CHAPTER ONE

THE MORPHOLOGY OF ADULT SCARIDS

1.1 Introduction

Various aspects of scarid morphology have been described in detail: cranial osteology by Gregory (1933), Gobalet (1980), Tedman (1980a) and briefly by Lubosch (1923, 1929, 1938); cranial myology by Lubosch (1923, 1929, 1938), Board (1956), Gobalet (1980) and Tedman (1980 b); jaw structure by Boas (1878), Randall and Nelson (1979) and Simoes and Domingos Andreucci (1982); pharyngeal mill by Boas (1878), Sagemehl (1855), Al-Hussaini (1946), Monod (1951), Schultz (1958), Hattori (1976, 1984), Gobalet (1980), Yamaoka (1980) and Liem and Greenwood (1981); viscera by Al-Hussaini (1945, 1947), Gohar and Latif (1959, 1961) and briefly by Suyehiro (1942); and the branchial arch by Nelson (1967).

These descriptions are restricted to a single, or a few 'typical', species, and differences in nomenclature make comparisons between them difficult. Comparative studies within the group are limited. Choat (1969) described variations in the ratio of the lengths of the premaxillary ascending and descending process in species from the Great Barrier Reef. Bruce (1979) likewise compared the form of the premaxilla, in addition to the dentary and pharyngeal plates, but based on species from Aldabra, Indian Ocean. Gobalet (1980) described the cranial osteology and myology of four species, two of which are restricted to the Eastern Pacific. With the exception of Boas (1878) all of the above works are restricted to adult fishes.

The present study is based upon Central Great Barrier Reef species. Particular attention is paid to those muscles and structures directly involved in feeding. Previously, a detailed comparative analysis of these structures and observations of ontogenetic changes in morphology were lacking. This study, therefore, considers the morphology of both adults and juveniles of representative species in the subfamily Scarinae. The morphology of adults will be described in this chapter and the morphology of juveniles in Chapter 2.

1.2 Materials, Methods and Terminology

Specimens were collected from several reefs and islands near to Lizard Island (14° 40'S, 145° 28'E) and off Townsville, Queensland, between August, 1981 and January, 1984. Large fish were taken by using a conventional rubber-powered spear gun, while smaller individuals were obtained by using a Hawaiian sling and multiprong spear. A list of the scarid species recorded from the Great Barrier Reef is given in Table 1.1.

Myological descriptions are based upon dissections of fresh, frozen, and preserved specimens, which were fixed and stored in 10% seawater-formalin. Observations of the jaw articulation mechanisms were made on fresh specimens. Osteological material was prepared by boiling the head of fresh or frozen specimens in water, then removing most of the flesh. Any remaining flesh decomposed when the skulls were left in water at room temperature (25°C) for a few days and was easily washed off. The bones were air-dried before labelling and, where necessary, were reassembled using a clear glue.

Table 1.1 A partial synonomy of the Scaridae of the Great Barrier Reef.

	Identification reference	Previous names used for G.B.R. species
Sparisomatinae		
Leptoscarus vaigiensis (Quoy & Gaimard)	B	-
Calotomus carolinus (Valenciennes)	B,H	-
Scarinae		
Cetoscarus bicolor (Rüppell)	A,G	-
Bolbometopon muricatum (Valenciennes)	A,G	-
Hipposcarus longiceps (Valenciennes)	G	*H. harid,H. schultzi*
Scarus bleekeri (de Beaufort)	F	-
Scarus frontalis Valenciennes *	D,G	*S. jonesi*
Scarus gibbus Rüppell	F	*S. microrhinos*
Scarus japanensis (Bloch)	F	-
Scarus sordidus Forsskål	B	-
Scarus brevifilis (Günther)	B	*S. chlorodon*
Scarus dimidiatus Bleeker	F	-
Scarus flavipectoralis Schultz	F	-
Scarus frenatus Lacepède	C	*S. servittatus*
Scarus ghobban Forsskål	B,G	-
Scarus globiceps Valenciennes	F	-
Scarus longipinnis Randall & Choat	F	-
Scarus niger Forsskål	B	-
Scarus oviceps Valenciennes	F	-
Scarus psittacus Forsskål	E	*S. forsteri*
Scarus rivulatus Valenciennes	F	*S. fasciatus*
Scarus rubroviolaceus Bleeker	B,G	-
Scarus schlegeli (Bleeker)	F	*S. venosus*
Scarus spinus (Kner)	F	*S. formosus*
Scarus tricolor Bleeker **	F	*S. lepidus*
Scarus sp. +	G	*S. lunula*

A = Smith (1956)
B = Schultz (1958)
C = Randall (1963)
D = Masuda *et al.* (1975)
E = Randall & Ormond (1978)
F = Randall & Choat (1980)
G = Randall & Bruce (1983)
H = Russell (1983)

* Visual record only (D.R.Bellwood & J.H. Choat, Lizard Island, December 1983).

** This G.B.R. species may be *S. forsteni* Bleeker (pers.comm. J.E. Randall) *cf. S. tricolor* in Randall & Bruce (1983).

\+ This species is presently being described (Choat & Randall, pers. comm.).

Table 1.2 The morphology of adult scarids: Material examined.

Species	Gapes		Dissections	
	No.	S.L. range in mm	No.	S.L. range in mm
Scarinae				
S. bleekeri	-	-	2	54-193
S. gibbus	4	208-340	7	249-455
S. sordidus	10	108-248	22	106-238
S. brevifilis	2	183-266	3	183-340
S. dimidiatus	1	233	2	214-233
S. flavipectoralis	2	200-217	4	186-222
S. frenatus	10	83-205	11	110-293
S. ghobban	-	-	3	106-360
S. globiceps	6	154-190	21	122-204
S. longipinnis	-	-	1	75
S. niger	2	82-239	6	107-240
S. oviceps	-	-	6	163-304
S. psittacus	-	-	5	63-196
S. rivulatus	9	69-235	6	58-235
S. rubroviolaceus	1	275	1	275
S. schlegeli	3	96-213	3	96-253
S. spinus	2	188-218	2	197-218
S. tricolor	1	176	1	176
S. sp. (*cf. lunula*)	1	170	5	164-233
Cetoscarus bicolor	-	-	5	183-486
Bolbometopon muricatum	-	-	4	530-775
Hipposcarus longiceps	-	-	1	329
Labridae				
Choerodon schoenleinii	-	-	1	790
Choerodon fasciata	-	-	1	164
Others				
Arothron reticularis	-	-	1	380
Opistognathus papuensis	-	-	1	340
Promicrops lanceolatus	-	-	1	1900

Gape = the maximal distance between the jaws when fully open.
S.L. = Standard Length, the distance from the tip of the snout to the caudal base.
Adult specimens (> 110 mm S.L.) were used for the descriptions although some sub-adult specimens were examined.

Table 1.3 Abbreviations used in the figures.

A1; A1α,A1β,	-	Adductor mandibulae section 1 subsections
A1βI, II, III, IV, V	-	Adductor mandibulae section 1 subdivisions
A2	-	Adductor mandibulae section 2
A3; A3α, A3β	-	Adductor mandibulae section 3
ALV.PR..	-	Alveolar process of premaxilla
ANG.PR.	-	Angular process of dentary
ANT.MAX.P.MAX.LIG.	-	Anterior maxillary premaxillary ligament
ART.	-	Articular
ART.ASC.PR.	-	Articular ascending process
ART.CON.	-	Articular condyle of quadrate (L.J.ART.)
ART.DEC.PR.	-	Articular descending process
ART.SOC.	-	Articular socket of dentary
ASC.PR.	-	Ascending process of premaxilla
A1T.	-	Adductor mandibulae tendon
Awα, Awβ, Awγ	-	Adductor mandibulae section Aw
CR.CON.	-	Cranial condyle of maxilla
CRU.LIG.	-	Cruciate ligaments of premaxilla
C.T.	-	Caniform tooth
DENT.	-	Dentary
DENT.L.FL.	-	Dentary lateral flange
DENT.PL.	-	Dental plate
EC.PTY.	-	Ectopterygoid (pterygoid)
EN.PTY.	-	Entopterygoid
EN.PTY.L.P.	-	Entopterygoid lateral process
HYO.	-	Hyomandibula
IN.	-	Insertion site
IN.A.	-	Adductor mandibulae insertion site
IN.ANT.MAX.P.MAX.LIG.	-	Insertion of anterior maxillary-premaxillary ligament
IN.I.	-	Intermandibularis insertion site
IN.P.H.	-	Protractor hyoideus insertion site
I.MAX.LIG.	-	Intermaxillary ligament
I.OP.	-	Interoperculum
I.OP.ART.LIG.	-	Interopercular-articular ligament
LAC.	-	Lacrymal
L.A.P.	-	Levator arcus palatini
L.J.ART.	-	Lower jaw articulation/articulatory socket of the lower jaw
L.O.	-	Levator operculi
MAX.	-	Maxilla
MAX.ARM	-	Maxillary arm
MAX.CON.	-	Maxillary condyle
MAX.FAC.	-	Maxillary facet of premaxilla
MAX.FOS.	-	Maxillary fossa
MAX.HD.	-	Maxillary head
MAX.L.R.	-	Maxillary lateral ridge
MED.PR.	-	Medial process of maxillary head
MED.SP.	-	Medial spine of the articular
MED.SUT.	-	Sutures of dentary medial symphysis
M.PTY.	-	Metapterygoid

NA.	–	Nasal
NAS.LAC.MAX.PAL.C.	–	Nasal-lacrymal-maxillary-palatine complex
NC.	–	Neurocranium
OP.	–	Operculum
OR.A1β	–	Adductor mandibulae muscular origin
P.H.	–	Protractor hyoideus
P.MAX.	–	Premaxilla
P.MAX.CON.	–	Premaxillary condyle of maxilla
P.MAX.PR.	–	Premaxillary process of maxilla
P.OP.	–	Preoperculum
P.OP.ART.LIG.	–	Preopercular-articular ligament
PAL.	–	Palatine
PAL.D.PR.	–	Palatine dorsal process
PAL.P.MAX.LIG.	–	Palatine-premaxillary ligament
PD.PR.	–	Postero-dorsal projection of the maxillary arm
POST.MAX.P.MAX.LIG.	–	Posterior maxillary-premaxillary ligament
QUA.	–	Quadrate
QUA.ART.	–	Quadrate-articular ligaments
QUA.L.R.	–	Quadrate lateral ridge
RO.C.	–	Rostral cartilage
S.OP.	–	Suboperculum
SYM.	–	Symplectic

Additional specimens were cleared for examination following the technique of Wasserburg (1976). A list of the material examined is given in Table 1.2.

Most specimens were dissected under a Wild M-5 dissecting miscroscope. Pencil drawings of whole head preparations were made using a Grant projector. Drawings of small preparations were made with the aid of a camera lucida. In all drawings, the shading conventions of Figure 1.10 are followed. A key to the abbreviations used in the figures is given in Table 1.3. Unless stated otherwise, all the figures in this chapter are in lateral view with the dorsal edge uppermost and the anterior edge on the left hand side.

Osteological terminology follows that of Gregory (1933), Rognes (1971), Bruce (1979), Gobalet (1980) and Yamaoka (1980), and unless stated otherwise, the myological terminology follows that of Winterbottom (1974 a). Intestinal descriptions follow the techniques and terminology of Mok (1977).

A - The Muscular and Skeletal System

1.3 Observations

From the external appearance of the head and the form of the superficial adductor muscle blocks, the species examined can be divided into two distinct groups, designated here as the 'sordidus' group and the 'frenatus' group (Section 1.3.4). *Scarus sordidus* and *S. frenatus* are described in detail as representatives of their respective groups. The osteological figures in this chapter were drawn from a 234 mm S.L. T.P. *S. sordidus* and a 263 mm S.L. T.P.

S. frenatus. The myological figures were drawn from a 238 mm S.L. T.P. *S. sordidus* and a 293 mm S.L. T.P. *S. frenatus*.

1.3.1 External appearance and integument (Figs 1.1 A, B)

The most striking difference between *S. sordidus* and *S. frenatus* is the dissimilarity in head shape (Figs 1.1 A, B). *S. sordidus* has a rounded profile with a distinct bump on the snout, above the terminal mouth. *S. frenatus* has a more angular profile and a slightly inferior mouth. The dental plates are exposed in *S. sordidus*, whereas in *S. frenatus* they are almost completely covered by the lips. Both species have large scales on the head with those of *S. frenatus* being more numerous.

The integument in both species is tightly connected to the nasal, lacrymal, circumorbitals, preopercular ascending ridge, quadrate lateral process and articular descending process. It has a flexible association with the premaxilla and dentary and has a strong fibrous connection at the angle of the jaws, where the maxillary arm, dentary lateral flange and premaxillary alveolar process meet.

1.3.2 Osteology

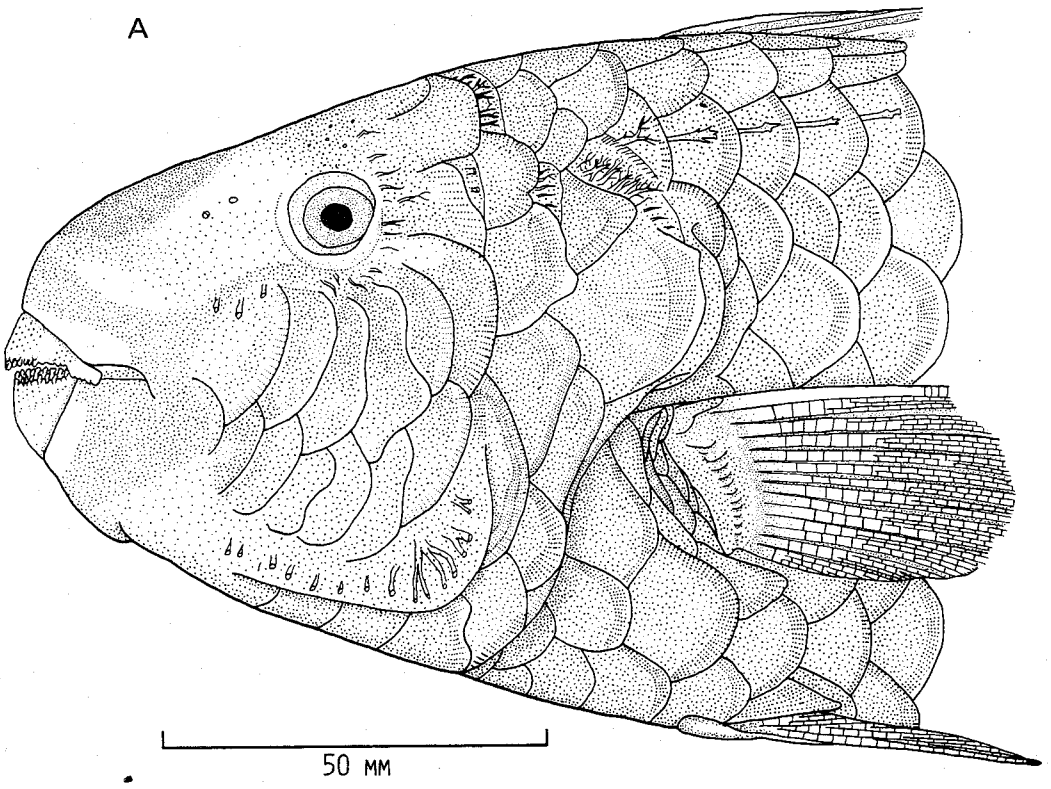
S. sordidus and *S. frenatus* differ considerably in their osteology. The descriptions below separate the 'sordidus' and 'frenatus' groups and form a basis for further myological descriptions.

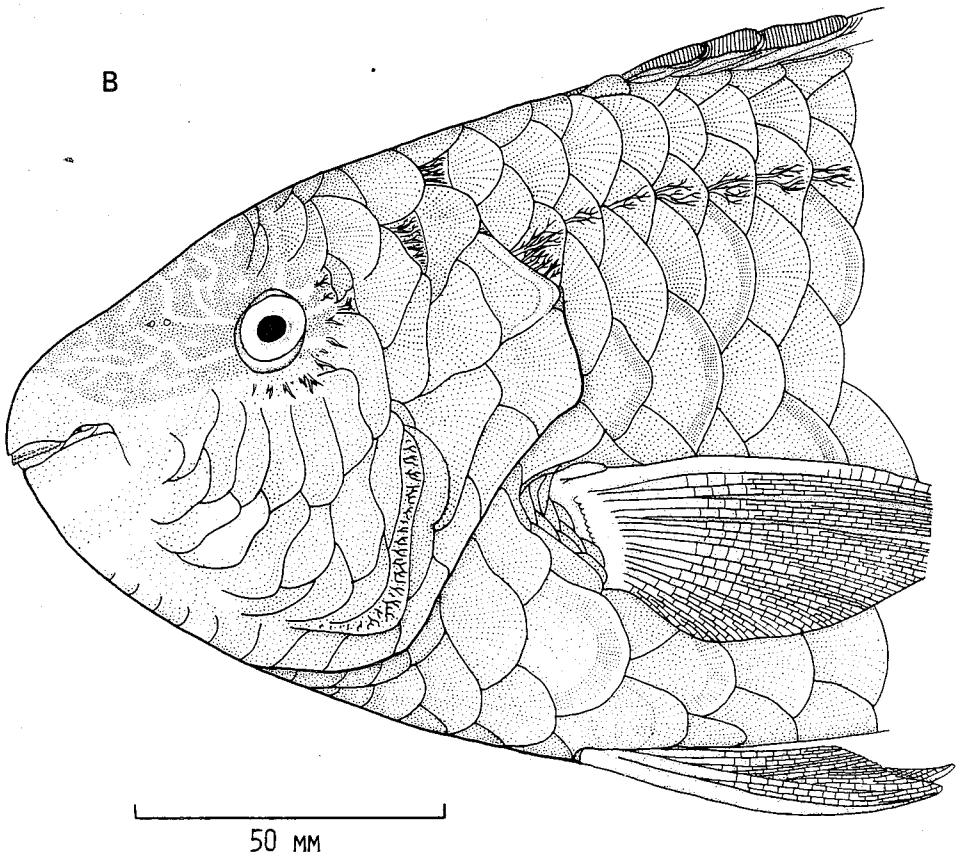
Figure 1.1 A

The external anatomy of the head of *Scarus sordidus*.

Figure 1.1 B

The external anatomy of the head of *Scarus frenatus*.


A
50 MM


B
50 MM

The suspensorium (Figs 1.2, 1.3, 1.4 A, B)

The suspensorium is of a similar shape in both species. It is roughly square with a protruded anterodorsal corner and a deep dorsal notch. It articulates with the neurocranium by two posterolateral condyles on the hyomandibula (HYO., Figs 1.2, 1.3, 1.4 A, B). A third condyle on the posterior edge of the hyomandibula bears a vertical groove into which the anterior edge of the ascending arm of the preoperculum (P.OP.) inserts (Figs 1.4 A, B). A ridge extending along the length of the preopercular arm and part of the horizontal limb to the posterior edge of the quadrate (QUA.), defines the posterior and posteroventral edge of the adductor mandibulae fossa, which occupies the central region of the suspensorium (Figs 1.2, 1.3).

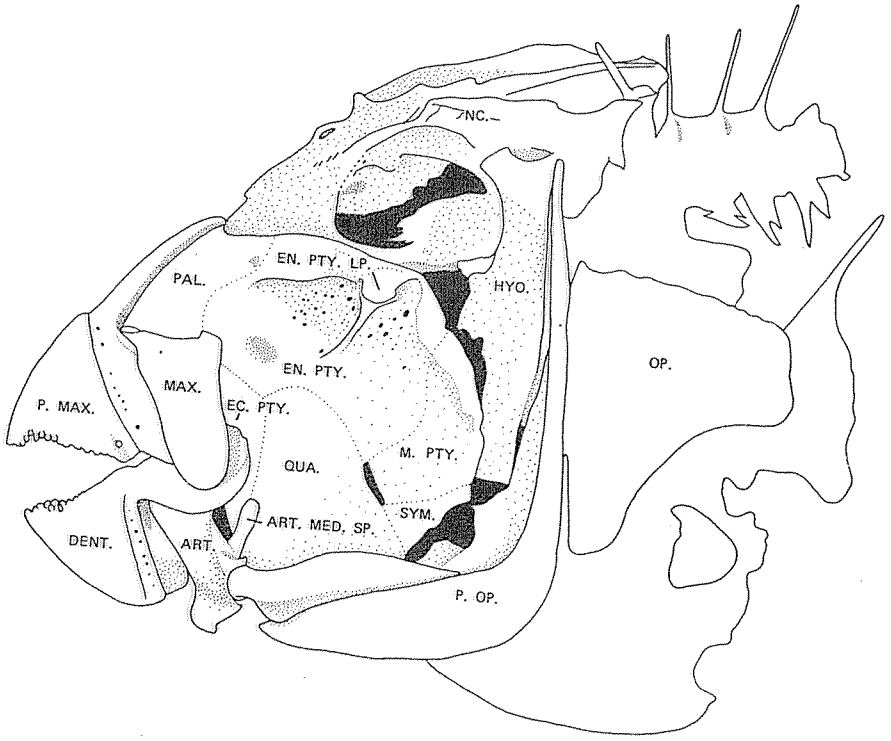
The connection between the horizontal limb of the preoperculum and quadrate, however, differs in the two species (Figs 1.4 A, B). In *S. sordidus* (Fig. 1.4 A), the quadrate lies dorsal to the preopercular horizontal limb, with the ventral edge of the quadrate inserting into a dorsal groove along the preopercular horizontal limb, except for the most anterior section where the narrow anterodorsal edge of the preopercular horizontal limb inserts into a narrow groove in the anteroventral extremity of the quadrate. In *S. frenatus* (Fig. 1.4 B), the anterior preopercular horizontal limb inserts into a shallow groove on the ventral surface of the quadrate and posteriorly, the quadrate lies lateral to the preopercular horizontal limb and does not interdigitate.

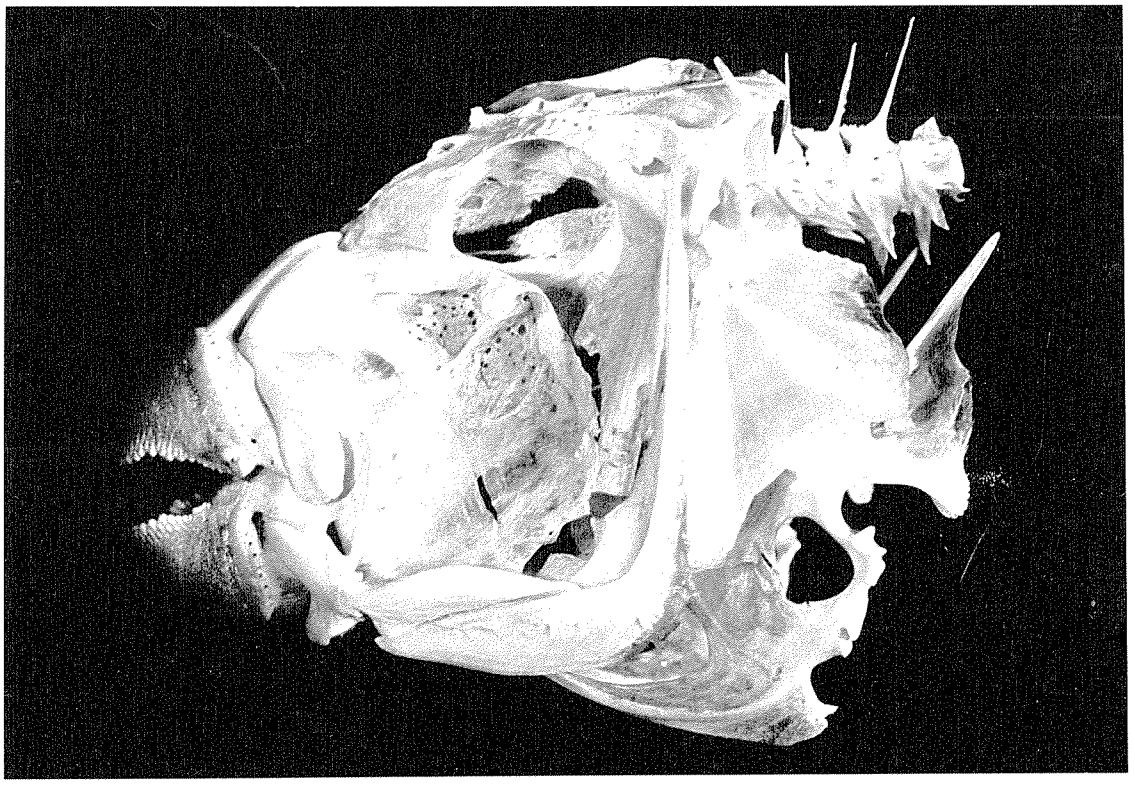
Figure 1.2

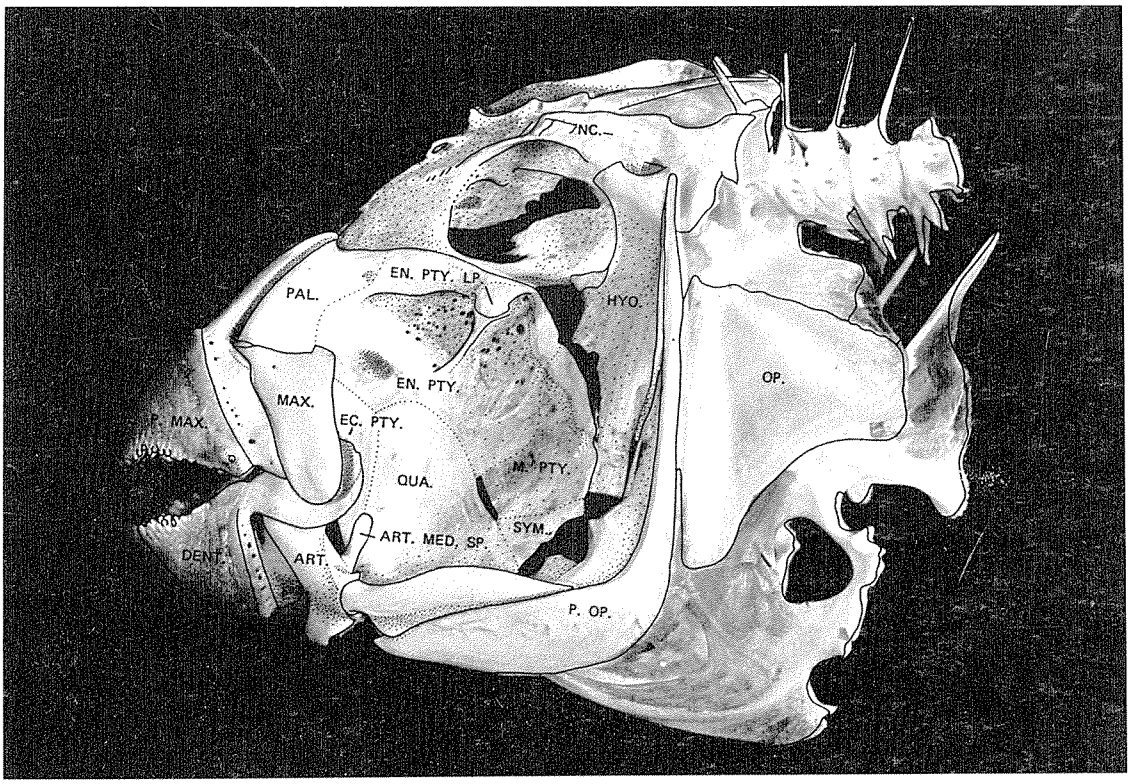
The bones of the head of *Scarus sordidus*, showing the location of the bones of the suspensorium and jaws.

Abbreviations used in this figure:

ART.	Articular
ART.MED.SP.	Articular medial spine
DENT.	Dentary
EC.PTY.	Ectopterygoid
EN.PTY.	Entopterygoid
EN.PTY.LP.	Entopterygoid lateral process
HYO.	Hyomandibula
M.PTY.	Metapterygoid
MAX.	Maxilla
NC.	Neurocranium
OP.	Operculum
P.MAX.	Premaxilla
P.OP.	Preoperculum
PAL.	Palatine
QUA.	Quadrate
SYM.	Symplectic


NC.
EN. PTY. LP.
PAL.
HYO.
EN. PTY.
OP.
MAX.
P. MAX.
EC. PTY.
M. PTY.
QUA.
SYM.
ART. MED. SP.
DENT.
ART.
P. OP.




NC.
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PAL.
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OP.
MAX.
EC. PTY.
P. MAX.
M. PTY.
QUA.
SYM.
ART. MED. SP.
DENT.
ART.
P. OP.

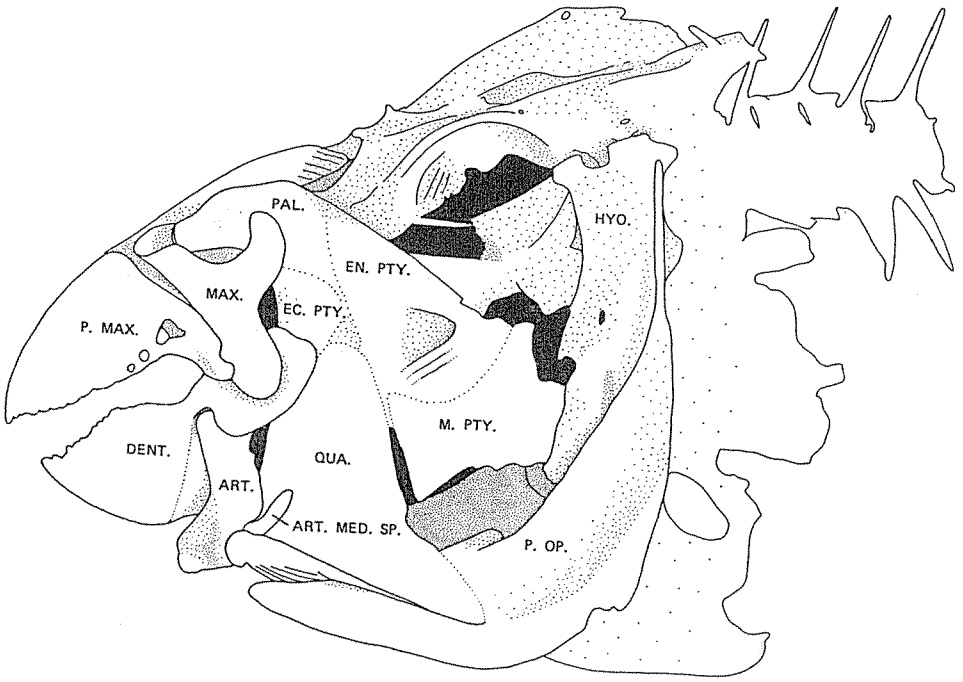
Figure 1.3

The bones of the head of *Scarus frenatus*, showing the location of the bones of the suspensorium and jaws.

Abbreviations used in this figure:

ART.	Articular
ART.MED.SP.	Articular medial spine
DENT.	Dentary
EC.PTY.	Ectopterygoid
EN.PTY.	Entopterygoid
HYO.	Hyomandibula
M.PTY.	Metapterygiod
MAX.	Maxilla
P.OP.	Preopercular
P.MAX.	Premaxilla
PAL.	Palatine
QUA.	Quadrate

The symplectic is not figured.


PAL.
HYO.
EN. PTY.
MAX.
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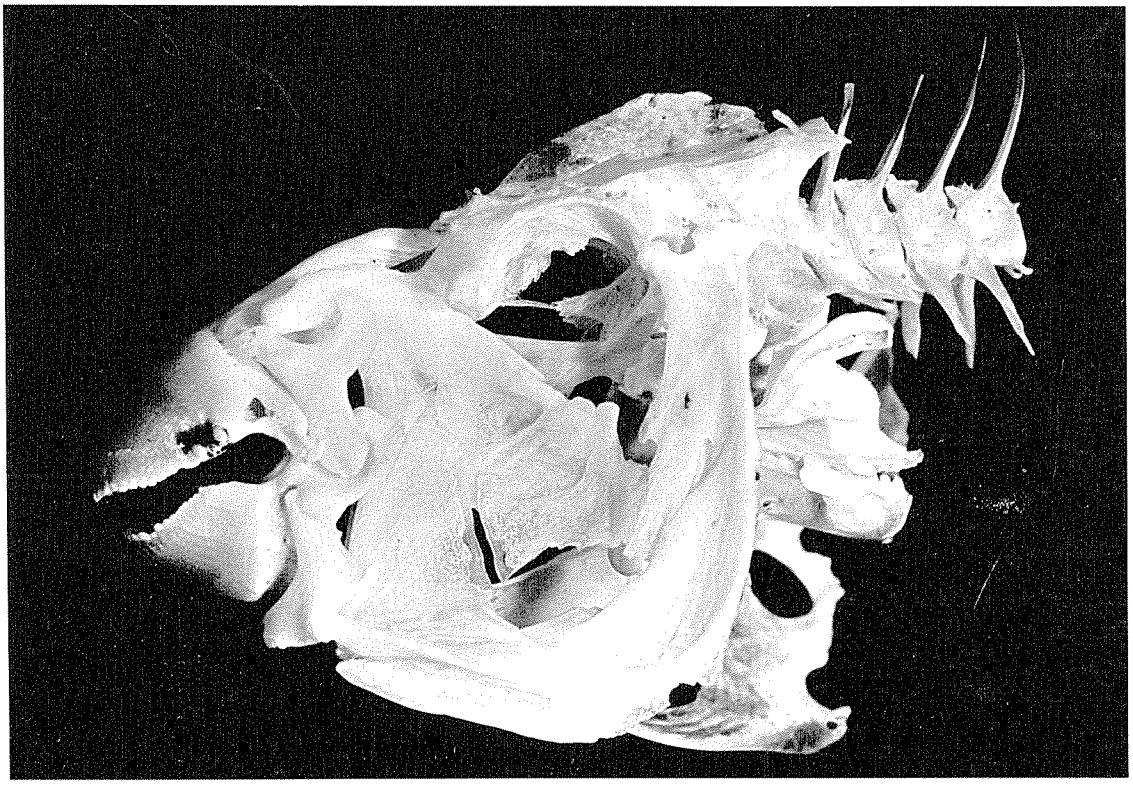
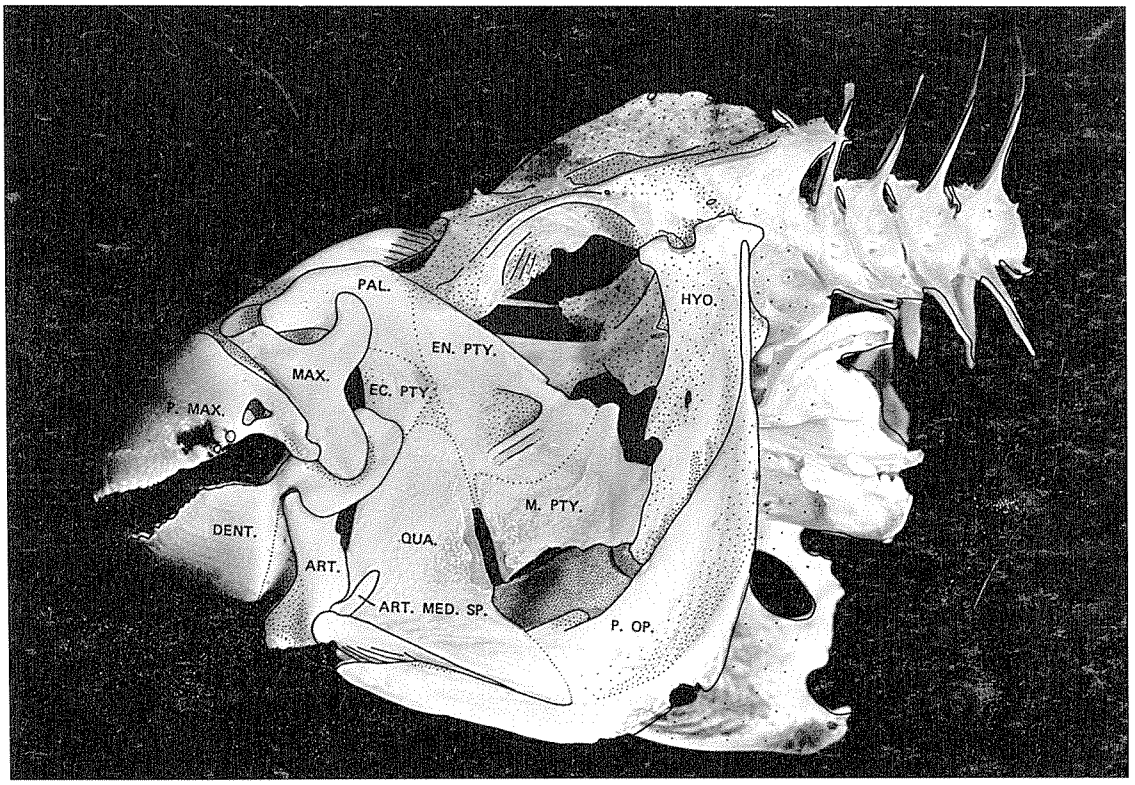
P. MAX.
M. PTY.
DENT.
QUA.
ART.
ART. MED. SP.
P. OP.




PAL.
HYO.
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MAX.
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P. MAX.
M. PTY.
DENT.
QUA.
ART.
ART. MED. SP.
P. OP.

A lateral ridge is present along the horizontal edge of the triangular quadrate (QUA.L.R., Figs 1.4 A, B). It forms a broad dorsal groove and represents the ventral edge of the adductor mandibulae fossa. In *S. sordidus* this ridge is well developed and extends to the posterior extremity of the quadrate, whereas in *S. frenatus* it is only developed anteriorly. Anteriorly the lateral ridge supports a rounded lateral articular condyle (ART.CON.). This condyle is connected by a horizontal ridge to a smaller ovoid medial condyle on the medial anteroventral extremity of the quadrate.

The symplectic (SYM.) inserts into a broad shallow depression on the posteromedial surface of the quadrate and extends posterodorsally to fuse with the ventral edge of the metapterygoid (M.PTY., Figs 1.4 A, B). This connection is stronger in *S. sordidus* than in *S. frenatus*. A large, irregular interspace is present between the symplectic, hyomandibula and the angle of the preoperculum. A smaller, narrow interspace is present between the quadrate and metapterygoid.

The entopterygoid (EN.PTY.) is the deepest of the sections in the adductor mandibulae fossa (Figs 1.4 A, B). It is tightly fused along its posteroventral edge to the metapterygoid, the posterior edge of which is in close association with the ventral portion of the anterior edge of the hyomandibula. Anteroventral laminae from the entopterygoid fuse with the medial surface of the dorsal portion of the quadrate and the anterior portion of the metapterygoid.

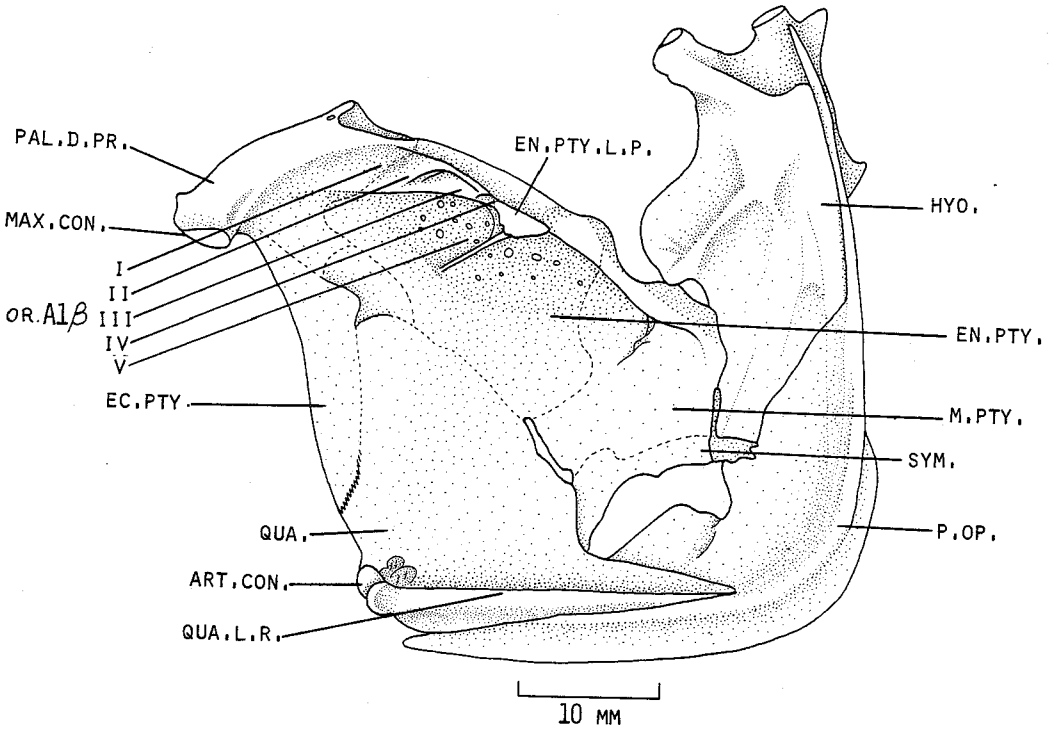
Posterior laminae from the ectopterygoid (EC.PTY.) likewise fuse with the anterodorsal medial surface of the quadrate and the anterior medial surface of the entopterygoid (Figs 1.4 A, B). The

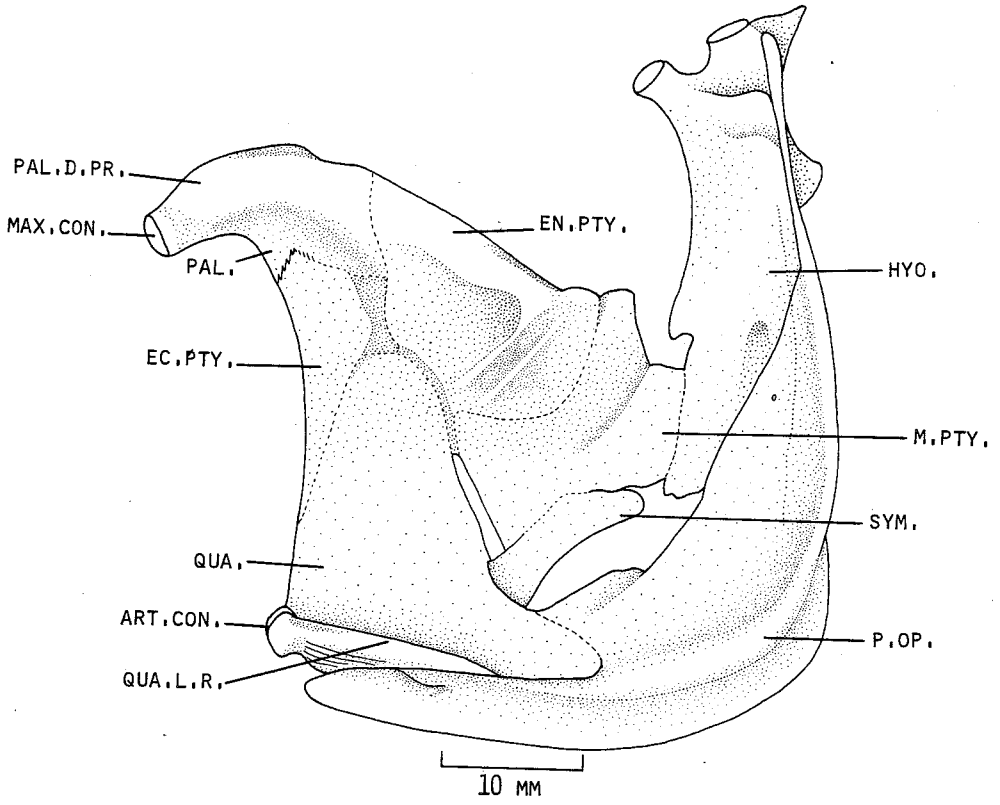
Figure 1.4 A

A lateral view of the suspensorium of *S. sordidus*.

Figure 1.4 B

A lateral view of the suspensorium of *S. frenatus*.


PAL.D.PR.
MAX.CON.
I
II
OR.Alβ III
IV
V
EC.PTY.
QUA.
ART.CON.
QUA.L.R.
EN.PTY.L.P.
HYO.
EN.PTY.
M.PTY.
SYM.
P.OP.
10 MM


PAL.D.PR.
MAX.CON.
PAL.
EC.PTY.
QUA.
ART.CON.
QUA.L.R.
EN.PTY.
HYO.
M.PTY.
SYM.
P.OP.
10 MM

posteroventral edge of the ectopterygoid fuses with the anterodorsal portion of the quadrate. In *S. sordidus* the ectopterygoid extends more ventrally than in *S. frenatus* and forms the greater part of the leading edge of the suspensorium. Dorsally the ectopterygoid is tightly bound by a serrate suture to the anteroventral edge of the palatine (PAL.), which is strongly ankylosed along its posterior edge to the leading edge of the entopterygoid.

The palatine has a dorsal process (PAL.D.PR.) that extends beyond the anterior edge of the suspensorium and bears the maxillary condyle (MAX.CON.) distally (Figs 1.4 A, B). In *S. sordidus*, the dorsal process is short and the rounded condyle faces ventro-anteroventrally, whereas in *S. frenatus*, the dorsal process is relatively elongate, with the ovoid condyle facing antero-anteroventrally.

The posterodorsal edge of the suspensorium, anterior to the hyomandibula, differs considerably in the two species. In *S. sordidus* (Figs 1.2, 1.4 A), the central area of the adductor fossa is deep, with a steeply sloping quadrate and metapterygoid and a strongly concave palatine and entopterygoid. The entopterygoid differs in structure from the other bones. It has an interlocking network of bone, which gives a latticed appearance in large individuals, and has a septum dividing two deep triangular concavities, which occupy the greater proportion of the dorsomedial area of the bone. This septum protrudes laterally, and at its posterodorsal extremity, fuses with a thickened ridge that extends along the dorsal edge of the suspensorium from the dorsal metapterygoid to the palatine. Where the ridge and septum meet, the

entopterygoid is expanded laterally to form a lateral process (EN.PTY.L.P., Fig. 1.4 A), with the septum between the two concavities having a buttress-like appearance. This lateral process lies directly below the circumorbitals. The mandibular branch of the trigeminal (fifth cranial) nerve passes through a hole in the lateral apex of the dorsal concavity of the entopterygoid, directly medial to the lateral process.

In *S. frenatus* (Figs 1.3, 1.4 B), the central area of the adductor fossa is broad and shallow. A slight recess in the lateral surface of the entopterygoid is bordered posteroventrally by two small anteroventrally sloping ridges close to the entopterygoid-metapterygoid suture. These ridges define the lower point of origin of A1β (Section 1.3.3, Fig. 1.12 B) and form a groove which carries the mandibular branch of the trigemial nerve from a notch in the dorsal edge of the entopterygoid towards the lower jaw. The posterodorsal edge of the suspensorium, anterior to the hyomandibula, is formed by the thickened dorsal edges of the metapterygoid, entopterygoid and palatine. It is irregular along its length and is notably thicker anteriorly.

Jaw apparatus (Figs 1.2, 1.3)

The jaw structure in scarids is the most distinctive of all their features. *S. sordidus* and *S. frenatus* both possess the fused teeth and modified articular-dentary joint associated with scarids, although there are many differences between the two species.

Upper jaw

There are two pairs of bones in the upper jaw, the maxillae and the premaxillae.

The maxilla (Figs 1.2, 1.3, 1.5 A, B, C, D)

The maxilla (MAX.) has two main parts, the maxillary arm (MAX.ARM.) and the maxillary head (MAX.HD., Figs 1.5 A, B, C, D). The maxillary arm is the longest and most lateral part. It is elongate dorsoventrally with a flattened posterodorsal projection. The maxillary arm in *S. sordidus* is broader than in *S. frenatus*, but lacks the well developed curved posterodorsal process (PD.PR.). A lateral ridge (MAX.L.R.) is present on the anterodorsal part of the maxillary arm of both species, although it is only well developed in *S. frenatus* (Figs 1.5 A, C). In addition, *S. sordidus* possesses a small poorly developed condyle midway along the anterior edge of the maxillary arm.

The maxillary head (Figs 1.5 A, B, C, D) is anterior and dorsomedial to the maxillary arm and forms the only point of articulation between the maxilla and palatine (Figs 1.2, 1.3). In this respect, it strongly reflects the differences in articulation between the two species. In *S. sordidus*, the maxillary head is relatively small with a single large posterodorsal facet on the dorsal extremity (Figs 1.5 A, B). The size and position of this concave facet and of the palatine maxillary condyle (Fig. 1.4 A) suggest an articulation that is limited to a rotation about a single point. In contrast, *S. frenatus* has a well developed maxillary head with a deep rounded groove extending from the dorsal extremity of the maxillary head to a concavity dorsomedial to the origin of the

Figure 1.5 A

A lateral view of the maxilla of *S. sordidus*.

Figure 1.5 B

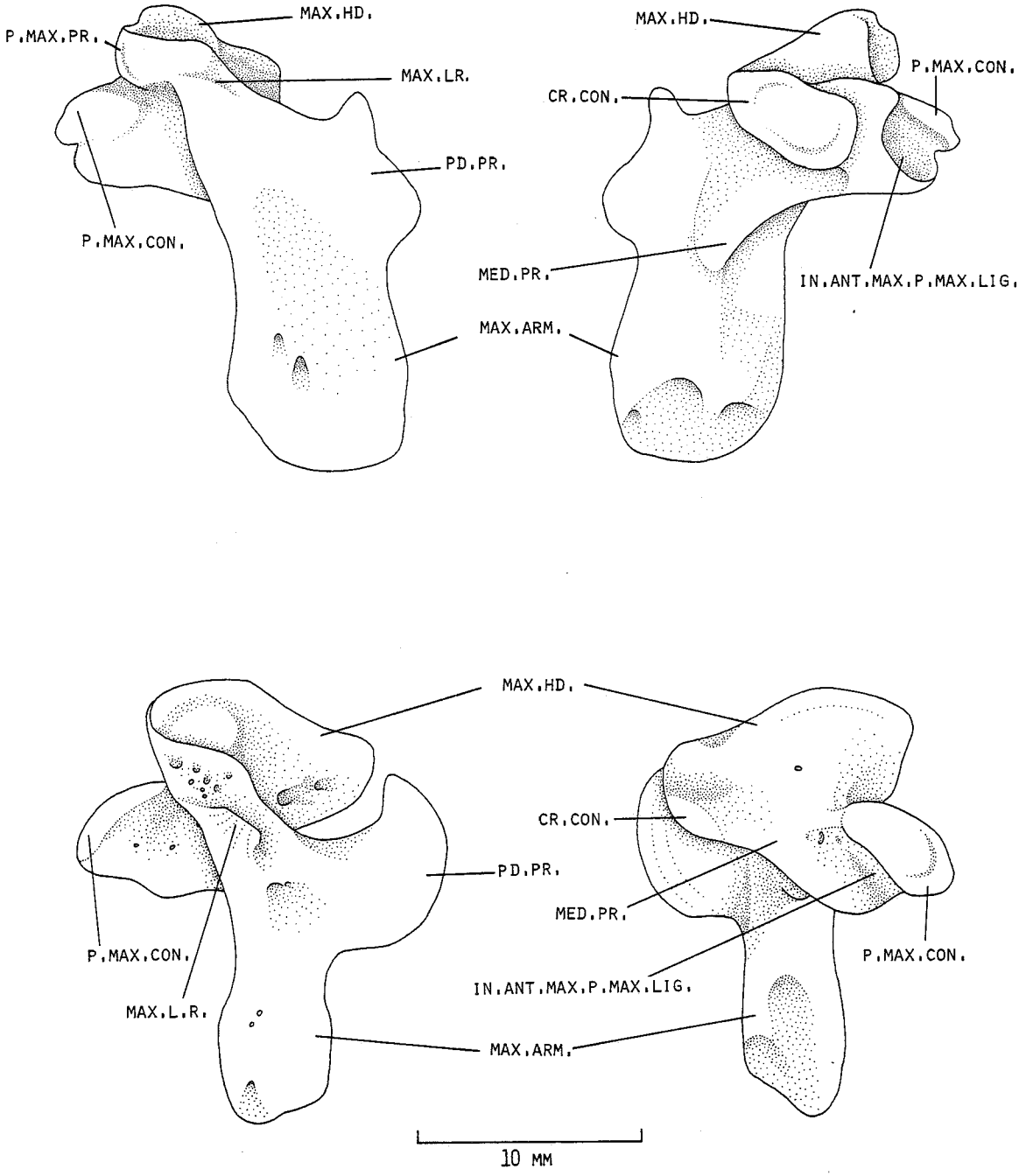
A medial view of the maxilla of *S. sordidus*.

Figure 1.5 C

A lateral view of the maxilla of *S. frenatus*.

Figure 1.5 D

A medial view of the maxilla of *S. frenatus*.


P.MAX.PR.
MAX.HD.
MAX.LR.
PD.PR.
P.MAX.CON.
MAX.HD.
P.MAX.CON.
CR.CON.
MED.PR.
IN.ANT.MAX.P.MAX.LIG.
MAX.ARM.
MAX.HD.
CR.CON.
PD.PR.
MED.PR.
P.MAX.CON.
P.MAX.CON.
IN.ANT.MAX.P.MAX.LIG.
MAX.L.R.
MAX.ARM.
10 MM

posterodorsal process of the maxillary arm (Figs 1.5 C, D). The groove is vertical except for a short horizontal section dorsally, which results in a complex articulation. *S. sordidus* possesses an important additional structure on the anterior surface of the maxillary head, the premaxillary process (P.MAX.PR., Fig. 1.5 A). This structure is absent in *S. frenatus* (Fig. 1.5 C). *S. sordidus* also possesses a small poorly developed facet on the anterior edge of the maxillary arm.

Differences in the medial process (MED.PR.) of the maxillary head strongly reflect the differences in the interrelationship between the maxilla and premaxilla (P.MAX.) of the two species. There are two condyles on the medial process, the premaxillary condyle (P.MAX.CON.), with two facets, and the cranial condyle (CR.CON., Figs 1.5 A, B, C, D). In *S. sordidus*, the anterodorsal facet of the premaxillary condyle is well developed, although the medial facet of this condyle is considerably smaller (Figs 1.5 A, B). The anterodorsal facet is associated with the maxillary facet of the premaxilla (MAX.FAC., Fig. 1.6 A), whilst the medial facet lies beneath the relatively immobile anterior maxillary-premaxillary ligament (ANT.MAX.P.MAX.LIG., Fig. 1.13 A). The large anterodorsally facing concavity which lies ventromedial to the premaxillary condyle is the insertion point of the anterior maxillary-premaxillary ligament (Fig. 1.5 B).

In *S. frenatus*, the premaxillary condyle has a large anterolateral facet and an equally large medial facet (Figs 1.5 C, D). The anterolateral facet is associated with the maxillary facet of the premaxilla (Fig. 1.6 D), as in *S. sordidus*. The well

developed medial facet, however, is in a synovial sheath beneath the anterior maxillary-premaxillary ligament (Fig. 1.13 B). On the medial surface below the medial facet is a shallow groove, the lower edge of which bears the insertion scar of the anterior maxillary-premaxillary ligament (Fig. 1.5 D).

A cranial condyle (CR.CON.) is present in both species. It is considerably larger in *S. sordidus* than in *S. frenatus*, although in both species the surface of the condyle is only slightly raised above the surface of the bone (Figs 1.5 B, D). The insertion scar of the posterior maxillary-premaxillary ligament (POST.MAX.P.MAX.LIG.,Figs 1.13 A, B) is posterodorsal to the cranial condyle in *S. sordidus* and dorsal to the condyle in *S. frenatus*.

The insertion scar of Alα in *S. sordidus* is on the medial posteroventral surface of the medial process of the maxillary head (Figs 1.11 B, 1.13 A). In *S. frenatus*, the insertion scar of Alα/A2tl is directly posteroventral to the deep concavity in the maxillary head, and medial to the base of the posterodorsal process of the maxillary arm (Figs 1.12 B, 1.13 B).

The premaxilla (Figs 1.2, 1.3, 1.6 A, B, C, D)

There is considerable dissimilarity in the structure of the premaxilla (P.MAX.) between the two species. *S. sordidus* has a short, deep dental plate (DENT.PL.) and a stout ascending process (ASC.PR.), whereas *S. frenatus* has a long, narrow dental plate and an elongate ascending process (Figs 1.2, 1.3, 1.6 A, B, C, D).

Figure 1.6 A

A lateral view of the premaxilla of *S. sordidus*.

Figure 1.6 B

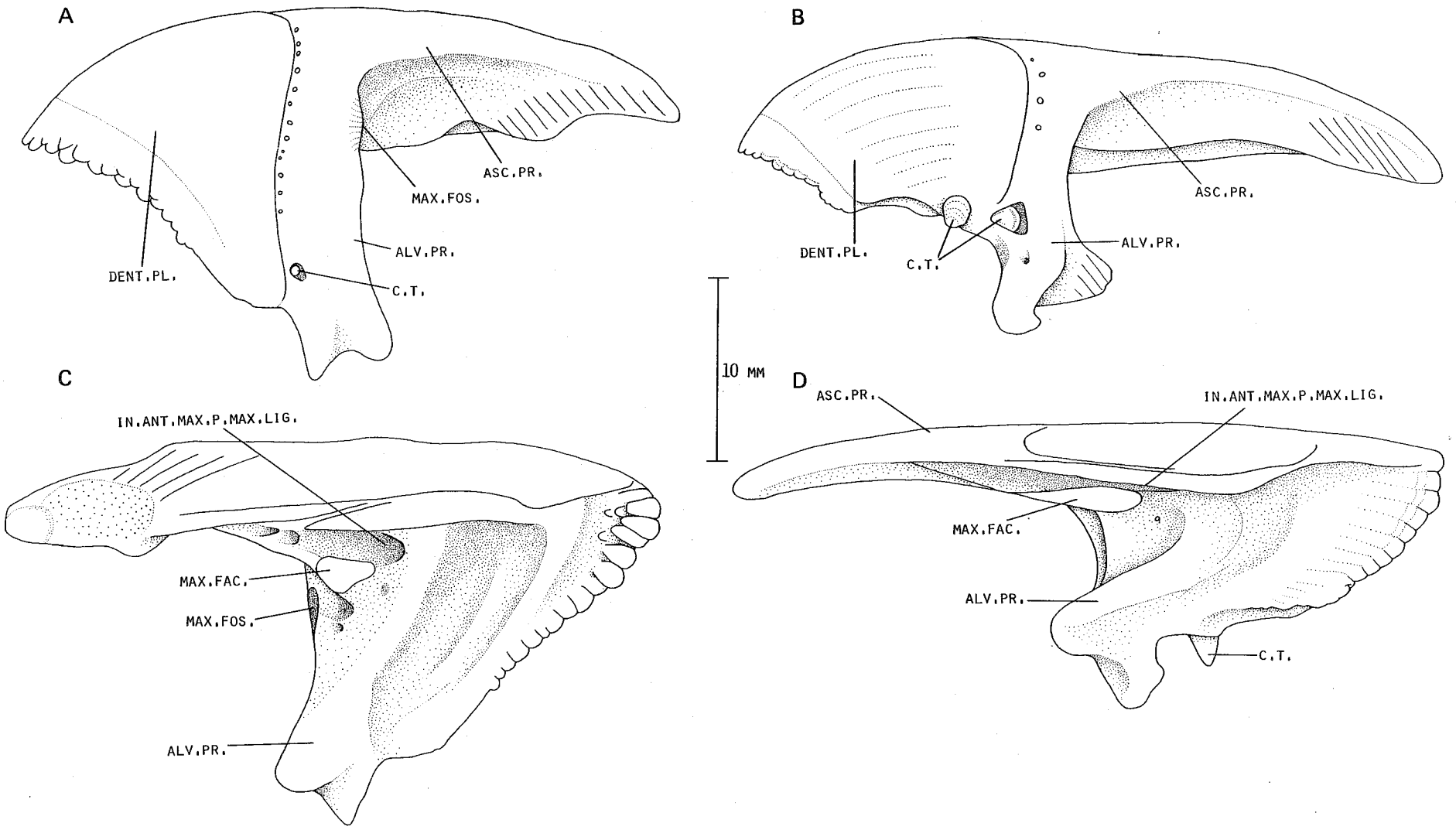
A lateral view of the premaxilla of *S. frenatus*.

Figure 1.6 C

A ventro-medial view of the premaxilla of *S. sordidus*.

Figure 1.6 D

A ventro-medial view of the premaxilla of *S. frenatus*.


A
ASC.PR.
MAX.FOS.
ALV.PR.
DENT.PL.
C.T.
B
ASC.PR.
DENT.PL.
C.T.
ALV.PR.
10 MM
C
IN.ANT.MAX.P.MAX.LIG.
MAX.FAC.
MAX.FOS.
ALV.PR.
D
ASC.PR.
IN.ANT.MAX.P.MAX.LIG.
MAX.FAC.
ALV.PR.
C.T.

The ascending process of *S. sordidus* is relatively short, with a broad concavity in the anterior lateral surface (Fig. 1.6 A). In *S. sordidus*, the palatine dorsal processes are in close proximity to each other with the anteromedial edges inserting into the lateral concavities of the ascending process (Fig. 1.2). In *S. frenatus*, the palatine dorsal processes are well spaced on either side of the premaxillary ascending processes (Fig. 1.3) and the lateral concavities are absent (Fig. 1.6 B). The distal ventral surface of the ascending process in *S. sordidus* is concave (Fig. 1.6 C) in the area of attachment to the rostral cartilage (RO.C., Fig. 1.13 A). This concavity is absent in *S. frenatus* (Fig. 1.6 D).

There is a deep concavity in the ventral surface of the premaxilla, at the medial base of the ascending and alveolar processes (ALV.PR., Figs 1.6 C, D). In *S. sordidus* it is short and wide, whereas in *S. frenatus* it is long and narrow and extends along the greater part of the ventral surface of the ascending process. In *S. sordidus*, the insertion of the anterior maxillary-premaxillary ligament (IN.ANT.MAX.P.MAX.LIG., Fig. 1.13 A) occupies the whole concavity, whereas in *S. frenatus*, it extends only over the anteromedial surface of the lateral side of the gully (Fig. 1.13 B).

The maxillary facet of the premaxilla (MAX.FAC.) is medially adjacent to the above mentioned ventral concavity and at the medial base of the alveolar process (ALV.PR., Figs 1.6 C, D). In *S. sordidus*, this facet is short and wide, whereas in *S. frenatus*, it is narrow and elongate, and tapers posteriorly as it extends onto the ventral surface of the ascending process.

In *S. sordidus*, a slightly raised crater-shaped posteriorly facing maxillary fossa (MAX.FOS.) is present on the proximal posterior surface of the alveolar process (Figs 1.6 A, C). It is into this fossa that the premaxillary process of the maxillary head is inserted (Figs 1.2, 1.5 A). This fossa is absent in *S. frenatus* (Figs 1.6 B, D).

In both species, the distal end of the alveolar process is bifid (ALV.PR., Figs 1.6 A, B, C, D), although the two processes are longer and more rotund in *S. frenatus*. In both species the posteromedial process is tightly bound to the medial surface of the maxillary arm (Figs 1.2, 1.3). The anterolateral process of *S. sordidus* lies flush with the maxillary arm (Fig. 1.2), and has a small, poorly developed facet on the posterior edge which corresponds with the facet on the anterior edge of the maxillary arm. In *S. frenatus* the distal end of the anterolateral process protrudes posterolaterally, forming a concavity into which the leading edge of the maxillary arm inserts (Figs 1.3, 1.6 B, D).

The anterior teeth of the premaxilla differ little from the dentary (DENT.) and will be discussed below. However, the premaxilla differs from the dentary in that often it possesses lateral 'canine' teeth (C.T., Figs 1.6 A, B). Of the thirteen initial phase specimens of *S. sordidus* examined (range 111 - 203 mm S.L.), no 'canine' teeth were found in the seven specimens below 129 mm S.L. The remaining six initial phase specimens all possessed 'canine' teeth, as did seven of the eight terminal phase individuals examined (169 - 238 mm S.L.). The teeth varied in number from 1 to 4 (usually 3) and typically form a horizontal row, although in two

specimens, the medial tooth on one side was dorsal to the other two. The colour of the dental plate (DENT.PL., Figs 1.6 A, B) in initial phase specimens varied from olive green in smaller specimens, to grey, olive green or deep blue-green in larger specimens. The blue-green colour was most prominent near to the alveolar region and extended anteriorly in terminal phase specimens, giving a dark green or dark blue-green colour to the dental plates.

Of the six initial phase specimens of *S. frenatus* examined (range 112 - 248 mm S.L.), only the largest individual had any trace of 'canine' teeth, which were represented by three small denticles. However, of the nine terminal phase specimens examined (range 257 - 293 mm S.L.), all possessed 'canine' teeth which were considerably larger than those found in *S. sordidus*. They varied in number from 1 to 3 (usually 3) and were invariably in a horizontal row. The colour of the premaxillary dental plate in initial phase specimens was predominantly white, whilst in terminal phase specimens, it was predominantly pale blue-green.

Lower jaw

There are two pairs of bones in the lower jaw, the articulars and the dentaries.

The articular (Figs 1.2, 1.3, 1.7 A, B, C, D)

The articular (ART.) has two main sections, a dorsolateral ascending process (ART.ASC.PR.) and a ventromedial descending process (ART.DEC.PR., Figs 1.7 A, B, C, D). It is composed of two bones, the angulo-articular and the smaller retro-articular which

Figure 1.7 A

A lateral view of the articular of *S. sordidus*.

Figure 1.7 B

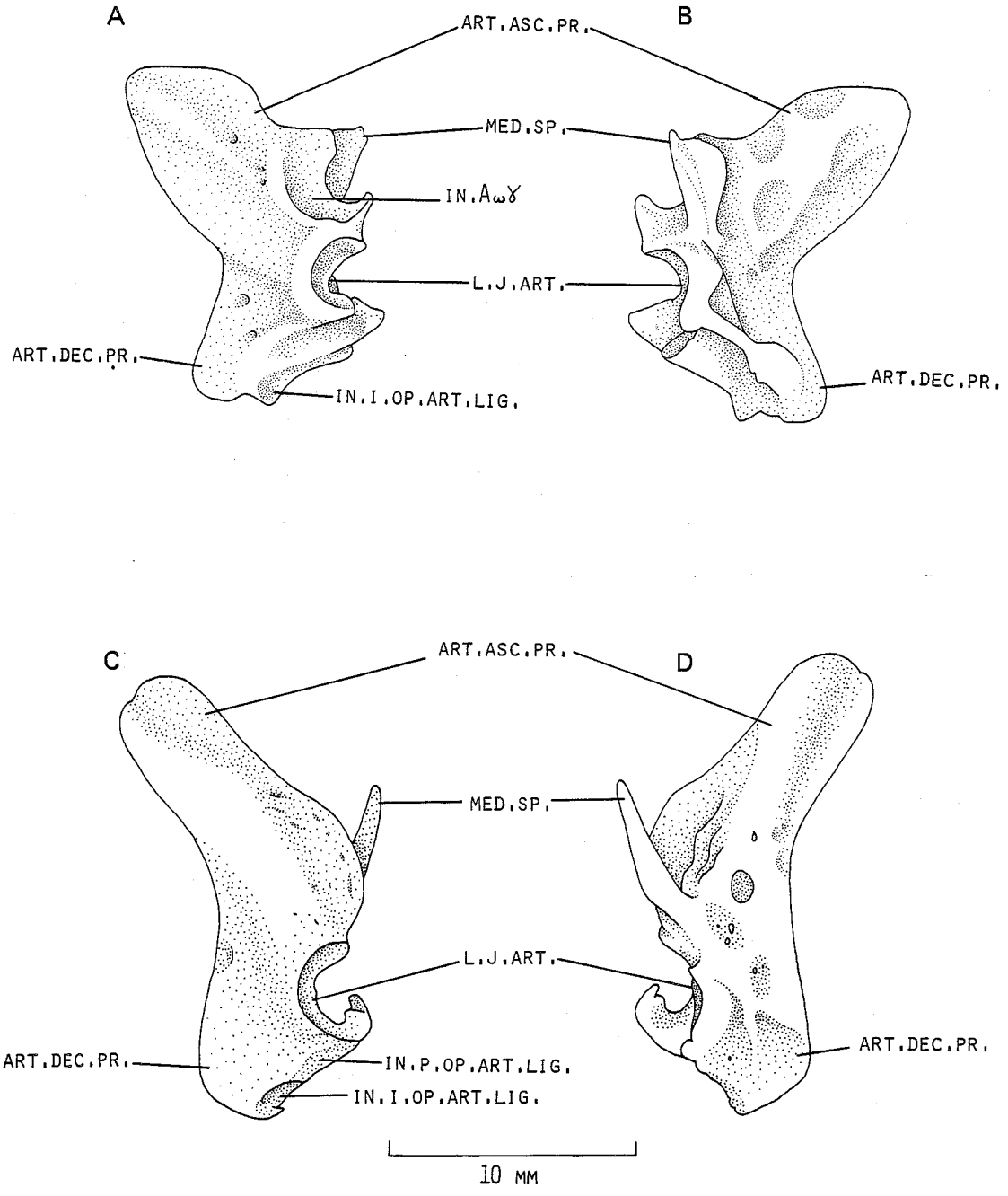
A medial view of the articular of *S. sordidus*.

Figure 1.7 C

A lateral view of the articular of *S. frenatus*.

Figure 1.7 D

A medial view of the articular of *S. frenatus*.


A
B
ART.ASC.PR.
MED.SP.
IN.Aω8
L.J.ART.
ART.DEC.PR.
IN.I.OP.ART.LIG.
ART.DEC.PR.
C
D
ART.ASC.PR.
MED.SP.
L.J.ART.
ART.DEC.PR.
IN.P.OP.ART.LIG.
IN.I.OP.ART.LIG.
ART.DEC.PR.
10 MM

forms the ventrocaudal face of the ventromedial descending process. On the posterior surface of the articular, at the base of the two processes, is a large posteriorly facing concavity formed by two concave fossae, the smaller of which lies medial to the other. These fossae correspond to the two condyles on the anterior quadrate (Figs 1.4 A, B) and form the articulatory socket of the lower jaw articulation (L.J.ART., Figs 1.7 A, B, C, D). In both species, there is a posterior protrusion ventral to this articulatory socket, which inserts into a cavity that lies directly ventral to the quadrate articular condyles.

The articular ascending process differs in the two species. In *S. sordidus*, it is stout with a tapered distal end and a distinct anterodorsal - posteroventral ridge on the lateral surface (Fig. 1.7 A), whereas in *S. frenatus*, it is elongate with a truncate distal end (Fig. 1.7 C). In addition, *S. sordidus* has a concavity on the proximal dorsal surface of the ascending process which has protruding anteromedial and ventromedial edges. This is the point of insertion of Awy (IN. Awy, Figs 1.7 A; 1.11 B, 1.14 A). In *S. frenatus*, a lobate dorsal ridge is present in this position (Fig 1.7 C).

The articular descending process of *S. sordidus* is relatively shorter than in *S. frenatus* (Figs 1.17 A, C). Both possess depressions on the posterior edge (of the retro-articular) which are the points of insertion for the preopercular-articular and interopercular-articular ligaments (Figs 1.11 A, 1.12 A). These depressions are most notable in *S. sordidus*, although this is not apparent in Figures 1.17 A and 1.17 C because of the angle at which

these bones were drawn.

On the medial surface of the articular, there is a prominent vertical spine (MED.SP.) arising from a point anterodorsal to the articulatory socket of the lower jaw. In *S. sordidus*, it bears a projecting lamina on the anterior edge and is relatively shorter than in *S. frenatus*.

The dentary (Figs 1.8 A, B, C, D)

As in the premaxilla, the form of the dentary differs in the two species. *S. sordidus* has a robust dentary with deep dental plates and a large lateral flange (DENT.L.FL., Figs 1.8 A, C), whereas *S. frenatus* has weaker protruding dental plates and a smaller lateral flange (Figs 1.8 B, D).

The two halves of the dentary are fused along a medial symphysis. The symphysis in *S. sordidus* is deep and has a large number of complex medial sutures (MED.SUT.) that zigzag posteriorly (Fig. 1.8 C). In *S. frenatus*, the symphysis is shorter with fewer simple medial sutures (Fig. 1.8 D). A round insertion scar lateral to the ventral extremity of the medial symphysis marks the point of tendinous insertion of the protractor hyoideus (IN.P.H., Figs 1.14 A, B).

The teeth are one of the most characteristic features of the 'sordidus' group, as exemplified by *S. sordidus* (Fig. 1.9 A). They are pear-shaped when viewed anteriorly and are arranged as a mosaic, with distinct lateral, vertical and diagonal rows. Because of the size and shape of the teeth and their arrangement in the dental

Figure 1.8 A

A lateral view of the dentary of *S. sordidus*.

Figure 1.8 B

A lateral view of the dentary of *S. frenatus*.

Figure 1.8 C

A medial view of the dentary of *S. sordidus*.

Figure 1.8 D

A medial view of the dentary of *S. frenatus*.

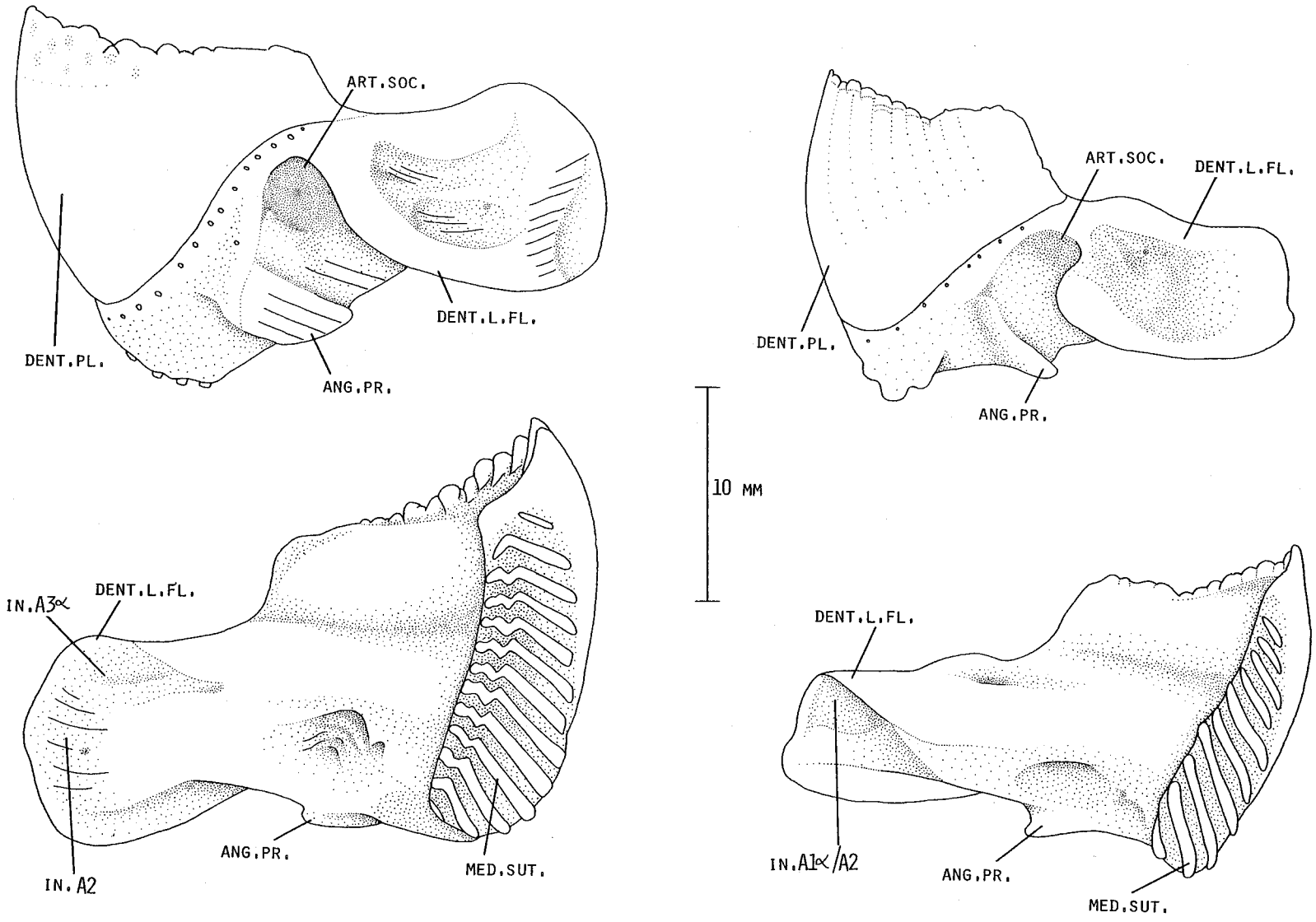
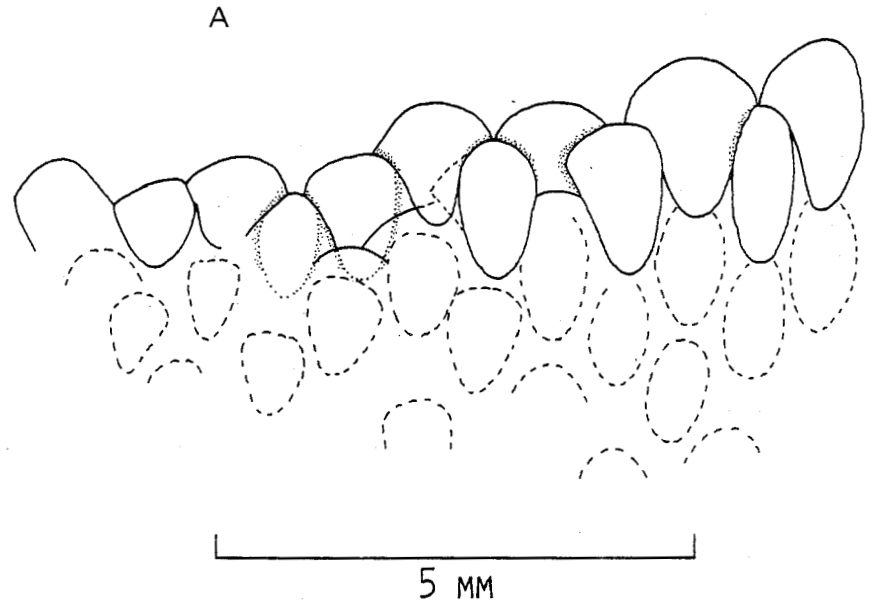

ART.SOC.
DENT.PL.
DENT.L.FL.
ANG.PR.
ART.SOC.
DENT.L.FL.
DENT.PL.
ANG.PR.
10 MM
IN.A3∝
DENT.L.FL.
ANG.PR.
IN.A2
MED.SUT.
DENT.L.FL.
IN.A1∝/A2
ANG.PR.
MED.SUT.

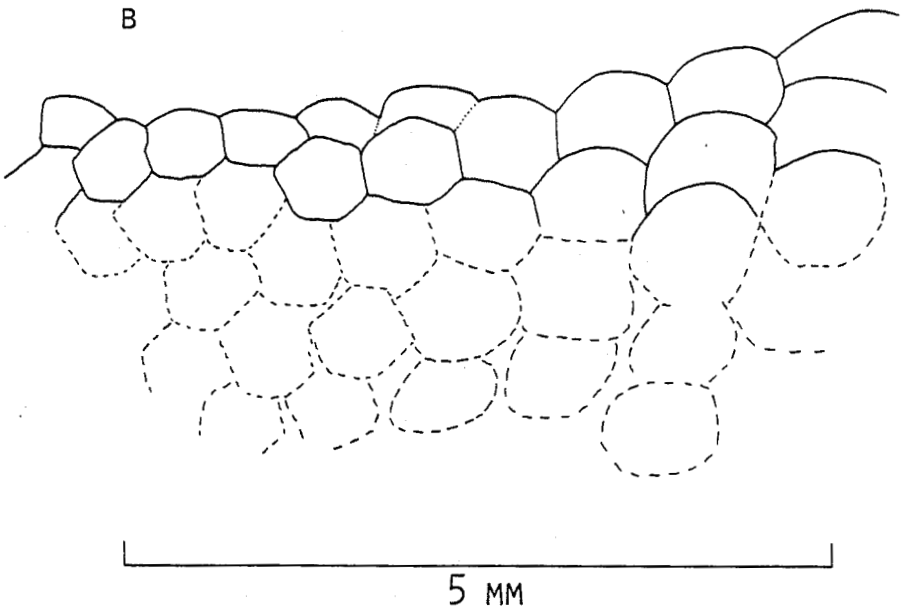
Figure 1.9 A

An anterior view of the dentary cutting edge of *S. sordidus*.

Figure 1.9 B

An anterior view of the dentary cutting edge of *S. frenatus*.


A
5 MM


B
5 MM

plate, the vertical rows alternate in possessing a tooth on the cutting edge. This results in a scalloped cutting edge which is maintained by the loss, rather than wear, of exposed teeth.

The teeth of *S. frenatus* (Fig. 1.9 B) are likewise characteristic of the 'frenatus' group. They are irregularly ovoid when viewed anteriorly and appear to be compressed dorsoventrally. They develop in vertical rows as in *S. sordidus* and form a mosaic during development, but lack the organized arrangement near the cutting edge and display a smaller degree of interdigitation between teeth in adjacent rows. Diagonal rows are present but occur at a more oblique angle than in *S. sordidus*. The main difference between *S. frenatus* and *S. sordidus* is that in *S. frenatus*, each vertical row has a tooth on the cutting edgewhich, when combined with a degree of wear, results in an even cutting edge. No specimens of either species were found to bear 'canine' teeth on the dentary.

The articulatory socket (ART.SOC., Figs 1.8 A, B) is located in the middle of the lateral surface of the dentary and is considerably deeper in *S. sordidus* than in *S. frenatus*. The socket is bordered on three sides by the angular process (ANG.PR.), dental plate and lateral flange. It has a posteroventral opening into which the ascending process of the articular inserts (Figs 1.2, 1.3). This forms the second articulatory joint of the lower jaw, which is a distinctive feature of the more specialized scarid species.

In both species, the dentary lateral flange bears prominent insertion scars on the medial surface. *S. sordidus* has two insertion scars, one on the posterodorsal edge and the other on the posterior extremity of the medial surface. These are the insertion

points of A3α and A2 respectively (Figs 1.8 C, 1.14 A). *S. frenatus* has only one insertion scar, that of Aiα/A2 t2, on the midposterior edge of the medial surface (Figs 1.8 D, 1.14 B).

The neurocranium (Figs 1.18 D, E, 1.21 B, C)

The neurocranium of both species is similar. It is relatively short and flattened dorso-ventrally. Of the two species, *S. sordidus* is the more robust and dorsoventrally compressed. In this species, the ethmoid is fused with the frontals and is developed extensively between the orbits (Fig. 1.21 B), whereas in *S. frenatus*, there is a gap between the ethmoid and frontals and the ethmoid is restricted to the anterior part of the orbit (Fig. 1.21 C). The most striking difference between the two species is in the form of the ethmoid-vomerine process (ETH.VOM.PR., Figs 1.21 B, C). In *S. sordidus*, it is moderately well developed and bears a pair of poorly developed lateral maxillary condyles. These condyles are absent in *S. frenatus* which has a short anteriorly directed ethmoid-vomerine process.

From a dorsal aspect, the neurocranium of *S. sordidus* tapers slightly anteriorly and possesses well developed lateral ethmoids. The anterior part of the frontals meet in the midline and the supraoccipital bears a relatively small crest. In *S. frenatus*, the overall shape is oblong, and is considerably wider than in *S. sordidus*. The lateral ethmoids are well developed, and the frontals are separated by the anterior incursion of the supraoccipital, which bears a large crest posteriorly.

Both species have one major fossa on the ventral surface (the site of origin of the posterior part of the fourth levator externus [fossa number 1 in Fig. 1.18 D, E]). The second fossa (number 2 in Figs 1.18 A, B), which forms part of the site of origin of the levator posterior in *Cetoscarus bicolor* and *Bolbometopon muricatum*, is not developed. There is only a small depression in this region. The flanges around the sites of origin of the pharyngeal muscles are more prominent in *S. sordidus* than in *S. frenatus*.

The pharyngeal apparatus

The pharyngeal osteology has been described already by Schultz (1958) and Hattori (1976, 1984) and in detail by Bruce (1979) and Gobalet (1980). A detailed description will therefore not be included here. The main features that differ between the two species, however, will be described.

The upper pharyngeal bones are similar in the two species, although the dorsal cranial articular surfaces are slightly larger in *S. sordidus*. The main differences between the two species are the size and number of teeth and tooth rows. *S. sordidus* typically has three rows of teeth on each upper pharyngeal bone, although some larger specimens may have lost the outer row. The innermost row contains the largest teeth, the relative widths being 20:5:1 from innermost to outermost. There are fewer teeth in the medial row of *S. sordidus* than in that of *S. frenatus* (*S. sordidus* mean = 9.31, s = 0.63, n = 12, *S. frenatus* mean = 12.17, s = 0.75, n = 6) although each tooth is larger and more rounded when viewed ventrally. *S. frenatus* typically has only two rows of teeth, the larger of

which is medial with a relative width of approximately 4.7:1. In one specimen, however, a much smaller third row was present on a part of the outer edge of one of the upper pharyngeal bones. In both species, the bone around the outer row(s) shows some degree of wear, although the teeth show little wear. These outer rows have only limited contact with the lower pharyngeal plate especially in *S. sordidus*, and are believed to be a vestige of the large, functionally important outer rows found in less specialized scarids (i.e. *C. bicolor*, *B. muricatum* and the Sparisomatinae).

There are two main differences in the form of the lower pharyngeal bone between the two species. Firstly, *S. sordidus* has a relatively broad pharyngeal plate, with a medial area that is less concave than the elongate pharyngeal plate of *S. frenatus*. Secondly, *S. sordidus* has a broad robust keel (the ventrally directed anterior process of the lower pharyngeal) with an origin extending from a point mid-way between the two lateral muscular processes to a point near the anterior end of the ventral surface of the pharyngeal plate. In comparison, *S. frenatus* has a narrow thin keel with a short site of origin near to the anterior end of the ventral surface of the pharyngeal plate. (The form of the keel can be seen in Figures 1.15 A and 1.15 B, as it is marked by the site of origin of the second transversus ventralis [T.V.2]).

1.3.3 Myology

The adductor mandibulae

The adductor mandibulae are the largest and most distinctive muscles of the jaw. It is in these muscles that the differences between *S. sordidus* and *S. frenatus* are most pronounced.

In the scarids, the form of the adductor mandibulae sections A1, A2 and A3 follow the general descriptions given by Winterbottom (1974 a), and therefore, confusion between these and homologous muscles in different families is avoided. The Aw section, however, is highly modified and differs from other families. This section and part of A3 have been variously described by several authors. In this study, the conventions of Winterbottom (1974 a) are followed when describing muscles in section Aw, although for clarity, the names used by other authors are also given. The figures in this section follow the shading conventions of Figure 1.10.

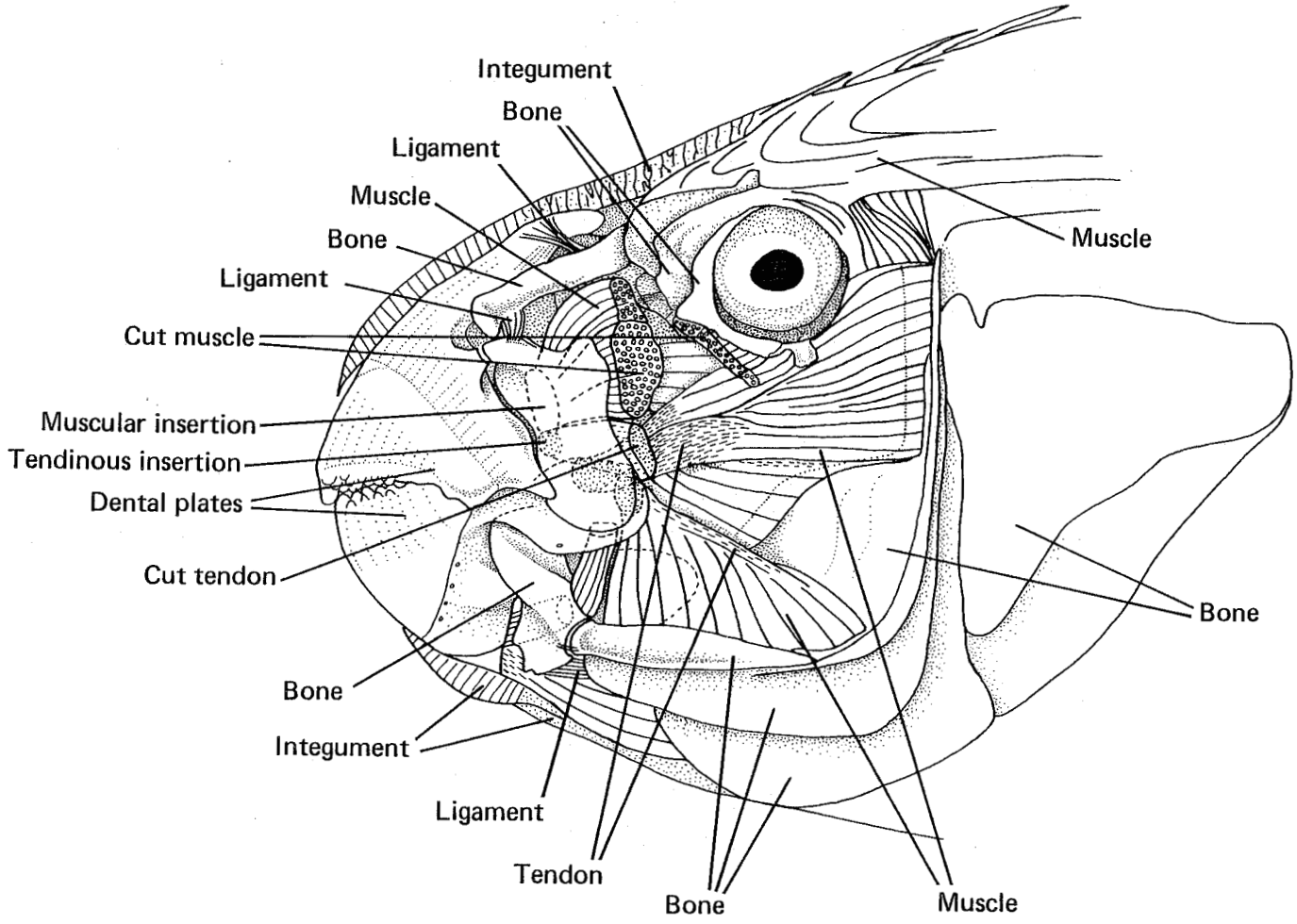
S. sordidus

Section A1 (Figs 1.11 A, B, 1.13 A)

By definition, this section has a dorsal position and inserts on the maxilla (Edgeworth, 1935). In *S. sordidus*, section A1 is subdivided into two subsections, designated A1α and A1β (Figs 1.11 A, B). Subsection A1α arises from the preoperculum, symplectic, ventral extremity of the hyomandibula and metapterygoid, and from the outer tendinous sheet that covers the adductor muscle mass which extends from the quadrate lateral ridge to the entopterygoid lateral process and ascending limb of the

Figure 1.10

The head of *Scarus sordidus* with the integument, nasal, lacrymal, circumorbitals, Alα and part of Alβ removed, showing the shading conventions used in this section.


Integument
Bone
Ligament
Muscle
Bone
Ligament
Cut muscle
Muscular insertion
Tendinous insertion
Dental plates
Cut tendon
Bone
Integument
Ligament
Tendon
Bone
Muscle
Muscle
Bone

preopercular. It is multipinnate with a thick tendon (Alαt, Fig. 1.11 B) inserting onto the medial surface of the maxillary arm at the base of the maxillary medial process. A narrow tendon described in *S. rivulatus* by Tedman (1980 b) as Alt3 is present in *S. sordidus*, connecting the medial surface of Alα to the base of the articular ascending process.

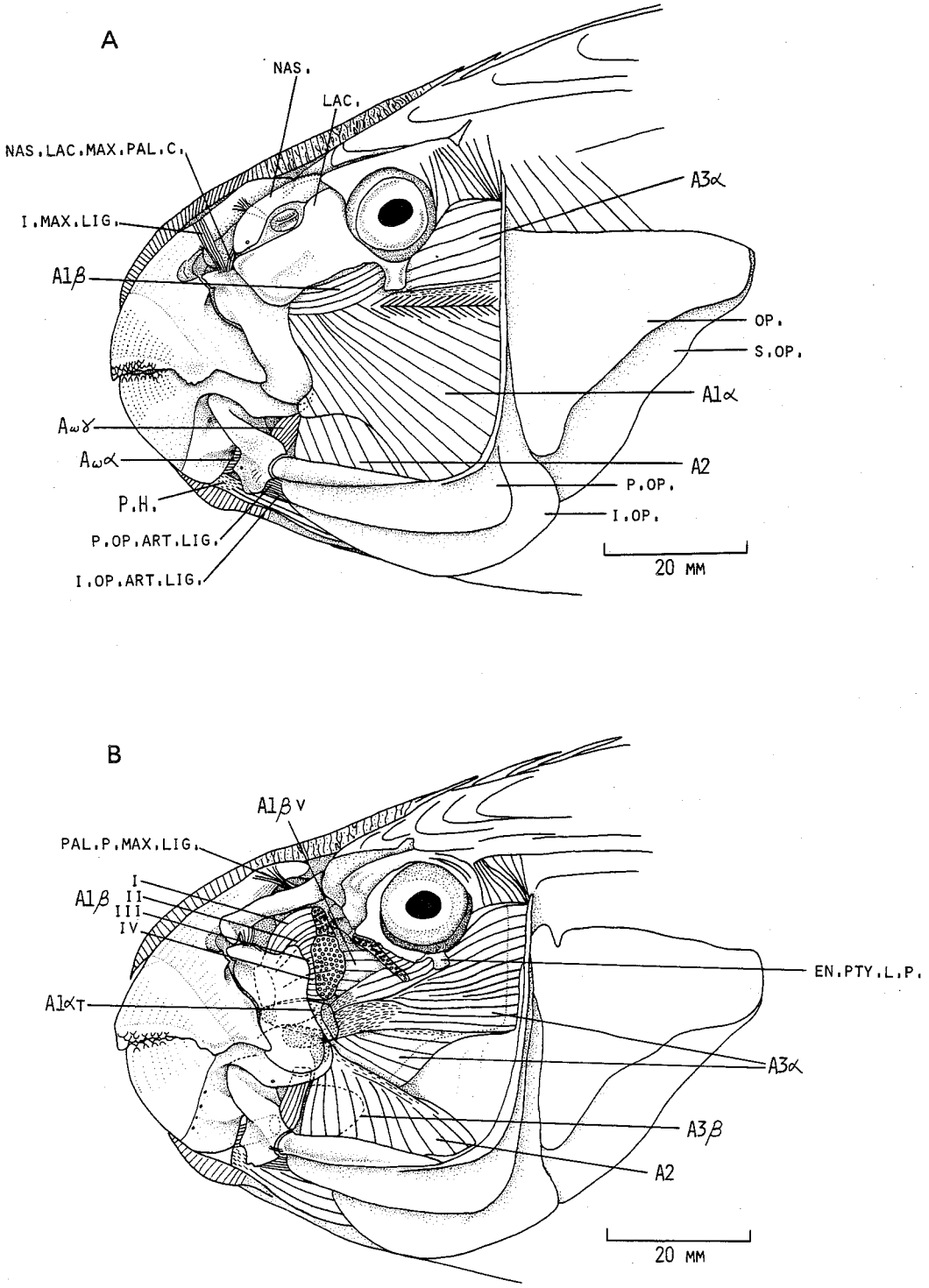
Subsection Alβ is the most dorsal of the adductor muscles and is divided into five subdivisions : four superficial (i, ii, iii and iv) and one deep (v) (Fig. 1.11 B). The four superficial subdivisions are most easily visible in large individuals. Each subdivision corresponds to a separate site of origin (Fig. 1.4 A). The most dorsal, Alβi arises from a slight concavity on the palatine and entopterygoid. Alβ ii, iii and iv arise from separate concavities on the anteriorly facing dorsal edge of the entopterygoid. In some specimens Alβ iii and iv appear to have further subdivisions. All four subdivisions fuse medially. Alβiv is strongly attached to the anterolateral edge of the entopterygoid lateral process, and is in close association with Alα from this point to the point of insertion. The superficial subdivisions of Alβ are fused medially with the deep subdivision Alβv. Alβv arises from the deep anterodorsal concavity of the specialized entopterygoid. The main body of Alβv passes medially to Alβ iii and iv. It inserts on the medial surface of the maxilla at the base of, and on the maxillary medial process, dorsal to the insertion of Alα and medial to the insertion of the superficial subdivisions of Alβ (Figs 1.11 B, 1.13 A).

Figure 1.11 A

The head of *S. sordidus* with the integument and circumorbitals removed.

Figure 1.11 B

The head of *S. sordidus* with the integument, nasal, lacrymal, circumorbitals, Alα and part of Alβ removed.


A
NAS.
LAC.
NAS.LAC.MAX.PAL.C.
I.MAX.LIG.
A1β
A3α
OP.
S.OP.
A1α
Aωγ
Aωα
A2
P.OP.
P.H.
I.OP.
P.OP.ART.LIG.
I.OP.ART.LIG.
20 MM
B
A1β v
PAL.P.MAX.LIG.
I
A1β II
III
IV
EN.PTY.L.P.
A1αT
A3α
A3β
A2
20 MM

The insertion of A1β is muscular, although in larger individuals the superficial subdivisions develop a tendinous sheath anteriorly. A tendinous sheet may also be present between the superficial and deeper subdivisions of A1β. The fibres are all parallel with the exception of those fibres which insert on the anterior sheath and those which fuse with the tendon of A1α.

Section A2 (Figs 1.11 A, B, 1.14 A)

Section A2 is the most ventral of the adductor muscles in *S. sordidus* (Figs 1.11 A, B). The main site of origin is the ventral half of the quadrate, but includes part of the symplectic, preopercular and the tendinous sheet covering the adductor mass. It is bipinnate and possesses a thin medial tendinous septum, as in A1α. The fibres slope anterodorsally and some fuse with a tendinous aponeurosis which extends along the dorsal edge of the muscle. This aponeuroris and the medial septum fuse to form a strong tendinous insertion on the posterior part of the medial surface of the dentary lateral flange (Fig. 1.14 A).

Section A3 (Figs 1.11 A, B, 1.14 A)

Section A3 is the deepest of the adductor muscles. *S. sordidus* possesses two divisions, A3α and A3β (Fig. 1.11 B). The A3 section arises from the quadrate, entopterygoid (including the deep posteroventral cavity), metapterygoid and hyomandibula, and in A3α, from the posterodorsal part of the tendinous sheet covering the adductor muscle mass. All the fibres at the bony site of origin are relatively short. Those fibres from the anteroventral part of the

quadrate develop a tendinous covering which forms a small tendon anteriorly. These represent the unipinnate subsection A3β (Figs 1.11 B, 1.14 A). The remaining fibres all attach to a tendinous sheet surrounding a bipinnate bundle of fibres. The fibres in this bundle arise from the surrounding tendinous sheet and have no direct connection to the bones. This combined mass of fibres forms the large multipinnate superficial section A3α. The tendon of A3α (A3αt) passes under Alαt to insert on the dorsal part of the medial surface of the dentary lateral flange (Fig. 1.14 A). A3β inserts *via* a small tendon (A3βt) on the medial surface of the articular ascending process, near to the base of the medial spine (Fig. 1.14 A). It also has muscular insertions ventral to the tendinous insertion and along the posterolateral edge of the articular medial spine.

Section Aw (Figs 1.11 A, B, 1.14 A)

In *S. sordidus*, there are three muscles that can be ascribed to Aw. These are Awα, Awβ and Awγ. Awα is attached anteriorly to the caudal extremity of the dentary angular process, lateral to the insertion of the protractor hyoidei. Posteriorly, it attaches to the medial surface of the articular and along the leading edge of the articular medial spine (Fig. 1.14 A). Awβ connects the midmedial surface of the dentary lateral flange to the distal end of the articular medial spine (Fig. 1.14 A). Awγ connects the ventromedial edge of the dentary lateral flange to a concavity on the dorsal surface of the articular ascending process, dorsal to the lower jaw articulation (Figs 1.11 A, B, 1.14 A). All the sections of Aw have parallel fibres and muscular insertions.

S. frenatus

Sections A1 and A2 (Figs 1.12 A, B, 1.13 B, 1.14 B)

In *S. frenatus*, section A1 has divided into two parts, the large superficial, medial subsection is designated A1α and the deeper, small, dorsal subsection, A1β. Subsection A1α and section A2 have fused to form a single large muscle block (Figs 1.12 A, B).

The A1α/A2 complex arises from the hyomandibula, preoperculum, metapterygoid, entopterygoid, quadrate and a fibrous sheet covering the medial portion of section A3. In most specimens there is no superficial division between A1α and A2 although upon dissection, a division may be found in the medial surface of the muscle, extending from a point near to the caudal extremity of the dentary lateral flange, towards the posteroventral angle of the preoperculum. The fibres of the A1α/A2 complex are long and almost parallel. They attach to a strong aponeurosis which inserts onto the dentary and maxilla *via* two thick tendons, A1α/A2t1 and A1α/A2t2 (Figs 1.13 A, B, 1.14 B). A1α/A2t1 inserts on the medial surface of the maxilla, at the base of the medial process. A1α/A2t2 inserts on the dorsal part of the medial surface of the dentary lateral flange. As in *S. sordidus*, a third narrow tendon is present (A1αt3). However, in *S. frenatus*, it connects a point anterodorsal to the division on the medial surface of the A1α/A2 complex to the base of the articular ascending process, ventrolateral to the insertion of A3t.

A1β arises from the entopterygoid. The site of origin includes the two small ridges on the ventral edge of the entopterygoid and the slight concavity which lies dorsal to the first ridge (Fig.

Figure 1.12 A

The head of *S. frenatus* with the integument removed.

Figure 1.12 B

The head of *S. frenatus* with the integument, nasal, lacrymal, circumorbitals and part of A1α/A2 removed.

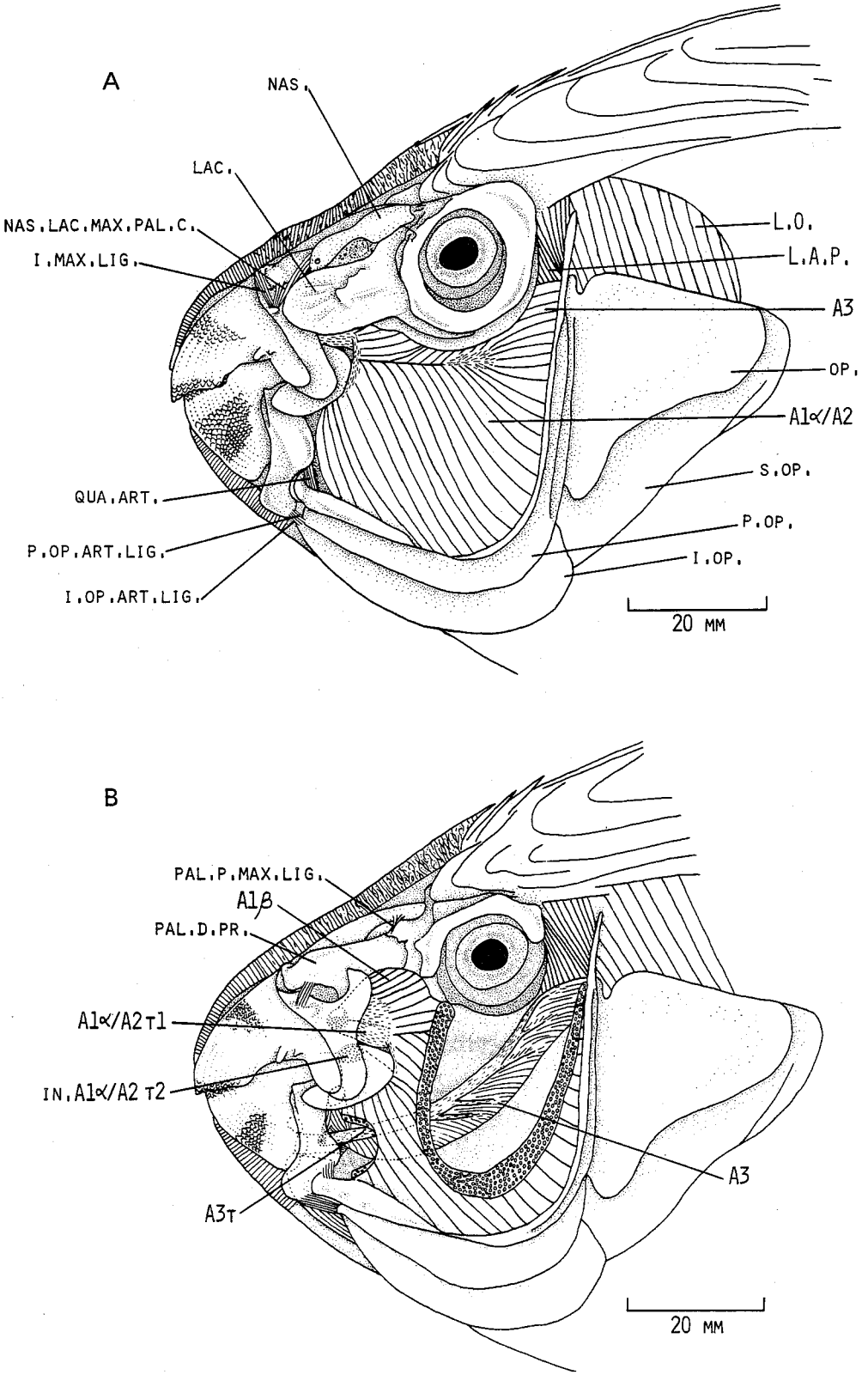
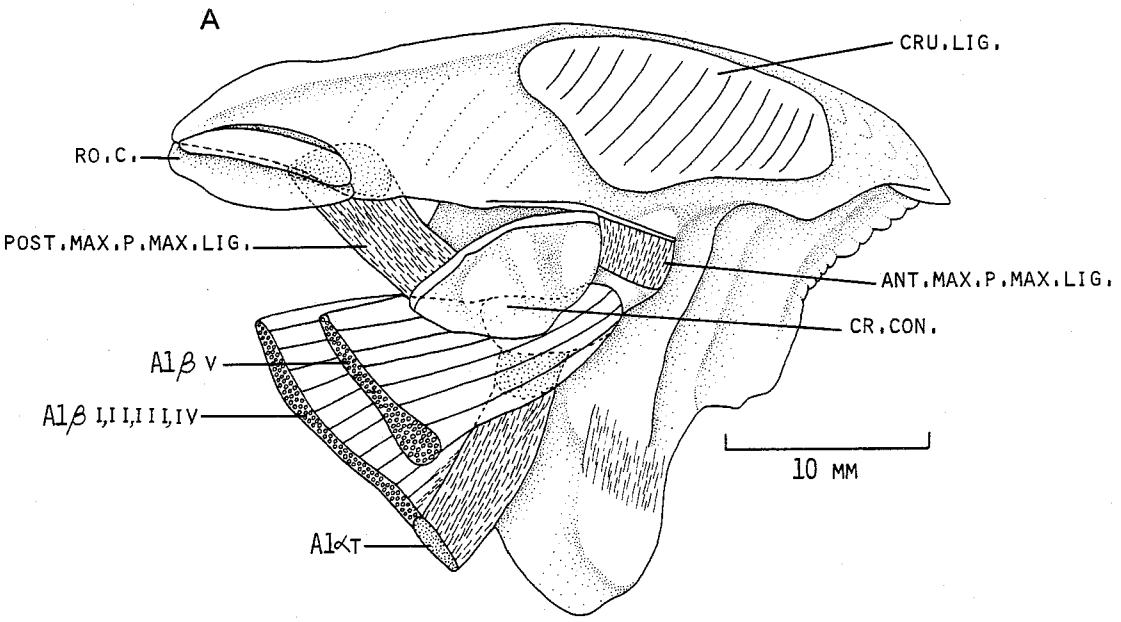

A
NAS.
LAC.
NAS.LAC.MAX.PAL.C.
I.MAX.LIG.
L.O.
L.A.P.
A3
OP.
A1α/A2
S.OP.
QUA.ART.
P.OP.
P.OP.ART.LIG.
I.OP.
I.OP.ART.LIG.
20 MM
B
PAL.P.MAX.LIG.
A1β
PAL.D.PR.
A1α/A2 T1
IN.A1α/A2 T2
A3
A3T
20 MM

Figure 1.13 A

A medial view of the upper jaw musculature of *S. sordidus*.

Figure 1.13 B

A medial view of the upper jaw musculature of *S. frenatus*.


A
CRU.LIG.
RO.C.
POST.MAX.P.MAX.LIG.
ANT.MAX.P.MAX.LIG.
CR.CON.
A1β V
A1β I,II,III,IV
10 MM
A1αT

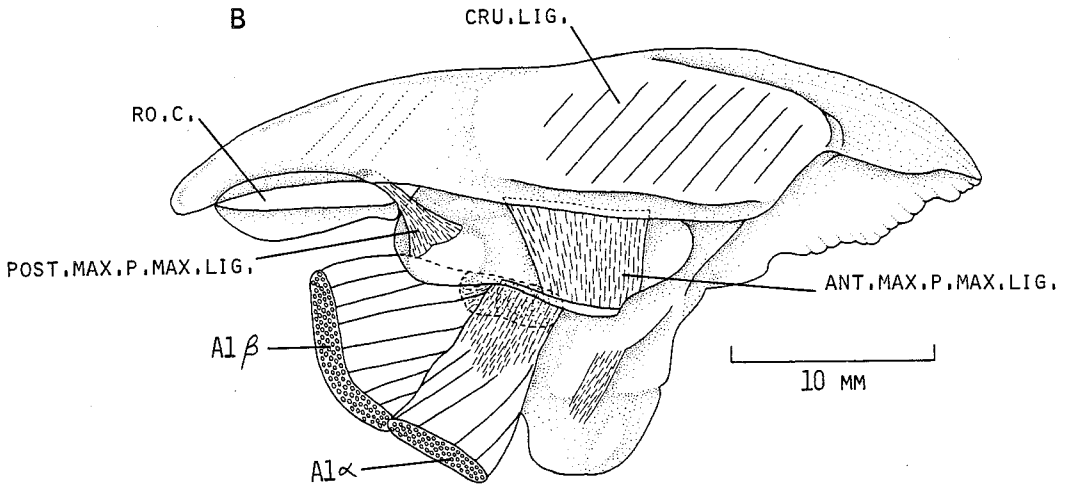

B
CRU.LIG.
RO.C.
POST.MAX.P.MAX.LIG.
ANT.MAX.P.MAX.LIG.
A1β
10 MM
A1α

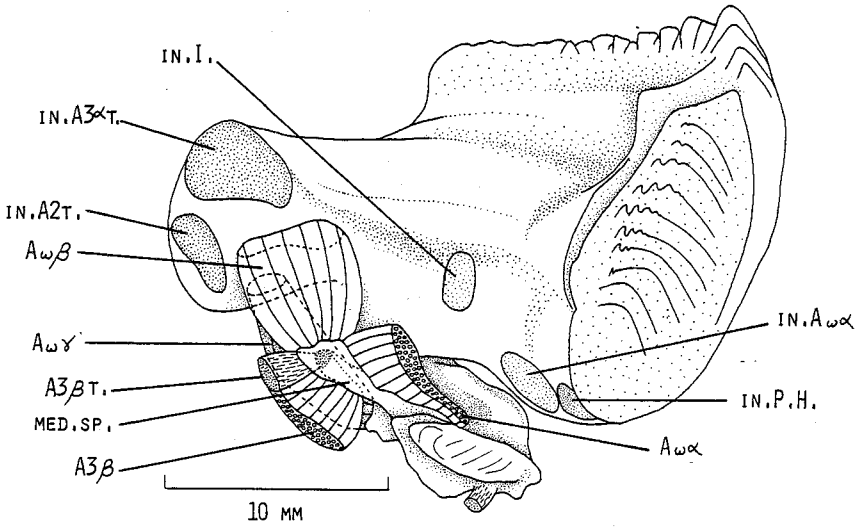
Figure 1.14 A

A medial view of the lower jaw musculature of *S. sorditdus*.

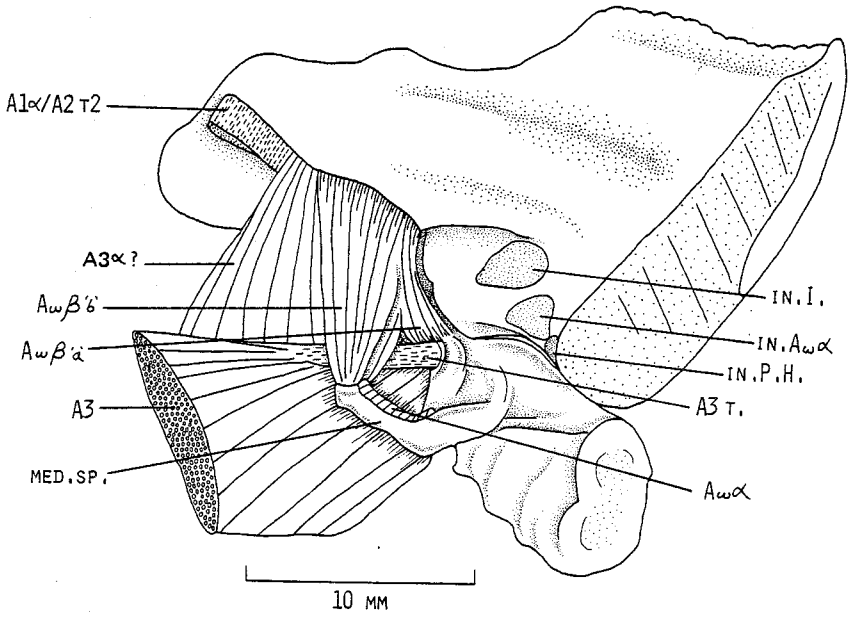
Figure 1.14 B

A medial view of the lower jaw musculature of *S. frenatus*.

A


IN.I.
IN.A3αT.
IN.A2T.
Aωβ
Aωγ
A3βT.
MED.SP.
A3β
IN.Aωα
IN.P.H.
Aωα
10 MM

B


A1α/A2T2
A3α?
Aωβ'b'
Aωβ'a'
A3
MED.SP.
IN.I.
IN.Aωα
IN.P.H.
A3T.
Aωα
10 MM

1.4 B). The ventral fibres of Alβ insert on the dorsal surface of Alα/A2t1 (Fig. 1.13 A). The dorsal fibres insert directly on the medial surface of the maxilla at the base of the medial process, dorsal to the insertion of Alα/A2t1. The insertions of Alβ are muscular but may possess a superficial tendinous sheath anteriorly. This is most notable in large individuals. The superficial adductor muscles have both pinnate and parallel fibres. Alα/A2 and the ventral part of Alβ are weakly pinnate whilst the dorsal part of Alβ is parallel.

Section A3 (Figs 1.12 A, B, 1.14 B)

Section A3 in *S. frenatus* is a deep, thin unipinnate muscle. The only superficially visible part is a small area posterodorsal to Alα/A2, just below the levator arcus palatini (L.A.P., Figs 1.12 A, B). The A3 section arises from the hyomandibula, metapterygoid, symplectic and quadrate, and fuses with an elongate dorsal aponeurosis which inserts on the medial surface of the articular, dorsal to the base of the articular medial spine. Some fibres originating from the quadrate insert directly onto the articular, ventral to the insertion of A3t (Fig. 1.14 B). In addition, a series of fibres from the anterodorsal edge of A3t insert on the medial surface of the dentary lateral flange, anterior and dorsomedially to the insertion of Alα/A2t2 (A3α?, Fig. 1.14 B). Anteriorly, these fibres are in close association, but not joined, to Awβ. The myological development of this species (Chapter 2) and the form of this muscle in adult specimens of other members of the subfamily Scarinae (Section 1.3.7), suggest that these fibres are a vestige of the dorsal section of A3 (A3α) which inserts on the

dentary. This series of fibres was described by Lubosch (1923) as the M. tendo-dentalis and later (Lubosch, 1929), as the M. tendo-articulari-dentalis. Gobalet (1980) described it as an adductor portion of Aw.

Section Aw (Fig. 1.14 B)

S. frenatus possesses two distinct divisions of Aw, Awα and Awβ (Fig. 1.14 B). Awα connects the posteroventral extremity of the dentary lateral to the insertion of the protractor hyoideus, to the leading edge of the articular medial spine, as in *S. sordidus*. This muscle was described by Lubosch (1923) as the adduktor-symphysialer and later, the Aw (Lubosch, 1929). Gobalet (1980) described it as the abductor portion of Aw.

Awβ connects the medial surface of the dentary lateral flange to two areas on the articular (Fig. 1.14 B). The dentary connection is anterior to the insertion of A3α and anteromedial to the connection of Alα/A2t2. The connections on the articular are 'a', to the medial surface of the articular (dorsal to the insertion of A3t), and 'b', to the distal end of the articular medial spine (Fig. 1.14 B). A muscle corresponding to part 'b' was described as the M. articulari-dentalis by Lubosch (1923) and as a fraction of the adductor portion of Aw by Gobalet (1980).

Other muscles of *S. sordidus* and *S. frenatus*

The intermandibularis (Figs 1.14 A, B)

The intermandibularis is present in both *S. sordidus* and *S. frenatus*, connecting the medial surfaces of the dentary. The fibres are parallel with a muscular insertion (IN.I., Figs 1.14 A, B) dorsolateral to the anterior insertion of Awα, and posteroventral to a deep pit in the medial surface of the dentary.

The protractor hyoideus (Figs 1.11 A, 1.14 A, B)

The protractor hyoideus (P.H., Fig. 1.11 A) is similar in both species, although it appears slightly larger in *S. sordidus*. It is a flattened muscle arising from the anteroventral lateral surface of the epihyal, the posteroventral lateral surface of the ceratohyal, and from the bases of the branchiostegal rays. It inserts on the caudal edge of the dentary, lateral to the medial symphysis (IN.P.H., Figs 1.14 A, B). The insertion is tendinous ventrolaterally and by a mass of connective tissue medially. The two parts of the muscle fuse in the midline anterior to the first branchiostegal ray.

The pharyngeal muscles (Figs 1.15 A, B)

There are ten major pairs of muscles associated with the pharyngeal apparatus of scarids (Figs 1.15 A, B). The pharyngeal muscles of *S. sordidus* and *S. frenatus* are similar, and closely resemble those figured by Liem and Greenwood (1981) and those described in *Calotomus japonicus* by Yamaoka (1980). The muscles of the pharyngeal apparatus of some species in the 'frenatus' group

Figure 1.15 A

A lateral view of the pharyngeal apparatus of *S. sordidus* (left side faces anteriorly).

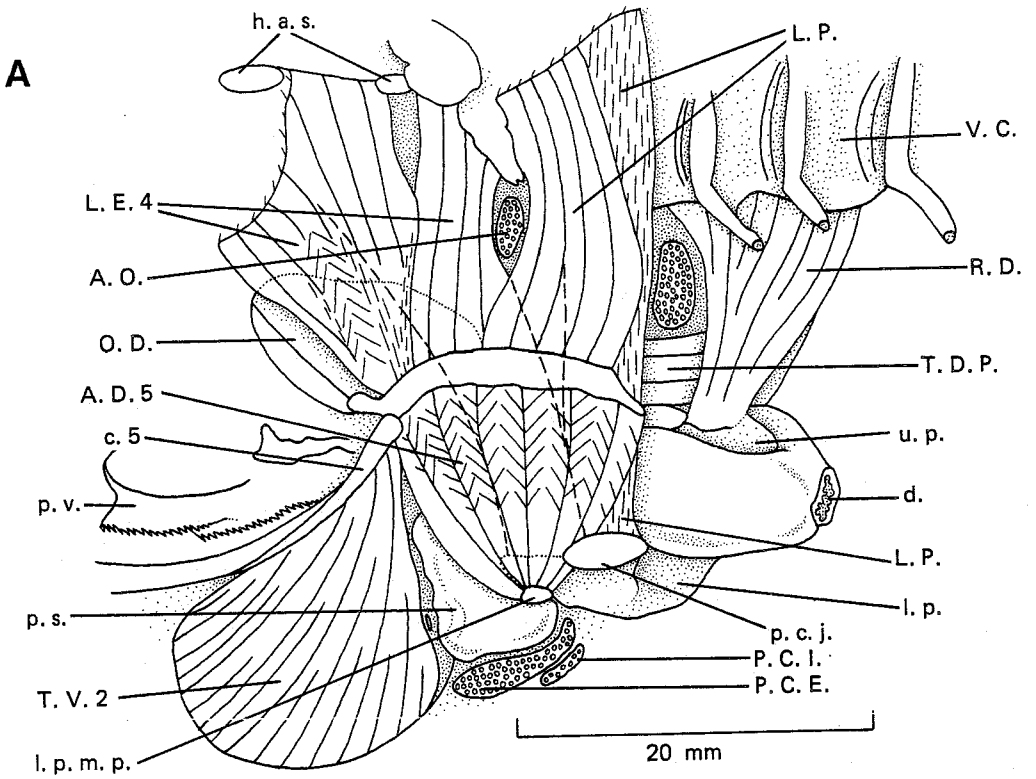
Figure 1.15 B

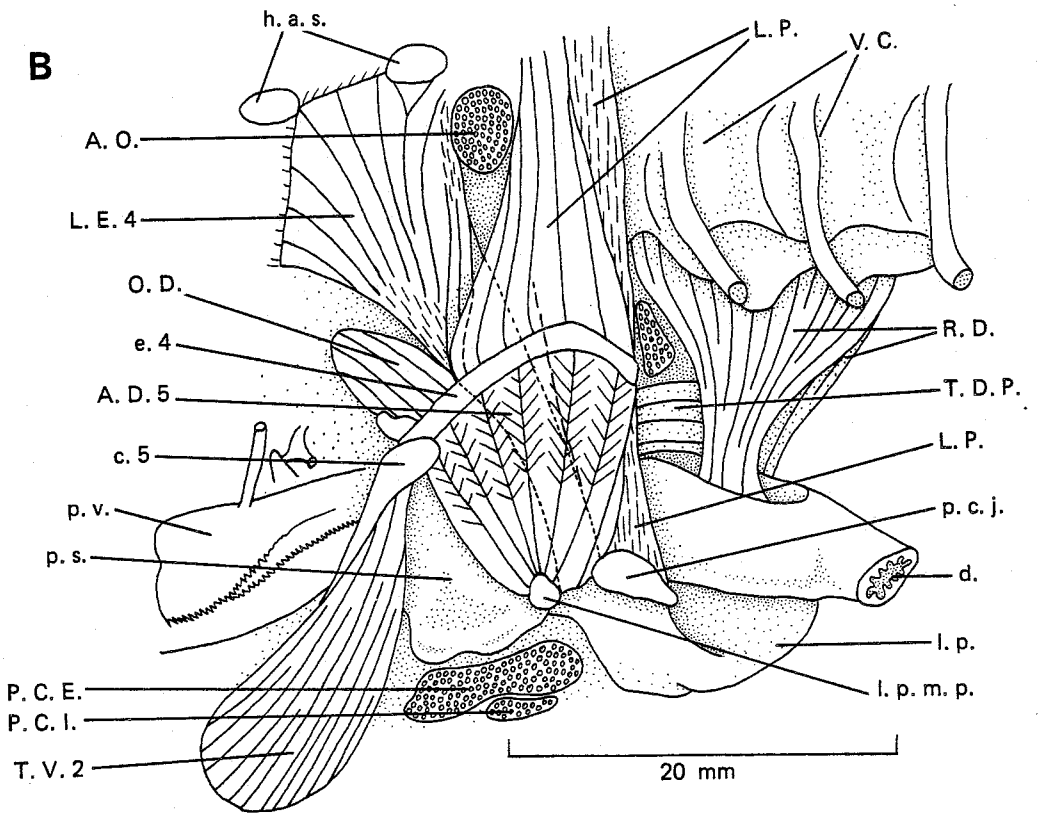
A lateral view of the pharyngeal apparatus of *S. frenatus* (left side faces anteriorly).

Abbreviations used in this figure:

A.D.5	Fifth adductor
A.O.	Adductor operculi
c.5	Fifth ceratohyal
d.	Duodenum
e.4	Fourth epibranchial
h.a.s.	Hyomandibular articulation sockets
L.E.4	Fourth levator externus
L.P.	Levator posterior
l.p.	Lower pharyngeal bone
l.p.m.p.	Muscular process of the lower pharyngeal bone
O.D.	Obliquus dorsalis
P.C.E.	Pharyngocleithralis externus
P.C.I.	Pharyngocleithralis internus
p.c.j.	Pharyngocleithral joint, lower pharyngeal facet
p.s.	Pharyngeal sacs
p.v.	Pharyngeal valve
R.D.	Retractor dorsalis
T.D.P.	Transversus dorsalis posterior
T.V.2	Second transversus ventralis
u.p.	Upper pharyngeal bone
V.C.	Vertebral column

The location of the pharyngeal apparatus *in situ* is shown in Appendix 1.


A
h. a. s.
L. P.
V. C.
L. E. 4
A. O.
R. D.
O. D.
T. D. P.
A. D. 5
u. p.
c. 5
d.
p. v.
L. P.
l. p.
p. s.
p. c. j.
P. C. I.
P. C. E.
T. V. 2
l. p. m. p.
20 mm


B
h. a. s.
L. P.
V. C.
A. O.
L. E. 4
O. D.
R. D.
e. 4
T. D. P.
A. D. 5
L. P.
c. 5
p. c. j.
p. v.
p. s.
d.
l. p.
P. C. E.
l. p. m. p.
P. C. I.
T. V. 2
20 mm

have been described in detail by Gobalet (1980). For clarity, a brief description of each muscle will be given below:

The *fourth levator externus* (L.E.4) is a large muscle which arises from the neurocranium, particularly from a deep triangular fossa on the ventral face (fossa number 1 in Figs 1.18 D, E). The primary (tendinous) insertion is onto the muscular process of the lower pharyngeal bone, although some lateral fibres may insert on the fourth epibranchial (e.4).

The *third levator internus* is a small muscle connecting the anterior upper pharyngeal bone to the neurocranium, at a point posterior to the orbit.

The *levator posterior* (L.P.) is a large muscle which arises from a groove in the posterior face of the neurocranium (occipital region). Medial fibres have a tendinous insertion on the muscular process of the lower pharyngeal bone (l.p.m.p.) whilst lateral fibres have a muscular insertion on the fourth epibranchial.

The *pharyngocleithralis internus* and *externus* (P.C.I. & P.C.E.) are both small strap-like muscles connecting the ventral surface of the lower pharyngeal bone (l.p.) and the cleithrum.

The *retractor dorsalis* (R.D.) is a moderately sized muscle arising from the ventral surface of the first three vertebrae with an insertion on the posterolateral extremity of the upper pharyngeal bone (u.p.).

The *fifth adductor* (A.D.5) is a moderately sized muscle arising from the ventral face of the fourth epibranchial and has a tendinous insertion on the muscular process of the lower pharyngeal bone.

The *obliquus dorsalis* (O.D.) is a moderately sized muscle connecting the fourth epibranchial to the anterolateral portion of the upper pharyngeal bone.

The *second transversus ventralis* (T.V.2) is a small to moderately sized muscle arising from the 'keel' of the lower pharyngeal bone, and inserting on the fifth ceratohyal (c.5) near to its connection with the fourth epibranchial.

The *transversus dorsalis posterior* (T.D.P.) is a small muscle connecting the posteromedial surface of the fourth epibranchial and the posterior lateral surface of the upper pharyngeal bone.

S. sordidus ans *S. frenatus* differ considerably in the overall development of the pharyngeal musculature, with *S. sordidus* possessing the more powerful musculature. The form of the muscles, however, differed only in one respect. In *S. frenatus*, the fourth levator externus inserts predominantly on the muscular process of the lower pharyngeal bone (Fig. 1.15 B). In some specimens, a few of the lateral fibres insert on the outer edge of the fourth epibranchial. In *S. sordidus*, the primary insertion of the fourth levator externus is likewise on the muscular process of the lower pharyngeal bone. However, a small proportion of the lateral fibres insert (often tendinously) on the anterolateral edge of the fourth epibranchial (Fig. 1.15 A).

Ligaments

The ligaments that are important in feeding, especially those which contrast the two morphological types are described below. For a more extensive description see Gobalet (1979) and Tedman (1980 b).

The *palatine-premaxillary* ligament (PAL.P.MAX.LIG., Figs 1.11 B, 1.12 B) connects the medial surface of the palatine to the dorsal surface of the premaxillary ascending process. It is more robust in *S. sordidus*.

In both species the two halves of the premaxilla are strongly bound by a series of *cruciate ligaments* (CRU.LIG., Figs 1.13 A, B).

An *intermaxillary* ligament (I.MAX.LIG.) is present in both species (Figs 1.11 A, 1.12 A). It is a broad band of fibrous tissue that connects the two maxillary heads, from a point on the maxillary lateral ridge, anterior to the maxillary connection of the nasal-lacrymal-maxillary-palatine complex. The intermaxillary ligament crosses above the premaxillary ascending processes and is in close association with the integument.

In the *nasal-lacrymal-maxillary-palatine* complex (NAS.LAC.MAX.PAL.C., Figs 1.11 A, 1.12 A), the more robust fibres connect the anterior edge of the nasal to the lateral ridge on the maxillary head. The more ventral fibres in this connection attach to the anterodorsal edge of the lacrymal (LAC.). Medial to the main nasal-maxillary fibrous bundle is a smaller series of fibres that bind the maxillary lateral ridge to the ventrolateral surface of the palatine dorsal process.

The two *maxillary-premaxillary* ligaments (Figs 1.13 A, B), differ in the two species. In *S. sordidus*, the anterior maxillary-premaxillary ligament (ANT.MAX.P.MAX.LIG.) is short and thick (Fig. 1.13 A). It connects a deep concavity on the medial anterodorsal extremity of the maxillary medial process to a concavity on the medial surface of the premaxilla at the base of the alveolar and ascending processes and medial to the maxillary facet. In *S. frenatus* (Fig. 1.13 B), this ligament is developed as a broad band of fibres connecting a ridge on the posteroventral edge of the medial surface of the premaxillary condyle to the lateral side of the medial ridge of the premaxillary ascending process, at the junction of the ascending and alveolar processes. The anterior maxillary-premaxillary ligament in *S. frenatus* permits a greater movement of the premaxilla (movement between the dorsal edge of the two bones is 5.5% of the S.L. in *S. frenatus* [n=3] and 0.6% of the S.L. in *S. sordidus* [n=3]). This protrusion of the premaxilla is the 'type A' (mandible depression model) mechanism of jaw protrusion described by Motta (1984).

The posterior maxillary-premaxillary ligament (POST.MAX.P.MAX.LIG.) is well developed in *S. sordidus* (Fig. 1.13 A). It consists of a broad strong ligament connecting the posterodorsal extremity of the premaxillary medial process, and the distal ventrolateral surface of the premaxillary ascending process. The ligament passes under the anterolateral edge of the rostral cartilage before inserting on the premaxilla. Although the ligament connects the same surfaces in *S. frenatus* (Fig. 1.13 B), it tapers into a narrow band before inserting on the premaxilla, and a few fibres from this ligament connect with the anterior edge of the

rostral cartilage.

The *maxillary-dentary-premaxillary* complex is a series of ligaments that binds the distal ends of the premaxillary alveolar process and maxillary arm and the lateral surface of the dentary lateral flange. The maxillary-premaxillary fibres tightly bind these two bones, especially in *S. sordidus*, whereas the fibres connecting the maxilla/premaxilla to the dentary allow free movement between these bones. The superficial parts of this complex are in close association with the integument.

There are two *articular-dentary* ligaments in each species. The anterior articular-dentary ligament connects the anteroventral part of the distal end of the articular ascending process to the lateral surface of the dentary angular process, ventral to the articular notch. The posterior articular-dentary ligament connects the posterodorsal part of the distal end of the articular ascending process to the medial surface of the articular notch formed by the dentary lateral flange. These ligaments are more robust in *S. sordidus*.

A *preopercular-articular* ligament (P.OP.ART.LIG.) and *interopercular-articular* ligament (I.OP.ART.LIG.) are present in both species (Figs 1.11 A, 1.12 A). The preopercular-articular ligament connects the anterior extremity of the preopercular horizontal limb to the posterior edge of the proximal end of the articular descending process. The interopercular-articular ligament connects the anterior extremity of the interopercular to the posterior edge of the distal end of the articular descending process. The interopercular-articular ligament is stronger than,

and lies ventromedial to, the preopercular-articular ligament.

There are two distinct *quadrate-articular* ligaments, one dorsal and one medial to the lower jaw articulation. The dorsal ligament binds the posterior proximal end of the articular ascending process to the quadrate, posterodorsal to the articular condyles (QUA.ART., Fig. 1.12 A). The medial ligament connects a posteromedial concavity on the proximal end of the articular descending process, to a similar concavity on the medial surface of the quadrate, ventrolateral to the articular condyles. In addition, there is a considerable quantity of connective tissue binding the two bones.

Synovial Joints

There are two synovial joints that play important roles in the feeding mechanism. Of these, the palatine-maxillary joint is of particular interest as it is the main point of articulation for the upper jaw and, as such, reflects the type of jaw movement. This joint differs in the two species.

In *S. sordidus*, the area of contact between the palatine and maxilla is relatively large. The palatine maxillary condyle (Fig. 1.4 A) and the articulatory facet on the maxillary head are both large and rounded, and the rotation of the maxilla (and hence premaxilla) about the palatine is a simple arc.

In *S. frenatus*, the area of contact between the palatine and maxilla is relatively small. The more anteriorly facing palatine maxillary condyle is oval with the wider part in the dorsomedial-ventrolateral axis (Fig. 1.4 B). The articulatory groove on the maxillary head consists of a large ventral concavity,

an elongate vertical groove and a short dorsal horizontal groove which curves gently to join the vertical groove. The rotation of the maxilla about the palatine is uneven.

In *S. sordidus*, the maxilla and premaxilla are tightly bound by the maxillary-premaxillary ligaments (Fig 1.13 A), and the two bones act as one functional unit. In *S. frenatus*, however, there is considerable movement between the two bones. The lateral surface of the broad anterior maxillary-premaxillary ligament forms a synovial cavity in which the medial facet of the premaxillary condyle slides (Fig. 1.13 B), resulting in the protrusion of the premaxilla relative to the maxilla.

The protrusion of the premaxilla and the uneven rotation of the maxilla about the maxillary condyle result in a complex movement of the premaxilla. As the mouth opens, the premaxilla protrudes and ascends smoothly; upon closure (if against a force), the premaxilla moves in three distinct phases. Firstly, the tip of the premaxilla recedes. In this stage, the premaxilla moves back to the maxilla and there is a slight rotation of the large ventral concavity (of the articulatory groove of the maxillary head) about the maxillary condyle. Secondly, the tip of the premaxilla descends steeply with little caudal movement. As this stage occurs, the maxilla descends and the maxillary condyle passes from the ventral concavity in the maxillary head and along the vertical groove. Finally, the tip of the premaxilla arcs posteroventrally to the closed position, as the maxillary condyle passes from the vertical groove to the horizontal groove in the maxillary head.

Summary

1. Osteology

S. sordidus possesses a deep premaxilla and dentary with strong robust teeth in alternating rows on the cutting edge; an interdigitating maxilla and premaxilla at the site of the premaxillary process; a relatively small maxillary head; a simple maxillary-palatine articulation; a deep suspensorium with a specialized lateral process on the entopterygoid; a large quadrate lateral ridge and upper pharyngeal bones typically bearing three rows of teeth on each.

S. frenatus, has a less robust premaxilla and dentary, with each vertical tooth row having a tooth on the cutting edge; no premaxillary process; a large maxillary head; a complex maxillary-palatine articulation; a simple, shallow suspensorium; a small quadrate lateral ridge and upper pharyngeal bones typically bearing two rows of teeth on each.

2. Myology

In *S. sordidus*, the Alα, Alβ, A2 and A3α are all well developed. Of these, Alα, A2 and A3α are strongly pinnate. A3α is the largest of the adductor muscles and inserts on the dentary. A3β is small and inserts on the articular. Three divisions of Aw are present, Awα, Awβ and Awγ.

In *S. frenatus*, the Alα and A2 have fused to form a single weakly pinnate unit, the Alα/A2. The A3 is weak and strap-like and inserts on the articular. Only two divisions of Aw are present, Awα and Awβ.

3. Ligaments and Joints

S. sordidus has a short, strong anterior maxillary-premaxillary ligament which binds the two bones into a single functional unit. This unit has a simple rotational joint with the maxillary condyle of the palatine dorsal process.

S. frenatus has a broad anterior maxillary-premaxillary ligament that permits protrusion of the premaxilla relative to the maxilla. In this species, the maxilla has a complex articulation with the maxillary condyle of the palatine dorsal process.

1.3.4 The 'sordidus' and 'frenatus' groups.

The species within the genus *Scarus* can be divided into two groups. A description of the main morphological features characteristic of species in each group is given below, with a brief description of some of the members of each group.

1.3.4.1 The 'sordidus' group

The two diagnostic features of species referable to this group are: the possession of an entopterygoid lateral process and a third division of Aw, Awy. Characteristic features include: a deep robust premaxilla and dentary, exposed dental plates with a thick cement covering, alternating tooth replacement by adjacent vertical tooth rows, a separate A1 and A2, a well developed A3 inserting on the dentary, a slightly raised maxillary fossa on the premaxilla with a corresponding premaxillary process on the maxilla, three rows of teeth (two in large individuals) on each upper pharyngeal bone, with the outer row(s) reduced, and a type III intestinal pattern (Section 1.5).

From published descriptions, no species of *Scarus* can be referred to the 'sordidus' group. However, Randall and Nelson (1979) described the premaxilla of *S. japanensis* (Bloch) which had a strong resemblance to that of *S. sordidus*, and referred to a related species complex that included; *S. bowseri* (Snyder), *S. frontalis* Valenciennes, *S. perspicillatus* Steindachner, *S. capistratoides* Bleeker, *S. rhodruropterus* (Bleeker), *S. troschelli* Bleeker and *S. (Ypsiscarus) oedema* (Snyder). In addition, from the published descriptions in Randall and Bruce (1983), the following species also

show a strong likelihood of belonging to the 'sordidus' group: *S. atrilunula* Randall & Bruce, *S. cyanescens* Valenciennes, *S. enneacanthus* Lacepède, *S.genazonatus* Randall & Bruce and *S.* (*Ypsiscarus*) *ovifrons* Temmink & Schlegel. These species, along with *S. sordidus*, *S. gibbus* and *S. bleekeri* (de Beaufort), are thought to form a large proportion of the species belonging to the 'sordidus' group. All of the above species are present in the Indo-Pacific but are absent from the Atlantic and Caribbean.

In the present study, three species which may be referred to the 'sordidus' group, as defined above, have been examined: *S. bleekeri*, *S. gibbus* and *S. sordidus*. *S. sordidus* has been described in detail above (Section 1.3). A brief description of the two other species is given below.

S. bleekeri

Two specimens of *S. bleekeri* have been examined. Both were almost identical to *S. sordidus* of a similar size, in terms of osteology and myology. These species possess a lateral process on the entopterygoid, alternating tooth rows on the cutting edge of the premaxilla and dentary, a short palatine dorsal process, a large A3α inserting on the dentary, an Awγ and A1β, a posteriorly extended quadrate lateral ridge and a premaxillary process (developing in the 54 mm S.L. individual). The pharyngeal osteology and musculature do not differ notably from that of *S. sordidus*.

S. gibbus

The myology and osteology of *S. gibbus* are almost identical to that of *S. sordidus*, although the characteristic modifications of the former are more pronounced. This may, however, be a reflection of the larger size attained by *S. gibbus*; in *S. sordidus*, the characteristic features of the group become more pronounced with increasing size. The adductor mandibulae and pharyngeal musculature of *S. gibbus* are identical to those of *S. sordidus* and each upper pharyngeal bone typically bears three rows of teeth. *S. gibbus* differs from *S. sordidus* most notably in the possession of: a more posterodorsal position of the entopterygoid lateral process, a shorter palatine dorsal process, the protrusion of the maxillary fossa on the premaxilla with a corresponding invagination of the premaxillary process on the maxilla in larger individuals and a broader quadrate lateral ridge.

1.3.4.2 The 'frenatus' group.

The diagnostic features of species referable to this group are the presence of a deep, thin strap-like A3 muscle which inserts only on the articular, and the sequential replacement of premaxillary and dentary teeth, where each vertical tooth row bears a tooth on the cutting edge. The closely related genus *Hipposcarus* possesses only the latter feature and is therefore excluded from the 'frenatus' group. Features characteristic of 'frenatus' group species include: a simple, shallow adductor fossa, an elongate palatine dorsal process, the absence of a maxillary fossa on the premaxilla, two divisions of Aw, a large posterodorsal process on the maxilla, a well developed maxillary head, slightly protruding jaws, dental

plates covered by the lips and a type I or type II intestinal pattern (Section 1.5). Each upper pharyngeal bone typically bears two rows of teeth, the outer one of which is greatly reduced. The A1α and A2 are frequently fused.

Species that can be included in this group from published descriptions include: *S. rivulatus* Valenciennes (Tedman,1980), *S. compressus* Osburn & Nichols, *S. ghobban* (Forsskål), *S. perrico* Jordan & Gilbert and *S. rubroviolaceus* Bleeker (Gobalet, 1980), *S. aeruginosus* Valenciennes (=?) and *S. ferrugineus* Forsskål (as *S. coerulescens* Valenciennes in Lubosch, 1923, 1929). In addition, the osteological description of *S. guacamaia* Cuvier in Gregory (1933) bears a strong resemblance to members of the 'frenatus' group. The 'frenatus' group is thought to include the majority of Indo-Pacific species presently in the genus *Scarus* and all Atlantic and Caribbean species of *Scarus*.

In this study, sixteen species which may be referred to the 'frenatus' group, as defined above, have been examined: *S. brevifilis* (Gunther), *S. dimidiatus* Bleeker, *S. flavipectoralis* Schultz, *S. frenatus* Lacepède, *S. ghobban* Forsskål, *S. globiceps* Valenciennes, *S. longipinnis* Randall & Choat, *S. niger* Forsskål, *S. oviceps* Valenciennes, *S. psittacus* Forsskål, *S. rivulatus* Valenciennes, *S. rubroviolaceus* Bleeker, *S. schlegeli* (Bleeker), *S. spinus* (Kner), *S. tricolor* Bleeker and *Scarus* sp. (*cf. lunula*). A brief description of the morphology of these species is given below. This is based on morphological features rather than individual species descriptions because of the degree of morphological similarity between many of the species.

Within the 'frenatus' group, there is some degree of variation between species, with the most disparate forms being *S. rubroviolaceus* and *S. flavipectoralis*. The group may be divided into two subroups, designated 'a' and 'b'. The two subgroups share a large number of characters but may be separated by the form of the intestine and the degree of fusion between Alα and A2. Subgroup 'a' includes: *S. flavipectoralis*, *S. psittacus*, *S. schlegeli* and *Scarus* sp. (*cf. lunula*). Subgroup 'a' species have a separate Alα and A2 and typically possses a type I intestinal pattern (Section 1.5). The body shape is relatively elongate with light osteological structures and relatively weak protruding jaws. Subgroup 'b' includes *S. brevifilis*, *S. dimidiatus*, *S. frenatus*, *S. ghobban*, *S. globiceps*, *S. longipinnis*, *S. niger*, *S. oviceps*, *S. rivulatus*, *S. rubroviolaceus*, *S. spinus* and *S. tricolor*. Members of this subgroup have a fused Alα/A2 complex and typically possses a type II intestinal pattern. The body of subgroup 'b' species is relatively deep, with more robust jaws and osteological structures than species in subgroup 'a'.

Osteology of 'frenatus' group species

The premaxilla and dentary

The deepest and most robust dentaries are found in *S. rubroviolaceus* and *S. ghobban*. Those of *S. brevifilis*, *S. dimidiatus*, *S. frenatus*, *S. niger*, *S. oviceps*, *S. rivulatus*, *S. spinus* and *S. tricolor* are less robust, whilst those of *S. flavipectoralis*, *S. globiceps*, *S. longipinnis*, *S. psittacus*, *S. schlegeli* and *Scarus* sp. (*cf. lunula*) are the weakest. In *S. flavipectoralis*, *S.* sp. and especially *S. schlegeli*, the

premaxilla is relatively elongate whilst the dental plate of the dentary is relatively shallow. Variations in the depth of the dentary have been described quantitatively by Bruce (1979) and will not be considered in detail here.

The form of the teeth also varies within the group. In *S. rubroviolaceus* and *S. ghobban*, the teeth are large with convex lateral and distal edges. When viewed anteriorly, they appear rounded and exhibit little wear. Although the anterior vertical tooth rows all have a tooth on the cutting edge, the lateral vertical tooth rows may have variable prominence on the cutting edge because of the size and shape of the teeth. The cutting edge is strongly scalloped.

In *S. brevifilis*, *S. dimidiatus*, *S. frenatus*, *S. globiceps*, *S. longipinnis*, *S. niger*, *S. oviceps*, *S. rivulatus* and *S. tricolor*, the teeth are broad with a convex distal edge. When viewed anteriorly, they are subrectangular, with a scalloped cutting edge which was worn, even in large individuals. In *S. spinus*, the teeth, especially in the premaxilla, are longer than in the other species in subgroup 'b'. When viewed anteriorly, these teeth are roughly hexagonal and form a mosaic but, because of wear, the cutting edge remains even.

The remaining four species (subgroup 'a') all possess elongate teeth, particularly *S. flavipectoralis*, *S. schlegeli* and *Scarus* sp. These elongate teeth are most notable in the premaxilla. Although the teeth in adjacent rows do not reach the cutting edge simultaneously, the cutting edge is only weakly scalloped due to wear.

Lateral 'canine' teeth are present in both subgroups. In the four species examined in subgroup 'a', lateral canines were present on both upper and lower jaws. In subgroup 'b', canines may be present on both jaws (*e.g. S. rivulatus, S. globiceps, S. longipinnis* and *S. spinus*), or only on the upper jaw (*e.g. S. frenatus, S. ghobban, S. niger, S. rubroviolaceus* and *S. tricolor*), or may be completely absent (as in *S. dimidiatus* and *S. oviceps*) (Randall & Choat, 1980, Randall & Bruce, 1983 and the present study).

An analysis of the maximum gape of freshly collected specimens from the 'sordidus' group and the 'frenatus' group (see Table 1.2 for species and lengths) revealed no significant difference between the two groups (Mann Whitney U-test [MWU-test] $p > 0.1$, n1/n2 = 40/14, U1/U2 = 206/354; 'sordidus' group species' gapes = 12.12 ± 0.54 [in 100ths of the S.L.; mean ± 95% C.I.], 'frenatus' group species gapes = 12.51 ± 2.57).

The suspensorium

The basic form of the suspensorium resembles that of *S. frenatus*. There are, however, several variable features. In *S. rubroviolaceus*, and to a lesser extent *S. oviceps*, a thickening of the posterodorsal edge of the entopterygoid and metapterygoid is present, with a well developed dorsal notch and a lateral groove carrying the mandibular branch of the trigeminal nerve.

Rounded protrusions of variable sizes are found on the posterodorsal edge of the suspensorium, near the notch through which the mandibular branch of the trigeminal nerve passes. A small,

rounded protrusion is present anterior to this notch in *S. flavipectoralis*, *S. oviceps* and *S. rubroviolaceus*, and posterior to the notch in *S. dimidiatus*, *S. psittacus* and *S. schlegeli*. The sizes of these protrusions are variable within and between species. A lateral expansion of the posterodorsal edge of the entopterygoid may be present in *S. globiceps*, and is well developed in *S. spinus*. In *S. spinus*, this entopterygoid lateral process closely resembles that of juvenile *S. sordidus* (at about 50mm S.L.). The entopterygoid lateral process of *S. spinus* is broad and thin, with no lateral thickening and does not possess associated septa or concavities. In *S. spinus*, the mandibular branch of the trigeminal nerve does not pass through the entopterygoid lateral process as in *S. sordidus*, but passes along a groove posterior to it, as in other members of the 'frenatus' group.

In all species, the palatine dorsal process appeares to undergo some ontogenetic changes, with a reduction in length as the individual grows. In most species, the maxillary condyle faces anteriorly throughout development but it may become more ventrally orientated in large individuals of some species (*e.g.* *S. flavipectoralis* and *S. ghobban*), as a result of the curvature of the long palatine dorsal process.

Finally, there is some variation between species in the form of the quadrate-preopercular attachment. In most species it has a frenatus-like form but it may approach the interlocking sordidus-like form. This type of attachment between the two bones is found in *S. rubroviolaceus*, *S. flavipectoralis* and, to a lesser extent, *S. ghobban*.

The neurocranium

In all species the neurocranium closely resembles that of *S. frenatus*, with a short ethmoid-vomerine process bearing poorly developed maxillary condyles and lacking any degree of fusion between the ethmoid and frontals. As in the 'sordidus' group, all species have straight basipharyngeal facets and a single pair of triangular fossae in the ventral surface. The most distinctive species is *S. spinus*, which has a particularly short neurocranium with a large supraoccipital crest. In overall form, the neurocranium of species in subgroup 'a' is weaker than that of species in subgroup 'b'. In addition, the basipharyngeal facets are relatively short and broad in species of subgroup 'a', particularly *S. flavipectoralis*.

The pharyngeal jaws

The upper pharyngeal jaws of species in the 'frenatus' group differ little from those of *S. frenatus*. All the specimens examined had two rows of teeth in the upper jaw, with the exceptions of: *S. rubroviolaceus* which has only one row, one specimen of *S. frenatus* which had three rows on one side and a single specimen of *S. globiceps*, from a collection of 14 individuals, which had three small teeth in a third row on one side of the upper pharyngeal jaw. There is considerable variation within and between species in the size, shape and number of teeth.

The lower pharyngeals are likewise similar to those of *S. frenatus*. The differences between many of the species examined have been analysed quantitatively by Bruce (1979) and will therefore

not be considered in detail here. The only notable feature is the relatively large area of the grinding surface in species of subgroup 'a'.

Myology of 'frenatus' group species

The degree of fusion between Alα and A2 is used as a character to divide subgroups 'a' and 'b', although considerable variation in the degree of fusion exists within the two subgroups. In subgroup 'a', the division between Alα and A2 is complete in *Scarus* sp., but in the remaining three species, a weak fibrous bridge of connective tissue is present between the two main tendons of Alα and A2. In subgroup 'b' species, the muscles are fused, but some degree of separation near the muscular origin and on the medial surface is present in some individuals. The extent of separation is dependent upon the species, the size of the specimen and individual variation which, often as a result of variations in the extent of the tendinous sheet that covers the adductor mandibulae in large individuals, may conceal any separation. A superficial subdivision near to the site of origin has been found in the following species (numbers of individuals in parentheses): *S. frenatus* (3), *S. niger* (1), *S. rubroviolaceus* (1), *S. brevifilis* (1) and *S. oviceps* (1). In all cases, this division corresponds to the dividing line described in *S. frenatus* (Section 1.3.3). In subgroup 'a' species, the two muscles are completely divided along this line.

The other form of myological variation recorded is the size of Alβ, which was relatively elongate in *S. flavipectoralis* and *S. schlegeli*. In the other species the variation within a species exceed differences between species, making comparisons between

species unreliable. Intraspecific variation appeared to be a result of the increase in the proportion of muscle covered by the outer tendinous layer in larger individuals.

The form of the musculature of the pharyngeal apparatus is similar in all of the 'frenatus' group species examined. The only difference being the degree of development. The most robust musculature was recorded in *S. rubrovioiaceus*.

Within *S. sordidus* and *S. frenatus*, most variation in the osteology, myology and intestinal patterns are size-related and are discussed in Chapter 2. In adults, there was no notable variation in the osteology or intestinal patterns (Sections 1.3.2 and 1.5), whilst the limited myological variation was primarily dependent upon the extent of the tendinous layer covering the adductor muscles (Section 1.3.3). The level of within-species variability in other species is comparable. Between-species variability within each group or subgroup is greater than within-species variability although it was still limited (Sections 1.3.4.1, 1.3.4.2 and 1.5).

Summary

1) Within the genus *Scarus* there are two distinct morphologial groups designated the 'sordidus' group and the 'frenatus' group.
2) 'Sordidus' group species possess teeth on the cutting edge of the jaws from alternating vertical tooth rows, an Awy, an entopterygoid lateral process and three upper pharyngeal tooth rows. This group includes: *S. bleekeri*, *S. gibbus* and *S. sordidus*.
3) 'Frenatus' group species possess teeth on the cutting edge of the jaws from each vertical tooth row, a thin strap-like A3 and two

upper pharyngeal tooth rows.

4) The 'frenatus' group is divided into two subgroups designated 'a' and 'b'. Species in subgroup 'a' typically have a separate Alα and A2, whereas species in subgroup 'b' have a fused Alα/A2 complex. Subgroup 'a' includes: *S. flavipectoralis*, *S. psittacus*, *S. schlegeli* and *S.* sp. (*cf. lunula*). Subgroup 'b' includes: *S. brevifilis*, *S. dimidiatus*, *S. frenatus*, *S. ghobban*, *S. globiceps*, *S. longipinnis*, *S. niger*, *S. oviceps*, *S. rivulatus*, *S. rubroviolaceus*, *S. spinus* and *S. tricolor*.

1.3.5 *Cetoscarus bicolor*

This species most closely resembles members of the 'sordidus' group, but lacks many of the derived characters present in 'sordidus' and 'frenatus' group species, including the articulatory articular-dentary joint, interdigitating upper pharyngeal tooth rows, cement covered dental plates, an entopterygoid lateral process and the dorsal subsection of A1, A1β. *C. bicolor* is an interesting species as it shares many characters with genera within the Sparisomatinae and, as the least specialized member of the Scarinae, forms a link between the Sparisomatinae and Scarinae.

Osteology (Figs 1.16, 1.17 B, 1.18 A)

The suspensorium

Although *C. bicolor* lacks a specialized entopterygoid, the suspensorium (Fig. 1.16) is similar to that of species in the 'sordidus' group. The palatine dorsal process is short, with a ventrally orientated maxillary condyle, and the entopterygoid has a perforated area formed by an interlocking network of bone. The quadrate lateral ridge extends to the posterior extremity of the quadrate with the mid and posterior portion of the ventral part of the quadrate lying in a dorsal groove in the preoperculum as in 'sordidus' group species. Characteristic features include a dorsal extension of the entopterygoid and a medial extension of the preopercular which fuses with the symplectic to create a small interspace bordered by the preopercular, symplectic and hyomandibula.

The jaw apparatus

The maxilla and premaxilla

The maxilla and premaxilla of *C. bicolor* are distinctive. Of the two groups they most closely resemble the form of species in the 'sordidus' group. The maxilla is broad, with a moderately well developed head and medial process (Fig. 1.16). It has, however, many distinctive features. The maxillary arm bears a small premaxillary facet on the leading edge below a small protrusion, and possesses a broad posterodorsal process similar to those of species in the 'frenatus' group. The maxillary head has a small medial flange and bears a large, simple rounded facet with which it articulates with the palatine. Anteriorly, the maxillary head bears a large premaxillary process which projects forward but tapers on the ventromedial surface. The medial process is poorly developed. It bears a single dorsolaterally orientated premaxillary condyle and a large cranial condyle which are both poorly developed. The insertion scars of the anterior maxillary premaxillary ligaments lie along the edge of the medial process, the larger one lying medial to the premaxillary condyle and the smaller posterior one lateral to the cranial condyle. The unusual insertion sites found in 'sordidus' group species are not present. On the medial surface of the maxillary arm, a prominent ridge is present, extending from the base of the medial process to the midpoint of the maxillary arm, where it terminates at the A1 insertion scar.

The premaxilla is robust (Fig. 1.16). It has a long stout ascending process with a deep ventral groove terminating near the base of the alveolar process. In *C. bicolor*, the maxillary fossa is

a simple deep pit, with the strongest bone on the ventromedial surface corresponding with the strong ventromedial part of the premaxillary process on the maxilla. On the distal posterior face of the bifid alveolar process, a fossa and a facet are present. These correspond with the protrusion and premaxillary condyle on the leading edge of the maxillary arm (Fig. 1.16). On the medial surface, the maxillary facet is poorly developed. The two insertion scars of the anterior maxillary-premaxillary ligaments are poorly differentiated. The anterior scar is a shallow depression medial to the maxillary facet, whilst the posterior scar (site) is in the deep groove on the ventral surface of the ascending process. This groove is similar to, but much shorter than, the corresponding groove in *S. frenatus*.

The teeth of *C. bicolor* are characteristic of the species (Fig. 1.16). Of the two groups, they most closely resemble those of the 'sordidus' group. They are arranged in a mosaic and are subovoid when viewed anteriorly. Each vertical row is represented on the cutting edge but with alternating prominence. This results in a strongly crenate cutting edge. Unlike 'sordidus' and 'frenatus' group species, there is no distinct cement covering over the dental plates, and the newly developed teeth protrude through the alveolar wall (as in *Euscarus* [Board, 1956] and *Sparisoma* [Boas, 1879 and Gygi, 1975]). There are no canine teeth in either jaw.

The articular and dentary

The articular and dentary differ markedly from those of the 'sordidus' group, primarily as a result of the non-articulatory nature of the joint between the two bones (Fig. 1.16). The

articular has three processes: the anterior and posterior ascending processes, and the descending process. The posterior ascending process is not present in 'sordidus' and 'frenatus' group species. The anterior ascending process of *C. bicolor* is considerably longer than in 'sordidus' or 'frenatus' group species. Overall the appearance of the articular is similar to that in the less specialized scarids (e.g. *Sparisoma cretense* [Board, 1959] and *Nicholsina* [Gobalet, 1980]) and labrids (Gobalet, 1980, Rognes, 1973, Tedman 1980 and Van Hasselt, 1979). On the medial surface, a medial articular spine is present, with the anterior edge attached to a large flange which extends along the anterior border of the descending process.

The dentary has an elongate lateral process, the dorsal edge of which is almost confluent with the cutting edge (Fig. 1.16). There is no articular socket, merely a groove between the lateral flange and a well developed angular process. The sutures at the medial symphysis are characteristically complex and branched. The dental plates and teeth are comparable to those of the premaxilla.

The pharyngeal apparatus

The pharyngeal jaws differ from those of 'sordidus' and 'frenatus' group species and bear a close resemblance to members of the Sparisomatinae, particularly *Euscarus* and *Sparisoma* (figured in Schultz, 1958). The lower pharyngeal bone is robust with a convex toothed surface (figured in Schultz, 1958 and Hattori, 1976, 1984). Each of the upper pharyngeal bones bear three rows of teeth, with relative widths of approximately 4.2:2.9:1 from innermost to outermost (figured in Schultz, 1958 and Hattori, 1976, 1984). There

is no interdigitation between the medial tooth rows.

The neurocranium (Figs 1.17 B, 1.18 A)

The neurocranium of *C. bicolor* is distinctive (Fig. 1.17 B). It is elongate and laterally compressed. The ethmoid-vomerine process is long and curved, with two lateral maxillary condyles on the anterior extremity. The parasphenoid forms a deep 'keel' anteriorly and the pharyngeal apophysis posteriorly. The latter bears the strongly curved facets of the basipharyngeal joint (c. in Fig. 1.17 B). In this species, the ridges on either side of the sites of origin of the fourth levator externus and levator posterior are well developed.

From a ventral perspective, the neurocranium displays two deep fossae (Fig. 1.18 A, 1, 2). The largest and deepest of these fossae (#1 in Fig. 1.18 A) is homologous with the large fossa found in all other scarids, namely, the site of origin of the posterior part of the fourth levator externus. Between this deep fossa and the posterior groove marking the site of origin of the posterior part of the levator posterior lies a smaller, deep triangular fossa (#2 in Fig. 1.18 A). This is the site of origin of the lateral section of the levator posterior, the fibres of which have a muscular insertion on the fourth epibranchial. Such a fossa has, so far, been recorded only from two species, *C. bicolor* and *B. muricatum*.

Myology (Fig. 1.16)

The myology of *C. bicolor* strongly resembles that of 'sordidus' group species. The three adductor muscle blocks, A1, A2 and A3 are all well developed.

The adductor mandibulae

Section A1

Section A1 covers a large superficial area of the adductor muscle mass (Fig. 1.16). It arises from the preoperculum, hyomandibula, metapterygoid and symplectic, and has a tendinous insertion on the medial surface of the maxilla.

Section A2

Section A2 is ventral to A1 and arises from the preoperculum, symplectic and quadrate (Fig. 1.16). It has a tendinous insertion on the posterior medial surface of the dentary lateral flange and, to a limited extent, on the medial surface of the posterior ascending process of the articular.

Section A3

Section A3 is the largest and deepest of the adductor muscle blocks (Fig. 1.16). It lies dorsomedially and arises from the palatine, entopterygoid, metapterygoid, hyomandibula and quadrate. The main tendinous insertion is on the dorsal part of the medial surface of the dentary lateral flange, with an additional smaller tendinous insertion on the medial surface of the articular, at the base of the anterior ascending process.

Figure 1.16

The head of a 388 mm S.L. *Cetoscarus bicolor* with the integument, nasal, lacrymal, circumorbitals and part of A1 removed.

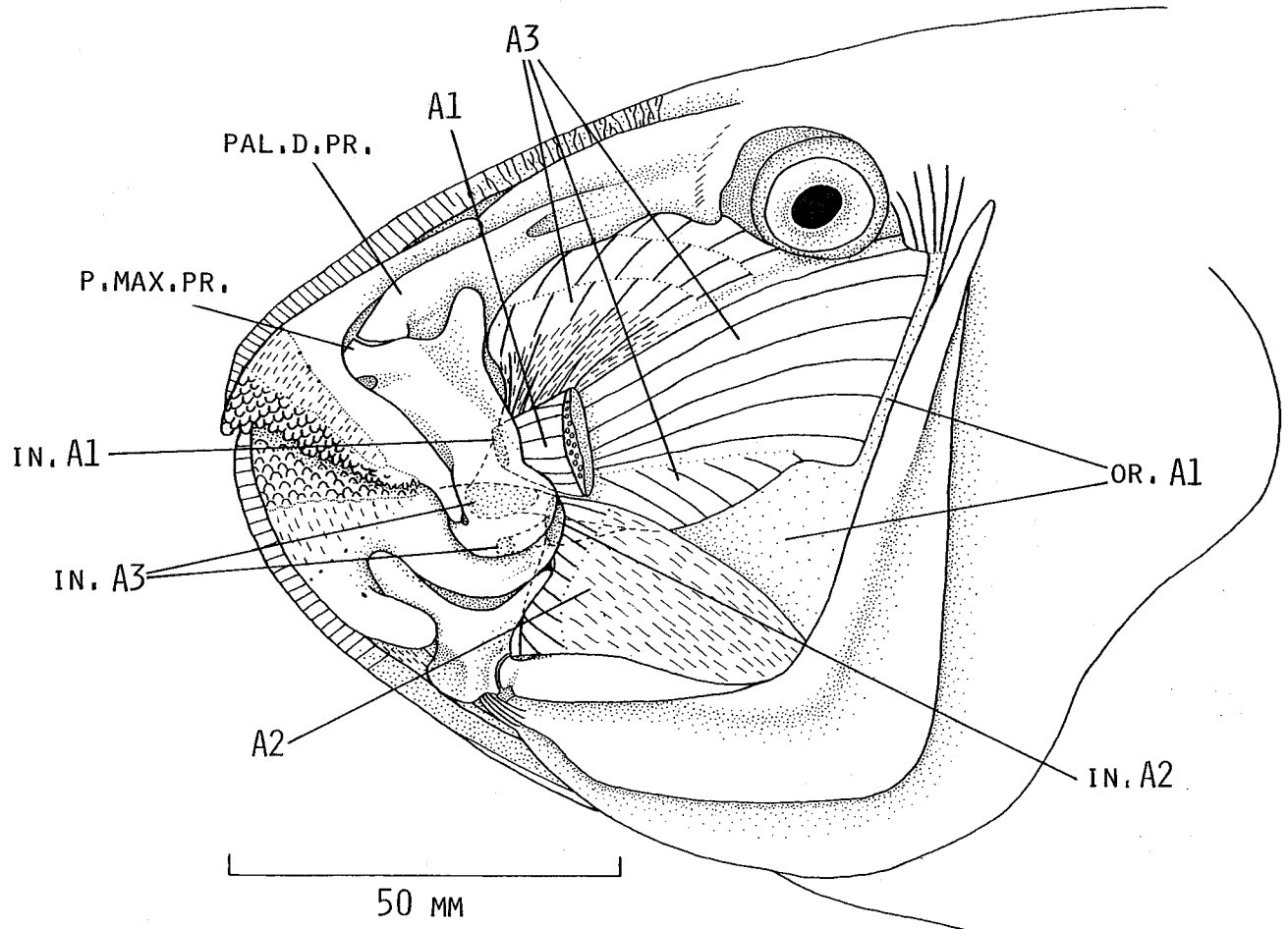

A3
A1
PAL.D.PR.
P.MAX.PR.
IN.A1
IN.A3
A2
OR.A1
IN.A2
50 MM

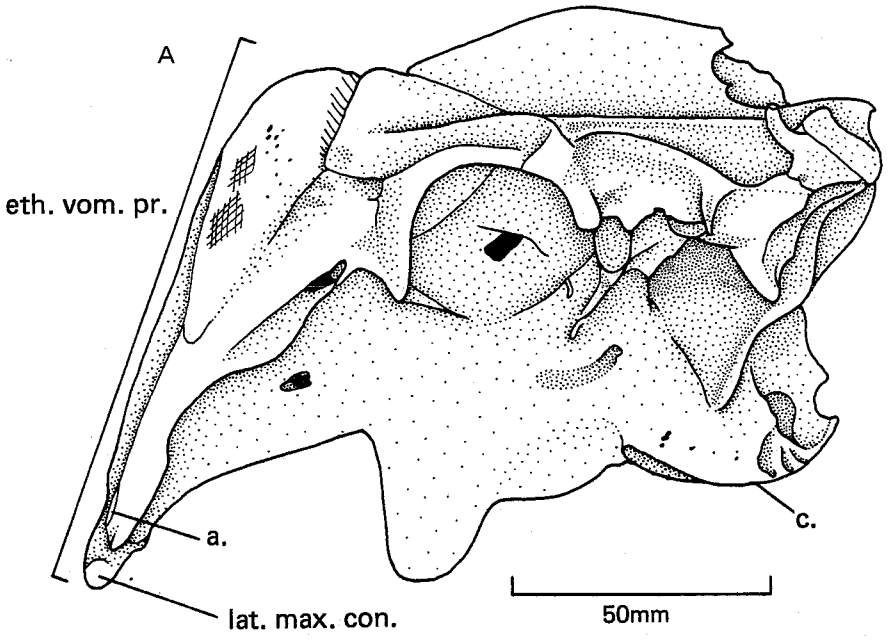
Figure 1.17 A

A lateral view of the neurocranium of *Bolbometopon muricatum*.

Figure 1.17 B

A lateral view of the neurocranium of *Cetoscarus bicolor*.

eth.vom.pr.	Ethmoid-vomerine process.
lat.max.con.	Lateral maxillary condyle of the ethmoid-vomerine process.
a.	Anterior premaxillary condyle of the ethmoid-vomerine process.
c.	Curved facets of the basipharyngeal joint.


A
eth. vom. pr.
a.
c.
lat. max. con.
50mm

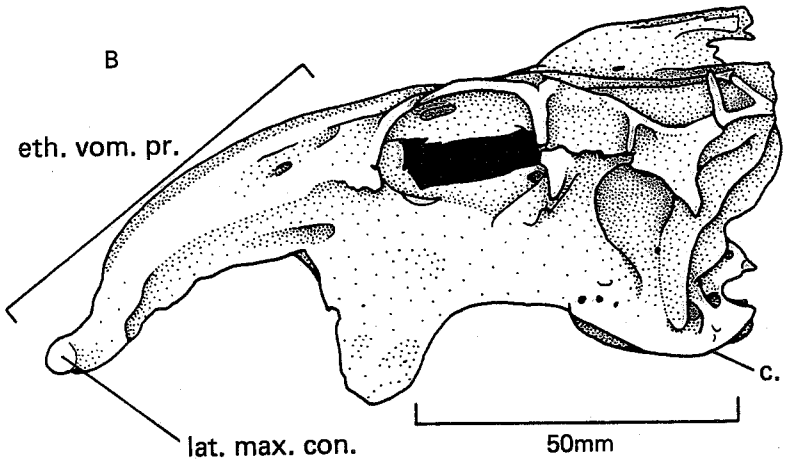

B
eth. vom. pr.
c.
lat. max. con.
50mm

Figure 1.18 A

A ventral view of the neurocranium of *Cetoscarus bicolor*.

Figure 1.18 B

A ventral view of the neurocranium of *Bolbometopon muricatum*.

Figure 1.18 C

A ventral view of the neurocranium of *Hipposcarus longiceps*.

Figure 1.18 D

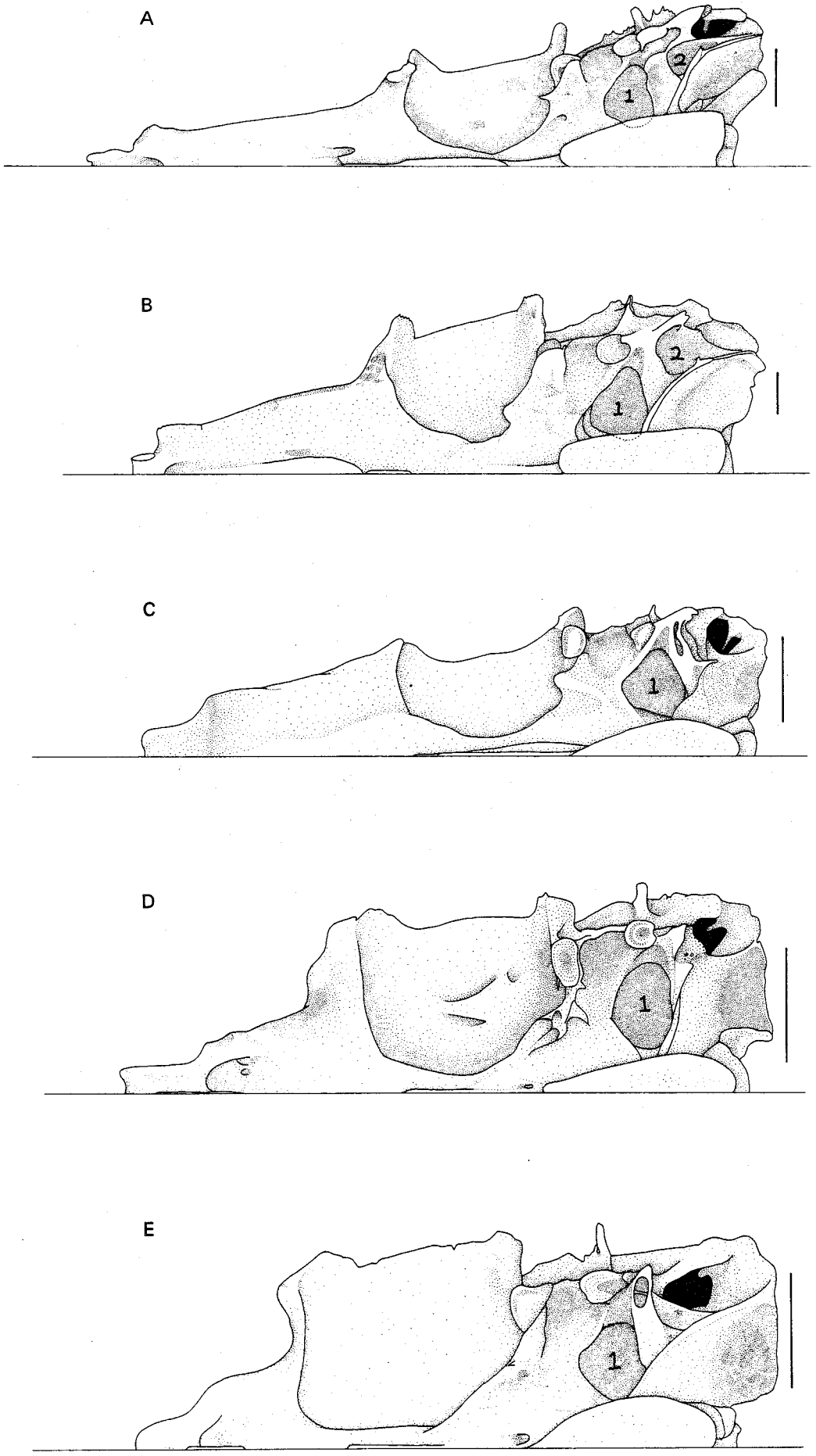
A ventral view of the neurocranium of *Scarus sordidus*.

Figure 1.18 E

A ventral view of the neurocranium of *Scarus frenatus*.

In each figure the vertical scale bar is 10 mm.

1 = A deep fossa; the site of origin of the posterior part of the fourth levator externus.
2 = A smaller fossa; the site of origin of the levator posterior.


A
1
2
B
1
2
C
1
D
1
E
1

The adductor muscles are covered superficially by a strong, tendinous sheet that extends from the orbit to the preoperculum and quadrate, with only the anterior section remaining uncovered. This sheet is an important site of origin for the superficial part of the adductor muscles.

A1 is primarily unipinnate with a small, deep bipinnate portion, A2 is bipinnate posteriorly and tripinnate anteriorly and A3 is primarily tripinnate, with some bipinnate portions posteriorly. As in *S. sordidus*, the degree of pinnation is strong, with relatively short fibres.

Other muscles

Intermandibular and Aw sections are developed in *C. bicolor*. There are two divisions of Aw: Awα and Awβ. The attachment sites of both sections are similar to those found in 'sordidus' and 'frenatus' group species.

An additional muscle which is absent in 'sordidus' and 'frenatus' group species is present in *C. bicolor*. It connects the anterior edge of the medial surface of the quadrate to the the posterior face of the flange connecting the articular medial spine and descending process. An homologous muscle was described in *Leptoscarus vaigiensis* (as *Scarichthys coeruleopunctatus*) by Lubosch (1923), who named it the M. adductor mandibulae medialis and later, the M. quadrato mandibularis internus (Lubosch, 1929). A comparable muscle is figured, but not labelled, by Board (1956) in *Euscarus cretense* (as *Sparisoma cretense*). This muscle is present also in *Hipposcarus longiceps* (Section 1.3.7). A similar muscle is present

in labrids (Van Hasselt, 1979). Winterbottom (1974), however, considers this muscle and the quadrato-mandibularis internus in scarids to be a posterior extension of the Aw.

There is little difference between the pharyngeal musculature of *C. bicolor* and that of 'sordidus' group species. It is strong as in 'sordidus' group species, with the only notable differences being the specialized fossa which forms the site of origin of the lateral fibres of the relatively well developed levator posterior and the lack of a fourth epibranchial insertion of the fourth levator externus (as in 'frenatus' group species).

Ligaments

The ligaments of *C. bicolor* are similar to those of *S. sordidus* with two notable exceptions: the maxillary-premaxillary ligaments and the articular-dentary ligaments. The anterior maxillary-premaxillary ligament connects the anteromedial edge of the maxillary medial process to the ventral surface of the premaxilla. It binds the two bones tightly but lacks the distinctive insertion sites found in *S. sordidus*. The posterior maxillary-premaxillary ligament connects the posterodorsal maxillary head to the ventral ascending process of the premaxilla with a few fibres connecting to the anterior edge of the rostral cartilage. This ligament is similar to that of *S. sordidus*. Both ligaments, however, have a more strap-like form than those of *S. sordidus*.

The articular-dentary ligament differs from members of the 'sordidus' and 'frenatus' groups because of the non-articulatory nature of the articular-dentary joint. However, it resembles

closely the form of species within the Sparisomatinae. The anterior articular ascending process is strongly bound to the dentary by ligaments along the dorsal and ventral edges corresponding to the anterior and posterior articular-dentary ligaments in *S. sordidus*. A third ligament is present connecting the distal end of the posterior articular ascending process to the posterior edge of the dentary lateral flange. In *S. sordidus* the posterior ascending process and ligament are both absent.

Summary

1) *C. bicolor* is the most primitive of the Scarinae and shares many features with species in the Sparisomatinae (especially *Sparisoma* and *Euscarus*). These include:
   a) The absence of an articular-dentary articulation.
   b) Upper pharyngeals each bearing three rows of teeth with the inner two rows being well developed and the absence of interdigitation between the medial rows.
   c) The deep jaws with crenate cutting edges, no cement over the dental plates and no lateral canines.
   d) The presence of a quadrato-mandibularis-internus.
2) Of the two groups, *C. bicolor* most closely resembles the species in the 'sordidus' group but lacks many of the specialized features associated with this group. These include the muscle sections A1β and A$w\gamma$ and the entopterygoid lateral process, all of which are absent in *C. bicolor*.
3) The anterior maxillary-premaxillary ligament binds the two bones and is relatively thin and strap-like.
4) The premaxillary process and maxillary fossa are well developed but have a simple structure.

5) The neurocranium possesses two deep fossae on the ventral surface. These are the sites of origin of a part of the fourth levator externus and levator posterior.

1.3.6 *Bolbometopon muricatum*

Bolbometopon muricatum is a distinctive species with a deep body and a hump on the forehead. This species is closely related to *C. bicolor* and shares many morphological characters including: a non-articulatory articular-dentary joint, teeth which visibly protrude through the alveolar wall, curved facets of the basipharyngeal joint, three rows of teeth in the upper pharyngeal bones (the inner two rows of which are well developed), an elongate ethmoid-vomerine process and a specialized fossa at the site of origin for the lateral part of the levator posterior. Despite its similarity to *C. bicolor*, it also shares some characters with members of the 'sordidus' group. These are: the form of the premaxillary process on the maxilla and the form of the anterior maxillary-premaxillary ligament.

Osteology (Figs 1.17 A, 1.18 B, 1.19)

The suspensorium

The suspensorium (Fig. 1.19) bears a strong resemblance to that of *C. bicolor* (Fig. 1.16). It is broad and shallow, with the deepest area of the entopterygoid bearing several small perforations. The dorsal edge has no thickening, no entopterygoid lateral process and possesses a short palatine dorsal process with a ventrally directed condyle.

It has, however, several distinctive features which differ from both *C. bicolor* and the 'sordidus' group. The overall shape is ventrally narrower than *C. bicolor* and *S. sordidus*. It is

relatively deeper (mean width/depth: *B. muricatum*, 0.66; *C. bicolor*, 0.80; *S. sordidus*, 0.87), with the palatine dorsal process in a more ventral position. The posterior part of the quadrate lies lateral to the preoperculum as in 'frenatus' group species, and lacks the deep dorsal groove that extends to the posterior extremity as found in 'sordidus' group species, some members of the 'frenatus' group and *C. bicolor*. In *B. muricatum*, the posterior part of the quadrate has an irregular medial surface which interdigitates with similar irregularities on the preoperculum. The medial ventral surface, and to a lesser extent, the anterior ventral surface of the quadrate bear a deep ventral groove into which the preoperculum inserts. This connection is stronger than that of *C. bicolor* or *S. sordidus*. Finally, the most characteristic feature of the suspensorium of *B. muricatum* is the raised network of bony laminae on the anterodorsal surface of the palatine (not apparent in Fig. 1.19). This feature has, so far, only been recorded in this scarid species.

The jaw apparatus

The maxilla and premaxilla

The maxilla and premaxilla (Fig. 1.19) are similar to those of *C. bicolor* (Fig. 1.16). The maxilla does, however, differ in several important features: the premaxillary process is shorter, the medial flange of the maxillary head is reduced, there is a large cavity for the insertion of the anterior maxillary - premaxillary ligament on the medial process (as in *S. sordidus*), the cranial condyle is reduced and the raised medial ridge

bearing the insertion scar of A1 is short (and therefore nearer to the medial process). With the exception of the reduced cranial condyle, these features all tend towards the state found in 'sordidus' group species. *B. muricatum* also lacks the small condyle mid-way along the anterior edge of the maxillary arm, which is present in both *C. bicolor* and *S. sordidus*.

The premaxilla likewise differs from that of *C. bicolor* in several features: the maxillary fossa is raised (as in *S. sordidus*), the relatively short ascending process has no marked lateral groove for the palatine dorsal process and has a poorly developed maxillary condyle (both are developed in *C. bicolor* and *S. sordidus*), the maxillary facet is relatively well developed, and a deep concavity is present in the proximal medial surface of the ascending process (the insertion site of the anterior maxillary - premaxillary ligament).

The dental plates of *B. muricatum* (Fig. 1.19) are deeper than those of *C. bicolor* (Fig. 1.16). The teeth form a mosaic comparable to that of *C. bicolor* but are covered by a thin layer of cement near the base of the dental plate. The most characteristic feature of the jaws is the presence of a small rounded protrusion (tubercule) at the base of each tooth. The taxonomic importance of this character was noted by Valenciennes (Cuvier & Valenciennes, 1839, p208-9) in his original description of this species (as *Scarus muricatus*). The cutting edges of the jaws are strongly crenate as in *C. bicolor*.

The articular and dentary

As in *C. bicolor*, there is no articular-dentary articulation in *B. muricatum* (Fig. 1.19). The articular is almost identical to that of *C. bicolor*, the only differences being the relative proportions. For example, in *B. muricatum*, the medial flange is narrower, the anterior ascending process is shorter and the flange joining the two ascending processes is larger. The dentary likewise closely resembles that of *C. bicolor*. The insertion scars and medial sutures are similar, although the overall shape is deeper. The teeth have the characteristic rounded protrusion and there is a thin layer of cement near the alveolar base. Although there is no articular-dentary articulation, the dentary has a short recessed groove into which the anterior articular ascending process inserts. This condition approaches the state found in those species with an articulatory articular-dentary joint.

The pharyngeal apparatus

The pharyngeal jaws of *B. muricatum* are almost identical to those of *C. bicolor*. The upper pharyngeal bones have three rows of teeth, the inner two of which are well developed, with relative widths of approximately 4.5:3.3:1 from innermost to outermost. In the specimens examined, the outer row was not as well developed as in *C. bicolor*. The degree of interdigitation between the medial tooth rows is minimal but greater than *C. bicolor*. The lower pharyngeal is robust, with a broad grinding surface. The pharyngeal bones of *B. muricatum* are figured in Schultz (1958) (as *Chlorurus gibbus*).

The neurocranium (Figs 1.17 A, 1.18 B)

The neurocranium of *B. muricatum* is strongly characteristic of the species (Figs 1.17 A, 1.1 B). It is deep, and possesses a ventrally protruding vomer, an ethmoid with a protruding areolar network of laminae and a large supraoccipital crest (Fig. 1.17 A). The basic form of the neurocranium resembles that of *C. bicolor*, and shares two specific characters that have, so far, been recorded only in these two species of Scarinae. These are: the curved facets of the basipharyngeal joint (c. in Fig. 1.17 A) and the second pair of deep triangular fossae on the ventral surface (the site of origin of the external part of the levator posterior, No. 2 in Fig. 1.18 B). As in *C. bicolor*, *B. muricatum* possesses a deep 'keel' on the anterior parasphenoid, well developed ridges at the sites of origin of the fourth levator externus and levator posterior, and a well developed pair of lateral maxillary condyles on the vomer. In *B. muricatum*, a pair of anteriorly facing facets (a. in Fig. 1.17 A) are present on the anterior face of the vomer. These facets have been recorded only in this species, and appear to form a compression point between the neurocranium and the premaxilla *via* the rostral cartilage.

Myology (Fig. 1.19)

Adductor mandibulae

Section A1

Section A1 is the most superficial of the adductor muscles (Fig. 1.19). It arises from the preoperculum, hyomandibula, metapterygoid and symplectic, and from a tendinous layer covering the adductor muscle mass. It inserts onto a raised process at the base of the maxillary medial process, the former being marked by a rounded insertion scar.

Section A2

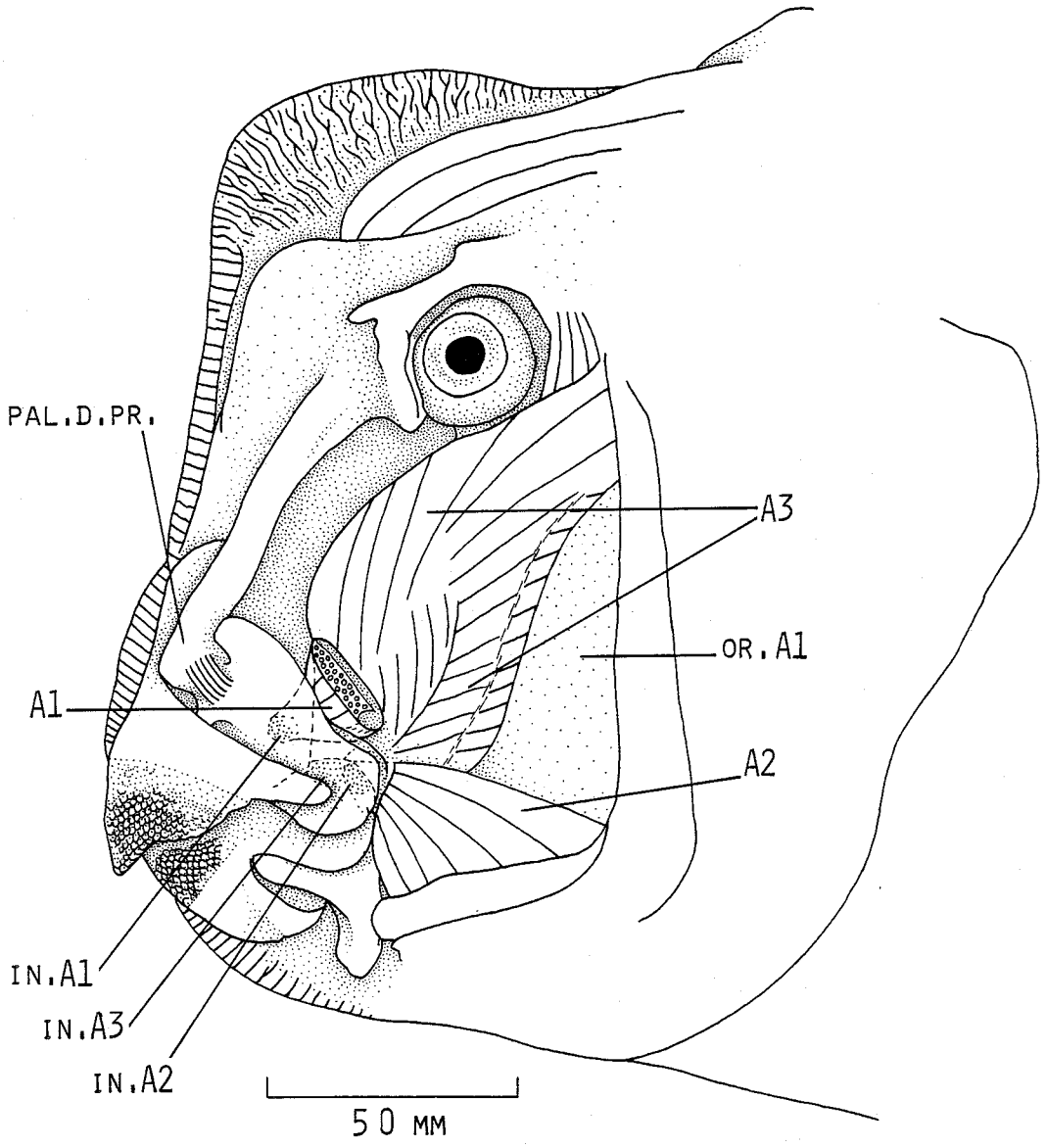
Section A2 lies ventral to the other muscles (Fig. 1.19), with origins on the quadrate, symplectic and preoperculum. It has two tendinous insertions: the larger insertion is on the posterior medial surface of the dentary lateral process, whilst the smaller insertion is on the distal medial surface of the posterior articular ascending process.

Section A3

Section A3 is the deepest of the main adductor muscles (Fig. 1.19), with origins on the entopterygoid, metapterygoid, hyomandibula and quadrate. It inserts on both the dentary and articular. The main insertion is onto the dorsal medial surface of the dentary lateral flange, with a small posterior part of this tendon inserting onto the medial surface of the articular, medial to the articular insertion of A2.

Figure 1.19

The head of a 530 mm S.L. *Bolbometopon muricatum* with the integument, nasal, lacrymal, circumorbitals, tendinous sheet covering the adductor muscle mass and part of A1 removed.


PAL.D.PR.
A3
OR.A1
A1
A2
IN.A1
IN.A3
IN.A2
50 MM

The A1 muscle mass is bipinnate whilst both A2 and A3 are multipinnate.

Other muscles

The intermandibular and Aw sections are developed in *B. muricatum*, and as in *C. bicolor*, the quadrato-mandibularis is relatively well developed. The pharyngeal musculature closely resembles that of *C. bicolor*, with a relatively well developed fourth levator externus and levator posterior, and no discernible insertion of the fourth levator externus on the fourth epibranchial.

The ligaments

The ligaments of *B. muricatum* differed little from those of the 'sordidus' group and *C. bicolor*. Of particular interest are the anterior maxillary-premaxillary ligament and articular-dentary ligaments. The anterior maxillary-premaxillary ligament is similar to that of *S. sordidus*. It is short and thick, and possesses deep insertion sites, in contrast to that of *C. bicolor*. The articular-dentary ligaments, however, are identical to those of *C. bicolor*, reflecting the non-articulatory nature of the articular-dentary joint in the two species.

The overall form of *B. muricatum* is similar to that of *C. bicolor* and reflects the close relationship between the two species. However, many features tend towards the form found in 'sordidus' group species. This suggests that *B. muricatum* is more closely related to the 'sordidus' group than *C. bicolor* is, and may represent an intermediate form. These 'sordidus'-like

features include: the form of the anterior maxillary-premaxillary ligament, the maxillary fossa of the premaxilla and the articular-dentary joint, the presence of cement on the dental plates and the increased interdigitation of the medial tooth rows on the upper pharyngeal jaw bones.

Summary

1) The overall shape of *B. muricatum* is unusual with a deep body and bulbous protrusion on the head.
2) *B. muricatum* closely resembles *C. bicolor* and shares many features. These include:
   a) A non-articulating articular-dentary joint.
   b) No Alβ and Awγ.
   c) Teeth in a mosaic form with a crenate cutting edge.
   d) No lateral canines.
   e) Upper pharyngeals having three rows of teeth, the inner two of which are well-developed and do not interdigitate medially.
3) Several morphological features in *B. muricatum* show a degree of similarity with those of *S. sordidus*. The premaxillary process, maxillary fossa and the anterior maxillary-premaxillary ligament closely resemble the form in *S. sordidus*, whilst the layer of cement at the base of the dental plates and the form of the articular-dentary joint both tend towards a *S. sordidus*-like form.
4) *B. muricatum* has three unique morphological features:
   a) A rounded bump (tubercule) at the base of each tooth.
   b) Protrusions on the ethmoid and palatine dorsal process formed by a network of bony laminae.

c) A pair of anteriorly facing facets on the vomer.

1.3.7 *Hipposcarus longiceps*

Hipposcarus longiceps is a member of one of the most morphologically distinct genera of scarids, characterized by a protruding angular snout. *H. longiceps* is particularly interesting as it possesses many features in common with 'frenatus' group species, but lacks the diagnostic, strap-like A3 muscle. It has, in addition, several features which bear a closer resemblance to *Cetoscarus bicolor* or 'sordidus' group species than 'frenatus' group species. It is unusual in that it lacks the dorsal division of A1, A1β, which is present in both the 'sordidus' and 'frenatus' group species, but absent in *C. bicolor* and *B. muricatum*.

Osteology (Figs 1.18 C, 1.20, 1.21 A)

The suspensorium

The suspensorium (Fig. 1.20) bears a superficial resemblance to that of 'frenatus' group species. It is elongate, with a shallow adductor fossa, no dorsal thickening and has a protruding palatine dorsal process with an anteriorly facing maxillary condyle. The most characteristic feature is a shallow fossa near the anterodorsal edge of the dorsal notch. The suspensorium does, however, differ from 'frenatus' group species in several major features. As in *C. bicolor* and *B. muricatum* (Sections 1.3.6 and 1.3.7), it has a small dorsal notch and a palatine dorsal process that lies below the lower level of the orbit. The quadrate lateral ridge extends almost to the posterior extremity of the quadrate, and with the exception of a small anterior section, the ventral edge lies in a deep groove in the preoperculum. The groove formed by the quadrate lateral

ridge is deep and V-shaped compared with the broad and U-shaped groove in *C. bicolor*, 'sordidus' group species and some members of the 'frenatus' group.

The jaw apparatus

The maxilla and premaxilla

The maxilla (Fig. 1.20) resembles those of species in the 'frenatus' group (Figs 1.5 C, D). It has a well developed posterodorsal process on the maxillary arm, a well developed maxillary head with a complex articulatory socket, and a large medial premaxillary condyle. However, it possesses a small premaxillary process on the maxillary head as in *C. bicolor*, *B. muricatum* and 'sordidus' group species. A large but poorly developed cranial condyle is also present.

The form of the premaxilla (Fig. 1.20) is intermediate between that of 'frenatus' group species and *C. bicolor*. The overall appearance is similar to that of *C. bicolor* but it has several structural features closely resembling those of 'sordidus' and 'frenatus' group species. The ascending process is elongate but lacks the ventrolateral concavity found in *C. bicolor*. The alveolar process possesses a maxillary fossa of a similar size to that of *B. muricatum* or of 'sordidus' group species, but it has a more basic pit-like form as in *C. bicolor*.

When viewed anteriorly, the form of the anterior teeth of the premaxilla appears intermediate between those of 'sordidus' and 'frenatus' group species. Each vertical tooth row has a representative on the cutting edge but, because of the size of the

teeth, they have alternating prominence. The resultant irregularities are, however, reduced due to wear. Laterally, the teeth closely resemble those of 'frenatus' group species, with developmental rows at an angle to the cutting edge and a weakly scalloped cutting edge (Fig. 1.20). Towards the angle of the jaws, the teeth become distinctly angular and form a short, serrated row. Lateral 'canine' teeth are present in this region but are not as well defined as in *S. sordidus* or *S. frenatus*. They bear a close similarity to the angular teeth on the cutting edge and there appears to be some continuity between these two sets of teeth. The premaxilla has a cement covering over the dental plates, which is translucent white in colour. The overall appearance is similar to that of *C. bicolor*, but the structure is closer to that of 'sordidus' and 'frenatus' group species.

The articular and dentary

H. longiceps has an articulatory articular-dentary joint (Fig. 1.20) as in 'sordidus' and 'frenatus' group species. The articular most closely resembles that of 'frenatus' group species. It has a long, simple medial spine and a characteristic ridge on the dorsal edge of the ascending process. The dentary, however, more closely resembles that of *C. bicolor*, but is more elongate with the dorsal edge of the narrow lateral flange almost confluent with the cutting edge. It has a well developed angular process and the medial sutures have a single inflection. The teeth of the dentary are similar to those of *S. frenatus*, with the exception of those near the angle of the jaws which are weakly pointed, resembling the angular teeth on the cutting edge of the premaxilla. Each vertical

tooth row is represented on the scalloped cutting edge which may appear even due to wear. The dental plates are covered in cement as in the premaxilla.

The pharyngeal apparatus

The pharyngeal jaws bear a close resemblance to those of 'frenatus' group species. The upper pharyngeal bones have large medial tooth rows which interdigitate medially. Unlike the 'frenatus' group species, however, a third small outer tooth row is present on each upper pharyngeal bone. In the specimen examined, two teeth were present in each outer row (*cf.* seven in the inner two rows), with the relative widths of the teeth in each row being 7.1:2.9:1 from innermost to outermost.

The neurocranium (Figs 1.18 C, 1.21 A)

The form of the neurocranium is intermediate between that of *C. bicolor* and *S. sordidus*. The ethmoid-vomerine process bears a pair of distal maxillary condyles and is of a moderate length. The main body closely resembles the 'sordidus' and 'frenatus' groups in overall shape. Only one pair of fossae are developed on the ventral surface. The second pair of fossae which form the insertion sites for the external part of the levator posterior in *C. bicolor* and *B. muricatum* (No. 2 in Figs 1.18 A, B) are not developed. (Only a small depression is present). The facets of the basipharyngeal joint on the pharyngeal apophysis are straight.

Myology (Fig. 1.20)

The myology of *H. longiceps* is unusual. It has a superficial resemblance to *C. bicolor*, as it lacks the dorsal division of A1, the A1β, which is found in both 'sordidus' and 'frenatus' group species. Upon closer examination, however, the musculature bears a closer resemblance to members of the 'frenatus' group.

The adductor mandibulae

Section A1

Section A1 occupies the greater proportion of the superficial area of the maxillary fossa (Fig. 1.20). It is the largest adductor muscle and arises from the hyomandibula, metapterygoid, symplectic, preoperculum, and to a lesser extent, from a superficial tendinous layer covering part of the adductor muscle mass. The fibres are relatively long and weakly bipinnate in lateral section. The main insertion site is on the medial surface of the maxilla as in the 'frenatus' group, although an additional smaller tendinous insertion is present on the medial posterodorsal extremity of the dentary lateral flange. A small tendinous attachment is also present between the anterior medial surface of A1 and the anterodorsal surface of A2, similar to the connections found in some members of subgroup 'a' of the 'frenatus' group (Section 1.3.4.2). Unlike 'sordidus' and 'frenatus' group species, there is no A1β.

Section A2

Section A2 (Fig. 1.20) is the most ventral of the three main adductor muscles. It arises from the quadrate, has weakly pinnate fibres and has a tendinous insertion on the middle of the posterior

Figure 1.20

The head of a 329 mm S.L. *Hipposcarus longiceps* with the integument, nasal, lacrymal and circumorbitals removed.

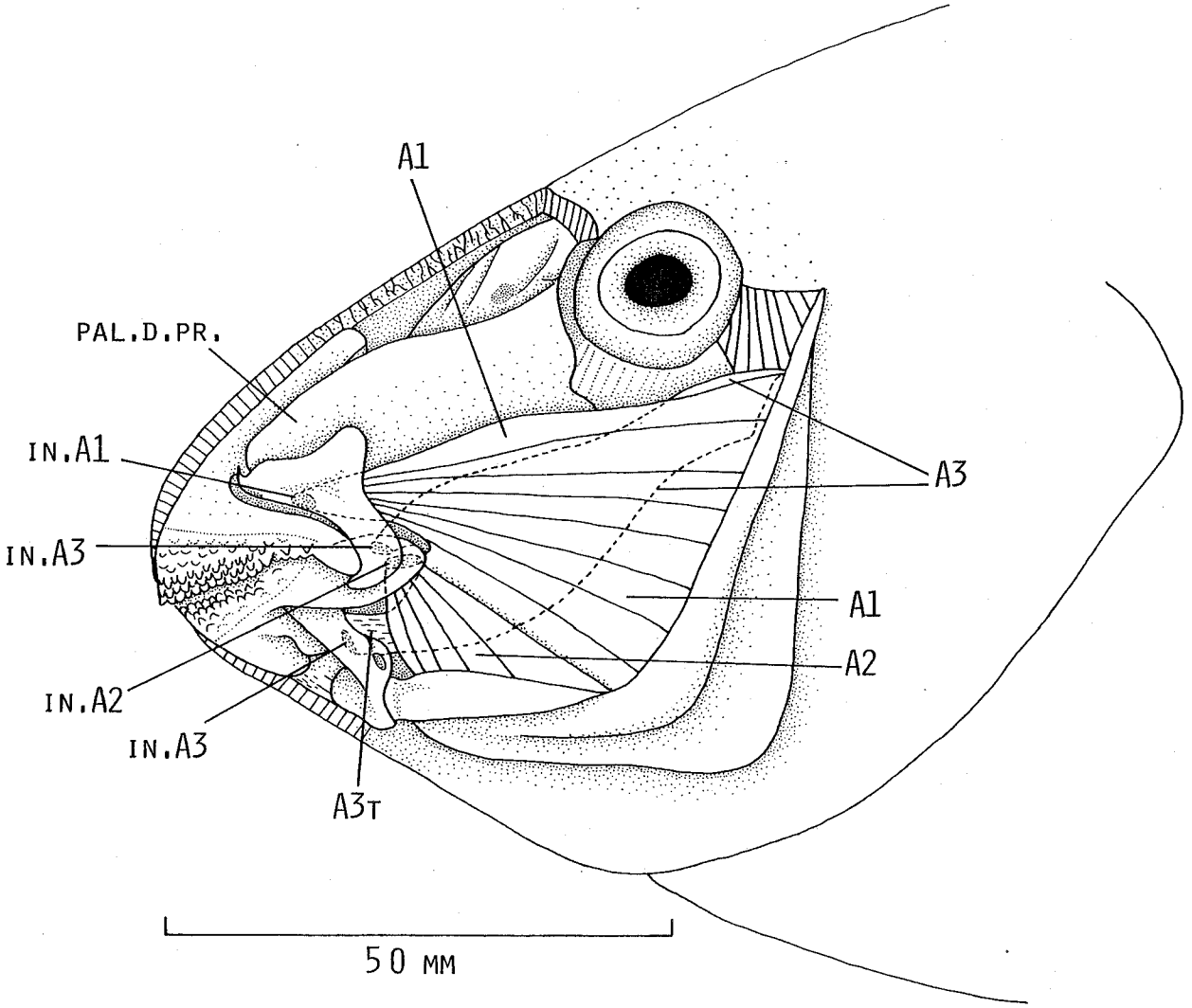

A1
PAL.D.PR.
IN.A1
A3
IN.A3
A1
A2
IN.A2
IN.A3
A3T
50 MM

Figure 1.21 A

A lateral view of the neurocranium of *Hipposcarus longiceps*.

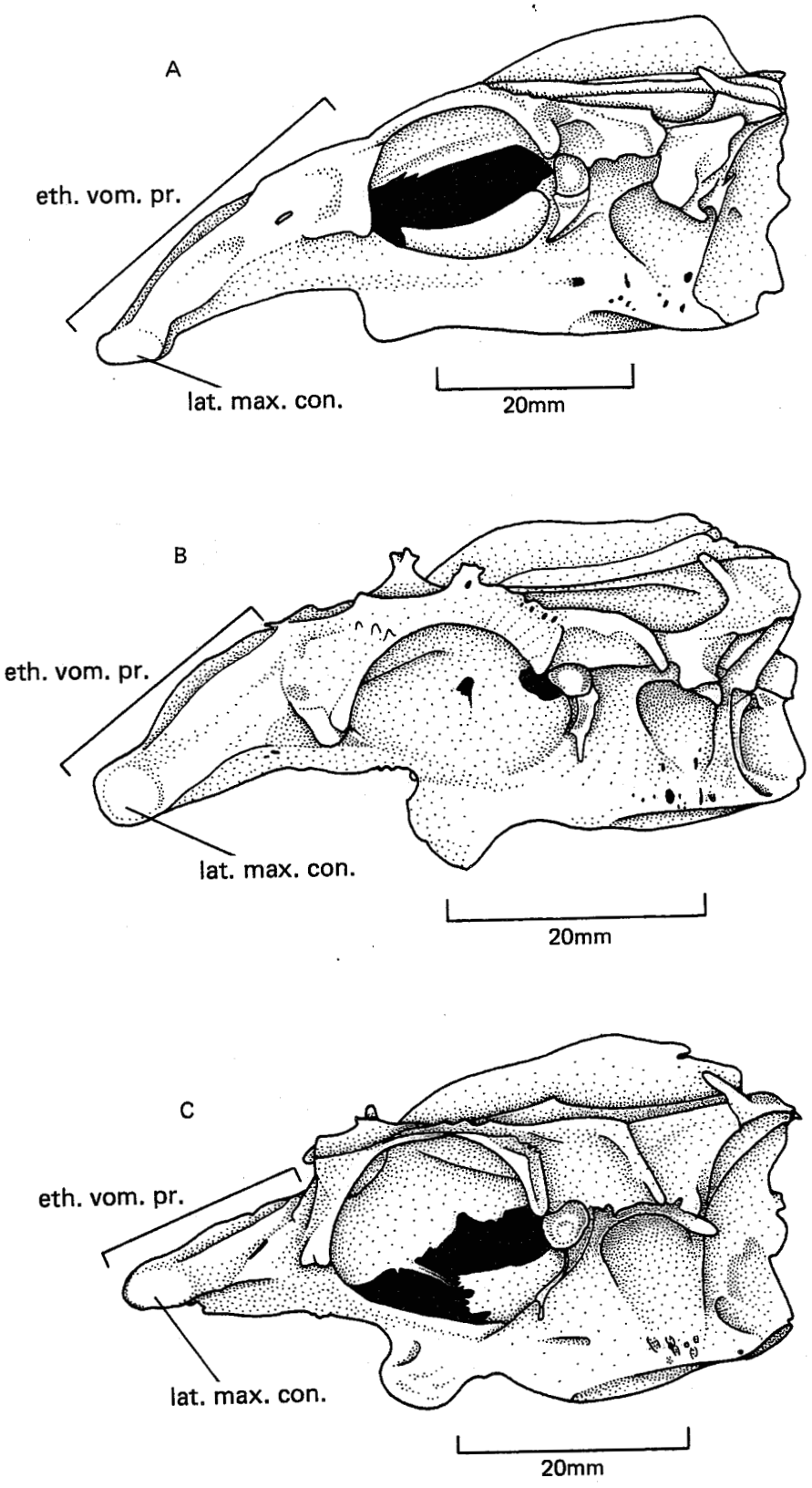
Figure 1.21 B

A lateral view of the neurocranium of *Scarus sordidus*.

Figure 1.21 C

A lateral view of the neurocranium of *Scarus frenatus*.

eth.vom.pr.	Ethmoid-vomerine process.
lat.max.con.	Lateral maxillary condyle of the ethmoid-vomerine process.


A
eth. vom. pr.
lat. max. con.
20mm
B
eth. vom. pr.
lat. max. con.
20mm
C
eth. vom. pr.
lat. max. con.
20mm

medial surface of the dentary lateral flange.

Section A3

H. longiceps differs most markedly from species in closely related genera in the form of section A3. In *H. longiceps*, section A3 is intermediate between *C. bicolor*, 'sordidus' group species and 'frenatus' group species. It is multipinnate as in *C. bicolor* and 'sordidus' group species, but is much smaller. It remains, however, larger than that of 'frenatus' group species. It arises from the quadrate, entopterygoid and hyomandibula, with two approximately equally sized tendinous insertions (Fig. 1.20). The dorsal insertion (A3α) is onto the dorsomedial surface of the dentary lateral flange, dorsal to the insertion of A2 and posteriorly adjacent to the dentary insertion of Awβ. The ventral insertion (A3β) is onto the medial surface of the articular ascending process and to the distal end of the articular medial spine.

The ventral insertion and associated fibres bear a strong resemblance to the A3 section of *S. frenatus* (Fig. 1.12 B). Likewise, the anterior fibres of the dorsal insertion bear a strong resemblance to the fibres in *S. frenatus*, designated as the remnants of A3α (*i.e.* the M. tendo-articulari-dentalis of Lubosch, 1929) (Fig. 1.14 B). In *H. longiceps*, these fibres are a part of a much larger sheet of fibres that extend along the dorsal segment of section A3.

Other muscles

An Aw section and an intermandibularis are present. The Aw has two divisions, Awα and Awβ. They arise and insert in a manner similar to those in members of the 'sordidus' and 'frenatus' groups, although the section Awβ 'a', as found in *S. frenatus*, (Fig. 1.14 B) is not present.

A small additional muscle is present, the quadrato mandibularis internus (*sensu* Lubosch, 1929), connecting the anterior medial surface of the quadrate to the connective tissue between the intermandibularis and Aw, near to the insertion of the intermandibularis. A similar muscle is present in *C. bicolor* and *B. muricatum*.

The pharyngeal musculature is indistinguishable from that of *S. frenatus* and other members of the 'frenatus' group.

Ligaments

The ligaments of *H. longiceps* are similar to those of *S. sordidus* and *S. frenatus*. The main differences are: a well developed ethmoid-entopterygoid ligament that joins the dorsal entopterygoid and lateral ethmoid and the form of the maxillary-premaxillary ligaments. These ligaments are of interest as they have a form intermediate between those of 'sordidus' and 'frenatus' group species.

The anterior maxillary-premaxillary ligament is longer and broader than in *S. sordidus* but narrower than in *S. frenatus*. The dorsal (premaxillary) insertion is on the dorsal and medial surfaces

of a groove along the ventral surface of the premaxilla. This groove is slightly wider than the corresponding groove in *S. frenatus* (Fig. 1.6 D), but not as wide as in *S. sordidus* (Fig. 1.6 C). The ventral (maxillary) insertion is on the middle and ventral edge of a depression directly below the medial facet of the premaxillary condyle, intermediate between the depression of *S. sordidus* (Fig. 1.5 B) and the ridge of *S. frenatus* (Fig. 1.5 D). The ligament has a more anterior position than in *S. frenatus* (Fig. 1.13 B) but not as far as in *S. sordidus* (Fig. 1.13 A). The overall appearance is similar to that of *S. frenatus* and, as in this species and other members of the 'frenatus' group, considerable movement between the two bones is possible.

The posterior maxillary-premaxillary ligament resembles that of *S. frenatus* (Fig. 1.13 B), but does not taper dorsally. The sites of insertion are the same as in *S. sordidus* and *S. frenatus*.

H. longiceps is unusual as it possesses many features which are common with *C. bicolor* (one of the least specialized scarine genera) and members of the 'frenatus' group (the most specialized scarine group). It has features in common with almost every genus or group. The main characteristics that link it to 'sordidus' and 'frenatus' group species are the form of the articular-dentary articulation and the pharyngeal mill.

Summary

1) The profile of the head of *H. longiceps* is unusual, with an angular protruding snout.
2) Many structures are intermediate between other genera and groups.

The most notable intermediates between *C. bicolor* and the 'frenatus' group are the suspensorium, premaxilla, dentary/articular and myology; between *C. bicolor* and the 'sordidus' group, the maxilla and neurocranium; and between the 'frenatus' and 'sordidus' groups, the premaxillary teeth, pharyngeal jaws and maxillary-premaxillary ligaments.

3) The articular-dentary joint articulates.

4) Caniform teeth are present on the cutting edge near the angle of the jaws.

5) Three rows of teeth are present on each upper pharyngeal bone. The two outermost are reduced, whilst the innermost rows interdigitate.

6) The A1β is absent and a quadrato-mandibularis is present.

1.4 Functional Implications

Scarids feed by biting or scraping algal covered coral rubble or live corals. This mode of feeding is dependent upon the possession of several morphological specializations. Bruce (1979) observed considerable morphological variation within the family Scaridae and noted that, in some cases, the observed feeding behaviour may be correlated with morphological specializations.

From the preceding morphological descriptions, there are two distinct morphological types within the subfamily Scarinae, typified by the 'sordidus' and 'frenatus' groups. These morphological variations not only divide the types in terms of structure but also in terms of function and, as such, divide the species into two functional groups, the 'biters' and the 'scrapers'.

1.4.1 'Sordidus' group species as 'biters'.

The morphological structures characteristic of 'sordidus' group species are consistent with the features that are necessary for biting the substratum. Structures that one would associate with this type of feeding strategy are all found in 'sordidus' group species, *i.e.* powerful musculature, uneven cutting edges to localize forces, articulatory systems to maximise localized forces, and strong supportive structures to withstand the forces exerted during feeding.

The supportive structures in 'sordidus' group species are notably stronger than in 'frenatus' group species. This is shown by: the more intimate junction between the quadrate and preoperculum, the development of a large quadrate lateral ridge, an

entopterygoid lateral process, the thickened dorsal ridge along the metapterygoid and entopterygoid, and the short, stout palatine dorsal process. The maxilla and articular are both robust and the premaxilla and dentary both possess deep dental plates. In addition, the dentary has a well developed lateral flange and a large number of complex medial sutures. All of these features assist 'sordidus' group species to withstand the strong forces experienced during feeding.

The form of the articulatory systems in 'sordidus' group species serves to both withstand the forces exerted during feeding and enhance the localized biting forces. The maxilla and premaxilla are tightly bound to each other by the maxillary-premaxillary ligaments, with the two bones interlocking where the premaxillary process of the maxilla inserts into the maxillary fossa of the premaxilla. These two bones, therefore, act almost as one, increasing the strength of the upper jaw and avoiding a weak point of articulation between the distal ends of the premaxillary alveolar process and the maxillary arm. The articulation of the upper jaw is simple with a single rounded concavity on the maxillary head rotating against the stout palatine maxillary condyle. This joint is strong and is likely to have a relatively consistent ability to withstand stress when compared to the more complex joint found in 'frenatus' group species. In addition, the well developed articulation between the maxilla and vomer (between the cranial and maxillary condyles, respectively) will further assist in withstanding the forces experienced during the articulatory movements of the upper jaw.

The lower jaw articulation between the quadrate and articular, and the articulation between the articular and dentary are similar in both 'sordidus' and 'frenatus' group species. However, the 'sordidus' group species possess stronger components, a deeper articulation socket, and most importantly, a larger in lever : out lever ratio about the articulo-dentary joint (Fig. 1.22 A). Thus for any given force exerted by the muscles on the dentary, the force exerted upon the substratum will be approximately 25% greater in *S. sordidus* than in *S. frenatus*.

In 'sordidus' group species, the teeth are relatively large and strong, with little evidence of wear. The low number of rounded teeth on the cutting edge makes the jaws inefficient for scraping surfaces. It does, however, enable the jaws to localize the force in several discrete points. As coral and coral rubble have a brittle crystalline stucture (Barnes, 1970), these localized stress points will help fracture or crack the substratum.

The jaw musculature in 'sordidus' group species has many features that are well suited to a biting feeding strategy. The three main adductor muscle blocks A1, A2 and A3 are all well developed, with the deep subdivision A1β and part of A3 both possessing specialized sites of origin on the entopterygoid. These specialized sites and the deep adductor fossa help to accommodate the large adductor muscle blocks. The superficial subdivision of A1β and A2 likewise have well developed sites of origin, on the dorsal ridge of the entopterygoid and palatine and in a dorsal groove formed by the quadrate lateral ridge, respectively. The 'sordidus' group possesses an important additional muscle, the Awy.

Figure 1.22 A

The dentary of *S. sordidus* showing the theoretical forces acting upon the dentary during muscle contraction.

The action of the dentary approximates that of a simple lever pivoting about the articular in the articulatory socket. In a lever, the forces are governed by the following equation:

$$Fi \times Li = Fo \times Lo$$

where

Fi = The force acting upon the inner part of the lever (*i.e.* the muscle force)
Fo = The force acting upon the outer part of the lever (*i.e.* the force of the dentary cutting edge upon the substratum or vice-versa)
Li = The length of the inner part of the lever
Lo = The length of the outer part of the lever

In *S. sordidus*, Li/Lo = 0.85, whilst in *S. frenatus*, Li/Lo = 0.68 (each value is a mean of four TP specimens). As the action of the dentary approximates that of a simple lever system, the force exerted upon the substratum (Fo), for a given muscular force (Fi), will be approximately 25% greater in *S. sordidus* than in *S. frenatus*.

Figure 1.22 B

A diagramatic figure describing the relationship between the angle of a muscle and its mechanical efficiency.

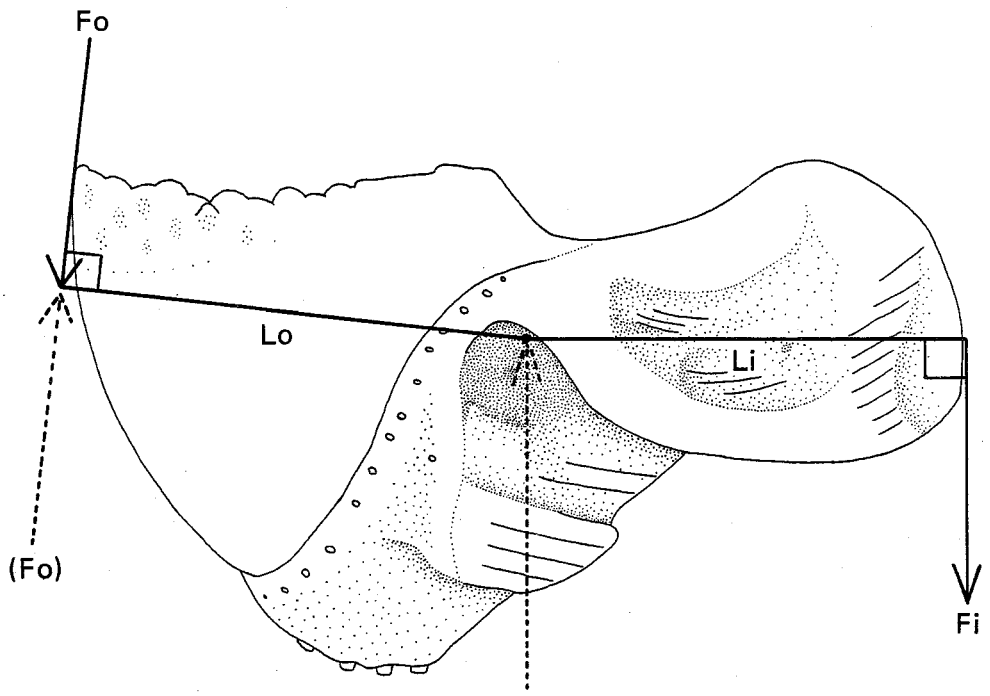
At angles below 90°, the force of a muscle or muscle fibre (in this example, the A1) can be divided into two components: one at 90° to the limb being rotated, the other at 90° to the first component. The first component results in useful work, rotating the limb, whilst the second component results in unproductive work. The proportion of unproductive work increases as the angle of the muscle decreases. The size of the component which results in useful work can be calculated using the following equation:

$$UF = TF \cos. \theta$$

where

UF = The component which results in useful work
TF = The total force exerted by the muscle
θ = The angle of the muscle to the limb being rotated

A

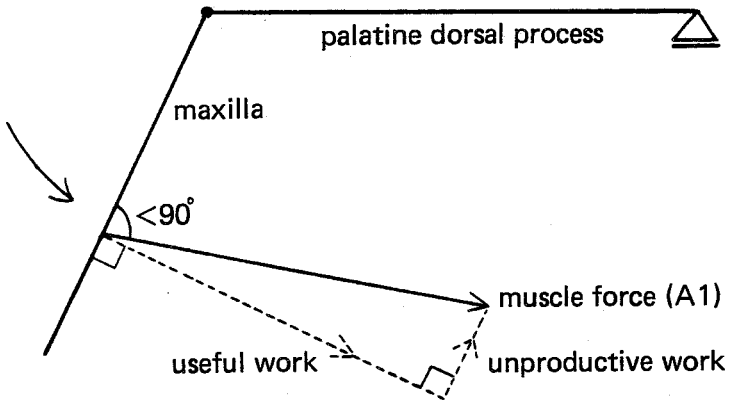


$Fi \times Li = Fo \times Lo$

S. sordidus $Fo = 0.85 \times Fi$

S. frenatus $Fo = 0.68 \times Fi$

B



This muscle is small, but it is in a good position to adduct the dentary, particularly with the increased leverage potential of the articular-dentary joint in 'sordidus' group species.

The orientation of the major muscle blocks in 'sordidus' group species differs from those of 'frenatus' group species. To maximise the force realized when rotating a bone about a fixed articulation, the main muscular force is ideally perpendicular to the rotating bone (Fig. 1.22 B). In 'frenatus' group species, the main adducting force is created by a single muscle block, the Alα/A2. The angle of the tendons and fibres within this system must, therefore, be a compromise between the optimal requirments of each part of the jaw. In the 'sordidus' group, however, the main adducting force is shared between three muscle blocks, Alα, A2 and A3α. Although the connection between the dentary and maxilla means that no muscle can be considered in isolation, the separation of the muscles permits each to work at an angle approaching the optimal angle for that part of the jaw which it rotates. Thus Alα is approximately perpendicular to the maxilla, A2, to the dentary and A3α, to the articular. The result is likely to be an overall increase in the force applied by the jaws, although the maximal force will only be available in one jaw position.

The function of Alα, A2 and A3α is to close the jaws during feeding. Alβ, A3, A3β and Awα, Awβ and Awγ will also close the jaws during the main bite but, because of their size and/or position, will contribute only a small proportion to the total force exerted during the closure of the jaws. They may, however, play an important role in the final closure of the mouth. The function of

A3 was described by Lubosch (1923, 1929) (in specimens now placed in the 'frenatus' group) as a "living tendon" serving to fix the articular against the dentary and quadrate, ensuring that the isolated bones of the lower jaw are able to function as a single unit at any angle. This function is herein attributed to both the A3 of 'frenatus' group species and the A3β of 'sordidus' group species.

Depending upon the orientation of the muscle fibres, there are two extreme muscle forms, pinnate or parallel, with a complete gradation between the two. In pinnate muscles, the fibres converge on a central axis (usually a tendon), whereas in parallel muscles, the fibres lie parallel to each other (Fig. 1.23). Both types are present in 'sordidus' group species. Sections Alα, A2 and A3 are strongly pinnate, whilst Aω, Alβ and the intermandibularis are parallel.

The properties of pinnate and parallel muscles have been described briefly by Winterbottom (1974 b) and Liem (1977), and in detail by Gans and Bock (1965). Parallel muscles have maximum excursion and can be arranged in thin sheets, whereas pinnate muscles are able to insert onto restricted sites on small bony elements by attaching to a narrow tendon. This ability is essential for the formation of optimal lever systems. Pinnate muscles can also be accommodated in restricted spaces and may, by asymmetric contraction, be able to move the tendon in two planes.

Theoretically, however, there are two disadvantages associated with pinnate muscles. Firstly, the effective force exerted in the direction of the tendon is only a proportion of the force exerted by

the fibres (Fig. 1.23). The force developed by a fibre in a pinnate muscle can be resolved into two components, one in the direction of the tendon, the other at 90° to this. Only the former results in effective work, the latter force which increases disproportionately as the angle of pinnation increases, is lost as unprofitable work (Fig. 1.22 B). Secondly, the range of excursion (*i.e.* the distance over which the muscle can work) is decreased in a pinnate muscle (Fig. 1.23). It must be noted, however, that for a given contraction of the fibres, the tendon will have a relatively greater excursion, although the range of excursion is reduced (Liem, 1977).

It appears initially that in 'sordidus' group species there has been a compromise between the main advantage of pinnate muscles *i.e.*, the localization of muscular forces, and the inherent weakness of the pinnate system. The only parallel adductor muscles are sections Aw and Alβ. These muscles are short and are present in areas where space for insertion is either unlimited or as large as the muscular site of origin.

The advantages of localized insertions may be the primary reason for the pinnate muscle system in 'sordidus' group species, although such advantages can also be realized in a weakly pinnate system as in 'frenatus' group species. It is therefore proposed that the strongly pinnate muscles found in 'sordidus' group species are adapted to deliver a powerful, cracking bite, with a minimal movement but with a large force which can fracture the brittle (crystalline) substratum (Fig. 1.23).

Figure 1.23

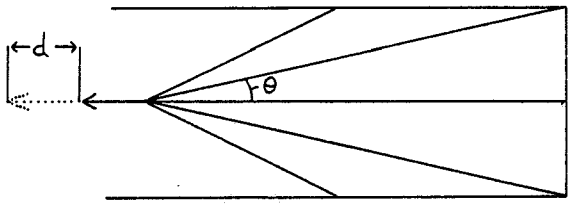
A diagramatic figure describing the properties of muscles with weakly pinnate or strongly pinnate fibres.

This figure describes muscles with weakly or strongly pinnate fibres. The properties of the weakly pinnate muscle approaches that of a parallel fibred muscle. In a parallel fibred muscle, the excursion of the tendon (d) is equal to the contraction of the fibres, and the force to the tendon (F) is equal to the force from the fibres. The calculations in this figure are based on the principles outlined in Figure 1.22 B. The effect of different angles of pinnation of the fibres in a muscle can be summarized as follows:

Fibre orientation:	Weakly pinnate or parallel	Strongly pinnate
Excursion of tendon (d)	Large	Small
Force exerted by tendon (F)	Larger	Smaller
Force per unit distance (F/d)	Small	Large

Figure 1.23 The mechanics of pinnate and parallel muscles.

A Weakly pinnate fibres *e.g. S. frenatus*

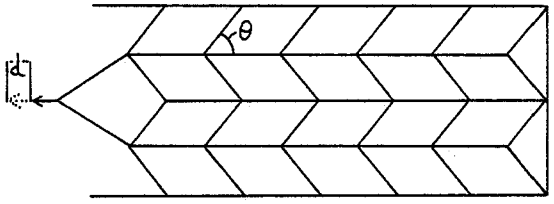


θ = 15°
mean fibre length = 40 mm
force from fibres = 10 units

force to tendon (F) = 9.66 units (10 cos. θ)
contraction of fibre = 4 mm
excursion of tendon (d) = 4.14 mm (4/cos. θ)

=> force per unit distance (F/d) = 2.33 units/mm

B Strongly pinnate fibres *e.g. S. sordidus*



θ = 40°
mean fibre length = 8 mm
force from fibres = 10 units

force to tendon (F) = 7.66 units (10 cos. θ)
contraction of fibre = 0.8 mm
excursion of tendon (d) = 1.04 mm (0.8/cos. θ)

=> force per unit distance (F/d) = 7.34 units/mm

θ = mean angle of fibres throughout contraction

Assumptions:

1) the fibres contract by 10 % of their total length and that they exert an even tension (force) throughout this period.
2) both systems have the same weight of muscle and the fibres in these muscles are capable of exerting the same force = 10 units.
3) the space available is the same in the two systems.

The disadvantageous limitation of the excursion range in pinnate muscle systems becomes an advantage when one considers a cracking bite. By having many fibres arranged in pinnate layers, a thin layer of muscle can be used to deliver a powerful force with little tendinous excursion. A parallel muscle occupying the same narrow space would result in a far larger tendinous excursion, and although the force is greater, the force per unit distance moved by the tendon is much smaller (Fig. 1.23). The benefit of a pinnate muscle of a greater force per unit distance will therefore outweigh the problem of a decreased force due to fibre orientation. This is particularly significant when the space available is limited, for example, to the adductor fossa.

The overall function of the morphological features found in 'sordidus' group species is in concordance with one capable of delivering a short, powerful bite, which cracks rather than scrapes the substratum. It is therefore proposed that the 'sordidus' group species are functional 'biters'.

1.4.2 'Frenatus' group species as 'scrapers'.

The morphology of species belonging to the 'frenatus' group differs considerably from that of members of the 'sordidus' group. The characteristics of 'frenatus' group species strongly suggest a feeding mode which involves a scraping the substratum. Morphological features leading to this suggestion include: a jaw structure that maximises the degree of contact between the cutting edges of the jaws and the substratum, an articulatory and muscular system that maximises the jaw movement for a minimal muscular effort and, wherever possible (to minimise energetic and hydrodynamic

costs), osteological and myological structures that are reduced or streamlined. The comparisons made in this section are between species in the 'sordidus' and 'frenatus' groups only, and do not include other members of the family.

The suspensorium of 'frenatus' group species is lighter than that of 'sordidus' group species. The quadrate typically has a loose association with the preoperculum and has a small lateral ridge. The overall adductor fossa is shallow with only a slight degree of thickening along the posterodorsal edge of the metapterygoid, entopterygoid and palatine, and only rarely possesses additional protrusions (as in *S. spinus*). The palatine dorsal process is elongate with a more terminal maxillary condyle. This permits protrusion of the jaw and greater mobility of the palato-maxillary joint.

The relative mobility of the premaxilla is far greater in 'frenatus' group species than in 'sordidus' group species. This is evident in the mobility permitted by the anterior maxillary - premaxillary ligament and the large, elongate maxillary facet on the premaxilla. There is no interdigitation between the two bones which articulate at the distal end of the premaxillary alveolar process and maxillary arm. The ability to protrude the premaxilla relative to the maxilla and the lack of excessive mechanical stress during feeding are further supported by the reduction in the articulatory surfaces between the maxilla and neurocranium (*i.e.* vomer) and the relatively weak, but highly mobile, maxillary - palatine joint. This joint is complex and results in a large downward movement of the tip of the premaxilla for a correspondingly small degree of

posterior movement of the maxilla, resulting in an effective scraping movement.

The dentary and articular differ little from those of 'sordidus' group species but as in *S. frenatus*, they are both of a lighter form. The dental plates of the dentary and premaxilla are relatively shallow and frequently protrude. As such, these structures are capable of a scraping bite but lack the strength for a powerful bite. In addition, the articular-dentary system of 'frenatus' group species has a smaller in lever : out lever ratio. This results in a greater movement of the dentary. Although this movement is weaker, it is suitable for scraping, where strength is less important than the distance moved.

The tooth structure of 'frenatus' group species is likewise well adapted for scraping the substratum. The presence on the cutting edge of one tooth from each vertical tooth row and the shape of the individual teeth ensure that the cutting edge is relatively even. This increases the area of contact between the cutting edge and the substratum. The broad tooth shape, its susceptibility to wear, and the lack of interdigitation between vertical tooth rows help to maintain the even cutting edge but weaken the overall structure.

As seen in 'sordidus' group species, the form of the muscles can have important functional implications. The 'frenatus' group possesses both parallel (intermandibularis, Aw and Aiβ) and pinnate (Aiα A2 and A3) muscles. With the exception of Awγ, which is absent, the parallel muscles of 'frenatus' group species are almost identical to those of 'sordidus' group species, and are likely to

have similar functions. The structural similarity is presumably a result of comparable restrictions upon the muscle length and the size of the insertion sites in the two groups. The form of the primary adductor muscle block(s) of 'frenatus' group species, however, differs from that of 'sordidus' group species. (The role of A3 as a "living tendon", maintaining the articular in the lower jaw articulatory system has been discussed already [Section 1.3.3]).

The weakly pinnate nature of the major adductor muscle block(s), Alα, A2 or Alα/A2 is in accord with the requirements of a scraping feeding strategy. The pinnation of the muscles is necessary because of the need to localize forces by the insertion of narrow tendons onto restricted optimal sites. However, it is advantageous to minimise the degree of pinnation in order to avoid the inherent 'problems' associated with a pinnate structure, (*i.e.* decreased efficiency and reduced extension) which increase disproportionately with the angle of pinnation. The large excursion characteristic of parallel (or weakly pinnate) muscles is desirable in a scraping scarid where the requirement is for a prolonged, weaker force rather than a brief, powerful contraction. These muscles are required to move the jaws over the substratum efficiently and for a scraper, a strong bite would be inefficient in terms of material collected when compared to several relatively weak bites.

The evidence used to define the 'frenatus' group as scrapers applies equally well to species in both subgroup 'a' and subgroup 'b'. The presence of a separate Alα and A2, and a type I intestinal pattern in members of subgroup 'a' (Section 1.5) may be correlated

with their more elongate body form (as in juvenile scarids, Section 2.3). The elongate body form is particularly marked in *S. flavipectoralis*, and to a lesser extent, *S. schlegeli*. The combination of an elongate body, separate Alα and A2, weak osteological structures, protruding, easily worn premaxilla, and shallow dentary are all indicative of a relatively weak scraping ability, which may be reflected in the feeding strategies of the species in subgroup 'a'.

The functional advantage of a fused Alα and A2 is not immediately obvious, and appears to be related to the form of the adductor fossa. However, the fusion can be explained in terms of optimal muscle fibre orientation. During adduction of the jaws, the angles of the main muscular force of Alα and A2 are only approximately perpendicular to the bone that is being rotated. The force applied to the rotating bone can be resolved into two vectoral components, the first, perpendicular to the rotating bone, results in useful work, whilst the second, at 90° to the first is lost as unproductive work (Fig. 1.22 B). In Alα, the main loss of force is in a posterodorsal direction. In A2, the complex articulation and variability in fibre direction make the major loss of force difficult to estimate. However, any posteriorly directed force from A2, if transferred to Alα, will be of some use; conversely, the posterodorsal force from Alα is of benefit if transferred to A2. The fusion of the two muscle blocks may therefore, facilitate the transfer of unproductive forces, *via* an interconnecting tendon, from one muscle block to the other, where such directional forces are capable of useful work.

The functional abilities of the morphological features of 'frenatus' group species strongly suggest a 'scraping' feeding strategy, with weak bites that scrape rather than bite the substratum. It is therefore proposed that 'frenatus' group species are functional 'scrapers'.

1.4.3 *Cetoscarus bicolor* and *Bolbometopon muricatum*

Much of the evidence supporting the hypothesis that 'sordidus' group species are 'biters' applies equally well to *Cetoscarus bicolor* and *Bolbometopon muricatum*. The jaws and suspensorium closely resemble those of 'sordidus' group species, the adductor mandibulae are strongly pinnate and the crenate cutting edge of the jaws are suited to a biting strategy. Both species, however, lack many of the derived characters found in members of the 'sordidus' group (Chapter 3), some of which play an important role in the biting mechanism. These include the lateral process of the entopterygoid, Awγ, Alβ and the articulatory articular-dentary joint. These species, although functional 'biters' may therefore be regarded as 'proto-biters'.

It is interesting to consider the function of the hump on the forehead of *B. muricatum*. Several explanations have been forwarded previously: some popular books have reported this species ramming coral heads to break them open (cited in Bruce, 1979); Wheeler (1975) stated that the gristly hump is usually abraded suggesting that it is pressed against the coral or rock whilst the fish is grazing, and Bruce (1979) suggested that the hump may act as a counterbalance during feeding.

In the present study, *B. muricatum* were not observed breaking corals open with the hump nor were they observed to press the hump against the substratum during grazing. Few of the specimens observed had abrasions on the anterior face of the hump. The abrasions recorded by Wheeler (1975) may have been caused by the means of capture. The counterbalance effect proposed by Bruce (1979) is questionable in view of the large proportion of time that *B. muricatum* is not actively feeding, when such a protrusion would be unproductive and increase the overall energetic costs of maintenance. In addition, the gristly hump has a density only slightly greater than seawater (pers. obs.) and relative to the total weight of the animal, the potential counterbalance effect of the hump is likely to be minimal.

Humps comparable to that of *B. muricatum* are present in a wide range of species, including: *S. gibbus*, *S. perrico*, *S. cyanescens*, *S. frontalis*, *Ypsiscarus oedema* (Snyder) and *Y. ovifrons* Temminck and Schlegel in the Scaridae; *Cheilinus undulatus* Rüppel, *Bodianus diplotaenia* (Gill), *Semicossyphus reticulatus* (Valenciennes), *Coris bulbifrons* Randall and Kuiter and *Coris aygula* Lacepède in the Labridae, and *Haplochromis moorii* (Boulenger) in the Cichlidae.

All these species have several factors in common. They are large with respect to confamilial species, with a deep body and a mouth below the midline, they all swim slowly in a labridiform manner relying primarily upon the pectoral fins for propulsion (see Blake, 1981) and they have a bony pharyngeal apparatus. In all cases, the hump increases in relative size with growth. All the above species have a potential swimming problem. The deep body and

ventral mouth produce a long sloping forehead, which will force the head down when swimming. This problem is further enhanced by the weight of the jaws (in scarids) and the pharyngeal apparatus, and the labridiform swimming motion which minimises sinusoidal movements. The ventrally directed force on the head will increase disporportionately with growth as the relative size of the forehead increases in large individuals (as demonstrated in the figures of *B. muricatum* in Smith [1956]). The relative importance of this ventrally directed force is also likely to change with growth due to changes in the form drag (friction) and the surface area to volume ratio. This 'nose diving' due to the ventrally directed force on the forehead can either be counteracted by increasing the uplifting effect of the pectoral and pelvic fins or alleviated by altering the profile of the forehead. The former, active technique is thought to be more energetically expensive than the latter passive technique.

From a consideration of the above factors, it is suggested that the hump in *B. muricatum* and the other species has a hydrodynamic function. A hump results in a more vertical profile and will therefore decrease the ventrally directed force on the forehead. In some species where the hump protrudes, it may even provide a small vertically directed force. The hydrodynamic function of the hump is supported by its gristly nature, its density which is only slightly greater than sea water and the limited bony supporting structures. The areolar development of the ethmoid in *B. muricatum* presumably provides a broad site of attachment for the unusually large hump. The elongate horn on the forehead of relatively fast swimming *Naso* species (including *N. brevirostris* Valenciennes, *N. rigoletto* Smith, *N. unicornis* Forsskål and *N. annulatus* [Quoy and Gaimard]) may have

a similar function. The function of the hump may be resolved by flow tank experiments using models or fresh specimens with or without the hump.

1.4.4 *Hipposcarus longiceps*

H. longiceps has an intermediate structure between that of 'sordidus' and 'frenatus' group species. It shares with the 'frenatus' group a weakly pinnate A1 and A2, a complex palatine-maxillary articulation and a tooth from each vertical tooth row on the cutting edge. These features strongly suggest a scraping strategy. However, *H. longiceps* possesses several characters in common with 'sordidus' group species, *C. bicolor* and *B. muricatum*, although these characters are either modified or of limited functional significance, *e.g.* the form of section A3 and the presence of a maxillary-premaxillary process. Because of the presence of important functional characters associated with a 'scraping' strategy, *H. longiceps* is regarded as a functional 'scraper', although the presence of several ancestral characters (Chapter 3) may suggest a less well specialized scraping ability when compared to species in the 'frenatus' group. *Hipposcarus longiceps* may therefore represent a more primitive scraper or 'proto-scraper'. This functional status is likely to be shared by other *Hipposcarus* species.

1.4.5 The pharyngeal apparatus

The primary function of the pharyngeal apparatus in scarids is the trituration of ingested matter. 'Sordidus' and 'frenatus' group species have a similar pharyngeal morphology and presumably,

therefore, similar functional abilities. The small differences in the form of the jaws may, however, be related to differences in the size of ingested particles. For example, 'sordidus' group species have relatively strong robust pharyngeal jaws that are suited for grinding the large particles that are likely to result from a 'biting' strategy. In contrast, species in subgroup 'a' of the 'frenatus' group have a weak pharyngeal musculature and osteology but a large lower pharyngeal tooth plate. Although such a system has little grinding or crushing power, it can efficiently triturate material containing small carbonate particles resulting from a 'scraping' strategy. These particles require little crushing, but remain highly abrasive. Species in subgroup 'b' of the 'frenatus' group have a form intermediate between that of species in the 'sordidus' group and subgroup 'a' of the 'frenatus' group and, presumably, have an intermediate function.

In comparison with the 'primitive' labrid-like scarids (*e.g. Cryptotomus, Calotomus* and *Nicholsina*), *Scarus* species have large lower pharyngeal tooth plates. This may be a reflection of the shift from a diet consisting primarily of algal fragments to one with a high proportion of particulate carbonate material. In the labrid-like scarids, a powerful chopping or crushing action would be ideally suited for processing ingested material which includes a large proportion of algae or plant fragments (Suyehiro, 1942 and Bruce, 1979). The small area of contact between the pharyngeal jaws would enhance the chopping or crushing action by increasing the force per unit area between the two jaws. In *Scarus* species, the ingested material is composed of much smaller filamentous or turf algae and a high proportion of calcareous material (Choat, 1969,

Bruce, 1979 and pers. obs.). A chopping or crushing action would be less efficient in this situation than a fine grinding action utilizing the calcareous particles as an abrasive. Such a system would benefit from an increased area of contact between the two opposable grinding surfaces, and may account for the increased area of the lower pharyngeal tooth plate and the form of the musculature found in *Scarus* species.

The pharyngeal jaws of scarids and labrids are strikingly different in both their osteology and myology. The tooth plates of the pharyngeal jaws of labrids are broad and short, with variable tooth forms which may be related to food types (Randall & Springer, 1973 and Yamaoka, 1978). The myology of the pharyngeal jaws of labrids is variable but differs markedly from that of scarids in the degree of development of the retractor pharyngeus superior (= retractor dorsalis), levator posterior and fourth levator externus. In scarids, the latter is particularly well developed, whereas, the former two muscles are relatively well developed in labrids (Yamaoka, 1978, 1980 and pers. obs.).

The observations in this study concur with the functional implications of the pharyngeal apparatus in scarids proposed by Yamaoka (1980), who suggested that the increased importance of the fourth levator externus of *Calotomus japonicus* may be related to the angle of the pharyngeal dental plates, which in turn may be related to the herbivorous, rather than carnivorous nature of scarids.

These differences between the scarids and labrids are interpreted here as the result of dissimilar food types and processing requirements. In labrids, the food is ingested as

discrete and often large pieces that require crushing and/or tearing prior to digestion. Hence, the importance of the levator posterior as a strong 'crushing' muscle and the retractor pharyngeus superior which facilitates both transport (Yamaoka, 1978) and possibly, tearing of ingested material. It is proposed that in labrids, the action of the pharyngeal jaws during feeding consists of a basic raising of the lower pharyngeal jaw (crushing) by the levator posterior, followed by a caudally-directed movement of the upper pharyngeal jaw (tearing) by the retractor pharyngeus superior. This action may, in part, be maintained in some primitive labrid-like scarids that feed on macroalgae and/or angiosperms. *Calotomus japonicus*, for example, has a retractor pharyngeus superior that arises from the first five vertebrae, as in many labrids (first four, in some species) (Yamaoka, 1978, 1980). In comparison, the genera examined in this study, possessed a retractor pharyngeus superior (retractor dorsalis) which arose only from the first three vertebrae. In addition, the fourth levator externus of *Calotomus japonicus* is smaller than that of *Scarus* species, whilst the levator posterior is larger. Both features are typical of the labrid pharyngeal apparatus (Yamaoka, 1978).

In scarids, especially *Scarus* species, a more complex grinding movement of the pharyngeal jaws is proposed, where the lower pharyngeal jaw is forced against the upper pharyngeal jaw with a swinging anterior movement accompanied by a slight caudal movement of the upper pharyngeal jaw. This results in a substantial degree of contact between the two jaws as they pass over each other. The levator posterior is able to maintain pressure between the two jaws but because of the angle of the upper pharyngeal tooth plate, it

does not facilitate a grinding action as it restricts the anterior movement of the lower pharyngeal jaw. A grinding action requires an anteriorly directed movement of the lower pharyngeal jaw, which probably accounts for the increasing importance of the fourth levator externus and decreasing importance of the levator posterior in scarids. These changes were noted in *Calotomus* by Yamaoka (1980) and are particularly notably in *Scarus* species (Section 1.3.3).

A grinding action of the pharyngeal apparatus with a swinging movement of the lower pharyngeal bone is supported by the differential development of the scarid pharyngeal musculature. The fourth levator externus, fifth adductor, second transversus ventralis and obliquus dorsalis are all well developed. The former three muscles adduct the pharyngeal bones whilst facilitating an anterior movement of the lower pharyngeal bone. The obliquus dorsalis draws the upper pharyngeal bones caudally producing a shearing movement of the upper pharyngeal bone against the lower pharyngeal bone. It will also give an anteriorly directed force to the fourth epibranchial which may be transmitted *via* the fifth adductor to the lower pharyngeal bone (Figs 1.15 A, B).

The decreased development of the levator posterior and the retractor pharyngeus superior likewise reflect a grinding action of the scarid pharyngeal apparatus. Although the levator posterior is the strongest crushing muscle in labrids (Yamaoka, 1978), it would impede the swinging abilities of the lower pharyngeal bone in scarids. The decreased relative size of this muscle, therefore increases the swinging abilities of the lower jaw. The decreased size, however, also reduces the crushing abilities of this muscle,

and may account for the increased size of the second major crushing muscle, the fourth levator externus. The reduced size of the retractor pharyngeus superior may be a result of a modified function, as it is no longer required to tear or transport material, merely to move the upper pharyngel bones over the lower pharyngeal bones. This movement is aided by the obliquus dorsalis, the second transversus ventralis, the wedge-shaped upper pharyngeal bones, the decreased crushing power, the rows of even rounded pharyngeal teeth (rather than conical or molariform teeth as in labrids [Yamaoka, 1972]), a mobile lower pharyngeal bone, and the nature of the material ingested.

The antagonistic muscles in the proposed grinding action are the transversus dorsalis posterior and the third levator externus (on the upper pharyngeal bones) and the pharyngocleithralis internus and externus (on the lower pharyngeal bone). It is proposed that the abduction of the pharyngeal tooth plates to admit material for grinding is primarily associated with the pharyngocleithralis internus and externus (and therefore the associated muscles of the cleithrum), with the levator posterior assisting in the rotation of the lower pharyngeal bone about the pharyngocleithral joint. This action is comparable to the protraction-abduction phase of the generalized cichlid mechanism described by Liem (1973). The relatively weak form of the pharyngocleithral joint irrespective of the feeding type and its presence in labrids, suggests a role in the opening of pharyngeal jaws rather than in the crushing phase.

An intermediate stage between the labrids and *Scarus* may be found in the more 'primitive' scarids, *e.g. Calotomus*, *C. bicolor* and *B. muricatum*, which retains a relatively well developed levator posterior. In *Calotomus*, it is of an intermediate size between labrids and *Scarus* (Yamaoka, 1978, 1980 and Section 1.3.3), whilst in *C. bicolor* and *B. muricatum*, it is slightly larger than in 'sordidus' group species, with a well developed anterolateral section arising from a specialized triangular fossa in the base of the neurocranium. All three species resemble *Scarus* (especially the 'frenatus' group form) in the development of the obliquus dorsalis and fourth levator externus. In these species, the degree of development of the levator posterior limits the anterior movement of the lower pharyngeal bone. *C. bicolor* and *B. muricatum* may have partially overcome this problem by the curvature of the basipharyngeal joint. This decreases the vertical movement of the upper pharyngeal teeth which are in use during grinding, and reduces the degree of movement required of the lower pharyngeal bone to maintain contact between the pharyngeal tooth plates. The associated musculature of the lower pharyngeal bone therefore retains the crushing action as found in labrids, but because of the shape of the upper pharyngeal bone, a slight grinding action is also pssible.

The functional advantage of a mobile (swinging) lower pharyngeal bone may be an increase in grinding efficiency despite a diminished crushing ability. The grinding efficiency (*i.e.* reduction of particle size and trituration of algal cells) can be increased by increasing the area of contact between the pharyngeal tooth plates, particularly if smaller areas come into contact

sequentially, thereby maintaining a relatively high pressure per unit area. This proposal is supported by the increased length of the lower pharyngeal tooth plates of *Scarus* when compared to sparisomatine genera (Schultz, 1958 and Bruce, 1979), and the increased area of worn teeth (as a % of total upper pharyngeal bone length) in *Scarus* (38-52 %, n=8) in comparison to *C. bicolor* and *B. muricatum* (26-32 %, n=7).

The functional interpretations of this section may be investigated by feeding experiments, but ideally require sequential x-ray photography (or x-ray cinematography) and/or detailed electromyographical analyses comparable to the studies of Liem (1973) and Liem and Greenwood (1981).

Summary

1) The genus *Scarus* has two functional groups, the 'sordidus' group and the 'frenatus' group.
2) 'Sordidus' group species are described as functional 'biters'. Morphological features which give rise to such a capability include:
   a) strong bones and specialized osteological structures
   b) articulatory systems that enhance the power of the bite
   c) robust teeth and an uneven cutting edge which localize the biting force, and
   d) additional muscles and pinnate adductor muscles which deliver a powerful force with little movement.
3) 'Frenatus' group species are described as functional 'scrapers', as indicated by:
   a) relatively light osteological structures

b) articulatory systems to enhance the movement of the jaws

c) smooth cutting edges to increase contact with the substratum, and

d) weakly pinnate adductor muscles which enhance jaw movement but provide little force.

4) *C. bicolor* and *B. muricatum* are functional 'biters' but lack many of the specialized morphological characters associated with biting in 'sordidus' group species, and are therefore considered 'proto-biters'.

5) *Hipposcarus longiceps* is a functional 'scraper' but retains ancestral characters. It is, therefore, considered a 'proto-scraper'.

6) The comparative morphology of the pharyngeal apparatus in scarids and labrids is discussed with regards to the type of food processing, *i.e.* crushing or grinding, as a result of dietary differences.

1.5 Visceral Anatomy

Two aspects of the visceral anatomy have been examined, the liver and the intestine.

Materials and methods

The viscera were examined in two collections of fish. The first was collected from Heron Island, Orpheus Island and Lizard Island between the 16th December 1980 and 20th January 1981. The second collection was from Pandora, Rib and Myrmidon reefs. Specimens in the former collection were frozen, and those from the latter collection fixed and preserved in 10% formalin. In all cases, the liver weight is expressed as a percentage of the cleaned body weight (*i.e.* with the intestine, liver, gonads and swim bladder removed), to allow for variations in the weight of the gut contents, liver and reproductive organs. Intestinal patterns were examined in both the fixed and fresh material from the above collections in addition to fresh material from Lizard Island. Comparative analyses of intestinal lengths were based solely on fixed material from the second collection.

Results

A. Liver

The livers of all scarids examined were large and oily, with a yellow - orange to tan colour. There are two major lobes with the sinistral typically larger than the dextral, the only exception was one specimen of *S. flavipectoralis* which had a large dextral lobe.

The data from the first collection are given in Table 1.4 and from the second collection in Table 1.5 A. In the second collection, *S. sordidus* and *S. globiceps* were examined as representatives of the 'sordidus' and 'frenatus' groups respectively. There is no significant difference in the relative liver weights of the two species (MWU-test $p > 0.1$, Table 1.5 A).

Because of potential seasonal variation and the small sample size, the data on relative liver sizes are not conclusive *per se*. They do, however, support the general observations of Al Hussaini (1945, 1947) and Gohar and Latif (1959), who described the liver of scarids as large and fatty, representing 1.5 to 7.4% ($\bar{x}$ = 3.8%) of the body weight. The data from the second collection of material suggest that there is little or no difference in liver size between the two species.

B. Intestine

The pattern and form of the intestinal tract varied both within and between species. Ontogenetic changes are the main form of variation within a species and will be described in Chapter 2. However, the intestinal pattern is relatively consistent within a species above 60 mm S.L. and therefore, for comparative purposes, only specimens above this size are considered here. Three main intestinal patterns were found, designated type I, II and III (Fig. 1.24). These patterns do not resemble any of the 'typical' actinopterygian gut patterns described by Mok (1980). Type I is the most simple. It possesses a duodenal - ilial loop and dextral loop 'a' but is characterized by the absence of both anterior sinistral loops

Table 1.4 A comparative list of relative liver weights

Species	Number	S.L.range (mm)	Mean Liver Weight†
Scarids:			
Scarus rivulatus	1	280	4.13
Scarus sp. (*cf. lunula*)	1	295	3.10
Scarus gibbus	1	370	2.93
Scarus sordidus	1	310	2.13
Non-scarid herbivores:			
Naso unicornis (Forsskål) *	2	235-370	1.83
Naso tuberosus (Lacepède) *	1	345	2.17
Siganus lineatus (C & V) *	2	355	1.20
Siganus spinus (L.) *	1	290	1.80
Acanthurus dussumieri (C & V)	1	285	0.67
Carnivores/omnivores:			
Lutjanus carponotatus Richardson	4	280-300	0.76
Plectrorhynchus flavimaculatus (C & V)	1	380	1.20
Spilotichthys pictus (Thunberg)	1	410	0.78
Lethrinus sp.	2	305-320	1.14
Epinephelus flavocaeruleus (Lacepède)	1	370	0.67
Plectropomus leopardus (Lacepède)	1	325	0.91
Epinephelus merra Bloch	6	240-330	0.82
E. fasciatus (Forsskål)	4	260-330	0.56
Choerodon schoenleinii	1	235	2.44
Chaetodon lineolatus (C & V)	1	160	1.41
Pomacanthus semicirculatus (C & V) *	1	270	0.90
Sargocentron spiniferum (Forsskål)	2	310	1.00
Caesio cuning (Bloch)	1	280	1.10

† = As a % of the cleaned body weight.

* = These species possess fat deposits around the intestine.

Table 1.5 A The liver weights of two *Scarus* species

Species	Intestinal Pattern	Number	S.L.Range (mm)	Mean Liver Weight A	$S\bar{x}$	U1/U2
S. sordidus	III	15	106-186	2.787	0.225	68 †
S. globiceps	II	14	122-204	2.307	0.153	142 †

A = As a % of total cleaned body weight.
† - No significant difference, MWU-test p> 0.1.

Table 1.5 B The intestinal length vs. standard length of two *Scarus* species

Species	Intestinal Pattern	Number	S.L.Range (mm)	R.G.I.+	$\bar{x}$	U1/U2
S. sordidus	III	13	106-186	2.14	0.05	42.5 *
S. globiceps	II	14	122-204	1.98	0.03	139.5 *

+ = Relative Gut Index (gut length/standard length).
* - Significantly different, MWU-test p< 0.02.

Table 1.5 C The intestinal length vs. body weight of two *Scarus* species

Species	Intestinal Pattern	Number	S.L.Range (mm)	R.G.I.+	$S\bar{x}$	U1/U2
S. sordidus	III	14	106-186	3.5	0.38	81.5 †
S. globiceps	II	14	122-204	3.11	0.27	114.5 †

+ = Relative Gut Index (gut length/cleaned body weight).
† - No significant difference, MWU-test p> 0.2.

Figure 1.24

The three types of intestinal pattern found in *Scarus* species.

In these figures, the intestine is represented by a simple line. The sacculated nature of the intestine is not shown. The positions of the two main loops 'a' and 'b' are indicated by hatching or stippling as shown in the lower figure. The species distribution of the intestinal pattern types are given in Table 1.6.

Intestinal type

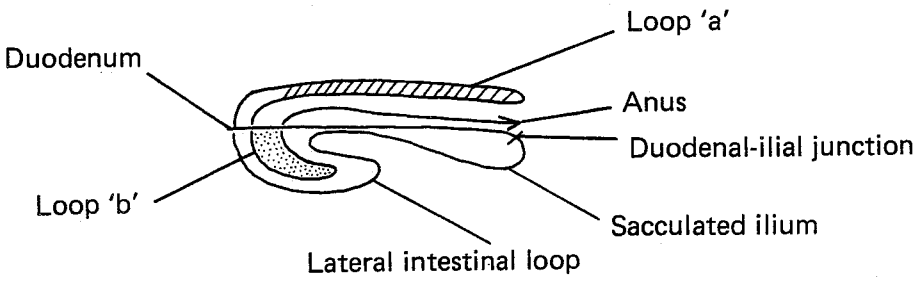
Type I

Lateral view

Dorsal view

Type II

Type III



(lateral and loop 'b'). Type II possesses four loops: the duodenal - ilial loop, the lateral intestinal loop (sinistral), loop 'a' (dextral) and loop 'b' (sinistral). It is characterized by having loop 'b' lying within the lateral intestinal loop. Type III likewise has all four loops but is characterized by loop 'b' lying lateral to the lateral intestinal loop. A list of those species possessing each intestinal type is given in Table 1.6. From this table, it is apparent that there is a marked division in the species possessing the three intestinal types, with types I and II being restricted primarily to 'frenatus' group species, in subgroups 'a' and 'b' respectively, and type III to 'sordidus' group species.

The intestinal pattern of *Cetoscarus bicolor* (n = 5, S.L. 124-486 mm) is intermediate between type II and III, with loop 'b' lying within the lateral intestinal loop anteriorly but lateral to it posteriorly. *Bolbometopon muricatum* (n = 2, S.L. 613-775 mm) has a type III intestinal pattern but with posteriorly extended lateral loops.

Exceptions to the typical patterns include: *Scarus* sp. (*cf. lunula*) which is unusual as adults possess type I, type II and intermediate patterns, one specimen of *S. oviceps* which lacked loop 'b', and a specimen of *S. schlegeli* which lacked the lateral intestinal loop. One *S. spinus* specimen had a type II intestinal pattern, but differed slightly as the lateral intestinal loop and loop 'b' extended dorsomedially over the duodenum. Another *S. spinus* specimen had a type II/III intestinal pattern with a short loop 'b' and an additional

Table 1.6 The distribution of intestinal types in *Scarus* species

Intestinal type	Species	Group or subgroup	Number	S.L. Range (mm)
I	*S. flavipectoralis*	†	3	200–217
	S. longipinnis	‡	1	75
	S. psittacus	†	7	63–196
	S. schlegeli	†	3	95–213
	S. sp.(*cf. lunula*)	†	1	164
II	*S. breviftlis*	‡	2	183–266
	S. dimidiatus	‡	2	214–233
	S. frenatus	‡	6	194–272
	S. ghobban	‡	1	106
	S. globiceps	‡	17	122–204
	S. niger	‡	5	107–214
	S. oviceps	‡	6	163–237
	S. rivulatus	‡	6	121–250
	S. rubroviolaceus	‡	1	275
	S. spinus	‡	1	218
	S. sp (*cf. lunula*)	†	1	222
III	*S. bleekeri*	*	2	54–193
	S. gibbus	*	6	208–455
	S. sordidus	*	24	60–234

† = 'Frenatus' group species subgroup 'a'.
‡ = 'Frenatus' group species subgroup 'b'.
* = 'Sordidus' group species.

ventrally directed fold in the lateral intestinal loop. One 253 mm S.L. *S. brevifilis* specimen was intermediate between types II and III. The characteristic sacculated form was found in all species examined.

The relative intestinal length was compared in two species, *S. sordidus* and *S. globiceps*, as representative species possessing type III and type II intestines respectively. The intestinal lengths were compared relative to the standard body length and the cleaned body weight (Table 1.5 B, C). The difference between the two species is significant when compared in terms of gut length : S.L. (MWU-test $p < .02$, Table 1.5 B), but not significant in terms of gut length : cleaned body weight (MWU-test $p > 0.2$, Table 1.5 C).

1.6 Functional Implications

A. The liver

Two factors are considered important when accounting for the relatively large liver size in scarids. Firstly, unlike some herbivores which store fat around the intestine (Table 1.4), scarids appear to use the liver as the primary lipid storage organ. Secondly, as in other herbivorous species, the liver of scarids appears to be larger than in non-herbivorous species (Table 1.4). This may be a general herbivorous response to the large number of toxic compounds in the diet (Hashimoto *et al.*, 1972 and Norris & Fenical, 1982) and the need to detoxify them.

B. The intestine

Within the genus *Scarus*, there is a marked division in the pattern of the intestinal tract. Members of the 'frenatus' group typically have type I or type II intestines, whereas only type III intestines are found in 'sordidus' group species. Within 'frenatus' group species, the division between those species possessing type I and type II intestines is also distinct, with only one species (*Scarus* sp.) possessing both forms.

There is a strong correlation between the intestinal pattern, the structure of the adductor mandibulae muscles, and the general body shape. Species with type I patterns are typically elongate with little or no connection between Alα and A2. Species with type II patterns are typically less elongate and have a strong connection between Alα and A2, whilst species with type III patterns are deep bodied with typical 'sordidus'-form adductor muscles.

The observed differences in the intestinal pattern are probably a result of optimal space utilization rather than a physiological or direct functional requirement. The space available for the gut i.e. the peritoneal cavity, is dependent upon the general body shape, which is in turn dependent to some extent on the morphology of the feeding apparatus. Therefore, in those members of the 'frenatus' group with an elongate head and body (species in subgroup 'a' and *S. longipinnis*), the peritoneal cavity is likewise long and narrow. Assuming that the intestinal diameter is limited by the functional factors described below, the most efficient intestinal pattern in such a cavity is a

series of simple loops i.e. a type I pattern.

In the remaining members of the 'frenatus' group (primarily species in sub-group 'b') the head and body are deeper. In these species, the peritoneal cavity is deeper but not markedly wider, hence a type II pattern, with loop 'b' lying within the lateral intestinal loop as the width is still limiting. The posterior extension of these loops is limited by the tapering of the body. In 'sordidus' group species, the feeding apparatus (head) is considerably wider than in species in either of the 'frenatus' sub-groups. The concomitant increase in the width of both the body and peritoneal cavity facilitates the development of the two sinistral lateral loops and because of the increased width loop 'b' is able to lie lateral to the lateral intestinal loop (= type III).

The dependence of the intestinal pattern upon the shape of the peritoneal cavity has been noted by Mok (1977, 1980) and Mok & Shen (1982), who found that at the species level, the intestinal pattern of chaetodontids is independent of intestinal length or diet (Mok, 1982). A similar lack of correlation between diet and intestinal pattern has been found in several species of acanthurid (Jones, 1968 and Mok, 1977).

The total intestinal lengths of *S. globiceps* and *S. sordidus*, with a type II ('frenatus' group) and a type III ('sordidus' group) intestinal pattern respectively, are significantly different (MWU-test $p < .02$) when compared in terms of total intestinal length: standard length (S.L.) (Table 1.5 B). However, the functional implications of this observation

are inconclusive, as the two species differ markedly in body shape. To allow for this variability in body shape, the intestinal lengths were compared in relation to the cleaned body weight. This revealed no significant difference (MWU-test $p > 0.2$) between the two species (Table 1.5 C). The difference between the two species using the former measurement is regarded as a reflection of body shape whilst the latter more accurately represents the relative intestinal lengths. The lack of any such difference suggests that the two groups may have similar digestive capabilities.

In general, herbivorous fishes have longer intestines than omnivorous or carnivorous species (Suyehiro 1941, Al Hussaini 1947 and Al Hussaini & Kohly 1954), although the relationship between ingested plant matter and gut length is not rigid (Suyehiro 1941, Al Hussaini 1947, 1949, Jones 1968, Emery 1973 and Mok 1982). As noted by Al Hussaini (1949), a comparison between various herbivorous groups is particularly difficult because of the wide range of feeding mechanisms and digestive systems.

In comparison with non-herbivorous species, scarids have a relatively long intestine (Gohar & Latif 1959 and Al Hussaini 1947). However, when compared to other groups of reef herbivores they have, as a group, some of the shortest intestines (Table 1.7). Two factors are considered particularly important when accounting for this relatively short intestine.

Table 1.7 Gut lengths of herbivorous reef fishes.

Species	R.G.I.+	Number of Species	Number of Individuals	Source
Scaridae				
Scarus spp.	1.62–2.66	17	55	A
Scarus spp.	1.44–1.88	2	6	D
Scarus sordidus	2.40–2.70	1	2	B
Scarus spp.	2.10–2.80	4	40	C
Acanthuridae				
Acanthurus spp.	3.80–4.60	2	19	C
Acanthurus spp.	3.00–6.90	12	@40	E
Zebrasoma veliferum	5.10	1	12	C
Zebrasoma spp.	3.70	2	@8	E
Naso unicornis	6.00	1	1	C
Naso unicornis	4.90	1	1	A
Naso spp. (herbivorous)	2.20–3.20	3	@12	E
Ctenochaetus spp.	3.50	2	@8	E
Siganidae				
Siganus spp.	4.60	2	16	C
Siganus spp.	2.70–4.40	2	4	A
Pomacentridae				
(herbivorous species)**	1.20–5.30	–	*	*
Kyphosidae				
Kyphosus tahmel	4.10	1	2	C
Blenniidae				
Salarius fasciatus	4.10	1	4	C

A= present study B= Al Hussini (1945) C= Al Hussini (1947)
D= Gohar & Latif (1959) E= Jones (1969)

+ = Relative gut index (*i.e.* gut length/standard length).
* = Values estimated from data expressed as graphs in Emery (1973) (only fish over 30 mm S.L. were used).
** = The strict herbivorous nature of some of these species is uncertain, see Lobel (1980) and Lassuy (1984).

Firstly, many herbivorous species appear to rely upon acid secretions to lyse algal cells before digestion, e.g. some acanthurids, pomacentrids, pomacanthids (Lobel, 1981) and cichlids (Moriarty, 1973). In these species, a long intestine would be advantageous as it increases the passage time and facilitates extended sequential chemical processing and absorption. In scarids the use of mechanical, rather than chemical (acid or enzyme), means of disrupting algal cells reduces the need for extended intestinal processing and with it the requirement for a long intestine. The presence of a relatively short intestine in species which mechanically process ingested algae has been noted in several species of acanthurids and in two species of scarids (Lobel, 1981).

Secondly, an important factor to consider when comparing the relative lengths of intestines is the mucosal surface area in relation to a given serosal length (Al Hussaini, 1949). The sacculated nature of the intestine in scarids increases the relative surface area of the intestine (Al Hussaini, 1945 and Gohar & Latif, 1959) and may therefore, further reduce the need for an elongate intestine.

The unusual sacculated nature of the intestine of scarids has been known for many years. Cuvier and Valenciennes (1839, p 133) state that Aristotle was the first to describe scarids as ruminants, and they refer to "l'estomach different" of scarids (based on *Spartsoma* (*Euscarus*) *cretense* (L.), see Board, 1956). This characteristic intestinal structure has since been described in detail (Al Hussaini, 1945 and Gohar & Latif, 1959). The

sacculations are interpreted as a means of increasing the mucosal surface area and decreasing the passage rate, thus increasing the time available for enzyme activities and absorption (Al Hussaini, 1945 and Gohar & Latif, 1959). The relatively long intestine of scarids in comparison with labrids, is seen as a consequence of the low nutritional content of the diet (Gohar & Latif, 1959).

Sacculation of the intestine has been recorded in all scarid genera examined, including *Calotomus* (as *Leptoscarus japonicus* in Suyehiro, 1941), which is one of the most 'primitive' scarid genera. The more 'primitive' labrid-like genera typically feed on large leafy algae or marine angiosperms (Suyehiro, 1941 and Bruce, 1979). A sacculated intestine in these species suggests that this feature may have originally evolved in response to such a diet. The presence of relatively specialized scarid-like pharyngeal jaws in these genera and the absence of a gastric stomach are indicative of a digestive strategy based on mechanical, rather than chemical, means of cellular disruption. The products of feeding that pass into the intestine of 'primitive' scarids is therefore, in many respects, similar to the material that passes into the intestines of the more 'advanced' scarids, i.e. a thick, ground slurry of little nutritional value. It is the nature of this material that is thought to have led to the unusual form of the scarid intestine.

The similarity of the scarid intestine to the human colon was first noted by Al Hussaini (1945). It is remarkable that both groups have such a similar structure. In both cases, the structure is interpreted as a means of increasing the mucosal

surface area for absorption (Roberts, 1971 and Gohar & Latif, 1961). This can, however, be achieved by other means (*e.g.* mucosal folds or pyloric caeca [Barrington, 1957]). It is suggested therefore, that although an increase in the mucosal surface area may be the primary consideration, the factor that has resulted in a sacculated structure in both scarids and humans was the nature of the luminal contents which is of a somewhat viscous nature (usually). The sacs increase the area of contact between the viscous luminal contents and the mucosa and maintain a degree of mixing throughout their passage.

The sacculation of the intestine is most marked in the sub-family Scarinae, where, unlike *Calotomus*, the ilial section of the intestine is fully sacculated. A sacculated intestine has many potential advantages when considered with respect to the feeding behaviour of the Scarinae (Chapter 5). Their feeding strategies result in the ingestion of large quantities of calcium carbonate which reduces the nutritive value of the ingested material and increases the density of the luminal contents. The large mean intestinal diameter will enable a prolonged passage time to be maintained and will reduce the relative speed with which the luminal contents passes the mucosal surface. This will decrease the friction between the luminal contents and the intestinal wall and will therefore, make the movement of large volumes of material energetically more efficient whilst decreasing the abrasion of the delicate mucosa by the large quantities of particulate calcium carbonate in the luminal contents.

It is interesting to note that both the labrids and scarids lack a gastric stomach (Gohar & Latif, 1959). In labrids, the lack of an acidic stomach is attributed to the large quantity of calcium carbonate ingested in the form of bivalve and echinoderm fragments (Gohar & Latif, 1959). As in extant labrids and scarids, it is likely that the ancestral labrid-like scarids also lacked an acidic stomach. The absence of an acidic stomach and the possession of a grinding pharyngeal mill are regarded as the two key preadaptive morphological characters that resulted in the unusual feeding strategies of the scarids.

Many fishes possess an acidic stomach and it is typically associated with a carnivorous diet (Barrington, 1957). An acidic stomach is also preadapted for the digestion of certain algae by acid lysis (Lobel, 1981), and may account for the widespread use of acid as a means of algal disruption in herbivorous fishes, as in the Acanthuridae, Chanidae, Pomacentridae, Pomacanthidae (Lobel, 1981) and Cichlidae (Moriarty 1973).

If primitive labrid-like scarids lacked an acidic stomach they would have no means of disrupting algal cell walls other than mechanical trituration in the pharyngeal mill. This feeding method, in association with a basic (alkaline) intestinal system would, however, make available new feeding niches, for example, the scraping of algal covered limestone, calcareous algae and corals, and eating tough algal species. These niches are unavailable to acid secreting species because of the problem of the buffering effect of ingested carbonate (Lobel, 1981). The large quantities of calcium carbonate ingested would also enhance

the masticatory processes by acting as an abrasive.

In this way, a unique feeding niche may have been available to the early scarids and resulted in the diversification of the group. This diversification is most notable in the form of the collecting apparatus, giving rise to such disparate forms as *Leptoscarus vaigiensis*, *Bolbometopon muricatum*, and *Scarus psittacus*. The fundamental role of the pharyngeal apparatus in the explosive speciation of African cichlids has been described by Liem (1973). In the family Labroidei (*sensu*. Kaufman & Liem, 1982), the pharyngeal jaws likewise appear to have played an important role in the adaptive radiation of the group.

Cellulase activity has been found in the intestines of several teleost species although it has most frequently been associated with ingested material rather than a result of a permanent microbial fauna or a secretory ability of the fish (Stickney & Shurnway, 1974, Prejs & Blaszczyk, 1977, Lindsay & Harris, 1980 and Weinstein *et al.*, 1982). The lack of cellulase or other enzymes capable of digesting plant cell walls in fishes has been suggested in several other studies (Randall, 1961 a, Gohar & Latif, 1961b, Hickling, 1966, Gunn *et al.*, 1977, Van Dyke & Sutton, 1977, Olatunde & Ogunbiyi, 1977, Ogden & Lobel, 1978 and Lobel, 1980, 1981). Although scarids have been regarded as ruminants and have an unusual intestinal structure (Sagemehl, 1885 and Board, 1956), no detailed investigation into the presence of cellulase has been undertaken. However, cellulase activity in scarids is unlikely in view of the evacuation of the intestinal contents at dusk and nocturnally empty intestines

(Smith & Paulson, 1974). Despite the lack of conclusive evidence of cellulase activity in fishes, there is a possibility that at least one herbivorous reef fish species possesses some ability to digest cellulose. Microbial analyses of the contents of the enteric diverticulum of rudderfishes (*Kyphosus* spp) have revealaed a microbial fauna which includes forms potentially capable of cellulase secretion (D.J.W. Moriarty, pers. comm. and Rimmer & Wiebe, in press).

Summary

1) Scarids have a large oily liver which is approximately 2.5% of the cleaned body weight.
2) Within the genus *Scarus* three distinct intestinal patterns are found: type I and II, typical of 'frenatus' group species, and type III, typical of 'sordidus' group species.
3) When compared relative to the standard length, a type III pattern is significantly longer than a type II pattern. When compared relative to the gutted body weight, however, there is no signicicant difference between the two.
4) The intestinal pattern is explained in terms of the general body shape and size of the feeding mechanism.
5) The intestine of scarids is shorter than that of other herbivorous reef fish families. This is interpreted as a result of mechanical, rather than chemical, food breakdown and the unusual form of the intestine.
6) The characteristic form of the scarid intestine is discussed as a means of increasing the surface area and as a specific adaptation to the unusual diet and feeding strategy of scarids.

7) The evolution of the scarid feeding mechanism is considered with reference to a preadapted 'labrid' stage which possesses pharyngeal jaws and lacks an acidic stomach.

1.7 Discussion

Morphological analyses have many applications in biology, with important roles in the study of ecology, behaviour, functional anatomy, physiology and systematics. In the present study, morphological analyses formed the basis for two areas of further study, 1) systematic analyses and 2) behavioural ecology.

1) Systematic analyses.

In the systematic studies of higher ichthyological taxa, internal morphological analyses are often of value (*e.g.* Schultz, 1958 and Mayr, 1969). The morphological descriptions in the present chapter form an ideal basis for comparisons between genera within the subfamily Scarinae. The systematics of the Scaridae using these descriptions are therefore considered in detail in Chapter 3.

2) Behavioural ecology.

Previous studies have found a strong correlation between the morphology and ecology of many fish species (*e.g.* Jones, 1968, De Martini, 1969, Emery 1973, Motta, 1980 and Stoner & Livingston, 1984), including scarids (Choat, 1969 and Bruce, 1979). In these studies, morphological analyses provided a useful tool in the investigation and interpretation of the ecology of fishes. In the present study, morphological analyses have also been used as a tool and as a basis for the investigation of the ecology of scarids. The

functional analyses, discussed above, provide for a more detailed understanding of the relationship between the morphology and ecology of scarids and of the mechanisms that enable the scarids to exploit their coral scraping niche.

The importance of morphology in the understanding of biological systems has been described by Bock (1977, 1980), who states that the only valid method for judging adapted features is by using the synthetic method. This method requires a study of the forms and functions of the feature in the laboratory, and of the biological roles of the feature in the field, and the selective demands of the environment. Bock (1980) highlights the need for ecological morphology to support functional morphology. The use of morphology in assessing competition and its ecological importance has also been noted by Schoener (1982).

The results of this chapter indicate that two morphological groups are present in the genus *Scarus*. Functional interpretations of species in these groups have indicated distinct differences that separate the two groups as 'biters' and 'scrapers'. These observations, however, form only part of the information necessary to assess these morphological diffrences and their ecological significance, following the synthetic method of Bock (1980). These morphological observations and functional interpretations give rise to one basic question: Is there any correlation between the functional morphology and the behavioural ecology of scarids? This question can only be answered by field observations and forms the basis for such studies in Chapter 5, where the ecological significance of morphology will be considered in more detail.

Finally, it is of interest to consider the morphology of scarids in a broader context. The most distinctive character is the fusion of the teeth, forming a solid dental plate which because of its beak-like appearance has given rise to the common name 'parrotfishes'. The fusion of the teeth is not, however, limited to scarids and has been recorded in many families, including the Oplegnathidae, Odacidae (Neoodacidae), Siganidae, Molidae, Diodontidae and Tetraodontidae (Gregory, 1933 and Wheeler, 1975). Of these, only two families commonly occur on coral reefs: the Diodontidae and Tetraodontidae. An examination of *Arothon reticularis* Schneider revealed a striking similarity between this species and scarids in the 'sordidus' group. Many of the morphological features associated with the enhanced biting capabilities of the 'sordidus' group are present or developed further in *A. reticularis*. In this species, the jaws have a powerful multipinnate musculature and simple articulations. Bones which are held tightly by ligaments in scarids are ankylosed in *A. reticularis*, *e.g.* the maxilla and premaxilla, and the articular and dentary. The jaws are strengthened further by deep dental plates with inflected medial sutures joining both the premaxillae and dentaries. A comparative study of the Scaridae and Tetraodontidae would be particularly valuable in assessing morphological adaptations and their ecological implications, as both families possess species that exploit a similar niche (*i.e.* feeding on large pieces of live coral [Glynn, *et al.*, 1972, Randall, 1974, Neudecker, 1977, Wellington, 1982 and Section 5.3]) and display a strong degree of morphological similarity, even though the two families are distantly related (Greenwood *et al.*, 1966).

CHAPTER TWO

THE MORPHOLOGY OF JUVENILE SCARIDS

2.1 Introduction

There have been numerous studies of the morphological changes that occur during the ontogeny of fishes. Many of these are descriptions of the external morphology and are primarily concerned with taxonomically important features (*e.g.* Leis & Rennis, 1983). Studies of the internal anatomy of fishes are often restricted to osteological descriptions (*e.g.* Potthoff, 1975, 1980, Mook, 1977, Jolie, 1980, Morris & Gaudin, 1982 and Potthoff *et al.*, 1984), although myological and intestinal descriptions are relatively common (*e.g.* Edgeworth, 1939, Smyly, 1952, Frost, 1954, Tanaka, 1969 a, b, 1971, Bryan & Madraisau, 1977, Mok, 1982, Claeys & Aerts, 1984).

Many of these studies are, however, primarily descriptive, and the functional implications of the observed developmental changes are not often considered. There are relatively few examples of comparative studies which assess both the morphological and behavioural changes that occur during the ontogeny of fishes (*e.g.* Stoner, 1980, Schmitt & Holbrook, 1984 and Labelle & Nursall, 1985).

In scarids, there have been few studies which have considered the morphological changes that occur during ontogeny. Randall and Randall (1963) described the spawning and early development of a sparisomatine scarid, whilst Leis and Rennis (1983) described the form of larval scarids. Boas (1883) briefly described the form of the premaxilla and dentary of a juvenile (or small IP) *Spartsoma*

species and a *Scarus* species (as *Scarus* sp. and *Pseudoscarus* sp. respectively).

Ontogenetic changes play an important role in the biology of a species (Werner, 1977 and Helfman, 1978). The potential importance of morphology during ontogeny has been demonstrated in crustaceans by Neill (1975). In this study the morphological changes that occur during the ontogenetic development of scarids are examined. Two species (*S. sordidus* and *S. frenatus*) are described in detail as representative species from the two morphological forms found in the genus *Scarus* although, for comparative purposes, other *Scarus* species were examined.

During the planktonic larval stage, the various scarid species are very similar in form. Within the genus *Scarus*, species or 'forms' can only be distinguished by the distribution of pigment cells (J. Leis, pers. comm.). Leis and Rennis (1983) describe the post-flexion larvae (over 3.3 to 4.2 mm S.L.) as elongate and laterally compressed, with a deep caudal peduncle. At this stage, no teeth are visible in the jaws and the eye is ovoid or rectangular. In the late post-flexion larvae the eye becomes rounded and, shortly before settlement, teeth are present in the jaws. The largest planktonic scarine larva reported by Leis and Rennis (1983) was 7.9 mm S.L.

In the present study, only those specimens that had been recruited to the reef were examined (*i.e.* post-settlement). (Settlement, as used here, refers to the action of moving from the water column to the substratum, *i.e.* reef. Recruitment refers to the permanent occupation of a restricted area of the reef for an

extended period of time). The smallest specimens examined were 6.8 mm S.L. (provisional *S. sordidus*) and 7.7 mm S.L. (*S. frenatus*).

2.2 Materials and Methods

Specimens were collected from the reef around Lizard Island during November - December, 1981, November, 1982 - February, 1983 and November, 1983 - January, 1984. Small specimens were collected using large (615 x 940 mm), clear polythene bags as traps. Larger specimens were obtained by using a Hawaiian sling and multiprong spear. Specimens were fixed in 10% formalin and preserved in 70% ethanol. A list of the material examined is given in Table 2.1.

Specimens were dissected using a dissecting microscope and examined under both dissecting and compound microscopes. Drawings were made with the aid of camera-lucida attachments.

2.3 Results

A. Osteological and myological changes.

New and recently recruited specimens of *S. sordidus* and *S. frenatus* (6.8 - 9.07 mm S.L.) are elongate and laterally compressed, with a rounded or slightly pointed snout. The two species are extremely similar in their morphology at this size. The suspensorium is narrow, with an open 'u' shape accommodating the large eye. The palatine dorsal process is elongate and protrudes beyond the point of articulation of the quadrate and articular. The jaws of both species possess a series of well developed caniform teeth which curve slightly inwards (Fig. 2.1. The apparent angle of the teeth in this figure is due to the curvature of the

Table 2.1 The morphology of juvenile scarids: material examined.

Species	Number	Standard Lengths (S.L.) in mm
S. sordidus	28	6.8 - 146 A
S. frenatus	18	7.7 - 154 B
S. gibbus	3	14.1 - 94
S. ghobban ?	2	13.1 - 14.5
S. globiceps/rivulatus ?	3	10.4 - 13.5
S. psittacus/schlegeli	18	10 - 26
S. rubroviolaceus	3	13.5 - 15.5
S. spinus ?	3	14.6 - 26
S. sp.(*cf. lunula*) ?	5	11.7 - 25.3
S. spp.	8	8 - 14.5

A = 6.8,8.2,9,9.7,10,11.3,11.8,12.8,15,15,18,19,19,27,35,43,52, 53,54,56,56,58,94,107,111,112,129,146 mm S.L.

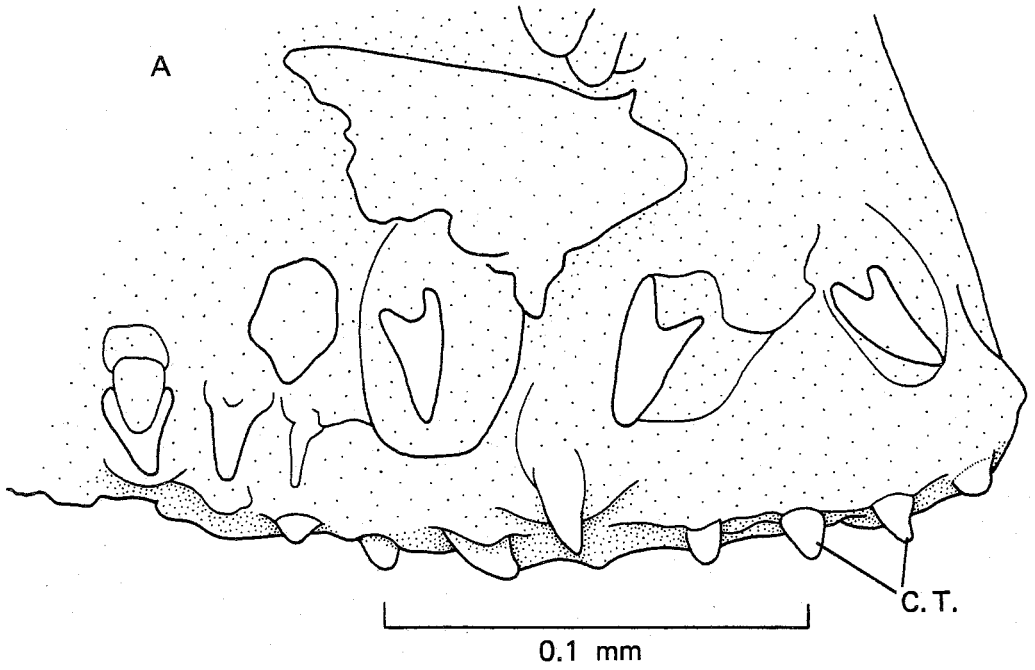
B = 7.7,7.8,8.7,8.7,8.8,10.2,11.1,12,14,14.7,22,26.5,31.5,77,92, 112,114,154 mm S.L.

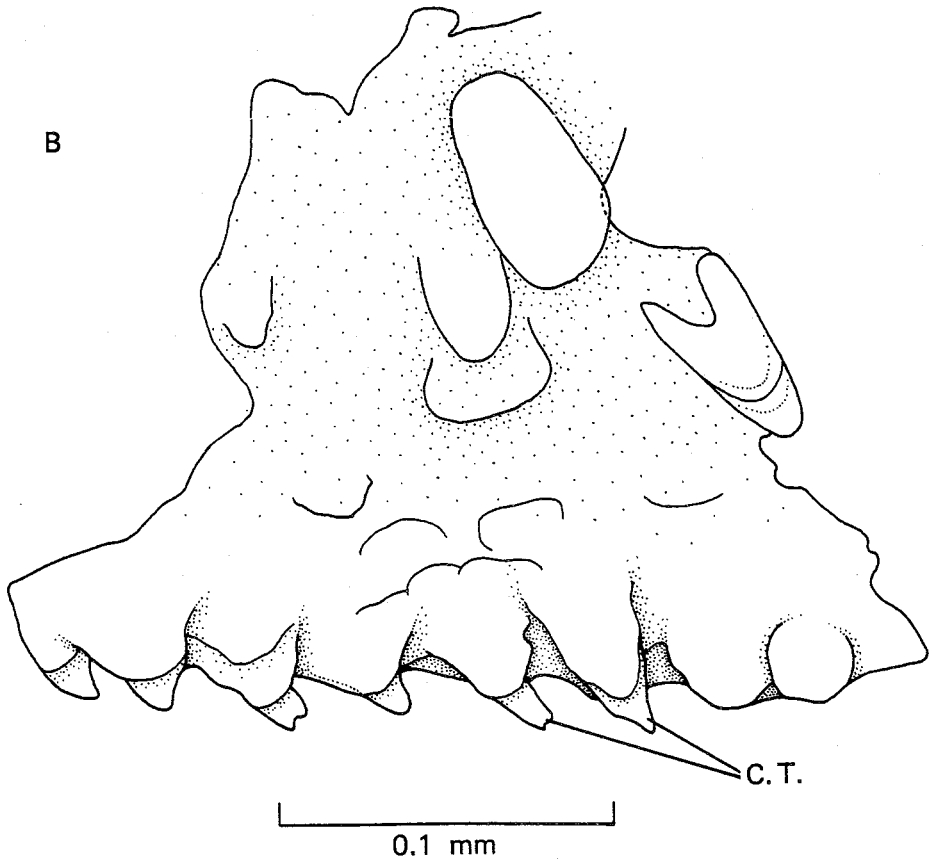
Figure 2.1 A

A lateral view of the anterior edge of the premaxilla of a 9.0 mm S.L. *S. sordidus*. (C.T. = caniform teeth).

Figure 2.1 B

A lateral view of the anterior edge of the premaxilla of a 8.7 mm S.L. *S. frenatus*. (C.T. = caniform teeth).


A
C. T.
0.1 mm


B
C. T.
0.1 mm

premaxilla). At this size, the developing teeth are also caniform (Fig. 2.1). The articular is elongate in both species and there is an articulatory articular-dentary joint.

A detailed examination of the myology was not undertaken at this size. However, the major muscle blocks (A1, A2 and A3) closely resemble the form in slightly larger specimens. The only notable difference is that in new or recently recruited specimens, the posterodorsal extremity of the adductor muscle mass does not extend above the level of the lower edge of the orbit and, unlike in larger specimens, it has no contact with the ventral edge of the levator arcus palatini (Fig. 2.3).

By 10 to 12 mm S.L., the caniform teeth on the anterior edge of the jaws are lost, leaving a smooth scraping edge. Small, pointed or strongly rounded teeth remain only at the angle of the jaws. The developing teeth are scale-shaped. In both species, the maxillary head is well developed. The palatine dorsal process is still elongate, with a terminal maxillary condyle. The palatine dorsal process and maxillary head of both species closely resemble those of adult *S. frenatus*. The movement of the upper jaw in juveniles is of a highly mobile form, as in adult *S. frenatus*, rather than the strong form, as found in adult *S. sordidus* (Sections 1.4.1 and 1.4.2). The quadrate in both species also closely resembles that of adult *S. frenatus*.

At 10 to 12 mm S.L., the muscles are clearly visible and are very similar in the two species. In both species, section A1 inserts *via* a long tendon to the maxilla. There is no A1β and no muscle fibres arise from the leading edge of the orbit. A2 is in

close association with A1 but has a distinct insertion onto the dentary lateral flange. At this size, there is no distinct link between the A1 and A2 sections in *S. frenatus*. In both species, the A3 section is well developed with a strong tendinous insertion on the articular and a weaker muscular insertion on the dentary lateral flange. The relative size of the A3 muscle is considerably larger than that which attaches to the articular in adult *S. sordidus* (*i.e.* A3β) or *S. frenatus*. Subsections Awα and Awβ are present but there is no Awγ in either species. Sections A1 and A2 have weakly pinnate fibres while A3 has pinnate fibres and Aw, parallel fibres.

Above 12 mm S.L., the morphology changes rapidly and the differences between the two species become more distinct. At 14 to 15 mm S.L., the relative depth of the suspensorium increases, corresponding with the decrease in the relative size of the orbit. The anterior cutting edges of the jaws are even although the teeth in the posterior region remain small and pointed. In both species, a few fibres of the A1 section arise from the anteroventral edge of the orbit, representing the early stage of development of A1β. Section A1 inserts by a long tendon on the maxilla and section A2 inserts by a short tendon to the dentary lateral flange. In *S. frenatus*, these tendons are closely bound near to their bases, whereas in *S. sordidus*, they remain distinctly separate. Section A3 possesses two subsections: a dorsal subsection inserting on the dentary lateral flange (A3α) and a ventral subsection inserting on the articular (A3β). In *S. sordidus*, the dorsal subsection (A3α) is particularly well developed, whilst the ventral subsection lacks the strong tendon found in smaller specimens and similarly sized *S. frenatus*. A third subsection of Aw, Awγ is present in

S. sordidus by 15 mm S.L. (This muscle was not located in a 12.8 mm S.L. *S. sordidus* specimen). At this size, there is no notable difference between the two species in the site of origin of the major muscle blocks.

Above 16 mm S.L., the two species continue to diverge and will therefore be considered separately.

1) Osteology

S. sordidus (Fig. 2.2)

S. sordidus starts to develop a lateral process on the entopterygoid at about 18 - 19 mm S.L. and at this size, it has a tendinous connection with A1β. As the individual grows, the entopterygoid lateral process becomes thicker and more protruded laterally. At 43 mm S.L., the entopterygoid at the base of the process is deeply concave and the septum has started to form. By 53 mm S.L., the two concavities at the base of the process are distinct and by 94 mm S.L, the lateral process, septum and concavities are fully formed.

The quadrate retains a 'frenatus-like' form until about 53 mm S.L., when, as a result of the slow dorsal movement of the ventral edge, this edge lies in a groove along the dorsal edge of the preopercular horizontal limb, the typical 'sordidus-like' postion. The degree of interdigitation between the preoperculum and quadrate increases until the adult form is reached at about 94 mm S.L.

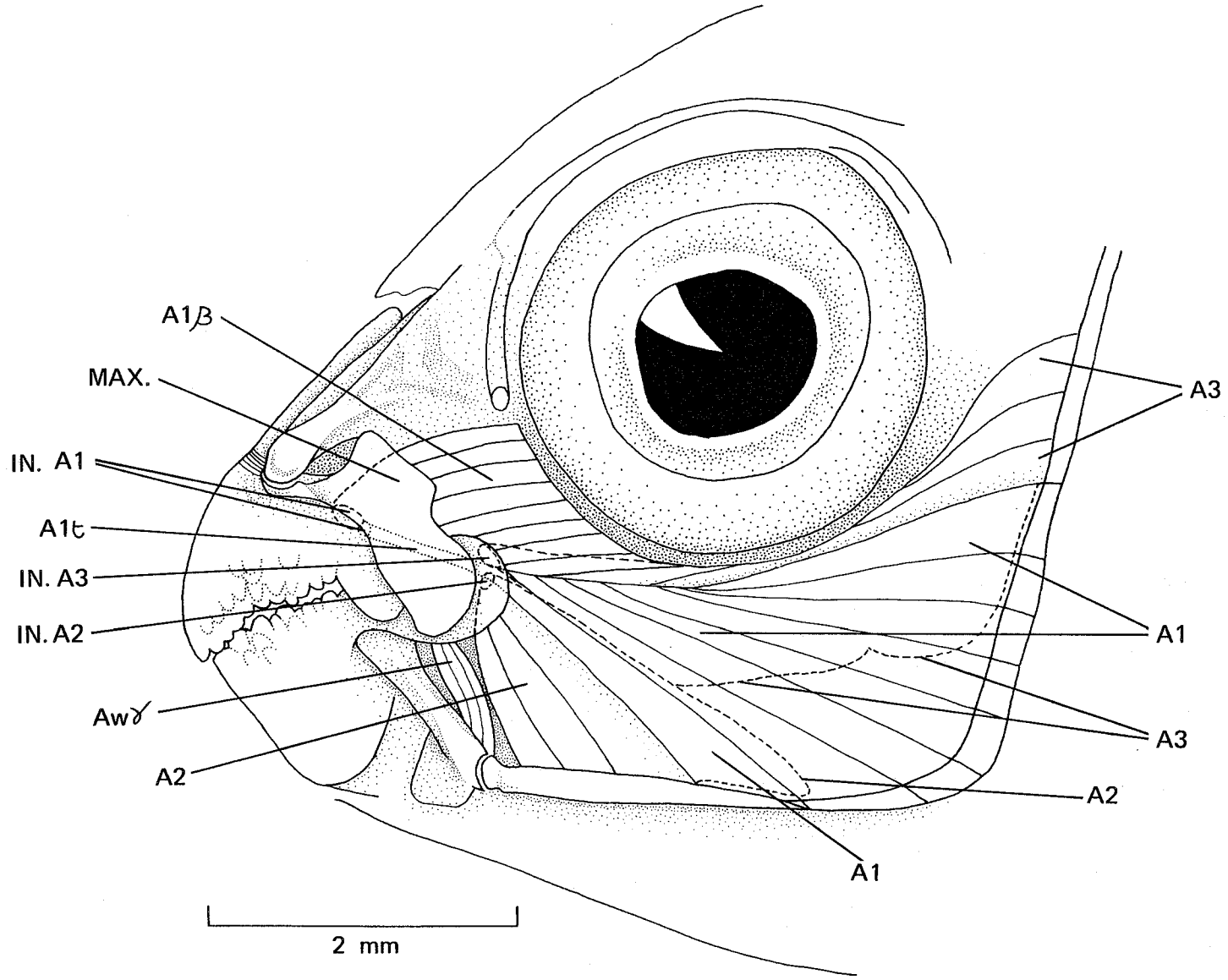
The palatine dorsal process becomes relatively shorter with growth and the terminal maxillary condyle becomes more ventrally oriented. At 8 - 9 mm S.L., the palatine dorsal process has a

Figure 2.2

The head of *S. soraidus* at 25.0 mm S.L. with the integument, nasal, lacrymal and circumorbitals removed.

Abbreviations used in this figure:

A1, A2, A3, Aw	Adductor mandibulae sections 1, 2, 3 and w
A1β	Adductor mandibulae section A1 subsection A1β
A1t	Tendon of adductor mandibulae section A1
Awγ	Adductor mandibulae section Aw subsection Awγ
IN. A1	Insertion site of A1
MAX.	Maxilla


A1β
MAX.
IN. A1
A1ε
IN. A3
IN. A2
Awγ
A2
A3
A1
A3
A2
A1
2 mm

length:width ratio of about 4.7:1 but by 94 mm S.L., this becomes 1:1 and in adults, is about 0.9:1.

The overall shape of the suspensorium deepens dorsoventrally throughout the juvenile phase, from a broad 'u'-shape at 8 - 9 mm S.L. to a more oblong shape at 16 - 20 mm S.L. It has a roughly square appearance at about 80 mm S.L. which is similar to that of the adult. These changes correspond with the decrease in the relative size of the orbit and its decreasing incursion into the dorsal edge of the suspensorium. The relative depth of the adductor fossa and the strength of the suspensorium also increase with growth.

Throughout development, the vertical tooth rows on the premaxilla and dentary alternate in the possession of a new tooth on the cutting edge, although the cutting edge of small specimens remains even due to wear. With increasing size, the teeth become progressively stronger, changing shape, when viewed anteriorly, from being scale-shaped to pear-shaped, with an increase in interdigitation between adjacent vertical tooth rows. As a result of these changes, the cutting edge becomes uneven at 18 - 27 mm S.L. and by 43 mm S.L., it appears scalloped and worn. The adult state, with distinctly alternating vertical tooth rows represented on an uneven cutting edge with minimal tooth wear, is achieved at about 111 mm S.L. The small pointed teeth at the angle of the jaws are lost between 19 and 27 mm S.L.

The first sign of the maxillary fossa on the premaxilla appears at about 43 mm S.L. as a hardening of the bone in the region later occupied by the maxillary fossa. This hardening is more apparent in

larger specimens and by 94 mm S.L., this area is marked by a depression. The rim of this depression is slightly raised at 107 mm S.L. and the adult form is complete by 112 mm S.L. During the development of the maxillary fossa, there is a corresponding hardening and development of the premaxillary process on the maxilla.

The dentary medial sutures increase in number and complexity with growth. At 18 - 19 mm S.L., there are 4 - 5 simple (\-shaped) sutures. At 58 mm S.L., there is a single short inflection in the sutures and by 107 mm S.L., there are 9 - 12 sutures with three inflections. In adults, there are 11 - 12 sutures with up to five inflections.

The only major change in the form of the articular is a rapid decrease in its relative length between 9 and 20 mm S.L., followed by a slight thickening. The articular medial spine increases in relative size with growth.

The pharyngeal apparatus of *S. sordidus* also changes during development. The number of teeth in each tooth row increases in both the upper and lower bones, and on the upper pharyngeal bones the relative size of the teeth in each row changes. At 11.8 mm S.L., there are five teeth per row and above 94 mm S.L., 8 - 11 teeth per row. In juvenile *S. sordidus*, there are three rows of teeth on each upper pharyngeal bone. The ratio of the widths of the teeth from the innermost to outermost row are 5.25:1.75:1 at 11.8 mm S.L. and 5.7:2.2:1 at 15.2 mm S.L. The outermost rows continue to decrease in relative size, resulting in a ratio of 20:5:1 at 129 mm S.L. and the eventual loss of the outermost row in some large

adults. At 11.8 mm S.L., the teeth are raised and have a rounded shape, with little interdigitation between the innermost rows and with no signs of wear. In progressively larger specimens, the teeth become more ovoid and the degree of interdigitation and wear increases. The lower pharyngeal tooth plate is relatively short in small specimens and becomes elongate in larger specimens.

S. frenatus (Fig. 2.3)

In comparison to *S. sordidus*, few new structures arise during the development of *S. frenatus*. The major changes are primarily as a result of allometric growth patterns. As in *S. sordidus*, the relative depth of the suspensorium of *S. frenatus* increases as the relative size of the orbit and its incursion into the dorsal part of the suspensorium decreases. The space between the orbit and maxilla increases in relative size and the angle of the jaws moves to a more medial position relative to the adductor fossa as a result of the deeper suspensorium and shortening of the articular. Unlike *S. sordidus*, however, there is only a slight shortening of the relative length of the palatine dorsal process and the terminal maxillary condyle is retained. The maxilla changes little with only a slight increase in the relative size of the posterodorsal process. The quadrate-preopercular joint remains unchanged.

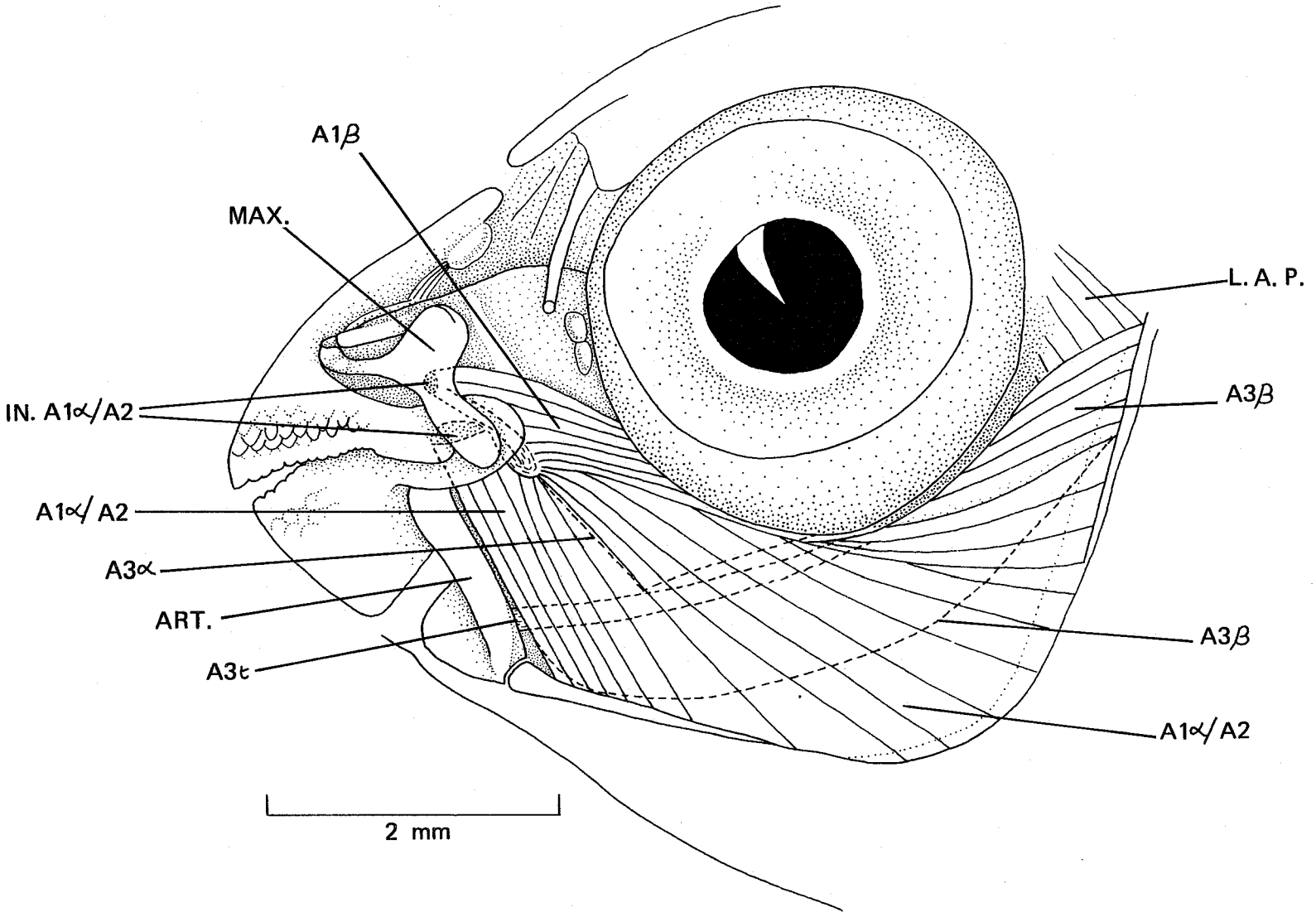
The teeth of the premaxilla and dentary of *S. frenatus* become progressively stronger but remain weaker than those of *S. sordidus*. They change from being scale-shaped, when viewed anteriorly, to roughly oblong, with the longest edge forming part of the cutting edge. The interdigitation between adjacent vertical tooth rows decreases in progressively larger specimens. These changes,

Figure 2.3

The head of *S. frenatus* at 26.5 mm S.L. with the integument, nasal, lacrymal and circumorbitals removed.

Abbreviations used in this figure:

A3, A3α, A3β	Adductor mandibulae section 3, subsections
Aiβ, A3α, A3β	Subsections of A1 and A3
Aiα/A2	Adductor mandibulae complex, comprising subsection Aiα and A2
A3t	Tendon of adductor mandibulae section A3
ART.	Articular
IN. Aiα/A2	Insertion point of Aiα/A2
L.A.P.	Levator arcus palatini
MAX.	Maxilla


A1β
MAX.
L. A. P.
IN. A1α/A2
A3β
A1α/A2
A3α
ART.
A3β
A3ε
A1α/A2
2 mm

however, have little impact on the form of the cutting edge. At 77 mm S.L., the teeth arise on the cutting edge from alternating vertical rows but they are rapidly worn and form an even cutting edge. In larger specimens (above about 154 mm S.L.) each vertical tooth row has a tooth on the cutting edge, which, when combined with a relatively large degree of wear results in an even cutting edge. This relatively even cutting edge persists even in adults due to the constant presence of teeth from each vertical tooth row on the cutting edge and the limited ability of these teeth to withstand wear. As in *S. sordidus*, the small pointed teeth at the angle of the jaws are lost between 14 and 22 mm S.L.

The dentary medial sutures remain simple throughout development but increase in number from 5 - 6 at 22 - 26 mm S.L. to 8 - 10 in adults.

S. frenatus possesses only two rows of teeth on each upper pharyngeal bone but as in *S. sordidus*, the number of teeth per row increases in larger specimens whilst the relative size of the teeth in the outer row decreases. At 10.2 mm S.L., there are 5 teeth per row, with a ratio of the innermost to outermost tooth widths being 2:1. At 14 - 15 mm S.L., there are 7 - 8 teeth per row with a ratio of 2.6:1 to 2.8:1. Above this size, this trend continues with adults having 12 - 13 teeth per row and a ratio of about 4.7:1. As in *S. sordidus*, the teeth of larger specimens become more ovoid, the degree of interdigitation and wear increases, and the lower pharyngeal plate becomes more elongate.

2) Myology

S. sordidus (Fig. 2.2)

At 18 - 19 mm S.L., all the major adductor muscle blocks can be easily located. Subsections A1β, Awα, Awβ and Awγ possess parallel fibres, A1α and A2 have weakly pinnate fibres and A3 is strongly pinnate when viewed laterally. The form of the muscles at 25 mm S.L. (Fig. 2.2) differs from that of smaller specimens primarily as a result of an increase in the relative size of sections A1β and A3.

In progressively larger specimens, the central tendon of A1α increases in relative length whilst the relative length of the muscle fibres decreases. As a result, A1α becomes increasingly pinnate. The anterior fibres of the muscle are the first to arise from the thin tendinous sheet covering the adductor muscle mass at about 53 mm S.L. With growth, the relative length of the fibres continues to decrease, the angle of pinnation increases and the proportion of muscle fibres arising from the tendinous sheet increases. The muscle is fully bipinnate by 94 mm S.L. The site of origin of A1α remains restricted to the posteroventral angle of the adductor fossa throughout development.

Subsection A1β slowly increases in relative size during development. By 18 mm S.L., the dorsal border is on the same level as the lower edge of the pupil. The muscle continues to expand dorsally and laterally (Fig. 2.2), with the first signs of subdivisions becoming apparent at about 43 mm S.L. The muscle is fully developed by about 54 mm S.L. although the proportions may change slightly with growth.

Section A2 develops in a similar manner to Alα. In progressively larger specimens, there is a decrease in the relative fibre length, an increase in the angle of pinnation and an increase in the relative length of the central tendon. By 94 mm S.L., there are several fibres arising from the tendinous sheet covering the adductor muscle mass. The proportion of fibres arising from this tendinous sheet and the degree of fibre pinnation increase with growth. The site of origin of A2 remains restricted to the anteroventral region of the adductor fossa throughout development.

At 18 - 19 mm S.L., the dorsal subsection of A3 (A3α) is slightly less than twice the length and three times the area of the ventral subsection (A3β). The bipinnate structure which was apparent when viewed laterally is lost. At about 25 mm S.L., a series of short fibres develop, arising from the dorsal part of the hyomandibula (Fig. 2.2). By 43 mm S.L., these fibres have formed a discrete layer, giving A3α a bipinnate structure. The increasing pinnation of the fibres around the medial tendon result in adult-form tripinnate structure at about 94 mm S.L. (The pinnation of the fibres is in the lateral plane and is most easily seen if the muscles are sectioned along their length). As in A3α, A3β has lost its bipinnate appearance by 26 mm S.L. Above this size, A3β remains unipinnate and slowly decreases in relative size. It decreases from about 65% of the length of A3α, at 19 mm S.L., to 25% at 114 mm S.L. The strongly unipinnate fibres of A3β in large individuals are continuous with the deepest muscle layer of A3α. The site of origin of A3β remains on the quadrate, but decreases in its relative area. The site of origin of A3α, however, remains in the mid- and posterodorsal part of the suspensorium, but increases in relative

area as the suspensorium expands dorsally. The increased area and the new structures that arise during the development of the suspensorium form a large proportion of the site of origin of A3α.

All three subsections of Aw are clearly visible above 18 mm S.L. They maintain their positions throughout development but decrease in relative length, as a result of the decreased length of the articular.

The degree of pinnation and proportion of fibres arising from the tendinous sheet covering the adductor muscle mass increase with size throughout the juvenile and adult phases.

S. frenatus (Fig. 2.3)

With the exception of section A3, the myology of *S. frenatus* changes little during development. By 22 mm S.L., A1α and A2 have formed a single unit, the A1α/A2 complex, with muscle fibres joining a tendinous aponeurosis that inserts on the maxilla and dentary (the aponeurosis is formed by the fusion of the A1α and A2 tendons). The A1α/A2 complex has an adult form at 26 mm S.L. (Fig. 2.3). The only modification found in larger individuals is the increased relative size of the muscle and the presence of a thin tendinous sheet covering the posterior part of the adductor muscle mass in some individuals. The A1α/A2 complex arises from the whole of the adductor muscle fossa and from the tendinous sheet covering subsection A3β. The site of origin does not change during development but the relative area, especially of the upper portion, increases as the suspensorium deepens. The fibre orientation remains weakly pinnate.

Subsection A1β develops slowly. Although fibres arising from the anterior edge of the orbit are present at 22 mm S.L., they do not form a distinct A1β subsection as the fibres insert *via* A1α/A2 t1. At 26 mm S.L., A1β is present with a muscular insertion on the maxilla but is poorly developed (Fig. 2.3). In larger specimens, the site of origin becomes more dorsal and the muscle thickens. The adult form is reached at approximately 77 mm S.L. The muscle fibres are predominantly parallel.

At 22 - 26 mm S.L., section A3 is relatively smaller than that in smaller specimens, particularly subsection A3α. Subsection A3β retains a tendinous insertion on the articular. The site of origin of A3α is reduced to a part of the tendon of A3β. It still inserts muscularly on the dentary (Fig. 2.2B). In larger specimens, the relative size of the muscle decreases further. Subsection A3β retains its position and tendinous insertion whilst A3α is reduced to a small sheet of fibres (the M. tendo-articulari-dentalis of Lubosch [1929]). The decrease in the size of A3α appears to correlate with the decreasing length of the articular. The adult form is reached by 77 mm S.L. The site of origin of both A3α and A3β does not change in specimens above 22 mm S.L., although the relative areas decrease. The fibres of A3α are parallel and those of A3β are weakly pinnate when viewed laterally.

The two subsections of Aw, Awα, and Awβ are retained, but both decrease in length as the articular shortens. Both subsections retain their sites of origin/insertion throughout development and have parallel fibres.

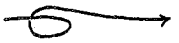
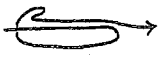
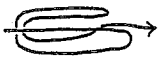
3) The intestinal tract

The intestinal tract of scarids changes markedly throughout ontogeny. There is an increase in the relative intestinal length and in the complexity of the coiling pattern and of the structure of the intestinal wall. The changes in the relative intestinal length of juvenile scarids are summarized in Table 2.2.

In preflexion scarid larvae, the intestine is a simple, straight tube. The first coil appears shortly after flexion (Leis & Rennis, 1983) and is present in newly settled larvae. At 8.5 mm S.L., an invagination of the dextral part of the loop is present. This invagination enlarges and results in an elongate loop (loop 'a') by about 11 mm S.L. This stage is equivalent to a type I intestinal pattern. (A description of the loops and types of intestinal pattern are given in Section 1.5, Fig. 1.24). At 14 mm S.L., a sinistral folding of the anterior parts of the intestine produces two sinistral loops (the lateral intestinal loop and loop 'b'). The intestinal patterns of *S. sordidus* and *S. frenatus* remain indistinguishable until approximately 24 mm S.L. Above this size, the form of the sinistral loops start to diverge resulting in a type II or type III intestinal pattern at about 50 mm S.L. in *S. frenatus* and *S. sordidus*, respectively.

In planktonic scarid larvae, the intestine is rugose (Leis & Rennis, 1983). This form remains after settlement until about 11 mm S.L., when a raised zig-zag pattern is visible on the mucosal surface of the ileal part of the intestine. This pattern is restricted to the anterior part of the ileum, the remaining part having a series of smaller raised ridges in an irregular pattern.

Table 2.2 Ontogenetic changes in the morphology of the intestinal tract of juvenile scarids.

S.L. (mm)	R.G.I.	Intestinal pattern (dorsal view)	Notes
< 4.2†	0.33‡		Preflexation
3.3–7.9†	0.4–0.6‡		Postflexation
6.8	0.37		Newly settled
8.2–8.7	0.54–0.71		Wearing of 'canine' teeth
11.1	1.25		No anterior 'canine' teeth
		S. frenatus *S. sordidus*	
14–15	0.98–0.15		Scarid-like jaws, first signs of sacculation.
18–22	1.1–1.65		Distinct sacculation anteriorly
26–27	1.36–1.74		Almost fully sacculated intestine
53–77	2.4		Fully sacculated intestine
		Type II Type III	Adult form

R.G.I. = Relative Gut Index = gut length/S.L.
† = From Leis and Rennis (1983)
‡ = Estimated from figures in Leis and Rennis (1983)

By 14 mm S.L., the patterning is lost from the anterior part of the ileum which now possesses a few constrictions in the serosal surface. In larger specimens, these constrictions deepen, producing sacs whilst the mucosal patterning is completely lost. By 22 mm S.L., several ileal sacs are present near the duodenal-ileal junction. The extent of sacculation increases, with most of the ileum being sacculated or bearing constrictions by 27 mm S.L. A lateral intestinal bulb is visible near the pharyngeal-duodenal junction in specimens above 11 mm S.L., although the relative size of this bulb decreases rapidly with growth. The adult intestinal form is complete at approximately 50 mm S.L.

2.4 Functional Interpretations

There are two particularly striking features found in the early ontogenetic development of scarids. Firstly, the size of the eye and the role it plays in influencing the morphology of the jaw apparatus and secondly, the presence of relatively large caniform teeth in newly recruited individuals.

It has been suggested that the main factors that are likely to cause mortality in planktonic fish larvae are predation and starvation, and the interaction between them (Moser, 1981). The eye is one of the main organs that can be modified in response to these factors (Moser, 1981). If one assumes that mortality in newly recruited fish is dependent upon similar factors (*i.e.* predation and starvation) then the eye is likewise likely to play a significant role in the survival of newly recruited fish.

The size of the eye is independent of body size, although in general, smaller animals have disproportionately large eyes (Noback, 1977 and Romer & Parsons, 1977). In theory, a larger eye will have a larger image on the retina. This image will cover more light sensitive cells and will therefore give the eye a higher resolution (Land, 1981). For a juvenile scarid, a large eye would theoretically increase its ability to locate prey and avoid predation and therefore, have a strong influence upon its survival. In recently settled scarid larvae, it appears that the eye is of primary importance, with other structures (*e.g.* the jaw apparatus) being of secondary importance. The morphology of these structures may therefore be dictated by the spatial requirements of the eye. The advantages of an efficient prey catching mechanism appear to be of secondary importance when compared to the importance of prey location and predator avoidance. The dominant role of the eye in influencing the form of the head and jaw apparatus of cichlids during ontogeny has been described by Otten (1983). The importance of the eye in determining the shape of the suspensorium in cichlids has also been noted by Barel (1984).

In recently recruited scarids, the mouth is terminal (possibly for streamlining?) but because of the size of the eye, the jaw musculature is ventral to the jaws. In this position, the adductor muscles will have reduced efficiences because of their angle in relation to the direction of movement of the jaws. (This principle is discussed in Sections 1.4. and 1.4.2). In adults, subsection A3β may act as a 'living tendon' maintaining the connection between the bones in the lower jaw (Section 1.4.1) and as such, probably contributes little to the adduction of the jaws. In recently

recruited scarids, however, the relative size of A3β suggests that it is one of the primary jaw adductors. Because of the length of the articular, a small contraction of A3β would result in a relatively large movement of the dentary. The need for only a small excursion by A3β, may account for its pinnate structure especially in small specimens. (The properties of pinnate muscles are discussed in Section 1.4.1). In larger specimens, the relative size of the eye and the relative length of the articular both decrease. This decreases the efficiency of jaw adduction by the indirect action of A3β upon the articular, whilst increasing the efficiency of A1 (in *S. frenatus*, especially), A2 and A3α (in *S. sordidus*, especially). These changes correspond with the observed changes in the relative size of the major adductor muscle sections and subsections. Sections A1 and A2 and subsection A3 increase in relative size whilst Subsection A3β decreases.

In recently recruited scarids, the jaws possess a series of relatively large caniform teeth (Figs 2.1 A, B). This may be a vestigial feature, in view of the close relationship between the scarids and labrids. However, the presence of relatively large teeth during the vulnerable settlement and early post-settlement period are more likely to have a functional role, since a useless vestigial feature would be strongly selected against. The absence of teeth in planktonic scarid larvae, with the exception of large pre-settlement larvae (Leis & Rennis, 1983), and the presence and maintainance (as evidenced by developing caniform teeth, Fig. 2.1 A) of caniform teeth in recently recruited scarids, suggests that these teeth are adapted for use during the settlement and early post-settlement period.

Recently recruited scarids (between 6.8 and 10 mm S.L.) have relatively large eyes, weak jaw musculature, caniform teeth, relatively few rounded, unworn upper pharyngeal teeth and a short, simple (non-sacculated) intestine. This combination, strongly suggests a carnivorous diet. The large eyes enable prey to be located, whilst the caniform teeth facilitate the capture of the prey. Jaw strength is not required, especially if prey is ingested whole. The few rounded upper pharyngeal teeth are more suited to crushing (as in carnivorous labrids, Section 1.4.5) than grinding. The short intestine (Table 2.2) is comparable to that of adult carnivores (Section 1.6) whilst the lack of sacculation suggests that the diet contains less inorganic matter and is of a higher nutritive value than that of adult scarids (Section 1.6). In the reef environment, the most likely prey for carnivorous fishes of this size is microcrustacea.

Above 10 mm S.L., the caniform teeth are lost and the jaws have a scarid-like 'scraping' form. The jaw musculature increases in relative size and efficiency, and the intestine increases in length with the first signs of sacculation at about 15 mm S.L., and the first fully formed sacs at about 20 mm S.L. Between 10 and 20 mm S.L., the jaws are of a 'scraping' form but because of the small size of the individual, 'scraping' behaviour may not be possible. At this size, individuals may be able to select discrete algal filaments and therefore feed as browsers rather than grazers (*sensu* Hiatt & Strasburg, 1960 and Jones, 1968). A moderately nutritive diet is suggested by the length and form of the intestine which is relatively longer than in small 'carnivorous-phase' juveniles but lacks the length and sacculation associated with the nutritionally

low diet of adults (Section 1.6). A moderately nutritive diet in individuals between 10 and 20 mm S.L. may be the result of selective browsing, although feeding upon small invertebrates is still possible, especially in smaller specimens.

Above 20 mm S.L., the ability of individuals to select individual algal filaments or catch small mobile invertebrates is likely to decrease with increasing size, and as a result of larger non-selective bites, the volume of ingested inorganic matter is likely to increase. Such dietary changes are reflected in the form of the alimentary tract. The upper pharyngeal teeth show increasing wear (as a result of increasing grinding activity?) and the relative length and degree of sacculation of the intestine increases. By 50 mm S.L., the intestine has a fully developed adult form. This strongly suggests a high bulk/low nutritive value diet (Section 1.7). The even, worn cutting edges of the jaws and the weakly pinnate adductor muscles strongly suggest that between 20 and 50 mm S.L., both *S. sordidus* and *S. frenatus* are functionally 'scrapers' (*cf.* Section 1.4.2).

Between 50 and 90 mm S.L., *S. sordidus* slowly develops features associated with a 'biting' strategy. The adult state with a full compliment of these features is only reached at about 90 mm S.L. At this size, *S. sordidus* is probably capable of delivering a 'cracking' bite, although the efficiency of these bites probably increases in larger specimens. Throughout this period, *S. frenatus* remains a functional 'scraper'.

The changes in the morphology of juvenile scarids do not occur rapidly. The transfer from one morphological stage to the next is gradual and therefore, functional and dietary changes are also likely to be gradual. The morphology, functional interpretations and implied diet are summarised in Table 2.3.

2.5 Discussion

As in Chapter 1, this chapter forms the basis for further behavioural and ecological studies following the 'synthetic' method of Bock (1980). This chapter addresses the first part of the basic question: Is there any correlation between the functional morphology and behavioural ecology of juvenile scarids? The second part of this question will be addresed in Chapter 6.

The morphological relationships betweeen juvenile *Scarus* species differs markedly from that of adults. In adults, there are two distinct morphological forms, each with differing functional abilities that are likely to reflect differing feeding strategies. In juvenile *Scarus* species, however, species-related differences in the morphology and functional abilities only become apparent above 50 mm S.L. Below this size, most morphological and functional differences are size- rather than species-related. The morphological similarity between juveniles suggests that all juvenile *Scarus* species will have similar feeding strategies at a given size. The extent of interspecific variation in juvenile scarid feeding patterns will be assessed in Chapter 6.

Table 2.3 The functional morphology of juvenile scarids.

S.L. in mm	Primary morphological features	Implied diet and feeding strategy
7 - 10	Large eye, canniform teeth, simple intestine	Carnivorous phase: highly nutritive diet, mobile invertebrates - micro-crustacea ?
10 - 22	Large eye, even cutting edge on jaws, simple intestine	Intermediate, carnivorous/browsing phase: moderately nutritive diet, selected algae or occasional micro-crustacea ?
20 - 50	Even cutting edge on jaws, sacculated intestine	Grazing phase 1: diet low nutritive value & high inorganic content, both species functional 'scrapers'
50 - 90	*S. sordidus* develops features for 'biting'	Grazing phase 2: divergence. Both species ingesting quantities of algae and carbonate, *S. sordidus* may bite slightly deeper than *S. frenatus*
above 90	*S. sordidus* = 'biter' *S. frenatus* = 'scraper'	Grazing phase 3: 'biters' and 'scrapers'. Both species ingest algae and carbonate particles - the adult diet. *S. sordidus* has a 'biting' strategy and *S. frenatus* a 'scraping' strategy

In addition to forming a basis for ecological studies, observations on the morphology of juvenile scarids also yield useful data for taxonomic and phylogenetic studies. There are two particularly important taxonomic features: the number of upper pharyngeal teeth rows and the articular-dentary articulation. The presence of three upper pharyngeal teeth rows in juvenile 'sordidus' group species and two in 'frenatus' group species enables the two groups to be distinguished at sizes above 11.5 mm S.L. The presence of an articulatory articular-dentary joint in specimens above 8.2 mm S.L. is indicative of the taxonomic importance of this feature, as the older a character, the more likely it is to be laid down early in ontogeny, and the older a taxonomic character, the higher its taxonomic weight (Mayr, 1969 p 214). This character may therefore, be valuable in distiguishing higher taxa, although studies of the morphological changes occurring during the ontogeny of labrid and sparisomatine genera are still required.

There is a large degree of parallelism between the ontogeny of *Scarus* species and the proposed phylogeny of the Scaridae (Chapter 3). This is most appararent in the form of the teeth, jaws, pharyngeal apparatus and intestine. A transformation from jaws bearing caniform teeth to incisor-like teeth and on to cement covered dental plates is followed both during the ontogeny of *Scarus* species and in the phylogeny of the Scaridae, from the labrids and the labrid-like sparisomatine genera to *Sparisoma*, *Euscarus*, *C. bicolor* and *B. muricatus* through to *Scarus*. During the ontogeny of *Scarus* species, there is a reduction in the size of the teeth in the outermost row of the upper pharyngeal teeth rows, leading to a loss of the outer row in some large specimens. In addition, there

is an increase in the degree of interdigitation between the innermost upper pharyngeal teeth rows and an elongation of the lower pharyngeal dental plate. These changes are parallel with the sequence of changes described in the proposed phylogeny of the Scaridae (Section 1.4.5 and Chapter 3). Finally, the transformation of the intestine from a form with a single loop, to a type I pattern (described in Section 1.5) and on to a type II or III pattern, with a progressive increase in the degree of sacculation is apparent during both the ontogeny of *Scarus* species (Table 2.2) and in the proposed phylogeny of the Scaridae (Chapter 3), from labrids (1 loop and no sacs), to *Calotomus* (type I and few sacs), to the Scarinae (types I, II and III, all being fully sacculated). The above ontogenetic changes are considered in the phylogenetic studies in Chapter 3.

The relationship between ontogeny and phylogeny has been known for many years. The Biogenetic Law of Müller-Haeckel (1868), a modified version of Baer's Law, states that "ontogeny is a shortened and modified recapitulation of phylogeny" (cited in Balinsky, 1975). The possibility that older characters are laid down earlier in ontogeny is tentatively accepted by Mayr (1969). However, the possibility of an organism during ontogeny recapitulating the adult stages of its phylogeny is questioned as a result of the lack of evidence (Mayr, 1969 p 214).

There is a striking similarity between adult *S. frenatus* and juvenile *Scarus* species. The presence of juvenile characters in adult *S. frenatus* and other 'frenatus' group species, however, is not interpreted as evidence for the 'frenatus' group being an

ancestral form. Several lines of evidence indicate that the 'frenatus' group is the most specialized scarid group or genus (Chapter 3). The similarity of this group to juvenile *Scarus* species is regarded as a result of neoteny. Neotenic features are not necessarily ancestral, and have been associated with several specialized groups (Alexander, 1975), including humans (McFarland *et al.*, 1979).

Summary

Morphology

1) Juvenile *Scarus* species between 8 and 9 mm S.L. are extremely similar and possess caniform teeth and a simple intestine with a single loop.
2) Between 15 and 50 mm S.L., *S. sordidus* and *S. frenatus* are superficially similar but possess adult muscle formations including an Awγ in *S. sordidus* and a fused Alα/A2 in *S. frenatus*. By 50 mm S.L., both species have fully sacculated intestines with an adult pattern.
3) Between 50 and 90 mm S.L., the two species diverge. *S. sordidus* changes rapidly, increasing the angle of pinnation of the adductor muscles and acquiring several modified osteological features including an uneven cutting edge on the jaws and an entopterygoid lateral process. *S. frenatus* does not change markedly.
4) Both *S. sordidus* and *S. frenatus* have an adult form at 90 mm S.L.

Functional interpretations

1) In small juvenile *Scarus* species, the relatively large eye appears to be of primary importance, limiting the structure and

function of the jaw apparatus.

2) The functional interpretations of the morphology of juvenile *Scarus* species suggests changes in the feeding strategies and diet during ontogeny. These changes are not discrete, as the morphology and functional abilities gradually change from one stage to the next. The five basic stages are:

   a) 7 - 10 mm S.L.: carnivorous.

   b) 10 - 20 mm S.L.: selective carnivore/browser/grazer.

   c) 20 - 50 mm S.L.: grazer 1, *S. sordidus* and *S. frenatus* both 'scrapers'.

   d) 50 - 90 mm S.L.: grazer 2, both species 'scrapers' but *S. sordidus* has increasingly stronger bites.

   e) Above 90 mm S.L.: grazer 3, adult stage; *S. sordidus* a 'biter' and *S. frenatus* a 'scraper'.

CHAPTER THREE

SYSTEMATICS OF THE SCARIDAE: THE PHYLOGENY AND GENERIC CLASSIFICATION

Morphological analyses frequently form the basis of systematic ichthyological studies. These studies often rely upon external, rather than internal, characteristics because it is easier to examine external characters both in fresh and preserved museum specimens. External features provide many useful characters for discrimination at the species level, whilst internal (anatomical) characters are uften used in the classification of higher taxa (Mayr, 1969). Such internal characters include osteology (*e.g.* Tyler, 1970, Fraser, 1972 and Greenwood, 1978), myology (*e.g.* Winterbottom, 1974 b, Stiassny, 1981, Liem & Greenwood, 1981, Marino & Dooly, 1982 and Howes, 1983 a, b) and intestinal anatomy (Mok, 1977 and Mok & Shen, 1982).

The classification of scarids has been in a state of confusion for many years, primarily due to the lack of reliable diagnostic morphological characters (Schultz, 1958). Many early descriptions were therefore, based upon colour patterns. However, the use of colour as a primary taxonomic character has several inherent problems. This is particularly marked in the Scaridae where colour is dependent upon age, sexual status, and to a lesser extent, geographical location (Randall & Bruce, 1983). The colours also change upon death and are lost during fixation (Smith, 1956).

Initial museum-based works by Smith (1956, 1959) and Schultz (1958, 1969) clarified some of the problems of scarid taxonomy, although the problem of sexual dichromatism was not resolved. Apart

from the re-examination of early descriptions and material (Randall & Ormond, 1978 and Randall & Nelson, 1979), the major contribution to scarid classification since the work of Smith (1959) and Schultz (1969) has been that involving the linkage of initial phase and terminal phase colour patterns. The marked difference between the initial and terminal phase colour patterns was first described by Brock and Yamaguchi in 1954, but it is only recently, with the greatly increased number of field studies, that the majority of initial and terminal phase colour patterns have been linked (*e.g.* Randall, 1963, Randall & Ormond, 1978, Randall & Choat, 1980, Randall, 1983 and Randall & Bruce, 1983).

The generic status of scarids within the subfamily Scarinae has been as confused as the identifications at the species level, primarily as a result of the same problem, namely, the lack of described diagnostic morphological features. Colour patterns are of little or no use at the generic level.

Schultz (1958) listed several morphological characters that he considered important in relation to the phylogeny of the Scaridae. These are:

1) number of rows of pharyngeal teeth on each upper pharyngeal bone
2) presence or absence and nature of incisor-like external teeth or dental plates
3) overlapping of jaws at tips
4) number of median predorsal scales
5) number of branched pectoral fin rays.

Schultz (1958) found the number of upper pharyngeal tooth rows to be a particularly useful characteristic at the generic level, and the use of this characteristic was welcomed by Smith (1959). The only internal morphological character examined by Schultz (1958) was vertebral counts which were of limited use at the generic level.

However, genera continued to be described solely on the basis of external morphological characters, particularly scale counts, for example, *Xanothon*, *Cetoscarus*, *Bolbometopon*, *Hipposcarus*, *Margaritodon*, *Chlorurus* and *Callyodon* (Smith, 1956, 1959), *Scarops*, *Scarus* and *Chlorurus* (Schultz, 1958) and *Ypsiscarus* (Schultz, 1969).

After detailed analyses of Eastern Pacific scarid species, Rosenblatt and Hobson (1969) recommended that until the internal anatomy of a large number of parrotfish species is known, the most reasonable way to arrange the species of the Scarinae would be to recognize only two genera, *Bolbometopon* Smith, 1956 and *Scarus* Forsskål, 1775. However, in the recent paper by Randall and Bruce (1983), four genera within the Scarinae were recognized: *Bolbometopon* Smith, 1956, *Cetoscarus* Smith, 1956, *Hipposcarus* Smith, 1956 and *Scarus* Forsskål, 1775. This generic system was based on external morphological characters.

The systematic aspects of the present morphological study are restricted to the interrelationships between the genera in the subfamily Scarinae. The proposed classification is based primarily on internal morphological characters, and is supported by external morphological characters, juvenile colouration, and adult behaviour.

A cladogram describing the proposed phylogeny of genera within the Scarinae is shown in Fig. 3.1. This cladogram is based on the shared derived characters (synapomorphies) listed in Table 3.1, and follows the method proposed by Hennig (1966). Reversion and/or convergent events have been considered using a parsimonious approach. The outgroup comparison rule was applied when considering the polarity of the character states, with outgroup comparisons being made with the Labridae, Sparisomatinae and *Euscarus*, and within the Scarinae.

It is believed that the labrid and scarid fishes arose from a common ancestral stock, with labrids possessing the more generalized percoid characters (Schultz, 1958, Greenwood, *et al*, 1966, Liem & Greenwood, 1981 and Kaufman & Liem, 1982). In the present study, as in Schultz (1958), the most ancestral character state is regarded as that which bears the closest resemblance to the form found in the labrids. In this respect, the Sparisomatinae possesses the most primitive, *i.e* labrid-like, scarids. Within this group, however, the lack of anatomical studies precludes the construction of a detailed phylogeny. The phylogeny proposed in the present study is therefore restricted to the Scarinae, with the addition of the genus *Euscarus* (subfamily Sparisomatinae) which has been described in detail by Board (1956).

From the limited morphological studies of Schultz (1958), *Euscarus* and *Sparisoma* appear to be the genera most closely related to the Scarinae. This observation is supported by the detailed anatomical studies on *Euscarus* by Board (1956). However, the generic status of *Euscarus* is questionable as it differs from

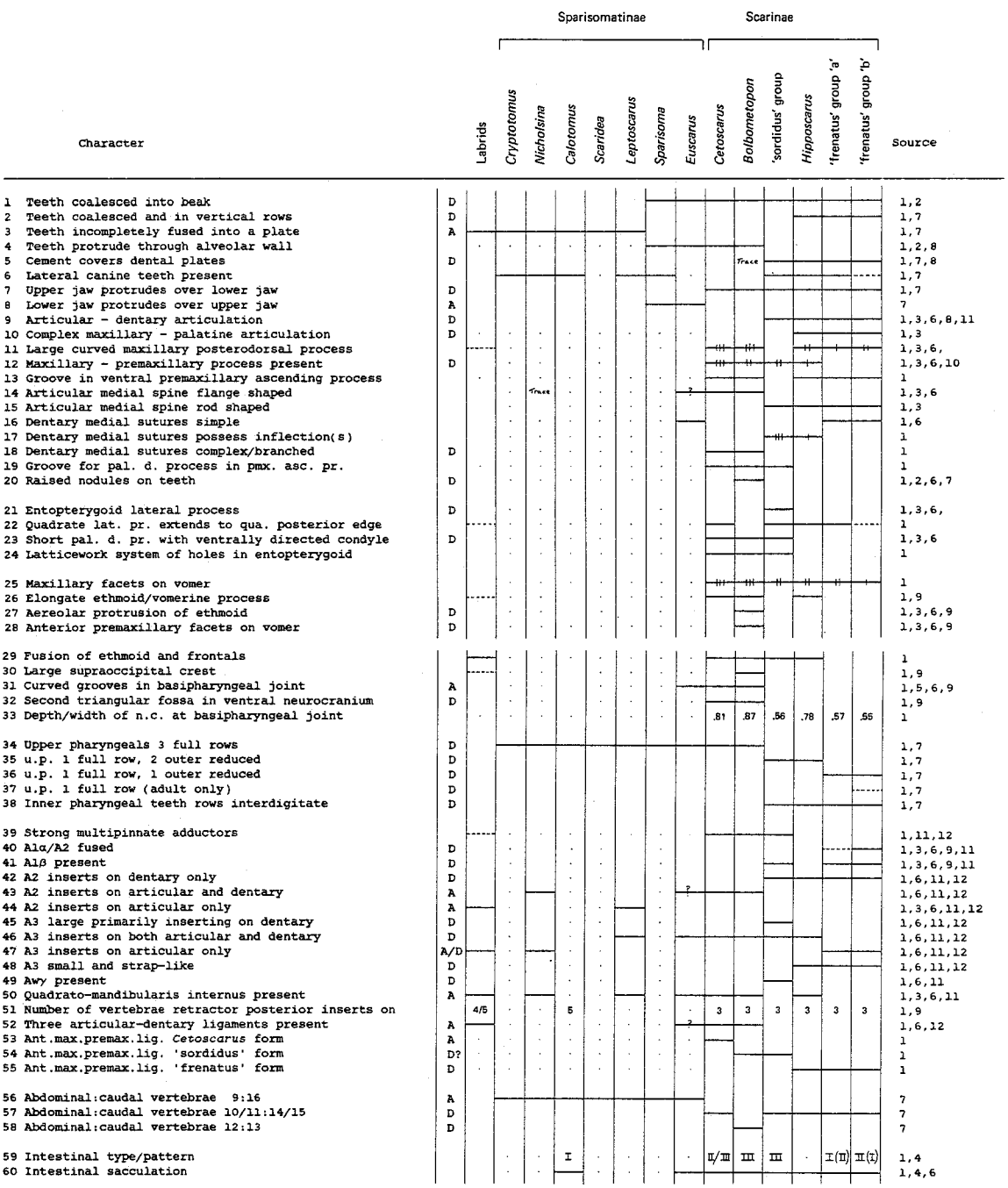
Figure 3.1

A cladogram showing the proposed phylogeny of the genera within the Scarinae, based on the morphological observations listed in Table 3.1.

In this figure, each bar is numbered corresponding to a character in Table 3.1. The sparisomatine genus *Euscarus* is included as the sister group of the Scarinae.


Euscarus
Cetoscarus
Bolbometopon
'sordidus' group
Hipposcarus
'frenatus' group
28
27
20
49
21
50
41
50
47
12
40
36
55
48
10
2
42
41
38
35
9
5
18
32
57 + 58
12
7
45
1
loss or convergence
synapomorphies

Table 3.1 The distribution of morphological characters among the scarid genera.



Source: 1 = Present study 2 = Boas (1879) 3 = Lubosch (1923,1929) 4 = Suyehiro (1942)
5 = Monod (1951) 6 = Board (1956) 7 = Schultz (1958) 8 = Frydl (1975)
9 = Yamaoka (1978,1980) 10 = Bruce (1979) 11 = Gobalet (1980) 12 = Tedman (1980b)
Labrid data was based on: Lubosch (1929); Rognes (1973); Yamaoka (1978); Van Hasselt (1979); Tedman (1980a,b) and the present study.

Legend: ├──┤ = present; │ │ = absent; │ · │ = not recorded; ├┈┈┤ = present in some species
┼┼┼ = strongly developed; ┼┼ = moderately well developed; ┼ = poorly developed
A = ancestoral D = derived
A key to the abbreviations used in this table are given in Section 1.3

Sparisoma only in the form of a single external character, *i.e.* an additional median predorsal scale (Schultz, 1958). The relationship between *Sparisoma* and *Euscarus* requires reanalysis.

Because of the lack of detailed anatomical studies of *Sparisoma*, *Euscarus* is proposed in this study as the sister group of the Scarinae and was used as the outgroup when assessing the polarity of characters in genera or groups within the Scarinae. If the overall difference between *Euscarus* and *Sparisoma* is found to be insufficient to separate the two genera, then *Sparisoma* (including *Euscarus*) would represent the sister group. From the known morphology of *Sparisoma*, such a fusion would not alter the results of the outgroup comparisons with *Euscarus*. In the present study, the Sparisomatinae (excluding *Euscarus* and *Sparisoma*) as a whole was only used for outgroup comparisons when the character state considered was shared by all members of the group.

In the proposed phylogeny (Fig 3.1), five of the characters are tentatively included because of their strikingly unusual nature, even though the state of these characters for all genera in the Sparisomatinae is not known. These characters are:

a) The second triangular fossa in the ventral surface of the neurocranium, which forms the site of origin for the anterior levator posterior muscle in *Cetoscarus* and *Bolbometopon* (No. 32, Table 3.1). This structure is absent in *Calotomus* (Yamaoka, 1980) and in labrids (Rognes, 1973 and Yamaoka, 1978). All other scarine genera (and groups) examined only have a small depression in this region. This fossa is therefore tentatively regarded as a derived feature (although an examination of *Sparisoma* and

Euscarus is necessary).

b) The unusual branching nature of the dentary medial sutures in *Cetoscarus* and *Bolbometopon*; this has only been recorded from these genera, and is absent in *Euscarus* (Board, 1956) and all remaining scarine genera (and groups) (No. 18, Table 3.1). This character state is therefore considered a uniquely derived feature.

c) The form of the A3 section of the adductor mandibulae in *Euscarus*, *Cetoscarus*, *Bolbometopon* and the 'sordidus' group. This has been designated derived by comparison with the state of the A3 section in *Leptoscarus*, *Calotomus* and *Nicholsina* (Table 3.1); a decision which should be considered as tentative and could only be confirmed after further analysis of the other sparisomatine genera.

d) Anterior premaxillary facets on the vomer of *Bolbometopon*. This feature was not apparent in the published descriptions of *Leptoscarus* (Lubosch, 1923, 1929), *Calotomus* (Yamaoka, 1980) and *Euscarus* (Board, 1956), and was absent from all scarine genera (and groups) examined, with the exception of *Bolbometopon* (No. 28, Table 3.1). Therefore, this feature is considered a uniquely derived character.

e) Maxillary-premaxillary processes (No. 12, Table 3.1). These processes were not figured or described in the published illustrations of *Euscarus* by Board (1956) or in the description of *Sparisoma* by Frydl (1975), and are absent in *Calotomus* and *Leptoscarus* (Bruce, 1979). Their presence in *Cetoscarus*, *Bolbometopon* and the 'sordidus' group is therefore, regarded as derived, with the reduction in size in *Hipposcarus* and absence in

the 'frenatus' group representing a secondary loss.

In addition to outgroup comparisons, ontogenetic development was considered when assessing the status of various character states. Features present in juveniles but absent in adults were regarded as potentially ancestral, whilst characters or forms that are only found in adults were regarded as being more likely to be a derived (specialized) state (Section 2.5). For example, the reduction in the relative size of the outer tooth rows on the upper pharyngeal bones and the presence of the entopterygoid lateral process in adult members of the 'sordidus' group (Chapters 1 and 2), are both regarded as derived states. This status is based on outgroup comparisons but is also supported by developmental observations (Section 2.3).

As noted by Schultz (1958), the number of upper pharyngeal tooth rows is a useful character at the generic level, there being a progressive diminution of the outer rows leading to specialized forms possessing only one or two tooth rows on each upper pharyngeal bone (Table 3.1). (These findings are supported by ontogenetic observations [Section 2.3]). However, the number of upper pharyngeal tooth rows is not a consistent characteristic as there are within-species variability (*e.g.* in *S. frenatus* and *S. globiceps*, Sections 1.3.2 & 1.3.4.2) and ontogenetic changes (*e.g.* in *S. sordidus*, *S. gibbus* and *S. rubroviolaceus*, Sections 1.3.2, 1.3.4.1 and Rosenblatt & Hobson, 1969). In considering the phylogeny of the Scarinae, the number of upper pharyngeal tooth rows was based on the maximum number of rows regularly found in each genus or group. Juvenile counts were taken into consideration but

infrequent adult variations were regarded as atypical and were disregarded.

The main difference between the phylogeny of the Scarinae proposed in this study (Fig. 3.1) and that of Schultz (1958) (Fig. 3.2) is the relationship between members of the Sparisomatinae and Scarinae. Schultz (1958) proposed an early division between the two subfamilies (Fig. 3.2). The two subfamilies differ in vertebral counts and the overlapping of the jaws at the tips (and possibly the egg and larval form [Leis and Rennis, 1983]) but these differences are not necessarily evidence of an early divergence between the two groups. Such a division would require a shared derived character to be present in all sparisomatine genera arising from the main sparisomatine - scarine division. No such character has been found.

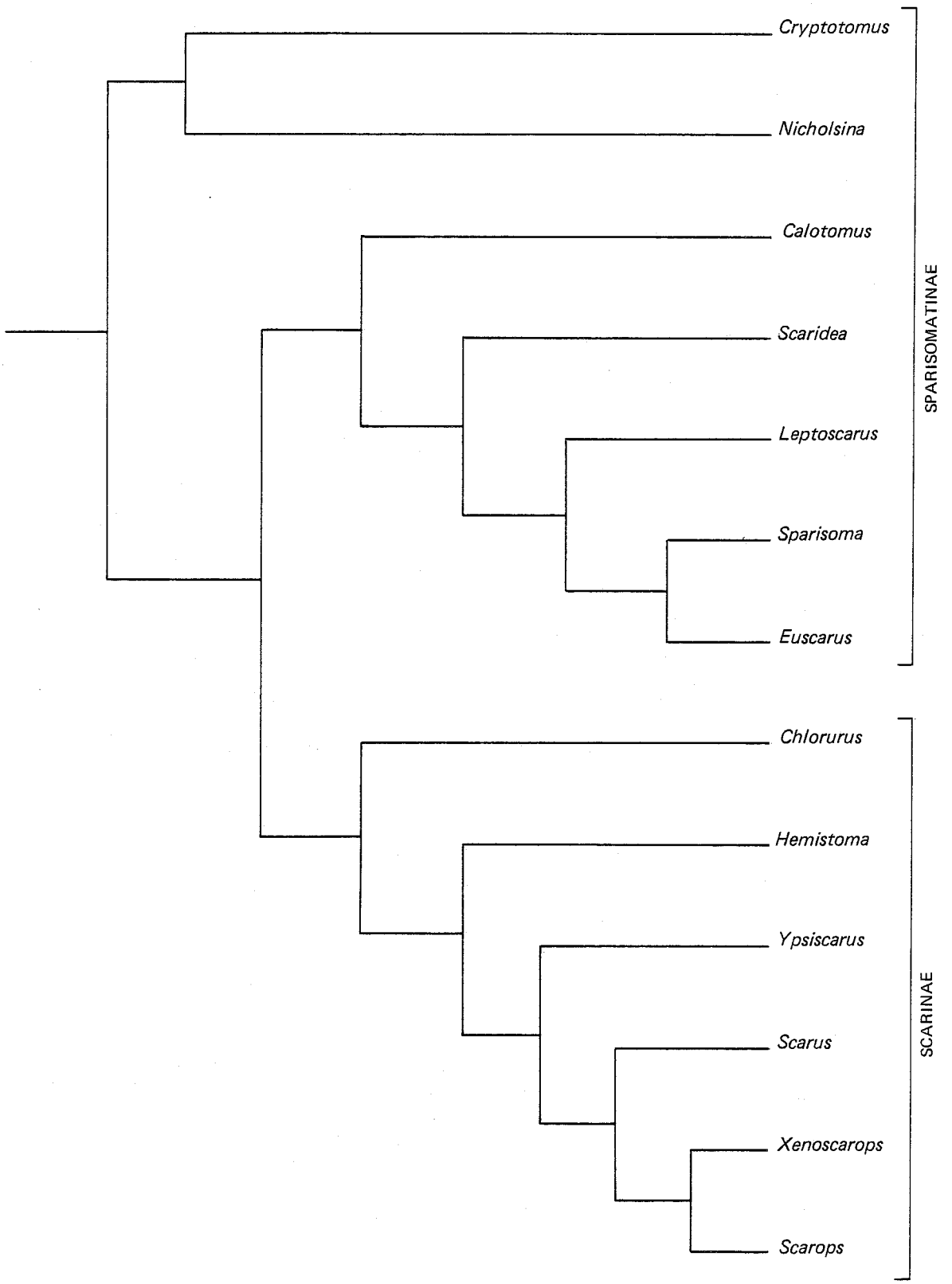
The presence of shared ancestral (primitive) characters within this group of sparisomatine genera does not support the division proposed by Schultz (1958).

It is believed that the Scarinae arose from a group in common with the more advanced sparisomatine forms, *i.e. Euscarus* and *Sparisoma*, and at an evolutionary stage much later than proposed by Schultz (1958) (Fig. 3.2). A recent division between the Scarinae and the advanced sparisomatine forms as proposed in this study, would account for the relatively large number of character states shared by *Euscarus* and *Cetoscarus* (Table 3.1). This suggested relationship is tentative and will require more morphological analyses of the Sparisomatinae, particularly *Sparisoma* and *Euscarus*.

Figure 3.2

The phylogeny of the genera in the family Scarinae as proposed by Schultz (1958).

This figure is modified from Figure 1 in Schultz (1958).


Cryptotomus
Nicholsina
Calotomus
Scaridea
Leptoscarus
Sparisoma
Euscarus
SPARISOMATINAE
Chlorurus
Hemistoma
Ypsiscarus
Scarus
Xenoscarops
Scarops
SCARINAE

The proposed phylogeny of the Scarinae (Fig. 3.1) is based primarily upon examinations of scarine genera (and groups) from the Great Barrier Reef. As a result, the genus *Ypsiscarus* is not included (and needs a separate examination). At present, there is a lack of detailed knowledge of the morphology of the sparisomatine genera which is essential as a basis for constructing a cladogram of the Scarinae and of the Scaridae as a whole.

The above phylogenetic considerations have revealed that several distinct phyletic lines are present within the Scarinae. Some of these comply with existing generic divisions, but others differ markedly. From the morphological descriptions in Section 1.3, two major groups have been described in the genus *Scarus*. These groups are believed to represent distinct phyletic lines (Fig. 3.1), and may differ sufficiently to demand full generic status within the subfamily Scarinae. It is proposed that the following genera be recognized within the Scarinae: *Cetoscarus*, *Bolbometopon* and *Hipposcarus*, with due consideration to the status of the 'sordidus' and 'frenatus' groups, presently in the genus *Scarus*. (The status of *Ypsiscarus* was not examined in this study).

In assessing the generic status of species within the Scarinae, the full list of characters given in Table 3.1 was considered. The three basic types of internal morphological characteristic that were regarded as important in the recognition of genera are:

1) Cranial osteology, including the premaxilla, maxilla, dentary, articular, suspensorium, neurocranium and pharyngeal apparatus
2) Jaw myology, with emphasis on the adductor mandibulae

3) Intestinal patterns.

The value of each taxonomic character is, in part, dependent upon its variability within the species or genus considered. In this study, little within-genus (or group) variation was found in the osteological and myological characters used. More variation was observed in the form of the intestinal pattern, but as in the osteological and myological studies, this variability was less than that found between genera or groups (Sections 1.3 and 1.5).

When assessing the relative importance of each character, the functional role in the biology of the species was considered. This enabled whole functional complexes to be identified (primarily the jaw apparatus, its component parts, and the pharyngeal apparatus) and the relationship between characters to be estimated. When two characters were functionally related, their relative taxonomic value was decreased correspondingly (following Mayr, 1969, p 221). This approach is, however, limited by the degree of information relating to the function of the character. The application of such information in the systematics of higher taxa has been suggested by Liem and Greenwood (1981).

The five morphological groups (and/or genera) recognized in this study are outlined below, with a key based primarily on internal morphological characters. The decision to maintain the genus *Cetoscarus* is based on its possession of a unique combination of characters. Although it is closely related to *Bolbometopon*, this genus possesses a sufficient number of unique characters to separate and distinguish it from *Cetoscarus*. The other genera and groups possess distinctive combinations of characters and each has at least

one unique character.

A key to the Great Barrier Reef genera and species groups in the subfamily Scarinae, based primarily on internal morphological characters of adults.

1) a) Dental plates not covered in cement, no articular-dentary articulation..... 2

   b) Dental plates covered in cement, articular-dentary articulation..... 3

2) a) Teeth simple, ethmoid-vomerine process long and curved..... *Cetoscarus*

   b) Round nodule on each tooth, ethmoid-vomerine process straight with areolar process on ethmoid..... *Bolbometopon*

3) a) Vertical tooth rows alternate in possessing a tooth on cutting edge, entopterygoid lateral process and Awy present, large A3..... 'sordidus' group

   b) Vertical tooth rows all possess a tooth on cutting edge, entopterygoid lateral process and Awy absent, small A3..... 4

4) a) A3 tendinous insertion on articular only, no premaxillary process, upper pharyngeal tooth rows two or less, Aiβ present..... 'frenatus' group

   b) A3 tendinous insertion on articular and dentary, premaxillary process present, three upper pharyngeal tooth rows, Aiβ absent..... *Hipposcarus*

Genus: *Cetoscarus* Smith, 1956

Diagnostic characters:

Cetoscarus may be identified by the following combinations of characters:

1) Upper jaw over lower jaw, teeth without nodules, no articular-dentary articulation, and has complex branched dentary medial sutures
2) Anterior maxillary-premaxillary ligaments arise from ridges on the maxilla
3) Ethmoid-vomerine process elongate and characteristically curved, but lacking anterior premaxillary facets and the areolar swelling of *Bolbometopon*
4) Two pairs of triangular fossae present in ventral face of neurocranium, basipharyngeal joint curved, the three upper pharyngeal tooth rows having a ratio of approximately 4:3:1 and no interdigitation of the inner two rows.

Characteristic features include: maxillary condyles on the vomer, 10-11 abdominal vertebrae, a crenate cutting edge on the jaws, the absence of A1β and Awy, the presence of a large A3 inserting on the dentary and articular, a quadrato-mandibularis and a type III intestinal pattern.

Genus: *Bolbometopon* Smith, 1956

Diagnostic characters:

1) Areolar protrusion of the ethmoid
2) Premaxillary facets on the anterior face of the vomer

3) Rounded nodules on each tooth

4) Steeply sloping ethmoid-vomerine process

5) Twelve abdominal vertebrae.

Characteristic features include: upper jaw overlapping lower jaw, no articular-dentary articulation, traces of cement on jaws, crenate cutting edges on jaws, complex dentary medial sutures, a maxillary-premaxillary process, maxillary condyles on vomer, short palatine dorsal process with simple maxillary articulation, two pairs of triangular fossae in ventral face of neurocranium, curved basipharyngeal grooves, three upper pharyngeal tooth rows, with a width ratio of 4.5:3:1, and inner pair of rows not interdigitating, no A1β or Awy, a large A3 inserting on the dentary and to a slight extent on the articular, a quadrato-mandibularis and a type III intestinal pattern.

Genus: *Hipposcarus* Smith, 1956

Diagnostic character:

1) A small A3 inserting tendinously on the dentary and articular.

In addition, *Hipposcarus* may be identified by the following combinations of character states:

1) A complex palatine-maxillary articulation and a premaxillary process on the maxilla.
2) An articular-dentary articulation, cement covered dental plates and no A1β.

Characteristic features include: each vertical tooth row having a tooth on the cutting edge of the jaws, dental plates off white in colour, poorly developed canine teeth, inflected dentary

medial sutures, three upper pharyngeal tooth rows with a width ratio of 7:3:1 and inner pair of rows interdigitating, a single pair of triangular fossae in ventral face of neurocranium and a poorly developed quadrato-mandibularis.

Genus: *Scarus* Forsskål

The 'sordidus' group

Diagnostic characters:

1) Each vertical tooth row alternating in the possession of a tooth on the cutting edge.
2) A specialized entopterygoid lateral process.
3) An Awy.

Characteristic features include: an articular-dentary articulation, deep robust cement covered dental plates which may be coloured, lateral canines, if present, well developed but only on upper jaw, inflected dentary medial sutures, a premaxillary process on the maxilla, a short palatine dorsal process with a simple maxillary articulation, three upper pharyngeal tooth rows (in small juveniles and adults but may be reduced to two in some large individuals) with a ratio of 20:5:1 and interdigitating inner rows, a large A3 inserting primarily on the dentary, an A1β, no quadrato-mandibularis and a type III intestinal pattern.

The 'frenatus' group

Diagnostic characters:

1) No maxillary-premaxillary process.
2) A thin strap-like A3 with a single tendinous insertion on the articular.

3) Two (or one) upper pharyngeal tooth rows in both juveniles (including recently recruited specimens, Section 2.3) and adults.

In addition, the 'frenatus' group may be identified by the following combinations of characters:

1) A tooth from each vertical tooth row is present on the cutting edge of the jaws, the dental plates may be coloured and canines, if present, are well developed and may occur on both jaws.
2) The palatine-maxillary articulation is complex and an A1β is present.

Characteristic features include: an articular-dentary articulation, simple dentary medial sutures, two upper pharyngeal tooth rows with a ratio of 4.7:1 and interdigitating medial rows, and a type I or II intestinal pattern. In some species, the A1α and A2 are fused.

A detailed list of the anatomical characters found in each genus or group is given in Table 3.1.

The proposed divisions of the Scarinae are based primarily upon internal morphological characters. These are, however, inconvenient when identifying specimens in the field and in preserved collections, as they require detailed dissections to ascertain the state of many characters. Fortunately, the proposed classification is supported by externally visible morphological characters and for convenience, a key and a brief description of these are given below.

A key to genera and species groups within the Scarinae, based on externally visible morphological characters of adults.

1) a) Dental plates not covered in cement..... 2

   b) Dental plates covered in cement..... 3

2) a) No hump on forehead, shallow body, 2 rows of scales on interopercle, 14 (rarely 15) pectoral fin rays..... *Cetoscarus*

   b) Large hump on forehead, deep body, 1 row of scales on interopercle, 15/16 pectoral fin rays..... *Bolbometopon*

3) a) Teeth on cutting edge from alternate vertical tooth rows, pectoral fin rays 15 or more, median predorsal scales 4 or less with no anterior pair..... 'sordidus' group

   b) Teeth on cutting edge from each vertical tooth row, pectoral fin rays 15 or less, median predorsal scales 4 or more, some species with anterior pair..... 4

4) a) Elongate angular snout, triangular pattern of cheek scales, white dental plates..... *Hipposcarus*

   b) Rounded snout, simple 2/3 cheek scale rows, dental plates may be coloured..... 'frenatus' group

Remarks and notes on field identifications.

Cetoscarus and *Bolbometopon*.

Although *Cetoscarus* and *Bolbometopon* are closely related and have a similar internal anatomy, they can be easily distinguished both in the field and from preserved collections. Both are monotypic genera. *Bolbometopon* possesses a deep body, a large hump on the forehead, a drab uniform colouration and has a much larger adult size than *Cetoscarus*. *Bolbometopon* differs from *Cetoscarus* in that it has only one row of scales on the interopercle (*cf.* two in *Cetoscarus*), fewer median predorsal and cheek scales, modally one more pectoral fin ray and no sexual dimorphism (Randall and Bruce, 1982). Initial and terminal phases of *Cetoscarus* are both distinctly marked (Randall and Bruce, 1982). The colour of the juvenile of *Bolbometopon* is drab (J.H. Choat pers. comm.), whilst that of *Cetoscarus* is both gaudy and distinctive (Section 4.3.2).

Hipposcarus

Species in this genus are easily distinguished in the field because of their elongate angular snouts. The unusual cheek scale formation and the invariably off-white dental plates assist in the identification of preserved specimens. The juvenile of this species is both unique and distinctive. The shape, colouration and behaviour more closely resemble *Lethrinus* species than *Scarus* species (Section 4.3.2).

'Sordidus' and 'frenatus' groups.

Species in these two groups, which are at present listed in the same genus, exhibit a wide variety of forms. There are, however, several characters which aid in separating species in the two groups in the field. Members of the 'sordidus' group have exposed dental plates and a low feeding rate, whilst members of the 'frenatus' group typically have dental plates which are either covered by the lips or slightly exposed, and have a high feeding rate (Section 5.3). Exceptional 'frenatus' group species with more exposed dental plates include *S. rubroviolaceus* and TP *S. ghobban*. Juveniles of the two groups have a common basic colour pattern (Chapter 4), although members of the 'sordidus' group have a tendency towards black banding or an overall dark colouration (Section 4.3).

Preserved specimens may be identified using dental characters in conjunction with scale and pectoral fin ray counts. Both groups show a wide variety of scale and ray counts, with considerable variation within and between species (Schultz, 1958 and Randall and Bruce, 1983). 'Sordidus' group species typically have 15 or more pectoral fin rays and four or less median predorsal scales, with no anterior paired median predorsal scales. 'Frenatus' group species typically have 14 pectoral fin rays (rarely 15) and four or more median predorsal scales, often with an additional anterior pair of scales. The combination of 15 pectoral fin rays and four median predorsal scales (with no anterior pair) is typical for 'sordidus' group species but exceptional in 'frenatus' group species. (The fin ray and median predorsal scale counts for most *Scarus* species are tabulated in Schultz, 1958 and Randall & Bruce, 1983). The two

groups may also be separated by counting the number of upper pharyngeal tooth rows, as 'sordidus' group species possess three rows of teeth, whilst 'frenatus' group species typically possess two rows. This technique can be useful in the examination of specimens as small as 11.5 mm S.L.

The classification of genera and groups within the Scarinae proposed here has limitations. Firstly, the observations were based on species from a single zoogeographical region, the Great Barrier Reef (although many of the species are recorded as having extensive Indo-Pacific ranges [Randall & Choat, 1980 and Randall & Bruce, 1983]). Secondly, only a limited number of species and individuals were examined in each genus or group, and thirdly, the genus *Ypsiscarus* was not examined, because of its rarity in the Great Barrier Reef region (Choat & Randall, pers. comm.).

Before such a suggested classification can be accepted, further analyses of the internal morphology of other scarid species are required. If these analyses support the findings of this study, the following classification is proposed:

Family : Scaridae

Subfamily : Scarinae

Genus : *Cetoscarus* Smith, 1956
Syn: *Callyodon* Gronow, 1763 (in part)
Scarus Forsskål, 1775 (in part)
Chlorurus Swainson, 1839 (in part)
Pseudoscarus Bleeker, 1861 (in part)

Bolbometopon Smith, 1956
Syn: *Callyodon* Gronow, 1763 (in part)
Scarus Forsskål, 1775 (in part)
Chlorurus Swainson, 1839 (in part)
Pseudoscarus Bleeker, 1861 (in part)

Hipposcarus Smith, 1956
Syn: *Scarus* Forsskål, 1775 (in part)
Pseudoscarus Bleeker, 1861 (in part)

'Sordidus' group (new genus)
Syn: *Callyodon* Gronow, 1763 (in part)
Scarus Forsskål, 1775 (in part)
Chlorurus Swainson, 1839 (in part)
Pseudoscarus Bleeker, 1861 (in part)
Xanothon Smith, 1956 (in part)

Scarus Forsskål, 1775 ('frenatus' group)
Syn: *Callyodon* Gronow, 1763 (in part)
Callyodon Scopoli, 1777 (subgenus)
Calltodon Walbaum, 1792
Erychthys Swainson, 1839
Hemistoma Swainson, 1839
Petronason Swainson, 1839
Pseudoscarus Bleeker, 1861 (in part)
Loro Jordan & Evermann, 1896
Xanothon Smith, 1956 (in part)
Margarittodon Smith, 1956
Scarops Schultz, 1958
Xenoscarops Schultz, 1958 (subgenus)

The genus *Scarus* when initially described by Forsskål in 1775 included species presently placed in both the 'sordidus' and 'frenatus' groups (*i.e. S. ghobban, S. niger, S. ferrugineus, S. psittacus* in the 'frenatus' group, and *S. sordidus* in the 'sordidus' group). The generic description of *Scarus* (in Schultz, 1958) is in accord with those characters possessed by members of the 'frenatus' group, but not the 'sordidus' group. In addition, the type species of the genus, *S. psittacus*, is a member of the 'frenatus' group. (The identity of Forsskål's *S. psittacus* is discussed by Randall & Ormond [1978]). It is therefore proposed that the genus *Scarus* be restricted in its application to members of the 'frenatus' group. The 'sordidus' group differs from the generic description of *Scarus* given by Schultz (1958) in that it possesses three rather than two rows of teeth on each upper pharyngeal bone. There is no existing genus which is based on the features that define the 'sordidus' group or that exclusively contains 'sordidus' group species. It is therefore proposed that the 'sordidus' group

be recognised at the generic level.

At present, the Scaridae is divided into two subfamilies, the Sparisomatinae and the Scarinae. This division is supported by some internal morphological characters (*e.g.* abdominal vertebrae counts, Table 3.1), several external morphological characters (Schultz, 1958) and to a limited extent by early life history characters (Leis & Rennis, 1983). This division may be questioned in view of the close relationship between some sparisomatine and scarine genera (*e.g. Sparisoma* and *Cetoscarus*), and the fact that taxonomically important characters, including the form of the articular-dentary joint (Section 2.5), have not been considered. However, it is suggested that until further analyses of the anatomy and early life histories of *Cetoscarus*, *Bolbometopon* and the sparisomatin genera have been undertaken, the present subfamilial classification should be retained as a convenient taxonomic division.

In this study, the widely accepted nomenclature of the parrotfishes has been followed, *viz.* the family Scaridae with two subfamilies: the Sparisomatinae and the Scarinae (*sensu.* Schultz, 1958). The familial status of the parrotfishes has, however, been questioned. Kaufman and Liem (1982) proposed a classification, based on the structure of the pharyngeal apparatus, wherein the Labridae, Odacidae and Scaridae are represented by a single family, the Labridae. The Scaridae therefore, is reduced to a subfamilial group. However, observations of early life history characters by Richards and Leis (1983) do not support the proposal of Kaufman and Liem (1982). Until such discrepancies are resolved and more detailed analyses of the families concerned are undertaken, the

conventional nomenclature of the Scaridae is considered the most reasonable system available.