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Biochemical Systematics and Evolution in the South American Turtle Genus *Platemys* (Pleurodira: Chelidae)

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Phenetic and phylogenetic methods of analysis of allozymic data were used to determine relationships among members of the South American genus *Platemys* (*P. pallidipectoris, P. spixii, P. macrocephala, P. radiolata,* and *P. platycephala*). Two members of the related genus *Phrynops* (*P. gibbus* and *P. rufipes*) were used in the phylogenetic analysis to determine character state polarities. Comparison of the biochemical analyses to those from chromosomal and morphological data indicated a general concordance between the data sets and supports specific status for all five members of the *Platemys* group. *Platemys platycephala* appears to be the most divergent member of the genus.

As currently recognized, the genus *Platemys* comprises five species distributed exclusively in South America. *Platemys platycephala* is the best known member of the genus and occurs throughout the Amazonian drainage in Venezuela, Colombia, Ecuador, Peru, Bolivia, Guyana, Suriname, French Guyana, and Brazil (Rhodin et al., 1984a). Two subspecies are recognized with *P. p. platycephala* broadly distributed and the recently described *P. p. melanonota* (Ernst, 1983a) known only from a few river systems in Peru and Ecuador. *Platemys radiolata* has a disjunct range in Brazil including a narrow eastern coastal strip and a geographically isolated western population (Rhodin et al., 1984b). *Platemys spixii* occurs in eastern Brazil and adjacent Argentina and Uruguay (Ernst, 1983b; Rhodin et al., 1984b). *Platemys pallidipectoris* is geographically separated from the above species, occurring in the Chaco Region of northern Argentina and perhaps into southern Bolivia and Paraguay (Rhodin, 1982; Rhodin et al., 1984b; Ernst, 1983c). The recently described *P. macrocephala* occurs in central Bolivia and adjacent Brazil (Rhodin et al., 1984a).

Standard karyotypes for all five *Platemys* species document an unusual range of intrageneric chromosomal variation for turtles (McBee et al., 1985). The diploid number (2n) ranges from 48–64 and the number of autosomal arms (fundamental number, FN) ranges from 60–64. *Platemys spixii* and *P. pallidipectoris* have indistinguishable karyotypes (2n = 50, FN = 62) whereas *P. platycephala, P. radiolata* and *P. macrocephala* each have unique karyotypes. In this study we examine allozymic divergence from representatives of the five species of *Platemys* and compare these data with chromosomal and morphological information to further clarify phylogenetic relationships among these little known South American turtles.

Materials and Methods

Heart, kidney, and liver samples were extracted from each specimen and frozen at −80 C. Approximately 1 g of tissue was homogenized in an equivalent volume of buffer (0.1 M Tris, 0.001 M EDTA, pH adjusted to 7.0 with HCl). Excess lipids were removed from liver homogenates by addition of an equal volume of toluene followed by centrifugation to separate the aqueous sample from the solvent. The use of this technique resulted in improved separation and resolution of electromorphs. Subsequent procedures for tissue preparation, horizontal starch gel electrophoresis and histochemical staining were similar to those described by Selander et al. (1971) and Sites et al. (1981, 1984). All protein systems were visualized using at least two different buffer systems in an attempt to detect cryptic variation. Buffer systems used in the final analyses and the protein systems examined are listed in Table 1. At each locus the most anodally migrating electromorph was designated as 100 and other allozymes at that locus were designated as the percent of migration compared to the 100 electromorph. Allozyme similarities were determined through side-by-side comparisons of all variant electromorphs. Enzyme nomenclature follows the recommendations of the No-

menclature Committee of the International Union of Biochemistry (1984), Murphy et al. (1983), and Murphy and Crabtree (1985).

Allelic variation was analyzed with the use of the BIOSYS-1 program (Swofford and Selander, 1981). The input data were in the form of individual genotypes. Estimates of genic identity (I; Nei, 1978), similarity (S; Rogers, 1972), and distance (D; Nei, 1972) were calculated from the 15 loci scored for all paired combinations of taxa.

Cladistic methods used to infer phylogenetic relationships from electrophoretic data have been recently reviewed by Buth (1984). There is, however, no consensus among researchers as to the appropriate method of treating intraspecific electromorphic polymorphisms and as a result a number of opposing approaches have been presented including both distance/similarity treatments (Felsenstein, 1984) and discrete character/state methods of coding (Mickevich and Mitter, 1981). The cladistic analysis employed in this study recognizes the locus as the character and the allelic composition of the locus as the character state. As discussed by Buth (1984) character states recognized by this method may be vulnerable to sampling error. To minimize the potential effects of frequency differences due to sampling error, low frequency alleles which did not significantly contribute to the array of a locus were omitted from the cladistic analysis. The coded data were then analyzed using verson 2.4 of Phylogenetic Analysis Using Parsimony (PAUP algorithm written by D. L. Swofford, Illinois Natural History Survey). The branch-and-bound option was used to evaluate all possible most parsimonious trees and the CONTREE option was used to produce a strict consensus tree. The outgroup used to determine character state polarities included the composite data from *Phrynops gibbus* and *P. rufipes*. Members of this genus were chosen based on the work of Gaffney (1977) who has shown, using synapomorphic cranial character states, that *Phrynops* is phylogenetically the closest extant South American genus to *Platemys*.

Results

Electrophoretic variation.—Of the 15 presumptive gene products resolved electrophoretically, three (Ap-A, Hex-A, and M-Mdh-A) were monomorphic in all specimens examined. Of the remaining 12 protein systems, six were found to vary within species (Gpi-A, Ldh-B, Me-A, S-Mdh-A, Pep-1, and Pgm-A) and six varied only among species (Ck-A, S-Icdh-A, Ldh-A, Mpi-A, Pgm-B, and S-Sod-A). Allelic designations and frequencies of the 12 polymorphic and polytypic loci are provided in Table 2.

TABLE 1. BUFFER SYSTEMS AND HISTOCHEMICAL STAINING PROCEDURES USED IN THIS STUDY. Tissue extracts were liver (L) or heart/kidney (HK). Buffer systems include: (A) Tris-citrate pH 8.0 (Ridgeway et al., 1970); (B) Tris-citrate pH 6.7 (Selander et al., 1971); (C) Poulik pH 8.6 (Selander et al., 1971); (D) Tris-citrate pH 7.0 (Ayala et al., 1972); and (E) Histidine pH 7.8.

Enzyme	Enzyme commission number	Tissue	Buffer
Aminopeptidase (Ap-A)	3.4.11.1	HK	A
Creatine kinase (Ck-A)	2.7.3.2	L	B
Glucose-6-phosphate isomerase (Gpi-A)	5.3.1.9	L	C
Hexokinase (Hex-A)	2.7.1.1	HK	B
Isocitrate dehydrogenase (S-Icdh-A)	1.1.1.42	L	B
L-Lactate dehydrogenase (Ldh-A, Ldh-B)	1.1.1.27	L/HK	B
Malic enzyme (Me-A)	1.1.1.40	HK	B
Malate dehydrogenase (M-Mdh-A, S-Mdh-A)	1.1.1.37	L	B
Mannose-6-phosphate isomerase (Mpi-A)	5.3.1.8	L	D
Peptidase-A (Pep-A)	3.4.1.1	L	C
Phosphoglucomutase (Pgm-A, Pgm-B)	5.4.2.2	L	D
Superoxide dismutase (S-Sod-A)	1.15.1.1	L	E[a]

[a] Histidine buffer: electrode buffer: Tris 7.26 g, histidine 3.88 g, conc. HCl 3.83 ml, and distilled water to a volume of 1 liter, gel buffer: 1:5 dilution of electrode buffer and distilled water.

Phenetic analysis.—Coefficients of genetic similarity, identity and distance were calculated for all paired combinations of taxa examined (Table 3). Similarity values (S; Rogers, 1972) among the *Platemys* species ranged from a high of 0.767 (*P. pallidipectoris* and *P. spixii*) and 0.710 (*P. macrocephala* and *P. radiolata*) to a low of 0.400 (*P. pallidipectoris* and *P. platycephala*). Although *P. platycephala* was the most allozymically distant of the species of *Platemys*, mean coefficients from the combined values in Table 2 show greater affinity between *P. platycephala* and the other species of *Platemys* ($\bar{S}$ = 0.476, $\bar{I}$ = 0.478, $\bar{D}$ = 0.751) than to either member of the genus *Phrynops* ($\bar{S}$ = 0.358, $\bar{I}$ = 0.360, $\bar{D}$ = 1.03).

TABLE 2. ALLELE DESIGNATIONS AND FREQUENCIES OF THE VARIANT LOCI RESOLVED IN THIS STUDY. Three loci (Ap-A, Hex-A, and M-Mdh-A) were monomorphic and are not shown in this table.

	Platemys					*Phrynops*	
	pallidipectoris	*spixii*	*macrocephala*	*radiolata*	*platycephala*	*rufipes*	*gibbus*
N	1	1	4	4	20	1	3
Ck-A	70	50	100	83	83	91	91
Gpi-A	61	61 (.50) 100 (.50)	61 (.50) 60 (.50)	61 (.50) 60 (.50)	29	80	80
S-Icdh-A	100	100	100	100	70	100	100
Ldh-A	72	72	100	100	100	100	100
Ldh-B	86	86	100	100	100	40	100 (.67) 71 (.33)
Me-A	72	54	89 (.25) 81 (.75)	84	58	92	100
S-Mdh-A	100	100	100	100	100	100	75 (.75) 57 (.25)
Mpi-A	70	70	83	70	74	83	100
Pep-1	87	93	89 (.67) 63 (.33)	100 (.25) 89 (.75)	81	63	74
Pgm-A	84	84	100 (.25) 84 (.75)	59	84	50	100
Pgm-B	100	100	100	100	100	100	74
S-Sod-A	82	82	25	25	60	50	100

Cladistic analysis.—Two of the 12 polymorphic protein systems listed in Table 2 (S-Mdh-A and Pgm-B) exhibit no ingroup variation and were cladistically uninformative for an analysis of *Platemys*. These systems along with the three monomorphic protein systems (Ap-A, Hex-A, and M-Mdh-A) were omitted from the cladistic analysis. All remaining protein systems were considered unordered with the exception of S-Icdh-A, Ldh-A, and Ldh-B each of which had only two character states. With these systems the character state shared with the composite outgroup was recognized as primitive.

Ck-A was considered autapomorphic in *Platemys pallidipectoris* (Ck-A 70), *P. spixii* (Ck-A 50), and *P. macrocephala* (Ck-A 100) whereas the Ck-A (83) allele was shared between *P. radiolata* and *P. platycephala*. The Gpi-A locus includes a Gpi-A (60) allele that was shared between two taxa, *P. macrocephala* and *P. radiolata*, and a Gpi-A (61) allele that was shared between the two aforementioned taxa plus *P. pallidipectoris* and *P. spixii*. Due to the very small sample sizes of *P. pallidipectoris* and *P. spixii* the lack of the Gpi-A (60) allele may be due to sampling error and we have conservatively coded all taxa associated with the Gpi-A (61) allele as sharing a single trait.

All taxa were coded as having unique character states of Me-A. Mpi-A (83) was considered primitive (*P. macrocephala* and the composite outgroup) with Mpi-A (70) coded as a shared condition in *P. pallidipectoris*, *P. spixii*, and *P. radiolata* and Mpi-A (74) considered as unique to one taxon (*P. platycephala*). *Platemys pallidipectoris*, *P. spixii*, and *P. platycephala* each possessed unique character states of Pep-1 with *P. macrocephala* and *P. radiolata* conservatively coded as having the same Pep-1 (89) character state. The Pgm-A (84) allele was considered shared in all *Platemys* taxa with the exception of *P. radiolata* which had the unique Pgm-A (59) character state. S-Sod-A (82) was shared between *P. pallidipectoris* and *P. spixii* whereas S-Sod-A (25) was shared between *P. macrocephala* and *P. spixii* and S-Sod-A (60) was unique to *P. platycephala*. The S-Sod-A (50/100) allelic array was unique to the composite outgroup.

The coded data set resulting from these character state determinations is provided in Table 4. The PAUP analysis yielded five equally parsimonious trees each with a length of 25 steps

TABLE 3. GENIC SIMILARITY (S; ROGERS, 1972), DISTANCE (D; NEI, 1978), AND IDENTITY (I; NEI, 1972) COEFFICIENTS FOR PAIRED COMBINATIONS OF THE SEVEN TAXA EXAMINED.

Taxon		2	3	4	5	6	7
1 *Phrynops gibbus*	S	.479	.279	.288	.423	.403	.316
	D	.737	1.297	1.280	.846	.910	1.143
	I	.478	.273	.278	.429	.403	.319
2 *Phrynops rufipes*	S		.400	.409	.578	.487	.400
	D		.916	.899	.528	.723	.916
	I		.400	.407	.590	.485	.400
3 *Platemys pallidipectoris*	S			.767	.498	.538	.400
	D			.249	.667	.590	.916
	I			.780	.513	.555	.400
4 *Platemys spixii*	S				.498	.511	.409
	D				.685	.671	.899
	I				.504	.511	.407
5 *Platemys macrocephala*	S					.710	.540
	D					.340	.600
	I					.711	.549
6 *Platemys radiolata*	S						.554
	D						.590
	I						.555
7 *Platemys platycephala*							

and a consistency index of 1.00, indicating no homoplasy. All five most parsimonious trees recognize *Platemys pallidipectoris,* and *P. spixii* as sister taxa. The remaining three taxa (*P. macrocephala, P. radiolata,* and *P. platycephala*) form an unresolved trichotomy below the *P. pallidipectoris* and *P. spixii* clade. From the output matrix of these five most parsimonious trees, a strict consensus tree was derived (Fig. 1).

DISCUSSION

Within the genus *Platemys, P. pallidipectoris,* and *P. spixii* represent the most closely related sister taxa. These two species possess indistinguishable standard karyotypes (McBee et al., 1985) and the highest and lowest interspecific genic identity (I = 0.780) and distance values (D = 0.249), respectively. Additionally, the phylogenetic analyses revealed three unambiguous synapomorphies (Ldh-A 72, Ldh-B 86, and S-Sod-A 82) which support the association of these two taxa as a dichotomously branching clade within the genus.

The specific status of *P. macrocephala* was only recently recognized, with specimens having previously been included within *P. radiolata* (Rhodin et al., 1984a). *Platemys macrocephala* has been distinguished from *P. radiolata* by its greater head width, slightly deeper shell, skull osteology and serum protein patterns (Frair, 1982; Rhodin et al., 1984a). Subsequently, McBee et al. (1985) found that these two taxa are distinguishable on the basis of two fewer microchromosomes in *P. macrocephala* and a possible heterochromatic addition to two pairs of group A macrochromosomes in *P. radiolata.* The bio-

TABLE 4. CHARACTER MATRIX OF THE ELECTROPHORETICALLY DEFINED GENE PRODUCTS LISTED IN TABLE 2. S-Mdh-A and Pgm-B were nonvariant within *Platemys* and were omitted from this analysis. The coding scheme for state recognition does not imply ordered relationships. See text for ordering and character state definitions. The characters from left to right are: Ck-A, Gpi-A, S-Icdh-A, Ldh-A, Ldh-B, Me-A, Mpi-A, Pep-1, Pgm-A, and S-Sod-A.

Taxa	Character state									
P. pallidipectoris	1	1	0	1	1	1	1	1	1	1
P. spixii	2	1	0	1	1	2	1	2	1	1
P. macrocephala	3	1	0	0	0	3	0	3	1	2
P. radiolata	4	1	0	0	0	4	1	3	2	2
P. platycephala	4	2	1	0	0	5	2	4	1	3
Phrynops (outgroup)	0	0	0	0	0	0	0	0	0	0

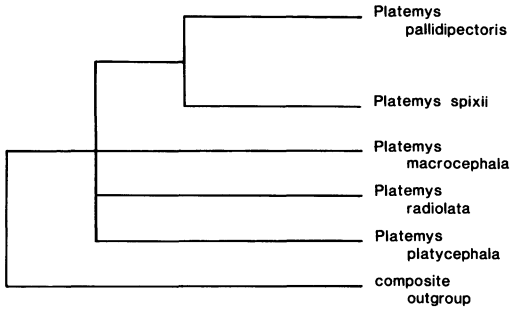

Fig. 1. Strict consensus tree based on the output matrix generated from the five most parsimonious trees resulting from the analysis of the coded character states presented in Table 4.

chemical data support the karyotypic and morphologic distinctions for these two taxa in that their allozymic divergence (I = 0.711, D = 0.340) strongly suggests their specific distinction. These two taxa share a number of unique character states (Gpi-A 60/61, Pep-1 89, and S-Sod-A 25) but the most parsimonious arrangement of the complete data set does not recognize these as synapomorphies between sister taxa.

Our biochemical data suggest that *P. platycephala* is phenetically the most divergent member of the genus. *Platemys platycephala* is genetically most similar to *P. radiolata* (S = 0.554) but cladistically forms an unresolved trichotomy with *P. macrocephala* and *P. radiolata*. Of the 10 phylogenetically informative protein systems resolved, *P. platycephala* possessed six autapomorphic character states (Gpi-A 29, S-Icdh-A 70, Me-A 58, Mpi-A 74, Pep-1 81, and S-Sod-A 60). Although autapomorphic states are of no use in defining cladogenetic events, these data indicate a high degree of divergence within the lineage leading to *P. platycephala*. In fact, *P. platycephala* has more than twice the number of autapomorphic character states than any other species within the genus. Considerable divergence is also evident in that the karyotype of this species has the highest known diploid number of all pleurodiran turtles and is the only turtle with an entirely acrocentric chromosomal complement (McBee et al., 1985). The karyotype of *P. platycephala* cannot be related to other members of the genus *Platemys* without invoking at least six Robertsonian fission/fusion events (Bickham and Carr, 1983). Furthermore, *P. platycephala* displays an unusual diploid-triploid mosaicism unlike that known in any other vertebrate species (Bickham et al., 1985).

Based on chromosomal variation, McBee et al. (1985) suggested the removal of all species but *P. platycephala* from the genus *Platemys*. This arrangement is also supported by morphological studies currently being conducted by Rhodin and Mittermeier. The biochemical information presented in this report, although falling short of fully resolving the phylogenetic relationships among all members of the genus *Platemys*, is generally consistent with and strengthens the inferences from the chromosomal and morphological data. The remaining four species may represent a distinct monophyletic genus with close taxonomic relationships to both *Phrynops* and *Platemys platycephala*.

Material examined.—AK numbers refer to karyotype numbers, Wildlife Genetics Laboratory, Texas A&M University. Representive voucher specimens have been placed in the Texas Cooperative Wildlife Collection (TCWC), the reptile collection of The University of Utah (UU) and The Museum of Comparative Zoology (MCZ), Harvard University. *Phrynops gibbus* (3) Venezuela: AK1434, 1386, 1387 (TCWC); *P. rufipes* (1) Colombia: AK1439 (TCWC); *Platemys pallidipectoris* (1) unknown origin; AK1408 (MCZ); *P. spixii* (1) unknown origin: AK1488 (MCZ); *P. macrocephala* (4) Bolivia: AK1450, 1474; unknown origin: AK6593, 6596 (TCWC); *P. radiolata* (4) unknown origin: AK1453, 1454, 6594, 6595 (TCWC); *P. platycephala* (20) Bolivia: AK1418–1422, 1428, 1435–1438, 1440–1444, 1447–1449 (TCWC); Suriname: AK6609 (TCWC); unknown origin: AK1427 (UU).

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