, either loss of exposed neurals has occurred independently many times, or well developed neurals have been secondarily derived independently many times, or a combination of the two is true.

It is not clear whether the well developed neurals of *Chelodina oblonga* or *Elseya* sp. aff. *latisternum* (Manning) are ancestral or secondarily derived. Consideration of the currently hypothesized phylogeny for Australian chelids (Georges and Adams, 1992) indicates that if exposed neurals are ancestral for both species, then loss of exposed neurals must have occurred independently at least five times in their evolutionary history, and twice in *Chelodina* alone (Fig. 3, hatched squares).

We suggest instead that the presence of exposed neurals is a retained ancestral state in only *Elseya* sp. aff. *latisternum* (Manning), possessed in common with *Phrynops gibbus* and *Pelomedusa subrufa*, whereas in *Chelodina oblonga* it is secondarily derived. In this scenario, the loss of exposed neurals would have occurred independently only four times, and only once in *Chelodina* (Fig. 3, open squares). Compelling evidence is building to suggest that the closest living

Table 1. Neural formulae of specimens examined possessing exposed neurals. Also shown is the number of pleural pairs which make midline contact. Pleural pairs numbered I to VIII, anterior to posterior.

Species	Specimen	N1	N2	N3	N4	N5	N6	N7	N8	Pleural Pairs in Contact
Aspideretes hurum	UC 0167	6P	6P	6P	6P	6A	6A	6A	5A	VIII
Pelomedusa subrufa	UC 0221	6A	6A	6A	6A	6A	6A	—	—	VIII
Chelodina longicollis	UC 0166	—	4	3P	5	—	—	—	—	ALL
Chelodina oblonga	QM 59283	5P	7A	5A	5A	6A	6A	5A	5	I, VII, VIII
	QM 59272	6P	5P	4A	5A	5A	6A	7A	—	I, VIII
	QM 59273	6P	5P	4P	4P	5A	5A	5A	3	I, VI, VII, VIII
	UC 0163	—	6A	7A	5A	5A	6A	5A	5	I, VII, VIII
	UC 0162	—	3A	8A	8A	—	5	—	—	I, II, V, VI, VII, VIII
	UC 0161	—	5A	6P	5A	—	5A	—	—	I, V, VI, VII, VIII
Chelus fimbriatus	PCHP 3985	6P	6A	6A	6A	6A	6A	6A	—	VIII
Elseya novaeguineae	AM 42662	—	—	—	—	—	—	3	—	ALL
Elseya sp. (Manning)	AM 123040	—	—	6A	6A	6A	6P	—	—	I, VI, VII, VIII
	AM 123042	—	—	5A	6A	6A	—	—	—	I, II, V, VI, VII, VIII
	QM 59289	—	5P	6A	6A	6A	5A	—	—	I, VI, VII, VIII
	QM 59290	—	6A	6A	6A	6A	5A	—	—	I, II, VI, VII, VIII
Elseya sp. (S. Alligator)	QM 59286	—	—	—	—	—	—	5	—	ALL
Phrynops gibbus	UC 0222	5	6A	6A	6A	6A	—	—	—	I, V, VI, VII, VIII

relatives of *Chelodina oblonga* are among the *Chelodina longicollis* group of species (including *C. novaeguineae*, *C. steindachneri*, *C. mccordi*, *C. reimanni*, and *C. pritchardi*) rather than the *C. expansa* group to which it bears the closest superficial similarity (including *C. parkeri*, *C. rugosa*, and *C. siebenrocki*). Electrophoretic comparisons yielded five synapomorphies uniting *C. oblonga* with the *C. longicollis* group (Georges and Adams, 1992), a result confirmed by recent comparisons of 12S mitochondrial gene sequences (J. Seddon, *pers. comm.*). A more distant relationship may explain the presence of well developed neurals in *C. oblonga* and the absence of exposed neurals in the *C. expansa* group of species.

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Literature Cited

BOULENGER, G.A. 1889. Catalogue of the Chelonians, Rhynchocephalians and Crocodiles in the British Museum (Natural History). London: Taylor and Francis, 311 pp.

BURBIDGE, A.A., KIRSCH, J., AND MAIN, A.R. 1974. Relationships within the Chelidae (Testudines: Pleurodira) of Australia and New Guinea. Copeia 1974:392-409.

GAFFNEY, E.S. 1977. The side necked turtle family Chelidae: a theory of relationships using shared derived characters. Amer. Mus. Novitates 2620:1-28.

GEORGES, A., AND ADAMS, M. 1992. A phylogeny for Australian chelid turtles based on allozyme electrophoresis. Austral. J. Zool. 40:453-476.

PRITCHARD, P.C.H. 1988. A survey of neural bone variation among recent chelonian species, with functional interpretations. Acta Zool. Cracov. 31(26):625-686.

RHODIN, A.G.J., AND MITTERMEIER, R.A. 1977. Neural bones in chelid turtles from Australia and New Guinea. Copeia 1977:370-372.

RHODIN, A.G.J., AND MITTERMEIER, R.A. 1983. Description of *Phrynops williamsi*, a new species of chelid turtle of the *P. geoffroanus* complex. In: Rhodin, A.G.J., and Miyata, K. (Eds.). Advances in Herpetology and Evolutionary Biology. Cambridge: Museum of Comparative Zoology, pp. 58-73.

WAITE, E.R. 1929. The Reptiles and Amphibians of South Australia. Handbooks of the Flora and Fauna of South Australia. Adelaide: British Science Guild, 270 pp.

WILLIAMS, E.E. 1953. Fossils and the distribution of chelid turtles. 1. "*Hydraspis*" *leithii* (Carter) in the Eocene of India is a Pelomedusid. Breviora 13:1-8.

ZANGERL, R. 1969. The turtle shell. In: Gans, C., Bellairs, A.d'A., and Parsons, T.S. (Eds.). Biology of the Reptilia. Vol. 1. Morphology A. London: Academic Press, pp. 311-340.

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Temperature-Dependent Sex Determination and Hatching Success in the Gopher Tortoise (*Gopherus polyphemus*)

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The gopher tortoise (*Gopherus polyphemus*) is a large terrestrial turtle once common in the lower coastal plain of the southeastern United States. Gopher tortoise numbers have been dramatically reduced throughout their range, but the species now has local protection in each of the six states in which it occurs, as well as federal protection in Louisiana, Mississippi, and western Alabama. Conservation measures are diverse, and include suggestions that in some cases eggs may be collected and incubated, with hatchlings released in the wild.

Potential success of such conservation tactics depends on information about hatching success rates and sex determination mode for the species. If captive hatching rates are low, an artificial incubation program is unlikely to be very successful and other management actions may be more appropriate. Information on sex determination mode is important because application of naive incubation techniques may yield undesirable sex ratios in species with temperature-dependent sex determination (TSD) (Morreale et al., 1982). Alternatively, knowledgeable incubation techniques may facilitate favorable manipulations to fit management objectives of TSD species (Vogt, 1994). Although the congener *Gopherus agassizii* is known to have TSD (Spotila et al., 1994; Lewis-Winokur and Winokur, 1995), sex determination mode is not known for *G. polyphemus*. As variation in the mode of sex determination within a single genus has been reported in other turtles (e.g., *Clemmys*, Ewert and Nelson, 1991), as well as in lizards (Viets et al., 1994), it is appropriate to assess the sex determination mode of *G. polyphemus*.

Methods. — Eggs for this study were collected on 12 June 1992 by oxytocin injection (Ewert and Legler, 1978) of four gopher tortoises recently captured on the Tillman Sand Ridge in Jasper County, South Carolina. This population is