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Freshwater fishes of the genus *Craterocephalus* (Artherinidae) from the southern drainages of Papua New Guinea and Irian Jaya with reference to *C.s. stercusmuscarum* from Australia.

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Abstract

A new species, *Craterocephalus pimatuae*, from tributaries of the Purari River (Papua New Guinea), is described. It differs from all other Papua New Guinea hardyheads osteologically (shape of premaxilla) as well as morphologically (midlateral and transverse scale counts, gill raker number in first lower gill arch). *C. nouhuysi, C. lacustris* and *C. randi* the other Papua New Guinea/Irian Jaya species are redescribed and distinguished on the basis of their external morphology, osteology and electrophoresis. *C. randi* is compared with the redescribed Australian species, *C. stercusmuscarum stercusmuscarum* since these species have often been confused in the past. *C. annator* on the basis of osteology, external morphology and electrophoresis is placed into the synonymy of *C. randi*. The relationships of *C. s. stercusmuscarum* with hardyheads from the southern drainages is examined with reference to the geologic history of the region.

Introduction

The systematics and relationships of the Papua New Guinea species of hardyheads have never been examined. The descriptions of each of the species by their authors were clear and unequivocal. However, Whitley in 1938, did compare specimens from Fly River with *C. nouhuysi* and *C. randi* and concluded that his new species, *Craterocephalus annator* was different on the basis of measurements, counts, colour and pattern. In subsequent years, *C. randi* and *C. stercusmuscarum* were confused because of similarity of colour and marking (e.g. Allen and Hoese, 1980). The status of *C. lacustris* has never been questioned. The new species, *Craterocephalus pimatuae,* appears to be most similar to *C. randi* and is a typical member of the *stercusmuscarum* group (Ivantsoff *et al.,* 1987a). The northern drainage of Papua New Guinea is almost devoid of hardyheads with *C. kailolae* (Ivantsoff *et al.,* 1987a) being the only exception.

The southern half of the island of Papua New Guinea/Irian Jaya is regarded as part of the Australian plate (Pigram and Davies, 1987) and its history appears to be inextricably associated with it. Papua New Guinea and Australia were connected in Tertiary and Quaternary during periods of low sea level. This resulted in common radiation of freshwater fishes with some 35 species belonging to 16 families (Munro, 1964). It could be assumed that radiation of hardyheads would have followed a similar pattern, with species in common to both sides of Torres Strait. Electrophoretic evidence, however,

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suggests that periodic geographic isolation was sufficient to initiate speciation but with none of the extant species of hardyheads from Papua New Guinea found living in Australia.

Material and Methods

Methods for morphological proportions and meristic counts follow those of Ivantsoff *et al.* (1987a). Specimens for osteology were stained following the methods of Taylor (1967). Cluster analysis (Figure 8a) of the species examined was made by using 57 osteological characters (represented by binary notation — 1/0 to indicate presence or absence; large or small etc.). The procedure was based on an algorithm modified from Sneath and Sokal (1973) by Dr. George McKay of Macquarie University. Electrophoresis, following the methods of Richardson *et al.* (1986), was used to assess the genetic differences of all species except *C. pimatuae* of which only 5 specimens are known. Six specimens from each of the populations of *C. randi* and *C. s. stercusmuscarum* were assayed, with 10 specimens of each of the other species *(C. lacustris* and *C. nouhuysi)* being used. Nineteen enzymes (21 loci) were examined. Genetic distances were calculated using Rogers' (1972) R formula where R = Distance. The R values were used in a cluster analysis programme (Figure 8b) based on an algorithm of Sneath and Sokal (1973) modified by Dr. George McKay of Macquarie University.

Areas of collection for specimens used in electrophoresis:

C. lacustris: Lake Kutubu (PNG).

C. nouhuysi: Tabubil, creek south of Ok Tedi on Kiunga Road; Sawmill Creek, Ok Tedi; South Sawmill Creek, about 10 km along Kiunga Road, all in PNG.

C. randi: Samongas, 5 km from Kiunga; Ok Mac, small creek 1 km south Kiunga; Rupi Creek, Kiunga (tributaries of Fly River near d'Albertis Junction, type locality of *C. annator* Whitley (1938). Kubuna River, Kubuna (type locality), all in PNG.

C. s. stercusmuscarum: Edith River, Northern Territory; Roper River, Mataranka Thermal Spring Road, 6 km from Stuart Highway, N.T.; Mulgrave River, Qld; Rollingstone Creek, 51 km north of Townsville; River Dee, 1/2 km west of Dululu, Qld, all in Australia.

Enzymes assayed: ADA; ADH; AK; ALD; CK; FDP; FUM; GAPD; GLDH; αGPD; GPI (2 loci); GOT (2 loci); IDH; LDH; MDH; ME; MPI; PGM; XDH. (for methods and stains, see Richardson *et al.*, 1986).

Material from the following institutions was examined: American Museum of Natural History, New York (AMNH); The Australian Museum, Sydney (AMS); British Museum of Natural History, London (BMNH); Commonwealth Scientific and Industrial Research Organization, Hobart, Tasmania (CSIRO); Kanudi Fisheries Research Station, Kanudi, Papua New Guinea (KFRS); Macquarie University, North Ryde (MQU); Late Dr. D.E. Rosen, personal collection (DR); Western Australian Museum, Perth (WAM); Zoologisch Museum, Amsterdam (ZMA).

Key to the Hardyheads of the Southern Drainages of Papua New Guinea

1a. Gill rakers in first lower gill arch never less than 10 (10-13); narrow interorbital, 3.2 (2.9-3.6) in head for this species. Lower lip protruding in adults. Anal plate short; interdorsal pterygiophores lacking well developed ventral processes. PGM^a allele present .... *C. lacustris*

1b. Gill rakers in first lower gill arch 6-11, rarely more than 10, interorbital 2.4-3.2 in head, for all species following. Lower lip never protrusive. Anal plate elongate; interdorsal pterygiophores with well developed ventral processes. PGM^a allele never present. 2

2a. Dorsal process of premaxilla in eye never more than 1.6; midlateral scale count never less than 35; pectoral rays 12-15; ventral wings of 5th ceratobranchial always lateral; basihyal cartilage either as long as basihyal bone or almost rudimentary 3

2b. Dorsal process of premaxilla in eye 1.6 (1.2-2.0); midlateral scale count 34.4 (32-37), usually less than 35; pectoral rays 11-13; ventral wings of 5th ceratobranchial medial; basihyal cartilage about half length of basihyal bone .... *C. randi*

3a. Transverse scale count 8.1 (8-8.5). Dorsal process of premaxilla robust, 1.5 (1.4-1.6) in eye; snout in eye 1.1 (1.1-1.3). 5th ceratobranchials incompletely fused; basihyal bone and cartilage about equal in length; sensory canals never enclosed ... *C. pimatuae*

3b. Transverse scale count always 7. Dorsal process of premaxilla long and slender, 1.1 (1.1-1.3) in eye; snout in eye 1.0 (0.9-1.1). 5th ceratobranchials completely fused; basihyal bone long; basihyal cartilage rudimentary; sensory canals of nasal and post-temporal bones enclosed or nearly so .... *C. nouhuysi*

Systematics

Craterocephalus pimatuae sp. nov.

Figure 1

Holotype

WAM P26971-004 25.4 mm SL. Small seine, Junction of Pima and Tua Rivers, 6°25'S 144°49.5'E. Papua New Guinea. Collected by G.R. Allen, September 1980.

Paratypes

WAM P26971-004 (3), data as for holotype; WAM P26971-004, prepared alizarin specimen, data as for holotype. Size range 24-35 mm SL.

Diagnosis

A freshwater species of hardyhead belonging to *C. stercusmuscarum* group (see Ivantsoff *et al.*, 1987a) and superficially similar to all Papua New Guinea members of this genus. Distinguished from those species by its robust dorsal process of premaxilla

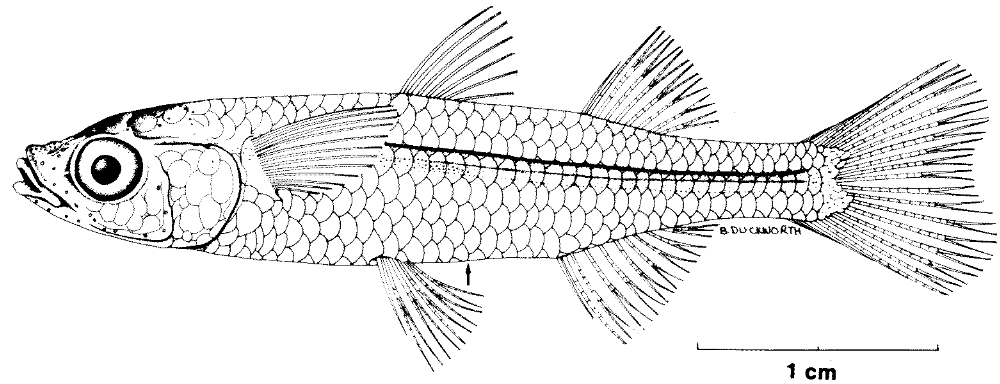


Figure 1. Holotype of *Craterocephalus pimatuae* WAM P.26971-004, 25.4 mm SL., Junction of Pima and Tua Rivers, Papua New Guinea.

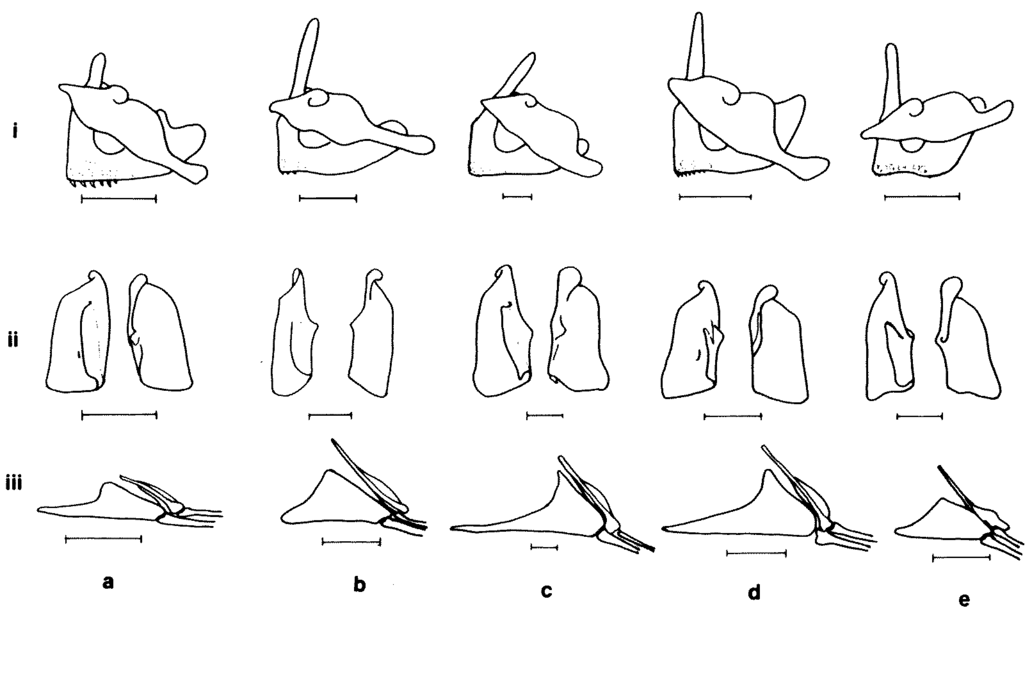


Figure 2. i) Premaxilla and maxilla, ii) dorsal and ventral aspects of nasal bone and iii) anal plate of: a. *Craterocephalus pimatuae;* b. *C. lacustris;* c. *C. nouhuysi;* d. *C. randi;* e. *C. s. stercusmuscarum.* Bar represents 1 mm.

Table 1. Morphometrics and meristics for the holotype and four paratypes of *Craterocephalus pimatuae* also morphometrics and meristics for three other species of hardyheads from the southern drainages of Papua New Guinea. Data expressed as mean, range and standard deviation.

Character Species						
Morphometric proportions		*C. pimatuae*	*C. nouhuysi*	*C. lacustris*	*C. randi*	*C. s. stercusmuscarum*
Number of specimens	Holotype	4 paratypes	30	42	25	44
In SL						
Head	3.4	3.4 (3.3-3.5) 0.10	3.7 (3.4-4.2) 0.16	3.4 (3.2-3.8) 0.15	3.7 (3.4-4.1) 0.60	3.6 (3.2-3.9) 0.18
Pec Length	4.9	5.3 (4.9-5.7) 0.28	5.4 (4.8-6.1) 0.35	6.4 (5.1-9.4) 0.62	6.2 (5.3-7.3) 0.61	6.3 (5.2-9.2) 0.86
H. max	4.8	4.8 (4.7-4.8) 0.06	4.8 (4.1-5.7) 0.59	4.6 (3.5-6.0) 0.44	5.1 (4.5-5.7) 0.27	5.1 (3.5-5.7) 0.38
H. min	10.8	10.6 (10.4-10.9) 0.22	9.7 (7.6-13.0) 1.65	11.7 (10.6-12.9) 0.68	10.8 (9.8-12.5) 0.56	10.9 (9.1-12.6) 0.88
Pec/anus	3.2	3.2 (3.1-3.2) 0.06	3.3 (2.9-3.4) 0.14	3.4 (3.0-4.0) 0.22	3.5 (3.0-3.8) 0.19	3.4 (2.9-3.7) 0.16
SnOD1	2.0	2.0 -	2.1 (2.0-2.1) 0.05	2.1 (2.0-2.2) 0.06	2.1 (2.0-2.2) 0.05	2.0 (1.8-2.2) 0.07
SnOD2	1.4	1.4 -	1.4 -	1.4 (1.4-1.5) 0.04	1.4 (1.3-1.5) 0.05	1.4 (1.3-1.5) 0.04
SnOV	2.1	2.2 (2.1-2.2) 0.04	2.3 (2.2-2.5) 0.08	2.3 (2.2-2.4) 0.06	2.3 (2.2-2.6) 0.08	2.3 (2.1-2.4) 0.09
SnTV	1.6	1.6 -	1.7 (1.6-1.8) 0.06	1.7 (1.6-1.8) 0.05	1.7 (1.6-1.8) 0.05	1.7 (1.6-1.8) 0.06
SnOA	1.5	1.5 -	1.4 (1.4-1.5) 0.04	1.5 (1.4-1.6) 0.04	1.4 (1.4-1.6) 0.04	1.4 (1.4-1.5) 0.04
SnTA	1.2	1.3 (1.2-1.3) 0.06	1.2 (1.2-1.3) 0.09	1.2 (1.0-1.5) 0.07	1.2 (1.1-1.3) 0.05	1.2 (1.0-1.3) 0.05
In Head						
Eye	3.1	3.3 (3.1-3.5) 0.17	3.5 (3.0-3.8) 0.15	3.4 (2.9-5.0) 0.53	3.3 (2.7-3.9) 0.10	3.1 (2.6-3.7) 0.24
Interorb	2.9	2.8 (2.8-2.9) 0.04	2.8 (2.4-3.2) 0.24	3.2 (2.9-3.6) 0.22	2.7 (2.5-3.1) 0.70	2.9 (2.2-3.3) 0.24
Postorb	2.4	2.4 (2.3-2.4) 0.05	2.4 (2.2-2.7) 0.11	2.3 (2.0-2.7) 0.17	2.3 (2.0-2.5) 0.13	2.5 (2.1-2.8) 0.17
In Eye						
Sn	1.2	1.1 (1.1-1.2) 0.02	1.0 (0.9-1.1) 0.07	1.2 (0.7-1.5) 0.23	1.2 (0.9-1.5) 0.18	1.3 (1.0-1.7) 0.18
Pmax	1.1	1.1 (1.0-1.1) 0.06	1.1 (0.9-1.3) 0.12	1.1 (0.7-1.4) 0.17	1.3 (1.0-1.5) 0.11	1.4 (1.1-1.7) 0.17
PmaxP	1.6	1.5 (1.4-1.6) 0.10	1.1 (1.0-1.3) 0.09	1.3 (0.8-1.9) 0.26	1.5 (1.0-2.1) 0.29	1.6 (1.3-2.0) 0.21
Lips/Pmax	2.3	2.5 (2.2-2.8) 0.21	2.0 (1.7-2.2) 0.13	2.0 (1.5-2.4) 0.20	1.9 (1.4-2.4) 0.20	1.8 (1.5-2.2) 0.16
Meristic Counts						
Midlateral	37	36.0 (35-37) 0.82	36.9 (36-38) 0.83	34.3 (32-38) 1.31	34.4 (32-37) 1.20	32.9 (32-34) 0.76
Transverse	8	8.1 (8-8.5) 0.25	7.0 -	7.3 (6-8) 0.60	7.3 (6.5-8) 0.60	7.0 (6.5-7) 0.11
Interdorsal	7	7.5 (7-8) 0.58	8.0 (7-9) 0.69	7.4 (6-9) 0.72	7.8 (6-9) 1.00	7.2 (6-9) 0.59
Predorsal	16	16.4 (16-19) 1.00	15.8 (14-18) 1.12	13.8 (11-18) 1.96	15.4 (11-19) 2.08	16.1 (12-18) 1.40
Vertebrae	36	37.2 (36-38) 0.58	38.0 (37-38) 0.91	36.5 (35-39) 1.04	36.0 (34-39) 1.41	36.7 (35-38) 1.22
D1	5	6.5 (5-7) 0.58	6.9 (5-8) 0.76	7.1 (5-8) 0.77	6.6 (5-8) 0.76	6.6 (5-8) 0.62
D2	7	7.3 (7-8) 0.50	7.3 (6-8) 0.53	7.2 (6-8) 0.54	7.1 (6-8) 0.81	6.1 (4-7) 0.50
A	9	8.5 (8-9) 0.58	8.8 (7-10) 0.73	8.1 (7-9) 0.57	7.8 (6-10) 0.88	7.1 (6-8) 0.53
Pec	13	14.3 (13-15) 0.96	13.5 (12-15) 0.68	12.6 (11-15) 1.69	11.9 (11-13) 0.78	11.7 (10-13) 0.66
Gr	9	9.3 (9-10) 0.50	7.9 (6-10) 1.07	11.7 (10-13) 0.77	8.6 (7-11) 1.23	10.3 (9-12) 0.81
Posit A	F3	F2.0 (F1.5-3) 0.41	F2.0 (F1-2.5) 0.60	F1.0 (F0-2) 0.53	F1.2 (F0-2) 0.36	F1.2 (F0-2) 0.61
OD1-TV	F6	F5.8 (F5-6) 0.50	F4.1 (F3-6) 0.92	F5.2 (F3-7.5) 1.01	F4.5 (3-6) 0.95	F4.5 (F3-6) 0.56
OD1-Tpec	B0	B0.5 (B0.5-1.0) 0.41	B2.2 (B0-4) 1.00	B0.8 (F1-B3) 0.99	B1.6 (F0.5-B4) 1.18	B2.5 (B0-4) 1.00
Ov-Tpec	F0	F1.0 (F0-1.5) 0.29	F1.6 (F0-3) 0.86	F1.5 (F0-3) 0.70	F1.3 (B1-F4) 1.07	F0.7 (B1-F2) 0.67

and by basihyal bone and cartilage being about equal in length, with basibranchial bone longer than cartilage in all other species. Nasal bone rounded anteriorly, lateral margin not straight (see Figure 2). Also distinguished from *C. nouhuysi* and *C. lacustris* by gill raker count and by length of dorsal process of premaxilla.

No fresh material for genetic studies was available.

Description

Slender freshwater species of the genus, most closely related to *C. stercusmuscarum* species, but lacking completely fused 5th ceratobranchials common to other members of the group. Mouth small with gape restricted by labial ligament to about two thirds of length of premaxilla. Lips moderately thin; lower lip not protrusive as in *C. lacustris.* Premaxilla not reaching anterior margin of orbit; dorsal process of premaxilla robust, with very long medial symphysis; dorsal process barely reaching interorbital space. Teeth large, in two distinct rows in upper and lower jaws. Other bones in mouth edentulous. Wings of partially fused 5th ceratobranchial lateral, high and rounded anteriorly. Gill rakers about half diameter of eye, lacking spinules. Scales dorso-ventrally elongated, in even rows along sides of body.

For morphometric and meristic differences between species, see Table 1.

Colour:

Live specimens olive to light brown above midlateral stripe, whitish below; silver midlateral stripe from upper pectoral to hypural joint. Fins clear. Preserved specimens pale cream colour with faint brownish reticulate pattern on uppermost scales along sides of body; body below midlateral stripe pale cream to whitish with no markings; midlateral stripe brownish, solid above, remainder of stripe below formed by light speckling anteriorly, to about vertical through tips of ventral fins, then solid throughout to hypural joint. Midlateral stripe not extending to head. All fins pale with no markings. Eye silvery with dark blotch along top; dorsum of head and interorbital speckled brownish; snout speckled with two distinct dark blotches on either side of median line; single distinct dark blotch on upper lip; rest of upper and lower lips slightly speckled.

Etymology

pimatuae, refers to the locality from which the new species was collected, i.e. the junction of Pima and Tua Rivers.

Distribution

Known only from the Pima and Tua Rivers in Papua New Guinea, located directly south of Mount Hagen. These rivers are tributaries of the Purari River in the central Highlands of Papua New Guinea. The fish were collected in deep pools in quiet backwaters near the junction of these tributaries. Presently, the area is inaccessible except by helicopter.

Craterocephalus lacustris Trewavas
Figure 3

Craterocephalus lacustris Trewavas, 1940: 286, type locality: Lake Kutubu, Papua New Guinea, holotype in BMNH (1940: 3.11.7-8); paratype in BMNH (1940.3.11.7-8); Schultz, 1948:20; Munro, 1958:155, 1964:166, 1967:174; Ivantsoff, 1978: 272.

Material examined

BMNH 1940.3.11.7-8, Lake Kutubu, Papua New Guinea, holotype and paratype of *Craterocephalus lacustris;* AMS IA. 8087 (1); CSIRO C3174 (1); MQU 70-40c (156). 42 specimens measured and counted, size range 25-115 mm SL. Other material examined but not used for measurements and counts: WAM P.28159-002 (65); WAM P.28258-002 (72). Material examined for osteology WAM P28159-002 (1); MQU W170-40 (1); MQU W170-41(2), all of the above collected in Lake Kutubu.

Diagnosis

Lacustrine species of genus *Craterocephalus,* most closely related to other Papua New Guinea members of *C. stercusmuscarum* group. Distinguished from those species by possessing highest gill raker count (10-13 in lower gill arch), narrow interorbital space (2.9-3.6 in head) and from all other species of *Craterocephalus* by protruding lower lip, especially in adults. Interdorsal pterygiophores lacking ventral process. Anal plate not elongate. Anterior of nasal bone not rounded; lateral margin of nasal straight (see Figure 2). Uniquely different from all other Papua New Guinea species in possessing a PGM^a allele (see Table 2).

Description

Robust fish, deep bodied in large adults, smaller fish seemingly more slender (Figure 3a,b) but not supported by measurements (Figure 4). Lips very fleshy and fusing about half way along premaxilla. In adults lower lip very protrusive, about twice thickness of upper. Premaxilla robuts, its dorsal process reaching into interorbital space. Distinct secondary lateral process also present. Teeth in two rows in upper and lower jaws not large. Basihyal bone long; basihyal cartilage small. Urohyal with narrow shallow ventral pocket. 5th ceratobranchial fused; occasionally only partially fused in specimens <30 mm SL; ventral wings for attachment of *pharyngoclavicularis* muscle lateral, not markedly high or rounded anteriorly. Gill rakers moderately long with small spinules. Scales not thin; dorsoventrally elongated, in even rows along sides of body. Preopercles and opercles scaled.

For morphometric and meristic differences between species see Table 1; for genetic differences see Tables 2 and 3.

Colour

Live specimens silvery golden colour; midlateral band dark and iridescent; opercles and abdomen silvery; dorsum of head darker than lower part of head. Some spots apparent along sides of body above and below midlateral band. Preserved specimens pale creamy anteriorly to light tan posteriorly. Reticulate marking of scales not apparent, with light speckling of melanophores present on scales above midlateral band. Midlateral band, dark, of even width from upper origin of pectoral fin to caudal peduncle. Dorsum of head with very dark, H shaped marking. Double row of spots apparent below midlateral band and single row above. Abdomen without melanophores. Snout very dark to above upper lip. Lips and chin unpigmented. Eye dark.

Table 2. Table of genetic frequencies for Papua New Guinea *Craterocephalus* together with *C. s. stercusauscarus*. Only loci with different alleles are shown.

Locus/allele		Species			
		C. lacustris	*C. nouhuysi*	*C. randi*	*C. s. stercusauscarus*
ADA	b	0.25	0.75	—	—
	c	0.75	0.25	0.61	0.75
	d	—	—	0.39	0.25
CK	a	—	1.00	0.90	0.25
	b	0.75	—	0.10	0.75
	c	0.25	—	—	—
FUM	b	0.18	—	—	1.00
	c	0.82	1.00	1.00	—
GAPD	a	1.00	1.00	1.00	0.88
	b	—	—	—	0.12
αGPD	a	0.30	0.75	—	0.25
	b	0.70	0.25	1.00	0.75
LDH	a	0.73	0.50	1.00	1.00
	c	0.27	0.50	—	—
MDH	b	0.30	0.50	0.39	0.55
	c	0.70	0.50	0.61	0.45
GPI-1	a	—	1.00	—	—
	b	—	—	—	—
	c	—	—	0.39	1.00
	d	1.00	—	0.61	—
GPI-2	c	—	0.62	0.36	0.21
	d	1.00	0.38	0.64	0.79
IDH	b	1.00	0.87	1.00	1.00
	c	—	0.13	—	—
ME	a	—	—	0.36	1.00
	b	1.00	1.00	0.64	—
MPI	a	—	—	—	0.25
	b	0.90	1.00	1.00	0.75
	c	0.10	—	—	—
PGM	a	0.50	—	—	—
	b	0.50	1.00	1.00	1.00
XDH	b	1.00	0.75	0.75	0.75
	c	—	0.25	0.25	0.25

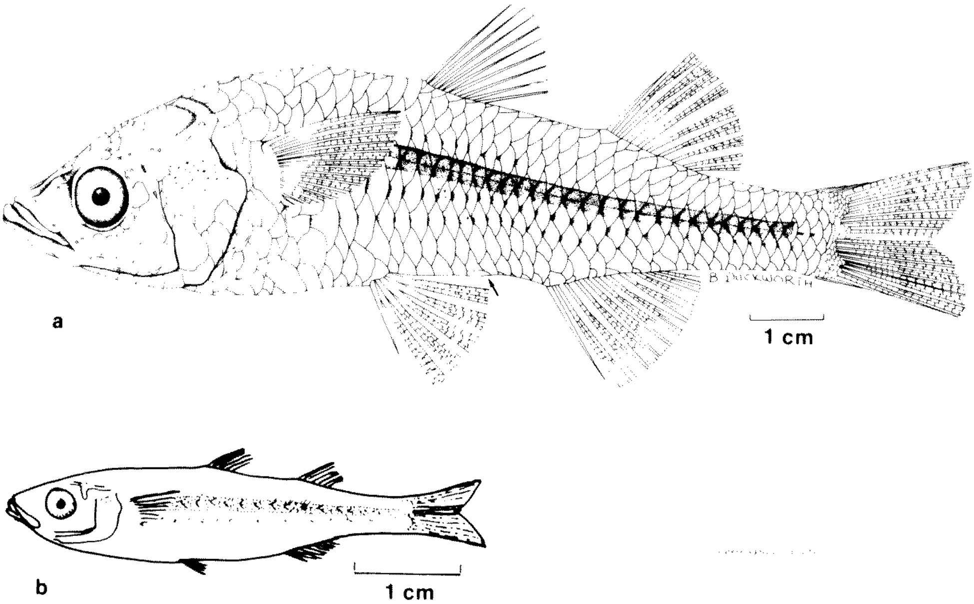


Figure 3a, b *Craterocephalus lacustris*, Lake Kutubu, Papua New Guinea.

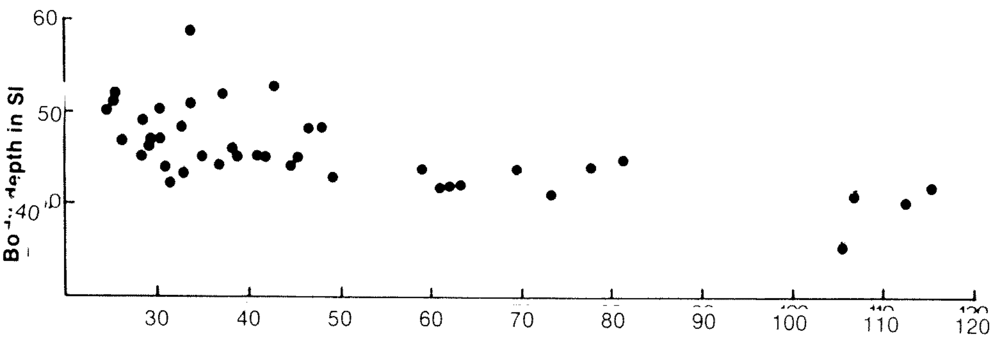


Figure 4. Graph to show relationship between standard length (SL) and maximum body depth as a proportion of SL of *C. lacustris*.

Distribution

All specimens of *C. lacustris* examined were collected in Lake Kutubu. Allen & Hoese (1986) in their description of Lake Kutubu, point out that the lake is drained by the Soro, Hegigio and ultimately the Kikori Rivers, to the Gulf of Papua. Presumably the species may occur in those rivers also. Kailola (1975) reported that this species was also present in Boboa (Lake Murray) and Balimo Lagoon. However, specimens available from that region to the present authors were not *C. lacustris*.

Table 3. Matrix table of R (Rogers, 1972) values for *Craterocephalus* species from Papua New Guinea (calculated from gene frequencies).

	C. lacustris	*C. nouhuysi*	*C. randi*	*C. s. stercusmuscarum*
C. lacustris	0.00	—	—	—
C. nouhuysi	0.25	0.00	—	—
C. randi	0.17	0.18	0.00	—
C. s. stercusmuscarum	0.25	0.30	0.19	0.00

Craterocephalus nouhuysi (Weber)
Figure 5

Atherinichthys nouhuysi Weber, 1910: 229, type locality: Bibis (van der Sande) River, West Irian, lectotype in ZMA (103.175). Paralectotypes in ZMA unless otherwise indicated: Alkmaar, Lorentz River, West Irian, paralectotypes ZMA 103.176 (12) (two specimens exchanged, now AMNH 9577, AMS I.17319-001 [alizarin]); paralectotype, ZMA 103.177 (1), side branch to the right of Lorentz River; paralectotypes ZMA 103.178 (8), rivulet near Alkmaar, Lorentz River; paralectotype ZMA 103.179 (1), Lorentz River, a little north of Alkmaar; paralectotype ZMA 103.180 (1), Beaufort River, 225 km upstream from Bibis River; paralectotype ZMA 103.181 (9), Lorentz River, south west Irian; Weber, 1913a:555; Regan 1914:276.

Craterocephalus nouhuysi: — Jordan and Hubbs, 1919:46; Weber and de Beaufort, 1922:278; Schultz, 1948:20; Munro, 1958:155; Hoedeman, 1960:212; Munro, 1967:172; Nijssen *et al.*, 1982:72.

Remarks

Type designation

Hoedeman (1960), in his list of type specimens in ZMA, designated a holotype and paratypes of *Atherinichthys nouhuysi* Weber. Nijssen *et al.* (1982) correctly redesignated the same specimens as lectotype and paralectotypes. The specimens are listed in the synonymy above.

Material examined

Paralectotypes ZMA 103.176 (5) Alkmaar, Lorentz River, West Irian; ZMA 103.177 (1); ZMA 103.178 (4); ZMA 103.179 (2); ZMA 103.180 (1); ZMA 103.181 (2); WAM P 27806-005 (15), Tributary of Ok Tedi River, 15 km S of Tabubil, Papua New Guinea. Material examined for osteology: paralectotype ZMA 103.176 (1); WAM P.27806 (3). Size range 62.1-95.4 mm SL.

Diagnosis

A freshwater species of *Craterocephalus stercusmuscarum* group most closely related to *C. randi.* Differing from all Papua New Guinea species in having longest basihyal

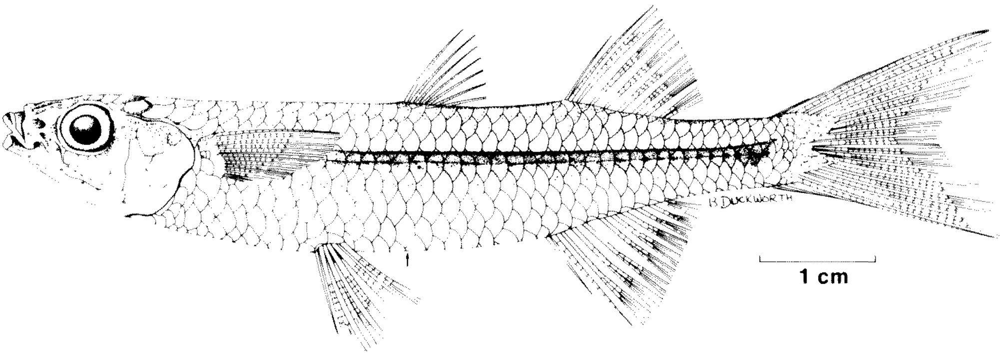


Figure 5. *Craterocephalus nouhuysi*, Tabubil, Papua New Guinea.

bone and rudimentary basihyal cartilage. Sensory canals of nasal and post temporal bones almost completely enclosed. Also differing in shape of nasal bone (see Figure 2). Transverse scale count always 7. Unique amongst the southern drainage species in having $GPI\text{-}1^{a}$ allele. Differing genetically from *C. randi* in frequencies at several loci *(ADA, α GPD, LDH).*

For genetic comparison with other species, see Tables 2 and 3.

Description

One of the two largest of all members of the genus and superficially resembling *C. randi.* Mouth small with gape restricted by labial ligament. Dorsal process of premaxilla long, slender, reaching well into interorbital space. Teeth in jaws small, barely visible. Gill rakers short, stumpy but slightly longer in angle of arch. Body scales large, dorsoventrally elongated with circuli apparent posteriorly. Dorsum of head with large, almost rectangular scales. Preopercle and opercle scaled.

For morphometrics and meristics, see Table 1.

Colour

Live specimens yellowish with midlateral stripe silvery above and dark below, extending from snout to hypural joint with midlateral band running from snout through eye to hypural joint, but not ending in crescent. No spots along sides of body; body above and below midlateral band uniform in colour. Dorsum of head, snout and upper lip dusky; opercles and eye silvery; preopercle sometimes iridescent. Paired fins clear, caudal fin golden. Preserved specimens cream to yellowish with dark midlateral stripe, paler through opercle, eye and snout. Melanophores on scales above midlateral stripe not forming reticulate pattern; no pigmentation below midlateral stripe. Paired fins and caudal fin with faint markings along rays. Eye dark to silvery. Dorsum of head, snout and upper lip dusky with lower lip cream to whitish.

Distribution

Known originally from Lorentz River in West Irian, now also from the upper tributaries of Fly River (Tedi River near Tabubil). The specimens from the latter are similar to the paralectotype material from the type locality, with only minor differences in some of the body proportions. Although the two river systems are quite separate, the coastal lowlands may allow dispersal. It is therefore possible that this species may also occur in rivers between. Further collecting is necessary to determine whether the present distribution is indeed disjunct.

Comments

The unique sharing of the *GPI-1*^{a} allele together with an osteological similarity in the sensory canals between *C. kailolae* and *C. nouhuysi* is difficult to explain. The former belongs to the *eyresii* group, the latter to *stercusmuscarum*. *C. kailolae* occurs in the northern drainage of Papua New Guinea, with all the other members of the species group occurring in Australia. Similarly, the distribution of several species of *Pseudomugil* shows that they too are disjunct (Saeed, Ivantsoff and Allen, 1989).

Craterocephalus randi Nichols and Raven
Figure 6

Craterocephalus randi Nichols and Raven, 1934:3, type locality: Kubuna (Kubuna river), British Papua; holotype in AMNH (12477), paratypes (4), in AMNH (12525); Whitley, 1938:226; Schultz, 1948:20; Munro, 1958:155, 1967: 174.

Craterocephalus annator Whitley, 1938:226, type locality, Fly River, Papua, about 50 km above d'Albertis Junction; holotype in AMS (IA.7228), paratypes (7), in AMS (IA.7228); Schultz, 1948:20; Munro, 1958:155, 1967:174.

Material examined

Holotype AMNH 12477, Kubuna (Kubuna River), British Papua. Partypes AMNH 12525 (4), as for holotype; Holotype of *C. annator* AMS IA.7228 Fly River, Papua, 30 miles above d'Albertis Junction. Paratypes *C. annator* AMS IA.7228(7), as for holotype; AMS IB.7054-7059 (9) Lake Murray (Mawa) New Guinea; MQUWI 70-41a (16) Weam (Torassi and Bensbach Rivers); KFRS FO.4009 (9) Nomad, Papua

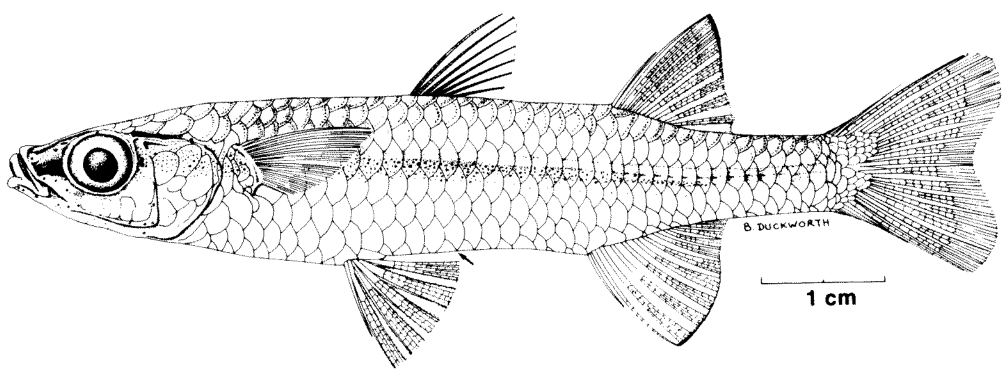


Figure 6. *Craterocephalus randi*, Kubuna, Papua New Guinea.

New Guinea; KFRS FO.4012 (7) Sinamre; downstream from Rumginae; MQUWI 70-41b (2) Balimo, north of Fly River. 25 specimens examined, size range 36.2-71.9 mm SL. Other material examined but not used for measurements and counts: WAM P.28139-005 (1), 10 km north of Kiunga; WAM P.28140-003 (6), 2 km north of Kiunga; WAM P.28141-004 (5) Elevelak, 17 km east of Kiunga; WAM P.28147-004 (8), Fly River, near Dora Village, in the vicinity of Kiunga; WAM P.28149-005 (3), 5 km west of Oboe near Kaviananga, south of Kiunga. Material used for osteology: MQU WI70-41a (3), Fly River, Papua New Guinea.

Diagnosis

Freshwater species belonging to *C. stercusmuscarum* group, most closely resembling *C. stercusmuscarum stercusmuscarum* on counts and measurements and *C. lacustris* on electrophoretic data. Uniquely distinct from other Papua New Guinea species in shape of nasal bone (see Figure 2) and with lateral ramus of premaxilla more highly elevated than in other species; basihyal bone long; cartilage about half length of bone. Ventral wings of fused 5th ceratobranchial medial position and lateral in all others. Sharing only with *C. nouhuysi* and *C. pimatuae* elongate anal plate and interdorsal pterygiophores with well developed ventral processes. Differing from other Papua New Guinea species by gene frequencies at several loci *(ADA, CK, αGPD, GPI-1, GPI-2).*

For genetic differences see Tables 2 and 3. Only distinguishable by combination of meristic and morphometric characters.

Description

Slender bodied freshwater fish, externally most closely resembling *C. s. stercusmuscarum.* Mouth small, gape restricted by labial ligament. Dorsal process of premaxilla moderately short, not reaching into interorbital space. Teeth moderately long, in two rows in upper and lower jaws. Gill rakers very short, pointed and very sparse. Scales with circuli apparent in smaller specimens. Preopercle and opercles scaled. Dorsum of head with large scales.

For meristics and morphometrics see Table 1.

Colour

Live specimens closely resembling *C. s. stercusmuscarum,* often with deep golden abdomen, jet black spots along sides of body and silvery sheen. Eye usually dark, opercles silvery-blue; midlateral band obvious and unbroken from snout, through eye and pectoral fin to caudal peduncle, ending in upward pointing crescent. Preserved specimens similar to *C. s. stercusmuscarum,* often with intense spotting along sides of body frequently fading with time when preserved. Reticulate pattern on scales above midlateral band. Midlateral band as in live specimens. Fins dusky with melanophores apparent on rays; tips of caudal dusky; base of all fins dark. Opercle silvery below midlateral band and cream above. Dorsum of head and snout dark; lips and chin peppered with melanophores.

Distribution

Known from the Fly, Bensbach, Kubuna and Strickland Rivers, from Lake Murray (also see Kailola, 1975). This species appears to be fairly common in the lower reaches of southern rivers in Papua New Guinea. Further collecting may prove its range to be more extensive as there are areas of the country still not readily accessible.

Comments

Craterocephalus randi has been often confused with *C. stercusmuscarum* (e.g. Allen and Hoese, 1980; Taylor, 1964). The colour pattern of both species is very similar but varies in intensity from locality to locality, within a locality and from time to time. Genetically, *C. randi* is distinct from *C. stercusmuscarum* at *FUM* (fixed gene difference) with alternate alleles at *CK*, polymorphic versus monomorphic at *GPI-1*. Genetically *C. randi* appears to be most closely allied to *C. lacustris*, differing at *PGM* locus. The status of *C. annator* had been questioned by Ivantsoff in 1978 although the Fly River population is usually pale in colour and without marking, unlike *C. randi* from other localities. Present electrophoretic study shows that the placement of *C. annator* into the synonymy of *C. randi* is correct as no differences could be found between specimens from Kubuna (the type locality for *C. randi*) and those from Fly River streams and tributaries (the type locality of *C. annator*).

Craterocephalus stercusmuscarum stercusmuscarum (Günther)
Figure 7

Atherina stercus muscarum Günther, 1867: 64, type locality: Cape York, Queensland; syntypes in BMNH (1867.5.6.61-62 [2]).

Atherina stercus-muscarum: — Macleay, 1881: 40.

Atherinichthys maculatus Macleay, 1883: 207, type locality: Lillismere Lagoon, Burdekin River; types lost.

Craterocephalus maculatus: — McCulloch, 1913: 52.

Craterocephalus stercus-muscarum: — Jordan and Hubbs, 1919: 45.

Craterocephalus stercus-muscorum: — Nichols and Raven, 1934: 4.

Craterocephalus stercusmuscarum: — McCulloch, 1929: 110; Whitley, 1957: 16; Munro, 1958b: 102; Lake, 1971: 28; Grant, 1982: 773; Pollard, 1974: 1-32; Merrick and Schmida, 1984: 148.

Craterocephalus worrelli Whitley, 1948: 86, type locality: Mataranka, Roper River system, Northern Territory; holotype in AMS (IB.1915); Munro, 1958b: 102; Allen, 1975: 92.

Craterocephalus tanii?: — Hansen, 1987: 167 (misnomer, presumably for *randi.*)

Craterocephalus randi: — Allen and Hoese, 1980: 55 (misidentification).

Craterocephalus stercusmuscarum stercusmuscarum: — Ivantsofft *et al.*, 1987b: 172.

Material examined

Holotype of *C. worrelli*, AMS IB.1915*, Mataranka, Roper River System, Northern Territory; CSIRO A.1224-6 (3)*, Mataranka, Roper River System; AMS IB.3700 (1)*, Darwin; AMS IB.4125-7 (25), Bamaroogjaja Swamp, South Alligator River; AMS I.17728-001 (3)*, Muddy Lagoon off Jim Jim Creek; AMS I.17727-001 (10), Lily Lagoon near Barramundie Creek; AMS I.177730-001 (10), Red Lily Lagoon, near Daly River Police Station; DR 1969-119 (1), Wildman Creek at Oenpelli-Darwin Road; AMS I.16859-007 (62), Magela Creek, Jabiru. All of the above localities in the Northern Territory, Australia.

BMNH 1867.5.6.61-62 (2), Cape York Peninsula, syntypes of *Atherina stercusmuscarum;* AMS I.18542-001 (6)*, Black River, about 25 km north of Townsville; MQU W175-21 (15)*, Cairns environs; MQU W176-41 (4)*, Rockhampton; MQU W176-40 (2)*, Bob's Creek, Rockhampton; AMS IB.5055 (5)*, Barron River, Kuranda; AMS IB.781 (1)*, Charters Towers; AMS IA.2386 (2)*, AMS IB.3722 (1)*, Alligator Creek, Townsville; AMS I.12767 (45), Burnett River, Eidsvold; AMS IA.3674 (174), Lake Barrine, Atherton Tableland; AMS IB.28732 (2), Pioneer River, Mackay; AMS IB.3503 (2), Gayndah; AMS I.18014-001 (5), O'Shanassy River; AMS I.17989-002 (24), Leura Homestead, McKenzie River; AMS I.17957-005 (1), Gregory River near Riversleigh Station. All of the above localities in Queensland, Australia.

*Specimens used for measurements and counts.

Material used for osteology: MQU W175-21 (4) Cairns; MQU Ia-129 (1) Hervey Creek, south of Cairns, Australia.

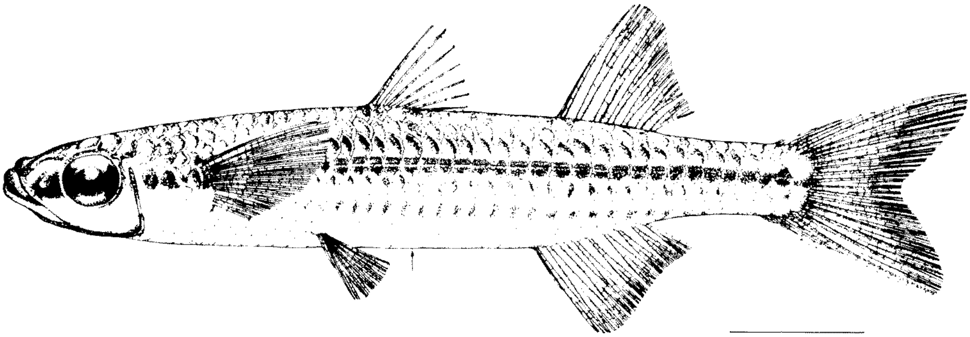


Figure 7. *Craterocephalus stercusmuscarum stercusmuscarum* Mataranka, Northern Territory.

Diagnosis

Widespread species of Australian hardyhead closely related to Papua New Guinea species but distinguished from them by shape of nasal bone, anal plate not elongate (Figure 2), gill rakers leaf-like and covered with spinules; with small teeth in 2-3 rows in both jaws. Distinguished genetically at *FUM* locus and in some allele frequencies *(ADA, CK, αGPD, ME, MPI)*.

For genetic differences see Tables 2 and 3.

Description

Slender freshwater species, closely related to all southern Papua New Guinea species and to the Australian subspecies *C. s. fulvus*. Lips fleshy, mouth small, with gape restricted by labial ligament. Premaxilla not reaching vertical through anterior margin of orbit; dorsal process moderately long, just reaching interorbital space in most specimens. Teeth small, in 2 or 3 rows in upper and lower jaws. Other bones of mouth edentulous. Wings of fused 5th ceratobranchial lateral, not high and rounded anteriorly. Gill rakers moderately long and leaf-like but less than half diameter of pupil with distinct spinules present. Small, round scales, in even rows on side of body. Distinct concentric circuli on all body scales.

For morphometrics and meristics see Table 1.

Colour

Live specimens extremely variable from locality to locality, within locality and from time to time; ranging from greenish yellow and translucent, with only faint markings but with midlateral stripe obvious, to solid silvery gold with deep golden abdomen and distinct black spots. All fins yellowish. Black mark near vent in females when running ripe, abdomen of male becoming bright gold when sexually mature (Lake, 1978). Preserved specimens yellow to light brown with grey or dusky fins. Centre of each scale if pigmented forming black spot, with latter often appearing confluent with adjacent spot to form black lines along side of body. Midlateral band running from snout through eye, opercle to hypural joint. Dorsum of head black and dorsal surface of body darker than ventral. Preserved specimens losing colour with time.

Distribution

Craterocephalus stercusmuscarum stercusmuscarum is a widespread Australian species inhabiting rivers and creeks of northeastern Queensland and extending as far south as Dee River at Dululu. This species is also common in the rivers west of the Dividing Range draining into the Gulf of Carpentaria and the northern rivers of Northern Territory including the Roper, Alligator and Edith Rivers. Occasionally single specimens which may be attributed to *C. s. stercusmuscarum* are found further to the south in South Australian waters (Finnis River, Nilpena Springs) but genetic affinities of the latter are yet to be determined.

Comments

The justification for the recognition of two subspecies of *C. stercusmuscarum* is recorded in Ivantsoff *et al.* (1987) but in the context of the newly described subspecies, *C. s. fulvus*. The redescription of *C. s. stercusmuscarum*, however was omitted. Additional studies (electrophoretic and osteological) now allow a detailed comparison of this species, not only with its other subspecies but also with *C. randi*, its other close relative.

The confusion between *C. s. stercusmuscarum* and *C. randi* has already been discussed. Failure to recognize the variability of coloration had also led to a description of several species which are now regarded as indistinct from *C. stercusmuscaraum*. A thorough description of *Atherinichthys maculatus* by it's author (Macleay, 1867) has left no doubt that it is indistinct from Günther's flyspecked hardyhead (Jordan and Hubbs, 1919). Examination of the type of *C. worrelli* and subsequent collection of additional specimens from the type locality also leaves no doubt that *C. worrelli* is not different from *C. s. stercusmuscarum*. Genetic analysis of Mataranka specimens shows that they are indistinct from other populations of *C. s. stercusmuscarum* and are genetically conservative.

Discussion

Most of the land mass which is now Papua New Guinea, is geologically young. However, some areas date from Eocene and Oligocene (Dow, 1977; Pigram and Davies, 1987). Whilst the northern half of Papua New Guinea is an accretion of islands derived from the Asian plate, the southern half is the leading edge of the Australian tectonic plate. The two collided during Tertiary (Pigram and Davies, 1987).

The species of hardyheads from the southern drainages of Papua New Guinea are closely related to *C. s. stercusmuscarum* from northern and north eastern Australia. This relationship is not unexpected as Australia and Papua New Guinea have been connected by the Torres Land Bridge intermittently during Tertiary and Quaternary, with the present marine transgression separating the landmasses only about 7-10 thousand years ago.

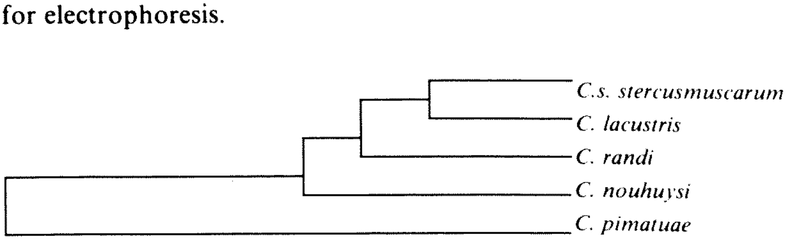
It is well documented that a large lake (Lake Carpentaria) formed in the Torres Land Bridge during the last glacial maximum when the sea level was below —53 m (Smart, 1977; Jones and Torgersen, 1988). Whether this lake was brackish or fresh is debatable. It may have been closed to the sea and containing only internal drainage fresh water (Jones and Torgersen, 1988) or it may have always been joined to the Arafura Sea by a narrow channel with brackish water (Galloway and Löffler, 1972). With this internal drainage, whether brackish or entirely fresh, dispersal was possible for euryhaline fish species such as atherinoids and allowed them to cross from one land mass to the other. It is now known (Allen and Cross, 1982; Saeed *et al.*, 1989) that some species of rainbowfishes and blue-eyes are found on either side of Torres Strait. Genetic comparison of populations of these species of fish should nonetheless be made to determine whether divergence has already begun.

Radiation of *Craterocephalus* species and possibly others appears to be a recent phenomenon, from about Plio/Pleistocene. During Miocene, most of southern New Guinea was under shallow marine transgression (Dow, 1977). Crowley (in press) suggests that invasion of freshwaters by the ancestor of the *C. stercusmuscarum* group occurred in that area (northern Australia/southern Papua New Guinea).

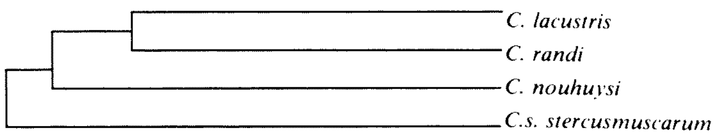
With the subsequent fall of sea level, swampy lowlands around the mouth of Fly River emerged. These lowlands, together with seasonal flooding during Pleistocene and Holocene appear to have allowed movement of fish between the rivers which drained into the same flood plain, much as species today move between rivers of the Gulf of Carpentaria during the wet season when the area becomes a vast flood plain (Simpson and Doutch, 1977). Judging by genetic distance (Table 3), there appears to have been very little opportunity for speciation to occur. Isolation occurred nevertheless, resulting in distinct and localized species such as *C. lacustris* and *C. pimatuae*. The Torres Strait Barrier had allowed for recent separation between *C. randi* and *C. s. stercusmuscarum* with the genetic distance between them being quite small (R=0.19) but similar to the distances between all Papua New Guinea species in the southern drainage (Figure 8b). No specimens of *C. pimatuae* were available for electrophoresis. The comparison of Figure 8a and 8b is therefore not possible since one of the species is excluded from the genetic study. The latter study, nonetheless gives an indication of the recency of speciation between Australian and New Guinea hardyheads available for analysis.

Examination of cluster analysis (Figure 8a) shows that the osteological differences set *C. pimatuae* apart from other Papua New Guinea species. Considering the apparent osteological conservatism of atherinids (see Todd, 1976) the differences of *C. pimatuae* suggest that separation of this species had taken place prior to separation of other Papua

New Guinea hardyheads. This hypothesis cannot be verified until fresh material is available for electrophoresis.



a



b

Figure 8. Cluster analysis of Papua New Guinea species of *Craterocephalus* and *C. s. stercusmuscarum* using a) osteological characters and b) Rogers' genetic distance values.

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ARC funding has allowed us to collect extensively in many remote parts of Papua New Guinea and Australia. We thank Mr John Paska, Dr Doug Hoese, Mr Kent Hortle, for assistance in the field. The management of Ok Tedi Mining Co. was very helpful with logistics. Ms B. Duckworth is thanked for her drawings of the specimens. We also wish to express our gratitude to all the museum curators who were kind enough to lend us specimens during the course of our study.

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