xestus. Also helpful during various stages of the work, was the technical assistance of D. Fridman, H. Segal and Sh. Lifshitz.

Literature Cited

Bertin, L. 1958a. Glands cutanés et organes lumineux, p. 459–481. *In*: Traité de Zoologie. P. P. Grassé (ed.) 13. Masson, Paris.

———. 1958b. Appareil digestif, 1248–1302. *Ibid.*

Cameron, A. M., and R. Endean. 1966. The venom apparatus of the scorpion fish *Notesthes robusta*. Toxicon 4:111–121.

Endean, R. 1968. A study of the distribution, habitat, behaviour, venom-apparatus, and venom of the stone-fish. Austr. J. Mar. Freshw. Res. 12:177–196.

Genaro, J. F., Jr., A. H. Anton and D. F. Sayers. 1968. The fine structure of pit viper venom and additional observations on the role of aromatic amines in the physiology of the pit viper. Comp. Biochem. Physio. 25:285–293.

Halstead, B. W. 1970. Class Osteichthyes, Poisonous and Venomous Marine Animals of the World. 2:149–594.

Krölling, O., and H. Grau. 1960. Lehrbuch der Histologie und Vergleichenden Mikroskopischen Anatomie der Haustiere.

Palade, G. E., P. Siekewitz and L. G. Caro. 1962. Structure, chemistry and function of the pancreatic exocrine cell, p. 23–49. *In*: The exocrine pancreas Renck, A. V. and M. P. Cameron (eds.). H. and A. Churchill.

Skeie, E. 1962. The venom organs of the Weaverfish (*Trachinus draco*). Meddel. Danm. Fisk. Hovound. 3:327–338.

Smith-Vaniz, W. F. 1969. A new species of *Meiacanthus* (Pisces, Blenniidae, Nemophidinae) from the Red Sea, with a review of the Indian Ocean species. Proc. Biol. Soc. Washington 82. 349–354.

Springer, V. G. 1968. Osteology and classification of the fishes of the Family Blenniidae. Nat. Mus. Bull. 284.

———, and W. F. Smith-Vaniz. 1972. Mimetic relationships involving fishes of the family Blenniidae. Smithsonian Contr. Zoology, 12.

Wallace, L. B. 1893. The structure and development of the axillary gland of *Batrachus*. J. Morph. 8:563–568.

Marine Biology, Department of Zoology, Tel Aviv University, Tel Aviv, Israel.

Relationships Within the Chelidae (Testudines: Pleurodira) of Australia and New Guinea

Andrew A. Burbidge, John A. W. Kirsch and A. R. Main

A comparative study of the Chelidae of Australia and New Guinea based on morphological and serological data showed that *Pseudemydura umbrina* has no close relatives. It is as distantly related to the long-necked *Chelodina* as it is to the other short-necked genera, *Elseya* and *Emydura*. The latter genera are separated on both morphological and serological grounds but are more closely related to each other than to any other group. *Chelodina oblonga* is unique among Australian chelids in possessing neural plates and the remaining species of *Chelodina* can be divided into two groups about as distinct from each other as *Emydura* is from *Elseya*.

We believe that *P. umbrina* and *C. oblonga* have been isolated in the south-west of Australia since the Cretaceous. Speciation in the other groups is believed to be due to isolation resulting from increasing aridity since the Oligocene. Pleistocene land bridges allowed movement between Australia and New Guinea but no migration occurred between the south-east and southwest of Australia. The lack of extant species in Tasmania is attributed to its relatively cool climate, both now and in the Pleistocene.

Apart from marine species and the specialized *Carretochelys*, turtles are represented in Australia by a single family, the Chelidae, which also occurs in New Guinea and South America. The present study was initiated to investigate the relationships of *Pseudemydura umbrina* as part of a broader study on the reasons for its restricted distribution and extreme rarity (Burbidge and Main, unpublished; Burbidge, 1967).

The systematics of the Australian and New Guinean Chelidae are not well established. Wermuth and Mertens (1961) listed 19 spe-

cies, with 13 from Australia, while Worrell (1963), considering only Australia, listed 11. The only revision of the group since Boulenger (1889) was that of Goode (1967), which was not based on any substantial morphological analysis. Goode's classification has been used as a basis for the present studies. He listed the following 13 species: *Chelodina longicollis* (Shaw), *C. novaeguineae* Boulenger, *C. steindachneri* Siebenrock, *C. expansa* Gray, *C. oblonga* Gray, *C. seibenrocki* Werner, *Elseya dentata* (Gray), *El. latisternum* Gray, *El. novaeguineae* (Meyer), *Emydura macquaria* Cuvier, *Em. kreffti* (Gray), *Em. australis* (Gray), *Pseudemydura umbrina* Siebenrock.

Goode divided the genus *Chelodina* into two groups, one containing *C. longicollis*, *C. novaeguineae* and *C. steindachneri*, and the other the remaining three species. He synonymized *C. rugosa* Ogilby (1890) with *C. siebenrocki* Werner (1901) although the former has priority. The type-locality of *C. rugosa* is Cape York, Australia, while that of *C. siebenrocki* is New Guinea. Consistent, if minor, differences occur between individuals of these taxa from Australia and New Guinea and they are considered here as different species.

Goode also synonymized the New Guinea species *Emydura subglobosa* Krefft with the Australian *Em. kreffti*. However, for the same reasons as above we also consider these as separate species. Goode further suggested that *Em. australis* should be placed in a separate species-group but he did not recognize species-groups within *Elseya*.

Thus, using morphological criteria, 15 species of chelid tortoises (as they are known in Australia) are recognized in this paper. Many of these are allopatric and there remains the possibility that what now appear to be morphological distinctions may be bridged by intergrades. There is also uncertainty about the groupings and relationships within and between the various species. For example, the information available from earlier morphological studies has been insufficient to evaluate groupings within *Chelodina*, to support the separation of *Elseya* and *Emydura*, or to establish the affinities of *Pseudemydura*. These uncertainties have now been investigated by more extensive morphological analysis. In addition, the basis for understanding intergroup and interspecific relationships has been broadened by introducing serological evidence.

Methods

Morphology.—There are no extensive osteological collections available in Australia and most of the material described here was prepared by us or borrowed from John Goode. Much alcoholic material is available in Australian museums. Shells of the following were prepared: *Chelodina oblonga* (10), *C. steindachneri* (1) and *Pseudemydura umbrina* (3). We used the descriptions of *Emydura macquaria* and *C. longicollis* from Waite (1929), Worrell (1963) and Goode (1967).

Skulls and mandibles were prepared as follows: *C. oblonga* (3), *C. steindachneri* (1) and *P. umbrina* (3). Two additional *P. umbrina* skulls were borrowed from the Western Australian Museum and skulls and mandibles of *C. expansa* (2), *C. longicollis* (1), *Em. macquaria* (1) and *Elseya latisternum* (1) were borrowed from John Goode. The mandible of *Em. macquaria* was incomplete. The authors' collection is now in the Western Australian Museum.

Serology.—One or more individuals of each of the following species (with localities) were used for serological studies. Museum numbers are given where available.

1) *Pseudemydura umbrina* Twin Swamps Wildlife Sanctuary, Warbrook, Western Australia.
2) *Elseya latisternum* Burnet River, Gayndah, Queensland.
3) *El. dentata* North Johnstone River, Malanda, Qld.
4) *El. novaeguinea* Lake Murray, Papua. A.M. (Australian Museum).
5) *Emydura macquaria* Patho, Victoria.
6) *Em. kreffti* Woodstock, Qld.
7) *Em. subglobosa* Lake Murray, Papua. A.M.
8) *Em. australis* Parry's Creek, near Wyndham, West. Aust. W.A.M. (Western Australian Museum) R 29412.
9) *Chelodina steindachneri* Wiluna, West. Aust.
10) *C. longicollis* Patho, Victoria.
11) *C. novaeguineae* Woodstock, Qld.
12) *C. oblonga* Northam, West. Aust.
13) *C. expansa* Patho, Vic.

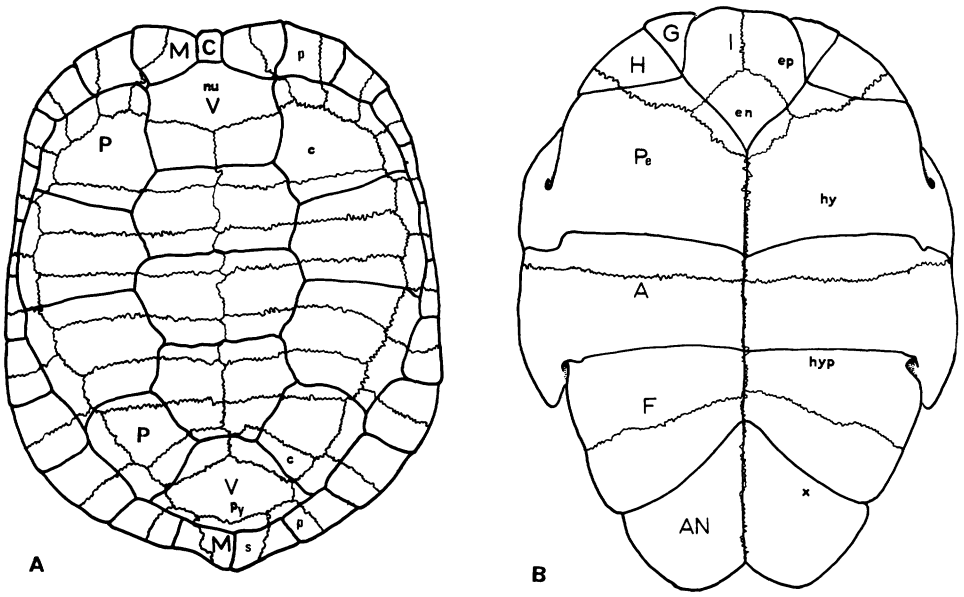

Fig. 1. *Pseudemydura umbrina* Carapace (A) and Plastron (B) Scutes: A, abdominal; AN, anal; P, pleural; F, femoral; G, gular; H, humeral; I, intergular; M, marginal; C, cervical; Pe, pectoral; V, vertebral. Plates: c, costal; s, suprapygal; en, entoplastron; ep, epiplastron; hy, hyoplastron; hyp, hypoplastron; p, peripheral; n, neural; nu, nuchal; py, pygal; x, xiphiplastron.

14) *C. ?rugosa* Kalumburu, West. Aust. W.A.M. R 29411.
15) *C. rugosa* Darwin, Northern Territory. A.M. R 26940.
16) *Testudo graeca* Locality unknown.

The *C. ?rugosa* above differed from typical *C. rugosa* by having radiating markings on each carapacial scute instead of longitudinal wavy grooves. Its taxonomic status is uncertain.

Blood was obtained by cardiac puncture and antisera to *Elseya latisternum, Emydura macquaria* and *Chelodina oblonga* were produced in rabbits (New Zealand Whites) by Freund's (1956) adjuvant technique. Immunoelectrophoresis (IEP) was carried out according to the micromodification of Scheidegger (as described by Hirschfield, 1960), using Oxoid Ionagar No. 2, made up to 1% in pH 8.6 Veronal buffer. Electrophoresis was carried out at 8–9 v/cm for 45 min., and the slides were incubated with antiserum for two days at 20 C. The precipitin patterns in the dried agar were stained with Azocarmine B.

Aliquots of each antiserum were absorbed with different heterologous sera and reacted with the 16 sera listed above. The reactions for each series of tests were scored by expressing the number of precipitin lines in the heterologous pattern as a percentage of the number of lines in the homologous pattern, and assigning a number from 0–5, corresponding to the percentages 0, 1–24, 25–49, 50–74, 75–99, and 100. Because of the low number of lines involved, these scores generally corresponded to discrete intervals.

After scoring, the data were analyzed by two methods of numerical taxonomy. Goodall's (1966) probabilistic similarity index was computed on a Digital PDP-6 computer using Goodall's programs, and routines were used from NT-SYS, the set of coordinated multivariate statistical programs developed by Rohlf, Kishpaugh and Bartcher and in general use for systematic studies at the University of Kansas. These routines included computation of a correlation of variables matrix from the data and a principal components analysis of that matrix which provided coordinates for a three-dimensional representation of the affinities of the 16 species.

Nephelometry was carried out with one antiserum according to the method of Boyden (1942) as modified by Kirsch (1967), and Boyden curves plotted for the titrations.

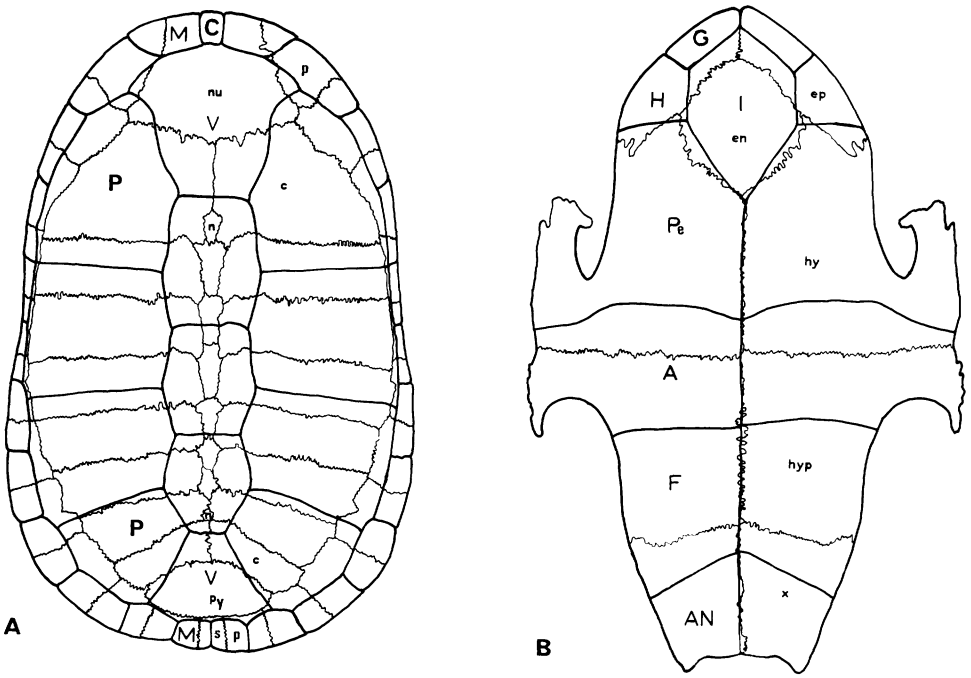

Fig. 2. *Chelodina oblonga* Carapace (A) and Plastron (B). Abbreviations as for Fig. 1.

Nephelometry is a photoelectric technique for measuring the reaction between antiserum and antigen mixtures over an antigen dilution series representing the range from antigen excess to antibody excess.

Boyden curves were plotted for the titrations and the heterologous reactions were also expressed as percentages of the homologous reactions, obtained in each case by summing the turbidities for the entire titration. Negative values in the zone of antigen excess were treated as zero values.

Results

Morphology.—Nomenclature of plates and scutes follows that of Zangerl (1969).

Patterns of the carapacial scutes of all species were very similar. The presence or absence of the cervical has been used to diagnose species and even genera. However, members of a single population may or may not possesss a cervical although one condition usually predominates. *Chelodina steindachneri*, for example, usually has a cervical but occasional specimens lack it. Similarly, members of *Elseya* usually, but not invariably, lack a cervical.

The arrangement of the plastral scutes, in particular the relationship of the intergular to the gulars and humerals, differs between species and is of great utility when defining taxa. In *Elseya* and *Emydura* the intergular is small, marginal and extends far enough posteriorly to only partially separate the humerals. The intergular of *Elseya* is smaller and more rectangular than in *Emydura*, in which it is dilated posteriorly. *Pseudemydura* has a much larger intergular which extends posteriorly to completely separate the humerals and partially separate the pectorals (Fig. 1). In *Chelodina* (Fig. 2) the intergular is similar to that of *Pseudemydura* in relative size and in the way it divides the pectorals, but it is completely enclosed anteriorly by the gulars, which meet at the midline. In some specimens, such as the holotype of *C. intergularis* Fry (1915), the anterior end of the intergular is marginal and separates the gulars.

The bony plates of the carapace are similarly arranged in all species but one. It has been stated that the Australian Chelidae, unlike most of the South American species, do not possess neurals and that the costals meet at the midline (Waite, 1929; Zangerl, 1948; Williams, 1953). This appears to be

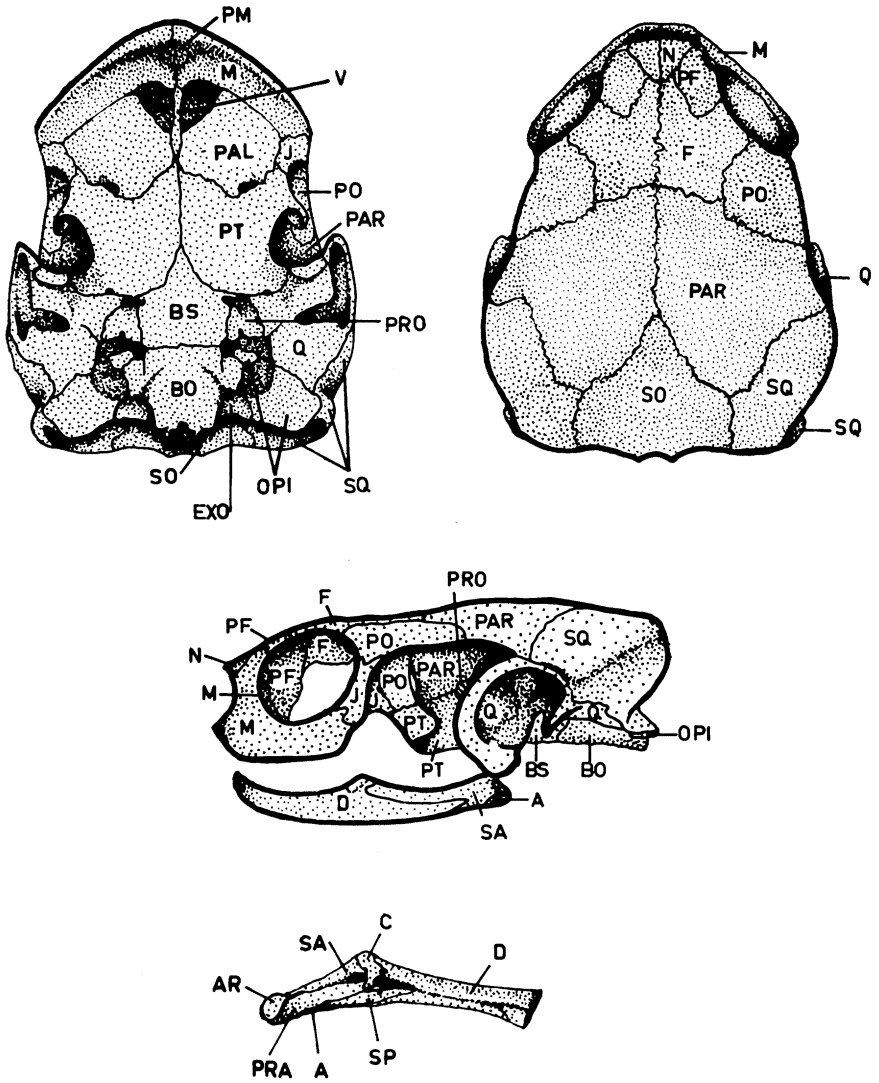

Fig. 3. *Pseudemydura umbrina* Skull and Mandible A—angular; AR—articular; BO—basioccipital; C—coronoid; D—dentary; EX—exoccipital; F—frontal J—jugal; M—maxilla; N—nasal; PAL—palatine; PAR—parietal; PF—prefrontal; PM—premaxilla; PO—postorbital; PRA—prearticular; PRO—pro-otic; PT—pterygoid; OPI—opisthotic; SA—surangular; SO—supraoccipital; SP—splenial; SQ—squamosal; V—vomer.

true in all species (e.g. *P. umbrina*, Fig. 1) except *Chelodina oblonga* (Fig. 2). Nine shells from near Perth, Western Australia were examined, together with a sub-fossil carapace from a cave near Augusta, 300 km south of Perth. One had five neurals, three had six, four had seven and two had eight. The specimen figured has eight. Those with fewer than eight neurals lack one or more of the most anterior or the two most posterior. Zangerl (1948) reported that *C. oblonga* does not possess neurals but he probably examined specimens of *C. rugosa* or *C. siebenrocki*, as these species have been synonymized with *C. oblonga* by other workers (e.g. Siebenrock, 1915; Wermuth and Mertens, 1961). Examination of *C. rugosa* and *C. siebenrocki* in the Western Australian Museum and the Australian Museum has confirmed that they do not possess neurals.

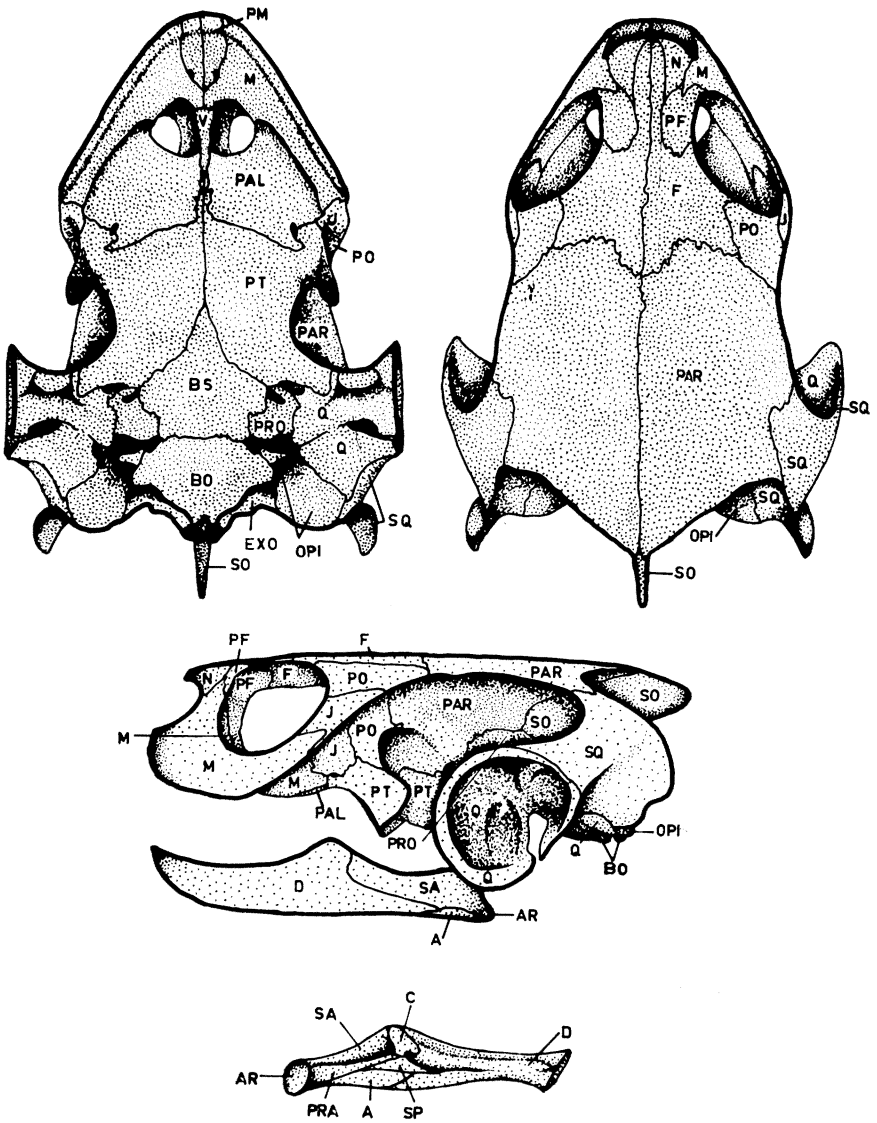

Fig. 4. *Elseya latisternum* Skull and Mandible. Abbreviations as for Fig. 3.

Arrangement of bony plastral plates does not vary significantly among the four genera.

The chief difference in the arrangement of various skull elements is the amount of temporal emargination. *Pseudemydura umbrina* (Fig. 3) has no posterior emargination and little ventral emargination, so that the parietal narrowly contacts the quadrate and broadly contacts the squamosal. The supraoccipital makes up a large part of the skull roof and is broadly in contact with the squamosal. *Elseya latisternum* (Fig. 4) and *Emydura macquaria* (Fig. 5), which have very similar skulls, have extensive posterior and ventral emargination. There is no contact between the supraoccipital and squamosal and the contact between the supraoccipital and parietal is much reduced. Similarly, there is no contact between the parietal and quadrate and the contact between the parietal and squamosal is reduced to a narrow bar. In *Chelodina oblonga* (Fig. 6) the posterior and ventral emarginations have joined and there is no contact between the

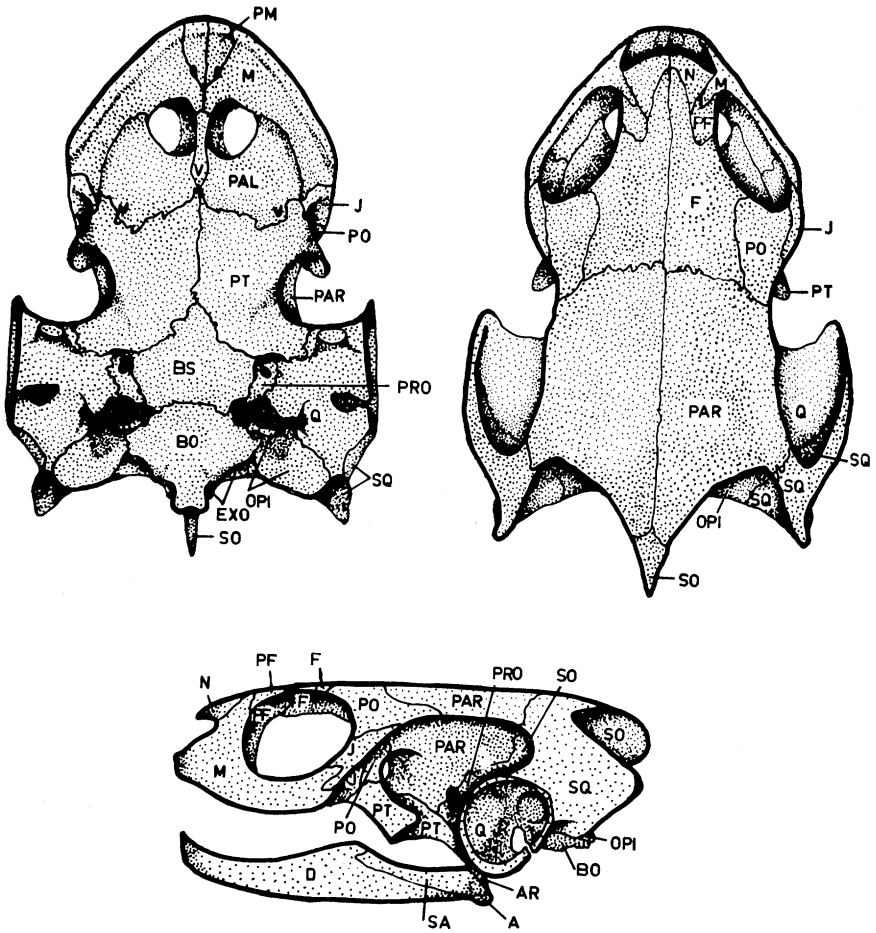

Fig. 5. *Emydura macquaria* Skull and Mandible. Abbreviations as for Fig. 3.

parietal and squamosal. The parietals, and particularly the supraoccipital, are much reduced dorsally. Skulls of *Chelodina expansa, C. longicollis,* and *C. steindachneri* have exactly the same structure.

Further differences between the skulls are as follows. In *P. umbrina* the premaxillae are much reduced and the anterior processes of the frontals do not separate the nasals; in the other groups this separation is almost complete. In *Chelodina* the frontals are fused and the maxillae extend dorsally so they contact the frontal and separate the prefrontals from the nasals.

Certain minor differences are evident between the skulls of *Elseya latisternum* and *Emydura macquaria*; in particular the snout of *El. latisternum* is more elongate and the frontals are correspondingly longer and extend further forward. Also, emargination has proceeded further in *Em. macquaria.* Although all the species of *Elseya* examined had longer, narrower heads than in *Emydura,* it is not known if the other differences noted above occur consistently throughout each genus.

There are only minor differences in arrangement of the seven bones which make up the mandible. All species had well developed splenials and coronoides, but only in *Chelodina* is the coronoid visible laterally. In *Pseudemydura umbrina* the prearticular extends forward to separate the coronoid and splenial; in all other species these elements are in contact. The angular is much reduced in *P. umbrina* compared with other species.

Serology.—The immunoelectrophoresis reactions performed and their resulting scores are

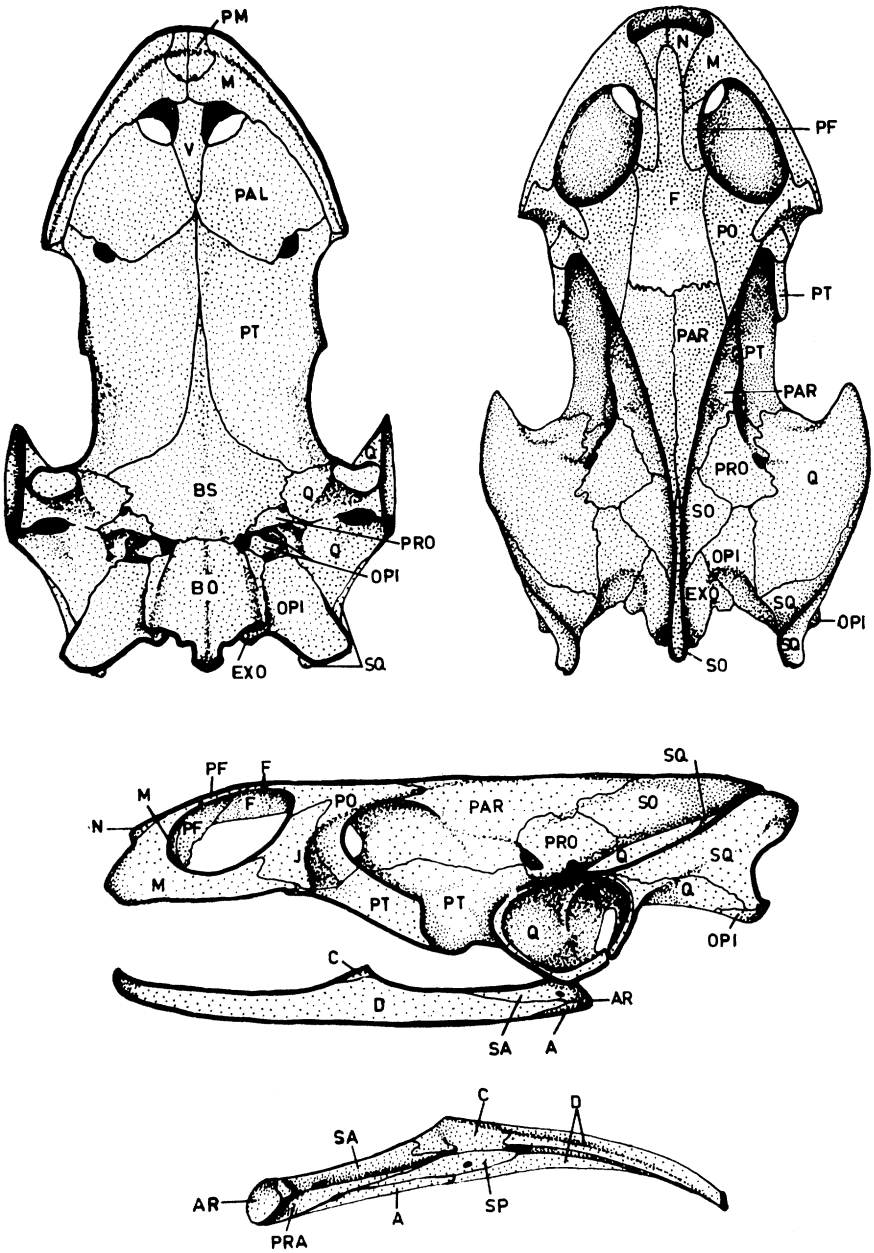

Fig. 6. *Chelodina oblonga* Skull and Mandible. Abbreviations as for Fig. 3.

shown in Table 1. Fig. 7 shows some absorbed and unabsorbed IEP reactions of anti-*Elseya latisternum*.

Some generalizations may be made about the reactions of each antiserum from inspection of Table 1. When anti-*El. latisternum* was absorbed with *El. dentata* or *Em. australis*, all activity disappeared for all species except the homologue. Absorption with *Chelodina steindachneri* or *C. longicollis* left strong activity only for *Emydura* spp. and *Elseya* spp. The effect of absorption with *P. umbrina* serum was similar to that with *Chelodina*. Absorption with *Testudo graeca*,

TABLE 1. IMMUNOELECTROPHORETIC REACTIONS OF ABSORBED RABBIT ANTISERA AGAINST THREE AUSTRALASIAN CHELIDS. Abbreviations are first two letters of the generic and specific names; identifying numbers correspond to listing in text (see "Methods").

Antiserum & absorbent	Sera tested															
	1 Ps. um.	2 El. la.	3 El. de.	4 El. no.	5 Em. ma.	6 Em. kr.	7 Em. su.	8 Em. au.	9 Ch. st.	10 Ch. lo.	11 Ch. no.	12 Ch. ob.	13 Ch. ex.	14 Ch. ?ru.	15 Ch. ru.	16 Te. gr.
anti-*Elseya latisterum* plus:																
1. Ps. um.*	1	5	3	3	3	3	3	3	1	1	1	1	2	2	2	1
3. El. de.	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5. Em. ma.	0	5	2	1	0	0	1	1	0	0	1	0	0	1	1	0
8. Em. au.	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9. Ch. st.	2	5	3	3	3	3	3	3	0	0	0	0	0	0	0	0
12. Ch. ob.	0	5	3	3	3	3	3	3	0	0	0	0	0	0	0	0
16. Te. gr.	2	5	3	3	3	3	3	3	2	2	2	2	2	2	2	0
anti-*Emydura macquaria* plus:																
1. Ps. um.	0	2	2	2	5	4	4	4	0	0	0	0	0	0	0	0
2. El. la.	0	0	0	2	5	5	5	4	0	0	0	0	0	0	0	0
3. El. de.	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0
6. Em. kr.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8. Em. au.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9. Ch. st.	2	3	4	3	5	5	4	5	0	1	1	1	1	1	1	0
12. Ch. ex.	0	3	3	3	5	4	4	4	0	0	0	0	0	1	0	0
16. Te. gr.	3	4	4	3	5	5	4	4	2	2	2	2	2	2	2	0
anti-*Chelodina oblonga* plus:																
1. Ps. um.	0	0	0	0	1	1	2	1	3	4	3	5	4	4	4	0
2. El. la.	1	0	1	0	0	0	0	1	4	4	3	5	4	4	4	0
3. El. de.	0	0	0	0	0	0	0	0	4	5	3	5	4	4	4	0
5. Em. ma.	1	1	1	1	0	1	1	1	4	4	3	5	4	4	3	0
9. Ch. st.	0	0	1	0	0	0	0	0	0	2	2	5	2	2	2	0
13. Ch. ex.	0	0	0	0	0	0	0	0	1	3	2	5	0	2	3	0
16. Te. gr.	2	2	2	2	2	2	2	2	4	4	4	5	4	4	4	0

* *Pseudemydura umbrina* serum incompletely absorbed anti-*Elseya latisternum*.

which was used as a taxonomically distant control, removed all antibodies only for itself.

Experiments with anti-*Emydura macquaria* complemented those with anti-*El. latisternum* in that absorption with other *Emydura* spp. removed all antibody activity. Absorption with *Elseya* sera left some activity for the *Emydura* species and in one case for an *Elseya*. Absorption with *Chelodina, Pseudemydura* or *Testudo* sera gave results similar to those obtained when these were used to absorb anti-*El. latisternum*. Reactions with anti-*Chelodina oblonga* are less easy to summarize; but in general absorption with *Emydura, Elseya* or *Pseudemydura* left strong activity for the *Chelodina* species. Absorption with *C. steindachneri* and *C. expansa* greatly reduced the activity for other *Chelodina* species and virtually eliminated reactions with species outside that genus. Absorption with *Testudo graeca* eliminated all activity against only itself.

Goodall's (1966) numerical taxonomic procedures produce a table showing the probabilities of association for each species pair within a larger grouping. The nature of the computation is such that a strong

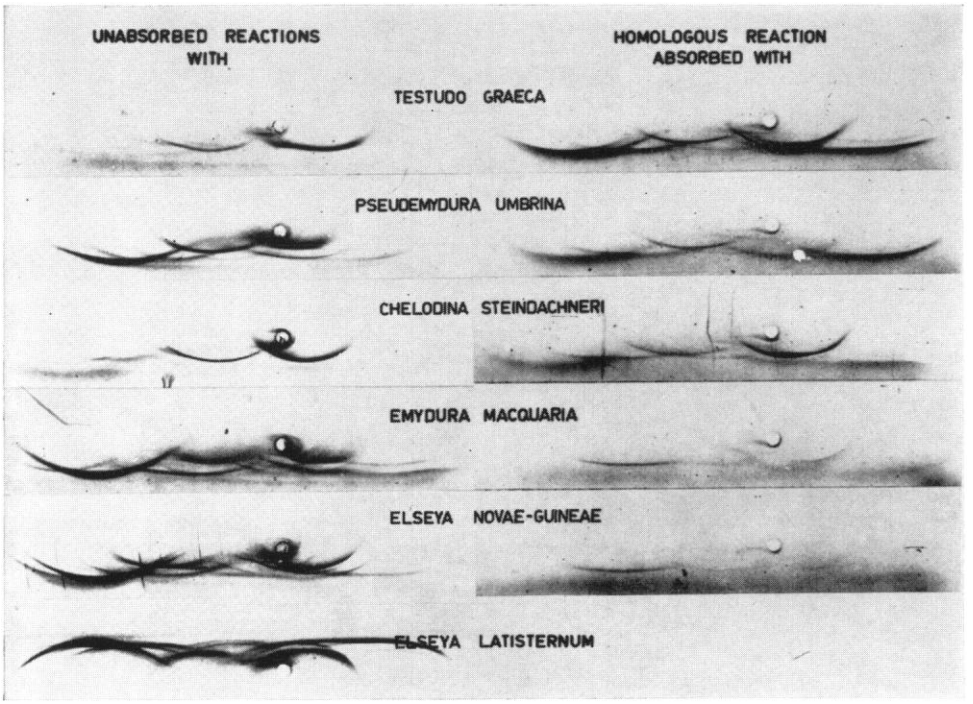

Fig. 7. Immunoelectrophoretic reactions with rabbit anti-*Elseya latisternum* serum. The photographs at left show reactions of several sera with unabsorbed anti-serum; those at right, of homologous serum (*El. latisternum*) when each of heterologous sera is used in turn as absorbent.

species grouping distorts the affinities of the less similar species. The data for the species in the strongest group must therefore be removed and the entire computation reperformed in order to reveal the next strongest group. Successive recomputation is continued until there are no more significant groups. Then the data for all species in each group are averaged and the affinities of the groups computed by treating each group as a single taxon.

The first computation showed a clear grouping of all *Emydura* species. The data for these were then removed and the next

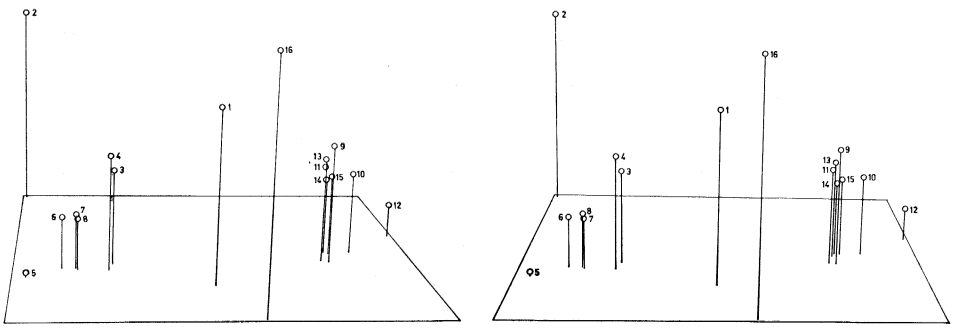

Fig. 8. Stereo pair representing affinities of 16 species in three-dimensional space, obtained by a principal components analysis of correlation matrix computed from data in Table 1. First three principal components account for over 85% of variation. Each circle shows location of a species, numbered as in text (see "Methods"). Length of each line joining a circle to plane corresponds to distance in the vertical dimension, while measurements on plane depict distances in other two dimensions.

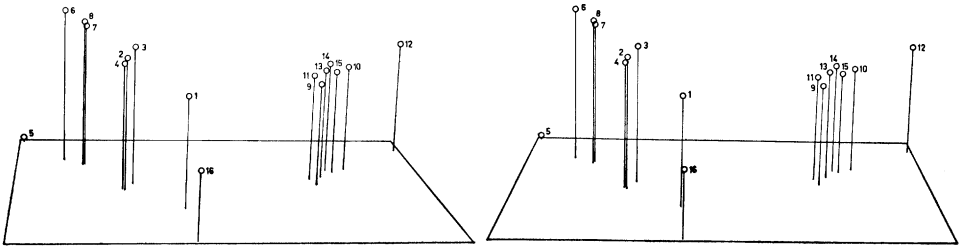

Fig. 9. Stereo pair as in Fig. 8 but with omission of data for anti-*Elseya latisternum*. First three principal components account for over 91% of variation.

run showed an association of *Elseya dentata* and *El. novaeguineae* and a weaker affinity between these two and *El. latisternum*. The three *Elseya* were removed and the next computation indicated a strong affinity between *Chelodina rugosa* and *C. ? rugosa*; the fourth computation grouped *C. longicollis* and *C. expansa* and the fifth gave no further groupings.

When group affinities were computed, the two groups of *Chelodina* showed affinities with each other at various levels of significance, but the other groups showed no clear affinities. A final run with all species of *Chelodina* averaged as a single input indicated no further groupings.

Fig. 8 represents the affinities of the 16 species in a three-dimensional projection, derived from a principal components analysis of the correlation matrix computed by the NT-SYS programs from the data of Table 1. With the exception of the distinct position of *Elseya latisternum* this analysis appears to agree with the results obtained by Goodall's method very closely; i.e. *Pseudemydura* is well separated from *Chelodina* and the *Emydura* and *Elseya* groups. Note that the species of *Chelodina* do group quite closely and that *Emydura* and *Elseya* (ignoring *El. latisternum*) form two close but distinct groups. *Testudo* is further removed than *Pseudemydura* from the other Australian chelids, as befits its classification as a separate sub-order.

Such anomalies as the separation of *Elseya latisternum* from related species are to be expected when a limited range of antisera are employed. One reason for this is that the large number of high values (5) for homologous sera tend to isolate these sera from those of other members of their genera. *C. oblonga* and *Em. macquaria* are also isolated by the effect from the other *Chelodina* and *Emydura*, respectively; but the anomaly is especially pronounced in *El. latisternum* because anti-*El. latisternum* is a weakly cross-reacting antiserum, and the discrepancy between homologous and heterologous values is marked (the next strongest reaction is 3). The NT-SYS analyses were recomputed after the omission of the data for anti-*El. latisternum* and the resulting stereogram (Fig. 9) does not show the anomalous separation. However, the remaining homologous sera, *Em. macquaria* and *C. oblonga*, remain somewhat isolated. In sum, certain apparent affinities indicated by analysis of serological data must be carefully distinguished as artifacts of the experimental coverage and should not be considered as truly definitive.

The grouping of the species as indicated by numerical analysis of the IEP data is as follows:

1. *Pseudemydura umbrina*
2. *Elseya* spp.
3. *Emydura* spp.
4. *Chelodina* spp.
5. *Testudo graeca*

The Boyden curves for the nephelometric reactions of anti-*C. oblonga* are shown in Fig. 10. The three other species of *Chelodina* which were tested gave the strongest reactions and were about equally similar to *C. oblonga* (reaction to *C. longicollis* not figured); while *P. umbrina, El. latisternum* and *Em. macquaria* were progressively less similar. *Testudo graeca* showed only a weak cross reaction.

Discussion

Consideration of the morphological evidence suggests that three divergent groups exist within the Australian Chelidae. These are:

1) *Emydura* and *Elseya*, which have short necks, a small marginal intergular and a narrow parieto-squamosal bar,

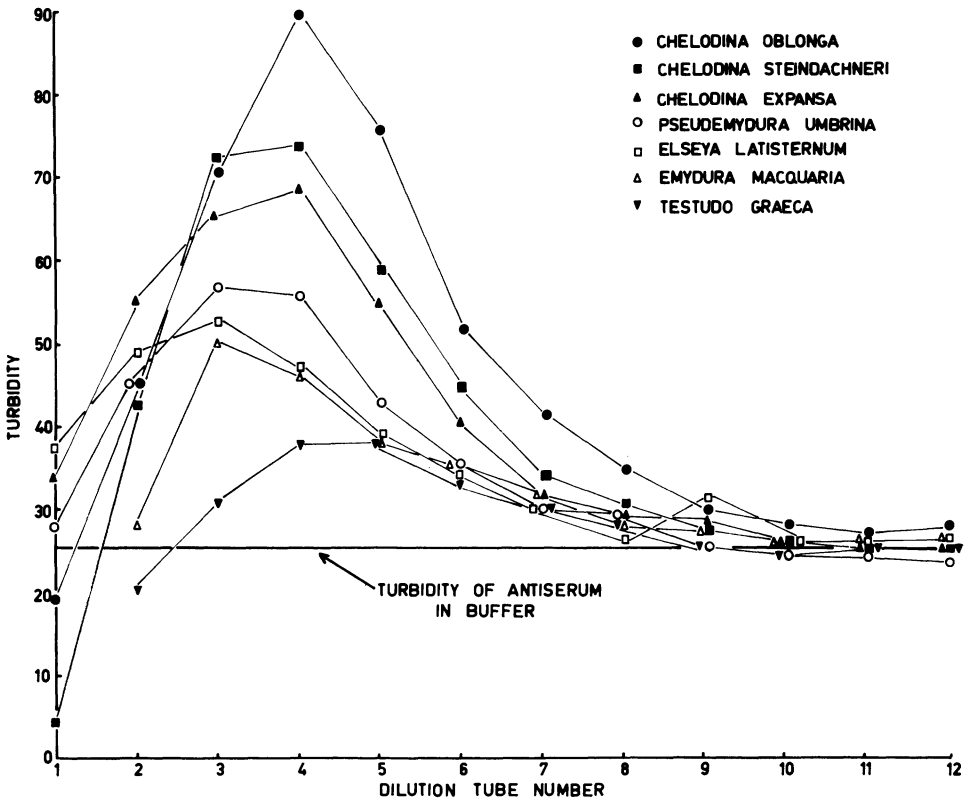

Fig. 10. Boyden curves for reactions of anti-*Chelodina oblonga*. Percent reactions are: *C. oblonga*, 100%; *C. steindachneri*, 77.6%; *C. expansa*, 75.8%; *C. longicollis*, 75.4% (not figured); *P. umbrina*, 59.1%; *El. latisternum*, 50.9%; *Em. macquaria*, 34.5%; *T. graeca*, 18.5%.

2) *Chelodina*, which have long necks, an enclosed intergular, and no parieto-squamosal bar, and
3) *Pseudemydura umbrina*, which has a short neck, a large marginal, and a completely roofed skull.

The first two groups can also be subdivided. *Elseya* and *Emydura* can be separated as shown in Table 2 (modified from Goode, 1967).

Boulenger (1889) characterized the genus *Elseya* as having a median alveolar ridge on the palate. As this character is present only in *El. dentata*, Boulenger placed *El. latisternum* and *El. novaeguinea* in *Emydura*. Gray (1867) had originally placed *latisternum* in *Elseya* but *novaeguineae* had been associated with *Emydura* until Goode (1967) relocated it. We consider the presence or absence of an alveolar ridge of minor importance, and in the light of the more consistent groupings above we believe that character should not be considered at the generic level.

TABLE 2.

	Elseya	*Emydura*
Intergular	narrow, rectangular	broad, dilated posteriorly
Cervical	usually absent	usually present
Skull cap	horny plate	smooth skin
Snout	prominent, long	flattened, short
Tubercles behind eye	few, prominent, large	many, flattened, small

TABLE 3.

	1.	2.	3.
Neck	Comparatively short, thin	very long, thick	very long, thick
Shape of Skull	small, not flattened height/width at rear of maxillae	large, flattened height/width	large, flattened height/width
	< 1:2.5	> 1:2.5	> 1:2.5
Carapace length of adult female	< 25 cm	> 25 cm	> 25 cm
Neurals in carapace	absent	absent	present, 5–8

Similarly, it is possible to divide *Chelodina* into three species groups:

1. *C. longicollis*
   C. novaeguineae
   C. steindachneri
2. *C. expansa*
   C. rugosa
   C. siebenrocki
3. *C. oblonga*

which differ as shown in Table 3.

C. oblonga could be placed in the second group, as Goode (1967) has done, but its possession of neurals suggests that it has been distinct from other members of that group for some time. Also, shells of all members of the *C. expansa* group are comparatively deeper, wider and more heavily built than the shell of *C. oblonga*.

The results obtained from the serological investigation largely agree with the groupings based on morphology. The important points are that the grouping of the short-necked species into three genera is confirmed and that *Pseudemydura* is as far, serologically, from *Emydura* and *Elseya* as it is from *Chelodina*. The morphologic evidence used to separate *Emydura* from *Elseya* is equivocal so it is noteworthy that serology does clearly separate them. Indeed the Goodall analysis does not show any relationship between them, but this is probably a computational artifact resulting from the increased discrimination within the *Emydura-Elseya* group because of the use of antisera against a species of each genus. That serology does show a close affinity of *Emydura* and *Elseya* is evident from the NT-SYS analysis and from inspection of Fig. 7 and Table 1.

The serological evidence does not support Goode's (1967) suggestion that *Emydura australis* should be separated from other *Emydura* because of minor differences in the structure of the skull and mandible, and the development in old adults of a differently shaped carapace and a head so large it cannot be withdrawn between the carapace and plastron (see also Worrell, 1963). Juveniles and young adults look much like other *Emydura* (C. Tanner, pers. comm.), so the changes in carapace shape and relative head size can probably be explained on the basis of unequal allometric patterns in old adults. Similar conditions have been found in other groups, such as *Kinosternon subrubrum steindachneri, Sternothernus carinatus minor* (Kinosternidae) and *Graptemys barbouri* (Emyidae) (Carr, 1952; Wermuth and Mertens, 1961), and none have warranted taxonomic distinction.

The serological results within *Chelodina* are somewhat confusing, for although *C. oblonga* is clearly separated, the other two morphological species-groups are not. The separation of *C. oblonga* from other *Chelodina* shown in the analysis of the IEP data could as easily be an anomaly of the experimental coverage (similar to that discussed above for *Elseya latisternum*) as a reflection of true relationship. However, the nephelometric measurements confirm that species of both other groups of *Chelodina* are serologically equidistant from *C. oblonga*. *C. oblonga* has probably been isolated from the other *Chelodina* for a considerable period of time (see below) and this phyletic relationship could superficially make the other spe-

TABLE 4. DISTRIBUTION OF THE CHELIDAE IN AUSTRALIA AND NEW GUINEA. The geographic regions are as shown in Figure 11. A dash (-) means that no member of that group is known to occur in the indicated region.

	Geographic Region							
Group	SW	W	SE		N			New Guinea
			WSE	ESE	NE		NW	
Chelodina longicollis	-	*steindachneri*	*longicollis*		*novaeguineae*			*novaeguineae*
Chelodina expansa	-	-	*expansa*		*rugosa*			*siebenrocki*
Chelodina oblonga	*oblonga*	-	-		-			-
Elseya	-	-	-	*latisternum*	*latisternum dentata*		*dentata*	*novaeguineae*
Emydura	-	-	*macquaria*	*kreffti*	*kreffti*		*australis*	*subglobosa*
Pseudemydura	*umbrina*	-	-		-			-

cies appear equally different from *C. oblonga*. For example, the Goodall analysis showed a grouping of *C. longicollis* and *C. expansa* which is not evident in the NT-SYS analysis and is not supported by morphology. In order to clarify these relationships the IEP experiments should be extended, using antisera prepared against members of the other two groups of *Chelodina*.

Although the serological results are equivocal, the morphological differences between the three groups of *Chelodina* are quantitatively similar to those between *Emydura* and *Elseya* and this, along with the zoogeographic evidence discussed below, suggests that they are in fact equally divergent groups.

The distributions of Australian and New Guinean chelids are not yet well documented, but from what is known (see Table 4 and Fig. 11) it is evident that their distribution does not conform to the patterns typical of faunas which have been greatly affected by Pleistocene climatic changes, e.g. birds (Serventy and Whittell, 1948) and frogs (Main, Lee and Littlejohn, 1958). Birds and frogs largely fit the three zoogeographic subregions (Torresian, Eyrean and Bassian) of Spencer (1896), with a mingling of Eyrean and Bassian species in the southwest corner of Australia. In the case of the tortoises, however, the Bassian region has only one chelid, *Chelodina longicollis*, which also occurs in parts of the Eyrean and Torresian regions, while the southwest has a unique chelid fauna of two species.

The evolution and present distribution of Australian chelids therefore requires a different interpretation.

Except for the most arid parts of Australia and the southwest corner, there is usually present in any area one member of the four polytypic species groups. This distribution appears consistent with the hypothesis that the ancestor of each species group was widespread throughout eastern and northern Australia during a period when the climate was wetter than at present, and that speciation has probably occurred in allopatry following fragmentation (resulting from increased aridity) of the original populations. The presence of *Emydura* spp. in isolated pools in central Australia supports this contention.

Fossil floras including *Nothofagus* of upper Eocene or lower Oligocene age have been reported in parts of inland southern Australia now receiving less than ten inches of

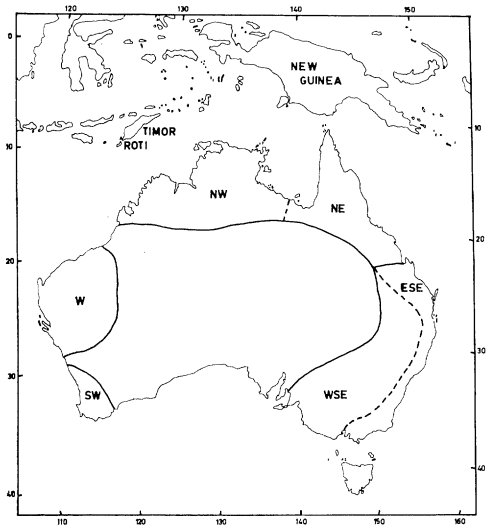

Fig. 11. Map of Australia and New Guinea showing extent of each geographic region listed in Table 4.

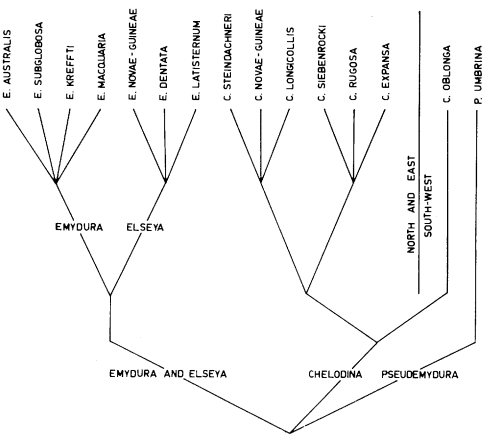

Fig. 12. Diagram showing relationships within the Chelidae of Australia and New Guinea.

rainfall per year (Balme and Churchill, 1959; Cookson, 1953; Cookson and Pike, 1953, 1954). As *Nothofagus* is at present restricted to rainforests in eastern Australia, New Guinea, and elsewhere in the Pacific region, this suggests that the climate in southern Australia may have become more arid during the late Tertiary and this may have caused fragmentation and speciation of the chelid groups. However, such a hypothesis also suggests that there would have been no climatic barriers between eastern and western Australia in pre-Oligocene time and this raises the question as to why the southwestern chelid fauna shows no eastern influence.

The southwest is at present isolated from the rest of Australia by areas of waterless desert. The region is noted for its high proportion of endemics, and the two chelids, *Pseudemydura umbrina* and *Chelodina oblonga*, are specialized and have no near relatives. Observations indicate that *C. oblonga* lives only in permanent water and is probably the least dry-adapted of all the Australian Chelidae (Burbidge, 1967). This suggests that the climate could never have become dry enough to eliminate the other chelid groups, for it would also have eliminated *C. oblonga*. Thus, the southwest appears never to have been occupied by other chelid groups.

In the Cretaceous a sea divided Australia from the Gulf of Carpentaria to the south coast (Keast, 1960; Glaessner and Parkin, 1957; Hill and Denmead, 1960), and any land connection would have been tenuous. In the Tertiary the sea receded to the Nullarbor Plain and the resulting limestones there have produced a riverless and edaphic barrier since. As a result of these events, the ancestor of *C. oblonga* could have been isolated from the eastern *Chelodina* before they diverged and lost their neurals. *Pseudemydura* could also have been isolated in the Cretaceous and its eastern representative (if there was one) may later have become extinct. The absence of a progenitor to the *Emydura-Elseya* group in the southwest suggests that this group did not inhabit southern Australia at that time but was restricted to the north.

Pleistocene climatic changes have affected the distribution of chelids in northern Australia. A land bridge which allowed rain forest frogs to enter Australia from New Guinea (Straughan and Main, 1966; Main, 1968) also allowed the passage of chelids. Thus, *C. novaeguineae* is reported from Australia, New Guinea and the island of Roti near Timor. The interspecific relationships of these populations are not well understood, however. Similarly other groups have species-pairs in northern Australia and New Guinea. These are *C. rugosa* and *C. siebenrocki*, *Em. krefftii* and *Em. subglobosa* and *El. dentata* and *El. novaeguineae*. A Pleistocene land connection was also present between Australia and Tasmania, but no extant chelids

are known from Tasmania. We attribute this absence to Tasmania's relatively cool climate, which would have been even colder when the bridge was present. During the *Pleistocene*, moister conditions than at present prevailed in southern Australia, but although moisture conditions were sufficient to allow the east-west migration of some frogs (Main et al., 1958; Main, 1968), it was evidently not wet enough to allow chelids to establish populations over much of this area.

A phylogeny incorporating the views expressed above is presented in Fig. 12.

The previous discussion allows, we believe, a better interpretation of the scant fossil record of the Chelidae in Australia. Apart from reports of a few small fragments from the Pleistocene of Queensland (Lydekker, 1889; de Vis, 1897; Longman, 1929), there have been only two significant fossil discoveries. Warren (1969a) reported a fossil chelid of Oligocene-Miocene age from Tasmania which cannot be distinguished from recent *Emydura macquaria*. This fossil supports the hypothesis that populations ancestral to the four main species groups were widespread in eastern and northern Australia during the Oligocene. The presence of this fossil in Tasmania also suggests that the climate of that island has become cooler since the Oligocene. The other record is of a specimen from Victoria which was originally identified as *Em. macquaria* and assigned a Pleistocene age (Chapman, 1919). Warren (1969b), however, has shown that the specimen was incorrectly described and that it possesses well developed posterior neurals. He named it *Chelycarapookus arcuatus* and placed it in a new family of unknown suborder. It appears to be early Cretaceous in age. The relationships of the Victorian fossil are uncertain, but we suggest that it represents one of the three main chelid groups before they lost their neurals.

The origin of the Australian Chelidae is unknown, and the family is reported only from Australasia and South America. The weight of morphological evidence leaves little doubt that the family is monophyletic in origin, although Friar's (1964, 1972) serological data showed an African pelomedusid giving a stronger cross-reaction than *Chelodina longicollis* when tested with an antiserum prepared against *Chelus fimbriatus*. We have recently extended the serological tests using an additional antiserum prepared against *Mesoclemmys* sp. and sera from *Mesoclemmys* sp., *Platemys* sp., Australian, and New Guinean chelid species, and non-chelid tortoises. Briefly, the results showed:

1) The South American species of *Mesoclemmys* and *Platemys* are more like each other than like any Australasian chelid. Using an anti-*Chelus fibriatus* serum, Friar (1972) similarly obtained a stronger reaction with another American species (*Batrachemys nasuta*) than with *Chelodina longicollis*.
2) The Australasian chelids are all more similar to each other than to *Mesoclemmys* or *Platemys*.
3) Of the Australian chelids, *Chelodina* is closest to *Mesoclemmys* and *Platemys*.
4) Although the Chelidae form two distinct serological groups, they are more similar to each other than to the non-chelid genera *Testudo* and *Clemmys*.

While this work is incomplete (ideally pelomedusids should be treated as well as cryptodires), the available information confirms the morphological evidence.

One explanation of the present distribution of the Chelidae is that the family was once widespread in the northern hemisphere but has since disappeared from there. This is the case with Pelomedusidae (Zangerl, 1948). However, no fossil chelids are known from outside their present range (Williams, 1953, 1954). Considering the wealth of pelomedusid and other turtle fossils known, it seems surprising that no chelid fossils have been found in the Northern Hemisphere and this suggests that they never occurred there. Thus the family is probably of southern hemisphere origin and its distribution may be explained by continental drift, or by rafting or swimming from one continent to another at a time when they were closer together.

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clemmys. J. W. Warren of Monash University, Clayton, Victoria, gave valuable advice on the fossil record and Merilyn Burbidge drew the figures.

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Literature Cited

Balme, B. E., and D. M. Churchill. 1959. Tertiary sediments at Coolgardie, Western Australia. J. Roy. Soc. W. Australia 42:37–42.

Boulenger, G. A. 1889. Catalogue of the Chelonians, Rhychocephalians and Crocodilians in the British Museum (Natural History), London.

Boyden, A. 1942. Systematic serology: A critical appreciation. Physiol. Zool. 15:109–145.

Burbidge, A. A. 1967. The Biology of Southwestern Australian tortoises. Ph.D. Thesis, University West. Australia, Perth.

Carr, A. 1952. Handbook of Turtles. Constable, London.

Chapman, F. 1919. On a fossil tortoise in ironstone from Carapook, near Casterton. Proc. Roy. Soc. Victoria. 32:11–13.

Cookson, I. C. 1953. The identification of the sporomorph of *Phyllocladites* with *Dacrydium* and its distribution in southern Tertiary deposits. Australian J. Bot. 1:64–70.

———, and K. M. Pike. 1953. The Tertiary occurrence and distribution of *Podocarpus* (section *Dacrycarpus*) in Australia and Tasmania. *Ibid*. 1:71–82.

———. 1954. The fossil occurrence of *Phyllocladis* and two other podocarpaceous types in Australia. *Ibid*. 2:60–68.

De Vis, C. W. 1897. The extinct freshwater turtles of Queensland. Ann. Queensland Mus. 3:3–7.

Freund, J. 1956. The mode of action of immunologic adjuvants. Adv. Tuberc. Res. 7: 130–148.

Friar, W. 1964. Turtle family relationships as determined by serological tests. *In*: Taxonomic Biochemistry and Serology. C. A. Leone (ed.), Ronald Press Co., New York.

———. 1972. Taxonomic relations among chelydrid and kinosternid turtles elucidated by serological tests. Copeia 1972:97–108.

Fry, D. B. 1915. On a new *Chelodina* from Australia with a key to the genus. Proc. Roy. Soc. Queensland 27:88–90.

Glaessner, M. F., and L. W. Parkin. 1957. The geology of South Australia. J. Geol. Soc. Australia 5:1–163.

Goodall, D. W. 1966. A new similarity index based on probability. Biometrics 22:882–907.

Goode, J. 1967. Freshwater tortoises of Australia and New Guinea (in the family Chelidae). Lansdowne Press, Melbourne.

Gray, J. E. 1867. Description of a new Australian tortoise (*Elseya latisternum*). Ann. Mag. Nat. Hist. London 20:43–44.

Hill, D., and A. K. Denmead. 1960. The geology of Queensland. J. Geol. Soc. Australia 2:1–474.

Hirschfield, J. 1960. Immunoelectrophoresis-procedure and application to the study of group specific variations in sera. Sci. Tools 7:18–25.

Keast, A. 1960. The unique plants and animals of south western Australia. Australian Mus. Mag. 13:152–157.

Kirsch, J. A. W. 1967. Comparative serology of marsupials. Ph.D. Thesis, Univ. West. Australia, Perth.

Krefft, G. 1867. Australian animals in New Guinea. Annali Museo Storia Civicio Naturale 8:390.

Longman, H. A. 1929. Palaeontological notes: specimens from a well at Brigalow. Mem. Queensland Mus. 9:247–252.

Lydekker, R. C. 1889. Catalogue of fossil amphibians and reptiles in the British Museum (Natural History), part 3.

Main, A. R. 1968. Ecology, systematics and evolution of Australian frogs. Adv. Ecol. Res. 5:37–86.

———, A. K. Lee and M. J. Littlejohn. 1958. Evolution in three genera of Australian frogs. Evolution 12:224–233.

Ogilby, J. D. 1890. Description of a new Australian tortoise. Rec. Australian Mus. 1:56–59.

Serventy, D. L., and H M. Whittell. 1948. A handbook of the birds of Western Australia. Paterson Brokensha Ltd., Perth.

Siebenrock, F. 1915. Die schildkrotengattung *Chelodina* Fitzinger. Sber. Akad. Wiss. Wein 124:13–35.

Spencer, W. B. 1896. Report on the work of the Horn scientific expedition to central Australia. Dulau and Co., London.

Straughan, I. R., and A. R. Main. 1966. Speciation and polymorphism in the genus *Crinia* (Anura, Leptodactylidae) in Queensland. Proc. Roy. Soc. Queensland 78:11–28.

Waite, E. R. 1929. The reptiles and amphibians of South Australia. Government Printer, Adelaide.

Warren, J. W. 1969a. Chelid turtles from the mid-Tertiary of Tasmania. J. Palaeont. 43: 179–182.

———. 1969b. A fossil Chelonian of probable lower Cretaceous age from Victoria, Australia. Mem. Nat. Mus. Victoria (29):23–28.

Wermuth, H., and R. Mertens. 1961. Schildkroten Krokodile Bruckenechsen. Gustav Fischer, Jena.

Werner, F. 1901. Reptilien und Batrachier von Ecuador und Neu-Guinea. II Reptilien und Batrachier von Deutsch Neu-Guinea. A. Chelonia. Verh. zool-bot Ges. Wien 51:602–603.

WILLIAMS, E. E. 1953. Fossils and the distribution of Chelyid turtles (1). Breviora No. 13.
———. 1954. Fossils and the distribution of Chelyid turtles (2). Breviora No. 32.
WORRELL, E. 1963. Reptiles of Australia. Angus and Robertson, Sydney.
ZANGERL, R. 1948. The vertebrate fauna of the Selma formation of Alabama. Part II. The Pleurodiran turtles. Fieldiana Geol. Mem. 3: 23–56.
———. 1969. The turtle shell, p. 311–339. *In*: Biology of the Reptilia, Vol. 1. Morphology A. C. Gans, A. d'A. Bellairs and T. S. Parsons (eds.), Academic Press.

DEPARTMENT OF ZOOLOGY, THE UNIVERSITY OF WESTERN AUSTRALIA, NEDLANDS, W.A. 6009, AUSTRALIA. (PRESENT ADDRESSES AAB: DEPARTMENT OF FISHERIES AND FAUNA, 108 ADELAIDE TERRACE, PERTH, W.A. 6000, AUSTRALIA; JAWK: BINGHAM LABORATORY, YALE UNIVERSITY, NEW HAVEN, CONNECTICUT 06520.)

A Review of the Microdesmidae (Pisces: Gobioidea) 1. *Cerdale* and *Clarkichthys* with Descriptions of Three New Species

C. E. DAWSON

The family includes *Gunnellichthys* Bleeker, *Paragunnellichthys* Dawson, *Microdesmus* Günther, *Clarkichthys* J. L. B. Smith and *Cerdale* Jordan and Gilbert. Relationships of *Allomicrodesmus* Schultz are unclear but it is not a microdesmid fish. Diagnoses are provided for *Clarkichthys* and *Cerdale*, removed from synonymy with *Microdesmus*, and nominal species are redescribed and illustrated. *Cerdale prolata* and *C. paludicola*, from the tropical eastern Pacific, and *C. fasciata* from Brazil are described as new. Data are provided on morphometry, distribution and ecology together with a key to genera and treated species.

THE family Microdesmidae (wormfishes) includes some 28 species of small (to about 300 mm total length), burrowing or burrow inhabiting, elongate to anguilliform fishes. They occupy a variety of low-temperate to tropical habitats ranging from coral reefs to muddy estuaries and occur to depths of at least 37 m. Regan (1912), Berg (1940) and others included the group among the blennioid fishes, but osteological studies by Gosline (1955) showed that wormfishes should be referred to the perciform suborder Gobioidei. In the first review of the family, Reid (1936) synonymized *Cerdale* Jordan and Gilbert and *Leptocerdale* Weymouth with *Microdesmus* Günther. Reid did not treat Indo-Pacific forms and included all eastern Pacific and Atlantic species within *Microdesmus*. Smith (1958) followed Reid's treatment of *Cerdale* and *Leptocerdale*; established *Clarkichthys* to accommodate *Cerdale bilineata* Clark; synonymized *Paragobioides* Kendall and Goldsborough, with *Gunnellichthys* Bleeker; treated *Gunnellichthys*, *Microdesmus* and *Clarkichthys* as subgenera of *Gunnellichthys*; and changed the family name to Gunnellichthidae. Robins and Manning (1958) treated *Microdesmus* and *Gunnellichthys* as separate genera in the Microdesmidae, but withheld comment on *Clarkichthys*. Schultz (1966) retained the family name Microdesmidae, elevated Smith's subgenera to generic status, and described *Allomicrodesmus dorotheae* as the type species of *Allomicrodesmus*.

The holotype and only known specimen of *A. dorotheae* is a damaged postlarva of uncertain relationships. Contrary to the original description and figure, all but the 1st two dorsal fin rays are segmented and unbranched; there are no branched caudal or anal fin rays; the separated pelvic fins are badly distorted but the inner margin of the left fin bears a ragged tissue fragment suggesting that the pelvic fins were originally united; there is a distinct pore on the posterodorsal margin of the orbit. The combination of reduced dorsal spines, orbital pore and described gill opening morphology (membrane united, forming a free fold