A NEW SPECIES OF SKATE FROM WESTERN AUSTRALIA WITH COMMENTS ON THE STATUS OF *PAVORAJA* WHITLEY, 1939 (CHONDRICHTHYES: RAJIFORMES)

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Abstract.—The genus Pavoraja is resurrected for the Australian skates Raja nitida and Pavoraja alleni, n. sp., which differ from all recognized genera of skates in clasper and rostral structure, and by their combination of derived character states. Pavoraja alleni is described and diagnostic characters are given for Pavoraja and P. nitida.

Raja nitida, which occurs off Tasmania, Victoria, and southern New South Wales (Whitley 1940), was placed in a new genus *Pavoraja*, along with another eastern Australian skate, *Raja polyommata* Ogilby, 1916 by Whitley (1939). Whitley (1939) only briefly described *Pavoraja* and gave no characteristics that distinguish it from other skate genera. The following year Whitley (1940) offered little to augment his description, but stated that *P. nitida* resembles the South American skate, *Malacorhina scobina* (=*Psammobatis scobina* Philippi, 1857), that the type locality of *P. nitida* may be South America rather than Australia, and that the Australian specimen of *P. nitida* may represent a new species or subspecies. More recent authors (Fowler 1941, Bigelow and Schroeder 1953) considered *Pavoraja* synonymous with the genus *Raja*, because of Whitley's lack of a generic diagnosis.

During investigations of the skate fauna of Western Australia a new species was discovered which closely resembles Raja nitida Günther, 1880. Herein we describe the taxonomically important anatomical characters of R. nitida, comment on the taxonomic status of Pavoraja, describe the new species, and then comment on the relationship of R. polyommata to the other species.

Materials and Methods

Specimens of *Raja nitida*, *R. polyommata*, and the new species were obtained from the Australian Museum, Sydney (AMS); British Museum (Natural History) (BMNH); Tasmanian Museum, Hobart (TMH); and Western Australian Museum, Perth (WAM). Several individuals of *R. nitida* and one of the three specimens of the undescribed species were dissected to reveal the structure of the claspers, neurocrania, and scapulocoracoids. Several additional specimens of *R. nitida* and all three specimens of the new species were radiographed to verify the anatomical observations based on dissections and to count vertebrae, pectoral radials, and pelvic radials. Methods for making measurements and counts are described by McEachran and Compagno (1979, 1982).



Fig. 1. Lateral view of right clasper, partially expanded to show components: a, *R. nitida*, AMS 1B.5275; b, *Pavoraja alleni*, WAM P19118 (Holotype). cf—cleft, hy—hypopyle, pr—pseudorhipidion, rh—rhipidion, sl—slit, sp—spike, sr—spur, st—sentinel.

Results

Claspers.-Raja nitida has very slender, short claspers which are constricted rather than expanded at origin of glans (Fig. 1a); without dermal denticles or pseudosiphon; inner dorsal lobe with pseudorhipidion extending from level of hypopyle to about distal one-third of glans, continuing distally as a fold of integument; slit located lateral to pseudorhipidion; spur well developed; cleft medial to spur; rhipidion well developed, running from level of hypopyle to distal onethird of glans, distal section rotated laterally and running over base of sentinel; sentinel rod-shaped and covered with integument, extending from level of slit to near tip of glans; spike ventral to sentinel, located within sentina, disc-shaped with a sharp, naked lateral margin; axial cartilage forming a slender tip (Fig. 2a, b, c); dorsal marginal little expanded distally, distal margin truncate, with an inner distal extension entering glans and forming pseudorhidion; ventral marginal with a evenly convex distal margin; dorsal terminal 1 and ventral terminal membranous, broadly joined on ventral aspect of glans, forming a sheath-like covering of glans; dorsal terminal 2 broad, fused to distal and distolateral surface of dorsal marginal; dorsal terminal 3 fused with dorsal terminal 2, small with a distally pointed and laterally curved extension forming spur; ventral terminal V-shaped, lacking a sharp lateral margin, lying on dorsal surface of accessory terminal 1; accessory terminal 1 Y-shaped, fused with distal surface of ventral marginal, S-shaped distal extension forming sentinel; accessory terminal 2 short, attached to accessory terminal 1, with a dorsoventrally flattened, disc-shaped extension forming spike.



Fig. 2a, b, c. Right clasper cartilages of *R. nitida*, AMS 1B5275: a, Lateral view, partially expanded with dorsal terminal and ventral terminal cartilages shown separately; b, Dorsal view; c, Ventral view; d, e, f, right clasper cartilages of *P. alleni*, WAM P19118 (Holotype), d, Lateral view, partially expanded with dorsal terminal and ventral terminal cartilages shown separately; e, Dorsal view; f, Ventral view. Atr₁—accessory terminal 1, atr₂—accessory terminal 2, ax—axial, dmg—dorsal marginal, dtr₁—dorsal terminal 1, dtr₂—dorsal terminal 2, dtr₃—dorsal terminal 3, vmg—ventral marginal, vtr—ventral terminal.

Neurocranium.—The neurocranium of R. nitida has a short, slender rostral shaft, fused to flattened rostral node and appendices at tip of snout (Fig. 3a), widely separated from rostral base and neurocranium; rostral appendices free of rostral shaft posteriorly and possessing two foramina; propterygia of pectoral girdle reaching rostral appendices; nasal capsules of moderate size, set at about a 40° angle to transverse axis of neurocranium; foramen for profundus nerve on leading edge of nasal capsule; anterior foramen for preorbital canal on anterior margin of kidney-shaped basal fenestra of nasal capsule; precerebral space narrow, inner walls of nasal capsules moderately bulging into precerebral space; interorbital region narrow (Table 1); preorbital processes poorly developed, separated from supraorbital crests by shallow notch; postorbital processes well developed; anterior fontanelle tear-shaped; posterior fontanelle trapezoid-shaped;



Fig. 3. Neurocranium of *R. nitida*, AMS 1B.5275: a, Dorsal view; b, Lateral view; c, Posterior view; d, Ventral view. ac—anterior cerebral vein foramen, af—anterior fontanelle, antc—antorbital condyle, bf—basal fenestra, end—endolymphatic foramen, es—efferent spiracular artery foramen, hf—hyomandibular facet, ic—internal carotid artery foramen, into—intercerebral vein foramen, ja—jugal arch, ibX—lateralis branch of vagus nerve foramen, nc—nasal capsule, obf—otic branch of facial nerve foramen, of—orbital fissure, onc—orbitonasal canal, os—optic stalk, peri—perilymphatic foramen, pf—posterior fontanelle, poc—preorbital canal foramen, postp—postorbital process, prep—preorbital process, prof—profundus nerve foramen, ra—rostral appendix, rb—rostral base, rn—rostral node, rs—rostral shaft, II—optic nerve foramen, III—oculomotor nerve foramen, IV—trochlear nerve foramen, VII—hyomandibular branch of facial nerve foramen, IX—glossopharyngeal nerve foramen, X—vagus nerve foramen.

foramen for anterior cerebral vein posterior to line connecting foramina for preorbital and orbitonasal canals (Fig. 3b); trochlear nerve foramen posterior and dorsal to optic nerve foramen; oculomotor nerve foramen situated above optic stock; orbital fissure located on posterior aspect of orbit, anterior to foramen for hyomandibular branch of facial nerve and posterior to foramen for interorbital vein; efferent spiracular artery foramen on ventral rim of orbit; jugal arches moderately slender; vagus nerve foramen immediately ventral to foramen for lateralis branch of vagus nerve and medial to foramen for glossopharyngeal nerve (Fig. 3c); basal plate moderately narrow (Fig. 3d).

Scapulocoracoid.—The scapulocoracoids of R. nitida are moderately short and anteroposteriorly elongated (Table 2), without an anterior bridge (Fig. 5a); anterior fenestra little expanded; postdorsal fenestra moderately expanded; meso-condyle not expanded; three postventral foramina, first greatly enlarged; neo-pterygial ridge between mesocondyle and metacondyle incomplete.

Comments.—Raja nitida differs from all other species of *Raja* in clasper and rostral structure and differs from all other genera of skates in its combination of derived character states, suggesting that the genus *Pavoraja* should be resurrected for this species. "*Raja*" *nitida* differs from *Raja* in possessing claspers with membranous dorsal terminal 1 and ventral terminal cartilages which are broadly joined along the ventral aspect of the glans and disc-like accessory terminal 2 cartilages; a reduced and incomplete rostral shaft which is widely sepa-

VOLUME 95, NUMBER 1



Fig. 4. Neurocranium of *P. alleni*, WAM P19117 (Paratype): a, Dorsal view; b, Lateral view; c, Posterior view; d, Ventral view. Abbreviations as in Fig. 3.

rated from the rostral base, and propterygia of pectoral fins which reach rostral appendices. Reduction of the rostral base precludes this species from being classified in *Raja* (Ishiyama 1958, Stehmann 1970, Hulley 1972, McEachran and Compagno 1982).

	<i>P. alleni</i> 278 mm TL ♀	P. nitida 335 mm TL ð	P. nitida 357 mm TL ð	
Nasobasal length (mm)	26.7	36.2	40.1	
Cranial length	185	168	151	
Rostral cartilage length	23	20	24	
Prefontanelle length	84	70	70	
Cranial width	92	80	80	
Interorbital width	26	27	25	
Rostral base	13	10	11	
Anterior fontanelle length	33	29	28	
Anterior fontanelle width	14	9	8	
Posterior fontanelle length	42	47	34	
Posterior fontanelle width	12	17	11	
Rostral appendix length	16	14	11	
Rostral appendix width	15	10	11	
Rostral cleft length	6	6	5	
Cranial height	24	23	22	
Width across otic capsules	58	50	51	
Least width of basal plate	24	25	24	
Greatest width of nasal capsule	37	37	37	
Internasal width	13	10	11	

Table 1.—Neurocranial measurements of *P. alleni* and *P. nitida* expressed as percentage of nasobasal length.

	<i>P. alleni</i> 278 mm TL ♀	P. nitida 335 mm TL ♂	P. nitida 357 mm TL さ		
Scapulocoracoid length (mm)	16.3	21.5	25.1		
Scapulocoracoid height	71	74	75		
Premesocondyle	39	40	41		
Postmesocondyle	61	60	58		
Postdorsal fenestra length	32	32	33		
Postdorsal fenestra height	24	25	19		
Anterior fenestra length	17	15	15		
Anterior fenestra height	25	24	22		
Rear corner	53	59	58		

Table 2.—Scapulocoracoid measurements of *P. alleni* and *P. nitida* expressed as percentage of scapulocoracoid length.

Pavoraja Whitley, 1939

Type species.—Raja nitida Günther, 1880.

Diagnosis.—Snout with small laterally compressed rostral process; caudal fin poorly developed, with an epichordal lobe and with or without a hypochordal lobe; claspers constricted at origin of glans; dorsal marginal with a distomedial extension forming pseudorhipidion; dorsal terminal 1 and ventral terminal membranous and broadly joined along ventral aspect of glans; dorsal terminal 3 with free distal tip forming spur; accessory terminal 1 with an S-shaped distal extension forming sentinel; accessory terminal 2 with a disc-shaped extension forming spike; rostral shaft slender and reduced, separated by a wide distance from narrow rostral base; rostral appendices short, propterygia of pectoral girdle extending to rostral appendices; nasal capsules with basal fenestrae; anterior fontanelle and internarial plate moderately narrow; interorbital region narrow; preorbital processes poorly developed; foramen for anterior cerebral vein posterior to line



Fig. 5. Lateral view of scapulocoracoid: a, *R. nitida*, AMS 1B.8274; b, *Pavoraja alleni*, WAM 19117 (Paratype). af—anterior fontanelle, msc—mesocondyle, mtc—metacondyle, pdfe—postdorsal fenestra, prc—procondyle, pvf—postventral foramina, scp—scapular process.

connecting foramina for precerebral and orbitonasal canals; scapulocoracoid subrectangular to almost rectangular, moderately short and anteroposteriorly expanded; without anterior bridge; three postventral foramina; precaudal monospondylous vertebrae ranging from 26 to 29 and predorsal caudal diplospondylous vertebrae ranging from 66 to 79.

Remarks.—Arhynchobatis, Bathyraja, Breviraja, Gurgesiella, Psammobatis, Pseudoraja, "Raja" waitei, and Sympterygia also possess reduced rostra, a derived state (McEachran and Compagno 1979, 1982). Rostra of Arhynchobatis, Bathyraja (in part), Psammobatis, "Raja" waitei, and Sympterygia are basally segmented and could presumably have evolved into the P. nitida state by distal retraction of the rostral shaft. The rostral shaft in Psammobatis is partially retracted while that of Pseudoraja is nearly absent (McEachran and Compagno 1979). However, all of these taxa differ from P. nitida in structure of the claspers, neurocrania and scapulocoracoids (Compagno and McEachran, in prep.) and thus it seems likely that rostral reduction has occurred separately several times within the skates. Pavoraja nitida shows a closer relationship to the genera with reduced but basally unsegmented rostra (Breviraja and Gurgesiella) in structure of the neurocranium and scapulocoracoid, and to a lesser degree, in clasper structure, and possibly could have been derived from a common ancestor of either of these taxa. Breviraja possesses a distally segmented rostral shaft which could have evolved into the P. nitida state by basal retraction of the proximal, unsegmented part of the shaft. However, uniqueness of the clasper and rostral structure of P. nitida precludes its classification with either Breviraja or Gurgesiella and supports the resurrection of Pavoraja.

Based on the examination of several small immature specimens of R. polymmata, this species is classified in Raja rather than Pavoraja. It possesses a stout rostral shaft and in all aspects agrees with the anatomical character states within Raja. Further comments on its relationships must await the procurement of large, mature specimens to make more extensive anatomical observations and to examine the claspers.

Pavoraja nitida (Günther, 1880) (Fig. 6, Table 3)

Diagnosis.—Disc width greater than 54% of total length; orbital length 1.7 to 2.1 times as long as spiracle; anterior margin of pelvic fins less than 75% of distance from origin of anterior lobe to extreme posterior margin of fin; second dorsal fin and epichordal lobe of caudal fin confluent; epichordal lobe shorter than base of second dorsal fin; hypochordal lobe of caudal fin absent; dorsal surface dark brown with small light spots, some of which are arranged into occelli; mature males range from 312 to 363 mm TL.

Comments.—It is very unlikely that the type locality of P. nitida is South America rather than Australia, as suggested by Whitley (1940). The holotype of P. nitida does not differ significantly from the specimens from Australia. No specimens resembling P. nitida have been reported from South America, and specimens resembling this species have not been discovered in the large samples of South American skates studied by McEachran.

Material examined.-BMNH 1879.5.14.417 (Holotype), Two Fold Bay, New



Fig. 6. Pavoraja nitida, BMNH 1879.5.14.417 (Holotype).

South Wales, Australia, HMS Challenger, 6 April–4 June 1874. AMS 1A.2493 (1), AMS 1A.3904.05 (1), AMS 1B.4324.25 (2), AMS 1B.5275 (2), AMS 1B.8274 (3), AMS E.2165 (1), AMS E.5453 (1), AMS I.10823.24 (2), AMS I.16564.001 (1), AMS IA.3904.05 (1), TMH D816 (1).

Pavoraja alleni, new species

Holotype.—WAM P19118, 297 mm TL, mature male, collected off northwestern Australia, near Rowley Shoals, 17°17.0'S, 119°57.0'E, 350 m, 20 December 1969.

Paratypes.—WAM P19117, 278 mm TL, female, collected with holotype; WAM P8226, 159 mm TL, female, collected December 1963 or January 1964 in the eastern Indian Ocean, 17°05′S, 119°48′E, aboard the *Umitaka Maru*.

Diagnosis.—Disc width less than 52% of total length; orbital length 2.2 to 3.2 times as long as spiracle; anterior margin of pelvic fins 81 to 104% of distance from origin of anterior lobe of fin to extreme posterior margin of fin; second dorsal fin and epichordal lobe of caudal fin not confluent, distance from posterior margin of base of second dorsal fin to tip of tail considerably greater than length of base of second dorsal fin; hypochordal lobe of caudal fin small but present; dorsal surface light tan with minute dark spots loosely concentrated into ill defined blotches but not forming ocelli; males mature at 297 mm TL.

Description.—Disc 1.1 times as broad as long; maximum angle in front of spiracles 107° in holotype (110° to 112° in paratypes); margin of disc convex except concave opposite orbits and spiracles; outer corners of disc broadly round-

VOLUME 95, NUMBER 1

	P. alleni (holotype)	P. alleni (paratype)	P. alleni (paratype)	P. alleni x	P. nitida (holotype)	<i>P. nitida</i> n = 15	P. nitida x
Sex	3	Ŷ	Ŷ		3		
Total length (mm)	297	278	159		209	242-358	
Disc width	50.8	49.3	47.2	49	59	54-62	59
Disc length	44.4	43.5	42.8	44	50	45-52	51
Snout length (preocular)	10.4	9.6	11.7	10.4	11.0	8.3-11.4	9.5
Snout length (preoral)	9.8	10.5	12.9	10.7	11.8	9.3-12.6	10.6
Snout to maximum width	28.6	26.3	27.0	27	29	25-31	28.7
Prenasal length	8.1	8.0	9.7	8.4	8.2	6.3-9.1	7.7
Orbit diameter	4.7	3.9	4.7	4.4	5.7	5.2-6.1	5.6
Distance between orbits	2.7	3.1	3.3	3.0	3.2	2.9-3.7	3.3
Orbit and spiracle length	5.3	4.6	5.2	5.0	6.3	6.2-8.9	6.6
Spiracle length	1.5	1.8	1.4	1.6	3.2	2.7-6.3	3.2
Distance between spiracles	6.6	6.0	6.4	6.3	6.5	4.2-6.7	6.3
Mouth width	6.9	6.1	5.8	6.3	6.3	5.9-7.9	6.9
Nare to mouth	3.5	3.5	4.5	3.7	3.5	3.2-4.7	4.2
Distance between nostrils	4.8	4.5	5.2	4.8	4.1	3.2-4.7	3.9
Width of first gill opening	0.9	1.0	0.8	0.9	1.7	1.6-2.1	1.7
Width of third gill opening	1.0	1.1	0.8	1.0	1.9	1.5-2.0	1.7
Width of fifth gill opening	0.7	0.9	0.8	0.8	1.6	1.3-1.6	1.4
Distance between first gill openings	12	12	12	12	13	15-12	12
Distance between fifth gill openings	8	8	7	8	7	6–8	6
Length of anterior pelvic lobe	12	11	13	12	12	12–14	13
Length of posterior pelvic lobe	13	14	13	14	16	17–18	17
Distance-snout to cloaca	41	41	40	41	44	41-45	43
Distance-cloaca to 1st dorsal fin	47	47	48	47	46	43-47	45
Distance-cloaca to caudal origin	55	57	55	55	54	51-56	53
Distance-cloaca to caudal tip	59	59	61	60	57	54-59	57
Number of tooth rows (upper jaw)	38	35	45	39	34	31-36	33.9
Sample size of radiographs				3		4	
Number of trunk vertebrae	26	28	26	26.7	27	26-29	27.5
Number of predorsal caudal vertebrae	79	71	74	74.6	66	66–72	70.2
Number of pectoral radials	63	67		65.5	72	62-73	69.8
Number of pelvic radials	16	15		15.5	20	19–20	19.7

Table 3.—Proportional measurements and meristic values for *P. alleni* and *P. nitida*. Proportions are expressed as percentage of total length.

ed. Tip of snout with small, laterally flattened process. Axis of greatest width 76% (67 to 68%) of distance from tip of snout to axil to pectoral fins. Pelvic fins deeply incised, anterior lobe narrow and acutely pointed; anterior margin 85% (81 to 104%) as long as distance from origin of anterior lobe to posterior extreme of fin. Tail slender, little depressed, its width at midlength about two-thirds diameter of eye. Tail with narrow lateral fold along ventrolateral surface running from near tip of pelvic fins to origin of hypochordal lobe of caudal fin, widening near tip of tail fold to equal height of epichordal lobe of caudal fin. Length of tail from center of cloaca to distal tip 1.4 times (1.5 times) distance from tip of snout of center of cloaca.

Preocular length 2.5 times (2.2 to 2.5 times) as long as orbit; preoral length 2.0 times (2.4 to 2.5 times) internarial distance. Interorbital distance 0.6 (0.7 to 0.8) times length of orbit, orbit length 3.1 (2.2 to 3.3) times as long as spiracles.



Fig. 7. Pavoraja alleni, WAM P19118 (Holotype): a, Dorsal view; b, Ventral view; c, Ventral view of head.



Fig. 8. Pavoraja alleni, WAM P19117 (Paratype).

VOLUME 95, NUMBER 1

Anterior and posterior nasal flaps without fringes; without nasal pits. Upper and lower jaws moderately arched (little arched). Teeth with pointed cusps near symphyses of jaws, with rounded cusps near margin of jaws (with rounded cusps throughout jaws), teeth arranged in more or less transverse series (in quincunx).

Distance between first gill slits 2.5 (2.4 to 2.8) times as great as between nares; distance between fifth gill slits 1.6 (1.3 to 1.8) times as great as between nares; length of first gill slits 1.4 (1.1 to 1.2) times length of fifth gill slits and 0.1 (0.1 to 0.2) times mouth width. First dorsal fin slightly higher and longer than second; interspace between dorsal fins equal to or slightly shorter than base of first dorsal fin; second dorsal fin separated from epichordal caudal-fin lobe by distance equal to one-half base of second dorsal fin; epichordal lobe low, length of base about equal to that of second dorsal fin; distance from end of base of second dorsal to tip of tail considerably greater than length of base of second dorsal fin; hypochordal caudal lobe small.

Upper surface of disc, pelvics and tail densely covered with denticles. Ventral surface naked. Orbit with 3 thorns on anteromedial margin and 3 thorns on posteromedial margin; 3 prenuchal and 1 nuchal thorns; 3 irregular rows of thorns on dorsal surface of tail, no interdorsal thorns. Holotype with 5 alar spines on left and 4 on right lateral aspect of disc and a patch of malar thorns on anterolateral aspect of disc.

The claspers of P. alleni are similar to those of P. nitida with the following exceptions: claspers very slender; rhipidion poorly developed; sentinel curved laterally and extending to tip of glans (Fig. 1b); dorsal terminal 1 only loosely connected to ventral terminal along ventral aspect of glans; dorsal terminal 3 with a longer distal extension forming spur (Fig. 2d, e, f); ventral marginal with a truncated distal margin; accessory terminal 1 with a relatively longer and less curved distal extension forming sentinel; accessory terminal 2 with a more elongated shaft supporting disc-like extension forming spike.

The neurocranium of P. alleni is similar to that of P. nitida with the following exceptions: nasal capsules set at about a 30° angle to transverse axis of neurocranium (Fig. 4); rostral base better developed, extending nearly to leading edge of nasal capsules; precerebral space broader (Table 1), inner walls of nasal capsules not appreciably bulging into precerebral space; postorbital processes poorly developed; jugal arches relatively slender.

The scapulocoracoids of P. alleni are similar to those of P. nitida (Table 2) with the following exceptions: the anterior vertical margin is more perpendicular to horizontal axis (Fig. 5b); posterior corner more posteriorly located; postdorsal fenestra is oval-shaped rather than elliptical.

Color.—Dorsal surface uniformly light tan with minute dark spots loosely concentrated into ill defined, symmetrically arranged blotches; tail darker with four obscure brown bands; dorsal fins tan with brown blotches. Ventral surface light tan.

Etymology.—Named after Gerald R. Allen (WAM) who furnished us with the specimens of the new species.

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