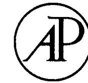
Zoological Journal of the Linnean Society (1996), *118:* 241–260. With 2 figures



Electrophoretic delineation of species boundaries within the short-necked freshwater turtles of Australia (Testudines: Chelidae)

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Received November 1995, accepted for publication February 1996

A total of 222 specimens from 55 populations of short-necked chelid turtle was collected from drainages in Australia and Papua New Guinea. Two populations were initially considered to belong to different diagnosable taxa if all individuals in one population could be distinguished from all individuals in the other by fixed allozyme differences. When two populations or diagnosable taxa shared allozymes at all presumptive loci, their profiles were combined into a single diagnosable taxon. Comparisons between populations and emerging diagnosable taxa were repeated until no further changes were possible. The species *Elseya dentata* comprised five clearly diagnosable taxa, differing by between 4 and 19 fixed allozyme differences. The currently recognized *El. latisternum* and *El. novaeguineae* were each a single diagnosable taxon, and there were three diagnosable taxa, including a sibling pair, that could not be assigned to a currently described *Elseya* species. In contrast, all forms of *Emydura* were very closely related, with no two taxa differing by more than three fixed allozyme differences. There were three diagnosable taxa in the north (*Em. victoriae, Em. subglobosa* and one new form), though support for them was marginal. In the south, *Em. macquarii, Em. krefftii* and *Em. signata* formed only a single diagnosable taxon, even sharing rare alleles. If the phylogenetic species concept is adopted, there is support for recognition of 16 species of short-necked turtle in Australia, including *Pseudemydura umbrina.* Currently only 10 are described. Our data also provide evidence of reproductive isolation in some cases (sympatric or parapatric), and comparative evidence (*sensu* Mayr) in others, than the traditional biological species concept applies also to these diagnosable taxa.

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ADDITIONAL KEY WORDS:—Phylogenetic species concept – molecular systematics – pleurodire.

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0024–4082/96/011241 + 20 $25.00/0

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INTRODUCTION

Freshwater turtles in the family Chelidae occur in Australia, New Guinea, the island of Roti in Indonesia, and South America. No fossil material has been found outside their present range (Pritchard, 1979) so the family is considered to be of Gondwanan origin (Burbidge, Kirsch & Main, 1974). The current classification of Australian forms (Cogger, Cameron & Cogger, 1983; Cann & Legler, 1994) includes 16 species in six genera: six in *Chelodina*, two in *Elseya*, five in *Emydura*, *Pseudemydura umbrina*, *Rheodytes leukops* and *Elusor macrurus*. The only other freshwater turtle from Australia is *Carettochelys insculpta* of the family Carettochelydidae.

Chelid turtles are conservative in many morphological features, and their present classification is poorly founded and in dire need of review. Wermuth & Mertens (1961) listed nine species of *Emydura*: *Em. australis, albertisii, branderhorsti, kreffti, macquarrii, subglobosa, latisternum, schultzei* and *novaeguineae*, to which Worrell (1963) added *Em. victoriae*. Goode (1967) recognized only three species — *macquarii, krefftii* and *australis* — synonymizing *branderhorsti* and *schultzei* with *novaeguineae* which he transferred with *latisternum* to the genus *Elseya*. He synonymized *Em. subglobosa* and *Em. albertisii* with *Em. krefftii*. Cogger (1975) recognized six species: *Em. australis, krefftii, macquarii, signata, subglobosa* and *victoriae*, though he later synonymized *Em. australis* with *Em. macquarii* (Cogger *et al.*, 1983). In addition to those recognized by Cogger *et al.* (1983), several authors have referred to what they regard as potentially undescribed species of *Emydura* from Fraser Island of coastal Queensland (Cann, 1978; Georges & Legler, 1996), Cooper Creek in central Australia (Goode, 1967; Legler, 1981), and several rivers from coastal New South Wales (Cann, 1967, 1978; Legler, 1981). The recent synonomizing of *Emydura australis* with *E. macquarii* (Cogger *et al.*, 1983) throws into question the status of the northern yellow-faced turtle formerly assigned to *Em. australis*.

In the classification of Goode (1967), adopted also by Cogger *et al.* (1983), three species of *Elseya* are recognized — *El. dentata, El. latisternum* and *El. novaeguineae*. However, suspected new species of *Elseya* have been reported from the Namoi/Gwydir drainages of north central New South Wales (Legler, 1981), the Manning and Bellingen drainages of coastal New South Wales (Cann, 1978; assigned to *Elseya latisternum* by King & Heatwole, 1994a,b) and the coastal rivers of Queensland (Goode, 1967; Cann, 1978; Legler, 1981).

Allozyme electrophoresis complements traditional morphological approaches to resolving species boundaries (Avise, 1975; Buth, 1984; Richardson, Baverstock & Adams, 1986; Hillis, 1987). It provides a large number of characters with discrete character states that are genetically determined. Sufficient is known of the enzyme systems in use to ensure that these characters are largely independent of each other and any morphological characters used, and that they are usually expressed in all individuals regardless of age or sex. Moreover, when compared with morphological studies, fewer individuals may need be sampled per population to adequately represent the variation present in character states and to identify diagnostic character states.

In this paper, we use allozyme electrophoresis to delimit species within the short-necked chelid genera of Australia, testing boundaries between both currently recognized species and suspected new forms for consistency with the allozyme data. Our approach was to use an objective procedure to identify diagnosable taxa within these genera (Davis & Manos, 1991), which can be regarded operationally as phylogenetic species. Levels of divergence between those diagnosable taxa were compared with levels of divergence observed between forms that are well accepted as biological species, as an alternative basis for decisions on species status.

MATERIAL AND METHODS

Specimen collection and identification

A total of 222 specimens from 55 populations of short-necked chelid turtle were collected from drainages in the five Australian mainland states, the Northern Territory and Papua New Guinea (Fig. 1). *Pseudemydura umbrina* was unavailable for study, but all other recognized short-necked species are represented (Table 1), including many distinctive forms thought to be separate species (Table 2). The sampling strategy involved obtaining a minimum of five turtles (not always achieved) from each of several populations of species in the genera *Elseya, Emydura* and *Rheodytes*. *Elseya novaeguineae* (Meyer), endemic to New Guinea, was obtained from Baitetta (145°44' 5°00') and Warabruk (145°05' 5°23') in the Madang Province (Fig. 1). *Emydura subglobosa* has been reported from the northern tip of Cape York Peninsula, Queensland, but specimens used in this study were collected from near Port Moresby in New Guinea.

All turtles representing described species were identified with the aid of keys provided by Cogger (1983). Distinctive populations and undescribed species were assigned to genera using these keys and were associated with literature references on the basis of locality and comparisons with published photographs or descriptions. One exception, a form called 'short-necked alpha' could not be assigned to any known genus on morphological grounds and its natural distribution was, until recently, unknown. For nearly 25 years, short-necked alpha was known to science only from pet-shops in Victoria, but has been recently described as *Elusor macrurus* from the Mary River in Queensland (Cann & Legler, 1994). With few exceptions, the specimens were lodged with Australian museums (see Specimens Examined) and cross-referenced to tissue samples for future reference.

Specimens were returned to the laboratory alive where they were killed by intra-cranial injection of sodium pentabarbitone (Nembutal). Samples of liver, heart, muscle, kidney, whole blood and plasma were removed, immediately frozen by immersion in liquid nitrogen and stored at −70° C prior to use.

In a supplementary survey, whole blood samples were collected from populations of *Elseya* sp. aff. *dentata* from the Mary, Burdekin and Nicholson drainages of Queensland (Fig. 1), immediately frozen by immersion in liquid nitrogen and stored at −70° C prior to use.

Electrophoresis

A pilot study identified liver and muscle as the most suitable tissues for

electrophoretic analysis. Liver and muscle homogenates were stored and prepared as detailed in Adams *et al.* (1987) and screened electrophoretically on 'Cellogel' (Chemetron, Milan) using techniques described previously (Richardson *et al.* 1986).

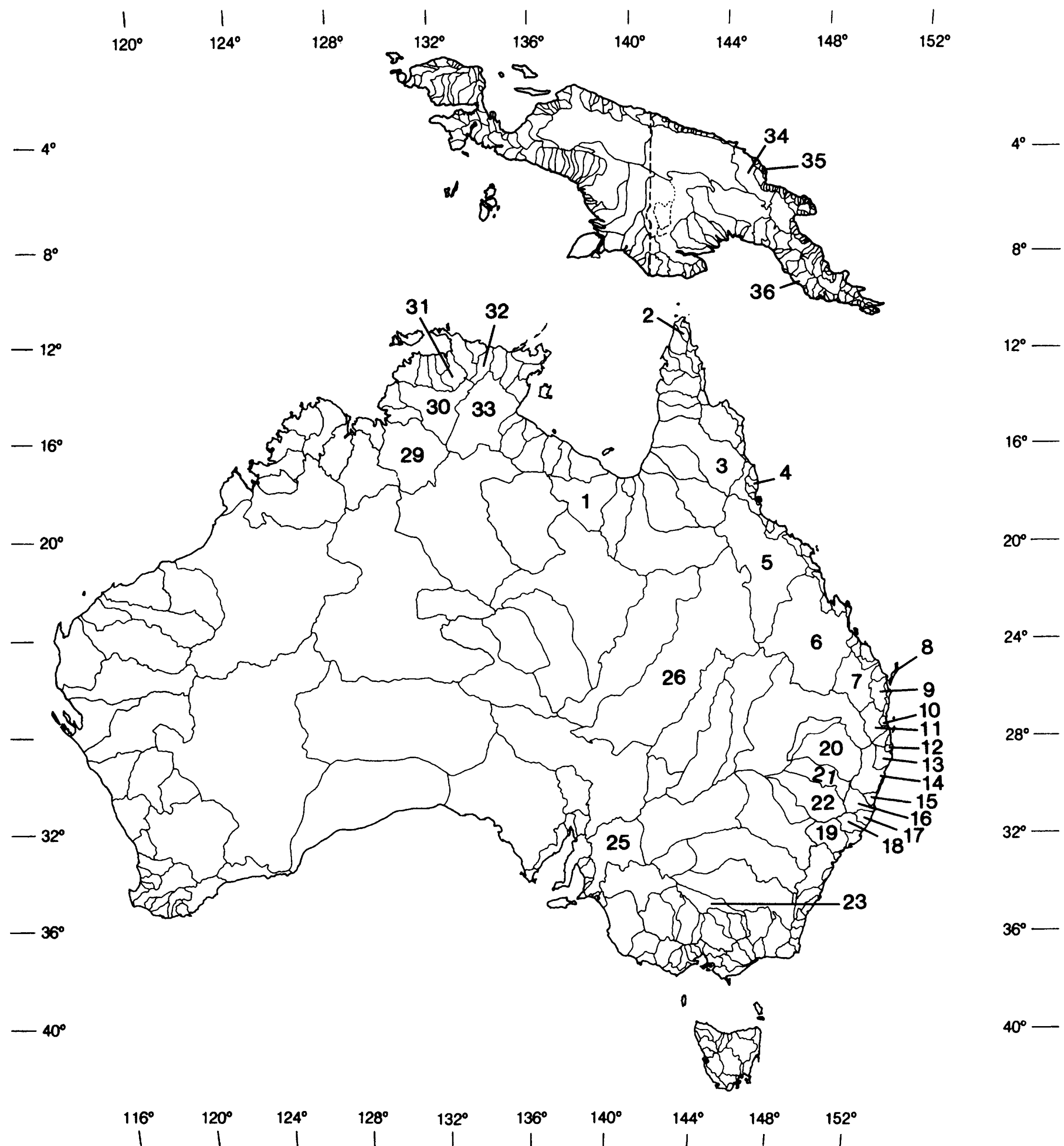

Figure 1. A map of Australian and New Guinean drainage basins showing the 33 drainages from which samples were collected. Drainage basins are numbered as follows. Queensland: 1, Nicholson R. (ELL, EMS); 2. Jardine R. of Cape York Peninsula (ELL); 3. Mitchell R. (EM*a*); 4. Johnstone R. (EL*b*); 5. Burdekin R. (EMM); 6. Fitzroy R. (EL*c*, EMM, RHE); 7. Burnett R. (EL*c*, ELL, EMM); 8. Fraser Is. (EMM); 9. Mary R. (ELL, EMM, SNA); 10. Pine R. (ELL); 11. Brisbane R. (EMM). New South Wales: 12. Tweed R. (ELL, EMM); 13. Richmond R. (ELL, EMM); 14. Clarence R. (EMM); 15. Bellingen R. (EL*e*); 16. Macleay R. (EMM); 17. Hastings R. (including Nambucca R.) (EMM); 18. Manning R. (EL*f*); 19. Hunter R. (EMM); 20. Border Rivers (Severn R., Dumeresque R.) (EMM); 21. Gwydir R. EL*d*); 22. Namoi R. (EMM). Victoria: 23. Murray Riverina Basin. (EMM). South Australia: 25. Lower Murray R. (EMM); 26. Cooper Creek. (EMM). Northern Territory: 29. Victoria R. (ELD, EMV); 30. Daly R. (ELD, EMV, EM*a*, EMS); 31. South Alligator R. (EL*a*, ELL, EM*a*); 32. Liverpool R. of Arnhem Land (including Mann R.) (ELL); 33. Roper R. (EMS). Papua New Guinea: 34: Ramu R. (ELN); 35: un-named drainage, Madang Province (ELN); 36: Lokoti R., Port Moresby (EMS). Numbering is not consecutive, so as to be consistent with that of Georges & Adams (1992). The taxa following each locality are the species proposed in Table 5.

TABLE 1. Described species of Australian chelid turtle, drainages from which they were collected, and sample sizes. *Elseya novaeguineae*, also included in the present study, is endemic to New Guinea. Classification follows that of Cogger *et al.* (1983), with the addition of *Elusor macrurus* (Cann & Legler, 1994). Location numbers correspond to those used in Figure 1

Code	Species	Locations sampled	*n*
ELD	*Elseya dentata* (Gray, 1863)	29, 30, 31	14
ELL	*Elseya latisternum* Gray, 1867	1, 2, 7, 9, 10, 12, 13, 31, 32	29
ELN	*Elseya novaeguineae* (Meyer, 1874)	34, 35	5
SNA	*Elusor macrurus* Cann & Legler, 1994	9	5
EMK	*Emydura krefftii* (Gray, 1871)	5, 6, 7, 9	19
EMM	*Emydura macquarii* (Gray, 1830)	20, 22, 23, 25	23
EMI	*Emydura signata* Ahl, 1932	11	5
EMS	*Emydura subglobosa* (Krefft, 1876)	36	3
EMV	*Emydura victoriae* Gray, 1842	29, 30	14
RHL	*Rheodytes leukops* Legler, & Cann, 1980	6	1

The principles used to assign mobility states, conduct allozymic interpretations and confirm electromorph identity are also detailed in Richardson *et al.* (1986). The enzyme products of 54 presumptive loci gave staining of sufficient intensity and resolution to be scored.

Specimens collected in the supplementary survey were scored for 38 loci in blood, with gels run for comparisons among *Elseya novaeguineae*, *Elseya dentata* (*sensu stricto*) and the Queensland forms of *Elseya* sp. aff. *dentata* only. These data were analysed separately from the main data set because of the limited set of comparisons made.

Species delimitation

Diagnosable taxa, that is, collections of populations whose individuals can all be distinguished from all individuals of other populations on the basis of a unique combination of character states, were identified using the procedure of Davis & Manos (1991). Potential errors resulting from this procedure are discussed in detail by Davis & Nixon (1992).

Each local population (group of individuals collected at a particular site) was provisionally considered as a single biological population. If previous studies suggested that two morphologically distinguishable species were present in

TABLE 2. Populations of Australian short-necked turtle considered on the basis of literature reference to be of uncertain status. Listed also are the drainages from which they were collected and sample sizes. Location numbers correspond to those of Figure 1

Code	Commonly used name	Current designation	Locations sampled	*n*	References
EL*b/c*	Queensland dentata	*Elseya dentata*	1, 4, 5, 6, 7, 9	25	Goode, 1967; Cann, 1978
EL*d*	Namoi/Gwydir Elseya	*Elseya latisternum*	21	10	Cann, 1978
EL*e/f*	Bellingen/Manning Elseya	*Elseya latisternum*	15, 18	10	Cann, 1978; King & Heatwole, 1994a,b
EM*c*	Fraser Island Shortneck	*Emydura krefftii*	8	4	Cann, 1978; Georges & Legler, 1996
EM*d*	Cooper Creek Turtle	*Emydura krefftii*	26	12	Goode, 1967
EM*a/b*	Northern Yellow-faced Turtle	*Emydura* "australis"*	1, 3, 30, 31, 33	19	Worrell, 1963

**Emydura australis* was synonymized with *Emydura macquarii* by Cogger *et al.* (1983).

microsympatry (i.e. syntopic), then the two distinguishable forms were regarded as separate biological populations. In such cases, the probability of their having been drawn from a panmictic population was calculated and used as the basis for a decision. Profiles of allozyme frequencies were determined for each population, and fixed differences between populations were tabulated. A fixed difference occurs when two populations fail to share any allozymes at a given locus (Richardson *et al.*, 1986). Two populations were considered notionally to belong to different diagnosable taxa if all individuals in one population could be distinguished from all of the individuals in the other by one or more fixed differences.

If two populations, two diagnosable taxa or a population and a diagnosable taxon displayed no fixed differences at all presumptive loci, then they were considered to belong to the same diagnosable taxon and their profiles were combined. Note that by this procedure it is possible for two populations to differ by one or more fixed differences yet belong ultimately to the same diagnosable taxon. This occurs when, for example, the first population is fixed for allozyme *a*, the second population is fixed for allozyme *b* and a third population possesses both allozymes.

Following repeated application of this procedure to all populations and diagnosable taxa present at each step, the analysis yields either a single diagnosable taxon or two or more diagnosable taxa, each distinct from all others on the basis of one or more fixed differences.

There is an asymmetry in proof here, which applies to both molecular and morphological analyses. If two populations share allozymes at all of their loci for the sample of individuals examined, then without doubt, the populations from which the individuals were taken share those allozymes. In contrast, an observed fixed difference between two populations may reflect either a true fixed difference or a statistical sampling error, owing to the finite number of individuals examined. Statistical analysis is required to properly interpret fixed differences observed in electrophoretic studies of species boundaries. Unfortunately, no appropriate statistical test appears to be available for any but the restrictive case of microsympatry, where a panmictic population can be assumed as the basis of a null hypothesis. As a rule of thumb in the application of the above procedure to cases of allopatry, we required at least two fixed differences when sample sizes were large (n_1 and $n_2 \geq 10$), and at least three fixed differences when sample sizes were small (n_1 or $n_2 < 10$) to regard populations as separate diagnosable taxa. This rule of thumb was applied only as a final step in the procedure, by which time diagnosable taxa included sufficient populations to raise sample sizes.

Enzymes examined

ACON*, aconitate hydratase (Enzyme Commission No. 4.2.1.3); ACP, acid phosphatase (No. 3.1.3.2); ADA*, adenosine deaminase (No. 3.5.4.4); ADH, alcohol dehydrogenase (No. 1.1.1.1); AK*, adenylate kinase (No. 2.7.4.3); CA*, carbonate dehydratase (No. 4.2.1.1); CK, creatine kinase (No. 2.7.3.2); CS, citrate synthase (No. 4.1.3.7); DIA, diaphorase (No. 1.6.99.--); ENOL, enolase (No. 4.2.1.11); EST, esterases (No. 3.1.1.--); FDP*, fructose bisphosphatase (No. 3.1.3.11); FUM*, fumarate hydratase (No. 4.2.1.2); GAPD, glyceraldehyde-3-phosphate dehydrogenase (No. 1.2.1.12); GLO, lactoyl-glutathione lyase (No. 4.4.1.5); GOT*, aspartate aminotransferase (No. 2.6.1.1); GPD, glycerol-3-phosphate dehydrogenase (No. 1.1.1.8); GPI*, glucose-phosphate isomerase (No. 5.3.1.9); GPT, alanine aminotransferase (No. 2.6.1.2); GSR, glutathione reductase (No. 1.6.4.2); HBDH,

3-hydroxybutyrate dehydrogenase (No. 1.1.1.30); IDH*, isocitrate dehydrogenase (No. 1.1.1.42); LAP, leucine amino-peptidase (No. 3.4.11.1); LDH, lactate dehydrogenase (No. 1.1.1.27); MDH, malate dehydrogenase (No. 1.1.1.37); ME*, 'malic' enzyme (No. 1.1.1.40); MPI*, mannose-phosphate isomerase (No. 5.3.1.8); NP*, purine nucleoside phosphorylase (No. 2.4.2.1) PEP-A*, dipeptidase (No. 3.4.13.--); PEP-B, tripeptide aminopeptidase (No. 3.4.11.--); PEP-D, proline dipeptidase (No. 3.4.13.--); 6PGD*, 6-phosphogluconate dehydrogenase (No. 1.1.1.44); PGK, phosphoglycerate kinase (No. 2.7.2.3); PGM*, phosphoglucomutase (No. 5.4.2.2); PK*, pyruvate kinase (No. 2.7.1.40); SOD*, superoxide dimutase (No. 1.15.1.1); SORDH*, 1-iditol dehydrogenase (No. 1.1.1.14); TPI*, triose-phosphate isomerase (No. 5.3.1.1); UGPP, UTP-glucose-1-phosphate uridylyltransferase (No. 2.7.7.9); XO, xanthine oxidase (No. 1.1.3.22).

Details of the number of loci examined for each enzyme system are shown in Appendices 1 and 2. Conventions for naming loci and allozymes follow that of Adams *et al.* (1987). All loci were scored from liver except for *Adh-2, Ald, Ca-2, Ck, Est, Fdp-2* and *Gpd-2* which were scored from muscle. Those loci bearing and asterisk were scored also from blood of Queensland specimens of *Elseya* sp. aff. *dentata* collected during the supplementary survey.

Specimens examined

Elseya dentata (NTM R12231, R13317–20, R13436, R13510/21/23), *Elseya latisternum* (AM R120997–8, R123032–9, R125474–5; NTM R13516/17/24; QM J47988/90/95, J48001/6/11/17/21/22/24/54/55/63/66), *Elseya novaeguineae* (AM R124696–8, R124702–3), *Elseya* sp. (Burnett, aff. *dentata*) (AM R123067, R128007; QM J47987/98, J48002/10/12/26/27/29/39/46/52), *Elseya* sp. (Burdekin, aff. *dentata*) (QM J58174, J60262), *Elseya* sp. (Johnstone, aff. *dentata*) (AM R125468, QM J48059/62/64/65/68), *Elseya* sp. (Nicholson, aff. *dentata*) (QM J60255), *Elseya* sp. (Magela, aff. *dentata*) (AM R128001–4; NTM R13512), *Elseya* sp. (Gwydir, aff. *latisternum*) (AM R123027–31; QM J48023/28/30/38/57), *Elseya* sp. (Bellingen) (AM R120965, R123043–6), *Elseya* sp. (Manning) (AM R120966–7, R123040–2), *Elusor macrurus* (AM R125482–5, R128006), *Emydura krefftii* (AM R125473, R125486–9; QM J47993/6/7/9, J48003/4/7/9/13/16/19/25/42/51), *Emydura macquarii* (AM R120953–9, R123047–9; QM J48033–37, J48040/44/45/47/50; SAM R21229–31), *Emydura signata* (AM R120971/78/89/93/94, R123001–11, R123013–26; QM J48031/41/48/53/56), *Emydura subglobosa* (AM R124793–4), *Emydura victoriae* (AM R125490/95/97; NTM R13438, R13511, R13513–15, R13518–20, R13522), *Emydura* sp. (Cooper, aff. *krefftii*) (SAM R18427/29/32/37, R20598, R31125–31), *Emydura* sp. (Fraser, aff. *krefftii*) (QM J47989, J47991–2, J48008), *Emydura* sp. (Sleisbeck, aff. *subglobosa*) (AM R128005; NTM R13428–9, R13431–3; QM J48058/61/67), *Emydura* sp. (Daly Mission, aff. *victoriae*) (AM R125469–72, R125491–4 R125498–9), *Rheodytes leukops* (AM R125481).

Museum abbreviations

AM, Australian Museum, Sydney; ANC, Australian National Wildlife Collection, CSIRO Gungahlin, Canberra; QM, Queensland Museum, Brisbane; NTM; Museums and Art Galleries of the Northern Territory, Darwin; SAM, South Australian Museum, Adelaide.

RESULTS

Allozyme profiles for 23 populations of *Elseya*, 30 populations of *Emydura* and one population each of *Elusor macrurus* and *Rheodytes leukops* are shown in Appendices 1 and 2. A matrix of fixed differences between populations was constructed from these profiles and reduced to a matrix of differences between diagnosable taxa (Table 3) as outlined in Material and Methods. The diagnosable taxa of Table 3 are grouped for convenience into the phylogenetic groups identified by Georges & Adams (1992), namely: the *Elseya dentata* group, the *Elseya latisternum* group, the *Emydura, Rheodytes leukops* and *Elusor macrurus*.

Elseya dentata, including the populations of northern Australia and Queensland but excluding for the moment those sampled during the supplementary survey, comprises four diagnosable taxa. There is *Elseya dentata* proper, incorporating populations from the Victoria (type locality) and Daly Rivers of the Northern Territory, a diagnosable form from the Alligator Rivers region of the Northern Territory and two diagnosable forms from Queensland, one from the Johnstone Rivers near Cairns and one from the Fitzroy and Burnett drainages of mid-coastal Queensland. Single fixed differences in allopatry between the Victoria River ($n = 2$) and Daly River ($n = 7$) populations, and between the Burnett River ($n = 7$) and the Fitzroy River ($n = 6$) populations were each regarded as artifacts of limited sampling. The clearest boundary is that between the Queensland and Northern Territory forms which are distinguished by between 16 and 19 fixed differences. The diagnosable taxon in the South Alligator Rivers region occupies adjacent drainages to those inhabited by *Elseya dentata* proper, and is distinguished from it by four fixed differences. The north Queensland (Johnstone River) and mid-coastal Queensland

TABLE 3. Counts of fixed differences (lower matrix) and percentage fixed differences (upper matrix) among the 15 diagnosable taxa identified in the primary survey. Abbreviations: El*a*, *Elseya* (South Alligator); EL*b*, *Elseya* (Johnstone); EL*c*, *Elseya* (Burnett); ELD, *Elseya dentata*; EL*d*, *Elseya* (Gwydir); EL*e*, *Elseya* (Bellingen); El*f*, *Elseya* (Manning); ELL, *El. latisternum*; ELN, *El. novaeguineae*; EM*a*, *Emydura* (Daly Mission); EM*b*, *Emydura* (Sleisbeck); EMM, *Em. macquarii*; EMS, *Em. subglobosa*; EMV, *Em. victoriae*; RHL, *Rheodytes leukops*; SNA, *Elusor macrurus*. EMV and EM*a* were microsympatric (synoptic) at Daly Mission and sympatric with EM*b* in the Daly drainage. ELD & EL*a*, and ELL & EL*d* were in shallow allopatry, occupying adjacent drainages. The raw data are presented in Appendices 1 and 2

		EMV	EMa	EMb	EMM	ELD	ELa	ELb	ELc	ELN	ELL	ELd	ELe	ELf	SNA	RHL
Emydura	EMV	—	2	2	4	30	34	32	30	40	40	43	47	45	46	42
	EMa	**1**	—	2	6	30	36	32	30	40	40	40	43	43	46	40
	EMb	**1**	**1**	—	4*	30	32	28	25	36	36	38	42	42	40	40
	EMM	**2**	**3**	**2***	—	32	32	32	30	30	36	36	43	42	37	36
Elseya	ELD	16	16	16	17	—	7	31	30	33	41	44	48	46	22	21
dentata	ELa	18	19	17	17	**4**	—	35	33	35	43	44	48	46	23	22
group	ELb	17	17	15	17	**17**	**19**	—	11	33	43	48	54	50	24	18
	ELc	16	16	13	16	**16**	**18**	**6**	—	31	39	46	54	46	23	18
	ELN	19	19	17	14	**16**	**17**	**16**	**15**	—	40	50	54	50	24	20
Elseya	ELL	21	21	19	19	22	23	23	21	19	—	7	13	15	27	25
latisternum	ELd	23	21	20	19	24	24	26	25	24	**4**	—	13	15	30	27
group	ELe	25	23	22	23	26	26	29	29	26	**7**	**7**	—	20	30	30
	ELf	24	23	22	22	25	25	27	25	24	**8**	**8**	**11**	—	28	28
Elusor	SNA	24	24	21	19	42	43	45	43	50	51	57	57	53	—	42
Rheodytes	RHL	22	21	21	19	39	41	33	33	42	46	50	56	52	**22**	—

*a shared allozyme at the 0.03 level for *Me-2* was interpreted as convergence.

forms (Fitzroy/Burnett) were distinguishable by six fixed differences, but this result was thrown into question by the subsequent discovery of a population in the Burdekin River which separates the Johnstone and Fitzroy drainages. This intervening population may have shared alleles that distinguish the northern and mid-coastal populations, thus combining them all into a single diagnosable taxon. However, subsequent electrophoretic comparisons involving the additional forms of Queensland *dentata* collected in the supplementary survey, showed that this was not the case. These subsequent comparisons revealed an additional diagnosable taxon from the Nicholson drainage which flows into the Gulf of Carpentaria. It differs from other Queensland forms of *El. dentata* by between 5 and 7 fixed differences and from *Elseya dentata* proper by 13 fixed differences (Table 4). Phylogenetically, the Nicholson River form represents a third branch of an unresolved trichotomy including also the mid-coastal forms and north Queensland forms of *Elseya dentata* (see Georges & Adams, 1992). The Mary River population joins the mid-coastal form of the Burnett and Fitzroy drainages as a single diagnosable taxon.

Electrophoretic evidence in support of a distinctive white-headed *Elseya* from the Burdekin drainage is problematic. It differs from its closest relative in the Johnstone drainage by two fixed differences in allopatry (Table 4), but sample sizes were small (n = 3 and 6 respectively). Two fixed differences in allopatry are insufficient by our rule of thumb to demonstrate a true fixed difference between the populations from which the sampled individuals were drawn. Its white head is diagnostic and it will soon be described as a new species (John Cann, pers comm).

Elseya novaeguineae, also in the *Elseya dentata* group but endemic to New Guinea, is also a diagnosable taxon, distinct from all Australian forms by between 15 and 16 fixed differences (Table 3).

The *Elseya latisternum* group, including the form of *Elseya* of uncertain status from the Manning/Bellingen Rivers of coastal New South Wales, comprises four diagnosable taxa. Coastal populations from the Richmond River of northern NSW to the Jardine River of Cape York, the Gulf of Carpentaria and Arnhem Land formed a single diagnosable taxon, *Elseya latisternum*. Single fixed differences in allopatry between each of the Arnhem Land (n = 3) and Cape York (n = 1) populations compared to remaining populations were regarded as artifacts of limited sampling. A diagnosable taxon from the Gwydir tributary of the Murray-Darling drainage of north-central NSW is also found in the Namoi and Severn tributaries

TABLE 4. Counts of fixed differences (lower matrix) and percentage fixed differences (upper matrix) for *Elseya dentata* (*sensu stricto*), *El. novaeguineae* and the diagnosable taxa within the Queensland forms of *Elseya dentata* at 38 loci (37 for *El. novaeguineae*). Locations corresponding to those shown in Figure 1 are given in square parentheses. Sample sizes for each population are presented in round parentheses

		Mid-coastal Qld [6,7,9], (15)	Burdekin. R. [5], (3)	Johnstone R. [4], (6)	Nicholson R. [1], (1)	*Elseya dentata* [29,30], (14)	*Elseya novaeguineae* [34,35], (5)
Mid-coastal Qld	El*c*	—	18.4	13.2	15.8	31.6	35.1
Burdekin R.	El*h*	7	—	5.3	18.4	42.1	40.5
Johnstone R.	El*b*	5	2	—	13.2	34.2	35.1
Nicholson R.	El*g*	6	7	5	—	34.2	29.7
Elseya dentata	ELD	12	16	13	13	—	37.8
Elseya novaeguineae	ELN	13	15	13	11	14	—

and so occupies adjacent drainages to those inhabited by *Elseya latisternum.* It is distinguished from *Elseya latisternum* by four fixed differences in shallow allopatry (Table 3). Surprisingly, the *Elseya* from the two coastal drainages of NSW, the Manning and Bellingen, are a sibling species pair. Formerly cryptic in the sense that morphological differences were so slight as to have them regarded as a single taxon, they differ at 20% of their loci (11 fixed differences, Table 3).

Populations within the *Emydura* were problematic. Only four diagnosable taxa could be distinguished among the *Emydura,* and support for them was much more tenuous than for the *Elseya.* We could find no evidence to support the current recognition of *Emydura krefftii* (including the Fraser Island and Cooper Creek forms), *Em. signata* (including the coastal NSW forms) and *Em. macquarii* as separate diagnosable taxa. They even shared rare alleles (Appendix 2). In northern Australia, the red-faced turtle, *Emydura victoriae,* could be distinguished from a second taxon, a yellow-faced turtle, in microsympatry (Daly Mission, Daly River, Northern Territory). They differed by one fixed allelic difference and three concordant fixed morphological differences (colour of the eye-stripe, presence/absence of leading and trailing black spots on the iris, presence/absence of a fused triturating surfaces to form a plate on the roof of the mouth). A third form of *Emydura,* in sympatry with the above two, but not in microsympatry, could be distinguished from them by a single fixed difference in each case. This third form together with *Emydura subglobosa* from New Guinea, joined to form a single diagnosable taxon.

Elusor macrurus and *Rheodytes leukops* are clearly diagnosable taxa distinguished from each other by 22 fixed differences and all other taxa by at least 19 fixed differences (Table 3).

DISCUSSION

The *Elseya latisternum* group comprises four diagnosable taxa, one assignable to *Elseya latisternum* (*sensu stricto*) which occupies coastal rivers probably in a continuous series from northern NSW to Cape York, the Gulf of Carpentaria and Arnhem Land, a sibling species pair in the Bellingen and Manning Rivers of coastal NSW, and a distinct taxon from the Gwydir drainage of north central NSW. Genetic uniformity, in terms of fixed allozyme differences, across the extensive distribution of *Elseya latisternum* contrasts strongly with the structure among populations of what is currently regarded as *Elseya dentata* distributed over a similarly extensive range. The present study has identified six diagnosable taxa in the *Elseya dentata* group which currently contains only *Elseya dentata* and *Elseya novaeguineae* (Table 4). In contrast to the diversity revealed within the genus *Elseya,* the *Emydura* are all very closely related, and presumably result from a recent radiation. Our inability to find diagnostic differences between populations of *Emydura krefftii, Em. signata* and *Em. macquarii,* including the forms from Fraser Island, Cooper Creek and coastal NSW, strongly suggests that they should be regarded as a single species. The three currently recognized species lack clear morphological differences to distinguish them, with allocation of specimens to species based on presence of a yellow eye-stripe and a relatively deep shell in *Em. krefftii,* absence of a yellow eye-stripe and a relatively shallower shell in *Em. signata* and *Em. macquarii,* and on geographic range. Nowhere are they found in sympatry, despite abutting distributions, an indication that when populations do exchange individuals, differences are not maintained because of interbreeding. The eye-stripe is a highly variable character, absent in some but not

all populations of the Fraser Island form (Georges & Legler, 1996), present in many young individuals of all three species, and present in a substantial proportion (*c.* 15%) of adult individuals of *Em. macquarii* from the Severn River of the Queensland-NSW border. Shell shape is equally variable, and variation in both traits may be explained adequately as a geographic cline. *Emydura signata* was described from two juvenile specimens (*c.* 75 mm in length) and said to differ from *Emydura macquarii* by the serrated posterior of the marginals (Ahl, 1932), but the level of serration on the holotype is slight (Ahl, 1932:127) and at this level of expression, is a highly variable character both developmentally and geographically within *Emydura*. In the absence of concrete evidence to the contrary, the three currently recognized species should be synonymized, together with the Cooper Creek form and the Fraser Island form.

Populations of *Emydura* (EM*b*) from the upper reaches of the Daly, Roper and Nicholson Rivers of northern Australia were not diagnostically different from populations of *Emydura subglobosa* from New Guinea. These three Australian populations lack the red flushing of the ventral surfaces of the shell, limbs and gular region of the New Guinea form and the population in the Jardine River of Cape York (no tissues available). Nevertheless, we regard these forms to comprise a single species, once a contiguous series of river populations bordering Lake Carpentaria, now the Gulf of Carpentaria, with Australian forms separated from those of New Guinea only when the sea levels rose again approximately 12 000 years ago (Torgersen *et al.*, 1988).

While absence of diagnostic differences between populations, either molecular or morphological, is an indication of conspecificity, there remains the vexed question of whether the diagnosable taxa identified in this study are species. Populations belong to different biological species (*sensu* Mayr, 1969) if they are reproductively incompatible when given the opportunity to breed under natural conditions. In cases of microsympatry, evidence of separate species status is direct; fixed allozyme differences in what otherwise should be a panmictic population is evidence of reproductive incompatibility. This criterion establishes the separate species status of the red-faced turtle, *Emydura victoriae*, and the closely related yellow-faced turtle (EM*a*), as yet undescribed, found together at Policeman's Crossing on the Daly River, Northern Territory.

When turtle populations occupy adjacent drainages, there is presumably opportunity over time for exchange of individuals between populations, so fixed differences are also regarded as evidence of separate species status. Hence, the four fixed differences between *Elseya latisternum* and the undescribed form of *Elseya* from the Gwydir River of NSW establishes the Gwydir River form as a new species. Four fixed differences in shallow allopatry stands in stark contrast to the absence of fixed differences among populations of *Elseya latisternum* ranging from the Richmond River in NSW to Cape York and Arhnem Land (Fig. 1). A similar argument can be mounted for the distinctive population of *Elseya dentata* in the Alligator Rivers region.

In cases of allopatry, the biological species concept is particularly problematic, as has long been recognized. With the above exceptions, cases of uncertain species status among the Australian chelids can be resolved only through comparisons among allopatric populations. Here, there appear to be two alternatives: we can base a decision on inferential evidence, along the lines recommended by Mayr (1969:197) or we can dispense with the biological species concept and the criterion of

reproductive incompatibility and adopt one of the recently formulated phylogenetic species concepts.

Consider the approach of Mayr (1969) first. If within a given genus, or closely related genera, there is a well defined level of divergence between valid biological species, then this level of divergence, be it morphological or molecular, can be used as a yardstick to determine the status of isolated populations in the same genus. The amount of divergence between populations within valid biological species of the same genus or closely related genera, can also be added to the yardstick as an indication of the level of divergence that may occur without reproductive isolation. This approach depends on an association between level of divergence and attainment of reproductive isolation. Morphological divergence and the attainment of reproductive incompatibility can be uncoupled events in time and space (Mishler & Donoghue, 1982), as for example in many salamanders (Larson, 1984, 1989). However, there is evidence that an association exists between level of genetic divergence, as revealed by electrophoresis, and attainment of reproductive isolation. In non-avian species of vertebrate, Nei's distances between 97% of species reviewed by Thorpe (1982) were greater than 0.16, whereas Nei's D was less than this value in 98% of comparisons between populations of the same species. It appears that, with the notable exception of some avian species, reproductive isolation in vertebrates evolves slowly over long periods of geographical isolation, concomitant with the accumulation of measurable genetic differences. Thus the yardstick approach of Mayr has some foundation for molecular studies, more so than for morphological studies.

In practice, this approach requires identification of those species beyond dispute as valid biological species. Those of uncertain status become the basis of hypotheses to be tested in comparison with the yardstick constructed from data on the valid biological species. Unfortunately, while the species used to construct the yardstick are generally regarded as valid biological species, evidence of reproductive incompatibility among Australian chelids is lacking except in cases of sympatry. Hence, we are reduced to comparing levels of genetic divergence for disputed forms against a yardstick constructed from populations of what are regarded as valid species on the basis of similar subjective judgments previously made using morphology. This is a circularity. Nevertheless, for the purposes of this exercise, we have considered *Elseya latisternum* (excluding the Gwydir, Bellinger and Manning populations), *Emydura victoriae, Chelodina longicollis, C. expansa, C. Rugosa, C. steindachneri, Elusor macrurus* and *Rheodytes leukops* as valid biological species, drawing upon the additional allozyme data of Georges & Adams (1992) for the *Chelodina.*

The yardstick, showing distances between populations of the same species, populations of different species in the same genus and populations of different species in different genera is shown in Figure 2. Note that the pairwise comparisons used to construct this figure necessarily involve considerable redundancy (results of comparisons between populations A and B, and B and C constrain the possible outcomes for A and C, for example). This does not alter the shape or extent of any of the groupings shown, and since no statistical analyses are involved, this redundancy was disregarded. Included on the figure are the distances between each form of uncertain status and its taxon of closest affinity. It is clear that the interspecific differences between populations of *Emydura macquarii, Em. krefftii* and *Em. signata* respectively, are of a magnitude comparable to interpopulation differences only. In contrast, the differences between the Gwydir form of *Elseya latisternum* and the coastal form, between the cryptic Manning and Bellingen forms of *Elseya,*

between the Queensland and Northern Territory forms of *Elseya dentata*, and between *Elseya dentata* proper and the South Alligator form are of a magnitude consistent with differences between currently recognized species that are not in dispute.

Under the alternative phylogenetic species concepts, formulated by Nixon & Wheeler (1990) with contributions by Eldridge & Cracraft (1990), Nelson & Platnick (1981), Cracraft (1983, 1989) and others, species level classification is required to reflect phylogenetic history, in much the same way as higher level classifications reflect phylogeny. Paraphyletic species, that is, species comprising populations whose common ancestor has descendent populations belonging to another species, are unacceptable under a phylogenetic species concept. Paraphyly at the species level is demonstrated by application of the cladistic method to populations of the species and other closely related species, yet the cladistic method can only be expected to extract the pattern of ancestry and descent among these populations if there is no gene flow between them. As diagnostic differences between populations are required to be reasonably certain of absence of gene flow, a phylogenetic species concept considers diagnosable taxa, such as those identified in this paper, as the fundamental units of analysis. Indeed, one such concept regards species as "the smallest aggregation of populations (sexual) or lineages (asexual) diagnosable by a unique combination of character states in comparable individuals (semaphoronts)" (Nixon & Wheeler,

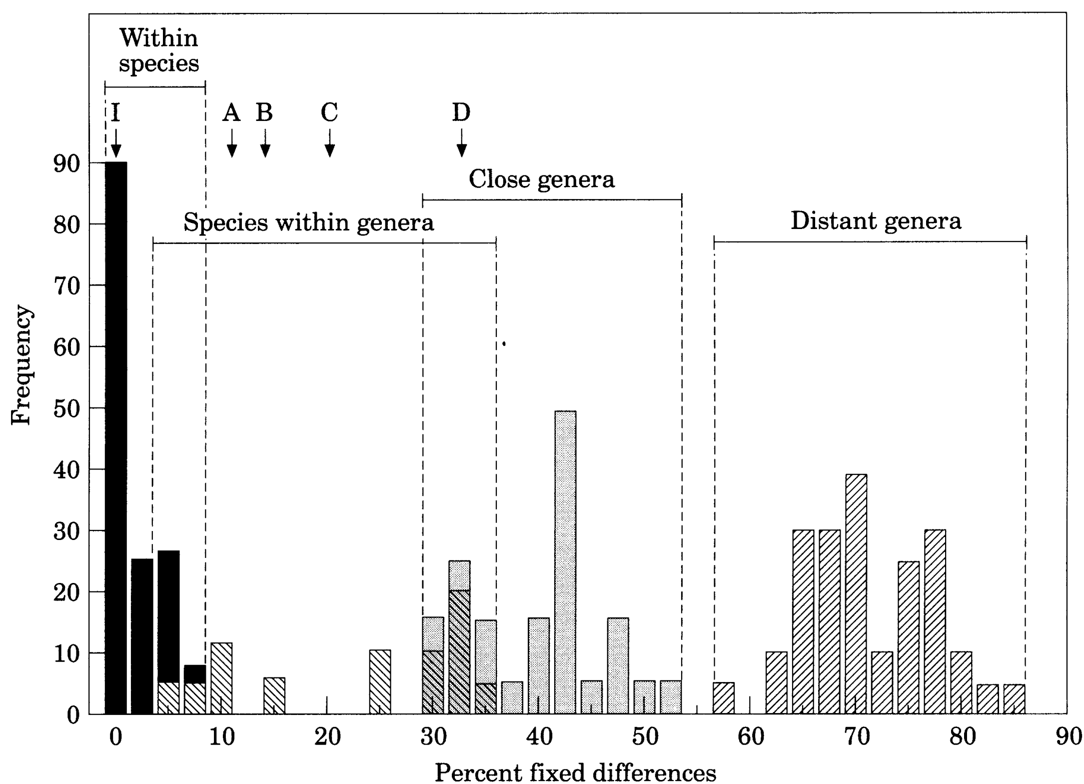

Figure 2. Comparison of the genetic distances between allopatric diagnosable taxa of uncertain species status with distances between populations of the same species (■), distances between populations of different species in the same genus (▧), distances between populations of different species in closely related genera (▒), and distances between populations of species in distantly related genera (▨). Arrows are labelled as follows: **A**, EL*b* (Johnstone) vs EL*c* (Burnett) (11%); **B**, EL*e*/*f* (Bellingen/Manning) vs ELL (*El. latisternum*) (13–15%) and El*b* (Johnstone) vs El*g* (Nicholson) (13.2%); **C**, EL*e* (Bellingen) vs EL*f* (Manning) (20%), **D**, ELD (*El. dentata*) vs EL*b*/*c* (Queensland *dentata*) (30–35%). The distances among populations of *Em. macquarii*, *Em. krefftii* and *Em. signata* (labelled **I**, 0 to 2%) are well within the range expected for populations of a single species.

1990:218). Under this concept, the diagnosable taxa identified in the present study are species by definition, and instances of paraphyly do not arise.

Operationally, this approach is far more satisfactory than the biological species concept, shackled as it is by the requirement to demonstrate or infer reproductive incompatibility, often in allopatry. However, the biological species concept has three key advantages. First, it provides a criterion for distinguishing between true species (i.e. reproductively isolated) and 'phena', that is, diagnosable variants resulting, say, from developmental, sexual or environmental influences. For example, macrocephalic *Emydura* have been erroneously regarded for at least a century as distinct species separate from other members of the same gene pool (Legler, 1981). Second, biological species are not ephemeral entities. Their evolution typically remains, from the time of speciation, independent of genetic changes in other related species, regardless of events that open up avenues for exchange of individuals among sister species. Demographic processes alone lead to their extinction. Third, it is a useful concept, in the same way as the higher level categories are useful, by focussing attention on both differences (among populations of related species) and similarities (among populations of the same species).

Modern molecular techniques have, to a large degree, reduced the possibilities for mistakenly recognizing diagnosable variants within a species as separate species, because many of the characters used are expressed in all individuals regardless of environment, age or sex. However, if we adopt the phylogenetic species concept, operationalized in the way described in the present paper, we accept that the species identified are not necessarily reproductively isolated either in theory or in practice. Some, therefore, may be transitory entities, that can be subsequently extinguished by both the demographic processes of extinction and by events that renew avenues for the exchange of individuals among sister taxa. This is a real conceptual cost. In its defence, it can be argued that the phylogenetic species concept respects phylogenetic history, which is measurable as accrued diagnostic differences, but ignores what might happen in the future, which cannot be measured (Frost & Hillis, 1990).

A second difficulty with the phylogenetic species concept arises through refinement of molecular approaches to systematics. Under this concept, any lineage in which a mutation occurs and becomes fixed is theoretically diagnosable with a technique of sufficient sensitivity and therefore will be regarded as a separate species. While this is not a problem for allozyme electrophoresis, it opens the possibility that we will ultimately be regarding entities as transitory as demes as species (Frost & Hillis, 1990), and that, while admirably reflecting the full scope of variations in nature, the vast majority may be diagnosable on molecular examination only.

With the controversy on the species concept as yet unresolved, it is important to clearly identify the basis upon which populations are assigned to species. If we adopt the phylogenetic species concept, then this study supports the recognition of 16 species of short-necked chelid turtle in Australia (Table 5), including *Pseudemydura umbrina*. Our data also provide evidence of reproductive isolation in cases of sympatry or parapatry, and comparative evidence (*sensu* Mayr) is presented for the remainder, to establish that the traditional biological species concept also applies to these diagnosable taxa.

ACKNOWLEDGEMENTS

We thank John Cann for sharing his extensive knowledge of Australian freshwater

TABLE 5. A list of currently recognized species of short-necked chelid turtle of Australia, together with a recommended list of species following the electrophoretic analysis. *Pseudemydura umbrina* was not available for study. Status of the Burdekin form of *Elseya dentata* remains unclear

Current	Abbrev.	Proposed	Locations sampled
Elseya dentata	ELD	*Elseya dentata*	29, 30
	EL*a*	*Elseya* sp. aff. *dentata* (Sth Alligator)	31
	EL*b*	*Elseya* sp. aff. *dentata* (Johnstone)	4
	EL*c*	*Elseya* sp. aff. *dentata* (Burnett)	6, 7, 9
	EL*g*	*Elseya* sp. aff. *dentata* (Nicholson)	1
Elseya latisternum	ELL	*Elseya latisternum*	1, 2, 7, 9, 10, 12, 13, 31, 32
	EL*d*	*Elseya* sp. aff. *latisternum* (Gwydir)	21
	EL*e*	*Elseya* sp. aff. *latisternum* (Bellingen)	18
	EL*f*	*Elseya* sp. aff. *latisternum* (Manning)	15
Emydura macquarii			
Emydura krefftii	EMM	*Emydura macquarii*	5, 6, 7, 8, 9, 11, 12, 13, 14, 16,
Emydura signata			17, 20, 22, 23, 25, 26
Emydura victoriae	EMV	*Emydura victoriae*	29, 30
Emydura "australis"	EM*a*	*Emydura* sp. aff. *victoriae* (Daily Mission)	3, 30, 31
Emydura subglobosa	EMS	*Emydura subglobosa*	1, 30, 33, 36
Elusor macrurus	SNA	*Elusor macrurus*	9
Rheodytes leukops	RHE	*Rheodytes leukops*	6
Pseudemydura umbrina	—	*Pseudemydura umbrina*	—

turtles and their distribution and Peter Baverstock for his generous and enthusiastic support of this project. We are grateful also to the many people who provided specimens or assisted in the field, and in particular G. Georges, M. Palmer-Allen, J. Cann, H. Cooper-Preston, K. Day, J. Covacevich, R. Fairfax, A. Allison, R. Kennett, A. White, T. Press, J. Parmenter, T. Reardon, A. Pryor, J. Wombey, B. Clay and Gordon Elmer. C. Banks supplied specimens of *Elusor macrurus* from the collection of the Royal Melbourne Zoological Gardens and T. Schwaner gave us access to tissues held at the South Australian Museum. P. Baverstock and S. Donnellan provided critical comments on the manuscript. J. Birrell and M. Palmer-Allen provided outstanding technical assistance. This study was supported by the Canberra C.A.E. Research Fund, the Conservation Commission of the Northern Territory, and by an Australian Research Council Grant to the Evolutionary Biology Unit of the South Australian Museum. The University of Queensland and the Northern Territory Museum provided laboratory space and equipment.

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APPENDIX 1. Allozyme profiles for 23 populations of *Elseya*, and one population each of *Rheodytes leukops* and *Elusor macrurus*, at 54 enzyme loci. Drainages corresponding to those shown in Figure 1 are given in square parentheses, with different localities within a drainage identified by a lower case letter. Loci marked with an asterisk were screened in muscle. Sample sizes for each population are presented in round parentheses (liver:muscle). The conventions for designating allozymes and multiple loci follow Adams *et al.* (1987); in particular, alleles are designated alphabetically according to increasing mobility. The body of the table contains percentages. Species abbreviations: EL*a*, *Elseya* (Sth Alligator); El*b*, *Elseya* (Burnett); El*c*, *Elseya* (Johnstone); ELD, *Elseya dentata*; EL*d*, *Elseya* (Gwydir); EL*e/f*, *Elseya* (Bellingen/Manning); ELL, *Elseya latisternum*; SNA, *Elusor macrurus*; ELN, *Elseya novaeguineae*; RHL, *Rheodytes leukops*. Locations areas shown in Figure 1. Details of undescribed forms are given in Table 2.

	Nominal taxon																								
	ELL										ELd	ELe/f		ELD									ELN	SNA	RHL
Locus	[32] (3:3)	[31a] (2:2)	[2] (1:1)	[1] (1:1)	[7] (5:0)	[9] (2:0)	[10a] (2:0)	[10b] (3:0)	[12] (5:5)	[13] (5:5)	[21] (10:5)	[15] (5:5)	[18] (5:5)	[29] (2:2)	[30a] (2:2)	[30c] (5:5)	[31b] (4:4)	[31a] (1:1)	[4a] (1:1)	[4b] (5:5)	[6] (6:1)	[7] (7:1)	[34,35] (5:0)	[9] (5:5)	[6] (1:1)
Acon-1	b	b	b	b	b	b	b=75 a=25	b=67 a=33	b=50 a=50	b=40 a=60	b	b	b	c	c	c	f	f=50 d=50	c	c	c	c	c=90 a=10	b	c
Acon-2	d=67 b=33	d=50 b=50	b	b	b	b	b	b	b	b	b	e	b	f	f=75 d=25	f=60 d=40	f	f	d	d	d	d	b=70 a=30	f	f
Acp	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	b	a
Ada	d	d=25 b=75	d	d	d	d	d	d	d	d	d	d	d	f	f	f	f	f	e	e	e	e	h	g	i
Adh	b	b	b	b	b	b	b	b	b	b	b	b	c	b	b	b	b	b	e	e	f	f	—	—	d
Ak-1	b	b	b	b	b	b	b	b	b	b	b	b	b	a	a	a	a	a	a	a	a	a	a	a	a
Ak-2	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	c=33 a=67	c=64 a=36	a	a	d
**Ald*	b	b	b	b	—	—	—	—	b	b	b	b	b	b	b	b	b=37 a=63	a	b	b	b	b	—	b	b
Ca-1	e	e	e	e	e	e	e	e	e	e	a	a	a	d	f=25 d=75	f=30 d=70	f	f	c	c	c	c	b	b	b
Ca-2	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	b	c	c
Ca-3	b	b	b	b	b	b	b	b	b	b	b	b	b	e	f	f	e	e	a	a	e	e	e=70 d=30	e	c
**Ck*	a	a	a	a	—	—	—	—	a	a	a	a	b	b	b	b	b	b	b	b	b	b	—	b	b
Dia	a	a	a	a	a	a	a	a	a	a	b	a	b	a	a	a	a	a	a	a	a	a	a	a	a
**Enol-2*	a	a	a	a	—	—	—	—	a	a	a	a	a	a	a	a	b	b	a	a	a	a	—	a	a
Fdp-1	b	b	b	b	b=90 a=10	b	b	b	b	b	b	b	b	a	a	a	a	a	a	a	a	a	a	a	a
Fum	a	b	b	b	b=90 a=10	b	b	b	b	b	b	b	c=10 b=90	b	b	b	b	b	b	b	c=17 b=83	c	d	b	b
Glo	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	b	b
Glo-2	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	b	b	b	c=7 b=93	a	a	a
Got-1	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	b=25 a=75	a	a	a	a	a	a	b	b
Got-2	e	e	e	e	e	e	e	e	e	e	e	e	e	d	d	d	e	e	e	e	e	e	e	c	e
Gpd-1	b	b	b	b	b	b	b	b	b	b	b	b	b	a	a	a	a	a	a	—	a	a	a	b	a
**Gpd-2*	c	c	c	c=50 a=50	—	—	—	—	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c=70 a=30	b	c

Appendix 1. *Continued*

Locus	ELL [32] (3:3)	ELL [31a] (2:2)	ELL [2] (1:1)	ELL [1] (1:1)	ELL [7] (5:0)	ELL [9] (2:0)	ELL [10a] (2:0)	ELL [10b] (3:0)	ELL [12] (5:5)	ELL [13] (5:5)	ELd [21] (10:5)	ELe/f [15] (5:5)	ELe/f [18] (5:5)	ELD [29] (2:2)	ELD [30a] (2:2)	ELD [30c] (5:5)	ELD [31b] (4:4)	ELD [31a] (1:1)	ELD [4a] (1:1)	ELD [4b] (5:5)	ELD [6] (6:1)	ELD [7] (7:1)	ELN [34,35] (5:0)	SNA [9] (5:5)	RHL [6] (1:1)
Gpi	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	a	a	a	a	a	f=80 a=20	e
Gpt	d	d	d	d	d	d	d	d	d	d	c	e	d	i=50 g=50	i	i=12 g=88	i	i	b	b	f=25 d=75	b	j=75 g=12 d=13	g	a
Gsr	c	c	c	c	c	c	c	c	c	c	c	b	c	c	c	c	c	c	c	c	c	c	c	d	c
Hbdh	c	c	c	c	c	c	c	c	c	c	b	c	c	b	b	b	b	b	b	b	b	b	c	d	b
Idh-1	e	e	e	e	e	e	e	e	e	e	e=95 b=5	b	e	e	e	e	e	e	f	f	e	e	c	e	d
Idh-2	a	a	a	a	a	a	a	a	a	a	a	c	a	a	a	a	a	a	a	a	a	a	a	a	a
Lap	a	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	c	b
Mdh-1	c	c	c	c	c	c=75 b=25	c	c	c	c	c=95 a=5	c	c	c	c	c	c	c	c	c	c	c	c	c	c
Mdh-2	a	a	a	a	a	a	a	a	a	a	a	a	a	b	b	b	b	b	b	b	b	b	b	b	b
Me-2	g	g	g	g	g	g	g	g	g	g	g	g	g	h	h	h	h	h	e	e	f	f	g=30 d=70	c	f
Mpi	c	c	c	c	c	c	c	c	c	c	c	c	c	b	b	b	b	b	b	b	a	a	b	b	b
Np	a	a	a	b	b=40 a=60	b	b=50 a=50	b=33 a=67	c=50 b=40 a=10	c=40 b=60	a	a	a	p=25 m=50 e=25	h=50 d=50	m=30 h=30 d=40	h=62 e=38	e	o	o=30 h=70	g	g	s=20 r=60 q=20	f	q
Pep-A	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	b	a	a
Pep-B	c=33 a=67	a	c	a	c=30 a=70	c=75 a=25	a	a	a	a	a	a	a	e	e	e	i=25 g=75	g	d	d	d	d=79 b=21	f	f	e
Pep-D	d=33 c=67	d=25 c=75	c	c	c=80 a=20	d=25 c=50 a=25	d=50 c=50	d=33 c=67	d=10 c=80 a=10	d=10 c=70 a=20	d=20 c=80	c	d=30 c=70	e	e	e	e	e	f	f	f	f	f	b	f
6Pgd	a	a	a	a	a	a	a	a	a	a	a	a	e	c	c	c	c	c	c	c	c=75 b=25	c	c	h=20 g=80	d
Pgm	b=17 a=83	b	a	a	a	a	a	a	a	a	a	a	a	c	c	c	c	c	b	b	b	b	b=90 a=10	b	b
Pk	a	a	a	a	a	a	a	a	a	a	a	a	c	a	a	a	a	a	b	b	b	b	a	b	b
Sod	c	c	e	a	c	c	c	e=17 c=83	c	c	c	b	b	b	b	b	b	b	c	c	c	c	c	b	c
Sordh	a	a	a	a	a	a	a	a	a	a	a	a	c=80 a=20	b	d	d=90 b=10	d	d	d	d	d	d	d	d	a
Tpi	a	a	a	a	a	a	a	a	a	a	a	a	a	b	b	b	b	b	a	a	a	a	b	a	a
Xo	d	d	d	d	d	d	d	d	d	d	d	d	c	a	a	a	a	a	b	b=90 a=10	a	a	a	e	f

Allozymes fixed in all populations: Cs^a, $Gapd^a$, $Ldh\text{-}1^a$, $Ldh\text{-}2^b$, and $Ugpp^a$. Allozymes fixed in most populations: $Enol\text{-}1^a$ (El*d*[21] a=95, b=5), *Est^c (El*d*[21] c=10, d=90), *$Fdp\text{-}2^c$ (El*d*[21] c=50, d=50; ELD [30] b=10, c=90), $Me\text{-}1^c$ (ELD[4] –) and $Pgka^a$ (RHL a=50, b=50).

APPENDIX 2. Percentage allozyme frequencies for 30 populations of *Emydura* at 54 enzyme loci. Drainages corresponding to those shown in Figure 1 are given in square parentheses, with different localities within a drainage identified by a lower case letter. Loci marked with an asterisk were screened in muscle. Sample sizes for each population are presented in round parentheses (liver:muscle). The conventions for designating allozymes and multiple loci follow Adams *et al.* (1987); in particular, alleles are designated alphabetically according to increasing mobility. Species abbreviations: EM*a/b*, *Emydura* (Northern Yellowface); EM*c*, *Emydura* (Fraser Island); EM*d*, *Emydura* (Cooper Creek); EMI, *Emydura signata*; EMK, *Emydura krefftii*; EMM, *Emydura macquarii*; EMS, *Emydura subglobosa*; EMV, *Emydura victoriae*. Details of undescribed forms are given in Table 2.

	Nominal Taxon																													
	EMV					EMa/b				EMS		EMK				EMd		EMM					EMc	EMI						
Locus	[29] (5:5)	[30a] (6:6)	[30b] (3:3)	[30b] (4:4)	[30c] (1:1)	[31] (2:2)	[33] (5:5)	[1] (3:3)	[3] (4:4)	[36a] (1:1)	[36b] (2:2)	[5] (5:5)	[6] (5:0)	[7] (4:0)	[9] (5:0)	[26a] (7:0)	[26b] (5:5)	[20a] (9:4)	[20b] (1:1)	[22] (5:0)	[23a] (5:5)	[23b] (3:0)	[8] (4:0)	[11] (5:0)	[12] (5:5)	[13] (4:4)	[14] (5:5)	[16] (5:5)	[17a] (5:5)	[17b] (6:6)
Acon-1	c	c	c	c	g	c	g=70 e=10 c=20	g=83 c=17	c	c	c	c	c	c	e=10 c=90	c	c	e=22 c=78	e=50 c=50	c	e=10 c=90	c	c	c	c	c	c	c	c	c
Acon-2	d	d	d	d	d	d	d	d	d	d	d	f=80 d=20	f=50 d=50	f=12 d=50 a=38	f=40 d=60	f=79 d=21	f=50 d=50	f=22 d=78	f=50 d=50	f=80 d=20-	g=10 f=40 d=50	f=50 d=50	g=25 f=25 c=37	d=80 a=20	d=70 c=10 a=20	d=87 b=13	d=90 c=10	d=90 b=10	d	d
Ada	c	c=16 b=67 a=17	C=33 b=67	c=87 a=13	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c
Adh	b	c=17 b=83	b	b	c	b	c=40 b=60	c=17 b=83	b	b	c=50 b=50	b	b	b	b	b	b=50 a=50	b	b	b	b	b	b	b	b	b	b	b	b	b
Ak-2	d	e=17 d=75 b=8	d	d	d	d	d	d	d	d=50 a=50	d	d	d=90 b=10	e=12 d=88	d	d	d	d	d	d	d	d	d	d	d	d	d	d	d	d
**Ald*	a	a	a	b	a	b	b=30 a=70	b=17 a=83	b	b	b	a	—	—	—	—	a	a	a	—	a	—	—	—	a	a	a	a	a	a
Ca-3	f	f	f	f	e	f	e	e	f	e	e	b	e	e=62 b=38	e=80 b=20	b	b	e	e	e	e	e	e	e	e	e	e	e	e	e
**Est*	c	c	c	c=62 a=38	c	c	c	c	c	c	c	c=80 b=20	—	—	—	—	c	c	c	—	c=90 b=10	—	—	—	c	c	c	c	c	c
**Fdp-2*	c	c	c	c	c	c=75 a=25	c	c	e=37 c=63	c	c	d=80 c=20	—	—	—	—	c	c=87 b=13	c	—	c	—	—	—	e=20 c=80	c	c	c	c	c
Fum	b=80 a=20	b	b	b	b	b	b	b	b	b	b	c=10 b=90	b	c=50 b=50	c=50 b=50	b	b	b	b	b	b	b	c	c=80 b=20	c=80 b=20	c=37 b=63	c=70 b=30	c=40 b=60	c=70 b=30	c=92 b=8
Glo	a	a	a	a	a	a	a	a	a	a	a	a	a	b=37 a=63	b=30 a=70	a	a	a	a	a	a	a	b	a	a	a	a	a	a	a
Got-1	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	c=14 a=86	a	a	a	a	a	a	a	a	b=10 a=90	b=25 a=75	a	a	a	a
Got-2	e	e=59 h=8 a=33	e=67 a=33	e=25 a=75	e	b=50 a=50	e=90 b=10	e	e=25 b=12 a=63	e	e	f	f	f	f	f=71 e=29	f=70 e=30	g	g	g	h=10 g=90	g=83 f=17	f	g=10 f=90	g=10 f=90	g=12 f=88	g=10 f=80 e=10	f	f	f=67 e=33
Gpi	a	a	a	a	a	d=25 a=75	a	c=33 a=67	a	a	c=50 a=50	a	c=10 a=90	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
Gpt	i=62 h=38	h=42 f=58	h=50 f=50	h=75 f=25	h	h	h	h	h	h=50 f=50	h=75 f=25	h	h	h	h	h	h	h=83 g=17	h	h=90 g=10	h=80 g=20	h	h	h=50 g=50	h=70 g=30	h=87 g=13	h	h	h	h

APPENDIX 2. *Continued*

Locus	Nominal Taxon: EMV [29] (5:5)	EMV [30a] (6:6)	EMV [30b] (3:3)	EMa/b [30b] (4:4)	EMa/b [30c] (1:1)	EMa/b [31] (2:2)	EMa/b [33] (5:5)	EMa/b [1] (3:3)	EMa/b [3] (4:4)	EMS [36a] (1:1)	EMS [36b] (2:2)	EMK [5] (5:5)	EMK [6] (5:0)	EMK [7] (4:0)	EMK [9] (5:0)	EMd [26a] (7:0)	EMd [26b] (5:5)	EMM [20a] (9:4)	EMM [20b] (1:1)	EMM [22] (5:0)	EMM [23a] (5:5)	EMM [23b] (3:0)	EMc [8] (4:0)	EMI [11] (5:0)	EMI [12] (5:5)	EMI [13] (4:4)	EMI [14] (5:5)	EMI [16] (5:5)	EMI [17a] (5:5)	EMI [17b] (6:6)
Gsr	c	c	c	c	c	c	c	c	c	c	c	c=90 a=10	e=10 c=90	c	c	e=67 c=33	e=40 c=60	e=57 c=43	c	e=30 c=70	e=10 c=90	e=67 c=33	c	c	c	c	c	c	c	c
Gpi	a	a	a	a	a	d=25 a=75	a	c=33 a=67	a	a	c=50 a=50	a	c=10 a=90	a	a	a	a	d=78 b=22	d	d=40 b=60	d=90 b=10	d=50 b=50	b	b	b	b	b	b	b	b
Gpt	i=62 h=38	h=42 f=58	h=50 f=50	h=75 f=25	h	h	h	h	h	h=50 f=50	h=75 f=25	h	h	h	h	h	h	a	a	a	b=10 a=90	a	a	a	a	a	a	a	a	a
Gsr	c	c	c	c	c	c	c	c	c	c	c	c=90 a=10	e=10 c=90	c	c	e=67 c=33	e=40 c=60	b=17 a=83	b=50 a=50	b=40 a=60	b=40 a=60	b=17 a=83	b	c=10 b=90	b	b	b	b	b	b
Hbdh	b	b	b	b	b	b	b	b	b=87 a=13	b	b	b	b	d=12 b=88	d=20 b=80	d	d	b	b	b	b	b	b	b	b	b	d=10 b=90	b	d=20 b=80	d=25 b=75
Idh-2	a	a	a	a	b=50 a=50	a	b=40 a=60	b=67 a=33	a	b=50 a=50	a	a	a	a	a	a	a	b	b	b	b	b	b=12 a=88	b=60 a=40	b=90 a=10	b	b	b	b	b
Lap	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	c=11 a=89	a	a	a	a	d=25 c=75	c	c	c	d=10 c=80 a=10	c=80 a=20	c=90 a=10	c
Ldh-2	b	b=83 a=17	b	b	b	b	b	b	b	b	b	b=90 a=10	b	b	b	c=36 b=64	c=60 b=40	b	b	b	b	b	b	b=70 a=30	b=90 a=10	b	b	b	b	b
Mdh-2	b	b	b	b	b	b	b	b	b	b	b	b	b=90 a=10	b=37 a=63	b=70 a=30	b	b													
Me-1	c	c	c	d=37 c=63	c	c	c	c=50 b=50	d=37 c=63	c	c	c=90 a=10	c=40 a=60	c=87 a=13	d=10 c=50 a=40	d=25 c=75	d=40 c=60	l=11 k=17 j=72	k=50 j=50	l=10 k=40 j=40 i=10	l=10 k=40 j=50	k=83 j=17	j	k=80 j=20	k=10 j=90	j	j	j	j	j
Me-2	c	c=25 a=75	c=33 a=67	c=87 a=13	c=50 a=50	c=75 a=25	c=90 a=10	c=33 a=67	c	c	c	b	c=10 b=90	b	b=87 a=13	b	b	g=56 f=44	g	g	g=40 f=60	g=67 f=33	g=25 f=75	g	g	g	g	g	g	g
Np	j	j	j=83 i=17	j	j	j	j	j	k=12 j=88	k=50 j=50	j	j	k=70 j=30	k=62 j=38	k=60 j=40	j	j													
																		i=50 g=50	i=50 g=50	i=40 g=60	i=50 g=50	i=67 g=33	i=12 g=88	i=20 g=80	i=10 g=90	i=62 g=38	i=40 g=60	i=50 g=50	i=20 g=80	i=75 g=25
Pep-B	j=10 g=90	j=33 g=67	g	g	k	g	k	k=50 g=50	g=75 e=25	g	g	j=10 h=10 g=70 f=10	h=10 g=30 f=60	h=12 g=50 f=38	g=10 f=90	k=15 j=64 g=21	k=10 j=80 g=10	c b	c b	c b	c b	c b	c b	c b	c b	c b	c b	f=30 c=70 b	c b	c b
Pep-D	h	h	h	h	h	h	h	h	h	h	h	i=50 g=50	i=10 g=90	i=37 g=63	i=10 g=90	g	g	a	a	a	a	a	a	a	a	a	a	a	a	a
6Pgd	c	c	c	c	c=50 b=50	c	c=70 b=30	c	c	c	c	c	c	c	c	c	c	b	b	b	b	b	c	b	c=20 b=80	c	c=90 b=10	c	c	c
Pgm	b	b	b	b=87 a=13	b	a	b	b	b=25 a=75	b	b	b	b	b	b	b	b	a	a	a	a	a	a	a	a	a	a	a	a	a
Pk	a	b=8 a=92	a	a	b=50 a=50	a	b=20 a=80	b=83 a=17	a	a	a	a	a	a	a	a	a	h=83 g=17	h	h=90 g=10	h=80 g=20	h	h	h=50 g=50	h=70 g=30	h=87 g=13	h	h	h	h
Sod	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	e=57 c=43	c	e=30 c=70	e=10 c=90	e=67 c=33	c	c	c	c	c	c	c	c

Allozymes fixed in all populations: *Acp*^{a}, *Ak-1*^{a}, *Cs*^{a}, *Dia*^{c}, *Enol-1*^{a}, **Enol-2*^{a}, *Fdp-1*^{a}, *Gapd*^{a}, *Glo-2*^{a}, *Gpd-1*^{b}, **Gpd-2*^{c}, *Ldh-1*^{a}, *Mdh-1*^{c}, *Mpi*^{c}, *Pgk*^{a}, *Tpi*^{a}, and *Ugpp*^{a}. *Ca-1*^{c} (EMa/b[30b] –), *Ca-2*^{c}, (EMV[29] a=10, c=90), **Ck*^{b}, (EMa/b[1] a=17, b=83, *Idh-1*^{b} (EMI[17a] a=10, b=90), *Pep-A*^{b} (EMI[17a] b=83, c=17) and *Sordh*^{d} (EMI[14] d=60, e=40). The enzyme *Xo* was not scorable in *Emydura*, with most populations segregating for one or more of the *b*, *c* or *d* allozymes.