Description of a new subfamily, genus and species of a freshwater atherinid, *Bleheratherina pierucciae* (Pisces: Atherinidae) from New Caledonia

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Abstract

Bleheratherina pierucciae is described from Tontouta (26°56.9'S 166°14'E) and Pirogues Rivers, New Caledonia. The new species has been compared with other Indo-Pacific atherinids, both freshwater and marine (representatives of genera *Atherinason, Atherinomorus, Atherinosoma, Atherion, Craterocephalus*, *Hypoatherina, Kestratherina, Leptatherina* and *Stenatherina)* and an atherionid *(Atherion).* Dyer & Chernoff's (1996) division of Atherinidae into three subfamilies has been briefly reviewed and a fourth subfamily, Bleheratherininae, is now added to this list since the new species is distinct and different from all known atherinids. *Bleheratherina pierucciae* can be immediately recognised by the unusual structure of its mouthparts. Other distinct osteological characters confirm that it merits a subfamilial status. The evolutionary history of this new species must have commonality with the Australian coastal and marine fishes, having probably been derived from a common ancestor likely to have occurred in a marine environment i.e. Arafura Sea. The zoogeographic events, which led to the separation of New Caledonia from Australia and its emergence as a separate island, post Palaeocene, must have led to a divergence of the ancestral fauna which invaded the freshwaters of New Caledonia.

Zusammenfassung

Beschrieben wird *Bleheratherina pierucciae* von Tontouta (26°56.9'S 166°14'O) und Pirogues Rivers, New Caledonia. Die neue Art wird mit anderen indo-pazifischen Atheriniden verglichen, sowohl Süßwasser- als auch Meeresbewohnern (Vertretern der Gattungen *Atherinason, Atherinomorus, Atherinosoma, Atherion, Craterocephalus, Hypoatherina, Kestratherina, Leptatherina* und *Stenatherina)* sowie mit einem Atherioniden *(Atherion).* Die von Dyer & Chernoff (1996) stammende Unterteilung der Atheriniden in drei Unterfamilien wurde überarbeitet und eine vierte Unterfamilie, Bleheratherininae, hinzugefügt, denn die neue Art unterscheidet sich deutlich von den bisher bekannten Ährenfischen. *Bleheratherina pierucciae* lässt sich an der ungewöhnlichen Struktur des Maulbereichs leicht erkennen. Weiterhin sprechen osteologische Merkmale für einen besonderen Subfamilien-Status. Die Evolutionsgeschichte dieser neuen Art dürfte einen gemeinsamen Ausgangspunkt mit australischen Küsten- und Meeresfischen haben, wahrscheinlich gab es einen gemeinsamen Vorfahren in der marinen Umwelt, speziell im Arafura-Meer. Erst die zoogeografischen Ereignisse am Ende des Paläozäns, die zur Abtrennung Neu-Kaledoniens von Australien und zur Bildung einer eigenen Insel führten, dürften zur Eigenentwicklung der damaligen Arten und ihrer Eroberung der Süßgewässer in Neukaledonien geführt haben.

Résumé

Bleheratherina pierucciae est décrit, originaire des rivières Tontouta (26°56.9'S 116°14'E) et Pirogues, Nouvelles-Calédonie. La nouvelle espèce a été comparée avec d'autres Athérinidés de l'Indo-Pacifique, aussi bien d'eau douce que marins (représentants des genres *Atherinason, Atherinomorus, Atherinosoma, Atherion, Craterocephalus, Hypoatherina, Kestratherina, Leptatherina* et *Stenatherina)* et avec un Athérinidé *(Atherion).* La subdivision des Atherinidae, de Dyer & Chernoff (1996) en trois sous-familles a été brièvement revue et une quatrième sous-famille, Bleheratherininae, s'ajoute maintenant à cette liste, vu que la nouvelle espèce se distingue de tous les Athérinidés connus. *Bleherateriна pierucciae* se reconnaît facilement par la structure inhabituelle des parties de la bouche. D'autres caractères ostéologiques distincts confirment son statut de sous-famille. L'histoire de l'évolution de cette nouvelle espèce doit avoir des points communs avec les poissons côtiers et marins d'Australie, dans la mesure où elle descend probablement d'un ancêtre commun qui a dû vivre dans un environnement marin, en l'occurrence la Mer d'Arafura. Les événements zoogéographiques qui ont présidé à la séparation entre la Nouvelle-Calédonie et l'Australie et son occurrence en tant qu'île après le Paléocène, a dû provoquer une différenciation de la forme ancestrale qui a investi les eaux douces de Nouvelle-Calédonie.

Sommario

Bleheratherina pierucciae è descritta sulla base di esemplari raccolti nei torrenti Tontouta (26°56.9'S 166°14'E) e Pirogues, Nuova Caledonia. La nuova specie è stata comparata ad altri aterinidi dell'Indo-Pacifico, sia d'acqua dolce sia marini (rappresentanti dei generi *Atherinason,*

Atherinomorus, Atherinosoma, Atherion, Craterocephalus, Hypoatherina, Kestratherina, Leptatherina e *Stenatherina)* e al genere *Atherion.* La suddivisione degli Atherinidae in tre sottofamiglie secondo Dyer & Chernoff (1996) è stata brevemente riesaminata e una quarta sottofamiglia, Bleheratherininae, è ora aggiunta a questa lista poiché la nuova specie si distingue da tutti gli altri aterinidi noti. *Bleheratherina pierucciae* può essere immediatamente riconosciuta per la struttura insolita delle parti boccali. Altre caratteristiche osteologiche confermano che la specie merita la collocazione in una sottofamiglia separata. La sua storia evoluzionistica deve contenere elementi comuni con i pesci marini che abitano le coste australiane, poiché probabilmente si è originata da un antenato comune che abitava l'ambiente marino del mare di Arafura. Gli eventi zoogeografici che hanno portato alla separazione della Nuova Caledonia dall'Australia e la sua comparsa come isola separata nel tardo Paleocene devono aver portato ad una divergenza della fauna ancestrale che ha colonizzato le acque dolci della Nuova Caledonia.

INTRODUCTION

Atherinids are small marine, estuarine and freshwater fishes not exceeding 120 mm SL (a soon to be described species of *Craterocephalus* may reach 300 mm SL), occurring predominantly in the Old World, with only *Alepidomus evermanni* (freshwaters of Cuba) and two marine species, *Atherinomorus stipes* and *Hypoatherina harringtonensis* (predominantly in the shore waters of the Caribbean) known from the New World. In the Southeast Pacific, the family is only known only from Tumaco, Colombia, according to Dyer (2006). All other New World silversides have been separated into a family of their own the Atherinopsidae by Saeed et al. (1994).

All freshwater atherinid species are derived from marine ancestors and until recently have only been known from the rivers of Australia, New Guinea and some islands in the vicinity of the latter. No "freshwater" atherinids are present in Africa or Europe other than those found in lakes and lagoons, which may be brackish or freshwater, in the vicinity of the Mediterranean, Black, Aral and Caspian Seas. These are euryhaline fish, all probably derived from *Atherina boyeri* Risso, 1810 (Trabelsi et al. 2004). It appears, however, that freshwater atherinids do occur on islands in the south Pacific other than in Australia and the island of New Guinea. In 2005, Larson et al. described a freshwater species *Craterocephalus laisapi* from East Timor. The present description is an account of the discovery and identification of a new freshwater atherinid collected by Heiko Bleher and Paola Pierucci from the Tontouta River, some 45 km north-east of Noumea. Another collection was made from the Pirogues River, New Caledonia, about 15 km south east of Noumea, during the Pedcal Field Survey in 1996, with specimens now deposited in the Muséum national d'Histoire naturelle in Paris. Atherinids have a long evolutionary history, they are known from Eocene European deposits (Ivantsoff 1978) and the relationship between descendants *(Atherina* spp.) of the Tethys

Fig. 1. Approximate position of New Caledonia in Late Cretaceous. Note that New Guinea is under water at this time. Modified after Griffiths (1971).

forms and those found off the eastern coast of Australia have been shown to be close (Ivantsoff 1978).

The zoogeography of New Caledonia is related to a set of zoogeographical events which encompass the separation of what is now New Caledonia and New Zealand from eastern Australia and Antarctica (see Fig. 1). Prior to the Late Cretaceous, a single landmass which is now separated into New Zealand, New Caledonia, the Campbell Plateau, the Lord Howe Rise and the Norfolk Ridge, separated away, moving northward and by the Palaeocene the separation from Australia was complete (Sanmartin & Ronquist 2004). During most of this time, most of New Zealand and New Caledonia were submerged. This would indicate that the ancestral species, which gave rise to the modern freshwater New Caledonian atherinid was marine. Crowley (1990) suggested that dispersal of at least one ancestral species of *Craterocephalus (C. stercusmuscarum)* took place from the present north of Australia, from the Arafura Sea, spreading to the east coast of Australia and at some point in time invading the rivers along the coast. Whilst *C. stercusmuscarum* and *C. marjoriae* along the east coast of Australia occur in freshwater, *C. honoriae,* another hardyhead, is almost exclusively estuarine, occurring in coastal lakes from Queensland border (approximately 28°30'S) to the north of Newcastle in New South Wales (30°S). There are also freshwater species of *Craterocephalus* in southern New Guinea rivers, in many landlocked lakes (e.g lakes Lakamora, Kamaka, Kutubu, Yamur) and Aru Islands (H. Bleher, pers. com.) suggesting a local centre of origin somewhere beyond what is presently northern Australia. The ancestor to the New Caledonian freshwater fish must have also come from this region but separated from ancestral atherinid species early during the Tertiary to give rise to a distinct new form, which invaded the freshwaters of New Caledonia.

MATERIALS AND METHODS

Five specimens were collected from the Tontouta River New Caledonia (Figs 2-3) about 12 km inland (approximately 26°56.9'S 166°14'E) New Caledonia, by Heiko Bleher and Paola Pierucci, in November 1997. Specimens collected in 1996 from the Pirogues River, New Caledonia and deposited in the Muséum national d'Histoire naturelle (MNHN) in Paris were also examined and identified being the same as those from Tontouta River. Specimens were measured from the tip of the snout to the hypural joint and standard lengths were recorded to the nearest 0.1 mm. Measurements were recorded as means and range (in brackets). Standard deviations were calculated and recorded in Table I. Cleared specimens were stained with Alizarin Red S (Pirogues River) and with alcian blue (Tontouta River).

Measurements were made with electronic calipers with data entered into an Excel file, which converted raw data into proportions of standard length

Fig. 2. The mouth of the Tontouta River, is located approximately 35 km north-west of Noumea. Red asterix is the type locality, about 45 Km north-east of Noumea. Courtesy of maps of New Caledonia.

(SL), head length and eye diameter. Counts were made using the technique recommended by Hubbs & Lagler (1958) so as to make comparisons with previously described atherinid species. Two specimens were cleared and stained using the method of Taylor (1967), Taylor & Vandyke (1985) and Dingerkus & Uhler (1977). These were measured and counted prior to clearing. Drawings were made with the assistance of a stereomicroscope. Osteological comparisons were made with representatives of marine Indo-Pacific atherinds and an atherionid (Table II). Specimens collected by H. Bleher's party were deposited in the Australian Museum Sydney, those borrowed from the MNHN were returned to that institution. All of the specimens that have been examined are designated as types.

Institutional identification is as follows: AMS – The Australian Museum, Sydney; MNHN – Muséum national d'Histoire naturelle, Paris; MQU – Macquarie University Fish collection. The following species were examined: *Atherinomorus lacunosus* AMS I3227 (**5**, 36-44 mm); *Atherinosoma microstoma* MQU-IA 22- 26 (**1**, 75 mm); *Atherinason hepsetoides* MQU-Ia48 (**1**, 69 mm); *Atherion elymus* MQU unregistered (**3**, 41-44 mm); *Craterocephalus capreoli* MQU-I WI 75-27 (**3**, 34-40 mm); *C. honoriae* MQU-I JMP 75-5 (**5**, 36-44 mm); *C. mugiloides* MQU-I KB 75-35 (**3**, 43-48 mm); *Hypoatherina barnesi* MQU-I(a)-107 (**2**, 42-53 mm); *Kestratherina esox* MQU-I 45 (**1**, 67 mm); *Leptatherina presbyteroides* MQU-IA57 (**10,** 42-90 mm); *Stenatherina panatela* MQU-I 176 (**1**, 70 mm).

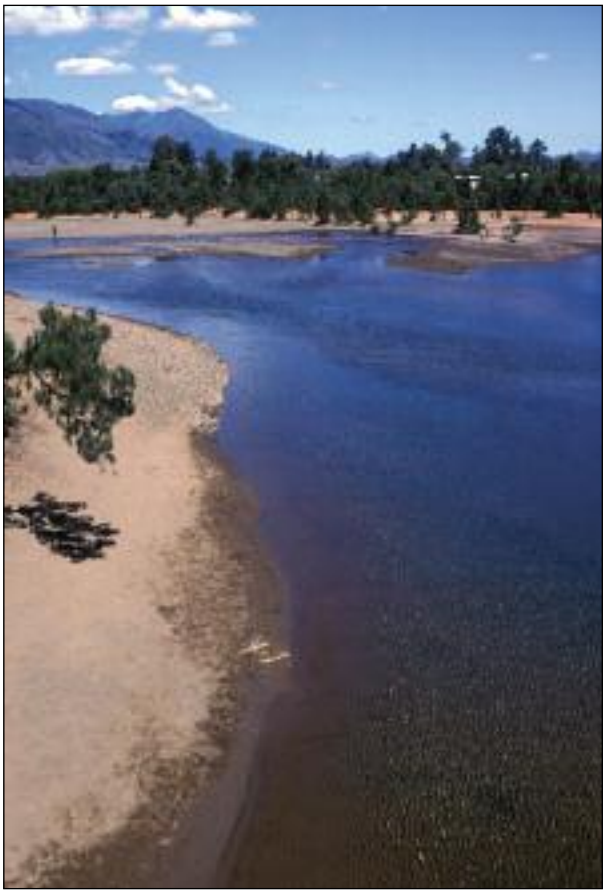


Fig. 3. Tontouta River, New Caledonia collection site.

SYSTEMATIC ACCOUNT

Bleheratherininae n. subfam.

Diagnosis: Labial ligament very thick; premaxilla and its anterior process uniquely different from other Atherinidae with a highly expanded triangular posterior ramus and with small lateral process immediately preceding; its anterior process very long and slender; maxilla highly curved; coronoid process of dentary large and squarish, articular peak very low (Fig. 5); mesethmoid absent or possibly cartilaginous (not observed in the alcian blue preparation); palatine, finger-like, with blunt top; ligament to nasal somewhat elongated; nasal lacking ventral palatine process; first infraorbital free, second and third appear to be fused (Fig. 6): hypurals 1 and 2 fused, 3, 4, 5 not fused (Fig. 7); teeth in premaxilla and dentary very minute, sparse, in about 2 rows as are teeth on mesopterygoid; vomer edentulous; teeth on basibranchials in very small, sparse, tooth patches; fifth ceratobranchial shallow, triangular, teeth small anteriorally becoming slightly larger posteriorly; four small and poorly developed interdorsal pterygiophores present.

Bleheratherina n. gen.

Type species: *Bleheratherina pierucciae* Aarn and Ivantsoff. *Bleheratherina* is presently monotypic.

Diagnosis: The diagnostic characters for the genus are given under the subfamily account.

Bleheratherina pierucciae n. sp.

Holotype: AMS I.44680-001, 39.3 mm SL, Tontouta River, New Caledonia, about 12 km inland in freshwater, water temperature 28°C. Collected by H. Bleher and P. Pierucci with seine, 8 November 1997.

Paratypes: AMS I.44680-002, (4, 22.0-38.3 mm SL) data as for holotype. AMS I.44680-003 (1, 32.9 mm SL, cleared specimen, stained with alcian

blue), data as for holotype. MNHN 1996-442 (5, 19.9-32.9 mm SL), Pirogues River, New Caledonia, collected by PEDCAL Field Survey. MNHN 1996-442 (1, 36.1 mm SL, cleared specimen stained with alizarin red S). Data as for non-stained paratypes from Pirogues River.

Diagnosis: See subfamily account. A small species of fish, the largest specimen so far collected about 47 mm total length.

Description: A very slender fish with large mouth, distal end of premaxilla reaching vertical through anterior edge of orbit; not attributable to any other atherinid genus or species on basis of its osteology. Superficially similar in body shape to some species of *Craterocephalus* or *Atherinosoma* externally, but much more slender than members of those genera; identifiable by its mouthparts, by unique shape of maxilla (Figs 5, 9, 10), long and slender premaxillary process (Figs 5, 9) and coronoid process of dentary (Fig. 9); maxilla covered by infraorbitals and not visible externally; distal end of premaxilla and maxilla covered by labial ligament, restricting gape; premaxilla with very fine caniniform teeth; preopercle covered by scales; gill filaments visible through translucent opercle in preserved specimens; body depth same from head to origin of second dorsal fin; body tapering from origin of anal fin with peduncle more slender than rest of body; body scales small, thin and in regular rows to hypural joint; anus usually about one scale in front of ventral fin tips; gill rakers thin, long, about half diameter of pupil and numerous (19-22) on first lower gill arch; fin elements fine and relatively long (Fig. 4) about height of 4 midlateral scales; spines in first dorsal about diameter of orbit, branched rays of other fins slightly shorter, becoming smaller distally.

All data recorded as proportions and calculated as means and ranges: Head in 4.0 (3.5-6.1), greatest body depth 7.0 (6.7-8.0); least depth at caudal peduncle 14.8 (13.4-16.4) all in SL; eye in head 2.9 (1.9-3.2); snout 1.1 (1.0-1.2); premaxilla 0.8 (0.8-0.9); dorsal process of premaxilla 0.7 (0.7-0.9) last 3 recorded as proportion of eye; midlateral scales 40.3 (40-41); transverse scale rows 5; predorsal scales 16.7 (15-17); interdorsal scales 6.7 (6-7); vertebral count (2 specimens only) 40-41; dorsal fins V-VII Ii10-12; anal fin Ii12-14; pectoral fin Ii12-13; ventrals always I5; caudal fin 9+8 (dorsal and ventral) principal rays; gill rakers in first lower gill arch 20.4 (19-22); origin of first dorsal fin from 2 scales in front to one scale behind vertical through tips of ventrals; origin of ventrals 3 to 5 scales in front of tips of pectorals. Table I includes all meristic and morphometric characters of the specimens examined.

Colour in live: The collector's photograph was taken at the time of capture providing the colours of the fish when live. This is a very colourful atherinid. Body above midlateral band grey, with all scales clearly delineated with melanophores; black spot present at origin of caudal; thin green-blue line forming upper third of midlateral band, becoming broader below first dorsal fin and disappearing beyond distal end of second dorsal fin; midlateral band thin, less than half width of midlateral scales, blue above with brown patch beneath pectoral, then continuing as blue line above and diffuse narrow brown band below, extending to distal end of second dorsal, then becoming thin dark brown band to caudal peduncle; base of fins delineated by darker chromatophores; second dorsal and anal fins dusky, first dorsal, ventral and pectoral fins hyaline; base of

Fig. 4. *Bleheratherina pierucciae* Tontouta River, New Caledonia. Photo taken at the site of the collection by Heiko Bleher. The photograph shows one of the specimens designated as a paratype.

caudal fin also dusky; opercle iridescent, with blotches of chromatophores towards free edge; iris golden, surrounding black pupil; snout peppered with melanophores at anterior edge; lower part of dentary outlined by melanophores.

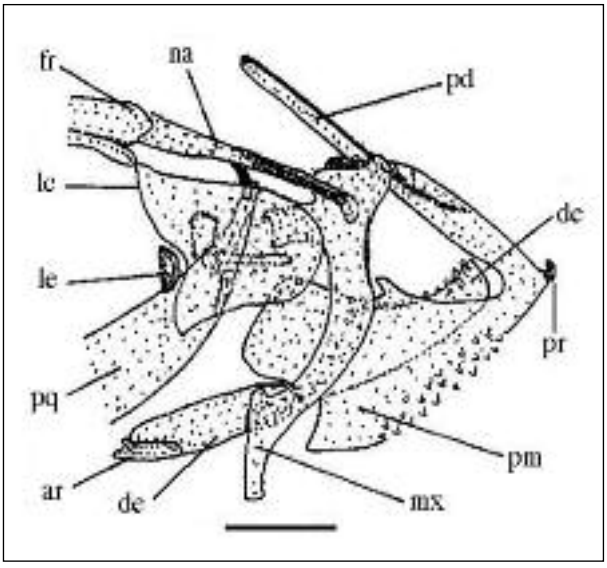


Fig. 5. Mouthparts of *Bleheratherina pierucciae,* MNHN 1996-442, 37 mm SL. Snout in lateral aspect, right side. Abbreviations: **ar,** articular; **de,** dentary; **fr,** frontal; **lc,** lacrimal; **le,** lateral ethmoid; **mx,** maxilla; **na,** nasal; **pd,** premaxilla dorsal process; **pm,** premaxilla; **pq,** palatoquadrate; **pr,** premaxilla rostroventral spinous process. Scale bar: 1 mm.

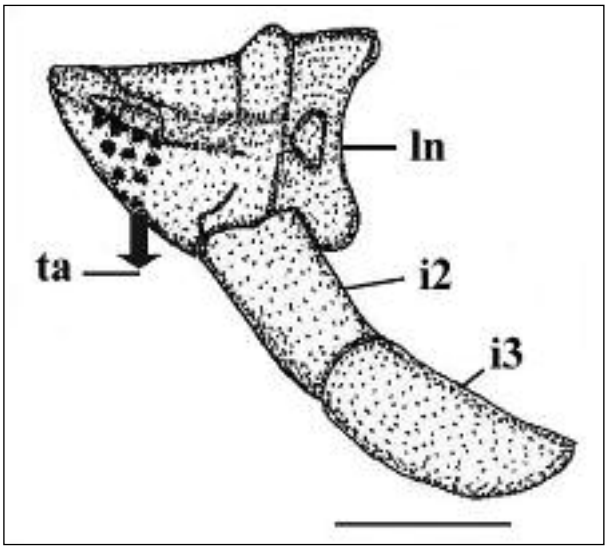


Fig. 6. *Bleheratherina pierucciae,* MNHN 1996-442, 37 mm SL. Infraorbitals in lateral aspect. Abbreviations: **i2,** infraorbital 2; **i3,** infraorbital 3; **ln,** lacrimal notch; **ta,** adductor tendon (not shown). Scale bar: 1 mm.

Colour in alcohol: The preserved specimens are uniformly brown, with a thin (about half a scale width) midlateral band. The fins are duskier than in life. Chromatophores so distinct in live specimens, faded. Eyes are black and prominent.

Osteological description: Ethmoid cartilage forming rostromedian margin of orbits; ethmomaxillary ligament absent; lateral ethmoid lateral angle developed as prominent condyle, articulating with lacrimal caudal margin (Fig. 5); mesethmoid absent; rostral cartilage distorted elongate hourglass shape, dorsal to ethmoid (Fig. 8); rostral cartilage rostral angle attached to maxillary internal rostral processes.

Vomer edentulous, elongate, bearing paired condyles projecting rostroventrally, ventral to ethmoid; condyle contacting cylindrical submaxillary meniscus, and giving rise to caudoventrally coursing vomeropalatine ligament (Fig. 11); parasphenoid dorsal to vomer, in median interorbital plane; parasphenoid ventral ridge not extended caudally, parasphenoid fossa absent (Dyer & Chernoff 1996); basisphenoid trabecular.

Nasal falcate, rostral angle directed caudally, attached ligamentously to lacrimal (Fig. 11); nasal ventral process attached ligamentously to palatine dorsal angle; frontals broadly separated rostrally, ventral to rostral cartilage, but caudally conjoined in median asymmetric symphysis; maxilla with internal and external rostral processes, and tall

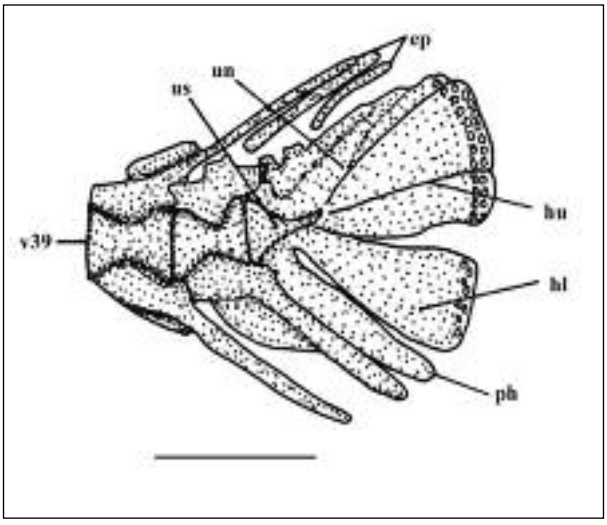


Fig. 7. *Bleheratherina pierucciae*, caudal fin and last few vertebrae, fin rays removed. Abbreviations: **ep,** epural; **hl,** lower hypural plate; **hu,** upper hypural plate; **ph,** parhypural; **un,** uroneural; **us,** urostyle; **v39,** vertebra 39. Posterior edges of hypurals cartilaginous. Scale bar: 1 mm.

Table I: Seven specimens (holotype and all paratypes) of *Bleheratherina pierucciae.* Morphometric (in mm) and meristic attributes are recorded in columns 1- 7. Measurements are calculated as proportions of standard length (SL), head and eye. Raw data in columns 1-7 are used to calculate means X, standard deviation (SD) and range (Max, Min). **Pec. L.** length of pectoral fin; **H max,** greatest body depth; **Width max,** greatest width taken across head; **H min,** least body depth; **Pec-anus** distance from snout to anal opening; **Sn,** snout; **OD1,** origin of first dorsal fin;**OD2** origin of second dorsal fin; **OV,** origin of ventral fin; **TV** tips of ventral fins; **OA** origin of anal fin; **TA** origin of last ray of anal fin; **Caud. Ped.,** caudal peduncle; **Prem. Proc.** Dorsal process of premaxilla; **Midlat sc.** Scale count along midlateral line; **Trans. Rows,** number of scale rows along side of body; **Pred. sc,** predorsal scales; **Interdor. Sc.,** interdorsal scales; **D1 Fin,** number of spines in the first dorsal fin; **D2 Fin,** number of branched rays in second dorsal fin; **Pect. Fin,** pectoral fin rays; **Gill rak,** number of gill rakers in first lower gill arch including one in the angle of the arch; **Anus pos.** position of anal opening in relation to tips of ventral fin, negative number means in front of. **OD1 to TV,** position of first dorsal fin in relation to vertical through tips of ventral fin., **OD1 to T. Pec,** position of first dorsal fin in relation to vertical through tips of pectoral fin; **OV to T. Pec,** position of tips of ventrals to vertical through tip of pectoral fin, negative sign indicates in front of. Vertebral count made on alizarin preparations and includes terminal half centrum.

Specimens	1	2	3	4	5	6	7				
Total length	46	46.9	32	27	43	35	39				
SL (in SL)	38.3	39.3	25.8	22	36.1	28.5	33	X	SD	MAX	MIN
Head	10.5	11.1	4.23	5.95	10.1	7.88	9.2	3.97	0.87	6.099	3.54
Pec.L.	6.21	5.82	3.75	3.61	6.04	5.31	6.4	6.06	0.59	6.88	5.18
Hmax.	5.36	5.89	3.84	2.76	5.22	4.15	4.8	7.03	0.41	7.975	6.68
Width Max.	4.83	5.06	3.19	2.83	4.39	3.42	4	8.05	0.21	8.326	7.77
H. Min.	2.66	2.39	1.65	1.65	2.5	1.98	2.2	14.8	0.93	16.44	13.4
Pec-anus	10.5	11.2	6.34	5.67	10.3	7.94	8.9	3.7	0.19	4.073	3.5
Sn-OD1	20.1	20	13.1	10.9	17.9	14.4	17	1.97	0.04	2.024	1.91
Sn-OD2	28.4	27.6	18.3	15.2	25.5	20.1	24	1.41	0.03	1.442	1.35
Sn-OV	16.2	16.8	10.8	9.49	15.2	12.5	14	2.35	0.04	2.398	2.28
Sn-TV	20.4	21.5	14.2	12.8	20.1	16.2	18	1.8	0.05	1.876	1.72
Sn-OA	26.8	27.7	17.5	15.3	24.7	19.9	23	1.44	0.02	1.472	1.42
Sn-TA	32.4	31.8	21.1	18.2	30.3	24.4	28	1.2	0.02	1.237	1.17
IN HEAD	10.5	11.1	4.23	5.95	10.1	7.88	9.2				
Eye	3.42	3.45	2.28	1.95	3.37	2.52	3.2	2.89	0.43	3.225	1.86
Interorbital	2.68	3.15	1.73	1.42	2.4	2.02	2.2	3.76	0.57	4.221	2.45
Postorbital	3.97	3.69	2.52	2.2	3.64	2.86	3.3	2.62	0.4	3.015	1.68
Caud. Ped.	8.11	6.61	4.92	4.28	6.97	5.19	5.4	1.43	0.28	1.698	0.86
IN EYE	3.42	3.45	2.28	1.95	3.37	2.52	3.2				
Snout	3.05	3.16	1.87	1.92	2.74	2.41	2.5	1.14	0.09	1.24	1.02
Premaxilla	3.92	4.54	2.73	2.32	3.75	3.36	3.6	0.83	0.05	0.899	0.75
Prem. proc.	4.17	4.92	2.7	2.07	3.79	2.91	3.5	0.85	0.07	0.942	0.7
Lips/ premax.	2.06	1.69	0.98	0.75	1.69	0.74	1.3	2.87	0.78	4.534	1.91
MERISTICS											
Midlat. sc.	41	40	40	40	40	41	40	40.3	0.45	41	40
Trans. rows	5	5	5.5	5.5	5.5	5.5	5.5	5.36	0.23	5.5	5
Pred.sc.	17	17	17	15	17	17	17	16.7	0.7	17	15
Interdor. sc.	7	7	6	6	7	7	7	6.71	0.45	7	6
Vert. count										40	41
D1 Fin	5	7	6	6	5	6	6	5.86	0.64	7	5
D2Fin	11	11	10	10	11	12	11	10.9	0.64	12	10
Anal fin	14	12	12	12	13	14	13	12.9	0.83	14	12
Pect. fin	12	12	13	12	13	13	13	12.6	0.49	13	12
Gill rak.	20	21	19	20	22	21	20	20.4	0.9	22	19
Anus pos.	-1	1	0	-1	-1	-1	-1	-0.6	0.73	1	-1
OD1 to TV	1	1	0	0	-2	-1	1	0	1.07	1	-2
OD1 to T.Pec.	5	4	4	3	3	4.5	4.5	4	0.71	5	3
OVtoT.Pec.	-1.5	-2	-1	-1.5	-2	-1.3	-1	-1.5	0.35	-1	-2

accessory process (Fig. 9); external rostral process joined to contralateral structure by thick intermaxillary ligament, enclosing premaxilla dorsal process; maxillary condyle located dorsomedially, at level of rostral bifurcation, attached to elongate submaxillary meniscus; ligament from small spine on maxilla accessory process to articular; tendon from musculus adductor mandibulae inserting on internal face of maxilla; maxilla ramus narrow; small ligament from spine on dorsal aspect of ramus to dentary coronoid process; labial ligament from caudal angles of maxilla and premaxilla, coursing deep to premaxilla to insertion at mandibular symphysis.

Premaxilla dorsal process very elongate; premaxilla rostroventral angle bearing narrow rostroventral spinous process, projecting across median plane; process of left premaxilla dorsal to contralateral structure; premaxilla alveolar ramus expanded, with sharp body process and semi-rounded caudal angle; rostral two-thirds of premaxilla alveolar ramus bearing small caniniform teeth.

Dentary (Fig. 9) with moderately elevated coronoid process, bearing small caniniform teeth; moderate rostrally directed incisure in lateral face of dentary, articular rostral process extending rostral to base of incisure and coursing along medial face of dentary; mandibular cartilage elongate, originating from caudal angle of articular, coursing on medial surfaces of articular and dentary to termination deep to rostromedian margin; suspensorium not unlike that of craterocephalines (cf. Dyer & Chernoff 1996); palatine coursing rostrodor-

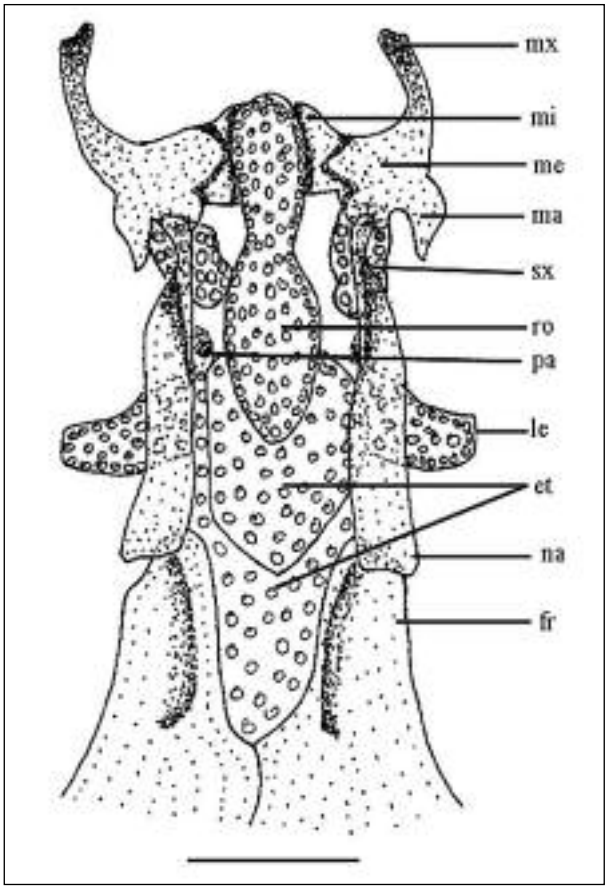


Fig. 8. *Bleheratherina pierucciae,* MQU-I566, 38 mm SL. Rostrum in dorsal aspect, slightly eccentric, lacrimal and premaxilla removed. Abbreviations: **et,** ethmoid; **fr,** frontal; **le,** lateral ethmoid; **ma,** maxilla accessory process; **me,** maxilla external rostral process; **mi,** maxilla internal rostral process; **mx,** maxilla; **na,** nasal; **pa,** palatine; **ro,** rostral cartilage; **sx,** submaxillary meniscus. Stippling: cartilage. Scale bar: 1 mm.

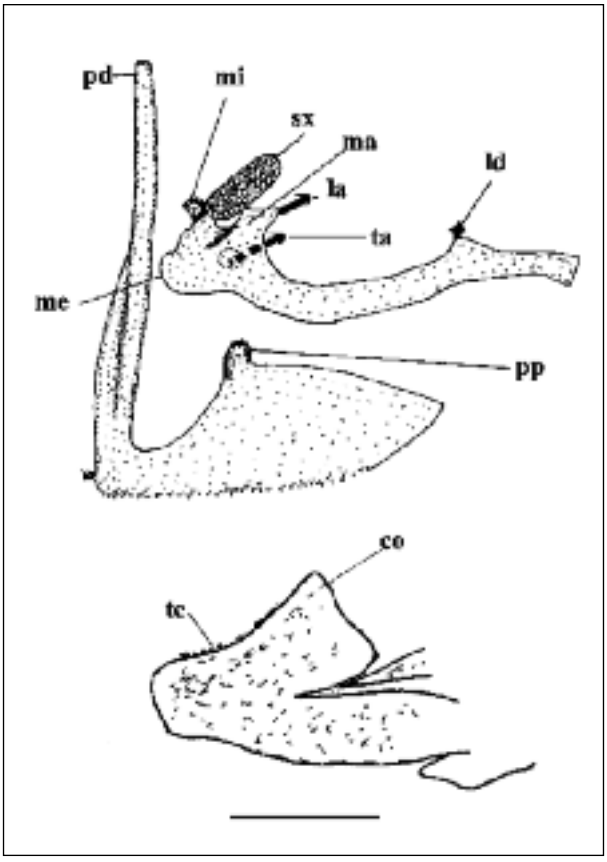


Fig. 9. *Bleheratherina pierucciae,* MNHN 1996-442, 37 mm SL. Maxilla, premaxilla and dentary in lateral aspect. Abbreviations: **co,** coronoid process of dentary; **la,** ligament to articular; **ld,** ligament to dentary; **ma,** maxilla accessory process; **me,** maxilla external process; **mi,** maxilla internal process; **pd,** premaxilla dorsal process; **pp,** premaxilla body process; **pr,** premaxilla rostroventral spinous process; **sx,** submaxillary meniscus; **ta,** adductor tendon; **te,** minute teeth. Scale bar: 1 mm.

Table II. Comparison of *Blehatherina* with the genera of Australian marine silversides.**1**. Note that the 3 species of *Craterocephalus* are marine. *Atherion,* a close relative of Atherinidae is now placed into a family of its own, Atherionidae. Abbreviations **b,** broad; **l,** low; **n,** narrow;; p, pointed. * data unavailable.

Character ↓ sp.→	*Blehertatherina* **1**	*Atherinason* **2**	*Atherinoorus* **3**	*Atherinosoma* **4**	*Atherion* **5**	*C. capreoli* **6**	*C. honoriae* 7	*C. mugiloides* **8**	*Hypoatherina* **9**	*Kestratherina* **10**	*Leptatherina* **11**	*Stenatherina* **12**
Vomerine teeth present (+) or absent	-	-	+	+	+	*	*	*	-	+	-	+
Submaxillary meniscus elongate (+) or not	+	+	-	-	-	+	+/-	+/-	-	+	+	-
Maxilla ramus broad (b) or narrow (n)			n			b	b	b	n	n	n	n
Labial ligament to mandibular synthesis (+) or not (-)	+ o	+	-	+	-	+	-	+	+	*	+	+
Premaxilla dorsal process very elongate (+) or not (-)	+	+	-	-	-	+	+	-	-	+	+	+
Premaxilla rostrocaudal spinous process present (+)	+	-	-	-	-	-	-	-	-	-	-	-
Premaxilla body process punctuate (p) or low (l)	p	p	l	p	l	l	l	p	p	l	p	p
Palatine with rostrally directed 'head' (+) or not (-)	-	-	+	+	-	-	-	-	-	-	*	+
Mesopterygoid teeth present (+) or absent (-)	+	-	+	+	-	-	+	+	+	+	+	+
Basibranchial toothplate present (+) or absent (-)	+	*	+	+	+	+	+	+/-	+	+	*	+
Hypobranchials I, II elongate (+) or not (-)		-	+	-	-	-	-	-	+	+	-	+
Total gill rakers on ceratobranchial I	19-22	15-16	16-17	12	10-11	8-10	11-12	11-12	10-11	15-16	10-14	14-15
Total vertebrae	40-41	48	42	42	40-4	32-34	37-38	37	42	48	45-48	46
Pelvic attached to pleural rib no.?	4	7	4	6	4	5	5	5	4	6	7	5
Pelvic dorsolateral process relatively large (+) or not	+	+	+/-	+	-	-	-	-	+	-	-	-

sally, lacking anterior process, joined to nasal by short ligament, not contacting maxilla (Fig. 11).

Circumorbital series consisting of three rostral and one caudal elements; lacrimal quadrilateral, horizontal axis elongate (Fig. 6); caudal margin notched, articulating with lateral ethmoid; medial face bearing extended subnasal shelf, shelf acting as insertion for tendon from musculus adductor mandibulae. Lateral face of lacrimal bearing open, vertical sensory canal, towards caudal border. Dermosphenoid small, open laterally.

Hyobranchial apparatus similar to that of other Atheriniformes (e.g. Aarn & Ivantsoff 1997); basihyal elongate, rostrally joined to elongate glossohyal cartilage, both elements edentulous; basihyal caudally articulating with first basibranchial, caudolaterally articulating via large condyles with dorsal hypohyal; basibranchials elongate, second and third basibranchials overlain by small toothplates; short, rostrally contacting basihyal and ventral hypohyals, caudally contacting second basibranchial; first and second hypobranchials rela-

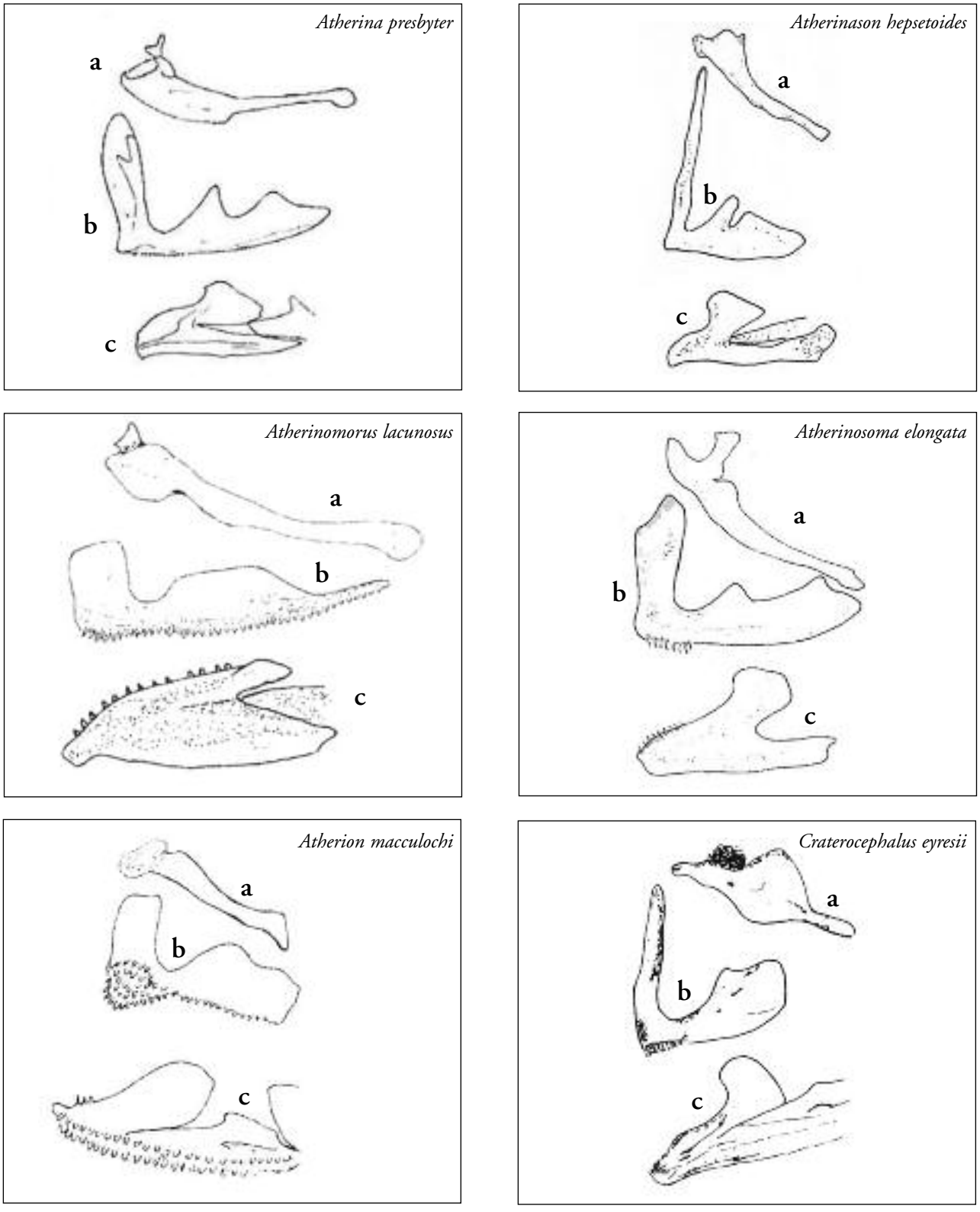


Fig. 10. Mouth parts of Old World atherinid genera. An atherionid, *Atherion maccullochi* is also included for comparison. Generic identification can be made by comparing: **a**. maxilla, **b**. premaxilla and **c**. dentary. Mouthparts of *Bleheratherina pierucciae* (Fig. 9) are uniquely different from all other atherinid genera.

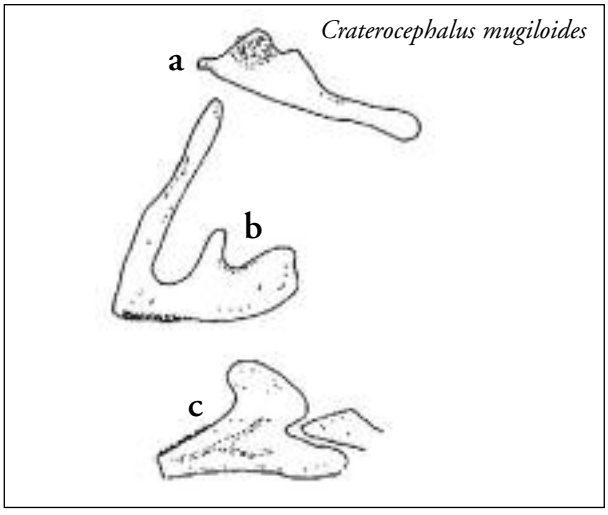
tively elongate, first hypobranchial bearing 6-8 gill rakers; first ceratobranchial bearing 19-22 gill rakers.

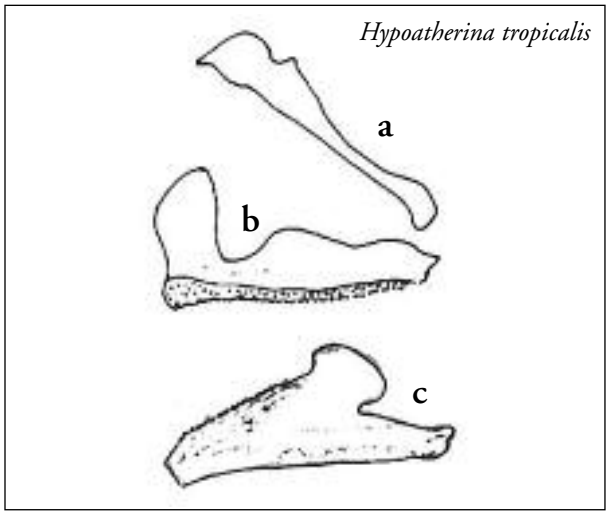
Total vertebrae (including terminal half centrum) 40-41, precaudal 18-19, caudal 22-23; Dorsal angle of pleural ribs contacting caudal surface of parapophyses from third to last precaual vertebrae; epineurals on all precaudal vertebrae.

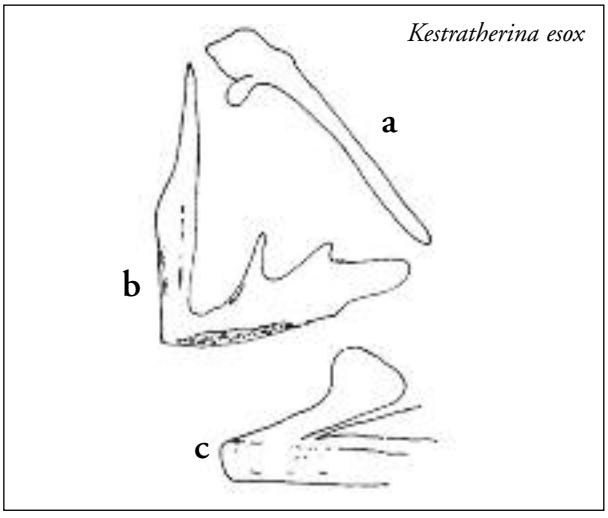
First vertebra with narrow, reduced neural process (Fig. 12); second vertebral neural plate large, third element largest of series, subsequent processes progressively diminishing; neural processes produced as spines rather than plates after eighth vertebra; penultimate vertebra lacking neural spine (Fig. 7).

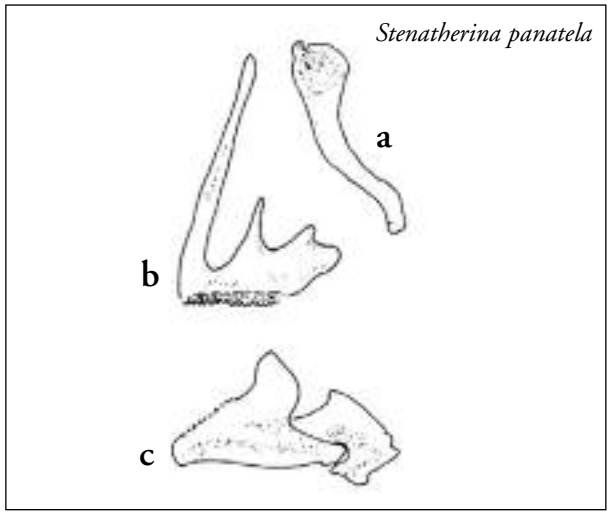
Two epurals dorsal to penultimate vertebra, cranial epural more elongate; terminal hemivertebra fused to urostyle, coursing caudodorsally; truncated uroneural on rostral face of urostyle; caudal face of urostyle supporting hypural fan, consisting of upper and lower hypural plates; upper plate of unfused hypurals 3-4, lower plate of unfused hypurals 1-2; horizontal cleft separating plates; hypurapophysis originating cranial to parhypural foramen, directed caudolaterally, below horizontal plane through vertebral centrae; large preural ventral cartilage located distally between haemal spine of penultimate and second preterminal vertebrae.

First dorsal fin originating at level of transverse plane through vertebra 11-13; single large triangular pterygiophore supporting cranial two spines, caudal spine(s) supported individually by single pterygiophore(s); five interdorsal pterygiophores; second dorsal fin originating at level of transverse plane through vertebra 24-25, each element supported individually by single deep pterygiophore, except caudal two rays, supported by single pterygiophore with distally-fused stay; anal fin commencing at level of vertebra 22-23 (Fig. 13).









Spine and first ray contacting large triangular pterygiophore; other rays individually supported by series of pterygiophores, the caudal ray supported by stay; caudal fin (Fig. 7) commencing at level of penultimate vertebra with 8-10 dorsal and ventral procurrent rays, caudal principal rays originating on caudal margins of hypural plates; pectoral fin falcate, extending dorsally almost to horizontal plane through vertebral centrae, caudally contacting second pleural rib (Fig. 14); cleithrum bearing compact dorsal spinous process and extended caudodorsal process; dorsal incisure interposed between spine and process.

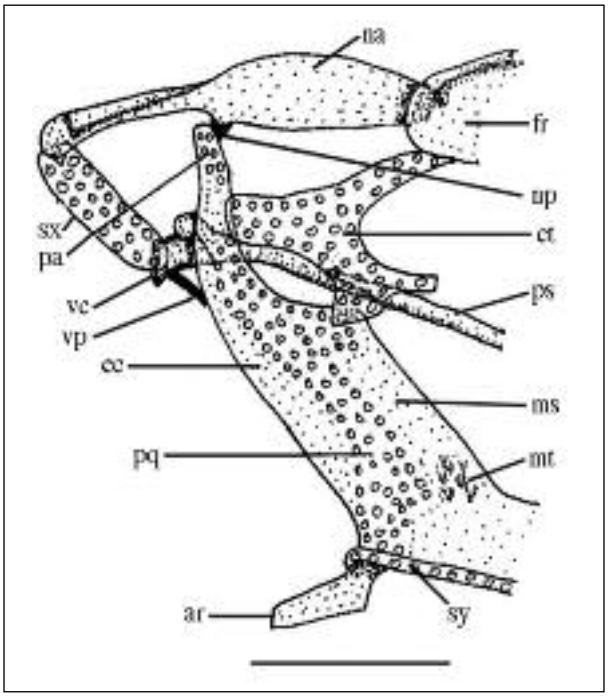


Fig. 11. *Bleheratherina pierucciae,* MNHN 1996-442, 37 mm SL. Snout in lateral aspect, jaws and infraorbitals removed. Abbreviations: **ar,** articular; **ec,** ectopterygoid; **et,** ethmoid; **fr,** frontal; **ms,** mesopterygoid; **mt,** mesopterygoid tooth patch; **na,** nasal; **np,** nasopalatine ligament; **pa,** palatine; **pq,** palatoquadrate; **pr,** premaxilla rostroventral spinous process; **ps,** parasphenoid; **sx,** submaxillary meniscus; **sy,** symplectic; **vc,** vomerine condyle; **vp,** vomeropalatine ligament. Small circles indicate cartilage. Scale bar: 1 mm.

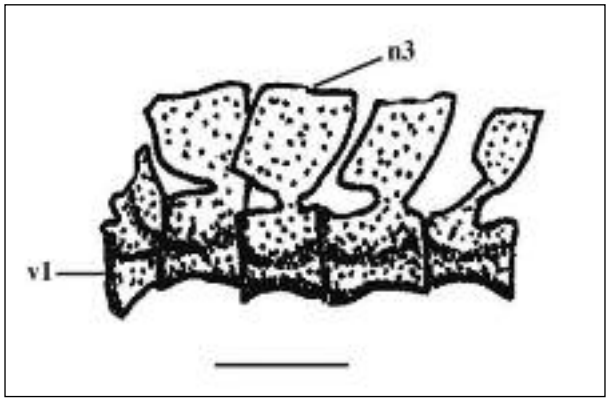


Fig. 12. *Bleheratherina pierucciae* , MNHN 1996-442, 37 mm SL. First five vertebrae in lateral aspect. Abbreviations: **n3,** neural process of third vertebra; **v1,** first vertebra. Scale bar: 1 mm.

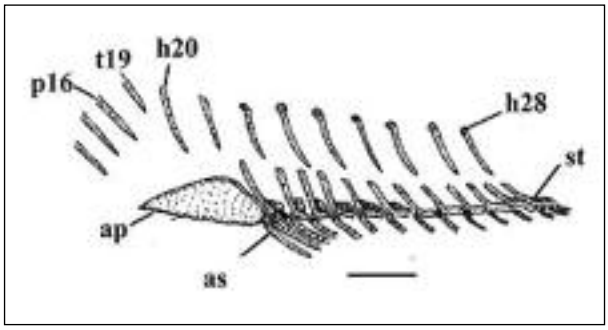


Fig. 13. *Bleheratherina pierucciae,* MNHN 1996-442, 37 mm SL. Anal fin and supports. Abbreviations: **ap**, anal plate; **h20**, haemal spine of vertebra 20; **h28**, haemal spine of vertebra 28; **p16**, pleural rib 16; **sp**, anal fin spine; **st**, fin stay; **t19**, transverse process of vertebra 19. Scale bar: 1 mm.

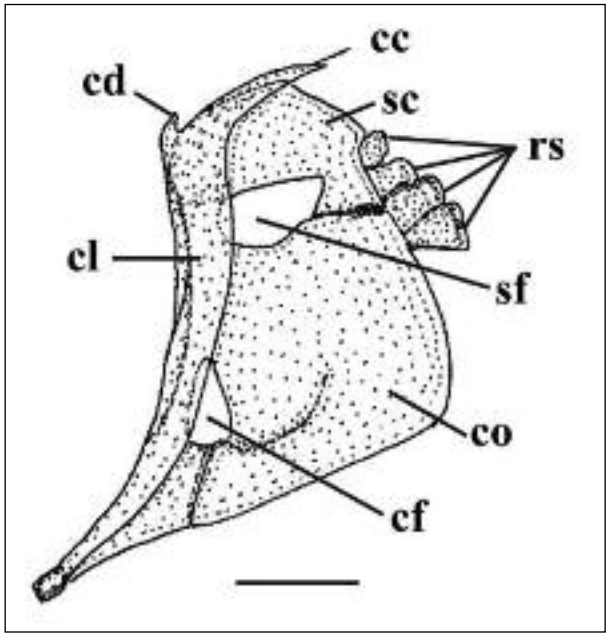


Fig. 14. *Bleheratherina pierucciae,* MNHN 1996-442, 37 mm SL. Pectoral fin. Abbreviations: **cc**, cleithrum caudodorsal process; **cd**, cleithrum dorsal spinous process; **cf**, coracoid foramen; **cl**, cleithrum; **co**, coracoid; **rs**, proximal radial; **sc**, scapula; **sf**, scapula foramen; Scale bar: 1 mm

Baudelot's ligament inserting on medial face of incisure; scapula irregular, scapular foramen at ventral border; four proximal radials uniformly broad; pectoral spur and first two rays supported by scapula, ventral rays supported by proximal radials; supracleithrum elongate, attached to lateralface of cleithrum about dorsal incisure; postemporal medially attached to lateral face of supracleithrum; posttemporal dorsal ramus contacting epiotic, horizontal ramus developed in ligament from intercalary; dorsal postcleithrum ovoid, contacting first two epineurals, deep to angle of cleithrum caudodorsal process; ventral postcleithrum elongate, coursing from lateral face of second pleural rib to distal angle of first pleural rib.

Pelvic fin elongate, dorsolateral process attached to fifth pleural rib; two muscular processes on ventral aspect of pelvic fin; pelvic medial process well developed, overlapping contralateral structure, bearing elongate cranial and caudal spinous processes (Fig. 15).

Etymology: The names refer to the discoverers of this new fish, Heiko Bleher and Paola Pierucci, both having collected in the most inaccessible parts of the world frequently under the most difficult conditions. The suffix "ae" in *pierucciae* pertains to the gender of the collector.

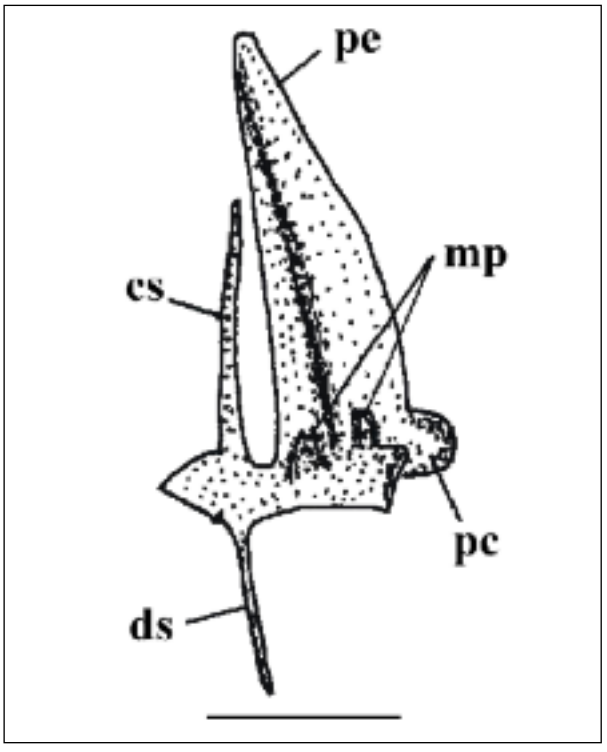


Fig. 15. *Bleheratherina pierucciae*, MNHN 1996-442, 37 mm SL. Pelvic fin in ventral aspect. Abbreviations: **cs,** pelvic medial cranial spinous process; **ds,** pelvic medial caudal spinous process; **mp,** muscular process; **pc,** pelvic caudodorsal process; **pe,** pelvic lateral plate. Scale bar: 1 mm.

DISCUSSION

Dyer & Chernoff (1996) defined Atherinidae, comprising 12 genera grouped into three subfamilies. These subfamilial definitions are outlined below.

Atherinomorinae comprises *Atherinomorus, Hypoatherina* and *Stenatherina, Teramulus* and *Alepidomus.* This subfamily is diagnosed by: the postemporal sensory canal oriented along the dorsal arm of postemporal bone, the parasphenoid fossa with ventral fenestra, the fibrocartilagenous submaxillary meniscus and the presence of hyomandibular nerve foramen.

Craterocephalinae are defined by two characters: a nasal ventromedial ligament to the palatine and the anterior palatine process directed dorsally, supported by the presence of a large submaxillary meniscus. The inclusion of *Allanetta* and *Quirichthys* as two nominal genera in this family is disputed by the present authors (see Crowley 1990, Patten 1978, Aarn 1998) who do not consider these genera distinct from *Craterocephalus* despite Dyer & Chernoff's (1966) arguments to the contrary.

External morphology of *Bleheratherina pierucciae* suggests that it could be a close relative to *Craterocephalus*, which includes marine, estuarine and freshwater species. For this reason, several species of this genus (Table II) were included in this study.

Atherininae includes *Atherina, Atherinason, Atherinosoma, Kestratherina* and *Leptatherina,* defined by these same authors as those members, which have the A1 muscle mandibular tendon and the posterior position of the pelvic girdle.

Dyer & Chernoff's (1996) recognition of the three atherinid subfamilies is borne out by a much earlier study by Ivantsoff (1978). Using a BMDP2M cluster analysis of cases based on 40 meristic and morphometric characters and an examination of about 1300 specimens and 32 nominal atherinid species had shown that all species of *Craterocephalus* clustered together, then with species of *Atherinosoma. Atherinomorus, Hypoatherina* and *Stenatherina* which clustered together as did the species of *Atherina. Atherinason* clustered with *Atherina* suggesting close affinity there as well (Fig. 16).

Bleheratherininae is now added to the family Atherinidae. Whilst this work does not include a cladistic analysis to define this new subfamily or use of the cluster analysis procedure at this point in time, the new species clearly represents a distinct new group which can be distinguished by:

1. A very thick labial ligament
2. The unique shape of the maxilla not observed in any other species of atherinid
3. A very long premaxillary process
4. The mesethmoid appearing to be absent, a feature which may be variable as it is in species of *Craterocephalus*
5. A finger-like palatine with a blunt top; there is a longish ligament to the nasal
6. The nasal lacking a ventral palatine process
7. The first infraorbital being free, the second and third appearing to be fused
8. Hypurals 1 and 2 being fused, unlike hypurals 3, 4, 5
9. The premaxilla being triangular laterally rather than curved
10. The coronoid process of the dentary being very large and squarish
11. The articular peak being very low

A comprehensive osteological comparison of all

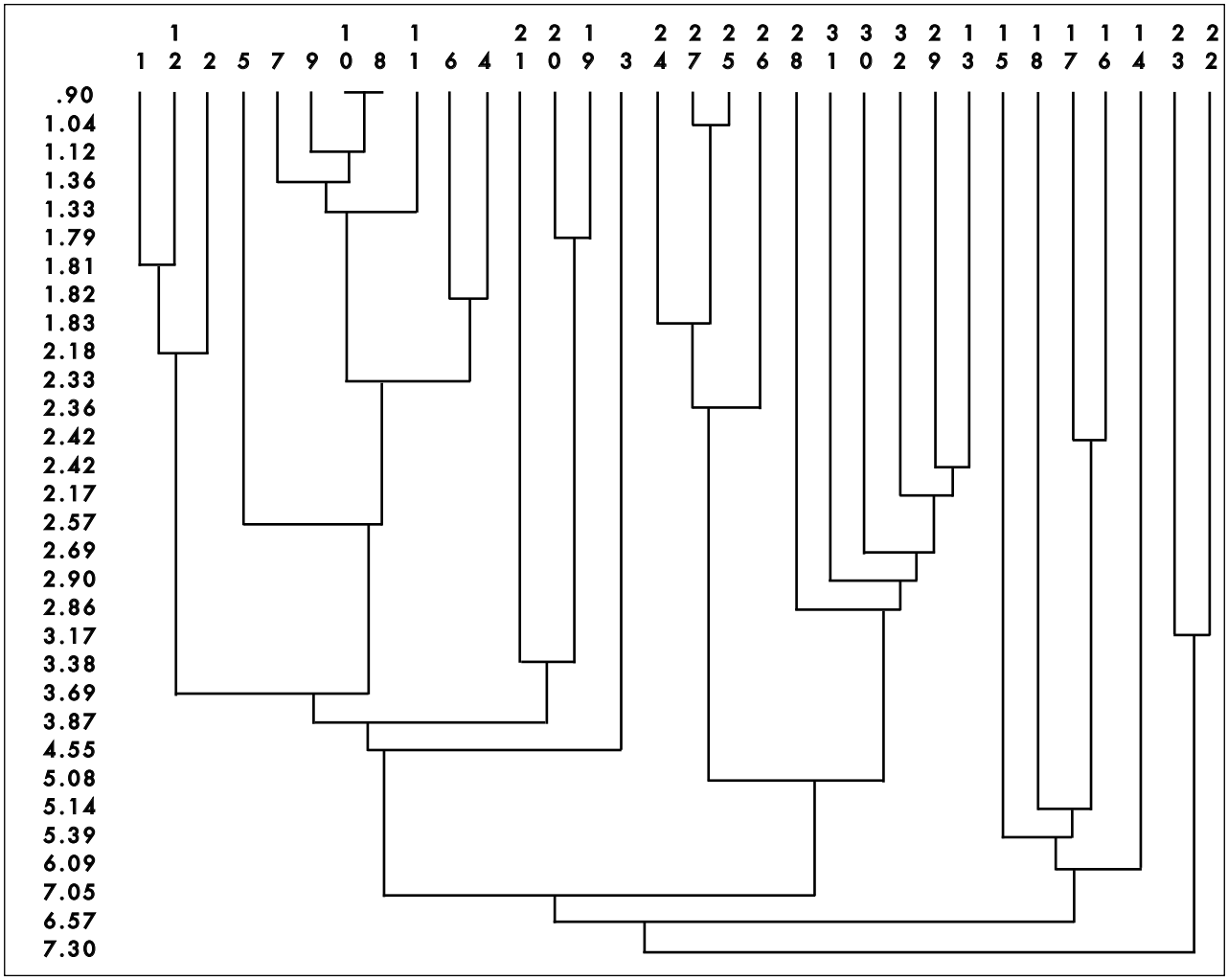


Fig. 16 Meristic and morphometric attributes examined by BMDP2M cluster analysis of 32 species of atherinids (Ivantsoff 1978). The analysis is based on 40 characters and about 1400 specimens. 1. *Craterocephalus honoriae,* 2. *C. pauciradiatus,* 3. *C.eyresii,* 4. *C. cuneiceps,* 5. *C. marjoriae,* 6. *C. dalhousiensis,* 7. *C. lacustris,* 8. *C.s. stercusmuscarum,* 9. *C. randi,* 10. *C. s. fulvus,* 11. *C. nouhuysi,* 12. *C. mugiloides,* 13. *Stenatherina panatela,* 14. *Atherinason hepsetoides,* 15. *Kestratherina esox,* 16. *Atherina boyeri,* 17. *A. presbyter,* 18. *A. hepsetus,* 19. *Atherinosoma microstoma* 20. *Atherinosoma elongata,* 21. *Leptatherina presbyteroides, 22. Atherion elymus,* 23. *A. maccullochi,* 24. *Atherinomorus endrachtensis,* 25. *Atherinomorus ogilbyi,* 26. *A. capricornensis,* 27. *A. lacunosus,* 28. *Hypoatherina tropicalis,* 29. *H. temminckii,* 30. *H. barnesi,* 31. *H. valenciennei, 32. H. ovalaua.*

then known Atherinidae was done by Patten (1978). The above features are based on present observations as well as Patten's earlier studies.

The mouthparts in *Bleheratherina pierucciae* are very different to those of any members of the three subfamiliies defined by Dyer & Chernoff (1996). The combination of other features, which make *Bleheratherina. pierucciae* distinct, are:

1. The teeth in jaws are sparse and quite small. They are also small on the mesopterygoids and absent on vomer.
2. Teeth on basibranchials are very small, sparse and distributed in tooth patches.
3. The fifth ceratobranchial is shallow, triangular, with small teeth anteriorly, becoming larger posteriorly.

It is not at all surprising that all of the Old World atherinids bear relationships to one another. As previously mentioned, atherinids are known from the late Eocene and Early Miocene (Svichenskaya 1973) as well as Pliocene (Gaudant 1978). Prior to the formation of the Mediterranean, the Tethys Sea allowed continuous distribution of atherinids into what is now the Indian and the western Pacific Ocean. Consequently, atherinids occur to the south along the west African coast *(Atherina* spp.*, Teramulus),* east along the Indian Ocean coastline *(Atherinomorus, Hypoatherina* spp., *Atherion)*, Indonesian and Philippine Archipelagos and north as far as Japanese waters *(Atherinomorus, Hypoatherina, Stenatherina* spp.), New Guinea and adjacent islands (freshwater *Craterocephalus* spp. as well as the marine species of the western Pacific) and Australia where speciation has resulted in new genera *(Atherinason, Kestratherina, Leptatherina* and *Atherinosoma)* with much inland and coastal speciation of *Craterocephalus* spp. New Caledonia is now known to have a fresh water atherinid.

Whether speciation occurred due to vicariant events as continents drifted, or dispersal, would be a matter of conjecture without a serious analysis of post Mesozoic geological events. Suffice it to say that conditions were conducive to speciation. Apart from atherinids, other closely related families such as Bedotiidae, Rheoclidae, Telmatherinidae Melanotaeniidae and Pseudomugilidae, have also evolved to mostly occupy freshwater habitats in Madagascar, Sulawesi, New Guinea and Irian Jaya, and Australia as well as some small adjacent islands in the Banda and Arafura Seas.

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REFERENCES

AARN 1998. Aspects of the biology of Melanotaeniiidae (Teleostei; Atherinomorpha. Unpublished Ph.D. thesis, Macquarie University, Sydney.

AARN & IVANTSOFF, W. 1997. Descriptive anatomy of *Cairnsichthys rhombosomoides* and *Iriatherina werneri* (teleostei: Atheriniformes, and a phylogenetic analysis of Melanotaeniidae. *Ichthyological Exploration of Freshwaters* **8** (2): 107-50.

CROWLEY, L. E. L. M. 1990. Biogeography and the systematics of the endemic fresh water fish genus *Craterocephalus* (Family Atherinidae). Unpublished Ph.D. thesis, Macquarie University, Sydney.

DYER, B. S. 2006. *Hypoatherina harringtonensis.* Fish Base. http://fishbase.org/

DYER, B. S. & Chernoff, B. 1996. Phylogenetic relationships among the atheriniform fishes (Teleostei, Atherinomorpha). *Zoological Journal of the Linnean Society* **117**: 1-69.

DINGERKUS, G. & UHLER, L. D. 1977. Enzyme clearing of Alcian blue stained whole small vertebrates for demonstration of cartilage. *Stain Technology* **52** (4)**:** 229-232.

GAUDANT, J. 1978. L'Ichthyofaune des Marine Messiniennes des Environs de Gabbro (Toscane, Italie): Signification Paleoecologique. *Geobios* **11** (6):905-910.

GRIFFITHS, J. R. 1971. Reconstruction of the South-West Pacific margin of Gondwanaland. *Nature* **234:** 203-207.

HUBBS, C. L. & LAGLER, K. F. 1958. *Fishes of the Great Lakes Region.* University of Michigan Press, Ann Arbor, Michigan, 213 pp.

IVANTSOFF, W. 1978. Taxonomic and systematic review of the Australian fish species of the family Atherinidae with reference to related species of the Old world. Unpublished Ph.D. thesis, Macquarie University, Sydney.

LARSON, H. K., IVANTSOFF, W. & CROWLEY, L. E. L. M.

2005. Description of a new species of freshwater hardyhead, *Craterocephalus laisapi* (Pisces, Atherinidae) from East Timor. *aqua, Journal of Ichthyology and Aquatic Biology* **10** (2): 81-88.

PATTEN, J. M. 1978. Osteology, relationships and classification of hardyheads of the subfamily Atherininae (Pisces, Atherinidae). Unpublished M.Sc. Thesis, Macquarie University, Sydney.

SANMARTIN, I. & RONQUIST, F. 2004. Southern Hemisphere Biology Inferred by Event-Based Models: Plant versus Animal Patterns. *Systematic Biology* **53** (2): 216-243).

SAEED, B., IVANTSOFF, W. & CROWLEY, L. E. L. M. 1994. Systematic relationships of atheriniform families within Division 1 of the Series Atherinomorpha (Acanthopterygiii) with relevant historical perspectives. *Journal of Ichthyology* **34** (9): 27-72.

SVICHENSKAYA, A. A. 1973. Mullet-like fossils in the U.S.S.R. *Trudi Instituta Akademii Nauk SSSR. (Moscow)* **138**: 1-64. (In Russian).

TAYLOR, W. R. 1967. Outline of a method of clearing tissues with pancreatic enzyme and staining bones of small vertebrates. *Turtox News* **45** (12): 308-309.

TAYLOR, W. R. & VAN DYKE, G. C. 1985. Revised procedures for staining and clearing small fishes and other Vertebrates for bone and cartilage study. *Cybium,* **9** (2): 107-119.

TRABELSI, M., MAAMOURI, F., QUIGNARD, J-P., BOUSSAID, M. & FAURE, E. 2004. Morphometric or morpho-anatomal and genetic investigations highlight allopatric speciation in Western Mediterranean lagoons within the *Atherina lagunae* species (Teleostei, Atherinididae). *Estuarine Coastal and Shelf Science* **61** (2004): 713-723.