Systematics of *Callogobius* (Teleostei: Gobiidae)

by

Naomi Rachel Delventhal

A Thesis submitted to the Faculty of Graduate Studies of
The University of Manitoba
in partial fulfillment of the requirement of the degree of

DOCTOR OF PHILOSOPHY

Department of Biological Sciences
University of Manitoba
Winnipeg

Abstract

Callogobius is a large genus of gobies characterized by fleshy ridges of papillae on the head in both horizontal and vertical rows. The taxonomy and phylogenetics of the genus are difficult and poorly understood. The purpose of my research is to better categorize the diversity within *Callogobius* by identifying and describing morphological characters and using them to aid species identification and discovery of monophyletic sub-groups within the genus. In this thesis, I construct separate phylogenetic hypothesizes for the intrarelationships of *Callogobius* using morphological and molecular data, respectively. Parsimony analysis using morphological characters (external anatomy and osteology) supports the presence of three monophyletic groups within *Callogobius*, the *hasseltii*, *sclateri* and *maculipinnis* groups. A fourth group, the *tutuilae* group, contains several species, at least some of which share some characters with members of the *sclateri* group. A molecular phylogenetic approach using four genes (*zic1,* a partial fragment containing *12S*, $tRNA^{Val}$ and *16S*, *rag1* and *sreb2*) and analyzed using maximum parsimony, maximum likelihood and Bayesian inference supports the monophyly of *Callogobius*, the *hasseltii*, *sclateri* and *maculipinnis* groups; the *tutuilae* group is resolved as paraphyletic with respect to the *sclateri* group. Reductive traits, such as small size and loss of head pores appear to have evolved multiple times independently. In addition to phylogenetic analyses, I address some of the taxonomic issues within *Callogobius* through the descriptions of two new species, *C. winterbottomi* and *C. pilosimentum*, a redescription of *C. clarki*, removal of *Gobiopsis liolepis* from *Callogobius*, and a regional review of the Red Sea species (including a key). My taxonomic and phylogenetic study demonstrates that it is possible to find concordance between multiple methods even in taxa characterized by diversity and reductive characters.

Acknowledgements

As I finish this dissertation, I feel the desire to thank just about everyone with whom I've interacted in the last twelve years since I've started my degree. For the sake of brevity, however, I'll keep this section short and concise.

I am grateful to the continuous support from my advisor R. Mooi and my committee members B. Ford, J. Hare and B. Sharanowski. Their suggestions, along with those of my external examiner L. Parenti, have greatly improved the final version of this dissertation.

I received funding from the University of Manitoba Graduate Fellowship, an NSF Graduate Research Fellowship, a field work grant from the Leonard P. Schulz fund, and a grant from the Foundation for Science and Disability. A. Gill provided additional financial aid through an NSF grant and R. Mooi provided financial support through an NSERC Discovery Grant 327844-06.

I am indebted to countless individuals for loan of specimens and/or hosting my visits (institutional names abbreviated following Fricke & Eschmeyer [2017]). These individuals include, but are not limited to: M. Sabaj Pérez (ANSP), K.-T. Shao (ASIZP), Y. Ikeda (BLIP), J. Maclaine (BMNH), A. Suzumoto (BPBM), H. Endo (BSKU), D. Catania (CAS), M. Rogers (FMNH), D. Golani (HUJ), H. Wellendorf (NMW), K. Matsuura (NSMT), G. Shinohara (NSMT), I-S. Chen (NTOUP), M. van Oijen (RMNH), R. Winterbottom (ROM), O. Gon (SAIAB), T.J. Alpermann (SRI), L. Parenti (USNM), J. Williams (USNM), S. Morrison (WAM), K. Hagiwara (YCM), N. Bogutskaya (ZIN), Z. Jaafar (ZRC) and R. Barman (ZSI).

I thank J.Van Tassell, R. Robertson, I-S. Chen & students, U. Satapoomin & staff, M. Aizawa, and Y. Ikeda for putting up with me on field trips to collect gobies. H. Ho took me to collect specimens from the fish markets in Taiwan. I have enjoyed many interesting and helpful

conversations about *Callogobius* taxonomy; in particular I thank A. Gill, H. Larson, R. Winterbottom, D. Hoese, J. Williams, Y. Ikeda, and Akihito.

I am grateful to Department of Biological Sciences support staff M. Stopchyki (nee Foster) and J. Stringer, who tirelessly problem-solve for graduate students. I thank J. Anderson (former Department Head, Biological Sciences) for her understanding and support as I completed my Ph.D. amidst unforeseen challenges. I would not have been able to complete my degree without assistance from the University of Manitoba Accessibility Services; in particular I am grateful to L. Banash, J. Duong, A. Matheson and J. Cordovan. L. McDonald assisted in data collection from *C.* sp. 20, and K. Gardner helped with creating tables. J. Klapecki provided support at the Manitoba Museum. Finally, I thank my family for their support and patience with me over the years.

TABLE OF CONTENTS

Abstract ii
Acknowledgments iii
Table of contents v
List of tables viii
List of figures x

Chapter One. Introduction 1
  Challenges in *Callogobius* alpha taxonomy 3
  History of *Callogobius* phylogeny 4
  Research objectives and approach 6
  Chapter outline 7

Chapter Two. Intrarelationships of *Callogobius* (Teleostei: Gobiidae): a morphological perspective 9
  SUMMARY 10
  INTRODUCTION 11
  METHODS 13
    Taxon selection 14
    Character selection and coding 15
    Phylogenetic analysis 16
  RESULTS 17
    Character descriptions 19
    Phylogenetic hypotheses 57
    Description, membership and phylogenetic diagnoses of proposed *maculipinnis*, *sclateri* and *hasseltii* groups 61
    tutuilae group (unassigned species) 67
  DISCUSSION 69
  MATERIAL EXAMINED 72

Chapter Three. Molecular phylogenetics of *Callogobius* (Teleostei: Gobiidae) 74
  SUMMARY 75
  INTRODUCTION 76
  METHODS 82
    Gene sampling and DNA sequencing 86
    Sequence assembly, alignment and substation model selection 87
    Phylogenetic inference 87
  RESULTS 89
  DISCUSSION 95

Chapter Four. *Callogobius winterbottomi*, a new species of goby (Teleostei: Gobiidae) from the Western Indian Ocean 98
SUMMARY 99
INTRODUCTION....100
MATERIALS AND METHODS 101
  Meristics 101
  Morphometrics 102
  Sensory papillae rows....103
Callogobius winterbottomi sp. nov 104
DISCUSSION 114

Chapter Five. Redescription of *Callogobius clarki* (Goren) (Teleostei: Gobiidae), not a synonym of *C. bifasciatus* (Smith) 116
SUMMARY 117
INTRODUCTION....118
METHODS....119
Callogobius clarki (Goren 1978) 122
DISCUSSION 130
MATERIAL EXAMINED....131

Chapter Six. *Callogobius liolepis* Bleeker, a senior synonym of *Gobiopsis aporia* Lachner and McKinney (Teleostei: Gobiidae: *Gobiopsis*)....133
SUMMARY 134
INTRODUCTION....135
MATERIAL EXAMINED....136
METHODS....138
RESULTS....138
SYNONOMY OF *Gobiopsis liolepis* (BLEEKER) 143
DISCUSSION 144
BLEEKER'S UNPUBLISHED DESCRIPTION OF *Callogobius liolepis* WITH TRANSLATION 148

Chapter Seven. A review of the *Callogobius* (Teleostei: Gobiidae) from the Red Sea with the description of a new species 152
SUMMARY 153
INTRODUCTION..154
MATERIALS AND METHODS 155
Callogobius pilosimentum sp. nov. 157
Callogobius amikami Goren, Miroz & Baranes...169
Callogobius clarki (Goren 1978) 174
Callogobius dori Goren 1981...178
Callogobius flavobrunneus (Smith 1958) 181
Callogobius sclateri (Steindachner 1879)...184
DISCUSSION 187
Key to seven *Callogobius* species of the Red Sea 188

Chapter Eight. Discussion and conclusions..190
Why challenges remain in *Callogobius* taxonomy 191
How my research contributes to *Callogobius* alpha taxonomy on a broader level.................192
The evolution of small size and pore loss in *Callogobius*...194
Conflict between morphological and molecular data...197

References...199

Appendix A. The status of nominal *Callogobius* 212

LIST OF TABLES

TABLE 2.1 Morphological data matrix with 55 characters scored for 16 *Callogobius* species and two outgroup species (*Yongeichthys criniger* and *Drombus* sp.). Numbers in the columns (0, 1, or 2) indicate coded character states; a question mark (?) in the columns indicate that the character is variable or inapplicable. For reference, species in the outgroup are not highlighted, species in the *maculipinnis* group are highlighted in dark grey, species in the *tutuilae* group are highlighted in medium grey, species in *sclateri* group are highlighted in light grey, and species in the *hasseltii* group are highlighted in very light grey.

TABLE 3.1 Genus and species of specimens used in this study, their Lukas Rüber (LR) tissue collection number, and collection locality.

TABLE 3.2 *Callogobius* species sampled in this study with comparison of their species-group designation of McKinney (1980) and Delventhal & Mooi (unpublished, Chapter 2).

TABLE 4.1 Selected measurements of the holotype and two paratypes of *Callogobius winterbottomi* in mm; the values in parentheses indicate the percentage of standard length (SL) or head length (HL).

TABLE 4.2 Akihito & Meguro's (1977) numbering system for *Callogobius* sensory papillae rows, followed by our assigned descriptive names. The intermandibular row was not originally identified by Akihito & Meguro (1977), but incorporated here as Row 24. Asterisks indicate those rows that are particularly useful in describing interspecific variation in *Callogobius* and are commented on in the description of *C. winterbottomi*. Two groups of papillae rows (usually less well defined; ridges may or may not be raised) are found on the temporal and posttemporal/predorsal regions; we refer to these as the temporal and posttemporal groups, respectively. These rows are illustrated but not labelled in Figure 4.5.

TABLE 5.1 Selected morphometric characters for *Callogobius clarki* and *C. bifasciatus*. The holotype values of *C. clarki* are compared with values of a similarly sized specimen of *C. bifasciatus* (BMNH 2000.4.19.761) as the holotype of the latter is a small juvenile in poor condition. Pooled values are presented as averages followed by range in parentheses. Values for specimens smaller than 15 mm SL (standard length) are not included.

TABLE 5.2 Pectoral-fin ray count frequencies for *Callogobius clarki* (n = 21) and *C. bifasciatus* (n = 22). Holotype values are marked by *. Bilateral counts included when available.

TABLE 5.3 Lateral scale count frequencies for *Callogobius clarki* (n = 18) and *C. bifasciatus* (n = 21). Holotype values are marked by *. Bilateral counts included when available.

TABLE 5.4 Predorsal and transverse scale count frequencies for *Callogobius clarki* (n = 17) and *C. bifasciatus* (n = 20 for predorsal and 21 for transverse). Holotype values are marked by *; that of transverse series for *C. bifasciatus* from Smith (1958) as specimen condition did not permit counts at time of our observation.

TABLE 5.5 Transverse mandibular papillae row (Row 16) count frequencies for *Callogobius clarki* (n = 19) and *C. bifasciatus* (n = 14); counts taken bilaterally. Holotype values for *C. clarki* are marked by *; counts were not taken from the holotype of *C. bifasciatus* at time of observation.

TABLE 6.1 Selected distinguishing characters comparing the lecto- and paralectotype of *Gobiopsis liolepis* (Bleeker) with the most similar species of *Gobiopsis* as presented in Lachner and McKinney (1978); all other *Gobiopsis sensu stricto* have scale and pectoral-fin ray counts that are too low. Koumans (1932) reported ± 45 LL (lateral line) scales for Bleeker's specimens, Bleeker about 45. Modes are presented in parentheses (when available); LL scale and pectoral-fin ray counts for types are provided for left and right sides, respectively; ? = not observed in type specimens, presumably due to poor condition.

TABLE 7.1 Selected measurements of the holotype and paratypes of *Callogobius pilosimentum sp. nov*.; standard length is provided in mm, values for other morphometrics are as percentage of standard length (SL) or head length (HL), as indicated. For paratypes, the range is followed by an average value for all types in parentheses. The two largest specimens (63 and 67 mm SL) were males (M), the next 3 largest specimens (55.8, 50.3, 49.3 mm SL) were females (F).

TABLE A.1 Nominal species of *Callogobius*, their current or provisional allocation, catalog numbers of type materials, and status of holotype (examined/not examined by the present author, missing or destroyed.) All species marked as "uncertain" under the "Current allocation" column include in parentheses a possible senior synonym, however, it is probable that many of these uncertain species will prove to be valid with continued investigation.

LIST OF FIGURES

FIGURE 2.1 Lateral view of the external sensory system of the head in two *Callogobius* species. Headpores are indicated diagrammatically, rather than as short tubes; headpores and papillae rows are labelled following Delventhal et al. (2016, Chapter 7) and Delventhal & Mooi (2013, Chapter Four). Scale bars = 2 mm. **A.** *C. pilosimentum* (SMF 35756, 36.4 mm SL female holotype) showing the preopercular canal (Char. 6, state 0), the temporal canal (Char. 7, state 0) and transverse mandibular rows in groups of four (Char. 3, state 1). **B.** *C. winterbottomi* (ROM 92690, 22.9 mm SL male paratype) showing widely separate preopercular and transverse opercular papillae rows (Char. 2, state 0) and transverse mandibular rows in groups of 10 or more (Char. 3, state 0). Sensory pores are absent in this species (Char. 4, state 1).

FIGURE 2.2 Scale morphology in *Callogobius*. Scale bar = 0.5 mm. **A.** (left) A mid lateral scale from *C. winterbottomi* (ROM 92690, 32.2 mm SL male paratype) with a distinctly outlined centre (Char. 8, state 1); (right) slightly elongate ctenii from a caudal peduncle scale (Char. 11, state 1) on the same individual. Scale bar = 1 mm. **B.** A caudal peduncle scale from *C. flavobrunneus* (CAS 63904, 35.5 mm SL female) with dramatically elongate ctenii (Char. 11, state 1).

FIGURE 2.3 Female urogenital papilla morphology in *Callogobius*. Scale bar = 1 mm. Abbreviations: An = anus, UP= urogenital papilla, LF = lateral flaps, AS=anal spine. **A.** *C.* sp. 20 (USNM 412481, 25.9 mm SL) showing the absence of lateral flaps (Char. 13, state 0). **B.** *C. clarki* (USNM 341181, 31.0 mm SL) showing the presence of lateral flaps (Char. 13, state 1).

FIGURE 2.4 *Callogobius* pelvic fin morphology. Scale bar = 2 mm. Abbreviations: F = frenum, S = spine, M = membrane. **A.** Pelvic fins of *C.* sp. 20 (USNM 412481, 31.7 mm SL male) which are joined, with the fifth ray approximately the same length as the fourth (Char. 14, state 0), pelvic frenum present (Char. 15, state 0) and fifth pelvic-fin ray highly branched (Char. 16, state 0). **B.** Pelvic fins of *C. winterbottomi* (ROM 92690, 32.2 mm SL male paratype) which are partially joined, with the fifth ray shorter than the fourth (Char. 14, state 1), pelvic frenum present (Char. 15, state 0) and fifth pelvic-fin ray highly branched (Char. 16, state 0). **C.** Pelvic fins of *C. sclateri* (ROM 60877, 32.7 mm SL female) which are separate with a minute membrane (Char. 14, state 2), pelvic frenum absent (Char. 15, state 1) and fifth pelvic-fin ray branched only once (Char. 16, state 1).

FIGURE 2.5 Dorsal view of the anterior portion of the cranium in in *Callogobius*. Scale bars = 1mm. Abbreviations: EML=ethmo-maxillary ligament, VO=vomer, ME=mesethmoid, LE=lateral ethmoid, FR=frontal.**A.** *C. andamanenis* (ROM 68202, 39.1 mm SL female) showing lateral ethmoids that are small and loosely joined to the mesethmoid (Char. 19, state 0), and the mesethmoid process for the ethmo-maxillary ligament a small nubbin (Char. 22, state 0). **B.** *C. bifasciatus* (ROM 39892, 33.2 mm male) showing lateral ethmoids that are small and loosely joined to the mesethmoid (Char. 19, state 0), and the mesethmoid process for the ethmo-maxillary ligament a small nubbin (Char. 22, state 0). **C.** *C. maculipinnis* (USNM 241882, 28.3 mm SL, female) showing lateral ethmoids that are large and firmly joined to the mesethmoid (Char. 19, state 1), and the mesethmoid process for the ethmo-maxillary ligament long and narrow (Char. 22, state 1).

FIGURE 2.6 Dorsolateral view of the cranium of *Callogobius* with suspensorium, gill arches and eye removed. The pterosphenoid is dark grey and the expansion of the frontals is light grey. Scale bar = 2 mm. Abbreviations: ME = mesethmoid, VO = vomer, FR = frontal, PA = parasphenoid, PTS = pterosphenoid, SP = sphenotic, PR = prootic, PT = pterotic, IC = intercalar, BO = basioccipital, EO = exoccipital, SO = supraoccipital. **A.** *C. andamanensis* (ROM 68202, 39.1 mm SL female) showing the absence of frontal and parasphenoid expansion into orbit (Char. 20, state 0) and absence of mesethmoid strut (Char. 21, state 2). **B.** *C. bifasciatus* (ROM 39892, 33.2 mm male) showing limited frontal expansion and no parasphenoid expansion into orbit (Char. 20, state 1) and an ossified mesethmoid strut that does not contact the vomer/parasphenoid (Char. 21, state 1). **C.** *C. shunkan* (BLIP 19810168, 40.0 mm SL female) showing extensive frontal and parasphenoid expansion into orbit (Char. 20, state 2) and absence of mesethmoid strut (Char. 21, state 2).

FIGURE 2.7 Lateral view of the suspensorium of *Callogobius*. Two suspensorium characters, the palatine dorsal arm angle (Char. 30) and palatine shaft width (Char. 31), are not labeled because the palatine does not lie flat while articulated with the remainder of the suspensorial bones. Scale bars = 2 mm. Abbreviations: PM = premaxilla, DE = dentary, ART = anguloarticular, RET = retroarticular, QU = quadrate, MX = maxilla, PA = palatine, EC = ectopterygoid, SYM = symplectic, MET = metapterygoid, HYO = hyomandibula, OP = opercle, POP = preopercle, IOP = interopercle, SOP = subopercle, GAP = symplectic gap. **A.** *C. bifasciatus* (ROM 39892, 33.2 mm male) showing enlarged canine teeth in the lower jaw (Char. 23, state 2), an open maxilla head (Char. 24, state 0), the dorsal lamina of the quadrate without right-angle-forming anterior expansion (Char 25, state 0), an anterior flange on the metapterygoid which reaches the quadrate (Char. 26, state 0), posterior region of the metapterygoid without ventral extension (Char. 27, state 2), quadrate without expansion into the symplectic gap (Char. 28, state 0), bony protuberance present at the preopercular ligament (Char. 29, state 1), palatine with short anterolateral arm (Char. 32, state 1) and a curve at the junction between the anterolateral and posterolaterial arm (Char. 33, state 2), ectopterygoid broad with tapered shaft (Char. 34, state 1) and a broad dorsal margin without a second bony protuberance (Char. 35, state 1), preopercle with dorsal truncation (Char. 36, state 1) and no ventral groove (Char. 37, state 1), hyomandibula with short posterodorsal condyle (Char. 38, state 1). **B.** *C. depressus* (USNM 214728, 63.2 mm SL female) showing lack of enlarged canine teeth in the lower jaw (Char. 23, state 0), an open maxilla head (Char. 24, state 0), the dorsal lamina of the quadrate without right-angle-forming anterior expansion (Char 25, state 0), no anterior flange on the metapterygoid (Char. 26, state 1), posterior region of the metapterygoid without ventral extension (Char. 27, state 2), quadrate without expansion into the symplectic gap (Char. 28, state 0), no bony protuberance present at the preopercular ligament (Char. 29, state 0), palatine with long anterolateral arm (Char. 32, state 1) and no curve at the junction between the anterolateral and posterolateral arm (Char. 33, state 0), ectopterygoid broad with tapered shaft (Char. 34, state 1) and a broad dorsal margin with a second bony protuberance (Char. 35, state 2), preopercle without dorsal truncation (Char. 36, state 0) but with a ventral groove (Char. 37, state 0), hyomandibula without short posterodorsal condyle (Char. 38, state 0). **C.** *C. maculipinnis* (ROM 57704, 45.3 mm SL) showing lack of enlarged canine teeth in the lower jaw (Char. 23, state 0), a closed, bowl-shaped maxilla head (Char. 24, state 1), dorsal lamina of the quadrate with right-angle-forming anterior expansion (Char 25, state 1), no anterior flange on the metapterygoid (Char. 26, state 1), posterior region of the metapterygoid with ventral extension at the point of articulation of the symplectic and hyomandibula (Char. 27, state 1), quadrate with expansion into the symplectic gap (Char. 28, state 1), no bony protuberance present at the preopercular ligament (Char. 29, state 0), palatine with long anterolateral arm (Char. 32, state 1) and no curve at the junction between the anterolateral and posterolateral arm (Char. 33, state 0), ectopterygoid very broad with a distinct shaft (Char. 34, state 2) and a broad dorsal margin without a second bony protuberance (Char. 35, state 1), preopercle without dorsal truncation (Char. 36, state 0) but with a ventral groove (Char. 37, state 0), hyomandibula without short posterodorsal condyle (Char. 38, state 0).

FIGURE 2.8 Pharyngobranchial tooth morphology in *Callogobius*. Scale bars = 0.25 mm. **A.** Pharyngobranchial 3 tooth type A (from *Callogobius depressus*, USNM 214728, 63.2 mm SL female). **B.** Pharyngobranchial 3 tooth type B (from *Callogobius clarki*, USNM 220031 39.9 mm SL). **C.** Pharyngobranchial 3 tooth type C (*Callogobius hastatus*, CAS 63897, 26.9 mm SL). **D.** Pharyngobranchial 3 tooth type D (*Callogobius maculipinnis*, USNM 241882, 28.3 mm SL, female).

FIGURE 2.9 Dorsal gill arch morphology in *Callogobius*. Scale bar = 1 mm. Abbreviations: EB1 = epibranchial 1, EB2 = epibranchial 2,EB3 = epibranchial 3, EB4 = epibranchial 4, IAC = interarcual cartilage, PB2 = pharyngobranchial 2 PB3 = pharyngobranchial 3, PB4T = pharyngobranchial 4 toothplate. **A.** *C. maculipinnis* (MPM 45773, 30.0 mm SL) showing distinct arm of pharyngobranchial 2 to interarcual cartilage (Character 41, state 1) and broad dorsolateral head of epibranchial 3 (Character 44, state 0). Epibranchial tooth patches not illustrated. **B.** *C. tanegasimae* (uncataloged, 32.8 mm SL female) showing no distinct arm of pharyngobranchial 2 to interarcual cartilage (Character 41, state 0) and a relatively narrow dorsolateral head of epibranchial 3 (Character 44, state 1).

FIGURE 2.10 Dorsal view of the anterior portion of ventral gill arch and hyoid arch of *Callogobius*. Scale bar = 1 mm. Abbreviations: BH = basihyal, VHH = ventral hypohyal, DHH = dorsal hypohyal, ACH = anterior ceratohyal, BB1 = basibranchial 1, BB2 = basibranchial 2, CB1 = ceratobranchial 1, HB1 = hypobranchial 1. **A.** *C. hastatus* (17.0 mm SL) showing a narrow basihyal (Char. 45 state 1), and hypobranchial 1 with a laterally directed anterolateral process (Char. 42, state 1) and short posterior arm (Char. 43, state 0). Scale bar = 6.5 mm. **B.** *C. maculipinnis* (MPM 45773, 30.0 mm SL) showing a moderately broad basihyal (Char. 45, state 0) which is distinctly bilobed, and hypobranchial 1 with an anteriorly directed anterolateral process (Char. 42, state 0) and long posterior arm (Char. 43, state 1).

FIGURE 2.11 Pectora-fin osteology of *Callogobius*. Scale bar = 1 mm.Abbreviations: PT = posttemporal, SCL = supracleithrum, LF = lateral flange of cleithrum, CL = cleithrum, CO = coracoids, DP = dorsal processes of cleithrum, PR = proximal radial. **A.** *C. mucosus* (USNM 341205, 66.4 mm SL male) showing the narrow and closely spaced dorsal processes of the cleithrum (Char. 47, state 1) and a dorsally-directed lateral flange of the cleithrum (Char. 48, state 0). Scale bar = 2mm. **B.** *C. bifasciatus* (ROM 39892, 33.2 mm male) showing the broad and widely separated dorsal processes of the cleithrum (Char. 47, state 0) and a dorsoposteriorly directed lateral flange of the cleithrum (Char. 48, state 1).

FIGURE 2.12 Morphology of the first and second pectoral-fin ray of *Callogobius*. Scale bar = 0.5 mm. **A.** (top) Lateral view of *C. mucosus* (USNM 341205, 66.4 mm SL male) showing no blade on the medial hemitrich of the penultimate (second) ray (Char. 50, state 0). (bottom) Medial view of the same specimen. Scale bar = 1 mm. **B.** (top) Lateral view of *C. bifasciatus* (ROM 39892, 33.2 mm male) showing a triangular blade on the medial hemitrich of the penultimate ray (Char. 50, state 1). (bottom) Medial view of the same specimen.

FIGURE 2.13 Morphology of the first through sixth vertebrae of *Callogobius*, ribs and associated epineurals not shown. Scale ba r= 2 mm. Abbreviations: V1 = first vertebra, EN = epineurals, PP = parapophyses, V4 = fourth vertebra, V6 = sixth vertebra. **A.** (top) Lateral view of *C. okinawae* (USNM 241882, 31.8 mm female) showing the absence of expanded wings on the parapophyses (Char. 54, state 0). (bottom) Ventral view of the same specimen. **B.** (top) Lateral view of first through sixth vertebrae of *C. maculipinnis* (USNM 241882, 32.6 mm SL female) showing the presence of expanded wings on the parapophyses beginning with the fourth vertebra (Char. 54, state 2). (bottom) Ventral view of the fourth vertebra of the same specimen.

FIGURE 2.14 Phylogenetic hypotheses for the inter-relationships of *Callogobius*. Four equally most parsimonious trees, computed using maximum parsimony, with 55 morphological characters and 19 taxa. Tree length = 95, CI = 0.695, RI = 0.858.

FIGURE 2.15 Strict consensus tree based on the four most parsimonious trees from Figure 2.14. Bootstrap values greater than 50% were added to appropriate branches. The *maculipinnis* group is indicated by dark grey, the *tutuilae* group is indicated by medium grey, the *sclateri* group is indicated by light grey, and the *hasseltii* group is indicated by very light grey.

FIGURE 2.16 McKinney's (1980) phylogenetic tree of *Callogobius* based on morphology. Copyright J.F. McKinney.

FIGURE 3.1 (previous page) Bayesian analysis for the concatenated data set, with posterior probabilities. Nodes supported by at least 95 percent ML bootstrap replicates indicated with an asterisk (*). LR numbers refer to Lukas Rüber's tissue collection numbers; these numbers are used in the tree to differentiate individuals of the same species. Delventhal & Mooi's (unpublished, Chapter Two) species groups are indicated by colour. Very light grey = *hasseltii* group, light grey = *sclateri* group, medium, grey = *tutuilae* group, dark grey = *maculipinnis* group.

FIGURE 3.2 Maximum parsimony consensus tree for the reduced data set, with most of the duplicate taxa removed. Bootstrap values of at least 50% have been mapped onto nodes. LR numbers refer to Lukas Rüber’s tissue collection numbers; these numbers are used in the tree to differentiate individuals of the same species. Delventhal & Mooi’s (unpublished, Chapter Two) species groups are indicated by colour. Very light grey = *hasseltii* group, light grey = *sclateri* group, medium, grey = *tutuilae* group, dark grey = *maculipinnis* group.

FIGURE 3.3 Summary of the interrelationships of *sclateri*, *maculipinnis, hasseltii* and *tutuilae* groups as inferred by the present molecular analysis and Delventhal & Mooi's (unpublished, Chapter Two) morphological analysis.

FIGURE 4.1 Left lateral views of type specimens of *Callogobius winterbottomi*. Scale bar = 5 mm.A. Holotype, ROM 58914, 33.8 mm SL male. **B.** Paratype, ROM 92690, 32.2 mm SL male. **C.** Paratype, ROM 92690, 22.9 mm SL male.

FIGURE 4.2 Scale morphology in *Callogobius winterbottomi*, illustrated from male paratype, ROM 92690, 32.2 mm SL. Left, entire mid-lateral scale from region below last spine of first dorsal fin showing distinctly outlined centre and single row of ctenii of normal length. Circuli are not illustrated, although note that they do not occur within the outlined centre. Right, slightly elongate ctenii of postero-dorsal caudal peduncle scale for comparison. Scale bar = 1 mm.

FIGURE 4.3 Ventral view of pelvic fins of *Callogobius winterbottomi*, illustrated from male paratype, ROM 92690, 32.2 mm SL. Scale bar = 2 mm. Abbreviations: F = weak frenum, M = extent of membrane uniting pelvic fins, about two thirds length of fins (reconstructed, membrane damaged in all specimens available), S = pelvic spine.

FIGURE 4.4 Right lateral view of *Callogobius winterbottomi*, SAIAB 057357, 37.7 mm SL female. Scale bar = 5 mm.

FIGURE 4.5 Sensory papillae pattern in *Callogobius winterbottomi* paratype, ROM 92690, 22.9 mm SL, male. **A.** Lateral view. Arrow indicates anterior extent of gill opening. **B.** Dorsal view. Numbers refer to Akihito & Meguro’s (1977) sensory papillae system (see Table 5.2). Scale bar = 2 mm.

FIGURE 5.1 *Callogobius clarki*, holotype, HUJ 10065, 36.3 mm SL female: (A) left lateral view; (B) right lateral view.

FIGURE 5.2 Female urogenital papilla of *Callogobius clarki*, USNM 341181, 31.0 mm SL, ventral view. Note the broad lateral flaps of skin. An = anus; AS = anal-fin spine; LF = lateral flap; UP = urogenital papilla. Scale bar = 1 mm.

FIGURE 5.3 *Callogobius clarki*, USNM 220038, 48.6 mm SL, male (illustration P09712 by Jack R. Schroeder, Smithsonian Institution, NMNH, Division of Fishes): **A.** dorsal view of head; **B.** lateral view of head and body; **C.** lateral view of head enlarged from B. Numbers are added to identify papillae rows used in the redescription (numbers follow Akihito and Meguro, 1977; names follow Delventhal and Mooi, 2013): 2 postnasal row; 9 anterior suborbital row; 10 mid-suborbital row; 11 posterior suborbital row(s); 12 longitudinal cheek row; 13 transverse cheek row; 14 longitudinal maxillary row; 15 longitudinal mandibular row; 16 transverse mandibular rows; 17 postorbital row; 20 preopercular row; 21 transverse opercular row.

FIGURE 6.1 Type specimens of *Gobiopsis liolepis* (Bleeker): **A.** lectotype, RMNH.PISC.4411, 44.0 mm SL; **B.** paralectotype, RMNH.PISC.36383, 42.0 mm SL. Photos by M. Aizawa.

FIGURE 6.2 X-ray images of the type specimens of *Gobiopsis liolepis* (Bleeker): **A.** lectotype, RMNH.PISC.4411, 44.0 mm SL; **B.** paralectotype, RMNH.PISC.36383, 42.0 mm SL. Photos by M. Aizawa.

FIGURE 6.3 Head barbels and sensory papillae of *Gobiopsis liolepis* (Bleeker): **A.** dorsal view; **B.** lateral view; **C.** ventral view. Arrows and labels indicate distinctive barbels and papillae found in the lecto- and paralectotype (RMNH.PISC.4411; RMNH.PISC.36383), barbel terminology following Lachner and McKinney (1978): ACT, anterior cheek tuft; AGB, anterior gular barbels; CB, chin barbels; IMB, inter-mandibular barbels; IOP, interorbital papillae row [portion of the nasal papillae row of Lachner & McKinney (1978:7) confluent with the suborbital papillae and unique to this species]; PMB, posterior mandibular barbels. Due to condition of the specimens, not all of these features were observed in both types (see text). Base illustration modified from Lachner and McKinney (1978: plate 1a,b and plate 2a) of USNM 209247 (male paratype of *G. aporia*) from plates P09253 and P09357 by Jack R. Schroeder, Smithsonian Institution, NMNH, Division of Fishes, with permission. Scale bar is approximate.

FIGURE 7.1 Sensory pore and papillae pattern on the head of *Callogobius pilosimentum sp. nov.*, SMF 35756, holotype, female, 36.4 mm SL. Scale bar = 2 mm. **A.** Lateral view; **B.** Ventral view. Letter abbreviations of sensory pores follow Akihito & Meguro (1977) and descriptive names are modified from Takagi (1957). Papillae row numbering follows Akihito and Meguro and descriptive names are from Delventhal & Mooi (2013). Sensory pores: B = posterior nasal; C = anterior interorbital; D = posterior interorbital; E = supraotic; F = anterior otic; G = posterior otic; H = intertemporal; M,N,O = preopercular; K = anterior temporal; L = posterior temporal. Papillae rows: 2 = postnasal; 9 = anterior suborbital; 10 = mid suborbital; 11 = posterior suborbital; 12 = longitudinal cheek; 13 = transverse cheek; 14 = longitudinal maxillary; 15 = longitudinal mandibular; 16 = transverse mandibular; 17 = postorbital; 20 = preopercular; 21 = transverse opercular (rows 20 and 21 continuous).

FIGURE 7.2 *Callogobius pilosimentum sp. nov.*, live colouration: **A.** SMF 35756, holotype, female, 36.4 mm SL, Farasan Island, Saudi Arabia; **B.** Fresh colouration, uncatalogued, Farasan Island, Saudi Arabia, illustrating pattern frequently induced by stress; **C.** SMF 35760, paratype, female, 55.8 mm SL, Obhur, Jeddah, Saudi Arabia. Photos by S. Bogorodsky.

FIGURE 7.3 *Callogobius amikami* Goren, Miroz & Baranes: **A.** Preserved specimen, TAU P-10321, holotype, sex uncertain, 26.2 mm SL, Eilat, Israel; **B.** Aquarium specimen in 1993, Coral World, Eilat, about 40 mm TL, collected by A. Miroz. **C.** *Callogobius cf. amikami*, live colouration, SMF 35770, juvenile, 7.2 mm SL, Al Wajh bank, Saudi Arabia. Photos by N. Delventhal (A), J.E. Randall (B) used with permission, S. Bogordsky (C).

FIGURE 7.4 *Callogobius clarki* (Goren), live colouration: **A.** SMF 35766, female, 41.4 mm SL, Al Wajh, Saudi Arabia; **B.** BPBM 41243, male, 52.0 mm SL, Dahab, Egypt. S. Bogordsky.

FIGURE 7.5 *Callogobius dori* Goren, live colouration, SMF 35762, male, 23.8 mm SL, Farasan Island, Saudi Arabia. Photo by S. Bogordsky.

FIGURE 7.6 *Callogobius flavobrunneus* (Smith): **A.** Fresh colouration, uncatalogued, 36.0 mm SL, Shams Alam, southern Egypt; **B.** Preserved specimen, SMF 35771, female, 27.3 mm SL, Al Wajh, bank, Saudi Arabia. Photos by S. Bogordsky (A), R. Mooi (B).

FIGURE 7.7 A. *Callogobius sclateri* (Steindachner), preserved specimen, USNM 298419, female, 22.1 mm SL, Ras Burqa, Gulf of Aqaba, Egypt. **B.** *Callogobius* sp. A, live colouration, SMF 35772, juvenile, 14.5 mm SL, Yabua Island, Saudi Arabia. Photos by R. Mooi (A), S. Bogordsky (B).

FIGURE 8.1 *Callogobius* sp. 20, an undescribed species of *Callogobius* in the *hasseltii* group used in the morphology-based analysis. Photo by J. Williams.

Chapter One. Introduction

Gobioids (suborder Gobioidei), referred to as the Gobiiformes by some authors (e.g. Betancur-R et al. 2013) comprise one of the largest groups of fishes with over 2100 extant species (Nelson et al. 2016). Some are tiny and paedomorphic, others are adapted to a semi-terrestrial habitat (mudskippers); still others are elongate and blind, or have modifications for torrential freshwaters or cave life (Zander 2011). Many gobioids have mutualistic associations with other organisms (including shrimps and other fishes). Nearly all gobioids display complex brood care behavior and hermaphroditism is common (usually sequential hermaphroditism – they change sex from one to the other, e.g., from female to male or vice versa) (Mazzoldi et al. 2011).

Because of their incredible diversity, gobioids are superb organisms for a wide range of studies in evolutionary biology such as adaptive radiation, functional morphology, physiology, and developmental and reproductive biology (Rüber & Agorreta 2011). However, studies exploiting the vast potential of gobioids are few due to current inadequate systematic knowledge of the group. Some of the challenges presented by gobies are their small size (usually less than 3 inches) and trends of independent evolution towards reduction in derived lineages, such as loss of bones and sensory pores (Thacker 2011). An extreme example of reduction is the genus *Schindleria*, one of the world's smallest vertebrates (Johnson & Brothers 1993); the largest specimen of *S. brevipinguis* is 8.4 mm SL (Watson and Walker 2004).

Among derived gobioids, the subfamily Gobiinae (sensu Pezold 1993) of the family Gobiidae, comprise a particularly large and poorly known group, with approximately 130 genera (Nelson 2006). Some authors (e.g., Thacker 2009, Nelson et al. 2016) recognize the Gobiinae and several small imbedded families as a distinct family (which they refer to as the Gobiidae), removing some of the traditionally recognized gobiids to the family Gobionellidae (= the family Oxcudercidae), but I follow Gill and Mooi (2012) and continue to recognize it as a subfamily because goby classification is still in a state of flux.The gobiine genus *Callogobius* includes more than 40 nominal species (Eschmeyer and Fricke 2016), with perhaps 25 or more undescribed species (D. H. Hoese, pers. comm.), making it one of the most speciose gobioid genera. Species of *Callogobius* inhabit a variety of shallow marine environments including coral reefs, reef rubble, and tidepools; a few species also occur in mangrove streams. The taxonomy is poorly known. Most species have brown, cryptic colouration, some occur only in specific habitats, and most museum specimens are in poor condition due to many species having fragile skin and deciduous scales. Several of the holotypes are more than 100 years old and in poor condition. As a result, many new *Callogobius* species take years of study, with extended time required for specimen collection and comparison with holotypes of previously described species. For example, there are more than seven undescribed species known in Japan (Y. Ikeda pers. comm.), one of which has been under study for more than 30 years, first reported and illustrated by Akihito (1984).

Most museum specimens of *Callogobius* are small, drab and often in poor condition, but when viewed under a dissecting microscope, a distinctive trait is visible. The sensory papillae (superficial neuromasts) of the head are on raised ridges in a unique pattern (Winterbottom 2003; see Figure 4.5, Chapter Four). Below the genus level, however, all is chaos in *Callogobius*. There is bewildering variation in characters such as scale size and shape, vertebral number, body shape and size, colour pattern, pelvic-fin structure, and presence and position of sensory canals and pores (McKinney 1980). Many of these characters are commonly used to diagnose genera; vertebral number was used to define larger groups within gobioids in a classic study that forms the basis for much of our knowledge of higher gobioid relationships (Birdsong et al. 1988). Given that *Callogobius* is monophyletic, it is an ideal group to study character evolution and explore hypotheses of convergence and divergence within gobiines, as trends in *Callogobius* appear to reflect general trends in the Gobiinae.

Challenges in* Callogobius *alpha taxonomy

Clearly, a well supported phylogeny is a prerequisite for testing evolutionary hypotheses. To undertake a phylogenetic study of *Callogobius*, the alpha taxonomy must first be clarified. Akihito and Meguro (1975, 1977) examined type material and identified the taxa known at that time in Japan, and McKinney & Lachner (1978b) provided a summary table of selected characters obtained mostly from types when available. These works continue to be important to the systematics of *Callogobius*, as they form a basis for the recognition of *Callogobius* as currently circumscribed. Most subsequent taxonomic papers on *Callogobius* consisted of descriptions of one or two new species (e.g., Goren 1978, Goren 1979a, Goren et al. 1991, Chen & Shao 2000, Chen et al. 2006) with comparisons to other species and regional keys based on literature alone (rather than comparisons to type material or other positively identified specimens). As a result, errors have crept into the literature and continue to be perpetuated. Identification attempts using published keys and/or checklists, even by ichthyologists familiar with gobies, more often than not result in incorrect conclusions. This situation is made worse by the plethora of undescribed species, and correct identification is largely impossible. Many (in some collections, most) museum specimens of *Callogobius* are unidentified or misidentified at the species level (pers. obs).

Taxonomic problems and lack of adequate literature continue to hinder advances by recent workers. For example, *Callogobius nigromarginatus* was described by Chen & Shao (2000) and distinguished from *C. maculipinnis* by colour pattern, fin-spine proportions, and slightly lower scale counts. However, the colour pattern of *maculipinnis*-like species can vary in response to ichthyocide useage (Y. Ikeda, pers. comm.), and scale-count ranges and fin-spine proportions of most species have not been adequately documented, making comparisions based on the literature nearly impossible.. These characters appear to vary individually, regionally, and between species; scale counts may vary among individual researchers or be inconsistent even if performed by the same researcher, since most *Callogobius* have irregularly placed (and often small) scales; like other gobiids, they lack a lateral line. Due to the extreme diversity of *Callogobius* species, it cannot be ruled out that *C. nigromarginatus* is a valid species, although additional morphological characters (and possibily the use of genetic studies) will be needed to demonstrate whether this can be corroborated.

Most undescribed *Callogobius* species are from poorly surveyed regions, with the overwhelming diversity of species easily resulting in a variety of major or minor errors during the species description process. For example, when I examined the paratypes of another recently described species, I found a second, distinct undescribed species to be included. Until this can be properly documented, the true identity of both species will be obscured.

History of* Callogobius *phylogeny

As expected for a diverse, taxonomically challenging group, intrarelationships of *Callogobius* are poorly known. Diagnostic characters for *Callogobius*, as well as current circumscription, were not recognized until the 1970s. Prior to this time, species of *Callogobius* were placed in as many as 13 genera (Eschmeyer & Fricke 2016). Several authors have attempted to divide *Callogobius* into two or more species groups, the purpose of which was either to provide phylogenetic hypotheses or to allow easier taxonomic comparisons. Lachner & McKinney (1974) remarked that a specific subgroup within *Callogobius,* which they called the *hasseltii* species group, displayed distinct morphology, but they did not provide further details. McKinney (1980) provided a "cladistic" analysis using characters of the osteology and external morphology, sampling 14 *Callogobius* species. He ultimately recognized two species groups, a stout-bodied (*maculipinnis*) and a slender-bodied (*hasseltii*) group. These groups were named following the taxonomic convention of using the name of the first described species in each group. Although he did discover one interesting character – a modification in the ectopterygoid which he interpreted as a socket for articulation with the palatine – resolution at the species level was generally supported only by potentially troublesome characters, such as degree of pelvic fin fusion (highly variable among gobies [Hoese 1986]). McKinney & Lachner (1984) proposed a group, which they simply called the "stout-bodied group" with ctenoid scales and a smaller number of segmented dorsal fin elements. Goren et al. (1991) recognized a group of species with a relatively low number of scale rows; their work focused on species identification rather than phylogeny reconstruction.

A sister taxon to *Callogobius* has never been proposed, although Lachner and McKinney (1974) suggested a possible relationship between *Pipidonia* (later synonymised with *Gobiopsis* [Lachner & McKinney 1978]), *Barbuligobius* and *Callogobius.* Miller & Wongrat (1979) discussed a similarity in arrangement of the sensory papillae in *Callogobius* and *Egglestonichthys*. Winterbottom (2003) summarized possible similaries between goby genera that possess folds or ridges of sensory papillae on the head (*Cristatogobius, Mangarinus,* *Callogobius*, *Feia* and *Gobiopsis*). In *Callogobius,* however, the sensory papillae arrangement is consistent and unique; in all species the basic pattern with the 24 rows as illustrated in Figure 4.5 (Chapter Four) is present, and occurs in no other taxon. Moreover, the osteology of these potentially related genera is not obviously similar (pers. obs.). Molecular research (summarized in Chapter Three) has thus far failed to identify likely candidates for *Callogobius* relatives among among other gobiines.

Research objectives and approach

My research focuses on understanding and categorizing the diversity within *Callogobius*. My first objective is to address the current state of *Callogobius* systematics, which has been problematic due to the extreme diversity in species and their morphology and the inadequate communication tools for use between researchers (e.g. lack of standardized character sets used in species descriptions and keys). I begin to clarify the alpha taxonomy of *Callogobius* through two new species descriptions, a species redescription, a regional review and the removal of an incorrectly assigned species species. This is only a first step , but in this work my goal has been to identify and begin using a number of characters that have not been consistently employed by previous *Callogobius* workers. For example, I create a naming system for papillae rows designed to be more user-friendly than previous systems; my hope is that the use of these characters in *Callogobius* taxonomic work will become standardized over time. This will make the process of new species descriptions quicker and less likely to produce errors.

My philosophy regarding species identification is pragmatic; I recognize a group of individuals as representing a distinct species if they share a unique combination of characters, and my confidence in this assessment is increased if those individuals also share a geographic range (or are endemic to a specific region). I work under the assumption that these species are monophyletic units, and any evidence to the contrary would prompt me to re-evaluate my conclusions.

In my phylogenetic work, I focus on morphological characters and character systems that vary at the intrageneric level, since the focus of my work is to identify monophyletic groups within the genus, rather than determine the relative placement of *Callogobius* within the gobies. Most of the osteological characters used here were surveyed in *Callogobius* for the first time; a number of them have not yet been described in other gobies to my knowledge. My approach to character discovery was to lay out trays of dissected specimens or their parts, and compare them under the microscope for differences and similarities. Some of the characters used in this study were discovered accidentally, other promising characters had to be abandoned because I could not devise a way to describe them or condense the variation into character states. One of the major questions I address is simply: Is it possible to find meaningful monophyletic subgroups within a large, unwieldy genus? By "meaningful" I mean morphologically distinctive and supported by multiple character systems (such as external sensory system, body shape and osteology). I also sought to determine whether it is possible to find congruence between morphological and molecular data sets at a low taxonomic level.

Chapter outline

In this thesis, I address some the current problems in phylogenetics and taxonomy of *Callogobius*. Four out of the eight chapters have been published, and the chapters are not presented sequentially in the order in which they were written. Thus, some of the conclusions may be modified from how they were first presented, the notable example being the definition of the *sclateri* group, which was first presented in Chapter Four, but later revised in Chapter Two in light of new information from additional species. The naming system for papillae rows is first presented in Chapter Four, but cited throughout the dissertation in most chapter methods sections.

In Chapter Two (not yet published), I construct a phylogenetic hypothesis for relationships within *Callogobius* using morphological data taken from the external anatomy, suspensorium, cranium, gill arches, pelvic-fin osteology, and axial skeleton, and four subgroups are identified within *Callogobius*; for three of them, I provide evidence of monophyly. In Chapter Three (not yet published), I test the relationships proposed in Chapter Two using molecular data from nuclear and mitochondrial DNA. In Chapter Four (published in *Zootaxa* and written sequentially first among all the chapters, hence, cited extensively in Chapter Two and elsewhere), I describe a new species of *Callogobius*, propose a standardized naming system for the papillae rows (one of the most important character systems for distinguishing species within the genus) and introduce characters that help define subgroups within *Callogobius* including unusal morphology of the female urogenital papilla in some *Callogobius* species. In Chapters Five and Six (published in *Copeia* and *Zootaxa* respectively), I deal with common problems in alpha taxonomy – I redescribe a species that has been incorrectly synonymized with an existing species, and I remove a species that has been incorrectly placed in *Callogobius* and identify its correct generic placement. In Chapter Seven (published in *Zootaxa*), I build on the framework of Chapters Four and Five, and examine all the known species of *Callogobius* in a geographically defined region (the Red Sea), describe an undescribed species, and provide a dichotomous key for all known species in the Red Sea.

2. Chapter Two. Intrarelationships of *Callogobius* (Teleostei: Gobiidae): a morphological perspective

Publication status: This chapter has not been published; however, most of this paper will be published in the future with Randy Mooi. For this reason, I have used "we" throughout the text. In later chapters of this thesis, I cite this chapter as Delventhal & Mooi (unpublished).

My contribution: I designed the study, obtained and prepared specimens, identified most of the characters, coded all of them, ran the analyses, and drafted the manuscript. R. Mooi identified some of the characters and reviewed all of them as well as the manuscript. I drafted about half of the illustrations, which were inked and prepared by R. Mooi, who drafted and prepared the remaining illustrations.

SUMMARY

Callogobius is a large Indo-Pacific goby genus characterized by raised ridges of sensory papillae in both horizontal and vertical rows. There are more than 40 nominal species and numerous undescribed species. Although *Callogobius* is thought to be monophyletic, the relationships to other gobiine genera and the relationships among the species are not well known. We examined cleared and stained specimens of 16 *Callogobius* species, and identified 55 variable, parsimony informative characters from osteology and external morphology. These characters were analyzed using parsimony, resulting in the identification of three monophyletic subgroups among sampled species of *Callogobius*. These subgroups can be distinguished by external morphology and/or osteology. We refer to these subgroups as the *maculipinnis*, *sclateri*, and *hasseltii* groups and provide a phylogenetic diagnosis of each. We are aware of two described species, *C. tutuilae* and *C. centrolepis*, and several undescribed species that exhibit a combination of characters not consistent with the *maculipinnis*, *sclateri*, or *hasseltii* groups. Lacking evidence for monophyly, we informally refer these to an assemblage we call the *tutuilae* group. Our examination of the osteology of a specimen we identify as *C.* cf. *centrolepis* indicates that it shares a number of synapomorphies with members of the *sclateri* group. The memberships of our *hasseltii* and *maculipinnis* groups are not identical to McKinney's (1980) *hasseltii* and *maculipinnis* groups.

INTRODUCTION

Callogobius Bleeker comprises more than 40 nominal species (Eschmeyer et. al. 2016, Appendix A, Table A.1), and numerous undescribed species found throughout the Indo-Pacific in marine (and occasionally estuarine) environments. Historically, species of *Callogobius* have been placed in several separate, often monotypic, genera; *Batracheleotris* Fowler, *Crossogobius* Koumans, *Doryptena* Snyder, *Galera* Herre, *Gunnamatta* Whitley, *Herrea* Whitley, *Intonsagobius* Herre, *Macgregorella* Seale, *Metagobius* Whitley, *Mucogobius* McCulloch, and *Ulcigobius* (subgenus of *Drombus*) Fowler are all considered synonyms of *Callogobius*. Several species of *Callogobius* were originally described as species of *Gobius*, *Eleotris*, *Drombus* or *Gobiomorphus*, which are distinct and demonstrably different genera. McKinney and Lachner (1978) provided a summary table of selected characters obtained mostly from types when available. Their paper formed the basis for the recognition of *Callogobius* as currently circumscribed. Unfortunately, McKinney and Lachner never completed their planned revision, and most subsequent taxonomic papers on *Callogobius* were regional or consisted of the description of a single species, e.g., Goren (1978), Goren (1979), Goren (1980), McKinney & Lachner (1984), Goren et al. (1992), Chen & Shao (2000), and Chen et al. (2006).

Callogobius is diagnosed by a single putative synapomorphy – the sensory papillae (superficial neuromasts) of the head are on raised ridges in a unique pattern with both longitudinal and transverse rows, a strong indication that the genus is monophyletic (Winterbottom 2003). Since the 1970s, several authors attempted to define smaller groups within *Callogobius*. Lachner & McKinney (1974, p. 878) remarked that *Callogobius* is an “impractical, heterogeneous assemblage of two, possibly more, species groups.” They suggested that a group they called the *hasseltii* species group, displayed major differences from other nominal species, but did not indicate which characters were used or which species were included. McKinney, in an unpublished Master's thesis (1980) provided an analysis using characters of the osteology and external morphology, sampling 14 *Callogobius* species but no outgroup. His analysis supported a stout-bodied (*maculipinnis*) and slender-bodied (*hasseltii*) group. Presumably based on McKinney's work, McKinney & Lachner (1984) subsequently proposed a group, which they simply called the "stout-bodied group" with ctenoid scales and a smaller number of segmented dorsal fin elements group. This comprised *C. bauchotae, C. centrolepis*, *C. crassus*, *C. flavobrunneus*, *C. maculipinnis*, *C. plumatus*, and *C. sclateri*. Goren et al. (1991) modified this arrangement slightly when they recognized a group of species with a relatively low number of scale rows that included *C. amikami*, *C. bauchotae*, *C. centrolepis*, *C. crassus*, *C. dori*, *C. maculipinnis* and *C. plumatus*. Chen & Shao (2000) continued to recognize Goren et al.'s group, adding a new species, *C. nigromarginatus*. In 2013, Delventhal & Mooi (Chapter Four) identified a group of *Callogobius* which share a number of external features including modified scales on the caudal peduncle with unusually long ctenii (present in some other goby genera), female urogenital papilla with small lateral flaps of skin, a configuration of the preopercular papillae row (Row 20) in which it is always separate from the transverse opercular row (Row 21), preopercular pores absent, and caudal and pectoral fins not elongate. This group included *C. sclateri* (Steindachner), *C. bifasciatus* (Smith), *C. flavobrunneus* (Smith), *C. clarki* (Goren), and *C. winterbottomi* Delventhal & Mooi.

A variety of hypotheses have been proposed regarding the relationships between *Callogobius* and other gobies. Previous authors have noted similarities in the sensory papillae pattern with *Egglestonichthys* (Miller & Wongrat 1979). Other gobies share the presence of raised ridges, but in a different pattern; these genera include *Gobiopsis*, *Cristatogobius,* *Mangarinus*, and *Feia* (Winterbottom 2003). Lachner & McKinney (1974) proposed a possible relationship between *Pipidonia* (= *Gobiopsis*), *Barbuligobius* and *Callogobius.* Molecular studies that sample widely among gobies (Thacker 2003, Thacker 2009, Neilson & Stepien 2009, Thacker and Roje 2011, Thacker et al. 2011, Chakrabarty et al. 2012, Agorreta et al. 2013, Tornabene et al. 2013) consistently place *Callogobius* among the Gobiinae (sensu Pezold 1993) and imbedded families (the Gobiidae sensu Thacker [2009]), but collectively fail to identify likely candidates for close relationships.

In this study, we examine the intrarelationships among *Callogobius* species using morphology. Our objective is to determine if there are morphologically distinct, monophyletic subgroups within *Callogobius*. We evaluate McKinney's (1980) hypothesis of relationships, as well as Delventhal and Mooi's (2013, Chapter Four) *sclateri* group. We do not specifically evaluate the monophyly of *Callogobius,* or attempt to place it among a particular lineage of gobiines (or gobiine derivatives). Our preliminary observations suggest that many of the characters surveyed in this paper vary widely among gobies, either showing a high degree of homoplasy or being difficult to code due to the sheer amount of variation in morphology and the large number of potential character states. Thus, a study designed to evaluate the relationships of *Callogobius* among other gobies would likely require different characters or reinterpretation of existing characters used in the present study. This is beyond the scope of this paper.

METHODS

Abbreviations for institutional codes follow Fricke & Eschmeyer (2017) and/or Sabaj Pérez (2016). External morphology was examined using cyanine blue dye following the method of Akihito et al. (1993). Measurements and counts follow the methods outlined by Delventhal &

Mooi (2013, Chapter Four) and Delventhal et al. (2016, Chapter Seven), except caudal-fin length which was recorded as a proportion of head length, rather than standard length. Terminology for sensory papillae rows follows Delventhal & Mooi (2013, Chapter Four); row numbers follow Akihito and Meguro (1977); terminology for head pores and sensory canals follows Delventhal et al. (2016, Chapter Seven).

Cleared and stained specimens were prepared for osteological examination following the method of Tayler & Van Dyke (1985); at least one C&S specimen of each species was dissected following Weitzman (1974). Some of the osteological characters are described on the basis of proportions, which are discussed in the description of each character. All illustrations were made with the assistance of a camera lucida.

Taxon selection: We selected *Callogobius* species for inclusion in the study primarily on two criteria - they were relatively common in collections (and therefore available for clearing and staining with dissection), and they could be identified to species level with a high degree of certainty. We ignored the latter criterion for species identified as *C. maculipinnis*, even though we could not be certain they were in fact *C. maculipinnis* (rather than a similar species in the *maculipinnis* species complex - *C. bauchotae*, *C. irrasus*, *C. kuderi*, *C. nigromarginatus*, *C. snelliusi* or *C. vanclevei* - but not the distinctive *C. shunkan* or *C. pilosimentum*). All species identified as *C. maculipinnis sensu lato* scored consistently the same for characters used in this study and thus, we assume this species complex represents a monophyletic unit. We also ignored this criterion with the inclusion of *C.* cf. *centrolepis*; even though we are uncertain of the correct identification of our specimen, we included this species because it represented otherwise unsampled diversity, belonging to a group which we have previously informally referred to as the *tutuilae* group. Moreover, McKinney (1980) included a species identified as *C. centrolepis* in his analysis, and we chose to include this species to improve comparison between the two studies. Unfortunately, specimens closely matching the types/description of *C. hasseltii* were not available, so we were unable to sample this species in this study. Although we cleared and stained a significant number of undescribed species, we did not include them in the analysis. We discussed the placement of all valid or potentially valid species of *Callogobius* (as identified in Appendix A and Table A.1). We included *C*. sp. 20 in this paper even though it remains undescribed at the time of writing.

We examined a number of cleared and stained gobiines to determine appropriate outgroups and eventually chose two taxa: *Drombus* sp. and *Yongeichthys criniger*. These species were chosen based on availability and examination of their osteology which is relatively similar to other non-specialized gobiines (i.e., they displayed few automorphies in the characters studied). Both have been placed along with *Callogobius* within the Gobiinae of Pezold (1993) and the *Priolepis* group of Birdsong et al. (1988) (a non-monophyletic subgroup of gobiines defined by similarities in the axial skeleton); this supports their suitability as outgroup taxa for a study of the intrarelationships of *Callogobius*.

Character selection and coding: Characters were selected through direct examination of fluid preserved and cleared and stained (C&S) specimens. We identified characters that were consistent within the majority of species, easily defined, and variable among our species. We only included parsimony informative characters in the final matrix. In addition, we reviewed McKinney's (1980) characters, incorporating many of them (usually with significant modification in description and/or interpretation), but rejecting characters which we found to be difficult to code and inconsistent within a species (such as the presence/absence of a thin plate or hook at the posteriomedial corner of the upper pharyngeal tooth plate). In certain cases we did include polymorphic characters, and our coding strategy is discussed in the description of each character. The character state was coded as (?) in species where the character was variable, except in situations where the character was present or absent depending on the ontogenetic stage or specimen condition. In these cases the character was coded as present for a species if it was present in any individuals (example: ctenoid scales in *C. bifasciatus*). Whenever possible, we coded characters as binary, but we included a limited number of multistate characters. Many of the characters we included were continuous characters, including characters that are defined on the basis of proportions (such as caudal fin length as a proportion of head length). There are a number of statistical methods available for coding continuous characters in morphological studies (Garcia-Cruz and Sosa 2006, Lawing et al. 2008). However, we chose to define states in such a way as to reduce the number of taxa with intermediate states. We have not attempted to polarize characters directly, given their variability within gobiids as a whole. In general we do not make any claim that the characters used in this study are appropriate to hypothesize relationships between genera. Where characters are discussed in the text, character number is listed in parentheses for reference.

Phylogenetic analysis: We assembled the character matrix in MacClade (Maddison & Maddison 2005). Phylogenetic analysis was performed using PAUP* (Swofford 2002) with parsimony used as the optimality criterion; the branch-and-bound method was used to search for trees. In all analyses, characters were treated as unordered and were weighted equally. The trees were rooted with *Drombus* sp. and *Yongeichthys criniger*. A consensus tree was computed using all of the most parsimonious trees. In addition, to test the robustness of our phylogenetic hypotheses, we ran a bootstrap analysis using a full heuristic search and 1000 pseudoreplicates; groups with at least 50% frequency were retained in the consensus.

RESULTS

See Table 2.1 for the completed character matrix; detailed character descriptions are below.

TABLE 2.1 Morphological data matrix with 55 characters scored for 16 *Callogobius* species and two outgroup species (*Yongeichthys criniger* and *Drombus* sp.). Numbers in the columns (0, 1, or 2) indicate coded character states; a question mark (?) in the columns indicates that the character is variable or inapplicable. For reference, species in the outgroup are not highlighted, species in the *maculipinnis* group are highlighted in dark grey, species in the *tutuilae* group are highlighted in medium grey, species in *sclateri* group are highlighted in light grey, and species in the *hasseltii* group are highlighted in very light grey.

Character No.	*C. andamanensis*	*C. depressus*	*C. dori*	*C.hastatus*	*C. mucosus*	*C. okinawae*	*C. producta*	*C. tanegasimae*	*C.* sp. 20	*C. bifasciatus*	*C. clarki*	*C. flavobrunneus*	*C. sclateri*	*C.* cf. *centrolepis*	*C. maculipinnis*	*C. pilosimentum*	*C. shunkan*	*Y. criniger*	*Drombus* sp.
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0
2	1	1	1	1	1	1	1	1	1	0	0	0	0	1	?	?	?	?	?
3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	?	?
4	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
5	1	1	1	?	1	1	1	1	1	1	?	1	1	1	1	1	1	0	0
6	1	0	1	?	0	1	1	1	1	1	?	1	1	1	0	0	0	0	0
7	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0
8	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0
9	1	?	0	?	?	1	1	1	?	0	0	0	0	0	0	0	0	0	0
10	?	2	2	2	2	?	?	?	2	2	2	2	2	1	0	0	0	1	0
11	?	0	0	0	0	?	?	?	0	1	1	1	1	0	0	0	0	0	0
12	1	1	0	?	1	1	1	1	0	0	0	0	0	0	0	0	0	1	0
13	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0
14	0	0	0	0	0	1	0	0	0	1	1	2	2	0	0	0	0	0	0
15	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
16	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
17	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0
18	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0
20	0	0	0	0	0	0	0	0	0	1	1	1	1	0	2	2	2	0	0
21	2	2	2	2	2	2	2	2	2	1	1	1	1	0	2	2	2	0	0
22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0
23?	0	0	0	0	0	0	0	0	0	2	2	?	2	0	0	0	0	0	1

24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0
25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0
26	1	1	1	1	1	1	1	1	1	0	0	0	0	0	1	1	1	0	0
27	2	2	2	2	2	2	2	2	2	2	2	2	2	2	1	1	1	0	0
28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0
29?	0	0	0	1	0	0	1	0	0	1	1	1	?	1	0	0	0	0	0
30	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	1
31	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0
32	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	1
33	0	0	2	2	0	1	1	0	2	2	2	2	2	0	0	0	0	0	0
34	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	2	2	0	0
35	2	2	1	2	2	2	2	2	2	1	1	1	1	1	1	1	1	0	0
36	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0
37	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0
38	0	0	0	1	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0
39	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0
40	?	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	1	0
41	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0
42	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0
43	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0
44	0	1	0	0	1	0	1	0	0	0	0	0	0	1	1	1	1	1	0
45	1	0	1	1	0	1	1	1	1	1	1	1	1	1	0	0	0	0	1
46	1	1	1	1	?	1	1	1	1	1	1	1	1	0	0	0	0	0	0
47	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0
48	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0
49	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0
50	0	2	1	0	0	0	0	0	1	1	1	1	1	1	1	1	1	0	0
51	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
52	0	1	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0
53	?	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
54	0	0	0	0	0	0	1	1	0	1	1	1	1	1	2	2	2	0	0
55	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0

Character descriptions

External characters

1. Raised papillae rows

This basic arrangement of raised papillae ridges in a specific pattern with both horizontal and vertical rows is unique to *Callogobius* and present (with some minor variation) in all species, but absent in all other goby species (Figure 2.1).

Character states: absent (0), present (1).

2. Preopercular papillae row and transverse opercular row

The arrangement of the preopercular papillae row (row 20) and transverse opercular row (row 21) is distinctive in several *Callogobius* species. In the species sampled in this study, these two rows are always continuous with each other on each side in *C. andamanensis, C.* cf. *centrolepis, C. depressus*, *C. dori*, *C. hastatus*, *C. mucosus*, *C. okinawae*, *C. producta*, *C. tanegasimae*, and *C.* sp. 20. They are always widely separate (with the preopercular row positioned above and anterior to the transverse opercular row) in *C. bifasciatus*, *C. clarki C. flavobrunneus*, and *C. sclateri*. In *C. maculipinnis*, *C. pilosimentum* and *C. shunkan*, the condition of these rows is variable; they may be continuous or separate, the preopercular row may be anterior to or simply above the transverse opercular row and the condition may vary bilaterally on a single individual. We scored species that display this variability as (?). This character was also scored (?) for outgroup species because they lack the raised papillae rows (Figure 2.1).

Character states: always widely separate (0), always continuous (1), variable or N/A (?).

3. Transverse mandibular rows

Transverse mandibular rows (Row 16) occur on each side of the underside of the lower jaw in all species of *Callogobius*. In species sampled in the study, *C. maculipinnis*, *C. pilosimentum* and *C. shunkan* normally have 3-4 rows on each side, followed by a series of individual papillae that extend posteriorly towards the edge of the preopercle; all the other species normally have 10 or more rows. This character was scored (?) for outgroup species that lack the characteristic raised ridges (Figure 2.1).

Character states: 10 or more rows (0), 3-4 rows (1), N/A (?).

4. Presence of sensory canals and pores

In *Callogobius*, head pores are present in most species as larger juveniles and adults. They are absent in a number of species including two species sampled in this study, *C. clarki* and *C. hastatus*. All other species examined in this study, as well as the outgroup species *Drombus* sp. and *Yongeichthys criniger* have head pores and canals (Figure 2.1).

Character states: Present (0), absent (1).

5. Head pores ending as short tubes

All pored species of *Callogobius* have pores ending in short tubes, a trait distributed widely among gobies. The pores of the outgroups end as a simple opening. *C. clarki* and *C. hastatus* lack all pores and canals so this character was scored (?).

Character states: pores end as simple opening (0), pores end as short tubes (1), N/A (?).

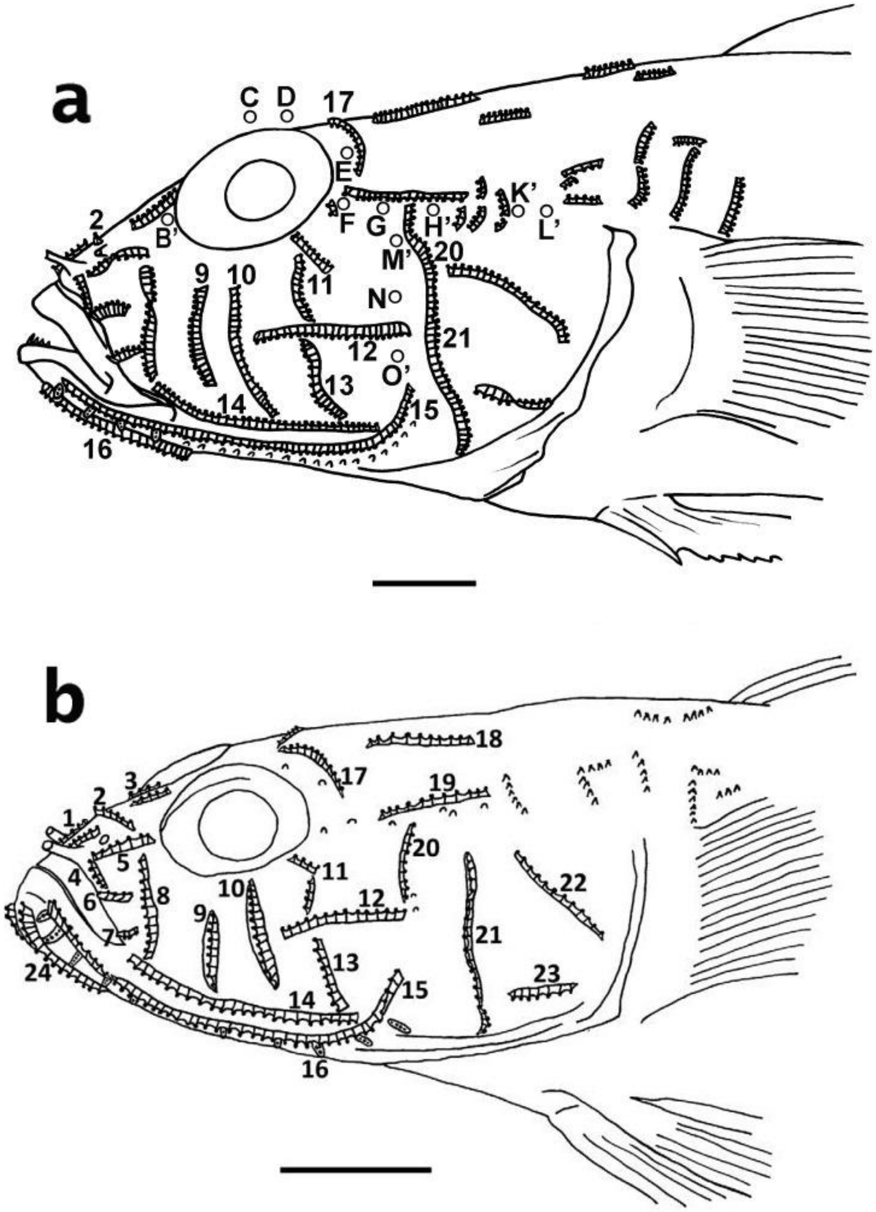

FIGURE 2.1 Lateral view of the external sensory system of the head in two *Callogobius* species. Headpores are indicated diagrammatically, rather than as short tubes; headpores and papillae rows are labelled following Delventhal et al. (2016, Chapter 7) and Delventhal & Mooi (2013, Chapter Four). Scale bars = 2 mm. **A.** *C. pilosimentum* (SMF 35756, 36.4 mm SL female holotype) showing the preopercular canal (Char. 6, state 0), the temporal canal (Char. 7, state 0) and transverse mandibular rows in groups of four (Char. 3, state 1). **B.** *C. winterbottomi* (ROM 92690, 22.9 mm SL male paratype) showing widely separate preopercular and transverse opercular papillae rows (Char. 2, state 0) and transverse mandibular rows in groups of 10 or more (Char. 3, state 0). Sensory pores are absent in this species (Char. 4, state 1).

6. Preopercular canal

The preopercular canal, when present, is bilateral and in *Callogobius* usually contains three (or sometimes two) pores. When the peropercular canal is present, a distinct groove is visible in the preopercle. In the species sampled in this study, the preopercular canal is absent in adult specimens of *C. andamanensis*, *C. bifasciatus*, *C.* cf. *centrolepis, C. clarki*, *C. dori*, *C. flavobrunneus*, *C. okinawae*, *C. producta*, *C. sclateri*, *C. tanegasimae* and *C.* sp. 20; it is present in *C. depressus*, *C. maculipinnis*, *C. mucosus*, *C. pilosimentum*, *C. shunkan*, *Yongeichthys criniger* and *Drombus sp*. *C. clarki* and *C. hastatus* lack all pores and canals so this character was scored (?) (Figure 2.1).

Character states: Present (0), absent (1), N/A (?).

7. Temporal canal

The temporal canal, when present, is bilateral and contains two pores (K' and L'). It is present in all adult specimens of *Callogobius maculipinnis*, *C. pilosimentum* and *C. shunkan*, and absent in all other *Callogobius* species sampled. *C. clarki* and *C. hastatus* lack all canals so this character was scored (?). The temporal canal is present in the outgroup species (Figure 2.1).

Character states: present (0), absent (1), N/A (?).

8. Scales with distinctly outlined centres

All *Callogobius* species examined had scales with distinctly outlined centres. These distinct centres are more easily viewed with the application of cyanine blue dye. They are distributed widely across the head and body in many species, but are restricted regionally in some species or individuals. They are typically less widely distributed in species with tiny scales, and the centres are often very tiny in these species. The scales of the two outgroup species lack distinctly outlined centres (Figure 2.2).

Character states: all scales without distinctly outlined centres (0), some scales with distinctly outlined centres (1).

9. Ctenoid scales

Ctenoid scales are present in all specimens of *Callogobius* cf. *centrolepis, C. dori, C. flavobrunneus, C. maculipinnis, C. pilosimentum, C. sclateri, C. shunkan*, juveniles and most adult *C. bifasciatus*, and *C. clarki*. They are present on *Drombus* sp. and *Y. criniger*. They are distributed in the posterior part of the body and in some species are present only on the caudal peduncle. They are absent in *C. andamanensis, C. tanegasimae, C. producta*, and *C. okinawae*. They are rarely present in *C. depressus, C. hastatus, C. mucosus* and *C.* sp. 20; when present they are found on the mid-lateral region, between the anal and caudal fins. We scored ctenoid scales as present (0) in *C. clarki* and *C. bifasciatus* because they seem to be invariably present in juveniles; but we scored *C. depressus, C. hastatus C. mucosus,* and *C.* sp. 20 as (?) since the presence or absence in these species cannot be correlated with a specific life stage.

Character states: present at least as juveniles (0), absent at all life stages (1), present rarely on some individuals (?).

10. Ctenii size and number

Callogobius maculipinnis, *C. pilosimentum*, *C. shunkan* and *Drombus* sp. have very fine, numerous ctenii, typically 30-37 on average-sized, regularly shaped mid-lateral scales. *C. bifasciatus, C. clarki*, *C. depressus C. dori, C. flavobrunneus*, *C. hastatus, C. mucosus C. sclateri*, and *C.* sp. 20 typically have 18 or fewer ctenii on average-sized, regularly shaped mid-lateral scales (or in caudal peduncle scales in species with limited ctenoid scale distribution). *Yongeichthys criniger* and *Callogobius* cf. *centrolepis* normally have an intermediate number of ctenii (about 28). Most specimens have a small number of irregularly shaped scales that may have greater or fewer numbers of ctenii.

Character states: usually more than 30 fine ctenii per scale (0), usually 20-29 ctenii per scale (1), usually fewer than 19 medium to large sized ctenii (2), N/A (?).

11. Caudal peduncle scales with elongate ctenii

We observed scales with particularly elongate ctenii on specimens of *Callogobius bifasciatus*, *C. clarki, C. flavobrunneus,* and *C. sclateri*; this elongation can be particularly remarkable in juvenile and subadult specimens. We scored this state as present (1) for a species if we observed it in any individuals, as caudal peduncle scales may be missing or damaged on some specimens. In many individuals, these elongate ctenii are dorso-ventrally asymmetrical in length. Other *Callogobius* species examined in this study and *Drombus* sp. lack elongate ctenii. *Yongeichthys criniger* has scales with elongate ctenii, but they are distributed differently and are most strongly elongate in the midflank region; we scored this character as absent (0) for this species (Figure 2.2).

Character states: absent (0), present (1), N/A caudal peduncle lacks ctenoid scales (?).

12. Predorsal scales

The predorsal scales are small, unevenly and sometimes scarcely distributed and imbedded in the skin in *Callogobius andamanensis, C. depressus, C. mucosus, C. okinawae*, *C. producta,* and *C. tanegasimae*. Undamaged specimens of these species, especially *C. okinawae, C. producta* and *C. tanegasimae* may appear to lack all predorsal scales. The predorsal scales are not deeply imbedded in *C. bifasciatus, C.* cf. *centrolepis, C. clarki, C. dori*, *C. flavobrunneus, C. maculipinnis, C. pilosimentum, C. sclateri, C. shunkan, C.* sp. 20, nor in the outgroup *Drombus* sp. In *Yongeichthys criniger*, imbedded predorsal scales are present just anterior to the dorsal fin. McKinney and Lachner **(**1978**)** described *Callogobius hastatus* as lacking predorsal scales; we found none on superficial examination of our specimens. However, we found a small number of imbedded scales in some species for which McKinney and Lachner (1978) recorded none. Hence, we score this character as unknown (?) for *C. hastatus*.

Character state: predorsal scales not imbedded (0), predorsal scales imbedded (1), predorsal scales appear absent (?).

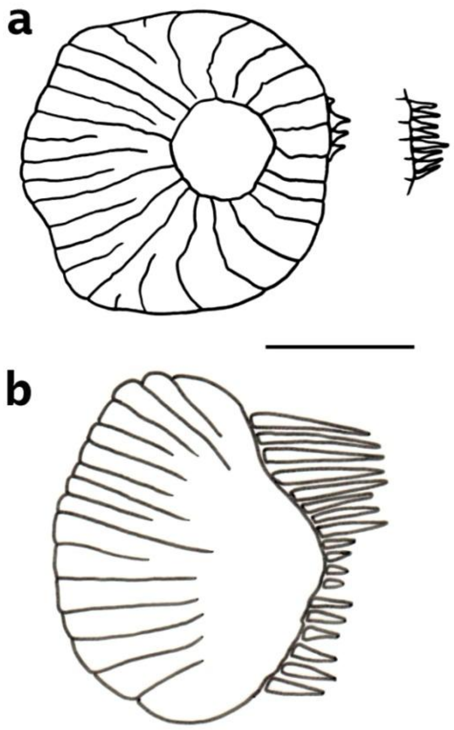

FIGURE 2.2 Scale morphology in *Callogobius*. Scale bar = 0.5 mm. **A.** (left) A mid lateral scale from *C. winterbottomi* (ROM 92690, 32.2 mm SL male paratype) with a distinctly outlined centre (Char. 8, state 1); (right) slightly elongate ctenii from a caudal peduncle scale (Char. 11, state 1) on the same individual. Scale bar = 1 mm. **B.** A caudal peduncle scale from *C. flavobrunneus* (CAS 63904, 35.5 mm SL female) with dramatically elongate ctenii (Char. 11, state 1).

13. Female urogenital papilla

In *Callogobius bifasciatus, C.* cf. *centrolepis, C. clarki C. flavobrunneus,* and *C. sclateri,* the female urogenital papilla is broad with small lateral, distal, flaps adjacent to the opening. In the remaining species as well as *Drombus* sp. and *Y. criniger*, the female urogenital papilla lacks distal lateral flaps (although sometimes folds of skin near the opening may appear flaplike) (Figure 2.3).

Character states: female urogenital papillae without distal lateral flaps (0), female urogenital papillae with distal lateral flaps (1).

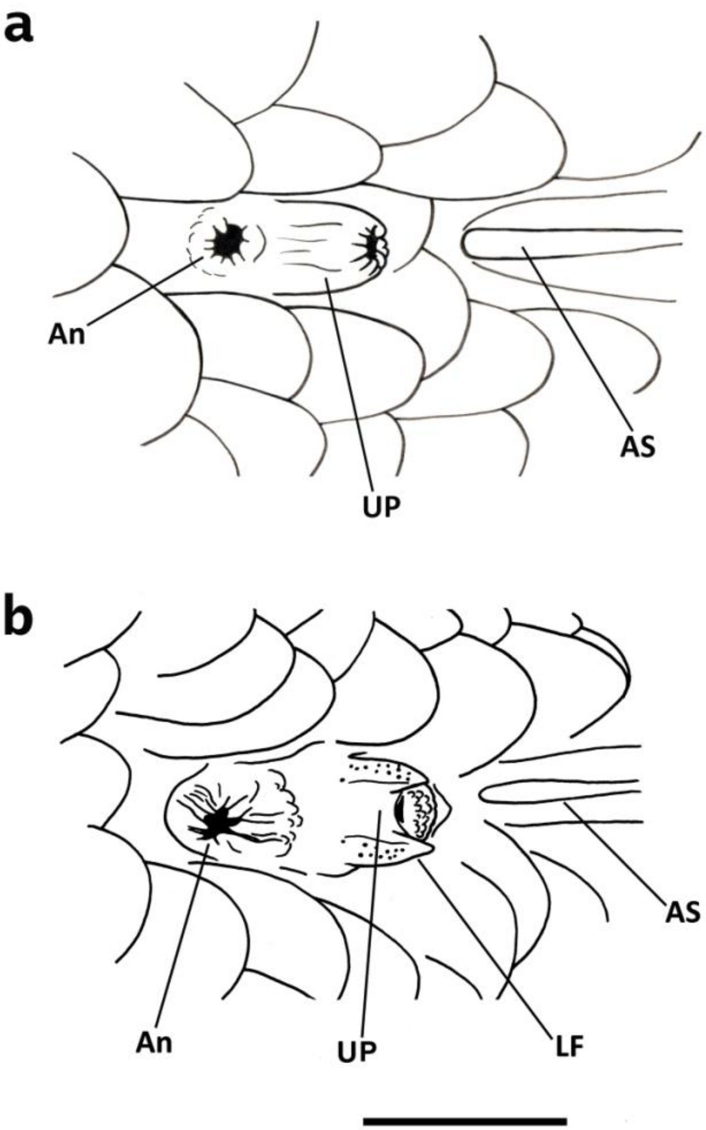

FIGURE 2.3 Female urogenital papilla morphology in *Callogobius*. Scale bar = 1 mm. Abbreviations: An = anus, UP = urogenital papilla, LF = lateral flaps,
AS = anal spine. **A.** *C.* sp. 20 (USNM 412481, 25.9 mm SL) showing the absence of lateral flaps (Char. 13, state 0). **B.** *C. clarki* (USNM 341181, 31.0 mm SL) showing the presence of lateral flaps (Char. 13, state 1).

14. United pelvic fins

The pelvic fins are united to form a margin in *Callogobius andamanenis*, *C.* cf. *centrolepis*, *C. depressus C. dori, C. hastatus, C. maculipinnis*, *C. mucosus*, *C. pilosimentum*, *C. producta*, *C. shunkan*, *C. tanigasimae, C.* sp. 20*, Drombus* sp. and *Yongeichthys criniger.* In these species the fifth ray is the same length or slightly longer than the fourth. In *C. bifasciatus*, *C. clarki* and *C. okinawae*, the pelvic fins are partially joined with the fifth ray shorter than the fourth. In *C. flavobrunneus* and *C. sclateri*, the fins are separate or connected by a minute inner membrane and the fifth ray is shorter than or subequal to the fourth (Figure 2.4).

Character states: fully united, rounded cup (0), partially united (1), separate or with minute membrane (2).

15. Pelvic frenum

A pelvic frenum is present in *Callogobius andamanenis*, *C. bifasciatus*, *C.* cf. *centrolepis, C. clarki C. depressus C. dori, C. hastatus,C. maculipinnis*, *C. mucosus, C. okinawae, C. pilosimentum, C. producta, C. shunkan, C. tanigasimae*, *C.* sp. 20*, Drombus* sp. and *Y. criniger;* it is absent in all specimens of *C. sclateri* and *C. flavobrunneus* (Figure 2.4).

Character states: present (0), absent (1).

16. Fifth pelvic-fin ray branching

In all included *Callogobius* and outgroup species except *C. sclateri* and *C. flavobrunneus,* the fifth pelvic-fin ray is branched at least twice in adults, with the second branch occurring in the proximal two-third of the fin ray. In *C. sclateri* and *C. flavobrunneus* it is branched only once, or branched a second time at the extreme tips (Figure 2.4).

Character states: branched at least twice (0), branched once or, if branched twice, the second branching only at tips (1).

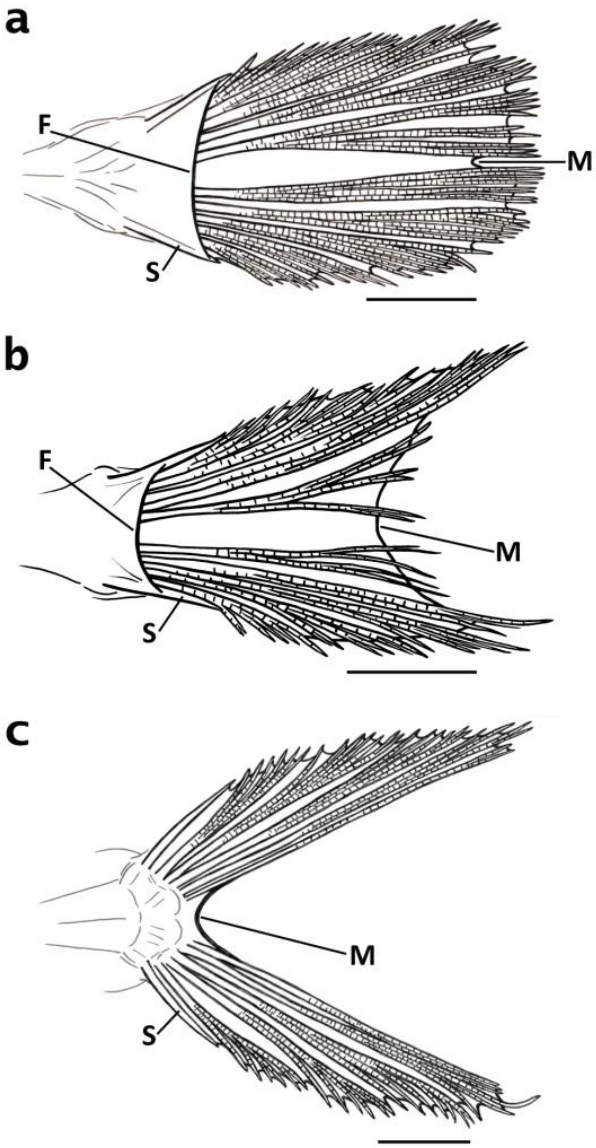

FIGURE 2.4 *Callogobius* pelvic fin morphology. Scale bar = 2 mm. Abbreviations: F = frenum, S = spine, M = membrane. **A.** Pelvic fins of *C.* sp. 20 (USNM 412481, 31.7 mm SL male) which are joined, with the fifth ray approximately the same length as the fourth (Char. 14, state 0), pelvic frenum present (Char. 15, state 0) and fifth pelvic-fin ray highly branched (Char. 16, state 0). **B.** Pelvic fins of *C. winterbottomi* (ROM 92690, 32.2 mm SL male paratype) which are partially joined, with the fifth ray shorter than the fourth (Char. 14, state 1), pelvic frenum present (Char. 15, state 0) and fifth pelvic-fin ray highly branched (Char. 16, state 0). **C.** Pelvic fins of *C. sclateri* (ROM 60877, 32.7 mm SL female) which are separate with a minute membrane (Char. 14, state 2), pelvic frenum absent (Char. 15, state 1) and fifth pelvic-fin ray branched only once (Char. 16, state 1).

17. Caudal fin elongation

The caudal fin is relatively elongate (its length significantly greater than head length) in *Callogobius andamanenis, C. depressus, C. dori, C. hastatus, C. mucosus, C. okinawae, C. producta*, *C. tanigasimae* and *C.* sp. 20. In these species, the pectoral fins also show a degree of elongation. In *C. bifasciatus*, *C.* cf. *centrolepis, C. clarki*, *C. flavobrunneus*, *C. maculipinnis*, *C. pilosimentum*, *C. sclateri*, *C. shunkan*, *Drombus* sp and *Yongeichthys criniger*, the caudal fin is relatively short, approximately the same length as or shorter than the head.

Character states: caudal fin not elongate (0), caudal fin elongate (1).

18. Black spot on dorsal edge of caudal fin

In the species sampled in this study, a distinct black spot is present on the dorsal edge of the caudal fin in *Callogobius dori*, *C. okinawae* and *C.* sp. 20. It is absent in all other examined species including the outgroups.

Character states: black spot absent on dorsal edge of caudal fin (0), black spot present on dorsal edge of caudal fin (1).

Cranium

19. Lateral ethmoids

In *Callogobius maculipinnis*, *C. pilosimentum* and *C. shunkan*, the lateral ethmoids are large and usually very firmly attached to the mesethmoid. In the remaining *Callogobius* species and the outgroup species, the lateral ethmoids are relatively small and easily disarticulated (Figure 2.5).

Character states: lateral ethmoids small, easily disarticulated from mesethmoid (0), lateral ethmoids large, firmly attached to mesethmoid (1).

20. Frontal expansion

In *Callogobius maculipinnis*, *C. pilosimentum* and *C. shunkan* the frontals are expanded deeply ventrally into the posterior region of the orbit and contact the medial parasphenoid processes, forming a bony interorbital septum. In both specimens of *C. pilosimentum* and two specimens of *C. maculipinnis* (ROM 57704), there is greater than normal dorsal expansion of the parasphenoid which meets the ventral expansion frontals. In *C. bifasciatus*, *C. clarki*, *C. flavobrunneus* and *C. sclateri* there is shallow frontal expansion into the posterior region of the orbit and this expansion is excluded from contact with the parasphenoid by the pterosphenoid. In the remaining species and the outgroups, there is little or no frontal expansion into the posterior region of the orbit (Figure 2.6).

Character states: frontals with little or no expansion (0), frontals expanded shallowly (1), frontals expanded deeply (2).

21. Mesethmoid strut

In *Callogobius bifasciatus, C. clarki, C. flavobrunneus* and *C. sclateri* the mesethmoid has an ossified medial strut that extends ventrally towards (but does not contact) the vomer/parasphenoid. In the remaining *Callogobius* species, an ossified strut is absent. In *Drombus* sp. and *Yongeichthys criniger*, this strut is present and reaches the vomer/parasphenoid (Figure 2.6).

Character states: ossified mesethmoid strut contacts vomer/parasphenoid (0), ossified mesethmoid strut does not contact vomer/parasphenoid (1), ossified mesethmoid strut absent (2).

22. Mesethmoid processes for ethmo-maxillary ligament

The mesethmoid process for origin of the ethmo-maxillary ligament is long and narrow, extending anterior to the articulation of the dorsoposterior arm of the palatine with the ethmoids in *Callogobius maculipinnis*, *C. pilosimentum* and *C. shunkan*. In other *Callogobius* and the outgroups the mesethmoid process is never larger than a small bump or nubbin and is posterior to the articulation of the palatine with the ethmoids. Winterbottom (1990) described a similar process in some species of *Trimmatom* and *Trimma* (Figure 2.5).

Character states: mesethmoid process for ethmo-maxillary ligament a small nubbin posterior to the articulation of the dorsoposterior arm of the palatine (0); long, narrow mesethmoid process for origin of the ethmo-maxillary ligament extending anteriorly to the articulation of the dorsoposterior arm of the palatine (1).

Suspensorium

23. Lower jaw canine teeth

Enlarged canine teeth, normally in pairs, are present on each side in all examined cleared and stained specimens of *Callogobius sclateri*, *C. bifasciatus*, and *C. clarki*. They are present in some lots identified as *C. flavobrunneus* (ROM 642CS and ANSP 162299) but not others (CAS 63904); we are currently examining the taxonomic relevance of this since specimens identified as *C. flavobrunneus* show geographic variation in colouration and may include more than one species. In the meantime, we have scored this character as present for *C. flavobrunneus*. A single enlarged canine tooth is present on each side of *Drombus* sp. but absent in *Yongeichthys criniger* and the other *Callogobius* species included in this study (Figure 2.7).

Character states: enlarged canine teeth absent (0), present singly (1), present in pairs (2).

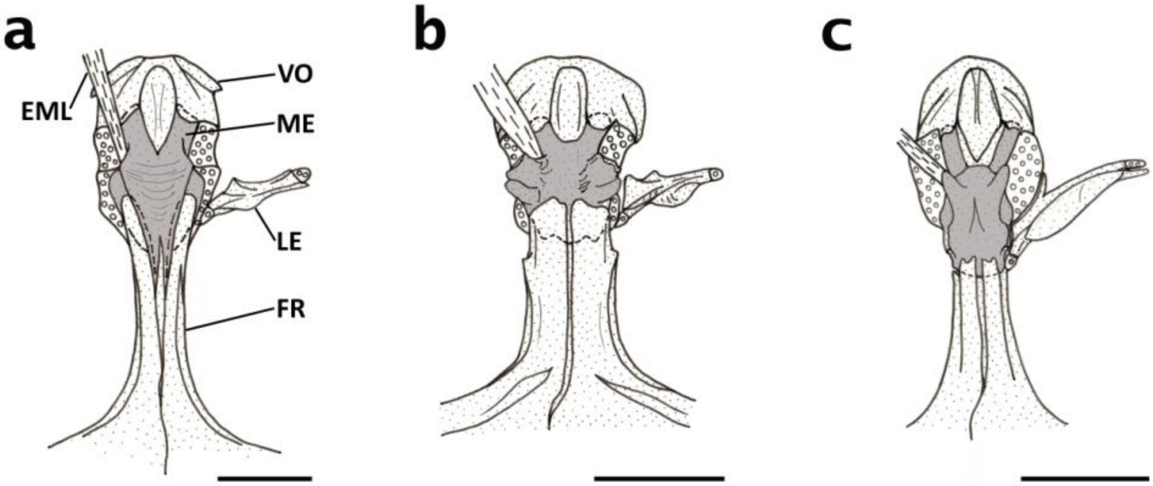

FIGURE 2.5 Dorsal view of the anterior portion of the cranium in in *Callogobius*. Scale bars = 1mm. Abbreviations: EML=ethmo-maxillary ligament, VO=vomer, ME=mesethmoid, LE=lateral ethmoid, FR=frontal.**A.** *C. andamanenis* (ROM 68202, 39.1 mm SL female) showing lateral ethmoids that are small and loosely joined to the mesethmoid (Char. 19, state 0), and the mesethmoid process for the ethmo-maxillary ligament a small nubbin (Char. 22, state 0). **B.** *C. bifasciatus* (ROM 39892, 33.2 mm male) showing lateral ethmoids that are small and loosely joined to the mesethmoid (Char. 19, state 0), and the mesethmoid process for the ethmo-maxillary ligament a small nubbin (Char. 22, state 0). **C.** *C. maculipinnis* (USNM 241882, 28.3 mm SL, female) showing lateral ethmoids that are large and firmly joined to the mesethmoid (Char. 19, state 1), and the mesethmoid process for the ethmo-maxillary ligament long and narrow (Char. 22, state 1).

24. Maxilla head

In all *Callogobius* examined, the anterolateral portion of the maxilla head is bowl-shaped and articulates with the anterolateral arm of the palatine. In *C. maculipinnis*, *C. shunkan*, and *C. pilosimentum*, this bowl is completely closed (or rarely has a minute opening in the center of the bone). In all other species examined as well as *Drombus* sp. and *Yongeichthys criniger*, this bowl is open (ring-shaped) and not filled in with bone (Figure 2.7).

Character states: open (0), closed (1).

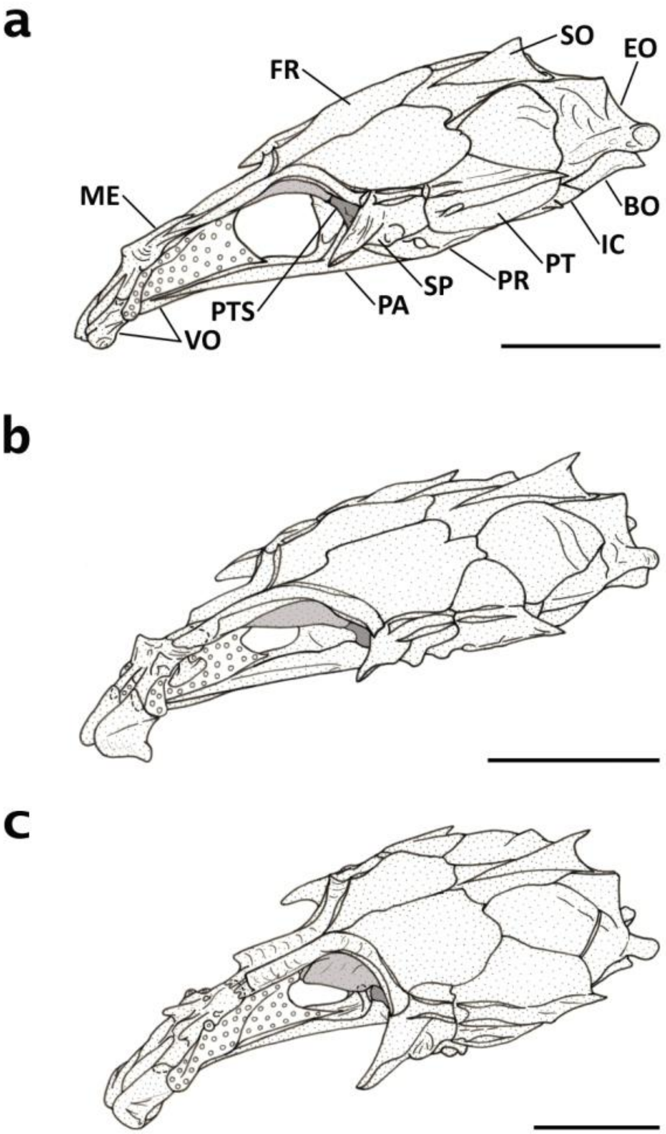

FIGURE 2.6 Dorsolateral view of the cranium of *Callogobius* with suspensorium, gill arches and eye removed. The pterosphenoid is dark grey and the expansion of the frontals is light grey. Scale bar = 2 mm. Abbreviations: ME = mesethmoid, VO = vomer, FR = frontal, PA = parasphenoid, PTS = pterosphenoid, SP = sphenotic, PR = prootic, PT = pterotic, IC = intercalar, BO = basioccipital, EO = exoccipital, SO = supraoccipital. **A.** *C. andamanensis* (ROM 68202, 39.1 mm SL female) showing the absence of frontal and parasphenoid expansion into orbit (Char. 20, state 0) and absence of mesethmoid strut (Char. 21, state 2). **B.** *C. bifasciatus* (ROM 39892, 33.2 mm male) showing limited frontal expansion and no parasphenoid expansion into orbit (Char. 20, state 1) and an ossified mesethmoid strut that does not contact the vomer/parasphenoid (Char. 21, state 1). **C.** *C. shunkan* (BLIP 19810168, 40.0 mm SL female) showing extensive frontal and parasphenoid expansion into orbit (Char. 20, state 2) and absence of mesethmoid strut (Char. 21, state 2).

25. Quadrate shape

In *Callogobius maculipinnis*, *C. shunkan* and *C. pilosimentum*, the leading anterior edge of the dorsal lamina of the quadrate is expanded anteriorly and forms a right angle; the posterodorsal corner is blunted where it articulates with the metapterygoid (resulting in a five-sided shape). In the remaining species, as well as the outgroup species, the leading anterior edge expands only slightly or not all and does not form a right angle; the posterodorsal edge is usually curved abruptly downward where it articulates with the metapterygoid (resulting in a three- or four-sided shape) (Figure 2.7).

Character states: dorsal lamina of quadrate without right-angle-forming anterior expansion (0), dorsal lamina of quadrate with right-angle-forming anterior expansion (1).

26. Metapterygoid flange over quadrate

In *Callogobius bifasciatus, C.* cf. *centrolepis, C. clarki*, *C. flavobrunneus* and *C. sclateri*, there is an anterior flange-like extension of the metapterygoid that usually forms a bridge to the quadrate, although in some specimens only appears as a slight extension on the upper edge of the metapterygoid over the cartilage separating the metapterygoid and the quadrate. This flange is absent in the other *Callogobius* species examined, but present in *Drombus* sp. and *Yongeichthys criniger* (Figure 2.7).

Character states: anterior flange present (0), absent (1).

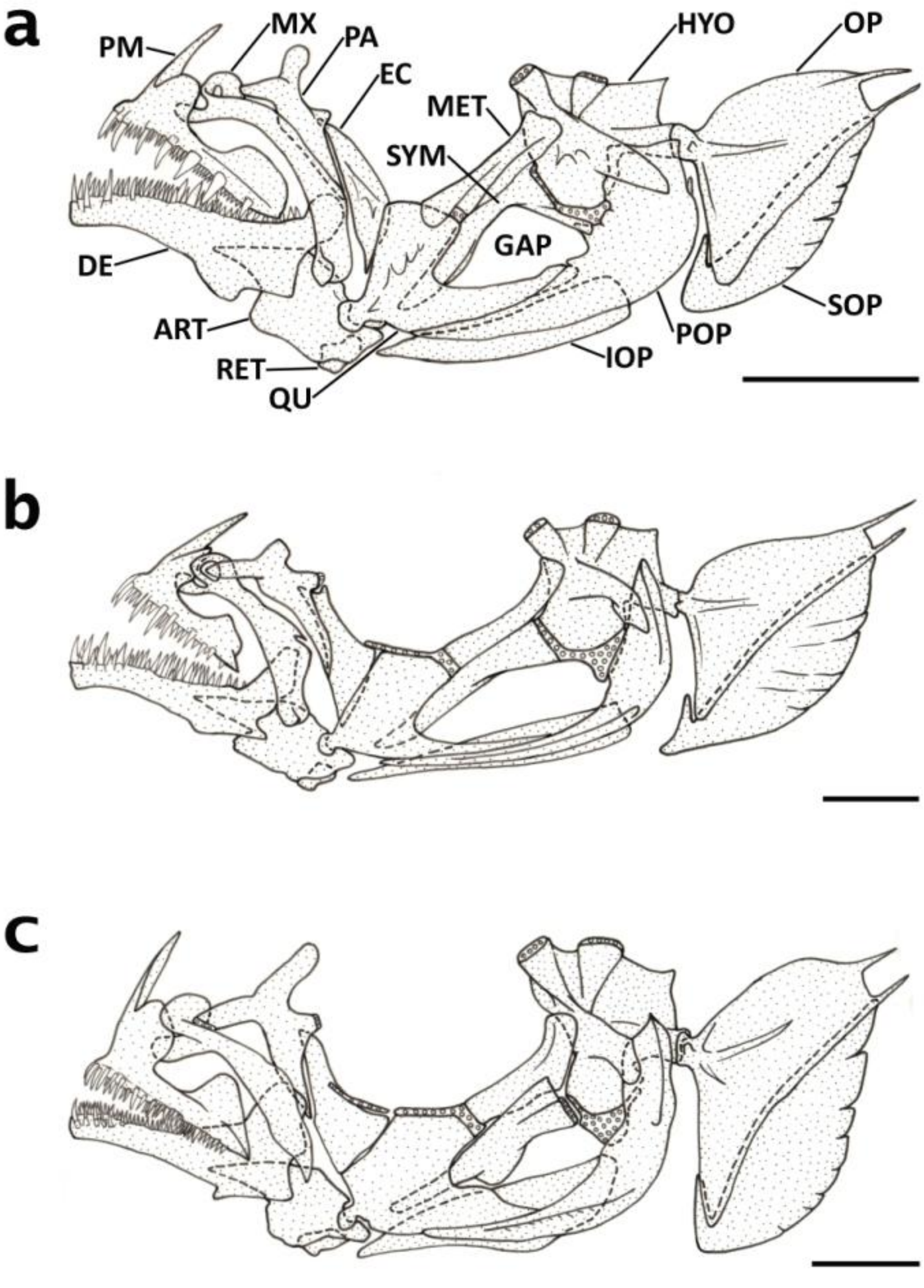

Figure 2.7 Caption on next page.

FIGURE 2.7 Lateral view of the suspensorium of *Callogobius*. Two suspensorium characters, the palatine dorsal arm angle (Char. 30) and palatine shaft width (Char. 31), are not labeled because the palatine does not lie flat while articulated with the remainder of the suspensorial bones. Scale bars = 2 mm. Abbreviations: PM = premaxilla, DE = dentary, ART = anguloarticular, RET = retroarticular, QU = quadrate, MX = maxilla, PA = palatine, EC = ectopterygoid, SYM = symplectic, MET = metapterygoid, HYO = hyomandibula, OP = opercle, POP = preopercle, IOP = interopercle, SOP = subopercle, GAP = symplectic gap. **A.** *C. bifasciatus* (ROM 39892, 33.2 mm male) showing enlarged canine teeth in the lower jaw (Char. 23, state 2), an open maxilla head (Char. 24, state 0), the dorsal lamina of the quadrate without right-angle-forming anterior expansion (Char 25, state 0), an anterior flange on the metapterygoid which reaches the quadrate (Char. 26, state 0), posterior region of the metapterygoid without ventral extension (Char. 27, state 2), quadrate without expansion into the symplectic gap (Char. 28, state 0), bony protuberance present at the preopercular ligament (Char. 29, state 1), palatine with short anterolateral arm (Char. 32, state 1) and a curve at the junction between the anterolateral and posterolaterial arm (Char. 33, state 2), ectopterygoid broad with tapered shaft (Char. 34, state 1) and a broad dorsal margin without a second bony protuberance (Char. 35, state 1), preopercle with dorsal truncation (Char. 36, state 1) and no ventral groove (Char. 37, state 1), hyomandibular with short posterodorsal condyle (Char. 38, state 1). **B.** *C. depressus* (USNM 214728, 63.2 mm SL female) showing lack of enlarged canine teeth in the lower jaw (Char. 23, state 0), an open maxilla head (Char. 24, state 0), the dorsal lamina of the quadrate without right-angle-forming anterior expansion (Char 25, state 0), no anterior flange on the metapterygoid (Char. 26, state 1), posterior region of the metapterygoid without ventral extension (Char. 27, state 2), quadrate without expansion into the symplectic gap (Char. 28, state 0), no bony protuberance present at the preopercular ligament (Char. 29, state 0), palatine with long anterolateral arm (Char. 32, state 1) and no curve at the junction between the anterolateral and posterolateral arm (Char. 33, state 0), ectopterygoid broad with tapered shaft (Char. 34, state 1) and a broad dorsal margin with a second bony protuberance (Char. 35, state 2), preopercle without dorsal truncation (Char. 36, state 0) but with a ventral groove (Char. 37, state 0), hyomandibula without short posterodorsal condyle (Char. 38, state 0). **C.** *C. maculipinnis* (ROM 57704, 45.3 mm SL) showing lack of enlarged canine teeth in the lower jaw (Char. 23, state 0), a closed, bowl-shaped maxilla head (Char. 24, state 1), dorsal lamina of the quadrate with right-angle-forming anterior expansion (Char 25, state 1), no anterior flange on the metapterygoid (Char. 26, state 1), posterior region of the metapterygoid with ventral extension at the point of articulation of the symplectic and hyomandibula (Char. 27, state 1), quadrate with expansion into the symplectic gap (Char. 28, state 1), no bony protuberance present at the preopercular ligament (Char. 29, state 0), palatine with long anterolateral arm (Char. 32, state 1) and no curve at the junction between the anterolateral and posterolateral arm (Char. 33, state 0), ectopterygoid very broad with a distinct shaft (Char. 34, state 2) and a broad dorsal margin without a second bony protuberance (Char. 35, state 1), preopercle without dorsal truncation (Char. 36, state 0) but with a ventral groove (Char. 37, state 0), hyomandibula without short posterodorsal condyle (Char. 38, state 0).

27. Metapterygoid ventral expansion

In *Callogobius maculipinnis*, *C. shunkan* and *C. pilosimentum*, the posteroventral region of metapterygoid is expanded ventrally towards the point of articulation with the symplectic and hyomandibula. As a result, the anteroventral portion of the hyomandibula is relatively smaller than in other species. In all the other *Callogobius* species examined, the ventral expansion of the metapterygoid is relatively shallow, if present at all. In *Drombus* sp. and *Yongeichthys criniger* the metapterygoid expands ventrally but the area of maximum extension is posterior to the point where the symplectic articulates with the hyomandibula (Figure 2.7).

Character states: posterior region of metapterygoid with ventral extension posterior to point of articulation of the symplectic and hyomandibula (0), posterior region of metapterygoid with ventral extension at point of articulation of the symplectic and hyomandibula (1), posterior region of metapterygoid with minimal or no ventral extension (2).

28. Quadrate expansion into symplectic gap

In *Callogobius maculipinnis, C. shunkan, C. pilosimentum*, the posteriorly-directed ventral arm of the quadrate extends dorsally into the symplectic gap region towards the symplectic. In approximately half the specimens in this group, the symplectic also extends ventrally, reaching or nearly reaching the quadrate extension. This symplectic extension appears to be bilateral when present, although we are not able to correlate it with particular species or collection localities. In all other *Callogobius* species examined, as well as *Drombus* sp. and *Yongeichthys criniger*, the quadrate and symplectic do not expand into the symplectic gap region (Figure 2.7).

Character states: quadrate does not extend into symplectic gap region (0), quadrate extends into symplectic gap region (1).

29. Bony protuberance for preopercular/hyomandibula ligament

Two ligaments are present on the posterior edge of the preopercle. One connects with the articulating arm of the opercle; the second, which attaches anterodorsally relative to the first, connects with the ventral edge of the posterior condyle of the hyomandibula. The base of the second ligament forms a short bony protuberance on the preopercle in *Callogobius bifasciatus*, *C.* cf. *centrolepis, C. clarki*, *C. flavobrunneus*, *C. hastatus* and *C. producta*. This protuberance was present on one (of two) specimens of *C. sclateri*; we scored this character as variable (?) for this species. In some individuals, there is also a protuberance at the point of attachment of the ligament onto the hyomandibula (Figure 2.7).

Character states: preopercle without bony protuberance at ligament origin (0), preopercle with bony proteuberance at ligament origin (1).

30. Palatine dorsal arm angle

The dorsal portion of the palatine has two large articular processes – an anteroventrally-directed arm that articulates with the maxilla (hereon referred to as the anterolateral arm), and a dorsomedially directed arm that articulates with ethmoids (posterodorsal arm). There is also a smaller posteroventrally directed arm that overlaps the dorsal tip of the ectopterygoid. In *Callogobius*, the angle between the two dorsal arms varies. When measured along the upper outer edge of the bone, the angle between the two arms is greater than 135 degrees in *C.* cf. *centrolepis, C. maculipinnis*, *C. pilosimentum* and *C. shunkan*. The angle is less than or approximately equal to 135 degrees in the remaining species. In *Yongeichthys criniger*, the angle is greater than 135 degrees and in *Drombus* sp. it is approximately equal to 135 degrees.

Character states: angle between dorsal arms of the palatine greater than 135 degrees (0), angle between arms less than or equal to 135 degrees (1).

31. Palatine shaft width

The shaft of the palatine is relatively broad in *Callogobius maculipinnis, C. pilosimentum* and *C. shunkan*. The anterior mid lateral edge forms a distinct point which is set ventral to the ligament which joins to the vomer; the palatine shaft usually appears roughly rhomboid in shape. The palatine shaft is relatively narrow in the other examined *Callogobius* species and *Yongeichthys criniger*; the anteriolateral point (not always present) is positioned at approximately the same level as the ligament which attaches to the vomer and the palatine shaft appears tapered in shape. The palatine shaft is very narrow in *Drombus* sp. Character states: palatine shaft broad (0), palatine shaft narrow (1).

32. Palatine anterolateral arm length

In *Callogobius bifasciatus, C. clarki, C. flavobrunneus, C. sclateri* and *Drombus* sp., the anterolateral arm of the palatine is relatively short, so that there is little or no gap between the upper edge of the palatine shaft and maxilla when the specimen is at rest in a closed-mouth position. In the remaining species including *Yongeichthys criniger*, the arm is relatively long, and there is a gap between the maxilla and the upper edge of the palatine shaft (Figure 2.7). Character states: palatine anterodorsal arm relatively long (0), palatine anterolateral arm relatively short (1).

33. Palatine anterolateral arm curve

In *Callogobius bifasciatus*, *C. clarki*, *C. dori*, *C. flavobrunneus*, *C. hastatus*, *C. sclateri* and *C.* sp. 20, there is a distinct curve at the junction between the anterolateral and posterodorsal arm. In these species, the anterolateral arm (which continues to be curved proximally) is directed more anteriorly and the posterodorsal arm is directed more medially; the flat shaft of the palatine rests in a relatively medial direction. In *C. andamanensis*, *C.* cf. *centrolepis, C. depressus, C. maculipinnis*, *C. mucosus*, *C. tanegasimae*, *C. pilosimentum*, *C. shunkan*, *Drombus* sp. and *Yongeichthys criniger*, there is little or no distinct curve at the junction between the anterolateral and posterodorsal arms. In these species, the anterolateral arm, if curved, is curved distally, and the flat shaft of the palatine rests in a relatively lateral direction. In *C. okinawae* and *C. producta*, there is a slight curve between at the junction of the anterolateral and posterodorsal arms (Figure 2.7).

Character states: little or no curve at the junction of the anterolateral and posterodorsal arms (0), slight curve at the junction of the anterolateral and posterodorsal arms (1); distinct curve at the junction of the anterolateral and posterodorsal arm (2).

34. Ectopterygoid shape

In *Callogobius maculipinnis*, *C. pilosimentum* and *C. shunkan*, the ectopterygoid is very broad ventrally, with the anteriodorsal region appearing to be a distinct, curved narrower shaft. In the remaining examined *Callogobius* species, the ectopterygoid is moderately broad and the shaft is relatively tapered. In *Drombus* sp. and *Yongeichthys criniger* the ectopterygoid is narrow and tapered (Figure 2.7).

Character states: ectopterygoid narrow and tapered (0), ectopterygoid broad with tapered shaft (1), ectopterygoid very broad with distinct shaft (2).

35. Ectopterygoid dorsal process

In *Callogobius andamanenis, C. depressus*, *C. hastatus, C. mucosus, C. okinawae*, *C. producta, C. tanigasimae* and *C.* sp. 20, the dorsal margin of the ectopterygoid has a distinct bony process resulting in double tip. McKinney (1980) interpreted this morphology as a socket for articulation with the palatine; we are uncertain of this interpretation, although the process seems to be associated with the point of attachment of a ligament which joins to the lateral ethmoid. The remaining *Callogobius* species have a relatively broad dorsal margin to the ectopterygoid; it may be abruptly curved in some individuals, but lacks a distinct second protuberance. In *Drombus* sp. and *Yongeichthys criniger*, the dorsal margin of the ectopterygoid forms a simple, narrow point (Figure 2.7).

Character states: ectopterygoid dorsal margin a narrow point (0), ectopterygoid dorsal margin broad, often with abrupt curve (1), ectopterygoid dorsal margin broad with a second bony process (2).

36. Preopercle dorsal truncation

In *Callogobius bifasciatus*, *C.* cf. *centrolepis, C. clarki*, *C. flavobrunneus* and *C. sclateri* the dorsal edge of the preopercle is truncate (with only a slight anteroventral slope as it approaches the point where the preopercle is overlapped by the hyomandibula flange). In the remaining *Callogobius* examined as well as *Drombus* sp. and *Yongeichthys criniger*, the dorsal edge of the preopercle is tapered or more dramatically sloped. In our specimen of *C. bifasciatus,* there is a bony bridge between the symplectic and preopercle; we did not observe this in any other *Callogobius* specimen (Figure 2.7).

Character states: preopercle dorsal edge with dramatic slope (0), preopercle dorsal edge truncate (1).

37. Ventral groove on preopercle

In all *Callogobius* lacking the preopercular canal, there is no corresponding posterior bony groove in the preopercle (see Character 6). Furthermore, *C. bifasciatus, C.* cf. *centrolepis, C. clarki*, *C. flavobrunneus* and *C. sclateri* lack a ventral groove on the anterior arm of the preopercle; a ventral groove is present on all other examined *Callogobius* species as well as *Drombus* sp. and *Yongeichthys criniger* (Figure 2.7).

Character states: ventral groove on preopercle present (0), ventral groove on preopercle absent (1).

38. Hyomandibula dorsal condyle relative height

In *Callogobius bifasciatus*, *C.* cf. *centrolepis, C. clarki*, *C. flavobrunneus*, *C. hastatus* and *C. sclateri*, the posterodorsal condyle of the hyomandibula appears relatively short compared to the anterodorsal condyle; its maximum bony height at its highest (anterior) edge is approximately equal (or subequal) to the maximum bony height of the lowest (anterior) edge of the anterodorsal condyle. In the remaining species including the outgroups, the posterodorsal condyle is similar in height to the anterodorsal condyle; the maximum bony height of the anterior edge of the posterodorsal condyle is greater than the maximum bony height of the anterior edge of the anterodorsal condyle (Figure 2.7).

Character states: posterdorsal condyle similar height to anterodorsal condyle (0), posterodorsal condyle relatively short (1).

Gill arches

39. Pharyngobranchial 3 teeth

In *Callogobius*, the teeth on pharyngobranchial 3 display a range of morphologies. They may be conical and tapered (which we refer to as tooth type A), or have an abruptly curved tooth tip preceded by slight bulging (tooth type B; similar to Character 8 of Parenti and Thomas [2008]). The bulge may be flattened distally (sometimes appearing hook-like (tooth type C), or have a shorter, second tip (tooth Type D). Many individuals display two or more morphologies on a single tooth plate. Tooth types C and D are present on all individuals of *C. maculipinnis, C. shunkan*, *C. pilosimentum* and *Yongeichthyscriniger*. The remaining examined species lack tooth type D, and are usually restricted to tooth types A or B, expect tooth type C which is present on some *C. hastatus* (Figure 2.8).

Character states: tooth type D absent (0), tooth type D present (1).

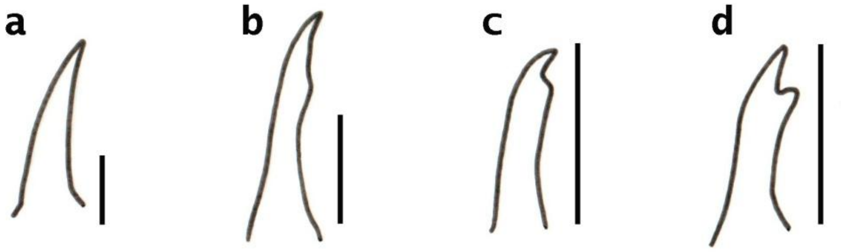

FIGURE 2.8 Pharyngobranchial tooth morphology in *Callogobius*. Scale bars = 0.25 mm. **A.** Pharyngobranchial 3 tooth type A (from *Callogobius depressus,* USNM 214728, 63.2 mm SL female). **B.** Pharyngobranchial 3 tooth type B (from *Callogobius clarki*, USNM 220031 39.9 mm SL). **C.** Pharyngobranchial 3 tooth type C (*Callogobius hastatus*, CAS 63897, 26.9 mm SL). **D.** Pharyngobranchial 3 tooth type D (*Callogobius maculipinnis*, USNM 241882, 28.3 mm SL, female).

40. Epibranchial tooth patches

We observe tooth patches on epibranchial 2 on all specimens of *Callogobius bifasciatus, C.* cf. *centrolepis, C. clarki, C. flavobrunneus, C. maculipinnis, C. pilosimentum, C. sclateri, C. shunkan,* and *Drombus sp.*; many individuals had tooth patches on epibranchials 1 and 3 as well. The arrangement (when present) is sometimes irregular and may not be symmetrical. Our dissected specimen of *C. andamanensis* had a tooth patch on epibranchial 2 on one side; we scored this species (?). We were unable to find any epibranchial tooth patches on the remaining examined species or *Yongeichthys criniger*.

Character states: epibranchial tooth patches present (0), or absent (1), variable (?)

41. Pharyngobranchial 2 with arm to interarcual cartilage

Pharyngobranchial 2 articulates with the interarcual cartilage through connective tissue. In *Callgobius maculipinnis*, *C. shunkan*, and *C. pilosimentum*, there is a narrow, clearly defined arm on pharyngobranchial 2 that projects dorso-medially towards interarcual cartilage. The remaining species as well as the outgroup species lack a clearly defined arm, although there may be dorso-medial bulging toward the interarcual cartilage (Figure 2.9).

Character states: pharyngobranchial 2 arm to interarcual cartilage absent (0), present (1).

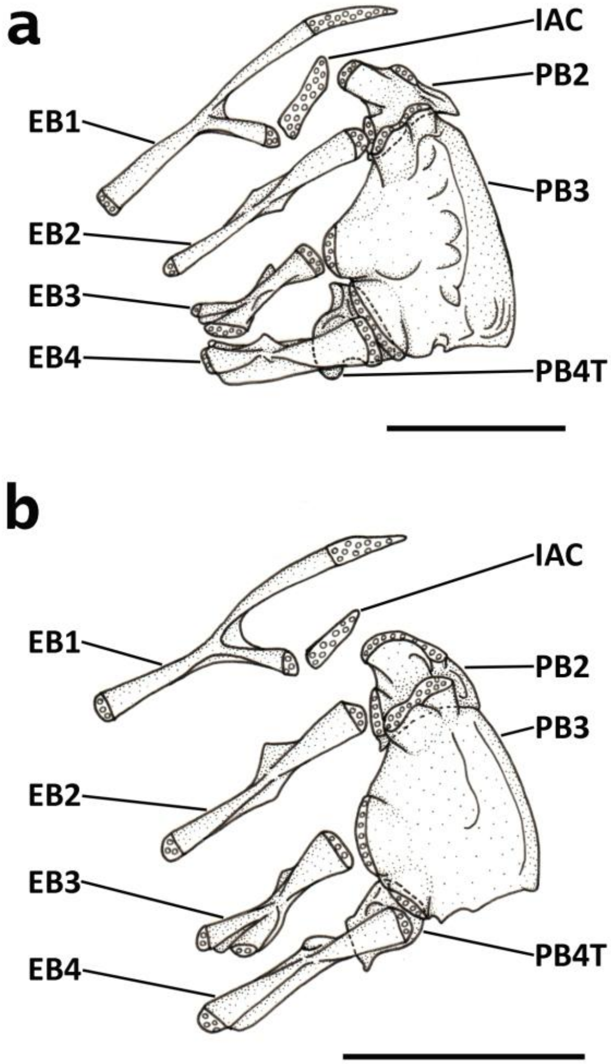

Figure 2.9 Caption on next page.

FIGURE 2.9 Dorsal gill arch morphology in *Callogobius*. Scale bar = 1 mm. Abbreviations: EB1 = epibranchial 1, EB2 = epibranchial 2,EB3 = epibranchial 3, EB4 = epibranchial 4, IAC = interarcual cartilage, PB2 = pharyngobranchial 2 PB3 = pharyngobranchial 3, PB4T = pharyngobranchial 4 toothplate. **A.** *C. maculipinnis* (MPM 45773, 30.0 mm SL) showing distinct arm of pharyngobranchial 2 to interarcual cartilage (Character 41, state 1) and broad dorsolateral head of epibranchial 3 (Character 44, state 0). Epibranchial tooth patches not illustrated. **B.** *C. tanegasimae* (uncataloged, 32.8 mm SL female) showing no distinct arm of pharyngobranchial 2 to interarcual cartilage (Character 41, state 0) and a relatively narrow dorsolateral head of epibranchial 3 (Character 44, state 1).

42. Hypobranchial 1 anterolateral process

In *Callogobius maculipinnis, C. shunkan, C. pilosimentum*, *Drombus* sp. and *Yongeichthys criniger*, the anterolateral process of hypobranchial 1 is directed anteriorly, or within 45 degrees of the anterior direction. In the remaining species, this process is directed laterally or within a 45 degree angle of the lateral direction. The exact angle of the process may vary within a species and may be slightly asymmetrical in a single individual (Figure 2.10).

Character states: anteriorly directed (0), laterally directed (1).

43. Hypobranchial 1 proportions

In *Callogobius maculipinnis*, *C. shunkan*, *C. pilosimentum*, and *Yongeichthys criniger* the length of the posterior arm of hypobranchial 1 arm is relatively long, at least 2/3 of the medial arm. In all other included *Callogobius* and *Drombus sp.*, the posterior arm is relatively short, approximately half the length of the medial arm (Figure 2.10).

Character states: hypobranchial 1 posterior arm short (0), hypobranchial 1 posterior arm long (1).

44. Epibranchial 3

Epibranchial 3 has two lateral heads - a dorsolateral head which attaches via a ligament to an anterodorsal projection on epibranchial 4 and a ventrolateral head which articulates with ceratobranchial 3. In *Callogobius* cf. *centrolepis, C. depressus, C. maculipinnis, C. mucosus, C. shunkan, C. pilosimentum, C. producta,* and *Yongeichthys criniger,* the dorsal head is significantly broader than the ventral head. In all other *Callogobius* examined and *Drombus sp.*, the two lateral heads are approximately the same width (the dorsal head is may be slightly narrower or slightly broader); it is not always symmetrical (Figure 2.9).

Character states: dorsolateral head significantly broader than ventrolateral head (0), dorsal lateral head approximately the same width (1).

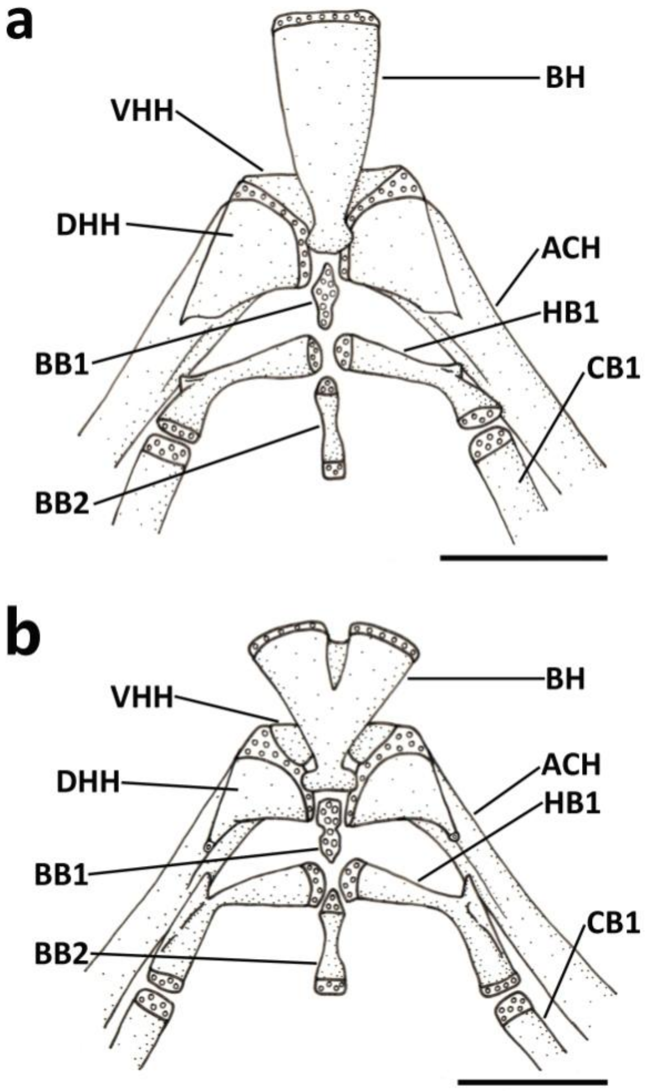

FIGURE 2.10 Dorsal view of the anterior portion of ventral gill arch and hyoid arch of *Callogobius*. Scale bar = 1 mm. Abbreviations: BH = basihyal, VHH = ventral hypohyal, DHH = dorsal hypohyal, ACH = anterior ceratohyal, BB1 = basibranchial 1, BB2 = basibranchial 2, CB1 = ceratobranchial 1, HB1 = hypobranchial 1. **A.** *C. hastatus* (17.0 mm SL) showing a narrow basihyal (Char. 45 state 1), and hypobranchial 1 with a laterally directed anterolateral process (Char. 42, state 1) and short posterior arm (Char. 43, state 0). Scale bar = 6.5 mm. **B.** *C. maculipinnis* (MPM 45773, 30.0 mm SL) showing a moderately broad basihyal (Char. 45, state 0) which is distinctly bilobed, and hypobranchial 1 with an anteriorly directed anterolateral process (Char. 42, state 0) and long posterior arm (Char. 43, state 1).

45. Basihyal

The basihyal is moderately broad, with a bony width at least three-fourths of its length in *Callogobius depressus*, *C. maculipinnis*, *C. mucosus*, *C. pilosimentum*, and *C. shunkan* it may be slightly to distinctly bilobed in some individuals, to a degree that is not consistant within species. It is moderately broad in *Yongeichthys criniger*. It is narrow, with a bony width less than three-fourths of its length in the remaining sampled *Callogobius* species and *Drombus sp.* (Figure 2.10).

Character states: moderately broad (0), narrow (1).

Pectoral-fin osteology

46. Postcleithrum

The ventral postcleithrum is long and slender in *Callogobius* cf. *centrolepis, C. maculipinnis*, *C. pilosimentum*, *C. shunkan*, *Drombus* sp. and *Yongeichthys criniger*. It is relatively small and short in *C. andamensis, C. bifasciatus, C. clarki, C. dori, C. flavobrunneus, C. okinawae*, *C. producta*, *C. sclateri*, *C. tanegasimae* and *C.* sp. 20. We were unable to find a postcleithrum in *C. mucosus* (McKinney [1980] also reported it absent) so we scored this character as (?). Like other gobiids, species of *Callogobius* lack a dorsal postcleithrum (Akihito, 1969, 1986; Gill and Mooi, 2012).

Character states: ventral postcleithrum long (0), ventral postcleithrum short (1).

47. Dorsal processes of cleithrum

The dorsal processes of the cleithrum are relatively broad and widely separated in *Callogobius bifasciatus*, *C.* cf. *centrolepis, C. clarki*, *C. flavobrunneus*, *C. maculipinnis*, *C. pilosimentum*, *C. sclateri*, *C. shunkan*, *Drombus* sp. and *Yongeichthys criniger*. In *C. andamanenis, C. depressus, C. dori, C. hastatus, C. mucosus, C. okinawae, C. producta, C. tanigasimae* and *C.* sp. 20, the dorsal processes are narrow and closely spaced (the tip of the anterior dorsal process is usually directed slightly posteriorly (Figure 2.11).

Character states: dorsal processes of cleithrum broad and widely separated (0), dorsal processes of cleithrum narrow and closely spaced (1).

48. Lateral flange of cleithrum

The dorsal portion of the lateral flange of the cleithrum (a site of attachment for pectoral fin musculature) is curved posteriorly in *Callogobius bifasciatus*, *C. clarki*, *C. flavobrunneus*, and *C. sclateri*. In these species, the dorsal tip points towards the area between the first and second proximal radials. In the remaining species, the dorsal portion of the lateral flange is not curved posteriorly; in these species the dorsal tip points towards one or both of the dorsal processes of the cleithrum (Figure 2.11).

Character states: lateral flange of cleithrum directed dorsally towards dorsal processes of the cleithrum (0), lateral flange of cleithrum directed dorsoposteriorly towards area between first and second proximal radial (1).

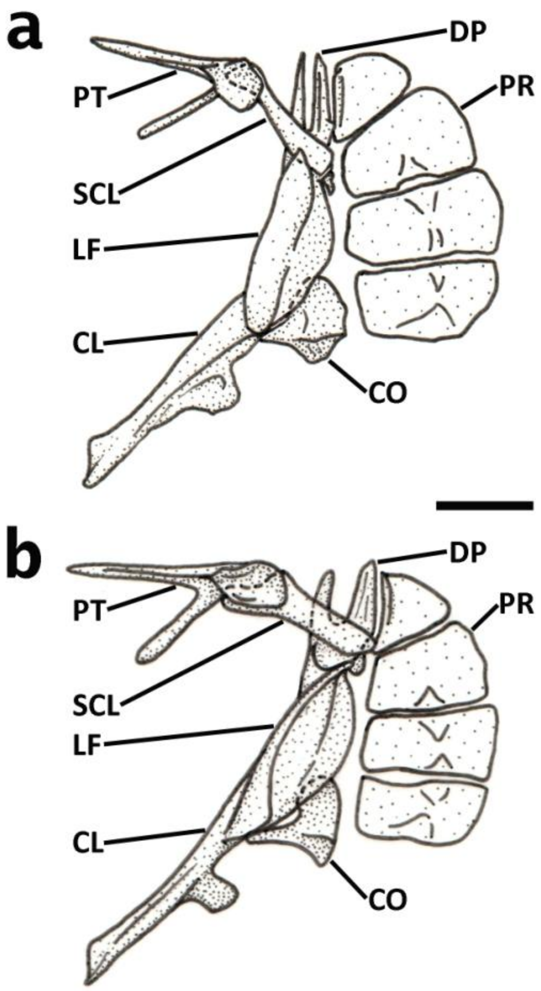

FIGURE 2.11 Pectoral-fin osteology of *Callogobius*. Scale bar = 1 mm.Abbreviations: PT = posttemporal, SCL = supracleithrum, LF = lateral flange of cleithrum, CL = cleithrum, CO = coracoids, DP = dorsal processes of cleithrum, PR = proximal radial. **A.** *C. mucosus* (USNM 341205, 66.4 mm SL male) showing the narrow and closely spaced dorsal processes of the cleithrum (Char. 47, state 1) and a dorsally-directed lateral flange of the cleithrum (Char. 48, state 0). Scale bar = 2mm. **B.** *C. bifasciatus* (ROM 39892, 33.2 mm male) showing the broad and widely separated dorsal processes of the cleithrum (Char. 47, state 0) and a dorsoposteriorly directed lateral flange of the cleithrum (Char. 48, state 1).

49. Medial expansion of cleithrum

In *Callogobius maculipinnis*, *C. pilosimentum* and *C. shunkan* the cleithrum is expanded medially, especially in the region of the second proximal radial, forming a subtriangular surface for muscle attachment; the width of the expansion is approximately 3/4 the width of corresponding lateral expansion. In the remaining species including the outgroups, any medial expansion of the cleithrum is 1/4 or less the width of the lateral expansion.

Character states: cleithrum expanded medially 1/4 or less the width of lateral expansion (0), cleithrum expanded medially about 3/4 the width of lateral expansion to form a roughly triangular surface (1).

50. Blade on medial hemitrich of penultimate dorsal pectoral-fin ray

In *Callogobius bifasciatus*, *C. clarki*, *C. dori*, *C. flavobrunneus*, *C. maculipinnis*, *C. pilosimentum*, *C. sclateri*, *C. shunkan*, and *C.* sp. 20 there is a distinct, dorsally-directed roughly triangular blade located proximally on medial hemitrich of the penultimate dorsal pectoral-fin ray. In *C. depressus* there is a low, long blade in the same region. In the remaining species, including the outgroups, there is no blade on the medial hemitrich of the penultimate dorsal pectoral-fin ray. (Figure 2.12)

Character states: no blade on the medial hemitrich of the penultimate dorsal pectoral-fin ray (0), distinct triangular blade on the medial hemitrich of the penultimate dorsal pectoral-fin ray (1), low flat blade on the medial hemitrich of the penultimate dorsal pectoral-fin ray (2)

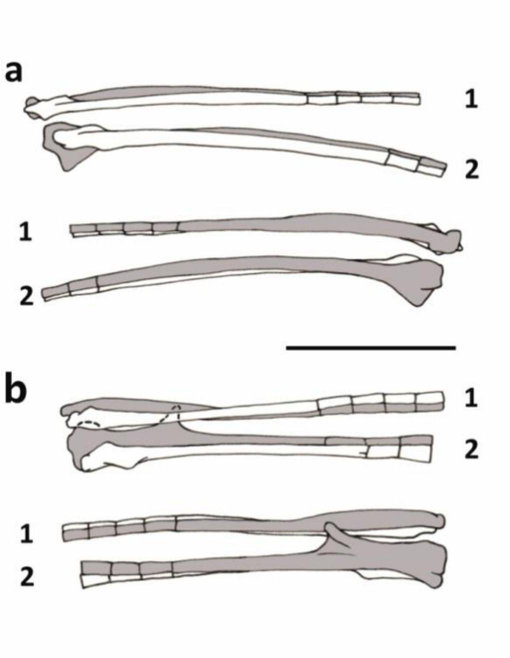

FIGURE 2.12 Morphology of the first and second pectoral-fin ray of *Callogobius*. The lateral hemitrich is white and the medial hemitrich is grey. Scale bar = 0.5 mm. **A.** (top) Lateral view of *C. mucosus* (USNM 341205, 66.4 mm SL male) showing no blade on the medial hemitrich of the penultimate (second) ray (Char. 50, state 0). (bottom) Medial view of the same specimen. Scale bar = 1 mm. **B.** (top) Lateral view of *C. bifasciatus* (ROM 39892, 33.2 mm male) showing a triangular blade on the medial hemitrich of the penultimate ray (Char. 50, state 1). (bottom) Medial view of the same specimen.

Axial skeleton

51. Number of precaudal vertebrae

Callogobius producta normally has 11 precaudal vertebrae; *C. tanegasimae* normally has 11 or 12. The remaining sampled *Callogobius* species and *Drombus* sp. and *Yongeichthys criniger* normally have 10 precaudal vertebrae.

Character states: usually 10 precaudal vertebrae (0), usually 11 or more precaudal vertebrae (1).

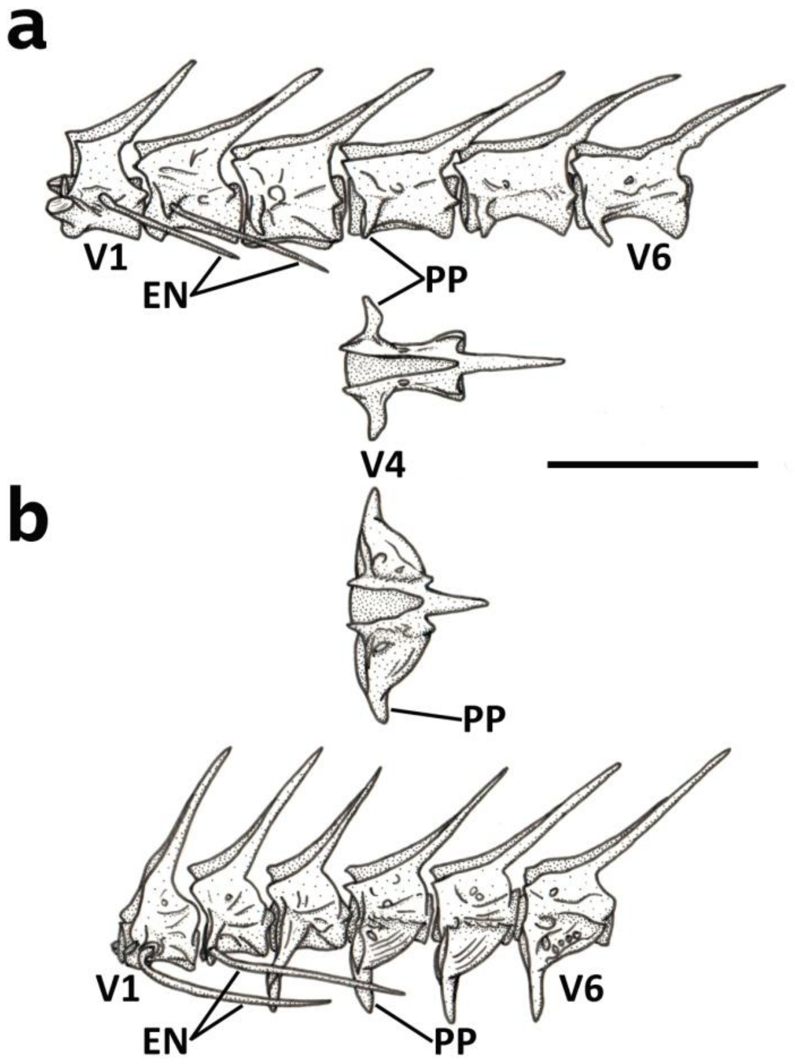

FIGURE 2.13 Morphology of the first through sixth vertebrae of *Callogobius*, ribs and associated epineurals not shown. Scale ba r= 2 mm. Abbreviations: V1 = first vertebra, EN = epineurals, PP = parapophyses, V4 = fourth vertebra, V6 = sixth vertebra. **A.** (top) Lateral view of *C. okinawae* (USNM 241882, 31.8 mm female) showing the absence of expanded wings on the parapophyses (Char. 54, state 0). (bottom) Ventral view of the same specimen. **B.** (top) Lateral view of first through sixth vertebrae of *C. maculipinnis* (USNM 241882, 32.6 mm SL female) showing the presence of expanded wings on the parapophyses beginning with the fourth vertebra (Char. 54, state 2). (bottom) Ventral view of the fourth vertebra of the same specimen.

52. Number of caudal vertebrae

Callogobius depressus, *C. mucosus* and *C. producta* have 17 caudal vertebrae; *C. tanegasimae* has 17 or 18. The remaining sampled species including *Yongeichthys criniger* have 16 caudal vertebrae. Exceptional individuals may have unusual counts; none were included in our samples. One of two C&S specimens of *Drombus* sp. has 17 caudal vertebrae (the other has 16). Birdsong et al. reported *Drombus palackyi* as having 16 caudal vertebrae; we scored *Drombus* sp. as having 16.

Character states: usually 16 caudal vertebrae (0), usually 17 or more caudal vertebrae (1).

53. Parapophyses with expanded anterior process

In *Callogobius producta* and our adult specimens of *C. tanegasimae*, the parapophyses of the third (and usually other) vertebrae are broad, expanded and with an anterior process. In our two cleared and stained specimens of *C. andamanensis*, the larger specimen has similar (although less distinctive) anterior expansion of the parapophyses, but the smaller specimen lacks it; we scored this species as variable (?). The remaining species examined including the outgroup species lack this expansion on the third vertebrae.

Character states: parapophyses of adults with expanded anterior process (0), parapophyses of adults not with expanded anterior process (1).

54. Parapophyses with expanded proximal wings

In *Callgobius maculipinnis*, *C. pilosimentum* and *C. shunkan*, the paraphosyses have substantial wing-like posterior expansion starting by the 4th vertebra. In *C. bifasciatus*, *C.* cf. *centrolepis*, *C. clarki*, *C. flavobrunneus*, *C. producta*, *C. sclateri* and *C. tanegasimae* the parapophyses have a narrow to moderate wing-like expansion, which does not start before the 5th vertebra and usually well posterior. The remaining examined species including the outgroup species lack wing-like expansion of the parapophyses. (Figure 2.13)

Character states: no wing-like expansion of parapophyses (0), slight wing-like expansion of parapophyses starting no earlier than the 5th vertebra (1), marked wing-like expansion of parapophyses starting by the 4th vertebra (2).

55. Epineurals on caudal vertebrae

In *Callogobius andamanensis*, *C. producta* and *C. tanegasimae*, there are no epineurals associated with caudal vertebrae. In the remaining examined species including the two outgroup species, at least one (and as many as five) caudal vertebrae have associated epineurals.

Character states: epineurals associated with caudal vertebrae present (0), epineurals associated with caudal vertebrae absent (1).

Phylogenetic hypotheses

Parsimony analysis yielded 4 most parsimonious trees with a tree length of 95 (Figure 2.14), a consistency index (CI) of 0.695 and a retention index (RI) of 0.858. In each of the most parsimonious trees, *Callogobius* is monophyletic and a clade containing *C. maculipinnis*, *C. pilosimentum* and *C. shunkan* is sister to all the remaining species (henceforth, we refer to this as the *maculipinnis* group, named for the first described species in the group). Among the remaining species, *C.* cf. *centrolepis* (the only species sampled in a group we refer to as the *tutuilae* group) is sister to a clade containing *C. bifasciatus*, *C. clarki*, *C. flavobrunneus* and *C. sclateri* (the *sclateri* group). The *sclateri* group + *C.* cf. *centrolepis* are sister to a clade containing *C. dori*, *C.* sp. 20, *C. okinawae*, *C. hastatus*, *C. mucosus*, *C. depressus*, *C. tanegasimae*, *C. producta* and *C. andamanensis*; we refer to the latter as the *hasseltii* group. Within the *hasseltii* group, *C. dori* is recovered as sister to the remaining group members. These trees differed in the relative placement of two taxa. *Callogobius andamanensis* is either recovered as sister to *C. producta* + *C. tanegasimae* or as sister to a clade containing *C. producta* + *C. tanagasimae* and *C. depressus* + *C. mucosus*. *Callogobius bifasciatus* and *C. clarki* are either recovered as sister taxa or as unresolved within the *sclateri* group. Figure 2.15 depicts the strict consensus tree, with bootsrap values of at least 50% marked on the tree. The *maculipinnis* and *sclateri* groups each received 100% bootstrap support, the *hasseltii* group received 69 % bootstrap support and the *hasseltii* + *sclateri* group + *C.* cf. *centrolepis* clade received 93% bootstrap support. Only three terminal species-level relationships were supported by more than 50% bootstrap analysis - the sister taxon relationships between *C. flavobrunneus* + *C. sclateri*, *C. producta* + *C. tanegasimae* and *C. depressus* + *C. mucosus*.

The monophyly of *Callogobius* received 68 % bootstrap support. Only one of four characters supporting this node, raised papillae rows in a specific horizontal and vertical pattern (Char. 1), is unique to *Callogobius* among fishes. The other three characters [head pores ending as short tubes (Char. 5), broad dorsal margin of the ectopterygoid (Char. 35) and scales with distinctly outlined centres (Char. 8)] are known to occur in other gobioid taxa outside of those surveyed here.

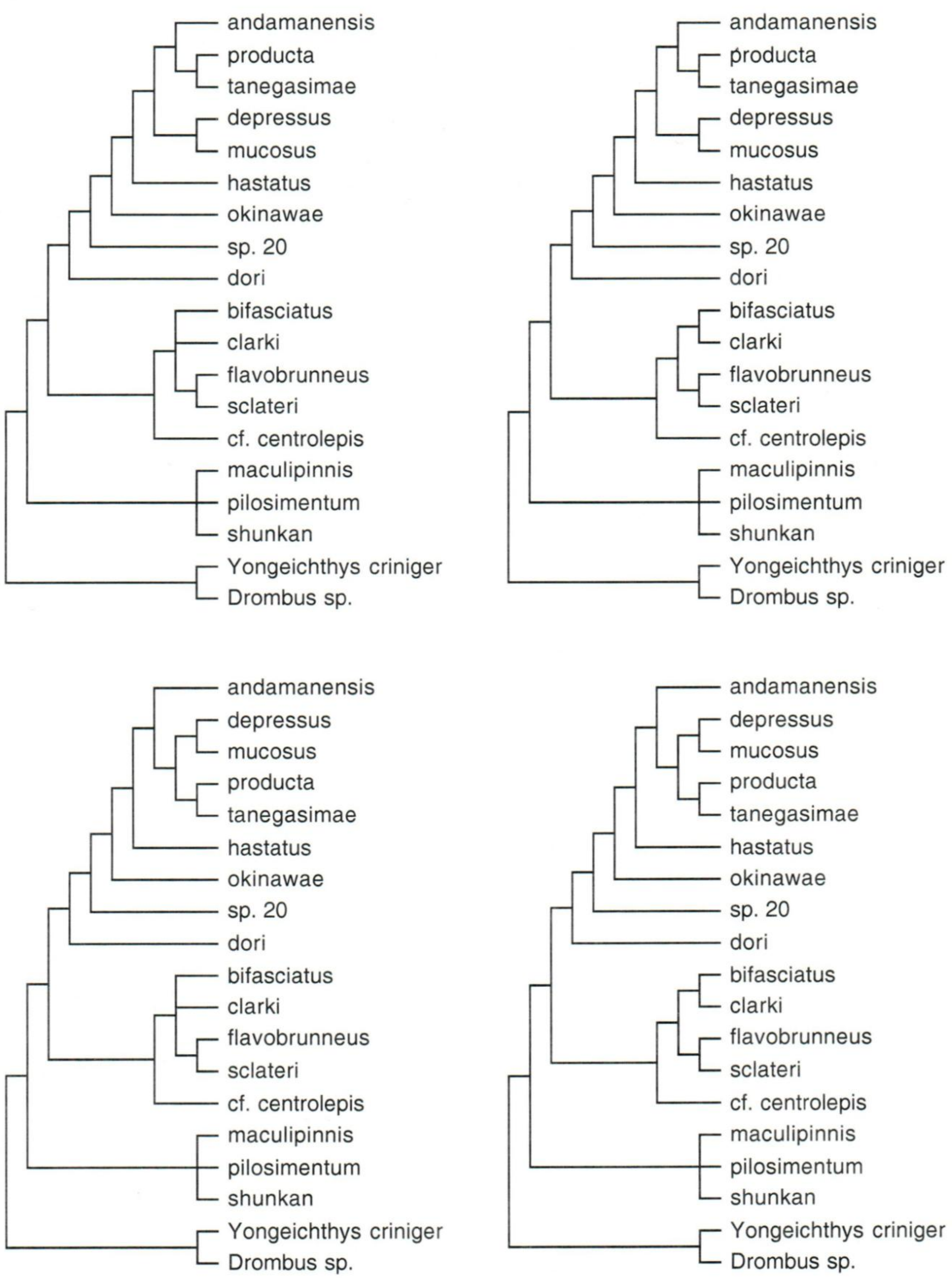

FIGURE 2.14 Phylogenetic hypotheses for the inter-relationships of *Callogobius*. Four equally most parsimonious trees, computed using maximum parsimony, with 55 morphological characters and 19 taxa. Tree length = 95, CI = 0.695, RI = 0.858.

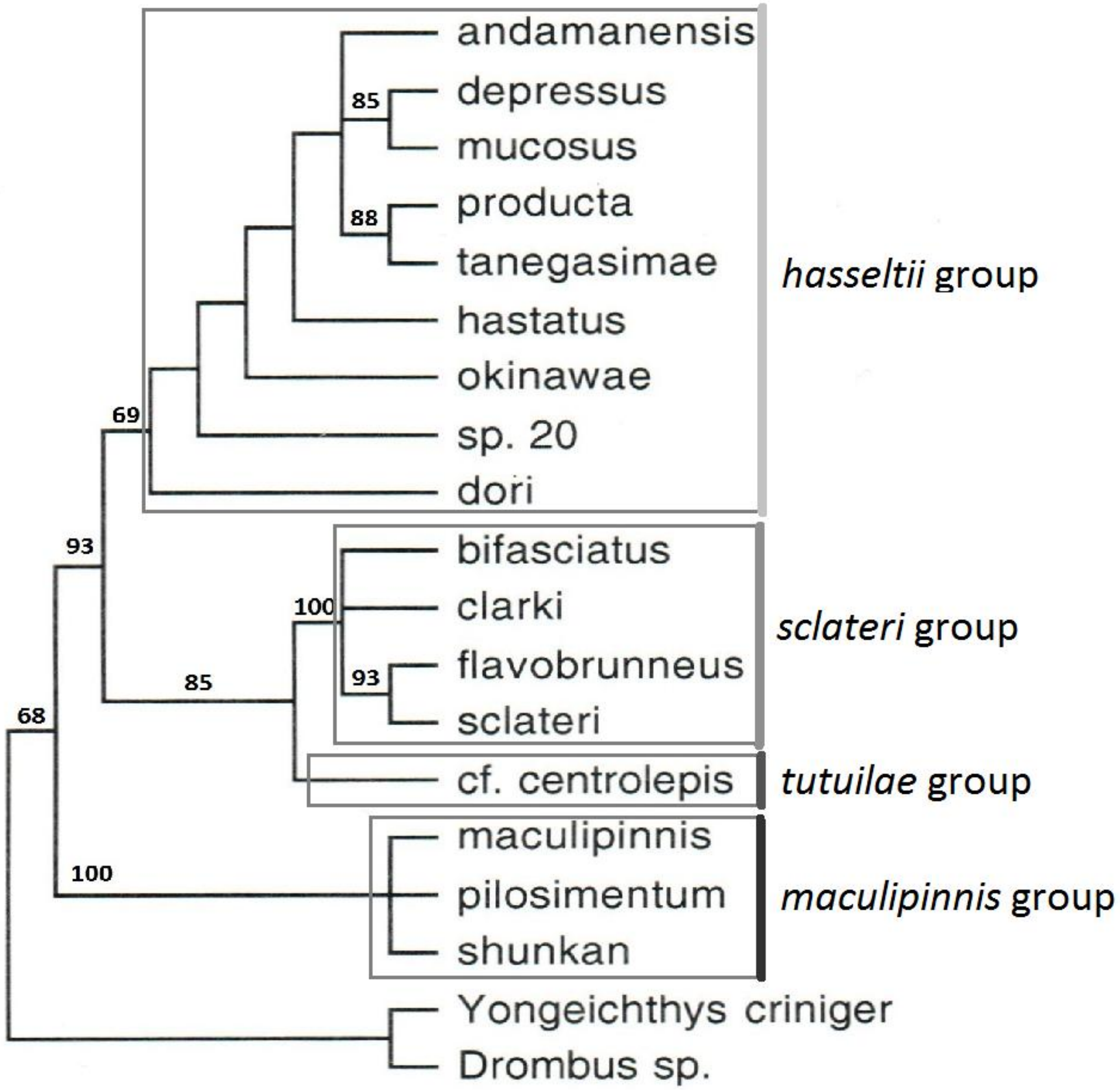

FIGURE 2.15 Strict consensus tree based on the four most parsimonious trees from Figure 2.14. Bootstrap values greater than 50% were added to appropriate branches. The *maculipinnis* group is indicated by dark grey, the *tutuilae* group is indicated by medium grey, the *sclateri* group is indicated by light grey, and the *hasseltii* group is indicated by very light grey.

Description, membership and phylogenetic diagnoses of proposed *maculipinnis*, *sclateri* and *hasseltii* species groups

Characters listed in the group diagnoses are hypothesized synapomorphies, shared by all members of the group, and absent in other *Callogobius* species and the outgroup species *Drombus* sp. and *Yongeichthys criniger*. Listed species in each group are marked with a star (*) if they were examined both externally and osteologically in this study, other species (not marked with a star) were assigned to groups based on external characters alone through examination of type material (see Delventhal & Mooi 2013, Chapter Four) and/or non-type specimens.

maculipinnis group

Included species: *Callogobius bauchotae* (if valid) *C. irrasus* (if valid), *C. kuderi* (if valid), *C. maculipinnis**, *C. nigromarginatus* (if valid), *C. pilosimentum**, *C. shunkan**, *C. snelliusi* (if valid) and *C. vanclevei* (if valid)

Diagnosis: Only 3-4 transverse mandibular rows on each side (Char. 3, state 1), lateral ethmoids large and firmly attached to mesethmoid (Char. 19, state 1), frontals ventrally expanded into orbit forming bony interorbital septum (sometimes with parasphenoid expansion) (Char. 20, state 2), mesethmoid process for ethmo-maxillary ligament long and narrow (Char. 22, state 1), dorsal lamina of quadrate with anterior expansion (Char. 25, state 1), quadrate extends dorsally into symplectic gap (sometimes with symplectic expansion) (Char. 28, state 1), (Char. 30, state 0), palatine shaft broad and rhomboid shaped (Char. 31, state 1), ectopterygoid very broad ventrally with distinct shaft (Char. 34, state 2), pharyngobranchial 2 with arm to interarcual cartilage (Char. 41, state 1), cleithrum with medial expansion (Char. 49, state 1), expanded wings of parapophyses beginning by 4th vertebra (Char. 54, state 2).

Description and remarks: Members of the *maculipinnis* group are usually brown with lighter spots or bars. The colouration in preservation is influenced by the capture conditions (stressed individuals often developed deeply contrasting bars). All species in this group can be distinguished from other *Callogobius* externally based on the presence of 3-4 transverse mandibular rows per side, and the presence of the temporal canal. All species have preopercular canals, relatively low lateral scale counts (28 or fewer), ctenoid scales with numerous very fine ctenii, and large, non-imbedded predorsal scales. There are no enlarged canine teeth on the lower jaw. Pelvic fins are fully united with a well-developed pelvic frenum, and no species have distal lateral flaps on the female urogenital papillae. They are stout-bodied with normally 16 caudal vertebrae, and a caudal fin that is shorter than the head length. Osteologically, they are highly distinctive. The frontals are expanded further ventrally into the orbit (Char. 20) than those of any other *Callogobius* species, and the wing-like expansions of the parapopyses (Char. 54) are more marked and begin anteriorly compared to those in other species.. The ossified mesethmoid strut is absent (it is also absent in members of the *hasseltii* group) and the angle between the palatine dorsal arms greater than 135 degrees (as it is in *Yongeichthys. criniger*). Pharyngobranchial 3 teeth have a second tip (tooth types C and D; also present in *Y. criniger* and some *C. hastatus*).

Intra-group relationships: All three species in the *maculipinnis* group scored the same for all of the characters used in this analysis, thus the relationships within this group have not been resolved and are indicated by a polytomy.

***sclateri* group**

Included species: *Callogobius bifasciatus*, C. clarki*, C. flavobrunneus*, C. sclateri**

Possibly included species (pending osteological examination): *C. winterbottomi, C. trifasciatus* (if valid)

Diagnosis: Ossified mesethmoid strut extends ventrally towards (but does not touch) vomer/parasphenoid (Char. 21, state 1), anterolateral arm of palatine short (Char. 32, state 1), and lateral flange of cleithrum curved posteriorly (Char. 48, state 1).

Description and remarks: Members of the *sclateri* group are typically barred in colouration or at least exhibit mottled bars. All species have 10 or more transverse mandibular rows per side, widely separate preopercular and transverse opercular papillae rows, and lack the preopercular and temporal canals. Lateral scale counts are low to moderate (about 23-48). All species have ctenoid scales, but some may be restricted to the caudal peduncle in smaller individuals. There are relatively few large ctenii per scale and elongate ctenii are found on some caudal penduncle scales (also found on some *tutuilae* group species); predorsal scales are not imbedded. Most specimens have a pair of enlarged canine teeth on each side of the lower jaw. Pelvic fins may or may not be united, and a frenum is present or absent depending on the species. The female urogenital papillae have distal lateral flaps (which are also present on some *tutuilae* group species), and bodies may be short or moderately elongate but typical specimens do not have more than 16 caudal vertebrae. The caudal-fin length is less than the head length. In addition to the osteological characters listed in the diagnosis, the metapterygoid has a flange-like extension over the quadrate (common among gobies but uncommon in *Callogobius*), the posterodorsal condyle of the hyomandibula is relatively short (but it is also short in *C. hastatus*), and all species of low to moderate wing-like expansions of the parapophyses not starting before the 5th vertebra (also shared by *C. producta* and *C. tanegasimae*). There is shallow frontal expansion into orbit but no parasphenoid expansion, and the preopercle exhibits dorsal truncation and lacks a ventral groove (the preopercle is similar in at least some *tutuilae* group species).

Callogobius winterbottomi appears similar to members of this group externally, and was placed in the *sclateri* group as first proposed by Delventhal and Mooi (2013, Chapter Four). However, unlike the *maculipinnis* and *hasseltii* groups, membership in the *sclateri* group as defined in this paper cannot be determined by external morphology alone. The changes to our definition of the *sclateri* group and the placement of *C. winterbottomi* is addressed in the discussion section. *C. trifasciatus* was synomized with *C. flavobrunneus* by McKinney and Lachner (1984). If distinct from *C. flavobrunneus, C. trifasciatus* is expected to fit within this group, although osteological examination will be necessary for corroboration.

Intragroup relationships: A sister taxon relationship beween *C. flavobrunneus* and *C. sclateri* was recovered in each of our analyses. These species share three characters related to the pelvic fin morphology: pelvic fins separate or with minute membrane (Char. 14, state 2), pelvic frenum absent (Char. 15, state 1) and fifth pelvic-fin ray usually branched once (Char. 16, state 1). However, these are also found in some other *Callogobius* species not included in this study (such as *C. crassus,* which we assign to the *hasseltii* group).

***hasseltii* group**

Included species: *Callogobius amikami*, *C. andamanenis**, *C. badia* (if valid), *C. bothriorrhynchus* (if valid), *C. clitellus*, *C. coelidotus* (if valid), *C. crassus*, *C. depressus**, *C. dori**, *C. hasseltii, C. hastatus*, C. insolita* (if valid), *C. gobiosoma* (if valid), *C. mannarensis, C. moroana* (if valid), *C. mucosus*, C. okinawae*, C. plumatus, C. producta*, C. sheni, C. stellatus, C. tanegasimae** and *C.* sp. 20*

Diagnosis: Caudal-fin length is greater than head length (Char. 17), dorsal processes of cleithrum narrow and closely spaced (Char. 47, state 1).

Description and remarks: Colouration is variable among members of the *hasseltii* group. The basic pattern may include vertical bars and/or fine horizontal lines or flecks; some species have a black spot on the upper edge of the caudal fin. All species have 10 or more transverse mandibular rows per side, continuous preopercular and transverse opercular papillae rows, and lack the temporal canals. Preopercular canals may be present or absent. Lateral scale counts are very low to very high (about 18-80). Some species have ctenoid scales, others only cycloid scales; a number of species usually have cycloid scales with rare individuals having a small number ctenoid scales. There are relatively few large ctenii per scale, and no elongate ctenii on caudal penduncle scales; depending on the species predorsal scales may or may not be deeply imbedded. Canine teeth are not enlarged. Pelvic fins vary from fully united with a well-developed frenum to separate/with a minute membrane and no frenum. The female urogenital papilla lacks distal lateral flaps. Body shape may vary from short to highly elongate, with 10-11 precaudal vertebrae and 16-18 caudal vertebrae depending on the species. As indicated in the diagnosis, the caudal fin length is greater than the head length. The mesethmoid strut is absent (it is also absent in members of the *maculipinnis* group), and the ectopterygoid dorsal margin broad with a second bony process in almost all species (absent in *C. dori*). Epibranchial tooth patches are usually absent (but present on at least some individuals of *C. andamanensis*; also absent in *Yongeichthys criniger*).

This is the largest and most morphologically diverse group within *Callogobius*. There are only two characters shared by all members of this group, the elongate caudal fin with a length greater than head length the narrow and closely spaced dorsal processes of the cleithrum. However, in addition to the characters listed in the diagnosis, certain characters appear unique to some members of this group among *Callogobius,* including body with cycloid scales only, a black spot on the caudal fin, predorsal scales that are deeply imbedded or absent, a second bony process on the dorsal margin of the ectopterygoid, epibranchial tooth patches absent, epineurals absent from caudal vertebrae, 11 or more precaudal vertebrae, 17 or more caudal vertebrae, and the absence of a blade on medial hemitrich of penultimate dorsal pectoral-fin ray.

We were unable to include a specimen identifiable as *Callgobius hasseltii,* the first named species in this group, due to the taxonomic problems in this species (see Appendix A). However, all of Bleeker's presumed *C. hasseltii* specimens are consistent with other members of this group in having an elongate caudal fin.

Intragroup relationships: Although we sampled nine species within the *hasseltii* group, only two clades within this group received more than 50% bootstrap support. Each clade contains only two species, and neither is supported by exclusive synapomorphies. One clade, *C. producta* + *C. tanegasimae* is supported by the presence of 11 or more precaudal vertebrae (Char. 51, state 1), 17 or more caudal vertebrae (also shared by *C. depressus* and *C. mucosus*) (Char. 53, state 1), parapophyses with expanded anterior processes (also shared by some *C. andamensis*) (Char. 54, state 1), parapophyses with wing-like expansion starting no earlier than the 5th vertebra (also shared by *C. bifasciatus*, *C. clarki*, *C. flavobrunneus* and *C. sclateri*) (Char. 54, state 1) and the absence of epineurals on caudal vertebrae (also shared by *C. andamensis*) (Char. 55, state 1). A second clade, consisting of *C. depressus* and *C. mucosus* is supported by the presence of 17 or more caudal vertebrae (also shared by *C. producta* and *C. tanegasimae*) (Char. 53, state 1), and a moderately broad basihyal (also shared by *C. maculipinnis*, *C. pilosimentum* and *C. shunkan*) (Char. 45, state 0).

***tutuilae* group (unassigned species)**

All known described species, except *Callogobius trifasciatus*, *C. winterbottomi*, *C. tutuilae* and *C. centrolepis* have been placed in one of the three groups. *Callogobius trifasciatus*, if distinct from *C. flavobrunneus*, is expected to fit within the *sclateri* group. Externally, *C. winterbottomi* is consistent with members of the *sclateri* group, and we provisionally retain it there, awaiting osteological examination.

We have informally considered *Callogobius tutuilae* and *C. centrolepis* (which are poorly understood taxonomically) along with several similar-looking undescribed species to be part of a poorly defined assemblage (lacking known synapomorphies) which we call the *tutuilae* group. Species in this group are relatively rare in collections, and are usually in poor condition. They resemble members of the *maculipinnis* or *sclateri* group in general appearance, but they differ from each in several characters. Unlike species of the *maculipinnis* group, *C. centrolepis* and *C. tutuilae* have 10 or more transverse mandibular rows, and they lack the preopercular and temporal canals. However, unlike species of the *sclateri* group, *C. centrolepis* and *C. tutuilae* have continuous preopercular and transverse opercular papillae rows (although these rows are separate in some very similar looking species). At least some species in the *tutuilae* group lack scales with elongate ctenii and enlarged canine teeth, however, the mature females of most but not all species have lateral flaps on the urogenital papilla. No species in this group have a caudal-fin length greater than the head length which differentiates them from members of the *hasseltii* group.

We included in the present study a single specimen which we identified as *Callogobius* cf. *centrolepis*. Like members of the *sclateri* group there was a distinct flange-like extension of the metapterygoid that reaches the quadrate (Char. 26, state 0), the preopercle was truncated dorsally and lacks a ventral groove (Chars. 36-37, state 0), and the posterior condyle of the hyomandibula was relatively short (Char. 38). Unlike members of the *sclateri* group an ossified mesethmoid strut is absent (Char. 21, state 2), canine teeth are not enlarged (Char. 23, state 0), the palatine dorsal arm angle was greater than 135 degrees (like members of the *maculipinnis* group) (Char. 30, state 0), the palatine anterolateral arm was long and uncurved (Chars. 32 -33, state 0), the ventral postcleithrum was long and slender (like members of the *maculipinnis* group) (Char. 46, state 0) and the lateral flange of the cleithrum was directed dorsally (Char. 48, state 0). The external anatomy revealed no scales with elongate ctenii (Char. 11, state 0) and ctenii size and number was intermediate (between typical counts in the *maculipinnis* and *hasseltii* group) (Char. 10, state 1). The specimen, a female, displayed a urogenital papilla with lateral flaps (Char. 13). Based on the morphology of the female urogenital papilla and the preopercle, we were not surprised that *C.* cf. *centrolepis* was recovered as sister to the *sclateri* group as we have defined it in this paper. Further examination of cleared and stained *tutuilae* group specimens (and species) is required to determine whether this group forms its own lineage sister to the *sclateri* group, or if these species form a basal grade or are imbedded within an expanded *sclateri* group defined by a smaller subset of derived characters.

DISCUSSION

Re-definition of the *sclateri* group: In this paper, we revise our original definition of the *sclateri* group (Delventhal and Mooi 2013, Chapter Four), which was first identified by having modified caudal peduncle scales and a female urogenital papilla with distal lateral flaps of skin, initially presumed diagnostic among *Callogobius* (Characters 11 & 13 of the present study). Although all species in our newly defined *sclateri* group do exhibit the above external character states, these are also present in some (but not all) unassigned (*tutuilae* group) species. Hence, we have expanded the diagnosis of the *sclateri* group to include several osteological synapomorphies [ossified mesethmoid strut (Char. 21, state 1), short anterolateral arm of palatine (Char. 32, state 1), and posteriorly curved lateral flange of cleithrum (Char. 48, state 1)]. Unfortunately, we have not been able to examine the osteology of *C. winterbottomi* in the current study, as only four individuals are known in collections, making distructive sampling inadvisable. Thus, the placement of *C. winterbottomi* in the *sclateri* group is uncertain.

Evaluation of McKinney's (1980) hypothesis: McKinney included 14 species in his phylogenetic study, identified as *Callogobius maculipinnis*, *C. centrolepis*, *C.* new species B (= *C. dori*), *C.* new species A (= *C. clarki*), *C. flavobrunneus*, *C. sclateri*, *C. mucosus*, *C. producta*, *C. hastatus*. *C. okinawae*, *C.* species h-1 (= *C.* cf. *hasseltii* 1), *C.*species h-2 (= *C.* cf. *hasseltii* 2), *C. stellatus*, and *C. mannarensis* (Figure 2.17). He discussed approximately 20 characters, although it is not clear how many he ultimately used in the construction of his phylogenetic hypothesis nor was the method by which he constructed his phylogenetic hypothesis explicitly described. McKinney (1980) recognized two major groups within *Callogobius*. His stout-bodied (*maculipinnis*) group included *C. maculipinnis*, *C. centrolepis*, *C. dori* (= new species B), *C.*

clarki (= new species A), *C. flavobrunneus*, and *C. sclateri*; he defined this group to include species with enclosed sensory canals of the frontal bones and the presence of epibranchial tooth patches (except in *C. dori*). The second group, his slender-bodied (*hasseltii*) group included *C. mucosus*, *C. producta*, *C. hastatus*. *C. okinawae*, *C.* cf. *hasseltii* 1 (= species h-1), *C.* cf. *hasseltii* 2 (= species h-2), *C. stellatus*, and *C. mannarensis*, is defined by having socket-type palatine-ectopterygoid articulation (reinterpreted in our Char. 35) and lacking epibranchial tooth patches. McKinney's *maculipinnis* group is largely equivalent to our combined *maculipinnis*, *sclateri* and *tutuilae* groups. Notable departure from McKinney's hypothesis are our recognition of *C. dori* as a member of the *hasseltii* group based on the elongate caudal fin, lack of epibranchial tooth patches, and narrow gap between the dorsal processes of the cleithrum, as well as our inclusion of synapomophies defining our *maculipinnis* and *sclateri* groups. McKinney and Lachner (1984) later added *C. crassus* to their "stout-bodied" group (apparently equivalent in membership to McKinney's *maculipinnis* group), which we consider belongs to the *hasseltii* group based on its elongate caudal fin (we have not examined cleared and stained specimens). McKinney considered *C. maculipinnis* and *C. centrolepis* to have a close relationship based on pectoral girdle osteology and the presence of a well-developed ventral postcleithrum. Our examination of the pectoral girdle of *C.* cf. *centrolepis* corroborates his observations but not his interpretation; these characters appear to be plesiomorphic within *Callogobius*, and our specimen of *C.* cf. *centrolepis* fails to exhibit synapomorphies associated with *C. maculipinnis*, but rather exhibits some synapomorphies shared with our *sclateri* group. McKinney placed *C. sclateri* as sister to *C. flavobrunneus* in a clade with *C. clarki*. This agrees with our topology (all are members of our *sclateri* group), although McKinney's grouping was based only on pelvic fin shape (slightly shortened in *C. clarki* and separate in *C. flavobrunneus* and *C. sclateri*). Our analysis also recovered *C. sclateri* and *C. flavobrunneus* as sister taxa, based on three pelvic-fin characters. We did not examine the osteology of *C. mannarensis* or *C. stellatus*, but based on external anatomy and radiographs, we agree with McKinney's assessment of the close relationship between these two species. McKinney based the relationship between *C. okinawae, C.* cf. *hasseltii* 1 and *C.* cf. *hasseltii* 2 on the character of shortened pelvic fin rays; he based the relationship between *C. hastatus*, *C. producta* and *C. mucosus* on having fifth pelvic-fin rays not shortened. He stated, however, that he had little confidence in the relationships beyond the division into two major groups.

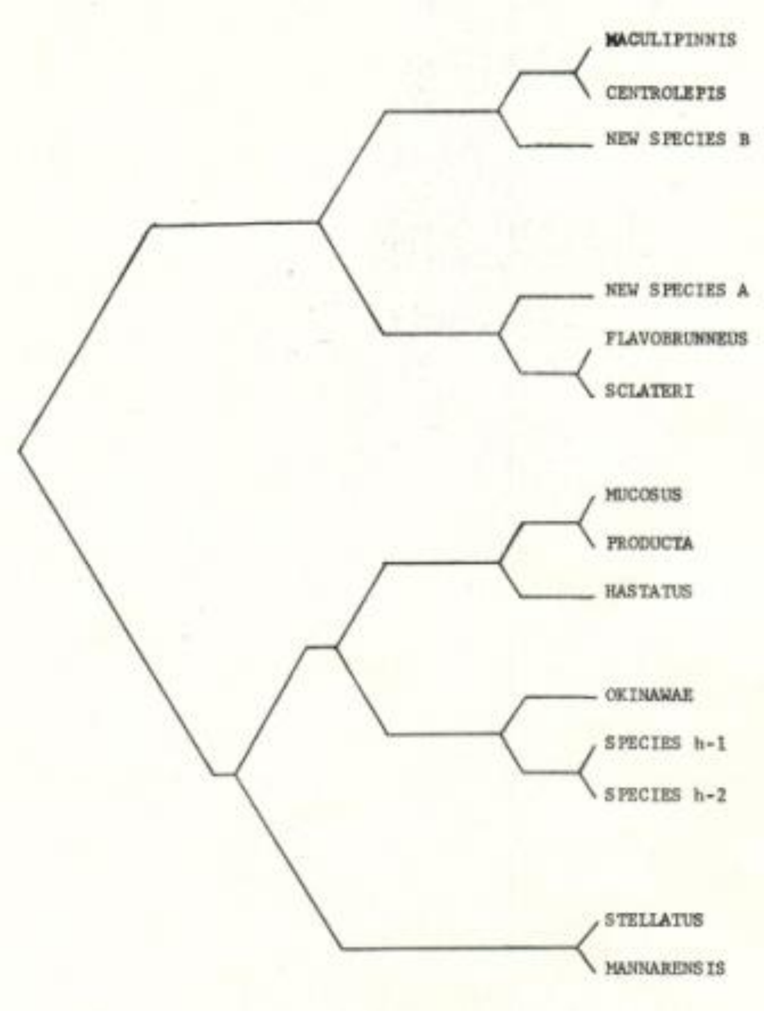

FIGURE 2.16 McKinney's (1980) phylogenetic tree of *Callogobius* based on morphology. Copyright J.F. McKinney.

Implications for biogeography: Our study identifies three monophyletic groups within *Callogobius*, which include the great majority of the diversity within the genus. No particular group is geographically restricted to a specific region within the range of *Callogobius* as a whole. The Red Sea is currently the best documented region for *Callogobius* (Delventhal et al. 2016, Chapter Seven), with only seven species known, but with representatives from all three monophyletic groups: *C. amikami* and *C. dori* (*hasseltii* group); *C. clarki*, *C. flavobrunneus* and *C. sclateri* (*sclateri* group); *C. pilosimentum* (*maculipinnis* group) and *C.* sp. A (*sclateri* group or *tutilae* group).

MATERIAL EXAMINED

Cleared and stained specimens:

Callogobius andamanensis: ROM 68202 (2 specimens); *C. bifasciatus*: ROM 39892 (1 specimen); *C. clarki*: USNM 220031 (3 specimens); *C. depressus*: USNM 214728 (1 specimen); *C. dori*: USNM 220030 (1 specimen), USNM 220929(1 specimen); *C. flavobrunneus*: ANSP 162299 (4 specimens); *CAS 63904* (4 specimens); ROM 642CS (3 specimens - Chagos); USNM 300025 C. (2 specimens); CAS 63897 (2 specimens); *C. hastatus*: USNM 300025 (2 specimens); *C. maculipinnis*: ANSP 162296 (4 specimens); USNM 241882 (2 specimens); ROM 57704 (2 specimens); MPM 45773 (1 specimen); *C.mucosus*: USNM 341205 (2 specimens); *C. okinawae*: CAS 63991 (4 specimens); ROM 63898 (2 specimens);USNM 241882 (2 specimens); *C. pilosimentum*: BMNH 1978.9.8.12-16 (1 specimen); SMF 37757 (1 specimen); *C. producta*: USNM 241874 (1 specimen); *C. sclateri*: ROM 60877 (1 specimen); ROM 728CS (1 specimen); *C. shunkan*: BLIH 19810168 (1 specimen); *C. tanegasimae*: uncat. (7 specimens); *C.* sp. 20

USNM 410662 (1 specimen); *C.* cf. *centrolepis*: BPBM 31367 (1 specimen); *Drombus* sp.: MPM 31412 (2 specimens); *Yongeichthys criniger*: USNM327958 (1 specimen).

Fluid specimens:

Callogobius andamanensis: ROM68202 (46 specimens, from the same lot as two C&S specimens); *C. bifasciatus:* ROM 39892 (3 specimens, from the same lot as the C&S specimen), ROM 39899 (4); *C. clarki*: HUJ 10065 (HOLOTYPE, 1), USNM 220031 (8 specimens, from the same lot as three C&S specimens); *C. depressus*: USNM 341205 (24 specimens - mixed lot new number TBA); *C. dori:* BMNH 1978.9.8.8-11 (4 specimens), USNM 220929 (2 specimens, from the same lot as one C&S specimen); *C. flavobrunneus:* USNM 220091 (2 specimens), ROM 60837 (4 specimens) USNM 313818 (20 specimens); *C. hastatus:* USNM 30025 (23 specimens, from the same lot as two C&S specimens); *C. maculipinnis:* USNM 241882 (31 specimens, from the same lot as two C&S specimens); *C. mucosus:* USNM 341205 (19, from the same lot as two C&S specimens); *C. okinawae:* USNM 241882 (20 specimens, from same lot as two C&S specimens - mixed lot new number TBA); *C. pilosimentum*: SMF 35756 (1 specimen, holotype); BMNH 1978.9.8.12-16 (5 specimens, paratypes); *C. producta:* USNM 241874 (10 speciemens, from the same lot as one C&S specimen); *C. sclateri:* ROM 60877 (12 specimens, from the same lot as one C&S specimen); *C. shunkan*: BLIP 19920029 (1 specimen), BLIP 19810167 (1 specimen); *C. tanegasimae:* NSMT-P 28273 (5 specimens); *C.* sp. 20: USNM 409430 (1 specimen, holotype), USNM 411406 (1 specimen), USNM 412487 (17 specimens); *C.* cf. *centrolepis*: BPBM 31367 (1 specimen, from same lot as one C&S specimen); *Drombus* sp.: MPM 31412 (8 specimens, from the same lot as 2 C&S specimens); *Yongeichthys criniger*: USNM327958 (1 specimen, from the same lot as one C&S specimen).

Chapter Three. Molecular phylogenetics of *Callogobius* (Teleostei: Gobiidae)

Publication status: This paper has not been published; however, portions of this paper will be rewritten in the future (with additional material added) and published with Ainhoa Agorreta and Lukas Rüber. For this reason, I have used "we" throughout the text.

My contributions: I designed the study, acquired the tissue samples through field collection and exchange with colleagues, ran the analyses and wrote the paper. Ainhoa Agorreta taught me the lab work (extraction and sequencing) all of which we did together. Lukas Rüber provided lab space, discussed analyses and methods, and identified appropriate molecular markers for use within gobies.

SUMMARY

The genus *Callogobius* is a large group of gobioid fishes containing at least 65 species, over one third of which are undescribed. Relationships to other goby genera and relationships among species within the genus are poorly known. In this study, we infer the phylogenetic relationships among 15 *Callogobius* species using mitochondrial (partial fragment containing *12S*, $tRNA^{Val}$ and *16S)* and nuclear (*zic1*, a, *rag1* and *sreb2*) genes via analysis through maximum likelihood, Bayesian inference and maximum parsimony. Our results indicate that McKinney's (1980) *hasseltii* and *maculipinnis* groups are not monophyletic, however our results support the monophyly of Delventhal & Mooi's (unpublished) *hasseltii*, *maculipinnis*, and *sclateri* groups. Delventhal and Mooi's undiagnosed *tutuilae* group assemblage is paraphyletic with respect to their monophyletic *sclateri* group. There is evidence that a great deal of genetic diversity occurs among specimens identified as *C. hasseltii*; this is consistent with morphological evidence and suggests a complex of very similar species.

INTRODUCTION

Gobioids (suborder Gobioidei) comprise one of the largest groups of fishes with over 2100 extant species (Nelson et al. 2016), but there is currently inadequate systematic knowledge of the group. Some of the challenges of gobioid systematics (both at the species level and generic/family level) include the tremendous number of species, their small size (usually less than 10 cm) and independent trends towards reduction in derived lineages, such as inferred loss of bones and sensory pores (Thacker 2011). The composition and nomenclature of higher taxa within the gobioids are still in dispute, but for the purposes of this paper, we recognize two subfamilies within the Gobiidae, the Gobiinae (composed of the subfamily Gobiinae + the families Kraemeriidae, Schindleriidae and Microdesmidae and the Gobionellinae (composed of the subfamilies Gobionellinae, Amblyopinae, Oxudercinae and Sicydiinae). This classification is consistent with recent phylogenetic evidence (e.g. Thacker 2003, 2009; Gill and Mooi 2012), although some authors (e.g. Thacker 2009, Nelson et al. 2016) recognize these groups as families (the Gobiidae and the Gobionellidae/Oxcudercidae)

The genus *Callogobius* (family Gobiidae) includes more than 40 nominal species (Eschmeyer et. al. 2017, Delventhal unpublished, Appendix A), making it one of the largest gobioid genera. Species of *Callogobius* are widespread in Indo-Pacific shallow marine and brackish environments, including coral reefs, tidepools and mangrove streams. Because of cryptic colouration, habitat specialization, and poor condition of most specimens (many species have fragile skin and deciduous scales), the taxonomy is poorly known and at least 25 undescribed species are likely to exist (D. Hoese pers. comm.).

Callogobius is unique among gobies in having the sensory papillae (superficial neuromasts) of the head on raised ridges in a unique transverse pattern (Winterbottom 2003, Delventhal and Mooi, unpublished, Chapter Two). This monophyly is in contrast to many gobiine genera that are loosely held together by a variety of plesiomorphic and/or likely non-homologous characters, or a suite of reductive characters thought to have evolved multiple times due to heterochrony (such as small size and reduced superficial sensory system [Thacker 2011]).

Relationships of *Callogobius* to other gobiids are uncertain, and a sister taxon to *Callogobius* has not been proposed. Lachner & McKinney (1974) suggested a possible relationship between *Pipidonia* (later synonymised with *Gobiopsis* [Lachner & McKinney 1978]), *Barbuligobius* and *Callogobius.* They differentiated *Callogobius* from *Gobiopsis (Pipidonia)* and *Barbuligobius* (the former with which it has often been confused [Hoese 1986]) by the characteristic development of raised fleshy, papillose ridges, absence of chin and snout barbels, and variably reduced sensory pores. Miller & Wongrat (1979) noted a similarity in arrangement of the sensory papillae in *Callogobius* and *Egglestonichthys* (although unlike *Callogobius*, the sensory papillae of *Eggelstonichthys* are not on raised ridges). Winterbottom (2003) discussed similarities between *Feia* and *Callogobius*. He suggested that *Callogobius* is monophyletic based on possession of both horizontal and vertical papillose ridges on the cheek. He noted that only a few goby genera (*Cristatogobius*, *Mangarinus*, *Callogobius*, *Feia* and *Gobiopsis*) possess folds or ridges of sensory papillae on the head, but in *Callogobius* the sensory papillae arrangement is consistent and unique.

Two large morphological studies sampled broadly within the gobioids, and included species of *Callogobius* (Birdsong *et al.* 1988, Pezold 1993). Despite having surveyed only a limited number of character complexes, they have proven useful as a starting place for hypotheses of relationships and have been widely cited. In their landmark paper, Birdsong *et al.* (1988) divided gobioids into 32 groups based on characters of the axial skeleton. They placed

Callogobius within a group of gobiids they called the *Priolepis* group, which contained 54 genera. The *Priolepis* group was their largest group, and also contained most of the other goby genera suggested by subsequent authors as possible *Callogobius* relatives. Pezold (1993) identified synapomorphies in the head pore patterns in a subset of gobiids he called the Gobiinae that included members of the *Priolepis, Gobius, Bathygobius, Gobiosoma, Pomatoschistus* and *Kellogella* groups of Birdsong et al. (1988). He distinguished the Gobiinae from a subfamily Gobionellinae, which he considered “a smaller assemblage of convenience” (although later molecular work [Thacker 2013, Tornabene et al. 2013, Agorreta et al. 2013] supported a relationship with members of the *Pomatoschistus* group and gobionellines). Delventhal and Mooi (unpublished, Chapter Two) used two *Priolepis* group gobiines, *Drombus* sp. and *Yongeichthys criniger* as outgroups for a morphological study of the intrarelationships of *Callogobius*, chosen due to their availability and unspecialized osteology. They did not attempt to evaluate the relationship among these taxa and *Callogobius*.

Several molecular studies have sampled one or two species of *Callogobius* as part of a larger gobioid phylogeny. Thacker (2003), in a phylogenetic analysis using mitochondrial DNA (ND1, ND2 and COI) that sampled 66 taxa, recovered *Callogobius* (represented by *C. sclateri*) in a clade containing the genera *Ctenogobiops*, *Fusigobius, Asterropteryx* and *Amblyeleotris.* Rüber (2006, an unpublished presentation) sampled nuclear DNA (*rag1*) of 103 taxa and placed *Callogobius* (represented by *C. hasseltii*) in a clade containing *Yongeichthys, Amoya, Drombus, Favonogobius, Istigobius* and *Cryptocentrus.* Neilson & Stepien (2009) included the *C. sclateri* COI sequence from Thacker (2003) in an analysis examining the relationships of the benthophiline gobies. Their analysis placed *C. sclateri* as sister to *Chromogobius zebratus* but the relationship was not well supported. Agorreta & Rüber (2012) reanalyzed Neilson &

Stepien's dataset and found *C. sclateri* in a clade containing eleotridids and *Odontobutis*, but with low support values. In general, they recovered poor support values for most nodes (especially within lower gobioid relationships) (Agorreta & Rüber 2012), suggesting that *COI* alone is of limited value for inferring relationships at lower taxonomic levels. Thacker (2009) again using mitochondrial DNA (*ND1*, *ND2*, *COI* and *cytb*) found *Callogobius sclateri* and *C. bifasciatus* (the only two *Callogobius* species sampled) as sister taxa in a clade containing *Bathygobius, Cabillus, Cryptocentroides*, and *Acentrogobius.* Thacker and Roje (2011) sequenced 3 mitochondrial (*ND1*, *ND2* and *COI*) and 3 nuclear genes (*rag2*, *Rho*, *RNF213*) for 102 goby species. In their study, *C. sclateri* and *C. bifasciatus* were recovered as a clade within the family Gobiidae, although their relationship to other taxa was uncertain. Thacker and Roje (2011) proposed a group which they called "flapheaded gobies" to include *Barbuligobius, Callogobius*, *Discordipinna*, *Drombus*, *Feia*, *Gobiopsis*, *Mangarinus, Palutrus*, *Phoxacromio*n, and *Platygobiopsis*. However, only *Callogobius* was sampled in their phylogeny, and grouping with the other genera was based on unspecified overall morphological commonalities (Thacker and Roje 2011). Agorreta et al. (2013) sampled five genera among Thacker and Roje's (2011) "flapheaded gobies," *Discordipinna*, *Drombus*, *Gobiopsis*, *Feia* and *Callogobius*. They found these genera scattered among the gobiines, with no close relationship with each other except for *Drombus* and *Gobiopsis*, which were recovered in a clade containing *Silhouettea*, *Exyrias*, *Istigobius*, *Amoya*, *Favonigobius*, *Arenigobius*, *Acentrogobius* and *Porogobius*; *Drombus* itself was recovered as polyphyletic. They also recovered *Callogobius* as its own lineage within the gobiines with no clear close relationships. Thacker et al. (2011) in an examination of shrimp goby relationships, included sequences of *C. sclateri* and *C. bifasciatus* (*ND1*, *ND2*, *COI, rag2* and *Rho*) in their study. They found *Callogobius* to be sister to a clade containing *Asterropteryx* and the shrimp goby genera *Ctenogobiops*, *Vanderhorstia* and *Amblyeleotris*, however, they did not sample widely among non-shrimp gobies. Chakrabarty et al. (2012) included *C. bifasciatus* in an analysis that used mostly published sequences from *ND1*, *ND2*, *cytB* and *COI*; they found *Callogobius* sister to *Cabillus* in a clade also including *Glossogobius*, *Trimmatom*, *Trimma* and *Priolepis*. Tornabene et al. (2012) in an analysis using nuclear (*Rag1* and *Rho*) sequences found *Callogobius sclateri* to be sister to a large clade including European gobies, *Priolepis*, *Lythrypnus*, microdesmines, ptereleotrines, sevenspined gobies, *Valenciennea*, *Amblygobius*, *Coryphopterus*, *Lophogobius*, *Asterropteryx*, and *Gladiogobius*.

There is no consensus regarding the placement of *Callogobius* within the Gobiidae. Moreover, these studies showed relatively poor support for many of the hypothesized relationships. However, all studies, regardless of taxon sampling and regions sequenced, concurred in placing *Callogobius* within a subfamily Gobiinae that includes the Microdesmidae, Ptereleotridae and Schindleridae (these small families were traditionally recognized on the basis of many autapomorphies; in recent years they are hypothesized to be nested within the Gobiinae [Thacker 2011, Gill and Mooi 2012]). Published molecular phylogenetic results suggested that members of the "*Priolepis* group" of Birdsong *et al.* (1988) are "generalized" gobiines and paraphyletic with respect to other gobiines and Microdesmidae, Ptereleotridae, and Schindleridae. Several studies (Thacker 2003, Thacker 2009, Rüber 2006, unpublished) indicate a possible relationship between *Callogobius* and some groups of gobiines such as the *Acentrogobius*-type gobies (including *Drombus*, *Amoya*, *Acentrogobius* and *Yongeichthys*) and Indo-Pacific shrimp gobies (including *Cryptocentrus, Amblyeleotris,* and *Ctenogobiops*). Others contradict this (Chakrabarty et al. 2012, Agorreta et al. 2013, Tornabene et al. 2013). Given the results of previous molecular studies, the potential relatives to *Callogobius* remain open to question, although would be found among the Gobiinae.

Within *Callogobius* remarkable variation occurs in characters such as scale type and scale type distribution, body and fin shape, presence and distribution of sensory pores and papillae rows, and osteology (McKinney 1980); Delventhal and Mooi unpublished, Chapter Two). Several authors attempted to divide the genus into smaller groups, in part to simplify species identification. Lachner & McKinney (1974) suggested that one assemblage, which they called the *hasseltii* group, displayed major differences from other nominal species, but did not indicate which characters were used or which species were included. McKinney (1980) proposed relationships among 14 *Callogobius* species using osteological and external characters, but did not sample outgroups. His analysis supported stout-bodied (*maculipinnis*) and slender-bodied (*hasseltii*) groups. Later, McKinney & Lachner (1984) defined a “stout-bodied group” with ctenoid scales and a smaller number of segmented dorsal fin elements. Goren et al. (1991) modified this arrangement only slightly when they recognized a group of species with relatively few scale rows. Delventhal & Mooi (2013, Chapter Four) proposed a subgroup of *Callogobius* which they termed the *sclateri* group to include *C. bifasciatus*, *C. clarki*, *C. flavobrunneus*, *C. sclateri* and a newly described species, *C. winterbottomi*. They distinguished this group based on external morphology. Delventhal & Mooi (unpublished, Chapter Two) redefined the *sclateri* group based on osteology. They redefined two additional hypothesized monophyletic groups, the *hasseltii* group and the *maculipinnis* groups (which differed in membership to some degree from McKinney's [1980] circumscription). In addition, Delventhal & Mooi (unpublished, Chapter Two) discussed several species, including two nominal species, *C. tutuilae* and *C. centrolepis*, which did not appear to fit clearly into the *maculipinnis*, *sclateri* or *hasseltii* groups.

They provisionally placed these remaining *Callogobius* species into an assemblage they called the *tutuilae* group, for which monophyly could not be corroborated.

In the present study, we propose a phylogenetic hypothesis for the relationships among 15 species of *Callogobius*. Because of its uncertain relationship to other gobies, we have chosen to include outgroups in the families Eleotridae, Gobionellinae, and Gobiinae. This is consistent with well-accepted hypotheses of gobioid relationships in which the Gobionellinae and Eleotridae are successive outgroups with respect to the Gobiinae (e.g. Thacker 2009, Gill & Mooi 2012). We obtained tissues of only three genera previously cited as possible *Callogobius* relatives based on morphology (*Feia*, *Gobiopsis* and *Discordipinna*), thus, our study does not address the relationship of *Callogobius* to other gobiines nor does it evaluate the monophyly of Thacker and Roje's "Flapheaded gobies". However, we evaluate support for the monophyly of *Callogobius* and for previously identified species groups – the *hasseltii* and *maculipinnis* groups of McKinney (1980) and the *hasseltii*, *maculipinnis*, *sclateri* and *tutuilae* groups of Delventhal & Mooi (unpublished).

METHODS

To infer the interspecies relationships of *Callogobius*, we sampled 62 *Callogobius* individuals representing 15 different species. Most of our samples are from Japan, due to the field work by scientists from Biological Laboratory of the Imperial Palace (BLIP) and the National Museum of Nature and Science (NSMT). This includes species from all four species groups defined by Delventhal & Mooi (unpublished, Chapter Two) and both of McKinney's (1980) species groups. Of these species, 6 are undescribed and currently under study by scientists at the Biological Laboratory of the Imperial Palace (BLIP) in Tokyo. These species are referred to here as *C*. sp. 1, *C*. sp. 2, *C*. sp. 3, *C*. sp. 6, *C*. sp. 7 and *C*. sp. 8. Specimens of these species were examined at the beginning of the present study, and the external morphology places *C*. sp. 1, *C*. sp. 7 and *C*. sp. 8 in the *hasseltii* group *sensu* Delventhal & Mooi, *C*. sp. 6 in the *maculipinnis* group *sensu* Delventhal & Mooi, and *C*. sp. 2 and *C*. sp 3 in the *tutuilae* group. Two "species" sampled in this study would be better represented as complexes; these are *C. hasseltii* and *C. maculipinnis*. Both are likely to encompass several similar species with widespread distribution and poorly understood taxonomy (Delventhal et al. 2016, Chapter Seven, Delventhal & Mooi unpublished, Chapter Two). In this paper we do not attempt to address these issues and refer to as yet indistinguishable members of these complexes as *C. hasseltii* and *C. maculipinnis* respectively. We also selected 18 taxa representing successive outgroups: Gobiinae (*Trimma, Priolepis, Feia, Istigobius, Gobiopsis, Discordipinna, Bathygobius and Glossogobius*), Gobionellinae (including Oxudercinae and Sicydiinae) (*Sicyopterus, Awaous, Oligolepis, Pseudapocrytes, Boleophthalmus*) and Eleotridae (*Eleotris*). Ideally, we would have sampled *Drombus* sp. and *Yongeichthys criniger*, gobiine species used as outgroups by Delventhal and Mooi (unpublished, Chapter Two), but these taxa were not available at the time of sequencing. Phylogenetic trees were rooted on *Eleotris*. Table 3.1 lists the specimens sampled in this study, collection locality and voucher specimen location. Abbreviations for institutional codes follow Fricke & Eschmeyer (2017).

TABLE 3.1 (next page) Genus and species of specimens used in this study, their Lukas Rüber (LR) tissue collection number, and collection locality.

LR number	**Genus**	**Species**	**Locality**	
LR07408	*Awaous*	*flavus*	Aquarium trade	
LR07409	*Pseudapocryptes*	*elongates*	Commercial trade	
LR07411	*Glossogobius*		Commercial trade	
LR07412	*Oligolepis*		Aquarium trade	
LR07415	*Boleophthalmus*		Taiwan	
LR07416	*Istigobius*	sp.2	Taiwan	
LR07417	*Priolepis*		Taiwan	
LR07419	*Trimma*	*okinawae*	Taiwan	
LR07420	*Gobiopsis*	*arenaria*	Taiwan	
LR07422	*Bathygobius*	sp.1	Taiwan	
LR07423	*Bathygobius*	sp.2	Taiwan	
LR07424	*Istigobius*	sp.1	Taiwan	
LR07425	*Sicyopterus*		Taiwan	
LR07426	*Eleotris*		Taiwan	
LR07428	*Bathygobius*		Taiwan	
LR07429	*Callogobius*	*hasseltii*	Malaysia	
LR07430	*Callogobius*	*hasseltii*	Japan	Amami-oshima I.
LR07431	*Callogobius*	*hasseltii*	Japan	Amami-oshima I.
LR07432	*Callogobius*	*hasseltii*	Japan	Kochi
LR07433	*Callogobius*	*maculipinnis*	Japan	Amami-oshima I.
LR07434	*Callogobius*	*maculipinnis*	Japan	Amami-oshima I.
LR07435	*Callogobius*	*okinawae*	Japan	Yakusima I.
LR07436	*Callogobius*	*okinawae*	Japan	Yakusima I.
LR07437	*Callogobius*	*okinawae*	Japan	Yakusima
LR07438	*Callogobius*	*okinawae*	Japan	Yakusima
LR07439	*Callogobius*	*okinawae*	Japan	Okinawa
LR07440	*Callogobius*	*okinawae*	Japan	Iriomote-jima
LR07441	*Callogobius*	*shunkan*	Japan	Kochi
LR07442	*Callogobius*	*hasseltii*	Japan	Amami-oshima
LR07443	*Callogobius*	*tanegasimae*	Japan	Yakusima
LR07444	*Callogobius*	*tanegasimae*	Japan	Iriomote-jima
LR07445	*Callogobius*	*crassus*	Japan	Ishigaki-jima
LR07446	*Callogobius*	*flavobrunneus*	Japan	Okinawa-jima
LR07447	*Callogobius*	*flavobrunneus*	Japan	Okinawa-jima
LR07448	*Callogobius*	*flavobrunneus*	Japan	Iriomote-jima
LR07449	*Callogobius*	*hasseltii*	Japan	Okinawa-jima
LR07450	*Callogobius*	*hasseltii*	Japan	Okinawa-jima
LR07451	*Callogobius*	*hasseltii*	Japan	Amami-Oshima
LR07452	*Callogobius*	*hasseltii*	Japan	Amami-Oshima
LR07453	*Callogobius*	*hasseltii*	Japan	Shizuoka Pref.
LR07454	*Callogobius*	*hasseltii*	Japan	Shizuoka Pref.

LR07455	*Callogobius*	*hastatus*	Japan	Iriomote-jima
LR07456	*Callogobius*	*hastatus*	Japan	Iriomote-jima
LR07457	*Callogobius*	*hastatus*	Japan	Iriomote-jima
LR07458	*Callogobius*	*maculipinnis*	Japan	Zamami-jima
LR07459	*Callogobius*	*maculipinnis*	Japan	Zamami-jima
LR07460	*Callogobius*	*maculipinnis*	Japan	Zamami-jima
LR07461	*Callogobius*	*okinawae*	Japan	Okinawa-jima
LR07462	*Callogobius*	*okinawae*	Japan	Okinawa-jima
LR07463	*Callogobius*	*okinawae*	Japan	Iriomote-jima
LR07464	*Callogobius*	*okinawae*	Japan	Iriomote-jima
LR07465	*Callogobius*	*sclateri*	Japan	Yaku-shima
LR07466	*Callogobius*	*sclateri*	Japan	Zamami-jima
LR07467	*Callogobius*	*sclateri*	Japan	Zamami-jima
LR07468	*Callogobius*	*sclateri*	Japan	amami-Oshima
LR07469	*Callogobius*	*shunkan*	Japan	Shizuoka Pref.
LR07470	*Callogobius*	*shunkan*	Japan	Chiba Pref.
LR07471	*Callogobius*	*shunkan*	Japan	Shizuoka Pref.
LR07472	*Callogobius*	*tanegasimae*	Japan	Okinawa-jima
LR07473	*Callogobius*	*tanegasimae*	Japan	Okinawa-jima
LR07474	*Callogobius*	*tanegasimae*	Japan	Iriomote-jima
LR07475	*Callogobius*	*tanegasimae*	Japan	Iriomote-jima
LR07476	*Callogobius*	sp. 1	Japan	Iriomote-jima
LR07477	*Callogobius*	sp. 2	Japan	Zamami-jima
LR07478	*Callogobius*	sp. 2	Japan	Zamami-jima
LR07479	*Callogobius*	sp 2	Japan	Zamami-jima
LR07480	*Callogobius*	sp 3	Japan	Zamami-jima
LR07481	*Callogobius*	sp 3	Japan	Zamami-jima
LR07482	*Callogobius*	sp 3	Japan	Zamami-jima
LR07483	*Callogobius*	sp. 6 cf. *maculipinnis*	Japan	Zamami-jima
LR07484	*Callogobius*	sp. 6 cf. *maculipinnis*	Japan	Zamami-jima
LR07485	*Callogobius*	sp. 6 cf. *maculipinnis*	Japan	Zamami-jima
LR07486	*Callogobius*	sp. 7	Japan	Amami-Oshima
LR07487	*Callogobius*	sp. 7	Japan	Amami-Oshima
LR07488	*Callogobius*	sp. 7	Japan	Zamami-jima
LR07489	*Callogobius*	sp. 7	Japan	Zamami-jima
LR07490	*Callogobius*	sp. 8 cf. *crassus*	Cebu	
LR07491	*Callogobius*	sp. 8 cf. *crassus*	Cebu	
LR07492	*Discordipinna*	*griessingeri*	Japan	Zamami-jima
LR07493	*Feia*	*nympha*	Japan	Iriomote-jima
LR07494	*Gobiopsis*	*arenaria*	Japan	Okinawa-jima

Gene sampling and DNA sequencing

For all specimens, total genomic DNA was isolated from ethanol-preserved fin or muscle tissue using the QIAamp® DNA Mini Kit (QIAGEN, Valencia, CA, USA) following the manufacturer's instructions. We sequenced four molecular markers: one 1835 bp mitochondrial (mt) fragment containing partial *12S*, a partial fragment of *16S* and *tRNA*^{Val} (which connects the 12S and 16S fragments [Rüber et al. 2003]), 1428 bp of the recombination activating gene 1 (*rag1*); 828 bp partial fragment of the zic family member I (*zic1*); and a 870 bp partial fragment of the super conserved receptor expressed in brain 2 (*sreb2*). Mt ribosomal fragments were amplified using the primers reported by Kocher et al. (1989) for 12S, Palumbi et al. (1991) for 16S, and Rüber et al. (2003) for *tRNA*^{Val}. Nuclear markers were amplified using the primers reported by López et al. (2004) for *rag1*, and Li et al. (2007) for *zic1* and *sreb2***.** PCR amplifications were conducted using 67mM Tris-HCl pH 8.3, 1.5mM $MgCl_2$, 0.4mM of each dNTP, 2.5µM of each oligonucleotide, template DNA (10-100ng), and *Taq* DNA polymerase (1 U, PromegaGoTaq® DNA Polymerase) and purified water for a total volume of 25µl . PCR conditions for mt ribosomal fragments (*12S*, *16S*, *tRNA*^{Val}) were: initial denaturing step at 94ºC for 5 minutes, 35 cycles of 94ºC for 45 seconds, 50ºC for 45 seconds, and 72ºC for 1 minute, with a final extension at 72ºC for 7 minutes. PCR conditions for nuclear fragments (*rag1*, *zic1*, *sreb2*) were: initial denaturing step at 94ºC for 5 minutes, 40 cycles of 94ºC for 45 seconds, 58ºC (52 for *rag1*) for 45 seconds, and 72ºC for 90 seconds, with a final extension at 72ºC for 7 minutes. PCR products were purified with Millipore Purification Plates and sequenced in an automated DNA sequencer (ABI 3730xl DNA Analyzer) at the sequencing facilities at the Natural History Museum, London (BMNH), using the BigDye Terminator v1.1 Cycle sequencing kit (Applied Biosystems) and the corresponding PCR primers.

Sequence assembly, alignment and substitution model selection

Sequence assembly and trimming was performed using Sequencher® version 4.8 sequence analysis software (Gene Codes Corporation, Ann Arbor, MI USA; http://www.genecodes.com). Alignments were prepared separately for each mitochondrial ribosomal and nuclear molecular marker using the default setting of MAFFT version 6.818 (Katoh et al. 2002; Katoh and Toh 2008). Individual alignments were first analyzed separately to determine the phylogeny inferred from individual genes; the separate gene alignments were also combined into a single concatenated dataset that was used in all subsequent phylogenetic analyses.

For each individual gene and concatenated alignment the best-fitting models of nucleotide substitution were identified using the Akaike information criterion (AIC; Akaike 1973) as implemented in jModeltest version 0.1.1 (Posada 2008). In all cases, the resulting best-fit model was general time reversible (GTR) (Rodríguez et al. 1990) + invariant sites (I) (Reeves 1992), + gamma (Γ) (Yang 1994).

Phylogenetic inference

The combined datasets were analyzed using maximum likelihood (ML; Felsenstein 1981) Bayesian inference (BI; Huelsenbeck et al. 2001), and maximum parsimony (MP) analysis. Individual gene trees were done using BI only. ML analysis was performed with RAxML version 7.2.6 (Stamatakis 2006) using the rapid hill-climbing algorithm (Stamatakis et al. 2007) on CIPRES. BI was performed with MrBayes version 3.1.2 (Huelsenbeck & Ronquist 2001, Ronquist & Huelsenbeck 2003) running four simultaneous Markov chains for 10 million generations, sampling every 1000 generations, and discarding the first one million generations as burn-in (as judged by plots of ML scores and low standard deviation of split frequencies). Two independent BI runs were performed as an additional check that the chains mixed well and so converged using the GTR + Γ+ I model for each partition. Support for internal branches was evaluated by non-parametric bootstrapping with 2,000 replicates (RAxML) and posterior probabilities (MrBayes) in the ML and BI analyses, respectively.

To facilitate computationally feasible MP analyses, a subset of taxa was compiled which generally excluded multiple individuals of a given *Callogobius* species. This is justified since all species were resolved as monophyletic in the ML and BI analyses, and with the exception of specimens identified as *C. hasseltii*, there was relatively little difference in the sequences of different individuals within each species. Specimens identified as *C. hasseltii* demonstrated a large amount of genetic diversity, so two specimens were included. The following taxa were included in this subset: *Eleotris* LR7426, *Awaous flavus* LR7408, *Sicyopterus* LR7425, *Oligolepis* R7412, *Pseudapocryptes elongates* LR7409, *Boleophthalmus* LR7415, *Glossogobius* LR7411, *Bathygobius* sp1 LR7422, *Bathygobius* sp2 LR7423, *Bathygobius* LR7428, *Istigobius* sp1 LR7424, *Istigobius* sp2 LR7416, *Gobiopsis arenaria* LR7420, *Gobiopsis arenaria* LR7494, *Discordipinna griessingeri* LR7492, *Priolepis* LR7417, *Trimma okinawae* LR7419, *Feia nympha* LR7493, *Callogobius hasseltii* LR7429, *Callogobius hasseltii* LR7430, *Callogobius okinawae* LR7435, *Callogobius tanegasimae* LR7444, *Callogobius hastatus* LR7456, *Callogobius* sp1 LR7476, *Callogobius crassus* LR7445, *Callogobius* sp8 LR7491, *Callogobius* sp7 LR7487, *Callogobius flavobrunneus* LR7446, *Callogobius sclateri* LR7465, *Callogobius* sp3 LR7481, *Callogobius* sp2 LR7477, *Callogobius maculipinnis* LR7460, *Callogobius* sp6 LR7483 and *Callogobius shunkan* LR7469. MP analyses were conducted using PAUP* version 4.0a151 (Swofford 2002). All characters were equally weighted and unordered. A heuristic search was run with random taxon addition, all minimal trees saved and TBR branch swapping was employed on the best trees only. In order to evaluate support for each node, MP bootstrap analysis was run as a heuristic search with 1000 replicates, random addition of taxa and identical settings to the previous analysis.

RESULTS

Most species were successfully sequenced for most individual genes. The mitochondrial ribosomal alignment was comprised of 1833 base pairs, of which 932 were variable and 713 parsimony informative. The *rag1* alignment was comprised of 1428 base pairs, of which 499 were variable and 352 were parsimony informative. Two species, *Awaous flavus* and *Callogobius crassus*, were not successfully sequenced for this gene. The *zic1* alignment was comprised of 828 base pairs, of which 123 were variable and 76 were parsimony informative. *Awaous flavus* and *C. crassus* were also not successfully sequenced for this gene. The *sreb2* alignment was comprised of 870 base pairs, of which 201 were variable and 145 were parsimony informative. *Istigobius* sp.1 and *C. crassus* were not successfully sequenced for this gene. The combined phylogenetic analyses were based on an alignment from 4962 nucleotide sites, 1755 of which were variable and 1288 parsimony informative.

See figure 3.1 for the BI tree marked with ML bootstrap values greater than 95 %. In each of the three analyses, the gobiid subfamilies Gobionellinae+Oxcudercinae (represented by *Awaous*, *Sicyopterus*, *Oligolepis*, *Pseudapocryptes* and *Boleophthalmus*) and Gobiinae (represented by *Glossogobius*, *Bathygobius*, *Istigobius*, *Gobiopsis*, *Discordipinna*, *Feia*, *Trimma*, *Priolepis* and *Callogobius*) were recovered as monophyletic, with high support values. In each analysis *Callogobius* was recovered as monophyletic with posterior probability of 1.0 (BI) or a bootstrap value of 100% (both ML and MP analysis). This well-supported monophyly is consistent with morphological evidence from the unique arrangement of sensory papillae rows (Winterbottom, 2003, Delventhal and Mooi, unpublished, Chapter Two). However, we acknowledge that the present study has sampled a relatively small assortment of outgroup taxa.

Table 3.2 lists the *Callogobius* species sampled in this study and compares the species group allocation by McKinney (1980) (if available), by Delventhal and Mooi (unpublished, Chapter Two), and results from this study. Undescribed species not included in Delventhal and Mooi (unpublished, Chapter Two) were allocated to one of their groups based on direct examination of external morphology prior to being sequenced. Bayesian inference of the combined dataset (Figure 3.1) demonstrated strong support (posterior probability of 1.0) for the monophyly of *Callogobius* and the *maculipinnis*, *sclateri* and *hasseltii* species groups suggested by Delventhal & Mooi (unpublished, Chapter Two). In this topology, the *hasseltii* group was recovered as sister to the remaining *Callogobius* species. The *maculipinnis* group is sister to a clade consisting of the *sclateri* group (represented here by *C. sclateri* and *C. flavobrunneus*) and two species of a paraphyletic *tutuilae* group (here represented by *C*. sp. 2 and *C*. sp. 3, which form successive sister taxa to the two species of the *sclateri* group). The ML tree resulted in an identical topology to the Bayesian tree, with similar high support values for the clades of interest. Most sampled members of McKinney's (1980) *maculipinnis* group and *hasseltii* group were recovered together. However, *C. crassus*, was placed in the stout-bodied group by McKinney and Lachner 1984 (= *maculipinnis* group *sensu* McKinney [1980]). In the present phylogeny, it is placed in the *hasseltii* group, as Delventhal & Mooi (unpublished, Chapter Two) had predicted (Table 3.2). Although this analysis placed the clade containing *Priolepis*, *Trimma* and *Feia* as sister to *Callogobius*, we have not sampled widely in the *Gobiinae*, and we do not necessarily propose a close relationship among these taxa. Moreover, support values for this relationship are relatively low, with a BI posterior probability of 0.98 and an ML bootstrap value of 63%.

TABLE 3.2 *Callogobius* species sampled in this study with comparison of their species-group designation of McKinney (1980) and Delventhal & Mooi (unpublished, Chapter 2).

Species	McKinney (1980)	Delventhal & Mooi (unpublished)	This study
C. cf *hasseltii*	*hasseltii* group	*hasseltii* group	*hasseltii* group
C. hastatus	*hasseltii* group	*hasseltii* group	*hasseltii* group
C. tanegasimae	*hasseltii* group	*hasseltii* group	*hasseltii* group
C. okinawae	*hasseltii* group	*hasseltii* group	*hasseltii* group
C. crassus	*maculipinnis* group*	*hasseltii* group	*hasseltii* group
C. sp. 1	N/A	*hasseltii* group**	*hasseltii* group
C. sp. 7	N/A	*hasseltii* group**	*hasseltii* group
C. sp. 8	N/A	*hasseltii* group**	*hasseltii* group
C. cf *maculipinnis*	*maculipinnis* group	*maculipinnis* group	*maculipinnis* group
C. shunkan	N/A	*maculipinnis* group	*maculipinnis* group
C. sp. 6	N/A	*maculipinnis* group**	*maculipinnis* group
C. sclateri	*maculipinnis* group	*sclateri* group	*sclateri* group
C. flavobrunneus	*maculipinnis* group	*sclateri* group	*sclateri* group
C. sp. 2	N/A	*tutuilae* group**	paraphyletic *tutuilae* group
C. sp. 3	N/A	*tutuilae* group**	paraphyletic *tutuilae* group

*This species was not included in McKinney (1980), but described by McKinney & Lachner (1984) as being closely allied with a group of stout-bodied species whose membership was identical to McKinney's (1980) *maculipinnis* group.

**These undescribed species were not included in Delventhal & Mooi (unpublished, Chapter Two), but examined by N. Delventhal prior to the beginning of this study and assigned to groups based on diagnostic morphological characters.

MP analysis of the reduced taxon set found three most parsimonious trees. Figure 3.2 depicts the strict consensus tree with mapped bootstrap values of at least 50%. The MP consensus tree differed in topology from the BI/ML tree in only two respects. In the MP tree, *Callogobius okinawae* was recovered as sister to the remaining *hasseltii* group species (a relationship supported by fewer than 50 % of bootstrap replicates); in the BI/ML trees as sister to a clade containing *C*. sp. 1, *C. tanegasimae*, *C. hastatus* and *C. hasseltii* albeit with posterior probability of 0.78 and low ML bootstrap support. In the MP tree,he clade containing *Discordipinna*, *Gobiopsis* and *Istigobius* was recovered as sister to *Callogobius*, although this relationship was supported by less than 50% of bootstrap replicates. None of the relationships that differ between analyses are strongly supported by the BI or ML tree; if nodes with BI posterior probability of less than 0.99 and supported by fewer than 80% of ML bootstrap replicates are collapsed, the topologies are identical with that of the MP bootstrap tree.

Individual BI gene runs largely resulted in similar support for the clades of interest, with exceptions as noted. In the mitochondrial ribosomal and *rag1* trees the monophyly of the four clades of interest (the genus *Callogobius*, the *hasselti* group, the *maculipinnis* group and the *sclateri* group) were supported with a posterior probability of at least 0.91 for each clade. The *sreb2* and *zic1* trees were more poorly resolved or showed lower support values, presumably because of the lower number of variable characters in these sequences. In the *sreb2* tree, *Callogobius* as a whole and the *maculipinnis* group were monophyletic (posterior probability 1.0), but other clades were either not present or supported by posterior probability of less than 0.90. In the *zic1* tree, only the *maculipinnis* group was supported by a high posterior probability (1.0).

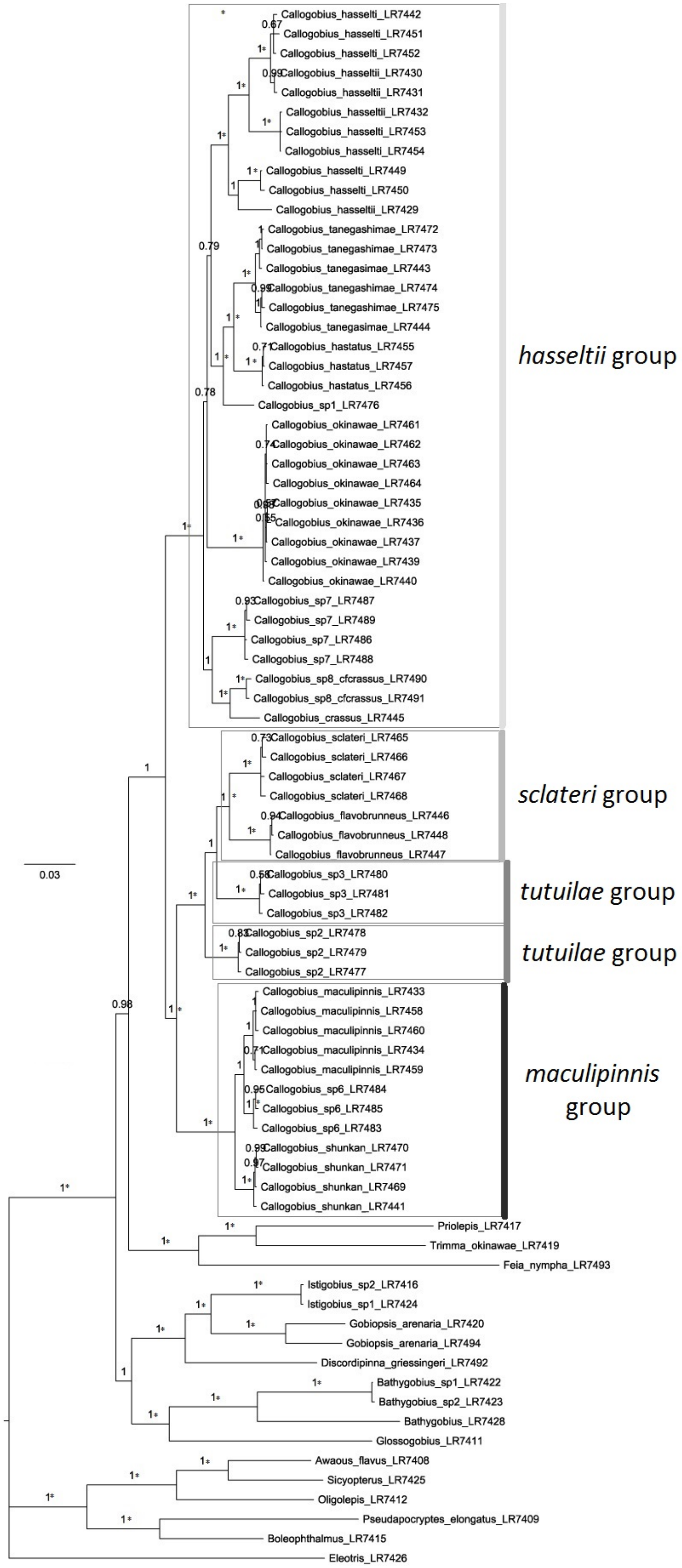
Callogobius_hasselti_LR7442
0.67
Callogobius_hasselti_LR7451
1*
Callogobius_hasselti_LR7452
0.99
Callogobius_hasseltii_LR7430
Callogobius_hasseltii_LR7431
1*
1*
Callogobius_hasseltii_LR7432
Callogobius_hasselti_LR7453
Callogobius_hasselti_LR7454
1*
1*
Callogobius_hasselti_LR7449
1
Callogobius_hasselti_LR7450
Callogobius_hasseltii_LR7429
1
Callogobius_tanegashimae_LR7472
0.79
1
Callogobius_tanegashimae_LR7473
Callogobius_tanegasimae_LR7443
1*
0.99
Callogobius_tanegashimae_LR7474
1
Callogobius_tanegashimae_LR7475
1*
Callogobius_tanegasimae_LR7444
0.71
Callogobius_hastatus_LR7455
1*
1*
Callogobius_hastatus_LR7457
Callogobius_hastatus_LR7456
0.78
Callogobius_sp1_LR7476
Callogobius_okinawae_LR7461
0.74
Callogobius_okinawae_LR7462
Callogobius_okinawae_LR7463
Callogobius_okinawae_LR7464
0.68
Callogobius_okinawae_LR7435
0.55
Callogobius_okinawae_LR7436
1*
1*
Callogobius_okinawae_LR7437
Callogobius_okinawae_LR7439
Callogobius_okinawae_LR7440
0.93
Callogobius_sp7_LR7487
Callogobius_sp7_LR7489
1*
Callogobius_sp7_LR7486
Callogobius_sp7_LR7488
1
1*
Callogobius_sp8_cfcrassus_LR7490
1*
Callogobius_sp8_cfcrassus_LR7491
Callogobius_crassus_LR7445
hasseltii group
0.73
Callogobius_sclateri_LR7465
Callogobius_sclateri_LR7466
1*
Callogobius_sclateri_LR7467
1
Callogobius_sclateri_LR7468
1 *
0.94
Callogobius_flavobrunneus_LR7446
1*
Callogobius_flavobrunneus_LR7448
Callogobius_flavobrunneus_LR7447
sclateri group
1
0.03
0.58
Callogobius_sp3_LR7480
1*
1*
Callogobius_sp3_LR7481
Callogobius_sp3_LR7482
tutuilae group
0.83
Callogobius_sp2_LR7478
1*
Callogobius_sp2_LR7479
Callogobius_sp2_LR7477
tutuilae group
Callogobius_maculipinnis_LR7433
1
0.98
Callogobius_maculipinnis_LR7458
1 *
1
Callogobius_maculipinnis_LR7460
0.71
Callogobius_maculipinnis_LR7434
1
Callogobius_maculipinnis_LR7459
0.95
Callogobius_sp6_LR7484
1*
Callogobius_sp6_LR7485
1*
Callogobius_sp6_LR7483
0.99
Callogobius_shunkan_LR7470
0.97
Callogobius_shunkan_LR7471
1*
Callogobius_shunkan_LR7469
Callogobius_shunkan_LR7441
maculipinnis group
1*
1*
Priolepis_LR7417
1*
Trimma_okinawae_LR7419
Feia_nympha_LR7493
1*
Istigobius_sp2_LR7416
1*
Istigobius_sp1_LR7424
1*
1*
Gobiopsis_arenaria_LR7420
Gobiopsis_arenaria_LR7494
Discordipinna_griessingeri_LR7492
1
1*
Bathygobius_sp1_LR7422
1*
Bathygobius_sp2_LR7423
1*
Bathygobius_LR7428
Glossogobius_LR7411
1*
Awaous_flavus_LR7408
1*
Sicyopterus_LR7425
1*
Oligolepis_LR7412
1*
Pseudapocryptes_elongatus_LR7409
Boleophthalmus_LR7415
Eleotris_LR7426

FIGURE 3.1 (previous page) Bayesian analysis for the concatenated data set, with posterior probabilities. Nodes supported by at least 95 percent ML bootstrap replicates indicated with an asterisk (*). LR numbers refer to Lukas Rüber's tissue collection numbers; these numbers are used in the tree to differentiate individuals of the same species. Delventhal & Mooi's (unpublished, Chapter Two) species groups are indicated by colour. Very light grey = *hasseltii* group, light grey = *sclateri* group, medium, grey = *tutuilae* group, dark grey = *maculipinnis* group.

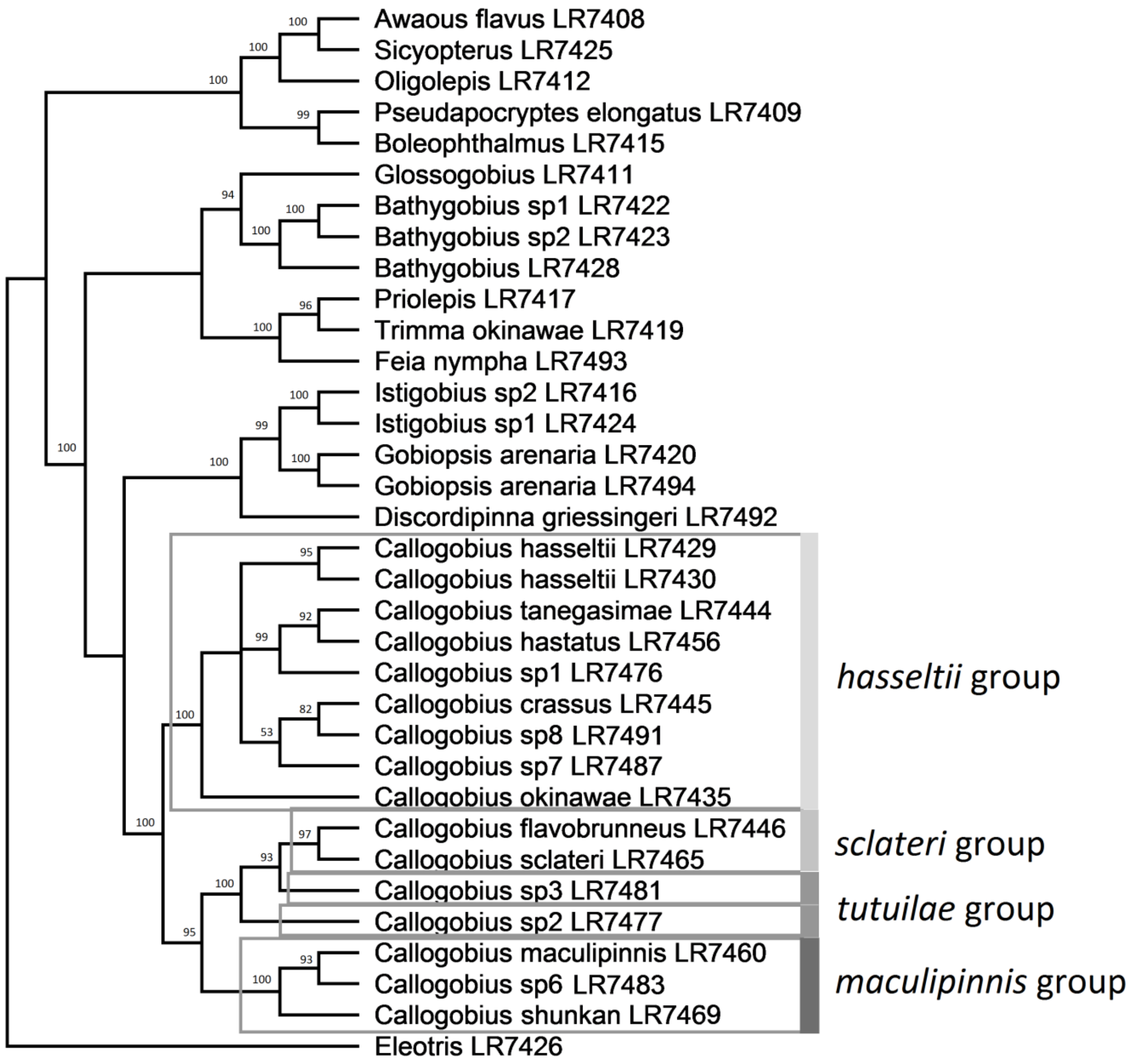

FIGURE 3.2 Maximum parsimony consensus tree for the reduced data set, with most of the duplicate taxa removed. Bootstrap values of at least 50% have been mapped onto nodes. LR numbers refer to Lukas Rüber's tissue collection numbers; these numbers are used in the tree to differentiate individuals of the same species. Delventhal & Mooi's (unpublished, Chapter Two) species groups are indicated by colour. Very light grey = *hasseltii* group, light grey = *sclateri* group, medium, grey = *tutuilae* group, dark grey = *maculipinnis* group.

DISCUSSION

Overall, we observed a high degree of concordance between results from the morphological data set of Delventhal & Mooi (unpublished, Chapter Two) and the present molecular data set. The genus *Callogobius*, the *sclateri* group, the *maculipinnis* group and the *hasseltii* group were recovered as monophyletic in each analysis. Hence, the morphological diagnoses are corroborated and these three monophyletic groups can be used to narrow comparisons for species descriptions.

Figure 3.3 depicts a summary of the relationships between the *sclateri*, *maculipinnis*, *hasseltii* and *tutuilae* groups as inferred by the present molecular analysis and Delventhal & Mooi's (unpublished, Chapter Two) morphological analysis. In Delventhal & Mooi's (unpublished, Chapter Two) morphological analysis, the single species sampled from the *tutuilae* group was recovered as sister to the *sclateri* group; in the present molecular study both *tutuilae* group species were recovered as paraphyletic with respect to the *sclateri* group. The most significant difference was that in the morphological tree the *maculipinnis* group was recovered as the sister to the remaining *Callogobius* species, whereas in the molecular tree the *hasseltii* group was recovered as sister to the remaining species. We re-examined the character matrix from Delventhal & Mooi (unpublished, Chapter Two) to determine whether any support existed for the alternative topology as identified by the molecular dataset. The morphological hypothesis - the relationship between the *hasseltii*+*tutuilae*+*sclateri* groups - was supported by two characters shared by all included members but not shared by members of the *maculipinnis* group, *Drombus* sp. or *Yongeichthys criniger*: the absence of the temporal canal, the hypobranchial 1 process directed laterally. However, both of these characters are known to vary widely within gobiids. During a re-examination of Delventhal & Mooi's (unpublished, Chapter Two) character matrix, we noted that the *maculipinnis* group shared a large number of apomorphic characters. These character states were not shared with the outgroup taxa, therefore long branch attraction cannot explain the discordance between the morphological and molecular phylogenetic hypotheses. Morphological support for the molecular hypothesis was absent; we found no characters shared by the *maculipinnis*+*tutuilae*+*sclateri* groups not shared by members of the *hasseltii* group, *Drombus* sp. or *Yongeichthys criniger*. However, we cannot rule out the possibility that the topology supported by Delventhal and Mooi's (unpublished, Chapter Two) morphological dataset is the result of outgroup selection. At least one of the two characters supporting the monophyly of their *hasseltii* group (elongate caudal fin) is found in other gobiids and may be the state found in basal *Callogobius*. Likewise, we cannot rule out that incongruence between the two hypotheses is a result of the molecular tree being poorly rooted due to distant outgroups; inevitable because no sister taxon to *Callogobius* has been identified.

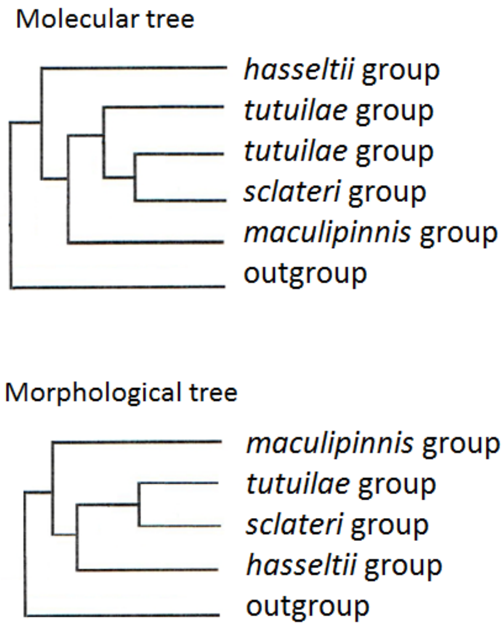

FIGURE 3.3 Summary of the interrelationships of *sclateri*, *maculipinnis*, *hasseltii* and *tutuilae* groups as inferred by the present molecular analysis and Delventhal & Mooi's (unpublished, Chapter Two) morphological analysis.

It is interesting to note the relative branch lengths between groups of individuals identified as *Callogobius hasseltii* (i.e. the members of the *C. hasseltii* species complex). All but one of our samples are from Japan (LR 7429 is from Malaysia) yet the distances between many individuals is comparatively large. Our results suggest that at least 4 major clades exist within this species complex. One clade contains LR 7454, LR 7453 and LR 7432 (from Shizuoka, Shizuoka and Kochi, respectively) and is sister to a clade containg LR 7451, LR 7452, LR 7431 and LR7430 (from Amami-oshima). More distinct to them is a clade containing LR 7450 and LR 7449 (from Okinawa-jima) and LR 7429 (from Malaysia). By comparison, in other species with 5 or more representatives, *C. tanegasimae* and *C. okinawae*, the branch lengths between specimens from different locations within the Japanese islands are relatively short. Morphological studies by the first author and Y. Ikeda suggest that *C. hasseltii* (a widespread taxon as currently circumscribed) is a complex of several very similar species (2 or more of which may occur in a single locality) with differing, but overlapping morphometric and meristic values including subtle differences body proportions, fin-ray counts, lateral series-scale counts, and previously undocumented cheek-scale counts. This confusion has existed since the original description, since Bleeker's three syntype specimens (RMNH 1852) appear to represent two species (Delventhal unpublished, Appendix A). We expect that further, detailed morphological data collection along with additional genetic sampling will reveal several cryptic species within this complex.

Chapter Four. *Callogobius winterbottomi*, a new species of goby (Teleostei: Gobiidae) from the Western Indian Ocean

NAOMI R. DELVENTHAL[1] & RANDALL D. MOOI[1,2]
[1]*Department of Biological Sciences, 212B Biological Sciences Bldg., University of Manitoba, Winnipeg MB, R3T 2N2 Canada. E-mail: naomi.delventhal@gmail.com*
[2]*The Manitoba Museum, 190 Rupert Ave., Winnipeg MB, R3B 0N2 Canada. E-mail: rmooi@manitobamuseum.ca*

Published in *Zootaxa* 19 March 2013

My contribution: I first identified the species as undescribed based on the literature and extant types, planned the study, travelled to all the listed institutions to examine the included type and non-type specimens, determined the characters appropriate for examination, wrote the methods section and developed the new naming system for sensory papillae (with comments from R. Mooi and Y. Ikeda, who is not a co-author), and drafted the remarks section including the hypothesis for relationships, with comments from R. Mooi. I photographed Figure 4.4 and illustrated Figure 4.5; R. Mooi photographed Figure 4.1 and illustrated Figures 4.2 and 4.3 Most meristic data from the type series were recorded independently by myself and R. Mooi (to ensure similar technique and accuracy); the recorded measurements of the type series were taken by R. Mooi; I recorded papillae row data and all data taken from specimens not on loan to the Manitoba Museum. R. Mooi arranged the figures.

SUMMARY

Callogobius winterbottomi new species is described from the 33.8 mm SL holotype and two paratypes (32.2 mm SL and 22.9 mm SL) from the Comoros, Western Indian Ocean. It is distinguished from all other known *Callogobius* species by the following combination of characters: sensory pores absent, 23–26 scales in lateral series, and sensory papillae pre-opercular row not continuous with transverse opercular row. One additional specimen of *Callogobius winterbottomi* was located from South Africa. A new standardized naming system for *Callogobius* sensory papillae rows is presented for identification and clarification of character states among *Callogobius* species. The new species is tentatively placed among what we term the "*sclateri* group", a clade including *C. sclateri* (Steindachner) and three other species that exhibit a modified female urogenital papilla with lateral distal flaps and elongate ctenii on the caudal peduncle scales. *Callogobius tutuilae* (Jordan & Seale) is removed from synonymy with *C. sclateri* because it has partially united pelvic fins (vs. separate) and the preopercular sensory papillae row is continuous with the transverse opercular row (vs. separate).

INTRODUCTION

The genus *Callogobius* Bleeker comprises more than 40 nominal species (Eschmeyer 2012) and is widespread in Indo-Pacific shallow marine and brackish environments, including coral reefs and coral rubble, tidepools, and mangrove streams. Because of cryptic colouration, habitat specialization, and poor condition of most museum specimens (many species have fragile skin and deciduous scales), the taxonomy is poorly known. A revision of *Callogobius* has never been completed. In the 1970s some inroads were made; Akihito & Meguro (1975, 1977) examined type material and clarified the taxa from Japan, and McKinney & Lachner (1978a) provided a summary table of selected characters obtained mostly from types. The latter authors provided a complete list of included species of *Callogobius* at the time, and formed a basis for the recognition of *Callogobius* as currently circumscribed. Unfortunately, McKinney & Lachner never completed a planned revision, although they did synonymize several species in a later publication (McKinney & Lachner 1984), but without detailed evidence. Goren (1979b) reviewed the *Callogobius* species of the Red Sea, whereas other taxonomic papers on *Callogobius* since McKinney & Lachner (1978a) consist primarily of descriptions of one or two new species (e.g., Goren 1978; Goren 1979a; McKinney & Lachner 1978b; McKinney & Lachner 1984; Chen & Shao 2000; Chen *et al*. 2006).

During a visit by the first author to the Royal Ontario Museum, three male specimens of an unknown *Callogobius* species were encountered in a single collection from the Comoros. After a thorough search, only one additional specimen of this species, a female, was located from South Africa. In this paper, we describe this species as new, briefly discuss its relationships among congeners, and suggest removal of a possible relative, *C. tutuilae* (Jordan & Seale), from synonymy with *C. sclateri* (Steindachner). We also provide a new standardized naming system for *Callogobius* sensory papillae rows for identification and clarification of character states among species of this genus.

MATERIALS AND METHODS

Abbreviations for institutional codes follow Fricke & Eschmeyer (2012) and/or Sabaj Pérez (2010). Comparisons to other described species are based on the holotypes of the following species and data from McKinney & Lachner (1978a): *Callogobius amikami* Goren, Miroz & Baranes, TAU P-10321; *C. andamanensis* Menon & Chatterjee, ZSI F7105/2; *C. badia* (Herre), FMNH 17373; *C. bauchotae* Goren, MNHN 1976-0184; *C. bifasciatus* (Smith), SAIAB 235; *C. bothriorrhynchus* (Herzenstein), ZIN 9684; *C. centrolepis* Weber, ZMA 111745; *C. clarki* (Goren), HUJ 10065; *C. clitellus* McKinney & Lachner, USNM 209249; *C. coelidotus* (Sauvage), MNHN 0000-2968; *C. crassus* McKinney & Lachner, USNM 220088; *C. depressus* (Ramsay & Ogilby), AMS B.9758; *C. dori* Goren, BMNH 1978.9.8.7; *C. flavobrunneus* (Smith), SAIAB 211; *C. hastatus* McKinney & Lachner, USNM 216811; *C. irrasus* (Smith), SAIAB 186; *C. kuderi* (Herre), SU 36815; *C. maculipinnis* (Fowler), ANSP 47549; *C. mucosus*(Günther), BMNH 1871.9.13.169; *C. okinawae* (Snyder), USNM 62240; *C. plumatus* (Smith), SAIAB 208; *C. santa* (Herre), FMNH 17374; *C. sclateri* (Steindachner), NMW 30901; *C. sheni* Chen, Chen & Fang, MNNB P6980; *C. shunkan* Takagi, NSMT-P 110000 (formerly TUFLFB); *C. snelliusi* Koumans, RMNH 20289; *C. snyderi*(Fowler), ANSP 72078; *C. stellatus* McKinney & Lachner, USNM 217429; *C. tanegasimae* (Snyder), USNM 62241; *C. trifasciatus* Menon & Chatterjee, ZSI F 7144/2; *C. tutuilae* (Jordan & Seale), USNM 51770; *C. vanclevei* (Herre), USNM 202513.

Meristics. Lateral series scale counts were taken from the dorsalmost extent of the opercular opening to the mid-posterior edge of the hypural plate. Scale counts were taken on both sides when possible as most *Callogobius* species have irregularly sized and unevenly spaced scales. Cyanine blue dye (following the method of Akihito *et al.* 1993) was used to identify scale pockets on specimens missing scales. Predorsal scales were counted from the origin of the first dorsal spine along the midline towards the occiput. Since these scales typically do not form a natural line, scales with at least one-third of their width crossing the midline, as well as any emarginate scales partially encircling the first dorsal-fin spine, were included. Transverse scale rows were counted diagonally from the origin of the first dorsal fin, downward and backward, to the ventral midline at or near the anal-fin base. The last segmented ray in the anal- and second dorsal fins is divided at its base and was counted as a single ray. Pectoral-fin ray counts were taken on both sides when possible. Caudal-fin rays are provided as counts of segmented rays on the upper + lower hypural plates, with the number of branched rays recorded as Arabic numerals and number of unbranched rays as lower case Roman numerals. Procurrent (unsegmented) caudal rays are provided as upper + lower counts.

Morphometrics. Measurements were taken with either dial calipers or microscope graticule and recorded to the nearest 0.1 mm (Table 4.1). Standard length (SL) was taken from the anterior tip of the upper jaw (snout) to the mid-posterior edge of the hypural plate (as identified by folding the caudal fin to find the hypural crease). Head length was measured from the tip of the upper jaw to the upper posterior margin of the operculum. Head depth was taken vertically at the preopercular edge, which is usually the deepest point. Head width was taken at the widest point of the preopercular edge (usually a mid-lateral point). Bony interorbital width was measured by finding the narrowest interorbital distance and pinching it gently with the calipers. Predorsal length was taken from the tip of the upper jaw to the base of the first dorsal-fin spine. Preanal length was taken from the tip of the upper jaw to the base of the first anal-fin spine. Prepelvic length was taken from the tip of the upper jaw to the base of the pelvic-fin spine. Pectoral-fin length was taken from the base of the uppermost ray to the tip of the longest ray. Pelvic-fin length was taken from the base of the spine to the tip of the longest ray, whether the longest ray was the 4th or 5th was recorded. Caudal-fin length was taken from mid-lateral edge of the hypural plate to the tip of the longest ray. Caudal peduncle depth was taken vertically, at the narrowest point, usually just anterior to the posterior edge of the hypural plate.

Sensory papillae rows. Superficial neuromasts are referred to as "sensory papillae" following common usage in goby systematics. Individual papillae rows are identified using Akihito and Meguro's (1977) numbering system, in addition to descriptive names presented in Table 4.2. The descriptive names are intended to clarify states of papillae rows observed among different species within *Callogobius* (including intraspecific variation), but are not appropriate for use with other goby genera. In the species description we have commented only on papillae rows whose length and orientation are variable among *Callogobius* species and generally consistent within a given species. We report each condition along with the number of observations (taken bilaterally, if possible) in parentheses. Relative length of a given row is determined by its base; two rows are considered joined or continuous only if the base is shared; when breaks occur, the two rows are considered separate.

Individual sensory papillae are present in the interorbital, temporal and preopercular regions where pores would normally be found in *Callogobius* species having sensory canal pores. Because we are uncertain of their developmental origin, we are reluctant to identify them as the primary replacement neuromasts of Coombs et al. (1988) and Wongrat & Miller (1991). However, we suggest the term pore replacement papillae for these neuromasts, not to suggest a developmental connection (necessarily), but only to differentiate these individual papillae from unrelated named and numbered papillae rows in these regions.

Callogobius winterbottomi **sp. nov.**

Holotype. ROM 58914, 33.8 mm SL male. Stated locality: Indian Ocean, Comoros, Moheli Bay, on south coast about 3 nautical miles west of Nioumachoua at southwest tip of island at Drondroni River, 12°21’15” S, 43°40’00” E, rotenone, depth 9–17 m, R. Winterbottom, W. Holleman, 27 Nov. 1988.

Paratypes. ROM 92690, 2 specimens (32.2 mm SL male and 22.9 mm SL male). Collected with the holotype.

Other material. SAIAB 057357, 1 specimen (37.7 mm SL female). Stated locality: Indian Ocean, South Africa, Aliwal Shoal off Scottburgh, 30°18’01” S 30°48’58” E, 26-28 m, P.C. Heemstra, 7 Feb. 1998.

FIGURE 4.1 Left lateral views of type specimens of *Callogobius winterbottomi*. Scale bar = 5 mm.A. Holotype, ROM 58914, 33.8 mm SL male. **B.** Paratype, ROM 92690, 32.2 mm SL male. **C.** Paratype, ROM 92690, 22.9 mm SL male.

Diagnosis. *Callogobius winterbottomi* is distinguished from all other known *Callogobius* species by the following combination of characters: head pores absent, 23–26 scales in lateral series, and preopercular papillae row (Row 20) not continuous with transverse opercular papillae row (Row 21).

Description. Holotype values are indicated by an asterisk. Parentheses enclose the number of counts in the type specimens with the particular value; counts are made on both sides when applicable or possible. Dorsal fin rays VI, I,9 (3*); anal fin rays I,8(3*); pectoral fin rays 16(2*), 17(4); pelvic fin rays I,5 (6*); segmented caudal fin rays 9 + 7i (1*), i8 + 7i (2); procurrent rays 4 + 4 (3*); scales in lateral series 23(1), 24(3), 26(2*); predorsal scales 8(2), 9(1*); transverse scales 10(1), 11(2*). Counts for these characters in the non-type female fall within the ranges reported for the type specimens.

All scales are large and deciduous, with distinctly outlined centres without circuli (Figure 4.2). Scales on the head and anterior half of the body are cycloid; cycloid scales are present in the spaces between the papillae rows on the cheeks, preoperculum and operculum, on the lateral side of the pectoral fin bases, prepelvic and predorsal regions, and on the belly. Scales on the posterior half of the body are ctenoid; ctenoid scales first appear on the mid-flank region below the 5th or 6th spine of the first dorsal fin. Ctenii are roughly triangular and pointed, and increase in number per scale towards the caudal peduncle. Slightly elongate ctenii occur on scales of the dorsal and ventral edges of the caudal peduncle (near or above the procurrent caudal-fin rays) (Figure 4.2).

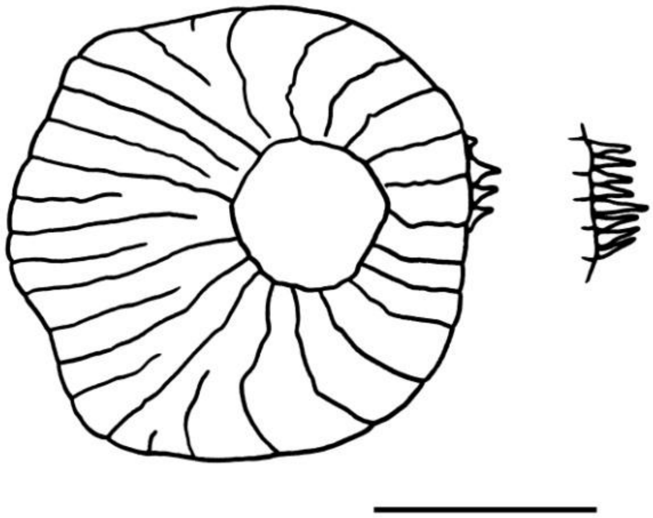

FIGURE 4.2 Scale morphology in *Callogobius winterbottomi*, illustrated from male paratype, ROM 92690, 32.2 mm SL. Left, entire mid-lateral scale from region below last spine of first dorsal fin showing distinctly outlined centre and single row of ctenii of normal length. Circuli are not illustrated, although note that they do not occur within the outlined centre. Right, slightly elongate ctenii of postero-dorsal caudal peduncle scale for comparison. Scale bar = 1 mm.

Teeth of upper and lower jaws (based on paratype, ROM 92690, 32.2 mm SL) are conical and slender; outer teeth larger, slightly curved and spaced at a distance of two thirds to twice the height of the tooth. There are 2–3 rows of inner teeth tightly spaced, about half the height of the outer teeth. The tongue is of medium-width with a slightly bilobed tip. Anterior nostrils are long, slender tubes, reaching almost to the outer edge of the upper lip; the posterior nostrils are very short upright tubes.

Pelvic fins are partially united with the membrane reaching two thirds the length of the fin (Figure 4.3). The fifth segmented pelvic-fin ray is about three quarters the length of the fourth ray; all segmented pelvic-fin rays are branched. The pelvic frenum is present, but somewhat weak (Figure 4.3).

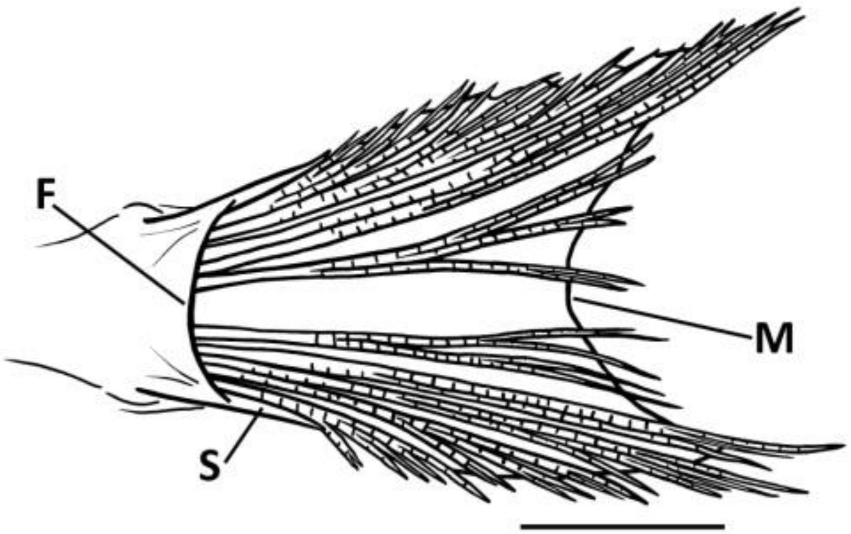

FIGURE 4.3 Ventral view of pelvic fins of *Callogobius winterbottomi*, illustrated from male paratype, ROM 92690, 32.2 mm SL. Scale bar = 2 mm. Abbreviations: F = weak frenum, M = extent of membrane uniting pelvic fins, about two thirds length of fins (reconstructed, membrane damaged in all specimens available), S = pelvic spine.

TABLE 4.1 Selected measurements of the holotype and two paratypes of *Callogobius winterbottomi* in mm; the values in parentheses indicate the percentage of standard length (SL) or head length (HL).

	Holotype	Paratype	Paratype
Sex	M	M	M
Standard Length (SL)	33.8	32.2	22.9
Head length (HL) (% of SL)	11.5 (34.0)	11.0 (34.2)	8.3 (36.2)
Head depth (% of HL)	5.9 (50.9)	5.1 (46.4)	4.1 (49.4)
Head width (% of HL)	7.8 (67.8)	7.3 (66.4)	5.3 (63.9)
Interorbital width (% of HL)	0.78 (6.9)	0.68 (6.2)	0.63 (7.6)
Predorsal fin distance (% of SL)	13.1 (38.8)	13.2 (41.0)	9.4 (41.0)
Preanal fin distance (% of SL)	20.2 (59.8)	19.6 (60.9)	13.9 (60.7)
Prepelvic fin distance (% of SL)	11.8 (34.9)	10.6 (32.9)	7.5 (32.8)
Pectoral fin length (% of SL)	10.4 (30.8)	9.5 (29.5)	6.5 (28.4)
Pelvic fin length (% of SL)	7.5 (22.2)	7.2 (22.4)	5.4 (23.6)
Caudal fin length (% of SL)	11.1 (32.8)	10.3 (32.0)	6.7 (29.3)
Caudal peduncle depth (% of SL)	4.4 (13.0)	4.2 (13.0)	3.2 (14.0)

The male urogenital papilla is very long, slender and darkly pigmented. In the female (SAIAB 057357), the papilla is broad and darkly pigmented with small, distal flaps of skin laterally (E. Heemstra & W. Holleman, pers. comm.).

Head pores are absent. Pore replacement papillae are present in the interorbital, temporal and preopercular regions where pores would normally be found in *Callogobius* species having sensory canal pores (Figure 4.5).

FIGURE 4.4 Right lateral view of *Callogobius winterbottomi*, SAIAB 057357, 37.7 mm SL female. Scale bar = 5 mm.

TABLE 4.2 Akihito & Meguro’s (1977) numbering system for *Callogobius* sensory papillae rows, followed by our assigned descriptive names. The intermandibular row was not originally identified by Akihito & Meguro (1977), but incorporated here as Row 24. Asterisks indicate those rows that are particularly useful in describing interspecific variation in *Callogobius* and are commented on in the description of *C. winterbottomi*. Two groups of papillae rows (usually less well defined; ridges may or may not be raised) are found on the temporal and posttemporal/predorsal regions; we refer to these as the temporal and posttemporal groups, respectively. These rows are illustrated but not labelled in Figure 4.5.

Row 1	Internasal row
Row 2	Postnasal row*
Row 3	Interorbital row
Row 4	Oblique premaxillary row
Row 5	Preorbital row
Rows 6	Upper longitudinal premaxillary row
Rows 7	Lower longitudinal premaxillary row
Row 8	Transverse maxillary row
Row 9	Anterior suborbital row*
Row 10	Mid suborbital row*
Row 11	Posterior suborbital row(s)*
Row 12	Longitudinal cheek row*
Row 13	Transverse cheek row*
Row 14	Longitudinal maxillary row*
Row 15	Longitudinal mandibular row*
Rows 16	Transverse mandibular rows*
Row 17	Postorbital row*
Row 18	Upper cranial row
Row 19	Lower cranial row
Row 20	Preopercular row*
Row 21	Transverse opercular row*
Row 22	Oblique opercular row
Row 23	Subopercular row
Row 24	Intermandibular row

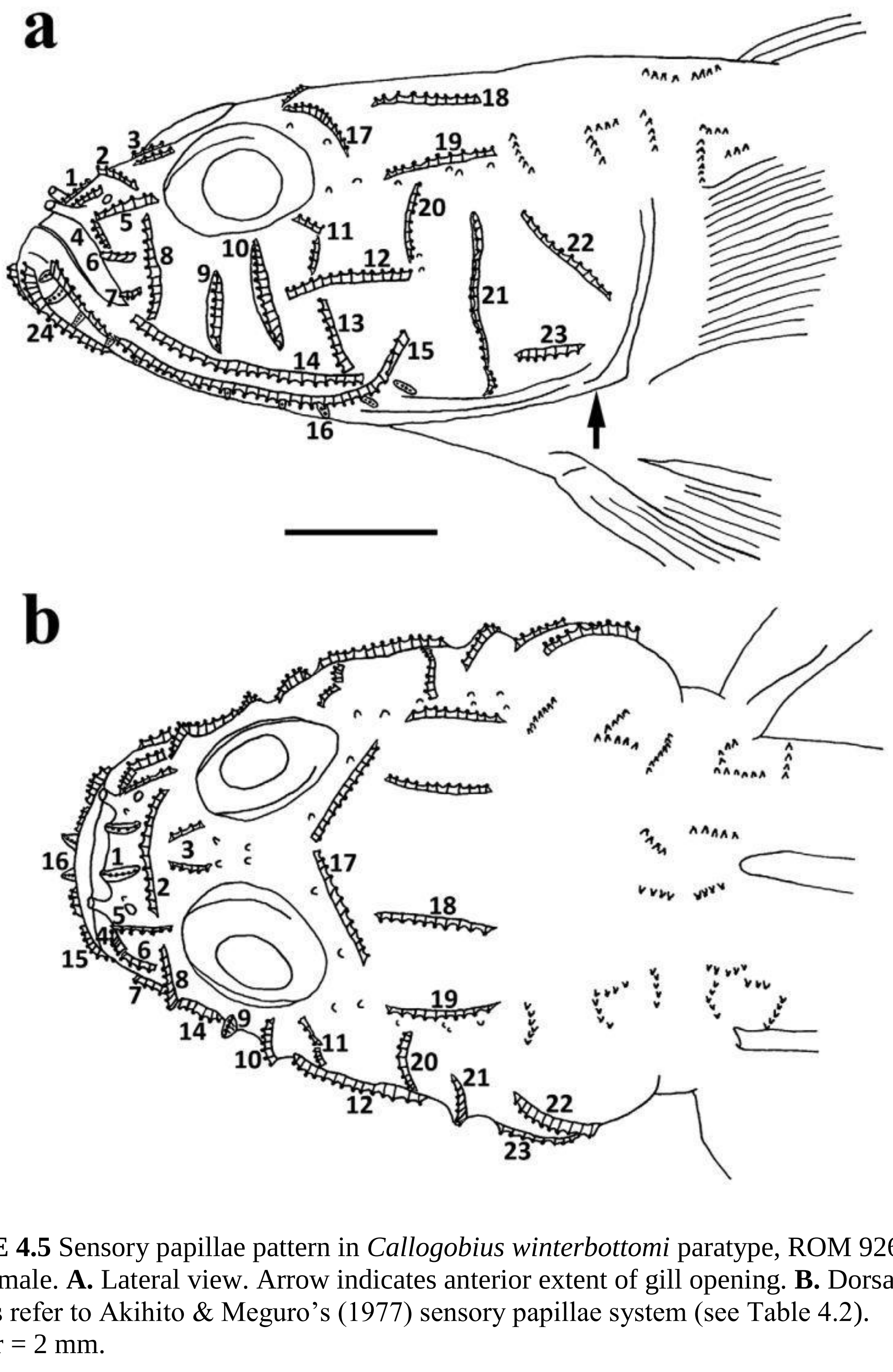

FIGURE 4.5 Sensory papillae pattern in *Callogobius winterbottomi* paratype, ROM 92690, 22.9 mm SL, male. **A.** Lateral view. Arrow indicates anterior extent of gill opening. **B.** Dorsal view. Numbers refer to Akihito & Meguro's (1977) sensory papillae system (see Table 4.2).
Scale bar = 2 mm.

Papillae Row Configuration (Figure 4.5): The postnasal rows (Row 2) are long and joined across the midline (3*). The anterior suborbital row (Row 9) is moderately long and does not reach the eye (6*); the mid suborbital row (Row 10) reaches or nearly reaches the eye (4*) or is of moderate length (2). The posterior suborbital rows (Row 11) are short; they may be separate but touch (2*), slightly overlap (2) or be well separated (2). The longitudinal maxillary row (Row 14) is unbroken and extends posteriorly to just below (2) or usually beyond (4*) the transverse cheek row (Row 13), which is short (6*). The longitudinal mandibular row (Row 15) is unbroken (6*). There are approximately 10(1), 11(4*), or 12(1) transverse mandibular rows (Row 16) on each lower jaw. The postorbital rows (Row 17) are short (less than 2/3 the length of the distance from the dorsal mid-line to the bony edge of the cranium) (4) to medium, (more than 2/3 the length of the distance from the dorsal mid-line to the bony edge of the cranium) (2*), and may nearly reach the midline (4*). The preopercular row (Row 20) is positioned anterior to, and not continuous with, the transverse opercular row (Row 21) (6*). The non-type female specimen exhibits papillae row configurations identical to that of the holotype.

Colour in Preservative (Figure 4.1): General colour pattern consists of brown dusky bars and mottling on a pale yellow-brown head and body. Head markings are poorly defined, consisting of lateral dusky blotches and a more evenly pigmented region from the snout through the post-orbital region, dorsally. The ventral region of the head is lightly pigmented. Papillae rows are more distinctly pigmented than surrounding regions. A wide dusky bar extends dorsally over the operculum and pectoral-fin base towards the first dorsal-fin spine; the ventral region of this bar may be darker than the remainder. The trunk has a wide bar extending below the first dorsal fin, reaching to, but not across, the belly. The belly is pale. A narrow, irregular, mottled bar or partial bar may be visible between the dorsal fins, particularly in the smallest specimen;

this marking is more defined ventrally. A wide, slanted bar extends from the second dorsal fin to the posterior edge of the anal fin and around the anterior portion of the caudal peduncle. A wide bar encircles the posterior caudal peduncle, the edge of the hypural plate and the proximal regions of the caudal fin. The fins are pigmented with a darker brown; the first and second dorsal fins have irregular rows of pale spots and/or bands; the outermost edges are mostly pale. The pectoral fins are darkly mottled; there is greater pigment concentration medially. The pelvic and anal fins are evenly dark, except for the margins, which are pale. The caudal fin is dark, with fine, irregular and indistinct vertical bands. The urogenital papilla is dark.

Etymology. Named in honour of Rick Winterbottom who, along with Wouter Holleman, collected the type series. Rick has made substantial contributions to the systematics of gobies and other Indo-Pacific fishes, and to the development of both authors' respective careers. Suggested vernacular name: Winterbottom's flapheaded goby.

Distribution and habitat. Known only from the Comoros (3 specimens, the type series) where the field station was described as "base of vertical wall with numerous caves" at 9–17 m, and South Africa (1 specimen), collected at a depth of 26–28 m.

Comparisons. Only three other described *Callogobius* species lack all head pores: *C. hastatus*, *C. crassus* and *C. clarki*. *C. winterbottomi* can easily be distinguished from *C. hastatus* and *C. clarki* by lower lateral scale counts (23–26 vs 32–37 in *C. hastatus* and 33–41 in *C. clarki*). *C. winterbottomi* differs from *C. crassus* by higher lateral scale counts (23–26 vs 19–21) and papillae row configuration (preopercular row not continuous with transverse opercular row, longitudinal maxillary row and longitudinal mandibular row not broken in *C. winterbottomi* vs preopercular row continuous with transverse opercular row, longitudinal maxillary row and longitudinal mandibular row broken and displaced in *C. crassus*). We are aware of at least two undescribed species of *Callogobius* lacking head pores, but these both differ from *C. winterbottomi* in having the preopercular row (Row 20) continuous with the transverse opercular row (Row 21).

In the Western Indian Ocean, *C. winterbottomi* may also be confused with *C. maculipinnis*, *C. sclateri*, *C. bifasciatus*, *C. flavobrunneus* or *C. plumatus*. These species develop head pores by the time they reach 14 mm but may be more difficult to distinguish as juveniles. *C. winterbottomi* differs from small *C. maculipinnis* by having 10 or more transverse mandibular rows (vs 3–4) and the fifth segmented pelvic fin ray shorter than the fourth (vs. fifth pelvic fin ray as long or longer than the fourth); from *C. sclateri* by having a pelvic frenum and connecting membrane between the fifth segmented pelvic fin rays (vs. pelvic frenum and connecting membrane absent) and by pectoral fin darkest medially (vs. pectoral fin with dark upper edge in small *C. sclateri*); from *C. bifasciatus* and *C. flavobrunneus* by lateral scale counts (23–26 in *C. winterbottomi* vs. 37–48 in *C. bifasciatus* and 34–38 in *C. flavobrunneus*); and from *C. plumatus* by having preopercular row not continuous with transverse opercular row (vs. continuous) and by having the anterior nostril longer than the posterior nostril (vs. shorter).

Remarks. SAIAB 057357 was not assigned type status because of the difference in collection locality. Although this specimen is slightly larger and darker than the Comoros specimens (cf. Figs. 1, 4), these differences are unlikely to be of taxonomic or biological significance. SAIAB 057357 is a female and all three type specimens are males, but we have not observed sexual dichromatism or dimorphism in other *Callogobius* species, except in the shape of the urogenital papilla, and do not expect them in *C. winterbottomi*.

DISCUSSION

In *Callogobius*, the sensory papillae are on raised ridges or flaps in an arrangement that makes species in the genus easily distinguishable from all other gobies. Winterbottom (2003) hypothesized that *Callogobius* is monophyletic based on the presence of both longitudinal and transverse raised ridges. We recognize that naming systems for sensory papillae are controversial in gobies, and that similarly oriented rows have not been demonstrated to be homologous among different goby taxa (see Van Tassell *et al*. 2011 for a brief review). It is not uncommon for individual specimens of *Callogobius* to exhibit slight differences in papillae rows not normally found within a given species (e.g., in a species where the post nasal rows are usually long and overlapping slightly over the midline, occasional specimens may be found where the rows are joined at the midline). These variations generally do not hamper species identification, since in most cases other characters are used in conjunction with papillae row arrangements.

With the description of *C. winterbottomi*, there are now four described species of *Callogobius* that lack all head pores as adults; the others are *C. hastatus*, *C. crassus*, and *C. clarki*. Lack of head pores was not mentioned in the original description of *C. clarki*; we redescribe *C. clarki* in a separate paper. Two additional undescribed species of poreless *Callogobius* are currently under study by the first author and Y. Ikeda (BLIP). There is no additional evidence that poreless *Callogobius* species form a monophyletic group.

However, we hypothesize that *Callogobius winterbottomi* is a member of a monophyletic sub-group having the following external characters that are unique among *Callogobius*: modified scales on the caudal peduncle with unusually long ctenii (occasionally found in other goby genera), and female urogenital papilla with small distal flaps of skin (not previously reported in gobiids). This sub-group, with *C. winterbottomi*, includes *C. sclateri* (Steindachner), *C.*

bifasciatus (Smith), *C. flavobrunneus* (Smith), and *C. clarki* (Goren). All members of this "*sclateri* group" also have the preopercular papillae row (Row 20) separate from the transverse opercular row (Row 21), lack preopercular pores, and lack elongate caudal and pectoral fins (Figure 4.5). We are currently preparing a description of osteological characters that lend additional support for the monophyly of the "*sclateri* group" that will be published in an upcoming paper.

Callogobius tutuilae (Jordan & Seale 1906) has similar body and fin proportions to members of the "*sclateri* group." The only specimen, the holotype (USNM 52770), is very small and in poor condition and was synonymized with *C. sclateri* by both Koumans (1953) and McKinney and Lachner (1984). However, we recognize *C. tutuilae* as a valid species because, unlike *C. sclateri*, *C. tutuilae* has partially united pelvic fins (the pelvic fins are completely separate in even tiny juveniles of *C. sclateri*), and the preopercular papillae row (Row 20) is continuous with the transverse opercular row (Row 21) (separate in *C. sclateri*).

Chapter Five. Redescription of *Callogobius clarki* (Goren) (Teleostei: Gobiidae), not a synonym of *C. bifasciatus* (Smith)

NAOMI R. DELVENTHAL[1] & RANDALL D. MOOI[1,2]

[1]*Department of Biological Sciences, 212B Biological Sciences Bldg., University of Manitoba, Winnipeg MB, R3T 2N2 Canada. E-mail: naomi.delventhal@gmail.com*
[2]*The Manitoba Museum, 190 Rupert Ave., Winnipeg MB, R3B 0N2 Canada. E-mail:rmooi@manitobamuseum.ca*

Published in *Copeia* March 2014

My contribution: I conducted the specimen examination and literature review and determined that *C. clarki* was a valid species; I planned the study, drafted the paper except the final paragraph in the Discussion section which was drafted by R. Mooi, and recorded specimen data except for morphometric data which was recorded by R. Mooi (most meristic data was recorded independently by R. Mooi to ensure technique consistency). R. Mooi photographed Figure 5.1 and illustrated Figure 5.2.

SUMMARY

Callogobius clarki (Goren) is redescribed based on 21 specimens from the Red Sea. This species was originally described from a single specimen collected from the Red Sea, but subsequent workers have placed it in synonymy with the Western Indian Ocean species *C. bifasciatus* (Smith). However, it differs from *C. bifasciatus* in lacking all head pores, and having a lower range in several meristic values (pectoral-fin rays usually 15-17 vs 16-18, lateral scale rows usually 33-39 vs 39-46, predorsal scale rows 12-15 vs 16-20, transverse scale rows usually 17-18 vs 18-22, and transverse mandibular papillae rows usually 11 vs 12). Within the genus, *C. clarki* is a member of the *sclateri* group, exhibiting a female urogenital papilla with small distal flaps of skin, elongate ctenii on some caudal peduncle scales, and preopercular sensory papillae rows not continuous with the transverse opercular rows.

INTRODUCTION

Callogobius clarki (Goren, 1978) was originally described as a species of *Drombus* from a single specimen collected from the Red Sea. In that description, Goren (1978) compared *clarki* with two other Western Indian Ocean and Red Sea gobies then assigned to *Drombus*, *D. irrassus* Smith and *D. plumatus* Smith (later placed in *Callogobius* [Goren, 1980]). Goren did not initially compare *C. clarki* with other *Callogobius* species. Although Smith (1958) had described *C. bifasciatus* (Smith) and *C. flavobrunneus* (Smith) in the Western Indian Ocean one year previous to the description of *C. irrasus* and *C. plumatus*, he had placed them in a different genus, *Mucogobius*, and a different family, Eleotridae, presumably because of the separate pelvic fins in the former two species (Goren, 1980). The condition of the sensory pores of the head of *C. clarki* was not specifically noted by Goren (1978, 1979, 1980), although a key to Red Sea *Callogobius* used this feature to differentiate *clarki* from all other local species (Goren et al., 1991). Randall et al. (1994) and Randall (1995) synonymized *C. clarki* with *C. bifasciatus* without comment.

During the first author's study of *Callogobius* taxonomy, a striking trend was noted. All *C. bifasciatus* specimens (following Randall et al., 1994) from the Red Sea lacked sensory pores, but pores were present on every specimen from outside the Red Sea. Examination of the types of *C. clarki* (HUJ 10065) and *C. bifasciatus* (SAIAB 235) confirmed the absence and presence of sensory pores in these two specimens, respectively. This suggested that *C. clarki* was a distinct and valid species endemic to the Red Sea as suggested by Goren et al. (1991), and led to a search for other possible distinguishing characters between *C. clarki* and *C. bifasciatus*. In this paper, we redescribe *C. clarki* (Goren, 1978), with particular attention given to a comparison with *C. bifasciatus* (Smith, 1958). In addition to sensory pore distribution, we provide evidence that *C.*

clarki and *C. bifasciatus* exhibit different (but overlapping) ranges for several meristic values; morphometric characteristics examined did not differ between the two species.

METHODS

Institutional abbreviations are as listed at http://www.asih.org/codons.pdf. Methods for morphometric and meristic data collection follow Delventhal and Mooi (2013, Chapter Four). Morphometric data were limited to specimens that had reached sexual maturity and that had not become compressed, folded or otherwise distorted during preservation and storage. Data reported in the text are followed, in parentheses, by the number of specimens exhibiting that feature; the holotype condition is indicated by an asterisk (*). Bilateral observations are used when possible. Terminology for sensory papillae rows follows Delventhal and Mooi (2013, Chapter Four). In the redescription we have commented only on papillae rows whose length and orientation are variable among *Callogobius* species and generally consistent within a species.

Callogobius clarki (Goren, 1978)

Clark's Flapheaded Goby

Figures 5.1 – 5.3; Tables 5.1 – 5.5

Drombus clarki Goren, 1978:200-201, fig. 6. – Goren, 1979:36-37, fig. 19, tab. 1 [description]; Golani, 2006:34 [type list].

Callogobius new species A. – McKinney, 1980:2, fig. 1 (drawing reproduced here as Figure 5.3).

Callogobius clarki (Goren). – Goren, 1980:213, 216, tabs. 1,2; Dor, 1984:241 [list]; Goren et al., 1991:300 [key]; Goren and Dor, 1994:63 [list]; Delventhal and Mooi, 2013:162-163 [species comparison, relationships].

Callogobius bifasciatus (non Smith, 1959). – Randall et al., 1994:240-241, fig. 8 [in part, description, synonymy of *C. clarki* with *C. bifasciatus*]; Randall, 1995:300, fig. 937 [in part, description, synonymy of *C. clarki* with *C. bifasciatus*]; Golani and Bogorodsky, 2010:46 [list].

FIGURE 5.1 *Callogobius clarki*, holotype, HUJ 10065, 36.3 mm SL female: (A) left lateral view; (B) right lateral view.

Holotype. HUJ10065 (ex HUJ 56976): 1 specimen (36.5 mm SL female), Red Sea, Egypt (formerly Israel), Et Tur, Gulf of Suez, 1972, HUJ team.

Non-type material. 20 specimens. BMNH 1978.9.8.6: 1 specimen (38.8 mm SL male), Red Sea, Sudan, Mersa Ar-Rakiyai, "Manihine", 1951. ROM 50227: 1 specimen (34.9 mm SL male), Red Sea, Egypt (formerly Israel), Tiran Island, Foul Bay, M. Goren, 1981. USNM 220031: 11 specimens (14.1 – 35.1 mm SL, 4 male, 3 female, 1 juvenile, 3 specimens cleared and stained), Red Sea, Egypt, Gulf of Aqaba, bay at El Himeira, V. Springer et al., 1969. USNM 220038: 2 specimens (34.6 – 48.6 mm SL, males), Red Sea, Eritrea (formerly Ethiopia), Melita Bay (mouth of Melita Bay), V. Springer et al., 1969. USNM 220090: 1 specimen (43.7 mm SL male) Red Sea, Egypt, Reef near road at Marsa Muqabla [= Marsa el Muqabila, approx. 29°22'N 34°47'E], NW of coast Gulf of Aqaba, V. Springer et al., 1969. USNM 296954: 2 specimens (16.8 – 24.2 mm SL, 1 male, 1 juvenile), Red Sea, Egypt, Strait of Jubal, NW Edge of Sha'b al Fanadir reef, 27°17'23"N 33°48'52"E, H. Fehlmann et al., 1965. USNM 341181: 2 specimens (31.0 – 47.9 mm SL, 1 male, 1 female), Red Sea, Egypt, Strait of Jubal, small reef ca. 300 yds. North of pier at Institute of Oceanography & Fisheries, Ghardaqa, 27°16'38"N 33°47'01"E, H. Fehlmann et al., 1965.

Diagnosis. *Callogobius clarki* is distinguished from all other described *Callogobius* species by the following combination of characters: head pores absent, 33-41 scales in lateral series, and preopercular row (Row 20) not continuous with transverse opercular row (Row 21).

Description. See Table 5.1 for selected morphometric values, with comparisons to values for *C. bifasciatus*.

See Tables 5.2-5.4 for meristic values. Starred values indicate those of the holotype. Dorsal fin elements VI, I,10 (19*), VI, I,11 (1); anal fin elements I,9 (20*); pectoral fin elements

12 (1), 15 (3), 16 (27*), 17 (9); pelvic fin elements I,5 (40*); unbranched and branched principle caudal fin rays i8 + 7i (18*), i8 + 8 (2); procurrent rays 4 + 4 (5), 4 + 5 (1), 5 + 4 (5), 5 +5 (8*), 6 +6 (1); scales in lateral series 33 (2), 34 (2), 35 (8), 36 (5), 37 (7*), 38 (6), 39 (2), 41 (1); scales in predorsal series 12 (1), 13 (3), 14 (7), 15 (6*); scales in transverse series 17 (9), 18 (7*), 19 (1).

Teeth and tongue based on 3 cleared and stained specimens from USNM 220031. Teeth of upper jaw conical, slender and slightly curved inward; outer row enlarged and spaced at a distance of about 2/3 to 1/3 the height of the tooth; about one to four tightly spaced inner rows of smaller teeth (one posterior row gradually increasing to about four inner rows anteriorly. Teeth in lower jaw conical, slender and slightly curved inward; an anterior outer row with about 3-5 somewhat enlarged teeth on each side; a mid-posterior innermost row of enlarged (some greatly enlarged) teeth; one to four rows of smaller teeth extending between and beyond (posterior to) the enlarged outer and inner rows. Tongue rather slender, tip rounded. Anterior nostril a slender tube, may reach the outer edge of the upper lip in some specimens; posterior nostril a short, upright tube.

Pelvic fins partially joined, membrane probably reaching between 2/3 – 5/6 the length of the fin (all of our specimens have torn pelvic fins); the fifth pelvic-fin ray shortened, about nine tenths the length of the fourth pelvic-fin ray on the holotype, frequently shorter on other specimens; all pelvic-fin rays branched. Frenum present, but relatively weak. Urogenital papilla with little or no pigment, long and tapering in males; broad with distal flaps of skin in females (Figure 5.2).

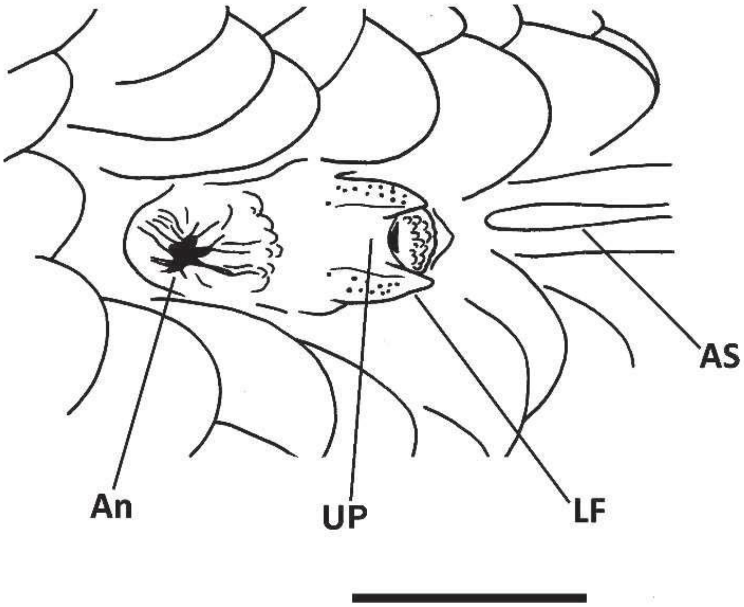

FIGURE 5.2 Female urogenital papilla of *Callogobius clarki*, USNM 341181, 31.0 mm SL, ventral view. Note the broad lateral flaps of skin. An = anus; AS = anal-fin spine; LF = lateral flap; UP = urogenital papilla. Scale bar = 1 mm.

Pores absent. Individual pore replacement papillae (or occasionally short ridges of up to 4 papillae) are present in the interorbital, temporal and preopercular regions.

Papillae row configuration (Figure 4.3): The postnasal rows (Row 2) are long and joined across the midline (17*), or occasionally separate (2). The anterior suborbital row (Row 9) is moderately long to long, approaching the eye (38*); the mid suborbital (Row 10) nearly reaches or reaches the eye (38*). The posterior suborbital rows (Row 11) are short to moderate length, well separated (26), nearly touching (5*), or slightly overlapping (7*). The longitudinal maxillary row (Row 14) is unbroken and extends posteriorly below (9) or below and beyond (29*) the transverse cheek row (Row 13). The longitudinal mandibular row (Row 15) is unbroken (38*). There are approximately 10 (2), 11 (30*) or 12 (6*) transverse mandibular rows on each lower jaw. The post orbital (Row 17) rows are medium length (between 2/3 and 4/5 the distance from the dorsal midline to the bony edge of the cranium) (5) or long (more than 4/5 the distance from the dorsal midline to the bony edge of the cranium) (14*); they may be well separated (11), nearly touch or touch (6*) or continuous across the midline (2). The preopercular row (Row 20) is positioned anterior to and not continuous with the transverse opercular row (Row 21) (38*).

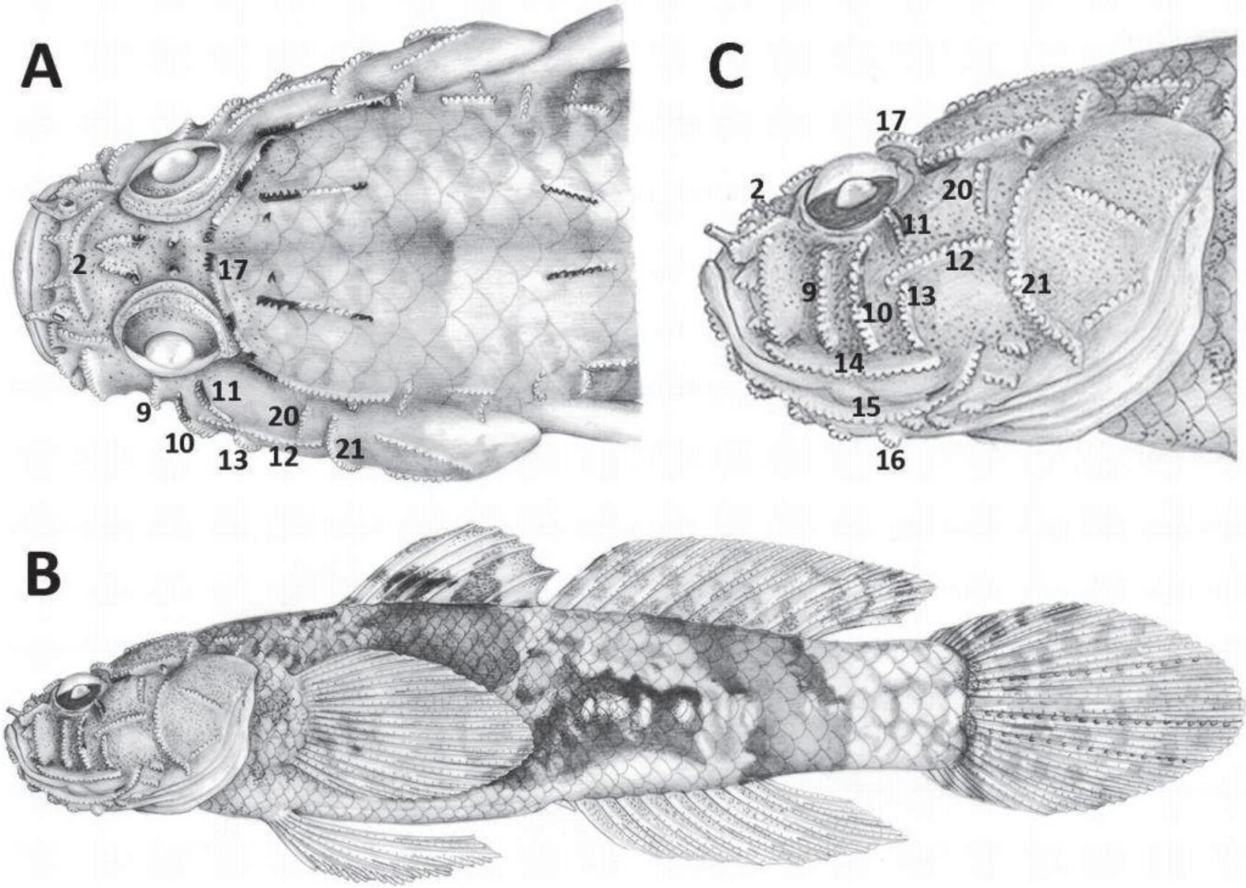

FIGURE 5.3 *Callogobius clarki*, USNM 220038, 48.6 mm SL, male (illustration P09712 by Jack R. Schroeder, Smithsonian Institution, NMNH, Division of Fishes): **A.** dorsal view of head; **B.** lateral view of head and body; **C.** lateral view of head enlarged from B. Numbers are added to identify papillae rows used in the redescription (numbers follow Akihito and Meguro, 1977; names follow Delventhal and Mooi, 2013): 2 postnasal row; 9 anterior suborbital row; 10 mid-suborbital row; 11 posterior suborbital row(s); 12 longitudinal cheek row; 13 transverse cheek row; 14 longitudinal maxillary row; 15 longitudinal mandibular row; 16 transverse mandibular rows; 17 postorbital row; 20 preopercular row; 21 transverse opercular row.

Colour in preservation (Figure 5.1): General colour pattern consists of brown dusky mottling and bars on pale yellow-brown head and body. Head markings poorly defined, mottled even in small specimens. Ventral region of head with little pigment. Papillae row colouration continuous with surrounding markings but with greater contrast, typically alternating light and dark. Trunk with a wide vertical bar extending below the first dorsal fin, reaching to, but not across the belly, which is pale. An irregular, mottled marking may be visible between the dorsal fins; this marking is often wide ventrally. A wide, slanted bar extends from the second dorsal fin to the posterior edge of the anal fin and around the caudal peduncle. A wide bar may or may not be well defined on the caudal peduncle, the edge of the hypural plate and the proximal regions of the caudal fin. The first and second dorsal fins display irregular rows of pale spots and/or bands. The pectoral fins are mottled; there is often a small spot medially on the pectoral fin base. The pelvic fins are mostly pale, the anal fin darker. The caudal fin displays fine irregular bands. The urogenital papilla is pale; in female, lateral and distal flaps lightly pigmented (Figure 5.2).

TABLE 5.1 Selected morphometric characters for *Callogobius clarki* and *C. bifasciatus*. The holotype values of *C. clarki* are compared with values of a similarly sized specimen of *C. bifasciatus* (BMNH 2000.4.19.761) as the holotype of the latter is a small juvenile in poor condition. Pooled values are presented as averages followed by range in parentheses. Values for specimens smaller than 15 mm SL (standard length) are not included.

	Callogobius clarki		*Callogobius bifasciatus*	
	Holotype	n=16	BMNH 2000.4.19.761	n=16
Gender	F	10M, 6F	F	6M, 10F
Standard Length (SL) (mm)	36.5	16.8-48.6	37.8	22.4-46.5
Head length (HL) (% of SL)	30.1	31.2 (28.6-32.5)29.4	29.7	(27.3-32.0)
Head depth (% of HL)	52.7	48.3 (43.6-54.6)48.6	47.1	(44.0-54.9)
Head width (%of HL)	66.4	67.9 (60.2-79.4)71.2	70.0	(60.4-78.9)
Interorbital width (% of HL)	7.9	7.7 (6.4-9.7)	9.6	8.7 (7.3-10.1)
Pre-dorsal fin distance (% of SL)	39.5	38.3 (35.5-41.0)36.5	37.0	(34.6-39.0)
Pre-anal fin distance (% of SL)	62.7	61.5 (58.0-63.6)61.9	60.4	(58.4-62.2)
Pre-pelvic fin distance (% of SL)	32.1	32.8 (30.2-34.5)29.9	30.4	(29.1-32.2)
Pectoral fin length (% of SL)	23.8	25.5 (23.5-27.1)24.3	24.2	(20.6-27.1)
Pelvic fin length (% of SL)	18.6	21.8 (18.6-24.2)22.0	19.9	(17.8-22.0)
Caudal fin length (% of SL)	23.6	26.9 (22.0-31.0)25.4	25.2	(21.7-28.2)
Caudal peduncle depth (% of SL)	12.6	12.5 (11.2-13.7)12.7	12.6	(10.9-13.6)

TABLE 5.2 Pectoral-fin ray count frequencies for *Callogobius clarki* (n = 21) and *C. bifasciatus* (n = 22). Holotype values are marked by *. Bilateral counts included when available.

	Pectoral-fin ray number			
	15	16	17	18
clarki	3	27*	11	
bifasciatus	1	15	13	13*

TABLE 5.3 Lateral scale count frequencies for *Callogobius clarki* (n = 18) and *C. bifasciatus* (n = 21). Holotype values are marked by *. Bilateral counts included when available.

	Lateral Series															
	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48
clarki	2	2	8	5	7*	6	2		1							
bifasciatus					1	1	2	7*	7	7	3	4		3		1

TABLE 5.4 Predorsal and transverse scale count frequencies for *Callogobius clarki* (n = 17) and *C. bifasciatus* (n = 20 for predorsal and 21 for transverse). Holotype values are marked by *; that of transverse series for *C. bifasciatus* from Smith (1958) as specimen condition did not permit counts at time of our observation.

	Predorsal Series									Transverse Series					
	12	13	14	15	16	17	18	19	20	17	18	19	20	21	22
clarki	1	3	7	6*						9	7*	1			
bifasciatus					1	6*	7	4	2		5*	6	3	3	4

TABLE 5.5 Transverse mandibular papillae row (Row 16) count frequencies for *Callogobius clarki* (n = 19) and *C. bifasciatus* (n = 14); counts taken bilaterally. Holotype values for *C. clarki* are marked by *; counts were not taken from the holotype of *C. bifasciatus* at time of observation.

	10	11	12
clarki	2	30*	6*
bifasciatus		1	27

Etymology. Goren named this species in honor of Dr. Eugenie Clark "for her outstanding contributions to the knowledge of the fish fauna of the Red Sea." We suggest the vernacular name Clark's Flapheaded Goby for this species.

Distribution. Known only from the Red Sea.

Comparisons. Four described species of *Callogobius* are known to lack all head pores as adults: *C. clarki, C. crassus, C. hastatus,* and *C. winterbottomi*. *Callogobius clarki* differs from *C. crassus* in having higher lateral scale counts (33-41 vs. 19-22), higher second dorsal and anal fin element counts (normally I,10 and I,9 vs. I,7-8 and I,6-7 respectively), preopercular row not continuous with transverse opercular row (vs. continuous), longitudinal maxillary row and longitudinal mandibular row continuous (vs. broken and displaced), and pelvic fins joined at least 2/3 length (vs. joined only at the base). *Callogobius clarki* can be distinguished from *C. hastatus* by colour pattern (mottled with wide bars vs. speckled with or without narrow bars), body shape (moderately stout with rounded fins vs. very slender with elongate fins), preopercular row not continuous with transverse opercular row (vs. continuous) and fifth pelvic fin ray shorter than the fourth and pelvic fins partially joined with a weak/moderate frenum (vs. rounded pelvic disc with a strong frenum). *Callogobius clarki* differs from *C. winterbottomi* in having higher lateral scale counts (33-41 vs. 23-26) and higher second dorsal and anal fin ray counts (I,10 and I,9 vs. I,9 and I,7 respectively). All other described species of *Callogobius* can be distinguished from *C. clarki* by the presence of head pores on all specimens larger than 10-15 mm. Tiny juveniles of *C. sclateri, C. flavobrunneus*, or *C. bifasciatus* that have not yet developed pores could be confused with *C. clarki;* these species share a similar body shape, colour pattern, and configuration of preopercular row and transverse opercular row. *Callogobius sclateri* and *C. flavobrunneus* can be distinguished by separate pelvic fins (joined at least 2/3 length in *C.*

clarki), and in addition *C. sclateri* has a lower lateral scale count (28-31). *Callogobius bifasciatus* generally has higher counts for several meristics (pectoral-fin rays, lateral scale rows, predorsal scale rows, transverse scale rows, transverse mandibular papillae rows) (Tables 5.2-5.5); it has not been collected from the Red Sea.

Remarks. Goren (1978, 1980) reported a collection date of 20 January 1970 for the holotype. This is in contrast to the specimen label and the HUJ written catalog, both of which record the date as 20 January 1972. The latter date is probably correct (and is the date reported in the present paper) because on this date a collection was made at Et Tur (D. Golani, pers. comm., Por et al., 1972).

Our scale counts for the holotype vary slightly from those reported by Goren (1978), although some variation in reported values might be expected from worker to worker given the irregular scale rows in many *Callogobius* species. In the present study, both authors independently completed scale counts for the majority of specimens; these were consistent, and used for comparison between *C. clarki* and *C. bifasciatus*.

The larger specimen of USNM 220038 (a 48.6 mm SL male) was formerly designated as *Callogobius simulus* Lachner and McKinney holotype MS, but remained unpublished. USNM 220031 (8 specimens alcohol, 3 specimens cleared and stained) were also designated *Callogobius simulus*. McKinney (1980) refers to *C. clarki* as “*Callogobius* new species A” and presents two illustrations (a dorsal view of the head and a lateral view of the head and body) of the larger specimen of USNM 220038. These images, by Jack R. Schroeder are printed here with permission of the Smithsonian Institution, NMNH, Division of Fishes (Figure 5.3).

DISCUSSION

With reference only to the original descriptions and apparently with only one Red Sea specimen at hand, Randall et al. (1994) synonymised *Callogobius clarki* and *C. bifasciatus* without comment. Randall (1995) and Golani and Bogorodsky (2010) followed this decision. Our study indicates that *C. clarki* is a valid Red Sea endemic species. Not only does *C. clarki* differ strikingly in lacking sensory pores, it differs in count frequencies of pectoral-fin rays (Table 5.2), lateral scale rows (Table 5.3), predorsal and transverse scale rows (Table 5.4), and transverse mandibular papillae rows (Table 5.5). Moreover, the anterior suborbital row (Row 9) is relatively longer in most *C. bifasciatus* specimens, nearly reaching the eye in 13 out of 14 specimens examined for this character. All *C. bifasciatus* specimens examined as comparative material in this study had dorsal fin element counts of VI I,10 and anal fin element counts of VI I,9. We observed a lateral scale count range of 37-48 (40 for the holotype), and predorsal scale range of 16-20 (17 on the holotype). In contrast, Randall et al. (1994) reported *C. bifasciatus* having "dorsal rays VI-I, 9-10 (usually 9); and rays I, 8-9 (usually 8); … longitudinal scale series 47-53; … predorsal scales 21-23." Of their material, all but one specimen (from the Red Sea), is from the Arabian Gulf or Oman, as is most of our *C. bifasciatus* material. Randall et al. (1994) reported about 47 lateral series scales on the holotype of *C. bifasciatus*, but our counts agree with those of Smith (1958), who recorded 40.

Both *C. clarki* and *C. bifasciatus* belong to the *sclateri* group defined by Delventhal and Mooi (2013) as a subgroup of *Callogobius* having a modified female urogenital papilla with lateral distal flaps, and elongate ctenii on caudal peduncle scales. The modified female urogenital papilla (Figure 5.2) may be unique to the *sclateri* group among gobies, although we have yet to examine representatives of all goby genera for this character.

Of the five species of *Callogobius* reported from the Red Sea, two are endemic (*C. clarki*, *C. dori*); *C. amikami* is known from one Red Sea specimen and a photo record from Oman (Randall, 1995), whereas *C. flavobrunneus* and *C. maculipinnis* are widespread throughout the Indo-West Pacific. Randall (1998) estimated Red Sea endemism in fishes to be about 14%, although he included species that extended their ranges into the Gulf of Aden; for example, no chaetodontids are restricted to the Red Sea, but Randall suggested 7 of 17 were endemic. However, some families exhibit extremely high endemism. Of twelve species of pseudochromids listed for the Red Sea (Golani and Bogorodsky, 2010), nine are found only there. This supports Randall's (1998) expectation that smaller fishes will exhibit higher endemism due to more rapid generation times, amplified by life history traits such as demersal eggs and parental care. However, the Gobiidae (sensu Gill and Mooi, 2012) does not support this generalization. Despite being small with short generation times and having demersal eggs with parental care, gobiids exhibit less than 16% Red Sea endemism (19 of 120 presumed native species as listed in Golani and Bogorodsky, 2010), only marginally higher than Red Sea fishes as a whole. However, our knowledge of small, cryptic fishes is far from complete; better understanding of taxonomy is likely to reduce the number of apparent widespread species and increase the number of recognized endemics.

MATERIAL EXAMINED

Callogobius bifasciatus (30 specimens): SAIAB 235 (holotype): 1 specimen (21.0 mm SL female?), Tanzania, Pemba Island, J.L.B. Smith. BMNH 2000.4.19.760-766: 7 specimens (22.4 – 39.9 mm SL, 1 male, 1 male?, 5 females), United Arab Emirates, Abu Dhabi, 24°39’23”N 54°31’16”E, A. Gill 1999. BMNH 1994.1.18.163-166: 4 specimens (26.9-40.1 mm

SL, 2 male, 2 female), Kuwait, Arabian Gulf, Qaru Island, N. Downing 1985. BMNH 2000.4.19.756: 1 specimen (44.5 mm SL female), United Arab Emirates, Abu Dhabi, Ushsh Island, 24°18’15”N 52°52’18”E, A. Gill et al. 1999. BMNH 2000.4.19.758-759: 2 specimens (24.5-39.3 mm SL, 1 male, 1 female), United Arab Emirates, Abu Dhabi, Ghasha Island, 24°25’27”N 52°38’44”E, A.C. Gill et al. 1999. BMNH 2000.4.19.755: 1 specimen (40.2 mm SL male), United Arab Emirates, Abu Dhabi, JaziratDagalah, 24°12’18”N 52°56’6” E, A.C. Gill et al. 1999. ROM 39892: 4 specimens (33.9 – 45.0 mm SL, 2 male, 1 female, 1 specimen cleared and stained), Oman, B.N.G. Simm 1981. ROM 39899: 4 specimens (14.8 – 34.8 mm, 3 female, 1 juvenile), Oman, NE of Sur, B.N.G. Simm 1982. ROM 39919: 3 specimens (40.6 – 46.5 mm SL, 3 male), Oman, near Kalhat (Qalhat), B.N.G. Simm 1981. SAIAB 003419: 1 specimen (63.4 mm SL male), Tanzania, Pemba Island, J.L.B. Smith 1952. SAIAB 46417: 1 specimen (24.2 mm SL male), South Africa, Aliwal Shoal, Cathedral, C. Buxton et al., 1994. SAIAB 46477: 1 specimen (28.5 mm SL male), South Africa, Natal, Aliwal Shoal, Hospital Reef, off Scottburgh, C. Buxton et al., 1994.

Type specimens of other *Callogobius* species were examined as listed in Delventhal and Mooi (2013).

Chapter Six. *Callogobius liolepis* Bleeker, a senior synonym of *Gobiopsis aporia* Lachner and McKinney (Teleostei: Gobiidae: *Gobiopsis*)

NAOMI R. DELVENTHAL[1] & RANDALL D. MOOI[1,2]

[1]Department of Biological Sciences, 212B Biological Sciences Bldg., University of Manitoba, Winnipeg MB, R3T 2N2 Canada. E-mail: naomi.delventhal@gmail.com
[2]The Manitoba Museum, 190 Rupert Ave., Winnipeg MB, R3B 0N2 Canada. E-mail: rmooi@manitobamuseum.ca

Published in *Zootaxa* 13 February 2014

My contribution: I conducted the background specimen examination and literature review and determined that *Gobiopsis liolepis* was not a species of *Callogobius*, but rather a senior synonym of *G. aporia*; I planned the study, recorded the observations of the types and drafted the paper, with comments from R. Mooi, except the translation of Bleeker's description which was drafted by R. Mooi. The photographs and x-ray photographs were taken by M. Aizawa (not a co-author). R. Mooi arranged the figures.

SUMMARY

Callogobius liolepis Bleeker in Koumans was briefly described from two specimens from Ambon. A later, more detailed description by Koumans was apparently based on Bleeker's unpublished description and specimens of *C. okinawae* (Snyder), considerably complicating the taxonomy of several species. Re-examination of the syntypes identifies *C. liolepis* as a species of the genus *Gobiopsis* Steindachner due to the absence of raised vertical ridges of papillae that characterise *Callogobius* and the presence of barbels in a pattern unique among gobiids to a subset of *Gobiopsis*. *Gobiopsis liolepis* (Bleeker) is determined as the senior synonym of *G. aporia* Lachner and McKinney based on the absence of head pores combined with the presence of a series of tightly spaced papillae over the eye, lateral scale counts of 36–42, pectoral-fin ray counts of 20–21, dorsal-fin ray counts VI+I,10 and anal-fin ray counts of I,9. The larger syntype is designated the lectotype and the smaller the paralectotype. Specimens identified as *C. liolepis* in museums or the literature are likely referable to *C. okinawae* (Snyder) or *C. bifasciatus* (Smith).

INTRODUCTION

The taxonomy of many gobiid genera and species has been complicated by enormous numbers of synonyms generated through inadequate descriptions of small and diverse taxa. Despite many alpha taxonomic issues, *Gobiopsis* Steindachner, 1861 and *Callogobius* Bleeker, 1874 are relatively well-defined compared to most gobiid genera and are easily differentiated externally by the presence of barbels or distinctive raised ridges of papillae, respectively (e.g. Larson & Murdy 2001). In a review of gobioid genera, Koumans (1931:75) introduced *Callogobius liolepis* as an unpublished Bleeker name and provided a short description borrowed from Bleeker's notes: "*Callogobius liolepis* Blkr. (Museum name) differs from *C. hasselti* [sic] in having the base of the preoperculum and operculum naked, distance between the eyes broader, all scales being cycloid, snout longer." Although authorship of this species has generally been attributed to Koumans (e.g. Eschmeyer 2013), Koumans' (1931) unqualified attribution to Bleeker and use of his description indicates that Bleeker should retain authorship (International Commission on Zoological Nomenclature 1999: Article 50.1.1). Koumans (1932:14) later provided a more detailed description. Since that time, the species has been mentioned only infrequently in taxonomic literature and faunal lists. McKinney and Lachner (1978) questioned the placement of this species within the genus *Callogobius*, but made no taxonomic recommendations. We examined the type materials of *C. liolepis* in 2007 to discover that, despite their poor condition, the two specimens could be determined as a species of *Gobiopsis*. In this paper we designate them as a lectotype and a paralectotype while presenting evidence to reassign the species to *Gobiopsis* and, further, to support synonymization of *G. liolepis* (Bleeker in Koumans 1931) as a senior synonym with *G. aporia* Lachner & McKinney, 1978. We also clarify misidentifications in the literature.

FIGURE 6.1 Type specimens of *Gobiopsis liolepis* (Bleeker): **A.** lectotype, RMNH.PISC.4411, 44.0 mm SL; **B.** paralectotype, RMNH.PISC.36383, 42.0 mm SL. Photos by M. Aizawa.

MATERIAL EXAMINED

Abbreviations for institutional codes follow Fricke and Eschmeyer (2013) and/or Sabaj Pérez (2013).

Callogobius liolepis Bleeker in Koumans, 1931: RMNH.PISC.4411, lectotype, 44.0 mm SL, East Indies, Ambon, P. Bleeker (prior to 1860) (EtOH and x-ray image); RMNH.PISC.36383, paralectotype, 42.0 mm SL, collected with lectotype (EtOH and x-ray image).

Gobiopsis aporia Lachner & McKinney, 1978: USNM 209731, holotype, 39.9 mm SL, Ambon Island, Moluccas, off Tandjung Suli, V.G. Springer and M.F. Gomon, 11 Jan 1973; USNM 211983, paratypes, 13: 29.5– 49.3 mm SL (39.3 mm SL specimen cleared and stained), Indonesia, off the coast of Karmundjawa Is., V.G. Springer et al., 29 Mar 1974; USNM 209240, paratypes, 2: 36.3–41.5 mm SL (larger cleared and stained), Sri Lanka, Kalkudah Bay, T.

Iwamoto, 9 June 1970; CAS 65720, 48.6 mm SL, Papua New Guinea, Madang Province, S.G. Poss, D. Catania et al., 12 May 1987; ROM 68690, 46.8 mm SL, Andaman Sea, Thailand, Malacca Strait, Phuket, Kata Bay, R. Winterbottom, W. Holleman, R. D. Mooi, U. Satapoomin, 14 Nov 1993; ROM 68691, 2:13.0–37.2 mm SL, Andaman Sea, Thailand, Malacca Strait, Phuket, NW tip of Ko Mai Thon, R. Winterbottom, W. Holleman, R. D. Mooi, U. Satapoomin, 23 Nov 1993; WAM 30920.015, 45 mm SL, Western Australia, Kimberley, Montgomery Reef, J.B. Hutchins, 22 Nov 1997; WAM P.31805-031, 4: 37–54 mm SL, Western Australia, Kimberley, Vansittart Bay, Long Island, J.B. Hutchins, 24 Nov 1995; WAM P.31250-042, 6: 32–51 mm SL, Western Australia, Kimberley, east side of Wildcat Reefs, S.M. Morrison, 2 Dec 1996;WAM P.31251-036, 47.0 mm SL, Western Australia, Kimberley, Montgomery Reef, S.M. Morrison, 3 Dec 1996.

Callogobius okinawae (Snyder): RMNH.PISC.20176, 23.1 mm SL, Indonesia, Ambon, Snellius Expedition, 11–14 Sept 1930; RMNH.PISC.20293, 26.9 mm SL, Indonesia, Haroekoe, Snellius Expedition, 3–7 May 1930; RMNH.PISC.20597, 39.5 mm SL, Indonesia, Flores, Endeh, 6–8 Nov 1930; RMNH.PISC.20607, 3: 22.6–35.8 mm SL, Indonesia, Halmahera, Ake Selaka, Kaoe Bay, Snellius Expedition, 28 May 1930.

Mucogobius bifasciatus Smith, 1958 (= *Callogobius bifasciatus*): SAIAB 235, holotype, 21.0 mm SL, Tanzania, Pemba Island, J.L.B. Smith.

Mucogobius liolepis (= *Callogobius bifasciatus*): SAIAB 3419, 63.4 mm SL, Tanzania, Pemba Island, J.L.B. Smith.

Comparisons to other described species of *Gobiopsis* are based on Lachner & McKinney (1978, 1979), Shibukawa (2010) and the holotypes of the following species: *G. angustifrons* Lachner & McKinney, USNM 213492; *G. arenaria* (Snyder), USNM 62237; *G. asanai*

(Koumans) ZSI F5283/2; *G. bravoi* (Herre), SU 33120; *G. malekulae* (Herre) FMNH 17385; *G. pinto* (J.L.B. Smith), SAIAB 197; *G. quinquecincta* (H.M. Smith), USNM 90317; *G. springeri* Lachner & McKinney, USNM 210011; *G. woodsi* Lachner & McKinney, USNM 212249. Comparisons to *Callogobius* species are based on McKinney and Lachner (1978) and data from holotypes listed in Delventhal and Mooi (2013).

METHODS

Standard length was taken using dial calipers. Methods for counting fin rays, lateral scales, vertebrae, and terminology used to specify barbel groups follows Lachner and McKinney (1978). Scale counts must be considered approximate as *G. liolepis*, *C. okinawae* and *C. bifasciatus* have small, irregularly-shaped, slightly deciduous scales. Cyanine blue was used to provide temporary contrast to aid in the observation of scales, barbels and sensory papillae following the method first outlined in Akihito et al. (1993b:1089) and described in English by Saruwatari et al. (1997). Observations of osteology were made using radiographs or cleared and stained specimens. Due to the condition of the type material, detailed morphometrics and colour are not re-described in detail.

RESULTS

The types of *Callogobius liolepis*, the larger here designated as lectotype and the smaller as paralectotype, were in very poor condition (Figure 6.1), as reported by Akihito and Meguro (1975), apparently having been desiccated sometime in the past. Despite this, it is evident that the specimens have no raised vertical ridges of papillae, ruling out their membership with *Callogobius* as cladistically defined by Winterbottom (2003). The specimens do, however, exhibit several of the diagnostic features of *Gobiopsis* listed by Lachner and McKinney (1978), including short, well-developed barbels on the head in specific groupings (including the chin, anterior and posterior internasals, anterior cheek tuft, and anterior gular barbels common to all species in that paper), and a roughly horizontal fleshy fold on the midcheek. Although not as definitive, the Bleeker specimens also share the general physiognomy of *Gobiopsis*, including a depressed, broad head with a wide interorbital (about 19% of head length or 6% SL for lectotype and paralectotype, approximate due to condition of specimens), a broad snout with a protruding lower jaw, and stout body. Fin and vertebral counts (dorsal fin VI+I,10; anal fin I,9; 10+16 abdominal plus caudal vertebrae) are consistent with *Gobiopsis*, as is the first dorsal-fin pterygiophore formula of 3(221100) for both types (cf. Lachner & McKinney 1978) (Figure 6.2). The specimens were very dark due to poor preservation. The few melanophores and pigmented areas that could be discerned were consistent with the general *Gobiopsis* colour pattern of a series of dark saddles and mottling found in most species, with a dark spot on the upper pectoral-fin base (Figure 6.1). Bleeker's original colour notes (p. 258, translated from the Latin; see Appendix) state, in part: "…head and body variegated with dark in a cloud-like pattern, on the flanks the dark colour forms wide irregular transverse bands [saddles]… dark spot on the upper base of the pectoral fins, caudal base with a larger dark spot, rays with small darkish spots arranged in 5 or 6 transverse stripes."

As a result of their poor condition, certain barbels were visible only on one specimen or even only on one side as indicated in Figure 6.3. We found two pairs of chin barbels at the symphysis of the lower jaw of each specimen. A cheek tuft with at least one or more barbels was present at the anterior edge of the mid-cheek fold on either side of each specimen. The lectotype exhibited three posterior mandibular barbels on the skin covering the posterior portion of the dentary, and the paralectotype had three anterior gular barbels and at least two inter-mandibular barbels along the hyoid region and below the lower jaw. This distinctive arrangement is unique to *Gobiopsis sensu stricto*, a group we define (following Lachner & McKinney 1979) as including those ten species treated in Lachner and McKinney (1978): *G. angustifrons*, *G. aporia*, *G. arenaria*, G. bravoi, G. canalis Lachner & McKinney, G. macrostoma Steindachner, G. malekulae, *G. pinto*, *G. quinquecincta*, *G. woodsi*. This arrangement is not found in *Gobiopsis* species included later by Lachner and McKinney (1979: *G. atrata* (Griffin), *G. exigua* Lachner & McKinney, and *G. springeri*) or by Shibukawa (2010: *G. namnas* Shibukawa), nor in any other gobiid.

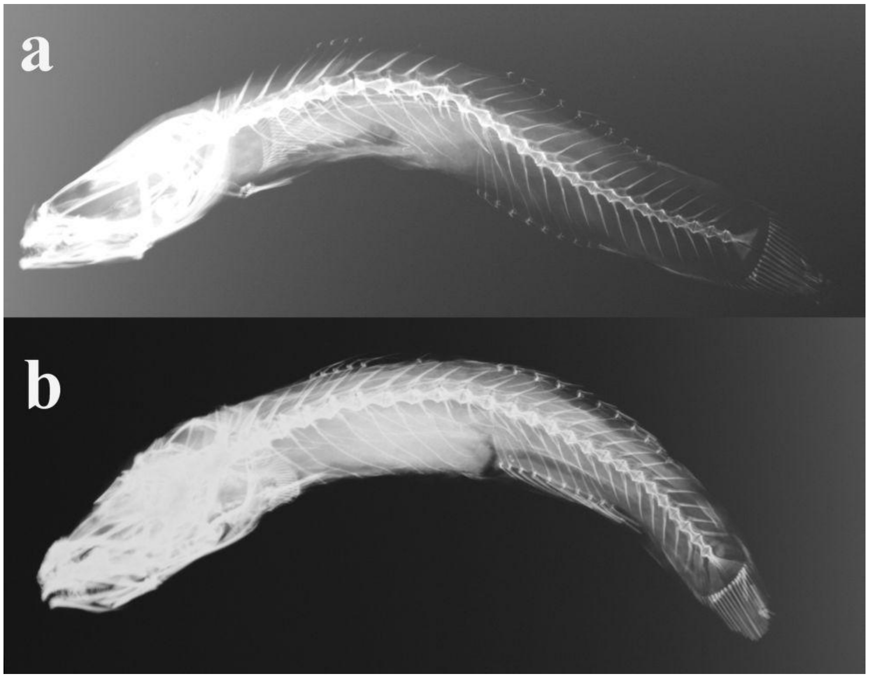

FIGURE 6.2 X-ray images of the type specimens of *Gobiopsis liolepis* (Bleeker): **A.** lectotype, RMNH.PISC.4411, 44.0 mm SL; **B.** paralectotype, RMNH.PISC.36383, 42.0 mm SL. Photos by M. Aizawa.

Specific characters identify the species of *Gobiopsis sensu stricto* equivalent to Bleeker's specimens (Table 6.1). Neither type specimen has any head pores, but each exhibits a row of numerous, tightly spaced papillae medial to each eye; *G. aporia* is the only member of *Gobiopsis sensu stricto* lacking head pores and is the only species having a continuous series of sensory papillae around the eye in the interorbital space, described as "the nasal papillae row…confluent with the suborbital row" (Lachner & McKinney, 1978:7, Pattern 1) (Figure 6.3A,B). In addition, lateral scale counts of 36–42 and pectoral-fin ray counts of 20–21 in both specimens is consistent with the description and type material of *G. aporia* (Table 6.1). Only *G. canalis*, *G. macrostoma*, *G. pinto*, and *G. woodsi* also have pectoral-fin ray counts of 20 or higher. Among these, *G. macrostoma* is the most similar to Bleeker's specimens as it has lateral scale counts in the appropriate range, but, in addition to having cephalic sensory pores and no papillae medial to the eye, this species differs from Bleeker's specimens in having ctenoid scales and no posterior mandibular barbels (Table 6.1).

We conclude that *Callogobius liolepis* Bleeker in Koumans, 1931 is a species of *Gobiopsis* Steindachner, 1861 and that it is a senior synonym of *G. aporia* Lachner & McKinney, 1978.

For a complete species description and comparison, we refer to Lachner and McKinney (1978, 1979). Because Koumans (1940, 1953a,b) confounded the original *C. liolepis* with other species and altered the description to fit those, subsequent workers have misidentified specimens using these altered descriptions. Specifics surrounding these issues are provided in the Discussion.

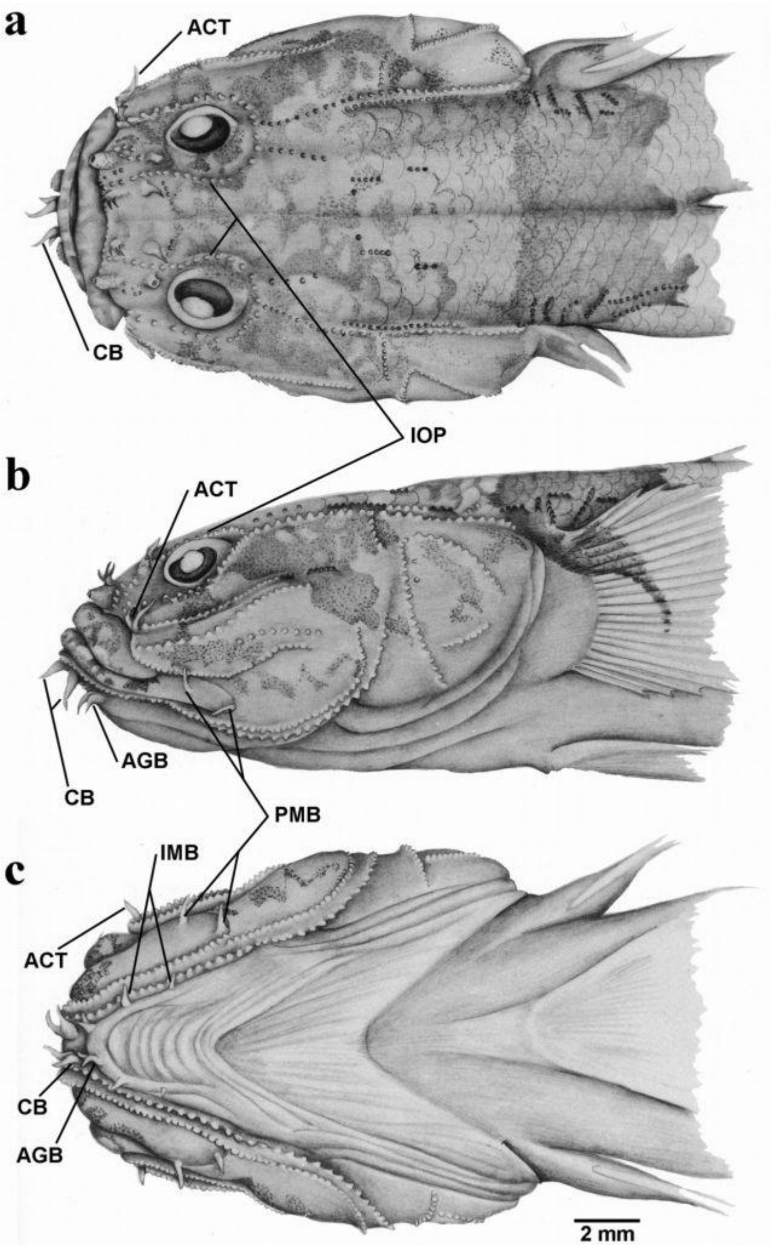

FIGURE 6.3 Head barbels and sensory papillae of *Gobiopsis liolepis* (Bleeker): **A.** dorsal view; **B.** lateral view; **C.** ventral view. Arrows and labels indicate distinctive barbels and papillae found in the lecto- and paralectotype (RMNH.PISC.4411; RMNH.PISC.36383), barbel terminology following Lachner and McKinney (1978): ACT, anterior cheek tuft; AGB, anterior gular barbels; CB, chin barbels; IMB, inter-mandibular barbels; IOP, interorbital papillae row [portion of the nasal papillae row of Lachner & McKinney (1978:7) confluent with the suborbital papillae and unique to this species]; PMB, posterior mandibular barbels. Due to condition of the specimens, not all of these features were observed in both types (see text). Base illustration modified from Lachner and McKinney (1978: plate 1a,b and plate 2a) of USNM 209247 (male paratype of *G. aporia*) from plates P09253 and P09357 by Jack R. Schroeder, Smithsonian Institution, NMNH, Division of Fishes, with permission. Scale bar is approximate.

SYNONYMY OF *Gobiopsis liolepis* (BLEEKER)

Callogobius liolepis Bleeker in Koumans 1931:75 [from Bleeker, unpublished, p. 258]. Koumans 1932:14 [description from Bleeker specimens, table of morphometrics and meristics]; Koumans 1940:168, 207 [comparison with *C. atratus* Griffin = *Gobiopsis atrata* (Griffin)], 168 [comparison with *Gunnamatta insolita* Whitley = *Callogobius depressus* (Ramsay & Ogilby)]; Koumans 1953a:248 [in part, list of *C. okinawae* of the Snellius Expedition]; Koumans 1953b:97 [in part, description based in part on *C. okinawae*]; Rangarajan 1968:347, 350– 352, tab. II [following Koumans 1953b, comparison with *C. mannarensis*, key]; Menon & Chatterjee 1974:127– 128 [comparison with *C. andamanensis*, key]; Akihito & Meguro 1975:112, table 1 [listing as syntypes, comparison with *C. hasseltii* (Bleeker) and C. okinawae (Snyder)]; Goren 1979a:43 [key]; Goren 1979b:216, table II [comparison with *C. clarki* (Goren), data from Koumans 1953b]; Chen & Yu 1986 [listed for Taiwan, basis unknown]; Larson & Murdy 2001:3595 [listed for western central Pacific, based on original description?].

Callogobius hasseltii (non Bleeker 1851).—Fowler 1949:133 [uncertainly synonymised from description in Koumans 1931; correctly assigning authorship to Bleeker].

Gobiopsis aporia Lachner & McKinney 1978:11–15, key, fig. 6, tabs. 1–6, pls. 1, 2b, 7a. Lachner & McKinney 1979:5 [comparison with *G. atrata* (Griffin)]; Akihito 1984:267, fig. 142, pl. 354D [brief description, distribution]; Böhlke 1984:104 [type list]; Ibarra & Stewart 1987:41 [type list]; Akihito et al. 1993a: 1042 [description, schematic drawing, key]; Akihito et al. 1993b: 1103, fig. 3 [schematic illustration of head barbels and papillae pattern]; Larson (in Randall & Lim) 2000:638 [listed for South China Sea]; Hutchins 2001:43 [listed for Western Australia]; Larson & Murdy 2001:3598 [listed for western central Pacific, based on original description]; Akihito et al. 2002:1249 [brief description, distribution, key, schematic illustration], fig. 37–6;

Allen & Adrim 2003:59 [list]; Shibukawa et al. (in Kimura & Matsuura) 2003:185 [brief description and photo, Bitung Sulawesi]; Hoese & Larson 2006:1658 [list]; Shibukawa 2010:97 [general description of genus]; Allen & Erdmann 2012:976 [brief description and photo].

TABLE 6.1 Selected distinguishing characters comparing the lecto- and paralectotype of *Gobiopsis liolepis* (Bleeker) with the most similar species of *Gobiopsis* as presented in Lachner and McKinney (1978); all other *Gobiopsis sensu stricto* have scale and pectoral-fin ray counts that are too low. Koumans (1932) reported ± 45 LL (lateral line) scales for Bleeker's specimens, Bleeker about 45. Modes are presented in parentheses (when available); LL scale and pectoral-fin ray counts for types are provided for left and right sides, respectively; ? = not observed in type specimens, presumably due to poor condition.

	Headpores	**Intermandibular barbells**	**Posterior mandibular barbels**	**LL scales**	**Scale type**	**Pectoral-fin rays**
G. liolepis lectotype	absent	?	3	37, 42	cycloid	20, 21
G. liolepis paralectotype	absent	2	?	36, 42	cycloid	21, 21
G. aporia	absent	1–3(2)	2–6(3)	36, 42	cycloid	19–21(20)
G. canalis	present	absent	absent	50–55	cycloid	22–23
G. macrostoma	present	0–4(2)	absent	36–44	ctenoid	19–22(21)
G. pinto	present	0–3(1)	absent	50–60	cycloid	20–21(21)
G. woodsi	present	0–2(2)	2–5(3)	30–36	ctenoid	20–22(21)

DISCUSSION

The identity of *Callogobius liolepis* Bleeker has had a confused history. Based on two specimens 58 and 60 mm total length collected from Ambon, Bleeker (unpublished, p. 258; see Appendix) wrote a Latin description, intending this to form a part of the text of his multi-volume Atlas Ichthyologique des Indes Orientales Néêrlandaises (1862–1877). In that manuscript, now archived at the RMNH in Leiden, Bleeker emphasized that this new species had cycloid scales, and a wide interorbital distance compared to *C. hasseltii* Bleeker, 1851, the only species assigned to *Callogobius* at that time. More significantly, he noted that it had no head pores and much more highly developed papillae (presumably barbels), including: "the two anterior mandibular papillae [= chin barbels?] longer than the rest" (see Appendix). Upon Bleeker's death in 1878 the publication of the Atlas, including the description of *C. liolepis*, was halted. The specimens intended to be the syntypes of *C. liolepis* were obtained by the RMNH. In 1983, plates for the planned volumes XI–XIV were published by the Smithsonian (Bleeker 1983). Plate 430, which should have included the illustration of *C. liolepis*, was among several that were lost (Boeseman 1983:5).

We found no mention of *C. liolepis* in published literature until 1931, when Koumans, then curator of fishes at RMNH, made a brief note referring to *C. liolepis*, which he regarded as a Bleeker museum name (Koumans 1931:75) and where he used Bleeker's unpublished description to differentiate the species from *C. hasseltii*. This appears to satisfy the criteria to establish Bleeker as the author of *C. liolepis* (ICZN 1999: Article 50.1.1). It seems Koumans became aware that his 1931 note amounted to the original description, because he later published a more detailed description using Bleeker's two original specimens (Koumans 1932:14).

In 1940, Koumans regarded *Callogobius atratus* Griffin, 1933 as "very close" (p. 168) or "allied" (p. 207) to *C. liolepis*. Griffin's species was reassigned to *Gobiopsis* by Lachner and McKinney (1979). His later descriptions of the species (Koumans 1940, 1953b) seem to be based partially on a translation of Bleeker's unpublished text and partially on specimens of *C. okinawae* (Snyder 1908). We examined six specimens of *Callogobius* collected by the Snellius Expedition (1929–1930) that had been reported as *C. liolepis* by Koumans (1953a:248), and determined that they were *C. okinawae* (RMNH.PISC.20176, 20293, 20597, 20607). Koumans (1940, 1953b) synonymised *C. santa* (Herre 1935) with *C. liolepis*; however, *C. santa* is presently considered a synonym of *C. okinawae* (Akihito & Meguro 1975). Koumans (1940, 1953b) considered *C. okinawae* a synonym of *C. hasseltii*.

The generic placement of *C. liolepis* was first questioned by McKinney and Lachner (1978) in a paper describing two new species of *Callogobius* and summarizing data on the nominal species. They stated that *C. liolepis* lacked the fleshy papillose head ridges of *Callogobius* and indicated they intended to relegate *C. liolepis* and four other nominal species to other genera in their subsequent studies. However, this planned work never materialized. McKinney and Lachner's unpublished notes indicate that they examined the *C. liolepis* syntypes in the 1970's. A label found in the jar containing the *C. liolepis* syntypes reads: "Not a species of *Callogobius* Bleeker; possibly related to *Pipidonia* H.M. Smith because: 1) barbels present; 2) papillae rows similar; 3) dentition like *Pipidonia*; 4) general body physiognomy similar. *C. liolepis* cannot be identified with any known species of *Pipidonia* or *Pipidonia*-like species. The presence of barbels and absence of vertical and transverse ridges on the head excludes *C. liolepis* from *Callogobius. C. liolepis* is therefore considered a *nomen dubium* with its exact generic affinities being unknown. J.F. McKinney 4 June 1976." Lachner and McKinney (1978) synonymised *Pipidonia* Smith with *Gobiopsis* Steindachner but made no mention of *C. liolepis* in this or subsequent papers.

Callogobius liolepis has been included sporadically in faunal lists in literature since its description. Our studies indicate that most of these identifications are based on Koumans (1953b), and are likely referable to *C. okinawae*. Another possible source of confusion is *C. bifasciatus*.J.L.B. Smith (1958) described and illustrated an 80 mm TL specimen as *Mucogobius* *liolepis* (Koumans) in the same paper in which he described *M. bifasciatus* Smith 1958 [= *Callogobius bifasciatus* (Smith); Randall et al. 1994; Delventhal & Mooi 2013]. Both specimens were collected from Pemba Island; the type of *C. bifasciatus* (SAIAB 235) is a 21 mm SL juvenile. Smith distinguished *C. bifasciatus* from *C. liolepis* by scale counts and colouration (noting that they shared the presence of cycloid scales). However, the scale-count difference falls within intraspecific variation (40 vs 45; *C. bifasciatus* scales are unevenly sized and spaced) and the colouration difference is consistent with ontogenetic change in *C. bifasciatus* (juveniles are distinctly bi-coloured, becoming more mottled with age). Smith must have realized his error, as *C. liolepis* is not mentioned in later publications. A specimen of *C. bifasciatus* from Pemba Island (SAIAB 3419, 63.4 mm SL) is consistent with Smith's description and illustration of his *Mucogobius liolepis* (Smith 1958:147, pl. IIIK). Jones and Kumaran (1970:329) followed Smith (1958) and identified specimens from Minicoy (Laccadive Archipelago, India) as *Mucogobius liolepis* (Koumans), providing a figure and description. As would be expected, their specimens appear to be a *Callogobius* and not *Gobiopsis liolepis* (Koumans), but we cannot determine the species. Some aspects of the description do match *Callogobius bifasciatus* (Smith), but others do not and this species has not been recorded from this part of the Indian Ocean.

Takagi (1963) collected specimens from Japan that he identified as *Callogobius liolepis*. Akihito and Meguro (1975) examined type specimens of *C. okinawae*, *C. hasseltii* and *C. liolepis* and determined that Takagi's specimens were *C. okinawae*. Goren (1979a,b) included *C. liolepis* in a key to *Callogobius* species and in a table of species and diagnostic characters for Red Sea and Indian Ocean Callogobius. Data were from Kouman's (1953b), but the species was likely included among Indian Ocean taxa through reference to Smith's (1958) identification of adult C. *bifasciatus* as Kouman's *liolepis* (as noted above).

Gobiopsis liolepis (Bleeker) is a relatively common species of the genus known from the Andaman Sea eastward to southern Japan and south through Indonesia, New Guinea and northern Australia (Lachner & McKinney 1978; museum collections).

BLEEKER’S UNPUBLISHED DESCRIPTION OF *Callogobius liolepis* WITH TRANSLATION

Bleeker’s unpublished description of *Callogobius liolepis* with translation following (translations edited by Ineke Loots and Martien van Oijen). Comments additional to translation appear in square brackets.

Tome XI p. 258 Callogobius liolepis Blkr. Atl. Tab. 430, Gob. Tab. 5 fig. 9.

Callog. corpore elongate antice cylindraceo postice compresso, altitudine 5 circ. in ejus longitudine absque, 6 ad 6½ in ejus longitudine cum pinna caudali; capite acutiusculo 3½ circ. in longitudine corporis absque, 4⅓ circ. in longitudine corporis cum pinna caudali; altitudine capitis 2 circ., latitudine capitis 1½ circ. in ejus longitudine; linea rostro-frontali declivi rostro tantum convexa; oculis magis sursum quam lateraliter spectantibus, diametro 5 circ. in longitudine capitis , diametro 1 circ. distantibus; regione interoculari poro conspicuo nullo; plicis et papillis capite superne lateribus et inferne pluribus, papillis mandibularibus 2 anterioribus ceteris longioribus; rostro convexo multo latiore quam longo, oculo non breviore, apice ante oculum sito; tubule narium anteriore posterior longiore; maxilla superiore maxilla inferiore paulo breviore sub oculi parte posteriore desinente; rictu valde oblique; dentibus maxillis acutis serie externa ceteris longioribus et paucioribus; lingua obtuse rotundata; apertura branchiali paulo infra basin pinnae pectoralis desinente; capite vertice tantum squamato, rostro genisque rugoso; sulco oculo-suprascapulari poro conspicuo nullo; squamis toto corpore cycloideis, serie longitudinali 20 circ. frontem et dorsalem anteriorem, 45 circ. angulum aperturae branchialis superiorem inter et basin pinnae caudalis, serie transversa 15 circ. initium pinnae analis inter et dorsalem radiosam; squamis trunco postrorsum magnitudine parum accrescentibus; appendice anali oblonga obtuse; pinnis dorsalibus distantibus, magnitudine parum accrescentibus; appendice anali oblonga obtuse; pinnis dorsalibus distantibus, spinosa obtusiuscula corpore humiliore spinis mediis ceteris longioribus; dorsali radiosa dorsali spinosa vix altiore postice quam antice altiore acute vel acutiuscula; pectoralibus non filosis subaequali sed ea breviore; caudali lanceolata acutiuscula capite non longiore; coloure corpore superne viridi-roseo inferne dilutiore; iride viridi margine pupillari aurea; capite corporeque fusco nebulato-variegatis, fusco lateribus fascias latas transversas efficiente; pinnis roseis vel aurantiacis dorsalibus vittis vel fasciis 2 vel 3 longitudinale [?] transversis; pectoralibus basi superne macula fusca; caudali basi macula fusca majore, radiis maculis parvis fuscentibus in vittulas 5 vel 6 transversas dispositis. B. 5. D. 6-1/8 vel 6-1/9. P. 21. V. 1/5-5/1. A. 1/8 vel 1/9. C. 5/14/5 circ. Hab. Amboina, in mari. Longitudo 2 speciminum 58’’’ et 60’’’.

Elongate body, cylindrical anteriorly, compressed posteriorly, depth about 5 times in length without, 6 to 6½ in length with caudal fin; head somewhat acute, about 3½ in body length without, about 4⅓ with caudal fin; head depth about 2, head width about 1½ in its length, rostro-frontal profile sloping, only on the snout convex, eyes looking upwards more than laterally, diameter about 5 in head length, about 1 diameter apart; no visible pores in interocular region, many folds and papillae on the lateral and lower sides of the head, the two anterior mandibular papillae longer than the rest [presumably what are now termed chin barbels]; snout convex, much wider than long, not shorter than eye, tip located in front of the eye; anterior nasal tube longer than posterior one; upper jaw a little shorter than lower jaw, ending under the posterior part of the eye; gape very oblique; jaws with sharp teeth, teeth in outer series longer and fewer than the others; tongue bluntly rounded; branchial opening ends a little below the base of the pectoral fin; only top of head scaled, snout and cheeks wrinkled; no pores visible in oculo-suprascapular groove; all body scales cycloid, about 20 scales in longitudinal series between the forehead and anterior dorsal fin, about 45 scales between the superior angle of the branchial opening and the base of the caudal fin, about 15 scales in transverse series from anal fin origin to rayed dorsal fin; trunk scales slightly increasing in size towards the posterior part, anal appendage [urogenital papilla] oblong, blunt; dorsal fins separate [literally: dorsal fins apart], spiny fin somewhat blunt, lower than the body, middle spines longer than the others, rayed dorsal fin hardly higher than spiny dorsal fin, posterior part higher than anterior part, acute or somewhat acute, ventral fin a little shorter than pectoral fins, in the middle united for almost the whole length; anal fin nearly equal in shape and height to second dorsal fin [litt. rayed dorsal fin], but shorter; caudal fin lanceolate, somewhat acute, no longer than the head; body colour green-pink dorsally, of a fainter colour ventrally; iris green, margin of the pupil golden, head and body variegated with dark in a cloud-like pattern, on the flanks the dark colour forms wide irregular transverse bands, fins pink or orange, dorsal fins with 2 or 3 longitudinal transverse dark stripes or bands; dark spot on the upper base of the pectoral fins, caudal base with a larger dark spot, rays with small darkish spots arranged in 5 or 6 transverse stripes. B. 5, D. 6-1/8 or 1/9, P. 21, V. 1/5.5/1, A. 1/8 or 1/9, C. 5/14/5 approximately. Hab. Amboina, in sea. Length of 2 specimens 58 and 60 mm. [TL]

Rem. Cette espèce est fort distincte de l’Hasseltii par la nature cycloïdes de toutes les écailles, par l’absence d’écailles sur les joues et les opercules, par la caudale pas plus longe que la tête, par la tête plus grande et plus large et à sillons et papilles beaucoup plus développés, etc. Les deux espèces ne sont connues jusqu’ici que de l’Insulinde. Remarks.

This species is very distinct from Hasseltii by having all scales cycloid, by the absence of scales on the cheeks and opercles, by the caudal being not as long as the head, by having the head much larger and wider, and by much more developed grooves and papillae etc. The two species till now are only known from the East Indies.

Chapter Seven. A review of the *Callogobius* (Teleostei: Gobiidae) from the Red Sea with the description of a new species

NAOMI R. DELVENTHAL[1], RANDALL D. MOOI[1,2], SERGEY V. BOGORODSKY[3,4] & AHMAD O. MAL[5]

[1]Department of Biological Sciences, 212B Biological Sciences Bldg., University of Manitoba, Winnipeg MB, R3T 2N2 Canada. E-mail: naomi.delventhal@gmail.com
[2]The Manitoba Museum, 190 Rupert Ave., Winnipeg MB, R3B 0N2 Canada. E-mail: rmooi@manitobamuseum.ca
[3]Senckenberg Research Institute and Natural History Museum Frankfurt, Senckenberganlage 25, 60325 Frankfurt a.M., Germany
[4]Station of Naturalists, Omsk, Russia. E-mail: ic187196@yandex.ru
[5]Marine Biology Department, Faculty of Marine Sciences, King Abdulaziz University, Jeddah, Saudi Arabia. E-mail: aomal@kau.edu.sa

Published in *Zootaxa* 31 October 2016

My Contribution: I planned the study with assistance from R. Mooi, acquired loans of the available Red Sea material to determine which species are present, examined all specimens and wrote the manuscript (with comments from R. Mooi and S. Bogorodsky) including the key and species accounts; R. Mooi wrote the synonymies for each species account. I recorded all specimen data except for morphometric data which was recorded by R. Mooi (most meristic data was recorded independently by R. Mooi to ensure technique consistency), drew Figure 7.1 in pencil (R. Mooi inked it) and photographed one preserved specimen; S. Bogorodsky collected some of the material, provided most of the photographs and commented on the manuscript; O. Mal organized S. Bogorodsky's field work.

SUMMARY

Five species of *Callogobius* Bleeker have been previously reported from the Red Sea: *C. amikami* Goren, Miroz & Baranes, *C. clarki* (Goren), *C. dori* Goren, *C. flavobrunneus* (Smith), and *C. maculipinnis* (Fowler). Records of *C. bifasciatus* (Smith) in the Red Sea are referable to *C. clarki*. *Callogobius amikami* has been previously known only from a single specimen, the holotype from the Red Sea, and two photographs, a live juvenile from Oman and a live specimen at an aquarium at Coral World, Eilat. We obtained a possible additional juvenile from the Red Sea, although we are unable to definitively determine its identity. Red Sea specimens previously identified as *C. maculipinnis* [or *C. irrasus* (Smith)] represent a new species, distinguished from the latter by normally having four sets of transverse mandibular rows on each side (rather than three); this species is described here as *Callogobius pilosimentum* sp. nov. Four specimens of an additional, undescribed species of *Callogobius*, *C*. sp. A, have been collected from the Red Sea, but we withhold a formal description because this species is currently under study by colleagues. *Callogobius sclateri* (Steindachner), previously known from the Indo-West Pacific, is reported from the Red Sea for the first time. A key to all seven species is provided. Each species is photographed, habitat is described and a brief description with detailed comparisons is provided. The new species and *C. clarki* are endemic to the Red Sea.

INTRODUCTION

Callogobius Bleeker 1874 is a genus of moderately small gobies characterized by distinctive raised ridges of papillae on the head and comprising more than 40 nominal species (Eschmeyer & Fricke 2016). It is widespread in Indo-Pacific shallow marine and brackish environments, including coral reefs and coral rubble, tidepools, and mangrove streams. Species are cryptic and rarely seen out of shelter, making them difficult to survey. Despite considerable collecting and research over almost 200 years, relatively few specimens and only five species have been reported from the Red Sea (Golani & Bogorodsky 2010). The first described Red Sea endemic *Callogobius* was *C. clarki* (Goren 1978); Goren (1980) reviewed four species of *Callogobius* in the Red Sea, *C. clarki*, *C. irrasus* (Smith 1959), *C. flavobrunneus* (Smith 1958), and described a new Red Sea endemic, *C. dori* Goren. *Callogobius irrasus* was considered a synonym of *C. maculipinnis* (Fowler 1918) by McKinney & Lachner (1984). Goren *et al.* (1991) described yet another Red Sea endemic species, *C. amikami* Goren, Miroz & Baranes. *Callogobius clarki* was synonymized with *C. bifasciatus* (Smith 1958) by Randall *et al*. (1994), a decision followed by other authors including Randall (1995) and Golani & Bogorodsky (2010), until *C. clarki* was resurrected as a valid species by Delventhal & Mooi (2014).

In this paper we report the first record of *Callogobius sclateri* (Steindachner 1879) for the Red Sea, a species with an otherwise widespread distribution in the Indo-West Pacific. In addition, we have identified four Red Sea specimens that, though resembling *C. sclateri*, represent an undescribed species: BPBM 18213 (male, 38.3 mm SL and female, 34.5 mm SL), SMF 35772 (KAU 13-631; juvenile, 14.5 mm SL), and KAUMM 383 (KAU 13-32; juvenile, 17.0 mm SL). This species can be distinguished from *C. sclateri* and other Red Sea species by the lower lateral scale counts (22–25), partially united pelvic fins (about two-thirds of length in intact specimens), and the fifth pelvic-fin ray no more than four-fifths the length of the fourth. These appear to be representatives of a widespread species in the Indo-West Pacific that is presently under study by scientists at the Biological Laboratory of the Imperial Palace, Japan. We include this species in our key as *C*. sp. A, but do not provide a formal species description; one is forthcoming from these colleagues.

Our examination of the head papillae row patterns of Red Sea specimens identified as *Callogobius maculipinnis* revealed a subtle difference compared to specimens outside the Red Sea. With rare exception, specimens of members of the *C. maculipinnis* species complex collected outside the Red Sea have three sets of transverse mandibular rows on each side of the lower jaw. In contrast, almost all Red Sea specimens have four sets of transverse mandibular rows on each side of the lower jaw; we describe the Red Sea specimens as a new species.

We provide a key to all seven Red Sea *Callogobius* along with brief descriptions of each species, detailed comparisons, habitat descriptions, and photographs.

MATERIALS AND METHODS

Specimens from the Red Sea are listed in their respective species accounts. In addition, we examined type specimens of the *Callogobius* species listed in Delventhal & Mooi (2013), and representatives of *C. maculipinnis* as identified from other geographic localities is provided in the new species account. The full account of the new species is provided first, followed by the remaining Red Sea species summaries in alphabetical order.

Abbreviations for institutional codes follow Fricke & Eschmeyer (2015) and/or Sabaj Pérez (2014) excepting KAUMM (King Abdulaziz University Marine Museum, Jeddah, Saudi Arabia – specimens temporarily housed at SMF). Specimens that have been tissue-sampled are provided with a KAU number after the catalogue number. Methods for morphometrics and meristics follow Delventhal & Mooi (2013), with the following additions. Whenever possible, morphometric data were taken from specimens that had reached sexual maturity and that had not become compressed, folded or otherwise distorted during preservation and storage. Full collection data are provided for previously unreported material.

Scales. We recorded the anterior-most limits of ctenoid scales with appropriate landmarks (e.g., from the first spine of the second dorsal fin, meaning, from a vertical line drawn from the first spine of the second dorsal fin) or simply recorded a general pattern with its variation (e.g., ctenoid scales, if present, restricted to the caudal peduncle).

Sensory pores and papillae rows. The alphabetical naming system for the sensory pores follows Akihito & Meguro (1977) and descriptive names for pores and canals are modified from Takagi (1957). Figure 7.1 illustrates the sensory pores and canals found in the new species. Cyanine blue dye prepared by the method of Akihito *et al*. (1993) was applied when distinguishing between pores (which often end in short tubes) and pore replacement papillae, the latter normally located where pores would be positioned in pored species (see Delventhal & Mooi 2013). Terminology for sensory papillae rows follows Delventhal & Mooi (2013). We comment only on papillae rows whose length and orientation are variable among *Callogobius* species and generally consistent within a species (these rows are labeled in Figure 7.1).

Colour pattern. In each species account, we recorded a range in the number of dark bars (e.g. 4–5 bars). In general, each species has a specific number of possible bars in a distinct and consistent orientation, but the bars themselves may or may not be visible due to changes in contrast caused by the environment and behavioural response of the fish (e.g., Figure 7.2). In addition, many *Callogobius* become increasingly dark and/or mottled as they age. In these species, juveniles tend to be distinctly bi-coloured, but the barring pattern becomes obscured in larger fish. The colour patterns of the pectoral and first dorsal fins are often useful in distinguishing species. Unfortunately, the first dorsal fin is usually compressed in preserved specimens. The pattern on the pectoral fin often changes with age. Photographs by the third author (SVB) are of live specimens usually under anesthetic; this can sometimes result in different colour patterns than might be seen before collection, but are usually more representative than patterns in freshly dead specimens.

***Callogobius pilosimentum* sp. nov.**

Hairy-chinned Flapheaded Goby

(Figures 7.1–7.2, Table 7.1)

Drombus irrasus (non Smith) – Goren 1979b: 36.

Callogobius irrasus (non Smith) – Goren 1980: 213; Dor 1984: 241.

Callogobius maculipinnis (non Fowler) – Goren *et al*. 1991: 299; Goren & Dor 1994: 53; Golani & Bogorodsky 2010: 46.

Material examined. All specimens collected from the Red Sea.

Holotype. SMF 35756 (KAU12-0224), female, 36.4 mm SL, Saudi Arabia, Farasan Island, N16°43.083' E42°03.934' , isolated coral patch of lagoon, 3–5 m, S.V. Bogorodsky & T.J. Alpermann, 20 February 2012 (Figs. 1, 2A).

Paratypes (17 specimens, 25.5–67.0 mm SL). **Egypt**: BPBM 21518, male?, 41.5 mm SL, El Hameira, coral knoll in 12 m, J.E. Randall & O. Gon, 25 April 1977; **Saudi Arabia**: KAUMM 373, male, 47.1 mm SL, Maqna, N 28°26'13.40" E 034°45'47.80", steep slope, 7 m, S.V. Bogorodsky, 13 April 2011; KAUMM 374, female, 28.3 mm SL, Jeddah, Obhur (Sharm Obhur), N21°42'33.12" E39°05'48.26", base of rocky reef, 2 m, S.V. Bogorodsky, 19 April 2011; KAUMM 375 (KAU12-0220), male, 25.5 mm SL, collected with the holotype; KAUMM 376, male, 37.0 mm SL, Farasan Island, N16°43.083' E42°03.934', isolated coral patch of lagoon, 3–5 m, S.V. Bogorodsky & T.J. Alpermann, 20 February 2012; KAUMM 377 (KAU13-378), male, 28.5 mm SL, 30 km south of Al Wajh, N26°03'30.36" E36°38'34.98", fringing reef, 8 m, S.V. Bogorodsky & T.J. Alpermann, 14 June 2013; SMF 35757, 2 males, 29.7 mm SL (C&S) & 47.3 mm SL, Farasan Island, N16°54' 93.30" E41°50'76.10", lagoon, isolated small coral patch, 1 m, S.V. Bogorodsky, 01 April 2011; SMF 35758 (KAU12-0218), male, 38.4 mm SL, collected with the holotype; SMF 35759 (KAU12-0538), female, 35.8 mm SL, Farasan Island, N16°43.083' E42°03.934', isolated coral patch of lagoon, 3–5 m, S.V. Bogorodsky & T.J. Alpermann, 28 February 2012; SMF 35760, male, 67.0 mm SL and female, 55.8 mm SL (Figure 2C), Jeddah, Obhur (Sharm Obhur), N21°42'32.28" E39°05'47.16", steep slope with patches of corals and small sandy flats, 14–16 m, S.V. Bogorodsky, 01 July 2013; **Sudan**: BMNH 1978.9.8.12-16, 5 specimens (4 females with 1 C&S, 1 male, 44.5–61.9 mm SL), Suakin, coral crevices in seawall, Manihine collections, 5 December 1950.

Other material. BMNH 1978.9.8.17-26, 10 specimens (6 females, 4 males, 36.9–70.7 mm SL), Sudan, Suakin Archipelago, around seawall and from crevices, Manihine collections, 12 January 1951.

Tentative identification: USNM 296956, female, 44.3 mm SL, Red Sea, Egypt, just north of Ras Burqa, V.G. Springer *et al*., 23 July 1969.

Diagnosis. *Callogobius pilosimentum* is distinguished from all other known *Callogobius* species by the following combination of characters: interorbital canal normally containing pores B', C, D, E, F, G and H'; preopercular canal containing pores M', N, and O'; temporal canal containing pores K' and L'; scales in lateral series 21–25 (usually 24); normally four transverse mandibular papillae rows (Row 16) on each side.

Description. Holotype values indicated by an asterisk. Parentheses enclose number of type specimens with the particular value, counts made on both sides when applicable or possible. Dorsal fin VI+I,9(17*), VI+I,10(1); anal fin I,6(1), I,7(17*); pectoral-fin rays 15(2), 16(11), 17(15*), 18(5); pelvic-fin rays I,5(36*); segmented caudal-fin rays 9+8(1), i8+8(4*), i8+7i(12), ii7+8(1); procurrent rays 4+4(2), 5+4(15*), 5+5(1); scales in lateral series 21(1), 22(3*), 23(4), 24(20*), 25(5); predorsal scales 6(5), 7(13*); transverse scales 8(3), 9(13*), 10(2).

See Table 7.1 for selected morphometrics. Body moderately robust for the genus (Figure 7.2). Head depressed, broader than deep. Snout obtuse. Mouth slightly oblique, forming an angle of about 45° with body axis; lower jaw slightly beyond tip of upper jaw, posterior end of jaws at or just before vertical through anterior margin of orbit. Anterior nostril moderately long, slender tube, reaching halfway to anterior outer edge of upper lip; posterior nostril very short, upright tube. Eye moderately large; upper margin of orbit slightly elevated above profile of head. Interorbital narrow. Gill opening ending ventrally at lower edge of pectoral-fin base. Tongue broad, tip slightly bilobed. Urogenital papilla long, slender and darkly pigmented in males; broad and darkly pigmented in females, no lateral flaps. Vertebral count (based on two cleared and stained specimens) 10 precaudal + 16 caudal.

Dentition. Teeth in jaws conical and slender in rows; outer teeth slightly larger than inner teeth. Outer teeth present on anterior two-fifths of toothed portion of lower jaw; inner teeth of lower jaw tightly packed anteriorly, about 6 irregular rows merging to single row posteriorly. Outer teeth of upper jaw extend over entire toothed portion of upper jaw, about 5 irregular rows of inner teeth merging to single row parallel to row of outer teeth.

Fins. First dorsal fin-base short; anterior fin membranes incised, first three interspinous membranes incised with spine tips free up to one-fourth their length, occasionally more for second and third spine (particularly in males that have longer, filamentous fin spines), posterior interspinous membrane only slightly incised; second spine longest. Second dorsal fin-base about twice that of first dorsal; segmented rays branched, penultimate ray longest. Anal fin-base short; segmented rays branched, penultimate ray longest. Pectoral fin-rays branched except for dorsalmost one or two rays; fin reaching to level of second or third anal-fin ray. Pelvic fins fully united with membrane over entire length of medial rays; fourth segmented pelvic-fin ray barely shorter or subequal to fifth ray, fifth ray almost reaching to anus; all segmented pelvic-fin rays branched. Pelvic frenum present and well developed. Caudal fin rounded, length < 40% SL.

Squamation. All scales large and deciduous, with distinctly outlined centres. Scales cycloid on head and anterior half of body; cycloid scales present on nape to interorbital, in spaces between papillae rows on cheeks, preoperculum and operculum, on lateral side of pectoral-fin bases, prepelvic and predorsal areas, and belly. Scales ctenoid on posterior half of body from mid-flank region below first to third spines of first dorsal fin. Ctenii numerous, long, slender and pointed; no elongate ctenii on caudal peduncle. Most specimens with single large cycloid scale in centre of pelvic disc (visible under pelvic frenum).

Cephalic sensory systems. Pores present (Figure 7.1). Interorbital canal with pair of posterior nasal pores (pore B), anterior interorbital pore (pore C), posterior interorbital pore (pore D), pair of supraotic pores (pore E), pair of anterior otic pores (pore F), pair of posterior otic pores (pore G), and pair of intertemporal pores (pore H); preopercular canal with three preopercular pores (pores M, N and O); each temporal canal with anterior and posterior temporal pore (pores K and L, respectively).

Papillae row configuration (Figure 7.1): Postnasal rows (Row 2) long and joined across midline (16*) or overlapping (1). Anterior suborbital row (Row 9) short to moderately long, not reaching eye (34*). Mid suborbital row (Row 10) short to moderately long, not reaching eye (34*). Posterior suborbital rows (Row 11) long and overlapping (32*) or rarely short or irregular (2). Longitudinal maxillary row (Row 14) rarely irregular (1), normally continuous and extending posteriorly to below and beyond (33*) transverse cheek row (Row 13), latter short (31*) or rarely irregular (1). Longitudinal mandibular row (Row 15) continuous (21*) or irregular (3). With 4(31*), 5(2), or 2(1) transverse mandibular rows (Row 16) on each side of lower jaw, all but one specimen with 4 on at least one side; 15 of 17 type specimens with 4 on both sides. One specimen with 5 on one side and 4 on the other (SMF 35760, 67 mm SL), and one with 5 on one side and 2 on the other (SMF 35759, 35.8 mm SL); latter exhibits irregular patterns in several other papillae rows (Rows 13, 14, 15, 17, 20, 21). Postorbital rows (Row 17) short (less than two-thirds of distance from the dorsal mid-line to bony edge of cranium) (8) or medium (more than two-thirds of distance from dorsal mid-line to bony edge of the cranium) (24*), rarely irregular (1). Preopercular row (Row 20) continuous with the transverse opercular row (Row 21) (25*) or separate (5).

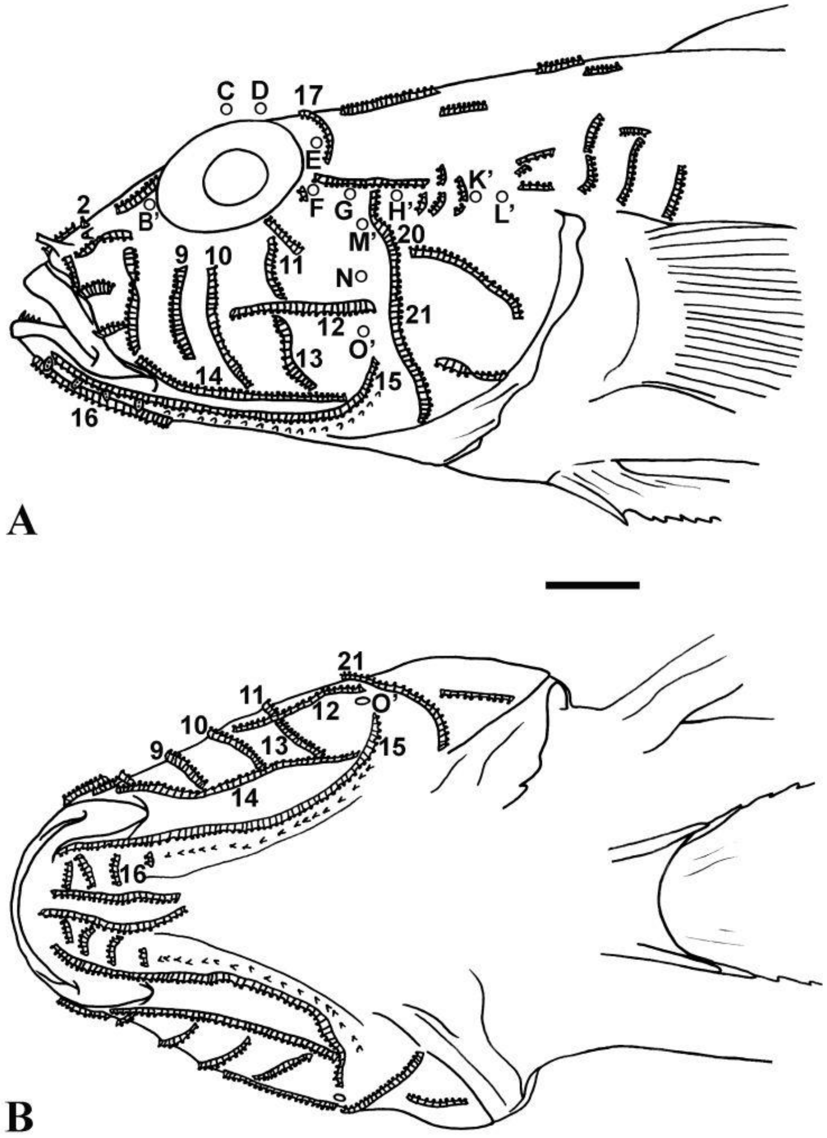

FIGURE 7.1 Sensory pore and papillae pattern on the head of *Callogobius pilosimentum sp. nov.*, SMF 35756, holotype, female, 36.4 mm SL. Scale bar = 2 mm. **A.** Lateral view; **B.** Ventral view. Letter abbreviations of sensory pores follow Akihito & Meguro (1977) and descriptive names are modified from Takagi (1957). Papillae row numbering follows Akihito and Meguro and descriptive names are from Delventhal & Mooi (2013). Sensory pores: B = posterior nasal; C = anterior interorbital; D = posterior interorbital; E = supraotic; F = anterior otic; G = posterior otic; H = intertemporal; M,N,O = preopercular; K = anterior temporal; L = posterior temporal. Papillae rows: 2 = postnasal; 9 = anterior suborbital; 10 = mid suborbital; 11 = posterior suborbital; 12 = longitudinal cheek; 13 = transverse cheek; 14 = longitudinal maxillary; 15 = longitudinal mandibular; 16 = transverse mandibular; 17 = postorbital; 20 = preopercular; 21 = transverse opercular (rows 20 and 21 continuous).

Colour in life (Figure 7.2). General colour pattern brown to dark brown with paler patches (Figure 7.2A), or pale grayish-brown with up to five dark brown mottled vertical bars on body and dark brown blotchy patterns with varying contrast on head. Body bars, when visible (e.g. Figs. 2B & C, but not Figure 7.2A), appear as follows: irregular bar may extend dorsally over operculum and pectoral-fin base, slightly indented at first dorsal fin spine; wide bar extends below first dorsal fin; two wide, slightly oblique bars extend below mid and posterior portions of second dorsal fin; narrow bar encircles posterior caudal peduncle, edge of hypural plate and proximal regions of the caudal fin. Underside of head light brown or dusky, papillae rows may show great colour contrast. First dorsal fin with dark brown basal spot centered on fourth ray and continuous with dark body bar; may exhibit yellow markings on distal margin. First and second dorsal fins dark brown with irregular, oblique, pale bands or rows of spots, some individuals with irregular dark and pale pattern; caudal fin dark brown usually with pale spots forming irregular bars. Pelvic and anal fins dusky or dark brown with or without paler blotches. Pectoral fin with dark irregular bands or rows of spots and a dark medial mark at base. Urogenital papilla dark.

Colour in preservative. As in life, although older specimens can be orange-brown with little pattern on body. Most museum specimens damaged (species with fragile skin and deciduous scales) and body colour pattern often reduced to light brown or grey with dark outlines of scale pockets.

TABLE 7.1 Selected measurements of the holotype and paratypes of *Callogobius pilosimentum sp. nov.*; standard length is provided in mm, values for other morphometrics are as percentage of standard length (SL) or head length (HL), as indicated. For paratypes, the range is followed by an average value for all types in parentheses. The two largest specimens (63 and 67 mm SL) were males (M), the next 3 largest specimens (55.8, 50.3, 49.3 mm SL) were females (F).

	Holotype	Paratypes
Gender	F	9M,8F
Standard Length (mm)	36.4	25.5–67.0 (42.8)
Head length (% of SL)	33.0	29.1–34.1 (32.3)
Head depth (% of HL)	59.2	50.6–64.6 (58.8)
Head width (% of HL)	73.3	64.6–75.8 (70.2)
Interorbital width (% of HL)	5.4	4.1–7.8 (5.7)
Predorsal fin distance (% of SL)	38.5	34.3–40.4 (37.0)
Preanal fin distance (% of SL)	59.6	57.8–62.8 (60.3)
Prepelvic fin distance (% of SL)	33.0	29.6–35.8 (32.8)
Pectoral-fin length (% of SL)	31.3	29.7–35.4 (32.6)
Pelvic-fin length (% of SL)	23.9	22.0–28.1 (24.9)
Caudal-fin length (% of SL)	32.4	26.4–37.3 (31.9)
Caudal peduncle depth (% of SL)	13.7	12.3–15.5 (13.8)

Etymology. The species name is derived from the Latin *pilosus* meaning “hairy” and *mentum* meaning “chin”, referring to the extra rows of papillae on the chin. Specific epithet to be treated as a noun in apposition. Suggested common name: hairy-chinned flapheaded goby.

Distribution and habitat. Restricted to the Red Sea. It is usually collected in shelters or close to shelters on small sand flats (about 0.5–1m across) of steep slopes, sometimes at the base of coral reefs, in closed areas in bays and lagoons, at depths of 1–20 m.

Remarks. Goren (1980) listed *Drombus irrasus* Smith in the Red Sea as a first record. This species is considered a synonym of *Callogobius maculipinnis* by most authors (e.g. McKinney & Lachner 1984, Goren *et al*. 1991); Eschmeyer and Fricke (2016) incorrectly attributed Delventhal & Mooi (2013) as recognizing this species when the type was listed as comparative material. Although we have not examined Goren’s (1980) *C. irrasus* material, we suspect that these specimens will belong to *C. pilosimentum*. Two lots of specimens that we identify as *C. pilosimentum* (BMNH 1978.9.8.12-16 and BMNH 1978.9.8.17-26) were examined by Goren (1980) and identified as *C. irrasus*.

Callogobius pilosimentum belongs to a "*maculipinnis* species complex" including the following nominal species: *C. bauchotae* Goren 1979, *C. irrasus* (Smith 1959), *C. kuderi* (Herre 1943), *C. maculipinnis* (Fowler 1918), *C. nigromarginatus* Chen & Shao 2000, *C. shunkan* Takagi 1957, *C. snelliusi* Koumans 1953, and *C. vanclevei* (Herre 1950). Species of this complex are characterized by having the temporal canal with pores K and L (absent in all other *Callogobius*) and normally four or fewer transverse mandibular rows on each side (all other *Callogobius* normally have more than 10). McKinney & Lachner (1984) synonymised *C. irrasus*, *C. kuderi*, *C. shunkan*, *C. snelliusi*, and *C. vanclevei* with *C. maculipinnis*; they did not examine *C. bauchotae* (or *C. nigromarginatus* as it was described after their work). However, their synonymies should be considered questionable because all included species are poorly defined. Based on the first author's examination of the types, we are confident that several, or even most, of these species will prove to be valid after complete investigation. Despite this, *C. pilosimentum* can readily be distinguished from the other members of this complex, all of which normally have three transverse mandibular rows on each side. We previously examined the types of all the above species in the *maculipinnis* complex except *C. nigromarginatus.* They all have three sets of transverse mandibular rows, except *C. shunkan* which has extra irregular rows and is easily differentiated by other characters (Y. Ikeda pers. comm.). These observations of the types were recently confirmed by Y. Ikeda (*C. bauchotae, C. snelliusi*, and *C. shunkan*), M. Sabaj Pérez (*C. maculipinnis*) and D. Catania (*C. kuderi*). L. Parenti re-examined the holotype of *C. vanclevei*, a distorted specimen that appears to have no fourth transverse mandibular row on either side. The holotype of *C. nigromarginatus* was unavailable, but the illustration and text indicate that three transverse mandibular rows are present (Chen & Shao 2000).

We found only a single Red Sea specimen (USNM 296956, female, 44.3 mm SL) that has three transverse mandibular rows on each side. We tentatively identify it as *Callogobius pilosimentum*, but we have not designated it as a paratype. We presume that this is simply unusual variation in a species that normally has four on each side. To evaluate variation in transverse mandibular papillae rows (Row 16, Figure 7.1) in specimens outside of the Red Sea, we examined 174 adult specimens identified in collections as *C. maculipinnis* ranging across the Indian Ocean eastward to Mangareva (Gambier Islands, French Polynesia) in the Pacific Ocean (listed in Comparative material below).

Of these 174 specimens examined from outside of the Red Sea, only three (< 1.7%) exhibited the condition of *C. pilosimentum* of having four transverse mandibular papillae rows on both sides of the jaw. Even among these, only one (WAM P27935-024) exhibited a normal, sequential four-row anatomy, and this specimen belongs to an Australian ‘population’ that has distinctly higher meristic counts than other members of the complex (D. Hoese pers. comm.). The other two specimens (USNM 332226 and ZRC 40669) have unusual morphologies where the fourth transverse mandibular row on one side follows a free papilla and/or the first row is a branch of the intermandibular row. An additional 11 specimens had four rows on only one side and three or fewer on the other (6.3% of all specimens). From localities with the largest representation, an Indonesian lot (USNM 241882) had three of 32 specimens having four transverse mandibular papillae rows on one side only and of 42 specimens in 11 lots from Fiji only two specimens had four such rows on one side. This is in contrast to the condition in *C. pilosimentum* in the Red Sea where all specimens exhibited four or more transverse mandibular rows on each side except one that had five on one side and two on the other, and one that had three on each side (USNM 296956).

In *Callogobius pilosimentum*, the anterior first dorsal-fin spines are usually free of membrane for one-fourth or more of the spine length, particularly the second spine. Although clearly evident on some live specimens (Figure 7.2), this can be difficult to assess on preserved specimens. This feature is common to most, if not all, members of the *maculipinnis* species complex so is not diagnostic, but is potentially of value to distinguish live or particularly well-preserved specimens from Red Sea congeners.

Comparative material. *Callogobius maculipinnis* (listed west to east): Comoros – ROM 92691 (4); Oman – ROM 39895 (6); Chagos – ROM 55107 (4); Sri Lanka – USNM 220035 (5); Cocos-Keeling – WAM P29928-022 (4); Western Australia – WAM 27935-024 (3); Thailand – ROM 58036 (1), 68041 (4); Indonesia – USNM 241882 (32), WAM P33093-002 (2); Singapore – ZRC 40669 (1); Philippines – ROM 53339 (3), USNM 297102 (2); Taiwan – BPBM 23242 (1), USNM 298439 (8); Palau – BPBM 37767 (2), ROM 75955 (1); 76134 (1); Papua New Guinea – BPBM 32638 (1), 32674 (2), USNM 297051 (2); Australia – MPM 48365 (1), ROM 38903 (1), USNM 297048 (3); One Tree Island – BPBM 14432 (4); Lord Howe Island – BPBM 14862 (1); Coral Sea – BPBM 33517 (1), 33629 (3); New Caledonia – BPBM 34270 (1), ROM 64155 (1), 64160 (2), 64416 (3); Vanuatu – BPBM 5765 (1), MPM 32132 (1), 46721 (1); Marshall Islands – BPBM 8296 (1), 17739 (1), 22349 (1); Fiji – BPBM 39866 (1), 40082 (1), ROM 57700 (5), 57701 (1), 57703 (3), 57705 (6), 57707 (2), 57708 (1), 57709 (2), 57710 (1), USNM 332226 (19); Tonga – BPBM 38115 (3), USNM 339828 (7); Tahiti – BPBM 8315 (2); Rapa – BPBM 17317 (1); Mangareva – BPBM 13595 (3).

Comparisons to other described *Callogobius* species are based on our data from the available holotypes listed in Delventhal & Mooi (2013).

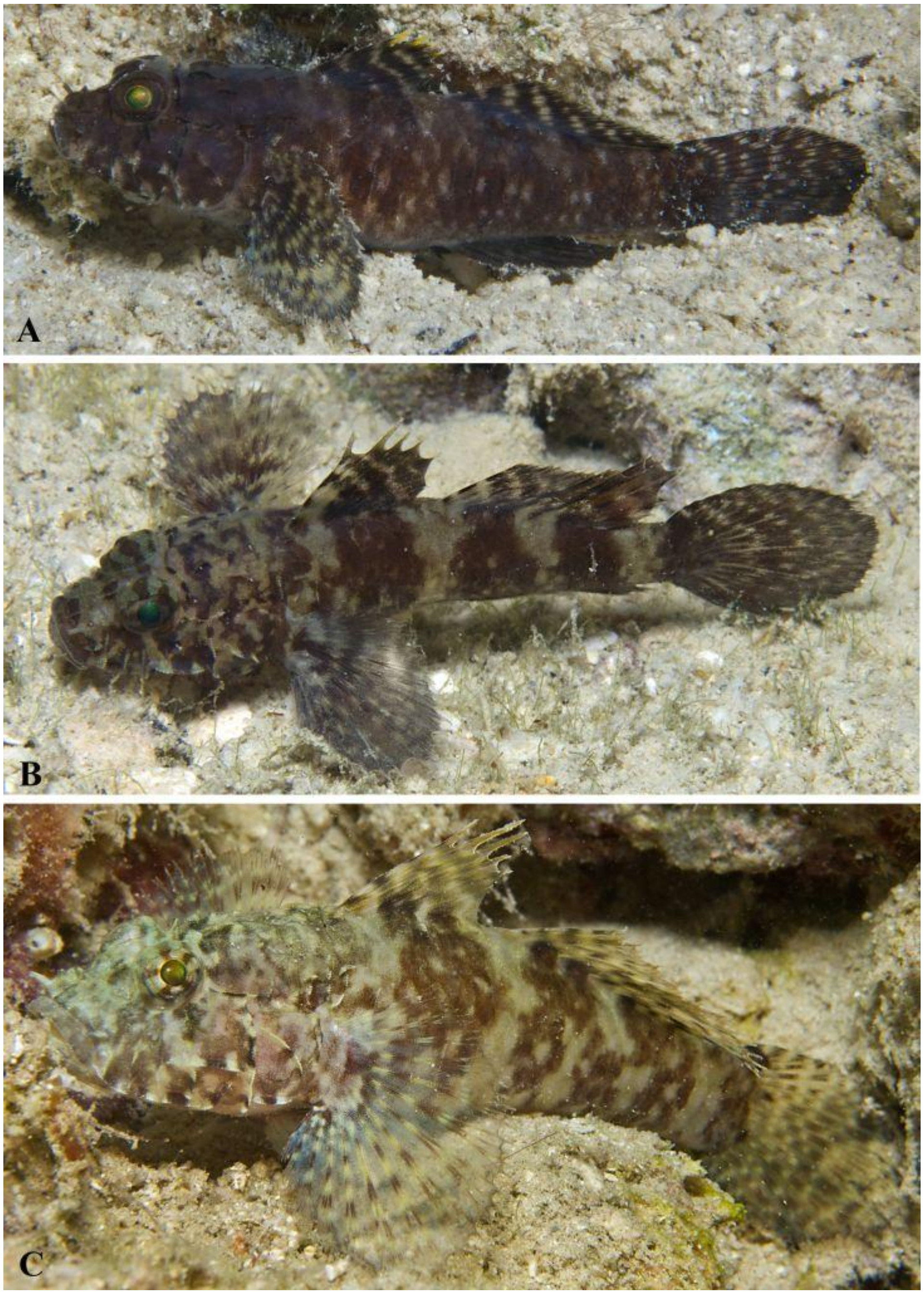

FIGURE 7.2 *Callogobius pilosimentum sp. nov*., live colouration: **A.** SMF 35756, holotype, female, 36.4 mm SL, Farasan Island, Saudi Arabia; **B.** Fresh colouration, uncatalogued, Farasan Island, Saudi Arabia, illustrating pattern frequently induced by stress; **C.** SMF 35760, paratype, female, 55.8 mm SL, Obhur, Jeddah, Saudi Arabia. Photos by S. Bogorodsky.

Callogobius amikami Goren, Miroz & Baranes 1991

(Figure 7.3)

Callogobius amikami Goren, Miroz & Baranes 1991: 300 (Eilat, Israel, Gulf of Aqaba, Red Sea; holotype TAU P-10321). – Goren & Dor 1994: 63; Randall 1995: 329; Golani & Bogorodsky 2010: 46.

Diagnosis. *Callogobius amikami* is distinguished from congeners by the following combination of characters: interorbital pores B’, D, E, F, G and H’ present; preopercular canal absent; temporal canal absent; dorsal fin VI+I,10; anal fin I,8; scales in lateral series about 27; scales ctenoid from the first spine of the second dorsal fin to the caudal-fin base; preopercular papillae row (Row 20) continuous with transverse opercular row (Row 21); body colouration with strongly contrasting wide dark bars and narrow horizontal lines.

Brief description. Moderately stout-bodied species with slightly elongate and round-tipped caudal fin > 40% SL in length. Scales large, cycloid anteriorly, ctenoid from first spine of second dorsal fin to caudal-fin base, scales in lateral series about 27. Dorsal-fin rays VI+I,10, anal-fin rays I,8, pectoral-fin rays 18; pelvic fins fully united with fifth ray equal to fourth (resulting in blunt-ended appearance), frenum weak. Anterior nostril slightly longer than posterior nostril. Head pores present with interorbital canal normally containing pores B’, D, E, F, G, and H’, preopercular and temporal canals absent. Preopercular papillae row (Row 20) continuous with transverse opercular row (Row 21), more than 10 transverse mandibular papillae rows (Row 16) on each side.

Body of adults pale grey with about nine narrow black stripes following scale rows, short broad black bar dorsally below posterior half of first dorsal fin, a slightly curved black bar below rear of second dorsal fin, and black bar at caudal-fin base. Head whitish with three dark bars radiating from eye, one oblique across side of snout anteriorly to chin, one across cheek and opercle, and one dorsoposteriorly across occiput. Broad irregular oblique black bar from origin of first dorsal fin to upper part of opercle. Two papillae rows on cheek below eye black. Both dorsal fins black, each with broad white dash anteriorly, oblique rows of white spots, and narrow white to hyaline border. Caudal fin with large central brown area crossed by rows of black spots, margin white and broadest dorso-posteriorly. Pectoral fin dark dorsally and basally, white ventrally. Presumed juveniles (see Remarks) white with four narrow black bars on body, one on nape, one dorsally extending into first dorsal fin, one posteriorly extending through anal fin and second dorsal, and one at caudal-fin base; bars in dorsal fins with orange spot; pelvic fin white; pectoral fin mostly white with broad black dorsal and posterior margin with orange submarginal band; caudal fin white with black bar in posterior third with orange bar within it.

Distribution and habitat. Confirmed only from the Red Sea. First reported by Goren *et al*. (1991) in the original description of a single specimen (TAU P-10321) from Eilat, Israel collected at 6 m among coral pieces and rocks away from the coral reef. A possible photographic record from Oman is discussed below.

Remarks. *Callogobius amikami* is most likely to be confused with *C. dori*. It differs in second dorsal- and anal-fin ray counts (D2 I,10 and A I,8 in the holotype of *C. amikami* vs. D2 I,9 and A I,7 in *C. dori*), and in adult colour pattern (distinct vertical bars present vs. absent). Our measurements and lateral scale counts taken from the holotype (Figure 7.3A) differ slightly from those of Goren *et al*. (1991), who measured the holotype at 28.4 mm SL and counted 24 scales in lateral series. Our shorter SL measurement is likely due to stiffening of the specimen in preservation; our higher lateral scale count can be attributed to uneven scale distribution and individual researcher technique. Goren *et al*. (1991) stated that the holotype is a male; we found the gender to be ambiguous.

A second specimen of *C. amikami* was photographed by J.E. Randall in 1993 at Coral World in Eilat (Figure 7.3B). We were unable to determine if the specimen was eventually preserved and added to a collection.

Debelius (1993: 263) provided a photograph of a single live juvenile *Callogobius* taken in Muscat, Oman (Western Indian Ocean) that he identified as *C. amikami*, but no specimens were taken. The photographed individual displays sharply contrasting narrow bars, with the bars having bright orange central markings on the pectoral, first and second dorsal fins, and caudal fins. Randall (1995) followed Debelius (1993) in listing *C. amikami* as occurring in Oman. We consider this identification to be uncertain. The colour pattern of *C. amikami* differs slightly from the photograph (although some differences would be expected from developmental change); the holotype of *C. amikami* has much wider bars and darker fins. The live photograph of the holotype in Goren *et al*. (1991) does indicate orange on the first dorsal fin, supporting the identification of the Oman specimen as C. *amikami*, however, the latter appears to have an anal fin ray count of I,7 (as opposed to I,8 in the holotype *C. amikami*).

The third author collected and photographed a 7.2 mm juvenile from Al Wajh bank, Saudi Arabia (Figure 7.3C) that resembles the specimen in Debelius's photograph. This individual was very secretive, hidden inside the base of dead coral in fringing seaward reefs at a depth of 3–5m. Microscopic examination revealed that the lateral scales are not yet fully developed on this specimen and second dorsal- and anal-fin ray counts are I,9 and I,7 respectively, lower than the counts on the holotype of *C. amikami*. Instead, these counts match those of *C. dori*, although no tiny juveniles of the latter are known. We are uncertain that this specimen represents *C. amikami*.

Representative Red Sea Material (2 specimens, 7.2 &26.2 mm SL)**. Israel**: TAU P-1032, holotype, sex uncertain, 26.2 mm SL. **Saudi Arabia**: SMF 35770 (KAU13-142), juvenile (tentative identification), 7.2 mm SL, Al Wajh bank, N25°35'52.86" E36°41' 01.80", seaward slope of unnamed island, sediment with coral patches, 3–5 m, coll. S.V. Bogorodsky & T.J. Alpermann, 12 June 2013.

FIGURE 7.3 *Callogobius amikami* Goren, Miroz & Baranes: **A.** Preserved specimen, TAU P-10321, holotype, sex uncertain, 26.2 mm SL, Eilat, Israel; **B.** Aquarium specimen in 1993, Coral World, Eilat, about 40 mm TL, collected by A. Miroz. **C.** *Callogobius cf. amikami*, live colouration, SMF 35770, juvenile, 7.2 mm SL, Al Wajh bank, Saudi Arabia. Photos by N. Delventhal (A), J.E. Randall (B) used with permission, S. Bogordsky (C).

Callogobius clarki (Goren 1978)

(Figure 7.4)

Drombus clarki Goren 1978: 200 (El-Tur, Sinai coast, Egypt, Gulf of Suez, Red Sea; holotype HUJ 10065). – Goren 1979b: 36.

Callogobius bifasciatus (non Smith) – Randall *et al*. 1994: 240; Randall 1995: 330; Golani & Bogorodsky 2010: 46.

Callogobius clarki – Goren 1980: 213; Dor 1984: 241; Goren *et al*. 1991: 300; Goren & Dor 1994: 63; Delventhal & Mooi 2014: 143.

Diagnosis. *Callogobius clarki* is distinguished from congeners by the following combination of characters: head pores absent; scales in lateral series 33–41; scales mostly cycloid except for ctenoid scales occasionally on caudal peduncle; preopercular papillae row (Row 20) not continuous with transverse opercular row (Row 21).

Brief description. Moderately stout-bodied with rounded caudal fin < 40% SL in length. Scales small, cycloid except for a few rows at caudal-fin base (larger specimens may lack ctenoid scales although exceptionally long ctenii may be present on caudal peduncle scales), scales in lateral series 33–41. Dorsal-fin rays VI+I,10–11 (rarely 11); anal-fin rays I,8–9 (usually 9); pectoral-fin rays 15–17; pelvic fins united two-thirds of their length, with fifth ray shorter than fourth with weak frenum. Anterior nostril slightly longer than posterior nostril. Head pores absent. Preopercular papillae row (Row 20) not continuous with transverse opercular row (Row 21); more than 10 transverse mandibular papillae rows (Row 16) on each side.

Head, body and median fins finely mottled whitish and grey-brown with irregular broad, dark brown bar below first dorsal fin extending onto fin as one or two spots at base. Second broad, oblique, dark bar extending from mid to posterior base of second dorsal fin to posterior base of anal fin and anterior caudal peduncle. A dark bar posteriorly on caudal peduncle at caudal-fin base. Wide, diffuse brown bar or blotch present on ventral half of body below origin of second dorsal fin. Sensory papillae ridges on head with dark brown spots. Pectoral fin mostly translucent with diffuse vertical, narrow, brown bands and sometimes dense markings medially. Colouration of preserved material similar to fresh colouration.

Distribution and habitat. Reported only from the Red Sea. *Callogobius clarki* is often found under stones or at the base of corals in fringing seaward reefs and patches of corals in lagoons and bays at a depth of up to at least 12 m.

Remarks. *Callogobius clarki* differs from all other *Callogobius* species in the Red Sea in lacking head pores. Juvenile specimens of *C. flavobrunneus* and *C. sclateri* that have not yet developed head pores may be confused with *C. clarki*. Unlike *C. flavobrunneus*, *C. clarki* has ctenoid scales only on the caudal peduncle, pelvic fins united, and a weak frenum (vs. ctenoid scales on the posterior half of the body, separate pelvics or united by only a minute membrane, and no frenum). *Callogobius clarki* has higher lateral scale counts than *C. sclateri* (33–41 vs. 28–31) and pelvic fins partially united with a weak frenum (vs. separate with no frenum). Live *C. clarki* may closely resemble *C. flavobrunneus*, due to similar body shape and colouration (they may have *flavobrunneus*-like medial markings on the pectoral fins); examination with the aid of a microscope may be needed to distinguish them.

Representative Red Sea material (35 specimens, 16.8–52.0 mm SL)**. Egypt**: BPBM 41226, female, 23.9 mm SL; BPBM 41243, male, 52.0 mm SL, Dahab, large coral block, 14 m, coll. S.V. Bogorodsky, 01 August 2015; HUJ 10065, holotype, female, 36.5 mm SL; ROM 50227, male, 34.9 mm SL; USNM 220031, 11 specimens, 4 males, 3 females, 1 juvenile, and 3 specimens cleared and stained, 14.1–35.1 mm SL; USNM 220090, male, 43.7 mm SL; USNM 296954, 1 male and 1 juvenile, 16.8–24.2 mm SL; USNM 341181, male and female, 31.0–47.9 mm SL; USNM 300015, female?, 23.6 mm SL; **Eritrea**: USNM 220038, 2 males, 34.6–48.6 mm SL; **Saudi Arabia**: KAUMM 380 (KAU13-218), male, 25.2 mm SL, Al Wajh bank, fringing reef of small island, 5–8 m, coll. S.V. Bogorodsky & T.J. Alpermann, 12 June 2013; KAUMM 381 (KAU13-292), male, 29. 4 mm SL, 25 km south of Al Wajh, fringing reef, 5–7 m, coll. S.V. Bogorodsky & T.J. Alpermann, 13 June 2013; KAUMM 382 (KAU13-491), female, 34.6 mm SL, 25 km south of Al Wajh, fringing reef, 11–14 m, coll. S.V. Bogorodsky & T.J. Alpermann, 16 June 2013; SMF 35755, male, 21.5 mm SL, Amaq, fringing reef, 7 m, coll. S.V. Bogorodsky & T.J. Alpermann, 31 March 2011; SMF 35763, female, 23.7 mm SL, Farasan Island, isolated coral patch of lagoon, 3–5 m, coll. S.V. Bogorodsky & T.J. Alpermann, 28 February 2012; SMF 35765 (KAU13-212), female, 36.4 mm SL, Al Wajh bank, sediment with coral patches, 3–5 m, coll. S.V. Bogorodsky & T.J. Alpermann, 12 June 2013; SMF 35766 (KAU13-291), female, 41.4 mm SL, 25 km south of Al Wajh, fringing reef, 5–7 m, coll. S.V. Bogorodsky & T.J. Alpermann, 13 June 2013 (Figure 7.7); SMF 35767 (KAU13-217), male, 37.2 mm SL, Al Wajh bank, fringing reef of small island, 5–8 m, coll. S.V. Bogorodsky & T.J. Alpermann, 12 June 2013; SMF 35768 (KAU13-381 & 382), 2 females, 31.6 –33.6 mm SL, 30 km south of Al Wajh, fringing reef, 8 m, coll. S.V. Bogorodsky & T.J. Alpermann, 14 June 2013; SMF 35769 (KAU13-454), male, 42.3 mm SL, 25 km south of Al Wajh, fringing reef, 11–14 m, coll. S.V. Bogorodsky & T.J. Alpermann, 16 June 2013; **Sudan**: BMNH 1978.9.8.6, male, 38.8 mm SL.

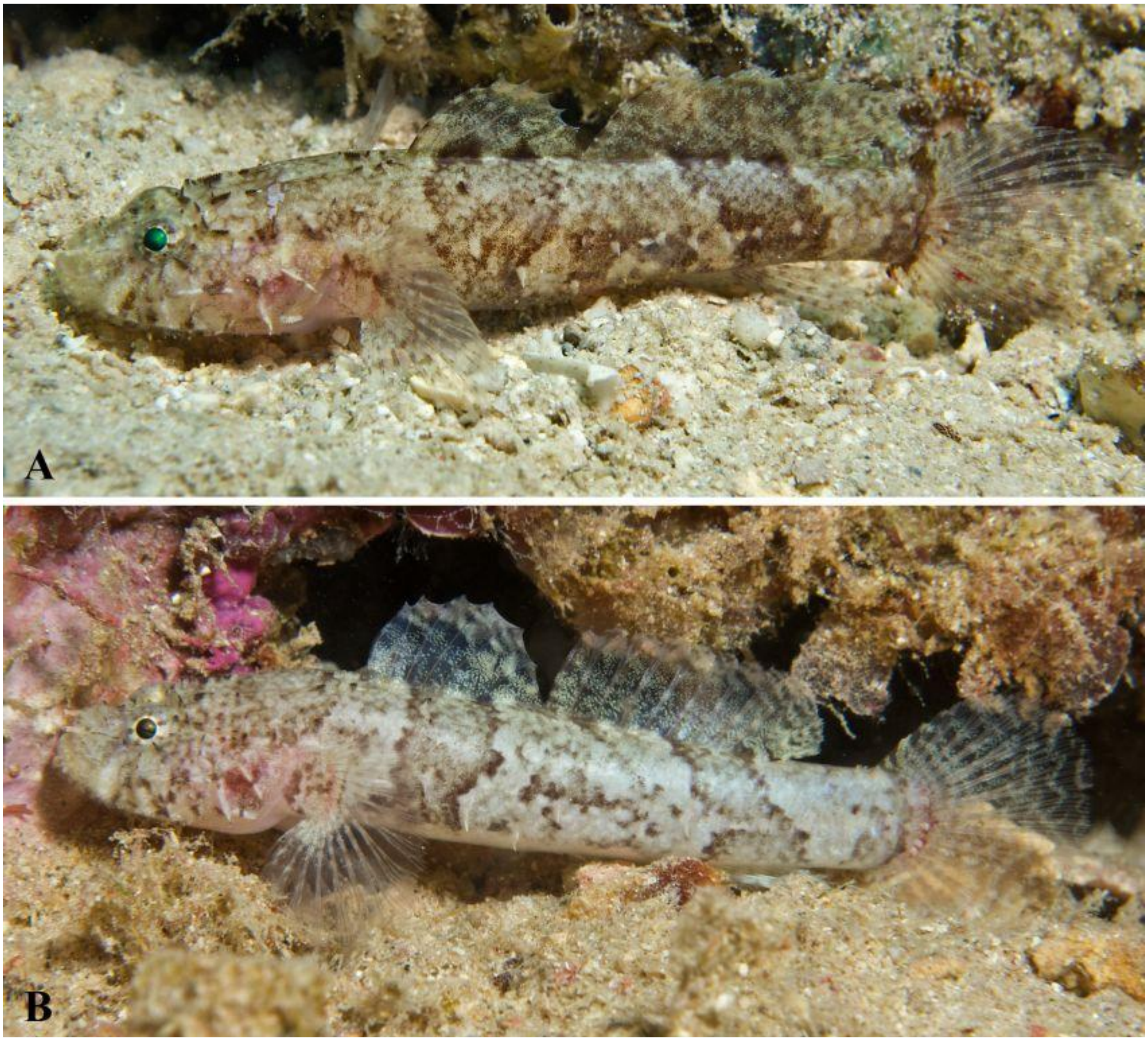

FIGURE 7.4 *Callogobius clarki* (Goren), live colouration: **A.** SMF 35766, female, 41.4 mm SL, Al Wajh, Saudi Arabia; **B.** BPBM 41243, male, 52.0 mm SL, Dahab, Egypt. S. Bogordsky.

Callogobius dori Goren 1980

(Figure 7.5)

Callogobius dori Goren 1980: 210 (Suakin, Sudan, Red Sea; holotype BMNH 1978.9.8.7).

Callogobius dori – Dor 1984: 241; Goren *et al*. 1991: 299; Golani & Bogorodsky 2010: 46.

Diagnosis. *Callogobius dori* is distinguished from congeners by the following combination of characters: interorbital pores B', D, E, F, G and H' present; preopercular canal absent; temporal canal absent; dorsal fin VI+I,9; anal fin I,7; scales in lateral series 24–26; body tan to dark brown with narrow, dark longitudinal stripes; a large diffuse black spot dorsally in caudal fin.

Brief description. Moderately stout-bodied with elongate, broadly rounded, caudal fin > 40% SL in length. Scales large, deciduous, cycloid anteriorly, ctenoid from first spine of second dorsal fin to caudal-fin base, scales in lateral series 24–26. Dorsal-fin rays usually VI+I,9, anal-fin rays usually I,7, pectoral-fin rays 17–18, pelvic fins fully united with moderate frenum. Anterior nostril longer than posterior nostril. Head pores present with interorbital canal normally containing pores B', D, E, F, G and H', preopercular and temporal canals absent. Preopercular papillae row (Row 20) continuous with transverse opercular row (Row 21), more than 10 transverse mandibular papillae rows (Row 16) on each side.

Head, body and fins tan to brown. About seven or eight narrow, dark, longitudinal stripes usually visible on body. First dorsal and pectoral fins dark. Our specimens very faded, unable to discern whether or not vertical bars or head markings present. Dark spot as large as eye on upper part of caudal fin often present, depending on the condition of the specimen. Colouration in preservation similar.

Distribution and habitat. Western Indian Ocean and Red Sea. *Callogobius dori* specimens have been collected from the base of coral patches on silty sand of a closed lagoon, depth 5–7 m, although one collection reached 21–27 m.

Remarks. In the Red Sea, *C. dori* is most likely to be confused with *C. amikami* and *C. pilosimentum*. *Callogobius dori* shares a similar body shape and usually dark colouration with *C. pilosimentum*; it differs from the latter in lacking preopercular and temporal canals (vs. present), dorsal-fin spines not prolonged (vs. dorsal-fin spines prolonged, the second spine occasionally as a short filament), caudal fin > 40% SL in length (vs. < 40% SL), and more than 10 transverse mandibular papillae rows on each side (vs. 4). *Callogobius dori* shares a similar body shape and proportions with *C. amikami*; it differs from the latter in having second dorsal- and anal-fin ray counts of I,9 and I,7 respectively (vs. I,10 and I,8 respectively in holotype of *C. amikami*) and in colour pattern (cf. Figs. 3, 5).

McKinney (1980) in an unpublished Master's thesis refers to this species as *Callogobius* new species B. One lot of *C. dori* examined by McKinney (USNM 220030, Red Sea, Gulf of Aqaba, Bay at El Himeira, 4 specimens) was labeled as "*C. aquilus*"; this name was never published.

Callogobius dori has been considered a Red Sea endemic, but we have located three specimens from the Seychelles (USNM 385746, Amirante Islands, St. Joseph Atoll, south of Ressource Island, 0–4 m, 7 March 1964), considerably expanding the known range of this species and suggesting it might be found elsewhere in the Western Indian Ocean.

Representative Red Sea material (24 specimens, 15.8–35.5 mm SL)**. Egypt**: HUJ 11092, male, 28.1 mm SL; ROM 43205, 1 male and 1 female, 17.0–20.5 mm SL; USNM 220030, 2 males, 2 females, and 1 specimen cleared and stained, 15.8–24.0 mm SL; USNM 220095, female?, 19.2 mm SL; USNM 220098, male, 28.7 mm SL; USNM 220929, 1 male and 2 females, 18.4–21.5 mm SL; **Eritrea**: USNM 220099, female, 24.0 mm SL; **Saudi Arabia**, Farasan Island: KAUMM 378 (KAU12-318), female, 23.9 mm SL, base of fringing reef of small island, 7 m, coll. S.V. Bogorodsky & T.J. Alpermann, 22 February 2012; SMF 35761 (KAU12-219), male, 24.6 mm SL, isolated coral patch of lagoon, 3–5 m, coll. S.V. Bogorodsky & T.J. Alpermann, 20 February 2012; SMF 35762, male, 23.8 mm SL (Figure 7.5), collected with SMF 35761; **Sudan**: BMNH 1978.9.8.7, holotype, male, 33.5 mm SL; BMNH 1978.9.8.8-11, paratypes, 3 males and 1 female, 27.5–35.5 mm SL; BPBM 20387, male, 26.8 mm SL.

FIGURE 7.5 *Callogobius dori* Goren, live colouration, SMF 35762, male, 23.8 mm SL, Farasan Island, Saudi Arabia. Photo by S. Bogordsky.

Callogobius flavobrunneus (Smith 1958)

(Figure 7.6)

Mucogobius flavobrunneus Smith 1958: 145 (Pinda, Mozambique; holotype SAIAB 211).

Callogobius flavobrunneus – Goren 1980: 214; Dor 1984: 241; Goren *et al*. 1991: 300; Goren & Dor 1994: 63; Golani & Bogorodsky 2010: 46.

Diagnosis. *Callogobius flavobrunneus* is distinguished from congeners by the following combination of characters: interorbital pores present; preopercular canal absent; temporal canal absent; scales in lateral series 34–40; scales ctenoid posteriorly on body from below first spine of the second dorsal fin; preopercular papillae row (Row 20) not continuous with transverse opercular row (Row 21); pectoral fin densely pigmented medially

Brief description. Moderately stout-bodied with rounded caudal fin < 40% SL in length. Scales medium-sized, cycloid anteriorly, ctenoid posteriorly on body from below first spine of second dorsal fin to the caudal-fin base (exceptionally long ctenii on caudal peduncle scales), scales in lateral series 34–40. Dorsal-fin rays VI+I,9–10 (rarely 10), anal-fin rays I,7–8 (usually 8), pectoral-fin rays 15–17, pelvic fins separate (or with very short connecting membrane) with fifth ray significantly shorter than fourth (only about three-fourths of length) and frenum absent. Anterior nostril longer than posterior nostril. Head pores present with interorbital canal normally containing pores B’, D, E, F, G, and H’ (rarely containing pore C), preopercular and temporal canals absent. Preopercular papillae row (Row 20) not continuous with transverse opercular row (Row 21), more than 10 transverse mandibular papillae rows (Row 16) on each side.

Head, body and fins densely mottled brown (sometimes pale and lightly mottled). Depending on intensity of mottling, up to four broad, diffuse, dark brown bars, frequently two being more obvious, one below first dorsal fin and one obliquely below second dorsal fin. Base of pectoral-fin rays darkly marked with a vertical bar, connecting anteriorly to a dark pectoral-fin base, resulting in an H or sideways T mark. First dorsal fin with irregular, dark basal spot. Caudal fin brown with vertical rows of white speckles, margin of fin usually pale. Colouration in preservation similar to colour in life, although generally paler and barring more distinct.

Distribution and habitat. Widespread in the Indo-West Pacific. In the Red Sea, often found under stones or at the base of coral heads in fringing seaward reefs, depth 3–15 m.

Remarks. In the Red Sea, *C. flavobrunneus*, *C. sclateri*, and *C. clarki* are frequently confused, due to similarly-shaped moderately stout bodies, and colour pattern of four wide bars. *Callogobius flavobrunneus* differs from *C. clarki* in having head pores in specimens at least 14 mm SL (vs. absent in specimens of any size), ctenoid scales from the origin of the second dorsal fin (vs. only on caudal peduncle), and pelvic-fin morphology (frenum absent and membrane uniting medial rays minute or absent vs. frenum present and fins united over most of length medial ray). *Callogobius flavobrunneus* differs from *C. sclateri* in having higher lateral series scale counts (34–40 vs. 27–32), fifth pelvic-fin ray significantly shorter than fourth (about three-fourths length of fourth ray vs. subequal), and pectoral-fin colour pattern (medial dark markings vs. dark upper edge or diffuse vertical bands). *Callogobius flavobrunneus* differs from *C.* sp. A in having higher lateral series scale counts (34–40 vs. 22–25), and pelvic fins with connecting membrane very short or absent (fins separate vs. united along most of length of medial rays).

Representative Red Sea material (5 specimens, 14.3–41.3 mm SL)**. Egypt**: HUJ 11564, male, 24.9 mm SL; USNM 298438, male, 31.8 mm SL; **Eritrea**: USNM 297159, female, 41.3 mm SL; USNM 300014, female, 14.3 mm SL; **Saudi Arabia**: SMF 35771 (KAU13-211), female, 27.3 mm SL, Saudi Arabia, Al Wajh bank, seaward slope of unnamed island, sediment with coral patches, 3–5 m, coll. S.V. Bogorodsky & T.J. Alpermann, 12 June 2013.

FIGURE 7.6 *Callogobius flavobrunneus* (Smith): **A.** Fresh colouration, uncatalogued, 36.0 mm SL, Shams Alam, southern Egypt; **B.** Preserved specimen, SMF 35771, female, 27.3 mm SL, Al Wajh, bank, Saudi Arabia. Photos by S. Bogordsky (A), R. Mooi (B).

Callogobius sclateri (Steindachner 1879)

(Figure 7.7A)

Eleotris sclateri Steindachner 1879: 157 (Society Islands; holotype NMW 30901).

Diagnosis. *Callogobius sclateri* is distinguished from congeners by the following combination of characters: interorbital pores present; preopercular canal absent; temporal canal absent; scales in lateral series 27–32; pelvic fins separate or with only a minute basal membrane, without frenum and with fifth ray subequal to fourth; preopercular papillae row (Row 20) not continuous with transverse opercular row (Row 21).

Brief description. Moderately stout-bodied with rounded caudal fin < 40% SL in length. Scales medium-sized, cycloid anteriorly, ctenoid from the first to third spine of the first dorsal fin to the caudal-fin base (exceptionally long ctenii on caudal peduncle scales), scales in lateral series 27–32. Dorsal-fin rays VI+I,9, anal-fin rays I,7; pelvic fins separate or joined by a minute basal membrane, fifth ray just slightly shorter or about equal to length of fourth and frenum absent. Anterior nostril slightly longer than posterior nostril. Head pores present with interorbital canal normally containing pores B’, C, D, E, F, G and H’ (pore C sometimes absent), preopercular and temporal canals absent. Preopercular papillae row (Row 20) not continuous with transverse opercular row (Row 21), more than 10 transverse mandibular papillae rows (Row 16) on each side.

Head, body and fins usually with fine speckling, particularly in larger specimens. Head with dark brown bars extending from eye, one oblique anteriorly to upper lip, one posteriorly to preopercular margin, and one ventral just posterior to gape. Body with up to four brown bars, one from base of first dorsal fin extending from basal fin spot and narrowing to below outer third of pectoral fin, an oblique brown bar linking posterior bases of second dorsal and anal fins extending irregularly into second dorsal-fin membranes, a broad dark brown bar at base of caudal fin, and another short bar on lower half of body below origin of second dorsal fin. First dorsal fin mostly dark, second dorsal fin mottled or broadly striped. Pectoral fin with dark diagonal marking along upper margins in juveniles, which can become broader, more vertical, curved and/or diffuse in larger specimens. Caudal fin with faint, fine barring to dark. Colouration in preservation similar to live colouration.

Distribution and habitat. *Callogobius sclateri* is distributed in the Indo-West Pacific and the Red Sea. Habitat information not recorded in the Red Sea, although capture depth ranges from 0–16 m.

Remarks. In the Red Sea, *Callogobius sclateri*, *C. flavobrunneus*, and *C. clarki* are frequently confused due to similarly-shaped moderately stout bodies, and colour pattern of four wide bars. *Callogobius sclateri* differs from *C. clarki* by having head pores in specimens at least 14 mm SL (vs. none) and in having separate pelvic fins (vs. united at least two-thirds length). *Callogobius sclateri* shares the separate pelvic fins with *C. flavobrunneus*, but differs in having lower counts of scales in lateral series (27–32 vs. 34–40), fifth pelvic-fin ray subequal to fourth (vs. significantly shorter), and pectoral-fin colour pattern (dark upper edge or diffuse vertical bands vs. medial dark markings). *Callogobius sclateri* has a similar colour pattern to *C*. sp. A (Figure 7.7B), but the latter has partially united pelvic fins and fewer scales in lateral series (22-25 vs. 27–32). These differences were confirmed through examination of the holotype of *C. sclateri* (NMW 30901) by NRD and SVB.

Representative Red Sea material (4 specimens, 14.0–21.8 mm SL)**. Egypt**: USNM 298412, 1 male and 1 female, 14.0–20.5 mm SL; USNM 298419, sex uncertain, 1 specimen, 21.8 mm SL; USNM 296964, male, 21.4 mm SL.

FIGURE 7.7 A. *Callogobius sclateri* (Steindachner), preserved specimen, USNM 298419, female, 22.1 mm SL, Ras Burqa, Gulf of Aqaba, Egypt. **B.** *Callogobius* sp. A, live colouration, SMF 35772, juvenile, 14.5 mm SL, Yabua Island, Saudi Arabia. Photos by R. Mooi (A), S. Bogordsky (B).

DISCUSSION

Of the seven species of *Callogobius* identified from the Red Sea, at least two have been found nowhere else: *C. clarki* and *C. pilosimentum*. Two others were originally described from the Red Sea and considered endemic. *Callogobius amikami* is known only from the holotype (Figure 7.3A) and a possible juvenile specimen (Figure 7.3C), both from the Red Sea. There are two photographic records, the only certainly identifiable image being a Red Sea specimen (Figure 7.3B). The remaining photograph is of a tiny juvenile from Oman that has yet to attain characters that can confirm identification (Debelius 1993). If this latter record is of *C. amikami*, the species would lose its Red Sea endemic status. We found specimens of *C. dori* in a mixed lot with one *C. flavobrunneus* from the Seychelles of the Western Indian Ocean, removing it as a Red Sea endemic. The remaining *Callogobius* species found in the Red Sea are widespread across the Indo-Pacific; *C. sclateri* has not been previously reported from the Red Sea.

It is possible, even likely, that continued study of these species, particularly the widespread taxa, will reveal undiscovered diversity and geographic differentiation. Even so, the endemism of *Callogobius* in the Red Sea (28%) is higher than that reported for the region as a whole (13%; DiBattista *et al*. 2015), and is perhaps indicative of the tendency for demersal, egg-guarding species to have more restricted ranges. For example, *Pseudochromis* (Pseudochromidae) exhibits about 75% endemism in the Red Sea (Gill 2004; Golani & Bogorodsky 2010). Thorough sampling of *Callogobius* with techniques that result in intact specimens, colour photographs and genetic material, along with monographic treatment will provide a much more complete picture of the taxonomy and biogeography of this difficult group.

Key to seven *Callogobius* species of the Red Sea

(To be used for specimens at least 15 mm SL. Counts of scales in lateral series can vary by ± 2 depending on the user or the condition of the specimen)

1a. Chin with 4 transverse mandibular papillae rows (Row 16) on each side; temporal canal present with 2 pores (K', L') above operculum; scales in lateral series 21–25, usually 24; in intact adult specimens, anterior first dorsal-fin spines free of membranes for about one-quarter or more of spine length …………….. *Callogobius pilosimentum* n. sp. (Fig. 7.2)

1b. Chin with more than 10 transverse mandibular papillae rows (Row 16) on each side (the rows extending posteriorly to the lower edge of the preoperculum); temporal canal absent (no pores above operculum); scales in lateral series 22–41, more than 24 in most species; in intact adult specimens, anterior first dorsal-fin spines free of membranes for less than one-quarter spine length ..…………………………………………………...…….. 2

2a. Pelvic fin united and frenum weak to moderately well-developed; preopercular row (Row 20) continuous with transverse opercular papillae row (Row 21) ….……………………. 3

2b. Pelvic fins separate or partially united and frenum weak or absent; preopercular papillae row (Row 20) not continuous with transverse opercular row (Row 21) …...……………… 4

3a. Head with strongly contrasting markings including bars radiating from eye, body with dark bars and horizontal stripes; D VI+I,10; A I,8 ………..… *Callogobius amikami* (Fig. 7.3)

3b. Head, body and fins mostly dark with narrow dark horizontal stripes on body, dark vertical bars usually not obvious; D VI+I,9; A I,7 ..………..... *Callogobius dori* (Fig. 7.5)

4a. Scales in lateral series 33–41 ..…………..…………………………………..……...… 5

4b. Scales in lateral series 22–32 ………………………………………………………………. 6

5a. Head pores absent; scales mostly cycloid, except for a few on caudal peduncle; pelvic fins united about two-thirds of length of medial rays, frenum weak ………………………..
……………..……………………………………………… *Callogobius clarki* (Fig. 7.4)

5b. Head pores present; scales ctenoid on posterior half of body; pelvic fins separate or with a minute membrane, frenum absent …………….… *Callogobius flavobrunneus* (Fig. 7.6)

6a. Scales in lateral series 27–32; pelvic fins separate or with a minute basal membrane
…………………………………..…………….….... *Callogobius sclateri* (Fig. 7.7A)

6b. Scales in lateral series 22–25; pelvic fins united about two-thirds of the length of pelvic fin
…………………………………………………….…….… *Callogobius* sp. A (Fig. 7.7B)

Chapter Eight. Discussion and conclusions

At the beginning of my tenure as a PhD student, I outlined a plan to revise the entire genus *Callogobius*, construct phylogenetic trees using both morphology and DNA sequences, and use the phylogenetic trees to test biogeographic and/or character-related hypotheses. My plans changed slightly as my program progressed, in part due to unanticipated challenges and in part due to the nature of *Callogobius* itself. Despite these challenges, significant progress was made in all aspects of *Callogobius* taxonomy and systematics, providing a framework for future work. In this thesis, I accomplished the following objectives to better categorize the diversity within *Callogobius*:

1. Addressed alpha taxonomic problems, with the description of two new species, the redescription of an existing species, and the removal of a species erroneously placed in *Callogobius* to another gobiid genus, *Gobiopsis*.

2. Described morphological character systems to facilitate the work of other taxonomists and morphology-based phylogeneticists. In some cases, these characters were identified here for the first time.

3. Used morphology to infer phylogenetic relationships within *Callogobius*, and to identify hypothesized monophyletic subgroups within *Callogobius*. The identification of morphologically distinct species groups will allow for fast-tracking descriptions of new species.

4. Used DNA sequences to test the relationships inferred using morphology, demonstrating a very high degree of congruence between the morphological and molecular hypotheses. This indicates that significant phylogenetic signal exists in goby morphological characters, and morphology should not be ruled out as a source of meaningful data in goby phylogeny reconstruction at the intrageneric level.

5. Completed a review of all the known species in a geographically distinct region known for its diversity and high level of endemism, the Red Sea.

Why challenges remain in *Callogobius* alpha taxonomy

I am aware of at least 18 undescribed species (some of which I have plans to describe, others of which are under study by scientists at BLIP). I consider 12 *Callogobius* species to be of uncertain status, meaning I lack sufficient data to determine whether they are synonyms of existing species or valid species in their own right. There are several reasons why so many species are still of uncertain status. In some cases, holotype specimens have been lost or destroyed, and extant material from near the type locality is either lacking, or includes two or more very similar species making it difficult to determine which (if any) are appropriate for comparisons (or to designate as a neotype).

Callogobius are generally very small, most are fragile, and most species lack bright colours. The colours also change depending on the capture method. Y. Ikeda (pers. comm.) has determined that certain characters such as the colour pattern of the first dorsal fin are useful in distinguishing between species, yet the dorsal fin is usually either torn or pinched to the body in preserved specimens, so this character may not be determinable for the majority of museum specimens, including types. In order to use this character effectively for species identification, specimens need to be treated very carefully at capture and at the time of preservation. Many traditional characters such as scale counts are difficult to determine in *Callogobius* because so many species have either deciduous scales or extremely uneven scale rows. Non-traditional characters such as fin-ray branching patterns, cheek squamation, scale-type distribution, nostril length, stress colour patterns etc., require a great deal of time to explore for usefulness, are difficult to define, and are not recorded for previously described species, whose types may be lost or in poor condition. Nearly all species vary in colour ontogenetically and some vary geographically, making it difficult to determine which differences define species. Finally, some of the undescribed species are known from very few specimens, suggesting overall that the diversity within *Callogobius* is probably poorly represented in collections.

How my research contributes to *Callogobius* alpha taxonomy on a broader level

My research defines a naming system for papillae rows designed to facilitate identification of taxonomically meaningful differences between *Callogobius* species**.** Sensory papillae row patterns have been used as primary characters to define *Callogobius* and to distinguish different species within the genus. However, there has not been a standardized naming system to describe the papillae patterns used among different workers. Many authors simply illustrated the sensory system with or without brief description (including relatively recent authors such as Rangarajan 1968, Menon and Chatterjee 1974, McKinney and Lachner 1978a, McKinney and Lachner 1978a, McKinney and Lachner 1984, Goren 1978, Goren 1979b, Goren 1980, Goren et al. 1991). This approach, however, does not allow papillae row differences to be discussed in keys or species diagnoses. In the case of *C. bauchotae* (Goren 1979), the papillae rows were incorrectly illustrated suggesting a reduced sensory system unlike that of other *Callogobius* species, which obscured the relationship of this species with other *maculipinnis*-like species. Other authors (e.g. Miller and Wongrat 1979, Chen and Shao 2000, Chen et al. 2006) used a lettering system based on Sanzo (1911) and applied this to all gobies. I chose not to use a naming system for *Callogobius* that attempts to be universal to gobies because homology cannot be established between similarly-positioned rows among different genera. For my naming system (Delventhal & Mooi 2013, Chapter Four), I chose to employ a numbering system based on Akihito (1975, 1977) because of the clarity of its use, and its specificity to *Callogobius*. My naming system was created with accessibility to other researchers in mind, so that subtle differences in papillae patterns (such as relative row lengths) can be used to distinguish between similar species, and my species accounts and diagnoses begin to employ papillae row differences that had not previously been published to distinguish existing species (Delventhal & Mooi 2014, Chapter Five, Delventhal et al. 2016, Chapter Seven). My hope is that my system allows researchers to better describe papillae for taxonomic usage, and that in the future the homology of various papillae rows may be tested using a variety of means such as examination of innervations patterns and/or development.

My research defines three large monophyletic groups within *Callogobius* that are easily distinguishable - two by both external anatomy and osteology (*maculipinnis* and *hasseltii* group), and one by osteology (*sclateri* group). All three of these groups are supported by molecular phylogenetics. I identified two described and a number of undescribed species as belonging to a non-monophletic assemblage of which at least some members appear to be basal to the *sclateri* group. For an unwieldy genus with at least 65 species (a third or more of which are undescribed), this has direct application not only for understanding species diversity and evolution but also for determining which species need to be emphasized as comparisons in new species descriptions. An example of this application has been with the relatively recent new species discovery, *Callogobius* sp. 20, which was brought to my attention by its original collector, Jeff Williams (USNM). This species is small and non-descript, but it shares several characters found only among *hasseltii* group species, including cycloid scales and an elongate caudal fin with a black spot on the upper edge. I obtained permission to clear and stain a specimen to add it to the morphological analyses, and the relationship to other *hasseltii* group members received further support based on osteology. Because I understand which species are most likely to be similar to *C*. sp. 20, I have been able to fast-track the species description.

FIGURE 8.1 *Callogobius* sp. 20, an undescribed species of *Callogobius* in the *hasseltii* group used in the morphology-based analysis. Photo by J. Williams.

The evolution of small size and pore loss in *Callogobius*

Small body size and reductive features are common among gobies (Thacker 2003, 2011, Tornabene et al. 2016) and believed to have evolved independently in multiple lineages. At least 9 miniature (maximum adult size rarely exceeding 30 mm SL) and 5 poreless *Callogobius* species are known (Tables 8.1- 8.2), making them an interesting group to test whether reductive characters can evolve multiple times within a genus. Only four miniature species (*C. hastatus*, *C.* SK sp.7, *C.* SK sp.8, and *C. crassus*) and three species lacking headpores (*C. hastatus*, *C.* SK sp.8, and *C. crassus*) were sampled as part of the molecular portion of my study. All of these species were placed in the *hasseltii* group but in two separate lineages (Figure 3.1, Chapter Three). One lineage includes *C. crassus*, *C*. SK sp.7 and *C*. SK sp.8; all members of this lineage are miniature and have unusually broad papillae ridges (personal observation). A second lineage contains only one miniature poreless species (*C. hastatus*) but also two large, pored species (*C. tanegasimae*, *C.* SK sp. 1). Compared to other *Callogobius* species, members of this clade are all relatively elongate and slender, including *C. hastatus*. Three additional species lacking headpores are known, *C. clarki*, *C. winterbottomi*, and *C.* ND sp. 2. *Callogobius clarki* was found to be in the *sclateri* group in the morphological analysis by Delventhal & Mooi (unpublished, Chapter Two; Fig. 2.14-2.16, Chapter Three), and *C. winterbottomi* was determined to be either placed in the *sclateri* or *tutuilae* group based on examination of external characters. Although these species were not sampled in the molecular study, the monophyly of the *sclateri* group is well-supported in each study, suggesting that the poreless condition has evolved at least three times in *Callogobius*. Miniature *Callogobius* species occur in the *hasseltii* and *tutuilae* groups suggesting that small body size and the absence of head pores have each evolved independently (or have been secondarily lost) several times within *Callogobius*.

Tornabene et al. (2016), in a study of a sub-group of seven-spined gobies (gobiines not thought to be closely related to *Callogobius*), also found that the presence or absence of head pores and canals was not correlated with relationships as determined by molecular sequence analyses. This is in contrast to several other morphological characters that were correlated with hypothesized relationships (including pelvic-fin fusion and ray branching, specific papillae pattern, the presence of modified basicaudal scales, and anal-fin pterygiophore insertion) (Tornabene et al. 2016). This indicates that, although reductive characters my indeed be problematic, non-reductive characters found in taxa known for reductive features may be present and carry significant phylogenetic signal.

Thacker (2003) pointed out the benefits of using molecular sequence data for resolving the phylogenetic relationships of gobies, because they are independent of the reduction that can confound morphological character analysis. However, Tornabene et al. (2016) demonstrated that a number of gobioid morphological characters, even if highly variable, do in fact contain significant phylogenetic signal. My study lends additional support to the hypothesis that morphologically-based phylogenetic study within gobies can indeed be viable, and show significant congruence with molecular results. Although morphological reduction is hypothesized to be found independently in several lineages within *Callogobius*, most of the characters used in my study were not reductive and many were previously unreported (such as the frontal expansion in the orbit and mesethmoid morphology). Thus, my recommendation to gobioid morphological phylogeneticists is to look beyond obvious reductive characters and emply novel morphological features not previously surveyed.

Table 8.1 Dwarf species of *Callogobius* (adult size usually 30 mm SL or less), with their species group assignment based on Delventhal & Mooi (unpublished). Undescribed species are identified according to ND numbers (which refer to my personal ordering system for unidentified species), but where applicable SK numbers are also included (and refer to the BLIP ordering system for unidentified species). In the text, SK numbers are used, except for C. sp. 20, which does not have an SK number.

Dwarf species	Species group	Sampled
crassus	*hasseltii*	molecular
dori	*hasseltii*	morphological
hastatus	*hasseltii*	morphological, molecular
sheni	*hasseltii*	Not sampled
ND sp. 4	*tutuilae*	Not sampled
ND sp. 5 (SK sp. 7)	*hasseltii*	molecular
ND sp. 12 (SK sp. 8)	*hasseltii*	molecular
ND sp. 15	*hasseltii*	Not sampled
ND sp. 20	*hasseltii*	morphological

Table 8.2 Poreless species of *Callogobius*, with their species group assignment based on Delventhal & Mooi (unpublished).

Poreless species	Species group	Sampled
clarki	*sclateri*	morphological
crassus	*hasseltii*	molecular
hastatus	*hasseltii*	morphological, molecular
winterbottomi	*sclateri*	Not sampled
ND sp. 2	*hasseltii*	Not sampled
ND sp. 12 (SK sp. 8)	*hasseltii*	molecular

Conflict between morphological and molecular analyses

Although my molecular and morphological-based phylogenetic hypotheses show a high degree of concordance, a point of conflict does exist; in the morphological hypothesis the *maculipinnis* group is placed as sister to the remaining *Callogobius* whereas the molecular hypothesis places the *hasseltii* group sister to the remaining species. In Chapter Three, I discuss whether morphological characters exist that could support the molecular hypothesis, concluding that the discrepancy is most likely a result of outgroup selection in one or both analyses. I conclude that the discrepancy is a rooting issue possibly caused by too-distant outgroups in one (or both) of the analyses. McMahan et al. (2015) took the investigation of incongruent morphological and molecular phylogenies a step further. They investigated the discordance between morphological and molecular approaches to squamate relationships by mapping molecular data onto a morphological-based topology. Surprisingly, they found that a larger number of unambiguous (unique and unreversed) molecular apomorphies supported the morphological hypothesis and suggested that the problem of incongruence between analyses was not due to homoplasy in the morphological data but suggesting an inherent analytical problem in the molecular data, perhaps caused by distant outgroups. Distant outgroups are inevitable in many analyses because sister groups have not been identified for many taxa. For gobioids as a whole, monophyly is well supported but neither morphological (e.g. Johnson and Brothers 1993, Winterbottom 1993) nor molecular (e.g. Thacker & Hardman 2005, Thacker 2009) analyses have been consistent in their identification of a sister taxon, although numerous candidates have been proposed. A similar situation is true for *Callogobius* (see Chapter Three for a review). Although Harrington et al. (2016) argued that McMahan et al.'s study suffers from serious methodological shortcomings, I am intrigued by the possibility of using a morphological scaffold method in the future to explore discrepancies between morphological and molecular hypotheses in my own research. However, the congruence between the morphological and molecular hypotheses presented in this thesis is much more striking than any conflict.

References

Agorreta, A. & L. Rüber. 2012. A standardized reanalysis of molecular phylogenetic hypotheses of Gobioidei. *Systematics and Biodiversity*. 10(3): 375–390.

Agorreta, A., D. San Mauro, U. Schliewen, J.L. Van Tassel, M. Kovačić, R. Zardoya & L. Rüber. 2013. Molecular phylogenetics of Gobioidei and phylogenetic placement of European gobies. *Molecular Phylegenetics and Evolution*. 69(3): 619–633.

Akaike, H., 1973. Information theory as an extension of the maximum likelihood principle. In: Petrov, B.N., Csaki, F. (Eds.), *Second international symposium of information theory*. AkademiaiKiado, Budapest, Hungary, pp. 267–281.

Akihito.1984. Suborder Gobioidei. *In*: Masuda, H., K. Amaoka, C. Araga, T. Uyeno, & T. Yoshino (eds.). *The Fishes of the Japanese Archipelago*. Tokai University Press, Tokyo, pp. 236–289.

Akihito, A. Iwata, K. Sakamoto, & Y. Ikeda.1993a. Suborder Gobioidei. *In*: Nakabo, T. (ed.), *Fishes of Japan with pictorial keys to the species*. Tokai University Press, Tokyo, pp. 997–1087. (In Japanese.)

Akihito, K. Sakamoto, A. Iwata, & Y. Ikeda. 1993b. Cephalic sensory organs of the gobiod fishes. *In*: Nakabo, T. (ed.), *Fishes of Japan with pictorial keys to the species*. Tokai University Press, Tokyo, pp. 1088–1116. (In Japanese.)

Akihito, Prince & K.Meguro. 1975. On a goby *Callogobius okinawae. Japanese Journal of Ichthyology,* 22(2): 112–116. (In Japanese.)

Akihito, Prince & K. Meguro. 1977. Five Species of the Genus *Callogobius* found in Japan and their relationships. *Japanese Journal of Ichythyology.* 24(2): 113–127. (In Japanese.)

Allen, G.R. & M. Adrim. 2003. Coral reef fishes of Indonesia. *Zoological Studies,* 42(1): 1–72.

Allen, G.R. & M.V. Erdmann. 2012. *Reef fishes of the East Indies. Volumes I–III.* v. I: x + 1–424 + end note; v. II: 425–855; v. III: preface, map, contents and 857–1260; including Appendix 1 (new species descriptions) and Appendix II (addendum). Tropical Reef Research, Perth, Australia.

Betancur-R. R, R.E. Broughton, E.O. Wiley EO, K. Carpenter, J.A. López, C. Li, N.I. Holcroft, D. Arcila, M. Sanciangco, J.C. Cureton II, F. Zhang, T. Buser, M.A. Campbell, Ballesteros JA, Roa-Varon A, Willis S, Borden WC, Rowley T, Reneau PC, Hough DJ, G. Lu, T. Grande, G. Arratia, and G. Ortí. 2013. The Tree of Life and a New Classification of Bony Fishes. *PLOS Currents Tree of Life*. 1-41.

Birdsong, R.S, E.O. Murdy & F.L. Pezold. 1988. A study of the vertebral column and median fin osteology in gobioid fishes with comments on gobioid relationships. *Bulletin of Marine Science.* 42(2): 174–214.

Bleeker, P. 1851. Over eenige nieuwe soorten van Blennioïden en Gobioïden van den Indischen Archipel. *Natuurkundig Tijdschrift voor Nederlandsch Indië. 1(3): 236-258*

Bleeker, P. 1862–1877. *Atlas Ichthyologique de Indes Orientales Néerlandaises, publié sous les auspices du Gouvernement colonial Néerlandaises.* Tomes I–IX. Amsterdam.

Bleeker, P. 1874. Esquisse d'un système naturel des Gobioïdes. *Archives Néerlandaises de Sciences Exacte et Naturelles,* 9: 289–331.

Bleeker, P. 1983. *Atlas Ichthyologique de Indes Orientales Nééȓlandaises*. Plates originally prepared for planned tomes XI–XIV. Smithsonian Institution Press, Washington.1–22. Pls. 421–575.

Bleeker, P. (Unpublished) *Callogobius liolepis* Blkr. Page 258 in Manuscript for Vol. XI of the *Atlas Ichthyologique de Indes Orientales Nééȓlandaises*. In the archives of RMNH.

Borges, R., C. Faria, F. Gil & E.J. Goncalves. 2011. Early development of gobies. *In*: Patzner, R.A., J.L. Van Tassell, M. Kovačić. and Kapoor, B.G. (eds.), *The Biology of Gobies.* CRC Press, Taylor and Francis Group, Science Publishers, Enfield, New Hampshire, pp. 403–462.

Boeseman, M., in Bleeker, P. 1983. *Atlas Ichthyologique des Indes Orientales Neerlandaises. Plates for Volumes XI–XIV*. Smithsonian Institution Press, Washington D.C.

Böhlke, E.B. 1984. Catalog of type specimens in the ichthyological collection of the Academy of Natural Sciences of Philadelphia. *Special Publication, Academy of Natural Sciences of Philadelphia*. No. 14, i–viii + 1–216.

Castresana, J., 2000. Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Molecular Biology and Evolution.* 17(4): 540–552.

Chakrabarty, P., M.P. Davis & J.S. Sparks. 2012. The first record of a trans-oceanic sister-group relationship between obligate vertebrate Troglobites. *PLoS ONE*. 7(8): e44083.

Chen, I-S., J.-P. Chen, & L.-S. Fang. 2006. A new marine goby of genus *Callogobius* (Teleostei: Gobiidae) from Taiwan. *Ichthyological Research*. 53(3): 228–232.

Chen, J.P. & K.T. Shao. 2000. *Callogobius nigromarginatus*, a new species of Goby (Pisces: Gobiidae) from Taiwan. *Bulletin of Marine Science.* 66(2): 457–466.

Chen, J.T.F. & M.J., Yu. 1986. *A Synopsis of the Vertebrates of Taiwan*. Commercial Books Co., Taipei, Taiwan. 1092 pp. (In Chinese.)

Coombs, S., J. Janssen, & J.F. Webb. 1988. Diversity of lateral line systems: evolutionary and functional considerations. *In*: Atema, J., R.R. Fay, A.N. Popper, and W.N. Tavolga (eds.), *Sensory Biology of Aquatic Animals*. Springer-Verlag, Berlin, Germany, pp. 553–593.

Debelius, H. 1993. *Indian Ocean Tropical Fish Guide*.Aquaprint, Neu Isenberg. Germany. 321 pp.

Delventhal, N.R., & R.D. Mooi. 2013. *Callogobius winterbottomi,* a new species of goby (Teleostei: Gobiidae) from the Western Indian Ocean. *Zootaxa.* 3630(1):155–164.

Delventhal, N.R. & R.D. Mooi. 2014. Redescription of *Callogobius clarki* (Goren) (Teleostei: Gobiidae), not a synonym of *C. bifasciatus* (Smith). *Copeia*. 2014(1): 143–148.

Delventhal, N.R. & R.D. Mooi. 2014. *Callogobius liolepis* Bleeker, a senior synonym of *Gobiopsis aporia* Lachner and McKinney (Teleostei: Gobiidae: *Gobiopsis*). *Zootaxa*. 3764(5): 571-580.

Delventhal, N.R., R.D. Mooi, S.V. Bogorodsky & A.O. Mal. 2016. A review of the *Callogobius* (Teleostei: Gobiidae) from the Red Sea with the description of a new species. *Zootaxa*. 4179(2): 225-243.

DiBattista, J.D., M.B. Roberts, M.B., J. Bouwmeester, *et al*. 2015. A review of contemporary patterns of endemism for shallow water reef fauna in the Red Sea. *Journal of Biogeography*, 43(3): 423–439.

Dor, M. 1984. *Checklist of the Fishes of the Red Sea*. CLOFRES. Israel Academy of Sciences and Humanities. Jerusalem.

Eschmeyer, W.N. (ed.) 2012. *Catalog of Fishes: Species, References*. California Academy of Sciences, San Francisco. (http://research.calacademy.org/research/ichthyology/catalog/fishcatmain.asp). Electronic version accessed May 2012.

Eschmeyer, W.N. (ed.) 2013. *Catalog of Fishes: Genera, Species, References*. California Academy of Sciences, San Francisco. (http://research.calacademy.org/research/ichthyology/catalog/fishcatmain.asp). Electronic version accessed 2 Aug 2013.

Eschmeyer, W.N. & R. Fricke (eds.). 2016. *Catalog of Fishes: Genera, Species, References.* California Academy of Sciences, San Francisco. (http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp). Electronic version accessed 5 January 2016.

Eschmeyer, W.N., R. Fricke, & R. van der Laan (eds). 2017. *Catalog of Fishes: Genera, Species, References.* California Academy of Sciences, San Francisco. (http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp). Electronic version accessed June 2017.

Fowler, H.W. 1918. New and little-known fishes from the Philippine Islands. *Proceedings of the Academy of Natural Sciences of Philadelphia*. 70: 2–71.

Fowler, H.W. 1946. A collection of fishes obtained in the Riu Kiu Islands by Captain Ernest R. Tinkham, A.*U.S. Proceedings of the Academy of Natural Sciences of Philadelphia*. 98: 123-218.

Fowler, H.W. 1949. The fishes of Oceania – supplement 3. *Memoirs of the Bernice P. Bishop Museum*. 12(2): 37–186. (from 1967 authorized reprint by Johnson Reprint Corp., NewYork)

Felsenstein, J. 1981. Evolutionary trees from DNA sequences: a maximum likelihood approach. *Journal of Molecular Evolution.* 17(6): 368–376.

Fricke, R. & W.N. Eschmeyer. 2012. *Guide to Fish Collections*. California Academy of Sciences, San Francisco. Available from: http://researcharchive.calacademy.org/research/Ichthyology/catalog/collections.asp. Electronic version accessed 31 May 2012.

Fricke, R. & W.N. Eschmeyer. 2013. *Guide to Fish Collections*. California Academy of Sciences, San Francisco. Available from: http://research.calacademy.org/research/ichthyology/catalog/collections.asp. Electronic version accessed 2 Aug 2013.

Fricke, R. & W.N. Eschmeyer. 2015. *Guide to Fish Collections*. California Academy of Sciences, San Francisco. Available from: http://researcharchive.calacademy.org/research/ichthyology/catalog/collections.asp Electronic version accessed 10 Sept 2015.

Fricke, R. & W.N. Eschmeyer. 2017. *Guide to Fish Collections*. California Academy of Sciences, San Francisco. Available from: http://researcharchive.calacademy.org/research/ichthyology/catalog/collections.asp Electronic version accessed June 2017.

Garcia-Cruz, J. & V. Sosa. 2006. Coding quantitative character data for phylogenetic analysis: a comparison of five methods. *Systematic Botany*. 31(2): 302–309.

Gill, A.C. 2004. Revision of the Indo-Pacific dottyback fish subfamily Pseudochrominae (Perciformes: Pseudochromidae). *Smithiana Monograph 1*. 1–213 (12 plates).

Gill, A.C. & R.D. Mooi. 2012. Thalasseleotrididae, new family of marine gobioid fishes from New Zealand and temperate Australia, with a revised definition of its sister taxon, the Gobiidae (Teleostei: Acanthomorpha). *Zootaxa*. 3266: 41–52.

Golani, D. 2006. An annotated list of types in the Hebrew University fish collection. *Haasiana: a newsletter of the biological collections of the Hebrew University*. 2006(3):20–40.

Golani, D. & S.V. Bogorodsky. 2010. The fishes of the Red Sea – reappraisal and updated checklist. *Zootaxa*. 2463: 1–135.

Gomon, M.F., J.C.M. Glover & R.H. Kuiter (eds). 1994. *The fishes of Australia's south coast. Flora and Fauna of South Australia Handbooks Committee.* State Printer, Adelaide. 992 pp.

Goren, M. 1978. A new gobiid genus and seven new species from Sinai coasts (Pisces: Gobiidae). *Senckenbergiana Biologica*. 59(3/4): 191–203.

Goren, M. 1979a. *Callogobius bauchotae* new species from Marshall Island (Gobiidae, Pisces). *Cybium 3e série. Bulletin de la Société Française d'Ichtyologie* No. 7: 41–44.

Goren, M. 1979b. The Gobiinae of the Red Sea (Pisces: Gobiidae). *Senckenbergiana Biologica*. 60(1/2):13–64.

Goren, M. 1980. Red Sea fishes assigned to the genus *Callogobius* Bleeker with a description of a new species (Teleostei: Gobiidae). *Israel Journal of Zoology*. 28: 209–217.

Goren, M. & M. Dor. 1994. *An Updated Checklist of the Fishes of the Red Sea. CLOFRES II.* The Israel Academy of Sciences and Humanities. Jerusalem. 120 pp.

Goren, M., A. Miroz & A. Baranes. 1991. *Callogobius amikami* a new species of goby (Gobiidae) from the Red Sea. *Cybium*. 15(4): 299–302.

Günther, A. 1872. Report on several collections of fishes recently obtained for the British Museum. *Proceedings of the Zoological Society of London.* 1871(3): 652-675.

Harrington, S.H. D.H. Leavitt, and T.W. Reeder. 2016. Squamate Phylogenetics, Molecular Branch Lengths, and Molecular Apomorphies: A Response to McMahan et al. *Copeia*: 104(3): 702–707.

Herre, A.W.C.T. 1927. Gobies of the Philippines and the China Sea. *Monographs, Bureau of Science Manila Monograph*. 23. 352 pp.

Herre, A.W.C.T. 1935. New fishes obtained by the Crane Pacific expedition. *Field Museum of Natural History, Publications,Zoölogical Series*. 18 (12): 383-438.

Herre, A.W.C.T. 1943. Notes on fishes in the Zoological Museum of Stanford University. XI.Two new genera and species. With key to the genera of gobies with vomerine teeth. *Proceedings of the Biological Society of Washington*. 56:91–95.

Herre, A.W.C.T. 1950. Two new gobies from the Philippines with notes on a third rare goby. *Proceedings of the Biological Society of Washington*. 63:73–76.

Herzenstein, S.M. 1896. Über einige neue und seltene Fische des Zoologischen Museums der Kaiserlichen Akademie der Wissenschaften. *Ezhegodnik, Zoologicheskago Muzeya Imperatorskoi Akademii Nauk*. 1(1): 1-14.

Hoese, D.F. 1986. Family No. 240: Gobiidae. In *Smiths' Sea Fishes*, M.M. Smith and P.C. Heemstra (eds.) J.L.B. Smith Institute of Ichthylology, Grahamstown. 774-807.

Hoese, D.F. & H.K. Larson. 2006. Gobiidae. *In*: Wells, A., D.F. Hoese, D.J. Bray, G.R. Allen, J.R. Paxton, and P.L.Beesley (eds.). *Zoological Catalogue of Australia, Volume 35. Fishes*. CSIRO Publishing, Collingwood, Australia, pp. 1612–1697.

Huelsenbeck, J.P., and F.R. Ronquist. 2001. MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* 17(8): 754–755.

Huelsenbeck, J.P., F.R. Ronquist, R. Nielsen, & J.P. Bollback. 2001. Bayesian inference of phylogeny and its impact on evolutionary biology. *Science* 294(5550): 2310–2314.

Hutchins, J.B. 2001. Checklist of the fishes of Western Australia. *Records of the Western Australian Museum Supplement.* 63: 9–50.

Ibarra, M. & D.J. Stewart. 1987. Catalogue of type specimens of Recent fishes in Field Museum of Natural History. *Fieldiana Zoology (New Series)*. 35: 1–112.

International Commission on Zoological Nomenclature. 1999. *International Code of Zoological Nomenclature. Fourth Ed*. International Trust for Zoological Nomenclature. On-line edition, http://iczn.org/code.

Jacob, J. and K. Rangarajan 1960. *Callogobius seshaiyai* the name proposed for the gobiid from the Vellar Estuary, Porto Novo. *Journal of the Zoological Society of India*.12(1): 20-21.

Johnson, G.D. & E.B. Brothers. 1993. *Schindleria*: a paedomorphic goby. *Bulletin of Marine Science*. 52(1): 441–471.

Jordan, D.S. & A. Seale. 1906. The fishes of Samoa. Description of the species found in the archipelago, with a provisional check-list of the fishes of Oceania. *Bulletin of the Bureau of Fisheries.* 25: 173–455.

Jones, S. & M. Kumaran. 1970. New records of fishes from the seas around India – Part VI. *Journal of the Marine Biological Association of India*. 10(2): 321–331.

Katoh, K., K. Misawa, K. Kuma & T Miyata. 2002. MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Research* 30(14): 3059–3066.

Katoh, K., & H. Toh. 2008. Recent developments in the MAFFT multiple sequence alignment program. *Briefings in Bioinformatics.* 9(4): 286–298.

Kocher, T.D., W.K. Thomas, A. Meyer, S.V. Edwards, S. Pääbo, F.X. Villablanca & A. C. Wilson. 1989. Dynamics of mitochondrial DNA evolution in animals: amplification and sequencing with conserved primers. *Proeedings of the National Academy of Sciences*. 86(16): 6196–6200.

Koumans, F.P. 1931. *A preliminary revision of the genera of the gobioid fishes with united ventral fins.* Drukkerj Imperator N.V., Lisse. 1–174.

Koumans, F.P. 1932. Notes on gobioid fishes (1-5). *Zoologische Mededelingen*. 15: 1–16.

Koumans, F.P. 1940. Results of a Reexamination of Types and Specimens of Gobioid Fishes, with Notes on the Fish Fauna of the Surroundings of Batavia. *Zoologische Mededeelingen.* 22: 121–210.

Koumans, F.P. 1953a. Biological Results of the Snellius Expedition, XVI: The Pisces and Leptocardii of the Snellius Expedition. *Temminckia.* 9: 177–275.

Koumans, F.P. 1953b. Gobioidea. In: Weber and de Beaufort. *The Fishes of the Indo-Australian Archipelago*. E. J. Brill, Leiden. 10: 1–423.

Lachner, E.A & J.F. McKinney. 1974. *Barbuligobius boehlkei*, a new Indo-Pacific genus and and species of Gobiidae (Pisces), with notes on the genera *Callogobius* and *Pipidonia. Copeia.* 1974(4): 869–879.

Lachner, E.A. & J.F. McKinney. 1978. A revision of the Indo-Pacific fish genus *Gobiopsis* with descriptions of four new species (Pisces: Gobiidae). *Smithsonian Contributions to Zoology*. No. 262. 52 pp.

Larson, H.K. & D.F. Hoese. 1997. A new species of *Egglestonichthys* (Teleostei: Gobiidae) from the Indo-West Pacific, with discussion of the species of the genus. *The Beagle, Records of the Museums and Art Galleries of the Northern Territory*. 13: 45–51.

Larson, H.K. & E.O. Murdy. 2001. Families Eleotridae, Gobiidae. In: Carpenter & Niem 2001. *Species identification guide for fishery purposes*. *Bony fishes part 4* v. 6: 3574–3603.

Lawing, A.M., J. M. Meik, W.E. Schargel & N. MacLeod. 2008. Coding Meristic Characters for Phylogenetic Analysis: A Comparison of Step-Matrix Gap-Weighting and Generalized Frequency Coding. *Systematic Biology*. 57 (1): 167–173.

Li, C., G. Ortí, G. Zhang, & G. Lu. 2007. A practical approach to phylogenomics: the phylogeny of ray-finned fish (Actinopterygii) as a case study. *BMC Evolutionary Biology.* 7: 7–44.

López, J.A., W.-J. Chen & G. Ortí. 2004. Esociform phylogeny. *Copeia.* 2004(3): 449–464.

Maddison, D.R. & W.P. Maddison. 2005. MacClade v.4.08. Sinauer Associates, Sunderland, Massachusetts.

Mazzoldi, C., R.A. Patzner & M.B. Rasotto. 2011. Morphological organization and variability of the reproductive apparatus in gobies. *In*: Patzner, R.A., J.L. Van Tassell, M. Kovačić. and Kapoor, B.G. (eds.), *The Biology of Gobies.* CRC Press, Taylor and Francis Group, Science Publishers, Enfield, New Hampshire, pp. 367–402.

McKinney, J.F. 1980. Morphological variation among 14 species of *Callogobius* Bleeker (Pisces: Gobiidae). Old Dominion University, Norfolk, Virginia. (Unpublished Master's thesis.)

McKinney, J.F. & E.A. Lachner. 1978a. Two new species of *Callogobius* from Indo-Pacific waters (Teleostei: Gobiidae). *Proceedings of the Biological Society of Washington*. 91(1):203–215.

McKinney, J.F. & E.A. Lachner. 1978b. A new species of gobiid fish, *Callogobius stellatus*, from Flores Island, Indonesia (Teleostei: Gobiidae). *Proceedings of the Biological Society of Washington.* 91(3):715–723.

McKinney, J.F. & E.A. Lachner. 1984. *Callogobius crassus*, a new fish from the Indo-Pacific region (Teleostei: Gobiidae). *Proceedings of the Biological Society of Washington.* 97(3): 627–631.

McMahan, C. D., L. R. Freeborn, W. C. Wheeler, & B. I. Crother. 2015. Forked tongues revisited: molecular apo-morphies support morphological hypotheses of squamate evolution. *Copeia.* 103: 525–529.

Menon, A.G.K. & T.K. Chatterjee. 1974. *Callogobius andamanensis*, a new gobioid fish from Curlow Island, Middle Andamans, with key to species of *Callogobius* of the seas of India and Malay Archipelago. *Current Science*. 43(4): 126–128.

Menon, A.G.K. and T.K. Chatterjee. 1976. *Callogobius trifasciatus*, a new gobioid fish from Mayabunder, Middle Andaman Island. *Mahasagar -- Bulletin of the National Institute of Oceanography*. 7(3-4): 205-207.

Miller, P.J. & P. Wongrat. 1979. A new goby (Teleostei: Gobiidae) from the South China Sea and its significance for gobioid classification. *Zoological Journal of the Linnean Society.* 67(3): 239–257.

Nelson, J.S. 2006. *Fishes of the World,* 4th ed. John Wiley & Sons, Hoboken, New Jersey. 601 pp.

Nelson, J.S., T.C. Grande & M.V.H. Wilson. 2016 *Fishes of the World,* 5th ed. John Wiley & Sons, Hoboken, New Jersey. 752 pp.

Neilson, M.E. & C.A. Stepien. 2009. Escape from the Ponto-Caspian: Evolution and biogeography of an endemic goby species flock (Benthophilinae: Gobiidae: Teleostei). *Molecular Phylogenetics and Evolution*. 52(1): 84–102.

Palumbi, S.R., A. Martin, S. Romano, W.O. MacMillan, L. Stice, & G. Grabowski. 1991. *The simple fool's guide to PCR*. Department of Zoology, University of Hawaii, Honolulu.

Pezold, F. 1993. Evidence for a monophyletic Gobiinae. *Copeia.* 1993(3): 634–643.

Por, F.D., H. Steinitz, I. Ferber & W. Aron. 1972. The biota of the Red Sea and the Eastern Mediterranean (1967–1972) a survey of the marine life of Israel and surroundings. *Israel Journal of Zoology*. 21(3-4): 459–523.

Posada, D., 2008. jModelTest: phylogenetic model averaging. *Molecular Biology and Evolution.* 25(7): 1253–1256.

Ramsay, E.P. & J.D. Ogilby. 1886. Descriptions of some new Australian fishes. *Proceedings of the Linnean Society of New South Wales (Series 2)*. 1(1): 4-7.

Randall, J.E. 1995. *Coastal Fishes of Oman*. Crawford House Publishing. Bathurst. 439 pp.

Randall, J.E. 1998. Zoogeography of shore fishes of the Indo-Pacific region. *Zoological Studies*. 37(4): 227–268.

Randall, J.E., N. Downing, L.J. McCarthy, B.E. Stanaland & A.B. Tarr**.** 1994. Fifty-one new records of fishes from the Arabian Gulf. *Fauna of Saudia Arabia*. 14: 220–258.

Randall, J.E. & K.K.P. Lim. 2000. A checklist of the fishes of the South China Sea. *The Raffles Bulletin of Zoology*. 8: 569–667.

Rangarajan, K. 1970. A new species of *Callogobius* (family Gobidae: Pisces) from Gulf of Mannar, India. *Journal of the Marine Biological Association of India*. 10(2): 347–353.

Reeves, J.H. 1992. Heterogeneity in the substitution process of amino acid sites of proteins coded for by mitochondrial DNA. *Journal of Molecular Evolution.* 35(1): 17–31.

Rodríguez, F., J.F. Oliver, A. Marín & J.R. Medina. 1990. The general stochastic model of nucleotide substitution. *Journal of Theoretical Biology.* 142(4): 485–501.

Ronquist, F., & J.P. Huelsenbeck. 2003. MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics.* 19(12): 1572–1574.

Rüber, L. & A. Agorreta. 2011. Molecular systematic of gobioid fishes. *In*: Patzner, R.A., J.L. Van Tassell, M. Kovačić. and Kapoor, B.G. (eds.), *The Biology of Gobies.* CRC Press, Taylor and Francis Group, Science Publishers, Enfield, New Hampshire, pp. 23-50.

Rüber, L., J.L.Van Tassell & R. Zardoya. 2003. Rapid speciation and ecological divergence in the American seven-spined gobies (Gobiidae, Gobiosomatini) inferred from a molecular phylogeny. *Evolution.* 57(7): 1584–1598.

Sabaj Perez, M.H. (ed.). 2010. *Standard symbolic codes for institutional resource collections in herpetology and ichthyology: an online reference. Version 2.0* (8 November 2010). American Society of Ichthyologists and Herpetologists, Washington, DC. Available at http://www.asih.org/ Electronic version accessed 31 May 2012.

Sabaj Perez, M.H. (ed.). 2013. *Standard symbolic codes for institutional resource collections in herpetology and ichthyology: an online reference*. Verson 4.0 (28 June 2013). American Society of Ichthyologists and Herpetologists, Washington, DC. Available at http://www.asih.org/ Electronic version accessed 21 May 2013.

Sabaj Perez, M.H. (ed.). 2014. *Standard symbolic codes for institutional resource collections in herpetology and ichthyology: an online reference*. *Version 5.0*. American Society of Ichthyologists and Herpetologists, Washington, DC. Available at http://www.asih.org/ Electronic version accessed 22 September 2014.

Sabaj M.H. 2016. *Standard symbolic codes for institutional resource collections in herpetology and ichthyology: an online reference. Version 6.5* (16 August 2016). American Society of Ichthyologists and Herpetologists, Washington, DC. Available at http://www.asih.org/ Electronic version accessed June 2017.

Sanzo, L. 1911. Distribution delle paille cutanee (organiciatiforme) e suo valore sistematico nei gobi. *Mitteilungen Zoologische Station zu Neapel*. 20: 249–328.

Saruwatari, T., J.A. López & T.W. Pietsch. 1997. Cyanine blue: a versatile and harmless stain for specimen observation. *Copeia.* 1997(4): 840–841.

Sauvage, H.-E. 1880. Description des Gobioïdes nouveaux ou peu connus de la collection du Muséum d'histoire naturelle. *Bulletin de la Société philomathique de Paris (7th Série).* 4: 40-58.

Seale, A. 1910. New species of Philippine fishes. *The Philippine Journal of Science*. 4(6): 491-543.

Shibukawa, K. 2010. *Gobiopsis namnas,* a new deep-dwelling goby (Teleostei: Perciformes: Gobiidae: Gobiinae) from Japan. *Bulletin of the National Museum of Nature and Science, Series A. Supplement*. 4:97–106.

Shibukawa, K., T. Peristiwady & S.R. Suharti. 2003. Gobiidae. *In*: Kimura, S.and K. Matsuura (eds.), *Fishes of Bitung, northern tip of Sulawesi, Indonesia*. Tokyo, pp. 175–194.

Smith, J.L.B. 1958. The fishes of the family Eleotridae in the western Indian Ocean. *Ichthyological Bulletin of the J.L.B. Smith Institute of Ichthyology*. 11: 137–163.

Smith, J.L.B. 1959**.** Gobioid fishes of the families Gobiidae, Periophthalmidae, Trypauchenidae, Taenioididae, and Kraemeriidae of the Western Indian Ocean. *Ichthyological Bulletin, Department of Ichthyology, Rhodes University*. 13: 185–225.

Snyder, J.O. 1908. Descriptions of eighteen new species and two new genera of fishes from Japan and the Riu Kiu Islands. *Proceedings of the United States National Museum*. 35 (1635): 93-111.

Stamatakis, A. 2006. RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22(21): 2688–2690.

Stamatakis, A., F. Blagojevic, D. Nikolopoulos, & C. Antonopoulos. 2007. Exploring new search algorithms and hardware for phylogenetics: RAxML meets the IBM Cell. *The Journal of VLSI Signal Processing*. 48(3): 271–286.

Steindachner, F. 1861. Beiträge zur Kenntniss der Gobioiden. *Sitzungsberichte der Adademie der Wissenschaften, Wien, Mathematische-naturwissenschaftliche Klasse*. 42(23): 283–292.

Steindachner, F. 1879. Ichthyologische Beiträge (VIII). *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften. Mathematisch-Naturwissenschaftliche Classe*. 80(1–2): 119–191, Pls. 1–3.

Swofford, D.L. 2002. PAUP*: phylogenetic analysis using parsimony (* and other methods). Version 4. Sunderland: Sinauer Associates.

Takagi, K. 1957. Descriptions of some new gobioid fishes of Japan, with a proposition on the sensory line system as a taxonomic appliance. *Journal of the Tokyo University of Fisheries*. 43(1): 97–126.

Takagi, K. 1963. Studies of the Gobioid Fishes on the Japanese Waters on the Comparative Morphology, Phylogeny, Taxonomy, Distribution and Bionomics. Tokyo University. (In Japanese, unpublished.) 273 pp.

Taylor, W.R. & G.C. Van Dyke. 1985. Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study. *Cybium*. 9(2): 107–119.

Thacker, C.E. 2003. Molecular phylogeny of the gobioid fishes (Teleostei: Perciformes: Gobioidei). *Molecular Phylogenetics and Evolution.* 2003(26): 354–368.

Thacker, C.E. 2009. Phylogeny of Gobioidei and placement within Acanthomorpha, with a new classification and investigation of diversification and character evolution. *Copeia*. 2009(1): 93–104.

Thacker, C. 2011. Systematics of Gobiidae. *In*: Patzner, R.A., J.L. Van Tassell, M. Kovačić. and Kapoor, B.G. (eds.), *The Biology of Gobies.* CRC Press, Taylor and Francis Group, Science Publishers, Enfield, New Hampshire, pp. 129–136.

Thacker, C.E. 2013. Phylogenetic placement of the European sand gobies in Gobionellidae and characterization of gobionellid lineages (Gobiiformes: Gobioidei). *Zootaxa*. 3619(3): 369–382.

Thacker, C.E. & M. A. Hardman. 2005. Molecular phylogenetics of basal gobioid fishes: Rhyacichthyidae, Odontobutidae, Xenisthmidae, Eleotridae (Teleostei: Perciformes: Gobioidei). *Molecular Phylogenetics and Evolution*. 37(3): 858–871.

Thacker, C.E. & D.M. Roje. 2011. Phylogeny of Gobiidae and identification of gobiid lineages. *Systematics and Biodiversity*. 9(4): 329-347.

Thacker, C.E., A.R. Thomson & D.M. Roje. 2011. Phylogeny and evolution of Indo-Pacific shrimp-associated gobies (Gobiiformes: Gobiidae). *Molecular Phylogenetics and Evolution*. 59: 168–176.

Tornabene, L., Y. Chen & F. Pezold. 2013. Gobies are deeply divided: phylogenetic evidence from nuclear DNA (Teleostei: Gobioidei: Gobiidae). *Systematics and Biodiversity*. 11(3): 345–361.

Tornabene, L., J.L. Van Tassell, R.G. Gilmore, D.R. Robertson, F. Young, Forrest and C.C. Baldwin. 2016. Molecular phylogeny, analysis of character evolution, and submersible collections enable a new classification of a diverse group of gobies (Teleostei: Gobiidae: *Nes* subgroup), including nine new species and four new genera. *Zoological Journal of the Linnean Society*. 177(4): 764–812.

Van Tassell, J.L., L. Tornabene & M.S. Taylor. 2011. A history of gobioid morphological systematics. *In*: Patzner, R.A., J.L. Van Tassell, M. Kovačić. and Kapoor, B.G. (eds.), *The Biology of Gobies.* CRC Press, Taylor and Francis Group, Science Publishers, Enfield, New Hampshire, pp. 3–22.

Watson, W. & H.J. Walker. 2004. The world's smallest vertebrate, *Schindleria brevipinguis*, a new paedomorphic species in the family Schindleriidae (Perciformes: Gobioidei). *Records of the Australian Museum*. 56:139-142.

Weber, M. 1909. Diagnosen neuer Fische der Siboga-Expedition. *Notes from the Leyden Museum.* 31(4): 143-169.

Whitley, G.P. 1928. Studies in ichthyology. No. 2. *Records of the Australian Museum*. 16 (4): 211-239.

Whitley, G.P. 1931. New names for Australian fishes. *Australian Zoologist*. 6(4): 310-334, Pls. 25-27.

Winterbottom, R. 1990. The *Trimmatom nanus* species complex (Actinopterygii, Gobiidae). phylogeny and progenetic heterochrony. *Systematic Biology*. 39 (3): 253–265.

Winterbottom, R. 1993. Search for the gobioid sister group (Actinopterygii: Percomorpha). *Bulleton of Marine Science*. 52(1): 395–414.

Winterbottom, R. 2003. *Feia ranta,* a new species of gobiid fish (Acanthopterygii; Perciformes) from Vietnam. *Aqua, Journal of Ichthyology and Aquatic Biology.* 7(3): 97–102.

Wongrat, P. & P.J. Miller. 1991. The innervations of head neuromast rows in eleotridine gobies (Teleostei: Gobioidei). *Journal of Zoology, London*. 225: 27–42.

Yang, Z. 1994. Maximum likelihood phylogenetic estimation from DNA sequences with variable rates over sites: approximate methods. *Journal of Molecular Evolution.* 39(3): 306–314.

Zander, C.D. 2011. Morphological adaptations to special environments of gobies. *In*: Patzner, R.A., J.L. Van Tassell, M. Kovačić. and Kapoor, B.G. (eds.), *The Biology of Gobies.* CRC Press, Taylor and Francis Group, Science Publishers, Enfield, New Hampshire, pp. 345–366.

Appendix A. The status of nominal *Callogobius*

During the course of my research, I reviewed the literature and examined the majority of extant *Callogobius* type specimens to determine the status of each nominal species. In Table A.1, I list species included in *Callogobius* as circumscribed by McKinney and Lachner (1978b) and all subsequently described species; nominal species are listed alphabetically by species names but with their original combination (generic assignment used in the original description). When discussing *Callogobius* species names in the text of this appendix, I first refer to them using the original combination, but subsequently use their current generic assignment. My general conclusion is that the majority of nominal species are likely distinct (and their names should not be considered junior synonyms) but I withhold formal redescription until additional material collected near the original type locality can be located and examined.

TABLE A.1 Nominal species of *Callogobius*, their current or provisional allocation, catalog numbers and status of holotype (examined/not examined by the present author, missing or destroyed.) All species marked as "uncertain" under the "Current allocation" column include in parentheses a possible senior synonym, however, it is probable that many of these uncertain species will prove to be valid with continued investigation.

Nominal species	**Current allocation**	**Holotype**
Callogobius amikami Goren , Miroz & Baranes 1991	*C. amikami*	TAU P-10321(examined)
Callogobius andamarensis Menon & Chatterjee 1974	*C. andamanensis*	ZSI F7105/2 (examined)
Macgregorella badia Herre 1935	Uncertain (*C. hasseltii*)	FMNH 17373 (examined)
Callogobius bauchotae Goren 1979	Uncertain (*C. maculipinnis*)	MNHN 1976-0184 (examined)
Mucogobius bifasciatus Smith 1958	*C. bifasciatus*	SAIAB 235 (examined)
Gobius bothriorrhynchus Herzenstein 1896	Uncertain (*C. hasseltii*)	ZIN 9684 (examined)
Callogobius centrolepis Weber 1909	*C. centrolepis*	ZMA 111745 (examined)
Drombus clarki Goren 1978	*C. clarki*	HUJ 10065 (examined)
Callogobius clitellus McKinney & Lachner 1978	*C. clitellus*	USNM 209249 (examined)
Gobius coelidotus Sauvage [ex Cuvier & Valenciennes] 1880	Uncertain (*C. hasseltii*)	MNHN 0000-2968 (examined)
Callogobius crassus McKinney & Lachner 1984	*C. crassus*	USNM 220088 (examined)
Gobius depressus Ramsay & Ogilby 1886	*C. depressus*	AMS B.9758 (examined)
Callogobius dori Goren 1980	*C. dori*	BMNH 1978.9.8.7. (examined)
Mucogobius flavobrunneus Smith 1958	*C. flavobrunneus*	SAIAB 211 (examined)
Mucogobius gobiosoma Whitley 1931	*C. mucosus* (tentative)	AMS I.11480 (not examined)
Eleotris hasseltii Bleeker 1851	*C. hasseltii*	RMNH 1852 (examined)
Callgobius hastatus McKinney and Lachner 1978	*C. hastatus*	USNM 216811 (examined)
Gobiomorphus illotus Herre 1927	Uncertain (*C. sclateri*)	BSMP 11531 (destroyed)
Gunnammata insolita Whitley	*C. depressus* (tentative)	AMS IA.2517 (not examined)
Macgregorella intonsa Herre 1927	*C. okinawae*	BSMP 3575 (destroyed)
Drombus irrasus Smith 1959	Uncertain (*C. maculipinnis*)	SAIAB 186 (examined)
Intonsagobius kuderi Herre 1943	Uncertain (*C. maculipinnis*)	SU 36815 (examined)
Drombus maculipinnis Fowler 1918	*C. maculipinnis*	ANSP 47549 (examined)
Callogobius mannarensis Rangarajan 1968	*C. mannarensis*	CMFRI 102 (missing)
Magregorella moroana Seale 1910	Uncertain (*C. hasseltii*)	BSMP 3575 (destroyed)
Gobius mucosus Günther 1872	*C. mucosus*	BMNH 1871.9.13.169 (examined)
Callogobius nigromarginatus Chen & Shao 2000	Uncertain (*C. maculipinnis*)	ASIZP 057693 (missing)
Doryptena okinawae Snyder 1908	*C. okinawae*	USNM 62240 (examined)
Callogobius pilosimentum Delventhal et al.	*C. pilosimentum*	SMF 35756 (examined)
Drombus plumatus Smith 1959	*C. plumatus*	SAIAB 208 (examined)
Galera producta Herre 1927	*C. producta*	BSMP 7417 (destroyed)
Macgregorella santa Herre 1935	*C. okinawae*	FMNH 17374 (examined)
Eleotris sclateri Steindachner 1879	*C. sclateri*	NMW 30901 (examined)
Callogobius sheni Chen, Chen & Fang 2006	*C. sheni*	MNNB P6980 (examined)
Callogobius shunkan Takagi 1957	*C. shunkan*	LFBKU (examined)
Callogobius snelliusi Koumans 1953	Uncertain (*C. maculipinnis*)	RMNH 20289 (examined)
Doryptena snyderi Fowler 1946	*C. okinawae*	ANSP 72078 (examined)
Callogobius stellatus McKinney & Lachner 1978	*C. stellatus*	USNM 217429 (examined)
Doryptena tanegasimae Snyder 1908	*C. tanegasimae*	USNM 62241 (examined)
Callogobius trifasciatus Menon & Chatterjee 1976	Uncertain (*C. flavobrunneus*)	ZSI F 7144/2 (examined)
Drombus tutuilae Jordan & Seale 1906	*C. tutuilae*	USNM 51770 (examined)
Intonsagobius vanclevei Herre 1950	Uncertain (*C. maculipinnis*)	USNM 202513 (examined)
Callogobius winterbottomi Delventhal & Mooi 2013	*C. winterbottomi*	ROM 58914 (examined)

The first described goby species to subsequently be placed in *Callogobius* is *Eleotris hasseltii* Bleeker 1851 (type locality, Java). The specimens considered to be syntypes (RMNH 1852) appear to include two species, and there is no evidence that they were collected from the same locality. Examination of additional material suggests that what has been identified as *C. hasseltii* is a complex of several widespread, similar-looking species that may also differ regionally. I therefore chose to withhold a redescription of this species, awaiting access to more material collected in the vicinity of the type locality. The holotype and only specimen of *Gobius bothriorrhynchus* Herzenstein 1896 (type locality, Philippines), appears similar to at least one species of the presumed *C. hasseltii* syntypes; however, the condition of the specimen (like many other older *Callogobius* specimens) is poor and it is difficult to determine with confidence. I consider the status of *C. bothriorrhynchus* uncertain and will revisit it as more material becomes available. Koumans (1940) examined the holotype of *Macgregorella moroana* Seale 1910 (type locality, Jolo, Sulu Province, Philippines) and considered it a synonym of *C. hasseltii*; it was subsequently destroyed. I consider the status uncertain. Likewise, the types of *Macgregorella badia* Herre 1935 (type locality, Fiji) and *Gobius coelidotus* Sauvage 1880 (type locality, Java) appear to be specimens of a *hasseltii*-like species and these names have been considered synonyms of *C. hasseltii* (Akihito and Meguro 1975), but I consider their status uncertain.

The holotype of *Eleotris sclateri* Steindachner 1879 (type locality Society Islands) is in remarkably good condition considering its age. *Drombus tutuilae* Jordan & Seale 1906 (type locality, American Samoa) was previously considered a synonym of *C. sclateri* by Koumans (1953) and by McKinney and Lachner (1984). The holotype (USNM 51770) is small and in very poor condition but Delventhal and Mooi (2013, Chapter Four) were able to demonstrate that it differs from *C. sclateri* and represents a distinct species. It appears to be part of a poorly defined species complex that also includes *C. centrolepis* Weber 1909 (type locality, Sulawesi). Examination of the type of *C. centrolepis* suggest that it is most likely distinct, although I have not been able to rule out that it is a synonym of *C. tutuilae* (because of the poor condition of both specimens). A number of undescribed species similar to *C. tutuilae* and *C. centrolepis* exist; they are usually relatively small, easily damaged, sparsely collected and often lack strong distinguishing characteristic (personal observation).

Doryptena okinawae Snyder 1908 (type locality Okinawa Island, Japan) represents a distinctively shaped and coloured species easily distinguished from other *Callogobius* species by the papillae pattern. The types of *Macgregorella intonsa* Herre 1927 (type locality Mindanao, Philippines) were destroyed; Koumans (1940) considered it a synonym of *C. hasseltii*, but I follow Akihito and Meguro (1975) in recognizing this species as a synonym of C. *okinawae* based on the illustration and description. *Macgregorella santa* Herre 1935 (type locality, Vanuatu) has been considered a synonym of *C. okinawae* by Akihito and Meguro (1975) and others; I have examined the holotype (FMNH 17374) and agree with their assessment.

Callogobius trifasciatus Menon & Chatterjee 1976 (type locality Andaman Islands) was synonymised with *Mucogobius flavobrunneus* Smith 1958 (type locality, Mozambique) by McKinney and Lachner (1984). However, specimens identified as *C. flavobrunneus* differ in colour pattern throughout their range, so I consider this synonymy tentative, pending further investigation. According to Central Marine Fisheries Research Institute (CMFRI) staff, the type material of *Callogobius mannarensis* Rangarajan 1968 was not available for examination during my 2007 visit to India. However, the distinctiveness of this species is well-corroborated based on the description and non-type material.

I have not examined the types of *Gunnammata insolita* Whitley 1928 or *Mucogobius gobiosoma* Whitley 1931; I tentatively recognize them as synonyms of *Gobius depressus* Ramsay & Ogilby 1886 and *Gobius mucosus* Günther 1872 following Gomon et al. (1994) and Larson & Murdy (2006).

Delventhal et al. (2016, Chapter 7) recently discussed the status of nine *maculipinnis*-like nominal species: *Callogobius bauchotae* Goren 1979, *Drombus irrasus* Smith 1959, *Intonsagobius kuderi* Herre 1943, *Drombus maculipinnis* (Fowler 1918), *C. nigromarginatus* Chen & Shao 2000, *C. shunkan* Takagi 1957, *C. snelliusi* Koumans 1953 and *Intonsagobius vanclevei* (Herre 1950). They described a new species, *C. pilosimentum* Delventhal, Mooi, Bogorodsky & Mal 2016. They suggested that a substantial number (possibly most) of these species will be demonstrated to be distinct following additional investigation. This investigation is challenging, however, due to the often continuous variation of external characters within this species complex, and the unusually fragile nature of most specimens. Two described species within this complex are readily distinguished from the others; *C. pilosimentum* which has a specific variation in the papillae pattern on the chin (normally 4, rather than 3 transverse mandibular rows [Row 16] on each side) (Delventhal et al. 2016, Chapter 7), and *C. shunkan* which differs slightly in body shape, colouration and meristics. *Callogobius shunkan* is currently being redescribed by colleagues at the Biological Laboratory of the Imperial Household (BLIP).

In addition to the species already dicussed, I recognize the following to be distinct species of *Callogobius* with no synonyms: *Callogobius amikami* Goren , Miroz & Baranes 1991, *Callogobius andamanensis* Menon & Chatterjee 1974, *Mucogobius bifasciatus* Smith 1958, *Drombus clarki* Goren 1978, *Callogobius clitellus* McKinney & Lachner 1978, *Callogobius crassus* McKinney & Lachner 1984, *Callogobius dori* Goren 1980, *Callgobius hastatus*

McKinney and Lachner 1978, *Drombus plumatus* Smith 1959, *Galera producta* Herre 1927, *Callogobius sheni* Chen, Chen & Fang 2006, *Callogobius stellatus* McKinney & Lachner 1978, *Doryptena tanegasimae* Snyder 1908 and *Callogobius winterbottomi* Delventhal & Mooi 2013.

Callogobius seshaiyai Jacob & Rangarajan 1960 (type locality, Southern India) is not a species of *Callogobius*. It lacks the specific pattern of raised sensory papillae characteristic of other *Callogobius* species, and appears to be a species of *Mangarinus* Herre, based on examination of the types, and collections of similar looking specimens I collected while in Phuket, Thailand. *Callogobius liolepis* Bleeker is likewise not a species of *Callogobius*, but rather a senior synonym of *Gobiopsis aporia* Lachner and McKinney1978 (as demonstrated in Chapter Six of this thesis).