A Review of Species Previously Identified as *Craterocephalus eyresii* (Pisces: Atherinidae)

L. E. L. M. CROWLEY and W. IVANTSOFF

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Recent electrophoretic and osteological work has shown that geographically widely separated populations of fish, all previously identified as *Craterocephalus eyresii*, are attributable to four distinct species. These are *C. eyresii* (Steindachner, 1884), *C. fluviatilis* McCulloch, 1913, and two new species, *C. centralis* and *C. amniculus*. Osteological differences between the first three species are minor, whilst the maxilla and premaxilla of *C. amniculus* are distinctly different. Electrophoretic studies indicate only a single fixed gene difference between *C. amniculus* and *C. fluviatilis* but the other three species differ considerably at a number of loci. There are three fixed gene differences between *C. eyresii* and *C. centralis* and at least seven between all other pairs. Morphologically, *C. eyresii*, *C. fluviatilis* and *C. centralis* are very similar. *C. amniculus* is distinguished from the other three by having a greater number of midlateral and transverse scales.

L. E. L. M. Crowley and W. Ivantsoff, School of Biological Sciences, Macquarie University, North Ryde, Australia 2109; *manuscript received 18 April 1989, accepted for publication 20 June 1990.*

INTRODUCTION

In separate studies in 1978, both Ivantsoff and Patten recognized and reviewed 10 species of hardyheads in the genus *Craterocephalus*. With recent work and more comprehensive collecting the number has now risen to 24 (see Ivantsoff *et al.*, 1987a, b; Crowley and Ivantsoff, 1988). Populations of hardyheads with a broad but disjunct distribution (central and South Australia, through the Murray-Darling Drainage System in New South Wales and in the Hunter River Region of central eastern New South Wales) were recognized as *C. eyresii*, (Ivantsoff, 1978, Patten, 1978) or as *C. fluviatilis* (McCulloch, 1913- see Ivantsoff *et al.*, 1987a). Some slight morphological variations between these populations were apparent, but were accepted as population variability in a single, widespread species.

In 1884, Steindachner described the atherinid species *Atherinichthys eyresii (= Craterocephalus eyresii)* but failed to designate type material or to give a particular type locality. McCulloch and Waite (1918) carefully examined specimens obtained from Coward and Strangways Springs in South Australia and identified them as indistinct from those described by Steindachner. They also pointed out that the Lake Eyre hardyhead was closely allied to *Craterocephalus fluviatilis* (McCulloch, 1913). Jordan and Hubbs (1919), in their review of atherinids, suggested Coward and Strangways Springs as the type locality basing their interpretation on a statement 'wärhend der Lake Eyre-Expedition gesammelt'.

Re-examination by Ivantsoff (1978) of McCulloch's type material, on which the original description of *C. fluviatilis* is based, showed that the holotype and two paratypes were distinct from the other paratypes; the former were identified at that time as *C. eyresii*, but recent work has shown this identification to be incorrect. The three other paratypes, one of which was figured, are now recognized as *C. stercusmuscarum fulvus* (see Ivantsoff, 1978; Ivantsoff *et al.*, 1987a).

In his study of variability in populations, Ivantsoff (1978) noted that midlateral and transverse scale counts in hardyheads from the Peel and Namoi Rivers were much

higher than those from southern reaches of the Murray-Darling River system, South Australian waters and the type locality.

The objectives of this study were: to examine morphological, osteological and genetic variation in populations identified as *C. eyresii*; to re-assess the relationships between the populations from the Finke River and Lake Eyre Drainage on the western side of the Flinders and Barrier Ranges and from the Murray-Darling Drainage to the east of those ranges.

Materials and Methods

Procedures used for measurements and counts are as reported in Crowley and Ivantsoff (1988); values were taken from thirty specimens of each species wherever possible. Alizarin stained specimens — following the method of Taylor (1967) — were used for osteology with three or more specimens of each species examined.

Electrophoresis was carried out following the methods of Richardson *et al.*, (1986). Fixed gene differences as suggested by those authors were used to indicate genetic relationships between populations. Ten specimens of each species were examined at twenty-one loci (see Table 1 for enzymes assayed).

Specimens designated as holotypes and paratypes are now deposited in The Australian Museum, Sydney (AMS); Northern Territory Museum of Arts & Sciences (NTM); University of Michigan Museum of Zoology, Ann Arbor Michigan (UMMZ); American Museum of Natural History, New York (AMNH); Western Australian Museum, Perth (WAM). Additional material from the following institutions has also been examined: Museum of Victoria, Melbourne (NMV); South Australian Museum, Adelaide (SAM), Macquarie University, (MQU).

Systematic Descriptions

Craterocephalus amniculus sp. nov.
(Fig. 1)

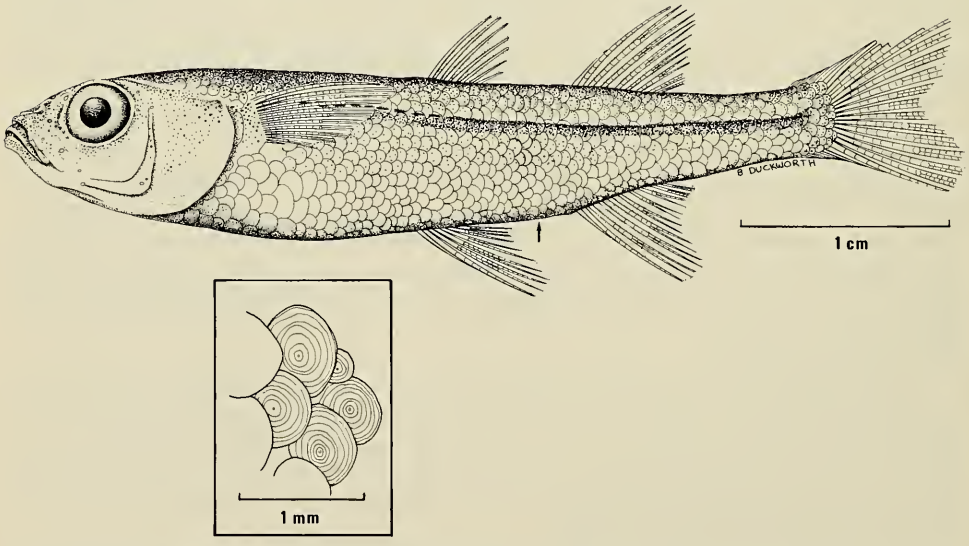

Fig. 1. Holotype of *Craterocephalus amniculus*, AMS I.28880-001, 40.0mm SL. Arrow indicates position of anus.

Craterocephalus eyresii: Lake, 1978:41 (in part); Ivantsoff 1978:245 (in part), 1980:133 (in part); Llewellyn, 1983:13 (in part); Merrick and Schmida, 1984:145 (in part).

Holotype: AMS I.28880-001. 40.0mm standard length (SL), collected with 2.5m seine, in shallow water over gravel, in Cockburn River, Nemingha, N.S.W. 31°07′S, 150°59′E. Collected by A. L. Crowley and L. E. L. M. Crowley, 13 February, 1987. For morphometrics and meristics of the holotype, see Table 2.

Paratypes: (21), AMS I.28880-002 (10, 25.8-44.2mm SL); WAM P.29891.001 (4, 32.0-40.6mm SL); NTM S.12526-001 (3, 36.6-45.5mm SL); UMMZ 214855 (2, 36.7-43.4mm SL); AMNH 58688 (2, 42.7-43.4mm SL). Locality and collectors for all paratypes as for the holotype.

TABLE 1

Enzymes assayed, number of loci scored, buffer and staining-system used following the methods of Richardson et al., *(1986)*

Enzyme Name and abbreviation	E.C. Number	Loci scored	Buffer
Adenosine deaminase ADA	3.5.4.4	1	B
Alcohol dehydrogenase ADH	1.1.1.1	1	B
Adenylate kinase AK	2.7.4.3	1	B
Aldolase ALD	4.1.2.13	1	D
Creatine kinase CK	2.7.3.2	1	D
Fructose-1,6-diphosphatase FDP	3.1.3.11	1	B
Fumarate hydratase FUM	4.2.1.2	1	B
Glyceraldehyde-3-phosphate dehydrogenase GAPD	1.2.1.12	1	D
Glucose dehydrogenase GLDH	1.1.1.47	1	B
Aspartate aminotransferase GOT	2.6.1.1	2	B
Glycerol-3-phosphate dehydrogenase αGPDH	1.1.1.8	1	B
Glucose-phosphate-isomerase GPI	5.3.1.9	2	B
Isocitrate dehydrogenase IDH	1.1.1.42	1	A
Lactate dehydrogenase LDH	1.1.1.27	1	B
Malate dehydrogenase MDH	1.1.1.37	2	A
Malic enzyme ME	1.1.1.40	2	B
Mannose phosphate isomerase MPI	5.3.1.8	1	B
Phosphoglucomutase PGM	2.7.5.1	1	B
Xanthine oxidase XO	1.2.3.2	1	D

Additional Material Examined: (included in counts and measurements) (Table 2): MQU I.77-3 (1, 31.8mm SL), Peel River, at Tamworth, N.S.W., 31°04′S, 150°53′E; MQU I-086 (5, 30.7-33.0mm SL) Glennies Creek, N.S.W., 32°33′S, 148°29′E; MQU I-001 (1, 40.7mm SL) Bowmans Creek, N.S.W., 32°25′S, 151°03′E. Material examined for osteology: AMS IA.333 (2), Warialda Creek, N.S.W., 29°36′S, 150°50′E; MQU IA.90 (1), Peel River, Tamworth, N.S.W., 31°04′S, 150°53′E; MQU IA.70-52 (2), Peel River, Tamworth, N.S.W. 31°04′S, 150°53′E.

Diagnosis: A species of the atherinid genus *Craterocephalus*, superficially appearing to be most closely allied to *C. eyresii* but differing from that species in the following: midlateral scale counts, 40.6 (37-48); transverse scale counts 15.9 (14-18). For a comparison of morphometric and meristic values of *C. amniculus, C. centralis, C. eyresii* and *C. fluviatilis* see Tables 2, 4, 5, 6. Differing osteologically from *C. eyresii*: in shape of maxilla; in ratio of symphysial part of dorsal process to total length of dorsal process of premaxilla; in shape of nasal bone; in medial process of pelvic girdle (see Fig. 2). Exhibiting fixed gene differences at 8 loci (see Table 3), when compared with *C. eyresii*.

Differing from all other species of the genus *Craterocephalus* by the combination of the following: midlateral 40.6 (37-48); transverse scale counts 15.9 (14-18); gill raker count 10.2 (9-11); shape of anterior medial process of maxilla. Scales of head and body smaller than in any other *Craterocephalus* species; scales with obvious circuli (see Fig. 1).

Description: Small, moderately robust fish, maximum known size 44.2mm SL. Mouth protractile, lips thin. Gape restricted by labial ligament, one third of way along mouth. Teeth few, moderately long and pointed, restricted to anterior part of both jaws. Other bones edentulous. Premaxilla short and not reaching vertical through anterior edge of orbit; dorsal premaxillary process reaching into interorbital space. Gill rakers moderately short, less than half diameter of pupil, first four often tuberculate. Scales small, almost circular, thin, but with circuli complete and obvious, appearing barely to overlap. Scales usually absent from dorsum of head, or if present, well spaced, small and circular. Opercles naked.

Colour: Live specimens (from Nemingha) dusky gold above dark silvery midlateral stripe and silvery gold below. Abdomen, chin, opercles and eyes, silvery. Dorsum of head, snout and lower jaw very dark. Caudal fin golden, dorsal fins dusky gold. Anal fin pale gold; ventral fins clear. Fish from other areas (e.g. Boiling Down Creek) paler than Nemingha specimens but similar in other features. Preserved specimens — cream to light brown, depending on length of preservation. Eyes dark. Upper half of body brownish and heavily peppered with melanophores. Lower half peppered lightly with melanophores, except for abdomen. Upper and lower body scales never outlined to form reticulate pattern. Dark peritoneum visible through body wall from origin of ventral fins to anus. Opercles, snout, premaxilla, maxilla and lower lip, speckled; dorsum of head very dark. Pectoral, first and second dorsal, anal and caudal fins with melanophores forming contours along spines and rays. Ventral fins clear.

Etymology: *amniculus* — meaning a small creek or stream, referring to the habitat where these fish are often found.

Distribution: *C. amniculus* has been collected in the Macintyre River, Warialda Creek, Peel and Cockburn Rivers, the Namoi River, and Boiling Down Creek which are all tributaries of the upper Darling River. Some specimens have also been collected from Glennies Creek and Bowmans Creek in the Hunter River region on the eastern side of the Liverpool Range (see comments below).

Comments: Specimens in the Hunter River drainage tentatively recognized as *Craterocephalus amniculus* present a problem: only 6 specimens have ever been collected, one from Bowmans Creek in 1976 and 5 from Glennies Creek in 1980. At this stage, it is not possible to determine whether the hardyhead populations are established in this

TABLE 2

Morphometric proportions and meristic counts of the holotype and 24 paratypes and 7 other specimens of Craterocephalus amniculus

Size and Range In SL	Holotype 40.0m SL	Paratypes and 7 other specimens 31 (25.8-44.2mm SL) Mean	Range	SD
Head	3.4	3.4	(3.3-3.6)	.08
H. max	4.5	4.4	(4.0-5.3)	.28
H. min	11.0	10.8	(9.9-11.9)	.55
Pec/anus	2.8	2.9	(2.6-3.1)	.12
Sn-OD1	2.0	2.0	(1.8-2.1)	.06
Sn-OD2	1.5	1.5	(1.4-1.5)	.05
Sn-OV	2.0	2.1	(2.0-2.2)	.07
Sn-TV	1.6	1.7	(1.6-1.8)	.06
Sn-OA	1.4	1.5	(1.4-1.5)	.05
Sn-TA	1.3	1.3		
In Head				
Eye	3.5	3.5	(3.0-3.9)	.25
Interorb.	2.9	2.9	(2.6-3.3)	.18
Postorb.	2.2	2.2	(2.0-2.4)	.09
In Eye				
Snout	1.0	1.0	(0.8-1.2)	.12
Premaxilla	1.0	1.0	(0.9-1.1)	.07
Lips	2.3	2.4	(2.2-2.6)	.12
Premax. process	1.2	1.2	(1.0-1.5)	.14
Scales				
Midlateral	39	40.6	(37-48)	3.00
Transverse	16	15.9	(14-18)	1.03
Predorsal	18	17.7	(16-20)	1.04
Interdorsal	6	6.4	(5-8)	0.63
Fin rays				
1st dorsal	7	6.2	(5-7)	.54
2nd dorsal	6	5.8	(5-7)	.48
Anal	7	6.5	(5-8)	.63
Pectoral	12	12.0	(11-14)	.78
Other				
Gill rakers	10	10.2	(9-11)	0.54
Posit. anus	B0.5	B0.3	(B0.5-F0.5)	0.51
OD1-TV	F6	F6.9	(F5-9)	1.03
OD1-TPec	B2	B1.5	(B3-F1)	1.09
OV-TPec	F0	F0.3	(B2-F2)	0.95
Vertebrae	34	*34.9	(33-36)	.88

* 15 specimens.

Abbreviations in morphometric/meristic tables: — H, height or body depth; — max, maximum; — min, minimum; — Pec, pectoral; — Sn, snout; — OD1, origin of first dorsal fin; — OD2, origin of second dorsal fin; — OV, origin of ventral fins; — TV, tips of ventral fins; — OA, origin of anal fin; — TA, insertion of last ray of anal fin; — TPec, tips of pectoral fin; — Interorb., interorbital; — Postorb., postorbital; — Premax. process, dorsal process of premaxilla; — Posit. anus, position of anus in relation to tips of ventral fins, expressed in a number of scales (B), behind, (F), in front of; — SL, standard length; — SD, standard deviation.

region or are a result of accidental or deliberate translocation. Systematic collecting in the Hunter River drainage system between Maitland and Muswellbrook N.S.W., over the last 5 years by both authors, has failed to find any more of this hardyhead in that region. A specimen from Glennies Creek, closely resembles members of the population now identified as *C. amniculus* in dentition, the shape of the maxilla and the length of the premaxillary symphysis. An electrophoretic analysis would confirm the status of the Hunter River hardyhead. Until such a study is made, the Hunter River hardyhead is considered to be indistinct from *C. amniculus*.

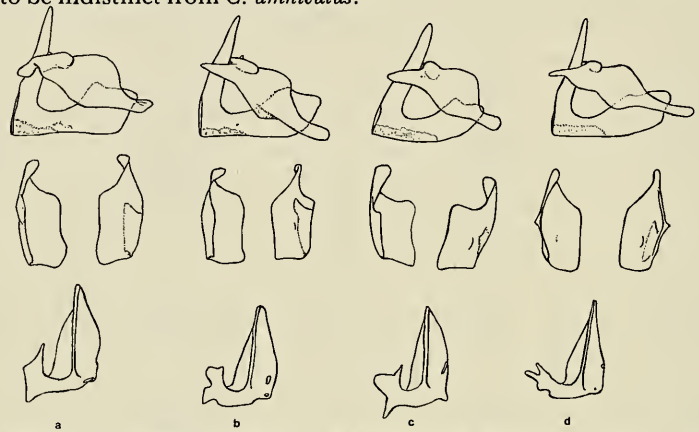

Fig. 2. Left maxilla and premaxilla; dorsal and ventral aspects of left nasal; left pelvic girdle, ventral aspect; of a) *C. amniculus*; b) *C. centralis*; c) *C. fluviatilis;* d) *C. eyresii.*

Craterocephalus centralis sp. nov.
(Fig 3)

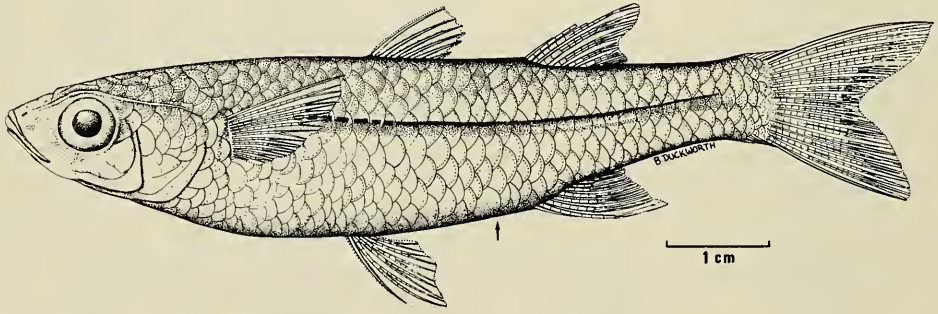

Fig. 3. Holotype of *Craterocephalus centralis*, AMS I.28888-001, 52.2mm SL.

Craterocephalus eyresii: Munro, 1958:102 (in part); Scott, Glover and Southcott, 1974:153 (in part).

Holotype: AMS I.28888-001 52.2mm SL. Finke River, Glen Helen Gorge, Northern Territory, 23°41′S, 132°40′E. Collected with 30m seine, in a shallow billabong (0.25-0.50m), overgrown with weeds and with a muddy bottom. Collected by L. E. L. M. Crowley and W. Ivantsoff, 13 September, 1987. For morphometrics and meristics of the holotype, see Table 4.

Paratypes: (29), AMS I.28874-001 (8, 43.8-56.1mm SL) Glen Helen Gorge, 23°42′S 132°40′E, collected 26 September 1983; AMS I. 28875-001 (1, 64.0mm SL) Salt Hole,

Finke River, Northern Territory, 24°02′S, 132°50′E, collected 26 September 1983; AMS I. 28875-002 (4, 34.3-43.9mm SL) Salt Hole, Finke River, Northern Territory, collected 19 September 1983; WAM P.29893.001 (2, 44.3-56.6mm SL) Pioneer Creek, 23°39′S 132°43′E, collected 28 April 1983; WAM P.29892.001 (4, 40.7-45.6mm SL) Palm Creek Crossing, 24°03′S 132°43′E, collected 20 December 1983; NTM S.12527-001 (4, 39.5-45.6mm SL) Finke River — Ellery Creek Junction, 24°06′S 132°48′E, collected 21 December 1983; NTM S.12528-001 (3, 40.9-51.9mm SL) Hermannsburg Mission, Rock Hole, Northern Territory, 23°57′S 132°46′E, collected 25 April 1983; UMMZ 214856 (2, 41.2-56.8mm SL) Finke River, 24°04′S 132°40′E collected 7 June 1983; AMNH 58689 (2, 46.0-52.3mm SL) as for UMMZ, collected 7 June 1983. All paratypes collected by D. Liddle. Material examined for osteology: AMS IA 24687.001 (4) as for holotype.

Diagnosis: A species of the atherinid genus *Craterocephalus*, superficially appearing to be closely allied to *C. eyresii*, but differing from that species in the following: transverse scales 10.5 (10-11); second dorsal fin rays 5 (4-6); anal fin rays 5.9 (5-7); gill rakers 10.2 (9-11). For a comparison of morphometric and meristic values of *C. centralis*, *C. amniculus*, *C. eyresii* and *C. fluviatilis*, see Table 2, 4, 5, 6. Differing osteologically from *C. eyresii*: in shape of premaxilla and nasal bones (see Fig. 2); in position of ventral wings of 5th ceratobranchial for attachment of *pharyngoclavicularis* muscle; in shape of basihyal; in length of posterior process of urohyal. Genetically distinct from *C. eyresii* in having fixed gene differences at two loci, high alternate allele frequencies at one locus (see Table 3). Having in common an allele at the GPI-2 locus only with *C. eyresii*.

Differing from all other species of genus *Craterocephalus* by the combination of the following: snout 0.9 (0.8-1.0); premaxilla 0.9 (0.8-1.0), both as proportion of diameter of eye; gill raker count 10.2 (9-11); transverse scale count: usually 4 (rarely 5) above midlateral band; in shape of medial process of pelvic girdle.

Description: A moderately robust fish, maximum known size 64.0mm SL. Mouth small but protractile; lips moderately thin. Gape restricted by labial ligament one third of way along mouth. Teeth in jaws sparse, minute, other bones edentulous. Premaxilla short, not reaching vertical through anterior edge of orbit; dorsal process of premaxilla barely reaching into interorbital space. Gill rakers tuberculate and widely spaced. Scales moderately large, strong, in even rows above midlateral stripe. Rows not always even below midlateral stripe. Scales on dorsum of head large, irregular; opercles scaled.

Colour: Live fish rich silvery-golden colour above prominent green/gold midlateral stripe; paler below; abdomen whitish. Opercles and eyes silver. Dorsum of head dark down to eye, pale silver below. Scales outlined above midlateral stripe; some scales below also showing reticulate pattern. Preserved fish from creamy yellow to light brown, depending on length of preservation. Eye silvery. Body with melanophores peppering scales above midlateral band, also forming reticulate pattern at edge of scales; reticulate pattern apparent below midlateral band in some specimens. Snout and lips peppered with melanophores. Dorsum of head very dark. Abdomen pale but with dark peritoneum visible through body wall, from origin of ventral fins, to anus. Pectoral, anal and dorsal fins with light dusting of melanophores. Ventral fins clear.

Etymology: *centralis* — indicating the species' provenance — Central Australia.

Distribution: This species of hardyhead is known only from the Finke River and bodies of water immediately associated with it. During times of dry weather or prolonged drought, the fish of this area seek refuge in pools formed by natural springs in the river bed.

Comments: *C. centralis* and *C. eyresii* are morphologically similar. *C. centralis* appears to be more robust but morphometric proportions for maximum body depth do not demonstrate any difference (*cf.* Tables 4, 5).

The close relationship of the specimens from the Finke River (*C. centralis*) and from Lake Eyre (*C. eyresii*), is further indicated by sharing of an allele (see Table 3) which is not found in any other species of hardyhead (Crowley, unpublished data). There is no doubt, however, that they are two distinct species since even at this locus (*GPI*-2), *C. eyresii* is polymorphic whilst *C. centralis* is monomorphic for the b allele. The absence of genetic flow between the populations indirectly confirms Kotwicki's (1989) belief that the Lake Eyre and the Finke River drainages are no longer contiguous.

TABLE 3

Enzyme loci which show allelic frequencies and fixed gene differences for four species of hardyheads, C. eyresii, C. centralis. C. amniculus *and* C. fluviatilis. *Alleles not present in these species are omitted*

Locus	Allele	*C. eyresii*	*C. centralis*	*C. amniculus*	*C. fluviatilis*
ADA	d	–	–	0.25	0.18
	e	–	–	0.75	0.82
	f	0.36	0.29	–	–
	g	0.64	0.71	–	–
CK	a	1.0	1.0	–	–
	b	–	–	–	1.0
	c	–	–	1.0	–
FUM	a	–	1.0	–	–
	b	0.54	–	1.0	1.0
	c	–	–	–	–
	d	0.46	–	–	–
GAPD	b	1.0	1.0	–	–
	c	–	–	1.0	1.0
GLDH	a	–	0.5	–	–
	b	–	0.5	0.2	–
	c	1.0	–	0.8	1.0
GOT-1	a	1.0	1.0	–	–
	c	–	–	1.0	1.0
GOT-2	b	–	–	1.0	1.0
	c	1.0	1.0	–	–
GPI-1	c	1.0	1.0	–	–
	d	–	–	0.8	0.9
	e	–	–	0.2	0.1
GPI-2	a	0.45	–	–	–
	b	0.55	1.0	–	–
	c	–	–	1.0	0.67
	d	–	–	–	0.33
IDH	a	–	–	1.0	1.0
	b	–	0.17	–	–
	c	1.0	0.83	–	–
MDH	a	0.39	0.31	–	–
	b	0.61	0.69	1.0	1.0
ME	b	0.75	0.3	–	–
	c	0.25	0.7	1.0	1.0
MPI	b	1.0	0.9	0.38	1.0
	c	–	0.1	0.62	–

The two loci for Glucose-phosphate isomerase (E.C. number 5.3.1.9) found in all *Craterocephalus* spp., support findings of Echelle and Echelle (1984) and Shaklee and Keenan (1986) who have found at least two loci for this enzyme in fish. This is contrary

to a report by Richardson *et al.* (1986) who suggested that only one locus for that enzyme was present in vertebrates.

Craterocephalus eyresii Steindachner, 1884
(Fig. 4)

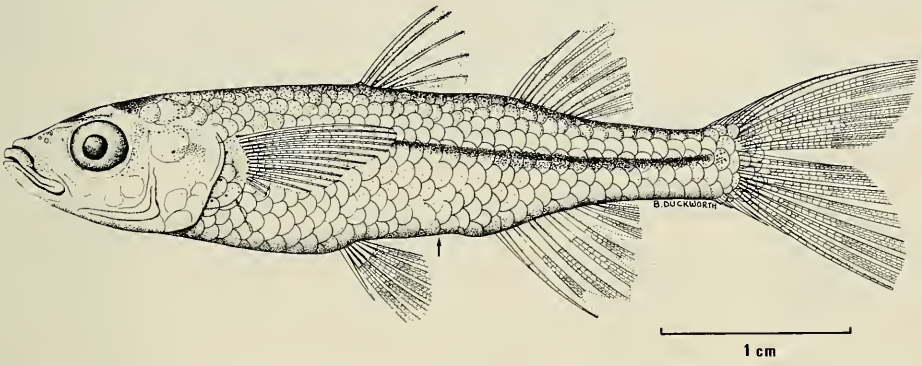

Fig. 4. Neotype of *Craterocephalus eyresii*; AMS I.28788-001, 40.0mm SL.

Atherinichthys eyresii Steindachner, 1884:1075, type locality: Coward and Strangways Springs (suggested by Jordan and Hubbs, 1919). Neotype designated herein.

Atherina interioris Zeitz, 1909:264 (*Nomen nudum*).

Craterocephalus eyresii: McCulloch and Waite, 1918:43; Jordan and Hubbs, 1919:45; McCulloch, 1929:109; Whitley, 1957:15; Munro, 1958:102; Scott, 1962:136: Scott, Glover and Southcott, 1974:153 (in part); Ivantsoff, 1978:245 (in part); Merrick and Schmida, 1984:145 (in part).

Craterocephalus fluviatilis: (not of McCulloch), Ivantsoff, Crowley and Allen 1987:174.

Designated Neotype: AMS I.28788-001 (40.0mm SL), collected by pole-seine at Strangways Springs, South Australia 29°09′S 136°34′E. Collected by W. Ivantsoff and L. E. L. M. Crowley, 12th June 1985. The designation of the neotype is strictly defined in Article 75 of International Code of Zoological Nomenclature (1985). The circumstance admitted (b) (I-III) and the qualifying conditions (d) (1-6) allow the designation in exceptional circumstances. As *C. eyresii* is now known to be a complex of four species, the designation of the neotype is considered to be essential.

Material examined: MQU WI-356 (20, 28.1-51.2mm SL), as for designated neotype; AMS I.13662 (10, 34.9-43.3mm SL) Strangways Springs. Additional material examined: MQU I-335 (4) Gregory Creek, 29°45′S 137°19′E; SAM F3545 (2) Johnsons No. 3 Bore 29°32′S 136°14′E; SAM F3958 (2) Lake Eyre 29°20′S 137°20′E; SAM F3986 (2) Peakes Bore, South Australia; SAM F4207 (2) Frome Creek, 29°19′S 137°58′E; SAM F4218 (2) Emu Creek 29°41′S 136°18′E; NMV A6159 (5) Lake Callabonna 29°40′S 140°01′E. Material examined for osteology: MQU IA 170 (4, 32.0-37.2mm SL) Strangways Springs.

Diagnosis: A freshwater species of the genus *Craterocephalus* most closely related to *C. centralis* but differing from that species in the following: snout to insertion of last ray of anal fin in SL 1.3 (1.2-1.3); transverse scale count 12.2 (11-14); predorsal scale count 16.3 (13-20); second dorsal fin rays 5. 8 (5-7); anal fin rays 6.5 (5-8); 5 or more scales above midlateral stripe, 6-8 scales below; in shape of nasal bone (see Fig. 2); in position of ventral wings of 5th ceratobranchial for attachment of *pharyngoclavicularis* muscle; in

shape of basihyal; in length of posterior portion of urohyal. Differing genetically from *C. centralis* at two loci (see Table 3).

TABLE 4

Morphometric proportions and meristic counts for the holotype and 30 paratypes of C. centralis

Size and Range In SL	Holotype 52.2mm SL	Paratypes 30 (34.3-64.0mm SL) Mean	Range	SD
Head	3.5	3.4	(3.2-3.7)	.15
H. max	4.0	4.3	(3.6-4.9)	.34
H. min	9.7	9.4	(8.6-10.8)	.56
Pec/anus	2.6	2.8	(2.4-3.0)	.13
Sn-OD1	2.0	2.0	(1.9-2.2)	.06
Sn-OD2	1.4	1.4	(1.4-1.5)	.04
Sn-OV	2.1	2.1	(1.9-2.2)	.07
Sn-TV	1.6	1.6	(1.5-1.7)	.04
Sn-OA	1.4	1.4	(1.4-1.5)	.03
Sn-TA	1.3	1.3		
In Head				
Eye	3.4	3.7	(3.4-4.1)	.17
Interorb.	3.0	2.9	(2.6-3.1)	.13
Postorb.	2.3	2.2	(2.0-2.3)	.07
In Eye				
Snout	1.0	0.9	(0.8-1.0)	.07
Premaxilla	0.9	0.9	(0.8-1.1)	.08
Lips	2.3	2.4	(2.0-2.7)	.19
Premax. process	1.1	1.3	(1.1-1.5)	.12
Meristics				
Scales				
Midlateral	32	31.9	(31-33)	.63
Transverse	10	10.5	(10-11)	.51
Predorsal	15	15	(13-16)	.98
Interdorsal	6	5.6	(4-7)	.68
Fin rays				
1st dorsal	6	5.8	(5-6)	.43
2nd dorsal	6	5.0	(4-6)	.61
Anal	6	5.9	(5-7)	.61
Pectoral	12	12.4	(11-13)	.67
Other				
Gill rakers	11	10.2	(9-11)	.57
Posit. anus	B2	B0.5	(B0-2)	.65
OD1-TV	F4	F4.6	(F3.5-6)	.66
OD1-TPec	B1.5	B1.4	(B0-4)	.90
OV-TPec	F1	F0.7	(B2-F2)	.72
Vertebrae	34	*32.7	(32-34)	.69

* 17 specimens.

Distinguished from all other species of *Craterocephalus* by the combination of: transverse scale count 12.2 (11-14); minimum body depth in SL 10.1 (8.3-12.0); unique in having the GPI-2 a allele but sharing GPI-2 b allele with *C. centralis*.

Description: Moderately robust fish, but seemingly varying in body depth with age. Mouth protractile; lips moderately fleshy. Gape restricted by fusion of lips from about half to two thirds way along premaxilla. Teeth in jaws small, other bones edentulous. Premaxilla short, not reaching vertical through anterior edge of orbit; dorsal process of premaxilla just reaching interorbital space. Gill rakers short, less than half diameter of pupil, occasionally tuberculate. Scales moderately small, strong, not always in even rows above or below midlateral stripe; circuli obvious on all scales. Scales on dorsum of head irregular, usually larger than body scales; opercles scaled.

TABLE 5

Morphometric proportions and meristic counts for the designated neotype and 29 specimens of C. eyresii *from Strangways Springs (suggested type locality by Jordan and Hubbs, 1919)*

Size and Range In SL	Neotype 40.0mm SL	Other specimens 29 (28.1-51.2mm SL) Mean	Range	SD
Head	3.3	3.4	(3.2-3.8)	.18
H. max	4.1	4.4	(3.8-5.3)	.30
H. min	9.7	10.1	(8.3-12.0)	.77
Pec/anus	2.9	2.8	(2.5-3.1)	.12
Sn-OD1	2.0	2.0	(1.9-2.1)	.07
Sn-OD2	1.4	1.4	(1.3-1.5)	.05
Sn-OV	2.1	2.1	(1.9-2.3)	.08
Sn-TV	1.6	1.6	(1.5-1.8)	.06
Sn-OA	1.5	1.4	(1.4-1.5)	.05
Sn-TA	1.3	1.3	(1.2-1.3)	.04
In Head				
Eye	3.8	3.7	(3.2-4.3)	.23
Interorb.	2.9	3.0	(2.7-3.3)	.16
Postorb.	2.3	2.2	(2.1-2.4)	.07
In Eye				
Snout	0.9	0.9	(0.7-1.1)	.09
Premaxilla	0.8	0.9	(0.7-1.1)	.09
Lips	2.6	2.6	(2.2-3.0)	.23
Premax. process	1.1	1.2	(0.9-1.5)	.12
Meristics				
Scales				
Midlateral	32	32.2	(30-34)	0.94
Transverse	12	12.2	(11-14)	0.89
Predorsal	16	16.3	(13-20)	1.64
Interdorsal	7	6.1	(4-7)	0.77
Fin rays				
1st dorsal	5	5.9	(4-7)	.83
2nd dorsal	5	5.8	(5-7)	.62
Anal	6	6.5	(5-8)	.71
Pectoral	13	12.5	(12-14)	.61
Other				
Gill rakers	11	11.1	(10-12)	0.68
Posit. anus	F0.5	B0.4	(F1-B1.5)	0.54
OD1-TV	F6	F5.4	(F3-8)	1.12
OD1-TPec	F1	B0.3	(B3-F2)	1.33
OV-TPec	F2	F1.4	(0-F3)	0.94
Vertebrae	33	*32.3	(31-34)	0.83

* 17 specimens.

Colour: Live specimens usually bright yellow with distinct silvery midlateral stripe. Opercles and abdomen iridescent green or silvery. Fins clear to yellowish. Preserved specimens from pale yellow to dark brown, depending on method and length of preservation. Eyes dark. Midlateral stripe either silvery or very dark, thin from origin of pectoral fin but becoming wider caudally and ending in series of small spots. Scales above midlateral stripe speckled with melanophores but reticular pattern not obvious; melanophores sparsely scattered below midlateral stripe. First and second dorsal, anal and pectoral fins with rows of melanophores along spines and rays; ventral fins clear.
Distribution: The species is found in the Lake Eyre Drainage. It has been collected from the Frome River and other rivers, streams and bores of South Australia. It appears that sufficient numbers survive dry seasons in refuge areas, dispersing and breeding rapidly in favourable conditions, only to die out again due to increasing salinity and evaporation of the water (see Ruello, 1976).
Comments: The integrity of the Lake Eyre Drainage is well discussed by Kotwicki (1989). From that study, it appears that the system is isolated from other drainage systems. These data are in agreement with the findings presented. *C. eyresii* is genetically isolated from the Finke River *C. centralis*, a river which even in the highest flood years does not reach Lake Eyre. The drainages to the south east are also not connected with the Lake Eyre Drainage System (Kotwicki, 1989). The separation of these drainages has allowed speciation to occur, resulting in close but distinct species, *C. fluviatilis* in the lower reaches of the Murray-Darling and *C. amniculus* in the higher reaches of the same drainage. A full biogegraphic review of the genus *Craterocephalus* is in preparation by the authors.

Craterocephalus fluviatilis McCulloch, 1913

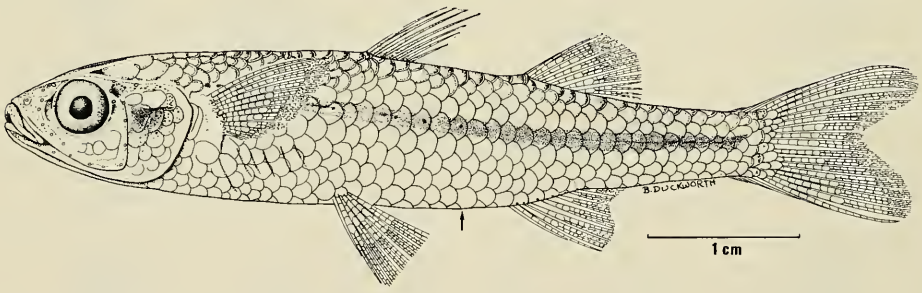

Fig. 5. Specimen of *Craterocephalus fluviatilis*; NMV A6161, 49.7mm SL.

Craterocephalus eyresii: Scott, Glover and Southcott 1974:153 (in part); Ivantsoff, 1978:245 (in part); Lake, 1978:41 (in part); Cadwallader and Backhouse, 1983:94 (in part); Merrick and Schmida, 1984:145 (in part); Ivantsoff, Crowley and Allen, 1987a:174.
Holotype Examined: AMS I.12456 (1, 47.2mm SL), North Yanko Creek, Narrandera, N.S.W.
Paratypes Examined: AMS I.12457 (2, 27.8-46.9mm SL), as for holotype. Remaining paratypes identified as *C. stercusmuscarum fulvus* (Ivantsoff *et al.*, 1987a).
Additional Material Examined: NMV A6157 (13) Lake Wandella, Vic., 35°45′S 143°53′E; NMV A6161 (14), Lake Hawthorn, Mildura, Vic., 34°12′S 142°06′E; MQU I.470 (5), Lake Hawthorn, Mildura, Vic. Material examined for osteology: MQU IA 73-4 (5) Lake Bonney, South Australia, 37°45′S 140°20′E; MQU IA 99 (2)

North Yanko, New South Wales, 34°52'S 146°18'E; MQU IA 100 (1) Murray River, N.S.W. 34°11'S 142°10'E.

Diagnosis: Moderately small fish most closely related to *Craterocephalus amniculus* and *C. eyresii* but differing from those species by a combination of the following: least body depth 11.6 (10.6-12.6) in SL; eye 3.4 (3.2-3.9); interorbital 3.0 (2.7-3.4) both in head; premaxillary process 1.4 (1.1-2.1) in eye. Midlateral scale count 33.1 (31-35); transverse scale count 10.9 (10-12); position of anus 1.2 (0-2) scales behind tips of ventral fins; in shape of basisphenoid; position of dorsal flange of 5th ceratobranchial. Differing: from *C. eyresii* in size and length of urohyal; in shape of medial process of pelvic girdle; from *C. amniculus* in shape of anterior process of maxilla (see Fig. 2). Differing genetically from *C. amniculus* at a single locus (CK); and from *C. eyresii* at 8 loci (ADA, CK, GAPD, GOT-1, GOT-2, GPI-1, GPI-2, IDH). For genetic differences and similarities between species, see Table 3.

Distinguished from all other members of the genus by a combination of the following: least body depth 11.6 (10.6-12.6); distance from origin of pectoral to anus 2.9 (2.6-3.2), both as proportion of SL; midlateral scale count 33.1 (31-35); transverse scale count 10.9 (10-12); predorsal scale count 14.3 (12-17); position of anus 1.2 (0-2) scales behind tips of ventral fins; origin of first dorsal 4.9 (3.5-6.5) scales in front of tips of ventral fins; single row of small, inward pointing teeth in upper and lower jaws; anterior arms of lateral ethmoids not fusing strongly to vomer as in other species.

Description: Small, moderately deep bodied freshwater fish, maximum size known 60.0mm SL. Most similar superficially to *Craterocephalus eyresii* as suggested by McCulloch (1913). Mouth small, protrusible, lips not thick, gape restricted by labial ligament from one third to half way along premaxilla. Teeth small, in single row and restricted to anterior part of both jaws. Premaxilla not reaching vertical through anterior margin of orbit; dorsal process of premaxilla not reaching interorbital space. Body scales small, thin, deciduous, almost circular, with circuli obvious and complete. Opercle, preopercle and dorsum of head with larger scales; scales on dorsum of head reaching to anterior margin of orbit. Gill rakers on lower ramus of 1st gill arch, short, tuberculate, last 2-3 slightly longer.

Colour: Live specimens varying from silver to dark golden dorsally with silver midlateral stripe; abdomen always pale with silvery iridescent sheen. Opercles, eye, bright silver; dorsum of head darker than snout. Fins clear to creamy. Preserved specimens pale creamy-yellow to light tan with midlateral band not prominent; melanophores forming light reticulate pattern on scales above midlateral band; scales below unmarked. Dorsum of head, snout and chin lightly peppered with melanophores; opercle with distinct triangular dark patch. Ventral contour of spots from end of anal fin to procurrent rays of caudal fin. Dorsals, anal and caudal fins with some melanophores outlining spines and rays; pectoral and ventral fins clear.

Distribution: According to McCulloch (1913), this species was reported to have a wide distribution in the upper Murray River Drainage (Yanko Creek, Murrumbidgee River as far east as Cooma). The occurrence of *C. fluviatilis* in northern tributaries of the Darling is doubtful, despite the reports of its presence in that river (McCulloch, 1913). Its present range appears to be restricted to Victoria, in some small lakes associated with the Murray River, where it is presently abundant. Recent collecting in the Murray River, south of Renmark and in Lake Bonney, South Australia, failed to yield any specimens, where previously, this species had been reported by Lloyd & Walker (1986) from five sites in the lower Murray, in 1976.

Comments: Although McCulloch was aware that specimens from the Namoi and Barwon Rivers had 7 rows of scales whilst of those from Narrandera, 3 had 10, two had 8 and one had 7 transverse scale rows, he described the populations as a single species.

Ivantsoff *et al.* (1987a) concluded that the type material of *C. fluviatilis*, McCulloch (1913) included two separate species which they then identified as *C. eyresii* and *C. stercus-muscarum fulvus*. Clearly, specimens from Narrandera and the Namoi and Barwon Junction with 7-8 transverse scale rows are *C. s. fulvus*; the three specimens with 10 scale rows are *C. fluviatilis*.

TABLE 6

Morphometric proportions and meristic counts for the holotype and 2 paratypes (McCulloch's 1913 material) and 33 other specimens of C. fluviatilis

Size and Range In SL	Holotype 47.6mm SL	2 paratypes and 33 other specimens 35 (24.1-58.4mm SL) Mean	Range	SD
Head	3.8	3.5	(3.1-4.0)	.20
H. max	4.8	4.6	(4.0-5.1)	.28
H. min	12.5	11.6	(10.6-12.6)	.61
Pec/anus	2.9	2.9	(2.6-3.2)	.16
Sn-OD1	2.0	2.1	(1.9-2.2)	.06
Sn-OD2	1.5	1.5	(1.4-1.5)	.03
Sn-OV	2.1	2.1	(2.0-2.3)	.10
Sn-TV	1.7	1.7	(1.6-1.8)	.06
Sn-OA	1.5	1.5	(1.4-1.6)	.04
Sn-TA	1.3	1.3	(1.1-1.3)	.04
In Head				
Eye	3.5	3.4	(3.2-3.9)	.19
Interorb.	2.8	3.0	(2.7-3.4)	.18
Postorb.	2.2	2.3	(2.2-2.4)	.08
In Eye				
Snout	1.1	1.0	(0.8-1.5)	.12
Premaxilla	1.2	1.0	(0.9-1.4)	.12
Lips	2.2	2.4	(2.1-2.7)	.14
Premax. process	1.4	1.4	(1.1-2.1)	.27
Meristics				
Scales				
Midlateral	32	33.1	(31-35)	0.84
Transverse	10	10.9	(10-12)	0.59
Predorsal	15	14.3	(12-17)	1.28
Interdorsal	6	5.7	(5-7)	0.60
Fin rays				
1st dorsal	6	5.8	(4-7)	.79
2nd dorsal	6	6.2	(5-8)	.71
Anal	7	7.2	(6-9)	.61
Pectoral	–	11.9	(11-13)	.52
Other				
Gill rakers	11	10.8	(10-12)	0.73
Posit. anus	0	B1.2	(0-B2)	0.78
OD1-TV	F6	F4.9	(F3.5-6.5)	0.90
OD1-TPec	B0.5	B1.6	(F1-B3.5)	1.04
OV-TPec	0	F0.2	(B2-F2)	1.06
Vertebrae	34	34	(33-35)	0.59

* 18 specimens.

McCulloch's (1913) records of distribution of *C. fluviatilis* must now be considered equivocal since other specimens which he attributed to this species may be either *C. s. fulvus* or *C. amniculus*.

Discussion

Morphological and osteological conservatism of atherinids appears to be commonplace. Fossil fish from the Miocene (Messinian) deposits in northern Italy are similar to the extant species *Atherina boyeri* (Gaudant, 1981: ". . . les athérines de Cherasco présentent beaucoup d'affinités avec *Atherina (Hepsetia) boyeri* Risso"). Pliocene atherinids from Arizona (Todd, 1976) are not very different from the extant species of *Colpichthys*. Harman *et al.* (1982) consider that there is probably only one species of *Pranesus* (=*Atherinomorus*, see Whitehead and Ivantsoff, 1983) in the Pacific and Indian Oceans, rather than a much larger number that has been described over the last hundred and fifty years. Bamber and Henderson (1985) on the basis of their meristic and morphological studies concluded "that *A. presbyter* and *A. boyeri* reflect the tails of a continuum. . . . It is best to consider the single species *Atherina boyeri* . . .". Whilst it might be considered that morphologically *C. centralis* and *C. amniculus* represent the "tails of a continuum" (*sensu* Bamber and Henderson, 1985), genetically this appears to be unlikely. The fixed gene differences between the populations from the Finke River (which rarely, if ever, flows into Lake Eyre — Kotwicki, 1989), and the populations from the Lake Eyre drainages, indicate that speciation has occurred.

Similarly, despite the presence of only a single fixed gene difference between *C. fluviatilis* and *C. amniculus*, the differences in morphology and osteology indicate that these also are separate species. Flooding in the Murray-Darling drainage system has been well documented (Russell, 1892) allowing interbreeding in the recent past; but a single fixed gene difference between populations in contiguous waterways indicates that interbreeding no longer occurs.

Speciation of freshwater fish in Australia is considered to be recent, according to some workers (Whitley, 1959; Allen and Cross, 1982; Merrick and Schmida, 1984). Extrapolating from the data of Echelle and Echelle (1984) it would appear that, whilst *C. eyresii*, *C. centralis* and *C. fluviatilis* are morphologically and osteologically conservative, these species are more genetically divergent than the morphologically conservative atherinid species flocks of *Chirostoma*, from the Mesa Central (Mexico), which Echelle and Echelle (1984) suggested date only from Plio/Pleistocene. Higher numbers of fixed gene differences (see Table 3) between populations from either side of the Flinders and Barrier Ranges, all previously considered to be *C. eyresii*, indicate that separation has been longer than is found between *Chirostoma* species.

Reasons for the absence of small native species from previously known areas (e.g. the hardyheads from the Hunter and Murrumbidgee Rivers) are a matter of conjecture. There is a paucity of information on whether small endemic fishes can compete successfully with introduced species; if they can withstand the changes due to agricultural and pastoral practices; or how they react to the use of fertilizers, weedicides and insecticides. Studies on the decline of endemic species exist (e.g. Cadwallader, 1978) but these tend to apply to larger and commercially important fish.

Extinction of Australian aquatic organisms has become a matter of concern in recent years. A report by Michaelis (1985) lists the threatened fishes of inland waters of Australia and includes some useful biological and geographical data on each. The proceedings of the conference on Australian threatened fishes (Harris, 1987) propose strategies to protect and conserve the native inland fishes.

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