

*DIAGRAMMA MELANACRUM* NEW SPECIES OF HAEMULID FISH FROM INDONESIA, BORNEO AND THE PHILIPPINES WITH A GENERIC REVIEW

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The haemulid fish *Diagramma melanacrum* is described from 5 specimens: 1 S of Lombok, 1 off Bali, 1 off Halmahera, and 2 from Bonebetang Is., Sulawesi. The species is known also from underwater photographs at the islands of Moyo and Romang, S Indonesia, Sipadan and Mabul off NE Borneo, Tomini Bay in Sulawesi, Bohol in the Philippines and Ashmore Reef, Timor Sea. It is distinct among haemulids in having 1X-X, 22-24 dorsal rays; 55-57 lateral-line scales; swimbladder with 3 small anterior projections; dorsal spine 3 or 4 longest, 1.8-2.9 in head; first dorsal spine about half length of second; pelvic fins reaching vent or slightly beyond, 1.2-1.3 in head; and in colour: pale yellow dorsally, shading through grey to whitish ventrally, with numerous small dark brown spots on head, body and dorsal fin, and caudal fin with lower fourth black; anal and pelvic fins mainly black. *Diagramma pictum* is divided into 5 geographically separate subspecies: *D. pictum pictum* (Thunberg), from the western Pacific and Indo-Malay Archipelago, excluding Australia and S New Guinea; *D. pictum labiosum* Macleay, from N Australia and S New Guinea; *D. pictum cinerascens* Cuvier, from the Bay of Bengal to the Persian Gulf; *D. pictum punctatum* Cuvier, from the Red Sea; and *D. pictum centurio* Cuvier, from East Africa. □ *Diagramma*, *Haemulidae*, *Indonesia*, *Philippines*, generic review.

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Haemulid fishes of *Plectorhinchus* and *Diagramma* (commonly Thicklips, Sweetlips, Rubberlips or Slateys) are important components of the fish fauna of coral reefs and adjacent habitats of the Indo-Pacific region. Indo-Pacific species of *Plectorhinchus* (23) and *Diagramma* (2) are strikingly different in colour as juveniles, and some have intermediate phases that differ from either the juvenile or the adult. Association of juveniles to adults is still not complete for all species. Like other haemulids, *Plectorhinchus* and *Diagramma* are primarily nocturnal. They tend to form small, nearly stationary aggregations on coral reefs by day and disperse at night for feeding on a wide variety of small benthic invertebrates.

In 1988, while diving in 36m on a reef off NW Moyo Island (8°13'N, 117°30'E) in S Indonesia, one of us (JER) encountered a small group of an unknown haemulid fish that was believed to be a species of *Plectorhinchus* Lacepède. A photograph (Fig. 3D) was sent to Roland J. McKay at the Queensland Museum who reported that it appeared to be undescribed.

The Queensland Museum has a specimen of this species, taken by trawl S of Lombok in the

Lesser Sunda Islands. It had been misidentified as *P. picus* and was reported and illustrated as such (Gloerfelt-Tarp & Kailola, 1984). Burgess et al. (1988, pl. 221) followed Gloerfelt-Tarp & Kailola with their artist's impression. Re-examination of the QM specimen revealed that it has X dorsal spines (XI-XIV in species of *Plectorhinchus*) and a swimbladder with 3 small anterior projections (not known in *Plectorhinchus*). These are features of *Diagramma* Cuvier to which it is now assigned.

Additional specimens are known from Denpasar, Bali and Halmahera, Indonesia and Bonebetang Is., Sulawesi. Underwater photographs by JER at Romang Island, Indonesia (7°34'S, 127°27'E); by Klaus E. Fiedler at Sipadan Island, Sabah; by Dieter Eichler at Bohol Island, Philippines; by Rudie Kuitert at Mabul, Borneo (QMNR 44-45) and the S edge of Tomini Bay, central-eastern Sulawesi (QMNR 46-47, QMNP 200); and by J. Barry Hutchins at Ashmore Reef, Timor Sea indicate that the species is widespread in the East Indian region.

*Diagramma* has generally been regarded as monotypic (Smith, 1962; McKay, 1983), although Kuitert & Debelius (e.g. 1994)

recognised 2 closely related species. Apart from the species described here, 5 apparently allopatric colour forms of *D. pictum* (Thunberg) occur, with the SE Asian form most distinctive. These variants are most readily recognisable in the large juvenile to subadult colour phases. All forms have previously been assigned specific names; however, with the exception of *D. labiosum* Macleay from Australia, these species have generally been regarded as junior synonyms of *D. pictum*. Attempts were made using colour and morphometric and meristic data, as well as through analysis of mitochondrial DNA, to determine whether some of these forms represent distinct species. The results of both methods were inconclusive. DNA analysis suggested that there may be almost as much genetic divergence among widely separated Australian populations of *D. 'labiosum'* as there is between some of these populations and *D. pictum* from Singapore. From these comparisons, as well as non-genetic examination of other colour forms from the Indian Ocean, it was concluded that more detailed genetic study would be necessary. All colour varieties appear to form geographically separate populations and should be afforded interim recognition as subspecies of *D. pictum*.

#### METHODS

The following measurements were taken: Standard length (SL) = tip of snout (not upper lip) to base of caudal fin (hypural plate flexure); body depth = maximum depth from base of dorsal spines; body width = maximum width just posterior to gill opening; head length (HL) = tip of snout (not including upper lip) to posterior margin of opercular membrane; snout length = tip of snout (not including lip) to fleshy margin of orbit; interorbital space = least fleshy width; preorbital depth = least depth from lower edge of orbit to above end of maxilla; caudal peduncle length = rear of anal fin base to base of caudal fin; spine and ray lengths were measured to the base of these elements; diameter of spots on the body were taken from spots of most common width on the upper body.

The last ray of the dorsal and anal fins was counted as one, although divided to base; pectoral ray counts include the upper rudimentary ray; lateral-line scale counts were made to the caudal flexure and include tubed scales only; gill-raker counts were made on the first arch and include all rudiments that are at least long as wide; the upper-limb gill-raker count was given first; the lower-limb count

includes the raker at the angle. Figures for the holotype are given in parentheses. Total length (TL) is quoted where size was estimated from photographs of fish not collected, and in the key, to assist in field identification of fresh or live material. Institutional abbreviations: Australian Museum, Sydney (AM); The Natural History Museum, London (BMNH); Bernice P Bishop Museum, Honolulu (BPBM); CSIRO Marine Laboratories, Hobart (CSIRO); Museum National d'Histoire Naturelle, Paris (MNHN); Miyazaki University, Miyazaki (MUFS); Northern Territory Museum, Darwin (NTM); Phuket Marine Biological Centre, Phuket (PMBC); Queensland Museum, Brisbane (QM); JLB Smith Institute of Ichthyology, Grahamstown (RUS1); Museum für Naturkunde an der Universität Humboldt zu Berlin (ZMB).

**DNA EXTRACTION, PCR AND SEQUENCING.** The genetic analyses and its statistical treatment were carried out by SC. Total genomic DNA was isolated from muscle tissue using sequential phenol/chloroform extractions following digestion with Proteinase K (Sambrook et al., 1989). Two oligoprimers were used to amplify a 420bp fragment of the mitochondrial Cytochrome B gene, L 1475 (Meyer, 1991) and CB2H (Palumbi et al., 1991). PCR mixtures contained 5µl of 1.25mM dNTP's (Promega), 5µl of Promega Polymerase reaction buffer, 1 unit of Promega *taq* DNA polymerase (#1662), 5µl of MgCl<sub>2</sub>, 2.5µl of each primer (10µM), 1µl of genomic template DNA, made up to a volume of 50µl with autoclaved distilled water and overlaid with 30µl of light mineral oil. The mixture was subjected to 35 cycles of the following thermal profile: 5min at 94°C (only on initial cycle), 30sec at 94°C, 30sec at 55°C, 1min at 72°C and 5min at 72°C (on final cycle only).

PCR-amplified DNA was then purified for sequencing using an agarose gel purification kit (QIAGEN). Light strand sequences were generated for each individual using Automated DNA Sequencing Technology (Applied Biosystems Inc.) following the manufacturers directions. Nucleotide sequences were aligned by eye and identical sequences were assigned the same haplotype number for subsequent statistical analysis.

Nucleotide diversity and nucleotide divergence statistics (Nei, 1987) were calculated within and among each pair of samples using REAP (McElroy et al., 1991). The phylogenetic relationships among haplotypes was represented

as a minimum spanning network. Minimum spanning trees were reconstructed with the aid of a program supplied by L. Excoffier.

### SYSTEMATICS

#### ***Diagramma melanacrum***

Johnson & Randall, sp. nov.

(Common name: Blackfin Slatey)

(Figs 1A-F, 8)

*Plectorhinchus picus* (non Valenciennes) Gloerfelt-Tarp & Kailola, 1984: 198 (fifth fig.), 199, 340.

*Plectorhinchus picus* (non Valenciennes) Burgess, Axelrod & Hunziker, 1988: pl. 221, lower right fig.

**ETYMOLOGY.** Greek *melanos*, black; and *akros*, tip or at the end; refers to black outer part of anal and pelvic fins and lower part of caudal fin.

**MATERIAL.** HOLOTYPE: QMI20291, 410mm SL, Indonesia, S of Lombok, 8°24'S, 116°01'E, trawl, T. Gloerfelt-Tarp, 1982. PARATYPES: QMI30725, 187mm SL, Indonesia, Kampung Loleba, Wasile district, Halmahera, 00°58'N, 127°56'E, trawl, H. Singou, 1/2/1979; QMI20285, 133mm SL, Indonesia, Denpasar, Bali, 8°46'S, 115°10'E, trawl, T. Gloerfelt-Tarp, 1982; BPBM 26719, (2) 219-254mm SL, Sulawesi, W side Bonebetang Is., spear, 20m, sand at reef edge, J.E. Randall, 8/9/1978. (Fig. 8).

**DIAGNOSIS.** Dorsal rays X-XI, 22-24; tubed lateral-line scales 55-57; outer row of teeth in jaws slightly enlarged, movable; swimbladder with 3 short anterior projections; third or fourth dorsal spine longest, 1.8-2.9 in head; first dorsal spine 1.7-2.3 in length of second; interspinous membranes of dorsal fin not incised; pelvic fins reaching vent or slightly beyond, 1.2-1.3 in head; body light yellow dorsally, shading to pale silvery grey on sides and ventrally, with numerous small dark brown spots, which are smaller and form oblique rows on body below lateral-line; head light purplish grey with numerous small brown spots, opercular membrane black; dorsal fin and upper 3/4 of caudal fin with small dark spots; lower 1/4 of caudal fin black; anal and pelvic fins mainly black. Juveniles from 133mm SL with spots about size of pupil on head, body, dorsal and caudal fins becoming progressively smaller and more numerous with age. Juveniles and subadults up to 254mm SL with narrow discontinuous wavy lines on operculum and cheeks, extending to about level of anterior margin of eye; these lines breaking up into spots in larger specimens.

**DESCRIPTION.** (Table 1) Dorsal rays X-XI, 22-24 (X, 22); anal rays III, 6-7 (III, 6); pectoral rays 17 (first ray rudimentary, second

unbranched); pelvic rays I, 5; tubed lateral-line scales 55-57 (56); scales above lateral-line to origin of dorsal fin 14-15(14); gill rakers 6-7+13-14 (6+14).

Body oblong and moderately deep, depth 38.0-41.5% SL (41.5%); body compressed, width 31.6-40.8% depth (39.4%); caudal peduncle depth 10.7-11.8% SL (10.7%); caudal peduncle length 22.6-25.2% SL (23.4%); head length 29.5-33.2% SL (31.2%); snout length 21.6-28.7% HL (27.3%); orbit diameter 21.1-29.3% HL (21.1%); interorbital space convex, width 25.8-33.6% HL (33.6%); preorbital depth 22.2-27.3% HL (27.3%).

Mouth small, slightly inferior, maxilla reaching a vertical from just beyond anterior margin to nearly the anterior third of eye, upper-jaw length 25.6-35.5% HL (35.5%); numerous rows of small slightly curved conical teeth at front of jaws, narrowing to a single row posteriorly, outer row slightly enlarged and somewhat movable; lips fleshy; chin with 3 pairs of prominent pores.

Scales small and ctenoid; lateral line gently curved, following dorsal contour of body; head scaled except snout just forward of anterior nostrils (to anterior nostrils in holotype), and a naked band to eye; small scales basally on median fins, those on dorsal extending about 1/4 distance to margin; opercle with a single flat blunt spine; margin of preopercle very finely serrate, serrae slightly larger at corner.

Dorsal fin scarcely notched, interspinous membranes not incised; base of spinous portion of dorsal fin 26.9-31.2% SL (27.8%); base of soft portion of dorsal fin 36.6-41.1% SL (36.6%); first dorsal spine about half length of second, 43.2-60.4% (49.3%); longest dorsal spine the third or fourth, 34.0-55.9% HL (third, 34.0%); longest dorsal soft ray 44.5-61.5% HL (44.5%); base of anal fin 28.9-35.7% HL (28.9%); first anal spine very short, 7.0-12.9% HL (7.0%); second anal spine 25.8-45.1% HL (25.8%); third anal spine 28.1-45.4% HL (28.1%); longest anal ray 53.1-69.6% HL (53.1%), reaching when adpressed more than half distance to caudal-fin base; caudal fin truncate to slightly emarginate, its length 20.0-23.8% SL (20.7%); longest pectoral ray 21.1-21.9% SL (21.5%); pelvic fins reaching to or slightly beyond vent, 24.1-27.4% SL (24.1%).

Colour in alcohol of holotype: light brown with numerous small dark brown spots on head, dorsally on body, dorsal fin, and upper 3/4 of



TABLE 1. Proportional measurements of the type specimens of *Diagramma melanacrum* expressed as a percentage of standard length.

	Holotype	Paratypes			
	QMI20291	QMI30725	QMI20285	BPBM 26719	BPBM 26719
Standard length (mm)	410.0	187.0	133.0	219.0	254.0
Body depth	41.5	38.0	38.7	40.4	41.3
Body width	16.3	15.5	12.8	12.8	14.4
Head length	31.2	33.2	30.8	29.5	31.7
Snout length	8.5	9.5	7.9	6.4	8.3
Upper jaw length	11.1	9.4	7.9	9.0	9.4
Orbit diameter	6.6	8.0	9.0	8.2	7.9
Preorbital depth	8.5	7.5	6.8	6.8	7.7
Interorbital width	10.5	8.6	8.4	9.2	9.8
Caudal peduncle depth	10.7	11.4	11.8	11.7	11.7
Caudal peduncle length	23.4	22.6	25.2	24.0	23.4
Spinous dorsal base	27.8	29.4	29.3	31.2	26.9
Soft dorsal base	36.6	36.7	36.6	38.8	41.1
First dorsal spine	4.3	7.5	10.2	6.1	6.0
Second dorsal spine	8.7	15.2	16.9	13.9	13.7
Third dorsal spine	10.6	16.7	16.8	14.3	14.7
Fourth dorsal spine	10.0	16.8	17.2	13.6	14.2
Fifth dorsal spine	9.9	15.8	15.6	13.0	13.4
Longest dorsal ray	13.9	20.3	15.8	18.2	16.1
Anal fin base	9.0	11.2	10.9	10.5	10.9
First anal spine	2.2	4.3	4.0	3.3	2.5
Second anal spine	8.0	13.0	13.9	12.1	11.6
Third anal spine	8.8	14.2	14.0	12.8	12.6
Longest anal ray	16.6	20.9	19.5	20.5	19.7
Caudal fin length	20.7	23.8	23.3	21.5	20.0
Longest pectoral ray	21.5	21.9	21.1	21.8	21.7
Longest pelvic ray	24.1	27.4	25.9	25.3	25.1

caudal fin; spots below lateral-line smaller, not as dark, very close-set, following centres of oblique scale rows; spots on snout and interorbital smaller and more close set than those on remainder of head and upper body; opercular membrane dark brown; lower 1/4 of caudal fin and all but basal part of anal and pelvic fins dark brown; pectoral fins dusky, the upper half of base with a dark brown bar that curves over dorsal edge of fin base to axilla. Paratypes, 133-254mm SL: Similar to holotype except spots on head, body and caudal fins progressively smaller and greater in number with increasing size. Operculum and cheeks with narrow discontinuous wavy longitudinal lines extending to about level of anterior of eye. Anteriorly, on snout, lines replaced by small dark brown spots as in holotype.

Colour in life from underwater photographs

(specimens not collected): snout, interorbital, nape, body mostly above lateral-line, dorsal fin, and upper 3/4 of caudal fin pale yellow with numerous small dark brown spots; body below lateral-line light grey with numerous faint close-set orange brown spots, smaller than those dorsally on body, and arranged in oblique rows; head light purplish grey with numerous small dark orange brown spots; ventral part of head and body whitish; opercular membrane black; lower 1/4 of caudal fin black; anal and pelvic fins whitish basally, soon shading to black distally, the leading edge of pelvics narrowly whitish; pectoral fins pale with dusky rays and a narrow dark reddish brown bar at base. Subadults of about 250mm TL with narrow discontinuous wavy longitudinal dark brown lines on head, extending from about anterior margin of eye to opercles. The colour pattern of small juveniles is unknown.

REMARKS. Kuitert (1993; 1996), Kuitert & Debelius (1994) and Eichler & Myers (1997) recognised 2 species of *Diagramma*, *D. pictum*

(Thunberg), widespread in the Indo-west Pacific excluding Australia and S PNG, and *D. labiosum* Macleay from Australia and S PNG. Sightings of both species from Flores, Indonesia were reported by Rudie H. Kuitert (pers. comm., 1996), but the presence of *D. 'labiosum'* in this area has not been substantiated by specimens or photographs. J. Barry Hutchins reported (pers. comm., 2000) that *D. 'labiosum'* was absent from Ashmore Reef. This is not surprising as the fish fauna of this reef has close affinities to Indonesia and includes species typically Indo-Malaysian, some of which are not known from Australian inshore waters (Allen, 1993). Another haemulid, *Plectorhinchus vittatus* (Linnaeus) is recorded from offshore reefs at Ashmore, Hibernia and Rowley Shoals, but not from other Australian waters.

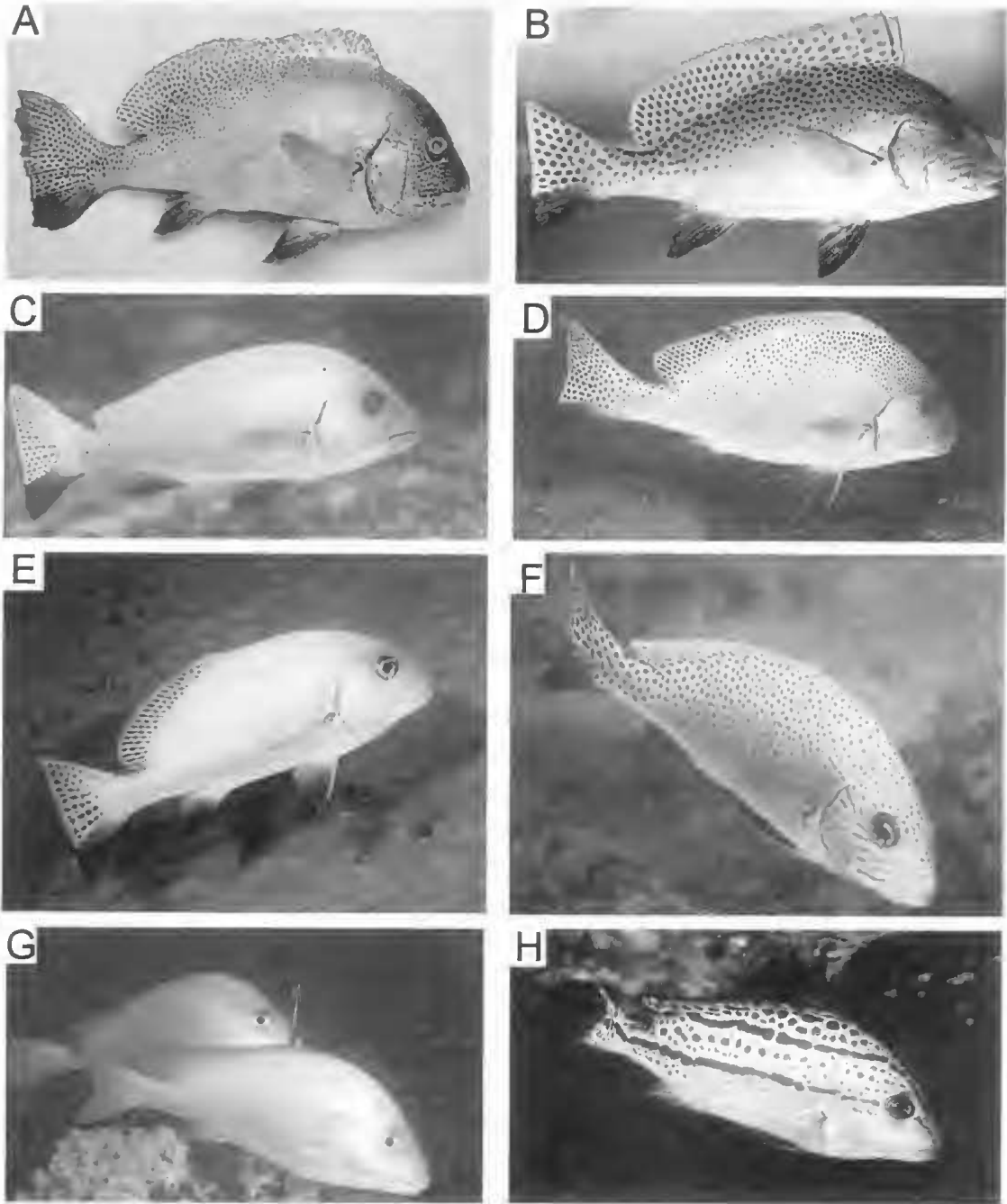


FIG. 1. A, *Diagramma melanacrum* Holotype, QM 1.20291, 410mm SL, Lombok, Indonesia, T. Gloerfelt-Tarp. B, *Diagramma melanacrum* Paratype, BPBM 26719, 254mm SL, Off Ujung Pandang, Sulawesi, J.E. Randall. C, *Diagramma melanacrum* ~350mm TL, Romang Island, Indonesia, J.E. Randall. D, *Diagramma melanacrum* ~330mm TL, Moyo Island, Indonesia, J.E. Randall. E, *Diagramma melanacrum* ~350mm TL, Tomini Bay, Sulawesi, R.H. Kuiter. F, *Diagramma melanacrum* ~250mm TL, Mabul, Borneo, R.H. Kuiter. G, *Diagramma pictum labiosum*, 300mm TL, Lizard Is., Australia, J.E. Randall. H, *Diagramma pictum labiosum*, ~130mm TL, Sydney Harbour, Australia, R.H. Kuiter.

TABLE 2. Meristic data of *Diagramma* species.

	Tubed Lateral-line Scales																											
	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78				
<i>melanaerum</i>	2	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>pictum labiosum</i>	-	-	-	-	2	1	-	1	1	1	1	4	7	6	7	10	3	2	4	4	2	4	-	1	-	-	-	
<i>pictum pictum</i>	-	-	4	3	5	5	3	1	1	5	9	4	2	5	2	3	2	1	-	2	-	-	-	-	-	-		
<i>pictum cinerascens</i>	1	5	1	7	3	2	1	2	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
<i>pictum centurio</i>	-	2	1	3	8	1	1	2	2	3	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
<i>pictum punctatum</i>	2	1	1	2	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		

	Gill Rakers																		
	Upper					Lower						Total							
	5	6	7	8	9	11	12	13	14	15	16	17	17	18	19	20	21	22	23
<i>melanaerum</i>	-	4	1	-	-	-	-	4	1	-	-	-	-	-	3	2	-	-	-
<i>pictum labiosum</i>	3	33	22	3	-	-	1	19	37	4	-	-	-	1	14	26	16	3	1
<i>pictum pictum</i>	1	18	26	7	1	-	-	9	36	6	1	1	-	-	6	14	21	6	5
<i>pictum cinerascens</i>	-	6	15	3	-	1	5	11	7	-	-	-	1	1	6	8	8	-	-
<i>pictum centurio</i>	-	1	9	16	2	-	-	-	12	16	-	-	-	-	-	6	9	13	-
<i>pictum punctatum</i>	-	6	2	-	-	-	-	2	3	3	-	-	-	-	2	3	1	2	-

	Dorsal Spines			Dorsal Rays						Pectoral Rays			
	IX	X	XI	20	21	22	23	24	25	26	16	17	18
<i>melanaerum</i>	2	3	-	-	-	1	-	4	-	-	-	5	-
<i>pictum labiosum</i>	12	50	-	-	-	3	16	29	12	2	-	16	13
<i>pictum pictum</i>	13	43	-	1	6	17	13	14	5	-	-	48	6
<i>pictum cinerascens</i>	2	21	1	-	3	11	8	2	-	-	-	20	4
<i>pictum centurio</i>	7	22	-	-	1	5	11	10	2	-	-	25	3
<i>pictum punctatum</i>	-	8	-	-	-	2	4	2	-	-	-	5	1

*Diagramma pictum* and *D. 'labiosum'* are distinguished on few characters other than colouration, with all meristic and morphometric values strongly overlapping (Tables 2, 3). Small juveniles are difficult if not impossible to separate. Given the similarity between *pictum* and *'labiosum'* there was some doubt as to whether they should be separated at the specific or subspecific level (as geographically separate colour forms). With no firm evidence of sympatry, which would lend support to the premise of separate species status, it was decided that some tests would be conducted to determine the genetic variability among and between Australian and SE Asian populations, and to see if these indicated more conclusive separation.

**DNA ANALYSIS.** Fresh frozen specimens of *D. 'labiosum'* were obtained from the following widely separated Australian localities: 1) Comboyuro Point, Moreton Bay, Qld (4 fish); 2) North West Island, Capricorn Group, Qld (4 fish); 3) Gulf of Carpentaria, Qld (3 fish); 4) off Port Headland, WA (3 fish). Specimens of *D. pictum* were obtained from Senoko Fishery Port, Singapore (4 fish). One specimen of

*Plectorhinchus flavomaculatus* (Ehrenberg, 1830) from off Mackay, Queensland, Australia was used to gain an outgroup sample. Frozen muscle tissue from the lower caudal peduncle was removed from each specimen for analysis.

TABLE 3. Selected morphometric data of *Diagramma melanaerum*, *D. pictum pictum* and *D. pictum labiosum*.

	<i>D. melanaerum</i>	<i>D. p. pictum</i>	<i>D. p. labiosum</i>
Number of specimens	5	33	40
Standard length (mm)	133-410	130-503	129-620
Percentage of standard length			
Depth	38.0-41.5	35.8-40.6	31.3-41.3
Head length (HL)	29.5-33.2	26.8-31.5	25.7-32.6
Orbit diameter	6.6-9.0	5.4-9.5	4.5-8.7
Caudal peduncle length (CPL)	22.6-25.2	22.9-27.9	24.2-28.9
Caudal peduncle depth (CPD)	10.7-11.8	9.6-11.9	8.7-12.3
Pelvic fin length	24.1-27.4	18.7-23.8	17.0-24.3
Ratio CPL:HL	1.2-1.5	1.0-1.3	0.9-1.3
Ratio CPD:CPL	2.0-2.2	2.0-2.8	2.2-3.1

TABLE 4. Cytochrome B nucleotide diversity within (bold) and among pairs of samples of *D. pictum* (5) and *D. 'labiosum'* (1-4).

		1	2	3	4	5
1	Moreton Bay (n = 4)	<b>0.000</b>	0.000	0.003	0.002	0.005
2	North West I. (n = 4)	0.000	<b>0.000</b>	0.003	0.002	0.005
3	Gulf of Carpentaria (n = 3)	0.005	0.005	<b>0.003</b>	0.001	0.003
4	North West Shelf (n = 3)	0.005	0.005	0.006	<b>0.006</b>	-0.001
5	Singapore (n = 4)	0.005	0.005	0.005	0.003	<b>0.000</b>

Our aim with the mitochondrial DNA analysis was to determine if each of the *D. 'labiosum'* and *D. pictum* forms formed monophyletic mtDNA clades. Such a pattern would have allowed us to conclude that the 2 colour forms have existed allopatrically for a considerable amount of time (at least 4N generations (Avise et al., 1984)) and may have provided an insight to the 2 forms being separate species. The results are however inconclusive as mtDNA haplotypes do not cluster by colour form or location (Tables 4, 5). That haplotype 4 is shared between forms in the North West Shelf and Singapore provides evidence of gene flow between the 2 forms (Fig. 2). It should be noted however that several Indo-Pacific species of butterflyfishes *Chaetodon* are paraphyletic for Cytochrome B sequences despite being considered good species (McMillan & Palumbi, 1995). This may reflect the rapid diversification of the *Chaetodon* species complex and suggests that there has not been sufficient time since speciation for complete mtDNA lineage sorting. Such a situation cannot be rejected for *D. 'labiosum'* and *D. pictum* on the basis of our cytochrome B data set.

Thus mitochondrial DNA analysis alone does not provide a perfect test of species status due to its haploid non-recombining nature (Avise, 1994). An assay of nuclear genes from areas where the two forms are sympatric would have provided a more powerful test of the taxonomic status of the two forms. This luxury was not afforded in the present study for two reasons. First, reports of the two forms existing in sympatry are anecdotal at best. The one report from southern Indonesia is based only on sightings of large adults, in which colour is a less reliable distinguishing feature. No specimens of *D. 'labiosum'* from this region have been located. Despite extensive collecting efforts off northern

TABLE 5. Cytochrome B haplotype frequencies for samples of *D. pictum* and *D. 'labiosum'*.

Location	Haplotype Frequencies				
	1	2	3	4	5
Moreton Bay	4	-	-	-	-
North West Is.	4	-	-	-	-
Gulf of Carpentaria	-	2	1	-	-
North West Shelf	-	1	-	1	1
Singapore	-	-	-	4	-

Australia, no specimens of the *D. pictum* form have been found. Second, tissue material could not be transported back to the laboratory from SE Asian sites in good enough condition to permit allozyme electrophoresis to be carried out.

On this basis, and results enunciated below, it was decided that the separate colour forms be recognised as subspecies of *D. pictum* Thunberg.

**Diagramma pictum pictum** (Thunberg, 1792)  
(Common name: Yellow-spotted Slatey)  
(Figs 3A-H, 8)

*Perca picta* Thunberg, 1792 (Japan).  
*Perca pertusa* Thunberg, 1793 (Japan).  
*Holocentrus radjaban* Lacepède, 1802 (East Indies).  
*Diagramma balteatum* Cuvier, 1830 (Java).

REMARKS. *D. pictum pictum* is known from the W Pacific and Indo-Malay Archipelago, N to Japan and S to New Caledonia, but excluding Australia and S New Guinea. Various stages are figured in colour, from Japan (Burgess & Axelrod, 1972, pls 392-393; Masuda et al., 1984; Masuda & Kobayashi, 1994:162, pls 1-3, 5-6 (note fish in pl. 4 are *D. pictum labiosum* from the Great Barrier Reef, Australia); Okamura et al., 1997: 352, 12 pls of specimens 2.5 to 65cm; Masuda, 2000: 96), through Taiwan (Shen, 1984:

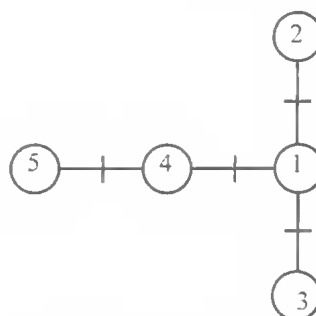


FIG. 2. Minimum spanning network of the relationships among Cytochrome B sequences. Each dash represents a single nucleotide substitution.

pl. 65 no. 327-6a,b,c, pl. 66 no. 327-8b&c; Burgess & Axelrod, 1974: pls 271, 275-276), the Philippines (JER photo QM NR63), Palau (Myers, 1999, pl. 67, a&b), Indonesia (Gloerfelt-Tarp & Kailola, 1984; Kuitert & Debelius, 1994; photos JER (QM NR62) and R.H. Kuitert (QM NR52)), Rabaul, New Britain (Allen & Steene, 1987, pls 50-8), New Caledonia (Fourmanoir & Laboute, 1976: 99; JER photo QM NX793-795) and Santo, Vanuatu (Burgess & Axelrod, 1975, pl. 222-223). Fowler (1931) illustrated in black and white a range of 12 juvenile colour variations, one of which (fig. 22, lower left) is similar to a juvenile paratype of *D. melanacrum* (QMI20284), but lacks the width and intensity of black pigmentation to the lower caudal lobe.

*D. pictum pictum* is distinguished by relatively large, close-set, yellow to burnt orange spots on head, body and unpaired fins in juveniles from about 160mm TL, subadults, and at least smaller adults. This subspecies progresses from the striped to fully spotted phase at 160-200mm TL. Diameter of the spots varies from about 1-3 times in the pupil or 2-5.3 times in the eye diameter. Short bars and wavy lines of the same colour are often present, mostly on the suborbital and operculum, in specimens larger than 160mm TL, but usually break up into spots in large specimens. Specimens to about 600mm TL usually retain conspicuous, although relatively smaller, spots on the body and particularly the cheeks. In fish above 800mm TL, spots on the body have often faded into a generally plain slate or silver-grey ground colouration, but there are usually at least some yellowish spots remaining on the lower head. We have no records of specimens with scattered dusky blotches, as is common in other large *D. pictum* subspecies. This subspecies also lacks the rows of bronze centres to individual scales present in *D. pictum punctatum*. The only other subspecies to share yellowish spots, or yellow pigmentation on the unpaired fins of all but small juveniles, is *D. pictum cinerascens*. However, in the latter the spots fade and disappear from the body at a much earlier stage, at about 300 to 400mm TL. Other subspecies have darker, usually brownish spots. The median tubed lateral-line scale count of 65 (range 57-74) is lower than the median of 69 recorded for *D. pictum labiosum* (range 59-78), but is higher than that for all other *pictum* subspecies (median 58-59, range 55-66). The median dorsal ray count (23) is lower than for *D. pictum labiosum* (24), but higher than that of *D.*

*pictum cinerascens* (22). The median total gill raker count (21) is higher than that for *D. pictum labiosum* and *D. pictum cinerascens* (20) and lower than that for *D. pictum centurio* (22).

**Diagramma pictum labiosum** Macleay  
(Common name: Australian Slatey)  
(Figs 1G-H, 4A-H, 8)

*Diagramma labiosum* Macleay, 1883 (Wide Bay, Queensland).

REMARKS. *D. pictum labiosum* is known from S New Guinea and N Australia, from Houtman Abrolhos, WA, E to Lord Howe Island and Sydney, NSW. It is figured in Burgess & Axelrod (1976: pls 345 & 350-354), Coleman (1980: 160), Grant (1982: pl. 190; 1987: pl. 456), Sainsbury et al. (1985: 215), Allen & Steene (1987: pls 51-2), Randall et al. (1990 & 1997: 191), Kuitert (1993, 1996) and Masuda & Kobayashi (1994: 162, pl. 4).

Macleay (1883) described *D. labiosum* from a single 300mm specimen. The type is no longer extant (Eschmeyer, 1998). Macleay made reference to dense spotting on the soft dorsal and caudal fins, but not to any spots on the head and body. He stated that 'the general colour is a dark silvery bluish grey'. This is consistent with fresh specimens from Australian waters, some of which had lost all spots on the head and body by 250mm TL, and all by 300-350mm TL. It is usual for other subspecies, except for *D. pictum centurio* from E Africa, to exhibit spots at 300mm.

*D. pictum labiosum* has relatively small, close-set dark brown to bronze spots on the head and body in specimens from about 150-300mm TL. These spots vary in diameter from 2.6-6.5 times in pupil or 4.7-11.6 times in eye, rapidly diminishing in size on fish from 150-200mm TL. The stripes of the juvenile stage break up into a larger number of much finer spots than in any other subspecies. Golden-brown to dusky spots and short bars may be present on the suborbital and operculum of juveniles, but fade and disappear by about 200mm TL. Small dark brown spots gradually fade and disappear from the anterior toward the posterior part of the body with age. From 200-300mm TL spots on the body have reduced to a cluster of spots less than 1/4 pupil diameter, peppered on the upper half of the caudal peduncle. Beyond 350mm TL, all spots have disappeared and the head and body are plain slate to sooty silver-grey, often with some violet reflections on the cheeks. Adults, especially those in excess of 500mm TL, often develop scattered diffuse dusky blotches. In most



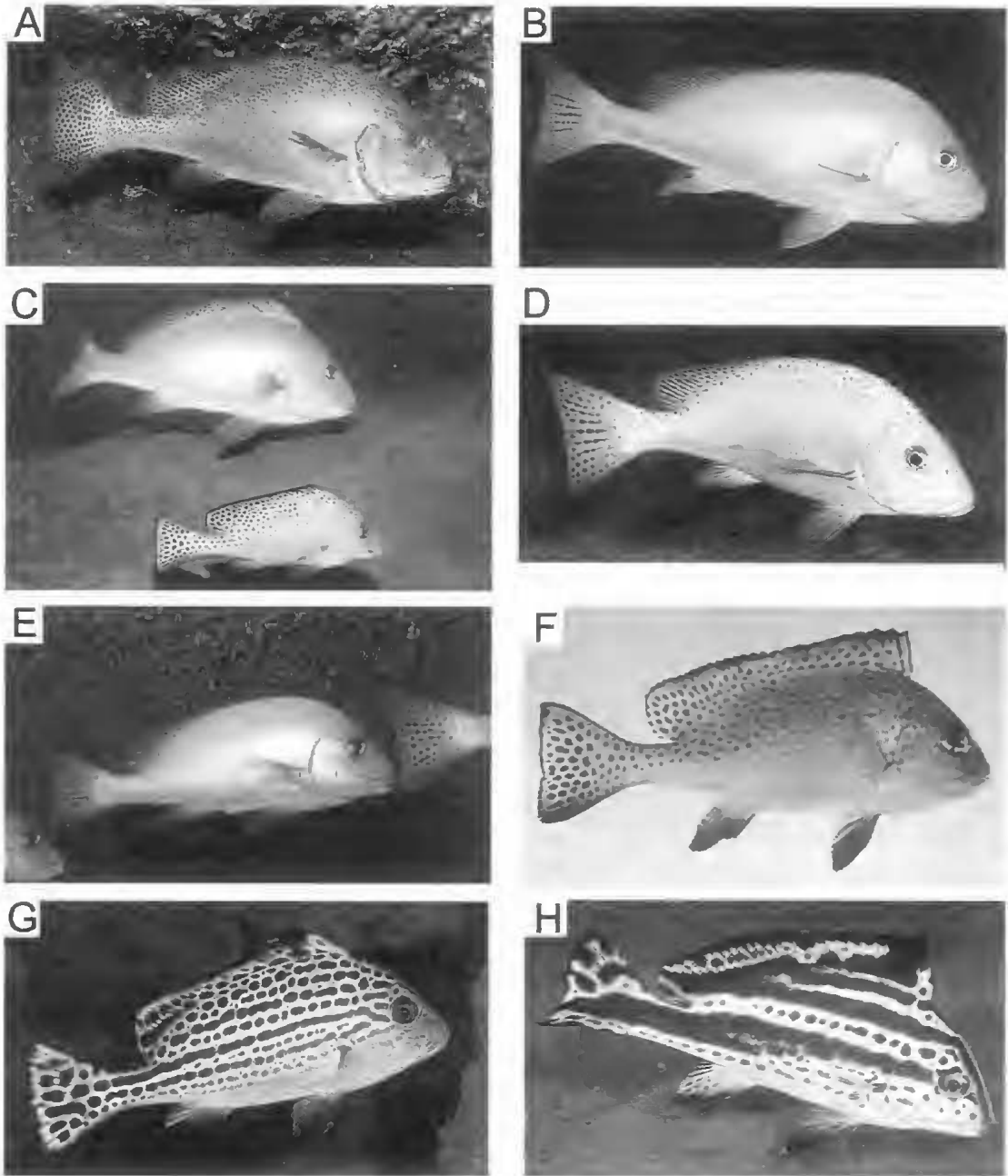


FIG. 3. *Diagramma pictum pictum*; A, ~800mm TL, Maumere, Flores, R.H. Kuiter; B, 800mm TL, Menjangan Is., Bali, R.H. Kuiter; C, ~550mm TL and ~250mm, Flores, Indonesia, R.H. Kuiter; D, ~350mm TL, Tomini Bay, Sulawesi, R.H. Kuiter; E, ~300mm TL, New Caledonia, J.E. Randall; F, 236mm TL, Dumaguete, Philippines, J.E. Randall; G, ~200mm TL, Amed, Bali, R.H. Kuiter; H, ~150mm TL, Bitung, Sulawesi, R.H. Kuiter.

individuals numerous small spots persist on the caudal and rear of the soft dorsal fin, even in specimens of 1000mm TL. At all comparable

sizes, spots on these fins are greater in number and smaller in diameter than in *D. pictum pictum*. In specimens 350-500mm TL, a maximum of

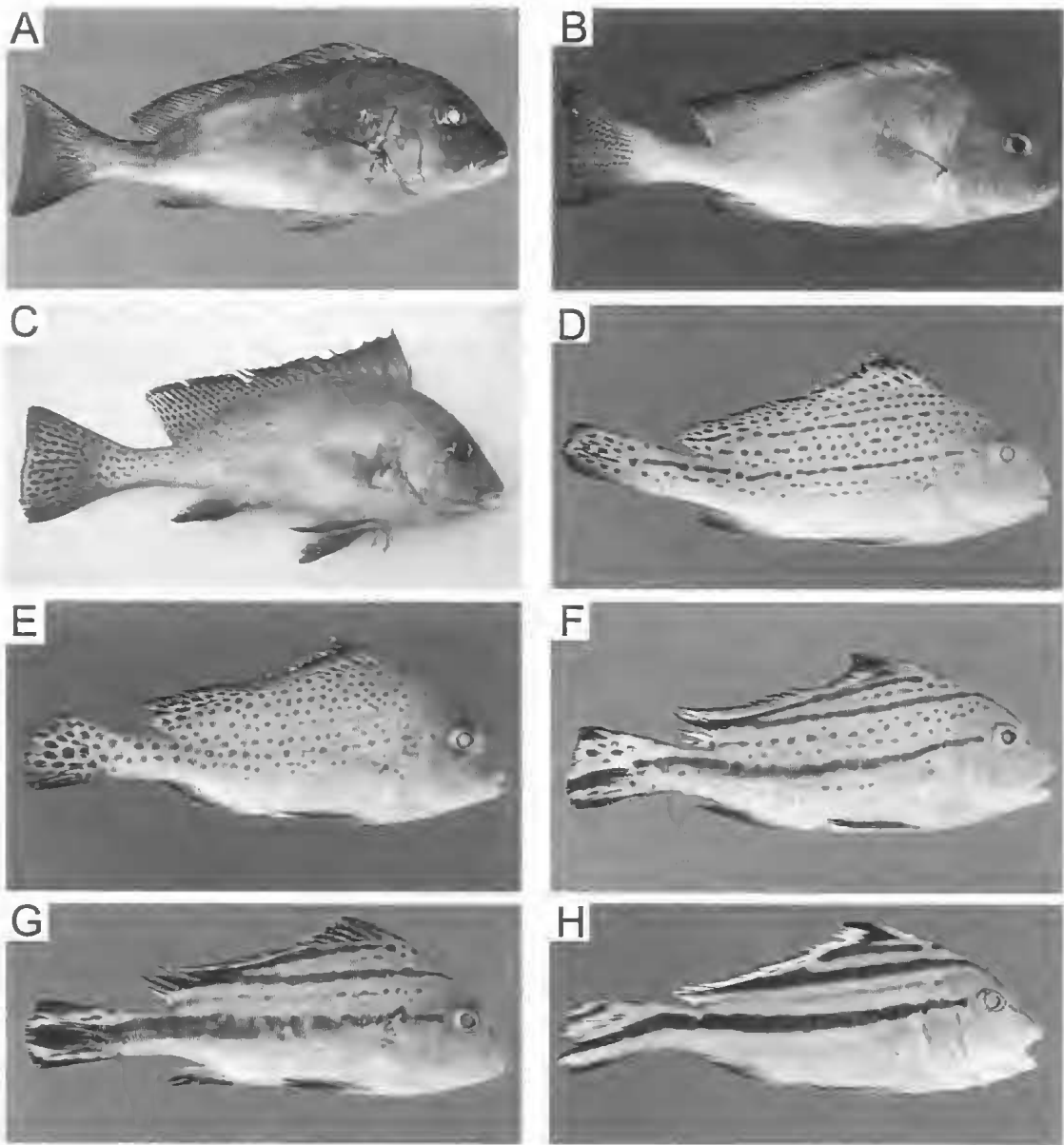


FIG. 4. *Diagramma pictum labiosum*; A, 392mm TL, Moreton Bay, Australia, J.W. Johnson; B, 335mm TL, North West Is., Great Barrier Reef, Australia, J.W. Johnson; C, ~220mm TL, Shark Bay, Western Australia, R.J. McKay; D, 160mm TL, Gulf of Carpentaria, Australia, J.W. Johnson; E, 146mm TL, Gulf of Carpentaria, Australia, J.W. Johnson; F, 136mm TL, Gulf of Carpentaria, Australia, J.W. Johnson; G, 126mm TL, Gulf of Carpentaria, Australia, J.W. Johnson; H, 108mm TL, Gulf of Carpentaria, Australia, J.W. Johnson.

9-14 rows of spots on the soft dorsal fin membrane and 12-20 rows of spots on the caudal fin membrane parallel to the fin rays were recorded, versus a maximum of 4-6 and 6-10 respectively for *D. pictum pictum*. This species lacks yellow or orange spots at any size and has

no bars or wavy lines on the head, except occasionally in small juveniles. Adults have a scarlet to crimson-red throat, from the rear of the palate to the interior of the operculum and branchiostegal membranes, as well as the outer

gill arch membranes, broadly in common with other subspecies.

*D. pictum labiosum* progresses from a striped to a fully spotted stage at a smaller size than other subspecies of *Diagramma* (130-160mm TL); and spots, while present, are smaller and more close-set at any given size than other subspecies. Subadults lose all markings on head and body at a smaller size (300-350mm TL) than all other subspecies, except some *D. pictum centurio* from E Africa. It differs from other subspecies by a higher median lateral-line scale count (69 versus 57-65) and, more importantly, the upper range of lateral line scale counts in all other *Diagramma* (except *D. pictum pictum* with 74), is below the median for *D. pictum labiosum*. The median total gill raker count (20) is lower than for all other *D. pictum* subspecies (21 or 22), except *D. pictum cinerascens*; and the median soft dorsal ray count (24) is higher than all other *D. pictum* subspecies (22 or 23).

***Diagramma pictum cinerascens* Cuvier**  
(Common name: Fork-striped Slatery)  
(Figs 5A-H, 8)

*Diagramma cinerascens* Cuvier, 1830 (Trincomalee, Sri Lanka).

*Diagramma blochii* Cuvier, 1830 (Trincomalee, Sri Lanka).

*Diagramma poecilopterum* Cuvier, 1830 (Pondicherry, India).

REMARKS. *Diagramma pictum cinerascens* occurs in the Indian Ocean from the Bay of Bengal to the Persian Gulf. It is figured in colour photographs taken by R.H. Kuiter (QM NR48-49), Kuiter (1998:104), JER (QM NL742) and H. Voigtman (in Debelius, 1999: 100, top left) from the Maldives; from Sri Lanka (Debelius, 1999: 100); from the Persian Gulf by Randall (1992, pl. 130a) and J. Hoover (in Randall, 1995, pls 528-530) and from the Gulf of Oman by P. Woodhead (in: Debelius, 1993: 127 top left, p. 128 centre, and Debelius, 1998: 88 centre) from Ras al Hamra, Oman.

The brief original description of *D. cinerascens* is from a 256mm SL specimen, MNHN 7803 (Bauchot et al., 1983). The holotype has a uniform brown body and small darker brown spots on the rays of the dorsal and anal fins. Cuvier (1830) gave a dorsal ray count of 'XII/16?' for *D. blochii*, which suggests a species of *Plectorhinchus*, however his description was based on a drawing by Raynaud and the query given after the count suggests he had difficulty in discerning the true fin formula from the drawing. His dorsal, anal and pectoral

fin formulae for *D. poecilopterum* are also shown to be erroneous by Smith (1962). Smith examined the holotype and paratype (MNHN 7811 from Pondicherry and 7810 from Trincomalee, respectively) and obtained counts consistent for this form (Table 2). Stripes on the 155mm SL holotype, as depicted in Smith (1962: fig. 22), are usual for specimens of this size.

This subspecies differs from others in the configuration of the body stripes of juveniles, the size of the spots, and nature of the lines on the cheeks and operculum of large juveniles to small adults. Juveniles progress from a striped to a fully spotted phase at 180-240mm TL. Juveniles of about 150mm TL often have broad, clearly defined body stripes, not yet beginning to break into broken lines or numerous spots, as is usual for other *Diagramma* of this size. As mentioned by Day (1878), unlike juvenile stages of any other form of *Diagramma*, the second and third stripes on the body merge to form a single stripe above the posterior half of the pectoral fin (Day, 1878, pl. 21, fig. 3; Debelius, 1993, fig. p. 127; Randall, 1992, pl. 130a; Smith, 1962, fig. 22). At the point where the stripes merge, there is often a small break or up-curved interruption in the stripe. The front of the head, including the snout to the interorbital and suborbital, as well as much of the dorsal and caudal fin membrane, may be bright yellow in fish of up to about 200mm TL. In specimens from about 200-350mm TL, there are usually wavy yellowish lines or spots on the operculum and cheeks. The lines are narrow in larger specimens, but vary in width in small specimens. Spots on the body are tan to orange-brown, in longitudinal rows. In specimens about 180-300mm TL, the spots range from 3.1-6 in eye diameter. The spots are generally smaller and more close-set than *D. pictum pictum*, larger and more close-set than *D. pictum centurio* and larger and more sparse than in *D. pictum labiosum*. Unlike the latter, they do not fade and disappear first from the dorso-anterior region, producing a life-stage with a cluster of spots on the upper part of the caudal peduncle only. The only other subspecies to have lines or bars on the head of specimens above 180mm TL is *D. pictum pictum*, however, in the latter, these are usually broader and accompanied by yellow or orange spots on the body. Specimens in excess of 400mm TL are generally plain slate to silver-grey, often with scattered irregular dusky blotches on the head and body, similar to large *D. pictum labiosum*. However, unlike the latter, narrow wavy yellowish lines or small spots may still be evident

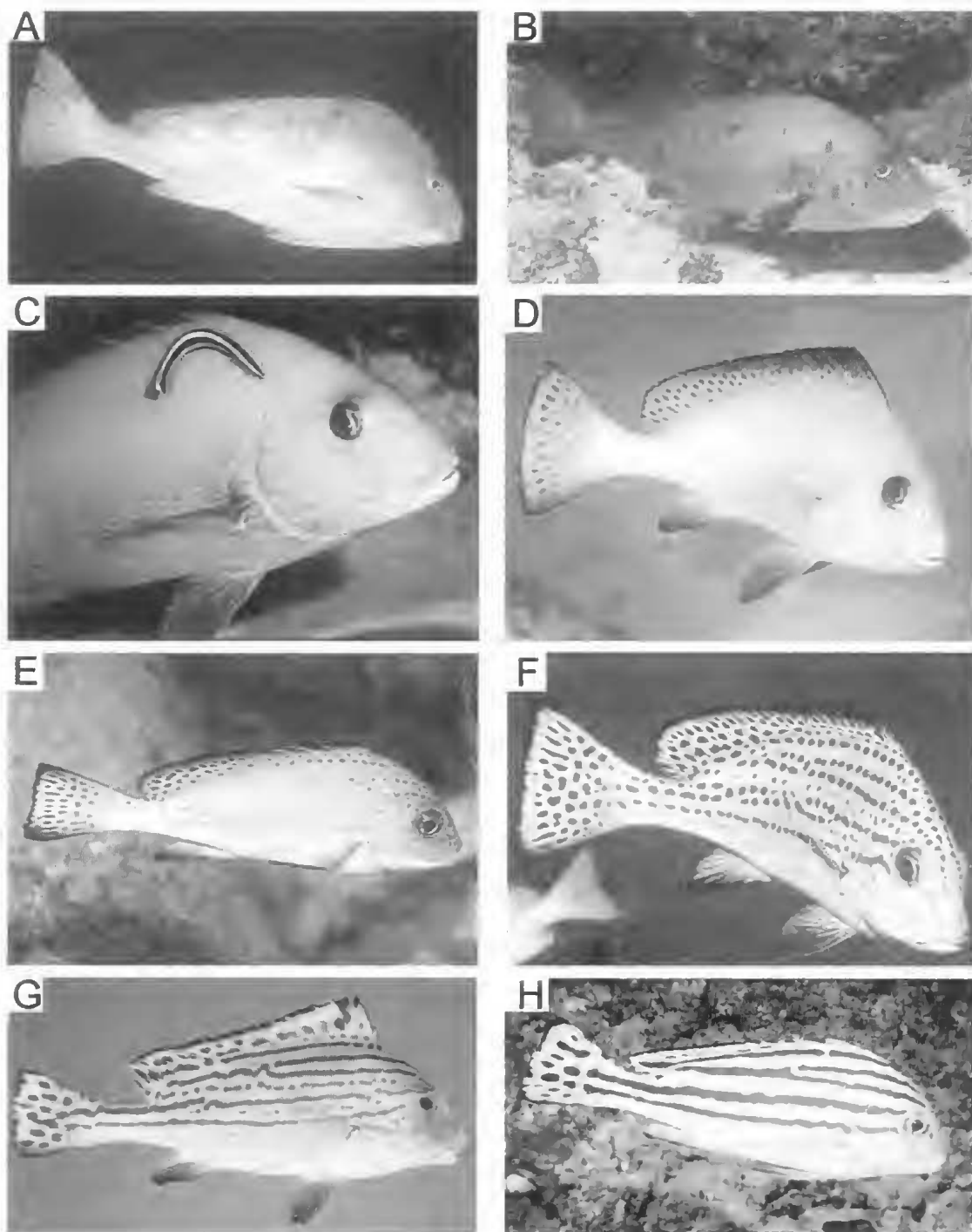


FIG. 5. *Diagramma pictum cinerascens*; A, ~800mm TL, Oman, J.P. Hoover; B, ~500mm TL, Great Basses, Sri Lanka, R.C. Anderson; C, ~450mm TL, Maldives, R.H. Kuiter; D, ~300mm TL, Oman, J.P. Hoover; E, ~240mm TL, Trincomalee, Sri Lanka, R.C. Anderson; F, ~200mm TL, Trincomalee, Sri Lanka, R.C. Anderson; G, 172mm TL, off Bahrain, Persian Gulf, J.E. Randall; H, ~150mm TL, Oman, P. Woodhead.



from the suborbital to the rear of the operculum in some larger specimens. This subspecies is best distinguished by the unique striped pattern of the juvenile and by the narrow yellowish wavy lines or spots on the head in small adults. It has a lower median lateral line scale count (58) than *D. pictum pictum* (65) and *D. pictum labiosum* (69); fewer median total gill rakers (20) than other *D. pictum* subspecies (21 or 22), except *D. pictum labiosum*; and fewer median dorsal fin rays (22) than all other subspecies (23 or 24).

***Diagramma pictum punctatum* Cuvier**  
(Common name: Red Sea Slatey)  
(Figs 6A-H, 8)

*Diagramma punctatum* Cuvier, 1830 (Red Sea).

*Diagramma punctatum* Rüppell, 1830 (Northern Red Sea).

*Diagramma cinerascens* (non Cuvier) Rüppell, 1830 (Red Sea) - name preoccupied by *D. cinerascens* Cuvier.

REMARKS. *Diagramma pictum punctatum* is known only from the Red Sea. It is figured in colour photographs by G.R. Allen at Jeddah (QMNR54-55); JER at Sudan and Nuweiba, Egypt (McKay, in Fischer & Bianchi, 1984: vol. II, pl. 2; Randall, 1983: pl. 111; Randall, 1992: pl. 130b); JER photos at Gulf of Aqaba (QMNX806) and Dahab, Egypt (QMNX807); R. Kuitert photo at Egypt (QMNX800); D. Eichler photo (QMNX798) and H. Debelius photos at Sinai, Egypt (Debelius, 1998: 88 upper left (adult) and upper right (large juvenile)), QMNX799.

Cuvier (1830) in his account of *D. punctatum*, initially referred to 3 specimens collected by Ehrenberg. A description and meristic formulae for this material was quoted separately and a single specimen 9 inches in length was listed. These specimens were from the Red Sea and are represented by one unregistered specimen in the Natural History Museum, Humboldt University, Berlin (Eschmeyer, 1998). Cuvier went on to mention other material of *Diagramma* sourced by Kuhl and van Hasselt from Java (RMNH D 2172); Stadhouder from the Indian Archipelago (MNIIN 7836 (1), MNIIN A.7832 - latter specimen is the holotype of *D. radjaban* Lacepède, 1802); Raynaud from Batavia (MNHN 7801 (1)); and Quoy & Gaimard from Vanicolo (MNHN 7802 (2)). The museum catalog numbers for these specimens were listed by Bauchot et al. (1983) and Eschmeyer (1998). Cuvier recognised all the material from the East Indies as *D. radjaban* of Lacepède (1802), and surmised that the Ehrenberg material from the Red Sea was 'the same species, or very near' to it. However, Cuvier's description of *D. punctatum* was not a compilation of the Red Sea and East Indian forms of *Diagramma*. The Ehrenberg material was treated separately in the initial

stages of the paper, followed by an account of other specimens from the east, including a redescription of the type material of *Holocentrus radjabau*. Also, Cuvier, by his equivocal comments above, cast doubt on whether the other specimens were conspecific with the Red Sea material. The unregistered ZMB specimen from the Ehrenberg collection is implicitly the holotype and the rest constitute other material, rather than part of a syntypic series. Rüppell (1830) also proposed *D. punctatum* for specimens from the N Red Sea, catalogued SMF 2215 (2), but appears to have been pre-empted by Cuvier (Eschmeyer, 1998).

*D. pictum punctatum* has dark brown, orange-brown to golden tan spots on the head and body of most specimens in excess of 140mm TL. In smaller specimens the spots are usually slightly elongate, and individual spots along the rows may be slightly inclined obliquely. Juveniles transform at about 135-145mm TL from a colour pattern including 3 broad dark stripes, to a phase that is uniformly marked with spots of approximately equal size. The spots on the body of large juveniles and subadults (180-350mm TL) are smaller than in *D. pictum pictum*, similar to *D. pictum cinerascens*, but larger than other *Diagramma* subspecies. They are fewer than in *D. pictum labiosum* and usually greater than in *D. pictum centurio*. From about 140-350mm TL spots generally decrease from about 1/2 to 1/4 pupil diameter, or 4.1-6.6 in eye diameter. At this size, there is no bright yellow pigmentation to the head, body or fin membranes, as in some *D. pictum cinerascens* and *D. pictum pictum*. The ground colour of adults is plain silver-grey to grey-bronze. Adults usually have small round dark brown spots on the upper head and along the upper body to the caudal peduncle, above the lateral-line. The only other subspecies to have distinct spots on the body in adults is *D. pictum pictum*, however in the latter the spots (when present) are larger, usually lighter in colour and not confined to the upper margin of the body. In adults there are bronze centres to individual scales, forming rows, a feature absent or very ill-defined in other forms. Few specimens were available for examination; however the lateral-line scale counts obtained (55-61) are at the low end of the range for the genus and modally well below that for *D. pictum labiosum*.

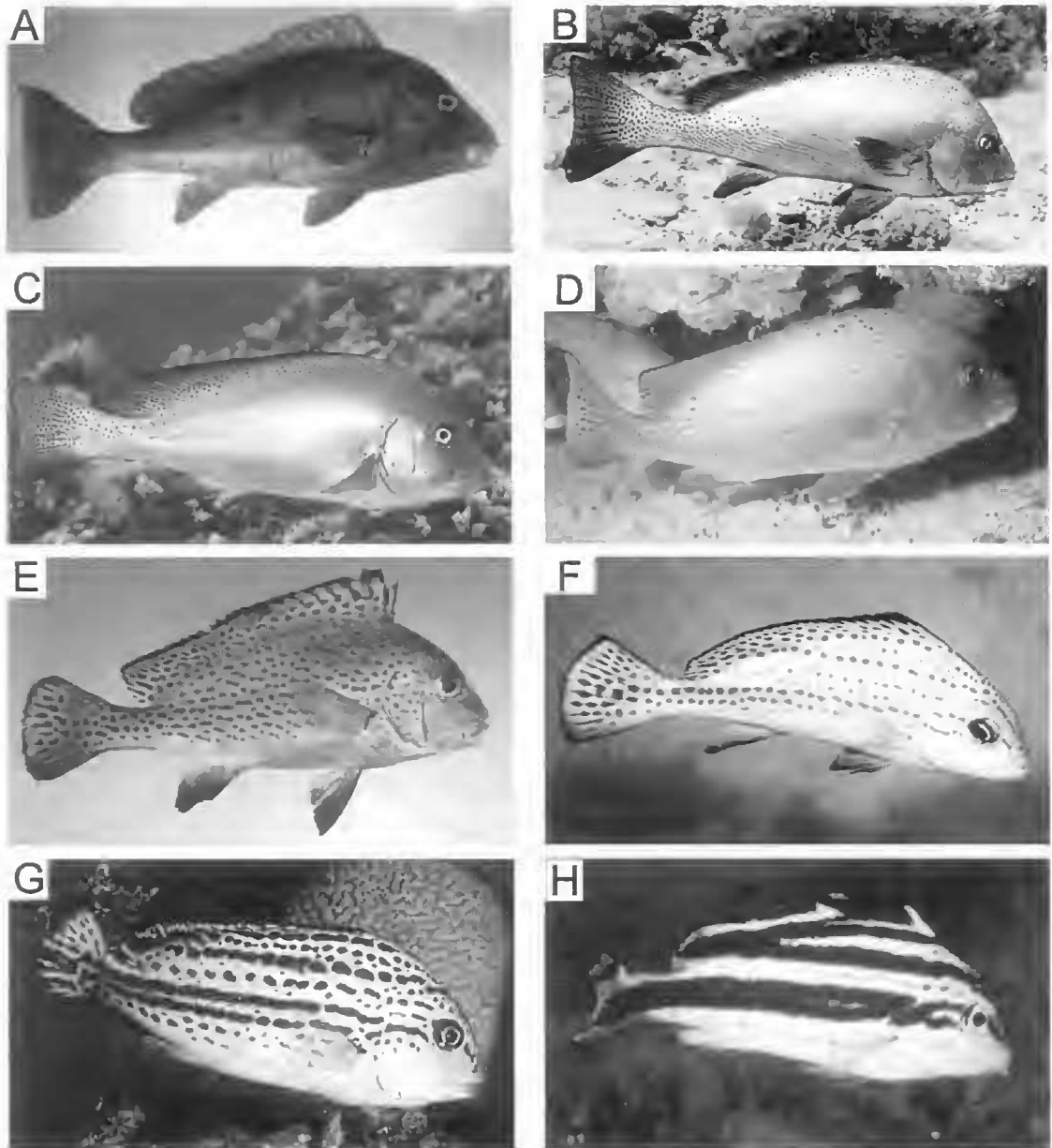


FIG. 6. *Diagramma pictum punctatum*; A, 594mm TL, Sudan, Red Sea, J.E. Randall; B, ~500mm TL, Ras Muhammad, Sinai, Red Sea, H. Debelius; C, ~400mm TL, Daheb, Sinai, Red Sea, J.E. Randall; D, ~300mm TL, Jeddah, Red Sea, G.R. Allen; E, 222mm TL, Nuweiba, Sinai, Red Sea, J.E. Randall; F, ~200mm TL, Egypt, Red Sea, R. H. Kuiter; G, 180mm TL, Red Sea, J.E. Randall; H, 132mm TL, Eilat, Gulf of Aqaba, Red Sea, J.E. Randall.

***Diagramma pictum centurio* Cuvier**  
 (Common name: East African Slaty)  
 (Figs 7A-F, 8)

*Diagramma centurio* Cuvier, 1830 (Seychelles).

REMARKS. *D. pictum centurio* is known from the Seychelles to E Africa and S to Durban. It has been photographed by JWJ (QM NR53, subadult), G.R. Allen (QM NR56, large juvenile), N. Coleman (subadult) and H. Debelius

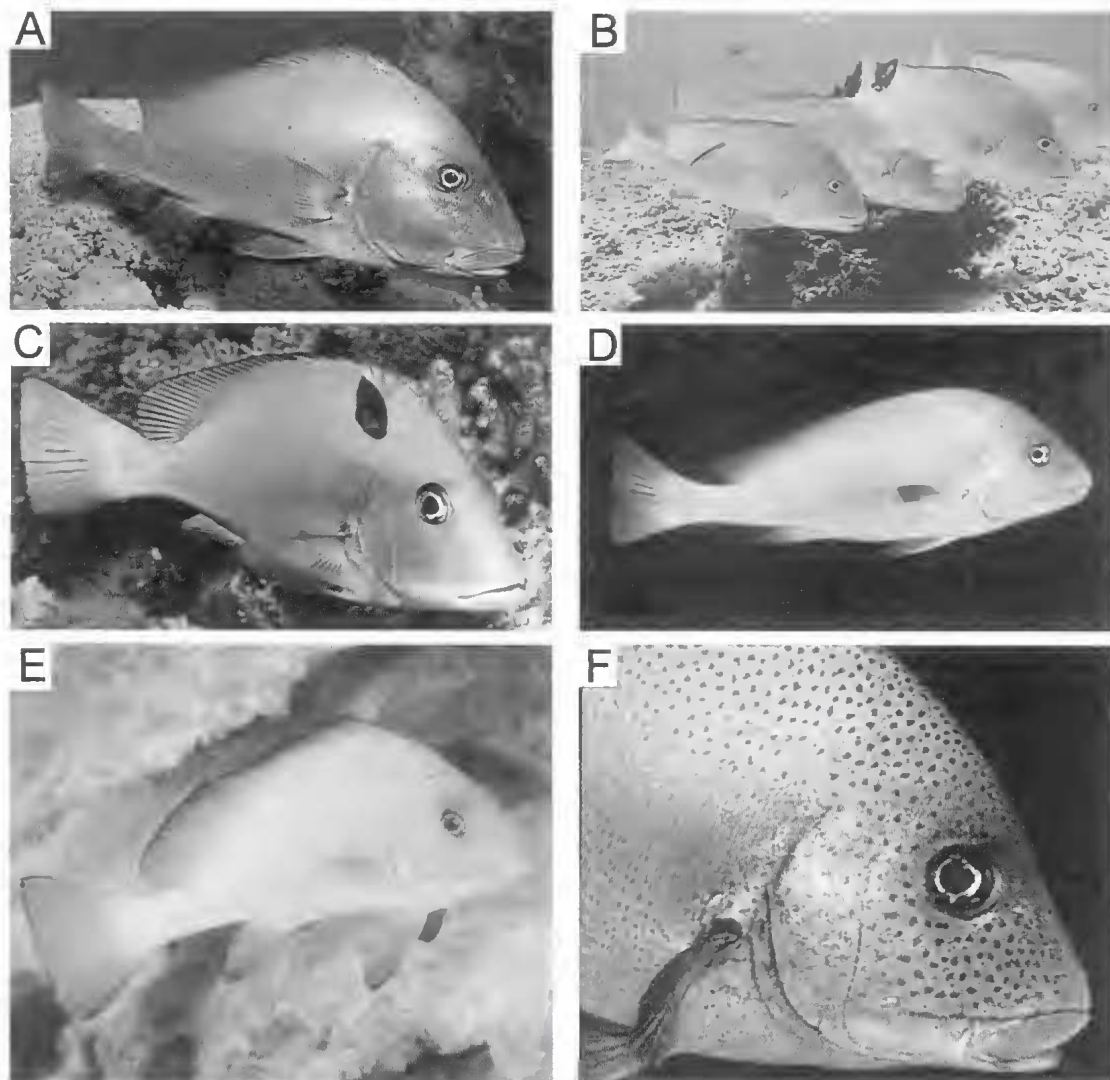


FIG. 7. *Diagramma pictum centurio*; A, ~500mm TL, Mahe, Seychelles, H. Debelius; B, ~350mm TL, Pemba, Kenya, D. Eichler; C, ~250mm TL, Pemba, Kenya, D. Eichler; D, ~300mm TL, Mahe, Seychelles, N. Coleman; E, ~230mm TL, Mahe, Seychelles, G.R.Allen; F, ~200mm TL, Mahe, Seychelles, H. Debelius.

(Debelius, 1999: 99 (adult and juvenile) from Mahe, Seychelles; by D. Eichler (Eichler & Lieske, 1994: 132, from Pemba, Kenya; and a 340mm specimen from Inhaca, Mozambique and a 750mm specimen from Shimoni, Kenya are illustrated (Smith, 1949, pl. 42, fig. 688; Smith, 1962, figs 1, 2).

Cuvier's description of 257mm SL holotype (MNNH8526) of *D. centurio* mentioned scattered small brown spots on the nape, upper body and caudal region. Playfair & Günther (1867) reported a specimen 16 inches from the

Seychelles, with 'head, back, sides, upper part of tail, dorsal and sometimes caudal with brownish-yellow spots'.

No small juveniles from the Seychelles were available for examination, however Debelius (1999: 99 left) illustrated a specimen estimated to be about 200mm TL, with numerous small dark brown spots peppered on the head and upper body. Subadults from this area have slightly larger, sparsely distributed, orange-brown spots on the upper head, body mostly above the lateral line, and on the caudal peduncle. The spots are

smaller than in similar sized *D. pictum pictum*, *D. pictum cinerascens* or *D. pictum punctatum*, and are more sparse than in *D. pictum labiosum*. Adults are slate to silver-grey on the head and body, and may retain a few scattered small spots on the upper body, near the base of the dorsal fin. The soft dorsal and caudal fins may have numerous small close-set dark brown spots, similar to *D. pictum labiosum*.

There appears to be some variability in colouration between individuals from the Seychelles and those from E. Africa. Preserved specimens of in excess of 170mm TL from coastal E. Africa lack spots on the head and body, and spots on the dorsal and caudal fins, if present, are faint. Fish of this size illustrated in underwater photographs were uniformly silver-grey with no distinctive markings, however few photographs from this region were available for examination. Juveniles are striped to about 150mm TL, but the stripes rapidly regress, forming profuse rows of small dark spots by about 150-160mm TL. Smith's (1949, 1962) figures of a 340mm subadult from Mozambique, however, clearly illustrate fine dark spots on the body and unpaired fins, similar to those in the photograph of Debelius (1999) from Mahe. These spots appear to have been somewhat artist-enhanced in Smith's latter reproduction, but prior to his expedition to the Seychelles in 1954, Smith (1949) alluded briefly to the spots in adults.

Identification of this subspecies is complicated by some variability between regions, however large juveniles (beyond the striped phase) may be peppered with tiny dark brown spots, and the subadult stage may best be distinguished by the presence of small, sparse orange-brown spots on the body. Alternatively, large juveniles and subadults lacking any distinctive markings (some E. African specimens) are separable in that all other subspecies, except some *D. pictum labiosum*, have spots of some type at 160-350mm TL. Also, the median upper, lower and total gill raker counts are highest for all *Diagramma*; the median dorsal ray count (23) is higher than in *D. pictum cinerascens* (22) but lower than in *D. pictum labiosum* (24); and the median lateral-line scale count (59) is lower than in *D. pictum pictum* (65) and *D. pictum labiosum* (69).

#### DISCUSSION

*D. melanacrum* is the most distinctive member of the genus, with its low scale count, more robust body and unique colouration. The subspecies of *D. pictum*, although differing considerably in

colouration between one another at certain ontogenetic stages, are remarkably similar as adults. Only *D. pictum pictum* retains obvious spots on the body as an adult. *D. melanacrum* differs from all *D. pictum* subspecies in having the third or fourth dorsal spine longest (second dorsal spine usually longest in the latter, fourth always shorter than second); a taller first dorsal spine; 1.7-2.3 in length of second (2.3-3.9 in the latter); a stouter caudal peduncle, depth of peduncle in its length 2-2.2 (2.2-3.1 in specimens greater than 130mm SL of the latter) and in having pelvic fins that at least reach the vent in all life stages (pelvic fins reach to or slightly beyond the vent in most juveniles up to 200mm SL, but become increasingly remote with growth, large adults falling short by over half length of fin in *D. pictum* subspecies). The tubed lateral-line scale count of 55-57 is lower than that of *D. pictum labiosum* (59-78, usually higher than 65), but overlaps the extreme lower end of the range for other *D. pictum* subspecies (cumulative ranges 55-74). Scale rows above the lateral line to the origin of the dorsal fin, at 14-15, are lower than *D. pictum labiosum* (17-19) and usually lower than other *D. pictum* subspecies (15-18). The range of scale counts for *D. melanacrum*, however, could reasonably be expected to expand when further specimens are available for examination. There are also noteworthy differences in colour. Adults of *D. pictum pictum* have orange to yellow spots on the head and usually also on the body; adults of *D. pictum punctatum* have brown spots on the upper head and body, but they are smaller, more evenly rounded and more sparsely distributed; adults of other *D. pictum* subspecies are slate or silvery-grey, sometimes with large irregular scattered dark blotches. They all lack numerous small close-set dark brown spots on a yellowish background (bronze spots to centres of scales in *D. pictum punctatum* are vague, smaller, lighter in colour and generally follow along the scale rows); and the prominently black lower part of the caudal fin. Other subspecies also usually lack the intensity of black pigmentation to outer part of the anal and pelvic fins, although some juveniles may have dusky fins. *D. melanacrum* is light yellow dorsally on the body, as well as the dorsal fin and upper 3/4 of the caudal fin, and the dark spots on the upper part of the body and on these fins are larger, darker and not arranged one per scale; also there are no large dark blotches on the body.

*Diagramma melanacrum* appears to be rare compared to most other Indo-Pacific haemuljids.



JER has observed it only 3 times in Indonesia and not in the Philippines, Borneo or New Guinea, in spite of many hours underwater at numerous localities in the East Indies region. Nor was it encountered in fish markets. Pieter Bleeker apparently failed to find this species during his many productive years of research on the fishes of Indonesia.

#### KEY TO *DIAGRAMMA* SPECIES

N.B. Differences in colouration between most subspecies of *D. pictum* is limited mainly to certain ontogenetic stages. Small initial stage juveniles are generally patterned with broad longitudinal black stripes on a cream to creamish yellow background, and are generally not separable using this key. Transformation from striped to spotted colour phases occurs at various lengths between subspecies. Large adults of *labiosum*, *cinerascens* and *centurio* are all generally silver-grey to slate-grey, often with scattered dusky blotches, but differ medially in several meristic features. The colouration of small *D. melanacrum* juveniles is unknown.

1. Lower 1/4-1/3 of caudal fin black; upper body and head with numerous small close-set dark brown spots; third or fourth dorsal spine longest; first dorsal spine 1.7-2.3 in length of second; pelvic fins reaching to or beyond anus; caudal-peduncle depth 2.0-2.2 in its length; tubed lateral-line scales about 55-57  
 . . . . . *D. melanacrum*  
 (Philippines, Borneo, Sulawesi and southern Indonesia)
- Lower 1/4-1/3 of caudal fin not black (often dusky to black near lower margin in juveniles and subadults); upper body and head of adults without small close-set dark brown spots; second dorsal spine usually longest; first dorsal spine 2.3 or more in length of second; pelvic fins not reaching anus in adults (may extend to anus in juveniles); caudal-peduncle depth usually greater than 2.2 in its length; tubed lateral-line scales 55-78 . . . . . 2
2. Lemon yellow, orange to orange-tan spots on head and body of large juveniles and subadults; spots large, 2-6 in eye diameter; adults either lacking spots on the head and body, or with large yellow to orange spots, at least on head; short bars or wavy lines usually on head of large juveniles and subadults; ground colour of median fins often bright yellow in juveniles to subadults; juveniles transform from striped to fully spotted phase at 160-240mm TL . . . . . 3
- Dark brown, bronze or orange-brown spots on head and body of large juveniles and subadults; spots usually smaller, 4-11 in eye diameter; adults generally silver-grey to slate grey, often with scattered dusky blotches, sometimes with small brown spots, but never with large yellow or orange spots; no short bars or wavy lines on head of juveniles and subadults; ground colour of median fins never bright yellow (except occasionally in initial stage juveniles of up to about 100mm TL); juveniles transform from striped to fully spotted phase at 130-160mm TL . . . . . 4
3. Tubed lateral-line scales 57-74 (median 65); second and third body stripes of juveniles not merging near pectoral

fin; large yellow to burnt orange spots usually present on head and body of adults (if not, then at least on cheeks); no scattered irregular dusky blotches on head and body of adults; head of subadults and adults usually with combination of spots, short bars and broad wavy lines; spots present on head and body of large juveniles to adults, 2-5 in eye diameter; total gill rakers 19-23 (median 21) . . . . . *D. pictum pictum*  
 (New Caledonia north to southern Japan and west to the Indo-Malay Archipelago, excluding Australia and southern New Guinea)

- Tubed lateral-line scales 55-64 (median 58); second and third body stripes of juveniles merging above posterior half of pectoral fin (in specimens of about 150mm TL); no spots on body of adults; scattered irregular dusky blotches often present on head and body of adults; head of subadults and adults with narrow wavy lines, small spots or unmarked; spots present on head and body of large juveniles to subadults, 3-6 in eye diameter; total gill rakers 17-21 (median 20) . . . . . *D. pictum cinerascens*  
 (Northern Indian Ocean, from Bay of Bengal to the Persian Gulf)
4. Spots on head and body of large juveniles to subadults (180-350mm TL) larger, 4.1-6.6 in eye diameter, often slightly elongate and oblique; adults usually with small scattered round spots on upper head and along body near dorsal fin base and caudal peduncle; adults with small bronze centres to individual scales, forming rows  
 . . . . . *D. pictum punctatum* (Red Sea)
  - Spots on head and body of large juveniles to subadults (180-350mm TL) smaller, 6.5-11.6 in eye diameter, always round; adults either lacking or with only few spots on head and body; adults without small bronze centres to individual scales . . . . . 5
  5. Tubed lateral-line scales 59-78 (median 69); total gill rakers usually 19-21 (median 20); spots on body (when present) bronze to dark brown, always close-set, gradually disappearing from anterior toward posterior part of body with growth, ultimately leaving a small patch of spots at upper part of caudal peduncle, before fading completely . . . . . *D. pictum labiosum*  
 (northern Australia, from Houtman Abrolhos, WA to Sydney Harbour, NSW; southern New Guinea)
  - Tubed lateral-line scales 56-66 (median 59); total gill rakers 21-23 (median 22); spots on body (when present) usually orange-brown, peppered finely in some large juveniles, but sparsely distributed in subadults, not gradually disappearing from anterior toward posterior part of body with growth, not leaving a small patch of spots at upper part of caudal peduncle, before fading completely . . . . . *D. pictum centurio*  
 (East Africa to Seychelles)

#### OTHER MATERIAL EXAMINED (Fig. 8)

(Numbers in brackets are lengths of specimens in mm. Catalogue numbers refer to single specimens unless otherwise indicated by number in italics)

*D. pictum labiosum*. QUEENSLAND: QMI3371 (148); QMI3442 (124); QMI3946 (203); QMI6079 (187); QMI6678 (168); QMI7094 (261); QMI7579 (238); QMI7804 (283); QMI7853 (115); QMI11555 (266); QMI12535 (129); QMI12536 (127); QMI12710 (268); QMI12616 (292); QMI12724-30 7 (224-337); QMI12908

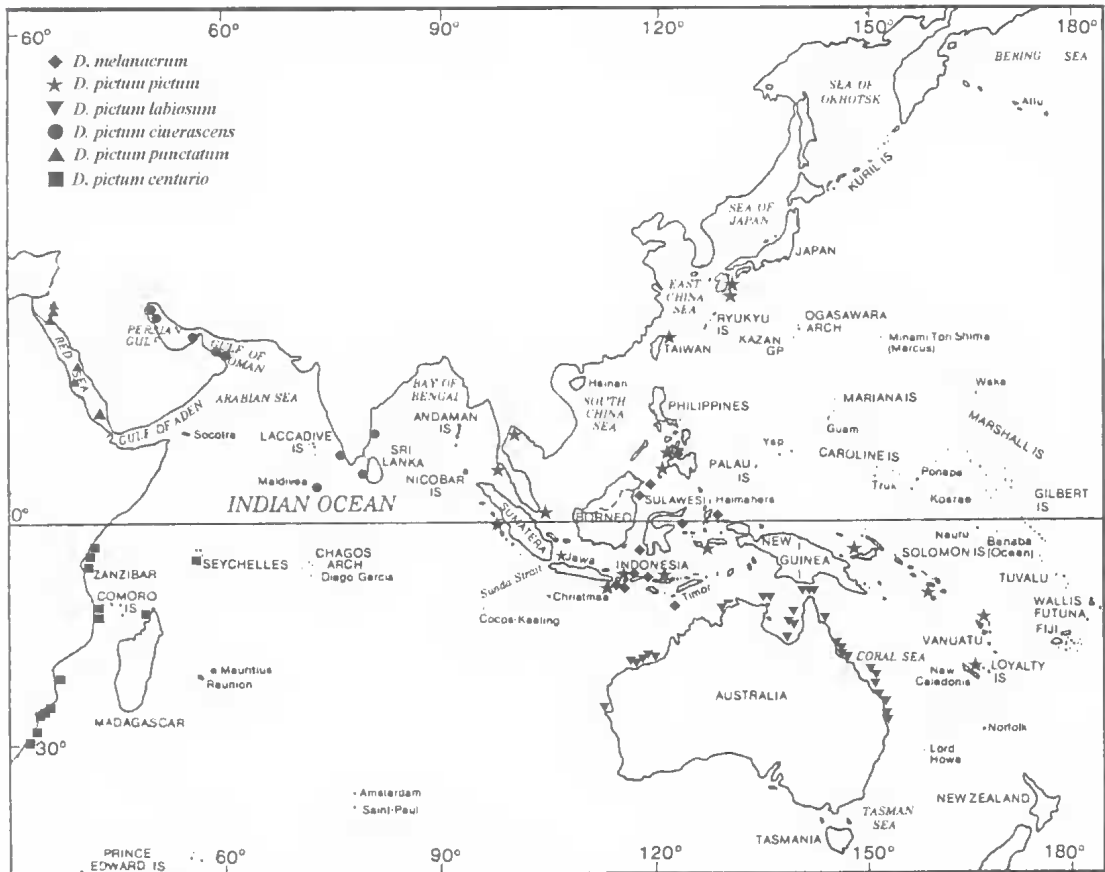


FIG. 8. Confirmed distributional records of examined *Diagramma* species

2 (117-119); QMI15058 (156); QMI15097 (118); QMI15965 (98); QMI16467 (116); QMI16852.2 (96-127); QMI20132 (192); QMI20850 (107); QMI20884 (123); QMI21223 (110); QMI21334 (151); QMI23229.2 (84-126); QMI30757 (401); QMI30758 (434); QMI30759 (370); QMI30760 (380); QMI30761 (601); QMI30762 (620); BPBM14335 (349); BPBM14465 (138). Northern Territory: NTMS10577-001 (222); NTMS11613-028 (356); NTMS13318-002.3 (175-213). WESTERN AUSTRALIA: QMI10225.2 (83-105); QMI14230 (112); QMI30726.2 (123-196); QMI30727 (255); QMI30728 (232); QMI30729 (238); QMI31110 (468); QMI31111 (519); QMI31112 (511); NTMS10987-002 (436); CSIROH3834-02 (341).

*D. pictum pictum*. JAPAN: MUFS12534 (192); MUFS12847 (245); MUFS11816-7.2 (136-156.5); MUFS12162 (142); MUFS12226 (114.5); QMI31403-4.2 (372-377). INDONESIA: BMNH1858.4.21:364 (85); QMI20383 (304); QMI20284 (136); QMI20286 (100); QMI20287 (186); QMI20288 (503); QMI20289 (302); QMI20304 (61); BPBM36675 (38); BPBM18593 (99); BPBM20678 (239); BPBM30100.2 (60-61); NTMS11037-001 (332); NTMS11127-016 (95).

THAILAND: QMI21687.12 (58-212); PMBC14425 (152); PMBC5884 (190), PMBC5885 (185), PMBC5890 (175) and PMBC5891 (187). MALAYSIA: AMIA3343 (94); QMI30873 (311); QMI30874 (325); QMI31076.3, 136-188); QMI31113 (224). PHILIPPINES: AMI10568 (118); AMI10503 (120); BPBM28550 (95); BPBM22143 (187). TAIWAN: BPBM18687 (200). VANUATU: AMI17142-015 (173). NEW CALEDONIA: AMB2410 (275). SOLOMON ISLANDS: BPBM17371.2 (172-245). PAPUA NEW GUINEA: BPBM15709 (104).

*D. pictum cinerascens*. INDIA: AMI15599-006 (125); AMB8320 (141); BMNH1888.11.6:7-8.2 (147-181); BMNH1889.2.1:2961 (45); BMNH1847.11.22:134-136.2 (74-90); BPBM20666.2 (67-86); PMBC5886 (181), PMBC5887 (181), PMBC5892 (167), PMBC5893 (169) and PMBC5894 (197). GULF OF OMAN: BMNH1888.12.29:48 (172). PERSIAN GULF: BMNH1904.5.25:184 (78); BMNH2000.4.19:1113 (155); BPBM33174 (68); BPBM21181.3 (63-132); BPBM29495.3, 117-144).

*D. pictum punctatum*. RED SEA: BMNH 1860.11.9:93 (157); BMNH1960.3.15:763 (36); BMNH1871.4.13:9.2,

(192-237); RUSI7989 2 (113-128); BPBM19856 (180); BPBM31867 (100).

*D. pictum venturio*. SEYCHELLES: AMI32067-001 (232). KENYA: RUSI41682 (168); RUSI41677 2, (50-61). TANZANIA: BMNH1985.7.9:193 (203). MOZAMBIQUE: RUSI41656 4, (59-125); RUSI41681 (161); RUSI41680 (141), RUSI42227 (127); RUSI41679 (122); RUSI56386 2, (98); RUSI41678 (76). MADAGASCAR: RUSI52829 10, 73-105). SOUTH AFRICA: RUSI3846 (68); RUSI12754 (46); BMNH1919.9.12:24 (193).

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