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A CONTRIBUTION TO THE TAXONOMY OF THE MARINE FISH GENUS ARGYROSOMUS (PERCIFORMES: SCIAENIDAE), WITH DESCRIPTIONS OF TWO NEW SPECIES FROM SOUTHERN AFRICA

by

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ABSTRACT

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Study of the biology, anatomy and taxonomy of the sciaenid fishes of the genus *Argyrosomus* from South Africa and Namibia revealed that three species were confused under the name "*Argyrosomus hololepidotus* (Lacepède, 1801)". Comparison of morphometric and meristic data, otoliths, swim-bladders, drumming muscles, and other morphological features, of specimens from southern Africa, Madagascar, the Mediterranean Sea, the eastern Atlantic Ocean, Japan and Australia, established that the "*A. hololepidotus*" of recent authors is a complex of four species: *A. japonicus* (Temminck & Schlegel, 1843), which occurs off southern Africa, Japan and Australia; *A. inodorus* sp. nov., which is known from Namibia to the Kei River (32°40'S) on the east coast of South Africa; *A. coronus* sp. nov., which is known from central and northern Namibia and Angola, and *A. hololepidotus*, which appears to be endemic to Madagascar. These four species are compared with *A. regius* (Asso, 1801) of the Mediterranean and eastern Atlantic, *A. thorpei* Smith, 1977 from South Africa, Mozambique and the west coast of Madagascar, and *A. beccus* Sasaki, 1994 known only from Durban harbour. To promote stability in the nomenclature and to resolve the confusion in the taxonomy of *Argyrosomus* species, neotypes are selected for *A. hololepidotus* and *A. japonicus*. The biology, distributions and fisheries of six species are reviewed. Distribution patterns for the southern Africa and Madagascar (*A. regius, A. japonicus, A. inodorus, A. coronus, A. thorpei, A. beccus*, and *A. hololepidotus*) are provided. The composition and distinction of the genus *Argyrosomus* are briefly discussed.

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Marc H. Griffiths¹ and Phillip C. Heemstra²

INTRODUCTION

Sciaenid fishes of the genus *Argyrosomus* occur in the eastern Atlantic and Indo-West Pacific regions, and are important food species wherever they are found. Close similarity in the external appearance of these species has resulted in a difficult and sometimes confused taxonomy. Correct identification of *Argyrosomus* species is essential from a management perspective, as different species often exhibit different life history traits, and therefore require separate conservation strategies.

Since 1977 two species of Argyrosomus, "A. hololepidotus" and A. thorpei, were recognised as important recreational and commercial fishes off South Africa. In 1990, a project initiated by the first author (MHG) to study the biology of "Argyrosomus hololepidotus", revealed that two species were confused under this name. In order to establish their identity, these two species were compared with other species of Argyrosomus. The results are presented in this paper, together with descriptions of A. hololepidotus, A. regius, A. japonicus and A. thorpei. Neotypes are designated for A. hololepidotus and A. japonicus. Two new species, A. inodorus and A. coronus are also described from southern Africa, bringing the total number of Argyrosomus species to ten.

Taxonomic differences between A. *inodorus* and A. *japonicus* were studied in detail, as both species are important in recreational and commercial fisheries in South Africa. The habitats and distributions of the Southern African Argyrosomus species are discussed, and the biology and fisheries of the six African species are reviewed.

MATERIALS AND METHODS

The specimens examined are listed after each description. Institutional abbreviations follow Leviton et al. (1985). Sex is indicated by the letters M (male) and F (female); juveniles, too small to be sexed, are indicated by "J". In cases where additional fresh specimens were examined but not preserved, the total sample number (n) includes these fresh specimens. Except as indicated below, measurements and counts used in this study were based on the methods of Hubbs and Lagler (1964). Counts of gill-rakers and swimbladder appendages exclude rudiments (structures wider than long). Swim-bladder appendages were counted on the left side of the swim-bladder. Orientation of swim-bladder appendages may vary depending on the amount of fat in

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² J.L.B. Smith Institute of Ichthyology, Private Bag 1015, Grahamstown, 6140. which they are embedded. Our descriptions of appendage orientation for the species treated here are based (when possible) on specimens with little or no fat.

Vertebral counts were made on skeletons (see below) or on radiographs. Caudal vertebrae were taken as those with fused transverse processes or distinct haemal spines. Body depth was measured between the origins of the first dorsal and the pelvic fins. Caudal peduncle length was measured obliquely from the end of the second dorsal fin base to the lateral line at the base of the caudal fin. Pre-pelvic length was taken from the tip of the lower jaw to the origin of the pelvic fin. The least fleshy interorbital width was measured. As specimen treatment causing shrinkage of the eve (e.g. storage in alcohol or freezing), generally also caused shrinkage in this measurement, data for fresh specimens is provided in the key where relevant. Pectoral fin length was measured from the origin of the most dorsal ray to the tip of the longest ray. Anal and pelvic fin lengths were taken from the fin origin to the distal tip of the fin. The first lower-limb gill-raker (next to the raker at the angle), and the longest gill filament of the first gill arch were measured. The heights and lengths of scales on the body at the tip of the adpressed left pectoral fin were measured. The length of the longest urinary bladder (left or right, Fig. 1) of



Figure 1. Ovaries (O) and urinary bladders (UB) of South African: A) Argyrosomus inodorus, 825 mm TL; B) Argyrosomus japonicus, 860 mm TL, illustrating differences in size of bladders and the bladder length measurement (UBL).

A. japonicus and A. inodorus was measured to the nearest millimetre. The size of the bladder was influenced by the degree of fullness at the time of death. In order to compensate for bladder fullness, measurements were taken from fresh material after the bladders were emptied and straightened. The shape of the caudal fin varies with species, specimen size and expansion. To compensate for variable expansion, the fin was fully splayed (while still wet) on a smooth surface, and then allowed to contract to the "natural" position. Variation in caudal fin shapes and terminology are illustrated in Figure 2. Notes on life colour were taken from fresh specimens. The examination of more than five hundred live A. inodorus and A. japonicus suggest that both species darken after death.

Sonific (drumming) muscles run in a narrow longitudinal band (one on each side) along the inside of the ventrolateral wall of the posterior part of the body cavity. The muscle fibres run transversely to the long axis of the muscle and are attached to the medial surface of the peritoneum. They are not connected to the swimbladder.

Morphometric ratios are expressed as percentages of head length (HL) (measurements on head only) and standard length (SL). Unless indicated as "TL", all fish lengths are of SL. For statistical analyses, measurements were expressed as fractions of SL and then arcsine-transformed. Meristic data and morphometric ratios (except *A. hololepidotus* with n = 2 or 3) were compared using ANOVAs and Tukey studentized range tests. Morphometric ratios for *A. inodorus* and *A. japonicus* were also analyzed according to 100 mm SL size classes to compare characters that show allometric growth (e.g. eye diameter) or those which grow at different rates in the two species (e.g. pectoral fin length).



Figure 2. Argyrosomus caudal fin shapes and terminology. A) elongate pointed; B) elongate S-shaped; C) Sshaped; D) bi-concave; E) wedge-shaped; F) rounded; G) truncate.



Figure 3. Otolith terminology and measurements: DM = Dorsal Margin, OL = Otolith Length, OH = OtolithHeight, OCD = Ostium to Cauda Distance, PM = PosteriorMargin, VM = Ventral Margin.

In addition to comparing the general morphology of the sagittae of five Argyrosomus species, the relationships between sagittal measurements (and weight) and TL for A. inodorus and A. japonicus were compared using regression analysis. Total length (TL) was used instead of SL, because it could be measured more rapidly when recording data from commercial catches. Otoliths were taken from all sizes (A. inodorus, 60 - 1378 mm TL; A. japonicus, 36 - 1750 mm TL) represented in the catch. Otolith weight (to the nearest milligramme) and measurements (to the nearest 0.01 mm, see Fig. 3) were taken from the left sagitta. Fish lengths and otolith measurements (including weight) were log-transformed and straight line regressions were calculated. The corresponding regression lines for A. inodorus and A. japonicus were tested for differences in slope and intercept (Myers, 1990).

Twelve skeletons of A. inodorus, 7 of A. japonicus, 2 of A. thorpei and 1 of A. coronus were compared. Measurements of cranial features (Figs 4 & 5) were taken as follows: pre-supraoccipital crest length (PSOCCRL) was measured point-to-point along the median axis from dorsoanterior tip of mesethmoid to dorsal end of frontal/supraoccipital suture; supraoccipital crest length (SOCCRL) was measured similarly to PSOCCRL from frontal/supraoccipital suture to the posterior edge of supraoccipital crest, immediately below the dorso-posterior angle; neurocranial length (NCL) was taken from the anterior tip of the vomer to the posterior tip of the basioccipital; neurocranial width (NCW) is the distance between the anterior ends of the sphenotic bones. The left dentary was measured from the anterior tip to the posterior tip of the ventral processes (Fig. 6). The length of the left premaxilla was measured as the maximum straight line distance between anterior and posterior tips.









Figure 4. Neurocrania (lateral view): A) Argyrosomus inodorus, 365 mm SL; B) A. japonicus, 365 mm SL; C) A. coronus, 495 mm SL; D) A. thorpei, 452 mm SL. IOW = Interorbital Window; LLC = Lateral Line Canal; NCL = Neurocranial Length; PSOCCRL = Pre-Supraoccipital Crest Length; SOCCRL = Supraoccipital Crest Length. Scale bar = 10 mm.



Figure 5. Dorsal view of neurocrania: A) Argyrosomus inodorus, 365 mm; B) A. japonicus, 365 mm; C) A. coronus, 495 mm; D) A. thorpei, 461 mm. Neurocranial width is the distance between the anterior ends of the sphenotic bones (arrows); LLC = Lateral Line Canal. Scale bar = 10 mm.



Figure 6. Left dentaries (lateral view): A) Argyrosomus japonicus, 525 mm; B) A. thorpei, 461 mm; C) A. inodorus, 433 mm; D) A. coronus, 495 mm. DL = Dentary Length

In order to establish the habitat and distribution patterns of A. inodorus, A. japonicus and A. thorpei, the southern African coastline was divided into ten regions (Fig. 7). Regional boundaries within each country do not necessarily coincide with political boundaries. Whole specimens (or otoliths of specimens) from four habitats (estuary, surf zone, nearshore hard bottom and nearshore soft bottom) within each region were examined. The "nearshore habitat" is defined as the marine coastal waters between depths of 10 and 100 m. Argyrosomus species are infrequently caught deeper than 100 m in South African waters. Catch methods included gill netting (estuaries), seine netting (estuary and surf zone), line fishing (estuary, surf zone and nearshore hard bottom) and trawling (nearshore soft bottom). The percentage contributions (by number) of each species to the total Argyrosomus catch in each regional habitat were calculated. For Natal nearshore hard bottom (reef) catches, numerical contributions were calculated by dividing the total catch of each relevant species (over the period 19881992) by the average individual weight of the respective species in the catch. This was possible as the commercial fishermen who provided the catch data differentiate between *A. thorpei* and *A. japonicus*, and examination of 3852 specimens of *Argyrosomus* from Natal revealed that *A. inodorus* does not occur there.

Biological and fishery notes are based on a three year (1990-92) sampling programme during which over 10 000 fish were examined from localities along the entire South African seaboard. Catch statistics (where not referenced) are from the databases of the Sea Fisheries Research Institute in Cape Town.

Argyrosomus Pylaie, 1835

Argyrosomus Pylaie, 1835: 532. Type species Argyrosomus procerus Pylaie, 1835 (substitute name for "Sciaena aquila Cuvier" = Cheilodipterus aquila Lacepède, 1803, = Perca regia Asso, 1801 = Argyrosomus regius) by monotypy. See Trewavas (1977) for details of synonymy.

DESCRIPTION: Body fairly elongate and moderately compressed; dorsal profile more convex than ventral profile. Mouth terminal, slightly oblique; jaws equal anteriorly, or lower jaw protrudes slightly. Chin without barbel but with three pairs of mental pores: the median pair rounded, the second oval or elongate, and third pair narrow slits, each pair progressively further apart. No large canines; teeth differentiated in size; upper jaw with outer row of enlarged teeth and narrow inner band of smaller teeth; lower jaw with single inner row of enlarged teeth and outer row of smaller teeth; smaller teeth in both jaws less visible in larger specimens. Anterior nostril round to oval, the posterior one slightly larger and oval to slit-like. Preopercle serrated; operculum ending in two weak, flattened spines (often hidden by skin).

Pectoral fins relatively short (15-23% SL), with a dark fleshy axillary fold at upper end of fin base. Caudal fin pointed (in small juveniles) to S-shaped, rhomboid, rounded or even truncate (in young and adults). Lateral-line scales 47-53 (usually 51) to base of caudal fin; lateral-line tubules arborescent; lateral-line scales extend to end of caudal fin.

Sagitta moderately elongate, with prominent postcentral umbo on outer surface; inner (medial) surface convex, with enlarged, spoon-shaped ostium and strongly curved, J-shaped cauda with bluntly rounded tip; otoliths of adults generally deepest within posterior third, close to tip of cauda. The sagitta of the type species (*A. regius*) is indistinguishable from that of *A. hololepidotus* or *A. japonicus* (Figs 11, 14 & 15). Since *A. regius* is the type-species of the genus, this general otolith morphology is referred to as the *Argyrosomus* form.

Swim-bladder typically carrot-shaped (tapering posteriorly) with 21-45 short appendages that may or may not (individual variation) be embedded in a wedge of fatty tissue; no appendages enter the head (i.e. pierce the transverse septum); most appendages arborescent, divided initially into two distinct limbs which are often orientated dorso-posteriorly and ventro-anteriorly, respectively; last 2-6 appendages reduced in size and bud-like or weakly



Figure 7. Map illustrating localities and the 10 southern African regions used in the distribution analysis of Argyrosomus species.

branched (last appendage not tubular). Drumming muscles of *Argyrosomus* species may be present in both sexes or in males only. Generally 11 abdominal and 14 caudal vertebrae.

REMARKS: In her excellent revision of the Indo-West Pacific sciaenids, Trewavas (1977) recognized five species of Argyrosomus: A. regius, hololepidotus, japonicus, miiuy and amoyensis. Mohan (1984) added Sciaena heinii Steinachner, 1902 to the genus (Trewavas [1977: 451] treated S. heinii as a "doubtful species", because she had not examined any specimens and was unsure of its generic assignment). Mohan's (1984) description of the swim-bladder, otolith, dentition and external morphology of this species agrees with those of Argyrosomus (as described above).

A comprehensive revision of the genus *Argyrosomus* was beyond the scope of our present work, but some comments (we hope constructive) on the currently accepted limits and definition of this genus are in order. Sasaki

(1989) recognized the genus Miichthys Lin, 1983 for Sciaena miluy Basilewsky, 1855 and put this species in a new monotypic tribe, Miichthyini, "distinguished by the combination of well curved sulcus tail [cauda of the sagitta], absence of enlarged swim-bladder appendages, absence of cephalic swim-bladder appendages, scaly dorsal fin.". As discussed by Sasaki (1989: 81, 90-92), the otolith and swimbladder features that distinguish Sciaena miluy from A. japonicus and other members of his tribe Argyrosomini are relatively primitive (plesiomorphic) character states. The presence of enlarged anterior swim-bladder appendages is a dubious synapomorphy for the tribe Argyrosomini, because it appears only in larger specimens. Enlarged appendages are known in A. regius, A. japonicus, and A. inodorus, but they were not present in 46 cm SL specimens of A. thorpei. They are not known for A. hololepidotus, A. coronus or A. amoyensis, but this may be because the swim-bladders of larger individuals of these three species have not been examined.



Figure 8. Argyrosomus beccus Sasaki, holotype, 175 mm SL, USNM 325504, Durban; after Sasaki, 1994.

The two autapomorphies: ("frontal projecting downward" and "caudal fin being truncate to lunate in adults") cited by Sasaki (1989: 118) for A. japonicus are also dubious as defining character states for the genus Argyrosomus. The "frontal projecting downward" refers to the increased ossification of the interorbital septum in A. japonicus (Fig. 4B), in which the frontals are fused ventrally into a median lamina that extends ventrally and fuses with similar lamina arising from the median ethmoid and parasphenoid bones. In A. coronus (Fig. 4C) the frontal and parasphenoid bones are also fused, but in A. inodorus (Fig. 4A) and A. thorpei (Fig. 4D), the interorbital septum is not so well ossified, and the median frontal lamina does not contact the parasphenoid bone. The state of the interorbital septum in A. hololepidotus, A. amoyensis, and the type-species (A. regius) are unknown. The value of this character state (increased ossification of interorbital septum) as an indication of a monophyletic genus is further diminished by its homoplastic development in more distantly related genera (e.g., Johnius and Kathala, Sasaki, 1989).

Judging from several thousand South African specimens and eight specimens from Japan (including the photograph of Masuda et al., 1988: Pl. 147, Fig. E), it is not quite accurate to describe the caudal fin of *A. japonicus* as "truncate to lunate in adults". The caudal fin of adults is most commonly S-shaped (Fig. 2C, with the rear margin of the upper half of the fin concave and the lower half convex), less frequently bi-concave (Fig. 2D) and seldom wedge shaped (Fig. 2E) or truncate (Fig. 2G). In view of the ontogenetic variation in caudal fin shape, and the fact that other (distantly related) sciaenids also have s-shaped or truncate caudal fins, the value of the caudal fin shape as a defining character state for the genus *Argyrosomus* is also questionable.

Although Sasaki's (1989) evidence for recognition of *Miichthys* and the tribes Miichthyini and Argyrosomini is not convincing, we do not have sufficient information to contest or support these taxa.

Sasaki (1994) described Argyrosomus beccus as a new species from South Africa based on three specimens (175, 191 & 230 mm SL) collected from Durban Harbour in 1969.

No further specimens of this anomalous species have been collected in South African waters. Anatomically, it differs strikingly from other species of *Argyrosomus* in having an unusually short beak-like snout, with a slight concavity in the dorsal head profile just before the eye (Fig. 8). The snout length (6.1-6.3% SL, 20-21% HL) is shorter than the eye diameter (7.3-8.3% SL, 24-27% HL); whereas, in the six species that we measured, the snout lengths (7.4-9.6% SL, 24-31% HL) are always longer than the eye diameters (4.7-7.9% SL, 14-24% HL). The interorbital width of *A. beccus* is also much narrower (4.7% SL, 15.2-15.6% HL) than in the other five species (6.0-8.5% SL, 19-29% HL).

KEY TO SPECIES OF ARGYROSOMUS FROM AFRICA AND MADAGASCAR

- 2a. Axillary skin fold above pectoral fin base scaly; anterior part of lateral line strongly curved; peritoneum pigmented with fine black dots; fins orange brown or dusky yellow in life; otolith (sagitta) with tip of cauda expanded and truncate A. thorpei

(Algoa Bay to southern Mozambique)

3

- 2b. Axillary skin fold of pectoral fin without scales; anterior part of lateral line slightly curved; peritoneum unpigmented; otolith cauda J-shaped, the tip rounded and not expanded . . .
- 3a. Caudal peduncle depth 58-74% peduncle length; ostium to cauda distance 37-63% otolith height; drumming muscles absent in females; length of body scales at tip of pectoral fin 1.8-2.5% SL; interorbital width 20-25% HL (23-26% in fresh specimens); swim-bladder appendages 31-42

. A. inodorus sp. nov. (Namibia to Kei River)

3b.	Caudal peduncle depth 68-94% peduncle
	length; ostium to cauda distance 23-34%
	otolith height; drumming muscles present
	in both sexes of adults (> 27 cm SL) 4
4a.	Interorbital width 24-29% HL (27-30% in
	fresh specimens)
4b.	Interorbital width 20-24% HL (22-25% in
	fresh specimens) 6
5a.	Swim-bladder appendages 36-45; caudal
	peduncle depth 68-82% peduncle length;
	length of midlateral body scales
	1.8-2.3% SL, lower jaw 44-48% HL A. regius
	(Mediterranean, eastern Atlantic, and Red Sea)
5b.	Swim-bladder appendages 28-38; caudal
	peduncle depth 76-94% peduncle length;
	length of midlateral body scales 2.2-2.7% SL,
	lower jaw 46-50% HL A. coronus sp. nov.
	H (Namibia and Angola)
6a.	Suborbital width 10.5-12% &L swim-bladder
	appendages 34-36 A. hololepidotus
	u (Madagascar)
6b.	Suborbital width 8.4-10.5% &L swim-bladder
	appendages 21-31 A. japonicus
	(Indo-West Pacific to False Bay, South Africa)

Argyrosomus regius (Asso, 1801) (Fig. 9)

Sciaena umbra var. Brünnich, 1786: 99.

Perca regia Asso, 1801: 42 (coasts of Spain).

Cheilodipterus aquila Lacepède, 1803: 685, Pl. 21, Fig. 3 (French Atlantic).

Sciaena umbra (non Linnaeus): Cuvier, 1814: 13, Pl.

Sciaena aquila: Cuvier, 1816: 298; Risso, 1826: 411 (Mediterranean); Cuvier, in Cuvier & Valenciennes, 1830: 28, Pl. 139; Day, 1880-1884: 150, Pl. L (Great Britain); Smitt, 1892: 50, Fig. 13. Pseudosciaena aquila: Bleeker, 1863: 142; Bleeker, 1876: • 329.

- Perca vanloo Risso, 1810: 298, Pl. 9, Fig. 30 (Western Meditteranean).
- Argyrosomus procerus Pylaie, 1835: 532 (substitute name for Sciaena aquila Cuvier).
- Johnius hololepidotus (non Lacepède): Fowler, 1936: 884 (described from Mediterranean specimens).
- Argyrosomus regius: Trewavas, 1966: 4; 1973: 397; 1977: 324, Fig. 8; Seret, 1981: 266.
- For additional references see Trewavas, 1973.
- Neotype: MNHN 7511, La Rochelle, French Atlantic; designated by Trewavas (1966) quoting a description by P.J.P. Whitehead (MS).

DIAGNOSIS: A species of *Argyrosomus* with the following combination of characters: dorsal fin rays 26-30; gillrakers 3-5 + 8-10; swim-bladder carrot shaped, with 36-45 arborescent appendages; caudal peduncle length 11-13% SL; peduncle depth 68-82% peduncle length; interorbital width 7.3-8.5% SL (24-29% HL); suborbital width 8.4-11% HL; lower jaw length 45-48% HL; midlateral body scale length 1.8-2.3% SL; drumming muscles present in both sexes; urinary bladders large; sagitta typically *Argyrosomus* (Fig. 10), OCD 26-32% OH; pectoral fins 18-21% SL, not reaching past vertical at tip of pelvic fins; pectoral fin axillary fold scaleless; peritoneum unpigmented; anterior part of lateral line slightly curved.

DESCRIPTION: Based on 19 whole specimens (173-433 mm) plus otoliths, swim-bladders, interorbital widths, head lengths and SL of 7 others collected for us by Bernard Séret. Due to the poor condition of five specimens (MNHN 7511, MNHN 7533, MNHN 7945, MNHN 1524, and the neo-type), only the interorbital width and SL measurements of these fish were included in the following description. Trewavas' (1977) data (10 specimens 135-965 mm SL) are given in parentheses.



Figure 9. Argyrosomus regius, North Sea (after Smitt, 1892)



Figure 10. Medial (above) and lateral (below) views of sagittae of Argyrosomus regius (top and third rows) and A. coronus (second and bottom rows). The largest specimen for A. regius, was redrawn from Chaine (1938). Scale bar = 10 mm.

Dorsal fin X+I,26-30 (IX-X+I,26-29); anal fin II,7; pectoral-fin rays 16-18; lateral-line scales 49-53(47-51); gill-rakers 3-5 + 8-10 (2-5 + 9); swim-bladder appendages 36-45 (40-42); vertebrae 11 + 14.

Proportions as %SL: head length 28-34 (27-35); predorsal length 33-37; pre-pelvic length 29-39, usually 30-34; body depth 24-34 (25-36); caudal peduncle length 11-13; peduncle depth 7.9-10.8; snout 8.1-9.6; eye diameter 5.5-6.5 at 173-222 mm, 4.1-5.1 at 261-339 mm and 4.3 at 433 mm SL; interorbital width 7.3-8.5; suborbital width 2.7-3.5; upper jaw 12-14; lower jaw 14-16; pectoral fin 18-21 (18-23); pelvic fin 19-21 at 173-198 mm, 17-19 at 261-342 mm and 17 at SL 433; anal fin 14-18; third dorsal spine 11-16; second anal spine 7.0-8.9 (6-9); gill-raker 1.6-2.4; gill-filament 2.8-3.3.

Proportions as % HL: snout 26-29 (26-31); eye diameter 17-19 at 173-222 mm, 12-16 at SL 261-342 mm and 14 at 433 mm SL (15-19 at SL 193-494 mm and 10-11 at SL 950-965 mm); interorbital width 24-29 (21-26); suborbital width 8.5-11; upper jaw 38-42 (39-44); lower jaw 45-48 (42-49); gill-raker 5.0-7.2; gill-filament 9.1-11.

Proportions as % eye diameter: gill-raker 32-45; gill-filament 49-56 at 173-198 mm, 63-69 at 261-342 mm and 76 at 433 mm SL.

Scales cycloid on snout and below eye, otherwise finely ctenoid. Lateral line evenly curved. Caudal fin elongate pointed in small specimens, S-shaped in those of medium size, and according to Trewavas (1977), bi-concave ("symmetrically concave") in very large individuals. Drumming muscles well developed in both sexes. Urinary bladders large, as in A. japonicus.

Swim-bladder appendages proximally divided into two limbs (Fig. 11) that are orientated dorsoposteriorly and ventroanteriorly along entire length of bladder. Branches arising from both limbs project posteriorly and lie against the bladder (throughout length); but in specimens where large quantities of fat are present the branches project laterally (Fig. 11). Disproportionate appendage enlargement was not observed in any *A. regius* (173-480 mm) examined by us, but it was illustrated by Cuvier (1814).

Otoliths (Fig. 10): Description as for A. japonicus; OCD 24-34% OH.

COMPARISONS: Specific differences between A. regius and the congeners described in this paper are dealt with



Figure 11. Swim-bladder appendages (anterior view) from mid-way along left side of swim-bladder: A) Argyrosomus hololepidotus, 465 mm SL, neotype; B) A. regius, 430 mm SL; C) A. coronus, 471 mm SL. Scale bar = 10 mm.

under the "comparisons" sections of the respective species (below) and in Tables 2-6.

DISTRIBUTION: A. regius occurs throughout the Mediterranean and Black Sea, northwards along the Atlantic coasts of Europe to the British Isles, southern Norway and Sweden; it has been recorded along the west coast of Africa to the Gulf of Guinea (Trewavas, 1977; Chao & Trewavas, 1981; Séret, 1981; Chao, 1986). A. regius has entered the Red Sea through the Suez canal (Steinitz, 1967; Mohan, 1984). The species occurs in inshore and shelf waters, close to the bottom or near the surface (depth range 15-200 m); it also enters estuaries and coastal lagoons (Chao, 1986).

FISHERIES: A. regius is an important food fish in the Bay of Biscay (French Atlantic) and along the coasts of Senegal and Mauritania (Moal, 1957; Balguerias, 1985; Quéro & Vayne, 1987). It is caught with hook and line, trawl nets, gillnets, circular nets and seines. The flesh is sold fresh, salted or dried.

BIOLOGY: Although sexual maturity is attained by some individuals at 80 cm TL, most adults off the west coast of Africa are larger than 110 cm TL (Moal, 1957). Spawning occurs during May to July in the Bay of Biscay, from April to July in the southern Mediterranean (Chao, 1986) and from January to May off west Africa (Mauritania, Moal, 1957; Tixerant, 1974 in Champagnat & Domain, 1978). Both adults and juveniles are migratory, moving longshore or offshore/onshore in response to change in water temperature (Moal 1957; Champagnat & Domain, 1978; Oliver & Lafon, 1981; Quéro & Vayne, 1987; Quéro, 1989). The largest size recorded is 182 cm TL and 103 kg (Quéro & Vayne, 1987).

MATERIAL EXAMINED:

MEDITERRANEAN SEA: Israel: HUJ 6906 (F 325 mm); HUJ 14451 (J 173 mm); HUJ 16342 (F 198 mm); RUSI 30254 (M 261 mm); RUSI 30255

(M 269 mm); RUSI 30256 (F 227 mm). Egypt: HUJ 5182 (M 255mm & 300 mm); MNHN 4978 (F 222 mm); MNHN 7495 (J 189 mm); MNHN 7533 (M 264mm, 286 mm [gonads missing]); MNHN 1524 (286 mm [gonads missing]). ATLANTIC OCEAN: France: MNHN 7511 (Neotype, no gonads, 425 mm, La Rochelle); RUSI 40772 (M 433 mm); RUSI 40776 (M 430 mm); RUSI 40777 (F 325 mm including otoliths); RUSI 40972 (355 mm, otoliths & swim-bladder only); RUSI 40973 (455 mm, otoliths & swim-bladder only); RUSI 40973 (455 mm, otoliths & swim-bladder only); RUSI 40977 (460 mm, otoliths & swim-bladder only); RUSI 40977 (480 mm, otoliths & swim-bladder only); RUSI 40977 (480 mm, otoliths & swim-bladder only); RUSI 40977 (M 322 mm); RUSI 40971 (M 342 mm, F 319 mm, including otoliths).

Aryrosomus japonicus (Temminck & Schlegel, 1843) (Fig. 12)

- Sciaena japonica Temminck & Schlegel, 1843: 58, Pl. 24, Fig. 1 (vicinity of Nagasaki, Japan; based on description and plate in unpublished manuscript of D.W. Burger; specimen not preserved).
- Sciaena antarctica Castelnau, 1872: 100, Pl. 1 (Melbourne market); Macleay, 1881: 520; Tenison-Woods, 1883: 53, Pl. 16; Stead, 1906: 113, Fig. 42; Ogilby, 1908: 66, Pl. 37; Roughley, 1916: 112, Pl. 35, 1951: 70, Pl. 28; McCullock, 1922: 58, Pl. 58; Waite, 1923: 129. (Australia).
- Sciaena margaritifera Haly, 1875: 269 (off Natal, South Africa).
- Sciaena aquila (non Lacepède): Castelnau, 1878: 381.
- Corvina axillaris (non Cuvier): De Vis, 1884: 538 (Brisbane River; so synonymized by Ogilby, 1918).
- Sciaena neglecta Ramsey & Ogilby, 1886: 941 (coast of New South Wales; so synonymized by Ogilby, 1918).
- Sciaena hololepidota antarctica: (non Lacepède); Ogilby, 1918: 70, Pl. 21 (Queensland).



Figure 12. Argyrosomus japonicus, 454 mm SL, RUSI 38457; Eastern Cape Province.

- Nibea japonica: Matsubara, 1937: 41, Figs 9 & 10 (near Tokyo); Chu, Lo & Wu, 1963: 55, Figs 31, 57, 83; Taniguchi, 1969: Figs 4 A & B; Masuda et al. 1988: Pl. 147 E.
- Argyrosomus japonicus: Lin, 1938: 170; Lin, 1940: 244, Fig. 1 (Hong Kong); Matsubara, 1955: 645, Pl. 67, Fig. 229 (Japan); Chu, 1956: 25, Pl. 2, Fig. 3 (Taiwan); Kamohara, 1964: 50 (Japan); Fischer & Whitehead, 1974: SCIAEN Argyr 4; Sasaki, 1994.
- Johnius hololepidotus (non Lacepède): Smith, 1949: 226, Fig. 552; Smith & Smith, 1966: 43.
- Pseudosciaena antarctica: Ogilby & Marshall, 1954: 70, Fig. 85 (Queensland).
- Argyrosomus hololepidotus (non Lacepède): Smith & Smith, 1966: 43; Fischer & Whitehead, 1974: SCIAEN Argyr 3; Trewavas, 1977: 326, Figs. 9, 12, 47 & 54 (Australia & South Africa); van der Elst, 1981: 261; Mohan, 1984: SCIAEN Argyr 3; Heemstra, 1986: 616, Pl. 71; Grant, 1987: 221, Fig. 493; Kailola et al. 1993: 318; Kuiter 1993: 199; Gomon, 1994; Branch et al. 1994: 250.

Johnius antarctica: Grant, 1978: 474, Pl. 201 (Australia). Argyrosomus sp.: Sainsbury et al., 1984: 230, fig.

Neotype: RUSI 44704, 499 mm SL, Meitsu, Nango-Cho, Miyazaki Prefecture, southeast coast of Kyushu, Japan, depth 50 m; 21st October 1993. Collected by Yukio Iwatsuki.

DIAGNOSIS: A species of *Argyrosomus* with the following combination of characters: dorsal fin rays 25-30; gill-rakers 4-5 + 10-12; swim-bladder carrot shaped, with 21-31 arborescent appendages; caudal peduncle length 11-13% SL; peduncle depth 70-92% peduncle length; interorbital width 6.4-7.4% SL (21-24% HL); suborbital width 8.4-10.5% HL; lower jaw length 48-52% HL; midlateral body scale length 2.4-3.1% SL; drumming muscles present in both sexes; urinary bladder length 2.0-9.6% SL; otolith shape like *A. regius* (Figs 13-15; see description below), OCD 23-41% OH; pectoral fins 17-21% SL, usually not reaching vertical at tips of pelvic fins; pectoral axillary fold scaleless; peritoneum unpigmented; anterior part of lateral line slightly curved.

DESCRIPTION: Based on 66 preserved specimens (119-638 mm), seven skeletons (318-590 mm) and the otoliths of 543 fish that were not preserved. Data from the neotype are in parenthesis. Dorsal fin X+I,25-30 (X,29); anal fin II,7; pectoral-fin rays 15-17 (17); lateral-line scales 50-53 (51); gill-rakers 4-5 + 9-12 (4 + 9); swim-bladder appendages 21-31 (30); vertebrae 11 + 14.

Proportions as % SL: head length 28-33 (28.5); pre-dorsal length 32-36 (33); pre-pelvic length 31-36 (31); body depth 25-30 (25); caudal peduncle length 11-13 (13); peduncle depth 8.8-10.6 (9.0); snout length 7.7-9.0 (8.3); eye diameter 5.2-7.0 at 119-298 mm, 4.4-5.2 at 301-387 mm and 3.9-5.0 (3.9) at 403-638 mm SL; interorbital width 6.4-7.4 (6.8); suborbital width 2.6-3.2 (2.6); upper jaw 12-13.5 (12); lower jaw 13.5-16 (14.0); pectoral fin 17-21 (17); pelvic fin 17-22 at 119-298 mm, 17-20 at 301-387 mm and 15-18 (16) at 403-634 mm SL; anal fin 15-19 at 119-298 mm, 15-17 at 301-387 mm and 12-15 (14) at 403-638 mm SL; third dorsal spine 11-15 (12); second anal spine 7.5-12 at 119-298 mm and 5.7-7.9 at 301-638 mm SL; gill-raker 1.8-2.8 at 119-298 mm, 1.8-2.2 at 301-387 mm and 1.6-2.1 (2.0) at 403-638 mm SL; gill-filament 2.6-3.4 (2.9).

Proportions as % HL: snout 26-30 (29); eye diameter 16-23 at 119-298 mm, 15-18 at 301-387 mm and 13-16 (13.6) at 403-638 mm SL; interorbital width 21-24 (24); suborbital width 8.5-10.4 (9.2); upper jaw 40-45 (42.5); lower jaw length 48-52 (49); gill-raker 6.2-8.9 at 119-298 mm, 6.3-7.1 at 301-387 mm and 5.3-9.0 (6.9) at 407-664 mm SL; gill-filament 8.5-11.4 (10.1).

Proportions as % eye diameter: gill-raker 32-57 (51); gill-filament 45-63 at 130-298 mm, 55-68 at 301-387 mm and 57-80 (74) at 407-664 mm SL.

Dorsal profile generally has a hump or "shoulder" behind the head. Axillary fold at base of pectoral fin scaleless. Scales weakly ctenoid on body (including belly and chest), nape, interorbital region, preoperculum and below eye; those on body not easily lost; length of midlateral body scales 2.4-3.1% SL. Lateral line evenly curved. Pectoral fin of most fish less than 100 cm not reaching vertical at tip of pelvic fins, but on some fish the pectoral and pelvic tips are equal. Caudal fin typically pointed (Fig. 2A) in fish less than 10 cm, becoming elongate S-shaped (Fig. 2B) in fish 15-35 cm SL and S-shaped (Fig. 2C) in fish larger than 40 cm SL; the caudal fin of large adults is occasionally bi-concave, wedge shaped or slightly rounded (Fig. 2F). Drumming muscles well developed in males and females but thicker in mature males than in mature females; although poorly developed in small individuals, drumming muscles were observed in all specimens greater than 27 cm. Peritoneum not pigmented. Urinary bladders large (Fig. 1). Pyloric caeca 7-10 (n = 64).

Swim-bladder (Figs 13B, D & 14B) appendages 21-31, those along anterior half of bladder divided basally into dorsoposterior and lateroanterior limbs, but along posterior half of bladder, the lateroanterior limbs become ventroanteriorly orientated, and the branches arising from them are orientated posteriorly, lying against the bladder (Fig. 14B). As a result, the arborescent appendages of the posterior half of the swim-bladder are not clearly visible in ventral view (Figs 13B & D). Disproportionate enlargement of 1-6 appendages (Figs 13D & 14B) occurs with increased size (16 of 61 specimens); the smallest specimen with enlarged appendages was 360 mm SL. The enlargement begins as a swelling at the base of the appendage, proceeding through the branches to the distal ends. Ventral surface of swimbladder covered with small black/grey dots (more obvious in smaller individuals) which apparently disperse, becoming less concentrated with growth.

Otoliths: Sagitta (Figs 15-17) typically Argyrosomus (like that of A. regius): moderately elongate and roughly triangular; ventral margin evenly rounded in smaller otoliths, becoming straighter with growth, with a bulge in the posterior third; margin of ventral bulge often denticulate; dorsal margin slightly convex and, in specimens 15 - 33 cm TL, commonly with a mediodorsal denticle (Fig. 17, first row); posterior margin generally straight and posterodorsal angle 90° or less; posteroventral angle becomes more acute with size; ostium to cauda distance (OCD) 23-41% OH. The



Figure 13. Ventral view of left half of swim-bladders: Argyrosomus inodorus: A) 355 mm, RUSI 38480; C) 640 mm, RUSI 42240. A. japonicus: B) 325 mm, RUSI 38450; D) 638 mm, RUSI 38452. DEA = Disproportionately Enlarged Appendage. Scale bar = 10 mm. otolith dimension/fish length relationships are given in Table 1; statistically there is no difference between the sexes. Intraspecific variation in otolith morphology is illustrated in Fig. 17.

Neurocranium (Figs 4 & 5): Length of neurocranium (NCL) 20-22% SL. Pre-supraocciptal length 10-11% SL and 49-53% NCL. Supraoccipital crest length 9.2-10.2% SL and 43-49% NCL (318-560 mm). Neurocranial width 7.3-8.4% SL and 34-39% NCL. Premaxilla 8.1-8.9% SL and 39-42% NCL. Dentary 9.5-10.1% SL and 44-48% NCL. Third and fourth neural spines 7.5-8.3 and 8.9-9.9% SL respectively.

Colour: In life, silvery grey becoming darker above and lighter below; dorsal surface with a bluish bronze sheen that may become coppery on head. Larger fish (>80 cm) are golden brown; dorsal and caudal fins grey/brown, becoming darker with age, often with a reddish hue - due to vascular distension or haemorrhaging (possibly during capture). Pectoral and anal fins white in fish less than 10 cm, changing to yellow and finally to grey or grey/brown in fish greater than 35 cm, also becoming darker with size. Mouth lining of juveniles white, becoming yellow and finally yellowish grey in large adults. Axillary fold of pectoral fin grey to black, generally with an irregular coppery-bronze patch.

Preserved specimens vary in colour according to treatment; usually grey but sometimes brown; darker above and lighter below. Dark patches on scales may give appearance of oblique stripes. Fins grey, sometimes with one or two longitudinal stripes on dorsal fin; the pelvic and pectoral fins usually pale.

COMPARISONS (see Tables 2-6): A. japonicus differs from A. regius in having a lower modal number of pectoralfin rays; longer midlateral scales; longer lower jaw; narrower interorbital width (Fig. 18); fewer and smaller arborescent swim-bladder appendages that, on the anterior half have ventral limbs that are orientated anterolaterally (vs anteroventrally), and branches arising from these project laterally (vs posteriorly and against the bladder); and a higher modal number of gill-rakers. Our comparison of otoliths from A. regius (Fig. 10) and A. japonicus (Figs 15-17) using our material and the illustrations of Chaine (1938) and Schwarzhans (1993) for both smaller and larger A. regius specimens, revealed no differences in the sagittae of these two species.

REMARKS: The original description of Temminck and Schlegel (1843: 58, Pl. 24, Fig. 1) was based on the description and plate in Burger's unpublished manuscript. According to Boeseman (1947: 62) "there never was a specimen in Burger's or Von Siebold's collection,". Boeseman (1947: 62) also pointed out "that Burger's descriptions without exception proved to be rather inexact. Temminck and Schlegel generally corrected and completed Burger's data with characters from the specimen(s) [from Burger's collection] ... Burger's plates too often show inaccuracies, but these also sometimes have been corrected by the authors [Temminck & Schlegel]...In this case, however, there was no way to verify Burger's data and plate. On account of this, it is very difficult, if not impossible, to make a final statement as to the identity and synonymy of Temminck & Schlegel's species." In view of the uncertainty of the identity of *Sciaena japonica* from Temminck & Schlegel's original description and illustration, the absence of a type specimen, and the presently confused taxonomy of *Argyrosomus* species, we believe that designation of a neotype for *Sciaena japonica* will promote stability of nomenclature and help to resolve the taxonomic confusion associated with these species.

Trewavas (1977: 330) commented: "As Lin (1940) pointed out, the resemblence [of *A. japonicus*] to *A. hololepidotus* is striking. The apparent differences are mostly correlated with size and are due to allometry." Trewavas' concept of "*A. hololepidotus*" was based on South African and Australian specimens of *A. japonicus*, as she did not examine any specimens from Madagascar. Her account of *A. japonicus* was compiled from published descriptions of specimens from Japan and China, and she went on (1977: 331) to observe that "there is no inherent improbability in Lin's suggestion (1940) that the relationship between *A. japonicus* and *A. hololepidotus* may be that of races of one species".

Our comparison of specimens from South Africa, Japan and Australia confirms that these populations are conspecific. Previous recognition of "A. *hololepidotus*" and A. *japonicus* as separate species was due to taxonomic inertia and the fact that none of the previous authors had directly compared specimens from Japan with those from South Africa or Australia.

Although the South African, Japanese and Australian populations of *A. japonicus* seem to be well isolated geographically (see below), and the smaller size of Australian

specimens (see below) implies some genetic differences between South African and Australian populations, the absence of any significant morphological (including branching patterns in the swimbladder appendages) or meristic differences in the specimens that we have examined from these populations requires that we recognize them as single species. Examination of molecular characters (proteins, DNA, etc) or some morphological features that we may have overlooked may show significant differences between these allopatric populations; but until such evidence is discovered, we accept the null hypothesis of conspecific identity of these populations by default (i.e., the burden of proof for recognition of separate species requires some tangible evidence other than apparent allopatry).

DISTRIBUTION: A. japonicus is found on the African southeast coast from the Cape of Good Hope to southern Mozambique; in Australia it is known along the entire southern seaboard from North West Cape (north of Shark Bay) in Western Australia to the Burnett River (north of Brisbane) in Queensland (Trewavas, 1977; Grant, 1978; Sainsbury et al., 1984; Kailola et al., 1993; Starling, 1993); in the northern Indian Ocean, it occurs off Pakistan and the northwest coast of India (Mohan, 1984) (as "A hololepido-tus"); and in the Northern Pacific it has been reported from Hong Kong northwards along the Chinese coast to southern Korea and Japan (Trewavas, 1977).

Along the South African coast *A. japonicus* occurs abundantly from Cape Agulhas to northern Natal (Table 7). It is found in estuaries (preferring those that are turbid), in the surf zone, and in the nearshore zone to depths of about 50 metres. In the nearshore environment, the species rarely



Figure 14. Lateral view of swim-bladders and anterior view of middle appendage: A) *Argyrosomus inodorus*, 640 mm, RUSI 38480; B) *A. japonicus*, 638 mm, RUSI 38452. DEA = Disproportionately Enlarged Appendage. Scale bars = 10 mm.



Figure 15. Medial view of *Argyrosomus* sagittae, showing inter-specific differences and morphological changes with growth. Those for *A. inodorus* and *A. japonicus* were chosen as typical of the size classes represented. Fish sizes given are of TL. Scale bar = 10 mm.



Figure 16. Lateral and ventral views of some sagittae illustrated in Figure 15. Scale bar = 10 mm.



Figure 17. Intraspecific variation of sagittae from South African Argyrosomus japonicus and similar-sized specimens from Japan and Australia.



Figure 18. Relationship between interorbital width and head length (HL) for *Argyrosomus regius* (squares), *A. japonicus* (circles), *A. hololepidotus* (crosses) and *A. coronus* (triangles).

ventures onto the "soft" (flat) substrates exploited by trawlers, but prefers "linefish grounds" (especially wrecks or high profile reefs that are associated with sand). West of Cape Agulhas, the relative proportion of *A. japonicus* found in *Argyrosomus* catches declines markedly, and the species is not known in the cold waters from the Cape of Good Hope to Namibia north of Lüderitz (Table 7).

FISHERIES: Due to its large size, palatability and abundance, *A. japonicus* is perhaps the premier angling species of the inshore environment (estuaries and surf zone) along the South African east coast (Cape Agulhas to Natal). Commercial line boat fishermen operating in the nearshore environment catch an average of 197 tons per annum (1988-1992). Recreational boat-fishermen often target this species and are believed to catch at least as much, and possibly more than the commercial fishermen. The flesh is generally sold fresh, but sometimes frozen.

In Australia A. *japonicus* (previously identified as *Sciaena antarctica, Johnius antarctica*, or more recently as *"Argyromosus hololepidotus"*) is an important commercial and recreational angling species known as the "mulloway". It is caught in estuaries, in the surf and offshore, using hook and line, gill nets, seine nets and trawl nets (Roughley, 1951; Ogilby, 1954; Grant, 1978; Hall, 1985; Jones, 1991; Kailola et al., 1993; Starling, 1993). From 1964 to 1990, the annual Australian catch has fluctuated between 175 and 575 tons (Kailola et al., 1993).

BIOLOGY: In South African waters, 50% sexual maturity for *A. japonicus* is attained at 110 cm TL for females and at 95 cm TL for males (Griffiths & Hecht, 1993 [species A]). Although there is strong evidence for a spawning migration of adult fish to Natal in spring, reproductive activity is also observed in the Cape Province (as far west as Cape Infanta). Adult fish are found mainly in the nearshore environment (beyond the surf zone) but at times visit inshore habitats. Juvenile fish (<100 cm TL) remain exclusively in the inshore habitats (surf and estuaries) with small juveniles (<15 cm TL) found only in estuaries. Juvenile recruitment to estuaries occurs at about 30 mm TL. The maximum size recorded is 75 kg (181 cm TL). Fish of 45 kg are common, and those between 50-60 kg are not unusual.

In Australia, A. *japonicus* attains sexual maturity at 75 cm TL, and spawning apparently occurs in the summer months (Hall, 1986). According to Kailola et al. (1993), the maximum size in Australia is 43 kg, but Gomon (1994) states that the mulloway attains a length of over 2 metres and a weight of nearly 60 kg.

MATERIAL EXAMINED:

JAPAN: BMNH 1987.5.7.1 (M 297 mm); BMNH 1987.5.7.2 (M 339 mm); BMNH 1987.5.7.3 (F 268 mm). MIYAZAKI: RUSI 44704 (F 499 mm, neotype); RUSI 43674 (F 491 mm); RUSI 40776 (M 267 mm, F 275 mm). Otoliths from four fish 325 - 610 mm TL. AUSTRALIA: AMS I 4453 (347 mm); AMS I 7658 (M 301 mm); AMS I 25605-002 (360 mm); AMS I 27322-007 (J 190 mm); AMS I 17178039 (J 168 mm) RUSI JB1 (J 195 mm). Otoliths from 75 fish 53 mm-880 mm TL). SOUTH AFRICA: Natal: BMNH 1862.11.9.13-14 (230 & 237 mm, Syntypes of S. margaritifera, Haly, 1875); RUSI 37391 (J 194 mm & 195 mm). Eastern Cape Province: BMNH 1994.11.30:4 (F 285 mm); MNHN 1994-0570 (F 270 mm); RUSI 11924 (447 mm); RUSI 30147 (F 635); RUSI 32506 (M 370 mm & F 363 mm); RUSI 32507 (F 360 mm); RUSI 32508 (M 387 mm); RUSI 33459 (M 403 mm); RUSI 35450 (F 447 mm); RUSI 37049 (F 436 mm); RUSI 37053 (F 344 mm); RUSI 37055 (F 526 mm); RUSI 37321 (M 382 mm); RUSI 37322 (M 231 mm, F 368 mm); RUSI 38050 (M 338 mm, F 298mm & J 250 mm); RUSI 38064 (Js 134mm & 120 mm); RUSI 38064 (J 168mm & 192 mm); RUSI 38065 (J 148, 202 & 216 mm); RUSI 38066 (J 218 mm & 143 mm); RUSI 38081 (J 158 mm); RUSI 38448 (F 416 mm); RUSI 38449 (F 471 mm); RUSI 38450 (M 355 mm); RUSI 38451 (M 484 mm); RUSI 38452 (F 638 mm); RUSI 38453 (M 424 mm); RUSI 38454 (F 430 mm); RUSI 38455 (F 415 mm); RUSI 38456 (F 574 mm); RUSI 38457 (M 454 mm); RUSI 38458 (F 537 mm); RUSI 38460 (F 612 mm); RUSI 38461 (M 571 mm); RUSI 41130 (298 mm); RUSI 42165 (J 218 mm, 221 mm & 189 mm and one F 245 mm). Southern Cape Province: RUSI 39136 (M 320 mm); RUSI 39138 (F 304 mm); RUSI 39140 (F 340 mm); SAM 33472 (M 330 mm); USNM 332447 (M 290 mm). Otoliths from 543 fish (37-1750 mm TL) collected from various localities along the South African east coast.

Argyrosomus hololepidotus (Lacepède, 1801) (Fig. 19)

- Labrus hololepidotus Lacepède, 1801 (3): 517, Pl. 21, Fig. 2 (based on the unpublished figure of Philibert Commerson, who [according to Cuvier & Valenciennes, 1830] obtained the specimen from Fort Dauphin, Madagascar).
- Sciaena aquila (non Lacepède): Pellegrin 1914: 225 (Madagascar).
- Argyrosomus hololepidotus: Bauchot & Bianchi, 1984: 88; Mohan, 1984, SCIAEN Argyr 3 (in part).

Holotype: none

- Iconotype: Lacepède, 1801, Pl. 21, Fig. 2 (from Philibert Commerson's drawing).
- Neotype: RUSI 41433, female 465 mm, Fort Dauphin, Madagascar; collected by Marc H. Griffiths, 3rd April 1993. According to Cuvier and Valenciennes (1830),



Figure 19. Argyrosomus hololepidotus, neotype, 465 mm SL, RUSI 41433; Madagascar.

Commerson's original specimen from Fort Dauphin, Madagascar and his description of the species were lost. Because sciaenid taxonomy depends heavily on internal anatomy (Trewavas, 1977), the iconotype (an engraving of Commerson's figure) contains too little detail to differentiate between *Argyrosomus* species. It is therefore necessary to designate a neotype to resolve the taxomomic confusion that besets this name.

ADDITIONAL MATERIAL: RUSI 41432, J 204 mm, and a fresh specimen (M 615 mm) examined at the Fort Dauphin fish market. Meristic data from the third specimen were recorded, and the otoliths were collected; otoliths of four larger specimens were also collected.

DIAGNOSIS: A species of *Argyrosomus* with the following combination of characters: dorsal fin rays 27-28; gill-rakers 4-5+9; swim-bladder carrot shaped, with 34-36 arborescent appendages with lateroanterior limbs throughout length of bladder; caudal peduncle length 12-13% SL; peduncle depth 75-77% peduncle length; interorbital width 6.3-7.3% SL (22% HL); suborbital width 11-12% HL; lower jaw length 50% HL; midlateral body scale length 2.5-2.8% SL; drumming muscles present in both sexes; sagitta similar to that of *A. regius*, OCD 28-34% OH; pectoral fins 17-18% SL, not reaching vertical at tip of adpressed pelvic fins; pectoral fin axillary fold scaleless; peritoneum unpigmented; anterior part of lateral line moderately curved.

DESCRIPTION: Data for the neotype in parentheses. Dorsal fin X+I,27-(28); anal fin II,7; pectoral fin rays 16-(17); lateral-line scales 50 - (51); gill-rakers 4-(5) + 9; swim-bladder appendages (34)-36; vertebrae 11 + 14.

Proportions as % SL: head length (29)-30; pre-dorsal length 34; pre-pelvic length 32; body depth (26)-27; caudal peduncle length (12)-13; peduncle depth (9.0)-9.7; snout length (7.4)-7.8; eye diameter (4.7)-5.5; interorbital width (6.3)-6.7; suborbital width (3.0)-3.4; upper jaw (12)-12.5; lower jaw (14)-15; pectoral fin (17)-18; pelvic fin (18)-20; anal fin (14)-16; third dorsal spine (13); second anal spine (6.7)-8.5; gill-raker (1.8)-1.9; gill-filament 2.9-(3.2); scale length (2.5)-2.8.

Proportions as % HL: snout (26)-27; eye diameter (16.5)-18; interorbital width (22)-23; suborbital width (10.5)-12; upper jaw 42-(43.5); lower jaw 50; gill-raker (4.2)-6.3; gill-filament 10-(11).

Proportions as % eye diameter: gill-raker 34-(39); gillfilament 54-(68).

Dorsal profile of *A. hololepidotus* includes a hump or "shoulder" behind the head. Pectoral fins not reaching vertical at tip of pelvic fins (for fish 204-615 mm). Scales ctenoid on body, belly, nape, interorbital region, operculum and below eye. Caudal fin elongate S-shaped (Fig. 2B) in smallest fish and S-shaped (Fig. 2C) in two larger specimens examined; it is probable (as in *A. japonicus*) that the caudal fins of fish less than 10 cm SL are pointed. Gill-raker at angle shorter than outer gill-filaments (at angle) in larger fish, and equal to gill-filaments in 204 mm specimen. Drumming muscles present in both sexes. Urinary bladders large, as in *A. japonicus*. Pyloric caeca 8 or 9.

Swim-bladder carrot shaped (Fig. 20) with 34-36 appendages. Proximal two limbs of arborescent appendages orientated dorsoposteriorly and lateroanteriorly throughout length of bladder. Branches arising from anterior limb project at 90° to the bladder, and those from the dorsal limb project posteriorly and lie against the bladder. In specimens with significant quantities of appendage fat, the lateroanterior limb becomes orientated ventroanteriorly and the branches of both limbs project laterally at 90° to the bladder (with only slight posterior orientation at their tips) (Fig. 20). Last two appendages on each side of the bladder bud-like, and the four preceding these, weakly branched.

Otoliths: Comparisons of sagittae from A. hololepidotus, A. japonicus (Figs 15 & 16) and A. regius (Fig. 11 and the illustrations of Chaine, 1938 and Schwarzhans, 1993) revealed no significant differences. The denticles observed along the dorsal margin of the smallest otolith figured for A. hololepidotus (Figs 15 & 16) are also sometimes found in small specimens of A. japonicus and A. regius. The OCD is 28-34% OH for A. hololepidotus.

Colour: Fresh colour of neotype silvery grey becoming darker and bluish above and white below; flanks and dorsal surface with a distinctly bronze sheen. Pectoral, dorsal and



Figure 20. Swim-bladder of *Argyrosomus hololepidotus* 465 mm, Neotype, RUSI 41433: A) lateral and B) ventral (left half) views. The orientation of the swim-bladder appendages of this specimen was modified by the large quantity of fat that was removed from between the appendages (see description).

caudal fins brownish grey; pelvic and anal fins almost white with streaks of grey. Fleshy fold at axil of pectoral fin black and scaleless. After fixation the neotype darkened, becoming distinctly brown; this dark brown colour is possibly due to the use of paraformaldehyde (to prepare the formalin solution). Mouth lining pale grey; inner aspect of operculum dark grey. Peritoneum unpigmented.

COMPARISONS (Tables 2 - 4): A. hololepidotus differs from A. japonicus by having a wider suborbital, more swimbladder appendages and fewer lower gill-rakers. Furthermore, the branches arising from the ventral limbs along the posterior half of the swim-bladder (Fig. 20), project laterally from the bladder and do not lie against it as in A. japonicus (Figs 13 & 14), and in specimens with little or no appendage fat, the ventral limb is orientated lateroanteriorly (vs ventroanteriorly) in the posterior half of the bladder.

A. hololepidotus differs from A. regius by having fewer and smaller swim-bladder appendages (Fig. 11), which have ventral limbs (in specimens with little or no appendate fat) that are orientated anterolaterally (vs anteroventrally) and branches arising from these which project at 90° from the bladder (vs posteriorly and lying against the bladder); wider suborbital; shorter pectoral fin; longer scales; narrower interorbital; and longer lower jaw.

A. hololepidotus was also compared with data and illustrations of A. amoyensis from Trewavas (1977), Mohan (1984) and the original description of Nibea miichthioides Chu et al. 1963. A. hololepidotus differs in having 9 (vs 8) lower gill-rakers, interorbital width 22-23% HL (vs 19% HL), and suborbital width 11-12% HL (vs 9% HL). The swim-bladder of A. amoyensis is spindle shaped (tapering anteriorly and posteriorly), there are only 22-29 appendages, and they are not obviously divided into dorsal and ventral limbs. The sagitta of A. hololepidotus (Figs 15 & 16) is similar to that of A. amoyensis (Trewavas, 1977: Fig. 9b; Chu et al., 1963: Fig. 82), but it lacks the protuberance found on the posterodorsal corner in A. amoyensis.

DISTRIBUTION: A. hololepidotus is known only from Madagascar. The neotype, Commerson's original specimen (Cuvier & Valenciennes, 1830) and the specimens listed by Pellegrin (1914) were all collected from Fort Dauphin on the southeast coast of Madagascar. Although Mohan (1984) indicated that A. hololepidotus is found along the entire east coast and northern parts of the island, fisheries personnel in Madagascar report that it is common only on the southeast coast.

FISHERY: A. hololepidotus or the "fyandava" (Malagasy name) is generally caught by artisanal fishermen using dugout canoes and handlines in 20 - 40 m of water.

BIOLOGY: All three specimens (204-615 mm) examined in this study were immature, suggesting a large size at sexual maturity (similar to *A. japonicus* and *A. regius*). The maximum size, as measured from marks on the oars and gaffs of fishermen, was 135 cm TL.

Argyrosomus thorpei Smith, 1977

- Argyrosomus thorpei Smith 1977: 561, Pls. I & II; van der Elst, 1981: 262; Mohan, 1984: SCIAEN Argyr 7; Heemstra, 1986: 617, Pl. 71.
- Afroscion thorpei: Trewavas, 1977: 337; Schwarzhans, 1993: 134, Figs. 244-245.
- Holotype: RUSI 674 (320 mm SL from Natal)

Paratypes: RUSI nos 675-680, 2651A & B, BMNH 1976.10.18.1

DIAGNOSIS: A species of *Argyrosomus* with the following combination of characters: dorsal fin rays 26-28; gill-rakers 4-6 + 10-12; swim-bladder carrot shaped, with 25-33 arborescent appendages; caudal peduncle length 12-14% SL; peduncle depth 65-79% peduncle length; interorbital width 6.0-7.9% SL (19-26% HL); suborbital width 10-12% HL; lower jaw length 47-52% HL; midlateral body scale length 2.6-3.3% SL; drumming muscles present in both sexes; urinary bladders large; sagitta with anterior two-thirds expanded, posterodorsal angle >90°, posterior margin straight, cauda with distal portion expanded and tip truncate, OCD 34-44% OH; pectoral fins 20-23% SL, reaching past vertical at tip of pelvic fins; pectoral fin axillary fold scaly; peritoneum pigmented; anterior half of lateral line strongly curved.

DESCRIPTION: Based on 16 preserved specimens (166-474 mm), two fresh specimens, two skeletons (452 & 461 mm) and otoliths of 53 other fish. Dorsal fin X+I,26-30; anal fin II,7; pectoral-fin rays 15-17; lateral-line scales 49-52; vertebrae 11 + 14. Proportions as % SL: HL 29-32; pre-dorsal length 33-37; pre-pelvic length 32-34; body depth 24-30; caudal peduncle length 12-14; peduncle depth 8.4-10.2; snout 8.1-8.9; eye diameter 6.8-7.9 at 166-238 mm, 4.8-5.4 at 315-390 mm and 4.0-4.2 at 441-474 mm SL; interorbital width 6.0-7.9; suborbital width 3.0-3.7; upper jaw 12-14; lower jaw 14-16; pectoral fin 20-23; pelvic fin 16-21 at 166-238 mm, 17-18 at 315-390 mm and 16-17 at 403-634 mm SL; anal fin 15-17 at 166-238 mm, 14 at 315-390 mm and 13 at 460 mm SL; third dorsal spine 10-15; second anal spine 4.4-7.9 at 166-238 mm and 6.7-7.7 at 315-474 mm SL; gill-raker 2.7-3.0 at 166-238 mm, 2.4-3.0 at 315-390 mm and 2.3-2.5 at 441-474 mm SL; gill-filament 2.6-3.4.

Proportions as % HL: snout 26-29; eye diameter 19-21 at 166-238 mm, 17-19 at 315-390 mm and 15-17 at 403-474 mm SL; interorbital width 19-26; suborbital width 10-12; upper jaw 39-44; lower jaw 47-52; gill-raker 9.0-9.8 at 166-238 mm, 8.1-10.0 at 315-390 mm and 8.1-8.5 at 441-474 mm SL; gill-filament 9.1-11.6.

Proportions as % eye diameter: gill-raker 42-56; gill filament 51-55 at 166-238 mm, 53-68 at 315-390 mm and 66-74 at 441-474 mm.

Scales cycloid on snout, below eye, on interorbital region and on extreme anterior part of chest; ctenoid on rest of body. Anterior half of lateral line strongly curved. Caudal fin elongate S-shaped in juveniles, becoming slightly S-shaped and occasionally truncate in adults (Fig. 2). The correction made to the caudal fin in the photograph of the holotype (Smith, 1977) is probably erroneous. Gill-raker at angle of first arch at least equal to outer (shorter) gill-filaments in fish less than 46 cm, but gill-raker shorter than gill-filaments in larger fish. Smith (1977) reported no sonific muscles for *A. thorpei*, but we found drumming muscles in both sexes (n = 48) in specimens larger than 23 cm (including the paratypes listed). Urinary bladders large (as in *A. japonicus*).

Swim-bladder carrot shaped, with 25-33 appendages (for illustration see Smith 1977, Pl. 2); the ventral limb is orientated lateroanteriorly, rather than venteroanteriorly and the branches arising from it project laterally and at no stage lie against the bladder. The dorsal limb is orientated dorsoposteriorly, but along the posterior three quarters of the bladder it curves through 150° so that the tip points anteriorly. The branches on this limb project posteriorly to dorsally; and lie against the swim-bladder; last 1-3 appendages are bud-like and the 1-3 preceding appendages weakly branched. Disproportionate swim-bladder enlargement not observed in any *A. thorpei* that we examined.

Otoliths: Sagittae of A. thorpei (Figs 15 & 16) very distinctive, moderately elongate, the anterior two-thirds expanded, resulting in a broadly rounded apex; dorsal and posterior margins relatively straight; posterodorsal angle $>90^{\circ}$; ventral margin convex in smaller fish, becoming \circ concave with growth; cauda strongly curved with distal portion expanded and tip truncate.

Neurocranium (Figs 4 & 5) and skeleton: Length of neurocranium (NCL) 20-21% SL; pre-supraoccipital crest length 10-11% SL and 49-51% NCL; supraoccipital crest length 8.5-8.9% SL and 41-44% NCL (452-461 mm SL); neurocranial width 8.1-8.4% SL and 40-41% NCL. Pre-

maxilla 8.6-8.7% SL and 42-43% NCL; dentary 9.8-10% SL and 48% NCL; interorbital septum relatively unossified. Third and fourth neural spines 8.9% and 8.5-8.7% respectively.

Colour: Silvery grey becoming darker and blue (with a coppery sheen) above and lighter below; fins yellow grey to orange brown, occasionally reddish (particularly caudal) as a result of vascular distension and haemorrhaging; mouth lining pale yellow; inside of operculum grey/black with yellow tinge; peritoneum pigmented with grey/black dots. After preservation the colour depends on treatment, and may vary from dark brown to grey, or even silver. A dark spot on each dorsal body scale may give the appearance of oblique stripes; fins greyish or brown; peritoneum and ventral surface of swim-bladder with fine black/grey dots.

COMPARISONS (Tables 2-6): The body of Argyrosomus thorpei is slightly more compressed than the other species described in this paper. Teeth of lower jaw with Argyrosomus pattern of differentiation, but smaller than in equalsized specimens of the other species (Fig. 6).

Differences between A. thorpei and A. japonicus include: a wider suborbital, scaly pectoral fin axillary fold, anterior half of lateral line more strongly curved, longer caudal peduncle, longer gill-rakers; sagitta with a more obtuse posterodorsal corner, anterior two-thirds of otolith and distal portion of the cauda expanded (Fig. 15); neurocranium wider, with wider lateral line canals (Fig. 5) and larger inter-orbital window (Fig. 4).

A. thorpei differs from A. hololepidotus in having fewer swim-bladder appendages, more lower gill-rakers, longer pectoral fin, anterior half of lateral line more strongly curved, scaly pectoral fin axillary fold, pigmented peritoneum; sagitta with a more obtuse posterodorsal corner and anterior two-thirds of otolith and distal portion of the cauda expanded (Fig. 15).

REMARKS: Based on otolith shape, Trewayas (1977) established the monotypic genus, Afroscion, for Argyrosomus thorpei Smith, 1977. This genus was not recognized by Mohan (1984), Heemstra (1986) or Sasaki & Kailola (1988). The recent discovery of Afroscion trewavasae Schwarzhans 1993, based on otoliths from the Lower Pliocene of Morocco, led Schwarzhans to reinstate the genus Afroscion. arguing that it represents a lineage separated from Argyrosomus for a considerable period of time. According to him, "the shape of the dorsal rim and the absence of a concavity at the ventral rim (of the otolith) are the most obvious diagnostic differences" for the genus. Schwarzhans (1993), however, described the dorsal margins ("rims") of both genera as being flat, and we found that the ventral margin of Argyrosomus sagittae becomes concave with growth (Fig. 15). Although A. thorpei differs from other species of Argyrosomus by its scaly pectoral axillary fold, pigmented peritoneum, strongly curved lateral line, and distinctive otolith morphology, we believe these differences are insufficient to justify a separate generic status.

DISTRIBUTION: A. thorpei is known from the southeast African coast from Port Elizabeth to Mozambique and also from the west coast of Madagascar. In South Africa it is mostly caught beyond the surf zone (to depths of 80 m) and seldom found south of Natal (Table 7).

FISHERIES: Natal commercial lineboat fishermen catch an average of 107.1 tons and the recreational line-boat sector land an estimated 23 tons (ORI unpublished data) per annum (1988-1992). Shore anglers occasionally catch this species at selected sites on the Natal north coast. *A. thorpei* is also caught in large numbers by line-boat fishermen operating in Mozambique.

BIOLOGY: The size at 50% sexual maturity is 33 cm TL, and spawning occurs during winter (van der Elst et al., 1990). Juveniles are found on sand or mud substrata and the adults predominantly on reef (Fennessy, 1994). Maximum size recorded is 12.0 kg.

MATERIAL EXAMINED:

SOUTH AFRICA: Natal: RUSI 675 (M 365 mm); RUSI 676 (F 365 mm); RUSI 677 (M 474 mm); RUSI 678 (M 375 mm); RUSI 680 (F 315 mm); RUSI 2651 (M 390 mm); RUSI 10264 (F 385 mm); RUSI 10694 (J, 166 mm and 2 F, 171 & 185 mm); RUSI 11613 (F, 238 mm); RUSI 13065 (1 M 460 mm and 2 F, 379 mm & 441 mm); RUSI 28382 (M 231 mm). Plus otoliths from 30 fish (14 - 110 cm TL). Eastern Cape Province: Algoa Bay: RUSI 10264 (M 385 mm). MOZAMBIQUE: RUSI 39881 (M 203 mm); RUSI 48480 (F 452 mm, skeleton); RUSI 48481 (F 461 mm, skeleton); the meristic counts of the two fish from which the skeletons were prepared, were also recorded.

Argyrosomus inodorus sp. nov. (Fig. 21)

- Sciaena hololepidota (non Lacepède): Cuvier & Valenciennes, 1830: 38 (in part); Smith, 1849 Pl. 15 (in part); Pappe, 1853: 15; Barnard, 1927: 569 (in part) Pl. 23, Fig. 3; Biden, 1930: 108 (in part) Pl. 13.
- Johnius hololepidotus (non Lacepède): Smith, 1949: 226 (in part, not Fig. 552, which is A. japonicus).
- Argyrosomus hololepidotus (non Lacepède): Trewavas, 1977: 327 (in part, not figs); Heemstra, 1986: 616 (in part, not figs); Bianchi et al., 1993: 164; Schwarzhans, 1993: 138, Fig. 255.

Holotype: RUSI 44705, male, 447 mm SL, South Africa, False Bay, depth 10 m; collected by M. H. Griffiths, 5 June 1994.

Paratypes: 78 specimens (131-860 mm). NAMIBIA: Walvis Bay: RUSI 15257 (M 605 mm). Swakopmund: RUSI NP (M 392 mm); RUSI 48475 (F 415 mm); RUSI 48476 (F 424 mm); RUSI 48477 (M 338 mm); RUSI 48478 (F 332 mm); RUSI 48479 (M 315 mm). SOUTH AFRICA: Eastern Cape Province: AMS I. 34965-001 (F 462 mm, M 308 mm); BMNH 1994.11.30:2 (M 305 mm); BMNH 1994.11.30:3 (F 266 mm); MNHN 1994-0568 (M 558 mm); MNHN 1994-0569 (F 307 mm); NSMT-P 46548 (M 348 mm); NSMT-P 46549 (F 521 mm); RUSI 11924 (F 470 mm); RUSI 38464 (F 306 mm); RUSI 38466 (F 274 mm); RUSI 38467 (F 330 mm); RUSI 38469 (F 283 mm); RUSI 38471 (F 304 mm); RUSI 38474 (F 374 mm); RUSI 38476 (F 258 mm); RUSI 38478 (F 289); RUSI 38479 (M 299 mm); RUSI 38480 (F 325 mm); RUSI 38481 (F 265 mm); RUSI 41138 (F 368 mm); RUSI 41141 (F 293 mm); SAM 33473 (F 276 mm); SAM 33474 (M 381 mm); USNM 331636 (F 357 mm, M 296 mm). Western Cape Province: RUSI 37390 (J 131-157 mm); RUSI 38475 (F 275 mm); RUSI 39836 (5 M 211-287 mm & 3 F 212-227 mm); RUSI 41129 (F 301 mm); RUSI 41132 (M 308 mm); RUSI 41133 (F 362 mm); RUSI 41134 (M 240 mm); RUSI 41136 (F 369); RUSI 41139 (J 154 mm); RUSI 41140 (M 366 mm); RUSI 41143 (M 306 mm); RUSI 41145 (M 364 mm); RUSI 41147 (F 267 mm); RUSI 41148 (F 219 mm); RUSI 41149 (F 267 mm); RUSI 41150 (F 202 mm); RUSI 41151 (F 235 mm); RUSI 41153 (F 234 mm); RUSI 41154 (J 167 mm); RUSI 41156 (F 407 mm); RUSI 41160 (J 179 mm); RUSI 41161 (M 595 mm); RUSI 41162 (J 161 mm); RUSI 41163 (F 227 mm); RUSI 41167 (F 234 mm); RUSI 41435 (J 141 mm); RUSI 42241 (M 660 mm); RUSI 42242 (F 510 mm); RUSI 42246 (M 664 mm); RUSI 42240 (F 640 mm); RUSI 42243 (F 527 mm); RUSI 42244 (M 387 mm); RUSI 42245 (M 383 mm); RUSI 42247 (F 650 mm); RUSI 42248 (F 860 mm); RUSI 44706 (453 mm); RUSI 44707 (435 mm).

DIAGNOSIS: A species of *Argyrosomus* with the following combination of characters: dorsal fin rays 25-29; gill-rakers 4-6 + 10-12; swim-bladder carrot shaped with 31-42 arborescent appendages, the latero-anterior limb of appendages present throughout length of bladder; caudal peduncle length 12-15% SL; peduncle depth 58-74% peduncle length; interorbital width 6.3-7.8% SL (20-25% HL); suborbital width 8.6-10.9% HL; lower jaw length 47-51% HL; midlateral body scale length 1.8-2.5% SL; drumming muscles present only in males; urinary bladders rudimentary, length 0.1-3.3% SL; sagitta (Figs 15, 16 & 22) elongate, with pronounced bulge in posterior third of ventral margin; OCD 37-63% OH; pectoral fins 19-23% SL, reaching to or beyond vertical at tip of adpressed pelvic fins of fish 25-90 cm SL (in South African specimens); pectoral fin axillary



Figure 21. Argyrosomus inodorus sp. nov., holotype, 447 mm SL, RUSI 44705; South Africa: False Bay.

fold naked; peritoneum unpigmented; anterior part of lateral line slightly curved.

DESCRIPTION: Based on 79 preserved specimens (131-860 mm), 12 skeletons (300-517 mm) and otoliths and total lengths of 623 fish from South Africa, and 85 from Namibia, that were not preserved. Counts and measurements for the holotype are in parentheses. Dorsal fin X+I,25-29 (27); anal fin II,7 [one specimen from Walvis Bay with 8 rays]; pectoral fin rays 16-17 (17); lateral-line scales 50-53 (51); gill-rakers 4-6 + 10-12; swim-bladder appendages 31-41; vertebrae 11 abdominal and 14 caudal.

Proportions as %SL: HL 28-33 (30); pre-dorsal length 32-36 (33); pre-pelvic length 30-36 (34); body depth 24-28 (25.5); caudal peduncle length 12-15 (13.5); peduncle depth 7.7-9.6 (9.2); snout 7.1-9 (8.5); eye diameter 5.8-7.3 at 131-299 mm, 4.9-6.2 at 301-387 mm, 4.0-5.0 (5.0) at 404-664 mm, and 3.3 at 860 mm SL; interorbital width 6.3-7.8 (7.2); suborbital width 2.6-3.3 (3.0); upper jaw 12-14 (12); lower jaw 14-18 (14.5); pectoral fin 19-23 (21.6); pelvic fin 16-20 at 131-387 mm, 15-17 (17) at 407-664 mm, and 14 at 860 mm SL; anal fin 14-18 at 131-299 mm, 13-15 at 301-387 mm, 12-14 (13.9) at 407-664 mm and 12 at 860 mm SL; third dorsal spine 11-15 (12); second anal spine 5.1-11.7 (7.2); gill-raker 2.0-2.9 at 131-299 mm, 1.8-2.6 at 301-387 mm, 1.6-2.1 at 407-664 mm and 1.2 at 860 mm SL; gill-filament 2.6-3.6.

Proportions as % of HL: snout 24-30 (28.5); eye diameter 18-24 at 131-299 mm, 16-20 at 301-387 mm, 13-17 (17) at 407-664 mm SL, and 11 at 860 mm SL; interorbital width 20-25 (24); suborbital width 8.6-10.9 (10.1); upper jaw 39-44 (40); lower jaw 47-51 (49); gill-raker 6.7-9.1 at 131-299 mm, 6.0-8.8 at 301-387 mm, 5.3-7.0 at 407-664 mm and 3.9 at 860 mm SL; gill- filament 8.9-13.3.

Proportions as % eye diameter: gill-raker 32-46; gillfilament 37-53 at 131-299 mm, 46-77 at 301-387 mm, 55-88 at 407-664 mm and 107 at 860 mm SL.

Dorsal profile evenly rounded. Eye obliquely egg shaped. Nostrils as for A. japonicus. Scales deciduous, weakly ctenoid on body (including belly and chest), nape of neck, interorbital region, operculum and below eye. Skin fold at base of pectoral fin scaleless. Pectoral fins reach to or beyond vertical at tip of adpressed pelvic fins for South African specimens 25-90 cm SL, but on smaller fish the pelvic fins extend past tip of pectorals. Caudal fin shape changes with growth; it may be pointed (<10 cm SL, Fig. 2A), elongate and S-shaped (10-22 cm SL, Fig. 2B), or strongly to slightly S-shaped (>30 cm, Fig. 2C). Caudal fin of larger specimens occasionally wedge-shaped to slightly rounded or truncate (Figs 2 E, F & G). Gill-raker at angle of first arch equal to or longer than outer gill-filaments at angle for specimens less than 55 cm, but gill-filaments longer than gill-raker at angle in larger individuals. Drumming muscles present only in larger males, and are poorly developed (or even absent) in most males less than 25 cm SL (n = 8350). Urinary bladders (Fig. 1) rudimentary or sometimes absent in South African specimens, but possibly larger in those from Namibia. Pyloric caeca 7-10 (n = 335).

Swim-bladder (Figs 13A & C & 14A) carrot-shaped, tapering posteriorly, with 31-42 appendages. Most appendages arborescent, basally divided into dorsoposterior and



Figure 22. Intraspecific variation of sagittae from 5 size classes of South African *Argyrosomus inodorus*; sizes are total lengths. Lower two rows of drawings (otoliths from fish 1002 - 1227 mm) have been reduced (x 0.75) for purposes of reproduction.

lateroanterior (rather than ventroanterior) limbs, none of which significantly overlap the bladder. Branches arising from anterior limb project at 90° to bladder throughout its length and at no stage lie against it. The last 1-3 pairs of appendages are bud-like and the 1-3 pairs preceding these, weakly branched. Disproportionate appendage enlargement (see *A. japonicus*) was observed only in the 860 mm specimen, which was the largest of 86 *A. inodorus* examined. Ventral surface of swim-bladder with a sparse pattern

of small black/grey dots that do not appear to increase in size or number, but disperse, with growth.

Otoliths: Sagitta (Figs 15, 16 & 22) elongate; posterior margin rounded, posterodorsal angle usually greater than 90° ; ventral margin evenly curved in juveniles, but with a prominent, often denticulate, bulge in posterior third of otoliths of adults; OCD large (37-63% OH). A lateral process (Fig. 16, top row) often occurs just below umbo in larger specimens. Otolith dimension/TL relationships are given in Table 1; statistically, there were no differences between the sexes.

Neurocranium (Figs 4 & 5) and skeleton: Length of neurocranium (NCL) 20-22% SL; pre-supraoccipital crest length 10-12% SL and 51-56% NCL; supraoccipital crest length 8.0-8.8% SL and 39-43% NCL (300-546 mm SL); neurocranial width 8.1-9.2% SL and 39-45% NCL. Pre-maxilla 8.1-9.1% SL and 40-42% NCL; dentary 9.3-10.3% SL and 46-49% NCL; interorbital septum relatively unossified. Third and fourth neural spines 6.9-8.0 and 8.2-9.3% SL respectively.

Colour: In life, body silvery becoming green/brown above and white below. Dorsal surface with a copper to bronze sheen which may be very pronounced on head; dorsal and caudal fins pale yellow grey to pale grey/brown; anal, pelvic and pectoral fins from almost white to brown/grey; fins (particularly caudal) occasionally reddish as a result of vascular distension and haemorrhaging. Pectoral fin axillary fold black with a copper/bronze patch. Mouth lining varies from pale yellow to yellow/grey; inner aspect of operculum grey to black, sometimes with a yellow tinge.

In alcohol, body silvery to grey, with a dark spot on each dorsal body scale, sometimes giving rise to oblique stripes;

fins pale to dark grey. One or two longitudinal stripes may be visible on dorsal fins.

COMPARISONS (Tables 1-6 & 8): A. inodorus differs from A. japonicus in having a more even dorsal profile, larger eye (Fig. 23, Table 8) longer pectoral fins (Fig. 24; significant for fish >30 cm SL, Table 8), which reach to or beyond vertical at tip of pelvic fins in fish 25-90 cm SL, shorter scales (Fig. 25), which are more easily lost; a longer and shallower caudal peduncle (Figs 26-28); no drumming muscles in females; rudimentry urinary bladders (Figs 1 & 29); and a higher modal number of lower gill-rakers (Tables 4 & 5). A. inodorus also has more swim-bladder appendages (Tables 2 & 3), the appendages are larger (particularly along anterior part of bladder), with the lower limbs orientated anterolaterally (vs anteroventrally) throughout length of bladder (Figs 13 & 14), and the branches arising from the dorsal and ventral limbs of the appendages along the posterior half of the swim-bladder project at right angles from the bladder (in A. japonicus these branches extend posteriorly and lie against the bladder, Figs 13 & 14).

The sagitta of *A. inodorus* (Figs 15, 16 & 22) is longer than that of *A. japonicus* (Fig. 30, Table 1), it has a more obtuse posterodorsal angle, rounded (vs straight) posterior margin, pronounced bulge on ventral margin, a greater OCD (Fig. 31, Table 1), and lower OCD:OH ratio (Fig. 32, Table 2).

The neurocranium is wider than that of *A. japonicus* (Fig. 33), it also has an enlarged lateral-line canal system (Figs 4 & 5), a larger interorbital window with frontal and parasphenoid bones not connected (Fig. 4), and shorter supraoccipital crest (Fig. 34, Table 2).

The fish weight/TL and otolith weight/TL relationships for A. *inodorus* and A. *japonicus* are also significantly different (P < 0.0001, Table 1). The OCD:OH ratio was not



Figure 23. Relationship between eye diameter and SL for Argyrosomus inodorus (squares) and A. japonicus (circles).



Figure 24. Relationship between pectoral fin length and SL for Argyrosomus inodorus (squares) and A. japonicus (circles).

allometric for either *A. inodorus* or *A. japonicus* (see Fig. 32) and consequently should assist in the identification of these two species when only otoliths are available (e.g. studies on the feeding of *Argyrosomus* predators or on the middens of ancient southern African man).

Differences between A. *inodorus* and A. *hololepidotus* (Tables 2-4) include: more lower gill-rakers; narrower suborbital width; longer pectoral fin and caudal peduncle; shorter scales; reduced urinary bladders; and drumming muscles in males only. The sagitta of A. *inodorus* (Figs 15, 16 & 22) has a more obtuse posterodorsal angle, rounded (vs straight) posterior margin, pronounced bulge in posterior portion of ventral margin, greater OCD (Fig. 15), and a lower OCD:OH ratio (Table 2).

A. inodorus differs from A. regius (Tables 2 & 3-6) in having more lower-limb gill-rakers, narrower interorbital, longer pectoral fin, caudal peduncle and lower jaw, smaller urinary bladders, drumming muscles in males only, and lower limb of arborescent swim-bladder appendages orientated anterolaterally (vs ventroanteriorly), with branches projecting at 90° to the bladder (vs projecting posteriorly and against the bladder). The sagitta of A. inodorus (Figs 15, 16 & 22) has a more obtuse posterodorsal angle, rounded (vs straight) posterior margin, pronounced bulge in posterior



Figure 25. Relationship between midlateral body scale length and SL for Argyrosomus inodorus (squares) and A. japonicus (circles).



Figure 26. Relationship between caudal peduncle length and SL for Argyrosomus inodorus (squares) and A. japonicus (circles).

portion of ventral margin, greater OCD (Fig. 15), and lower OCD:OH ratio (Table 2).

A. *inodorus* differs from A. *thorpei* (Tables 2-6) in having a slightly curved lateral line, shorter midlateral body scales, narrower suborbital width, more swim-bladder appendages, reduced urinary bladders, drumming muscles in males only, and naked pectoral axillary fold. The sagitta has a rounded posterior margin, anterior two-thirds of otolith tapering to form a sharply rounded apex, tip of cauda not expanded and OCD greater (Fig. 15). A. inodorus was compared with data and illustrations of A. amoyensis from Trewavas (1977), Mohan (1984) and the original description of Nibea miichthioides Chu et al. (1963). A. inodorus has more lower gill-rakers (10-12 vs 8); a carrot-shaped (vs spindle-shaped) swim-bladder with more appendages (31-41 vs 22-29); wider interorbital (width 20-25% vs 19% HL); and longer pectoral fin (19-23% vs 17% SL). The sagitta of A. inodorus (Figs 15, 16 & 22) is also distinct from that of A. amoyensis (Trewavas, 1977: Fig. 9b; Chu et al., 1963: Fig. 82); it is more elongate,



Figure 27. Relationship between caudal peduncle depth and SL for Argyrosomus inodorus (squares) and A. japonicus (circles).



Figure 28. Relationship between CPD (caudal peduncle depth) as % CPL (caudal peduncle length) and SL for Argyrosomus inodorus (squares) and A. japonicus (circles).

with a prominent bulge on posterior sector of ventral margin, rounded (vs straight) posterior margin, greater OCD, more elongate ostium with concave ventral and dorsal margins, and it lacks the protuberance on the posterodorsal corner in *A. amoyensis*.

A. inodorus differs from A. beccus Sasaki (1994) in having 10-12 lower gill-rakers (vs 8-9); swim-bladder appendages 31-41 (vs 23); longer snout (8-9% SL (vs 6.1-6.3% SL), snout convex (concave in A. beccus); eye diameter 5.8-7.3% SL (vs 7.3-8.3% SL, for fish of comparable size); wider interorbital 6.3-7.8% SL (vs 4.7% SL), and pelvic fin length 16-20% SL (vs 22-23% SL, for fish of comparable length). The sagitta of A. inodorus (Figs 15, 16 & 22) is easily distinguished from that of A. beccus (Sasaki, 1994: Fig. 2B); it is more elongate, with concave (vs convex) dorsal and ventral margins, a longer ostium, pronounced bulge in posterior third of ventral margin, angle of posterodorsal corner > 90° (vs 80-90°), posterior margin rounded (vs straight in *A. beccus*), OCD distinctly greater, and postcentral umbo on lateral surface of sagitta less than 50% of otolith length (about 75% in *A. beccus*).

Based on descriptions of *A. heinii* by Steindachner (1907) and Mohan, (1984), *A. inodorus* can be distinguished by lower limb gill-rakers 10-12 (vs 9); dorsal-fin rays 25-29 (vs 32-33) and an S-shaped (vs emarginate) caudal fin in adults.

Based on the description of A. miluy by Trewavas (1977), A. inodorus has lower limb gill-rakers 10-12 (vs



Figure 29. Relationship between urinary bladder length and TL for South African Argyrosomus inodorus (squares; n = 265) and A. japonicus (circles; n = 312).



Figure 30. Relationship between otolith length and TL for Argyrosomus inodorus (squares) and A. japonicus (circles).

9-10), snout length 24-30% HL (vs 22-24% HL), interorbital width 20-25% HL (vs 19-21% HL), upper jaw length 39-44% HL (vs 44-46% HL) and lower jaw length 47-51% HL (vs 53-55% HL). The swim-bladder appendages are much longer in *A. miiuy*, and at about 27 cm SL, almost completely enwrap the bladder (Trewavas, 1977). The caudal fin is also more elongate in *A. miiuy* than in *A. inodorus*, and at 305 mm SL is pointed (Chu et al., 1963) as opposed to S-shaped. Comparisons of the sagitta of *A. inodorus* (Figs 15, 16 & 22) and *A. miiuy* (Chu et al., 1963: Fig. 90; Schwarzhans 1993: Figs 239-240) reveal that the otolith of *A. miiuy* is more slender, with concave to straight (vs straight or convex) dorsal margin, posterodorsal corner more obtuse, posterior margin sharply rounded to pointed (vs rounded), the cauda is less curved, and the postcentral umbo on the lateral surface of the otolith is about 65% of the otolith length (less than 50% in *A. inodorus*).

ETYMOLOGY: *Inodorus*, Latin for "without smell". *A. inodorus* was first suspected of being a different species because it lacked the strong brassy/metallic smell that is typical of *A. japonicus* found in South African waters.

REMARKS: For many years *A. inodorus* has been confused with *A. japonicus* (as "*A. hololepidotus*"). However, based on the distribution patterns of the two species (this study), the catch localities, the sizes of the specimens examined and the descriptions of the caudal fin, it is almost certain that all of the authors mentioned in the synonymy (above)



Figure 31. Relationship between ostium to cauda distance and TL for Argyrosomus inodorus (squares) and A. japonicus (circles).



Figure 32. Relationship between OCD (ostium to cauda distance) as a ratio of OH (otolith height) and TL for Argyrosomus inodorus (squares) and A. japonicus (circles).

were inadvertently referring to A. *inodorus* (in part or in full).

DISTRIBUTION: A. inodorus occurs from Namibia southwards around the Cape of Good Hope and northwards at least as far as the Kei River (Fig. 7). In the area between the Kei River and Cape Agulhas, A. inodorus rarely enters estuaries or the surf zone, and is caught mostly by skiboat fishermen and trawlers at depths of 10-100 metres (Table 7). However, as one rounds Cape Agulhas and enters the cooler waters of the west coast, the species becomes more abundant in the surf zone. The proportion of A. inodorus in Argyrosomus catches declines in northern Namibia, where water temperatures are higher, and the species is not known in Angola.

FISHERIES: A. inodorus is highly regarded as a table fish (mostly sold fresh, but sometimes frozen) and it is an important commercial and recreational species wherever it is found. The majority of the South African catch is made between the Cape of Good Hope and the Kei River. Commercial line-fishermen operating from vessels of between 5 and 15 m in length, catch an average of 835 tons per annum (1988-1992). Although no statistics are available for recreational boat fishermen, their catches are expected to be of a similar magnitude. The South African trawl fishery is responsible for an average by-catch of 217 tons per annum, and Western Cape shore angling and beach seine catches are estimated at 26 and 4 tons respectively (Lamberth et al. 1994).

In Namibia A. inodorus is most abundant north of Meob (200 km south of Walvis Bay). Line-boat fishermen catch an average (1989/93) of 413 tons per annum (unpublished data, Namibian Ministry of Sea Fisheries), and shore anglers land in excess of 40 000 fish (approx. 130 tons) a year (Lenssen et al. 1991). Namibian A. inodorus are restricted to a narrow coastal band of 1-20 m, apparently as a result of an anoxic zone which extends beyond this depth (Hart & Curry, 1960; Boyd, 1983; Bailey et al., 1985).

BIOLOGY: In South Africa A. *inodorus* attains 50% sexual maturity at 31 cm TL (males) and 34 cm TL (females), with spawning activity observed throughout its distribution, from the Cape of Good Hope to the Kei River Mouth, during spring/summer (Griffiths & Hecht, 1993 [species B]). Nursery grounds consist of soft-bottom bay areas at depths less than 50 m (Wallace et al., 1984; Smale & Badenhorst, 1991; as "A. *hololepidotus*"). Maximum size recorded was 145 cm TL (36.3 kg). Common to 115 cm TL (15 kg).

Argyrosomus coronus sp. nov. (Fig. 35)

- Sciaena aquila (non Lacepède): Poll, 1954: 234 Fig. 71, Pl. II, Figs 2, 6 & 7 (Atlantic Ocean off Angola).
- Argyrosomus hololepidotus (non Lacepède): Trewavas, 1977: 327 (in part not figs); Chao & Trewavas, 1981: SCIAEN Argyr 3. Bianchi et al. 1993: 164 (in part).
- Holotype: RUSI 48468, female, 430 mm SL, northern Namibia, 4 km south of Hoarusib River, surf zone, collected by M.H. Griffiths, 15 March 1995.

Paratypes: 18 specimens (147-595 mm). ANGOLA. IISNB 9723 (J 202 mm, J 220 mm); IISNB 9724 (F 523 mm); IISNB 9725(J 147 mm). NORTHERN NAMIBIA. RUSI 48458 (F 408 mm); RUSI 48459 (F 385 mm); RUSI 48460 (F 440 mm); RUSI 48461 (M 408 mm); RUSI 48462 (F 408 mm); RUSI 48463 (M 424 mm); RUSI 48464 (M 361 mm); RUSI 48465 (F 365 mm); RUSI 48466 (M 595 mm); RUSI 48467 (M 471 mm); RUSI 48469 (F 355 mm); RUSI 48467 (M 281 mm); RUSI 48471 (M 312 mm); RUSI 48472 (M 370 mm); RUSI 48473 (M 495 mm, skeleton).

DIAGNOSIS: A species of *Argyrosomus* with the following combination of characters: dorsal fin rays 26-30; gillrakers 4-5 + 8-10; swim-bladder carrot shaped, with 28-38 arborescent appendages; caudal peduncle length 10-12% SL; peduncle depth 76-94% peduncle length; interorbital width 7.5-8.3% SL (24-27% HL); suborbital width 8.2-10.2% HL; lower jaw length 46-50% HL; midlateral body scale length 2.2-2.7% SL; drumming muscles present in both sexes; urinary bladders large; sagitta typically *Argyrosomus* (Fig. 11), OCD 26-34% OH; pectoral fins 18-21% SL, not reaching past vertical at tip of pelvic fins; pectoral fin axillary fold scaleless; peritoneum unpigmented; anterior part of lateral line slightly curved.

DESCRIPTION: Based on 19 preserved (147-595 mm), 7 fresh specimens (486-598 mm), one skeleton (495 mm) and 107 otolith pairs (281-1110 mm). Counts and measurements for the holotype are in parentheses.

Dorsal fin X+I,26-30 (27); anal fin II,7; pectoral-fin rays 16-18 (18); lateral-line scales 50-53 (51); gill-rakers 4-5 + 8-10; swim-bladder appendages 28-38; vertebrae 11 + 14.

Proportions as % SL: head length 31-32 (31); pre-dorsal length 33-36 (35); pre-pelvic length 33-36 (34); body depth 25-28 (27); caudal peduncle length 10-12 (12); peduncle depth 8.6-10 (10); snout 8.4-9.3 (9.2); eye diameter 6.7 at 147 mm, 5.2-6.0 at 202-281 mm, 4.7-5.0 at 312-385 mm, 4.2-4.7 (4.5) at 408-471 mm and 3.8-4.4 at 523-595 mm SL; interorbital width 7.5-8.3 (8.2); suborbital width 2.6-3.2 (2.9); upper jaw 12-14 (13); lower jaw 15-16 (15); pectoral fin 18-21 (20); pelvic fin 21 at 147 mm, 19-20 at 202-281 mm, 17-18 at 312-385 mm, 16-18 (17) at 408-471 mm and 15-18 at 523-595 mm SL; anal fin length 18 at 147 mm, 15-17 at 202-281 mm, 15-16 at 312-385 mm, 14-15 (15) at 408-471 mm and 13-14 at 523-595 mm SL; third dorsal spine 13-15 at 202-281 mm, 11-13 at 312-385 mm, 11-13 (13) at 408-471 mm and 11 at 595 mm SL; second anal spine 9.7 at 147 mm, 7.5-8.7 at 202-281 mm, 6.4-8.3 at 312-385 mm, 6.8-8.3 (7.2) at 408-471 mm and 5 at 595 mm SL; gill-raker 1.6-2.3; gill-filament 3.0-3.8.

Proportions as % HL: snout 27-31 (30); eye diameter 22 at 147 mm, 17-19 at 202-281 mm, 15-16 at 312-385 mm, 14-15 (14) at 408-471 mm and 14 at 523-595 mm SL; interorbital width 24-27 (27); suborbital width 8.2-10.4 (9.2); upper jaw 38-43 (43); lower jaw 46-50 (49); gill-raker 5.0-7.4; gill-filament 9.9-12.1.

Proportions as % eye diameter: gill-raker 31-53; gillfilament 56 at 147 mm, 60-62 at 202-281 mm, 65-73 at 312-385 mm, 67-78 at 408-471 mm and 83 at 523-595 mm SL.

Dorsal profile of *A. coronus* includes a hump or "shoulder" behind the head. Pectoral fins not reaching past vertical at tip of pelvic fins (for fish 147-595 mm). Nostrils as for *A. japonicus*. Caudal fin mostly S-shaped (281-595 mm), but sometimes wedge shaped, bi-concave or rounded. Lateral line evenly curved, axillary skin fold at base of pectoral fin scaleless.

Scales cycloid below eye, but ctenoid on body (including belly and chest), nape of neck, interorbital region, and operculum. Gill-rakers at angle shorter than outer gill-filaments at angle (281-593 mm). Drumming muscles well developed in both sexes. Pyloric caeca 8-10. Urinary bladders large, as in *A. japonicus*.

Swim-bladder (Fig. 36) carrot shaped with 28-38 appendages, each proximally divided into two limbs. The



Figure 33. Relationship between NCW (neurocranial width) and NCL (neurocranial length) for Argyrosomus inodorus (squares), A. japonicus (circles), A. coronus (triangles) and A. thorpei (crosses).



Figure 34. Relationship between SOCCRL (supraoccipital crest length) and SL for *Argyrosomus inodorus* (squares), *A. japonicus* (circles), *A. coronus* (triangles) and *A. thorpei* (crosses).



Figure 35. Argyrosomus coronus sp. nov., 368 mm TL, Angola (after Poll, 1954).

ventral limb is orientated lateroanteriorly, rather than ventroanteriorly and the branches arising from it project laterally and at no stage lie against the bladder. The dorsal limb is orientated dorsoposteriorly, but along the posterior three quarters of the bladder it curves through 150° so that the tip points anteriorly. The branches on this limb project posteriorly to dorsally and lie against the swim-bladder. In specimens with large quantities of appendage fat, the lateroanterior limb is orientated more ventroanteriorly and the branches arising from both limbs project at 90° to the bladder. The last 0-3 appendages bud-like and the 1-3 proceeding these weakly branched. Disproportionately enlarged appendages were not observed in any *A. coronus* (147-595 mm) examined by us.

Otoliths (Fig. 10): Description as for A. *japonicus*, but cauda more strongly curved (less angular) and posterior margin of cauda more rounded; OCD 26-34% OH.

Neurocranium (Figs 4 & 5) and skeleton: Length of neurocranium (NCL) 21% SL; pre-supraoccipital crest length 11% SL and 52% NCL; supraoccipital crest length

9.1% SL and 44% NCL (495 mm); neurocranial width 8.4% SL and 41% NCL. Interorbital septum relatively well ossified with frontal fused with medial ethmoid and parasphenoid bones. Premaxilla 7.7% SL and 37% NCL; dentary 9.2% SL and 44% NCL. Third and fourth neural spines 8.9 and 8.3% SL.

Colour: In life, silvery grey/brown becoming darker above and lighter below; dorsal surface with a bluish bronze sheen that may become coppery on head. Some individuals darker brown than others; fins dark grey/brown; mouth lining yellow, some with a touch of grey; inside of operculum yellow and dark grey. Axillary fold of pectoral fin grey to black, generally with an irregular coppery-bronze patch.

Preserved specimens vary, usually grey, darker above and lighter below. Dark patches on scales may give appearance of oblique stripes. Fins grey, sometimes with one or two longitudinal stripes on dorsal fin.

COMPARISONS (Tables 2-6): A. coronus generally has a more pointed head (resulting from a less convex snout, Fig.



Figure 36. Swim-bladder of Argyrosomus coronus, 360 mm SL: A) lateral view and B) ventral (left half) views.

35) than the other species described in this paper, including *A. regius* (Figs 9, 12, 19 & 21).

A. coronus differs from A. regius in having a higher modal number of lower limb gill-rakers; a slightly longer lower jaw; longer midlateral scales (Fig. 37); a shorter and deeper caudal peduncle (Fig. 38); fewer arborescent swimbladder appendages, in which the lower limb is orientated latero-anteriorly (vs ventro-anteriorly) with branches that project at 90° to the bladder (vs project posteriorly and lie against the bladder). The otoliths of A. coronus are more elongate (Figs 10 & 39) than those of A. regius; the cauda is more curved, with a more rounded posterior margin (Fig. 40); and the curvature of the posterior margin of the ostium is more acute.

Differences between A. coronus and A. japonicus include a lower modal number of upper gill-rakers, a higher modal number of pectoral fin rays, a wider interorbital (Fig. 18), shorter lower jaw; a wider neurocranium (Fig. 33), with wider lateral line canals on the dorsal surface (Fig. 5); and a shorter pre-maxilla (7.7% vs 8.1-8.8% SL) and dentary (9.2% vs 9.3-10.1% SL). A. coronus also has more arborescent swim-bladder appendages, and in the posterior half of the bladder the lower limbs are orientated anterolaterally (vs anteroventrally) with branches projecting at 90° to the bladder (vs projecting posteriorly and lying against the bladder, Figs 13, 14 & 36). The saggitta of A. coronus has a more strongly curved cauda, which is less angular, and has a more acutely rounded posterior margin (Figs 10 & 15). Fresh specimens of A. coronus also lack the strong metallic odour of South African A. japonicus.

A. coronus differs from A. hololepidotus in having a wider interorbital (Fig. 18), a narrower suborbital, and a shorter and deeper caudal peduncle. The saggitta of A. coronus (Fig. 10) has a more strongly curved cauda, which is less angular, and has a more rounded posterior margin than that of A. hololepidotus (Fig. 15).

Differences between A. coronus and A. thorpei include fewer lower limb gill-rakers, a higher modal number of pectoral fin rays and swim-bladder appendages, a wider interorbital, a narrower suborbital, a naked (vs scaled)



Figure 37. Relationship between scale length and SL for *Argyrosomus regius* (circles) and *A. coronus* (squares).

pectoral axillary fold, a shorter caudal peduncle, shorter midlateral body scales, and a slight (vs strong) anterior curve of the lateral line. The sagitta of *A. coronus* is not expanded in the anterior two-thirds, it has a more acute posterodorsal angle, a cauda which is neither expanded in the distal portion nor truncated at the tip, and a shorter OCD (Figs 11 & 15).

A. coronus differs from A. inodorus in having lower modal numbers of upper and lower gill-rakers, a lower modal number of swim-bladder appendages, a wider interorbital (Fig. 41 and Table 2), a shorter and deeper caudal peduncle (Fig. 42 and Table 2), a smaller orbital diameter



Figure 38. Relationship between CPD (caudal peduncle depth) as % CPL (caudal peduncle length) and SL for Argyrosomus regius (circles) and A. coronus (squares).



Figure 39. Relationship between otolith length and SL for *Argyrosomus regius* (circles) and *A. coronus* (squares).

(Fig. 43), larger urinary bladders, drumming muscles in both sexes (vs in males only), a longer supraoccipital crest (Fig. 34 and Table 2), a smaller interorbital window (frontal and parasphenoid bones connected, Fig. 4) and shorter premaxilla (7.7 vs 8.1-9.1% SL) and dentary (9.2 vs 9.3-10.2% SL). The sagitta of *A. coronus* (Fig. 10) has a more acute posterodorsal angle, a smaller OCD (Fig. 44), a lower OCD:OH ratio (Fig. 45), a straight (vs rounded) posterior margin, and it lacks the prominent bulge found on the ventral margin in *A. inodorus* (Fig. 15). *A. coronus* is generally darker and more brown in colour (body) than *A. inodorus*, and the fins are dark grey/brown (vs yellow/grey).



Figure 40. Superimposed sagittae of Argyrosomus regius, 516 mm TL (solid line) and A. coronus, 512 mm TL, (broken line).

A. coronus was also compared with data and illustrations of A. amoyensis (from Trewavas, 1977; Mohan, 1984 and the original description of Nibea miichthioides Chu et al., 1963). A. coronus differs in having 8-11 (vs 8) lower gill-rakers, interorbital width 24-27% HL (vs 19% HL). The swim-bladder of A. amoyensis is spindle shaped (tapering anteriorly and posteriorly), there are only 22-29 appendages (vs 28-38), and they are not obviously divided into dorsal and ventral limbs. The sagitta of A. coronus (Fig. 10) is similar to that of A. amoyensis (Trewavas, 1977: Fig. 9b; Chu et al., 1963: Fig. 82), but it is slightly more elongate, has a more strongly curved (less angular) cauda, and lacks the protuberance found on the posterodorsal corner in A. amoyensis.

A. coronus differs from A. beccus Sasaki (1994) in having swim-bladder appendages 28-38 (vs 23); longer snout (8.4-9.3% vs 6.1-6.3% SL), snout convex (concave in A. beccus); eye diameter 5.2-6.7% SL (vs 7.3-8.3% SL, for fish of comparable size); wider interorbital 7.5-8.3% SL (vs 4.7% SL), and pelvic fin length 19-21% SL (vs 22-23% SL, for fish of comparable length). The sagitta of A. coronus (Fig. 10) is distinguished from that of A. beccus (Sasaki, 1994: Fig. 2B); in that it is more elongate, with a longer ostium, a more strongly curved cauda, and the postcentral umbo on the lateral surface of the otolith is less than 50% of the otolith length (about 75% in A. beccus).

Based on descriptions of *A. heinii* by Steindachner (1907) and Mohan (1984), *A. coronus* can be distinguished by dorsal-fin rays 26-30 (vs 32-33) and an S-shaped (vs emarginate) caudal fin in medium sized fish.

Based on the description of A. miluy by Trewavas (1977), A. coronus has snout length 27-31% HL (vs 22-24%) HL), interorbital width 24-27% HL (vs 19-21% HL), upper jaw length 38-43% HL (vs 44-46% HL) and lower jaw length 46-50% HL (vs 53-55% HL). The swim-bladder appendages are much longer in A. miiuy, and at about 27 cm SL, almost completely enwrap the bladder (Trewavas, 1977). The caudal fin is also more elongate in A. miiuy than in A. coronus, and at 305 mm SL is pointed (Chu et al., 1963) as opposed to S-shaped. Comparisons of the sagitta of A. coronus (Fig. 10) and A. miiuy (Chu et al., 1963: Fig. 90; Schwarzhans, 1993: Figs 239-240) reveal that the otolith of A. miluy is more slender, with concave or straight (vs straight or convex) dorsal margin, sharply rounded or pointed (vs straight) posterior margin, posterodorsal corner more obtuse, cauda less curved, and the postcentral umbo on the lateral surface of the otolith about 65% of the otolith length (less than 50% in A. coronus).

ETYMOLOGY: This species is named Argyrosomus coronus in honour of Corona Griffiths, wife of the first author, in appreciation of her contributions to the illustrations of this paper and her help with field work. The specific name is treated as a noun in apposition.

REMARKS: Although morphometric differences between A. coronus and A. regius are subtle, and possibly would not justify species recognition, we have placed much weight on swim-bladder appendage counts, and on differences in otolith morphology for the following reasons: Swim-bladders of A. regius specimens from the Mediterranean, French



Figure 41. Relationship between interorbital width as % HL and SL for *Argyrosomus coronus* (circles) and *A. ino-dorus* (squares).

Atlantic and north Africa provided no evidence for a cline in appendage counts. Counts of *A. coronus* specimens from Namibia and Angola were also similar. In addition the numbers of appendages of other *Argyrosomus* species were found to be consistent over wide distributional ranges e.g. *A. japonicus* from South Africa, Australia and Japan; and *A. inodorus* from the eastern seaboard of South Africa and from central Namibia. Differences in the morphology of the otoliths of specimens from the northern and southern hemispheres were also regarded as important because these structures often do not differ between recognized *Argyrosomus* species e.g. *A. regius*, *A. japonicus* and *A. hololepidotus*.

The recognition of *A. coronus* as a separate species also assists with species identification in Namibia. This species has a shorter and deeper caudal peduncle and a lower number of swim-bladder appendages than *A. regius*, and together with interorbital width is therefore more easily separated from *A. inodorus*.

DISTRIBUTION: Known from Namibia and Angola. It becomes more abundant in *Argyrosomus* catches as one moves northwards (Table 7) indicating that it prefers warmer waters. Found in estuaries, the surf zone and further offshore. Reports of "*A. hololepidotus*" from the west coast of Africa, south of the equator (Trewavas, 1977; Mohan, 1984; Heemstra, 1986), are probably based on specimens of *A. coronus*.

FISHERIES: In Namibia A. coronus is caught by commercial and recreational fishermen in fairly low numbers. Areas further north are closed to the public. In southern Angola it is caught with hand lines, gillnets, trapnets and occasionally purse seines; mostly in depths of 20-40 m, but also in the surf zone and in depths to 100 m (B.Bennett pers comm).



Figure 42. Relationship between CPD (caudal peduncle depth) as % CPL (caudal peduncle length) and SL for *Argyrosomus coronus* (circles) and *A. inodorus* (squares).

BIOLOGY: The biology of this species has not been studied. Personnel of the Namibian Ministry of Sea Fisheries found fish up to 13 kg to be immature, suggesting a large size at maturity, similar to that of *A. japonicus* and *A. regius*. Adults are rarely found in Namibia but according to Bruce Bennett (pers comm) are abundant in southern Angola (common to 50 kg). Maximum size 77 kg. The lack of permanent estuaries in southern Angola suggests that this habitat type does not play an important role in the life history of *A. coronus*.



Figure 43. Relationship between orbital diameter and HL for *Argyrosomus coronus* (circles) and *A. inodorus* (squares).



Figure 44. Relationship between OCD (ostium to cauda distance) and TL for *Argyrosomus coronus* (circles) and Namibian *A. inodorus* (squares)



Figure 45. Relationship between OCD (ostium to cauda distance) as a ratio of OH (otolith height) and TL for Argyrosomus coronus (circles) and Namibian A. inodorus (squares).

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Table 1. Regression equations for data from *Argyrosomus japonicus* (J) and *A. inodorus* (I) from South African waters for weight/total length (W/TL), otolith dimension/TL, and standard length/total length (SL/TL) relationships. OL = otolith length, OH = otolith height, OC = ostium to cauda distance and OW = otolith weight. The asterisk (*) denotes a significant difference (P < 0.01) between the slopes and/or intercepts of the corresponding relationships, after log - transformation.

	Relationship	r	n	Range (TL)	F-ratio	Р
J	$W(g) = 8.391 \times 10^{-6} TL (mm)^{3.025}$	0.999	1215	37-1750 mm	29.6	<0.0001*
I	$W(g) = 6.832 \times 10^{-6} TL (mm)^{3.055}$	0.997	3146	60-1378 mm		
J	$OL(mm) = TL(mn)^{0.706}/5.678$	0.995	543	37-1750 mm	1238.3	<0.0001*
I	$OL(mm) = TL(mm)^{0.699}/4.691$	0.993	623	60-1310 mm		4
J	$OH(mm) = TL(mm)^{0.630}/5.931$	0.989	542	37-1750 mm	19.0	<0.0001*
I	$OH(mm) = TL(mm)^{0.603}/4.932$	0.990	623	60-1310 mm		
J	$OC(mm) = TL(mm)^{0.589}/14.821$	0.969	539	50-1750 mm	3251.2	<0.0001*
I	$OC(mm) = TL(mm)^{0.607}/10.717$	0.972	616	60-1310 mm		
J	$OW(g) = TL(mm)^{2.008}/479004$	0.989	542	37-1750 mm	138.6	<0.0001*
I	$OW(g) = TL(mm)^{1.896}/195344$	0.989	623	60-1310 mm		
J	SL = 0.877 TL - 10.882	0.999	167	35-1790 mm	-	-
I	SL = 0.886 TL - 14.882	0.999	408	140-970 mm	-	-

Table 2. Diagnostic characters of *Argyrosomus* species. CPD = caudal peduncle depth, CPL = caudal peduncle length, F = female, M = male, OCD = ostium-cauda distance, OH = otolith height,*Argyr.*= as for*A. regius*.

	hololepidotus	inodorus	japonicus	regius	coronus	thorpei
Gill-rakers (lower limb)	9	10-12	9-11	8-10	8-10	10-11
Swim-bladder appendages	34-36	32-41	21-31	36-45	28-38	25-33
Interorbital width (%HL)	22-23	20-25	21-24	24-29	24-27	20-21
Suborbital width (%HL)	10.5-12	8.6-10.9	8.4-10.5	8.5-11	8.2-10.2	10-11.5
Lower jaw length (%HL)	50	46-51	48-52	44-48	46-50	49-53
CPD as %CPL	75-77	58-74	70-92	68-82	76-94	65-79
CPL as %SL	12-13	12-15	11-13	11-13	11-12	12-14
Pectoral fin length (%SL)	17-18	19-23	17-21	18-21	17-21	20-23
Midlateral body scale length (%SL)	2.5-2.8	1.8-2.5	2.4-3.1	1.8-2.3	2.2-2.7	2.6-3.3
Supraoccipital crest length (%SL)	-	8.0-8.8	9.2-10.2	-	9.1	
Urinary bladder length (%TL)	large	0.1-3.3	2.0-9.6	large	large	large
OCD as %OH	28-34	37-63	23-41	26-32		34-44
Otolith morphology	Argyr.	distinct	Argyr.	Argyr.	Argyr.	distinct
Anterior curve of lateral 'line	slight	slight	slight	slight	slight	strong
Pectoral fin axillary fold	scaleless	scaleless	scaleless	scaleless	scaleless	scaly
Drumming muscles	M & F	M only	M & F	M & F	M & F	M & F

Table 3. Frequency distributions for swim-bladder appendage counts in Argyrosomus hololepidotus (H), A. inodorus (I), A. japonicus (J), A. coronus (C), A. regius (R), and A. thorpei (T).

																			_	_							
										S	wim-	bla	dde	r ap	pen	dage	es										
	n	x	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
н	3	35														1	1	1									
I	77	35.8											1	3	9	9	15	8	10	7	7	4	3	2			
J	63	26.3	1	2	6	6	12	5	15	5	4	6	1														
с	24	31.9								3	4	2	1	4	4	2	1	1	1	1							
R	23	39.3																3	4	2	1	5	3	2	1	1	1
т	18	29.4					1	1		3	3	4	4	2													

Table 4. Frequency distributions for meristic characters in Argyrosomus hololepidotus (H), A. inodorus (I), A. japonicus (J), A. coronus (C), A. regius (R) and A. thorpei (T)..

	U	pper G	111-ra	akers					L	ower	Gill-1	akers			
	n	x	3	4	5	6		n	x	8	9	10	11	12	
н	3	4.7		1	2		н	3	9		3				
I	76	5.2		1	59	16	I	76	11			17	48	11	
J	66	4.6		24	42		J	66	9.9		11	51	13		
с	25	4.1		23	2		с	25	9.5	1	11	12	1		
R	17	4.3	1	10	6		R	19	9.1	1	16	2			
т	18	5.1		1	15	2	т	18	11.1			1	15	2	
	I	ectora	l fin	-rays						Dorsa	l fin	-rays			
	n	x	15	16	17	18		n	x	25	26	27	28	29	30
н	2	16.5		1	1		н	3	27.3			2	1		
I	393	16.5	11	193	185	4	I	381	27.1	10	85	160	99	26	1
J	68	16.1	3	50	12		J	61	26.7	4	28	23	12	2	
с	23	16.7	1	5	16	1	с	24	27.2		5	12	5	1	1
R	19	16.9		5	11	3	R	18	27.6	1	1	6	6	3	1
					•			10	07.1		2		2	1	
т	18	16	3	12	3		Т	18	27.1		3	11	2	1	

Table 5. ANOVA: Multiple range tests of meristic characters that show significant differences (P < 0.0001). Mean values increase from left to right; * indicates a significant difference at the 1% level and # a difference at the 5% level. *Argyrosomus inodorus* (I), *A. japonicus* (J), *A. regius* (R), and *A. thorpei* (T).

Table 6. ANOVA: Multiple range tests of arc-sine transformed morphometric ratios that show significant differences (P < 0.0001). Mean values increase from left to right; * signifies a difference significant at the 1% level and # a difference at the 5% level. *Argyrosomus inodorus* (I), *A. japonicus* (J), *A. regius* (R), and *A. thorpei* (T).

Character	Species
Pectoral fin-rays	<u>T J</u> * I # R
Gill-rakers (upper)	R * J * <u>T I</u>
Gill-rakers (lower)	R * J * <u>I T</u>
Swim-bladder appendages	J * T * I * R

Character	Species
Suborbital width	J * <u>I R</u> * T
Interorbital width	<u>j t i</u> * r
Pre-dorsal length	I * <u>T J R</u>
Body depth	<u>I R</u> * J # T
Caudal peduncle length	J # R * <u>T I</u>
Caudal peduncle depth	<u>i r</u> * <u>t j</u>
Scale height	R * I * J * T
Scale length	<u>R I</u> * <u>J T</u>
Gill-raker length	<u>R J I</u> * T

Table 7. The distribution of South African Argyrosomus species, based on relative contributions (% by number) to catches made in four habitat types of 10 regions (see Fig. 7 for regional boundaries). A. inodorus (I), A. japonicus (J), A. coronus (C), A. thorpei (T).

	Estuary	Surf zone	Nearshore reef	Nearshore sand/mud
S. Mozambique	-	-	99.8%T:0.2%J (n=1021)	-
N. Natal	100% J (n=45)	35 %T:65%J (n=32)	95% T: 5% J (n=557955)	100% T (n=832)
S. Natal	100% J (n=13)	100% J (n=36)	85%T:15%J (n=87456)	-
Transkei	100% J (n=410)	100 %J (n=16)	-	-
E. Cape	100% J (n=670)	98% J: 2%I (n=590)	1.3% J: 98.7% I (n=2629)	100% I (n=1050)
S. Cape	100% J (n=168)	100% J (n=58)	1.5% J: 98.5% I (n=22128)	100% I (n=1473)
S.W. Cape	Rare	3.3% J: 96.7% I (n=333)	100%I (n=558)	100%I (n=33)
W.Cape	Rare	100%I (n=9)	100% I (n=42)	Rare
S. Namibia	no estuaries	100% I (n=229)	-	-
C. Namibia	no estuaries	93% I:7%C (n=740)	100% I (n=225)	100% I (n=52)
N. Namibia	no estuaries	50%1:50%C (n=408)	100% I (n=220)	-
S. Angola	-	100% C (n=30)	100% C (n=10)	100% C (n=6)

Table 8. Arcsine-transformed morphometric ratios for *A. inodorus* and *A. japonicus* that showed significant difference (ANOVA) only when analysed according to size class. 1 = 100-199 (n = 7+10), 2 = 200-299 (n = 28+13), 3 = 300-399 (n = 21+13), 4 = 400-499 (n = 6+11), 5 = 500-599 (n = 4+5) * = 5% level (p<0.05), ** = 1% level (p<0.01). Size class ranges are of mm SL.

Character	Size	clas	3 8 es	(100mm)	
	1	2	3	4	5
Eye diameter	*	**	**	*	*
Pectoral fin length			**	*	*
Anal fin length		**	**	٠	

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STYLE OF THE HOUSE

Hyphens: Certain substantive compounds are hyphenated: gill-raker, soft-ray, swim-bladder, type-species, type-locality, type-series, type-specimen. Other words often used together are not hyphenated unless they are used in adjectival expressions before a noun: anal fin / anal-fin rays; lateral line / lateral-line scales; gill arch / gill-arch filaments, etc.

Word usage: Although the following word pairs are often used interchangeably, we believe that consistent use of the first word as a noun and the second as an adjective will improve the precision of our writing: mucus / mucous; maxilla / maxillary; opercle / opercular; operculum / opercular. The operculum (= gill cover) comprises (usually) four separate bones: opercle, subopercle, preopercle and interopercle. The words preoperculum, suboperculum and interoperculum are unnecessary substitutes and not to be used for preopercle, subopercle and interopercle. The plural of operculum is opercula.

Decimal comma versus decimal point: Contrary to most journals published in South Africa and some European countries, we will not use a comma in place of a decimal point. Most computers do not read a comma as a decimal point. In addition, it is common in ichthyological papers to give sequences of measurements that include decimal numbers, with each measurement separated by a comma. If the comma is used to separate items in a series, as well as being used to indicate a decimal number, it will cause considerable confusion.

Fin formulae: Fin formulae will be designated as follows: D XII, 10-12 indicates one continuous fin with 12 spines and 10-12 soft (segmented) rays; D X/I, 10-12 indicates a fin divided to the base in front of the last spine; and D X+I, 12 indicates two separate dorsal fins, the first with 10 spines and the second with 1 spine and 12 soft rays. If it is necessary to differentiate branched and unbranched soft-rays, lower-case Roman numerals will be used for unbranched rays and Arabic numerals for branched rays, e.g. D iii,8. Principal caudal-fin rays are defined as those that touch the hypural bones. The number of principal caudal rays is usually the number of branched rays plus two. If the principal caudal rays are in two separate groups, the number of rays in the dorsal group is given first: thus, "principal caudal rays 8+7" means that there are 15 principal caudal rays, with 8 rays in the dorsal group and 7 in the ventral group.

Abbreviations: Abbreviations normally end with a full stop: et al., e.g., etc., n.b., (note: these commonly used abbreviations of Latin words are not italicized). Compass directions (north, west, northwest, etc.) are abbreviated using capital letters without the full stops: N, W, NW. Dr (Doctor) and Mr (Mister) will be used without a period. We recommend the following abbreviations for ichthyological terms: Standard length — SL, total length — TL, gill-rakers — GR, lateral line — LL.