Osteology and Systematic Position of the Butterfly Mackerel, *Gasterochisma melampus*

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(Received February 10, 1983)

Abstract   A detailed description of the osteology of *Gasterochisma melampus* is presented, and the systematic position of the species is discussed through comparison with other perciform species from nine families.   Of the 13 osteological characters considered in this study to be diagnostic of the Scombridae, 12 are shared by *G. melampus*.   On the other hand, in perciform families other than the Scombridae, there are no characters of a particular family shared only by *G. melampus*, except for the ethmoid of the Coryphaenidae.   In addition to the above scombrid characters, *G. melampus* possesses 15 characters which are seen in none of the other species, and these characters are mostly seen in the neurocranium.   The osteological characters of *G. melampus* represent both primitive and advanced states in the Scombridae.   On the basis of these osteological observations, *G. melampus* can be considered to have been derived from the scombrid stem at an early time and to have undergone its own specialization.   *G. melampus* is regarded as an aberrant form but still within the taxonomic limits of the family Scombridae.

Richardson (1845: 346) described the monotypic genus *Gasterochisma* (type-species: *Gasterochisma melampus* Richardson) as a member of his "familiae Scomberidarum." Since then, this genus has attracted attention of many workers on account of its unique characters. Günther (1860: 387) re-examined the type-specimen of *G. melampus*, and placed the genus in the Nomeina, one of the five groups of the Scombridae in his classification. Regan (1902: 120) suggested the systematic position of *Gasterochisma* to be in the Scombridae, and he later (1909: 72) defined the family Scombridae as including the genus.

Although many investigators have followed Regan's (1909) scheme (Fraser-Brunner, 1950; Greenwood et al., 1966; Lindberg, 1971; Nelson, 1976), the relationships of *Gasterochisma* with the Scombridae have been a subject of different interpretations. Gosline (1968: 32) felt that *Gasterochisma* bore at least as much resemblance to the Bramidae as to the Scombridae. Collette and Gibbs (1963: 24–25), Gosline (1971: 163–164) and Collette (1978: 26, 38) questioned whether *Gasterochisma* is a member of the Scombridae.

On the systematic position of *Gasterochisma* within the family Scombridae, Regan (1902: 120) suggested the resemblance of the genus to *Cybium* (=*Scomberomorus*). Fraser-Brunner (1950) regarded *Gasterochisma* as the most primi-

tive form of the family. Tominaga (1966: 44) emphasized the necessity of re-examining the views of Fraser-Brunner (1950). Gosline (1968: 32) and Collette and Chao (1975: 590) stated that even if *Gasterochisma* is included in the Scombridae, it is a very aberrant form in the family.

All the studies mentioned above are based mainly on the external characters of *Gasterochisma*. Klawe (1980) correctly suggested the need to study the internal characters of *G. melampus*.

The purpose of this study is to describe the osteological features of *Gasterochisma melampus* in detail, and discuss the systematic position of the species through osteological comparison with other perciform species.

Material and methods

Terminology used in this study is based mainly on Harrington (1955), Patterson (1964), Monod (1968), Nelson (1973) and Uyeno (1975).

Gasterochisma melampus: Five specimens, which consist of four dissected and cleaned skeletal specimens and one preserved specimen in alcohol, were used in this study. Almost all observations were based on the four skeletal specimens, while the preserved one was X-rayed and partially dissected with alizarin staining for examining the branchial arch.

NSM-PO 381 (National Science Museum, Tokyo, Department of Paleontology, Osteological Collection); 35°49′6S, 89°19′0W, 203.4 mm in neurocranium length, 5 January 1980 (whole skeletal parts).

NSM-PO 382; no collecting and measurement data (incomplete skeletal specimen).

NSM-PO 511; 35°49′6S, 89°19′0W, 1950.0 mm in FL (fork length), 254.8 mm in neurocranium length, 5 January 1980 (whole skeletal parts).

One specimen deposited in Far Seas Fisheries Research Laboratory, Japan; 39°23′0S, 89°43′3W, 252.4 mm in neurocranium length, 8 December 1963 (axial skeleton only).

ZUMT 52313 (Department of Zoology, University Museum, University of Tokyo); 40°00′0S, 40–50°W, 355.0 mm in head length, July 1965 (head region only, preserved in alcohol).

Comparative material. In order to determine the systematic position of *Gasterochisma melampus*, a total of 29 specimens of 23 species belonging to 9 families and 4 suborders of the order Perciformes was examined.

Suborder Percoidei. Family Scombropsidae: *Scombrops boops*; FUMT-P 3826 (Department of Fisheries, University Museum, University of Tokyo), 87.6 mm in SL (standard length) (CS; cleared and stained specimen).

Family Coryphaenidae: *Coryphaena hippurus*; NSM-PO 118, 657.0 mm in SL (DC; dissected and cleaned specimen); NSM-PO 244, 900.0 mm in FL (DC); NSM-PO 523, no measurement data (DC).

Family Bramidae: *Taractes rubescens*; NSM-PO 651, 856.0 mm in TL (total length) (DC). *Taractichthys longipinnis*; NSM-PO 652, 601.0 mm in SL (DC); NSM-PO 653, 768.0 mm in TL (DC).

Family Sparidae: *Pagrus major*; FUMT-P 3797, 92.1 mm in SL (CS).

Suborder Scombrolabracoidei. Family Scombrolabracidae: *Scombrolabrax heterolepis*; NSM-PO 660, 176.2 mm in SL (CS).

Suborder Scombroidei. Family Gempylidae: *Nealotus tripes*; NSM-PO 661, 223.7 mm in SL, (DC). *Ruvettus pretiosus*; NSM-PO 547, 1160.0 mm in SL (DC).

Family Trichiuridae: *Trichiurus lepturus*; NSM-PO 201, no measurement data (DC).

Family Scombridae: *Acanthocybium solandri*; NSM-PO 561, 1560.0 mm in FL (DC). *Auxis thazard*; NSM-PO 182, 335.0 mm in SL (DC). *Euthynnus affinis*; NSM-PO 38, 445.0 mm in FL (DC). *Grammatorcynus bicarinatus*; NSM-PO 211, no measurement data (DC); FUMT-P 3796, 285.0 mm in SL (CS). *Gymnosarda unicolor*; NSM-PO 31, 313.0 mm in SL (DC). *Katsuwonus pelamis*; NSM-PO 657, 547.2 mm in SL (DC). *Rastrelliger kanagurta*; NSM-PO 439, 205.0 mm in TL (DC); FUMT-P 1817, 179.7 mm in SL (CS). *Sarda orientalis*; NSM-PO 28, 455.0 mm in SL (DC). *Scomber australasicus*; NSM-PO 205, 228.0 mm in SL (DC). *S. japonicus*; NSM-PO 203, no measurement data (DC); NSM-PO 207, 306.0 mm in SL (DC). *Scomberomorus niphonius*; NSM-PO 659, 587.0 mm in SL (DC). *Thunnus alalunga*; NSM-PO 656, 895.0 mm in FL (DC), *Thunnus albacares*; NSM-PO 212, no measurement data (DC).

Suborder Stromateoidei. Family Centrolophidae: *Psenopsis anomala*; NSM-PO 658, 144.8 mm in SL (DC).

Description

Neurocranium. The neurocranium is divided into four regions: ethmoid, orbit, otic and basicranial regions. Preceding the description of each region, the gross morphology of the neurocranium is discussed.

Gross morphology. The dorsal view of the neurocranium is unique in shape (Fig; 1); nearly parabolic in conic section rather than triangular or trapezoidal as in other scombrid fishes (Kishinouye, 1923; Gibbs and Collette, 1967; Collette and Chao, 1975; Devaraj, 1977). Although the frontoparietal foramen is absent, the frontal, parietal and supraoccipital are very thin around their junction on each side. The pineal foramen is also absent. The only ridge on the dorsal surface of the neurocranium is the conspicuous supraoccipital crest, in contrast to other scombrids which possess five crests (Kishinouye, 1923). The centroposterior part of the neurocranium is markedly expanded dorsally to form a "box-like brain case". The roof of the brain case is composed of the posterior part of the frontals, inner part of the parietals, anterior part of the epiotics and posterior part of the supraoccipital.

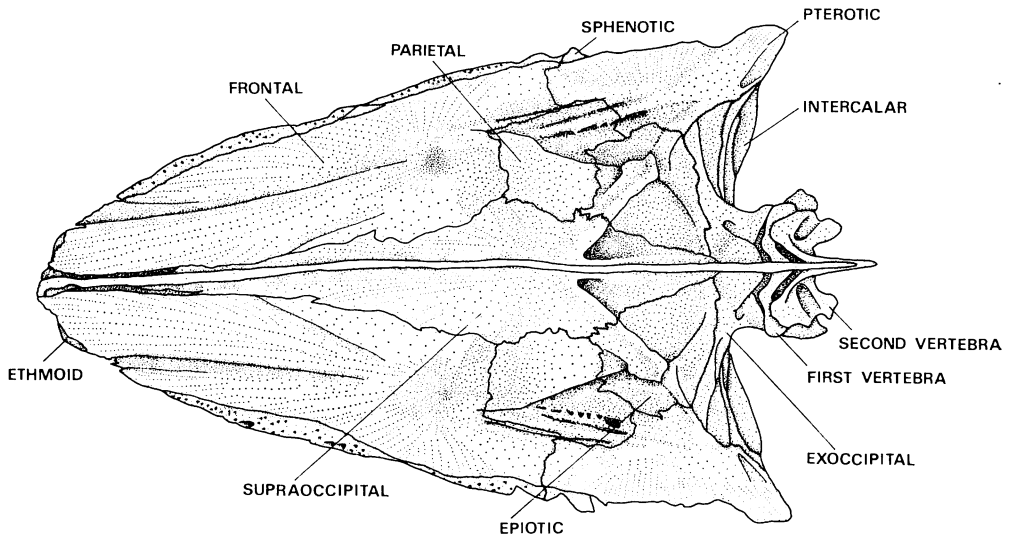In ventral view (Fig. 2), the prelateral ethmoid

Fig. 1. Neurocranium of *Gasterochisma melampus* (NSM-PO 511, 1590.0 mm in FL, 254.8 mm in neurocranium length), dorsal view.
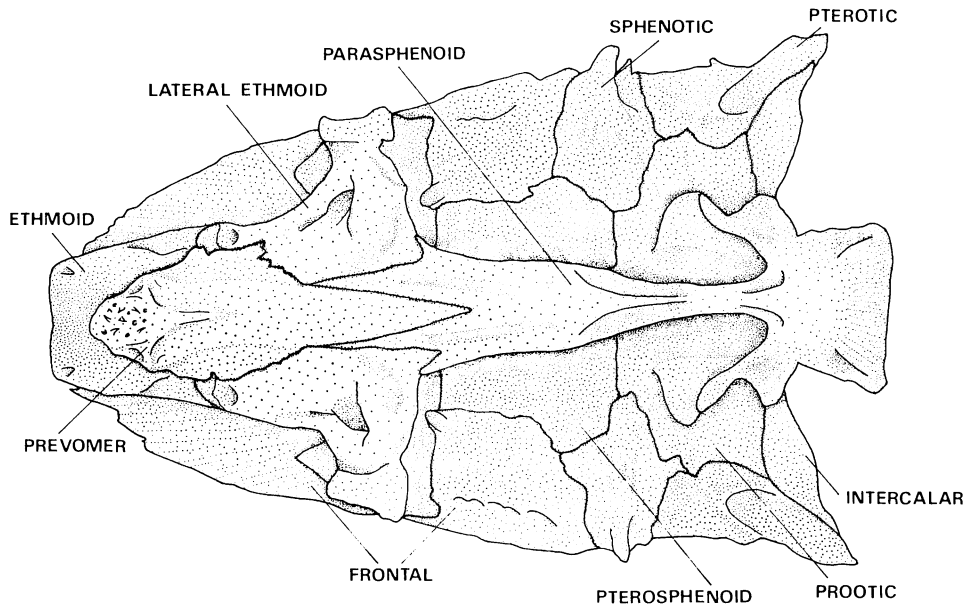

Fig. 2. Neurocranium of *Gasterochisma melampus* (NSM-PO 511), ventral view.

region, formed by the ethmoid and lateral ethmoids, is long and narrow as in primitive scombrids (Allis, 1903; Gnanamuttu, 1966). The posterolateral process of the lateral ethmoid is well developed and located at the anterior two-thirds of the neurocranium. The auditory capsule is not developed.

The supraoccipital crest runs along the entire dorsal edge of the neurocranium (Fig. 3). The anterior margin figured by the ethmoid and prevomer is deeply concave when viewed laterally. The orbit is lower and shorter than in other scombrids. No prominent lateral shelf is formed at the junction of the frontal, pterotic and
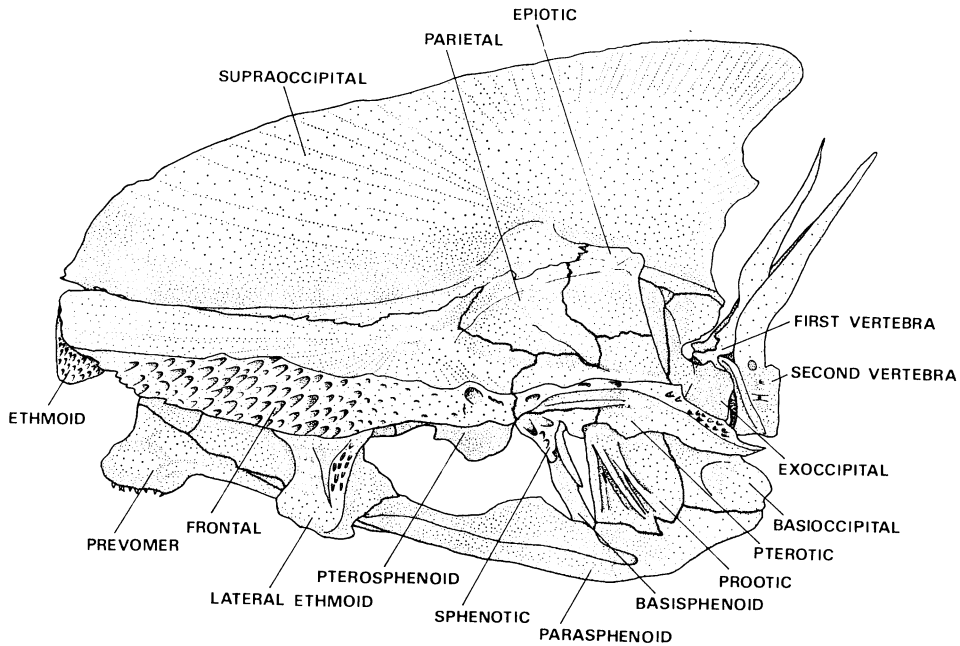
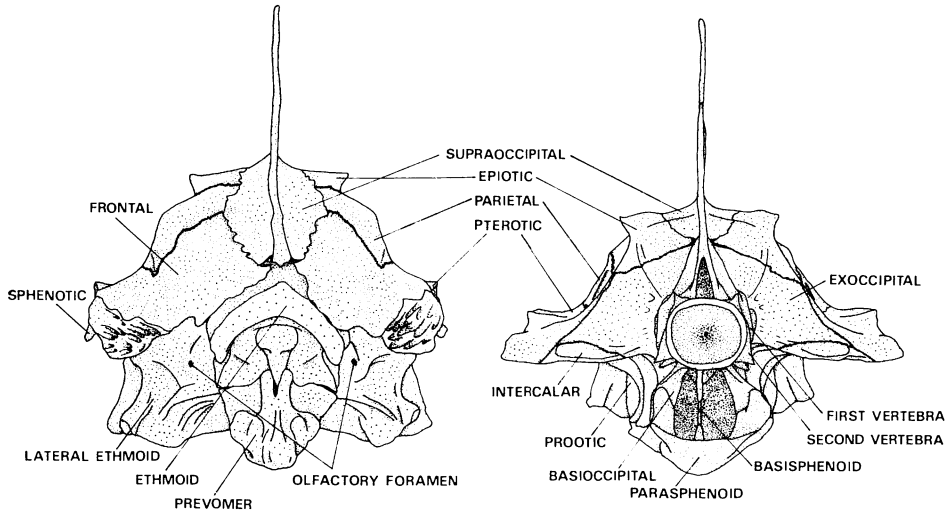Fig. 3. Neurocranium of *Gasterochisma melampus* (NSM-PO 511), lateral view.

Fig. 4. Neurocranium of *Gasterochisma melampus* (NSM-PO 511), frontal view (left) and rear view (right).

sphenotic on each side. The vertebral column is received by the upper half of the posterior part of the neurocranium, and the lower half of the neurocranium formed by the parasphenoid and basioccipital is free and convex posteriorly. The anteroventral part of the first vertebral column attaches obliquely to the posterodorsal region of the basioccipital, and its anterior part is inserted into the posterior receptive capsule of the exoccipitals. The myodome, bounded by the parasphenoid, prootics and basioccipitals, is large and opens posteriorly to the exterior (Fig. 4).

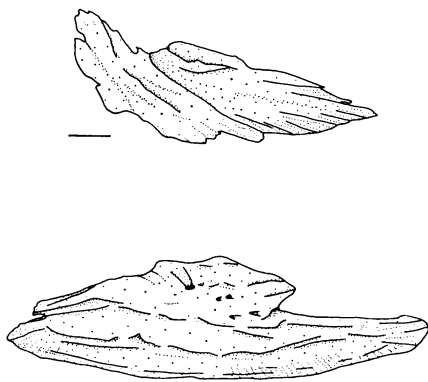**Ethmoid region.** Ethmoid: The ethmoid is an

Fig. 5. Lateral view of left nasal (top) and lachrymal (bottom) of *Gasterochisma melampus* (NSM-PO 511). Scales indicate 10 mm.

unpaired bone, located at the anterodorsal part of the neurocranium. In dorsal view, the ethmoid is almost completely hidden by the frontals. It is in contact posterolaterally with the lateral ethmoids and posteroventrally with the prevomer. The anteroventral part of the ethmoid is free, and, in anterior view, it shows an arched shape (Fig. 4). The anterior border of the ethmoid is straight, lacking both the anteromedian projection and anterolateral horns which are observed in other scombrid fishes.

Lateral ethmoid (prefrontal, parethmoid): The paired lateral ethmoids are irregular in shape and form the anterior wall of the orbit. Each lateral ethmoid is united at the median line. The posterior part of the lateral ethmoid extends laterally on both sides to form the posterolateral process. The lateral ethmoids are connected anterodorsally to the ethmoid, anteroventrally to the prevomer, posterodorsally to the frontals, posteroventrally to the parasphenoid, and posteriorly to the pterosphenoids. A relatively small olfactory foramen is present in the centroinner part of the posterolateral process of the bone (Fig. 4).

Prevomer (vomer): The prevomer is the most anteroventral bone of the neurocranium. Its anterior border is convex in ventral view. The anterior part of the prevomer projects ventrally and conical teeth are present on it. The prevomer tapers posteriorly and fits into the V-shaped anterior projection of the parasphe-

noid. In lateral view, the anterodorsal edge of the prevomer is concave and in contact dorsally with the posteroventral region of the ethmoid.

Nasal: The nasal is thickened in the anterior part and becomes thinner towards its posterior end (Fig. 5).

Orbital region. Frontal: The frontals cover the anterior half of the dorsal surface of the neurocranium. The frontals are very large, and the ethmoid and lateral ethmoids are concealed by the frontals when viewed dorsally. The dorsal surface of each frontal, on which no conspicuous grooves are developed, is provided with radiations originating from the central region. The auxiliary crest, which is a unique character of *Scomberomorus* (Devaraj, 1977), is not developed. The frontals do not meet along the median line, but are interrupted by the supraoccipital. Dorsally the frontals meet the parietals and pterotics posteriorly. Ventrally they are connected posteriorly to the sphenotics and medially to the pterosphenoids. The frontals are thin in the median part and become greatly thickened laterally. No shelf is formed on the posterolateral part of each frontal. In other scombrids a dilater groove (Allis, 1903) or outer crest (Collette and Chao, 1975) is formed there.

Basisphenoid: The basisphenoid is an unpaired Y-shaped bone. Dorsally the basisphenoid meets the prootics posteriorly and the pterosphenoids anteriorly. Ventrally it extends downward and attaches to the parasphenoid. A posteroventrally directed process is present on the central part of the main axis.

Pterosphenoid (alisphenoid): The paired pterosphenoids form the central part of the roof of the orbit. They are connected to the lateral ethmoids, frontals, sphenotics, prootics, and basisphenoid. Anteriorly the pterosphenoids meet each other along the median line. The central inner margin of each pterosphenoid projects downward but does not extend to the parasphenoid.

Lachrymal (preorbital): The lachrymal is an elongate elliptical bone (Fig. 5). The dorsal margin is deeply concave just behind its midpoint. The posterior portion is slender.

Otic region. Parietal: The parietals are paired thin bones. They are in contact with the supraoccipital along their inner margins. The inner halves of the parietals form the posterior

part of the roof of the box-like brain case. Their outer halves form a part of the lateral walls of the brain case. A deep, short groove is present obliquely in the foot of the lateral wall. The parietals meet the frontals anterolaterally, the pterotics posterolaterally, and the epiotics posteriorly.

Epiotic: The epiotics are massive and irregular in shape. They constitute the posterior roof and wall of the box-like brain case. The epiotics are in contact with the parietals, supraoccipital, pterotics, and exoccipitals. A blunt process, known as the epiotic process, is found on the dorsal surface of each epiotic.

Supraoccipital: The supraoccipital is an unpaired bone, bounded by the frontals, parietals, epiotics and exoccipitals. In dorsal view, the base of the supraoccipital shows a flat diamond-shape. This base runs along the median line of the neurocranium from end to end. Posteriorly the base separates the exoccipitals at the surface. The supraoccipital crest is very high, semiparabolic-shaped in lateral view, originating from the anterior end of the base and extending posterodorsally to the posterior margin of the second vertebral column.

Pterotic: The pterotics are paired bones, triangular in shape, and situated at the most posterolateral region of the neurocranium. Dorsally they are in contact with the epiotics, parietals, exoccipitals and frontals, ventrally with the sphenotics and prootics, and posteriorly with the intercalars. The posterior process of each pterotic is short and blunt. This process projects posterolaterally.

Prootic: The paired prootics are irregular in shape. The prootics meet each other along the ventromedian line of the brain case. They are connected to the pterosphenoids, basisphenoid, sphenotics, pterotics, intercalars, exoccipitals, basioccipitals and parasphenoid. The prootic pit and foramen are absent. The anterior part of the bone is greatly extended laterally to form a wing on either side (Fig. 4), and the wing serves as the posterior wall of the orbit. Several longitudinal thin bony wings are developed on the lateral region of each prootic.

Sphenotic: The sphenotics are paired bones, forming the posterodorsal part of the roof of the orbit. The sphenotics are in contact anteriorly with the frontals and pterosphenoids, and

posteriorly with the pterotics and prootics. The lateral process of the sphenotic is short, blunt, and almost totally concealed by the frontal in dorsal view.

Intercalar (opisthotic): The paired intercalars ankylose with the symphysis of the exoccipitals, pterotics and prootics. The bones do not interpose between the exoccipitals and pterotics as in the primitive scombrids (Starks, 1910). The posterior margin of the intercalar is smooth in dorsal view.

Basicranial region. Parasphenoid: The parasphenoid is a long bone, forming most of the basal portion of the neurocranium. It meets the lateral ethmoids anterodorsally and the prevomer anteroventrally. Posteriorly both sides of the parasphenoid project dorsally and are connected to the ventral flanges of the basioccipital and to the posteroventral parts of the prootics. The posterior margin of the parasphenoid is straight and does not bifurcate when viewed ventrally. Immediately anterior to the projections, a lateral wing is developed on either side of the parasphenoid. The anterior edge of the lateral wings of the parasphenoid is deeply concave and the wings are joined dorsovertically to the prootics. The parasphenoid extends posteriorly nearly to a vertical through the middle of the second vertebral column. A dorsally projecting keel is developed anterior to the connection with the basisphenoid.

Basioccipital: The basiocciptial is an unpaired bone, situated at the posteroventral part of the neurocranium. It is connected dorsally to the exoccipitals and anteriorly to the prootics. A posteroventrally directed lateral flange is developed on each side and is connected to the dorsal projections of the parasphenoid. The posterodorsal part of the basioccipital is attached obliquely to the anteroventral part of the first vertebra. Posteriorly the basioccipital extends to the posterior edge of the second vertebra.

Exoccipital: The exoccipitals are in contact anterodorsally with the epiotics, laterally with the pterotics, posterolaterally with the intercalars, anteroventrally with the prootics, posteroventrally with the basioccipital. The bones of both sides are interposed by the supraoccipital on the surface, but they meet each other below the surface. The posteroinner part of the exoccipitals projects posterolaterally, forming a cap-
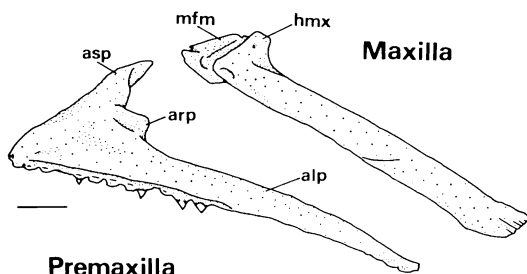
Fig. 6. External view of left premaxilla and maxilla of *Gasterochisma melampus* (NSM-PO 511). alp, alveolar process of premaxilla; arp, articular process of premaxilla; asp, ascending process of premaxilla; hmx, head of maxilla; mfm, median flange of maxilla. Teeth on premaxilla are badly broken. Scale indicates 20 mm.
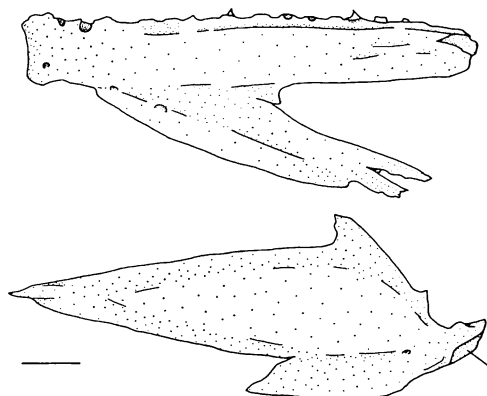

Fig. 7. External view of left dentary (top) and angular with retroarticular (bottom) of *Gasterochisma melampus* (NSM-PO 511). Line indicates a position of retroarticular. Teeth on dentary are badly broken. Scale indicates 20 mm.

sule. The first vertebra is inserted into this capsule, and the vertebra is nearly completely hidden in lateral view.

Branchiocranium. The branchiocranium is divided into five sections: mandibular, palatine, hyoid, and branchial arches and opercular apparatus.

Mandibular arch. The supramaxilla was not available for this study, because it was lost in the specimens examined.

Premaxilla: The premaxilla is a slightly curved long bone with a row of slightly compressed conical teeth (23–25 in number) on the ventral edge (Fig. 6). It is composed of an ascending, an articular and an alveolar process. The ascending process projects posterodorsally, making an acute angle with the alveolar process. The tip of the ascending process is more or less pointed. The articular process is small and blunt, situated immediately posteroventral to the ascending process. The alveolar process serves as the main axis of the bone, and its posterior end is thin and somewhat sharp. The small anterior projection observed in higher scombrids (Collette and Chao, 1975) is not developed on the bone.

Maxilla: The maxilla is a long curved bone, mounted on the premaxilla (Fig. 6). Anteriorly it is composed of two parts; the articular head and median flange. The articular head articulates with the prevomer. The posterodorsal part of the articular process of premaxilla

fits into the outer surface of the median flange. The posterior margin of the bone is broad.

Dentary: The dentary is a large bone with a row of teeth (27–30 in number) on the dorsal edge (Fig. 7). The bone is forked posteriorly, the dorsal branch being longer than the ventral one. The anterior margin of the dentary is slightly concave. A deep notch is present on the anterior part of the ventral edge of the dentary.

Angular (articular) and retroarticular (angular): The angular is a spear-shaped bone with anterodorsally and anteroventrally directed projections on the posterior part (Fig. 7). A hooked process, to which the quadrate attaches, is present on the posteroventral corner of the bone. The V-shaped main body fits into the dentary. Both the dorsal and ventral projections are pointed, and the dorsal projection is smaller than the ventral one. The retroarticular is a small bone attaching to the posteroventral margin of the angular (Fig. 7).

Palatine arch. The endopterygoid was damaged and is not available for this study.

Palatine: Each of the palatines is composed of the dorsal and ventral ridges (Fig. 8). Small conical teeth (about 20 in number) are present on the ventral ridge. Anteriorly, the dorsal ridge is projected and hooked, while the ventral ridge is projected but not hooked. The anteri-
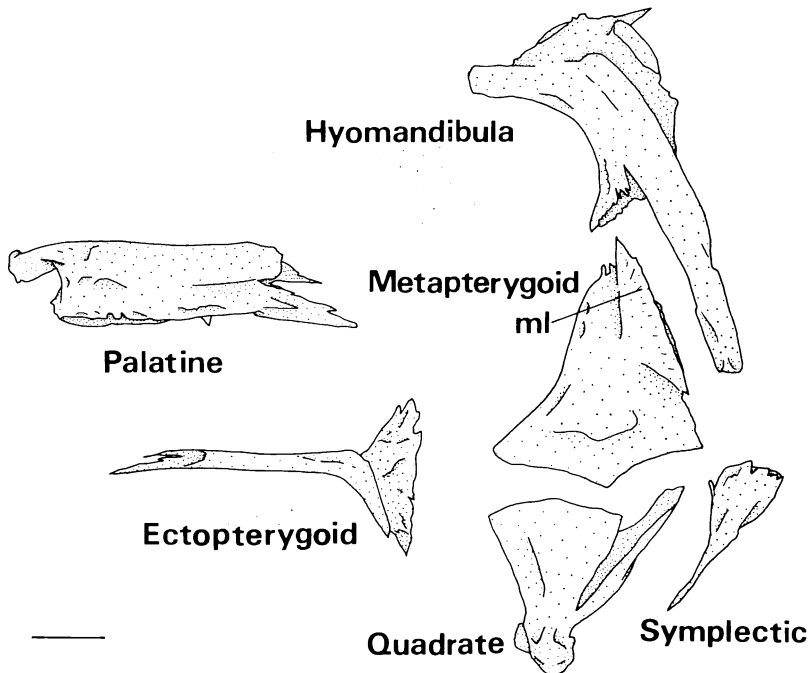
Fig. 8. Internal view of right palatine and quadrate, and external view of left ectopterygoid, metapterygoid, hyomandibula and symplectic of *Gasterochisma melampus* (NSM-PO 511). ml: metapterygoid lamina. Scale indicates 20 mm.

or part of the ventral ridge is round. The posterior end of both the dorsal and ventral ridges is thin. The ventral ridge extends more posteriorly than the dorsal one.

Ectopterygoid: The ectopterygoid is a T-shaped bone (Fig. 8). Its dorsal and ventral projections are pointed. The ventral projection is slightly longer than the dorsal one. The posterodorsal part of the main axis is curved gently.

Metapterygoid: The metapterygoid is a somewhat triangular-shaped bone (Fig. 8). It is in contact with the hyomandibula dorsally and posteriorly, with the symplectic posteroventrally and with the quadrate anteroventrally. The dorsal projection of the ectopterygoid attaches to the inner side of the anteroventral part of the metapterygoid. A groove, into which the hyomandibula fits, is developed on the upper three-fourths of the posterior margin of the metaptergyoid. The metapterygoid lamina is present. On the posteroventral edge of the metapterygoid a groove is developed to receive the symplectic.

Hyoid arch. Hyomandibula: The hyomandibula is an inverted L-shaped bone (Fig. 8), connecting the opercular apparatus and suspensorium to the neurocranium. There condyles are present on the dorsal part of the hyomandibula. A pointed posteriorly directed process is developed on the posterodorsal corner of the bone. An anteriorly directed wing is developed along the upper half of the anterior margin of the long axis. The posterolaterally directed wing runs along the long axis, and a little deep groove, to which the preopercle attaches, is developed between the wing and the posterior condyle.

Symplectic: The symplectic is a small bone, fitting into the deep groove of the quadrate ventrally and into the metapterygoid dorsally (Fig. 8). The upper part of the bone is thin and broad, while its lower part is a needle-like spine.

Quadrate: The quadrate is nearly triangular in shape (Fig. 8). Its lower part is a large articulating facet attaching to the posterior hooked process of the angular. The dorsal edge of the quadrate connects to the metapterygoid. There is a deep groove on the posterior part of the bone for receiving the symplectic. The posterior portion of the groove extends upward to
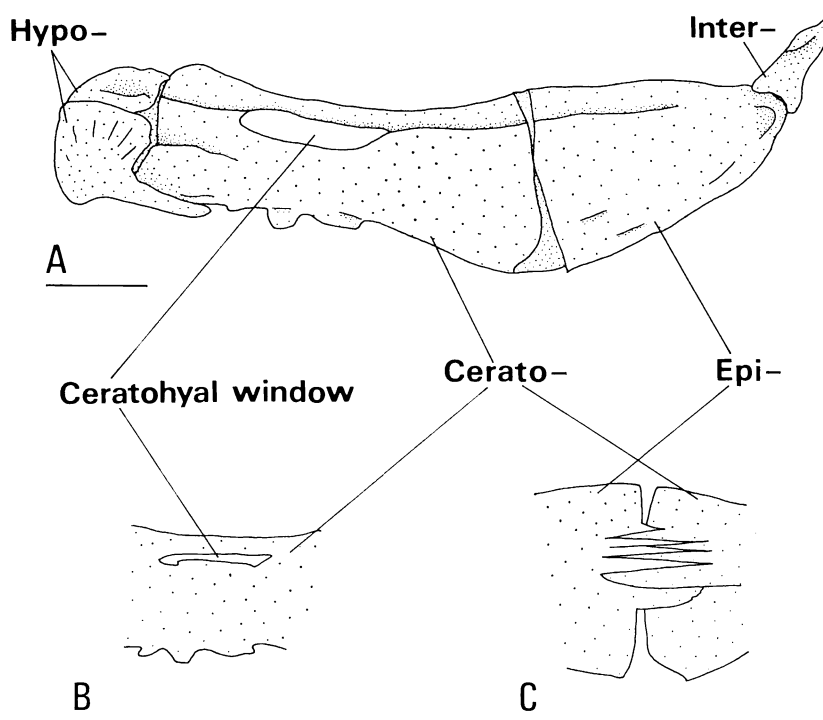
Fig. 9. A, external view of left hyoid complex (hypohyal, ceratohyal, epihyal and interhyal) of *Gastero-chisma melampus* (NSM-PO 381). B, ceratohyal window of *G. melampus* (NSM-PO 511). C, internal view of epihyal-ceratohyal suture of *G. melampus* (NSM-PO 381). Scales indicate 20 mm.

form a process on the posterodorsal corner of the quadrate.

Hypohyal: The hypohyal has two ossification centers, (Fig. 9A): the dorsal segment is smaller than the ventral one. The dorsal segment has an inner projection on the anterodorsal corner. The ventral segment has a posteriorly directed process on the posteroventral corner. The anterior margin of the hypohyal is slightly convex.

Ceratohyal: The ceratohyal is a thin, rectangular-shaped bone (Fig. 9A). Both the dorsal and ventral edges are concave. A blunt projection is present on the anteroventral corner. Three notches, to which branchiostegals attach, are developed along the ventral margin. A large ceratohyal window, the beryciform foramen of McAllister (1968), is present on the central part of the ceratohyal. This window is smaller in a larger specimen (NSM-PO 511, Fig. 9B). The groove runs along the upper edge of the ceraohyal window, extending anteriorly to the end of the ceratohyal and posteriorly to the central part of

the epihyal.

Epihyal: The epihyal is roughly triangular-shaped (Fig. 9A). On the inner surface, the anteromedial edge of the epihyal interlocks with the posteromedial edge of the ceratohyal by means of interlocking processes, the epihyal-ceratohyal suture of McAllister (1968) (Fig. 9C). The two bones are connected to each other by a cartilaginous connection on the outer surface.

Interhyal: The interhyal is a small, elongate bone (Fig. 9A) that connects the hyoid arch to the suspensorium.

Glossohyal: The golssohyal is a small unpaired bone supporting the tongue (Fig. 10). It is triangular in shape in dorsal view. No teeth are present on the bone.

Urohyal: The urohyal is a median bone located between the hypohyals (Fig. 10). It is roughly rectangular in shape. A blunt process projects ventrolaterally on each side of the anteroventral corner of the urohyal. A deep groove is developed on the anterior half of the ventral edge of the bone.
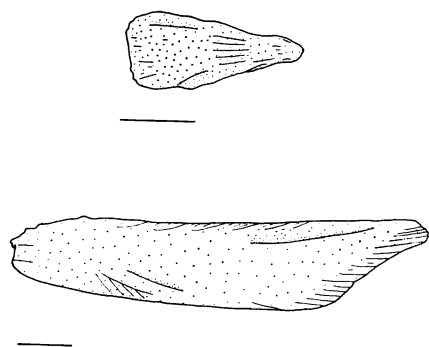
Fig. 10. Dorsal view of glossohyal (top) and lateral view of urohyal (bottom) of *Gasterochisma melampus* (NSM-PO 511). Scales indicate 20 mm.

Branchial arch. The elements and their arrangement of branchial arch are much the same as those in other scombrids (Fig. 11A, B; Iwai and Nakamura, 1964; de Sylva, 1955; Mago Leccia, 1958; Gnanamuttu, 1966; Collette and Chao, 1975; Devaraj, 1977). The gill rakers are, on the other hand, unique in their shape (Fig. 11C); instead of being elongate, they are swelling type with pointed spines. The number of gill rakers in the first gill arch of the right side is 17 on the lower arch of the hypobranchial and ceratobranchial, 1 on the junction of the upper and lower arches, and 8 on the upper arch of the epibranchial. A small, plate-like ossicle with small spines is present between each gill raker (Fig. 11C).

It should be noted that according to Collette et al. (1984), the cartilaginous tip of the second epibranchial is unique extending over the top of the third infrapharyngobranchial to connect with the third epibranchial. However, this could not be confirmed in this study; rather, the cartilaginous tip of the second epibranchial is a small projection and inserts into a cartilaginous socket of the second infrapharyngobranchial (Fig. 11D). Further information needs to confirm the above reported observation.

Opercular apparatus. Opercle: The opercle is a broad, thin, pentagonal-shaped bone (Fig.
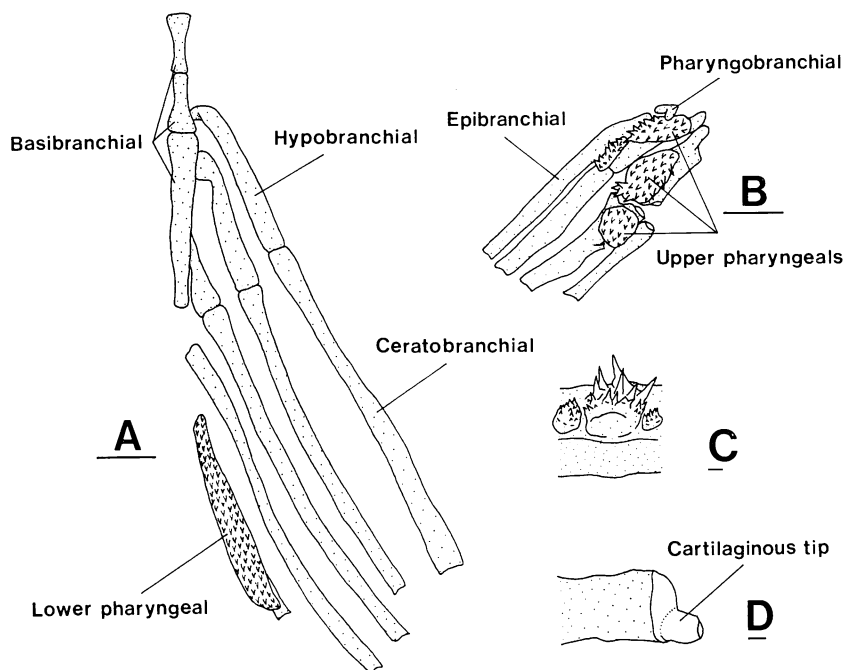

Fig. 11. Branchial arch of *Gasterochisma melampus* (ZUMT 52313). A, dorsal view of right lower gill arches. B, ventral view of right upper gill arches. C, fifth gill raker from junction of upper and lower arches of the first gill arch of the right side. D, lateral view of a cartilaginous tip of second epibranchial. A and B are traced from radiographs. Scales: 20 mm for A and B, 2 mm for C and D.
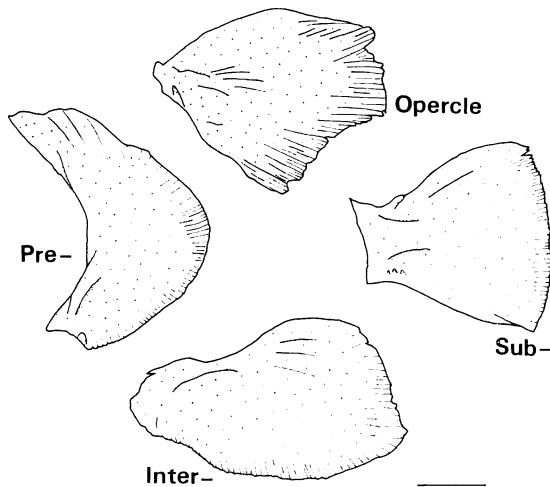
Fig. 12. Lateral view of left opercular apparatus (opercle, subopercle, preopercle and inter-opercle) of *Gasterochisma melampus* (NSM-PO 511). Scale indicates 40 mm.

Fig. 13. Lateral view of vertabrae of *Gastero-chisma melampus* (NSM-PO 511). Numerals below each vertebra indicate vertebral number from anterior. Top, first closed haemal arch on midmost vertebra is shown. Middle, first caudal vertebra (middle one) is shown. Bottom, inferior foramina (if) on caudal vertebrae are shown. Scales indicate 20 mm.

12). An articular facet, articulating with the hyomandibula, is present on the anterior end of the opercle.

Subopercle: The subopercle is flat and trapezoidal in shape (Fig. 12). The anterior part of both the dorsal and ventral edge is concave, and a triangular projection is formed on both the anterodorsal and anteroventral corners of the bone.

Preopercle: The preopercle is a broad thin, crescent-shaped bone (Fig. 12). The ventral edge of the bone is concave, and its anteroventral projection is pointed.

Interopercle: The interopercle is roughly elliptical (Fig. 12). Deep grooves, lined with bony ridges, are sculptured on the inner surface of the bone.

Axial skeleton. The axial skeleton is described in three sections; the vertebral column, caudal fin-rays, and caudal complex.

Vertebral column. The vertebral number is $19+25=44$ including the hypural plate in the specimens examined. The first vertebral column, the atlas, is slightly shorter than the second one. This vertebra inserts into the capsule of the exoccipitals (Fig. 3).

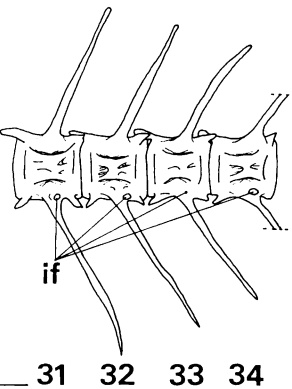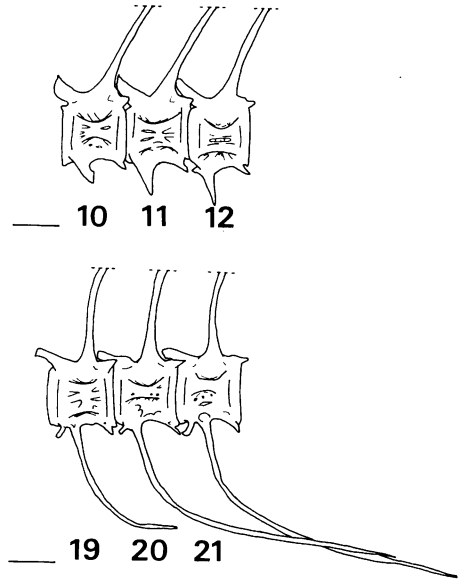The neural arches and spines on the first to sixth vertbrae are stout and laterally compressed. The neural spine on the first vertebra fits into the anterior groove of the second neural spine. An elongate haemal spine occurs on the 20th vertebra and posteriorly (Fig. 13, middle). Posterior to the 34th vertebra, both the neural and haemal spines come to bend backward gradually and lie above the next spine. Laterally directed parapophyses appear on the anterior part of
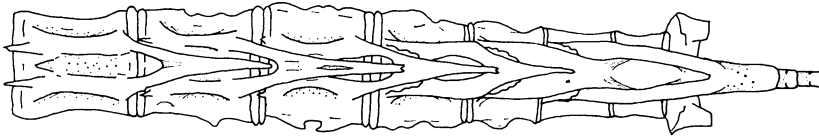
Fig. 14. Dorsal view of last eight vertebrae (including urostyle) of *Gasterochisma melampus* (NSM-PO 511). Scale indicates 20 mm.
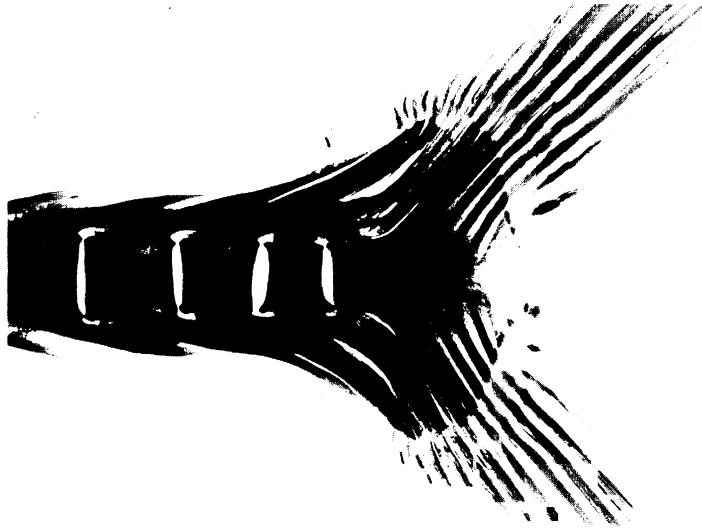

Fig. 15. Radiograph of caudal region of *Gasterochisma melampus* (NSM-PO 381).

the ventral margin of the first to seventh vertebrae. On the eighth to tenth vertebrae, the parapophyses gradually shift to the anteroventral part of the respective centra and point ventrally. The first closed haemal arch is formed on the 11th vertebral column (Fig. 13, top).

The neural prezygapophyses were not clearly observed on the first vertebra. The first neural prezygapophysis is found on the base of the second neural spine. On the last six vertebrae, the neural prezygapophyses are reduced in size and become small ridges at the base of each neural spine. Neural postzygapophyses are present on all but the first vertebra and last seven vertebrae. The neural pre- and postzygapophyses overlap each other. A lateral keel, connecting the neural prezygapophysis with the parapophysis, is developed vertically on the second, third and fourth vertebrae.

Haemal prezygapophyses were observed from the 11th vertebra posteriorly. The last six vertebrae lack haemal prezygapophyses. The haemal prezygapophysis projects obliquely from the base

of the haemal arch. Haemal postzygapophyses are developed on all but the anterior four and last seven vertebrae. The haemal postzygapophysis is on the posterior part of each centrum. The haemal pre- and postzygapophyses barely overlap each other.

Inferior foramina are small and developed on the 30th to 33rd vertebrae (Fig. 13, bottom). There are faint traces of a keel on the vertebrae (Fig. 14).

Caudal fin-rays. Each proximal end of the caudal fin-rays is deeply forked to receive and completely cover the hypural plate (Fig. 15). The procurrent spur is not developed and the base of the preceding ray is not shortened (e.g., Johnson, 1975).

Caudal complex. The caudal complex, supporting the caudal fin-rays, is composed of three preurals and the hypural plate (Fig. 16). The last preural centrum, i.e., preural centrum 2, is slightly reduced in size compared with the anterior centra. Preural centrum 4 has a neural and a haemal spine, fused to the centrum. Pre-
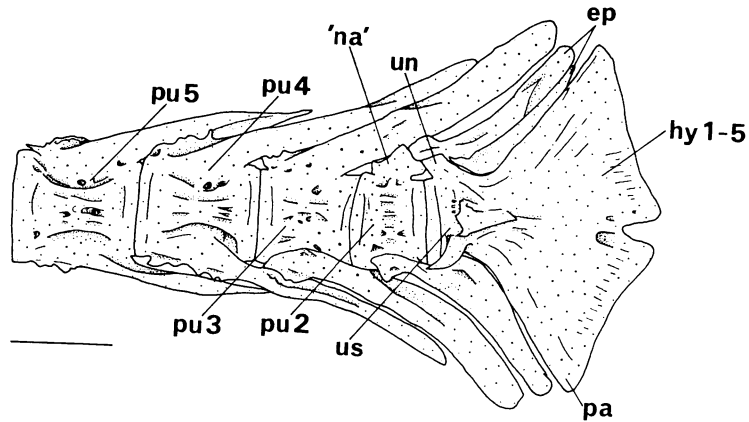
Fig. 16. Lateral view of caudal complex of *Gasterochisma melampus* (NSM-PO 511). ep, epural; hyl–5, hypurals 1 to 5; 'na', specialized neural arch; pa, parhypural; pu 2–5, preural centra 2 to 5; un, uroneural; us, urostyle; preural centrum 1+ural centrum. Scale indicates 20 mm.
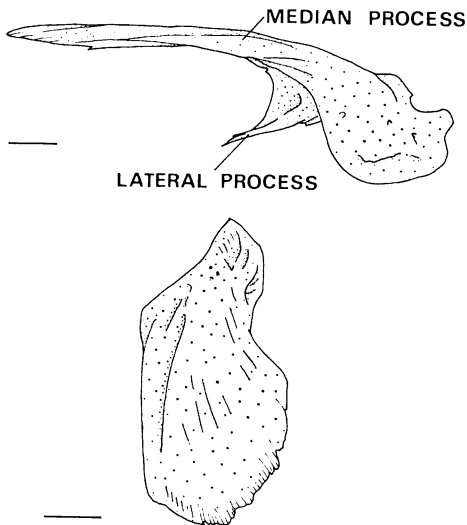

Fig. 17. Lateral view of left posttemporal (top) and supracleithrum (bottom) of *Gasterochisma melampus* (NSM-PO 511). Scales indicate 20 mm.

ural centrum 3 has a fused neural spine and an autogenous haemal spine. Preural centrum 2 has a specialized neural arch (Potthoff, 1975) and an autogenous haemal spine. Two epurals are present between the neural spine on preural centrum 3 and the hypural plate. The anterior epural is not fused with but inserted into the specialized neural arch on preural centrum 2. The

urostyle is a fusion of preuarl centrum 1 and the ural centrum (Nybelin, 1973; Kohno et al., 1983). The uroneural is fused with the urostyle. The hypural plate is formed by means of the fusion of the hypurals 1 to 5, the urostyle and the parhypural (e.g., Potthoff, 1975; Kohno and Taki, 1983; Kohno et al., 1984). The parhypurapophysis is a large wing projecting laterally. A hypural notch is present on the posterior margin of the hypural plate. The suture is absent between the upper and lower halves of the hypural plate.

Pectoral girdle. In this study the supratemporal was not available because it was lost in the specimens examined. The number of pectoral fin-rays is 21; the uppermost ray is attached to the pectoral condyle of the scapula, and other rays are attached to the radials.

Posttemporal: The posttemporal is a thin, elliptical bone with two anteriorly directed processes (Fig. 17). The median process, the upper one, is long and flat, and connects with the epiotic. The lateral process, the lower one, is a short rod-shaped bone and connects with the intercalar. A thin inner shelf bone connects the median and lateral processes. The lower part of the posttemporal body is thin and connected with the median process anteriorly to form an outer shelf. A deep cave is formed between the two shelves. Two notches are present in the posterior and posterodorsal edges of the
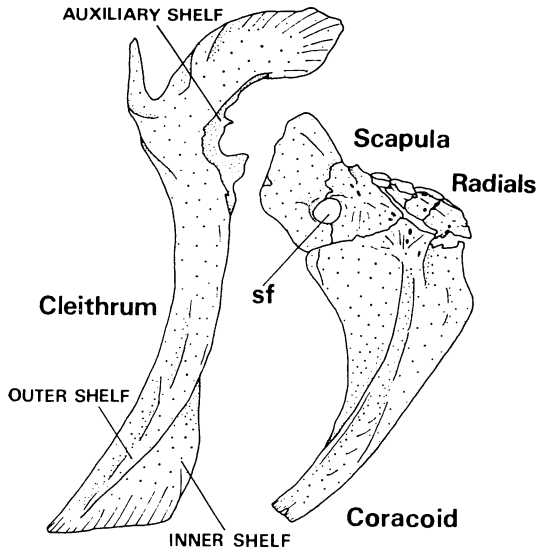
Fig. 18. Lateral view of cleithrum, scapula, coracoid and radials of *Gasterochisma melampus* (NSM-PO 511). sf, scapular foramen. Scale indicates 40 mm.

Fig. 19. Lateral view of left postcleithrum 1 (left) and 2 (right) of *Gasterochisma melampus* (NSM-PO 511). Scale indicates 20 mm.

posttemporal body.

Supracleithrum: The supracleithrum is roughly oval in shape (Fig. 17). It connects the cleithrum to the posttemporal. The anterior part is thickened into a ridge, and the posterior part is thin. Dorsally a triangular-shaped projection is present. The anterodorsal edge is slightly concave and extends to the triangular projection. The upper part of the posterior edge is deeply concave.

Cleithrum: The cleithrum is a long, curved bone with two projections at the upper end (Fig. 18). The anterior projection forms a more or less sharp spine. The posterior projection is broad and wing-like. The main body of the cleithrum has an inner and an outer shelf. These shelves join each other along the main axis. The ventral edge of the cleithrum is not pointed but is a broad plate. The inner shelf ends at the upper one-third of the cleithrum. An auxiliary shelf is developed in the inner side of the inner shelf, starting at the lower one-third of the cleithrum and ending at the mid-point of the *posterior* edge of the dorsal wing. The outer shelf also ends there.

Scapula: The scapula is roughly trapezoidal in shape (Fig. 18). It connects antero-

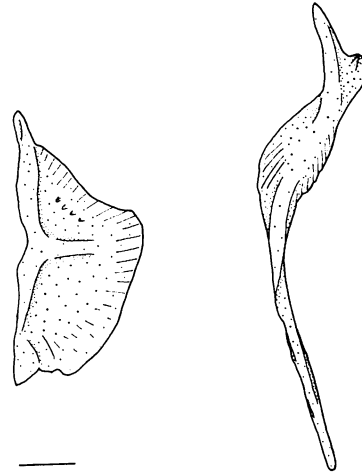dorsally with the cleithrum. In internal view, the scapula extends nearly to the anterior edge of the dorsal wing of the cleithrum. Ventrally the scapula is in contact with the coracoid. The scapular foramen is large. The pectoral condyle, to which the uppermost pectoral fin-ray is attached, is located at the posterodorsal part of the scapula. The first two radials and upper half of the third radial attach to the scapula immediately posteroventral to the pectoral condyle. A groove runs vertically along the median line of the scapula.

Coracoid: The coracoid is roughly triangular in shape (Fig. 18). Its anterior edge is deeply concave. The posterior half of the coracoid is elevated with a less steep fault along the main axis of the coracoid. The coracoid connects dorsally to the scapula, and anterodorsally to the cleithrum. The squarish anteroventral part of the coracoid attaches to the inner side of the inner shelf of the cleithrum. The fourth radial and lower half of the third radial attach to the posterodorsal part of the coracoid. A small fenestra is formed between the posterior part of the coracoid and the lowermost radial.

Radials: Four radials are present and attached to the scapula and coracoid as mentioned above (Fig. 18). The radials become larger and thinner downward.

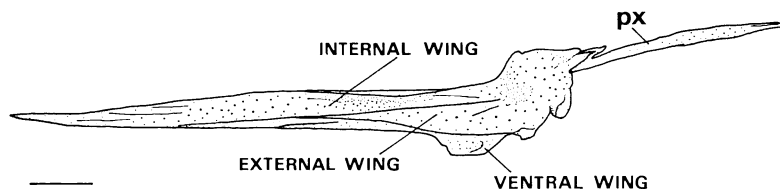Postcleithra 1 and 2: Postcleithrum 1 is a

Fig. 20.　External view of left basipterygium of *Gasterochisma melampus* (NMS-PO 511).　px, posterior xiphoid process.　Scale indicates 20 mm.

more or less triangular-shaped bone with a sharp process at the dorsal end (Fig. 19).　Postcleithrum 2 is elongate and spine-like with a broad wing at the upper part (Fig. 19).

Pelvic girdle.　One spine and five soft rays attach directly to the basipterygium.

Basipterygium: The basipterygium is a long slender bone with three anterior wings, i.e., external, internal, and ventral wings (Kishinouye, 1923), and a posterior process (Fig. 20).　The three anterior wings form a flat plate in the anterior half of each wing.　The anteroventral edge of the ventral wing is concave.　The posterior half of the internal wing is folded outside.　A deep groove is formed by the folded dorsal edge of the internal wing and the base of the external wing.　At their posterior portions the internal and ventral wings unite together to form a broad plate extending vertically.　The anterior xiphoid process (de Sylva, 1955) is not developed.　The posterior xiphoid process (de Sylva, 1955) is formed into a very long, slender spine, protruding from the posterior portion of the internal wing.

Systematic position of
Gasterochisma melampus

In addition to the comparative materials listed in the earlier section, the following studies were referred to for determining the systematic position of *Gasterochisma*: Allis (1903), Starks (1910), Kishinouye (1923), Godsil (1954), Mago Leccia (1958), Nakamura (1965), Nakamura and Mori (1966), Gibbs and Collette (1967), Collette and Chao (1975), Uyeno and Fujii (1975), Devaraj (1977) (all studies on scombrids); Matsubara and Iwai (1958) for the gempylids; Gregory (1933) for the skull; Monod (1968) for the caudal complex.

Scombrid features.　Based on osteological comparison between the scombrids (here excluding *Gasterochisma*) and other families, the following characters are recognized as osteological characteristics of the scombrids: the bones are generally sturdy and greasy, and the suture of the neurocranium is strong and rigid; the auditory capsule is not appreciable externally; the supraoccipital crest is a gentle crest formed by the frontals anteriorly and high, extending posteriorly to at least the first vertebral column; the supraoccipital does not extend between the exoccipitals and epiotics of both sides; each lateral ethmoid is broadly united at the median line; the myodome is very large and opens posteriorly to the exterior; the ascending process of premaxilla is short, heavy and triangular-shaped; canine teeth are never developed; the preopercle is not armed with spines, and the opercular bones are closely united to each other to form a broad plate; the cleithrum is not much developed above the pectoral fin, placed more or less obliquely, and sloping forward; vertebral number is 31–64; the caudal fin-rays insert deeply over and completely cover the hypural plate; the last vertebra is fused with the hypurals and uroneurals to form the hypural plate.

Unique characters of *Gasterochisma*.　On the basis of osteological comparison between *Gasterochisma* and other perciform species, *Gasterochisma* is unique in possessing the following characters: the neurocranium is nearly parabolic when viewed dorsally; the outer crest is not formed; the "box-like brain case" is developed on the dorsal surface of the neurocranium; the vertebral column attaches to the upper half of the posterior part of the neurocranium, and the lower part formed by the parasphenoid and basioccipital is free and convex posteriorly; the frontal is very large with a round anterior edge,

and covers the ethmoid and lateral ethmoid dorsally; the supraoccipital base and crest extend to the anterior edge of the neurocranium, and in the lateral view the crest is semiparabolic in shape; the prootic foramen or groove is absent; the dorsal keel is developed on the parasphenoid anterior to the connection with the basisphenoid; the receptive capsule, into which the first vertebral column is inserted, is formed on the exoccipitals; the projection is developed at the posteroventral corner of the hypohyal; the parapophysis is developed on the first vertabral column; the median process of the post-temporal is remarkably long, and the notch is present on the posterodorsal edge of the bone; the ventral edge of the cleithrum is broad and squarish; the ventral edge of the coracoid is squarish; the anterior xiphoid process of the basipterygium is absent, and the posterior half of its internal wing is folded outside.

Familial classification of *Gasterochisma*. Of the 13 characters recognized as osteological characteristics of the Scombridae in this study, only one is at variance with that of *Gasterochisma*: the supraoccipital creast is not formed by the frontals anteriorly but by the supraoccipital extending to the anterior edge of the neurocranium. On the contrary, *Gasterochisma* differs from other perciform families. In the other families studied, no characters are shared with *Gasterochisma* except for the ethmoid of the Coryphaenidae. In *Gasterochisma* and the coryphaenids, no projections are developed on the ethmoid. The 15 unique characters of *Gasterochisma*, on the other hand, are seen mostly in the neurocranium as mentioned by Tominaga (1966). These unique characters do not, in my opinion, justify a separate family for *Gasterochisma*. On the basis of these osteological observations, it is concluded that *Gasterochisma* should remain in the family Scombridae.

It is noted that *Gasterochisma* possesses three well-developed predorsal bones (Nakamura and Fujii, 1983; pers. comm. with Dr. Bruce B. Collette). In my opinion, it is unreasonable to exclude the genus from the Scombridae based on the predorsal bones alone. It should be mentioned that in the family Gempylidae only the genera of *Ruvettus*, *Thyrsitops* and *Tongaichthys* have a small predorsal bone (Nakamura

and Fujii, 1983).

In addition to the osteological characters mentioned above, it should be pointed out that this conclusion is supported by such external characters of *Gasterochisma* as follows (cf., Fraser-Brunner, 1950; Tominaga, 1966; Collette, 1978): the body is slightly compressed; the caudal fin is strong; the caudal peduncle is slender; a pair of lateral keels is developed on the caudal peduncle; several finlets are present posterior to both the dorsal and anal fins; there are two dorsal fins and the first one folds into a dorsal groove; both the second dorsal and anal fins are sickle-shaped; the interpelvic process is developed.

A resemblance between *Gasterochisma* and the Bramidae was suggested by Gosline (1968). The shape of the supraoccipital crest creates this similarity. However, they are essentially different. The crest is formed only by the supraoccipital extending forward in *Gasterochisma*, whereas in the Bramidae it is formed by the frontals anteriorly. No other character indicating their close relationship was detected. Regan (1902), on the other hand, noted the similarity of the high supraoccipital crests in *Gasterochisma* and *Coryphaena*, but that of latter is formed by the frontals anteriorly as in the Bramidae.

Character distribution in *Gasterochisma*. On the assumption that characters observed in *Scomber* are primitive (Starks, 1910; Kishinouye, 1923; Gosline, 1968), osteological characters of *Gasterochisma* are of a mixture of both primitive and advanced scombrid features. The following characters of *Gasterochisma* are regarded as primitive: the prelateral ethmoid region is long and narrow; prootic pit is absent; the intercalar does not interpose between the pterotic and exocciptial; the parasphenoid is not bifurcated in the ventral surface of the posterior end; a small anterior projection is not developed on the premaxilla; the posterior caudal vertebrae are not reduced in size; the notch is present at the posterior margin of the hypural plate; the anterior epural is not fused with the specialized neural arch on the second preural centrum.

In addition to the primitive characters, those regarded as advanced are as follows: the orbit is low and short in the lateral view; the postero-lateral process of the lateral ethmoid is well

developed; the pterosphenoid projects downward; the basisphenoid is thick and connected with the parasphenoid; the anterior part of the prootic projects laterally as a thin wing which forms the posterior wall of the orbit; the angle between the ascending process and the alveolar process of the premaxilla is not perpendicular but somewhat acute; a deep notch is developed on the anteroventral edge of the dentary, and the posterior dorsal branch of the dentary is slightly broad; the ventral ridge of the palatine projects anteriorly; the groove is developed on the upper three-fourths of the posterior margin of the metapterygoid; the anterior wing is developed only along the anterior margin of the main axis of the hyomandibula; the opercle is pentagonal in shape and broader horizontally; a bony caudal peduncle keel is slightly developed; the suture between the upper and lower parts of the hypural plate is absent; the posterior xiphoid process of the basipterygium is long.

Relationships of *Gasterochisma* within the Scombridae. Regan (1902) suggested that *Gasterochisma* resembles *Cybium* (=*Scomberomorus*) and Berg (1940) adopted Regan's idea and mentioned that it is allied to the Cybiidae of Kishinouye (1923). Devaraj (1977) described 29 osteolgical characters as unique features of *Scomberomorus*. These unique features of *Scomberomorus* do not occur in *Gasterochisma*, with the exception of the vertebral number. It is, consequently, unreasonable to consider *Gasterochisma* as closely related to *Scomberomorus*.

Based on the uniqueness in osteological characters and the mosaic occurrence of both primitive and advanced characters in *Gasterochisma*, I am of the opinion that *Gasterochisma* has been derived from the scombrid stem at an early time and undergone its own specialization.

This conclusion is in agreement with Fraser-Brunner (1950), Collette and Chao (1975) and Collette and Russo (1978) in which *Gasterochisma* deserves a subfamily by itself, but not with Fraser-Brunner's conclusion of the scombrid phylogeny in that *Gasterochisma* is regarded as a "groundplan" of the Scombridae.

Distribution of *Gasterochisma*. According to Warashina and Hisada (1972), the distribution of *Gasterochisma melampus* is confined to the south of 35°S in the Pacific, Indian and Atlantic oceans. This geographic range overlaps with that of *Thunnus maccoyii* (Castelnau) and *Allothunnus fallai* Serventy, and the ranges of these three species are peripheral to the geographic range of the Scombridae (Klawe, 1980). However, the similarity in distribution of these species seems to have been achieved by different processes of dispersal. *T. maccoyii* has been evidently derived from *Thunnus* species complex (Iwai et al., 1965). The genus *Thunnus* is a highly advanced group in the Scombridae, and the present-day distribution of the genus has been achieved through a gradual spread of its members from a certain neritic tropical region (Parin, 1968; Shubnikov, 1974). *A. fallai* also belongs to the advanced group in the family (cf., Collette et al., in press), and its present-day distribution has been achieved in a similar way as *T. maccoyii*. On the other hand, the derivation of *G. melampus* can be considered as an early event in the evolution of the Scombridae, as concluded earlier in this study. I agree with Parin's (1968) opinion that the present-day range of *G. melampus* is explained by the displacement of the species from the original region of habitat by more specialized derivative forms.

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ウロコマグロの骨格系と系統的位置

河野　博

　ウロコマグロの骨格系を記載した．それに基づいて，スズキ目に属する9科との比較を行い，ウロコマグロの系統的位置を考察した．

　ウロコマグロはサバ科魚類の特徴とみなされた13形質のうち12形質を保有していた．これに対して，サバ科以外のスズキ目魚類では，ウロコマグロとだけ共有されている形質はシイラ科の篩骨以外に見出すことはできなかった．さらに，ウロコマグロには15の特異な形質が認められた．これらの形質は主に頭部に集中しており，これらの形質に基づいて単一の科を提唱することは本質的ではないと判断した．以上のことから，ウロコマグロはサバ科に属すると結論した．

　ウロコマグロと他のサバ科魚類を比較すると，ウロコマグロにはサバ科の原始的・派生的形質がモザイク状に分布していることが判明した．先に述べた15の特異形質とサバ科魚類の形質状態がモザイク状に分布していることから，ウロコマグロは早い時期にサバ科の主幹から分化して独自の特化方向へむかったものと推論した．

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