ISSN 0968-0470

Bulletin of The Natural History Museum

Zoology Series

THE
NATURAL
HISTORY
MUSEUM

VOLUME 65 NUMBER 1 24 JUNE 1999

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World List abbreviation: *Bull. nat. Hist. Mus. Lond.* (Zool.)

Zoology Series
Vol. 65, No. 1, pp. 1–72

ISSN 0968–0470

The Natural History Museum
Cromwell Road
London SW7 5BD

Issued 24 June 1999

Typeset by Ann Buchan (Typesetters), Middlesex
Printed in Great Britain by Henry Ling Ltd., at the Dorset Press, Dorchester, Dorset

Bull. nat. Hist. Mus. Lond. (Zool.) **65**(1): 1–13 Issued 24 June 1999

Phylogenetic relationships of Toad-headed lizards (*Phrynocephalus*, Agamidae) based on morphology

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CONTENTS

SYNOPSIS. *Phrynocephalus* together with its sister-group, *Bufoniceps* is most closely related to other advanced Palaearctic and African agamids. They have been regarded as the sister-group of all these species or derived from African *Agama* (Moody, 1980, morphological data) or as the sister of *Laudakia* (Joger, 1991, albumin immunology) but reassessment of morphology suggests a relationship to *Trapelus*. Parsimony analysis of 46 morphological characters, involving 54 derived states, of 25 species of *Phrynocephalus* indicates that successive branches arising from the main lineage of the genus are as follows: *P. mystaceus*; *P. maculatus*; *P. arabicus*; the *P. interscapularis* group – (((*P. clarkorum*, *P. ornatus*) ((*P. euptilopus*, *P. luteoguttatus*) (*P. interscapularis*, *P. sogdianus*))); *P. scutellatus*; *P. golubevi*; *P. reticulatus; P. raddei*. There is then a group of 11 species in which relationships are generally poorly resolved, although within this *P. theobaldi*, *P. roborowskii* and *P. vlangalii* are clearly closely related to each other and perhaps to *P. forsythii*, and the tuberculated species, *P. helioscopus*, *P. persicus*, *P. rossikowi* and *P. strauchi* may also form a clade. There is no clear morphological evidence that the northeastern species, *P. axillaris*, *P. versicolor*, *P. przewalskii*. and *P. guttatus* (which also extends far to the west) form a holophyletic group. *Phrynocephalus* does not appear to share its general phylogeographic pattern with other Asian reptiles and this may consequently result from dispersal rather than vicariance events. The phylogeny suggests the ancestor of *Phrynocephalus* occurred in Arabia-NW India area whence there were three independent invasions of Central Asia: by the ancestors of *P. mystaceus*, of *P. interscapularis* + *P. sogdianus*, and of *P. golubevi* and its sister group, the latter later extending north and eastwards into Mongolia, China and Tibet. *Phrynocephalus* appears to have primitively occupied aeolian sand habitats but to have spread to harder substrates from which sandy habitats were sometimes reinvaded. Degeneration of the outer and middle ear occurred in the early history of *Phrynocephalus* but was partly reversed in *P. axillaris* and the *P. theobaldi* group.

INTRODUCTION

Toad-headed agamids, *Phrynocephalus* Kaup 1825, are a found in the mainly Palearctic desert regions of Asia, from Eastern Turkey and Russia to Mongolia, and southwards to southern Arabia and Pakistan. Species in the south and centre of the range of the genus are, in the main, well defined but, in the northeast, boundaries between them are often less clear and numerous nominal taxa have been described (see e.g. Zhao & Adler, 1993). This makes the total number of species in the genus uncertain but it is likely to be in excess of 30. In this paper, an estimate of phylogeny is made for 25 of the better defined species using morphological characters, including external features and some internal ones derived from the skeleton, middle ear, shoulder muscles and abdominal arteries.

RELATIONSHIPS OF PHRYNOCEPHALUS

Phrynocephalus is the sister group of the monotypic *Bufoniceps* Arnold 1992 which was created for *Phrynocephalus laungwalaensis* Sharma, 1978. Moody (1980) placed *Phrynocephalus* (including *P. laungwalaensis*) with what at the time was usually called *Agama* Daudin 1802, in his group 6 of the Agamidae. Within *Agama*, as then understood, this author recognised several separate genera: *Agama* s. str., *Xenagama* Boulenger 1895, *Pseudotrapelus* Fitzinger 1843, *Trapelus* Cuvier 1817 and *Stellio* Laurenti 1768. However, the name *Stellio* is unavailable (Stejneger, 1933) and the assemblage it was used to denote by Moody is paraphyletic, comprising distinct Palaearctic and mainly African assemblages (Joger, 1991; Baig & Böhme, 1997) of which the former is probably a clade and the members of the latter more closely related to such taxa as *Agama*, *Pseudotrapelus* and *Trapelus* (personal observations). Leviton, Anderson, Adler & Minton (1992) argue for the use of *Laudakia* Gray, 1845 for the Palaearctic forms, a course followed here. The more recent suggestion (Henle, 1995), that *Laudakia* should be confined to some members of this assemblage and the rest placed in *Placoderma* Blyth, 1854, requires more thorough assessment of the relationships of these lizards before it is adopted. The name *Acanthocercus* Fitzinger, 1843 is available for the remainder of the

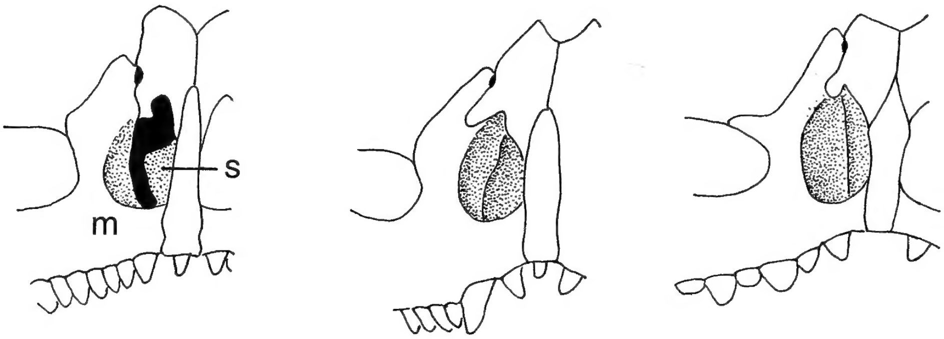

Fig. 1 Anterior views of right nasal area of skulls showing differences in contribution of the maxilla (m) to the posterior wall of the narial opening. a. Small, does not contact septomaxilla (s) (*Bufoniceps laugwalaensis*). b. More extensive contribution, especially dorsally, and broad contact with septomaxilla (*Phrynocephalus mystaceus*). c. More extensive still, both dorsally and ventrally, broad contact with septomaxilla maintained (*P. euptilopus*).

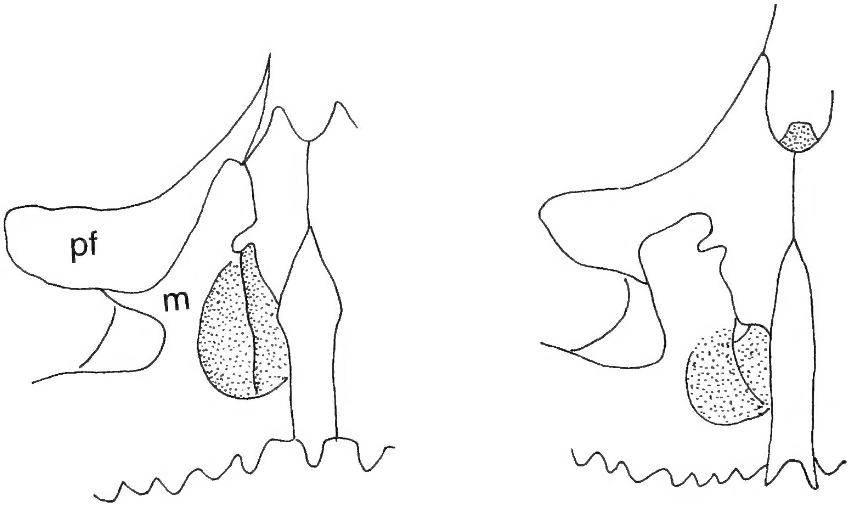

Fig. 2 Anterior views of right nasal area of skulls. a. Dorsal process of maxilla (m) tapering upwards, maxilla extending outwards below lateral process of prefrontal bone (pf) which is large (*P. euptilopus*). b. Dorsal process of maxilla blunt above, maxilla not extending markedly outwards below lateral process of premaxilla which is relatively small (*P. persicus*).

forms that Moody allocated to *Stellio* (Schätti & Gasperetti, 1994; Henle, 1995; Baig & Böhme, 1997).

Unweighted Wagner tree analysis of the morphological data presented by Moody (1980) indicated that *Phrynocephalus* was derived from a paraphyletic *Agama* s. str., while compatability analysis, and Wagner tree analysis where characters were weighted according to their consistency index in an initial run, suggested that *Phrynocephalus* was sister to all other members of Moody's Group 6 (Moody, 1980).

Results of isozyme analysis have been interpreted as indicating that *Phrynocephalus* is the sister group of *Laudakia* (Ananjeva & Sokolova, 1990), a result in agreement with immunological studies (Joger, 1991). In contrast, a reassessment of morphology (pers. obs.) suggests that the sister group of *Phrynocephalus* + *Bufoniceps* is *Trapelus*. Shared features that appear derived within Moody's Group 6 include the following: maxillae in contact beneath premaxilla, lateral prefrontal processes very large, palatine roof of interorbital canal narrow or absent, vomers fused, squamosal spatulate with no hook-shaped projection on its lateral margin, presacral vertebrae usually 22 or fewer; nostrils directed forwards rather than sideways, no enlarged subocular scales (reversed in some *Phrynocephalus*), external ear opening reduced in size, no spinous scales on dorsum of neck (reversed in some *Phryncocephalus*), no caudal autotomy, scales on tail not in regular whorls; nasal passage long and flexed, depressor mandibulae muscle extends partly over tympanum.

MORPHOLOGICAL CHARACTERS USED TO ESTIMATE PHYLOGENY

Skull

1. *Contribution of the maxilla to the posterior wall of the narial opening of the skull* (Figure 1). Small, does not contact septomaxilla (0); more extensive especially dorsally, broad contact with septomaxilla (1); more extensive still both dorsally and ventrally, broad contact with septomaxilla maintained (2).
2. *Dorsal process of maxilla* (Figure 2). Tapering upwards (0); broad and ending bluntly above (1).
3. *Maxilla extends clearly outwards below the anterior surface of the lateral process of the prefrontal bone* (Figure 2). No (0); yes (1).
4. *Relationship of maxillary and nasal bones below the lateral process of the nasal* (Figure 3). Widely separated (0); more narrowly separated (1); in contact (2).

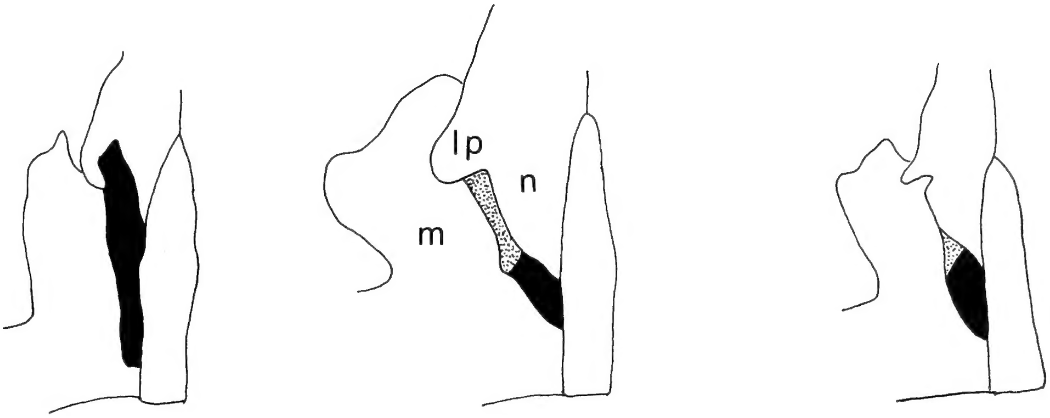

Fig. 3 Anterior views of right nasal area of skulls showing differences in arrangement of maxilla (m), septomaxilla (stippled)) and nasal bones (n). a. maxilla and nasal widely separated below lateral process (lp) of nasal (*P. scutellatus*). b. Maxilla and nasal more narrowly separated below lateral process of nasal and the space filled by the septomaxilla (*P. versicolor*). c. Maxilla and nasal in contact below lateral process of nasal (*P. persicus*).

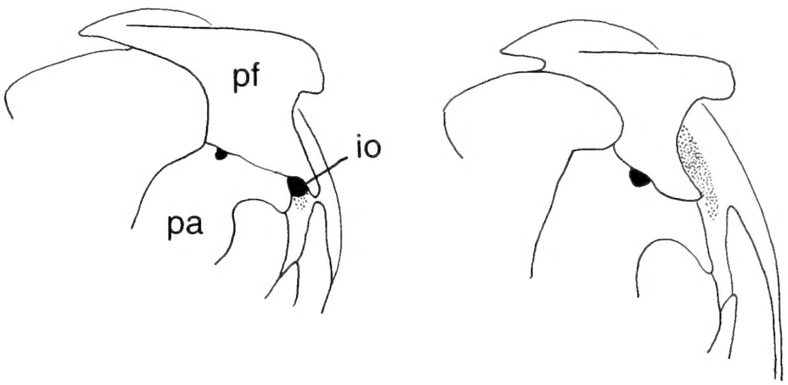

Fig. 4 View into anterior right orbit, showing width of posterior face of prefrontal bone (pf) relative to that of the posterior platine (pa) and variation in lateral extension of the prefrontal relative to the infraorbital canal (io). a. Posterior face of prefrontal broad, extends laterally across infraorbital canal. b. Posterior face of prefrontal narrow, does not extend across infrarorbital canal

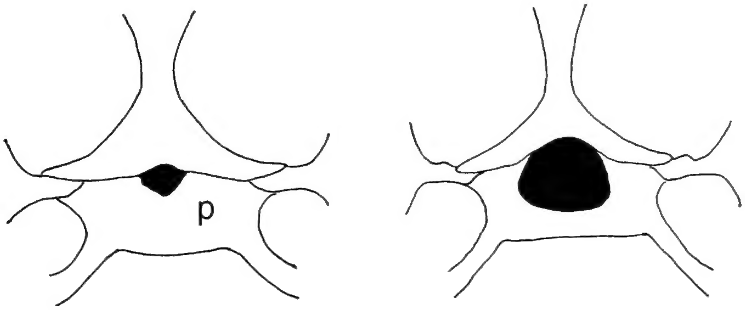

Fig. 5 Difference in size of the parietal foramen (black) in adults. a. Small, diameter less than distance from the lateral edge of the parietal bone (p) (*P. scutellatus*). b. Large, diameter more than distance from lateral edge of parietal bone (*P. persicus*).

5. *Maxilla in contact with septomaxilla on surface of skull below lateral process of nasal* (Figure 3). No (0); yes but does not reach nasal (1); yes and reaches nasal (2).
6. *Nasal bone projects laterally over maxilla anteriorly*. No (0); yes (1).
7. *Size of lateral process of prefrontal* (Figure 2). Relatively small (0); large and extended laterally (1).
8. *Width of posterior face of prefrontal bone in orbit relative to width of posterior part of palatine* (Figure 4). Relatively broad (0); narrowed (1).
9. *Prefrontal bone extends laterally across infraorbital canal* (Figure 4). No (0); yes (1).
10. *Size of parietal foramen in adults* (Figure 5). Relatively small, its lateral diameter less than its distance from the lateral edge of the parietal bone (0); large, its lateral diameter more than its distance from the lateral edge of the parietal bone (1).
11. *Body of parietal bone relative to its supratemporal processes* (Figure 6). Upper surface of body of parietal bone relatively flat

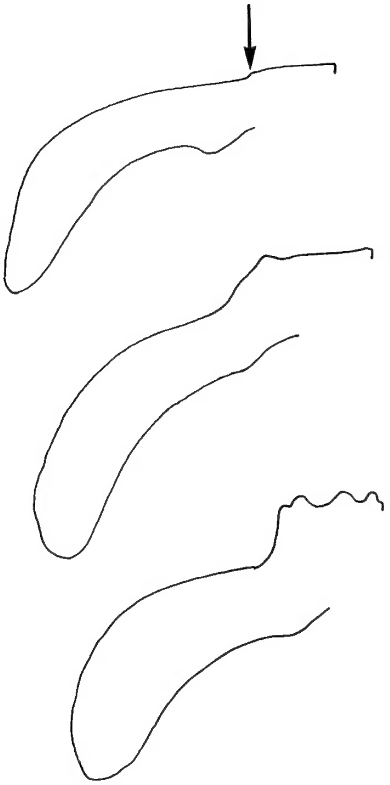

Fig. 6 Lateral profiles of supratemporal process (left) and body of parietal bone (right), arrow indicates border between the two regions. a. Upper surface of body of parietal bone running more or less smoothly into upper margin of supratemporal process (*P. mystaceus*). b. Upper suface of body of parietal abruptly raised relative to upper margin of the supratemporal process (*P. persicus*). c. Similar, but upper surface of body of parietal tuberculated (*P. scutellatus*).

and running more or less smoothly into upper margin of supratemporal processes which is relatively flat (0); upper surface of body of parietal bone abruptly raised relative to upper margin of supratemporal processes (1).

Other skeletal features

12. *Number of scleral ossicles.* Twelve (0); eleven (1); ten in some individuals (2).
    Acrodonta including Agamidae usually have 12 scleral ossicles in each eye instead of the usual lizard number of 14. While *Bufoniceps* possesses 12 there is further reduction in *Phrynocephalus*: most species and individuals have 11 ossicles but some members of at least a proportion of species in the *P. interscapularis* group have 10. This is true of *P. interscapularis*, *P. luteoguttatus*, *P. sogdianus* and *P. ornatus*. Occurrence of 10 ossicles may in fact be wider, but the other two members of the *P. interscapularis* group (*P. eutilopus* and *P. clarkorum*) are known from relatively few specimens, so checks on ossicle number have been very limited in these.
13. *Number of presacral vertebrae.* Usually 22, occasionally 23 in some species (0); usually 21, occasionally 20 (1).
    Substantial data on presacral vertebral number are given by Whiteman (1978) and my own observations confirm his. Exceptions to the usual numbers occur in some species but nearly always constitute a small minority of not more than about 15% of individuals.
14. *Number of caudal vertebrae.* Usually 40–50 or more (0); usually less than 40 (1).
    Again, my own observations confirm data given by Whiteman (1978).

External features

15. *Largest individuals exceed 60mm from snout to vent.* Yes (0); no (1).
16. *Outline of body viewed from above.* Robust and rounded (0); more slender (1).
17. *Position of nostrils relative to line joining anterior corners of eyes when head viewed from in front* (Figure 7). Nostrils clearly below line (0); nostrils intersecting line or above it (2); intermediate (1).
    Differences in position of the nostril are associated with differences in the conformation of the distal limb of the tubular nasal vestibule. The proximal limb of the vestibule is more or less vertical in all cases, running downwards from its connection with the primary nasal chamber. Where the nostril is low, the distal limb of the vestibule is relatively short and runs obliquely upwards and outwards from the base of the proximal limb to the nostril. In animals where the nostril is high the distal limb runs more or less vertically upwards parallel to the proximal limb and is about as long as this.
18. *Number of internasal scales between the nasal scales* (Figure 7). Usually two or more – 0; usually one or nil – 1.

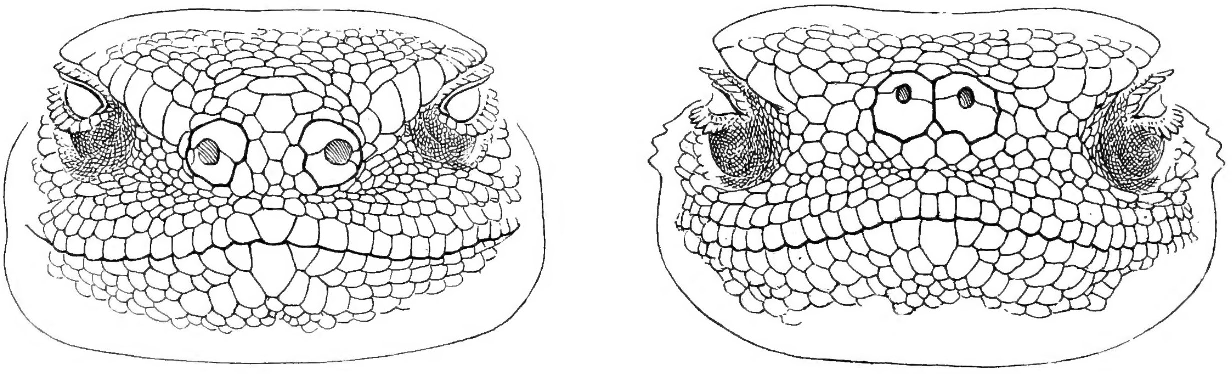

Fig. 7 Anterior views of heads showing differences in nostril position and in number of scales between nasal scales. a. Nostrils lower and separated by two or more internasal scales (*P. theobaldi*). b. Nostrils high and nasal scales in contact or separated by a single internasal scale (*P. arabicus*).

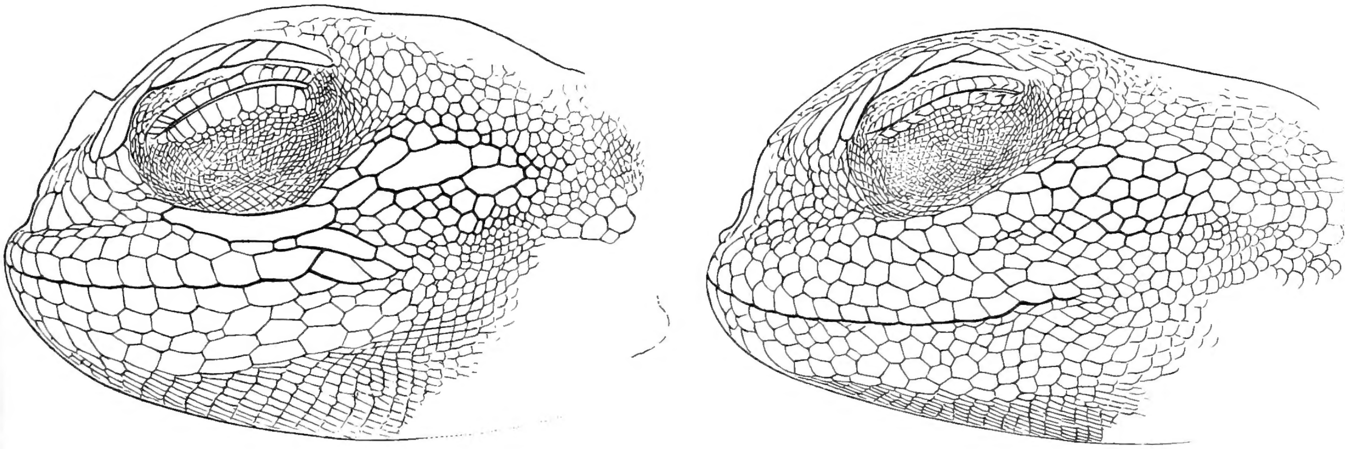

Fig. 8 Left side of head showing differences in number of horizontal rows of scales immediately above the supralabials counted below the anterior eye, and in the size of the subocular and anterior temporal scales. a. 2 or 3 rows above supralabials, subocular and one or more anterior temporals enalarged and elongate (*P. clarkorum*); b. 4–5 rows above supralabials, suboculars and anterior temporals not enlarged (*P. golubevi*).

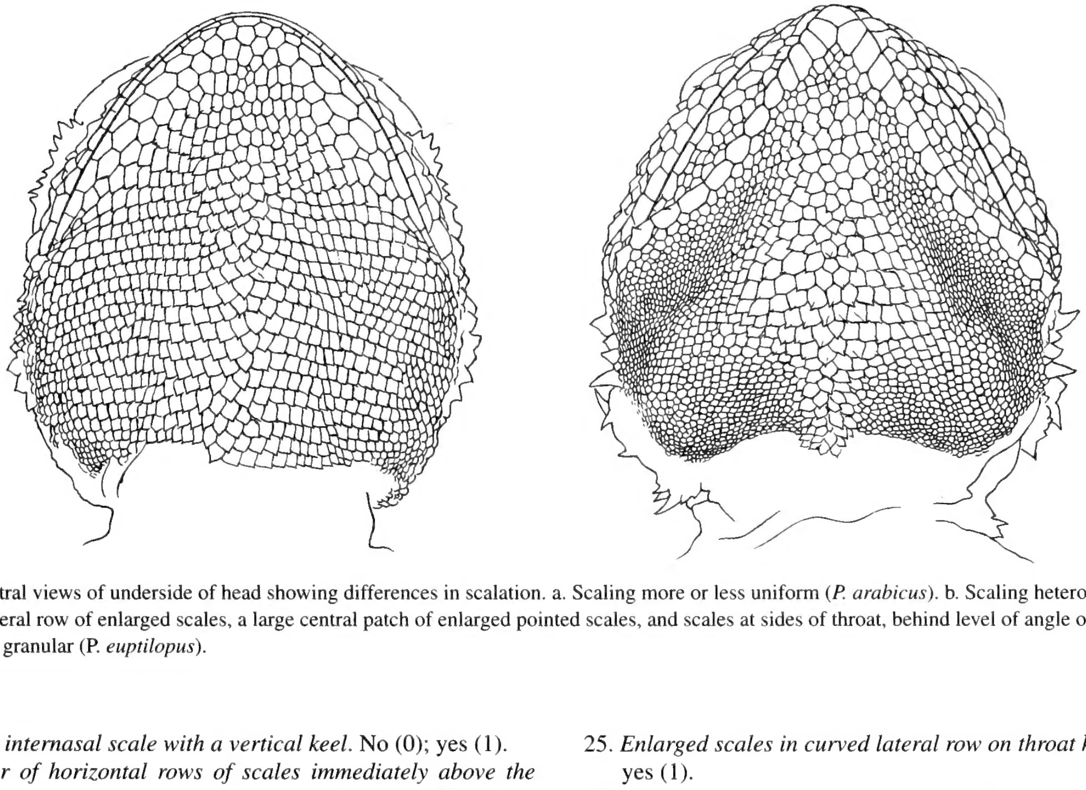

Fig. 9 Ventral views of underside of head showing differences in scalation. a. Scaling more or less uniform (*P. arabicus*). b. Scaling heterogeneous, with curved lateral row of enlarged scales, a large central patch of enlarged pointed scales, and scales at sides of throat, behind level of angle of mouth, very small and granular (P. *euptilopus*).

19. *Single internasal scale with a vertical keel.* No (0); yes (1).
20. *Number of horizontal rows of scales immediately above the supralabials, counted below anterior part of eye* (Figure 8). Usually three rows, occasionally two (0); usually four or even five rows (1).
21. *Enlarged subocular scales* (Figure 8). Not or only weakly differentiated (0); one or more enlarged, keeled, antero-posteriorly elongated scales (1).
22. *One or more enlarged, diagonally keeled and elongated scales on anterior temporal region* (Figure 8). No (0); yes (0).
23. *External ear opening*. Present (0); absent (1).
24. *A lateral row of enlarged throat scales beginning in mental area and curving backwards and outwards usually to the vicinity of the angle of mouth, separated from lower labial scales anteriorly by one to three rows of scales* (Figure 9). No (0); yes (1).
25. *Enlarged scales in curved lateral row on throat keeled.* No (0); yes (1).
26. *A large central patch of enlarged pointed scales on throat, the more postero-lateral ones directed outwards and backwards* (Figure 9). No (0); yes (1).
27. *Scales at sides of throat, behind level of angle of mouth very small and granular* (Figure 9). No (0); yes (1).
28. *Some scales on posterior temporal region and on sides of anterior neck enlarged, elongate and pointed, and directed outwards and upwards.* No (0); yes (1).
29. *Distinct enlarged, raised, often pointed tubercles on dorsum of body*. No (0); yes (1).

Tubercles are enlarged scales that project markedly above the general level of the dorsal body skin. They may be sexually dimorphic in *Phrynocephalus*, often being more strongly

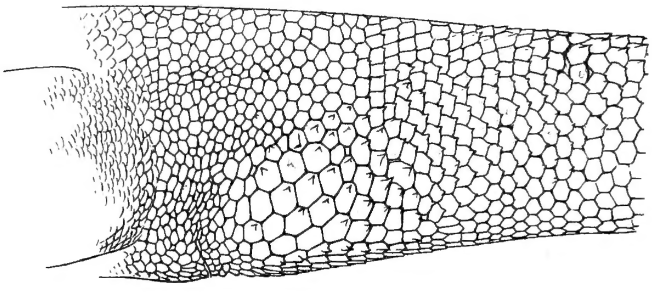

Fig. 10 Left side of tail base in *P. roborowskii*, showing enlarged spinose scales.

developed in males than females. Tubercles are frequently clumped, especially anteriorly, and there is considerable variation in the number associated in such groupings. Tubercle form is also variable and is especially narrow, pointed and elongate in *P. forsythii*, which also shows particularly strong sexual dimorphism. Although the presence of tubercles is usually a clear-cut condition, their development is sometimes sporadic and weak. For instance, many *P. theobaldi* lack them but a few animals have somewhat enlarged scales that are raised and form weak tubercles posteriorly.

30. *Scales at sides of tail base distinctly enlarged and often spinose* (Figure 10). No (0); yes (1)
31. *Horizontal fringe of pointed upturned scales on posterior surface of proximal thigh*. No (0); yes (1).
32. *Subdigital lamellae on distal part of fourth toe of pes* (Figure 11). With two or more keels or at least projections from the free edges of the lamellae (0); with a single keel or none (1;
33. *Narrow light longitudinal stripes often present on flanks*. No (0); yes (1).
34. *Dark pigment frequent in mid-line area of belly in adults*. No (0); yes (1).
35. *Distal tail often with substantial dark pigment at least ventrally, where it may form transverse bars*. No (0); yes (1).

Soft parts

36. *Palatal flaps*. Large (0); reduced or absent (0)
37. *Tympanum*. Well developed and robust(0); reduced to a delicate membrane (1); absent (2). This and other ear features of *Bufoniceps* and *Phrynocephalus* are discussed further elsewhere (Arnold, submitted).

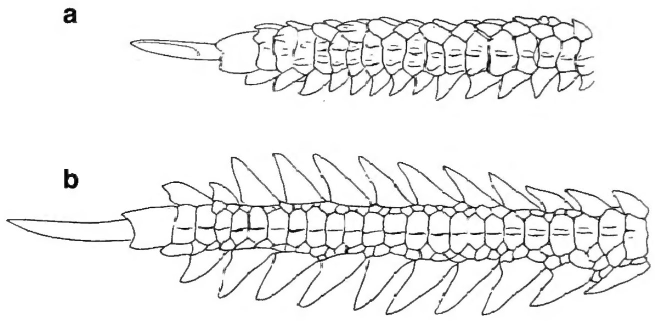

Fig. 11 Underside of fourth toes of pes (anterior edge above), showing extent of lateral fringes of pointed scales and number of keels on subdigital lamellae. a. Fringes small, especially anteriorly, two keels distally (*P. theobaldi*). b. Large fringes, single keels (*P. mystaceus*).

38. *Pars inferior of extracolumella*. Large (0); small or absent (1)
39. *Pharyngeal opening of middle ear*. Large, length 15–25% of head length (0); distinctly reduced, length about 10–14% of head length (1); minute or absent (2).
40. *Episterno-cleidomastoideus muscle present* (Figure 12).Yes (0); very reduced (1); absent (2).
41. *Episterno-cleidomastoideus muscle a single strap* (Figure 12). Yes (0); with two branches (1).
42. *Episterno-cleidmasoideus muscle extends anteriorly to occiput* (Figure 12). No (0); yes (1).
43. *Scapulodeltoideus muscle extends upwards immediately anterior to insertion of acromiotrapezius muscle on scapula*. No (0); yes (1).
44. *Origin of caecal artery on doral aorta* (Figure 13). Anterior and close to mesenterica cranialis artery and well posterior to coeliac artery (0); close to and usually in front of coeliac artery, occasionally behind (1).

The caecal artery, which arises from the dorsal aorta and supplies the intestine, exhibits interspecific variation in the position of its origin on the aorta, relative to the origins of the coeliac artery, which runs to the stomach, and the mesenterica cranialis artery, which like the caecal artery supplies the intestine (Henke, 1974). In at least some *Sitana* and *Draco*, and in *Acanthocercus*,

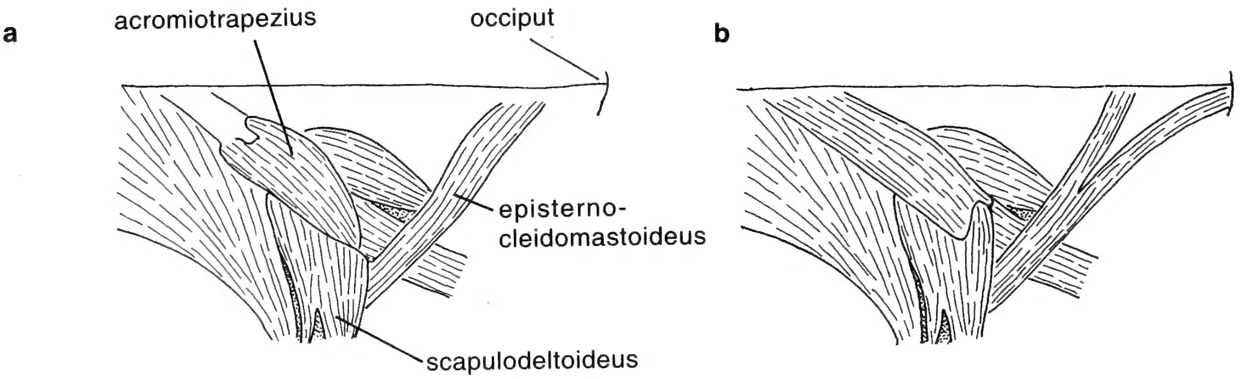

Fig. 12 Diagramatic representations of superficial muscles of the right shoulder and neck. a. Episterno-cleidomastoideus muscle a single strap not extending to the occiput; no dorsal extension of scapulodeltoideus muscle anterior to insertion of acromotrapezius muscle. b. Episterno-cleidomastoideus muscle divided, the anterior branch reaching the occiput; a dorsal extension of scapulodeltoideus muscle anterior to insertion of acromiotrapezius muscle present.

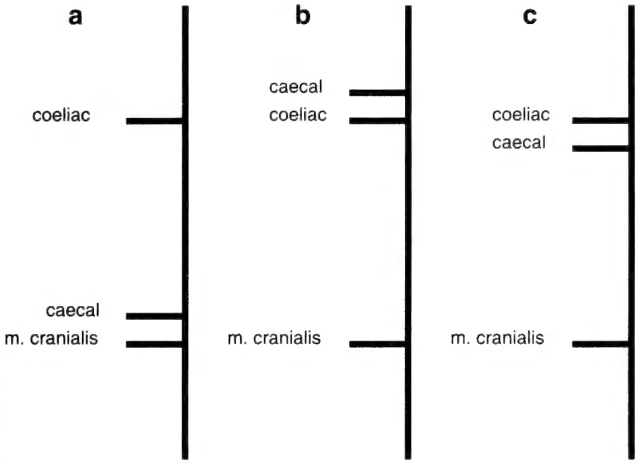

Fig. 13 Variation in position of the origin of the caecal artery on the dorsal aorta in *Phrynocephalus*. a. close to origin of mesenterica cranialis artery. b, c. Close to origin of coeliac artery.

Xenagama, *Agama* s. str., *Pseudotrapelus* and *Trapelus*, the caecal artery originates well posterior to the coeliac artery and close to and anterior to the mesenterica cranialis artery (Figure 13a). In a wide range of agamids, including *Laudakia*, the caecal and coeliac arteries originate close together, with the former usually, although not always, anterior (Figure 13b, c). (Information from Henke, 1974 and personal observations).

Within *Phrynocephalus* some species exhibit an anterior origin of the caecal artery, either a short distance in front of that of the coeliac artery or, much less commonly, just posterior to it. In contrast, the remaining members of the genus and *Bufoniceps* show a posterior origin close to the mesenterica cranialis artery.

Other characters

45. *Viviparous, giving birth to fully-formed young*. No (0); yes (1).
46. *Tail used frequently in intraspecific signalling*. No (0); yes (1).

Hemipenial features

It has been suggested that features of the hemipenis delineate species groups within *Phrynocephalus* (Semenov & Danayev, 1989). These authors illustrate apparent differences in lobe length and in whether calyces are present on the lobes. However, personal observations of a wide range of species, including *P. mystaceus*, *P. maculatus*, *P. arabicus*, *P. euptilopus*, *P. interscapularis*, *P. helioscopus*, *P. theobaldi*, *P. vlangalii*, *P. guttatus*, *P. versicolor* and *P. przewalskii*, suggest that the hemipenis in these forms is consistently deeply lobed with a honeycomb structure on the outer lobe surfaces. Possibly the differences described by Semyonov and Danayev result from examining hemipenes preserved in different stages of eversion.

PHYLOGENETIC ANALYSIS

The data set (Appendix 1) consists of 46 characters most of which are binary but eight include three states. *Trapelus* and *Laudakia* were used as alternative outgroups. Analysis was initially carried out using the Hennig86 program (Farris, 1988) with the options ie- and bb*, which apply branch swopping to a single tree certain to be of minimum length. When characters were ordered and *Trapelus* used as the outgroup, two trees of 110 steps were produced with a consistency index of 0.49 and a retention index of 0.79. With *Laudakia* as the outgroup two trees were again produced, with a length of 112 steps, consistency index 0.48 and retention index 0.79.

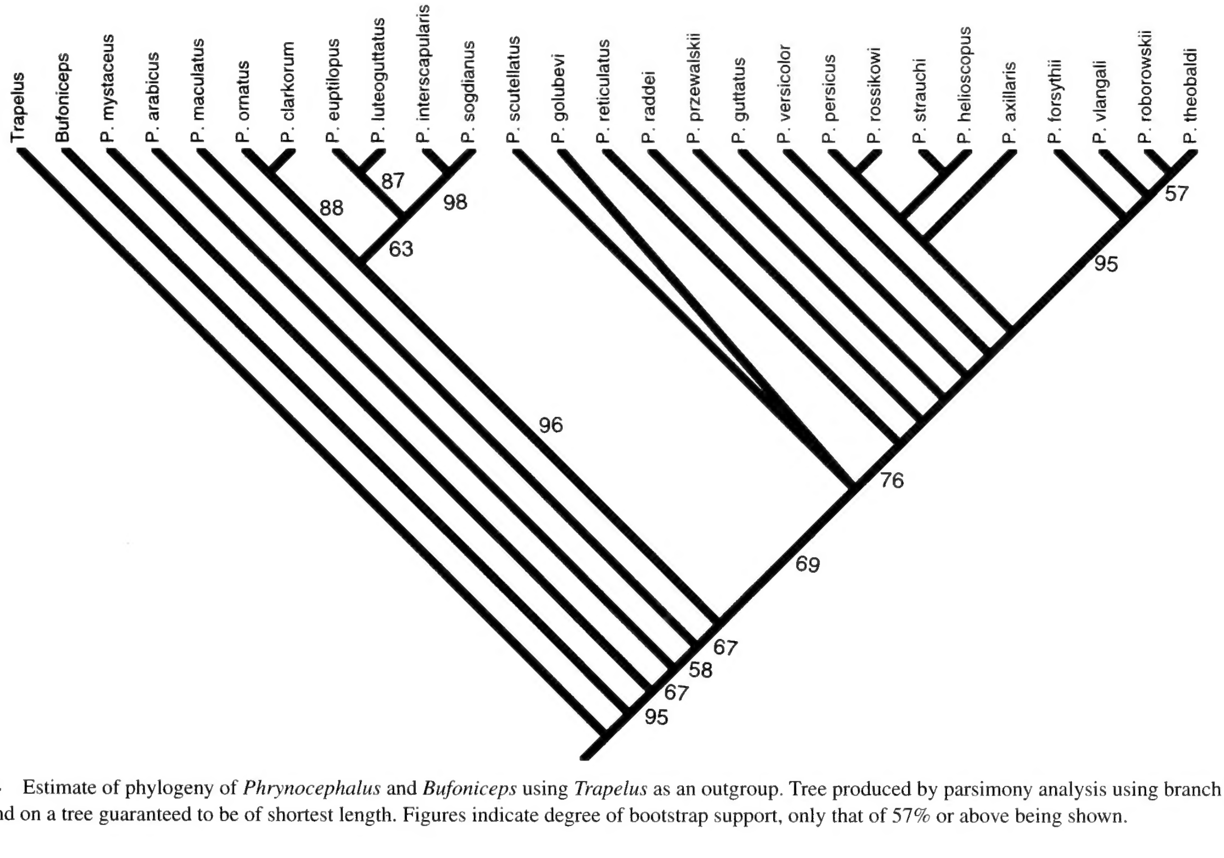

Fig. 14 Estimate of phylogeny of *Phrynocephalus* and *Bufoniceps* using *Trapelus* as an outgroup. Tree produced by parsimony analysis using branch and bound on a tree guaranteed to be of shortest length. Figures indicate degree of bootstrap support, only that of 57% or above being shown.

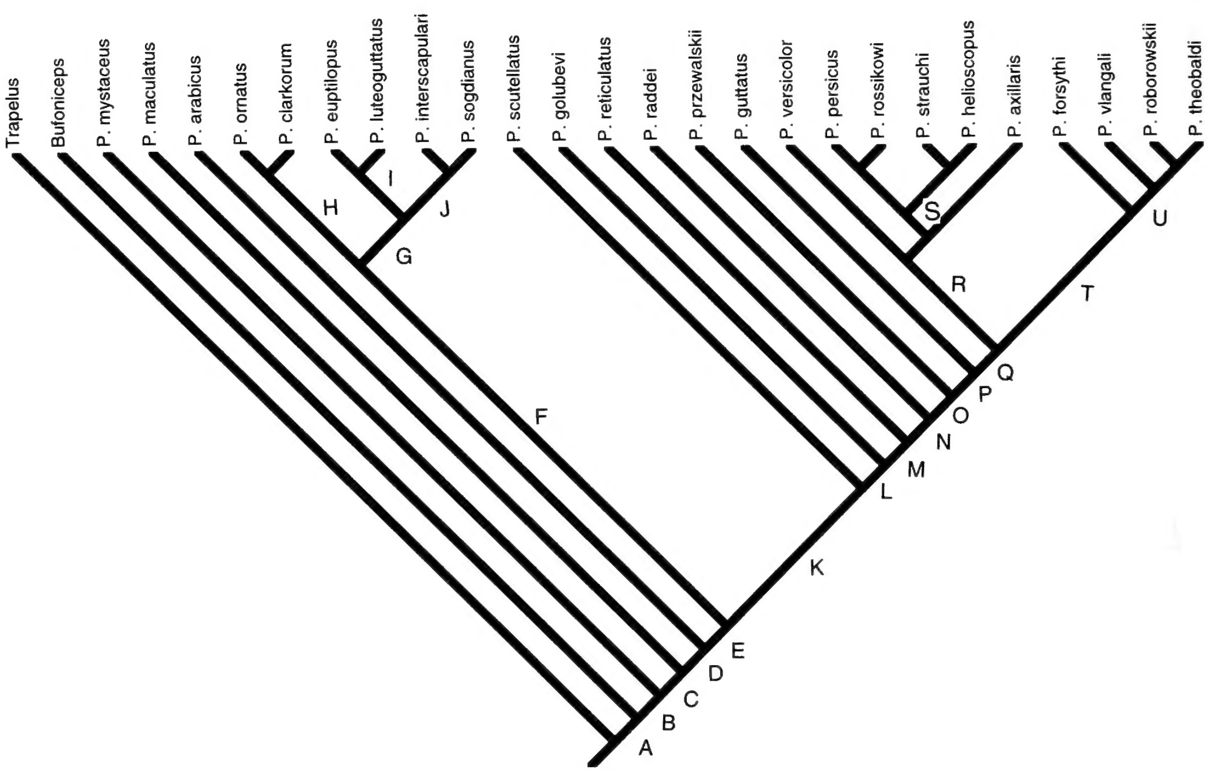

Fig. 15 Tree in Figure 14 after being subjected to successive approximations character weighting using Hennig86 program (Farris, 1988), resulting in *P. scutellatus* and *P. golubevi* being resolved as successive branches. Characters that define lettered nodes are as follows (brackets indicate some degree of parallelism; R indicates reversal). A 17, 18, (32); B 1.1, 12.1, 23, 35, 37.1, 46; C 1.2, 44; D 15; E 37.2, 38, 39.2; F 3, 12.2?, (21), 24, (36), 42; G (14), 28, 43; H 16, 22, 33; I 25, 26, 27; J (8), 19, 31; K 13, 32R; L 10, 20; M (4), 17.2R; N 17.1R; O 18R, 44R; R (29); S 29; T 30; U 6, (8), (34), 38R, (39.2R), 45.

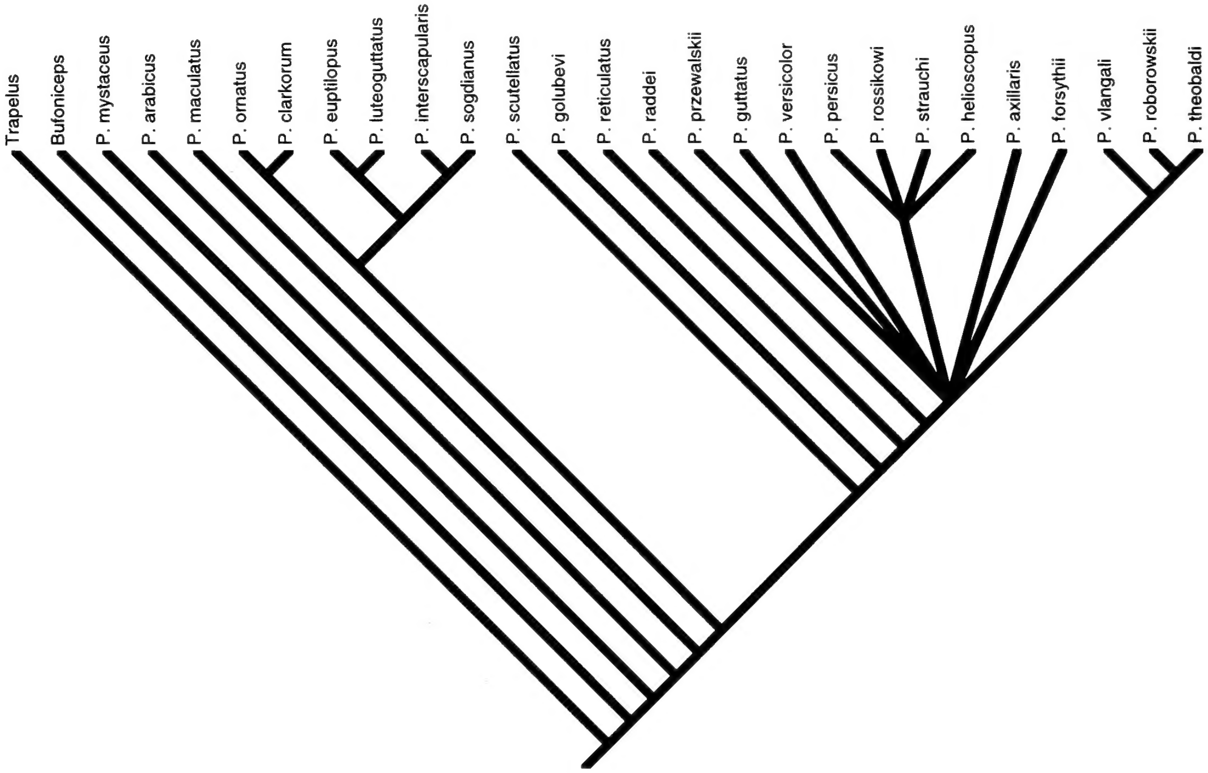

Fig. 16 Conservative estimate of phylogeny for *Phrynocephalus* and *Bufoniceps*. Only nodes supported by two or more characters of low homoplasy are shown.

In both cases the consensus has the same topology (Figure 14). When all characters were unordered, trees of 102 steps were produced which are congruent with those where characters were ordered, but with less resolution in the clade consisting of *P. przewalskii* and its nearest relatives (the topology of this region of the tree is the same as that shown in Figure 16.).

When all these analyses were repeated using the 'heuristic search' option of the PAUP 3.1.1 programme (Swafford, 1993), results were identical. Bootstrapping (100 replicates), using this programme, was also applied to the ordered tree rooted on *Trapelus* and nodes with bootstrap support over 50% are indicated in Figure 14.

Use of the successive approximations character weighting option in Hennig86 produced little change in the original tree based on unordered characters and rooted on *Trapelus*, merely resolving the trichotomy in the consensus tree involving *P. scutellatus* and *P. golubevi*, by making them successive branches on the main lineage of *Phrynocephalus*.

Principal states supporting nodes are shown in Figure 15. It will be seen that some 13 nodes are supported by two or more conservative characters that show little or no homoplasy. The other nodes are defined by single or noisy characters. A conservative tree recognising the nodes based on the former features, or with bootstrap support above 50% (and in many cases both) is shown in Figure 16.

Several nodes on the main lineage of *Phrynocephalus* are quite well supported and a number of other subclades can be recognised. Thus six species constituting a holophyletic group with marked internal structure form the *Phrynocephalus interscapularis* group consisting of *P. interscapularis*, *P. sogdianus*, *P. euptilopus*, *P. luteoguttatus*, *P. clarkorum* and *P. ornatus*. The clade has geographical coherence, occurring in western Pakistan, Afghanistan, eastern Iran and adjoining central Asia. Another well defined clade, the *P. theobaldi* group, includes *P. theobaldi*, *P. roborowskii* and the rather more different *P. vlangalii*. The similar tuberculated species, *P. helioscopus*, *P. persicus*, *P. strauchi* and *P. rossikowi* may form another unit, although it lacks marked bootstrap support.

DISCUSSION

Biogeography

Ananjeva and Tuniyev (1992) speculate about the history and biogeography of *Phrynocephalus* in the former USSR. Their complex hypothesis is difficult to assess as it is not based on an estimate of phylogeny for the species concerned and does not include other members of the *Phrynocephalus* clade.

Phrynocephalus is a characteristic element of the deserts of Palaearctic Asia, like the lacertid genus *Eremias* and the gecko assemblage including *Cyrtopedion*, *Agamura*, *Bunopus*, and *Crossobamon* etc. Its area cladogram is not shared with these other taxa and there is substantial sympatry between species and species groups. It therefore seems likely that parts of the genus dispersed into at least some areas of its huge range. The estimate of phylogeny suggests that the ancestor of the present species occurred in the south of the present distribution of *Phrynocephalus*, possibly within the area running from western Arabia to northwestern India. This region appears to contain the primary range of *Trapelus*, which may be the sister of the *Bufoniceps* + *Phrynocephalus* clade, and *Bufoniceps* itself occurs in northwest India. Many of the basal branches of main *Phrynocephalus* lineage are found wholly or partly in this area, including *P. maculatus* (Arabia to Pakistan), *P. arabicus* (Arabia), some members of the *P. interscapularis* group (S. Afghanistan, SW. Pakistan) and *P. scutellatus* (central and eastern Iran, S. Afghanistan and SW. Pakistan).

From this putative source area, there may have been at least a triple invasion of the presently warm and arid lowland regions of central Asia (Turkmenistan, Uzbekistan, Tadzhikistan, Kirgizstan, southern Khazakstan): by the *P. mystaceus* and *P. interscapularis-sogdianus* lineages and by the ancestor of *P. golubevi* and the members of its sister group (shown in Figure 15, 16). The latter invasion has given rise to a series of taxa in the area (including *P. golubevi*, *P. reticulatus*, *P. raddei* and the *P. helioscopus* group).

There was then apparently eastward spread: into the Tibetan region, by the ancestor of the *P. theobaldi* group and perhaps *P. forsythii*, and further north into Northwest China and southern Mongolia. On the basis of morphology, it is not clear whether extension into the latter region represents a single invasion and radiation or independent invasion by several lineages.

A variety of additional movements by particular lineages has also occurred. For instance, although within the *P. helioscopus* group *P. strauchi* and *P. rossikowi* have relatively small allopatric ranges, *P. helioscopus* is widespread in former Soviet Central Asia and the very similar *P. persicus* on the soutwestern periphery of the range of this species extends into eastern Turkey and Iran. *P. guttatus* now has a broad distribution from northwest China westwards as far as the north Caspian area.

Unfortunately, there is little or no fossil record of *Phrynocephalus* and its immediate relatives. Material assigned to *Phrynocephalus* has been reported from the Pliocene of eastern Turkey (Zerova & Chkhikvadze, 1984), but the precise relationships of these fossils are unknown and it is not even certain whether they represent a member of the clade made up of all present species of *Phrynocephalus* or if they fall outside this grouping.

This arrangement of branches on the main lineage of the *Phrynocephalus-Bufoniceps* clade correlates with species distinctness. As noted, the older southern side-branches comprise very well differentiated taxa, whereas later ones in central Asia often involve more similar species and this trend is especially marked among the relatively recent, more terminal branches in the Northwest China-Southern Mongolia region, where species are very variable, their boundaries poorly defined and their taxonomy often confused.

Structural niche

Most members of the majority of genera in Moody's Group 6 (Moody, 1980) climb to some extent. This is true of *Laudakia*, most *Acanthocercus* and *Agama* s. str., *Pseudotrapelus* and most *Trapelus*. Members of the latter genus, the likely sister-group of *Bufoniceps* + *Phrynocephalus*, spend a lot of time on the ground but many of them also climb in bushes. In contrast to these, *Bufoniceps* and *Phrynocephalus* themselves are strictly ground-dwelling, a derived condition.

There has been dispute as to whether the ancestral spatial niche of *Phrynocephalus* is soft, wind-blown sand. This is suggested by Chernov (1948), Whiteman (1978) and Semenov (1987), but Golubev (1989) and Ananjeva & Tuniyev (1992) consider the group arose in gravel and sandstone deserts. The estimate of phylogeny presented here supports the former hypothesis, with *Bufoniceps* and three of the four basal external branches of the main *Phrynocephalus* lineage being found in loose-sand habitats. (References to use of soft-sand habitats: *P. mystaceus* – Ananjeva & Tuniyev, 1992; *P. arabicus* – Arnold, 1984, Gallagher & Arnold, 1988; *P. clarkorum* and *P. ornatus* – Clark, 1992; *P. luteoguttatus* – Minton, 1966; *P. euptilopus* – Smith, 1935; *P. interscapularis* – Ananjeva & Tuniyev, 1992; *P. sogdianus* – Bannikov *et al.*, 1979). Shifts to firmer ground occurred in *P. maculatus* and independently in the ancestor of the clade containing *P. scutellatus* and its sister group. There was some subsequent shift back to looser substrates in *P. guttatus* (Ananjeva & Tuniyev, 1992) and *P. przewalskii*.

Another indication that aeolian sand habitats are primitive is that a number of features conferring performance advantage in such environments first appear on the internal branch of the phylogeny on which these habitats are entered, that is the ancestral lineage of the *Bufoniceps* + *Phrynocephalus* clade. These are discussed below.

Changes in morphological features

Principal changes in morphology in the history of the *Bufoniceps-Phrynocephalus* clade are listed in the caption of Figure 15. A high proportion of the characters in the data set (Appendix 1) show a single change on the phylogeny. Overt reversals occur in such features as size (in *P. euptilopus*) and the pattern of arteries arising from the aorta. Simple parallelisms are quite frequent in the remaining characters, but few of these are really noisy.

Body size decreases early in the history of the main lineage of *Phrynocephalus*. Many features that appear likely to confer performance advantage in aeolian sand habitats develop at the base of the *Bufoniceps* + *Phrynocephalus* clade and, as noted, are concurrent with entry into such habitats. These features include: lateral fringes of elongate scales on the digits that prevent the feet sinking into soft surfaces (Carothers, 1986); reduction of the keeling on the digital lamellae, which may be less necessary to reduce heat intake in soft-sand environments (Arnold, 1998); fringes of elongate scales along the edges of the eyelids, countersunk jaws, valvular nostrils, and a U-shaped nasal vestibule consisting of vertically parallel and subequal proximal and distal limbs, all of which features appear to exclude sand (Stebbins, 1943, 1944, 1948), although very long nasal passages may also protect the main nasal cavity from desiccation; skin covering the tympanum that may protect it from damage during burial activity, and lateral prefrontal processes that possibly protect the eyes during the same process.

Some of these features initially associated with aeolian sand habitats persist in less basal forms that occur on firmer substrata. Thus, toe and eyelid fringes and countersunk jaws occur in all *Phrynocephalus*, although they are less marked in species that are not found on loose sand. The outer limb of the nasal vestibule is shortened in most firm-ground forms, a shift associated with the changed position of the nostril (p. 5). This feature represents a reversion towards the primitive condition found in other Group 6 agamids. It is also associated with increased contact between the maxillary and nasal bones, either directly or via the septomaxilla. These nasal features occur in more terminal *Phrynocephalus* species on the main lineage of the genus and have developed in parallel in *P. maculatus*.

Other changes loosely associated with shift to firmer substrates include reduction in size of the lateral processes of the prefrontal bones, reduction in number of presacral vertebrae, increase in number of scale rows above the upper labial scales, increase in size of the parietal foramen of the skull and reversal in the pattern of the arteries arising from the aorta.

The high altitude *P. theobaldi* group is characterised by a number of features, including viviparity, something that often develops in cold conditions (Shine, 1985). Within this group, *P. vlangalii* develops a nostril structure that is even more reversed than in other firm-ground forms.

The external and middle ear is heavily modified in the early history of the main *Phrynocephalus* lineage, the tympanum disappearing, the extracolumella decreasing in size and the pharyngeal opening becoming very reduced or absent. These changes may be associated with greater use of subterranean rather than aerial vibration in hearing when lying under the sand. They partly reverse in the *P. theobaldi* group and perhaps independently in *P. axillaris*. Certainly the former species do not usually bury directly in the substratum and use permanent burrows instead (K. Autumn, pers. comm.)

Members of the *P. interscapularis* group possess a range of features that are rare or absent in other *Phrynocephalus* (see caption of Figure 15); their functional significance is uncertain.

Behaviour

Phrynocephalus has a number of distinctive behaviour patterns. The appearance of burial by fast lateral oscillation of the flattened body (discussed by Arnold, 1995) is concurrent with entry into aeolian sand habitats at the base of the *Bufoniceps-Phrynocephalus* clade and, like some morphological features already discussed, is likely to be an adaptation to this environment. In line with this, such shimmy burial is best developed in more basal species (e.g. *Bufoniceps* – Sharma (1978), *P. mystaceus*, *P. interscapularis* – Ananjeva & Tuniyev (1992), *P. arabicus*, *P. scutellatus*, *P. reticulatus* (pers. obs.)). Lateral oscillation often persists in species secondarily occurring on harder substrata, for instance in *P. maculatus* (pers. obs) and *P. helioscopus* (Ananjeva & Tuniyev, 1992). In such cases this behaviour may be modified and not necessarily always used for burial.

When sprayed with water, *P. helioscopus* adopts a distinctive posture in which the hindquarters are raised and the head lowered. Any liquid on the back then moves forward by capillary action in the channels between the scales (and probably by gravity when enough water is present) towards the mouth where it is ingested (Schwenk & Greene, 1987). Presumably, such behaviour permits advantage to be taken of even minor precipitation and condensation, something likely to be a significant benefit in the arid regions where *P. helioscopus* lives. *P. arabicus* from the United Arab Emirates responds to spraying very similarly (pers. obs.). As these two species are widely separated on the estimate of phylogeny for *Phrynocephalus*, this stereotyped behaviour may well be more widespread than presently known. It could not be demonstrated in *Trapelus flavimaculatus*, also from the United Arab Emirates, so it may be confined to *Phrynocephalus* and possibly *Bufoniceps*.

Phrynocephalus species are also distinctive in using the tail for intraspecific signalling (e.g. Arnold, 1984; Ross, 1989, 1995). For instance, it may be raised, curled upwards in the sagittal plane and wagged laterally. Movements usually expose conspicuous markings on the underside of the tail, such as a dark tip and transverse bars and sometimes areas of bright pigment as well. Tail signalling has been investigated for a number of Central Asian species by Dunayev (1996), who recognises seven distinct ways in which the tail may be used (Dunayev, Figure 3). Of the species considered in the present paper, the following are listed as investigated: *P. mystaceus*, *P. maculatus*, *P. interscapularis*, *P. sogdianus*, *P. reticulatus* (as *P. ocellatus*), *P. raddei*, *P. strauchi*, *P. helioscopus*, *P. versicolor* and *P. guttatus*. When data for *P. arabicus* (Ross, 1995) is incorporated, it is apparent that more basal forms on the main *Phrynocephalus* lineage have less complex tail displays than the others. When the seven display features are treated as two-state characters (absent or present) and subjected to parsimony analysis on their own, they produce the following consensus tree which is congruent with the estimate of phylogeny based on morphology: (*P. mystaceus*, *P. maculatus* (*P. arabicus* (all other species))). However, the supposed *P. maculatus* on which Dunayev's observations were based are from the small area of Tadjikistan where *P. golubevi* occurs, a species which was previously not separated from *P. maculatus*. If the animals concerned are in fact *P. golubevi*, the tree based on tail signalling is no longer congruent with that from morphology.

Ecological analogues of *Phrynocephalus*

Small diurnal lizards, that are sit-and-wait foragers, have high body temperatures when active and in many cases signal with their tails, are found in several desert systems. Apart from *Phrynocephalus*, they include the agamids *Ctenophorus* and *Tympanocryptis* in Australia, the phrynosomatid sand lizards in North America (*Uma*, *Callisaurus*, *Holbrookia* and *Cophosaurus*), tropidurines in south America (*Leiolaemus*), geckoes in southern Arabia and Somalia (*Pristurus*) and lacertids in Southwest Africa (*Meroles anchietae*). However, although they show significant parallels in morphology and behaviour, these derived features are not necessarily assembled in the same order (Arnold, 1994).

Nomenclature

As presently understood, *Phrynocephalus* is a well-defined clade defined by six synapomorphies not found in closely related agamids (numbers 1.1, 12.1, 23, 35, 37.1 and 46 in the present data set). Besides lacking these, *Bufoniceps*, the sister taxon of *Phrynocephalus*, possesses at least one apomorphy not found in the latter genus, namely a very short tail. Golubev & Dunayev (1997) suggested that *Bufoniceps* should be expanded to include *P. mystaceus*, *P. maculatus*, *P. arabicus*, *P. ornatus*, *P. clarkorum*, *P. luteoguttatus*, *P. euptilopus*, *P. interscapularis* and *P. sogdianus*. These are all basal members of *Phrynocephalus* and their inclusion in *Bufoniceps* would create a new grouping that is clearly paraphyletic and reduce *Phrynocephalus* to a smaller and less well defined clade. The suggestion should consequently be rejected.

ACKNOWLEDGEMENTS. I am grateful to Jens Vindum (California Academy of Sciences for the loan of material of *Phynocephalus roborowskiii*, *P. rossikowi* and *P. strauchi*. Ed Wade drew Figures 7–11.

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Appendix 1 Data set for *Phrynocephalus and its relatives*. Figures above columns refer to characters listed on pp. 2–7. – indicates no data or character uncheckable or intermediate; v indicates character variable.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
1	Laudakia	0	0	0	0	0	0	0	v	v	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	Trapelus	0	0	0	0	0	0	0	0	1	0	0	0	v	v	0	v	0	0	0	0	0	0	0	0	0
3	Bufoniceps	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	2	1	0	0	0	0	0	0	0
4	P. mystaceus	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	2	1	0	0	0	0	1	0	0
5	P. maculatus	2	0	0	2	0	0	1	0	0	0	0	1	0	0	0	0	2	1	0	1	0	0	1	0	0
6	P. arabicus	2	0	0	0	0	0	1	0	1	0	0	1	0	0	1	0	2	1	0	0	0	0	1	0	0
7	P. ornatus	2	0	1	0	0	0	0	0	0	0	0	2	0	0	1	1	2	1	–	0	1	1	1	1	0
8	P. clarkorum	2	0	1	0	0	0	0	0	0	0	0	1	0	0	1	1	2	1	–	0	1	1	1	1	0
9	P. euptilopus	2	0	1	0	0	0	1	0	1	0	0	1	0	1	0	0	2	1	–	0	0	0	1	1	1
10	P. luteoguttatus	2	0	1	0	0	0	1	0	1	0	0	2	0	1	1	0	2	1	–	0	1	0	1	1	1
11	P. interscapularis	2	0	1	0	0	0	0	1	0	0	1	2	0	1	1	0	2	1	1	0	1	0	1	1	0
12	P. sogdianus	2	0	1	0	0	0	0	1	0	0	1	2	0	1	1	0	2	1	1	0	1	0	1	1	0
13	P. scutellatus	2	0	0	0	0	0	1	0	1	0	1	1	1	0	1	0	2	1	0	0	0	0	1	0	0
14	P. golubevi	2	0	0	0	0	0	1	0	0	1	0	1	1	0	1	0	2	1	0	1	0	0	1	0	0
15	P. reticulatus	2	0	0	1	2	0	–	0	0	1	–	1	1	0	1	0	1	1	0	v	0	0	1	0	0
16	P. raddei	2	1	0	2	2	0	1	0	1	1	1	1	1	0	1	0	0	1	0	1	0	0	1	0	0
17	P. rossikowi	2	0	–	2	1	0	–	0	0	1	1	1	1	1	1	0	0	0	0	1	0	0	1	0	0
18	P. strauchi	2	1	0	1	0	0	–	0	0	1	1	1	1	0	1	0	0	v	0	1	0	0	1	0	0
19	P. persicus	2	1	0	2	2	0	0	0	1	1	1	1	1	1	1	0	0	0	0	1	0	0	1	0	0
20	P. helioscopus	2	1	0	1,2	0	0	0	0	–	1	1	1	1	0	1	0	0	0	0	v	0	0	1	0	0
21	P. forsythii	2	0	0	1	2	0	0	0	0	1	1	1	1	–	1	0	0	0	0	1	0	0	1	0	0
22	P. roborowskii	2	0	0	1	2	1	0	1	0	1	0	1	1	1	1	0	0	0	0	1	0	0	1	0	0
23	P. theobaldi	2	0	0	1	2	1	0	1	0	1	0	1	1	1	1	0	0	0	0	1	0	0	1	0	0
24	P. vlangalii	2	0	1	1	2	1	0	1	–	1	0	1	1	1	1	0	0	0	0	v	0	0	1	0	0
25	P. axillaris	2	1	0	1	2	0	0	0	0	1	0	1	1	0	1	0	0	v	0	v	0	0	1	0	0
26	P. guttatus	2	0	0	1	2	0	0	0	–	1	0	1	1	0	1	0	0	0	0	1	0	0	1	0	0
27	P. versicolor	2	1	0	1	2	0	0	0	0	1	0	1	1	0	1	0	0	0	0	1	0	0	1	0	0
28	P. przewalskii	2	0	0	1	2	0	1	–	–	1	0	1	1	0	0	0	0	0	0	1	0	0	1	0	0

Appendix 1 continued

		26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46
1	Laudakia	0	0	1	–	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
2	Trapelus	0	0	0	–	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0
3	Bufoniceps	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
4	P. mystaceus	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	1	1	0	0	0	1
5	P. maculatus	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	1
6	P. arabicus	0	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0	0	1	0	1
7	P. ornatus	0	0	0	0	0	0	1	1	0	1	1	2	1	2	0	1	1	0	1	0	1
8	P. clarkorum	0	0	0	0	0	0	1	1	0	1	1	2	1	2	0	1	1	0	1	0	1
9	P. euptilopus	1	1	1	0	0	0	1	0	0	1	1	2	1	2	0	0	1	1	1	0	1
10	P. luteoguttatus	1	1	1	0	0	0	1	0	0	1	1	2	1	2	0	0	1	1	1	0	1
11	P. interscapularis	0	0	1	0	0	1	1	0	0	1	1	2	1	2	0	1	1	1	1	0	1
12	P. sogdianus	0	0	1	0	0	1	1	0	0	1	1	2	1	2	0	1	1	1	1	0	1
13	P. scutellatus	0	0	0	1	0	0	0	0	0	1	0	2	1	2	2	–	–	0	1	0	1
14	P. golubevi	0	0	0	0	0	0	0	0	0	1	0	2	1	2	2	–	–	0	1	0	1
15	P. reticulatus	0	0	0	0	0	0	0	0	0	1	0	2	1	2	0	0	0	0	1	0	1
16	P. raddei	0	0	0	0	0	0	0	0	0	1	0	2	1	2	0	0	0	0	1	0	1
17	P. rossikowi	0	0	0	1	0	0	0	0	0	1	0	2	1	2	2	–	–	0	0	–	1
18	P. strauchi	0	0	0	1	0	0	0	0	0	1	0	2	1	2	2	–	–	0	0	–	1
19	P. persicus	0	0	0	1	0	0	0	0	0	1	0	2	1	2	2	–	–	0	0	0	1
20	P. helioscopus	0	0	0	1	v	0	0	0	0	1	0	2	1	2	2	–	–	0	0	0	1
21	P. forsythii	0	0	0	1	1	0	0	0	0	1	1	2	0	2	0	0	0	0	0	0	1
22	P. roborowskii	0	0	0	0	1	0	0	0	1	1	0	2	0	1	2	–	–	0	0	1	1
23	P. theobaldi	0	0	0	v	1	0	0	0	1	1	0	2	0	1	2	–	–	0	0	1	1
24	P. vlangalii	0	0	0	0	0	0	0	0	1	1	0	2	0	1	0	0	0	0	0	1	1
25	P. axillaris	0	0	0	0	0	0	0	0	0	1	0	2	1	1	0	0	0	0	0	0	1
26	P. guttatus	0	0	0	0	0	0	0	0	0	1	–	2	1	2	0	0	0	0	0	0	1
27	P. versicolor	0	0	0	0	0	0	0	0	0	1	0	2	1	2	1	0	0	0	0	0	1
28	P. przewalskii	0	0	0	0	0	0	0	0	1	1	0	2	1	2	0	0	0	0	0	0	1

Bull. nat. Hist. Mus. Lond. (Zool.) **65**(1): 15–21 Issued 24 June 1999

Rita sacerdotum, a valid species of catfish from Myanmar (Pisces, Bagridae)

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SYNOPSIS. *Rita sacerdotum* Anderson, 1879, is the valid name for the only species of the south Asian bagrid catfish genus *Rita* that resides in Myanmar. This species is distinguished from other species of *Rita* by a comparatively short dorsal-fin spine that never extends to the adipose fin base; palatal tooth patches, composed primarily of uniformly sized molariform teeth, that are in broad contact across the midline anteriorly, but diverge posteriorly and terminate in an acute point; and a small eye that is only about one-eighth to one-tenth the length of the head. *Rita sacerdotum* resides in the Sittoung and Ayeyarwaddy rivers, at least as far north as Myitkyina, Kachin State. This species is redescribed and a new key to the species of *Rita* is provided.

INTRODUCTION

The south Asian catfish genus *Rita* is broadly distributed in India, Bangladesh, Nepal, the Indus plain of Pakistan, and the Ayeyarwaddy system of Myanmar. Jayaram (1966) provided a systematic account of the species of the *Rita*, and subsequent reviews have been provided by Misra (1976), Jayaram (1977, 1981), and Talwar & Jhingran (1991). In each of these treatments, four species of *Rita* are recognized, although the specific names used for some of the species differ.

The identity of the single species of *Rita* that inhabits the Ayeyarwaddy River, the focus of this paper, also varies among these studies. This uncertainty has existed since the earliest accounts of the presence of *Rita* in Myanmar waters, its persistence due in part to the dearth of material available for study and an enigmatic proposal of a name for the Ayeyarwaddy species. I recently obtained additional specimens of this species, and this prompted me to reexamine the question of their identity. The discovery of the holotype of *Rita sacerdotum* Anderson, 1879, a specimen that has, for all intents and purposes, been lost since the species was named, revealed that there is only one species of *Rita* in the Ayeyarwaddy system, and that *Rita sacerdotum* is the valid name for that species.

METHODS AND MATERIALS

Measurements are all straight line distances. Specimen lengths are all reported as standard length. Institutional abbreviations follow Leviton *et al.* (1985). Other abbreviations used herein are: HL – head length; SL – standard length.

When refering to previously published accounts of the region and in the list of the specimens examined, I repeat the name Burma (or Burmah), for the country now known as Union of Myanmar. In all other places, I use Myanmar. Throughout the text, I use the officially accepted spellings: Yangon for Rangoon, Ayeyarwaddy for Irrawaddy, Bago for Pegu, and Sittoung for Sittang or Sitang.

MATERIAL EXAMINED

Rita chrysea, 54 specimens, 61–205 mm.
INDIA: *Orissa*, Mahanadi River at Cuttack, K. Jayaram, CAS 54540 (6:107–130 mm, 1 cleared & stained). Mahanadi River basin, Sonepur fish market, T. Roberts, 19–22 Feb 1985, CAS 61855 (43:61–205 mm). Mahanadi River at Amicut, Cuttack, K. Jayaram, 23 Oct 1954, SU 48799 (2:110–118 mm). *Bihar*, Sheonath River at Bisrampur, A. Herre, 13 Dec 1940, SU 41043 (1:106 mm).

Rita gogra, 6 specimens, 112–205 mm.
INDIA: *Andhra Pradesh*, Poona, Bombay Pres., A. Herre, 1940, SU 41044 (1:123 mm). *Maharashtra*, Godavari River, Nanden market, K. Jayaram, 10 Feb 1955, USNM 11494 (1:112 mm). *Karnataka*, Krishna River basin, Tungabahdra River or reservoir at Hospet, Hampi, or Kampli, T. Roberts, 28 Jan–3 Feb 1985, CAS 62088 (5:138–205 mm).

Rita kuturnee, 8 specimens, 57–97 mm.
INDIA: *Andhra Pradesh*, Tungabhadra River, K. Jayaram, 10 Feb 1955, USNM 114950 (3:61–88 mm); Tungabhadra River, at Kurnool, K. Jayaram, 10 Feb 1955, SU 48798 (2:57–59 mm). *Karnataka*, Krishna River basin, Tungabahdra River or reservoir at Hospet, Hampi, or Kampli, T. Roberts, 28 Jan–3 Feb 1985, CAS 62077 (1:59 mm). *Maharashtra*, Poona, A. Herre, 9 Apr, 1937 SU 34868 (2:83–97 mm).

Rita rita, 16 specimens, 24–258 mm.
INDIA: *Bihar*, Ganges River at Patna, T. Roberts, Apr–May 1996, CAS 92501 (1:61 mm). *Uttar Pradesh*, Allahabad, Ganga River, 8–12–1974 [sic], USNM 317823 (1:214 mm). *West Bengal*, Hugli River at Pulta, A. Herre, 23 Oct 1954, SU 34866 (10:70–94 mm, one additional specimen in lot, not examined). Calcutta, A. Herre, 9 Apr 1937, SU 34867 (2:187–194 mm). Calcutta, A. Herre, 6 Apr 1937, SU 14132 (1:258 mm). BANGLADESH: *North Central Region*, Tangail District, Ganges River basin, 5 Nov 1992, CAS 92411 (1:24 mm).

Rita sacerdotum, 23 specimens, 22–690 mm.
MYANMAR: '3rd Defile of Irrawaddy River, Upper Burmah, Dr. Anderson', BMNH 1875.8.4.7 (1:690 mm, holotype of *Rita sacerdotum*). Sittoung River, E. Oates, BMHN 1891.11.30:242 (1:285 mm), BMNH 1891.11.30.343 (1, disarticulated dry skeleton, not measured). *Ayeyarwaddy Division*, Wa-ke-ma town market, 17 Sep 1996, Myint Pe, NRM 40631 (4:107–135 mm). *Bago Division*, Bago market, 25 Oct 1997, C. J. Ferraris, Myint Pe, Mya Than Tun, BMNH 1998.3.11.1 (1:150 mm), CAS 99210 (1:126 mm). *Yangon Division*, Hlaing River, 31 Oct 1997, C. J. Ferraris, Mya Than Tun, CAS 99309 (10:22–70 mm). Insein market (northern Yangon), July 1996, Myint Pe, AMNH 224490 (1:195 mm). Insein market, Nov 1997, Pe, C. J. Ferraris, Mya Than Tun, USNM 348211 (2:191–203

mm). Rangoon Market, A. Herre, 14 Nov 1940, SU 39869 (2:172–184 mm).

HISTORY OF THE IDENTIFICATION OF THE AYEYARWADDY *RITA*

Day (1873) provided the first mention of *Rita* from the Ayeyarwaddy River in his account of the fishes of India and British Burma, under the name *Rita ritoides* (Valenciennes, 1840), a name now considered a junior synonym of *Rita rita* (Hamilton, 1822) (Jayaram, 1966). Several years later Day (1877) included the Ayeyarwaddy within the range of *Rita buchanani* Bleeker 1853, another junior synonym of *Rita rita*. Day acknowledged that *Rita ritoides* might have been the appropriate name for the species, but departed from his earlier use of that name and, without explanation, used *R. buchanani* instead.

The name *Rita sacerdotum* was proposed in Anderson (1878 [1879]) for a species from the middle reaches of the Ayeyarwaddy River. As noted by Jayaram (1966), several authors have attributed the description of this species to Francis Day, presumably on the basis of a statement in the book's acknowledgements (Anderson, 1878 [1879]: xxiv) which states that Day 'favored me with a list of fishes collected on the First Expedition, and undertook the description of certain species'. However, the species described by Day are those published elsewhere (Day 1870a, 1870b, 1871) and not the ones that first appeared in Anderson (1878 [1879]). The style of writing and the choice of anatomical characters are significantly different from that of Day's other published species descriptions. It is important to note that the actual publication date for the species description, and for the volume as a whole, differs from that on the title page. A statement in the published corrigenda that follows the title page clearly indicates that publication was unexpectedly delayed past 1878, the date on the title page, and was issued, instead, in 1879.

Anderson's (1878 [1879]) description of *Rita sacerdotum* was based on his field observations of living examples of the species that were treated as pets by the residents of a Buddist temple as well as a single specimen that was secured and illustrated. The account was published in a summary of an expedition to western Yunnan, along with accounts of other species from Yunnan and 'upper Burmah'. Because of the title of the publication, some accounts have mistakenly cited the type locality of this species as Yunnan.

In neither Day's (1888) Supplement to the fishes of India, nor his modified and updated version of his earlier book (Day, 1889) is Anderson's *Rita sacerdotum* (or the other two fish species described by Anderson) mentioned. The reason for this curious omission is unknown. It is possible, but highly unlikely, that Day was unaware of Anderson's book with its included species accounts. Day and Anderson must have known each other, as evidenced by the above mentioned acknowledgement of Day's assistance by Anderson. Day may have considered the species to lie outside the scope of his own book, as it was described from Upper, rather than British, Burma. For whatever reason, Day's failure to include mention of *Rita sacerdotum* in either of the two accounts he published on fishes of southern Asia appears to have been a major factor in the subsequent oversight of Anderson's name.

Vinciguerra (1890) reported on a specimen of *Rita* from the vicinity of Yangon, under the name *Rita ritoides*. He noted that his specimen differed from the typical form of *R. ritoides* in the relative length of the dorsal spine and the shape of the humeral process. Vinciguerra compared his specimen with the description of *Rita sacerdotum*, and decided that it too differed from his specimen on several features, but that the two specimens shared a comparatively short dorsal-fin spine. On that basis, he concluded that two distinct forms of *Rita ritoides* existed, one in Myanmar and one in India.

After a period of more than a half century without any mention of *Rita* from the Ayeyarwaddy, Jayaram (1966) revised the genus *Rita* and concluded that two species were found in Myanmar: *Rita rita* and *R. kuturnee* (Sykes, 1839). Inclusion by Jayaram of *Rita rita* in the fauna of Myanmar appears to be based solely on the literature accounts of Day (1873) and Vinciguerra (1890). Jayaram tentatively placed *Rita sacerdotum* into the synonymy of that species. All of the specimens from the Ayeyarwaddy River, or elsewhere in Myanmar, that were cited as having been examined by Jayaram were listed in the account of *Rita kuturnee*. However, *Rita kuturnee*, and its widely used junior synonym *Rita hastata* (Valenciennes, 1840), is a species otherwise known only from the rivers of peninsular India. Talwar & Jhingran (1991) doubted that *R. kuturnee* actually occurs in Myanmar, even though Jayaram (1977, 1981) had continued to list it in subsequent accounts of the distribution of that species.

Misra (1976) included Myanmar in the distribution of *Rita rita*, but not that of *R. kuturnee*. In his abbreviated synonymy for *R. rita*, there is no mention of *R. sacerdotum*, and the publication of Anderson (1878 [1879]) is likewise missing from the literature cited. Talwar & Jhingran (1991) similarly listed *Rita rita* as the only species of *Rita* from Myanmar, but they tentatively included *Rita sacerdotum* in the synonymy of that species.

IDENTITY OF THE AYEYARWADDY SPECIES OF *RITA*

Although much of the recent literature suggests that the *Rita* species inhabiting the Ayeyarwaddy River is *Rita rita*, the species in that basin is, in fact, clearly distinct from *R. rita*. During this study, specimens of *R. rita*, from various parts of the Ganges basin, the type locality of the species, were found to exhibit characters lacking in specimens from the Ayeyarwaddy. As first noted in Jayaram (1966), the palatal teeth of the Ayeyarwaddy *Rita* specimens are not arranged in the broad, elliptical patches characteristic of *R. rita* but, instead, in 'pear-shaped' patches that tapered posteriorly nearly to a point (Figure 1a). In addition, the dorsal-fin spine of *R. rita* is long and stout with its length at least equal to the head length. The adpressed spine usually extends well past the adipose-fin origin, at least in large individuals. Day (1877) noted that the relative size of the spine was apparently allometric, and that in small individuals it may only equal the head length, but that in larger individuals it may exceed 1.3 times HL. In Ayeyarwaddy specimens, in contrast, the dorsal-fin spine is never as long as the head and, more typically, it is shorter than the head minus the snout, even in the largest specimens.

In contrast to the prevailing view, Jayaram (1966) identified the Ayeyarwaddy specimens as *R. kuturnee*. It appears that his conclusion is based primarily, but erroneously, on the similarity of the palatal tooth patches in the two species. In placing the Ayeyarwaddy *Rita* into *R. kuturnee*, he also looked beyond several striking differences between the two species. For example, the eye size of *R. kuturnee* is significantly larger than that of the Ayeyarwaddy *Rita*. In his diagnosis of *R. kuturnee*, Jayaram (1966) lists the eye size as 'Eye 3.07 (2.70 to 4.70 of up to 8.80 in specimens from Burma) in head length; 1.35 (1.00 to 1.50 or 3.90) in interorbital space width; 1.39 (1.00 to 1.50 or 3.00) in snout length.' It is possible that Jayaram interpreted the consistant disparity in eye proportions between the Indian and Ayeyarwaddy specimens as a result of allometric growth in *R. kuturnee*. All of the specimens he examined from

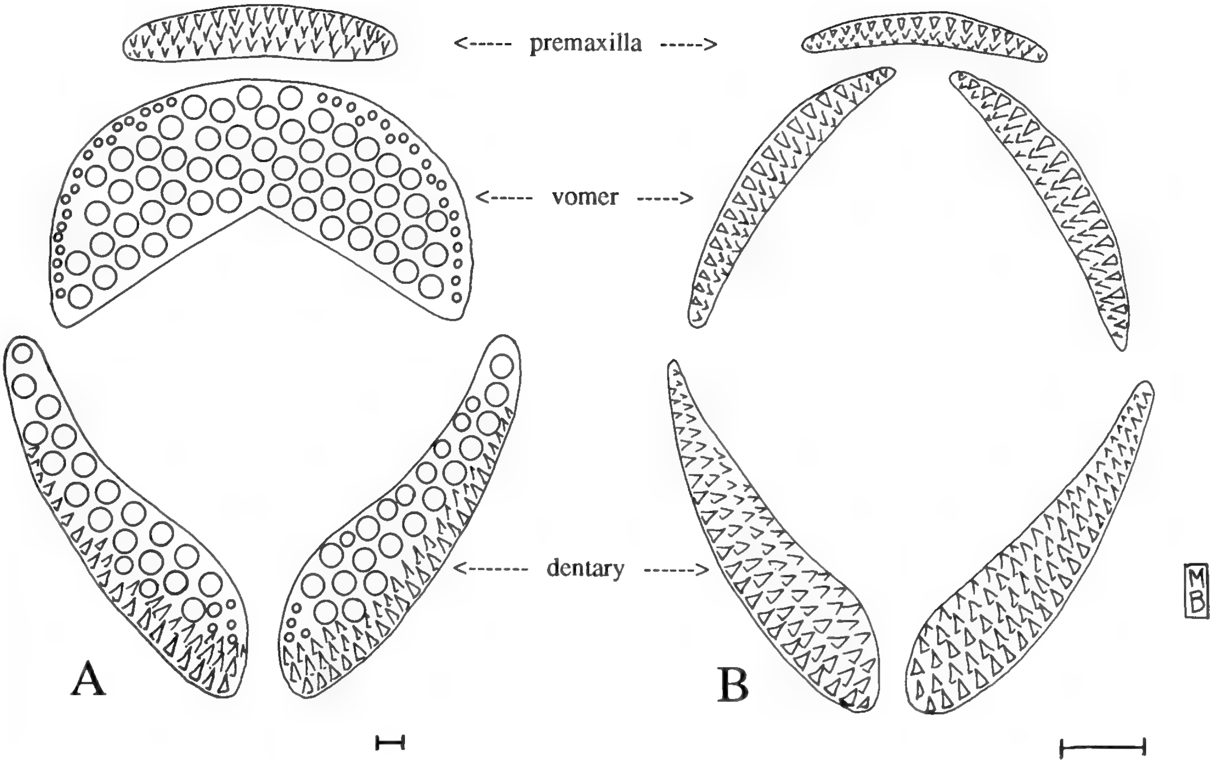

Fig. 1 Diagrammatic representation of tooth patches on jaws and palate of *Rita* species. A. *Rita sacerdotum* Anderson, 184 mm, SU 39869. Scale bar = 1 mm.; B. *Rita kuturnee* (Sykes), 97 mm, SU 34868.

peninsular India are substantially smaller (36 to 103 mm) than any of the specimens listed from Myanmar (184 to 318 mm). In the Ayeyarwaddy specimens that I examined (22 to 285 mm), the eye length is always 8 to 10 times in the head length. Curiously, despite the observation that the Ayeyarwaddy specimens has small eyes, Jayaram used the eye size of *R. kuturnee* to help distinguish it from *R. chrysea*, a species for which he lists the eye diameter as '3.76 (2.83 to 5.22)' in head length. Clearly he did not take into account the Ayeyarwaddy specimens in this diagnosis of *R. kuturnee*.

The shape of the palatal tooth patches, a characteristic on which Jayaram placed heavy emphasis, also differs between *Rita kuturnee* and the Ayeyarwaddy form. The 'pear-shaped' tooth patches that Jayaram (1966, Figure 1b) described and illustrated as characteristic of *R. kuturnee* appear, in fact, to be those of the Ayeyarwaddy river species, and not *R. kuturnee*. In all of the specimens of *R. kuturnee* that I examined, the palatal tooth patches are slender, crescent-shaped arches that are either separated at the midline (Figure 1b), or meet only for the width of a single row of teeth. The palatal tooth-patches in *Rita kuturnee* have stout conical teeth, larger in size than those of the premaxilla, rather than the broadly rounded, or molariform ones that predominate in the palate of the Ayeyarwaddy species (Figure 1a). As with the size of the eye, it is possible that Jayaram assumed that his specimens of *R. kuturnee* from peninsular India were juveniles, with incompletely developed palatal tooth patches, and that the adult condition in the peninsular population is like that in the Ayeyarwaddy specimens. Even in the smallest examined specimens from the Ayeyarwaddy basin the palatal tooth patches are broadly in contact across the midline and are composed primarily of molariform teeth. Thus, I conclude that the Ayeyarwaddy form is not conspecific with *Rita kuturnee*.

The Ayeyarwaddy River *Rita* population has never been considered conspecific with either of the two other Indian *Rita* species, *R. chrysea* Day, 1877 and *R. gogra* (Sykes, 1839), and I have found no reason to assign either name to the Ayeyarwaddy fishes. *Rita chrysea*, restricted to the Mahanadi River and nearby tributaries in Orissa and considered to be the smallest species of *Rita* (Talwar & Jhingran, 1991), is characterized by a large eye (2.8 to 5.2 in HL) and by having a broad, nearly rectangular, patch of molariform teeth that extends across the midline of the palate (Jayaram, 1966). *Rita gogra*, which is sometimes listed as *Rita pavimentata* (Valenciennes, 1840) (e.g., Misra, 1976; Talwar & Jhingran, 1991), is known only from rivers of the Deccan region of peninsular India, including the Krishna, Harda, Godavari, Tungabhadra, Manjra, Bhima, and Mutha-Mula (Jayaram, 1966). Although similar in overall appearance with the Ayeyarwaddy *Rita*, *R. gogra* can be distinguished immediately by the unusual shape of its head. The dorsal surface of the head, posterior to the orbits, is dominated by a bilaterally symmetrical swelling formed by massive extensions of the adductor mandibulae muscle that cover the cranial roofing bones. All other species of *Rita*, including the Ayeyarwaddy species, have the dorsal surface of the cranium covered only with skin, through which the cranial roofing bones can easily be palpated. In addition, the Ayeyarwaddy *Rita* can be distinguished from *R. gogra* by the color of the mental barbel (black in *R. gogra*, white in the Ayeyarwaddy species). The palatal tooth-patch in *R. gogra* has finely conical teeth anteriorly and increasingly large molariform teeth posteriorly (Jayaram, 1966).

Thus, it must be concluded that the Ayeyarwaddy *Rita* is not conspecific with any of its Indian congeners. The only remaining name that might apply is *Rita sacerdotum*, which was described from the Ayeyarwaddy. The description and published illustration of that species, however, only vaguely resembles a *Rita*, and characteristics of the Ayeyarwaddy species are either absent from the description, or in variance with the illustration. Although Jayaram (1966) followed Vinciguerra (1890) in placing *Rita sacerdotum* into the synonymy of *Rita rita*, he place the specimens he examined from the Ayeyarwaddy into a second species of *Rita*. I have been unable, so far, to find any specimens that represented a second species from Myanmar. Clearly, an examination of the holotype of *Rita sacerdotum* was necessary to determine whether it indeed represented a species of *Rita* different from the one that I, and others, have observed.

THE HOLOTYPE OF *RITA SACERDOTUM* ANDERSON

Anderson (1878 [1879]) did not indicate where the holotype of *Rita sacerdotum*, or any of the other species described in the same paper, were deposited. Although I expected to find the specimen in The Natural History Museum, London, the holotype was not listed in its type catalog, and there was no entry for *R. sacerdotum* in their species catalog. In fact, no specimen of *Rita* collected by Anderson was listed in the catalog. An exhaustive search through the registers did uncover a *Rita sacerdotum* collected by Anderson, without any indication that it was a holotype. With the assistance of the staff of the Fish Section of the Zoology Department, the specimen was found among the collection of stuffed, dried fish specimens. Its identity as the holotype was promptly made by comparsion of the stated locality information and by direct comparision with the published illustration.

It is puzzling that the specimen was never recognized as the holotype of *Rita sacerdotum*. Although the specimen was registered in 1875, prior to Anderson's publication, the register entry (BMNH 1875.8.4.7) lists the name and is surrounded by entries for the other species named by Anderson. It is even more suprising that although the specimen was registered with the new name during Albert Günther's tenure, he did not include the specimen in his personal annotated copy of his catalog (Günther, 1868) or annotate the register entry to indicate that the specimen was a holotype. Nonetheless, with the discovery of the holotype, it is now possible to clarify some peculiar features in the illustration of *Rita sacerdotum* and, with that information, finally resolve the identity of theAyeyarwaddy *Rita*.

The holotype of *Rita sacerdotum* is a dried, stuffed specimen, 69 cm in standard length (Figure 2). The specimen appears to have been placed on display at two different times, based on the fact that the stuffed skin has two forms of wire attachments. One set of mounts, extending from the ventral surface of the body, indicate that the specimen was at one time mounted freestanding, probably on a

Fig. 2 *Rita sacerdotum* Anderson, holotype, 69 cm, BMNH 1875.8.4.7.

Fig. 3 Published illustration of holotype of *Rita sacerdotum*, reproduced from Anderson (1878 [1879], pl. 79, Fig. 3).

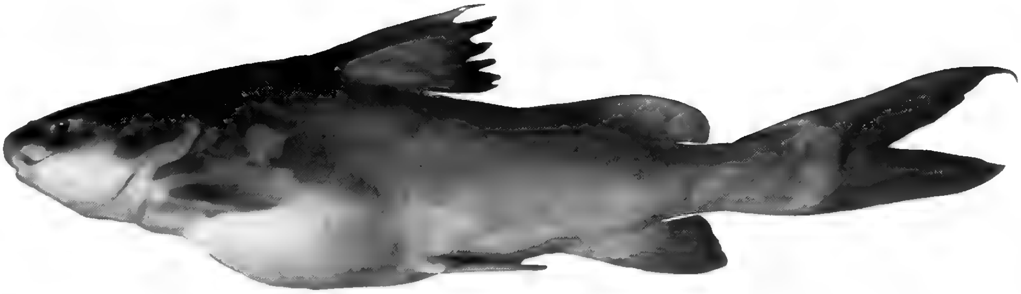

Fig. 4 *Rita sacerdotum* Anderson, 150 mm, BMNH 1998.3.11.1.

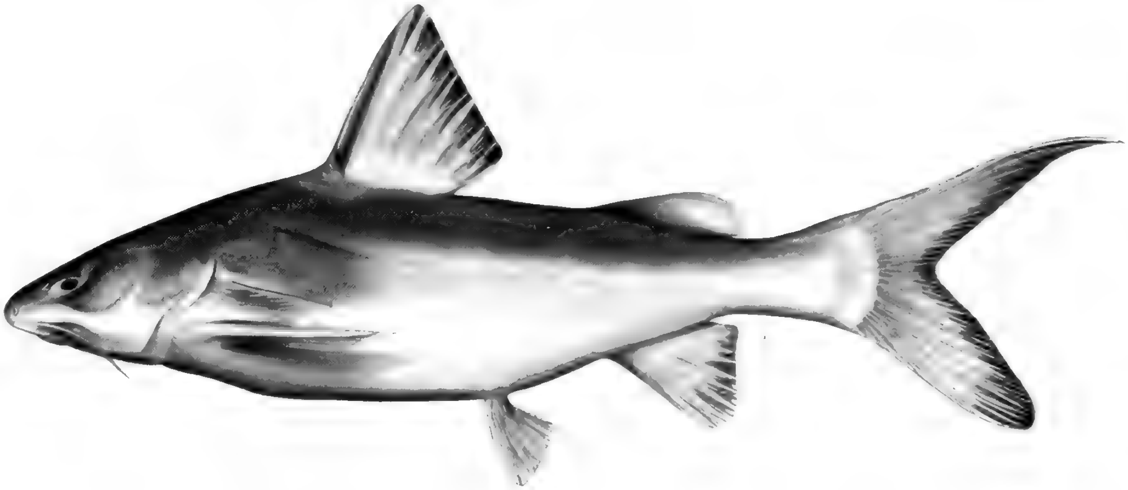

Fig. 5 *Rita sacerdotum* Anderson, 126 mm, CAS 99210.

wooden stand. A second pair of wires protrudes from the left side of the body, suggesting that the specimen was mounted on a wall, with the right side of the body on display.

The published illustration of the holotype (Figure 3) resembles the mounted specimen quite closely, except for some damage to the fins. Most importantly, the elongated caudal region of the body, which is identical in proportion to that in the illustration, suggests that the illustration was probably prepared from the dried mount rather than the freshly collected specimen. The body of the specimen is disproportionally long and the caudal region is far more slender and cylindrical than other specimens of *Rita* from the Ayeyarwaddy (Figures 4, 5). This unusual body form, and the illustration that resulted from drawing the dried specimen, have made comparison between the illustration and fresh specimens of the species problematic. On close inspection, it appears that the body of the mounted specimen must have been stretched well beyond the normal proportions of the species when it was stuffed. As Anderson collected only a single specimen, it is reasonable to assume that he or his taxidermist had no model to use to shape his specimen, once it was skinned and the vertebral column removed. Although the general shape of the body does not closely resemble the other specimens from the Ayeyarwaddy, other features of the body are, in fact, quite similar and clearly indicate that the holotype and the other available specimens are conspecific. The shape of the palatal tooth patches, the unusually short dorsal spine, and small eye combine to distinguish this species from its congeners. All of the specimens that I have examined exhibit this same suite of characters, albeit with some ontogenetic variation. It appears therefore that there is only one species of *Rita* in the Ayeyarwaddy system, and that the oldest available name for that species is *Rita sacerdotum*.

DIAGNOSIS AND REDESCRIPTION OF *RITA SACERDOTUM*

As noted above, the inaccurate taxidermic preparation of the holotype of *Rita sacerdotum* made the specimen longer than it would have been in life, and this precludes using the specimen for any proportional measurements standardized against the body length. Therefore, any statement in the description that relates a body measurement to the standard length does not include the holotype.

Diagnosis

Rita sacerdotum is readily distinguished from all congeners by the following combination of characteristics: eye small, its diameter 10–13% head length; dorsal-fin spine length no greater than the length of the head posterior to the snout; adpressed dorsal-fin spine does not extend to adipose-fin origin; and palate with a single crescent-shaped patch of primarily large, bluntly conical, teeth of approximately uniform size.

Description

Body elongate, slightly compressed anteriorly, progressively more compressed toward caudal fin. Body deepest at dorsal-fin origin, its depth at that point approximately equal to distance from nasal barbel to opercular margin; body depth decreases gradually to adipose-fin origin, more rapidly thereafter. Least depth at caudal peduncle approximately equals snout length. Skin of body and head covered with thick coat of mucous, anchored by fine filamentous projections from skin surface; filaments largest and most dense on chin and opercular margin of head, and, especially, on lateral surface of body ventral to dorsal fin.

Vent slightly anterior to anal-fin origin. Lateral line midlateral and straight from past tympanum to hypural plate; anterior portion of lateral line more dorsally situated; lateral line bent sharply in the dorsal direction onto base of upper caudal-fin lobe posterior of hypural plate margin. Lateral line pores extend laterally from canal, through thick mucous coat. Anterior canal pores ramify and spread in asymmetric pattern over pectoral-girdle elements and tympanum. Cephalic canal pores similarly branch over dorsum of head and onto opercle.

Head large, its length approximately 3½ times in SL; head slightly depressed, at pectoral-fin origin its depth approximately 80% its width; head depth at orbit approximately 2/3 its width. Dorsal profile of head straight from orbit to snout, slightly convex posteriorly; ventral profile nearly straight. Mouth nearly terminal; upper jaw slightly overhangs lower. Teeth in upper jaw conical and sharply pointed, in 6 to 8 irregular rows. Tooth-bearing surface of premaxilla long and nearly transverse, its long axis four to five times its short axis. Tooth-bearing surface of mandible elongated, tapering posteriorly. Teeth in lower jaw pointed and conical along anterior margin of jaw, approximately equal in size to those of upper jaw; two rows of bluntly rounded teeth, much larger in size than conical teeth, present mesially; only blunt teeth present along posterior part of mandible. Palate with coalesced tooth patch extending across midline. Tooth patch convex anteriorly, concave posteriorly, with nearly parallel lateral margins. Teeth on palate nearly all in form of bluntly rounded pegs, slightly larger in diameter posteriorly, except for one or two rows of somewhat smaller teeth along lateral and anteriolateral margins of toothplate. Gill rakers 24 to 29; anterior 8 to 10 rakers on lower arch rudimentary, shorter than intervening spaces; posterior rakers moderately long and thick.

Eye small, ovoid, with long axis parallel to body length; long diameter of orbit approximately 1/3 snout length, 1/5 interorbital width, and equal to or slightly greater than 1/10 head length. Orbital margin free.

Anterior naris situated along anterior margin of snout, its opening a short tube, flared at margin, directed anteriorly. Posterior naris remote from anterior naris, and slightly more laterally situated; its anterior margin located midway between snout tip and anterior margin of orbit. Naris surrounded by short rim, connected to nasal barbel anteriorly.

Head with three pairs of barbels. Maxillary barbel extends from fold between upper lip and skin of snout; barbel filamentous, without fleshy attachment to snout. Maxillary barbel short, not extending to margin of bony opercle. Nasal barbel short, its length approximately equal to orbital diameter; adpressed barbel reaches only to anterior margin of orbit. Ventral surface of head with single pair of mandibular barbels; barbel originates at vertical through anterior orbital margin; barbel filamentous, extending to, or nearly to, vertical through pectoral spine origin.

Dorsal surface of supraoccipital, posttemporal and pterotic bones granular, remainder of head covered with smooth skin. Adductor mandibulae does not extend onto dorsal surface of cranium.

Upper lip with several rows of short papillae along margin; papillae often multifurcated at tip. Lower lip broadly connected to skin of chin, separate laterally. Lip margin with papillae comparable to those of upper lip, at least medially.

Opercular membrane free from isthmus at margin, but attached more basally; membranes broadly connected across midline, but separated posterior to isthmus connection. Branchiostegal rays 7 or 8.

Dorsal-fin origin at approximately 40% of SL. Fin quadrangular, first ray longest and approximately two times that of last ray; last ray without membranous extension to body; fin margin straight. Fin base approximately 1/2 of HL and shorter than interspace between dorsal fin and adipose fin. Dorsal-fin spine stout, with sharply pointed tip. Spine length equals head length minus snout, or approximately 15% SL. Anterior margin of spine produced into sharp keel, without serrations; lateral and posterior surfaces smooth. Dorsal spine preceded by fully formed spinelet. Dorsal fin preceded by coarsely granular predorsal bone; lateral extent of predorsal bone approximately equals that of supraoccipital spine. Dorsal fin rays II,7; posterior two rays appear as one, split at base.

Adipose fin large; anterior fin margin straight, convex distally. Fin extends posteriorly well past its posterior insertion.

Caudal fin deeply forked, lobes with acutely pointed tips; lobes slightly asymmetrical, dorsal lobe longer and sometimes with filamentous extension. Length of dorsal most primary ray approximately three times length of middle rays. Procurrant rays few, short, not extending anteriorly onto caudal peduncle. Caudal fin rays i,7,8,i.

Anal fin quadrangular, anterior rays longest; posterior rays progressively shorter, fin margin straight. Last ray not connected to caudal peduncle by membrane. Fin base short, approximately equal to that of adipose fin. Anal-fin origin slightly posterior to vertical through adipose fin origin. Anal-fin rays iv, 9–10.

Pelvic fin abdominal, its origin posterior to vertical through posterior insertion of dorsal fin. First branched ray longest, following rays only slightly shorter. Adpressed fin just reaches anal-fin origin. Pelvic-fin rays i,6.

Pectoral fin acutely pointed; first branched ray longest, its length approximately three times posterior-most ray. Pectoral-fin spine stout, sharply pointed at tip. Spine with short filament at tip, length of filamentous extension approximately equals snout length. Outer margin of spine produced into acute keel; keel very finely serrated for basal quarter, smooth for remainder of its length; in small specimens, most of spine margin covered with tiny transverse serrations. Inner spine margin with densely packed, pointed, retrorse serrations; serration height greater than length of space between successive serrations. Humeral process acutely pointed posteriorly, with a slightly rounded tip. In larger specimens, process becomes more rounded posteriorly, as in holotype (Figures 2, 3). Surface of humeral process granular, with granulations less coarse than those of cranial surface. Pectoral-fin rays I,10 or I,11.

Coloration in preservative

Body gray, darker dorsally, gradually becoming lighter ventrally; abdomen nearly white. Head dark gray dorsally, white ventrally; transition between gray and white regions fairly abrupt, occuring ventral to eye and approximately in line with maxillary barbel origin. Operculum gray with white margin. Orbit surrounded by distinct white ring. Maxillary barbel dark grey, mental barbel nearly white.

Dorsal, anal, and pectoral fins pale, with broad black margin. Pelvic fin uniformly pale or with some indication of dark margin. Caudal fin with fine dark margin on middle rays; darkened margin progressively larger toward lobe tips.

Distribution

Rita sacerdotum appears to be distributed widely through the Ayeyarwaddy River basin of Myanmar. Specimens examined during this study were all from the lower portions of the basin, but I observed a few large individuals in markets as far upriver as Mandalay. In addition, *Rita* is seen occasionally in the Myitkyina market (U Tun Shwe, pers. comm.). Outside of the Ayeyarwaddy basin and its extensive delta, there is one record of specimens from the Sittoung River (BMNH 1891.11.30.242–243), and two from the Bago River (BMNH 1998.3.11.1 and CAS 99210).

Natural History

Little is known about *Rita sacerdotum*. While small specimens, up to about 25 cm, are routinely found in markets of Yangon and smaller delta villages, at least during the rainy season (April to September; U Myint Pe, pers. comm.), large specimens are only rarely seen in markets. All of the specimens examined during this study appear to be juveniles and there is no published indication of the size of maturity for this species.

Individuals as small as 22 mm were obtained from the tidal rivers in the vicinity of Yangon in November, 1997. The presence of these tiny individuals in the lower course of the river suggests that *Rita* may reproduce in the estuarine part of the river and disperse more widely throughout the river at a larger size. This idea is supported by anecdotal reports that large numbers of large *Rita* appear at an island pagoda, in the middle reaches of the Ayeyarwaddy River, for a short period of time during monsoon season (U Nyi Nyi Lwin, pers. comm.). This may be indicative of a spawning migration.

Examination of the gut contents of a few specimens revealed that *Rita sacerdotum* feeds on a variety of aquatic and terrestrial invertebrates. Several specimens contained fragments of small glass prawns, and others contained pieces of winged insects. A comprehensive study of the food habits is not possible at this time due to the relatively small number of specimens available and the fact that the specimens in collections represent only juveniles.

KEY TO SPECIES OF *RITA*

1. Dorsal surface of head, between eyes and occipital spine, covered with thick layer of muscle; pelvic fin black .... *Rita gogra* (rivers of the Deccan region of peninsular India)

   Dorsal surface of head covered only with skin; pelvic fin pale 2

2. Eye small, 10–13% HL 3

   Eye large, 30–40% HL 4

3. Dorsal-fin spine as long, or longer than length of head, adpressed spine extends to or beyond adipose-fin origin (in specimens greater than 100 mm); palatal teeth in two elliptical patches, not meeting at midline; teeth on posterior extent of lower jaw and palate molariform, much larger than anterior teeth .... *Rita rita* (Ganges River basin)

   Dorsal-fin spine no longer than head minus snout, adpressed spine not reaching adipose-fin origin; palatal teeth in a single crescent patch that extends across midline of palate; teeth on palate more or less uniform in size (Figure 1A) ....
   Rita sacerdotum (Myanmar: Ayeyarwaddy and Sittoung River basins)

4. Palatal teeth in slender patches along lateral margin of palate, no larger than teeth in upper jaw and not meeting at midline (Figure 1B), dorsal-fin spine smooth anteriorly, except for few serrae basally .... *Rita kuturnee* (rivers of Deccan region of peninsular India)

   Palatal teeth in large quadrangular patch that covers most of palate; teeth large and molariform in middle of patch, smaller laterally; dorsal-fin spine with single row of antrorse serrae, for at least basal 2/3 of spine length .... *Rita chrysea* (Mahanadi River and nearby tributaries in Orissa)

ACKNOWLEGEMENTS. Examination of specimens for this study was facilitated by David Catania and William Eschmeyer (CAS), Darrell Siebert and Oliver Crimmon (BMNH), and Richard Vari (USNM). Tyson Roberts provided valuable insights during early stages of this study. The photograph of the holotype of *Rita sacerdotum* was arranged by Darrell Siebert and taken by Phil Hurst (BMNH). Al Leviton provided the photographic reproduction of the published illustration of *Rita sacerdotum*, from his personal copy of Anderson (1878 [1879]). Molly Brown drew figure 1 and Alison Schroeer drew figure 5. Travel to Myanmar was undertaken as part of a series of consultancies for the United Nations Food and Agriculture Organization. Kent Carpenter and Dora Blessich of that organization were instrumental in making these trips possible. Collection of specimens in Myanmar was made possible by the Myanmar Department of Fisheries; several individuals, including U Hla Win, U Nyi Nyi Lwin, U Myint Pe and U Mya Than Tun, provided me with assistance and valuable information. Financial support to travel to London and to examine specimens at The Natural History Museum was provided by TWA and the Inhouse Research Fund of the California Academy of Sciences. Without the help of all of these persons and organizations, this study could not have been undertaken. The manuscript was improved by comments from James Atz, Nigel Merrett, Darrell Siebert and Richard Vari.

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Bull. nat. Hist. Mus. Lond. (Zool.) **65**(1): 23–29 Issued 24 June 1999

Indian Ocean echinoderms collected during the *Sindbad Voyage* (1980–81): 4. Crinoidea

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CONTENTS

SYNOPSIS. Thirty species of shallow-water Crinoidea, representing eighteen genera in six families, are recorded from collections made during the *Sindbad Voyage* (Oman to China) from the Lakshadweep (Laccadive) Islands, Sri Lanka and Pula Wé Sumatra). Following the zoogeographic subdivisions of Clark and Rowe (1971), extensions of range are recorded for at least six of the species: *Clarkcomanthus albinotus* (Indonesia/East Indies); *Comanthus briareus* (Sri Lanka area); *Comanthus gisleni* (Sri Lanka area & Indonesia/East Indies); *Comanthus suavia* (Sri Lanka area & Indonesia/East Indies); *Comanthus wahlbergii* (Maldive area, Sri Lanka area & Indonesia/East Indies), and *Oxycomanthus bennetti* (Indonesia/East Indies); and possibly also *Comaster parvicirrus* (Sri Lanka area – doubt about earlier record) and *Comaster multifidus* (Maldive area – specimens poorly preserved). In addition to the taxonomic treatment, ecological information for each crinoid species (habitat types, depth range) is provided and broadly analysed.

INTRODUCTION

Systematically, crinoid taxonomy has undergone relatively few changes since the monumental works of A.H. Clark (1915–1967), the major exception to this being the recent revisions to the family Comasteridae by Hoggett and Rowe (1986) and Rowe, Hoggett, Birtles and Vail (1986).

This paper is the fourth in a series reporting the collection of echinoderms made during a cruise by one of us (ARGP) across the Indian Ocean from Oman to China. The expedition was undertaken in a replica of an ancient Arab sailing vessel, 'Sohar'. Systematic accounts of the other echinoderm classes have already been published (Price & Reid, 1985; Marsh & Price, 1991; Price & Rowe, 1996).

Thirty species of shallow-water crinoids from six families are listed, including nine new distribution records. Generally, comments are made where the record extends or modifies a range of distribution, or to clarify the identification. Where no comment is offered, the species was already known from the region and is widespread in the Indo-West Pacific.

MATERIALS AND METHODS

Specimens were collected by one of us (ARGP) and other expedition members at localities from Chetlat Island, Lakshadweep (Laccadives), Sri Lanka and Pula Wé, Sumatra (Indonesia). Details of sampling localities are shown in Figure 1. Sampling was undertaken principally on coral reefs using scuba. At each locality, details of habitat type and depth range were recorded, along with the number of individuals of each species. The number of specimens collected is placed in parenthesis after each sample number in the Material lists for each species. Material was fixed and preserved using standard methods (Lincoln & Sheals, 1979). Conditions on board and for specimen storage on 'Sohar' were not as sophisticated as on modern research vessels. Hence not all specimens returned were in good condition.

Specimens were identified by JIMC. Where the identification was uncertain, due to the changes to crinoid taxonomy by Rowe, Hoggett, Birtles and Vail (1986) and Hoggett and Rowe (1986), confirmation was sought from one of the authors of those papers. In some cases, subsequent re-examination of specimens has engendered doubt, and this doubt is expressed in the text of this paper.

Where three or more specimens of a species were collected, representative specimens of that species were sent to the Singapore Museum (SM), as the regional museum; otherwise material was divided between the Natural History Museum (NHM), London, and the Western Australian Museum (WAM), Perth.

Species are listed in families, and within each family, alphabetically by genus and species.

RESULTS

Throughout this account synonymy has been confined, where possible, to a single reference from which the original reference can be traced.

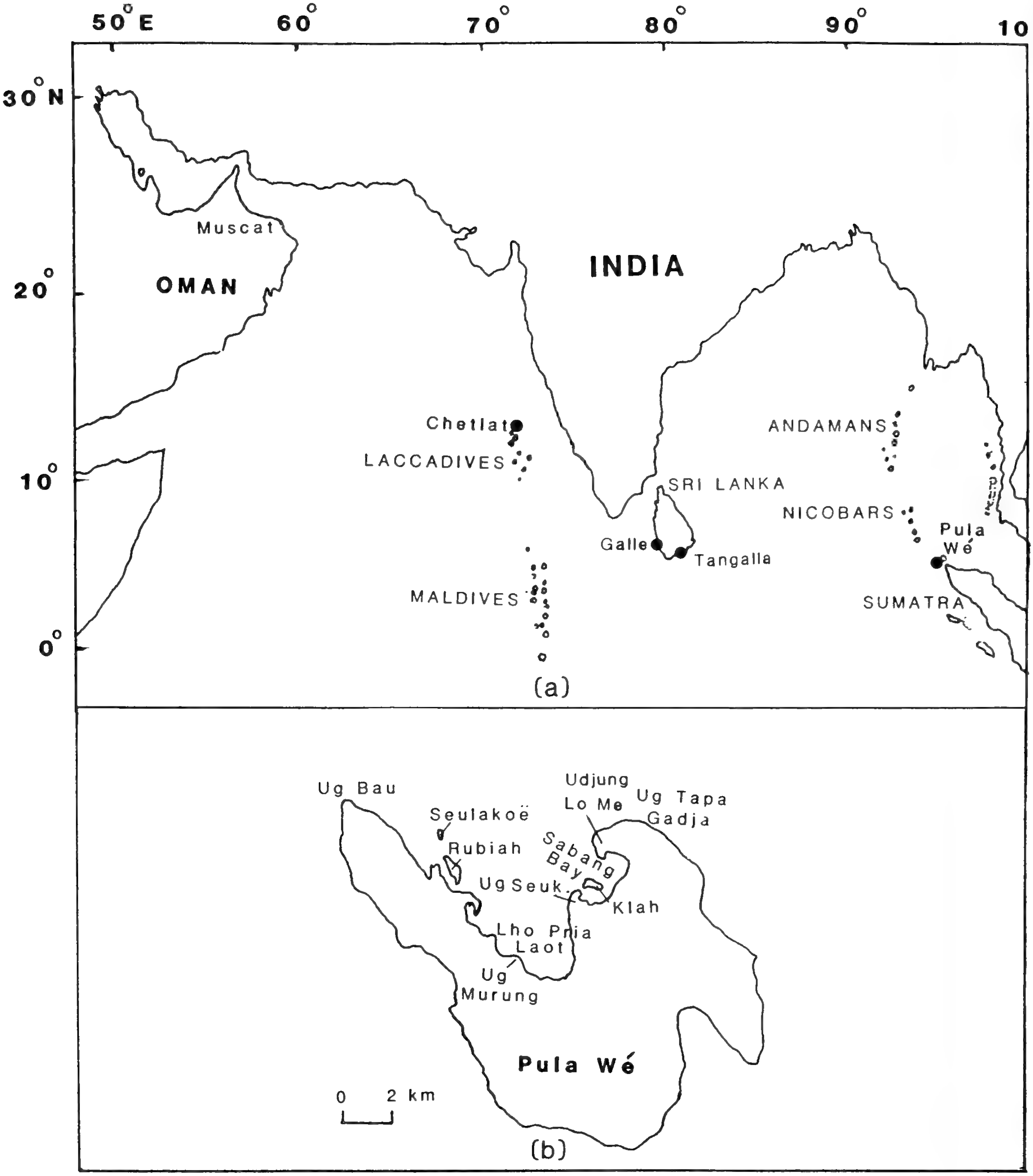

Fig. 1 (a) Map of northern Indian Ocean showing sampling areas (●) during *Sindbad Voyage*, with insert (b) for Pula Wé Sumatra.

Class Crinoidea

Family COMASTERIDAE

1. *Alloeocomatella pectinifera* (A.H. Clark, 1911)

See. Clark and Rowe, 1971:6–7; Hoggett and Rowe, 1986:122; Messing, 1995: 644.

Material. NHM – 810501C/2 (2), 810505C/1 (1); WAM – 810425F/2 (1); SM – 810421A/1 (1).

Collection sites. Sabang Bay, Seukundo, and Ug Seukundo, Pula Wé, Sumatra.

Habitats and depth range. Subtidal rock/coral, coral reef, on gorgonian; 2–30m.

Comments. The species was described by A.H. Clark (1911) and placed (with reservation) in the genus *Comissia*, later to be included in a new genus *Alloeocomatella* by Messing (1995). The species has been found in the Maldives, Indonesia, the Great Barrier Reef (GBR) of Australia, Papua New Guinea, New Caledonia and the Marshall Islands.

2. *Capillaster multiradiatus* (Linnaeus, 1758)

See. Clark and Rowe, 1971:6–7.

Material. NHM – 810422E/3 (1), 810423C/4 (2), 810425F/2 (4), 810426B/1 (1), 810427D/3 (2), 810428D/2 (1), 810430A/1 (1), 810430A/7 (1), 810430A/23 (1), 810430A/30 (1), 810430A/31 (1), 810504A/2 (1); WAM – 810422C/3 (1), 810422D/9 (1), 810424D/5 (1), 810425B/1 (2), 810525E/1 (2), 810425E/2 (2), 810427D/1 (1), 810428D/1 (1), 810430A/11 (1), 810430A/22a (1), 810430A/25 (1 of 2), 810430A/24b (1), 810430A/29 (1); SM – 810422C/4 (1), 810422D/7 (1), 810424B/4 (1), 810425F/1 (4), 810425F/4 (2), 810425F/5 (1), 810426A/1 (1), 810430A/10 (1), 810430A/21b (1), 810430A/21d (2), 810430A/25 (1 of 2).

Collection sites. Klah, Seulakoe, Sabang Bay, Ug Murung, Ug Tapa Gadja, Ug Seukundo and Rubiah, Pula Wé, Sumatra.

Habitats and depth range. Subtidal rock, coral reef, coral rubble, fire coral, soft coral and gorgonian; 2–30m.

Comment. This species is well-known across the Indo-Pacific region. However, its habitat varies; in some regions it inhabits exposed situations, in others it is cryptic. Specimens have been recorded from 0.5–1 m in Madagascar, to 77 m in the Bay of Bengal (Clark, 1972). In this collection, habitat and depth also varied.

3. *Capillaster sentosus* (Carpenter, 1888)

See. Clark and Rowe, 1971: 6–7.

Material. WAM – 810501C/4 (1).

Collection site. Ug Seukundo, Pula Wé, Sumatra.

Habitat and depth. Subtidal rock; 20m.

4. *Clarkcomanthus albinotus* Rowe, Hoggett, Birtles and Vail, 1986.

See. Rowe, Hoggett, Birtles and Vail, 1986: 238.

Material. WAM – 810428E/1(1).

Collection sites. Ug Tapa Gadja, Pula Wé, Sumatra.

Habitat and depth. Soft coral, 2–10m.

Comment. This is a marked extension of range for this species, previously only recorded from the Great Barrier Reef, Papua New Guinea (Messing, 1994) and Japan.

5. *Clarkcomanthus littoralis* (Carpenter, 1888)

See. Rowe, Hoggett, Birtles and Vail, 1986: 236.

Material. NHM – 810423D/1 (broken), 810425C/3 (1), 810428C/4 (2); WAM – 810420A/2 (fragmented), 810430A/12 (1), 810501A/3 (1), 810504C/4 (1); SM –810421C/2 (1), 810428E/2 (1), 810430A/19 (1).

Collection sites. Klah, Seukundo, Ug Bau, Subang Bay, Ug Tapa Gadja and Ug Seukundo, Pula Wé, Sumatra.

Habitats and depth range. Subtidal rock/coral, coral reef; 2–10m.

6. *Clarkcomanthus luteofuscum* (H.L. Clark, 1915)

See. Rowe, Hoggett, Birtles and Vail, 1986: 233.

Material. WAM – 810427D/1 (1).

Collection sites. Ug Murung, Pula Wé, Sumatra.

Habitat and depth. Soft coral, 2–10m.

7. *Comanthina nobilis* (Carpenter, 1884)

See. Rowe, Hoggett, Birtles and Vail, 1986: 243.

Material. NHM – 810425A/18d (2), 810425D/1 (1), 810430A/34 (1); WAM – 810425A/18e (2), 810430A/16 (1); SM – 810425A/18 (1), 810430A/2 (1), 810501A/5 (2).

Collection sites. Ug Murung and Ug Seukundo, Pula Wé, Sumatra.

Habitats and depth range. Subtidal rock/coral, coral reef; 6–30m.

8. *Comanthina schlegelii* (Carpenter, 1881)

See. Clark and Rowe, 1971:6–7; Rowe, Hoggett, Birtles and Vail, 1986: 244.

Material. NHM – 810422D/4 (1), 810423A/2 (1), 810430A/13 (1), 810504C/3 (1); WAM – 810423C/2a (1), 810430A/6 (1), 810504C/1 (1); SM – 810421C/1 (1), 810421C/4 (1), 810424D/3 (1).

Collection sites. Seukundo, Klah, Ug Bau and Ug Seukundo, Pula Wé, Sumatra.

Habitat and depth range. Subtidal rock and coral reef; 5–20m.

9. *Comanthus briareus* (Bell, 1882)

See. Rowe, Hoggett, Birtles and Vail, 1986:218

Material. NHM – 810424B/5 (1); WAM – 810204A/8 (1).

Collection sites. Kalpitiya, Sri Lanka; Seulakoe, Pula Wé, Sumatra.

Habitat and depth range. Coral reef; 3–5m, 20–30m.

Comment. The Sri Lankan specimen is a new locality record for this species, and extends its range west into the Indian Ocean from Indonesia.

10. *Comanthus gisleni* Rowe, Hoggett, Birtles and Vail, 1986.

SEE. Rowe, Hoggett, Birtles and Vail, 1986: 219.

MATERIAL. NHM – 810124A/1 (1), 810204A/3 (1),810430A/14 (1), 810430A/22a (3), 810504B/1 (1); WAM – 810124A/1 (1), 810124A/6 (1), 810204A/2 (1), 810425F/1 (1), 810430A/15 (1); SM – 810422D/5 (1), 810430A/4 (1), 810430A/14 (1), 810504A/1 (1).

COLLECTION SITES. Galle and Kalpitiya, Sri Lanka; Klah, Sabang Bay, Ug Bau, Ug Seukundo and Rubiah, Pula Wé, Sumatra.

HABITATS AND DEPTH RANGE. Subtidal rock, coral rubble, coral reef, soft coral; 2–20m.

COMMENT. All these specimens represent extension of the range of this species into the northern Indian Ocean. It has been recorded from the coast of Western Australia, but otherwise only from the Pacific Ocean coasts and islands, Thailand, Papua New Guinea and Japan (Rowe *et al.*, 1986: 221; Messing, 1994).

11. *Comanthus mirabilis* Rowe, Hoggett, Birtles and Vail, 1986.

SEE. Rowe, Hoggett, Birtles and Vail, 1986: 226.

MATERIAL. NHM – 810501F/2 (1); WAM – 810427C/1 (1); SM – 810430A/5 (1).

COLLECTION SITES. Ug Bau and Ug Seukundo, Pula Wé, Sumatra.

HABITATS AND DEPTH RANGE. Subtidal rock/coral, coral reef; 5–30m.

COMMENT. The WAM specimen has 45 arms. The IIIBr series are mostly 2; where an arm has broken off and regenerated there is usually another devision series and extra arms, otherwise division series beyond IIIBr are randomly distributed. Most pinnules beyond P_2 are broken, so comb distribution further out cannot be ascertained.

12. *Comanthus parvicirrus* (Müller, 1841)

SEE. Rowe, Hoggett, Birtles and Vail, 1986:211; Hoggett and Rowe, 1986: 125.

MATERIAL. NHM – 810123A/1 (1),810123B/2 (1), 810203A/1 (1 of 3), 810206A/1 (1), 810212A/2 (1), 810420A/1 (1), 810425F/1 (1), 810427C/2 (1 of 3), 810428C/2 (1); WAM – 810126B/5 (1),810124A/6 (1);810203A/1 (1 of 3), 810204A/2 (1), 810204A/6 (1), 810425F/3 (1), 810427C/2 (1 of 3), 810428C/5 (1),810430A20a (1); SM – 810125A/2 (1), 810126B/6 (1), 810203A/1 (1 of 3), 810204A/5 (1), 810204A/7 (1), 810425A/18d (1), 810427C/2 (1 of 3), 810430A/20c (1), 810430A/21a (1), 810501E/10 (1).

COLLECTION SITES. Galle, Hikkaduwa, Kandakkuliya, Kalpitiya, Negombo and Unawatuna, Sri Lanka; Klah, Sabang Bay, Ug Murung, Ug Bau, and Ug Seukundo, Pula Wé, Sumatra.

HABITATS AND DEPTH RANGE. Subtidal rock/coral, coral reef; 2–20m.

COMMENT. The specimens from Sri Lanka may constitute a new record *for C. parvicirrus* as it is now defined (Rowe *et al.*, 1986), depending on the correctness of H.L. Clark's (1915) identification of a specimen from the region.

13. *Comanthus suavia* Rowe, Hoggett, Birtles and Vail, 1986.

SEE. Rowe, Hoggett, Birtles and Vail 1986: 222.

MATERIAL. NHM – 810501B/1 (1); WAM – 810123A/2(1), 810124A/6, 810501B/4 (1).

COLLECTION SITES. Galle, Sri Lanka; Rubiah, Pula Wé, Sumatra.

HABITATS AND DEPTH RANGE. Subtidal rock, coral reef; 5–20m.

COMMENTS. This is a major extension of range, as the species was originally thought to be restricted to the northern Great Barrier Reef and New Guinea. Two specimens, whose identity was originally in doubt, have now been confirmed as this species. One, 810124A/6, has 7–9 triangular comb teeth, recurved but with bases not in contact; terminal tooth small, proximal tooth usually saucer-shaped. Combs appear irregularly, e.g. on P_1, P_3, P_6 or P_2, P_3, P_4, P_6. The centrodorsal is stellate with cirrus buds and cirrus scars, and subradial clefts are present. Specimen 810501B/4 has short combs with 4+2 teeth, triangular but not in lateral contact, a saucer-shaped proximal tooth, and a smaller secondary tooth on some pinnules.

14. *Comanthus wahlbergii* (Müller, 1843)

SEE. Rowe, Hoggett, Birtles and Vail, 1986: 228.

MATERIAL. NHM – 810123B/1 (1), 810421A/5(1); WAM – 810204A/2 (1); SM – 8101423B/3 (1), 810204A/4 (1).

COLLECTION SITES. Chetlat I., Laccadive Islands; Galle and Kalpitiya, Sri Lanka; Seukundo, Pula Wé, Sumatra.

HABITATS AND DEPTH RANGE. Subtidal rock, coral reef; 3–30m.

COMMENT. The collection of *C. wahlbergii* from the Laccadives, Sri Lanka and Sumatra, Indonesia fills the gaps in the distribution of this species around the Indian Ocean.

15. *Comaster multifidus* (Müller, 1841)

SEE. Clark and Rowe 1971: 6.

MATERIAL. NHM – 810421A/4 (1); WAM – 810425E/1 (1); SM – 801210B/5 (1, fragmented), 801212A/2 (1, fragmented).

HABITATS AND DEPTH RANGE. Subtidal rock and coral; 10–30m.

COLLECTION SITES. Chetlat I., Laccadive Is; Sabang Bay and Seukundo, Pula Wé, Sumatra.

COMMENT. This species is well known from Indonesia and northern Australia, and from the South Pacific. The record from the Laccadives is a marked extension of range, but identification is not positive because of the condition of the specimens.

16. *Oxycomanthus bennetti* (Müller, 1841)

SEE. Clark and Rowe, 1971:6–7; Rowe, Hoggett, Birtles and Vail, 1986:259.

MATERIAL. NHM – 810421B/3 (1), 810422D/9 (1),810423C/5 (1), 810423C/5 (1),810424D/2 (1),810424D/4 (1), 810425A/18b (1), 810425A/18 (1), 810425E/1 (1), 810425F/2 (1), 810425F/3 (3), 810428B/2 (1); WAM – 810422D/6 (1), 810423C/2b (1), 810423C/3 (2), 810423C/6 (1), 810424A/3 (1), 810424D/6 (1),810424D/7

(1), 810425A/18c (1), 810427D/1 (2), 810428A/5 (1), 810428B/3 (1), 810504C/2 (1); SM – 810421C/5 (1), 810422D/8 (1), 810423A/1 (1), 810423C/1 (1), 810424D/1 (1), 810427D/1 (1), 810427D/2 (1), 810428A/6 (1), 810430A/8 (2),810430A/35 (1), 810430A/36 (1), 810501C/4 (2).

COLLECTION SITES. Seukundo, Klah, Ug Bau, Seulakoe, Sabang Bay, Ug Murung and Ug Seukundo, Pula Wé, Sumatra.

HABITATS AND DEPTH RANGE. Subtidal rock/coral, coral reef, soft coral; 2–30m.

COMMENT. Rowe *et al.* (1986) do not record this species from Indonesia, although it was recorded from Papua New Guinea by Messing (1994); therefore this collection fills in the gap between the Andaman Islands and the Philippines.

Family **HIMEROMETRIDAE**

17. ***Amphimetra tessellata*** (Müller, 1841)

SEE. Clark and Rowe, 1971:6–7.

MATERIAL. WAM – 810425E/2 (1).

COLLECTION SITE. Sabang Bay, Pula Wé, Sumatra.

HABITAT AND DEPTH. On gorgonian; 10–20m.

18. ***Himerometra robustipinna*** (Carpenter, 1881)

SEE. Clark and Rowe, 1971:8–9.

MATERIAL. NHM – 810423E/1 (1).

COLLECTION SITES. Ug Bau, Pula Wé, Sumatra.

HABITAT AND DEPTH. On a wreck, 5m.

Family **MARIAMETRIDAE**

19. ***Lamprometra palmata*** (Müller, 1841)

SEE. Clark and Rowe, 1971: 8–9.

MATERIAL. NHM – 810425E/1 (1), 810504D/2 (1 of 2); WAM – 810124A/7 (1), 810212A/4 (1); SM – 810425F/3 (1), 810504D/2 (1 of 2).

COLLECTION SITES. Galle and Unawatuna, Sri Lanka.

HABITATS AND DEPTH RANGE. Subtidal rock, coral, coral reef; 2–20m.

20. ***Oxymetra finschi*** (Hartlaub, 1890)

SEE. Clark and Rowe, 1971: 8–9.

MATERIAL. WAM – 810430A/33 (1).

COLLECTION SITE. Ug Seukundo, Pula Wé, Sumatra.

HABITAT AND DEPTH RANGE. Subtidal rock; 12–13m.

21. ***Stephanometra indica*** (Smith, 1876)

SEE. Clark and Rowe, 1971:8–9.

MATERIAL. NHM – 81020A/3 (1); WAM – 801212A/1 (fragmented); SM – 810421C/3 (fragmented).

COLLECTION SITES. Chetlat I., Laccadive Islands; Klah and Seukundo, Pula Wé, Sumatra.

HABITAT AND DEPTH RANGE. Coral reef; 4–8m.

COMMENT. Even though two of the three specimens are fragmented, they are easily identifiable as this widely-distributed Indo-Pacific species.

22. ***Stephanometra spinipinna*** (Hartlaub, 1890)

SEE. Clark and Rowe, 1971:8–9.

MATERIAL. NHM – 810423D/1 (1).

COLLECTION SITE. Ug Bau, Pula Wé, Sumatra.

HABITAT AND DEPTH. Coral reef; 2–8m.

Family **COLOBOMETRIDAE**

23. ***Cenometra bella*** (Hartlaub, 1880)

SEE. Clark and Rowe, 1971:10–11; Meyer and Macurda, 1980:88–89.

MATERIAL. NHM – 810423C/7 (1).

COLLECTION SITE. Ug Bau, Pula Wé, Sumatra.

HABITAT AND DEPTH. On gorgonian; 10–20m.

24. ***Colobometra perspinosa*** (Carpenter, 1881)

SEE. Clark and Rowe, 1971:10–11.

MATERIAL. NHM – 810421B/5 (1), 810425F/2 (2); WAM – 810427C/1 (2), 810501D/3 (1); SM – 810424A/2 (1), 810501A/1 (1), 810501B/2 (1).

COLLECTION SITES. Seukundo, Klah, Sabang Bay, Ug Murung and Ug Seukundo, Pula Wé, Sumatra.

HABITATS AND DEPTH RANGE. Subtidal rock/coral, coral reef on gorgonian; 2–30m.

25. ***Decametra brevicirra*** (A.H. Clark, 1912)

SEE. Clark and Rowe, 1971:10–11.

MATERIAL. WAM – 810425D/2 (1).

COLLECTION SITE. Sabang Bay, Pula Wé, Sumatra.

HABITAT AND DEPTH. Subtidal rock and sand; 25m.

COMMENT. Clark & Rowe (1971) implied that the main key characteristic of *D. brevicirra*, the similarity in segment numbers in P_1 and P_2, distinguishing this species from its congeners *D. mylitta* (A.H. Clark, 1912) and *D. chadwicki* (A.H. Clark, 1911), would not 'hold good' when more specimens from the type locality, the Bay of Bengal, had been collected. This specimen, from Sumatra, clearly has 10 segments on both proximal pinnules. It differs from the other specimen of this genus collected in the same area, which clearly keys out to *D. parva* (below) on the basis of having a higher cirrus segment number. It may be time for a thorough re-examination of the genus, as there are doubtless more records than there were in 1971.

26. ***Decametra parva*** (A.H. Clark, 1912)

SEE. Clark and Rowe, 1971:10–11.

MATERIAL. NHM – 810428A/11 (1).

Collection site. Ug Bau, Pula Wé, Sumatra.

Habitat and depth. Subtidal rock and coral, 20–30m.

27. ***Oligometra carpenteri*** (Bell, 1884)

See. Clark and Rowe, 1971:10–11.

Material. WAM – 810124A/7 (1).

Collection site. Galle, Sri Lanka.

Habitat and depth. Subtidal rock; 10–15m.

Comment. This is an extension of range for the species, which is well known along much of the Great Barrier Reef and has been recorded in Indonesia. This specimen has much less well-developed keels on the proximal pinnules than in specimens from the GBR, where the two species of the genus are quite distinct. However, the pinnules are wider than long, and lack flaring of their distal ends of segments. Only *O. serripinna* has been previously recorded from the Sri Lanka area.

28. ***Oligometra serripinna*** (Carpenter, 1881)

See. Clark and Rowe, 1971:10–11.

Material. NHM – 810425D/2 (1); WAM – 810425E/2 (1); SM – 810422C/5 (1).

Collection sites. Klah and Sabang Bay, Pula Wé, Sumatra.

Habitats and depth range. Subtidal rock/sand, coral reef, on gorgonian; 10–30m.

Comment. See above.

Family **TROPIOMETRIDAE**

29. ***Tropiometra carinata*** (Lamarck, 1816)

See. Clark and Rowe, 1971:10–11.

Material. NHM – 810126B/5 (4), 810428D/3 (1); WAM – 810123B/3 (1), 810213A/2 (4), 810428D/6; SM – 810123A/1 (1), 810212A/4 (3).

Collection sites. Galle, Hikkaduwa, Unawatuna and Tangalla, Sri Lanka; Ug Tapa Gadja, Pula Wé, Sumatra.

Habitats and depth range. Subtidal rock/coral, coral reef; 3–15m.

Comment. *T. carinata* is well known from Indian Ocean reefal areas.

Family **ANTEDONIDAE**

30. ***Antedon parviflora*** (A.H. Clark, 1912)

See. Clark and Rowe, 1971: 10–11.

Material. NHM – 810425D/2 (1).

Collection site. Sabang Bay, Pula Wé, Sumatra.

Habitat and depth. Subtidal rock and sand, 25m.

Table 1 Regional distribution of crinoids from the *Sindbad Voyage* (names in parenthesis are equivalent zoogeographic subdivision of sampling area, following Clark & Rowe, 1971)

Laccadives **(Maldive area)**	**Sri Lanka (Sri Lanka area)**	**Pula Wé, Sumatra (Indonesia/East Indies)**
Comanthus wahlbergii	*Comanthus briareus*	*Alloeocomatella pectinifera*
Comaster multifidus	*Comanthus gisleni*	*Capillaster multiradiatus*
Stephanometra spinipinna	*Comanthus parvicirrus*	*Capillaster sentosus*
	Comanthus suavia	*Clarkcomanthus albinotus*
	Comanthus wahlbergii	*Clarkcomanthus littoralis*
	Lamprometra palmata	*Clarkcomanthus luteofuscum*
	Oligometra carpenteri	*Comanthina nobilis*
	Tropiometra carinata	*Comanthina schlegelii*
		Comanthus briareus
		Comanthus gisleni
		Comanthus mirabilis
		Comanthus parvicirrus
		Comanthus suavia
		Comanthus wahlbergii
		Comaster multifidus
		Oxycomanthus bennetti
		Amphimetra tessellata
		Himerometra robustipinna
		Oxymetra finschii
		Stephanometra indica
		Stephanometra spinipinna
		Cenometra bella
		Colobometra perspinosa
		Decametra brevicirra
		Decametra parva
		Oligometra serripinna
		Tropiometra carinata
		Antedon parviflora

DISCUSSION

The crinoids of the tropical Indo-west Pacific region (Africa, Indonesia, Philippines, tropical Australia and the South Pacific) are relatively well-documented (Clark & Rowe, 1971). The region between the Red Sea and Indonesia has to date produced a relatively depauperate crinoid record, but the reasons for this are not clear. Unfortunately, the *Sindbad* collection does not resolve the problem. The low number of crinoids in this collection from the Laccadives and from Sri Lanka is probably due to a combination of two factors: lower abundance and diversity of this group in the localities collected, and limited sampling time available in those regions. This situation is unfortunate, as the areas of the northern Indian Ocean, except for the western fringe of Indonesia, are not well-represented in any collections of echinoderms, so that species and even generic distributions within the region are not well-known. In fact, the majority of specimens collected during the *Sindbad Voyage* are from around the small island of Pula Wé, at the western tip of Sumatra, Indonesia. SE Asia is the region of the Indo-West Pacific associated with greatest echinoderm species richness (Clark & Rowe, 1971), and Indonesia in particular is commonly regarded as the centre of distribution for coral reefs, other invertebrate groups and marine tropical diversity in general (Veron, 1995; Gray, 1997).

Crinoid records from this voyage's collection are divided into the different regions sampled in Table 1, which also shows the equivalent zoogeographic subdivisions adopted by Clark & Rowe (1971). The observed distribution is highly skewed, with all but two of the 30 species collected in Sumatra, eight in Sri Lanka and only three in the Laccadives. Regional comparison based on more comprehensive records, including Indian Ocean data of Clark and Rowe (1971) and the results of James (1989) for the Laccadives (13 additional species) and Sri Lanka (14 additional species), shows species distributions to be less uneven. Nevertheless, the resulting pattern reveals a progressive increase in species richness from the Maldive area to Sri Lanka to East Indies/Indonesia, as suggested in the *Sindbad* data (Table 1). However, the Laccadives, in particular, probably remain undersampled. These islands are a prohibited area under the control of India, and access will probably continue to be restricted.

Range extensions, to the western fringe of Indonesia (Pula Wé) and into the Indian Ocean, are recorded for at least six of the 30 crinoid species collected during the *Sindbad Voyage*, as follows: *Clarkcomanthus albinotus* (Indonesia/East Indies); *Comanthus briareus* (Sri Lanka area); *Comanthus gisleni* (Sri Lanka area & Indonesia/East Indies); *Comanthus suavia* (Sri Lanka area & Indonesia/East Indies); *Comanthus wahlbergii* (Maldive area, Sri Lanka area & Indonesia/East Indies); *Oxycomanthus bennetti* (Indonesia/East Indies); and possibly also *Comaster parvicirrus* (Sri Lanka area – depending on validity of an earlier record) and *Comaster multifidus* (Maldive area?– specimens poorly preserved).

Of the crinoids represented, *Capillaster multiradiatus* and *Oxycommanthus bennetti* were the most common, each occurring in 19% of the samples, followed by *Comanthus parvicirrus* which occurred in 9% of the samples. The first two species also occupied a relatively wide range of depths (2–30 m) and habitats compared to most other species collected. A more comprehensive ecological and biogeographic assessment of echinoderms of Pula Wé, Sumatra is currently in progress.

ACKNOWLEDGEMENTS. We are grateful to Dr R. Dalley, P. Hunnam, P. Dobbs and D. Tattle for their considerable assistance during field work. One of us (A.R.G.P.) would also like to thank T. Severin, leader of the *Sindbad Voyage*, for the kind invitation to participate in the expedition which was made possible by generous support from the Ministry of Natural Heritage and Culture, Sultanate of Oman. Financial assistance to A.R.G.P. from the Leverhulme Trust is gratefully acknowledged. Thanks are also due to Dr Anne Hoggett (Lizard Island Research Station, GBR, Australia) for assistance with identification of specimens in doubt; and to Dr Frank Rowe for confirming several identifications.

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Bull. nat. Hist. Mus. Lond. (Zool.) **65**(1): 31–50 Issued 24 June 1999

On the hybrid status of Rothschild's Parakeet *Psittacula intermedia* (Aves, Psittacidae)

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Synopsis. The name *Psittacula intermedia* was attached to seven dataless specimens sent from India to England between 1895 and 1907, six of which are now at the American Museum of Natural History, the other being at The Natural History Museum, Tring, U.K. Their origins and taxonomic standing have long puzzled authorities, since they look intermediate between male Plum-headed Parakeet *P. cyanocephala* and Slaty-headed Parakeet *P. himalayana*, and no definite field records exist. Although a hybrid origin has been suggested, *intermedia* has recently been considered a valid species on the bases of: (a) uniformity of characters; (b) a single origin; (c) a non-captive origin; (d) an old description of hybrid *cyanocephala* × *himalayana* which does not match *intermedia*; (e) reports of captive *intermedia* in the 1990s; and (f) biochemical analysis of captive birds.

For this study, we examined all published *intermedia* specimens. For hybrid diagnoses we compared morphology of adult males qualitatively and mensurally with the putative parental species, including also Grey-headed Parakeet *P. finschii* and Blossom-headed Parakeet *P. roseata*. We examined six live adult hybrid *cyanocephala* × *himalayana* bred by two different aviculturists, as well as one live bird in India claimed to be *intermedia*, and we considered published avicultural evidence.

Our analyses showed all the defences of the specific status of *intermedia* to be wanting, as follows: (a) considerable variation exists in the original material; (b) the specimens could not all have had a single origin; (c) six of the seven specimens showed signs of captivity; (d) the 65-year-old account of *cyanocephala* × *himalayana* only furnishes passing descriptions of juveniles, and is therefore not comparable with the adult *intermedia* specimens; (e) all the specimens examined in Bombay are hybrid *cyanocephala* × *krameri*, while other captive *intermedia* in Austria and India are of uncertain provenance (but the former appear to be *cyanocephala* × *finschii*); and (f) the biochemical analysis was seriously flawed, most importantly in that the specimens used were not *intermedia* but hybrid *cyanocephala* × *krameri*.

Neither *cyanocephala* nor *himalayana* shows any morphological characters incompatible with being parent to *intermedia*, and all features of the latter are explained by a combination of the two former species. Moreover, mensurally the AMNH *intermedia* fall midway between *cyanocephala* and *himalayana*. All known male *cyanocephala* × *himalayana* possess plumage features and measurements matching AMNH's five adult male *intermedia*, while the previously undescribed female hybrid has the head paler than *himalayana* and drabber than female *cyanocephala*. This evidence leaves no doubt that *intermedia* is a hybrid of *cyanocephala* and *himalayana*.

INTRODUCTION

Rothschild's or the Intermediate Parakeet *Psittacula intermedia* was described from a single dataless specimen (Rothschild 1895) backed up by a later series which also lacked data but had been exported from Bombay (Rothschild 1907, Hartert 1924). However, apart from being listed in Peters (1937), this parakeet was overlooked until mentioned by Ripley (1953) as a species of Indian origin. Of subsequent authors who have considered the status of *intermedia* and treated it as taxonomically valid, only Biswas (1959) had examined Rothschild's entire series. Walters (1985) had access only to a single specimen in the bird collections of The Natural History Museum, Tring, U.K. (BMNH); in Bombay, Sane (1975, 1977, Sane *et al.* 1987) had only his own captive birds; while Inskipp and Inskipp (1995) simply reviewed the literature on *intermedia*; and Bhargava (1998) had only his own specimens in India. *Psittacula intermedia* has been accepted uncritically as a species by several authors (e.g. Howard and Moore 1991, Monroe and Sibley 1993). However, Salvadori (1907), in reference to the type, had stated that *intermedia* was '. . . not improbably established on a hybrid!'. Immediately after Salvadori's comment, Rothschild (1907) mentioned having obtained six more specimens, which he maintained '. . . should certainly dispose of any doubt regarding the distinctness of *intermedia*'. Conversely, Husain (1959), on the basis of the single skin at the BMNH, considered that *intermedia* was a hybrid between Plum-headed Parakeet *Psittacula cyanocephala* and Slaty-headed Parakeet *P. himalayana*, while Forshaw (1973) concluded the same after examination of the series at the American Museum of Natural History, New York (AMNH); Wolters (1975) also treated it as a probable hybrid. Still other authors have remained undecided as to its status (Peters 1937, Ali and Ripley 1969, 1981, Wirth 1990); Juniper and Parr (1998) and Collar (1997) tentatively gave it a species account pending publication of the present study. *Psittacula intermedia* is currently listed as a globally threatened species with IUCN status Vulnerable, but for which no specific threats have been identified (Collar *et al.* 1994), although its possible extermination by collectors has been suggested (Walters 1985).

The fact that the phenotype of *Psittacula intermedia* places it midway between *cyanocephala* and *himalayana* was acknowledged in both the original description and in the specific epithet chosen (Rothschild 1895). Since then, no characters of *intermedia* have been identified that either differ from those of *cyanocephala* or *himalayana* or are not manifestly intermediate between these two (*contra* Inskipp *et al.* 1996, whose cited references nowhere demonstrate non-intermediacy). Moreover, the area of origin of *intermedia* has never been accurately pinpointed, despite fairly extensive subsequent ornithological work in many presumably likely areas; even Rothschild (1907) admitted that 'speculations as to its exact locality were useless, as these collections contained forms exclusively found in the Eastern Himalaya as well as others occurring only in the north-western portions of India.' A statement by Ali and Ripley (1969) concerning *intermedia* – 'never consciously seen alive in the wild state by any ornithologist' – remains true today. Recent reports within India (R. Bhargava pers. comm. 1996, *in litt.* 1997, 1998; Ahmed *et al.* 1996, Anon. 1997, 1998a, b; Mookerjee 1997; Bhargava 1998; Them 1998), and three birds identified as *intermedia* (Sane 1975, 1977, Sane *et al.* 1987, S. R. Sane pers. comm. 1997), do not clear up the mystery, as all refer to captive birds of uncertain provenance, and some of these are of problematic identification as well (Rasmussen and Collar 1998, Bhargava 1998). Appeals for information (Rothschild 1907, Sane 1977, Wirth 1990, Inskipp and Inskipp 1995) have not led to the discovery of a wild population.

If *intermedia* were a typical diurnal, noisy *Psittacula*, it would be a most unusual bird, not only for having escaped the attentions of field ornithologists for over a century in one of the best-known parts of tropical Asia, but also for showing complete intermediacy in numerous characters between two clearly differentiated congeners. There are two possible explanations for this double circumstance: the first is that it is an extremely rare species and therefore requires concerted conservation attention; the second is that it is not a species at all, but a hybrid. Only the second explanation accounts for both of its unusual traits. In this paper we reexamine the evidence for specific status vs. hybrid origin of *intermedia*, based on plumage and mensural analyses both of museum specimens and of newly located captive birds of known parentage.

METHODS

SPECIMENS EXAMINED

Eight museum specimens have been published in the primary literature as *Psittacula intermedia*, although one (AMNH 621545) has been considered an immature *himalayana* (Biswas 1959, 1990, Forshaw 1973). Each was thoroughly examined, photographed, and measured for this study: AMNH 621539 (holotype), 621540–621542, 621544–621545; BMNH 1980.3.1; and BNHS (Bombay Natural History Society) 26758. In addition, we examined another uncatalogued specimen belonging to Mr. Sane, as well as a photograph of three unaccessioned specimens in the possession of R. Bhargava.

In the early 1930s, Rothschild's entire series of *intermedia* went to AMNH along with most of the rest of his collection. Subsequently, one (BMNH 1980.3.1, formerly AMNH 621543) was exchanged to the then British Museum (Natural History) (M.P. Walters, pers. comm. 1997), where it had already resided since 1959 on long-term loan (Knox and Walters 1994). The BMNH specimen was lent to AMNH so that we could compare it there with the remainder of the series.

A colour transparency of AMNH 621540 (placed with the specimens; date and photographer unknown) taken sometime after 1973 – based on an accompanying note: '*Psittacula* '*intermedia*' believed to be a hybrid *himalayana* × *cyanocephala* see Forshaw (1973: 336)' – shows that it had long central rectrices when the photo was taken, but these were lacking when the specimen was first photographed by PCR in 1993, and it cannot now be determined if the rectrices were fully grown. Estimates of lengths of the tail and of the yellow tip of the central rectrix of AMNH 621540 were made from the transparency, in which the subject is 1/3 natural size and photographed from the side.

BNHS 26758 is essentially dataless (label data: male, aviary bird, S. R. Sane, Bombay, 12/90), as is Sane's second uncatalogued specimen; these are two of the three birds examined from his collection. The first may or may not be the specimen described in Sane (1975, 1977), referred to as having died in 1978, and as being in the BNHS collection (Sane et al. 1987), but if '12/90' refers either to date of death or to date of accession it can hardly be the same individual.

The only other specimens reputed to be *intermedia* of which we are aware are those preserved by R. Bhargava, and we have seen photos of three of those. However, adult female and especially immature *intermedia* (see below) would readily escape notice among series of similar congeners, and may well exist undetected in museum collections.

We assessed variability among the eight published putative *intermedia* specimens in the plumage and mensural characters listed in Tables 1–4 and the Appendix.

PHOTOGRAPHIC EVIDENCE

Most of the published information on *intermedia* was recently summarized by Inskipp and Inskipp (1995). Through perusal of the avicultural literature we located an additional, previously unrecognized, published photograph of an *intermedia*-like bird, and correspondence with aviculturists and researchers (after the main statistical analyses for this paper were complete) resulted in additional unpublished information, including the location of several more captive birds, some of documented parentage.

HYBRID DIAGNOSES

For hybrid diagnoses (Graves 1990), plumage, other external characteristics, and measurements of adult males were compared among the species of *Psittacula* that either had been suggested previously as possible parental taxa (Husain 1959, Forshaw 1973, Wolters 1975) or for which the phenotype of the presumptive hybrids indicated the likelihood of those species being involved. Sane's birds were compared indirectly with the other *intermedia* specimens (Table 1) and with series of adult male *cyanocephala* and Rose-ringed Parakeets *P. krameri* (Table 2), while other *intermedia* were compared with series assembled at the National Museum of Natural History (USNM) of each of the potential parental species: *cyanocephala* ($n = 21$), *himalayana* ($n = 26$), Grey-headed Parakeet *P. finschii* ($n = 17$), *krameri* ($n = 10$), and Blossom-headed Parakeet *P. roseata* ($n = 11$). Additionally, all adult males of these species in the collections of AMNH, the Academy of Natural Sciences of Philadelphia (ANSP), the Museum of Comparative Zoology (MCZ), and the University of Michigan Museum of Zoology (UMMZ), as well as several smaller collections, were examined and measured; their plumage characters (which did not differ materially from those of the series assembled at USNM) were not included in the analyses, but their measurements are included in the Appendix and in the statistical analyses. A few unsexed specimens with plumage characteristics diagnostic of males were included. All other species of *Psittacula* were ruled out as potential parental species as they have plumage characters strongly incompatible with the phenotype of specimens reputed to be *intermedia*.

Mensural characters of adult males (listed in Appendix) were used to evaluate which (if any) of the species listed above could potentially be parental species of the *intermedia* specimens. Measurements taken as far as possible for each specimen were: culmen length (from distal edge of cere); height and width of maxilla (upper mandible, at distal edge of cere); minimum distance between nares; width of (lower) mandible; wing length (straightened and flattened); shortfalls of each primary (P1–P10, with P1 outermost) from wingpoint; for P1, distance from notch on inner web to feather tip, maximum width, and width at notch; widths of P2–5, each taken at

Table 1 External qualitative characters of individual specimens attributed to *Psittacula intermedia*.

Character	AMNH 621539	AMNH 621540	AMNH 621541	AMNH 621542	AMNH 621544	AMNH 621545	BMNH 1980.3.1	BNHS 26758	Sane uncatalogued
Age class	adult	adult	adult	subadult?	adult	immature	adult	adult	adult
HEAD									
Extent of orange/red on maxilla	¾ orange	½ orange	⅓ orange	minimal	½ orange	none	¼ orange	all red	all red
Depth of orange/red on maxilla	strong	strong	pale	very pale	strong	none	moderate	bright red	bright red
Extent of dark on mandible	none	none	none	none	⅕	none	none	complete	complete
Colour of lores	purplish-pink	purplish-pink	purplish-pink	deep pink	purplish-pink	yellow-green	yellowish-pink	greyish-lilac	greyish
Colour of rear crown/nape	grey-blue	grey-blue	grey-blue	grey-blue	grey-blue	dusky grey	blue-grey	bright cerulean blue	bright cerulean blue
BODY									
Color of nape collar	pale blue-green	pale blue-green	pale blue-green	pale blue-green	pale blue-green	dusky blue-green	pale blue-green	viridian	viridian
Extent of blue on collar	broad	moderate	very broad	very narrow	very narrow	none	moderate	moderate	moderate
Color of back	yellow-olive	yellow-olive	yellow-olive	sl. dkr yel.-olive	sl. dkr yel.-olive	cool green	sl. darker yel-olive	bright yellow-olive	bright yellow-olive
Extent of blue tinge on rump	moderate	moderate	strong	moderate	strong	strong	lacking	slight	slight
WING									
Presence of shoulder patch	present	present	present	present	present	none	none	none	slight rusty tinge
Blue tinge to upperwing coverts	present	present	present	lacking	present	none	none	slight	slight
Shape of P3	broad, square	moderate, square	moderate, square	broad, square	moderate, elliptical	moderate, pointed	moderate, elliptical	moderate, elliptical	moderate, elliptical
TAIL									
Colour of midsection of R1	missing	royal blue	dark blue	royal blue	dark blue	cool green	greenish-blue	missing	pale greenish-blue
Colour of tip of R1	missing	yellow	pale yellow	pale yellow	primrose yellow	pure yellow	yellowish-white	missing	uniform bluish to tip
Breadth of R1 tip	missing	moderate	broad	moderate	rather narrow	narrow	narrow	missing	slightly spatulate

Table 2 Qualitative characters used in hybrid diagnosis between *Psittacula cyanocephala*, *P. krameri*, and S. R. Sane's specimens and living bird.

Character	*P. cyanocephala*	Sane's birds	*P. krameri*
Maxilla	all yellowish	all red	all red
Mandible	black	black	black
Cere shape	moderately wide, rounded	narrow, nearly straight	narrow, straight
Cere colour	medium grey	pale greyish-horn	whitish
Orbital skin	dark grey	fleshy whitish	orange
	rather wide, not prominent	rather narrow, very prominent	rather narrow, very prominent
Lores pattern	no line	slight line	strong line
Forehead	reddish-purple	greenish tinge	green
Auriculars and central face	reddish-purple	dull purplish-blue	bluish-green
Lower face	purplish	cerulean blue	lime green
Rear crown	shining mauve	cerulean blue	powder blue
Lower border neck collar	as nape	broken orange-chestnut	nearly complete rose-orange
Nape	bright bluish-green	viridian	slightly bluish-green
Upper wing coverts	variably bluish-green	slightly bluish	lacking bluish
Shoulder patch	maroon	slight tinge on one	absent
Underwing coverts	pale turquoise-blue	slightly bluish	yellowish-green
Rump	variably bluish-green	slightly bluish	yellowish-green
Uppertail	rich dark blue	pale blue-green	lime-green
Tail tip	white, moderate width, spatulate	concolorous with rest or narrow whitish; slightly spatulate	concolorous with rest, not spatulate
Foot	dark pinkish-grey	pale pinkish-grey	whitish

tip of next shortest feather; lengths of longest (R1, central) and next more lateral (R2) rectrices (both taken from insertion of central rectrices); maximum width of yellow or white tip and approximate maximum width at distal end of blue or green area of R1 (with feathers flattened out); distances between tips of each rectrix (except R1) of one side and the next shortest (next more lateral) rectrix; widths of each rectrix of one side at the tip of the next shortest one; approximate distance from tips of R1 and R2 to definite blue or green part of feather (= length of pale tip); tarsus length; minimum width of tarsus; length of claw of middle toe (from distal edge of scute); length of hindclaw (from distal edge of scute). Feathers in sheath or in a damaged or heavily worn state were not measured, and if there was a difference in length between rectrices of a pair, the longer one was measured. Maximum skull width was measured over skin and compressed feathers for specimens in which palpation and/or x-rays indicated that the widest portion of the skull was intact and not padded with stuffing.

Two specimens from the Rothschild series (BMNH 1980.3.1 and AMNH 621545) showed very different plumage and mensural characters from each other and from the remainder of the specimens in this series, and so were treated as unknowns in the analyses. AMNH 621545, although thought a female *intermedia* by Rothschild (1907), was considered by Biswas (1959, 1990) and Forshaw (1973) to be an immature *himalayana*, the latter opinion being shared by us after examination. We therefore compared its plumage characters with known immature *himalayana* and *finschii*, and its measurements with nine juveniles (sexes combined) of the former.

Univariate statistics and principal components analyses (PCAs) using correlation matrices were run on external and skeletal measurements using SYSTAT for Windows (Version 5.0) on an IBM-compatible PC. Variables for PCAs were chosen to allow the inclusion of selected individual *intermedia* specimens without estimation of missing data, which would be inadvisable owing to the small sample size of *intermedia*.

EVALUATION OF ORIGIN OF SPECIMENS

To test the idea that the Rothschild Collection series of *intermedia* had the same origin – an argument first put forward long ago by Hartert (1924) – we compared preparation styles and materials used among these specimens by external examination and study of x-rays. We also compared them with native-prepared (e.g., 'Bombay preparation', 'India', and 'Madras') skins of other *Psittacula* species (*cyanocephala*, *himalayana*, *roseata*, *finschii*) at AMNH, MCZ, and USNM. To permit analysis of certain aspects of preparation styles and materials used, radiographs (x-rays) were taken of the Rothschild *intermedia* specimens, and of native skin specimens of *himalayana*, *finschii*, and *cyanocephala* for comparison. X-rays (ventral and lateral views) were made of the AMNH and BMNH *intermedia* (including the putative immature *himalayana*) by M. N. Feinberg, Department of Ichthyology, AMNH (30 kV and 3 mA for 2 min, using Kodak Industrex-M Ready-pack film), and for the other specimens by PCR in the Fish Division, National Museum of Natural History (USNM; 25 kV and 5 mA for 30 sec, using Kodak Industrex SR film).

To evaluate whether the Rothschild Collection series originated from wild, not captive birds – an argument used by Biswas (1959) to support species status – we examined the Rothschild specimens for presence of: overgrown bill and claws; broken remiges and rectrices; overly worn feathers due to delayed moult; abrasion damage to feathers of the type resulting from repeated contact with cage bars; and dirt on plumage, bill, and feet consistent with a confined environment.

EXAMINATION OF CAPTIVE BIRDS

We examined five living adult hybrids belonging to Mr M. Sedgemore that are the progeny of an experimental pairing of a male *cyanocephala* and a female *himalayana*. The female parent, which died in the nest shortly after producing the second of two hybrid broods in successive years, was considered unsalvageable as a specimen; the male parent died more recently and the skin is preserved as BMNH 1998.33.2. We took hand-held photographs and aviary videotape of all five hybrids, as well as several measurements (taken by PCR while the birds were held by Sedgemore) of bill, wing, and tail. All the hybrids were in some stage of moult, so certain measurements could not be taken. The recently moulted central rectrices of the single female hybrid are now at the BMNH, and Sedgemore also gave us several photographs of the hybrids, both as juveniles with their parents and as adults. PCR also examined and videotaped the single live bird claimed to be *intermedia* remaining in Sane's collection in December 1997. We also studied photos sent by

Mr L. Critchley of yet another adult male hybrid and its parents. This bird was one of five hybrids in a single brood that Critchley incidentally produced by housing a male *cyanocephala* in a mixed aviary with a female *himalayana*, but he sold the other four hybrids to a pet shop in the U.K. before they attained adult plumage. Photos of all captive birds discussed in this paper are on file both with BirdLife International HQ and the senior author, and selected photos showing each specimen will appear on a colour plate accompanying a short article on *Psittacula intermedia* (Rasmussen and Collar in press).

RESULTS

SANE'S CAPTIVES

BNHS 26758 and Sane's other two birds, one stuffed and one alive as of December 1997, are all captive, dataless males identified as *intermedia*. However, all proved to be considerably different from the Rothschild specimens, possessing characters of both *cyanocephala* and *krameri*, but none inconsistent with their being hybrids between the latter two species (Tables 1 and 2; Appendix). Sane's birds have much bluer, paler sides to the head and a greener mid- and hindcrown than do any of the Rothschild Collection *intermedia*; like the latter they have mainly lilac cheeks, but many feathers of the head are multicoloured, at least on the two skin specimens. On the sides of the crown and edge of the black moustache, most of the individual feathers have peach-coloured bases and blue tips; on the cheek the bases tend to be peach and the tips lilac; while the feathers of the centre of crown and nape have green centres and blue tips. The specimens have entirely black lower mandibles and all-red upper mandibles except for the paler tips. Their soft-part colours and the feathering at the bill base are all unlike AMNH *intermedia*. The maxillae of Sane's birds are smoothly rounded on lateral view and not particularly robust proximally, being very similar in shape to *krameri*, not *himalayana*. Two of the three individuals bear no indication of the red shoulder patches (and they are very vague in the third) that are shown by both male *cyanocephala* and *himalayana*, and that are present in five of Rothschild's six adult *intermedia*, but that are always lacking in male *krameri*. However, of all the features in which Sane's three birds differ from AMNH *intermedia*, none is more telling than the broken orange-chestnut neck ring of the former (Table 2), which (assuming that the birds are hybrids) can hardly have come from any source other than *krameri* or the much larger Alexandrine Parakeet *P. eupatria*. Also, in both of the individuals with the central rectrices present, the feathers have very small pale tips, consistent only with the latter two species.

In 1990, one of two '*intermedia*' then alive in Sane's possession was photographed in Bombay by R. Wirth. The published photo (Wirth 1990) shows a bird very similar to BNHS 26758 and Sane's uncatalogued specimen, and from the date it may be either the bird still living as of 1997 or the uncatalogued specimen; it possesses the same suite of features consistent with its being a hybrid *krameri* × *cyanocephala* (or possibly *krameri* × *roseata*). A description of the second live bird was not provided, but Sane considered both to be *intermedia*, and Wirth (*in litt.* 1997) noticed no differences between

Table 3 Component loadings for PCAs of (A) bill width, wing, and tail measures for a model including juvenile *Psittacula himalayana*; (B) bill, wing length, and rectrix 5 measures, including Sane's mounted specimen and three of Sedgemore's living birds; and (C) head and wing measures, including BNHS 26758 (Sane's study skin).

	Factor						
	A		B		C		
Measurement	1	2	1	2	1	2	3
HEAD							
Culmen length	–	–	0.93	0.03	0.82	–0.49	0.06
Maxilla height	–	–	0.96	0.06	0.87	–0.36	0.10
Bill width	0.67	0.06	0.95	0.05	0.85	–0.38	–0.20
Skull width	–	–	–	–	0.84	–0.24	–0.02
WING							
Wing length	0.95	0.11	0.93	–0.12	0.92	–0.20	0.12
P3 shortfall	–	–	–	–	–0.09	0.81	0.06
P4 shortfall	–	–	–	–	0.67	0.57	0.24
P5 shortfall	–	–	–	–	0.86	0.41	0.09
P6 shortfall	0.93	0.16	–	–	0.92	0.29	0.10
P7 shortfall	0.93	0.24	–	–	0.95	0.16	0.13
P8 shortfall	0.97	0.14	–	–	0.95	0.21	0.11
P9 shortfall	0.96	0.19	–	–	0.96	0.13	0.12
P10 shortfall	0.96	0.19	–	–	0.95	0.11	0.16
P1 notch length	–	–	–	–	0.68	–0.55	0.12
P1 maximum width	0.68	–0.43	–	–	–	–	–
P1 notch width	–	–	–	–	0.36	–0.57	–0.45
P2 width	0.62	–0.59	–	–	0.58	0.56	–0.42
P3 width	–	–	–	–	0.66	0.31	–0.49
P4 width	–	–	–	–	0.81	0.11	–0.34
P5 width	–	–	–	–	0.86	–0.16	–0.27
TAIL							
R1 width	0.83	0.02	–	–	–	–	–
R2 width	0.75	–0.50	0.56	0.76	–	–	–

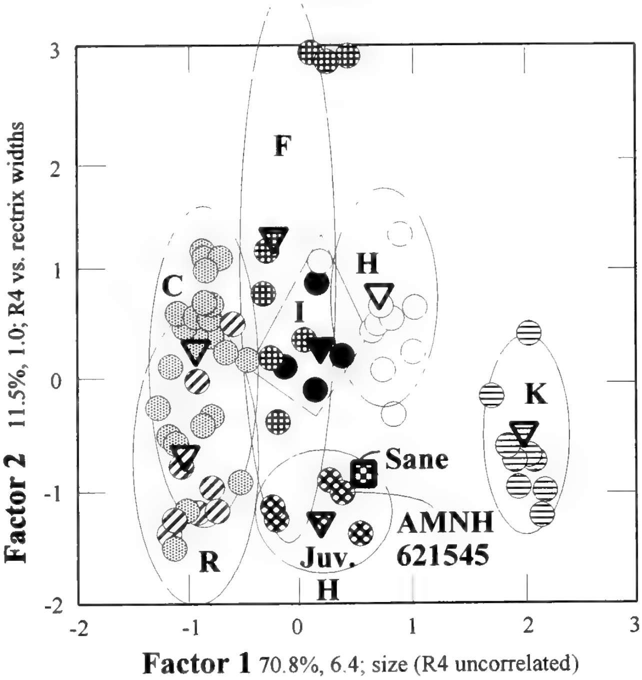

Fig. 1 Identity of AMNH 621545 with immature *Psittacula himalayana*: graphs of individual scores (circles), group means (triangles), and 95% confidence intervals (open ovals) of factor scores from principal components analysis (PCA) on measurements of adult male *P. cyanocephala* (C, grey-filled circles), *P. himalayana* (H, white), AMNH *P. intermedia* (black), immature *P. himalayana* of both sexes (diagonal hatching); *P. roseata* (R, diagonal cross-hatching), both populations of *P. finschii* (F, horizontal cross-hatching), one of Sane's specimens (checkered), and *P. krameri* (K, horizontal bars). A polygon outlines the scores for AMNH *P. intermedia* specimens due to small sample size. Summary statistics presented in the axis labels are percent variance explained and eigenvalues, respectively, followed by important measures for each axis. Component loadings for PCA are given in Table 3A.

the two. PCR examined all three of Sane's birds in the space of two days and concluded that they lacked salient differences, all being apparent *krameri* × *cyanocephala* hybrids.

IMMATURE SPECIMEN

AMNH 621545, considered to be a female *intermedia* by Rothschild (1907), but thought by others to be an immature *himalayana* (Biswas 1959, 1990, Forshaw 1973), shows no relevant plumage differences from the series of immature *himalayana* at AMNH with which we directly compared it, nor from others at USNM and other museums with which photos of it were compared. In a PCA of several measurements, AMNH 621545 falls within the 95% confidence limits of immature *himalayana* of both sexes (Figure 1, component loadings in Table 3, summary statistics in Appendix). In body plumage 621545 resembles *himalayana* in being generally cooler green and less yellowish than immature *finschii*, although some juveniles of the two species overlap in this. AMNH 621545 is unlike juvenile hybrid *cyanocephala* × *himalayana* (see below) in its bigger, duskier maxilla, brighter green nape, lack of yellowish collar, bluer-green overall body colour, and especially in its bright green upper tail surface with a bright yellow tip. Thus, on the basis of both plumage and measurements, all evidence supports the hypothesis that AMNH 621545 is an immature *himalayana*, and we therefore exclude this specimen from further analyses.

BMNH SPECIMEN

Comparison of photos and measurements of BMNH 1980.3.1 with those of the adult male AMNH *intermedia* showed that the former has several differences from all other *intermedia*, although it is part of the Rothschild series, and despite the seemingly inexplicable fact that the BMNH specimen was the one upon which Husain (1959) based his conclusion that *intermedia* was a hybrid *himalayana* × *cyanocephala*. This bird was therefore lent to AMNH for our comparisons, where we confirmed (Table 1, Appendix) that it has a smaller maxilla with only a slight reddish tinge basally (less than in all AMNH birds except 621542, the specimen said by Biswas [1959] to be completing post-juvenile moult); it has a slightly duller head with paler reddish-purple on the face (washed yellowish in front of the eye) and paler greyish-blue on the crown and nape; and it totally lacks maroon shoulder patches. Its P3 is narrower and less squared at the tip than in all adult AMNH specimens except 621544. The tail is greener at the base, more turquoise for most of its length, and has the pale tip whiter and shorter. This specimen is the only one of the Rothschild series that has a measurable, fully grown tail, so its rectrix length cannot be directly compared with the other *intermedia*. The salient differences between BMNH 1980.3.1 and typical *roseata* are: the former lacks reddish shoulder patches; it has an entirely pale lower mandible (though this is nearly all-pale in a few *roseata*; Table 4); its hindneck has a turquoise tinge; it has a slightly broader tail tip; the front of its face is slightly redder; and its P3 tip is broader (Table 1). In most statistical analyses, BMNH 1980.3.1 falls within the *roseata* and *cyanocephala* groups (Figures 2–5).

REMAINING *INTERMEDIA* SPECIMENS

The other five AMNH specimens attributed to *intermedia* (including the holotype), and also Bhargava's three specimens, are quite similar to one another. However, although most previous authors (Rothschild 1907, Hartert 1924, Husain 1959) have treated the first five under one description as if they were identical, they are in fact variable in most of the characters that separate them from any of the putative parental species (Table 1). Only Biswas (1959) mentioned variation among these five, but even he called them 'exceedingly similar'. All have fairly large bills with varying amounts of orange at the base of the maxilla. All have nearly or entirely pale lower mandibles, although AMNH 621544 has a broad black stripe down one side of the lower mandible. Each has the front of the face bright purplish- to deep pink, grading into the duller grey-blue crown, nape, and lower portions of the face. All have a pale blue-green collar, but this is highly variable in breadth and prominence, even allowing for differences in preparation. In addition, all have a bluish wash of variable strength on the wing coverts and/or rump. Only three of the specimens now have the central rectrices present, and in none of these (*contra* Biswas 1959) are they fully grown (this cannot now be determined in AMNH 621540, the fourth *intermedia* that once had central rectrices, but the fact that they are now missing from this specimen suggests they were loosely attached and thus moulting). Thus, original tail lengths presented in previous treatments – Biswas (1959): 185, 202, 221mm; Husain (1959): about 220 mm; Forshaw (1973): 167–195 mm (mean = 180.7, $n = 3$), 206 ($n = 1$) – would be expected to be too short. However, we measured the central rectrices of the three specimens in which they are now mostly grown as 157, 200 and 170 mm, and the now-missing rectrices of AMNH 621540 were estimated at ca. 200 mm. The central rectrices of all four of these birds show (or showed) long, at least moderately broad, pale to pure yellow tips and dark or royal blue upper tail surfaces. The breadth and length of the yellow tail tip are quite variable, however, and the length of the yellow R1 tip of AMNH 621540 is estimated to have been 48 mm, compared with a mean tip length of 41.6 mm for the others (Appendix). From the photograph of Bhargava's two specimens for which the central rectrices are present (both photographed next to a cm rule), these rectrices appear to be ca. 234 and 229 mm (although it cannot be determined from the photos whether these rectrices are full-grown), while the yellowish tips are ca. 51 and 54 mm, respectively.

We found no external qualitative characters in AMNH *intermedia* or Bhargava's specimens that differ from those exhibited by at least one member of one of the two species groups (*roseata/cyanocephala* and *finschii/himalayana*), or that are not intermediate between them (Table 4). Among the potential parental species, *roseata* exhibits the most plumage features incompatible with the AMNH *intermedia* phenotype, while *finschii* also has a few characters inconsistent with *intermedia*, mostly in tail shape and colour. Neither *cyanocephala* nor *himalayana* shows any plumage features incompatible with their being parental species of AMNH *intermedia*, and a combination of the former two readily explains all plumage features of the latter.

STATISTICAL RESULTS

Summary statistics for measurements of the putative *intermedia* specimens (with the BMNH specimen treated separately), Sedgemore's hybrids, Sane's specimens, and comparative samples of the five putative parental species are given in the Appendix. For almost all measures, the AMNH *intermedia* are intermediate between *cyanocephala* and adult *himalayana*, and in many cases also between others of the putative parental species. Bivariate scatter plots of selected measurements overwhelmingly demonstrate this pattern, e.g. Figure 2A showing culmen length from cere vs. culmen width, in which all AMNH *intermedia* and Sedgemore's hybrids fall between the *cyanocephala/roseata* pair and the *himalayana/finschii* pair. Furthermore, *krameri* is larger than, and Sane's two specimens are as large as, the *himalayana/finschii* pair. A slightly different pattern is shown in Figure 2B (wing length vs. culmen length): here again, AMNH *intermedia* and Sedgemore's hybrids fall between *cyanocephala/roseata* and *himalayana* but, because of the shorter wing of *finschii* compared with *himalayana*, there is slight overlap between *finschii* and *intermedia*. *Psittacula krameri* is similar in wing length to *himalayana* but is bigger-billed, and Sane's birds fall between *cyanocephala/roseata* and *krameri*, being considerably

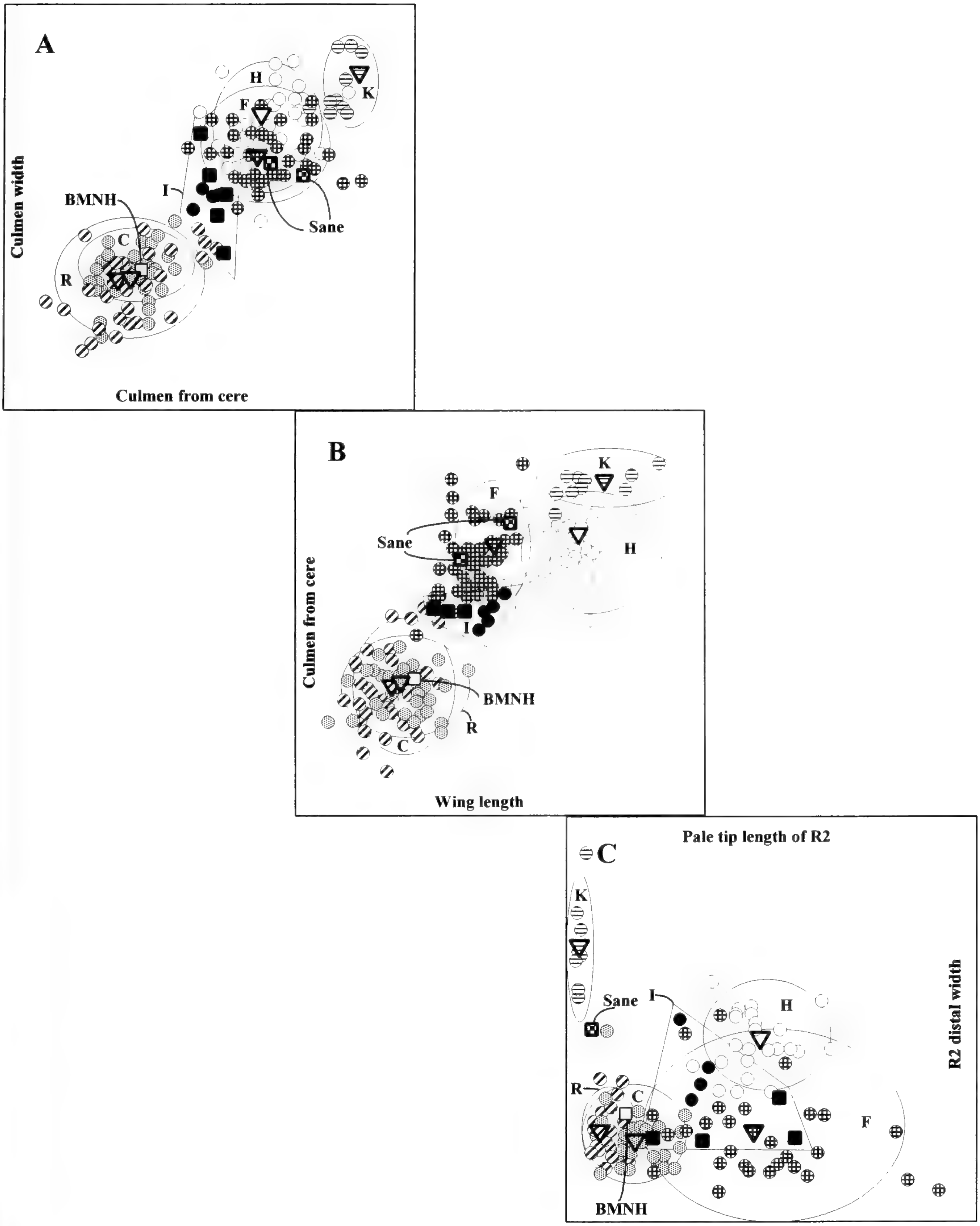

Fig. 2 Bivariate scatter plots of measurements of putative parental species and hybrids: (A) culmen length from cere vs. culmen width; (B) wing length vs. culmen length from cere; (C) R2 pale tip length vs. R2 tip width. Symbols are as for Figure 1, with the addition of the BMNH *intermedia* specimen (white square) and Sedgemore's hybrids (black squares).

Table 4 Characters used in hybrid diagnosis of *Psittacula cyanocephala* ($n = 21$), *P. roseata* ($n = 11$), AMNH *P. intermedia*, Sedgemore's hybrids ($n = 4$), *P. himalayana* ($n = 26$), and *P. finschii* ($n = 17$). Variation indicated for all but *intermedia*, for which see Table 1.

	'Blossom-headed' superspecies		*P. intermedia*		'Slaty-headed' superspecies	
	P. cyanocephala	*P. roseata*	AMNH *intermedia*	Sedgemore's hybrids	*P. himalayana*	*P. finschii*
HEAD						
Colour of base of maxilla	yellowish-horn (19/20[a])	yellowish-horn	orange	orange	red-orange	orange-red
Size of maxilla	small	small	moderate	moderate	heavy	rather heavy
Colour of mandible	black[b]	black[c]	yellowish-horn	yellowish-horn	yellowish-horn	yellowish-horn
Colour of cere	medium-grey[d]	*blackish	neutral to warm horn	warm horn	pale orange	pale orange-horn
Shape of cere	fairly wide, no or slight division	fairly wide, no or slight division	fairly wide, slight division	fairly wide, slight division	wide, partly divided	wide, partly divided
Width of bare orbital skin	relatively wide	relatively wide	?moderate	moderate	narrow	narrow
Colour of lores	bright pink (8) to bright red	*salmon-pink 5 bright, 5 pale	purplish-pink	purplish-pink	green-tinged grey	slaty grey
Colour of rear crown/nape	shining mauve[e]	*lilac[f]	grey-blue	grey-blue	cold slaty grey	warm slaty grey
BODY						
Colour of nape collar	bright bluish-green	*lime green	pale blue-green	pale blue-green	pale greenish-blue to pale bluish-green	bright greenish-blue
Extent of blue on collar	usually narrow	*none	narrow to very broad	moderate	moderate to broad	narrow, well-defined
Colour of collar/mantle border	bright olive (≥mantle)	olive (=mantle)	dull yellow-olive (=mantle)	dull yellow-olive (=mantle)	cool olive (=mantle)	*prominent, yellow-green (>>mantle)
Colour of rump	variably bluish-green	*pure bright green	bluish-green	bluish-green	cool green	bright yellowish-green
WING						
Colour of lesser coverts	variably bluish-green	*pure green	blue-tinged (4/5)	blue-tinged	cool green[g]	yellowish-green
Colour of red wing patch	bright maroon	dark maroon	mid-maroon	maroon	very dark maroon	dark maroon
Shape of P3	very broad, square	*narrow, elliptical	moderate (3/5), square (4/5)	moderate, squarish	moderate, square	moderate, ellipical
Colour of underwing coverts	pale turquoise-blue	*yellow green	pale bluish-green	pale bluish-green	pale bluish-green	pale bluish-green
TAIL						
Colour of midsection of R1	rich dark blue	*deep turquoise-blue	royal to dark blue	royal blue	dull purplish-blue	dull bluish-purple
Colour of R1 shaft at middle	black	black	black	black	dark brown	*pale brown to whitish
Colour of tip of R1	white[h]	very pale yellow	pale to pure yellow	pale yellow	bright pure yellow	*glaucous, orange-tinged yellow
Breadth of tip of R6	moderate	*thin	rather narrow to broad	moderate, slightly spatulate	broad	*thin
Toe colour	dark pinkish-grey	?dark grey	medium rosy-grey	medium rosy-grey	pale grey	pale grey
Claw colour	same as toes	?dark horn	?same as toes	same as toes	darker, greyer than toes	darker, greyer than toes

An asterisk (*) denotes characters not likely to contribute to an *intermedia*-like phenotype in combination with characters of either member of the other superspecies.

[a] Blackish patch at base in one; [b] 5/20 have ⅓ or more of mandible pale; [c] 3/11 have ⅓ or more of mandible pale; [d] 1/20 has lores pale grey; [e] Variable, always strongest at lower edge of nape; very dull in one specimen from Sri Lanka; [f] Dull in 3 worn specimens; washed greenish in another; [g] Bluish in 3 worn specimens; [h] Slightly yellow-tinged in one.

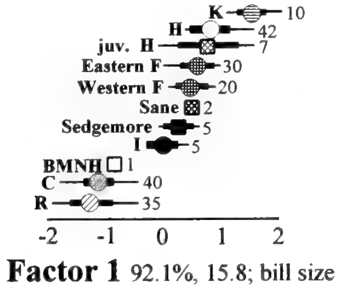

Fig. 3 Graph of means (squares), standard deviations (heavy bars), and ranges (narrow bars) of individual scores for putative parental species and hybrids on Factor 1, the only significant axis in a PCA of culmen length (component loading 0.95), maxilla height (0.96), and maxilla length (0.97). The number to the right of the range bar is *n*. Symbols are as for Figure 1 and 2; eastern and western *finschii* are included as separate groups.

larger than *intermedia*. In the plot of the distal width of rectrix 2 (R2) vs. the pale tip length of that feather (Figure 2C), *intermedia* fall between *cyanocephala/roseata* and *himalayana*, but not most *finschii*. *Psittacula krameri* is unique in its combination of a broad, very short pale tail tip, and in this Sane's specimen is intermediate between *krameri* and *cyanocephala/roseata*, and certainly not *himalayana*.

On a PCA of three bill measures (Figure 3, Table 3) selected to allow inclusion of as many specimens and live hybrids as possible, the only significant axis was Factor 1, a very strong size axis. On this axis, *cyanocephala* and *roseata* had the smallest mean factor scores, with the BMNH *intermedia* slightly larger. The other putative *intermedia* and known hybrids fell between these and the successively larger *finschii* and *himalayana* groups. *Psittacula krameri* was much the largest, and Sane's specimens were the largest of the putative hybrid groups, again showing the influence of *krameri*.

In a PCA for which variables were selected to allow inclusion of one of Sane's specimens (Figure 4A, Table 3), the AMNH *intermedia* and Sedgemore's birds group near each other, and between the widely spaced *roseata/cyanocephala* and *himalayana* groups, but overlap considerably with *finschii*. Sane's bird, however, falls between the *roseata/cyanocephala* and *krameri* groups.

Another PCA for which the variables selected allowed inclusion of Sane's other specimen (Figure 4B, Table 3) showed AMNH *intermedia* grouping out halfway between *cyanocephala* and *himalayana*, with the mean of *roseata* falling out more distantly. In this case, the second Sane specimen falls out much closer to *cyanocephala* than to *krameri*.

WING AND TAIL FORMULAE

In mean shortfalls of each primary tip from the wingpoint (Figure 5A), the AMNH *intermedia* are completely intermediate between *himalayana* and *cyanocephala*. However, BMNH 1980.3.1 is very like the mean of *cyanocephala* in pattern of primary shortfalls from the wingpoint. AMNH *intermedia* are closer in mean primary shortfalls to *roseata* than to *cyanocephala* (and thus less intermediate between *roseata* and *himalayana*; Figure 5B), but neither *roseata* nor *finschii* could be ruled out as parental species on this basis alone. Sane's single specimen on which these characters are measurable is nearly intermediate in primary shortfall pattern between *cyanocephala* and *krameri* (Figure 5C), although again these data do not rule out some other parental combinations.

On mean widths of primaries, AMNH *intermedia* were again intermediate between *himalayana* and *cyanocephala* except in width of P2, a measurement that is highly dependent on shortfall of P3 (Figure 6A). In spacing between tips of rectrix pairs 3–6 (Figure 6B),

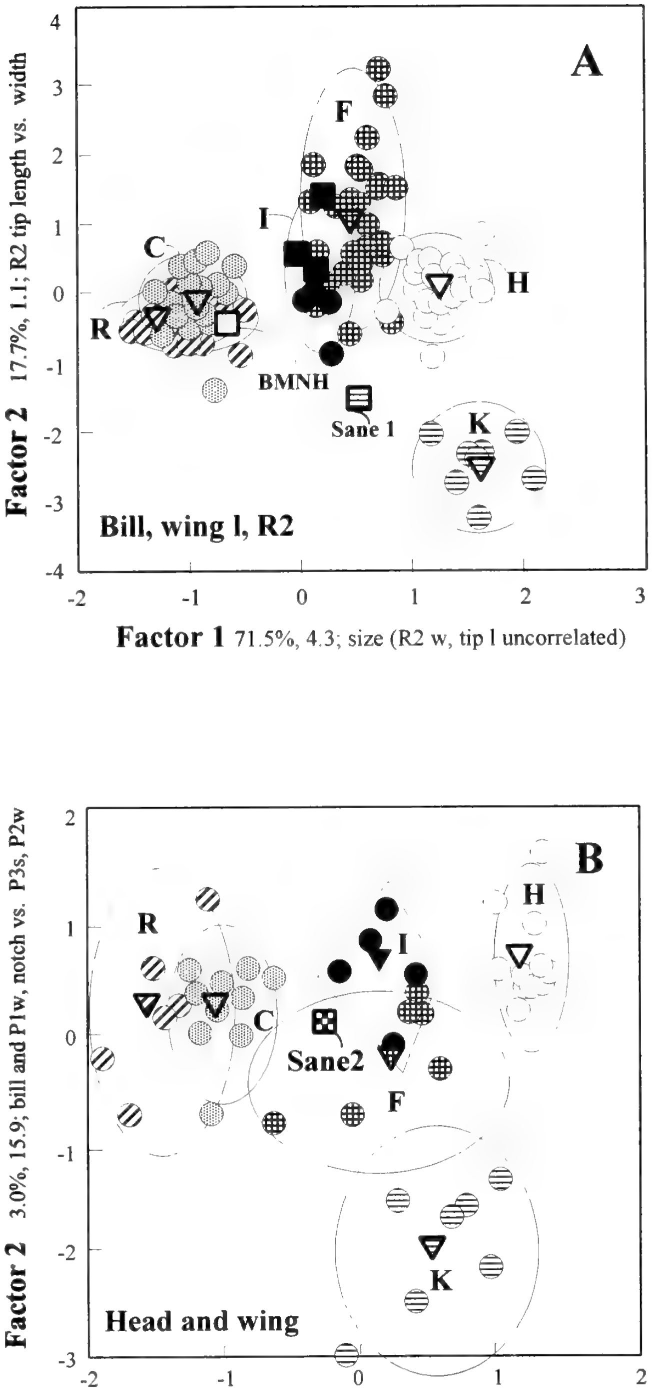

Fig. 4 Identity of AMNH *intermedia* with Sedgemore's hybrids, distinctness from Sane's specimens, and intermediacy of all the above between putative parental species: graphs of individual scores on Factors 1 and 2 from PCAs on measurements of adult males of putative parental species and hybrids. Symbols are as for preceding figures. Summary statistics of PCAs are given in Table 3B and C. (A) Variables chosen to allow inclusion of Sedgemore's hybrids and Sane's first specimen; (B) variables chosen for inclusion of Sane's second specimen.

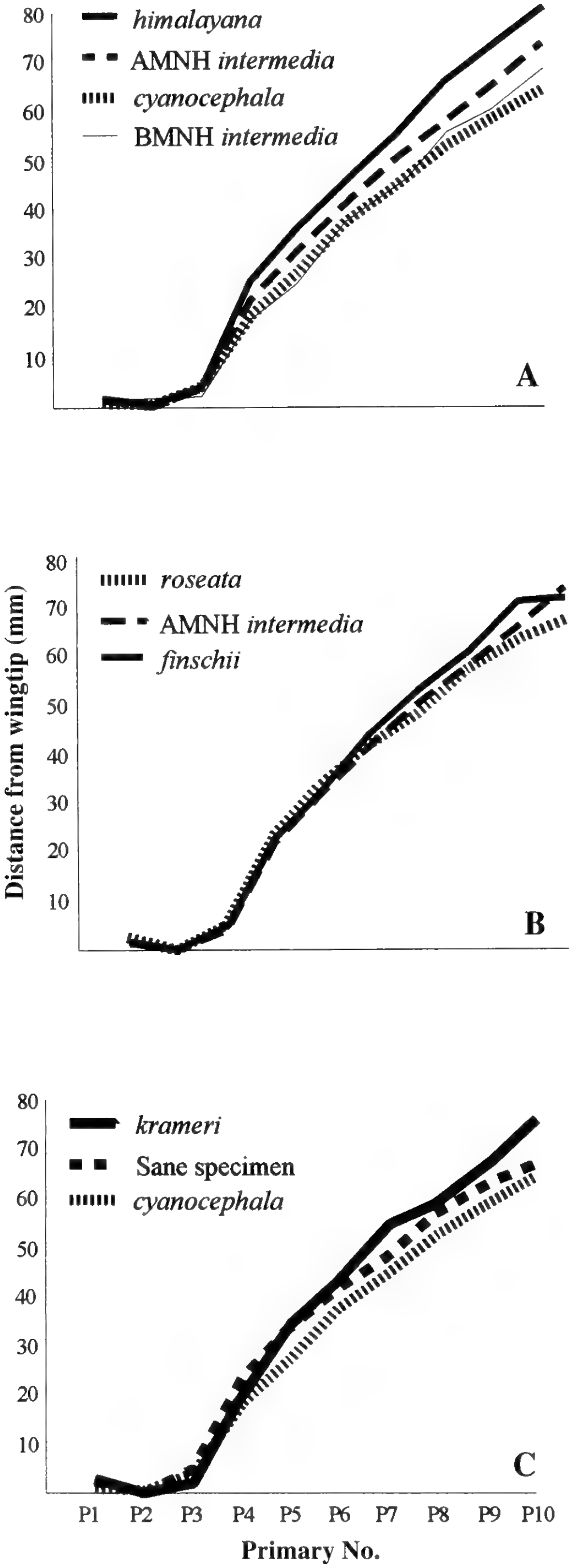

Fig. 5 Graphs of mean shortfalls of primaries from wingpoint for: (A) *Psittacula cyanocephala*, *P. himalayana*, and *P. intermedia* (BMNH specimen separate); (B) *P. cyanocephala*, *P. roseata*, and *P. intermedia* (BMNH specimen separate); (C) *P. krameri*, *P. cyanocephala*, and one of Sane's specimens. Full data are presented in Appendix.

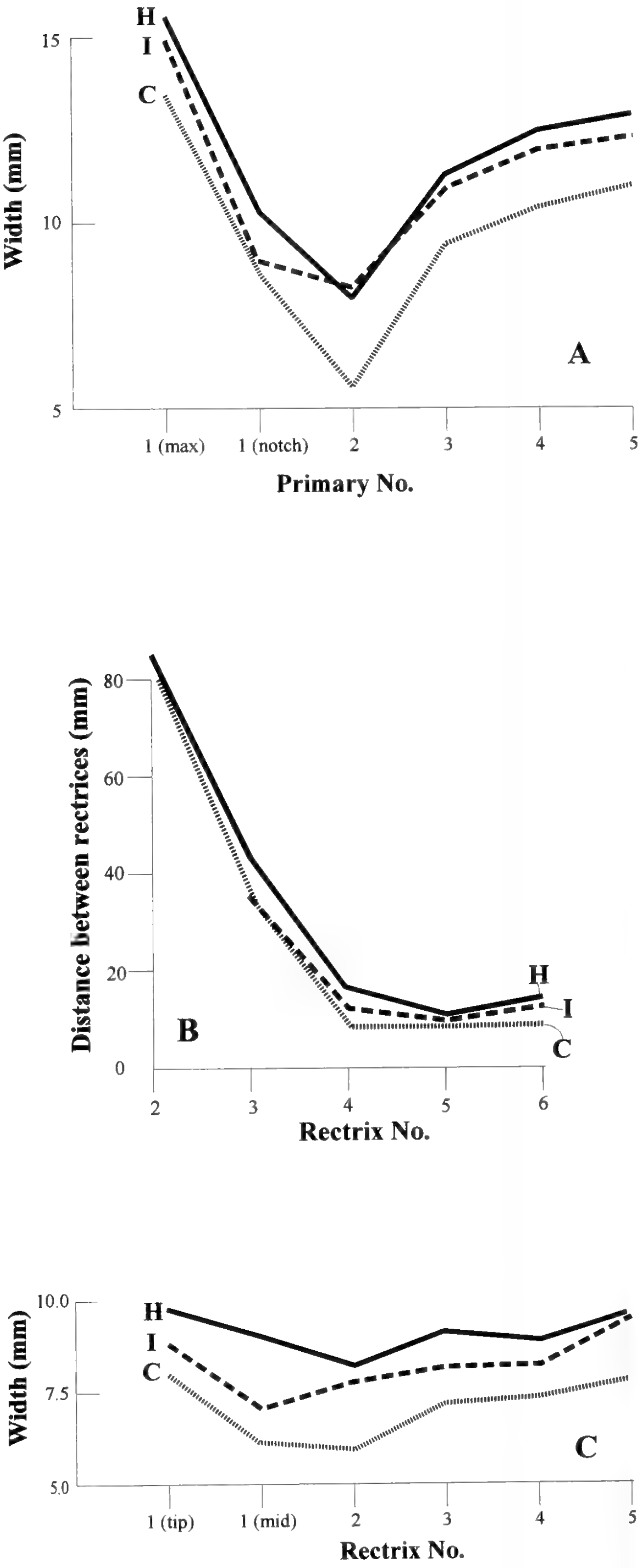

Fig. 6 Remex and rectrix width and spacing for *Psittacula cyanocephala*, *P. himalayana*, and *P. intermedia*: (A) mean widths of primaries, maximum and at notch for P1 (outermost), and width of P2–P5 at next innermost remex; (B) mean spacing between rectrices; (C) mean rectrix widths at next more lateral rectrix. Full data are presented in Appendix.

the AMNH *intermedia* are again totally intermediate, but BMNH 1980.3.1 differs from *intermedia* and is very like *roseata* (Appendix). In rectrix widths (Figure 6C), AMNH *intermedia* are more or less intermediate, although the central rectrices are somewhat closer in width to those of *cyanocephala*, while the outer rectrices are closer to those of *himalayana*; BMNH 1980.3.1 differs here as well (Appendix).

STYLES OF SPECIMEN PREPARATION

Examination of preparation styles of the Rothschild *intermedia* (Figure 7) other than the type (which predated the others) but including the juvenile *himalayana* (AMNH 621545), showed that one (AMNH 621541) has a longish neck and understuffed throat (vs. short necks and breast nearly touching the bill on the others); another (AMNH 621542) has the bill slightly open, while in three (AMNH 621544–5, BMNH 1980.3.1) the maxilla is extended far beyond the mandible (vs. naturally positioned in AMNH 621540–1). The wings are positioned far forward and low on the body on two (AMNH 621544–5), and low but to the sides on two others (AMNH 621540–1) vs. well-positioned to the sides on the remaining two (BMNH 1980.3.1, AMNH 621542). The body is compressed dorsoventrally in all but one (BMNH 1980.3.1). The tail is twisted in relation to the body in all but two (BMNH 1980.3.1, AMNH 621541); one with a twisted tail (AMNH 621542) has one of its central rectrices rotated 180° and its rectrices are spread, while they are folded tightly in the others. One specimen (AMNH 621542) is filled with dirty cotton, while another (AMNH 621544) has the body made of a tightly but roughly wound ball of coarse brown fibres each about 0.5 mm in width, and the rest of the Rothschild specimens are stuffed with rough bundles of straw. Support sticks in two (AMNH 621542, 621544) are thin (ca. 3 mm diameter), whittled, and orange-brown; thicker (3.4 mm), rougher, and grey-brown in another (AMNH 621540); and very thick (ca. 7 mm), coarse, crudely broken, and dark brown in yet another (AMNH 621545), while sticks are not visible externally in the other specimens.

All the Rothschild *intermedia* share the following external preparation features: the eyes are not stuffed and are dried shut; the breast is crudely stuffed so that the feathers of the upper breast are pushed outwards and upwards; the abdominal incision is rough; the tibiotarsi are broken medially and the feet were not secured, now being entirely missing in three (presumably having been lost after preparation). Strangely, the only published photograph of any of the Rothschild *intermedia* specimens (AMNH 621540, in Arndt 1996) was digitally enhanced to add in a lifelike eye and periorbital skin, even though it lacks a wing on the side photographed.

Radiographs (Figure 8) elucidate additional pertinent preparation features of the Rothschild *intermedia* specimens: AMNH 621541 and 621545 both had similar loose-woven cloth wound around the top of the support sticks and pushed into the open back of the skulls, while the others have little or no stuffing in the skulls. The X-rays confirm the similarity between the straw used in stuffing of five specimens (AMNH 621539–621541, 621545, BMNH 1980.3.1), and show that straw is lacking in two others (AMNH 621542, 621544). The body of AMNH 621540 is fusiform, while in AMNH 621544 the rear body is nearly empty. BMNH 1980.3.1 lacks a support stick altogether. In some of the specimens (AMNH 621540–1, 621545) the support stick is jammed into the braincase, while in AMNH 621544 the tip lies between the orbits, and in AMNH 621542 it projects into the base of the maxilla. In all specimens, the wings are positioned carelessly and variably, and those of the holotype are positioned differently to the rest. Similarities among the specimens visible in the x-rays include: most or all of the radii and the entire humerus have been removed; much of the back of the skull was removed but in an inconstant manner; the bones were often haphazardly broken and bone chips are embedded inside five specimens; and sacral vertebrae were left in five specimens.

Other dateless specimens examined by us that had been prepared in this characteristic native skin style (the 'Bombay preparation': Rothschild 1895) include the following abnormally plumaged specimens: a partial lutino *cyanocephala* (AMNH 454031); a yellow-tinged (flavistic?) *cyanocephala* (AMNH 621491); and a near-lutino *krameri* (AMNH 454030). Bombay preparation *Psittacula* skins with normal plumage at AMNH include: three *cyanocephala* (621490, 621492, 621537); five *himalayana* (621551–621554, 621556); two *finschii* (621550, 621557); and one *krameri* (621337). Further Bombay preparation skins are now in other collections (e.g. MCZ 38324–5). No skins of the Bombay preparation were found among the AMNH series of other Indian *Psittacula* species, although other presumed native skin styles are represented among them.

EVIDENCE FOR CAPTIVE ORIGIN

We found the following features among the Rothschild *intermedia* that are consistent with their having been held in captivity: (1) breakage or damage of primaries in three (AMNH 621542, 621544–5); (2) loss of central rectrices on AMNH 621539 and ongoing replacement of central rectrices on at least three others (AMNH 621541–2, 621544 and presumably 621540, showing that a high proportion of the sample is in moult); (3) irregular dark worn areas on feathers of the carpal area and heavily frayed wing coverts in AMNH 621544; (4) a featherless patch on the left side of the upper breast, and damaged feathers on the forehead of AMNH 621544 and shoulder of AMNH 621542; and (5) dirt on the feathers of the breast and/or belly of four (AMNH 621539, 621544–5, BMNH 1980.3.1), dirt on the right wing of BMNH 1980.3.1, and apparent whitewash on the upper tail surface of BMNH 1980.3.1.

PHOTOGRAPHS AND OTHER REPORTS OF CAPTIVE *INTERMEDIA*

A photograph of a parakeet published in Herrmann (1994) as a male *cyanocephala* is instead much like the five AMNH adult male *intermedia* specimens. This individual (which has now been sold) and its mate (which has died and for which no details are available) were said to be wild-caught from an unknown locality and were held in captivity in Austria, where the photograph was taken by F. Pfeffer in 1985 (T. Arndt, *in litt.* 1997). Based on a copy of Pfeffer's photograph, the male differs from *cyanocephala* (and agrees with AMNH *intermedia*) in having two-thirds of the upper mandible red-orange and fairly large; a pale yellowish lower mandible; a large head with more extensive, slatier-blue areas on the rear face and head; a weaker blue wash on nape, wing coverts, and rump; and the tail tip longer and yellowish. From the photograph of the male, it appears to differ from the AMNH *intermedia* in having a paler, less pure yellow tail tip; narrower central rectrices; a yellow-green area between the mantle and the hindcollar; and a dark maroon shoulder patch.

A second male (also of unknown provenance but from around 1985) was recently located in captivity at Turnersee Bird Park in Austria by R. Low (*in litt.* 1997) and F. Pfeffer (T. Arndt *in litt.* 1997), and was almost immediately published (with colour photos) as a true *intermedia* (Fuchs 1997). Photos of this bird (which is missing parts of its toes) from all three above sources show it to be very similar to the previously mentioned captive bird in Austria, except that its bill looks smaller and less orange-red. Some of the photos clearly show very narrow central rectrices with very long pale yellow tips and whitish shafts encroaching into the blue portion at least as far proximally as the level of the R2 tips. R. Low (*in litt.* 1997) stated it was the same size as the female *cyanocephala* with

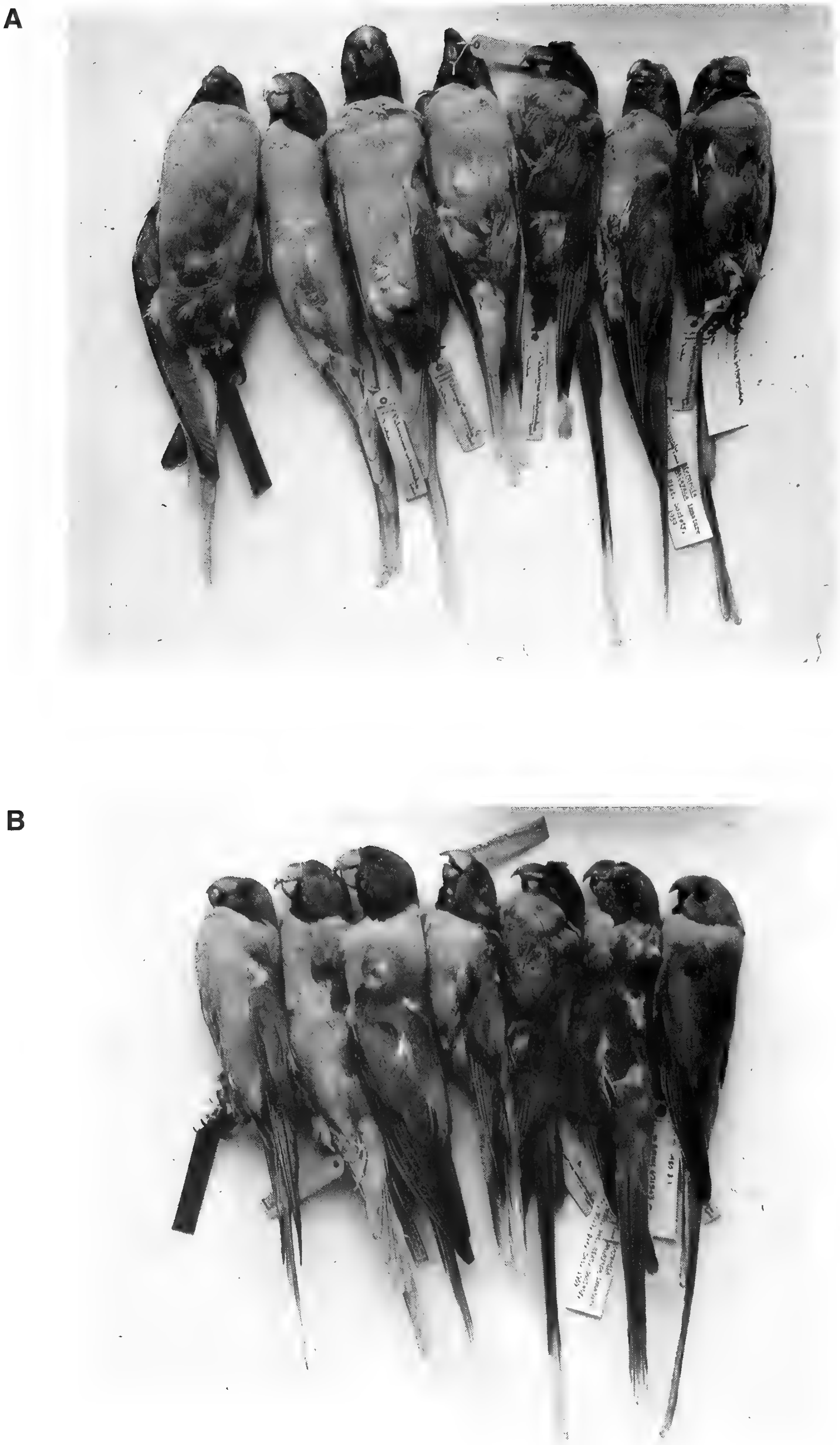

Fig. 7 Photo of all Rothschild *Psittacula intermedia* skins to show preparation styles: (A) ventral view of (left to right) AMNH 621539 (holotype), 621540-2, 621544-5, BMNH 1980.3.1; (B) lateral view.

Fig. 8 X-rays of all Rothschild *Psittacula intermedia* skins to show preparation styles and materials. Ventral view of (left to right, top row) AMNH 621544, BMNH 1980.3.1, AMNH 621539 (holotype), 621540, (bottom row) 621545, 621542, 621541.

which it was kept, and that the owners informed her that it had been bred from *cyanocephala* at Vogelpark Turnersee. However, the article about this individual (Fuchs 1997), which claimed that it was a great rarity, does not mention its parentage nor even the possibility that *intermedia* is a hybrid.

Sane (1977) recalled that in 1972 or 1973 he had seen a bird similar to his first '*intermedia*', but that it had been purchased by H. H. Jamsaheb, Nawanagar, India. He had also been told in about 1976 that someone in Britain had two or three *intermedia*, and that 8–10 had been imported into Holland in 1976. An individual was offered for sale in 1976 as 'probably the only known specimen in captivity in the world' (Inskipp and Inskipp 1995). However, we know of no documentation for any of these claimed *intermedia*.

In a poster session at the 1996 BirdLife Asia Conference in Coimbatore, India, R. Bhargava exhibited a photo of a captive bird that closely matched the AMNH specimens already examined by PCR. Bhargava (pers. comm. 1996) informed us that such birds were not rare in the pet trade within India, but that the illegality of this trade makes documentation difficult. He had obtained as many as five individuals from traders at one time, although one of these has since been ringed and released at a news conference (Anon. 1998) and three have died and been preserved as specimens. Bhargava's three specimens appear from photographs to be indistinguishable from AMNH *intermedia*, but definite, verifiable data on their provenance appear to be lacking.

KNOWN HYBRID *CYANOCEPHALA* × *HIMALAYANA*

After the publication of Walters (1985), Sedgemore informed M. P. Walters (pers. comm., 1995) that he had crossed *himalayana* and *cyanocephala* in captivity and obtained *intermedia*-like hybrids. Beginning in the late 1970s Sedgemore tried pairing captive *himalayana* and *cyanocephala* to determine whether Husain's (1959) hypothesis was correct (M. Sedgemore, *in litt.* 1997), but his adult male *cyanocephala* (age unknown) and five-year-old female *himalayana* refused to bond. In the mid-1980s he tried pairing different individuals of the same species, but again without result (M. Sedgemore, *in litt.* 1997). Then in 1991 he housed an immature female *himalayana* and immature male *cyanocephala* together, and these showed pair behaviour that year but did not breed. In 1992, of three eggs laid, two were clear and one was fertile but did not hatch, and in 1993 three more eggs were produced, only one of which hatched but the chick died at two weeks of age. Finally, in 1994, all three eggs laid hatched and the chicks fledged, as did chicks from two of three eggs laid in 1995 (M. Sedgemore, *in litt.* 1997). All the hybrids – four males and one female – were still alive and in adult plumage when we saw them in September 1997.

Photos of Sedgemore's hybrids with their parents show that the mother was a typical *himalayana* and the male parent a typical *cyanocephala*, the latter being additionally confirmed by the specimen. All these photos and our direct examination, photographs, and measurements confirm the identity of the hybrids with AMNH *intermedia*. The heads of all four adult male hybrids were coloured as in the five AMNH adult specimens, with only slight variability among them. Their ceres were pale fleshy horn; their maxillae orange-red on the basal two-thirds and with yellowish tips; their lower mandibles were pale; their eyering skin was pale greyish; and their feet and claws were pale greyish-pink. All had a broad pale greenish-blue hindcollar, lesser wing coverts, rump, and underwing coverts, the undersurfaces of the rectrices yellow with the outer webs bluish proximally, and the tail tips slightly broadened and pale yellowish from above.

The single female hybrid was less distinctive but still possessed characteristics which should enable recognition of specimens or captives. It would be immediately distinguishable from adult *himalayana* or *finschii* by its much paler, duller grey head and lack of a narrow black collar, and from males of the above two species by its lack of a maroon wing patch. Its head was drabber grey than adult female *cyanocephala*, with a pale area in front of the eye much as in juvenile *cyanocephala*; its upper mandible was heavier and was strongly tinged orange at the base; its lower mandible was pale; it had a slight yellowish collar on the sides of the neck (paler and duller than in adult female *cyanocephala* and less ochraceous than in female *roseata*); and it had long, slightly broadened, pale yellow tail tips, which extend much farther proximally on the feather than in *cyanocephala*.

Sedgemore (1995) briefly described the juveniles of the first brood. His photos of four of these same hybrids as fresh-plumaged juveniles show that they would be difficult but not impossible to distinguish from those of either parental species. All four hybrids had a pale area on the front of the face (on the forehead, lores, and area around the bill base); greenish-grey auriculars; a dull green crown and nape; and a pale yellowish-green collar contrasting with the head and mantle. From below, the tails of the hybrids were narrowly yellow-tipped. The upper tail surfaces are visible only on two individuals, in which they were greenish-blue with a pale yellow tip. Note that the latter character disagrees with Tavistock's (1933) statement (see below) that the tails of his hybrids were brighter blue than in young *cyanocephala* and were white-tipped. A photo of one of Sedgemore's 1995 hybrids in direct comparison with its 1994-hatched brother (an adult by then) shows that the juvenile has the upper tail surface more turquoise than the adult male. The young hybrids differed from juvenile *himalayana* by their smaller bills, their lack of blackish blotches at the bases of the maxillae, their duskier ceres, yellower collar, bluer upper tail surface, and narrower rectrices, and from juvenile *cyanocephala* by their duller, less yellow collar, and yellowish tail tips. It is uncertain whether juvenile hybrids between *cyanocephala* and *himalayana* could reliably be discriminated from young *finschii*, which would be more similar in size and proportions.

Successful hybridization of male *cyanocephala* × female *himalayana* was also achieved earlier by Critchley, who placed an adult male *cyanocephala* whose mate had just died in a mixed aviary with a placid adult female *himalayana* that had lived in a pet shop for several years (L. Critchley, *in litt.* 1998). The birds paired up during the first spring (1989) that they were kept together; from all five eggs laid, chicks hatched and were reared successfully. The fates of four of the young which were sold to a pet shop are unknown, but the remaining male moulted into adult plumage in August 1990 and was in Critchley's aviaries as of May 1998. Several photos, including one of the adult hybrid with its parents, show that Critchley's hybrid matches in every plumage detail the AMNH *intermedia* series and Sedgemore's male hybrids, and confirm the specific identity of the parents. Finally, a male *cyanocephala* and female *himalayana* also hybridized successfully in the aviaries of Mr E. Beale (now deceased, M. Sedgemore, pers. comm. 1997), and the pair reared two chicks in 1980. These had yellow tail tips as juveniles (Beale 1981), but this brief description does not enable evaluation of whether they match Rothschild's *intermedia* in other respects.

DISCUSSION

SANE'S CAPTIVES

Recognizing that the bird in Sane's collection photographed by Wirth (1990) was different from the AMNH material, Arndt (1996) stated that 'specimens caught on the plain of the Indian state of

Uttar Pradesh and described in literature as *Psittacula intermedia* do not probably belong to this species'. It has been noted elsewhere (Inskipp and Inskipp 1995) that the insufficient descriptions and the lack of photos in Sane *et al.* (1987) prevent independent evaluation both of their putative *intermedia* and their statement that 'each year between 1979 and 1984, one or two live specimens of this species were available in the Indian bird market most of which could not however be acquired by us. . . .' The following facts, however, show their true identity: (a) all Sane's birds share characters of *krameri* and *cyanocephala*, but not *himalayana*; (b) Sane (1975, 1977) himself described his immature bird as looking like a hybrid *krameri* × *cyanocephala*, with 'some reddish colour resembling somewhat that on the nape of the Rose-ring Parrakeet'; (c) trappers informed Sane that his birds were caught with, and were natural hybrids between, *krameri* and *cyanocephala* (Sane 1975, 1977); and (d) Sane *et al.* (1987) were confused about soft part coloration, post-mortem changes, and sexual dimorphism in their birds (see below, also Inskipp and Inskipp 1995). Sane (1977) also stated that 'the call of my bird is more like a Ringneck than a Blossom-head' [here meaning *cyanocephala*]. This evidence, coupled with our new data on Sane's three birds, demonstrates that all the *intermedia* reported by Sane (1975, 1977) and Sane *et al.* (1987) are *krameri* × *cyanocephala* rather than *intermedia.* Sane (1977) identified his birds as *intermedia* from the description in Biswas (1959), and related that when Biswas saw Sane's first bird, he indicated that it appeared to be *intermedia* but that measurements were needed for confirmation. Sane later took measurements which he said 'confirmed [sic] with the original' (Sane *et al.* 1987).

The lack of red shoulder patches in two of Sane's birds virtually rules out the possibility of *eupatria* (in which both sexes have shoulder patches) as a parental species, but it is consistent with *krameri*. In addition, the great size difference between *eupatria* and *cyanocephala* makes their hybridization unlikely, and the bill shapes of the Bombay specimens and live bird do not resemble that of *eupatria*. The only other possible combination that could result in such a phenotype would be *krameri* × *roseata*. However, all Sane's birds have a slight bluish tinge to the nape and wing coverts, so *roseata* could hardly be a parent, since this colour is lacking on both *krameri* and *roseata*.

The assumption by Sane *et al.* (1987) of reversed sexual dimorphism in *intermedia* based on the presumed sex of two of their living captives has already been called into question by Biswas (1990), and Inskipp and Inskipp (1995) also queried this as well as their statements on post-mortem changes in bill coloration. Now that we know that these birds are *krameri* × *cyanocephala* (explaining why two of them lack shoulder patches), the only remaining published corroboration for Sane *et al.*'s (1987) hypothesis of reversed sexual dimorphism is, by their own account, 'another male in the collection, which . . . had mated with a female Roseringed parakeet. However, the eggs laid were infertile.' Their 'subadult female' *intermedia* must presumably have been sexed by inference on the basis of its shoulder patches after Sane *et al.* (1987) had concluded that those lacking this feature were males. Its measurements were then compared with those published for AMNH *intermedia*, which Sane *et al.* (1987) termed 'female', but which surely must be males. However, even though male *krameri* lack shoulder patches, male *cyanocephala* possess them, so some male *krameri* × *cyanocephala* could have patches as well, and thus Sane *et al.*'s (1987) sexing of their subadult bird as a female on this basis is not upheld. In addition, the unaccessioned stuffed specimen (presumably the 'female') showed only a hint of a shoulder patch. Thus, even if Sane's birds really were *intermedia* and even if *intermedia* was a valid species, it is untenable to presume that it would exhibit reversed sexual dimorphism with respect to other *Psittacula* species.

Clearly, the specimens (number not stated) whose blood was used in the electrophoretic analyses reported in Sane *et al.* (1987) must have been *krameri* × *cyanocephala*, rendering the results inapplicable to the question of the taxonomic status of *intermedia*. In addition, the four loci examined do not form an acceptable sample, the methods of analysis and interpretation of results are problematic (R. Fleischer, pers. comm. 1997), and the major differences claimed between *intermedia* and other *Psittacula* species are improbable, especially given the apparent parentage of the individuals sampled.

BMNH SPECIMEN

One of the original Rothschild Collection *intermedia* specimens, BMNH 1980.3.1, was the one on which Husain's (1959) analysis of the hybrid origin of *intermedia* was primarily drawn. It is, moreover, more like the illustration of male *intermedia* in Inskipp and Inskipp (1995) than are any of the AMNH *intermedia*. However – and despite Hartert's (1924) assertion that specimens in the Rothschild Collection are alike – BMNH 1980.3.1 differs in several respects from the remaining five adults (Table 1). It is closer in overall appearance to adult male *roseata* than are the others, and is mensurally similar to both *roseata* and *cyanocephala*; except for the pale lower mandible and lack of shoulder patches it could be a hybrid *cyanocephala* × *roseata*. It could also be an F2 hybrid, or if bred in captivity, a trigen. Its tail tips are broader than in either *roseata* or *finschii*, while the turquoise upper tail surface and tail tip coloration, shape, and length are as in *roseata*. The slightly brighter red on the front of its face than in *roseata* cannot be explained as *roseata* × *himalayana* or *finschii*. However, its complete lack of reddish shoulder patches is unique among the *intermedia* series, is not due to feather loss, moult, or immaturity, and defies ready explanation. On present evidence we cannot resolve its parentage, but it does not appear to be an F1 offspring of a *cyanocephala* × *himalayana* cross.

EVIDENCE FROM THE AMNH SPECIMENS

As far as we can determine, all characters of adult AMNH *intermedia* are either (a) shared with the *himalayana/finschii* species pair or the *roseata/cyanocephala* pair, or (b) intermediate between one or both members of these two species groups. If for the moment we accept *intermedia* as a hybrid (to be further substantiated below), then we must assume (as did Husain 1959) that one member of each of the above species pairs was the parental species. *Psittacula roseata* cannot have been involved, as its facial coloration is not bright or deep enough to result in an *intermedia* phenotype, and its P3 is much too narrow (Table 4). In addition *roseata* lacks bluish on its hindneck, wing coverts, and rump, while most AMNH *intermedia* have the blue tint in these areas stronger than on the *himalayana/finschii* pair, and the upper tail surface of *roseata* is a paler, greener blue than in the other species and in AMNH *intermedia*.

However, hybridization of *cyanocephala* with either *himalayana* or *finschii* would involve none of the problematic characters of *roseata*. Nevertheless, *finschii* has narrow central rectrices that make it unlikely to be a parental species, whether mated with *cyanocephala* or *roseata*, since the mean distal width of the central rectrices is greater in *intermedia* than for any of those three species (Appendix; see also Husain 1959). In addition, a *finschii* × *cyanocephala* or *roseata* cross could hardly result in the bright yellow tail tips of AMNH *intermedia* (as already noted by Husain 1959). Finally, unlike *intermedia*, *finschii* has a bright yellow-green band above the mantle and pale shafts on the upper tail surface. Incidentally, the tail tips of the individual illustrated as *himalayana* in Inskipp and Inskipp (1995) are actually those of *finschii*.

Mensural and statistical analyses show the intermediacy of AMNH *intermedia* between one or both members of the *himalayana/finschii* and *roseata/cyanocephala* species pairs in every character set examined. Because *roseata* and *cyanocephala* are similar in size and proportions, *roseata* is not mensurally ruled out as a parental species, but it is ruled out on plumage (see above). However, *finschii* is smaller than *himalayana*, particularly in wing characters, and its tail proportions are different from any other species and AMNH *intermedia*, so it is unlikely to have been parent to the latter. We know of no cases in which a good species, which is intermediate between two patently different congeners in numerous phenotypic characters, totally lacks distinctive features of its own. Also, it is scarcely conceivable that a wild species would duplicate exactly the character states found in known hybrids between two quite distinct taxa. Thus both plumage and mensural analyses very strongly support the hypothesis that AMNH *intermedia* are of hybrid origin, and this is further validated by their identity with known hybrids between *himalayana* and *cyanocephala*.

ARGUMENTS PREVIOUSLY USED IN FAVOUR OF SPECIFIC STATUS

Hartert (1924) stated that if *intermedia* were a hybrid, 'so many specimens would not very likely have come at the same time,[2] and one would expect them to vary, but they are all alike', with footnote 2 disclosing that 'Our six males were selected by Mr. Dunstall, a dealer in feathers, from a greater number of these birds, he told us'. These statements have often been repeated as evidence of specific status (Biswas 1959, Walters 1985, Inskipp and Inskipp 1995), but both are flawed. First, the holotype did not originate with the other *intermedia*. Second, one of the six remaining specimens is a typical immature *himalayana* (see above), leaving only five *intermedia* supposedly of similar origins and identity. Hartert's assertion that these came from a greater number (though not 'a much greater number', *contra* Walters 1985) in the possession of *and selected by* Dunstall implies that Hartert himself did not see additional *intermedia* but had taken the London plumassier's word for it. There is nothing to indicate that Dunstall would have recognized the difference between *intermedia* and *cyanocephala*, and (our third objection) there seems no compelling evidence that he actually had more specimens of *intermedia*: the 'greater number of these birds' may have referred to the rest of a shipment of other *Psittacula* parakeets, a possibility supported by one of the six '*intermedia*' being a juvenile *himalayana*. There was a considerable millinery trade in *Psittacula* skins around this time (Hartley 1907), and only a very small percentage would have ended up in reference collections.

Fourth, preparation styles and materials used in the five Dunstall *intermedia* plus the immature *himalayana* differ strikingly among the skins. These differences strongly suggest that, although all are native skins, they were not all prepared at the same time and place. They may have come to Rothschild's museum at the same time, but not necessarily so to Dunstall or his supplier. Additional support for staggered acquisition of the material lies in the fact that native skins of *cyanocephala* and *himalayana* strongly resemble, in style and materials, not only those of *intermedia* but also those of *finschii*, which (given their distribution) must have originated farther east. Conversely, one adult *intermedia* (AMNH 621541) and the immature *himalayana* are so similar in preparation materials as to make it highly probable that they were prepared together. Many of the 'Bombay preparation' parakeet skins very likely came from bird markets to which captive birds had been brought from afar. Indeed, the incidence of at least three partial lutino specimens of this same preparation suggests selective breeding for this trait, which has long been highly desired by Indian aviculturists (Greene 1884).

After restating Hartert's (1924) contentions that *intermedia* is a valid species, Biswas (1959) indicated he had concluded the same independently. However, his only further evidence was as follows: 'Besides, if they were man-made hybrids, they would necessarily have been cage birds. But the character of their toes does not indicate this. *Psittacula intermedia* may, therefore, be regarded as a genuine wild species'. Besides the obvious fact that bird hybrids are not necessarily 'man-made', Biswas (1959) gave no indication of which features of the toes were found inconsistent with captive origin.

Our examination showed that the *intermedia* specimens exhibit to varying degrees several conditions consistent with their having been in captivity under suboptimal conditions (Harrison and Harrison 1986). It thus seems likely that most or all of the *intermedia* specimens in existence were captives for some period immediately prior to their death. In India, *Psittacula* parakeets have long been extremely popular cagebirds (Finn 1906, Ali 1927, Dharmakumarsinjhi 1954, Sinha 1959), and although most are taken from nests (Hume 1890), others are captive-bred commercially (H. S. A. Yahya, pers. comm. 1997), and they have long been bred for the Indian aristocracy (Greene 1884). Mutations in particular are bred in captivity in India (S. R. Sane, pers. comm. 1997), garnering up to Rs. 20,000 (Ahmed 1997). From the prices of cagebirds considered to be *intermedia* (Rs. 2,000 vs. less than Rs. 25 for ordinary *cyanocephala*: A. Rahmani *in* Inskipp and Inskipp 1995), it is self-evident that captive-breeding of such hybrids would be well worth the trouble.

Walters (1985) drew attention to previously overlooked descriptions of captive-reared *cyanocephala* × *himalayana* (Tavistock 1932–1938) which do not match Forshaw's (1973) description of *intermedia*. Based on this, as well as Hartert's (1924) arguments, Walters (1985) concluded that *intermedia* could not be a hybrid between those species and must therefore be a valid species, and in this he has been followed by most recent authors. Presumably also on the basis of this captive-breeding event, Arndt (1996) stated 'it has been discovered that hybrids between [*himalayana* and *cyanocephala*] differ considerably from *Psittacula intermedia*. . . .' However, a reevaluation of the aviculturist Tavistock's writings shows some relevant discrepancies.

First, although Tavistock (1932–1938) did repeatedly pair a male *himalayana* with a female *cyanocephala*, rearing at least seven young over a period of five years, he published only a very brief description of just two of those young, which were nestmates (Tavistock 1933), and did not describe their adult plumage. Thus there is no assurance that the other hybrids resembled these two, nor is there information enabling comparison between his hybrids and AMNH *intermedia*.

Second, while it is true that Tavistock's (1933) description of the two young *cyanocephala* × *himalayana* as having white tail tips does not match the specimens of *intermedia* (the discrepancy noted by Walters), other statements Tavistock made throw doubt upon his entire account. His remark that 'they resemble young Plumheads, but their central tail feathers are brighter blue with white tips and their heads have a dusky tinge' is nonsensical, as young *cyanocephala* do have white tips to their tails, and their heads may have a dusky tinge much like juvenile *himalayana*. Also, it is counterintuitive that hybrids would have brighter blue central rectrices than those of young *cyanocephala*, since juvenile *cyanocephala* have these feathers considerably bluer than do juvenile *himalayana*, which are green-tailed. Sedgemore stated that his juvenile *cyanocephala* × *himalayana* had 'blue green' upper tail surfaces (Sedgemore 1995), and this is confirmed by photos of them as juveniles. The central rectrices of the adult plumage of both parental species are bluer than in the juvenile plumage, while those of adult *cyanocephala* are bluer and less purple than for adult *himalayana*. Since the two young hybrids described by Tavistock (1933) had only hatched that year, presumably in the spring or summer of 1933, they could scarcely have moulted into diagnostic adult rectrices before Tavistock's article went to press. These inconsistencies indicate that little weight should be given to Tavistock's rather off-hand description.

Although not in connection with *intermedia*, Low (1992: 118) mentioned hybrids bred by the Duke of Bedford (then the Marquess of Tavistock), stating that the Duke had paired a male *finschii* with a female Blossom-headed Parakeet. However, Tavistock (1932) specifically stated he used a male 'Hodgson's Slaty-headed Parakeet' and female Plumheads (Tavistock 1932–1938). While *cyanocephala* has often gone by the common name of Blossom-headed Parakeet, to our knowledge *roseata* (earlier known as *rosa*) has not been called Plum-headed Parakeet, so he probably used *cyanocephala*. 'Hodgson's Slaty-headed' can refer only to nominate *himalayana*, not *finschii*. However, whether or not Tavistock had used true *himalayana*, some progeny of a cross between yellow-tipped and white-tipped parents might well show white tail tips, and in any case the tail tips of *finschii* are glaucous yellow, not white.

GEOGRAPHIC PROVENANCE

Biswas (1959) indicated that the Rothschild Museum label of the type specimen of *intermedia* states 'India Nat. Skim' and considered it uncertain whether 'native skin' or 'Native Sikkim' (= then-autonomous Sikkim) was meant. This was then taken by Ripley (1961) and Ali and Ripley (1969) as indicating that the type probably originated in Sikkim. However, the type's original label (the only one borne by the specimen, in Hartert's handwriting) clearly reads 'Nat. Skin', by which was meant the Bombay preparation of these trade skins, and thus there is no evidence pointing to Sikkim as the region of origin.

On the basis of Rothschild (1895) and Hartert (1924), it has also been assumed that *intermedia* is from the Western Himalayas (Forshaw 1973, Sibley and Monroe 1990), an idea reinforced by Sane *et al.*'s (1987) birds that we now know are *krameri* × *cyanocephala*, although the latter were reputedly from the plains just to the south (Sane 1977, Sane *et al.* 1987, Knox and Walters 1994). However, there is no basis for this assumption regarding either lot of Rothschild Collection skins that contained *intermedia* specimens. In the description, Rothschild (1895) stated that the type came to him with two skins of *Palaeornis schisticeps* and, because it was shipped from Bombay, it most likely came from the 'Western Provinces'. However, later Rothschild (1907) stated that speculation was useless, as the same shipment contained birds from various parts of the Himalayas; still later, Hartert (1924) stated that the birds evidently came from some part of the Himalayas. Subsequently it has been assumed without comment (Biswas 1959, Ali and Ripley 1969, Walters 1985) that by *schisticeps* Rothschild meant *Psittacula himalayana* of the western and central Himalayas. However, Rothschild did not differentiate between *himalayana* and the eastern form, *finschii*, both of which were then known as *schisticeps*, in his description of *intermedia*. Since at least two native skins of *finschii* of the 'Bombay preparation' (AMNH 621550, 621557) are present in the Rothschild Collection, but were not identified as such until later in a different hand (the former specimen is listed in the AMNH register as *himalayana* ssp., the latter erroneously as *P. h. himalayana*), it is by no means certain which form was meant by Rothschild, and the lack of a register for his collection prior to its accession at AMNH makes it impossible to determine this now.

CAPTIVE *INTERMEDIA* OF UNKNOWN PROVENANCE

The male '*intermedia*' located in Austria are probably both hybrids between *cyanocephala* and *finschii*, as indicated by the uniformly narrow central rectrices with very long pale yellow tips and pale shafts midway up the feathers, the yellow-olive band between the bluish nape collar and olive-green mantle, and the bright yellowish-green underparts. None of these features is consistent with *himalayana* as a parental species. Also, R. Low (*in litt.* 1997) thought the Turnersee bird was the same size as the female *cyanocephala* with which it was kept, which further supports *finschii* rather than *himalayana* as a parental species, as does this individual's small bill. Both of the Austrian '*intermedia*' have the front of the face bright rose-red, a feature incompatible with *roseata* being one of the parental species.

KNOWN *CYANOCEPHALA* × *HIMALAYANA*

Sedgmore's captive hybrids of known parentage are virtually identical in both plumage and measurements to AMNH *intermedia*. The slight mensural differences shown in Figure 3 are almost certainly due to measurement error, as the live birds had to be measured with great care to avoid injuring them, and thus they are probably slightly too large. Also, slight shrinkage of museum specimens is well-known. The identity of these hybrids with the type and only known series of *intermedia* cannot be ascribed to coincidence.

CONCLUSIONS

There is no evidence that *intermedia* is a valid species, and there is abundant circumstantial and unambiguous direct evidence that the AMNH series is comprised of hybrid *himalayana* × *cyanocephala* specimens. The discovery in the 1990s of more birds matching the phenotype of AMNH *intermedia* does not negate the above, particularly as they may well originate in captivity. In addition, Rothschild's original series not only contained a juvenile *himalayana*, but also another hybrid of uncertain parentage; Sane's '*intermedia*' are from a third hybrid combination (*krameri* × *cyanocephala*), and the two cage birds in Austria are probably from a fourth (*finschii* × *cyanocephala*). Thus the literature refers entirely to birds putatively of four different hybrid combinations, and the supposed species *Psittacula intermedia* has no taxonomic standing.

ACKNOWLEDGEMENTS. Special thanks go to Mr M. Sedgemore of Codsall, near Wolverhampton, U.K., for sending photos of his captive hybrids, allowing us personally to examine the birds, and sharing his notes with us. In addition we owe thanks to T. Arndt, R. Wirth, F. Pfeffer, R. Low; to R. P. Prŷs-Jones, M. P. Walters, and M. Adams, The Natural History Museum, Tring, U.K. (BMNH); C. Blake, M. LeCroy, P. Sweet, and M. N. Feinberg, American Museum of Natural History (AMNH); L. Bevier, Academy of Natural Sciences of Philadelphia (ANSP); D. E. Willard, Field Museum of Natural History (FMNH); R. A. Paynter, Jr., Museum of Comparative Zoology, Harvard University (MCZ); R. B. Payne and J. Hinshaw, University of Michigan Museum of Zoology (UMMZ); G. R. Graves and S. L. Olson, National Museum of Natural History (USNM); A. Rahmani, S. Unnithan, S. R. Sane, and A. Aktar, Bombay Natural History Society (BNHS); R. Bhargava and H. S. A. Yahya, Aligarh Muslim University; T. P. and C. Inskipp, K. Kazmierczak, L. Critchley, Cumbria, U.K.; and P. J. K. McGowan. Funding for PCR's travel to Bombay on two occasions was provided by the Research Opportunities Fund, National Museum of Natural History, and by British Airways, through M. Sitnik and T. Shille, Office of Biodiversity Programs/NOAHS, Smithsonian Institution. The manuscript was substantially improved by comments from G. R. Graves, R. P. Prŷs-Jones and M.D. Gottfried.

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Appendix Summary statistics of measurements (l = length, w = width, h = height; mm) of adult male *Psittacula cyanocephala, P. roseata,* AMNH *P. intermedia,* live hybrids in Sedgemore's collection (including one female); specimens from Sane's collection ($n = 2$); adult *P. himalayana,* then juveniles in parentheses; *P. finschii* specimens from western and eastern populations, respectively, and *P. krameri.* All are given as mean ± standard deviation (range, *n*). Measurements for BMNH 1980.3.1 given in parentheses following summary statistics of AMNH *intermedia* specimens. Descriptions of measurements given in Methods section.

Measure	*P. cyanocephala*	*P. roseata*	AMNH *P. intermedia* (BMNH 1980.3.1)	Sedgmore's hybrids	Sane specimens	adult (immature) *P. himalayana*	*P. finschii* W/E	*P. krameri*
HEAD								
Culmen	17.8±0.8	17.7±1.1	20.0±0.4 (18.0)	20.1±0.3	21.2±0.6	21.7±0.9 (21.1±1.1)	21.7±1.0/21.4±0.9	23.8±0.4
length	16.5–19.9, 40	15.3–20.2, 35	19.5–20.6, 5	19.7–20.5, 5	21.8–22.7	19.7–24.0, 41 (19.8–23.1, 7)	20.2–24.4, 32/19.3–23.4, 20	22.9–24.4, 10
Maxilla	10.7±0.4	10.3±0.4	11.8±0.5 (11.3)	12.8±0.3	11.9±0.1	12.8±0.6 (12.8±0.7)	12.5±0.3/12.3±0.4	13.4±0.7
height	9.8–11.4, 46	9.5–11.1, 38	11.4–12.8, 5	12.6–13.2, 5	11.8–12.0	11.3–13.8, 42 (11.8–13.8, 9)	11.7–13.1, 31/11.4–12.9, 20	12.4–14.4, 10
Narial	4.7±0.4	4.5±0.4	4.6±0.2 (3.8)	–	–	5.5±0.4 (5.7±0.4)	5.1±0.3/5.1±0.3	7.6±1.2
width	3.6–5.8, 43	3.7–5.5, 39	4.3–4.9, 5	–	–	4.8–6.2, 38 (5.0–6.3, 8)	4.4–5.8, 30/4.9–5.7, 20	6.5–10.0, 9
Maxilla	12.0±0.3	11.8±0.5	13.3±0.2 (12.1)	13.2±0.7	13.6±0.1	14.2±0.5 (14.2±0.6)	13.8±0.4/13.8±0.3	14.8±0.4
width	11.1–12.8, 46	10.9–12.7, 38	13.0–13.7, 5	12.3–14.1, 5	13.5–13.7	12.8–15.2, 42 (13.1–15.1, 9)	13.0–14.6, 31/13.2–14.4, 20	14.4–15.4, 10
Mandible	9.8±0.9	9.6±0.8	10.9±1.0 (10.0)	–	11.8±0.4	10.9±0.5 (11.1±0.7)	10.9±0.5/–	11.7±0.4
width	8.6–11.7, 23	8.5–11.6, 23	9.8–12.2, 4	–	11.5–12.1	9.8–12.7, 32 (10.2–12.1, 7)	10.1–11.5, 14/–	11.0–12.3, 10
Skull	22.6±1.1	21.5±0.9	24.3±1.1 (24.1)	–	23.0	25.4±1.0 (25.1±1.9)	24.2±1.0/24.0±0.7	25.6±1.0
width	20.5–24.7, 40	19.4–22.7, 35	23.0–26.0, 5	–	–	23.9–28.8, 30 (23.2–28.0, 5)	22.7–27.0, 21/22.3–25.1, 18	23.9–26.9, 10
WING AND REMIGES								
Wing	138.5±5.0	136.2±4.5	153.5±1.6 (142.0)	146.3±2.1	152.5±6.4	167.2±6.0 (155.1±3.3)	152.6±3.3/148.4±3.5	171.1±6.1
length	126–150, 44	129–145.5, 40	152–156, 5	144–148, 3	148–157	154–187, 38 (150–160, 9)	147–159, 30/141–155, 19	165–183, 10
P1	1.6±1.3	0.5±0.9	0.9±1.0 (0.0)	–	1.6±0.2	2.2±1.5 (0.2±0.4)	2.5±2.1/1.7±1.0	2.1±0.6
shortfall	0.0–4.1, 29	0.0–2.7, 31	0.0–1.9, 4	–	1.4–1.7	0.0–5.0, 24 (0.0–1.1, 8)	0.0–7.6, 13/0.0–4.2, 15	1.1–3.1, 9
P2	0.0±0.2	0.7±0.9	0.0±0.0 (0.5)	–	0.0	0.2±0.5 (0.2±0.4)	0.2±0.6/0.0±0.0	0.0±0.0
shortfall	0.0–1.0, 28	0.0–2.7, 31	0.0, 4	–	–	0.0–1.7, 25 (0.0–1.2, 9)	0.0–2.1, 13/0.0–0.0, 15	0.0–0.0, 9
P3	4.3±0.9	6.2±1.5	5.4±1.0 (3.0)	2.7	5.6	5.3±1.0 (5.8±1.4)	3.7±1.0/3.5±1.2	2.3±0.9
shortfall	2.1–6.1, 29	3.0–8.6, 37	4.0–6.4, 5	–	–	3.3–7.2, 23 (4.4–8.2, 9)	1.9–5.2, 13/1.4–5.7, 14	1.0–3.7, 9
P4	19.7±1.5	19.4±2.1	21.8±3.0 (18.3)	–	22.1	26.1±1.5 (19.9±1.8)	23.7±1.6/24.1±2.0	19.5±1.8
shortfall	16.4–22.2, 31	15.0–25.3, 36	16.7–24.1, 5	–	–	23.8–30.0, 27 (17.9–22.8, 8)	21.2–26.3, 13/20.0–28.5, 19	16.6–21.8, 9
P5	28.9±1.5	28.8±2.0	33.1±1.2 (26.9)	–	31.1	37.4±2.1 (28.7±2.0)	34.1±1.6/34.6±2.5	31.4±2.3
shortfall	25.9–32.5, 30	23.0–33.2, 37	31.5–34.6, 5	–	–	33.3–43.8, 26 (26.0–31.4, 7)	31.7–37.1, 13/30.1–41.7, 19	28.5–34.9, 9
P6	37.6±1.8	37.9±2.5	42.4±1.0 (37.3)	–	41.6	46.8±2.3 (38.0±1.8)	44.0±2.4/43.9±2. 8	42.7±2.8
shortfall	34.6–41.5, 30	33.7–44.0, 37	41.3–43.5, 5	–	–	43.4–53.1, 27 (35.2–40.9, 9)	39.5–47.8, 13/38.4–50.6, 19	37.5–45.6, 9
P7	45.3±1.9	45.5±2.7	50.3±1.7 (45.8)	–	48.7	56.0±2.3 (46.8±1.9)	52.1±2.6/51.9±3.3	52.2±2.9
shortfall	42.1–49.9, 28	41.2–51.0, 38	47.5–52.1, 5	–	–	52.1–62.1, 27 (43.8–49.9, 9)	47.7–56.4, 13/43.7–60.0, 19	47.0–56.4, 9
P8	52.5±2.1	53.0±3.2	58.8±1.7 (54.7)	–	56.0	65.7±2.6 (56.5±1.7)	60.0±2.8/59.6±2.6	60.5±3.6
shortfall	48.7–57.3, 29	48.2–60.3, 37	56.0–60.1, 5	–	–	59.3–71.2, 28 (54.1–59.5, 9)	55.5–63.9, 12/54.5–64.7, 18	53.9–65.1, 9
P9	59.2±2.4	59.6±3.2	67.8±1.2 (61.2)	–	62.1	73.5±3.0 (64.3±1.6)	67.4±2.8/66.8±3.0	68.7±2.9
shortfall	54.5–65.2, 28	54.5–65.8, 38	66.5–69.7, 5	–	–	68.0–81.8, 27 (62.7–66.9, 9)	63.4–72.8, 11/61.9–71.4, 18	73.3–73.0, 9
P10	64.6±2.6	66.0±3.6	74.7±2.3 (67.1)	–	68.7	81.0±3.5 (71.4±2.1)	74.2±3.0/72.8±3.4	76.2±3.6
shortfall	57.9–70.5, 26	60.5–72.7, 38	72.4–77.9, 5	–	–	73.9–88.3, 25 (67.8–75.6, 9)	70.0–78.9, 11/67.1–79.6, 17	69.7–81.9, 7
P1 notch-	18.0±1.5	18.1±1.6	19.2±0.7 (18.4)	–	21.1	21.1±1.5 (17.4±1.4)	19.0±1.5/8.1±1.6	24.4±1.5
tip distance	15.5–21.4, 31	14.5–21.0, 33	18.1–19.9, 5	–	–	17.4–24.3, 31 (15.1–19.8, 7)	16.7–22.7, 17/14.5–21.0, 33	22.0–26.3, 7
P1 maximum	13.1±1.4	13.2±0.7	14.9±0.9 (14.9)	–	–	15.3±1.2 (14.6±1.1)	14.2±1.0/14.5±0.6	14.3±3.2
width	8.9–15.3, 24	11.9–14.5, 12	14.3–16.3, 4	–	–	12.8–17.7, 25 (12.7–16.3, 9)	12.5–16.2, 11/13.5–15.4, 15	10.5–18.4, 7
P1 width	8.4±0.6	8.1±0.7	8.8±1.4 (8.9)	–	4.9	9.1±0.6 (8.4±0.7)	8.6±0.8/8.1±0.7	13.3±3.6
at notch	7.2–9.8, 25	7.4–9.8, 10	7.6–11.1, 5	–	–	8.1–10.2, 25 (7.4–9.6, 7)	7.8–10.7, 12/7.4–9.8, 10	9.6–18.0, 8
P2 width	6.2±0.8	5.8±0.4	8.0±1.4	–	5.9	7.8±0.7 (7.2±0.9)	6.5±0.9/6.3±1.0	5.9±0.7
	4.3–7.5, 26	5.3–6.4, 11	6.8–10.3, 5	–	–	6.6–8.7, 17 (6.2–9.0, 8)	5.6–6.9, 4/4.7–7.6, 8	4.9–6.8, 8
P3 width	9.6±1.0	8.3±0.6	11.0±1.0	–	9.7	11.4±0.6 (10.1±0.6)	10.9±0.5/10.5±0.6	9.6±1.2
	6.5–11.4, 25	7.4–9.1, 10	9.9–12.5, 5	–	–	10.7–12.5, 16 (9.0–10.8, 7)	10.4–11.8, 6/9.5–11.5, 9	8.2–11.9, 8

Appendix *Continued*

Measure	*P. cyanocephala*	*P. roseata*	AMNH *P. intermedia* (BMNH 1980.3.1)	Sedgmore's hybrids	Sane specimens	adult (immature) *P. himalayana*	*P. finschii* W/E	*P. krameri*
P4 width	10.4±0.7	9.3±0.5	11.7±1.3	–	11.4	12.5±1.0 (10.4±1.2)	11.6±0.3/11.4±0.8	11.5±0.8
	8.8–11.8, 24	8.5–10.4, 10	10.0–12.9, 5	–	–	10.2–14.2, 16 (8.7–11.2, 4)	11.1–12.1, 6/10.4–12.8, 9	10.3–12.5, 8
P5 width	11.0±0.6	10.2±0.6	12.1±0.5	–	12.0	12.8±0.8 (11.9±0.6)	11.3±0.8/10.2±0.6	13.1±0.8
	9.9–12.0, 16	9.0–11.0, 10	11.3–12.7, 5	–	–	11.7–14.7, 16 (11.0–12.7, 5)	10.4–12.8, 8/10.2–11.0, 10	12.1–14.3, 8
RECTRICES								
R1	203.1±15.8	166.1±15.4	157+, 170+, 200+ (182+)	262.0±11.6	176	234.7±15.0	264.7±18.9/250.6±19.7	231.4±10.4
length	166–231, 35	141–229, 33	–	246–273, 4	–	207–261, 27	232–302, 12/211–271, 16	222–254, 8
R2	115.7±17.3	103.6±8.1	127.0±13.1 (102)	–	[131.8]	146.1±12.2	137.0±22.8/132.7±14.0	194.1±36.0
length	91–194, 37	89–131, 37	106–138, 5	[96–116, 4]	–	115–180, 40	98–184, 19/113–1760, 16	165–255, 8
R1–R2	88.76±11.9	55.8±7.8	–	155.0±8.8	44.2	83.6±9.5	114.2±4.7/116.8±14.8	59.1±20.3
difference	47–109, 23	43.7–71.4, 17	–	145–166, 4	–	71–111, 16	110–121, 4/93–140, 15	23–76, 8
R2–R3	34.5±9.4	24.3±5.8	35.2±10.0 (20.1)	41.5±12.0	29.3	44.1±6.9 (16.9±1.9)	50.4±13.8/41.8±15.4	37.9±4.6
difference	10.0–49.7, 42	15.8–45.5, 35	18.8–44.0, 5	33.0–50.0, 2	–	32.0–63.0, 38 (14.9–20.2, 6)	14.7–75.0, 34/14.7–69.0, 17	31–47, 9
R3–R4	8.6±1.2	9.7±1.5	11.7±1.2 (8.9)	–	16.2±1.1	15.3±5.5 (11.2±0.6)	13.9±2.4/12.6±1.8	22.3±4.3
difference	6.2–10.7, 30	6.7–13.4, 36	10.1–13.2, 5	–	15.5–17.0	9.0–41.1, 31 (10.5–12.1, 6)	10.6–18.1, 16/9.6–16.1, 17	17–32, 9
R4–R5	7.3±2.1	8.5±1.8	8.9±1.0 (9.3)	–	12.9±0.0	10.3±1.9 (8.6±1.5)	9.6±1.6/78.4±1.0	17.6±1.9
difference	4.3–17.2, 32	6.0–15.1, 36	7.7–10.5, 5	–	12.9–12.9	7.0–16.1, 33 (6.1–10.1, 6)	7.4–13.3, 19/6.4–10.3, 16	15–20, 9
R5–R6	9.6±1.7	10.3±1.3	11.9±0.8 (10.2)	–	15.0±2.7	13.5±2.0 (11.3±1.4)	11.1±2.3/10.5±1.5	19.4±1.8
difference	6.9–14.4, 32	6.2–13.1, 37	11.2–13.1, 5	–	13.1–16.9	10.0–17.6, 32 (9.4–13.4, 8)	7.8–15.0, 19/8.3–13.5, 16	17–22, 9
R1 distal	7.7±1.3	5.3±0.6	8.3±1.2 (6.1)	9.3±1.1	7.0	9.7±0.9	5.1±0.7/4.6±0.4	7.7±0.8
width	4.9–10.2, 27	3.9–6.7, 20	7.5–9.7, 3	8.0–1.0, 3	–	8.0–11.8, 30	4.0–6.3, 25/3.9–5.4, 13	6.6–8.4, 6
R1 proximal	6.0±0.7	5.2±0.6	7.0±0.5 (5.5)	–	–	8.5±0.7	5.1±0.7/5.5±0.4	–
width	4.9–7.9, 30	4.1–6.8, 32	6.4–7.3, 3	–	–	7.0–10.0, 34	3.3–6.6, 19/4.8–6.1, 15	–
R2 width	6.0±0.7	6.2±0.5	7.8±0.7 (6.6)	6.2±0.5	8.7	8.4±0.7 (8.7±0.8)	5.8±1.1/6.5±0.9	10.7±1.1
	5.1–8.7, 33	5.3–7.5, 28	7.0–9.0, 5	6.0–7.0, 4	–	7.2–9.9, 27 (8.1–9.7, 5)	4.7–8.8, 18/5.3–9.0, 15	9.6–13.1, 9
R3 width	6.8±1.0	6.4±0.8	8.2±1.1	–	8.8±0.1	8.9±0.9 (8.5±0.6)	7.6±0.5/7.2±0.5	11.2±1.1
	5.2–10.7, 25	5.2–8.1, 10	7.1–9.7, 5	–	8.8–8.9	7.0–10.5, 16 (7.7–9.2, 4)	7.2–8.4, 4/6.4–7.9, 9	8.7–12.3, 9
R4 width	7.0±0.9	7.0±0.7	8.2±0.7	–	9.2±0.0	8.6±0.6 (7.6±0.7)	7.7±0.7/7.2±0.5	11.8±1.0
	5.6–9.3, 25	5.8–8.3, 10	7.6–9.4, 5	–	9.2–9.2	7.8–9.6, 14 (6.5–8.6, 7)	7.1–8.8, 5/6.7–7.9, 8	9.9–12.8, 9
R5 width	7.6±1.2	7.3±0.8	9.3±1.0	–	9.2	9.4±0.7 (8.5±0.8)	8.2±1.1/7.8±0.4	12.3±0.9
	4.3–9.5, 24	6.6–9.4, 10	8.4–11.0, 5	–	–	8.8–10.8, 10 (7.0–10.0, 8)	6.6–9.7, 5/7.1–8.4, 8	11.1–13.9, 7
R1 tip length	29.3±6.7	16.5±4.6	41.6±3.5 (33.9)	48.2±13.8	4.0	81.4±10.7	115.5±19.6/107.7±13.0	2.8±1.2
	11.0–38.5, 36	7.3–25.7, 31	39.1–44.1, 2	30.0–62.0, 4	–	58.0–105.0, 38	85.0–165.0, 23/90–130, 13	0.0–4.1, 8
R2 tip length	13.1±4.8	7.7±2.0	25.3±2.4 (11.8)	32.7±13.1	5.0	38.6±6.5	42.2±13.7/28.8±9.9	2.8±0.7
	5.3–23.2, 41	5.0–13.0, 36	22.4–27.8, 4	17.0–45.0, 4	–	25.0–55.0, 39	17.3–73.0, 21/14–50, 14	2.0–4.4, 8
HINDLIMB								
Tarsus	14.2±0.9	13.6±0.9	14.8±0.1 (15.6)	–	15.8	15.3±1.1 (15.4±0.4)	15.4±0.9/4.7±0.9	17.6±0.6
length	12.4–16.1, 33	12.0–15.9, 32	14.7–14.9, 3	–	–	13.0–18.4, 32 (14.8–15.7, 6)	12.2–17.0, 25/12.3–15.9, 16	16.8–18.7, 10
Minimum	3.3±0.4	3.2±0.4	3.0±0.1	–	3.4	3.4±0.3 (3.5±0.4)	3.4±0.4/3.6±0.3	4.2±0.5
tarsus width	2.4–4.5, 23	2.7–4.1, 11	2.9–3.1, 3	–	–	3.1–4.3, 21 (3.0–4.1, 4)	2.9–4.0, 5/3.1–4.1, 10	3.5–5.0, 8
Midclaw	7.9±0.5	7.9±0.6	8.6±0.2 (7.5)	–	8.8±0.4	9.2±0.5 (8.6±0.7)	8.5±0.4/8.4±0.5	9.9±1.0
length	7.1–9.0, 23	7.0–9.2, 13	8.3–8.8, 3	–	8.5–9.1	8.2–10.5, 29 (7.4–9.5, 8)	7.9–9.4, 12/7.6–9.4, 15	8.0–11.0, 8
Hindclaw	6.1±0.5	6.6±0.4	8.0±0.7 (6.0)	–	7.0	7.0±0.3 (6.7±0.3)	6.6±1.0/6.4±0.8	7.9±0.3
length	5.5–7.0, 13	6.1–7.0, 5	7.5–8.5, 2	–	–	6.3–7.4, 23 (6.3–7.2, 8)	5.1–8.5, 7/5.8–8.3, 9	7.5–8.3, 6

Bull. nat. Hist. Mus. Lond. (Zool.) **65**(1): 51–72 Issued 24 June 1999

A review of the genus *Bargmannia* Totton, 1954 (Siphonophorae, Physonecta, Pyrostephidae)

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CONTENTS

SYNOPSIS. Two new species of the physonect siphonophore genus *Bargmannia* are described, and *B. elongata* Totton (1954) and *B. lata* (Mapstone, 1998) are redescribed. The status of the genus and its retention within the family Pyrostephidae are discussed.

INTRODUCTION

Totton (1954) established the genus *Bargmannia*, named after his colleague Dr Helene Bargmann, to include the single species, *B. elongata*; nectophores of which he had found in thirteen *Discovery* samples, plus one from the *Michael Sars* Expedition (Leloup, 1955). Because the structure of the nectophores differed so markedly from those of all other known physonect siphonophores, Totton did not give a detailed description of them; remarking only that the lateral radial canals on the nectosac had straight courses. Totton (1965) later noted that, although *B. elongata* was one of the most easily recognised siphonophore species, nothing more had been published on it since its original description. In fact, by the time of publication of Totton's monograph, only Alvariño (1963, 1964) had mentioned it; and then only in lists of siphonophore species collected in the western Pacific. Totton included a brief description of a further specimen collected at *Discovery* St 4246 (37°50'N, 13°22'W), remarking on the orange coloration of the stem.

Since that time several authors have reportedly identified this species from various collections. However, examination of both Totton's material and that from more recent *Discovery* collections (Mackie, Pugh & Purcell, 1987) appeared to indicate that Totton's (1954, 1965) illustrations of *Bargmannia elongata* could be referred to two species, and that his material also included a third species. However, it was not until submersibles collected specimens of this genus that this contention could be proved beyond doubt. Study of this submersible material, together with that from the *Discovery* collections, shows that there are at least four species that may be referred to the genus *Bargmannia*. The second species that Totton illustrated under the name *B. elongata* has recently been described under the name *B. lata*. More detailed descriptions of both these species, together with descriptions of two previously undescribed species, are given herein.

Totton (1954) did not refer the genus *Bargmannia* to any of the physonect families, although his description appears at the end of a section dealing with various species of the family Agalmatidae. Later, Totton (1965) placed the genus in the family Pyrostephidae, which previously had been monotypic for the species *Pyrostephos vanhoeffeni* Moser, 1925. However, his diagnosis of that family applied only to the genus *Pyrostephos*, and included such features as marked bends in the dorsal and lateral radial canals on the nectosac of the nectophores. This character alone would exclude the genus *Bargmannia*. Since then, Stepanjants (1967) placed the genus in the catch-all family Agalmatidae, whereas Daniel (1974) retained it within the family Pyrostephidae. Now that intact specimens have been collected by submersibles it is possible to review the systematic position of the genus *Bargmannia*. It is concluded that, for the present at least, it should be retained within the family Pyrostephidae, the diagnosis of which is adjusted accordingly.

Family **PYROSTEPHIDAE** Moser, 1925

DIAGNOSIS. Long-stemmed physonect siphonophores. Nectophores with large triangular thrust block; with lateral wedge-shaped processes reduced or absent. With apico-, infra- and vertical (meso-) lateral ridges; apico-laterals divide above ostial level. Adaxial wall of nectosac lacking musculature; deeply hollowed. Long pallial canal; short pedicular canal, giving rise, on nectosac, to only dorsal and ventral radial canals; lateral radial canals arise separately from dorsal. Dorsal and lateral radial canals either looped or straight. Tentillum with straight (or twisted, but not tightly coiled) cnidoband; lacking an involucrum; with terminal filament. Dactylozooids either absent or modified to form peculiar palpacle-less oleocysts. Individual specimens of single sex (dioecious), with gonophores budded one from another to form a small gonodendron; female gonophores contain two or more eggs.

REMARKS. In *Pyrostephos vanhoeffeni*, the triangular thrust block is best seen on smaller nectophores. On larger, preserved ones it is bent up dorsally (see also Discussion section).

Genus ***BARGMANNIA*** Totton, 1954

DIAGNOSIS. Pyrostephids with distinctive elongate nectophores. Mature nectophores with large, triangular thrust block; without apical wedge-shaped processes; with extensive ventro-lateral wings. Basic ridge pattern may be augmented by additional ridges branching from apico-laterals. Nectosac basically cylindrical; dorsal and ventral radial canals straight; lateral radial canals arise separately, but in close proximity, from the dorsal canal. Pneumatophore without apical pore.

Siphosome diffuse; devoid of fully formed dactylozooids. Bracts specifically variable in shape. Each cormidium; with simple tentacle-like structure attached to stem midway between successive gastrozooids; with single gonodendron; with four bud-like structures (?vestigial dactylozooids) with sexually dimorphic arrangement. Second tentacle and fifth bud occasionally present proximal to a gastrozooid.

REMARKS. The meso-lateral ridges on the nectophores, as referred to in the above diagnosis, are homologous with the vertical lateral ridges, as defined by Pugh and Youngbluth (1988), found on the nectophores of certain agalmatid species. In these latter species these ridges run vertically, or slightly obliquely, between the apico- and infra-lateral ridges, although they may not reach the latter. However, in *Bargmannia* spp. their arrangement is strikingly different in that they have a very oblique course; and it is the infra-lateral ridges that may or may not join them basally. For these reasons the term meso-lateral ridges will be used herein.

In contrast, the outer of the two branches of the apico-lateral ridges should not be compared with the lateral ridges of agalmatid species, as defined by Pugh and Youngbluth (1988). They more closely resemble the near-ostial branching of the apico-laterals in agalmatid species such as *Lychnagalma utricularia* (Claus, 1879) (see Pugh & Harbison, 1986) and *Halistemma transliratum* Pugh & Youngbluth, 1988, which also possess normal lateral ridges.

The long, median canal that runs up the thrust block (see Figure 2), just below its ventral surface, has been variously referred to as a pallial (e.g. Daniel, 1974) or a pedicular canal (e.g. Daniel, 1985). In accord with the definitions given by Totton (1965) here the canal will be referred to as the pallial canal; and the short canal, passing through the mesogloea from the stem to the nectosac, the pedicular canal.

Recently, it has been brought to my attention (Dr S. Haddock, personal communication) that the generic name *Bargmannia* was used by Herre (1955) in a description of a genus of an extinct salamander. *Bargmannia* Totton, 1954 clearly has priority of publication.

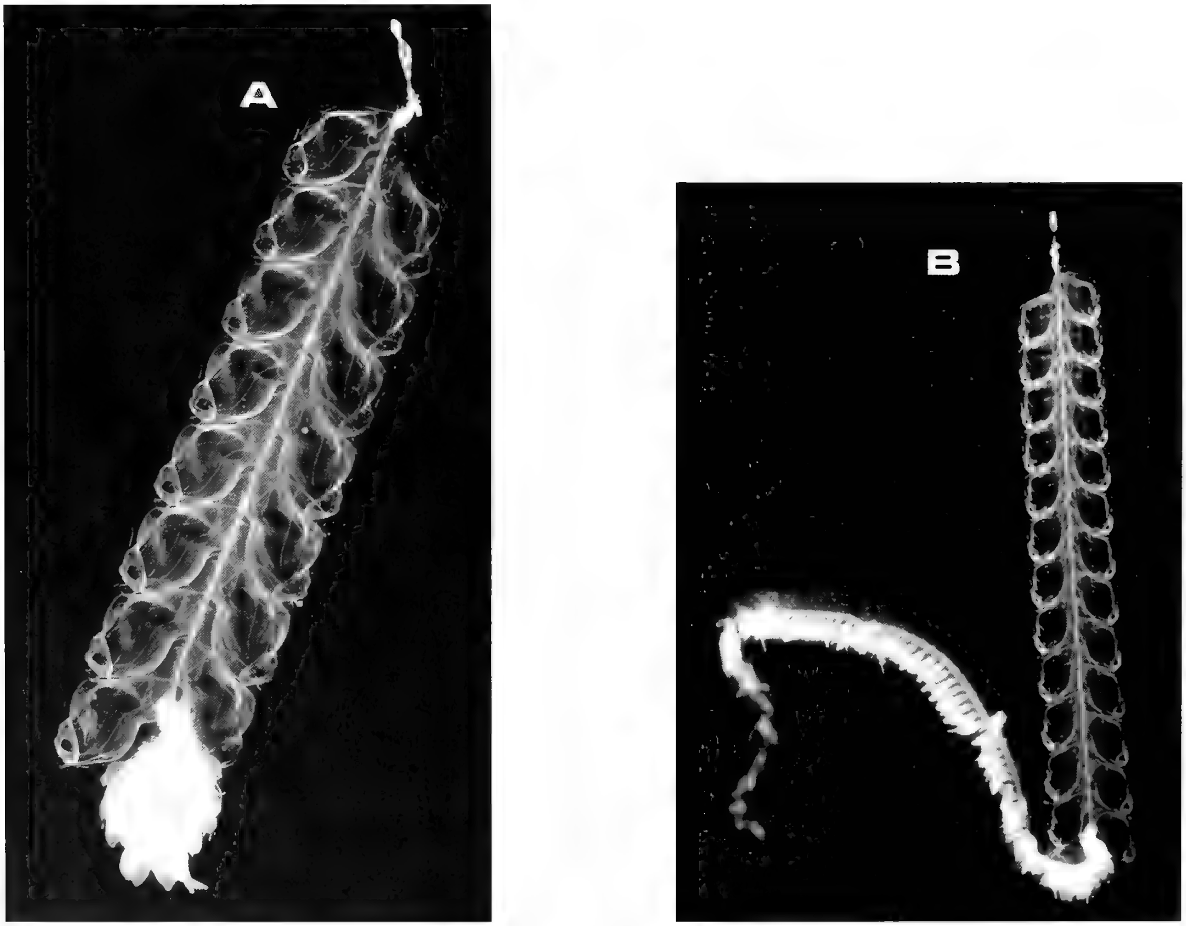

Fig. 1 *Bargmannia elongata*. A. Photograph (reproduced by kind permission of Larry Madin, WHOI) of live specimen collected during *Alvin* Dive 961. B. Photograph (reproduced by kind permission of Steve Haddock, UCSB) of live specimen collected during *JSL* I Dive 2673. Nectosomal length c. 9 cm.

Bargmannia elongata Totton, 1954

(Figures 1–5)

Bargmannia elongata Totton 1954 (Text-Figure 28 A–D only); Totton 1965 (Figure 45, A–D only); Kirkpatrick & Pugh, 1984: Figure 11.

HOLOTYPE. BMNH 1952.11.19.7, designated by Totton (1954): one nectophore from *Discovery* II St. 699; 14° 27.3'N, 30° 02.3'W; 14–v–1931; 0–370m. The specimen was figured by Totton (1954, text-Figure 28 C, D; 1965, Figure 45 C, D).

PARATYPES. As designated by Totton (1954): eighteen nectophores from the same sample as the holotype. BMNH 1952.11.19.8–25.

MATERIAL EXAMINED. The holotype and paratype material have been re-examined in order to establish to which of the presently recognised *Bargmannia* spp. the name *elongata* should be applied. Totton's (1954) other material also has been re-examined and, although all the material is in poor condition, it appears that only the nectophores from two other *Discovery* stations belong to this species. These are St. 681 (21°13'S, 29°55.25'W; 1–v–1931) where a TYFV net was fished over a depth range 1500–1000m; and St. 107 (43°03'S, 17°03'E; 4–xi–1926) where the net used was a N450 and the depth range was 850–950m. The nectophore from the former of these stations was figured by Totton (1954, text-Figure 28 A, B; 1965, Figure 45 A, B). The other nectophore, from *Discovery* St. 1769, also illustrated in the same figures (E, F) does not belong to *B. elongata*, but to *B. lata*.

Several nectophores of this species have been found in more recent *Discovery* collections, as is discussed below. However, the major part of the redescription will be based on two specimens collected by DSRV *Alvin* off San Diego, California, U.S.A. in 1979, during Dives 961 (32°14'N 117°22'W; 5–ix–1979; water depth 833m) and 966 (33°04'N 118°16'W; 8–ix–1979; water depth 747m). The *Alvin* Dive 961 specimen, preserved in Steedman's solution, has been deposited in The Natural History Museum London (BMNH 1998.2163). The exact depths of collection for both *Alvin* specimens were not recorded.

DIAGNOSIS. Nectophores with central thrust block broadly rounded or obliquely truncate apically. Pair of short ridges, directed toward mid-line, branch from apico-laterals where latter bend out sharply at a right angle. Outer branches of apico-laterals end, basally, on, or just apical to, enlarged processes lateral to ostium. In preserved specimens ostium opens dorso-basally and nectosac, with apparently dense musculature, has distinct dorso-ventral undulations. The ratio of the overall length of the nectophore to the length of the nectosac averaged 1.31. Delicate, foliaceous bracts; typically with patches of ectodermal cells on distal half of dorsal surface.

DESCRIPTION. A photograph of the living specimen collected during *Alvin* dive 961 is shown in Figure 1A. By the time it was taken, in a tank on board the mother ship, several nectophores had become detached and the siphosomal stem had contracted. A second living specimen, collected during *Johnson-Sea-Link* (*JSL*) I Dive 2673 (27°02.7'N, 85°01.5'W, depth 780m), is shown in Figure 1B.

PNEUMATOPHORE. The pneumatophore measured c. 2.2 mm in length and 1 mm in width, but was distorted and ruptured. No pigmentation was apparent. In the *Alvin* dive 961 specimen, the main gas cavity, the pneumatosaccus (height 1.8 mm), was separated from the small gas secreting region, the pneumadenia, by a narrow collar. Below the pneumatophore was a long stalk, up to 7.6 mm in length. Immediately above the nectosome, this stalk narrowed and was flattened to form a hinge-like structure, which could facilitate the use of the pneumatophore as a means of orientating the animal.

NECTOPHORE (Figures 2–3). The nectophores had a biserial, staggered arrangement down the nectosome (Figure 1). Forty two nectophores were found with the *Alvin* dive 961 specimen, though many were small or immature; and 26, mostly mature ones, were found with the *Alvin* dive 966 specimen. The mean dimensions, for the fully developed nectophores of each specimen, were:- length: 21.29 ± 0.93 mm and 16.49 ± 0.75 mm; width: 9.58 ± 0.56 mm and 7.40 ± 0.32 mm; and the ratios of total length of the nectophore to the length of the nectosac were 1.29 ± 0.02 and 1.34 ± 0.04, respectively. For net collected nectophores, damage and distortion by preservation, particularly to their basal halves, made it difficult to assess this ratio accurately.

The nectophores of the dive 966 specimen were noticeably smaller than those from dive 961 but, as will be seen in the description of the following species, the size range of the nectophores can vary greatly between individual specimens. In general, the thrust block was roundly, and often slightly asymmetrically, truncate (Figure 2A, *tb*; 2B), although for a few of the nectophores of the smaller specimen it was distinctly tapered. The latter was also apparent on several net collected nectophores where the apex of the thrust block was drawn out to form a small digitiform process that could be folded over ventrally.

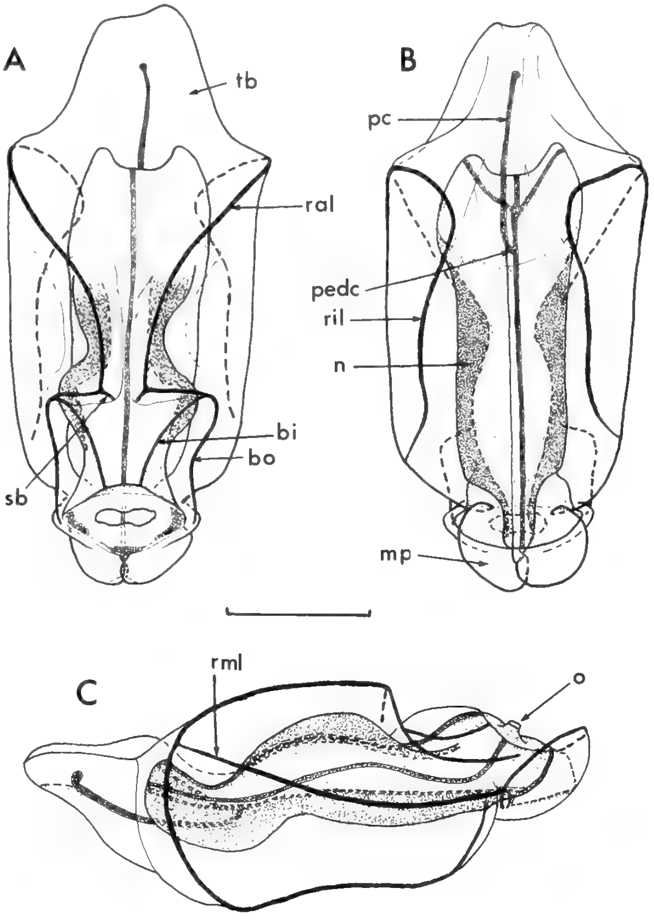

Fig. 2 *Bargmannia elongata*. A. Upper, B. lower, and C. lateral views of mature nectophore. Scale bar = 5 mm. *bi*, *bo*: inner and outer branches of apico-lateral ridge; *mp*: mouth-plate; *n*: nectosac; *o*: ostium; *pc*: pallial canal; *pedc*: pedicular canal; *ral*, *ril*, *rml*: apico-, infra- and meso-lateral ridges; *sb*: side branch; *tb*: thrust block.

The basic *Bargmannia* ridge pattern is supplemented by a pair of short ridges (Figures 2A, *sb*; 3 A) that branch from the apico-laterals (Figure 2A, *ral*) at the point where the latter bend sharply, through 90°, away from the mid-line. This sharp bend typically can be seen in less well preserved specimens and is characteristic for this species. The side branches are directed, for a short distance, toward the deep median furrow. In many specimens, particularly net collected material, they were difficult to discern but often can be seen after staining. Basally, the inner branch of each apico-lateral ridge curves inwards and then down to reach the ostium (Figure 2 A, *bi*), except for immature nectophores (Figure 3A) where it ends slightly above that level. Each outer branch (Figures 2A, *bo*; 3C) typically terminates on or just above one of the small, but prominent, lateral processes on either side of the ostium.

Basal extensions of the meso-lateral ridges form the baso-lateral margins of the bilobed mouth-plate (Figure 2B, *mp*; 2C), each lobe being thickened ventrally, particularly toward the mid-line. Basally, the two lobes typically overlap and unite, in the mid-line, at about half the height of the mouth-plate (Figure 3C). The lower nerve tract (see Mackie, 1964), which can be traced down the nectophore, beneath its ventral surface in the mid-line, recurves at this point and continues obliquely to the baso-ventral margin of the ostium (Figure 3C). In immature nectophores the mouth-plate is not thickened and has a U-shaped emargination in the mid-line (Figure 3A, B) which is deepest in the youngest nectophores.

Above the mouth-plate, the basal extensions of the meso-lateral ridges curve round toward the mid-line, on the ventral surface of the nectophore (Figure 2 B), before looping back outwards as the meso-laterals proper (Figure 2C, *rml*). The infra-laterals are weakly defined in the region where they divide from the meso-laterals, and in younger nectophores clearly terminate before reaching the latter (Figure 3 B). The meso-laterals curve up, obliquely, across the lateral surface to reach the junction with the other main ridges at a level slightly below the apex of the nectosac (Figure 2C). The connection with the other ridges is weak, and often the meso-laterals appear to end slightly below the junction, as was found for younger nectophores (Figure 3 A).

The infra-laterals (Figure 2B, *ril*) demarcate the ventral margins of the thickened walls of the more basal part of the ventro-lateral wings. In lateral view these wings are slightly emarginate in outline. Apical to where the infra-laterals curve up to join the other ridges, the wings remain well developed and are thickened with mesogloea.

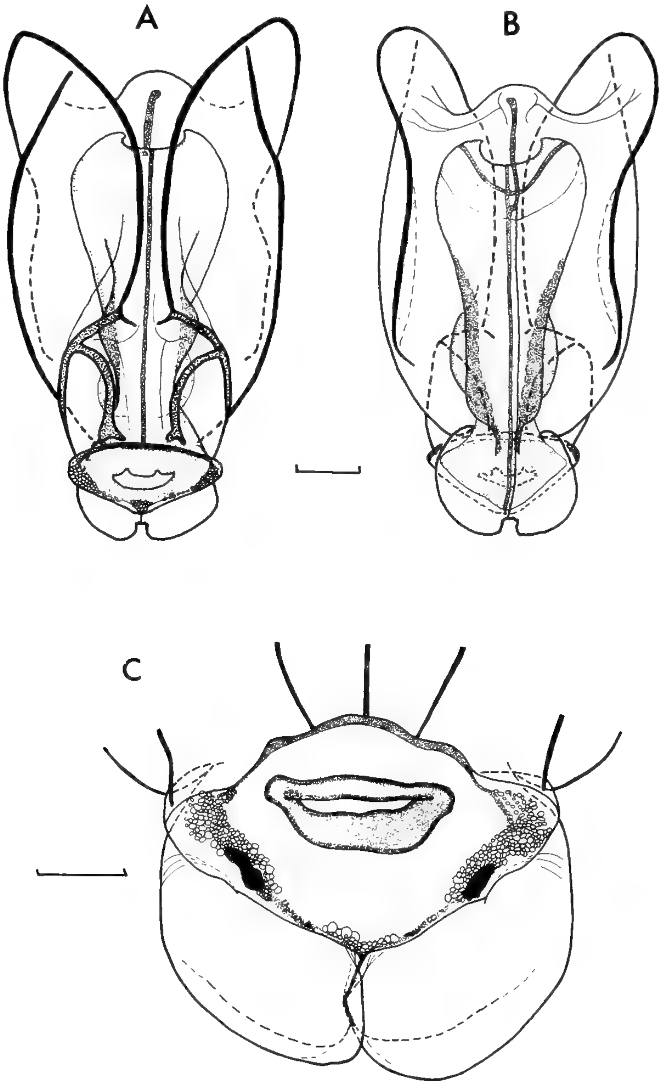

Fig. 3. *Bargmannia elongata*. A. Upper and B. lower views of young nectophore; C. detail of ostial region of mature nectophore. Scale bar = 1 mm.

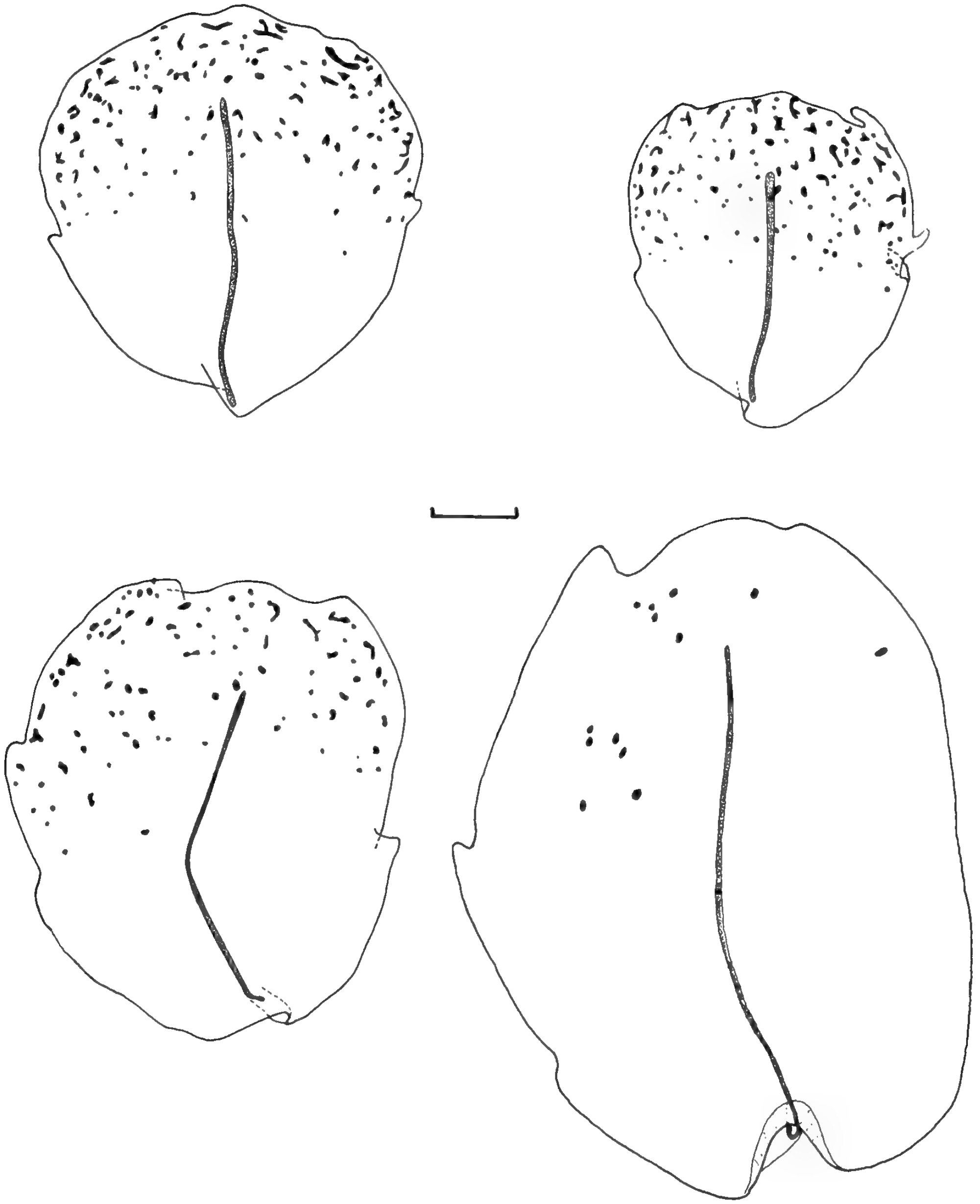

Fig. 4 Bracts of *Bargmannia elongata*. Scale bar = 1 mm.

This thickening diminishes in the region of the thrust block, but there is still a shallow median gutter that enfolds the nectosomal stem in the region of attachment of the nectophore (Figure 2 B).

In the preserved nectophores, the nectosac is a dorso-ventrally undulating tube (Figure 2B, *n*; 2C), with prominent dorso-lateral extensions in the mid region, and ventro-lateral ones both apically and basally. However, this arrangement is not apparent in the nectophores of the living animal (Figure 1). The nectosac is broadest at about two-thirds its length, narrowing slightly towards its apex. It has a distinct apical emargination; U-shaped in the younger nectophores (Figure 3 A). Typically, the ventral, adaxial region towards the apex of the nectosac is distinctly undercut and, from a level just basal to the point of insertion of the pedicular canal, its wall is devoid of musculature (Figure 2 B). The musculature of the remainder of the nectosac appears well developed and gives it a distinctly opaque appearance. The ostium, in the preserved material, opens onto the dorso-basal (abaxial) surface (Figure 2C, *o*) and is roughly rhomboidal in shape. However, this probably is distortion due to preservation (see Figure 1). In the *Alvin* specimens it has a large velum, with a relatively small central opening, but in net collected material often the velum is destroyed. The lateral walls of the ostium extend out to form lateral processes (Figure 3C) that, typically, are covered by patches of ectodermal cells of varied size. Further such patches are present on the ventral margin of the velum, but not on the dorsal margin, except for the youngest nectophores. Some, if not all, of these cells probably produce bioluminescent material since this has been found to be the case in another *Bargmannia* spp. (Dr S. Haddock, personal communication).

The long pallial canal (Figure 2B, *pc*) extends up into the median thrust block, where it ends with a short dorsal inflection into the

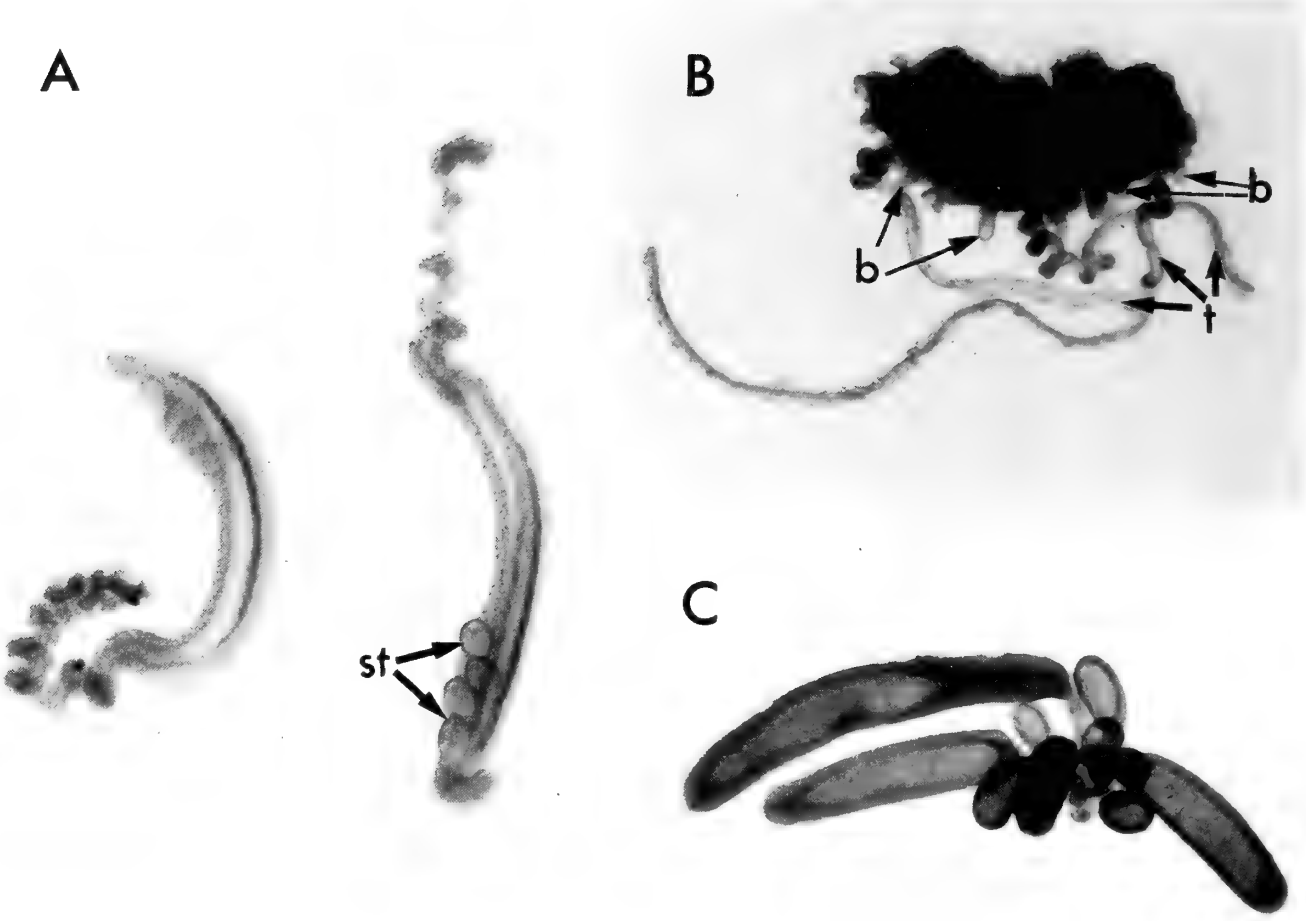

Fig. 5 *Bargmannia elongata.* A. Young tentilla with stenoteles (*st*) at proximal end of cnidoband (magn. 50×); B. Part of siphosome showing three siphosomal tentacles (*t*) and several buds (*b*) (magn. 16×); C. Male gonophores (magn. 30×).

mesogloea. At its base the lower nerve tract can be seen to leave its proximity and to continue down beneath the ventral surface of the nectophore to reach the ostium. The short pedicular canal (Figure 2B, *pedc*) extends through the mesogloea, from the base of the pallial canal, to the nectosac. There it gives rise to only the dorsal and ventral radial canals. The lateral canals arise separately, but in close proximity to each other, from the dorsal canal, and initially are directed toward the apico-lateral margins of the nectosac. They then continue down the lateral margins of the nectosac and, although their courses show undulations (Figures 1C, 2C), they are merely following the dorso-ventral undulations in the nectosac itself; the latter being a preservation artefact.

The youngest nectophores (Figure 3A, B) typically show the absence of a median thrust block, and the apico-lateral margins are demarcated by the apico- and infra-lateral ridges. The basal portions of the apico-lateral ridges are particularly well marked, and the inner branches are distinctly broadened, often appearing almost bifurcate at their basal ends, which lie just above the ostium (Figure 3A). There are two short tracts of cells extending out from the lateral processes of the ostium just ventral to the outer branch of the apico-lateral ridges. These could not be discerned in the mature nectophores.

BRACT (Figure 4). The bracts are extremely delicate, foliaceous structures, the largest of which measures 9 mm in length. The dorsal surface is slightly convex, the ventral one slightly concave. For many the proximal region is bent up dorsally, or one side is folded over the other resulting in a distinct asymmetry. The bracteal canal extends, approximately in the mid-line and in close proximity to the ventral wall, to about four-fifths the length of the bract. The distal end of the bract is slightly truncate and bears two lateral processes, which vary in shape from merely rounded corners to distinct teeth. The region between them usually is roundly pointed. Additional processes may be present on the lateral margins of the bract. Again these can form distinct teeth, but quite often are indiscernible. The maximum number of lateral processes found was two on one side, and one on the other. The distal half of the dorsal side of the bract is dotted with distinctive patches of small round ectodermal cells. These patches are densely packed on the smallest bracts; but more spread out on the larger ones, where some patches have been lost by abrasion. These cells probably are sites of bioluminescence.

GASTROZOOID AND TENTACLE. The larger gastrozooids in the *Alvin* material measured up to 10 mm in length. They are brown in colour, in their preserved state, and are comprised of a short, narrow basigaster, to the base of which the tentacle is attached; a large, expanded stomach, the inside of which is covered with thickened patches of endodermal cells; and a long proboscis, with longitudinal endodermal hepatic stripes. Several younger, smaller gastrozooids also are present, which are largely colourless and transparent, with only small patches of endodermal cells in the stomach region.

No mature tentilla remained with the specimens. The immature tentilla (Figure 5A) conformed to the basic *Bargmannia* design, with the cnidoband ranging from being straight to curved or slightly twisted. There was a maximum of only six large nematocysts, probably stenoteles, that measure c. 120 by 80μm, irregularly arranged on the proximal region of the cnidoband. About half the circumference of the cnidoband is covered with rows of two other types of nematocysts; one is ovoid, measuring c. 16 × 11 μm; and the other is spherical, measuring c. 8.5μm in diameter. Similar nematocysts are also present on the terminal filament. It has not been confirmed that these nematocysts are the acrophores and desmonemes that are typically found on the terminal filaments of many physonect species. It is, however, unusual to find such small nematocysts on the cnidoband. The terminal filament obviously can extend to a considerable extent, but in the preserved specimens it is generally tightly coiled.

SIPHOSOMAL TENTACLES AND BUDS (Figure 5B). Midway between each gastrozooid a peculiar tentacular structure is attached directly to the siphosomal stem. In the preserved specimens they are usually tightly coiled, but some relaxed ones can reach lengths of 8 mm. Along one side there is a biserial arrangement of spherical nematocysts, c. 13 μm in diameter, similar to those on the cnidoband of the tentacle. The gastrovascular canal is lined by an irregular honeycomb of large endodermal cells.

In addition to the siphosomal tentacle, small bud-like structures were noted protruding from the stem. Because the siphosome in both specimens was tightly coiled it was not possible to assess the precise disposition of these buds. However, their arrangement may be similar to that which will be described for the following species.

GONOPHORE (Figure 5C). Both the *Alvin* specimens are male and bear numerous gonodendra at various stages of development. The gonophores measure up to 4 mm in length, including the pedicel. They appear to bud one from another to form a small gonodendron. If the gonophores becomes detached, their thin-walled pedicels remain, giving the false impression of the presence of gonopalpons. Again, since the stem is highly contracted, it is difficult to ascertain their exact disposition.

REMARKS CONCERNING THE IDENTIFICATION OF *BARGMANNIA ELONGATA*. Complete and well-preserved specimens of *B. elongata* easily can be distinguished from the other *Bargmannia* spp., particularly as the form of the bracts is very distinctive. For the nectophores, the arrangement of the apico-lateral ridges, with their distinct right-angled bend and the presence of the short extra ridges branching from them, also are characteristic features. However, in the case of net collected material, which is usually damaged or distorted, the nectophores of this species may be difficult to distinguish from those of the following species, as is discussed further after its description.

Bargmannia amoena sp. nov.

HOLOTYPE. BMNH 1998.2164, preserved in Steedman's solution, collected during *JSL* II Dive 1458 off Dry Tortugas, Florida; 24°00.6'N 82°17.4'W; 3.ix.1987; 841m.

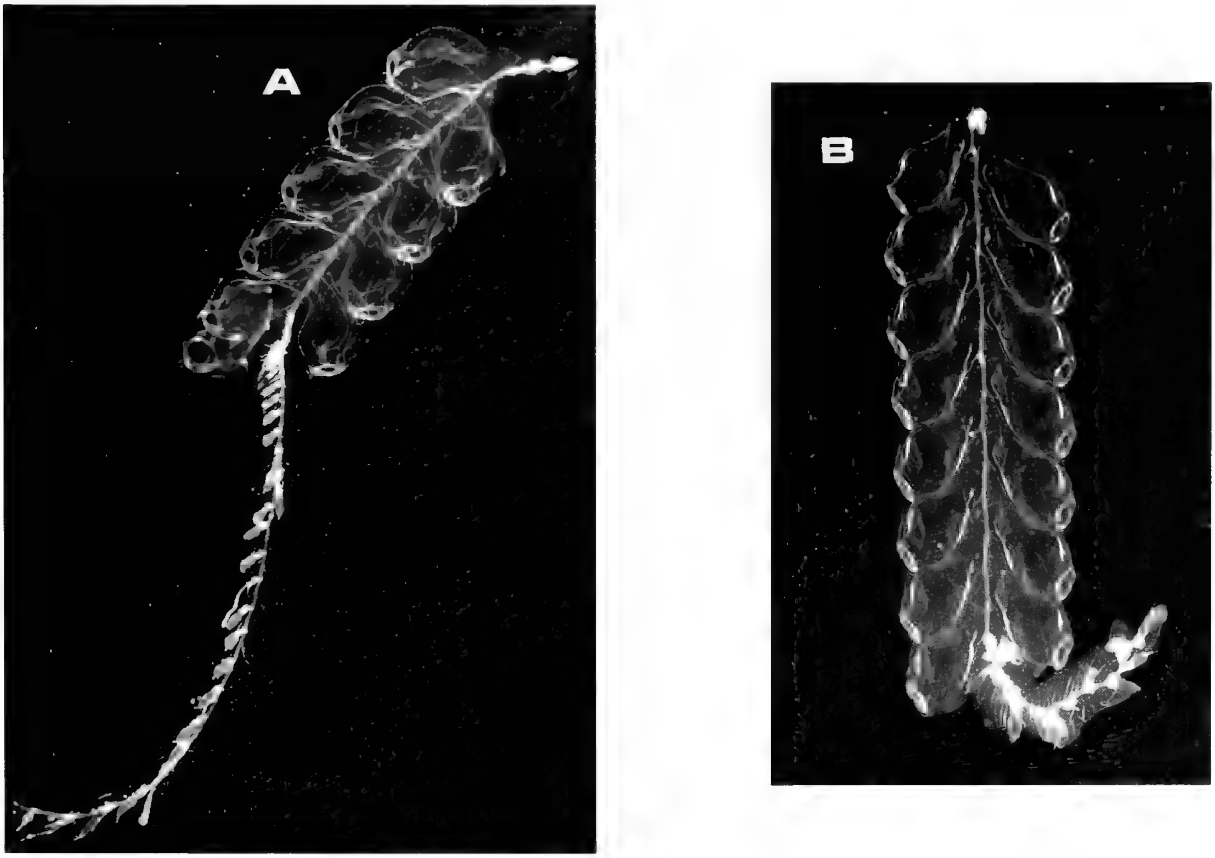

Fig. 6 *Bargmannia amoena* sp. nov.. Photographs (taken by Ron Gilmer) of live specimen collected during JSL II Dives 968 (A) and 1687 (B). Nectosomal lengths: A. c. 5 cm, B. c. 7 cm.

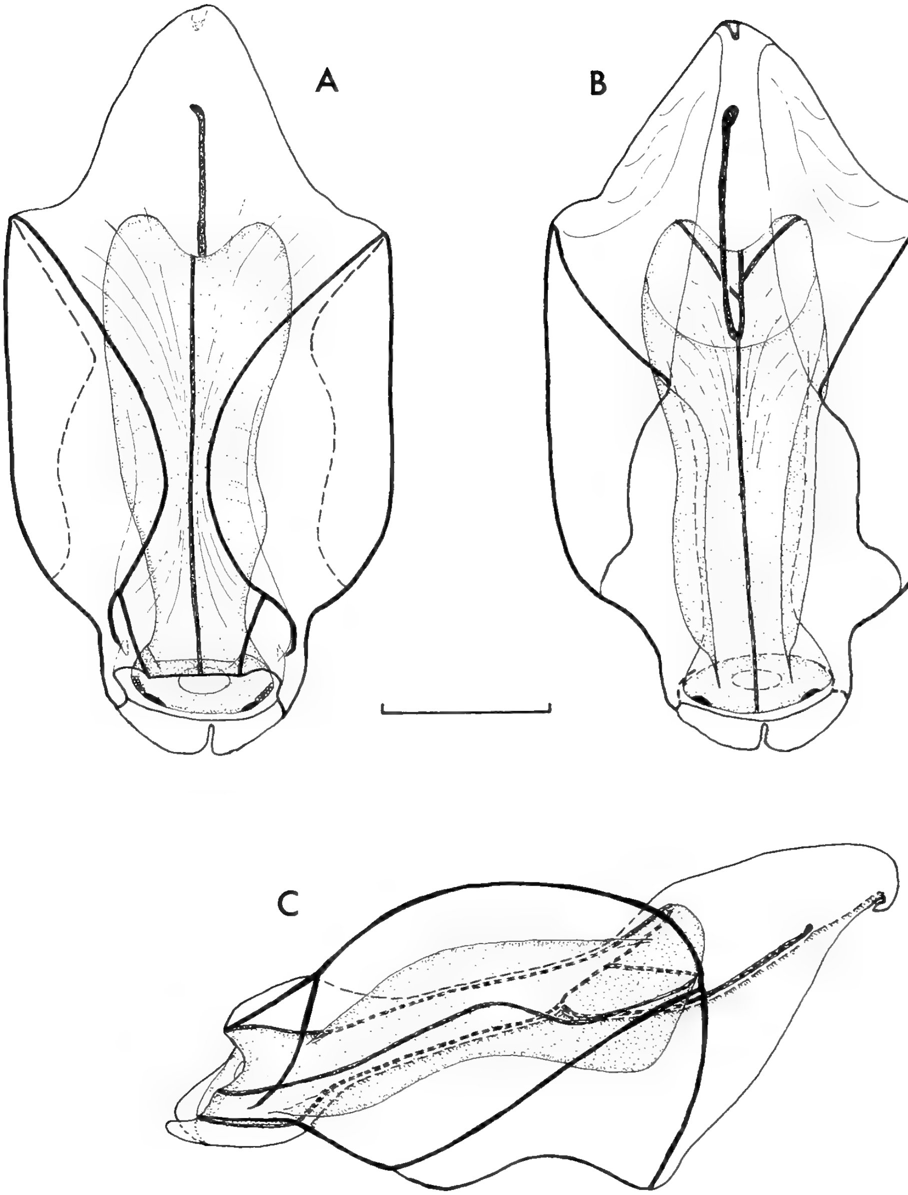

Fig. 7 *Bargmannia amoena* sp. nov. A. Upper, B. lower, and C. lateral views of mature nectophore from type specimen collected during JSL II Dive 1458. Scale bar = 5 mm.

PARATYPE. BMNH 1998.2165, preserved in Steedman's solution, collected during *JSL* I Dive 2636 off The Bahamas; 25°53.2'N 77°48.3'W; 5–xi–1989; 890m.

MATERIAL EXAMINED. 67 specimens have been collected during 40 dives by the submersibles *JSL* I and II. Of these, 52 have been re-examined for this description. Some of the material originally ascribed to *B. elongata* by Totton (1954) probably belongs to this species. In addition, some poorly preserved nectophores have been found in recent *Discovery* collections.

DIAGNOSIS. Apico-lateral ridges of nectophores smoothly curved, without pronounced bends; their outer branches terminating well above the ostium, before reaching the relatively small lateral ostial processes. No additional ridges. In smaller specimens central thrust block pointed with small digitiform process apically; in larger ones, latter folded over ventrally so that, in upper view, thrust block appears roundly truncate. In preserved specimens, ostium opens basally. Nectosac more translucent than that of *B. elongata*. Ratio of overall length of nectophore to that of nectosac averages 1.42, varying slightly according to the size of specimen. Bracts of two types; both delicate and foliaceous, with two pairs of lateral teeth; without patches of large ectodermal cells.

DESCRIPTION. Photographs of living specimens collected during *JSL* II dives 968 and 1687 are shown in Figure 6. The specimens from the *JSL* collections fall within three size classes, based on the length of the mature nectophores, but also reflected by the degree of sexual maturity. All the smaller specimens were colourless, while the largest ones had bright orange-red basigasters; the basal part of the gastrozooid.

PNEUMATOPHORE. The pneumatophore measured approximately 3 mm in height and 1.5 mm in width, but was highly distorted and

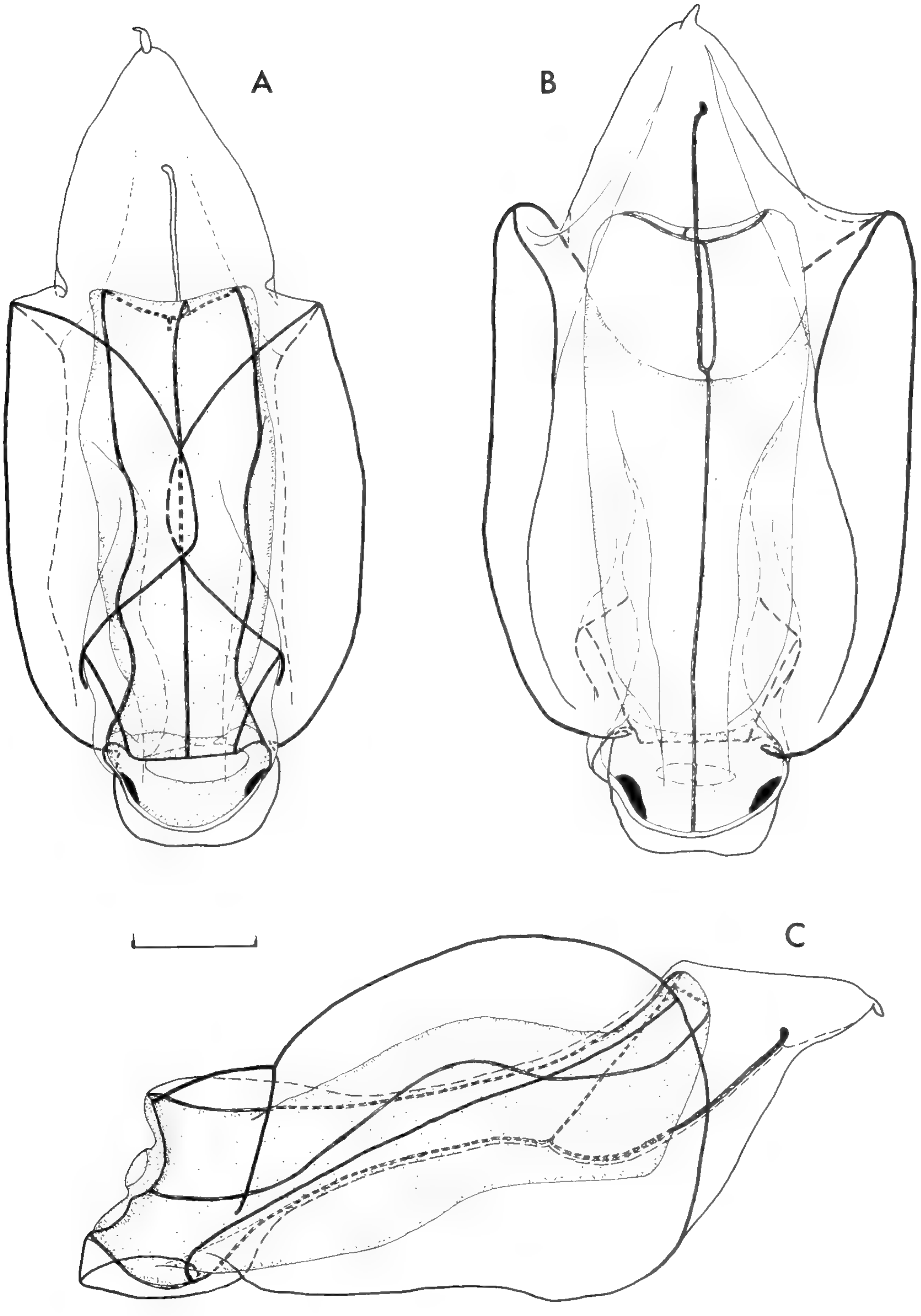

Fig. 8 *Bargmannia amoena* sp. nov. A. Upper, B. lower, and C. lateral views of mature nectophore from small specimen collected during JSL II Dive 976. Scale bar = 1 mm.

ruptured by the expansion of the gas within it. No pigmentation is apparent. The pneumatophore is inserted onto the apical end of a long stalk that, depending on the degree of contraction, can be 5–6 mm in length. As in *B. elongata*, this stalk is flattened at its base, where it joins the nectosome, to form a hinge-like structure.

NECTOPHORE (Figures 7–9). The nectophores had a biserial, staggered arrangement down the nectosome (Figure 6). The number of nectophores found with each specimen varied from 5 to 32. Depending on the mean length of their nectophores, these specimens can be divided into three size categories. Seven specimens, all collected during the same cruise in 1984, bore c. 10 relatively small nectophores whose lengths were less than 8 mm. The mean length, for the mature nectophores, was 7.41 ± 0.43 mm; the mean width 3.10 ± 0.22 mm; and the ratio of the overall length to that of the nectosac averaged 1.41 ± 0.06. None of these specimens was sexually mature. The bulk of the specimens was included in second size category, where the length of the mature nectophores ranged from 9 to 19 mm. These specimens bore distinct, but immature, gonophores. Each specimen averaged about 20 nectophores, whose mean length was 13.70 ±

1.86 mm; mean width 6.71 ± 0.88 mm; and the ratio of the overall length to that of the nectosac averaged 1.42 ± 0.06. Finally six specimens had even larger nectophores and were sexually mature. They averaged 13.5 nectophores, whose mean length was 20.94 ± 2.36 mm; mean width 10.58 ± 2.18 mm; and the ratio of the overall length to that of the nectosac averaged 1.44 ± 0.05.

As was the case for *B. elongata*, the apex of the thrust block of the smaller specimens was drawn out to form a small digitiform process (Figure 8A). In the larger specimens, this process usually became folded over onto the ventral side of the nectophore (Figure 7C), so that, in upper view, the thrust block appeared roundly truncate (Figure 7A).

The apico-lateral ridges are, in their preserved state, smoothly curved and have no pronounced bend or side branches (Figures 7 & 8), as was found for *B. elongata*. After these ridges divide, the inner branches extend obliquely down to reach the ostium; while the outer branches curve down the sides of the nectophore, but peter out well above ostial level. The latter is particularly marked on the smaller nectophores (Figure 8C).

Basal extensions of the meso-lateral ridges form the baso-lateral margins of the mouth-plate (Figures 7 & 8). The structure of the mouth-plate varies with the size of the mature nectophore. In the smallest specimens, the mouth-plate is only slightly truncate basally (Figure 8A). In the middle size range of specimens, the mouth-plate becomes more and more emarginate and, in the largest ones, it has a narrow U-shaped median indentation stretching up to the ostium (Figure 7A). The mouth-plates of the immature nectophores of all sizes of specimens show the same features as the corresponding mature ones (Figure 9).

Above the mouth-plate, in the small and medium sized specimens, the basal extensions of the meso-lateral ridges curve slightly in toward the mid-line (Figure 8B), before curving out again to form the meso-laterals proper. In addition the infra-laterals do not unite with the latter. On the largest specimens, there is no inward curve of the meso-laterals (Figures 7B, 9B), but the infra-laterals have a very weak connection with them (Figure 7B); However, the apical junction of the meso-laterals with the other ridges is always clearly defined. The arrangement of the infra-lateral ridges, in the small (Figure 8C) and medium sized specimens, is very similar to that described for *B. elongata*. However, in the largest specimens, the ventro-lateral wings are more extensive in the region where the infra-laterals curve up to join the other ridges. The ventral margins of these wings are distinctly emarginate.

The nectosac, in its preserved state, appears as a dorso-ventrally undulating tube; but this is probably a preservation artefact. The dorso-lateral extensions, in the mid region of the nectosac, are slightly more extensive than in *B. elongata*. At its apex the nectosac has a shallow U-shaped indentation, and the adaxial wall is distinctly undercut and devoid of musculature. On the remainder of the nectosac the musculature appears much less dense that of *B. elongata*, and the nectosac is considerably more translucent. The arrangement of the pallial and pedicular canals, and the radial canals on the nectosac is similar to that of *B. elongata*.

In the preserved specimens, the ostium opens almost basally and has a large velum. Its lateral walls are only slightly extended to form small lateral processes. The pattern of the patches of ectodermal cells is similar to that of *B. elongata*, but the cells are more uniform in size, and the patches more diffuse laterally. In addition, there are two ventro-lateral patches of deeply granulated cells that are relatively large and almost spherical.

The youngest nectophores (Figure 9) typically show the absence of a median thrust block. The inner branches of the apico-lateral ridges reach the ostium. The degree of emargination of the apex of the nectosac is variable, according to the developmental stage. It ranges from a narrow, median U-shaped indentation to a marked emargination across most of the width of the nectosac. As noted above the shape of the mouth-plate varies according to the size of the specimen. On either side of the ostium there is a tract of small ectodermal cells extending up toward the end of the outer branch of the apico-lateral ridges. These tracts are longer than those seen on the young nectophores of *B. elongata* and, again, are difficult to discern on the adult nectophores.

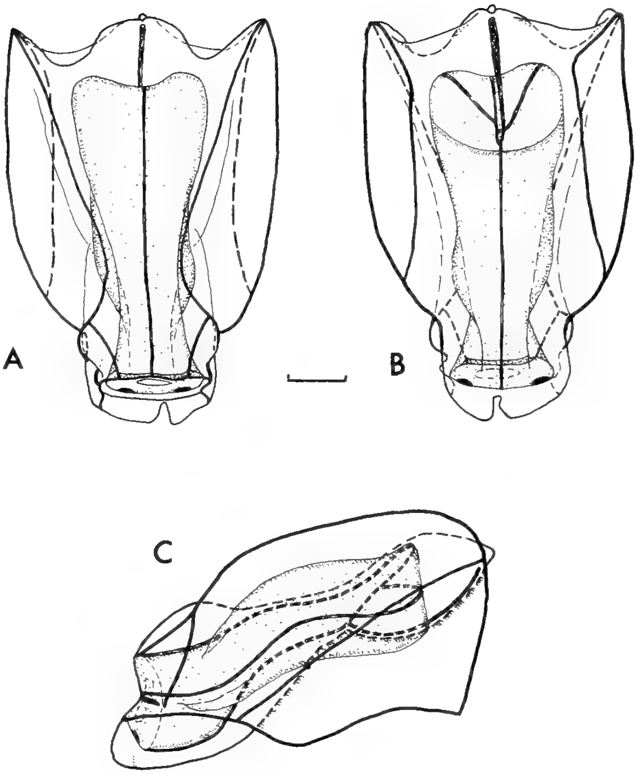

Fig. 9 *Bargmannia amoena* sp. nov. A. Upper, B. lower, and C. lateral views of young nectophore from specimen collected during JSL II Dive 1449. Scale bar = 2 mm.

BRACT (Figure 10). There are three pairs of bracts per cormidium. Each is thin and leaf-like, with a slight thickening in the central region of the proximal half. The dorsal surface is slightly convex, and the ventral one slightly concave. In general their size is in proportion with that of the nectophores, with those of the largest specimens measuring up to 18 mm in length. No patches of ectodermal cells were observed. However, in each cormidium, each successive pair of bracts tends to be slightly larger than the pair proximal to it. The proximal part of each bract is slightly asymmetrical to allow for insertion onto the stem. The bracteal canal extends to about two-thirds to four-fifths the length of the bract. It remains in close contact with the ventral wall of the bract at all times.

There is much variation in the shape and form of the bracts, but two basic types can be distinguished; both having two pairs of lateral teeth. In one type, which make up the first two pairs of bracts in each cormidium, the bracts are relatively symmetrical. The more distal pair of lateral teeth are very variable in shape, ranging from being virtually absent to being quite marked (Figure 10A, B, D). In the second type (Figure 10C, E), which are the distal pair, the bracts are asymmetrical, and the bracteal canal can have a distinct proximal curve. The distal pair of lateral teeth are well developed and closer

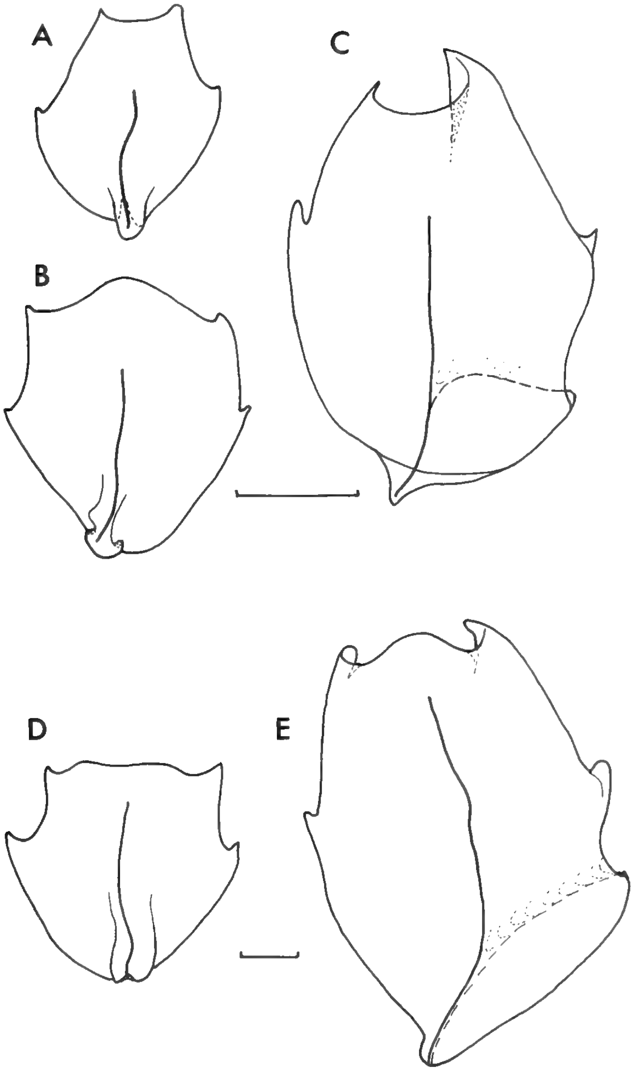

Fig. 10 Bracts of *Bargmannia amoena* sp. nov. Scale bars: A, B, C = 1 mm, D, E = 2 mm.

together than on the first type, so that the distal end of the bract is relatively narrow. One of the proximal pair of teeth is usually more developed than the other, and on that side the lateral wall of the proximal part of the bract often extends out as a rounded notch.

GASTROZOOID AND TENTACLE (Figure 11A, C). The largest gastrozooids measure up to 10 mm in length. In the preserved state they are suffused with a brown coloration with, in the largest specimens, the basigaster having bright orange-red pigmentation. The latter (Figure 11C, *bg*), typically, is cup-shaped, enclosing the base of the stomach region, and is covered in large rounded ectodermal cells. The stomach region (Figure 11C, *s*) appears relatively thin and the endodermal hepatic villi can be seen within. The proboscis region can be extended to some distance.

The tentacle can be several centimetres in length. It is a simple, narrow, unsegmented tube, bearing a haphazard and irregular arrangement of the two sorts of small nematocysts that are also found on the tentilla. In the present specimens, only a few tentilla, up to 10, remain attached close to its base. In their preserved state, the tentilla (Figure 11A) typically are highly contracted and are comprised of a short pedicel; an irregularly twisted cnidoband; and, for the most part, a regularly coiled terminal filament. The cnidoband is a simple tube that, in life, is generally straight or slightly curved, and can extend to a length greater than 0.5 cm. One side of the cnidoband appears to consist of a primitive elastic strand. It is not tightly folded, as is the case in some other physonect species, but a few pleats are present. The other side of the tentillum is comprised of numerous rows of small nematocysts of two types, as was the case in *B. elongata*. These are ovoid, measuring 20 × 14 μm and 12 × 11 μm, and occur in roughly equal proportions and possibly in alternating rows, although this could not be determined with certainty. Similar nematocysts are found along the length of the terminal filament. Again, it has not been determined whether these nematocysts are the acrophores and desmonenes found in other physonect siphonophores. At the proximal end of the cnidoband there is a paired series of up to 26 stenoteles that measure 135 × 105 μm.

SIPHOSOMAL TENTACLES AND BUDS (Figure 11B, C). As several of the siphosomal stems of the specimens examined remained relaxed, it was possible to study the disposition of the siphosomal tentacles and buds in detail. The primary siphosomal tentacle (Figure 11B, *t*) is inserted midway between successive gastrozooids and can be tightly coiled or extend to several millimetres in length. As in *B. elongata*, its surface is covered in large ectodermal cells and there is a paired series of nematocysts along one side.

On each cormidium there are, at least, four solid bud-like structures, whose arrangement is sexually dimorphic. In the female specimens (Figure 11B), the first bud (*b1*) lies a short distance distal to the gastrozooid (*gz1*), while the second (*b2*) is inserted about one quarter the length of the cormidium. The gonodendron is then inserted between the latter and the central siphosomal tentacle (*t*). The third bud (*b3*) lies a short distance distal to this tentacle, and the last (*b4*) is inserted immediately proximal to the next gastrozooid (*gz2*). In the male specimens (Figure 11C), the gonodendron is situated immedietly distal to the gastrozooid. The first bud (*b1*) then lies distal to the gonodendron at about one quarter the length of the cormidium; that is approximately in the same position as the second bud on the female specimens. The second bud lies immediately proximal to the central siphosomal tentacle; and the third midway between that tentacle and the next gastrozooid. The fourth, as in the female specimens, is inserted immediately proximal to the next gastrozooid. These arrangements pertain in the great majority of the specimens examined, but in the largest ones another tentacle, and possibly another bud, are found in close proximity to the fourth bud. Usually, this tentacle is much smaller than the central tentacle, but otherwise appears to be identical; including the double row of nematocysts.

GONOPHORE. (Figure 11B, C). As noted above, the degree of sexual maturity of the specimens appears to be directly related to their size, as assessed by the length of the nectophores. Thus in the smallest specimens, at most, only gonophore buds can be seen. The major group of medium sized specimens have better developed gonophores, while the largest are obviously sexually mature. All seven of the largest specimens are male.

There is only a single gonodendron per cormidium. In male specimens the gonodendron lies immediately distal to a gastrozooid and proximal to the first siphosomal bud. The mature male gonophores (Figure 11C, *mg*) measure up to 5.5 mm in length and 1.1 mm in diameter The female gonophores (Figure 11B, *fg*) are attached to the stem by a short stalk that is inserted approximately midway between the second siphosomal bud and the central siphosomal tentacle. Between one and six gonophores, in various stages of development, are attached to it by short pedicels. Each

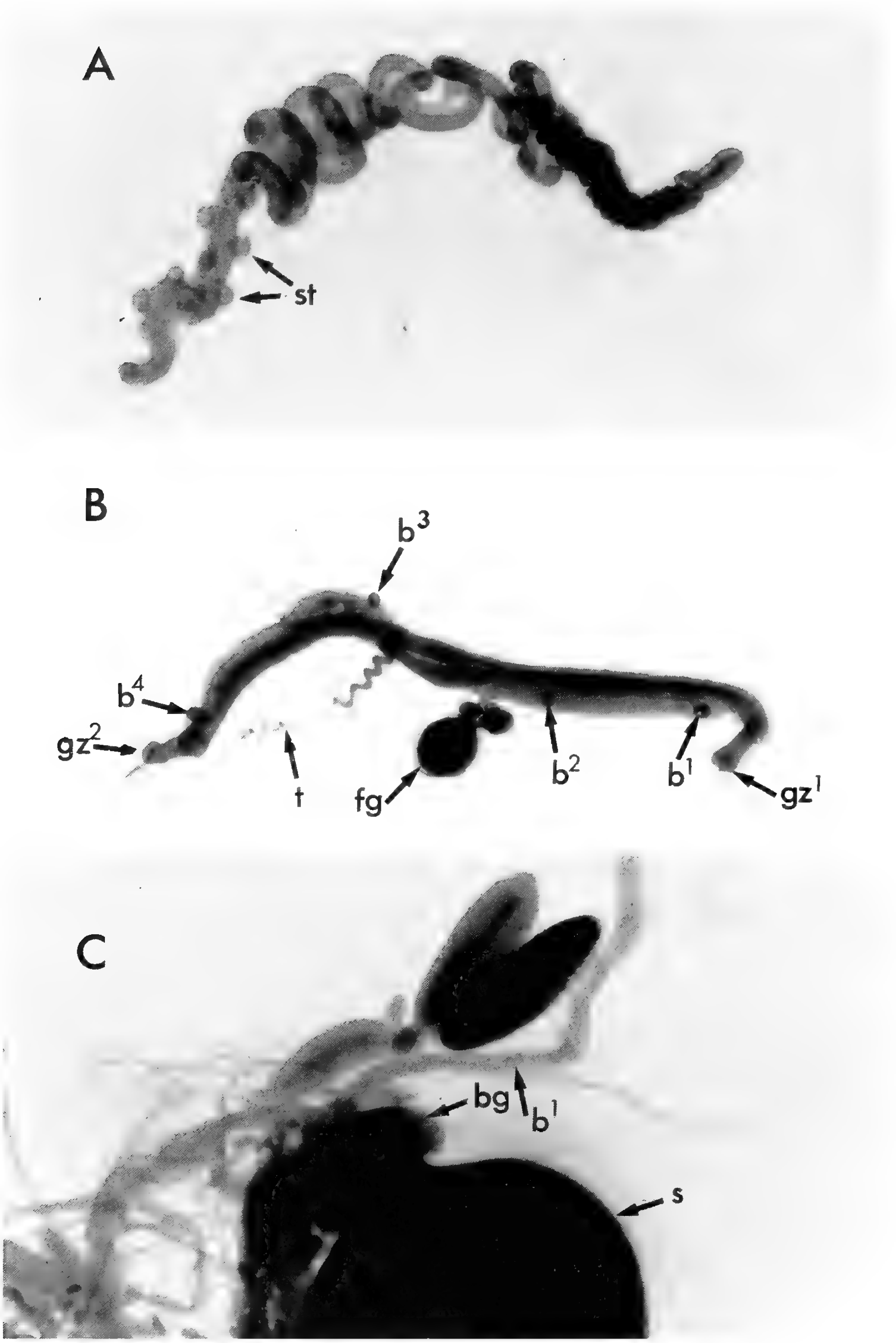

Fig. 11 *Bargmannia amoena* sp. nov. A. Mature tentillum, with stenoteles (*st*) at base of cnidoband (magn. 25×); B. Cormidium of siphosome, with gastrozooids detached (gz^1 and gz^2 mark their attachment points) showing the siphosomal tentacle (*t*), four buds (b^{1-4}) and female gonophores (*fg*) (magn. 25×); C. Male gonophores (*mg*) attached just distal to gastrozooid, with its basigaster (*bg*) and stomach (*s*), and proximal to the first bud (b^1) (magn. 12.5×).

gonophore contains two eggs. This is a highly unusual situation as, according to Carré and Carré (1995) all other physonect siphonophores have only one egg in each gonophore. However, Totton (1965) states that the gonophores of *Pyrostephos vanhoeffeni* contain from three to five eggs.

DISTRIBUTION. Much of Totton's (1954, 1965) *Bargmannia* material, from early *Discovery* collections, is so poorly preserved that it is difficult to be certain to which species it belongs. However, as noted earlier, the nectophores from *Discovery* Sts. 699 and 681, from the South and North Atlantic Ocean respectively, belong to *B. elongata*; as does that from *Discovery* St. 107 from south of South Africa. Several other of his nectophores probably belong to *B. amoena*, but this has not been established with certainty.

The great majority of the 8500+ nectophores of *Bargmannia* spp. that have been identified from over 300 recent *Discovery* samples, mainly from the North east Atlantic Ocean, belong to either *B. elongata* or *B. amoena*. However, these identifications were made before it was realised that two similar species were present. A re-examination of some of the material, however, typically showed that the material was too poorly preserved for specific identification. However, it was clear that *B. amoena*, not *B. elongata*, was the predominant species of the genus at c. 44°N, 13°W, where an extensive series of collections was made (Pugh, 1984). Collectively, both species have a widespread distribution in the North-east Atlantic Ocean; from the equator to 60°N, with possibly *B. elongata* being more common at lower latitudes and *B. amoena* at higher ones. Nectophores have been collected at all depths from the surface to 4520 m, but the vast majority were found in samples from between 200 and 600 m.

Most of the 67 specimens of *B. amoena* collected by the submersibles *JSL* I and II came from a relatively small area in the region of The Bahamas, from 25°03' to 26°36'N and 77°23' to 78°44'W. Five others were collected near the Dry Tortugas, between Florida and Cuba, at c. 24°30'N, 83°45'W. All were collected over a wide depth range, from 435 to 910 m, with a mean depth of 625 ± 130 m. This mean depth is slightly deeper than the depth range for both *B. elongata* and *B. amoena* found in *Discovery* net collections. However, both figures probably are biased because, in the case of the submersible, most observations and collections were made within the 600–900 m depth range, while at 44°N, 13°W for instance, most of the net sampling was concentrated in the top 600 m of the water column.

REMARKS CONCERNING THE IDENTIFICATION OF *BARGMANNIA AMOENA*. Complete and well-preserved specimens of *B. amoena* easily can be distinguished from the other *Bargmannia* spp. as they have very distinctive bracts. However, if only poorly preserved nectophores are present, then there may be some difficulty in separating this species from *B. elongata*. They cannot be confused with *B. gigas*, because of the relatively enormous size of the latter's nectophores; and should not be confused with *B. lata*. The much narrower nectosac of the latter species, together with the greater depth of the furrow between its deep lateral wings, should easily distinguish it.

As noted above, the best feature distinguishing *B. elongata* and *B. amoena* is the arrangement of the apico-lateral ridges. In *B. elongata* these have a pair of side branches, running down toward the mid-line, while in *B. amoena* such side branches are absent. In addition, in *B. elongata*, at the point where these side branches arise, the apico-laterals bend sharply outwards, through 90°, while in *B. amoena* the apico-laterals only curve gently away from the mid-line. Unfortunately, it is this region of the nectophore that most often becomes distorted in poorly preserved specimens and these distinguishing features can be masked. This can result in the distinct, right-angle bend in the apico-lateral ridges of *B. elongata* coming to resemble the much smoother curve in *B. amoena* or, conversely, those of the latter species becoming distorted to form distinct bends resembling those of the former. The side branches to the apico-laterals in *B. elongata* often are difficult to discern, but usually show up after staining.

Another obvious difference, despite its subjectiveness, is the density of the musculature on the nectosac. Nectophores with almost opaque nectosacs appear to belong to *B. elongata*, while those with translucent nectosacs belong to *B. amoena*. In addition, the ratio of the total length of the nectophore to that of the nectosac may be of use. In *B. elongata* this ratio, in well-preserved specimens, averages 1.31, while in *B. amoena* it averages 1.42. However, with poorly preserved material, particularly when the basal half of nectophore is damaged, both measurements could be underestimated, which would lead to a corresponding increase in the ratio.

Other features of the nectophore that might be considered include the fact that in *B. amoena* the outer branch of the apico-lateral ridges peters out higher above the ostium than in *B. elongata*. Also, the lateral processes to the ostium are much larger in *B. elongata*. In addition, the angle at which the ostium opens is very characteristic in well-preserved material. In *B. elongata* the ostium is directed dorso-basally while in *B. amoena* it opens basally. However, all these features might be difficult to discern in poorly preserved nectophores The structure of the mouth-plate may be important but, as has been shown for *B. amoena*, this may vary according to the size of the specimens. More well preserved specimens of *B. elongata* are needed in order to assess this. Similarly, this applies to the arrangement of the meso-lateral ridges and their basal extensions; and to the profile of the ventral margins of the ventro-lateral wings.

ETYMOLOGY. *Amoena* is Latin for 'pleasing, delightful'.

Bargmannia lata Mapstone 1998

Bargmannia elongata Totton 1954 (partim) (text-Figure 28, E–F only), 1965 (partim) (Figure 45 E–F only).
Bargmannia lata Mapstone 1998: 141–146, figs 1–3.

HOLOTYPE. In the collections of the British Columbia Provincial Museum, BCPM 996-203-1; one nectophore and one bract collected at St. LC10 (48°22.4'N 126°20.2'W; 24–iv–1987; 700–0m) off British Columbia, Canada;

PARATYPES. As designated by Mapstone; **1.** 7 nectophores and 7 bracts (BCPM 996-204-1#1), and **2.** 6 nectophores and 6 bracts (BCPM 996-205-1#2) from the same sample as the holotype; **3.** 11 nectophores (BCPM 996-206-1#3), and **6.** 1 bract (BMNH 1996.1239-1240#6) from St.A4 (48°15'N 126°40'W; 21.iii.87; 500 m); **4.** 8 nectophores (0–700m; BCPM 996-207-1#4), and **5.** 14 nectophores and 2 bracts (BMNH 1996.1234-1238#5) from St. LB17 (47°56.5'N 126°26.1'W; 21.iii.87; 700m).

MATERIAL EXAMINED. One specimen collected during *Alvin* Dive 966 off San Diego, California, U.S.A.; 33°04'N 118°16'W; 8–ix–1979; water depth 747m. The depth of collection of the specimen was not recorded.

Two nectophores collected at *Discovery* St. 1769, and figured by Totton (1954, Text-Figure 28, E, F; 1965, Figure 45, E, F) as *B. elongata*; 33°43.3'S 8°38.5'E; 20–v–1936; 1000–750 m; NHML 1957.5.15.110.

In addition, the specimens that Totton included under the name *B. elongata* have been re-examined. Although not all are in good condition, the following appear to belong to *B. lata*:-

Table 1 Geographical distribution of *Bargmannia lata* from recent *Discovery* collections.

Station	Date	Position	Depth (m)	Nects	Bracts
8565# 1	1–viii–74	3°03.1'N 23°14.3'W	700–800	5	
6662#37	21–ii–68	10°34.9'N 19°43.7'W	1060–1300	24	16
6662#32	20–ii–68	10°45.3'N 19°51.7'W	1210–1450	3	4
6662#30	19–ii–68	10°47.4'N 19°52.7'W	730–795	17	
6662#15	16–ii–68	10°57.0'N 19°56.6'W	600–695	27	
6662#20	17–ii–68	10°57.5'N 19°49.0'W	810–900	8	
6662#22	17–ii–68	10°57.6'N 19°57.3'W	610–680	25	3
6662#16	16–ii–68	10°59.4'N 19°52.1'W	810–890	18	2
7824#39	10–iii–72	11°01.1'N 19°55.8'W	895–1000	5	
6662#10	15–ii–68	11°03.1'N 19°59.2'W	910–985	4	
6662# 7	14–ii–68	11°04.6'N 19°48.2'W	715–800	33	
6662# 8	15–ii–68	11°08.2'N 19°47.8'W	910–985	7	
7831# 1	16–iii–72	13°18.4'N 25°33.2'W	10–1000	12	
7803# 2	19–ii–72	18°06.4'N 25° 8.1'W	1015–1250	13	
11261#16	28–vi–85	31°13.1'N 25°18.3'W	1000–1100	16	
8281#29	17-iii–73	31°42.5'N 63°43.6'W	1259–1500	26	
11794#36	26–vi–88	47°14.2'N 19°31.2'W	1200–1300	10	
11794#83	2–vii–88	47°17.9'N 19°21.4'W	1300–1395	7	
11794#31	26–vi–88	47°27.1'N 19°18.0'W	2500–2750	17	2
12096# 2	3–vi–90	47°57.8'N 16°49.6'W	1100–1200	16	20

4 nectophores from John Murray Expedition St. 34; 13°05.6'N, 46°24.7'E; 16–x–33; 0–1022 m. BMNH 1949.11.10.378; and
4 nectophores from *Discovery* St. 206; 16°36'S, 6°25.1'W; 1–v–37; 1900–1500 m. BMNH 1957.5.15.111.

Several nectophores and bracts also have been identified from more recent *Discovery* material from the N.E. Atlantic (Table 1).

DIAGNOSIS. Nectophores with relatively long median thrust block; with extensive ventro-lateral wings, emarginate on ventral margins. Nectosac a relatively short, narrow tube without any pronounced dorso-ventral undulations; squarely truncate apically. Ratio of overall length of nectophore to that of nectosac, on average, exceeds 1.59. Bracts large, robust, distally truncate; with semicircular dorsal ridge connecting tips of baso-lateral processes and delimiting a dorso-basal facet; with prominent tooth on outer lateral margin.

DESCRIPTION. A photograph of the live specimen collected by *Alvin* and taken on board the mother ship is shown in Figure 12. Unfortunately, prior to photography, several nectophores had become detached and the siphosomal stem had contracted. No pigmentation is apparent in the preserved specimen, but the original colour photograph indicates that the whole of the endodermal lining of the stem was suffused with an orange-red colour.

PNEUMATOPHORE. The highly distorted pneumatophore of the *Alvin* specimen measured 2 mm in height. It is borne on a very short, but probably highly contracted, stalk.

NECTOPHORE (Figures 13–15). A total of 16 nectophores was found with the *Alvin* specimen. The mean dimensions for the fully developed nectophores of this specimen were:- length 19.44 ± 2.73 mm (range 14.79–23.86 mm); width 9.72 ± 1.07 mm, and the ratio of total length to that of the nectosac was 1.59 ± 0.09. Nectophores of the earlier *Discovery* material, in the NHM, are somewhat larger with an average length of 24.94 ± 6.02 mm (range 17.74–31.94 mm). The ratio of total length to that of the nectosac also was slightly greater ratio (1.67 ± 0.10; n = 10); the same as that for Mapstone's (1998) material. Similarly, the nectophores of more recent *Discovery* material also are larger: length 22.89 ± 4.04 mm (range 15.8–29.6 mm; n = 48). These nectophores have the greatest length:nectosac-length ratio of 1.73 ± 0.11. However, this increase in ratio probably

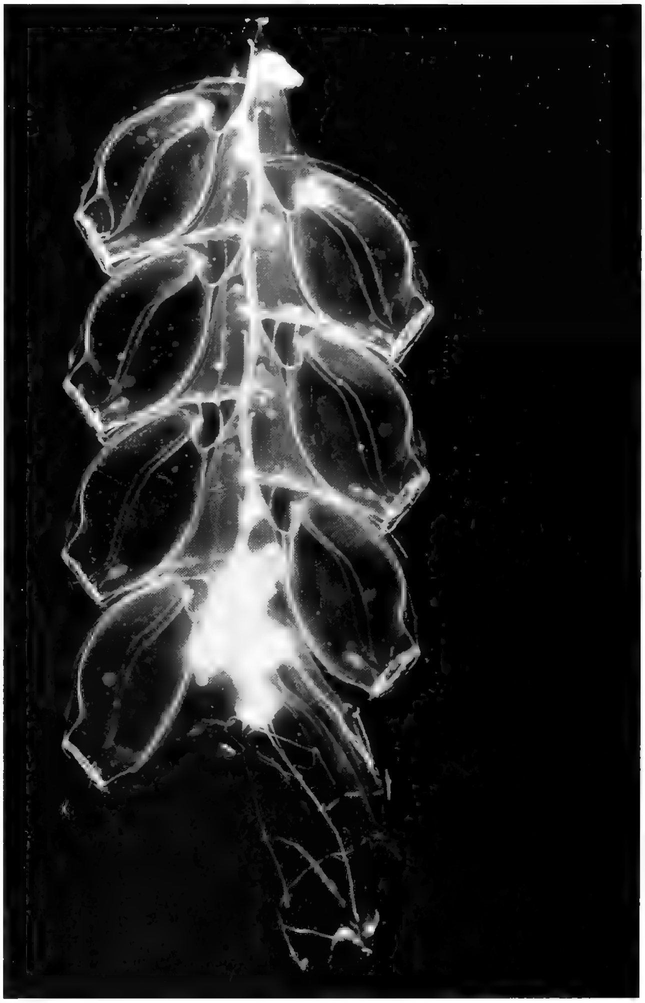

Fig. 12 *Bargmannia lata*. Photograph (reproduced by kind permission of Larry Madin, WHOI) of live specimen collected during *Alvin* Dive 966. Nectosomal length c. 5 cm.

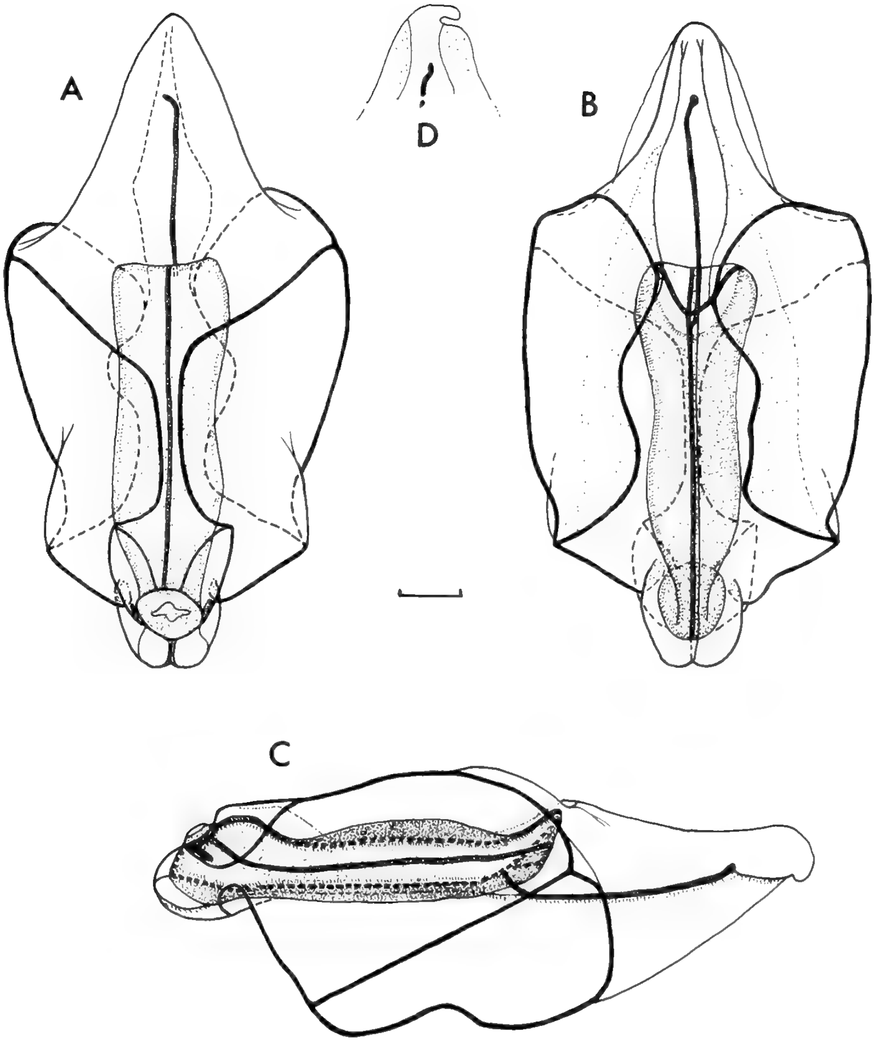

Fig. 13 *Bargmannia lata*. A. Upper, B. lower, and C. lateral views of mature nectophore collected during DSRV *Alvin* Dive 966. D. Ventral view of the apex of another nectophore. Scale bar = 2 mm.

is due to the fact that the base of the nectophore frequently is damaged, resulting in an underestimate of both measurements, and a consequent increase in their ratio.

The central thrust block forms an extensive triangular process whose apex is often roundly pointed Figure 13A). However, on several nectophores one side is drawn out to form a small digitiform process that may be folded over laterally or ventrally (Figure 13D). The ridge pattern conforms to the basic *Bargmannia* design, with no extra ridges being present.

From their junction with the meso- and infra-lateral ridges on the 'shoulder' of the nectophore, the apico-laterals are directed obliquely toward the mid-line. They closely approach each other, and continue for some distance in a basal direction; leaving a narrow median furrow between them. At about one quarter the length of the nectophore, in the *Alvin* material, they rapidly curve out laterally, before giving rise to the typical inner and outer branches (Figures 13–15). The inner branch curves obliquely toward the mid-line and joins the ostium on its dorsal surface. The outer branch curves down and then round and ends on the lateral margin of ostium, although it can be difficult to discern basally. The angle between the apico-lateral ridge and its inner branch is acute (Figure 13A). However, in less well preserved nectophores, this pronounced angle is not always apparent (Figure 14B) and the inner branch can appear as a simple continuation of the main ridge.

The mouth-plate is small and made up of two rounded lobes that unite in the mid-line, slightly basal to the ostium. The ventro-lateral margins of these lobes are, as usual, formed by basal extensions of the meso-lateral ridges. Above the ostium, on the ventral surface of the nectophore, these basal extensions curve round toward the mid-line, before looping back out as the meso-laterals proper and continuing apically. After a relatively long distance, in comparison with *B. elongata* and *B. amoena*, the infra-laterals branch from them (Figures 13C, 15C). The meso-laterals then continue obliquely up and across the lateral margins of the nectophore to join the apico- and infra-laterals on the 'shoulder' of the nectophore. The junctions with the other ridges, both apically and basally, are obvious, unlike in *B. elongata*.

In the basal two-thirds of the nectophore, the infra-lateral ridges form the ventral margins to the ventro-lateral wings (Figure 13C, 15C). These wings are relatively large in comparison with those of *B. elongata* and *B. amoena*, occupying more than half the depth of the nectophore. They are distinctly emarginate in the mid region of

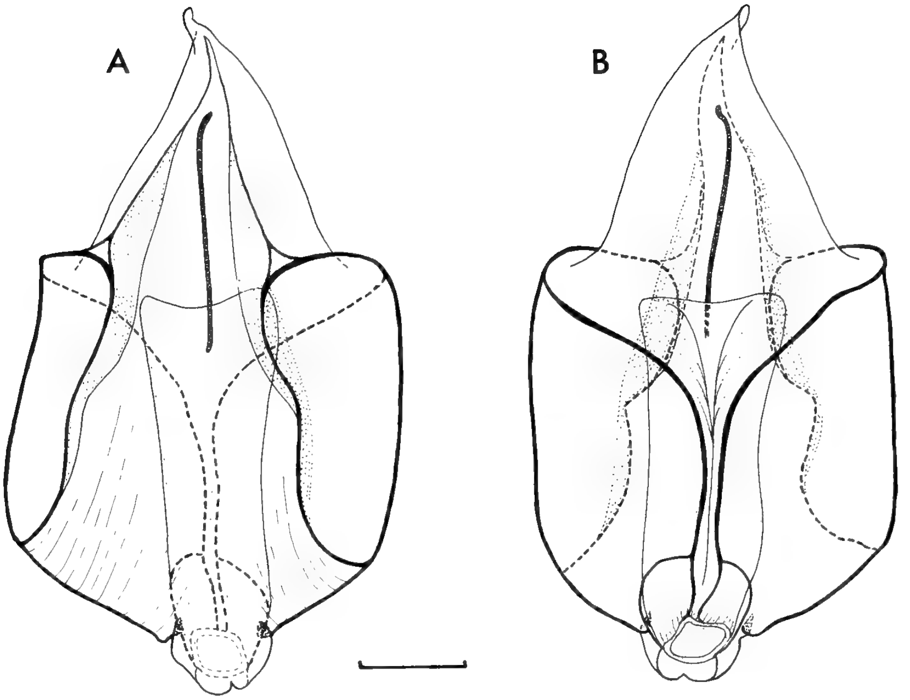

Fig. 14 *Bargmannia lata*. A. Lower and B. upper views of nectophore from *Discovery* St. 1769. Scale bar = 5 mm.

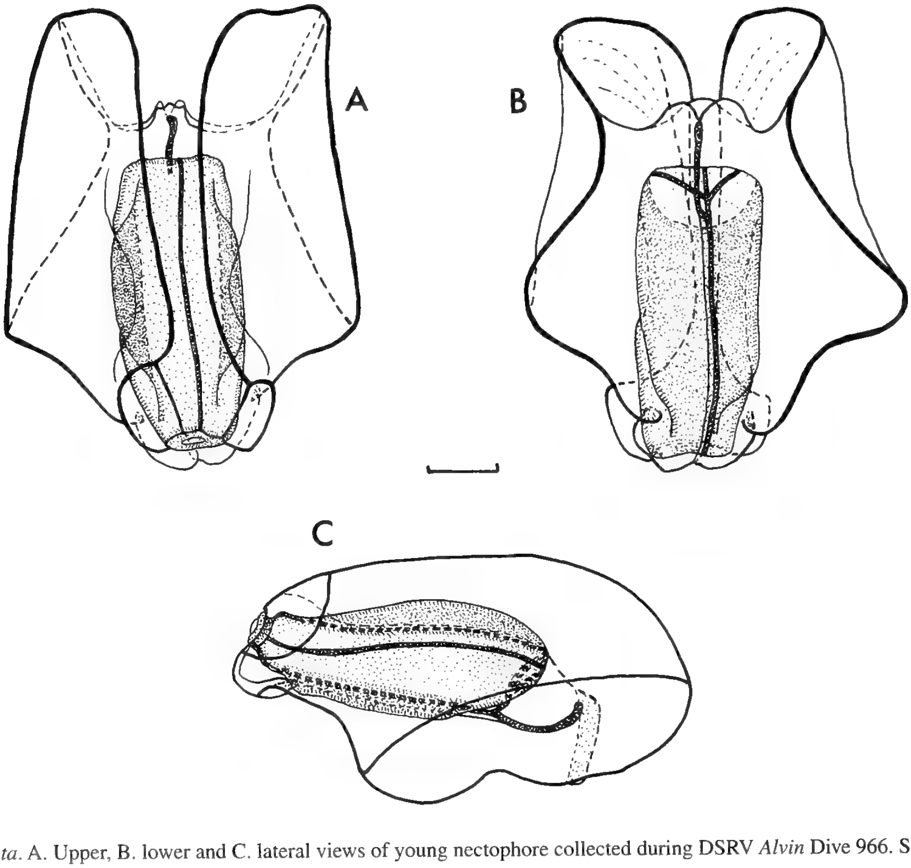

Fig. 15 *Bargmannia lata*. A. Upper, B. lower and C. lateral views of young nectophore collected during DSRV *Alvin* Dive 966. Scale bar = 1 mm.

the nectophore. In the region where the infra-laterals leave the ventral margins of the ventro-lateral wings, the latter begins to thicken toward the mid-line. These thickened, rounded, unridged lateral walls continue up to the apex of the nectophore and, on the thrust block, delimit a narrow gutter that enfolds the nectosomal stem (Figures 13B, 14A).

The nectosac is a relatively short and narrow tube without any marked dorso-ventral undulations (Figures 13, 14) in the preserved specimens. Its apex lies approximately on a level with the 'shoulder' of the nectophore. The nectosac occupies only c. 38% of the width of the nectophore, as measured across its 'shoulder'. This results from the fact that the extensive ventro-lateral wings not only increase the depth of the nectophore, but also increase its relative width. The apex of the nectosac is squarely truncate, without any marked indentation. Its adaxial surface is distinctly undercut and, typically, is devoid of musculature. The remaining musculature on the nectosac appears much less dense in comparison with that of *B. elongata*.

The canal system follows the basic *Bargmannia* plan. The long pallial canal ends, apically, with a short dorsad inflection into the mesogloea. On the nectosac the pedicular canal gives rise to only the dorsal and ventral radial canals. In contrast to *B. elongata* and *B. amoena*, in the preserved material the lateral radial canals have straight courses down the lateral margins of the nectosac. However, in life, their courses appeared to be slightly undulating (Figure 12). In the original colour photograph there are indications that the pallial, dorsal, ventral, ostial ring, and proximal parts of the lateral canals were suffused with a light orange-red colour.

The ostial opening, in the preserved nectophores, typically is displaced slightly dorsad and has a well-developed velum, but no pronounced lateral processes. There are no marked patches of ectodermal cells, although some nectophores show a single row around the basal half of the ostium and/or a short, narrow band of small cells that lies just dorsal to the outer branch of the apico-lateral ridge. These cells, again, are presumed to be sites of bioluminescence.

BRACT (Figure 16). Only seven bracts were retained with the *Alvin* material. However, because of their very characteristic shape, several more have been identified from recent *Discovery* material. The bracts measured from 13.5 to 27 mm in length and were remarkably robust. They had a convex dorsal and a concave ventral surface. In the *Alvin* specimen, there were two types of bract, with one type being represented by only a single small bract. The key feature that distinguishes them is the presence of only a single lateral tooth on the outer margin (Figure 16A, B) of the larger ones; while the smaller one has lateral processes on both sides (Figure 16C). The

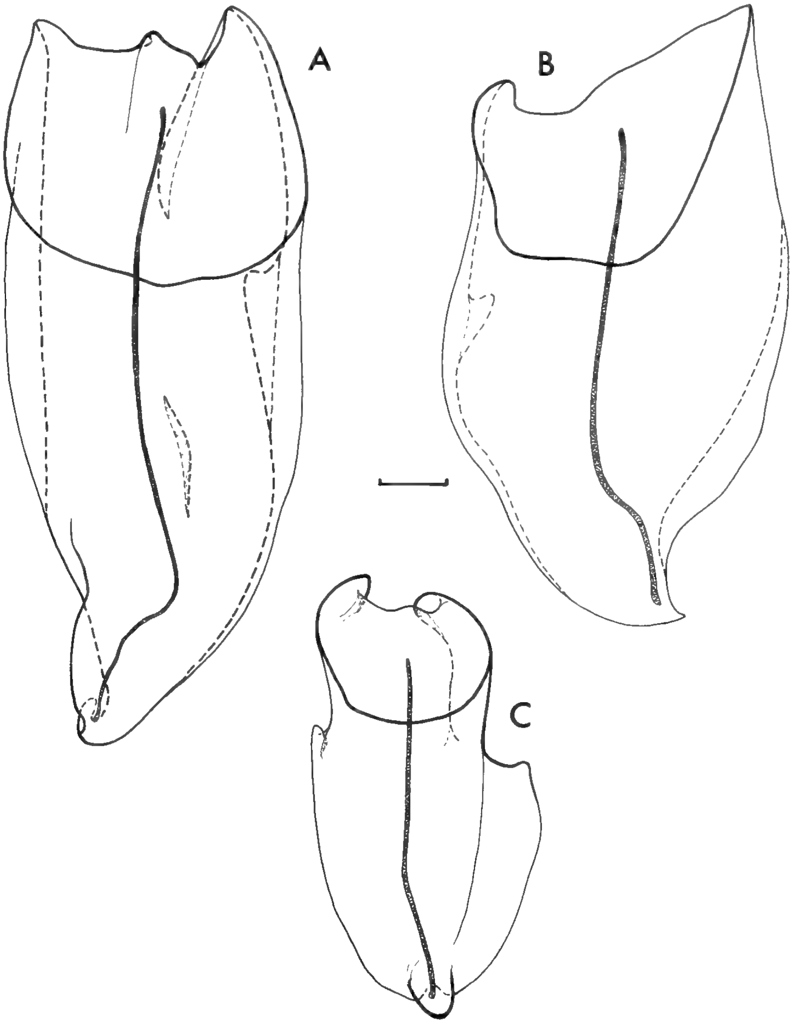

Fig. 16 Bracts of *Bargmannia lata* collected during DSRV *Alvin* Dive 966. Scale bar = 2 mm.

larger ones also were distinctly asymmetric proximally; and the bracteal canal made a right-angled bend. These differences may be just the result of growth, or may related to their point of attachment on the cormidium, as was noted for *B. amoena*. Both types of bract are distally truncate, and possess a semicircular dorsal ridge that delimits a rounded distal facet. The ridge connects the tips of two distal processes.

The shape of the distal margin of the larger bracts varied considerably. On some, the inner margin of one of the distal process extended up the ventral side of the bract forming a flap-like structure; while on others this flap was absent. Another small ventral flap can be present, approximately in the mid line, in the proximal half of the bract. The bracteal canal lies just above the ventral surface of the bract and ends close to its distal margin. The original colour photograph of the *Alvin* dive 966 specimen indicated that, in life, some of the bracteal canals had an orange-red pigmentation like that of the remainder of the stem.

GASTROZOOID AND TENTACLE. Only a small portion of the proximal end of the siphosome was preserved from the *Alvin* specimen, so that only a few young gastrozooids were present. These measured up to 7 mm in length, and showed no distinguishing features. No pigmentation is apparent in the preserved material, but in life they had a deep red pigmentation.

The tentacles attached to the gastrozooids mainly bore young tentilla; with a c. 1 mm pedicel; a 2.5 mm cnidoband, apparently devoid of large nematocysts; and a c. 4 mm uncoiled terminal filament, apparently without a terminal process. However, a few more mature tentilla had cnidobands extending to more than 8 mm, with 4–6, possibly more, large nematocysts (stenoteles), arranged biserially and arranged alternately, at their proximal ends. Small nematocysts, possibly of two types, are present throughout the cnidoband and terminal filament.

SIPHOSOMAL TENTACLES AND BUDS. The peculiar tentacular processes, previously noted in specimens of *B. elongata* and *B. amoena*, are present on the small part of the siphosomal stem remaining but, because of the contracted state of the latter, it was not possible to ascertain their exact disposition. They are narrow, delicate structures, measuring up to c. 4 mm in length, and are covered in large, rounded ectodermal cells. Small nematocysts are present but, without destroying the tentacle, it was no possible to assess whether they had a biserial arrangement, as noted for the previously described species. Siphosomal buds also appear to be present, but their arrangement could not be discerned.

GONOPHORE. A few loose male gonophores are present with the *Alvin* material. They are identical to those previously described for *B. elongata* and *B. amoena*.

DISTRIBUTION. A total of 288 nectophores and 27 bracts of *B. lata* have been found in recent *Discovery* collections (Table 1). The data indicated that, in the North-east Atlantic Ocean, *B. lata* was more commonly collected at lower latitudes and at deeper mesopelagic depths; with a mean depth of c. 1000 m. Totton's material came from two sites in the South Atlantic Ocean and one in the Gulf of Aden; the *Alvin* material came from off San Diego, California, USA; and Mapstone's (1998) from off British Columbia, Canada; thus indicating a widespread geographical distribution for this species.

REMARKS CONCERNING THE IDENTIFICATION OF *BARGMANNIA LATA*. *B. lata* can now be easily distinguished from other *Bargmannia* spp. The nectophores are relatively broad, with extensive ventro-lateral wings, that are markedly emarginate along their ventral margins. The median thrust block is relatively long so that the ratio of the total length of the nectophore to that of the nectosac is high, c. 1.6, or more for net collected material, as compared with c.1.31 in *B. elongata* and c. 1.41–1.44 in *B. amoena*. The nectosac appears as a relatively short, narrow, straight-sided tube, without any pronounced dorso-ventral undulations, and squarely truncate apically. It occupies only c. 38% of the width of the nectophore, as compared with 45% in *B. elongata*. The large, robust bract, with a semicircular dorsal ridge connecting the tips of the baso-lateral processes, also is distinctive.

Despite these differences it is clear that Totton (1954, 1965), had little reason to suspect that he was dealing with at least two *Bargmannia* spp., particularly as he had so few, poorly preserved nectophores. However, with the collection of complete specimens of *Bargmannia* spp. by submersibles the specific differences between the various types of nectophore that Totton illustrated can now be established.

Bargmannia gigas sp. nov.

HOLOTYPE. BMNH 1998.2166 one nectophore, preserved in Steedman's solution, collected at *Discovery* St. 8560#2 (0°03.1'N, 22°44.2'W; 27–vii–1974; 1510–2000 m; RMT8 net).

PARATYPES. Three nectophores, preserved in Steedman's solution, from the same *Discovery* sample. BMNH 1998.2167–69.

MATERIAL EXAMINED. The type and paratypes, and a further ten nectophores from the same station, which are retained in the *Discovery* collections at the Southampton Oceanography Centre. All the nectophores are presumed to have originated from a single specimen.

DIAGNOSIS. Nectophores relatively enormous, up to 52 mm in length; with large ventro-lateral wings; with small mouth-plate deeply divided. Basic ridge pattern supplemented by three pairs of ridges, all dividing from apico-laterals; two pairs short, directed toward mid-line; third pair directed laterally. Nectosac without dorso-ventral undulations; apex only slightly emarginate; ostial opening large. Ratio of overall length of nectophore to that of nectosac averages 1.63.

DESCRIPTION. NECTOPHORES (Figures 17 and 18). The relatively enormous nectophores varied in size from 14.5 × 8 mm (length × width) for the smallest, immature one, to 52 × 20 mm, respectively, for the largest. The mean dimensions for the fully developed nectophores were length: 41.0 ± 6.96 mm and width: 19.1 ± 2.52 mm, and the ratio of total length to that of the nectosac was 1.63 ± 0.10. The nectophores, in their present state of preservation, are devoid of pigmentation and, in most cases, the muscular lining of the nectosac has become detached and/or lost. The large, thickened, central thrust block is roundly truncate.

The basic pattern of the prominent ridges conforms with that of the genus, and both the inner and outer branches of the apico-laterals appear to reach the dorso-lateral margins of the ostium. In addition there are three pairs of ridges that branch from the apico-laterals (Figures 17A, 18). Two of these pairs of ridges are very short and run down into the shallow median gutter, towards the mid-line. One pair arises at a level of about two-fifths the length of the nectosac, while the other originates from the inner branches of the apico-laterals, close to the ostium. The other pair arises from the outer branches of the apico-laterals and extends up the sides of the nectophore between the apico- and meso-laterals. These ridges peter out approximately at the mid-length of the mature nectophore. Below them the lateral walls of the nectophore often show prominent thickenings (Figure 17C).

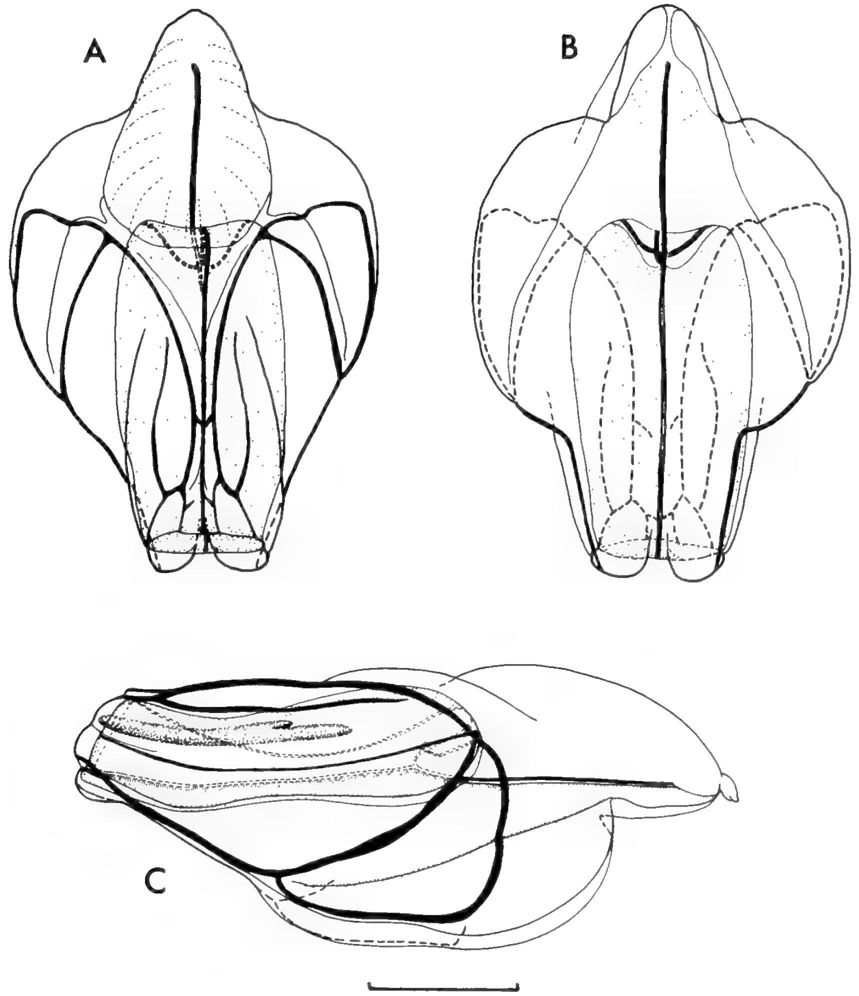

Fig. 17 *Bargmannia gigas* sp. nov. A. upper, B. lower, and C. lateral views of mature nectophore. Scale bar = 1 cm.

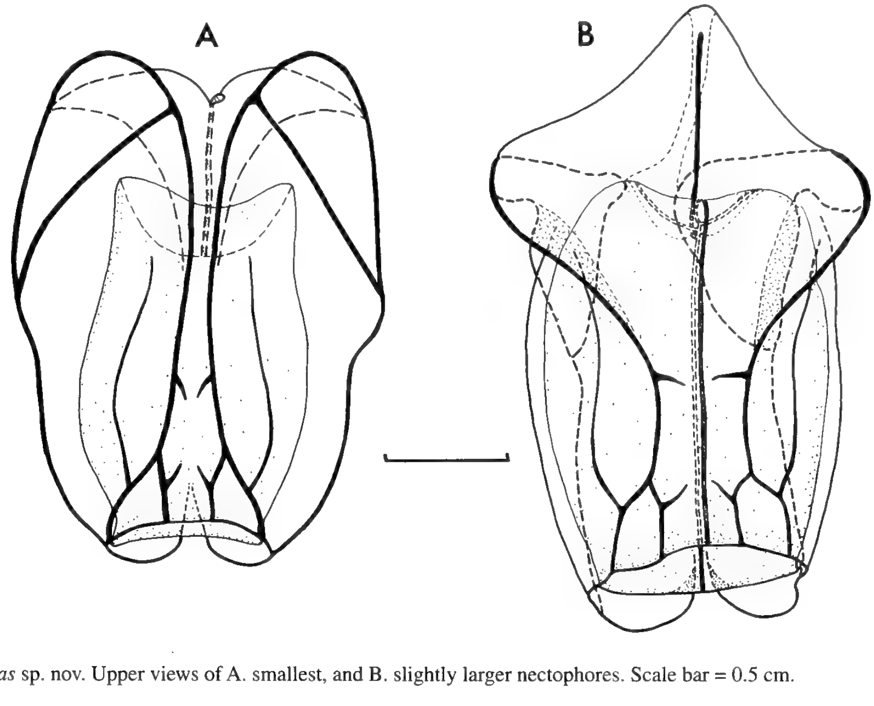

Fig. 18 *Bargmannia gigas* sp. nov. Upper views of A. smallest, and B. slightly larger nectophores. Scale bar = 0.5 cm.

The broad, but relatively short, mouth-plate consists of two rounded processes whose basal margins are marked by basal extensions of the meso-lateral ridges. These ridges peter out, without apparently uniting, on the lower surface of the nectophore a short distance above ostial level. The infra-lateral ridges branch from the meso-laterals approximately on a level with the mid-length of the nectosac. The meso-laterals then run obliquely up the sides of the nectophore to join the other ridges, approximately on a level with the top of the nectosac. The infra-laterals form the ventral margins of the ventro-lateral wings up to a level just above the top of the nectosac. They then bend through 90° and run up to join the apico- and meso-laterals (Figure 17C). The thickened ventro-lateral wings are well developed and enclose a deep groove, which at its deepest occupies half the height of the nectophore (Figure 17C). They are roundly truncate apically at about four-fifths the length of the nectophore.

The nectosac is a long tube, with only a slight apical emargination, that occupies most of the main body of the nectophore, and has no obvious dorso-ventral undulations. It is distinctly undercut adaxially and is presumed to have a muscle-free zone in that region, although this could not be established with certainty. The ostial opening is very large and is only slightly directed towards the upper surface. The pedicular canal (Figure 17B) typically only gives rise to the dorsal and ventral radial canals. The course of all the canals is straight.

Typically, the youngest nectophores show the absence of a central thrust block (Figure 18A), but with a clearly defined ridge pattern. A slightly larger nectophore shows the gradual development of the thrust block and the ventro-lateral wings (Figure 18B).

REMARKS CONCERNING THE IDENTIFICATION OF *BARGMANNIA GIGAS*. *B. gigas* is known only from the nectophores of what is presumed to be a single specimen, collected in the equatorial Atlantic at a depth of 1510–2000m. The nectophores easily can be distinguished from other *Bargmannia* sp. by their incredible size and the distinctive pattern of ridges.

ETYMOLOGY. The specific name *gigas* refers to the giant size of the nectophores.

DISCUSSION

As was noted in the Introduction, the content of the genus *Bargmannia* is debated. Although Totton (1965) included it in the family Pyrostephidae, some of the characters that he listed in his diagnosis of that family apply exclusively to the scope accorded to the genus *Pyrostephos*, which is monotypic for *P. vanhoeffeni*. In particular, these are the looping of the lateral radial canal on the nectosac of the nectophore, and the three to four marked bends of the dorsal canal. In *Bargmannia* all the canals are held to be straight, or only slightly sinuous. Other characters, such as the number of tentilla on the tentacle, and the structure of the bracts and gastrozooids probably are more specific than familial. However, in both genera the nectosome is long but again this is not a good familial character.

At first glance, the nectophores of *Pyrostephos vanhoeffeni* (see Totton, 1965, Figure 41) and *Bargmannia* species look strikingly different. However, there are several similarities. Specimens of *P. vanhoeffeni* have been collected recently by SCUBA divers (G.R. Harbison, personal donation) and by net (Pagès, Pugh & Gili, 1994). It is apparent from these that the mature nectophores can vary greatly in size; ranging from 8 × 5 mm (length × width) in the SCUBA collected material (Figure 19B) to 15 × 18 mm, respectively, in the net collected specimens (Figure 19C). Such large size ranges of the mature nectophores of physonect species have not often been observed, although such is so in *Nanomia bijuga* (delle Chiaje, 1841) (Pugh, *pers. obs.*). It is also known to be so in at least two *Bargmannia* spp. In *B. amoena* (Figure 19A), the size variation of mature nectophores is even greater than that of *P. vanhoeffeni*, ranging from c. 6 × 3 mm (length × width) to 25.5 × 12.5 mm respectively. Although the general shape of mature *Bargmannia* nectophores does not change with size, it appears that that of *P. vanhoeffeni* does. In the smaller specimens of the latter (Figure 19B) there is a large triangular thrust block, reminiscent of that on mature *Bargmannia* nectophores. However, in the larger, preserved specimens (Figure 19C) the thrust block is folded upwards producing a deep transverse furrow on the dorsal surface, just basal to it. Neither *P. vanhoeffeni* nor *Bargmannia* spp. have large apico-lateral processes.

The nectophores of both genera have the same basic ridge pattern; comprising apico-, infra, and vertical (meso-) laterals, but no lateral ridges. In addition, in both, the apico-laterals divide into two branches close to the ostium. The inner branch ('frontal ridge') of the larger nectophores of *Pyrostephos vanhoeffeni* (see Totton, 1965, Figure 40) is relatively short, in comparison with *Bargmannia* spp., and directed only toward the mid-line. However, the present material, particularly that of the smaller specimens, shows that these ridges can curve round basally and continue for a short distance towards the ostium before petering out. Nonetheless, the species of these two genera are not the only physonects to show this basic pattern of ridges. It is also found on the nectophores of two others namely, *Frillagalma vityazi* Daniel, 1966 (see Pugh, 1998) and *Erenna richardi* Bedot, 1904 (P.R.Pugh, personal observation). In addition, an even simpler arrangement, in which the vertical lateral ridges are absent, is found in two *Marrus* species, namely *M. antarcticus* Totton, 1954 and *M. orthocanna* Kramp (1942). For these, the branching of the apico-lateral ridges is weak and difficult to discern. A third species, namely *M. orthocannoides*, that Totton (1954) include in the latter genus probably does not belong there as its nectophores do not have an adaxial muscle-free zone on the nectosac.

Species referred to both *Bargmannia* and *Pyrostephos* have an adaxial zone on the nectosac of the nectophore that is muscle-free and deeply embayed. In addition, the lateral radial canals arise separately from the dorsal canal. These appear to be important characteristics. Of the other species previously mentioned *Marrus antarcticus* and *M. orthocanna* show all of these characters. However, in *Frillagalma vityazi*, there is no deeply embayed, muscle-free adaxial zone; although the lateral radial canals do arise separately from the dorsal one, albeit very close to the point of insertion of the pedicular canal (Pugh, 1998). Further, this species has many marked differences from the others under consideration and need not be considered further in this discussion. *Erenna richardi* does have a muscle-free zone, but it lies at the apex of the nectosac, which is not deeply embayed adaxially. Thus, from the basic arrangement of the ridges and nectosac, the nectophores of *Bargmannia*, *Pyrostephos* and *Marrus* species are very similar. Another common feature is that they all have relatively short pedicular and relatively long, ascending pallial canals. But how do their siphosomal elements compare?

Most siphonophores are believed to be hermaphrodite (monoecious), bearing both male and female gonophores. However, specimens of *Physalia*, the Portuguese Man O'War, and probably all other cystonect siphonophores, are single sexed (dioecious). It should be noted that Mackie, Pugh & Purcell (1987, p.100) used the terms monoecious and dioecius erroneously. In physonect siphonophores, species of the benthic family Rhodaliidae appear to be dioecious (Pugh, 1983), as are *Marrus antarcticus*, *Pyrostephos vanhoeffeni* (Totton, 1965), and from the present study *Bargmannia* spp. According to Andersen (1981) *M. orthocanna* is monoecious, but the male gonophores he illustrated were only minute, bud-like

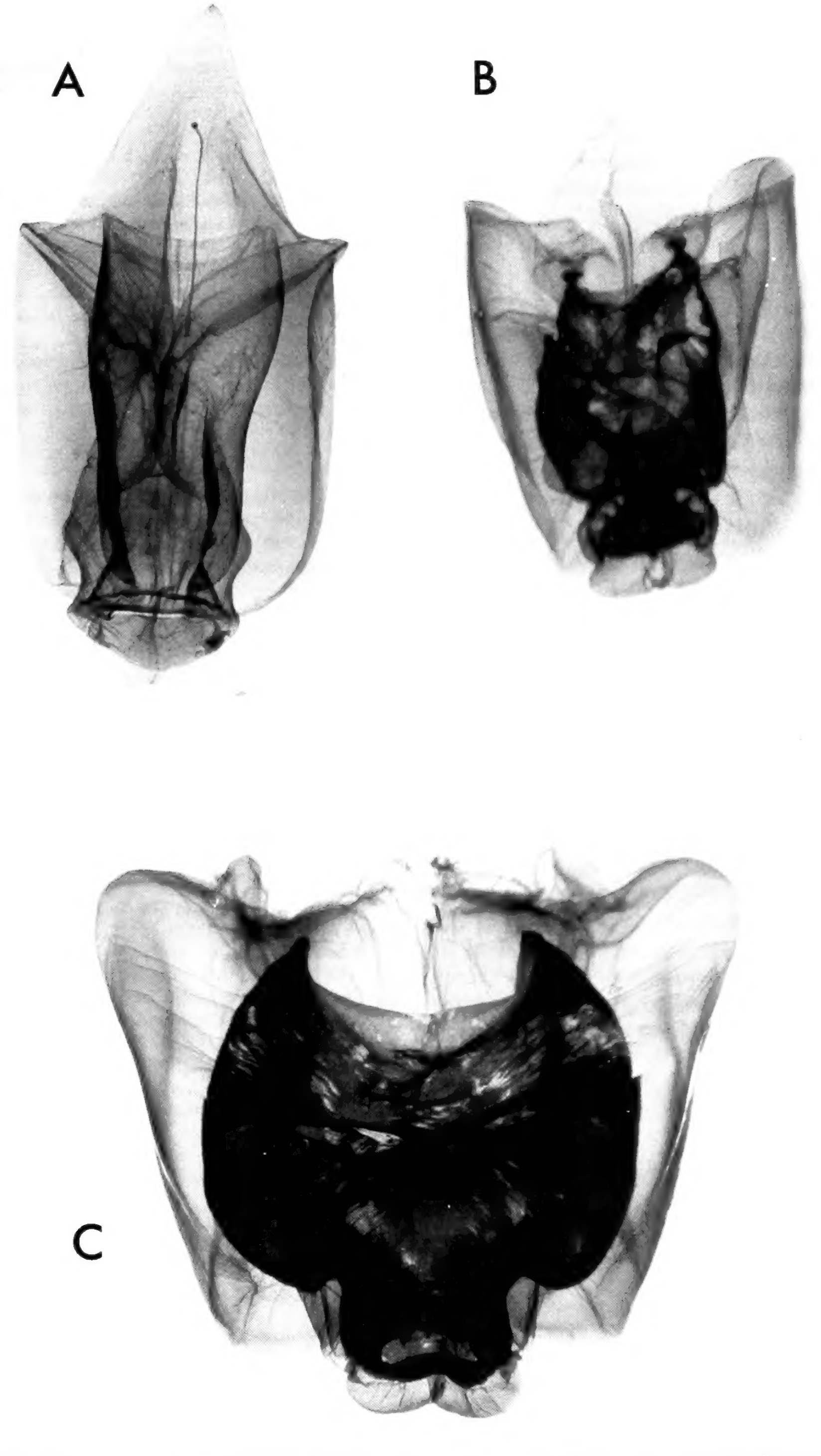

Fig. 19 Nectophores of A. *Bargmannia amoena* sp. nov. (magn. 10); B, C. *Pyrostephos vanhoeffeni* collected by SCUBA (B, magn. 11×) and by net (C, magn. 7.5×).

structures. Since only female gonophores could be identified on submersible collected specimens, this point could not be checked (P.R.Pugh, personal observation). Whether *Erenna richardi* is monoecious or dioecious remains unknown. Nonetheless, it is of interest to note that, of the physonect species whose female gonophores are known, only those of *P. vanhoeffeni* and *B. amoena* contain more than one egg; 3–5 in the former species (Totton, 1965) and two in the latter.

The structure of the tentillum is another feature in which close similarities between *Bargmannia* species and *Pyrostephos vanhoeffeni* appear. In both the cnidoband is straight, or slightly twisted, but not tightly coiled, and is without a basal involucrum. In addition, they both have long terminal filaments. Even more striking is the presence of large nematocysts, probably stenoteles, only in the proximal region of the cnidoband of both species. However, those of *Bargmannia* spp. are considerably larger than those of *P. vanhoeffeni*, which measure c. 40 × 28 mm. Further, the other nematocysts present on the cnidoband and terminal filament are very similar. Two types of small nematocysts were found in *Bargmannia* spp. and similar ones, measuring 13–17 × 9.5–10.5 µm and 6.5 × 6.5 µm, were found in *P. vanhoeffeni*. Although the tentillum of *Erenna* has a straight cnidoband, and that of *Marrus* is loosely coiled or straight, the types and distribution of the nematocysts are quite different. The cnidoband of *Erenna* is massively armed with two types of elongate nematocysts, measuring c. 160 × 37 µm and c. 35 × 18 µm, while the terminal process appears to be devoid of any nematocyst. The cnidoband of *Marrus* contains heteronemes and haplonemes, measuring c. 55 × 20 µm and c. 35 × 7 µm of the type often seen in other agalmatid species. The terminal filament of the latter species contains only small nematocysts, probably desmonemes, acrophores or anacrophores, measuring c. 16 × 9.5 µm and c. 10 × 10 µm. These differences in the nematocyst types alone seem sufficient to indicate that *Bargmannia* and *Pyrostephos* are more closely related to each other than either is to *Marrus* or *Erenna*.

Despite all these similarities between *Bargmannia* spp. and *Pyrostephos vanhoeffeni*, there are at least two major differences: *Bargmannia* spp. are the only physonect siphonophores known to have siphosomal tentacles, though apolemiid species have nectosomal ones; they also lack dactylozooids, although the bud-like structures may be vestigial ones. In addition, *P. vanhoeffeni* is the only species known to have highly modified dactylozooids, the oleocysts, without palpacles. The only other species in which dactylozooids are thought to be absent is *Marrus orthocanna* (Andersen, 1981). However, Totton (1965) reported that palpons are present on the gonodendra of *M. antarcticus*. Further work needs to be carried out on well-preserved specimens of these *Marrus* species in order to investigate this apparent difference, and whether each is monoecious or dioecious.

Although there are major differences between *Bargmannia* spp. and *Pyrostephos vanhoeffeni*, there appear to be sufficient similarities to warrant the retention of the genus *Bargmannia* in the family Pyrostephidae. The alternative would be to propose a new family for it, since the genus certainly does not fit neatly into the family Agalmatidae. This might also apply to the genera *Marrus* and *Erenna* but their species are too little known.

ACKNOWLEDGEMENTS. I am extremely grateful to Drs Richard Harbison and Edie Widder for inviting me to participate in several cruises involving the use of submersibles, and for donating the siphonophore material collected to me. I thank Dr Paul Cornelius for his helpful comments on the manuscript.

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