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Bulletin of the British Museum (Natural History)

Zoology series Vol 34 1978-1979

British Museum (Natural History)
London 1979

Dates of publication of the parts

No 1	29 June 1978
No 2	30 November 1978
No 3	21 December 1978
No 4	22 February 1979
No 5	29 March 1979
No 6	26 April 1979

ISSN 0007-1498

Printed in Great Britain by Henry Ling Ltd, at the Dorset Press, Dorchester, Dorset

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Zoology Volume 34

Bulletin of the
British Museum (Natural History)

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Zoology series Vol 34 No 1 29 June 1978

The *Bulletin of the British Museum (Natural History)*, instituted in 1949, is issued in four scientific series, Botany, Entomology, Geology and Zoology, and an Historical series.

Parts are published at irregular intervals as they become ready. Volumes will contain about four hundred pages, and will not necessarily be completed within one calendar year.

Subscription orders and enquiries about back issues should be sent to: Publications Sales, British Museum (Natural History), Cromwell Road, London SW7 5BD, England.

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

ISSN 0007-1498

Zoology series
Vol 34 No 1 pp 1-64

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London SW7 5BD

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The anatomy and relationships of the cyprinid fish *Luciobrama macrocephalus* (Lacepède)

G. J. Howes
Department of Zoology, British Museum (Natural History), Cromwell Road, London SW7 5BD

Contents

Synopsis

The osteology and cranial myology of the long-headed cyprinid fish, *Luciobrama macrocephalus*, is described and aspects of its cranial functional morphology are considered. On the basis of shared derived characters the closest relatives of *Luciobrama* are identified as *Aspiolucius*, *Pseudaspius*, *Aspius* and *Elopichthys* which together form a monophyletic assemblage termed the aspinine group. It is suggested that this group is related to an as yet unidentified monophyletic aggregate of the 'Leuciscinae'. The osteological characters of many other cyprinid genera are compared and commented upon in the light of their usefulness as indicators of relationship and in terms of function. The cranial myology of *Elopichthys bambusa* and *Barilius bola* is described and figured.

Introduction

Although the Cyprinoidei display a great degree of diversity in their morphology and trophic specializations, there appear to be fewer piscivorous taxa than amongst their presumed sister group of ostariophysans, the Characoidei. This is undoubtedly due, in part at least, to the fact that jaw teeth are lacking in cyprinoid fishes. On the other hand, a characteristic of cyprinoids is the protusile mechanism of the upper jaw and the correlated development of a suction method of feeding (see Alexander, 1964, 1966 & 1967). Because of this particular type of jaw mechanism, the evolution of pike-like piscivores, a habitus (of piscivore) so prevalent amongst the characoids and other teleost groups, has been severely limited. To my knowledge, only one such fish has evolved amongst the cyprinids, namely, *Elopichthys* (which is discussed in this paper). The reasons for the absence of this type of predatory facies, and those which account for the other types manifest in present day old-world cyprinid lineages, are presented on page 61.

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In a previous paper (Howes, 1976) I described, in part, the cranial anatomy of a piscivorous cyprinid, *Macrochirichthys macrochirus*. From this initial study my attention was drawn to other piscivorous cyprinids and in particular to *Luciobrama macrocephalus*. Because *Luciobrama* is so obviously specialized, it seemed that it might offer clues to the recognition of primitive and advanced character states in other groups of cyprinids. In order to detect these and to find the closest relatives of *Luciobrama* on the basis of shared specializations, comparisons have been made with a number of other cyprinid genera (see p. 25).

As pointed out later (p. 61) the classification of cyprinid fishes is in an unsatisfactory state and it would be futile and pretentious at this stage to offer any phylogenetic scheme for subfamilial classification. What has become clear during this study is that few of the presently recognized cyprinid subfamilies are monophyletic groups.

List of study material

Species	BMNH register number	Type of preparation and standard lengths (mm) of alcohol preserved specimens	Locality
Abramis brama	1864.4.2:12	Skeleton	Holland
Abramis brama	Unregistered	Skeleton	Unknown
Alburnus alburnus	Unregistered	Alizarins; 37, 40, 58	Thames
Aspidoparia morar	1872.4.17:81	92	Bengal
Aspiolucius esocinus (Types)	1897.7.5:31–32	244, 107	Amu-Daria
Aspiopsis merzbacheri (Type)	1914.3.2:1	166	Central Asia
Aspius aspius	Unregistered	Two skulls	Danube
Aspius aspius	1860.3.7:34	225	Danube
Aspius aspius	1976.4.1:1	110	Mures R.
Aspius vorax	1920.3.3:127–146	235	Basra
Aspius vorax	1874.4.28:30	Skeleton	Tigris R.
Barbus altianalis	Unregistered	Skeleton	Lake George
Barbus altianalis	Unregistered	142	Lake George
Barbus altus	1882.2.11:314	145	Thailand
Barbus argenteus	1907.6.29:217	Skeleton	Angola
Barbus aspilus	1909.4.29:14	Skeleton	Ja R.
Barbus barbus	Unregistered	Skeleton	England
Barbus barbus	1908.12.28:123	Skeleton	England
Barbus callensis	1869.1.29:4	Skeleton	Algeria
Barbus callipterus	1975.1.17:201–210	53	Togo
Barbus camptacanthus	Unregistered	Skeleton	W. Africa
Barbus canis	1864.8.23:24	Skeleton	Jordan
Barbus capensis	Unregistered	Skeleton	Burg R.
Barbus fritschii	1904.11.18:59	Skeleton	Morocco
Barbus gonionotus	1974.10.10:823–824	144	E. Java
Barbus guirali	1902.11.12:119	Skeleton	Kribi R.
Barbus harterti	1902.7.28:35	Skeleton	Morocco
Barbus harterti	1903.10.29:16	Skeleton	Morocco
Barbus holotaenia	1902.11.12:122	Skeleton	Kribi R.
Barbus intermedius	1902.12.13:291	Skeleton	Errer R.
Barbus kersteni	1961.12.1:156	Skeleton	Aswa R.
Barbus longiceps	Unregistered	Skeleton	Galilee
Barbus mariae	1936.12.22:35–39	370	Athi R.
Barbus nasus	1902.1.4:22	Skeleton	Morocco
Barbus natalensis	1862.8.28:8	Skeleton	Natal
Barbus orphoides	1974.10.10:865–872	90	Java
Barbus oxyrhynchus	1893.12.2:31	Skeleton	Thikathike R.

Species	BMNH register number	Type of preparation and standard lengths (mm) of alcohol preserved specimens	Locality
Barbus paludinosus	1902.1.4:72	Skeleton	Morocco
Barbus perince	1907.12.2:3745	Skeleton	Nile
Barbus progenys	1903.7.28:155	Skeleton	Cameroon
Barbus radiatus	1961.12.10239	Skeleton	Aswa R.
Barbus reinii	1903.10.29:10	Skeleton	Morocco
Barbus rocadasi	1911.6.1:26	Skeleton	Angola
Barbus sarana	1889.9.26:99–103	94	Deoli
Barbus setivemensis	1869.1.29:21	Skeleton	Unknown
Barbus somereni	1971.1.5:96–99	Alizarins; 76, 60	Ruimi R.
Barbus tor	1889.2.1:523	Skeleton	Assam
Barbus trimaculatus	1907.4.9:98	Skeleton	Transvaal
Barilius bendelisis	1889.10.29:37	Skeleton	Dehra Dun
Barilius bola	1889.2.1:1205	Skeleton	Assam
Barilius bola	1889.9.26:118–127	235	Deoli
Barilius bola	1867.5.12:20–22	135	Norar R.
Barilius gatensis	1889.2.1:1135–1139	107	Nilgherriss
Barilius loati	1907.12.2:1503–1512	132	Gondokoro
Barilius loati	1907.12.2.3748	Skeleton	Nile
Barilius microcephalus	1906.9.7:4	Skeleton	L. Malawi
Barilius microcephalus	1974.1.15:25–26	210	L. Malawi
Barilius moori	1974.3.19:1–5	102–137	L. Kivu
Barilius niloticus	Unregistered	Alizarins; 23·5–40	L. Rudolf
Barilius niloticus	1907.12.2:3764–3767	Skeletons	Nile
Barilius ornatus	1893.6.30:61–70	75–93	Shan States
Barilius ubangensis	1902.11.12:142–148	88	Kribi R.
Barilius ubangensis	1903.7.28:165	Skeleton	Kribi R.
Barynotus luteus	1874.4.28:23	Skeleton	Tigris R.
Catla catla	1908.12.28:122	Skeleton	Hooghly R.
Catostomus teres	1866.12.13:5	Skeleton	Montreal
Chela laubuca	1889.2.1:1356–1359	60	Madras
Chelaethiops sp.	Unregistered	Alizarins; 20·5–30·0	L. Rudolf
Chondrostoma nasus	1976.4.1:4–6	148	Romania
Chondrostoma polylepis	1885.1.29:30	Skeleton	Coruna
Ctenopharyngodon idellus	1888.5.15:25	Skeleton	Tchang
Culter brevicauda	1891.1.31:28	Skeleton	China
Cyprinus carpio	Unregistered	122	Lincolnshire
Cyprinus carpio	Unregistered	Skeleton	Unknown
Cyprinus carpio	Unregistered	Skeleton	Amoy
Cyprinus carpio	Unregistered	Skull	Unknown
Danio aequipinnatus	1894.5.21:56–60	72	Byingi
Elopichthys bambusa	1889.6.24:51	Skeleton	Kiu Kiang
Elopichthys bambusa	1936.10.19:20	Alizarin; 116	Tatung
Elopichthys bambusa	1936.10.19:13–19	185, 250	Tatung
Elopichthys bambusa	Unregistered	220	China
Erythroculter ilishaeformis	1936.10.19:31–34	176	Hankow
Erythroculter mongolicus	1889.6.24:57	Skeleton	Kiu Kiang
Esomus danricus	1863.12.8:108–114	85	Madras
Garra blandfordi	1902.12.13:420	Skeleton	Jerrer R.
Garra lamta	Unregistered	Skeleton	Unknown
Hemiculter leucisculus	1938.12.1:26	54	Chusan
Hemiculterella polylepis	1921.7.26:21–23	132	Yunnan Lake
Hypophthalmichthys molitrix	1895.5.31:22	Skeleton	China
Labeo bata	1889.2.1:206	Skeleton	Assam

Species	BMNH register number	Type of preparation and standard lengths (mm) of alcohol preserved specimens	Locality
Labeo coubie	1907.12.2:3744	Skeleton	Kosheh, Nubia
Labeo coubie	1911.3.31:21–29	Alizarin; 52	Aboina R.
Labeo chrysophekadion	1898.11.8:115	Alizarin; 63	Menam R.
Labeo cylindricus	1902.5.26:23	Skeleton	Tana
Labeo diplostomus	1889.2.1:163	Skeleton	Hardwar
Labeo macrostoma	1904.5.2:158–160	140	Angola
Labeo niloticus	1907.12.2:975–980	122	L. Menzaleh
Labeo rohita	1889.2.1:138–139	143	Calcutta
Labeo rohita	1858.8.15:50	Alizarin, 83	India
Labeo stoliczke	1891.11.30:286	Skeleton	Sittang R.
Leuciscus cephalus	1867.4.2:15	Skeleton	Holland
Leuciscus idus	1867.4.2:6	Skeleton	Holland
Luciobrama macrocephalus	1889.6.24:48	Skeleton	Kiu Kiang
Luciobrama macrocephalus	1928.4.24:15	273	Nanking
Luciobrama macrocephalus	1896.6.24:46	420	Kiu Kiang
Luciobrama macrocephalus	1888.5.15:31–32	458	Tchang
Luciosoma bleekeri	1898.11.8:114	Skeleton	Menam R.
Macrochirichthys macrochus	1898.11.8:121	Skeleton	Menam R.
Macrochirichthys macrochus	1898.4.2:243	212	Menam R.
Megalobrama bramula	1936.10.19:21	111	Hankow
Megalobrama macrops	Unregistered	Skeleton	Formosa
Myxocyprinus chinensis	1889.6.24:10	Skeleton	Kiu Kiang
Notropis hudsonius	1925.2.3:121–125	68	Mississippi R.
Ochetobius elongatus	1936.10.19:35–38	147	Tatung, China
Ochetobius elongatus	1889.6.8:56	330	Kiu Kiang
Opsariichthys uncirostris	1901.3.6:9	Skeleton	Ningpo
Opsariichthys uncirostris	1923.3.5:6–12	152	Seoul
Oreinus sinuatus	1889.2.1:64–72	177–205	Simla
Oreoleuciscus pewslowi	1975.1.17:259–265	118–178	Mongolia
Oreoleuciscus potanini	1891.10.7:26–27	174	Mongolia
Oxygaster anomalura	1881.3.21:3	195	Sarawak
Parabramis pekinensis	1936.10.19:22–23	125	Hankow
Parabramis pekinensis	1889.6.8:46–53	235	Kiu Kiang
Parapelecus argenteus	Unregistered	166	China
Pelecus cultratus	1879.11.14:36	Skeleton	Syr Darya
Pelecus cultratus	1966.2.22:1–2	174, 175	Romania
Phoxinus lagowskii	1974.8.6:21–30	81	Onon R. Mongolia
Phoxinus phoxinus	1967.12.18:1–13	66	Kysuka R.
Pseudaspius leptocephalus	1925.8.6:28	137	Amur R.
Pseudolaubuca sinensis	1889.6.24:61	Skeleton	Kiu Kiang
Pseudolaubuca sinensis	1889.6.24:59–60	195	Kiu Kiang
Pseudoxygaster gora	1934.10.7:54	137	Allahabad
Rasbora argyrotaenia	1974.10.10:1801–1805	50–79	Bali
Rutilus friesii	Unregistered	Skeleton	L. Derkus
Rutilus rutilus	Unregistered	Skeleton	England
Rutilus rutilus	Unregistered	Alizarins; 66, 76, 77	England
Salmostoma bacaila	1889.9.26:145–154	90, 107	Rajputana
Salmostoma sardinella	1891.11.30:374–383	85, 98	Sittang R.
Saurogobio dumerili	1889.6.24:21	Skeleton	Kiu Kiang
Scardinius erythropthalmus	1867.4.2:7	Skeleton	Holland
Schizothorax esocinus	1870.11.30:40	Skeleton	Kashmir
Schizothorax esocinus	1870.11.30:39	260	Kashmir
Schizothorax grahami	1969.4.15:118	184	Kuan Hsien

Species	BMNH register number	Type of preparation and standard lengths (mm) of alcohol preserved specimens	Locality
Semiplotus macclellandi	1889.2.1:869	Skeleton	Assam
Squaliobarbus curriculus	1889.6.8:34–38	138	Kiu Kiang
Squaliobarbus curriculus	1888.5.15:29	Skeleton	Tchang
Varicorhinus beso	1968.7.24:18–19	Alizarins; 80, 114	L. Tsana
Varicorhinus steindachneri	1910.11.28:158	Skeleton	Lucalla R.
Varicorhinus tanganicae	1906.9.6:11	Skeleton	L. Tanganyika
Zacco platypus	1865.5.2:30	Skeleton	China
Zacco platypus	Unregistered	80	Locality unknown
Zacco spilurus	1939.3.23:14–16	74	Kowloon
Zacco spilurus (Types)	1956.2.25:1–5	34·5–46	Hong Kong
Zacco temmincki	1905.6.7:61–65	150	Japan

In addition to being dissected, all the alcohol preserved specimens were radiographed.

Abbreviations used in text figures

Skeletal elements

AA	Anguloarticular
AHY	Anterohyal
APTE	Autopterotic
BB 1–4	Basibranchials
BO	Basioccipital
BSR	Branchiostegal rays
C 1–5	Ceratobranchials
CIM	Cranial intermuscular bones
CL	Cleithrum
CLA	Claustrum
COR	Coracoid
D	Dentary
DHY	Dorsohyal
DPT	Dermopterotic
DSP	Dermosphenotic
E	Ethmoid
ECT	Ectopterygoid
ENT	Entopterygoid
EP	Epural
EPI 1–4	Epibranchials
EPO	Epioccipital
ES	Extrascapular
EX	Exoccipital
F	Frontal
H	Hyomandibula
HB 1–4	Hypobranchials
HF	Hyomandibular fossa
HY 1–6	Hypurals
IC	Intercalar
IF	Infrapharyngobranchial
INC	Intercalarium
IO	Infraorbitals
IOP	Interoperculum
KE	Kinethmoid
LE	Lateral ethmoid

LF	Lateral foramen
LP1	Lateral process of the 1st vertebra
LP2	Lateral process of the 2nd vertebra
MAX	Maxilla
MC	Mesocoracoid
MET	Metapterygoid
METP	Metapterygoid process
N	Nasal
NC	Neural complex of Weberian apparatus
NP2	Neural plate of 2nd vertebra
NP3	Neural plate of 3rd vertebra
OP	Operculum
OS	Orbitosphenoid
OSS	Os suspensorium
PA	Parietal
PAL	Palatine
PE	Preethmoid
PC	Postcleithrum
PH	Parhypural
PHY	Posterohyal
PMX	Premaxilla
PO	Preoperculum
PP	Pharyngeal process
PR4	Lateral process of 4th vertebra (modified pleural rib)
PRO	Prootic
PS	Parasphenoid
PTF	Posttemporal fossa
PTS	Pterosphenoid
PTT	Posttemporal
PU1+U1	Fused preural and ural centra
Q	Quadrate
RA	Retroarticular
SCA	Scaphium
SCP	Scapula
SE	Supraethmoid
SN	Supraneural
SO	Supraoccipital
SOR	Supraorbital
SP	Autosphenotic
STF	Subtemporal fossa
SUB	Suboperculum
SY	Symplectic
TR	Tripus
UN	Uroneural
V	Vomer
VHY	Ventrohyal

Muscles and soft tissues

A1, A2, A3	Divisions of the *adductor mandibulae* muscle
aap	*Adductor arcus palatini*
ah	*Adductor hyomandibulae*
ct	Connective tissue
do	*Dilatator operculi*
hh	*Hyohyoidei*
im	*Intermandibularis*
km lig	Kinethmoid–maxillary ligament
lap 1, 2	Divisions of the *levator arcus palatini*
lig	Ligament
lo	*Levator operculi*

lsa	Ligamentous sheet connecting supraneural to supraoccipital
lsb	Ligamentous sheet connecting neural complex to supraoccipital
obv 1–3	*Obliqui ventrales*
pce	*Pharyngoclavicularis externus*
pci	*Pharyngoclavicularis internus*
ph	*Protractor hyoidei*
rv 1–3	*Recti ventrales*
sb	Swimbladder
sth	*Sternohyoideus*
tf	Tendinous fascia of *adductor mandibulae* A3
tlap	Ventral tendon of *levator arcus palatini*
tv	*Transversus*

Luciobrama macrocephalus (Lacepède)

(Fig. 1)

Synodus macrocephalus Lacepède, 1803, *Hist. Nat. Poiss.* **5** : 322, pl. IX, fig. 1 (described from a Chinese drawing).

Luciobrama typus Bleeker, 1870, *Versl. Meded. K. Akad. wet. Amst.* (2) **4** : 252 (Yangtse-Kiang).

Luciobrama macrocephalus: Bleeker, 1873, *Ned. Tijdschr. Dierk* 4 : 89 (re-description).

Luciobrama is a monotypic genus (see p. 60) of east Asian and Chinese piscivorous cyprinids (see Nichols, 1925 & 1943 for a general account of this habit in the cyprinids). Stomach contents that I have examined have revealed the remains of small (*ca* 80–100 mm SL) cyprinid fishes. Specimens of *Luciobrama macrocephalus* grow to large size; Kimura (1934) records total lengths of over 700 mm and weights of 1000 g.

The external morphology of this fish has been described adequately by Bleeker (1873), Rendahl (1928), Kimura (1934) and Lin (1935). Kimura (*op. cit.*) also cited all references to the species up to that date. Since then the following accounts have been published. Chu (1935) gave an account of scale morphology and described the pharyngeal bones and teeth; Nichols (1943) and Wu (1964) both gave descriptions and noted the distribution of the species. It is unnecessary to repeat the detailed descriptions of external characters given by these authors, save to note the absence of barbels, the ellipsoid shape of the orbit and the small scales (up to 155 in the lateral line). Nuptial tubercles have not been detected in any specimens examined, but have been reported as occurring in this species (see review by Wiley & Collette, 1970).

Osteology

Circumorbital series (Fig. 2)

The first *infraorbital* (lachrymal) is an almost square plate bearing 12 pores of the lateralis canal along its ventral border.

The second infraorbital is very narrow and borders the entire ventral margin of the orbit. It is joined to the third just below the posterior border of the eye.

The third infraorbital is lamellate, the lateralis canal bearing 6–7 pores. It is an elongate bone extending in an almost horizontal plane to a point well beyond the posterior margin of the eye before joining the fourth infraorbital.

The fourth infraorbital is reduced to the canal tube. It diverges from the third at an angle of about 45° across the postorbital part of the head.

The fifth is minute and is sometimes fragmented. It consists of only the canal tube.

(See page 26 for further discussion of these bones.)

The *supraorbital* (SOR, Figs 3 & 5) is large being bordered anteriorly by the lateral ethmoid and latero-posteriorly by the frontals.

Ethmo-vomerine region

The *kinethmoid* (KE, Fig. 7) is a short columnar bone, the dorsal surface bears a wedge-shaped groove and the ventral surface is rounded. It is connected by two ventral ligaments to the heads of the vomer and by laterally extending ligaments to the maxillary ascending processes.

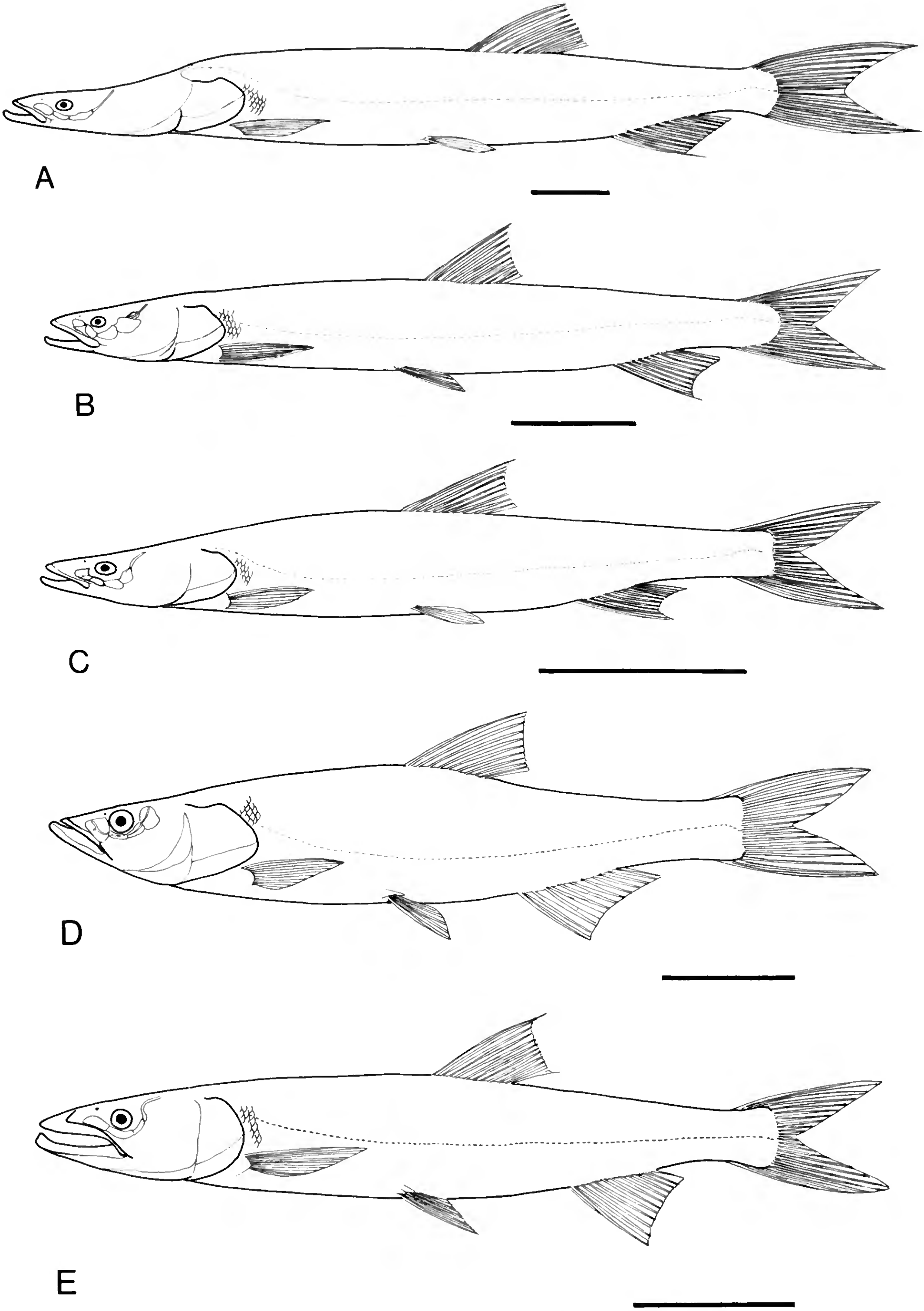

Fig. 1 Outline drawings of: A. *Luciobrama macrocephalus*, B. *Aspiolucius esocinus*, C. *Pseudaspius leptocephalus*, D. *Aspius vorax*, E. *Elopichthys bambusa*. Scale = 5 cm.

The *supraethmoid* (SE, Figs 3, 4 & 5) is narrow with thin wing-like extensions posteriorly. Laterally the bone is bordered by the nasals and posteriorly by the frontals. The anterior border is rounded with a median notch.

The *ethmoid* (E, Figs 3 & 4) underlies the supraethmoid and overlies the vomer. It is bifurcated anteriorly, the two short arms provide the medial surfaces of the fossae for the preethmoids. Antero-dorsally there is a small foramen separating the bone from the supraethmoid. Posteriorly there is a wide synchondrosis with the lateral ethmoid.

The *lateral ethmoids* (including fused prefrontals; LE, Figs 3, 4 & 5) extend to protrude well beyond the lateral margins of the cranium. Basally each bone is triangular, supporting anteriorly a thick, curved ascending wall which connects the supraorbital. Posteriorly it extends as a thin wall meeting the orbitosphenoid in a synchondrosis. Dorsally, each bone is overlain by its corresponding frontal; ventrally, contact is made with the parasphenoid. Medially, the lateral ethmoids are in contact.

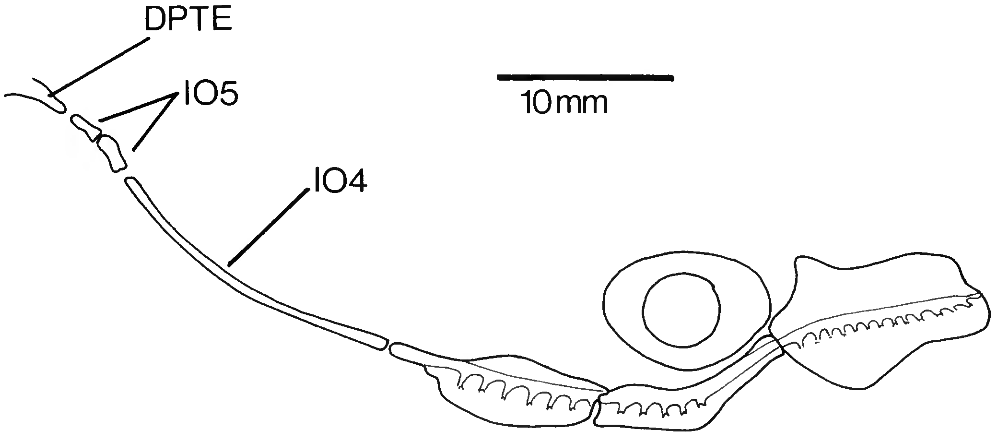

Fig. 2 *Luciobrama macrocephalus*, infraorbital series.

The *vomer* (V, Figs 4 & 5) is a thin, lamellate bone extending posteriorly to a point well beyond the centre of the orbit. It is overlain by the parasphenoid and the ethmoid. Anteriorly it flares into the shape of a double club, the arms of which provide the lower surfaces of the preethmoid fossae.

The *preethmoids* (PE, Figs 3 & 4) are irregular ovate bones articulating with the ethmoid and the vomer. They are covered by the cartilage upon which rest the autopalatines.

The *nasals* (N, Figs 3 & 4) border the supraethmoid anteriorly and the frontals posteriorly. They are in the form of long tubes bearing 9–10 pores. Laterally each nasal is attached by skin to the first infraorbital.

The *frontals* (F, Figs 3, 4, 5 & 6) are extremely long and narrow, sutured for their entire length. Anteriorly their lateral borders slope downward to contact the supraorbitals. The canal tube runs along the lateral edge of each bone from the anterior edge of the pterotic in an almost straight line to the nasal. It bears 22 pores.

Orbital region

The *orbitosphenoids* (OS, Figs 4, 5 & 6) are greatly depressed bones 'sandwiched' between the frontals and the parasphenoid. Contact with the parasphenoid is along a third of that bone's orbital length. Anteriorly, the orbitosphenoids join the lateral ethmoids by a wide synchondrosis. Dorso-posteriorly, each bone extends as a long arm which diverges slightly from its fellow. These arms contact similar anterior extensions of the pterosphenoid. Posteriorly, the lower part of each orbitosphenoid is directed medially and meets its partner in the midline to form a narrow, wedge-shaped septum. (This is not the 'orbitosphenoid septum' referred to later in this

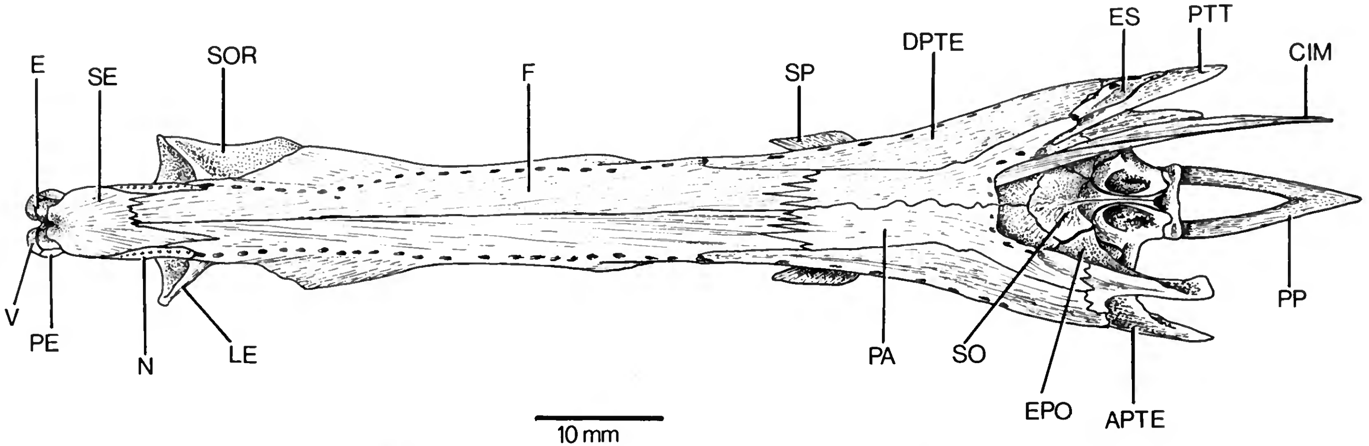

Fig. 3 *Luciobrama macrocephalus*, neurocranium, dorsal view.
Some bones are removed from the left-hand side of the skull to show the underlying elements.

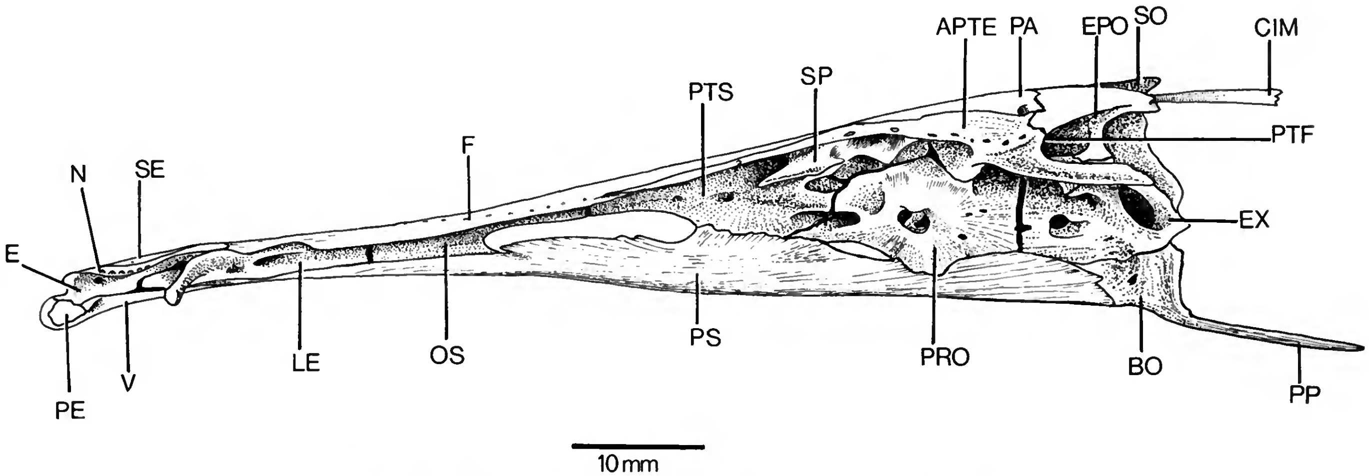

Fig. 4 *Luciobrama macrocephalus*, neurocranium, lateral view.

paper as occurring in other cyprinids (p. 32), in those cases the septum extends from the ventral surfaces of the bones.)

The *pterosphenoids* (PTS, Figs 4, 5 & 6) are extensive, forming almost half the length of the orbito-otic region. Each bone is produced into an anterior process along the ventral surface of the frontal which contacts the corresponding posterior extension from the orbitosphenoid. The posterior dorsal margin is sutured to the autosphenotic. Latero-posteriorly the bone extends as a wide branch which forms the anterior wall of the leading hyomandibular fossa. Below this the pterosphenoid border is concave, this concavity forming part of the border of the trigemino-facialis foramen; the lateral surface at this point is deeply grooved to allow for the nerve pathways. Ventrally, there is an extensive connection with the wide ascending wing of the parasphenoid. The pterosphenoids are narrowly separated from each other leaving only a small optic foramen.

The *parasphenoid* (PS, Figs 4, 5 & 6) is wide anteriorly, the ventral surface below the lateral ethmoids is flat but becomes concave below the orbitosphenoids; beyond this point the bone narrows and deepens, the sides becoming thin walls which rise gradually until, as wide ascending processes, they contact the ventral margins of the pterosphenoids. The posterior border of the ascending process is separated from the pterosphenoid and prootic by an extensive hypophysial foramen. The dorso-posterior part of the parasphenoid is first overlapped by, and then runs abutted with, the prootic, followed by the anterior part of the exoccipital. The posterior border of the parasphenoid is sutured against the basioccipital. The ventral surface of the parasphenoid is rounded below the ascending processes, flaring slightly and becoming flattened below the prootic with a slight medial groove developing posteriorly. This groove leads into the aortic foramen of the basioccipital. The posterior part of the parasphenoid forms the floor and walls of the myodome.

Otic region

The *prootics* (PRO, Figs 4, 5 & 6) are large, forming long dorsal connections with the autosphenotics. Anteriorly, the border of each prootic with the parasphenoid is interrupted by the large trigemino-facialis foramen. Postero-ventrally, part of the prootic extends to overlap the parasphenoid. Anteriorly, each bone is in the form of a wedge-shaped arm which inserts partly between the pterosphenoid and the parasphenoid; dorso-posteriorly, it contacts the pterotic. The area between the sphenotic and pterotic is bevelled and forms part of the hyomandibular facet. Postero-medially, the prootic forms the lower medial wall of the subtemporal fossa. Its posterior border is sutured to the epioccipital.

A posterior myodome is present (ascertained by radiographs) and appears similar to that described for *Aspius* by Oliva and Skořepa (1968).

The *pterotics* (APTE, Figs 3, 4, 5, 6 & 32) dorsally border the parietals and the frontals extending forward as narrow triangles overlying the autosphenotics. The outer margin of each bone bears the canal which contains 13 pores. Posteriorly, the pterotic is recessed as a facet for the hyomandibula (a continuation of that feature on the autosphenotic and prootic). Ventrolaterally, the surface is arched, the posterior foot of the arch joining the epioccipital and forming the outer roof of the subtemporal fossa (STF, Fig. 5). The lateral border continues posteriorly as a thick spine. Medially, the pterotic meets the epioccipital to form the high vaulted subtemporal fossa.

The pterotic also contributes substantially to the formation of the posttemporal fossa (PTF, Figs 4 & 32) where it provides the lateral wall, part of the roof and the floor.

The *basioccipitals* (BO, Figs. 4, 5 & 32) are sutured to the parasphenoid anteriorly and to the epioccipitals dorsally. Medially they extend forward between the prootics and form part of the roof of the posterior myodome. There is no obvious bulla acoustica lagenaris.

From the ventral surface of each bone there extends posteriorly two processes which fuse distally to form the pharyngeal process (PP, Figs 3, 4 & 5). The 'masticatory plate' is virtually absent.

The *supraoccipital* (SO, Figs 3, 4 & 32) is bordered anteriorly by the parietals and laterally by the epioccipitals, the whole area forming an almost flat platform. Medially, the bone rises as a low ridge which extends posteriorly as a thin plate-like process. This supraoccipital process barely rises above the highest level of the skull roof.

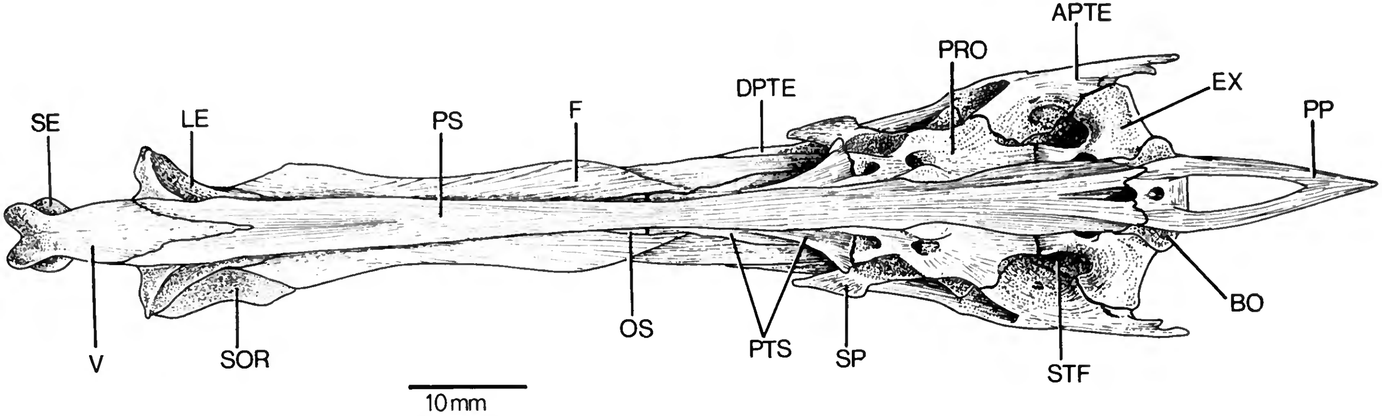

Fig. 5 *Luciobrama macrocephalus*, neurocranium, ventral view.

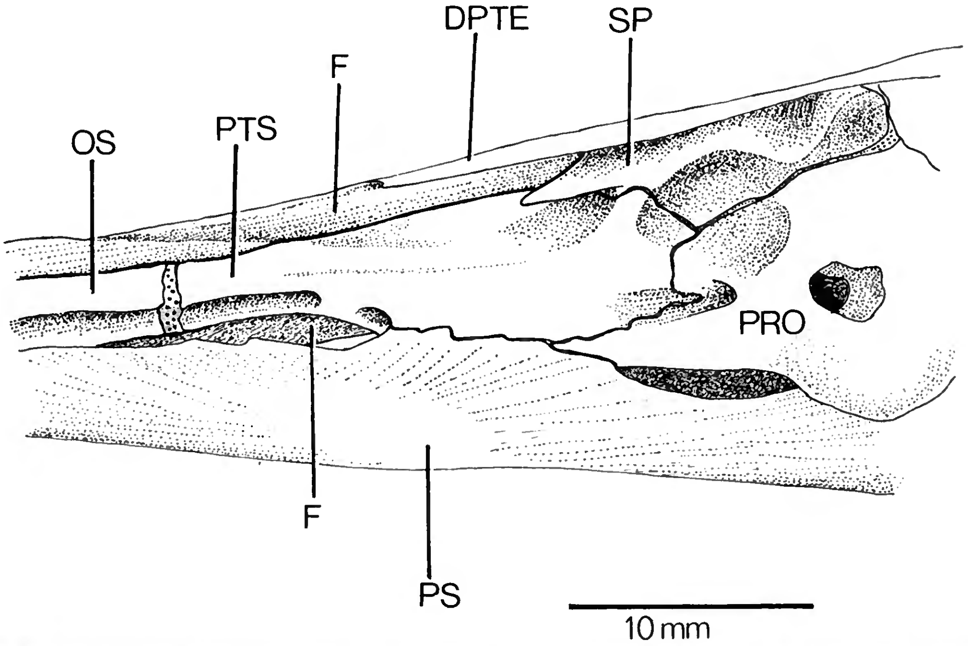

Fig. 6 *Luciobrama macrocephalus*, neurocranium, ventro-lateral aspect of the orbito-otic region.

The *intercalar* is absent.

The *parietals* (PA, Figs 3 & 4) are elongate and join the frontals anteriorly. Laterally they are bordered, for part of their length, by the pterotics. Posteriorly, the parietals are deeply recessed, the roof of this recess providing insertion for the epaxial musculature, and the lateral border origin for the cranial intermuscular bones.

The parietals gently slope posteriorly to join the supraoccipital. The presence of the transverse occipital sensory canal is indicated by four pores on the surface of each bone.

The *posttemporals* (PTT, Fig 3). Each is a paddle-shaped bone, the stem of which extends dorso-anteriorly at an angle of 45° to rest along the epioccipital. The lamellate 'paddle' of the bone is joined to the supracleithrum. Ventrally, between the posttemporal and the pterotic border, there lies a long narrow *extrascapular* (ES, Fig 3).

The *autosphenotics* (SP, Figs 3, 4, 5 & 6) are long depressed bones overlain by the pterotics. The anterior part of each sphenotic projects laterally from beneath the cranial border as a sloping shelf. Posteriorly, the dorsal surface of the bone presents two undulations which form a lateral cavity roofed by the pterotic. From this cavity arises the *dilatator operculi* muscle. The undulations of the bone also provide, ventro-laterally, the roofs of two deep facets for the hyomandibular condyles. The posterior facet is continued onto the pterotic and ventrally onto the prootic.

No *dermosphenotic* can be identified. (See page 28 for comments on this bone.)

The *exoccipitals* (EX, Figs 3, 4, 5 & 32) are seen laterally as almost square bones. Dorso-medially, each bone is in contact with the epioccipital and forms the inner surface of the subtemporal fossa. Posteriorly, the arm containing the semi-circular canal is compressed and is directed laterally to contact the descending arch of the pterotic. Medially, the exoccipital is curved around to form the border of the lateral occipital foramen. Its dorsal border is sutured to the epioccipital and supraoccipital. Ventrally, it is bordered by the epioccipital and the basioccipital. The glossopharyngeal foramen is situated in the centre of the bone's lateral face.

The *epioccipitals* (= epiotic; see Patterson, 1975) (EPO, Figs 3, 4 & 32). The lateral face of each bone forms the medial wall of the posttemporal fossa. Dorso-medially, it is suturally united with the supraoccipital and together the bones form a platform posterior to the parietal. Ventrally, the epioccipital contacts the exoccipital and prootic. Dorso-laterally, it joins the pterotic and forms the roof and the upper part of the lateral wall of the subtemporal fossa.

The upper jaw (Fig. 7)

Each *premaxilla* (PMX) is in the form of a slender rod with a large anterior ascending process which is ligamentously connected to the kinethmoid. Each premaxilla is curved gently mesad to meet its counterpart, to which it is attached by a thick band of ligamentous tissue.

Each *maxilla* (MAX) is a large triangular bone. Anteriorly, it is produced into a large knob-like process which fits into a concavity on the premaxilla. Ventrally there is a process which runs mesad below the premaxilla to contact its fellow from the opposite side.

The dorsal border of the maxilla is expanded into a large plate-like process (termed here the palatine process). Between this and the anterior ascending process runs the ligament joining the maxilla and the palatine. The posterior margin of the bone is concave, ventrally it contacts the premaxilla.

The lower jaw (Fig. 8)

Each *dentary* (D) is a long canoe-shaped bone curving gently mesad to join its partner. The coronoid process is deep with a narrow convex border. Ventrally the mandibular lateral line canal bears 20 pores.

The *anguloarticular* (AA) is a large bone sloping gently dorsad to meet the coronoid process of the dentary. The articular surface for the quadrate is almost rectangular. The anguloarticular bears 5 pores of the mandibular canal.

The *retroarticular* (RA) is a very thin wedge of bone lying ventrally.

Hyopalatine arch (Fig. 9)

The *hyomandibula* (H) is broad and flat dorsally, the border shaped into two broad articular

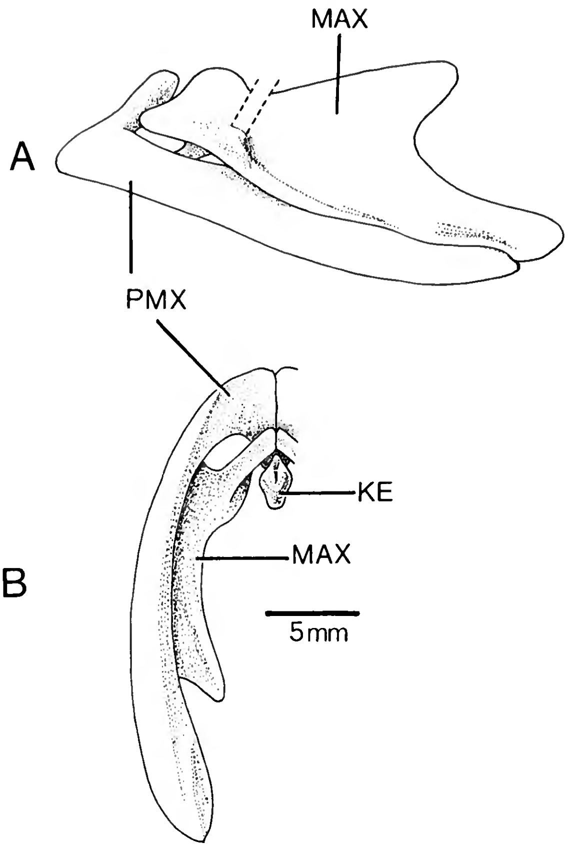

Fig. 7 *Luciobrama macrocephalus*, upper jaw. A. Lateral view. B. Ventral view.

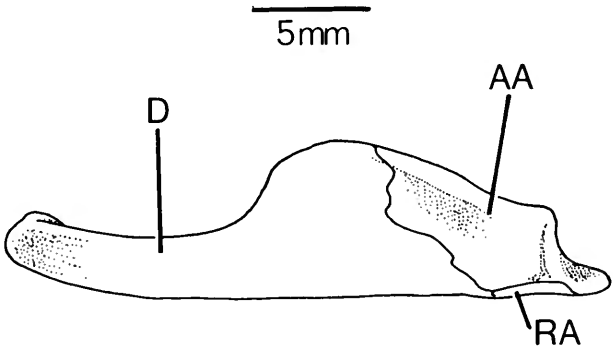

Fig. 8 *Luciobrama macrocephalus*, lower jaw, lateral view.

heads. The anterior of these heads fits into the facet formed by the sphenotic, posterior part of the pterosphenoid and the dorsal margin of the prootic. The posterior head fits into the facet formed by the sphenotic, the prootic and the pterotic.

The lower limb, or shaft, is long and broad, directed at an angle of 45° to the vertical.

The anterior border of the hyomandibula is concave, the posterior is produced into a small condyle which articulates with the operculum. The lateral face bears a weak depression.

The *quadrate* (Q) is a low elongate bone which is produced ventro-posteriorly into a triangular extension covered partially by the symplectic and preoperculum. The dorsal margin is horizontal and extends anteriorly to above the anguloarticular. Just posterior to the articulation with the anguloarticular is a large foramen. There appears to be no nerve or vessel of any kind passing through this aperture but only fibres of the connective tissue which line the floor of the branchial cavity.

There is a wide synchondrosis between the posterior border of the quadrate and metapterygoid.

The *symplectic* (SY) is a lanceolate bone and lies between the metapterygoid and the quadrate. The lateral surface bears a ridge from which originate some of the fibres of the *adductor mandibulae* muscle complex (see p. 21).

The *autopalatine* (PAL) is a thick rod-shaped element, forked anteriorly. The lateral fork provides the insertion for the maxillary ligament, the mesial process contacts the cartilage overlying the preethmoid.

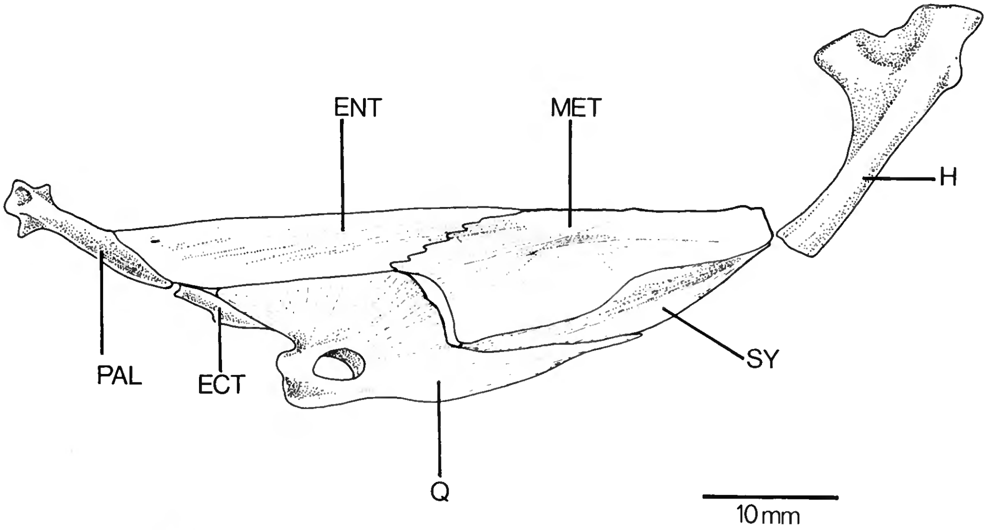

Fig. 9 *Luciobrama macrocephalus*, hyopalatine arch, lateral view.

No *dermopalatine is present.*

The *ectopterygoid* (ECT) is a thin gutter-like bone applied to the anterior border of the quadrate. Dorsally it contacts the entopterygoid. It is separated from the palatine by a wide area of cartilage.

The *entopterygoid* (ENT) is an extensive sheet of bone, the dorsal border of which is horizontal. Laterally it is overlapped by the quadrate and metapterygoid.

The *metapterygoid* (MET) overlaps the entopterygoid and ventrally partially overlaps the symplectic. The dorsal border is horizontal. The bone slopes mesad to the parasphenoid and a ridge is produced along the lateral face of the bone at the base of the slope.

The opercular series (Fig. 10)

The *preoperculum* (PO) is a large, broadly crescentic bone overlapping the anterior edge of the operculum and most of the interoperculum. There are 10 pores of the opercular–mandibular lateral line canal visible along its lower margin with 3 or 4 along the posterior border.

The *interoperculum* (IOP) is shaped like a broad knife blade. Its posterior border is rounded and overlaps the anterior margin of the suboperculum.

The *suboperculum* (SOP) is a narrow curved sheet of bone, its dorsal edge, apart from the posterior point, covered by the operculum.

The *operculum* (OP) is extensive. The dorsal margin is long and concave and is produced anteriorly into a long finger-like process to which is attached the *dilatator operculi* muscle. Mesially a thin strut, pierced ventro-anteriorly by three large foramina, extends caudal from the articular facet.

Hyoid arch (Fig. 11A)

The *interhyal* (IH) is a short flat element with a concave posterior border. The head bears a dorsally extended projection from which runs a ligament which passes between the symplectic and the shaft of the hyomandibula to insert on the ventro-posterior tip of the metapterygoid. This ligament is overlain by the connective tissue extending between the symplectic and the hyomandibula.

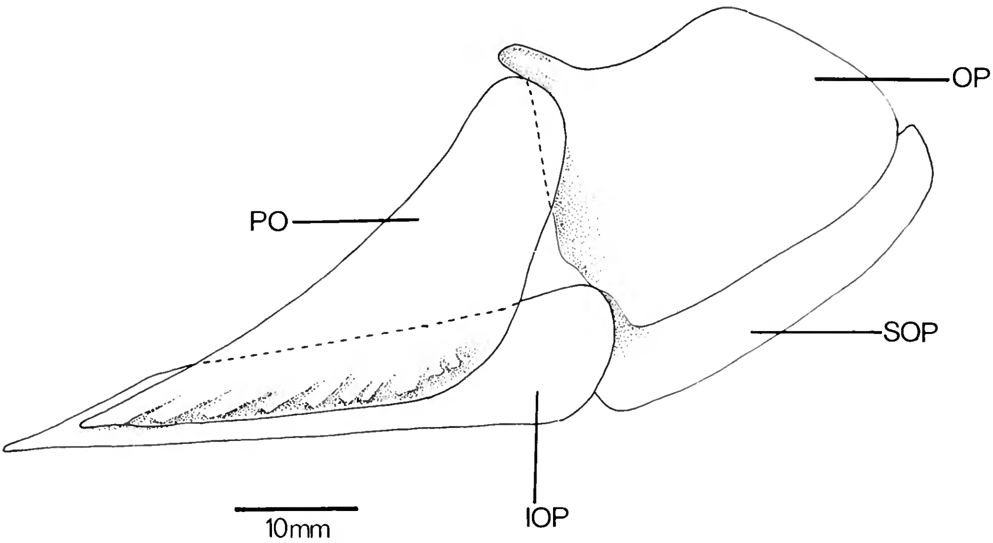

Fig. 10 *Luciobrama macrocephalus*, opercular series, lateral view.

Another ligament runs from the anterior edge of the interhyal to join the medial face of the preoperculum.

The *posterohyal* (PHY) is a thick triangular bone bearing one branchiostegal ray.

The *anterohyal* (AHY) is a thin-waisted element articulating anteriorly with the dorso- and ventrohyals. It bears two branchiostegal rays.

The *dorsohyal* (DHY) is small, and is in contact with the first basibranchial (basihyal); the *ventrohyal* (VHY) is thick, its lower surface bearing a fossa for the ligament connecting the urohyal. Its medial surface is joined to that of its opposite member by a ligament.

The *urohyal* (Fig. 11B) is extremely elongate, the ventral surface is flat, but bears a slight ridge posteriorly. A shallow vertical plate runs along the midline of the dorsal surface. Anteriorly the bone narrows into a neck from which arise two heads; these are connected to the ventrohyal by thick ligaments.

The *branchiostegal rays* (BSR 1, 2 & 3) are long lamellate bones, the first of which is thin and articulates with the ventral medial surface of the anterohyal; the second is expanded proximally into an anteriorly directed process. Articulation is on the lateral face of the anterohyal. The third is also expanded proximally and articulates with the lateral face of the posterohyal.

The branchial arches (Fig. 12)

There are two ossified *infrapharyngobranchials* (IF 2, 3), recognized as infrapharyngobranchials 2 and 3 (see Nelson, 1969). Cartilaginous elements are present between the first epibranchial and the second infrapharyngobranchial and between the fourth epibranchial and third infra pharyngobranchial. These elements most probably represent the 1st and 4th infrapharyngobranchials.

The *epibranchials* (EPI 1–4) number four. The first is wide with a blade-like posterior border overlapping the second. The third epibranchial bears a dorsal process overlapping the fourth.

The *certaobranchials* number the usual five (C 1–5). The first bears 6 long finger-like gill rakers; the second 9; the third 10 plus 6 along the medial surface; the fourth 7 plus 7. The fifth is the lower pharyngeal bone which bears a single row of 4–5 curved teeth. The bone is very thin and anteriorly elongate, curving gently mesad to ligamentously join its fellow. The pharyngeal bone and teeth have been described and figure by Chu (1935).

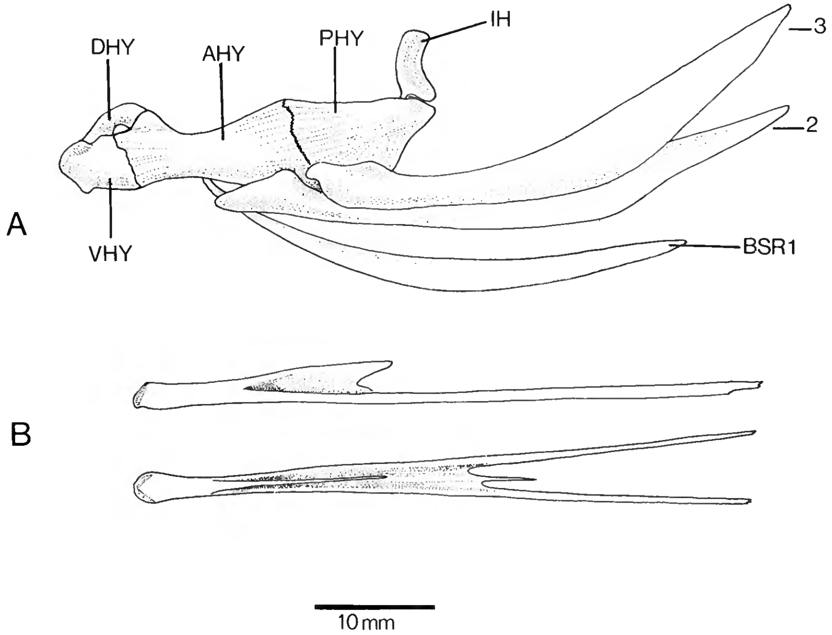

Fig. 11 *Luciobrama macrocephalus.* A. Hyoid arch, lateral view. B. Urohyal seen in (top) lateral and (bottom) dorsal views.

There are four *basibranchials* (BB 1–4). The first (basihyal) is a long thin rod in contact with the hypohyals. The second is flat and in contact with the 1st *hypobranchials* (HB1); the third is long, narrow-waisted and in contact with the 2nd hypobranchials; the fourth is thin and is curved ventrad.

Weberian apparatus and swimbladder (Fig. 13).

The 1st vertebra is a thin disc bearing lateral processes (LP1) from which a ligament extends to contact the medial face of the cleithra.

The second and third centra are fused dorsally, but ventrally they are clearly separated. The 2nd vertebra bears thick lateral processes which are inclined upward (LP2). The 3rd vertebra contains a lateral fossa for the articulation of the tripus. Extending dorsad from the second and third centra is the third neural plate (NP3). The dorsal border is triangular. On the anterior margin lies the second neural plate (NP2) which extends forward to contact the supraoccipital. Lying below the anterolateral border of the second neural plate is the *claustrum* (CLA) which is a cartilaginous cup-shaped structure. A ligament runs from each claustrum to insert upon the basioccipital.

Along the posterior margin of the third neural plate there rests part of the large neural complex (NC); see below.

The 4th vertebra bears stout lateral processes which become ventrally directed (pleural ribs, PR4). The medial surface of each extends inwards as an *os suspensorium* (OSS), a thin plate curving anteriorly so that its tip underlies the posterior edge of the 3rd vertebra. There is a short neural spine on the 4th vertebra, the dorso-anterior surface of the spine supports the posterior half of the neural complex.

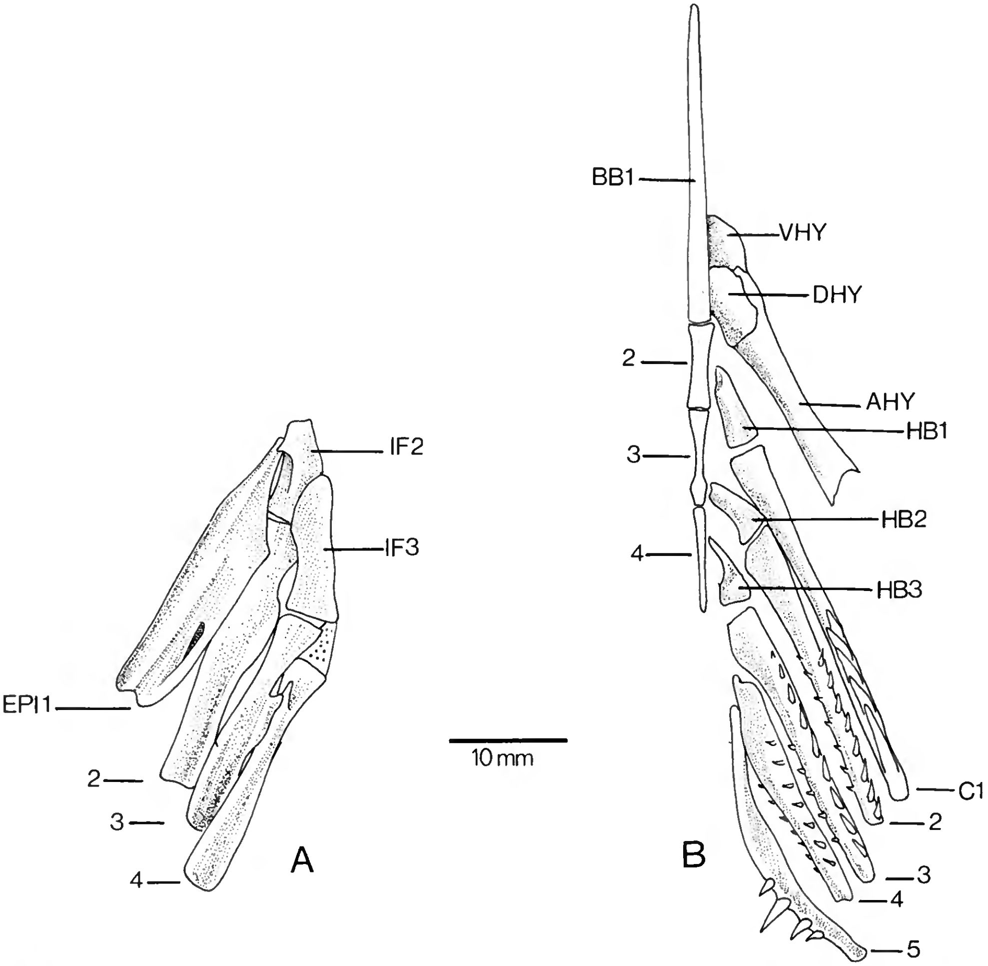

Fig. 12 *Luciobrama macrocephalus*, branchial arches. A. Upper arch, left side, dorsal view. B. Lower arch, right side and basibranchials, dorsal view.

The *scaphium* (SCA) is rounded and capped dorsally by the claustrum. Ventrally it articulates with a groove along the top of the first centrum and from a depression on its posterior face a ligament runs to connect this bone with the intercalarium.

The *intercalarium* (INC) articulates in a fossa situated below the third neural plate which overlaps the second vertebra. A ligament (a continuation of that extending from the scaphium) attaches ventrally and continues to insert upon the leading edge of the tripus.

The *tripus* (TR) is a thin triangular plate articulating with the third vertebra. Anteriorly it contacts the lateral process of the second vertebra (LP2); posteriorly its tip connects with the medial face of the process emanating from the 4th vertebra (PR4).

The *neural complex* (NC) which lies across the 3rd and 4th vertebrae is an irregularly shaped bone. The dorsal surface is grooved and posteriorly a supraneural plate (possibly two fused supraneurals) slides into the groove. This plate is connected to the supraoccipital by a ligamentous sheet (lsa) which runs across the anterior part of the grooved upper margin of the neural complex. The anterior border of the neural complex is concave and a separate ligamentous sheet (lsb) connects this to the supraoccipital.

The *swimbladder* (sb) is an elongate cigar-shaped structure extending posteriorly to above the first anal fin ray. It is bipartite.

The pneumatic duct is very long and runs along the dorsal surface of the gut from its exit at the anterior of the alimentary canal to its entry into the posterior division of the swimbladder.

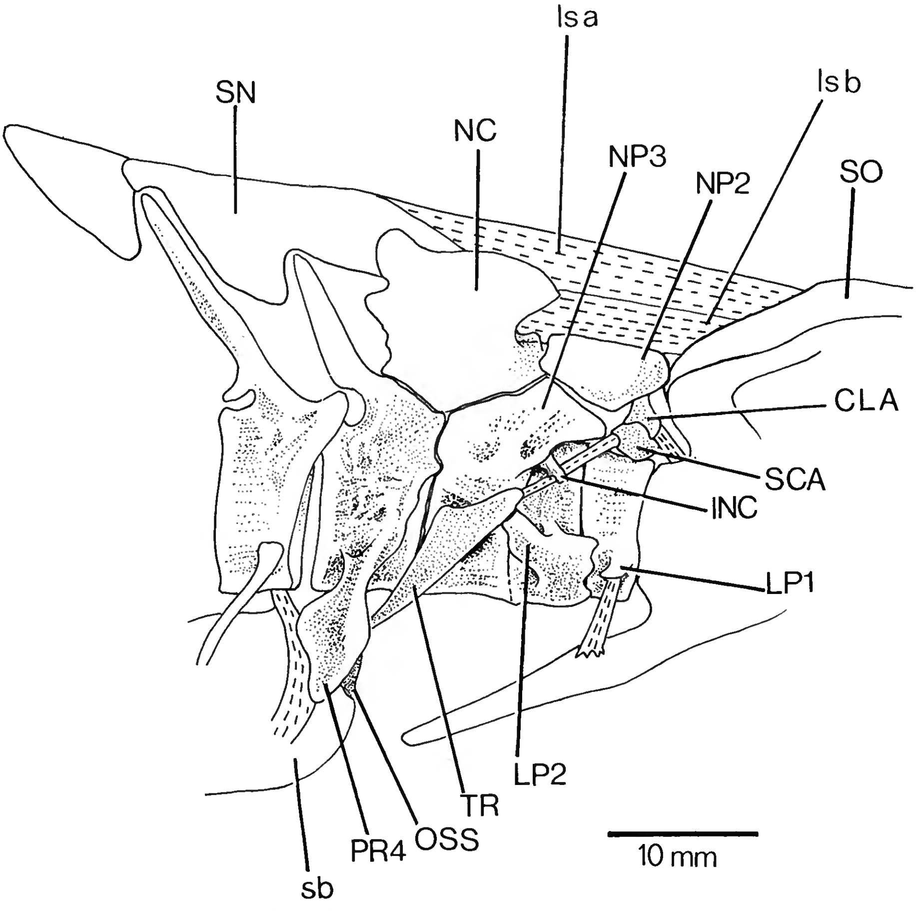

Fig. 13 *Luciobrama macrocephalus*, Weberian apparatus, lateral view.

Pectoral girdle (Fig. 14A)

The *cleithrum* (CL). The horizontal limb of the cleithrum is narrow and bifurcated anteriorly. The tip of the limb lies on a perpendicular with the posterior margin of the prootic. The ascending limb has a slightly curved hind margin; it is aligned almost vertically.

The *postcleithrum* (PC) is a short spine-like process.

The *supracleithrum* (SCL) is a small blunted crescentic element attached to the upper third of the cleithral limb. It attaches to the inner face of the posttemporal.

The *coracoid* (COR) is a narrow, flat bone posteriorly joined to the cleithrum along a flat lateral extension; anteriorly, there is a narrow area of attachment along the leading edge of the cleithrum. The coracoids diverge from each other and meet only along the anterior margin.

The *mesocoracoid* (MC) is a wide bridge of bone extending between the cleithrum and the coracoid.

The *scapula* (SCP) lies against the medial face of the cleithrum below the mesocoracoid. It joins the posterior border of the coracoid and provides an articular surface for the four plate-like *proximal radials.*

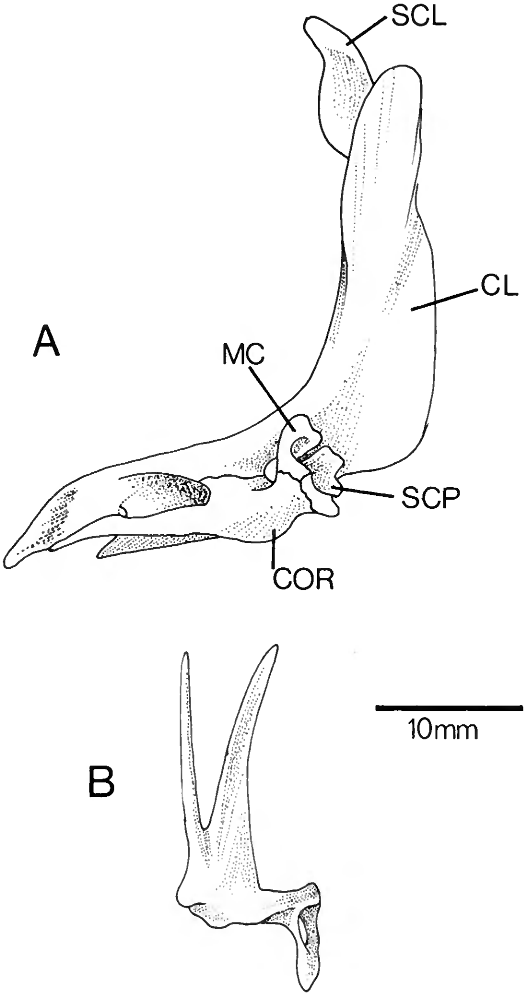

Fig. 14 *Luciobrama macrocephalus.* A. Pectoral girdle, lateral view. B. Pelvic girdle, left side, dorsal view.

Pelvic girdle (Fig. 14B)

The pelvic bones are deeply forked, the thin dagger-like arms narrowly diverging. The ischiac process is wide and is joined to its fellow along the apposed medial face.

Vertebral column

There is a total of 55 vertebrae (including the four forming the Weberian apparatus), comprising

30 precaudal (without a haemal spine), 20 caudal and the fused preural and first ural vertebrae. All the centra are of almost the same length.

There are 12 *supraneurals* lying between the neural spines of the 5th to 18th vertebrae. The first two supraneurals are expanded and contact the neural complex of the Weberian apparatus (see p. 18). The supraneurals become progressively thinner posteriorly; on a radiograph they are barely visible.

The *cranial intermuscular bones* (CIM, Figs 3 & 4) extend from the medial margin of the parietals and epioccipitals as thin rods which become lamellate and expand into 7 or 8 bones to lie above the Weberian apparatus.

The first of the *epipleurals* is associated with the 15th rib. They are exceedingly thin needle-like bones numbering 11–12. There are numerous *intermuscular bones* above the anal fin.

The first *pterygiophore* of the dorsal fin is expanded anteriorly. There are 9 dorsal and 11 anal pterygiophores. Two radials connect the pterygiophore with the fin ray (see p. 52).

Caudal fin skeleton (Fig. 15)

There are six hypurals (HY 1–6) of which the first is greatly expanded. The fused preural and ural centra (PU1 + U1) bear a knife-like neural spine. There is one large epural and a pair of small uroneurals (UN) above hypural 6. The parhypural (PH) bears only a slight hypurapophysis. The principal fin ray formula is I9 + 9I.

Cranial myology

Jaw and suspensorial muscles (Figs 16–19)

The postorbital region of *Luciobrama* is covered by thin skin, when this is removed there is exposed a large *adductor mandibulae* muscle. Two major divisions of this muscle can be distinguished, namely A1 and A2.

Adductor mandibulae A1 extends from the quadrate, symplectic and preoperculum. The anteroventral fibres run dorsad at an angle of 30°, those forming the dorsal border of the muscle run almost horizontally. Below the orbit the muscle is greatly thickened but becomes abruptly compressed prior to its insertion. The fibres insert upon a thick tendinous band which runs along the ventral border of the maxillary and is attached to that bone by connective tissue.

The maxilla has been described elsewhere (p. 13). A cartilaginous mass (car) fills the area bordered anteriorly by the concave dorsal edge of the maxilla, dorsally by the lateral ethmoid and medially by the dentary.

The large A2 extends from the lateral face of the preoperculum, the hyomandibula and the metapterygoid. The fibres running from the preoperculum and hyomandibula are orientated horizontally and form the lateral face of the muscle; those running from the metapterygoid are directed laterally at an angle of 40° to join the body of horizontal fibres. Anteriorly A2 is divided, each division inserting upon its own tendon. The tendon of the lateral division inserts upon the rim of the coronoid process of the dentary, that of the inner division on to the rim of the anguloarticular, just posterior to the outer tendon.

Adductor mandibulae Aw is absent. The medial face of the lower jaw is covered by a thick connective tissue which forms a cushion along the dorsal edge of the jaw (the lower lip), and at the articulation of the jaw is continuous with that tissue and skin covering the upper jaw.

The *levator arcus palatini* (lap) is an exceptionally well-developed muscle and to my knowledge is the most extensive described for any teleost although that of *Arapaima gigas* approaches this size (see Kershaw, 1976).

It originates from the ventral surface of the frontal, the pterotic and the sphenotic to insert upon the length of the entopterygoid, metapterygoid and on a sheet of thick connective tissue connecting the metapterygoid with the hyomandibula (ct, Fig. 17).

The ventral surface of the levator is bevelled to accommodate *adductor mandibulae* A2. The anterior border of the muscle forms the posterior border of the orbit.

When the outer layer of the muscle is removed (lap 1), two inner sections are revealed. The first (lap 2, Fig. 17) lies posteriorly and runs from a dorsal aponeurosis from which the *dilatator*

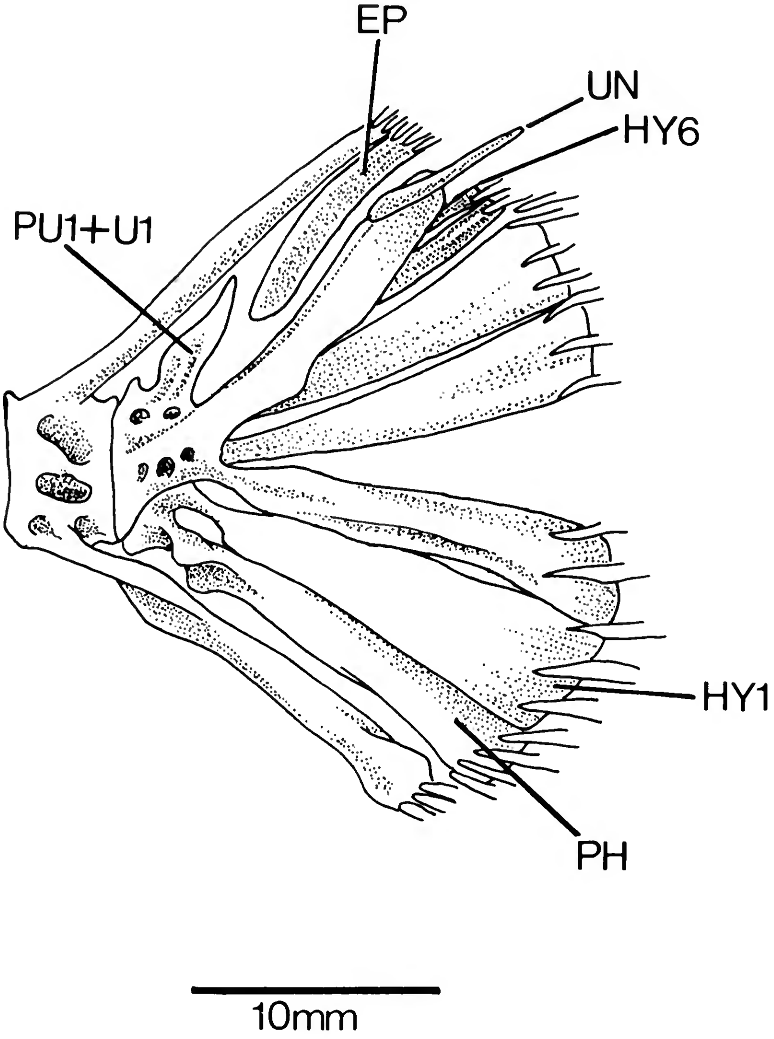

Fig. 15 *Luciobrama macrocephalus*, caudal fin skeleton, lateral view.

operculi also stems. The direction of its fibres is the same as that of the outer layer. Insertion is upon the lateral face of the hyomandibula.

The second element (ah, Fig. 17) lies against the pterosphenoid and parasphenoid. The fibres are orientated in the opposite direction to those of the other layers. Anteriorly, the muscle is bordered by a sheet of connective tissue which covers the lateral face of the pterosphenoid; posteriorly, it originates from the deep subtemporal fossa and inserts upon the medial face of the hyomandibula.

Ventral insertion of all the sections is along the medial dorsal edge of the ento- and metapterygoid.

The inner element is well differentiated from the rest of the *levator arcus palatini* and I interpret it as being the *adductor hyomandibulae* (which is also found in *Aspius* and some other genera; see p. 53).

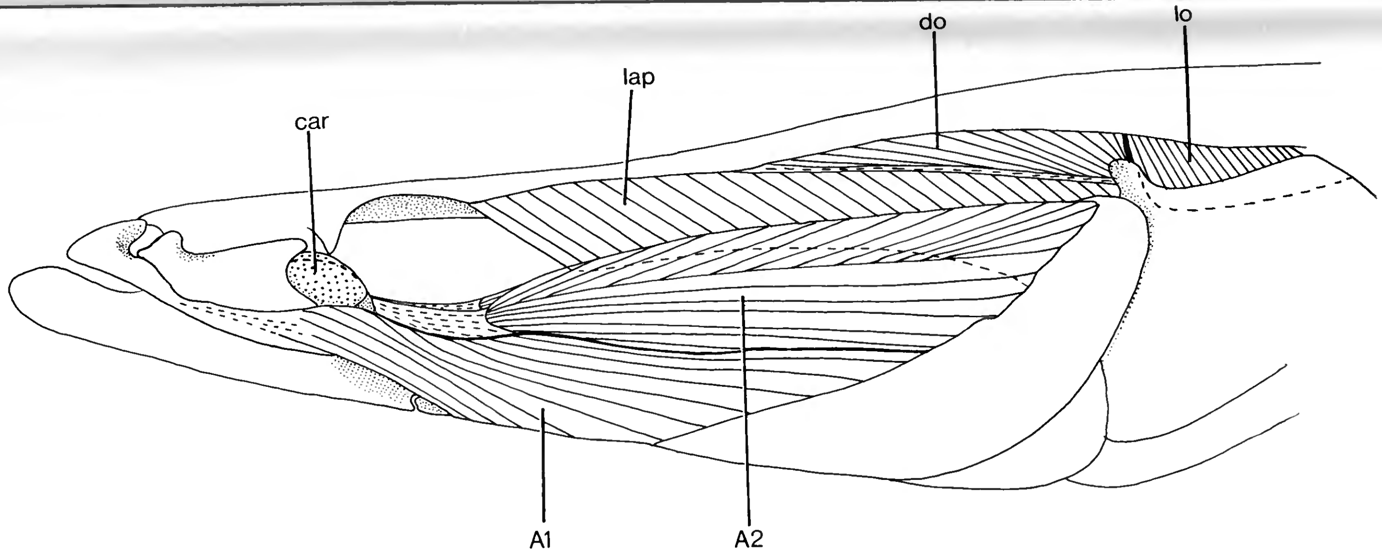

Fig. 16 *Luciobrama macrocephalus*, cranial musculature. Dotted lines indicate the ventral borders of the *levator arcus palatini* and the *levator operculi*.

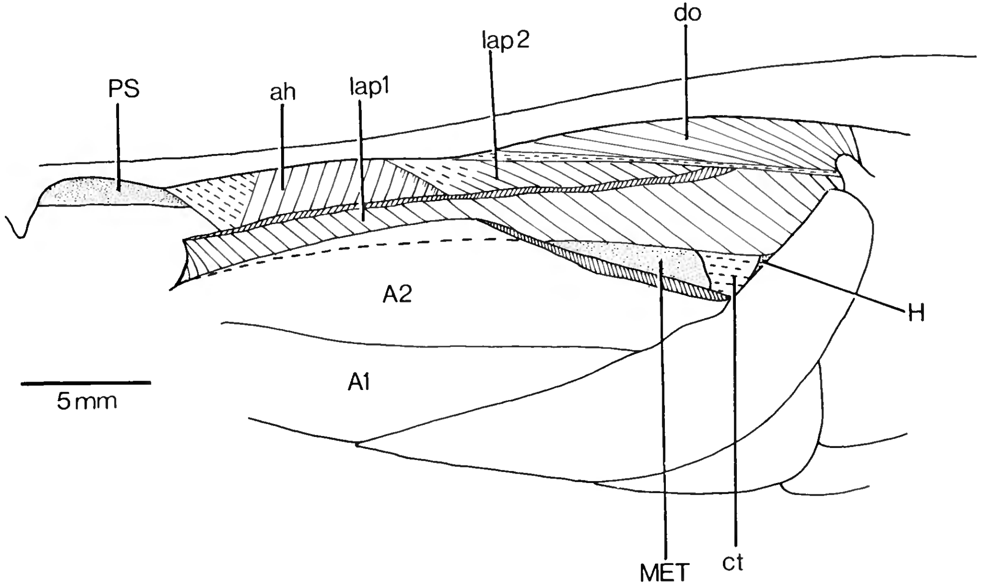

Fig. 17 *Luciobrama macrocephalus*, cranial musculature. Dissection of deeper muscle layers. The dorsal borders of the *adductor mandibulae* A1 and the *levator arcus palatini* 1 have been cut through.

The *adductor arcus palatini* is absent, but it would appear that the anterior extension of the *adductor hyomandibulae* is in fact fulfilling the function of the *adductor arcus palatini.*

The *dilatator operculi* (do) originates anteriorly from the aponeurosis which also gives rise to the inner section of the *levator arcus palatini*, and posteriorly from the lateral border of the pterotic. Some fibres also stem from the sphenotic process.

Insertion of the fibres is into a long tendon which forms the ventral border of the muscle and which joins the anterior process of the operculum. A thick band of tissue connects the lateral face of the opercular process with the pterotic.

The *levator operculi* (lo, Fig. 16) is a flat sheet of muscle running from the pterotic to the medial face of the operculum. The fibres run almost perpendicularly.

The *adductor operculi* is a thin conical muscle originating from the deep subtemporal fossa to insert upon the medial leading edge of the operculum anterior to the insertion of the *levator.*

Hyoid muscles (Fig. 18)

The *intermandibularis* (im) is very thin and ellipsoidal in cross-section. It is covered dorsally by skin and connective tissue, ventrally by the *protractor hyoideus.*

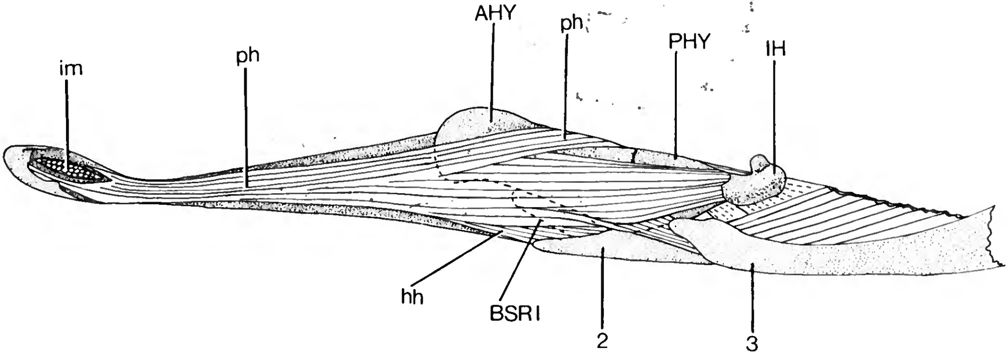

Fig. 18 *Luciobrama macrocephalus*, hyoid musculature. The hyal bones are those of the left side shown in lateral view. The first branchiostegal ray and ventral borders of other hyal bones are indicated by dashed lines. The dentary is of the right side and is shown in medial view.

The *protractor hyoidei* (ph) arise from the medial and lateral surfaces of the anterohyal and posterohyal. Those parts stemming from the internal surfaces of the bones overlap the dorsal edge of the anterohyal to pass laterally into the muscle body. The lateral origin is as far back as the interhyal. Small bundles of fibres also originate from the second and third branchiostegal rays. The two halves of the muscle join together and run as an elongate cone between the dentaries. Insertion is posterior to, and below, the *intermandibularis.*

The *hyohyoidei* (hh) are weakly developed. They lie as sheets of fibres between the branchiostegal rays. From the first branchiostegal ray the fibres run into tendinous bands which meet along a raphe below the dorso- and ventrohyals. Insertion is from the third branchiostegal ray onto the suboperculum.

It is not possible to distinguish *abductores* and *adductores* sections of this muscle and it would appear as Winterbottom (1974) noted in *Cyprinus* that the function of the *adductores* is taken over, in this case to a great extent, by the *protractor hyoidei.*

The *sternohyoideus* (sth, Fig. 19) originates from the forked leading edge of the cleithrum, the dorsal arm of the fork contributing a separate bundle of fibres which is directed ventrally into the main mass of horizontally arranged fibres. The lateral border of the muscle is marked by tendinous bands. Insertion is along the ventral and lateral faces of the urohyal.

Branchial arch muscles (Fig. 19)

I have not made a thorough investigation of the branchial arch muscles due to lack of material for deep dissection. As far as I can see, the arrangement of this musculature is essentially that described for *Opsariichthys* by Takahasi (1925).

The *obliqui ventrales* (obv1–3) are present on the first three ceratobranchials, they are very elongate well-developed muscles.

The fourth ceratobranchial bears a *transversus* muscle which meets its fellow along a median raphe into which inserts the *pharyngoclavicularis interni.*

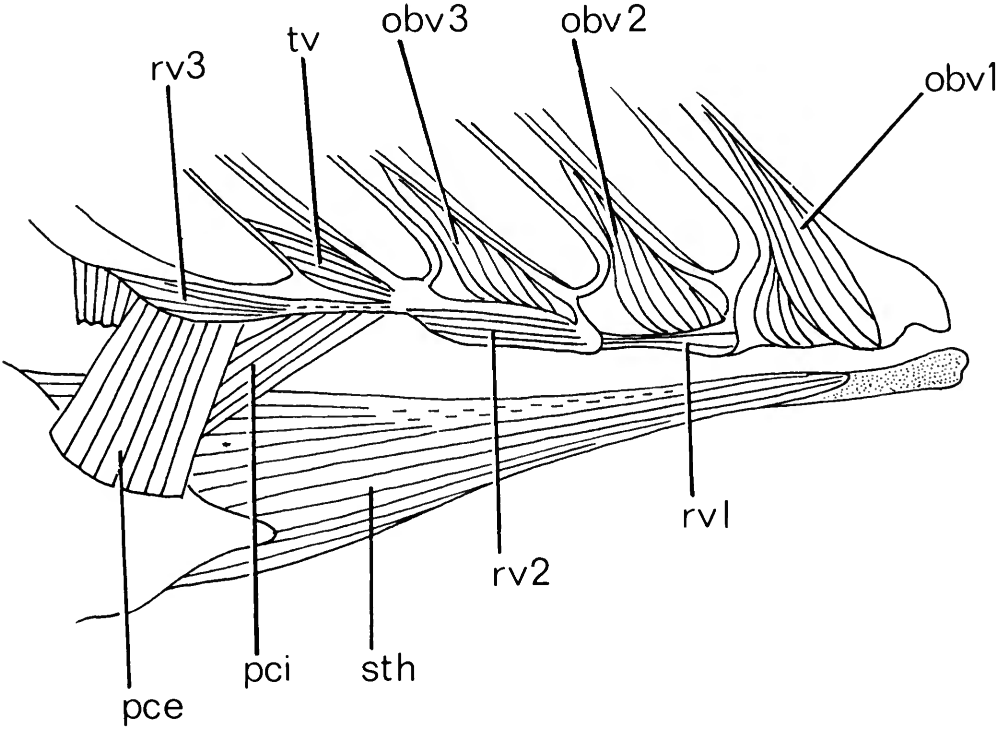

Fig. 19 *Luciobrama macrocephalus*, ventral branchial muscles of the right side shown in ventro-lateral view.

Connecting the second and third hypobranchials is a thin almost tendinous muscle, the *recti ventrales* (rv1); another larger element runs from the third to the fourth hypobranchial (rv2), a thin tendon then connecting the fourth hypobranchial to the *recti ventrales* of the fifth (pharyngeal) ceratobranchial.

These muscles are the *arcualis-hyoideus* of Takahasi (1925). Winterbottom (1974) refers to these as the *recti ventrales* and remarks that there are four to five in the cyprinids.

Comparative analysis

In order to determine the interrelationships of *Luciobrama*, it has been necessary to examine a wide range of cyprinid genera and to review a series of anatomical features to decide if they are derived or primitive characters.

The species that have been examined are listed on pages 2–5. These were chosen to represent those groups currently recognized as subfamilies (see p. 61). In referring to large genera such as *Barilius*, *Barbus* and *Labeo* it should be made clear that in the context of this paper such reference is only to those species examined and does not imply that any particular feature occurs in all congeners.

Although many genera have been examined, not all are cited in the following analysis. An initial study suggested those that could possibly be related to *Luciobrama*, those that displayed parallel features and those exhibiting marked differences. Examples of genera in all three categories have been used in this analysis.

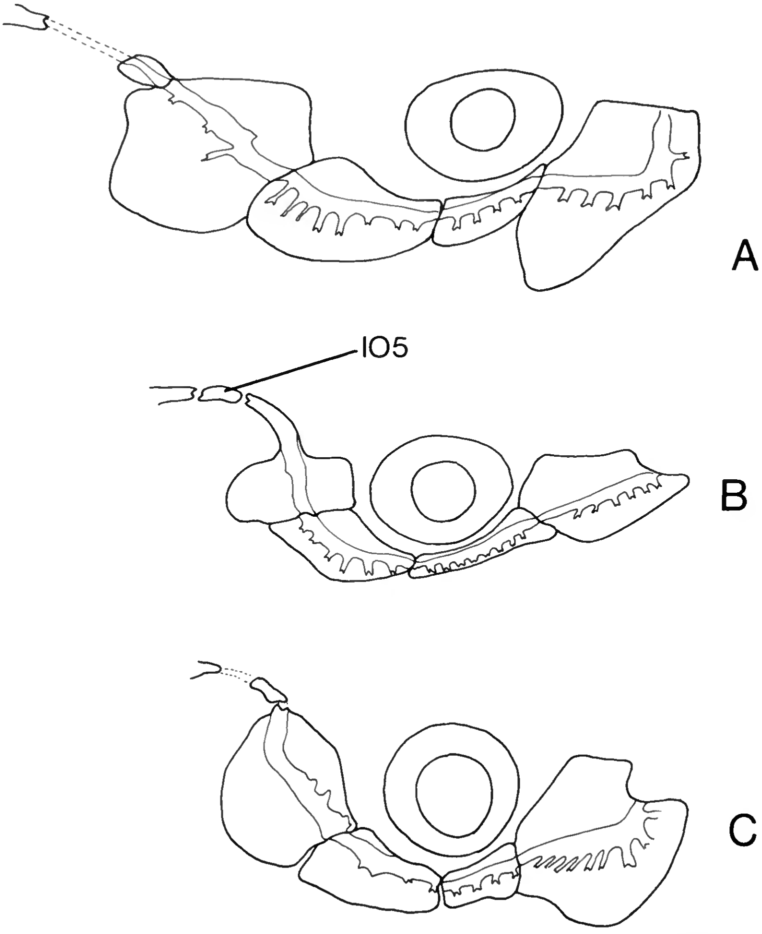

Fig. 20 Infraorbital bones of A. *Aspiolucius esocinus*, B. *Pseudaspius leptocephalus*, C. *Aspius vorax*.

Osteological characters

Circumorbital series

In *Luciobrama* all the infraorbitals, apart from the lachrymal, are reduced to a slender ossification around the sensory canal tube. This is not an unusual condition in cyprinids and is found in many genera (e.g. *Alburnus*, *Labeo*, *Barbus*, *Notropis*, *Chrosomus*). However, in all species of three genera, namely *Aspiolucius*, *Pseudaspius* and *Aspius*, the posterior infraorbitals are of similar morphology and arrangement to those in *Luciobrama* (*cf.* Fig. 2, Figs 20A, B & C). In these three genera the first infraorbital is large, and the canal bears 9–10 pores in *Aspiolucius*, 11 in *Pseudaspius* and 9–10 in *Aspius*. The second infraorbital is short in *Aspiolucius*, but in *Pseudaspius* and *Aspius* it approaches the proportions of that bone in *Luciobrama*. The third and fourth infraorbitals are expanded, the fourth being shield-shaped. The canal carried by the fourth infraorbital is diverted across the postorbital region as in *Luciobrama.* In all these species the fifth infraorbital is minute and reduced to an ossification around the canal tube.

In *Elopichthys* (Fig. 21A), although the reduction of ossification is similar to that found in the above-cited genera, the fourth infraorbital is orientated vertically, and the fifth curved dorso-posteriorly to join the pterotic canal. This arrangement is found in a number of genera (e.g. *Leuciscus*, *Alburnus*, *Culter*, *Pelecus*, *Paralaubuca*, *Oxygaster* and *Ochetobius*; Fig. 21D). However, in *Paralaubuca* and *Oxygaster* the fourth infraorbital is expanded.

A different situation is found in *Opsariichthys*, *Zacco*, *Barilius* and some other genera (see below, p. 29). Here all elements in the infraorbital series are expanded. In *Barilius bola* the second,

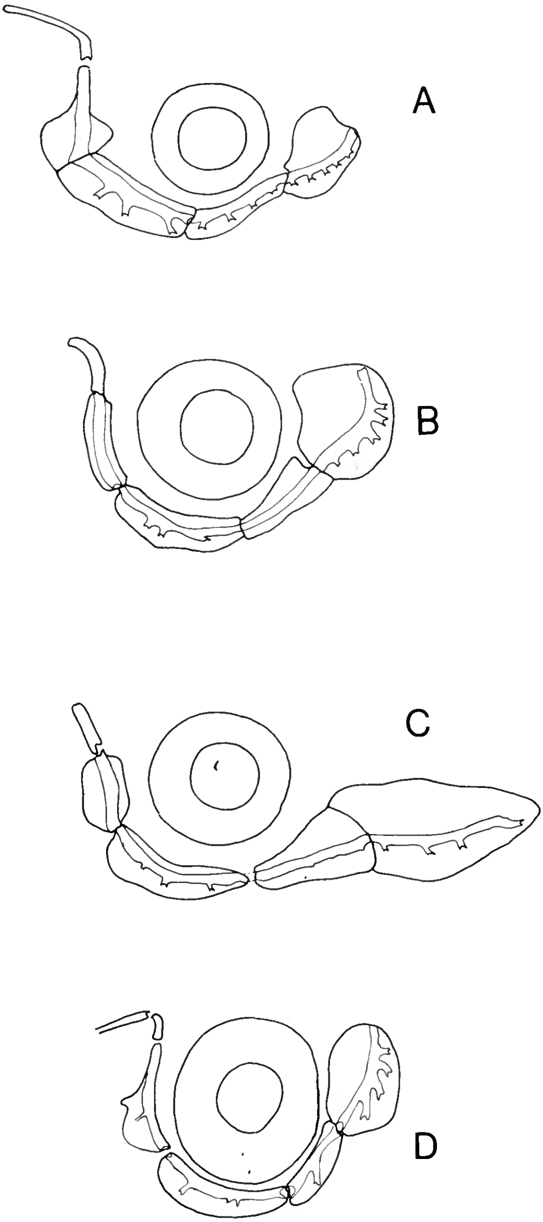

Fig. 21 Infraorbital bones of A. *Elopichthys bambusa*, B. *Erythroculter mongolicus*, C. *Schizothorax esocinus*, D. *Pelecus cultratus.*

third and fourth bones cover the entire cheek. In *Opsariichthys* the fourth and fifth infraorbitals are expanded posteriorly. Expansion of the second and third bones occurs in some *Rasbora* (Ramaswami, 1955b).

The fifth infraorbital is reduced to an ossification around the canal tube in *Opsariichthys* and is remote from the supraorbital, but in *Barilius* it is large and connected to the supraorbital. A similar arrangement is found in *Salmostoma*, *Luciosoma* and *Squaliobarbus* (see below, p. 29).

The *supraorbital* is variously developed in cyprinids (see Ramaswami, 1955b : 208). In *Aspiolucius*, *Pseudaspius* and *Aspius* (Fig. 20) it is, as in *Luciobrama*, relatively narrow, the frontal widening posteriorly to it and preventing its contacting the infraorbital series.

In narrow headed cyprinids, such as *Oxygaster*, *Pseudolaubuca* and *Macrochirichthys*, the bone is narrow and extends for almost the length of the lateral margin of the frontal but fails to make contact with the fifth infraorbital.

In most *Barbus* species the supraorbital is small and well separated from the infraorbital series by the frontal, but in *Barbus tor* the bone is very long and meets the fifth infraorbital. Gosline (1974 : 3) also noted the variability of contact in certain south-east Asian species of *Barbus*.

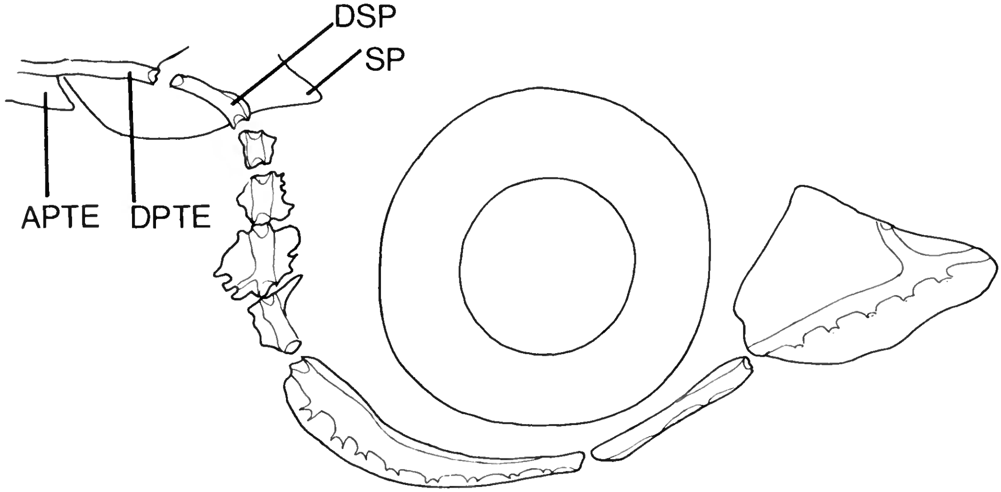

Fig. 22 Infraorbital bones of *Oreoleuciscus pewslowi*.

Comments on circumorbitals

Roberts (1973) states that in cyprinids there is an antorbital and six infraorbitals. I count only six including the first, here identified as the lachrymal (following Harrington, 1955). Gosline (1961) considered the first infraorbital in cyprinids as possibly a compound structure comprising the lachrymal and antorbital. It is not clear if Roberts considered the first infraorbital to represent two fused elements.

Harrington (1955) identified the sixth infraorbital in *Notropis bifrenatus* as the dermosphenotic, noting that it was reduced to a bony tube and was often lacking in that species.

Gosline (1975) discussed the dermosphenotic of cyprinids and thought the degree of development of this bone and its proximity to other circumorbitals could be an aid in assessing the primitive or specialized condition of a particular taxon. However, he considered that in *Aspius* there was a certain degree of difficulty in the identification of this bone. Gosline (1975 : 2; pl. 2, fig. 3) described a membranous tube connecting the fifth infraorbital with the cranium. In fact his fifth infraorbital is the fourth in the series and the 'membranous tube' is the fifth. In a series of specimens of *Aspius vorax* I have found quite some variation in the development of this bone. In some specimens there is a single completely ossified canal connecting the fourth infraorbital with the pterotic canal, in others the bony tube is fragmented into two components, the upper one of which probably represents the true dermosphenotic (sixth infraorbital) and overlies the autosphenotic. In a specimen of 110 mm SL on one side of the head there is no sign of an ossified element between the fourth infraorbital and the pterotic, although the canal is present as an epidermal tube. Yet, on the other side of the head the fifth infraorbital is well ossified.

In *Oreoleuciscus pewslowi* (Fig. 22) it is interesting to note that there is marked fragmentation of the posterior infraorbital. In one specimen the fourth infraorbital is fragmented into three separate lamellate elements and the sixth infraorbital (the dermosphenotic) is also present (see Jollie, 1975, on the fragmentation of these bones.).

In *Luciobrama* connection between the fifth infraorbital and the dermopterotic is made through an epidermal canal. This connection occurs far in front of the autosphenotic because of the forward extension of the overlying dermopterotic. Thus, there is no infraorbital bone connected with any part of the autosphenotic and which could be interpreted as a dermosphenotic.

In *Esomus*, Ramaswami (1955b) pointed out that the sphenotic occurred as a roofing bone. The bone he was referring to is, in fact, the dermosphenotic and in preparations to hand I have been able to separate this canal bearing bone from the underlying autosphenotic. Greenwood *et al.* (1966) refer to this feature in *Esomus* as being specialized, but it is probably a primitive condition for a cyprinid.

Gosline (1975) noted that in *Salmostoma* the dermosphenotic was large and contacted the supraorbital (which it also does in *Barilius*, *Cyprinus*, *Squaliobarbus*, *Luciosoma* and some other genera). He was of the opinion that contact between the dermosphenotic and supraorbital was a primitive character (Gosline, 1975 : 6) because such contact is found in the 'generalized' characoid *Brycon.*

It is so that in *Brycon* and other characoids the sixth infraorbital (dermosphenotic) is well developed and makes contact with the supraorbital (Weitzman, 1962; Roberts, 1969). However, this has little bearing on the situation in cyprinids. Indeed, if *Opsariichthys* is to be considered the 'primitive' cyprinid this argument fails because no such contact is found between the infraorbitals and supraorbital. In *Salmostoma* and other cyprinid genera in which such contact occurs, it is between the fifth infraorbital and supraorbital. No cyprinid I have examined shows any evidence of the interposition of a sixth infraorbital. This would suggest that either the dermosphenotic has been lost altogether in these genera or else it has become incorporated with the fifth infraorbital. Incorporation into another dermal head bone is suggested by an observation on *Chelaethiops*. A specimen of *Chelaethiops* sp. (29·5 mm SL) was found to possess a well-developed dermosphenotic, but in four other specimens of the same series (alizarin preparations) it was absent. However, in a fifth specimen (24·5 mm SL) a fragment of the dermosphenotic was visible, apposed to the posterior edge of the frontal (Figs 23A & B).

The dermosphenotic is also well developed in *Esomus danricus* (see above), and the fifth infraorbital, although small, maintains contact with the supraorbital; that area lying postero-dorsally to the infraorbital (i.e. above the *dilatator operculi* muscle) is covered by a 'normal' body scale, one bearing concentric radii. This scale appears to be in no way associated with any cranial bone.

The area covered by the fifth infraorbital is that which houses the *dilatator operculi* and *levator arcus palatini* muscles, and it seems likely that reduction of dermal bones in that region would be a necessary preadaptation or a response to the reorientation and expansion of the underlying musculature. It may be noted here that in some *Barilius* species where the fifth infraorbital is large, the *dilatator operculi* is covered by the *adductor mandibulae* muscle (see p. 55).

Tretiakov (1946) placed much emphasis in classifying the cyprinids on the development of the infraorbital series and suggested that those cyprinid genera with the broadest posterior bones (presumably in contact with the supraorbital) were the most primitive. He included *Cyprinus* in that category.

Gosline (1974) considered the cephalic canals of cyprinids and divided the old world genera into two groups on the basis of 'presence or absence of a gap between the supraorbital and infraorbital canals'. He stated (*loc. cit.* : 11) that all south-east Asian and African cyprinids have the supraorbital and infraorbital canals connected.

The connection between the infraorbital and supraorbital canals is dependent on the form of the last infraorbital (or dermosphenotic) already discussed above. There is always a connection between the two canal systems, be it through an ossified or an unossified tube. The 'gap' observed by Gosline is presumably the unossified condition. Such an unossified connection is found in some African *Barbus* (e.g. *B. somereni*), a group which Gosline included amongst those genera with a connection between the canal systems; whereas *Rutilus* and *Pelecus*, included in the group with a break between the canal systems, have a complete connection with the pterotic canal.

Ethmo-vomerine region

The *kinethmoid.* I have been unable to determine the condition of this bone in *Aspiolucius* and *Pseudaspius* owing to lack of material for dissection. In *Aspius* it is short and blunt as in *Luciobrama.*

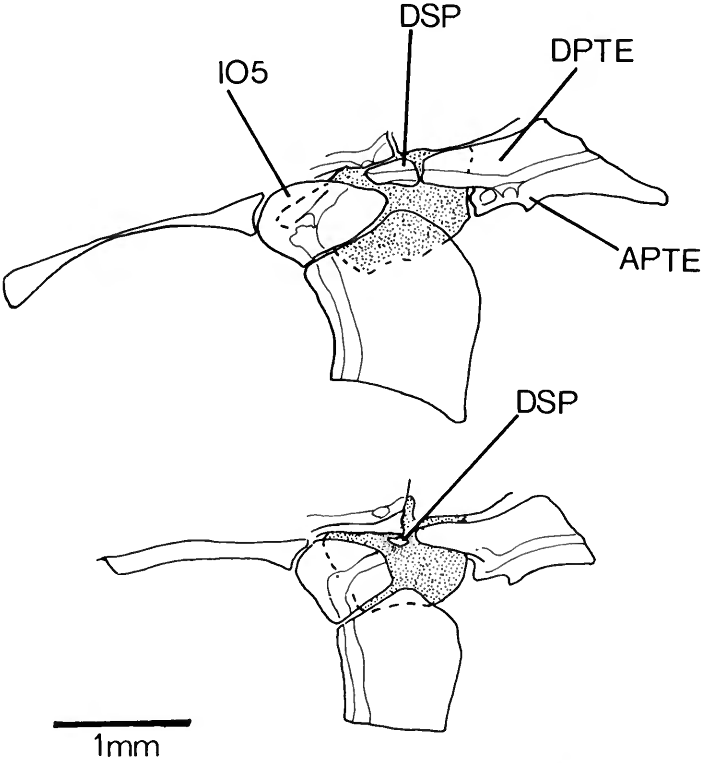

Fig. 23 Upper circumorbital bones of *Chelaethiops* sp. A. A specimen of 29·5 mm SL, B. A specimen of 24·5 mm SL.

In *Elopichthys* the dorsal surface of the kinethmoid is greatly expanded into a flat diamond-shaped plate separating the premaxillae posteriorly (Fig. 35, KE). It is attached by ligaments to the premaxillae and maxillae and rotates against the ethmoid when the jaw is opened.

In *Opsariichthys*, *Zacco* and some species of *Barilius* the kinethmoid is an elongate gutter-shaped bone the dorsal edges of which are slightly flared. However, in *Barilius bola* the dorsal surface is expanded as a solid plate similarly to that of *Elopichthys* although not as extensively (see p. 43). In other species of *Barilius* the kinethmoid is a rod-shaped structure which is notched dorsally. This is the 'usual' condition of the kinethmoid in other cyprinid genera and is probably the primitive one. Exceptionally, in the genus *Barbus*, the species *B. tor* and *B. mariae* possess very long kinethmoids, the posterior borders of which are convex, enabling the bone to rock in the anterior ethmoid groove. Current research on the genus *Macrochirichthys* has indicated an unusual feature of the kinethmoid (which is a triangular bone) whereby it articulates directly with the premaxillae.

I could only examine the features of the ethmo-vomerine region in *Aspiolucius* and *Pseudaspius* from radiographs. Both genera resemble *Luciobrama* in possessing a similar depression, elongation and contact of the lateral ethmoids with the parasphenoid.

Ramaswami (1955b) noted that in many genera including *Barbus*, *Opsariichthys* and *Aspius* the *preethmoid* articulated with the ethmoid only. However, in all the cyprinid genera I have examined the preethmoid is supported in a lateral fossa formed by the ethmoid and the vomer (the condition noted in *Labeo* by Starks, 1926 : 174). Ramaswami (1955b) also states that the preethmoid is completely lacking in, amongst other genera, *Esomus*, *Leuciscus* and *Notropis*. I can report that it is present in both the former genera and Harrington (1955) notes that it is present in *Notropis* but is supported only by the vomer. The size of the preethmoid varies considerably, being a very large laterally protruding structure in *Opsariichthys* to minute, partially ossified pads in *Chela* and *Esomus*.

The *supraethmoid* is variously developed in cyprinids. One condition appears for it to be broad and short with the anterior border notched medially; this is the type found in *Opsariichthys*, and some *Barilius* species. Although basically similar, the supraethmoid in the cultrines is narrow and the medial notch much deeper. In *Barbus* and *Labeo* the bone can become extensively developed (e.g. *Labeo cylindricus*) and the anterior border produced medially. In *Barbus tor* and *Barbus mariae* there is, however, a very deep medial groove which accepts the expanded kinethmoid; see above page 30. The usual condition is for the supraethmoid to interdigitate posteriorly with the frontals, the posterior border is mostly straight or somewhat irregular but without the long lateral forks found in *Luciobrama* and *Aspius*. However, in *Macrochirichthys*, *Chela* and some other genera the supraethmoid is overlain by the frontals. Work currently in progress suggests that this is a derived feature associated with the oblique orientation of the jaws and that it is indicative of close relationship of those genera in which it occurs.

Variability within the *ethmoid* appears to be mainly one of depth; being very deep in some genera such as *Pelecus* and shallow in others such as *Chela*. In all the cyprinids I have examined the ethmoid makes some contribution to the preethmoid fossa.

The *vomer* is usually short and wide as it is in *Opsariichthys* but in this genus and in some *Barilius* it is greatly thickened anteriorly. An extreme of this condition is found in *Elopichthys* where the ventral surface is swollen and posteriorly folds over to contact the parasphenoid (Fig. 24). The vomer in the majority of cyprinids is thin and the ventral surface is either flat or bears a shallow groove.

The *nasals* in *Aspiolucius* are long decurved bones containing 8 pores (Fig. 25); in *Pseudaspius* they are shorter, bearing 5 pores, and in *Aspius*, long with 6 pores (Fig. 26). *Elopichthys* resembles *Luciobrama* in possessing long, narrow nasals bearing 9 pores. In the majority of cyprinid genera studied the nasals are found to be short bones with 2–4 pores. In some cultrines they may be long as in *Erythroculter mongolicus* where the nasal bears a lateral flange and has 6 pores.

The *frontals* in *Pseudaspius*, but even more in *Aspiolucius*, are narrow, elongate and anteriorly are slightly separated from one another (Fig. 25). The lateral border posterior to the orbit, like that in *Luciobrama*, is markedly concave. No other cyprinid genus I have encountered has such elongate frontals as are present in *Aspiolucius* and *Luciobrama*. In most genera examined the frontals are relatively short and broad but in some *Barilius* species are narrow and elongate with a concave border above the orbit. The dorsal surface of the frontals is mostly flat or convex but in *Macrochirichthys*, *Pseudoxygaster*, *Pelecus* and some species of *Oxygaster* the frontals are medially depressed to allow for the cranial extension of the epaxial musculature (see Howes, 1976), and in *Nematabramis* there are transverse lamellate ridges across the frontal surfaces.

Orbital region

Each *orbitosphenoid* in *Aspiolucius* and *Pseudaspius* appears similar to that in *Luciobrama*; for some distance it is joined to the parasphenoid but lacks the dorsal posterior extensions seen in *Luciobrama*. (These observations were made entirely from radiographs.)

In *Aspius* the orbitosphenoids are short, deep and widely divergent (Fig. 27B). Medially, they fuse to form an interorbital septum which extends ventrally to join the parasphenoid. A similar development is found in *Elopichthys* but here the septum is reduced (Fig. 27A).

The orbitosphenoid septum is variable in its development within the Cyprinidae. Its purpose is to provide wide separation between the cranial roof and the parasphenoid. Such separation appears to have little to do with the size of the orbit but more with the angle at which the cranium is aligned to the vertebral column and the size of the buccal cavity. In piscivorous cyprinids the orbitosphenoids make direct contact with the parasphenoid without the intervention of a septum. This is also the case in those genera such as *Labeo* and *Garra* which are characterized by their depressed crania. In both cases this close union has resulted in increased rigidity of the cranium (in *Labeo cylindricus* the orbitosphenoids extend lateral wings which join similar processes from the parasphenoid), and increased area of the buccal cavity. When the orbitosphenoids are reduced in depth they often exhibit a cancellous surface and bear lateral ridges (e.g. *Labeo*, *Schizothorax*, *Barilius*).

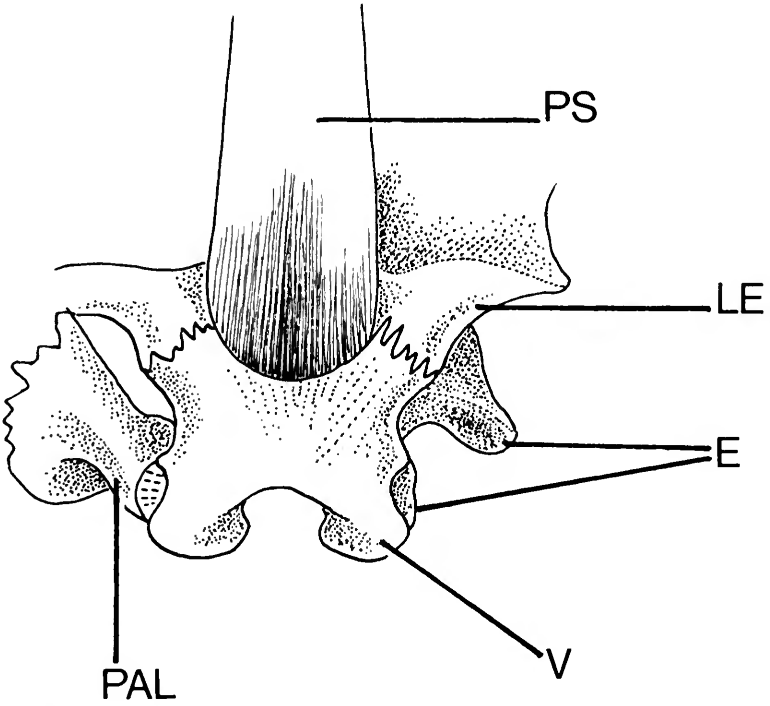

Fig. 24 *Elopichthys bambusa*, ethmo-vomerine region, ventral view.

The *pterosphenoid* in *Aspiolucius* and *Pseudaspius* is an extensive bone and is depressed as in *Luciobrama*, but in *Aspius* it is less extended antero-posteriorly, and that part of the bone forming the wall of the hyomandibular facet less well developed (Fig. 27B). The pterosphenoids of *Aspius* diverge widely and their borders are close to the lateral margins of the frontals.

In *Elopichthys* (Fig 27A, 28 & 29), the pterosphenoids present a condition not encountered in any other cyprinid. The bones are extensively developed and diverge to reach the lateral margins of the frontals. Unlike the genera mentioned above, the sphenotic is not continuous with the frontal and these two bones are separated by the intervention of the pterosphenoid, whose surface at this point is depressed to form a basin. The pterosphenoid basin provides the site of origin for the *adductor mandibulae* A3 muscle (see p. 53). As in *Luciobrama* there is an extensive connection with the parasphenoid.

The pterosphenoids of other cyprinid genera examined are generally small, almost hexagonal in outline and make contact with both the prootic and parasphenoid. However, in *Zacco*, *Cyprinus*, *Catla*, *Rutilus* and some species of *Barilius*, the pterosphenoid does not contact any

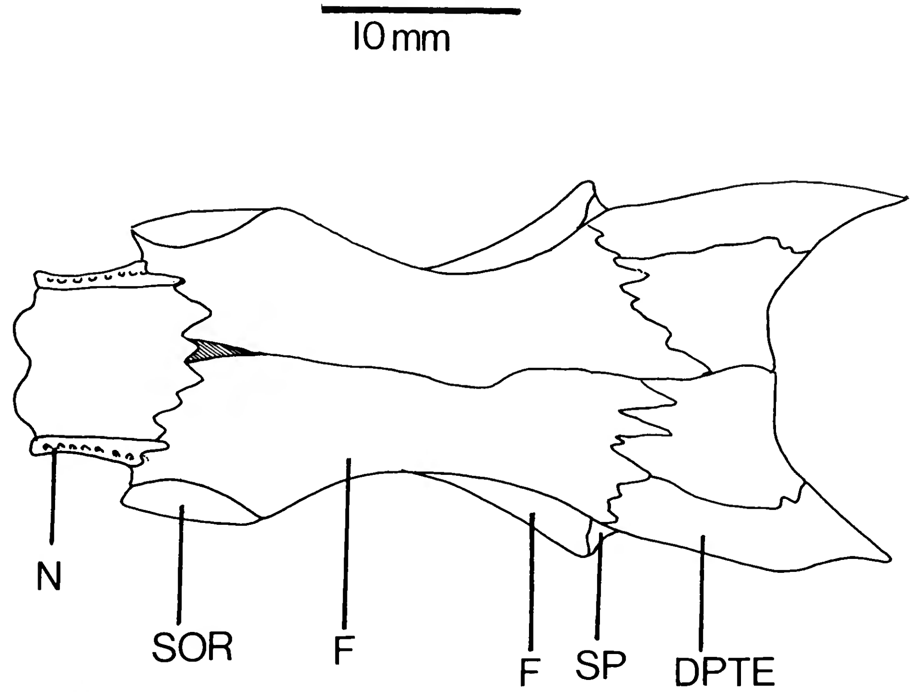

Fig. 25 *Aspiolucius esocinus*, part of the dorsal surface of the cranium. (Holotype.)

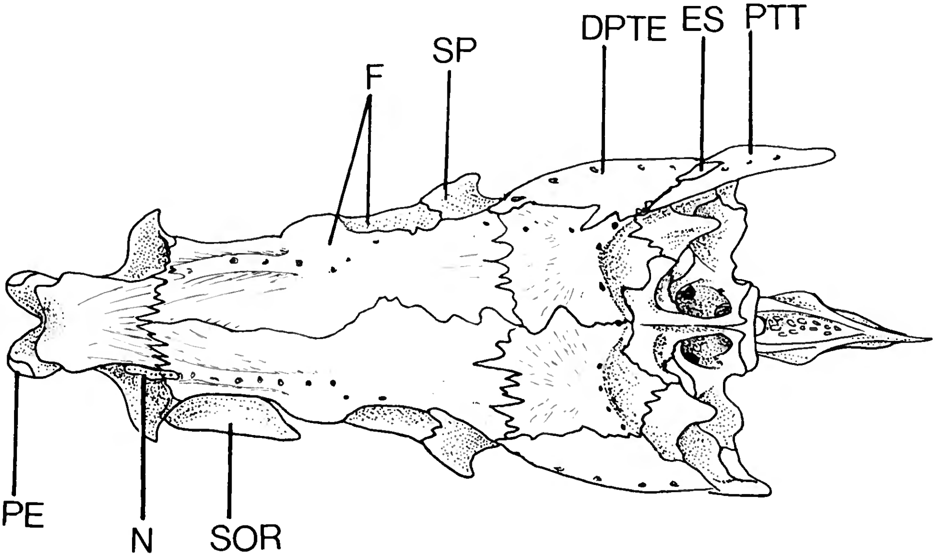

Fig. 26 *Aspius vorax*, neurocranium, dorsal view.

part of the parasphenoid but instead is sutured entirely to the prootic. (See later note on prootic, p. 35.)

The *parasphenoid* in *Aspiolucius* and *Pseudaspius* is thick and horizontally aligned, contacting the medial sections of the lateral ethmoids and the orbitosphenoids as in *Luciobrama*. In *Opsariichthys* the parasphenoid is thin, flared anteriorly, and bears a deep groove on its ventral surface. The lateral ascending wing of the parasphenoid which contacts the prootic and pterosphenoid is wide. Below the prootic the parasphenoid broadens into a triangular platform which is extended laterally by the contribution of the flattened ventral surfaces of the prootics. A similar contribution from the prootics to the parasphenoid platform is found in most *Barilius* species (Fig. 30). The lateral ascending wings of the parasphenoid in *Zacco*, some *Barilius* species, and *Leuciscus* are narrow, and as mentioned above, make contact only with the prootic and not the pterosphenoid.

Although Ramaswami (1955b) stated that the parasphenoid did not show any variation, in fact it does. In some genera the anterior part is very wide (e.g. some *Labeo* species) and there are present in others well-developed medial dorsal and ventral ridges, Again, in *Labeo* the ascending

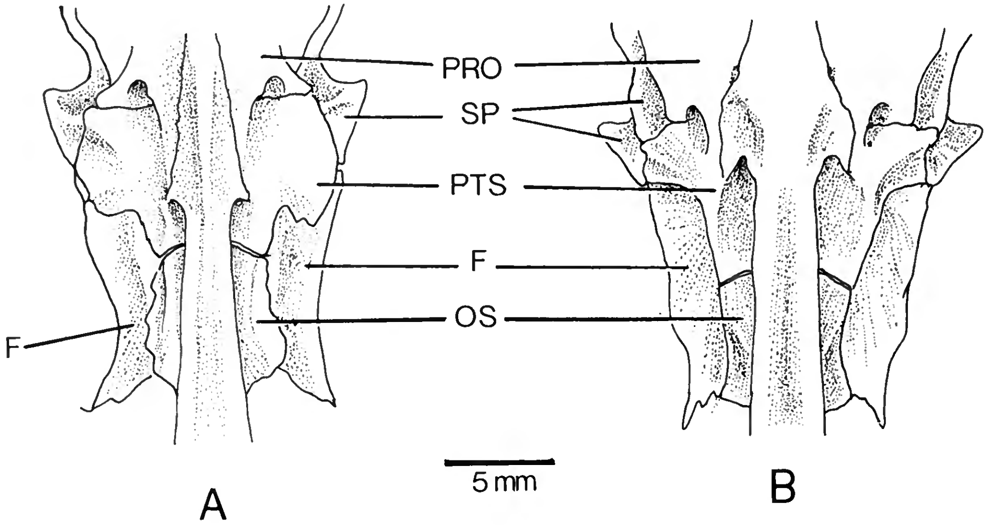

Fig. 27 Ventral views of the orbital regions of A. *Elopichthys bambusa*, B. *Aspius vorax.*

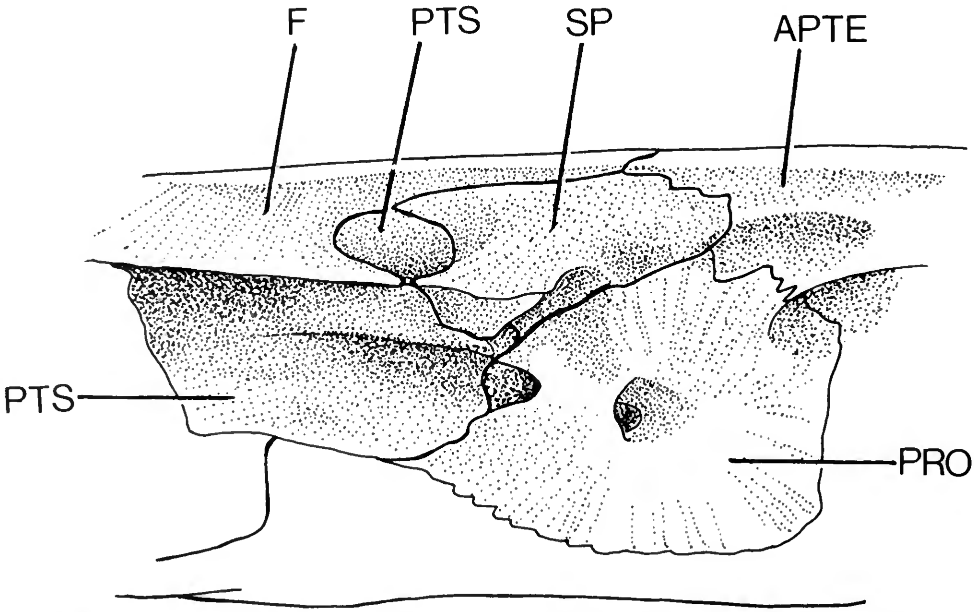

Fig. 28 *Elopichthys bambusa.* Lateral view of the orbital-otic region of the neurocranium. (Composite from three specimens.)

wing may be greatly extended laterally and there is sometimes developed a medial strut of the ascending wing which contacts the pterosphenoid. *Catla* and *Hypophthalmichthys* have the posterior part of the parasphenoid bent upwards, and the midline below the ascending wings bears a strong ventral process.

Otic region

The *prootic* in *Aspiolucius*, *Pseudaspius*, *Aspius* and *Elopichthys* is of a similar elongate shape to that in *Luciobrama* and the anterior foramen of the trigemino-facialis chamber is likewise situated on the anterior border of the bone which contacts the pterosphenoid. Also, as in *Luciobrama* the lateral commissure is wide. The large hypophysial foramen (Ramaswami, 1955b) between the parasphenoid and prootic in *Luciobrama* is absent in the above-mentioned genera.

In most cyprinid genera examined, the anterior foramen of the trigemino-facialis chamber interrupts the anterior border of the prootic, which is bounded by the pterosphenoid. However, in some species of *Barilius* the prootic bears the anterior opening of the trigemino-facialis chamber entirely in its lateral face, remote from the anterior border and in those species the lateral commissure is a narrow structure. There is much variation in the width of the lateral commissure throughout the cyprinids. Besides *Luciobrama* and the genera mentioned above, it is a wide structure in *Schizothorax*, *Erythroculter* and some *Barbus* species (all those taxa in fact, which have an elongation of the postorbital cranium). On the other hand, it is reduced to a narrow strut in *Opsariichthys*, *Zacco*, *Leuciscus* and *Labeo*.

The floor of the prootic forms the roof of the *posterior myodome* in all the genera examined. Again, the extent and depth of the myodome show great variation. As far as can be ascertained from radiographs, the myodome in *Aspiolucius* and *Pseudaspius* resembles that of *Luciobrama* which in turn bears similarity to that described in *Aspius* by Oliva and Skořepa (1968).

The topographic relationship between the prootic, parasphenoid and pterosphenoid in the cyprinids appears to have some significance in establishing phylogenetic relationships between various taxa. A particular study is being made of these bones in connection with current work on the genera *Opsariichthys*, *Zacco* and *Barilius*.

The *autosphenotic* is extensive in *Aspiolucius* and extends laterally from below the border of the cranium as a long shelf on which the *dilatator operculi* muscle originates (Fig. 25). In *Aspius* (Fig. 26) the sphenotic is not roofed by any part of the frontal or pterotic. Together with part of the frontal it extends laterally and forms the fossa for the *dilatator operculi* muscle.

The sphenotic in *Elopichthys* is bordered anteriorly by the basin-like pterosphenoid (see above, p. 32), and it extends laterally as a wide platform, the posterior ventral surface of which forms the anterior hyomandibula facet (Figs 27A, 28 & 29).

In *Opsariichthys*, *Zacco* and some *Barilius* the bone is overlapped along its medial margin by the frontal and forms a deep dilatator fossa. The anterior lateral process of the sphenotic in these genera is short and lamellate, in contrast to that of other species of *Barilius* (e.g. *bola*, *loati*) where the lateral process is long and thick.

In *Barilius microcephalus* the posterior dorsal border of the sphenotic is separated from the overlying pterotic to form a lateral foramen (LF, Fig. 31). Part of the *adductor mandibulae* A2 muscle originates from the ventral surface of the pterotic and passes through this foramen.

Some genera display a condition in which the laterally directed process of the sphenotic is separated from the overlying frontal, contact between the two bones being along their lateral margins. Thus, a foramen is formed which provides a passage for the *dilatator operculi* muscle which originates on the ventral surface of the frontal. This feature is found in *Esomus*, *Cyprinus* and *Catla*. It also occurs in some *Barbus* species and appears to be present in all European and north African species examined (*Barbus barbus*, *B. callensis*, *B. nasus* and *B. reinii*), a middle eastern species (*B. canis*), some eastern and southern African species (*B. altianalis*, *B. intermedius*, *B. oxyrhynchus*, *B. rocadasi*, *B. progenys*, *B. natalensis* and *B. capensis*) and in some Asian species (*B. altus* and *B. tor*). However, it is absent in all the other species of *Barbus* examined (see list of species on p. 2) where the dilatator fossa is of the 'usual' type (see p. 56).

In all the African and Asian *Labeo* species examined the sphenotic process is separated from the frontal in the same way as it is in *Barbus* and the other genera cited above. However, the sphenotic

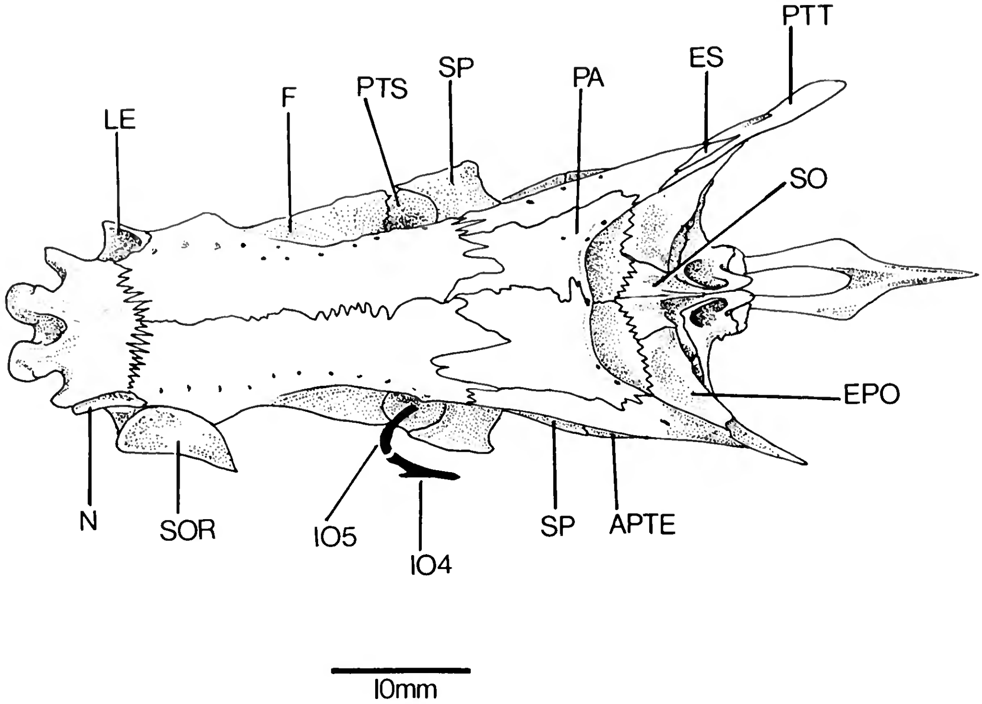

Fig. 29 *Elopichthys bambusa*, neurocranium, dorsal view. The position of infraorbitals 4 and 5 are indicated.

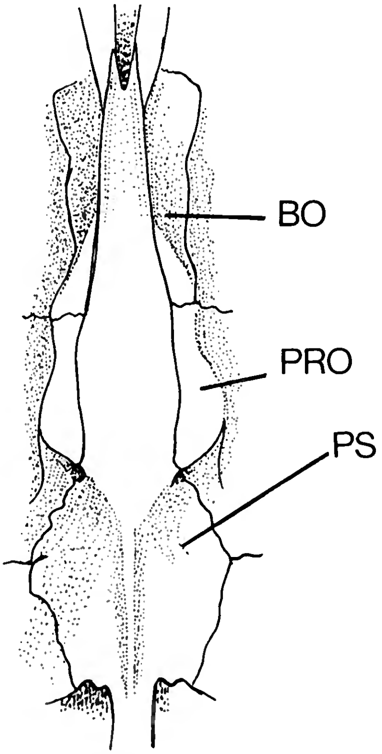

Fig. 30 *Barilius bola*. Ventral view of the parasphenoid and prootic. The parasphenoid platform is unshaded.

process, which in *Labeo* is usually reduced to a thin strut of bone, is also perforated by a foramen. These two openings allow for passage of a divided *dilatator operculi* muscle (see p. 57). A subsidiary foramen is also present in *Catla* and here too the *dilatator* muscle is divided through both apertures.

In *Squaliobarbus* the lateral process of the sphenotic is a wide platform covered for half its width by the frontal. The ventral surface of the bone provides a fossa for the articulation of the anterior condyle of the hyomandibula. Anteriorly, the sphenotic is deeply recessed, leaving only the thinnest wall between the orbital cavity and the dilatator fossa, perhaps an incipient condition for the development of this feature.

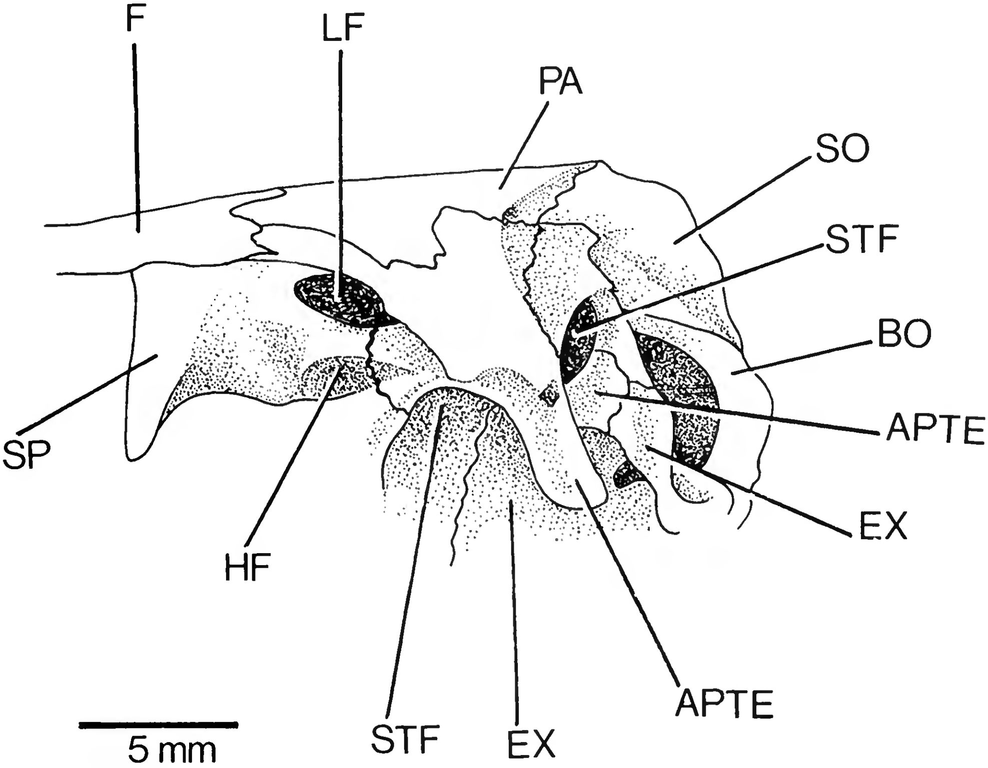

Fig. 31 *Barilius microcephalus.* Dorso-posterior section of neurocranium, lateral view.

Further discussion of the dilatator fossa is reserved until page 56.

The *pterotics* in *Aspiolucius* and *Elopichthys* (Figs 25 & 28) are wide bones contributing to the cranial surface and bordering the parietals and frontals as in *Luciobrama*. Also, as in that species, they overlie and extend anteriorly beyond the sphenotic shelf.

In *Aspius* there is only a narrow region of contact between the pterotics and the frontals. The fossa for the posterior condyle of the hyomandibular bone is almost entirely confined to the pterotics.

The cranial surface of the pterotics is narrow in *Opsariichthys* and most *Barilius* species. Medially the bones form a flat roof to the subtemporal fossa. Ventro-posteriorly their connection with the exoccipitals, through which passes the semi-circular canal, is greatly compressed. The posterior spine of each pterotic is short and is directed ventrally at an acute angle. The posterior hyomandibular fossa lies mainly in the pterotic, but the anterior third extends onto the sphenotic. In the long-jawed species of *Barilius* (e.g. *B. bola*, *B. loati*) this fossa is confined almost entirely to the pterotic.

The *posttemporal fossae* in *Luciobrama* are well developed (see p. 11 & Fig. 32A). As far as I can ascertain from radiographs such is also the case in *Aspiolucius* and *Pseudaspius*. Certainly in *Aspius* (Fig. 32B), *Elopichthys* (Fig. 33A), *Megalobrama*, *Culter*, *Erythroculter* and *Schizothorax* deep posttemporal fossae are developed. In other genera such as *Opsariichthys* (Fig. 33B) and *Pelecus* the fossae are present but are shallow. They are absent in *Leuciscus*, most *Barbus* species, *Labeo*, *Garra*, *Paralaubuca* and *Macrochirichthys*. In some *Barbus* species (*B. tor*, *B. longiceps*) 'pseudo-posttemporal' fossae are developed. That is to say, instead of the lateral wall of the fossa being formed from the pterotic, it is provided by the enlarged posttemporal, the pterotic contributing only slightly to the anterior part of the fossa (Fig. 33C).

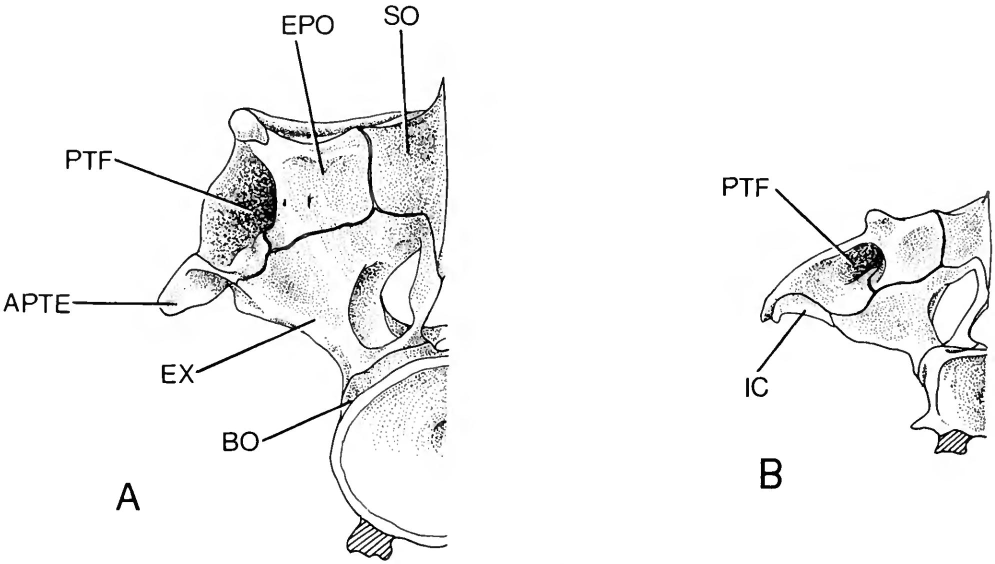

Fig. 32 Posterior views of the neurocrania of: A. *Luciobrama macrocephalus*, B. *Aspius vorax*.

A rather different situation is found in some *Barilius* species (*B. bola*, *B. microcephalus*, *B. loati*, *B. niloticus*) where there are no posttemporal fossae as such but a posterior (posttemporal) opening which invades the deep subtemporal fossa. Here, the pterotic contacts the epioccipital along the cranial surface and posterior border, forming the roof of the subtemporal fossa (Fig. 31).

Ramaswami (1955b : 222) notes that 'In some form or other all genera possess a posttemporal fossa in Cyprinidae', while Roberts (1973) stated that posttemporal fossae are entirely closed in Cyprinidae. Neither of these statements is correct.

Weitzman (1962) considered the presence of posttemporal fossae in cyprinids to be a specialized feature. Certainly the fossae take on a specialized form in *Luciobrama* and in long-headed representatives of other genera, but its presence in such relatively 'primitive' cyprinids as *Opsariichthys*, *Zacco* and *Barilius*, and the fact that this feature is much more widespread amongst the cyprinids than had previously been supposed, would indicate that it is a plesiomorph character.

The *exoccipitals* show little variation in the genera examined. In all of them the lateral occipital foramen of each bone is extensive, its border being defined by a narrow strip of bone. The lateral limb of the exoccipital is directed at an angle of 45° in *Luciobrama* (Fig. 32A) and in other long-headed cyprinids (Figs 32B & 33A).

In *Labeo* the bone is markedly modified. The lateral limb is directed horizontally (as it is in *Barbus*, Fig. 33C) and the lateral occipital foramen is reduced, being margined by a thickening of the bone.

The *epioccipital* in *Aspius* has the posterior face of this bone produced into a thick, caudally directed process. Such a feature is also noted in *Erythroculter* and *Schizothorax* but appears to be absent in *Aspiolucius* and *Pseudaspius*. Except in *Barbus tor*, where similar processes are present, such well-developed epioccipital features have not been found in the other genera examined. It is a feature no doubt associated with the elongation of the skull and the need to produce an extended surface for the attachment of epaxial muscle fibres.

The dorsal surface of the epioccipital in *Elopichthys* covers a large area which, together with the parietals and supraoccipital forms an extensive posterior cranial platform (see p. 13).

The *basioccipital* could not be examined in either *Aspiolucius* or *Pseudaspius* and the shape of the masticatory plate of the pharyngeal process cannot be ascertained. The plate is weakly developed in *Aspius* and *Elopichthys* as it is in *Luciobrama*, and the pharyngeal process itself is short and laterally compressed distally.

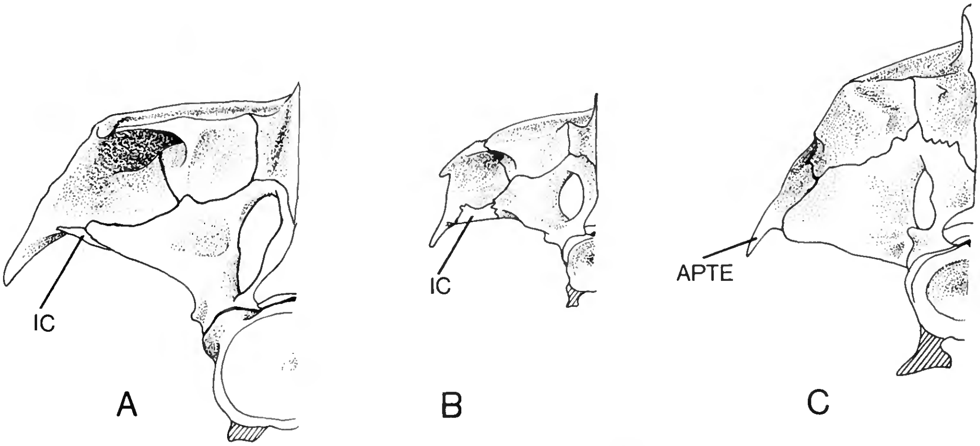

Fig. 33 Posterior views of the neurocrania of: A. *Elopichthys bambusa*, B. *Opsariichthys uncirostris*, C. *Barbus oxyrhynchus*.

Opsariichthys, *Zacco* and some *Barilius* have a pharyngeal process which is laterally compressed and steeply angled, the masticatory plate being moderately developed. The masticatory plate is particularly well-developed in many *Barbus* and *Labeo* species and in *Hypophthalmichthys* (see Ramaswami, 1955b), which in some cases, completely hides the aortic foramen. It appears that in those taxa which possess slender pharyngeal bones and teeth the masticatory plate is weakly developed (e.g. *Pelecus*, *Macrochirichthys* and long-jawed *Barilius* species).

The bulla acoustica is not well developed in any of the genera studied.

The *supraoccipital* is basically similar in all genera examined. The crest of the bone is variously developed; for example in *Labeo coubie* there are two diverging wings arising from the medial lamellae; in *Pelecus* the bone forms a high point to the cranium but the medial crest is virtually absent and in *Chela* the entire crest is truncated. Direct contact of the supraoccipital with the neural complex appears to occur only in *Labeo* (Reid, pers. comm.), connection normally being effected by ligamentous sheets (see p. 19).

The *intercalar* was said by Ramaswami (1955b : 216 -as opisthotic) to be 'normally absent'. However, in *Aspius* (IC, Fig. 32B) and *Erythroculter* the intercalar is extremely well developed and covers the area between the pterotic and epioccipital both dorsally and ventrally. Each intercalar in *Schizothorax* is reduced to a discoid bone lying ventral to the junction of the pterotic and epioccipital. The bone is also present in *Opsariichthys*, *Barilius*, *Squaliobarbus*, *Culter*, *Leuciscus* and some *Barbus* species. I have not found it in *Labeo*, *Pelecus* or *Macrochirichthys*.

The *parietals* are especially elongate in *Luciobrama*, *Aspiolucius* and *Pseudaspius*, a condition also encountered in *Hypophthalmichthys*. The 'normal' condition in the Cyprinidae is for the parietals to be short and wide, and the most extreme form of this condition is to be found in some *Labeo* species. As mentioned earlier (p. 39) the parietals in *Aspius*, *Elopichthys* and *Erythroculter* contribute to the formation of a posterior cranial platform (Figs 26 & 29).

The *posttemporals* in *Aspius*, *Pseudaspius*, *Aspiolucius* and *Elopichthys* are like those in *Luciobrama* (Figs 3, 26 & 29), namely, lamellate ventrally with a long anterodorsal extension, bordered ventrally by the lateral extrascapula.

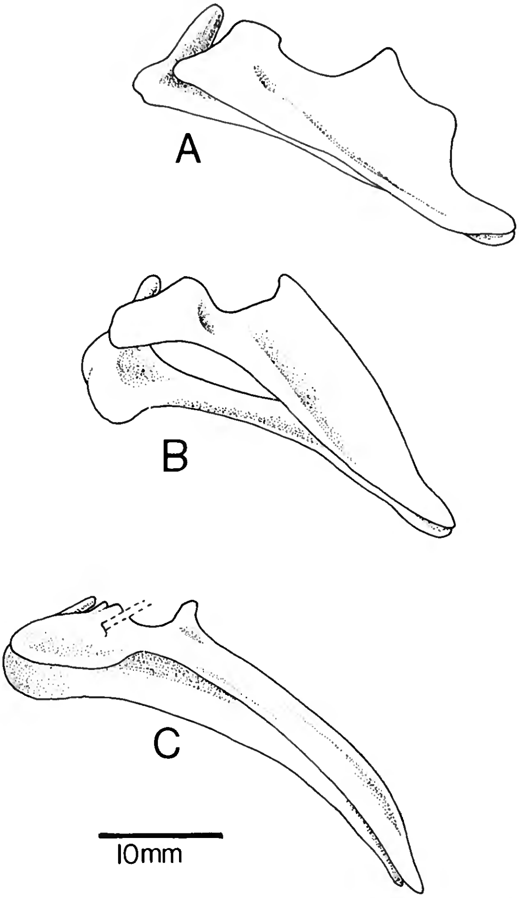

Fig. 34 Upper jaws, in lateral view of: A. *Aspius vorax*, B. *Opsariichthys uncirostris*, C. *Barilius bola*.

The *extrascapula* is variously developed in the cyprinids (noted by Ramaswami, 1955b : 218 -as supratemporal). I have found it as an ellipsoid bone in *Aspius*, thin and elongate in *Elopichthys* and varying from a plate-like element lying over the posterior part of the pterotic (as in *Squaliobarbus*) to a lamellate bone running between the posttemporal and pterotic (as in *Paralaubuca*).

The jaws

The *upper jaw* in *Aspiolucius* and *Pseudaspius* appears, from radiographs, to be similar to that of *Luciobrama* (Fig. 7). In *Aspius* the premaxilla is thin with a large plate-like ascending anterior process.

The premaxillae of *Elopichthys* are massive beak-like structures sutured along their midlines, except for a small anterior foramen. The ventral border of the bones is very sharp edged. The maxillae possess very long anterior medial processes, but the palatine processes are much reduced. The ventral border of the maxilla lies medial to the premaxilla and posteriorly it curves to project ventrally beyond the end of the premaxilla (Fig. 35).

The premaxillae in *Opsariichthys* are very slender bones. At the symphysis the ventral border is rounded. The dorsal border of the maxilla displays a marked concavity anteriorly which is the point of insertion of the maxillary-palatine ligament. The anterior medial process of each maxilla contacts its fellow from the opposite side along a narrow face. The maxilla is separated quite widely for part of its length from the premaxilla. The bones contact each other at their anterior and posterior margins.

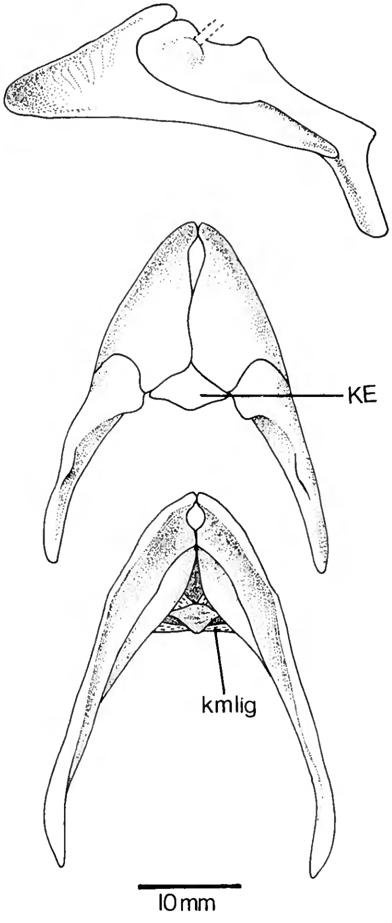

Fig. 35 *Elopichthys bambusa*, upper jaw. Lateral, dorsal and ventral views.

In *Barilius* the anterior tip of each maxilla is extended forward and curved medially so as to almost contact its counterpart. The medial process of each bone, which underlies the anterior ascending process of the premaxilla, meet each other along the midline and maintain contact along a wide surface. These medial processes (maxillary rostral process of Ramaswami, 1955b) do not appear to contact each other in other cyprinid genera examined but are connected across the midline by a ligament.

The upper jaw of *Barilius bola* is greatly elongate when compared with that of *Opsariichthys* (Figs 34B & C). The premaxilla is extremely long and thin, and dorso-laterally is overlapped for almost its entire length by the maxilla. The anterior ascending process of the premaxilla is beak-like and resembles that of *Elopichthys* (*cf.* Fig. 35) but is not so extensively developed.

Another cyprinid which is characterized by its long jaws is *Macrochirichthys* (see Howes, 1976). Here the upper jaw has a complex symphysial joint, mesial extensions being developed on the maxillae which serve to separate the two halves of the jaw to allow for the accommodation of the symphysial knob of the dentary when the jaws are closed.

In most *Barbus* and *Labeo* species examined the maxilla possesses a wide palatine process. The mesial processes are short and are connected with each other by a long ligament. The ventral border of the maxilla overlaps the premaxilla for only part of its length.

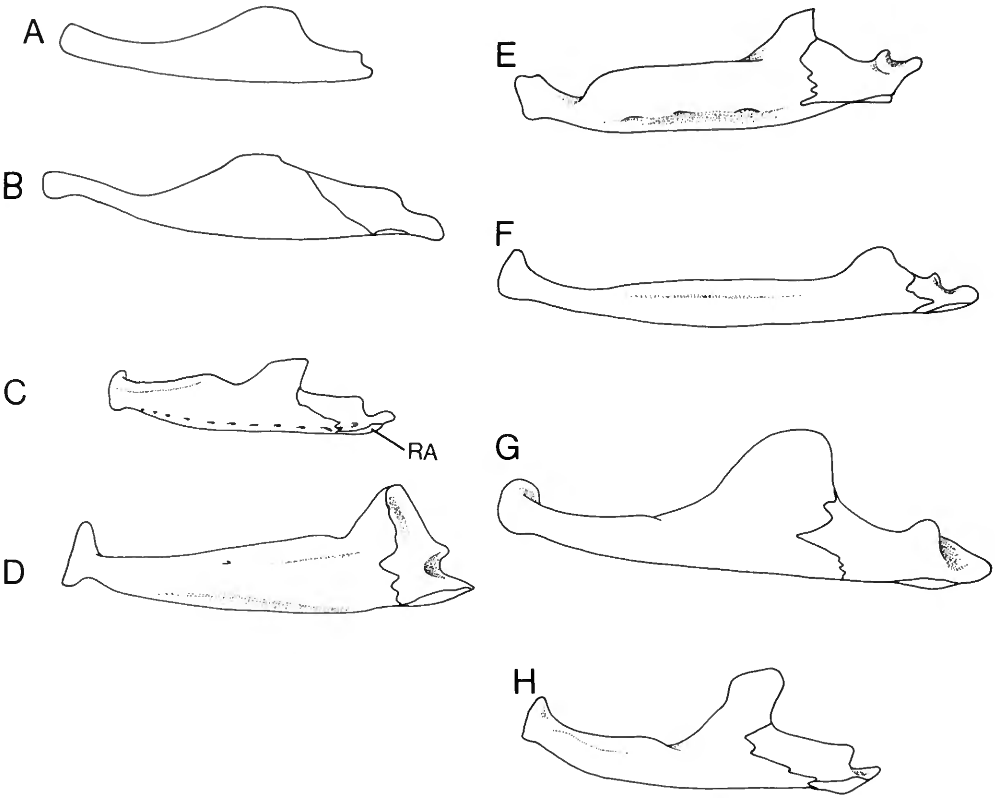

Fig. 36 Lower jaws of: A. *Pseudaspius leptocephalus*, B. *Oreoleuciscus pewslowi*, C. *Aspius vorax*, D. *Elopichthys bambusa*, E. *Opsariichthys unicirostris*, F. *Barilius bola*, G. *Schizothorax esocinus*, H. *Erythroculter mongolicus*.

The *lower jaw* in *Aspiolucius* and *Pseudaspius* is of the same narrow, canoe-shape as in *Luciobrama*. There are 14 pores in the mandibular canal on the dentary, plus 2 on the anguloarticular.

In *Aspius* (Fig. 36C) the dentary is proportionately thicker with an expanded symphysial process. The posterior border of the coronoid process is almost perpendicular, with the anguloarticular extending backwards from it at right angles. The dentary-anguloarticular junction in *Aspius* most closely resembles that of *Erythroculter* and *Opsariichthys* (Figs 36E & H).

In *Elopichthys* (Fig. 36D) the dentary is very thin, the tapered and hammer-shaped symphysial process fiting into the corresponding curvature of the upper jaw when the mouth is closed. Posteriorly the coronoid process rises steeply to meet the anguloarticular. Like *Luciobrama*, the dorsal border of this process is continuous and not broken as it is in the other genera.

The dentary of *Opsariichthys* (Fig. 36E) bears a strong symphysial process followed by a notch and then a curved thin wall which rises gradually to form the ascending process. A similar notch can be found in *Paralaubuca* and *Macrochirichthys* (see Howes, 1976 : 244).

In *Barilius bola* (Fig. 36F) the dentary is exceedingly thin and gently concave just before it enlarges to form the symphysial knob. There is a low ascending process. The other *Barilius* species examined exhibit a lower jaw similar to that of *Opsariichthys*. The number of mandibular pores ranges from 6 to 12 in both genera.

The dentary of *Leuciscus*, *Barbus* and *Labeo* is invariably short and narrow, tapering anteriorly in *Barbus* and *Leuciscus* but expanded in *Labeo*. In these genera the jaws curve sharply medially, whereas in all those genera mentioned previously the curve is a shallow one (see below).

The dentaries of *Luciobrama*, *Aspiolucius* and *Pseudaspius* have weakly developed symphysial processes; posteriorly the curve of the dorsal margin of the coronoid process is continued by the anguloarticular instead of there being an abrupt discontinuity as noted in *Aspius* (Fig. 36C). This form of articulation of the dentary with the anguloarticular is encountered in many 'primitive' teleosts (*Elops*, *Esox*, *Hoplias* and most of the characoids). In the case of *Luciobrama*, etc. it is likely that this type of lower jaw has been derived from the condition found in *Aspius* and *Opsariichthys*, the larger adductor mandibulae muscles requiring a greater area of bone for insertion. It is of interest to note that the posterior part of the lower jaw of *Oreoleuciscus* (Fig. 36B) greatly resembles that of *Luciobrama*, although the anterior part of the jaw is narrowed and curved like that of a 'typical' leuciscine.

Matthes (1963) and Liem (1970) pointed out that the presence of a high coronoid process on the lower jaw increased the power and speed at which the jaws could be closed. Only in *Elopichthys*, *Schizothorax*, *Erythroculter*, *Pelecus*, *Leuciscus* and some species of *Barbus* and *Labeo* can the coronoid process be considered as relatively high. In such exclusively piscivorous cyprinids as *Luciobrama*, *Barilius bola* and *Macrochirichthys* the process is low. In this respect it is probably the distance and angle of the coronoid process from the point of articulation with the quadrate which is more important. It will be noted by referring to Fig. 36 that in the long-jawed species in which the jaw is aligned at an angle (represented here by *Barilius bola*), the coronoid process is placed well posteriorly and is relatively low, whereas in *Elopichthys*, where the jaw is aligned horizontally, the coronoid is high, although still placed well back.

In some cyprinids the coronoid process is placed close to the anterior tip of the jaw. This apparent forward movement is due in part to the greater mesial curvature of the dentary and its subsequent foreshortening, seen particularly in *Labeo* and *Barbus* species where it is correlated with the broadening of the head. In these fishes the higher the coronoid region the greater the area available for the adductor mandibulae muscles which operate at a greater angle than those in the long-jawed species, where the muscle fibres lie partially horizontally. Dr Keith Banister has pointed out to me that in some species of *Barbus* this forward movement of the coronoid process is more real than apparent, and that it seems correlated with a definite shortening of the ethmoid region.

Ramaswami (1955b : 223) remarks that the upper jaw bones of cyprinids show a uniform morphology. Generally speaking this is true. Most cyprinids rely on protrusion of the upper jaw and employ suction feeding (Alexander, 1964, 1966, 1967 & 1969), and this requires a particular association between the maxilla and the premaxilla.

The extent of movement of the upper jaw in *Luciobrama* appears to be rather restricted. The ascending processes of premaxillae are not particularly long, and manipulation of preserved material shows that the upper jaw is not very protractile.

From measurements of the bones and manipulations of the jaws of *Barilius* it would seem that the shorter jawed species possess more mobile upper jaws than do the longer jawed species such as *B. bola* where, like *Macrochirichthys*, there appears to be very restricted movement of the premaxilla.

It must be emphasized that these observations have been made on preserved material only and so must be open to doubt.

In *Elopichthys* the upper jaw is so modified that the only kind of movement possible is rotation against the ethmoid (see p. 41), and jaw action here must be centred upon fast snapping action (an almost parallel jaw action can be seen in the African characoid, *Phagoborus*).

Greenwood (1974) noted that in piscivorous cichlids the long lower jaw is accompanied by a highly protrusile upper jaw (this is particularly noticeable in the South American cichlid genus *Petenia*). But in the long-jawed piscivorous cyprinids the reverse seems to be the case. Here the elongation of the jaws has been by posterior extension and this has necessitated a correlated movement of the hyopalatine arch so that the shaft of the hyomandibula is perpendicular and the jaw articulation is moved backward and downward to below the orbit. There has been no great extension of the anterior ascending process of the upper jaw nor of the ethmoid–vomerine region of the cranium. Only in *Elopichthys* has any marked modification been achieved in the forward extension of the upper jaw. However, I consider this fish to be a 'long-headed' rather than a 'long-jawed' cyprinid and in these species the hyopalatine arch is differently orientated (see further discussion on p. 61).

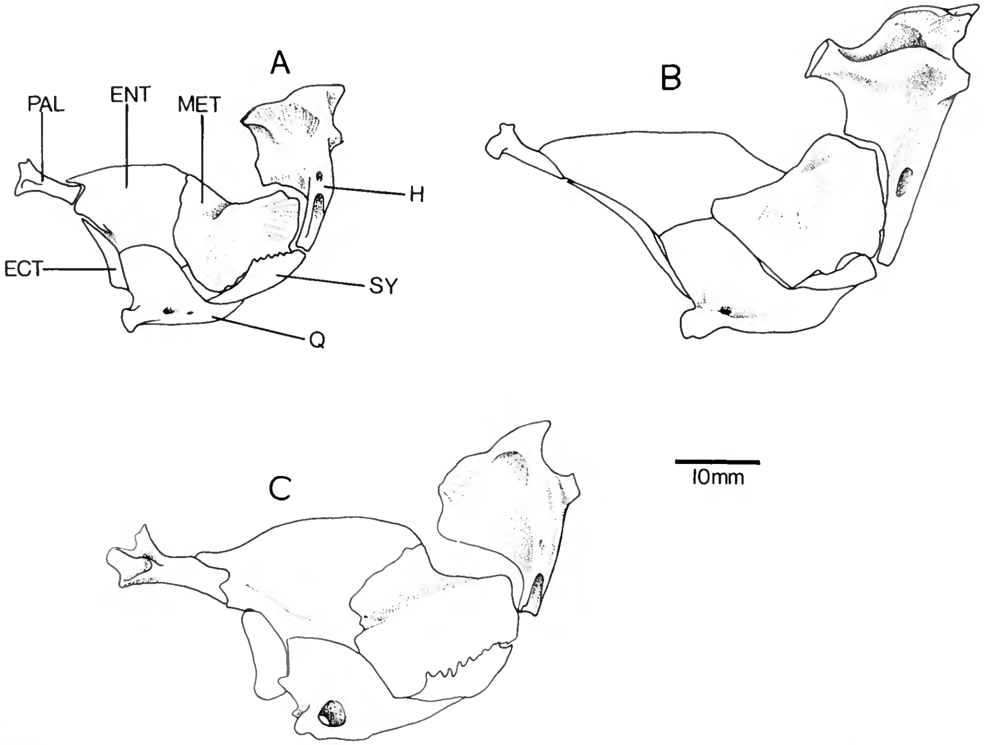

Fig. 37 Hypopalatine arches shown in lateral view of: A. *Aspius vorax*, B. *Elopichthys bambusa*, C. *Erythroculter mongolicus*.

Hyopalatine arch (Figs 37 & 38)

I am unable to determine the precise nature of the elements constituting the hyopalatine arch in *Aspiolucius* and *Pseudaspius*. From radiographs it is possible to follow the outline of the bones, and these closely resemble the description given below for *Aspius*.

In *Aspius* (Fig. 37A) the ventral limb of the *hyomandibula* is short, the posterior border of the bone is convex and the lateral face bears a shallow depression. By contrast, the hyomandibula of *Elopichthys* (Fig. 37B) has a well-developed flange in this position.

The hyomandibula in *Opsariichthys* and *Barilius* (Figs 38A & B) is vertically aligned; the ventral limb is thick and long. Here too the lateral face bears a wide flange along which the *dilatator operculi* muscle runs.

A lateral flange is also present on the hyomandibula of *Barbus tor* but is absent in other species of *Barbus* I have examined.

In *Macrochirichthys* the hyomandibula has a lateral process on which is inserted the *levator arcus palatini* muscle (see Howes, 1976). Similar lateral processes serving for muscle attachment are present in *Pseudolaubuca*.

In *Hypothalmichthys* the lateral surface of the hyomandibula is strongly curved outward so that the suspensorium lies beyond the cranial border.

The *quadrate* of *Aspius* (Fig. 37A) is a short high bone separated by a wide area of cartilage from the metapterygoid. The anterior border is perpendicular, the dorsal border curved. A small foramen is present posterior to the articulatory condyle, a feature shared with *Luciobrama* (see p. 15). I have found such a foramen in four other genera: *Elopichthys* and *Erythroculter*, in which it is large (in the skeleton of *Elopichthys* examined, the foramen is present only in the right quadrate); *Pseudoxygaster* and *Macrochirichthys*, in which it is minute.

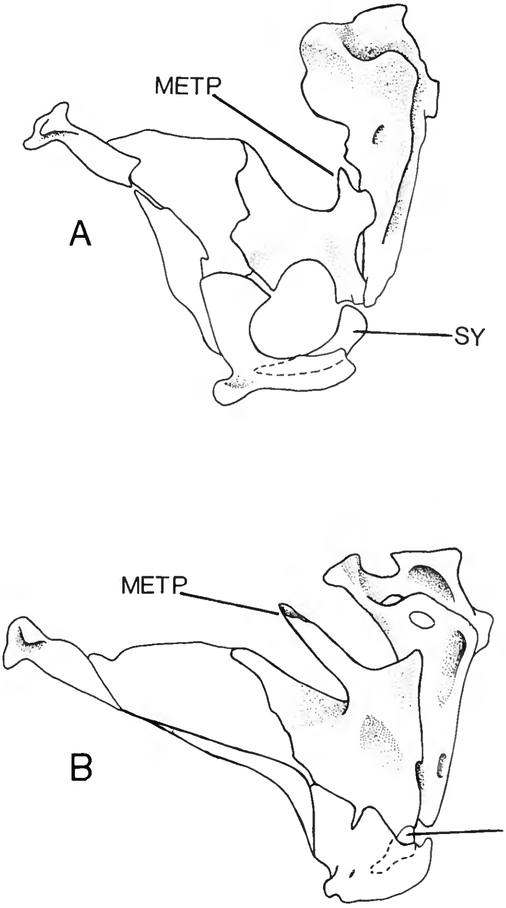

Fig. 38 Hyopalatine arches shown in lateral view of: A. *Opsariichthys uncirostris*, B. *Barilius bola*.

The quadrate of *Opsariichthys* is a thin, curved bone, the dorsal border being concave and forming the margin of a large fenestra. This feature is shared with *Zacco*, where the fenestra is not so well developed, with *Macrochirichthys*, in which it is about equally developed, with *Pseudoxygaster* and with *Salmostoma*. Further discussion of the metapterygoid–quadrate fenestra appears on page 46.

The *symplectic* is an extensive bone in most of the genera examined. Medially it overlaps the posterior extension of the quadrate. In *Opsariichthys* the symplectic forms the postero-ventral border of the metapterygoid–quadrate fenestra. In *Barilius* it is a small element lying medial to the quadrate (Fig. 38B). Ramaswami (1955b : 224) comments on the symplectic in other cyprinid genera.

A *dermopalatine* has not been found in any of the genera examined.

The *autopalatine* varies little in the genera examined. Differences involve the degree of development of the articular head with the ethmoid; it may be very wide and flat in this region as in *Hypophthalmichthys* or rod-shaped as in *Luciobrama*. The medial face of the palatine is almost always concave. There is also variation in its articulation with the entopterygoid. Usually this is by way of a right-angled indentation in the entopterygoid bnt sometimes as in the case of *Barilius bola* (Fig. 38B) and *Elopichthys* (Fig. 37B) the edge of the palatine may be sloped and partly overlapped laterally by the entopterygoid. In both *Opsariichthys* and *Barilius* the palatine is laterally compressed and in the former genus bears a ventral keel.

The *ectopterygoid* in most cyprinids is a thin sheet which partly underlies the medial face of the quadrate and the ventral margin of the entopterygoid. The 'generalized' condition of this bone appears to be wide with a slightly concave to convex anterior mrgin. In the long-jawed taxa such as *Elopichthys*, *Macrochirichthys* and *Barilius bola* the ectopterygoid is very narrow with a markedly concave anterior border, *Figs* 37B & 38B. Only in *Luciobrama* (and possibly in *Aspiolucius*) does the ectopterygoid appear to be rod-shaped.

The *entopterygoid* is generally short and deep, its dorsal border rounded. In *Luciobrama*, *Aspiolucius*, *Pseudaspius* and *Elopichthys* the bone is narrow and long with a straight dorsal margin. In broad-headed species of the genera *Barbus* and *Labeo* the entopterygoid is markedly medially directed and often bears a thick ridge along the fold for the insertion of the *adductor arcus palatini* muscle.

Ramaswami (1955a) notes the presence in *Labeo macrostoma* and *Cyprinus carpio* of a mesial facet on the entopterygoid which articulates with the lateral ethmoid. Other *Labeo* species I have examined have this facet variously developed and it seems to be well developed in those species with a long ethmoid but is virtually absent in those with a short ethmoid. In other cyprinid genera this part of the entopterygoid is usually a wedge-shaped platform and varies considerably in size.

The *metapterygoid* of almost all genera examined is deep with the lateral ridge developed to varying degrees depending on the angle at which the bone is directed mesially toward the parasphenoid. The dorsal border is invariably concave (the one exception to this rule being *Luciobrama*). In *Opsariichthys* (Fig. 38A) the metapterygoid is narrow and axe-shaped, its ventral border forming the dorsal margin of the metapterygoid–quadrate fenestra. Posteriorly it is sutured to the hyomandibula. There is a small ascending process on the dorso-posterior edge of the bone (METP). *Barilius bola* has a similar metapterygoid process but in this case it is developed as a long anteriorly directed spine which serves both as the point of origin for the *adductor mandibulae* A3 and for the insertion of the *levator arcus palatini* muscles. Posteriorly, the metapterygoid has a long perpendicular border in contact with the hyomandibula (Fig. 38B). A metapterygoid spine appears to be present in all the species of *Barilius* I have examined but in none it is developed to the same degree as in *B. bola*. There is no metapterygoid spine in *Zacco*.

The significance of the metapterygoid–quadrate fenestra has been discussed by Regan (1911)[1] and remarked on again by Ramaswami (1955b), Weitzman (1962), Gosline (1973, 1974 & 1975) and Howes (1976). Most authors, including Regan (1911), have assumed it to be a generalized or primitive character. Gosline (1973), however, expressed doubts about this, and was inclined to attach more significance to the state of the entire pterygoid complex.

In those genera with a long postorbital cranium (*Luciobrama*, *Aspiolucius*, *Pseudaspius*) the hyomandibula has a short ventral limb which is directed anteriorly, and there is also an increase in the length of the pterygoid bones but not in their depth. In the majority of cyprinids the hyomandibula is a deep bone with its shaft aligned almost perpendicular to the skull. The pterygoid bones are also short and deep and in those genera with wide and depressed crania the metapterygoid is often acutely directed mesad toward the parasphenoid (e.g. *Labeo*) thus providing a large space to accommodate the thick *adductor mandibulae* muscles.

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[1] Regan (1911) stated that a fenestra is present in *Chela* but he did not designate the species. I have been unable to detect it in any species now assigned to the genus *Chela* (Bănărescu, 1968) and I suspect that Regan was in fact referring to *Macrochirichthys*, which he knew as *Chela macrochir*. It would seem that the skeleton of *Macrochirichthys macrochirus* in the BMNH collection which was available to Regan was the only skeleton bearing the generic name *Chela* at the time he would have examined it.

If a comparison is made with the situation in characoids where the metapterygoid–quadrate fenestra is widespread the following points emerge.

In the majority of characoids there does not seem to be the same degree of dorsal extension of the pterygoid bones as occurs in cyprinids. The ectopterygoid and overlying entopterygoid are long (a correlate of the generally more elongate snouts and jaws of characoids). However, in broad-headed characoids such as *Erythrinus*, *Lebiasina*, *Citharinus*, and in some leporinids and prochilodontids the pterygoid bones are deep and directed acutely mesad as in the broad-headed cyprinids. In these cases the metapterygoid–quadrate fenestra is either absent or reduced. Furthermore, it is noted that the *adductor mandibulae* and *levator arcus palatini* muscles in the characoids do not utilize the surfaces of the pterygoid bones to the same degree as in the cyprinids and in those characoids where the *adductor mandibulae* muscles are particularly extensive (*Hepsetus*, *Ctenolucius*, *Acestrorhynchus*, *Salminus*) there has been a forward extension of the hyomandibula along the dorsal margin of the metapterygoid thereby providing the additional surface area of attachment (see Roberts, 1969).

The fenestra between the quadrate and metapterygoid is certainly a functional device which would seem to serve either to relieve stresses by directing forces generated in the lower jaw around the perimeter of the pterygoid bones and into the cranium or perhaps, more importantly, it acts as a type of hinge which enables the pterygoid bones to undergo lateral rotatory movements. Again, it is noted that those characoids in which the fenestra is reduced are those in which there is little or no development of the symphysial articulation of the lower jaw – as in most of the cyprinids. There are also differences in the articulation of the palatine with the ento- and ectopterygoids in the broad-headed and narrow-headed cyprinids which indicate different degrees of lateral rotation.

The exact functional significance of this fenestra is not obvious and may only be realized when all the vectors have been analysed. Whatever its use as a stress-relieving or force-directing device, one possible advantage of this feature seems that in *Macrochirichthys*, *Pseudoxygaster* and *Salmostoma* its presence has allowed the jaw articulation to move further forward than in other cyprinids. The jaws of *Macrochirichthys* are proportionately as long as those of *Barilius bola* and it might be supposed that retention of such a fenestra would also have been an advantage to this bariliine. However, in *Barilius* there is a well-developed *adductor mandibulae* A3 muscle extending from the dorsal process of the metapterygoid (see p. 55), whereas in *Macrochirichthys* and *Pseudoxygaster* A3 originates from the hyomandibula (see Howes, 1976 : 242). The development of this muscle and bone in *Barilius* as a functional unit could account for a ventral expansion of the hyomandibula so as to occlude any opening that may have been present in the ancestral form. Some confirmation of this comes from my current studies on *Salmostoma* in which there is a reduction in the size of the metapterygoid–quadrate fenestra in those species with the longer jaws.

My current researches on *Macrochirichthys* indicate that neither it, *Salmostoma* nor *Pseudoxygaster* are at all closely related to *Opsariichthys* or *Zacco* and so the metapterygoid–quadrate fenestra cannot therefore be regarded as a synapomorph feature. I conclude that it represents a primitive cypriniform character (widespread occurrence in the Characoidei) and that in *Opsariichthys* and those genera in which it occurs it should be considered as plesiomorph. Possibly the potentiality for its development was inherited in several lineages and was realised (as in *Macrochirichthys*) under the necessary combination of selective pressures.

Opercular series

In *Aspiolucius*, *Pseudaspius* and *Aspius* the morphology of the opercular elements closely resembles that in *Luciobrama*; the pre-, inter- and subopercula are extensive bones. The operculum has a long concave dorsal border and a well-developed anterior extension for the insertion of the *dilatator operculi* muscle. The medial strut contains two ventral foramina. The preoperculum has 9–10 pores along the ventral border.

In *Elopichthys* the vertical limb of the preoperculum is longer and the horizontal limb shorter, than in the genera mentioned above. The ventral border bears 6 pores. The medial strut of the operculum is feeble and contains a single large foramen.

In *Opsariichthys* and the majority of *Barilius* the lower limb of the preoperculum does not extend so far forward and the ascending process of the limb is almost vertical. Three pores of the mandibular lateral line canal are present on the ventral border. The operculum is deep, with a short dorsal border; it lacks the prominent anterior extension for the *dilatator operculi* muscle. The interoperculum in *Barilius bola* has been greatly reduced in length, a change in proportion correlated with the backward shift of the jaw articulation (see above, p. 43).

Most *Barbus* and *Labeo* species have a wide, vertically orientated preoperculum which has a short ventral limb. The operculum generally is deep, with a short dorsal border, but *Barbus tor*, *B. longiceps* and *B. barbus* all have a long dorsal border.

A large operculum with a long dorsal border appears characteristic of some predatory cyprinids, e.g. *Pelecus*, *Macrochirichthys* and *Erythroculter*, where it is associated with a shallow, acutely angled preoperculum. This is the situation encountered in *Luciobrama*, *Aspiolucius*, *Pseudaspius* and *Aspius* in which are present noticeably elongate pre-, inter- and subopercula. There is an opposite situation in the long-jawed *Barilius* species where an operculum with a short dorsal border is associated with deep and narrow opercular elements.

Hyoid and branchial arches

HYOID ARCH. There is little variation in the morphology of the elements comprising the hyoid arch in the genera studied.

All the branchiostegal rays, apart from the first, are expanded proximally.

The urohyal is variously developed, sometimes being channelled ventrally as in *Aspius* and *Opsariichthys*, or flat, as in *Barilius* and *Barbus*. The medial plate can be short and high as in *Schizothorax* or reduced to a slight ridge as in *Elopichthys*.

The basihyal is greatly elongated in *Luciobrama* (p. 17), a condition also encountered in *Aspiolucius* and *Elopichthys*.

THE BRANCHIAL ARCHES. Intergeneric comparison reinforces Ramaswami's (1955b) opinion that there is a general uniformity in the branchial elements of cyprinids.

I have not found either first or fourth infrapharyngobranchials represented as an ossified element.

There is some variation in the development of the dorsal processes on the epibranchials.

The *pharyngeal teeth* of *Aspiolucius* are arranged in two rows with 3–5 teeth, those of *Pseudaspius* in two rows (2–4), of *Aspius* in two rows (3–5) and of *Elopichthys* in three rows (5–3–2 or 5–4–2).

The whole problem of what constitutes a primitive pharyngeal dentition in the cyprinids has been discussed at length by numerous authors (see Nelson, 1969 : 513). In the case of *Luciobrama* it seems evident that a single row of pharyngeal teeth is a derived condition.

Weberian apparatus and swimbladder

In *Aspius*, *Elopichthys* and, as far as I can tell from radiographs, in *Aspiolucius* and *Pseudaspius*, the os suspensorium is curved anteriorly, the lateral processes of the fourth centrum (PR4) are short and thin, and those of the second centrum (LP2) are curved slightly dorsad. In all these genera, except *Aspius*, the second neural plate contacts the supraoccipital, and the fused neural complex is in contact with a supraneural plate.

In *Luciobrama*, *Aspius* and *Elopichthys* (Figs 39A & B) the second and third centra are not completely fused. Dorsally a distinct separation can be detected; ventrally this is not so clearly defined since the suture line is always visible and there is never the complete fusion seen in other cyprinids where the division between the centra has become completely obliterated.

In *Opsariichthys* and *Barilius* (Fig. 39D) the lateral processes of the fourth centrum (PR4) are weakly developed and directed posteriorly. The lateral processes of the second centrum are greatly expanded laterally and are not curved. The tripus in these genera is very elongate. The second and third centra are separated in *Opsariichthys* but they are fused in *Barilius*.

In *Schizothorax*, *Barbus* and *Labeo*, and in the majority of genera examined, the os suspensorium is curved anteriorly and the lateral processes of the fourth centrum are well developed; those of *Barbus* are often expanded distally.

In *Macrochirichthys* and *Pseudoxygaster* the os suspensorium is very short and vertically directed; the tripus is elongate and the second and third centra are separated and in *Pelecus* (Fig. 39C) the os suspensorium is almost horizontally directed. Although *Pelecus* has been included in the Cultrinae along with *Macrochirichthys* and *Pseudoxygaster* (see Bănărescu, 1967) there are many differences in the structure of the anterior part of the vertebral column. The first and second centra of *Macrochirichthys* and *Pseudoxygaster* are greatly modified, whereas in *Pelecus* these centra are of a generalized nature. (Work is in progress on the description and analysis of these elements in the Cultrinae.)

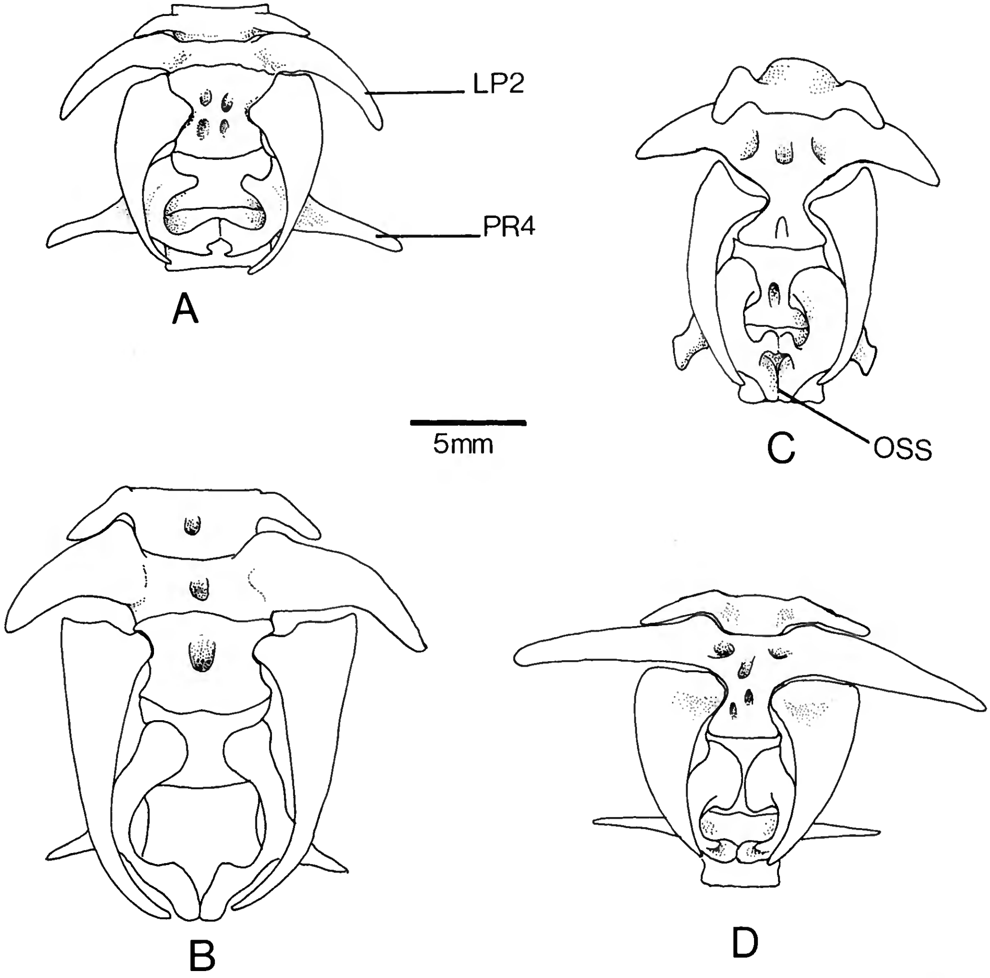

Fig. 39 Weberian apparatus shown in ventral view of: A. *Aspius vorax*, B. *Elopichthys bambusa*, C. *Pelecus cultratus*, D. *Barilius microcephalus*.

Sorescu (1972) studied the Weberian apparatus of representatives of the subfamilies Danioninae and Cultrinae. Her ideas of primitive and specialized characters exhibited by these skeletal elements are ill-defined and her conclusions concerning the relationships of the Cultrinae and Danioninae – neither of which are monophyletic assemblages – are, in my opinion, invalid.

As far as I am aware no comparative study has been made of the *swimbladder* throughout the Cyprinidae. Tchang (1933) frequently notes the condition of the swimbladder in various genera.

He mentions that the organ in *Opsariichthys* is enclosed in a bony capsule. I can find no evidence to justify this statement.

The swimbladder in most of the genera studied is a simple bipartite structure. In some genera at present included in the Cultrinae there is a further posterior division.

Pectoral girdle

In *Aspiolucius*, *Pseudaspius* and *Aspius* the pectoral girdle is similar to that of *Luciobrama*. In all these genera the horizontal limb of the cleithrum is directed forward to a point below the anterior border of the prootic, and (except in *Aspius*) it is bifurcated anteriorly. The coracoids are joined only anteriorly. The mesocoracoid in *Aspius* is a thin bridge of bone. The postcleithrum in *Aspiolucius* and *Aspius* is short, like that of *Luciobrama* but in *Pseudaspius* it is elongate. The supracleithrum is elongate in *Aspius*, while that of *Aspiolucius* and *Pseudaspius* is of a length intermediate between that of *Aspius* and *Luciobrama*.

In *Elopichthys* the anterior margin of the ventral limb of the cleithrum is very wide, the ascending limb short. The mesocoracoid is wide and the coracoids are joined medially for half of their lengths. The postcleithrum is very long and the supracleithrum as elongate as that of *Aspius*.

In both *Opsariichthys* and *Barilius* the vertical limb of the cleithrum is narrow. The coracoids are joined anteriorly, the mesocoracoids are long and narrow, the supracleithra elongate and the postcleithra very long and spine-like.

A similar kind of arrangement, but with the upright and horizontal arms of the cleithrum broadened, is found in *Barbus* and *Labeo*.

Throughout the cyprinids there appears to be considerable variation in the degree of development of the cleithral–coracoid fenestra which may, as in the case of *Chela*, be entirely lacking. The development of this feature appears to be associated with the variation of the pectoral fin muscles and ventral extension of the coracoids.

In *Salmostoma*, *Oxygaster*, *Pseudolaubuca*, *Paralaubuca*, *Pelecus*, *Pseudoxygaster*, *Chela* and *Macrochirichthys* there is a great expansion and complete, or almost complete, medial contact of the coracoids (see description of pectoral girdle of *Pelecus* by Rauther, 1950).

Regan (1911 : 28–29) states that '*Barilius*, *Danio* etc. agree with *Opsariichthys* in the form of the cleithra, rounded or pointed anteriorly, and these are connected by genera such as *Aspius* with *Leuciscus* and its allies, in which the cleithra are more expanded and truncated anteriorly . . . the *Barbus* group differs in that the cleithra are distinctly emarginate anteriorly'. Broadly speaking, the cleithra of all these genera are similar, but in *Barbus*, *Leuciscus* and *Alburnus* the curved dorso-lateral margin of the cleithral limb is raised into a blade-like ridge. Furthermore, it is not the case, as stated by Regan (see above), that all *Barbus* exhibit anteriorly emarginate cleithra. In *Barbus tor*, for example, the cleithra are forked anteriorly as in *Luciobrama*, providing two places of origin for the *sternohyoideus* muscle (see p. 19).

One variable element of the pectoral girdle is the postcleithrum. It is usually found as a long medially curved bone which reaches its most extensive development in *Macrochirichthys*. In some genera (e.g. *Salmostoma*) it is reduced to a short spike and in *Barilius* appears as a small scale-like bone, whilst in *Pseudoxygaster* it appears to be entirely lacking (although it may possibly be identified as a modified external scale above the pectoral fin).

Sorescu (1968) uses the morphology of the pectoral girdle as a principal character in differentiating cyprinid subfamilies. She has placed reliance on similarity of shape of the elements to indicate affinity. This has led, for example, to placing *Barilius zambezensis* in the Cultrinae without taking account of other *Barilius* species. Sorescu's failure to utilize other and probably more significant cranial characters, and her apparent failure to recognize parallelism, renders her conclusions doubtful.

Pelvic girdle

There is little variation in the pelvic girdle. In some genera the pelvic bone is only shallowly forked, but as far as I am aware there are no cyprinids with an unforked pelvic bone, the usual condition in characoids.

Appendicular skeleton

VERTEBRAL COLUMN. The total number of *vertebrae* in *Aspiolucius*, *Pseudaspius*, *Aspius* and *Elopichthys* ranges from 51 to 54 (*cf.* 55 in *Luciobrama*).

Of the other genera examined, only *Pelecus*, *Hemiculterella* and *Ochetobius* possess more than 50 vertebrae. It is to be noted that in *Ochetobius* the increased number is in the posterior abdominal region (i.e. between the dorsal and anal fin bases). No other member of the Cyprinidae has such a distance between the posterior ray of the dorsal and the origin of the anal fin. In all remaining genera examined the total number of vertebrae is from 41 to 49.

The more elongate cyprinid species show an increase in vertebral number (see Lindsey, 1975). The proportions of the centra in all cyprinid genera I have examined are virtually identical. Only in *Macrochirichthys* and *Pseudoxygaster* is there any appreciable elongation of the precaudal centra, but in none have the caudal centra been lengthened.

Table 1 Vertebral counts of some Cyprinid genera. These are arranged in groups of what I believe to be related genera. W = Weberian vertebrae. * = Second and third centra separate or partially separated. ? = Condition unknown. A = Abdominal. C = caudal vertebrae. T = total number. SN = Supraneurals

Genus	W	A	C	T	SN
Luciobrama	4*	30	21	55	12
Aspiolucius	4?	27	23	54	13
Pseudaspius	4?	26	21	51	11
Aspius	4*	25–26	24	51–52	13–14
Elopichthys	4*	25–27	22–23	52–54	15–16
Barilius spp	4	16	23–25	43–45	11
Barilius bola	4	22	21	48	13
Opsariichthys	4*	19	21	44	6–7
Oxygaster	4*	16	23	43	13
Pseudolaubuca	4*	17	26	47	15
Pseudoxygaster	4*	19	21	44	12
Macrochirichthys	4*	23	22	49	16
Hemiculterella	4*	17	23	44	10
Pelecus	4	24	24	52	22–23
Erythroculter	4	19	23	46	7
Parabramis	4	19	21–22	45–46	5–6
Paralaubuca	4	16	22	42	12
Schizothorax	4	22–25	19–20	45–49	11
Oreinus	4	22–24	20–21	47–48	12–13
Leuciscus	4	21–22	20–22	46–48	10–12
Abramis	4	20	22	46	10
Ochetobius	4	34	22–23	60–61	14

The total number of vertebrae in *Barbus* and *Labeo* never exceeds 48 (Banister and Reid, pers. comms).

The *supraneurals* vary considerably in their development and in their number, ranging from 5 to 6 in *Parabramis* to 23 in *Pelecus*. In *Luciobrama*, *Aspiolucius*, *Pseudaspius*, *Aspius* and *Elopichthys* they are thin rod-like structures, numbering 11–16, whereas those of *Schizothorax*, *Oreinus*, *Barbus* and *Labeo* are plate-like, numbering 10–13. In *Semiplotus* the supraneurals reach their most marked degree of development, expanding between the neural spines to form a rigid pre-dorsal septum along the vertebral column.

In *Macrochirichthys* the anterior supraneurals are horizontally aligned and are in contact with the enlarged neural spines (Howes, 1976 : 244). A similar arrangement is present in *Pseudoxygaster* and *Pseudolaubuca*.

MEDIAN FIN SKELETON. In all cyprinid genera examined the first proximal dorsal pterygiophore is expanded. In those with well-ossified anterior dorsal rays the corresponding proximal pterygiophores bear lateral struts.

Roberts (1973) comments on the number of radials (pterygiophores) supporting the dorsal and anal fin rays in cyprinids. He notes that there are three in *Opsariichthys* but that according to Bridge (1896) there are usually two in cyprinids. However, Bridge (*op. cit.*) did in fact identify three elements in all the cyprinids he examined, namely species of *Barbus*, *Cyprinus*, *Abramis* and *Tinca*.

In all the species I have examined there are three elements, distal, medial and proximal pterygiophores.

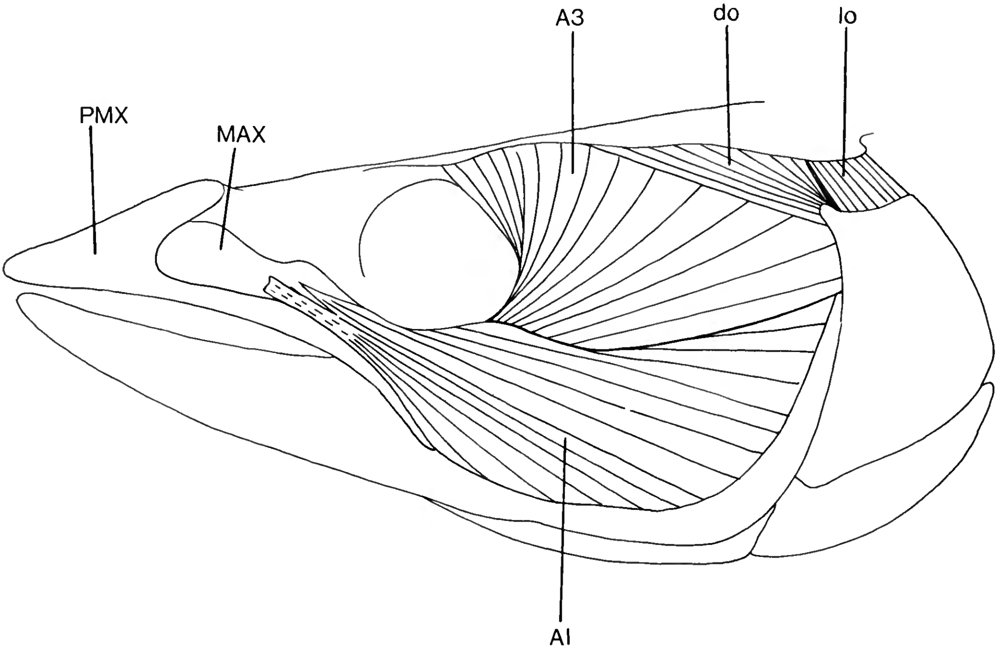

Fig. 40 *Elopichthys bambusa*, cranial musculature, superficial elements.

CAUDAL FIN SKELETON. In all the genera examined there is a marked consistency in the construction of the caudal fin skeleton. The only variation appears to be in the size of the first hypural and the number of epurals (either one or two).

Roberts (1973) gives 10+9 as the count for the principal caudal rays, but I count 9+9 in all genera examined.

Shukla & Verma (1972) have described the caudal fin skeleton of *Barilius bola*. They have, however, misidentified many of the elements and have used published descriptions of other cyprinids in their comparative treatment. Thus their conclusions concerning the 'primitive' nature of this species are very dubious.

Myological characters

Cranial muscles

Several workers have described the cranial muscles of various cyprinids (e.g. Takahasi, 1925, several genera; Ping *et al.*, 1958, *Cyprinus*; Saxena, 1960, *Garra*; Matthes, 1963, *Labeo*, *Barbus*, *Barilius* and other genera; Munshi & Singh, 1967, *Labeo* and *Cirrhina*; Meinel *et al.* 1970, *Barbus nasus*, *Ctenopharyngodon* and *Squalius*).

From a superficial dissection of the type specimen of *Aspiolucius esocinus* it would appear that the cranial muscles of this species are like those in *Luciobrama*. The *dilatator operculi* and *levator arcus palatini* are developed in the same way and the *adductor mandibulae* muscles are similarly arranged. I was unable to examine the arrangement of the deeper muscles. *Pseudaspius* and *Aspius* both exhibit the same basic arrangement as *Luciobrama*.

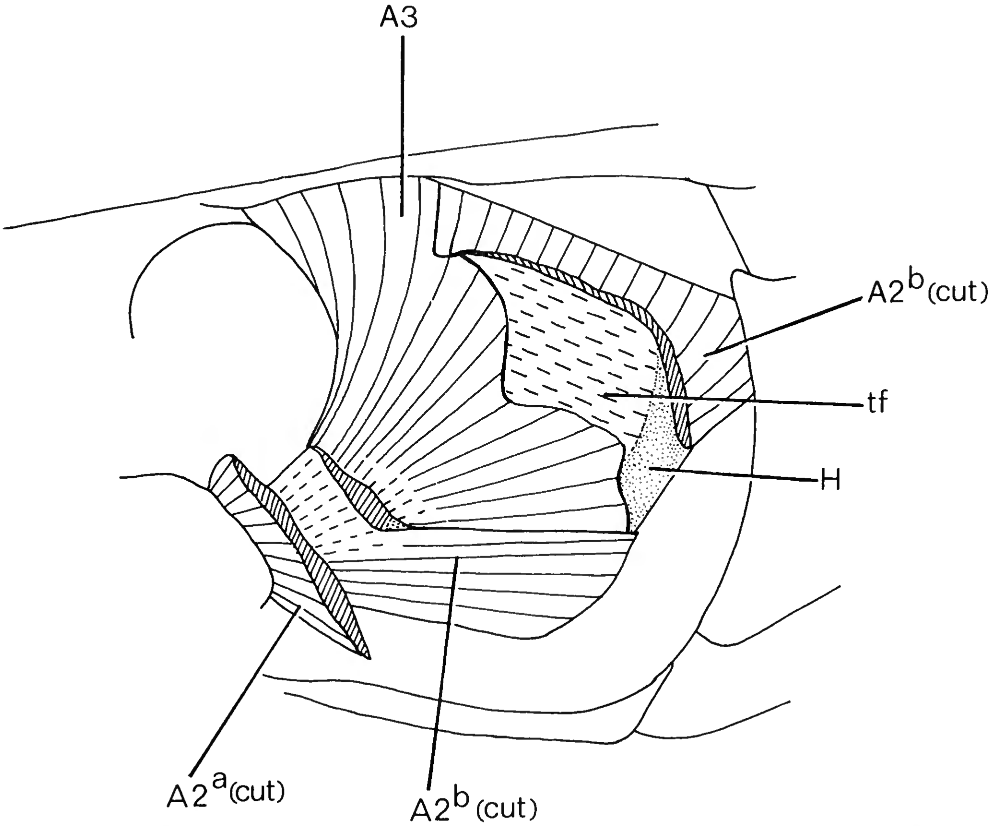

Fig. 41 *Elopichthys bambusa*, cranial musculature, deeper layers. *Adductor mandibulae* A2 is cut through to expose A3, which in turn is cut to show the tendinous fascia.

The cranial muscles of *Aspius aspius* have been described by Suslowska (1971). I have compared the muscles of *Aspius vorax* with those of *A. aspius* and find them to be of almost identical morphology. Suslowska (1971) does not recognize the conventional divisions of the *adductor mandibulae*. Although she points out that the external portion (A1) inserts on the maxilla, she does not state that it is bifurcated at this insertion.

The *levator arcus palatini* is extensive; a tendinous sheet extends through the lateral surface of the muscle to join the preoperculum and this provides a site of origin for part of the *adductor mandibulae* (A2). The *levator* is divided by A3. An *adductor arcus palatini* is present.

Suslowska (1971) noted the presence of an *adductor hyomandibulae*. The form of this and the other muscles she describes for *A. aspius* are as those in *A. vorax*.

The musculature of *Elopichthys* (Figs 40–44) resembles that of *Aspius* in that the *adductor mandibulae* is separable into its various parts only anteriorly. The *adductor mandibulae* A1 inserts via two tendons onto the maxilla (Fig. 40). A2 inserts onto the rim of the anguloarticular. Aw is poorly developed. The morphology of the inner element, A3, differs quite considerably from that described in any other cyprinid. This muscle originates partly from the frontal, partly from the pterosphenoid basin (see p. 32 & Fig. 42) and partly from the dorsal aspect of the sphenotic. Laterally it stems from the face of the sphenotic and pterotic and from a tendinous fascia covering the hyomandibula (tf, Fig. 41).

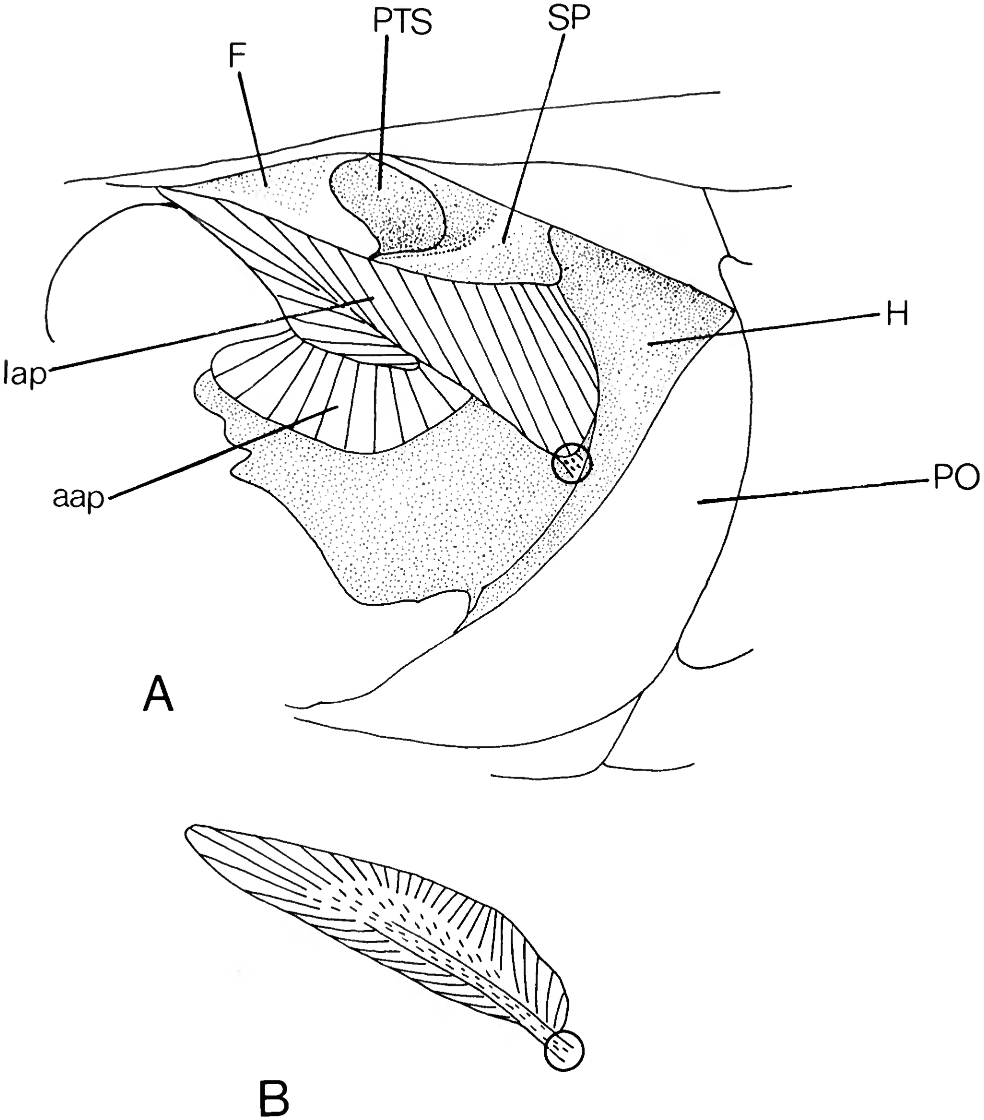

Fig. 42 *Elopichthys bambusa*, cranial musculature. A. Deep dissection to show *levator arcus palatini*; the *adductor mandibulae* muscles having been removed. B. Inner section of *levator arcus palatini*. The circle indicates that part of the tendon of the inner muscle which is visible before the outer layer is removed.

The *levator arcus palatini* in *Elopichthys* runs from the lower border of the frontal, the faces of the pterosphenoid and the sphenotic. The muscle is a complex one; the anterior bundle of fibres, which runs from the frontal, joins a medial pinnate sheet of fibres which originates from the face of the pterosphenoid and sphenotic to insert on the hyomandibula (Fig. 42A). The ventral border of this element is a stout tendon. When this outer layer is removed there is revealed a pinnate medial section with its fibres running in the opposite direction (Fig. 42B). When this medial layer is removed there is yet another, triangular sheet bordered anteriorly by a wide tendon (tlap, Fig. 43). This tendon stretches from the ventral surface of the frontal to insert upon the edge of the metapterygoid. The muscle fibres arise in part from the frontal but mostly from the sphenotic. Insertion is along the medial face of the hyomandibula. I would identify this medial element as an *adductor hyomandibulae*.

The *adductor arcus palatini* is a stout muscle which stems from the base of the prootic to insert ventrally upon the metapterygoid. The *dilatator operculi* runs across the upper border of the levator *arcus palatini* from the pterotic and sphenotic to the anterior process of the operculum. Medially the muscle originates in part from the face of the hyomandibula (a condition also found in *Pseudaspius*). Suslowska (1971) states that the *dilatator* inserts upon the hyomandibula in *Aspius*.

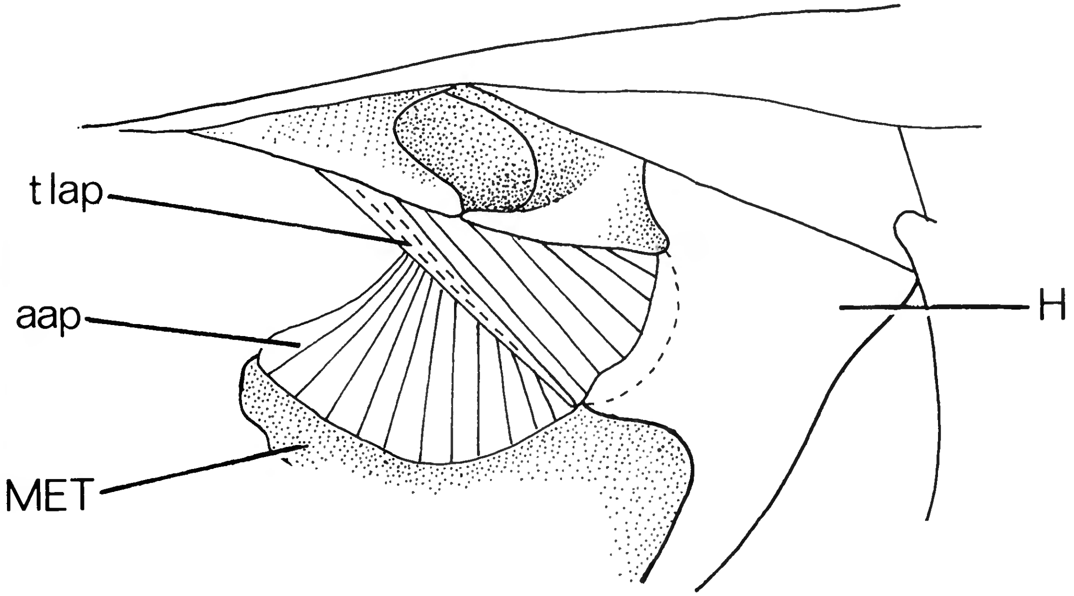

Fig. 43 *Elopichthys bambusa*, cranial musculature. The outer layers of the *levator arcus palatini* have been removed to expose the inner layer and the *adductor arcus palatini*.

In *Opsariichthys*, *adductor mandibulae* A1 is a single element inserting on the maxilla; A2 is a large muscle inserting on the anguloarticular and separated medially from A3 by the *levator arcus palatini*. Aw is present. The *dilatator operculi* originates from a discrete lateral fossa formed by the sphenotic. It is not covered by any part of the *adductor mandibulae* since this complex muscle originates below its ventral border.

In *Barilius* the *adductor mandibulae* A1 is a narrow, divided element (Matthes, 1963, recognized divisions A1a and A1b) the anterior part of which is bordered ventrally by a strong *ligamentum primordium*. It inserts along the lateral face of the maxilla. The larger element inserts via a thick tendon medial to the outer element. (In *Barilius bola* the medial section of A1 joins the maxilla along its distal border; there is no tendon of insertion, see Fig. 44.)

The A2 section of the *adductor* in *Barilius bola* and other long-jawed *Barilius* species is extensive, and originates from the preoperculum, pterotic and sphenotic; it gives rise to a reduced Aw section. A3 originates from the dorsal process of the metapteryoid (see p. 47). This process also provides the insertion area for the *levator arcus palatini* which originates from the ventral margin of the frontal and from the sphenotic. The *dilatator operculi* runs from the posterior part of the sphenotic process and is covered by A2. The *adductor arcus palatini* is well developed. In other, shorter-jawed *Barilius* species (e.g. *ubangensis*, *bendelisis*, *ornatus*) *adductor mandibulae* A2 is not as extensive, does not cover the *dilatator operculi* and does not originate from the sphenotic; the metapterygoid process is reduced and the *adductor arcus palatini* is small. In other words, the cranial muscle arrangement greatly resembles that of *Opsariichthys* (see Takahasi, 1925). Indeed, this basic type of morphology has been found in all the other cyprinid genera examined. There are, of course, modifications, as for example in *Oxygaster* and *Pseudolaubuca* where the anterior part of the *adductor mandibulae* A1 is narrowed and tubular; the dorsal part of the *levator arcus palatini* in *Pseudolaubuca* extends to insert upon the operculum together with the *dilatator operculi*; the *dilatator operculi* is divided in *Labeo*, and the *levator arcus palatini* is complexly divided, as described in this paper for *Elopichthys* and in *Macrochirichthys* (Howes, 1976).

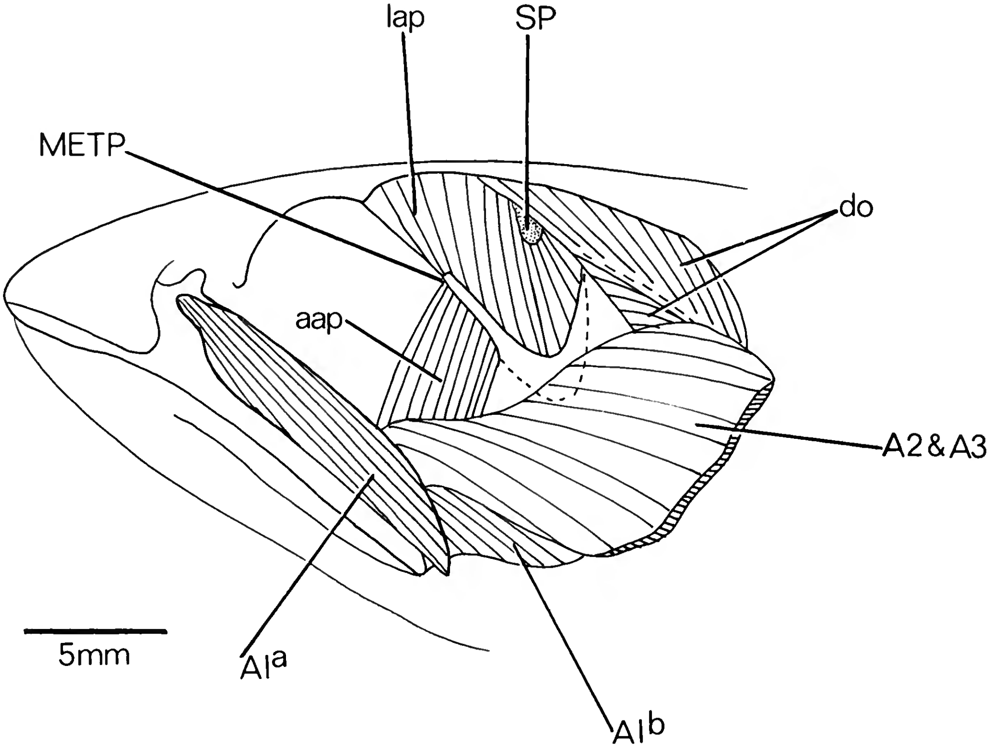

Fig. 44 *Barilius bola*, cranial musculature. *Adductor mandibulae* A2 and A3 are reflected to expose the deeper muscles.

A *ligamentum primordium* is not well developed in the syprinids studied. Only in *Barilius* have I have found it to be clearly differentiated and this not to the same extent as it is in most characoids. It may be a primitive character of cyprinids.

Earlier (p. 35), differences in the morphology of the *dilatator operculi* fossa were pointed out; four main types of fossa can be distinguished:

1. That involving mostly the sphenotic, with part of the frontal and pterotic, and lying laterally on the cranium, sometimes roofed by part of the frontal. This type of fossa is usually small and found in many cyprinid genera (e.g. *Opsariichthys*, *Zacco*, *Rasbora*, *Danio*, some *Barilius* and *Barbus* species and most cultrine species).
2. That involving a broad sphenotic process and a large area of the frontal, and which extends onto the cranial roof. This type of fossa is variously developed and can be extensive as in *Hypophthalmichthys*, where it occupies a large area of the frontal. It is characteristic of most genera currently assigned to the Leuciscinae. In Characoids a similar fossa is found in the Cynodontini (Howes, 1976).

3. That in which the sphenotic is developed below the frontal as a shelf. This type of fossa occurs in *Luciobrama* and its relatives. In characoids a similar type of fossa is found in *Salminus* (Roberts, 1969) and in *Brycon alburnus* (pers. obs.).
4. That in which the frontal and underlying sphenotic have become partly separated to form a foramen. This type of fossa is found in some *Barbus* species in *Cyprinus*, in *Labeo* and what are believed to be related genera (Reid, unpublished information). In characoids a similar foramen is found in some erythrinids, Acestrorhynchinae and Ctenoluciidae (Roberts, 1969; pers. obs.).

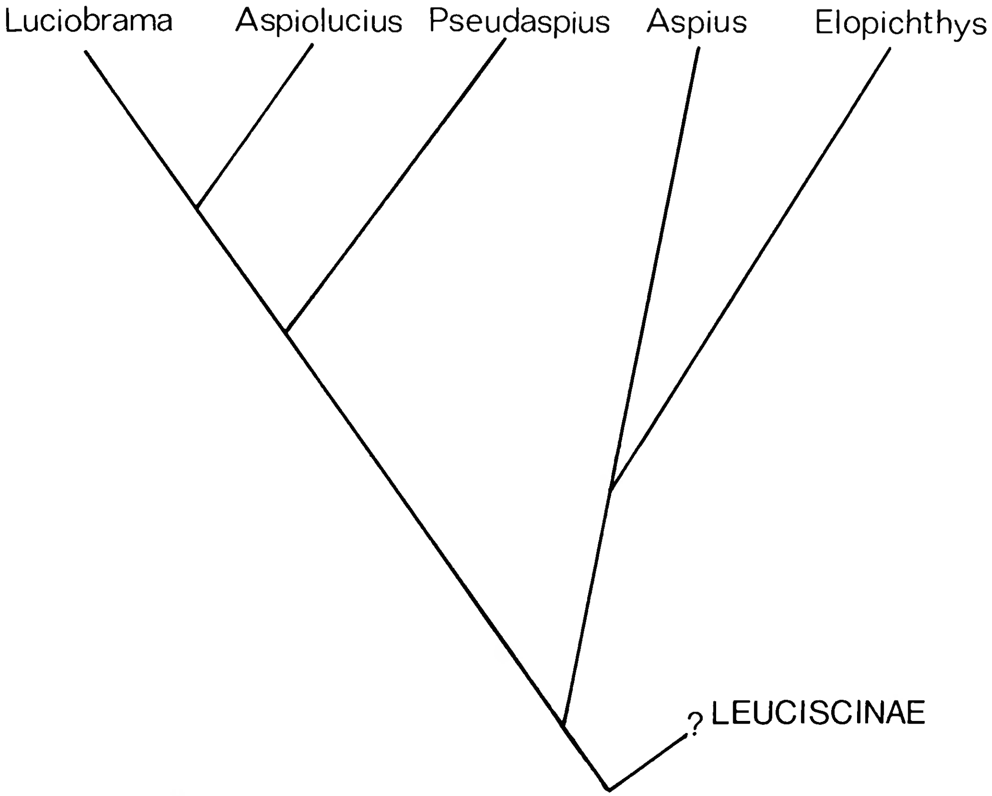

Fig. 45 Cladogram to illustrate the relationships of the aspinine genera.

There is also another condition, whereby the dilatator fossa is virtually absent. This occurs in the long-jawed *Barilius* species, e.g. *bola*, *loati*, and in *Macrochirichthys*. In these taxa the *dilatator operculi* muscle has either been so reduced (*Barilius*) or runs almost perpendicularly that the need of an inclined or horizontal shelf has been eliminated.

Roberts (1973) places little value on the condition of the dilatator fossa, believing it to be 'extremely labile'. Admittedly, we must be aware of parallelism in the formation of this as in any other character, but I believe the particular characteristics of this feature are indicators of relationships. Gosline (1975) also draws attention to the varying conditions of the dilatator fossa.

Hyoid and branchial muscles

During this present study no extensive comparison of these groups of muscles has been made. It is noted that the development of the hyoid muscles in *Luciobrama* and *Aspius* is relatively 'weak' when compared with that of the *Barbus* and *Labeo* groups of genera, where the hyohyoidei are well developed (see Matthes, 1963).

Various arrangements of the hyoid muscles are found in the cyprinids (i.e. *intermandibularis* absent; *protractor hyoidei* divided anteriorly), but the basic plan is little modified from that described in *Opsariichthys* by Takahasi (1925).

Concerning the branchial arch muscles, the only comments I am able to make at present concern the *retractor pharyngeus* of the upper branchial arches. Winterbottom (1974) points out two conditions of this muscle, one as observed in *Opsariichthys*, where it is undivided, and the other as in *Cyprinus*, where there are two divisions. In *Luciobrama*, *Aspius* and *Elopichthys* there appears to be a single element stemming from the basioccipital process and inserting along the medial edge of ceratobranchial 5.

Considerations of functional morphology in *Luciobrama*

The head of *Luciobrama* is enormously elongate, but as described in this paper, this elongation is entirely postorbital in extent. The preorbital part of the head is 'normal' and in fact greatly resembles that of *Aspius*, both in shape and proportions.

Suslowska & Urbanowicz (1957) have commented on the feeding mechanism of *Aspius*, and their comments may be of help in elucidating those of *Luciobrama*. These authors compared *Aspius* with *Cyprinus* and *Esox* and considered the morphology of the cranium and jaw in *Aspius* to be in accordance with development 'from an omnivore into a carnivore'. (See remarks on p. 61.) Suslowska (1971) again compared *Aspius* with *Cyprinus* and *Esox*. She comments that the form of the *levator arcus palatini* in *Aspius* closely resembles that of *Cyprinus*. However, there is a difference in the orientation of the fibres, those of *Aspius* being more horizontally directed (as in *Luciobrama*, see p. 21). Suslowska (*op. cit.*) also demonstrated a close resemblance between the arrangement of the *adductor hyomandibulae* in *Aspius* and *Esox*.

Woskoboinikoff (1932), Yeremeyeva (1950), Alexander (1964), Suslowska (1971) and Howes (1976) all draw attention to the form of the *dilatator operculi* and note that this muscle is developed to the greatest degree in those fishes with elongate heads in which the operculum has become greatly extended. The need for strong dilatation of the opercula is two-fold, providing an increased flow of water for respiration and enabling the prey to be moved into the buccal cavity.

In *Luciobrama*, the large operculum and long *dilatator operculi* may not necessarily be indicative of their principal role in the feeding action. The movement of the operculum at its articulation with the hyomandibula seems to be restricted and it seems likely that the muscle's action is concerned primarily with strong breathing movements (see Alexander, 1969).

The enormous elongation of the postorbital skull region in *Luciobrama* and the correlated development of both the pterygoid series and the *levator arcus palatini* suggest, as a consequence, a powerful abduction of the hyopalatine arch, which would provide a suction corridor and thus reinforce the feeding action.

Summary

The following characters in *Luciobrama* are considered to be specialized (apomorph):

1. Reduced and elongate fourth infraorbital, diverted across the postorbital face (pp. 7 & 26).
2. Elongate postorbital region (including lengthened and narrowed parietals) (pp. 11 & 35).
3. Long tubular nasals, bearing 9–10 pores (pp. 9 & 31).
4. Orbitosphenoid and pterosphenoid bearing posterior and anterior extensions respectively (pp. 9 & 31).
5. Autosphenotic underlying the frontal as a shelf (pp. 13 & 35).
6. Posttemporal fossa extending well forward (pp. 13 & 38).
7. Extensive postparietal platform (pp. 13 & 40).
8. Specialized form of the lower jaw and large number of pores in the mandibular lateral line canal (pp. 13 & 42).
9. Short, inclined hyomandibula (pp. 13 & 44).
10. Elongate pterygoids (p. 15 & 45).

11. Extensive opercular series (pp. 15 & 47).
12. Second neural plate contacting the cranium (pp. 17 & 48).
13. Total number of vertebrae 50 or more (pp. 20 & 51).
14. Enlarged and complex *levator arcus palatini* muscles (pp. 21 & 53).
15. Scales minute and numerous (p. 7).

Of these characters only 4 is confined to *Luciobrama*. Characters 2 and 10 are shared only with *Aspiolucius*. Characters 8 and 9 are shared with *Aspiolucius* and *Pseudaspius*. All the remaining characters are shared with *Aspiolucius*, *Pseudaspius* and *Aspius*.

Relationships of *Luciobrama*

Bleeker (1870) suggested that *Luciobrama* was near to *Aspius*. Since that perceptive statement was made no other worker has speculated upon the relationships of this genus.

Berg (1964) thought that *Pseudaspius* was close to *Leuciscus* but implied that *Aspiolucius* and *Aspius* were related.

Luciobrama has been placed in the Leuciscinae by Rendahl (1928), Chu (1935) and Lin (1935), and in the Cyprininae by Tchang (1933). *Aspiolucius*, *Pseudaspius* and *Aspius* are placed in the Leuciscinae by Chu (1935) and Nikolsky (1954).

From the summary of synapomorph characters presented above (p. 58) it would appear that *Luciobrama* is, as Bleeker (1870) supposed, closely related to *Aspius*, but with even closer ties to *Aspiolucius* and *Pseudaspius*. I regard *Luciobrama* and *Aspiolucius* as a sister group and *Pseudaspius* as the closest relative of those two genera. In turn, all three are the sister group to *Aspius* which, by virtue of the morphology of the jaw and relatively unmodified cranium, I consider to be the least specialized representative of this group of genera. The relationships of the aspinine group of genera are discussed below, page 61.

Relationships of *Elopichthys*

Elopichthys poses a difficult problem concerning relationships and I have included it here because I believe it belongs to the aspinine assemblage.

Gosline (1974 : 12) stated '. . . *Elopichthys* (with *Ochetobius*) and *Hypophthalmichthys* (with *Aristichthys*) seem to represent highly specialized cyprinid groups without close relatives'.

From this statement I assume that Gosline is considering *Ochetobius* to be related to *Elopichthys*. I have examined specimens of *Ochetobius elongatus*, but apart from an enlargement of the *levator arcus palatini* muscle and the numerous vertebrae (see p. 51) I am unable to find any specializations that would suggest close affinity with *Elopichthys*. The upper jaw of *Ochetobius* appears to be highly protractile, the premaxillae possess long anterior ascending processes, there is no expansion of the pterosphenoid and the lower jaw is short and deep. All these features represent marked differences between *Elopichthys* and *Ochetobius*. I believe *Ochetobius* to be a specialized leuciscine.

I agree with Gosline (1974) that *Elopichthys* is a highly specialized taxon and has diverged sufficiently from its ancestral lineage to almost 'stand alone'. Nevertheless, *Elopichthys* shares many derived characters with the aspinine genera (see list on p. 58). Particularly important are those characters shared only with *Aspius*: the lateral expansion of the pterosphenoid to the cranial borders, the close resemblance of the orbitosphenoids and the elongate supracleithrum.

I consider *Elopichthys* to be most closely related to *Aspius* and thus, together, these form the sister group to *Luciobrama*, *Aspiolucius* and *Pseudaspius*.

The aspinine group of cyprinids

For the present I do not intend to assign any formal taxonomic status to the assemblage of genera considered here as the aspinine group. The reasons for this are discussed below (p. 61).

No single character of those enumerated below will distinguish the aspinines from other groups of cyprinids but the following combination of characters will identify this assemblage.

Character	Character state
Barbels absent	? Plesiomorph
Scales small; 65–155 in lateral line	Apomorph
Vertebrae 51–55	Apomorph
Cranium elongate; in some cases the postorbital cranium is three times the length of the preorbital part	Apomorph
Sphenotic exposed as a shelf below the frontal margin	Apomorph
Orbitosphenoid making extensive contact with parasphenoid	Apomorph
Infraorbitals 2, 3, 4 and 5 narrow, the fourth elongate	Apomorph
Operculum antero-posteriorly extended with a long dorsal border	Apomorph
Posttemporal fossa present, extending well forward	Presence: Plesiomorph Condition: Apomorph
Pterosphenoid sometimes extended to the lateral margin of the frontal	Apomorph
Pterosphenoid makes extensive contact with the parasphenoid	Apomorph
12 or more pores in the mandibular lateral line canal	Apomorph
Nasals elongate with 9–10 pores	Apomorph
Second neural plate contacts the cranium	Apomorph
Levator arcus palatini muscle extensive and complex	Apomorph
Dilatator operculi muscle extended	Apomorph

The genera and species comprising the aspinine group are:

Aspius Agassiz, 1832
  Aspius aspius (Linn.) 1758
  Distribution: Europe
  Two subspecies are recognized by Berg (1964), *A. aspius aspius* (Europe) and *A. aspius taeniatus* (Caspian and Aral seas).
  Aspius vorax Heckel 1843
  Distribution: Tigris R.

Aspiolucius Berg 1907
  Aspiolucius esocinus (Kessler), 1874
  Distribution: Amu-Darya
  Berg (1964) and Nikolsky (1954) mention a second species, *A. harmandi* (Sauvage) from Tonkin. This is an error. The species originally described as *Gymnognathus harmandi* by Sauvage (1884) is a synonym of *Elopichthys bambusa* (see synonymy in Lin, 1935 and Wu, 1964). Tchang (1933) placed *Aspiopsis merzbacheri* Zugmayer, 1921 in the genus *Aspiolucius*. He gave no reason for this action. I have examined the type and can find no characters which would justify inclusion in this genus. I agree with Berg (1964 : 541) in treating *Aspiopsis* as a synonym of *Leuciscus* (*sensu latu*).

Pseudaspius Dybowski, 1869
  Pseudaspius leptocephalus (Pallas), 1776
  Distribution: Amur basin

Luciobrama Bleeker, 1870
  Luciobrama macrocephalus (Lacepède), 1803
  Distribution: Southern China
  Luciobrama longiceps Pellegrin, 1907
  Distribution: Hanoi
  Rendahl (1928) considered *L. longiceps* as possibly a subspecies or other populational variant.

Since the species is known from only a single specimen more material from a wide range of localities will have to be available before its supposed subspecific status can be evaluated.

Elopichthys Bleeker, 1859
Elopichthys bambusa (Richardson), 1844
Distribution: China

Discussion

Luciobrama is a highly specialized member of the aspinine group of cyprinids. Although this group can be seen as a monophyletic assemblage it is difficult to relate it to other groups; the crux of this difficulty is the fact that various classifications of the Cyprinidae have been made by attaching significance to superficial resemblances and by utilizing only single characters or a series of too few characters. In some cases the significance of these features has defied interpretation. For example, Saxena & Khanna (1965) in their work on the osteology of *Catla* state 'It is impossible to indicate any specific features of the osteocranium as representative of primitive or evolved conditions.'

Because cyprinids tend to present a uniformity in those characters previously analysed, several authors have concluded that the family cannot be divided readily into subfamilies or other well-defined groupings (Sagemahl, 1891; Regan, 1911; Ramaswami, 1955b; Hensel, 1970; Gosline, 1973). Hensel (1970) has presented a history of the classification of the Cyprinidae. It seems that certain genera were assigned to a subfamily on a purely arbitrary basis (see p. 59 concerning *Luciobrama*).

In view of this unsatisfactory state of affairs it is not possible to place the aspinine genera in any relevant framework of related groups. Although I suspect that the aspinines can be related to the 'Leuciscines', until the Leuciscinae can be identified on the basis of shared specializations it will not be possible to say exactly how they are related.

From the anatomical evidence presented in this paper it is apparent that the piscivorous facies characterizing the aspinines is a derived condition – derived no doubt from an ancestral form possessing a reasonably protractile jaw and narrow cranium, i.e. a 'leuciscine-type' fish. One representative of this related group may be *Oreoleuciscus* which shares affinities with the aspinines in the morphology of the lower jaw, infraorbitals and dilatator fossa; see page 43.

Some authors have considered a piscivorous or carnivorous habit to be a primitive character for the Cyprinidae (see Hubbs & Black, 1947 and Matthes, 1963). Roberts (1969) also noted this possibility in the characoids, referring specifically to *Hepsetus*. I take the contrary view to these authors and maintain that it is the omnivores of the respective cyprinid lineages which represent the 'primitive' type' Evidence for this point of view is presented in this paper where it is shown that the piscivorous facies are the result of derived anatomical features, or 'specializations'. (See also the remarks of Suslowska & Urbanowicz, 1957; quoted here on page 58.

Several lineages of old-world cyprinids have evolved as piscivores. One, the aspinines, is considered in this paper. The predatory morphology of this group has been achieved not by any marked changes in jaw structure (apart for *Elopichthys* which is considered below), but by an increase in length of the postorbital part of the cranium and modification of the hyopalatine arch so as to improve or modify the suction feeding method. Another, exemplified by *Barilius*, has evolved by the more 'usual' method of elongating the jaws but because of the particular type of protractile mechanism of the cyprinid upper jaw (involving the kinethmoid and not the median ethmoid), the jaw elements have lengthened posteriorly. This has meant a correlated deepening of the hyopalatine series coupled with a slightly increased length to the postorbital part of the cranium. *Macrochirichthys* represents another type in which there has also been a lengthening of the jaws but coupled with a forward movement of their articulation and modification to the anterior part of the vertebral column which has allowed an upward movement of the head (pers. obs.). In this case there has been no lengthening of the postorbital cranium. Some other genera such as *Erythroculter* and *Schizothorax* display attributes of both the aspinine type of morphology (increased postcranial length) and bariliine type (increased jaw length and deepening of the pterygoid series).

Only one cyprinid, the aspinine *Elopichthys*, has developed what may be termed the pike-like facies so characteristic of other teleost piscivores. This has been achieved by 'sacrificing' the evolutionary potential of the protrusile upper jaw. The 'early stages' of this particular evolutionary pathway may, however, be detected in *Barilius bola*.

Acknowledgements

I am greatly indebted to Dr P. H. Greenwood for his encouragement, advice and criticism of many earlier drafts of the manuscript.

I want to express my gratitude to Dr K. E. Banister and Mr G. McGregor Reid for so many helpful discussions concerning the phylogeny of cyprinids and for providing me with much unpublished information concerning their respective studies on the genera *Barbus* and *Labeo*.

Mr M. van Oÿen of Leiden University provided much help by discussing functional anatomical problems as did Dr Richard Vari in discussing characoids. I am most grateful to them both.

To Mr J. Chambers go my thanks for preparing so many alizarin specimens and to Mrs Margaret Clarke for assisting with radiographs and numerous other jobs.

Finally, I wish to thank Dr P. J. P. Whitehead for his helpful advice and criticism of the final draft of the manuscript.

References

Alexander, R. McN. 1964. Adaptation in the skull and cranial muscles of South American characinoid fish. *J. Linn. Soc. (Zool.)* **45** : 169–190.

—— 1966. The functions and mechanisms of the protrusible upper jaws of two species of cyprinid fish. *J. Zool. Lond.* **149** : 288–296.

—— 1967. *Functional design in fishes*. London. 160 pp.

—— 1969. Mechanics of the feeding action of a cyprinid fish. *J. Zool. Lond.* **159** : 1–15.

Bănărescu, P. 1967. Studies on the systematics of Cultrinae (Pisces, Cyprinidae) with description of a new genus. *Revue roum. Biol. (Zool.)* **12** (5) : 297–302.

—— 1968. Remarks on the genus *Chela* Hamilton-Buchanan (Pisces, Cyprinidae) with description of a new subgenus. *Annali Mus. civ. Stor. nat. Giacomo Doria* **77** : 53–64.

Berg, L. S. 1964. *Freshwater fishes of the USSR and adjacent countries*. **2**. (English translation of the fourth ed. of 1949.) 496 pp.

Bleeker, P. 1870. Nieuw vischsoorten van China. *Versl. Meded. K. Akad. wet. Amst.* **4** : 251–256.

—— 1873. Notice sur le *Synodus macrocephalus* Lac. (*Luciobrama typus* Blkr). *Ned. Tijdschr. Dierk* **4** : 89.

Bridge, T. W. 1896. The mesial fins of ganoids and teleosts. *J. Linn. Soc. (Zool.)* **25** : 530–602.

Chu, Y. T. 1935. Comparative studies on the scales and on the pharyngeals and their teeth in Chinese cyprinids, with particular reference to taxonomy and evolution. *Biol. Bull. St. John's Univ., Shanghai* 2 : 1–225.

Gosline, W. A. 1961. Some osteological features of modern lower teleostean fishes. *Smithson. Misc. Coll.* **142** (3) : 1–142.

—— 1973. Considerations regarding the phylogeny of cypriniform fishes, with special reference to structures associated with feeding. *Copeia*, 1973 (4) : 761–776.

—— 1974. Certain lateral-line canals of the head in cyprinid fishes, with particular reference to the derivation of North American forms. *Jap. J. Ichth.* **21** (1) : 9–15.

—— 1975. The cyprinid dermosphenotic and the subfamily Rasborinae. *Occ. Pap. Mus. Zool. Univ. Mich.* **673** : 1–13.

Greenwood, P. H. 1974. The cichlid fishes of Lake Victoria, East Africa: the biology and evolution of a species flock. *Bull. Brit. Mus. nat. Hist.* (Zool.), Suppl. 6 : 1–134.

Greenwood, P. H., Rosen, D. E., Weitzman, S. H. & Myers, G. S. 1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. *Bull. Am. Mus. nat. Hist.* **131** : 339–456.

Harrington, R. W. 1955. The osteocranium of the American cyprinid fish, *Notropis bifrenatus* with an annotated synonymy of teleost skull bones. *Copeia*, 1955 (4) : 267–290.

Hensel, K. 1970. Review of the classification and the opinions on the evolution of **Cyprinoidei** (Eventognathi) with an annotated list of genera and subgenera described since 1921. *Annotnes Zool. Bot. Bratislava*, **57** : 1–45.

Howes, G. J. 1976. The cranial musculature and taxonomy of characoid fishes of the tribes Cynodontini and Characini. *Bull. Brit. Mus. nat. Hist.* (Zool.) **29** (4) : 203–248.

Hubbs, C. L. & Black, J. D. 1947. Revision of *Ceratichthys*, a genus of American cyprinid fishes. *Misc. Publs. Mus. Zool. Univ. Mich.* **66** : 1–56.

Jollie, M. 1975. Development of the head skeleton and pectoral girdle in *Esox*. *J. Morph.* **147** (1) : 61–88.

Kershaw, D. R. 1976. A structural and functional interpretation of the cranial anatomy in relation to the feeding of osteoglossoid fishes and a consideration of their phylogeny. *Trans. zool. Soc. Lond.* **33** : 173–252.

Kimura, S. 1934. Description of the fishes collected from the Yangtse-Kiang, China by the late Dr K. Kishinouye and his party in 1927–1929. *J. Shanghai Sci. Inst.* **1** (3) : 11–247.

Liem, K. F. 1970. The comparative anatomy of the Nandidae (Pisces : Teleostei). *Fieldiana Zool.* **56** : 1–166.

Lin, S. Y. 1935. Contribution to the study of cyprinidae of Kwangtung and adjacent provinces. *Lingnan Sci. J.* **14** (4) : 651–663.

Lindsey, C. C. 1975. Pleomerism, the widespread tendency among related fish species for vertebral number to be correlated with maximum body length. *J. Fish Res. Bd. Can.* **32** (12) : 2453–2469.

Matthes, H. 1963. A comparative study of the feeding mechanism of some African Cyprinidae (Pisces, Cypriniformes). *Bijdr. Dierk.* **33** : 3–35.

Meinel, W. Von, Holl, A. & Schulte, E. 1970. Vergleichend-anatomische und funktionsanalytische Untersuchungen an der splanchnischen Muskulatur einiger Cyprinidae (Teleostei). *Zool. Beit.* **16** : 93–128.

Munshi, J. S., Datta. & Singh, B. R. 1967. The cranial muscles and the natural mechanism of opening and closing of mouth in two Indian major carps. *Zool. Anz.* 178 (1–2) : 49–60.

Nelson, G. J. 1969. Gill arches and the phylogeny of fishes, with notes on the classification of vertebrates. *Bull. Am. Mus. nat. Hist.* **141** art. 4 : 479–552.

Nichols, J. T. 1925. Chinese freshwater fishes. *Nat. Hist. N.Y.* **25** (4) : 346–352.

—— 1943. *Freshwater fishes of China*. Nat. Hist. of Central Asia. **9**. American Museum of Natural History, New York. 322 pp.

Nikolsky, G. V. 1954. *Special Ichthyology*. 2nd ed. Moscow. 458 pp.

Oliva, O. & Skořepa, V. 1968. The myodome in carp (*Cyprinus carpio* Linnaeus) and Repfen (*Aspius aspius* Linnaeus). *Vest. csl. Zool. Spol.* **32** (1) : 39–45.

Patterson, C. 1975. The braincase of pholidophorid and leptolepid fishes, with a review of the actinopterygian braincase. *Phil. Trans. Roy. Soc.* B 269 (899) : 275–579.

Ping, C., Pao, S. & Yang, H. Y. 1958. The skeletal musculature of the carp (*Cyprinus carpio*). *Acta zool. sin.* **10** : 289–315.

Ramaswami, L. S. 1955a. Skeleton of cyprinoid fishes in relation to phylogenetic studies: 6. The skull and Weberian apparatus in the subfamily Gobioninae (Cyprinidae). *Acta Zool.* **36** (2) : 127–158.

—— 1955b. Skeleton of cyprinoid fishes in relation to phylogenetic studies: 7. The skull and Weberian apparatus of the Cyprininae (Cyprinidae). *Acta Zool.* **36** (3) : 199–242.

Rauther, M. 1950. Über *Pelecus cultratus* (L.) in Vergleich mit anderen 'Beilfischen'. *Zool. Anz.* **145** : 794–804.

Regan, C. T. 1911. The classification of the teleostean fishes of the order Ostariophysi. 1. Cyprinoidei. *Ann. Mag. nat. Hist.* (8) **8** : 13–32.

Rendahl, H. 1928. Beiträge zur kenntnis der Chinesischen süswasserfische. 1. Systematischer Teil. *Ark. Zool.* **20A** (1) : 1–194.

Roberts, T. R. 1969. Osteology and relationships of characoid fishes, particularly the genera *Hepsetus*, *Salminus*, *Hoplias*, *Ctenolucius* and *Acestrorhynchus*. *Proc. Calif. Acad. Sci.* (4) **36** : 391–500.

—— 1973. Interrelationships of ostariophysans. *In*: *Interrelationships of fishes*, Greenwood, P. H., Miles, R. S. & Patterson, C. (Eds) : 373–395. London and New York.

Sagemahl, M. 1891. Beiträge zur vergleichenden Anatomie der Fische, IV. Das Cranium der Cyprinoiden. *Morph. Jahrb.* **17** : 489–495.

Sauvage, H. E. 1884. Contribution à la faune ichthyologique du Tonkin. *Bull. Soc. zool. Fr.* **9** : 209–215.

Saxena, S. C. 1960. The cranial musculature of a hill-stream cyprinid fish *Garra mullya* (Sykes). *Proc. Nat. Inst. Sci. India* B (4) **26** : 176–188.

Saxena, D. B. & Khanna, S. 1965. Osteology of the freshwater teleost *Catla catla* (Ham.). Part I. Osteocranium. *Vest. csl. Zool. Spol.* **29** : 127–145.

Shukla, G. R. & Verma, S. R. 1972. Appendicular skeleton of *Barilius bola* (Ham.). (With the remark of phylogenetic consideration.) *Anat. Anz.* **130** : 560–570.

Sorescu, C. 1968. Vergleichende Untersuchungen über den Schultergürtel der Cyprinidae. *Senck. biol.* **49** (5) : 387–397.

—— 1972. Comparative studies on the Weberian apparatus in the subfamily Danioninae and Cultrinae (Cyprinidae – Pisces). *Revue roum. Biol.* (Zool.). **17** (6) : 391–398.

Starks, E. C. 1926. Bones of the ethmoid region of the fish skull. *Stanf. Univ. Public. Biol. Sci.* **4** (3) : 139–338.

Suslowska, W. 1971. A comparative study of the muscles of the head of *Aspius aspius* (Linnaeus, 1758) and *Esox lucius* Linnaeus, 1758. *Acta Zool. Cracov.* **16** (16) : 695–713.

—— **& Urbanowicz, K.** 1957. Badania prownaweze nad wybranymi elementami szkieletu szezupala – *Esox lucius* L., bolenia – *Aspius aspius* (L.) i karpia – *Cyprinus carpio* L. *Zesz. nauk. Univ. Lodz* (2) **3** : 71–93.

Takahasi, N. 1925. On the homology of the cranial muscles of the cypriniform fishes. *J. Morph.* **40** : 1–109.

Tchang, T. L. 1933. *The study of Chinese cyprinoid fishes*, Part 1. Zool. Sinica 2 (1) : 1–247.

Tretiakov, D. K. 1946. Systematic groups of Cyprinidae. *Zool. Zh.* **25** (2) : 149–156.

Weitzman, S. H. 1962. The osteology of *Brycon meeki*, a generalized characin fish, with an osteological definition of the family. *Stanford ichthyol. Bull.* **8** (1) : 3–77.

Wiley, M. L. & Collette, B. B. 1970. Breeding tubercles and contact organs in fishes: their occurrence, structure and significance. *Bull. Am. Mus. nat. Hist.* **143** art. 3 : 143–216.

Winterbottom, R. 1974. A descriptive synonymy of the striated muscles of the teleostei. *Proc. Acad. nat. Sci. Philad.* **125** (12) : 225–317.

Woskoboinikoff, M. M. 1932. Der Apparat der Kiemenatmung bei den Fischen. *Zool. Jb. Anat. Jena* **55** : 315–488.

Wu, Hsien-Wen. 1964. *Cyprinid fishes of China.* **1.** Shanghai. 228 pp.

Yeremeyeva, E. F. 1950. Zavistimost miezdu stroieniem cherepa i stroiemiem rotovogo i golotochnogo apparatov kostistich ryb. *Trudy Inst. Morf. Zhivot.* **3** : 34–41.

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Bulletin of the British Museum (Natural History)

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Zoology series Vol 34 No 2 30 November 1978

The *Bulletin of the British Museum (Natural History)*, instituted in 1949, is issued in four scientific series, Botany, Entomology, Geology and Zoology, and an Historical series.

Parts are published at irregular intervals as they become ready. Volumes will contain about three hundred pages, and will not necessarily be completed within one calendar year.

Subscription orders and enquiries about back issues should be sent to: Publications Sales, British Museum (Natural History), Cromwell Road, London SW7 5BD, England.

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

ISSN 0007-1498

Zoology series
Vol 34 No 2 pp 65-82

British Museum (Natural History)
Cromwell Road
London SW7 5BD

Issued 30 November 1978

A new species of *Pteralopex* Thomas, 1888 (Chiroptera: Pteropodidae) from the Fiji Islands

J. E. Hill
Department of Zoology, British Museum (Natural History), Cromwell Road, London SW7 5BD

W. N. Beckon
Peace Corps, Suva, Fiji

Contents

Synopsis

The unusual megachiropteran genus *Pteralopex* is briefly reviewed and considered to include three species, two named many years ago from the Solomon Islands, and a third, here described as new, from the Fiji Islands, whence the genus is recorded for the first time. Cuspidation of the molariform teeth in *Pteralopex* is considered in detail, with especial reference to the new species, and compared with the similarly cuspidate condition of the molariform teeth of *Harpyionycteris*. Presumed homologies with the cusps of the dilambdodont teeth of the Microchiroptera are examined, with a discussion of the relevance of molariform cuspidation in the Megachiroptera to theories of their dental evolution.

Introduction

The known megachiropteran fauna of the Fiji Islands has been limited hitherto to two species of the widespread genus *Pteropus*, one the Pacific fruit bat *P. samoensis*, the other the Polynesian fruit bat *P. tonganus*, and to the long-tailed fruit bat *Notopteris macdonaldi*. None is endemic: *P. samoensis* is represented on the Fiji Islands by an endemic subspecies, *P. s. nawaiensis*, the other, nominate subspecies occurring in the Samoa Islands (Wodzicki & Felten, 1975), while *P. tonganus* is more widely distributed, its subspecies occurring variously from Dampier (Karkar) Island, off the northeastern coast of New Guinea and from Rennell Island, in the Solomon Islands, eastward to the Tonga and Samoa Islands and to Niue Island. This species may occur or have occurred even further to the east, in the Cook Islands, whence bats, apparently pteropodids, have been reported (Smith, 1902, Krzanowski, 1977 : 271) from Raratonga Island (21° 14′ S, 159° 46′ W) and where there is evidence of bats (Gill, 1876, Krzanowski, 1977 : 271) on Mangaia Island (21° 55′ S, 157° 55′ W). The subspecies of *P. tonganus* on the Fiji Islands, *P. t. tonganus*, occurs also in the Tonga and Samoa groups to the east, but to the west is replaced by *P. t. geddiei* on the Loyalty Islands, New Caledonia and the New Hebrides. The representatives of *Pteropus* on the Fiji Islands thus display a closer affinity to those of the more easterly islands than to their congeners on the islands to the west of the Fiji group. *Notopteris macdonaldi* has a rather different distributional pattern: one subspecies, *N. m. macdonaldi*, occurs on the Fiji Islands and in the New Hebrides (specimens reported from Ponape, Caroline Islands by Jentink (1887 : 268, 1888 : 158) are referred to this subspecies by Andersen (1912 : 798) who also (p. lxxiv) queries

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the veracity of the record) with a second subspecies, *N. m. neocaledonica*, in New Caledonia. The microchiropteran fauna of the Fiji Islands is similarly sparse with records only of *Emballonura semicaudata* and *Tadarida jobensis*. As among the Megachiroptera there is no endemic species: *E. s. semicaudata* occurs also in the Tonga and Samoa groups and in the New Hebrides, with a second subspecies in the Palau Islands, while the distribution of *T. jobensis* extends from the Fiji Islands to New Guinea and Australia. Specimens of the latter species from the Fiji Islands seem likely to represent *T. j. bregullae*, described originally from the New Hebrides (Felten, 1964*a* : 12).

The islands to the east of the Fiji group have fewer species, with *Pteropus tonganus* and *Emballonura semicaudata* in the Tonga Islands, occurring together with *Pteropus samoensis* in the Samoa Islands. To the west of Fiji, however, the islands and island groups have a more diverse bat fauna. Apart from *Notopteris macdonaldi* on New Caledonia and the New Hebrides, the Megachiroptera are represented by several species of *Pteropus*, all except *P. tonganus* usually restricted to particular islands or groups of islands. *Pteropus ornatus* occurs on the Loyalty Islands and New Caledonia, on the latter island with *P. vetulus* (Felten, 1964*c*); *P. anetianus*, its several subspecies (Felten, 1964*b*, Felten & Kock, 1972) and *P. fundatus* occur on the New Hebrides, while *P. tuberculatus*, *P. vanikorensis* and *P. nitendiensis* are found on various of the Santa Cruz Islands. By contrast, the Microchiroptera of these islands and island groups consist chiefly of species with a much wider general distribution, although one, *Miniopterus robustior*, is known only from the Loyalty Islands. Most are Australasian: *Minopterus australis* and *M. medius* extend to the Loyalty Islands and New Caledonia, *Hipposideros galeritus*, *Aselliscus tricuspidatus*, *Myotis adversus* and *Miniopterus tristis* to the New Hebrides. *Emballonura semicaudata*, widely distributed among the islands of the Pacific to the east, occurs also on the New Hebrides and *Chalinolobus gouldi*, otherwise an Australian species, is represented on New Caledonia (Koopman, 1971 : 4).

The bat species so far recorded from the Fiji Islands are quite clearly consistent with the position of the group in the long island chain that stretches eastward from New Guinea into the Pacific Ocean, the Fiji Islands lying near the eastern limit of bat distribution along the chain and somewhat widely separated from their nearest neighbours to the west. Although four of the five bat species hitherto known from the Fiji Islands occur also on the islands to the west, the absence from the Fijian fauna of the majority of the widespread microchiropteran species that extend eastward to the New Hebrides or even to New Caledonia and the Loyalty Islands suggests that for many the relatively wide oceanic strait between these islands and the Fiji group is an effective barrier to further dispersal. Of bat species found both east and west of this obstacle, only one megachiropteran and one microchiropteran occur further west than New Caledonia and the New Hebrides. Furthermore, differentiation is unusual among Fijian bats, until now there being no endemic species reported from this island group, and but one endemic subspecies. In these circumstances it is of particular interest to report the existence in the Fiji Islands of a hitherto undescribed and very distinct species of the aberrant genus *Pteralopex*, itself previously known only from the Solomon Islands.

Systematic descriptions

Genus *PTERALOPEX* Thomas, 1888

Pteralopex Thomas, 1888 : 155, 1889 : 473, pl. 20, fig. 3, pl. 21, figs 4–7. *Pteralopex atrata* Thomas, 1888.

The genus *Pteralopex* is characterized externally by the insertion of the wings at or near the mid-line of the back along the spinal line; cranially by an unusually well-developed sagittal crest, long postorbital processes which reach or nearly reach the zygomata, rather upwardly directed orbits and short, broad, nearly parallel-sided rostrum, but especially dentally by massive upper canines which have a prominent posterior supplementary cusp and by the exceptional size of the outer lower incisors (i_{2-2}).* The molariform teeth of *Pteralopex*, moreover, are variously cuspidate, on occasion displaying an extreme of the tendency towards lateral cuspidation seen in various

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* The dental notation adopted in this paper is that of Miller (1907).

ways and to varying degrees in some species of the related genus *Pteropus*, in *Hypsignathus*, *Nyctimene*, *Paranyctimene*, *Dobsonia* or in *Harpyionycteris*, although surface cusps or ridges such as occur in some of *Cynopterus*, in *Ptenochirus*, *Latidens*, *Dyacopterus*, *Thoopterus*, *Dobsonia* or in *Harpyionycteris* are lacking.

The dental formula of *Pteralopex* is $\mathrm{i}\,\frac{2}{2}$, $\mathrm{c}\,\frac{1}{1}$, $\mathrm{pm}\,\frac{3}{3}$, $\mathrm{m}\,\frac{2}{3} = 34$, as in *Pteropus*; the upper incisors (i^{2-3}) have very broad posterior ledges and the upper canines are short, very thick antero-posteriorly, with a large and prominent posterior secondary cusp extending halfway along the length of the tooth and a wide internal cingulum bearing small internal and postero-internal basal cusps, the anterior cusp sometimes indistinct. The first upper premolar (pm^2) is rudimentary, its crown only slightly differentiated; the second (pm^3) and third (pm^4) upper premolars and the first upper molar (m^1) have prominent, shelf-like raised anterior and posterior basal ledges, the labial lateral elevation in these teeth raised into a cuspidate structure, the lingual elevation usually similarly so but on occasion more ridge-like, while the second upper molar (m^2) lacks the anterior basal ledge and the cuspidate appearance is usually less evident.

The inner lower incisor (i_1) is very small, subterete, its edge slightly lobed, the outer lower incisor (i_2) much enlarged to twelve or fifteen times the bulk of i_1, its posterior ledge very long antero-posteriorly, the longitudinal diameter of the tooth greater than the transverse diameter of its crown, the cutting edge tricuspid or incipiently so. The lower canine is relatively short and stout, its cingulum with generally a small raised postero-external tubercle; the first lower premolar (pm_2) subequal in crown area to i_2, with similar broad inner ledge and tricuspid cutting edge, the central cusp the largest; the second lower premolar (pm_3) has a large main cusp, sometimes with a subsidiary anterior cusp, a short posterior basal ledge forming labially a small posterior basal cusp separated from the main cusp by a notch. The third lower premolar (pm_4) and the first (m_1) and second (m_2) lower molars are short and broad, with strong posterior basal ledges more developed lingually than labially and thus oblique, and their lateral elevations are variously cuspidate to differing degrees, the lingual elevation on occasion more ridge-like; third lower molar (m_3) usually subcircular, with a concave crushing surface, generally with a shallow notch in its labial margin, but sometimes may be more definitely cuspidate, its crown pattern more nearly similar to that of m_2.

A comprehensive review of *Pteralopex* as then understood was provided by Andersen (1912 : 432), who had earlier (1909*a* : 213) studied its affinities in considerable detail. The genus has hitherto included two named forms, *P. atrata* Thomas, 1888 (the type species) and *P. anceps* Andersen, 1909*b*, the former described from Guadalcanar Island, in the eastern Solomon Islands and later reported (Sanborn, 1931 : 21) from the nearby island of Ysabel, the latter apparently known only from Bougainville Island and from Choiseul Island (Phillips, 1968 : 792), in the more westerly part of the Solomons group. Andersen (1912 : 437) considered the two to be distinct species but Laurie & Hill (1954 : 40) and Phillips (1968 : 790) considered *anceps* a subspecies of *P. atrata*. There is much, however, to commend the original arrangement. The ears of the larger *anceps* have a trace of a blunt tip and although for the most part its pelage is blackish or seal brown, the hairs on the posterior part of the ventral surface are tipped with drab brown. The fur is long and rather woolly, extending to the dorsal surface of the tibia and of the metatarsals, which dorsally are densely haired. In contrast, the ears of *atrata* are more rounded and its pelage uniformly blackish or dark seal brown, rather short and not especially woolly, the fur not extending dorsally to the distal end of the tibia (the last fourth is naked) or to the metatarsals.

Although many dental features such as the enlargement of i^{2-3} and of i_2, and the presence of a secondary canine cusp are shared in equal measure by *anceps* and *atrata*, in others there is considerable divergence. In particular, the anterior basal ledges of pm^4 and m^1, and to a lesser extent of pm^3 are less developed in *anceps* than in *atrata*, and the lingual margins of pm_4, m_1 and m_2 are more ridge-like and less cusp-like. According to Andersen (1912 : 437, 438, fig. 22) the anterior basal ledge of pm^4 in *anceps* does not extend internally on to the inner surface of the lingual cusp as it does in *atrata*, but the lingual faces of pm^{4-4} have been damaged in the subadult holotype and only available specimen of *anceps*, and the observation cannot now be confirmed from this example: according to Phillips (1968 : 792) the anterior basal ledge of pm^4 in adult *anceps* extends to the labial surface. Certainly the anterior basal ledges of pm^3 and m^1 in *anceps* extend much less obviously on to the inner face of the lingual cusp than in the corresponding teeth of *atrata*. In *anceps* the lingual cusp of pm$_4$ is long and slightly ridge-like but in *atrata* the corresponding cusp is much more nearly conical: this contrast is more pronounced in m$_1$ which in *anceps* has a long, ridge-like lingual elevation, scarecely separated from the raised anterior rim of the tooth, but in *atrata* has a prominent, sharply defined antero-internal cusp, or in m$_2$ where the similarly long, rather low, ridge-like lingual elevation of *anceps* differs from the short, slightly raised corresponding elevation of *atrata*. Furthermore, the labial elevations of pm$_4$, m$_1$ and m$_2$ in *anceps* are much less definitely divided into two cusps than in *atrata*, the dividing fissure in pm$_4$ and m$_1$ scarcely reaching the labial face of the teeth and barely perceptible in m$_2$. In general terms the molariform teeth of *anceps* are nearer in appearance to those of many species of *Pteropus* than are those of *atrata*: the external and dental differences between *anceps* and *atrata* suggest that the two forms must be considered specifically distinct.

Key to species of *Pteralopex*

1 Smaller (length of forearm 116–120 mm); pelage brown overall; labial margin (excluding raised posterior ledge) of pm^4 and m^1 divided into three cusps, the anteriormost very small; pm$_3$ lacking any lingual cusp; crowns of m$_1$ and m$_2$ closely similar . . ***P. acrodonta*** sp. nov.

– Larger (length of forearm 139–171 mm); pelage predominantly black or blackish seal brown, especially dorsally; labial margin (excluding raised posterior ledge) of pm^4 and m^1 forming a single large cusp; pm$_3$ with prominent lingual cusp; crowns of m$_1$ and m$_2$ dissimilar . 2

2 Smaller (length of forearm 139–144 mm); ventral pelage uniformly black or blackish seal brown; fur short, not especially woolly, extending to entire dorsal surface of tibia and to dorsal surface of metatarsals; pm$_4$ with subconical lingual cusp; lingual elevations of m$_1$ and m$_2$ short, in m$_1$ forming a sharply defined subconical antero-internal cusp . . ***P. atrata***

– Larger (length of forearm 160–171 mm); ventral pelage black or blackish seal brown anteriorly, brownish posteriorly; fur long, woolly, not extending dorsally to distal end of tibia or to dorsal surface of metatarsals; pm$_4$, m$_1$ and m$_2$ with lengthened or long ridge-like lingual elevations . . . . ***P. anceps***

Pteralopex acrodonta sp. nov.

HOLOTYPE. BM(NH) 77.3097. Adult ♂. Ridge about 300 m NE of the Des Voeux Peak Radio Telephone Antenna Tower, Taveuni Island, Fiji Islands, 16° 50½′ S, 179° 58′ W, c. 3840 ft (1170 m). Collected 3 May 1977 by W. N. Beckon, died 6–7 May 1977. Caught in mist net on ridge summit: bulldozed land with secondary scrubby growth, adjacent to primary forest. Original number 104. Skin and skull.

OTHER MATERIAL. No. 101. Adult ♀. Des Voeux Peak, Taveuni Island, c. 3900 ft (1190 m). Collected 9 November 1976 by W. N. Beckon, died 12 November 1976. Caught in mist net on ridge summit. Skin and skull. To be deposited in the Fiji Museum.

DIAGNOSIS. Smaller externally (Table 1) than either *Pteralopex anceps* or *P. atrata*, differing sharply from these in overall brown rather than black or blackish seal brown pelage; skull smaller (Table 1) than in either of the related species, but with relatively wider interorbital region and relatively more massive zygomata which have a more pronounced upward deflection. Teeth, excepting m^2 and m$_3$, smaller (Table 2) than in *P. anceps* or *P. atrata*, pm^4, m$^{1-2}$ and m$_{1-3}$ more cuspidate, (Fig. 1) the labial margin (excluding raised posterior ledge) of pm^4 and m^1 divided into three cusps rather than elevated into a single cusp as in these species; m^2 little reduced, similar in size to m^2 of *P. anceps* or *P. atrata*; pm$_3$ lacking the prominent internal cusp of pm$_3$ in *P. anceps* or *P. atrata*, its internal vertical ridge merging smoothly into the tip of the tooth; m$_1$ and m$_2$ closely resembling each other, not markedly dissimilar in size and cuspidation as in *P. anceps* and *P. atrata*; crown of m$_3$ less basin-like than in the related species, its cusp pattern similar to that of m$_1$ and m$_2$.

DESCRIPTION. Ears small, short, almost concealed by surrounding fur; upper margin of ear semicircular as in *Pteralopex atrata*, with no indication of any tip; outer surface of conch nearly naked, a few sparse long hairs on its inner surface, clustered a little more thickly near the anterior

Table 1 External and cranial measurements (in millimetres) of *Pteralopex acrodonta*, *P. atrata* and *P. anceps*

	P. acrodonta[1] ♂ BM(NH) 77.3097 Taveuni I., Fiji Is	*P. acrodonta* ♀ No. 101 Taveuni I., Fiji Is	*P. atrata*[1] ♂ BM(NH) 88.1.5.9 Guadalcanar I.	*P. atrata* ♂ BM(NH) 89.4.3.3 Guadalcanar I.	*P. atrata* ♀ BM(NH) 89.4.3.1 Guadalcanar I.	*P. atrata* ♀ BM(NH) 34.7.2.31 Guadalcanar I.	*P. anceps*[1, 2] ♀ BM(NH) 8.11.16.7 Bougainville I.	*P. anceps*[4] 3 ♂ ♂, ♀ Bougainville I. ♀ Choiseul I.
Length of forearm	116·5	119·5	141·8	140·5	144·0	139·0	136·3	160–171
Total length of skull	58·6	57·5	69·9	67·5	65·8	68·0	64·5	77·0–78·9
Condylobasal length	57·0	56·4	66·6	63·5	63·2	64·7	62·5	73·8–75·5
Palatal length	32·2	31·8	36·7	36·1	34·7	37·2	34·4	
Length palation to incisive foramina	27·2	26·6	31·2	30·5	29·9	32·3	29·2	
Length front of orbit to tip of nasals	15·7	15·0	18·9	16·9	17·0	19·0	17·2	
Lachrymal width	13·5	13·4	12·8	13·3	13·1	13·3	13·9	
Interorbital width	9·1	9·7	8·8	8·4	8·7	8·9	9·3	
Postorbital width	7·2	8·1	5·4	6·2	6·9	6·6	8·7	
Orbital diameter	12·5	12·4	12·9	13·0	13·1	13·3	12·9	
Zygomatic width	32·5	35·1	38·4	38·0	39·4	39·9	–	42·2–45·4
Width of braincase	21·5	22·0	22·5	22·7	21·7	23·5	24·8	
Mastoid width	20·6	20·9	22·6	22·3	22·0	23·7	22·5	
c^1–c^1 (greatest external)	14·2	14·6	17·0	17·2	16·9	15·9	16·7	18·7–21·1
c^1–c^1 (external, alveoli)	13·3	13·3	15·2	16·0	15·3	14·4	15·1	
c^1–c^1 (least internal)	8·0	8·3	9·0	8·9	8·6	8·8	8·3	
pm^4–pm^4 (least internal)	9·4	9·5	10·6	11·1	11·3	11·1	–	
m^1–m^1 (external, crowns)	16·0	16·3	20·3	21·6	20·9	20·0	20·5	22·0–25·3
m^1–m^1 (external, alveoli)	15·1	15·9	18·5	19·9	19·5	18·5	18·7	
Width of mesopterygoid fossa	6·9	6·6	8·1	9·1	9·1	9·8	8·1	
c–m^2	21·9	22·0[3]	25·6	26·1	25·4	25·3	25·4	28·2–29.3
Length of complete mandible from condyles	44·5	43·3	54·3	53·2	50·2	51·4	48·9	
Length of right ramus from condyle	46·4	45·4	55·8	54·5	52·0	53·6	50·6	
c–m_3	24·2	24·2	27·8	28·0	27·4	27·4	28·2	31·4–32·8

[1] Holotype. [2] Subadult. [3] Left toothrow. [4] From Phillips (1968:792)

Table 2 Measurements (in millimetres) of cheekteeth of *Pteralopex acrodonta*, *P. atrata* and *P. anceps*

		P. acrodonta[1] ♂ BM(NH) 77.3097 Taveuni I., Fiji Is	*P. acrodonta* ♀ No. 101 Taveuni I., Fiji Is	*P. atrata*[1] ♂ BM(NH) 88.1.5.9 Guadalcanar I.	*P. atrata* ♂ BM(NH) 89.4.3.3 Guadalcanar I.	*P. atrata* ♀ BM(NH) 89.4.3.1 Guadalcanar I.	*P. atrata* ♀ BM(NH) 34.7.2.31 Guadalcanar I.	*P. anceps*[1, 2] ♀ BM(NH) 8.11.16.7 Bougainville I.
pm^3	Length	4·3	4·4	5·1	5·1	5·0	4·5	5·1
	Width	3·0	3·1	4·0	4·4	4·2	3·8	4·3
pm^4	Length	4·4	4·2	4·9	5·0	5·1	4·6	5·3
	Width	3·2	3·2	4·2	4·6	4·2	4·0	–
m^1	Length	4·0	3·9	4·5	4·4	4·6	4·0	5·0
	Width	2·8	2·8	3·7	3·9	3·8	3·5	4·2
m^2	Length	3·6	3·5[3]	3·2	3·3	3·1	2·7	3·2
	Width	2·7	2·6[3]	2·8	3·0	2·9	2·6	3·0
pm$_2$	Length	2·4	2·4	2·9	3·0	3·0	2·4	3·3
	Width	2·4	2·2	3·0	2·9	3·2	2·6	3·2
pm$_3$	Length	4·3	4·3	4·9	4·8	4·8	4·4	5·5
	Width	2·3	2·5	3·3	3·6	3·2	3·2	3·3
pm$_4$	Length	4·2	4·1	5·0	5·2	5·1	4·8	5·8
	Width	2·6	2·8	3·7	3·9	3·7	3·4	3·7
m$_1$	Length	4·3	4·3	4·5	4·9	4·8	4·5	5·5
	Width	2·8	2·8	3·8	3·7	3·6	3·3	3·8
m$_2$	Length	4·1	3·9	3·7	3·7	3·7	3·4	4·0
	Width	2·7	2·6	3·4	3·4	3·3	3·1	3·5
m$_3$	Length	2·7	2·3	2·7	2·8	2·7	2·4	2·5
	Width	2·4	2·4	2·8	2·7	2·7	2·4	2·7

[1] Holotype. [2] Subadult. [3] Left tooth.

margin of the ear; no antitragal lobe; wings inserted on the back at or near the spinal line, and posteriorly at the base of the first and second toes; second phalange of fourth digit subequal in length to first phalange, not conspicuously longer; uropatagium or interfemoral membrane a very narrow flange; calcar short. Pelage brown overall, dorsally with the hairs mid-brown at the base and for much of their length, over the head, mantle and rump tipped with paler shining brown to give a slightly bronzed appearance, paler hair tips on rump a little less evident than those of mantle; hairs in mid-dorsal region immediately behind mantle bright brown for their entire length, smooth, closely adpressed, forming a longitudinal band about 18–20 mm in width over the innermost part of the wing membranes at their insertion along the mid-line of the body; ventral pelage a drab brown, rather paler than the dorsal pelage, on the lower part of the neck and on the flanks with paler light brown tips. The colour of the new species contrasts sharply with the black coloration of *P. atrata* or with the black dorsal surface of the head and body in *P. anceps*; only in

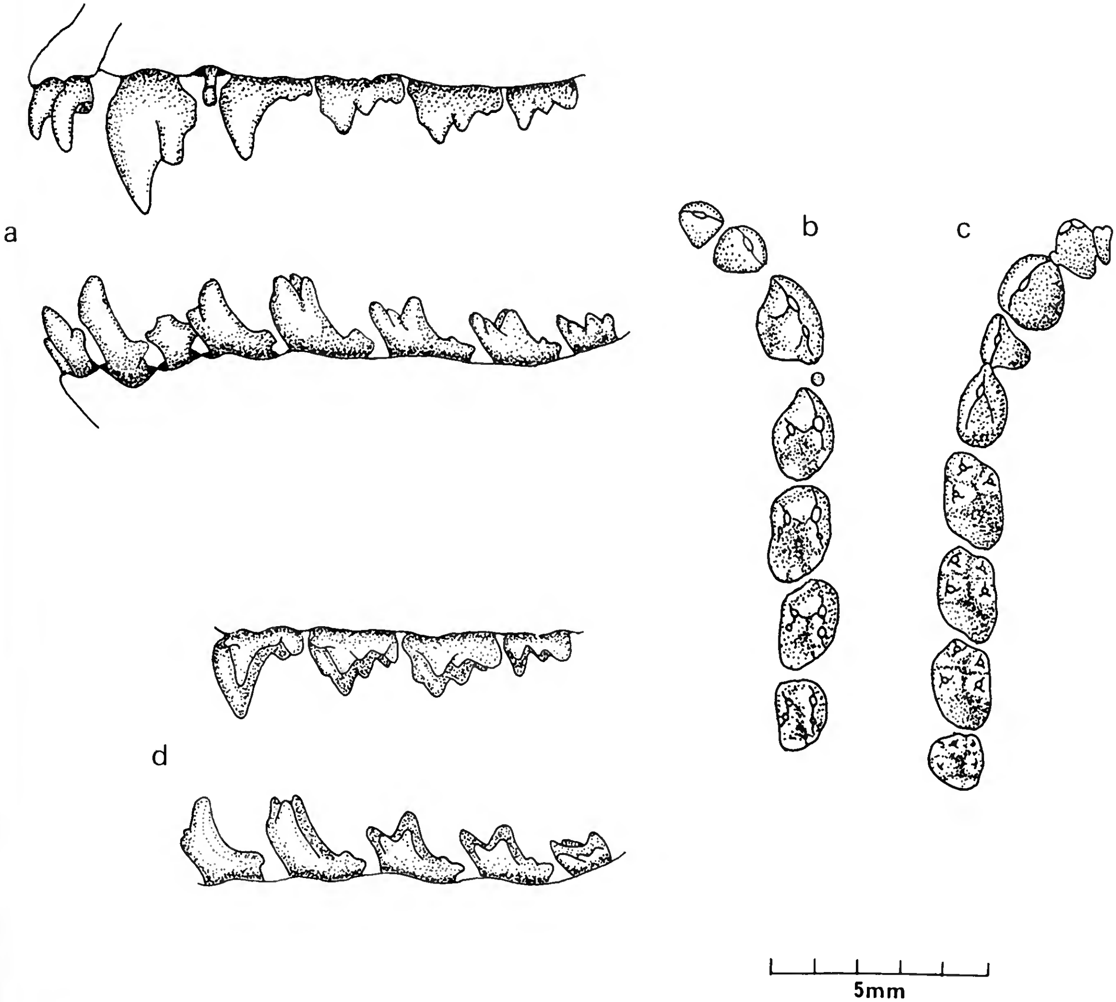

Fig. 1 *Pteralopex acrodonta*. Holotype ♂ BM(NH) 77.3097. a. Labial aspect of left toothrows. b. Ventral aspect of left upper toothrow. c. Dorsal aspect of left lower toothrow. d. Lingual aspect of right molariform teeth.

this latter species the blackish brown colour of the underparts is relieved by drab tipping to the otherwise dark seal brown hairs over the lower part of the chest and over the belly.

Fur long and woolly as in *Pteralopex anceps*; upper surface of forearm thickly clothed with moderately long, adpressed brownish hairs for the proximal two thirds of its length, the hair covering a little more extensive and denser near and at the elbow; tibia densely covered dorsally with thick long hair to the ankle, with a very thin scattering of moderately long, brownish hairs on the upper surface of the phalanges. Dorsal surface of wing and uropatagium or interfemoral membrane largely naked but a narrow band of quite dense, closely adpressed, long bright brown hairs extending along the junction of the mesopatagium with the proximal two thirds of the forearm, around the elbow and across the endopatagium to the rear of the mantle, the median longitudinal mid-dorsal band of long, smoothly adpressed bright brown hairs above the insertion of the endopatagium on the body extending over the proximal part of the membrane; a thin clustering of moderate, blackish brown hairs near the hind margin of the endopatagium at and near its junction with the foot; ventrally a denser band of moderately long brown hairs along the proximal two thirds of the junction of the mesopatagium with the forearm; ventral surface of forearm and tibia with no more than a few very sparse hairs.

Pteralopex anceps has a rather dense cover of long black hairs on the proximal third of the dorsal surface of the forearm and the dorsal surface of the tibia is densely clothed with quite long blackish chestnut brown fur, extending to the dorsal surface of the foot over the metatarsals and, more sparsely, to the dorsal surface of the phalanges; there is a band of moderate hairs on the mesopatagium both dorsally and ventrally adjacent to the lower part of the forearm, blackish above, brownish below, but the dorsal band does not extend across the surface of the endopatagium to the rear of the mantle. In *P. atrata* the proximal third of the dorsal surface of the forearm and the dorsal surface of the tibia have only a very sparse cover of moderate black hairs which extend and scatter on to the dorsal surface of the foot over the metatarsals and phalanges; there is no definite band of fur on the dorsal surface of the mesopatagium or of the endopatagium, but the ventral surface of the mesopatagium has a band of brownish hairs along the proximal two thirds of its junction with the forearm.

Skull similar to that of *Pteralopex anceps* or of *P. atrata*, with broad, nearly parallel-sided rostrum, but smaller; sagittal crest well developed but not especially prominent; interorbital region relatively wide; orbits less markedly upwardly directed than in its congeners; zygomata massive, deep, their upper margin forming a strongly pronounced upwardly sweeping curve; nasals terminating anteriorly at a line vertically above the rear of i^3 as in *P. anceps* rather than above the centre of this tooth as in *P. atrata*.

Inner upper incisor (i^2) with narrow posterior shelf, less sharply demarcated from the vertical cusp than in *Pteralopex anceps* or *P. atrata*, the junction smoothly curved rather than angular; i^3 with posterior shelf more prominently developed than in i^2 and more sharply demarcated from the vertical cusp, the internal cingulum of the tooth slightly raised as in *P. anceps* and lacking the postero-internal cingulum cusp of i^3 in *P. atrata*. Upper canine very similar to that of *P. anceps* or *P. atrata*, substantial, massively based, its antero-external face shallowly grooved, the principal cusp with sharp anterior and internal ridges and with a large, heavy posterior supporting cusp extending along about two thirds of the length of the tooth, a very small, poorly defined posterior cingulum cusp at its base; a small internal cingulum cusp at and just behind the base of the internal ridge, larger than the corresponding indistinct internal cingulum cusp of *P. anceps* but rather less developed than the corresponding cusp in *P. atrata*, in the unworn dentition followed by two small internal cusplets; postero-internal cingulum cusp small and undeveloped, in contrast to the substantial postero-internal cingulum cusp of the related species, but in these there is little or no trace of any posterior cingulum cusp.

Anterior upper premolar (pm^2) small, terete, its circular crown very slightly larger than its shaft; pm^3 with larger labial cusp and smaller lingual cusp as in *Pteralopex anceps* or *P. atrata*, its anterior basal ledge narrower than in those species but nevertheless also extending to the inner face of the tooth, a small basal supplementary postero-external cingulum cusp at rear of main labial cusp; pm^4 strongly cuspidate, labially with a higher central cusp supported by a small anterior subsidiary cusp and a rather more prominent posterior subsidiary cusp, separated from the posterior basal ledge by a small, undeveloped basal cusp, lingually with a lower but rather more massive cusp supported posteriorly by a small postero-internal basal cusp; anterior and posterior basal ledges well developed, raised, the anterior ledge extending to the inner face of the tooth as in *P. atrata*, the posterior ledge oblique as in *P. anceps*.

First upper molar (m^1) very similar to pm^4 with its labial elevation divided into a larger central cusp with smaller anterior and posterior supporting cusps, separated from the raised posterior ledge by a very small basal cusp integral with the ledge and with large lingual cusp, an incipient subsidiary postero-internal cusp at the base of its posterior face; m^2 relatively large, the tooth labially with a large anterior cusp supported posteriorly by a lower subsidiary cusp, the lingual elevation divided into two cusps, the anteriormost much the longer and higher, completely separated anteriorly from the labial elevation by a moderate fissure, the posterior basal ledge well developed, raised and cusp-like. In profile, the labial faces of pm^4 and m^1 present a more or less tricuspid appearance, the anteriormost cusp small and sometimes rudimentary, the second cusp much the largest, supported posteriorly by a well-developed subsidiary cusp, the basal cusp at the rear of this structure barely evident in profile, overshadowed by the large, massive elevated posterior basal ledge. In the same way, m^2 is bicuspid in labial profile, with a large anterior cusp and smaller posterior subsidiary cusp: as in pm^4 and m^1, the strongly developed, elevated posterior basal ledge appears in profile to be a further posterior cusp. There is a sharp contrast in labial profile between pm^4, m^1 and m^2 in *Pteralopex acrodonta* and the corresponding teeth in *P. anceps* and *P. atrata*, which present but a single large cusp, with posteriorly the prominent elevated posterior basal ledge: in *P. atrata* the extreme elevation of this ledge produces the appearance of a posterior cusp, especially in m^1 and m^2.

Inner lower incisor (i_2) as in *Pteralopex anceps* or *P. atrata*, very small, about one twelfth to one fifteenth the bulk of i_3, its edge slightly widened, faintly and irregularly lobed, its crown triangular in cross-section; i_3 much as in *P. anceps* or *P. atrata*, large, with high, rounded, chisel-like cutting edge, shallowly divided into a small inner and larger central cusp, the latter flanked at its base by a small external basal cusp, and with strong posterior shelf to give the crown a triangular outline; lower canine short and relatively massive, with narrow postero-internal shelf, not differing appreciably from the lower canine in the related species.

First lower premolar (pm_2) similar in cross-section to i_3, as it is in *Pteralopex anceps* or *P. atrata*, but a little smaller than that tooth as in *P. anceps*, its edge with larger central cusp, a rudimentary anterior cusp and a rather more developed posterior cusp; pm_3 faintly bicuspid in labial profile, its large labial cusp with a small anterior subsidiary cusp, the tooth lacking any trace of an internal lingual cusp, its internal ridge integral to the tip, not forming an incipient internal cusp as in *P. anceps* or a well-developed internal cusp as in *P. atrata*, the labial cusp in these species single, with no secondary or subsidiary anterior cusp; posterior basal ledge narrow as in the related species, terminating labially in a small postero-external basal cusp separated from the principal labial cusp by a distinct notch; pm_4 similar to pm_4 of *P. anceps* or *P. atrata*, labially with two well developed cusps, lingually with a single large cusp, the anterior part of the crown divided completely by moderate fissures, the labial cusps divided totally as in *P. atrata*, not partially as in *P. anceps*, the posterior basal ledge broad and oblique as in these species, elevated labially into a postero-external cusp-like structure separated by a distinct notch from the posterior of the larger labial cusps, but undeveloped lingually, as in *P. anceps* and *P. atrata*.

First lower molar (m_1) quite different from m_1 in either *Pteralopex anceps* or *P. atrata*, its crown anteriorly elevated as in these species but divided anteriorly by deep longitudinal and transverse fissures into four cusps, two labial and two lingual, the anteriormost labial cusp in the unworn dentition with a slight curving of its postero-external edge which may indicate a further slight degree of cuspidation. The anterior part of the crown thus displays a condition contrasting sharply with *P. anceps* in which the elevated part of the crown of m_1 is only partially divided by shallow fissures and is rather basin-like, the lateral ridges more or less integral with the raised anterior rim, which is divided by a shallow antero-internal groove; the labial ridge has a shallow fissure just extending to its outer face and the lingual ridge is rather long, with a similarly shallow fissure in its internal face. In *P. atrata* the fissures are deeper than in *P. anceps*, creating labially two well-developed cusps and lingually a single large cusp. As in *P. anceps* and *P. atrata*, the posterior basal ledge of m_1 in *P. acrodonta* is well developed, wide and oblique, elevated labially into a postero-external basal cusp but low lingually, the cusp rather less developed than in the related species.

Second lower molar (m_2) closely resembling m_1 but differing in the unworn dentition in having the labial elevation divided into three cusps, the large anterior labial cusp having a small subsidiary cusp shallowly divided from its postero-external face, the whole deeply separated from a more posteriorly placed large labial cusp, the two anterior cusps eroding with wear to a single, large flattened structure. The anterior part of the crown differs widely from the corresponding part of the crown of m_2 in *Pteralopex anceps* from which cusps are effectively lacking, the labial ridge only faintly divided and then incompletely, the lingual ridge long and undivided, both ridges integral with the raised anterior margin to form an elevated rim round much of the anterior part of the tooth. The anterior part of the crown of m_2 in *P. atrata* is similar to that of *P. anceps*, but the labial ridge is very shallowly divided by a slight fissure and the lingual ridge is relatively shorter and slightly cusp-like, faintly divided from the raised anterior margin. The posterior basal ledge of m_2 in *P. acrodonta* resembles that of m_1 and is similarly well developed, wide and oblique, elevated labially into a low basal cusp. In *P. anceps* the posterior basal ledge of m_2 is much developed postero-externally into a large cusp-like structure not clearly separated from the labial ridge but is similarly low lingually, while in *P. atrata* the ledge is elevated postero-externally into a distinct large cusp, separated from the main labial ridge by a deep notch. In *P. anceps*, therefore, the crown of m_2 is basin-like, its central depression opening postero-internally but otherwise surrounded by elevated ridges: in *P. atrata* shallow fissures appear in the anterior and labial of these ridges, the lingual ridge is shorter and more cusp-like and the labial ridge is quite clearly separated from the small cusp that forms the labial termination of the posterior basal ledge. In *P. acrodonta* the basin-like pattern is absent, the tooth with a group of elevated cusps anteriorly and a broad, low posterior basal ledge that is only slightly elevated labially.

Third lower molar (m_3) relatively large, similar in size to m_3 in *Pteralopex anceps* or *P. atrata*, the anterior cusp pattern in the unworn dentition similar to that of m_2, with three labial and two lingual cusps, the anterior labial cusp large, with a small subsidiary cusp shallowly divided from its postero-external face, deeply separated from a more posteriorly situated large posterior labial cusp, and much of the crown of the tooth traversed by relatively deep longitudinal and transverse fissures; posterior basal ledge narrow and short, elevated, shallowly divided into two small unequal basal cusps, the outer smaller, the inner rather larger. The cusp pattern is greatly eroded in the worn dentition to produce two flattened cusps anteriorly, one labial, one lingual, separated by a shallow longitudinal fissure, both separated by a deeper transverse fissure from the low, cusp-like remnants of the posterior labial and lingual cusps and of the raised posterior basal ledge. The crown of m_3 in *P. acrodonta* contrasts sharply with that of m_3 in *P. anceps* in which no cusps are evident and which has instead very short lateral ridges, contiguous with the raised anterior margin, the posterior margin greatly developed and elevated, separated from the labial ridge by a shallow notch, the central depressed area of the tooth opening postero-internally as in m_2 of that species. There are similar contrasts with the crown of m_3 in *P. atrata*, which has very similar short lateral ridges, the lingual ridge slightly cusp-like, separated from the raised anterior margin by a faint indentation, the posterior margin elevated labially into a rounded cusp, separated from the labial ridge by a shallow notch, and the central area of the tooth opening postero-internally as in *P. anceps*.

The anterior parts of pm_4 and m_1 in *Pteralopex acrodonta* are strongly bicuspid in labial profile, with m_2 and m_3 more or less tricuspid in the unworn dentition when the large anterior cusp and its associated subsidiary cusp are clearly defined, but bicuspid when wear has occurred. The small external basal cusp terminating the posterior basal ledge in pm_4, m_1 and m_2 suggests an additional, low posterior cusp behind the main elevation. The lower molariform teeth of *P. acrodonta* differ sharply in profile from those of *P. anceps* in which only a slight indication of a division of the labial ridge into two cusps can be seen in pm_4 and m_1, is imperceptible in m_2 and absent from m_3. In labial profile they more nearly resemble the lower molariform teeth in *P. atrata* where the labial ridge in pm_4 and m_1 is clearly bicuspid, that of m_2 faintly so but m_3 lacks any division of the labial ridge. The lingual profile of pm_4 is similar in the three species, but *P. acrodonta* differs markedly from *P. anceps* and *P. atrata* in the lingual profile of m_1 and m_2. The lingual elevation of these teeth in *P. acrodonta*, although long, is deeply divided into two cusps but in *P. anceps* presents an uninterrupted ridge-like lingual elevation which is shorter and raised into a single large cusp in *P. atrata*. The lingual profile of m_3 differs similarly. In the unworn dentition of *P. acrodonta* its lingual elevation is bicuspid although in the worn dentition the posterior cusp tends to erode into the posterior basal ledge: in *P. anceps* there is a low lingual ridge which in *P. atrata* is anteriorly higher and a little more cusp-like.

ETYMOLOGY. The specific name is derived from *ἄκρος*, pointed, and *ὀδών* = *ὀδούς*, tooth, in allusion to the many pointed summits of the molariform teeth in the new species.

BIOLOGY. Little is known of the biology of this species: the male was not reproductively active when captured, and the female not pregnant.

REMARKS. This interesting new species was discovered by the junior author and his wife, who obtained a single example on Taveuni in the latter part of 1976. They visited the island again in 1977 when two more specimens were caught, one of which escaped. It is possible that the species may be the 'white' fruit bat described by Mr Vasu Shankaran, an Indian resident of Taveuni, and known as the 'beka lulu' by the local population. This 'white' bat was reported in the lower forest of the Nasinu area, about 13½ km SSW of Waiyevo, but while camped there no specimens were netted although many bats were seen circling in the forest during the early evening. Mr Shankaran remarked that this bat usually roosted in pairs in the fern clumps growing some 6–10 m from the ground on the trunks of the larger trees in the open, tall forest, leaving the clump when disturbed but flying only a short distance before landing again, unlike the other Fijian fruit bats which are more colonial and which desert their roost when an intruder approaches. This observation is supported by Mr Robin Mercer, a planter and naturalist of Savusavu in Vanua Levu, who said that the Fijians of that island use the term 'beka lulu' for a light coloured fruit bat that circles the roost instead of flying away when disturbed: he had thought such bats to be old, hoary individuals of the known species. A different pattern of erratic, manoeuvring flight, suggesting the hunting of insects, was noted in large bats over Des Voeux Peak on Taveuni. The name 'beka lulu' or 'mbeka lulu' appears in a list of Fijian names (Macdonald, 1857 : 267) collected during an expedition up the Rewa River and its tributaries in 1856 and also in the New Fijian Dictionary of Capell (1973) where it is defined as a 'species of bat'. The term apparently refers to its reputed owl-like colour and large eyes: in life the eyes of *Pteralopex acrodonta*, although not unusually large, are bright orange and very conspicuous. From the pattern of bird distribution in the Fiji Islands, too, it seems possible that in due course the species will be found in Vanua Levu, across the narrow Somosomo Strait from Taveuni Island.

Relationships

Andersen (1909*a* : 218) discussed the diagnostic characters and affinities of *Pteralopex* in detail and concluded that it was closely related to the *pselaphon* group of *Pteropus* (including *P. insularis*, *P. phaeocephalus*, *P. pselaphon*, *P. pilosus*, *P. tuberculatus* and *P. leucopterus*), some members of this group displaying to a greater or lesser extent many of those features that appear in more exaggerated form in *Pteralopex anceps* or in *P. atrata*. The newly described species adds support to this opinion. The distribution of the fur, the shape of the skull, its long postorbital processes that do not reach the zygomata, the lack of postorbital zygomatic processes, its short, broad rostrum, heavy premaxillae and its high, broad coronoid rising at about a right angle from the horizontal ramus, with broad, steeply sloping gonys are all features of *Pteralopex* that are foreshadowed in the *pselaphon* group of *Pteropus*. The dentition of *Pteralopex acrodonta*, although more extreme and further removed from that of *Pteropus* than the dental structure either of *Pteralopex anceps* or of *P. atrata*, has nevertheless a number of interesting features that extend the parallels drawn by Andersen between the dental architecture of *Pteralopex* and that of the members of the *pselaphon* group of *Pteropus*, especially of *P. pselaphon*, *P. pilosus*, *P. tuberculatus* and *P. leucopterus*.

The posterior shelf of i^2 is narrower in *Pteralopex acrodonta* than in *P. anceps* or *P. atrata* and is slightly less sharply demarcated from the vertical cusp, with a smooth, more rounded transitional area rather than a right-angled junction such as occurs in these species, and i^3 is relatively smaller than in *P. anceps* or *P. atrata*, about one and one half times greater in bulk than i^2 rather than two times or more its bulk as in the other species of *Pteralopex*. In these features i^{2-3} of *Pteralopex acrodonta* resemble those of the members of the *Pteropus pselaphon* group and, indeed, approach the condition found in *P. leucopterus*. The upper canine in *Pteralopex acrodonta* resembles the upper canine of *P. anceps* or *P. atrata* in the structure of the principal cusp and its major subsidiary cusp, but the postero-internal basal cingulum cusp is smaller and lower than in these species. In the *Pteropus pselaphon* group internal cingulum cusps at the base of the canine are when present usually low and irregular, except in *P. pilosus* which has a large postero-internal basal cusp and a smaller internal basal cusp. The lower incisors and lower canines of the new species are characteristically those of *Pteralopex*.

Certain features of the post-canine dentition of *Pteralopex acrodonta* also find a precedent among the members of the *pselaphon* group of *Pteropus*. The second lower premolar (pm_3) in lacking any well-defined internal cusp in *Pteralopex acrodonta* differs sharply from pm_3 in *P. anceps* and *P. atrata*: in the *Pteropus pselaphon* group, *P. pselaphon*, *P. pilosus* and *P. tuberculatus* have an internal shoulder on pm_3 that clearly represents such a cusp but in *P. leucopterus* the internal ridge of pm_3 merges smoothly into the summit of the tooth, as in the new species. The third lower premolar (pm_4) and m_{1-2} are also of especial interest in *Pteralopex acrodonta*. In this species, as in *Pteralopex anceps* and *P. atrata*, these teeth are short and broad with oblique, labially more developed posterior ledge, but while pm_4 in *P. acrondonta* is otherwise very similar to pm_4 of *P. anceps* and more especially of *P. atrata*, the lingual elevation of m_1 and m_2 (and also of m_3) is divided into two cusps in contrast to the undivided lingual ridge of m_1 and m_2 in these species. As Andersen (1909 : 221) pointed out, in the *Pteropus pselaphon* group it is the inner or lingual ridge of pm_4 and m_1 that is divided in *P. pselaphon*, while in *P. leucopterus* the inner ridge of m_1 and m_2 is faintly divided, with a lesser or scarcely perceptible division in the outer or labial ridge of the same teeth. This author commented that in *Pteralopex*, as it was then understood, there was a further development of a tendency already apparent in the *Pteropus pselaphon* group but that division had shifted, so to say, from the inner or lingual elevation to the outer or labial elevation (there is in fact a shallow internal fissure in the internal face of the inner ridge of m_1 in *Pteralopex anceps* that does not extend to the edge of the tooth), but in *P. acrodonta* the cuspid condition appears very strongly in both the lingual and the labial elevations of m_1 and m_2. The crowns of these teeth in *P. acrodonta* present a multicuspid appearance that finds a weak parallel in *Pteropus leucopterus*, albeit very much less strongly emphasized. Furthermore, in *Pteralopex acrodonta* the much increased degree of cuspidation extends to m^2 and m_3, which are less reduced than in *P. anceps* or *P. atrata*, with m^2 at least three quarters rather than about one half or less the size of m^1 and larger than the corresponding tooth in the related species, and m_3 one half rather than one third the size of m_2, about the same size as m_3 of *P. anceps* or *P. atrata*. These features suggest a tendency to obtain a maximum of occlusal area in the teeth, despite the smaller size of the newly described bat when compared with its congeners. The geographical distribution of the dental characters among the three species of *Pteralopex* is also of interest. The least cuspidate molariform dentition, most like that of *Pteropus*, is to be found in the westernmost species, *P. anceps*. The most cuspidate dentition, least like that of *Pteropus*, is found in the easternmost species, *P. acrodonta*. A condition intermediate between these extremes occurs in the geographically central species, *P. atrata*.

Dental homologies and dental evolution

The larger of the pteropodid post-canine teeth have generally a rather characteristic appearance, consisting basically of a rectangular or more or less square crown, with a large labial and a small lingual elevation: these elevations are higher and more developed on the anterior teeth and less so in those that lie towards the rear of the toothrows, particularly in the last lower molar where they may be little more than longitudinal ridges along each side of the tooth. The elevations are higher in the anterior part of each tooth, with an oblique crushing surface, and lower in the posterior part, the crushing surface more nearly flat. The median division between the two elevations in the first of the larger teeth in each jaw is either obscured by a high, ridge-like commissure, or, often, they merge to form a single large cusp.

Miller (1907 : 41) suggested that it may be assumed (from analogy with the fruit-eating phyllostomatids) that in the upper molars the labial of these elevations is the paracone, the lingual elevation the protocone, while in the lower molars the labial elevation is the protoconid, its lingual counterpart the metaconid. More recently, Slaughter (1970 : 77) considered further that in the upper molars the metacone has been incorporated into the labial ridge and the hypocone into the lingual ridge, while the ridges of the lower molars similarly incorporate the hypoconid labially and the entoconid lingually. Additional small subsidiary cusps are present in several of the Pteropodidae, reaching an extreme in *Harpyionycteris* and *Pteralopex* but also present to some degree in *Hypsignathus*, *Dobsonia*, *Cynopterus*, *Ptenochirus*, *Dyacopterus*, *Thoopterus*, *Nyctimene* and *Paranyctimene*, while some division of the lateral ridges is apparent in a few species of *Pteropus*. The view adopted by Slaughter (p. 56, figs 1I, 1H, p. 77) is that the small subsidiary cusp on the posterior slope of the main labial cusp of the upper molariform teeth of *Dobsonia*, *Nyctimene* and sometimes *Cynopterus* is a rudimentary metacone and that likewise the small subsidiary cusp on the posterior slope of the principal labial cusp of the corresponding lower teeth is a rudimentary protostylid. On this basis Slaughter suggests or infers (p. 56, fig. 1H, p. 78) that in *Harpyionycteris* the last upper premolar (pm^4) consists labially of the paracone and metacone, lingually the protocone, pm_4 consisting of a tall protoconid flanked postero-labially by a well-developed protostylid, and lingually by a prominent metastylid, there being no metaconid. According to this author, the upper molars in *Harpyionycteris* retain the paracone and protocone, the metacone lying behind the paracone, and on occasion supporting a posterior metastyle. Lingually, the posteriormost cusp is the hypocone. The lower molars have anteriorly the protoconid and metaconid, the labial protoconid followed by a protostylid, the lingual metaconid by a metastylid: the third labial cusp is a small hypoconid, the third lingual cusp the entoconid, the stylids being as well developed as the other cusps.

Support for such close homology between the multiple cusps of the molariform teeth in certain of the Megachiroptera and the cusps of the Microchiropteran dentition is lacking or contradictory. Convincing palaeontological evidence has yet to be found: such cusps in the Megachiroptera occur sporadically, antero-internally, postero-externally, laterally, or on the crown of the tooth, sometimes as a short, raised ridge. In one form or another, or in combination, they are to be found in varying degrees in several of the megachiropteran genera. Even within the species their occurrence is irregular and variable: Peterson & Fenton (1970 : 5) have pointed out that in eight examples of *Harpyionycteris whiteheadi* no two specimens can be said to be even close to identical in the cusp pattern of m^1 and m^2. In this series the cusps vary in size, position and number, with the addition of accessory cusps to the basic pattern, or with the division of primary cusps into two elements, even between the corresponding right and left teeth of individuals, to the extent that these authors considered the variability of cusp patterns in *Harpyionycteris* to be unique among bats and certainly ranking high among mammals. It is difficult to avoid the conclusion that such multiple cusps cannot be properly homologized with the cusps of the Microchiroptera.

Thomas (1889 : 473), although admitting in an expanded description of *Pteralopex* that it might be thought at first sight that the genus was a highly specialized offshoot of *Pteropus*, considered that its cuspidate teeth most probably represented a survival from the cuspidate dentition that the ancestors of the Pteropodidae might be presumed to have possessed, largely on account of the 'tuberculo-sectorial' appearance of the third premolar and first molar. Later, Thomas (1896 : 243, 1898 : 384) also suggested that the cuspidate canines of *Harpyionycteris* might also owe their origin to a presumably cuspidate-toothed condition among the ancestors of the Pteropodidae. Miller (1907 : 41), although suggesting homology between the anterior of the molar cusps of the Pteropodidae and the protocone, paracone, protoconid and metaconid of the microchiropteran tooth, considered that additional cusps and ridges were not homologous and noted that the tendency to produce supernumerary cusps reached its extreme in *Pteralopex* and *Harpyionycteris*. A similar view was adopted by Andersen (1909*a* : 222; 1912 : xxix, 435) who considered *Pteralopex* to be a very specialized offshoot of *Pteropus*, more particularly of the *Pteropus pselaphon* group, the dental peculiarities of *Pteralopex* deriving in his opinion directly from tendencies already latent in the members of that group. Winge (1923 : 263; 1941 : 305) was also unable to recognize the tooth structure of the insectivorous bats in the multicuspidate cheek-teeth of *Pteralopex* and, indeed, found nothing else in its dentition to indicate primitive conditions, repeating the opinions of Miller and Andersen that *Pteralopex* is a highly modified pteropodid. Similarly, Tate (1951 : 4), in considering the dentition of *Harpyionycteris* in relation to the megachiropteran assemblage as a whole, suspected that its multicuspid molars, and the entire dentition, must be regarded as secondary rather than as a surviving example that represented a formerly widespread condition in the Megachiroptera. However, Phillips (1968 : 790) thought Thomas probably correct in considering *Pteralopex* to be an isolated relic.

Slaughter (1970 : 51) has examined possible evolutionary trends in the dentition of the Chiroptera. In discussing the Megachiroptera, this author (p. 77) reviewed the features reported for the fragmentary dentition of reputedly the earliest known megachiropteran, *Archaeopteropus transiens* Meschinelli, 1903, from the Oligocene of Italy, and concluded that only *Harpyionycteris* among living genera had a cuspidate molariform dentition that in any way approached the dentition ascribed to *Archaeopteropus*. However, little is known of the true nature of the ancestral dentition of the Megachiroptera, and Smith (1976 : 53) has remarked that there is apparently no dentition remotely similar to the 'primitive' dilambdodont condition among either the living or the fossil megachiropterans. The argument for megachiropteran dental evolution that Slaughter based on a supposed similarity between the dentitions of *Archaeopteropus* and *Harpyionycteris* was thought by Smith to be weak.

In developing his theme, Slaughter (1970 : 78) considered that the dentition of *Pteralopex* indicated that emphasis shifted very early from a cuspid state to one of U-shaped lophs, minimal dental erosion exposing a rodent-like pattern of dentine. Thus, in *Pteralopex*, the crown of a partially worn upper molar will present (Slaughter, p. 65, fig. 3H) a U-shaped fossette, opening labially, the lower molars presenting two similar lophs or fossettes, the anterior opening to the rear, the posterior opening forward. He considered that the origin of the dental patterns of *Pteralopex* could be easily understood by comparison with *Harpyionycteris* and, indeed, would derive the dentition of *Pteralopex* from that of a *Harpyionycteris*-like form. This presumed loph pattern is not entirely supported by the specimens examined in the course of the present study. In *Pteralopex anceps* m^1 and m^2 have clearly a labially opening fossette, but occasionally in *P. atrata* the high, anterior cusp-like part of each tooth is divided lingually from the elevated posterior basal ledge (hypocone and metastylar cusp of Slaughter) as deeply or almost as deeply as it is labially so that wear will expose an anterior and a posterior loph, rather than a U-shaped rim, or the fossette so formed may be rimmed lingually by a low, narrow unworn ridge rather than the broad ridge figured by Slaughter. The lingual ridge of pm^4 in *P. atrata* may also rarely be similarly deeply divided from the posterior basal ledge. The upper molariform dentition of *P. acrodonta* differs quite sharply from the concept of labially opening fossettes: the lingual division between the anterior part of the tooth and the posterior basal ledge in pm^4, m^1 and m^2 is deeper than the labial division so that the fossette opens lingually rather than labially, but with a depression in the postero-external part of its labial rim.

In the mandible, the anterior cusps of m_1, m_2 and m_3 in *Pteralopex anceps*, *P. atrata* and *P. acrodonta* provide the necessary basis for the posteriorly directed, U-shaped anterior loph postulated by Slaughter but it is more difficult to establish a foundation for a similar but anteriorly directed posterior loph in the specimens examined. There is little trace of such a loph in m_1 of any of these species: in this tooth the posterior basal ridge consists of little more than a low labial postero-external cusp, with no lingual elevation, the postero-internal part of the tooth flattened, the internal fossette thus opening postero-lingually. The posterior part of m_2 in *P. atrata* and *P. acrodonta* is similar to the corresponding area of m_1, except that in *P. atrata* the posterior basal ridge and its postero-external cusp is larger and more massive: in both species the crown is low and flat postero-internally, as in m_1, the posterior basal ridge extending rather more than half-way across the rear of the tooth, the internal fossette opening postero-lingually. In *P. anceps* the posterior basal ridge of m_2 has a very large postero-external cusp forming an internal part of the labial ridge, and extends across the rear of the tooth almost to its internal corner. Thus with wear the crown of the tooth will become more basin-like, its central fossette opening postero-lingually on to a small, flattened area. Posteriorly, m_3 in *P. atrata* is broadly similar to m_2 but the posterior basal ridge is a little heavier and extends a little further across the tooth, the internal fossette opening postero-lingually. In *P. anceps* the posterior basal ridge of m_3 is heavy, more or less integral with the labial ridge and extending to the inner corner of the tooth, much as in m_2, the fossette opening lingually, while in *P. acrodonta* the posterior basal ridge of m_3 although a little elevated is narrow and short and can scarcely enclose any internal fossette.

The suggestion that the dentition of *Pteralopex* might derive from a *Harpyionycteris*-like form also deserves close examination, especially since the extremely cuspidate molariform teeth of *Pteralopex acrodonta* have a number of similarities with the corresponding teeth in *Harpyionycteris*. They do, however, differ from the molariform teeth of *Harpyionycteris* in several features. The last upper premolar (pm^4) in *P. acrodonta* closely resembles its counterpart in *Harpyionycteris*, its major labial cusp with a small posterior subsidiary cusp as in that genus, but has additionally a smaller anterior cusp, not evident in *Harpyionycteris*, while the lingual cusp has small anterior and posterior basal cusps which are barely if at all evident in that genus. The anterior basal ledge of the tooth is a little wider and flatter in *P. acrodonta*, and the posterior basal ledge larger and heavier, not clearly divided into two cusps as in *Harpyionycteris*. The upper molars (m^{1-2}) of *P. acrodonta*, although basically with the same cusp pattern as those of *Harpyionycteris*, have more elevated crowns, with the cusps less clearly divided: the main labial cusp of m^1 has an additional rudimentary subsidiary cusp on its anterior face and in both teeth the anterior basal ledge is more developed, the posterior basal ledge more elevated, heavier and more massive, not divided into two cusps. In *Harpyionycteris* the posterior basal ledge in m^1 is divided into two cusps but in m^2 it forms an indistinctly divided postero-internal cusp: accessory cusps are sometimes present in these teeth (Peterson & Fenton, 1970 : 7, fig. 2) but usually lingually. As in *P. acrodonta*, m^2 is relatively unreduced.

The lower molariform dentitions of *Pteralopex acrodonta* and *Harpyionycteris* have similar resemblances and differences. The principal cusps of pm_4 in both form an anterior 'trigonid', but in *Harpyionycteris* the tooth has additionally an anterior basal cusp and there is a small subsidiary cusp on the posterior face of the principal lingual cusp. The first lower molar (m_1) of *P. acrodonta* has anteriorly a group of four well-divided cusps arranged laterally in two pairs, the antero-labial of these with perhaps a faint trace of further cuspidation. Posteriorly, the tooth has a small low external basal cusp and its internal part is low and flattened. This configuration resembles the crown of m_1 in *Harpyionycteris* except that in this genus the anterior part of the tooth has three rather than two lingual cusps. The second lower molar (m_2) in *P. acrodonta* is similar to m_1, with the anterior part of the crown clearly divided, but in the unworn dentition the large antero-labial cusp has a smaller subsidiary cusp divided from its postero-external face, so that effectively there are three labial cusps: lingually, m_2 in *P. acrodonta* has two cusps, as in m_1. Posteriorly, there is a low external basal cusp flanking the low, flattened internal part of the tooth. In contrast, the anterior part of m_2 in *Harpyionycteris* has two labial and three lingual cusps: posteriorly, the tooth resembles m_2 of *P. acrodonta*. The unworn cuspidation of the anterior part of m_3 in *P. acrodonta* is similar to that of the anterior part of m_2, with a group of three labial and two lingual cusps, the first two labially consisting of a larger cusp with a smaller subsidiary cusp divided from its postero-external face. Posteriorly, however, the tooth is strongly elevated and slightly cuspidate, its internal part not low and flattened. In *Harpyionycteris* the anterior part of m_3 has two labial and three lingual cusps: posteriorly, there is a low external basal cusp but the internal part of the tooth is low and flattened as it is in m_2. However, m_3 in *Harpyionycteris* is relatively unreduced, in this respect resembling m_3 in *P. acrodonta*.

It is clear, therefore, that *Pteralopex acrodonta* resembles *Harpyionycteris* quite closely in the major details of its molariform teeth, differing chiefly in a slightly greater degree of development of the basal ledges of pm^4, m^1 and m^2, in the greater elevation of the crowns of the latter two teeth, and in certain details of cuspidation. The degree and pattern of cuspidation, especially where accessory cusps are concerned, may prove variable to some extent: only the holotype of *H. whiteheadi whiteheadi* has been available for comparison but variability in the cusps of m^1 and m^2

in *H. w. negrosensis* has been clearly demonstrated by Peterson & Fenton (1970 : 5, 7, fig. 2). In other respects the dentition of *Harpyionycteris* differs widely from that of *P. acrodonta*, as in its reduced number of incisors with the specialized structure and proclivity of the upper pair, this latter a character shared with the upper canines, and the effective obsolescence of lower incisors with their apparent substitution by strongly tricuspidate, rather incisiform, slightly procumbent lower canines, supplemented by well-developed anterior lower premolars (pm_{2-2}). These extensive differences militate against the view that the dentition of *Pteralopex* can be derived from a *Harpyionycteris*-like form: Andersen (1909*a* : 220) considered that the structure of pm^3, pm^4 and m^1 in *Pteralopex* could be derived very easily from that of the corresponding teeth of any species of *Pteropus* and had most probably originated from teeth in which the posterior basal ledge was already more than usually developed, as for instance in the members of the *pselaphon* group of *Pteropus* or in *Pteropus samoensis*; in the *P. pselaphon* group the anterior cingulum of pm^3 and pm^4 is also raised. Furthermore, this author (pp. 217, 220) presented a detailed case for the progressive division of the lateral ridges of certain of the lower molariform teeth in *Pteropus*. In the majority of species the ridges are simple: in *P. samoensis* and *P. pilosus* a faint depression in the inner or lingual ridge of pm_4 suggested an initial division to Andersen, leading to *P. pselaphon* in which the inner ridges of pm_4 and m_1 are very distinctly divided and to *P. leucopterus* in which there is a depression in the inner ridges of m_1 and m_2, with usually a shallower depression in the outer or labial ridges of these teeth, although it may sometimes be absent or scarcely detectable. This same process can be discerned more vividly in the three species of *Pteralopex*, from a least emphatic, *Pteropus*-like condition in *Pteralopex anceps*, approaching the *pselaphon* group of *Pteropus* as exemplified by *P. pilosus*, *P. pselaphon* and *P. leucopterus*, through an intermediate stage in *Pteralopex atrata*, to the strongly multicuspidate condition of *P. acrodonta*.

The hypothesis that the multicuspidate molariform teeth of *Pteralopex* are an extreme in the Pteropodine dentition is attractive: an opposite extreme is to be found in the low, broadened and rounded cusps and ridges of the molariform teeth of *Styloctenium* or of *Aproteles* Menzies, 1977. Although Andersen (1909*a* : 220) suggested that the multicuspidate condition could be derived from the molariform dentition of *Pteropus*, it is perhaps more plausible to suggest that the smoother or laterally ridged crown represents a derived condition, the cuspidate crown a less modified state. The links between the dentition of *Pteralopex* and the *pselaphon* group of *Pteropus*, rather than indicating *Pteralopex* to be a specialized offshoot of *Pteropus* as Anderson (1909*a* : 222) thought at one time, may well indicate that *Pteralopex* and the *Pteropus pselaphon* group derive from a close common ancestor. Andersen (1912 : l) himself later adopted a similar view, considering it scarcely open to doubt that *Pteralopex* had developed from a bat closely related to the living species of the *Pteropus pselaphon* group, or, in other words, that the genus (as it was then understood) was a peculiarly modified representative of that group in the Solomon Islands.

The adaptive significance of the multicuspidate dentition in *Harpyionycteris* was discussed briefly by Peterson & Fenton (1970 : 7) who speculated that, like most of its allies, *Harpyionycteris* is a fruit eater, perhaps adapted for a particular type of tough-textured fruit, the multicuspidate teeth being valuable in extracting the juice. Similar considerations may apply to *Pteralopex* (Sanborn, (1931 : 21) reported *P. atrata* feeding on green coconuts) and especially to *P. acrodonta* which closely resembles *Harpyionycteris* in the extent of cuspidation and in the lack of reduction of the last molars, both adaptations that apparently maintain a maximum of occlusal area despite relatively small overall size. *Harpyionycteris* is rather isolated within the Pteropodidae, having been given subfamilial status by Miller (1907 : 77) and by Andersen (1912 : 799), who, however, remarked (p. 803) that but for the fact that the plan of his Catalogue of 1912 had been predetermined before detailed work had been undertaken the genus ought to have been classed in the Pteropodinae, immediately after *Dobsonia*. Tate (1951 : 4) doubted the association with *Dobsonia* (this author misinterpreted Andersen's action in according subfamilial rank to *Harpyioncteris* as a lack of conviction in his association of the genus with *Dobsonia*) and suggested a connection with *Nyctimene*. Koopman & Cockrum (1967 : 116) also accorded subfamilial rank to *Harpyionycteris* but more recently Koopman & Jones (1970 : 23) preferred tribal status for the genus, within the Pteropodinae. On the other hand, Schultz (1970) noted its isolated systematic position in the Megachiroptera and considered that its multicuspidate molars indicated that it did not live exclusively on fruit. He concluded that certain morphological features of the digestive tract (notably the structure of the intestinal mucosa) pointed to an early separation from other pteropodids, and consequently postulated familial rank as the Harpyionycteridae. Hitherto among the Megachiroptera, extreme cuspidation of the molariform teeth has been unique and diagnostic to *Harpyionycteris* and for any higher category based upon it. In contrast, the multicuspidate condition in *Pteralopex acrodonta* can be linked through *P. atrata* and *P. anceps* to the condition more general among the other members of the Pteropodinae.

Acknowledgements

Our thanks are due to Mrs W. N. Beckon for much essential assistance and support, particularly with the collection of specimens; to Mr Peter Thomson, District Officer, Taveuni Island, and his wife Marijcke, who offered hospitality and gave invaluable assistance with transport, accommodation and food during successive visits to the island, and to Mr Vasu Shankaran of Taveuni and Mr Robin Mercer of Vanua Levu for providing local information. We are grateful also to Dr J. D. Smith, of the Department of Biological Sciences, California State University, Fullerton, California, whose views in correspondence with the senior author have been most valuable during the preparation of this paper.

References

Andersen, K. 1909*a*. On the characters and affinities of '*Desmalopex*' and *Pteralopex*. *Ann. Mag. nat. Hist.* (8), **3** : 213–222.

—— 1909*b*. Two new bats from the Solomon Islands. *Ann. Mag. nat. Hist.* (8), **3** : 266–270.

—— 1912. *Catalogue of the Chiroptera in the Collection of the British Museum, 2nd ed. I. Megachiroptera.* London.

Capell, A. 1973. *A New Fijian Dictionary*. 4th ed. Suva.

Felten, H. 1964*a*. Zur Taxionomie indo-australischer Fledermäuse der Gattung *Tadarida* (Mammalia, Chiroptera). *Senckenberg biol.* **45** : 1–13, 7 figs.

—— 1964*b*. Flughunde der Gattung *Pteropus* von den Neuen Hebriden (Mammalia, Chiroptera). *Senckenberg. biol.* **45** : 87–92, 6 figs.

—— 1964*c*. Flughunde der Gattung *Pteropus* von Neukaledonien und den Loyalty-Inseln (Mammalia, Chiroptera). *Senckenberg. biol.* **45** : 671–683, 6 figs.

—— **& Kock, D.** 1972. Weitere Flughunde der Gattung *Pteropus* von den Neuen Hebriden, sowie den Banks- und Torres-Inseln, Pazifischer Ozean. *Senckenberg. biol.* **53** : 179–188. 3 figs, 1 tab.

Gill, W. W. 1876. The Mammalia of the Pacific. *The Leisure Hour*, 308–309. [N.V.].

Jentink, F. A. 1887. *In* H. Schlegel & F. A. Jentink, *Muséum d'Histoire Naturelle des Pays-Bas. Revue méthodique et critique des Collections déposées dans cet Etablissement. Tome 10. Catalogue Ostéologique des mammifères.* Leiden.

—— 1888. *In* H. Schlegel & F. A. Jentink, *Muséum d'Histoire Naturelle des Pays-Bas. Revue méthodique et critique des Collections déposées dans cet Etablissement. Tome 12. Catalogue Systématique des mammifères* (*Rongeurs, Insectivores, Cheiroptères, Edentés et Marsupiaux*). Leiden.

Koopman, K. F. 1971. Taxonomic notes on *Chalinolobus* and *Glauconycteris* (Chiroptera : Vespertilionidae). *Am. Mus. Novit.* No. 2451 : 1–10, 1 fig.

—— **& Cockrum, E. L.** 1967. *In* S. Anderson & J. K. Jones, Jr (Eds), *Recent Mammals of the World. A Synopsis of Families.* **6.** Bats, pp. 109–150, 11 maps. New York.

—— **& Jones, J. K., Jr** 1970. Classification of bats. *In* B. H. Slaughter & D. W. Walton (Eds), *About Bats. A Chiropteran Biology Symposium*, pp. 22–50, 11 figs, 2 tabs. Dallas.

Krzanowski, A. 1977. The easternmost occurrence of bats in Polynesia. *Acta theriol.* **22** : 271–272.

Laurie, E. M. O. & Hill, J. E. 1954. *List of Land Mammals of New Guinea, Celebes and adjacent Islands 1758–1952.* London.

Macdonald, J. D. 1857. Proceedings of the Expedition for the exploration of the Rewa River and its tributaries, in Na Viti Levu, Fiji Is. *Jl R. geogr. Soc.* **27** : 232–268, map.

Menzies, J. I. 1977. Fossil and subfossil fruit bats from the mountains of New Guinea. *Aust. J. Zool.* **25** : 329–336, 3 figs, 3 tabs.

Meschinelli, L. 1903. Un nuovo chirottero fossile (*Archaeopteropus transiens* Mesch.) delle ligniti de Monteviale. *Atti R. Inst. veneto Sci.* **62** (2) : 1329–1344, 1 pl.

Miller, G. S. 1907. The families and genera of bats. *Bull. U.S. natn. Mus.* **57** : i–xvii, 1–282, 49 figs, 14 pls.

Peterson, R. L. & Fenton, M. B. 1970. Variation in the bats of the genus *Harpyionycteris*, with the description of a new race. *Contr. Life Sci. Div. R. Ont. Mus.* No. 17 : 1–15, 6 figs, 3 tabs.

Phillips, C. J. 1968. Systematics of the Megachiropteran bats of the Solomon Islands. *Univ. Kans. Publs Mus. nat. Hist.* **16**: 777–837, 17 figs., 6 tabs.

Sanborn, C. C. 1931. Bats from Polynesia, Melanesia, and Malaysia. *Publs Field Mus. nat. Hist.* Zool. Ser. **18** : 7–29.

Schultz, W. 1970. Einige Bemerkungen zum Bau des Verdauungstraktes und der systematischen Stellung des Spitzzahnflughundes, *Harpyionycteris whiteheadi* Thomas, 1896 (Megachiroptera). *Z. Säugetierk.* **35** : 81–89, 7 figs.

Slaughter, B. H. 1970. Evolutionary trends of Chiropteran dentitions. *In* B. H. Slaughter & D. W. Walton (Eds), *About Bats. A Chiropteran Biology Symposium*, pp. 51–83, 5 figs. Dallas.

Smith, J. D. 1976. Chiropteran evolution. *In* R. J. Baker, J. K. Jones, Jr & D. C. Carter (Eds), Biology of bats of the New World family Phyllostomatidae. Part I. *Spec. Publs Mus. Texas Tech Univ.* No. 10 : 49–69, 2 figs.

Smith, S. P. 1902. Niue Island and its people. *J. Polynes. Soc.* **11** : 81–106. [N.V.]

Tate, G. H. H. 1951. *Harpyionycteris*, a genus of rare fruit bats. *Am. Mus. Novit.* No. 1522 : 1–9, 4 figs, 2 tabs.

Thomas, O. 1888. Diagnoses of six new mammals from the Solomon Islands. *Ann. Mag. nat. Hist.* (6) **1** : 155–158.

—— 1889. The mammals of the Solomon Islands, based on the collections made by Mr C. M. Woodford during his second expedition to the archipelago. *Proc. zool. Soc. Lond.* (1888) : 470–484, 3 pls.

—— 1896. On mammals from Celebes, Borneo, and the Philippines recently received at the British Museum. *Ann. Mag. nat. Hist.* (6) **18** : 241–250.

—— 1898. On the mammals obtained by Mr John Whitehead during his recent expedition to the Philippines. *Trans. zool. Soc. Lond.* **14** : 377–412, 7 pls.

Winge, H. 1923. *Pattedyr-Slaegter. I. Monotremata, Marsupialia, Insectivora, Chiroptera, Edentata.* København.

—— 1941. *The Interrelationships of the Mammalian Genera* (Ed. A. S. Jensen, R. Sparck & H. Vølsøe, translated E. Deichmann & G. M. Allen). *I. Monotremata, Marsupialia, Insectivora, Chiroptera, Edentata.* København.

Wodzicki, K. & Felten, H. 1975. The peka, or fruit bat (*Pteropus tonganus tonganus*) (Mammalia, Chiroptera), of Niue Island, South Pacific. *Pacif. Sci.* **29** : 131–138, 2 figs, 4 tabs.

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Zoology series Vol 34 No 3 21 December 1978

The *Bulletin of the British Museum* (*Natural History*), instituted in 1949, is issued in four scientific series, Botany Entomology, Geology and Zoology, and an Historical series.

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World List abbreviations: *Bull. Br. Mus. nat. Hist.* (Zool.)

ISSN 0007-1498

Zoology series
Vol 34 No 3 pp 83-124

British Museum (Natural History)
Cromwell Road
London SW7 5BD

Issued 21 December 1978

A revision of the spider genus *Portia* (Araneae : Salticidae)

F. R. Wanless
Department of Zoology, British Museum (Natural History), Cromwell Road, London SW7 5BD

Contents

Synopsis

The spider genus *Portia* Karsch is revised. All the 16 known species (of which 5 are new) are described and figured. Biological and distributional data are given and a key to the species is provided. Two species groups based on the structure of the male genitalia are proposed. The type-material (including 14 holotypes) of 22 nominate species was examined and 7 lectotypes and 1 neotype are newly designated. One genus is revived, 2 generic and 4 specific names are newly synonymized and 6 new combinations are proposed.

Introduction

Portia is a distinctive genus of long-legged ornate spiders which have attracted the attention of naturalists on account of their conspicuous leg fringes and abdominal hair tufts. The genus is represented in both the Oriental and Ethiopian regions and at present includes 16 species.

Portia, as recognized in this paper, has previously been divided between two genera *Portia* and *Linus* which Simon (1901) placed in separate suprageneric groups, the Boetheae comprising *Portia* and *Boethus*, and the monogeneric Lineae. In the same work Simon synonymized *Brettus* Thorell, 1895 with *Portia*, but recent studies on the type species of *Brettus*, *B. cingulatus* Thorell, have shown that this genus is valid, and furthermore that several species at present in *Portia* will have to be transferred back into *Brettus*. Simon's understanding of *Portia* seems to have been based in part on *Portia semifibriata* (Simon), from India and not on the type species *P. schultzii* Karsch from South Africa. *P. semifimbriata* agrees well with Simon's concept of Boetheae but it is not congeneric with *P. schultzii* and will have to be referred back into *Brettus*, i.e. its original combination. *P. schultzii*, in spite of uncertainties in respect of adult females (see below, p. 88), is clearly congeneric with *Portia fimbriata* (Doleschall), the type species of *Linus*. In fact a Madagascan record for *P. fimbriata* (Simon, 1901) probably refers to *P. schultzii* or even *P. africana* (Simon) both of which are now known to occur in Madagascar.

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The Ethiopian species have been revised by Roewer (1965) who recognized both *Portia* and *Linus* as valid, distinguishing them by the curvature of the first eye row and carapace shape. Unfortunately he based his descriptions and figures almost entirely on the literature and did not examine many of the type specimens. His new genus *Neccocalus*, proposed for *Cocalus africanus* Thorell, is a synonym of *Portia* as *C. africanus* is conspecific with the widespread West African species *P. africana.*

Genus *PORTIA* Karsch

Sinis Thorell, 1878, June : 269. Type species *Salticus fimbriatus* Doleschall, by original designation [Junior homonym of *Sinis* Heer, 1862 : 31]. Petrunkevitch, 1928 : 246. Bonnet, 1958 : 4061.

Portia Karsch, 1878 [December] : 774. Type species *Portia schultzii* Karsch, by original designation and monotypy. Peckham & Peckham 1885 : 267. Simon, 1901 : 400–403. Petrunkevitch, 1928 : 182. Bonnet, 1958 : 3766. Roewer, 1965 : 10.

Linus Peckham & Peckham, 1885 : 289 [Replacement name for *Sinis* Thorell]. Simon, 1901 : 400, 408, 410. Petrunkevitch, 1928 : 181. Sherriffs, 1931 : 538. Bonnet, 1957 : 2482. Roewer, 1965 : 14. **Syn. n.**

Boethoportia Hogg, 1915 : 501. Type species *Boethoportia ocellata* Hogg, by monotypy. Petrunkevitch, 1928 : 181. Strand, 1929 : 15. Roewer, 1954 : 933. Bonnet, 1955 : 892 [Synonymized by Prószyński, 1971 : 385].

Neccocalus Roewer, 1965 : 20. Type species *Cocalus africanus* Thorell, by original designation and monotypy. **Syn. n.**

Simon (1901), without giving his reasons, synonymized *Brettus* Thorell with *Portia* Karsch. However, preliminary studies on the holotype of the type species *Brettus cingulatus* Thorell have shown that the genus is valid and it is here removed from synonymy **gen. rev.** The genus will be revised in a paper in preparation.

Definition. Medium to large spiders ranging from about 4·5 to 9·5 mm in length. Sexes alike in general body form, but colour markings sometimes showing slight sexual dimorphism. Usually ornate with tufts of hair and leg fringes; colour patterns composed on setae (easily rubbed). *Carapace*: high, usually with marked slope from posterior lateral eyes to anterior row and to posterior thoracic margin; fovea elongate, just behind posterior lateral eyes; sculpturing not marked. *Eyes*: anteriors subcontiguous, apices procurved to recurved; posterior median eyes relatively large, about midway between anterior lateral and posterior lateral eyes or nearer to anterior laterals; posterior row usually narrower than anterior row; quadrangle length between 38 and 55 per cent of carapace length. *Clypeus*: high, concave. *Chelicerae*: medium to large, more or less vertical; promargin with three teeth, retromargin with three to six. *Maxillae*: elongate, usually divergent. *Labium*: subtriangular, about as long as broad. *Sternum*: scutiform to elongate scutiform. *Pedicel*: short. *Abdomen*: usually ovoid to elongate ovoid, rarely elongate; scuta lacking; spinnerets subequal in length, anteriors and posteriors robust, medians slender, usually hirsute; colulus apparently lacking, its position indicated by scanty hair tuft in front of spinnerets; trachea (Fig. 1D) unbranched, arising from transverse slit just in front of spinnerets and apparently limited to the abdomen. *Legs*: long and slender, usually with conspicuous fringes; spines numerous, generally robust; claw tufts present, scopula lacking, but female metatarsi I and tarsi I with minute ventral setae (Pl. 5c, d). *Female palp*: usually hirsute with terminal claw. *Male palp*: femoral apophysis usually lacking; tibia with prolateral and ventral apophyses; cymbium usually modified proximally and often with a prolateral flange (Fig. 1B, F); embolus moderately long and slender; conductor sometimes present; tegulum with peripheral seminal reservoir, a deeply curved furrow and a tripartite membraneous apophysis (adjacent to the embolic base) that sometimes extends laterally to form a small tegular apophysis (Fig. 10A, D); median apophysis lacking. *Epigyne*: relatively simple openings usually indistinct; seminal ducts generally short, wide and very dark, opening into large, dark, rounded spermathecae.

Remarks. The conductor (c) is very closely associated with the embolic shaft and would appear to have a supporting or protective function. In *P. labiata* (Thorell) and *P. crassipalpis* (Peckham & Peckham) the conductor is well developed (Figs 9B, 10A), but in *P. fimbriata* (Doleschall) it is greatly reduced, its presence being indicated by a shallow groove across the embolic shaft (Pl. 3a, b). This groove is not joined to another groove which extends along the inside of the embolus and terminates near the tip (Pl. 3e, f). In *P. schultzii* and several other species the conductor is apparently absent. The tripartite membraneous apophysis (m) is generally indistinct (Pl. 3b, c) and its prolateral extension is not always evident.

As might be expected preliminary observations with the scanning electron microscope have revealed additional characters which will undoubtedly be of phylogenetic significance. For example, the species examined in this study all have the same type of setae (Pl. 4, 5) which appear to show inter- and intraspecific differences. Unfortunately a detailed analysis of microsculpture cannot be presented as several species are known only from one or two specimens that are in poor condition and cannot be used for SEM studies.

BIOLOGY. Gravely (1921) reports an Indian species of '*Linus*' stalking and pouncing on a pholcid, *Smeringopus* sp., in its web. Another species (Bristowe, 1941) was seen devouring an Indian web-building pisaurid, *Euprothenops ellioti* (O. P.-C). Bristowe also records '*Linus fimbriatus*' feeding on *Smeringopus elongatus* (Vinson), on an *Araneus* and on a *Theridion*. In each case the '*Linus*' met with success in capturing its prey and remained in the victim's web to eat the owner before retiring. *P. fimbriata* has also been recorded from the web of *Nephila malabarensis* (Sherriffs, 1931).

An African *Portia* has been found in association with another spider's web by John and Frances Murphy, who collected two immature specimens of *P. schultzii* Karsch from an extensive diplurid web in Kenya. Important observations (previously unpublished) were made by Frances Murphy who successfully reared the above juveniles through four or five moults. The female died after its penultimate or final moult (see p. 88), but the male reached adulthood. In captivity both spiders made several webs which were apparently used for trapping and locating prey. The male's web was more flimsy than that of the female, but neither web appeared to be essential as both spiders readily caught wingless fruit flies when the cages were cleaned and the webs destroyed. Moulting was not observed, but several exuvia were found hanging upside down below the sheet-web and it seems reasonably certain that *P. schultzii* moults in the open. The adult male did not spin a web, but when placed on that of the female (Pl. 1a, b) found no difficulty in running about and adopted poses which had not been previously noticed and were taken to be part of a courtship routine. Another species, believed to be *P. durbanii* Peckham & Peckham collected by the author and Mr A. Russell-Smith in Durban, was also reared through several moults by Frances Murphy, but there was no web spinning activity. The specimen, apparently a subadult male, died just before its final moult.

Bristowe (pers. comm.) quite naturally assumed that *Portia* invaded spider webs for the purpose of feeding, but the above observations on captive specimens suggests that some *Portia* species may build and live in their own webs and use them for prey capture, either in isolation or in association with the webs of other spiders. Careful field observations are needed to resolve this aspect of behaviour as web building has not to my knowledge been reported for salticid spiders.

AFFINITIES. The affinities of *Portia* cannot be fully reviewed at present as numerous related genera have yet to be revised. The structure of the genitalia suggests that *Portia* is closely related to *Brettus* and some species of *Cocalus* (e.g. *C. lancearius* Thorell). Unfortunately the type species of *Cocalus*, *C. concolor* Koch, known only from a single male specimen, has no palps and I am unable to present a diagnosis at the moment.

Preliminary observations suggest that *Portia*, *Brettus*, *Cocalus* and other genera with large posterior median eyes may be related to lyssomanid spiders. For example, *P. adonis* (Simon), *P. albolimbata* (Simon) and *P. semifimbriata* (Simon) do not belong in *Portia* but represent another genus *Brettus* (type species *Brettus cingulatus* Thorell), which may form a link between *Asemonia* and *Portia*. If one considers Simon's concept of *Portia* (based in part on *P. semifimbriata*) and its affinities with *Boethus* (sensu Simon) then Simon's comment (Simon, 1901) that: 'Les *Boethus* (*Nealces* E. Sim.) me paraissent faire le passage des *Lyssomanes* aux *Cocalodes* et aux *Linus*' become significant. The affinities of *Cocalodes* are uncertain but the genus is probably close to *Brettus*.

The taxonomic status of lyssomanids has yet to be resolved. The presence of four eye rows has until recently been considered diagnostic of lyssomanids but it has already been shown (Galiano, 1976 and Wanless, 1978a) that several 'typical' salticid genera have similar eye formulae. The most aberrant example of a salticid with four eye rows is *Athamas whitmeei* O. P.-Cambridge, which has the anterior lateral eyes behind and almost exactly above the anterior medians. Even Simon (1901) remarked on the similarity with *Lyssomanes*, but as far as I am aware he has never suggested that the genera were closely related, presumably because the genitalia of *A. whitmeei* are of the type frequently found in the Salticidae. If *Portia* and related genera were transferred to the Lyssomanidae, then the large posterior median eyes might be considered as generally diagnostic of Lyssomanidae. However *Pandisus*, a small madagascan genus closely related to *Asemonia*, is exceptional in having small posterior median eyes.

Platnick (1971) has suggested that courtship behaviour in *Lyssomanes bradyspilus* Crane, as described by Crane (1949), indicates that lyssomanids should have family status, but Galiano (1976) holds the view that on anatomical grounds the group merits no more than subfamily rank. The decision is made difficult as our knowledge of the group is very limited. However, the web spinning behaviour of *P. schultzii*, the flimsy brooding webs of *Lyssomanes jemineus* Peckham & Wheeler (Eberhard, 1974) and *Asemonia* sp. n. (Murphy coll, vials 1549, 3661; F. Murphy unpublished observations) are in contrast to known salticid behaviour. Furthermore, the branched tracheal systems of several 'typical' Salticidae (Lamy, 1902; Hill, 1977 and Wanless, 1978a) are more complex than the unbranched systems found in *Asemonia* (Wanless unpublished observation), *Portia* (Fig. 1D) and *Lyssomanes* (Lamy, 1902 and Forster, pers. comm.). Forster (1970) has already argued that the general complexity of the tracheal system (i.e. branched or unbranched) is of more evolutionary significance than the presence or absence of tracheal intrusions into the cephalothorax. There is thus evidence to support Platnick's view, or at least suggest that lyssomanids should be accorded a higher taxonomic rank than other salticid subfamilies as they are understood at the present time.

List of species in the genus *Portia* Karsch, 1878

Portia africana (Simon, 1886)
P. albimana (Simon, 1900)
P. alboguttata (Lawrence, 1938)
P. assamensis sp. n.
P. cazomboensis sp. n.
P. crassipalpis (Peckham & Peckham, 1907)
P. durbanii Peckham & Peckham, 1903
P. falcifera sp. n.
P. fimbriata (Doleschall, 1859)
P. kenti Lessert, 1925
P. labiata (Thorell, 1887)
P. madagascarensis sp. n.
P. oreophila sp. n.
P. russata Simon, 1900
P. schultzii Karsch, 1878
P. solitaria Lessert, 1927

Key to species of *Portia*

Males

1 Tibial apophysis jointed (Figs 14C, F; 16B, C) (Africa, Madagascar) . . 2
– Tibial apophysis not joined (Ethiopian and Oriental regions) 4
2 Tibial apophysis very robust (Fig. 16B–D) (Madagascar) . . **madagascarensis** sp. n. (p. 114)
– Tibial apophysis slender (Fig. 14C, F) 3
3 Embolus short and slender (Fig. 14A) (South Africa) . . . . **kenti** Lessert (p. 111)
– Embolus long and robust (Fig. 14B) (Uganda) . . . . . **falcifera** sp. n. (p. 111)
4 Femora of palp with a distal blunt apophysis (Fig. 13B) (South Africa)
durbanii Peckham & Peckham (p. 109)

– Femoral apophysis lacking 5
5 Embolus relatively short (Fig. 12B) (Sri Lanka) ***albimana*** (Simon) (p. 107)
– Embolus relatively long 6
6 Tegular apophysis present (Fig. 10A, D, C, F) 7
– Tegular apophysis absent 8
7 Tibial apophysis slender (Fig. 10B) (Sri Lanka, India, Burma, Thailand, Malaysia, Sumatra) ***labiata*** (Thorell) (p. 103)
– Tibial apophysis robust (Fig. 10F) (Assam, Nepal) ***assamensis*** sp. n. (p. 105)
8 Conductor well developed (Fig. 9B) (Malaysia, Borneo) ***crassipalpis*** (Peckham & Peckham) (p100)
– Conductor poorly developed or lacking 9
9 Cymbial flange as in Fig. 1B, F; clypeus with a white spot below each AM (Zaire, Kenya, Tanzania, South Africa, Madagascar) ***schultzii*** Karsch (p. 88)
– Cymbial flange otherwise; white spots lacking 10
10 Cymbial flange as in Fig. 4D; clypeus with curved white 'moustache' (West and Central Africa) ***africana*** (Simon) (p. 93)
– Cymbial flange as in Fig. 7G; 'moustache' lacking ***fimbriata*** (Doleschall) (p. 99)

Females

1 Epigyne as in Fig. 17B; body with white longitudinal bands (Fig. 17D) (Madagascar) ***oreophyla*** sp. n. (p. 116)
– Epigyne and body otherwise 2
2 Epigyne as in Fig. 6B, spermathecae large, ducts apparently lacking; (Madagascar) ***russata*** Simon (p. 97)
– Epigyne otherwise 3
3 Anterior eye row strongly recurved in frontal view 4
– Anterior eye row procurved in frontal view 6
4 Epigyne with central curtain-like membrane (Fig. 2C) (Angola, South Africa) ***cazomboensis*** sp. n. (p. 90)
– Epigyne without central membrane 5
5 Epigyne with delicate septum (Fig. 13D) (South Africa) ***durbanii*** Peckham & Peckham (p. 109)
– Septum lacking; epigyne as in Fig. 3D–F (Guinea, Ivory Coast, Zaire) ***solitaria*** Lessert (p. 91)
6 Epigyne with sclerotized septum as in Fig. 5A, B, C (Africa) 7
– Epigyne otherwise 8
7 Septum central, ducts not extended posteriorly (Fig. 5A, B, F) ***africana*** (Simon) (p. 93)
– Septum distal, ducts extended posteriorly (5C, D, H) ***alboguttata*** (Lawrence) (p. 96)
8 Epigyne small and pale; spermathecae indistinct (Fig. 1G; Pl. 3b) (Africa) [? subadult ♀] ***schultzii*** Karsch (p. 88)
– Epigyne otherwise (Oriental region) 9
9 Epigyne as in Fig. 8A–F; clypeus not thickly white haired ***fimriata*** (Doleschall) (p. 99)
– Epigyne otherwise; clypeus thickly white haired 10
10 Epigynal orifice undivided (Fig. 11B) ***labiata*** (Thorell) (p. 103)
– Epigynal orifice divided (Fig. 11E) ***assamensis*** sp. n. (p. 105)

The *schultzii*-group

The *schultzii*-group occurs in both the Ethiopian and Oriental regions and is comprised of ten species. It is characterized by the presence of a fixed male palpal tibial apophysis that lacks the membraneous joint found in the *kenti*-group. The latter group is known only from males and it is not known if the epigynes of *schultzii*-group females show any diagnostic features relative to the *kenti*-group.

Two species, *P. cazomboensis* sp. n. and *P. solitaria* Lessert, resemble the *kenti*-group in having the first eye row recurved in frontal view. However, I have not placed them in the *kenti*-group as the males of both species are unknown and the resulting definition based on the female genitalia could be misleading. Furthermore, *P. russata* (Simon) is somewhat intermediate as the first eye row is only slightly recurved and not procurved as in other species of this group.

Portia schultzii Karsch

(Fig. 1A–G; Pls 1, 2, 4a, b)

Portia schultzii Karsch, 1878 : 774, ♀. Holotype ♀, South Africa, Port Natal (MNHU, Berlin) [examined].

P. schultzi: Simon, 1901 : 402, 403 [Unjustified emendation]. Petrunkevitch, 1928 : 182. Roewer, 1954 : 934. Bonnet, 1958 : 3767. Roewer, 1965 : 12. Prószyński, 1971 : 461.

Brettus martini Simon, 1900 : 31, ♀, South Africa, Natal, Zululand (? MNHN, Paris) [Not examined, presumed lost; synonymized by Simon, 1901 : 402, 403]. Roewer, 1954 : 934. Bonnet, 1958 : 3767.

Linus lesserti Lawrence, 1937 : 254, fig. 22, ♂. Holotype ♂, South Africa, Zululand, Hluhluwe Game Reserve (NM, Pietermaritzburg. No. 75) [Examined]. Roewer, 1954 : 935. Bonnet, 1957 : 2482. Roewer, 1965 : 17, fig. 16a–c. Prószyński, 1971 : 425. **Syn. n.**

Remarks. (i) Some parts of the holotype of *P. schultzii* including the epigyne have been preserved on a microscope slide and it compares well with a specimen collected in Kenya and reared through four or five moults by Mrs Frances Murphy. Both specimens have small pale epigynes (Pl. 4b; Fig. 1G) with obscure spermathecae unlike other species in the genus. The spermathecae may not be completely formed and it is probable that both specimens are subadult, but I could be mistaken and the 'subadult female' is described and provided for in the identification key. The identity of the male is based on a specimen from Kenya taken with the female referred to above and reared to adulthood. This male is conspecific with *Linus lesserti* which is now regarded as a junior synonym.

(ii) A vial labelled '19618 *Port scultzi* [sic] Karsch (= *martini* E.S) Natal' contains one female and several immatures of *P. durbanii* Peckham & Peckham. The female is possibly the type of *Brettus martini* Simon, as there is no other vial in the Simon collection (Paris), labelled *martini*. However, this assumption may not be correct and the name *Brettus martini* is regarded as *nomen dubium*.

Diagnosis. *P. schultzii* is very similar to *P. fimbriata* (Doleschall), but can be readily distinguished by the shape of the cymbial flange (Fig. 1F) and pale epigyne (Pl. 4b; Fig. 1G), but see remarks under (i) above.

Male from South Africa. *Carapace* (Fig. 1C): orange-brown with dark brown mottling; eye region shiny (when rubbed) with scattered long hairs, thoracic part has a metallic sheen under some angles of illumination; clothed in recumbent dark brown and whitish hairs with scanty thoracic white-haired tufts and broad white marginal bands from between coxae I–II and coxae IV. *Eyes*: anteriors subcontiguous with apices procurved, fringed by pale orange hairs and with tufts of orange to dark orange hairs above AM, outside of AL and inside PL. *Clypeus*: mottled orange and blackish with light orange-brown hairs and a white-haired spot below each AM. *Chelicerae*: orange-brown with darker markings and pale orange and white hairs; promargin with three teeth, retromargin with two. *Maxillae and labium*: orange-brown to brown-black. *Sternum*: scutiform; orange-brown with blackish median area and spots opposite coxae I–III and between coxae IV, the pattern reinforced by white hairs in pale areas and dark brown ones elsewhere. *Abdomen*: yellow-orange to orange-brown with blackish-mottling; clothed in black and light orange hairs with nine white dorsal hair tufts; venter and sides mottled orange-brown and black with scattered white tufts and obscure blackish band from epigastric furrow to spinnerets; spinnerets orange-brown with light orange and black hairs. *Legs*: orange-brown with darker markings and a metallic sheen under some lights; clothed in brownish hairs and scattered white tufts; tibiae and patellae ventrally fringed with long black hairs, medially scanty on tibiae III–IV; spines robust and numerous. *Palp* (Fig. 1A, B, E, F): clothed in yellow-white hairs, with strong prolateral white-haired fringes on tibiae and patellae.

Dimensions (mm): total length 5·36; carapace length 2·52, breadth 2·04, height 1·76; abdomen length 2·8; eyes, anterior row 1·76, middle row 1·56, posterior row 1·69; quadrangle length 1·10. *Ratios*: AM : AL : PM : PL :: 30 : 14 : 10 : 15, AL–PM–PL : 18–19, AM : CL :: 30 : 19.

Female from Kenya (? subadult). This specimen resembles the ♂ in body form, but it died just after moulting and appears rather pale. *Carapace*: similar to ♂ but white haired tufts and marginal bands inconspicuous. *Eyes*: more or less as in ♂. *Clypeus*: mottled yellow-brown and black with

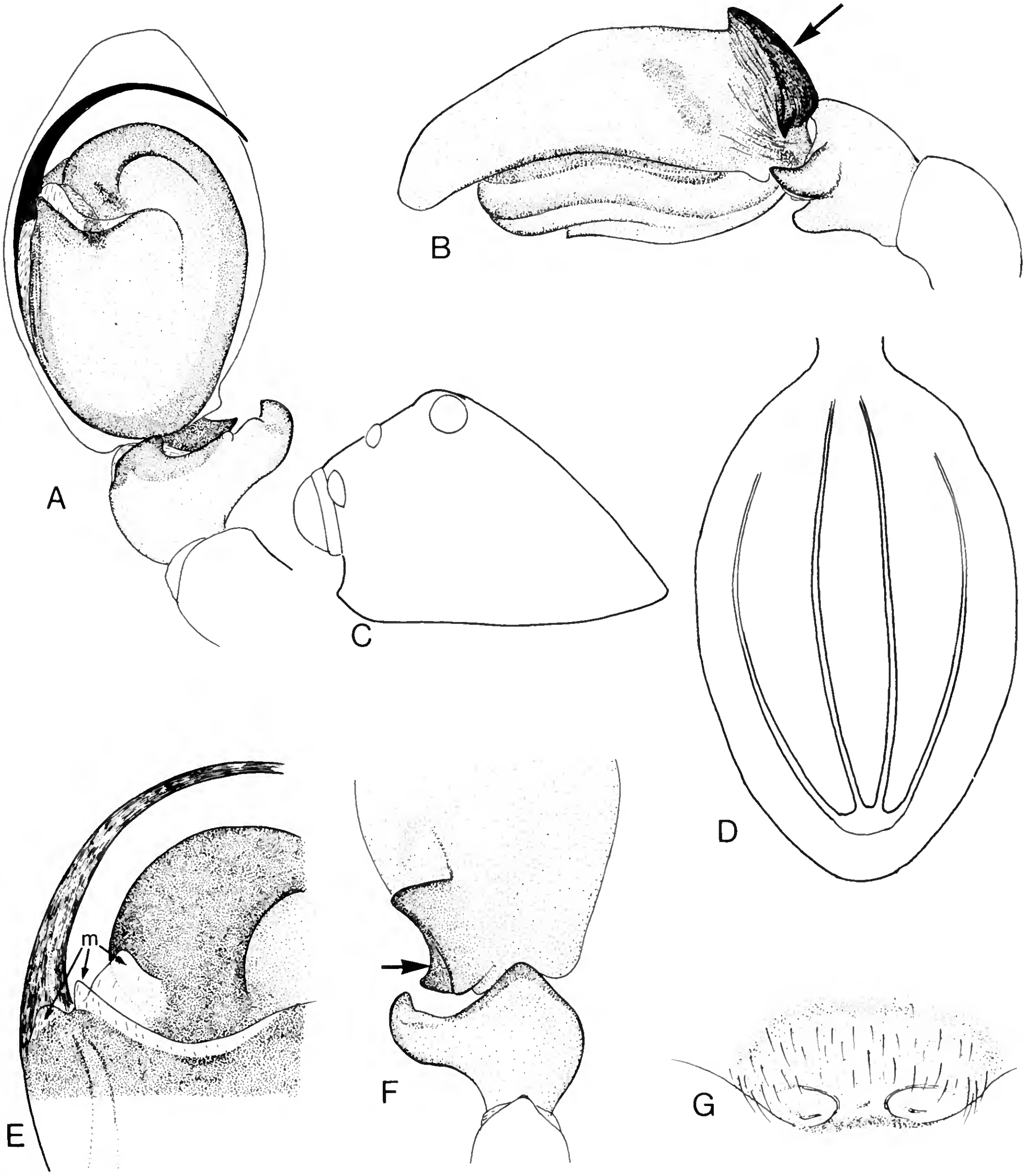

Fig. 1 *Portia schultzii* Karsch, ♂ from South Africa: (A) palp, ventral view; (B) palp, lateral view; (C) carapace, lateral view; (D) tracheal system, schematic; (E) palp, region of tripartite membrane; (F) tibia and cymbial flange from above. ♀ from Kenya: (G) epigyne, ? subadult.

marginal white-haired band. *Chelicerae*: pale yellow with black distal markings; sparsely clothed in whitish and light orange hairs. *Maxillae and labium*: similar to ♂, but paler. *Sternum*: more or less as in ♂. *Abdomen*: light yellow with black markings; generally rubbed, but with scattered white and orange-brown hairs; venter mottled blackish with two yellow spots in front of spinnerets; spinnerets dark brownish. *Legs*: light yellow with blackish markings and bands on femora and tibae; fringes as in ♂; spines more or less as in ♂. *Epigyne* (Pl. 4b; Fig. 1G): small and pale.

Dimensions (mm): total length about 4·8; carapace length 2·54, breadth 2·04, height 1·64; abdomen length 1·4; eyes, anterior row 1·68, middle row 1·48, posterior row 1·61; quadrangle length 1·12. *Ratios*: AM : AL : PM : PL :: 27 : 12·5 : 9·5 : 13, AL–PM–PL : 16–17, AM : CL :: 27 : 15.

VARIATION. ♂ total length varies from 4·8 to 7·7 mm; carapace length 2·2–3·12 mm (ten specimens). Variation not marked except for bare patches in rubbed specimens.

BIOLOGY. Important observations made by Mrs Frances Murphy on captive specimens from Kenya has been summarized elsewhere (p. 85) and additional data are given below.

DISTRIBUTION. Kenya, Madagascar, South Africa, Tanzania, Zaire.

MATERIAL EXAMINED. Type data given in synonymy. KENYA: Kilifi, beaten from diplurid web in shrub layer about 90 m from the sea, 2 juveniles, 13.8.74, reared in captivity, ♀ died iii.1975, ♂ matured i.1975, killed iv.1975 (*J. & F. Murphy*, vial 4340). MADAGASCAR: Mt Ankarana, 1 ♂, ii.1956 (*E. Renson*, MT 142.985) (MRAC, Tervuren). SOUTH AFRICA: Durban, 3 ♂♂ (*G. P. Staunton*); Port Natal, 1 ♂ (BMNH). Pietermaritzburg, 1 ♂ (*C. Akerman*, NM, 1497); Pietermaritzburg; 2 ♂♂, xii. 1939(*Arbuckle*, NM. 2883); 2 ♂♂, xii.1940 (*E. Praltgala*, NM. 3344); 1 ♂, xi.1962, 1 ♂, 1 juvenile ♀, xii,1953 (*R. F. Lawrence*, NM. 8793, 5953). Rosi Bay, 1 ♂ (*Toppin*, NM. 1957) (NM, Pietermaritzburg). TANZANIA: Tendaguru, British Museum (Natural History) Expedition to East Africa, 1 ♂, ii.1926 (*W. E. Cutler*) (BMNH). ZAIRE: Albertville, 1 ♂, 1959 (*J. Verhoustraite*, MT. 115072) (MRAC, Tervuren).

Portia cazomboensis sp. n.

(Fig. 2A–D)

DIAGNOSIS. *P. cazomboensis* is a distinctive species readily distinguished by the median epigynal membrane (Fig. 2C, arrowed). Its affinities are uncertain but it appears to be related to *P. solitaria* Lessert.

MALE. Unknown.

FEMALE HOLOTYPE. *Carapace* (Fig. 2A): yellow-orange with brownish mottling on lower thoracic sides; clothed in recumbent short white hairs. *Eyes:* with black surrounds except AM; anteriors subcontiguous with apices strongly recurved, fringed by whitish hairs and has a tuft of pale yellow hairs outside PM. *Clypeus*: yellow-orange with darker markings; sparsely white haired with several long pale hairs marginally. *Chelicerae*: pale yellow-orange with darker markings; fringed by long light yellow hairs with very scanty proximal and medial transverse bands composed of recumbent, short clear yellowish hairs; promargin and retromargin with three teeth. *Maxillae and labium*: light orange-brown, but maxillae blades and labial tip light yellow. *Sternum*: scutiform; pale orange lightly tinged black, and with orange margins. *Abdomen*: rubbed; dull yellow with central grey-black anterior band followed by two chevrons with a dark patch on either side; the front chevron is margined anteriorly by a white line extending laterally between patches, a similar but obscure line margins the posterior chevron; venter yellow with black markings and central black band from epigyne to spinnerets; clothed in fine silky hairs. *Legs*: Legs I pale brown to orange-brown with dense brown haired fringes on venter and dorsam of tibiae and venter of patellae and femora. Legs II–III yellow-brown with obscure darker femoral markings. Legs IV as III but femoral markings more distinct and with distal orange band on tibiae. Spines numerous, moderately robust. *Palp*: pale yellow with light orange tips and blackish femoral markings; fringed with long white hairs. *Epigyne* (Fig. 2B–D).

Dimensions (mm): total length 5·8; carapace length 2·6, breadth 2·04, height 1·56; abdomen length 3·3; eyes, anterior row 1·4, middle row 1·1, posterior row 1·2; quadrangle length 1·0. *Ratios*: AM : AL : PM : PL :: 11 : 6 : 5 : 6, AL–PM–PL : 7–9·5, AM : CL :: 11 : 6.

VARIATION. A ♂ from South Africa measures 6·5 mm total length, 2·84 mm carapace length.

DISTRIBUTION. Angola. South Africa.

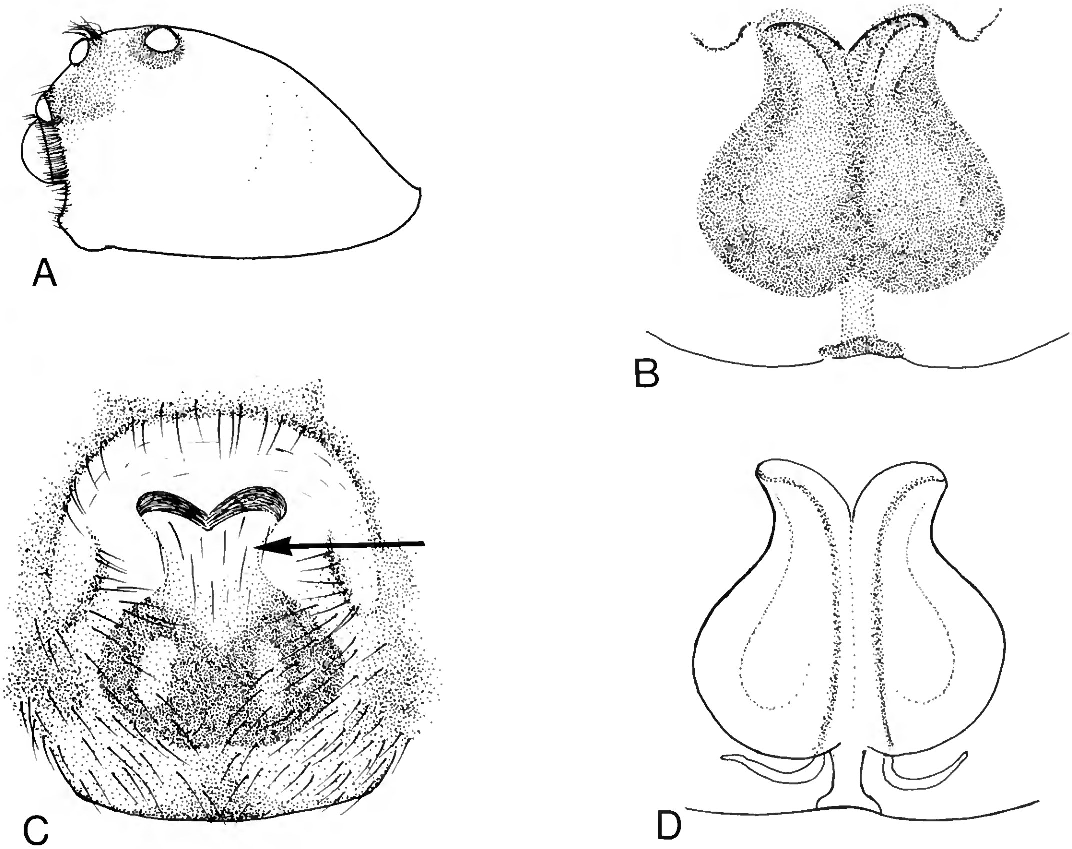

Fig. 2 *Portia cazomboensis* sp. n., holotype ♀: (A) carapace, lateral view; (C) epigyne. Paratype ♀: (B) vulva, ventral view; (D) vulva, dorsal view.

MATERIAL EXAMINED. Holotype ♀, ANGOLA: Cazombo, 13.ii.1955 (*A de Barros Machado*, Ang. 4909.22). Paratype: SOUTH AFRICA: Rosi Bay, 1 ♀ (*Toppin*, NM, 1957 part) (NM, Pietermaritzburg).

Portia solitaria Lessert

(Fig. 3A–F)

Portia solitaria Lessert, 1927 : 425, fig. 14, ♀. Holotype ♀, Zaire, Medje (AMNH, New York) [Examined]. Roewer, 1954 : 934. Bonnet, 1958 : 3767. Roewer, 1965 : 13, fig. 13. Prószyński, 1971 : 461.

Linus guineensis Berland & Millot, 1941 : 399, fig. 92, ♀. Holotype ♀, Guinea, Kankan (MNHN, Paris) [Examined]. Roewer, 1954 : 935; 1965 : 14. **Syn. n.**

Portia guineensis (Berland & Millot) Roewer, 1965 : 14.

REMARKS. Roewer (1965) correctly transferred *L. guineensis* Berland & Millot to *Portia*, but as he did not examine the type specimen he did not notice that the figures provided by Berland & Millot (1941, fig. 92, D and I) must be transposed for the captions to read correctly.

DIAGNOSIS. *P. solitaria* is similar to *P. cazomboensis*, but can be distinguished by the absence of a translucent epigynal membrane (Fig. 3E, D, F).

MALE. Unknown.

FEMALE HOLOTYPE. *Carapace* (Fig. 3A): orange-brown with darker mottling; clothed with recumbent white hairs. *Eyes*: with black surrounds except AM; anteriors subcontiguous with apices

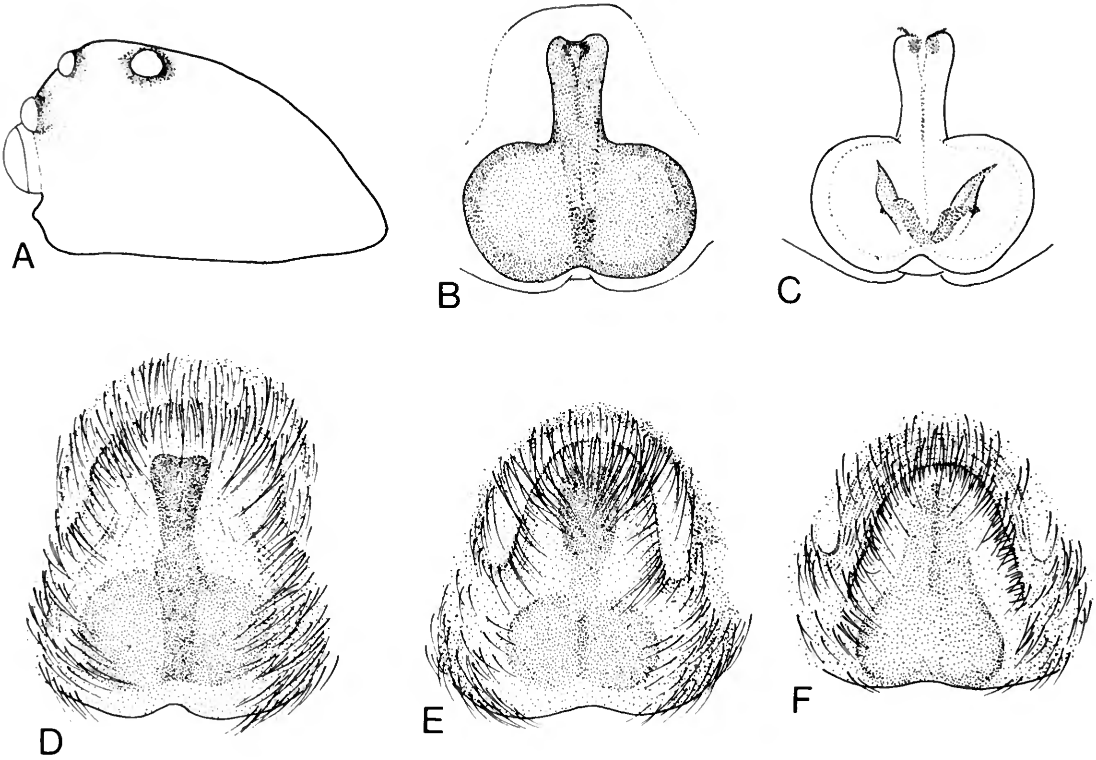

Fig. 3 *Portia solitaria* Lessert, holotype ♀: (A) carapace, lateral view; (E) epigyne. ♀ from Ivory Coast: (B) vulva, ventral view; (C) vulva, dorsal view; (D) epigyne. Holotype ♀ of *L. guineensis* Berland & Millot: (F) epigyne.

strongly recurved, fringed with whitish hairs. *Clypeus*: sparsely covered in short white hairs and fringed by long pale orange ones. *Chelicerae*: orange to light orange with blackish markings; thickly clothed in long light orange hairs; promargin with three teeth, retromargin with four. *Maxillae*: light orange with darker markings. *Labium*: orange-brown with light orange tip. *Sternum*: scutiform; light orange tinged by black and with clear dark orange margins; shiny with very scanty tufts of pale orange hair opposite coxae I–III and between coxae IV. *Abdomen*: more or less rubbed; light yellow-orange with sooty dorsal markings and a broad black band from epigyne to spinnerets; dorsam sparsely clothed with brown and white hairs, forming a pattern similar to that of *P. cazomboensis* sp. n.; tufts apparently lacking; spinnerets pale yellow-orange. *Legs*: orange-brown with brown-black markings especially on posteriors; fringes rubbed; spines strong and numerous. *Palp*: pale yellow with light orange tips and darker femoral markings; clothed in long whitish hairs. *Epigyne* (Fig. 3B, C, E).

Dimensions (mm): total length 5·44; carapace length 2·68, breadth 2·16, height 1·64; abdomen length 3·0; eyes, anterior row 1·52, middle row 1·20, posterior row 1·40; quadrangle length 1·16. *Ratios*: AM : AL : PM : PL :: 13 : 7 : 5·5 : 6·5, AL–PM–PL : 7–10·5, AM : CL :: 13 : 6.

VARIATION. Female total length varies from 5·44 to 6·64 mm, carapace length 2·68– 3·2 mm (three specimens). The leg fringes, composed of stiff brown-black hairs, are present on venter and dorsal of tibiae I and ventrodistally on femora I and tibiae IV. The epigyne varies in the degree of sclerotization but the general outlines are fairly characteristic.

DISTRIBUTION. Guinea, Ivory Coast, Zaire.

MATERIAL EXAMINED. Type data given in synonymy. IVORY COAST: Lisière, forest gallery, 1 ♀ (MNHN, Paris).

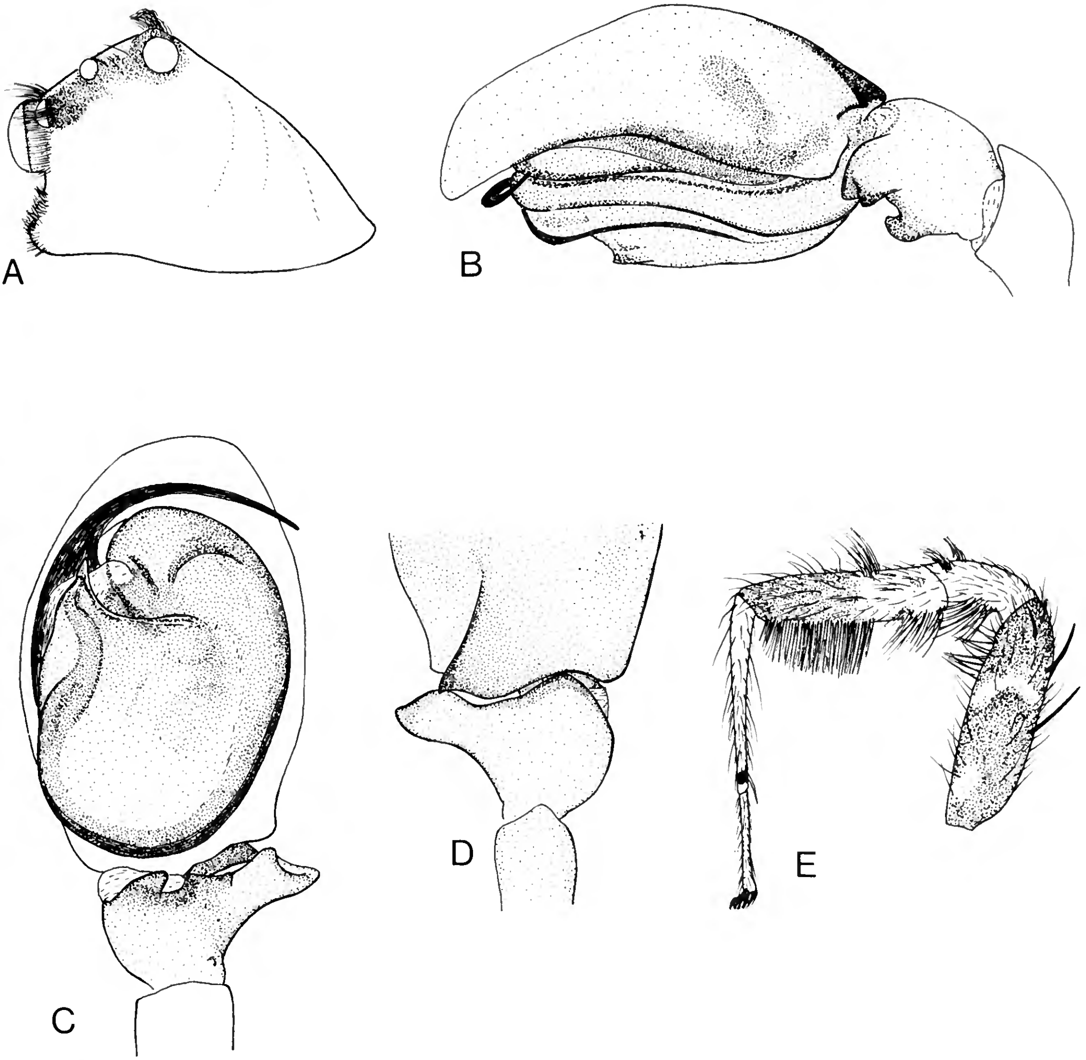

Fig. 4 *Portia africana* (Simon), ♂ from Sierra Leone: (A) carapace, lateral view; (B) palp, lateral view; (C) palp, ventral view; (D) tibia and cymbial flange from above; (E) leg I.

Portia africana (Simon) comb. nov.

(Figs 4A–E; 5A, B, F, G; Pl. 5b)

Linus africanus Simon, 1886 : 393, ♂. LECTOTYPE ♂ (here designated) Zaire, Landana (MNHN, Paris. No. 7547) [Examined]. Simon, 1901 : 409, 410; 1909 : 412. Berland & Millot, 1941 : 398–401, figs 91, 92. Roewer, 1954 : 935. Bonnet, 1957 : 2482. Roewer, 1965 : 16, fig. 15. Prószyński, 1971 : 425. Cutler, 1976 : 132.

Cocalus africanus Thorell, 1899 : 91, ♂. Holotype ♂, Cameroon (NR, Stockholm) [Examined]. Simon, 1901 : 407. Roewer, 1954 : 934. Bonnet, 1956 : 1173. **Syn. n.**

Neccocalus africanus (Thorell) Roewer, 1965 : 20, fig. 21 [Proposed as type species of monotypic genus *Neccocalus* Roewer, 1965].

Diagnosis. *P. africana* is closely related to *P. alboguttata* (Lawrence) known only from the female. It can usually be separated by the elongate epigynal septum (Fig. 5A, B), but this is variable and is sometimes clogged with waxy secretions (see also Berland & Millot, 1941 : 399, fig. 91). In some cases it may be necessary to examine the vulva in which the relatively short seminal ducts are fairly distinctive (Fig. 5G).

MALE FROM SIERRA LEONE. *Carapace* (Fig. 4A): orange-brown with light orange eye region and darker markings; faintly iridescent violet or green under some angles of illumination; clothed in recumbent white and light brown hairs with an irregular marginal band from coxae II to IV, and also with three rather sparse white haired tufts on thoracic part. *Eyes*: anterior row more or less contiguous with apices slightly procurved, fringed by whitish hairs with whitish to orange hair tufts above AM, outside of AL and inside PL. *Clypeus*: below AM a light orange transverse, crescent-shaped region clothed with short pale yellow hairs and a distinctive narrow white band just below AM. *Chelicerae*: orange-brown with darker markings; thinly clothed in fine light brown hairs with whitish hairs proximally; groove with three teeth on each margin. *Maxillae and labium*: orange-brown suffused with black, but inner margins of maxillae and labial tip lighter. *Sternum*: elongate scutiform; yellow-brown faintly tinged by black and with light orange margins; densely clothed with creamy white hairs, less dense medially and with very scanty tufts of long brown hairs opposite coxae I–III and between coxae IV. *Abdomen*: mottled yellow-brown and black with blackish markings; clothed in white, orange-brown and black hairs with conspicuous tufts composed of orange and creamy white hairs; venter yellow-brown with blackish markings; spinnerets brown with creamy white and light brown hairs. *Legs*: tarsi and metatarsi yellow-brown to orange-brown, the latter with longitudinal black stripes; remaining segments brown with darker brown and yellow-brown markings forming irregular bands on femora; tibiae and patellae partially fringed with long brown hairs, ventrally; spines strong and numerous. *Palp* (Fig. 4B–D): yellow-brown to orange-brown with blackish femoral bands; clothed in pale yellowish hairs with long white prolateral fringes on tibae and patellae.

Dimensions (mm): total length 6·08, carapace length 2·72, breadth 2·41, height 2·0; abdomen length 3·44; eyes, anterior row 1·86, middle row 1·64, posterior row 1·8; quadrangle length 1·28. *Ratios*: AM : AL : PM : PL :: 16 : 8 : 6 : 8, AL–PM–PL : 8–7, AM : CL :: 16 : 12.

FEMALE FROM SIERRA LEONE. *Carapace*: orange-brown with faint sooty markings and paler eye region; clothed with short fine recumbent white and light brownish hairs, with a scanty tuft behind fovea; marginal thoracic band apparently lacking. *Eyes*: more or less as in ♂. *Clypeus*: crescent-shaped region densely white haired. *Chelicerae*: orange with blackish markings; densely white haired proximally with long light brown hairs distally marginal teeth as in ♂. *Maxillae, labium and sternum*: more or less as in ♂. *Abdomen*: similar to ♂, but tufts composed of orange-brown to dark brown hairs. *Legs*: similar to ♂, but femoral and tibial bands slightly more distinctive. *Palp*: whitish yellow, tipped with orange-brown, and with blackish femoral bands; densely fringed with long white hairs. *Epigyne* (Fig. 5A, F, G): clothed with creamy yellow hairs.

Dimensions (mm): total length 7·84; carapace length 3·56, breadth 3·08, height 2·52; abdomen length 4·24; eyes, anterior row 2·26, middle row 2·04, posterior row 2·25; quadrangle length 1·52. *Ratios*: AM : AL : PM : PL :: 18 : 9 : 7 : 9·5, AL–PM–PL : 11–11·5, AM : CL :: 18 : 15.

VARIATION. ♂ total length varies from 5·2 to 7·2 mm, carapace length 2·6–3·2 mm (ten specimens). ♀ total length from 4·8–9·6 mm, carapace length 2·5–3·7 mm (11 specimens). Freshly preserved specimens have black leg fringes and some females have more regular, but indistinct marginal thoracic bands from coxae II to IV. Cheliceral teeth vary from two to three denticles on each margin. The tibial apophyses of the male palps show slight variations in form which is sometimes emphasized by small differences in the angle of view. The epigynal septum is variable (Fig. 5A, B) and normally obscured by hairs; the openings on either side are occasionally filled with secretions.

BIOLOGY. According to Berland & Millot (1941), *P. africana* shows a preference for the branches of bushes and can be recognized at a glance by the tufts of hairs which ornament the legs and abdomen.

DISTRIBUTION. Angola, Cameroon, Central African Republic, Gabon, Ghana, Ivory Coast, Sierra Leone, Zaire, Zambia.

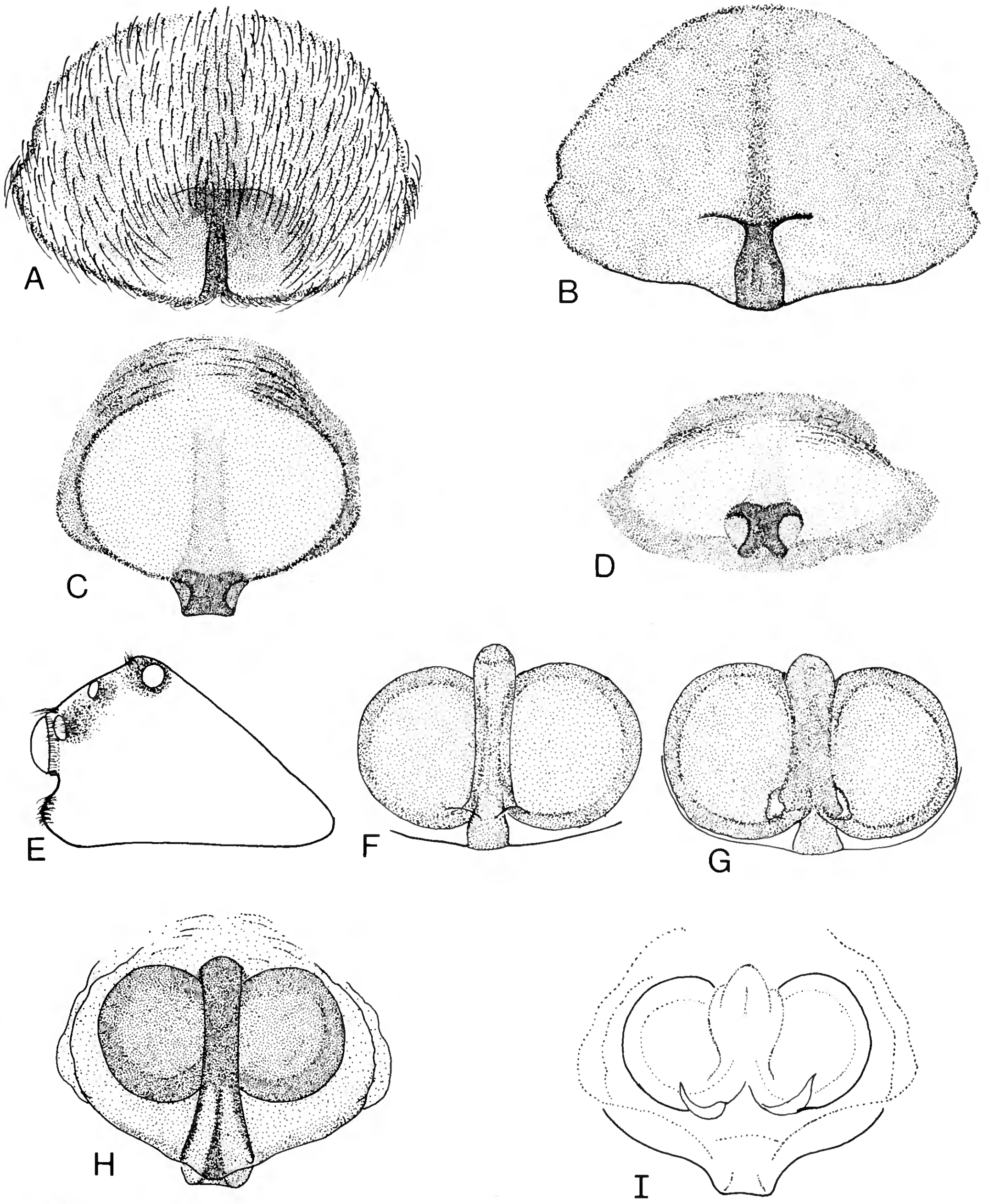

Fig. 5 (A, B, F, G) *Portia africana* (Simon), ♀ from Sierra Leone: (A) epigyne; (F) vulva, dorsal view; (G) vulva, ventral view. ♀ from Angola: (B) epigyne. (C, D, E, H, I) *Portia alboguttata* (Lawrence), ♀ from South Africa: (C) epigyne; (D) epigyne, viewed from behind; (E) carapace, lateral view; (H) vulva, ventral view; (I) vulva outline, dorsal view.

Material examined. Type data given in synonymy. Angola: Dundo: 1 ♀, 8.x.1946 (*A. B. Machado*, Ang. 65.10); in house, 1 ♂ (*A. Correia*, Ang. 22111); 1 ♀, 10.v.1962 (*A. B. Machado*, Ang. 16962); in garden, 1 ♂, 21.ii.1960 (*A. B. Machado*, Ang. 15375.1); laboratory garden, 1 ♀, 29.ix.1973 (*L. de Carvalho*, Ang. 23529) Parc Carrisso, 1 ♂, 31.x.1960 (*A. B. Machado*, Ang.

23019.2.16). Lobito, under stones, 2 ♀♀, 31.xii.1948 (*A. B. Machado*, Ang. 1268). CENTRAL AFRICAN REPUBLIC: Bambari, 3 ♀♀, ii.1969 (*G. Pierrard*, MT. 136626) (MRAC, Tervuren). GABON: Makokou, 2 ♂♂, xii.1965 (*R. P. Darchen*, MT. 130410) (MRAC, Tervuren). GHANA: Bibianaba, 1 ♂, 29.x.1911 (*H. G. F. Spurell*) (BMNH). IVORY COAST: Man, 3 ♂♂, 5 ♀♀, vii.1937 (*L. Berland, J. Millot*) (MNHN). Paris. SIERRA LEONE: Fourah Bay, 1 ♂, 1 ♀, 1.x.1958 (*E. White*) (BMNH). ZAIRE: Ht Katanga, Terr. de Jadotville, colline Kasompi W. 1 ♀, x.1956 (*Z. Bacq*. MT. 90998); Katanga, Lubumbashi, 1 ♀, iv–v.1966 (*J. Godeaux*, MT. 131508); Kivu: Terr. Uvira, entre Kalundu et Kavimvira, 1 ♀, vi. 1961 (*R. Kiss*, MT. 11926); Bukavu, 2 ♀♀, 1951 (*H. Bomans*, MT. 69321–22) (MRAC, Tervuren). ZAMBIA: Abercorn, 1 ♂, xi.1945 (*P. D. L. Guilbride*) (BMNH).

Portia alboguttata (Lawrence) comb. nov.

(Fig. 5C, D, E, H, I)

Linus alboguttatus Lawrence, 1938 : 520, ♀. Holotype ♀, South Africa, Port Shepstone, Natal (NM, Pietermaritzburg, No. 1484) [Examined]. Roewer, 1954 : 935; 1965 : 19, fig. 19. Prószyński, 1971 : 425. Cutler, 1976 : 132.

DIAGNOSIS. *P. alboguttata*, known only from the female, is closely related to *P. africana* (Simon), but can be distinguished by the structure of the epigyne (Fig. 5C, D, H, I), see remarks on page 93.

MALE. Unknown.

FEMALE FROM SOUTH AFRICA, PORT SHEPSTONE. *Carapace* (Fig. 5E): orange with darker cephalic sides and a band of blackish mottling encircling mid-thoracic region; iridescent violet under some angles of illumination; clothed with fine recumbent white and black hairs (the latter mostly restricted to mottled areas). *Eyes*: anteriors subcontiguous with apices slightly procurved, fringed by light yellow-orange hairs and with tufts of yellow-orange hairs outside AL. *Clypeus*: dark orange with distinctive white haired band. *Chelicerae*: reddish orange with white hairs proximally and long fine ones distally; groove with three teeth on each margin. *Maxillae and labium*: dark reddish orange, but inner margins of maxillae and labial tip lighter. *Sternum*: elongate scutiform; brownish orange with reddish orange margins; clothed in short white hairs and long brownish ones forming a pattern similar to that found in *P. africana*. *Abdomen*: mottled blackish and yellow-brown; clothed in white, light orange and blackish hairs with conspicuous tufts composed of orange to brown hairs tipped white; venter blackish; spinnerets brown, with white and brown hairs. *Legs*: tarsi and metatarsi yellow-brown, the latter with longitudinal black stripes; remaining segments brown to orange-brown with irregular yellow bands on posterior femora; tibiae and patellae with interrupted long black ventral fringes, incomplete on the tibiae; femora clothed ventrally with white hairs forming irregular horizontal stripes on legs I–II, but restricted to the yellowish bands on legs III–IV; spines moderately strong and numerous. *Palp*: whitish yellow tipped with orange-brown, and with blackish femoral bands and blotches on tibiae and patellae; fringed with long white hairs. *Epigyne* (Fig. 5C, D, H, I): clothed with white hairs, edged with black.

Dimensions (mm): total length 8·2; carapace length 3·4, breadth 3·0, height 2·4; abdomen length 4·8; eyes, anterior row 2·2, middle row 1·9 posterior row 2·0; quadrangle legnth 1·5. *Ratios*: AM : AL : PM : PL :: 17 : 8 : 6 : 8, AL–PM–PL : 10–12, AM : CL :: 17 : 13.

VARIATION. Female total length varies from 5·2 to 9·3 mm, carapace length 3·2–4·0 mm (eight specimens).

BIOLOGY. Unknown.

DISTRIBUTION. Malawi, South Africa.

MATERIAL EXAMINED. Holotype ♀, data given in synonymy. MALAWI: Lake Nyasa, 1 ♀ (BMNH). SOUTH AFRICA: Kruger National Park, Pafuri, 1 ♀ (*H. Braack*) (SIMR, Johannesburg); Swaziland, 1 ♀ (*R. C. H. Sweeney*) (BMNH); Pietermaritzburg 1 ♀, xii.1965 (*R. F. Lawrence*, NM, 9507), 1 ♀, 1917 (*C. Akerman*, NM. 1754); Port Shepstone, 1 ♀, xii.1936 (NM. 1367) (NM, Pietermaritzburg).

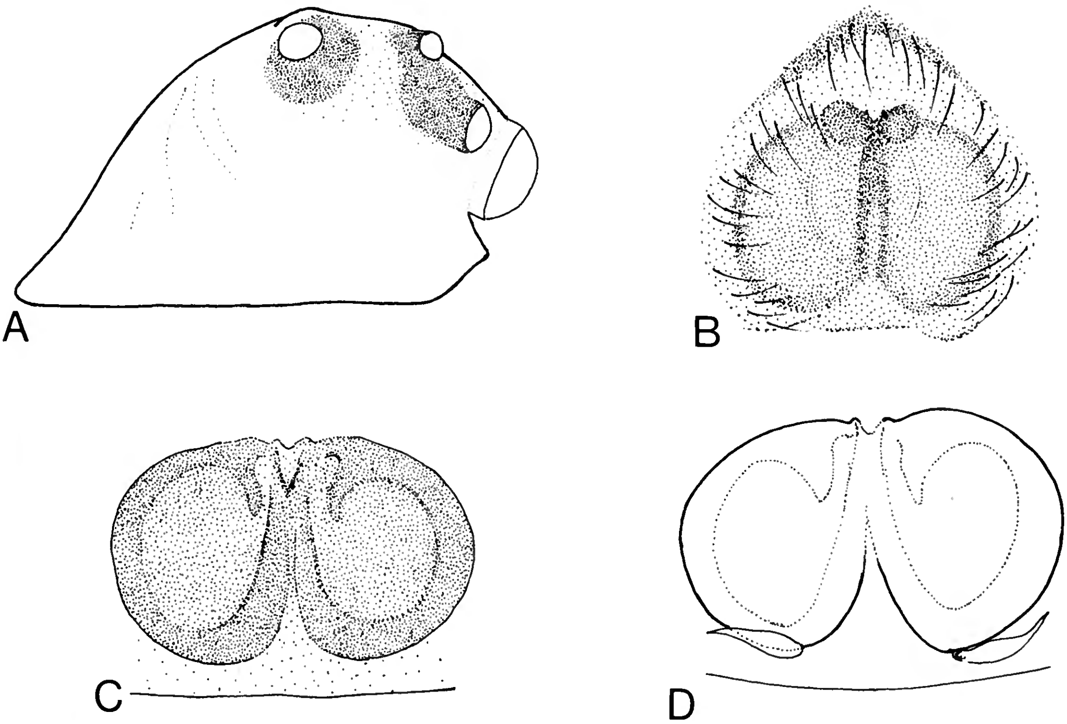

Fig. 6 *Portia russata* Simon, lectotype ♀: (A) carapace, lateral view; (B) epigyne; (C) vulva, ventral view; (D) vulva outline, dorsal view.

Portia russata Simon
(Fig. 6A–D)

Portia (*Brettus*) *russata* Simon, 1900*a* : 381, ♀. LECTOTYPE ♀ (here designated) Madagascar, Antongil (MNHN, Paris. No. 10257) [Examined].
Portia russata Simon, 1901 : 402. Roewer, 1954 : 934. Bonnet, 1958 : 3766. Roewer, 1965 : 13.

The vial labelled '10257 *Port russata* E. S. Antongil (type)' was found to contain two species, both represented by females. One of the specimens agrees more or less with Simon's original description of *P. russata* and is designated lectotype. The other species represents a new taxon described elsewhere in this paper (p. 116).

DIAGNOSIS. Although *P. russata* is placed in the *schultzii*-group it is not very closely related to the other species, and can be readily distinguished by the structure of the epigyne (Fig. 6B–D).

MALE. Unknown.

FEMALE FROM MADAGASCAR. *Carapace* (Fig. 6A): orange-brown with paler eye region; irregularly clothed with recumbent, short white hairs. *Eyes*: anteriors subcontiguous with apices slightly recurved, fringed by white hairs. *Clypeus*: orange-brown, edged with black; sparsely fringed by white hairs, with oblique white bands below AL. *Chelicerae*: orange-brown tinged with black; sparsely white haired proximally with fine, long orange hairs elsewhere; promargin with three teeth, retromargin with four. *Maxillae and labium*: orange-brown to light yellowish. *Sternum*: elongate scutiform: yellow-orange with very scanty patches of orange-hairs opposite coxae I–III and between coxae IV. *Abdomen*: rubbed; yellow-orange with blackish markings; clothed in scattered patches of orange and light yellow hairs. Spinnerets light yellow. *Legs*: yellowish orange to orange with obscure femoral bands; ventral fringes of orange-brown hair on tibiae I and II, of

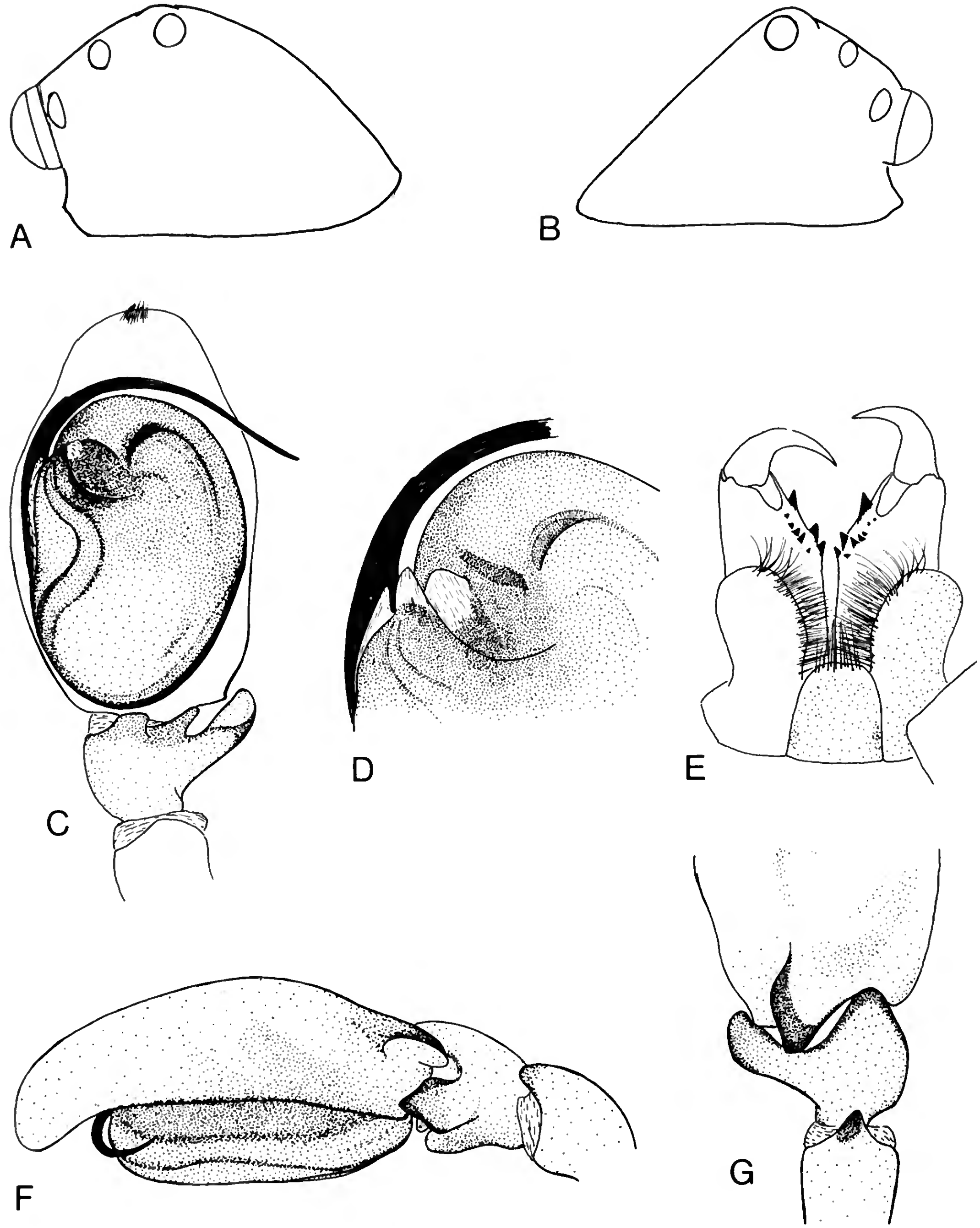

Fig. 7 *Portia fimbriata* (Doleschall), ♂ from Amboina: (A) carapace, lateral view; (C) palp, ventral view; (D) palp, region of tripartite membrane; (E) chelicerae, maxillae and labium; (F) palp, lateral view; (G) tibia and cymbial flange from above. Holotype ♀ of *L. alticeps* Pocock: (B) carapace, lateral view.

whitish hair on patellae I and mixed white and orange-brown hairs on femora I–II. Spines strong and numerous. *Palp*: light yellow with long white hairs. *Epigyne* (Fig. 6B–D).

Dimensions (mm): total length 6·8; carapace length 2·8, breadth 2·4, height 1·8; abdomen length 4·4; eyes, anterior row 1·8, middle row 1·6, posterior row 1·7; quadrangle length 1·4. *Ratios*: AM : AL : PM : PL :: 15 : 7·5 : 5 : 7·5, AL–PM–PL :: 9·5–14, AM : CL :: 15 : 8.

VARIATION. Lectotype ♀ measures 6·0 mm total length, 2·56 mm carapace length.

BIOLOGY. Unknown.

DISTRIBUTION. Madagascar.

MATERIAL EXAMINED. Lectotype ♀, data given in synonymy. MADAGASCAR: 1 ♀ (UM, Oxford).

Portia fimbriata (Doleschall) comb. nov.

(Figs 7A–G; 8A–F; Pls 3a–f; 4c–f; 5c, d, f)

Salticus fimbriatus Doleschall, 1859 : 22, pl. 5, fig. 2, ♂, ♀. LECTOTYPE ♂ (here designated) Amboina (RNH, Leiden, vial 5426) [Examined].

Attus fimbriatus: Hasselt, 1877 : 54.

Sinis fimbriatus: Thorell, 1878 : 270; 1881 : 499, 707. 1895 : 359.

Linus fimbriatus: Karsch 1891 : 299. Thorell, 1892 : 352, 475. Simon, 1901 : 409–11; 1901*a* : 70. Strand. 1909 : 97; 1911 : 177. Rainbow, 1911 : 278. Petrunkevitch, 1928 : 181. Sherriffs, 1931 : 538; 1939 : 196, Roewer, 1954 : 935. Bonnet, 1957 : 2482. Chrysanthus, 1968 : 49, figs 1–6. Prószyński, 1971 : 425.

Linus alticeps Pocock, 1899 : 117, fig. 14, ♀. Holotype ♀, Rubiana, New Georgia (Solomon Islands) (BMNH), reg. no. 1898.12.5.60) [Examined]. Simon, 1901 : 410. Rainbow, 1913 : 14. Blumental, 1935 : 711. Roewer, 1954 : 936. Bonnet, 1957 : 2482. Prószyński, 1971 : 425. **Syn. n.**

Boethoportia ocellata Hogg, 1915 : 502, fig. 1, ♂, ♀. LECTOTYPE ♂ (here designated) Dutch New Guinea (BMNH, reg. no. 1921.3.24.125–6) [Examined]. Petrunkevitch, 1928 : 181. Roewer, 1954 : 933. Bonnet, 1955 : 892. Prószyński, 1971 : 385. [Synonymy noted by D. J. Clark, and published with acknowledgement by Prószyński, 1971.]

The characters given by Pocock (1899) to separate *L. alticeps* Pocock from *P. fimbriata* (Doleschall) would appear to be artefacts. The nearly square posterior cephalic angle has been caused by a tear in the thorax; furthermore, the carapace is partly detached from the sternum and legs, thus increasing its apparent height. The specimen, is, in other respects, identical with *P. fimbriata*.

DIAGNOSIS. *P. fimbriata* is closely related to *P. crassipalpis* (Peckham & Peckham), but can be separated by the structure of the palp (Fig. 7C, F, G). The female of *P. crassipalpis* is unknown.

MALE FROM AMBOINA. *Carapace* (Fig. 7A): orange-brown with lighter eye region; clothed in short, recumbent orange-brown hairs; with a white haired band from fovea to posterior margin and broad, white marginal bands from coxae II to coxae IV. *Eyes*: anteriors more or less contiguous with apices procurved, fringed with orange-brown hairs. *Clypeus*: orange-brown with sooty markings; clothed in light orange-brown hairs. *Chelicerae*: orange-brown with darker markings: proximally a thin transverse band of white hairs, elsewhere thinly clothed in long fine light orange hairs; promargin with three teeth, retromargin with five. *Maxillae and labium*: orange-brown with sooty markings, but inner margins and labial tip paler. *Sternum*: scutiform; light yellowish with orange margins; densely covered in creamy white hairs, with very scanty tufts composed of long brown hairs opposite coxae I–III and between coxae IV. *Abdomen*: light yellowish with blackish markings clothed in light yellow and orange-brown hairs and five tufts composed of orange to creamy white hairs; yellow-brown with blackish markings; spinnerets orange-brown tinged by black, clothed in orange-brown hairs. *Legs*: orange-brown with lighter distal segments; tibae and patellae with long dark brown ventral fringes, incomplete on tibiae II–IV; very abrupt lateral and dorsal fringes also present on tibiae; spines moderately strong and numerous. *Palp* (Fig. 7C, D, F, G; Pl. 3a–f): yellow-brown to dark orange-brown with yellowish white hairs.

Dimensions (mm): total length 6·4; carapace length 2·82, breadth 2·76, height 2·24. abdomen length 3·6; eyes, anterior row 2·2, middle row 1·96, posterior row 2·08; quadrangle length 1·56. *Ratios*: AM : AL : PM : PL :: 19·5 : 9 : 6 : 9, AL-PM-PL :: 10–10, AM : CL :: 19·5 : 10.

FEMALE FROM NEW GUINEA. *Carapace*: orange with sooty markings and pale eye region; clothed in recumbent white hairs in eye region, with scattered short brown hairs and very scanty patches of white hair becoming denser behind fovea and forming thin irregular bands on the margins between coxae II and IV. *Eyes*: more or less as in ♂, anteriors fringed by white and orange hairs, with tufts of orange to dark brown hairs behind AM, outside AL and inside PL. *Clypeus*: orange with faint blackish markings; clothed in recumbent light orange-brown hairs with a poorly defined white stripe below AL and several long stout hairs below AM. *Chelicerae*: orange with sooty markings; thinly clothed in fine whitish hairs and stouter dark brown ones. *Maxillae, labium and sternum*: more or less as in ♂. *Abdomen*: light yellow clothed in white, light orange and brownish hairs with tufts composed of dark brownish orange to white hairs. *Legs*: similar to ♂, but femora and tibiae III–IV obscurely banded with light yellow; fringes very dense, ventrals incomplete on tibiae II to IV, dorsals present on tibiae and patellae, prolaterals on tibiae I–IV, retrolaterals on tibiae III–IV. *Palp*: light yellow to distally dark orange with a blackish femoral band; fringed by white and orange-brown hairs. *Epigyne* (Fig. 8C): clothed in whitish and dark brown hairs.

Dimensions (mm): total length 10·5; carapace length 3·84, breadth 3·52, height 2·72; abdomen length 5·68; eyes, anterior row 2·64, middle row 2·4 posterior row 2·56; quadrangle length 1·76. *Ratios*: AM : AL : PM : PL :: 22 : 10 : 7 : 10·5, AL–PM–PL :: 12–11, AM : CL :: 22 : 13.

VARIATION. ♂ total length varies from 5·2–6·5 mm, carapace length 2·32–2·8 mm (eight specimens). ♀ total length from 6·8–10·5 mm, carapace length 2·72–3·84 mm (six specimens). The male tibial apophysis shows slight variations in shape, but the greatest apparent differences are more often caused by the angle of view. The epigynes are sometimes plugged with waxy secretions; the lip of the lower margin varies in curvature and may be smooth or rough, also the anterior oriface margin (arrowed in Fig. 8A) can be distinct or obscure.

BIOLOGY. Unknown, but considered by P. T. Lehtinen (pers. comm.) to be synanthropic rather than cosmotropical. It has certainly been confused with *P. labiata* in the past and its distribution, given below, is now more restricted. Its occurrence in Sri Lanka needs confirmation.

DISTRIBUTION. Amboina, Mussau Island, New Georgia, New Guinea, Solomon Islands, Sri Lanka, Yule Island.

MATERIAL EXAMINED. Type data given in synonymy. AMBOINA: Ceram, 2 ♂♂, 3 ♀♀, (MNHN, Paris, no. 5568) (MNHN, Paris); 1 ♂ (BMNH); 1 ♀, Peckham coll. no. 4123 (MCZ, Harvard); 2 ♂♂, Peckham coll (*F. C. Muir*, *T. Barbour*) (MCZ, Harvard). MUSSAU ISLAND: Talumalas, 1 ♀, 5.ii.1962 (*Noona Dan Exp.* 1961–62) (BMNH). NEW GUINEA: Kokoda, Papua, 1200 ft, 2 ♂♂, v.1933 (*L. E. Cheesman*); Cyclops Mts, Sabron, 1 ♂, v.1936 (*L. E. Cheesman*); Waigea, Go Village, N. Mayalilrt Bay, 1 ♀, vii.1938 (*L. E. Cheesman*) (BMNH); 1 ♂, 1 ♀, early 1943 (*Capt Tinkham*); 1 ♂, ix–x.1944 (*R. B. Burrows*) (AMNH, New York). SRI LANKA: Galle, 1 ♂ (*E. Simon*, no. 16266) (MNHN, Paris). YULE ISLAND: 1 ♀ (NR, Stockholm).

REMARKS. This species has previously been recorded from Africa, Madagascar, India, Sri Lanka, Hong Kong, Java and Cape York, Australia. The Australian records are probably valid, but I have not seen the specimens concerned. A female from Madagascar, identified as *L. fimbriata* by Simon, is in fact *P. africana*; other specimens from Java and Sri Lanka, incorrectly determined as *P. fimbriata* by Simon, are *P. labiata*, although the Sri Lanka vial also contained a male *P. fimbriata*. The species is almost certainly absent from Africa, and its occurrence in India and Hong Kong cannot be accepted at present as the specimens may have been misidentified.

Portia crassipalpis (Peckham & Peckham) comb. n.

(Fig. 9A–D; Pl. 5a, e)

Linus crassipalpis Peckham & Peckham, 1907 : 605, ♂. Holotype ♂, Sarawak, Kuching (MCZ, Harvard) [Examined]. Roewer, 1954 : 936. Bonnet, 1957 : 2482. Prószyński, 1971 : 425.

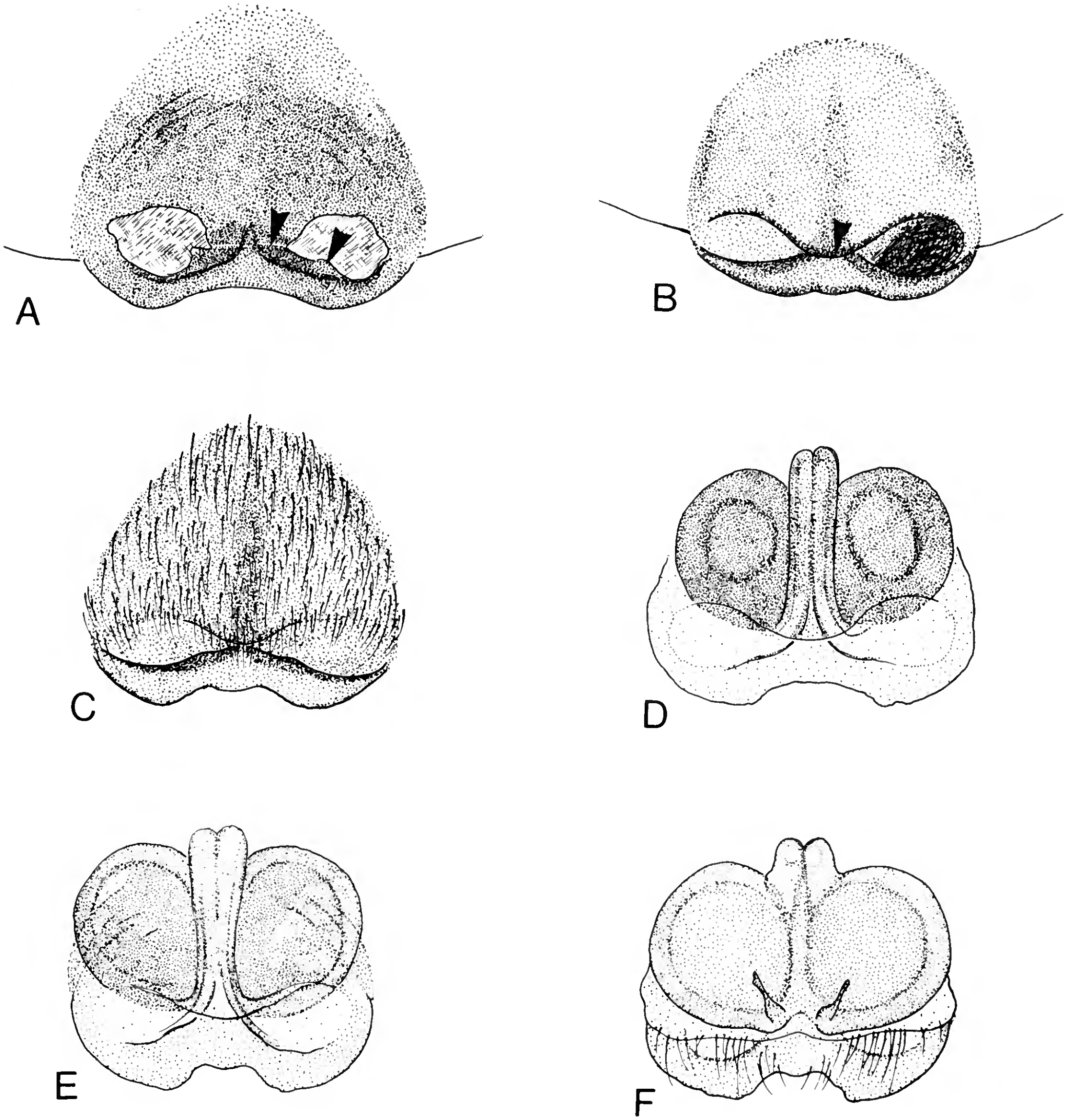

Fig. 8 *Portia fimbriata* (Doleschall), ♀ from Amboina: (A) epigyne 'plugged'; (D) vulva, ventral view; (E) vulva, ventral view of another specimen; (F) vulva, dorsal view. Holotype ♀ of *L. alticeps* Pocock: (B) epigyne 'plugged' on one side. ♀ from New Guinea: (C) epigyne with setae shown.

Diagnosis. *P. crassipalpis*, known only from the male, is closely related to *P. fimbriata*, but can be readily distinguished by the structure of the palp (Fig. 9B–D).

Female. Unknown.

Male from Borneo. *Carapace* (Fig. 9A): yellow-brown; clothed in recumbent orange hairs in eye region, with orange and brown-black ones on thoracic part; from fovea to posterior margin a white wedge-shaped band and from coxae II to coxae IV, broad white marginal bands. *Eyes*: anteriors contiguous with apices procurved, fringed by orange hairs with long black ones above AM, and with orange tufts outside AL and inside PL. *Clypeus*: yellow-brown with blackish markings; thinly clothed in pale yellow-orange hairs. *Chelicerae*: yellow-brown with blackish

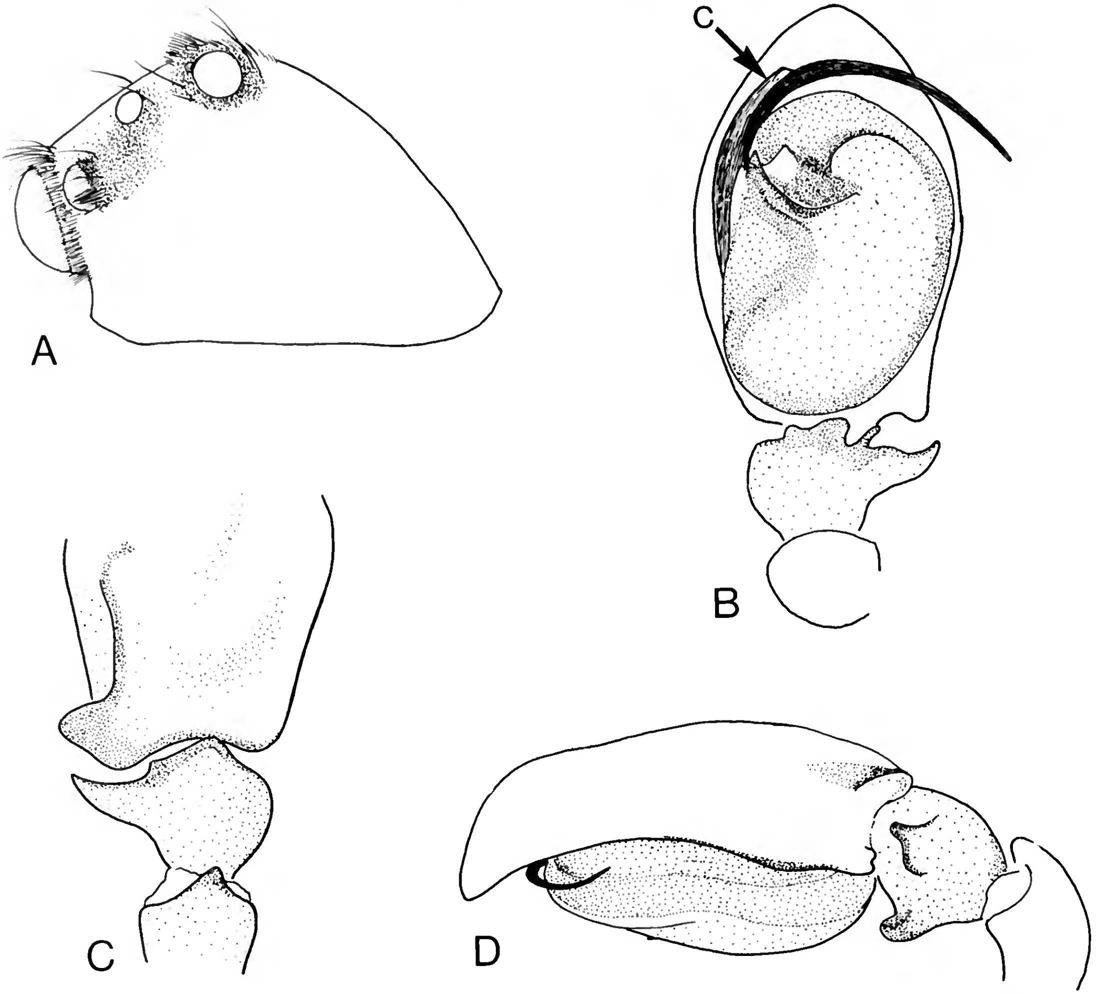

Fig. 9 *Portia crassipalpis* (Peckham & Peckham), ♂ from Borneo: (A) carapace, lateral view; (B) palp, ventral view; (C) tibia and cymbial flange from above; (D) palp, lateral view.

markings; sparsely clothed in long fine hairs; promargin with three teeth, retromargin with six. *Maxillae and labium*: yellow-brown tinged blackish. *Sternum*: elongate scutiform: yellow-brown with faint pattern of blackish spots; thinly clothed in whitish yellow hairs with long blackish ones opposite coxae I–III and between coxae IV. *Abdomen*: yellow-brown with blackish markings; clothed in whitish yellow hairs anteriorly, grading to orange posteriorly, with scattered long stiff brown hairs and a pair of very scanty creamy white tufts just beyond the middle; venter mottled yellow-brown and black; spinnerets brownish orange with orange hairs. *Legs*: generally yellow-brown tinged blackish, but tarsi and metatarsi lighter, the latter with blackish apices; also the posterior femora vaguely annulated with yellow-brown; tibiae and patellae with long black ventral fringes, incomplete on tibiae III–IV; spines strong and numerous. *Palp* (Fig. 9B–D): yellowish to yellow-orange with blackish proximal femoral bands; clothed in orange hairs with creamy white tufts on inside of tibiae and patellae; conductor well developed.

Dimensions (mm): total length 5·12; carapace length 2·28, breadth 1·98, height 1·76; abdomen length 2·44; eyes, anterior row 1·86, middle row 1·64, posterior row 1·8; quadrangle length 1·2. *Ratios*: AM : AL : PM : PL :: AL–PM–PL : 8–6, AM : CL :: 16 : 10.

VARIATION. Total length of ♂ varies from 4·8 to 5·12 mm, carapace length 2·24–2·56 mm (three specimens). The holotype and a male from Malaya have the eye region lighter than the thoracic part.

BIOLOGY. Unknown.

DISTRIBUTION. Borneo, Malaya.

MATERIAL EXAMINED. Type data, given in synonymy. BORNEO: East Coast, 1 ♂, 13.ix.1975 (*J. R. Thomson*, vial K20) (BMNH). MALAYA: Singapore, 1 ♂, 1898 (*H. N. Ridley*) (BMNH).

Portia labiata (Thorell) comb. nov.

(Figs 10A–C; 11A–C)

Sinus fimbriatus Doleschall; Hasselt, 1882: 50, pl. V, fig. 16 [Misidentification].

Linus labiatus Thorell, 1887: 354, ♀ and juvenile. LECTOTYPE ♀ (here designated) Burma, Bhamo (MCSN, Genoa) [Examined]. Thorell, 1895: 359. [= *S. fimbriatus*: Hasselt, non Doleschall, 1859; = *L. dentipalpis* Thorell]. Simon, 1901: 409–410, 1903: 749.

Linus (?) *dentipalpis* Thorell, 1890: 35, ♂. Holotype ♂, Sumatra, Boven Rawas [*S. fimbriatus*: Hasselt 1882] (RNH, Leiden, no. 5428) [Examined]. Thorell, 1892: 352, 475. Simon, 1901: 410, 1903: 749, 1048 [Transferred to *Erasinus*].

Erasinus labiatus: Simon, 1903: 749, 754. Roewer, 1954: 1068. Bonnet, 1956: 1725. Prószyński, 1971: 401.

DIAGNOSIS. *P. labiata* is closely related to *P. assamensis* sp. n., but can be distinguished by the more slender tibial apophysis in males (Fig. 10B) and undivided epigynal oriface in females (Fig. 11B).

MALE FROM MALAYA. *Carapace* (Fig. 11A): orange-brown,l ighter in eye region; clothed in short, recumbent brown-black hairs with a white wedge-shaped band from fovea to posterior margin and broad white marginal bands from coxae I to IV. *Eyes*: anteriors subcontiguous with apices procurved, anteriors fringed by orange hairs with scanty tufts of darker hairs behind AM and outside AL. *Clypeus*: orange-brown with blackish markings; clothed in light orange-brown hairs with fine whitish hairs centrally. *Chelicerae*: orange-brown with brown-black markings; sparsely clothed in fine light yellowish orange hairs; promargin with three teeth, retromargin with five. *Maxillae and labium*: brown-black with inner margin of maxillae and labial tip paler. *Sternum*: scutiform, yellow-brown tinged black; clothed in white hairs, less dense centrally and marginally, with very scanty tufts of long dark brown hairs opposite coxae I–III and between coxae IV. *Abdomen*: brownish with lighter markings; generally clothed in recumbent orange-brown hairs with a pattern of blackish ones posteriorly and a short, central white haired band flanked by black hairs anteriorly with a series of hair tufts composed of long orange to creamy white hairs; venter, yellow-brown with poorly defined central black band; spinnerets dark brown. *Legs*: Legs I–II generally dark brown with vague light femoral markings. Legs III similar but femoral markings slightly more distinct; tarsi and metatarsi lighter, the latter with dark brownish marks particularly around spine sockets. Legs IV as III but markings slightly more distinct; tibiae and patellae with long black ventral fringes, incomplete on tibiae II–IV; very abrupt mid-dorsal fringes also present on tibiae I–IV; spines moderately strong and numerous. *Palp* (Fig. 10A–C): orange-brown to dark brown; clothed in orange and white hairs, conductor well developed.

Dimensions (mm): total length 6·5; carapace length 2·64, breadth 2·44, height 2·0; abdomen length 3·52; eyes, anterior row 1·92, middle row 1·72, posterior row 1·84; quadrangle length 1·34. *Ratios*: AM : AL : PM : PL :: 17 : 8 : 5 : 8, AL–PM–PL : 9–9, AM : CL :: 17 : 12.

FEMALE FROM MALAYA. *Carapace*: orange-brown, lighter in eye region with sooty markings radiating from fovea and with a violet to green iridescent sheen in some lights; clothed in whitish hairs, with scattered long brown ones in eye region. *Eyes*: more or less as in ♂. *Clypeus*: conspicuously marked by transverse, crescent-shaped band of short white hairs with a marginal fringe of long whitish ones. *Chelicerae*: dark orange-brown; sparsely clothed in long clear white hairs with transverse white haired bands proximally; promargin with three teeth, retromargin with four.

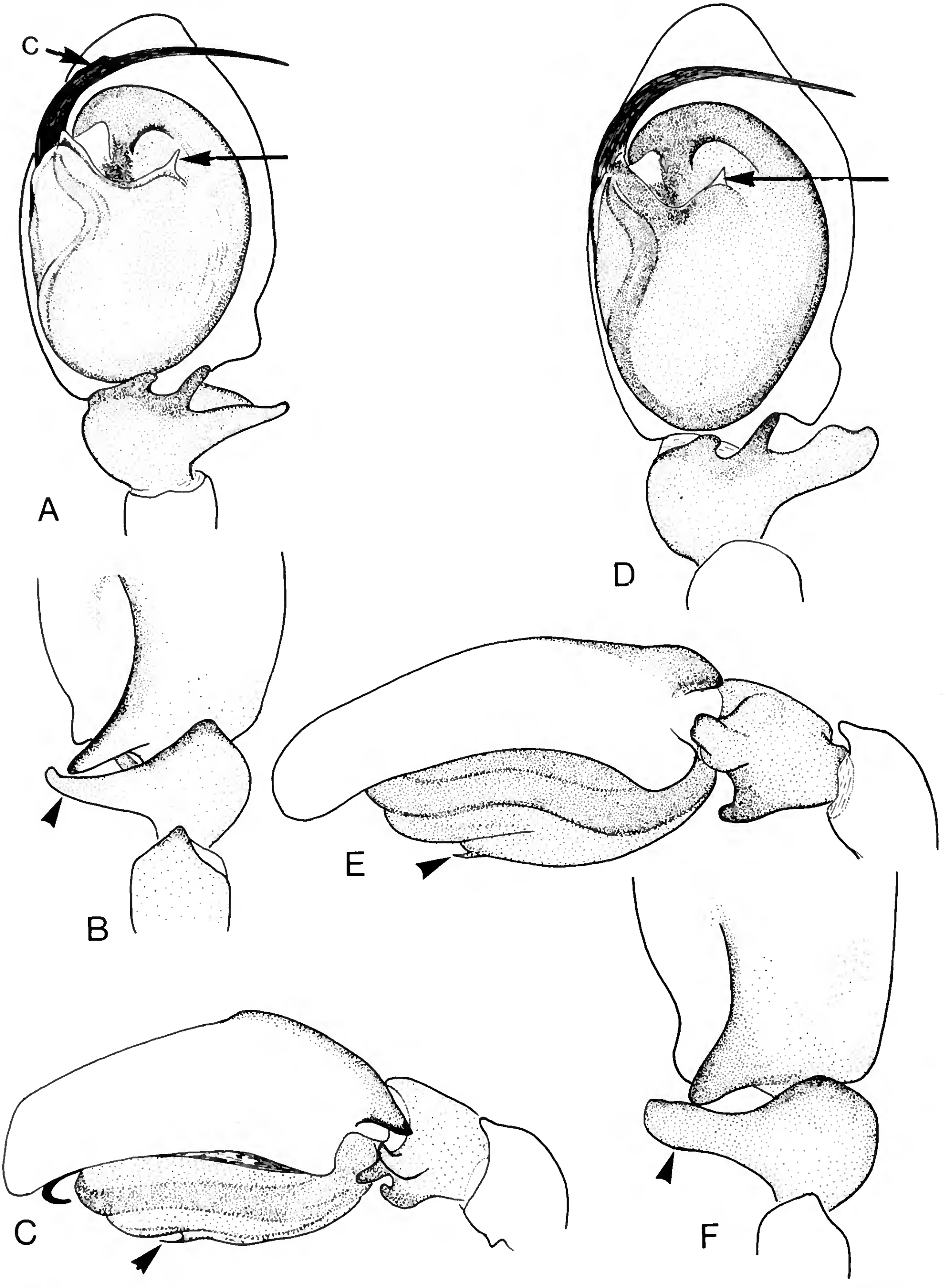

Fig. 10 (A–C) *Portia labiata* (Thorell), ♂ from Malaysia: (A) palp, ventral view; (B) tibia and cymbial flange from above; (C) palp, lateral view. (D–F) *Portia assamensis* sp. n., holotype ♂: (D) palp, ventral view; (E) palp, lateral view; (F) tibia and cymbial flange from above.

Maxillae, labium and sternum: as in ♂. *Abdomen*: mottled brown and black; covered with golden, whitish and black hairs with a series of tufts composed of brownish or creamy brown hairs tipped with white; spinnerets brown-black. *Legs*: more or less as in ♂, but with numerous long white hairs on underside of femora. *Palp*: light yellow with dark brown spots; fringed with long white hairs. *Epigyne* (Fig. 11B–C).

Dimensions (mm): total length 6·5; carapace length 2·88, breadth 2·62, height 2·0; abdomen length 3·6; eyes, anterior row 2·0, middle row 1·82, posterior row 1·96; quadrangle length 1·4. *Ratios*: AM : AL : PM : PL :: 17 : 8 : 5·5 : 8, AL–PM–PL : 10–10, AM : CL :: 17 : 11.

VARIATION. ♂ total length varies from 5·28 to 7·5 mm, carapace length 2·4–3·28 mm (eight specimens). ♀ total length from 6·56 to 9·44 mm, carapace length 2·76–3·84 mm (eight specimens). The tibial apophysis is sometimes more distinctly knob-shaped and the epigyne is often plugged.

BIOLOGY. Unknown, but one male has been taken from a pholcid web.

DISTRIBUTION. Burma, India, Malaya, Sarawak, Siam, Sri Lanka, Sumatra.

MATERIAL EXAMINED. Type data, given in synonymy. BURMA: Tenasserim, 1 ♀ (*E. W. Oates*); Tharrawaddy, 1 ♂ (*E. W. Oates*) (BMNH). INDIA: Madras, Nilghiri Hills, 1 ♂ (Sir *George Hampson*) (BMNH). MALAYA: Kuala Lumpur, Batu village, taken from a pholcid web in derelict hut, 1 ♂, 12.ix.1973 (*A. D. Blest*, vial 27(B)); Singapore, Seletar Reserve, about 1 mile from Nee Soon village, in natural clump of dead grass, 1 ♀, 17.ix.1973 (*A. D. Blest*, vial 36(C)); Kuala Lumpur, 1 ♂ (*C. Boden Kloss*); Singapore, 1 ♂, 1898 (*H. N. Ridley*) (BMNH). SARAWAK: Moss forest, 4000 ft, 1 ♀, 16.x.1932 (Oxford Univ. Sarawak Exped.) (BMNH). SIAM: Bangkok, 1 ♂ (*H. Hillman*) (BMNH). SRI LANKA: Franatim, 1 ♀, viii.1905 (*A. Willey*); Peralena, Botanical gardens, 1 ♂, 1♀ (Freeman); Colombo, 1 ♂ (*E. E. Green*); 1 ♀ (BMNH); 1 ♂ (UM, Oxford); Galle (*E. Simon*, vial 16266) (MNHN, Paris). SUMATRA: Hanan Kloof, 2 ♂♂, 2 ♀♀ (*E. Jacobson*, Reismoser coll) (NM, Wien); Forte de Kock, 1 ♂, 2 ♀♀, iv.1914 (*E. Jacobsen*, det Thorell vial 5424); Buo, 2 ♂♂, 1 sub ♀, ii.1914 (*E. Jacobson*, vial 5425) (RNH, Leiden).

Portia assamensis sp. n.

(Figs 10D–F; 11D–F)

DIAGNOSIS. *Portia assamensis* is closely related to *P. labiata* (Thorell), but may be distinguished by the robust tibial apophysis (arrowed, fig. 10F) in males, and the divided epigynal orifice in females (Fig. 11E). The white haired clypeus readily separates female *P. assamensis* from female *P. fimbriata* (Doleschall).

MALE HOLOTYPE. *Carapace* (Fig. 11D): orange-brown with paler eye region; clothed in recumbent, light orange hairs with median white band from fovea to posterior margin and broad white marginal bands from coxae I to coxae IV. *Eyes*: anteriors subcontiguous with apices procurved, fringed by whitish hairs. *Clypeus*: light orange-brown; very sparsely clothed in fine hairs. *Chelicerae*: orange-brown with darker markings; sparsely clothed in long fine hairs, teeth not examined. *Maxillae and labium*: orange-brown, inner margins of maxillae and labium lighter. *Sternum*: elongate scutiform; light yellow-brown with darker margins; densely clothed in creamy white hairs with several long fine brown ones opposite coxae I–III and between coxae IV. *Abdomen*: rubbed; yellow-brown to orange-brown with darker markings; clothed in fine whitish and light orange hairs; spinnerets brownish. *Legs*: dark orange; tibiae and patellae I clothed in light orange hairs with brown ventral fringes and mid-dorsal tufts on tibiae; remaining tibiae and patellae similar, but fringes more scanty and interrupted, with the dorsal tufts lacking on tibiae III–IV, spines moderately strong and numerous. *Palp* (Fig. 10D–F): orange to blackish red with white and creamy white hairs; large tibial apophysis similar to that of *P. africana*; the membraneous tegular apophysis (arrowed in fig. 10D) is best seen in lateral view.

Dimensions (mm): total length 7·4; carapace length 3·1, breadth 2·84, height 2·16; abdomen length 4·48; eyes, anterior row 2·28, middle row 2·0, posterior row 2·2; quadrangle length 1·6. *Ratios*: AM : AL : PM : PL :: 19 : 9·5 : 6 : 9, AL–PM–PL : 10–10, AM : CL :: 19 : 12.

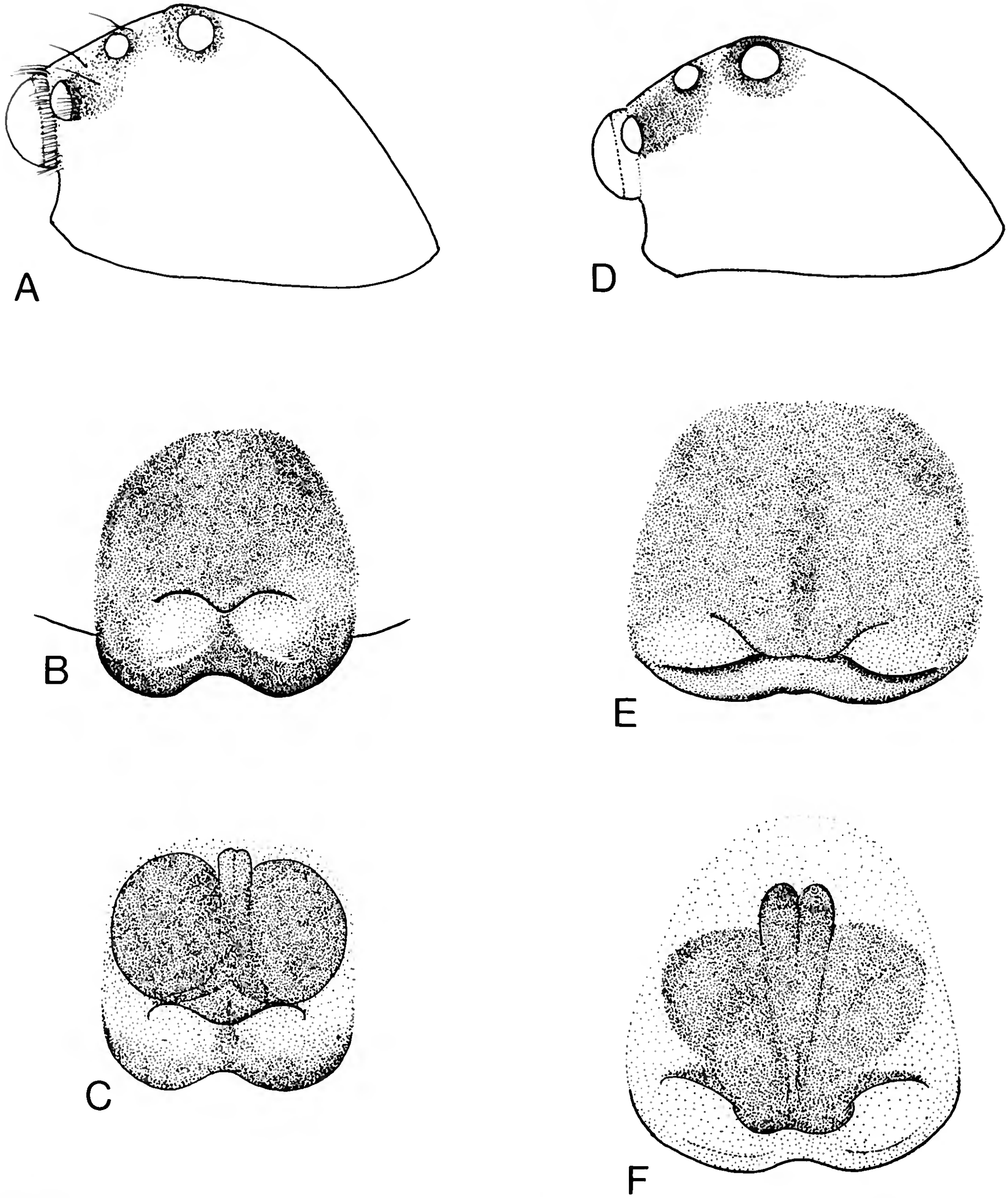

Fig. 11 (A–C) *Portia labiata* (Thorell), ♂ from Malaysia: (A) carapace, lateral view. ♀ from Malaysia: (B) epigyne; (C) vulva, ventral view. (D–F) *Portia assamensis* sp. n., holotype ♂: (D) carapace, lateral view. Paratype ♀: (E) epigyne; (F) vulva, ventral view.

Female from Nepal: *Carapace*: similar to ♂; orange with light sooty markings, thoracic part weakly iridescent; generally clothed in short whitish hairs with several long white hairs behind fovea. *Eyes*: more or less as in ♂; anteriors fringed by orange hairs with orange tufts outside AL and inside PL. *Clypeus*: orange with lower half densely white haired, except for median patch of very fine short hairs. *Chelicerae*: reddish orange with short white lanceolate and long fine hairs; pro- and retromargin with three teeth. *Maxillae and labium*: reddish black, inner margins of maxillae and labial tip lighter. *Sternum*: similar to ♂; light orange with darker margins; clothed in creamy white hairs with scattered long brownish ones. *Abdomen*: mottled yellow-brown and black; clothed in white, orange and dark brown hairs with tufts composed of dark brown to white hairs; spinnerets brown. *Legs*: dark orange-brown with lighter markings on posterior femora and tibiae, and dark dorsal stripe on metatarsi I–II; tibiae and patellae with long black ventral fringes, interrupted on legs II–IV; tibial mid-dorsal tufts also present; spines moderately strong and numerous. *Palps*: reddish black with yellow-orange markings; fringed with whitish and light brown hairs. *Epigyne* (Fig. 11E, F): clothed with white hairs.

Dimensions (mm): total length 9·0; carapace length 3·84, breadth 3·36, height 2·48; abdomen length 4·96; eyes, anterior row 2·54, middle row 2·34, posterior row 2·42; quadrangle length 1·76. *Ratios*: AM : AL : PM : PL :: 20 : 10 : 7 : 10, AL–PM–PL : 12–12, AM : CL :: 20 : 16.

VARIATION. A paratype ♂ measures 6·8 mm total length, 3·28 mm carapace length. ♀ total length varies from 7·1 to 10·7 mm, carapace length 3·1–3·7 mm (five specimens). The epigynes are sometimes plugged.

BIOLOGY. A female from Maewa Khola, Nepal, was taken with 21 second instar spiderlings from a silken retreat in a curled up dead leaf. Numerous exuvia were still in the nest, and it seems likely that in this species the mother remains with the young until they disperse.

DISTRIBUTION. Assam, Nepal.

MATERIAL EXAMINED. Holotype ♂, ASSAM, no other data (BMNH, reg. no. 1977.9.5.5). Paratypes: ASSAM: 1 ♂, in same vial as holotype. NEPAL: Between Bichipur Khola and Pokhara, on a stone, 3000 ft, 1 ♀, 9.vii.1954 (*K. H. Hyatt*, no. 256, Brit. Mus. Nepal Exped); Mayangdi Khola, west of Beni, on rocky ground, 3000 ft, 1 ♀, 16.vi.1954 (*K. H. Hyatt*, no. 155, Brit. Mus. Nepal Exped); Between Tilhar and Naudhara, 4–5000 ft, 2 ♀♀, 29.vii.1954 (*K. H. Hyatt*, no. 247, Brit. Mus. Nepal Exped); Maewa Khola, Sanghu, 6000 ft, 1 ♀ with young in curled up dead leaf, 10.x.1961 (*K. H. Hyatt*, no. 42a, Brit. Mus. Nepal Exped) (BMNH).

REMARKS. It is not known for certain if the females described above are conspecific with the males. They may represent a new taxon or even belong with *P. albimana*, originally described from North West India. The problem should be quickly resolved when additional material becomes available for study.

Portia albimana (Simon) comb. n.

(Fig. 12A–D)

Linus albimanus Simon, 1900 : 33, ♂. LECTOTYPE ♂ (here designated) India, Dehra-Dun (MNHN, Paris, no. 17764) [Examined]. Simon, 1901 : 409. Roewer, 1954 : 936. Bonnet, 1957 : 2482. Prószyński, 1971 : 425.

DIAGNOSIS. *P. albimana* is a fairly distinctive species distinguished from all other species of *Portia* by the relatively short embolus (Fig. 12B) and completely fringed tibiae I.

FEMALE. Unknown.

MALE FROM SRI LANKA. *Carapace* (Fig. 12A): orange-brown with paler eye region; clothed in recumbent light brownish hairs, with a white wedge-shaped band from fovea to posterior margin and broad white marginal bands from AM sides to coxae IV. *Eyes*: anteriors subcontiguous with apices slightly procurved, fringed by white hairs with light brown tufts outside AL. *Clypeus*: densely clothed in white hairs forming a crescent-shaped patch below AM. *Chelicerae*: orange-brown; clothed in long fine hairs and white ones along inner proximal margins (rubbed); promargin and retromargin with three teeth. *Maxillae and labium*: orange-brown, inner margin of maxillae and labial tip paler. *Sternum*: scutiform; orange-brown with darker margin; clothed in white hairs with longer brown ones opposite coxae I–III and between coxae IV. *Abdomen*: yellow-brown with darker markings; rubbed, but clothed in some minute iridescent setae; spinnerets brownish orange. *Legs*: Legs I orange to orange-brown; tibiae completely fringed by dense,

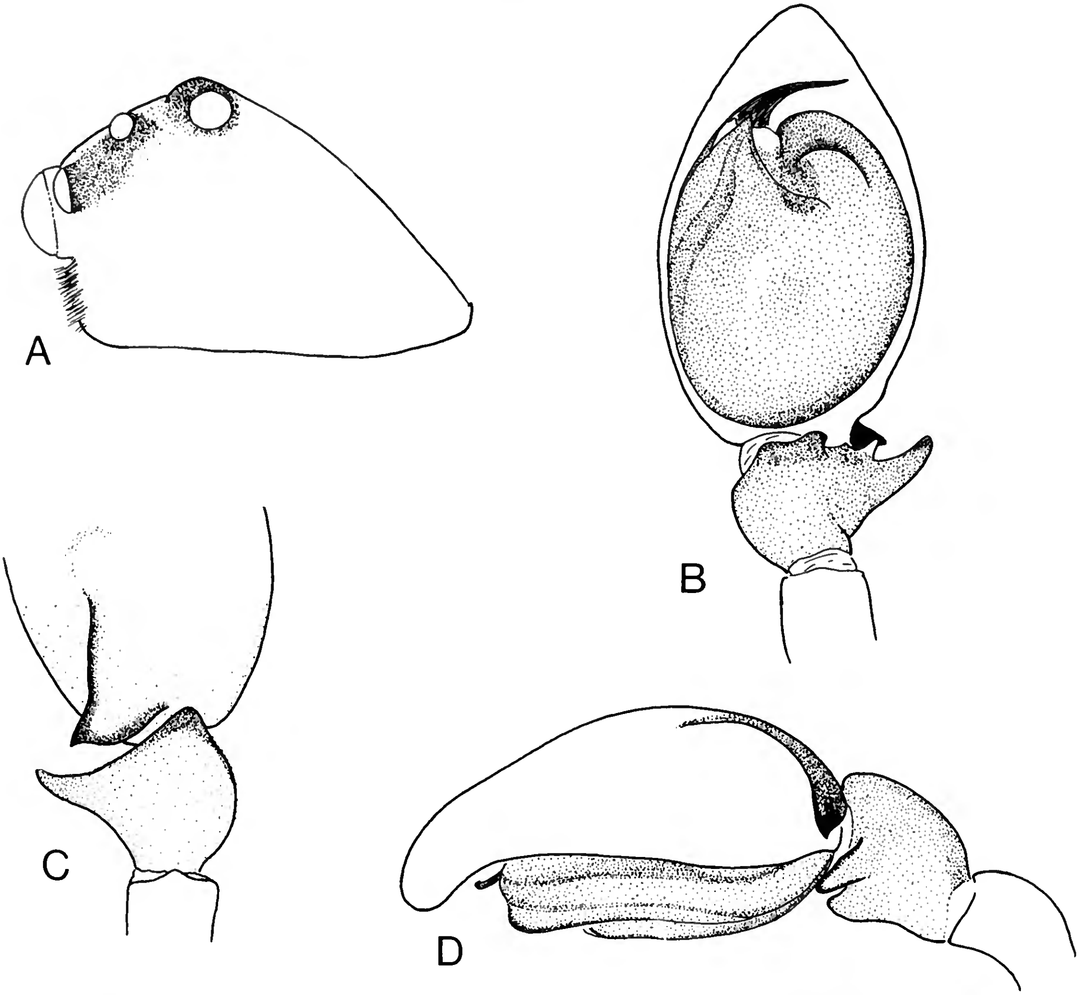

Fig. 12 *Portia albimana* (Simon), ♂ from Sri Lanka: (A) carapace lateral view; (B) palp, ventral view; (C) tibia and cymbial flange from above; (D) palp, lateral view.

stiff brownish hairs, those on venter longest; patellae with ventral fringe only. Remaining legs orange to dark orange, without fringes; spines numerous, moderately robust. *Palp* (Fig. 12B–D): orange-brown to dark brown with long white hairs on inside of tibiae and patellae; embolus short, cymbial flange with a strong downward slope.

Dimensions (mm): total length 6·08; carapace length 2·6, breadth 2·2, height 1·84; abdomen length 3·6; eyes, anterior row 1·83, middle row 1·66, posterior row 1·8; quadrangle length 1·28. *Ratios*: AM : AL : PM : PL :: 15 : 8 : 6 : 8, AL–PM–PL : 10–9, AM : CL :: 15 : 10·5.

VARIATION. Total length of ♂ varies from 4·9 to 7·3 mm, carapace length 2·16–3·0 mm (five specimens).

BIOLOGY. Unknown.

DISTRIBUTION. India, Sri Lanka.

MATERIAL EXAMINED. Type data, given in synonymy. SRI LANKA: Peralena, 1 ♂ (BMNH). 3 ♂ (UM, Oxford).

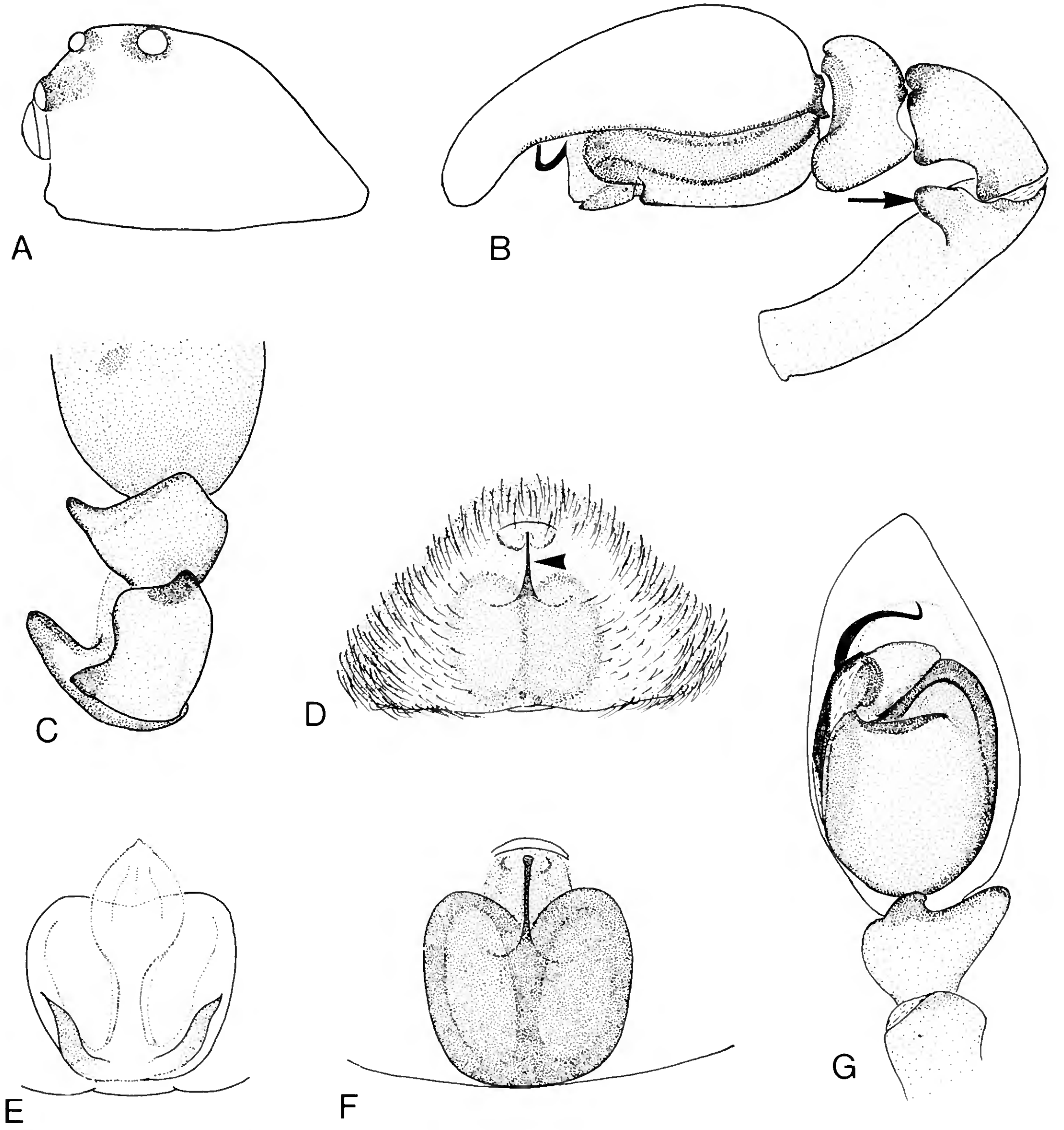

Fig. 13 *Portia durbanii* Peckham & Peckham, neotype ♂: (A) carapace, lateral view; (B) palp, lateral view; (C) tibia from above; (G) palp, ventral view. ♀ from Umkomas River: (D) epigyne; (E) vulva outline, dorsal view; (F) vulva, ventral view.

Species sola

Portia durbanii Peckham & Peckham

(Fig. 13A–G)

Portia durbanii Peckham & Peckham, 1903 : 183, figs 2, 2a, 2b, ♂♂. Neotype ♂ (here designated) South Africa, Durban (MCZ, Harvard) [Examined]. Warren, 1928 : 58. Lawrence, 1947 : 36. Roewer, 1954 : 933. Cutler, 1976 : 133.

P. durbanensis: Bonnet, 1958 : 3766 [Unjustified emendation]. Prószyński, 1971 : 461.

P. durbani: Roewer, 1965 : 12, fig. 11 [Unjustified emendation].

REMARKS. The Peckhams' (1903) state in their original description: 'we have three males from Durban, sent by Mr Quekett'. The vial labelled '(28) *Portia durbanii* Peck. Durban. Type. G. W. & E. G. Peckham Coll' contains six males, three subadult males and one female. Some of these specimens are probably syntypes, but as they cannot be positively recognized a neotype is designated.

DIAGNOSIS. *P. durbanii* is a species of uncertain affinities, but can be easily recognized by the presence of the palpal femoral spur in males (Fig. 13B) and slender epigynal septum in females (Fig. 13D).

MALE NEOTYPE. *Carapace* (Fig. 13A): orange-brown, clothed in fine recumbent white hairs, with scattered long brownish hairs in eye region. *Eyes*: with brown-black surrounds except AM; anteriors subcontiguous with apices recurved, fringed by whitish hairs. *Clypeus*: orange-brown clothed in fine whitish hairs. *Chelicerae*: light orange-brown with blackish markings; clothed in mixed lanceolate and normal long whitish hairs; promargin with three teeth, retromargin with four. *Maxillae and labium*: orange-brown, but inner distal margins of maxillae and labial tip paler. *Sternum*: elongate scutiform; pale-orange brown tinged blackish with clear orange margins, shiny; clothed in light orange hairs. *Abdomen*: pale yellowish orange with blackish ventral band and four impressed dorsal spots; sparsely clothed in long brownish hairs with very scanty longitudinal band composed of very fine iridescent setae; tufts apparently lacking; spinnerets light yellow-brown. *Legs*: generally orange-brown to light orange-brown; light brown ventral fringes present on femora, patellae and tibiae of legs I, also legs II but very scanty. Spines strong and numerous. *Palp* (Fig. 13B, C, G): orange-brown with light brown hairs.

Dimensions (mm): total length 5·8; carapace length 2·8, breadth 2·3, height 1·68; abdomen length 3·2; eyes, anterior row 1·68, middle row 1·38, posterior row 1·56; quadrangle length 1·2. *Ratios*: AM : AL : PM : PL :: 13 : 7·5 : 5·5 : 6, AL–PM–PL : 9–10, AM : CL :: 13 : 8.

FEMALE FROM LOWER UMKOMAAS RIVER, SOUTH AFRICA. General body form and colour similar to male. *Carapace*: orange-brown with eye region paler; clothed in very fine recumbent white hairs. *Abdomen*: pale yellow with black ventral band and four impressed dorsal spots; sparsely clothed in long orange hairs. *Palps*: whitish yellow with long white hairs. *Epigyne* (Fig. 13D–F): slender anterior septum distinctive.

Dimensions (mm): total length 5·2; carapace length 2·4, breadth 2·0, height 1·56; abdomen length 2·7; eyes, anterior row 1·56, middle row 1·3, posterior row 1·48; quadrangle length 1·08. *Ratios*: AM : AL : PM : PL :: 13 : 7·5 : 5 : 6, AL–PM–PL : 9–10, AM : CL :: 13 : 7.

VARIATION. Male total length varies from 5·12 to 6·4 mm, carapace length 2·32–2·8 mm (eight specimens). Females range from 5·1 to 6·5 mm total length, 2·3–2·8 mm carapace length. Hair tufts on the carapace and abdomen are apparently lacking. The fine carapace hairs appear light brownish under some angles of illumination and some males have vague abdominal chevrons, but iridescent hairs are usually rubbed.

BIOLOGY. A juvenile collected from bushes in Pietermartizburg, S. Africa, by the author and Mr A. Russell-Smith was reared through several moults by Mrs Frances Murphy. There was no evidence of web spinning activity as was the case with *P. schultzii*, unfortunately the specimen did not reach adulthood and died during moulting.

DISTRIBUTION. South Africa.

MATERIAL EXAMINED. Neotype data given in synonymy. SOUTH AFRICA: Durban: 1 ♂ (*G. P. Staunton*); 1 ♂, 1 ♀ (*J. F. Quekett*); 1 ♀ (*J. P. Crezoe*); Natal, Lower Umkomaas River, 3 ♀♀ (*G. F. Leigh*); Pietermaritzburg, low bushes, 1 juvenile, iv.1976 (*A. Russell-Smith & F. Wanless*) (BMNH). Natal, 1 ♀, 6 immatures (*C. Martin*, Simon coll, no. 19618) (MNHN, Paris). Maritzburg: 1 ♂ (*R. A. Holliday*, NM, 4236); xii.1959, 1 ♂ (*R. F. Lawrence*, NM. 6350); xii.1957, 1 ♀ (NM. 6749) (NM, Pietermaritzburg).

The *kenti*-group

The *kenti*-group, known only from males, is comprised of three species, *P. madagascarensis* sp. n. from Madagascar, *P. kenti* Lessert and *P. falcifera* sp. n. both from Africa.

The species appear to form a good monophyletic group which can be readily separated from the *schultzii*-group by the recurved anterior eye row and the membraneous joint of the palpal tibial apophysis (Figs 14C, F; 16B). In *P. kenti* the tibial apophysis shows some flexibility, but it is not known if the tibial apophysis can be moved naturally. *P. falcifera* and *P. madagascarensis* also appear to have flexible apophyses, but movement has not been demonstrated in the specimens at hand. In the ant-like genus *Belippo* (see Wanless, 1978) the male palpal tibial apophysis could be easily moved (by hand) and its membraneous base clearly allowed for flexibility. However, in this case I am not sure that the apophyses can be correctly described as moveable although their appearance suggests that there may be a limited degree of flexibility.

Portia kenti Lessert

(Figs 14A, C, D; 15A)

Portia kenti Lessert, 1925 : 339, fig. 8, ♂. Holotype ♂, South Africa, Natal, Umbilo (NM, Pietermaritzburg) [Examined]. Roewer, 1954 : 934. Bonnet, 1958 : 3766. Roewer, 1965 : 11, fig. 10. Prószyński, 1971 : 461. Cutler, 1976 : 133.

DIAGNOSIS. *P. kenti* is very closely related to *P. falcifera* sp. n., but can be separated by the shorter embolus, less robust tibial apophysis and shallow membraneous depression on the proximal ectal margin of the cymbium (Fig. 14A, C, D).

FEMALE. Unknown.

MALE FROM DURBAN. *Carapace* (Fig. 15A): yellow-brown, clothed with short, recumbent creamy white hairs that are iridescent under some angles of illumination. *Eyes*: anteriors subcontiguous with apices strongly recurved, fringed by whitish hairs with a tuft of light yellow-brown hairs behind PM. *Clypeus*: with several long stiff orange hairs. *Chelicerae*: yellowish orange, thinly covered in long pale hairs; promargin with three teeth, retromargin with four. *Maxillae and labium*: light yellowish brown. *Sternum*: elongate scutiform; yellowish faintly tinged with black; shiny, sparsely clothed in light orange-brown hairs. *Abdomen*: light yellow with obscure chevrons dorsally and a longitudinal blackish band ventrally; clothed in minute yellowish/iridescent hairs; spinnerets light yellow. *Legs*: yellowish orange to light yellow-orange; legs I with dense brown fringes on dorsam and venter of tibiae, venter of patellae and distal venter of femora; legs II with similar, but less dense fringes. Spines moderately strong and numerous. *Palp* (Fig. 14A, C, D): light yellow-brown to yellow-brown. Embolus short, conductor apparently lacking; tibial apophysis moveable (?); proximal ectal margin of cymbium with a shallow, somewhat membraneous triangular depression.

Dimensions (mm): total length 6·3; carapace length 2·9, breadth 2·5, height 1·76; abdomen length 3·56; eyes anterior row 1·54, middle row 1·55, posterior row 1·44; quadrangle length 1·16. *Ratios*: AM : AL : PM : PL :: 12·5 : 7 : 5 : 6·5, AL–PM–PL : 7·5–10, AM : CL :: 12·5 : 7.

VARIATION. The holotype measures 5·0 mm total length, 2·5 mm carapace length.

BIOLOGY. Unknown.

DISTRIBUTION. South Africa.

MATERIAL EXAMINED. Holotype ♂, data given in synonymy. SOUTH AFRICA: Durban, 1 ♂ (*G. P. Staunton*) (BMNH).

Portia falcifera sp. n.

(Figs 14B, E, F; 15B–D)

DIAGNOSIS. *P. falcifera* is closely related to *P. kenti* Lessert, from which it may be separated by

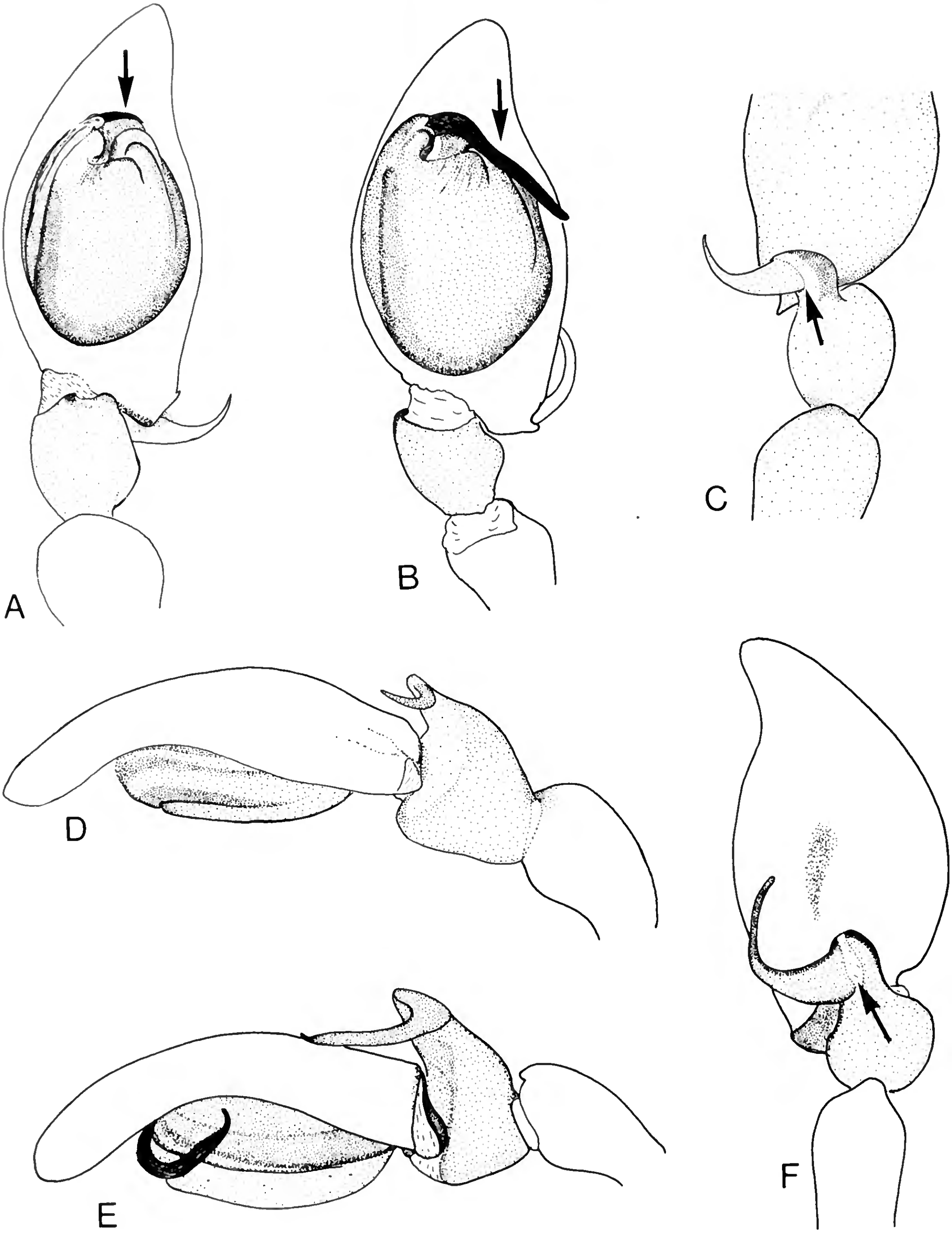

Fig. 14 (A, C, D) *Portia kenti* Lessert, ♂ from Durban: (A) palp, ventral view; (C) tibia from above; (D) palp, lateral view. (B, E, F) *Portia falcifera* sp. n., holotype ♂: (B) palp, ventral view; (E) palp, lateral view; (F) tibia from above.

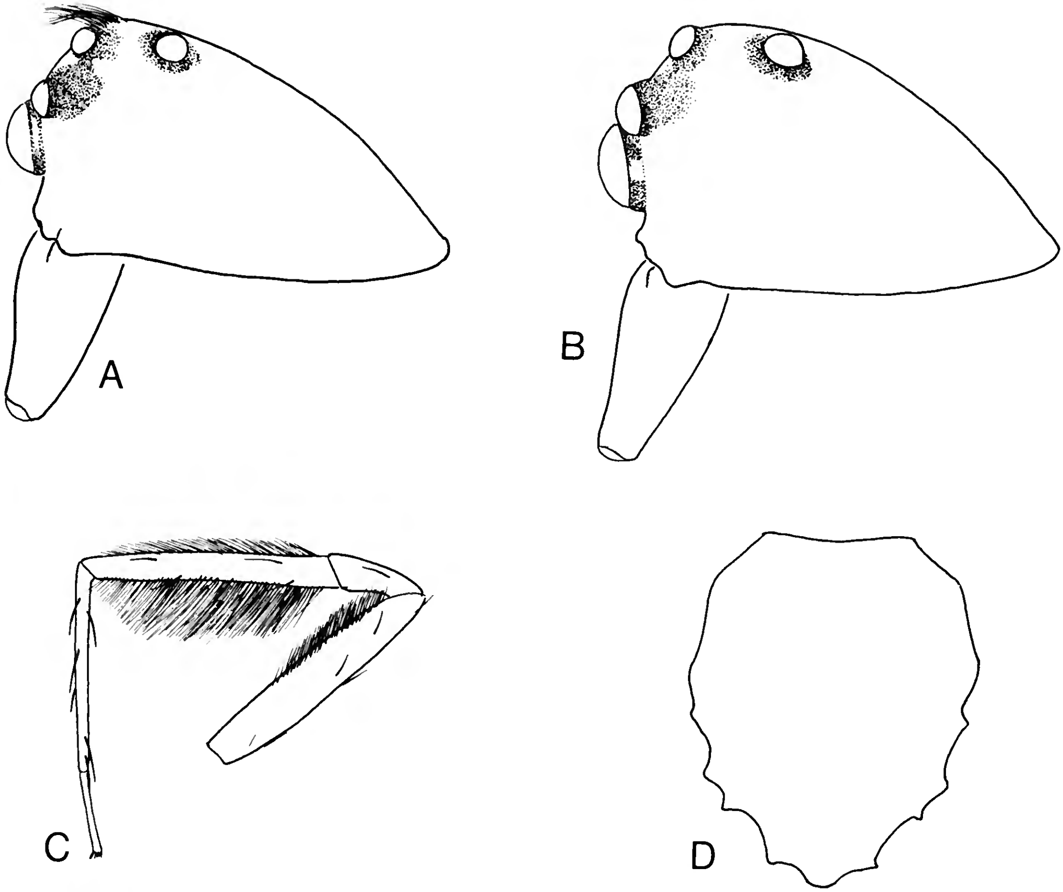

Fig. 15 (A) *Portia kenti* Lessert, ♂ from Durban: (A) carapace, lateral view. (B–D) *Portia falcifera* sp. n., holotype ♂: (B) carapace, lateral view; (C) leg I; (D) sternum.

the longer embolus, more robust tibial apophysis and deep excavation on the proximal ectal margin of the cymbium (Fig. 14B, E, F).

FEMALE. Unknown.

MALE HOLOTYPE. *Carapace* (Fig. 15B): orange-brown; clothed in fine recumbent whitish/iridescent hairs. *Eyes*: anteriors subcontiguous with apices strongly recurved, fringed by whitish hairs. *Clypeus*: thinly clothed in fine white hairs with long yellowish ones marginally. *Chelicerae*: orange-brown with obscure sooty markings; a scanty transverse white haired fringe proximally, elsewhere sparsely covered in long fine yellowish hairs. *Maxillae and labium*: yellow-orange tinged black, but inner margins of maxillae and labial tip lighter. *Sternum* (Fig. 15D): light yellow-orange with orange margins, shiny; thinly clothed in pale orange hairs. *Abdomen*: light yellow-brown with obscure blackish dorsal chevrons and a longitudinal black band ventrally; clothed in fine yellow-brown/iridescent hairs; spinnerets light yellow. *Legs*: light orange to orange-brown; dense black fringes present on venter and dorsam of tibiae I, and on distal venter of femora I and tibiae IV. Spines strong and numerous. *Palp* (Fig. 14B, E, F): yellow-brown to orange-brown. Embolus relatively long, conductor apparently lacking; tibial apophysis moveable (?); proximal ectal margin of cymbium clearly modified.

Dimensions (mm): total length 5·36; carapace length 2·52, breadth 2·12, height 1·52; abdomen length 2·8; eyes anterior row 1·46, middle row 1·04, posterior row 1·28; quadrangle length 1·12. *Ratios*: AM : AL : PM : PL :: 13 : 8 : 6 : 7, AL–PM–PL : 8–10, AM : CL :: 13 : 6.

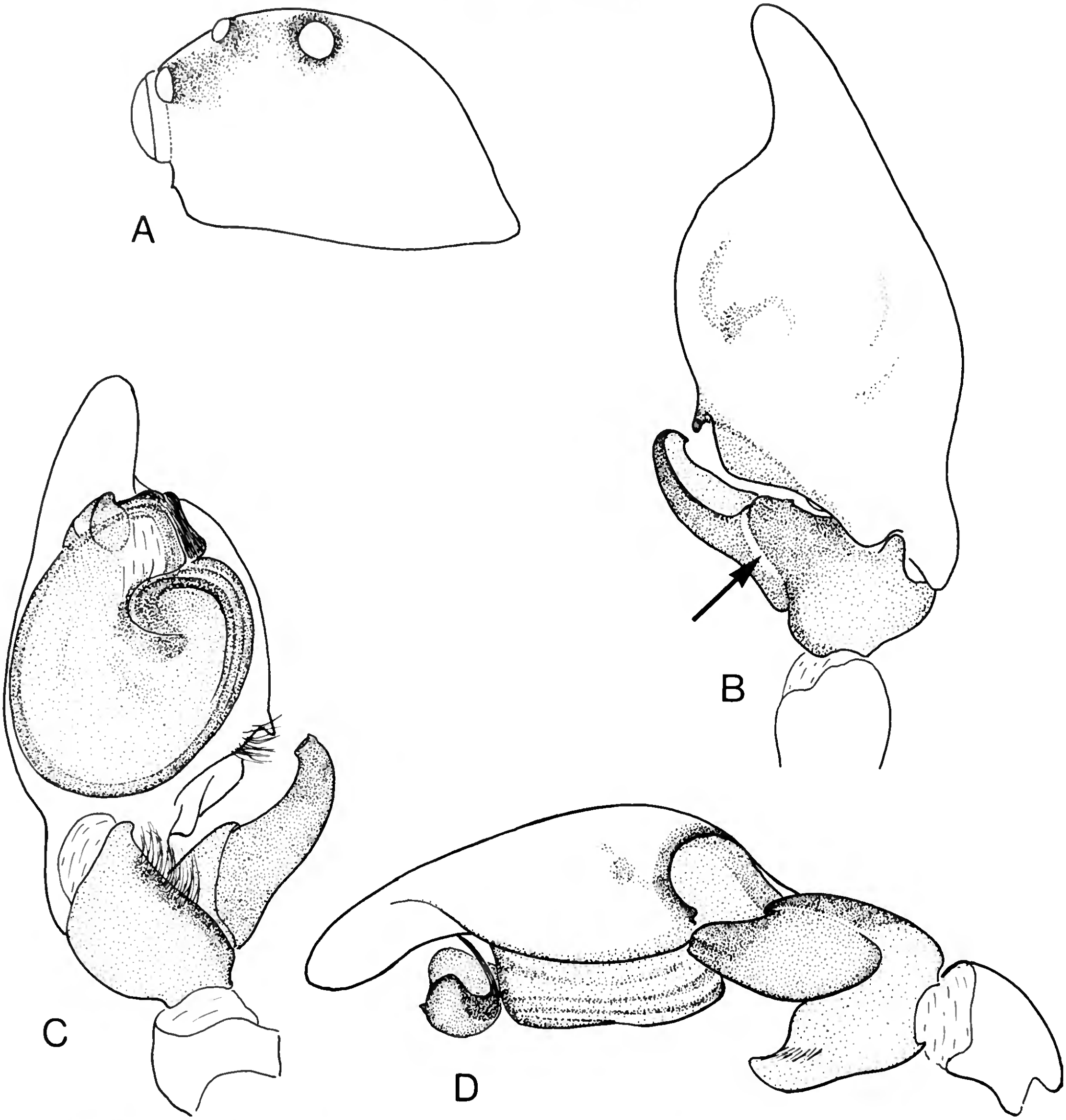

Fig. 16 *Portia madagascarensis* sp. n., holotype ♂: (A) carapace, lateral view; (B) palp, dorsal view; (C) palp, ventral view; (D) palp, lateral view.

VARIATION. Unknown.

BIOLOGY. Unknown.

DISTRIBUTION. Uganda.

MATERIAL EXAMINED. Holotype ♂, UGANDA, Mpanga forest, beaten from trees, 20.iii.1966 (*A. E. Squires*, Loughborough Naturalist's Club) (BMNH, reg. no. 1977.8.12.1).

Portia madagascarensis sp. n.

(Fig. 16A–D)

DIAGNOSIS. *P. madagascarensis* is a fairly distinctive species separated from other species in the *kenti*-group by the large palpal tibial apophysis (Fig. 16B) and lack of leg fringes.

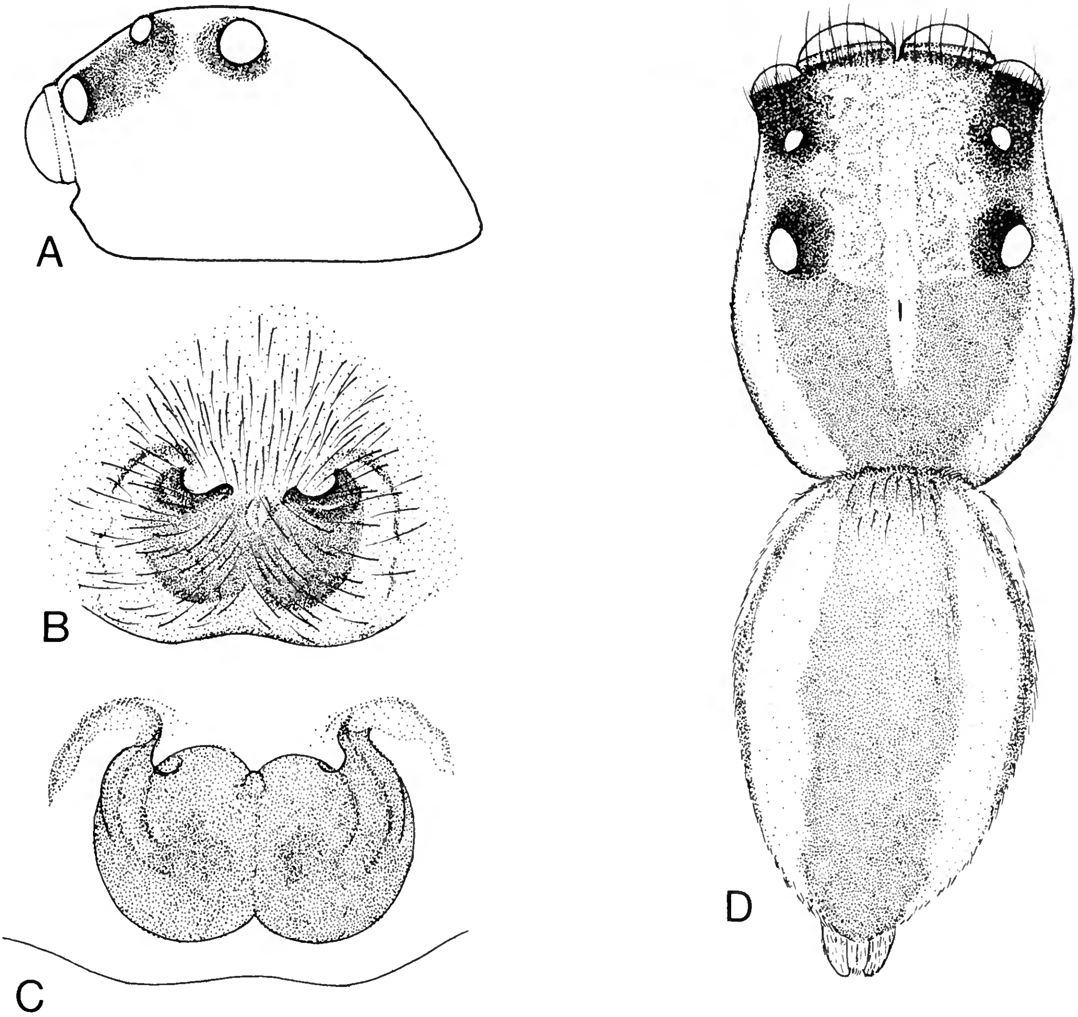

Fig. 17 *Portia oreophila* sp. n., holotype ♀: (A) carapace, lateral view; (B) epigyne; (C) vulva, ventral view; (D) dorsal view.

FEMALE. Unknown.

MALE HOLOTYPE. *Carapace* (Fig. 16A): light orange with yellowish guanin in eye region; clothed in fine recumbent whitish/iridescent hairs. *Eyes*: anteriors subcontiguous with apices slightly recurved, fringed by whitish hairs. *Clypeus*: sparsely fringed by whitish hairs. *Chelicerae*: light orange, shiny with fine long pale hairs; promargin with three teeth, retromargin with five. *Maxillae and labium*: light yellow-orange, but inner margins of maxillae and labial tip whitish. *Sternum*: scutiform; light yellowish orange, shiny. *Abdomen*: pale yellow; covered in fine iridescent hairs; spinnerets yellow-orange. *Legs*: light yellow-orange grading to dark orange distally especially legs I–II; fringes lacking. Spines numerous, moderately strong. *Palp* (Fig. 16B–D): yellowish with tibiae and cymbium orange to orange-brown. Embolus short, curved, originating from distinct base; conductor apparently lacking; tibial apophysis moveable (?); proximal ectal margin of cymbium clearly modified.

Dimensions (mm): total length 4·7; carapace length 2·2, breadth 1·8, height 1·4; abdomen length 2·5; eyes, anterior row 1·5, middle row 1·2, posterior row 1·4; quadrangle length 1·1. *Ratios*: AM : AL : PM : PL :: 13 : 7 : 4 : 6, AL–PM–PL : 9–9·5, AM : CL :: 13 : 6.

VARIATION. Unknown.

BIOLOGY. Unknown.

DISTRIBUTION. Madagascar.

MATERIAL EXAMINED. Holotype ♂, MADAGASCAR, Mt Ambohisanga, i.1951 (*A. Pierrard*, MT 142917) (MRAC, Tervuren).

Species sola

Portia oreophila sp. n.

(Fig. 17A–D)

DIAGNOSIS. *P. oreophila* is a fairly distinctive species which can be distinguished from other *Portia* species by the white longitudinal bands on the carapace and abdomen (Fig. 17D), and the epigyne structure (Fig. 17B, C). It may belong in the *kenti*-group, but I am unable to comment further on its affinities until the male is discovered.

MALE. Unknown.

FEMALE HOLOTYPE. *Carapace* (Fig. 17A, D): yellow-orange with yellow guanin in eye region; clothed in short, recumbent yellow to orange hairs; from AM to just beyond fovea a central narrow white haired band, also from clypeus to coxae IV a broad submarginal band of short, recumbent white hairs, somewhat silky under some angles of illumination. *Eyes*: anterior row subcontiguous with apices recurved, fringed by light yellowish hairs. *Clypeus*: sparsely fringed with white laceolate hairs. *Chelicerae*: light yellow-orange, shiny; sparsely covered in fine, yellowish hairs; promargin with three teeth, retromargin with five. *Maxillae and labium*: light yellow. *Sternum*: scutiform; light yellow, shiny; thinly clothed in fine yellowish hairs. *Abdomen* (Fig. 17D): whitish yellow; clothed in orange hairs, with lateral longitudinal white haired bands; spinnerets light yellow. *Legs*: pale yellow-orange with vague light yellowish bands on tibiae I–II; tibiae I ventrally fringed by short orange hairs with a region of white hairs medially; femora I scantly fringed by short white hairs. Spines strong and numerous. *Palp*: creamy white with white hairs. *Epigyne* (Fig. 17B, C).

Dimensions (mm): total length 4·64; carapace length 2·32, breadth 1·9, height 1·44; eyes, anterior row 1·58, middle row 1·27, posterior row 1·44; quadrangle length 1·16. *Ratios*: AM : AL : PM : PL :: 13 : 7 : 4·8 : 7, AL–PM–PL : 8–9, AM : CL :: 13 : 5.

VARIATION. A ♀ from Antongil measures 5·0 mm total length, 2·4 mm carapace length.

BIOLOGY. Unknown.

DISTRIBUTION. Madagascar.

MATERIAL EXAMINED. Holotype ♀, MADAGASCAR: Mt Ambohisanga (*A. Pierrard*, MT. 142913) (MRAC, Tervuren). Paratype ♀, MADAGASCAR: Antongil (*A. Mocqueries*) (MNHN, Paris, No. 10257a).

Species Incertae Sedis

Portia deciliata Strand

Portia (*Boethus* ?) *deciliata* Strand, 1907 : 745, ♂. Madagascar, Nossi Bé. Strand, 1908*a* : 182. Roewer, 1954 : 933. Bonnet, 1958 : 3766.

The type of this species is believed to have been deposited in the Museum of Natural History, Lübeck, which was destroyed during the 1939–45 war. The species cannot be positively identified from the original description.

Linus nigrolineatus Strand

Linus nigrolineatus Strand, 1908 : 482, subadult ♂. LECTOTYPE ? subadult ♂ (here designated) Madagascar, St Marie de Marovoay, 21.ix.1906 (NR, Stockholm) [Examined]. Roewer, 1954 : 935. Bonnet, 1957 : 2483.

This species was originally described from an immature specimen, and adults cannot be positively recognized at the present time.

Linus subvexus Thorell

Linus subvexus Thorell, 1890 : 79, ♂. Indonesia, Nias Island. Simon, 1901 : 410. Reimoser, 1925 : 90; 1929 : 130. Roewer, 1954 : 936. Bonnet, 1957 : 2483.

I have been unable to examine the type of this species and the original description in inadequate for its certain identification. Material labelled *L. subvexus* in RNH, Leiden (vials 5424, 5425), NM, Wien (2 ♂♂, 2 ♀♀, det. Reimoser) and FS, Frankfurt am Main (vial 1120, det. Reimoser; det Roewer) are all *P. labiata* (Thorell).

Portia strandi Caporiacco

Portia strandi Caporiacco, 1941 : 136, fig. 58, ♂, subadult ♀. Ethiopia Caschei. Roewer, 1954 : 934.

The type of this species has not been examined, but the original description, which is accompanied by a good figure, suggests that *P. strandi* may be a synonym of *P. africana* (Simon).

Acknowledgements

I am grateful to Mr & Mrs John Murphy, London for allowing me to study their collection of African salticid spiders. Mrs Frances Murphy kindly supplied the photographs for Plates 1 and 2 and allowed me to include her previously unpublished observations on the behaviour of *P. schultzii* and *P. durbanii*.

I am also indebted to Dr W. S. Bristowe for his comments on *Portia* behaviour and for bringing my attention to Gravely's observations (1921).

Colleagues kindly made types and other material available for study: Professor P. L. G. Benoit, Musée Royal d'Afrique Centrale, Tervuren, Belgium (MRAC, Tervuren); Dr M. Grasshoff, Forschungsinstitut Senckenberg, Natur-Museum, Senckenberg, Frankfurt am Main, West Germany (FS, Frankfurt am Main); Dr J. Gruber, Naturhistorisches Museum, Wien, Austria (NM, Wien); Dr L. H. van der Hammen, Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands (RNH, Leiden); M M. Hubert, Muséum National d'Histoire Naturelle, Paris, France (MNHN, Paris); Professor T. Kronestedt, Naturhistoriska Riksmuseet, Stockholm, Sweden (NR, Stockholm); Mr B. Lamoral, Natal Museum, Pietermaritzburg, South Africa (NM, Pietermaritzburg); Professor H. W. Levi, Museum of Comparative Zoology, Harvard, U.S.A. (MCZ, Harvard); Dr A. de Barros Machado, Lisbon; Dr M. Moritz, Museum für Naturkunde der Humboldt-Universität, Berlin, East Germany (MNHU, Berlin); Dr N. Platnick, American Museum of Natural History, New York, U.S.A. (AMNH, New York); Dr R. Poggi, Museo Civico di Storia Naturale, Genoa, Italy (MCSN, Genoa); Mr M. W. R. de V. Graham, The University Museum, Oxford (UM, Oxford).

Finally, I would like to thank Mr D. Macfarlane (CIE, London) for reading the manuscript and for linguistic help.

References

Berland, L. & Millot, J. 1941. Les araignées de l'Afrique occidentale française. I. Les Salticides. *Mém. Mus. Hist. nat. Paris* n.s. **12** : 297–424.

Blumenthal, H. 1935. Untersuchungen über das (Tarsalorgan) der Spinnen. *Z. Morph. Okol. Tiere* **29** (5) : 667–719.

Bonnet, P. 1945–61. *Bibliographia Araneorum* 3 vols. Imprimerie Douladoure, Toulouse.

Bristowe, W. S. 1941. *The comity of spiders.* **2** : 229–560. Ray Society: London.

Caporiacco, L. di 1941. Arachnida. *Missione Biol. Sagan-Omo.* **12** Zool. 6 : 159 pp.

Chrysanthus, Fr. 1968. Spiders from South New Guinea X. *Tijdschr. Ent.* **111** (2) : 49–74.

Crane, J. 1949. Comparative biology of salticid spiders at Rancho Grande, Venezuela. Part IV. An analysis of display. *Zoologica N.Y.* **34** : 159–214.

Cutler, B. 1976. A catalogue of the jumping spiders of southern Africa (Araneae: Lyssomanidae and Salticidae) *Cimbebasia* (A) **4** : 129–135.

Doleschall, C. L. 1859. Tweede bijdrage tot de kennis de arachniden van den Indischen Archipel. *Verh. natuurk. Ver. Ned. Ind.* **5** : 60 pp.

Eberhard, W. G. 1974. Maternal behaviour in a South American *Lyssomanes. Bull. Br. arachnol. Soc.* **3** (2) : 51.

Forster, R. R. 1970. The spiders of New Zealand. Part 3. *Otago Mus. Bull.* **3** : 183 pp.

Galiano, M. E. 1976. Comentarios sobre la categoria sistematica del taxon Lyssomanidae (Araneae). *Revta Mus. argent. Cienc. nat. Bernardino Rivadavia Inst. nac. Invest. Cienc. nat.* **5** (3) : 59–70.

Gravely, F. H. 1921. The spiders and scorpions of Barkuda Island. *Rec. Indian Mus.* **22** : 399–459.

Hasselt, A. W. M. van 1877. Araneae exoticae, quas quondam in India Orientali (praesertim Insula Amboina) collegit Cel. Dr. C. L. Doleschall, ac, pro Museo Lugdunensi. *Tijdschr. Ent.* **20** : 17–18.

—— 1882. Aranea. In Veth, P. J., *Midden Sumatra*, Naturlijke Histoire. **IV** (11, A) Leiden, E. J. Brill.

Heer, O. 1862. Beitrage zur insektenfauna Oeningens. *Maatsch. Wet. Haarlem* (2) **16** : 31.

Hill, D. E. 1977. The tracheae of jumping spiders. *Peckhamia* **1** (2) : 26–30.

Hogg, H. R. 1915. On spiders of the family Salticidae collected by the British Ornithologists' Union expedition and the Wollaston expedition in Dutch New Guinea. *Proc. zool. Soc. Lond.* **20** : 501–528.

Karsch, F. 1878. Exotisch – araneologisches. *Z. ges. naturw. Halle* **51** : 323–333, 771–826.

—— 1891. Arachniden von Ceylon und von Minikoy gesammelt von den Herren Doctoren P. und F. Sarasin. *Berl. ent. Z.* **36** (2) : 267–310.

Lamy, E. 1902. Recherches anatomiques sur les trachées des araignées. *Annls Sci. nat.* **8** : 149–280.

Lawrence, R. F. 1937. A collection of Arachnida from Zululand. *Ann. Natal Mus.* **8** (2) : 211–273.

—— 1938. A collection of spiders from Natal and Zululand. *Ann. Natal Mus.* **8** (3) : 455–524.

—— 1947. A collection of Arachnida made by Dr. I Trägårdh in Natal and Zululand (1904–1905). *Göteborgs K. Vetensk.-O. vitterhSamh. Handl.* Ser. B **5** (9) : 3–41.

Lessert, R. de 1925. Araignées du Sud de l'Afrique. *Revue suisse Zool.* **32** (21) : 323–365.

—— 1927. Araignées du Congo. Part 1. *Revue suisse Zool.* **34** (17) : 405–475.

Peckham, G. W. & Peckham, E. G. 1885. Genera of the family Attidae: with a partial synonymy. *Trans. Wis. Acad. Sci. Arts Lett.* **6** : 255–342.

—— 1903. New species of the family Attidae from South Africa, with notes on the distribution of the genera found in the Ethiopian region. *Trans. Wis. Acad. Sci. Arts Lett.* **14** : 173–278.

—— 1907. The Attidae of Borneo. *Trans. Wis. Acad. Sci. Arts Lett.* **15** : 603–653.

Petrunkevitch, A. 1928. Systema Aranearum. *Trans. Conn. Acad. Arts Sci.* **29** : 270 pp.

Platnick, N. 1971. The evolution of courtship behaviour in spiders. *Bull. Br. arachnol. Soc.* **2** (3) : 40–47.

Pocock, R. I. 1899. *Scorpions, Pedipalpi and spiders collected by Dr Willey in New Britain, The Solomon Islands, Loyalty Islands, etc. Willey's Zoological Results based on material from New Britain, New Guinea, Loyalty Islands, and elsewhere collected during the years* **1895, 1896** *and* **1897**. Part 1. Cambridge, pp. 95–120.

Proszynski, J. 1971. Catalogue of Salticidae (Aranei) specimens kept in major collections of the world. *Annls zool. Warsz.* **28** : 367–519.

Rainbow, W. J. 1911. A census of Australian Araneidae. *Rec. Aust. Mus.* **9** : 107–319.

—— 1913. Arachnida from the Solomon Islands. *Rec. Aust. Mus.* **10** : 16 pp.

Reimoser, E. 1925. Fauna sumatrensis. *Supplta ent.* **11** : 89–94.

—— 1929. Spolia Mentawiensia Araneae. *Bull. Raffles Mus.* **2** : 125–133.

Roewer, C. F. 1954. *Katalog der Araneae.* **2**, Abt. B : 924–1290. Institut Royal des Sciences Naturelle de Belgique, Bruxelles.

—— 1965. Die Lyssomanidae und Salticidae – Pluridentati der Äthiopischen Region (Araneae). *Annls Mus. r. Afr. cent.* No. **139** – 86 pp.

Sherriffs, W. R. 1931. South Indian Arachnology. Part 5. *Ann. Mag. nat. Hist.* (10) **7** : 537–546.

—— 1939. Hong Kong spiders. Part 5. *Hong Kong Nat.* **9** (3) : 133–140.

Simon, E. 1886. Études Arachnologiques 18e Mémoire (1) XXVI Matériaux pour servir à la fauna des arachnides du Sénégal. *Annls Soc. ent. Fr.* (6) **5** : 345–396.

—— 1900. Études Arachnologiques 30e Mémoire (1) XLVII Descriptions d'espèces nouvelles de la famille des Attidae. *Annls Soc. ent. Fr.* **69** : 27–61.

—— 1900*a*. Descriptions d'arachnides nouveaux de la famille des Attidae. *Annls Soc. ent. Belg.* **44** : 381–407.

—— 1901. *Histoire Naturelle des Araignées,* **2** (3) : 381–668. Roret, Paris: Libraire Encyclopédique.

—— 1901*a*. On the Arachnida collected during the (Skeat Expedition) to the Malay Peninsula. *Proc. zool. Soc. Lond.* (2) : 45–84.

—— 1903. *Histoire Naturelle des Araignées,* **2** (4) : 669–1080. Roret, Paris: Libraire Encyclopédique.

Strand, E. 1907. Diagnosen neuer spinnen aus Madagascar und Sansibar. *Zool. Anz.* **31** (23) : 725–748.

—— 1908. Arachniden aus Madagaskar, gesammelt von Herrn Walter Kandern. *Zool. Jb.* **26** : 453–488.

—— 1908*a*. Beitrage zur spinnenfauna Madagaskars. *Nyt Mag. Naturvid* 46 : 227 pp.

—— 1909. Sud-und ostasiatische spinnen 11. Fam. Clubionidae. Fam. Salticidae. *Abh. naturforsch. Ges. Gorlitz* **26** : 128 pp.

—— 1911. Araneae von den Aru- und Kei-Insen. *Abh. senckenb. naturforsch. Ges.* **34** : 129–199.

—— 1929. Zoological and palaeontological nomenclatorial notes. *Latav. Augstsk. Rak.* **20** (29) : 29 pp.

Thorell, T. 1878. Studi sui ragni Malesi e Papuani Part 2. Ragni di Amboina raccolti da Prof. O. Beccari. *Mus. civ. Stor. nat. Giacomo Doria* **13** : 317 pp.

—— 1881. Studi sui ragni Malesi e Papuani. Part 3. Ragni dell' Austro-Malesia e del Capo York, conservati nel Museo Civico di Storia Naturale di Genova. *Mus. civ. Stor. nat. Giacomo Doria* **17** : 720 pp.

—— 1887. Viaggio di L. Fea in Birmania e regioni vicine. 2 Primo saggio sui ragni Birmani. *Mus. civ. Stor. nat. Giacomo Doria* (2) **5** : 417 pp.

—— 1890. Studi sui ragni Malesi e Papuani (4) 1. *Mus. civ. Stor. nat. Giacomo Doria* (2) **8** : 419 pp.

—— 1892. Studi sui ragni Malesi e Papuani (4) 2. *Mus. civ. Stor. nat. Giacomo Doria* **31** : 490 pp.

—— 1895. *Descriptive catalogue of the spiders of Burma.* British Museum (Natural History). 406 pp.

—— 1899. Araneae Camerunenses (Africae occidentalis) quas anno 1891 collegerunt Cel. Dr Y Sjöstedt aliique. *Bih. K. svenska VetenskAkad. Handl.* **25** (4) 1 : 105.

Wanless, F. R. 1978. A revision of the spider genera *Belippo* and *Myrmarachne* (Araneae: Salticidae) in the Ethiopian region. *Bull. Br. Mus. nat. Hist.* (Zool.) 33 (1) : 1–139.

—— 1978*a*. A revision of the spider genus *Marengo* (Araneae: Salticidae) *Bull. Br. Mus. nat. Hist.* (Zool.) 33 (4): 231-296.

Warren, E. 1928. The comparative histology of the testis and the origin of the spermatozoa in certain South African spiders. *Ann. Natal Mus.* **6** (1) : 88 pp.

Plate 1 *Portia schultzii*, ♂. Note slender metatarsi and leg fringes characteristic of the genus.

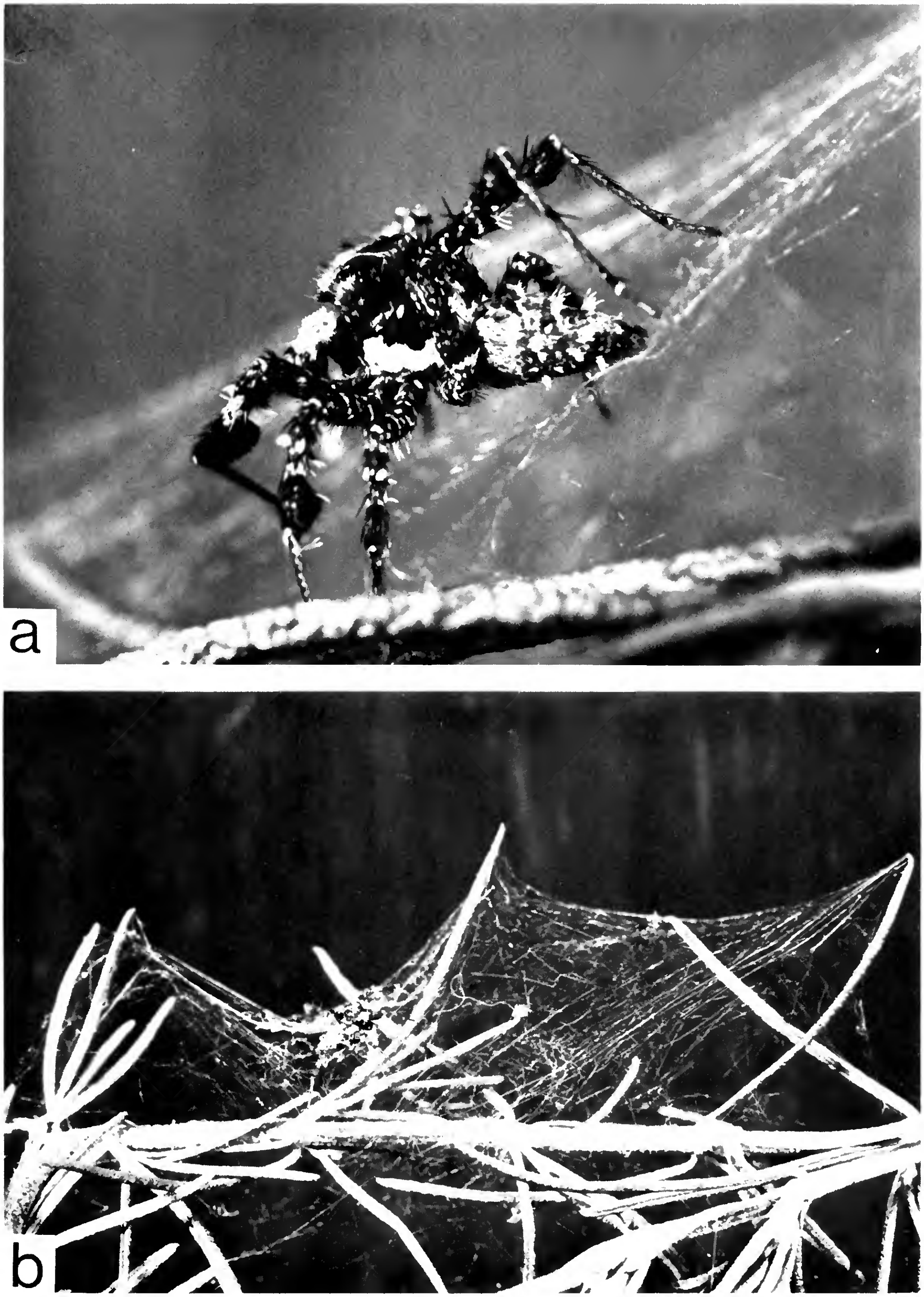

Plate 2 (a, b) *Portia schultzii*, male on female's web.

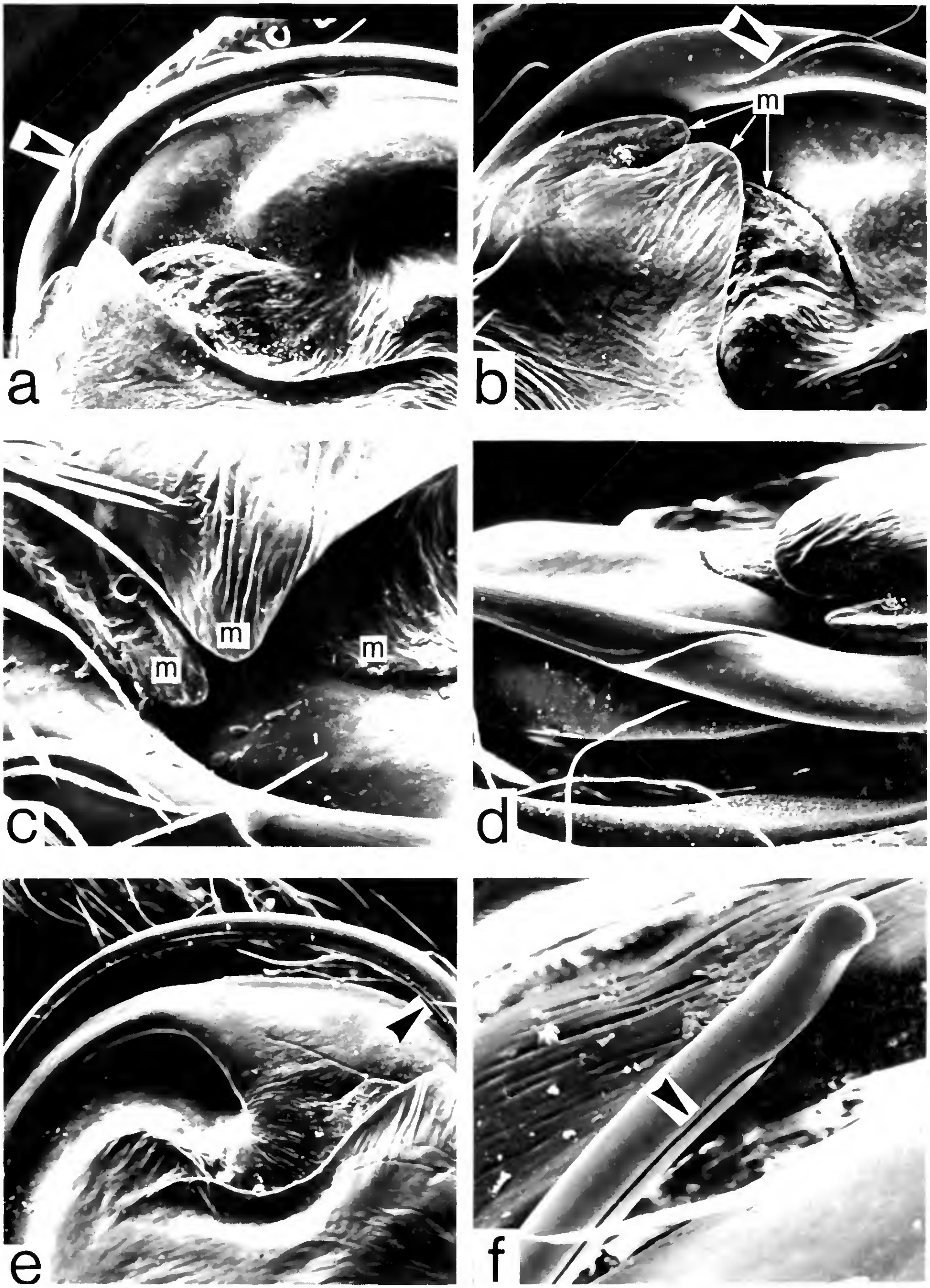

Plate 3 *Portia fimbriata* palp structure. (a, b) tripartite membrane and poorly developed conductor. × 200. (c) tripartite membrane in front view. × 500. (d) conductor in lateral view. × 200. (e) tegular furrow and embolic groove. × 200. (f) embolus tip, showing groove. × 2000.

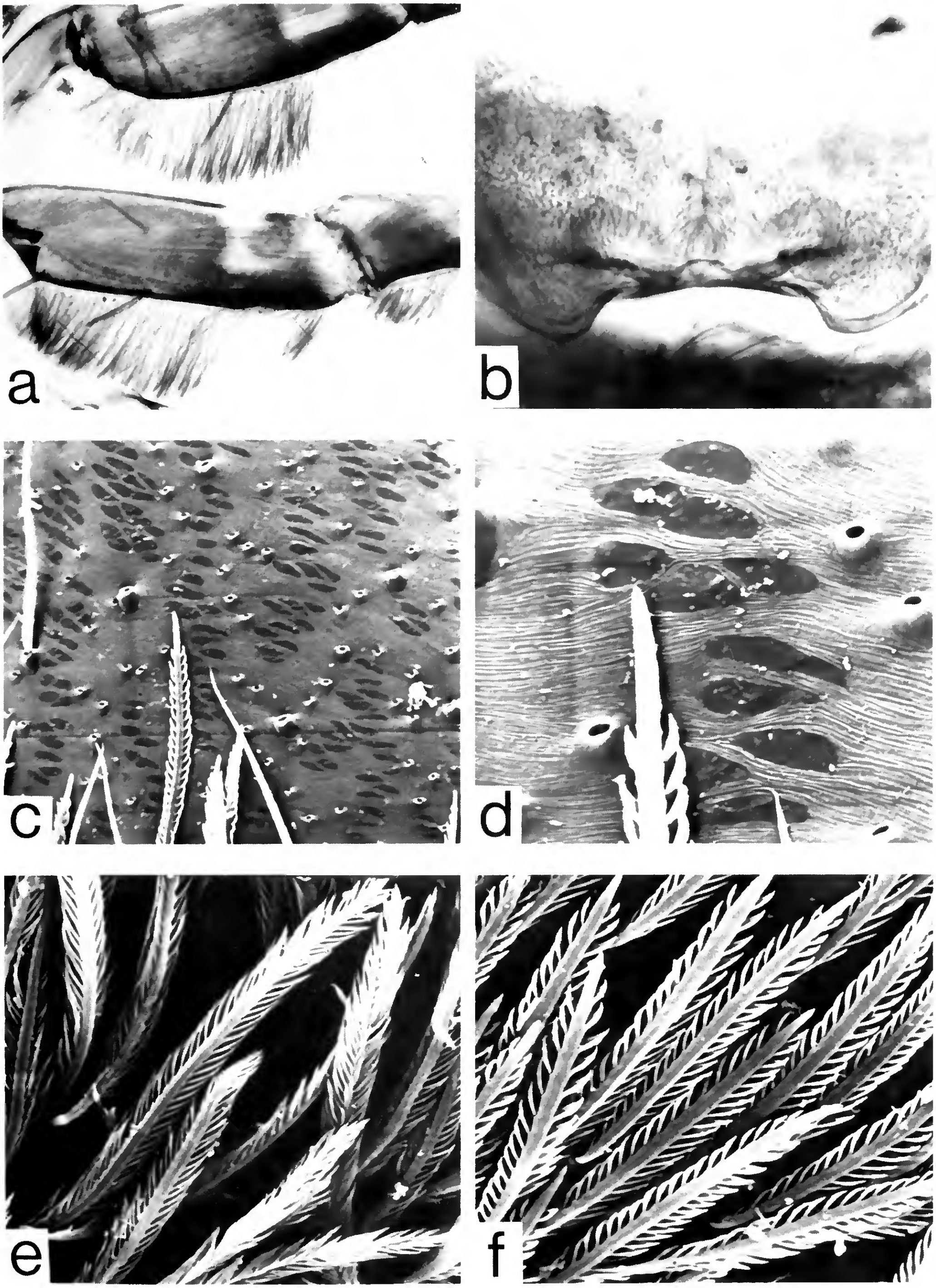

Plate 4 (a, b) *Portia schultzii*, holotype ♀. (a) legs, showing interrupted fringes; (b) vulva, dorsal view, ? subadult. (c–f) *Portia fimbriata*, ♀. (c, d) thoracic region below fovea, showing cuticle structure (striate with smooth spots) considered to be responsible for the weak iridescent sheen of many species. × 500, × 2000; (e) refractile white setae from thoracic marginal band. × 1000; (f) setae below and between PM and PL. × 1000.

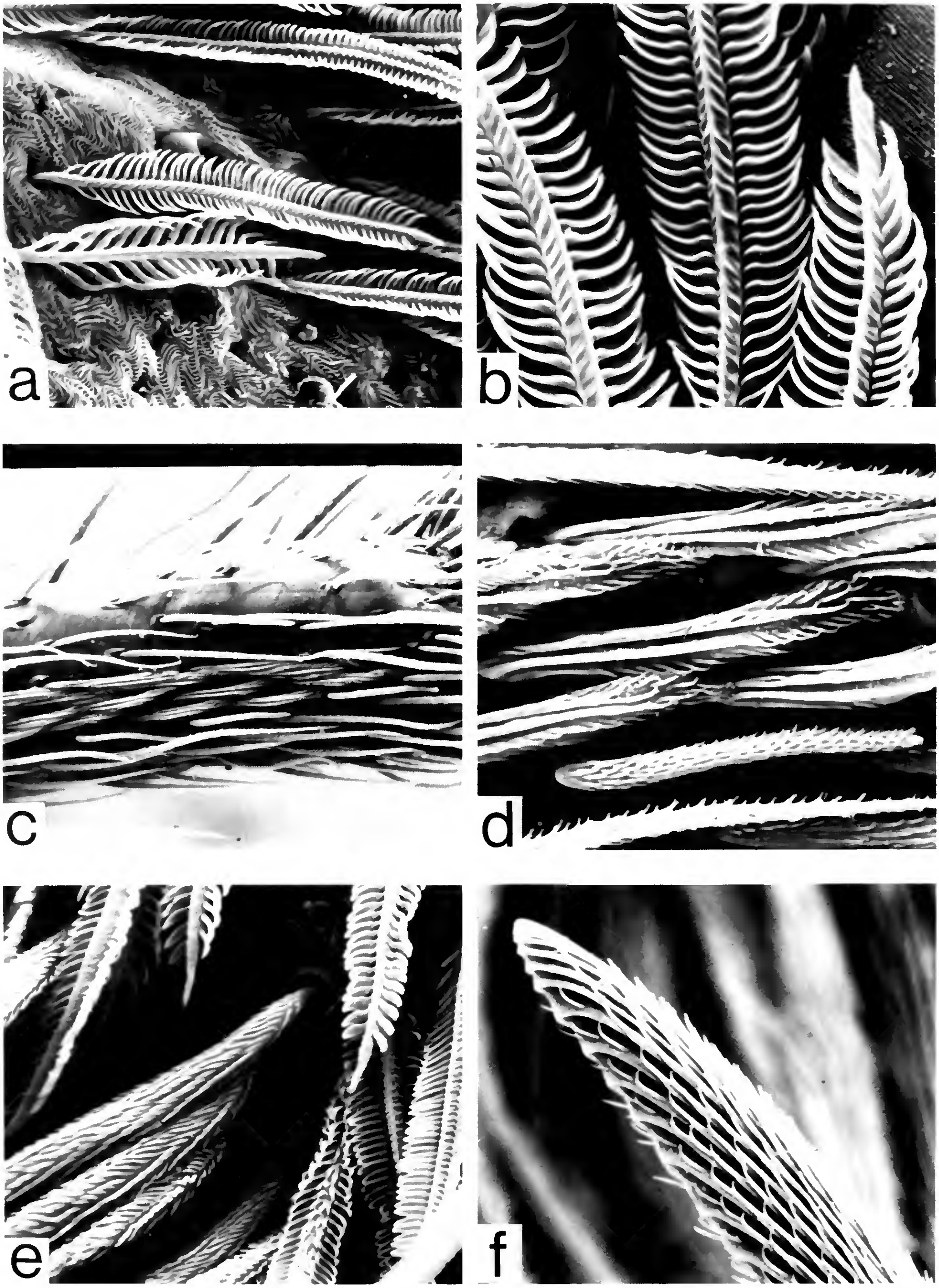

Plate 5 Examples of setae from several species of *Portia*. (a) *P. crassipalpis*, ♀ abdomen. × 1000. (b) *P. africana*, between PL. × 2000. (c, d) *P. fimbriata*, ♀ tarsi I, showing row of specialized setae. × 500, × 2000. (e) *P. crassipalpis*, base of abdominal hair tuft. × 1000. (f) *P. fimbriata*, tip of metatarsal spine, × 2000.

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**Bulletin of the
British Museum (Natural History)**

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Zoology series Vol 34 No 4 22 February 1979

The *Bulletin of the British Museum (Natural History)*, instituted in 1949, is issued in four scientific series, Botany, Entomology, Geology (incorporating Mineralogy) and Zoology, and an Historical series.

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

ISBN 0007–1498

British Museum (Natural History)
Cromwell Road
London SW7 5BD

Zoology series
Vol 34 No 4 pp 125–180

Issued 22 February 1979

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British Museum (Natural History), Tring, Hertfordshire HP23 6AP

Contents

Introduction

The major bird collections of the world were founded in an era when the merits of collecting were unquestioned, and the pressure of human activities on wildlife had not yet aroused widespread concern. Today, the picture is very different and, quite rightly, many countries now exercise strict control on collecting. Nevertheless, there is a continued need to collect birds on a more limited scale, and the reasons for this, and many of the issues involved, have recently been reviewed by a committee of the American Ornithologists' Union (A.O.U., 1975). In no area is this need more clearly seen than in that of anatomical specimens. Such collections – of pickled birds, or of skeletons – have lagged far behind those of bird skins. For example, those of the British Museum (Natural History) listed in this paper, though large by comparison with other institutions, form less than 2% of the whole (skins plus anatomical) in number of specimens, and are much less complete in their representation of genera and species. Although bird skins are the most practicable and convenient type of specimen for many studies, such a great disparity is quite unjustifiable, and in many cases little short of tragic. There are a variety of reasons why this situation has arisen. Skeletons are more troublesome to prepare than skins, while pickled birds are heavy and difficult to transport. Moreover, skin specimens were more suited to the interests of the numerous private individuals whose specimens form the basis of many museum collections. This factor, incidentally, has also adversely affected the skin collections themselves, since immature and moulting stages are often badly represented, presumably because they were of less interest to private collectors.

Whatever the causes, the relative paucity of anatomical specimens of birds is a matter for regret, and at present hinders much potential research, not only on systematics, but also in such fields as biomechanics and ecology. A fundamental step in redressing the balance is to take stock of the collections available at present. The only published information of this kind so far available is the list of avian anatomical specimens in the Peabody Museum, Yale University, by Ames and Stickney (1968). The present paper provides similar details for the collections of the British Museum (Natural History).

History of the collections

A detailed history covering both skins and anatomical specimens during the 19th century is given by Sharpe (1906). The skeleton collection is on the whole older than the spirit collection, although two birds in spirit probably collected on Cook's third voyage (Burton, 1969) are perhaps the oldest bird specimens in the Museum. Among the older specimens are included a series of

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skeletons of domestic breeds of duck, fowl and pigeon presented by Charles Darwin. Several extinct species are represented. The spirit collection apparently remained very limited until 1874, in which year 354 spirit specimens were registered. The growth of these collections subsequently has reflected the interests of successive members of staff. In the past two decades, their growth has accelerated considerably under the guidance of G. S. Cowles and P. J. K. Burton. This acceleration has been brought about partly by exploiting potential sources of dead birds such as zoos, lighthouses and animal welfare organizations, and also by active collecting in various parts of the world. In recent years a particularly important contribution has been that made by the Harold Hall Australian Expeditions, 1962–70 (Hall, 1974). The collection now includes about 13 000 spirit and 8000 skeleton specimens.

Curation and management

All specimens are given British Museum (Natural History) Registration Numbers, even though it is recognized that repeated dissection could, in theory, virtually destroy some spirit specimens – an event which has yet to happen in practice. In the case of skeletons, this number is written on various parts of the specimen, to reduce the risk of muddling components when several are examined together. Spirit specimens are preserved in 80% ethyl alcohol with the exception of a few very large species which are kept in 1% phenoxetol. Those collected recently are fixed in the field with 10% formaline solution, followed where possible by an injection of glycerine as recommended by Harrison and Cowles (1970). Older specimens were often preserved in alcohol at the time of collection, and some are more fragile than recent specimens. However, all are usable for the majority of purposes, and good histological preparations have been obtained even from eighty-year-old specimens. Most skeletons are now prepared by using beetles (*Dermestes maculatus*), though older specimens were prepared by hand after boiling or enzyme treatment.

Although it is hoped that investigators will be able to visit the Museum if possible to carry out their research, loans are made available throughout the world to competent research workers or postgraduate students under supervision. It is usual for copies of theses or publications resulting from the use of the collections to be deposited with the Sub-department of Ornithology, British Museum (Natural History). Where study involves dissection of specimens, it is a condition of loans that either such publications or at least a full record, in the form of notes and drawings, should be so deposited. Requests for loans should initially be addressed to Dr P. J. K. Burton, explaining the proposed research in some detail.

Representation

Of the 9016 bird species recognized by Morony, Bock and Farrand (1975), 3654 (41%) are represented in the anatomical collections. At the generic level, 1266 genera out of 2065 are represented (61%). One family (Atrichornithidae) is completely unrepresented by either skeleton or spirit specimens. Representation is generally much better for non-passerines (47% of species and 75% of genera represented) than for passerines (35% of species and 49% of genera). In general, the skeleton collection is the richer in large species, and the spirit collection in small ones. This has undoubtedly arisen from the practical difficulties of transporting large birds in fluid from remote parts of the world; nevertheless, the collecting policy now in operation should in time eliminate this imbalance.

Geographic coverage is wide and reasonably even; not surprisingly, the Western Palaearctic is best represented. The most poorly represented region is the southern half of South America.

Expansion policy

It is hoped that this list will be consulted by individuals or institutions contemplating any programme of field collecting; in this way, unnecessary collecting can be avoided, and effort can be concentrated on areas of genuine weakness. Hopefully, also, other museums holding similar collections may be able to produce lists of this kind* and thus improve coordination still further.

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*Note added in proof: an inventory of anatomical specimens is now available from the American Museum of Natural History.

All programmes of collecting must be prepared in consultation with the conservation authorities in the countries concerned. It has to be recognized that the collection of some rare species is quite out of the question, and for many others, the decision would require much heart searching. However, many quite scarce species are kept alive in zoos or private aviaries. Except in the few cases of captive breeding to restock wild populations, such individuals are just as severe a loss to their species as dead specimens would be. If their capture is to be fully justified, it is essential that they should be carefully studied while alive, and preserved for further research when they eventually die. This situation particularly affects birds of prey; a good example is the Harpy Eagle, *Harpia harpyja*, missing from this spirit collection and probably most others. Its large size and extreme raptorial adaptations make it an attractive subject for anatomical study, and it is to be hoped that the few examples of this species which exist in various aviaries throughout the world will be preserved in fluid when they die. Improved liaison between museums, zoos and private aviaries is essential to avoid the sad wastage which has occurred in the past, and we hope that this paper may in some measure help to bring this about. The same remarks apply to all whose activities may from time to time bring them into contact with potentially valuable specimens, from bird banders to conservation officials.

Systematic list

We have followed the classification and nomenclature of Morony, Bock and Farrand (1975) throughout. Only species represented in the anatomical collections in some form are listed; those which are entirely missing can be found by comparing our list with that of Morony *et al.* A numerical summary of representation is given for each family or subfamily.

Key to symbols

Spirit
A = complete spirit specimen
A^k = head only in spirit
a = skinned carcass
$A^\dagger$ = incomplete spirit specimen
E = eviscerated spirit specimen
A* = chick, embryo or juvenile in spirit

Skeleton
S = complete skeleton
K = skull only
$S^\dagger$ = incomplete skeleton
S* = chick or juvenile skeleton

STRUTHIONIFORMES
STRUTHIONIDAE

1 genus, 1 species

	Spirit	Skels
Struthio		
camelus	A,K	13S,4K,8S†

RHEIFORMES
RHEIDAE

2 genera. 2 species
1 genus & 1 species unrepresented

Rhea		
americana	12A†,7A, 13A*	6S,12S†,7K

CASUARIIFORMES
CASUARIIDAE

1 genus, 3 species

Casuarius		
casuarius	4†	S,10S†,3K
bennetti		4S†,2K
unappendiculatus	2†	K,2S†

DROMAIIDAE

1 genus, 2 species
1 species, unrepresented

Dromaius		
novaehollandiae	2†,5A,3*	S,7S†,11K

APTERYGIFORMES
APTERYGIDAE

1 genus, 3 species

Apteryx		
australis	A*,A†,2A	6S,7S†
owenii	A	3S,S†
haastii		2S,5S†

TINAMIFORMES
TINAMIDAE

9 genera, 47 species
3 genera & 35 species unrepresented

Tinamus		
tao	A	
major	A^k	
Crypturellus		
cinereus	A	
obsoletus		S
undulatus	A	5S
noctivagus	A	
tataupa	2A,2A†	
Rhynchotus		
rufescens	4A,3A*	4S,5S†
Nothoprocta		
perdicaria	2A	S
cinerascens	2A	
pentlandii	A	
Nothura		
maculosa	4A,2A*	9S,S†
Eudromia		
elegans	2A,A*	2S

SPHENISCIFORMES
SPHENISCIDAE

6 genera, 18 species
2 species unrepresented

	Spirit	Skels
Aptenodytes		
patagonica	a	4S,2K,3S†
forsteri	6A*	3S†,2S
Pygoscelis		
papua	2A,12A*	5S,S†,5K
adeliae	17A*	9S,2S†,K
antarctica		2S,K
Eudyptes		
pachyrhynchus		S
sclateri		S
crestatus	10A*,6A	8S,3S†,2K
chrysolophus	A	S†
Megadyptes		
antipodes		K
Eudyptula		
minor		3S
albosignata		S
Speniscus		
demersus	A,A^k	3S,K,S†
humboldti		S,S†
magellanicus		4S,S†
mendiculus		S,2K

GAVIIFORMES
GAVIIDAE

1 genus, 5 species
1 species unrepresented

Gavia		
stellata	A^k,3A	10S,2K,3S†
arctica		S,2S†
immer	A	6S,5K,S†
adamsii		K,S†

PODICIPEDIFORMES
PODICIPEDIDAE

5 genera, 19 species
8 species unrepresented

Tribe **PODILYMBINI**

Tachybaptus		
ruficollis	14A*,5A	12S,3S†
novaehollandiae	3A	
pelzelni	A	2S
Podilymbus		
podiceps	5A*,A	2S
Rollandia		
rolland		S,S†
micropterum	A,A*	

Tribe **PODICIPEDINI**

Podiceps		
major		S
dominicus	3A	
cristatus	4A	7S,4K,2S†
auritus	A*,3A	7S

PODICIPEDINI (cont.)

Podiceps (cont.)	Spirit	Skels
nigricollis	2A	
occipitalis		S,S†
Aechmophorus		
occidentalis		S

PROCELLARIIFORMES
DIOMEDEIDAE

2 genera, 13 species
1 species unrepresented

	Spirit	Skels
Diomedea		
exulans	A^k,2A	7S,10K,3S†
epomophora		S,K
irrorata		4S,2K
albatrus		S,2K
nigripes		S,K
immutabilis		S
melanophris	2A*	2S,6K,S†
cauta		S,K
chlororhynchos	A	3K
chrysostoma		S
Phoebetria		
fusca		4K
palpebrata	A	3S

PROCELLARIIDAE

12 genera, 66 species
27 species unrepresented

	Spirit	Skels
Macronectes		
giganteus	3A*,3A	6S,7K,S†
Fulmarus		
glacialis	5A,4A*	9S,K,10S†
Thalassoica		
antarctica	6A	2S,2K,S†
Daption		
capense	2A	4S,K,S†
Pagodroma		
nivea	3A	3S
Pterodroma		
macroptera		10S
lessoni		4S,3K,S†
cahow		S†
inexpectata		12S,K
solandri		S
brevirostris		S
neglecta		S
magentae		2K
arminjoniana	A	S
mollis	4A	S
phaeopygia		2S,K
externa		S
cooki		K
Halobaena		
caerulea		4S
Pachyptila		
vittata	3A	S,12K,4S†
salvini		5S
desolata	13A	12S,10K
belcheri	9A,2A*	7S,3K
turtur	A	8S,S†
Bulweria		
bulwerii	3A	2S,K,4S†
*fallax**	A,4A	
Procellaria		
cinerea		S,K,S†
aequinoctialis	2A	4S
Calonectris		
diomedea	3A	6S,K
Puffinus		
carneipes	2A,A*	S,S†,K
gravis		S,K
pacificus	2A*,A	2S,2K
bulleri		S
griseus	2A	6S,3S†,2K
tenuirostris		5S,K,2S†
puffinus	5A*	7S,2S†
gavia		2S
assimilis	A	6S,S†
lherminieri	2A	S†

HYDROBATIDAE

8 genera, 21 species
2 genera & 10 species unrepresented

	Spirit	Skels
Oceanites		
oceanicus	A*,28A	2S
Garrodia		
nereis	20A	
Pelagodroma		
marina	3A*,9A	3S,3S†
Fregetta		
tropica		2S
Hydrobates		
pelagicus	5A	6S
Oceanodroma		
tethys	A	3S
castro	A	4S,2K,S†
leucorhoa	A	15S,K
hornbyi		S
melania	2A	

PELECANOIDIDAE

One genus, 4 species
One species unrepresented

	Spirit	Skels
Pelecanoides		
magellani	2A	
georgicus	7A	
urinatrix	3A*,17A	6S,2K,2S†

PELECANIFORMES
PHAETHONTIDAE

1 genus, 3 species

	Spirit	Skels
Phaethon		
aethereus	8A	6S
rubricauda	A*	S†
lepturus	A*,8A	5S,2S†,K

PELECANIDAE

1 genus, 8 species

	Spirit	Skels
Pelecanus		
onocrotalus	a	5S
roseus		S
rufescens		K
philippensis		S,2S†,K
crispus		S
conspicillatus		2S,K
erythrorhynchos		S,2K
occidentalis	3A	4S,2K

SULIDAE

2 genera, 9 species
2 species unrepresented

	Spirit	Skels
Morus		
bassanus	5A*,4A	10S,6S†,K
Sula		
nebouxii		2K
variegata		S
abbotti		K
dactylatra	A	3S,S†
sula	2A*,5A	8S,K S†
leucogaster	2A^k,2A*,7A	S,2K

PHALACROCORACIDAE

3 genera, 33 species
14 species unrepresented

	Spirit	Skels
Phalacrocorax		
auritus		3S
olivaceus		S,K,S†
sulcirostris	3A	3S
carbo	3A,a	12S,7K,4S†
nigrogularis		4S,4K
aristotelis	3A*,3A	16S,4K,5S†
urile		S
magellanicus	A^k,2A*	
bougainvillii		S
varius	A^k	
carunculatus	2A*	3S†
verrucosus	A,A^k	
atriceps		S,S†,4K
albiventer	A	2S
Halietor		
melanoleucos	3A	S,2K
africanus	4A*	S,2K
niger		S
pygmeus	A	
Nannopterum		
harrisi	2a,4A	2S,S†,4K

ANHINGIDAE

1 genus, 4 species
1 species unrepresented

	Spirit	Skels
Anhinga		
rufa	3A*	S†
melanogaster		2S,K
anhinga	7A*,7A	S

FREGATIDAE

1 genus, 5 species
1 species, unrepresented

	Spirit	Skels
Fregata		
aquila	A*,2A^k,9A	3S,K
magnificens	3A	S
minor	A	2K
ariel		S

CICONIIFORMES

ARDEIDAE

16 genera, 64 species
30 species unrepresented

	Spirit	Skels
BOTAURINAE		
Botaurus		
stellaris	5A	4S,K,S†
poiciloptilus	2A	
Ixobrychus		
exilis		K
minutus	3A	3S,K
sinensis	A	
flavicollis	2A	
ARDEINAE		
Tribe **TIGRIORNITHINI**		
Tigrisoma		
lineatum	A^k,3A	S
Tribe **BYCTICORACINI**		
Gorsachius		
melanolophus		2K
Nycticorax		
nycticorax		8S,4K
caledonicus	3A	K
pileatus		2S†
violaceus	6A	3S,S†
Tribe **COCHLEARIINI**		
Cochlearius		
cochlearius	A*,A	S,2K,S†
Tribe **ARDEINI**		
Ardeola		
ralloides	A	S
grayii		3S
rufiventris	A	
ibis	3A*,A	2S,K,2S†
Butorides		
virescens		S,S†
striatus	10A	2S
Hydranassa		
caerulea	2A	3S
tricolor	2A*,4A	S
Egretta		
sacra	3A	2S
gularis	2A*	
garzetta	2A*	2S
intermedia	2A	
alba	A	3S,3K
Ardea		
purpurea		6S,K

ARDEINI (cont.)

Ardea (cont.)	Spirit	Skels
novaehollandiae	3A	2K,3S
pacifica	2A	
cinerea	11A*,4A	13S
cocoi		2S
melanocephala	A	S
goliath		4S
imperialis		S†

BALAENICIPITIDAE

1 genus, 1 species

Balaeniceps		
rex	A	3S,3K

SCOPIDAE

1 genus, 1 species

Scopus		
umbretta	A*,3A	3S,K

CICONIIDAE

6 genera, 17 species

2 species unrepresented

Tribe **MYCTERIINI**

Mycteria		
ibis		3K
leucocephala	2A	3S,S†
Anastomus		
oscitans	2A	2S,3K
lamelligerus		2S

Tribe **CICONIINI**

Ciconia		
nigra		2S,K
abdimii	5A*,2A	S
episcopus		3S,K
maguari		2S
ciconia	A*,A	4S,K

Tribe **LEPTOPTILINI**

Ephippiorhynchus		
asiaticus	A	4S
senegalensis		S,3K
Jabiru		
mycteria		4S
Leptoptilos		
javanicus	A	2S,K,S†
dubius		4S,3K
crumeniferus		3S,4K

THRESKIORNITHIDAE

20 genera, 33 species

8 genera & 16 species unrepresented

THRESKIORNITHINAE

	Spirit	Skels
Threskiornis		
aethiopica	2A	5S,4K
melanocephala	5A	3S,K
molucca	5A	
Carphibis		
spinicollis	A*	
Pseudibis		
papillosa		S†
Geronticus		
calvus		S
Hagedashia		
hagedash	A	S
Harpiprion		
caerulescens	2A^{k}	K
Theristicus		
caudatus	A^{k},A	2S
melanopis	A	
Eudocimus		
albus		2S
ruber	A*,5A	2S,S†
Plegadis		
falcinellus	2A	5S,S
Lophotibis		
cristata	A	S

PLATALEINAE

Platalea		
leucorodia	A*,A	4S,4K,S†
regia	3A	
Ajaia		
ajaja		2S,S†,K

PHOENICOPTERIDAE

3 genera, 6 species

1 species unrepresented

Phoenicopterus		
ruber	2A,A*	7S,S†,2K
chilensis	A	2S,K
Phoeniconaias		
minor	A,A^{k}	S,2K
Phoenicoparrus		
andinus	A	
jamesi	4A^{k},4A	S

ANSERIFORMES

ANHIMIDAE

2 genera, 3 species

1 genera & 1 species unrepresented

Chauna		
torquata	3A	3S,S†
chavaria	A*,A^{k},2A	S,3S†

ANATIDAE

43 genera, 146 species

24 species unrepresented

ANSERANATINAE

Anseranas		
semipalmata		4S

ANSERINAE

Tribe **DENDROCYGNINI**

Dendrocygna		
eytoni	A	
bicolor	2A*	2S
arcuata		S
javanica		2K
viduata	A*,A	2S,K
arborea		S
autumnalis	2A	S

ANSERINAE(cont.)

Tribe ANSERINI	Spirit	Skels
Cygnus		
(*Cygnus*)		
olor	3A*,2A	9S,S†,4K
atratus	A†	2S
melanocoryphus	A^{k}	4S
(*Olor*)		
cygnus	A	4S,7S†,2K
columbianus	A^{k}	5S,S†
Coscoroba		
coscoroba	A	S
Anser		
cygnoides	A	2S,5K
fabalis		5S,K,S†
albifrons	2A	6S,S†,2K
anser	A^{k}	4S,9K,S†
indicus		S
caerulescens	3A*	K
rossi		S
canagicus	A	
brachyrhynchus	2A	
hyperboreus	K	
Branta		
(*Nesochen*)		
sandvicensis		2S
(*Branta*)		
canadensis	A	3S
leucopsis	A	7S,2S†
bernicla	a,5A	6S,2K,S†
ruficollis	3A	2S
Cereopsis		
novaehollandiae	5A*	5S,S†
Tribe STICTONETTINI		
Stictonetta		
naevosa	A	2S
ANATINAE		
Tribe TADORNINI		
Cyanochen		
cyanopterus	A*	2S,K
Chloephaga		
melanoptera		S
picta	A†,A	4S,32K
hybrida	A	S
poliocephala	A^{k},A	2S
rubidiceps	A	S
Neochen		
jubatus	A	S
Alopochen		
aegyptiacus	A*,A	2S,2K,S†
Tadorna		
(*Casarca*)		
ferruginea	A*	7S,S†
cana	A*,2A	S
tadornoides		5S
(*Tadorna*)		
tadorna	2A*,2A	4S
radjah	9A	S

	Spirit	Skels
Tribe TACHYERINI		
Tachyeres		
patachonicus	6A*	2S
brachypterus		S
Tribe CAIRININI		
Plectropterus		
gambensis		5S
Cairina		
moschata		S,2K
scutulata		S
Sarkidiornis		
melanotos	A,2A	3S
Pteronetta		
nartlaubi		K
Nettapus		
pulchellus	7A	
coromandelianus	A	S,2K,S†
auritus	2A	S
Aix		
sponsa	3A*,2A	4S,K
galericulata	a,A*,3A	3S
Chenonetta		
jubata	2A	3S
Amazonetta		
brasiliensis	2A*,A	
Tribe ANATINI		
Hymenolaimus		
malacorhynchus	A	2S
Merganetta		
armata	2A	S
Anas		
(*Anas*)		
penelope	3A^{k},A	6S,3K
americana		S
sibilatrix	3A	2S,2K
falcata	A	
strepera	A	5S,K
formosa		S
spinicauda		S,S†
wyvilliana		S
superciliosa	A	2S
crecca	A*,4A	8S,2K,S†
flavirostris	A*,A	3K
capensis	A	
gibberifrons	A	S
castanea		2S
aucklandica	2A	
platyrhynchos	4A*,5A	15S,18K,3S†
rubripes		3S
melleri		S
poecilorhyncha		S,K
luzonica	A	S
specularis	2A	S,S†
specularioides	2A	K
acuta	6A*,A†,A	2S
georgica	2A	S
bahamensis		S,S†
erythrorhyncha	A†	3S

ANATINI (cont.)

Anas (cont.)	Spirit	Skels
versicolor	2A	S,K
querquedula	A*,2A	S,2K
discors	4A	
cyanoptera	a,2A	S
clypeata	A*,A	8S,K
Malacorhynchus		
membranaceus	3A^{k},A	2S
Marmaronetta		
angustirostris		2S,2K

Tribe AYTHYINI

Rhodonessa		
caryophyllacea	3A	S,S†
Netta		
rufina	A*	S†,S
erythrophthalma	6A*	
peposaca	A	
Aythya		
valisineria		S
ferina	A	5S
australis		S
nyroca		2S
innotata	A*,A	
novaeseelandiae		S
fuligula	2A	7S
marila	A†	6S,K

Tribe MERGINI

Somateria		
mollissima	2A*,7A	14S,K,2S†
spectabilis		S†
Polysticta		
stelleri		
Histrionicus		
histrionicus	A	2S
Clangula		
hyemalis	8A*,5A	10S,K
Melanitta		
nigra	4A	5S,S†
perspicillata	A	
fusca	3A	4S,K
Bucephala		
albeola	A*,2A	
islandica		2S
clangula	3A	9S
Mergus		
(*Lophodytes*)		
cucullatus	A	
(*Mergellus*)		
albellus	A	6S
(*Mergus*)		
serrator	2A*,A	6S,S†
merganser	3A	6S
australis	E,A	3S

Tribe OXYURINI

Heteronetta		
atricapilla		S

	Spirit	Skels
Oxyura		
(*Oxyura*)		
jamaicensis	4A	
vittata		2S
Biziura		
lobata		3S
Thalassornis		
leuconotos	2A*,2A	

FALCONIFORMES

CATHARTIDAE

5 genera, 7 species
2 species unrepresented

Cathartes		
aura	2A	6S,K,S†
Coragyps		
atratus	A	4S
Sarcoramphus		
papa	2A	7S,2K,S†
Gymnogyps		
californianus		2S
Vultur		
gryphus	A,A*	4S,2K

PANDIONIDAE

1 genus, 1 species

Pandion		
haliaetus	2A,A*	4S,3S†,K

ACCIPITRIDAE

64 genera, 217 species
14 genera unrepresented
106 species unrepresented

Aviceda		
subcristata	A	
leuphotes		S†
Leptodon		
cayanensis		K
Pernis		
apivorus	2A	4S,2K
Elanoides		
forficatus	A	2S
Machaerhamphus		
alcinus	A	S
Elanus		
leucurus	A*,A	S
caeruleus	2A	7S,K,S†
notatus	A	
Chelictinia		
riocourii	A	
Rostrhamus		
sociabilis	4A	
Harpagus		
bidentatus		K
Ictinia		
plumbea		4S
Milvus		
migrans	A*	4S,3S†,K
milvus	A*,A	3S,2K

ACCIPITRIDAE (cont.)

	Spirit	Skels
Haliastur		
sphenurus	A	5S
indus	A	4S,S†
Haliaeetus		
leucogaster		S,K
vocifer	A	3S,2K
leucoryphus		S†
leucocephalus		4S,2K
albicilla		6S,2S†,K
Ichthyophaga		
ichthyaetus		S†
Gypohierax		
angolensis	A	8S,K
Neophron		
percnopterus		6S
Gypaetus		
barbatus		11S,4S†,K
Necrosyrtes		
monachus	A,A^{k}	2S,K
Gyps		
bengalensis	A	2S,2S†
africanus		K
rueppellii		2S
himalayensis		K
fulvus	A*	3S,2K,S†
Torgos		
tracheliotus		3S,K
Sarcogyps		
calvus	2A	S
Aegypius		
monachus		2S,2K,S†
Trigonoceps		
occipitalis		2S,K,S†
Circaetus		
gallicus	E	4S
cinereus		S
cinerascens		S
Terathopius		
ecaudatus	A	4S
Spilornis		
cheela		6S
Eutriorchis		
astur	A	
Polyboroides		
typus	A	2S
radiatus		S,3S†
Circus		
assimilis		S,S†
aeruginosus	A†,4A*	5S,K,S†
ranivorus		S
cyaneus	A*,3A	4S,S†
cinereus	A	S†,K
pygargus		2S,2S†
Melierax		
metabates	A†	S
canorus		2S
gabar	2A	

	Spirit	Skels
Erythrotriorchis		
radiatus		S
Accipiter		
gentilis	A,E,A*	6S,S†,3K
henstii		2S†
gularis	A	
virgatus	A	K
cirrhocephalus		2S
nisus	E,8A,5A*	21S,3S†,3K
striatus		S
tachiro	A	2S,S†
trivirgatus	A	2S,2S†
fasciatus		S
novaehollandiae		S
soloensis		S
badius	4A	2S,S†
francesii		S,S†
cooperii		S
bicolor	A	S†
Butastur		
liventer		S
teesa	A	S†
indicus		S
Kaupifalco		
monogrammicus	3A	S,K
Leucopternis		
polionota		S
Buteogallus		
anthracinus	A	
urubitinga	A	S
Heterospizias		
meridionalis		3S
Busarellus		
nigricollis	A	S
Geranoaetus		
melanoleucus		3S
Parabuteo		
unicinctus		4S
Buteo		
nitidus	2A	4S
magnirostris	4A	3S
lineatus		2S
platypterus	A	
swainsonii	3A	
albicaudatus	A	
jamaicensis		2S,K
buteo	4A	6S,K
lagopus	4A*,A	S
rufinus		7S,K
regalis		S
rufofuscus	A	5S,S†
Morphnus		
guianensis		S
Harpia		
harpyja		3S
Pithecophaga		
jefferyi	A	2S

ACCIPITRIDAE (cont.)

	Spirit	Skels
Ictinaetus		
malayensis		S
Aquila		
pomarina		S,2S†
clanga		2S,S†
rapax		4S,2K
heliaca		S,S†
wahlbergi		S
chrysaetos	A	8S,S†,3K
audax	A	3S,K,S†
verreauxi		S
Hieraaetus		
fasciatus	A*	5S,2S†
pennatus	E	S,S†
morphnoides	A	
Lophoaetus		
occipitalis		3S
Spizaetus		
cirrhatus		2S
nipalensis		K
ornatus		S
Stephanoaetus		
coronatus		S,S†
Polemaetus		
bellicosus		3S,K

SAGITTARIIDAE

1 genus, 1 species

	Spirit	Skels
Sagittarius		
serpentarius	A†,A	10S,K

FALCONIDAE

10 genera, 61 species

1 genus & 26 species unrepresented

	Spirit	Skels
Daptrius		
ater		S,K
americanus	A^{k},3A	
Phalcoboenus		
megalopterus	A	S
australis		2S,K
Polyborus		
plancus	4A,A*	3S
Milvago		
chimango	4A*	2S,K
chimachima	3A	
Herpetotheres		
cachinnans	A^{k},3A	S,K
Micrastur		
ruficollis	2A	
Polihierax		
semitorquatus	7A	S
insignis	A	
Microhierax		
caerulescens	9A	S
fringillarius	A	S
melanoleucus	A	
Falco		
naumanni	4A	S,S†,K
sparverius	13A	6S,S†,K
tinnunculus	12A,13A*	21S,3S†,2K
newtoni		S
cenchroides	4A	S
vespertinus	A	4S
chicquera	2A	2S
columbarius	3A*,A	14S
berigora	4A	2S
novaezeelandiae	A	S,S†
subbuteo	3A	6S,5K
longipennis	A	S
eleonorae		S†
femoralis	2A	
biarmicus	A	3S
mexicanus		S
jugger	A	S,S†
cherrug		4S
rusticolus	A	5S,K
deiroleucus	A	S
peregrinus	8A	14S,5S†,K

GALLIFORMES

MEGAPODIIDAE

7 genera, 12 species

3 genera & 7 species unrepresented

	Spirit	Skels
Megapodius		
freycinet	A*,8A	2S
pritchardii	5A*,A,†4A	
Leipoa		
ocellata		S
Alectura		
lathami	A	3S,K
Macrocephalon		
maleo		2S

CRACIDAE

8 genera, 44 species

1 genus & 18 species unrepresented

	Spirit	Skels
Ortalis		
vetula		S
cinereiceps	A	
garrula	A	
ruficauda		2S
canicollis		3K
motmot		2S
Penelope		
argyrotis	A	
montagnii		S
marail	6A	S
superciliaris	A^{k}	4S
jacquacu	A*	S
purpurascens		2S
pileata		2S
Aburria		
pipile	A^{k}	
jacutinga		S

CRACIDAE (cont.)

	Spirit	Skels
Penelopina		
nigra	A^{k}	S†
Oreophasis		
derbianus		2S,2S†
Nothocrax		
urumutum		2S
Crax		
(*Mitu*)		
tomentosa		2S,K
mitu		4S,2K
(*Pauxi*)		
pauxi		S
(*Crax*)		
rubra	A^{k}	4S
alberti		4S
alector	3A	3S
globulosa	2A†	3S
fasciolata		4S

PHASIANIDAE

MELEAGRIDINAE

2 genera, 2 species

Meleagris		
gallopavo	A,2A^{k},7A*	6S,7K
Agriocharis		
ocellata		S

TETRAONINAE

6 genera, 16 species
6 species unrepresented

Dendragapus		
canadensis	A*	S
Lagopus		
lagopus	A†,11A*,2A	13S,13K
mutus	2A,5A	11S,6K,S†
Tetrao		
tetrix	5A†,11A*, 2A	8S,2S†,8K
urogallus	A†,A,7A*	4S,4S†,13K
Bonasa		
bonasia	2A	5S
umbellus		2S
Centrocercus		
urophasianus		S
Tympanuchus		
phasianellus		2S†
cupido		2S
Hybrids:		
Tetrao tetrix × *Phasianus colchicus*	A†	
Lagopus lagopus × *Tetrao tetrix*	2A*	

ODONTOPHORINAE

10 genera, 33 species
5 genera & 24 species unrepresented

	Spirit	Skels
Lophortyx		
californica	3A*	2S,K
Philortyx		
fasciatus	A	
Colinus		
virginianus		4S
leucopogon	A	
cristatus		S
Odontophorus		
gujanensis	3A	
guttatus	A	
Cyrtonyx		
montexumae	A	
ocellatus		S

PHASIANINAE

40 genera, 155 species
6 genera & 69 species unrepresented

Tribe PERDICINI

Lerwa		
lerwa		S,S†
Ammoperdix		
griseogularis	A	
heyi	A	3S
Tetraogallus		
caspius		S
tibetanus	A	
altaicus	A	S,K
himalayensis		4S
Alectoris		
graeca	2A*,6A	5S,S†
barbara		2S
rufa	2A	3S,S†,K
melanocephala	2A	S,2S†
Francolinus		
francolinus	A	5S,S†
pictus		2S,S†
pintadeanus	A	S
swainsonii	A	
leucoscepus	A	
jacksoni		S
ahantensis	2A*	
squamatus		S†
bicalcaratus		K
clappertoni		S
natalensis		S
capensis		S
sephaena	A	
levaillantii		S
albogularis	A†,A	
pondicerianus	A	2S,S†
gularis		S
Perdix		
perdix	16A*,2A,A	6S,S†,6K
Margaroperdix		
madagarensis	3A	
Melanoperdix		
nigra	A	
Corturnix		
coturnix	6A	4S,S†,15K
coromandelica	2A*	

PERDICINI

Corturnix (cont.)	Spirit	Skels
delegorguei	A	
pectoralis	A	2S
Synoicus		
ypsilophorus	4A*,4A	2S,K
Excalfactoria		
adansonii		S†
chinensis	7A	S
Perdicula		
asiatica		3S
Arborophila		
torqueola		S
rufogularis	A*,2A†,2A	
javanica		S
Tropicoperdix		
charltonii	A	K
Rollulus		
rouloul	2A*,3A	6S,S†
Ptilopachus		
petrosus	5A	
Bambusicola		
fytchii	2A*	
thoracica	A,A*,2A	S
Galloperdix		
lunulata		S
bicalcarata		2S

Tribe PHASIANINI

	Spirit	Skels
Ithaginis		
cruentus		S,S†
Tragopan		
satyra	A,A†	6S,K
temmincki		S
Pucrasia		
macrolopha	A	2S
Lophophorus		
impeyanus	A	5S,S†
Gallus		
gallus	33A*,A†	34S,16K,5S
lafayettei		S
sonnerati	2A*	2S
Lophura		
leucomelana	2A	3S,S†
nycthemera	A*	3S,2K
imperialis	A,3A*	
edwardsi	3A*,3A	
swinhoei	5A*	S
erythrophthalmus	A†	2S
ignita	A	3S
diardi	A*	S
bulweri	A*	
Crossoptilon		
mantchuricum	2A	2S,S†
auritum	A	2S
Catreus		
wallichi		2S,S†
Syrmaticus		
mikado	2A	S
soemmerringi		3S
reevesi	A*,10†,2A	2S
Phasianus		
colchicus	24A*,10A†, 10A	7S,16K,S†
versicolor		S
Chrysolophus		
pictus	A,A*	4S,2K
amherstiae	A*	S,K
Polyplectron		
chalcurum	3A	S,K
germaini	A	
bicalcaratum	2A,3A*	S†
malacense	A	
emphanum	3A	
Rheinartia		
ocellata	A	4S,S†
Argusianus		
argus	3A	3S
Pavo		
cristatus	A,4A*	4S,S†,K
muticus	A†	5S,K
Afropavo		
congensis	2A	S
Hybrid:		
Gallus gallus ×		
Phasianus colchicus	A	

NUMIDINAE

5 genera, 7 species
2 species unrepresented

	Spirit	Skels
Phasidus		
niger		S†
Numida		
meleagris	9A* 3A†,2A	7S,K
Guttera		
edouardi		3S
pucherani	3A†	
Acryllium		
vulturinum	A	

OPISTHOCOMIDAE

1 genus, 1 species

	Spirit	Skels
Opisthocomus		
hoazin	18A*,8A	4S,S†

GRUIFORMES

MESITORNITHIDAE

2 genera, 3 species

	Spirit	Skels
Mesitornis		
variegata		S
unicolor	A†,3A	S,K
Monias		
benschi	4A	2S

TURNICIDAE

2 genera, 14 species
7 species unrepresented

	Spirit	Skels
Turnix		
sylvatica	A*,6A	S
tanki	3A*	S,S†
suscitator	8A	S

TURNICIDAE (cont.)

Turnix (cont.)	Spirit	Skels
nigricollis	A*,A	S,S†
varia	2A,5A*	3S
velox	2A*,A	2S
Ortyxelos		
meiffrenii	A*,5A	2S

PEDIONOMIDAE

1 genus, 1 species

Pedionomus		
torquatus	A	

GRUIDAE

4 genera, 15 species
5 species unrepresented

GRUINAE

Grus		
grus	A*	S,2K
japonensis	A	S,K
americana		S
antigone	5A*,2A	5S
rubicunda	A†	2S,K
leucogeranus		S,K
Bugeranus		
carunculatus	A	2S
Anthropoides		
virgo	A*	7S
paradisea	A*	3S

BALEARICINAE

Balearica		
pavonina	2A†,2A	7S,K

ARAMIDAE

1 genus, 1 species

Aramus		
guarauna	2A	S

PSOPHIIDAE

1 genus, 3 species
1 species unrepresented

Psophia		
crepitans	A	3S
viridis	a,2A	S†

RALLIDAE

53 genera, 141 species
18 genera & 79 species unrepresented

RALLINAE

Rallus		
(*Rallus*)		
longirostris		S
elegans		S
limicola	A	
aquaticus	9A*,27A	5S,3S†,4K
madagascariensis		S
*mirificus**	A	
striatus	A,6A*	
(*Hypotaenidia*)		
philippensis	7A*,2A	2S,K
torquatus	A	S

	Spirit	Skels
Atlantisia		
rogersi	A,a	S
Ortygonax		
sanguinolentus	A	
nigricans	2A	
Tricholimnas		
sylvestris		2S
Pardirallus		
maculatus	A	
Dryolimnas		
cuvieri	2A	3S,S†
Rallina		
fasciata	8A	S†
eurizonoides	A	
Aramides		
cajanea	4A	S,S†
ypecaha	A*,4A	3S,K,S†
calopterus		S
Nesoclopeus		
poeciloptera	E ?,A	
Gallirallus		
australis	2A*,3A	4S
Himantornis		
haematopus	A	
Canirallus		
oculeus	3A	
Mentocrex		
kioloides	2A	S,2S†
Crecopsis		
egregia	A	K
Crex		
crex	7A,8A*	S,K,S†
Limnocorax		
flavirostra	A*,4A	2S,K
Porzana		
pava	A	S
pusilla	A	2S
porzana	A	4S
carolina	A,3A*	
fusca	A,3A*	2S†
tabuensis	A	
Porzanula		
palmeri	E,A*,2A	S
Pennula		
millsi	E,4A*,3A	
sandwichensis	E,4A*,3A	
Nesophylax		
ater	2A	
Laterallus		
viridis	3A	
leucopyrrhus		S
Coturnicops		
noveboracensis		K
Sarothrura		
pulchra	A*,2A	
insularis	A	
Poliolimnas		
cinereus	A	

RALLINAE (cont.)

	Spirit	Skels
Porphyriops		
melanops		S
Tribonyx		
ventralis		3S
mortierii	2A	3S,S*
Amaurornis		
phoenicurus	A*,3A	2S
Gallicrex		
cinerea	A^{k},4A	
Gallinua		
chlloropus	30A*,A†,9A	7S,2S†,5K
angulata	A	
Porphyriornis		
nesiotis		S†
comeri	A*,A†,3A	S,4S†
Pareudiastes		
pacificus	E ?,A	
Porphyrula		
alleni	4A	3S
martinica	8A	S
Porphyrio		
porphyrio	A,3A*	
madagascariensis	A	
poliocephalus	A	7S
Notornis		
mantelli		2S

FULICINAE

	Spirit	Skels
Fulica		
atra	5A*,3A	6S,2K
americana	7A*	
leucoptera	A,A	

HELIORNITHIDAE

3 genera, 3 species

	Spirit	Skels
Podica		
senegalensis	A†,4A	S
Heliopais		
personata	4A*	
Heliornis		
fulica	11A	S

RHYNOCHETIDAE

1 genus, 1 species

	Spirit	Skels
Rhynochetos		
jubatus	A^{k},A*,2A	5S

EURYPYGIDAE

1 genus, 1 species

	Spirit	Skels
Eurypyga		
helias	2A	2S

CARIAMIDAE

2 genera, 2 species

	Spirit	Skels
Cariama		
cristata	A^{k},A	6S,S†
Chunga		
burmeisteri	A	2S

OTIDIDAE

11 genera, 24 species
10 species unrepresented

	Spirit	Skels
Tetrax		
tetrax		3S,K
Otis		
tarda	A*,2†,3A	3S,K
Neotis		
nuba		K
Choriotis		
arabs		K
kori		K
australis	A	2S,K
Chlamydotis		
undulata		3S,K
Lophotis		
ruficrista	A	S
Afrotis		
atra		S
Eupodotis		
vigorsii		S
senegalensis	A†,A	S
Lissotis		
melanogaster		K
Houbaropsis		
bengalensis		S
Sypheotides		
indica		S†

CHARADRIIFORMES

Suborder **CHARADRII**

JACANIDAE

6 genera, 8 species
1 genus & 1 species unrepresented

	Spirit	Skels
Actophilornis		
africana	A*,8A	S
albinucha		2S
Irediparra		
gallinacea	8A	
Hydrophasianus		
chirurgus	4A	S†
Metopidius		
indicus	6A	2S,2S†
Jacana		
spinosa	4A*,7A	3S
jacana	2A*,3A	

ROSTRATULIDAE

2 genera, 2 species
1 genus & 1 species unrepresented

	Spirit	Skels
Rostratula		
benghalensis	4A*,12A	3S,3K,3S†

DROMADIDAE

1 genus, 1 species

	Spirit	Skels
Dromas		
ardeola	4A^{k},5A*, 2A†,2A	S,2K

HAEMATOPODIDAE

1 genus, 7 species
5 species unrepresented

	Spirit	Skels
Haematopus		
ostralegus	A*,61A	18S,15K,2S†
leucopodus	2A	K

IBIDORHYNCHIDAE

1 genus, 1 species

Ibidorhyncha		
struthersii	3A*,A	2S,2K,S†

RECURVIROSTRIDAE

3 genera, 13 species
5 species unrepresented

Himantopus		
himantopus	10A	6S,3K
mexicanus	3A	
leucocephalus	2A	
Cladorhynchus		
leucocephala		2S,K
Recurvirostra		
avosetta	5A	3S,2K
americana	A	
novaehollandiae	2A	K,S
andina		K

BURHINIDAE

2 genera, 9 species
1 genus & 4 species unrepresented

Burhinus		
oedicnemus	7A*,2A	7S,S†,3K
senegalensis	A,A*	
vermiculatus	A	
capensis		S
magnirostris	3A	2S,5K,2S†

GLAREOLIDAE

5 genera, 8 species
4 species unrepresented

CURSORIINAE

Pluvianus		
aegyptius	2A*,8A	2S,K
Rhinoptilus		
africanus	A	
cinctus	A	
chalcopterus	A*,3A	S
Cursorius		
cursor	A,A*	S,2K
coromandelicus	A	S,2K
temminckii	4A	K

GLAREOLINAE

Stiltia		
isabella	5A	
Glareola		
pratincola	2A,A*	2S,K
maldivarus		2S,K
nuchalis	A*,5A	
cinerea	A*	S

CHARADRIIDAE

8 genera, 64 species
2 genera & 15 species unrepresented

	Spirit	Skels
Vanellus		
vanellus	14A*,13A	6S
crassirostris	2A	
armatus	4A	
spinosus	A	
tectus	3A	
malabaricus	A	K
albiceps	A^k	
lugubris	A	
coronatus	3A,2A*	
senegallus	2A*,A	
leucurus	A	
cayanus	2A	
chilensis	13A*,6A	
indicus	A^k,2A	
tricolor	5A	3S,K
miles	4A	
Pluvialis		
apricaria	35A	7S,4S†,8K
sominica	8A	6K
squatarola	20A	5S,3S†,4K
obscura		2K
Charadrius		
hiaticula	4A*,17A	5S,9S†,3K
semipalmatus	2A	
placidus		K
dubius	7A*,2A	4K
wilsonia	4A	3S,S†,K
vociferus	4A	3K
melodus		2K
pecuarius	2A*,10A	K
sanctaehelenae		2S,K
tricollaris	8A	S,K
alexandrinus	9A	5K,3S
marginatus	2A†	
peronii	3A	2K
collaris		K
bicinctus	A	K
falklandicus	2A*,3A	K
mongolus	A	4S,2K
leschenaultii	7A,4A^k	4K
asiaticus	2A	2K
veredus		K
modestus	4A	K
melanops	2A*,23A	S
cinctus	4A	K
rubricollis		K
Anarhynchus		
frontalis	A	S
Peltohyas		
australis	A*,6A	
Eudromias		
morinellus	2A*	S†,K
ruficollis	4A	2S,K

SCOLOPACIDAE

9 genera, 31 species
7 species unrepresented

	Spirit	Skels
TRINGINAE		
Tribe **NUMENIINI**		
Limosa		
limosa	2A	8S
haemastica	2A	
lapponica	A*,22A	12S,6K,2S†
fedoa		K
Numenius		
minutus	8A	K
borealis	E ?	K
phaeopus	A*,6A	8S,5K,S†
arquata	13A*,33A	10S,3S†,5K
americanus		S,2K
Bartramia		
longicauda	3A*,5A	S

Tribe **TRINGINI**		
Tringa		
(*Totanus*)		
erythropus	11A*,A	S,2S†
totanus	31A	7S,5K,S†
stagnatilis	3A	
nebularia	A*,4A	S,4K
melanoleuca	3A	2K
flavipes	4A	S
(*Tringa*)		
ochropus	5A	2S,3K,6S†
solitaria	3A	S
glareola	3A*,4A	S†
Catoptrophorus		
semipalmatus	4A	2S,K
Xenus		
cinereus	3A	3K
Actitis		
hypoleucos	3A*,16A	S†,2K
macularia	9A	S,K
Heteroscelus		
brevipes	4A	2S,K
incanus	4A	

Tribe **PROSOBONIINI**		
Prosobonia		
cancellata	E,2A	S†,K

ARENARIINAE

1 genus, 2 species
1 species unrepresented

Arenaria		
interpres	20A	3S,9S†,2K

PHALAROPODINAE

1 genus, 3 species

Phalaropus		
tricolor	A	
lobatus	4A	3S,K
fulicarius	5A	S,K

SCOLOPACINAE

1 genus, 6 species
3 species unrepresented

Scolopax	Spirit	Skels
rusticola	8A*,15A	4S,4S†,14K
saturata	2A	
minor	A	

GALLINAGONINAE

4 genera, 20 species
8 species unrepresented

Coenocorypha		
aucklandica	A^k	S
Gallinago		
stenura	3A	K
megala	A	
macrodactyla		S
media		S,S†,K
gallinago	7A*,39A	7S,2S†,6K
paraguaiae	A	
nobilis	2A	
undulata		K
Lymnocryptes		
minimus	20A	5S,K,S†
Limnodromus		
griseus	7A	3K
semipalmatus		K

CALIDRIDINAE

7 genera, 24 species
1 species unrepresented

Aphriza		
virgata	2A	S
Calidris		
canutus	A*,33A	8S,2K,S†
tenuirostris	A	K
alba	11A	4S,K
pusilla	12A	S,2K
mauri	2A	S
ruficollis	7A	3S
minuta	7A,5A*	3S,K
temminckii	2A	S†
subminuta	5A	
minutilla	2A	K
fuscicollis	5A	
bairdii	A	
melanotos	2A	S
acuminata	8A	S
maritima	4A*,10A	4S,K
alpina	2A*,71A	12S,9K
ferruginea	2A	S
Eurynorhynchus		
pygmeus	2A	S
Limicola		
falcinellus	2A	K
Micropalama		
himantopus	8A	K
Tryngites		
subruficollis	7A	K
Philomachus		
pugnax	12A*,10A	11S,6K

THINOCORIDAE

2 genera, 4 species
1 species unrepresented

	Spirit	Skels
Attagis		
gayi		K
Thinocorus		
orbignyianus	4A	2S,K
rumicivorus	10A	2S,K,S†

CHIONIDIDAE

1 genera, 2 species

Chionis		
alba	A*,9A	4S,S†,3K
minor	9A*,7A	S,K

Suborder LARI

STERCORARIIDAE

2 genera, 5 species
1 species unrepresented

Catharacta		
skua	18A*,2A	6S,3K
Stercorarius		
pomarinus	A	
parasiticus	2A*,3A	6S,K,2S†
longicaudus	A*,A	

LARIDAE

17 genera, 90 species
3 genera & 39 species unrepresented

LARINAE

	Spirit	Skels
Gabianus		
pacificus		S
scoresbii	2A	S
Pagophila		
alba	4A*,2A	
Larus		
modestus	7A*	
hemprichii	2A*	S
delawarensis	2A	
canus		5S,S†,5K
argentatus	A,A*	12S,2S†,4K
fuscus	3A*,4A	3S
dominicanus	A†	S
marinus	A†,A,A*	6S,7K
hyperboreus	2A*	5S,2K,S†
glaucoides		2S
ichthyaetus		3S
atricilla		S
brunnicephalus		K
cirrocephalus	A*	
novaehollandiae	A	4S,K
melanocephalus		2S
maculipennis	A	S
ridibundus	4A*,7A	11S,4K
genei	A	4S,K
philadelphia		S
minutus	A	S
Rissa		
tridactyla	10A*,5A	7S,S†,6K
Creagrus		
furcatus		2S
Xema		
sabini	A†	2S

STERNINAE

Chlidonias		
hybrida		2S
leucoptera	A	
nigra	6A	2S
Hydroprogne		
caspia		S†
Sterna		
hirundo	9A*,4A	5S,2S†
paradisaea	2A*	12S,2K
vittata	19A*,3A	
dougallii	3A,A*	
striata		3S
repressa		7S
sumatrana		2S
anaethetus	8A*,5A	
fuscata	A,A*	3S
albifrons		2S
Thalasseus		
bergii	5A*	5S,3K
maximus	2A	
bengalensis		S
sandvicensis	A,A*	6S,2K
Larosterna		
inca	A	2S
Procelsterna		
cerulea		S
Anous		
stolidus	15A*,4A	5S,S†
tenuirostris		S
minutus	2A	
Gygis		
alba	A*,11A	6S

RYNCHOPIDAE

1 genus, 3 species
1 species unrepresented

Rynchops		
niger		4S
albicollis	A†,2A	

Suborder ALCAE

ALCIDAE

13 genera, 23 species
3 genera & 7 species unrepresented

Alle		
alle	A†,15A	8S,3S†,K
Alca		
torda	7A*,5A	17S,S†,12K
Uria		
lomvia		2S
aalge	4A*,2A†,5A	17S,S†,9K
Cepphus		
grylle	A	11S,S†
carbo	A	

ALCIDAE (cont.)

	Spirit	Skels
Synthliboramphus		
antiquus	A	
Ptychoramphus		
aleuticus	A	
Cyclorrhynchus		
psittacula		S,S†
Aethia		
cristatella	A	S
pusilla	A	
pygmaea		S
Fratercula		
arctica	3A*,5A†,5A	11S,S†
corniculata	A	S
Lunda		
cirrhata	2A	S,K

COLUMBIFORMES
PTEROCLIDIDAE

2 genera, 16 species
9 species unrepresented

Syrrhaptes		
paradoxus	A	4S
Pterocles		
alchata	2A*	4S
exustus	2A*	S†,6K
senegallus	2A*	2S†
orientalis		3S
lichtensteinii	2A	2S
quadricinctus	6A	S

RAPHIDAE

2 genera, 3 species
1 genus & 1 species unrepresented

Raphus		
cucullatus		S
solitarius		S†

COLUMBIDAE

42 genera, 303 species
6 genera & 180 species unrepresented

Columba		
livia	A	54S,4S†,5K
guinea	3A	3S
oenas	A*,2A	2S,S†,4K
palumbus	6A*,3A	18S,3S†,3K
trocaz	2A	S,S†
unicincta	A	
arquatrix		S
hodgsonii		S†
leucocephala	A	S
squamosa		S
picazuro		S
maculosa		S
fasciata	A	
nigrirostris	A	
Nesoenas		
mayeri	2A*	

Streptopelia	Spirit	Skels
turtur	5A	5S,S†
orientalis	A	
bitorquata		2S
decaocto	A*,5A	7S
roseogrisea		S
decipiens	A,A*	
semitorquata	2A*,2A	2S
capicola	4A	
vinacea		S
chinensis	3A	4S,S†
senegalensis	3A	S,K
Aplopelia		
larvata		S†
Macropygia		
unchall		S
amboinensis	A*	
phasianella	A	S
ruficeps		2S
Turacoena		
manadensis		S
Turtur		
chalcospilos	4A	
abyssinicus	A	
afer	10A	S
tympanistria	5A	4S
brehmeri	A	
Oena		
capensis	8A	S
Chalcophaps		
indica	2A*,14A	9S,K
stephani	3A	
Henicophaps		
albifrons	A	
Phaps		
chalcoptera	4A	S
elegans		2S
historionica		S
Ocyphaps		
lophotes	4A	3S
Petrophassa		
plumifera	7A	S
ferruginea	A	
scripta	A*	
smithii	7A	
rufipennis	A	
albipennis	4A	S
Geopelia		
cuneata	12A	6S
striata	A*,8A	4S
humeralis	7A	K,S
Leucosarcia		
melanoleuca		S
Ectopistes		
migratorius	E	S
Zenaida		
auriculata	6A*,A	S
aurita		S,2K
galapagoensis	A	

COLUMBIDAE (cont.)

	Spirit	Skels
Columbina		
passerina	A*,7A	2S
minuta	2A	S
talpacoti	5A	2S
picui	3A	
Claravis		
pretiosa	2A	
Metriopelia		
melanoptera		S
Scardafella		
squammata	2A,A*	2S
Leptotila		
verreauxi	4A	3S
rufaxilla	A	S
wellsi		S
jamaicensis		S
cassini	A	
Geotrygon		
versicolor	A	S
chrysia	A	
violacea	A	
montana		S
Starnoenas		
cayanocephala		3S
Caloenas		
nicobarica	A	
Gallicolumba		
luzonica	2A	
criniger		S
rubescens	A	
beccarii		S
Otidiphaps		
nobilis	A*,3A	
Goura		
cristata		2S,3S†,2K
scheepmakeri	A	
victoria		S,2S†
Didunculus		
strigirostris	6A	S,S†
Phapitreron		
leucotis		S†
Treron		
fulvicollis		S
olax	3A	
vernans	3A	S,S†,K
bicincta	A	3S,2K
pompadora		S
curvirostra	5A	S
phoenicoptera		S†
waalia	A	
australis	2A	S†
calva	3A	2S
apicauda	2A	S†
oxyura		S
sphenura		S†
Ptilinopus		
cinctus	A	S

Ptilinopus (cont.)	Spirit	Skels
jambu	4A	
magnificus	2A	
ornatus	A	
superbus	A	
porphyraceus	2A*,3A	
rarotongensis	A	
roseicapilla		2S
regina	A	S
greyii	2A	
dupetithouarsii	A	3S
coronulatus	A*	S
puchellus		S
rivoli		S
melanospila	3A,A*	S
Alectroenas		
madagascariensis	A	
pulcherrima	A	S,S†
Ducula		
badia		2S
forsteni		S
aenea	A	5S
galeata		S
whartoni		2S
lacernulata		2S
bicolor	A†	3S,S†
spilorrhoa	6A	S
Lopholaimus		
antarcticus		S
Hemiphaga		
novaeseelandiae	2A	

PSITTACIFORMES

LORIIDAE

81 genera, 344 species
18 genera & 181 species unrepresented

Chalcopsitta		
atra	A	
sintillata	A	S
Eos		
squamata		S
bornea		S
Trichoglossus		
ornatus		2S
haematodus	9A	3S,K
flavoviridis	A	
chlorolepidotus	3A	
euteles		S
versicolor	2A	S
Lorius		
lory		S
domicellus		S
garrulus		2S
Phigys		
solitarius	A	
Vini		
australis	A	
peruviana		S
ultramarina		2S

LORIIDAE (cont.)

	Spirit	Skels
Glossopsitta		
concinna	4A	3S
pusilla	3A	
porphyrocephala	3A	
Charmosyna		
palmarum	A	
placentis	4A	2S
papou	2A	
Neopsittacus		
musschenbroekii	A	

CACATUIDAE

CACATUINAE

Probosciger		
aterrimus		2S,3K
Calyptorhynchus		
funereus	13A	10S,4K
magnificus	3A	2S
Callocephalon		
fimbriatum		2S,S†
Eolophus		
roseicapillus	3A	3S
Cacatua		
leadbeateri		2S,K
sulphurea		2S,K
galerita		3S,K
moluccensis		2S,S†
alba		2S
sanguinea	3A	4S
tenuirostris		S
ducorps		

NYMPHICINAE

Nymphicus		
hollandicus	7A	4S,S†

PSITTACIDAE

NESTORINAE

Nestor		
notabilis	2A	2S
meridionalis	2A	S

MICROPSITTINAE

Micropsitta		
keiensis		S
finschii	6A	

PSITTACINAE

Pacific Taxa

	Spirit	Skels
Opopsitta		
diophthalma	3A	S
Psittinus		
cyanurus	5A	S
Geoffroyus		
geoffroyi	A	
Prioniturus		
luconensis	A	
Tanygnathus		
megalorynchos	A	
lucionensis		S
Eclectus		
roratus	4A	4S
Psittrichas		
fulgidus	A^{k},2A	
Prosopeia		
tabuensis	A	S†
Alisterus		
scapularis	4A	3S
chloropterus	4A	
Aprosmictus		
erythropterus	2A*,7A	3S
jonquillaceus		S
Polytelis		
swainsonii		S
anthopeplus	A	4S
alexandrae	A,2A*	
Purpureicephalus		
spurius	3A	S
Barnardius		
barnardi		S
zonarius	5A	6S,K
Platycercus		
caledonicus		5S
elegans		K,2S
eximius	7A	2S,S†,K
adscitus	7A	S,K
venustus	A*,3A	2S
icterotis	4A	3S
Psephotus		
haematonotus	2A	2S
varius	3A,A*	K
Cyanoramphus		
unicolor	A	S
novaezelandiae	A	S†
auriceps		3S
Eunymphicus		
cornutus	A	K
Neophema		
bourkii	2A	2S
chrysostoma	2A,A†	
elegans	8A	S
pulchella	3A	
splendida	A,A*	
Lathamus		
discolor	6A	S
Melopsittacus		
undulatus	20A	10S,2S†,2K
Pezoporus		
wallicus		K

Afro-Asian Taxa

Coracopsis		
vasa	A	S
nigra		2S
Psittacus		
erithacus	2A	9S,2K
Poicephalus		
robustus	3A	S
cryptoxanthus	A	
senegalus	A	S,S†

PSITTACINAE (cont.)

Poicephalus (cont.)	Spirit	Skels
rufiventris		S
meyeri	2A	3S
flavifrons	A	
Agapornis		
cana	2A	2S
pullaria	2A	5S,S†,K
taranta	5A	2S
roseicollis	4A	3S
personata	2A*,16A	6S,2S†
lilianae	3A	
nigrigenis	A	
Loriculus		
vernalis	A	S†
beryllinus		3K
galgulus	2A	S
aurantiifrons		S†
Psittacula		
eupatria	A*	S
krameri	3A	22S,2S†,S*
himalayana	A	
cyanocephala	3A	12S,4S†
columboides		S
calthorpae	2A	S
alexandri	4A	23S,7S†
longicauda	2A	S
echo	A	

New World Taxa

	Spirit	Skels
Anodorhynchus		
hyacinthinus	A	5S
Cyanopsitta		
spixii		S
Ara		
ararauna		S
militaris		2S,K
macao		4S,K
chloroptera		S,2S†
auricollis	A	
manilata	A	S†
maracana		S
nobilis	A	3S
Aratinga		
acuticaudata	A	3S
guarouba	2A,A*	
holochlora		S
mitrata		S
erythrogenys	A	2S
leucophthalmus	3A	2S
pertinax	3A	
cactorum	A	
Nandayus		
nenday		S
Conuropsis		
carolinensis	E	2S
Cyanoliseus		
patagonus	A†	S
Pyrrhura		
cruentata		S
frontalis	3A	S
leucotis	A	
picta	A	
Enicognathus		
ferrugineus	A	S
leptorhynchus		2S
Myiopsitta		
monachus	A	S
Bolborhynchus		
aymara		S
Forpus		
cyanopygius	2A	
passerinus	7A	2S
coelestis	A	
Brotogeris		
versicolurus		S
pyrrhopterus		S
sanctithomae		3S
Pionites		
melanocephala	A	
Pionus		
menstruus		S
maximiliani	2A	
seniloides		S
fuscus	A	S
Amazona		
leucocephala		2S
ventralis		2S
albifrons		3S
xantholora	A	
viridigenalis		S
dufresniana	A	S
festiva	A	
aestiva		4S,K
ochrocephala		3S
amazonica		4S
farinosa		3S
guildingii	3S	S,S†
Deroptyus		
accipitrinus	A	S
Triclaria		
malachitacea	A	

STRIGOPINAE

	Spirit	Skels
Strigops		
habroptilus	2A	4S,S†

CUCULIFORMES
MUSOPHAGIDAE

5 genera, 19 species
9 species unrepresented

	Spirit	Skels
Corythaeola		
cristata	A	2S,S†
Crinifer		
africanus	2A	2S,2S†

MUSOPHAGIDAE (cont.)

	Spirit	Skels
Corythaixoides		
concolor	A*,4A	
personata	A	
leucogaster	A	
Musophaga		
violacea	4A	2S
Tauraco		
corythaix	2A	
schuetii	A	
macrorhynchus	2A	S
leucotis	2A	S
porphyreolophus	A	
persa	A*	4S
livingstonii	2A	S†

CUCULIDAE

38 genera, 130 species
13 genera & 80 species unrepresented

CUCULINAE

	Spirit	Skels
Clamator		
glandarius	A,A†	2S
coromandus	2A*	S†
jacobinus	2A	
cafer		K
Cuculus		
varius	A	
clamosus	A	
canorus	3A*,35A	8S,5S†,2K
poliocephalus	A	
pallidus	7A	2S
Cacomantis		
merulinus	3A	2S,2S†
variolosus	A*	
pyrrhophanus	5A	
Misocalius		
osculans		S
Chrysococcyx		
cupreus	4A	
klaas	3A	2S
caprius	4A	2S
Chalcites		
xanthorhynchus		S†
basalis	4A	4S
lucidus	A	S
Surniculus		
lugubris	2A	
Eudynamys		
scolopacea	7A	2S,K
Urodynamis		
taitensis	2A	
Scythrops		
novaehollandiae	A	S†

PHAENICOPHAEINAE

	Spirit	Skels
Coccyzus		
erythropthalmus		2S
americanus	A	2S
minor	2A	
melacoryphus	3A	
Piaya		
(*Piaya*)		
cayana	4A	4S,K
(*Coccycua*)		
minuta	A	
Saurothera		
vetula		K
Ceuthmochares		
aereus	3A	
Rhopodytes		
diardi		S
tristis	A	S
Taccocua		
leschenaultii		
Rhinortha		
chlorophaea	2A	S
Zanclostomus		
javanicus		4S
Rhamphococcyx		
calyorhynchus		3S
curvirostris	2A	4S

CROTOPHAGINAE

	Spirit	Skels
Crotophaga		
major	3A†,3A	S
ani	12A	S,2K
sulcirostris	A	
Guira		
guira	2A*,5A	3S

NEOMORPHINAE

	Spirit	Skels
Geococcyx		
californiana	A	4S,S†
Carpococcyx		
radiceus	A	
renauldi	A	S

COUINAE

	Spirit	Skels
Coua		
cristata	3A	
caerulea	A	S

CENTROPODINAE

	Spirit	Skels
Centropus		
phasianius	5A	4S
sinensis	5A*,A	5S
toulou	2A	3S
bengalensis	3A	S
monachus	A,A*	K
senegalensis	A	S,K
superciliosus	A,4A*	S

STRIGIFORMES

TYTONIDAE

2 genera, 12 species
8 species unrepresented

TYTONINAE

	Spirit	Skels
Tyto		
alba	4A*,11A	17S,3K,S†
novaehollandiae		S,K
capensis		S

TYTONIDAE (cont.)

	Spirit	Skels
PHODILINAE		
Phodilus		
badius	A	K

STRIGIDAE

27 genera, 134 species
11 genera & 83 species unrepresented

	Spirit	Skels
BUBONINAE		
Otus		
rufescens	A	2S
spilocephalus	3A	6S
scops	2A*,9A	6S,2S†
senegalensis	5A	
rutilus		3S
insularis		S
bakkamoena	4A	4S,S†
asio		S
nudipes		S
leucotis	A	S
Bubo		
virginianus	4A*,3A	6S
bubo	4A*,6A	10S,S†,2K
capensis		2S
africanus	A*,4A	5S,K
nipalensis		2S†
sumatrana	A	
lacteus	A	S
coromandus		S,S†
Ketupa		
blakistoni		S
flavipes		S†
ketupu		5S,S†
Pulsatrix		
(*Pulsatrix*)		
perspicillata	3A	3S
Nyctea		
scandiaca	2A,A*	S,K
Surnia		
ulula	2A	5S
Glaucidium		
brodiei		S
passerinum	A	2S
jardinii	A	
brasilianum	5A	S,S†
perlatum	2A	
radiatum		S†
cuculoides	2A	S,2S†
Ninox		
connivens	A	
novaeseelandiae	6A	5S
scutulata	5A	S,2S†
philippensis		S
Sceloglaux		
albifacies	2A†	
Athene		
noctua	A*,15A	15S,3K,S†
brama	3A	S†
Speotyto		
cunicularia	3A*,12A	8S
Ciccaba		
virgata		S,S†
woodfordii	5A	
STRIGINAE		
Strix		
seloputo		S
leptogrammica		S†
aluco	A^k,A*,4A	9S,7K
varia		2S
uralensis	A	2S
nebulosa	2A	2S†
Rhinoptynx		
clamator		S
Asio		
otus	2A*,3A	9S,4K
madagascariensis		S,S†
flammeus	5A*,9A	10S,K,3S†
capensis		2S
Aegolius		
funereus	5A	

CAPRIMULGIFORMES
STEATORNITHIDAE

1 genus, 1 species

Steatornis		
caripensis	12A*,5A	2S

PODARGIDAE

2 genera, 13 species
8 species unrepresented

Podargus		
strigoides	7A	3S,3K
papuensis	2A	S
Batrachostomus		
auritus	5A	
harterti	A	
stellatus	3A	

NYCTIBIIDAE

1 genus, 5 species
4 species unrepresented

Nyctibius		
griseus	2A	K

AEGOTHELIDAE

1 genus, 8 species
7 species unrepresented

Aegotheles		
cristatus	3A	

CAPRIMULGIDAE

19 genera, 76 species
10 genera & 54 species unrepresented

CHORDEILINAE		
Chordeiles		
acutipennis	2A	S
minor	3A	S
Podager		
nacunda	3A	S

CAPRIMULGIDAE (cont.)

	Spirit	Skels
CAPRIMULGINAE		
Eurostopodus		
guttatus	2A	S
mystacalis		S
temminckii		S
Nyctidromus		
albicollis	3A	S,K
Phalaenoptilus		
nuttallii	A	S
Caprimulgus		
vociferus		S
ruficollis	A	
indicus	A,A*	S†
europaeus	2A*,7A	3S,2K,S†
madagascariensis	A	S
macrurus	2A	S†
pectoralis	A	
natalensis	A	
affinis		S
enarratus		3S,S†
Scotornis		
climacurus	3A,A*	2K
Macrodipteryx		
longipennis	5A*,6A	2S
Semeiophorus		
vexillarius	A,4A*	

APODIFORMES
APODIDAE

18 genera, 82 species
11 genera & 65 species unrepresented

	Spirit	Skels
CYPSELOIDINAE		
Streptoprocne		
(*Streptoprocne*)		
zonaris	3A	
APODINAE		
Collocalia		
(*Aerodramus*)		
francica	A*,8A	S
vanikorensis	4A	
fuciphaga	21A	
maxima	5A	
(*Collocalia*)		
esculenta	13A	
Raphidura		
leucopygialis	A	S
Hirundapus		
caudacuta	A	S†
gigantea	A	
Chaetura		
(*Chaetura*)		
pelagica	2A	3S
Cypsiurus		
parvus	4A*,7A	
Apus		
(*Tachymarptis*)		
melba		S†
aequatorialis		S
apus	10A	12S,2K,25*,4S
pacificus	A	S
caffer	2A*,A	
affinis	2A*	S

HEMIPROCNIDAE

1 genus, 4 species
2 species unrepresented

	Spirit	Skels
Hemiprocne		
longipennis	2A	
comata	5A	3S

TROCHILIDAE

116 genera, 338 species
75 genera & 274 species unrepresented

	Spirit	Skels
Glaucis		
hirusuta	4A	S
Threnetes		
ruckeri	A	2S
Phaethornis		
superciliosus	7A	2S
hispidus	A	
longuemareus	A	S
bourcieri	A	
Campylopterus		
rufus		S
Eupetomena		
macroura	4A	
Melanotrochilus		
fuscus	A	
Colibri		
delphinae		S
thalassinus		3S
serrirostris	2A	
Anthracothorax		
prevostii	A	
Eulampis		
jugularis	2A	K
Sericotes		
holosericeus	A	
Chrysolampis		
mosquitus	2A	
Orthorhyncus		
cristatus	9A	
Abeillia		
abeillei		S
Lophornis		
ornata	A	
magnifica	30A	
Discosura		
longicauda	A	
Chlorestes		
notatus	5A	S

TROCHILIDAE (cont.)

	Spirit	Skels
Chlorostilbon		
aureoventris	23A	K
ricordii	A	S
Thalurania		
furcata	16A	S
watertonii	A	
glaucopis	A	
Panterpe		
insignis		S
Damophila		
julie		S
Hylocharis		
(*Hylocharis*)		
sapphirina	A	
cyanus	A	
chrysura	A	
Trochilus		
polytmus		S,K
Amazilia		
(*Polyerata*)		
versicolor	43A	
fimbriata		S
lactea	A	
(*Saucerottia*)		
beryllina	2A	
(*Amazilia*)		
tzacatl		S†
Urochroa		
bougueri	A	
Patagona		
gigas	A	
Lafresnaya		
lafresnayi		8S
Coeligena		
coeligena	A	
torquata	A	11S
lutetiae		8S
iris		3S
Ensifera		
ensifera		5S
Sephanoides		
sephaniodes	A	
Boissonneaua		
mathewsii	2A	2S
Heliangelus		
strophianus		S
exortis		8S
viola		S
Eriocnemis		
vestitus		8S
luciani		S
Ocreatus		
underwoodii	2A	
Lesbia		
victoriae		S
nuna	2A	
Metallura		
tyrianthina		5S
Aglaiocercus		
kingi		S
Heliomaster		
furcifer	A	
Archilochus		
colubris	5A	
Calliphlox		
amethystina	13A	
Calypte		
anna		S
Acestrura		
mulsant	A	
Selasphorus		
rufus	2A	

COLIIFORMES
COLIIDAE

1 genus, 6 species
1 species unrepresented

	Spirit	Skels
Colius		
(*Colius*)		
striatus	4A*,14A	9S,K
castanotus	A	S
colius	4A	3S
(*Urocolius*)		
indicus	2A	
macrourus	2A	

TROGONIFORMES
TROGONIDAE

8 genera, 37 species
4 genera & 18 species unrepresented

	Spirit	Skels
Pharomachrus		
mocinno	A	K
fulgidus		S
auriceps		S,K
Trogon		
(*Curucujus*)		
massena	A	
melanurus	A	
Trogon)		
viridis	A	
citreolus	A	S
(*Trogonurus*)		
collaris	18A	S,K
rufus	A	
surrucura		S
curucui		2S
violaceus		S
Apaloderma		
narina	A	
Harpactes		
reinwardtii		S
kasumba	4A	
diardii	2A	4S
duvaucelii	4A	6S
erythrocephalus	A†,5A	S,2S†
wardi	A	

CORACIIFORMES

ALCEDINIDAE

14 genera, 90 species
1 genus & 43 species unrepresented

	Spirit	Skels
CERYLINAE		
CERYLE		
(*Megaceryle*)		
maxima	A	S
torquata	5A,A*	S†
alcyon	3A	2S,S†
(*Ceryle*)		
rudis	2A†,5A	S†,K
Chloroceryle		
amazona	4A	S
americana	13A	S
inda	3A	S
aenea	A	
ALCEDININAE		
Alcedo		
(*Alcedo*)		
atthis	5A	4S,2S
meninting	48A	S
coerulescens	19A	
(*Corythornis*)		
cristata	12A	2S,S†
leucogaster	4A	
Ispidina		
picta	21A	S
madagascariensis	2A	
Ceyx		
lepidus		3S
azureus	5A	S
erithacus	17A	S
rufidorsum	4A	2S
DACELONINAE		
Pelargopsis		
capensis	5A	S,2S
Lacedo		
pulchella	A	
Dacelo		
novaeguineae	6A,A*	8S
leachii	3A	2S
gaudichaud	2A	S
Clytoceyx		
rex	A	
Melidora		
macrorrhina	A	
Cittura		
cyanotis		S
Halcyon		
coromanda	A	
badia	A	
smyrnensis	6A	S2†,K
pileata	A	
cyanoventris	4A	
leucocephala	4A*,2A	
senegalensis	2A*,6A	S
malimbica	3A	
Halcyon (cont.)		
albiventris	2A*	
chelicuti	7A	
macleayii	6A	K
leucopygia	A	
farquhari	3A	
pyrrhopygia	3A	4S
sancta	29A	4S,K
chloris	34A	2S
saurophaga	A	
recurvirostris	3A*,3A	
concreta	3A	5S
Tanysiptera		
galatea	2A	

TODIDAE

1 genus, 5 species
4 species unrepresented

	Spirit	Skels
Todus		
todus	10A	S

MOMOTIDAE

6 genera, 9 species
2 genera & 4 species unrepresented

	Spirit	Skels
Aspatha		
gularis		2K
Electron		
platyrhynchum	3A	
Baryphthengus		
ruficapillus		S,2K
martii	A	
Momotus		
momota	6A	3S,K

MEROPIDAE

3 genera, 24 species
1 genus & 9 species unrepresented

	Spirit	Skels
Nyctyornis		
amicta	3A*,7A	S,K
athertoni		S†
Merops		
gularis	2A	
muelleri	A	
bulocki	A	
pusillus	18A	
variegatus	7A	
hirundinaceus	A	
albicollis	9A	S
viridis	18A*	
superciliosus	A*,5A	2S
ornatus	5A*,5A	4S
apiaster	2A,3A	S,K
malimbicus	A	
nubicus		S

CORACIIDAE

2 genera, 11 species
4 species unrepresented

	Spirit	Skels
Coracias		
garrulus	A*	2S,K
abyssinica	3A	2S†
caudata	2A,2A*	
benghalensis	A	S†

CORACIIDAE (cont.)

	Spirit	Skels
Eurystomus		
glaucurus	5A	2S
gularis	2A,A*	
orientalis	A*,9A	6S,2S†

BRACHYPTERACIIDAE

3 genera, 5 species

Brachypteracias		
leptosomus	A	
squamigera	A	
Atelornis		
pittoides	2A	2S
crossleyi		S†
Uratelornis		
chimaera	A	

LEPTOSOMATIDAE

1 genus, 1 species

Leptosomus		
discolor	2A	S,S†

UPUPIDAE

1 genus, 1 species

Upupa		
epops	A,11A,5A*	2S,2K,2S†

PHOENICULIDAE

2 genera, 8 species

4 species unrepresented

Phoeniculus		
purpureus	2A	3S
bollei	A	
aterrimus	A	
Rhinopomastus		
cyanomelas	A	S

BUCEROTIDAE

12 genera, 44 species

1 genus & 14 species unrepresented

	Spirit	Skels
Tockus		
birostris		K
fasciatus	A	K
alboterminatus	4A*	
nasutus	A*,7A	2S
hemprichii		K
griseus	2A	K
camurus	3A	
erythrorhynchus	3A	S,S†
deckeni	A†	
Berenicornis		
comatus	2A	
Anorrhinus		
galeritus	3A*	S
Penelopides		
panini		2S
Aceros		
nipalensis		K
corrugatus		S
undulatus	2A*	S,S†,K
plicatus		3S,3K
Anthracoceros		
malayanus		S,K
malabaricus	3A*	6S,S†
coronatus		2S
Bycanistes		
bucinator	A	2S,K
cylindricus	A	
subcylindricus	A*	
Ceratogymna		
atrata		2S,K
elata	A	
Buceros		
rhinoceros	4A*	2S,2K
bicornis	A	2S,5K
hydrocorax	A	2S
Rhinoplax		
vigil		S†,K
Bucorvus		
abyssinicus	2A	4S,2K
leadbeateri	A,A†	2K
Bycanistes		
brevis	7A,A†	S,K

PICIFORMES

GALBULIDAE

5 genera, 17 species

1 genus & 10 species unrepresented

Galbalcyrhynchus		
leucotis	A	S
Jacamaralcyon		
tridactyla	3A	S
Galbula		
galbula	3A	S
ruficauda	2A*,8A	
leucogastra		2S
dea	8A	
Jacamerops		
aurea	4A	

BUCCONIDAE

10 genera, 34 species

2 genera & 20 species unrepresented

Notharchus		
macrorhynchos	3A	2S
tectus	A	
Nystalus		
radiatus	3A	
chacuru	A	S
maculatus	A	
Malacoptila		
striata		S
fusca		S
panamensis	3A	
Micromonacha		
lanceolata		S
Nonnula		
ruficapilla	3A	

BUCCONIDAE (cont.)

	Spirit	Skels
Monasa		
atra	A	S
nigrifrons	A	
morphoeus	8A	S
Chelidoptera		
tenebrosa	9A	

CAPITONIDAE

13 genera, 80 species

1 genus & 32 species unrepresented

	Spirit	Skels
Capito		
niger	A	S
Eubucco		
richardsoni		S
bourcierii	A	
Semnornis		
frantzii	A	
ramphastinus	3A	
Psilopogon		
pyrolophus	3A	3S
Megalaima		
virens	A	2S,K
lagrandieri	2A	K
zeylanica	A†,8A	2S†,2K
viridis	A	2S
faiostricta	3A	
corvina		5S
chrysopogon	2A	2S
rafflesii	A	S,2K
mystacophanos	3A	S
javensis		S
flavifrons	A	
franklinii	A	S
Megalaima		
oorti	A	3S
asiatica	3A	2S,2S†
australis	3A	2S,S†
rubricapilla	2A	
haemacephala	5A	5S
henrici		3S
Calorhamphus		
fuliginosus	2A	S
Gymnobucco		
peli	6A	
bonapartei	2A	
Smilorhis		
leucotis	2A*,2A	
Pogoniulus		
duchaillui	3A	
scolopaceus	3A*,2A	S
chrysoconus	A	
bilineatus	9A	2S
subsulphureus	2A	
Tricholaema		
lacrymosum	2A	
diadematum	A	
melanocephalus	2A	
hirsutum	A	
Lybius		
vieilloti	3A	
torquatus	3A	
guifsobalito	A	
leucocephalus	2A	
melanopterus	A	
bidentatus	3A	
dubius	2A	
Trachyphonus		
purpuratus	A,A†	S
vaillantii	2A	
darnaudii	2A	
margaritatus		S

INDICATORIDAE

4 genera, 14 species

2 genera & 9 species unrepresented

	Spirit	Skels
Prodotiscus		
insignis	a	
regulus	A†	
Indicator		
maculatus	A	
indicator	3A	K
minor	A	S
archipelagicus	A	
Melichneutes		
robustus	A	

RAMPHASTIDAE

6 genera, 33 species

15 species unrepresented

	Spirit	Skels
Aulacorhynchus		
prasinus	A	S,S†
Pteroglossus		
viridis	4A	3S
inscriptus	3A	
flavirostris	A	
aracari	A	S
castanotis	A^{k},2A	
torquatus	2A	S
Selenidera		
maculirostris	2A	S
Sellnidera		
langsdorffii		S
reinwardtii		K,S
spectabilis	A	
Baillonius		
bailloni	A	S
Andigena		
laminirostris		S
Ramphastos		
discolorus	3A	
vitellinus	7A	2S
sulfuratus	A	3S,2S†
toco	A	4S
tucanus	A	S
ambiguus	A	

PICIDAE

27 genera, 204 species
3 genera & 128 species unrepresented

JYNGINAE	Spirit	Skels
Jynx		
torquilla	4A	4S,4K
PICUMNINAE		
Picumnus		
squamulatus		S
olivaceus	A	
innominatus	A	
Sasia		
ochracea	2A	
abnormis	9A	K
Nesoctites		
micromegas	A	
PICINAE		
Melanerpes		
candidus	A	
lewis	2A	S
formicivorus	4A	S
cruentatus	A	
flavifrons		2S
pucherani	3A	S
rubricapillus	2A	2S
aurifrons	2A	
Sphyrapicus		
varius	3A	
Campethera		
nubica	A	
bennettii	2A	
punctuligera	3A	
nivosa	4A	
Dendropicos		
fuscescens	3A	
namaquus	A	
xantholophus	A	
Picoides		
maculatus	A	
obsoletus	2A	
canicapillus	3A	
minor	2A	2S,3K,S†
macei		3S
auriceps	A	
dorae	2A	
darjellensis		S
major	2A*,9A	8S,4K
nuttallii		S
pubescens	A	2S
villosus	2A	S
tridactylus	3A	S,S†,2K
arcticus	A	
Veniliornis		
nigriceps		S
passerinus		S†
affinis	A	
Piculus		
flavigula	A	
aurulentus	A	S
Colaptes		
auratus		S
campestris	3A	4S,S†
Celeus		
loricatus	A	
brachyurus	A	S†
elegans	2A	
Dryocopus		
lineatus		2S
javensis	2A	
martius	A	3S
Campephilus		
melanoleucos	2A^{k},2A	
rubricollis		2S
magellanicus	5A	
Picus		
miniaceus	A	S
puniceus	3A	3S
chlorolophus	A	2S†
mentalis	2A	S
flavinucha	A	2S†
vittatus		2S
xanthopygaeus	5A	
canus		S,K
viridis	11A	9S,5K
Dinopium		
rafflesii	2A	
javanense	6A	
benghalense	3A	S
Chrysocolaptes		
lucidus	A	2S
Gecinulus		
grantia		S
Blythipicus		
rubiginosus	2A	S
pyrrhotis	2A†,A	
Reinwardtipicus		
validus	2A	
Meiglyptes		
tristis	5A	S
tukki	4A,A†	3S
Hemicircus		
concretus	A	
Mulleripicus		
fulvus		2S
pulverulentus	2A	

EURYLAIMIDAE

8 genera, 14 species
2 species unrepresented

EURYLAIMINAE		
Smithornis		
capensis	2A*,2A	
rufolateralis		S
sharpei		2S
Pseudocalyptomena		
graueri	A†	
Corydon		
sumatranus		2S

EURYLAIMINAE (cont.)

	Spirit	Skels
Cymbirhynchus		
macrorhynchos	8A*,15A	2S
Eurylaimus		
javanicus		S,K
ochromalus	6A	
Serilophus		
lunatus		2S†
Psarisomus		
dalhousiae	3A	2S†
Calyptomena		
viridis	3A	8S
whiteheadi	A	S

DENDROCOLAPTIDAE

13 genera, 52 species
4 genera & 36 species unrepresented

Dendrocincla		
fuliginosa	2A	
homochroa	A	
Deconychura		
longicauda	A	
Sittasomus		
griseicapillus	A	
Glyphorhynchus		
spirurus	8A	
Xiphocolaptes		
albicollis		K
Dendrocolaptes		
picumnus		S
platyrostris	A	
Xiphorhynchus		
picus	A	
guttatus	7A	S
flavigaster	A	
Lepidocolaptes		
angustirostris	3A	
affinis	4A	
fuscus		S
souleyetii		S
Campylorhamphus		
trochilirostris	A	2S

FURNARIIDAE

34 genera, 218 species
14 genera & 178 species unrepresented

FURNARIINAE

Geositta		
cunicularia	6A	
isabellina	A	
Upucerthia		
ruficauda	4A	
dumetaria	3A	
Cinclodes		
fuscus	A	
patagonicus	2A	
nigrofumosus		S
Furnarius		
leucopus	2A	
rufus	2A,2A*	K

SYNALLAXINAE

	Spirit	Skels
Aphrastura		
spinicauda	3A	
Leptasthenura		
platensis	2A	
aegithaloides	A	S
Synallaxis		
(*Schoeniophylax*)		
phryganophila	A	S
(*Synallaxis*)		
ruficapilla	2A	
frontalis	2A	
albescens	A	
spixi	A	
gujanensis		S
cinnamomea	6A	
Certhiaxis		
cinnamomea	2A	
Thripophaga		
pyrrholeuca		2S
Phacellodomus		
rufifrons	2A	
striaticollis	2A	
ruber	A	
Spartonoica		
maluroides	4A	
Phleocryptes		
melanops	2A	
Anumbius		
annumbi	2A*,5A	

PHILYDORINAE

Lochmias		
nematura	A	
Pseudoseisura		
lophotes	2A	
Pseudocolaptes		
lawrencii	A	
boissonneautii		S
Philydor		
(*Philydor*)		
rufosuperciliatus	A	
lichtensteini	2A	2S
rufus	2A	
Sclerurus		
albigularis	A*	
caudacutus	3A	
guatemalensis	4A	
Xenops		
minutus	A	S
rutilans	2A	
Pygarrhichas		
albogularis	A	

FORMICARIIDAE

51 genera, 228 species
27 genera & 192 species unrepresented

Batara		
cinerea	A	S

FORMICARIIDAE (cont.)

	Spirit	Skels
Mackenziaena		
severa		S
Taraba		
major	5A	
Sakesphorus		
canadensis		2S
Thamnophilus		
doliatus	2A	2S
nigriceps	4A	
punctatus	9A	4S
caerulescens	A	S
ruficapillus	4A	
Dysithamnus		
mentalis	2A	
Thamnomanes		
caesius	A	
Myrmotherula		
surinamensis	A	
fulviventris	4A	
axillaris	3A	
Herpsilochmus		
longirostris	A	
Formicivora		
grisea	3A	
Drymophila		
ferruginea	4A	
squamata	A	
Cercomacra		
tyrannina	A	
Pyriglena		
leuconota	2A	
atra	2A	
Myrmoborus		
leucophrys	3A	
Gymnocichla		
nudiceps	7A	S
Myrmeciza		
longipes	2A	
exsul	7A	S
ferruginea	2A	
Pithys		
albifrons	2A	
Gymnopithys		
rufigula	A	
leucaspis	7A	2S
Hylophylax		
naevioides	5A	S
poecilonota	2A	
Phaenostictus		
mcleannani	2A	
Formicarius		
analis	2A	S
Chamaeza		
campanisona		S
Grallaria		
(Grallaria)		
varia	A	S
Hylopezus		
perspicillatus	A	

CONOPOPHAGIDAE

2 genera, 11 species
8 species unrepresented

	Spirit	Skels
Conopophaga		
lineata	2A	
melanops	A	
Corythopis		
torquata	A	

RHINOCRYPTIDAE

12 genera, 30 species
9 genera & 28 species unrepresented

	Spirit	Skels
Pteroptochos		
megapodius	A	3S
Scelorchilus		
albicollis		S†

COTINGIDAE

27 genera, 79 species
16 genera & 58 species unrepresented

	Spirit	Skels
Ampelion		
rubrocristata	2A	
Pipreola		
riefferii	A	
chlorolepidota	A	
Lipaugus		
subalaris	A	S
vociferans	2A	K
Pachyramphus		
viridis	A	
rufus	2A	
cinnamomeus	3A	S
polychopterus	2A	
minor		S
Tityra		
cayana	2A	
semifasciata	A	S,K
inquisitor		S
Cotinga		
cayana		K
Gymnoderus		
foetidus	A	
Querula		
purpurata	2A	S
Perissocephalus		
tricolor	4A	S
Procnias		
alba	3A,A†	
nudicollis	A	2S
Rupicola		
rupicola	2A	S
peruviana	A*	S

PIPRIDAE

19 genera, 57 species
11 genera & 39 species unrepresented

	Spirit	Skels
Pipra		
aureola	A	
erythrocephala	10A	3S
rubrocapilla	2A	

PIPRIDAE (cont.)

Pipra (cont.)	Spirit	Skels
mentalis	A	2S
pipra	5A	
coronata	5A	S
serena	2A	
Antilophia		
galeata	A	
Chiroxiphia		
lanceolata	A	
pareola	17A	3S
caudata	A	
Masius		
chrysopterus	2A	
Ilicura		
militaris	2A	
Corapipo		
gutturalis	2A	
leucorrhoa	2A	
Manacus		
manacus	4A	
vitellinus	6A	2S
Chloropipo		
holochlora	A	

TYRANNIDAE

112 genera, 374 species

64 genera & 302 species unrepresented

FLUVICOLINAE

	Spirit	Skels
Xolmis		
coronata	A,A*	
irupero	A	
Muscisaxicola		
macloviana		2S
maculirostris	A	
Lessonia		
rufa	9A	
Myiotheretes		
striaticollis	3A	
Sayornis		
phoebe	2A	
nigricans		2S
saya	A	
Colonia		
colonus	2A	
Knipolegus		
nigerrimus	A	
Hymenops		
perspicillatus	7A	
Fluvicola		
pica	A	S
nengeta	A	
Arundinicola		
leucocephala	12A	S
Pyrocephalus		
rubinus	15A	S
Satrapa		
icterophrys	3A	
Machetornis		
rixosus	4A	
Sirystes		
sibilator	2A	
Muscivora		
forficata		S
tyrannus	4A	2S
Tyrannus		
tyrannus	6A	S
melanocholicus	4A,2A*	2S
dominicensis	8A	S†
caudifasciatus	2A	
Megarhynchus		
pitangua	A	S
Myiodynastes		
maculatus	4A	S
Myiozetetes		
cayanensis	3A	2S
similis		
Pitangus		
sulphuratus	A*,10A	S

MYLARCHINAE

	Spirit	Skels
Myiarchus		
ferox	2A	
tyrannulus	2A	
stolidus	2A	
magnirostris	9A	
Attila		
spadiceus	4A	S
cinnamomeus	A	
Laniocera		
hypopyrrha		S
Contopus		
virens	A	
cinereus	4A	
caribaceus	A	
Empidonax		
virescens	2A	
hammondii	A	
euleri	A	
Terenotriccus		
erythrurus	A	
Myiobius		
villosus	A	
barbatus	2A	S
Myiophobus		
fasciatus	A*,3A	
Onychorhynchus		
coronatus	A	K

PLATYRINCHINAE

	Spirit	Skels
Platyrinchus		
mystaceus	5A	
Tolmomyias		
sulphurescens	7A	
Rhynchocyclus		
olivaceus	3A	2S

EUSCARTHMINAE

	Spirit	Skels
Todirostrum		
poliocephalum	3A	

EUSCARTHMINAE (cont.)

Todirostrum (cont.)

	Spirit	Skels
cinereum	A	2S
plumbeiceps	2A	
sylvia	A	
Oncostoma		
olivaceum	A	
EUSCARTHMINAE		
Colopteryx		
galeatus	A	
Myiornis		
auricularia	A	
Hemitriccus		
diops	A	
Pogonotriccus		
eximius	A	
Phylloscartes		
ventralis	A	
SERPOPHAGINAE		
Tachuris		
rubrigastra	A	
Anairetes		
parulus		S
Serpophaga		
subcristata	6A	
Mecocerculus		
stictopterus		S
ELAENINAE		
Elaenia		
martinica	A	
spectabilis	A	
albiceps	2A	
pallatangae	2A	
Phyllomyias		
fasciatus	A	
Leptopogon		
amaurocephalus	A	
Minonectes		
olivaceus	5A	S
Pipromorpha		
oleaginea	6A	3S

OXYRUNCIDAE

1 genus, 1 species

Oxyruncus		
cristatus	A	

PHYTOTOMIDAE

1 genus, 3 species
1 species unrepresented

Phytotoma		
rutila	A	
rara		2S

PITTIDAE

1 genus, 24 species
12 species unrepresented

	Spirit	Skels
Pitta		
soror	A	
oatesi	4A	
caerulea		S
erythrogaster	A	
granatina	7A	
cyanea	A	
guajana	2A	S
baudii	A	S
sordida	24A	
brachyura	12A	S
angolensis	2A	
versicolor	A	K

XENICIDAE

2 genera, 4 species
1 species unrepresented

Acanthisitta		
chloris	6A	S
Xenicus		
longipes	7A	S
gilviventris	4A	

PHILEPITTIDAE

2 genera, 4 species
1 species unrepresented

Philepitta		
castanea	4A	S
schlegeli	2A	
Neodrepanis		
coruscans	A	

MENURIDAE

1 genus, 2 species
1 species unrepresented

Menura		
novaehollandiae		S,S†,2K

ATRICHORNITHIDAE

1 genus, 2 species
1 genus & 2 species unrepresented

None

ALAUDIDAE

15 genera, 77 species
3 genera & 53 species unrepresented

Mirafra		
javanica	3A	8S
hova		S
rufocinnamomea	2A	
poecilosterna	2A	
nigricans	A	
Eremopterix		
leucotis	A	
signata	3A	
nigriceps	2A	
Ammomanes		
cincturus	A	
Alaemon		
alaudipes	A	
Ramphocoris		
clotbey	A	

ALAUDIDAE (cont.)

	Spirit	Skels
Melanocorypha		
calandra		2S
maxima	2A*	
leucoptera	A	
yeltoniensis		S†
Calandrella		
cinerea	4A	4S
rufescens		S
Chersophilus		
duponti	A	
Galerida		
cristata	13A	S
theklae	3A	2S
Lullula		
arborea	A	3S,K
Alauda		
arvensis	29A	7S,S†,7K
gulgula	2A	
Eremophila		
alpestris	3A	2S

HIRUNDINIDAE

20 genera, 80 species

5 genera & 50 species unrepresented

PSEUDOCHELIDONINAE

Pseudochelidon		
eurystomina	A†	K

HIRUNDININAE

Tachycineta		
bicolor	7A	
leucorrhoa	2A	
Progne		
tapera	3A	
chalybea	2A	
modesta	4A	
Notiochelidon		
cyanoleuca	A	
Atticora		
fasciata	A	
Stelgidopteryx		
ruficollis	3A	
Cheramoeca		
leucosternum		S
Pseudhirundo		
griseopyga	2A	
Riparia		
paludicola		S,S†
riparia	2A	4S,K
cincta	A	S
Ptyonoprogne		
obsoleta	A	
fuligula	2A*	
Hirundo		
rustica	62A	16S,6K,S†,S*
tahitica	A*,12A	2S,S†
Cecropis		
cucullata	2A	
semirufa	3A	

Cecropis (cont.)	Spirit	Skels
senegalensis	3A	
daurica	3A	S†
Petrochelidon		
rufigula	A	
nigricans	3A	7S
pyrrhonota	5A	S
ariel		2S
Delichon		
urbica	9A	12S,2K,S*
Psalidoprocne		
(*Psalidoprocne*)		
albiceps	A	
holomelaena	3A	
obscura	A	

MOTACILLIDAE

5 genera, 5 species

1 genus & 28 species unrepresented

Dendronanthus		
indicus	2A	
Motacilla		
flava	17A	6S,2K
citreola		2S†
cinerea		2S,2S†,4K
alba	5A	11S,5S†,4K
aguimp	5A	
capensis	A	
flaviventris	A	
Macronyx		
croceus	3A	
ameliae	2A	
Anthus		
(Group A)		
novaeseelandiae	16A	4S
campestris		2K
similis	3A	
leucophrys	4A	S†
pratensis	2A	4S,S†,4K
trivialis	22A	S,2K
hodgsoni	A	2S†
roseatus	A	
cervinus	A	S
spinoletta	5A	2S,2K
(Group B)		
berthelotii	A	S
sokokensis	A	
(Group C)		
furcatus		S
lutescens	3A	S
correndera	6A	
antarticus	A	

CAMPEPHAGIDAE

9 genera, 70 species

3 genera & 42 species unrepresented

Coracina		
novaehollandiae	9A	9S
lineata	2A	
leucopygia	A	
papuensis	9A	2S

CAMPEPHAGIDAE (cont.)

Coracina (cont.)	Spirit	Skels
robusta	A	
caesia		3K
pectoralis	2A	
cinerea	2A	S
azurea	A	S
tenuirostris	4A	S
morio	A	
melaena	A	
melaschistos	A	3S†
fimbriata		S
Lalage		
nigra	5A	K
sueurii	27A	5S
leucomela	11A	S
maculosa	8A	
Campephaga		
phoenicea	7A	S
Pericrocotus		
divaricatus	A	
cinnamomeus	2A	S
brevirostris		S,2S†
flammeus	35A	2S†
solaris		6S
Hemipus		
picatus	8A	
hirundinaceus	4A	
Tephrodornis		
gularis	3A	S,2S†
pondicerianus	A	

PYCNONOTIDAE

15 genera, 123 species

4 genera & 60 species unrepresented

Spizixos		
semitorques	A	
Pycnonotus		
zeylanicus	A	
melanoleucos	2A	
melanicterus	3A	S,2S†
squamatus	A	S
cyaniventris	A	
iocosus	3A	8S
xanthorrhous	A	
leucogenys	3A	S
cafer	A	2S
aurigaster	11A	S
xanthopygos	2A	S†
barbatus	24A	2S
finlaysoni	2A	
flavescens	2A	
goiavier	3A	S
luteolus	A	
plumosus	12A	
blanfordi	A	
brunneus	2A	
erythropthalmos	3A	2S
virens	20A	S
gracilis	3A	

Pycnotus (cont.)	Spirit	Skels
curvirostris	2A	
importunus	A	
latirostris	18A	S
gracilirostris	4A	
simplex	A	S
Baeopogon		
indicator	A	
Ixonotus		
guttatus	3A	
Chlorocichla		
simplex	9A	
flavicollis	5A	
flaviventris	4A	
Phyllastrephus		
terrestris	5A	
strepitans		S
flavostriatus	A	
debilis	2A	S
albigularis	2A	
fishceri	13A	2S
icterinus	4A	
xavieri	3A	
cinereiceps	A	
Bleda		
syndactyla	5A	
eximia	5A	
canicapilla	A	
Nicator		
chloris	9A	S
vireo	A	
Criniger		
finschii		S
barbatus	A	
calurus	8A	
pallidus	2A	
ochraceus	3A	12S
bres	15A	5S
phaeocephalus	19A	12S
Setornis		
criniger	3A	
Hypsipetes		
viridescens	A	
charlottae	3A	
criniger	11A	9S,2S†
mcclellandii	2A	10S
flavala	2A	2S,S†
amaurotis	A	
madagascariensis	5A	2S,S†
Tylas		
eduardi	2A	S

IRENIDAE

3 genera, 14 species

5 species unrepresented

Aegithina		
tiphia	15A	
viridissima	A	
lafresnayei	3A	

IRENIDAE (cont.)

	Spirit	Skels
Chloropsis		
sonnerati	6A	
cyanopogon	A	3S
cochinchinensis	5A	2S
aurifrons	A	S,2S
hardwickei	2A	3S
Irena		
puella	17A	5S

LANIIDAE

12 genera, 74 species

40 species unrepresented

PRIONOPINAE

Eurocephalus		
ruppelli	A	

PRIONOPINAE

Prionops		
plumata	3A	S
caniceps	A	S
retzii	A	
scopifrons	A	

MALACONOTINAE

Lanioturdus		
torquatus	6A	
Nilaus		
afer	8A	
Dryoscopus		
gambensis	3A	
cubla	4A	
sabini	2A	
Tchagra		
senegala	6A	
australis	A	3S
Laniarius		
ferrugineus	2A	2K
barbarus	4A	S†
funebris	A	S
leucorhynchus		S
Telophorus		
bocagei	A	
sulfureopectus		S
multicolor	2A	
Malaconotus		
cruentus	A	
blanchoti		S

LANIINAE

Corvinella		
corvina	A	
melanoleuca	A	
Lanius		
tigrinus	6A	
cristatus	4A	
collurio	7A	7S,4K
collurioides	A	
schach	6A	4S†,K
minor	A	S
ludovicianus	A	
Lanius (cont.)	Spirit	Skels
excubitor	2A*,11A	4S,K
excubitoroides	A	
collaris	10A*,9A	
senator	A*,10A	2S,K

PITYRIASINAE

Pityriasis		
gymnocephala	7A	2S

VANGIDAE

9 genera, 13 species

2 species unrepresented

Calicalicus		
madagascariensis	5A	
Schetba		
rufa	2A	
Vanga		
curvirostris	4A	
Xenopirostris		
xenopirostris	A	
Falculea		
palliata	3A	2S
Leptopterus		
viridis	3A	S
chabert	4A	
madagascarinus	A	
Oriolia		
bernieri		2S†
Euryceros		
prevostii	2A	S
Hypositta		
corallirostris	A	S†

BOMBYCILLIDAE

5 genera, 8 species

1 genus & 4 species unrepresented

	Spirit	Skels
PTILOGONATINAE		
Ptilogonys		
caudatus	A	
Phainopepla		
nitens	4A	
Bombycilla		
garrulus	7A*,3A	5S
cedrorum	2A*,4A	K
HYPOCOLIINAE		
Hypocolius		
ampelinus	A†,3A	

DULIDAE

1 genus, 1 species

Dulus		
dominicus	2A	

CINCLIDAE

1 genus, 5 species

3 species unrepresented

Cinclus		
cinclus	3A*,7A	3S
pallasii		S†

TROGLODYTIDAE

14 genera, 59 species
10 genera & 49 species unrepresented

Campylorhynchus	Spirit	Skels
zonatus		S
Thryothorus		
fasciatoventris	2A	
coraya	2A	
nigricapillus	4A	S
ludovicianus	3A	
leucotis	4A	
longirostris	A	
Troglodytes		
troglodytes	5A*,16A	5S,3K
aedon	A*,3A	S
Henicorhina		
leucosticta	5A	

MIMIDAE

13 genera, 31 species
5 genera & 19 species unrepresented

Dumetella		
carolinensis	4A	2S
Melanoptila		
glabrirostris	A	
Melanotis		
caerulescens	A	
Mimus		
polyglottos	4A	2S
thenca		S
saturninus	3A	2S
Nesomimus		
trifasciatus	6A	
Toxostoma		
rufum	2A	2S
curvirostre	A	
redivivum	A	
Donacobius		
atricapillus	6A	
Margarops		
fuscatus	A	

PRUNELLIDAE

1 genus, 12 species
9 species unrepresented

Prunella		
collaris		2S
montanella		S
modularis	A*,3A	6S,2K,2S†

MUSCICAPIDAE

48 genera, 308 species
12 genera & 183 species unrepresented

TURDINAE

Brachypteryx		
stellata	A	
leucophrys	3A	
montana	A	

Erythropygia	Spirit	Skels
leucophrys	5A	
galactotes	3A	S†
quadrivirgata	A	
Drymodes		
brunneopygia	A	S†,S
Pogonocichla		
stellata	6A	
Erithacus		
erythrothorax	4A	
rubecula	9A*,10A	8S,2S†
sibilans	A	
luscinia	2A	S
megarhynchos	5A	2S,K
calliope	A	S
svecicus	7A	2S,K
pectoralis	3A	
pectardens	A	
brunneus	A	
cyane	19A	4S
cyanurus	A†,2A	
chrysaeus	2A	
Cossypha		
heuglini	2A	
cyanocampter	A	
caffra	A	
ansorgei		2S†
niveicapilla	4A	
albicapilla	2A	
Cichladusa		
arquata	2A	
Alethe		
diademata	14A	
Copsychus		
saularis	13A,A*	4S,2S
albospecularis	2A	
malabaricus	21A	5S,K
stricklandii	A	
pyrropygus	A*,A,A†	3S
Phoenicurus		
ochruros	7A,A*	3S
phoenicurus	4A*,34A	9S,K
frontalis	A	
moussieri	A	
erythrogaster	9A	
Rhyacronis		
fuliginosus	A	
Cinclidium		
leucurum	2A	
frontale	A	
Grandala		
coelicolor	A	S,2S†
Sialia		
sialis	2A	3S,2S†
mexicana	A	S
Enicurus		
velatus		S
ruficapillus	4A	5S
schistaceus	A	

TURDINAE (cont.)

	Spirit	Skels
leschenaulti	2A	2S
maculatus	A	
Cochoa		
viridis		S†
Myadestes		
unicolor	3A	
Stizorhina		
fraseri	A	
finschii	A	
Neocossyphus		
rufus	A	
poensis	6A	
Cercomela		
familiaris	A	S
Saxicola		
rubetra	A*,14A	4S,S†,4K
torquata	A*,27A	2S,2S†
caprata	A	
ferrea	9A	S†
Myrmecocichla		
aethiops	2A	
nigra	3A*,2A	
arnotti	2A	
melaena	A	
Thamnolaea		
semirufa	A	
Oenanthe		
isabellina	2A	
xanthoprymna		S
oenanthe	2A*,25A	2S,3S†
deserti	A	S
hispanica	A,2A*	
picata	A	
pleschanka	8A	
leucopyga	2A	
pileata	3A	
Chaimarrornis		
leucocephalus	A	
Saxicoloides		
fulicata	A	
Pseudocossyphus		
imerinus	A	5S
Monticola		
angolensis	5A	
saxatilis	2A	
cinclorhynchus	2A	
solitarius	A	3S
Myiophoneus		
glaucinus		S
caeruleus	5A	
Zoothera		
interpres	A*	S
citrinus	A	2S
sibirica	A	
guttata		S
mollissima	A	
dauma	2A*,3A	S,2S†
monticola		S

	Spirit	Skels
Nesocichla		
eremita	A*,8A	2S
Phaeornis		
obscurus		S
Catharus		
minimus	A	
ustulatus	4A	
guttatus	A	
Hylocichla		
mustelina	4A	
Platycichla		
flavipes	A	
Turdus		
olivaceus	4A	
abyssinicus	A	
libonyanus	A	
dissimilis	A*	
unicolor	A	S
torquatus		2S,K
boulboul	A	S†
merula	21A*,22A	24S,7K,4S†, S*
poliocephalus	2A*,4A	S,K
chrysolaus	2A	
obscurus	A	
ruficollis	A	S†
pilaris	5A*,13A	3S,3K
iliacus	19A*,52A	17S,5K
philomelos	10A	17S,S,K
viscivorus	4A	4S,2K
plumbeus	2A	
fuscater	A	S,K
serranus	2A	
rufiventris	3A*,2A	
falcklandii	A	
leucomelas	2A	
ignobilis		S
fumigatus	4A	
nudigenis	A	
albicollis	2A	
migratorius	8A	5S

ORTHONYCHINAE
9 genera, 17 species
6 genera & 14 species unrepresented

Orthonyx		
temminckii	A	
Psophodes		
olivaceus	2A	
Sphenostoma		
cristatum		S
Cinclosoma		
cinnamomeum	2A	

TIMALIINAE
49 genera, 255 species
19 genera & 149 species unrepresented

Pellorneum		
ruficeps	5A	
capistratum	4A	7S

TIMALIINAE (cont.)

	Spirit	Skels
Trichastoma		
tickelli	8A	
malaccense	14A	10S
rostratum	6A	
bicolor	2A	2S
albipectus	3A	
fulvescens	A	
puveli	A	
poliothorax	A	
pyrrhoptera	A	
Malacopteron		
magnirostre	2A	8S
cinereum	23A	7S
magnum	7A	7S
affine	A	3S
albogulare	5A,A†	
Pomatorhinus		
hypoleucos	3A	2S
schisticeps	2A	
montanus		3S
ruficollis	4A	
ochraceiceps	4A	
Pomatostomus		
temporalis	10A	8S
superciliosus	4A	3S
ruficeps	A	
Ptilocichla		
falcata	A	
Kenopia		
striata	A	S
Napothera		
atrigularis	5A	
macrodactyla	2A	2S
brevicaudata	2A	4S
epilepidota	A	
marmorata		S
Pnoepyga		
pusilla	4A	
Neomixis		
tenella		S
Stachyris		
ruficeps	A	
pyrrhops		S†
chrysaea	5A	S
nigriceps	14A	4S
poliocephala	5A	8S
striolata	A	
maculata	16A	7S
nigricollis	2A	S
thoracica		S
erythroptera	7A	4S
leucotis		5S
Macronous		
gularis	8A	
ptilosus	9A	2S
Timalia		
pileata	3A	K

	Spirit	Skels
Chrysomma		
sinense	2A	
Chamaea		
fasciata	A	S
Turdoides		
caudatus	2A	
squamiceps	A	
striatus	A	
melanops	A	2S*
plebejus	A	
jardineii	7A	
leucopygius	3A	
Garrulax		
perspicillatus		2S
albogularis		S†
leucolophus	10A	S,2S†
monileger		2S†
lugubris	2A	S
striatus		S
maesi	A	
chinensis	3A	S
davidi	A	
mitratus	A	4S
ruficollis		2S
merulinus	A	
canorus	3A	
sannio	A	
lineatus		S†
subunicolor	A	
affinis	A	
erythrocephalus	A	6S
milnei	A	
Leiothrix		
argentauris	10A	
lutea	47A	12S,S†
Cutia		
nipalensis	A	
Pteruthius		
rufiventer	A	
flaviscapis	A†	
melanotis	3A	
Gampsorhynchus		
rufulus	A	
Minla		
cynaouroptera	7A	
strigula	5A	2S
ignotincta	A	
Alcippe		
castaneceps	4A	5S
rufogularis	A	
brunnea		S
brunneicauda	7A	
poioicephala	3A	4S
peracensis	3A	
morrisonia	2A	
nipalensis	5A	5S
Crocias		
albonotatus		S

TIMALIINAE (cont.)

	Spirit	Skels
Heterophasia		
annectens	A	
capistrata	7A	
melanoleuca	3A	
picaoides	2A	2S,S†
Yuhina		
castaniceps	2A	
flavicollis	8A	S
gularis	2A	
nigrimenta	A	
Genera *Incertae Sedis*		
Myzornis		
pyrrhoura		2S†
Horizorhinus		
dohrni		S
Oxylabes		
madagascariensis	7A	
Mystacornis		
crossleyi	2A	S

PANURINAE

3 genera, 19 species

13 species unrepresented

	Spirit	Skels
Panurus		
biarmicus	6A	3K
Conostoma		
oemodium		S†
Paradoxornis		
guttaticollis	2A	
webbianus	4A	
gularis	A	
heudei	6A	

PICATHARTINA

1 genus, 2 species

	Spirit	Skels
Picathartes		
gymnocephalus	6A	5S
oreas	A*,2A,4A	S,3K

POLIOPTILINAE

3 genera, 12 species

1 genus & 8 species unrepresented

	Spirit	Skels
Ramphocaenus		
melanurus	2A	
Polioptila		
caerulea	A	
plumbea	A	
dumicola	2A	

SYLVIINAE

63 genera, 349 species

33 genera & 274 species unrepresented

	Spirit	Skels
Cettia		
(*Horeites*)		
brunnifrons	A	
(*Cettia*)		
cetti	5A	
Conopoderas		
caffra percensis	4A	2S
Locustella		
luscinioides		S
certhiola	8A	
naevia	46A	2S
lanceolata	53A	
Lusciniola		
melanopogon	A	
Acrocephalus		
paludicola	A	
schoenobaenus	A*,37A	3S,S†
scirpaceus	9A	S
palustris	2A	
stentoreus	A	S
arundinaceus	A	S
familiaris	E,A	
australis	2A	
vaughanii	A	
Nesillas		
typica		S
Thamnornis		
chloropetoides	A	
Chloropeta		
natalensis		S
Hippolais		
icterina	A,A*	
polyglotta	5A	
languida	A	S
pallida	7A	S
caligata	A	
Sylvia		
hortensis	8A	S,3K
borin	33A	2S
atricapilla	14A	S,2K
communis	25A	2S
curruca	4A	4S
minula	2A	
melanocephala	2A	S
cantillans	2A	S
undata		S
mystacea	A	
Sylvia		
cinerea	A	
Phylloscopus		
trochilus	54A	7S,2K
collybita	14A	S,S,2K
bonelli		S
sibilatrix	2A,A*	S
subaffinis	A	
fuscatus	A	
inornatus	3A	S†
borealis	13A	
coronatus	3A	
laurae	A	
Seicercus		
poliogenys	A	
Regulus		
calendula	A	S
regulus	2A*,5A	9S
ignicapillus	2A	3S,2K
satrapa	A	2S

SYLVIINAE (cont.)

	Spirit	Skels
Leptopoecile		
sophiae	A	
Scotocerca		
inquieta	3A	
Cisticola		
textrix	4A	
juncidis	12A	3S
cherina	2A	
natalensis	9A	
robusta	3A	
subruficapilla	A	
lais	2A	
chiniana	A	
brachyptera	2A	
fulvicapilla	A	
lateralis	4A	S
anonyma	8A	
erythrops	8A	
hunteri	A	
galactotes	9A	2S
Prinia		
subflava	4A	
inornata	2A	
leucopogon	2A	
gracilis	3A	
flaviventris	4A	
Apalis		
flavida	A	
melanocephala	A	
Elimina		
longicauda	2A	
Sphenoeacus		
(*Melocichla*)		
mentalis	4A	
Dromaeocercus		
brunneus	2A	
seebohmi	2A*,3A	
Orthotomus		
sutorius	2A	
atrogularis	2A	
sericeus	2A	
cucullatus		S
Camaroptera		
brachyura		S
brevicaudata	2A*,24A	S
superciliaris	A	
Eremomela		
scotops	5A	
pusilla	4A	
Sylvietta		
virens	A	
whytii	4A	
brachyura	A	
Macrosphenus		
concolor	2A	
Megalurus		
galactotes	A	
galactodea		S

Megalurus (cont.)	Spirit	Skels
timoriensis	A	S
palustris	A	S
gramineus		S
Bowdleria		
punctata	A	S
Cinclorhamphus		
cruralis	2A	S
mathewsi	3A	7S
Eremiornis		
carteri	A	
Hyliota		
flavigaster	A	
Hylia		
prasina	11A	S

MALURINAE

26 genera, 106 species

12 genera & 64 species unrepresented

Tribe **MALURINI**

Malurus		
cyaneus	8A	
melanotus		S
splendens	3A	7S
lamberti	19A	6S,S†
leuconotus	6A	3S
elegans	A	2S
dulcis	3A	
pulcherrimus	2A	2S
melanocephalus	8A	2S
coronatus	3A	S
callainus		S
Amytornis		
textilis	2A	S
striatus	A	4S
housei	A†,3A	5S†
Stipiturus		
malachurus	5A	4S

Tribe **ACANTHIZINI**

Gerygone		
olivacea	A	
magnirostris	A	6S
fusca	5A	2S
flavolateralis	6A	
Smicrornis		
brevirostris	24A	6S
Aphelocephala		
leucopsis	3A	2S
nigricincta	A	
Acanthiza		
lineata	A	S
pusilla	12A	12S
apicalis	A	
robustirostris	A	S
inornata	2A	3S
iredalei	2A	2S
reguloides	10A	
chrysorrhoa	7A	3S
uropygialis	7A	3S

ACANTHIZINI (cont.)

Sericornis	Spirit	Skels
frontalis	3A	
maculatus	3A	5S
Calamanthus		
fuliginosus	A	S
campestris	2A	
Hylacola		
cauta	A	S
Pyrrholaemus		
brunneus	4A	5S
Origma		
solitaria		S
Tribe **EPTHIANURINI**		
Epthianura		
albifrons		5S
tricolor	6A	4S
aurifrons		S
Genus *Incertae Sedis*		
Lamprolia		
victoriae	3A	3S
MUSCICAPINAE		
24 genera, 152 species		
9 genera & 96 species unrepresented		
Bradornis		
(*Bradornis*)		
microrhynchus	A	
pallidus	4A	
infuscatus		S
(*Empidornis*)		
semipartitus	2A	
Fraseria		
cinerascens	25A	
Rhinomyias		
olivacea	2A	
brunneata	A	S
umbratilis	8A,A*	3S
Ficedula		
(*Ficedula*)		
hypoleuca	31A	3S,K
albicollis	6A	
mugimaki	2A	
strophiata	4A	
solitaria	2A	S
hyperythra	8A	4S
nigrorufa	4A	
dumetoria		2S
Niltava		
(*Niltava*)		
grandis	2A	10S
macgrigoriae	2A	
sundara	A*,2A	S
concreta	A	
pallipes	A	
rubeculoides	4A	
banyumas	2A	
tickelliae	3A	
turcosa	A	
caerulata	A	

(*Muscicapella*)	Spirit	Skels
hodgsoni	A	
Muscicapa		
(*Muscicapa*)		
rufigastra	A	
striata	2A*,14A	6S,3K
sibirica	2A	
latirostris	14A	
adusta	A	
cassini	4A	
caerulescens	3A	
comitata		3S
gambagge	A	
(*Eumyias*)		
thalassina	6A	
Newtonia		
brunneicauda		S
Microeca		
leucophaea	14A	3S
flavigaster	4A	
Culcicapa		
ceylonensis		2S
Peltops		
montanus	A	
Petroica		
multicolor	7A	6S
goodenovii	6A	3S
phoenicea	5A	
rosea	A	
cucullata	8A	5S
macrocephala		2S
vittata		S
traversi	2A	
Eopsaltria		
australis	4A	2S
griseogularis	3A	4S
Peneoenanthe		
pulverulenta	4A	
Philentoma		
pyrrhoptera	5A	5S
velata	A	4S
Poecilodryas		
superciliosa	2A	S
PLATYSTEIRINAE		
4 genera, 25 species		
1 genus & 17 species unrepresented		
Bias		
(*Bias*)		
musicus	A	K
Batis		
capensis	A†	
molitor	2A	
senegalensis	A	
minor	4A	
Platysteira		
cyanea	5A	
concreta	A	
castanea	3A	
jamesoni	A	

MONARCHINAE

17 genera, 92 species
6 genera & 64 species unrepresented

	Spirit	Skels
Erythrocercus		
mccallii	A	
Trochocercus		
nigromitratus	A	
nitens	3A	
Terpsiphone		
viridis	4A	
rufocinerea	3A	
mutata	A	S
paradisi	12A	6S
Hypothymis		
azurea	5A	3S
Seisura		
inquieta	9A	4S
Machaerirhynchus		
nigripectus	A	
Mayrornis		
schistaceus	A	
lessoni	2A	S
Clytorhynchus		
pachycephaloides	A	
vitiensis	2A	S
hamlini	3A	
Monarcha		
alecto	7A	2S
castaneiventris	2A	
richardsii	A	
guttula		2S
trivirgata	5A	K
verticalis	2A	
chrysomela	6A	S
Arses		
kaupi	A	
telescophthalmus	3A	K
Myiagra		
rubecula	10A	S
ferrocyanea	4A	
vanikorensis	2A	S
azureocapilla	A	S

RHIPIDURINAE

2 genera, 40 species
1 genus & 29 species unrepresented

	Spirit	Skels
Rhipidura		
leucothorax	2A	
rufifrons	5A	
spilodera	A	
rennelliana	3A	
fuliginosa	5A	2S
nebulosa	2A	
albicollis	4A	7S
javanica	A*,5A	
rufiventris	10A	S
perlata	3A	2S
leucophrys	12A	2S

PACHYCEPHALINAE

10 genera, 46 species
4 genera & 33 species unrepresented

	Spirit	Skels
Falcunculus		
frontatus	2A	S
Oreoica		
gutturalis	4A	S
Pachycephala		
olivacea		S
simplex	4A	3S
pectoralis	22A	9S,S†
flavifrons	2A	
rufiventris	25A	9S
lanioides	6A	3S
Colluricincla		
megarhyncha	A	
parvula	A	2S
harmonica	18A	S
Pitohui		
kirhocephalus	A	2S
Genus *Incertae Sedis*		
Turnagra		
capensis		S

AEGITHALIDAE

3 genera, 8 species
1 genus & 5 species unrepresented

	Spirit	Skels
Aegithalos		
caudatus	9A*,A	4S
concinnus	4A	
Psaltriparus		
minimus	5A	

REMIZIDAE

4 genera, 10 species
2 genera & 6 species unrepresented

	Spirit	Skels
Anthoscopus		
flavifrons	A,3A*	
caroli	2A	
minutus	3A*	
Auriparus		
flaviceps	2A*	

PARIDAE

3 genera, 47 species
26 species unrepresented

	Spirit	Skels
Parus		
palustris	A	4S
montanus		S
atricapillus	3A	3S
carolinensis	2A	S
hudsonicus		S
rufescens	A	
rubidiventris	A	
ater	7A	2S,2K
elegans	A	
cristatus	4A	S
dichrous		2S†
afer	A	
niger	3A	

PARIDAE (cont.)

Parus (cont.)	Spirit	Skels
major	12A	10S,6K,S†
monticolus	A	
xanthogenys		S
caeruleus	2A*,19A	5S,2K
inornatus	A	
bicolor	A	
Melanochlora		
sultanea	2A	2S,2S†
Sylviparus		
modestus	A	

SITTIDAE

1 genus, 21 species
16 species unrepresented

SITTINAE

Sitta		
europaea	3A*,3A	5S,3K
nagaensis	A	
castanea		S†
canadensis	3A	
frontalis	3A	S

DAPHOENOSITTINAE

2 genera, 3 species
1 genus & 2 species unrepresented

Neositta		
chrysoptera	12A	4S

TICHODROMADINAE

1 genus, 1 species

Tichodroma		
muraria	2A	S

CERTHIIDAE

1 genus, 5 species
4 species unrepresented

CERTHIINAE

Certhia		
familiaris	7A	4S,2S†,2K
Salpornis		
spilonotus	3A	

RHABDORNITHIDAE

1 genus, 2 species
1 species unrepresented

Rhabdornis		
mysticalis	2A	

CLIMACTERIDAE

1 genus, 6 species
3 species unrepresented

Climacteris		
picumnus	5A	
rufa		2S
melanura	9A	7S
leucophaea	4A	

DICAEIDAE

7 genera, 58 species
36 species unrepresented

	Spirit	Skels
Melanocharis		
versteri	A	
Rhamphocharis		
crassirostris	2A	
Prionochilus		
maculatus	4A	5S
percussus	2A	S
xanthopygius	2A	
thoracicus	6A	
Dicaeum		
chrysorrheum	2A	
trigonostigma	11A	S
vulneratum	2A	
aeneum	6A	
hirundinaceum	24A	6S
ignipectus	4A	
cruentatum	A*,9A	S
trochileum	9A	
Oreocharis		
arfaki	A	
Paramythia		
montium	4A	2S
Pardalotus		
punctatus	3A	2S
xanthopygus	A	
rubricatus	4A	2S
striatus		S
substriatus	4A	3S
melanocephalus	16A	

NECTARINIIDAE

5 genera, 116 species
60 species unrepresented

Anthreptes		
fraseri	5A	
anchietae	4A	
simplex	2A	S
malacensis	16A	
longuemarei	10A	4S
collaris	2A*,A†,9A	
platurus	7A	
singalensis	A	
Hypogramma		
bypogrammicum	3A	7S
Nectarinia		
olivacea	28A	2S
balfouri	3A	
verticalis	8A	S
cyanolaema	2A	K
fuliginosa	5A	
rubescens	2A	
amethystina	3A	S
senegalensis	18A	2S
adelberti	2A	
zeylonica	7A	
sericea	4A	K

NECTARINIIDAE (cont.)

	Spirit	Skels
Nectarinia (cont.)		
calcostetha	6A	
jugularis	8A	2S
souimanga		S
venusta	8A	S†
talatala	4A	
oustaleti	A	
chalybea	2A	2S
mediocris	A	
preussi	A	
chloropygia	9A	
minulla	A†	
violacea		S
habessinica	3A	
cuprea	20A	
tacazze	4A	
mariquensis	3A	S†
bifasciata	2A	
coccinigastra	5A	
erythrocerca	A*,9A	
pulchella	6A	K
famosa	2A	
johnstoni		S
notata	A	
superba	3A	
kilimensis	3A	
reichenowi	A	
sperata	A	
Aethopyga		
nipalensis	3A	
saturata	2A	
siparaja	7A	
mystacalis	2A	
ignicauda		3S
Arachnothera		
longirostra	11A	7S
robusta	3A	
flavigaster	3A	
magna	4A	3S,S†
affinis		6S

ZOSTEROPIDAE

11 genera, 83 species

7 genera & 64 species unrepresented

	Spirit	Skels
Indo-Australian Taxa		
Zosterops		
erythropleura	A	S
japonica	2A	
palpebrosa	5A*,10A	
montana	A	
atrifrons	2A	
natalis	A,2A*	
lutea	8A	4S
rennelliana	2A,2A*	
explorator	A	
flavifrons	2A	
lateralis	10A	3S
tenuirostris	A	
Woodfordia		
superciliosa	3A	
Chlorocharis		
emiliae	5A	
African, Indian Ocean Taxa		
Zosterops (cont.)		
abyssinica	2A	
senegalensis	10A	
virens	2A	
maderaspatana	2A	
Genus *Incertae Sedis*		
Hypocryptadius		
cinnamomeus	A	

MELIPHAGIDAE

39 genera, 172 species

18 genera & 114 species unrepresented

Toxorhamphus		
novaeguineae		K
Lichmera		
indistincta	13A	9S
incana	A	
Myzomela		
obscura	7A	3S
erythrocephala	2A	2S
sanguinolenta	A	
cardinalis	A*,7A	
melanocephala	A	
Certhionyx		
niger	11A	
variegatus		S
Meliphaga		
analoga	21A	
notata	A	
lewinii		S
flava	A	
albilineata	A	S
virescens	13A	11S
fasciogularis	A	
fusca	6A	9S,S*
plumula	4A	4S
chrysops	2A	
cratitia	2A	3S
keartlandi	3A	2S
penicillata	13A	S
leucotis	5A	3S
melanops	3A	
unicolor	2A	
ornata		S
Foulehaio		
carunculata		S
Melithreptus		
brevirostris	3A	2S
lunatus	24A	4S
albogularis	12A	5S
laetior	3A	7S
Entomyzon		
cyanotis	8A	3S

MELIPHAGIDAE (cont.)

	Spirit	Skels
Philemon		
citreogularis	21A	3S
novaeguineae	5A	
argenticeps	5A	2S
corniculatus	5A	S
Gymnomyza		
samoensis	2A	
Phylidonyris		
novaehollandiae	7A	5S,K
nigra	A	S
melanops	2A	
albifrons		S
Ramsayornis		
fasciatus	2A	
Plectorhyncha		
lanceolata	6A	
Conopophila		
albogularis	6A	2S
rufogularis	3A	4S
Cissomela		
pectoralis	10A	2S
Acanthorhynchus		
tenuirostris	4A	
superciliosus	A	3S
Manorina		
melanophrys	A	
melanocephala	11A	S
flavigula	7A	7S
Anthornis		
melanura	7A*,A	S
Anthochaera		
rufogularis	5A	
chrysoptera	3A	2S
carnunculata	12A	9S
Prosthemadera		
novaeseelandiae	2A	4S,4K
Promerops		
cafer	2A	S

EMBERIZIDAE

65 genera, 279 species
29 genera & 186 species unrepresented

EMBERIZINAE

1st Group

	Spirit	Skels
Melophus		
lathami	A	
Emberiza		
calandra	3A	5S,2K
citrinella	2A*,7A	8S,S†,5K
cia	3A,A*	
hortulana	A	3S
caesia	3A	
cirlus	A	2S
striolata	A	
tahapisi	3A	
rustica	A	
flaviventris	A	
cabanisi	A	

Emberiza (cont.)	Spirit	Skels
bruniceps	4A	
schoeniclus	3A*,5A	6S,S†
Calcarius		
lapponicus	3A,A*	3S
Plectrophenax		
nivalis	7A,A*	2S,2S†,K
Zonotrichia		
iliaca	A	S†
melodia	6A	2S
georgiana	3A	2S
capensis	A	
querula	A	
leucophrys	2A	
albicollis	A	2S
atricapilla	2A	
Junco		
hyemalis	2A	2S
Ammodramus		
sandwichensis	4A	
maritimus		S
savannarum	A	
aurifrons	2A	
Spizella		
arborea	4A	
passerina	6A	S
pusilla	3A	S
Pooecetes		
gramineus	4A	
Chondestes		
grammacus	2A	

2nd Group

	Spirit	Skels
Phrygilus		
atriceps	A	
gayi	3A†,4A	
fruticeti	3A†	S
erythronotus		S
plebejus	2A	
carbonarius	3A†	
Melanodera		
melanodera	A	
Rowettia		
goughensis	4A	S,K
Nesospiza		
acunhae	A*,3A	S
Diuca		
diuca	A	
Idiopsar		
brachyurus		S
Poospiza		
thoracica		S
ornata	A	
nigrorufa	9A	S

3rd Group

	Spirit	Skels
Sicalis		
uropygialis	2A	
auriventris	4A	
flaveola	8A	4S,K
luteola	2A	S

EMBERIZINAE (cont.)

	Spirit	Skels
Emberizoides		
herbicola	A	S
Embernagra		
platensis	4A	
4th Group		
Volatinia		
jacarina	A	S
Sporophila		
americana		4S
lineola	2A	
nigricollis		S
caerulescens	3A	
albogularis	A	
leucoptera		K
Oryzoborus		
crassirostris	A	
angolensis	A	2S
Catamenia		
analis	2A	
Tiaris		
canora	A	
olivacea	3A	K
bicolor	A	
Loxigilla		
noctis	2A	
5th Group		
Geospiza		
magnirostris	9A	2S,K
fortis	11A	2S
fuliginosa	20A	2S,K
difficilis		K
scandens	2A	K
conirostris	2A	K
Camarhynchus		
crassirostris	7A	2S
pallidus	A	
Certhidea		
olivacea	3A	S,2K
6th Group		
Pipilo		
chlorurus	2A	
erythrophthalmus	8A	S,K
fuscus	A	S
Arremon		
taciturnus	A	S
flavirostris	3A	S
aurantiirostris	A	3S
Atlapetes		
pileatus	A	
leucopterus		S
brunneinucha		S,K
Pezopetes		
capitalis	A	
7th Group		
Genera *Incertae Sedis*		
Charitospiza		
eucosma	A	

Gubernatrix	Spirit	Skels
cristata	2A	
Coryphospingus		
pileatus	2A*,3A	
cucullatus	11A	
Paroaria		
dominicana	A	
gularis		S
CARDINALINAE		
9 genera, 36 species		
2 genera & 23 species unrepresented		
Spiza		
americana	A	S
Pheucticus		
chrysopeplus	2A	S
tibialis	3A	
ludovicianus	2A	
melanocephalus	2A	
Cardinalis		
cardinalis	23A	2S,K
sinuatus	3A	K
Caryothraustes		
canadensis	3A	
Pitylus		
grossus		S,K
Saltator		
maximus	3A	S
coerulescens	A	S
albicollis		S
Passerina		
cyanoides	A	6S
brissonii		S,K
cyanea	6A	S
versicolor	A	
ciris		S
leclancherii	3A	
caerulescens	2A	
THRAUPINAE		
57 genera, 238 species		
23 genera & 153 species unrepresented		
1st Group		
Schistochlamys		
ruficapillus	2A	S
melanopis		S
Neothraupis		
fasciata	A	
Cissopis		
leveriana	A	S
Chlorornis		
riefferii		2S
2nd Group		
Thlypopsis		
sordida	A	
Hemithraupis		
ruficapilla	A	
flavicollis		2S
Nemosia		
pileata	A	

THRAUPINAE (cont.)

	Spirit	Skels
3rd Group		
Rhodinocichla		
rosea	A	
Mitrospingus		
cassinii	3A	
Chlorothraupis		
olivacea	2A	
Orthogonys		
chloricterus		S
4th Group		
Eucometis		
penicillata	A	
Lanio		
fulvus		S
Tachyphonus		
cristatus	2A	
surinamus	A	
coronatus	5A	
rufus	4A	2S
Trichothraupis		
melanops		S
Habia		
gutturalis	A	
Piranga		
bidentata	4A	S,S†
rubra	2A	2S
olivacea		S
ludoviciana	A	
Calochaetes		
coccineus	A	
Ramphocelus		
nigrogularis		S
dimidiatus	2A	
carbo	4A	S,S†
bresilius	4A	S
passerinii	A	
flammigerus	3A	
5th Group		
Spindalis		
zena		2S
Thraupis		
episcopus	5A	2S
sayaca	A	2S†,K
cyanoptera	4A	4S
ornata		S
abbas	A	
palmarum	A	2S
bonariensis	A	
Buthraupis		
montana		S
Anisognathus		
igniventris	A	
flavinuchus	A	S
Stephanophorus		
diadematus	4A	2S
Pipraeidea		
melanonota	4A	

	Spirit	Skels
6th Group		
Euphonia		
plumbea	A	
chlorotica	2A	
violacea	2A	
laniirostris	10A	S
musica	5A	
rufiventris	A	
pectoralis		S
Chlorophonia		
cyanea	2A	3S
occipitalis	A	
Chlorochrysa		
calliparaea	2A	
Tangara		
mexicana	A	
chilensis	2A	S
fastuosa	3A	S
seledon	A	2S
desmaresti		2S
cyanoventris	A	
arthus		2S
icterocephala		S
xanthocephala	A	
parzudakii	A	
xanthogastra	A	
gyrola	A	S
cayana	15A	S†,K
cyanicollis	A	
larvata	A	
nigrocincta	2A	
nigroviridis	2A	
vassorii	A	
cyanoptera	A	
velia	5A	S
Dacnis		
lineata		S
cayana	16A	S
Chlorophanes		
spiza	4A	S
caeruleus	A	
cyaneus	8A	
7th Group		
Genera *Incertae Sedis*		
Diglossa		
baritula	2A	
lafresnayii	A	
glauca	A	
cyanea	2A	S
Euneornis		
campestris	A	

TERSININAE

1 genus, 1 species

	Spirit	Skels
Tersinia		
viridis	A	

PARULIDAE

28 genera, 126 species
12 genera & 88 species unrepresented

	Spirit	Skels
Mniotilta		
varia	7A	2S
Vermivora		
chrysoptera		S
peregrina	A	
ruficapilla		S
Parula		
americana	A	
pitiayumi	A	S
Dendroica		
petechia	5A	S
pensylvanica	3A	S
caerulescens	2A	
graciae	A	
dominica	A	
virens	3A	S
discolor	A	
tigrina		S
magnolia	3A	
coronata	5A	S†
palmarum	7A	
striata	5A	
castanea	A	S
Setophaga		
ruticilla	6A	2S,K
Seiurus		
aurocapillus	3A	2S
noveboracensis	4A	3S
Protonotaria		
citrea	2A	S
Geothlypis		
trichas	3A	S
aequinoctialis	3A	
formosa	A	
philadelphia	4A	S
Wilsonia		
citrinia		S
pusilla	A	2S
canadensis	2A	2S
Myioborus		
miniatus		S
Basileuterus		
culicivorus		S
rufifrons	A	
Phaeothlypis		
fulvicauda	2A	
Zeledonia		
coronata	A	K
Genera *Incertae Sedis*		
Icteria		
virens	A	S
Conirostrum		
cinereum		S
Coereba		
flaveola	15A	S,K

DREPANIDIDAE

10 genera, 23 species
2 genera & 9 species unrepresented

PSITTIROSTRINAE

	Spirit	Skels
Loxops		
(*Viridonia*)		
virens	8A	S
(*Paroreomyza*)		
maculata	26A	
(*Loxops*)		
coccinea	17A	S
Hemignathus		
(*Hemignathus*)		
procerus	A	
(*Heterorhynchus*)		
lucidus	2A	S
wilsoni	A	
Pseudonestor		
xanthophrys		2S
Psittirostra		
cantans	5A	S
bailleui	A	S
kona	E,A	

DREPANIDINAE

	Spirit	Skels
Himatione		
sanguinea	3A	S
Palmeria		
dolei	2A	2S
Ciridops		
anna	E,A†	
Vestiaria		
coccinea	4A	4S

VIREONIDAE

4 genera, 43 species
34 species unrepresented

CYCLARHINAE

	Spirit	Skels
Cyclarhis		
gujanensis	10A	3S,2S†

VIREOLANIINAE

	Spirit	Skels
Vireolanius		
(*Smaragdolanius*)		
leucotis		2S

VIREONINAE

	Spirit	Skels
Vireo		
(*Vireo*)		
griseus	2A	K
modestus	A	
flavifrons	2A	
(*Vireosylva*)		
philadelphicus	3A	
olivaceus	11A	2S
gilvus	A	
Hylophilus		
ochraceiceps	A	

ICTERIDAE

23 genera, 95 species
10 genera & 52 species unrepresented

ICTERINAE

	Spirit	Skels
Psarocolius		
(*Psarocolius*)		
decumanus	4A	
wagleri	4A	
(*Gymnostinops*)		
montezuma	3A	S
Cacicus		
(*Cacicus*)		
cela	4A	S
haemorrhous	A	S
uropygialis	A	
leucoramphus	A	
solitarius	2A	S†
melanicterus	A	
(*Amblycercus*)		
holosericeus	A	
Icterus		
cayanensis	5A	S
chrysater	A	S
nigrogularis		2S
mesomelas	3A	
pectoralis		S
icterus	2A	5S,S†
galbula	3A	S
spurius	3A	
bonana	A	
Xanthocephalus		
xanthocephalus	3A	S
Agelaius		
thilius	3A	
phoeniceus	A	4S
humeralis	A	
ruficapillus		S
Sturnella		
superciliaris	A	
militaris	7A	3S,K
magna		2S
neglecta	2A	
Amblyramphus		
holosericeus	A,5A*	
Gnorimopsar		
chopi		3S
Quiscalus		
(*Cassidix*)		
mexicanus	A	S
(*Quiscalus*)		
quiscula		2S
(*Holoquiscalus*)		
niger		S
lugubris	2A	2S
Euphagus		
carolinus	A	
cyanocephalus		S

	Spirit	Skels
Molothrus		
badius	3A	
rufoaxillaris	3A	
bonariensis	3A	S
aeneus	A	
ater	A	3S
Scaphidura		
oryzivora	5A	2S

DOLICHONYCHINAE

	Spirit	Skels
Dolichonyx		
oryzivorus		S

FRINGILLIDAE

1 genus, 3 species

FRINGILLINAE

	Spirit	Skels
Fringilla		
coelebes	48A	18S,S,3K
teydea	A	S
montifringilla	15A	3S,2K

CARDUELINAE

19 genera, 119 species
8 genera & 71 species unrepresented

	Spirit	Skels
Serinus		
pusillus	2A	3S
serinus	A*,4A	
canaria	7A	11S,4K
citrinella	4A	
citrinelloides		2S
capistratus	A	
koliensis		2S
leucopygius	A	S
mozambicus	12A	5S
flaviventris	A	
sulphuratus	A	
gularis	A	S,K
burtoni	4A	
totta		S
alario	A	S
Rhynchostruthus		
socotranus	2A,2A	
Carduelis		
chloris	7A	14S,6K
spinoides		K
spinus	2A	2S
yarrellii	2A	
magellanica	A*,8A	
notata	2A	S
atrata	2A	
barbata	A	
tristis	4A	S
psaltria	8A	K
lawrencei	A	
carduelis	7A	5S,3K
Acanthis		
flammea	A*,7A	4S,2K
hornemanni	A	
flavirostris		S
cannabina	3A	4S,S†,5K

CARDUELINAE (cont.)

	Spirit	Skels
Leucosticte		
nemoricola		2S,S†
brandti	A	
Rhodopechys		
githaginea	2A	K
Carpodacus		
purpureus	A	S
mexicanus	5A	
pulcherrimus	A	
rhodochrous		S
Pinicola		
enucleator	6A*,5A	6S,K
Loxia		
pytyopsittacus		S
curvirostra	8A	3S,S†
Pyrrhula		
nipalensis		2S
pyrrhula	A*,9A	3S,S†,2K
Coccothraustes		
(*Coccothraustes*)		
coccothraustes	A,3A	2S,S†,7K
personatus	2A	
(*Mycerobas*)		
melanozanthos	A	3S†,K
vespertinus	2A	

ESTRILDIDAE

28 genera, 127 species
5 genera & 61 species unrepresented

Waxbills (*Estrildae*)

	Spirit	Skels
Nigrita		
bicolor	3A	
canicapilla	3A	K
Pytilia		
phoenicoptera	2A	2S
melba	3A	2S
Mandingoa		
nitidula	5A	
Pyrenestes		
ostrinus	3A	
Spermophaga		
haematina	9A	S
Clytospiza		
monteiri	5A	
Hypargos		
niveoguttatus	2A	5S
Lagonosticta		
rara	A	
rufopicta		S
nitidula		S
senegala	18A	3S
rubricata	A*,5A	3S
larvata	2A	
Uraeginthus		
angolensis	8A	
bengalus	29A	12S
cyanocephala	A	3S,S†

	Spirit	Skels
Uraeginthus (cont.)		
granatina	2A	S
ianthinogaster	A	
Estrilda		
caerulescens	5A	
perreini		S
melanotis	14A	2S
paludicola	5A	3S
melpoda	12A	
rhodopyga		2S
troglodytes	3A	7S
astrild	14A	5S,K
nonnula	10A	S
atricapilla	3A	
Amandava		
amandava	3A	4S
formosa		2S
subflava	A*,3A	5S
Ortygospiza		
atricollis	A	

Grass Finches (*Poephilae*)

	Spirit	Skels
Aegintha		
temporalis	6A	2S
Emblema		
picta	5A	3S,K
oculata	A	
guttata	3A	4S,2S†,2K
Neochmia		
phaeton	3A	
ruficauda	2A	
Poephila		
(*Taeniopygia*)		
guttata	10A	6S
bichenovii	12A	
(*Poephila*)		
personata		S
acuticauda	6A	4S
cincta	4A	

Mannikins (*Lonchurae*)

	Spirit	Skels
Erythrura		
(*Erythrura*)		
prasina	55A	3S
(*Acalanthe*)		
psittacea	A	
cyaneovirens	3A	
Chloebia		
gouldiae	5A	2S
Aidemosyne		
modesta	2A	
Lonchura		
(*Euodice*)		
malabarica	3A	2S
(*Spermestes*)		
nana	A	S
cucullata	2A*,19A	2S
bicolor	5A	S
fringilloides	4A	S

ESTRILDIDAE (cont.)

	Spirit	Skels
(*Lonchura*)		
striata	5A	
fuscans	6A	
punctulata	10A	3S,S†,K
malacca	13A	4S,K
maja	14A	2S
castaneothorax	3A	S
melaena		S
(*Heteromunia*)		
pectoralis	8A	S
Padda		
oryzivora	22A	K
Amadina		
fasciata	2A	3S,K
Genus *Incertae Sedis*		
Pholidornis		
rushiae	2A	K

PLOCEIDAE

18 genera, 143 species

3 genera & 78 species unrepresented

BUBALORNITHINAE

	Spirit	Skels
Bubalornis		
albirostris	3A	K
Dinemellia		
dinemelli	4A	

PASSERINAE

	Spirit	Skels
Plocepasser		
mahali	6A	K
Pseudonigrita		
arnaudi	A	
Passer		
domesticus	7A*,21A	11S,7K,2S
hispaniolensis	3A	S
rutilans	A	S
iagoensis	5A	
griseus	15A	3S
montanus		3K,2S
luteus	3A	S
eminibey	A	
Petronia		
superciliaris	A	
dentata	2A	
Montifringilla		
adamsi	2A	
Sporopipes		
frontalis		2S

PLOCEINAE

	Spirit	Skels
Amblyospiza		
albifrons	10A*,A	
Ploceus		
baglafecht	A	S
pelzelni	3A	
luteolus	6A	
ocularis	2A	
nigricollis	16A	
capensis	A	S

Ploceus (cont.)	Spirit	Skels
subaureus	2A*,2A	
aurantius	2A	
castanops	2A	K
galbula		2S
taeniopterus	2A	
intermedius	A	
velatus	4A	
cucullatus	21A	2S,S
nigerrimus	12A	K
melanocephalus	6A	4S
jacksoni	A	4S
badius	A	
rubiginosus	3A	
nelivourvi	3A	S
sakalava	2A	
manyar	4A	
philippinus	2A	S,K
bicolor	A	K
Malimbus		
nitens	10A	
rubricollis	2A	K
malimbicus	2A	
rubriceps	2A	
Quelea		
erythrops	8A	
quelea	4A	2S
Foudia		
madagascariensis	A	4S,S†
rubra	A	S
Euplectes		
anomalus	2A	
afer	A*,10A	S
nigroventris		S
hordeaceus	12A	S
orix	9A	S,K
capensis	12A	2S
axillaris	3A	
macrourus	3A	S
hartlaubi	A	
albonotatus	3A	
ardens	5A	
progne	A	S

VIDUINAE

	Spirit	Skels
Vidua		
(*Hypochera*)		
chalybeata	6A	
funerea	A	S
(*Vidua*)		
hypocherina	2A	
macroura	10A	S
(*Steganura*)		
paradisaea	9A	

STURNIDAE

26 genera, 111 species

4 genera & 61 species unrepresented

STURNINAE

	Spirit	Skels
Aplonis		
atrifusca	4A	

STURNINAE (cont.)

Aplonis (cont.)	Spirit	Skels
corvina	E	S†,K
cinerascens	A	
tabuensis	7A	S
panayensis	3A	S
metallica	7A	S,2K
Poeoptera		
lugubris	A	
Onychognathus		
morio	A	
blythii	4A	
tenuirostris	A,A*	
salvadorii	2A	
Lamprotornis		
cupreocauda	A	
purpureiceps	A	S
purpureus		K
chalybaeus	4A	S
chloropterus	5A	
splendidus	2A*,A	
purpuropterus	A*,7A	
caudatus	4A	S
Cinnyricinclus		
leucogaster	2A	
Speculipastor		
bicolor	A	
Neocichla		
gutturalis	A	
Spreo		
superbus	9A	2S
pulcher	A*	S
Cosmopsarus		
regius	A	
Saroglossa		
aurata	2A	
spiloptera		S
Creatophora		
cinerea	2A	K
Sturnus		
malabaricus	A	
pagodarum	A*	
roseus	A	S†
vulgaris	A*,19A	19S,3S†,9K
contra	A	3S,2S
nigricollis	A	S
burmannicus	A	
melanopterus		S
Leucopsar		
rothschildi	A*	
Acridotheres		
tristis	3A	3S,3S†
ginginianus		2S†
fuscus		2S,3S†
cristatellus		2S
Ampeliceps		
coronatus	3A	K
Mino		
dumontii	A	S
Basilornis	Spirit	Skels
galeatus	A	
Streptocitta		
albicollis		2S
Sarcops		
calvus	4A	K
Gracula		
religiosa	4A	8S,2K
Enodes		
erythrophris		K
Scissirostrum		
dubium		3S

BUPHAGINAE

Buphagus		
africanus	A	
erythrorhynchus	3A	

ORIOLIDAE

2 genera, 28 species
14 species unrepresented

Oriolus		
sagittatus	9A	S
flavocinctus	2A	
xanthonotus	A	S
oriolus	4A,A*	S,K
auratus	3A	
chinensis	2A	2S
chlorocephalus	A	
brachyrhynchus	2A	
monacha	A	
larvatus		S†
cruentus	2A	
traillii	A	S†
Sphecotheres		
vieilloti	13A	
flaviventris	2A	2K

DICRURIDAE

2 genera, 20 species
1 genera & 10 species unrepresented

Dicrurus		
ludwigii	2A	
adsimilis	8A	S
forficatus	A	S
macrocercus	A	S†
leucophaeus	A	
annectans	A	
aeneus	2A	S†
remifer	A	12S
hottentottus	13A	2S,2S†,3K
paradiseus	15A	4S,S†

CALLAEIDAE

3 genera, 3 species

Callaeas		
cinerea	4A	
Creadion		
carunculatus	A	
Heteralocha		
acutirostris	E,6A	S,K

GRALLINIDAE

3 genera, 4 species
1 species unrepresented

GRALLININAE

	Spirit	Skels
Grallina		
cyanoleuca	A*,13A	3S

CORCORACINAE

Corcorax		
melanorhamphos	6A	
Struthidea		
cinerea	10A	2S

ARTAMIDAE

1 genus, 10 species
4 species unrepresented

Artamus		
fuscus	6A	
leucorhynchus	20A	10S,K
personatus		3S
superciliosus	2A	
cinereus	12A	9S
cyanopterus	2A	2S
minor	13A	K,6S

CRACTICIDAE

3 genera, 8 species
2 species unrepresented

Cracticus		
torquatus	8A	2S
nigrogularis	10A	2S
quoyi	2A	
Gymnorhina		
tibicen	4A	5S
Strepera		
graculina	2A	K
versicolor	2A	3S

PTILONORHYNCHIDAE

8 genera, 18 species
2 genera & 10 species unrepresented

Ailuroedus		
crassirostris	2A	
Scenopoeetes		
dentirostris		K
Amblyornis		
macgregoriae	A	
subalaris	A	S†,K
Sericulus		
chrysocephalus	A	S
Ptilonorhynchus		
violaceus	4A	S,2S†
Chlamydera		
maculata	4A	S
nuchalis	7A	5S

PARADISAEIDAE

20 genera, 42 species
9 genera & 22 species unrepresented

CNEMOPHILINAE

Loria		
loriae		K

PARADISAEINAE

	Spirit	Skels
Manucodia		
ater	A	S,K
comrii	A	S
Phonygammus		
keraudrenii	2A	K
Semioptera		
wallacei	A	K
Epimachus		
meyeri	A	
Astrapia		
mayeri	A	
stephaniae	A*,2A	
rothschildi	A	
Lophorina		
superba	A	S,K
Parotia		
sefilata	A†	
lawesii	2A	K
Cicinnurus		
regius	6A	2S,S†,2K
Diphyllodes		
magnificus	5A	S,K
respublica	4A	K
Paradisaea		
apoda	4A	S
raggiana	A	
minor		2S
rubra	6A,3A*	
rudolphi		S

CORVIDAE

26 genera, 105 species
3 genera & 50 species unrepresented

Platylophus		
galericulatus	5A	S
Platysmurus		
leucopterus	4A	S
Cyanocitta		
cristata	3A	2S
stelleri	2A	
Aphelocoma		
coerulescens	3A	
unicolor	A	
Cissilopha		
sanblasiana	A*,A	
Cyanocorax		
cristatellus	A	S,S†
affinis	2A	S
chrysops	2A	3S,S†,K
Psilorhinus		
morio		2S
Calocitta		
formosa		S
Garrulus		
glandarius	7A	7S,4S†,K
lanceolatus	2A	
lidthi	2A	

CORVIDAE (cont.)

	Spirit	Skels
Perisoreus		
infaustus	2A	3S,S†
Urocissa		
caerulea	A	S
erythrorhyncha	A	2S,2S†
whiteheadi	A	
Cissa		
chinensis	2A	
thalassina	A	S
Cyanopica		
cyana	A,2A*	S
Dendrocitta		
formosae	A†	S†,K
Crypsirina		
temia	A†,2A	S
Temnurus		
temnurus	2A	
Pica		
pica	2A*,3A	5S,7S†,2K
nuttalli	A	S
Zavattariornis		
stresemanni	A	
Podoces		
hendersoni	A	K
panderi		K
Pseudopodoces		
humilis	3A	2K

	Spirit	Skels
Nucifraga		
columbiana	3A	
caryocatactes	2A	3S,2S†,K
Pyrrhocorax		
pyrrhocorax	A	4S,S†
graculus		S
Ptilostomus		
afer		S,4K
Corvus		
monedula	6A	7S†,6K,S*
splendens		4S,4K,2S†
enca	A	2S
woodfordi		K
tristis	A	
frugilegus	2A	14S,9K,10S†, S*
brachyrhynchos		2S,S†
ossifragus		S
corone	A*,3A	4S,16S†,9K
macrorhynchos	A	3S,K
orru		5S
coronoides	3A	4S
albus		2S
ruficollis		3S,5K
corax	3A	6S,3S†,5K
rhipidurus		S,S†
albicollis		S†,K
crassirostris	A	
bennetti		2S

References

American Ornithologists' Union. 1975. Report of the A.O.U. Committee on Conservation, 1974–75. *Auk* 92 suppl.

Ames, P. L. & Stickney, E. H. 1968. Avian anatomical specimens in the Peabody Museum of Natural History, Yale University. *Postilla* **118** : 1–40.

Burton, P. J. K. 1969. Two bird specimens probably from Cook's voyages. *Ibis* **111** : 388–390.

Hall, B. P. 1974. *Birds of the Harold Hall Australian Expeditions.* London: British Museum (Natural History).

Harrison, C. J. O. & Cowles, G. S. 1970. *Instructions for collectors No. 2A: Birds.* London: British Museum (Natural History).

Morony, J. J., Bock, W. J. & Farrand, J. 1975. *Reference list of the birds of the world.* New York: American Museum of Natural History.

Sharpe, R. B. 1906. *The history of the collections contained in the Natural History Departments of the British Museum*, Vol. II. London: British Museum.

Titles to be published in Volume 34

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Bulletin of the
British Museum (Natural History)

Amphibians and reptiles from northern Trengganu, Malaysia, with descriptions of two new geckos: *Cnemaspis* and *Cyrtodactylus*

J. C. M. Dring

Zoology series Vol 34 No 5 29 March 1979

The *Bulletin of the British Museum (Natural History)*, instituted in 1949, is issued in four scientific series, Botany, Entomology, Geology (incorporating Mineralogy) and Zoology, and an Historical series.

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

ISSN 0007-1498

Zoology series
Vol 34 No 5 pp 181-241

British Museum (Natural History)
Cromwell Road
London SW7 5BD

Issued 29 March 1979

Amphibians and reptiles from northern Trengganu, Malaysia, with descriptions of two new geckos: *Cnemaspis* and *Cyrtodactylus*

J. C. M. Dring
22 Fryston Avenue, Croydon CR0 7HL

Synopsis

A collection from the area of Gunong Lawit, northern Trengganu, Malaysia, is described. Records of interest for West Malaysia are of *Microhyla borneensis*, *Rana p. paramacrodon* and *Rhacophorus pardalis*. Two new lizards, *Cyrtodactylus elok* and *Cnemaspis argus*, are described, and a key to the species of *Cnemaspis* in southeast Asia is given. *Goniocephalus herveyi* (Boulenger) is a synonym of *Goniocephalus liogaster* (Günther).

Introduction

Gunong Lawit is a mountain rising to a height of 1519 m (4982 ft) on the border between Ulu Trengganu and Ulu Besut in northern Trengganu State. During the period 22 February to 9 April 1974 an expedition of the British Museum (Natural History) collected certain groups of insects, amphibians, reptiles and some small birds and mammals on G. Lawit and in the lowlands to the east of it. Most collecting of amphibians and reptiles was conducted from three camps, at the Sungei Kelebang and on the east ridge and summit ridge of the mountain.

The Sungei Kelebang camp, 102° 45′ 0″ E 5° 27′ 40″ N, at 43 m elevation, in Mukim Ulu Setiu, Ulu Besut, was in an area of regenerating forest that had been selectively logged in 1971. The riverine forest (*Saracca* stream vegetation) had been little disturbed but the other areas were a mosaic of secondary forest and relatively untouched dipterocarp forest, intersected by logging tracks.

The Kelebang drainage is separated from that of the Sungei Petuang by a ridge, Bukit Bok, rising to a height of some 600 m and forming the boundary between Ulu Besut and Ulu Trengganu. A transit camp on the Sungei Petuang, 102° 38′ 20″ E 5° 26′ 20″ N, at 250 m, was beyond the reach of the loggers and was surrounded by primary rain forest on the steep hillsides leading to the mountain.

The east ridge camp on Gunong Lawit, 102° 37′ 18″ E 5° 25′ 25″ N, at 790 m, was on a ridge top in submontane forest covering the flanks of the mountain. Despite the well-lit forest floor the shrub story was sparse, including mainly palms, such as *Johannesteysmannia*. Most of the collecting was carried out along two swift streams, incised into each side of the ridge, which had their sources not far to the east of the camp. On the summit ridge, 102° 36′ 20″ E 5° 25′ 20″ N, at 1280 m, the camp was in montane rain forest, with *Leptospermum* and *Dacrydium* prominent among the trees, a thick understorey of shrubs and palms, and scattered areas of open 'padang', a heathy association of grasses, ferns and small shrubs.

Material collected

GYMNOPHIONA

Family ICHTHYOPHIIDAE

Ichthyophis sp.

MATERIAL. BM. 1974. 4229 (♂).

HABITAT. This specimen was found dead at the edge of a small rocky stream near the Sungei Kelebang camp. The stream had compact gravel beaches of very limited extent, and almost lacked silt, but may have drained from a more favourable area for caecilians.

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COLOUR. Dorsum dark brownish grey. A light mustard yellow lateral stripe crosses the nuchal collars, extends forwards to between the eye and the mouth commissure and is almost broken on the second nuchal groove only. The venter is slightly paler than the dorsum and there are no light dorsal or ventral spots or flecks.

REMARKS. The total length is 260 mm, the body width is 10 mm and the tail is very short. There are 318 folds in total, four or five interrupted by the vent and two posterior to it. The grooves fail to meet ventrally on the anterior $\frac{1}{2}$–$\frac{2}{3}$ of the body. The tooth counts are, premaxillary–maxillary 20–20, prevomeropalatine 21–21, dentary 18–18, splenial 12–12 (these are approximate counts since many of the teeth are missing).

This specimen may well belong to *Ichthyophis supachaii* Taylor, a Malay Peninsula species with a lateral stripe, a considerable number of splenial teeth (18–18) and 313–332 body folds. However, Taylor's description (1968) indicates that *supachaii* has fewer dentary teeth (about 8–8) and probably more teeth in the other series, as well as having a more acutely pointed tail and a flatter head. Since the specimen is also very similar to two other taxa, *I. atricollaris* Taylor, of Borneo, and *I. hypocyaneus* (van Hasselt), of Java, and since the extent of variation within and between populations has never been properly assessed I prefer not to apply a name to this specimen.

ANURA

Family PELOBATIDAE

Leptobrachium hasselti

Leptobrachium hasselti Tschudi, 1838.

MATERIAL. BM. 1974. 4228–4249 (16 ♂♂, 5 ♀♀, larvae).

HABITAT. Most specimens were collected along the logging tracks at the Sungei Kelebang camp (43 m). The species was also common around very slow streams in the disturbed forest. Choruses of males were found at a pair of shallow muddy pools at the track edge, at a similar stream a short distance from a track and at a swampy area where disturbance had left many shallow pools and slow streams. Males call from the cover of low vegetation and leaf litter. The pond-type larvae of this species were found only in one slow mud-bottomed stream having a maximum depth of about half a metre.

REMARKS. The call is a soft but carrying hup-hup (Fig. 1).

Leptobrachium heteropus

Leptobrachium heteropus Boulenger, 1900.

MATERIAL. BM. 1974. 4250–4275 (25 ♂♂, 1 ♀).

HABITAT. As reported by Grandison (1972). Specimens were collected in the upper stretches of two streams on the east ridge of G. Lawit at 790 m. The great majority were calling from the leaves of plants and were always less than 40 cm above the stream banks. One male was calling from below a dead leaf on the bank. A few specimens were found on rocks in the stream. A pair took up inguinal amplexus in the collecting bag.

COLOUR. The dorsal surfaces vary from slate grey through purplish grey to pinkish brown. There is frequently ochre mottling and an ochre area covering the snout. The ventral surfaces are grey except for the belly which is white, spotted with dark brown. A black canthal stripe and supratympanic mask, a grey W-shaped mark on the dorsum and pale areas on the elbows are typical. There are both pectoral and femoral glands, which are white.

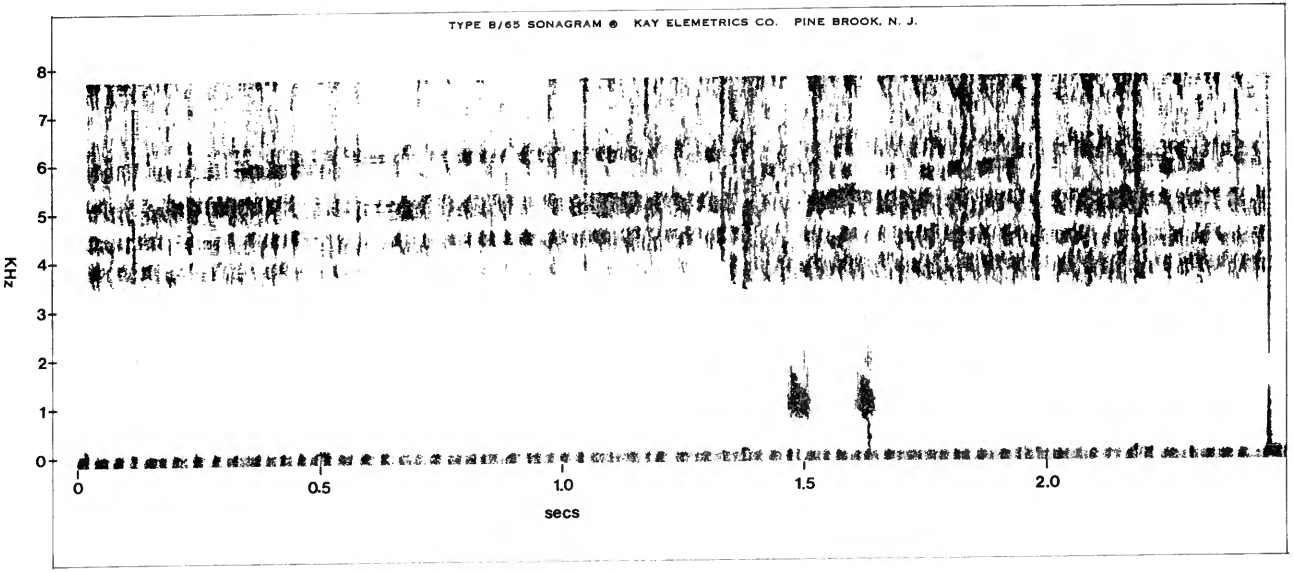

Fig. 1 Sonagram of the mating call of *Leptobrachium hasselti*, high frequency noise is background. Sonagrams were prepared using a Kay Electrometics Sonagraph 6061B, with the high shape and wide band settings. Calls were recorded on a Uher 4000 Report tape recorder with an AKG type D 190c microphone.

Megophrys aceras

Megalophrys montana var. *aceras* Boulenger, 1903.

MATERIAL. BM. 1974. 4276–4288 (4 ♂♂, 6 ♀♀, 2 juveniles, larvae).

HABITAT. Most of the sample were taken on the east ridge of G. Lawit (790 m) where specimens were caught equally along streams and along dry hillsides. Three were caught between the east ridge and the summit. At 1280 m a specimen was found in a sedgy valley at the edge of a padang, another was found on the summit (1520 m) in forest far from water. Larvae were taken in very shallow, gravelly sections of the east ridge streams. They were found feeding from the surface among stones and dead leaves.

REMARKS. Although Grandison (1972) has listed the differences between *M. aceras* and *M. monticola nasuta*, Berry (1975) has replaced *aceras* in the synonymy of *M. monticola monticola*, a subspecies confined to Java and western Sumatra. *M. monticola* and the Indochinese group comprising *feae*, *carinensis* and *intermedius* are the only *Megophrys* species having two pairs of dorsolateral folds. The inner pair converge slightly as they extend forwards on to the rear edge of the skull. *M. aceras* is like *M. baluensis*, *M. longipes* and the remaining Indochinese species in having only a single pair of dorsolateral folds which curve outwards to meet the posterior part of the supratympanic fold. Frogs of this group also generally have an X- or Y-shaped middorsal ridge. Hypothetically, *M. aceras* and *M. longipes*, montane endemics of the Malay Peninsula, and *M. baluensis*, the montane endemic of Borneo, can be regarded as close relatives of the Indochinese *Megophrys* (exclusive of the *feae* group) and not at all closely related to *M. monticola*. Perhaps these species are recent invaders of, or relicts in, the Sundan subregion.

A recent peninsular Malaysia record of *M. monticola nasuta* (Yong, 1974) has extended the altitudinal range of this form to above 1000 m. Both this form and *M. aceras* have been collected at 488–549 m near Kampong Janda Baik, Pahang, and *aceras* is known to occur as low as 300 m. The two species thus have a broad altitudinal overlap, although *monticola nasuta* is seldom collected at high altitudes in Malaya.

Megophrys monticola nasuta

Ceratophryne nasuta Schlegel, 1858.

MATERIAL. BM. 1974. 4289–4301 (10 ♂♂, 2 immature, larvae).

HABITAT. Males were calling throughout the collecting period from the banks of the Sungei Kelebang and its tributary streams at 43 m. Larvae were found under a stone in a shallow fast-running tributary and among pebbles at the edge of an exposed beach of the Kelebang. The immature frogs were both from 250 to 300 m on the lower slopes of G. Lawit, above the Sungei Petuang. The call is a loud, short honk.

Family **BUFONIDAE**

Ansonia malayana

Ansonia malayana Inger, 1960.

MATERIAL. BM. 1974. 4304–4319 (10 ♂♂, 5 ♀♀, 1 immature).

HABITAT. Two individuals were caught far from streams on ridge top trails, a male in a crack in a rock exposure near the east ridge camp (790 m) and an immature specimen among dry leaf litter on the forest floor at about 1000 m. The remaining 14 specimens were all caught along small rocky mountain streams. Two of these were among leaf litter and exposed rock faces by a torrent below the east ridge camp. Three were found on damp peat and among the leaves of palms near the summit ridge camp (1280 m). These were in humid, closed canopy forest around a small, stagnant stream. Nearby in an open, mainly grassy area (padang) with stunted *Leptospermum*, *Melostoma* and pitcher plants, nine examples were found along a small stream shaded by trees and shrubs. The toads were on rocks in the water or on overhanging vegetation as much as 1·5 m above the stream surface.

COLOUR. Dorsum black with fine yellow green to grey green vermiculation. Larger tubercles on dorsum mostly black, tending to form a black XX pattern. Tubercles on flanks and at mouth commissure chrome yellow. Dorsal surfaces of limbs as dorsum, with oblique, yellowish green crossbars. Upper and lower lips spotted with chrome yellow. Throat uniform greyish yellow, belly speckled with chrome yellow. Iris reddish gold to dark brown.

REMARKS. This series agrees closely with the type series of *A. malayana* Inger, from the Larut hills, Perak. The following description is based entirely on the G. Lawit specimens. Males having nuptial pads, mandibular asperities and vocal sac openings are 20·3–23·1 mm in snouth–vent length (mean 21·8 mm, N=10). Females with enlarged ova are 24·6–28·0 mm in length (mean 25·9 mm, N=4). Head width relative to SV length is 0·266–0·316 (mean 0·288, N=16) and tibia length relative to SV length is 0·440–0·517 (mean 0·471, N=16). The tips of the outer fingers are weakly expanded (about 1¼ times width of narrowest part of digit) and rounded. There is less sexual dimorphism in the extent of the toe web than in the type series. Females have the first and second toes webbed to the tips, the third and fifth with 1½–2 phalanges free and the fourth with 3 free phalanges. Males have the webbing marginally fuller, with the fleshy edges to the free parts of the digits better developed. In all the males examined the nuptial pad is confined to the dorsomedian part of the first finger and metacarpal. The mandibular asperities are small and closely set. They form about 2 rows posteriorly, two to four rows under the front of the lower jaw. The mandibular asperities of the holotype, another Larut hills male and 2 males from Bannang Satar, are identical with those of the G. Lawit males. There is no noticeable sexual dimorphism in the size of the tympanum, which is approximately equal to its distance from the mouth commissure. The yellow tubercle at the mouth commissure varies in size from ½ to ⅔ of the tympanum diameter. The dorsum is heterogeneously tuberculate, larger oval or rounded tubercles are separated by small conical ones. The smaller tubercles are capped by one, and the larger tubercles by up to six, white spicules. There is slight individual variation in the size and prominence of the dorsal tubercles. In all specimens there is a fine lichenate vermiculation of green on black covering the dorsal surfaces. In addition a characteristic XX pattern, which may be more or less broken up, is present on the dorsum. The first X extends from the supraocular area to above the scapulae, the second extends back on to the sacrum. There is frequently a pale middorsal patch enclosed by the arms of the two crosses. Chromatophores are absent from parts of the ventral surface of all specimens. These areas are transparent, apart from the whitish glands lying beneath the tubercles. The ventrolateral tubercles are each capped with yellowish pigment, as in the type series. In no specimens is there a ventral pattern of yellow marbling like that found in the series from Tasan and noted by Inger (1960). BM specimens referable to this species are from the Larut Hills and G. Keledang, Perak, from G. Tahan, Pahang, from G. Lawit and from Bannang Satar, Yala, Thailand. Measurements for the combined sample are similar to those from the G. Lawit series. SV adult ♂♂ 20·2–23·1 mm (mean 21·6 mm, N=14), adult ♀♀ 24·6–28·6 mm (mean 26·6 mm, N=8). HW/SV=0·266–0·316 (mean 0·286, N=25). Tibia/SV=0·440–0·517 (mean 0·475, N=25). Except for the specimens from Bannang Satar (a lowland locality), for which there are no data, this species has been collected between 640 and 1280 m. The call is a rapid metallic ticking (Fig. 2).

A. malayana belongs to a group of 3–5 species in the Malay peninsula, 4 in Borneo and 1 in south-west India having the following characters. Snout acuminate, tympanum visible externally, first finger does not reach disc of second when adpressed. Tips of digits rounded or weakly spatulate but not greatly expanded. Nuptial pad present or absent, if present covered with minute spicules, not larger spines. Mandibular asperities present or absent. Vocal sac present, or possibly absent in *A. tiomanica*. The Malay Peninsula forms of this group are discussed below.

Gunong Benom is one of the most isolated mountains in the southern Malay Peninsula. The *Ansonia* reported from *c.* 1000 m on the mountain by Grandison (1972) have been compared with material, including the types, of *A. malayana* and *A. tiomanica* Hendrickson. They are more similar to *malayana* than to *tiomanica* but differ from *malayana* in the following characters.

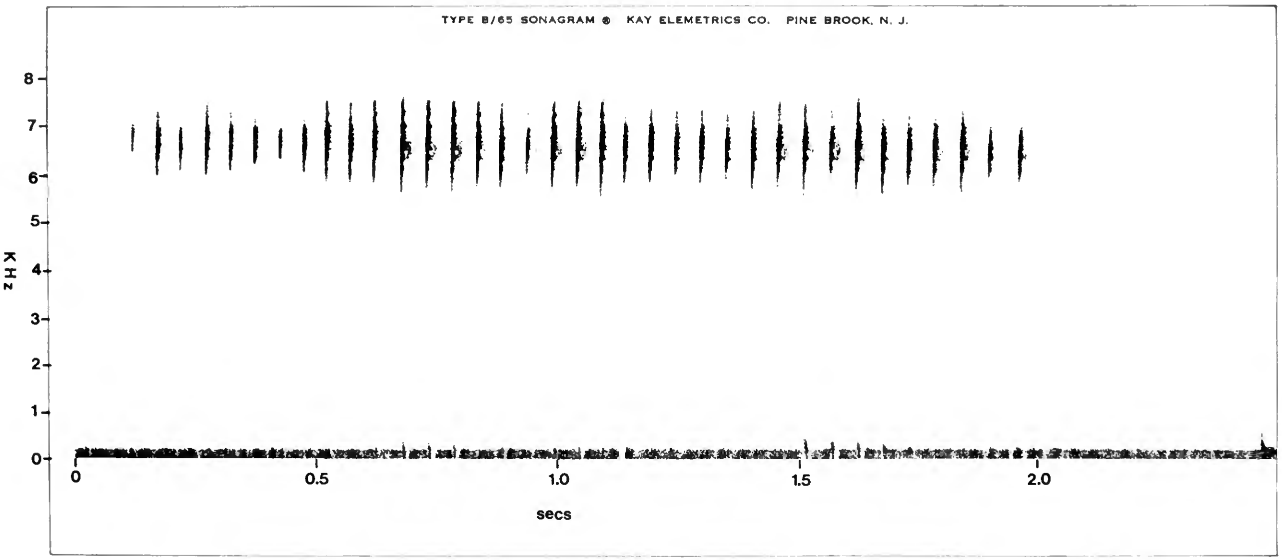

Fig. 2 Sonagram of the mating call of *Ansonia malayana*, recorded at 1280 m elevation.

Larger size, ♂ 25·4 mm, ♀ 30·2 mm in SV length.
♂ lacks a nuptial pad despite having a vocal sac and mandibular asperities.
♀ with enlarged tympanum, diameter twice as great as its distance from the mouth commissure.
Distinctive dorsal lichenation of *A. malayana* absent. XX pattern on dorsum indistinct or absent. Dark brown and chrome yellow in life without lichen green areas.

The examination of a larger series of *A. malayana* than was available to Grandison shows that there is variation in the extent of the webbing and in the development of the dorsal tubercles and tubercle at the mouth commissure. Nonetheless, the G. Benom specimens are extreme in these characters, as indicated by Grandison. The size and arrangement of the mandibular asperities, however, is identical to that in *malayana* (excluding the Tasan series reported by Inger (1960) which is discussed below). Head width of G. Benom frogs relative to snout–vent length 0·281–0·300 (mean 0·292, N=3). Tibia length relative to snout–vent length 0·474–0·496 (mean 0·482, N=3). These specimens may represent a species distinct from *A. malayana*.

The Tasan (Ban Tha San) frogs differ from *malayana* in the characters stated by Inger (1960) and in some others. Because of the 200 mile collecting hiatus between the Isthmus of Kra and the southern Malay Peninsula these differences may be due to geographic variation. They are as follows.

Larger size, adult ♂♂ 21·9–24·2 mm (mean 22·7 mm, N=14), adult ♀♀ 27·1–28·7 mm (mean 27·5 mm, N=7).
Nuptial pad extends on to basal part of dorso-median surface of second finger.
Mandibular asperities large, well separated and forming a single row.
Ventral surfaces of abdomen and thighs patched and marbled with yellow pigment which covers an area equal to or greater than the dark areas. (Ventral yellow pigment always confined to isolated tubercles in *A. malayana* and the G. Benom population.)
Head slightly wider. HW/SV 0·270–0·328 (mean 0·300, N=21).

The ratio of tibia length to snout–vent length falls within the range of *A. malayana*. Tibia/SV 0·453–0·508 (mean 0·487, N=16).

The remaining two Malayan species of this group are more similar to each other in size than to the three populations discussed above. *A. penangensis* (*sensu* Inger, 1960) was placed in the group of larger species having the first finger subequal to the second when adpressed. The two specimens described by Inger have been re-examined. The whole of one specimen, and the hind limbs of the other are desiccated. However, the first fingers of the better preserved specimen, and the first fingers of juveniles from the larval series described by Flower (1899) are much shorter than the second fingers. The tip of the first finger reaches only to the distal half of the penultimate phalange of the second, when the two fingers are adpressed. The tip of the first finger of *malayana* reaches the middle of the penultimate phalange when the first and second fingers are adpressed. *A. penangensis* is like *malayana* in other characters too. The first toe is webbed to the tip, the second to the terminal phalange. There are about 1½ phalanges of the third and fifth toes free and about 3 free phalanges of the fourth toe. The dorsum, although having scattered light coloured areas, also has a dark XX identical to that characteristic of *malayana*. There are oblique light stripes on the limbs and pale-tipped tubercles on the ventrolateral areas as in *malayana* too. This pattern is particularly distinct on the Penang juveniles which could as well be referred to *malayana* as to *penangensis*. *A. penangensis* is also similar in habitus to *A. malayana*, the ratios HW/SV (0·282 and 0·285 in *penangensis*, mean 0·286 in *malayana*) and tibia/SV (0·481 and 0·482 in *penangensis*, mean 0·475 in *malayana*) are identical in the two species. *Ansonia penangensis* (*sensu* Inger) appears to differ from *malayana* only, but markedly, in size, the gravid ♀ being 37·2 mm in length. The two adults and the larval series were collected on Penang Hill at 1800–2000 ft (550–610 m) in March 1898 by Captain S. S. Flower.

Ansonia tiomanica Hendrickson is similar to *A. penangensis* in size but is very different in habitus (see Hendrickson, 1966, Plate 10). This is perhaps reflected in the HW/SV ratio of 0·257 (♀) and 0·268 (♂) which is lower than that of *penangensis* and at the bottom of the range for *malayana*. The tips of the third and fourth fingers are weakly expanded (twice the width of the narrowest part of the digit) and weakly spatulate as stated by Hendrickson (1966). Again, as stated by Hendrickson, the toe webbing is greatly reduced.

First	Second	Third	Fourth	Fifth
1	2½ : 1½–2	2½ : 2	4 : 4	2–2½

There is much less webbing than in any of the forms discussed above, including the G. Benom population. The median edge of the outer metatarsal tubercle is frequently indistinct in preserved *Ansonia*. In *A. tiomanica* the tubercle is rather heart-shaped and in contact with the inner metatarsal tubercle as described by Hendrickson (1966), but there is a similar condition in some specimens of many other taxa. The dorsum is covered by close-packed, homogeneous, rounded tubercles which contrast strikingly with the heterogeneous tubercles of the three small forms. The Penang specimens are too poorly preserved to show whether the dorsal tuberculation was heterogeneous or homogeneous. The dorsal pattern also differs from the other populations, but is most similar to that of the G. Benom specimens. It is composed of discrete whitish spots covering 1–3 tubercles on a uniform dark brown background. Finally, the male, although having enlarged testes, differs in secondary sexual characteristics from sexually mature males of the small forms. It has no vocal sac (contrary to Hendrickson's statement), there is no nuptial pad (as in the G. Benom population) and the mandibular asperities are not distinct from those on the gular skin.

***Ansonia* sp.**

Ansonia leptopus, Grandison, 1972.

MATERIAL. BM. 1974. 4302–4303 (2 ♂♂).

HABITAT. This species was found in a small right bank tributary of the Sungei Kelebang at 43 m. Two other species, *Rana laticeps* and *Amolops larutensis*, were apparently also confined in the area to this fast, rocky stream, the only one of its type seen in the area. Both *Ansonia* specimens were caught at night on small rocks projecting from the water in shallow swift sections of the stream.

COLOUR. Dorsum dark reddish brown, canthal and tympanic areas and lips blackish. Throat and anterior belly dark grey or black, posterior belly grey brown. A dull reddish or orangy speckling on ventral surfaces. Hidden surfaces of limbs as venter. Iris dull orange, reticulated with black forming dark patches at the ends of the pupil.

REMARKS. Although no call was heard in the field one specimen gave a low clucking call in the collecting bag (Fig. 3). This call was quite unlike the ticking call of *A. malayana*.

These specimens, and two ♂♂ in the BM(NH) from the Ulu Tahan area, north Pahang, are identical with the series reported on by Grandison (1972) as *A. leptopus* (Günther). These Malay Peninsula specimens have the following characters. Gravid ♀ 51·0 mm in length, tibia/SV = 0·518. Mature ♂♂ 35·6–41·3 mm in length (mean 38·0 mm, N = 9), tibia/SV = 0·474–0·507 (mean 0·488, N = 8). Vocal sacs with bilateral openings in all 9 ♂♂. Nuptial pads always confined to dorsomedial surface of first metacarpal and first finger, covered with small brown spinules. Mandibular asperities formed by a single or double series of low ridged tubercles, each covered with a rounded cap of keratin and lacking spines. Similar asperities along the upper lip. No group of asperities under mandibular symphysis. Dorsum covered with low rounded tubercles with similar weakly keratinized tips. Because of their nuptial pads, because the nine similarly sized ♂♂ represent three independent collections, and because one male was collected in amplexus (Grandison, 1972) it is unlikely that the weak development of their asperities is due to the individuals not being at the peak of breeding condition. Free phalanges of toes in males as follows:

First	Second	Third	Fourth	Fifth
0	1½–2 : 0	2–2½ : 1–2	3⅓ : 3¼–3½	1½–2

Four Bornean taxa seem to be most closely related to this population. *Ansonia leptopus* (Günther) is similar to the Malay Peninsula population in having reduced toe webbing and weak mandibular

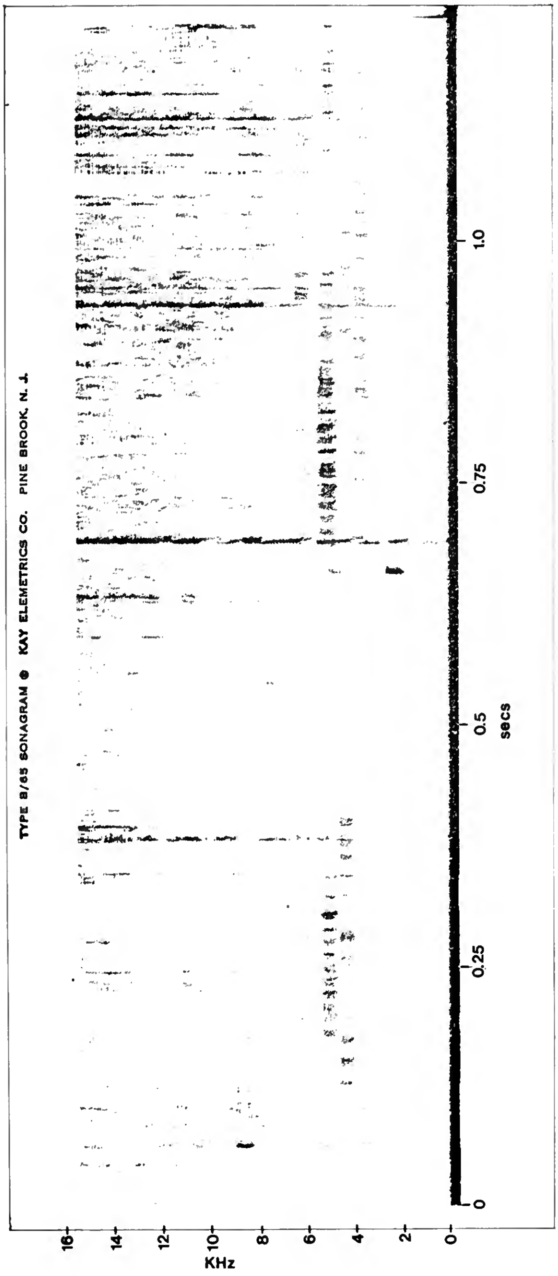

Fig. 3 Sonagram of a call of *Ansonia* sp., recorded in a collecting bag.

asperities. *A. longidigita gryllivoca* Inger is similar in lacking major sexual dimorphism in the development of the dorsal tubercles and in having weak mandibular asperities. The remaining two forms of this group, *A. l. longidigita* Inger and *A. guibei* Inger, are less similar to Malay Peninsula frogs than are either of the above forms. *A. leptopus* has marginally less extensive webbing than the Malayan frogs. Males have the web between the first and third toes more deeply incised so that the terminal phalange of the first and second toe is free; 2–2½ phalanges of the third and fifth toes are free, 3⅓–4 (usually 4) phalanges of the fourth toe are also free of web. Males have mandibular asperities in one or two rows as in Malayan frogs, but they are formed of conical tubercles capped by keratin spikes quite unlike the inconspicuous asperities of the Malayan sample. They also have a group of similar asperities under the mandibular symphysis (lacking in Malayan frogs) and lack asperities along the upper jaw (present in Malayan frogs). Finally, all males of *leptopus* except FMNH 77449 (Inger, 1960) have the dorsum covered with massive tubercles capped by high spines, while tubercles on the flanks and limbs are also spinose. Five mature males of *A. leptopus* have been reported (Inger, 1960) to be 34·2–35·8 mm in length but one BM male from Kinabalu, 42·5 mm long, shows that they may be as large as Malayan males. Male *A. longidigita gryllivoca* correspond with males of the Malayan population in having weak asperities along both the mandible and upper lip, and in the size and degree of keratinization of the dorsal tubercles. They differ in having the mandibular asperities conical, rather than ridge shaped, in having a group of asperities under the mandibular symphysis and in having more extensive webbing. Webbing on the third and fifth toes generally reaches the terminal phalanges and there are about three phalanges on the fourth toe unwebbed. They are also smaller, SV length 32·8–38·3 mm (mean 35·09 mm, N=24), and in about a third of males the nuptial pad extends onto the second finger (Inger, 1960). All the Bornean forms have been reported to have only one vocal sac opening, on left or right, while the Malay Peninsula males have bilateral vocal sac openings. On the basis of these differences I find it impossible to assign the Malayan population to either *A. leptopus* or *A. longidigita* and prefer to leave it unnamed. Further collecting of *Ansonia*, both in the lowlands and highlands of the peninsula should be rewarding.

Bufo asper

Bufo asper Gravenhorst, 1829.

MATERIAL. BM. 1974. 4320–4359 (2 ♂♂, 4 subadults, 29 juveniles).

HABITAT. Most specimens are recently metamorphosed juveniles, which were extremely common on stony river beaches of both the Kelebang (43 m) and the Petuang (250 m), from the start of collecting. Although adults and subadults were confined to the rivers, immature specimens were occasionally found along logging tracks and small streams at the Kelebang. On the east ridge of G. Lawit 3 specimens were caught in the valleys of small mountain streams at *c.* 790 m.

RANGE. Reports of this species from the Indochinese region appear in Boulenger (1893), Smith (1915) and Cochran (1930). Boulenger (1893) recorded the species from Tagata Juwa, Kawthoolei and there is one adult in the BM from the country along the Me Ping and Me Taw rivers, north west of Tak, nearby in Thailand. These are the northernmost locality records for both *B. asper* and *Rana blythi*, and apparently neither of these Sundan species is present beyond the hill tract between the Chao Phraya lowlands and the Andaman Sea, and north of about 17° N latitude.

Bufo parvus

Bufo parvus Boulenger, 1887*b*.

MATERIAL. BM. 1974. 4360–4407 (36 ♂♂, 4 ♀♀, 7 immature, larvae).

HABITAT. One subadult female was caught on the forest floor of Bukit Bok, the watershed between the Kelebang and the Petuang, at about 520 m. Mature males were caught along logging tracks at the Sungei Kelebang (43 m). Males were calling in chorus from among grass and low herbs at track edges and occasionally from bare mud or in the edges of the water. Gravid ♀♀ were also collected along the logging tracks, but one was among leaf litter on the bank of a small muddy stream in logged forest. Spawning sites were in water-filled ruts in the track and in a pair of shallow muddy pools at the track edge. Juveniles were caught in the camp site and along a small rocky forest stream.

REMARKS. The larvae are identical to those described by Smith (1916) from Khao Sebab in south-east Thailand.

Bufo quadriporcatus

Bufo quadriporcatus Boulenger, 1887*b*.

MATERIAL. BM. 1974. 4408–4409 (2 juveniles).

HABITAT. Both were caught in the vicinity of the Sungei Kelebang camp site.

COLOUR. The larger specimen was red brown dorsally with a dark-edged light canthal and dorso-lateral stripe. The throat was red brown with white spots, the belly dirty white with grey brown spots.

Cacophryne borbonica

Hylaplesia borbonica Tschudi, 1838.

MATERIAL. BM. 1974. 4410 (juvenile).

HABITAT. The specimen was caught on the forest floor on the hillside above the Sungei Petuang camp, at about 300 m.

Pedostibes hosei

Nectophryne hosii Boulenger, 1892.

MATERIAL. BM. 1974. 4411–4422 (11 ♂♂, 1 ♀).

HABITAT. Ten were caught on the banks of the Sungei Kelebang (43 m). During the first collecting period (22 February–8 March) males were calling from logs and branches above the river, either on the steep earth and rock banks or as high as 4 m from the forest floor and 5 m above the river. The female was found in a hole in the rock bank of the river. On the night of 8 March many males were heard calling from high in mature trees on the rocky banks of the Sungei Petuang, but none was caught. The call is a groaning croak. By 28 March breeding must have been over for no further calls were heard either at the Petuang or at the Kelebang. Two males collected at the Petuang were both on the steep rocky banks of a small tributary.

COLOUR. Males are khaki to chestnut brown on the dorsal surfaces. The throat is grey with small indistinct yellow spots, the belly is a dirty bluish white, also indistinctly marked with pale yellow. The back of the thigh is greyish. The female was more brightly coloured. The dorsum at night was dark purplish brown with yellow blotches. By day the dorsum was medium green, darkening over the vertebral area and fading to bluish on the flanks and hidden surfaces of the limbs. There were bright yellow markings ringed with darker green on the dorsum and flanks. The iris is golden brown reticulated with black and greyish at the ends of the pupil.

Family **MICROHYLIDAE**

Kalophrynus pleurostigma pleurostigma

Kalophrynus pleurostigma Tschudi, 1838.

MATERIAL. BM. 1974. 4423–4425 (2 ♂♂, 1 ♀).

HABITAT. Among leaf litter in secondary trackside vegetation and logged forest at the Sungei Kelebang (43 m).

REMARKS. Inger (1966) gave measurements of 21 Bornean *pleurostigma*. I have reexamined the 6 BM(NH) specimens which formed part of his material. The smallest adult female, from Gunong Dulit, is 35·2 mm in length and is probably the specimen on which Inger's lowest size limit for Bornean females was founded. On the basis of its dorsal pattern and short fourth finger it is not a *pleurostigma*. The smallest Bornean adult female which I have seen is 39·3 mm in length. Reinterpreting Inger's data on the basis of a little additional material, snout–vent lengths of adult *pleurostigma* are as shown in Table 1.

Table 1 Snout–vent lengths (mm) in three populations of *Kalophrynus pleurostigma*

	Males			Females		
	Range	Mean	N	Range	Mean	N
Borneo	36·8–50·4	43·6	16	? 39·3–57·8	48·0	10
Bunguran	42·8–46·2	44·3	4			
Peninsula*	35·0–41·2	37·9	7	38·2–45·8	42·9	6

* Malay Peninsula to just north of the Isthmus of Kra.

In comparison with this, 3 of the 7 Malayan specimens smaller than 35 mm in the BM(NH) are plainly adult. A male from 915 m on G. Tahan has nuptial pads like those of *pleurostigma*, is 28·8 mm in length and has a faint dorsal pattern unlike that of any *pleurostigma* and a massive inguinal dark patch extending onto the anterior face of the thigh. Two gravid females are 30·4 and 34·4 mm in length, lack a dorsal pattern, but have a well-developed dark inguinal spot without a light edge. They are from the base of G. Pulai, Johore and from Kampong Janda Baik, at about 500 m in Pahang. All 3 specimens have relative toe and finger lengths like those of *pleurostigma*. Unless there is remarkable size variation in *K. pleurostigma* these specimens represent one or two Malay Peninsula species, intermediate in size between *K. robinsoni* (five adults are 17–18 mm in length, altitudinal distribution 165–990 m) and *K. pleurostigma* (found in the lowlands of Malaya, but up to 2200 m on Kinabalu). Berry (1972) has shown that there are two types of *Kalophrynus* larvae in West Malaysia, one type was collected at Kampong Janda Baik.

Metaphrynella pollicaris

Phrynella pollicaris Boulenger, 1890.

MATERIAL. BM. 1974. 4426–4436 (11 ♂♂).

HABITAT. Found from 780 m to near the summit (1520 m), both in the tall forest of the intermediate zone and high altitude forest. Five males from the east ridge camp (790 m) were calling from elliptical holes in tree trunks and branches and were thus in a situation similar to that reported (Grandison, 1972) for Pahang examples. The minimum diameter of bole in which occupied holes were found was likewise found to be similar (about 8 cm). In two cases specimens were taken from holes in saplings used in the construction of the camp. On the east ridge the frogs were only heard calling at night. The five from the higher camp (1290 m) and one from just below the summit (*c.* 1500 m) occupied similar holes. At those elevations calling commenced in the late morning, perhaps due to the dull conditions, with very low cloud cover. Holes from which males called were found from ½ to 6 m above the ground, and were probably to be found at higher levels also. One specimen was calling from the outside of an inclined tree trunk, about a metre from a hole from which another male also called. Here tones of the call seemed to differ with the calling post, the specimen in the hole having a deeper call than that on the trunk. Around the higher camp *Metaphrynella* was found in both the more typical closed canopy forest and on the edges of padang where the trees were interspersed with grass, bushes and some stunted *Dacrydium*. The call is shown in Fig. 4.

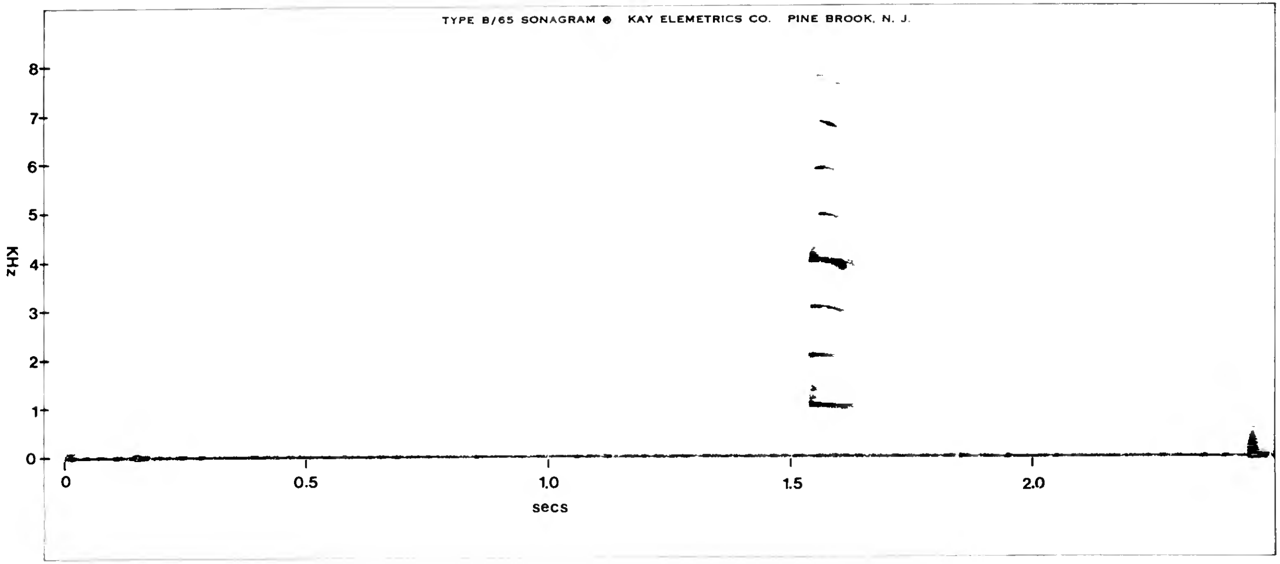

Fig. 4 Sonagram of the mating call of *Metaphrynella pollicaris*, recorded at 790 m elevation.

COLOUR. From dark greyish brown to pale ochre in life. A constant dark middorsal patch forking behind towards the posterior flanks and continuous, when the legs are flexed, with the dark crossbar on the thigh.

REMARKS. Grandison (1972) noted a size difference between low and high altitude populations on G. Benom. There are now 46 specimens of *M. pollicaris* in the BM(NH) (mostly from below 1500 m) which confirm this difference but do not suggest a cline of size increasing with altitude.

The lower altitude population is found from *c.* 500–1500 m but shows no evidence of a size cline over this range. At these elevations males with vocal sac openings and well-developed prepollices are 24·2–34·0 mm in length (mean 29·2 mm, N=27), females are 26·6–27·9 mm (mean 27·2 mm, N=3). Examples in the BM(NH) are from the Larut Hills (915–1370 m) and Jor (550 m), Perak; from Bukit Fraser, Selangor; from Kg. Janda Baik (*c.* 500 m) and from G. Benom (900–1220 m), Pahang; and from G. Lawit (790–1500 m).

The higher altitude population is known only from the males reported by Grandison (from 1680 to 1900 m on G. Benom) and from 2 males from about 1525 m on the Cameron Highlands. These specimens are 34·2–40·9 mm in length (mean 38·5 mm, N=12).

Microhyla berdmorei

Engystoma berdmorei Blyth, 1856.

MATERIAL. BM. 1974. 4437–4446 (4 ♂♂, 5 ♀♀ and larvae).

HABITAT. The whole sample was collected from logging tracks at the Sungei Kelebang camp. Some specimens were on mud or in flooded ruts but most were in trackside vegetation. In many areas this was a mass of grass and herbaceous plants with fallen branches and overhung by the low trees bordering the track. In one case at least a specimen was collected on clear ground with leaf litter between the saplings just behind the forest edge. This specimen was calling, apparently in chorus with *M. borneensis.* In other areas of trackside *M. berdmorei* was found with *M. heymonsi* and probably with *M. butleri* too.

Microhyla borneensis

Microhyla borneense Parker, 1928.

MATERIAL. BM. 1974. 4447–4452 (6 ♂♂).

HABITAT. Five specimens were collected on the nights of 4–6 April in one small area of secondary trackside growth. The vegetation consisted of slender saplings and rattan and the ground was dry and covered by dead leaves. A flooded rut in the otherwise dry track provided a possible breeding site. *M. berdmorei* was also present at this site, where a chorus of *Microhyla* were calling from the forest floor. The remaining specimen was calling from beneath a dead leaf on the forest floor at the edge of a swampy area from which the mature trees had been removed.

COLOUR. The pattern is as described by Inger (1966). The dorsum is brown to dark grey. There are two oval fawn patches between the scapular and middorsal expansions of the pattern. The throat is dark grey, the belly colourless to fawnish posteriorly. The iris is pale brown above, darker below.

REMARKS. This species has not previously been recorded outside Borneo. A further male, BM. 1928. 11.12.1, which was previously discussed as *M. annectans*, by Smith (1916*b*), Inger (1966) and Grandison (1972), is identical with this series and with two Bornean specimens including the holotype. It extends the range to Klong Bang Lai, *c.* 60 km north of the Isthmus of Kra. Snout–vent lengths of the six Malayan males, all of which have vocal sac openings, are 17·3–20·6 mm (mean 19·4 mm). Tibia lengths relative to snout–vent lengths are 0·563–0·659 (mean 0·613, N=5).

M. borneensis has two close relatives. *M. annectens* is endemic to mountains of the Malay Peninsula (Grandison, 1972). *M. annamensis* of the southern Vietnamese mountains has a warty dorsum, lacks an outer metatarsal tubercle and has a different pattern.

Microhyla butleri

Microhyla butleri Boulenger, 1900.

MATERIAL. BM. 1974. 4453 (♂).

HABITAT. From an overgrown mound of earth turned up at the edge of a logging track at the Kelebang.

Microhyla heymonsi

Microhyla heymonsi Vogt, 1911.

MATERIAL. BM. 1974. 4454–4467 (11 ♂♂, 4 ♀♀ and larvae).

HABITAT. *Microhyla heymonsi* was found calling in chorus from the edges of the logging tracks at the Sungei Kelebang. Males were collected from these choruses throughout the collecting period. One specimen was found half a metre above the track edge on a leaf in the low vegetation from which males were calling. All the others for which there are data were found on mud near the edges of flooded ruts and other pools or on earth at the edges of drier parts of the track. All these specimens were protected by fallen twigs and dead leaves, and often by a thin growth of vines and herbaceous plants. One pair, taken in amplexus, was located by the male's call. *M. heymonsi* was by far the commonest *Microhyla* at the Kelebang. The call is a rapid ticking (Fig. 5) like that of the other species of *Microhyla* heard calling around the camp.

Family **RANIDAE**

Amolops larutensis

Rana larutensis Boulenger, 1899.

MATERIAL. BM. 1974. 4468–4481 (5 ♀♀, 8 juveniles, eggs).

HABITAT. With *Rana laticeps* this was the only frog collected at all camps from 43 to 1280 m. It was taken only from the fast, clear, rocky streams and torrents which would provide a suitable habitat for the larva. Juveniles were found, with *R. laticeps* and *Ansonia* sp., along a gently inclined stream of this type near the Sungei Kelebang. None of these 3 species was present along nearby turbid streams. A mass of hundreds of eggs was suspended from the undersurface of a rock over a fast torrent of this stream.

Ooeidozyga laevis laevis

Oxyglossus laevis Günther, 1858.

MATERIAL. BM. 1974. 4482–4513 (3 ♂♂, 5 ♀♀, 24 immature and juveniles).

HABITAT. This was one of the commonest species along the logging tracks at the Sungei Kelebang camp, where it was found in flooded ruts and other shallow muddy pools. A single specimen was found by a shallow muddy stream in disturbed forest near a logging track but otherwise this frog, like *Rana limnocharis*, seemed to be unable to invade the regenerating forest.

Rana baramica

Rana baramica Boettger, 1901.

MATERIAL. BM. 1974. 4514–4518 (4 ♂♂, 1 gravid ♀).

HABITAT. All specimens were obtained in the disturbed forest around the Sungei Kelebang camp (43 m). This seems to be a secretive ground dwelling frog like *R. glandulosa* and *R. signata*. Five were heard calling, one at the beginning of March (the end of the first collecting period), the others

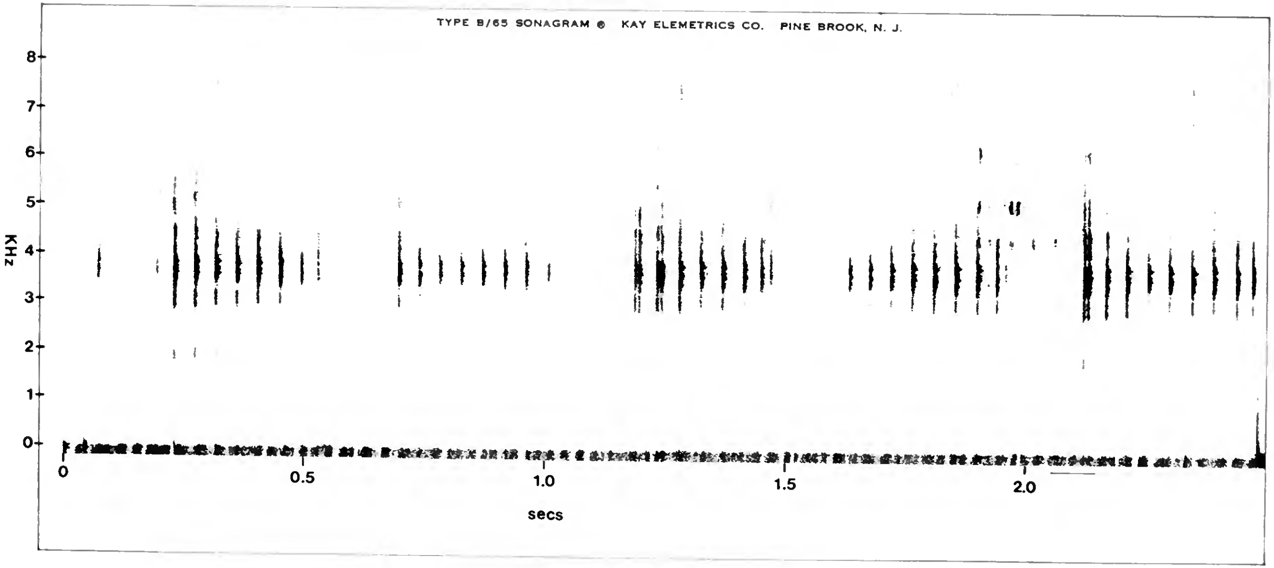

Fig. 5 Sonagram of the mating call of *Microhyla heymonsi*.

from 3 to 9 April. The first specimen heard was apparently in a tangle of sticks and leaves among the roots of a palm at the edge of a shallow earth banked stream. It was not collected. The first specimen caught was also calling from the roots of a bush, but in thick secondary trackside vegetation. It was about 30 cm above ground level. Two more specimens were caught while calling from a tangle of uprooted tree trunks and branches overgrown with creepers, on the banks of the Kelebang. Another specimen called from a large cavity in a rotten felled tree trunk in thick secondary growth. The female was found among a litter of rotten bark and wood by a log in thick secondary vegetation about 3 m from a logging track. It contains enlarged unpigmented ova. The calling sites of this frog were reminiscent of those of *R. signata*, which calls from tangles of roots and sticks, but on riverbanks. Calling was frequently heard at dusk, but continued into the night. The call is a loud 'yip yip yip . . .' (Fig. 6).

COLOUR. Dorsum and flanks very dark brown with pale dappling and a golden refracted gleam. Tympanum almost black. Edge of supraorbital area barred black and white or fawn. Upper lip the same, lower lip barred white on black. Ground colour of belly and lower flanks white to pale grey and almost obscured by rounded black and brown patches. Throat white to dark brown almost obscured by black mottling, with a white median line. Hind limbs very dark above with indistinct darker cross bars. Posterior thigh dark brown with black spots. Limbs greyish below mottled with black. Iris tin coloured to fawn in dorsal third, lower two-thirds very dark brown.

Rana blythi

Rana macrodon var. *blythi* Boulenger, 1920.

MATERIAL. BM. 1974. 4519–4550 (10 ♂♂, 9 ♀♀, 11 immature, eggs).

HABITAT. This was the commonest river frog at the Sungei Kelebang (43 m) and was also collected at the Petuang and at 790 m on the east ridge of G. Lawit. Around the Kelebang it was found in all areas close to water. Mature males and gravid females were taken equally on river beaches, along small streams in forest and by temporary trackside pools. Immature frogs of all sizes were taken in a similar range of habitats. The largest of the adult frogs, however, seemed to be confined to shingle river beaches. On the east ridge of G. Lawit this species occupied shallow gravel pools in mountain streams, where it must have been in competition with *R. kuhli.*

R. blythi has unpigmented eggs, which indicates (Salthe and Duellman, 1973) that the site of egg deposition may be specialized. A pebble nest, believed to belong to *R. blythi*, was found near the mouth of a tributary stream of the Sungei Petuang at 250 m. Eggs removed from the nest are unpigmented, 2–2·3 mm in diameter and 3–3·5 mm across the capsule. Mature oviducal ova from a preserved *blythi* are *c.* 2 mm in diameter. An outer ring of pebbles, about 60 cm in diameter, was built out into the stream from the pebble beach. Although the level of the stream fluctuated widely, at the time of observation this barrier broke the surface except on the upstream side, on which a current of water entered the nest. Stones had apparently been scraped up from within this ring to form a central pile, below the water surface, leaving an inner ring of smaller pebbles and gravel. No eggs were visible externally, but on removing a few large stones from the pile eggs were found dispersed through the pebbles and loosely adherent to them. During the day *R. blythi* was seen on the banks near the nest. Before collecting at night, the nest was revisited and a large *blythi* found on it. Later, 2 non-gravid females were caught in the nest area. Mackinnon (1975, pp. 147–148) records similar behaviour in an unnamed large *Rana* on the Sungai Segama in Sabah. Nest building may be important to *blythi* as a form of behaviour protecting the spawn and newly hatched larvae against the stream current. Territorial behaviour and parental guarding of the nest should be looked for in this species.

REMARKS. As already noted (p. 190) this Sundan species extends from the Malay Peninsula northwards to Changwat Tak, Thailand. It is apparently confined in the Indochinese subregion to the hill tract between the Andaman Sea and the Chao Phraya lowlands of Thailand.

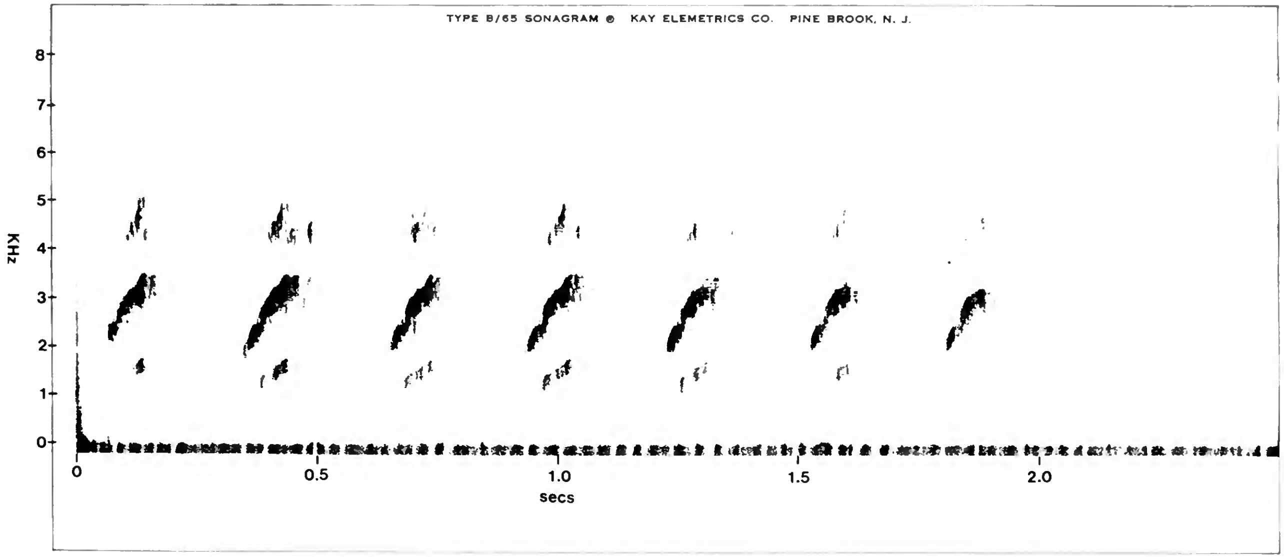

Fig. 6 Sonagram of the mating call of *Rana baramica*, background noise has been removed.

Rana chalconota raniceps

Polypedates raniceps Peters, 1871.

MATERIAL. BM. 1974. 4551–4626 (41 ♂♂, 19 ♀♀, 15 juveniles, larvae).

HABITAT. This riparian species was found in all areas near water at the Sungei Kelebang, including the flooded areas of logging tracks, and small streams in logged forest. Most were low on vegetation but some were up to 1½ m above ground. Males call from these positions. The call is a soft 'pink pink' like dripping water. The species was also found at the Sungei Petuang at 250 m.

Rana hosei

Rana hosii Boulenger, 1891*b*.

MATERIAL. BM. 1974. 4627–4640 (8 ♂♂, 6 ♀♀).

HABITAT. Six specimens were found at the Sungei Kelebang, on the river banks and up to 20 m from the river on vegetation. The other specimens were found along the Sungei Petuang (250 m), on the rocky river banks and up to 5 m from the water and 2 m above ground on shrubs. The ♂♂ all have nuptial asperities and the females are gravid or have convoluted oviducts.

Rana kuhli

Rana kuhlii Duméril and Bibron, 1841.

MATERIAL. BM. 1974. 4641–4654 (2 ♂♂, 4 ♀♀, 8 immature and larvae).

HABITAT. *Rana kuhli* was found only on the east ridge of G. Lawit (790 m) where it occupied small, rocky, mountain streams. Most specimens were found in shallow gravel-bottomed pools along the streams. Some were caught in a side pool of clear water with a light layer of silt and decomposing leaves. Two larvae were caught in a similar pool.

REMARKS. The 2 males have nuptial pads on the first finger covered with minute, white spicules. They have small unpigmented testes and are 61·4 and 93·0 mm in length. Only the larger male has significantly enlarged mandibular processes, which are 3–4 mm in height. Four gravid females are 66·0–81·3 mm in length. The mature ova are one-third pigmented and about 2·5 mm in diameter.

The larvae have I : 1–1 / 1–1 : II labial teeth, all the toes broadly webbed to the tips, the tibiae strongly tuberculate and the tail blotched and barred with black. They differ from Bornean larvae, however, in having acutely pointed tails twice as long as the body and in having 3 rows of papillae on the lower lip.

Rana laticeps

Rana laticeps Boulenger, 1882.

MATERIAL. BM. 1974. 4655–4702 (7 ♂♂, 5 gravid ♀♀, immature specimens).

HABITAT. As previously mentioned, this species and *Amolops larutensis* were the only frogs collected at all camps 43–1280 m. These records seem to extend both the upper and lower altitude limits slightly. In Borneo specimens come from 100 to 920 m. In the Malay Peninsula previous records are from 900 to 1220 m.

At the Kelebang *R. laticeps* could only be found in one stream and only four specimens, all caught on the same night, were found, despite frequent collecting both at night and in the day. This was the same rocky hillside stream in which *Amolops larutensis* and *Ansonia* sp. were found. The frogs were in shallow pools or between rocks at the stream edge.

Thirty-nine of these frogs came from two streams on the east ridge of G. Lawit (790 m). The species was found in areas of shallow gravel-bottomed pools and in shallow reaches with many dead leaves and some other detritus in the upper parts of the streams. During the night many were found in the water, from which the males seem to call. They were also found on the banks, mostly near the water but up to 2 m away in a few cases. During daylight the frogs hide among dead leaves in the water, in crevices under boulders and among the leaf litter along the banks. Juveniles were found in daylight among the leaf mould in seepages along the banks.

Only 2 specimens came from the summit ridge (1280 m). Both were in the small, semi-stagnant stream under closed canopy forest, along which most of the collecting was conducted. One was resting on matted roots in the edge of a pool between rocks, the other was in a shallow pool on a smooth rock base. A few calls were also heard along this stream.

Thus *R. laticeps* occupies a similar habitat throughout its altitudinal range. Apparently it also occupies a very similar habitat in Borneo (Inger, 1966).

REMARKS. The adult males are 34·5–46·9 mm (mean 43·8 mm, N=7) in snout–vent length. Gravid females are 36·7–45·0 mm long (mean 40·8 mm, N=5) and contain ova 2·8–3·0 mm in diameter, with only about one-fifth of the surface pigmented. The ova are therefore larger and less pigmented than those of *kuhli*. The call is a rising gurgle (Fig. 7).

Rana limnocharis limnocharis

Rana limnocharis Boie *in* Weigmann, 1835.

MATERIAL. BM. 1974. 4703–4724 (15 ♂♂, 4 ♀♀, 2 juveniles, larvae).

HABITAT. This commensal species was found only along logging tracks and in the camp clearing at the Sungei Kelebang (43 m).

Rana luctuosa

Limnodytes luctuosus Peters, 1871.

MATERIAL. BM. 1974. 4725–4726 (two larval series).

HABITAT. One series was collected in forest on the east ridge of G. Lawit at 790 m. The larvae were in a shallow gravelly pool separated from a small stream by two to three metres. The pool bottom was largely covered by a layer of decomposing leaves, with a little silt. At one end an inlet trickle had excavated a deeper hollow between roots. On each occasion on which the pool was approached tadpoles were seen to swim rapidly across it and disappear into this hollow. The other larvae were found in an exposed pool among long grass and *Melostoma* bushes in a boggy padang on the summit ridge at *c.* 1350 m. This very shallow pool was stagnant and had a deep mud base.

COLOUR. Very dark brown above and dark grey below. Ochre speckling on both dorsum and venter, on tail muscle and upper fin of tail.

REMARKS. The two series differ in the number and length of the papillae on the lower lip, but are otherwise very similar. Specimens from the summit ridge are in stages I–II (Taylor and Kollros, 1946), 12·0–18·0 mm in body length and 18·3–27·0 mm in tail length. Most have labial tooth formulae of I : 3–3 / 1–1 : III but one has I : 4–4 / 1–1 : III labial teeth. Most of the east ridge specimens are also in stages I–II. They have I : 4–4 / 1–1 : III labial teeth generally, although the posterior tooth row is very small in the smaller specimens. They are 15·2–19·5 mm in body length and 24·0–29·5 mm in tail length. A stage XIV larva is little different. It is 24·0 mm in body length, 32·5 mm in tail length and has I : 5–5 / 1–1 : III labial tooth rows. The east ridge specimens have one to three rows of papillae on the posterior lip and the posterior papillae are less than 0·3 mm in length. Summit ridge larvae have two rows of papillae. Alternate papillae of the lower row are greatly elongated, about 0·5 mm in length. Other Malayan larvae of stages I–XIX, with body lengths of 18·0–24·0 mm, and from 275 to 670 m elevation, have elongate papillae 0·4–0·6 mm in length, in proportion to their body lengths.

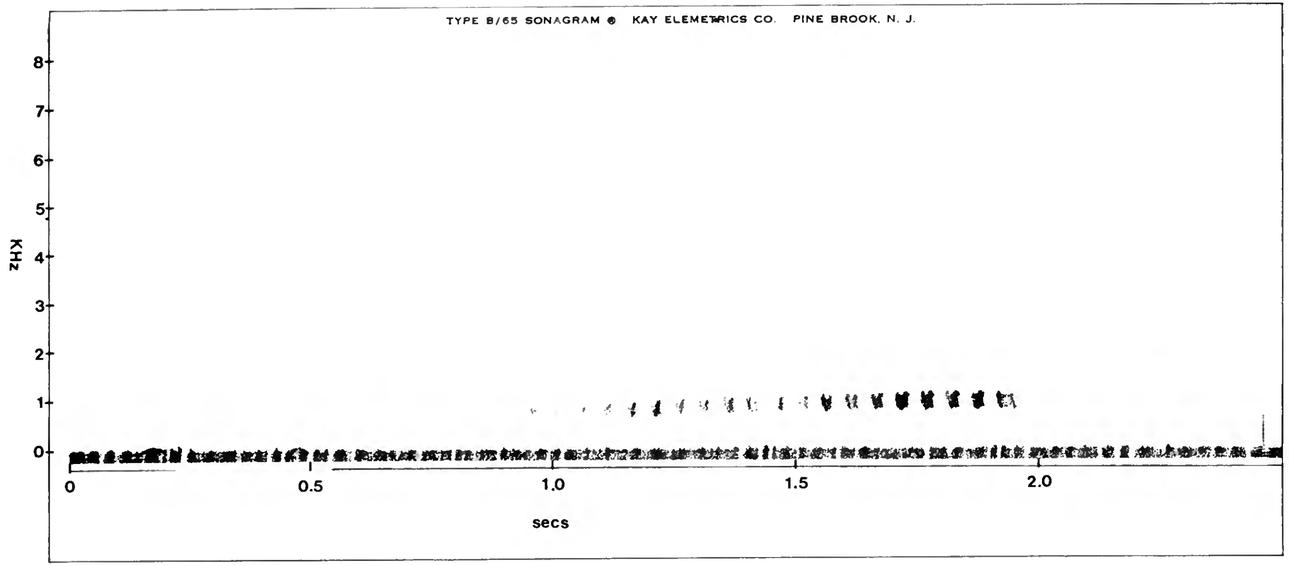

Fig. 7 Sonagram of the mating call of *Rana laticeps*, recorded at 790 m elevation.

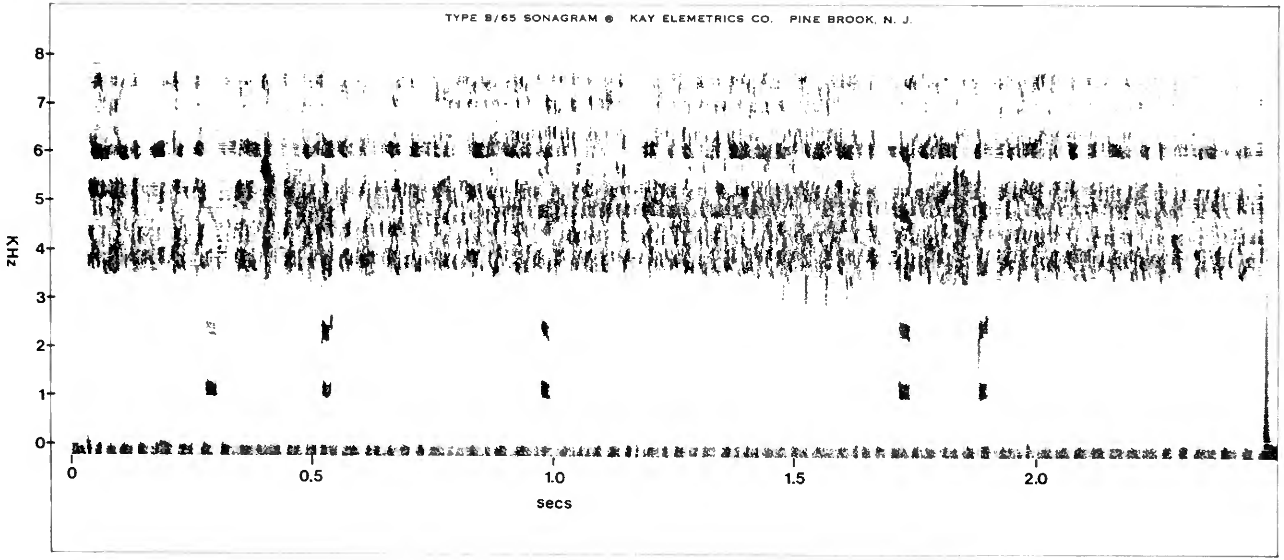

Fig. 8 Sonagram of the mating call of *Rana limnocharis*, most high frequency noise is background.

Rana macrodon

Rana macrodon Kuhl *in* Duméril and Bibron, 1841.

MATERIAL. BM. 1974. 4727–4728 (immature).

HABITAT. One specimen was caught in a flooded rut on a logging track, the other was caught shortly afterwards on the forest floor, between the buttresses of a tree. The second specimen ducked its head protectively between its fore limbs when approached. Both were collected in the Sungei Kelebang camp area (43 m).

COLOUR. The dorsum is medium brown with some yellowish paravertebral areas. There is some dark dorsal speckling, particularly at the edges of the weak dorsal tubercles. Anterior to the interocular bar the snout was fawn. There is a grey edged, fawn triangle below the eye and an oblique pinkish yellow band from the eye to the arm insertion. The black supratympanic stripe is narrow and covers the upper half of the tympanum, except its centre. The throat is mottled with grey, except where there is a broken median white stripe. The remainder of the venter is white with grey speckling. The hidden surfaces of the limbs are grey; the dorsal surfaces, including the outer two fingers and outer three toes, are the same brown as the dorsum. The posterior thigh is finely mottled with pale brown.

REMARKS. Kiew (1974) gives this species a new name, according to Berry (1975), but since I have not seen this thesis I prefer to use *macrodon*, *sensu* Inger. Berry gives a long list of Malay Peninsula records but without distinguishing between *R. macrodon* and *R. blythi*. The BM(NH) specimens of *R. macrodon* come from Singapore, from Kuala Teku, Pahang and from the Sungai Kelebang, in the Malay Peninsula. The Kelebang specimens, at 5° 28″ north, are thus the northernmost I have seen and with Inger's (1966) record from Selinsing, 4° 53″ north in Perak they mark the northern boundary of this species on the mainland.

Rana paramacrodon paramacrodon

Rana paramacrodon Inger, 1966.

MATERIAL. BM. 1974. 4729–4732 (3 gravid and 1 immature ♀♀).

HABITAT. The 4 specimens were believed to be *R. blythi* when collected and there are only brief field notes for them. Apparently all were collected in the same areas around the Sungai Kelebang in which *R. blythi* were found. Two were collected along the Sungai Kelebang, one of them while hiding among leaf litter by a shallow muddy side pool. Another was collected by one of the logging tracks, probably from a pair of very shallow clay-based trackside pools. The fourth was by a stream pool in a swampy area.

REMARKS. They agree closely with a paratopotype of *R. p. paramacrodon*. They range in size from 38·3 to 56·6 mm and the largest specimen contains enlarged pigmented ova. They have tibia to snout–vent length ratios of 0·537–0·575 and head length to snout–vent ratios of 0·364–0·373. The distal two phalanges of the fourth toe have a broad fringe of webbing on each side, such as is found in Bornean *paramacrodon*. On the inner edges of the second and third toes the web reaches the digit tips as a narrow sheet. All the frogs are a rather uniform dark brown dorsally, without a vertebral stripe, and all have a narrow light line along the thigh but not on the tibia. None has the distinct dorsal ridges found in some Bornean *paramacrodon*. There is a well-defined, lozenge-shaped, black tympanic mask. The entire surface of the throat is covered by fine grey mottling.

Kiew (1972) recorded *R. paramacrodon* from Tasek Bera, Pahang, and various localities in Selangor, although he noted that his frogs might represent an undescribed species. The specimens showed several distinctive features of *paramacrodon*, such as their small size and yellow ventral coloration. However, they lacked the equally distinctive black tympanic mask. This, then, is the first definite record of *paramacrodon* from the Malay Peninsula.

Rana plicatella

Rana plicatella Stoliczka, 1873.

MATERIAL. BM. 1974. 4733 (♂).

HABITAT. The frog was taken at night from a small stream on the east ridge of G. Lawit (790 m).

COLOUR. Dorsum dark ochre with blackish crossbars on the limbs. Throat white mottled with pale grey around the jaws. Chest, abdomen, undersurfaces of thigh and tibia golden yellow, speckled with brown on the distal femur and tibia.

Rana signata signata

Polypedates signatus Günther, 1872.

MATERIAL. BM. 1974. 4734–4757 (19 ♂♂, 5 ♀♀).

HABITAT. This common frog calls at night from tangles of roots and sticks up to 2 m from river edges. Its distinctive coloration makes it extremely difficult to see in such situations. Frogs were collected from this sort of site at both the Kelebang and the Petuang. At the Kelebang some males were also found by small streams in clearings or in forest. One of the females was found at a trackside about 100 m from the Kelebang, the others were in the same situations as the males. The call is shown in Fig. 9.

Rana tweediei

Rana tweediei Smith, 1935*b*.

MATERIAL. BM. 1974. 4758–4759 (immature).

HABITAT. Both were found on the forest floor away from streams. One was found during the afternoon on a dry ridge top track at about 600 m on the east ridge of G. Lawit. The other hopped across a trail at about 300 m on Bukit Bok, during a rainy afternoon.

COLOUR. The dorsal surfaces were reddish to dark brown with dark paravertebral blotches and narrow dark crossbars on the limbs. The larger specimen had a broad pale pinkish vertebral stripe from snout tip to vent. There was a ragged dark supratympanic marking and an orange pink oblique stripe behind the eye covering the lower edge of the tympanum. The lips have dark crossbars. The throat was colourless, the chest and abdomen pale yellow and the undersurfaces of the thigh and tibia yellow orange.

REMARKS. These two specimens, 30 and 21 mm in length, are virtually identical with two immature frogs from Pulau Tioman called by Hendrickson (1966) *Rana* (*Discodeles/Platymantis*) sp. There are small discs on the fingers and toes which have anterolateral grooves partly separating the dorsal and ventral surfaces. The dorsal portion of the disc, generally shorter than the ventral portion, is further subdivided by a median groove. I believe that these grooves are due to desiccation of the digit tips; similar structures can be seen on the discs of some preserved *Rana hascheana*, *microdisca* and *tweediei*. The finger discs are not wider than the basal portion of the digit, the first finger is short, the toe webbing is reduced, the outer metatarsals are separated in the distal part by web, the tympanum is distinct, there are weak dorsolateral glandular folds and the omosternum is deeply forked at the base. These characters, and their general appearance, place the specimens in the *ranae grunnientes* of Boulenger (1920), and close to *hascheana*, *microdisca*, *nitida* and *tweediei*. Their webbing is more extensive than that of *R. hascheana*, but is identical with that of the other species.

Rana tweediei Smith, which may be the Malay Peninsula representative of the *microdisca* group, was placed in the synonymy of *R. nitida* Smedley, 1931, by Kiew (1975) who showed that they do not differ in relative head or body proportions. Kiew noted the difference in size between his specimens of *tweediei* and the holotype of *nitida*, but did not consider it of specific value. Four fully adult males of *tweediei* in the BM(NH) are 36·5–41·8 mm in length (mean 39·4 mm). These

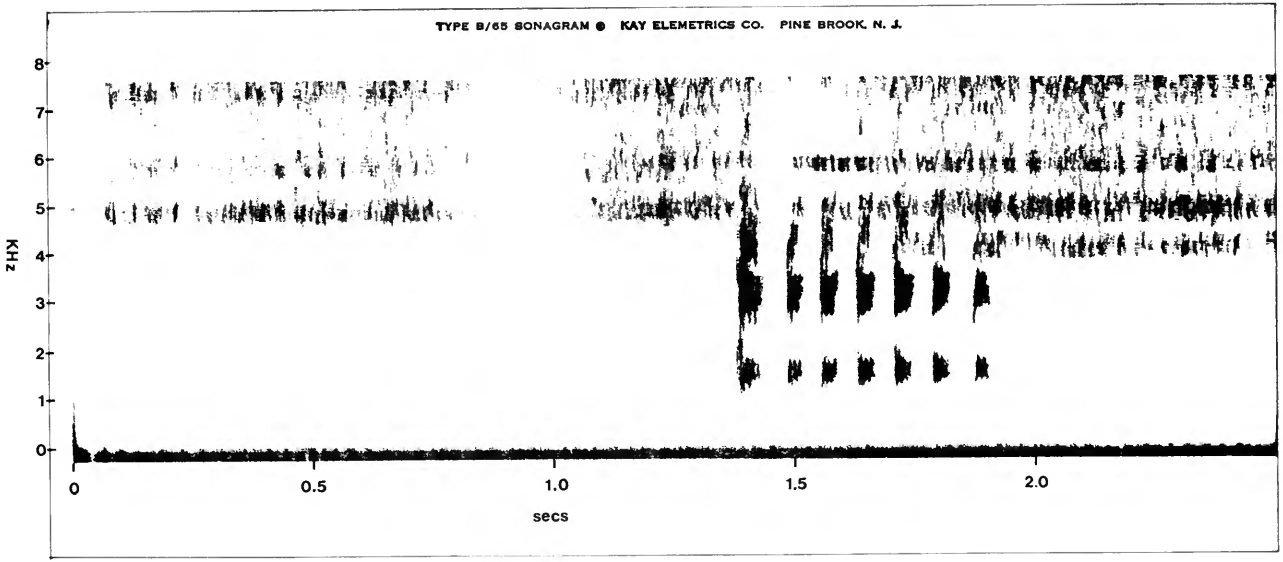

Fig. 9 Sonagram of the mating call of *Rana signata*, recorded at 43 m elevation. Most high frequency noise is background.

have enlarged heads and elongated mandibular processes, which in the largest specimen are 1·2 mm in height. This specimen has compact, unpigmented, rather rounded testes 3 mm in length. The male paratype of *nitida* is 53·5 mm in length, has short mandibular processes only 1 mm in height, and very large, compact, unpigmented and rather elongate testes 9·4 mm in length. Three gravid females of *tweediei* are 37·8–41·8 mm long (mean 39·8 mm), the gravid female holotype of *nitida* is 71·0 mm in length. Thus *tweediei* not only differs from *nitida* very markedly in size but may differ in male secondary sexual characters; and should be reinstated as a distinct species. One characteristic of *tweediei* is a jagged white (in preservative) stripe running from the eye over the lower edge of the tympanum. Since the Trengganu specimens share this characteristic, and since they were found within the known altitudinal range of *tweediei* (in lowlands up to 800–900 m) I refer them to this species, not to *nitida* which has only been found at 1370 m.

Family **RHACOPHORIDAE**

Edwardtayloria picta picta

Ixalus pictus Peters, 1871.

MATERIAL. BM. 1974. 4761 (gravid ♀).

HABITAT. From the east ridge of G. Lawit at 790 m. It was caught at night 2 m above the bank of a stream on a dead *Pinanga* stem.

COLOUR. The dorsum is cinnamon with creamy yellow spots. The discs of the first and second fingers and first to third toes are creamy yellow, the others are cinnamon. The throat and the undersurfaces of the fore limbs are yellowish with small cream speckles. The undersurfaces of the hind limbs are a light cinnamon. The belly is black with chalk white marbling. The iris is cinnamon, except for the upper anterior third which is cream.

REMARKS. This frog belongs to the genus, previously called *Hazelia* (see Liem, 1970), for which the new name *Edwardtayloria* was erected by Marx (1975), *Hazelia* being pre-occupied.

Philautus aurifasciatus

Hyla aurifasciata Schlegel, 1837.

MATERIAL. BM. 1974. 4762–4780 (14 ♂♂, 3 ♀♀ and 2 immature).

HABITAT. On the east ridge of G. Lawit (790 m) specimens were caught from ½ to 4 m above the ground on shrubs, along streams and on the hillsides above them. On the summit ridge at 1280 m 7 specimens were caught in closed canopy forest in the humid valley of a small stream. The species was also common at the summit (1500 m), where males were found calling from low foliage at night. There was no accessible ground water at the summit but in shallow valleys dry silty runnels among the leaf litter showed that during heavy rain there was some transitory surface water. These conditions must greatly favour frogs with direct development. *P. aurifasciatus* was never found in tree holes on G. Lawit, and was not collected in the heathy padang where *Nepenthes* grew.

REMARKS. This species has a number of characteristics that distinguish it from other Malay Peninsula species. The size does not show much geographic variation. Mature males have the following snout–vent lengths; G. Lawit, 21·9–26·9 mm (mean 24·1 mm, N=14); G. Benom, 20·6–26·2 mm (mean 23·8 mm, N=25); Borneo, 15·8–24·0 mm (mean 21·78 mm, N=13). Females with eggs or convoluted oviducts are considerably larger; G. Lawit, 27·8–31·7 mm (mean 29·7 mm, N=3); G. Benom, 31·0–36·7 mm (mean 33·7, N=7); Borneo, 23·9–33·3 mm (mean 29·9 mm, N=13). Data for Bornean specimens are from Inger (1966). Lingual papillae are generally present. Mature males have colourless nuptial pads on the dorsomedian surface of the first metacarpal. They have vocal sac slits which are generally small and near the jaw commissure. The gular skin is moderately folded to allow for extension of the vocal sac. Almost invariably adult males have weakly conical snout tips, while adult females have strongly conical ones. *P. aurifasciatus* is a strictly Sundan species and BM(NH) examples come from only as far north as the Larut Hills and G. Lawit.

Smith (1930) incorrectly reported this species from Thailand and Cambodia. Re-examination of his specimens shows that they have the characters below. A small species. 8 mature males from Changwat Tak are 16·7–20·3 mm in length (mean 19·2 mm). A female with kinked oviducts from north Thailand is 17·0 mm in length and 2 females with convoluted oviducts from south Cambodia are 19·0 and 19·4 mm long. Mature males have elongate vocal sac slits which reach forwards to about the middle of each mandible. The gular skin is massively folded to accommodate what must be a relatively large vocal sac. Lingual papillae are absent in all 37 specimens. There are nuptial pads like those of *aurifasciatus* and the snout shape is similar. Taylor (1962) collected a small *Philautus* in north Thailand which he called *P. parvulus* (Boulenger). I have compared Smith's material with two of the types of this species; the name *parvulus* appears to be applicable to these populations. The range of the species may extend south into the Malay Peninsula. *Philautus* have been collected in peninsular Thailand on Khao Luang and Ronpibun Hill, Nakhon Si Thannarat, and on Bukit Besar and at 'Patani' in the south east. Ten specimens from these localities all lack lingual papillae. Two mature males from 'Patani' and one of two from Ronpibun Hill have massively folded gular skin like *parvulus*. Snout–vent lengths of the 4 males are 18·5–21·2 mm (mean 19·6 mm). Immature specimens from Khao Luang and Bukit Besar have a pattern which includes a midventral pale line on the gular region (see Boulenger, 1903). All these specimens are tentatively referred to *P. parvulus*.

LARVAE. The breeding behaviour of *Philautus* is still poorly known. The ova are large and few (see Inger, 1966). This has led to hypotheses that the ova are deposited out of water. The Wolffian duct is simple, which suggests that no foam nest is produced (see Liem, 1970). *P. aurifasciatus* was observed by Mjoberg to lay its eggs in *Nepenthes* pitchers on G. Murud (Smith, 1925*a*). Frogs of the genus are frequently found calling far from water. Inger (1966) artificially fertilized eggs of *P. hosei* and raised larvae which developed to limb bud stage within the vitelline membrane. These larvae lack structures necessary for an active life (the horny beak, expanded lips, labial teeth, external gills, operculum and coiled gut) but have a very large yolk mass.

Larvae (BM. 1914. 5.12.3–17) were collected from *Nepenthes* pitchers on the summit of G. Santubong, Sarawak, and raised from pre-limb-bud state to metamorphosis. They were subsequently identified as *P. petersi* (=*aurifasciatus*) on the basis of the juveniles. These larvae agree with Inger's description of *P. hosei* larvae, except that the tail fins are well developed and highly vascularized, probably for respiration. According to the collector's notes, they did not leave the egg membranes until metamorphosis. Another series was collected from moss on tree trunks at 1280 m on G. Bunga Buah, Selangor, and discussed by Berry (1975) as *Megophrys longipes*. These agree closely with the Santubong larvae except that the tail fins are a little less well developed and not obviously vascularized. Neither series has the usual larval mouth parts or coiled gut, neither do they have external gills or an operculum with a spiracle. The eyes are well developed, there are olfactory pits, the fore and hind limb buds develop synchronously and there is a large yolk mass. *P. vermiculatus* males have also been collected among moss on tree trunks at this altitude on G. Bunga Buah. These larvae are reminiscent of those of *Rhacophorus microtympanum* (generic status uncertain according to Liem) described by Kirtisinghe (1946), which have an operculum and spiracle and non-functional gills.

A number of previous records of *Philautus* larvae have been based on aquatic larvae (Annandale, 1913, 1918, 1919; Rao, 1937; Roonwal and Kripalani, 1961; Smith, 1924, 1953). I have seen only the larvae assigned to *P. romeri* Smith (1953). They have I : 2–3 / III labial tooth rows and their characteristics, including extent of toe webbing and the size of the discs on the fingers and toes, support Smith's identification. Smith compared this species with *Chirixalus laevis*, belonging to a genus which has aquatic larvae with similar labial tooth row formulae. However, to me *P. romeri* does not appear similar to species currently assigned to *Chirixalus*, but to small *Philautus* species such as *P. annandalei*. Annandale (1913) recorded larvae which he assigned to *annandalei*. According to his account, they resembled *Polypedates leucomystax* larvae, and so should have had I : 3–3 / 1–1 : II labial teeth. The other records are less satisfactory. The supposed larvae of *P. variabilis* described by Annandale (1918, 1919) had II : 5–5 / 1–1 : V labial tooth rows, a higher number than is known in any other rhacophorid frog. Smith (1924) assigned larvae to *P. gryllus* but without giving his reasons. The larvae did not come from the same locality as his adults and had tooth row formulae of II : 3–3 or 4–4 / 1–1 : III. This formula is like that of *Chirixalus*, two species of which were found at nearby localities. Rao described larvae from 'streams of Kempholey' which he thought belonged to *P. hypomelas*, *P. leucorhincus*, *P. nassutus*, *P. pulcher* and *P. variabilis*. These appear from his description and plate to be generally stream adapted; they have somewhat expanded lips which lack labial teeth although a beak is present. The lips of some are multilobate. These larvae are unlike any yet known from the *Rhacophoridae*, but are similar to those described by Annandale (1918, 1919) and assigned to *Rana leptodactyla*, *Rana semipalmata* and *Nyctibatrachus*. Roonwal and Kripalani described a new species of *Philautus* from Assam on the basis of larvae and a juvenile. This species has webbing between the fingers, unlike any species assigned by Liem to *Philautus*. The finger webbing is however approximately as extensive as that in *Rhacophorus taronensis* Smith, from northern Burma. In summary, records of aquatic larvae for *Philautus* are suspect. They are probably based mainly on misidentifications, while some supposed *Philautus* may belong to other genera.

Colour. There is dorsal polychromatism as described by Grandison (1972). The ground colour of the dorsal surfaces varies from pinkish fawn to dark brown. The lips are cream spotted and the throat is mottled with grey and brown. The belly is greyish brown. The posterior flanks and anterior and posterior faces of the thigh are claret brown with oval fawn blotches. The iris was described in the field as gold to dark brown, and is never grey.

Philautus vermiculatus

Ixalus vermiculatus Boulenger, 1900.

Material. BM. 1974. 4781–4821 (30 ♂♂, 2 ♀♀, 8 immature).

Habitat. This Malay Peninsula endemic has the same altitudinal distribution as the more widespread *P. aurifasciatus*, it is known from 790 to 1530 m. Three specimens were taken at night from leaves 2–5 m above the forest floor on the east ridge of G. Lawit (790 m). One of them was calling from the top of a small tree on the steep valley side above a stream. Thirty specimens were caught around the summit ridge camp (1280 m). Half (12) of those with data were caught on leaves at night. Eight were taken from tree holes, holes in hollow branches, mostly at night. Males were found calling from both leaves and tree holes. The species was found equally in closed canopy forest in a humid stream valley (6) and in a nearby grassy padang (6). During a few hours' collecting in closed canopy forest at the summit 7 examples were obtained from low vegetation. Of the 6 caught there at night 4 males were calling from tree holes, another male was on a leaf near one of these calling males and a gravid female was caught a metre from another of the calling males.

It is possible that *P. vermiculatus* lays its eggs in tree holes and that males lead gravid females to these holes by calling. No clear ecological separation of *vermiculatus* and *aurifasciatus* was noticed in the field, but *aurifasciatus* was never found in tree holes or collected in a padang. It would be interesting to see whether the different colours of the two species lead to different choices of substrate. More precise observations need to be made before the mechanism by which these two similar species occupy the same areas can be understood. The quacking call is shown in Fig. 10.

Colour. In alcohol the 3 specimens from the east ridge are like all the BM(NH) examples of *vermiculatus* from other localities (the main range, G. Benom and G. Tahan, and from throughout the altitudinal range) in having the anterior and posterior faces of the thigh unpigmented. However, all the specimens from the summit and summit ridge have these areas darkly pigmented. From the field notes it appears that there were also differences in the life colours of the higher and lower populations on Lawit.

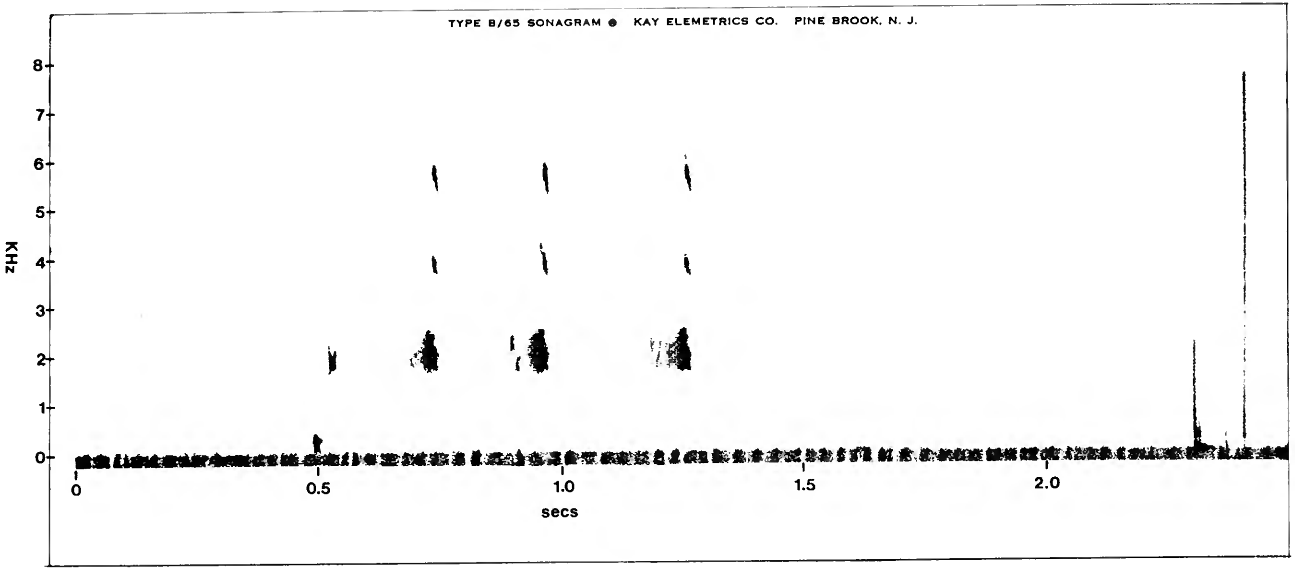

Fig. 10 Sonagram of the mating call of *Philautus vermiculatus*, recorded at 790 m elevation.

East ridge sample. Dorsal surfaces yellow brown to lichen green with darker vermiculations and other markings. Throat lemon yellow to fawn, mottled with brown. Other ventral surfaces and hidden surfaces of limbs golden yellow to orange. Lips cream spotted. Iris silver grey.

Summit and summit ridge sample. Throat creamish, belly greyish or colourless. Anterior and posterior faces of thigh pale ochre to medium brown. Dorsal surfaces and iris as above.

REMARKS. This species can be easily recognized in the field by its characteristic head shape (Grandison, 1972) and by its colour. *P. aurifasciatus* always lacks the greenish dorsal and yellowish ventral colours of *vermiculatus*. The iris is brown in *aurifasciatus*, silver in *vermiculatus*. This species shows only weak dorsal polychromatism compared to *aurifasciatus*. There is usually an hour-glass-shaped figure on the anterior dorsum sending back branches to the groin. Some *aurifasciatus* patterns are similar. *P. vermiculatus* invariably lacks a conical tip to the snout and a lingual papilla. Nuptial pads are also absent. In addition *vermiculatus* reaches a slightly larger size and has a relatively shorter tibia and narrower head. These differences are shown in Table 2.

Table 2 Data on West Malaysian *Philautus* (lengths in mm)

	P. vermiculatus	*P. aurifasciatus*
SV ♂♂	25·3–29·4 (mean 27·3, N=30)	20·6–26·9 (mean 23·9, N=39)
SV ♀♀	32·8–36·9 (mean 35·4, N=3)	27·8–36·7 (mean 32·4, N=10)
Tibia/SV	0·472–0·547 (mean 0·505, N=9)	0·515–0·603 (mean 0·562, N=9)
HW/SV	0·382–0·418 (mean 0·404, N=9)	0·412–0·438 (mean 0·427, N=9)

Polypedates colleti

Rhacophorus colleti Boulenger, 1890.

MATERIAL. BM. 1974. 4821–4823 (3 ♂♂).

HABITAT. All were collected on the same night, 1½–3 m above the ground on bushes and saplings around the edge of a swampy area in logged forest near the Sungei Kelebang camp (43 m).

COLOUR. By day the dorsum varied from pinkish grey to pale reddish chocolate. There was a darker hour-glass figure on the mid-dorsum surrounded by scattered dark and light speckling. The lip was dark edged with a pale line above. There were similar pale lines with dark lower edges on the outer surfaces of the limbs and the outer finger and toe, and above the vent. The throat was greyish, and the belly yellowish white. There are white tubercles below the vent. The iris was very pale brown.

REMARKS. Liem (1970) placed this species, along with *leucomystax*, *macrotis* and nine other species, in the revived genus *Polypedates*.

Polypedates leucomystax leucomystax

Hyla leucomystax Boie *in* Gravenhorst, 1829.

MATERIAL. BM. 1974. 4824–4835 (9 ♂♂, 1 gravid ♀, larvae).

HABITAT. On tracks or in secondary trackside vegetation in logged forest at the Sungei Kelebang.

Polypedates macrotis

Rhacophorus macrotis Boulenger, 1891*a*.

MATERIAL. BM. 1974. 4836 (♂).

HABITAT. It was caught at night 1½ m above the ground on a stem by a logging track at the Sungei Kelebang.

Rhacophorus appendiculatus

Polypedates appendiculatus Günther, 1858.

MATERIAL. BM. 1974. 4837–4845 (9 ♂♂).

HABITAT. All were collected in the disturbed areas around the Sungei Kelebang (43 m). Six were found in a dense thicket of saplings and other shrubs, rattan and vines at the intersection of two logging tracks. A large tree stump had been uprooted leaving a shallow, partly shaded hollow. This had flooded and a chorus of males were found around it on two successive nights. They were calling from 30 to 100 cm above ground level on shrubs. The other three specimens were caught in a similar, disturbed and swampy area. A moderately thick growth of rattan, ginger, banana and other shrubs had grown up where the larger forest trees had been removed. The swampy ground was criss-crossed with logs and covered by a network of very shallow pools. The frogs were on vegetation and 60–200 cm above ground level.

COLOUR. The dorsal surfaces are dark green to brown, with a dark interocular bar and hour glass figure on the abdomen. One specimen had russet dorsolateral markings. Throat is yellowish to greenish and may be colourless posteriorly. The belly is yellowish to dull orange. The anterior face of the thigh is brown to dark brownish red and the posterior face is dark blood red. The supra-anal scallops, the scalloped margin of the tarsus and fifth toe are white and there are white spots around the vent. The iris is sandy brown, orangey above.

REMARKS. The generic status of this species is uncertain (Liem, 1970). It is *Philautus*-like in appearance but has an aquatic larva. These males are similar in size to those from Sandakan, Sabah (Inger, 1966). Snout–vent length is 29·7–34·4 mm (mean 31·9 mm). Tibia length relative to snout–vent length is 0·489–0·532 (mean 0·505). Three males from Selangor and Negeri Sembilan are similar in size (mean 31·3 mm) and 2 Pahang females are 43·8 and 48·1 mm in length.

The call is shown in Fig. 11.

Rhacophorus bimaculatus

Leptomantis bimaculatus Peters, 1867.

MATERIAL. BM. 1974. 4846–4851 (3 ♂♂, 3 gravid ♀♀).

HABITAT. A male and 2 gravid females were caught in a bare and partly flooded logging clearing near the Sungei Kelebang camp, through which a fast deep affluent stream of the Kelebang was running. The male was above the stream surface on a pandan and the females were 1½–2 m up on shrubs of the clearing edge. Males, heard calling from undisturbed riverbank vegetation at the Sungei Petuang (250 m), were 1–2½ m above the steep rocky banks on shrubs and small trees. A gravid female was a metre above the river edge on a fern.

COLOUR. The dorsal surfaces are sandy to dark brown with five darker bars, on the interocular area, on the nape, the anterior dorsum, the sacrum and just anterior to the groin. The sacral bar is generally broken up into two dark patches over the sacral hypophyses. There is a conspicuous white spot below the posterior half of the eye. The lower jaw is brown edged, the venter is otherwise white. The posterior part of the flanks, the goin, the anterior and posterior faces of the thigh are dark brown with sky blue spots. There is some sky blue speckling on the ventral surface of the tibia, on the inner edge of the tarsus and foot, and in the axilla.

REMARKS. Liem (1970) examined the musculature and other characters of *R. bimaculatus* Boulenger, *R. bipunctatus* Ahl and *R. zamboangensis* (Taylor) separately, according to his appendix. However, *bipunctatus* Ahl is a replacement name for *bimaculatus* Boulenger, preoccupied by *Leptomantis bimaculatus* Peters, and so cannot be a distinct species. Since *bimaculatus* (Peters) appears superficially to be a *Rhacophorus*, and since *zamboangensis* (Taylor) was placed in its synonymy by Inger (1966), it is fair to assume that Liem's *R. bimaculatus* Boulenger was a *lapsus* for *R. bimaculatus* (Peters) and to treat this species as a *Rhacophorus* henceforth. It is found in the southern Philippines, Borneo and the Malay Peninsula.

The call is shown in Fig. 12.

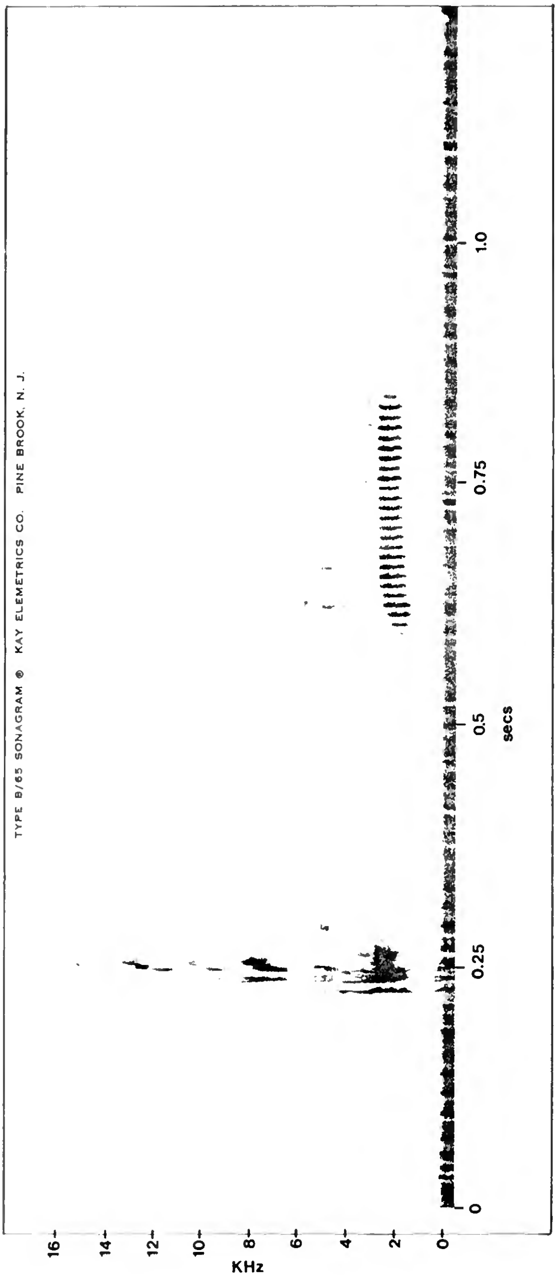

Fig. 11 Sonagram of the mating call of *Rhacophorus appendiculatus.*

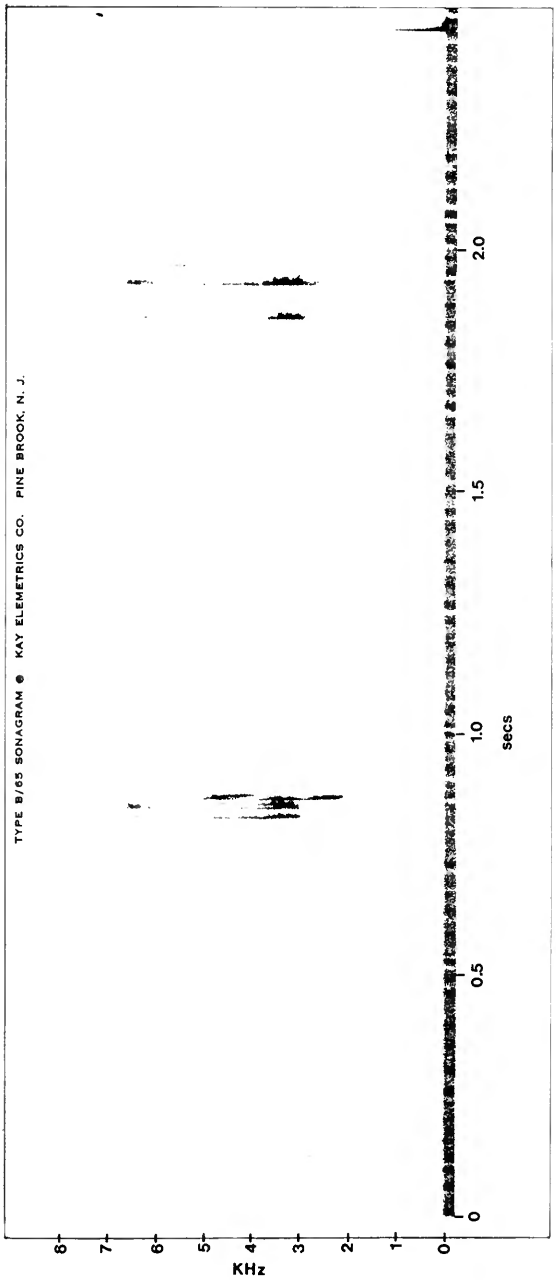

Fig. 12 Sonagram of the mating call of *Rhacophorus bimaculatus*, recorded at 250 m elevation.

Rhacophorus bipunctatus

Rhacophorus bipunctatus Ahl, 1927.

MATERIAL. BM. 1974. 4852–4882 (29 ♂♂, 1 ♀, juvenile and larvae).

HABITAT. Twenty-four of the specimens, including the female, were caught around the streamlet at the summit ridge camp at 1280 m. This small stream occupied a 100-m stretch of gently inclined valley bottom between a dry basin, overgrown with shrubs, and a mossy rockfall leading down into a steeper, drier section incised into the hillside. Collecting was carried out during a time of little rainfall and the only water available was in a series of still, clear rockpools up to ½ m deep. Shortly after the camp was left, however, a heavy rainfall transformed the water course into a torrent. The vegetation was a thick growth of *Licuala*, *Pinanga*, pandan, vines and woody shrubs such as *Melastoma* below a tree canopy at 10–15 m. Males were calling from ½ to 4 m above the ground on vegetation within a few metres of the stream. A pair in axillary amplexus were found on one of the lower branches of a tree, at 3–5 m above a shallow pool, and later laid a foam nest. Near the upper end of the stream bed a dry 'backwater', overgrown with low shrubs, but with several water-filled depressions, was searched. Near the back a shallow, pebble-bottomed pool below the bank contained well-developed larvae. A recently metamorphosed juvenile was found on the shrubs nearby. The other seven specimens were also caught at night, in a padang near the camp, at *c.* 1350 m. They were calling from shrubs and sedge and ½–2 m above the ground, at the margin of shallow muddy pools in a high grass area of open *Leptospermum* forest.

COLOUR. The dorsal colour is very changeable, from chestnut to yellow ochre, pale turquoise or even pale bluish grey. There is a slight, fine darker mottling sometimes forming an indistinct hour-glass pattern. The venter is white, or yellowish on the throat and anterior belly of some, and the hidden surfaces of the limbs and flanks are bright yellow, sometimes colourless or fleshy orange. The hand webs and all fingers except the outermost are yellow in males, but were described as pinkish and yellow streaked in the female. The outer toe webs and adjacent parts of those digits that are hidden at rest are a vivid brownish red, the inner webs are lighter. The vent, forearm and heel appendages are white edged. There may be white or cream spots on the dorsum. All specimens have a black or blue-black spot or linked pair of spots on the anterior flanks. The iris is brownish grey with a silver ring round the pupil.

Dorsal surfaces of the larvae are brown, turning golden green in older larvae. Ventral surfaces are colourless, the tail fades to grey distally.

REMARKS. This is the species found from the eastern Himalayas to West Malaysia, originally described by Boulenger (1882) as *R. bimaculatus*, and previously referred to in Malay Peninsula reports by this name. Measurements of Malayan specimens are: snout–vent length of males 37·1–40·0 mm (mean 38·3 mm, N = 10), of females 56·1–56·6 mm (N = 3); tibia in terms of snout–vent length is 0·466–0·504 (mean 0·483, N = 10).

The call is a harsh rattle, and is shown in Fig. 13.

Rhacophorus nigropalmatus

Rhacophorus nigropalmatus Boulenger, 1895.

MATERIAL. BM. 1974.4883–4897 (13 ♂♂, 1 ♀ and eggs).

HABITAT. The males were collected in trackside vegetation, 4–7 m above the ground, at the Sungei Kelebang camp. They were calling softly from trackside bushes throughout the collecting period, mostly in the vicinity of flooded ruts or other pools. The female was found in a torpid condition on felled vegetation in such an area. It spawned while alone in a collecting bag.

Rhacophorus pardalis

Rhacophorus pardalis Günther, 1858.

MATERIAL. BM. 1974. 4898–4904 (4 ♂♂, 2 ♀♀).

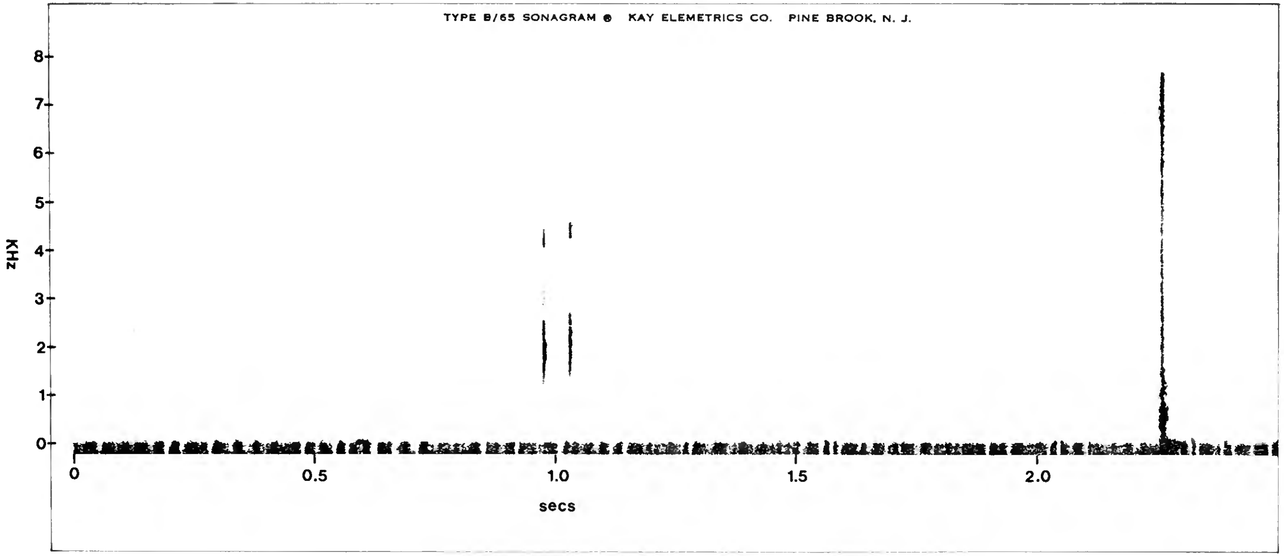

Fig. 13 Sonagram of elements of the mating call of *Rhacophorus bipunctatus*, recorded at 1280 m elevation.

Habitat. All were collected in the extensively disturbed areas around the Sungei Kelebang camp (43 m). Three males were in thick secondary vegetation at the sides of logging tracks and 2–5 m above the ground. Two were within a few metres of *R. nigropalmatus*, the other was near *R. reinwardti*. A pair in amplexus were traced by the male's call to a tree in a disturbed and swampy area. They were 5–10 m above ground. A gravid female was found in the same area about a metre up on a rattan stem.

Colour. Dorsal surfaces pale grey brown to orange brown. Irregular brown or grey markings and black, orange or lavender speckling. Flanks mottled yellow and orange. Belly creamy yellow marbled with orange. Throat whitish to yellow. Hidden surfaces of limbs fleshy orange to sulphur yellow. Webs orange and red. Lavender grey areas above vent and heels, and covering vent and heel appendages. Iris pale brownish grey.

Remarks. This lowland species which has been recorded from both Sumatra and Borneo was to be expected in the Malay Peninsula, and has also been recorded by Berry (1975) from Selangor. These Kelebang specimens roughly agree in size with Inger's (1966) Sarawak sample. Mature males 46·5–50·1 mm (mean 47·5 mm, N=4) in snout–vent length, the mature females 66·3 and 63·4 mm long.

Rhacophorus cf. *reinwardti*

Hypsiboas reinwardtii Wagler, 1830.

Material. BM. 1974. 4905–4907 (2 ♂♂, 1 immature ♀).

Habitat. These frogs came from a short stretch of logging track near the Sungei Kelebang camp at 43 m. They were traced by calls to the secondary trackside vegetation and forest edge where they were found 2, 5 and 7 m up in small trees. *Rhacophorus pardalis* was found at the same stretch of track and called from approximately the same level above ground at a nearby site, while *nigropalmatus* called from the same level at different logging track sites which offered apparently identical conditions.

Colour. As described by Grandison (1972).

Remarks. These specimens, with a male from Kampong Janda Baik, Pahang, and a gravid female from Khao Kala Kiri, extreme southern Thailand, confirm Grandison's description of the differences between the Javan and Malayan populations. Liem's (1973) notes on a Javan population of *reinwardti* show that the flash colours are more like those of *bipunctatus* than like those of the Malayan frogs, while the size of the Javan frogs is intermediate between those of the Malayan population and of *bipunctatus*. Calls and known larvae of the three groups are similar. In the Malay Peninsula '*reinwardti*' (43–*c*. 550 m) and *bipunctatus* (600–1350 m) are altitudinally separated. In Java *reinwardti* is or was of wide altitudinal distribution according to Liem. When the Sumatran populations are properly known it will probably be found that the specimens noted here represent a distinct species for which no name is yet available, *Rhacophorus reinwardti lateralis* Werner, 1900, being preoccupied by *Rhacophorus lateralis* Boulenger, 1883.

An element of the rattling, woodpecker-like call is shown in Fig. 14.

Theloderma horridum

Ixalus horridus Boulenger, 1903.

Material. BM. 1974. 4908 (♂).

Habitat. The specimen was caught at night in thick secondary trackside vegetation near the Sungei Kelebang at 43 m. It was about 2 m above ground on the rough bark of a large tree. When disturbed it climbed steadily up the trunk.

Colour. Dorsum medium brown with indistinct dark markings. Tympanum blackish with a pale rim. Lower flanks, belly and under surfaces of hind limbs pale greenish blue with rounded grey

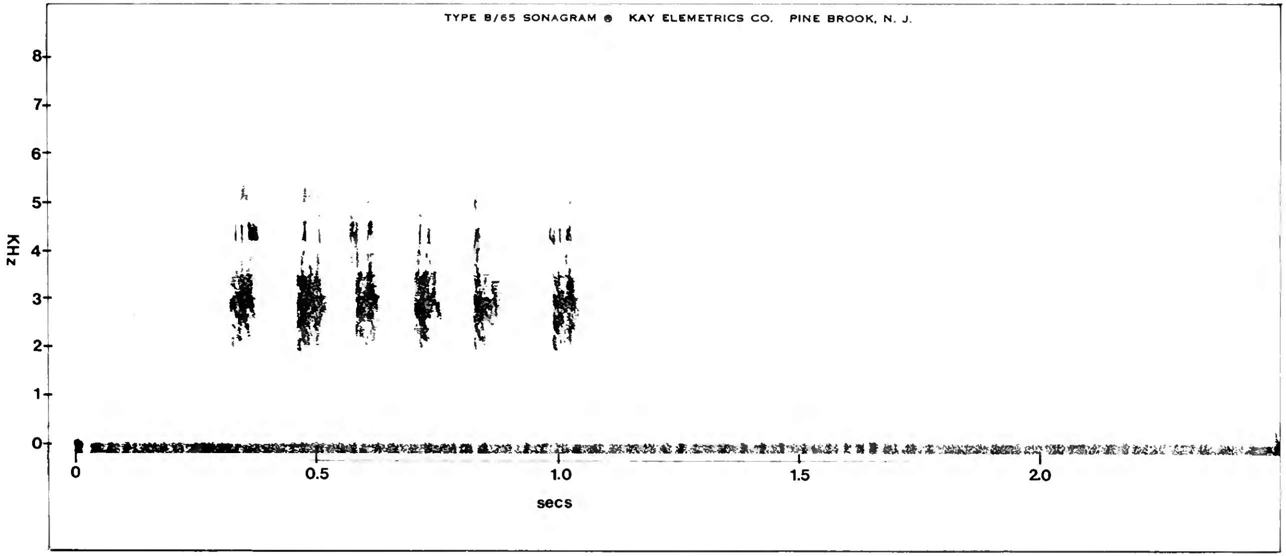

Fig. 14 Sonagram of the mating call of *Rhacophorus* cf. *reinwardti*.

brown patches. Gular region and under surfaces of fore limbs heavily mottled with dark grey brown. Upper surfaces of finger and toe discs with paired golden brown spots. The syntypes have four narrow distinct dark crossbars on the thighs, this specimen has three blotches. Iris bright golden brown above, duller below.

REMARKS. Boulenger's description and plate (1903) give most of the characteristics of this species. Snout–vent lengths of three adults 39·7–40·6 mm. The major part of the nuptial pad extends across the first metacarpal as far as the subarticular tubercle. There is also a separate small patch of spicules on the median edge of the finger, distal to the subarticular tubercle. There are no supernumerary tubercles at the bases of the fingers. Tibia length relative to snout–vent length is 0·521–0·554 (mean 0·537, N=3). The dorsal tubercles are rounded and less elevated than in *leprosa* and they do not form dorsolateral ridges. The asperities on the tibiae tend to form oblique ridges.

Theloderma leprosa

Hyla leprosa Schlegel, 1837–1844, p. 105.

MATERIAL. BM. 1974. 4909 (♂).

HABITAT. The specimen is from a hillside forest at 790 m on the east ridge of G. Lawit. It was caught at night, 1½ m from the forest floor on the leaf of a *Johannesteysmannia* (a fan-leaved palm).

COLOUR. Dorsum dark chocolate brown, upper flanks reddish brown. Dorsolateral tubercles and tubercles posterior to tympanum khaki. Venter pale grey, heavily blotched with very dark brown. Finger discs, discs of first to third toes, margin of toe web, subarticular, and inner metatarsal tubercles, and nuptial pad all pinkish red. Basal portion of toe web spotted with dark brown. Iris fawn, heavily streaked with black.

REMARKS. The snout–vent lengths of 4 mature males are 59·5–68·8 mm (mean 64·4 mm). The nuptial pad is covered with minute spicules. It extends from the wrist across the dorsomedian surfaces of the thumb pad and narrowly up the fleshy fringe of the first finger to the disc. There are supernumerary tubercles at the bases of all four fingers, but that under the first is indistinct. Broad webbing reaches the base of the disc on the first and fifth toes and the base of the disc or rather below on the outer edge of the second to third toes. It reaches above the subarticular tubercle on the inside of the second toe, as far as the distal tubercle on the inside of the third toe, and reaches the distal subarticular tubercle, on both sides of the fourth toe. Free parts of the digits have a fleshy ridge on the edge; on the fifth toe this is covered by tubercles. The inner metatarsal tubercle is not small as stated in previous descriptions, but moderately large, oval, and from 2·8 to 3·3 mm long in those specimens seen. Tibia length relative to snout–vent length is 0·535–0·546 (mean 0·541, N=3). Combined length of foot and tarsus relative to snout–vent length is 0·716–0·755.

Schlegel's description, based on Müller's specimen from Padang, Sumatra, which was deposited in the Leiden Museum, is the first to be valid by the rules of zoological nomenclature. Müller never published the name which has been ascribed to him, and Tschudi's (1838) diagnosis of *Theloderma* does not provide a recognizable description of the species.

SAURIA

Family **GEKKONIDAE**

Cnemaspis argus sp. nov.

Plate 1(a)

HOLOTYPE. BM. 1974. 4910, an adult male from 790 m on the east ridge of G. Lawit. Found in a cavity under a stone in or by the bed of a small stream, collected by Atan and Tiee at 1930–2030 hours, 9 March 1974.

Paratype. BM. 1974. 4911, female, with the same data as the holotype, from under a rock at the side of the stream.

Diagnosis. A large species of *Cnemaspis* (snout–vent length of ♂ 65·3 mm, of ♀ 62·8 mm) with 25 presacral vertebrae, keeled ventral scales, the fourth and fifth fingers subequal, and lacking a series of conspicuously enlarged median subcaudal scales.

Description of holotype. Nostrils directed upwards. Rostral ⅔ as high as wide, notched dorsally by a deep groove which does not reach the border of the mouth. A pair of drop-shaped supranasals bordering the nostrils above, and separated mesially by an elongated granule. Anterior border of the first supralabial reaches the nostril. Four or five indistinct granules behind the nostril, upper and lower largest. Eight supralabials to below the pupil, followed by about seven granules which border the mouth. Ten to twelve infralabials followed by two to four granules bordering the mouth. Mental subtriangular, almost as wide as long, border on the mouth 1⅓ width of rostral border. Two elongate postmentals separated by an almost circular scale and in contact with the first infralabials anteriorly. Canthus rounded, frontal, postnasal and preocular areas concave. Granules above supralabials and behind supranasals enlarged and weakly keeled. Small granules between the eyes. Elongated, erect ciliaries in front of the eyes. Pupil rounded, margin with a weak posterior notch and stronger dorsal and ventral notches. Ear opening as high as first supralabial, higher than wide.

Dorsal granules smaller than ventral scales, smallest along midline, and with up to 3 weak keels. Two paravertebral rows of dorsal tubercles separated posteriorly by 8–10 granules, on neck by 3–4 granules. Other tubercles irregularly scattered over dorsum and flanks and separated from each other by 2–5 granules. Tubercles variable in size, with 3–7 keels. Tubercle size decreases anteriorly over thorax and they become indistinguishable from the surrounding granules over the back of the skull. A pale tubercle above and in front of each ear opening with a smaller, flatter tubercle behind it. No distinct linear series of large pale tubercles on the nuchal region or on the sides of the neck.

Throat granules small, increasing in size towards infralabials and neck. Belly scales cycloid, subimbricate and keeled. About 60 scales in a midbody chevron across the belly between the lowest tubercles on the flanks, middle 20–40 are subimbricate. A chevron of 10 well-developed preanal pores occupying a low mound anterior to the ischia. Lateral edges of chevron separated from vent by 10–11 subimbricate scales and about 6 granules. Openings of the postanal sacs separated from vent by pigmented skin and held open by a colourless spongy substance.

Tail regenerated after fifth autotomy segment. An oblique row of three conical tubercles posterolateral to vent on sides of hemipenial swellings. Another conical tubercle on posterior margin of each swelling with two more tubercles on the sides of the tail above it. Six enlarged, weakly keeled scales near the posterior margin of each autotomy segment, two dorsolateral pairs and a lateral pair. On the first segment a further four enlarged scales, a dorsal pair anterior to the inner dorsolateral pair, and a lateral pair below the usual lateral tubercles. No row of distinctly enlarged median subcaudal scales. Subcaudals about as large as scales under femora, hexagonal and keeled.

Limbs moderately long and slender. Fourth finger moderately long, not longer than fifth (see Table 4). No rows or patches of very enlarged scales on ventral surfaces of femur, tibia, tibiotarsal articulation or first metatarsal. Ventral femoral scales not sharply distinguished from granules on posterior femur, largest proximally where they are flattened and barely larger than midbelly scales. No femoral pores. Sixteen to nineteen scales under first metatarsal, between the enlarged scale at the base of the first finger and the mound covering the tibial–metatarsal articulation. Subdigital scales tend to be broken up on the proximal phalanx and proximal part of the raised portion of each digit. The distal subdigital scales are those between the enlarged plate under the point of inflexion of the finger, and the claw.

Distal subdigital scales I : 15. II : 21. III : 24–25. IV : 23–24. V : 23–24.

Pattern as in Plate 1. In life, dorsal surfaces dark brown and fawn. Pale grey paravertebral blotches and bands on the tail. Chrome yellow oblique stripes radiating from the eye. Vertical disrupted bands of chrome yellow on the flanks. Indistinct yellowish markings on the fawn areas of the limbs. The undersurfaces pale pinkish grey. The iris bright copper.

Description of paratype. The female paratype agrees closely with the holotype. It has 9–10 supralabials followed by 6 or 7 granules, and 12 infralabials followed by 1–3 granules. It has no preanal pores or preanal mound, and the openings of the postanal sacs are empty. The scales under the femora are not differentiated and are smaller than the midbelly scales. There is a series of three to four tubercles posterolateral to the vent which are less well developed than in the male. The tail is entire. Enlarged scales are present near the posterior margins of the first fifteen autotomy segments. There are no conspicuously enlarged subcaudals anywhere along the length of the tail. The tail pattern is of longer black and shorter pale bands which are grey anteriorly and white, speckled with black posteriorly.

Distal subdigital scales I : 14–15. II : 22–23. III : 25. IV : 22–23. V : 24.

Table 3 Measurements (mm) of the holotype and paratype of *Cnemaspis argus*

	Holotype	Paratype
Snout–vent length	65·3	62·8
Tail length	–	91·6
Head length (to ear opening)	15·3	14·4
Head width	10·8	10·3
Distance between knees (with femora perpendicular to body)	36·0	35·4

Remarks. The species is not named for the hundred-eyed figure of mythology but for Argus Gathorne-Hardy, younger son of the expedition leader, Lord Medway.

Southeast Asian species of *Cnemaspis* have 25 presacral vertebrae as the usual number (29 specimens out of 32 examined) while the Indian species seen have 26 presacral vertebrae (17 specimens out of 21 examined). The single southeast Asian specimen of *kandianus* which I X-rayed had 26 presacral vertebrae. The species examined by X-ray were *affinis* (6), *argus* (2), *boulengeri* (1), *kendalli* (2), *kumpoli* (2), *nigridius* (18), *siamensis* (1), *beddomei* (6), *indicus* (11), *jerdoni* (1) and *kandianus* (3).

Only two of the southeast Asian group of species reach or exceed the size of *C. argus*. These are *nigridius* (Smith), which differs from *argus* in having a short fifth finger and enlarged smooth subcaudal scales, and *boulengeri* Strauch, which also has these characters and in addition has smooth ventral scales and enlarged subtibials. A group of taxa are like *argus* in having keeled

Table 4 *Cnemaspis*, fourth finger lengths

		Relative to SV length		Relative to forearm length	
Material	Number	Mean	Range	Mean	Range
species B	1		0·163		0·950
kendalli	4	0·149	0·142–0·158	0·829	0·777–0·845
nigridius	4	0·147	0·138–0·162	0·805	0·776–0·851
argus	2		0·134–0·144		0·785–0·839
siamensis (N)	4	0·112	0·105–0·120	0·722	0·685–0·754
siamensis (S)	4	0·119	0·114–0·125	0·761	0·714–0·807
affinis	4	0·121	0·112–0·133	0·773	0·729–0·847
flavolineatus	1		0·123		0·791
species A	2		0·116		0·686–0·741
kumpoli	1		0·112		0·712
boulengeri	4	0·127	0·122–0·132	0·698	0·678–0·719

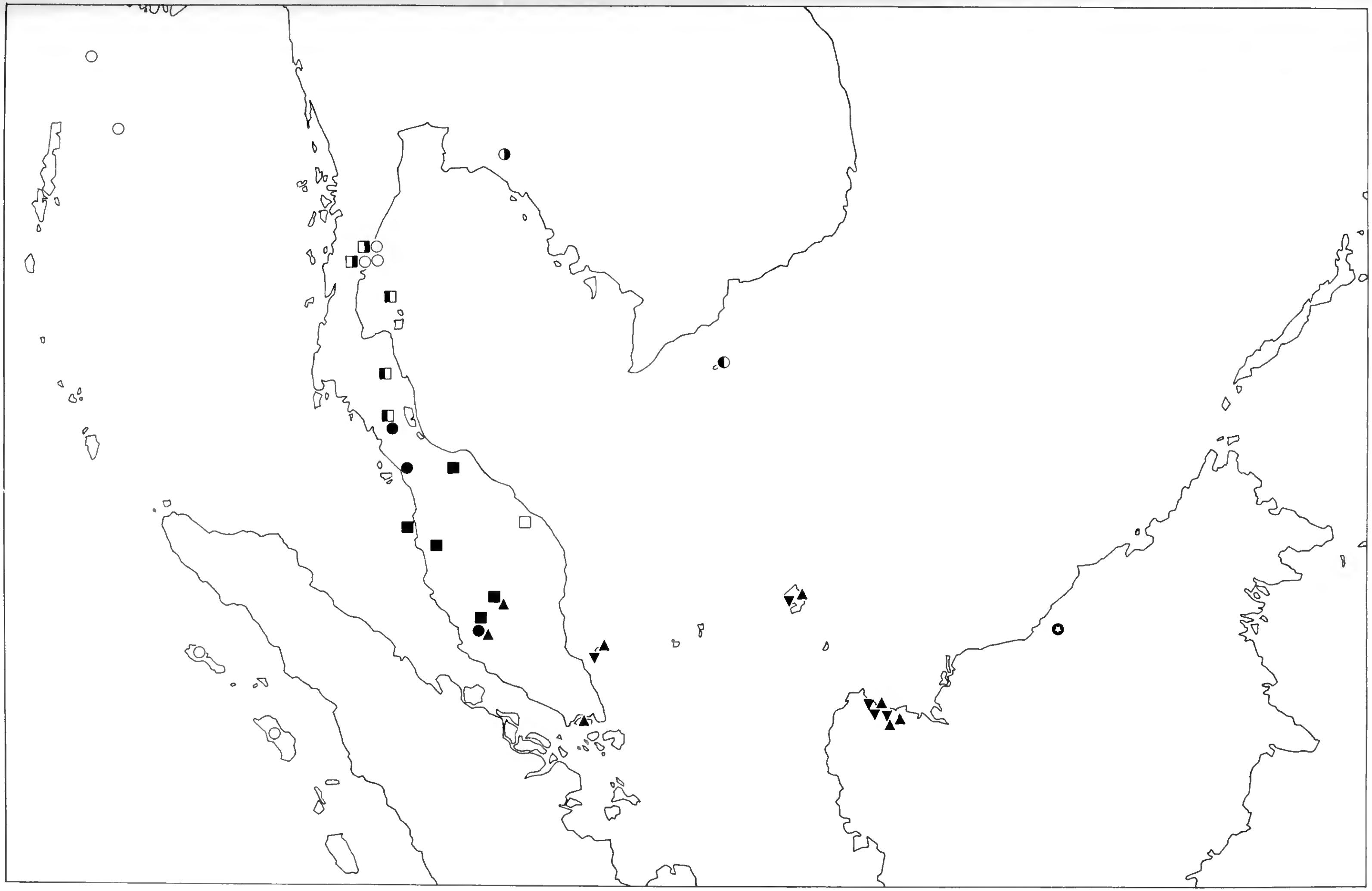

Fig. 15 The distribution of *Cnemaspis* in southeast Asia. *C. kandianus:* hollow circle. *C. boulengeri:* circle with left half filled. *Cnemaspis* sp. A: circle with right half filled. *C. kumpoli:* solid circle. *C. kendalli:* triangle. *C. nigridius:* inverted triangle. *Cnemaspis* sp. B: star in circle. *C. argus:* hollow square. *C. affinis* and *C. flavolineatus:* solid square. *C. siamensis:* half-filled squares to show the northern and southern populations separately. The southernmost records of *C. kandianus* (Sipora and Engano) and the northernmost record of *C. siamensis* (Ban Sadet) have been omitted.

ventral scales and the fifth finger equal in length to the fourth, these are *siamensis* (Smith), *affinis* Stoliczka and *flavolineatus* Nicholls. All are considerably smaller than *argus* and all have a rather lower number of distal subdigital scales under the toes and have relatively shorter fingers. In addition, *siamensis* differs in having a series of enlarged median subcaudal scales, and *affinis* has fewer preanal pores and tubercles at the side of the vent and differs in details of the colour pattern.

Because identification of *Cnemaspis* can be difficult I give below a key to the sundan-indochinese species, a table of data on finger length (see Table 4) and a map. This is based on most of the relevant material in the British Museum (Natural History), Field Museum of Natural History, United States National Museum and Bernice P. Bishop Museum, Hawaii.

Key to the southeast Asian species of *Cnemaspis*[1]

1A Males with femoral and preanal pores. Proximal subdigital scales much larger than distal scales which are 7–9 : 8–11 : 11–13 : 11–12 : 11–13 under the first to fifth toes. Adults 27–35 mm in snout–vent length. Ventral scales and proximal subcaudal scales smooth, distal subcaudals keeled. 26 presacral vertebrae are usual . . . . . ***kandianus***[2]

B Males lack femoral pores. Proximal subdigitals not, or little, larger than distal subdigitals which are 10 : 11 : 14 : 15 : 14 or more. 25 presacral vertebrae are usual . . . 2

2A Ventral abdominal scales smooth, subcaudals smooth 3

B Ventral abdominal scales keeled 5

3A Adults 59–66 mm in length. Fifth finger shorter than fourth. A series of shield-like subtibial scales almost as wide as the tibia, subcaudals almost as wide as the tail. No preanal pores. Digital subdigitals 11–15 : 13–15 : 16–19 : 16–18 : 16–20. Con Son (island), Vietnam ***boulengeri***

B Adults 51 mm or less. Fifth finger subequal to fourth. No series of shield-like subtibials, subcaudals less than half width of tail. Males with preanal pores 4

4A Snout relatively short and deep. Distal subdigitals 10–12 : 16–17 : 17–19 : 17–19 : 18–20. About 9 scales below the first metatarsal. Adult males 34–42 mm in length, with 8 preanal pores. About 28–30 scales around mid tibia. Southeast Thailand . . . . **species A**[3]

B Snout relatively long and flattened. Distal subdigitals 13–17 : 20–22 : 21–25 : 21–24 : 20–26. 12–17 scales below first metatarsal. Adult males 36–51 mm in length, with 8 preanal pores. About 24–32 scales around mid tibia. Malay Peninsula . . . . . . ***kumpoli***[4]

5A Terminal phalange of fifth finger reaches base or middle of penultimate phalange of fourth finger, which is relatively long (see table 4) 6

B Fifth finger subequal to fourth 8

6A Median subcaudal scales smooth, rounded and flat. Adult size to 85 mm, males with up to 16 preanal pores (Borneo) or preanal pores usually absent (P. Tioman). Enlarged postmentals present. Distal subdigitals 10–13 : 13–15 : 18–21 : 17–21 : 16–20 (Borneo and Bunguran populations) or 13–16 : 16–20 : 20–25 : 20–24 : 20–25 (P. Tioman) . ***nigridius***[5]

B Median subcaudals keeled, pointed and raised. Adult size to 58 mm 7

7A Preanal pores absent. Enlarged postmental scales present. Venter lightly pigmented, no black area covering the flanks. Adults to 58 mm. Distal subdigital scales 10–13 : 13–15 : 18–22 : 18–23 : 17–20 . . . . ***kendalli***[6]

B Preanal pores present (6). Enlarged postmental scales absent, mental deep and rounded. Venter heavily pigmented with the exception of scattered scales, flanks black with a few white patches (in alcohol). Adult male 46·7 mm. Distal subdigitals 13 : 14 : 20 : 20 : 19–20 **species B**[7]

8A Adults about 64 mm. Fingers relatively long. Distal subdigitals 14–15 : 21–23 : 24–25 : 22–24 : 24. Preanal pores 10. Subcaudals keeled, no enlarged median series . . . . ***argus***

B Adults less than 50 mm. Fingers relatively short. Distal subdigitals fewer, to 14 : 19 : 22 : 20 : 21 9

9A Median subcaudal scales keeled, not distinctly larger than adjacent scales, about five per autotomy segment proximally. Distal subdigitals 11–14 : 16–19 : 17–22 : 17–20 : 17–21, many of the more proximal of them broken up into smaller scales. Usually 2 tubercles at the side of the vent. Usually a dark blotch or ocellus above arm insertion. No median dark line on the throat. Males with 2–6 preanal pores are 27·7–46·7 mm in length . ***affinis***[8]

B Median subcaudal scales in a series of keeled, weakly pointed, enlarged scales, about four per autotomy segment proximally 10

10A Distal subdigitals 10–13 : 16–19 : 17–22 : 17–22 : 16–20, some of the more proximal members broken up into smaller scales. Usually one tubercle at the side of the vent. No dark blotch above arm insertion. No median dark line on throat. Males with 4–8 preanal pores are 30·7–39·7 mm in length. Northern Malay Peninsula . . . . ***siamensis***

B Distal subdigitals 9–11 : 11–15 : 14–20 : 15–21 : 14–19 and none are broken up. Usually 2 tubercles at the side of the vent. No dark blotch above arm insertion. A median dark line on the throat. Males lack preanal pores. Adults 32·9–38·0 mm in length. North of the Isthmus of Kra . . . . ***siamensis***[9]

Notes on the key

1 Not including the nominal species *timorensis* Duméril and Bibron.

2 Including the material called by Taylor (1963) *C. mysoriensis* (Jerdon).

3 BM 1917.5.14.5, BM 1926.12.7.2, FMNH 191479. Previously reported (Smith, 1925*b*; Taylor, 1963) as *C. siamensis.*

4 Three male specimens from Khao Chao, Trang (the holotype), from Kaki Bukit, Perlis and from the Batu caves, Selangor differ in size, in density of the dorsal tuberculation, in size of the scales under the tibia, in elements of the pattern and, possibly, in head shape. They are conveniently referred to *kumpoli.*

5 This species has been confused with *C. kendalli* and has also been referred to as *Cnemaspis* sp. (Hendrickson, 1966). The populations from the 1st Division, Sarawak, from Bunguran and from Pulau Tioman, Pahang, differ in presence or absence of preanal pores, numbers of distal subdigitals, density of dorsal tuberculation, number of scales along the first metatarsal and in the shape of the tubercles on the tail and at the sides of the vent.

6 One of the syntypes of *C. kendalli* (BM.XXII. 92b) is an immature specimen of *C. nigridius.* I therefore formally designate the other syntype, BM.XXII 92a (J. E. Gray's number), an adult male from Borneo, presented to the museum by Sir E. Belcher, as the lectotype.

7 FMNH 148588 from Labang camp, Bintulu district, Sarawak.

8 I have not been able to find clear differences between *flavolineatus* and *affinis.* The holotype of *flavolineatus,* with the preanal pores functioning, is 27·7 mm in length. Penang males are 39·1–46·7 mm in length (mean 43·9 mm, N = 7). Four males from Bukit Besar, south Thailand, are 31–41 mm in length and show variation in the shape of the mental shield, a character used by Nicholls (1949) to diagnose *flavolineatus.*

9 The two populations of *C. siamensis,* and *C. affinis,* seem to replace each other geographically. Most of the differences between them are comparable to the differences between the three populations I place in *nigridius.* A specimen from central north Thailand (Cochran, 1930) is too badly preserved to be definitely identified as *siamensis.*

Cyrtodactylus consobrinus

Gymnodactylus consobrinus Peters, 1871.

MATERIAL. BM. 1974. 4913 (juvenile).

HABITAT. Found 2½ m above the ground on the trunk of a large tree in secondary forest at the Sungei Kelebang (43 m).

COLOUR. Dorsal surfaces jet black, banded and reticulated by yellow cream, which is yellowest on head. Broad dark dorsal bands fade centrally into dark brown. Supralabials black and grey spotted with white. All ventral surfaces except tail pale grey. Tail dark ventrally with narrow pale bands broken on subcaudals. Iris chestnut reticulated with black.

Cyrtodactylus elok sp. nov.

Plate 1(b); Fig. 15

Cyrtodactylus ? brevipalmatus, Grandison, 1972.

HOLOTYPE. BM. 1967. 2783, adult male, at the base camp of the G. Benom expedition (215 m). Caught at night on leaf litter of the forest floor near the camp clearing and a stream.

PARATYPE. BM. 1974. 4912, adult male, near the Sungei Kelebang camp (43 m). Caught at night in thick secondary growth of palms and other shrubs among trees by a logging track. This gecko was seen moving slowly down a slender stem, apparently using its tail as a climbing aid. At rest the tip of the tail is coiled laterally.

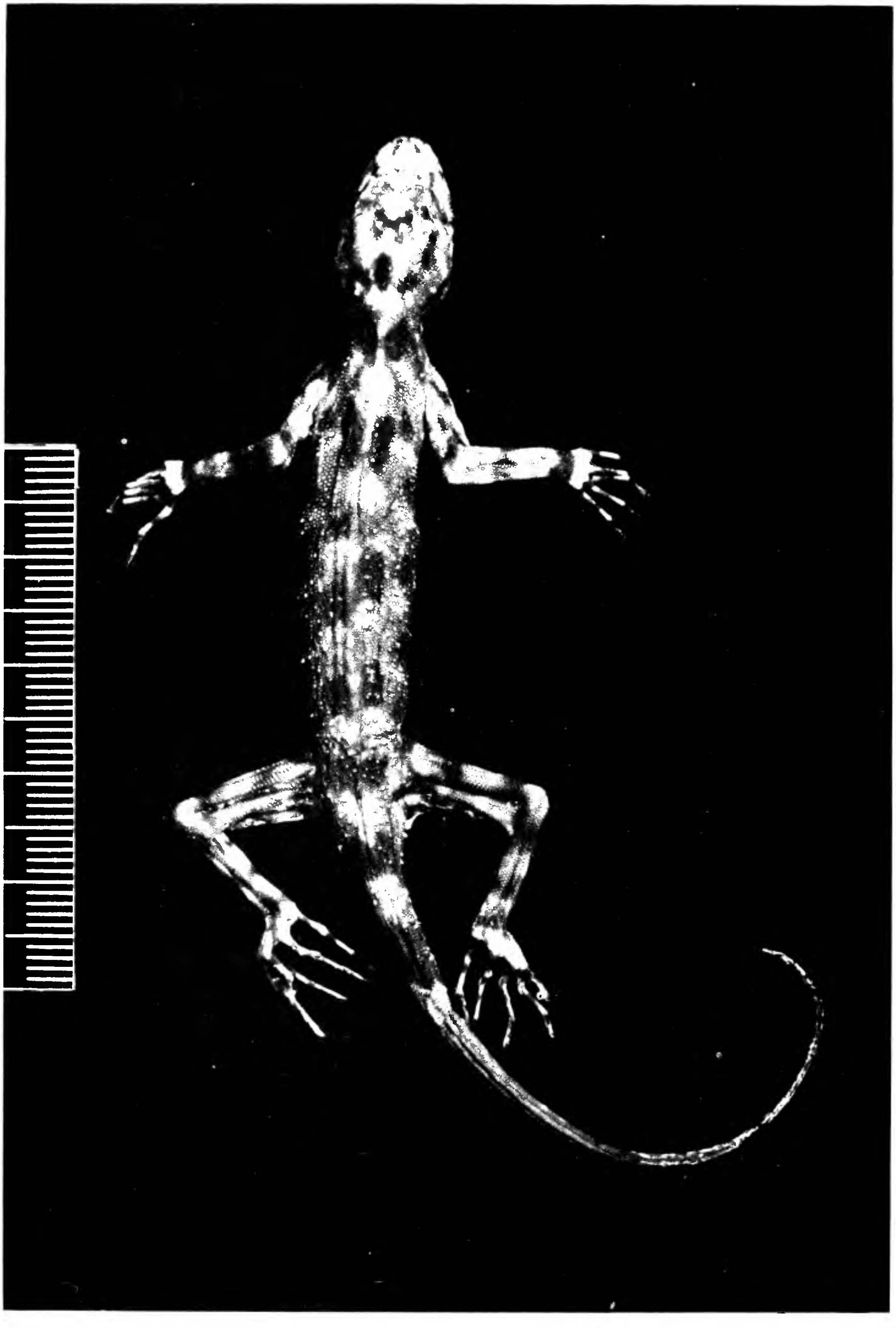

Plate 1 (a) *Cnemaspis argus* Holotype

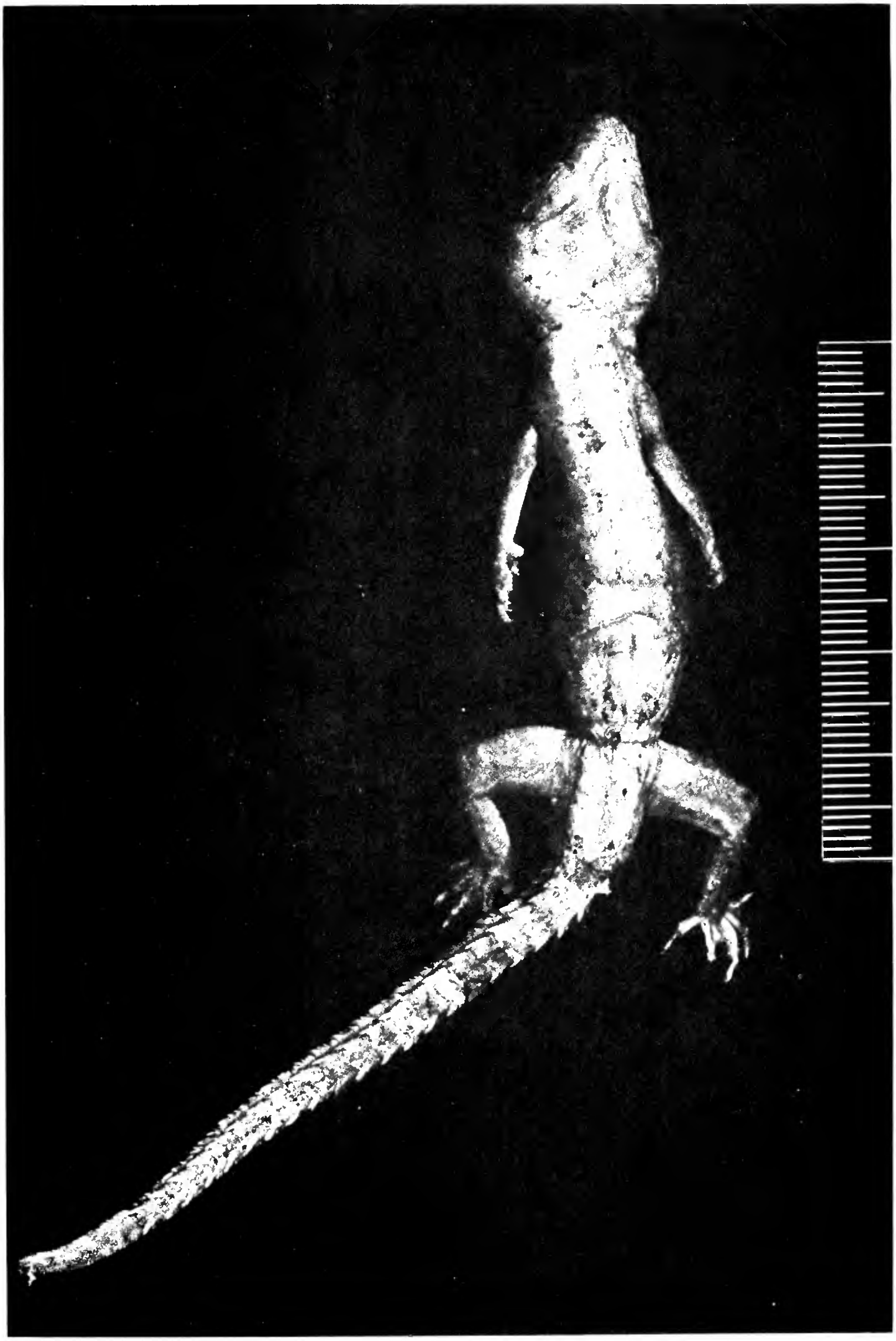

Plate 1 (b) *Cyrtodactylus elok* Holotype

DIAGNOSIS. A *Cyrtodactylus* with greatly enlarged proximal subdigital lamellae and with basally webbed toes, lacking femoral pores or enlarged femoral scales, but with a weakly arched series of preanal pores.

DESCRIPTION OF HOLOTYPE. Head oviform, forehead concave, snout obtusely pointed, its length 1½–1⅔ times eye diameter. Ear opening almost round, separated from eye by more than eye diameter. Eye with vertical *Gekko* type pupil. Nostril bordered in front by rostral, entered by the first supralabial, by an internasal and, posteriorly, by a concave scale bordered behind by five granules. Rostral large, quadrangular, with a vertical median groove in the upper part, and bordered behind by three internasals. Eight to nine supralabials extending to just behind centre of eye, followed by 3–4 scales little larger than the adjacent granules. Nine lower labials in total. A large, subtriangular mental followed by one pair of postmentals meeting on the midline and a second widely separated pair.

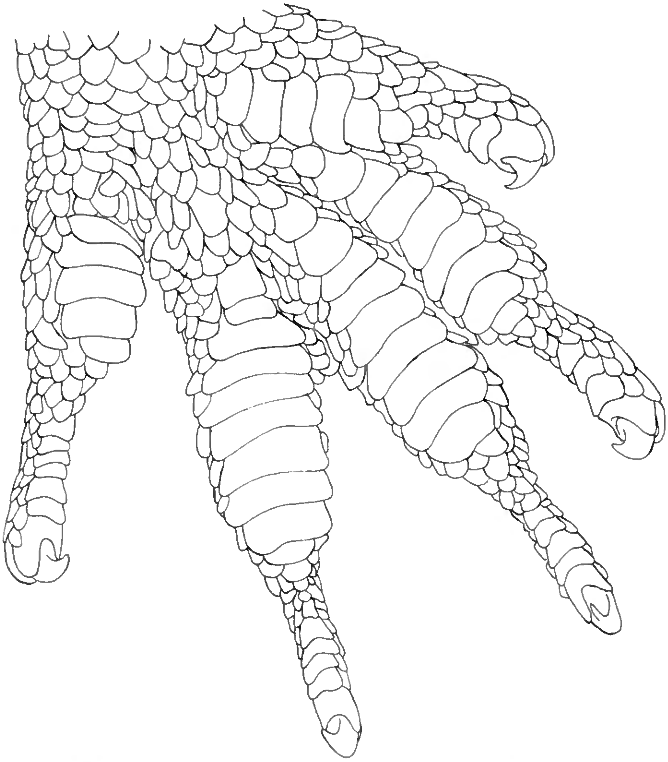

Fig. 16 Foot of the holotype of *Cyrtodactylus elok*.

Body slightly flattened, covered above by small flattened granules. Dorsal tubercles rather rounded and flattened with a weak median keel, irregularly arranged, 6–8 across middorsum, separated by 4–9 granules. Tubercles also on occiput and upper surfaces of limbs and tail base. A well-developed ventrolateral ridge with flattened imbricate scales generally larger than the adjacent granules. Ventral scales smooth, cycloid and about as large mesially as the dorsal tubercles, 44 across midbody. No preanal groove. Males with a weakly arched series of enlarged preanal scales, with 8 preanal pores. Surrounding scales larger than remaining ventral scales, separated from vent by a band of granules. Ventral surface of thigh lacking a series of enlarged femoral scales and without femoral pores. Anteroventral scales of thigh smaller than midbelly scales and merging into granules on posterior face of thigh without any distinct boundary. A pair of enlarged flattened scales to each side of vent on hemipenial swellings.

Proximal parts of each toe expanded and flattened, distal parts laterally compressed and raised. Subdigital lamellae of proximal parts many times width of adjacent scales, about five times width of scales on dorsal surface of toe. Fourth toe with 19 scales below (Fig. 16). Rudiment of web between toes I and II, well-developed web between toes II and III, III and IV. Well-developed proximal subdigital lamellae and rudimentary webbing also present on digits of hand.

Tail flattened, quadrangular in cross-section. Dorsolateral and ventrolateral edges of tail formed by denticulated series of elongate tubercles. Basally another paired series of tubercles on the dorsal surface of the tail, otherwise dorsal and lateral tail surfaces covered by granules. Ventral surface of tail covered with enlarged, flattened scales, the largest forming a mesial series two to four scales wide.

DESCRIPTION OF PARATYPE. Smaller but otherwise very similar to the holotype. Posterior border of nostril formed by 2 granules. Supranasals separated on midline by two small scales. Eleven supralabials, 8–9 to below centre of eye and 10 infralabials. About 10 dorsal tubercles counted across midbody. Two or three enlarged scales at the sides of the vent. Eighteen to nineteen scales beneath the fourth toe. A broad yellow to silver brown middorsal band crossed by seven darker brown bars on the body. Flanks and dorsal surfaces of limbs and head dark brown. Tail the same colour as the middorsal band with brown cross bars on the proximal part. A white streak from below the eye on to the posterior supralabials. Anterior labials barred cream and brown. Cream streaks behind the eye. Throat cream with white patches and dark speckling. Belly colourless except for dark speckling. Ventrolateral fold pale edged, with a series of four or five cream spots along it. Iris white with dark veins.

Table 5 Measurements (mm) of the holotype and paratype of *Cyrtodactylus elok*

	Holotype	Paratype
Snout–vent length	67·5	56·6
Head length (to ear opening)	18·2	14·6
Head width	14·3	11·2
Distance between knees (with femora perpendicular to body)	31·1	25·3
Tail length	75·7 (tip regenerated)	70·0

REMARKS. The name is Malay for beautiful. This species is closely related to *C. brevipalmatus* (Smith) which also has greatly enlarged proximal subdigital lamellae and basally webbed toes. Two adult *C. brevipalmatus* have weakly arched series of 7–9 enlarged preanal scales separated by 4–5 small scales from series of 7–9 enlarged femoral scales. The adult male holotype has 9 preanal and 6 and 7 femoral pores. The new species has a similar series of preanal scales and preanal pores but lacks enlarged femoral scales and lacks femoral pores. In no other species of *Cyrtodactylus* may enlarged femoral scales be either present or absent, although the number of femoral pores varies in some species (in three Javan *C. marmoratus* males which I have seen there are 7–18 femoral pores in total). Other differences of the new species from *brevipalmatus* are as follows.

There are fewer dorsal tubercles than in *brevipalmatus*. There are 6–10 tubercles counted across the midbody in a rough line, which are separated from each other by 4–9 granules. In *brevipalmatus* there are 14–18 tubercles across the midbody, separated by 1–5 granules.

The distal portions of the digits (that is, distal to the expanded subdigital lamellae) are shorter and have fewer subdigital scales as shown in Table 6.

Table 6 Numbers of distal subdigitals of *Cyrtodactylus elok* and *C. brevipalmatus*

Toe	I	II	III	IV	V
elok	5–6	6–7	9–10	9–10	9
brevipalmatus	8–9	9–11	11–13	11–13	11–13
Finger	I	II	III	IV	V
elok	4–5	6	8	8–9	7
brevipalmatus	7–8	9–10	10–11	10–12	9–10

Cyrtodactylus quadrivirgatus

Cyrtodactylus quadrivirgatus Taylor, 1962.

Material. BM. 1974. 4914–4924 (8 ♂♂, 2 ♀♀, 1 juvenile).

Habitat. All were collected at night, mostly above the ground and from as high as two metres above it, from the trunks of dead trees, the fissures of a log and from spiny palms, vines, saplings and other shrubby vegetation. Seven were from the Kelebang camp (43 m), near the river, at the edges of logging tracks, and in the intensely disturbed forest. Four were from the east ridge of G. Lawit (790 m) near streams and in ridge top forest.

Colour. The dorsal surfaces vary from fawn to dark grey brown with blackish brown markings, the venter is grey. The tubercles on the flanks and sides of the head, and the supraciliaries, may be yellowish. The iris was described variously as grey, ochre and dark brown in the field.

Remarks. All the geckos from the Malay Peninsula which were previously identified in the BM(NH) as *C. marmoratus* Kuhl, are referable to *C. quadrivirgatus.* This species differs from all other Sundan *Cyrtodactylus* (except *C. annulatus* Taylor and *C. sworderi* Smith) in lacking a pubic groove and femoral pores, as well as enlarged subcaudal scales and denticulated series of elongated tubercles on the ventrolateral folds or sides of the tail. *C. annulatus* of Mindanao and Bohol lacks enlarged femoral scales which are present in *quadrivirgatus. C. sworderi* of the Malay Peninsula, which is known only from the male holotype, differs in size (77 mm), in number of preanal pores (6), and in pattern (pale blotches on a dark ground). Adult males of *quadrivirgatus* are 51–65 mm in head and body length, females are up to 71 mm long. About half the males lack preanal pores, the remainder have up to four. The additional BM material comes from Bukit Besar, on the Pattani–Yala border in Thailand; from Penang Hill; from G. Keledang, the Larut Hills and Kuala Legap in Perak; from G. Benom, Pahang; from G. Bunga Buah, Selangor and from Singapore. *C. marmoratus* should be removed from the fauna of the Malay Peninsula, all records being presumably based on *quadrivirgatus* (and certainly those of Flower, 1899, Boulenger, 1903, Smith, 1935*b* and Grandison, 1972).

The range of *C. marmoratus* has been constantly reduced since de Rooij (1915) recorded it from New Guinea westwards to the Indian Ocean. Brongersma (1953) showed that records beyond Malaya, the Riouw Archipelago, Sumatra and the islands to its west, Java, Bali and Lombok were erroneous. He also indicated that the Christmas Island population was distinct. Taylor (1962) made comments on the diversity of the remaining assemblage. The type locality is Java. In three Javan males which I have seen there are up to 16 preanal pores separated from series of 3–10 femoral pores on each thigh by 4–7 poreless scales, but according to Brongersma (1953) the preanal and femoral pore series may be contiguous. The pore bearing preanal scales rim the pubic groove. The largest male is 74·4 mm in snout–vent length.

In three Sumatran males and an Engano male it is the scales anterior to the pore-bearing series that rim the pubic groove. The anterior median scale of the preanal series is greatly enlarged, occupies the bottom of the pubic groove, and bears the anterior preanal pore. It is followed by two continuous series of 8–15 pores extending on to the femora. The largest specimen is 66 mm long. Six males from Christmas Island, south west of Java and Sumatra, also differ from the Javan population. They have 9–11 preanal pores in an open series, not rimming a pubic groove, 11–13 femoral pores on each side and 3–8 poreless scales between the preanal and femoral series. These males are 73·0–78·9 mm long, while five females are 73·2–81·6 mm long. Possibly a proper study of the *marmoratus* group would show that a number of species are present in western Indonesia.

Gehyra mutilata

Hemidactylus (*Peropus*) *mutilatus* Weigmann, 1835.

MATERIAL. BM. 1974. 4925 (♀).

HABITAT. Under the bark of a dead tree in secondary trackside vegetation at the Sungei Kelebang camp.

Ptychozoon lionotum

Ptychozoon homalocephalum var. nov. *lionotum* Annandale, 1905.

MATERIAL. BM. 1974. 4926 (♂).

HABITAT. The gecko was 2–3 m up on a tree trunk in undisturbed forest near the Sungei Petuang (250 m), and was found at night.

REMARKS. Boulenger (1893) noted the presence of a *Ptychozoon* at Pegu which lacked dorsal tubercles, and Annandale gave it a name. Boulenger (1912) included *lionotum* in his discussion of *homalocephalum* (=*kuhli*), but Smith (1935*a*) raised it to the status of a species. Taylor (1963) was the first to record *lionotum* from the Malay Peninsula. He found it in near sympatry with *kuhli* in Changwat Nakhon Si Thannarat, and as far south as Changwat Trang, and also listed the differences between the two species. Material in the BM. shows that *lionotum* is also found in West Malaysia and Borneo, where it has been previously recorded as *kuhli* or *homalocephalum*. I have seen an embryo and hatchling from Bukit Besar, on the borders of Changwats Pattani and Yala (recorded by Boulenger, 1903 and Taylor, 1963), a male from Gunong Tahan, Pahang (recorded by Boulenger, 1908) and a male and female from the Baram district of Sarawak (recorded by Smith, 1935*a*).

P. lionotum differs from *kuhli* in lacking tubercles on the occiput, dorsum or dorsal surfaces of the tail segments, in having a notch largely separating the skin flap on the anterior edge of the forelimb from the first finger, and in having a smaller flap on the tail tip and the lateral tail flaps differently oriented. It also has fewer preanal pores, 16–24 in 6 males I have seen, 31 and 43 in two Malayan *kuhli*, one of which has the preanal pores in more than one row. Adult males of *lionotum* are 68–90 mm in snout–vent length and females are 84–103 mm long.

There is some geographical variation. Three specimens from north and east Thailand have a weak mound above the ear opening, covered with enlarged scales. The weak posterior lobe of the skin flap on the side of the neck is rounded and there is a single large tubercle on the side of the hemipenial swelling. The Malay Peninsula specimens have a free knob above the ear opening. This is followed by a strong fold to the posterior end of the neck flap where there is a further knob. The posterior lobe of the neck flap is triangular and the specialized tail-base tubercles are single. The two Bornean specimens are similar but the swelling above the ear opening is flap-shaped and the tubercles on the sides of the hemipenial swellings are divided.

Family **AGAMIDAE**

Aphaniotis fuscus

Otocryptis (*Aphaniotis*) *fusca* Peters, 1864.

MATERIAL. BM. 1974. 4927 (♂).

HABITAT. The single example was found about a metre from the ground on the trunk of a tree in the disturbed forest around the Sungei Kelebang camp (43 m).

Colour. The head and body are greenish ochre, the tail somewhat browner with a light tip. The lining of the mouth is bluish purple. The iris is bright blue.

Calotes cristatellus

Agama cristatella Kuhl, 1820.

Material. BM. 1974. 4928 (immature).

Habitat. The specimen was seen on the ground in the Sungei Kelebang camp site but when chased it ran up on to the palm-thatched roof of a hut.

Calotes sp.

Material. BM. 1974. 4929 (juvenile male).

Habitat. This lizard was caught near the summit ridge camp at 1280 m. It was found during the afternoon on a dead branch of a bush growing on the steep side of a dry gully, and was about half a metre above the ground.

Colour. Dorsum greyish fawn with five dark brown crossbars over the thorax and abdomen. Five dark bars radiating from the eye, three below it and two behind it. A small black v-shaped mark on the nape. The tail crossbarred fawn and dark brown. The midline of the throat and venter pale bluish, the remainder of the venter and upper lip whitish in life, now heavily scattered with melanophores. The area of the gular sac with an oval blue black ocellus enclosing a pinkish purple patch, which has become orange in the preserved specimen. Dark lines radiating from the area of the gular sac to the infralabials. The palate dark blue. The iris dark brown.

Remarks. This juvenile evidently belongs to the same species as the Gunong Tahan syntype of *C. floweri* Boulenger in the British Museum, a gravid female, BM. 1906.2.28.10. However, neither is conspecific with the Chantaburi syntype of *floweri*. Taylor and Elbel (1958) restricted the type locality of *floweri* to Chantaburi. I therefore formally designate the gravid female syntype from 'Chantaboon' (=Chantaburi), BM. 1946.8.11.25, collected by Captain S. S. Flower, as the lectotype.

The Gunong Tahan and Gunong Lawit specimens differ from *Calotes floweri*, in having a shorter head, fewer upper and lower labials, and scales along the canthus between the nasal and the supraciliaries, in having more scales under the fourth finger, and in being a smaller size.

These two specimens belong to the group of small, highland *Calotes* defined by Smith (1935*a*) as having the following characteristics: no fold or pit in front of the shoulder, dorsal and lateral scales pointing backwards and downwards and larger than the midventral scales, limbs relatively short (adpressed hind limb reaching shoulder). This group includes the Indochinese species *brevipes* Werner (see Mertens, 1954, for taxonomy), *floweri* Boulenger and *microlepis* Boulenger, and the Sundan species *flavigula* Smith and *tympanistra* Gray as well as this form. The three Indochinese species can be separated from the three Sundan species by the modified scales under the proximal part of the third toe (Fig. 17). In all six species the subdigital lamellae are bicarinate and the distal ends of the keel are raised to form spines, presumably as a modification for an arboreal life. In the Indochinese species the keels on the leading edge of the third toe are greatly enlarged and blade-like while the keels on the trailing edge of the toe at the base are reduced or absent. The Sundan species have normal bicarinate lamellae to the base of the third toe. Diagnoses of the species, based on the 14 specimens in the BM(NH), are given below.

Subdigital scales of the third toe are modified (see above).

C. floweri, range southeast Thailand and southwest Cambodia. Abdominal scales large, 50–54 round midbody, *c*. 35–41 dorsolateral scales. 20–24 scales under fourth toe, 16–19 scales under fourth finger. 10–11 upper and 9–10 lower labials. Male with a dark brown oval patch on the small gular sac. No enlarged paravertebral scales. Snout 1·5–1·85 times the length of the orbit. Snout–vent length of ♂ and two ♀♀ 90–99 mm.

C. brevipes, range northern Vietnam. Snout 1·5–1·6 times the length of the orbit. 10 upper and 8–10 lower labials. Male with a dark brown patch on the small gular sac. Abdominal scales moderate, 71–72 round midbody, *c.* 56–60 dorsolateral scales. Some spine-like scales on the occiput and a paravertebral series of enlarged dorsal scales. 20–22 scales under fourth toe, 18–19 scales under fourth finger. Snout–vent length of two ♂♂ 76 mm.

C. microlepis, range north Tenasserim and possibly to southern Vietnam. Snout 1·5–1·6 times the length of the orbit. 8–10 upper and 9–10 lower labials. Male with a small dark brown gular sac. Abdominal scales moderate, 70–71 round midbody, *c.* 56–62 dorsolateral scales. No series of enlarged paravertebral scales. 24–26 scales under fourth toe, 20–21 scales under fourth finger. Snout–vent of gravid ♀ from Tenasserim 62·2 mm, of gravid ♀ from southern Vietnam 85·5 mm.

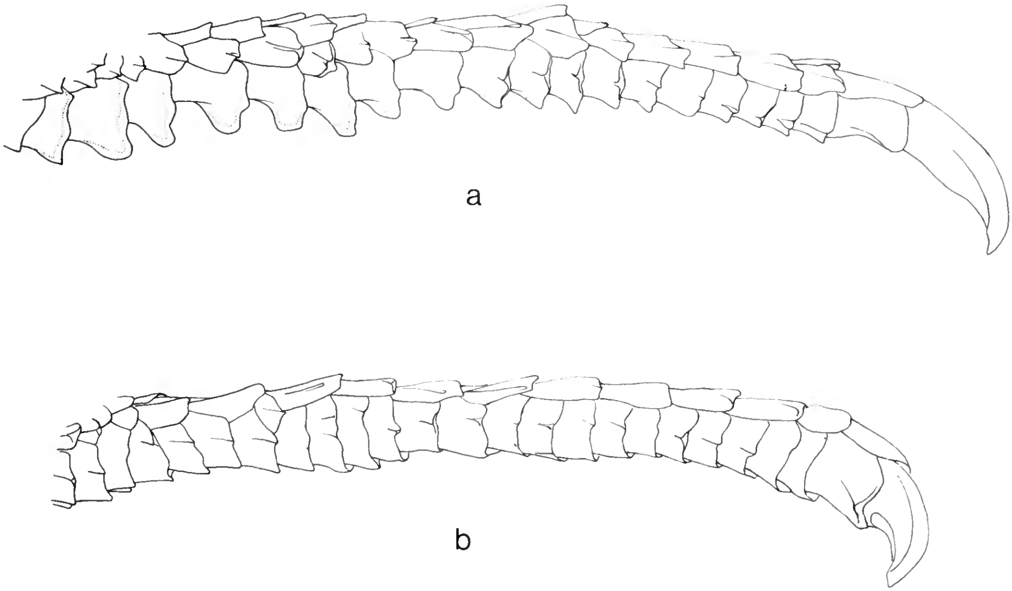

Fig. 17 Middle digit of the right foot of (a) *Calotes floweri* lectotype, and (b) *Calotes* sp. from Gunong Tahan.

Subdigital scales of the third toe are unmodified.

C. flavigula, range Malay Peninsula. Snout 1·3 times length of orbit. Seven upper and 8–10 lower labials. Male with a large bright yellow gular sac. Abdominal scales very large, 40 round midbody, *c.* 29 dorsolateral scales. No series of enlarged paravertebral scales. 31–32 scales under fourth toe, 26–27 scales under fourth finger. One ♂ 66·5 mm in length.

C. tympanistra, range Sumatra and Java. Snout 1·5–1·6 times length of orbit. 10–11 upper and 9–11 lower labials. Male with a small gular sac which is bluish grey in alcohol. Abdominal scales large, 46–54 round midbody, *c.* 38–46 dorsolateral scales. Some enlarged dorsal scales in the paravertebral area. 28–31 scales under the fourth toe, 23–26 scales under the fourth finger. Snout vent lengths of two ♂♂ and a ♀ 64–78 mm.

Calotes sp., range Malay Peninsula. Snout 1·4 times length of orbit. Eight upper and 7–8 lower labials. Gular sac of male is probably brightly coloured. Abdominal scales large, 48–50 or 57 round midbody, *c.* 36–37 dorsolateral scales. No series of enlarged paravertebral scales. 24–26 scales under fourth toe, 20–21 scales under fourth finger. Length of one ♀ is 70·3 mm.

The synonymy of the unnamed species includes *C. microlepis*, Boulenger (1908) and *C. floweri* Boulenger (1912) (part), Smith (1922), Smith (1930) and Smith (1935*a*) (part). The synonymy of *C. floweri* includes *C. microlepis*, Flower (1899) and *C. floweri* Boulenger (1912) (part), Smith (1935*a*) (part), Taylor and Elbel (1958) and Taylor (1963).

Draco formosus

Draco formosus Boulenger, 1900.

MATERIAL. BM. 1974. 4930–4933 (1 ♂, 1 ♀, 2 immature).

HABITAT. Of the three caught around the Sungei Kelebang camp at 43 m, two were knocked from saplings during the early morning. An immature specimen was shot while 3 m up on a 35 cm diameter tree in undisturbed forest at 790 m on the east ridge of G. Lawit.

COLOUR. As reported by Grandison (1972). The iris is yellowish green with a golden rim round the pupil.

Draco melanopogon

Draco melanopogon Boulenger, 1887*a*.

MATERIAL. BM. 1974. 4934–4950 (11 ♂♂, 3 ♀♀, 3 immature).

HABITAT. Only 1 specimen was caught at the Sungei Kelebang, probably because thick secondary growth interfered with observation rather than because of any altitudinal preference of the species. On the east ridge of G. Lawit (790 m) 1 specimen was found 2·5 m and the remainder 4·5–6·0 m above ground but the absence of specimens from higher up on trees reflects the difficulty of shooting them there. They were found on trees from a few to *c*. 50 cm in diameter. Many were found in forest with little undergrowth and few low branches on the trees on a flat-topped ridge between two streams. Others were on trees of forested slopes overhanging the streams or edging ridge top tracks.

COLOUR. As described by Grandison (1972), except that the orange brown of the throat extends on to the posterior basal third of the black gular pouch of the male. The gular pouch of the female is dark brown with a white to grey green tip. The ventral surface of the wattles is white in males, but in females is a continuation of the reddish brown colour of the base of the gular sac.

Draco quinquefasciatus

Draco quinquefasciatus Hardwicke and Gray, 1827.

MATERIAL. BM. 1974. 4951 (♀).

HABITAT. This was caught at night 'asleep' on the trunk of a tree in riverine forest near the Sungei Kelebang camp (43 m).

COLOUR. Dorsum pale greenish grey with darker grey green crossbars and black spots. A mask-shaped pinkish grey mark on the nape. The upper surfaces of the wings orangey brown fading to yellowish at the body, crossed by five black bars and by stripes of lighter scales over the ribs. Throat yellowish green and venter pinkish white flushed with yellow at the sides. Undersurfaces of the wattles orange yellow anteriorly, white posteriorly, with the posterior edge black. Undersurfaces of the wings yellowish white near the body, greyish towards the edge.

Goniocephalus armatus

Agama armata Hardwicke and Gray, 1827.

MATERIAL. BM. 1974. 4952 (♀).

HABITAT. This was found in a latrine pit near the river at the Sungei Kelebang camp (43 m).

Goniocephalus belli

Lophyrus Bellii Duméril and Bibron, 1836.

MATERIAL. BM. 1974. 4953 (♂).

HABITAT. This was caught on the east ridge of Gunong Lawit at 790 m. It was about a metre above the forest floor on the twig of a dead sapling in tall undisturbed hillside forest.

COLOUR. The head is brownish yellow dorsally with the tympanic scale and suborbital scales yellow green. The vertebral region and upper flanks are strongly banded with dark brown and yellow green. The first band forms a collar uniting ventrally behind the gular sac. The brown bands are broader than the yellow green ones and break up on the lower flanks to form a reticulated pattern enclosing enlarged yellow green scales. The tail is strongly banded dark brown and creamy yellow. The throat is fawn with longitudinal, black stripes and pink patches on the sides of the gular sac. The belly is creamy yellow in front, fading behind to cream. The iris is dull gold.

REMARKS. M. A. Smith (1935*a*) stated that he had examined Duméril and Bibron's type and that it was conspecific with *G. borneensis* (Schlegel). This species has been reported from lowlands to 1525 m.

Goniocephalus chamaeleontinus

Iguana chamaeleontina Laurenti, 1768.

MATERIAL. BM. 1974. 4954–4955 (2 ♀♀).

HABITAT. The first specimen was found at midday less than a metre from the ground on the trunk of a dead tree in undisturbed forest at *c*. 425 m on Bukit Bok, the ridge separating the Kelebang drainage from the Sungei Petuang. It tried to evade capture by moving to the hidden side of the tree. The other specimen was caught at night a few metres from a rocky stream on the east ridge of G. Lawit at 790 m. It was 3 m up on the trunk of a small sapling among mossy rocks. It was completely inactive, allowing itself to be picked up without attempting to escape. This was typical of all the *Goniocephalus* collected at night; presumably this is a diurnal genus.

COLOUR. The head and body are bright emerald green with black lines radiating from the eye and 2–6 enlarged yellow scales on the upper flanks. The lower flanks have 6 vertical rows of slightly enlarged yellow scales. The gular sac is yellow green and black with the conical scales forming its ventral edge, yellow. The belly is creamy yellow to dark fawn. Proximally the tail is coloured like the body but distally it is crossbarred with pale greenish grey and black. The iris is claret or rich chestnut.

Goniocephalus grandis

Dilophyrus grandis Gray, 1845.

MATERIAL. BM. 1974. 4956–4961 (4 ♂♂, 1 ♀ immature).

HABITAT. The specimens were all found on vegetation by the Sungei Kelebang or nearby streams at 43 m. Along the river there is mainly undisturbed *Saracca* stream vegetation. Two were collected one night on branches and vines overhanging the Kelebang, and one dived into the river when disturbed. Another three were found along a short stretch of a slow, earth-banked stream in disturbed forest not far from a logging track. Two were found on the midribs of palm leaves overhanging the water; they were within 10 m of each other. When disturbed, they dived into the water and swam rapidly under the surface; one was found submerged and sheltering under the bank.

Goniocephalus liogaster

Gonycephalus liogaster Günther, 1872.

MATERIAL. BM. 1974. 4962–4963 (♀ and immature).

HABITAT. The pair were collected within metres of each other on secondary trackside vegetation near the Sungei Kelebang camp (43 m). The female was about 2 m above ground on a slender branch and the immature specimen was about half a metre up on a twig.

COLOUR. They were described in the field as being similar to the *G. belli* but lacking the pink gular patches. The colour pattern is generally similar but the dark flank network includes more and smaller pale areas. The longitudinal dark streaks on the throat merge on the gular sac, but do not form a thick midgular band as in *belli*; in the smaller specimen they form a pair of small ocelli and open-fronted loops, in the female the pattern is similar, but indistinct. The outer rim of the iris is saxe blue.

REMARKS. Boulenger (1887*a*) described a new species from Malacca as *G. herveyi*. He stated that this differed from *liogaster* in having perfectly smooth dorsal scales, smooth or weakly keeled elongate scales at each side of the dorsal crest, the points on these scales shorter, and an unmarked throat. These slight differences do not seem to have been subsequently questioned. I have examined four specimens from the Malay Peninsula and seven from Pulau Laut in the Bunguran Islands (identified as *herveyi*) and 8 specimens from Borneo (identified as *liogaster*). This material includes the holotype of *herveyi* and five syntypes of *liogaster*.

The dorsal scales of all the specimens are smooth but with keels indicated as a weak median ridge. The scales at the sides of the dorsal crests (the supporting scales) are weakly keeled, the length of their points varies but any population differences are trivial (see below). There are minor differences in throat patterns. Malayan specimens have dark stripes which converge on to the gular pouch from the lower jaw. They are indistinct or absent in mature males. Bunguran specimens are similar, but the stripes may be somewhat broken up on the jaws. Bornean specimens may have completely spotted throats, but usually these spots are more or less confluent into broken stripes in the same position as those of Malayan or Bunguran specimens. One male has unbroken stripes converging on a dark coloured gular pouch. Data on the length of mature males, the height of their nuchal crests, the length of the points on the scales supporting these crests, and data on the subdigital scales of the toes and fingers are given in Table 7.

Table 7 Data on *Goniocephalus liogaster*

		Snout–vent length (mm)	Height of nuchal crest (mm)	Length of points of supporting scales (mm)
Malaya	2	133–135	20·0–22·0	1·3–2·0
Bunguran Is.	3	124–145	17·5–25·0	2·1–3·8
Borneo	4	116–131	17·0–27·8	1·2–2·2

		Subdigital scales of the toes				
		I	II	III	IV	V
Malaya	N=4	8–9	11–13	15–17	22–24	10–12
Bunguran Is.	N=6	7–9	12–13	14–17	21–24	11–12
Borneo	N=8	7–10	10–13	15–19	20–27	11–13

		Subdigital scales of the fingers				
		I	II	III	IV	V
Malaya	N=4	9–10	13–15	18–20	20–22	11–12
Bunguran Is.	N=6	9–10	13–14	18–19	18–20	10–13
Borneo	N=8	9–11	13–15	17–20	18–23	10–13

The few specimens at my disposal indicate that the differences which Boulenger noted between the types of *herveyi* and *liogaster* are due to individual variation, and suggest that the Malayan and Bornean populations are not significantly different. *Goniocephalus herveyi* (Boulenger) should be placed in the synonymy of *G. liogaster* (Günther).

Family **SCINCIDAE**

Mabuya multifasciata

Scincus multifasciatus Kuhl, 1820.

MATERIAL. BM. 1974. 4964–4987.

HABITAT. Several specimens, of which only one was collected, were seen among cut, dried *Johannesteysmannia* leaves lying next to a recently built hut on the bank of the Sungei Petuang (250 m). The rocky river banks were covered with sparse natural vegetation forming a community capable of withstanding periodic flooding. They were surrounded by miles of undisturbed, untracked forest. The remaining specimens were shot in secondary trackside vegetation among the logged forest at the Sungei Kelebang (43 m).

Sphenomorphus praesigne

Lygosoma praesigne Boulenger, 1900.

MATERIAL. BM. 1974. 4988 (♂).

HABITAT. Found by day in an emaciated state at the summit ridge camp site at 1280 m. The lizard was seen at the base of a rotten tree stump shortly after masses of peat had been pulled from the cavities under its roots.

COLOUR. The dorsal surfaces are chestnut brown with black mottling. There is a series of five to six large black patches on the side of the neck and the side of the thorax. The venter is immaculate except for black speckling at the sides of the throat and tail. The throat is dull grey green and the neck, belly, undersurface of the tail to its tip and undersurfaces of the limbs are golden yellow.

Family **VARANIDAE**

Varanus bengalensis nebulosus

Monitor nebulosus Gray *in* Cuvier, 1831.

MATERIAL. BM. 1974. 4989 (juvenile).

HABITAT. From a dry crevice in the trunk of a fallen tree in disturbed forest near the Sungei Kelebang (43 m).

SERPENTES

Family **COLUBRIDAE**

Boiga dendrophila cf. *melanota*

Dipsadomorphus dendrophilus var. *melanotus* Boulenger, 1896.

MATERIAL. BM. 1974. 4991 (♀).

HABITAT. Caught at night swimming upstream in a slow stretch of the Sungei Kelebang (43 m).

REMARKS. Brongersma (1934) referred Malay Peninsula *B. dendrophila* tentatively to the subspecies *melanota*. This specimen is typical of Malayan *dendrophila*. There are 223 ventrals, 92 subcaudals, 38 yellow bars on the flanks and 11 yellow spots on the sides of the tail.

Boiga drapiezii

Dipsas drapiezii Boie, 1827.

MATERIAL. BM. 1974. 4992 (immature).

Habitat. It was caught 1½ m above ground on the frond of a sessile palm (cf. *Eugeissona*) in logged forest near the Sungei Kelebang camp (43 m).

Colour. Head and dorsum were medium brown with a series of yellow brown diamond-shaped patches along the vertebral line. Between these patches were vertical crossbars. The upper labials were cream and the chin shields white. Ventral scales were similar to dorsal ground colour, anteriorly very pale brown, merging posteriorly to pinkish brown. The iris was pale ochre.

Remarks. Ventrals 269, subcaudals 156.

Boiga jaspidea

Triglyphodon jaspideum Dumeril and Bibron, 1854.

Material. BM. 1974. 4993 (♂).

Habitat. The specimen was caught at dusk climbing on a *Johannesteysmannia* palm about 1 m from the forest floor near the east ridge camp (790 m).

Colour. The dorsum was dusky pink with the vertebral scale row reddish brown and with a paravertebral series of black spots separated from each other by two to three vertebral scales. Alternating with the paravertebral spots is a series of dark bars on the flanks. There were white spots at the base of each bar, on the first dorsal scale row and the lateral edge of the ventral scale. On the posterior body there is a black mark on the lateral third of every other ventral corresponding with the white ventrolateral spots and lateral bars, anteriorly these dark marks are present on every ventral scale. The upper labials are white, spotted with dark brown and the chin shields and lower labials are cream. The anterior half of the belly was sulphur yellow, fading on the posterior ventrals through creamy fawn to pinkish fawn. The entire dorsum and posterior two-thirds of the venter are heavily speckled with black. The iris was pinkish brown.

Remarks. Ventrals 262, subcaudals 161.

Boiga nigriceps

Dipsas nigriceps Günther, 1863.

Material. BM. 1974. 4994 (immature).

Habitat. Found 1 m up in a spiny palm in hillside forest on the east ridge of G. Lawit, 790 m.

Colour. The dorsum was a light orange tan. The upper labials, except their dorsal edges, were white as were the chin shields and throat. The anterior ventrals were yellowish, on the posterior body the venter darkened through pinkish orange to orange brown on the tail. The entire dorsum except the upper labials is speckled with black and there is a series of black spots on the tenth and twelfth dorsal scale rows. The iris was pale orange.

Remarks. Ventrals 265, subcaudals 148.

Rhabdophis chrysargus

Tropidonotus chrysargus Schlegel, 1837.

Material. BM. 1974. 4990 (immature ♂).

Remarks. Caught by day in a hut at the Sungei Kelebang campsite (43 m). Ventrals 158+2, subcaudals 85.

Family **VIPERIDAE**

Trimeresurus popeorum

Trimeresurus popeorum Smith, 1937.

Material. BM. 1974. 4995–5000 (2 ♂♂, ♀ and immature).

HABITAT. Around the east ridge camp (790 m) specimens were caught on vegetation along streams both by night and by day. They were from a few centimetres to one metre above ground level on shrubs, palms and pandan. A male and female (BM. 1974. 4999–5000), from the summit ridge (1280 m), were within metres of each other on boulders in a small stream flowing through a padang.

COLOUR. The dorsum was emerald green and the ventral scales were lime green. The tail was pinkish brown above and the anterior subcaudals were lime green, the posterior subcaudals whitish or brownish. There is sexual dichromatism. The males have the dorsal scales speckled with black and the anterior part of each scale is blackish. The lower half of the first dorsal scale row is claret coloured, the upper half and adjacent edge of the second dorsal scale row is white. In females all the dorsal scales are uniform, except that the posterior edges of the scales of the first row and sometimes their keels, and the adjacent edge of the second scale row, are white. The black dorsal speckling and claret coloured ventrolateral line of the males are absent in females.

REMARKS. Sexual dimorphism is limited to colour, relative tail length and number of subcaudal scales. Data for the specimens are given in Table 8.

Table 8 Data on *Trimeresurus popeorum*

Specimen		Ventrals	Subcaudals	SV length (mm)	Tail length (mm)	Tail/SV
1974.4995	♂	161	79	350	88	0·252
1974.4996	imm. ♂	163	75	289	68	0·235
1974.4997	imm. ♀	164	65	338	68	0·201
1974.4998	imm. ♀	163	66	285	60	0·210
1974.4999	♀	163	66	416	83	0·200
1974.5000	♂	163	70	510	132	0·259

Trimeresurus sumatranus

Coluber sumatranus Raffles, 1822.

MATERIAL. BM. 1974. 5001–5003 (immature).

HABITAT. All specimens were caught during the day in undisturbed forest. 1974. 5001 is from above 250 m on G. Lawit, and 1974. 5002–5003 are from about 300 m on Bukit Bok, the watershed between the Kelebang and Petuang drainages.

COLOUR. Based on 1974. 5002. The dorsal scales are green, flecked with black. The dorsal half of the first scale row and the ventral edge of the second scale row are white in life, without any red. The ventral half of the first dorsal scale row is the same green as the dorsum. Every fourth to fifth dorsal scale along the body is edged anteriorly with black, to give the appearance of dark crossbars on the body. Anteriorly the dorsal surfaces of the tail are the same colour as the body, except that the white lateral line is on the edges of the subcaudals and adjacent dorsal scale row. The ventrals are lime green and the subcaudals and distal half of the tail are pinkish brown. There is a series of brown spots along the dorsal tail surfaces.

REMARKS. These specimens and two other immature examples (from Betong, extreme southern Thailand, and from G. Dulit, Sarawak) are the only material in the BM(NH) that I would refer to *T. sumatranus*. They have the characteristics given in Table 9.

None has a white postocular stripe, white spots on the sides or white spots or ocelli on the tail. They have three upper labials in contact with the subocular as the usual number, and all have two large scales on the dorsal surface of the snout between the supranasal and supraocular, with the anterior pair separated by their own width or less. These characters, and their comparatively short tails and low average numbers of subcaudals, help to separate them from the closely related species *hageni* (see Brongersma, 1933; Grandison, 1972). *T. hageni* has generally two or less upper labials in contact with the subocular, usually has small scales between the supranasal and supraocular, has 67–85 (mean 73·9, N = 13) subcaudals, and has the tail equal to 0·148–0·204 (mean 0·177, N = 13) of the total length.

Table 9 Data on *Trimeresurus sumatranus*

Specimen	Locality	Ventrals	Subcaudals	Tail length/ total length
1891.8.29.33	G. Dulit	193	59	0·130
1974.5001	G. Lawit	184	60	0·133
1974.5002	Bt. Bok	183	61	0·133
1974.5003	Bt. Bok	184	71	0·154
1936.9.12.3	Betong	181	63	0·160

The Trengganu specimens have the following scale row reduction formulae

1974.5001 $23\,\frac{5+6(17)}{5+6(16)}\;21\,\frac{4+5(115)}{4+5(114)}\;19\,\frac{4+5(122)}{4+5(120)}\;17\,\frac{3+4(148)}{3+4(148)}\;15$

1974.5002 $23\,\frac{11+12(14)}{11+12(12)}\;21\,\frac{5+6(112)}{5+6(113)}\;19\,\frac{5+6(118)}{5+6(119)}\;17\,\frac{4+5(152)}{4+5(149)}\;15$

1974.5003 $23\,\frac{5+6(13)}{5+6(14)}\;21\,\frac{5+6(112)}{4+5(109)}\;19\,\frac{5+6(116)}{5+6(116)}\;17\,\frac{4+5(134)}{4+5(128)}\;15$

TESTUDINATA

Family TRIONYCHIDAE

Dogania subplana

Trionyx subplanus Geoffroy, 1809.

MATERIAL. BM. 1974. 5004–5005.

HABITAT. One was in an area of interconnecting streams and shallow muddy pools in logged forest at the Sungei Kelebang (43 m). The other was caught at the Sungei Petuang camp at 250 m.

COLOUR. Dorsal surfaces grey brown, the plastron white, the remainder of the ventral surfaces pale grey. The dorsum of the smaller specimen was mottled with black and yellow brown and marked with a black median line and four ocelli edged with yellow brown spots. The iris is pale grey brown to match the dorsum.

Family TESTUDINIDAE

Geochelone emys

Testudo emys Schlegel and S. Müller, 1844.

MATERIAL. BM. 1974. 5006 (skeleton).

HABITAT. This adult was found in the afternoon on a disused logging track near the Sungei Kelebang camp at 43 m.

Acknowledgements

Miss A. G. C. Grandison, of the British Museum (Natural History), my colleague at the time of the expedition, organized the herpetological team, collected many of the specimens and made all the tape recordings of frog calls. I am also indebted to her for allowing me the facilities of the Museum during the preparation of this report, and for kindly reading and criticizing the manuscript.

Lord Medway, the expedition leader, gave us the use of his knowledge of the flora of the area and collected interesting material for us. My thanks are also due to Tie'e Sipang, Atan Busu and the late Busu Sain for their companionship on the trip and for their invaluable collecting skills.

I am particularly grateful to Dr T. J. Seller, Imperial College of Science, London, who very kindly prepared sonagrams of the frog calls for me.

I thank the following people and institutions for the loan of specimens in their care: Dr J. R. Hendrickson, Mr H. Marx and Frances I. McCullough; the Bernice P. Bishop Museum in Honolulu, the Field Museum of Natural History, Chicago, and the United States National Museum, Washington, D.C. I am also grateful to Dr E. N. Arnold, Mr A. F. Stimson, Mr Colin McCarthy and Mr Barry Clarke for their help with numerous problems and for their tolerance.

References

Ahl, E. 1927. Zur Systematik der asiatischen Arten der Frosch Gattung *Rhacophorus*. *Sber. Ges. naturf. Freunde Berl.* 1–3 : 35–47.

Annandale, N. 1905. Notes on some oriental geckos in the Indian Museum. *Ann. Mag. nat. Hist.* (7) **15** : 26–32.

—— 1913. Some new and interesting Batrachia and lizards from India, Ceylon and Borneo. *Rec. Indian Mus.* **9** : 301–307.

—— 1918. Some undescribed tadpoles from the hills of Southern India. *Rec. Indian Mus.* **15** : 17–24.

—— 1919. The tadpoles of *Nyctibatrachus pygmaeus* and *Ixalus variabilis*: a correction. *Rec. Indian Mus.* **16** : 303.

Berry, P. Y. 1972. Undescribed and little known tadpoles from West Malaysia. *Herpetologica.* **28** : 338–346.

—— 1975. *The amphibian fauna of peninsular Malaysia.* Kuala Lumpur. 133 pp.

Blyth, E. 1856. Proceedings of the Asiatic Society of Bengal, for October, 1855: report. *J. Asiat. Soc. Beng.* **24** : 711–725.

Boettger, O. 1901. Die Reptilien und Batrachier. Kükenthal's wissenschaftliche Reiseergebnisse. *Abh. Senck. Ges.* **25** : 321–402.

Boie, F. 1827. Bemerkungen über Merrem's Versuch eines Systems der Amphibien. 1. Ophidier. *Isis Jena* **20** : 508–566.

Boulenger, G. A. 1882. *Catalogue of the Batrachia Salientia s. Ecaudata in the Collection of the British Museum.* London. ed. 2, xvi + 503 pp.

—— 1883. New batrachians in the collection of the British Museum (Natural History). *Ann. Mag. nat. Hist.* (5) **12** : 161–167.

—— 1887*a*. Catalogue of the lizards in the British Museum (Natural History). London ed. 2, vol. 3, xii + 575 pp.

—— 1887*b*. On new batrachians from Malacca. *Ann. Mag. nat. Hist.* (5) **19** : 345–348.

—— 1890. List of the reptiles, batrachians and freshwater fishes collected by Professor Moesch and Mr Iversen in the district of Deli, Sumatra. *Proc. zool. Soc. Lond.* : 31–40.

—— 1891*a*. Descriptions of new oriental reptiles and batrachians. *Ann. Mag. nat. Hist.* (6) **7** : 279–283.

—— 1891*b*. On new or little-known Indian and Malayan reptiles and batrachians. *Ann. Mag. nat. Hist.* (6) **8** : 288–292.

—— 1892. An account of the reptiles and batrachians collected by Mr C. Hose on Mt. Dulit, Borneo. *Proc. zool. Soc. Lond.* : 505–508.

—— 1893. Concluding report on the reptiles and batrachians obtained in Burma by Signor L. Fea. *Annali Mus. civ. Stor. nat. Giacomo Doria* **13** : 304–347.

—— 1895. Description of four new batrachians discovered by Mr Charles Hose in Borneo. *Ann. Mag. nat. Hist.* (6) **16** : 169–171.

—— 1896. *Catalogue of the snakes in the British Museum (Natural History).* London, vol. 3, xi + 382 pp.

—— 1899. Descriptions of new batrachians in the collection of the British Museum (Natural History). *Ann. Mag. nat. Hist.* (7) **3** : 273–277.

—— 1900. Descriptions of new batrachians and reptiles from the Larut Hills, Perak. *Ann. Mag. nat. Hist.* (7) **6** : 186–193.

—— 1903. Report on the batrachians and reptiles. *Fasc. malayenses* **1** : 131–176.

—— 1908. Report on the Gunong Tahan expedition, May–September, 1905. III. Report on the fishes, batrachians and reptiles. *J. fed. Malay St. Mus.* **3** : 61–69.

—— 1912. *A vertebrate fauna of the Malay Peninsula from the Isthmus of Kra to Singapore including the adjacent Islands. Reptilia and Batrachia.* London. xiii + 294 pp.

—— 1920. A monograph of the South Asian, Papuan, Melanesian and Australian frogs of the genus *Rana. Rec. Indian Mus.* **20** : 1–226.

Brongersma, L. D. 1933. Herpetological notes I–IX. *Zool. Meded. Leiden* **16** : 1–29.

—— 1934. Contributions to Indo-Australian Herpetology. *Zool. Meded. Leiden* **17** : 161–251.

—— 1935. *Gymnodactylus marmoratus* (Gray). *Proc. Sect. Sci. K. ned. Akad. Wet.* **62** : 172–175.

Cochran, D. 1930. The Herpetological Collection made by Dr Hugh M. Smith in Siam from 1923 to 1929. *Proc. U.S. natn. Mus.* **77** : 1–39.

Cuvier, G. 1831. Edited by Griffith. *The Animal Kingdom. Reptilia. A synopsis of the species in the class reptilia.* London. 110 pp.

Duméril, A. M. C. and Bibron, G. 1836. *Erpetologie Generale.* Paris, vol. 3. iv + 517 pp.

—— 1841. *Erpetologie generale.* Paris, vol. 8. 792 pp.

—— 1854. *Erpetologie generale.* Paris, vol. 7. xvi + xii + 1536 pp.

Flower, S. S. 1899. Notes on a second collection of reptiles made in the Malay Peninsula and Siam. *Proc. zool. Soc. Lond.* : 600–696, 885–916.

Geoffroy-Saint-Hilaire, E. 1809. Sur les tortues molles, nouveau genre sous le nom de *Trionyx*, et sur la formation des carapaces. *Annls Mus. Hist. nat. Paris* **14** : 1–20.

Grandison, A. G. C. 1972. The Gunong Benom Expedition 1967. 5, Reptiles and amphibians of Gunong Benom with a description of a new species of *Macrocalamus. Bull. Br. Mus. nat. Hist.* (*Zool.*) **23** : 45–101.

Gravenhorst, J. L. C. 1829. *Deliciae Musei Zoologici Vratislaviensis.* fasc. 1. Lipsiae. xiv + 106 pp.

Gray, J. E. 1845. *Catalogue of the specimens of lizards in the collection of the British Museum.* London. xxviii + 389 pp.

Günther, A. 1858. *Catalogue of the Batrachia Salientia in the collection of the British Museum.* London. vi + 160 pp.

—— 1863. Third account of new species of snakes in the collection of the British Museum. *Ann. Mag. nat. Hist.* (3) **7** : 348–356.

—— 1872. On the reptiles and amphibians of Borneo. *Proc. zool. Soc. Lond.* : 586–600.

Hardwicke, T. and Gray, J. E. 1827. A synopsis of the species of saurian reptiles collected in India by Major-General Hardwicke. *Proc. zool. Soc. Lond.* **3** : 213–229.

Hendrickson, J. R. 1966. Observations on the fauna of Pulau Tioman and Pulau Tulai. 5, The Reptiles. 6, The Amphibians. *Bull. natn. Mus. St. Singapore* no. 34 : 53–71, 72–84.

Inger, R. F. 1960. A revision of the oriental toads of the genus *Ansonia* Stoliczka. *Fieldiana, Zool.* **39** : 473–503.

—— 1966. The systematics and zoogeography of the Amphibia of Borneo. *Fieldiana, Zool.* **52** : 1–402.

Kiew, B. H. 1972. The frogs of Tasek Bera. *Malay Nat. J.* **25** : 130–134.

—— 1974. The taxonomy, zoogeography and breeding biology of the *macrodon* complex of the genus *Rana*. Ph.D. thesis for the University of Malaya, Kuala Lumpur. *Not seen.*

—— 1975. A note on the genus *Rana: Rana tweediei* Smith is synonymous with *Rana nitida* Smedley. *Malay Nat. J.* **28** : 107–109.

Kirtisinghe, P. 1946. The presence in Ceylon of a frog with direct development on land. *Ceylon J. Sci.* (B) **23** : 109–112.

Kuhl, H. 1820. *Beiträge zur Zoologie und vergleichenden Anatomie.* Frankfurt am Main, vol. 1, viii + 152 pp.

Laurenti, J. N. 1768. *Specimen medicum, exhibens synopsin Reptilium emendatam cum experimentis circa venena et antidota Reptilium Austriacorum.* Vienna. 214 pp.

Liem, S. S. 1970. The morphology, systematics and evolution of the Old World treefrogs. *Fieldiana, Zool.* **57** : 1–145.

—— 1973. The frogs and toads of Tjibodas National Park, Mt. Gede, Java, Indonesia. *Philipp. J. Sci.* **100** : 131–161.

Mackinnon, J. 1975. *Borneo.* London. 184 pp.

Marx, K. W. 1975. A substitute name, *Edwardtayloria*, for a genus of tree frogs from southeast Asia (Anura : Rhacophoridae). *Scient. Publs sci. Mus. St. Paul* **2** : 1–3.

Mertens, R. 1954. Über die javanische Eidechse *Dendragama fruhstorferi* und die Gattung *Dendragama. Senckenbergiana* **34** : 185–186.

Nicholls, L. 1949. A new gekkonid from the Malay Peninsula. *Bull. Raffles Mus.* **19**: 47–49.

Parker, H. W. 1928. The Brevicipitid frogs of the Genus *Microhyla. Ann. Mag. nat. Hist.* (10) **2** : 473–499.

Peters, W. 1864. Über einige neue Säugthiere. *Mber. k. preuss. Akad. Wiss.*: 381–399.

—— 1867. Herpetologische Notizen. *Mber. k. preuss. Akad. Wiss.*: 13–37.

—— 1871. Über neue Reptilien aus Ostafrica und Sarawak (Borneo), vorzüglich aus der Sammlung des Hrn. Marquis J. Doria zu Genoa. *Mber. k. preuss. Akad. Wiss.*: 566–581.

Raffles, S. 1822. Description of a zoological collection made in Sumatra. *Trans. Linn. Soc. Lond.* **13**: 334.

Rao, C. R. N. 1937. On some new forms of Batrachia from South India. *Proc. Indian Acad. Sci.* **6B**: 387–427.

de Rooij, N. 1915. *The reptiles of the Indo-Australian archipelago.* I. Lacertilia, Chelonia, Emydosauria. Leiden. xiv + 384 pp.

Roonwal, M. L. and Kripalani, M. B. 1961. A new frog *Philautus gherrapungiae* from Assam, India, with field observations on its behaviour and metamorphosis. *Rec. Indian Mus.* **59**: 325–333.

Salthe, S. N. and Duellman, W. E. 1973. *In* J. L. Vial, *Evolutionary Biology of the Anurans. Contemporary Research on Major Problems.* Columbia. xii + 470 pp.

Schlegel, H. 1837–1844. *Abbildungen neuer oder unvollstandig bekannter Amphibien* . . . Dusseldorf. xiv + 141 pp.

—— 1858. *Handleiding tot de beoefening der Dierkunde.* Breda. Vol. 2, xx + 628 pp.

Smedley, N. 1931. Amphibians and reptiles from the Cameron Highlands, Malay Peninsula. *Bull. Raffles Mus.* no. 6: 105–123.

Smith, M. A. 1915. Notes on the fauna and flora of the Ratburi and Petchaburi districts. Reptiles and Batrachians. *J. nat. Hist. Soc. Siam* **1**: 153–156.

—— 1916*a*. Descriptions of five tadpoles from Siam. *J. nat. Hist. Soc. Siam.* **2**: 37–43.

—— 1916*b*. On a collection of reptiles and batrachians from Peninsula Siam. *J. nat. Hist. Soc. Siam.* **2**: 148–171.

—— 1922. On a collection of reptiles and batrachians from the mountains of Pahang, Malay Peninsula. *J. fed. Malay St. Mus.* **10**: 263–282.

—— 1924. New tree frogs from Indo-China and the Malay Peninsula. *Proc. zool. Soc. Lond.*: 225–233.

—— 1925*a*. On a collection of reptiles and amphibians from Mt. Murud, Borneo. *Sarawak Mus. J.* **3**: 5–14.

—— 1925*b*. Contributions to the herpetology of Borneo. *Sarawak Mus. J.* **3**: 15–34.

—— 1930. The Reptilia and Amphibia of the Malay Peninsula. *Bull. Raffles Mus.* no. 3: 1–149.

—— 1935*a*. *The fauna of British India including Ceylon and Burma. Reptilia and Amphibia. Vol. II – Sauria.* London. xiii + 440 pp.

—— 1935*b*. On a collection of reptiles and amphibians from Perak, Malay Peninsula. *Bull. Raffles Mus.* no. 10: 61–63.

—— 1937. The names of two Indian vipers. *J. Bombay nat. Hist. Soc.*: 730–731.

—— 1953. Description of a new species of frog of the genus *Philautus. Ann. Mag. nat. Hist.* (12) **6**: 477–478.

Stoliczka, F. 1873. Notes on some species of Malayan Amphibia and Reptilia. *J. Asiat. Soc. Beng.* **42**: 111–126.

Taylor, A. C. and Kollros, J. J. 1946. Stages in the normal development of *Rana pipiens* larvae. *Anat. Rec.* **94**: 7–23.

Taylor, E. H. 1962. New Oriental reptiles. *Kans. Univ. Sci. Bull.* **43**: 209–263.

—— 1963. The lizards of Thailand. *Kans. Univ. Sci. Bull.* **44**: 687–1077.

—— 1968. *The caecilians of the world. A taxonomic review.* Lawrence. viii + 848 pp.

—— **and Elbel, R. E.** 1958. Contributions to the herpetology of Thailand. *Kans. Univ. Sci. Bull.* **38**: 1033–1189.

Tschudi, J. J. 1838. *Classification der Batrachier, mit Berucksichtigung der fossilen Thiere.* Neuchatel. 100 pp. (reissued in *Mem. Soc. Sci. nat. Neuchatel* **2**: 1–100, 1839 (1840)).

Vogt, T. 1911. Beitrag zur Amphibienfauna der Insel Formosa. *Sitz. Ges. naturf. Freunde Berl.* no. 3: 179–184.

Wagler, J. 1830. *Natürliches System der Amphibien mit vorangehender Classification der Säugthiere und Vögel.* München, Stuttgart and Tübingen. vi + 354 pp.

Werner, F. 1900. Reptilien und Batrachier aus Sumatra. *Zool. Jb. Ab. Syst.* **13**: 32–508.

Wiegmann, A. F. A. 1835. *In* F. J. F. Meyen, Beiträge zur Zoologie gesammelt auf eine Reise um die Erde. *Nova Acta physico-med.* **17**: 185–268.

Yong, H. S. 1974. Notes on the horned frog. *Malay Nat. J.* **27**: 56–58.

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Bulletin of the
British Museum (Natural History)

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Zoology series Vol 34 No 6 26 April 1979

The *Bulletin of the British Museum (Natural History)*, instituted in 1949, is issued in four scientific series, Botany, Entomology, Geology (incorporating Mineralogy) and Zoology, and an Historical series.

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

This number completes Volume 34

ISSN 0007-1498

British Museum (Natural History)
Cromwell Road
London SW7 5BD

Zoology series
Vol 34 No 6 pp 243–321

Issued 26 April 1979

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P. F. S. Cornelius
Department of Zoology, British Museum (Natural History), Cromwell Road, London SW7 5BD

Contents

†, ††, †††, ? conspecific pairs.

Synopsis

The nominal species of hydroids belonging to the family Sertulariidae recorded from Britain and neighbouring seas are revised. Twenty-four valid species are provisionally recognized.

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Introduction

This report is one of a series produced to meet the current need for taxonomic revision of the western European hydroids (Cornelius, 1975*b*; Cornelius, in prep.) and contains a revision of the nominal species of the family Sertulariidae *sensu* Millard (1975). It is the first revision of British Sertulariidae since that of Hincks (1868), based largely on the works of Johnston (1838, 1847), so a new revision is long overdue.

The faunal area corresponds approximately with the local Continental Shelf (Cornelius, 1975*b* : Fig. 1). It comprises British waters westwards and northwards to the 183 m (600 ft) depth contour, the North Sea (excluding the cold trough off W & SE Norway), Oslo Fjord, Danish waters, the Swedish west coast, the coasts of Germany, the Netherlands and Belgium and the whole of the English Channel, south to the latitude of the Isle d'Oeussant (Ushant, 48° 28′ N). Most species treated are widespread in the North Atlantic. Some are limital within the area, but only *Diphasia delagei* seems to be restricted to it. None of the species considered has a medusa stage – indeed they are unknown in this family. *Dynamena pumila* is said to have 'eumedusoids' which, although released (Teissier, 1923), probably do not represent medusae.

The number of species of Sertulariidae recognized in this paper – 24 – happens to be the same as that recorded solely from British waters by Hincks (1868). There are, however, two additional species, *Diphasia delagei* and *Sertularia tenera* (although neither has been reliably recorded from Britain), while Hincks' *Sertularia argentea* and *S. fusca* are here reduced to synonyms of other species. Although Hincks' account of this family seems to be largely acceptable it needs revision in places in the light of much subsequent work, some of it contradictory. For example, there is scope for new species concepts in the genera *Salacia*, *Sertularella* and *Sertularia*.

Although it may seem that some taxonomic stability has at last been reached, the conclusions drawn must be regarded with some caution as they are based on the fauna of an arbitrary, restricted area. Indeed, none of the genera recognized is restricted to the Atlantic Ocean so the genera involved need to be revised on a world-wide basis. Similarly, many species are widely distributed; there being a high proportion of near-cosmopolitan and 'bi-polar' species in this as in many other groups of hydroids. Undoubtedly much of the taxonomic confusion in the past stems from attempts to prepare faunal accounts of restricted areas. I have attempted to show elsewhere (Cornelius, 1975*a*) the number of invalid species described in the genus *Obelia*, in which it seems that over 100 previously accepted species can be reduced to 3 nearly cosmopolitan species and perhaps 2 or 3 others. In British waters, Hincks (1868) referred 6 species to *Obelia;* but of these only 2 are now admitted. (The third cosmopolitan species of *Obelia* was unknown in European waters until the twentieth century.) It seems likely, therefore, that the present revision will be modified when each of the species recognized herein can also be evaluated as part of the world fauna.

On the other hand, a detailed study solely of the European hydroid fauna is defensible on the grounds that it will hopefully provide some basis for taxonomic revisions of non-European faunae. Indeed, the type species of many widely distributed hydroid genera were described first from Europe. First studied by the pre-Linnaean European botanists, their study received considerable impetus from the books of John Ellis (Ellis, 1755; Ellis & Solander, 1786); and Linnaeus (1758) based many of his hydroid species on those recognized in the earlier of Ellis' books. The subsequent works of Pallas (1766) and Linnaeus (1767) consolidated Europe's lead in hydroid systematics at that time. Many of the species described by those early workers – in general the large, conspicuous species – have subsequently proved to be very widely distributed throughout the world. It seems certain, therefore, that a European study will also contribute substantially to the stability of nomenclature throughout the group. Since in general the large, conspicuous species are those in which nomenclative problems are most acute, perhaps because they have been more widely collected than smaller species, the contribution to stability is important not only in providing ground work for a world-wide nomenclative stability but in addition in fulfilling a need for a widely accepted check-list of names of use to non-specialists. Nevertheless some name changes are inevitably introduced in the present paper, particularly in species of the genera *Diphasia* and *Sertularella*. Finally, there is the need to provide re-descriptions for identification purposes.

In the following revision the genera are arranged alphabetically, and within each genus also the species are treated in alphabetical sequence. To facilitate comparison between species the illustrations appear in a slightly different sequence from the descriptions. The morphological characters used in the present revision are discussed at length in the next section.

A problematical distribution record is dealt with towards the end of the account (p. 306) and 5 species unreliably recorded from the area are removed from the faunal list (p. 306). None of these was listed by Hincks, only one (*Sertularia evansi*) having been recorded before his work appeared. For convenience the generic diagnoses provided by Millard (1975) are followed where possible. Nomenclature of the genus *Tamarisca* is discussed here under the nominate species, *T. tamarisca*; but for the most part discussion of generic synonymies is avoided since generic limits in the family are widely regarded as arbitrary. It would seem desirable to consider all species of the family before redefining the genera and this is not attempted here.

The material examined was drawn mainly from the collections of the British Museum (Natural History) and carries registered numbers of the format 1865.3.4.2. The numbers reflect the approximate dates, in reverse, on which the specimens were first registered and not the dates of collection or of deposition in the Museum. Specimens loaned by other Museums are so indicated.

Scientific names of algae mentioned follow those in the check-list of Parke & Dixon (1968), and those of marine invertebrates other than coelenterates follow Marine Biological Association (1957) unless otherwise stated.

Morphological and other variation

(Variation is discussed also under each species.)

Colonial hydroids exhibit within a colony a range of morphological variation of the kind more usually associated with whole populations of solitary organisms. That there is any variation at all between members of a single colony is perhaps remarkable, and it is difficult to determine which of it is genotypic and which is phenotypic. Indeed, since the normal developmental processes of thecate hydroids are only now becoming understood (for example by Knight, 1965, and Beloussov, 1973) it seems as yet unwise to attempt to distinguish between the two types. The same difficulties apply also when between-colony comparisons are made, and the biggest current problem in hydroid taxonomy is to tell one kind of variation from the other. Although a few morphological characters are now believed from observation to vary in response to environmental factors the influence of these on the majority of characters is virtually unknown (see below; and Cornelius, 1975*a*, for remarks on environment-induced variation in the hydroid stage of *Obelia*). Nevertheless, there seems to be some value in comparing trends in intraspecific variation throughout the 24 species treated here. Hopefully, in due course, it will become possible for variation in the taxonomic characters used to be assessed and guidelines suggested for evaluating variation in these and other nominal taxa.

Environment-induced variation

(*a*) *In* Dynamena pumila. Lower shore specimens of this largely intertidal species are said to be more branched than those from higher shore levels (Broch, 1918). Preliminary observations (p. 271, below) suggest that low-level colonies are larger and more advanced reproductively at any one time than colonies at higher levels, perhaps reflecting differences in feeding opportunities. Colonies on sheltered shores appear to have thinner perisarc, and larger and proportionately longer hydrothecae, than those on more exposed shores.

(*b*) *Internode length.* Broch (1918) considered this to increase with depth in some species but a relation has not been proved conclusively. Probably other factors, either or both phenotypic and genotypic, also influence internodal length and for the present little taxonomic value can be placed on it.

(*c*) *Sterility.* The occasional intertidal specimens of *Sertularella polyzonias* that occur are thought to remain infertile (p. 289), perhaps in response to reduced feeding opportunity.

Variation of unknown cause

(*a*) *Dimensions.* The tables of measurements in the following account show that all dimensions of skeletal structures, particularly those of the hydrotheca, vary in length and only exceptionally does it seem justifiable to regard size as a taxonomic criterion. One such instance might be the distinction between the two *Abietinaria* species treated here (p. 254), but this is not certain. For the present it seems unwise to accept nominal taxa – whether specific or varietal – based on size differences alone, even when the differences seem striking.

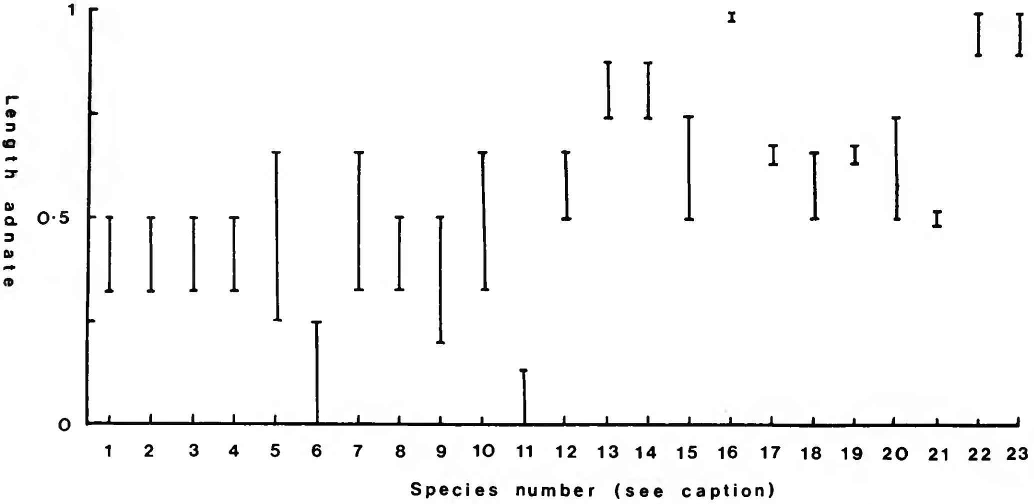


Fig. 1 Adnate portion of hydrothecal wall in species treated in the present paper (excepting *Sertularia tenera*). 1, *Symplectoscyphus tricuspidatus;* 2, *Sertularella gaudichaudi;* 3, *S. gayi;* 4, *S. polyzonias;* 5, *S. rugosa;* 6, *S. tenella;* 7, *Sertularia cupressina;* 8, *S. distans;* 9, *Abietinaria abietina;* 10, *A. filicula;* 11, *Hydrallmania falcata;* 12, *Diphasia attenuata;* 13, *D. delagei;* 14, *D. fallax;* 15, *D. margareta;* 16, *D. nigra;* 17, *D. pinastrum;* 18, *D. rosacea;* 19, *Dynamena pumila;* 20, *Amphisbetia operculata;* 21, *Tamarisca tamarisca;* 22, *Salacia articulata;* 23, *S. thuja.*

(*b*) *Hydrothecal characters.*

(i) Portion adnate. An evolutionary progression occurs in the thecate families from pedicellate hydrothecae through the adnate condition to a total inclusion of the hydrotheca within the hydrocaulus (Naumov, 1960, 1969); and although the precise evolutionary details have not been determined a similar progression also seems to occur in the present family. However, in some species the adnate proportion of the hydrothecal wall varies considerably (Fig. 1) and while there is on the one hand an overall systematic interest in the progressive incorporation of the hydrotheca into the hydrocaulus, on the other the precise degree of incorporation cannot be regarded a useful specific criterion.

(ii) Outward flexure of hydrotheca. Some species of Sertulariidae have hydrothecae which are out-turned, usually approximately midway between diaphragm and aperture. In many species the angle of outward flexure is variable, sometimes within a colony, while in others it seems more constant. In some there is a gradual curve, in others an abrupt bend with what appears to be a crease in the hydrothecal perisarc. Although in many genera (e.g. *Sertularia*) the angle of flexure is variable and probably of little taxonomic use, in others (e.g. *Diphasia*) it does seem useful in delimiting taxa.

In the genus *Sertularella* the narrow, distal third of the hydrotheca turns inward or outward from the hydrothecal axis or is straight. Variation in this has been used as a specific criterion in several publications by Millard (summary in Millard, 1975) but seems variable at least in the species here called *S. gaudichaudi* (p. 283) and should probably be used cautiously.

(iii) Number of cusps on hydrothecal rim. Although variable in some species (e.g. *Amphisbetia operculata*) the number of cusps, and to a greater extent their presence or absence, provide good taxonomic criteria at species level in the present faunal group. In addition, distinction between the genera *Symplectoscyphus* and *Sertularella* continues to be made on the basis of the number of cusps (three and four respectively). Although arbitrary, this distinction provides a working classification which can be used until more widely based generic limits can be worked out (Ralph, 1961).

(iv) Internal cusps in hydrothecae of *Sertularella* species. See page 283.

(v) External ornamentation. Regular patterning is rather unusual in hydroids. However, fine transverse ridging seems to be a diagnostic character of *Diphasia delagei* in which it occurs on both hydrotheca and gonotheca; but the occurrence of similar ridges on the hydrothecae of a single specimen of *Tamarisca tamarisca* (Fig. 29), a species in a closely related genus, gives grounds for caution. Similar ridging has been recorded as diagnostic of several species occurring outside the present faunal area (p. 260).

In the genera *Sertularella* and *Symplectoscyphus* a different and very much coarser ridging or corrugation is widespread. Although ridge number and size have been widely used as specific characters in these and other genera it is suggested below that they vary intraspecifically to such an extent that they do not always provide good taxonomic criteria (p. 293).

(vi) length : breadth ratio of hydrothecae. Although this seems approximately constant within a colony comparison of the ratio between colonies suggests that it is certainly not constant throughout the geographical range of most species treated here (see measurement tables for each species). At least in *Dynamena pumila* it seems to vary in response to environmental factors (p. 271), and hydrotheca length : breadth ratio does not seem a reliable specific character.

(vii) Arrangement of hydrothecae and hydrocladia. The species described here can be arranged in a series proceeding from those in which the hydrothecae are alternate (possibly the primitive condition) to those in which they are opposite. Stages in the series are here termed alternate, sub-alternate, sub-opposite and opposite for convenience of description, but the series is of course continuous. Although there is some intraspecific variation, position in the series seems to provide useful generic and sometimes specific characters.

All species in the present faunal group have a biseriate arrangement of the hydrothecae (with the exceptions of occasional triseriate specimens of *Diphasia fallax* and *Salacia thuja* and the secondary, pseudo-monoseriate arrangement in *Hydrallmania falcata*). Several arctic species are characteristically polyseriate (Naumov, 1960, 1969) but none has been recorded from the present area.

Two species, *Hydrallmania falcata* and *Amphisbetia operculata*, undergo a cataclysmic change in arrangement of the hydrothecae early in colony development. In *Sertularia cupressina* and *Salacia thuja* there is a similar cataclysmic change, in the arrangement of the hydrocladia. Possibly a comparable change occurs in *Sertularia tenera* also. In all 5 species the nature of these changes might give some phylogenetic clues; particularly in the case of *H. falcata* in which young colonies and occasional aberrant hydrocladia recall some of the characters of *Abietinaria* species (but see p. 274).

(*c*) *Hydranth characters*. The hydranths of many of the Sertulariidae species included here have not yet been adequately described. Accordingly, little systematic weight is at present attached to hydranth characters although further descriptive work might prove them useful. One feature which has been widely used as a generic (and even specific) criterion, however, is the offshoot of the enteron, or caecum, evident in contracted hydranths. It is perhaps significant that hydranths of preserved material are usually contracted if not relaxed before fixation. The taxonomic value of the presence or absence of caeca has been discussed recently by Mammen (1965) and Millard (1975) (see p. 279, below) and has been used as a generic character by the latter author and also by Naumov (1960, 1969). Probably it has little or only limited value as a *specific* character and, for example, its use as such in the genus *Salacia* is criticized below (p. 279). However, as discussed by Millard (1975), it seems often useful at genus level.

(*d*) *Gonothecal characters.* In all genera treated here, except *Sertularella*, gonothecal characters seem to provide reliable specific criteria, and a better understanding of that problematical genus might show them to be reliable there too. Male and female gonothecae are similar in some species of Sertulariidae, dissimilar in others. This usually varies from genus to genus (as at present diagnosed) but one species usually assigned to *Diphasia* seems exceptional in this respect (*D. pinastrum*, p. 267, being reported as having male and female gonothecae identical while in other *Diphasia* species included here they are dissimilar).

Fig. 2 Known depth ranges of Sertulariidae species occurring in Britain and nearby seas, based on data from various sources summarized in this paper. Almost certainly depth ranges in many species are incompletely known; and in 2 species (nos 1 and 10 in the figure) there is no data. Labels 1–23 as Fig. 1. Zero depth = ELWMST.

(*e*) *Habitat.* Not a useful specific criterion. Although exhaustive data is lacking no species in the present faunal group seems substrate-specific, most species occurring on a variety of substrates. Possibly there is only a generalized substrate selection by planulae in this family, but information on this point seems inadequate. Some species are characteristic of sandy bottoms, others of substrates of rock, shells, algae or other hydroids, but it seems that no species of the present faunal group enters a regular association.

Although colonies of several species can occasionally be found on the shore only *Dynamena pumila* occurs far from the low-water mark and alone can be considered partly intertidal. (See also habitat-induced variation, p. 245.) The depth ranges of many species treated here are rather wide (Fig. 2).

(*f*) *Reproductive season.* Most of the species included here have a rather long reproductive season (Fig. 3). Some are fertile in the cooler months and others in the summer, but apparently none is fertile in the autumn. Most breed later in the north than in the south, particularly *Sertularia cupressina.* Possibly the two rather similar *Abietinaria* species have different reproductive seasons but information is scant (p. 254). On the whole there seems little taxonomic value in this character.

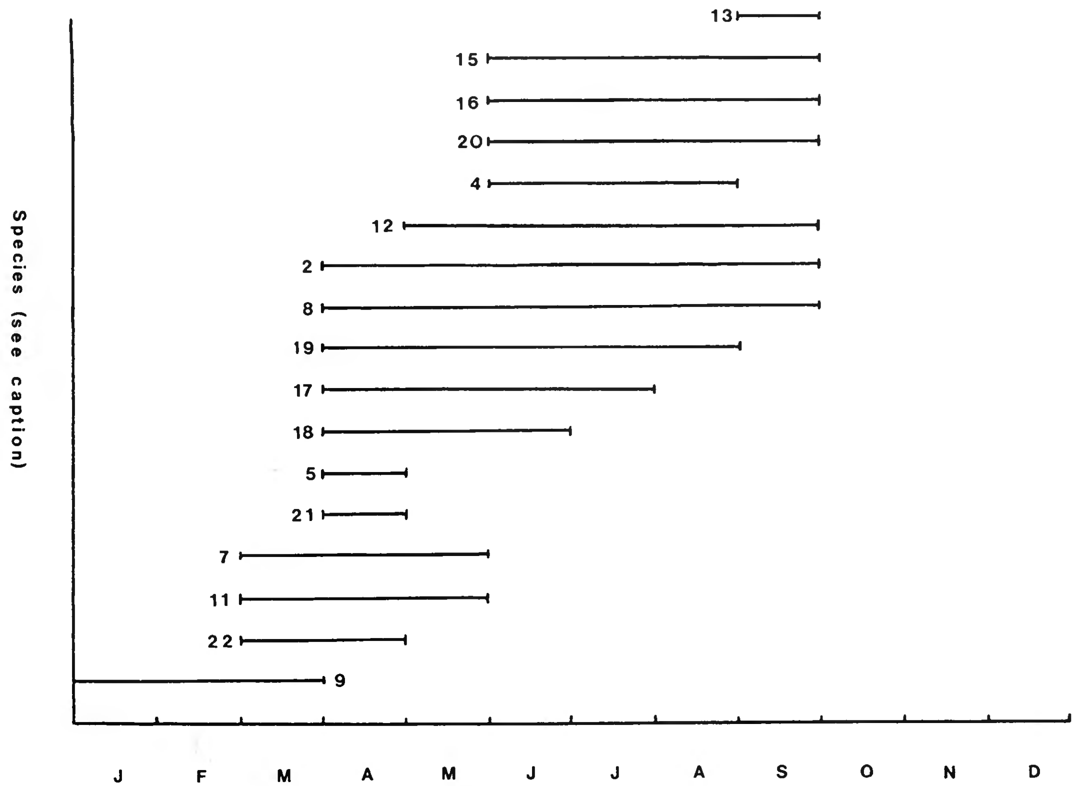


Fig. 3 Reproductive seasons of Sertulariidae species in the western English Channel, based largely on data presented by Marine Biological Association (1957) and Teissier (1965). Labels as for Fig. 1. See the entry 'Reproductive season' under each species for further data. Almost certainly the reproductive seasons of some species are incompletely known.

The scope of the genus *Sertularia*

The genus *Sertularia* Linnaeus, 1758, was formerly wider in scope, originally including species now assigned to families regarded distant as well as having once been applied to some bryozoan species. In addition most species in the present account have been referred to *Sertularia* at one time or another. There seemed little value in presenting a survey of past use of this generic name, and exhaustive accounts are already available in the synoptic lists of Bedot (1901, 1905, 1910, 1912, 1916, 1918, 1925: Hydrozoa) and Jelly (1889: Bryozoa). Early British usages of *Sertularia* were summarized by Johnston (1847: Bryozoa & Hydrozoa) and Hincks (1868: Hydrozoa). In addition, the index entries under *Sertularia* (p. 317) will serve as a guide to usages in the species treated here. Local uses in other hydroid families will be similarly covered in other papers (e.g. Cornelius, 1975*b*; Cornelius, in prep.). Pennington (1885) was probably the last synoptic author to employ the name *Sertularia* for bryozoan species.

Key to species

Only species which have been reliably recorded have been included (see pp. 306–308 for rejected and unreliable records). Provisional identifications can often be made from gonothecae by reference to the illustrations. Gonothecal characters are not included in the key, however, as many specimens lack them.

1	Rims of hydrothecae even; notched in some species but never cusped	2
–	Rims of hydrothecae cusped; not notched	11
2	Hydrothecae totally contained within perisarc or nearly so (*Salacia;* see also ***Diphasia nigra***, p. 265)	3
–	Terminal quarter or more of hydrothecae projecting from perisarc	4
3	Branches in one plane	***Salacia articulata*** (p. 276; Fig. 17)
–	Branches all round stem (except in young colonies)	***Salacia thuja*** (p. 280; Fig. 19)
4	Hydrothecae apparently on one side of stem only	***Hydrallmania falcata*** (p. 273; Fig. 15)
–	Hydrothecae biseriate (rarely triseriate, in *Diphasia fallax* & *Salacia thuja*)	5
5	Hydrothecal surfaces with fine transverse ridges [Also occasional specimens of *Tamarisca tamarisca* (p. 304; Fig. 29)]	***Diphasia delagei*** (p. 259; Fig. 10)
–	Hydrothecal surfaces not finely ridged	6
6	Axillary hydrothecae present and clearly associated with axils. (For distinctions see text, p. 253)	***Abietinaria abietina*** and ***Abietinaria filicula***
–	Axillary hydrothecae absent	7
7	Side branches narrower than main stem; colony regularly pinnate	8
–	Side branches same width as main stem; colony irregularly pinnate, or not pinnate at all	10
8	Adjacent walls of hydrothecae (almost) entirely adnate	***Diphasia nigra*** (p. 265; Fig. 12)
–	Adjacent walls of hydrothecae at most three quarters adnate	9
9	Hydrothecal flexure *c.* 45°; sides of main stems approximately parallel	***Diphasia pinastrum*** (p. 267; Fig. 13)
–	Hydrothecal flexure *c.* 90°; sides of main stems constricted below each hydrotheca	***Diphasia margareta*** (p. 263; Fig. 11)
10	Hydrothecae half adnate; flexure abrupt, *c.* 45°. (For distinctions see text, pp. 257–259)	***Diphasia attenuata*** and ***Diphasia rosacea***
–	Hydrothecae two thirds or more adnate; flexure gradual, less than 45°	***Diphasia fallax*** (p. 260; Fig. 9)
11	Number of cusps on hydrothecal rims two or three (one may be minute)	12
–	Number of cusps on hydrothecal rim four (*Sertularella*)	18
12	Two hydrothecal cusps	13
–	Three hydrothecal cusps	17
13	Hydrothecae in (sub)opposite pairs	14
–	Hydrothecae alternate	16
14	Hydrothecal cusps markedly unequal	***Amphisbetia operculata*** (p. 254; Fig. 6)
–	Hydrothecal cusps approximately equal	15
15	Nodal constrictions of one kind, all transverse	***Dynamena pumila*** (p. 271; Fig. 14)
–	Nodal constrictions of two kinds, transverse and oblique	***Sertularia distans*** (p. 296; Fig. 26)
16	One (rarely both) of the cusps on hydrothecal rims long (see p. 301 for distinctions; see also young *Amphisbetia operculata*, p. 254)	***Sertularia cupressina*** and ***Sertularia tenera***
–	Both cusps on hydrothecal rims short (young colonies, or aberrant branches on mature colonies)	***Hydrallmania falcata*** (p. 273; Fig. 15b)
17	Hydrothecae approximately straight; length : breadth ratio *c.* 2 : 1	***Symplectoscyphus tricuspidatus*** (p. 301; Fig. 28)
–	Hydrothecae curving outwards; length : breadth ratio *c.* 4 : 1	***Tamarisca tamarisca*** (p. 304; Fig. 29)
18	Length : breadth ratio of hydrothecae less than 2 : 1 (for distinctions see p. 293)	***Sertularella rugosa*** and ***Sertularella tenella***
–	Length : breadth ratio of hydrothecae 2 : 1 or more	19

19 Three (rarely one, two or four) sub-distal cusps on inside of hydrothecal wall; internodal perisarc and hydrothecal wall usually smooth . ***Sertularella gaudichaudi*** (p. 282; Fig. 20)
– No cusps on inside of hydrothecal wall; internodal perisarc and hydrothecal wall usually undulating to rugose (for distinctions see text, p. 287) ***Sertularella gayi*** and ***Sertularella polyzonias***

Systematic descriptions

Abietinaria abietina (Linnaeus, 1758)

(Fig. 4)

Corallina marina abietis forma . . . Ellis, 1755 : 4–5, pl. 1, figs B, b.
Sertularia abietina Linnaeus, 1758 : 808; Ellis & Solander, 1786 : 36–37; Hincks, 1868 : 266–268, pl. 55 (syn. *S. abietinula* Dalyell, 1847).
Abietinaria abietina: Broch, 1918 : 117–118; Kramp, 1935 : 184–185, fig. 77 A–B; Fraser, 1944 : 238–239, pl. 50, fig. 233; Vervoort, 1946 : 237–240, figs 103–105; Leloup, 1952 : 182–183, fig. 106; Naumov, 1960 : 375–376, fig. 264; Rees & Thursfield, 1965 : 139; Naumov, 1969 : 404–405, fig. 264; Calder, 1970 : 1525, pl. 5, fig. 6; Vervoort, 1972 : 98.

TYPE LOCALITY AND MATERIAL. Linnaeus (1758) gave the type locality as 'in Oceano'. The one sheet of herbarium material in the Linnaeus collection of the Linnean Society of London (catalogued 1298.4 by Savage, 1945) does not agree with the original diagnosis, and cannot be regarded as part of the original type series. The sheet bears a much branched infertile colony which incidentally does not resemble Ellis' (1755) illustration, which Linnaeus cited. Linnaeus' diagnosis mentioned gonothecae, which are absent from the specimen but present on Ellis' plate. Thus it seems that, as with many thecate hydroids, Linnaeus based his diagnosis on Ellis' illustration, and the illustrated specimen can be regarded as the holotype. Some Ellis material was preserved in the Museum of the Royal College of Surgeons of England until 1944 when much of the collections, including virtually all the hydroid material, was destroyed. It thus appears that the holotype specimen is no longer extant, although the original drawing of it survives (see Cornelius, 1975*a* : 267, footnote). Ellis did not give a locality for this species, but later collected it from Brighton (Ellis & Solander, 1786). The type locality of this species is accordingly here restricted to the south coast of England.

MATERIAL EXAMINED. This common and distinctive species is well represented in the BM(NH) collections and only specimens referred to in the text or illustrated are listed here. Isle of Man, ? 4 Sep 1894 (see notes under Reproductive season), fragments of ♀ colony on two microslides, coll. E. T. Browne, 1961.11.4.52–53 (Fig. 4b; Table 1). Lowestoft, Suffolk, part of colony on microslide, coll. G. J. Hinde, 1920.2.26.4 (Table 1). Off Wexford, Eire, 26 May 1901, 80 m ('Helga' sta. 54), hydrocladia on microslide, via E. T. Browne coll. 1967.6.15.21 (Fig. 4a).

DESCRIPTION. [Closely resembles *A. filicula* but is larger and more robust in appearance (see p. 253).] Colony erect, pinnate, monosiphonic, sturdy, up to 350 mm (Vervoort, 1946; Naumov, 1969) but often 50 mm or less; stolon tortuous. Hydrocaulus slightly flexuose, thicker and more robust than hydrocladia, which are straight; hydrocladia alternate, some second order branching; two rows of sub-alternate to alternate hydrothecae on both hydrocaulus and hydrocladia; axillary hydrothecae present. Hydrothecae variable, flask-shaped, bulbous proximally, tapering towards distal aperture; $\frac{1}{5}$–$\frac{1}{2}$ adnate; aperture circular, even, operculum attached on adjacent side, often deciduous; inner wall usually notched below aperture. Hydranth with diverticulum on outer side, *c.* 25 tentacles. Gonotheca ♂ = ♀, attached below hydrotheca, elongate-ovoid, walls thin, smooth to sinuous, tapering basally, ending distally in raised, circular aperture with *c.* 10 internal downward-pointing cusps (? desmocytes). Ova retained in acrocyst, embryos said (Hincks, 1868) to be bright yellow.

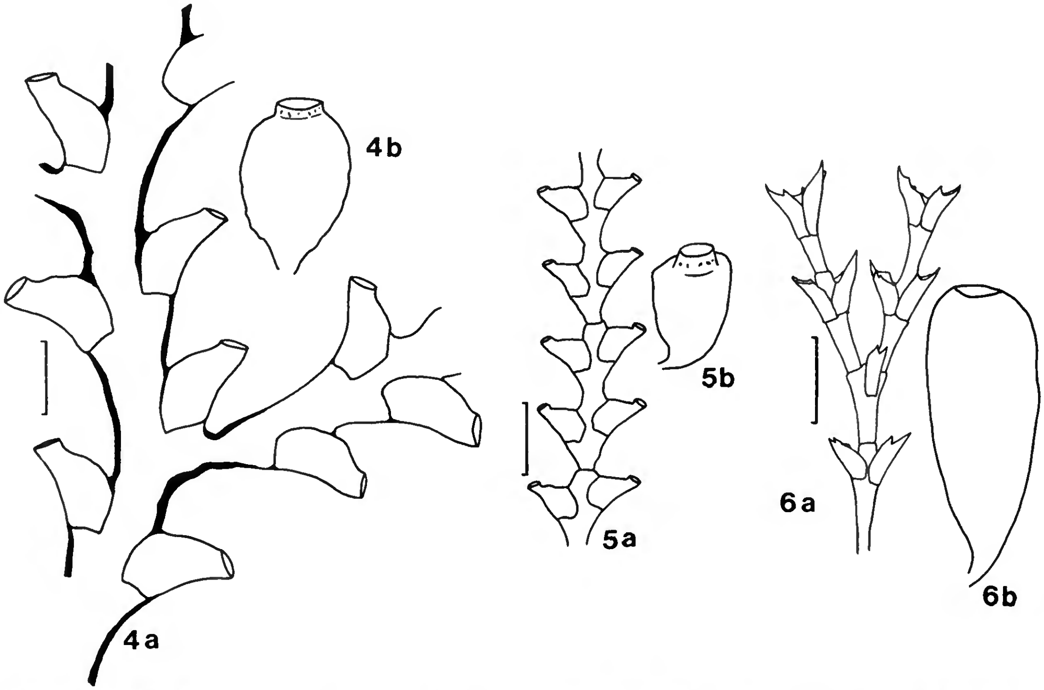
MEASUREMENTS. See Table 1.

Table 1 *Abietinaria abietina*. Measurements in μm

	Holland (Vervoort, 1946)	? U.S.S.R. (Naumov, 1969)	Isle of Man (1961.11.4.53)	SE England (1920.2.26.4)
Hydrotheca				
Outer side		600–1000	650–700	520–600
Inner side, length adnate			350–420	400–430
Inner side, length free			400–450	300–320
Diameter of aperture		190–300	230–270	180–220
Gonotheca				
Length	1300	1300 (max)	1200–1300	
Diameter	850	500–850	650–820	
Length/diameter	*1·53*	*1·53–2·6*	*1·58–1·84*	

REPRODUCTIVE SEASON. Fertile material recorded January to March at Roscoff (Teissier, 1965), during 'winter and spring' in British Isles (Ellis & Solander, 1786; Hincks, 1868, Hamond, 1957). A record of a fertile specimen reported from the Scilly Isles in July (Robins, 1969 : 333) seems exceptional. Two microslide preparations made by E. T. Browne from fertile material from the Isle of Man (1961.11.4.52–53) are dated 4 September 1894, but this date may simply be that on which the preparation was made, as Browne frequently noted this on the labels.

DISTRIBUTION. Common throughout the area on suitable substrates, occurring in the Kattegat but apparently not in the Baltic (Stechow, 1927; Broch, 1928; Kramp, 1935). The world distribution has been given by Broch (1918) and Naumov (1969).



Figs 4–6. **Fig. 4** *Abietinaria abietina*. (a) hydrocladia, SE Eire (1967.6.15.21); (b) gonotheca, sexed ♀ on contents (1961.11.4.53); scale (a–b) = 500 μm. **Fig. 5** *A. filicula*. (a) hydrocladium, NE England (1956.2.2.2); (b) gonotheca, Norway, 1962.11.7.15; scale (a–b) = 500 μm. **Fig. 6** *Amphisbetia operculata*. (a) Hydrocladia and (b) gontheca, SW England (1961.11.4.56); scale (a–b) = 500 μm.

HABITAT. Offshore, *c.* 10 m depth to edge of Continental Shelf. Common on sandy bottoms where it grows attached to pebbles, shells and similar objects. The species is washed ashore in large quantities where local currents are suitable (Hincks, 1868; Vervoort, 1946; Leloup, 1952).

REMARKS. *Abietinaria abietina* is a distinctive species, and no systematic revision seems necessary.

Abietinaria filicula (Ellis & Solander, 1786)

(Fig. 5)

Sertularia filicula Ellis & Solander, 1786 : 57, pl. 6, figs C, c; Hincks, 1868 : 264–266, pl. 53, fig. 3.
Abietinaria filicula: Broch, 1918 : 119–120; Kramp, 1935 : 185, fig. 77c; Fraser, 1944 : 240, pl. 50, fig. 224; Vervoort, 1946 : 240–242, fig. 106a; Naumov, 1960 : 381–383, fig. 272; Naumov, 1969 : 411–413, fig. 272.

TYPE LOCALITY AND MATERIAL. Scarborough, Yorkshire, England. Holotype (Ellis & Solander, 1786 : pl. 6, figs C, c) probably no longer extant (see notes under *A. abietina*, p. 251).

MATERIAL EXAMINED. The BM(NH) collection includes some 40 British specimens of this species, including all the herbarium material collected by George Johnston from Berwick Bay, the Firth of Forth and Scarborough, and mentioned by Gray (1848). Only the southernmost material, two Irish specimens and the measured material are listed. Vattlestraumen, Espegrend, nr Bergen, Norway, 30–40 m, 15 Aug 1962, fertile fragments on microslide, coll. W. J. Rees, 1962.11.7.15 (Fig. 5*b*, Table 2). Nr Ballantoy (= Ballycastle), Antrim, Northern Ireland, Dec 1797, colony in herbarium envelope, coll. R. Brown,[1] 1973.10.9.35. Bertraghboy, Connemara, Eire, 1874, colony in spirit, coll. A. M. Norman, 1912.12.21.358. Clachan Bridge, Seil, Argyll, Scotland, 1 Jun 1962, several fertile colonies in spirit, coll. W. J. Rees, 1962.6.19.1. Port Erin, Isle of Man, 14 Apr 1894, coll. E. T. Browne, 1948.10.1.15. Bridlington Bay, Yorkshire, 7 Nov 1921, fragments on microslide, coll. Ministry of Agriculture, Fisheries and Food, 1956.2.2.2 (Fig. 5a, Table 2). Plymouth, Devon, 8 Mar 1895, colony in spirit, coll. E. T. Browne, 1948.9.8.101.

DESCRIPTION. [Closely resembles *A. abietina* but is smaller and more delicate in general appearance (see p. 254).] Colony erect, pinnate, up to *c.* 100 mm (Vervoort, 1946). Main stem flexuose to straight; hydrocladia equal in width to main stem, alternate, with some second order branching. Hydrothecae in two rows, sub-alternate to alternate, on both main stem and branches and in axils; flask-shaped, bulbous basally, tapering distally to a neck which is said to be more defined than in *A. abietina;* $\frac{1}{3}$–$\frac{2}{3}$ adnate; aperture circular, even, inclined towards hydrocaulus or (less often) at right angles to long axis of hydrotheca; deciduous operculum attached to inner side; notch below aperture on inner side said to be deeper than that in *A. abietina.* Hydranth apparently undescribed. Gonotheca ♂ = ♀, elongate-ovoid, said to be proportionately longer than in *A. abietina* although measurements given here suggest proportions are similar (Tables 1, 2); aperture terminal, raised, with internal cusps.

MEASUREMENTS. See Table 2.

Table 2 *Abietinaria filicula.* Measurements in μm

	? Locality (Vervoort, 1946)	U.S.S.R. (Naumov, 1969)	Norway (1962.11.7.15)	NE England (1956.2.2.2)
Hydrotheca				
Outer side		330–350	320–360	310–340
Inner side, length adnate		210–250	190–230	200–220
Inner side, length free			150–180	170–190
Diameter of aperture		100–130	70–100	90–110
Gonotheca				
Length	900	900	1000	
Diameter	600	600	540	
Length/diameter	*1·5*	*1·5*	*1·85*	

REPRODUCTIVE SEASON. Apparently no published information. Collecting dates of two fertile specimens in the BM(NH) collection, taken 1 June 1962 in Argyll and 15 August 1962 near Bergen, Norway, perhaps indicate a difference in breeding season from *A. abietina* which breeds during winter and spring. Hamond (1957) recorded infertile material from Norfolk on 23 March 1952, at which time of year *A. abietina* would probably be fertile or at least bearing empty gonothecae.

DISTRIBUTION. Said to be boreal (Broch, 1918), recorded from most of the present area though regarded by Hincks (1868) as uncommon south of Scotland. The species has been considered local in occurrence (Hincks) and, in marked contrast to the similar but larger *A. abietina*, is poorly represented in the BM(NH) collections. The recorded world ranges of the two species are similar, though said (Naumov, 1969) not to be identical.

Southerly records of *A. filicula* are few, but include the following: Guernsey (Ansted & Latham, 1862, but not recorded there by Vervoort, 1949), Plymouth (present material), Ilfracombe (Cutcliffe, in Palmer, 1946, undated record), Liverpool (Byerley, 1854), Anglesey in 1940, 1948 and 1964 (Marine Science Laboratories, University College of North Wales, Bangor, unpublished records communicated by K. Hiscock) and Whitstable (Sorby, 1908; but not mentioned by Newell, 1954). The species has been recorded more often north of a line passing through the Isle of Man and Norfolk and published records suggest that from this line northwards it can at present be found offshore locally. The species has been reported from northern parts of Ireland but not from the south (Thompson, 1856; Stephens, 1905; present material), although recent information is apparently lacking. *A. filicula* is absent from the fauna lists of Dale, Plymouth, the Scilly Isles, Roscoff and the Glenan Isles (Marine Biological Association, 1957; Teissier, 1965; Crothers, 1966; Fey, 1969; Robins, 1969). Naumov (1969) stated that the species occurs southwards to 'the latitude of central France' but did not cite material. In the southern North Sea the species was not recorded from Belgium (Leloup, 1952), but there is an undated record from Holland (Vervoort, 1946) and it is recorded from the north-west coast of Germany (Broch, 1927), from Helgoland and Denmark (Kramp, 1935). Apparently the species does not occur in the Baltic (Stechow, 1927; Broch, 1928).

Almost all the records from the south of the area are from the last century and it seems that the southern limit of this species has moved northwards during the past 100 years.

HABITAT. Apparently no published information on substrate preference. In Russian seas reported from depths of 6–540 m, but not usually below 40 m (Naumov, 1969).

REMARKS. Specific status is retained for this poorly known form, although it shows a striking similarity to *A. abietina* in all but colony habit and dimensions. The apparent difference in reproductive season between the two species is not yet sufficiently documented for use as a specific criterion.

Amphisbetia operculata (Linnaeus, 1758)

(Fig. 6)

Corallina muscosa denticulata procumbens . . . Ellis, 1755 : 8, pl. 3, figs B, b.

Sertularia operculata Linnaeus, 1758 : 808; Hincks, 1868 : 263–264, pl. 54; Teissier, 1922 : 357–361; Teissier, 1929 : 647–650, figs 5–6; Vervoort, 1946 : 249–251, fig. 109; Blanco, 1966 : 1–6, figs 1–11.

Sertularia usneoides Pallas, 1766 : 132 (nom. nov. pro *S. operculata* Linnaeus, 1758).

Amphisbetia operculata: Agassiz, 1862 : 355; Stechow, 1923 : 199–200; Ralph, 1961 : 775–779, figs 8i–k; Rees & Thursfield, 1965 : 141; Vervoort, 1972 : 98–99 (syn. *Dynamena pulchella* d'Orbigny, 1846; *S. furcata* Trask, 1857).

Dynamena operculata: Naumov, 1960 : 330–331, fig. 220; Naumov, 1969 : 357–358, fig. 220.

TYPE LOCALITY AND MATERIAL. Linnaeus (1758) gave the type locality as 'in Oceano'. The Linnaeus collection in the Linnean Society of London contains no specimens (Savage, 1945; personal observation). The species almost certainly does not occur in Swedish waters (see Distribution, below) and as with other sertularian hydroids it seems plausible that Linnaeus based the designation of this species on previously published accounts (see also note 13, p. 309). One of the accounts cited by Linnaeus was that of Ellis (1755), and it seems likely that Linnaeus worked at least partly from Ellis' illustration (pl. 3, figs B, b). The illustrated specimen can be regarded the holotype. It is almost certainly no longer in existence (Cornelius, 1975*a* : 267). Ellis gave no locality for the specimen but since his book dealt with the British fauna it seems appropriate to restrict the type locality to coastal waters of the British Isles. Agassiz (1862) suggested a restriction to 'Europe' but this seems too wide as the species does not occur in several European countries.

MATERIAL EXAMINED. This species is well represented in the BM(NH) collections and only measured or illustrated material is listed below. Redcar Bay, Yorkshire, England, part of infertile colony on microslide, coll. J. Ritchie, 1964.8.7.149 (Table 3) (mentioned, Rees & Thursfield, 1965). Off Dungeness, Kent, 50° 47½′ N, 1° 10′ E, 28 Aug 1947, 35 m, part of fertile colony on microslide, coll. m.v. 'Manihine', 1947.10.6.18 (Table 3). Wembury Bay, Plymouth, Devon, part of fertile colony on microslide, coll. E. T. Browne, 1961.11.4.56 (Figs 6a–b, Table 3) (the microslide preparation is dated 29 Nov 1897 in Browne's hand but this is probably the date on which it was made since November is outside the normal breeding season). Valencia, SW Eire, 28 Jul 1895, part of infertile colony on microslide, coll. E. T. Browne, 1961.11.4.55 (Table 3).

DESCRIPTION. Colony a tuft of hair-like irregularly dichotomous hydrocauli, up to *c.* 350 mm. Hydrothecae in opposite pairs (alternate in very young colonies); one pair per internode and one hydrotheca in axil of each dichotomy; tubular, ½–¾ adnate, outer side straight to slightly concave; aperture sloping inwards towards stem, rim with long outer median spine and with or without two short lateral spines, one or (rarely) both of which may also be long, variation occurring within a hydrocaulus. Hydranth with 10–12 tentacles (Vervoort, 1949). Gonotheca probably ♂ = ♀ (see Variations section, below), large, ovoid but tapering conically basally; aperture distal, wide, circular, on very short collar; 1-piece operculum, usually deciduous. 'Medusoids' released (at dawn, Teissier, 1922), producing short-lived planktonic planulae.

MEASUREMENTS. See Table 3.

Table 3 *Amphisbetia operculata.* Measurements in µm

	English Channel (1947.10.6.18)	S Devon (1961.11.4.56)	NE England (1964.8.7.149)	SW Eire (1961.11.4.55)
Hydrotheca				
Length (tip of outer spine to inner corner)	370–400	300–370	300–380	350–430
Inner side, length adnate	200–230	200–210	160–170	180–230
Inner side, length free	60–70	70–100	70–90	70–90
Maximum diameter	90–110	120–130	120–140	110–130
Gonotheca (♂ = ♀)				
Length	1500	1800–2000		
Maximum diameter	800	800		
Diameter of aperture	350	280		

VARIATIONS. Hydrothecae in young colonies are often alternate (Teissier, 1929), paralleling growth changes in young colonies of *Hydrallmania falcata*, p. 273, and lack the long outer cusp characteristic of the rims of older *A. operculata* hydrothecae. Variation in the hydrothecal cusps of this species is described above (Description section). Narrower gonothecae were once thought to be male, broader ones female (Vervoort, 1949) but later evidence (Blanco, 1966) suggests that this variation is common to gonothecae of both sexes.

REPRODUCTIVE SEASON. June–September recorded from NW France (Teissier, 1965).

DISTRIBUTION. Widely distributed in the Atlantic Ocean, the northern limit probably passing through northern British waters. Recorded from throughout the present area but records are most numerous from the south and west. Common in the Irish Sea and English Channel (various authors) but unrecorded from the Scilly Isles (Robins, 1969); said to be common 'round the coast of Ireland' (Stephens, 1905) and recently (1975) reported common in Co Kerry (R. J. Lincoln, pers. comm.); common off Belgium (Leloup, 1952) and found off the Netherlands (Vervoort, 1946) and East Anglia (Morely, 1943; Hamond, 1957) although probably not common over most of the southern North Sea (Vervoort, 1949). Reported from two areas in Scotland – Caithness (in 1903, Rees & Thursfield, 1965) and Shetland (Norman, 1869; several sites in 1974, the late D. N. Huxtable, pers. comm.). The Shetland records appear to be the most northerly of the species. *A. operculata* has also been either found or reported off Yorkshire (BM(NH) collection) and the Durham coast (Hogg, 1829; Norman, 1905). The species is present around the Isle of Man (Bruce *et al.*, 1963) and Anglesey (K. Hiscock, pers. comm.), and has been reported from the Clyde Sea (Rankin, 1901, but not Ritchie, 1911, or Chumley, 1918). It is apparently unrecorded from the coasts of Germany, Denmark, Norway, Sweden, the Baltic and the Faroes (Broch, 1927, 1928; Kramp, 1929, 1935; Stechow, 1927; Rees & Rowe, 1969; Christiansen, 1972) apart from the unsupported statement of Naumov (1969) that it occurs northwards to Bergen, Norway.

HABITAT. Lower shore (including rock pools; Fowell, 1944) and shallow coastal waters down to 70 m (Bruce *et al.*, 1963) and perhaps slightly deeper. Hincks (1868) noted a substrate preference for *Laminaria* holdfasts.

REMARKS. No systematic revision of this distinctive species seems necessary.

Diphasia attenuata (Hincks, 1866)

(Fig. 7)

Sertularia attenuata Hincks, 1866 : 298–299.
Diphasia attenuata: Hincks, 1868 : 247–249, pl. 49, fig. 1; Broch, 1918 : 113; Vervoort, 1946 : 236, fig. 102; Rees & Thursfield, 1965 : 119.

TYPE MATERIAL AND LOCALITY. Hincks' original description of this species was based on material from 'North Devon, Cornwall, Brighton, Yorkshire coast and Peterhead', and also on the descriptions of Ellis (1755, part) and Johnston (1847, as *Sertularia rosacea*, part, and *S. pinaster*, part, based on material from Brighton and Orkney). Of this material only a microslide once in G. Busk's collection, identified by Hincks, could be located (Whitby, Yorkshire, 1850, part of ♀ colony on microslide, coll. G. Busk, det. T. Hincks, 1899.7.1.5854). It seems likely that this specimen is that or part of that on which Hincks based the Whitby locality record in his monograph (Hincks, 1868). However, it is not clear whether Hincks had seen the specimen before making the original description, although it closely resembles that description. The appropriate status for the specimen, therefore, seems to be neotype (see also Table 4). The type locality of the species, however, can be restricted more widely than the locality of the neotype specimen, to the British Isles.

OTHER MATERIAL EXAMINED. Off Mull, Argyll, Scotland, 1 Oct 1970, spirit material and part of ♀ colony on microslide, coll. P. F. S. Cornelius, 1971.5.11.34 (Fig. 7c, Table 4). Bridlington, Yorkshire, England, 7 Nov 1921, ♀ fragments on microslide, coll. Ministry of Agriculture, Fisheries and Food, 1956.2.2.7 (Fig. 7a). SE of Old Harry Rocks, Dorset, several colonies in spirit and one microslide preparation, coll. R. Kirkpatrick, 1897.8.9.22 (Table 4). English Channel, 50° 11′ N, 1° 47′ W, 70 m ('Manihine' sta. 9), 25 Jul 1947, ♀ fragment on microslide, 1947.9.4.13. English Channel, 49° 52′ N, 2° 10′ W, 85 m ('Manihine' sta. 48), ♀ fragment on microslide, 1948.9.6.2. Tenby, Pembrokeshire, Wales, small colony on microslide, coll. G. Busk, 1899.7.1.6346 (Fig. 7b).

DESCRIPTION. Colony erect but bending, loosely pinnate, monosiphonic; hydrocaulus and hydrocladia uniform in width, both sometimes ending in tendrils; some second order branching, axils *c.* 65°. Hydrothecae biseriate, in opposite pairs, tubular, $\frac{1}{2}$–$\frac{2}{3}$ adnate, gradually out-turned; aperture circular, rim even with deep notch on inner side; operculum approximately circular, attached on inner side, in present material apparently folded along mid-line with 'convex' surface outward. Hydranth with *c.* 16 tentacles; hypostome domed (Vervoort, 1949; present material). ♂ gonotheca (not seen) cylindrical, with 6 longitudinal ridges terminating distally in angular points; aperture on small distal cone. ♀ gonotheca 6-sided with 1–3 whorls of 6 spines distally;

spines tubular to conical, angle of insertion variable; aperture on small terminal cone; see also Remarks.

MEASUREMENTS. See Table 4.

Table 4 *Diphasia attenuata.* Measurements in μm

	NE England (Neotype)	S England (1897.8.9.22)	W Scotland (1971.5.11.34)
Hydrotheca			
Inner side, length adnate	310–340	330–380	260–340
Inner side, length free	200–280	380–420	270–320
Maximum diameter	120		
♀ Gonotheca			
Length (to ends of spines)	1950–2250	2350–2500	2250 (1 only)
Maximum diameter (excluding spines)	450–650	600–800	660

VARIATIONS. Both the present species and *D. rosacea* (p. 269) vary in the abruptness of the outward flexure in the hydrotheca, in the hydrothecal length : breadth ratio, in the robustness of the colony and in the structure of the ♀ gonotheca (for variations in which see Remarks).

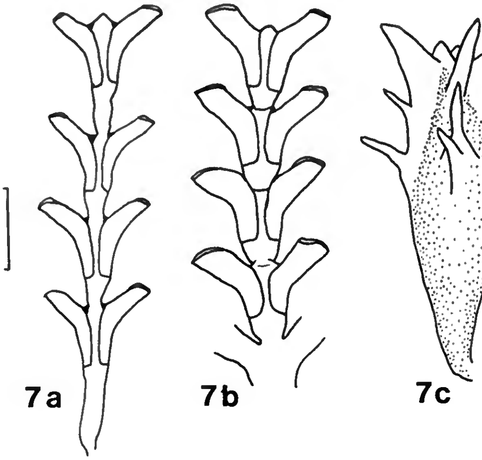
REPRODUCTIVE SEASON. Developing gonothecae found in July off Jersey (Vervoort, 1949); fertile material recorded May–September in NW France (Teissier, 1965). The fertile Mull specimen listed above was collected on 1 October 1970, and the Yorkshire specimen, which had an empty gonotheca, on 7 November 1921.

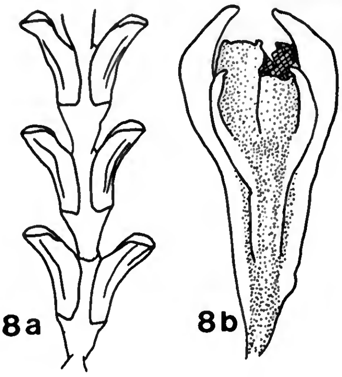
DISTRIBUTION. Found throughout the present area, but most frequent in the south and west. Common on both north and south coasts of the English Channel and in the Scilly and Channel Isles; and frequent in the southern North Sea[2] (Vervoort, 1949; Hamond, 1957; Marine Biological Association, 1957; Teissier, 1965; Robins, 1969), though unusual off Belgium (Leloup, 1952). Recorded also from Filey, Whitby and Peterhead (Hincks, 1868); Loch Lorn and the Sound of Canna (Rees & Thursfield, 1965); the Clyde Sea (Ritchie, 1911; Chumley, 1918), Isle of Man (Bruce *et al.*, 1963); Anglesey (K. Hiscock, pers. comm.); Bardsey (Knight-Jones & Jones, 1956); Pembrokeshire (Crothers, 1966); several localities in Eire and Northern Ireland (Stephens, 1905; also BM(NH) collection). There is BM(NH) material from the Shetlands, and Kramp (1929) recorded the species from the Faroes.

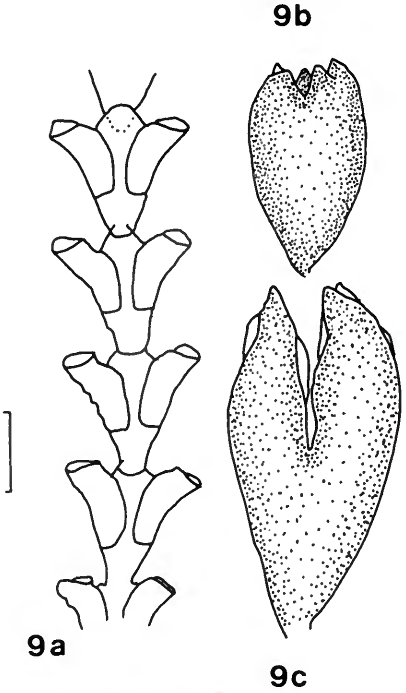
Table 5 Provisionally accepted differences between the two nominal species *Diphasia attenuata* and *D. rosacea*, arranged so far as understood in decreasing order of importance

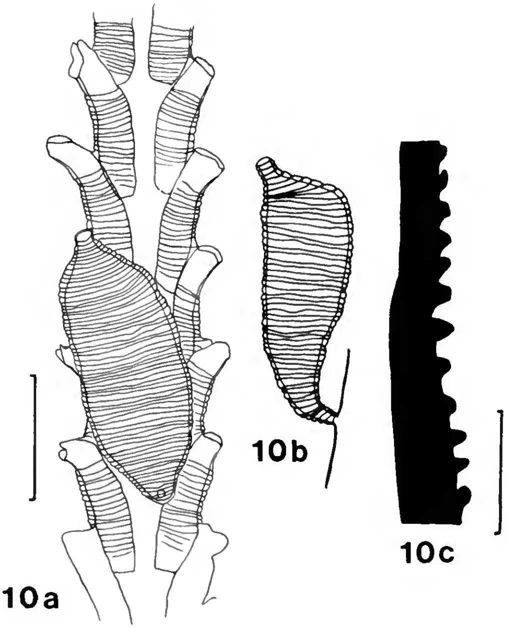
Character	*D. attenuata*	*D. rosacea*
♀ gonotheca	1–3 whorls of 6 spines irregularly arranged; no brood chamber; no inequality of spines within a whorl†	Eight distally-directed terminal spines enclosing brood-chamber; two of spines longer than rest†
Terminal tendrils	Often present	Rarely present
Hydrotheca	No grooves	Three grooves on outer wall (Leloup, 1952; Vervoort, 1959)
	Narrower	Broader
	Notch less wide	Rim with wide adcauline notch
Recording breeding season in W Europe	May–early October, possibly till early November	April–June, sometimes September

† But see p. 259.









Figs 7–10. Fig. 7 *Diphasia attenuata*. (a–b) hydrocladia, (a) NE England (1956.2.2.7) and (b) SW Wales (1899.7.1.6346); (c) ♀ gonotheca, W Scotland (1971.5.11.34); scale (a–c) = 500 µm. **Fig. 8** *D. rosacea*. (a) hydrocladium and (b) ♀ gonotheca, W Scotland (1956.1.1.17); scale as Fig. 7. **Fig. 9** *D. fallax*. (a) hydrocladium, (b) ♂ gonotheca and (c) ♀ gonotheca, monoecious colony, Faroe–Shetland Channel (1964.8.7.113); scale (a–c) = 500 µm. **Fig. 10** *D. delagei*. (a) hydrocladium with gonotheca, (b) lateral view of same gonotheca and (c) optical section of hydrothecal wall, external surface on right; all NW France (a–b, L. Cabioch personal collection; c, 1972.12.21.1); scales (a–b) = 500 µm, (c) = 50 µm.

The species is probably unrecorded from Denmark and the Baltic Sea (Stechow, 1927; Broch, 1928; Kramp, 1935).

HABITAT. Usually on other hydroids (Hincks, 1868); offshore, probably common at least to edge of Continental Shelf since Broch (1918) recorded material from a depth of 1470 m.

REMARKS. This species and *D. rosacea* (p. 269) are very similar but their separation is provisionally upheld on the basis of the characters in Table 5. However, all the characters seem variable and some specimens, particularly those lacking ♀ gonothecae, may be difficult to assign. Further, variations in the ♀ gonotheca of the two species approach each other, and gonothecal spines of the *attenuata* type may be joined by longitudinal ridges and tend to point upwards, recalling the arrangement in *rosacea*.

Diphasia delagei Billard, 1912

(Fig. 10)

Diphasia delagei Billard, 1912 : 466–467, figs 3–4; Billard, 1931 : 246–247; Teissier, 1965 : 22.

TYPE LOCALITY. Off Saint-Pol, NW France, 65 m; 4 August 1909; material not located.

MATERIAL EXAMINED. Numerous colonies, 8 miles NW of I de Batz, nr Roscoff, NW France, 85 m, September 1965, on *Diphasia rosacea*, coll. J. Bouillon & L. Cabioch, BM(NH) reg. no. 1972.12.21.1 (Figs 10a–c, Table 6).[3]

Table 6 *Diphasia delagei*. Measurements in μm

(I) Hydrocladia with vertically overlapping hydrothecae	Type series, NW France (Billard, 1912)	NW France (1972.12.21.1)†
Hydrotheca		
Inner side, length adnate	400–580	500–550
Inner side, length free	80–110	60–80
Diameter	110–120	140–170
Gonotheca		
Length		1150 (one only)†
(II) Hydrocladia with vertically separated hydrothecae	Type series, NW France (Billard, 1912)	
Hydrotheca		
Inner side, length adnate	270–300	
Inner side, length free	160–220	
Diameter	100–160	

† The measured gonotheca, although part of this series, was not registered (see Material examined).

DESCRIPTION. Branching stolon with erect hydrocauli, 25–35 mm. Hydrothecae usually absent from basal portion; in opposite pairs, separated laterally, often sub-opposite; tubular, $\frac{3}{4}$–$\frac{7}{8}$ adnate; 15–30 fine horizontal ridges on outer wall, 5–6 μm, high on outer edge, shallower towards inner side (Fig. 10); hydrothecal aperture circular, even, with single-flapped operculum attached on inner side. Hydranth contracted in present material, *c*. 15 tentacles. Gonotheca (hitherto undescribed) in present material elongate, with narrow terminal aperture at end of short eccentric tube; closely ridged throughout as hydrotheca; borne on hydrocladium on short pedicel just above base of hydrotheca; no gonothecal contents in present material.

MEASUREMENTS. See Table 6.

VARIATIONS. Billard (1912) reported that in some colonies only three-quarters of the inner wall of the hydrotheca was adnate and hydrothecal pairs were vertically distinct, while in others hydrothecae of one pair overlapped the bases of the next and about seven-eighths of the inner walls were adnate. Billard reported between-colony variations also in the lateral extent of the fine ridges on the surface of the hydrotheca. In the present material hydrothecae on a single hydrocladium projected by a varying amount and the precise proportion of the hydrothecal wall which is adnate in this species seems to have little systematic importance.

REPRODUCTIVE SEASON. September in NW France (Teissier, 1965). The present material, collected September 1965, had a single empty gonotheca. The apparent scarcity of gonothecae might indicate that reproduction is usually vegetative in this species, but present information is scant.

DISTRIBUTION. Apparently recorded from only a few localities in NW France and (Teissier, 1965) from the 'axial region of the English Channel', being recorded from nowhere else in the world.

HABITAT. Recorded on other hydroids [*Aglaophenia tubulifera* Hincks, 1861 (by Billard, 1912), *Diphasia margareta* (by Billard, 1931, as *D. pinaster*), *D. rosacea* (present material), 'other hydroids' (Teissier, 1965)] and on pebbles, gravel and shell-gravel (Teissier, 1965). Recorded from depths of 60–90 m (Teissier, op. cit.; other authors' records falling within these limits).

REMARKS. It is not clear why a distinctive species such as *D. delagei* should be so infrequently reported in a well-worked area like the western English Channel, or why it was not reported before 1912.

Several nominal species of *Diphasia*[4] having fine transverse ridges on the hydrotheca have been described from the Atlantic Ocean, but only two or perhaps three seem valid. *Diphasia tropica* Nutting, 1904, from the West Indies, was based on vegetative characters but the gonotheca is now known (Vannucci, 1949, as *Diphasiella ornata* sp. nov., from Colombo; van Gemerden-Hoogeveen, 1965) and the species seems well founded. *Sertularia hupferi* Broch, 1914, resembles *D. tropica* closely in vegetative characters and as suggested by Buchanan (1957) the two might well prove conspecific.[5] *Sertularia subtilis* Fraser, 1937, from Puerto Rico, described without gonotheca, resembles *D. tropica* closely on vegetative characters and might well prove conspecific. Secondly, *Geminella subtilis* Vannucci Mendes, 1946 (*non* Fraser, 1937), from Brazil, resembles *D. tropica* in vegetative characters but the described gonotheca is quite different. However, available evidence does not rule out the possibility that the two gonothecal types (of *D. tropica* and *G. subtilis*) are merely male and female of the same species. Finally, the present species, *Diphasia delagei* Billard, 1912, known only from the western English Channel, differs markedly from *D. tropica* in both vegetative and gonothecal characters and seems to be valid.

Diphasia fallax (Johnston, 1847)

(Fig. 9)

Sertularia fallax Johnston, 1847 : 73–74, pl. 11, figs 2, 5–6 (? syn. *Dynamena tubiformis* Lamouroux, 1821; see Remarks); Gray, 1848 : 71.
Diphasia fallax: Hincks, 1868 : 249–251; pl. 49, figs 2, 2a–b, text-fig. 31; Broch, 1918 : 108–111; Kramp, 1932 : 49–51 (syn. *D. wandeli* Levinsen, 1893); Kramp, 1935 : 181–182, fig. 75; Fraser, 1944 : 242, pl. 50, fig. 227a–c; Naumov, 1960 : 333–334, figs 223–224; Rees & Thursfield, 1965 : 120–121; Naumov, 1969 : 360–361, figs 223–224; Vervoort, 1972 : 103–105, fig. 31.
Diphasia fallax forma *wandeli:* Kramp, 1932 : 51.
Diphasia fallax forma *typica* Kramp, 1932 : 51.
Diphasia coronifera Allman, 1872 : 170 (nom. nud.); Allman, 1874a : 471, 474, pl. 66, figs 2, 2a; Rees & Thursfield, 1965 : 120.
Nigellastrum coroniferum: Stechow, 1923 : 160.

TYPE LOCALITIES AND MATERIAL. Extant type material and its localities are shown in Table 7. In addition, the syntype series originally included material from the coast of Aberdeen (coll. J. Macgillivray) and Scarborough, Yorkshire (coll. W. Bean), but this material was not located. The type locality can be restricted to the NE coast of Britain between Scarborough and Aberdeen, the limits of the original type series.

Table 7 *Diphasia fallax.* Syntype specimens extant in the BM(NH) collection. All are on herbarium sheets; see also text.

Locality	Collector	Gray (1848) cat. no.	BM(NH) reg. no.	Remarks
Dunstanburgh, Northumberland	R. Embleton	6a	1847.9.22.24a	Epizoic on lectotype of *Sertularia fusca* Johnston, 1847 (see p. 278)
Firth of Forth	J. Coldstream	6b–d	1847.9.22.29	
Whitburn, Durham	Miss M. Dale	6e	1847.9.22.31	Labelled 'Whitburn, Northumberland' in Johnston's hand, presumably in error
No data	G. Johnston	6f	1847.9.22.30	Probably correctly regarded a syntype

OTHER TYPE MATERIAL EXAMINED. Holotype of *Diphasia coronifera* Allman, 1874*a* [BM(NH) reg. no. 1912.12.21.108; see Remarks and Table 8].[6]

OTHER MATERIAL EXAMINED. This species is well represented in the BM(NH) collections and only mentioned, measured or illustrated material is listed here. Faroe–Shetland Channel, 61° 12′ N, 6° 33′ W ('Goldseeker' sta. 17), 10 Aug 1907, monoecious fragments on microslide, ex. coll. J. Ritchie, 1964.8.7.113 (mentioned, Rees & Thursfield, 1965: 120) (Figs 9a–c; Table 8). Firth of Lorn, Argyll, Scotland, 140–160 m, monoecious colonies in spirit, coll. J. Murray, 1888.6.9.16. Farland Pt, Gt Cumbrae Id, Buteshire, Scotland, 5–10 m, 20 May 1955, several fertile colonies in spirit+1 microslide preparation (♀), coll. W. J. Rees, 1956.1.1.4 (Table 8). Also examined was non-type material labelled '*Diphasia coronifera*' Allman, 1874*a*, from the Royal Scottish Museum, collected by James Ritchie and listed by Rees & Thursfield (1965).

DESCRIPTION. Colony erect, pinnate, up to *c.* 100 mm; monosiphonic main stem and branches straight to gently curved, some second order branching; terminal tendrils frequent, used (Hincks, 1868; Naumov, 1969) for attachment. Main stem thicker than branches. Hydrothecae biseriate, often triseriate in arctic regions (Kramp, 1932), opposite to sub-opposite, on both stem and branches; short, tubular, $\frac{3}{4}$+adnate, slightly out-turned distally; aperture circular, rim even, 1-flapped operculum attached on inner side. Perisarc annulus below each pair of hydrothecae.

Table 8 *Diphasia fallax.* Measurements in μm

	Russian seas (Naumov, 1969)	W Scotland (1956.1.1.4)	Faroe–Shetland Channel (1964.8.7.113; monoecious colony)	Holotype of *Diphasia coronifera* (1912.12.21.108; see Remarks)
Hydrotheca				
Inner side, length adnate	600–650	520–610	380–430	600
Inner side, length free		135–160	170–210	160
Maximum diameter		190–220	200–210	270
♂ gonotheca				
Length	900		1200 (1 only)	1200
Maximum diameter	400		650 (1 only)	700
♀ gonotheca				
Length	2000	2800–3100	2200–2450	
Maximum diameter	1000	950–1350	1050–1200	

Hydranth with *c.* 16 tentacles (Vervoort, 1946). Gonothecae on hydrocladia, attached below each hydrothecal pair. ♂ elongate, wider distally, with 4 erect spines (one to all of which may be bifid) surrounding the raised tubular aperture. ♀ similar but longer, with distal slender neck bearing terminal aperture, and four long conical processes arising from the four distal corners of the gonotheca joined above aperture to form brood chamber surrounding an acrocyst. Monoecious material reported several times but dioecious condition seems more usual (see Remarks).

MEASUREMENTS. See Table 8.

VARIATIONS. Kramp (1932) proposed that arctic forms of this species, having almost entirely sunken hydrothecae with strong tendency to bifid male gonothecal cusps and thick, dark main stems, should be referred to a variety, *wandeli* Levinsen, 1893 (based on the nominal species *Diphasia wandeli* Levinsen). Colonies more typical of warmer regions, having further projecting hydrothecae, male gonothecal cusps not bifid and paler (? younger) main stems he referred to a variety *typica* Kramp, 1932. It seems that the name *coronifera* Allman, 1874*a*, would have priority over *wandeli* (see Remarks); but Kramp showed the two 'formae' to be linked by a continuous series and it seems unnecessary to refer the extremes of the series to different taxa. No varieties are recognized here.

REPRODUCTIVE SEASON. Apparently no published information. Two fertile BM(NH) specimens were collected on 10 July 1907 in the Faroe–Shetland Channel (1964.8.7.113) and on 20 May 1955 from the R Clyde, W Scotland (1956.1.1.4).

DISTRIBUTION. A northern species which in the present area is probably widespread north of a line approximately between Glasgow and Hamburg but currently scarce or absent to the south. During the present century in British waters the species has not been recorded south of the R Clyde and Yorkshire (Ritchie, 1911; Broch, 1918; Chumley, 1918), although recorded present in the 'North Sea', Skagerrak and Kattegat (Broch, 1928; Kramp, 1935). Several nineteenth century records suggest the species then occurred further south [Ireland (Stephens, 1905); Isle of Man (Moore, 1937); N Wales (Penmaenmawr to Rhyl) in 1894 (Marine Science Laboratories, University College of North Wales, Bangor, unpublished records, via K. Hiscock); Holland (Vervoort, 1946); Channel Isles (Ansted & Latham, 1862, dubious record)]. However, Hincks (1868) recorded no localities further south than Yorkshire and Argyll. Thus the scant evidence available suggests that the species extended its range southwards during the last 30 years of the nineteenth century and later retreated to its original southern limit, but this is far from proven.

HABITAT. Naumov (1969) recorded a depth range of 13–250 m in Russian seas, with usual limits of 100–200 m. BM(NH) material suggests that in western Europe the species sometimes occurs in depths of only a few tens of metres, and although precise data are lacking it seems that the depth range in western Europe is similar to that in Russian seas as stated by Naumov.

Vervoort (1972) recorded colonies growing on hydroids of the genera *Aglaophenopsis* and *Salacia*.

REMARKS. The fragments from the Faroe–Shetland Channel and the colonies from the Firth of Lorn, Scotland, are monoecious, supporting Hincks' (1868) observation that this species sometimes bears male and female gonothecae on one colony. However, the bulk of the BM(NH) material is dioecious suggesting that this condition is usual.

When introducing the present species name Johnston (1847) tentatively included in its synonymy the older name *Dynamena tubiformis* Lamouroux (1821 : 12, pl. 66, figs 6–7). Lamouroux' collections were largely destroyed during the Second World War (Redier, 1967) but Billard (1909) had previously examined the type material of the present species. This material had been illustrated by Lamouroux. Billard considered it to be referable to an earlier species, *D. sertularioides* Lamouroux (1816 : 178), type material of which Billard examined, and also illustrated for the first time. Billard referred *sertularioides* (and of course with it *tubiformis*) to the genus *Synthecium* Allman, 1872, in the family Syntheciidae. Hence it seems usage of the species name *fallax* is not threatened by the two Lamouroux names; both of which were in fact applied to Australasian material.

Diphasia coronifera Allman, 1874*a*, was founded on male material resembling *D. fallax* in all features except, it was said, its eight projections (not four) surrounding the male gonothecal aperture. However, many of the male gonothecae on the holotype[6] bear four bifid projections, not eight undivided ones; while the present *D. fallax* material from W Scotland (1888.6.9.16) bears some male gonothecae with four simple projections, others with four bifid projections and still others intermediate, with one, two or three bifid projections. In addition, measurements of the holotype fall within the range of *D. fallax* dimensions (Table 8). Hence it seems that *D. coronifera* was based on typical *D. fallax* material, and the two taxa can be regarded conspecific. The non-type material in the James Ritchie collection of the Royal Scottish Museum, listed as *D. coronifera* by Rees & Thursfield (1965), was examined and found also to be *D. fallax. Thuiaria coronifera* Allman, 1876, originally described from material collected in Japanese waters, is a different species. It has recently been redescribed by Naumov (1960, 1969).

Diphasia margareta (Hassall, 1841)

(Fig. 11)

Sertularia margareta Hassall, 1841 : 284, pl. 6, figs 3–4; Johnston, 1847 : 72–73, text-fig. 13 [syn. *S. tudori* Rylands, in Johnston, 1847 (sic)].
Diphasia pinaster: Hincks, 1868 : 252–253, pl. 50, fig. 1; Teissier, 1965 : 22.
Diphasia elegans Sars, 1874 : 145–146, pl. 3, figs 23–26.
Diphasia pectinata: Vervoort, 1959 : 255–256, figs 23–24 (see p. 267).

TYPE LOCALITIES AND MATERIAL. Off Howth, near Dublin, Eire, and near Giant's Causeway, near Runkerry Point, Co Antrim, Northern Ireland. The type material was not located. As noted by Hincks (1868) the original description appears to have been of female material. See addendum.

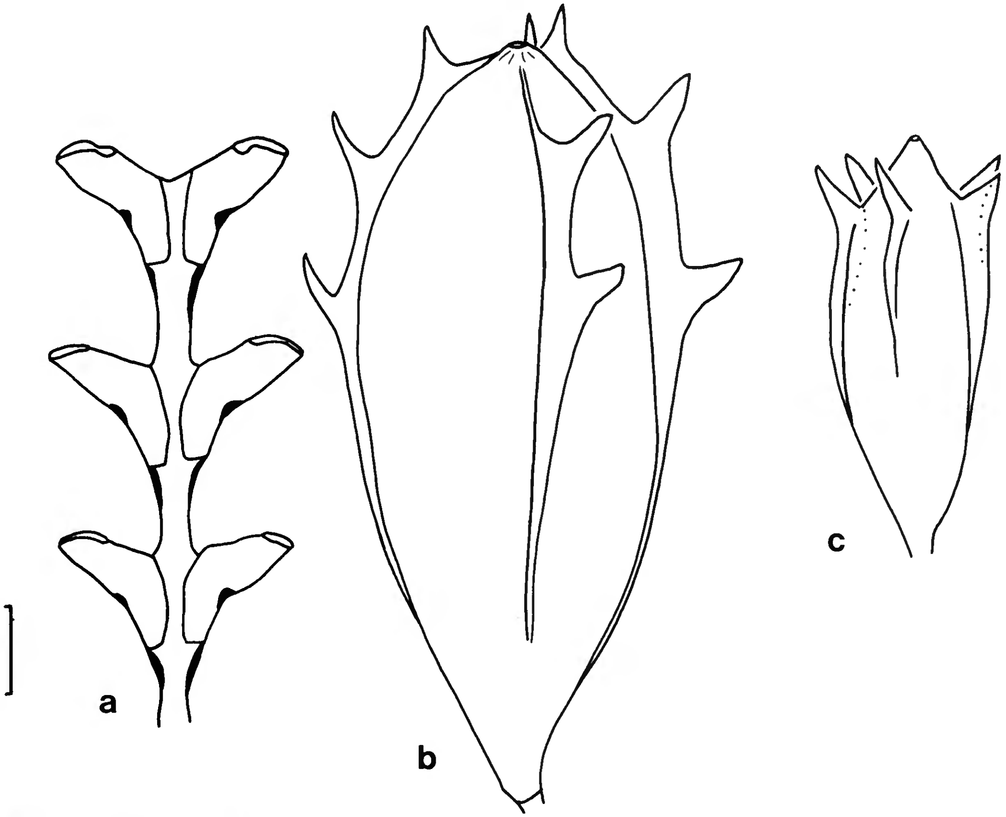


Fig. 11 *Diphasia margareta.* (a) terminal region of hydrocladium, North Sea (1964.8.7.114); (b) ♀ gonotheca, Azores (1888.11.13.52); (c) ♂ gonotheca with fifth, supernumerary spine, W Scotland (1955.10.15.5); scale (a–c) = 500 μm.

MATERIAL EXAMINED. Only measured, illustrated or otherwise mentioned material is listed. Campbeltown, Argyll, Scotland, 10 Jun 1952, fragments of ♂ colony on microslide, coll. R. B. Pike, 1955.10.15.5 (Fig. 11c; Table 9). W of Shetland Isles, 60° 02′ N, 3° 13′ W, 160 m, 19 Jun 1906, fragments of ♀ colony on microslide, coll. R.V. 'Goldseeker' (sta. 21a), via. J. Ritchie coll., 1964.8.7.114 (Fig. 11a; Table 9; mentioned, Rees & Thursfield, 1965 : 122, as *D. pinaster*). Peel, Isle of Man, ♀ hydrocaulus on microslide, ex E. T. Browne coll., 1961.11.4.31 (Table 9). Off Azores, 38° 38′ N, 28° 28½′ W, 900 m, Jun 1873, ♂ and ♀ fragments on microslide, coll. H.M.S. 'Challenger' (sta. 75), 1888.11.13.52 (Fig. 11b); mentioned, Allman, 1888 : 64, as *D. pinaster*).

DESCRIPTION. Colony erect, up to 150 mm, pinnate, side branches alternate, rather long, some second order branching. Hydrothecae on both stem and branches biseriate, opposite, grading proximally to sub-opposite, sharply out-turned in middle, ½–¾ adnate; inward projection of perisarc at angle of bend; shape of inward projection varies (Fig. 11a), sometimes (Vervoort, 1959) two projections; aperture oblique, circular, even rimmed, usually with adcauline notch; operculum circular, adcauline. Angle between inner edge of hydrotheca and hydrocaulus approximately 90°, although variable. Some hydrothecal renovation. Gonothecae – ♀ very large, elongate-ovoid, not pedicellate (Philbert, 1934), tetrangular, domed distally, with two [sometimes one (Vervoort) or three (Philbert)] spines on each edge near apex; internal structure complicated, described by Philbert; ♂ smaller than ♀, ovate, tapered basally, pedicellate (Philbert), tetrangular, with spine on each distal corner; aperture terminal, circular, raised.

MEASUREMENTS. See Table 9.

Table 9 *Diphasia margareta*. Measurements in μm

	SW Scotland (1955.10.15.5)	Isle of Man (1961.11.4.31)	North Sea (1964.8.7.114)
Hydrotheca			
Inner side, length adnate	400–420	450–500	550–560
Inner side, length free	390–410	450–500	520–540
♂ gonotheca			
Length	2100–2500		
Maximum diameter	700–900		
♀ gonotheca			
Length		3700–3800	3500–4000
Maximum diameter		1250–1300	1300

VARIATION. See Description.

REPRODUCTIVE SEASON. Fertile material recorded June–September in NW France (Teissier, 1965, as *D. pinaster*).

DISTRIBUTION. Recorded throughout the present area, but commonest in the south. Published and other records (mostly as *D. pinaster*) additional to the type localities include: 'most of the British Isles' (Hincks, 1868), Isle of Man (Bruce *et al.*, 1963), Clyde Sea (Ritchie, 1911; Vervoort, 1942), Strangford Lough, Northern Ireland (Williams, 1954), E & SW Eire (Stephens, 1905) S Devon (Marine Biological Association, 1957), Durham coast (Norman, 1905), Roscoff but no further East (Tessier, 1965), N Denmark, Kattegat & Norway S of Bergen (Kramp, 1935), strandline at Reculver, north Kent, 1970 (original).

HABITAT. Recorded (as *D. pinaster*) from depths greater than 75 m in W English Channel (Marine Biological Association, 1957; Teissier, 1965), down to 900 m in the Azores (Allman, 1888). These and other records indicate that the species is characteristically found in waters deeper than *c.* 75 m. Association with '*Smittina*' (Bryozoa) community noted by Teissier.

REMARKS. Nomenclature of the present species is discussed on pages 265, 267 and 269. *Diphasia elegans* Sars, 1874, is here considered conspecific.

Diphasia nigra (Pallas, 1766)
(Fig. 12)

Sertularia nigra Pallas, 1766 : 135–136; Johnston, 1838 : 128–130, text-fig. 13 [but not text-fig. 15, = holotype of *S. fusca* Johnston, 1847 (see Remarks under *Salacia articulata*, p. 279)]; Johnston, 1847 : 68–69, text-fig. 10, pl. 12, figs 1–2; Landsborough, 1852 : 126–127.

? *Sertularia pinnata* Pallas, 1766 : 136–137 (binominal for Baster, 1762 : pl. 1, figs 6a–b; ? = *S. cupressina* Linnaeus, 1758; see Remarks).

Sertularia pectinata Lamarck, 1816 : 116; Lamouroux, 1816 : 187 (see Remarks).

Sertularia pinnata: Johnston, 1847 : 69–70, pl. 12, figs 3–4 (syn. *S. fuscescens:* Turton, 1802); Landsborough, 1852 : 127 [non *Sertularia pinnata* Linnaeus, 1758 : 813, and Ellis & Solander, 1786 : 46–47 (= *Kirchenpaueria pinnata*, F. Plumulariidae; see Remarks); Templeton, 1836 : 468 (= *Sertularella gayi;* see p. 287)].

Diphasia pinnata: Hincks, 1868 : 255–257, pl. 52 (syn. *Sertularia nigra* Pallas); Vervoort, 1946 : 232–234, fig. 100 [syn. *S. nigra* Pallas, 1766; *Nigellastrum nigrum* Oken, 1815; *S. fuscescens* Linnaeus, 1791; *S. pectinata* Lamarck, 1816 (here referred to *Diphasia pinastrum* Cuvier, 1830; see p. 267)].

Diphasia nigra: Millard, 1975 : 261.

non *Diphasia pectinata:* Vervoort, 1959 : 255–256, figs 23–24 (= *D. margareta;* see Remarks).

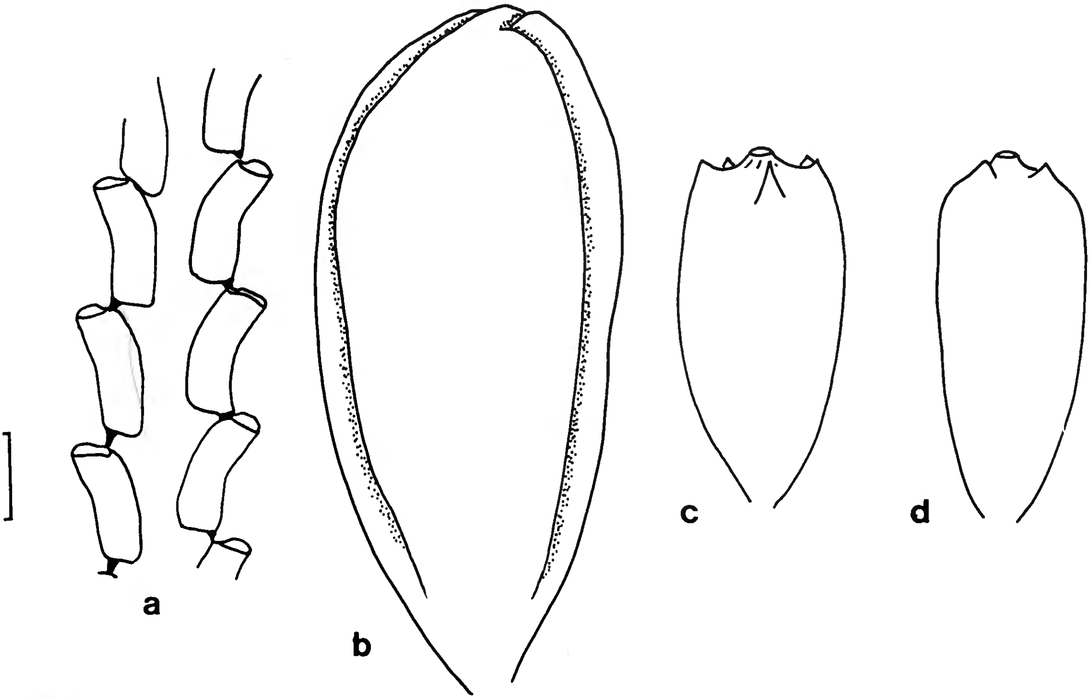


Fig. 12 *Diphasia nigra*. (a–b) part of hydrocladium and ♀ gonotheca, Bay of Biscay (1961.11.4.9); (c–d) two adjacent ♂ gonothecae with 5 and 2 terminal cusps, uncertain locality (1899.7.1.6344); scale (a–d) = 500 μm.

TYPE LOCALITY AND MATERIAL. Pallas based his description of *Sertularia nigra* on material from the 'Indian or American Oceans' growing on '*Mytilus margaritiferis*'[7] shells which he had seen in 'Belgian Museums', and some material of his own collected from the Lizard Peninsula, Cornwall, England. The type locality is here restricted to the Lizard Peninsula. None of the type material was located (see also Remarks).

TYPE MATERIAL OF OTHER NOMINAL SPECIES EXAMINED. *Sertularia pectinata* Lamarck, 1816 : 116; 'l'Océan des Grandes-Indes' [Indian Ocean]; collected by P. Sonnerat, presented to Lamarck; several fragments on microslide, Mus. nat. d'Hist. Nat., Paris, collection; mentioned, Billard, 1907 : 218.

NON-TYPE MATERIAL EXAMINED. Only measured, illustrated or otherwise mentioned material is listed. Guernsey, 1906, infertile colony in spirit, ex coll. A. M. Norman, 1912.12.21.117 (see comment under Distribution). Bay of Biscay, 48° 24′ N, 6° 33′ W, 150 m, Aug 1906, part of ♀ colony on microslide, coll. E. T. Browne, 1961.11.4.9 (Fig. 12a–b; Table 10); mentioned, Browne, 1907 : 16–17). 'Sydney, Australia', fragments of ♂ hydrocladia on microslide, ex coll. G. Busk, det. T. Hincks, 1899.7.1.6344 (Fig. 12c–d; Table 10; mentioned, Bale, 1884 : 99[8]).

DESCRIPTION. Colony large, up to *c.* 200 mm, robust, erect, rigidly pinnate, main stem thicker than the alternate side-branches; said (Hincks, 1868; Browne, 1907) to be deep red (carmine) to pink in life, preserved colonies being dark brown to black. Hydrothecae tubular, adnate, gently outcurved; rim even, operculum circular, attached on inner side; alternate, vertically contiguous or nearly so. ♂ gonotheca ovate, tapering basally to very short pedicel, terminal aperture on short cone surrounded by usually 4 (2–5 in present material) blunt spines. ♀ larger than ♂, obpyriform, without pedicel, with 4 longitudinal grooves meeting distally; internal structure described by Philbert (1934).

MEASUREMENTS. See Table 10.

Table 10 *Diphasia nigra.* Measurements in μm

	Locality uncertain (see material list; 1899.7.1.6344)	Bay of Biscay (1961.11.4.9)
Hydrotheca		
Length	600	480–530
Diameter	180	140–155
♂ gonotheca		
Length	1800	
Maximum diameter	850	
♀ gonotheca		
Length		4400
Maximum diameter		1700

REPRODUCTIVE SEASON. Fertile material recorded April–May off SW England (Marine Biological Association, 1957), June–September off NW France (Teissier, 1965), August in Bay of Biscay (Browne, 1907).

DISTRIBUTION. A warm water Atlantic species recorded in the present area only from SW England (Pallas, 1766; Hincks, 1868; Marine Biological Association, 1957) and NW France (Teissier, 1965). It has also been reported from the Glenan Isles, just south of the present faunal boundary (Fey, 1969). The BM(NH) specimen labelled 'Guernsey, 1906' lacks tissues so it might have drifted there, and the species was not recorded from the Channel Isles in the faunal survey of Vervoort (1949). Although recorded from the Netherlands in the eighteenth and nineteenth centuries, authentic material is apparently lacking (Vervoort, 1946) and the species has not been reported there this century.

HABITAT. Recorded from *c.* 80 m depth in the western English Channel (Marine Biological Association, 1957; Teissier, 1965); reported on bivalve shells (Pallas, 1766) and presumably occurs on other, similar substrates.

REMARKS. The present species has been known as *Diphasia pinnata* for the past 100 years[9] but it seems that this combination is inadmissible. The two nominal species *Sertularia pinnata* Pallas, 1766, and *S. nigra* Pallas, 1766, have been regarded conspecific by several authors[10] (e.g. Hincks, 1868; Bedot, 1901; Vervoort, 1946). Hincks, who was the first reviser, adopted the specific name *pinnata* and this has been widely followed; but *Sertularia pinnata* Pallas, 1766, is actually a junior primary homonym of *Sertularia pinnata* Linnaeus, 1758,[11] a plumularid currently referred to the genus *Kirchenpaueria* Jickeli, 1883 (for example by Rees & Thursfield, 1965). Thus the name *pinnata* Pallas, 1766, should not be used, leaving the once more widely used *nigra* available for the present species. In fact it is doubtful whether the two Pallas species are conspecific. *S. pinnata* Pallas was based on two illustrations of Baster (1762 : pl. 1, figs 6a–b). One illustration, of a pinnate colony, shows downward-curving branches unlike the straight, rigid branches of the present species; while the other shows gonothecae with two latero-distal horns, again unlike those of the present species. Although Vervoort (1946 : 233) likened Baster's illustrations to *Sertularia cupressina* Linnaeus, 1758, it seems that only the illustrated gonothecae resemble that species and that the illustrations as a whole should best be regarded as indeterminate. *S. pinnata* Pallas, 1766, based on them, should therefore also be regarded as indeterminate. The alternative, of referring the illustrations and hence *S. pinnata* Pallas to *S. cupressina* Linnaeus, has in fact no nomenclatural consequences since *S. pinnata* Pallas is in any case a junior homonym (see above). *S. nigra* Pallas, 1766, was not originally illustrated, but as the original diagnosis mentions sub-opposite hydrothecae and large, quadrangular gonothecae it seems that Hincks (1868) and other authors correctly identified their concepts of the present species with *S. nigra*, albeit employing the name *S. pinnata*.

The name *Sertularia pectinata* Lamarck, 1816, was applied by Bedot (1901 : 503) and Vervoort (1959 : 255–256) to the species here called *Diphasia margareta* (p. 263). However, as noted by Billard (1907 : 218), the holotype of *S. pectinata* Larmarck, re-examined here, is referrable to the present species (see also Remarks under *D. pinastrum*, p. 269). In addition to describing *S. pectinata* from type material Lamarck included *S. pinaster* Ellis & Solander, 1786, in its synonymy; but *S. pinaster* sensu Ellis & Solander seems to have been another species (here called *D. pinastrum*, p. 267). Lamarck evidently did not think that his new material and Ellis & Solander's account were of different species, but he seems to have been mistaken.

The homonym *Sertularia pectinata* Lamouroux, 1816 : 187, was considered to have been applied to indeterminate material by Bedot (1901 : 503); but Lamouroux *et al.* (1824 : 680) had already regarded it a synonym of the *S. pectinata* of Lamarck, 1816, and their view is followed here.

Diphasia pinastrum (Cuvier, 1830)

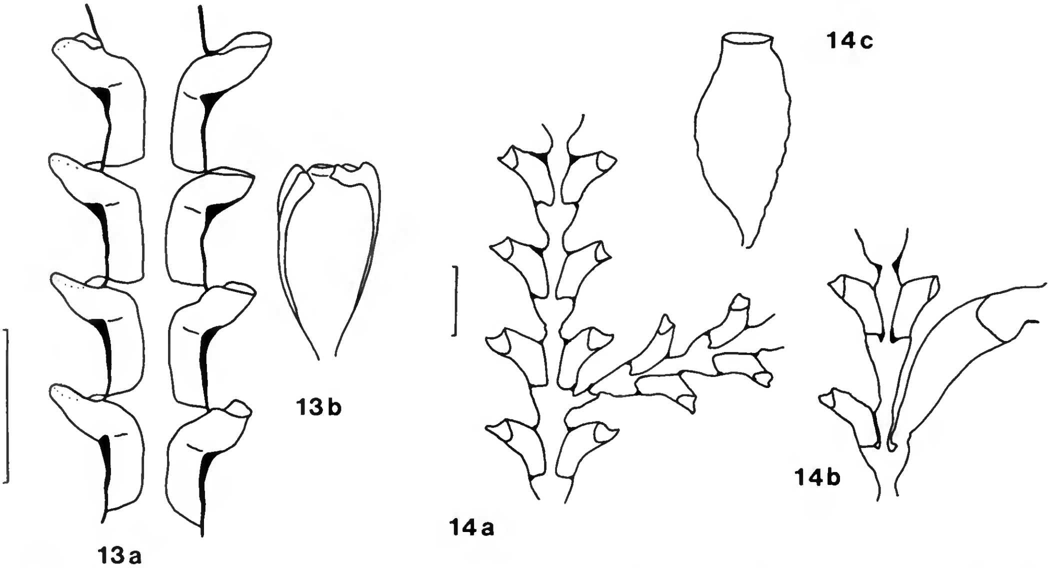
(Fig. 13)

Sertularia pinaster Ellis & Solander, 1786 : 55–56, pl. 6, figs B, b (non *S. pinaster* Lepechin, 1783; see Remarks).
Sertularia pinastrum Cuvier, 1830 : 301 (emend. pro *S. pinaster* Ellis & Solander; see Remarks).
Sertularia alata Hincks, 1855 : 127–128, pl. 2.
Diphasia alata: Hincks, 1868 : 258, pl. 48, figs 2, 2a–b; Browne, 1907 : 31; Broch, 1918 : 144; Kramp, 1935 : 183–184, fig. 76a; Rees & Thursfield, 1965 : 119.
non *Diphasia pinaster:* Hincks, 1868 : 252–253, pl. 50, fig. 1; Kramp, 1935 : 182–183, fig. 76b; [= *D. margareta* (Hassall, 1841); see Remarks].
non *Diphasia pectinata:* Vervoort, 1959 : 255–256, figs 23–24 [= *D. margareta* (Hassall, 1841); see Remarks].

TYPE LOCALITY AND MATERIAL. The type material of *Sertularia pinaster* Ellis & Solander, 1786, is almost certainly no longer extant (Cornelius, 1975*a* : 267, footnote). No locality was given in the original description. The type material of *Sertularia alata* Hincks, 1855, also seems lost. It comprised a fertile colony collected by George Barlee and 'Miss Cutler' in the Shetlands, and sent to Hincks by Miss Cutler. Two infertile colonies of this species collected in the Shetlands by Barlee and sent to A. M. Norman are now in the BM(NH) herbarium collection of Hydroida (reg. nos

1915.4.1.12) and it seems appropriate to select this material as neotype of *S. alata*. Unfortunately there is no evidence that the material was seen by Hincks. No neotype material of *Sertularia pinaster* Ellis & Solander is designated here.

Other material examined. The BM(NH) collections include examples of this distinctive species from a variety of localities within the present area and only the illustrated and measured material is listed here. Firth of Lorn, Argyll, Scotland, 120–140 m, part of infertile colony on microslide, coll. J. Ritchie, 1888.6.9.14 (mentioned, Rees & Thursfield, 1965 : 119, as *D. alata*) (Fig. 13a; Table 11). Bay of Biscay, 47° 48′ N, 7° 25–26′ W, 220 m, Aug 1906, several colonies, some fertile, on microslides, coll. E. T. Browne, 1961.11.14.16, 20 (mentioned, Browne, 1907 : 31, as *S. alata*) (Fig. 13b; Table 11).



Figs 13–14. Fig. 13 *Diphasia pinastrum*. (a) hydrocladium, W Scotland (1888.6.9.14); (b) ♀ gonotheca, Bay of Biscay (1961.11.14.20); scale (a–b) = 500 μm. **Fig. 14** *Dynamena pumila*. (a–b) hydrocladia, one showing unusual hydrotheca, SW England (1975.10.15.3); (c) gonotheca, SE England (1967.10.24.9); scale (a–c) = 500 μm.

Description. Colony robust, erect, usually simply and regularly pinnate but second order branching frequent; main stem thicker than branches. Stem and branches straight, usually monosiphonic but base of stem sometimes (Browne, 1907; Broch, 1918) polysiphonic. Branches alternate, like main stem bearing opposite to sub-opposite hydrothecae in two lateral rows. Hydrotheca long, S-shaped, ⅔ adnate, distal third sharply out-turned at *c.* 90° with immediate *c.* 45° upward flexure (Fig. 13); internal perisarc thickening at point of 90° flexure, conspicuous in optical section; aperture broad, rim even to sinuous, operculum 1-flapped, attached on inner side. Hydranth undescribed; one BM(NH) specimen had 18 tentacles (1961.11.4.17). Gonotheca ♂ = ♀ (Browne, 1907), roughly cylindrical but quadrangular in section, tapering basally; aperture terminal, raised, surrounded by 4 perisarc ridges ending centrally in rounded points.

Measurements. See Table 11.

Reproductive season. Fertile material recorded April–July in NW France (Teissier, 1965); June off SW England (Marine Biological Association, 1957).

Distribution. Recorded from eastern Atlantic waters from Bergen, Norway (Broch, 1918), to the Azores (Rees & White, 1966). The species might thus be expected to occur in suitable conditions throughout the present area, but published records are from scattered localities and the BM(NH) collections add no new information. All records are listed: Shetlands, Hebrides, Cornwall and S

Table 11 *Diphasia pinastrum.* Measurements in μm

	Bay of Biscay (1961.11.4.16)	W Scotland (1888.6.9.14)
Hydrotheca		
Inner side, length adnate	380–430	390–410
Inner side, length free	140–170	140–170
Gonotheca (♂ = ♀)		
♀† Length	620–670	
Maximum diameter	300–340	

† Contained ova.

Devon (Hincks, 1868; Marine Biological Association, 1957); N of Shetlands (61° 36′ N, 0° 44′ W) and Firth of Lorn, Argyll (Rees & Thursfield, 1965); Co Cork, Eire (Stephens, 1905); NW France (Teissier, 1965). Probably only once recorded from Denmark (Kramp, 1935) and absent from fauna lists relating to Oslo Fjord and the Baltic (Stechow, 1927; Broch, 1928; Naumov, 1969; Christiansen, 1972).

HABITAT. Waters deeper than 80 m off NW France (Teissier, 1965); 7–60 m off S Devon (Marine Biological Association, 1957); 120–140 m in W Scotland (Rees & Thursfield, 1965). Recorded 'on worm tubes' by Browne (1907) but substrate otherwise apparently not noted.

REMARKS. The similarity in colony habit between this species and that here called *Diphasia margareta* has caused some nomenclatural confusion. The present species was first given a binominal – *Sertularia pinaster* – by Ellis & Solander (1786). However, Vervoort (1959) has pointed out that this name is not available as it is a junior primary homonym of *Sertularia pinaster* Lepechin, 1783, a species currently referred to the genus *Selaginopsis* Allman, 1876. The illustrations provided by Ellis & Solander under *S. pinaster* clearly show their material to have been the species widely known as *Diphasia alata* Hincks, 1855,[12] and not as suggested by Vervoort (1959) that usually called *Diphasia pinaster* (e.g. *sensu* Hincks, 1868). The earliest available name for '*D. pinaster*' *sensu* Hincks seems to be *Sertularia margareta* Hassall, 1841; and that for the present species *Sertularia pinastrum* Cuvier, 1830. (See also Remarks under *D. nigra*, p. 267.)

Diphasia rosacea (Linnaeus, 1758)

(Fig. 8)

Corallina pumila pennata, denticulis terris . . . Ellis, 1755 : 8–9, pl. 4, fig. A, but not fig. C.
Sertularia rosacea Linnaeus, 1758 : 807.
Sertularia nigellastrum Pallas, 1766 : 129–130 (nom. nov. pro *S. rosacea* Linnaeus, 1758).
Diphasia rosacea: Hincks, 1868 : 245–247, pl. 48, figs 1, 1a–c; Broch, 1918 : 112–113; Kramp, 1935 : 182, fig. 74b; Vervoort, 1946 : 230–232, figs 98–99; Vervoort, 1959 : 257–258, fig. 25; Leloup, 1952 : 181–182, fig. 105; Naumov, 1960 : 332–333, figs 221–222; Rees & Thursfield, 1965 : 122; Naumov, 1969 : 358–359, figs 221–222.

TYPE MATERIAL AND LOCALITY. Linnaeus based his designation of this species on fig. A of Ellis' plate (not on fig. C, which in fact appears to represent *D. attenuata* (Hincks, 1866) and which was not given a binominal by Linnaeus). As with some other hydroids in the Linnean genus *Sertularia* it seems Linnaeus based his diagnosis solely on Ellis' illustration and not on material (see p. 251). Linnaeus provided a diagnosis but no description; and cited only Ellis' work. Thus the illustrated specimen, a female colony, can be regarded as holotype. Like other Ellis hydroid material it almost certainly no longer exists (Cornelius, 1975*a* : 267). Ellis' description was based on material from Brighton, Sussex, England, to which the type locality can be restricted.

MATERIAL EXAMINED. Only measured or illustrated material is listed. Vattlestraumen, Espegrend, nr Bergen, Norway, 15–25 m, 13 Apr 1962, ♀ hydrocaulus on microslide, coll. W. J. Rees, 1962.10.7.16 (Table 12). Millport, I of Cumbrae, Bute, Scotland, May 1962, ♀ colony on microslide, coll. W. J. Rees, 1962.6.19.15 (Table 12). Off Washbourne, W Cumbrae, Bute, 15–30 m, 18 May 1955, ♀ hydrocladia on microslide, coll. W. J. Rees, 1956.1.1.17 (Figs 8a–b). Off Wexford, Co Wexford, Eire, 80 m, 26 May 1901, ♂ and ♀ hydrocladia on same microslide (with one infertile hydrocladium of *D. attenuata*), coll. Irish Fisheries Board, via E. T. Browne, 1967.6.15.30 (Table 12).

DESCRIPTION. Colony erect but bending, up to 50 mm, delicate, loosely pinnate, some second order branching, branches and main stem uniform in width; branches often lacking hydrothecae proximally. Hydrothecae opposite to sub-opposite, tubular, $\frac{1}{2}$–$\frac{2}{3}$ adnate, gradually out-turned; aperture circular, rim even with slight notch on inner side; operculum circular, folded longitudinally, attached on inner side. ♂ gonotheca tubular, tapered basally, with 6–8 longitudinal ridges ending distally in blunt spines surrounding a conical process bearing the apical aperture. ♀ gonotheca tubular, tapering basally, with 8 longitudinal ridges ending distally in long inward-curving spines surrounding the central aperture and forming a brood-chamber; an opposite pair of the spines usually longer than the remaining six, and notched on the outer edge.

MEASUREMENTS. See Table 12.

Table 12 *Diphasia rosacea*. Measurements in μm

	SE Eire (1967.6.15.30)	SW Scotland (1962.6.19.15)	W Norway (1962.10.7.16)
Hydrotheca			
Inner side, length adnate	300–390	360–390	320–370
Inner side, length free	350–390	350–400	240–300
Maximum diameter	160–180	130–150	120–140
♂ gonotheca			
Length	1300–1700		
Maximum diameter	450–500		
♀ gonotheca			
Length (to ends of spines)	1800–1900	2000–2300	1800† (1 only)
Maximum diameter (excluding spines)	600–700	750–900	700

† Only one fully developed gonotheca on specimen.

VARIATION. See comments under *D. attenuata* (p. 256).

REPRODUCTIVE SEASON. Fertile material recorded March–April in SW England (Marine Biological Association, 1957), April–June and September in NW France (Teissier, 1965). All fertile BM(NH) material from W Europe was collected in April and May.

DISTRIBUTION. Found throughout the present area, also occurring north to Iceland and south at least to 9° N on the African coast (Vervoort, 1959).

HABITAT. Said to be commonest in the *Laminaria* zone of the sublittoral (Broch, 1918) and in depths shallower than 60 m (Kramp, 1935; Teissier, 1965), although some of the present material came from 80 m depth. The species has been found intertidally in places of fast water movement (Lewis, 1964).

REMARKS. Although this species has been widely regarded as distinctive, the differences from *Diphasia attenuata* are not great (see p. 257 for discussion and also Table 5).

Dynamena pumila (Linnaeus, 1758)
(Fig. 14)

Corallina pumila repens, minus ramosa . . . Ray, 1724 : 37; Ellis, 1755 : 9–10, pl. 5, figs A, a.
Sertularia pumila Linnaeus, 1758 : 807–808; Hincks, 1868 : 260–262, pl. 53, fig. 1; Winther, 1879 : 303–305, pl. 6, figs 1–4, 21–22 (? syn. *S. gracilis* Hassall, 1848, which is here referred to *S. distans* Lamouroux, 1816; see p. 299); Pennington, 1885 : 112–113, pl. 7, fig. 1.
Sertularia bursaria Linnaeus, 1758 : 814–815.
Cellularia bursaria: Ellis, 1768 : 434, pl. 19, fig. 12.
Dynamena pumila: Lamouroux, 1812 : 184; Lamouroux, 1816 : 179; Broch, 1918 : 115–116; Kramp, 1935 : 187–188, fig. 81A (syn. *Sertularia gracilis* auct.); Vervoort, 1946 : 252–254, fig. 110 (syn. *Sertularia pupa* Maratti, 1776; *S. thuia:* Fabricius, 1780; *Nigellastrum pumilum:* Oken, 1815; *Dynamena fabricii* Agassiz, 1860); Naumov, 1960 : 329–330, fig. 219; Naumov, 1969 : 356–357, fig. 219.
Dynamena distans Lamouroux, 1816 : 180, pl. 5, figs 1a, B.
non *Sertularia distans* Lamouroux, 1816 : 191; (see p. 299).

TYPE MATERIAL AND LOCALITY. Linnaeus (1758) gave the type locality as 'in Oceano', although citing the descriptions of both Ray (who gave the distribution as 'British Isles') and Ellis ('shores of Sheerness, Kent' and 'Brighton, Sussex'). Linnaeus' citation of Ellis' account lists only one of Ellis' figures, namely plate 5, fig. A (not fig. a). The illustrated specimen can be identified as the holotype.[13] It was said by Ellis to have been collected at Brighton, to which the type locality can accordingly be restricted. 'Brighton' is interpreted in the sense of the area currently administered by Brighton Borough Council. The area comprises the coast from Brighton town to Peacehaven inclusive. Suitable natural habitats for *D. pumila* do not at present exist on the coast of Brighton town, which is a more restricted area. The holotype specimen is almost certainly lost (Cornelius, 1975*a*) and the following neotype series is substituted: Rottingdean, Sussex, England, mean low tide level of neap tides, 24 June 1975, numerous fertile colonies on *Fucus serratus* L., in spirit, coll. P. F. S. Cornelius & J. Garfath, 1975.9.11.1.

OTHER MATERIAL EXAMINED. This distinctive species is well represented in the BM(NH) collections and only specimens referred to in the text or illustrated are listed here. Gåso Ranna, Gullmarsfjord, W Sweden, 27 Aug 1962, spirit material + 1 microslide preparation, coll. W. J. Rees, 1962.11.8.19. Caol Scotnish, Loch Sween, Argyll, Scotland, 30 May 1962, 1 m, fragment of colony on microslide, coll. W. J. Rees, 1962.6.19.22 (Table 13). Southern end of Lizard Peninsula, Cornwall, ELWST, 6 Oct 1975, fragment on microslide, coll. P. F. S. Cornelius, 1975.10.15.3 (Fig. 14a–b). Jennycliff Bay, Plymouth, Devon, Aug 1963, fragment of colony on microslide, coll. R. C. Vernon, 1967.10.24.14 (Table 13). Hastings, Sussex, 26 Jun 1963, coll. R. C. Vernon, 1967.10.24.9 (Fig. 14c; Table 13).

DESCRIPTION. Creeping stolon from which arise erect stiff monosiphonic hydrocauli up to *c.* 75 mm (Lewis, 1964), usually 50 mm or less; unbranched to sparsely and irregularly branched, sometimes loosely pinnate. Hydrothecae in opposite to sub-opposite pairs, with a nodal constriction between every one, two or three pairs; tubular, curved outwards, $\frac{2}{3}$ adnate; aperture 2-cusped, operculum fragile, 2-flapped, deciduous. Hydranth with 18–20 tentacles, said (Broch, 1918) to lack diverticulum. Gonotheca ♂ = ♀, pedicellate, ovoid, wall sometimes slightly rugose; aperture wide, often on short neck (development of gonophores described by Teissier, 1923); ♀ with *c.* 8 ova, retained in acrocyst; ♂ intracapsular.

VARIATIONS. Preliminary measurements were kindly made by Miss J. Garfath of intertidal material collected by the author from the very exposed and extremely sheltered sides of the peninsula south of Milford Haven, Dyfed (Pembrokeshire), Wales. The more sheltered population had hydrothecae approximately 30% longer and 10% broader than those on the more exposed shore; and exposed shore specimens had thicker perisarc than those from the sheltered shore (unpublished observations). Features of systematic importance were apparently not affected, however.

Broch (1918) found lower shore specimens to be more branched than upper shore ones while Johnston (1847) recorded that sublittoral colonies were more 'delicate' in all structures than those growing intertidally. It is possible, however, that Johnston based his remark on misidentified specimens of *Sertularia distans* Lamouroux.

MEASUREMENTS. See Table 13.

Table 13 *Dynamena pumila*. Measurements in μm

	SW England (1967.10.24.14)	SE England (1967.10.24.9)	W Scotland (1962.6.19.22)
Hydrotheca			
Inner side, length adnate	270–310	300–320	320–360
Inner side, length free	190–210	210–240	240–270
Maximum diameter	170–190	190–200	180–210
Internode			
Length (one pair of hydrothecae)	600–720	870–920	750–780
Gonotheca (♂ = ♀)			
Length, including pedicel		♂ 1400–1500	♀ 1200–1400
Maximum diameter		570–600	620–670
Diameter of aperture		290–300	350–400

On the date of collection of the fertile neotype material of *D. pumila* colonies of the same species at higher shore levels were infertile and smaller.

An unusual hydrotheca is shown in Fig. 14b.

REPRODUCTIVE SEASON. Fertile material recorded March–June in the Channel Isles (Vervoort, 1949), April–August in NW France (Teissier, 1965), May–June in the Kattegat (Rasmussen, 1973); May–September in N America (Agassiz, in Hincks, 1868).

DISTRIBUTION. Usually common on suitable shores and scarce in the sublittoral throughout the area, including the Baltic (Broch, 1918; Stechow, 1923). The species seems currently uncommon on many shores in Kent, England, perhaps in response to local pollution.

HABITAT. Characteristically intertidal ('middle and lower shore', Barrett & Yonge, 1958) but recorded also from shallow offshore waters (5 m, NW France, Fey, 1969; 20–30 m, W Sweden, present material; 75 m, Oslo Fjord, Christiansen, 1972). A record from 270 m (Naumov, 1969, apparently repeated in Christiansen, 1972) needs confirmation. The species occurs in brackish waters (Broch, 1918; Kramp, 1929), for example penetrating far into the Baltic (Stechow, 1923) and to the heads of both Scandinavian fjords (Broch, 1918) and Scottish sea lochs. Typically it occurs on fucoid and other algae, but particularly on shores exposed to strong wave action it attaches directly to rock. My own experience of *D. pumila* on shores in Scotland and Wales indicates that although present on shores of a variety of exposure to wave action the species nevertheless has a somewhat narrow tolerance range of water movement in terms of micro-environment. Thus, on very sheltered shores *D. pumila* usually occurs only on the middle to upper parts of fronds of fucoid algae, particularly *Ascophyllum nodosum* (L.) Le Jol., often the dominant alga on such shores; and then only in situations of maximal tidal flow, such as on the tops or sides of large rocks. On less sheltered shores *D. pumila* occurs lower down the algal fronds, evidently thus avoiding much of the wave action since it is there surrounded by the relatively huge algae – typically *Fucus serratus* L. on such shores. On shores sufficiently exposed that *F. serratus* is no longer entirely dominant on the mid-shore, but is replaced there in exposed micro-positions by barnacles, *D. pumila* occurs on the algae only near the bases of the stipes and is found also, still lower, on the rock itself. On very exposed shores – or parts of shores – where *F. serratus* is absent *D. pumila* occurs in still more sheltered micro-habitats, in crevices and beneath overhangs. Thus it seems that on sheltered shores *D. pumila* is found in micro-habitats having strong water movement, and on more exposed shores in situations where water-movement is least. This habitat 'preference' seems to be reflected also in the micro-distribution of the species on shores where a variety of exposure exists within a small area. More detailed study might show that the micro-distribution of this species can be correlated with biological wave-exposure scales of the kind postulated by Lewis (1964) and others. However, at present the influence of plankton- and silt-content of the water, and also of salinity, on the survival and growth of this species cannot be assessed. No doubt these and other factors than wave-exposure influence its micro-distribution; but at present it seems the correlation with wave-exposure is high.

Detailed habitat notes on the species in the Roscoff, NW France, area were provided by Prenant & Teissier (1924). Fowell (1944) recorded *D. pumila* as epizoic on the red coralline alga, *Corallina officinalis* L.

REMARKS. There seems little doubt that *Sertularia bursaria* Linnaeus, 1758, based on an earlier illustration of Ellis (1755) and later illustrated again by Ellis (1768, as *Cellularia*), is the present species. Bedot (1901 : 500) considered *bursaria* not to be a hydroid; but Ellis' illustrations leave no doubt. The specific name *pumila* Linnaeus, 1758, with which *bursaria* is here made a subjective synonym, is retained for the present species under the first reviser principle.

The nominal species *Dynamena distans* Lamouroux, 1816 : 180, appears not to differ from *D. pumila* (Linnaeus, 1758) and the two are here regarded conspecific. The first-mentioned should not be confused with *Sertularia distans* Lamouroux, 1816 : 191, which has been widely regarded as distinct (e.g. p. 296).

It was suggested by Winther (1879) and Kramp (1935) that *Sertularia gracilis* Hassall, 1848, and the present species are conspecific but following many authors (see p. 299) *S. gracilis* is here referred to *S. distans*.

A study of vegetative growth in *D. pumila* was made by Beloussov (1973).

Hydrallmania falcata (Linnaeus, 1758)

(Figs 15–16)

Corallina muscosa pennata ramulis & capillamentis falcatis. Ellis, 1755 : 12, pl. 7, figs A, a.
Sertularia falcata Linnaeus, 1758 : 810; Pallas, 1766 : 144–146 (syn. *S. stipulata* Linnaeus, 1758); Linnaeus, 1767 : 1309 (syn. *S. stipulata* Linnaeus, 1758).
Sertularia stipulata Linnaeus, 1758 : 813.
Serialaria falcata: Westendorp, 1843 : 34 (see Remarks).
Hydrallmania falcata: Hincks, 1868 : 273–275, pl. 58; Stechow, 1925 : 488, fig. 40; Vervoort, 1946 : 255–258, figs 111–113; Naumov, 1960 : 402–403, fig. 294; Naumov, 1969 : 433–435, fig. 294.
Further synonymy of this species was provided by Vervoort (1946).

TYPE MATERIAL AND LOCALITY. The two fragments preserved in the collections of the Linnean Society of London (Savage, 1945; numbered 1298.10) are both infertile. Since Linnaeus' original designation includes gonothecal characters (‘*calycibus ovatis*’) it seems unlikely that it was made from these fragments. As with several other Linnean hydroid species it seems probable that the designation was made from the illustration of Ellis (1755 : pl. 7, fig. A) which Linnaeus cited and which includes gonothecae. The illustrated specimen can, therefore, be regarded as holotype. It probably no longer exists (see notes under *Abietinaria abietina*, p. 251).

Ellis stated that the species was – as now – common off many British shores, mentioning by name only the coast at Sheerness, Isle of Sheppey, Kent. The type locality can thus be restricted to the coastal waters of N Kent.

MATERIAL EXAMINED. The BM(NH) collections include western European material from a wide variety of localities. The areas of origin and registered numbers of colonies having variant branches, shown in Fig. 16, are as follows: English Channel (1941.3.20.447; 1946.12.3.1; 1947.9.4.18; 1948.5.12.353; 1949.10.20.26); Irish coasts (1967.6.15.26, 43, 59, 79, 91, 107 & 151); W Scotland (1888.3.19.2) and Norway (1912.12.21.225; 1959.6.11.35; 1962.10.7.56; 1966.1.4.5). Details of the figured or measured specimens are as follows: Rongesund, Espegrend, nr Bergen, Norway, 25 m, 9 Apr 1962, colony in spirit + 1 microslide preparation, coll. W. J. Rees, 1962.10.7.56 (Fig. 15b). Port Erin, Isle of Man, 5 Oct 1894, two fertile hydrocladia on microslide, coll. E. T. Browne, 1961.11.4.61 (Fig. 15c). Kirkwall, Orkneys, Scotland, 2 Jul 1898, part of colony on microslide, coll. E. T. Browne, 1961.11.4.64 (Table 14). ‘SW England’, part of colony on microslide, coll. E. T. Browne, 1961.11.4.65 (Table 14). Reculver, Kent, strandline, Jul 1970, part of colony on microslide, coll. P. F. S. Cornelius, 1976.6.2.1 (Fig. 15a).

DESCRIPTION. Colony erect, tall, up to 640 mm recorded (Vervoort, 1946); main axis monosiphonic, in characteristic open spiral of pitch 10–30 mm, with lateral pinnate hydrocauli. Hydrothecae usually on one side of hydrocladia, but inclined alternately left and right; contiguous, in groups of 3–8 separated by nodal constrictions. Hydrothecae roughly tubular, broadening basally; aperture terminal, circular, even-rimmed; operculum circular, attached by inner edge. Some young colonies with alternate, biseriate hydrothecae (Fig. 15b) recalling arrangement in *Abietinaria* (see Variations, below). Hydranth 'minute and pure white' (Hincks, 1868), otherwise apparently undescribed. Gonotheca ♂ = ♀, ovoid to obpyriform, barely pedicellate; aperture terminal, broad, circular, sometimes (Naumov, 1969) with 4 internal 'denticles' (? = desmocytes). A colony 300 mm long had *c.* 4200 gonothecae (Vervoort, 1946).

MEASUREMENTS. See Table 14.

Table 14 *Hydrallmania falcata.* Measurements in μm

	Holland (Vervoort, 1946)	Russian seas (Naumov, 1969)	Orkneys (1964.11.4.64)	SW England (1961.11.4.65)
Hydrotheca				
Length	400–600	400–600	380–500	380–520
Maximum width	130–150	130–150	120–160	150–180
Diameter of aperture		80–100	60–80	80–100
Gonotheca				
Length	1500	1000–1500		1200–1700
Maximum width		400–600		550–700
Diameter of aperture	250	230–300		210–240

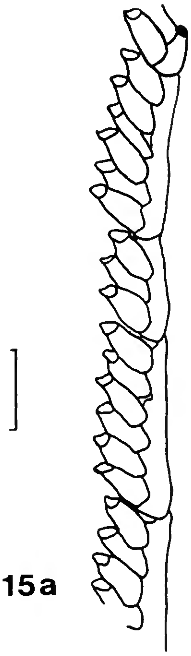
VARIATIONS. Young colonies and occasional branches of mature colonies have biseriate alternate hydrothecae, with two-cusped, not even, hydrothecal rims (Broch, 1918; Stechow, 1925; Vervoort, 1946; Naumov, 1969; Houvenaghel-Crèvecoeur, 1973). Mature colonies with occasional side-branches of this kind appear to occur sporadically within a population, and are not rare (Figs 15b, 16). They do not seem to deserve taxonomic recognition, and no name need be proposed for the variant. Although it resembles *Abietinaria* in many ways a phyletic relation with that genus should not be inferred automatically since the young stage of the rather different *Amphisbetia operculata* similarly resembles *Abietinaria* (see p. 255).

REPRODUCTIVE SEASON. Fertile specimens recorded March–May in NW France (Teissier, 1965), December–April in SW England (Marine Biological Association, 1957).

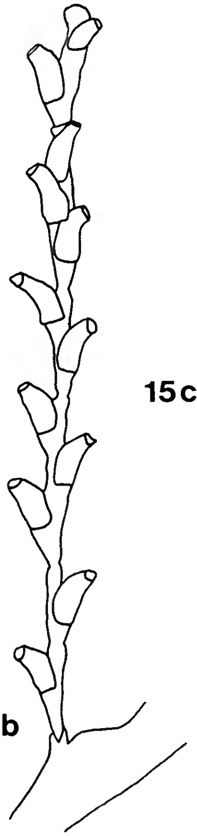
DISTRIBUTION. Common throughout most of the present area in suitable places, being recorded from the Kattegat but not the Baltic (Stechow, 1927; Broch, 1928).

HABITAT. Generally on sandy substrates, 20–100 m depth (Naumov, 1969). Detached colonies frequent on strand-line, sometimes occurring in large quantities.

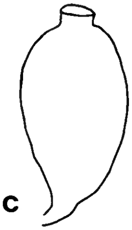
Figs 15–16 *Hydrallmania falcata.* **Fig. 15** (a) part of hydrocladium, lateral view, SE England (1976.6.2.1); (b) hydrocladium of abnormal but regularly observed growth form, W Norway (1962.10.7.56); (c) gonotheca, Isle of Man (1961.11.4.61); scale (a–c) = 500 μm. **Fig. 16** Localities of colonies in the BM(NH) collections with (solid circles) and without (open circles) abnormal hydrocladia. Four specimens having some abnormal hydrocladia had the imprecise locality 'Ireland' and are not represented on the map. See text for details of material (p. 273).



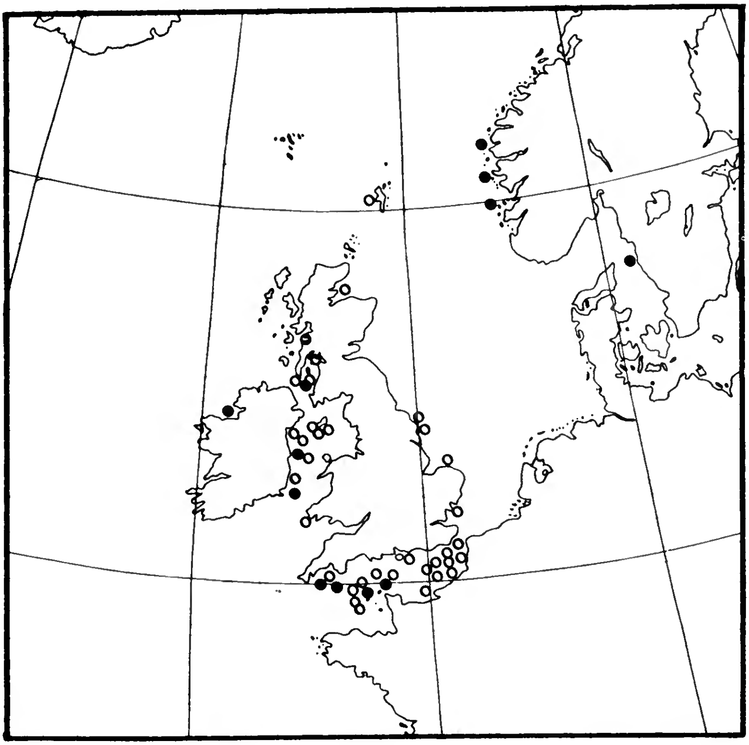
15a



15b



15c



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REMARKS. *H. falcata* is a distinctive and widely recognized species frequently known as the sickle hydroid. A habit photograph was shown by Rees (1966 : ii). The significance of the interesting abnormal hydrocladia is treated under Variations, above. Settlement of the planula and early development has been described by Houvenaghel-Crèvecoeur (1973).

The Linnean species *Sertularia stipulata* was based on the illustration of Ellis (1755 : pl. 38, fig. 5 but not fig. 6) and is undoubtedly the present species. There is almost certainly no extant type material. Pallas (1766) acted as first reviser when using the species name *falcata* in preference to *stipulata*.

The genus *Serialaria* Lamarck, 1816, was introduced to accommodate four bryozoan species and its use for the present species by Westendorp (1843; see synonymy) was wrong. Thus *Serialaria* does not threaten the widely used genus name *Hydrallmania* Hincks, 1868. Bedot (1901) noted another incorrect use of the name *Serialaria* for a hydroid species.

Salacia articulata (Pallas, 1766)

(Fig. 17)

Corallina erecta pennata, denticulis alternis . . . Ellis, 1755 : 11–12, pl. 6, figs A, a.

Sertularia lichenastrum Linnaeus, 1758 : 813 (part); Linnaeus, 1767 : 1313 (part); (see Remarks).

Sertularia articulata Pallas, 1766 : 137 (binominal proposed for Corallina erect pennata . . . Ellis, 1755).

Sertularia lonchitis Ellis & Solander, 1786 : 42 (nom. nov. pro *S. lichenastrum* Linnaeus; see Remarks).

Thuiaria articulata: Fleming, 1828 : 565; Fleming, 1842 : 565; Hincks, 1868 : 277–279, pl. 60 (syn. *Sertularia lonchitis* Ellis & Solander); Naumov, 1960 : 408–410, fig. 296; Naumov, 1969 : 440–441, fig. 296.

Sertularia nigra: Johnston, 1838 : text-fig. 13 only (= holotype of *S. fusca* Johnston, 1847; see Other type material examined).

Sertularia fusca Johnston, 1847 : 70–71, fig. 6 (p. 57), fig. 11 (p. 70); Landsborough,1852 : 127–128; Alder, 1857 : 26–27; Hincks, 1868 : 272–273, pl. 50, fig. 2 (syn. *S. nigra:* Jameson; Johnston; Fleming; but not Pallas).

Thuiaria ellisii Busk, 1851 : 119 (see p. 280).

Selaginopsis fusca: Norman, 1878 : 191; Rees & Thursfield, 1965 : 152; (non *S. fusca:* Allman, 1876, = *S. allmani* Norman, 1878, by designation by Norman).

Thuiaria lonchitis: Nutting, 1904 : 66–67, pl. 9, figs 5–8; Vervoort, 1946 : 262–263, fig. 115b (syn. *T. kolaensis* Jaderholm, 1907); Calder, 1970 : 1538, pl. 8, fig. 5; Vervoort, 1972 : 186–187.

Abietinaria fusca: Levinsen, 1913 : 310–311; Broch, 1918 : 120–122 (syn. *Thuiaria salicornia* Allman, 1847*a*); Vervoort, 1946 : 242–243, fig. 106b (syn. *Sertularia nigra:* Jameson); Naumov, 1960 : 400–401, fig. 292; Naumov, 1969 : 431, fig. 292.

Thuiaria lichenastrum: Kudelin, 1914 : 282–284, figs 92, 93, 93a.

Dymella articulata: Stechow, 1923 : 8; Vervoort, 1946 : 265–266, fig. 116 (syn. *Sertularia lichenastrum* Linnaeus; *Thuiaria persocialis* Allman; *T. neglecta* Kirchenpauer; *T. personalis* Kirchenpauer; *T. pectinata* Campenhausen); Vervoort, 1972 : 186.

Thujaria articulara Williams, 1954 : 49 (lapsus pro *articulata*).

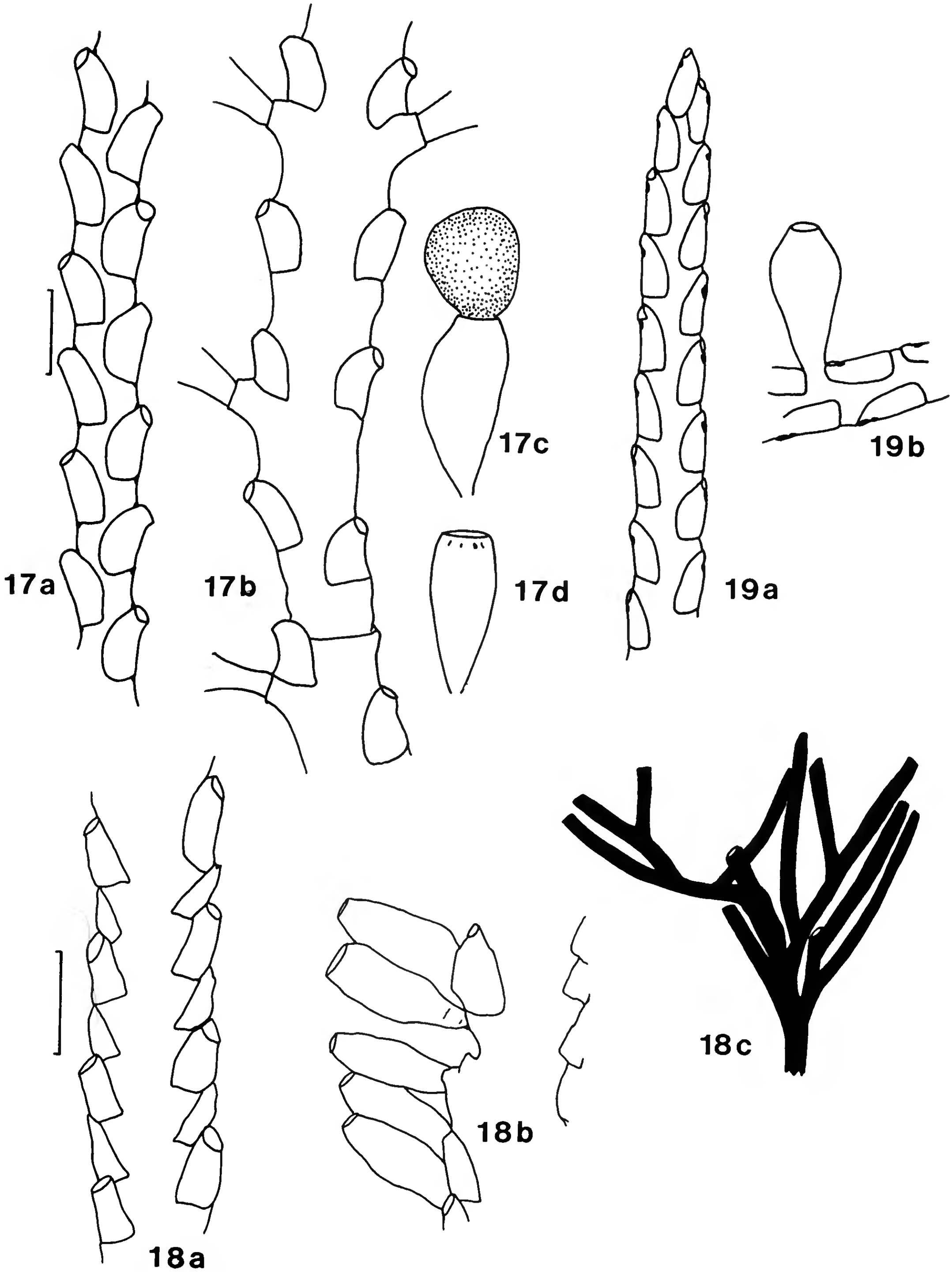
Salacia articulata: Millard, 1957 : 207 (syn. *Thuiaria persocialis* Allman; *T. pectinata* Allman); Rees & Thursfield, 1965 : 149 (syn. *Thuiaria pectinata* Allman); Millard, 1961 : 205 (syn. *Thuiaria ellisii* Busk).

Thuiaria barentsi Naumov, 1960 : 409–410, fig. 297, pl. 9, fig. 2; Naumov, 1969 : 442, fig. 297, pl. 9, fig. 2; (see Remarks).

? *Thuiaria uschakovi* Naumov, 1960 : 420–421, fig. 307, pl. 14, fig. 5; Naumov, 1969 : 452–453, fig. 307, pl. 14, fig. 5; (see Remarks).

TYPE MATERIAL AND LOCALITY. As explained in the Remarks section the original designation of *Sertularia articulata* Pallas, 1766, was based on plate 6 of Ellis (1755), drawn from a specimen from Dublin, Eire. It is virtually certain, however, that none of the hydroid specimens illustrated by Ellis (1755) survives (Cornelius, in prep.). The following series from the other side of the Irish Sea from Dublin is therefore designated neotype of *S. articulata* Pallas: off Lytham, Lancashire, England, 53° 44′ N, 2° 58′ W, several old colonies in spirit + 1 microslide (measured, Table 15), coll. R. L. Ascroft, 1893.2.28.13 (Figs 17a–b; Table 15).

OTHER TYPE MATERIAL EXAMINED. Lectotype of *Sertularia fusca* Johnston, 1847, single infertile colony comprising two pinnate hydrocauli, Dunstanburgh, Northumberland, deep water, coll.



Figs 17–19. **Fig. 17** *Salacia articulata.* (a) neotype, NE England, hydrocladium; (b) same, hydrocaulus; (c–d) gonothecae (? sex), W Scotland (1956.1.1.14); scale (a–d) = 500 μm. **Fig. 18** *S. lichenastrum,* syntype. (a) hydrocladium, scale = 500 μm; (b) same, gonothecae, scale as in (a); (c) silhouette of whole of syntype specimen on right of herbarium sheet (see note 14, p. 309), scale = 5 mm. **Fig. 19** *S. thuja.* (a) terminal region of hydrocladium, NE Scotland (1964.8.7.177); (b) gonotheca, NE England (1912.12.21.392); scale (a–b) as Fig. 17.

R. Embleton, 1847.9.22.24b (illustrated, Johnston, 1838: text-fig. 13, as *Sertularia nigra* Pallas, 1766; Johnston, 1847: text-fig. 6, as *S. fusca;* mentioned Gray, 1848 : 75, no. 26a). This specimen is the only one of the type series of *S. fusca* which could be located and is designated lectotype. It appears conspecific with the neotype material of *Sertularia articulata* Pallas, described above. Epizoic on it is a syntype specimen of *S. fallax* Johnston, 1847, regd no. 1847.9.22.24a; (see p. 261).

OTHER MATERIAL EXAMINED. Of the several dozen spirit and herbarium specimens from British localities in the BM(NH) collections, only material that has been measured, illustrated or specially mentioned here will be listed. Off Faroes, 61° 49′ N, 5° 36′ W, 160 m, 25 Aug 1906, part of colony on microslide, coll. m.v. 'Goldseeker', 1964.8.7.173 (Table 15; mentioned, Ritchie, 1911: 217, as *Thuiaria lonchitis;* Rees & Thursfield, 1965 : 150, as *Salacia lonchitis*). Off Washbourne, Cumbrae, Buteshire, Scotland, 15–30 m, 18 May 1955, many colonies in spirit + 1 microslide preparation showing acrocysts (?♀), coll. W. J. Rees, 1956.1.1.14 (Fig. 17c–d; Table 15) (? first record of acrocysts in this species).

Apart from the lectotype there is apparently almost no material labelled *Sertularia fusca* Johnston in the BM(NH) collection. The only three specimens labelled as this species are referrable to *Salacia articulata* (Pallas) (1922.6.23.1, Aberdeen, 1792; 1912.12.21.306–307, both off Durham, 1875).

DESCRIPTION. Colony erect, up to 250 mm (Hincks, 1868), pinnate, rigid, hydrocaulus flat and wide, hydrocladia alternate (sometimes opposite), inserted on small processes, angle with main stem 70–80°; no second order branching. End of main stem spiral in some long colonies (Broch, 1918). Hydrothecae in two rows, alternate, those in each row successively pointing left and right, tubular, tapered, turned sharply outwards below aperture, with flat base and angular bottom corner in lateral view; aperture flush to slightly projecting, rim circular, slight characteristic thickening on proximal side visible in optical section; operculum circular, abcauline. Lateral distance between hydrothecae variable, usually widest on hydrocaulus. Gonothecae ? ♂ = ♀, in one or two rows, on upper sides of hydrocladia, cylindrical, often with asymmetric bulge on one side, sharply tapering basally; aperture circular, nearly as wide as widest part of gonotheca, some internal cusps near rim (? desmocytes), pedicel short; acrocyst (? ♀) present in some BM(NH) material (1956.1.1.14; Fig. 17c).

MEASUREMENTS. See Table 15.

Table 15 *Salacia articulata*. Measurements in μm

	Neotype	North Sea (1964.8.7.173)	? North Sea (Vervoort, 1946)	U.S.S.R. (Naumov, 1969)	W Scotland (1956.1.1.14)
Hydrotheca					
Length	420–490	400–500	400–600		435–470
Diameter	220–300	150–160	150–250		180–210
Diameter of aperture	100–130	90–110		110	120–150
Diameter of base	120–180	100–120			110–120
Gonotheca					
Length			1500–3000	1100	1100–1200
Maximum diameter			800–1500	400	400–520
Diameter of aperture				200	400–470

VARIATIONS. Although the hydrocladia are usually inserted alternately, specimens in which some are opposite occur (e.g. BM(NH) 1842.12.7.16). The hydrothecal apertures may be flush with the hydrocladial perisarc or – as in the measured neotype microslide preparation – the proximal margin may be slightly raised and not parallel with the hydrocladial axis. Some gonothecae have an asymmetric bulge (Naumov, 1969 : fig. 269). Density of perisarc pigment varies between colonies, possibly with age. The vertical distance between hydrothecae varies but is usually roughly equivalent to one aperture diameter.

REPRODUCTIVE SEASON. March–April near Roscoff at 80 m depth (Teissier, 1965); empty gonothecae with acrocysts still attached collected by W. J. Rees, 18 May 1955, Cumbrae, Buteshire, W Scotland (1956.1.1.14) (see Fig. 17).

DISTRIBUTION. Arctic to northern boreal, circumpolar. Although reported widely from the present area records south of a line from Dublin to London are relatively few, and are from deeper waters. There are southerly records from Roscoff (Teissier, 1965), Cornwall and Devon (Hincks, 1868; Marine Biological Association, 1957), the Isle of Man [Bruce *et al.*, 1963, including an undated record probably about 1960 (A. A. Fincham, pers. comm.)], Swedish, Danish and Dutch coasts (Jägerskiöld, 1971; Kramp, 1935; Vervoort, 1946) but not Belgium (Leloup, 1952). In the BM(NH) collections there are specimens from many localities in Scotland, and a few from Northumberland, Durham, Cumberland and Lancashire. South of the present area Castric-Fey (1973) recorded the species at 30 m depth off the north-west coast of France.

HABITAT. Naumov (1969) recorded a depth range of 18–300 m in Russian seas, with more usual limits of 50–200 m. Hincks (1868) stated the usual substrates to be stones and shells.

REMARKS. Reasons for adopting the generic name *Salacia* Lamouroux, 1816, in place of the more widely used *Thuiaria* Fleming, 1828, were summarized by Cornelius (1975*b*).

For more than two centuries there has been nomenclatural confusion between the present species, the older of its synonyms and *Sertularia lichenastrum* Linnaeus (1758 : 813). The original diagnosis of *S. lichenastrum* was based partly on material pieces of which are currently in the collections of the Linnean Society of London.[14] Linnaeus mistakenly identified with the material plate 10 of Ellis (1755). Pallas (1766 : 138, 139) realized this confusion and, while recognizing *S. lichenastrum* Linnaeus, 1758, provided the new name *S. articulata* for the specimen depicted by Ellis. Linnaeus (1767 : 1313) later perpetuated his original error in recognizing only one species, regarding as conspecific both *S. lichenastrum* sensu Pallas (= *sensu* Linnaeus, 1758) and the specimen illustrated by Ellis. Subsequently, Ellis & Solander (1786 : 42) provided the new name *Sertularia lonchitis* in place of *S. lichenastrum* sensu Linnaeus, 1767, including Ellis' (1755) plate in the synonymy. It seems plausible that Ellis & Solander were unaware of Linnaeus' error and that they intended merely to attach a binomen of their own choice to the species which Ellis had been first to describe and illustrate. Thus it seems that the names *S. articulata* Pallas, 1766, and *S. lonchitis* Ellis & Solander, 1786, should be regarded as objective synonyms, both having been provided as names for the material illustrated by Ellis (1755). Although Hincks (1868) followed Pallas in recognizing only one species, some subsequent authors have discussed whether or not there are nevertheless two species involved (Nutting, 1904; Kudelin, 1914; Naumov, 1960, 1969; Rees & Thursfield, 1965; Vervoort, 1972). Naumov recognized only one species. Vervoort (1972) also inclined to this view but considered Stechow's (1923) assertion that *S. articulata* (auct.) lacked an abcauline caecum as sufficient reason to maintain a separation from *S. lonchitis* (auct.). If in reality there are two species then a new name will have to be provided for that hitherto called *S. lonchitis* (auct.). A caecum appears to be present in some British material with contracted hydranths (1955.11.15.7; 1956.1.1.14), but Mammen (1965) doubted the value of the presence or absence of a caecum in contracted hydranths as a systematic character and suggested that it is simply a fold in the hydrothecal wall which appears when the hydranth contracts. Millard (1975), however, has put forward a strong case that it can be used as a generic character; and implied (op. cit., p. 231) that it might be present in some species of the genus *Synthecium* Allman, 1872, and not in others (see also p. 247, above). It certainly seems improbable that the two nominal species of *Salacia* being discussed should differ solely in the presence or absence of a caecum, however formed, and as suggested by Pallas (1766) it appears that only one species need be recognized.

The lectotype specimen of *Sertularia fusca* Johnston, 1847, was found to be referrable to the present species. It seems that definitions of the two species have been centred on specimens in which the hydrothecae are closely packed (*articulata*) or vertically separated (*fusca*), but these extremes are connected by intermediates and the two taxa appear conspecific. Further indication that this view might be correct is that the supposed geographical range of *S. fusca* is a small area within that of *Salacia articulata*, being approximately northern England to southern Iceland and the European mainland coasts of similar latitudes (Kramp, 1929).

Thuiaria ellisii Busk, 1851, was referred to the present species by Bedot (1910), and also by Millard (1961) who examined the type material.

Thuiaria barentsi Naumov, 1960, seems identical with the present species. The features on which it was designated – large desmocytes inside the gonothecal aperture and completely sunken hydrothecae – are shared by some specimens of the present species. In fact some of the hydrothecae on a 'paratype' fragment of *T. barentsi* in the BM(NH) collection (1962.10.10.21, White Sea, 87 m, one hydrocladium in spirit, pres. D. V. Naumov) project beyond the hydrocladium and cannot be described as wholly sunken.

Thuiaria uschakovi Naumov, 1960, held to differ from *T. barentsi* in having alternately arranged hydrothecae and narrower stems and branches, similarly seems referable to *Salacia articulata* which also has alternate hydrothecae; but I have not seen specimens.

Acrocysts, possibly ♀, are present in some of the material examined here (see Description, Other material examined and Fig. 17c). They seem previously unrecorded in the present species.

Salacia thuja (Linnaeus, 1758)
(Fig. 19)

Corallina vesiculata, caule angulato rigido. Ellis, 1755 : 10–11, pl. 5, figs b, B.
Sertularia thuja Linnaeus, 1758 : 809.
Sertularia thuya: Lamouroux, 1816 : 193 (unjustified emendation).
Thuiaria thuia: Fleming, 1828 : 545; Fleming, 1842 : 545 (unjustified emendations).
Thuiaria thuja: Hincks, 1868 : 275–277, pl. 59; Nutting, 1904 : 62–63, pl. 7, figs 1–3; Kudelin, 1914 : 293–303, figs 97–98; Fraser, 1944 : 309–310, pl. 65, fig. 297; Vervoort, 1946 : 259–262, figs 114b, 115a; Naumov, 1960 : 417–419, fig. 305; Naumov, 1969 : 450–451, fig. 305; Calder, 1970 : 1538, pl. 8, fig. 6; Vervoort, 1972 : 185–186.
Thujaria thuja: Broch, 1918 : 139–141; Hamond, 1957 : 318.
Salacia thuja: Stechow, 1923 : 214; Rees & Thursfield, 1965 : 151; Robins, 1969 : 333.

TYPE LOCALITY AND MATERIAL. There is apparently no material of this species in the Linnaeus collection at the Linnean Society of London (Savage, 1945). Linnaeus (1758) gave the 'habitat' as 'in Oceano', and did not provide a description after the diagnosis. Thus it seems that he based the diagnosis on previously published accounts and not on specimens (cf. note 14 on p. 309). It is likely that he used the illustrations of Ellis (1755 : pl. 5, figs b, B) which he cited, and the illustrated specimen can be regarded as the holotype. It almost certainly no longer exists (cf. note 14, p. 309), but it is not felt necessary at present to designate neotype material. Ellis knew the species from Scarborough and 'Scotland'. The status of the species in English waters is not clear, however (see Distribution, below), and the type locality is here restricted to Scottish waters.

MATERIAL. Only mentioned, illustrated or measured material is listed. Off Caithness coast, NE Scotland, 70 m, 15 Sept 1903, part of colony on microslide, coll. J. Ritchie, 1964.8.7.177 (Fig. 19a; Table 16; mentioned, Rees & Thursfield, 1965 : 152). Durham coast, NE England, fertile colony in spirit and 1 microslide preparation, coll. A. M. Norman, 1912.12.21.392 (Fig. 19b; Table 16). Off Bell Rock (Inchcape Rock), Fife, Scotland, 30 Aug 1904, coll. J. Waterston, via J. Ritchie coll., young pinnate colony on microslide, 1964.8.7.177a (Table 16; mentioned, Ritchie, 1909b : 221). Several colonies in spirit, Bridlington Bay, Yorkshire, 7 Nov 1921, coll. s.s. 'George Bligh', 1956.2.2.5, 23–25. Infertile colony from strandline, Bridlington Bay, 28 May 1977, coll. P. F. S. Cornelius, 1977.6.1.1.

DESCRIPTION. Adult colony erect, up to *c.* 250 mm; in form of bottle brush, with branched hydrocladia arising all round stem. Main stem slightly flexuose, rigid, dark brown to black in older parts; lower branches deciduous on basal ⅔–¾ of stem. Young colonies alternate-pinnate; transition from pinnate to radial arrangement of hydrocladia apparently abrupt. Hydrocladial insertion close and radial in older colonies, hydrocladia dichotomously or less often alternately branched, ending in blunt points. Hydrothecae alternate, biseriate (rarely triseriate, BM(NH)

1964.8.7.177a; Ritchie, 1909*b*), cylindrical, entirely sunk, lateral circular aperture flush or nearly flush; circular one-flapped operculum attached on abcauline side. Distance between adjacent and successive hydrothecae variable. Naumov (1969) reported 'two rather distinct lateral denticles on the [aperture] margin' but these appear unusual. Adjacent side of hydrotheca convex, remote side straight to concave; length : breadth ratio from 2 : 1 to 5 : 1. Hydranth said (Leloup, 1952; Calder, 1970) to have abcauline diverticulum of enteron, but no BM(NH) material adequately preserved for this to be seen. Gonotheca ♂ = ♀, ovoid to inverted-conical, smooth (to rugose), tapering basally, no pedicel; widest just below aperture, which is circular, often on short collar; borne on hydrocladium below hydrotheca; Kudelin (1914) recorded ♀ acrocyst with one ovum in *S. thuja* 'subsp. *pacifica*' Kudelin.

MEASUREMENTS. See Table 16.

Table 16 *Salacia thuja*. Measurements in μm

	NE Scotland (1964.8.7.177)	NE Scotland† (1964.8.7.177a)	NE England (1912.12.21.392)
Distance between hydrocladial branches	1400–2000		
Hydrotheca			
Length	380–420	380–400	380–430
Maximum diameter	180–220	150–220	110–200
Diameter of aperture	90–100	90–110	60–80
Gonotheca (♂ = ♀)			
Length			830–1200
Maximum diameter			400–680
Aperture diameter			140–200

† Young (pinnate) colony with triseriate arrangement of hydrothecae (mentioned, Ritchie, 1909*b*).

VARIATIONS. Young colonies pinnate, older colonies having radially inserted hydrocladia which are branched dichotomously or alternately; hydrothecae alternate but variably spaced in all directions. Hydrothecal apertures flush to slightly prominent. See also Description.

REPRODUCTIVE SEASON. Apparently no data from boreal seas. Fertile material recorded May–October in N Russian seas (Kudelin, 1914), but no winter data available.

DISTRIBUTION. *Salacia thuja* has been recorded in European Continental Shelf waters from Portugal (Nobre, 1931) to the north of Scandinavia (74° 30′ N, 19° 03½′ E, 11 m; Kudelin, 1914). In the present area its distribution is patchy and seems to have contracted northwards during the past 100 years. Although present in the Kattegat it seems absent to the east of Copenhagen (Stechow, 1927; Broch, 1928; Kramp, 1935) and there are no recent records from the English Channel or the coasts of Belgium and Holland (Vervoort, 1946, 1949; Leloup, 1947, 1952; Marine Biological Association, 1957; Teissier, 1965; Robins, 1969). However, it has in the past been recorded from S Devon and Cornwall and the Dogger Bank (Hincks, 1868), the Scilly Isles (Clark, 1906), Sark (Ansted & Latham, 1862), Holland (pre 1766, Vervoort, 1946) and Belgium (Maitland, 1897). Ellis (1755) knew the species from only Scarborough on English coasts, and the only BM(NH) material from England in the present century is also from Yorkshire (see Material list). Hamond (1957) found occasional strand-line material from Norfolk in 1950 but his description of it suggests it might have drifted a long way. Possibly the present southern limit of the species in the southern North Sea is about 54° N.

On more westerly coasts there are no records from Wales, Lundy or the Isle of Man (Williams, 1954; Bruce *et al.*, 1963; Crothers, 1966; Hiscock, 1974 and pers. comm.; the late D. N. Huxtable, pers. comm.), although there is an undated record from Ilfracombe, N Devon (Cutcliffe, in Palmer, 1946) and old records from Londonderry in 1844, and Dublin, before 1878 (Stephens, 1905).

In Scottish waters the species is apparently less uncommon. The BM(NH) collection includes nineteenth-century herbarium material from Berwick Bay and the Firth of Tay; and Chumley (1918) recorded the species from the Clyde Sea, near which perhaps lies its present southern limit in W Scotland.

The apparent present British distribution of this species is difficult to explain since records from Portugal (Nobre, 1931) and the Mediterranean (Naumov, 1969; ? repeated by Christiansen, 1972) suggest that the species is tolerant of warmer sea temperatures than occur in southern England. However, the species was not recorded from the Adriatic by Riedl (1970) in a faunal survey and its presence in the Mediterranean should perhaps be regarded as unproven.

HABITAT. All depths to edge of Continental Shelf and slightly deeper. Naumov (1969) gave main depth limits of 50–200 m, with extremes of 2 and 800 m, in Russian seas. On shells and similar substrates (Johnston, 1847; Hincks, 1868).

REMARKS. No systematic revision of this distinctive species seems necessary. However, the similarity of *S. thuja* to *Thujaria laxa* Allman, 1874*a*, in all but colony shape is striking. Although *S. laxa* was recorded from 'as far south as the Shetlands' by Kramp (1943) he did not cite material and there are apparently no acceptable records from as far south as the British Isles. *S. laxa* has recently been redescribed by Naumov (1969), Calder (1970) and lastly Vervoort (1972), who placed it in the genus *Dymella* Stechow, 1923.

Sertularella gaudichaudi (Lamouroux, 1824)

(Fig. 20)

Sertularia gaudichaudi Lamouroux *et al.*, 1824 : 682 (but see addendum).
Sertularia fusiformis Hincks, 1861 : 253, pl. 6, figs 7–8.
Sertularella fusiformis: Hincks, 1868 : 234, 243, pl. 47, fig. 4, text-fig. 28; Hartlaub, 1901 : 85–86, text-fig. 55, pl. 5, figs 7–9 (syn. *S. simplex* Hutton, 1873); Ritchie, 1909c : 77–78, fig. 3; Bedot, 1912 : 353–354 (syn. *S. simplex* Hutton, 1873); Broch, 1918 : 105–106 (syn. *S. pellucida* Jaderholm, 1907); Millard, 1957 : 213–215, figs 10c–d (syn. *S. lineata* Stechow, 1923; non *S. fusiformis:* Warren, 1908); Millard, 1964 : 42–44 (syn. *S. ellisii* f. *ellisii* Picard, 1956).
Sertularella gaudichaudi: Billard, 1909 : 317–319, figs 5–6 [syn. *Sertularia picta* Meyen, 1834; *Sertularia exigua* (= *laxa*) Allman, 1888 (see Remarks); *Sertularella mediterranea* Hartlaub, 1901]; Billard, 1912 : 464–465 (syn. *S. mediterranea* auct.).
Sertularella ellisii: Picard, 1956 : 258–266, figs 1a, 2b, 3a–f.
Sertularella ellisii f. *fusiformis:* Teissier, 1965 : 23.
Sertularella mediterranea Hartlaub, 1901 : 10, fig. 6, 86–87, pl. 5, figs 10, 11, 15, 16; Broch, 1933 : 76–79; Vervoort, 1946 : 312–314; Vervoort, 1949 : 150–151, fig. 5; Hamond, 1957 : 316–317, fig. 24; Millard, 1957 : 215–216, figs 10e, 11b; Vervoort, 1959 : 272–273, figs 33a, 34a; Millard, 1964 : 45.
Sertularella polyzonias f. *mediterranea:* Leloup, 1952 : 168, fig. 97c; Picard, 1956 : 264, fig. 3b.
non *Sertularella ellisii* Deshayes & Edwards, 1836 = *S. polyzonias* (p. 290).

TYPE LOCALITY AND MATERIAL. The type material, now destroyed (Redier, 1967), was well described by Billard (1909). The type locality is the Falkland Isles (Billard, op. cit.). I have been unable to locate type material of either of the two main synonyms listed here (*S. fusiformis* Hincks, coasts of Devon; *S. mediterranea* Hartlaub, Rovinj, Yugoslavia), and in all probability none is extant. Professor Dr M. Dzwillo, Zoologisches Institut und Zoologisches Museum, Hamburg, informed me that no type material of the latter species is there although much of Hartlaub's collections survive. [The type material of *S. gaudichaudi* was described again by Billard (1922*b*).]

MATERIAL EXAMINED. This species is well represented in the BM(NH) collections, largely by material labelled *S. fusiformis* and *S. mediterranea*, and only measured and otherwise mentioned material is listed here. Burrafirth caves, Shetland Isles, Scotland, fertile hydrocladia on two microslides, coll. A. M. Norman, det. A. K. Totton, 1912.12.21.139A. 'Off Portugal' ('Porcupine' sta. 13), 1870, fertile fragments in spirit + 1 microslide preparation, coll. m.v. 'Porcupine', 1890.4.12.2–4 (Fig. 20a and Table 17). Naples, Italy, fertile colonies in spirit + 1 microslide preparation, coll. Stazione Zoologica, Naples, via. A. M. Norman, 1898.5.7.110 (Fig. 20b–c & Table 17).

DESCRIPTION. Hydrocauli erect, monosiphonic, flexuose, usually unbranched, up to 250 mm. Perisarc smooth to variably rugose; one hydrotheca per internode. Hydrothecae $\frac{1}{3}$–$\frac{1}{2}$ adnate, tubular to flask-shaped with sub-terminal constriction; walls smooth to rugose; aperture 4-cusped with 4-flapped operculum; 4 or fewer internal projections on wall near aperture, alternate in position with cusps on rim or in other positions (see Remarks); aperture usually perpendicular to hydrothecal axis but this variable. Gonotheca ovoid, length twice breadth, annulated throughout to smooth basally; aperture terminal, 3–4 cusped; ♀ said to be slightly larger than ♂. No acrocyst.

MEASUREMENTS. See Table 17.

Table 17 *Sertularella gaudichaudi.* Measurements in μm

	Portugal (1890.4.12.2–4)	Italy (1889.5.7.110)	S Africa (Millard, 1957, as *S. fusiformis*)
Hydrotheca			
Outer side	620–710	580–620	440–600
Inner side, length adnate	310–370	250–380	160–320
Inner side, length free	450–540	270–370	280–440
Diameter of aperture	200–250	160–190	200–250
Gonotheca (? ♂ = ♀)			
Length		1570–1650	1460–2160
Maximum diameter		740–800	780–990†

† Owing to a printer's error the maximum male gonothecal diameter was wrongly given as 1890 μm by Millard (1957 : 214). The correct figure was 890 μm. The maximum diameter of the female gonotheca was as stated, 990 μm (N. A. H. Millard, pers. comm.).

VARIATIONS. See Description and Remarks.

REPRODUCTIVE SEASON. Recorded fertile April–September in NW France (Teissier, 1965, as *S. mediterranea*).

DISTRIBUTION. Said to occur in warm and temperate Atlantic waters (Broch, 1918, as *S. fusiformis*). In the present area the species has been recorded as follows. As *S. fusiformis* – Clyde Sea (Ritchie, 1911; Chumley, 1918)*, the Hebrides and N & S Devon (Hincks, 1868), NW France (Teissier, 1965), the Scilly Isles (Robins, 1969) and the Isle of Man (Bruce *et al.*, 1963). As *S. mediterranea* – Shetlands (present material), E Anglia, the Solent, Hebrides & Breton coast (Hamond, 1957), the Channel Isles (Philbert, 1935; Vervoort, 1949), NW France (Teissier, 1965) and Pembrokeshire (Crothers, 1966).

HABITAT. Recorded intertidally (Hincks, 1868, as *S. fusiformis*) and from shallow waters throughout the present area.

REMARKS. There seems little doubt from Billard's (1909, 1922b) accounts of the type material of *S. gaudichaudi* Lamouroux that *S. mediterranea* Hartlaub and *S. fusiformis* Hincks can be regarded its junior synonyms. However, other accounts have sought to distinguish the two last-mentioned taxa, and ignored the first. *Sertularella mediterranea* Hartlaub, 1901, was proposed to accommodate material from Rovinj, Yugoslavia, differing from *S. polyzonias* (Linnaeus, 1758) in having smaller hydrothecae, in possessing internal cusps near the hydrothecal aperture and in lacking acrocysts. Hartlaub regarded the absence of acrocysts even from mature material as the most diagnostic character. Although *S. mediterranea* has since been widely recognized, chiefly (Millard, 1957, 1964) on the arrangement of the internal hydrothecal cusps and orientation of the hydrothecal aperture, it nevertheless seems conspecific with *S. fusiformis* and *S. gaudichaudi.* The two characters seem variable both within *S. fusiformis* s. str. and according to published descriptions of *Sertularella mediterranea* (see synonymy).[15] Further, Vervoort (1946, 1966, 1972) has

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* also Rankin, 1901

shown internal cusps to be variable in number in material assigned to *S. mediterranea* and also in *S. leiocarpa* (Allman, 1888), *S. parvula* (Allman, 1888) and *Symplectoscyphus elongatus* (Jaderholm, 1904). It thus seems that *S. mediterranea* and *S. fusiformis* can be regarded conspecific, and placed in *S. gaudichaudi*. Some authors (Leloup, 1952; Picard, 1956; Naumov, 1960, 1969) have referred *S. mediterranea* to *S. polyzonias* Linneaus, 1758, but this view seems mistaken.

The nominal species *Sertularia exigua* Allman, 1888, was labelled *S. laxa* on the caption to the original illustration. Allman found it necessary to change the name to *exigua* after the plates had been printed but before the text had been completed (Allman, 1888 : caption to pl. 26). *Thuiaria laxa* Allman, 1874*a*, is a different nominal species (p. 282).

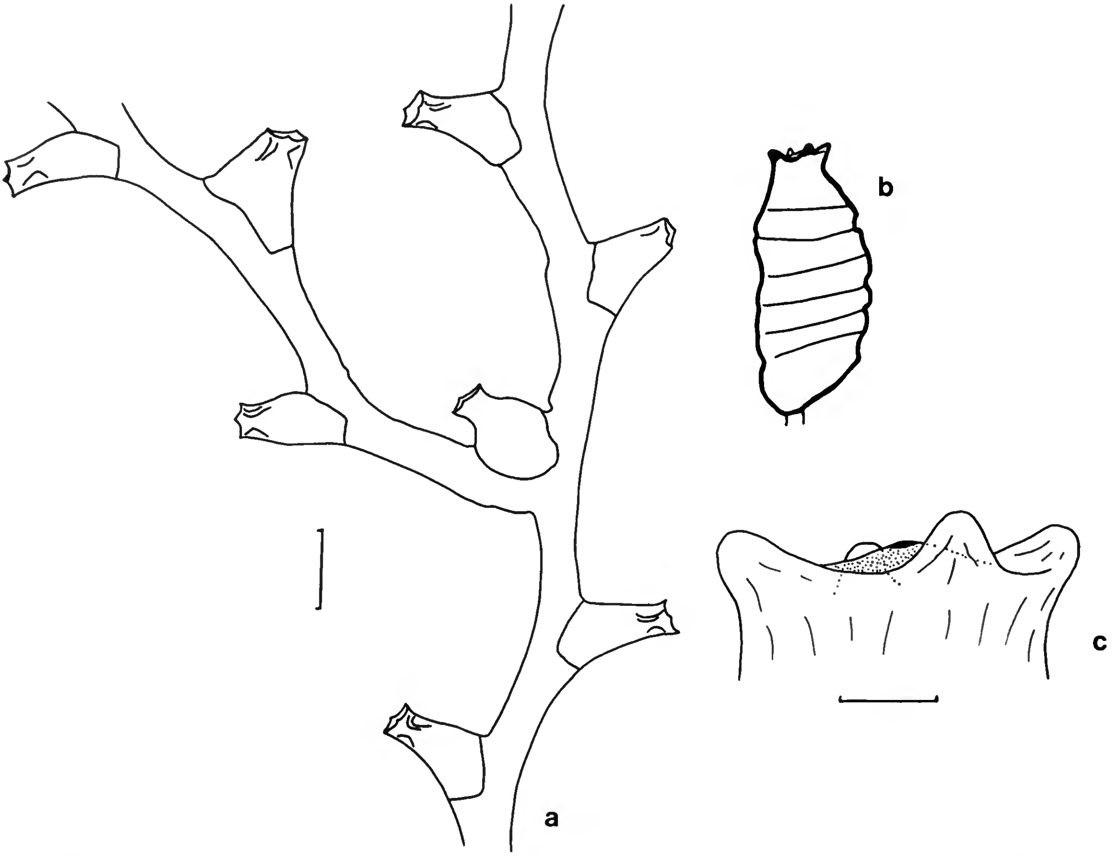


Fig. 20 *Sertularella gaudichaudi.* (a) part of colony, 'off Portugal' (1890.4.12.2–4), scale = 500 μm; (b) gonotheca, W Italy (1898.5.7.110), scale as in (a); (c) terminal region of (b), scale = 100 μm.

Sertularella gayi (Lamouroux, 1821)

(Fig. 21)

Sertularia gayi Lamouroux, 1821 : 12–13, pl. 66, figs 8–9; Lamouroux, Bory de Saint-Vincent & Deslongchamps, 1824 : 682; Deshayes & Edwards, 1836 : 152.

Sertularia pinnata Templeton, 1836 : 468.

Sertularella gayi: Hincks, 1868 : 237–239, pl. 46, fig. 2; Vervoort, 1959 : 273–275, figs 33b–c, 34b; Ralph, 1961 : 833–834, figs 24d–f; Vervoort, 1966 : 127–128, fig. 30; Vervoort, 1972 : 116–120, figs 36a–d.

TYPE LOCALITY AND MATERIAL. Coasts of English Channel (Lamouroux, 1821). If any type material was selected by Lamouroux it is almost certain that it was destroyed by a bomb at Caen on 7 July 1944, along with the bulk of the Lamouroux collection (Redier, 1967).

MATERIAL EXAMINED. Brattholmen, Hjeltefjord, Espegrend, nr Bergen, Norway, 40–90 m, 9 Apr 1962, two fertile colonies in spirit + 1 microslide preparation, coll. W. J. Rees, 1962.10.7.27. Shetland, fertile fragments in spirit and on microslide, coll. A. M. Norman, 1912.12.21.324 (Fig. 21a, Table 18). Lousy Bank, 60° 20′ N, 12° 40′ W, 200–400 m, several colonies in spirit, coll. Ministry of Agriculture and Fisheries, 1921.5.17.1. Loch Buie, Isle of Mull, W Scotland, 20–30 m, fragment of fertile hydrocaulus on microslide, coll. J. Murray, 1888.12.21.3. Whitsand Bay, Cornwall, England, 40 m, Aug 1962, two hydrocauli with ♂ gonothecae on microslide, coll. R. C. Vernon, 1967.10.24.10. Plymouth, Devon, 10 Sep 1897, ♀ colony in spirit + 1 microslide preparation showing acrocysts, coll. E. T. Browne, 1941.3.20.350 (Fig. 21b; Table 18). Mewstone Ledge, nr Plymouth, 20 m, several colonies in spirit, coll. R. Davis, 1962.8.8.1. 'Mountain Foot', Eire, 40–50 m, 24 Jul 1902, hydrocladia with ♀ acrocysts on 2 microslides, coll. E. T. Browne, 1967.6.15.86–87. Bay of Biscay, 800–850 m, two jars of spirit material + 4 microslide preparations including ♂ & ♀ gonophores, coll. E. T. Browne, 1941.3.20.352–3 (Figs 21c–d; Table 18), 1961.11.4.3.

DESCRIPTION. Colony erect, up to *c.* 250 mm, main stem and main branches polysiphonic, arrangement of smaller branches pinnate to subpinnate with some second and third order branching. Hydrocladia flexuose to almost straight, perisarc smooth to slightly rugose, internodal constrictions diagonal. Hydrothecae alternate, flask-shaped, narrowing just below aperture which is usually at *c.* 90° to long axis of hydrotheca; rim 4-cusped, depth of intervening bays variable; operculum 4-flapped; $\frac{1}{3}$–$\frac{1}{2}$ adnate, free portion smooth to slightly rugose, outer side smooth. With axillary hydrothecae. Hydranth apparently undescribed. Gonothecae ♂ = ♀, ovoid to club-shaped, distal $\frac{1}{3}$–$\frac{2}{3}$ horizontally ridged to rugose, aperture terminal, 2–3 (rarely 4) cusps, more prominent than in *polyzonias* s. str.; if 2 then typically one larger than the other; dioecious; eggs retained after fertilization in acrocyst (hitherto undescribed; Fig. 21b) identical with that of *S. polyzonias* s. str.

MEASUREMENTS. See Table 18.

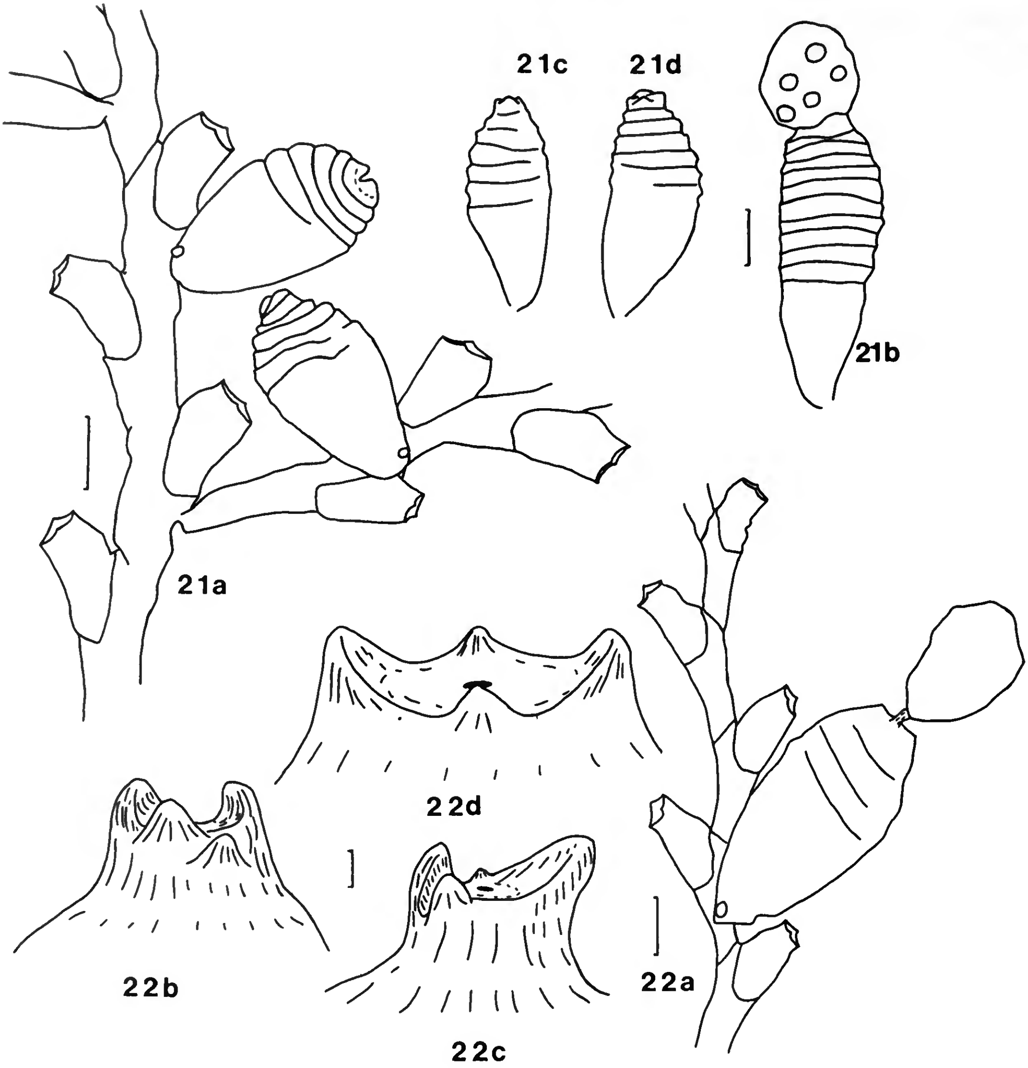
Table 18 *Sertularella gayi.* Measurements in μm

	SW England (1941.3.20.350)	Bay of Biscay (1941.3.20.353)	Shetland Isles (1912.12.21.324)
Hydrotheca			
Outer side	650–730	740–800	580–670
Inner side, length adnate	500–610	640–730	510–600
Inner side, length free	380–480	650–720	350–400
Diameter of aperture	300–370	200–280	320–350
Internode			
Length	980–1070	950–1080	800–920
♂ gonotheca			
Length		1900–2030	1550–1800†
Maximum diameter		780–860	730–810†
♀ gonotheca			
Length	2100–2400		
Maximum diameter	750–920		

† Sex uncertain.

VARIATION. Colony habit is usually erect and pinnate with polysiphonic main stem, but small colonies are barely recognizable as pinnate and are difficult to distinguish from colonies of *S. polyzonias* s. str. Distinctions between the two species are considered under Remarks.

The hydrothecae vary in the same way as do those of *S. polyzonias* (see p. 289). The gonothecal aperture has typically two opposite subequal rounded cusps (Fig. 21a) but in some specimens



Figs 21–22. **Fig. 21** *Sertularella gayi.* (a) hydrocladia with gonothecae, N Scotland (1912.12.21.324), scale = 500 μm; (b–d) gonothecae, scale = 500 μm, (b) ♀ gonotheca with acrocyst, SW England (1941.3.20.350), (c) ♂ gonotheca with 3 cusps, Bay of Biscay (1941.3.20.353), (d) ♀ gonotheca with 4 cusps, Bay of Biscay (1941.3.20.352). **Fig. 22** *S. polyzonias.* (a) hydrocladium and ♀ gonotheca with acrocyst and no terminal cusps, NE Ireland (1967.6.15.82), scale = 500 μm; (b–d) terminal regions of three gonothecae, scale = 100 μm, (b) 'abnormal', ♀, ? locality (1912.12.21.593), (c) 'abnormal', ♂, NE Ireland (1967.6.15.88), (d) 'normal', ? sex, NE Ireland (1967.6.15.83).

there are three, and in others two small pointed intermediate cusps between the main ones (Fig. 21d).

Reproductive season. Apparently no published information. Among the present material the following was fertile: 'Ireland', 27 Jul 1902 (1967.6.15.86); Bay of Biscay, Aug 1906 (1941.3.20.352–3); SW England, 10 Sep 1897 (1941.3.20.350).

Distribution. Widespread in North Atlantic coastal waters and common throughout the present area.

HABITAT. Recorded from all Continental Shelf depths. Similarities between this species and *S. polyzonias* make it unclear whether one species or both occurs intertidally.

REMARKS. Although the two nominal species *Sertularella polyzonias* and *S. gayi* have been recognized by several authors the recorded differences are few and apparently only three accounts have made a critical appraisal of them (Table 19). The main recorded differences, respectively, have been whether the colony is ramified and monosiphonic or pinnate and polysiphonic; whether the gonothecal aperture is 4- or only 2-cusped; and whether the free part of the adcauline hydrothecal wall is smooth or ridged. Many specimens show intermediate colony habits. Some small and ramified colonies have occasional polysiphonic stems and sometimes an incipient pinnate arrangement of the branches, and it is possible to arrange the colonies in a series so that those of the *polyzonias* type appear simply to be the younger specimens and *gayi* type colonies the older ones.

Table 19 Recorded differences between *Sertularella gayi* (Lamouroux, 1821) and *S. polyzonias* (Linnaeus, 1758)

Author	Characters ascribed to:	
	S. gayi	*S. polyzonias*
Hincks, 1868	Pinnate branching; gonothecal aperture 2-cusped	Irregular branching; gonothecal aperture 4-cusped
Picard, 1956	Pinnate branching; main stem and side-branches polysiphonic; gonethecal aperture with two unequal cusps	Irregular branching; main stem monosiphonic; gonothecal aperture 4-cusped
Millard, 1961	Free part of adcauline hydrothecal wall ridged; surface of gonotheca ridged distally, smooth basally	Free part of adcauline hydrothecal wall smooth; surface of gonotheca ridged throughout

The presence or absence of ridges on the free part of the adcauline hydrothecal wall is not correlated with either colony habit or gonothecal aperture cusps in the present material and seems unreliable as a specific character. The number and shape of the gonothecal aperture cusps were, however, loosely correlated with colony form, small ramified colonies having 2–4 pointed cusps and larger, pinnate colonies having 2–3 rounder cusps. However, the relation between the rounded and pointed cusps is not known and the two forms may nevertheless prove to be opposite ends of a series. The gonothecal 'contents' in large, pinnate colonies have not been previously described. The present material shows them be identical in both sexes with those of *S. polyzonias* s. str., an acrocyst being produced in the female (Fig. 21b).

Although the two species are very similar specific status is retained for each pending a fuller study of the characters on which they have been separated.

The original description of *Sertularia pinnata* Templeton, 1836, mentions thick main stems and pinnate branching. It thus seems referable to *S. gayi* s. str., and not to *S. polyzonias* s. str. as suggested by Johnston (1847) and Gray (1848). The combination *Sertularia pinnata* had previously been applied by Linnaeus (1758) and Pallas (1766) to other hydroid species (see p. 267).

Sertularella polyzonias (Linnaeus, 1758)

(Fig. 22)

Corallina minus ramosa alterna vice denticulata, . . . Ellis, 1755 : 5–6, pl. 2, figs A, B (part), pl. 38, fig. 1A.

Sertularia polyzonias Linnaeus, 1758 : 813 (part); Lamouroux, Bory de Saint-Vincent & Deslongchamps, 1824 : 681 (syn. *S. ericoides* Pallas); Johnston, 1847 : 61–63, pl. 10, figs 1–3 (syn. *S. flexuosa* Linnaeus, *S. ericoides* Pallas, *S. gayi* Lamouroux, 1821, *S. pinnata* Templeton[16], *S. hibernica* Johnston, 1838, *S. ellisii* Deshayes & Edwards).

Sertularia flexuosa Linnaeus, 1758 : 814.
Sertularia ericoides Pallas, 1766 : 127–128 (nom. nov. pro *S. polyzonias* Linnaeus and *S. flexuosa* Linnaeus).
? *Sertularia gayi* Lamouroux, 1821 : 12–13, pl. 66, figs 8–9 (see p. 287).
Sertularia ellisii Deshayes & Edwards, 1836 : 142–143.
Sertularella polyzonias: Gray, 1848 : 68–69 (syn. *Sertularia flexuosa* Linnaeus, *S. ericoides* Pallas, *Sertolara polizonia* Cavolini, 1785, *Sertularia gayi* Lamouroux, *S. pinnata* Templeton[16], *S. hibernica* Johnston, 1838, *S. ellisii* Deshayes & Edwards); Hincks, 1868 : 235–237, pl. 46, fig. 1 (syn. *Sertularia flexuosa* Linnaeus, *S. ericoides* Pallas, *S. pinnata* Templeton[16], *S. hibernica* Johnston, 1838, *S. ellisii* Deshayes & Edwards); Vervoort, 1946 : 224–226, fig. 96 (syn. *Sertularia flexuosa* Linnaeus, *S. ericoides* Pallas, *S. ciliata* Fabricius, 1780, *S. ellisii* Deshayes & Edwards, *S. hibernica* Johnston, 1838, *S. gigantea* Mereschkowsky, 1878, *S. quadricornuta* Hincks, 1880, *S. implexa* Hartlaub, 1901).

TYPE MATERIAL AND LOCALITY. Since Linnaeus' diagnosis of this species was not accompanied by a description and collecting data it is almost certain that he based the diagnosis on the illustrations of Ellis (1755 : pl. 2, figs A, B) which he cited (cf. note 13, p. 309).

It follows that material preserved on four herbarium sheets, numbered 1298.21–24 (Savage, 1945), in the collections of the Linnean Society of London was not used by Linnaeus when diagnosing the species and cannot be considered the type series. Probably the material reached Linnaeus after 1758 (see note 14, p. 309).

Herbarium sheet 1298.21 bears five colonies of the species here called *Symplectosyphus tricuspidatus;* sheet 1298.22 bears three infertile specimens of *Sertularella polyzonias*; sheet 1298.23 bears a fertile specimen of *S. polyzonias* without substrate, and an infertile specimen on a brown alga; and sheet 1298.24 bears a single, pinnately branched specimen of *S. polyzonias*. The three infertile specimens on sheet 1298.22 are here designated neotypes of *Sertularia polyzonias* Linnaeus, 1758.

Linnaeus stated the 'habitat' of this species to be 'in Oceano'. Ellis (1755) saw specimens of this species from the Isle of Sheppey and accordingly the type locality is here restricted to the north coast of Kent, England.

OTHER MATERIAL EXAMINED. Although the material listed had the characters of the present species as here defined, attention is drawn to the similarity of *S. gayi* (see Remarks). SW of Flattevossen, Espegrend, nr Bergen, Norway, 30 m, 9 Aug 1962, part of fertile colony on microslide, coll. W. J. Rees, 1962.11.7.39. Vattlestraumen, Espegrend, nr Bergen, Norway, 30–40 m, 15 Aug 1962, part of ♂ hydrocaulus on microslide, coll. W. J. Rees, 1962.11.7.13. Vattenholmen, Kosterfjord, Sweden, 80–120 m, 28 Sep 1964, parts of ♂ hydrocladia on microslides, coll. W. J. Rees, 1965.1.14.147–148. Löken, Gåsö Ränna, Gullmarsfjord, Sweden, 25–30 m, 13 May 1959, fertile fragment on microslide, coll. W. J. Rees, 1959.6.11.31. N end of Loch Sween, Argyll, Scotland, 1 m, 30 Jun 1962, hydrocaulus with gonothecae and terminal tendril, coll. W. J. Rees, 1962.6.19.14. Caol Scotnish, Loch Sween, Argyll, 1 m, 30 May 1962, fertile fragment on microslide, coll. W. J. Rees, 1962.6.19.20. 1·6 km E of Old Harry Rocks, Dorset, England, 20 m, several ♀ colonies on *Flustra* sp. (Bryozoa) in spirit + 1 microslide preparation, coll. R. Kirkpatrick, 1897.8.9.19 (Table 20). Weymouth Bay, Dorset, 20 m, hydrocaulus with ♂ gonothecae on microslide, coll. R. Kirkpatrick, 1897.8.9.20 (Table 20). Mewstone Ledge, Plymouth, Devon, 20 m, several colonies and fragments on microslide with ♀ gonotheca, coll. R. Davis, 1962.8.8.1. 'Mountain Foot', nr Leestone Point, Co Down, N Ireland, 40–50 m, 24 Jul 1902, fragments on 3 microslides, coll. E. T. Browne, 1967.6.15.82 (Fig. 22a), 83 (Fig. 22d), 88 (Fig. 22c). Off Clogher Head, Co Kerry, Eire, coll. E. T. Browne, fragments on 4 microslides as follows: 1947.12.1.3 (coll. 17 Jan 1902), 1967.6.15.148–150 (coll. 23 Jul 1902, 60–70 m). No locality, ♀ colony on microslide, ex A. M. Norman colln, 1912.12.21.593 (Fig. 22b).

DESCRIPTION. Colony monosiphonic, irregularly branched, ramified, often with second and third order branches; some branches terminating in tendrils which (Millard, 1957) may fuse with the stolon network. Hydrocauli slightly flexuose, perisarc smooth to slightly rugose; internodal constrictions diagnonal. Hydrothecae, alternate, one per internode, flask-shaped, narrowing just below aperture which is approximately at right-angles to long axis of hydrotheca; rim 4-cusped, depth of intervening bays variable, operculum 4-flapped; inner side of hydrotheca $\frac{1}{3}$–$\frac{2}{3}$ adnate, free part smooth to slightly rugose; outer side smooth. With axillary hydrothecae. Hydranth tentacles 20+ (Hincks, 1868). Gonothecae ♂ = ♀, ovoid to club-shaped, distal $\frac{1}{3}$–$\frac{2}{3}$ horizontally ridged to rugose, aperture terminal, 2–5 cusped (usually 4, frequently 3), cusps variable in shape and length; colonies dioecious. Eggs formed both on blastostyle and reportedly (Weismann, 1880) in hydrocauline coenosarc; ♀ acrocyst present.

Measurements. See Table 20.

Table 20 *Sertularella polyzonias.* Measurements in μm

	SW England (1897.8.9.19)	SW England (1897.8.9.20)	S Africa (Millard, 1957)
Hydrotheca			
Outer side	550–600	530–600	450–590
Inner side, length adnate	370–430	400–430	270–380
Inner side, length free	350–410	320–360	270–350
Diameter of aperture	240–265	250–280	190–270
Internode			
Length	740–920	870–980	
♂ gonotheca			
Length		1780–2000	1570–1690
Maximum diameter		770–810	600–660
♀ gonotheca			
Length	1850–2000		2210–2230
Maximum diameter	750–850		920–930

Variations. The colony habit is usually ramified but some specimens show slight fusion of the hydrocauli which is more usual in *S. gayi* (p. 284). At present it is not clear whether the two species are distinct or whether the two colony types are simply opposite ends of a series of variation. Possibly colonies with a distinct polysiphonic stem are simply older specimens of the same species as the smaller, ramified colonies (see also Remarks under *S. gayi*, p. 287).

In colonies referrable to *S. polyzonias* s. str. there is some variation in hydrothecal characters. The aperture is typically at right angles to the long axis of the hydrotheca but it may slope slightly inwards or outwards. The adnate portion of the hydrotheca varies from $\frac{1}{3}$ to $\frac{2}{3}$. The free portion of the inner wall is usually smooth but is slightly rugose in some specimens. There is also variation in the gonothecal characters in both sexes. The length : breadth ratio of the gonotheca varies between colonies, while the condition of the cusps surrounding the aperture, on which systematic importance has been placed by some authors (e.g. Picard, 1956), varies strikingly both within and between colonies. In colonies here assigned to *S. polyzonias* s. str. on other characters the number of cusps varied between 2 and 4 (once 5), 4 being most usual and 3 frequent. The size of the cusps also varied (Fig. 22).

Reproductive season. Fertile material recorded July–August, Jersey (Vervoort, 1949), June–August, NW France (Teissier, 1965), August–September, SW England (Marine Biological Association, 1957).

Distribution. Widespread in the North Atlantic and common in suitable localities over the whole of the present area.

Habitat. Chiefly offshore to 50 m depth, less frequently down to 300 m (Naumov, 1969). Small colonies occur intertidally but (the late D. N. Huxtable, pers. comm.) probably remain infertile. Recorded substrates include rock, other hydroids and algae.

Remarks. The female gonosome of *S. polyzonias* was described by Ellis (1755 : pl. 38, fig. 1A) and Hincks (1868) among others while that of the male seems to have been described only by Weismann (1883 : 165–168, pl. 6, fig. 5).

The relation between *Sertularella gayi* Lamouroux, 1821, and the present species is discussed under *S. gayi* (p. 287).

Sertularella polyzonias was considered to comprise two species by Deshayes & Edwards (1836) who provided the name *S. ellisii* for the new taxon. *S. ellisii* was distinguished on the basis of characters now known to be variable, viz. a flexuose hydrocaulus, fat hydrothecae, large hydrothecal apertures with 4 marginal cusps, and 4-cusped gonothecal apertures. Several authors (Johnston, 1847; Gray, 1848; Hincks, 1868; Vervoort, 1946) have regarded the two taxa as conspecific, and this view is adopted here. The material described under the name *S. ellisii* by Picard (1956) is referred here to *S. gaudichaudi* (p. 282).

The nominal species *Sertularia ericoides* Pallas, 1766, is discussed both here and under *Symplectoscyphus tricuspidatus* (p. 301). The view of Pallas (1766) that *S. polyzonias* Linnaeus, 1758, and *S. flexuosa* Linnaeus, 1758, are conspecific is followed here. Following Johnston (1847; but apparently not 1838), who appears to have been first reviser, the specific name *polyzonias* is employed. (Pallas had included both species in his *S. ericoides*.) *S. flexuosa* was based on a clear illustration of Ellis (1755), showing a female acrocyst among other details.

Sertularella rugosa (Linnaeus, 1758)

(Fig. 23)

Corallina exigua repens, denticulis alternis, fructus medicae cochleatae aemulis. Ellis, 1755 : 26–27, pl. 15, figs A, a.
Sertularia rugosa Linnaeus, 1758 : 809.
Sertularella rugosa: Hincks, 1868 : 241–242, pl. 47, figs 2, 2a–b; Hartlaub, 1901 : 121–124, pl. 6, fig. 12; Broch, 1918 : 106–107, fig. 57; Vervoort, 1946 : 226–228, fig. 97a; Yamada, 1950 : 13, pl. 1, fig. 12; Leloup, 1952 : 170–171, fig. 98; Naumov, 1960 : 340–341, fig. 230; Naumov, 1969 : 367–368, fig. 230.
Ellisia rugosa: Westendorp, 1843 : 22, pl. 1, figs g, h (see Remarks).

TYPE LOCALITY AND MATERIAL. Linnaeus (1758) gave the type locality as '*in Oceano*'. No Linnean material is extant in the collections of the Linnean Society of London (Savage, 1945) and it seems likely that Linnaeus made his designation solely from the illustration of Ellis (1755 : pl. 15, fig. A, but not fig. a) as no other reference was cited. The specimen illustrated by Ellis (A) can be regarded as the holotype. The illustration shows several gonothecae but no hydrothecae. Ellis stated he collected it from Brighton, Sussex, England, during June 1754, and the type locality can be restricted to Brighton. The specimen was not located and is probably no longer extant.

MATERIAL EXAMINED. Various localities around Espegrend, nr Bergen, Norway, 10–25 m, 31 Mar–13 Apr 1962, numerous colonies in spirit (4 jars) + 1 microslide preparation, coll. W. J. Rees, 1962.10.7.15, 36, 43, 67. Sneholm, Kosterfjord, Sweden, 40 m, 28 Sep 1964, small colony on *Flustra* sp. (Bryozoa), coll. W. J. Rees, 1965.1.14.175. Shetland, 1861, fertile fragment in spirit, coll. A. M. Norman, 1912.12.21.338. Cromarty harbour, NE Scotland, 18 m, 8 Mar 1907, two fragments on microslide, coll. J. Ritchie, 1964.8.7.143 (mentioned, Rees & Thursfield, 1965 : 138). Off Sanda I., Argyll, Scotland, 20–30 m, several colonies on *Flustra* sp., coll.R. B. Pike, 1955.11.15.12. Redcar, Yorkshire, England, 1907, fertile fragments on 2 microslides, coll. and det. J. Ritchie, 1964.8.7.144–145 (Table 21; mentioned, Rees & Thursfield, 1965 : 138). Bridlington Bay, Yorkshire, 7 Nov 1921, two fragments on microslide, coll. Ministry of Agriculture & Fisheries, 1956.2.2.8 (Fig. 23a & Table 21). Port Erin, Isle of Man, 1893, fertile fragment from *Flustra* colony on microslide, coll. & det. E. T. Browne, 1961.11.4.49 (Fig. 23b & Table 21). Hastings, Sussex, fragments on *Flustra* on microslide, coll. G. Busk, 1899.7.1.5834. Ilfracombe, Devon, 25 m, 31 May 1904, several colonies in spirit + 1 microslide preparation, coll. A. M. Norman, 1912.12.21.590 (Fig. 23c–d & Table 21).

DESCRIPTION. Colonies usually described as being of two forms, but these probably intergrade. The first comprises creeping stolons with irregularly spaced erect hydrocauli which are usually unbranched, up to 40 mm; the second has hydrothecae and gonothecae borne directly on the stolon. Hydrocaulus in erect specimens variably flexuose, hydrothecae alternate, one per internode. Hydrothecae short, $\frac{1}{4}$–$\frac{2}{3}$ adnate (Naumov, 1969); sides with typically 3–4 horizontal grooves, variable in depth, sometimes slight and on outer wall only, but usually much deeper and completely encircling hydrotheca; characteristic deep furrow below aperture on outer side (Broch, 1918; Naumov, 1969), aperture consequently inclined outwards; aperture operculate, 4-cusped. Hydranth inadequately described, but known to have a diverticulum [Leloup, 1952: fig. 98 B1; BM(NH) material 1956.2.2.8, 1962.10.7.36]. Gonothecae ? ♂ = ♀, large, ovoid, variably furrowed, occasionally only distally; aperture terminal, 4 (or 3 long + 1 short)-spined. One poorly preserved ♀ specimen has structures which are possibly acrocysts [BM(NH) 1964.8.7.145].

Measurements. See Table 21.

Table 21 *Sertularella rugosa*. Measurements in μm

	Erect specimens		Stoloniferous specimens	
	NE England (1964.8.7.145)	NE England (1956.2.2.8)	SW England (1912.12.21.590)	Isle of Man (1961.11.4.49)
Hydrotheca				
Outer side	250–300	380–450	350–400	330–420
Inner side, length adnate	160–250	160–220		
Inner side, length free	260–390	380–450		
Diameter of aperture	180–220	190–240	180–220	200–220
Internode				
Length	370–440	280–380		
Gonotheca (? ♂ = ♀)				
Length	1100–1600†			1350–1850‡
Maximum diameter	950–1150†			850–1100‡
Maximum length of terminal spines	120			110

† ? ♀ from contents; ‡ ♂ from contents.

Variation. Hydrocauli of this species are variably flexuose. Depth of furrowing of hydrotheca and gonothecal walls varies from deep grooving to barely perceptible indentation (Fig. 23). The lateral subterminal notch below the hydrothecal aperture varies in depth so that the angle between aperture and hydrothecal axis varies within the approximate limits 30° and 70°. The portion of the inner hydrothecal wall which is adnate varies from $\frac{1}{4}$ to $\frac{2}{3}$.

Reproductive season. Fertile material recorded in April both off NW France and in Oslo Fjord (Teissier, 1965; Christiansen, 1972).

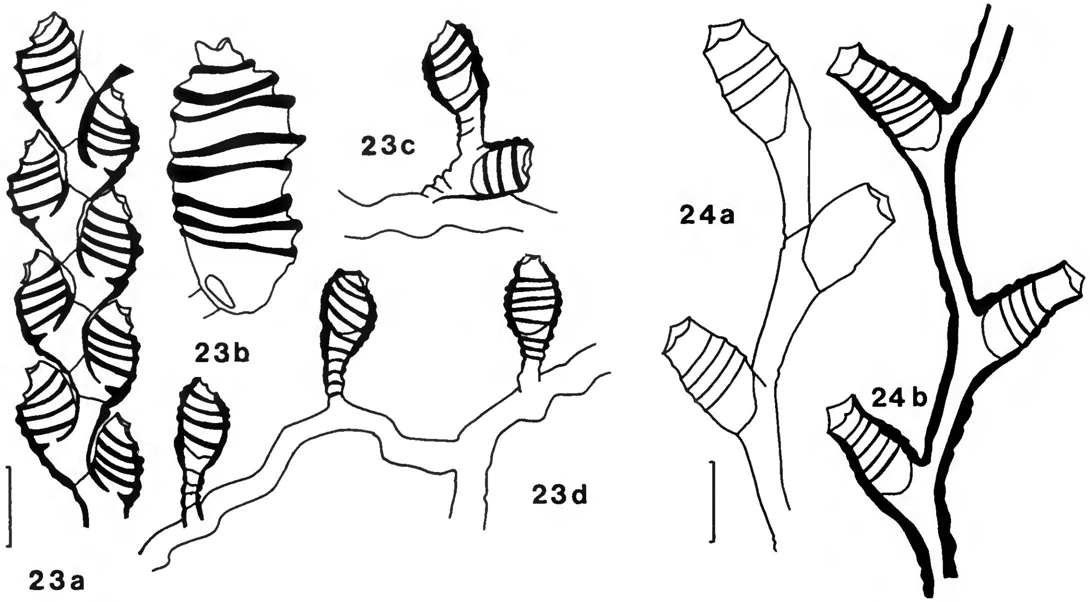
Distribution. Widely distributed in European coastal waters (Broch, 1918) and throughout the present area, including the Skagerrak, Oslo Fjord, Kattegat and the entrance to the Baltic (Stechow, 1927; Broch, 1928; Rees & Rowe, 1969; Christiansen, 1972; Rasmussen, 1973) but not the inner Baltic (Naumov, 1969; Christiansen, 1972).

Habitat. European specimens in the BM(NH) collection come from depths of 10–40 m. Naumov (1969) gives a normal depth range in Russian waters of 25–50 m with extreme limits of 0–263 m. The species has occasionally been recorded intertidally (Hincks, 1868; Broch, 1918). It commonly grows on *Flustra* spp. (Bryozoa), hydroids and brown algae (Hincks, 1868; Vervoort, 1946; Hamond, 1957); and has been recorded on lobster pots (Crothers, 1966). Hincks' statement that the species is commonly parasitic on *Flustra* almost certainly refers simply to substrate association.

Remarks. Differences from *S. tenella* are discussed under that species (p. 293). See also note 20, p. 309, for comments on *Ellisia* Westendorp, 1843.

Sertularella tenella (Alder, 1856)
(Fig. 24)

Sertularia rugosa var. Johnston, 1847 : 63.
Sertularia tenella Alder, 1856 : 357–358, pl. 13, figs 3–6; Alder, 1857 : 113–114, pl. 4, figs 3–6.
Sertularella tenella: Hincks, 1868 : 242–243, pl. 47, figs 3, 3a–c; Hartlaub, 1901 : 63–64, pl. 5, figs 21–23, pl. 6, figs 2, 4, 7, 9, 10 (syn. *S. geniculata* Hincks, 1874); Broch, 1918 : 104–105; Vervoort, 1946 : 228–229, fig. 97b; Yamada, 1950 : 12–13, pl. 1, fig. 11 (syn. *S. atlantica* Stechow); Naumov, 1960 : 341–342, fig. 231; Blanco, 1963 : 173–174 (syn. *S. geniculata* Hincks, *S. microgena* von Lendenfeld); Naumov, 1969 : 368–369, fig. 231; Calder, 1970 : 1529–1531, pl. 6, fig. 6.
Sertularella geniculata Hincks, 1874 : 152–153, pl. 7, figs 13–14.
Sertularella atlantica Stechow, 1920 : 21–22, fig. 2a; Stechow, 1923 : 183–184, fig. A^{1}a.



Figs 23–24. Fig. 23 *Sertularella rugosa.* (a) part of erect hydrocaulus, NE England (1956.2.2.8); (b) gonotheca, Isle of Man (1961.11.4.49); (c–d) part of stoloniferous colony, including (c) short erect hydrocladium, SW England (1912.12.21.590); scale (a–d) = 500 μm. **Fig. 24** *S. tenella.* (a) tip of thin walled hydrocladium, W Norway (1962.11.7.40); (b) part of thick walled hydrocladium, W Scotland (1888.12.21.3a); scale (a–b) = 500 μm.

TYPE LOCALITY AND MATERIAL. No type locality was given by Alder but Cornelius & Garfath (in press) have recently restricted it to the coast of Northumberland, England. Syntype herbarium material is extant in the Hancock Museum, Newcastle upon Tyne (several colonies on *Abietinaria abietina*, preserved on a herbarium sheet) and in the British Museum (Natural History) (two dried hydrocauli, 1857.8.3.49) (Cornelius & Garfath).

OTHER MATERIAL EXAMINED. (All infertile.) Dodd Narrows, Vancouver Island, Canada, 30 m, several fragments in spirit, coll. Miss Pixell, 1919.9.19.14. N side of Vattlestraumen, Espegrend, nr Bergen, Norway, 15–25 m, 13 Apr 1962, hydrocaulus in spirit, coll. W. J. Rees, 1962.10.7.14. SW of Flattevossen, nr Espegrend, 30 m, 9 Aug 1962, hydrocaulus in spirit + 1 microslide preparation, coll. W. J. Rees, 1962.11.7.40 (Fig. 24a). SE of Lilla Sneholm, Kosterfjord, W. Sweden, 40 m, 28 Sep 1964, colony in spirit, coll. W. J. Rees, 1965.1.14.177. Vattenholmen, Kosterfjord, 80–120 m, 28 Sep 1964, fragments in spirit, coll. W. J. Rees, 1965.1.14.98. Vädero Is, W Sweden, 80 m, 1 Oct 1964, fragments in spirit, coll. W. J. Rees, 1965.1.14.122. Gåsö Ranna, Gullmarsfjord, W Sweden, 20–30 m, 27 Aug 1962, several colonies in spirit + 1 microslide preparation, coll. W. J.

Rees, 1962.11.8.16. Smorhullen, Gullmarsfjord, 50 m, 13 Oct 1964, several colonies in spirit, coll. W. J. Rees, 1965.1.14.170. Loch Buie, Mull, Argyll, Scotland, 20–30 m, fragments on microslide, coll. J. Murray, 1888.12.21.3a (Fig. 24b). Sound of Mull, 40–200 m, 1 Oct 1970, several colonies in spirit, coll. P. F. S. Cornelius, 1971.5.11.42–43. Off Millport, Gt Cumbrae I., Bute, 40 m, Sep 1970, several colonies in spirit, coll. C. Edwards, 1971.5.11.44. Off Durham, England, 40–70 m, Jul 1874, several colonies in spirit + 1 microslide preparation, coll. A. M. Norman, 1912.12.21.333. Off NW Africa, 34° 57′ N, 11° 52′ W, 1070 m, colony on lopheliid coral, coll. J. Y. Buchanan, 1884.3.14.7.

DESCRIPTION. Colonies usually comprising creeping stolons with irregularly spaced, erect, usually unbranched hydrocauli up to 20 mm, but hydrothecae sometimes borne directly on the stolon. Hydrocaulus in erect specimens variably flexuose. Hydrothecae alternate, one per internode; up to $\frac{1}{4}$ adnate; walls with 5–6 annulations, sometimes (Bennitt, 1922) slight and on outer wall only, or entirely absent; rim 4-cusped, at 90° to hydrothecal axis, lacking notch below rim on outer side. Gonothecae ? ♂ = ♀, large, oval, rugose, terminal 3–4 spined aperture; similar to those of *S. rugosa* (see Remarks).

MEASUREMENTS. See Table 22.

Table 22 *Sertularella tenella.* Measurements in μm

	Russia (Naumov, 1969)	Canada (Calder, 1970)	Japan (Yamada, 1950)	W Europe (Vervoort, 1946)
Hydrotheca				
Outer side	500–540	660–790	450	500
Inner side, length adnate	140–230	310–350		
Inner side, length free	420–480	480–610		
Diameter of aperture	230–370	250–310	220	
Internode				
Length		1000–2100		
Gonotheca (? ♂ = ♀)				
Length	2000 (max)			900–1000
Maximum diameter	1000			550

VARIATIONS. See Remarks.

REPRODUCTIVE SEASON. There is apparently no published information from European waters, and there are no fertile specimens in the BM(NH) collection.

DISTRIBUTION. Widely distributed in the eastern North Atlantic (Broch, 1918) and found sporadically throughout the present area including the Kattegat and Skagerrak (Stechow, 1927; Broch, 1928; Rees & Rowe, 1969) but not east of the entrance to the Baltic (Broch, 1928; Naumov, 1969).

HABITAT. European specimens in the BM(NH) collection come from 10–120 m depth-range. Naumov (1969) gave a normal depth-range of 25–150 m with extreme limits of 25–1000 m. Recorded growing on other hydroids (Hincks, 1868; Vervoort, 1946).

REMARKS. The characters on which the two nominal species *Sertularella rugosa* (Linnaeus, 1758) and *S. tenella* (Alder, 1856) have been separated are rather few (Table 23), and until they can be re-assessed it is perhaps best to regard the continued separation of the two taxa as provisional. The single feature by which BM(NH) specimens can be separated is the presence or absence of the notch below the rim on the outer wall of the hydrotheca as seen from the side (Figs 23, 24). The depth of this notch in *S. rugosa* is variable, as is the general rugosity of the perisarc in both species, and it may be that the notch has no systematic value.

Sertularella geniculata Hincks, 1874, described from Icelandic material, was referred to the present species by Hartlaub (1901), whose opinion is followed here.

Table 23 Previously recorded differences between the nominal species *Sertularella rugosa* (Linnaeus, 1758) and *S. tenella* (Alder, 1856) (after Alder, 1856, 1857; Hincks, 1868; Hartlaub, 1901; Kramp, 1935; Vervoort, 1946; Yamada, 1950; Naumov, 1960, 1969)

Sertularella rugosa	*Sertularella tenella*
Hydrothecal aperture inclined outwards with respect to axis of hydrotheca	Hydrothecal aperture not inclined outwards
Notch below rim of hydrotheca on outer side	No notch
Hydrotheca ¼–½ adnate	Hydrotheca ¼ adnate
3–4 annuli on hydrotheca	5–6 annuli on hydrotheca

Sertularia cupressina Linnaeus, 1758
(Fig. 25)

Corallina muscosa alterna vice denticulata, . . . Ellis, 1755 : 6–7, pl. 2, figs C, c.
Corallina Cupressi forma, denticulis obtusis, . . . Ellis, 1755 : 7, pl. 3, figs A, a.
Sertularia cupressina Linneaus, 1758 : 808 (binomen for Corallina Cupressi forma, . . . of Ellis); Pallas, 1766 : 141–144 (syn. *S. argentea* Linnaeus); Linnaeus, 1767 : 1308; Hincks, 1868 : 270–272, pl. 57; Winther, 1879 : 308–309, pl. 6, figs 17–20; Broch, 1918 : 124–126 (syn. *S. argentea* Linnaeus); Vervoort, 1946 : 243–249, figs 107, 108, 114a (syn. *S. argentea* Linnaeus; *S. dentata* Lamouroux, 1816; *S. splendens* Lamouroux, 1816; *S. uber* Dalyell, 1834); Hancock *et al.*, 1956 : 307–325, figs 1a–d, 2c; Naumov, 1960 : 361–362, fig. 252 (syn. *S. argentea* Linnaeus); Naumov, 1969 : 390–391, fig. 252 (syn. *S. argenta* Linnaeus); Vervoort, 1972 : 183 (syn. *S. argentea* Linneaus); Cornelius, 1975b : 405 [syn. *S. echinata* Linnaeus (part)]; Calder, 1975 : 309–310, fig. 5f.
Sertularia argentea Linnaeus, 1758 : 809; Linnaeus, 1767 : 1308; Hincks, 1868 : 268–270, pl. 56; Hancock *et al.*, 1956 : 307–325, figs 1e–m, 2a–b, d–e, 3a–j, 5a–f; Calder, 1975 : 308–309, fig. 5e.
Sertularia echinata Linnaeus, 1761 : 541 (part); Pallas, 1766 : 152 (part); Linnaeus, 1767 : 1310 (part).
? *Sertularia pinnata* Pallas, 1766 : 136–137 (part); (see p. 267).
? *Sertularia cupressina* var. *tenera:* Winther, 1879 : 309–311, pl. 6, figs 7–16 (see p. 301).
Sertularia argentella Pennington, 1885 : 117, pl. 8, figs 1, 1a.

NOMENCLATURE. Pallas (1766) acted as first reviser when regarding *S. cupressina* Linnaeus, 1758, and *S. argentea* Linnaeus, 1758, as conspecific, and his adoption of the name *cupressina* for the species is followed here.

TYPE MATERIAL AND LOCALITY. The original diagnoses of the two nominal species *Sertularia cupressina* Linnaeus, 1758, and *S. argentea* Linnaeus, 1758, were not accompanied by descriptions or collecting data. It is, therefore, probable that the diagnoses were made from previously published accounts rather than from specimens (cf. note 13, p. 309). It follows that the material of *S. cupressina* in the Linnean collection of the Linnean Society of London (Savage, 1945 : 206) cannot be regarded as the original type series, and that the specimens illustrated by Ellis (1755 : pl. 3, figs A, a), the sole work cited by Linnaeus (1758), can be regarded the type series of *S. cupressina.* (Linnaeus cited several works under *S. argentea.*) It is virtually certain, however, that almost no Ellis hydroid material remains (Cornelius, in prep.), and that the original type series of *S. cupressina* is lost.

The Linnean Society of London collection contains (Savage, 1945) two herbarium sheets of hydroid material labelled *Sertularia cupressina.* For the reasons outlined above it seems Linnaeus received them after diagnosing this species, but nevertheless later identified them with it. Savage numbered the two sheets 1298.5–6. The first sheet bears a much branched infertile colony comprising four main hydrocauli *c.* 200 mm long, each with many side branches. The second bears a single *c.* 300 mm specimen forked near the tip, with many side branches. The specimen on sheet 1298.5 is here designated neotype of *Sertularia cupressina* Linnaeus. It is likely that the specimen came from Ellis (cf. Cornelius, 1975*a* : 273, footnote), and it seems appropriate to restrict the type locality of *S. cupressina* to the coasts of England, from whence Ellis obtained specimens. There is no material labelled *S. argentea* in the Linnean collection and no type material of that nominal species is identified here.

OTHER MATERIAL EXAMINED. *Sertularia cupressina* is exceptionally well represented in the BM(NH) collections and only measured, illustrated or otherwise mentioned specimens are listed. North Sound, Orkney, Scotland, 44 m, 13 Jul 1907, fertile fragments on microslide, coll. J. Ritchie, 1964.8.7.160 (mentioned, Rees & Thursfield, 1965 : 146, as *S. argenta*). Isle of Man, 10 Sep 1894, colony on microslide, coll. E. T. Browne, 1961.11.4.78 (Table 24). Various localities off south Devon, England, 4 microslide preparations of parts of colonies, coll. E. T. Browne, 1961.11.4.74, 77 (Table 24), 79. Hastings, Sussex, colony on microslide, coll. G. Busk, 1899.7.1.6134. Off Leigh, Essex, parts of colonies on 9 microslides, coll. F. J. Lambert, 1927.7.7.10 (Fig. 25; Table 24).

DESCRIPTION. Colonies erect, monosiphonic, long, with short side branches arranged spirally or (particularly in young specimens) in one plane; side branches themselves branched, dichotomously or alternately. Hydrothecae in sub-opposite to sub-alternate pairs, cylindrical basally, tapered distally and variably out-turned, outer wall straight to concave; inner side $\frac{1}{3}$–$\frac{2}{3}$ adnate; rim 2-cusped, cusps equal or outer longer, this varying along a hydrocaulus (longest cusps on oldest hydrothecae); frail 2-flapped operculum. Axillary hydrothecae present. Hydranth very extensile, *c.* 20 tentacles (Hincks, 1868). Gonotheca ♂ = ♀, changing shape during development; club-shaped when young, fully developed ones widest $\frac{2}{3}$–$\frac{3}{4}$ from base, with 1–2 opposite pairs of distal lateral horns usually developing later although (Broch, 1918) hornless mature gonothecae occur; aperture terminal, circular, on very short cylindrical process, with much-branched minute internal spines which are probably desmocytes; when mature, contents of ♂ creamy white, of ♀ pink; ♀ acrocyst widely recorded, ♂ acrocyst recorded by Hancock *et al.* (1956) only.

MEASUREMENTS. See Table 24.

Table 24 *Sertularia cupressina.* Measurements in μm

	SE England (1927.7.7.10)	SW England (1961.11.4.77)	Isle of Man (1961.11.4.78)
Hydrothecae			
Outer side	280–350	240–255	245–255
Inner side, length adnate	180–220	220–240	220–240
Inner side, length free	220–250	120–140	160–180
Maximum diameter	120–160	120–130	130–150
Gonotheca (? sex)			
Length	800–920	950–1100	
Maximum diameter	400–500	280–350	

VARIATIONS. See Description.

REPRODUCTIVE SEASON. Fertile material recorded May–November in Thames estuary (Hancock *et al.*, 1956), March at Plymouth (Marine Biological Association, 1957), March–May at Roscoff (Teissier, 1965), May–July in the Faroes (Kramp, 1929), February–September in Jersey (Vervoort, 1949), February–May and again in October–December in the Kattegat (Rasmussen, 1973).

DISTRIBUTION. Common throughout most of the area, particularly the southern North Sea where it is fished (Hancock *et al.*, 1956). Found in the Kattegat (Stechow, 1927; Rasmussen 1973) but rare (Broch, 1928) or absent (Naumov, 1969) further east in the Baltic and apparently absent from Oslo Fjord (Christiansen, 1972). The North Atlantic distribution was summarized by Broch (1918).

HABITAT. Sandy bottoms from 0 to 100 m, less commonly deeper. Not intertidal but common among strand refuse.

REMARKS. Although Hancock *et al.* (1956) emphatically retained specific status for *Sertularia argentea* Linnaeus, 1758, many authors have regarded it conspecific with *S. cupressina* Linnaeus, 1758 (e.g. Pallas, 1766; Broch, 1918; Kramp, 1935; Vervoort, 1946, 1972; Leloup, 1952; Naumov, 1960, 1969). Others, like Hancock, have upheld a separation (e.g. Linnaeus, 1767; Hincks, 1868;

Nutting, 1904; Fraser, 1944; Bruce *et al.*, 1963;[17] Rees & Thursfield, 1965;[17] Calder, 1975[17]). Nevertheless, the account of Broch (1918), accepting only one species, is particularly convincing and it and the opinions of almost all European workers this century are followed here.

Sertularia echinata Linnaeus, 1761, can be regarded a junior synonym of the present species for reasons given elsewhere (Cornelius, 1975*b*).

Sertularia pinnata Pallas, 1766, was founded on two illustrations of Baster (1762 : pl. 1, figs 6a–b) which Vervoort (1946) considered might represent *S. cupressina.* However, the identity of Baster's illustrations is doubtful. It is discussed under *Diphasia nigra* (p. 267).

Sertularia uber Dalyell, 1834, was referred to *S. argentea* by Johnston (1838), and can confidently be referred to the present species.

Sertularia distans Lamouroux, 1816

(Fig. 26)

Sertularia distans Lamouroux, 1816 : 191; Allman, 1877 : 25, pl. 16, figs 9–10; Billard, 1906 : 187–191, figs 10–11 (syn. *Sertularia gracilis* Hassall, 1848; *S. tenuis* Bale, 1884; *S. pourtalesi* Nutting, 1904; *S. stookeyi* Nutting, 1904; *Dynamena mediterranea* Marktanner-Turneretscher, 1890); Picard, 1951 : 348; Robins, 1969 : 333; Millard, 1975 : 306, figs 99e–h (syn. *S. gracilis* Hassall).

Sertularia gracilis Hassall, 1848 : 2223; Hassall & Coppin, 1852 : 162–163, pl. 21, fig. 3; Hincks, 1868 : 262–263, pl. 53, fig. 2; Winther, 1879 : 305–307, pl. 6, figs 5–6; Pennington, 1885 : 113; Pictet, 1893 : 48–50, fig. 41; Pictet & Bedot, 1900 : 23; Nutting, 1904 : 57–58, pl. 3, fig. 10; Fraser, 1944 : 282–283, pl. 61, fig. 270; Vervoort, 1946 : 251; Picard, 1951 : 348; Hamond, 1957 : 317; Teissier, 1965 : 25; Redier, 1967 : 399 (syn. *S. lamourouxi:* Bedot, 1925); Fey, 1969 : 401.

Sertularia pourtalesi Nutting, 1904 : 59, pl. 5, fig. 5 (nom. nov. pro *S. distans* sensu Allman, 1877); Fraser, 1944 : 286, pl. 61, fig. 273.

Sertularia heterodonta Ritchie, 1909*c* : 79–81, fig. 4.

Sertularia distans var *gracilis:* Billard, 1912 : 465; Leloup, 1935 : 47–48, figs 28–29; Vervoort, 1949 : 154, figs 4a–b; Millard, 1957 : 221–223, fig. 12; Rees & Thursfield, 1965 : 146–147; Redier, 1966 : 85; Rees & White, 1966 : 278.

Tridentata heterodonta: Stechow, 1923 : 205.

Tridentata gracilis: Stechow, 1925 : 208, fig. G.

Sertularia distans gracilis: Millard, 1964 : 49 (syn. *S. heterodonta* Ritchie, 1909*c*).

Tridentata distans: Hirohito, 1969 : 23, fig. 1.6.

non *Dynamena distans* Lamouroux, 1816 : 180, pl. 5, figs 1a, 1B; = *D. pumila* (Linnaeus, 1758); (see p. 273).

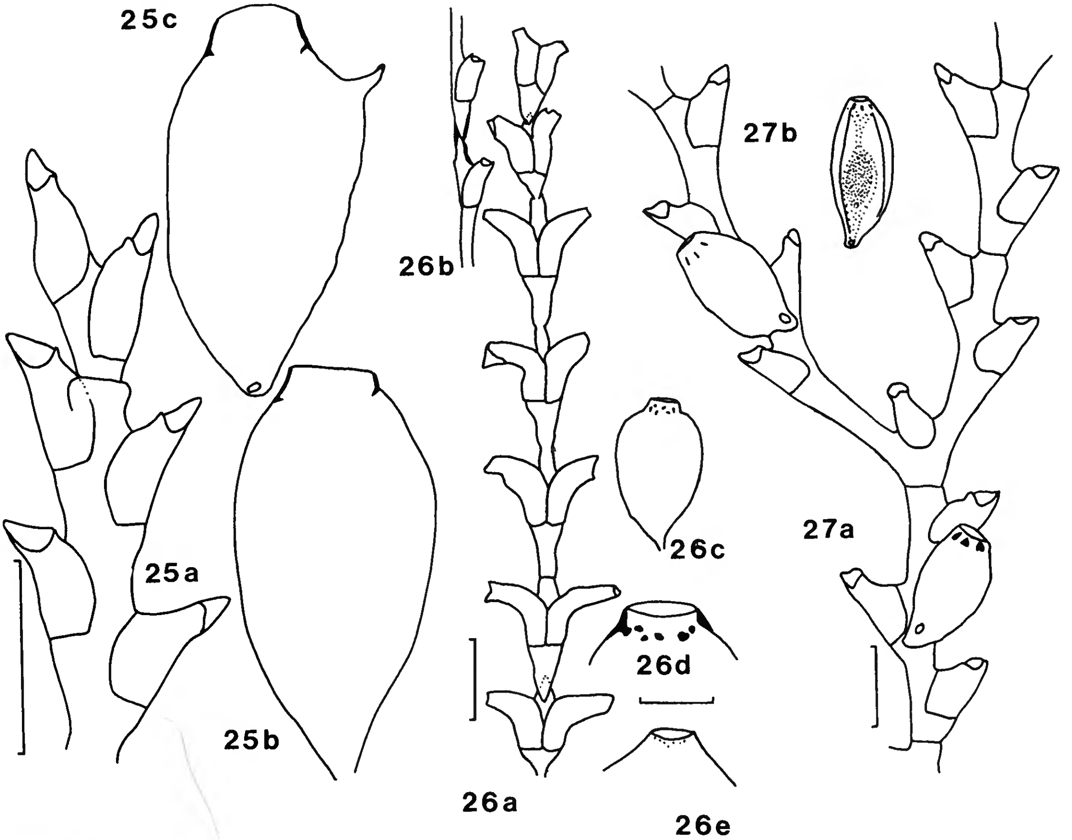
? Dynamena dubia Billard, 1922a : 344–348, fig. 1 (see note 21, p. 309).

TYPE LOCALITY AND MATERIAL. 'Australasia' (Lamouroux, 1816).[18] The type material of this species was formerly housed in the collections of the Botanical Institute, Faculty of Science, University of Caen, but was almost certainly destroyed along with the bulk of the Lamouroux collections during the Second World War (Redier, 1967). However, Billard (1906) had previously examined the material and found it to be identical with some non-type material he described and illustrated. The type material itself was apparently never illustrated.

TYPE MATERIAL OF OTHER NOMINAL SPECIES. *Sertularia gracilis* Hassall, 1848, two dense growths of fertile colonies on fragments of the red alga *Chondrus crispus* Stackh. (det. J. H. Price), 1848.7.14.6 (mentioned, Gray, 1848 : 150), and several fragments of hydrocauli on a microslide (1899.7.1.5867, ex G. Busk coll.); all material collected by J. Coppin, from Brighton, Sussex, England, and along with the next-mentioned to be regarded as the syntype series.

Two colonies in spirit and another on a herbarium sheet in the Hancock Museum, Newcastle upon Tyne, were formerly in Joshua Alder's collection (Cornelius & Garfath, in press). The spirit specimens are preserved together in a single tube, labelled '*Sertularia gracilis*, Brighton' in Alder's hand, the word 'Guernsey' having been added later by someone else. The colonies are on an alga (probably *Chondrus crispus*, det. J. H. Price). The herbarium specimen is a dense growth on an alga, also probably *Chondrus*, and is labelled 'Brighton, J. Coppin, Esq.' (the last very faint, in the lower right-hand corner of the sheet). It seems that both spirit and herbarium specimens can be regarded part of the type series.

NON-TYPE MATERIAL EXAMINED. 'Yarmouth', England, colony on alga, herbarium specimen, coll. 1807, 'Mr Wicks', 1956.6.2.23. (There is no indication whether the specimen is from Great Yarmouth, Norfolk, or Yarmouth, Isle of Wight.) R. Deben estuary, Suffolk, dense growth on dead colony of *Hydrallmania falcata* (Linnaeus, 1758), spirit, coll. D. L. Serventy, 1933.7.1.11. Off Enys Head, nr Kennack Sands, Lizard, Cornwall, 15 m, 28 May 1974, several colonies on *Laminaria* stipe, spirit, coll. J. D. George, 1975.5.14.1. Misery Point, R. Yealm estuary, S Devon, 4 Jul 1973, intertidal, several fertile hydrocladia on algae, spirit + 1 microslide preparation, coll. P. F. S. Cornelius, 1974.12.18.1–2 (Fig. 26c–e; Table 25). Swanage, Dorset, several fertile hydrocladia on microslide, coll. T. Hincks, 1899.5.1.177. Brighton, Sussex, 1806, infertile fragments on microslide, coll. 'Brodie', ex G. Busk coll., 1899.7.1.5862. Brighton, 1807, colony on brown alga, herbarium specimen, coll. 'Mr Wicks', 1956.6.2.22. Off Eastbourne, Sussex, 25 Sep 1948, fertile fragment on microslide, coll. s.s. 'Manihine' (sta. 55), 1948.9.28.83. Bridlington Bay, Yorkshire, 1928, fertile ♀ material with acrocysts (Zoological Museum, Amsterdam, colln) and 3 infertile microslide preparations (no. 172, Natural History Museum, Leiden, colln.); 'ex BM(NH) collection'! Altea, near Alicante, S Spain, 1 m, 5 Sep 1965, 8 microslides of material collected from algae,



Figs 25–27. Fig. 25 *Sertularia cupressina.* (a) terminal region of hydrocladium, (b–c) gonothecae, SE England (1927.7.7.10), scale (a–c) = 500 μm. **Fig. 26** *S. distans.* (a) terminal region of hydrocaulus, S Spain (1965.10.8.1–8); (b) an oblique node, lateral view, Azores (1962.2.10.15); (c–e) gonotheca, and aperture regions of two others, SW England (1974.12.18.1–2); scale (a–c) = 500 μm, (d–e) = 200 μm. **Fig. 27** *S. tenera.* (a–b) hydrocladia with ♂ gonothecae, and separate ♂ gonotheca, W Sweden (1911.12.8.23); scale = 500 μm.

coll. Miss J. Royston, 1965.10.8.1–8 (Fig. 26a; Table 25). Frodinhas, Azores, 10 m, Aug 1959, two hydrocladia on microslide, coll. Imperial College Azores Expedition, 1962.2.10.15 (Fig. 26b).

DESCRIPTION. Colony comprising a creeping stolon and irregularly spaced erect hydrocauli, 50–125 mm, occasionally branched. Hydrothecae often lacking from base of hydrocaulus; in opposite pairs, distance between successive pairs equal to or longer than attached part of hydrotheca, sometimes much longer. Hydrotheca tubular, sharply or gradually outward-curving (Fig. 26), length : breadth ratio from 2 to 8; aperture 2-cusped, occasionally with minute to small third cusp on outer margin, rim sometimes renovated; 2-flapped operculum. Members of a pair of hydrothecae often contiguous but (Millard, 1957; present material) this variable even along a hydrocaulus. About half inner wall adnate, but this proportion smaller in longer hydrothecae. Nodal contrictions of two kinds, oblique and transverse (Fig. 26a); oblique nodes between every second or third pair of hydrothecae, transverse nodes usually alternating with them. Occasional distal stolons (e.g. BM(NH) 1962.2.10.16). Hydranth said to have abcauline diverticulum of enteron when contracted (Billard, 1925; Millard, 1957; Hirohito, 1969); living ectoderm sometimes with dark speckling (Picard, 1951; Hamond, 1957). Gonotheca ♂ = ♀, ovoid, smooth, thin walled, aperture broad, terminal, on short collar of indefinite length or lacking; base pedicellate; borne on hydrocaulus below hydrothecae (Vervoort, 1949; Hirohito, 1969) or sometimes (Leloup, 1935) on stolon of colony; ♀ gonotheca said to contain a single egg by Vervoort (1949) but Millard (1975) illustrated several eggs, retained in an acrocyst.

MEASUREMENTS. See Table 25.

Table 25 *Sertularia distans*. Measurements in μm

	S Spain (1965.10.8.7)	SW England (1974.12.18.1)
Hydrotheca		
Outer side	420–450	230–250
Inner side, length adnate	270–300	110–130
Inner side, length free	260–290	190–220
Maximum diameter	110–130	90–120
Diameter of aperture	90–120	70–90
Gonotheca (♂ = ♀)		
Length		880–900
Maximum diameter		520–600
Diameter of aperture		130–170

VARIATIONS. The following morphological features have been used by various authors in defining the present species but appear to be sufficiently variable to be unreliable systematic characters: hydrothecal length, abruptness of hydrothecal flexure, distance between two hydrothecae of a pair (which may touch), vertical distance between one pair of hydrothecae and the next; presence or absence of speckling in living ectoderm of hydranth, presence or absence of collar beneath gonothecal aperture, presence or absence of hydrothecae near base of hydrocaulus, degree of distal tapering of each hydrotheca, number of pairs of hydrothecae between oblique internodes (1–3 pairs).

REPRODUCTIVE SEASON. Fertile material recorded April–September at Roscoff (Teissier, 1965), May–June in the Channel Isles (Vervoort, 1949), July in Norfolk (Hamond, 1957), July–September along south coast of England (present material).

DISTRIBUTION. Widespread in warm Atlantic coastal waters (Millard, 1957), reaching the south coast of England, NW Wales and Norfolk, and probably sporadically further north to Yorkshire. Apparently unrecorded from 'Ireland', Belgium or Holland (Vervoort, 1946; Leloup, 1952). Vervoort's (1949) appraisal of the species as 'comparatively rare along the Channel coasts of France and Great Britain' seems apt. However, widespread records of fertile specimens from the English Channel suggest that at least in some years the species finds suitable conditions there. All records are given: St Malo and Roscoff (Vervoort, 1949; Teissier, 1965), Channel Isles (Vervoort, 1949), Scilly Isles (Robins, 1969), S Cornwall (present material), Dorset (Hincks, 1868; Waddington, 1914), Sussex, Devon, Cornwall and Norfolk (Hincks, 1868), Kent (Sorby, 1908), Pembrokeshire (P. J. Hunnam, pers. comm.), Bangor and Bardsey Island, Anglesey, N Wales (Pennington, 1885; Pyefinch, 1943; K. Hiscock, pers. comm.), Suffolk (present material), Norfolk (Hamond, 1957), Yorkshire (present material). Records from Durham, Shetland, Blackpool and the Clyde Sea (Hincks, 1868; Norman, 1869; Pennington, 1885; Rankin, 1901) seem unusually far north and may be invalid.

HABITAT. Recorded in the present area from the intertidal zone (present material) down to 60 m (Teissier, 1965). Hamond (1957) found the usual substrate to be *Hydrallmania falcata* (Linnaeus, 1758) in Norfolk waters but use of a variety of plant, animal and inanimate substrates has been recorded in other places.

REMARKS. The nominal species *Sertularia gracilis* Hassal, 1848, type localities Brighton and Ramsgate (Hassal & Coppin, 1852), has been regarded as valid by some authors and as a variety or subspecies of *S. distans* Lamouroux, 1816, by others (see synonymy); but in agreement with Billard (1906, 1925) and Millard (1975) the two are here regarded conspecific. Distinguishing features between the two taxa were apparently not given until Picard (1951) presented a synopsis, and the widespread use of the combination '*S. distans* var. *gracilis*' seems ill founded. There seems little doubt that the type material of *S. gracilis* can be referred to *S. distans*.

Hirohito (1969) referred the present species to the genus *Tridentata* Stechow, 1920, since that genus was diagnosed as having an abcauline diverticulum of the enteron; but since *Sertularia* as restricted by Broch (1918), Millard (1975) and others has one too this transfer seems unnecessary.

Dynamena distans Lamouroux, 1816, is here referred to *D. pumila* (see p. 273).

The two similar-looking species here called *Dynamena pumila* (p. 271) and *Sertularia distans* (present species) probably occur together in some places at low shore levels and in the shallow sublittoral. A useful recognition mark seems to be the 'oblique' nodal constrictions of the present species, lacking in *D. pumila*, while the presence (in *S. distans*) or absence (in *D. pumila*) of a hydranth caecum might help with difficult material.

The present species was also redescribed by Millard (1975). The similar species *D. dubia* Billard, 1922a, is discussed in note 21 (p. 309).

Sertularia tenera Sars, 1874

(Fig. 27)

Sertularia tenera Sars, 1874 : 108–109, pl. 4, figs 1–4; Broch, 1910 : 171–173, figs 27–28, pl. 2, fig. 5; Kudelin, 1914 : 148–165, figs 21–24; Broch, 1918 : 127–130, fig. 67 [syn. *S. arctica* Allman; *S. albimaris* Thompson; *S. argentea* sensu Bergh; *S. dijmphnae* Bergh; *S. unilateralis* Bonnevie; *S. thomsoni* (sic) Schydlowsky]; Kramp, 1935 : 192–193, fig. 79B; Naumov, 1960 : 353–354, fig. 244; Rees & Thursfield, 1965 : 148; Naumov, 1969 : 382, fig. 244; Calder, 1970 : 1536, pl. 8, fig. 1; Christiansen, 1972 : 302; Vervoort, 1972 : 184 (syn. *S. arctica* Allman).

Sertularia arctica Allman, 1874*b* : 179; Allman, 1876 : 264, pl. 14, figs 1–2; Jaderholm, 1909 : 93–95, pl. 10, figs 5–13.

? *Sertularia cupressina* var. *tenera:* Winther, 1879 : 309–311, pl. 6, figs 7–16 (see p. 301).

Sertularia albimaris: Thompson, 1884 : 5, pl. 1, figs 1–3; (non Mereschkowsky, 1878 : 331–332, pl. 14, figs 3–5; see Remarks).

Sertularia thomsoni (sic) Schydlowsky, 1902 : 213–215, pl. 5, figs 55–61 (nom. nov. pro *S. albimaris* sensu Thompson, 1884); Jaderholm, 1909 : 92–93, pl. 9, figs 11–12 (but not 13).

Thuiaria tenera: Nutting, 1904 : 70, pl. 11, figs 9–12; Ritchie, 1911 : 218–220, figs 2–5; Fraser, 1944 : 308, pl. 65, fig. 295.

TYPE LOCALITY AND MATERIAL. 11 'miles' WNW of Skudesnäs, SW Norway (59° 09′ N, 5° 17′ E), 273 m ('150 fm'), infertile colony (Sars, 1874); material not located.

MATERIAL EXAMINED. (The Scottish records seem dubious; see Distribution.) All BM(NH) material of this species is listed. Spitzbergen, 3 infertile colonies, micro-preparations, pres. A. E. Eaton, 1874.4.4.57. Spitzbergen, several fragments in spirit and on 4 microslides, ♂ & ♀ gonothecae represented, coll. G. M. R. Levinsen, 1911.12.8.23 (Fig. 27; Table 26). Gåsö Ranna, Gullmarsfjord, W Sweden, 20–30 m, 27 Aug 1962, several infertile fragments in spirit, coll. and det. W. J. Rees, 1962.11.8.17. ? Off Tighnabruaich, Kyles of Bute, Argyll, Scotland, Jun 1910, fertile fragments of separate colonies on 2 microslides, coll. J. Ritchie, 1964.8.7.165–166 (mentioned, Ritchie, 1911; Rees & Thursfield, 1965) (see Remarks). ? Off Mull of Kintyre, Argyll, 100 m, infertile fragments taken from colony epizoic on *Halecium muricatum* (Ellis & Solander, 1786), preserved on microslide, coll. Sir John Murray, pres. J. Ritchie, 1964.8.7.164 (mentioned, Ritchie, 1911; Rees & Thursfield, 1965) (see Remarks). ? 'Between the Cumbraes', Firth of Clyde, W Scotland, 30–50 m, 8 Jul 1885, branched infertile specimen in spirit, coll. and det. A. M. Norman, 1912.12.21.375 (see Remarks).

DESCRIPTION. Colonies 100–150 mm, erect, monosiphonic, alternate-pinnate basally but often spiral distally, hydrocaulus slightly wider than hydrocladia, some secondary branching (dichotomous or alternate). Main stem straight to flexuose (Naumov, 1969). Hydrocladia usually without hydrothecae for basal 2–3 hydrotheca-lengths, characteristically much narrowed basally; axillary hydrotheca present. Hydrothecae in sub-alternate pairs with nodal constrictions between every second to sixth hydrotheca; widest in centre, tapering proximally and rather more distally; outer wall usually almost straight but often slightly concave with a bend midway along (Fig. 27a); if straight tending to form continuous line with edge of perisarc below [see Broch (1910) and Kudelin (1914) for longer accounts of variation in shape of hydrotheca]; aperture with two rounded cusps, equal or outer longer; operculum 2-flapped, outer larger (Calder, 1970). Hydranth with abcauline diverticulum (Calder, 1970); otherwise apparently undescribed. Gonothecae previously described as dimorphic (e.g. Broch, 1910, 1918; Ritchie, 1911; Kudelin, 1914; Naumov, 1969; Calder, 1970); either ovoid, 4–6 sided in cross-section, with as many longitudinal ribs, terminal aperture on short, wide collar, with branched internal spines (? desmocytes); or similar but circular in cross-section, terminal spines not recorded; sometimes with an equatorial constriction (see Remarks). Broch (1910) considered ♂ polygonal and ♀ circular in cross-section, but Naumov (1969) found both kinds on one colony. The present material includes both ♂ and ♀ polygonal gonothecae, so it seems unlikely that there is always sexual dimorphism. Possibly polygonal and tubular gonothecae represent ends of a continuous series. ♀ gonothecae in BM(NH) material appear to contain only one egg each.

MEASUREMENTS. See Table 26.

Table 26 *Sertularia tenera.* Measurements in μm

	U.S.S.R. (Naumov, 1969)	Canada (Calder, 1970)	W Scotland (?)† (Ritchie, 1911)	Spitzbergen (1911.12.8.23)
Hydrotheca				
Outer side	310–480			390–510
Inner side, length adnate	270–350	280–340	140–280	230–250
Outer side, length adnate	150–350	230–310	170–290	280–350
Maximum diameter			140–170	230
Diameter of base	150–210	140–200		180–220
Diameter of aperture			60–100	90–140
Gonotheca				
Length	830–940		810–1330	900–940
Maximum diameter	420–480		310–440	320–440
Diameter of aperture	200			130–170

† Locality dubious – See Remarks.

VARIATION. See under Description, above.

REPRODUCTIVE SEASON. Fertile material recorded 14 July to 24 August in Barents Sea and 28 July in White Sea (Kudelin, 1914). The fertile material said to have been collected by James Ritchie in Scotland, listed above, is dated June 1910, but the locality seems dubious (see Distribution).

DISTRIBUTION. Known in the present area from Gullmarsfjord, W Sweden (present material), from the Skagerrak and Kattegat (Kramp, 1935; Rasmussen, 1973) and dubiously reported from a few Scottish localities (see below). Although recorded from Oslo Fjord by Kramp (1935) this record was doubted by Christiansen (1972). The species has been widely recorded in arctic and sub-arctic Atlantic waters (summaries in Broch, 1918; Kramp, 1929; Naumov, 1969; Calder, 1970) and has been recorded on the edge of its normal range (and just outside the present area) from the Faroes (twice, Kramp, 1929) and from the type locality in SW Norway.

The Scottish records (see Material list), from the warm west coast, are thus surprising. The two Ritchie specimens from Tighnabruaich, Argyll, are dissimilar in detail and might well not be both from the same original collection. The Mull of Kintyre specimen came to Ritchie via Sir John Murray [cf. the here discredited record of *Sertularia mirabilis* (p. 307)]. For the present there seems no way of assessing further Ritchie's *S. tenera* records or that of A. M. Norman from the Firth of Clyde (present material), and they should be regarded sceptically. *S. tenera* was not listed by Rankin (1901) or Chumley (1918) in their detailed Clyde Sea fauna lists.

HABITAT. On stones and shells, sub-littoral to edge of Continental Shelf (Kramp, 1929); recorded on *Halecium muricatum* (by Ritchie, 1911; see present Material list), but record perhaps dubious (see under Distribution).

REMARKS. In vegetative morphological characters *S. tenera* resembles closely *S. cupressina* Linnaeus, 1758, and some infertile specimens may be difficult to identify. Indeed, Winther (1879) regarded *tenera* as a variety of *S. cupressina*. Nevertheless, *S. tenera* seems to be valid and can be identified on the basis of the following characters (largely after Broch, 1910). Compared with *S. cupressina*, hydrothecae of *S. tenera* are larger and more divergent from the hydrocaulus, usually with a straighter outer edge; hydrocladia are narrower than the stems and usually lacking hydrothecae basally in *S. tenera*, equal in thickness and having hydrothecae almost down to the base in *S. cupressina;* gonothecae are sometimes ovoid in both species but often have two or more terminal spines in *S. cupressina* (but sometimes no spines) while lacking terminal spines and often being polygonal in cross-section in *S. tenera*; ♀ acrocysts (once ♂ (? incorrect), Hancock *et al.*, 1956) are present in *S. cupressina* and have several eggs, whereas both ♂ and ♀ gonosomes are intracapsular in the present material of *S. tenera*, the ♀ having just one egg.

Naumov (1969) followed Broch (1910) in uniting *Sertularia arctica* Allman, 1874*b*, and *S. thomsoni* Schydlowsky, 1902, with the present species, and these synonymies seem correct. The type material of *S. arctica* was evidently unusual in that the gonotheca had an equatorial constriction. Ritchie (1911) recorded similar material.

Sertularia albimaris Mereschkowsky, 1878, has been distinguished from the present species in having hydrothecae which are shorter and largely fused with the hydrocaulus, and in having a lamellar hydrorhiza (Naumov, 1960, 1969). Naumov included *S. thomsoni* Schydlowsky, 1902, in its synonymy but following Kudelin (1914) *S. thomsoni* is here regarded conspecific with *S. tenera*. *S. albimaris* Mereschkowsky is a northern species reported from the North Sea by Naumov (1960, 1969) but it is not certain that this record comes within the present area, from which it seems unrecorded.

Symplectoscyphus tricuspidatus (Alder, 1856)

(Fig. 28)

Corallina minus ramosa alterna vice denticulata, . . . Ellis, 1755 : 5–6, pl. 2, figs A, a, B, b.

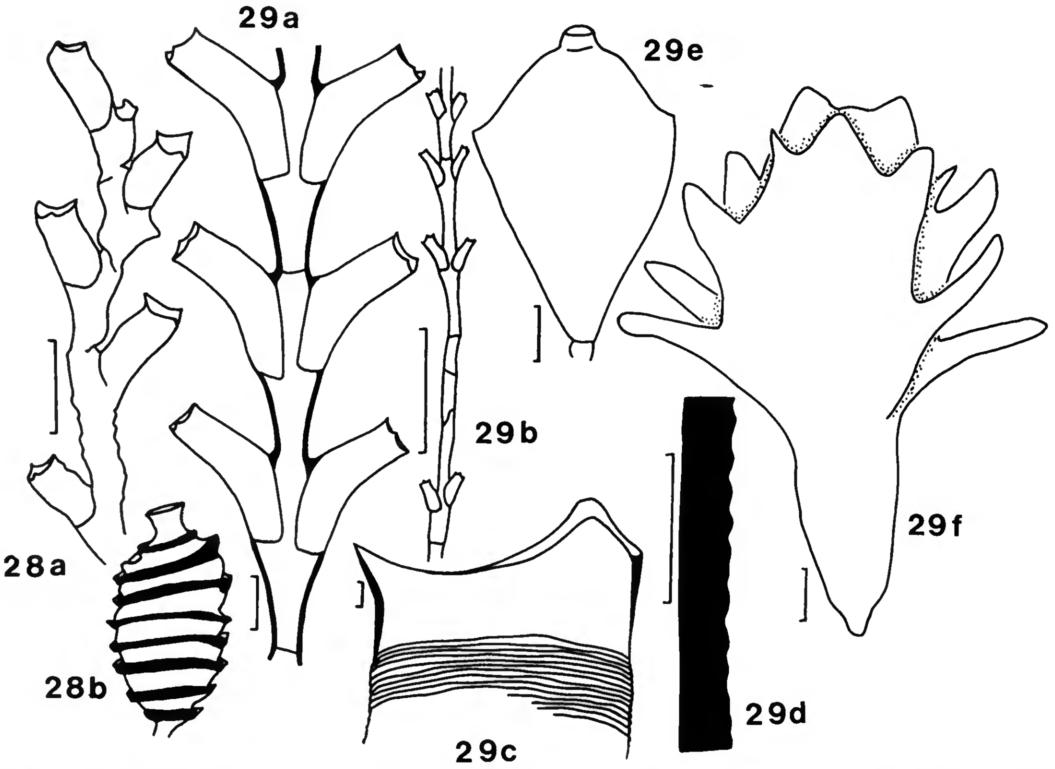
Sertularia polyzonias Linnaeus, 1758 : 813 (part); Linnaeus, 1767 : 1312 (part); Oken, 1815 : 92 (part); Esper, 1829 : 173–177 (part).

Sertularia ericoides Pallas, 1766 : 127–128 (part) (nom. nov. pro *S. polyzonias* Linnaeus and *S. flexuosa* Linnaeus); Pallas, 1768 : 158–160 (part); Oken, 1815 : 92 (part); Esper, 1829 : pl. 12, figs 1–2.

Sertularia tricuspidata Alder, 1856 : 356–357, pl. 13, figs 1–2; Alder, 1857 : 111–112, figs 1–2.

Sertularella tricuspidata: Hincks, 1868 : 239–240, pl. 47, fig. 1, text-fig. 30 (syn. *Sertularia ericoides* sensu Esper); Hartlaub, 1901 : 23, 127–129, pl. 2, figs 41–42 (syn. *S. ericoides* Pallas); Nutting, 1904 : 100–102, pl. 25, figs 3–7 (syn. *Sertularella pallida* Kirchenpauer, 1884; *S. hesperia* Torrey, 1902); Broch, 1910 : 168–170, 214–215, fig. 25; Broch, 1918 : 98–99; Kramp, 1929 : 22; Kramp, 1935 : 179; Vervoort, 1942 : 292; Kramp, 1943 : 33–34; Fraser, 1944 : 274–277, pl. 60, fig. 264; Naumov, 1960 : 348–349, fig. 240; Naumov, 1969 : 376–377, fig. 240; Calder, 1970 : 1531, pl. 6, figs 7–8. [non *Sertularella tricuspidata:* Ritchie, 1907a : 536 (= *Symplectoscyphus articulatus* (Allman) (Stechow, 1923 : 173; Rees & Thursfield, 1965 : 132)].

Symplectoscyphus tricuspidatus: Stechow, 1923 : 173; Yamada, 1950 : 10, pl. 1, fig. 9; Rees & Thursfield, 1965 : 132; Vervoort, 1972 : 166–168, fig. 54.



Figs 28–29. Fig. 28 *Symplectoscyphus tricuspidatus.* (a–b) terminal region of hydrocladium, and gonotheca, SW Canada (1898.6.4.2), scale = 500 μm. Fig. 29 *Tamarisca tamarisca.* (a) part of hydrocladium, Faroes (1964.8.7.109), scale = 500 μm; (b) hydrocaulus with unusually long internodes, 'E Coast of Britain' (1899.7.1.5923), scale = 5 mm; (c) detail of (?) unusual hydrotheca with finely ridged surface, NE Scotland (1964.8.7.110), scale = 50 μm; (d) optical section through hydrothecal wall of (c), external surface on right, scale = 50 μm; (e) ♂ gonotheca, as (b), scale = 500 μm; (f) ♀ gonotheca, Bay of Biscay (1961.11.4.5), scale = 500 μm.

Type locality and material. 'On zoophytes from deep water on the Northumberland coast' (Alder, 1856). Fragments in spirit, Hancock Museum, Newcastle upon Tyne, England, without collecting data but designated type material by Nutting (1904). Four herbarium specimens on one sheet in the BM(NH) collection (1919.4.5.6), presented by Alder in 1856 or 1857, labelled 'Northumberland Coast', can also be regarded part of the type series. Additional type material in the Hancock Museum has been listed by Cornelius & Garfath (in prep.)

Other material examined. *Eastern North Atlantic* Carl I., Spitzbergen, fragment in spirit, coll. A. E. Eaton, 1874.4.4.60. Bear I., Spitzbergen, strandline, fragments in spirit, coll. Oxford

University Spitzbergen Expedition, 1922.1.19.11. Bear I., 1930, fertile colonies in spirit, coll. J. A. Robertson, 1931.6.29.13. E of Faroes, 62° 00′ N, 6° 12′ W ('Goldseeker' sta. 16), 120 m, 25 Aug 1906, fragment of colony on microslide, ex coll. J. Ritchie, 1964.8.7.136 (mentioned, Rees & Thursfield, 1965 : 132). Off Northumberland, fragments of several colonies in spirit, coll. A. M. Norman, 1912.12.21.341. 'North Sea', pre-1857, three fragments on 2 microslides, purchased from L. Barrett, 1857.10.14.38 (Table 27).

North American waters R. St Lawrence, Canada, coll. 'Mr Whiteaves', ex coll. A. M. Norman, 1912.12.21.344. Off Cape Cod, Massachusetts, U.S.A., several colonies in spirit, coll. U.S. Fisheries Commission, pres. Smithsonian Institution, 1890.8.23.10. Unalaska I., Aleutian Is, several colonies in spirit, coll. d'A. W. Thompson, pres. Queen's College, University of Dundee, 1956.10.1.40. Vancouver, British Columbia, Canada, fertile colony on microslide coll. C. F. Newcombe, 1898.6.4.2. (Figs 28a–b).

DESCRIPTION. Hydrocauli erect, monosiphonic, branched, flexuose, bearing hydrothecae at the bends. Hydrocladia similar to hydrocauli; typically 3–5 hydrothecae between bases of successive hydrocladia. Colonies up to 150 mm (Naumov, 1969), but usually 50 mm or less. Perisarc of hydrocaulus variably rugose. Usually transverse to slightly oblique annulus above each or every second hydrotheca. Hydrothecae tubular to barrel-shaped, smooth walled to coarsely rugose, 2–3 times longer than wide. Outer side of hydrotheca often forming continuous curve with side of hydrocaulus below, but this sometimes interrupted by rugosities of perisarc; $\frac{1}{2}$–$\frac{1}{3}$ of inner side adnate; rim tricuspid, roundly cleft to varying extent; usually one cusp proximal and two distal but often irregular; renovations common; operculum 3-flapped. Hydranth apparently undescribed. Gonotheca ♂ = ♀, elongate to ovoid, 7–9 washer-shaped annular ribs; aperture terminal, at end of short tube, even, slightly flared; gonothecal pedicel short, inserted below hydrotheca.

MEASUREMENTS. See Table 27.

Table 27 *Symplectoscyphus tricuspidatus*. Measurements in μm

	U.S.S.R. (Naumov, 1969)	N Canada (Calder, 1970)	Japan (Yamada, 1950)	N Atlantic (Vervoort, 1972)	North Sea (1857.10.14.38)
Hydrotheca					
Outer side	350–560	490–570	340	310–350	580–640†
Inner side, length adnate	230–350	230–260		220–250	230–320
Inner side, length free	370–520	390–470		310–330	270–320
Diameter of aperture	290–330	230–270	250	200–220	220–250
Maximum diameter				230–250	210–270
Internode					
Length		700–1200		720–880	480–580
Gonotheca (♂ = ♀)					
Length	1600 (max)		1700		
Maximum diameter	850				

† Measured to junction with hydrocaulus.

VARIATIONS. The three hydrothecal cusps are usually placed so that two are distal and one is proximal, but the reverse condition occurs commonly and the cusps are not always equally spaced. The indentations between them are of various depths, but seem to be constant within each hydrotheca. Broch (1910) described variations in hydrothecal morphology. Internode length also varies (Table 27).

DISTRIBUTION. Circumpolar, in arctic to northern boreal waters (Broch, 1918; Naumov, 1969), occurring at least as far north as $79\frac{1}{2}$° N (Jaderholm, 1909). Although recorded south to northern England the present status of the species in British waters is unclear, the most recent published British record being from the Moray Firth, Scotland, in 1935 (Vervoort, 1942). Previous records and specimens from the present area include only Northumberland (type locality; also Alder, 1865; these records repeated by Norman, 1905, and Robson, 1914); Cumberland (Pennington, 1885 – a dubious record since it is almost the only record from the British west coast, and also the most southerly record of the species in the Atlantic); an unsubstantiated record from the Clyde Sea by Rankin (1901), not repeated by Chumley (1918); and 'North Sea' (BM(NH) 1857.10.14.38; Broch, 1928; Naumov, 1969). The species was not recorded in faunal lists of the Baltic, Danish waters and Oslo Fjord (Stechow, 1927; Broch, 1928; Christiansen, 1972). Available evidence suggests that the southern limit of the species has moved northwards from the southern North Sea during the past 100 years.

A record of the species from sub-antarctic waters (Naumov & Stepan'yants, 1962) has been doubted (Vervoort, 1972), as has the antarctic record of Ritchie (1907*a*) which has been referred to *S. articulatus* (Allman, 1888) (Stechow, 1923; Rees & Thursfield, 1965). The species seems otherwise unrecorded from the southern hemisphere.

REMARKS. Although Ellis (1755) stated that there were two species included in his 'Great Tooth Coralline', Linnaeus (1758) united them in the single taxon *Sertularia polyzonias*.[19] Pallas (1766) provided the name *S. ericoides* to include both this Linnean species and also *S. flexuosa* Linnaeus, 1758. Subsequently, Linnaeus (1767) and Pallas (1768, 1787) each used his own name for the composite taxon. F. L. Hammer (in Esper, 1829) stated that the two names referred to a single species, and used the senior name *polyzonias*, of which *ericoides* is in fact a junior objective synonym. When Alder (1856) independently recognized the existence of two species within *S. polyzonias* sensu Linnaeus he provided the new name *S. tricuspidata* for specimens with three-cusped hydrothecal rims, confusingly commenting that his species resembled *S. ericoides* sensu Hammer. This was the first time since Ellis' (1755) account that the two species had been recognized and the first time that a binomen had been applied solely to the present species.

S. flexuosa Linnaeus, 1758, seems referable to *S. polyzonias* s. str. (see p. 290).

Tamarisca tamarisca (Linnaeus, 1758)

(Fig. 29)

Corallina vesiculata sparsim et alternatim ramosa . . . Ellis, 1755 : 4, pl. 1, figs A, a.
Sertularia tamarisca Linnaeus, 1758 : 808.
Diphasia tamarisca: Hincks, 1868 : 254–255, pl. 51.
Sertomma tamarisca: Stechow, 1919 : 853; Stechow, 1923 : 159; Rees & Thursfield, 1965 : 118–119.
Sertularella (*Tamarisca*) *tamarisca:* Kudelin, 1914 : 480, 509–514.
Tamarisca tamarisca: Naumov, 1960 : 327–329, fig. 218; Naumov, 1969 : 354–355, fig. 218; Vervoort, 1972 : 184–185.

TYPE MATERIAL AND LOCALITY. The collections of Linnaeus in the Linnean Society of London include a single herbarium sheet bearing an infertile colony labelled *Sertularia tamarisca* (numbered 1298.3 by Savage, 1945). It does not appear to be *S. tamarisca* Linnaeus *sens. auct.*, e.g. Hincks, 1868, however, but is probably a species of *Abietinaria* sens. Naumov, 1969. The specimen is not well preserved but some hydrothecae have the remains of single-flapped adcauline operculae. Meanwhile there are in the BM(NH) collections two microslide preparations evidently also of Linnean material. They were formerly in the collections of George Busk (a one-time Secretary of the Linnean Society) and were labelled by him as follows: 'Sertularia tamarisca. Linn. herb.! (ms)' [BM(NH) registered numbers 1899.7.1.6300–6301]. Each slide bears an infertile fragment of hydrocaulus identical in appearance with the hydrocauli of the Linnean Society specimen, of which the BM(NH) specimens appear to be sub-samples.

However, as Linnaeus' designation includes male gonothecal characters ('calycibus obovatis bidentatis') it seems probable that these specimens are non-type and that, as with other sertularian hydroids, Linnaeus based the designation on the very clear illustration of Ellis (1755 : pl. 1, figs A, a). The specimen in the illustration, which shows male gonothecae, can thus be taken as holotype. It is probably lost (p. 251). It was taken 'in very deep water, near the Island of Dalkey, at the entrance of the harbour of Dublin', Eire (Ellis, 1755 : 4). The type locality of the species may be restricted to this area.

OTHER MATERIAL EXAMINED. Faroes, 62° 00′ N, 6° 12′ W ('Goldseeker' sta. 16), 120 m, 25 Aug 1906, fragments of 2 hydrocladia on microslide, coll. J. Ritchie, 1964.8.7.109 (Fig. 29a; mentioned, Rees & Thursfield, 1965 : 118). NW of Shetlands, 61° 35′ N, 0° 47′ E ('Goldseeker' sta. 10), 204 m, 3 Sep 1906, part of colony on microslide, coll. J. Ritchie, 1964.8.7.108 (mentioned, Rees & Thursfield, 1965 : 118). N of Orkneys, 59° 46′ N, 2° 21′ W ('Goldseeker' sta. 21), 92 m, 29 Aug 1906, 4 hydrocladial fragments on microslide, coll. J. Ritchie, 1964.8.7.110 (Figs 29c–d; mentioned, Rees & Thursfield, 1965 : 118). Bridlington Bay, Yorkshire, infertile fragment on microslide, coll. s.s. 'George Bligh', 1956.2.2.11. East coast of Britain, ♂ colony on microslide, coll. G. Busk, 1899.7.1.5923 (Fig. 29b, e; Table 28). Bay of Biscay, 7 Jan 1922, fragments of female colony on 3 microslides, coll. E. T. Browne, 1961.11.4.5, 6 & 8 (Fig. 29f; Table 28).

DESCRIPTION. Colony up to 150 mm, upright, robust, branched loosely, alternately (sometimes opposite), in one plane; hydrocaulus monosiphonic; appearance of colony often reminiscent of finer branches of the tamarisc tree (*Tamarix* L.). Hydrothecae on both stem and branches; often very large (see Measurements); (sub)opposite, biseriate; nodal constrictions immediately above each pair and varying distance below; each hydrotheca roughly tubular, $\frac{1}{2}$ adnate, variably outward-curving; rim 3-cusped, sometimes renovated, with 3-flapped operculum; hydrothecal surface sometimes finely ribbed (Fig. 29). Hydranth ? undescribed, in present material (1961.11.4.8) lacking enteron diverticulum, having *c.* 15 tentacles. ♂ gonotheca flattened, heart-shaped; proximal, pointed end pedicellate; two distal outer corners approximately 90°; aperture terminal, central, circular, on short tube. ♀ gonotheca 'conical, its distal end bearing 3 large flattened lobes with ramified distal margins; with a pair of identical lobes covering the aperture of the gonotheca in the form of a gabled roof; with a third, narrower lobe situated on the adjacent side, located between the other two, bending inwards' (Naumov, 1969). Notes on reproduction were given by Allman (1864). Hincks (1868) recorded monoecious material.

MEASUREMENTS. See Table 28.

Table 28 *Tamarisca tamarisca.* Measurements in μm

	U.S.S.R. (Naumov, 1969)	Bay of Biscay (1964.11.4.5, 6, 8)	E coast of Britain (1899.7.1.5923)
Hydrotheca			
Outer side	1350–1600	1100–1420	1080–1230
Inner side, length adnate	900–1150	550–800	600–710
Inner side, length free	880–1050	600–750	600–710
Diameter of aperture	500–600	330–390	340–390
♂ gonotheca			
Length	3000		2400–2800
Maximum diameter	2000		500–720
♀ gonotheca			
Length	5000	4900–5100	
Maximum diameter		3000–3200	

VARIATION. The distance between the proximal end of a hydrothecal pair and the nodal constriction below may vary widely within a single hydrocladium (Fig. 29b), resulting in variation of internode length. In one of the illustrated specimens basal parts of the hydrocladia are devoid of hydrothecae. There is variation between colonies in the degree of outward curvature of the hydrothecae, some being almost straight.

REPRODUCTIVE SEASON. Fertile material recorded April, NW France (Teissier, 1965). Notes on reproduction were given by Allman (1864).

DISTRIBUTION. Scattering of records throughout the present area excepting certain regions, suggesting a patchy distribution. Not recorded from Dutch and Belgian waters (Vervoort, 1946; Leloup, 1952) and apparently not present in the Baltic (Stechow, 1927; Broch, 1928) or the Channel Isles (Vervoort, 1949). Said, however, to be common in northern Britanny (Teissier, 1965). Apparently no other records from north coast of France, but records from SW England are numerous. The species 'never seems to occur in abundance' (Vervoort, 1972). Hincks (1868), writing of the distribution in Britain, stated 'Though not an abundant species, [it] is very widely distributed'.

HABITAT. Little information. Apparently occurring over much of the Continental Shelf at depths greater than about 10 m.

REMARKS. There seems no reason for systematic revision of this distinctive species at present. There has, however, been some confusion in recent literature regarding the generic names *Tamarisca* Kudelin (1914 : 480, 508; as sub-genus of *Sertularella* Gray, 1848) and *Sertomma* Stechow (1919 : 853). The sub-genus *Tamarisca* was raised to generic status by Naumov (1960 : 327). Rees & Thursfield (1965), however, continued to use the name *Sertomma* in preference. *Sertularia tamarisca* Linnaeus, 1758, is type species of both the sub-genus *Tamarisca* Kudelin, 1914, and of the genus *Sertomma* Stechow, 1919 (in each case by both original designation and monotypy). The current conventions of zoological nomenclature give equal status to genera and sub-genera for the purpose of priority so that *Sertomma* can be considered a junior objective synonym of *Tamarisca*.

Problematical record

Sertularella cylindritheca (Allman, 1888)

Sertularia cylindritheca Allman, 1888 : 59–60, pl. 29, figs 1, 1a.
Sertularella cylindritheca: Vervoort, 1972 : 126, fig. 39a.

DISTRIBUTION AND REMARKS. Dr W. Vervoort has kindly shown me three infertile hydrocladia of this species collected from deep water off the coast of Norfolk (53° 19′ N, 0° 42′ E, 90 m, coll. r.v. 'Aurelia', 17 Oct 1975; Leiden Museum collection). The hydrocladia, which contain tissues and were evidently alive when collected, resemble the type material (off Bahia, Brazil, coll. H.M.S. 'Challenger', fragments of colony in spirit, BM(NH) reg. no. 1888.11.13.47) in all essential features.

The previously recorded distribution apparently extends no further north on the eastern side of the Atlantic Ocean than the Straits of Gibraltar (Vervoort, 1972). The present material was received by Dr Vervoort through the Leiden Museum collection sorting facilities and we are in agreement that the locality data should not be regarded as conclusively proved.

Species erroneously recorded

(See also notes on Distribution under *Sertularia tenera*, p. 301.)

Parascyphus simplex (Lamouroux, 1816)

Laomedea simplex Lamouroux, 1816 : 207.
Parascyphus simplex: Ritchie, 1911 : 160–162, fig. 1; Totton, 1930 : 179–180, fig. 29; Ralph, 1961 : 755, fig. 1b; Rees & Thursfield, 1965 : 117–118.

DISTRIBUTION AND REMARKS. Apart from a single specimen dubiously stated by Ritchie (1911) to have been collected between Sanda Island and Ailsa Craig, Scotland, the species has not been recorded from the North Atlantic. However, several authors (Chumley, 1918; Totton, 1930; Ralph, 1961; Rees & Thursfield, 1965) have accepted Ritchie's record, apparently only Kramp (1947) noting that the Scottish locality was unusual.

The specimen, a microslide preparation of part of a colony, carries two BM(NH) registered numbers: 1964.8.7.106 (not 107 as stated by Rees & Thursfield) and 1888.3.19. The latter number relates to a small collection of hydroids made from Sanda by Sir John Murray. However, none of the specimens in that collection is identified in the contemporary Museum Register as *P. simplex* or anything similar. As Ritchie's collection contained *P. simplex* material from other localities (Rees & Thursfield, 1965) it seems likely that Ritchie mistakenly ascribed a Scottish locality to a foreign specimen. Further, the specimen on Ritchie's microslide preparation of *P. simplex* from Gough Island (BM(NH) 1964.8.7.105; duplicate material mentioned by Rees & Thursfield, 1965) is morphologically identical with that said to have come from near Sanda, and could well have come from the same colony.

The species is probably best considered unrecorded in the North Atlantic. A detailed redescription and synonymy were given by Ralph (1961).

'*Sertularia evansi*' Ellis & Solander, 1786

DISTRIBUTION AND REMARKS. Although the only European record of this species north of the Mediterranean Sea – from Norfolk, by Ellis & Solander, 1786 – now seems erroneous it was formerly quoted in British faunal accounts (e.g. Johnston, 1838, 1847; Gray, 1848; Landsborough, 1852). Removal of the species from the British list has been discussed in detail by Cornelius (in prep.). Once referred to the genus *Dynamena*, the species is now known as *Synthecium evansi* and placed in the family Syntheciidae. The species is included here as the faunal accounts just mentioned referred it to the present family; and the Syntheciidae – which has no truly British representative – will not be treated in the present sequence of papers.

Sertularia mirabilis (Verrill, 1873)

Diphasia mirabilis Verrill, 1873 : 9–10.
Selaginopsis mirabilis: Nutting, 1904 : 128, pl. 38, figs 11–12 (syn. *Polyserias hincksii* Mereschkowsky); Ritchie, 1909a : 217–220, figs 1–2; Rees & Thursfield, 1965 : 153.
Sertularia mirabilis: Kudelin, 1914 : 224–233, figs 62–65, 65a (syn. *Polyserias hincksii* Mereschkowsky); Broch, 1918 : 133–134; Naumov, 1960 : 365–367, fig. 257, pl. 8, fig. 1; Naumov, 1969 : 394–395, fig. 257, pl. 8, fig. 1; Calder, 1970 : 1532, pl. 7, fig. 3.
Polyserias hincksii Mereschkowsky, 1877 : 226, pl. 6, figs 15–16.

Fuller synonymies of earlier accounts were provided by Nutting (1904) and Kudelin (1914).

DISTRIBUTION AND REMARKS. Not yet reliably recorded from the present area. One spirit specimen and 2 microslide preparations in the BM(NH) collections (1910.10.4.18 and 1964.8.7.181) are parts of those said to have been taken off the Yorkshire coast by James Ritchie (1909*a*). The first number refers to a fertile colony 100 mm long preserved in spirit, and a microslide made from it. The specimen was given by Ritchie to Sir John Murray who presented it to the BM(NH) in 1910. The second number refers to the microslide specimen illustrated by Ritchie (1909*a* : fig. 1) and mentioned by Rees & Thursfield (1965 : 153) who record that there is a duplicate microslide in the Royal Scottish Museum, Edinburgh. The two BM(NH) specimens appear to be parts of larger colonies mentioned by Ritchie, said to have been removed from a stone entangled in the net of a Hull trawler when it returned to port. The trawler had made its last hauls off Flamborough Head, Yorkshire, and since Ritchie was told by his collector that the specimens had been fresh it seems plausible that he assumed they had come from that locality. However, neither of the two BM(NH) specimens has any coenosarc or hydranth tissues preserved. Although these might have been lost after the specimen was collected, it nevertheless seems plausible that the specimens had become entangled in the net on a more distant haul. As there are no other records of this species from the present area it seems best to regard the record unproven. It is perhaps unlikely that such a distinctive species should not have been found by other collectors. *S. mirabilis* is otherwise recorded as being arctic and sub-arctic in the North Atlantic (Broch, 1918; Naumov, 1969). It has been found as far south as west of the Faroes in deep water (Broch, 1918), although on the east and west coasts of North America the species extends further south than on the west coast of Europe (Ritchie, 1909*a*; Rees & Thursfield, 1965; Naumov, 1969; Calder, 1970).

Sertularia robusta (Clarke, 1877)

Thuiaria robusta Clarke, 1877 : 227–228, pl. 15, figs 53–55.
Sertularia robusta: Naumov, 1960 : 364–365, fig. 255 (syn. *S. fabricii:* Nutting, 1904; Broch, 1918); Calder, 1970 : 1533, pl. 7, figs 5–6; Vervoort, 1972 : 183–184 (syn. *S. fabricii:* Levinsen, 1893; Hartlaub, 1901; Nutting, 1904; Broch, 1918).

DISTRIBUTION AND REMARKS. Although recorded from the 'North Sea' by Naumov (1969) this species has generally been regarded as sub-arctic in distribution and seems not to have been reported from the present area. The species has not been recorded south of the Faroes on the western side of the Atlantic (Broch, 1918; Vervoort, 1972), and Naumov's comment probably refers to the northern part of the North Sea, outside the present area. The species has been redescribed by Naumov (1969), Calder (1970) and Vervoort (1972).

Stereotheca elongata (Lamouroux, 1816)

Sertularia elongata Lamouroux, 1816 : 189, pl. 5, fig. 3; Ritchie, 1907*b* : 78–83, pl. 111.
Stereotheca elongata: Ralph, 1961 : 762–764, fig. 4e–k; Rees & Thursfield, 1965 : 144–145.

DISTRIBUTION AND REMARKS. This species is known from Australia, Tasmania, New Zealand and South Africa (Ralph, 1961; Millard, 1975). A single specimen said to have been dredged off NE Scotland by James Ritchie in 1904 was supposed to have drifted to Britain attached to floating vegetation (Ritchie, 1907*b*; repeated by Millard). However, as there is no other North Atlantic record of this distinctive species it seems probable that Ritchie's record is erroneous. The specimen said to have come from Scottish waters is a microslide preparation in the Royal Scottish Museum (RSM No. 1959.33.535) (Rees and Thursfield, 1965). The BM(NH) collection includes 2 microslides from the Ritchie collection taken in Australian waters, numbered 1964.8.7.158–159, but these differ in detail from the 'Scottish' specimen.

Redescriptions of the species were provided by Ralph (1961) and Millard (1975).

Notes

[1] Robert Brown was the first Keeper of Botany at the British Museum. Thompson (1856 : 455) listed a specimen of this species collected by Brown from Ballycastle, in the collection of a one J. L. Drummond. [p. 253]

[2] The species was not listed among the North Sea fauna by Broch (1928), perhaps indicating its scarcity there at that time. [p. 257]

[3] The only fertile hydrocladium was returned to Dr Cabioch prior to registration of the remainder of the material, for his detailed study. All the material remaining in the BM(NH) is infertile. [p. 259]

[4] as well as *Tamarisca tamarisca* (see Fig. 29 and p. 305); and also *Tulpa diverticulata* Totton, 1930 (family Campanulariidae, by Millard, 1977). [p. 260]

[5] *Sertularia rugosissima* Thornely, 1904, based on infertile material from Sri Lanka (Ceylon), was referred to *S. hupferi* Broch by Thornely (1916) in a later paper and might, therefore, be conspecific with *D. tropica*. Jaderholm (1919) pointed out the similarity between *S. rugosissima* and *S. hupferi*, but did not propose a formal synonymy. [p. 260]

[6] There is an inconsistency in Allman's (1874*a*) paper concerning the type locality. In the unnumbered table (page 471) he gave it as 60° 14′ N, 6° 17′ W, depth 632 fm; while in the text (page 474) it was given as 64° 15′ N, 6° 15′ W, again 632 fm. Other collecting stations cited in the paper are no further north than 62° 1′ N; and while the stated depth at the first locality corresponds closely with that shown on modern Admiralty charts the depth at the more northerly locality is shown as approximately 1360 fm. The 60° 14′ N, 6° 17′ W locality thus seems the more likely of the two to be correct and a specimen collected from H.M.S. 'Porcupine' bearing these coordinates in the BM(NH) collection (1912.12.21.108, male colony in spirit, probably figd., Allman, 1874*a*; via A. M. Norman collection) appears to be type material. The first line of Allman's (1874*a*) account of *D. coronifera* suggests that the description was based on only one specimen, almost certainly the present one, which is thus holotype. [p. 263]

[7] The mollusc was probably the Indo-Pacific species now known as *Pinctada margaritifera* (Linnaeus, 1758) (P. B. Mordan, pers. comm.). [p. 265]

[8] Bale (1884) recorded material (as *D. pinnata*) from 'Sydney' and 'South Africa'. However, the species seems otherwise unrecorded outside the North Atlantic and the records seem dubious. Millard (1975) doubted the South African record. Both were quoted uncritically by Hincks (1868). [p. 266]

[9] except by Millard (1975 : 261), who called it *Diphasia nigra* in a brief zoo-geographical comment. [p. 267]

[10] although Johnston (1847) mistakenly referred male material to one species and female to the other. This was realized by Hincks (1868) and briefly noted in his synonymy under *Diphasia pinnata*. [p. 267]

[11] which was based on a clear illustration of Ellis (1755). The species has been widely regarded as valid. [p. 267]

[12] Evidence for this is the markedly bent, half adnate hydrothecae and regularly pinnate colony habit with close-set branches depicted by Ellis & Solander. [p. 269]

[13] None of the specimens in the collections of the Linnean Society of London (Savage, 1945 : 1298.1–2, 1298.28) resembles those described by Ellis, and as with most other sertularian hydroids it seems likely that Linnaeus based his designation on Ellis' illustration and not on specimens (see also p. 251). [p. 271]

[14] Unlike Linnaeus' (1758) diagnoses of most hydroids in his genus *Sertularia*, the diagnosis of *S. lichenastrum* and three other species are accompanied by short descriptions, a locality – Kamtchatka – and a collector's name – G. W. Steller. Although so late as 1 January 1767 Linnaeus wrote to John Ellis stating that until then Ellis had supplied all his hydroids (Smith, 1821 : 196; Cornelius, 1975*a* : 273) it seems that this was not so and that a few at least had already come from Steller's executors. Dr W. T. Stearn kindly examined the original description and designation of *S. lichenastrum* and informed me that there is little doubt that the provision of a description and locality indicates that Linnaeus made his designation from a specimen rather than from another author's account. It is known (Stejneger, 1936 : 543–544, 548) that soon after Steller's death in 1746 all his plant collections (then including hydroids) went to Linnaeus, who removed fragments before returning the material to Leningrad (then St Petersburg). Almost certainly the two fragments in the Linnean Society of London collection, labelled *Sertularia lichenastrum* in Linnaeus' hand and preserved on herbarium sheet 1298.26 (Savage, 1945), are Steller's specimens and those or parts of those on which the diagnosis of the species was based. The fragments (Fig. 18) are here regarded as syntypes of *S. lichenastrum* Linnaeus, 1758. (The remainder of the material might still be in the Leningrad collections (Stejneger, 1936 : 545), but was not mentioned by Kudelin (1914) in his detailed material lists and could not be located through the normal channels by the present author.) The herbarium sheet has two specimens, on the right and left sides of the page. The right hand specimen, labelled VI (probably to correspond with plate 6 of Ellis, 1755), is a piece of main stem 15 mm long with 4 side-branches, 3 of which are branched. Each final branch has a row of slightly projecting hydrothecae on each side, alternate hydrothecae pointing left and right. No operculae are visible. The specimen has numerous ovoid gonothecae with apertures only slightly less wide than their maximum diameters. The second fragment, on the left of the sheet, is of the same species and probably came from the same colony. It is a short piece of main stem with two side branches, and like the other fragment has numerous gonothecae.

Linnaeus gave the locality 'Kamtchatka' for the species. Stejneger recorded that many of Steller's collecting labels were separated from the specimens, and Hultén (1927 : 6) considered that Linnaeus wrongly ascribed the type locality 'Kamtchatka' to many Steller plant specimens. Possibly Linnaeus received them without labels. Certainly much of Steller's collecting was done in Kamtchatka but he also collected for differing periods in Alaska, Bering Island and several localities in the Sea of Okhotsk (Stejneger, 1936), so that the locality of the present specimen was not necessarily Kamtchatka. The Linnean Society fragments of *S. lichenastrum* seems conspecific with *Thuiaria sachalini* Kudelin, 1914, as redefined by Naumov (1960, 1969), and *Sertularia lichenastrum* Linnaeus, 1758, can be regarded its senior synonym. The combination by which the species should be known is *Salacia lichenastrum*. Naumov states that 'Salacia sachalini' is widespread in the seas of north-east Russia, and the type locality of *S. lichenastrum* can confidently be restricted to Kamtchatka, from which Linnaeus – perhaps mistakenly – supposed the type material to have come.

Fertile syntype material of *Thujaria alternitheca* Levinsen, 1893, in the BM(NH) collection (1896.8.15.4, two microslide preparations) seems identical with the syntypes of *S. lichenastrum* Linnaeus, 1758, and the two taxa appear conspecific. The gonothecae of the two type series are truncate and appear very similar but the gonothecae illustrated by Naumov (1969 : fig. 309) as *T. alternitheca* differ in tapering distally. Although the vegetative characters of Naumov's material seem similar to those of the type material of both *S. lichenastrum* and *T. alternitheca*, the Naumov material should perhaps not be referred to *S. lichenastrum* until its gonothecal characters can be better evaluated. [p. 279]

[15] Millard's (1957) suggestion that the internal cusps are easily lost through damage seems a less likely explanation of the recorded variation in their arrangement than that the variation is genotypic, as the cusps are in a protected position inside the hydrothecae; but a full explanation is lacking. [p. 283]

[16] *Sertularia pinnata* Templeton is here referred to *Sertularella gayi* Lamouroux (see p. 287). [p. 287]

[17] following Hancock *et al.* (1956). [p. 296]

[18] Millard's (1975) designation of the type locality as 'Atlantic Ocean' seems erroneous. [p. 296]

[19] The material labelled *S. polyzonias* in the collection of the Linnean Society of London includes 5 specimens of *Symplectoscyphus tricuspidatus* in addition to several specimens of *Sertularella polyzonias* as here defined. The specimens are discussed under *S. polyzonias* (p. 288). [p. 304]

[20] The genus name *Ellisia* was introduced by Westendorp (1843 : 22) to accommodate the present species alone. There seems no need for a separate genus for *Sertularella rugosa*, however; and *Ellisia* Westendorp should be considered a senior synonym of the genus name *Sertularella* Gray, 1848, which although more recent is wider in scope. As Bedot (1905 : 74) pointed out the name *Ellisia* had been introduced still earlier, by Forbes & Goodsir (1840), for an entirely different genus of hydroids, so that *Ellisia sens.* Westendorp is a junior homonym; and the widely used name *Sertularella* Gray, 1848, remains available. [p. 291]

[21] *Dynamena dubia* Billard, 1922*a*, type locality La Pallice, W France (by subsequent designation by Billard, 1927), has been recorded from several localities along the west coast of France including the Glenan Isles just south of the faunal boundary adopted here. *D. dubia* seems very close to *Sertularia distans* and may prove conspecific, but I have not seen material. Billard (1927) and Fey (1969) referred the species to the genus *Salacia*, but this seems quite unjustified. [p. 299]

Acknowledgements

I am grateful to Dr W. Vervoort for discussing nomenclatural changes proposed here in the genera *Diphasia* and *Sertularella*, and to Miss A. M. Clark for advice on many points of nomenclature and other matters. I am grateful also to Dr A. G. Long, Hancock Museum, Newcastle upon Tyne, and to T. O'Grady, Linnean Society of London, for access to the collections respectively of Joshua Alder and Linnaeus held in their institutions.

The Distribution sections of this paper benefited greatly from a manuscript file of published locality records prepared under the direction of the late W. J. Rees by his assistants over some years. Similarly, it is a pleasure to record the usefulness of a card catalogue of the old and valuable BM(NH) herbarium collection of hydroids, prepared recently by Miss J. Garfath.

An observation on distribution in *Sertularia distans* was made while on a visit to the Rijksmuseum van Natuurlijke Historie, Leiden and the Instituut voor Taxonomische Zoölogie, Zoölogisch Museum, Universiteit van Amsterdam, funded by the Stichting Jan Joost ter Pelkwijk Fonds, to which I am much indebted.

Other acknowledgements are made in the appropriate places in the text.

References

Agassiz, L. 1860. *Contributions to the natural history of the United States of America. Second monograph.* Volume 3. Boston.

—— 1862. *Contributions to the natural history of the United States of America. Second monograph.* Volume 4. Boston.

Alder, J. 1856. A notice of some new genera and species of British hydroid zoophytes. *Ann. Mag. nat. Hist.* (2) **18** : 353–362.

—— 1857. A catalogue of the zoophytes of Northumberland and Durham. *Trans. Tyneside. Nat. Fld Cl.* (1856) **3** : 93–162. (This reference bears the date 1856 but a footnote on page 87 of a previous paper in the same journal indicates that it was still in press on 29 January 1857.)

—— 1865. Report on the zoophytes. *Nat. Hist. Trans. Northumb.* **1** : 45–50. *In* Brady, G. S. (editor), Reports of deep sea dredging on the coasts of Northumberland and Durham, 1862–64. *Loc. cit.*, pp. 1–58. (Dating this publication follows Cornelius & Garfath, in prep.)

Allman, G. J. 1864. Report on the present state of our knowledge of the reproductive system in the Hydroida. *Rep. Br. Ass. Advmt Sci.* (1863) (1) : 351–426.

—— 1872. *A monograph of the gymnoblastic or tubularian hydroids. Conclusion of part I, and part II, containing descriptions of the genera and species of the Gymnoblastea.* London.

—— 1874*a*. Report on the Hydroida collected during the expeditions of H.M.S. 'Porcupine'. *Trans. zool. Soc. Lond.* **8** : 469–481.

—— 1874*b*. No title. [On several collections of Hydroida studied by G. J. Allman.] *Nature, Lond.* **11** : 179.

—— 1876. Diagnoses of new genera and species of Hydroida. *J. Linn. Soc.* (Zool.) **12** : 251–284.

—— 1877. Report on the Hydroida collected during the exploration of the Gulf Stream by L. F. de Pourtalès, Assistant, United States Coast Survey. *Mem. Mus. comp. Zool. Harv.* **5** (2) : 1–66.

—— 1888. Report on the Hydroida dredged by H.M.S. Challenger during the years 1873–1876. Part II. The Tubularinae, Corymorphinae, Campanularinae, Sertularinae, and Thalamophora. *Rept scient. Results Voy. Challenger*, **23** : 1–90 + i–lxix.

Ansted, D. T. & Latham, R. G. 1862. *The Channel Islands.* London.

Bale, W. M. 1884. *Catalogue of the Australian hydroid zoophytes.* Sydney.

Barrett, J. H. & Yonge, C. M. 1958. *Collins pocket guide to the sea shore.* London.

Baster, J. 1762. *Opuscula subseciva, observationes miscellaneas de animalculis et plantis.* Volume I. Haarlem, Holland.

Bedot, M. 1901. Matériaux pour servir à l'histoire des hydroïdes. 1re période. *Revue suisse Zool.* **9** : 379–515.

—— 1905. Matériaux pour servir à l'histoire des hydroïdes. 2me période (1821 à 1850). *Revue suisse Zool.* **13** : 1–183.

Bedot, M. 1910. Matériaux pour servir à l'histoire des hydroïdes. 3me période (1851 à 1871). *Revue suisse Zool.* **18**: 189–490.

—— 1912. Matériaux pour servir à l'histoire des hydroïdes. 4me période (1872 à 1880). *Revue suisse Zool.* **20** : 213–469.

—— 1916. Matériaux pour servir à l'histoire des hydroïdes. 5me période (1881 à 1890). *Revue suisse Zool.* **24** : 1–349.

—— 1918. Matériaux pour servir à l'histoire des hydroïdes. 6me période (1891 à 1900). *Revue suisse Zool.* **26** (Suppl.) : 1–376.

—— 1925. Matériaux pour servir à l'histoire des hydroïdes. 7me période (1901 à 1910). *Revue suisse Zool.* **32** (Suppl.) : 1–657.

Beloussov, L. V. 1973. Growth and morphogenesis of some marine Hydrozoa according to histological data and time-lapse studies. *Publs Seto. mar. biol. Lab.* **20** : 315–336.

Bennitt, R. 1922. Additions to the hydroid fauna of the Bermudas. *Proc. Am. Acad. Arts Sci.* **57** : 241–259.

Billard, A. 1906. Hydroïdes. *Expéd. scient. Travailleur-Talisman* (1906) : 153–243.

—— 1907. Hydroïdes de la collection Lamarck du Muséum de Paris. II. Campanulariidae et Sertulariidae. *Annls Sci. nat. Zool.* (9) **6** : 215–219.

—— 1909. Revision des espèces types d'hydroïdes de la collection Lamouroux conservée à l'Institut Botanique de Caen. *Annls Sci. nat. Zool.* (9) **9** : 307–336.

—— 1912. Hydroïdes de Roscoff. *Archs Zool. exp. gén.* **51** : 459–478.

—— 1922*a*. Note sur une espèce nouvelle d'hydroïde des côtes de France (*Dynamena dubia*). *Bull. Soc. zool. Fr.* **47** : 344–348.

—— 1922*b*. Note critique sur quatre espèces de Sertularella. *Revue suisse Zool.* **30** : 103–114.

—— 1925. Note sur le *Sertularia distans* (Lamouroux). *Bull. Mus. Hist. nat. Paris*, **31** : 197–202.

—— 1927. Les hydroïdes de la côte Atlantique de France. *C. r. Congr. Socs sav. Paris, Sect. Sci.* (1926) : 326–346.

—— 1931. Hydroïdes récoltés dans les campagnes du 'Pourquoi-Pas?' en 1920, 1921, 1924, 1927, 1929 et 1930. *Bull. Mus. Hist. nat. Paris*, (2) **3** : 244–247.

Blanco, O. M. 1963. Sobre algunos sertularidos de la Argentina. *Notas Mus. La Plata*, **20** : 163–180.

—— 1966. Observaciones sobre la morfologia de '*Sertularia operculata*' L. *Revta Mus. La Plata* (N.S.) (Zool.) **9** : 1–6.

Broch, H. 1910. Die Hydroiden der arktischen Meere. *Fauna arct.* **5** : 127–248.

—— 1914. Hydrozoa benthonica. *Beitr. Kennt. Meeresfauna Westafr.* **1** : 19–50.

—— 1918. Hydroida. (Part II). *Dan. Ingolf Exped.* **5** (7) : 1–206.

—— 1927. Hydrozoen. *Tierwelt Dtl.* **4** : 95–160. [Although dated 1928 this publication was received in the Zoology Library, British Museum (Natural History), on 20 December 1927.]

—— 1928. Hydrozoa I. *In* Grimpe, G. & Wagler, E. (editors), *Tierwelt N.- u. Ostsee*, **3** (b) : 1–100.

—— 1933. Zur Kenntnis der adriatischen Hydroidenfauna von Split. *Skr. norske VidenskAkad. mat.-nat. Kl.* (1933) **4** : 1–115.

Browne, E. T. 1907. The hydroids collected by the 'Huxley' from the north side of the Bay of Biscay in August, 1906. *J. mar. biol. Ass. U. K.* **8** : 15–36.

Bruce, J. R., Colman, J. S. & Jones, N. S. 1963. Marine fauna of the Isle of Man. *L.M.B.C. Mem. typ. Br. mar. Pl. Anim.* **36** : 1–307 + i–ix.

Buchanan, J. B. 1957. The hydroid fauna of the Gold Coast. *Revue Zool. Bot. afr.* **56** : 349–372.

Busk, G. 1851. A list of sertularian zoophytes and Polyzoa from Port Natal, Algoa Bay, and Table Bay, in South Africa; with remarks on their geographical distribution, and observations on the genera *Plumularia* and *Catenicella*. *Rep. Brit. Ass. Advmt Sci.* (1850) (2) : 118–120.

Byerley, I. 1854. The fauna of Liverpool. *Proc. lit. phil. Soc. Lpool* **8** (Appendix) : 1–125.

Calder, D. R. 1970. Thecate hydroids from the shelf waters of northern Canada. *J. Fish. Res. Bd Can.* **27** : 1501–1547.

—— 1975. Biotic census of Cape Cod Bay: hydroids. *Biol. Bull. mar. biol. Lab. Woods Hole* **149** : 287–315.

Castric-Fey, A. 1973. Hydraires et bryozoaires infralittoraux du plateau continental sud-armoricain. 1. – Plateau de Rochebonne et Ile d'Yeu. *Cah. Biol. mar.* **14** : 205–216.

Cavolini, F. 1785. *Memorie per servire alla storia de' polipi marini.* Naples.

Christiansen, B. O. 1972. The hydroid fauna of the Oslo Fiord in Norway. *Norw. J. Zool.* **20** : 279–310.

Chumley, J. 1918. *The fauna of the Clyde Sea area, being an attempt to record the zoological results obtained by the late Sir John Murray and his assistants on board the s.y. 'Medusa' during the years 1884–1892.* Glasgow.

Clark, J. 1906. Marine zoology. *In:* Page, W. (editor), *Victoria history of the county of Cornwall*, pp. 113–159. London.

Clarke, S. F. 1877. Report on the hydroids collected on the coast of Alaska and the Aleutian Islands, by W. H. Dall, U. S. Coast Survey, and party, from 1871 to 1874 inclusive. *Proc. Acad. nat. Sci. Philad.* (1876) : 209–238.

Cornelius, P. F. S. 1975*a*. The hydroid species of *Obelia* (Coelenterata, Hydrozoa : Campanulariidae), with notes on the medusa stage. *Bull. Br. Mus. nat. Hist.* (Zool.) **28** : 249–293.

—— 1975*b*. A revision of the species of Lafoeidae and Haleciidae (Coelenterata: Hydroida) recorded from Britain and nearby seas. *Bull. Br. Mus. nat. Hist.* (Zool.) **28** : 373–426.

—— Notes on the hydroid, *Synthecium evansi* (Ellis & Solander, 1786) (in prep.)

—— A revision of the species of Campanulariidae (Coelenterata : Hydroida) recorded from Britain and nearby seas. (In prep.)

—— **& Garfath, J.** The coelenterate taxa of Joshua Alder. (In prep.)

Crothers, J. H. (editor) 1966. Dale Fort marine fauna. Second edition. *Fld std.* 2 (Suppl.) : 1–169 + i–xxiv.

Cuvier, G. L. C. F. D. 1830. *Le règne animal, distribué d'après son organisation.* Vol. 3; 'new edition'. Paris.

Dalyell, J. G. 1834. No title. *Edinb. new phil. J.* **17** : 411–415. [*On* 'the propagation of Scottish zoophytes'.]

—— 1847–1848. *Rare and remarkable animals of Scotland, represented from living subjects: with practical observations on their nature.* Volume 1, 1847; volume 2, 1848. London.

Deshayes, G. P. & Edwards, H. M. (editors) 1836. *Histoire naturelle des animaux sans vertèbres, par J. B. P. A. de Lamarck.* Volume 2, second edition. Paris.

Ellis, J. 1755. *An essay towards a natural history of the corallines, and other marine productions of the like kind, commonly found on the coasts of Great Britain and Ireland.* London.

—— 1768. An account of the *Actinia sociata*, or clustered animal-flower, lately found on the sea-coasts of the new-ceded Islands. *Phil. Trans. R. Soc.* (1767) **57** : 428–437.

—— **& Solander, D.** 1786. *The natural history of many curious and uncommon zoophytes, collected from various parts of the globe.* Edited by M. Watt. London.

Esper, E. J. C. 1829. *Der Pflanzen-Thiere.* Volume 3, pp. 145–283. Edited by F. L. Hammer. Nürnberg.

Fabricius, O. 1780. *Fauna groenlandica.* Hafniae & Lipsiae.

Fey, A. 1969. Peuplements sessiles de l'archipel de Glénan. I. Inventaire: hydraires. *Vie Milieu.* (B) **20** : 387–413.

Fleming, J. 1828. *A history of British animals.* Edinburgh.

—— 1842. *A history of British animals.* Second edition. London.

Forbes, E. & Goodsir, J. 1840. On the *Corymorpha nutans* of Sars, a remarkable hydroid polype. *Ann. nat. Hist.* **5** : 309–315.

Fowell, R. R. 1944. The ecology of a rock pool. *Proc. Swansea scient. Fld Nat. Soc.* **2** : 192–212.

Fraser, C. M. 1937. New species of hydroids from the Puerto Rican region. *Smithson. misc. Collns* **91** (28) : 1–7.

—— 1944. *Hydroids of the Atlantic coast of North America.* Toronto.

Gemerden-Hoogeveen, G. C. H. van 1965. Hydroids of the Caribbean: Sertulariidae, Plumulariidae and Aglaopheniidae. *Stud. Fauna Curaçao* **22** (84) : 1–87.

Gray, J. E. 1848. *List of the specimens of British animals in the collection of the British Museum. Part 1. Centroniae or radiated animals.* London.

Hamond, R. 1957. Notes on the Hydrozoa of the Norfolk coast. *J. Linn. Soc.* (Zool.) **43** : 294–324.

Hancock, D. A., Drinnan, R. E. & Harris, W. N. 1956. Notes on the biology of *Sertularia argentea. J. mar. biol. Ass. U. K.* **35** : 307–325.

Hartlaub, C. 1901. Revision der Sertularella-Arten. *Abh. Geb. Naturw. Hamburg* **16** (2) : 1–143.

Hassall, A. H. 1841. Supplement to a catalogue of Irish zoophytes. *Ann. Mag. nat. Hist.* **7** : 276–287, 363–373.

—— 1848. Definitions of three new British zoophytes. *Zoologist* **6** : 2223.

—— **& Coppin, J.** 1852. Descriptions of three species of marine zoophytes. *Trans. microsc. Soc. Lond.* **3** : 160–164.

Hincks, T. 1855. Notes on British zoophytes, with descriptions of new species. *Ann. Mag. nat. Hist.* (2) **15** : 127–130.

—— 1861–1862. A catalogue of the zoophytes of south Devon and Cornwall. *Ann. Mag. nat. Hist.* (3) **8** (1861) : 152–161, 251–262, 290–297, 360–366; **9** (1862) : 22–30.

—— 1866. On new British Hydroida. *Ann. Mag. nat. Hist.* (3) **18** : 296–299.

—— 1868. *A history of the British hydroid zoophytes.* Two volumes. London.

—— 1874. On deep-water Hydroida from Iceland. *Ann. Mag. nat. Hist.* (4) **13** : 146–153.

—— 1880. On new Hydroida and Polyzoa from Barents Sea. *Ann. Mag. nat. Hist.* (5) **6** : 277–286.

Hirohito. 1969. Some hydroids of the Amakusa Islands. *Publ. Biol. Lab. Imp. Household, Tokyo* (1969) (9) : 1–32.

Hiscock, K. 1974. The marine fauna of Lundy. Coelenterata. *Rep. Lundy Fld Soc.* **25** : 20–32.

Hogg, J. 1829. On the natural history of the vicinity. *In* Brewster, J., 1829, *The parochial history and antiquities of Stockton-upon-Tees*. London. Appendix II.

Houvenaghel-Crèvecoeur, N. 1973. Sur le mode le fixation de la planule de *Hydrallmania falcata* L. (hydroïde thécate, Sertulariidae). *C. r. hebd. Séanc. Acad. Sci. Paris* (D), **276** : 2813–2815.

Hultén, E. 1927. Flora of Kamtchatka and the adjacent Islands. I. Pteridophyta, Gymnospermae and Monocotyledonae. *Kungl. svenska. VetenskAkad. Handl.* (3) **5** (1) : 1–346.

Hutton, F. W. 1873. On the New Zealand sertularians. *Trans. Proc. N. Z. Inst.* (1872) **5** : 256–259.

Jaderholm, E. 1904. Mitteilungen ueber einige von der Schwedischen Antarctic-Expedition 1901–1903 eingesammelte Hydroiden. *Archs Zool. exp. gén.* (4) **3** (Notes et revue) : I–XIV.

—— 1907. Über einige nordische Hydroiden. *Zool. Anz.* **32** : 371–376.

—— 1909. Northern and arctic invertebrates in the collection of the Swedish State Museum (Riksmuseum). IV. Hydroiden. *K. svenska VetenskAkad. Handl.* **45** (1) : 1–124.

—— 1919. Zur Kenntnis der Hydroidenfauna Japans. *Ark. Zool.* **12** (9) : 1–32.

Jägerskiöld, L. A. 1971. A survey of the marine benthonic macro-fauna along the Swedish west coas 1921–1938. *Acta R. Soc. scient. litt. gothoburg.* (Zool.) **6** : 1–146.

Jelly, E. C. 1889. *A synonymic catalogue of the recent marine Polyzoa, including fossil synonyms*. London.

Jickeli, C. F. 1883. Der Bau der Hydroidpolypen. *Morph. Jb.* **8** : 373–416, 580–680.

Johnston, G. 1838. *A history of the British zoophytes*. London.

—— 1847. *A history of the British zoophytes*. 2nd edition, two volumes. London.

Kirchenpauer, G. H. 1884. Nordische Gattungen und Arten von Sertulariden. *Abh. Geb. Naturw. Hamburg* **8** (3) : 1–54.

Knight, D. P. 1965. Behavioural aspects of emergence in the hydranth of *Campanularia flexuosa* (Hincks). *Nature, Lond.* **206** : 1170–1171.

Knight-Jones, E. W. & Jones, W. C. 1956. The fauna of rocks at various depths off Bardsey. *Rep. Bardsey Bird Fld Obs.* (1955) : 23–30.

Kramp, P. L. 1929. Marine Hydrozoa. *Zoology Faroes* **1** (5) : 1–59.

—— 1932. The Godthaab Expedition 1928. Hydroids. *Meddr Grønland* **79** : 1–86.

—— 1935. Polypdyr (Coelenterata). I. Ferskvandspolypper og Goplepolypper. *Danm. Fauna*, **41** : 1–208.

—— 1943. The Zoology of East Greenland. Hydroida. *Meddr. Grønland* **121** (11) : 1–52.

—— 1947. Hydroids collected by the 'Skagerak' expedition in the eastern Atlantic, 1946. *Göteborgs K. Vetensk. Vitter. Samh. Handl.* (B) **5** (8) : 1–16.

Kudelin, N. V. 1914. *Fauna de la Russe et des pays limitrophes. Hydraires* (Hydroidea). *Volume II. Plumulariidae, Campanulinidae et Sertulariidae*. Petrograd.

Lamarck, J. B. P. A. de 1816. *Histoire naturelle des animaux sans vertèbres*. Volume 2. Paris.

Lamouroux, J. V. F. 1812. Extrait d'un mémoire sur la classification des polypiers coralligènes non entierement pierreux. *Nouv. Bull. Soc. philom. Paris* **3** : 181–188.

—— 1816. *Histoire des polypiers coralligènes flexibles, vulgairement nommés zoophytes*. Caen.

—— 1821. *Exposition méthodique des genres de l'ordre des polypiers*. Paris.

—— 1824. *Corallina; or, a classical arrangement of flexible coralline polypidoms, selected from the French of J. V. F. Lamouroux*. London. [Translated anonymously.]

—— **Bory de Saint-Vincent, J. B. G. M. & Deslongchamps, E.** 1824. *Histoire naturelle des zoophytes, ou animaux rayonnés, faisant suite à l'histoire naturelle des vers, de Bruguiére*. In *Encyclopédie methodique* (Suppl.). Paris.

Landsborough, D. 1852. *A popular history of British zoophytes, or corallines*. London.

Leloup, E. 1935. Hydraires calyptoblastiques des Indes Occidentales. *Mém. Mus. r. Hist. nat. Belg.* (2) **2** : 1–73.

—— 1947. Les coelentérés de la faune Belge. Leur bibliographie et leur distribution. *Mém. Mus. r. Hist. nat. Belg.* **107** : 1–73.

—— 1952. Coelentérés. *Fauna Belg.* pp. 1–283.

Lepechin, J. 1783. Sertulariae species duae determinatae. *Acta Acad. Scient. Imp. Petropol.* (1780) (1) : 223–225.

Levinsen, G. M. R. 1893. Meduser, Ctenophorer og Hydroider fra Grønlands Vestkyst, tilligemed Bemaerkninger om Hydroidernes Systematik. *Vidensk. Meddr dansk naturh. Foren.* (1892) : 143–220.

—— 1913. Systematic studies on the Sertulariidae. *Vidensk. Meddr dansk naturh. Foren.* **64** : 249–323.

Lewis, J. R. 1964. *The ecology of rocky shores*. London.

Linnaeus, C. 1758. *Systema naturae*. 10th edition. Holmiae.

Linnaeus, C. 1761. *Fauna Svecica, sistens animalia Sveciae regni.* 2nd edition. Stockholm.

—— 1767. *Systema naturae.* 12th edition. Tom I, Pars II. Holmiae.

—— 1791. *Systema naturae.* Tom 1, Pars VI (pp. 3021–3910). 13th edition, edited by J. F. Gmelin. Lipsiae. [Dating of this part follows the information given in: *Catalogue of the books, manuscripts, maps and drawings in the British Museum (Natural History), vol. III, L–O.* London, 1910.]

Maitland, R. T. 1897. *Prodrome de la faune des Pays-Bas et de la Belgique flamande.* Leiden.

Mammen, T. A. 1965. On a collection of hydroids from south India. II. Suborder Thecata (excluding family Plumulariidae). *J. mar. biol. Ass. India* **7** : 1–57.

Maratti, J. F. 1776. *Plantis zoophytis et lithophytis in mari mediterraneo viventibus.* Rome.

Marine Biological Association. 1957. *Plymouth marine fauna.* 3rd edition. Plymouth, England.

Marktanner-Turneretscher, G. 1890. Die Hydroiden des k. k. naturhistorischen Hofmuseums. *Annln naturh. Mus. Wien* **5** : 195–286.

Mereschkowsky, C. 1877. On a new genus of hydroids from the White Sea, with a short description of other new hydroids. *Ann. Mag. nat. Hist.* (4) **20** : 220–229.

—— 1878. Studies on the Hydroida. *Ann. Mag. nat. Hist.* (5) **1** : 239–256, 322–340.

Meyen, F. J. F. 1834. Über das Leuchten des Meeres und Beschreibung einiger Polypen und anderer nieder Thiere. *Nova Acta Acad. Caesar. Leop. Carol.* **16** (Suppl. 1) : 125–216.

Millard, N. A. H. 1957. The Hydrozoa of False Bay, South Africa. *Ann. S. Afr. Mus.* **43** : 173–243.

—— 1961. A report on Busk's collection of South African hydroids. *Ann. Mag. nat. Hist.* (13) **4** : 203–208.

—— 1964. The Hydrozoa of the south and west coasts of South Africa. Part II. The Lafoeidae, Syntheciidae and Sertulariidae. *Ann. S. Afr. Mus.* **48** : 1–56.

—— 1975. Monograph on the Hydroida of southern Africa. *Ann. S. Afr. Mus.* **68** : 1–513.

—— 1977. Hydroids from the Kerguelen and Crozet Shelves, collected by the cruise MD.03 of the *Marion-Dufresne. Ann. S. Afr. Mus.* **73** : 1–47.

Moore, H. B. 1937. Marine fauna of the Isle of Man. *Proc. Lpool biol. Soc.* **50** : 1–293.

Moreley, C. 1943. The total living fauna of Suffolk. *Trans. Suffolk Nat. Soc.* **5** : 74–91.

Naumov, D. V. 1960. Gidroidy i gidromeduzy morskikh, solonovatovodnykh i presnovodnykh basseinov S.S.S.R. *Fauna S.S.S.R.* **70** : 1–626.

—— 1969. Hydroids and hydromedusae of the U.S.S.R. *Fauna S.S.S.R.* **70** : 1–660. Israel Program for Scientific Translations.

—— **& Stepan'yants, S. D.** 1962. Gidroidy podotryada Thecaphora, sobrannye v antarkticheskikh i subantarkticheskikh vodakh sovetskoi antarkticheskoi ekspeditsiei na dizel'-elektrakhode 'Ob'. In *Resultaty biologicheskikh issledovanii sovetskoi antarkticheskoi ekspeditsii* (1955–1958 gg), I. *Isledd. Fauny morei* **1** (9) : 69–104.

Newell, G. E. 1954. The marine fauna of Whitstable. *Ann. Mag. nat. Hist.* (12) **7** : 321–350.

Nobre, A. 1931. *Contribuïções para o estudo dos coelenterados de Portugal.* Pôrto.

Norman, A. M. 1869. Shetland final dredging report. Part II. On the Crustacea, Tunicata, Polyzoa, Echinodermata, Actinozoa, Hydrozoa, and Porifera. *Rep. Brit. Ass. Advmt Sci.* (1868) (1) : 247–336.

—— 1878. Note on *Selaginopsis* (= *Polyserias hincksii*, Mereschkowsky), and on the circumpolar distribution of certain Hydrozoa. *Ann. Mag. nat. Hist.* (5) **1** : 189–192.

—— 1905. Marine zoology. *In:* Page, W. (editor), *The Victoria history of the counties of England: a history of Durham.* Volume 1, pp. 83–86. London.

Nutting, C. C. 1904. American hydroids. Part II. The Sertularidae. *Spec. Bull. U.S. natn. Mus.* **4** (2) : 1–325.

Oken, L. 1815. *Okens Lehrbuch der Naturgeschichte.* Jena.

d'Orbigny, A. 1839, 1846. *Voyage dans l'Amérique méridionale, executé pendant les années 1826–1833.* Zoophytes, **5** (4) : 17–28. (1–16, 1839; 17–28, 1846.)

Pallas, P. S. 1766. *Elenchus zoophytorum.* The Hague.

—— 1768. *Lyst der Plant-Dieren.* Utrecht.

—— 1787. *Charakteristik der Thierpflanzen.* Vol. I. Nürnberg.

Palmer, M. G. 1946. *The fauna and flora of the Ilfracombe district of north Devon.* Exeter.

Parke, M. & Dixon, P. S. 1968. Check-list of British marine Algae – second revision. *J. mar. biol. Ass. U. K.* **48** : 783–832.

Pennington, A. S. 1885. *British zoophytes: an introduction to the Hydroida, Actinozoa, and Polyzoa found in Great Britain, Ireland, and the Channel Islands.* London.

Philbert, M. 1934. Note sur les gonothèques femelles de *Diphasia pinaster* (Ell. et Sol.) et de *Diphasia pinnata* (Pallas). *Bull. Inst. océanogr. Monaco* **647** : 1–8.

—— 1935. Contribution à l'étude des Hydraires dans les Iles Anglo-Normandes. *Bull. Mus. Hist. nat. Paris* (2) **7** : 85–88.

Picard, J. 1951. Notes sur les hydraires littoraux de Banyuls-sur-Mer. *Vie Milieu* **2** : 338–349.

—— 1956. Les espèces et formes méditerranéennes du genre *Sertularella. Vie Milieu* **7** : 258–266.

Pictet, C. 1893. Étude sur les hydraires de la Baie d'Amboine. *Rev. suisse Zool.* **1** : 1–64.

—— **& Bedot, M.** 1900. Hydraires provenant des campagnes de l'Hirondelle (1886–1888). *Résult. Camp. scient. Prince Albert I* **18** : 1–59.

Prenant, M. & Teissier, G. 1924. Notes éthologiques sur la faune marine sessile des environs de Roscoff. Cirripèdes, Bryozoaires, Hydraires. *Trav. Stn biol. Roscoff* **2** : 1–49.

Pyefinch, K. A. 1943. The intertidal ecology of Bardsey Island, North Wales, with special reference to the recolonization of rock surfaces, and the rock-pool environment. *J. anim. Ecol.* **12** (2) : 82–108.

Ralph, P. M. 1961. New Zealand thecate hydroids. Part III. Family Sertulariidae. *Trans. R. Soc. N. Z.* **88** : 749–838.

Rankin. J. 1901. Hydroida. *In* Elliot, G. F. S., Laurie, M. & Murdoch, J. B. (editors), *Fauna, flora and geology of the Clyde area.* Pp. 369–371. Glasgow.

Rasmussen, E. 1973. Systematics and ecology of the Isefjord marine fauna. *Ophelia* **11** : 1–495.

Ray, J. 1724. *Synopsis methodica stirpium Britannicarum.* Edn 3. London.

Redier, L. 1966. Hydraires et bryozoaires. *Cah. pac.* **9** : 77–122.

—— 1967. Révision de la collection du Muséum des hydraires de Lamouroux. *Bull. Mus. nat. Hist. Nat.* (2) **39** : 381–410.

Rees, W. J. 1966. *The Cnidaria and their evolution. Symp. zool. Soc. Lond.* **16** : 1–449. Edited by W. J. Rees.

Rees, W. J. & Rowe, M. 1969. Hydroids of the Swedish west coast. *Acta R. Soc. scient. litt. gothoburg.* (Zool.) **3** : 1–24.

Rees, W. J. & Thursfield, S. 1965. The hydroid collections of James Ritchie. *Proc. R. Soc. Edinb.* (B) **69** : 34–220.

Rees, W. J. & White, E. 1966. New records and fauna list of hydroids from the Azores. *Ann. Mag. nat. Hist.* (13) **9** : 271–284.

Riedl, R. 1970. *Fauna und flora der Adria.* Hamburg & Berlin. 2nd edition.

Ritchie, J. 1907*a*. The hydroids of the Scottish National Antarctic Expedition. *Trans. R. Soc. Edinb.* **45** : 519–545.

—— 1907*b*. On the occurrence of a supposed Australasian hydroid (*Sertularia elongata*) in the North Sea. *Proc. R. phys. Soc. Edinb.* **17** : 78–83.

—— 1909*a*. Is the hydroid, *Selaginopsis mirabilis*, a native of British seas? *Proc. R. phys. Soc. Edinb.* **17** : 217–220.

—— 1909*b*. Note on the probable origin of the hydroid genus *Selaginopsis. Proc. R. phys. Soc. Edinb.* **17** : 221–222.

—— 1909*c*. Supplementary report on the hydroids of the Scottish National Antarctic Expedition. *Trans. Roy. Soc. Edinb.* **47** : 65–101.

—— 1911. Contribution to our knowledge of the hydroid fauna of the west of Scotland. *Ann. Scot. nat. Hist.* **77** : 29–34, 158–164, 217–225.

Robins, M. W. 1969. The marine flora and fauna of the Isles of Scilly. Cnidaria and Ctenophora. *J. nat. Hist.* **3** : 329–343.

Robson, J. H. 1914. Catalogue of the Hydrozoa of the north-east coast (Northumberland and Durham). *Rep. Dove mar. Lab.* (N.S.) **3** : 87–103.

Sars, G. O. 1874. Bidrag til Kundskaben om Norges Hydroider. *Forh. VidenskSelsk. Krist.* (1873) : 91–150.

Savage, S. 1945. *A catalogue of the Linnaean herbarium.* London.

Schydlowsky, A. 1902. Matériaux relatifs à la faune des polypes hydraires des mers arctiques. 1. Les hydraires de la mer blanche le long du littoral des Jles Solowetzky. *Trudy Kharkov. Obshch. Ispyt. Prir.* (1901) **36** : 1–276.

Smith, J. E. 1821. *A selection of the correspondence of Linnaeus, and other naturalists, from the original manuscripts.* Two volumes. London.

Sorby, H. C. 1908. Marine zoology. *In* Page, W. (editor), *The Victoria history of the counties of England: a history of Kent in six volumes.* Volume 1, pp. 91–98. London.

Stechow, E. 1919. Zur Kenntnis der Hydroidenfauna des Mittelmeeres, Amerikas und anderer Gebiete, nebst Angaben über einige Kirchenpauer'sche Typen von Plumulariden. *Zool. Jb., Syst.* **42** : 1–172.

—— 1920. Neue Ergebnisse auf dem Gebiete der Hydroidenforschung. *Sber. Ges. Morph. Physiol. Münch.* (1919) **31** : 9–45.

—— 1923. Zur Kenntnis der Hydroidenfauna des Mittelmeeres, Amerikas und anderer Gebiete. II Teil. *Zool. Jb.* **47** : 29–270.

Stechow, E. 1925. Hydroiden der Deutschen Tiefsee-Expedition. *Wiss. Ergebn. dt. Tiefsee-Exped. 'Valdivia'* **17** (3) : 383–546.

—— 1927. Die Hydroidenfauna der Ostsee. *Zool. Anz.* **70** : 304–313.

Stejneger, L. H. 1936. *Georg Wilhelm Steller. The pioneer of Alaskan natural history.* Cambridge, Massachusetts.

Stephens, J. 1905. A list of Irish Coelenterata, including the Ctenophora. *Proc. R. Ir. Acad.* (B) **25** : 25–92.

Teissier, G. 1922. Observation des médusoides libres et des planulas de *Sertularia operculata* L. *Bull. Soc. zool. Fr.* **47** : 357–361.

—— 1923. Recherches sur *Dynamena pumila* (L.). *Trav. Stn biol. Roscoff* **1** : 3–59.

—— 1929. Morphologie des jeunes colonies de *Sertularia operculata* L. *Bull. Soc. Zool. France* **54** : 647–650.

—— 1965. *Inventaire de la faune marine de Roscoff. Cnidaires – cténaires.* Roscoff, France.

Templeton, R. 1836. A catalogue of the species of rayed animals found in Ireland, as selected from the papers of the late J. Templeton, Esq., of Cranmore, with notices of localities, and with some descriptions and illustrations. *Mag. nat. Hist.* **9** : 233–240, 301–305, 417–422, 466–472.

Thompson, W. 1856. *The natural history of Ireland. Volume 4. Mammalia, reptiles, and fishes. Also Invertebrata.* London. (Volume 4 was published posthumously, edited by R. Patterson, J. R. Garrett and G. Dickie.)

Thompson, d'A. W. 1884. The hydroid zoophytes of the 'Willem Barents' Expedition, 1881. *Bijdr. Dierk.* **10** (3) : 1–10.

Thornely, L. R. 1904. Report on the Hydroida collected by Professor Herdman, at Ceylon, in 1902. *Rep. Govt Ceylon Pearl Oyster Fish. Gulf Manaar, Suppl. Rep.* **8** : 107–126.

—— 1916. Report on the Hydroida collected by Mr James Hornell at Okhamandal in Kattiawar in 1905–6. In *Report to the Government of Baroda on the marine zoology of Okhamandal in Kattiawar.* Part ii. London. Edited by J. Hornell.

Torrey, H. B. 1902. The Hydroida of the pacific coast of North America. *Univ. Calif. Publs* (Zool.) **1** : 1–104.

Totton, A. K. 1930. Hydroida. *Nat. Hist. Rep. Br. antarct. 'Terra Nova' Exped.* **5** : 131–252.

Trask, J. B. 1857. On nine new species of zoophytes, from the Bay of San Francisco and adjacent localities. *Proc. Calif. Acad. Sci.* **1** : 100–103.

Turton, W. 1802. *A general system of nature. Translated from Gmelin's last edition of the Systema Naturae. Amended and enlarged by W. Turton.* Four volumes. London.

Vannucci Mendes, M. 1946. Hydroida Thecaphora do Brasil. *Archos Zool. S. Paulo* **4** : 535–597.

Vannucci, M. 1949. Hydrozoa do Brasil. *Bolm Fac. Filos. Ciênc. Univ. S. Paulo* (Zool.) **14** : 219–265.

Verrill, A. E. 1873. Results of recent dredging expeditions on the coast of New England. *Am. J. Sci.* (3) **5** : 1–16.

Vervoort, W. 1942. Northern Hydroida in the collections of the Rijksmuseum van Natuurlijke Historie and the Zoological Museum at Amsterdam, with notes on their distribution. *Zool. Meded. Leiden* **23** : 275–312.

—— 1946. Hydrozoa (C1). A. Hydropolypen. *Fauna Ned.* **14** : 1–336.

Vervoort, W. 1949. Notes on a small collection of hydroids from Jersey (Channel Islands). *Zool. Meded. Leiden* **30** : 133–162.

—— 1959. The Hydroida of the tropical west coast of Africa. *Atlantide Rep.* **5** : 211–325.

—— 1966. Bathyal and abyssal hydroids. *Galathea Rep.* **8** : 97–174.

—— 1972. Hydroids from the Theta, Vema and Yelcho cruises of the Lamont-Doherty Geological Observatory. *Zool. Verh. Leiden* **120** : 1–247.

Waddington, H. J. 1914. Marine fauna. In *A natural history of Bournemouth and district.* Edited by D. Morris. Bournemouth. Pp. 213–230.

Warren, E. 1908. On a collection of hydroids, mostly from the Natal coast. *Ann. Natal Mus.* **1** : 269–355.

Weismann, A. 1880. Zur Frage nach dem Ursprung der Geschlechtszellen bei den Hydroiden. *Zool. Anz.* **3** : 226–233.

—— 1883. *Die Entstehung der Sexualzellen bei den Hydromedusen.* Jena.

Westendorp, G. D. 1843. *Recherches sur les polypiers flexibles de la Belgique et particulièrement des environs d'Ostende.* Bruges.

Williams, G. 1954. Fauna of Strangford Lough and neighbouring coasts. *Proc. R. Ir. Acad.* **56** (B) : 29–133.

Winther, G. 1879. Om Internodiets bygning og Sammensaetning hos Sertularierne. *Naturh. Tidsskr.* **12** : 303–320. [Anonymous abstract in English in *Jl R. microsc. Soc.* (1) **3** (1880) : 462.]

Yamada, M. 1950. The fauna of Akkeshi Bay. XVII. Hydroids. *J. Fac. Sci. Hokkaido Univ.* (Zool.) (6) **10** : 1–20.

Index

Accepted names are shown in roman type, invalid names in *italic type*. Main page references are in *italics*.

Addenda

Some of the nomenclatural changes proposed here have been incorporated in Evans, F. O. (1978) [The marine fauna of the Cullercoats district. 6. Coelenterata and Ctenophora. *Rep. Dove mar. Lab.* (3) **19:** 1–165], with my agreement. The work provides further distribution data on many of the species included here. However, the distribution changes discussed above are not contradicted by Evans' data.

Type material of *Diphasia margareta* has recently been located (p. 263):—infertile fragment of colony on herbarium sheet, coll. A. H. Hassall, via G. Johnston; presumably from one of Hassall's Irish localities; BMNH regd no. 1842.12.7.10; syntypes (mentioned, Johnston, 1847: 72).

Sertularella gaudichaudi was first described by Lamouroux, in Freycinet, L. de (editor) (1824) [*Voyage autour du monde entrepris par ordre du Roi. Zoologie;* by Quoy, J. R. C. & Gaimard, J. P.; Paris; p. 615, pl. 90, figs 4–5] and later in the same year by Lamouroux *et al.* (see p. 282).

Titles to be published in Volume 34

The anatomy and relationships of the cyprinid fish *Luciobrama macrocephalus* (Lacepède). By G. J. Howes.

A new species of *Pteralopex* Thomas, 1888 (Chiroptera : Pteropodidae) from the Fiji Islands.
By J. E. Hill & W. N. Beckon.

A revision of the species of Sertulariidae (Coelenterata : Hydroida) recorded from Britain and nearby seas. By P. F. S. Cornelius.

Anatomical specimens of birds in the collection of the British Museum (Natural History).
By J. S. Blandamer & P. J. K. Burton.

Amphibians and reptiles from northern Trengganu, Malaysia, with descriptions of two new geckos: *Cnemaspis* and *Crytodactylus*.
By J. M. C. Dring.

A revision of the spider genus *Portia* (Araneae : Salticidae).
By F. R. Wanless.

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