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Article

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Description of two new species of sea bass (Teleostei: Latidae: *Lates*) from Myanmar and Sri Lanka

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Abstract

Two new species of *Lates* Cuvier are described. *Lates lakdiva*, new species, from western Sri Lanka, differs from its Indo-Pacific congeners by its lesser body depth, 26.6–27.6% SL; 5 rows of scales in transverse line between base of third dorsal-fin spine and lateral line; 31–34 serrae on the posterior edge of the preoperculum; third anal-fin spine longer than second; 47–52 lateral-line scales on body; and greatest depth of maxilla less than eye diameter. *Lates uwisara*, new species, from eastern Myanmar, is distinguished by possessing 7 scales in transverse line between base of third dorsal-fin spine and lateral line; eye diameter 4.4–4.7% SL; body depth 28.4–34.5% SL; and third anal-fin spine shorter than the second. Despite substantial genetic variation, *L. calcarifer* sensu lato is widely distributed, from tropical Australia through Indonesia, Singapore and Thailand, westwards to at least the west coast of India. Caution is urged in translocating *Lates* in the Indo-Pacific region as other yet unrecognized species likely exist. The status of the type specimens of *L. calcarifer* is discussed, and a common lectotype designated for *L. heptadactylus* and *L. nobilis*. While *Lates vacti* (type locality Bengal) may be a valid species, *L. cavifrons* and *L. darwiniensis* are considered synonyms of *L. calcarifer. Plectopomus* Goldfuss and *Ptertopomus* Goldfuss are shown to be incorrect subsequent spellings of *Plectropomus* Oken.

Key words: Australia, Burma, cryptic species, giant perch, barramundi, sibling species

Introduction

Known as sea bass or giant perch in Asia and barramundi in Australia, *Lates calcarifer* (Bloch, 1790) is among the most important food fishes in tropical Australasia and the Asian countries bordering the Indian Ocean (Pender & Griffin 1996; Rimmer & Russell 1998; Yingthavorn 1951; Rabanal & Soesanto 1982). The species has been recorded to attain a mass in excess of 44 kg and reach a total length of more than 135 cm in Australia (IGFA 2011). *Lates calcarifer* has long been of economic importance (e.g., it figures in Australian aboriginal rock art dating 15,000–8,000 ybp: Chaloupka 1997), and has been increasingly stocked for the recreational fishery and utilized in aquaculture for the past several decades. The existence of as many as 75 local names in 14 of the countries within its range (Mathew 2009; FAO 2011) is perhaps additional evidence of its popularity as a species of commercial significance.

While several freshwater species of *Lates* occur in the Nile basin (the Mediterranean having been connected to the Indian Ocean until the mid-Miocene: Harzhauser & Piller 2007), the only other non-African species currently considered valid is *L. japonicus* Katayama & Taki, 1984, restricted to estuaries and coastal waters in Japan. The range of *L. calcarifer* presently extends eastwards from the Persian Gulf to China and the Queensland coast of Australia, within an approximate latitude range of ±25 (FAO 2011; Pusey *et al.* 2004). The species is catadromous, with adults occurring in coastal waters, estuaries and sometimes rivers more than 700 km upstream of the tidal influence (Dunstan 1962). Species of *Lates* are, however, unknown from the East African coast, the Arabian Peninsula (which lacks perennial rivers and hence estuaries) apparently serving as a barrier to their southward dispersal.

Several studies suggest there is considerable genetic variation between populations of the fishes currently assigned to *L. calcarifer.* For example, Salini and Shaklee (1988) and Keenan and Salini (1990), based on an elec-

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trophoretic analysis, showed that as many as 14 widely-spaced locations in Western Australia and the Northern Territory harbour genetically distinct populations of *Lates*, a result supported also by the mitochondrial DNA study of Chenoweth *et al.* (1998). Following on this, Ward *et al.* (2008), in a study of the mitochondrial cytochrome *c* oxidase I (CO1) gene showed the Australian and Myanmarese populations of *L. calcarifer* to differ by a Kimura 2-parameter distance of *ca* 9.5% and a cytochrome-*b* distance of 11.3%, and mooted the existence of a cryptic species. More recently, Yue *et al.* (2009) genotyped populations of *L. calcarifer* from Southeast Asia and Australia and demonstrated that the Australian and Southeast Asian stocks showed substantial divergence. Because of the different methods involved, it is not possible reliably to combine the results of all these authors to elucidate the evolutionary relationships of the various populations studied. Nevertheless, it is clear that substantial genetic distances separate several *Lates* populations, which in turn warrant a taxonomic re-assessment.

While these genetic analyses suggest that *L. calcarifer* as hitherto understood likely comprises more than a single species, a morphological examination of samples from across its range, despite two excellent systematic treatments (Greenwood 1976; Otero 2004), has remained a desideratum. Dunstan (1958, 1962) noted some variation in colour and morphology in New Guinean and Australian populations of *L. calcarifer*, but these were not sufficiently unambiguous as to allow putatively distinct populations to be taxonomically differentiated (see also Grey 1987). Katayama *et al.* (1977) and Katayama and Taki (1983) showed the Australian and Japanese populations of *Lates* to be distinct and made available the name *L. japonicus* for the latter. However, they were unable to shed light on the true identity of *L. calcarifer* sensu stricto because the type/s were thought to be lost, and because the type locality, "Japan", had been in doubt since Cuvier (1828) argued that it was more likely Java. Specimens said to be types have since been found (Paepke 1999), providing an opportunity to address these questions.

Additionally, the taxonomy of *L. calcarifer* is complicated by the existence of several nominal species presently relegated to its synonymy (Eschmeyer 2011), all of them disadvantaged by scant original descriptions, poorly defined type localities and/or an absence of type specimens: *L. heptadactylus* (Lacepède, 1802), no type locality; *L. vacti* (Hamilton, 1822), no types, type locality Ganges River, Bengal, India; *L. nobilis* Cuvier, 1828, syntypes from multiple localities, type locality Pondicherry, India; *L. cavifrons* (Alleyne & Macleay, 1877), type lost, type locality "somewhere in Torres Straits or the coast of New Guinea"; and *L. darwiniensis* Macleay, 1878, type in poor condition, type locality "Darwin, Australia".

Here, in addition to reviewing briefly the taxonomy of *L. calcarifer*, we describe two new species of *Lates*, from Sri Lanka and Myanmar; and suggest, based on the external morphology of the size-class examined herein, that *Lates calcarifer* is a widely distributed species, with a range extending from the Queensland coast of Australia westwards at least to India.

Material and methods

A total of 45 specimens of *Lates* from Australia, India, Malaysia, Myanmar, Singapore, Sri Lanka and Thailand (Fig. 1) were examined. Counts of dorsal, anal and pelvic-fin spines and rays are presented, respectively, using Roman and Arabic numerals. Where supported by a single pterygiophore, dorsal- and anal-fin rays divided to the base were counted as a single ray. Caudal-fin ray counts are given as the number of dorsal procurrent rays + number of principal rays of upper lobe + number of principal rays of lower lobe + number of ventral procurrent rays. Measurements up to 200 mm were made to the nearest 0.1 mm with digital callipers, those greater than 200 mm to the nearest 1 mm with a meter rule. The following measurements were made—standard length, from snout tip to the hypural notch; total length, from snout tip to tip of caudal fin; head length, from snout tip to posterior (membranous) margin of opercle; and distances from snout tip to: base of last dorsal-fin ray, base of last anal-fin ray, anal-fin origin (preanal distance), pelvic-fin origin (prepelvic distance), base of last pectoral-fin ray (prepectoral distance), dorsal-fin origin (predorsal distance), posterior (serrated) margin of preoperle, tip of retrorse spine at angle of opercle, posterior margin of maxilla (maxillary length), and anterior margin of eye (snout length). Dorsal-fin and anal-fin base were measured from the fins' origins to the base of the last ray; post-dorsal distance, from dorsal-fin origin to hypural flexion; body depth, depth at dorsal-fin origin; caudal-peduncle depth, least depth of caudal peduncle; caudal-peduncle length, from base of last anal-fin ray to hypural flexion (notch); pectoral-fin length, from superior base to tip of pectoral fin; pelvic-fin length, from distal base to tip of pelvic fin; maxilla depth, greatest depth of maxilla; eye diameter, horizontal diameter of eye; internarial width, least distance between posterior nares; and interorbital width, least distance between bony margin of orbits. The lateral-line scale count includes all pored scales from the lateral-line origin to the hypural flexion (posterior to which the scales on the caudal-fin base are substantially reduced in size). Scales in transverse line on body were counted down from the base of the third (i.e. longest) dorsal-fin spine to the lateral line and up from the anus to the lateral line; and on the caudal peduncle (on each side) from the base of the last anal-fin ray backwards and up to the midline of the peduncle. Gill rakers were counted separately for the upper and lower limbs, respectively, of the first gill arch, the raker at the angle denoted by 1. Twenty-six of the 45 specimens examined were x-rayed and the number and length of fin spines and rays, and the number of abdominal and post-abdominal vertebrae, taken from radiographs. As a result of dorsal- and anal-fin spine measurements from specimens being subject to error because of the scaly sheath at the base of these fins, statistical analyses were done separately for spine-lengths measured from specimens and from radiographs. The predorsal scale-count is not recorded because the irregular arrangement of these scales makes repeatable counting impossible.

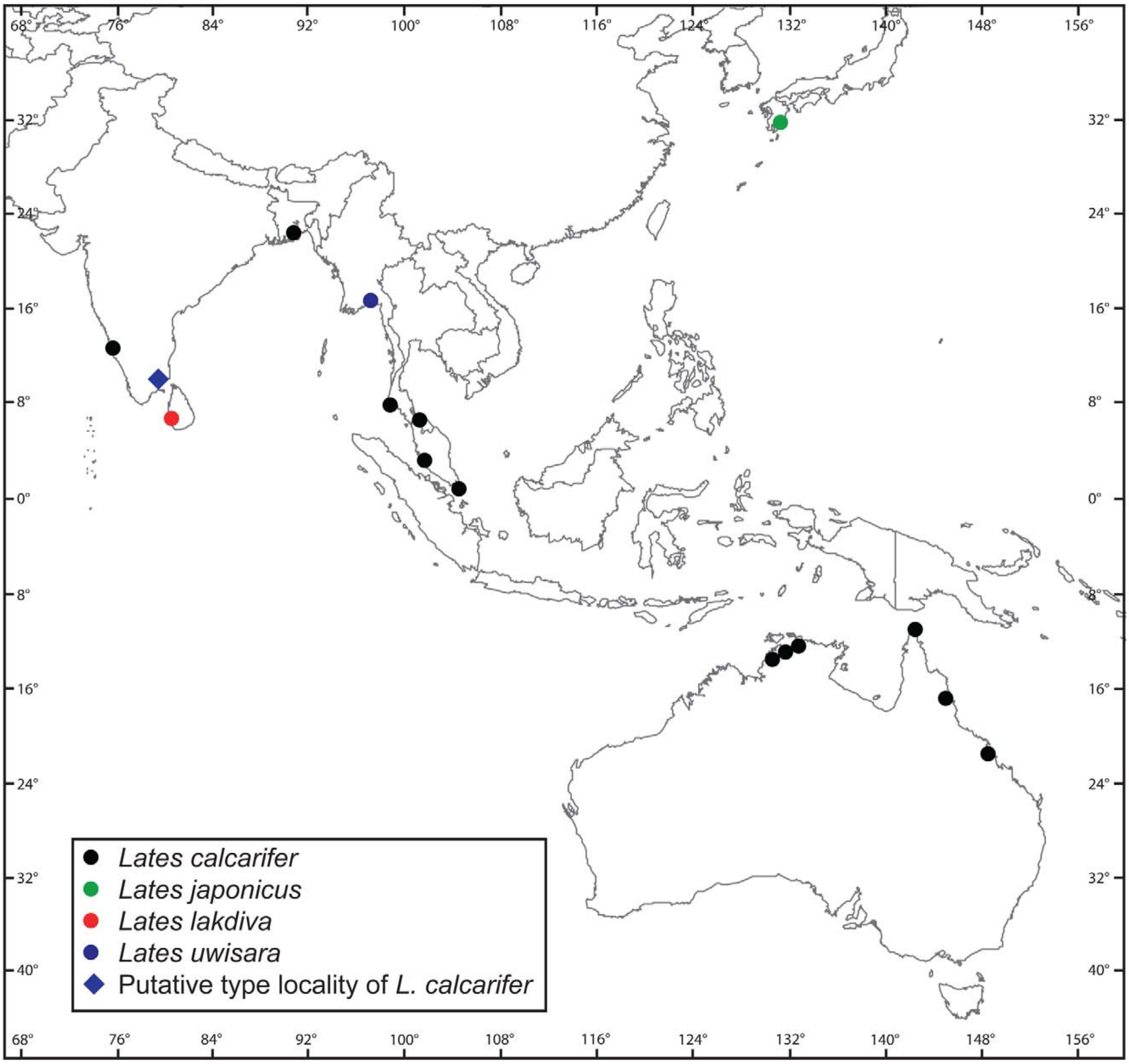

FIGURE 1. Locations from which species of *Lates* are reported in this study.

Principal components analysis (using Systat for Windows Version 11.00.01 and Microsoft Excel, with data regressed against SL) of the character correlation matrix was used to reduce dimensionality of the continuous morphological variables and to identify those variables that best discriminate among the species. Various axis rotations were tested and one selected for optimal interpretability of variation among the characters. Although the small sample sizes likely do not represent the full range of morphological variation, this analysis serves as a guide to the demarcation of species and helps to identify morphometric characters that contribute best to their diagnoses.

Institutional abbreviations used in the text are: AMS, Australian Museum, Sydney; ANFC, Australian National Fish Collection, Commonwealth Scientific and Industrial Research Organisation, Hobart; BMNH, Natural History Museum, London; CAS, California Academy of Sciences, San Francisco; IFS, Institute of Fundamental Studies, Hantana (Sri Lanka); IGB, Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Berlin; MAGNT, Museums and Art Galleries of the Northern Territory, Darwin; MAMU, Macleay Museum, University of Sydney, Sydney; NMNH, Smithsonian Institution National Museum of Natural History, Washington, D.C.; MNHN, Muséum National d'Histoire Naturelle, Paris; NSMT, National Museum of Nature and Science, Tokyo; QMB, Queensland Museum, Brisbane; WAM, Western Australian Museum, Perth; ZMB, Museum für Naturkunde, Berlin; and ZSI, Zoological Survey of India, Kolkata.

***Lates lakdiva*, new species**
(Fig. 2)

Material examined: holotype, AMS I.37516-001, 220 mm SL, St John's Fish Market, Colombo, Sri Lanka, 1994; paratypes, AMS I. 37516-001, 2, 239 mm SL and 256 mm SL, same data as holotype.

Diagnosis. *Lates lakdiva* is distinguished from *L. calcarifer* by its lesser body depth (26.6–27.6% SL, vs. 28.9–34.6% SL); possessing 5 (vs. 6) rows of scales between the base of the third dorsal-fin spine and lateral line; 31–34 (vs. 16–26) serrae on the posterior edge of the preoperculum; and having the third dorsal-fin spine 3.0–3.5 (vs. 2.1–2.8) times the length of the second. It differs from *L. japonicus* by having the third anal-fin spine longer (vs. shorter) than the second; and possessing 5 (vs. 7) rows of scales between the base of the third dorsal-fin spine and the lateral line, a lesser body depth (26.6–27.6% SL, vs. 30.3–33.7% SL), and 47–52 (vs. 58–63) lateral-line scales. *Lates lakdiva* differs from *L. uwisara* by having a greater eye diameter (5.5–5.6% SL, vs. 4.4–4.7% SL), a lesser body depth (26.6–27.6% SL, vs. 28.4–34.5% SL), a shorter dorsal-fin base (41.1–43.2% SL, vs. 43.3–45.0% SL), and by possessing 5 (vs. 7) rows of scales between the base of the third dorsal-fin spine and lateral line.

FIGURE 2. *Lates lakdiva*, holotype, AMS I.37516-001, 220 mm SL.

Description. See Table 1 for proportional measurements. Body compressed (body width 43.6–45.7% body depth), its depth 2.9–3.8 times in SL, deepest at dorsal-fin origin. Dorsal profile concave in interorbital region, rising steeply (convex) thereafter to dorsal-fin origin. Head moderately acute, its length 2.8 times in SL. Eye oval, height less than width, eye diameter 6.4–6.6 times in head length. Snout 5.3–5.4 times in head length. Interorbital space 90.6–95.2% eye diameter. Mouth oblique, lower jaw projecting beyond upper one when closed. Maxilla deep, its depth 82.1–92.7% eye diameter, extending posterior to level of eye. Villiform teeth present on jaws, palatines, pterygoids and vomer. Tongue smooth. Three sharp, strong spines on inferior margin of preoperculum, the first antrorse; a retrorse spine at angle of preoperculum, the posterior margin of which bears 31–34 serrae. A sharp spine at angle of operculum. Seven branchiostegal rays. Inferior margin of infraorbitals 1 and 2 finely serrated. Nares level with middle of eye, separated from eye by distance less than diameter of posterior naris. Gill rakers 3+1+8, densely denticulated on proximal side. Cleithrum and supracleithrum each with 4 or 5 serrae.

TABLE 1. Measurements as a percentage of standard length of holotype and 2 paratypes of *Lates lakdiva* (220–256 mm SL); holotype and 3 paratypes of *L. uwisara* (332–363 mm SL); 27 specimens of *L. calcarifer* (97.6–315 mm SL); and 11 specimens of *L. japonicus* (134–263 mm SL). Non-overlapping ranges between species are italicized. Specimen details are given in species accounts of *L. lakdiva* and *L. uwisara*, and Comparative Material.

	L. lakdiva		*L. uwisara*		*L. calcarifer*		*L. japonicus*	
	min	max	min	max	min	max	min	max
Total length	121	121	121	124	120	128	119	123
Snout to base of last dorsal-fin ray	82.4	83.2	82.6	85.2	82.0	88.4	82.0	85.8
Snout to base of last anal-fin ray	84.8	85.4	83.3	86.4	82.3	88.1	82.5	88.9
Preanal length	*73.9*	*74.8*	*72.9*	*75.6*	69.9	76.1	*67.5*	*72.3*
Prepelvic length	34.6	36.3	34.6	36.5	34.4	43.9	33.1	38.3
Prepectoral length	32.9	34.8	31.3	33.7	31.4	38.7	30.2	34.3
Predorsal length	44.8	45.0	44.7	47.2	42.0	47.4	42.3	45.7
Length of dorsal-fin base	*41.1*	*42.0*	*43.9*	*45.0*	41.3	46.3	42.8	45.5
Length of 1st dorsal-fin base	*19.4*	*19.4*	*21.1*	*23.0*	19.6	25.7	*22.3*	*26.6*
Length of 2nd dorsal-fin base	*18.3*	*19.2*	*21.0*	*21.8*	17.8	21.5	18.5	21.0
Dorsal-fin origin to caudal-fin base	60.2	60.2	59.3	62.3	58.6	65.0	60.9	65.2
Post-dorsal distance	18.7	18.7	16.0	19.4	14.3	19.5	17.9	20.2
Body depth	26.6	27.6	28.4	32.0	28.9	34.6	30.5	33.7
Depth from dorsal-fin origin to pelvic-fin origin	28.4	29.1	30.1	33.3	30.1	35.5	31.9	35.3
Depth at origin of 2nd dorsal fin	26.9	26.9	26.9	31.1	26.6	33.6	30.5	33.3
Caudal peduncle depth	*11.3*	*12.1*	11.6	13.3	11.9	14.6	*12.5*	*14.0*
Caudal peduncle length	*17.1*	*17.5*	*15.8*	*17.6*	14.3	19.6	*18.2*	*20.1*
Body width at dorsal-fin origin	*12.0*	*12.6*	14.0	16.1	11.7	17.6	11.8	16.4
Length of anal-fin base	*12.0*	*12.0*	*12.1*	*13.9*	*12.5*	*15.4*	*14.5*	*16.5*
Pectoral-fin length	*15.7*	*15.9*	*16.5*	*17.6*	14.2	17.5	14.7	16.6
Pelvic-fin length	20.1	20.7	18.5	20.7	18.4	21.9	20.1	21.6
Length of dorsal spine I	*2.2*	*2.8*	*3.3*	*3.6*	2.6	4.2	2.5	5.1
Length of dorsal spine II	*5.6*	*6.3*	*5.7*	*6.4*	5.8	7.8	*6.9*	*9.1*
Length of dorsal spine III	17.8	18.9	16.8	20.3	16.0	21.5	17.4	21.8
Length of anal-fin spine II	*4.3*	*4.5*	*4.2*	*5.0*	*4.3*	*6.8*	*8.5*	*11.5*
Length of anal-fin spine III	*7.4*	*7.4*	*6.4*	*7.1*	5.0	7.7	*7.3*	*9.3*
Head length	35.7	35.8	35.5	37.9	35.0	39.9	32.8	36.7
Snout length	*6.7*	*6.8*	*6.8*	*7.5*	6.6	8.4	7.2	8.7
Maxilla length	*14.6*	*14.6*	*15.2*	*16.8*	14.1	16.9	13.4	15.5
Maxilla depth	*4.6*	*4.6*	*4.9*	*5.4*	4.0	5.9	4.4	5.4
Internarial width	*4.8*	*4.8*	*4.1*	*4.3*	4.2	5.7	3.9	5.3
Eye diameter	*5.5*	*5.6*	*4.4*	*4.7*	*4.7*	*6.9*	4.9	6.7
Interorbital width	5.0	5.4	5.0	5.7	4.1	5.9	4.4	5.3
Snout to preopercular posterior margin	24.6	25.2	23.7	25.4	23.3	26.5	22.3	25.1
Snout to tip of spine at preopercular angle	26.3	26.6	26.3	27.9	25.2	29.6	24.1	27.2

First dorsal fin commencing slightly behind pelvic-fin, with 7 spines, third spine longest (III>IV>V>VI>II>VII>I). Base of first dorsal fin subequal to (97.5–110%) that of second dorsal fin. Second dorsal with 1 spine and 10 or 11 rays. Anal fin commencing beneath base of second-dorsal fin ray 4, with 3 spines, third one longest (III>II>I) and 7 or 8 rays. Pectoral fin with 14 rays, 76.7–81.1% length of pelvic fin, which has 1 spine and 5 rays. Pelvic-fin spine slightly shorter than dorsal spine IV, longer than dorsal spine V. Distal profiles of pectoral, pelvic, anal and second-dorsal fins rounded. Caudal fin rounded, with 7+9+8+7 rays. Caudal peduncle depth 66.1–69.1% its length.

Scales ctenoid; body and head scaled, except for snout, throat, preorbital and interorbital regions. Dorsal and anal fins reposed in a scaly sheath. Second-dorsal, caudal, anal and lateral area of pelvic fin densely covered with minute scales. Lateral line with 47–52 posteriorly notched scales on body, commencing immediately posterior to supracleithrum, extending almost to tip of caudal fin; two rows of pored scales on caudal fin, one above and one below median lateral line. Five scales in transverse line between base of third dorsal-fin spine and lateral line; 9 or 10 in transverse line between anus and lateral line; 22 circumpeduncular scales.

Coloration. In 70% alcohol (Fig. 2), head and body olive brown, darker above lateral line and on dorsal region of head, lighter below, ventrally creamy yellow. Fins dark olive, interradial membrane of dorsal fin white, dark-olive towards distal margin. Second dorsal fin, caudal and anal fins dark olive brown, pectoral and pelvic fins somewhat lighter, pelvic-fin spine almost white.

Etymology. The specific epithet Lakdiva is Sinhala for the island of Sri Lanka, here used as a substantive in apposition. We propose Sri Lankan Sea Bass as the common name for this species, which is also known by the local names ‘modha’ (Sinhala) and ‘koduwa’ (Tamil).

Conservation. The growth of the fisheries industry in Sri Lanka has seen the introduction of large numbers of juvenile *Lates* of unknown provenance into the island’s estuaries during the recent past (RP, pers. obs.). The effects of these introductions on the population of *L. lakdiva*, are unknown and warrant future investigation.

Lates uwisara, new species
(Fig. 3)

Material examined: holotype, ANFC H.6316-10, 353 mm SL, Myanmar, “river estuaries between Yangon and Sittang”, October 2005; paratypes, ANFC H.6316-09, 363 mm SL; ANFC H.6316-11, 332 mm SL; ANFC H.6316-12, 350 mm SL, same collection data as holotype.

Diagnosis. *Lates uwisara* is distinguished from *L. calcarifer* by possessing 7 (vs. 6) scales between the base of the third dorsal-fin spine and the lateral line; and having a lesser eye diameter (4.4–4.7% SL, n=3; vs. 4.8–6.9% SL, n=25). It differs from *L. lakdiva* by having a greater body depth (28.4–34.5% SL, vs. 26.6–27.6% SL), a longer dorsal-fin base (43.3–45.0% SL, vs. 41.1–43.2% SL), a lesser eye diameter (4.4–4.7% SL, vs. 5.5–5.6% SL), and by possessing 7 (vs. 5) rows of scales between the base of the third dorsal-fin spine and the lateral line. It is distinguished from *L. japonicus* by having the third anal-fin spine shorter (vs. longer) than the second; a shorter caudal peduncle (15.8–17.6 % SL, vs. 18.2–20.2% SL) and a greater preanal distance (72.9–75.6% SL, vs. 67.5–72.3% SL).

Description. See Table 1 for proportional measurements. Body compressed (body width 49.3–50.4% body depth), its depth 3.1–3.5 times in SL, deepest at dorsal-fin origin. Dorsal profile concave in interorbital region, rising steeply (convex) thereafter to dorsal-fin origin. Head moderately acute, its length 2.8 times in SL. Eye oval, height less than width, eye diameter 7.5–8.6 times in head length. Snout 4.7–5.2 times in head length. Interorbital space 114–122% eye diameter. Mouth oblique, lower jaw projecting beyond upper one when closed. Maxilla deep, its depth 104–120% eye diameter, extending posterior to level of eye. Villiform teeth present on jaws, palatines, pterygoids and vomer. Tongue smooth. Three sharp, strong spines on inferior margin of preoperculum, first antrorse; a retrorse spine at angle of preoperculum. Preoperculum posterior margin with 26–34 serrae. A sharp spine at angle of operculum. Seven branchiostegal rays. Inferior edge of infraorbitals 1 and 2 finely serrated. Nares level with middle of eye, separated from eye by distance less than diameter of posterior naris. Gill rakers 3+1+8–9, densely denticulated on proximal side. Cleithrum and supracleithrum each with 5–7 serrae.

First dorsal fin commencing slightly behind pelvic-fin, with 7 spines, third spine longest (III>IV>V>VI>II>VII>I). Second dorsal with one spine and 11 rays. Anal fin commencing beneath base of second-dorsal fin ray 3 or 4, with 3 spines, the third one longest (III>II>I) and 8 rays, the last one branched to base. Pectoral fin with 14 rays, 86.5–89.6% length of pelvic fin, which has 1 spine and 5 rays. Length of pelvic-fin spine equal to or slightly shorter than dorsal spine V, longer than dorsal spine VI. Distal profiles of pectoral, pelvic, anal and second-dorsal fins rounded. Caudal fin rounded, with 6–7+9+8+6–7 rays. Caudal peduncle depth 71.2–78.5% its length.

Scales, ctenoid; body and head scaled, except for snout, throat, preorbital and interorbital regions. Dorsal and anal fins reposed in a scaly sheath. Second dorsal, caudal, anal and lateral area of pelvic fin densely covered with minute scales. Lateral line with 56–59 scales on body, commencing immediately posterior to supracleithrum, extending almost to tip of caudal fin; two rows of pored scales on caudal fin, one above and one below median lateral line. Seven scales in transverse line between base of third dorsal-fin spine and lateral line; 10 or 11 in transverse line between anus and lateral line; 24 circumpeduncular scales.

Coloration. In 70% alcohol (Fig. 3), head and body olive-tan, darker above lateral line and dorsal region of head, lighter below, ventrally light yellowish-brown. Fins greenish-brown, interradial membrane of dorsal fin light greenish-brown, somewhat darker towards distal margin. Second dorsal fin, caudal and anal fins dark olive brown, pectoral and pelvic fins somewhat lighter.

FIGURE 3. *Lates uwisara*, holotype, ANFC H.6316-11, 332 mm SL.

Etymology. The species-name is a patronym honouring the Burmese patriot U Wisara; it is formed as a substantive in apposition. We suggest Myanmar Sea Bass as the common name of this species.

Remarks. Ward *et al.* (2008) investigated CO1 sequence divergence in *Lates* from Western Australia, Queensland, Singapore and Myanmar. While the former three populations were shown to be almost identical (0.5% divergence), the Myanmar specimens showed a divergence of 9.5%, sufficient to signify a distinct species (Page & Hughes 2010; Benziger *et al.* 2011). The type series of *L. uwisara* comprises the same specimens analysed by Ward *et al.* (2008). Interestingly, these authors also found a sample of *Lates* from French Polynesia to be identical to three of the Myanmar specimens. *Lates* does not occur naturally in French Polynesia where it has, however, been introduced for aquaculture (FAO 2011). While it is thus clear from Ward *et al.* (2008) that *L. uwisara* has already been used in aquaculture, it also raises a question over its type locality: is it indigenous to Myanmar waters, or might it have been introduced there, too? Data on three further Myanmarese specimens (ZSI FF 125, 177 mm SL, from Pegu [Bago]; ZSI FF 302, 141 mm SL, from Moulmein [Mawlamyaing]; and ZSI FF 410, 263 mm SL, from Akyab [Sittwe]) in the Francis Day collection at the ZSI (collected *ca*1880), kindly provided by S. Batuwita (pers. comm.), indicate they are examples of *L. uwisara*, leading us tentatively to regard the species as being originally from Myanmar. If the species has indeed entered into widespread use in aquaculture, however, it is likely to be recorded from additional localities in the future.

The specimens in our series of *L. uwisara* are significantly larger (mean 350 ± s.d. 13 mm SL) than those in the other species (*L. calcarifer*, 178 ± 45 mm SL; *L. japonicus*, 205 ± 39 mm SL; *L. lakdiva*, 238 ± 18 mm SL). It is possible, therefore, that at least one of the characters in the diagnosis of *L. uwisara*—viz., eye diameter less than depth of maxilla—is a consequence of allometry, which is particularly striking in the case of fish eyes (Howland *et al.* 2004). The number of scale rows between the third dorsal spine and lateral line, however, remains constant within species across the sample examined and, together with the relative lengths of the pelvic, dorsal and anal fin spines, may provide the best means of identifying this species.

Discussion

Identity of *Lates calcarifer*. Bloch (1790: 101) gave the locality of his *Holocentrus calcarifer* simply as Japan ("Das Vaterland dieses fisches ist Japan"). Cuvier (1828), however, observed that though Bloch believed *L. calcarifer* to be of Japanese origin, it could only have been from Java, as in the case of several Bloch fishes stated to be Japanese. He believed Bloch to have been misled by the Dutch traders who sold him the specimens: "We will have in what follows many opportunities to demonstrate that Bloch, either by ignorance, or because he was duped by the Dutch dealers whose fish he purchased, has almost always given as Japanese [what are] Javanese species" (Cuvier 1828: 100, our translation). Cuvier did not, however, mention the specific reasons that caused him to doubt the type locality mentioned by Bloch. Indeed, given that the Dutch East India Company had a trading post at Nagasaki at the time (Boxer 1950), it was entirely possible for Dutch traders to have provided Bloch with specimens that were in fact from Japan. Nevertheless, although there was at least one collection of fish Bloch believed he received from Japan ("In einer Unlängst [ohnlängst] erhaltenen Sammlung von japanischen Fischen", Bloch, 1787: 48), as pointed out by Paepke (1999: 27), many of the included specimens represent tropical species unknown from Japanese waters. Indeed, the vernacular 'Japanese' names of several fishes mentioned by Bloch, such as Jcan [Ican] boenak (*Bodianus boenak*), Ican ongo (*Holocentrus ongu*) and Ikan Lutjang (*Lutjanus lutjanus*) are Malay names, 'ikan' being Malay for fish.

In Bloch's own handwritten catalogue, he referred to the specimen of *L. calcarifer* depicted on Plate 244 of Bloch (1790) as "aus Tranquebar malaiisch Atukottalei" ("from Tranquebar, in Malay [language] Atukottalei"), making no mention of Japan. This appears plausible given that by the late 18th century Malay trading communities had become established in parts of India and Sri Lanka controlled by the Dutch East India Company (Hussainmiya 1987). "Atukottalei" was apparently a misspelling of Pattukottai, a town and maritime administrative region ('Taluk') in the Coromandel littoral of Tamil Nadu, India, some 90 km from Tranquebar (now Tharangambadi). It is credible that a specimen of *Lates* may have been purchased there.

In designating ZMB 13652 (290 mm SL) as lectotype of *Holocentrus calcarifer*, Paepke (1999) considered this specimen and ZMB 8735 (170 mm SL, a right skin) to be syntypes. Bloch (1790: 101), however, mentioned that his illustration was the same size as the fish ("Er ist in der Grösse, in der ich ihn erhalten habe, abgebildet"). The total length of the iconotype is 282 mm, whereas the total length of ZMB 13652 is 330 mm, a difference of 17%. It is even less certain that ZMB 8735 was part of the type series. Bloch's (1790) account is consistent with him having had only a single specimen before him (though he does not state this explicitly). While in some cases Bloch augmented the information provided in the original (1790) edition of *Allgemeine Naturgeschichte der Fische* in the subsequent French translation (Wells, 1981), the latter work too (Bloch 1797: 81), implies there was indeed only a single specimen: "Notre dessin a la grandeur de l'original de j'ai reçu". Bloch and Schneider (1801: 89), however, gave the (presumably maximum total) length of the specimen/s as "longa 10, lata 3 poll." [length 10, breadth 3 thumbs (inches)]. Several different systems of units were in use in pre-metric Europe (Klimpert 1896); assuming Bloch used the system that was official in Prussia until 1816, a thumb would have been 2.62 cm, making the maximum (total) length of this fish approximately 260 mm, which is closer to the size of the iconotype (282 mm TL). Given the 330 mm total length of ZMB 13652 and the 205 mm total length of ZMB 8735, the measurements of Bloch and Schneider (1801) seem consistent with neither specimen.

Unfortunately, it is also difficult to rely on the iconotype (Bloch, 1790: pl. 244; reproduced here as Fig. 4) for an accurate characterization of *L. calcarifer.* Although this figure is clearly inaccurate in some respects (e.g., the lateral line is not indicated but there are only 33 scales on the body in the lateral series, whereas all *Lates* measured in this study have a minimum of 49 lateral-line scales on the body), some characters can be discerned: e.g., dorsal spine III is shorter than the pelvic fin (longer in *L. japonicus*) and anal spine III is longer than anal spine II (shorter in *L. japonicus*). While these data do not allow the specimen depicted in the iconotype unambiguously to be allocated to the tropical Asian or Japanese populations of *Lates*, it lacks key characters observed in *L. japonicus*, for which reason we concur with Cuvier (1828: 100) that it was not from Japan. Based on its photograph (Fig. 5), the 'lectotype' of *L. calcarifer* (ZMB 13652) is consistent with the Asian and Australian specimens we list as belonging to this species: it possesses five cleithral and five supracleithral serrae, 21 serrations on the posterior margin of the preopercle, the lengths of the first, second and third spines of the dorsal fin 5.0%, 6.2% and 14.8% SL, and six scales in transverse line between the base of the third spine of the dorsal fin and the lateral line.

In conclusion, it appears that ZMB 8735 cannot have been a type of *Holocentrus calcarifer*: as at 1790 it seems Bloch had only a single specimen approximately 280 mm TL. While the type status of ZMB 13652 too, is moot, its total length (290 mm) is closer to that of the iconotype (282 mm), though somewhat larger than the size mentioned by Bloch and Schneider (1801), 260 mm. We treat it tentatively as the holotype, with type locality Pattukottai (10.4°N, 79.3°E) in Tamil Nadu, India.

FIGURE 4. Iconotype of *Holocentrus calcarifer* Bloch, 1790; pl. 244, laterally inverted.

FIGURE 5. Putative holotype of *Holocentrus calcarifer* Bloch, 1790, ZMB 13652, 273 mm SL; right skin, photograph laterally inverted. Photo: courtesy of Jörg Freyhof.

FIGURE 6. Lectotype of *Holocentrus heptadactylus* Lacepède, 1802, MNHN A-7330, 402 mm total length; right skin, photograph laterally inverted. Photo: courtesy of Romain Causse.

Synonymy of *Lates calcarifer.* The oldest available name in the synonymy of *L. calcarifer* is *Holocentrus heptadactylus* Lacepède, 1802, which too, lacks a type locality. Lacepède (1802: 391–392), while stating that he examined several specimens, specifically mentioned two: a juvenile of length rather under 20 cm and an older individual more than 40 cm long. These dimensions match the syntype skins in the MNHN: A-5739, 183 mm TL; and A-7330, 402 mm TL, the latter of which we here designate lectotype (Fig. 6). Based on its photograph, this specimen has 6 scales in transverse line between the origin of dorsal spine III and lateral line, 26 serrae on posterior margin of preoperculum, maxilla depth less than eye diameter, body depth 33.7% SL, third anal-fin spine longer than second, and length of pelvic spine greater than that of dorsal spine V. These characters serve to distinguish this specimen from *L. japonicus*, *L. lakdiva* and *L. uwisara*, and also place it within *L. calcarifer* as here understood.

The next oldest name in the synonymy of *L. calcarifer* is *Coius vacti* Hamilton, 1822. Hamilton (1822: 86–89, 369, pl. 16) provided a good description and illustration of this fish, which he described from the River Ganges. Specimens of *Lates* from the Ganges are rare in international collections, and we were ourselves able to examine only one, CAS SU 35744, 184.5 mm SL. While the morphometrics of this putative topotype differ slightly from those of our specimens of *L. calcarifer* from Australia, Singapore and Thailand (e.g., total length 128% SL, vs. 120–127% SL in *L. calcarifer*; caudal-peduncle length 14.3% SL, vs. 15.0–19.6% SL; pectoral-fin length 17.5% SL, vs. 14.2–17.0% SL; body width 11.7% SL, vs. 11.9–17.6% SL), it otherwise resembles *L. calcarifer* as understood here. The size of the specimen illustrated by Hamilton (1822, pl. 16) is unknown: he mentioned that they were best eaten at a [total] length of 2 feet (~60 cm), though they could reach up to 5 feet (~150 cm) in length. The proportions of this iconotype are broadly consistent with our specimens of *L. calcarifer*, though differing in detail, probably owing to artist's error (e.g. a lateral-line scale count of 37, vs. a minimum of 52 in our series). Although we retain *L. vacti* in the synonymy of *L. calcarifer* for the present, its identity warrants review when a larger series of topotypes becomes available.

The next-most senior name in the synonymy of *L. calcarifer* is *Lates nobilis* Cuvier, in Cuvier and Valenciennes, 1828. Its type locality, Pondicherry (Puducherry, in Tamil Nadu, India) is about 200 km north of Pattukottai, the putative type locality of *L. calcarifer.* Cuvier (1828) described *L. nobilis* both by indication to published descriptions as well as several specimens before him. As such, the type series of *L. nobilis* includes: one specimen obtained from Pierre Sonnerat, possibly from Pondicherry (the text is unclear), described on p. 97 (MHNG 148.01, 159 mm SL); one specimen obtained from Jean-Baptiste Leschenault, apparently also from Pondicherry (now MNHN A.6892, 242 mm TL); the specimen of *L. vacti* described and delineated in Hamilton (1822, pp. 86, 369; pl. 16), lost; the specimen described and delineated in Russell (1803, vol. 2, p. 23 and pl. 131) as 'Perca pandoomenoo', from Vizagapatam (Visakhapatnam, Andhra Pradesh, India), lost; two dry specimens (MNHN A.7330, 402 mm TL; MNHN A.5739, 183 mm TL) from the Indian Ocean, one 6–7 inches, one 15 inches, used by La Cepède to describe *L. heptadactylus* (Lacepède, 1802, himself noted that his specimens were "less than 20 cm" and "more than 40 cm”), the smaller of which was accompanied by a Dutch label, leading Cuvier to suspect it came from the Moluccas. The type series of *L. nobilis* would thus include these four specimens (MNHN A.6892, MNHN A.7330, MNHN A.5739, MHNG 148.01) plus the specimens figured in pl. 16 of Hamilton (1822) and pl. 131 of Russell (1803). From among these we select MNHN A.7330, the 402 mm TL specimen, as lectotype of *L. nobilis* Cuvier, 1828, which, having the same name-bearing type as *Holocentrus heptadactylus* Lacepède, 1802, becomes an objective synonym of the latter.

The two remaining available names in the synonymy of *L. calcarifer* are from Australian waters: *Pseudolates cavifrons* Alleyne & Macleay, 1877, type locality “somewhere in Torres Straits or the coast of New Guinea”; and *L. darwiniensis* Macleay, 1878, type locality Darwin. Eschmeyer and Fricke (2011), probably following Stanbury (1969), give the holotype of *P. cavifrons* as AMS I.514, which cannot be the type. It is a 201-mm TL specimen, whereas Alleyne and Macleay (1877) reported that their specimen was 2 feet long and nearly 6 inches deep. Whitley (1957) listed AMS I.513, a 180-mm SL specimen as a syntype, whereas Eschmeyer and Fricke (2011) mention ?AMS [ex MAMU F442(a)] (3) as possible paratypes. It is clear from the text of Alleyne and Macleay (1877), however, that the description of *P. cavifrons* was based on only a single specimen. It appears therefore that the type of *P. cavifrons* is lost (a search of the MAMU collection, the only other likely repository, also proved abortive: ACG, pers. obs.). Nevertheless, Alleyne and Macleay (1877) provided a good illustration of the holotype, which is sufficient to place *P. cavifrons* in the synonymy of *L. calcarifer.* The holotype of *L. darwiniensis* (type locality Darwin) exists (AMS I.16319-001, 179 mm SL), and appears to be in all respects a specimen of *L. calcarifer*, although it is in very poor condition.

A final ‘name’ remains to be clarified, ‘Perca maxima’ attributed to Sonnerat, in Cuvier and Valenciennes 1828: 96, by Eschmeyer and Fricke (2011), who observed that the name was “associated with [a] specimen described by Cuvier under the name *Lates nobilis*. Not available, considered a name in synonymy”. Cuvier (1828) mentioned only that Sonnerat, the collector, had referred to the species as ‘perca maxima’ (presumably on the label accompanying the specimen), but that he would call it *Lates nobilis* (“Feu Sonnerat, qui nous en avons dû le premier individu, lavait désign par le nom de perca maxima que nous lui aurions conserv, si notre distribution méthodique nous l’avait permis”). Taken together with the fact that Cuvier did not mention ‘perca maxima’ in either the table of contents or the plate of *L. nobilis*, he clearly did not intend the name to be used.

Pseudolates. Alleyne and Macleay (1877) also established a new genus, *Pseudolates*, for which *P. cavifrons* is the type species by monotypy. They distinguished this from *Lates nobilis* only by its “rough tongue and large scales”. The synonymy of *P. cavifrons* with *L. calcarifer* in effect makes *Pseudolates* a synonym of *Lates* (Paxton *et al.* 1989).

Ptertopomus. Commenting on the genus-group name *Ptertopomus* Cuvier in Goldfuss, 1820 (p. 66), Eschmeyer and Fricke (2011) give *Holocentrus calcarifer* Bloch as the type by monotypy, noting “Name perhaps overlooked, not in current literature; apparently predates *Lates* Cuvier, in Cuvier and Valenciennes, 1828, which apparently it should replace unless the ICZN is asked to set aside *Ptertopomus*.” It is clear from a wider examination of Goldfuss (1820), however, that his *Ptertopomus* was in fact a lapsus for *Plectropomus* Oken, 1817. In the preface to his *Handbuch der Zoologie*, Goldfuss (1820) states that he followed the handbooks of Oken (1817) and Cuvier (1816) in assigning some of their genera to larger genera as “Abtheilungen”: he was therefore aware of those works (Oken 1817, is in fact a review of Cuvier 1816). In the conspectus of genera at the beginning of Part 2 of Golfuss (1820), the name is spelt *Plectopomus*, whereas on p. 66, the spelling is *Ptertopomus*, clearly a lapsus in view of the index, which refers to p. 66, giving the spelling as *Plectopomus*. There is also the attribution of the name *Ptertopomus* to Cuvier by Goldfuss (1820) himself: no such Cuvier name exists. The spellings *Plectopomus* Goldfuss, 1820 and *Ptertopomus* Goldfuss, 1820, are therefore incorrect subsequent spellings of *Plectropomus* Oken, 1817: these names do not threaten *Lates*. It is also worth mentioning that Oken (1817: 1782) included only a single species in his *Plectropomus*, namely *Bod. macul*. (*Bodianus maculatus* Bloch, 1790), which becomes the type by, monotypy, not by subsequent designation by Jordan, Tanaka and Snyder (1913), as stated in Eschmeyer and Fricke (2011). *Bod. macul*. is also easily identified as *Bodianus maculatus* because it was one of the available names included by Cuvier (1816) in his ‘plectropomes’.

Multivariate analysis. *Lates uwisara* and *L. lakdiva* separate distinctly from each other in morphological space (Fig. 7, based on the 26 specimens for which radiographs were available). The first component (PC1) was composed primarily of the length of dorsal spines III–V, the length of the anal-fin base and the length of the second dorsal-fin base; while head length, maxilla length, caudal-peduncle length, and distance from snout to preopercular margin were the greatest contributors to PC2; and body depth, caudal peduncle depth and pelvic-fin length contributed most to PC3 (see Table 2). Together the first three principal components explain 71.4% of the variance. *Lates uwisara* separates distinctly from the other three species on the PC1 axis (Fig. 7A, B), while *L. lakdiva* separates distinctly from *L. calcarifer* and *L. japonicus* on the PC3 axis. Principal components analysis was also used to test for separation between the populations of *L. calcarifer*, using both the dataset for nine specimens that included measurements from radiographs and those from all 27 specimens included in the study, but none was found.

TABLE 2. Component loadings for axes 1–3 of the principal component analysis, variance explained and percentage of total variance explained for *Lates calcarifer* (AMS IA 1542, AMS I.21818-007, Northern Territories, Australia, n=2; QMB I 7125-27, 3; QMB I.7302; QMB I.22881, AMS I.514, Queensland, Australia, n=6; NSMT-P 21757, 2, Thailand, n=2), *L. japonicus* (NSMT-P 2251, NSMT-P 2837, 2, NSMT-P SK2838, 2, NSMT-P 102126, NSMT-P SK2834, AMS I.25746-001, Japan, n=8), *L. lakdiva* (AMS I.37516-001, 3, Sri Lanka, n=3) and *L. uwisara* (ANFC H.6316-09-12, 4, Myanmar, n=4). Asterisks indicate measurements made from radiographs. The largest five loadings for each axis in boldface.

Measurement	Component loadings		
	1	2	3
Total length	0.112	-0.539	**0.547**
Snout to base of last dorsal-fin ray	0.192	-0.248	0.489
Snout to base of last anal-fin ray	-0.099	-0.290	0.251
Preanal distance	0.067	-0.824	-0.088
Prepelvic distance	0.081	-0.460	0.322
Prepectoral distance	0.089	-0.796	0.104
Predorsal distance	0.362	-0.651	0.431
Post-dorsal distance	-0.071	0.729	0.098
Body depth at first dorsal-fin origin	0.236	0.304	**0.864**
Body depth at second dorsal-fin origin	0.127	0.507	**0.771**
Caudal-peduncle depth	0.010	0.493	**0.752**
Caudal-peduncle length	-0.254	**0.736**	0.143
Pectoral-fin length	0.250	-0.502	0.449
Pelvic-fin length	-0.194	0.185	**0.676**
Head length	0.305	**-0.788**	0.262
Maxilla length	0.280	**-0.736**	0.412
Maxilla depth	0.286	-0.590	0.153
Internarial width	-0.288	-0.463	-0.193
Eye diameter	-0.122	-0.215	-0.009
Interorbital width	0.920	-0.087	-0.185
Snout to posterior preopercle margin	0.417	**-0.795**	0.253
Snout to tip of spine at preopercle angle	0.318	**-0.865**	0.163
Body width at dorsal-fin origin	0.305	0.202	0.510
Snout length	0.338	0.114	0.353
Length of dorsal-fin spine I*	0.876	0.114	0.093
Length of dorsal-fin spine II*	0.917	0.157	-0.070
Length of dorsal-fin spine III*	**0.940**	0.003	-0.273
Length of dorsal-fin spine IV*	**0.964**	0.084	-0.214
Length of dorsal-fin spine V*	**0.940**	0.258	-0.062
Length of dorsal-fin spine VI*	0.876	0.367	0.086
Length of dorsal-fin spine VII*	0.869	0.378	0.045
Length of dorsal-fin spine VIII*	**0.966**	-0.051	-0.179
Length of anal-fin spine I*	0.653	0.483	0.194
Length of anal-fin spine II*	0.703	0.558	0.151
Length of anal-fin spine III*	0.911	0.091	-0.272
Distance between dorsal-fin spines VII and VIII*	0.927	-0.138	-0.248
Length of base of first dorsal fin*	0.922	-0.111	-0.224
Length of base of second dorsal fin*	**0.942**	0.016	-0.117
Length of base of anal fin*	**0.973**	0.037	-0.019
Variance explained by components	15.17	8.636	5.512
Percent of total variance explained	37.0	21.0	13.4

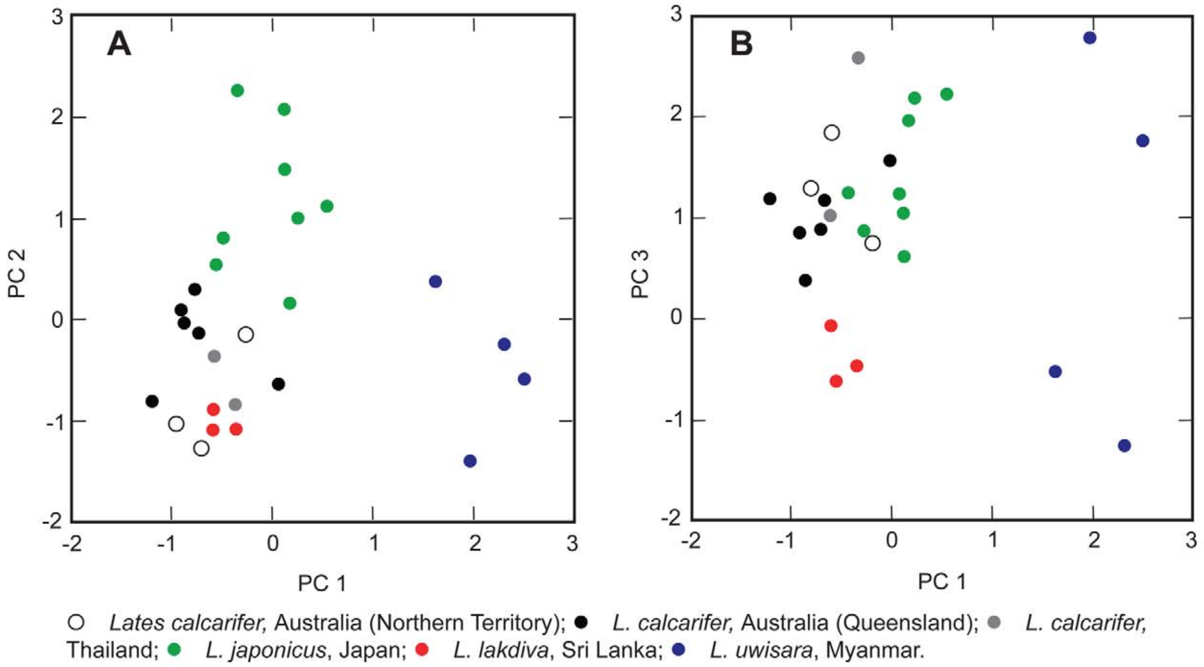

FIGURE 7. Factor scores of (A) PC1 vs PC2 and (B) PC1 vs PC3 of the principal components analysis of measurements (see Table 2) of *Lates calcarifer* (AMS IA 1542, AMS I.21818-007, AMS I.24691, Northern Territories, Australia, n=3; QMB I 7125-27, 3; QMB I.7302; QMB I.22881, AMS I.514, Queensland, Australia, n=6; NSMT-P 21757, 2, Thailand, n=2), *L. japonicus* (NSMT-P 2251, NSMT-P 2837, 2, NSMT-P SK2838, 2, NSMT-P 102126, NSMT-P SK2834, AMS I.25746-001, Japan, n=8), *L. lakdiva* (AMS I.37516-001, 3, Sri Lanka, n=3) and *L. uwisara* (ANFC H.6316-09-12, 4, Myanmar, n=4) based on 24 external and 15 osteological measurements.

Conservation and genetics. Since artificial spawning in *L. calcarifer* was first achieved in 1973 (Barnabe 1995) *Lates* have been increasingly translocated, cultivated and stocked in (or escape into) natural habitats throughout tropical Asia and Australasia, potentially endangering the integrity of indigenous geographically distinct populations and increasing the risk of hybridization (see Lintermans 2004, and references therein). This risk is perhaps highest in countries such as Malaysia, Thailand, India and Sri Lanka, in which extensive cross-country translocations and releases have occurred with scant or no records of brood-stock provenance being maintained (RP, pers. obs.). Indeed, several studies suggest that the genetic integrity of wild populations of *L. calcarifer* is maintained even at the level of individual rivers, making introductions, whether intended or accidental, potentially a threat (Shaklee & Salini 1985; Salini & Shaklee 1988; Keenan & Salini 1990; Shaklee & Phelps 1991; Shaklee *et al.* 1993; Keenan 1994; Marshall 2005). These reports add weight to the conclusion of Marshall (2005) that “Despite the barramundi’s catadromous life history, and ability to disperse through marine waters, the present genetic structure indicates a division principally among river drainages. From a population [genetics] viewpoint the species can be regarded as freshwater, rather than marine.”

The identification of two new species of sea bass—*L. lakdiva* and *L. uwisara*—in countries bordering the Bay of Bengal suggests that others await discovery in, e.g., countries bordering the Persian Gulf, Arabian Sea and South China Sea, from which *Lates calcarifer* is reported. In some of these countries it may already be too late, native stocks having become contaminated by introductions. This makes imperative not only the regulation of translocated *Lates*, but also the taxonomic evaluation of museum specimens that predate the era of introductions. The present data show that the external morphology of *L. calcarifer* is remarkably conserved despite substantial genetic variation (Salini and Shaklee 1988; Keenan and Salini 1990; Chenoweth *et al.* 1998; Ward *et al.* 2008; Yue *et al.* 2009), an example of morphologically static cladogenesis (Bickford *et al*. 2006). They also suggest that *L. calcarifer* is a widely distributed species within whose range pockets of distinct species of *Lates* occur. It is likely, therefore, that further species exist within the range of *L. calcarifer* as here understood, to be uncovered by future work.

Constraints. Material examined in this study was subject to two constraints. First, because of the increasing pace of translocations of *Lates* in recent years, we excluded specimens (except for the type series of *L. uwisara*) collected after 1995. Second, *L. calcarifer* become sexually mature only at about 50 cm SL (Dunstan 1958, 1962), a size above which they are seldom preserved in museum collections. As a result, the specimens examined in this study (range 97.6–363 mm SL, mean SL 203 mm, standard deviation 64.0 mm) are likely all juveniles. The morphology of adults, may be significantly different, especially given that *Lates* are protandrous hermophrodites, gender inversion occurring only at about 65 cm SL (Pusey *et al.* 2004). Specimens above this size may differ substantially from juveniles and also exhibit sexual dimorphism. Such specimens, however, are almost impossible to find in museums. A fuller understanding of the evolutionary relationships and taxonomy of Indo-Pacific *Lates* must, therefore, await a wide-ranging molecular study that samples *Lates* throughout its extensive range in this region.

Comparative material

Lates calcarifer. ZMB 13652, ('lectotype', probably the holotype), 273 mm SL, India, Tamil Nadu, Atukottalei [Pattukottai?]; ZMB 8735 (paralectotype), 170 mm SL, locality unknown; MNHN: A-5739 (paralectotype of *L. heptadactylus* and *L. nobilis*), 183 mm TL, locality unknown; MNHN A-7330 (lectotype of *L. heptadactylus* and *L. nobilis*), 402 mm TL, locality unknown; CAS SU 35744, 184.5 mm SL, India, West Bengal; AMS IA.1542, 190.7 mm SL, Australia, Northern Territory, Indian Island; AMS I.21818-007, 2 ex., 150.5, 175.3 mm SL, Australia, Northern Territory, East Alligator River, Cahill's Crossing, 65 km from coast; AMS I.24689-006, 213 mm SL, Australia, Northern Territory, Darwin, Buffalo Creek; AMS I.22044-004, 217 mm SL, Australia, Queensland, Daintree River, 8 miles from river mouth; AMS I.514, 201 mm SL, Australia, Queensland, Torres Strait; AMS I.22771-011, 144.6 mm SL, Australia, Queensland, 30 km from Proserpine, Conway Beach; QMB 12105, 150.1 mm SL, Australia, Queensland, Townsville; QMB 10377, 182.2 mm SL, Australia, Queensland, Port Stewart; QMB 7125-27, 2 ex., 170.3, 177.2 mm SL, Australia, Queensland, Townsville beach; QMB I.22881, 4 ex., 97.6–161.3 mm SL, Australia, Queensland, Murray River Swamps, near Cardwell, QMB I.7302, 171.1 mm SL, Australia, Queensland, Townsville, Deep Creek; NSMT-P 21756, 201.7 mm SL, NSMT-P 21757, 2 ex., 156.8, 189.6 mm SL, Thailand, Phuket, Andaman Sea, southern Thailand; NSMT-P 21758, 315 mm SL, NSMT-P 21759, 226 mm SL, Thailand, Songkhla Lake, Gulf of Thailand; ZRC 46467, 152 mm SL, Singapore, Palau Ubin; ZRC [uncat.], 181 mm SL, Singapore; ZRC NMS3339, 106 mm SL, Malaysia, Port Dickson.

Lates japonicus. NSMT-P 102126, 205.1 mm SL; NSMT-P 2251, 263 mm SL; NSMT-P 2837, 3 ex., 154.2-197.2 mm SL; NSMT-P SK2265, 246 mm SL; NSMT-P SK2838, 210 mm SL; NSMT-P SK2834, 253 mm SL: Japan, Ooyodo-gawa River: Miyazaki Pref., Miyazaki City; AMS I.25746-001, 204.4 mm SL, Japan, E. coast of Kyushu, Miyazaki Prefecture, mouth of Oyodo-Gawa River; AMS I.25742-001, 134.1 mm SL, Japan, Eastern Kyushu, Miyazaki Prefecture, mouth of Oyodo-Gawa River.

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