OSTEOLOGY AND RELATIONSHIPS OF THE SPANISH MACKERELS AND SEERFISHES OF THE TRIBE SCOMBEROMORINI

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ABSTRACT

Scomberomorus is distinct from all other scombrid genera in twenty-nine osteological characteristics. In most of these characteristics *Scomber, Rastrelliger, Acanthocybium, Gymnosarda, Allothunnus, Sarda, Auxis, Euthynnus, Katsuwonus* and *Thunnus* agree one with another. Since *Scomber* is assumed to be the most primitive genus of Scombridae (excluding *Gasterochisma*), these characteristics are considered to be primitive ones retained in all scombrids but *Scomberomorus*, in which they are modified to suit its own line of specialization towards an incomplete return to characters found in the Carangidae. *Acanthocybium* shares with *Scomberomorus* many features, seldom or rarely possessed by the other genera. Certain primitive percoid characteristics of *Scomber* are also retained in *Scomberomorus* and *Acanthocybium*. This evidence strongly suggests the closer affinities between *Scomberomorus* and *Acanthocybium* than the affinities of either with other scombrid genera, their common origin from or closer to the Scombrini, and the necessity to retain Scomberomorini as a tribe of the Scombridae. *Sarda* is remotely related to Scomberomorini. *Acanthocybium* is only superficially similar to the Xiphoidei.

Scomberomorus chinensis appears intermediate between *Acanthocybium* and the other species of *Scomberomorus* as well as a primitive species of the genus from which two groups of seerfishes diverged, the *cavalla* group consisting of *S. commerson* and *S. cavalla*, and the *guttatus* group consisting of *S. guttatus, S. koreanus, S. lineolatus, S. maculatus* and *S. regalis*. Within the latter group, *S. guttatus* and *S. koreanus* are more closely related to each other. *S. lineolatus* possesses many characteristics intermediate between the two groups. The *cavalla* group is very closely related to *Acanthocybium* and the major difference lies in the vertebral count. Specialized characters of each species are pointed out.

INTRODUCTION

The family Scombridae has been clearly defined by Regan (1909). Many investigators followed Regan's classification, maintaining this family as a natural unit (Starks 1910, Smith 1949, Fraser-Brunner 1950, de Beaufort and Chapman 1951, Rivas 1951, Jones and Silas 1960 and 1964, Collette and Gibbs 1963, Nakamura 1965, Gibbs and Collette 1967, Collette and Chao 1975). Kishinouye (1923) divided Regan's Scombridae into four families: Scombridae, Cybiidae, Katsuwonidae and Thunnidae. This classification although adopted by Berg (1940) and tentatively recognized by Godsil (1954), was shown long ago to be based on inadequate grounds (Takahasi 1926). Kishinouye (1923) treated *Cybium* (= *Scomberomorus*) and *Acanthocybium* together with *Grammatorcynus, Sarda* and *Gymnosarda* under Cybiidae. Starks (1910) placed *Scomberomorus, Acanthocybium* and *Sarda* within his subfamilies Scomberomorinae, Acanthocybinae and Sardinae respectively. On the basis of external and osteological characteristics, Jones and Silas (1960, 1964) recognized Scombrinae. Gasterochismatinae, Scomberomorinae and Thunninae as the subfamilies of Scombridae. They included *Scomberomorus* and the monotypic *Acanthocybium* within the Scomberomorinae, *Grammatorcynus* together with *Scomber* and *Rastrelliger* within the Scombrinae and placed *Sarda* and *Gymnosarda* within the Thunninae which also included *Auxis, Cybiosarda, Allothunnus, Thunnus, Katsuwonus* and *Euthynnus*. Nakamura (1965) tentatively recognized three subfamilies: Gasterochismatinae, Scombrinae and Thunninae and placed only *Thunnus* and *Euthynnus* (= *Katsuwonus*) within the Thunninae based on a study of the axial skeleton. It is implied in Nakamura's work that Scomberomorinae is suppressed, and as a result, *Scomberomorus* and *Acanthocybium* together with the other genera he displaced from Thunninae, ought to be alligned elsewhere (Scombrinae). Collette and Chao (1975) classified family Scombridae into two subfamilies: Gasterochismatinae and Scomberomorinae, and divided the Scombrinae into four tribes: Scombrini, Scomberomorini, Sardini and Thunnini. They placed *Grammatorcynus, Scomberomorus,* and *Acanthocybium* within the tribe Scomberomorini.

At least a dozen valid species of *Scomberomorus* exist on a global basis: *S. cavalla, S. maculatus* and *S. regalis* from the west Atlantic, *S. sierra* and *S. concolor* from the east Pacific and *S. commerson, S. chinensis, S. semifasciatus, S. lineolatus, S. niphonius, S. koreanus, S. guttatus, S. queenslandicus* and *S. multiradiatus* from the Indo-Pacific (Kishinouye 1923, Munro 1943 and 1967, Smith 1949, Fraser-Brunner 1950, de Beaufort and Chapman 1951, Deraniyagala 1952, Mago Leccia 1958, Jones and Silas 1961 and 1964, Williams 1960, Collette and Gibbs 1963, Silas 1964, Devaraj, in press). Munro (1943) divided *Scomberomorus* into nine subgenera which also included *Lepidocybium* (a gempylid) and *Cybiosarda*. Jones and Silas (1961) felt that excessive splitting of the genus is undesirable. Mago Leccia (1959) thought that *S. commerson* might deserve separate generic status on account of its closer affinities with *Acanthocybium*. According to Silas (1964), *S. koreanus* is identical with *S. guttatus* or varies only at a subspecific level. Based on morphometric and meristic comparisons, Devaraj (in press) established that *S. koreanus* is a distinct species. Uncertainties on the identity of some of *Scomberomorus* from the western Indian Ocean are evident from the works of Williams (1960), Smith (1964), and Silas (1964). Whether *S. tritor* and *S. sierra* are only geographical races of *S. maculatus*, as supposed to be by Munro (1943), or distinct species as indicated by Collette, Talbot and Rosenblatt (1963) and Collette (1970) has yet to be decided.

Solution of the existing species problems within *Scomberomorus* outlined above, necessitates studies on the comparative anatomy of the constituent species on a world-wide basis. Besides *Scomberomorus*, the tribe Scomberomorini includes two monotypic genera: *Grammatorcynus* and *Acanthocybium* (Collette and Chao 1975) and a knowledge of the anatomy of *Grammatorcynus bicarinatus* and *Acanthocybium solandri* is essential for the determination of their relationship with *Scomberomorus*. Elucidation of the relationship of the Scomberomorini with the other tribes of the Scombrinae and with the Gasterochismatinae, also calls for a comparative study on the anatomy of the various species included within these categories. Towards the part fulfillment of these objectives, osteological investigation on *S. commerson, S. lineolatus, S. koreanus, S. guttatus* and *A. solandri* from the Indian seas was undertaken in comparison with the data on the west Atlantic and other Indo-Pacific species of *Scomberomorus* available through the works of Mago Leccia (1958) and Kishinouye (1923). Osteological information for comparison at generic level within Scombridae were drawn from the material of *Sarda orientalis, Auxis thazard, Euthynnus affinis, Katsuwonus pelamis, Thunnus tonggol* and *Thunnus albacares* in the author's possession and from the contributions of Allis (1903) on *Scomber*, Gnanamuthu (1966) on *Rastrelliger*, Conrad (1938) on *Acanthocybium*, Nakamura and Mori (1966) on *Allothunnus*, Collette and Chao (1975) on Sardini, Gibbs and Collette (1967) on *Thunnus*, and Starks (1910), Kishinouye (1923), Godsil (1954) and Nakamura (1965) on their comparative osteology of Scombridae.

Adult specimens of the Indian species of *Scomberomorus* and *Acanthocybium solandri* landed in the commercial drift-net fisheries of the Rameswaram Island operating in Palk Bay and the Gulf of Mannar were utilized for the study. The disarticulated bones figured and described for each species are from a single specimen except when bones were lost. In such cases bones were taken from another specimen. A skull for each species was prepared from a separate specimen. For meristic counts of vertebrae, fins and gill rakers, many specimens were utilized; the data for the specimens from which bones were prepared are given in Table 1.

TABLE 1. *Details of the specimens used in osteological study.*

Species	Locality	Total Length (mm)	Fork Length (mm)	Sex	Bones studied
S. koreanus	Palk Bay	643	531	F	all bones except skull and branchial arches
S. koreanus	Palk Bay	650	542	F	skull
S. koreanus	Palk Bay	597	—	F	branchial arches
S. guttatus	Gulf of Mannar	575	482	F	all bones except skull and branchial arches
S. guttatus	Gulf of Mannar	679	565	F	skull
S. guttatus	Gulf of Mannar	490	402	F	branchial arches
S. lineolatus	Gulf of Mannar	767	652	F	all bones except skull and branchial arches
S. lineolatus	Gulf of Mannar	937	801	F	skull
S. lineolatus	Gulf of Mannar	660	560	M	branchial arches
S. commerson	Gulf of Mannar	803	695	F	all bones except skull and branchial arches
S. commerson	Gulf of Mannar	772	671	M	skull
S. commerson	Gulf of Mannar	585	505	F	branchial arches
A. solandri	Gulf of Mannar	1157	1069	F	all bones except skull, neurocranium and branchial arches
A. solandri	Andaman Sea	830	—	F	skull, neurocranium and branchial arches

Specimens were immersed in boiling water just long enough to enable loosening the flesh and cleaning the bones. All figures were drawn with the aid of a camera lucida to natural size or at 1.5-3.5 magnification. In general de Sylva (1955), Mago Leccia (1958), Weitzman (1962) and Collette and Chao (1975) were followed in naming the different bones and their parts. The terminology used in describing the branchial arches is after Nelson (1969) and that of the caudal skeleton is after Nybelin (1963) and Monod (1967, 1968).

ABBREVIATIONS USED IN FIGURES

alp anterolateral process
amp anteromesial process
ang angular
auc auxiliary crest
bf berciform foramen
bgry base of gill ray
boc basioccipital
br branchiostegal ray
bsp basisphenoid
cb-1 & 5 ceratobranchials, 1 & 5
cbb cartilaginous basibranchial
cerhy ceratohyal
clt cleithrum
co-2 & 3 copula, 2 & 3
cor coracoid
cp ciliary patch
dhy dorsal hypohyal
dn dentary
e (1) epural, 1
e (2) epural, 2
eb-1 & 4 epibranchial, 1 & 4
ect ectopterygoid
ent entopterygoid
ephy epihyal
epo epiotic
eth ethmoid bone
exo exoccipital
fcha first closed haemal arch
fphyp fused parhypural
fr frontal
gr gill raker
gry gill ray
hb 1 & 3 hypobranchial, 1 & 3
hm hypurale minimum
hpoz haemal postzygapophysis
hprz-1 haemal prezygapophysis, 1
hr horny rods
hs haemal spine
hsp-2 haemal spine (arch) of preural, 2
hsp-3 haemal spine (arch) of preural, 3
hyom hyomandibula
hyp hypural plate (Hypurals I + II & III + IV)
hyph hypurapophysis
ic intercalar
if-1 inferior foramen, 1
ihy interhyal
io-1 first infraorbital
io-2 second infraorbital
ioc infraorbital canal
iolc interorbital lateralis commissure
iop interopercle
ipb-1 to 3 infrapharyngobranchials, 1 to 3
iuptp independent upper pharyngeal tooth plate
le lateral ethmoid
lp lower pharyngeal
lptp lower pharyngeal tooth plate
mpt metapterygoid
mx maxilla
na nasal
npoz neural postzygapophysis
nprz neural prezygapophysis
ns neural spine
obb ossified basibranchial
op opercle
pa parietal
pap parapophysis
pas parasphenoid
pb pharyngobranchial
pcl lower postcleithrum
ped pedicel
pf pineal foramen
pgr pelvic girdle
phyp parhypural
pmp preoperculo-mandibular primary pores
pmx premaxilla
pop preopercle
pp posterior process
pro prootic
ptm posttemporal
pto pterotic
ptrs pterosphenoid
ptryg pterygials
pu-1 to 3 preurals, 1 to 3
qu quadrate
ra retroarticular
scap scapula
scl sclerotic capsule
sh shank
smx supramaxilla
soc supraoccipital
sop subopercle
sph sphenotic
st + hm stegurals + hypurale minimum
spt supratemporal
supcl supracleithrum
sym symplectic
uptp upper pharyngeal tooth plate
ver vertebra
vhy ventral hypohyal
vo vomer

Osteology

1. Skull

a. *Neurocranium*

The skulls of the different species are shown in Figs 1 and 2. The neurocranium (Figs 3-7) is nearly trapezoidal in dorsal view. It is elongate and flat especially at the anterior region and deepest at the posterior end of the orbit. The dorsal surface is provided with a median ridge, two pairs of lateral ridges (internal or temporal and external or pterotic), a pair of auxiliary ridges and three pairs of fossae: dialator, temporal and supratemporal, separated from each other by the lateral ridges.

The breadth of the neurocranium in relation to its length is greatest in *S. koreanus* and *S. guttatus*, tends to be less in *S. lineolatus* and *S. commerson* and is least in *A. solandri*. The supraoccipital crest extends forward over the frontals and together with the median crest of the frontals, forms the median ridge of the neurocranium in *Scomberomorus*, but it does not extend over the frontals in *A. solandri*. In *Scomberomorus*, the temporal ridge formed by the crests of the epiotic, parietal and frontal reaches as far as the anterior border of the frontal, but in *A. solandri* it stops at the level of the anterior end of the pineal window. Anteriorly, the temporal ridge tends to converge slightly with the midline of the neurocranium in *S. koreanus*, runs more or less straight in *S. guttatus*, and slightly diverges from the midline in *S. lineolatus* and *S. commerson*. In all these species including *A. solandri*, this ridge projects posteriorly in the form of a rough process known as the epiotic process which serves as a point of attachment of the posttemporal bone to the braincase. Mago Leccia (1958) remarked that while *S. maculatus* and *S. regalis* possess the epiotic process, *S. cavalla* lacks it. However, the dorsal surface of the neurocranium of *S. cavalla* illustrated in Fig. 1 (Pl. I) of Mago Leccia (1958) shows that the epiotic process is slightly developed in this species. In *S. commerson*, this process is very small, as in *S. cavalla*. The pterotic ridge extends anterior beyond the mid level of the orbit in *Scomberomorus*, but stops at about or before the mid level of the orbit in *A. solandri*. The auxiliary ridge is a small crest formed on the frontal, at the anterior level of the temporal fossa, in between the temporal and pterotic ridges. It is well-developed in *Scomberomorus* especially in *S. koreanus*, *S. guttatus*, *S. maculatus* and *S. regalis*, but reduced in size in *A. solandri*, being more so in larger specimens. The external margin of the auxiliary ridge is concave in *S. koreanus*, *S. guttatus*, *S. maculatus* and *S. regalis*, but nearly straight in *S. lineolatus*, *S. cavalla* and *S. commerson*. Among the investigated species of *Scomberomorus*, the height of the auxiliary ridge is less in *S. cavalla* and *S. commerson*. The height of the ridges and the depth of the intervening fossae are greater in *Scomberomorus* than in *A. solandri*. The dialator fossa is very much reduced in *A. solandri*. At the posterior part of each temporal fossa, anterior to the transverse ridge formed by the suturing of two processes, one each extending

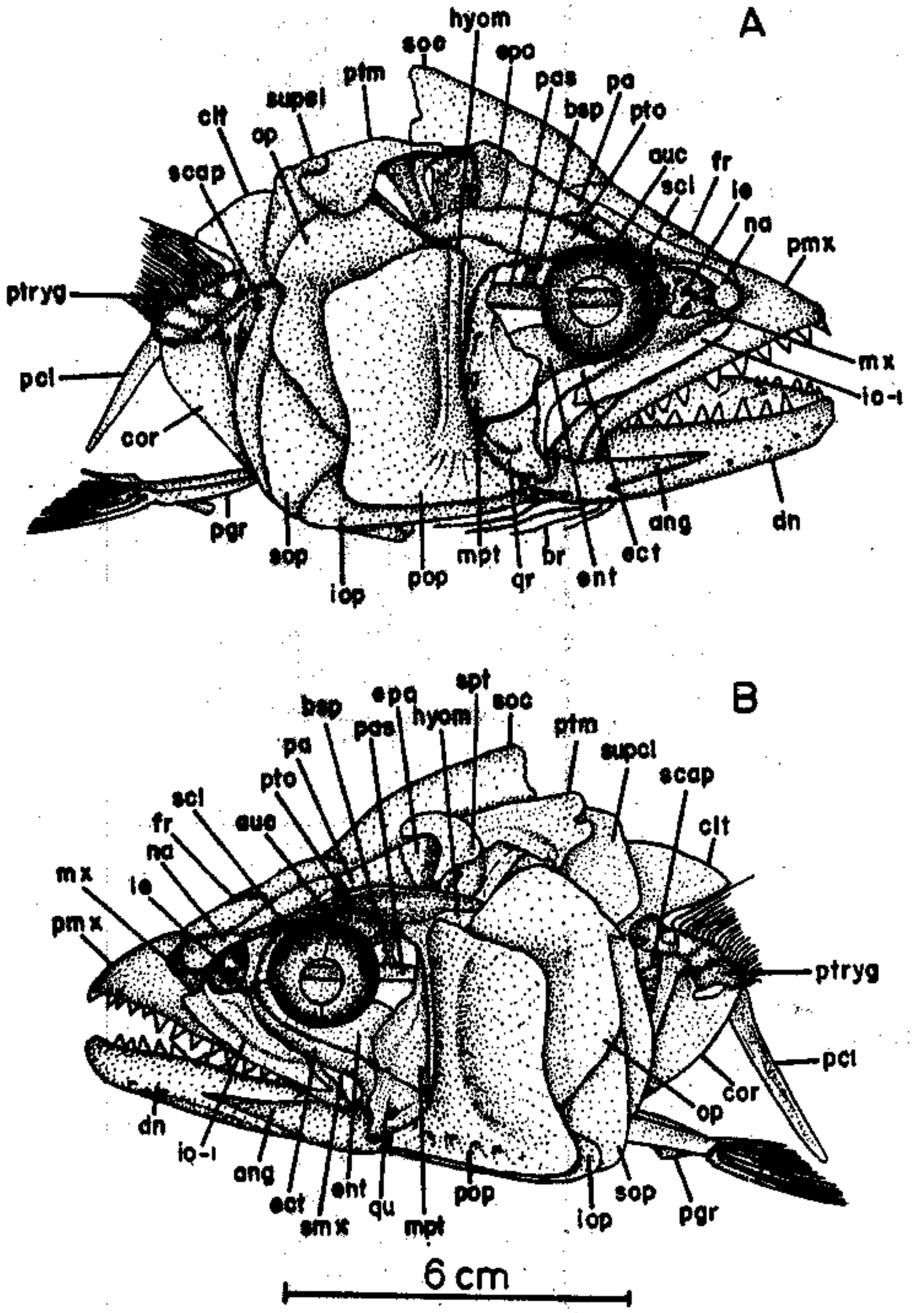

FIG. 1. Lateral view of skull of: A. *S. koreanus* (right side); B. *S. guttatus* (left side).

from the pterotic and the epiotic, is a small membrane-covered area bordered by the epiotic, pterotic and parietal in all the species including *A. solandri*, but excepting *S. koreanus*. Though this area is generally symmetrical, in some cases as in a specimen of *S. commerson*, the one on the right side was found separated into two tiny parts by means of a bony bridge that connected the pterotic with the parietal. This area appears to become a cleft after the neurocranium has been allowed to dry.

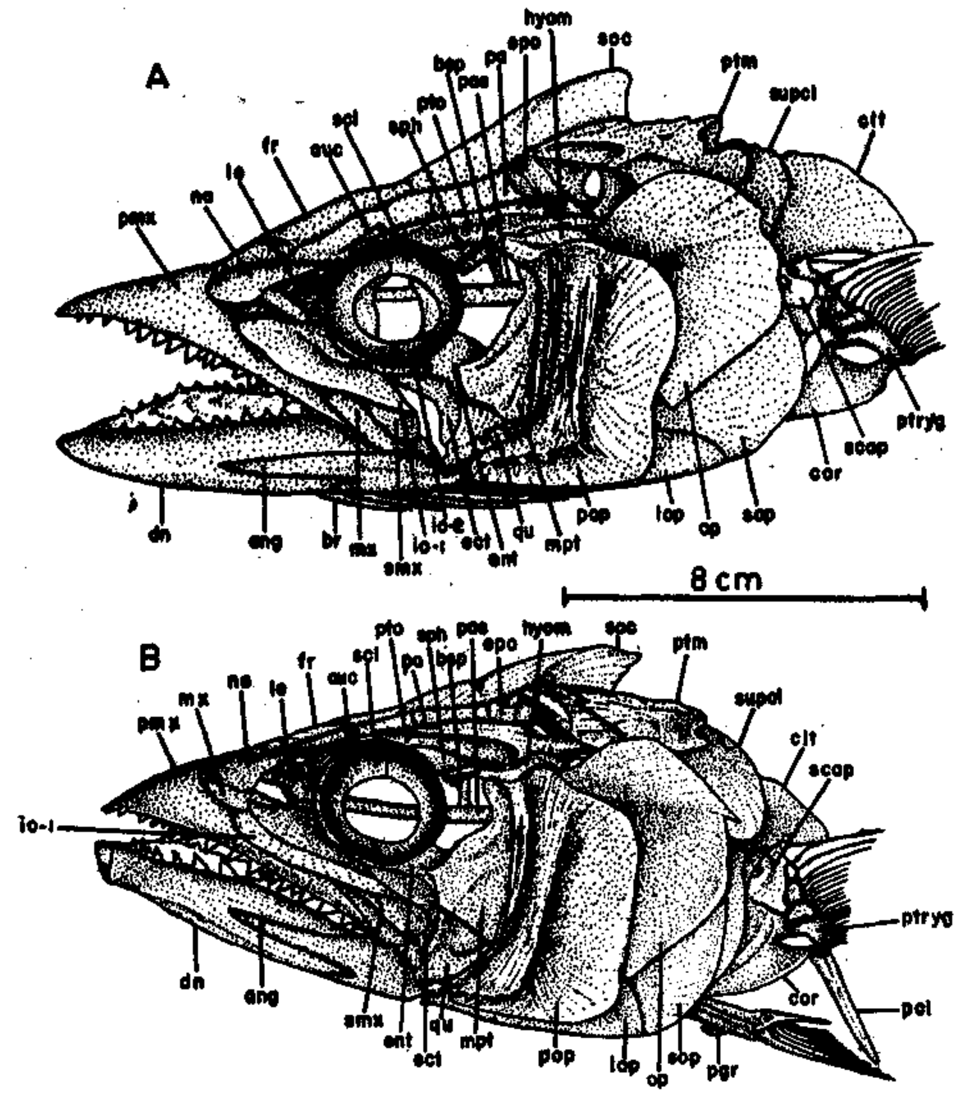

FIG. 2 A-B. Lateral view of skull (left side) of: A. *S. lineolatus*; B. *S. commerson*.

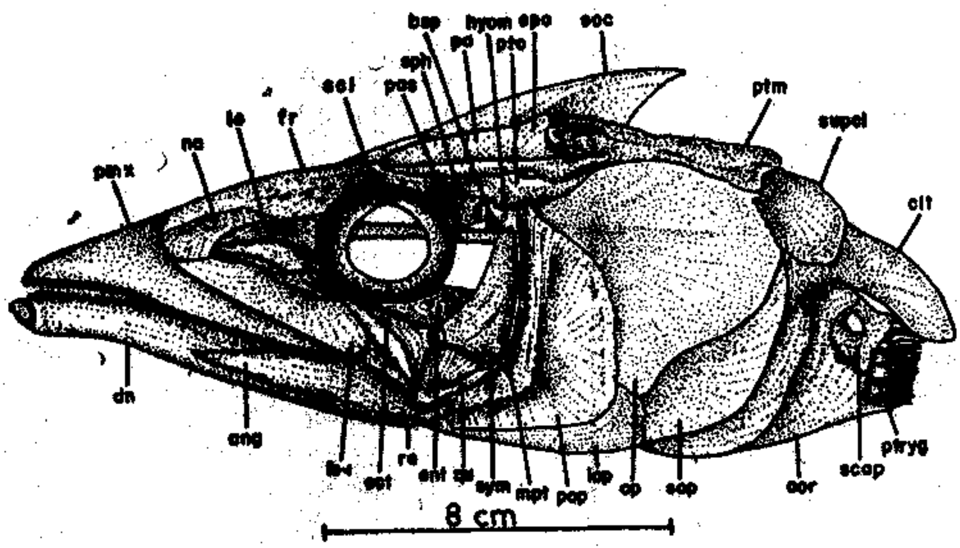

FIG. 2 C. Lateral view of skull (left side) of *A. solandri*.

i. *Ethmoid region — ethmoid, lateral ethmoid, vomer, nasal*:

The ethmoid bone (= dermethmoid or mesethmoid) is a forked median bone overlapped by the frontals above and bounded by the vomer and lateral ethmoid ventrally. The concave anterior surface articulates with the ascending process of the premaxilla. At its anterolateral aspect, the ethmoid bone supports the nasals.

In *Scomberomorus*, only the most anterior part of the ethmoid bone is exposed in dorsal view while the rest of it is overlapped by the frontal. In *A. solandri*, only the lateral aspects of the bone are overlapped by the frontals and a V-shaped dorsal median portion is exposed. The ethmoid bone is longer in *A. solandri* than in *Scomberomorus*.

The lateral ethmoids (= parethmoids) are massive paired bones which form the anterior boundary of the orbit and the posterior and mesial walls of the nasal cavity. The lateral portion of each bone extends downward as a prominent wall from the middle region of the frontals. The ventral surface of this wall mesially bears an articulating surface for the palatine and laterally another articulating surface for the first infraorbital (= lacrymal). The inner walls of the lateral ethmoids come closer to each other at the ventral median line of the skull and contact the anterior edge of the parasphenoid. The median half of each lateral ethmoid extends downward about three-fourths as far as the lateral portion and has a large round foramen for the olfactory nerve which is prominently seen on the anterior surface. On the dorsal surface, they abut against the nasals anteriorly, the frontals posteriorly and articulate with the ethmoid mesially. On the anterior surface, ventral to the foramen, each lateral ethmoid bears a process that extends anteriorly and mesially to contact the dorsolateral surface of the spear-shaped posterior portion of the vomer. No appreciable difference was noted in the lateral ethmoids of the different species.

The vomer (= prevomer) is an elongate spear-shaped anterior median bone thickened anteriorly. The spatula-shaped anterior part bears a large patch of fine teeth on its ventral surface. It connects with the ethmoid bone dorsally and lateral ethmoid dorsolaterally. The pointed posterior part is firmly ankylosed dorsally with the parasphenoid. On each side of the vomer, dorsolaterally and behind the spatulate anterior part, is a prominent articular surface for a loose articulation with the head of the maxilla through soft tissue. Posterior to this articular surface, facing ventrolaterally, is a very prominent sulcus for a similar movable articulation with the ventral branch of the anterolateral fork of the palatine.

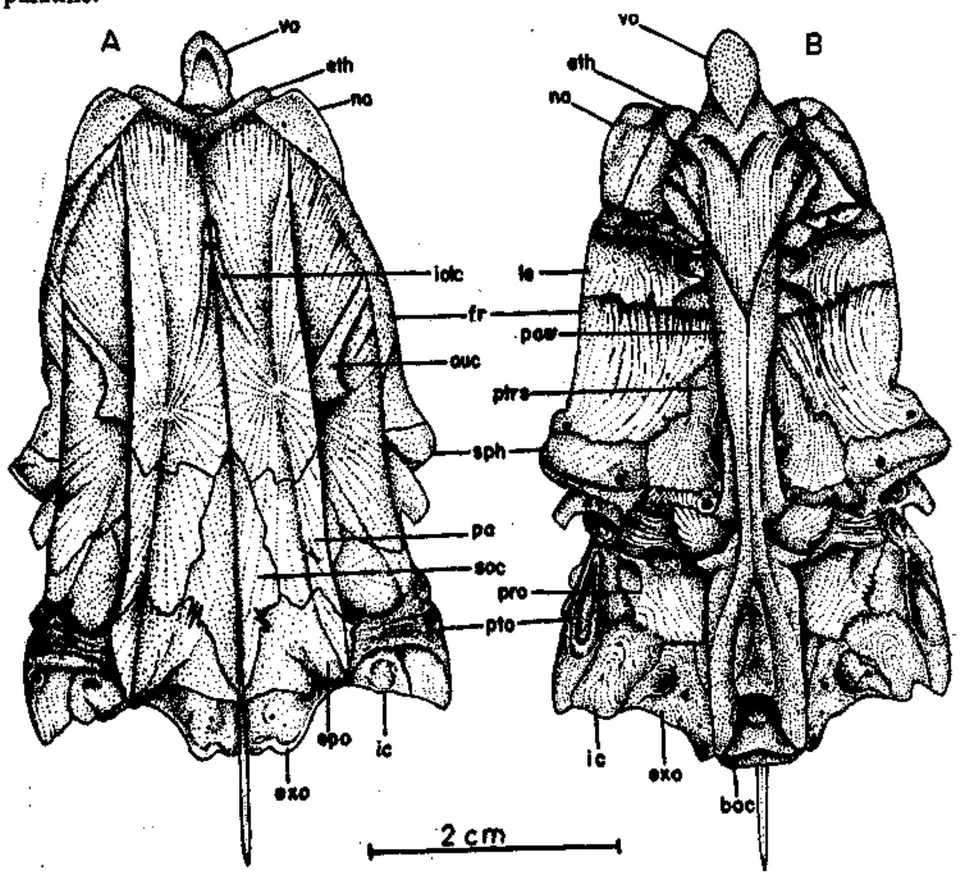

FIG. 3 A-B. Neurocranium of *S. koreanus*: A. dorsal view; B. ventral view.

The spatulate anterior part is very long and extends beyond the anterior margins of the nasal and ethmoid bones in *Scomberomorus*, but remains just hidden to the dorsal view i.e., its anterior tip lies a little posterior to the anterior border of the nasal in *A. solandri*. A notch found on each side of the middle of the vomer is more conspicuous in *A. solandri* than in *Scomberomorus*.

The nasal bones (Figs 1-7) are flat, nearly triangular bones with thickened external edges. They articulate with the anterior edge of the frontals and the extremities of the branches of the forked ethmoid bone. They are non-projecting in that their anterior margin is in level with that of the ethmoid bone. The nasal bones are very much alike in all the species.

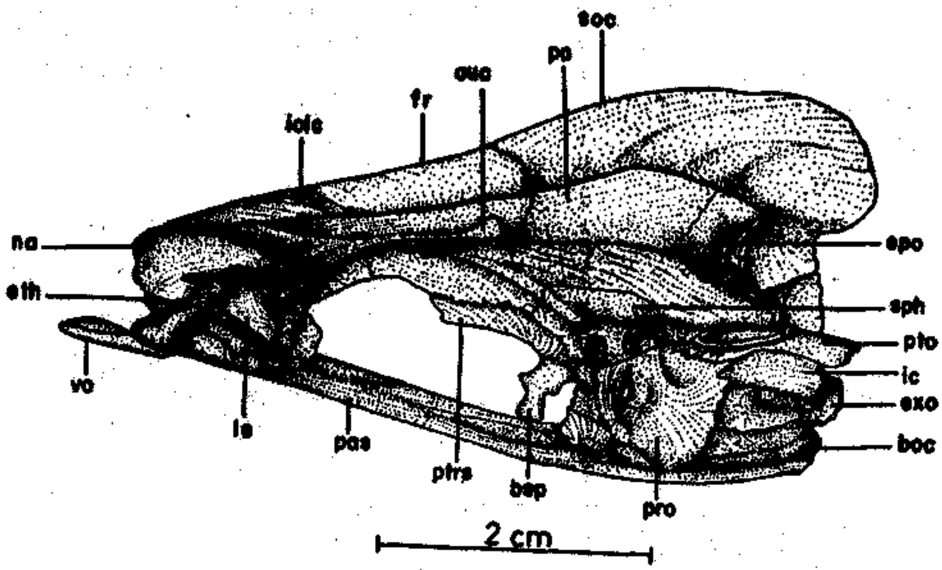

FIG. 3 C. Lateral view of the neurocranium of *S. koreanus*.

ii. *Orbital region — frontal, basisphenoid, pterosphenoid, first infraorbital (= lacrymal), second infraorbital (= suborbital), sclerotic:*

The frontals are paired bones that form the largest portion of the dorsal surface of the neurocranium. Anteriorly they are pointed, and posteriorly they become expanded. They display a series of growth lines which radiate from the central hollow region. The growth lines become prominent towards the anterior end. Anteriorly the frontals overlap the dorsal surface of the ethmoid bone, the inner edge of the nasals and the dorsal surface of the lateral ethmoid. The mid-lateral aspect is thickened to form the orbital roof. Posteriorly they are bounded by the supraoccipital and parietals. Posterolaterally they overlap the pterotics and just anterior to the pterotics, cover the sphenotics. Ventrally each frontal bears a sheet of bone, the orbital lamella, which is bounded by the sphenotic posteriorly, lateral ethmoid anteriorly and pterosphenoid mesially. On the base of the orbital lamella may be seen a number of small foramina for the branches of the supraorbital nerve trunk. The laterosensory canals of the frontals are evident on the pterotic crests as a series of pores.

In *A. solandri*, the frontals are separated from each other by the dorsomedian pineal fenestra lying just in front of the supraoccipital at the level of the pterosphenoids and another anterior fontanel just posterior to the ethmoid bone. When viewed through the pineal fenestra, a part of the dorsal surface of the parasphenoid is visible through the opening of the brain chamber in between the pterosphenoids. There is a deep depression on the frontals mesially, just anterior to the pineal fenestra. This depression becomes shallower anteriorly, becoming confluent with the dorsal surface of the frontals. In *Scomberomorus*, the frontals meet together mesially along the median line of the neurocranium, where they are raised to form the anterior half of the median ridge, whose posterior half is constituted by the supraoccipital crest. In the case of *S. koreanus*, *S. guttatus*, *S.*

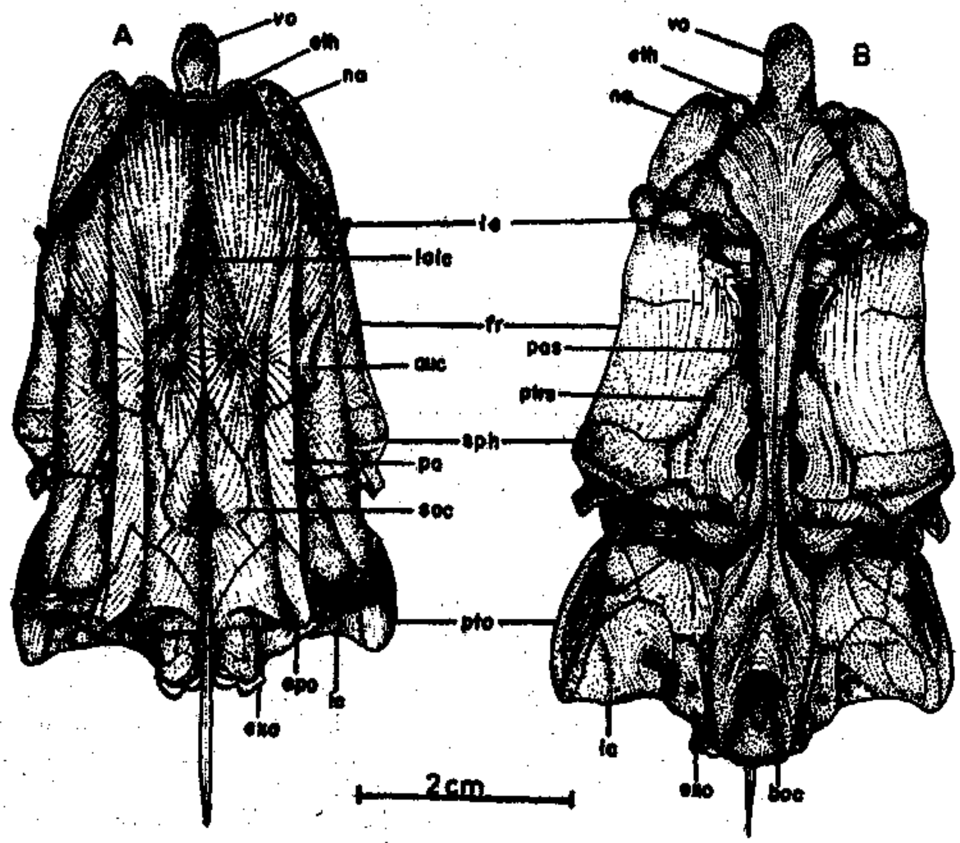

FIG. 4 A-B. Neurocranium of *S. guttatus*: A. dorsal view; B. ventral view.

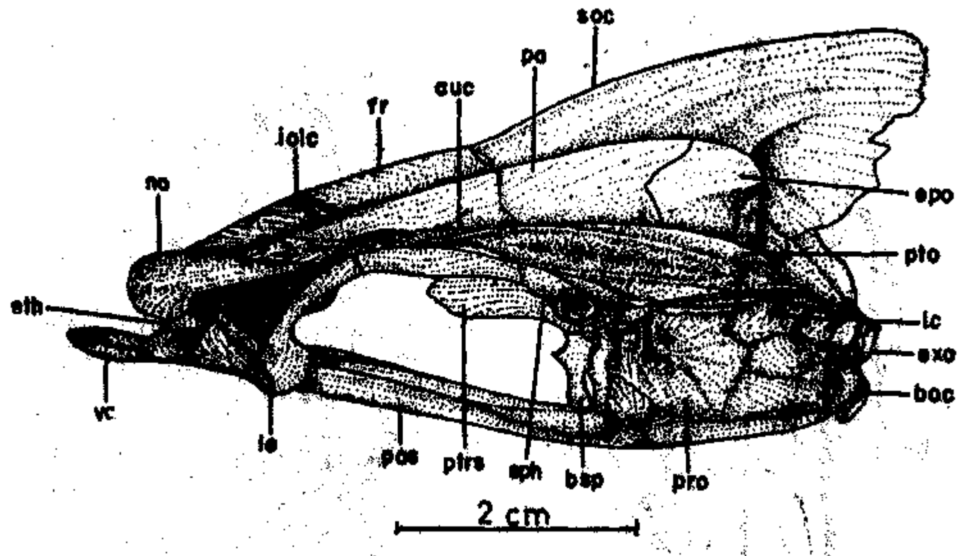

FIG. 4 C. Lateral view of the neurocranium of *S. guttatus*.

lineolatus, S. maculatus and *S. regalis*, the mesial walls of the frontals attach themselves so closely that they leave no slit in between, but in *S. commerson* and *S. cavalla*, a long narrow space is left in between the two walls at the posterior part of the frontals. This is not a fenestra in the true sense, as the lower part of the bones are very closely approximated. In *Scomberomorus*, the interorbital commissures of the lateralis system are developed at a little anterior to the middle of each frontal in the form of a hole at the margin of the median ridge which leads into an oblique tube downwards. Another pair of commissures of the lateralis system is developed at the anterolateral margin of the frontals. These sensory canals are not developed in *A. solandri*.

The basisphenoid is a small median Y-shaped bone that bridges the parasphenoid, prootics and pterosphenoids. The laterally compressed median vertical process bears an anterior median projection. The median vertical process is shorter with an anteriorly sloping base in *S. cavalla* and *S. commerson*. The anterior median process is shorter in the former, but very long in the latter. In the other species of *Scomberomorus*, the vertical process is long with posteriorly sloping base and a very small median process. In *A. solandri*, the vertical process is long with an anteriorly sloping base and a small median process.

The pterosphenoids (= pleurosphenoid or alisphenoid) form the posterodorsal region of the orbit. They abut the basisphenoid and prootics posteriorly and the frontals and sphenotics laterally. The brain chamber opens between the pterosphenoids. The pterosphenoids of *S. guttatus, S. cavalla, S. commerson* and

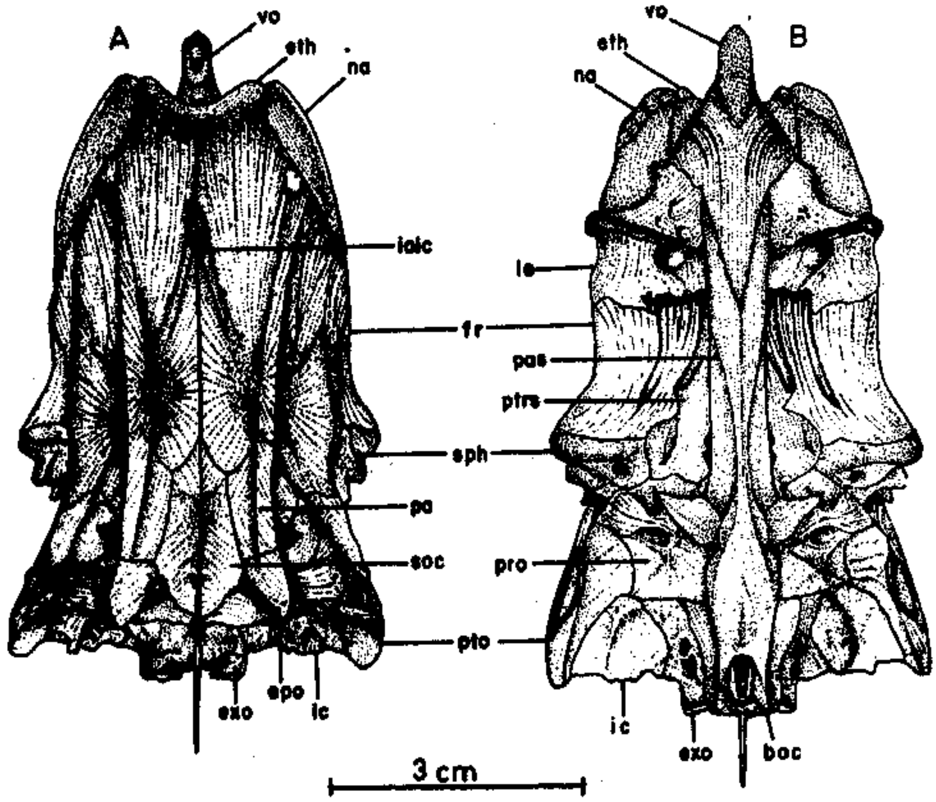

FIG. 5 A-B. Neurocranium of *S. lineolatus*: A. dorsal view; B. ventral view.

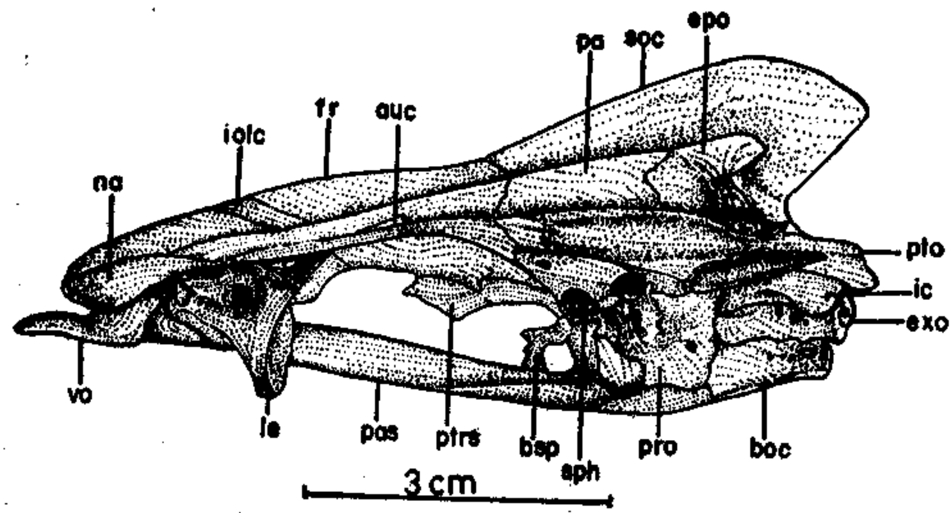

FIG. 5 C. Lateral view of the neurocranium of *S. lineolatus*.

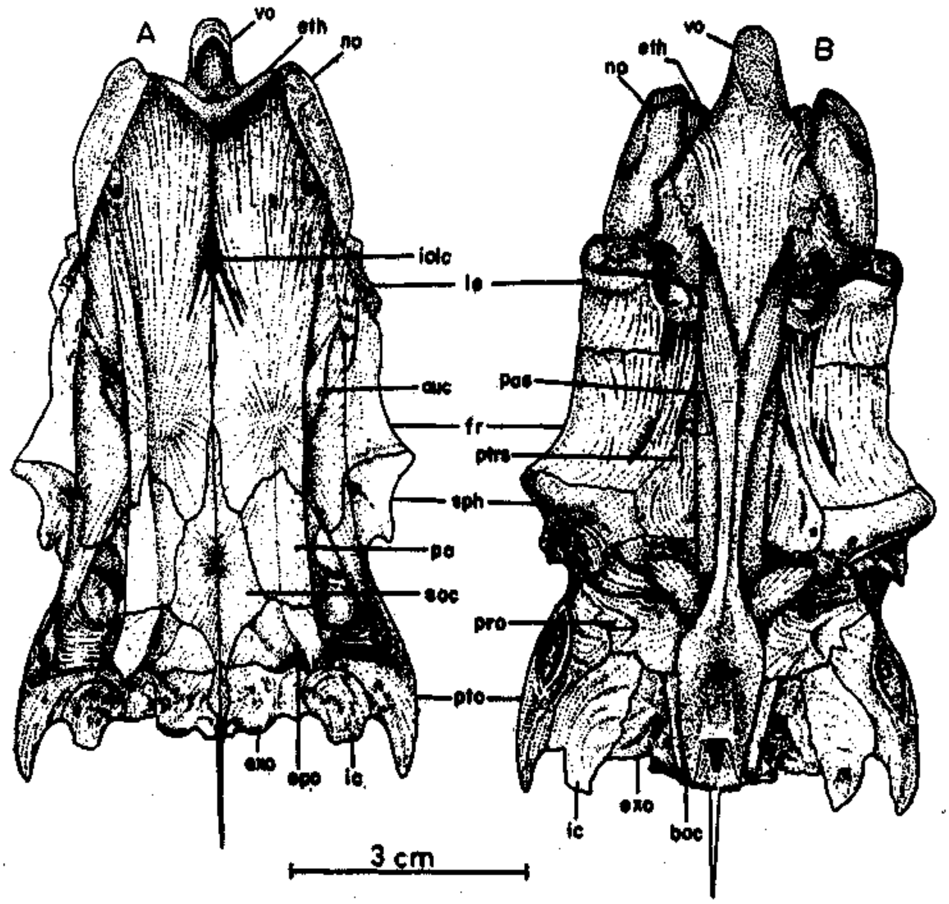

FIG. 6 A-B. Neurocranium of *S. commerson*: A. dorsal view; B. ventral view.

A. solandri are nearly rectangular in shape while those of *S. koreanus*, *S. maculatus* and *S. regalis* are club-shaped with narrow anterior part. The pterosphenoid of *S. lineolatus* is intermediate in that the anterior part is only slightly narrower than the posterior. Pointing from the inner margin of each pterosphenoid into the fenestra, is a small projection which is very prominent in *S. koreanus*. In *S. commerson*, this projection is insignificant and it is absent in *A. solandri*. The aperture of the brain chamber is wide and prominently visible on both sides of the parasphenoid in *S. koreanus*, *S. guttatus*, *S. maculatus* and *S. regalis*, less prominent in *S. lineolatus* and slightly visible or invisible in *S. cavalla*, *S. commerson* and *A. solandri*.

The first infraorbital (= lacrymal) (Fig. 8 A-E) which is the first bone of the orbital ring, is sculptured on the exterior surface, elongated posteriorly and possesses an articular facet on the dorsal surface which is accepted by the

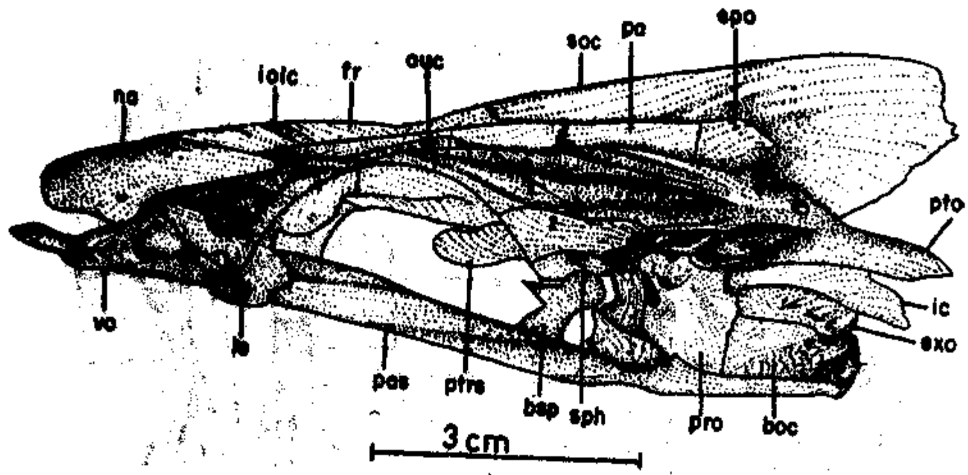

FIG. 6 C. Lateral view of the neurocranium of *S. commerson.*

ventrolateral corner of the lateral ethmoid. The first infraorbital is directed upward and forward and hides a major part of the maxilla. The portion lying posterior to the dorsal articular facet of the first infraorbital is very much elongated and pointed and is much longer than the anterior forked part in *Scomberomorus*, but is shorter and broader than the anterior part in *A. solandri*. Among the investigated species, the anterior part of the first infraorbital is forked in all except *S. cavalla*. The portion between the dorsal branch of the anterior part and the articular facet is concave in *S. koreanus*, *S. guttatus*, *S. lineolatus*, *S. maculatus* and *S. regalis*, but straight in *S. cavalla*, *S. commerson* and *A. solandri*. The bony anterior termination of the infraorbital laterosensory canal system in the first infraorbital is clearly seen in *Scomberomorus*, but indistinct in *A. solandri*.

The second infraorbital (= suborbital) (Fig. 8 F-J) is situated dorsal to the posterior region of the maxilla, mesial to the posterior part of the first infraorbital, and in between the ectopterygoid-entopterigoid region and the sclerotic capsule (Fig. 2 A). This bone forms part of the wall of the orbit, and consists of an outwardly facing thick rod, from which extends inwardly a bony lamina known as the subocular shelf. Since intra-specific variation is very frequently met within its shape (Figs 8 F1 and F2), the second infraorbital is unreliable for diagnostic purposes. In the case of *S. cavalla*, *S. maculatus* and *S. regalis*, Mago Leccia (1958) found that posterior to the first infraorbital, only one of the circumorbital bones which "has a flag-like appearance", was distinguishable from the thick scales surrounding the orbit. This bone seems to be the second infraorbital, as the subocular shelf is more or less flag-like. However, according to Lavett Smith and Bailey (1962), the subocular shelf was absent in the four species of Scombridae: *Auxis tapeinosoma*, *Sarda sarda*, *Scomber scombrus* and *Scomberomorus regalis*, examined by them. Dr. Bruce B. Collette, U.S. National Museum, Washington, states in a personal communication that all the scombrids he has looked at have an inwardly extending shelf on the second infraorbital.

The sclerotic capsules (Fig. 8 K-O) are rather thick and divided into an anterior and a posterior part. They are ovate rather than circular.

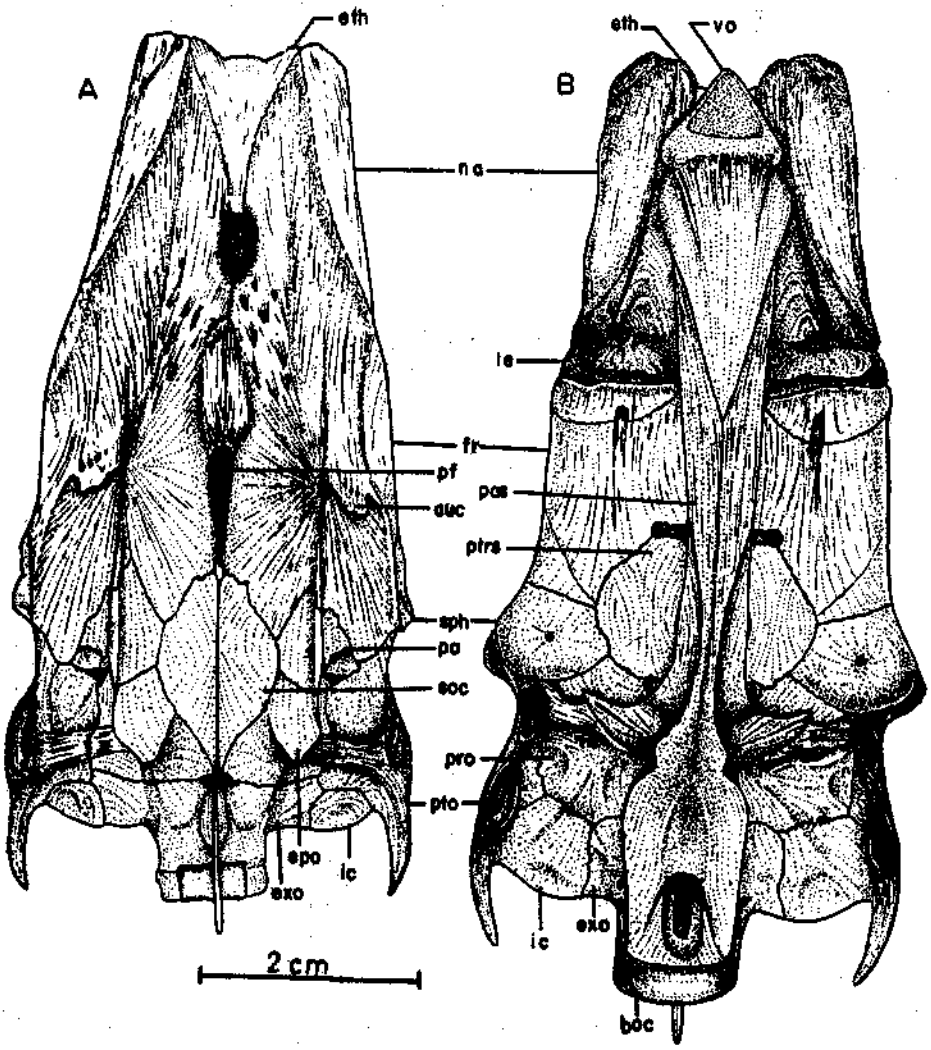

FIG. 7 A-B. Neurocranium of *A. solandri*: A. dorsal view; B. ventral view.

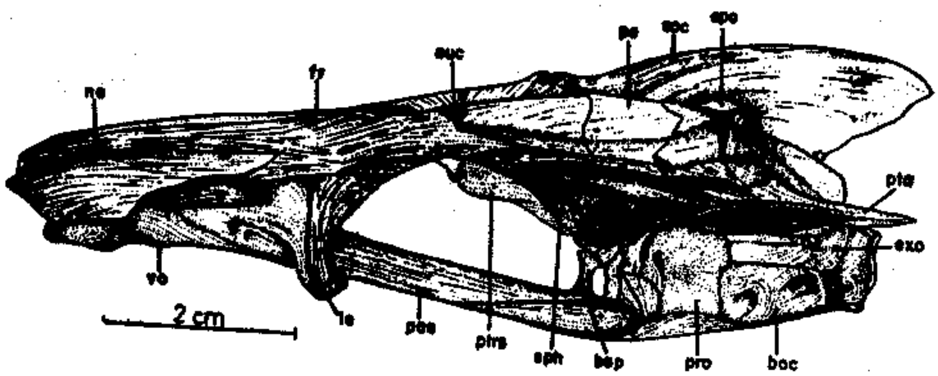

Fig. 7 C. Lateral view of the neurocranium of *A. solandri*.

iii. *Otic region — parietal, epiotic, supraoccipital, pterotic, prootic, sphenotic, and intercalar (= opisthotic)*:

The parietals are paired bones located lateral to the supraoccipital. Dorsally each bears an elevated longitudinal crest which forms part of the temporal ridge. The parietals suture with the frontals anteriorly, epiotics posteriorly, supraoccipital mesially and the pterotics laterally. They are excluded from contact with the sphenotics by the pterotic ridge formed by the pterotics and the frontals. According to Kishinouye (1923) the parietals are separated from the pterotics and take almost no part in the formation of the roof of the brain cavity. Mago Leccia (1958) reported the same condition in the case of *S. cavalla, S. maculatus* and *S. regalis*. In the present study the parietals are found joined to the pterotics except at the membrane-covered region; they are also found to contribute definitely to the roofing of the brain chamber together with other roof bones.

The epiotics are folded into two well-developed surfaces, dorsal and posterior, separated by a strong ridge. Dorsally, there is a rough process known as the epiotic process that receives the dorsal arm of the posttemporal, thus forming a link between the pectoral girdle and the neurocranium. The epiotic process forms the terminal posterior end of the temporal ridge. In *A. solandri*, the height of the temporal ridge at the level of the epiotics is so low that it renders the epiotic process a spatulate shape. Among the species of *Scomberomorus* studied, a slight tendency towards this condition was observed only in *S. commerson*. The epiotic process forms triangular projections at its lateral and posterior aspects in the case of *S. cavalla, S. commerson* and *A. solandri*. In *S. regalis*, there is a slight tendency towards the formation of these projections. Internally, the epiotics possess a deep sulcus to receive the posterior vertical semicircular canal. The epiotics attach posteriorly with the exoccipitals in an almost straight suture, anteriorly with the parietals, mesially with the supraoccipital and laterally with the pterotics.

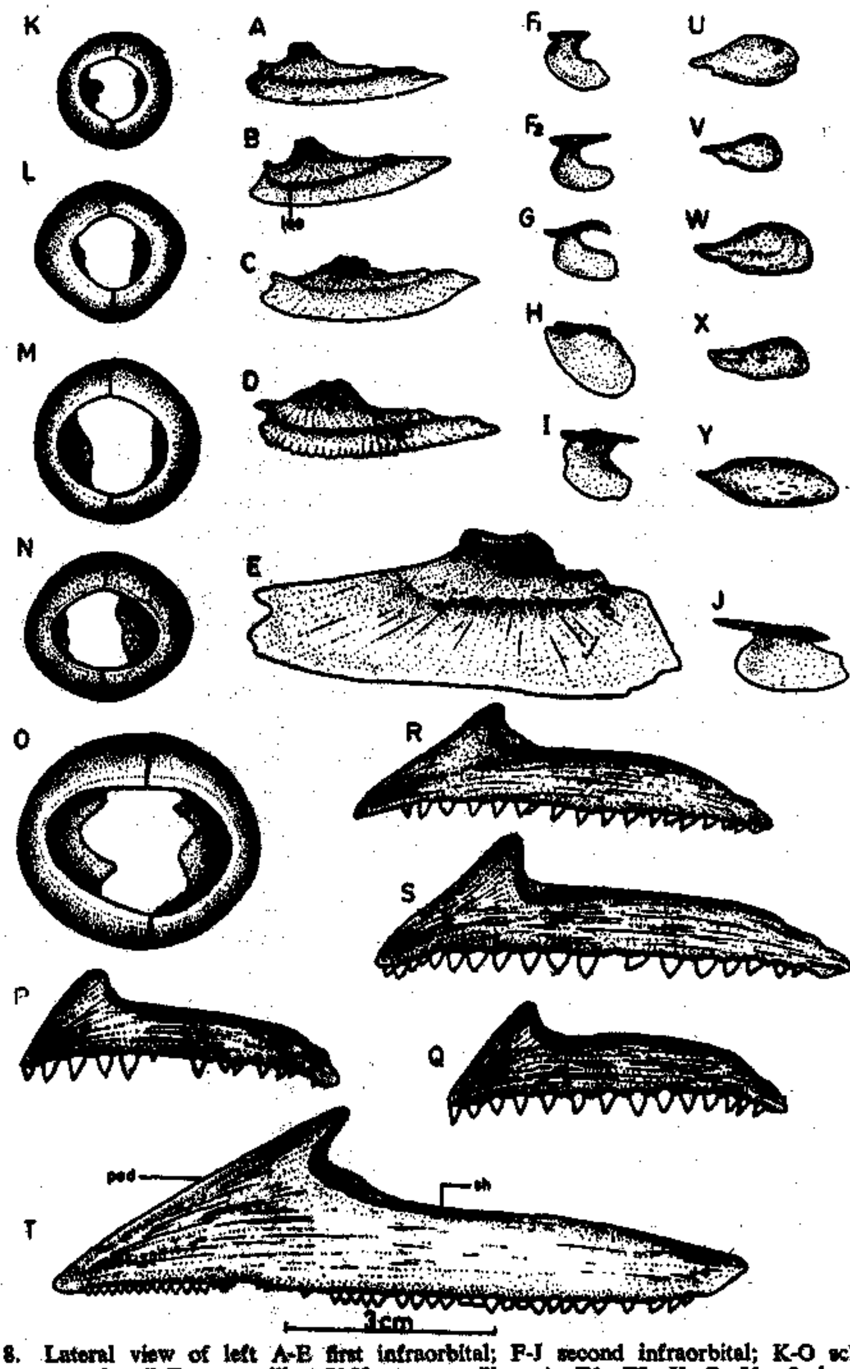

FIG. 8. Lateral view of left A-E first infraorbital; F-J second infraorbital; K-O sclerotic capsule; P-T premaxilla; U-Y supramaxilla. A, F1, F2, K, P, U *S. koreanus;* B, G, L, Q, V *S. guttatus;* C, H, M, R, W *S. lineolatus;* D, I, N, S, X *S. commerson;* E, J, O, T, Y *A. solandri.*

The supraoccipital forms the dorsomedial portion of the posterior end of the neurocranium and bears a well-developed ridge which continues anteriorly on the frontals and is pronounced posteriorly as a strong supraoccipital crest. The ridge extends down over the exoccipitals along the median line where the dorsal walls of the exoccipitals suture with each other, but not interposed between the exoccipitals. The supraoccipital is bounded anteriorly by the frontals and laterally by the parietals and epiotics.

The suture between the supraoccipital and the parietals in *S. koreanus* and *S. guttatus* forms a minor midlateral curve inward that renders the part anterior to it dome shaped. This formation is absent in *S. lineolatus, S. commerson* and *A. solandri*. In the three Caribbean species, it is present in varying degrees of development.

The pterotics form the lateral posterior corners of the neurocranium. Posteriorly each pterotic is produced into a truncate process or pointed spine. The main portion of the pterotic ridge is formed of the pterotic crest. On the posteroventral surface, the pterotic carries an oval depression to articulate with the hyomandibula. It constitutes a part of the temporal fossa mesially and dialator groove laterally. A strong, horizontal ridge from the pterotic firmly sutures with a corresponding ridge from the epiotic. The pterotics are overlaid by the frontals anteriorly leaving only the dorsal aspect of the crest. Anterolaterally they contact the sphenotics, dorsomesially the parietals and epiotics, posterodorsally the exoccipital and ventromesially the prootics. The intercalar contacts the pterotics both posterodorsally and ventrally. Three closely situated foramina are seen piercing each pterotic at the posterior-most region of the pterotic crest. One of these is dorsally placed and very prominent.

In the species of *Scomberomorus* examined by me, and those reported on by Mago Leccia (1958), but excepting *S. commerson*, the pterotics are produced backward into truncate processes. In *S. commerson*, these processes though broader, are very much elongated and approach the condition in *A. solandri* in which they are developed in the form of sharp spines.

The prootics are paired bones that occupy the major part of the ventral surface of the brain case. Ventrally each prootic is bordered by the parasphenoid, posteriorly by the basioccipital, exoccipital and intercalar, laterally by the pterotic and sphenotic, and anteriorly by the pterosphenoid and basisphenoid. On the ventral surface, extending from the lateral wing of the parasphenoid to the sphenotic, the prootic forms a thick bridge which protects the trigeminofacialis chamber for the great ganglia of the trigeminus and facialis nerves (Gregory 1933). The auditory foramen is situated at the posterior inner margin of this bridge. Anteriorly, just posterior to its contact with the pterosphenoid, the prootic is pierced by three foramina whose disposition and sometimes even the number are not constant between species or in different specimens of the same species. The prootic, as viewed internally, bears a shelf of bone above the cavity of the posterior myodome which extends inward to meet its counterpart of the other side. Near this shelf, extending from about the centra of the prootic to its posterior border, is the pocket-like recessus saccularis of the prootic which forms the interior region of the saccular cavity. The anterior part of the sagitta lies in this cavity. The shape of the prootic is very similar in all the species examined.

The sphenotics are paired flattened bones with a midlateral projection. The frontals and pterotics overlap the sphenotics to a certain extent to form the dialator fossa which provides the surface of origin for the dialator operculi muscle. A segment of the articular fossa for the head of the hyomandibula is afforded by the lateral wall of the sphenotic on the ventral surface. The sphenotic is pierced by a foramen for the ramus oticus nerve.

When viewed from the dorsal side, the sphenotics spread out on both sides more prominently in *Scomberomorus* than in *A. solandri*. The midlateral projection is large in *S. koreanus*, *S. guttatus*, *S. maculatus* and *S. regalis*, small in *S. lineolatus*, *S. cavalla* and *S. commerson* and absent in *A. solandri*.

The intercalars (= opisthotics) are flat bones that form part of the posterior border of the neurocranium interposed between the pterotics and exoccipitals. The anterior portion on the dorsal surface is concealed by the overlapping pterotic and, hence, the exposure of the bone on the dorsal surface is less than that on the ventral side. Each intercalar bears a protruberance on the dorsal surface to receive the ventral arm of the posttemporal.

The posterior end of each intercalar projects posteriorly as a prominent truncate process in *S. commerson*. *S. cavalla* approaches *S. commerson* closely in this respect. In *S. lineolatus*, *S. maculatus* and *S. regalis*, the posterior end projects in the form of a small backward projection. In *S. koreanus* and *S. guttatus*, such a projection is either insignificant or absent, but definitely absent in *A. solandri*. For the Caribbean species Mago Leccia (1958) described the projection as "two backward projections, which are more conspicuous in *regalis* than in the other two species". But in his figures, only one projection is seen, as in the present case and the process appears more prominent in *S. cavalla* than in *S. maculatus* or *S. regalis*.

iv. *Basicranial region — parasphenoid, basioccipital, exoccipital*:

The parasphenoid is a long ventromedian bone with a pair of ascending lateral wings in the posterior region. Posteriorly it connects with the prootic and basioccipital and bears on the ventral surface, a deep rectangular channel which forms the bottom of the eye-muscle canal. The posterior myodome lies above the posterior portion of the parasphenoid and between the ventral extensions of the prootics. The anterior end is bifurcate on the ventral surface to receive the spear-shaped posterior part of the vomer. There is a ventral median keel running from the level of the posterior margin of the wings anteriorly for some distance to separate the surfaces of insertion of the palatine adductor muscles of both sides of the head.

The parasphenoid of *S. lineolatus, S. cavalla, S. commerson* and *A. solandri* is broader than that of *S. koreanus, S. guttatus, S. maculatus* and *S. regalis*. The ventral face of the madian keel is rather broad in *S. cavalla* and *S. commerson* but narrow in the other species, especially *S. lineolatus*.

The basioccipital is a narrow median bone that expands a little anteriorly and is grooved on the ventral surface. This groove opens anteriorly into the posterior myodome. The basioccipital is bordered by the prootics anteriorly, the parasphenoid ventromedially and the exoccipitals dorsally. The concave rounded occipital condyle, which articulates with the atlas, forms the posterior extremity of this bone. The lower anterior portion of the basioccipital is divided into two bilateral lamellae that contact the two posterior processes of the parasphenoid. Between the bony lamellae formed by the prootics and basioccipital, above the parasphenoid, and between the bilateral posterior projections of the parasphenoid, lies the large posterior myodome. The basioccipital does not exhibit any appreciable difference between the species studied.

The exoccipitals enclose the foramen magnum and practically lie over the basioccipital. Their vertebral or paraoccipital condyles are large, concave and project some distance over the basioccipital. The slightly concave ventral surface is pierced by two large foramina for the vagus and glossopharyngeal (= glossohyal) nerves of which the latter is the smaller. The exoccipital does not show any significant variation in the species compared.

b. *Branchiocranium*

i. *Mandibular arch — premaxilla, maxilla, supramaxilla, dentary, angular, retroarticular*:

The premaxilla (Fig. 8 P-T) is a massive bone composed of an anterior ascending nasal process or pedicel and a posterior elongated shank with a row of teeth. There are two articular facets for the overlying maxilla at the junction of the posterior margin of the ascending process with the shank. The ascending processes of both premaxilla are closely approximated to each other mesially and fit into the median groove of the ethmoid bone.

The anterior wall of the ascending process forms an angle of 40-43° with the base of the shank (defined as the entering angle of the ascending process) and the length of this process is 38-39% of the total length of the premaxilla in *S. koreanus, S. guttatus, S. regalis* and *S. maculatus*. The pedicel makes an angle of 33° with the shank in *S. commerson* and *A. solandri*, but 23° in *S. lineolatus*.

S. cavalla seems to approach *S. commerson* with regard to this character. The pedicel length is 41-45% in the total length of the premaxilla in *S. lineolatus*, *S. cavalla* and *S. commerson*, but 50% in *A. solandri*. The number of teeth normally present on each premaxilla are 14 or 15 in *S. koreanus* and *S. guttatus*, 19 or 20 in *S. lineolatus* and *S. commerson* and about 50 in *A. solandri*. According to Mago Leccia (1958), larger specimens of *S. cavalla* possess large number of teeth.

The maxilla (Fig. 9 A-E) is a long curved bone surmounting the premaxilla dorsolaterally by means of an anterior head and a ventral sulcus. The head consists of a thick massive inner condyle and a small outer process. The former possesses a prominent knob at its dorsolateral aspect that fits into the articular surface of the vomer and an anterior deep concavity facing the inner wall of the premaxilla. Immediately posterior to the head is a shallow depression to receive the anterior articulating process of the palatine.

In both the Indian and the Caribbean species of *Scomberomorus*, the outer process of the maxilla head is well-developed except in *S. commerson* in which it becomes flimsier; this process is completely lost in *A. solandri*. In *Scomberomorus*, the condyle is pierced by a few tiny foramina, but in *A. solandri* there is a wide horizontal fenestra beneath the knob and a vertical one on the knob. The articulating surface for the palatine is well-developed in *A. solandri*. The maxilla is thicker and broader anteriorly, narrows posteriorly and broadens into a thin, flat fan (lamina) at the posterior end in *Scomberomorus*, but is laterally flattened, and posterodorsally notched with a small posterior end and narrow ventral sulcus in *A. solandri*.

The supramaxilla (Fig. 8 U-Y) is a fan-shaped bone with a narrow anterior handle broadening into a thin plate posteriorly. The handle is well-developed in the Indian species of *Scomberomorus*, but reduced in *A. solandri*.

The dentary (Fig. 9 F-J) is a large forked bone which forms the major part of the lower jaw. It is laterally flattened and bears a single row of triangular teeth on the dorsal margin. Posteriorly the dentary forms two arms. The ventral arm is relatively narrow and shorter than the dorsal arm and its inferior margin has a groove which accepts the angular and the anterior end of Meckel's cartilage. The base of the ventral arm has an external series of pores, which seem to be the preoperculomandibular pores (Allis 1903, Mago Leccia 1958) of a branch of the lateral-line system. The dentary is slightly curved, when viewed dorsally, and forms a single functional unit with the angular and Meckel's cartilage.

The length of the dentary from its anterior margin to the origin of its posterior arms is shorter than the length of its dorsal arm in *S. koreanus*, *S. guttatus* and *S. commerson*, but *vice versa* in *S. lineolatus*, *A. solandri* and the three Caribbean species. In general, there are two notches, one on the antero-

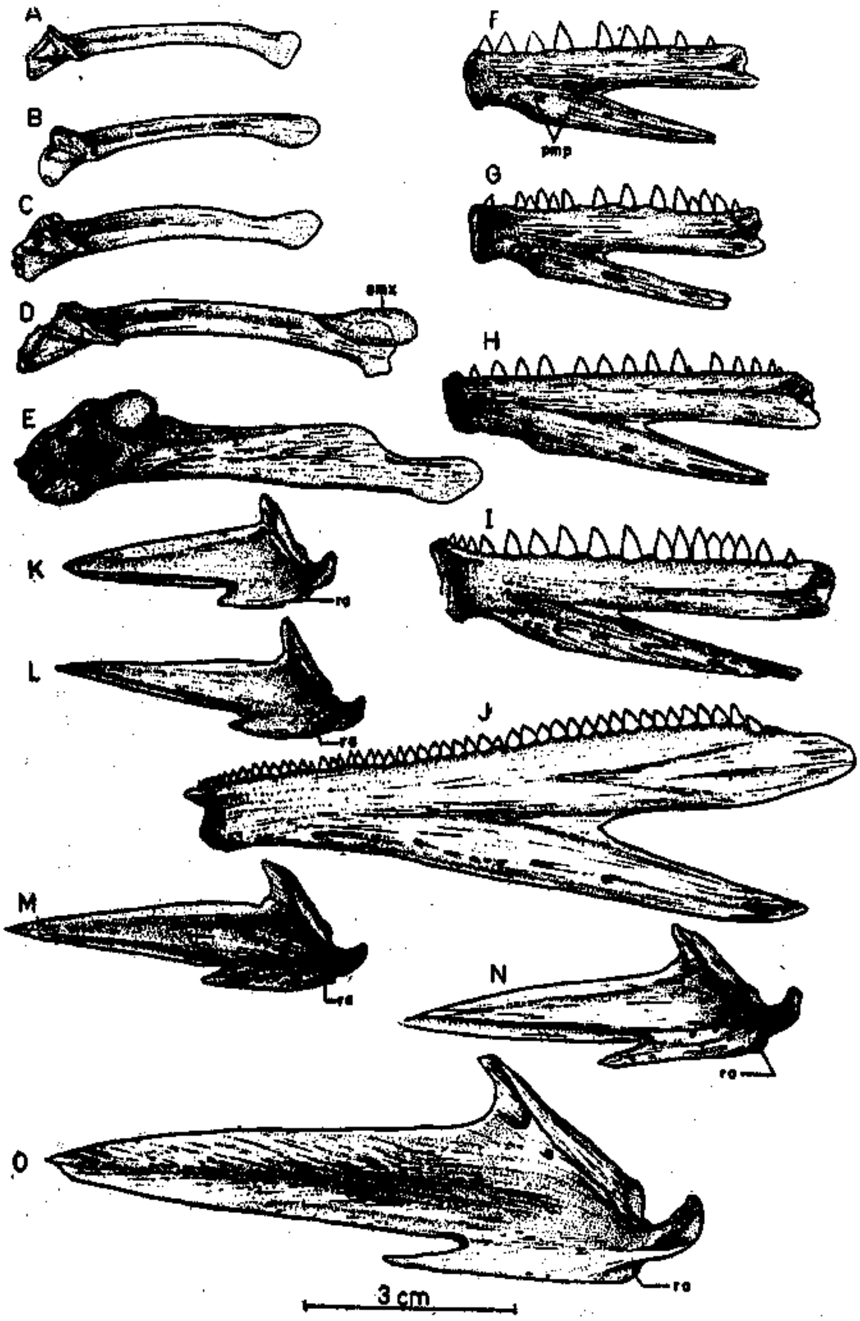

FIG. 9. Lateral view of left A-E maxilla; F-J dentary; K-O angular with retroarticular. A,F,K *S. koreanus*; B,G,L *S. guttatus*; C,H,M *S. lineolatus*; D,I,N *S. commerson*; E,J,O *A. solandri*.

ventral and the other on the anterior margins of the dentary. The anteroventral notch which is well-developed in all the species of *Scomberomorus* is almost obliterated in *A. solandri*. The anterior notch is quite indistinct in *S. koreanus*, *S. guttatus*, *S. lineolatus*, *S. maculatus* and *S. regalis*, distinct in *S. cavalla* and *S. commerson*, and well-developed in *A. solandri*. In all the species of *Scomberomorus* the posterior end of the upper arm is broad with a triangular depression, but narrow with no such depression in *A. solandri*. The number of teeth on each dentary is minimal in *S. koreanus* and *S. guttatus* (10-13), but increases to 13-14 in *S. maculatus*, 15-16 in *S. cavalla* and *S. regalis*, 17-19 in *S. lineolatus* and *S. commerson* and 50 in *A. solandri*.

The angular (Fig. 9 K-O) is a spear-shaped bone which is concave mesially and convex laterally. The convexity of the bone is adjusted to the general curvature of the dentary. The posterior end of the angular bears three large processes; the dorsal process which is directed forward and upward, the ventral process which is directed forward and the posterior process directed backward and upward. The latter process is hooked and carries a transverse articular facet to the quadrate. Between the dorsal and ventral processes is Meckel's cartilage which extends directly anterior into the space between the two arms of the dentary.

The ventral process of the angular is comparatively shorter and stumpier in *S. koreanus*, *S. guttatus*, *S. lineolatus*, *S. maculatus* and *S. regalis*, but longer and narrower in *S. commerson* and *A. solandri*. In *A. solandri* the dorsal process which is also relatively narrow, possesses a median groove externally. Meckel's cartilage ascends up to a little below the crest of the dorsal process in *A. solandri* unlike in *Scomberomorus*.

On the posteroventral surface of the angular is firmly joined the retroarticular (Fig. 9 K-O) a small irregular bone whose ventral edge projects downward beyond the ventral edge of the angular. The retroarticular is nearly alike in all the species examined.

ii. *Palatine arch — palatine, metapterygoid, ectopterygoid, entopterygoid*:

Mago Leccia (1958) described the palatine using different terminology and named the inner branch of the posterior fork "mid-dorsal projection". However, in order to bring out the salient features on a comparative basis, a different terminology is adopted in describing the bone in the present account.

The palatine (Fig. 10 A-E & A1-E1) is forked both posteriorly and anterolaterally. The dorsal branch of the anterolateral fork is hooked and its anterior end articulates with a facet on the maxilla, immediately ventral to the nasal. The ventral branch is cone-shaped. The exterior branch of the posterior fork carries on its dorsal surface the shank of the ectopterygoid and the inner, flat, thin branch is attached to the anterior end of the entopterygoid. The lateral

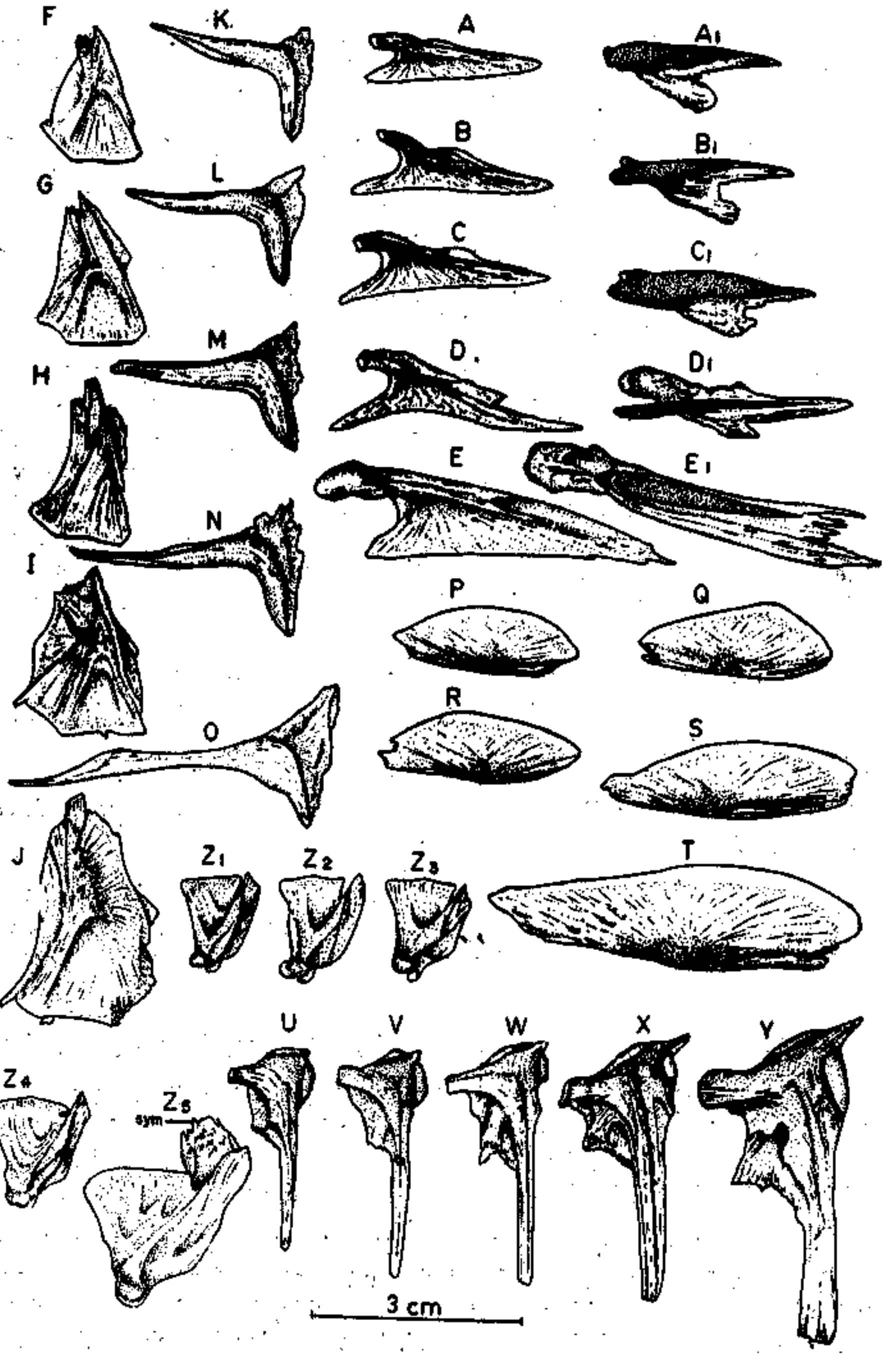

FIG. 10. Lateral view of left A-E palatine; F-J metapterygoid; K-O ectopterygoid; P-T entopterygoid; U-Y hyomandiblua; Z1-Z5 quadrate, and ventral view of left A1-E1 palatine. A,A1,F,K,P,U,Z1 *S. koreanus;* B,B1,G,L,Q,V,Z2 *S. guttatus;* C,C1,H,M,R,W,Z3 *S. lineolatus;* D,D1,I,N,S,X,Z4 *S. commerson;* E,E1,J,O,T,Y,Z5 *A. solandri.*

aspect of the palatine is roughly triangular and concave, and closely attached to the mesial wall of the maxilla.

The ventral branch of the anterolateral fork is longer than the dorsal branch in *Scomberomorus*, but shorter in *A. solandri*. The outer branch of the posterior fork is much longer than the inner branch in *Scomberomorus*, but equal to the inner in *A. solandri*. Bruce B. Collette states (personal communication) that the outer branch is not equal to the inner branch in a specimen of *A. solandri* examined by him. The dorsal surface of the bone is provided with two shallow facets for articulation with the ventral surface of the lateral ethmoid in *Scomberomorus*, but deeply depressed and provided with many furrows in *A. solandri*. The lateral wall is more concave and the ventral wall broadens laterally to form the broad toothed vertical lamina in *S. koreanus*, *S. guttatus* and *S. lineolatus*, but the lateral wall is less concave and the vertical lamina narrow in *S. commerson* and *A. solandri*. The vertical lamina is 'rather stout' in the Caribbean species (Mago Leccia 1958) as in the Indian species of *Scomberomorus*.

The metapterygoid (Fig. 10 F-J) is a flat, somewhat triangular bone. The posterodorsal margin of this bone is deeply grooved to receive the hyomandibula. The dorsal portion is strongly ankylosed to the lamellar region of the hyomandibula. The ventroposterior margin abuts against the lower-most portion of the symplectic process of the hyomandibula, but this edge does not touch the hymandibula, a relatively long slit being left between the two bones, through which the hyoidean artery passes (Allis 1903, Mago Leccia 1958). The ventral border is divided into two portions, the horizontal portion which is in contact with the quadrate, and the anterior oblique portion ankylosed to the ectopterygoid. Mesially the metapterygoid possesses a triangular-shaped articular facet which forms a beveled, interdigiting articulation with the upper arm of the ectopterygoid.

The posteroventral margin of the metapterygoid articulates with the dorsal end of the symplectic in *A. solandri*, but not so in any species of *Scomberomorus*. The posterior horizontal part of the ventral border is longer than the anterior oblique part in *Scomberomorus*, but *vice versa* in *A. solandri*. The anterior free border is convex or nearly straight in *S. koreanus*, *S. guttatus*, *S. maculatus*, *S. cavalla* and *S. commerson*, tends to be slightly concave in *S. lineolatus* and *A. solandri* and becomes decidedly concave in *S. regalis*. An anteroventral spine developed in *S. commerson* and *A. solandri* is absent in others.

The ectopterygoid (Fig. 10 K-O) is a T-shaped bone, the top of the T forming its posterior end. It is joined with the entopterygoid dorsally, the palatine laterally and anteriorly, and the quadrate and metapterygoid posteriorly. The shank of the T is slightly curved in dorsal view, concave dorsally and convex ventrally. The ventral convexity forms part of the margin of the buccal cavity. The dorsal arm of the ectopterygoid is shorter than the ventral arm in *Scomber-*

omorus and *vice versa* in *A. solandri.* The shank is moderately long in the former and very long in the latter.

The entopterygoid (= mesopterygoid) (Fig. 10 P-T) is a long, thin, flat bone, narrow at both ends, but wide in between. It connects with the palatine, metapterygoid and ectopterygoid. The mesial and posterior borders are free from contacts with other bony elements. The dorsal surface is concave and the smooth convex ventral surface forms the major part of the buccal roof.

The anterior end of the entopterygoid is narrower in *S. maculatus, S. regalis, S. cavalla, S. commerson* and *A. solandri* than in *S. koreanus, S. guttatus* and *S. lineolatus.* The width of the inner margin is more pronounced in *S. koreanus, S. guttatus, S. maculatus* and *S. regalis* than in the other species.

iii. *Hyoid arch — hyomandibula, quadrate, symplectic, hyoid complex (hypohyal, ceratohyal, epihyal, interhyal), glossohyal, urohyal:*

The hyomandibula (Fig. 10 U-Y) supports the opercular apparatus and suspends the oromandibular arch from the neurocranium. Dorsally this element displays a broad head, ventrally it forms a rod-shaped symplectic process. The head bears two condyles which are accepted by two facets on the neurocranium, the first on the posteroventral face of the sphenotic and the second on the ventral surface of the pterotic. A third condyle which is located on the posterior margin of the hyomandibula is accepted by the opercular. At the posterodorsal corner of the hyomandibula there is a small pointed process. The hyomandibula has a strong vertical ridge extending from the ventral margin to a little below the dorsal border from where it curves anteriorly to confluence with the anterior condyle. The portions lying anterior and posterior to this ridge are grooved for articulation with the metapterygoid and preopercle respectively so that *in situ* only the ridge and a portion of the upper broader surface are visible exteriorly. The upper surface of the symplectic is connected to the ventral border of the symplectic process of hyomandibula by way of a cartilage which is especially well developed in *A. solandri.*

The posterodorsal pointed process of the hyomandibula is very well-developed in *S. commerson* and *A. solandri,* but small in the other species. According to Kishinouye (1923) such a process is found in all scombroid fishes except in mackerel. Mago Leccia (1958), mistaking Kishinouye's terminology 'mackerel' for Spanish mackerel (*Scomberomorus*), felt that the presence of such a process in all the Florida (Caribbean) species of *Scomberomorus* was in contradiction with the observations of Kishinouye. Since Kishinouye meant species of *Scomber* by mackerel, no contradiction exists between the observations of the two authors. The vertical ridge approaches the dorsal margin more closely in *S. cavalla, S. commerson* and *A. solandri* than in the other species. Two deep fossae exist on the inner surface of the hyomandibula of *A. solandri,* but only one in the Indian species of *Scomberomorus.*

The quadrate (Fig. 10 Z1-Z5) is in the form of a triangle. The broad dorsal margin of the quadrate abuts against the ventral border of the metapterygoid while the deeply concave inferior articular surface fits into the corresponding surface on the hook-like posterior process of the articular. Externally the quadrate has a Y-shaped bony ridge with a saucer-shaped depression at the junction of the fork. The posterior branch of the fork extends upward beyond the dorsal margin as a strong process. This process receives the lower anterior portion of the preopercle along its lateral aspect. The junction of this process with the broader anterior portion is longitudinally grooved on the inner side to accommodate the symplectic.

The anterior arm of the fork of the Y-shaped bony ridge is not developed in *A. solandri* and consequently the depression also is absent. The posterior arm extends upward as a short process in *S. lineolatus*, but as a very prominent structure in all other species of *Scomberomorus;* the extending process is very long in *A. solandri.*

While the symplectic (Fig. 11 A-E) of *Scomberomorus* is a narrow bone, neither completely filling the groove in the quadrate, nor projecting beyond the upper margin of the quadrate, that of *A. solandri* is a stout prominently produced structure. There is a constriction at about the middle of the symplectic of all the Indian species of *Scomberomorus* which is well-pronounced in *S. guttatus.* No such constriction exists in *A. solandri.* There is an anterior horn on the upper half of the symplectic of *S. koreanus* and *S. guttatus.* The horn in the latter species is longer than in the former. In all the Indian species except *S. lineolatus,* the bone tends to broaden a little at the upper part; in *A. slandri,* the upper part is about eight times the size of the lower part.

The hyoid arch consists of the hypohyal (= basihyal of Mago Leccia 1958), ceratohyal, epihyal, interhyal (Fig. 12 A-E), glossohyal (Fig 12 F-J) and urohyal (Fig 12 K-O).

The hypohyal, ceratohyal and epihyal are closely associated and form a single functional unit (Fig. 12 A-E). The hypohyal consists of two centres of ossification, the dorsal hypohyal and the ventral hypohyal, firmly united by a fine indented suture. The dorsal hypohyal bears a sharp process at its upper interior corner, slightly curved posteriorly, which together with the articular surface on the ventral hypohyal establishes contact with their counterparts of the other side. The indentation suturing the dorsal and ventral hypohyals externally forms an upward curve anteriorly in *S. koreanus, S. lineolatus, S. regalis* and *S. niphonius* and runs nearly straight in the other species including *A. solandri.* In all but *S. commerson* among *Scomberomorus,* the dorsal hypohyal is slightly smaller than the ventral one. In *S. commerson,* both are of equal size. In *A. solandri,* the dorsal is much smaller than the ventral hypohyal. An anterior notch in the ventral hypohyal and an anterodorsal notch in the dorsal hypohyal are developed in *A. solandri,* but not in *Scomberomorus.*

The ceratohyal is the largest element of the hyoid complex. It is broadest at its posterior portion. Four acinaciform branchiostegal rays are attached to the respective articular surfaces at the ventral margin. The anterior end of the ceratohyal bears a lower process which joins the ventral hypohyal. Posteriorly the middle part of the ceratohyal interlocks with the epihyal by means of odontoid processes issuing forth from both elements (ceratohyal-epihyal suture of McAllister 1968), while the upper and lower portions are joined by cartilage. The dorsal margin of the ceratohyal is convex in *S. koreanus* and *S. lineolatus*, al-

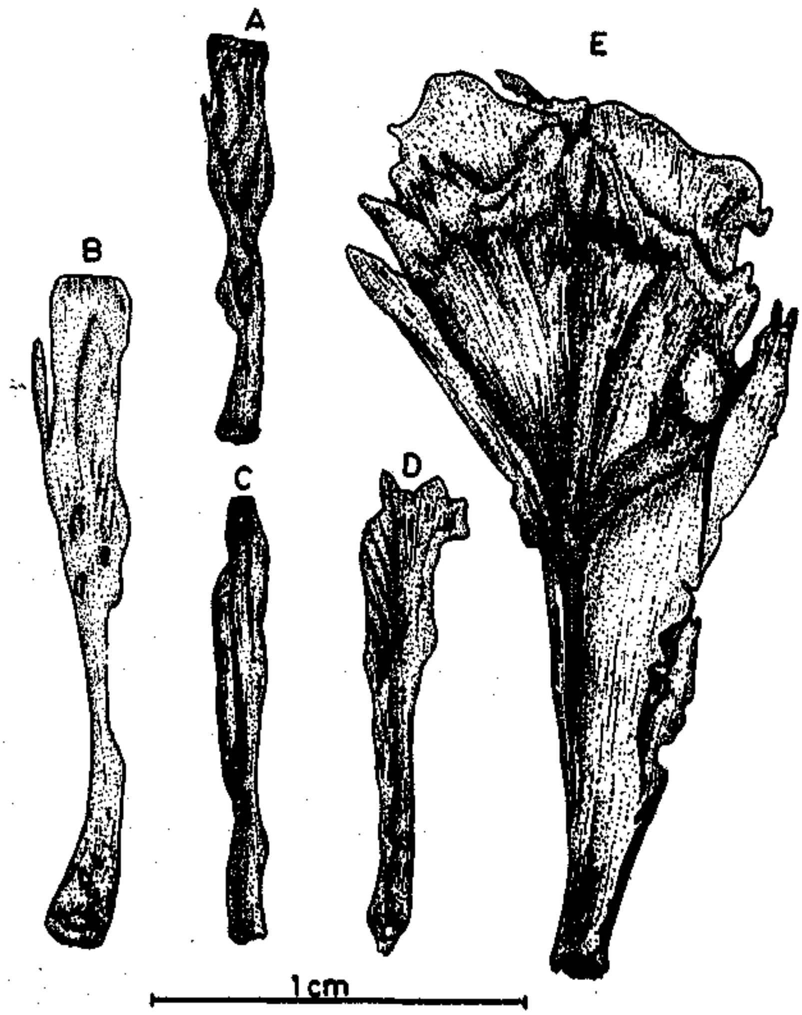

FIG. 11. Lateral view of left symplectic (surface touching the mesial wall of the quadrate). A *S. koreanus;* B *S. guttatus;* C *S. lineolatus;* D *S. commerson;* E *A. solandri.*

most straight in *S. guttatus* and *S. niphonius*, slightly concave in *S. commerson*, *S. maculatus*, *S. regalis* and *S. cavalla* and deeply concave and very much constricted in *A. solandri* so that the dorsal margin of the bone comes closer to the groove for the hyoidean artery.

The epihyal is roughly triangular and bears a posterior process to articulate with the interhyal. Its ventral margin presents an external sulcus to receive three acinaciform branchiostegal rays.

The groove for the hyoidean artery passes through the exterior surface of the hypo-cerato-epihyal unit. Issuing forth from a fossa on the inner surface of the hypohyal, the canal runs from the posterior portion of the dorsal hypohyal, through the ceratohyal to the posterior end of the epihyal. The course of the groove in the ceratohyal is nearly straight along the mid longitudinal line in the case of *S. lineolatus*, but slightly curved and displaced more dorsal in the other species. In *A. solandri*, it is very much curved and runs just beneath the dorsal margin. A portion of this groove in the ceratohyal is seen pierced by a narrow longitudinal slit, the ceratohyal window, also called the beryciform foramen, in *S. guttatus*, *S. lineolatus* and *S. commerson*. According to McAllister (1968) this foramen, characteristic of the Beryciformes is not present in Scombroidei, but is developed in such primitive Perciformes as the Serranidae,

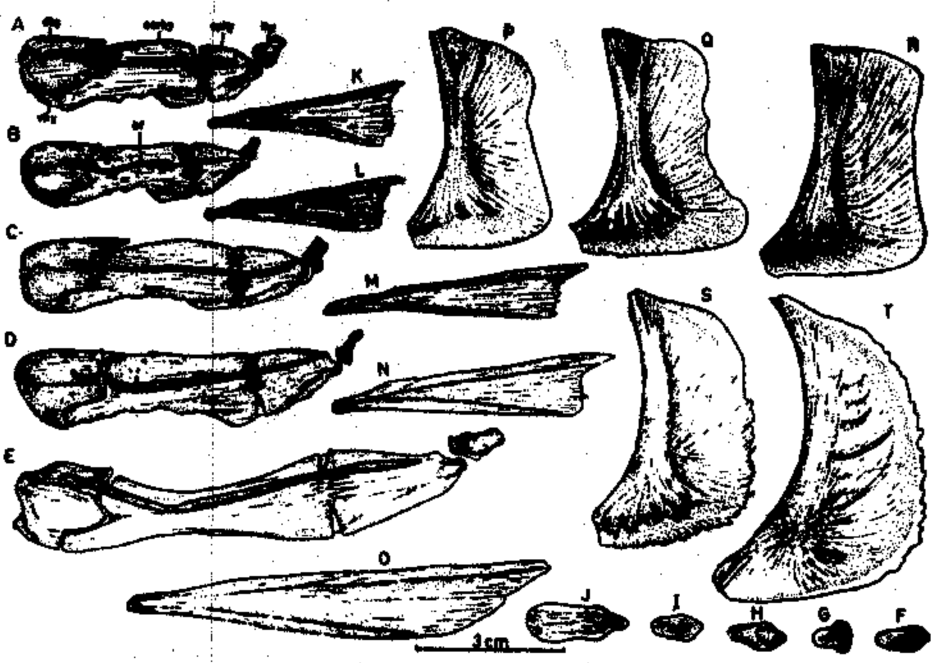

FIG. 12. Lateral view of left A-E hyoid arch; K-O urohyal; P-T preopercle; and dorsal view of F-J glossohyal. A,F,K,P *S. koreanus*; B,G,L,Q *S. guttatus*; C,H,M,R *S. lineolatus*; D,I,N,S *S. commerson*; E,J,O,T *A. solandri*.

Carangidae and Formionidae. This foramen is reported in *Allothunnus fallai* by Nakamura and Mori (1966) and an insignificant one is found in the ceratohyal of *Thunnus tonggol* in my collection.

The interhyal is a small flattened bone which links the hyoid complex with the hyomandibula and symplectic and is directed obliquely upward. It is relatively short and broad in *S. koreanus*, but constricted and narrow in *S. commerson*. The upper end is narrow in all the species that I examined.

The glossohyal (Fig. 12 F-J) is a median bone that supports the tissues of the tongue. The glossohyal of *Scomberomorus* is roughly rod-shaped or conical; it is narrow anteriorly and broadens posteriorly but terminates in the form of a small posterior cone; the bone is bulbus ventrally at the broadest portion. The glossohyal is rather wide in *S. guttatus* with less pronounced ventral bulb, but narrow and prominently bulbed in *S. lineolatus*. The glossohyal of *S. niphonius* seems to resemble that of *S. guttatus* in that it is rod-shaped with a thicker posterior part. As an exception, in one specimen of *S. guttatus* a thin scaly circular extension was observed in the posterior half of the bone. The glossohyal of *A. solandri* is spatulate with broad and round anterior end and furrowed dorsal and ventral surfaces.

The urohyal (Fig. 12 K-O) is an elongate medial bone located between the hypohyals. Its posterior end is broad and pointed at the dorsal corner. The posterior end of the urohyal is comparatively broader in *S. koreanus* than in other species of *Scomberomorus*. In *A. solandri*, the posteroventral margin is smoothed out in the form of a curve without forming a corner unlike *Scomberomorus*. At the dorsal margin, some distance posterior to the anterior end, is a tiny knob which projects in the form of a pointed process in *S. commerson*.

iv. *Opercular apparatus — opercle, subopercle, interopercle, preopercle*:

The opercle (Fig. 13 A-E) is a thin bone more or less broad and pentagonal in shape. It is divided into two portions by a horizontal smooth ridge which extends from the posterior margin to the upper-most part of the articular facet. The posterior margin is more or less serrated. The articular facet for the opercular process of the hyomandibula is narrow and elongate. There is a posterodorsal and an anteroventral projection in the opercle. The opercle is overlapped exteriorly on its anterior side by the posterior half of the preopercle. In the case of *S. commerson* and *A. solandri*, the course along which the posterior margin of the preopercle overlapped the opercle, is indicated by a clear line formed on the opercle.

The anteroventral projection and the notch below it is not well-developed in *S. koreanus, S. guttatus, S. maculatus, S. regalis* and *S. niphonius*. They tend to be prominent in *S. lineolatus* and are well-developed in *S. cavalla, S. commerson* and *A. solandri*. The anterior-posterior extent of the opercle is narrower in *S. koreanus*, *S. guttatus*, *S. maculatus* and *S. regalis*, gains additional breadth in *S. lineolatus* and *S. niphonius*, becomes broader in *S. cavalla* and *S. commerson* and is broadest in *A. solandri*.

The subopercle (Fig. 13 F-J) is a triangular flat bone with extended ascending and descending anterior projections. In *S. guttatus*, the projections are more acute than in the other species. The posteroventral margin bulges more and is well pronounced in *S. koreanus*, *S. guttatus*, *S. lineolatus*, *S. maculatus* and *S. regalis*, moderately pronounced in *S. niphonius* and *A. solandri* and less pronounced in *S. commerson* and *S. cavalla*. The dorsal edge is more acute in *S. guttatus* and *S. regalis*, less acute in *S. koreanus*, *S. lineolatus* and *S. maculatus* and blunt in *S. cavalla*, *S. commerson* and *A. solandri*.

The interopercle (Fig. 13 K-O) is somewhat oval in shape with a crest at the superior margin. There is a well-developed facet on the mesial side to receive an articular process of the epihyal.

The portion anterior to the superior crest is shorter and broadest in *S. koreanus*, *S. guttatus* and *S. regalis*, tends to be longer in *S. lineolatus* and *S. maculatus*, very much longer and pointed in *S. commerson* and *A. solandri*, especially in the latter. In *S. cavalla*, though this portion is shorter, it appears

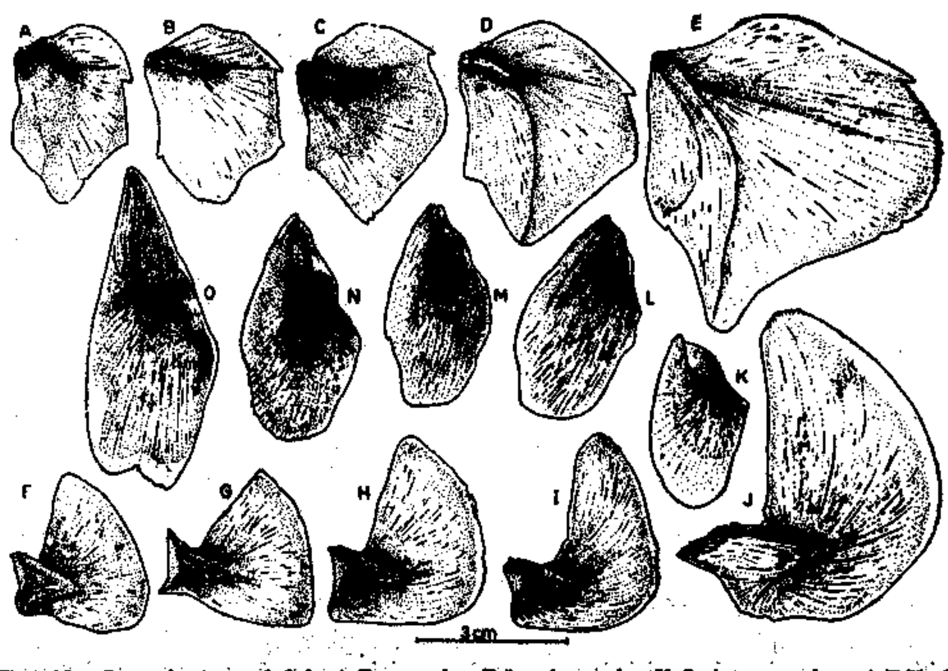

FIG. 13. Lateral view of left A-E opercle; F-J subopercle; K-O interopercle. A,F,K *S. koreanus*; B,G,L *S. guttatus*; C,H,M *S. lineolatus*; D,I,N *S. commerson*; E,J,O *A. solandri*.

narrower and more pointed. A well-formed notch anterior to the crest on the sloping margin in *Scomberomorus* is rather poorly developed in *A. solandri* rendering the superior margin nearly straight. The posterior margin is rounded in *Scomberomorus*, but divided into two by a mid notch in *A. solandri*. According to Conrad (1938), the interopercle of the latter resembles that of *Scomber*, and therefore, this notch may be presumed to be absent in his specimen of *A. solandri* from Bahama Islands as in the case of *Scomber*.

The preopercle (Fig. 12 P-T) is a large crescent-shaped flat bone, very broad at the lower posterior angle. The anterior portion of the bone is thickened into a bony ridge. A series of five or six pores along the lower margin of the ridge represents the preopercular laterosensory canal of the lateral-line system which continues into the dentary. On the mesial side, the ridge possesses a groove for receiving the hyomandibula and the quadrate.

The vertical anterior ridge of the preopercle is separated distinctly from the posterior thin flat surface by a vertical shallow depression on the exterior surface in *Scomberomorus*, but they become confluent with each other in *A. solandri*. A groove developed on the inferior end (horizontal limb of Kishinouye 1923) of the anterior ridge in *A. solandri* is absent in *Scomberomorus*. Pores of the laterosensory canal are distinct in the latter, but are obliterated in the former. The anterior ridge is forked at its upper part in all the Indian species of *Scomberomorus* except *S. commerson* in which the fork is either indistinct or absent; in *A. solandri*, this fork is completely lacking. The posterior margin is concave in all the species of *Scomberomorus* except *S. commerson* in which it is convex as in *A. solandri*. The concave posterior border makes the upper and lower parts appear like two limbs, of which the lower one is longer. In *S. guttatus*, the lower limb is much longer than in the other species.

v. *Branchial arch — basibranchials, hypobranchials, ceratobranchials, epibranchials, infrapharyngobranchials, gill rakers, gill rays* (Fig. 14 A-I):

The endoskeletal gill-arch elements in the Scomberomorini are: basibranchials, hypobranchials, ceratobranchials, epibranchials and infrapharyngobranchials. The basibranchial series in teleosts may be said to be formed of three copulae: one composed of the glossohyal (= basihyal of Nelson 1969) and two others, the anterior usually including three ossified basibranchials and the posterior consisting of a single cartilage representing two or three non-independent basibranchials (Nelson 1969). The dermal elements are the gill rakers and the tooth plates. The tooth plates found in Scomberomorini are: the lower pharyngeal tooth plate fused with the fifth ceratobranchial when the compound structure is termed the lower pharyngeal, the upper pharyngeal tooth plates fused with the second and third infrapharyngobranchials when they are termed "upper pharyngeals" or "pharyngeal bones" or sometimes "infrapharyngeals" and the independent fourth upper pharyngeal plate. In higher teleosts, the fourth upper

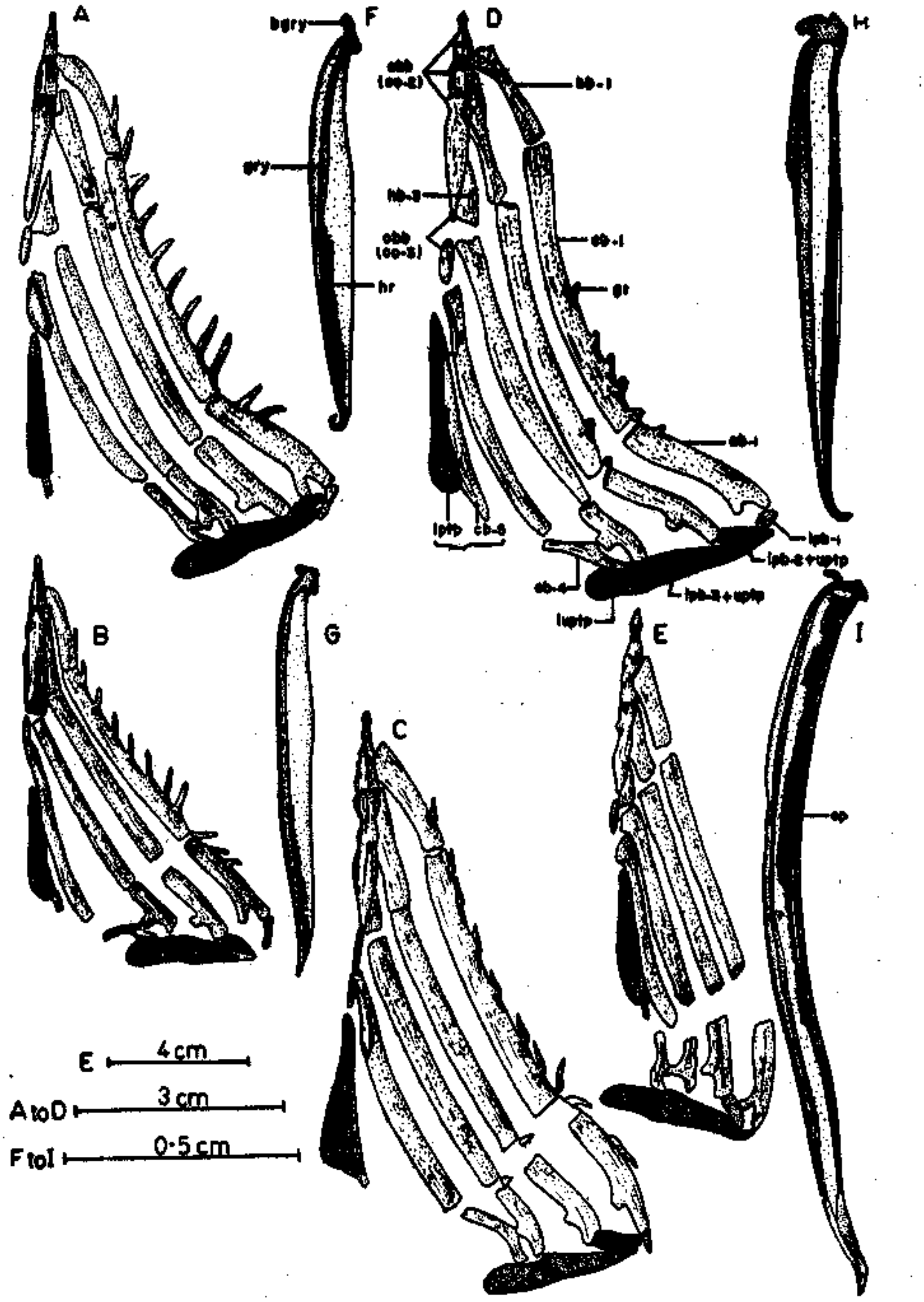

FIG. 14. Dorsal view of lower, and ventral view of upper right A-E branchial arches, and lateral view of F-I gill filaments with gill rays. A,F *S. koreanus;* B,G *S. guttatus;* C *S. lineolatus;* D,H *S. commerson;* E,I *A. solandri.*

pharyngeal plate almost invariably is considered as a fourth pharyngobranchial. Nelson (1969) determined the purely dermal origin of this element and established that there is no basis for believing that this toothed element includes a primitive ossified fourth infrapharyngobranchial, however primitive or advanced the fish in which it occurs might be. The numerous roughly rectangular tooth plates on the endoskeletal gill-arch elements, other than those mentioned above, in *Scomberomorus* and *Acanthocybium* are irregularly arranged as Nelson (1969) observed in most scombrids and hence require no special terminology.

In the Scomberomorini there are five pairs of gill arches basally attached to the basibranchials which form the median floor of the gill arches. Among the three ossified basibranchials of the anterior copula, the third one is the longest and the first and second are shorter. The first one articulates anteriorly with the glossohyal and laterally with the hypohyals through intervening cartilage. The posterior copula of *Scomberomorus* is a small cartilaginous rod lying immediately behind another small cartilage attached to the posterior end of the third basibranchial of the anterior copula. In the anterior three pairs, each gill arch consists of four bony elements — the hypobranchial, ceratobranchial, epibranchial and pharyngobranchial. The fifth gill arch represented by the lower pharyngeal lacks the epibranchial and the pharyngobranchial and both fourth and fifth arches are devoid of the hypobranchial. The first two hypobranchials are nearly the same size. The first one joins the second ossified basibranchial at about its mid portion and the second one joins the anterior part of the third ossified basibranchial of the anterior copula. The third hypobranchial, about half as long as the former two, lies along the posterolateral border of the third ossified basibranchial. There are five pairs of ceratobranchials. The anterior three articulate with the posterior end of the respective hypobranchials. The posterior two articulate with the cartilaginous pieces (posterior copula) lying behind the third ossified basibranchial. The ceratobranchials are the longest bones in the gill arches and all are nearly the same length. The compound bone formed by the fusion of the fifth ceratobranchial with the lower pharyngeal tooth plate is termed the lower pharyngeal. The lower pharyngeal is slightly expanded along the posterior border.

Epibranchials are present on the first four gill arches. Each of them articulates with the respective ceratobranchial forming an angle at the junction. They vary considerably in shape. The first three are rather straight, stout and forked at their anterior ends while the fourth, the most internal piece is thin and distorted to assume an approximately Y shape. There are three infrapharyngobranchials. The recurved first one articulates dorsally with the parasphenoid. The second triangular one is fused with the second upper pharyngeal tooth plate and the large third one with the third upper pharyngeal tooth plate. The fourth independent upper pharyngeal plate firmly contacts the third infrapharyngobranchial.

With regard to the major bones of the branchial arches, there is little variation except in the size of the third ossified basibranchial and the lower pharyngeal which appear broader in *S. cavalla* and *S. commerson* than in the other species, including *A. solandri*.

At its external margin, the first gill arch bears a series of gill rakers. They are curved inward and bear two or three series of minute teeth on the outer surface. The longer raker is at the angle of the arches. There may be none or one gill raker in the angle of the second and sometimes the third gill arches. There are 15-18 gill rakers in *S. regalis*, 13-15 in *S. maculatus*, 12-13 in *S. niphonius*, 10-13 in *S. koreanus*, 9-12 in *S. lineolatus*, 8-12 in *S. guttatus*, 11 in *S. chinensis*, 8-9 in *S. cavalla*, 4-8 in *S. semifasciatus* and *S. queenslandicus*, 2-6 in *S. commerson* and none in *A. solandri* (Table 2).

Each gill filament is supported by the flat, blade-like gill ray (Fig. 14 F-I). The gill rays are slender, bony laminae tapering towards the distal ends and structurally appear to be of membrane bone formed by direct calcification in the connective tissue. Basally they are buried in the connective tissue surrounding the afferent and efferent branchial arteries which lie along the concave surface of the ceratobranchial, epibranchial and hypobranchial. In all the gill arches, the gill rays occupy the axial parts of the blade-like gill filaments (Iwai and Nakamura 1964). The base of the gill ray is shoe-shaped with the middle of its attaching surface a little concave in *S. koreanus*, dome-shaped in *S. guttatus*, slightly dome-shaped in the middle with flat projecting extremities in *S. lineolatus*, club-shaped with an anterior large round portion separated by a mid notch from the posterior smaller curving handle in *S. commerson*, and club-shaped with a small anterior triangular part separated by a deep notch from the posterior narrow horn-like handle in *A. solandri*. A sloping notch is descernible at the rear margin of the descending part at about $\frac{1}{4}$th the distance of the ray from the base in *S. lineolatus*, *S. commerson* and *A. solandri*. A series of horny bars (40-45) extending from the ray transversely from the lower half to the tapering tip of the gill ray are developed in *S. koreanus* and *S. guttatus*. In *S. lineolatus*, a few such rods (10-15) are sometimes present in the lower part of the gill ray. These bars are longer in *S. koreanus* than in *S. guttatus*. The softer portion of the gill filament is plain in *S. koreanus* and *S. guttatus*, but provided with a row of thin cilia-like structures at the distal margin in *S. commerson* and sometimes in *S. lineolatus*. These cilia are reduced to concentrated patches in *A. solandri*.

2. Axial skeleton

a. *Vertebral column*

The vertebral column of *Scomberomorus* and *Acanthocybium* exhibits a remarkable simplicity when compared to most other scombrids. The haemal and neural processes are very slender, fragile and fibrous.

The first completely closed haemal arch (Fig. 15 A-D; F) occurs on the 10th vertebra in *S. cavalla*, 12th in *S. lineolatus* and *S. regalis*, 13th in *S. koreanus* and *S. commerson*, 14th in *S. guttatus*, 13th to 15th in *S. maculatus* and 27th in *A. solandri*. The first haemal postzygapophysis (Fig. 15 A-E) is formed on the 7th or 8th vertebra in *S. koreanus* and *S. lineolatus*, the 8th in *S. guttatus, S. commerson, S. cavalla, S. maculatus* and *S. regalis* and the 4th or 5th in *A. solandri*. The haemal postzygapophyses of the abdominal vertebrae are rather short and not produced, but quite prominent in all the species. The first haemal prezygapophysis (Figs 16 A, B; 17 A-C) occurs on the 14th vertebra in *S. commerson*, 17th in *S. lineolatus*, 18th in *S. koreanus*, 19th in *S. guttatus* and 23rd in *A. solandri*. The inferior foramina (Figs 16 A,B; 17 A,B) at the base of the haemal spines are small in lateral view and the first one is developed on the 26th vertebra in *S. koreanus* and *S. lineolatus*, 28th in *S. commerson* and 29th in *S. guttatus*. There is only one inferior foramen in *A. solandri* which is developed on the 49th vertebra. In *S. commerson*, a dorsally pointing spine is present at the basal posterior face of the haemal spine of the 26th and 27th vertebrae. The fusion of such a spine with the ventrolateral aspect of the centrum, forms the inferior foramen on the 28th vertebra. Such a sequence in the development of this foramen is not met with in the other species. The parapophysis (Fig. 15 A-E) first makes its appearance as an insignificant knob bordering the depression in the centrum for the articulation of the ribs on the

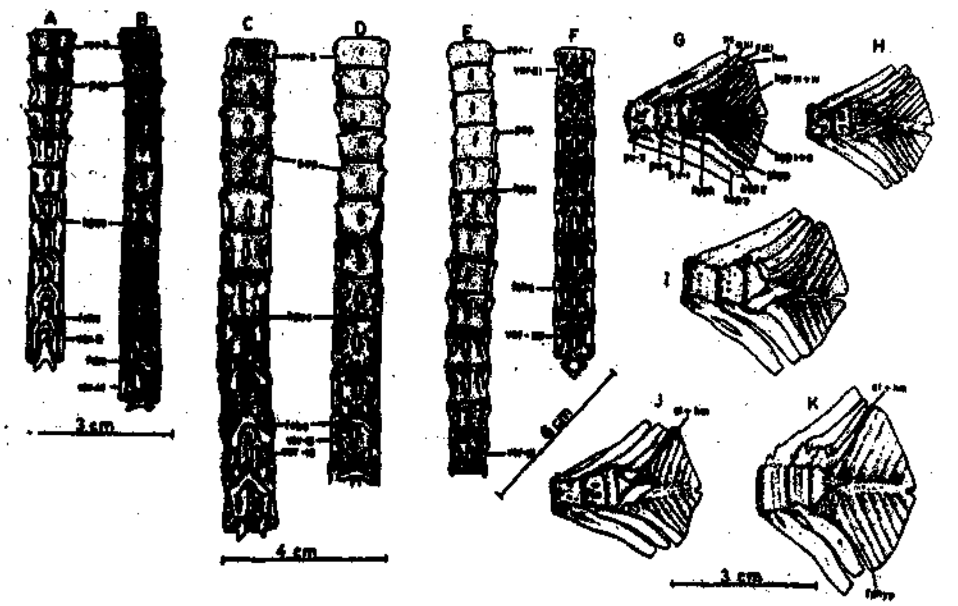

FIG. 15. Ventral view of A-F a portion of the vertebral column, and lateral view of G-K caudal skeleton. A,G *S. koreanus*; B,H *S. guttatus*; C,I *S. lineolatus*; D,J *S. commerson*; E,F,K *A. solandri*.

2nd vertebra in *A. solandri*, 3rd in *S. koreanus*, *S. guttatus*, *S. lineolatus*, *S. maculatus*, *S. regalis* and *S. cavalla* and 4th in *S. commerson*. It becomes progressively larger posteriorly.

From about the 7-9th to the 15-16th vertebrae, the parapophyses are directed obliquely forward, forming roughly an angle of 45-60° and from the 16-17th to the last precaudal vertebrae this angle increases so that the haemal arches are rendered nearly vertical in the case of *S. koreanus* (Fig. 16 A), *S. guttatus* (Fig. 16 B) and *S. lineolatus* (Fig. 17 A). In *S. commerson*, the parapophyses of the 11-15th vertebrae form an angle of about 60-70°, those of the 16-18th tend to be vertical to the vertebral column and those of the 18-20th incline posteriorly, forming an angle of about 100° (Fig. 17 B). In the case of *A. solandri*, the anterior abdominal parapophyses are not directed forward as in *Scomberomorus*, but directed almost vertically and after the 24th vertebra from where the haemal prezygapophysis gains prominence, they are inclined a little posterior to the vertical line making roughly 100-130° angle (Fig. 17 C).

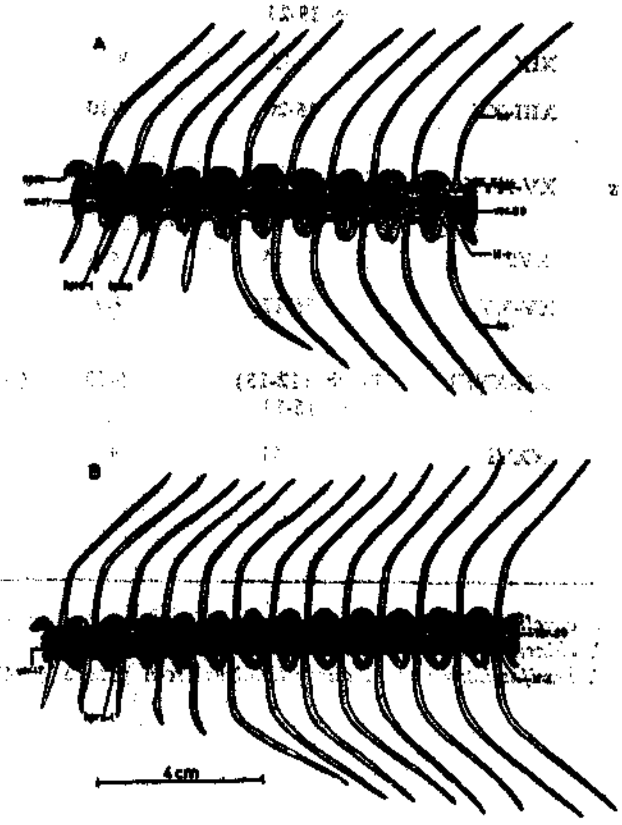

FIG. 16. Lateral view of a portion of the vertebral column. A *S. koreanus*; B *S. guttatus*.

TABLE 2. *Meristic counts of the*

Species	I dorsal Spine	II dorsal rays	Dorsal finlets	Anal rays
S. koreanus	XIV-XV	V + (14-18) = 19-23	8-9	(V-VI) + (16-18) = 21-23
S. guttatus	XIV-XVII	20-23	7-9	21-23
S. maculatus	XVI-XVIII	15-18	8-9	II + (15-17) = 17-19
S. regalis	XVI-XVIII	16	8-9	II + (14-15) = 16-17
S. lineolatus	XIV-XVII	(III-IV) + (12-16) = 19-23	8-10	(III-IV) + (16-19) = 19-23
S. nephonius	XIX	15	9	15-17
S. semifasciatus	XIII-XV	16-20	9-10	15-20
S. queenslandicus	XV-XVII	16-20	9-10	15-20
S. chinensis	XVI	15	8	16
S. cavalla	XV-XVI	16-17	8-9	II + (14-17) = 16-19
S. commerson	XII-XVIII	IV + (12-15) = 16-19	9-13	(III-IV) + (12-17) = 16-21
A. solandri	XXVI	11	9	11

Data for *S. cavalla*, *S. maculatus* and *S. regalis* from Mago Leccia (1958)
Data for *S. chinensis* and *S. niphonius* from Kishinouye (1923)
Data for *S. semifasciatus* and *S. queenslandicus* from Munro (1943)

different species of Scomberomorini.

Anal finlets	Gill rakers	Vertebrae	1st closed haemal arch at vertebra	1st haemal postzygapophysis at vertebra	1st haemal prezygapophysis at vertebra	1st inferior foramen at vertebra
7-9	10-13	20 + 26 = 46	13	7 or 8	18	26
7-9	8-12	(20-21) + (28-30) = 49-50	14	8	19	29
8-9	13-15	(21-23) + (30-31) = 52-53	13-15	8	—	—
8	15-18	(19-20) + (28-29) = 47-49	12	8	—	—
9-11	9-12	(18-20) + (25-28) = 45-48	12	7 or 8	17	26
8	12-13	22 + 28 = 50	17	7 or 8	17	31
9-10	4-8	(19-20) + (28-29) = 48-49	—	—	—	—
9-10	4-8	(19-20) + (28-29) = 48-49	—	—	—	—
7	11	18 + 22 = 40	11	8	21	21
8-10	8-9	(17-18) + 25 = 42-43	10	8	—	—
9-12	2-6	(19-20) + (23-25) = 42-45	13	8	14	28
9	0	32 + 31 = 63 (54 to 64 according to Mago Leccia, 1958)	27	7 or 8	23	49 (This is the only vertebra with an inferior foramen)

According to Conrad (1938) the first perceptible parapophysis in *A. solandri* is formed on the 16th vertebra. This appears a misconception which is explained as follows: The ventral fossa on the lateral aspect of the centrum begins to occupy a more lateral position from the 14th vertebra posteriorly and the septum separating it from the ventral median fossa also becomes well pronounced carrying at its anteroventral extremity the parapophysis. In the preceding vertebrae the parapophyses occupy a more lateral position at the anterior border of the depressions for the articulation of the ribs. When viewed from the ventral side, the knob-like protruberences appear well extended on both sides of the centrum posterior to the second vertebra and should definitely be considered as true parapophyses just as those occurring posterior to and including the 16th vertebrae.

In *S. koreanus* and *S. guttatus*, the parapophyses of each side of the 2nd or 3rd vertebrae, just preceding the first haemal arch, come very close and nearly touch each other (Fig. 15 A, B), but remain separate from each other in the other species (Fig. 15 C, D, F).

The anterior one or two haemal spines in *S. lineolatus* arch anteroposteriorly as they just leave the centrum (Fig. 17 A), but in *S. koreanus* and *S. guttatus* they pass vertically and veer obliquely backwards (Fig. 16 A, B) and in *S. commerson* and *A. solandri* tend to be oblique straight away (Fig. 17 B,C).

The atlas is slightly smaller than the second vertebrae. The neural spine of the atlas is more slender than the subsequent three or four massive spines. While in *S. koreanus* the first neural spine is nearly straight and does not touch the succeeding spine, it is arched, with its convex side facing anteriorly and the dorsal tip tending to touch that of the second spine in *S. guttatus* and *S. lineolatus*. In *S. commerson*, the first neural spine is of the same height as the second one and touches it throughout its length. In *A. solandri*, it is much shorter than the second and touches it all along its course except at the dorsal tip.

The relative length of the neural and haemal spines in the order of their decreasing length which is also reflected externally in the body depth of the different species is as follows: *S. koreanus, S. guttatus, S. lineolatus, S. commerson* and *A. solandri*.

The neural prezygapophysis of *S. koreanus* possesses a broader crest with a nearly straight dorsal margin (Fig. 16 A). In *S. guttatus*, the crest first elevates itself prominently, but suddenly slopes anteriorly (Fig. 16 B). In *S. lineolatus, S. commerson* and *A. solandri*, the crest is comparatively shorter and the dorsal margin gently slopes anteriorly (Fig. 17 A-C).

The vertebrae are more or less short particularly at both extremities. The vertebrae of *Scomberomorus* each has six longitudinal grooves: ventral median, dorsal median and two pairs of laterals. In the case of *S. koreanus*, beginning at the 11th caudal vertebra and continuing posteriorly a shallow median lateral groove is also present. *S. guttatus* also tends to have such a groove from the 9th or 10th caudal vertebra posteriorly. The centra of *S. lineolatus* are provided with many furrows, also those of *S. commerson*, to a certain extent, are provided with furrows (Fig. 17 A,B). *A. solandri* typically possesses three lateral grooves on each side of the centrum (Fig. 17 C). The number of vertebrae is 18 + 22 = 40 in *S. chinensis* (Kishinouye 1923), 17-18 + 25 = 42-43 in *S. cavalla* (Mago Leccia 1958), 19-20 + 23-25 = 42-45 in *S. commerson*, 20 + 26 = 46 in *S. koreanus*, 18-20 + 25-28 = 45-48 in *S. lineolatus*, 19-20 + 28-29 = 47-49 in *S. regalis* (Mago Leccia 1958), 19-20 + 28-29 = 48-49 in *S. queenslandicus* and *S. semifasciatus* (Munro 1943), 20-21 + 28-30 = 49-50 in *S. guttatus*, 22 + 28 = 50 in *S. niphonius* (Kishinouye 1923), 21-23 + 30-31 = 52-53 in *S. maculatus* (Mago Leccia 1958) and 32 + 31 = 63 in *A. solandri* (Table 5).

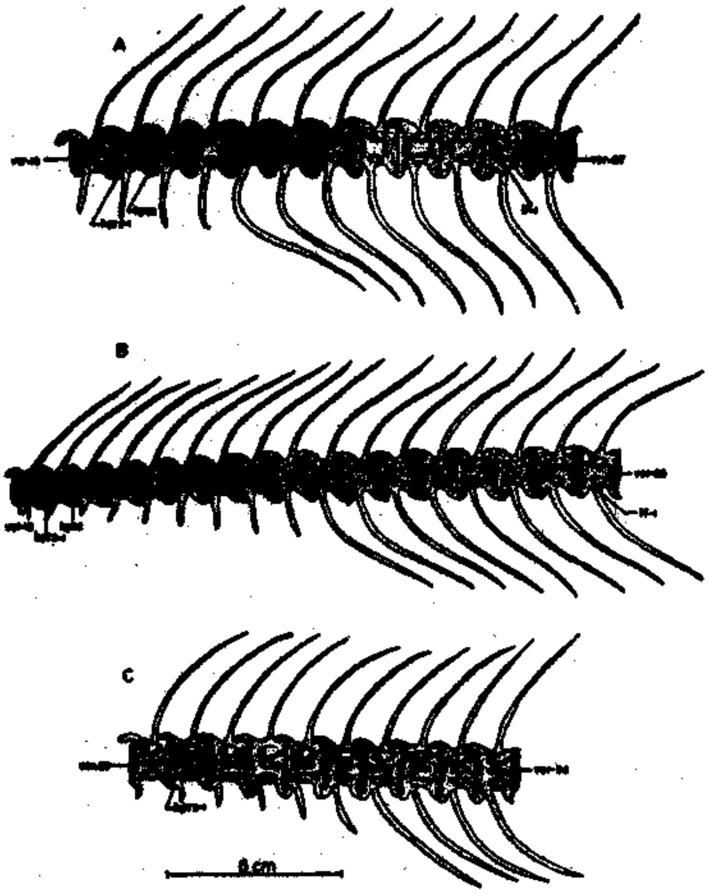

FIG. 17. Lateral view of a portion of the vertebral column. A *S. lineolatus*; B *S. commerson*; C *A. solandri*.

b. *Caudal skeleton*

Terminology for the caudal skeleton is based on Nybelin (1963) except for the modifications introduced by Monod (1967, 1968). The last haemal spine is considered a hypural by Gosline (1960), but a typical spine by Nybelin (1963). Following Monod (1967), this element is termed the parhypural which is functionally related to the hypurals, rather than to the haemal spines.

The caudal skeleton entering into the support of the caudal fin in the Scomberomorini consists of the hypural plates, the preurals (pu 1, pu 2, & pu 3) and their associated elements (Fig. 15 G-K). In a condition typical of many advanced fishes, both the first and second ural centra are co-ossified with the first preural centrum producing a compound centrum (Lundberg and Baskin 1969). This may be true with Scomberomorini also. The ventral hypural plate (hypurals I + II) and the dorsal hypural plate (hypurals III + IV) are fused into a single plate separated only by a posterior notch in both *Scomberomorus* and *Acanthocybium*. Anteriorly the hypural plate is fused with the first preural centrum. In *Scomberomorus*, the parhypural is free and the hypurapophysis is well-developed; but in *Acanthocybium*, the parhypural is completely incorporated into the ventral hypural plate and the hypurapophysis is reduced to a small process. The two haemal arches (hap 2 and hap 3) preceding the parhypural are autogenous in *Scomberomorus*, but fused with their centra in *Acanthocybium*. There are two epurals. The anterior or first epural lies over the modified neural process of the second preural centrum. The bony element separating the second epural from the dorsal hypural plate is a composite structure formed by the stegurals and the *hypurale minimum* in *A. solandri* and *S. commerson*. Monod (1968) is of the opinion that this piece is also a compound structure in *S. maculatus* (= *S. tritor*). A faint mark passing vertically on the surface of this bone indicates its compound nature in *S. lineolatus* too.

c. *Pleural ribs and intermuscular bones*

In *Scomberomorus*, the pleural ribs are slender, subequal and lie close to, but do not touch each other. The first rib articulates with the centrum of the third vertebra and the last one with the tip of the haemal arch of the last precaudal vertebra. In *A. solandri*, the anterior ribs are very broad and the first one articulates with the centrum of the second vertebra.

There are 21-22 intermuscular bones in *Scomberomorus* attached serially to the first 21 or 22 vertebral centra. The intermuscular bones on some of the centra at the anterior and posterior extremities are very short. In *S. koreanus*, an auxiliary intermuscular bone is present on the exoccipital. There are ten intermuscular bones in *A. solandri*, restricted to the precaudal region. The first one articulates with the centrum of the 1st vertebra and others with the head of the ribs and not with the vertebral centra as in other scombrid fishes. The second intermuscular bone and the first rib are sometimes fused at their heads.

3. Pectoral girdle

The pectoral girdle is formed of the following bones: supratemporal (= extrascapular), posttemporal, supracleithrum, cleithrum, scapula, coracoid and two postcleithra.

The supratemporal (Fig. 18 A-C) is a flat leaf-shaped bone lying just underneath the skin where its lateral process articulates with a dorsal articular surface on the pterotic. The anterior margin is concave and the convex posterior margin slightly overlaps the dorsal arm of the posttemporal. There is a small notch at the posterolateral corner. The portion lying lateral to this notch broadens in *S. commerson* and *A. solandri*.

The posttemporal (Fig. 18 D-H), a flat elliptical bone with two sturdy anterior processes, affords the principal articulation of the pectoral gridle with the neurocranium. The inner-most (dorsal) process is concave at its dorsal surface and articulates with the dorsal surface of the epiotic. The lateral (ventral) process is shorter, round in cross section and its hollow anterior end articulates with the dorsal protruberence of the intercalar. This branch extends posteriorly into a short process.

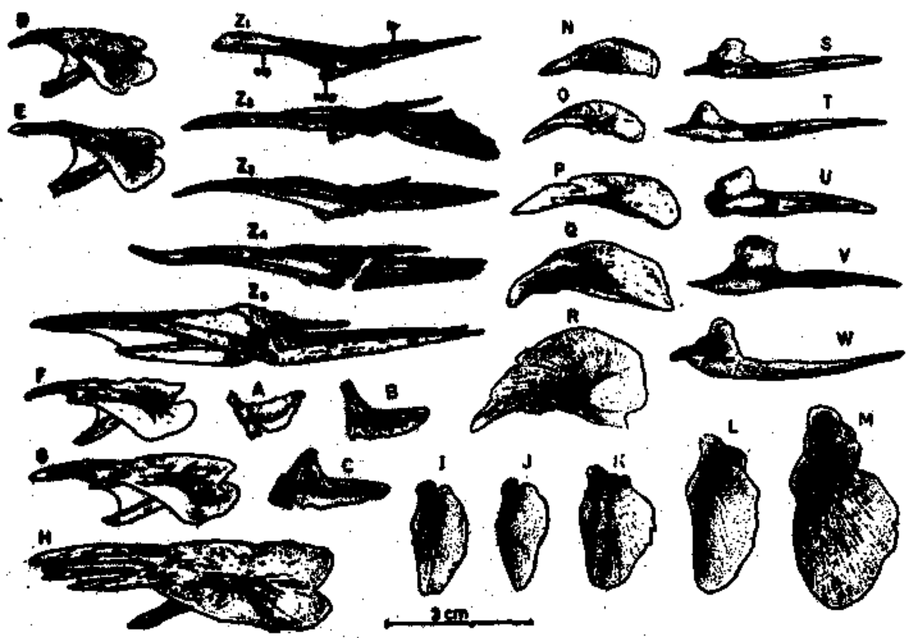

FIG. 18. Lateral view of left A-C supratemporal; D-H posttemporal; I-M supracleithrum; N-R upper postcleithrum; S-W lower postcleithrum; Z1-Z5 pelvic girdle. A,D,I, N,S,Z1 *S. koreanus*; B,E,J,O,T,Z2 *S. guttatus*; F,K,P,U,Z3 *S. lineolatus*; C,G,L, Q,V,Z4 *S. commerson*; H,M,R,W,Z5 *A. solandri*.

A lamina that connects the inner and lateral processes of the posttemporal of *Scomberomorus* is not well developed in *A. solandri*. In the latter, the lateral wall of the inner process extends anteriorly as a median process, separated from the inner one by an anterior notch. Kishinouye (1923) calls this the auxiliary process and Conrad (1938), the median process. The anterior end of this median process is made up of five or six spicule-like processes. The posterior end of the ventral process ends bluntly without any process in *S. guttatus*, forms a minute knob in *S. lineolatus*, projects distinctly in *S. commerson*, develops a prominent backwardly directed spine in *S. koreanus* and attains the form of a long process in *A. solandri*. The posterior margin of the bone is divided into two unequal halves: the smaller dorsal and the larger ventral in *Scomberomorus*, but into two equal halves in *A. solandri*. The inferior margin of the ventral half projects down as a cone in *Scomberomorus*, but remains straight in *A. solandri*.

The supracleithrum (Fig. 18 I-M) is an ovate bone, overlapped dorsolaterally by the posttemporal, but its lower half overlaps the anterior part of the dorsal wing-like extension of the cleithrum. The anterior border of the bone on the mesial side is thickened into a ridge. Dorsally there is a small handle-shaped process which curves into the posterior margin to end in a notch at the posterodorsal aspect. This notch tends to be more prominent in *S. commerson* than in the other species of *Scomberomorus* and is well pronounced in *A. solandri*.

The cleithrum (Fig. 19 A-J) is a long, curved, folded bone which forms the greater part of the pectoral girdle. The upper part of the bone consists of an anterior sharp process and a wing-like extension. The wing is bent inward to receive the supracleithrum laterally and the upper piece of the postcleithrum mesially. The lower part of the cleithrum is large and folded back upon itself as two walls: one lateral and the other mesial, which meet at their anterior margins and run parallel to each other. The mesial wall of the cleithrum forms a large triangular slit with the coracoid.

The wing of the cleithrum narrows posteriorly in *S. koreanus*, *S. guttatus* and *S. regalis*, but only narrows less in *S. lineolatus*, *S. commerson*, *S. cavalla* and *S. maculatus;* the wing is of uniform width in *A. solandri*. The major double-walled lower portion is broader in *S. koreanus*, *S. guttatus*, *S. lineolatus*, *S. cavalla*, *S. maculatus* and *S. regalis*, but tends to be less wide in *S. commerson;* this portion is very narrow in *A. solandri*, and consequently, the upper part of the slit which the mesial wall of the cleithrum forms with the coracoid, is not hidden by the lateral wall of the cleithrum, unlike in *Scomberomorus* in which the entire slit is hidden by the lateral wall. The mesial wall extends posteriorly very prominently in *S. koreanus*, *S. guttatus* and *S. lineolatus;* this posterior extension tends to be insignificant in *S. commerson* and becomes insignificant in *A. solandri*.

The scapula (Fig. 19 A-E) is a small bone connected to the cleithrum at the angle of its wing with the inner wall and to the dorsal border of the coracoid. It is pierced by a central, round foramen. Posteriorly the bone is thickened to receive the upper two and part of the third pterygials. The remaining part of the third and fourth pterygials are carried by the coracoid.

The central foramen in the scapula is very large in *S. koreanus*, *S. regalis* and *A. solandri* and smaller in other species.

The coracoid (Fig. 19 A-J) which joins the scapula dorsally and the inner fold of the cleithrum anteriorly, is spear-shaped and bears an external longitudinal sulcus close to its anterior border in *Scomberomorus*, but more towards the posterior in *A. solandri*. The coracoid is relatively broader in *S. koreanus*, *S. guttatus* and *S. lineolatus* than in *S. commerson* and *A. solandri*. The lowermost portion of the girdle presents a spear-shaped appearance in the last two species because of the reduced breadth of the two major components, the cleithrum and the coracoid.

There are two postcleithra. The lamellar upper postcleithrum (Fig. 18 N-R) is kidney-shaped with a narrow upper end, rounded lower margin, concave

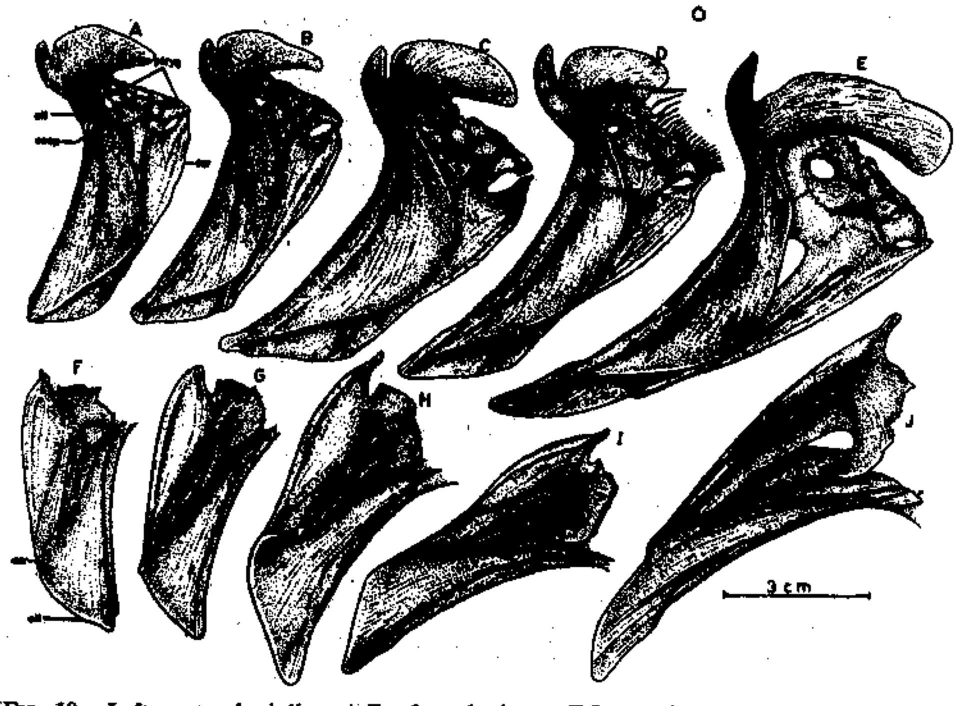

FIG. 19. Left pectoral girdle. A-E lateral view; F-J mesial surface of coracoid and lower part of cleithrum. A,F *S. koreanus*; B,G *S. guttatus*; C,H *S. lineolatus*; D,I *S. commerson*; E-J *A. solandri*.

anterior border and convex posterior margin. It is long and narrow in *S. koreanus*, *S. guttatus*, *S. lineolatus*, *S. maculatus* and *S. regalis*, broader in *S. cavalla* and *S. commerson* and massive in *A. solandri* with an anteroinferior notch.

The lower postcleithrum (Fig. 18 S-W) is broad and lamellar at the upper part with a short pointed ascending process and a long styliform descending process. There is little variation between species except that in *S. commerson* the lamella is comparatively broader. The ascending pointed process was absent in one specimen of *S. lineolatus* due to a malformation.

4. Pelvic girdle

The pelvic girdle (Fig. 18 Z1-Z5) is composed of a pair of bones united at the median line, imbedded in the ventral part of the abdominal wall free from contact with other bony elements. Each bone consists of three processes: anterolateral, anteromesial and posterior. The anterolateral is well-developed into a long, straight or slightly curved process and is provided with three longitudinal wings, the lateral, dorsal and ventral. These wings gain prominence posteriorly, but unite into a single entity anteriorly. In cross section the anterolateral process is vertical at its anterior part and triradiate posteriorly in all the species. The anteromesial process is thin, slender and about 1|3 or still less the length of the anterolateral process. The posterior process is short.

The anterolateral process of the pelvic girdle has its anterior end narrow in *S. lineolatus*, broad in *S. koreanus*, *S. maculatus* and *S. regalis* and of modest size in all other species including *A. solandri*. The posterior part of this process is broader in *S. cavalla*, *S. commerson*, and *A. solandri*. A notch is formed on the ventral wing of the anterolateral process before it joins the other wings in *A. solandri*, but is absent in *Scomberomorus*. When the pelvic girdle is viewed from the lateral side, the anterior end of the anteromesial process is distinctly visible in *S. koreanus*, *S. guttatus*, *S. lineolatus*, *S. maculatus*, *S. regalis* and *S. niphonius*, slightly visible or completely invisible in *S. cavalla* and *S. commerson* and completely invisible in *A. solandri*, being hidden by the anterolateral process.

RELATIONSHIPS

Based on a comparison of osteological characteristics, it is seen that while *Scomber*, *Rastrelliger*, *Acanthocybium*, *Allothunnus*, *Cybiosarda*, *Gymnosarda*, *Sarda*, *Auxis*, *Euthynus*, *Katsuwonus* and *Thunnus* are similar or nearly so in the following respects, *Scomberomorus* with rare exceptions, stands apart from them within the scombrinae. Comparison with *Gasterochisma* and *Grammatorcynus* is incomplete for want of adequate osteological information on these genera. The unique features of *Scomberomorus* are: (1) The neurocranium is nearly trapezoidal, elongate, more than one and a half times its breadth, flat at the anterior region and deepest at the hind end of the orbit. In *Grammatorcynus*, *Acanthocybium* and *Allothunnus*, the neurocranium although more elongate, is as nearly trapezoidal as in *Scomberomorus*. In *Scomber* and *Rastrelliger*, it is much elongated, gradually pointed towards the anterior and as high as broad. In the other genera, the neurocranium is short, only a little longer than broad and much broader than high. (2) The supraoccipital crest is high and the median ridge formed by the crest of the supraoccipital and frontals extends to the ethmoid region, except in *S. chinensis;* the supraoccipital crest is low and does not extend over the frontals in the other genera except *Gasterochisma*. (3) The interorbital lateralis commissure is always complete as in the Carangidae; but hardly discernible in any other scombroid genera including *Acanthocybium* in which its presence was presumed by Gosline (1968). In those species of *Scomberomorus* with a frontal crest, the two halves of the commissure extend up the outside surfaces of the halves of the frontal crest and open by separate exits on either side of its rim. In *S. chinensis*, in which the frontal crest is absent, the openings of the commissure are placed on either side of the rim of the frontals as they come closer to each other at the median line. (4) The pineal foramen is not developed except in *S. chinensis;* but in all other genera in which the frontal crest is not developed, either a pineal window or a transparent area is developed in the frontals directly under which is an expanded "pineal organ" (Rivas 1953). In those genera which possess a pineal window, the interorbital commissure is incomplete. If Rivas (1953) is correct in postulating the pineal body as a light receptor in scombrids, except *Scomberomorus*, then all scombrids have a rather different system of sensory perception on the top of the head than the system in the carangids (Gosline 1968). The presence of pineal window in *S. chinensis* indicates that pineal organ is developed in this species. It is interesting that, in *S. chinensis*, both the pineal organ for light reception as well as the interorbital commissure for sensory perception are simultaneously present. (5) The temporal ridges are directed straight forward towards the anterior border of the frontal, but are interrupted above the orbit by transverse ridges in *Scomber* and *Rastrelliger*, stop at the mid level of the orbit in *Acanthocybium* and diverge towards the anterolateral aspect of the frontal in others. (6) The anterior spatulate part of the vomer projects forward from the floor of the neurocranium beyond the anterior level of the nasal and the ethmoid bone; but remains entirely hidden to the dorsal view in others. (7) The posterior part of the first infraorbital is narrowly pointed; but broad and rounded in others. (8) The pterotics are produced posteriorly as blunt processes except in *S. commerson* in which they are produced as elongate spines; but as spines of varying length in the other genera, and the maximum length is attained in *Auxis*. (9) There are 10-19 large, triangular teeth with wide space in between, in each premaxilla and dentary. *Sarda* approaches *Scomberomorus* in number of teeth, but differs in the villiform shape. In the other genera, the teeth are small, more than 35 in number and very closely arranged. (10) The maxilla ends posteriorly in the form of a lamina; but narrow in others except *Scomber* which seems to approach the condition in *Scomberomorus*. (11) The posterior limit of the upper arm of the dentary is vertical with distinct corners, but gently curved in others. (12) The ventral branch of the anterolateral fork of the palatine is much longer than the dorsal branch, and the toothed surface of the vertical lamina is broader. However, the latter is narrow in *S. commerson*. In the other genera, the ventral branch is shorter and the lamina invariably narrow. (13) The posterodorsal aspect of the metapterygoid clasping the hyomandibula is not forked to the extent of extending the posterior branch across the symplectic process of the hyomandibula; in the other genera the posterior branch is well-formed and lies across the symplectic process of the hyomandibula. (14) The process at the posterodorsal aspect of the quadrate, though prominent, does not project far beyond the dorsal level of the anterior part of the quadrate. (15) The symplectic which is of nearly uniform width, is hidden to the exterior view, being confined to the groove on the mesial surface of the quadrate but in the other genera, it expands out well above the quadrate by more than 6 times the width of the base. (16) The dorsal hypohyal is equal to or slightly smaller than the ventral hypohyal; but distinctly smaller than the latter in others. (17) The superior margin of the ceratohyal is convex, straight or slightly concave, but deeply concave in others. (18) The posterior border of the urohyal is vertical with the posteroinferior corner forming an angle of about 90°; but gently curving down to the ventral margin in others. (19) The anterior limb of the subopercle is double-horned and the dorsal limb very much elongated; but the former single-horned, and the latter of medium length in all other genera except *Scomber* in which the lower limb is as long as the dorsal. (20) The posterior margin of the preopercle is concave, but crescent-shaped in others, being typically so in *Auxis* and *Euthynnus*. The preopercle of *S. commerson* nearly attains a crescent shape. (21) The posterior margin of the interopercle gently curves down as in *Scomber* and *Acanthocybium*; but descends obliquely straight in *Sarda* and vertically in *Rastrelliger, Auxis, Euthynnus* and *Thunnus*, with slightly concave inferior part. The posterior part of the interopercle posterior to its superior crest is longer than the part anterior to the crest in *Scomberomorus*; but *vice-versa* in all other genera. (22) The total number of vertebrae ranges from 40 in *S. chinensis* to 56 in *S. multiradiatus*, ranking next only to *Acanthocybium*. Only *Gasterochisma* and *Sarda* each having 45 vertebrae and *K. pelamis* with 41 vertebrae fall within the range of the count in *Scomberomorus*. (23) The hypurapophysis is very prominent; but very small in others. (24) The body of the posttemporal is lanceolate in that the inferior margin ventrally projects as a cone and anteriorly ascends up towards the dorsal process obliquely, exposing more than half of the lamina connecting the dorsal and ventral processes; the inferior margin is nearly straight in *Scomber*, *Sarda* and *Acanthocybium*, slightly concave in *Thunnus*, concave in *Euthynnus* and deeply concave in *Auxis*. (25) There is no shoulder-shaped anterior projection in the supracleithrum beneath the handle-shaped dorsal process; in *Acanthocybium*, only an insignificant projection is present; in *Scomber*, it is small and anteromedian in position, but in others it is well-developed. (26) The outer wall of the folded part of the cleithrum is so broad that it entirely conceals the window formed by the inner wall with the coracoid; in *Acanthocybium*, *Sarda* and *Thunnus*, it is less broad exposing the upper 1|3 of the window completely and most of the lateral surface of the inner wall. (27) The lower part of the cleithrum is nearly straight; it is slightly curved in *Sarda*, curved more in *Acanthocybium* and *Thunnus*, and attains the form of a bow in *Auxis* and *Euthynnus*; in *Scomber*, the lower-most region is deeply flexed. (28) The upper piece of the postcleithrum is rather narrow, but tends to be broader in *S. cavalla* and *S. commerson* as in the other genera. (29) The ventral wing of the anterolateral process of the pelvic girdle is narrow and not separated from the upper part by a notch; but broad and separated by a notch of varying depth in others.

With regard to the characteristics of the skeletal system, the species of *Scomberomorus* whose osteology has been investigated fall into two groups. *S. cavalla* and *S. commerson* form one group called the *cavalla* group by Mago Leccia (1958). *S. koreanus*, *S. guttatus*, *S. maculatus*, *S. regalis* and *S. lineolatus* form the *guttatus* group of Mago Leccia (1958) (Table 6). *S. lineolatus*, though identical with the *cavalla* group in certain characteristics, is closely alligned to the other group in many respects. The characteristic features of the *cavalla* group are: neurocranium relatively narrow; temporal ridge posteriorly with an insignificant epiotic process; auxiliary crests shallow with straight lateral margin; pineal foramen absent, but a narrow slit is left between the mesial crests of the frontals; brain-chamber opening slightly visible or not through either side of the relatively broad parasphenoid; median vertical process of the basisphenoid short with anteriorly sloping base; dorsal margin of the anterior part of the first infraorbital straight; epiotic develops lateral and posterolateral knobs; mid-lateral process of the sphenotic small; ventral surface of the median keel of the parasphenoid broad; entering angle of the premaxilla 33°; premaxilla with long nasal process, forming 41-45% of its length; anterior notch of the dentary distinct; ventral process of the angular long and narrow; lateral wall of the palatine less concave and its toothed lamina narrow; entopterygoid rather narrow; vertical ridge of the hyomandibula nearly approaches the dorsal margin of its head before meeting the anterior condyle; anteroventral projection of the opercle well-developed; anterior-posterior axis of the opercle broader; postero-inferior aspect of the subopercle not bulging prominently; dorsal edge of the subopercle blunt; third basibranchial and lower pharyngeal relatively broader; posterior margin of the descending part of the gill ray with a sloping notch and the gill filament with a row of ciliary structures*; gill ray without transverse horny bars; number of vertebrae 43 to 45; haemal and neural spines obliquely inserted on the centra; parapophyses of the anterior precaudal vertebrae nearly vertical; wing of the cleithrum slightly narrows itself posteriorly; coracoid rela-

* The nature of these structures is not known in *S. cavalla*.

TABLE 3. *Osteological characters of* Acanthocybium

No.	Bones	Characters (+)
1.	Auxiliary ridge, lateral margin	straight
2.	Auxiliary ridge, height	less
3.	Temporal fossa, depression	present
4.	Basisphenoid, median vertical process	long
5.	Basisphenoid, base	anteriorly sloping
6.	Basisphenoid, median process	small, pointed
7.	Pterosphenoids	nearly rectangular
8.	First infraorbital, anterior part	forked
9.	First infraorbital, anterodorsal aspect	straight
10.	Parietal sutural pattern	of similar type
11.	Epiotic process	well-developed
12.	Epiotic process, lateral and posterior sides	bulging
13.	Supraoccipital, mid lateral inward curve	absent
14.	Brain chamber, opening	slightly visible or invisible on either side of parasphenoid
15.	Parasphenoid	broader
16.	Parasphenoid, median keel	narrow bottomed
17.	Premaxilla, entering angle of pedicel	33°
18.	Dentary, length between anterior end to origin of posterior arms	longer than upper arm
19.	Angular, ventral process	long and narrow
20.	Palatine, lateral wall	less concave
21.	Palatine, toothed lamina	narrow
22.	Metapterygoid, anterior free border	slightly concave
23.	Metapterygoid, spine at anteroventral corner	present
24.	Entopterygoid	mesial border bulges slightly
25.	Hyomandibula, posterodorsal pointed process	well-developed
26.	Hyomandibula, vertical ridge elevation	reaches slightly below dorsal border
27.	Symplectic, anterior horn	absent
28.	Hypohyal, indentation	straight
29.	Opercle, anteroventral projection and notch	well-developed
30.	Opercle, line indicating course along which posterior border of preopercle overlapped opercle	present
31.	Subopercle, posteroventral area	bulges slightly
32.	Subopercle, dorsal edge	blunt
33.	Preopercle, posterior margin	convex
34.	Interopercle, portion anterior to crest	narrow and longer
35.	Third basibranchial	narrow
36.	Lower pharyngeal	narrow
37.	Gill ray, sloping notch at proximal margin	present
38.	Gill ray, horny transverse bars at lower part	absent
39.	Vertebrae, median lateral groove	present
40.	Bone separating 2nd epural from dorsal hypural plate	compound (stegurals + hypurale minimum)
41.	Supratemporal, portion lateral to notch	broadens
42.	Posttemporal, posterior projection of ventral process	as a long spine
43.	Supracleithrum, posterodorsal notch	well-developed
44.	Cleithrum, double-walled lower part	narrow
45.	Scapula, foramen	large
46.	Coracoid	narrow
47.	Upper postcleithrum	broad
48.	Pelvic girdle, posterior end of anterolateral process	broader
49.	Pelvic girdle, anterior end of anterolateral process	modest size

Symbol + is marked under those species which possess the character described under the
Symbol — is marked under those species which possess the character described under the
A.s = *A. solandri;* S.co = *S. commerson;* S.ca = *S. cavalla;* S.l = *S. lineolatus;* S.k =
Data for *S. cavalla, S. maculatus* and *S. regalis* from Mago Leccia (1958).

and the different species of Scomberomorus.

A.s	S.co	S.ca	Species S.l	S.k	S.g	S.m	S.r	Characters (—)
+	+	+	+	—	—	—	—	concave
+	+	+	—	—	—	—	—	more
+	+	+	+	—		+	+	ill-developed or absent
+	—	—	+	+	+	+	+	short
+	+	—	—	—	—	—	—	slightly sloping posteriorly
+	—	*	+	+	+	+	+	long, pointed (* broad)
+	+	+	—	—	+	—	—	rather club-shaped
+	+	—	+	+	+	+	+	not forked
+	+	+	—	—	—	—	—	concave
+	+	?	+	—	—	?	?	of another type (? = not known)
+	—	—	+	+	+	+	+	not well-developed
+	+	+	—	—	—	—	—	not bulging
+	+	?	+	—	—	?	?	present (? = not known)
+	+	+	—	—	—	—	—	wide and prominently visible
+	+	+	+	—	—	—	—	narrower
+	—	—	+	+	+	+	+	flat bottomed
+	+	+	*	—	—	—	—	40-43° (* 23°)
+	—	—	+	—	—	+	+	shorter than upper arm
+	+	+	—	—	—	—	—	short and stumpy
+	+	?	—	—	—	?	?	more concave (? = not known)
+	+	?	—	—	—	?	?	very broad (? = not known)
+	—	—	+	—	—	—	*	convex or nearly straight (* decidedly concave)
+	+	—	—	—	—	—	—	absent
+	+	+	+	—	—	—	—	mesial border bulges markedly
+	+	+	—	—	—	—	—	small
+	+	+	—	—	—	—	—	much below dorsal border
+	+	+	+	—	—	?	?	present (? = not known)
+	+	+	—	—	+	+	—	anteriorly curved
+	+	+	T	—	—	—	—	not so prominent
+	+	—	—	—	—	—	—	(T = intermediate) absent
+	+	+	—	—	—	—	—	bulges distinctly
+	+	+	—	—	—	—	—	acute
+	+	+	—	—	—	—	—	concave
+	+	+	T	—	—	T	—	shorter and less narrow (T = intermediate)
+	—	—	+	+	+	+	+	broad
+	—	—	+	+	+	+	+	broad
+	+	?	+	—	—	?	?	absent (? = not known)
+	+	?	—	—	—	?	?	present (? = not known)
+	—	—	—	+	+	—	—	absent
+	+	—	—1	—	—	—2	—	single (1, 2 = appears to be compound)
+	+	?	—	—	—	?	?	does not broaden (? = not known)
+	+	?	—	+	*	?	?	as a minute knob (* blunt; ? = not known)
+	+	—	—	—	—	—	—	less prominent
+	+	—	—	—	—	—	—	much wider
+	—	—	—	+	—	—	+	narrow
+	+	?	—	—	—	?	?	rather wide (? = not known)
+	+	+	—	—	—	—	—	long and narrow
+	+	+	—	—	—	—	—	rather narrow
+	+	+	*	—	+	—	—	broad (* very narrow)

left column.
extreme right column.
S. koreanus; S.g = *S. guttatus;* S.m = *S. maculatus;* S.r = *S. regalis.*

tively narrow; upper postcleithrum broader; and, the anterior part of the anteromesial process of the pelvic girdle hidden, or, only the tip visible to the lateral view of the girdle.

The species of the *guttatus* group differ from the *cavalla* group in the above aspects and their characteristic features are: neurocranium relatively broader; temporal ridge develops a prominent epiotic process posteriorly; auxiliary crest high with concave lateral margin; no slit is developed between the mesial crests of the frontals; brain-chamber opening broadly visible through either side of the narrow parasphenoid; median vertical process of the basisphenoid long; dorsal margin of the anterior part of the first infraorbital concave; lateral and posterolateral knobs absent in the epiotic; mid-lateral process of the sphenotic well-developed; median keel of the parasphenoid narrow; entering angle of the premaxilla 40-43°; premaxilla with short nasal process forming 38-39% of its length; anterior notch of the dentary faint; ventral process of the angular short and stumpy; lateral wall of the palatine deeply concave and its toothed lamina broader; mesial side of the entopterygoid more bulging; vertical ridge of the hyomandibula not closely approaching its head; anteroventral projection in the opercle insignificant; anterior-posterior axis of the opercle rather narrow; posteroinferior aspect of the subopercle more bulging; dorsal edge of the subopercle acute; third basibranchial and lower pharyngeal rather narrow; gill ray without a sloping notch and gill filament without ciliary structures *; horny bars in the gill ray present * number of vertebrae varying from 46 to 53 in the different species; haemal and neural spines longer and nearly vertically inserted to the centra; parapophyses of the anterior precaudal vertebrae directed anteriorly; wing of cleithrum narrow posteriorly; coracoid comparatively broader; upper cleithrum narrow; and, the posterior part of the anteromesial process of the pelvic girdle clearly visible to the lateral view of the girdle.

Except in a few characteristics such as the absence of a pineal foramen, the number of vertebrae etc., the *cavalla* group closely resembles *A. solandri* and in the few characters available for comparison, also resembles *S. chinensis*. The *guttatus* group differs from *A solandri* in all the above respects except in the size of the epiotic process of the temporal crest, median keel of the parasphenoid, basisphenoid, and the third basibranchial and lower pharyngeal.

Of the many species within the *guttatus* group, *S. koreanus* and *S. guttatus* are closely related to each other as indicated by the relatively shorter neurocranium, very high cranial crests, supraoccipital-parietal suture rendering the anterior half of the supraoccipital dome-shaped by an inward curve, absence of or insignificantly developed intercalar process, formation of an anterior horn on the simplectic, parapophyses of the one or two vertebrae just preceding the one with the first closed haemal arch nearly touching each other, and the devel-

* The nature of the gill filament and gill ray was investigated only in *S. koreanus*, *S. guttatus* and *S. lineolatus* of this species group.

opment of a mid-lateral furrow commencing from about the tenth caudal vertebrae posteriorly. Specialization in *S. guttatus* is indicated by the more acute anteroinferior limb of the subopercle, very long ventral limb of the preopercle, dome-shaped base of the gill ray, much elevated but suddenly sloping crest of the neural prezygapophyses, and the blind posterior end of the ventral process of the post-temporal. In *S. koreanus* specialization seems to have taken place in the temporal crest tending to converge anteriorly with the mid-longitudinal axis of the neurocranium, inward projection from the pterosphenoid into the opening of the brain chamber assuming special prominence, posterior end of the urohyal attaining the maximum vertical depth, and in the base of the gill ray assuming a shoe shape. Differences in the magnitude of the development of some of the characteristics considered common to both the species have also been observed, (e.g) the horny transverse rods extending from the gill ray are longer, anterior horn of the symplectic shorter, and the mid-longitudinal furrow of the posterior caudal centra deeper in *S. koreanus* than in *S. guttatus*. They differ also in the vertebral count which is 20 + 26 = 46 in *S. koreanus* but 20-21 + 29 = 49-50 in *S. guttatus*. Silas (1924) considered that *S. koreanus* and *S. guttatus* were identical or differed only at the subspecific level. Based on morphometric and meristic characteristics, Devaraj (in press) established that they are distinct species which is also supported by osteological evidence. Specialization in *S. maculatus* appears to have been towards an increase in the number of vertebrae to 53 which is second only to the maximum of 55-56 in *S. multiradiatus* within *Scomberomorus*.

S. lineolatus though closely alligned to the *guttatus* group, resembles the *cavalla* group in the relative size of the neurocranium, straight lateral margin of the auxiliary crest, relatively broader parasphenoid, longer nasal process of the premaxilla and the rather narrow entopterygoid. With regard to the extent of the brain chamber visible through either side of the parasphenoid, the anteroventral projection and the anteroposterior axis of the opercle tending to be prominent, the development of an incipient sloping notch and a few horny bars in the gill ray and the presence of a few cilia in the gill filament, *S. lineolatus* forms a transitional stage between the two groups. The smallest entering angle of the premaxilla (23°), straight mid-longitudinal course of the groove for the hyoidean artery in the hyoid arch, slightly dome-shaped base of the gill ray with flat projecting extremities, first one or two haemal spines arching anteroposteriorly, and the very narrow anterolateral process of the pelvic girdle appear to be the specialized characteristics of *S. lineolatus*.

The characteristics in which *S. commerson* seems to have specialized are: the prominent truncate process of the intercalar; shortening of the vertical process of the basisphenoid; much elongated median process on the vertical process of the basisphenoid; a posteriorly pointing tiny process projecting from a small knob on the superior margin of the urohyal; reduction of the number of gill rakers (2-6); club-shaped base of the gill ray; and, the more or less constant number of vertebrae (44). *S. commerson* is also unique in the possession of many characteristics of *A. solandri* not found in any of the other species of *Scomberomorus* studied. They are: the presence of a spine at the anteroventral corner of the metapterygoid, convex posterior margin of the preopercle, very well-developed and pointed posterodorsal process of the hyomandibula, relatively narrow double-walled lower part of the cleithrum, and the compound structure formed of the stegurals and the *hypurale minimum*. There are certain characteristics in *S. commerson* that seem to be in a state of transition between *A. solandri* and other species of *Scomberomorus*. They are: the relatively narrower neurocranium; temporal ridge tending to be low at the level of the epiotic; pterotic posteriorly produced into an elongated spine; mid-lateral process of sphenotic still smaller than that of *S. cavalla*, lateral branch of the anterior fork of the maxilla feebly developed; anterior notch of the dentary more distinct than in *S. cavalla;* upper fork of the anterolateral ridge on the preopercle indistinct or absent; the posterior extension of the lower part of the mesial wall of the cleithrum less significant; and, the upper postcleithrum larger than that of *S. cavalla* (Table 4). In the case of *S. cavalla*, the nearly convex temporal crest, very broad median process projecting from the vertical process of the basisphenoid, unforked anterior part of the first infraorbital and a low vertebral count of 43, appear to be specialized characteristics.

Osteological features of *S. chinensis* (Kishinouye 1923, p. 418, pl. 23, fig. 40, a-c) indicate that it is unique in the presence of the first haemal prezygapophysis and the first inferior foramen on the same vertebrae i.e., the third caudal vertebrae, the lowest number of vertebrae within Scomberomorini 18 + 22 = 40, and the development of both the pineal window as well as the interorbital lateralis commissure simultaneously. Within *Scomberomorus*, only *S. chinensis* shares with *Acanthocybium* such characteristics as the non-extension of the supraoccipital crest to the frontal, presence of a pair of very prominent depressions on the ventral surface of the vomer, and the well-developed pineal window. In the exposure of a broadly V-shaped dorsal surface of the ethmoid bone and the spatulate part of the vomer partly projecting beyond the anterior level of the ethmoid, it represents an intermediate condition between *Acanthocybium* and other species of *Scomberomorus*. It is identical with the *cavalla* group in the straight, shallow auxiliary crest, opening of the brain chamber, broad parasphenoid, development of epiotic knobs, oblique course of the neural and haemal spines and the low crest of the neural prezygapophysis. It resembles the *guttatus* group in the truncate pterotic process (also in *S. cavalla*), very small intercalar process, large number of gill rakers (2 + 9 = 11) and the incipient mid-lateral fossa in the caudal vertebrae as seen in *S. guttatus* and *S. koreanus*.

It could be inferred that *S. chinensis* forms a link between *Acanthocybium* and *Scomberomorus*, as well as the basis of the stem which diverged into

TABLE 4. *Transitional characters in* S. commerson (*and* S. cavalla *and* S. lineolatus) *intermediate between other species of* Scomberomorus *and* Acanthocybium.

Sl. No.	Bones	*A. solandri*	*S. commerson*	Other species of *Scomberomorus*
1.	Neurocranium, breadth in relation to length	narrow	tends to be narrower (in *S. lineolatus* also)	broad
2.	Temporal ridge	descends low at level of epiotic	slightly descends at level of epiotic	does not descend
3.	Pineal window	well-formed	as a pseudoslit (in *S. cavalla* also)	not formed
4.	Pterosphenoid, process at inner margin	absent	insignificant	prominent
5.	Pterotic process	as a long sharp spine	as an elongated wide process	short and truncate process
6.	Sphenotic, mid lateral process	absent	small (in *S. lineolatus* and *S. cavalla* also)	large
7.	maxilla, outer branch of anterior fork	absent	flimsy	well-developed
8.	Dentary, anterior notch	well-developed	distinct (*S. cavalla* also)	faint
9.	Preopercle, upper fork of anterior ridge	absent	indistinct or absent	well-developed
10.	Cleithrum, posterior extension at lower part of mesial wall	insignificant	tends to be insignificant	very well-developed
11.	Upper postcleithrum	massive	broader	narrow
12.	Pelvic girdle, anteromesial process	invisible to lateral view of girdle	anterior tip visible to lateral view of girdle (in *S. cavalla* also)	anterior 1/3 – 1/2 visible to lateral view of girdle

the two groups of seerfishes. Mago Leccia (1958) ramarked that *S. commerson* forms a link between the *cavalla* group and *Acanthocybium* and would merit separate generic treatment. Though the affinities of *S. commerson* to *Acanthocybium* are confirmed in this study, it does not appear to warrant a separate generic status as it does not deviate from any of the diagnostic characters of *Scomberomorus* already listed. Nor should a separate genus be recommended for *S. chinensis*. Moreover, Munro's (1943) splitting of *Scomberomorus* into nine subgenera fails to receive any support from the present investigation.

TABLE 5. *Osteological differences between* Acanthocybium *and* Scomberomorus.

Sl. No.	Bones	*Acanthocybium*	*Scomberomorus*
1.	Supraoccipital crest	does not extend over the frontals	extends over the frontals
2.	Temporal ridge	stops at anterior level of pineal window	reaches up to anterior end of frontal
3.	Pterotic ridge	stops posterior to mid level of orbit	extends up to mid level or still anterior of orbit
4.	Auxiliary ridge	reduced	
5.	Height of ridges and depth of fossae on the dorsal surface of neurocranium	less	well-developed more
6.	Dialator fossa	narrow	wide
7.	Ethmoid bone	long; V-shaped dorsomedian portion exposed	short to medium; only anterior border exposed
8.	vomer, anterior spatula	does not project beyond nasal	projects much beyond nasal level
9.	Pineal window	well-developed as a large fenestra	as a pseudoslit or absent
10.	Frontal, fenestra at posterior level of ethmoid bone	present	absent
11.	Frontal, interorbital commissure of the lateral line system	absent	present
12.	Frontal, broad depression in front of pineal window	well-developed	absent
13.	First infraorbital, posterior part	short and broad	long and pointed
14.	First infraorbital, infraorbital lateral line	obliterated	clearly seen
15.	Sphenotic	narrow	wide
16.	Sphenotic, mid lateral projection	absent	present
17.	Intercalar posterior process	absent	insignificant to well-developed

18. Pedicel length in total length of premaxilla	50%	35-45%
19. Premaxilla, number of teeth	about 50	14-24
20. Maxilla, lateral branch of anterior fork	absent	present
21. Maxilla, posterior end	reduced in size	lamellate
22. Supramaxilla, handle	reduced in size	well-developed
23. Dentary, number of teeth	about 50	10-20
24. Dentary, anteroventral notch	almost absent	present
25. Dentary, anterior notch	well-developed	faint to distinct
26. Dentary, posterior end of upper arm	narrow with no depression	broad with triangular depression
27. Angular, Meckel's cartilage	ascends to slightly below the crest of dorsal process	does not ascend to such a height
28. Palatine, anterolateral fork	ventral branch shorter than dorsal	ventral branch longer than dorsal
29. Palatine, posterior fork	outer branch equal to inner	outer branch much longer than inner
30. Palatine, dorsal surface	long depression with furrows	no depression, but with articular facets
31. Metapterygoid, posteroventral part	invaded by dorsal end of symplectic	not invaded
32. Metapterygoid, ventral border	anterior oblique part longer	horizontal part, longer
33. Ectopterygoid	dorsal arm longer	ventral arm longer
34. Hyomandibula, number of fossae on ventral surface	two	one
35. Quadrate, posterior process	very much longer	shorter to prominent
36. Quadrate, lateral surface	bony ridge not Y-shaped	Y-shaped bony ridge with saucer-shaped depression between the anterior arms
37. Symplectic, upper part	broad and produced beyond quadrate	small and not produced

TABLE 5. (*Continued*)

Sl. No.	Bones	*Acanthocybium*	*Scomberomorus*
38.	Symplectic, mid constriction	absent	present
39.	Hypohyal, dorsal hypohyal	much smaller than the ventral hypohyal	smaller than or equal to the ventral hypohyal
40.	Hypohyal, anterior and anterodorsal notches	present	absent
41.	Ceratohyal, dorsal margin	very deeply concave	convex to moderately concave
42.	Glossohyal, anterior end	broad	narrow
43.	Glossohyal, ventral bulbus thickening	absent	present
44.	Glossohyal, furrows on dorsal and ventral surface	present	absent
45.	Urohyal, posteroventral margin	curving without a corner	with a distinct corner
46.	Opercle, anteroposterior width	roadest	broad to broader
47.	Preopercle, vertical shallow depression along anterior ridge	absent	present
48.	Preopercle, upper fork of anterior ridge	absent	present
49.	Preopercle, lateral groove at the inferior end of the anterior ridge	present	absent
50.	Preopercle, lateral line pores	obliterated	distinct
51.	Interopercle, posterior border	divided by a mid notch	rounded, not divided
52.	Gill rakers	absent	present (2-18)
53.	Vertebral column, inferior foramina	only one	many
54.	First haemal prezygapophysis on vertebra	23rd	14-19th
55.	First closed haemal arch on vertebra	27th	10-15th

56. Number of vertebrae	63	40-56
57. Haemal spines of preural 2 and 3	fused with centra	autogenous
58. Parhypural	fused with compound centrum and hypural plate	autogenous
59. Hypurapophysis	small	large
60. Hypural plate, mid posterior notch	narrow	normal to broad
61. Number of intermuscular bones	10	21-22
62. Posttemporal, lamina between dorsal and ventral processes	absent	present
63. Posttemporal, median process	present	absent
64. Posttemporal, posterior border	divided into two equal halves	divided into two unequal halves
65. Posttemporal, ventral border of lower laminar part	straight	projects as a ventral cone
66. Cleithrum, wing	uniform width	posterior end narrowing
67. Cleithrum, space between anterior process and wing	very wide	narrow
68. Cleithrum, upper part of mesial slit with coracoid	visible to lateral view of cleithrum	not visible to lateral view of cleithrum
69. Coracoid, lateral longitudinal sulcus	near posterior border	close to anterior border
70. Pelvic girdle, notch on ventral wing of anterolateral process	present	absent
71. Pelvic girdle, anteromesial process	hidden to lateral view of girdle	visible in varying degrees to lateral view of girdle
72. First dorsal, number of spines	XXVI	XIII-XVIII
73. Second dorsal, number or rays	11	15-23
74. Anal, number of rays	11	15-24

Acanthocybium is one of those genera of Scombridae which differ from *Scomberomorus* in many osteological characteristics dealt with already. The differences of *Acanthocybium* and *Scomberomorus* are presented in Table 5. Hence, it becomes logical to question whether it should still be included in the Scomberomorini. The limited number of characteristics which it shares with *Scomberomorus* are the remarkably soft bones; concave anterior margin of the ethmoid bone (also in *Sarda*); flat, nearly triangular nasal with thickened edges joined to the external edge of the frontals and the extremities of the forked ethmoid bone, a shape not met with in any other scombrid genera; opercle with a posterior indention as in Scombrini and nearly straight anterodorsal margin (also in *Sarda*); premaxilla with broad shank, without distinct prominence separating the articular facets, and with low entering angle; ventral arm of the dentary shorter than its dorsal arm; posterior branch of the dorsal fork of the metapterygoid insignificant or absent; presence of a posterior notch in the hypural plate, two epurals and a compound structure consisting of the stegurals and *hypurale minimum*, and the absence of a bony caudal keel as in the Scombrini; the so-called lateral process of the supratemporal very small, occupying the posterolateral corner of the bone resulting in the loss of the typical Y shape met with in the other genera; supracleithrum without a special articulating surface for the cleithrum at the lower half of the anteromesial ridge; and, the mesial wall of the cleithrum forms a posterior bulging as it descends down towards the lower extremity. No other scombrid genera are smilar to *Scomberomorus* in the above respects except the Scombrini and *Sarda* agreeing in two or three characteristics. The characteristics in which Scomberomorini resembles Scombrini are the primitive percoid ones retained in the latter. Gosline (1968) has listed the primitive features of *Scomber*. The beryciform foramen, a primitive character present in some species of *Scomberomorus*, is absent in *Scomber*.

Since *Scomber*, considered to be primitive among Scombridae (Gosline 1968), is one of those genera agreeing one another in the twenty-nine characteristics already discussed, these must be considered as primitive features retained by all but *Scomberomorus* in which they are modified to suit its own line of specialization. These modifications render strong support to the retention of Scomberomorini as a distinct tribe to accommodate this specialized group of scombrid fishes. However, *Acanthocybium* has many important characters typical of *Scomberomorus* and hence its inclusion in the Scomberomorini should not appear questionable. The combination of these characteristics in *Acanthocybium* is concrete evidence of its common ancestry with *Scomberomorus*, although the latter has departed from the main line of evolution.

Acanthocybium solandri seems to have specialized in the following lines: absence of the mid-lateral process of the sphenotic, shortening of the post-articular part of the first infraorbital, development of deep mid notch at the posterior border of the interopercle, length of the nasal process of the premaxilla attaining nearly 50% of the total length of the premaxilla, absence of an anterior fork in the maxilla, longer dorsal arm of the ectopterygoid, loss of gill rakers, base of gill ray with a triangular anterior and horn-like posterior parts separated by a deep notch, vertebrae reaching the maximum number of 63 or above, occurrence of the first closed haemal arch on the 27th vertebrae, presence of only one inferior foramen developed on the 49th vertebra, vertically directed anterior abdominal parapophyses, development of a very deep midlateral fossa from the 9th to the 54th vertebra, complete fusion of the parhypural with the first preural centrum and the hypural plate, reduction of the number of intermuscular bones to 10, auxiliary process of the posttemporal ending in about four spicules, and the development of an anteroinferior notch on the upper postcleithrum.

OSTEOLOGICAL KEY TO THE INDIAN SPECIES OF SCOMBEROMORINI

1a. Flat, triangular nasal; premaxilla with broad shank and low entering angle; ventral arm of dentary shorter than its dorsal arm; posterior branch of dorsal fork of metapterygoid insignificant; lateral stem of supratemporal reduced; no articulating surface on anteromesial ridge of supracleithrum for the cleithrum; mesial wall of cleithrum posteriorly extended (Scomberomorini).

2a. Interorbital lateralis commissure absent; preorbital part of neurocranium evenly rounded and lengthened; postarticular part of first infraorbital shortened and blunt; mid lateral process of sphenotic absent; nasal process of premaxilla 50% in total length of premaxilla; maxilla not forked anteriorly; dorsal arm of ectopterygoid longer than its ventral arm; deep mid notch at posterior border of interopercle; gill rakers absent; base of gill ray with a triangular anterior and horn-like posterior parts separated by a deep notch; number of vertebrae 63 or more; first closed haemal arch on 27th vertebrae; only one inferior foramen, on 49th vertebra; deep mid-lateral fossa from 9th to 54th vertebrae; parhypural fused with hypural plate; number of intermuscular bones 10 (*Acanthocybium*)............ *A. solandri.*

2b. Interorbital lateralis commissure present; preorbital part of neurocranium not produced and with crests extending from the postorbital part; postarticular part of first infraorbital longer and pointed; sphenotic process present; nasal process of premaxilla 35-45% in total length of premaxilla; anterior fork of maxilla well-developed; dorsal arm of ectopterygoid shorter than its ventral arm; posterior border of interopercle not notched; 2-18 gill rakers; base of gill ray of a different shape; 40-56 vertebrae; first closed haemal arch on 10-15 vertebra; inferior foramen many, first one on any of the vertebra between 21 and 31; shallow mid-lateral fossae restricted to posterior caudal vertebrae in some species; parhypural autogenous; 21 to 22 intermuscular bones (*Scomberomorus*).

3a. Entering angle of nasal process of premaxilla 33-43°; first two haemal spines arch vertically or obliquely backwards; anterolateral process of pelvic girdle broad.

4a. Basisphenoid with long median process projecting from short vertical process; dorsal margin of anterior half of first infraorbital straight; pterotic and intercalar posteriorly produced into elongate processes; parasphenoid broad and brain chamber opening on either side of it slightly visible or invisible; entering angle of premaxilla 33°; toothed lamina of palatine narrow; superior margin of urohyal with a pointed process on a knob; broad opercle; gill rakers 2-6; base of gill ray club-shaped; vertebrae 42-45, usually 44; haemal and neural spines obliquely inserted to centra; no mid-lateral fossae on centra of posterior caudal vertebrae; upper postcleithrum broad...... *S. commerson.*

4b. Basisphenoid with broad median process projecting from long vertical process; dorsal margin of anterior half of first infraorbital concave; pterotic and intercalar processes insignificant or absent; parasphenoid narrow and brain chamber opening on its either side broadly visible; entering angle of premaxilla 40-43°; toothed lamina on palatine very broad; superior margin of urohyal devoid of any process; comparatively narrow opercle; gill rakers 8-13; base of gill ray dome- or shoe-shaped; vertebrae 46-50; haemal and neural spines vertically inserted to centra; shallow mid-lateral fossae present on centra of caudal vertebrae beginning at about 9th to 11th and continuing posteriorly; upper postcleithrum narrow.

5a. Vertical depth of posterior end of urohyal, of modest size; anteroinferior limb of subopercle more acute; ventral limb of preopercle much longer than its dorsal limb; base of gill ray dome-shaped; number of vertebrae 49-50; crest of neural process markedly elevated; posterior end of posttemporal ventral process blunt ......*S. guttatus.*

5b. Posterior end of urohyal attains maximum vertical depth among the Indian species; anteroinferior limb of subopercle rather blunt; ventral limb of preopercle only as long as the dorsal limb; base of gill ray shoe-shaped; number of vertebrae 46; crest of neural process not markedly elevated; posterior end of posttemporal ventral process in the form of a distinct spine .... *S. koreanus*.

3b. Entering angle of nasal process of premaxilla 23°; first two haemal spines arch anteroposteriorly; anterolateral process of pelvic girdle very narrow .... *S. lineolatus*.

1b. Nasal rather rod-like or club-shaped or bent anteriorly; premaxilla with very narrow shank and high entering angle; ventral arm of dentary equal to or longer than its dorsal arm; posterior branch of dorsal fork of metapterygoid very well-developed; supratemporal Y-shaped; articulating surface on anteromesial ridge of supracleithrum for the cleithrum present; mesial wall of cleithrum not posteriorly extended. (Fishes of the subfamily Scombrinae other than those of tribe Scomberomorini).

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