Anatomy of *Trigonognathus kabeyai*, with Comments on Feeding Mechanism and Phylogenetic Relationships (Elasmobranchii, Squalidae)

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Abstract   The skeleton and musculature of *Trigonognathus kabeyai* are described in detail.   The particular jaw dentition suggests that *Trigonognathus* has a clutching-type feeding action.   Several characters that might serve this function are discussed from the point of the functional morphology.   The phylogenetic relationships of *Trigonognathus* are not fully resolved, but it possesses three of the four synapomorphies of the Etmopterinae, i.e., two separate labial cartilages, no supraotic shelf, and prespinal radials.   Furthermore, three equally probable hypotheses of *Trigonognathus* relationships, a sister relationship with all etmopterine genera, *Etmopterus + Miroscyllium*, and *Aculeola + Centroscyllium*, are discussed.

Trigonognathus kabeyai Mochizuki et Ohe, a rare squaloid shark from southern Japan, is fairly attractive for its peculiar jaw morphology.   It has a slender and elongated body, dorsal fin spines with a lateral groove, and black body markings as in some *Etmopterus* species.   The head structure, unicuspid and canine-like jaw dentition, strongly elongated mouth gape, and narrow and triangular jaws are unexpected in morphology and probably feeding function among squaloid sharks.   In the original description (Mochizuki and Ohe, 1990), this strange species was placed in the Squalidae (*sensu* Compagno, 1984), but its relationships were not discussed.

We obtained another material of this species from Mimase Fish Market, Kochi Pref., and it is the first record of a female specimen.   The primary purpose of this paper is to describe and illustrate complete skeletal and myological structures of *Trigonognathus kabeyai*.   We also refer to the functional morphology of its peculiar feeding mechanism and to its phylogenetic relationships.

Material and methods

Study material is deposited in Kochi University (BSKU 44653, 258 mm TL).   Its internal structures were observed after the staining of the dissected specimen by the method of Dingerkus and Uhler (1977).   Illustrations were made using camera lucida images.   A specimen of *Centroscyllium excelsum* (HUMZ 69275, male, 588 mm TL; deposited in Hokkaido University) was used for comparative illustrative purposes.

Abbreviations used in figures are listed below:
AB —— abdominal vertebrae
ab —— adductor arcuum branchialium
abv —— anterior pelvic basal
acp —— articular condyle of pectoral fin
ad —— arcualis dorsalis
alc —— anterior upper labial cartilage
am —— adductor mandibulae
ams —— adductor mandibulae superficialis
bad —— basal cartilage (triangular basal) of dorsal fin
bb —— basibranchial
bd —— bile duct
bh —— basihyal
bv —— basipterygium of pelvic fin
bvp —— basiventral process
cb —— ceratobranchial
cbs —— constrictor branchialis superficialis
ccl —— cucullaris
CD —— caudal vertebrae
cd —— cardiac part of stomach
ch —— ceratohyal
chd —— constrictor hyoideus dorsalis
chv —— constrictor hyoideus ventralis
co —— coracoid
coa —— coraco-arcualis
cob —— coraco-branchialis
cod —— constrictor dorsalis
coh —— coraco-hyoideus

db ── dorsal bundle of body muscle
dbc ── calcified double corn (vertebra)
dic ── dorsal intercalary plate
dp ── depressor pectoralis
eb ── epibranchial
ec ── ethmoidal canal
ecr ── epichordal radial
ecs ── enamelled cap of dorsal fin spine
elf ── endolymphatic fossa
ep ── epiphysial pit
epg ── esophagus
es ── eye stalk
exb ── extrabranchial on branchial arch
exh ── extrabranchial on hyoid arch
fca ── foramen for carotid artery
feld ── foramen for endolymphatic duct
foa ── foramen for orbital artery
fops ── foramen for ophthalmicus superficialis
fxc ── flexor caudalis
g ── gill raker
gco ── genio-coracoideus
gop ── groove for orbital process
gr ── gill ray
hb ── hypobranchial
hm ── hyomandibula
hmf ── hyomandibular fossa
hmVII ── (foramen for) hyomandibular branch of facial nerve
ib ── interbranchialis
id ── inclinator dorsalis
im ── intermandibularis
int ── intestine
ipb ── interpharyngobranchialis
kp ── keel-process of basal cranii
lag ── lateral auditory groove
lb ── lateral bundle of body muscle
lbs ── ligament between shoulder girdle and epibranchial 5
lhe ── ligament between hyomandibula and epibranchial 1
li ── liver
llc ── lower labial cartilage
lp ── levator pectoralis
lpp ── lateral prepelvic process
lv ── levator ventralis
ma ── mandibula (Meckelian cartilage)
mag ── foramen magnum
mk ── mandibular knob of mandibula
ms ── mesopterygium of pectoral fin
mt ── metapterygium of pectoral fin
mtx ── metapterygial axis
nas ── nasal cartilage
ns ── nasal capsule
obi ── oblique inferior
obs ── oblique superior

oes ── constrictor oesophagus
ohc ── occipital hemicentrum
onc ── orbitonasal canal
op ── orbital process
opk ── oral pocket
otp ── otic process
pa ── palatine surface (of basicranium)
pb ── pharyngobranchial
pc ── pancreas
pcf ── precerebral fossa
pcm ── pericardial membrane
pff ── prefrontal fontanelle
plf ── perilymphatic fenestra
pmg ── posterior mandibular groove
poc ── preorbital canal
pop ── postorbital process
potp ── postotic process
pow ── preorbital wall
pq ── palatoquadrate
pr ── propterygium of pectoral fin
prop ── prootic process
psb ── foramen for pseudobranchial artery
psr ── prespinal radial
PT ── vertebrae of precaudal tail
ptr ── postspinal ray
pub ── puboischiadic bar
py ── pyloric portion of stomach
rb ── vertebral rib
rd ── radial of fins
rex ── rectus externus
rg ── rectal gland
rif ── rectus inferior
rit ── rectus internus
rod ── base of dorsal spine (rod)
rp ── rostral process
rsp ── rectus superior
sc ── scapular
sep ── supraethmoidal process
snf ── subnasal fenestra
so ── suborbitalis
soc ── supraorbital crest
sor ── ridge at supraotic region for constrictor dorsalis
sp ── spiracle
spl ── spleen
ssp ── subspinalis
tb ── trabecular region
tr ── transbasal canal
vb ── ventral bundle of body muscle
vic ── ventral intercalary plate
II ── (foramen for) optic nerve
III ── (foramen for) oculomotor nerve
V + VII – (foramen for) trigeminal and facial nerves
VI ── (foramen for) abducens nerve
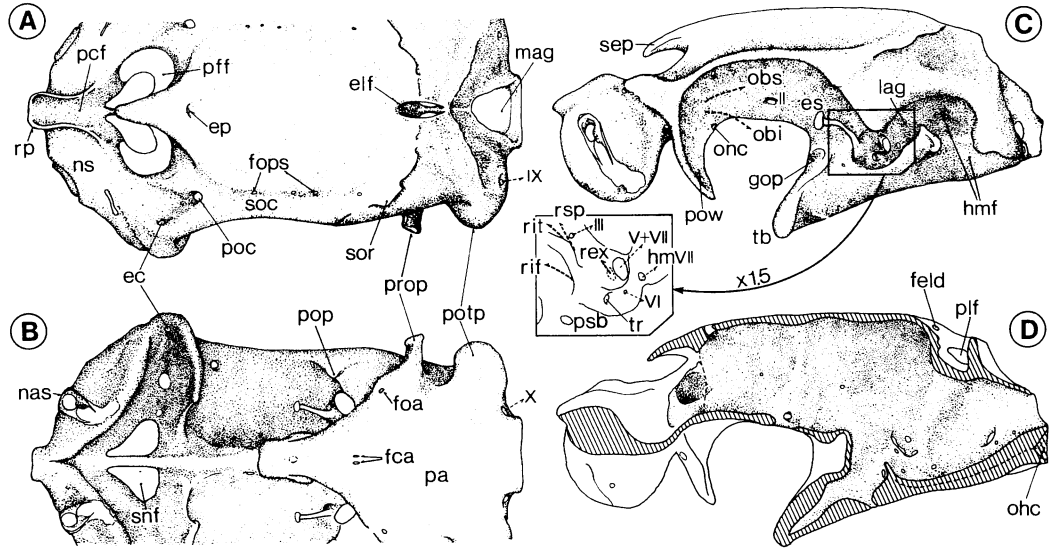IX ── (foramen for) glossopharyngeal nerve
X ── (foramen for) vagus nerve

Fig. 1. Dorsal (A), ventral (B), lateral (C), and internal (D) views of the neurocranium of *Trigonognathus kabeyai*. A thick broken line indicates the arising of muscle, and a thin broken line indicates a nerve lead out. Scale is 10 mm.

Description

Neurocranium (Fig. 1)

The neurocranium of *Trigonognathus kabeyai* is somewhat small with a squat profile. It is characterized by a rather snug nasal capsule, developed preorbital wall, well produced basal angle, and a deep fossa for the hyomandibula subdivided vertically.

Ethmoid region. The precerebral fossa (pcf) is large, waterdrop-like in shape. The anterior margin of the precerebral fossa makes a narrow and trough-like rostral process (rp), not elongated as in *Squalus*. The prefrontal fontanelle (pff) opens widely on the posterior wall of the precerebral fossa. Above this fontanelle, there is the supraethmoidal process (sep), an unpaired, anteriorly directed, horn-like projection. The epiphysial pit (ep) opens posterior to the base of this process. The nasal capsules (ns) are somewhat obliquely compressed and moderately separated from each other by the internasal septum; the subethmoidal ridge is inconspicuous. The ectethmoid chamber is narrow, and its floor has a subnasal fenestra (snf). The nostril, at the frontal end of the nasal capsule, is fringed by a U-shaped nasal cartilage (nas); an internal lobe is on the posterolateral side only (the mesonarial lobe is

absent).

Orbital region. The orbital region has a seriously concave lower profile, and the upper profile is gently convex. The preorbital wall (pow) is well expanded ventrally and somewhat laterally. There is a narrow interspace between the nasal capsule and preorbital wall. The supraorbital crest (soc) is moderately developed. A shallow longitudinal sulcus runs along the base of the supraorbital crest, into which some twigs of the ophthalmic superficial nerve perforate (fops). The preorbital canal (poc) opens dorsally on the outside of the base of the supraethmoidal process; the ophthalmicus profundus runs through the preorbital canal. The ethmoidal canal (ec) is a short tube from the dorsal to ventral sides at the interspace between the nasal capsule and preorbital wall. The postorbital process (pop), which is poorly developed with a low ventral crest, forms the posterior boundary of the orbit.

The interorbital wall is somewhat narrow. The trabecular region (tb) strongly expands anteroventrally to form a large, triangular projection; the basal angle is thus very conspicuous. The facet of the orbital articulation (gop) is at the anterolateral portion of the base of this projection. The orbitonasal canal (onc) and optic foramen (II) is near the ventral margin of the strongly notched interorbital wall.
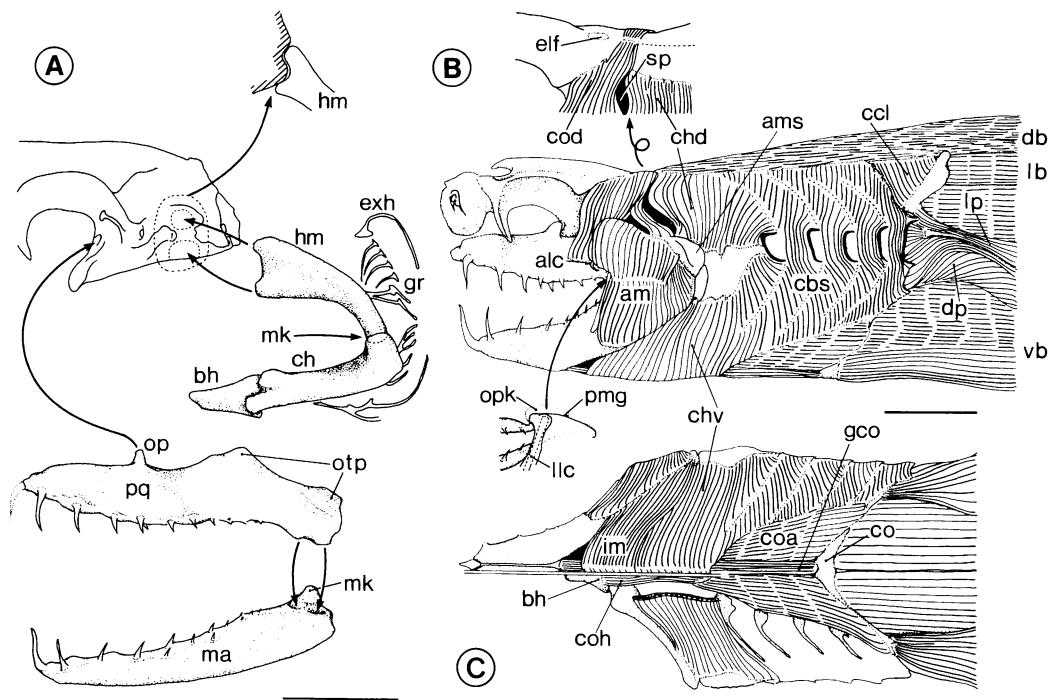
Fig. 2. A, mandibular and hyoid arches of *Trigonognathus kabeyai* showing jaw suspension, with an inset diagram of articulation between hyomandibula and neurocranium (right upper; frontal view). B-C, lateral (B) and ventral (C) views of head musculature; B, with dorsolateral view of occiput showing musculature (upper) and lateral view of mouth corner (lower); C, mandibula is omitted from lower half, below double line. Scales are 10 mm.

At the posterior margin of the orbital region, the bridged lateral commissure is absent. The foramen prooticum (V+VII), foramina for the hyomandibular facialis (hmVII) and abducens (VI), and the transbasal canal (tr) open in a deep concavity below the ventral crest of the postorbital process. The palatine nerve lacks a foramen of its own; it branches at the foramen for the hyomandibular facialis. The eye stalk (es) is elongated with a distal disc for supporting the eye ball.

Otico-occipital region. The otic region is high with a developed postotic process (potp), and the occipital region is strongly inclined posteriorly. The endolymphatic fossa (elf) is small and narrow, located at the posterior end of the supraotic region; the foramen for the endolymphatic duct (feld) is separate from the perilymphatic fenestra (plf). The supraotic shelf (sphenopterotic ridge) is absent; on the supraotic region, there is another low ridge (sor), to which the anterior margin of the constrictor dorsalis is adjacent. The foramen magnum (mag) opens

behind the endolymphatic fossa, in the middle of the occipital wall of the neurocranium. The occipital hemicentrum (ohc) is inserted onto the posterior end of the basicranium. The occipital condyle is weak. The glossopharyngeal (IX) and vagus nerves (X) have their foramina behind the postotic process.

The lateral surface of the otic region has a deep longitudinal groove (lag) for the hyomandibular nerve and jugular vein. The hyomandibular fossa (hmf) is well-developed and is composed of two deep depressions arranged vertically. A large prootic process (prop) is situated immediately in front of the hyomandibular fossa.

The palatine surface (pa) is flat and moderately wide without a medial longitudinal ridge. A paired foramen for the carotid artery (fca) is somewhat behind the basal angle. The orbital artery perforates the outer margin of the subotic region (foa).

Muscles on neurocranium. Two oblique muscles (obs, obi) originate separately from the preorbital wall. The rectus externus (rex) arises from its own
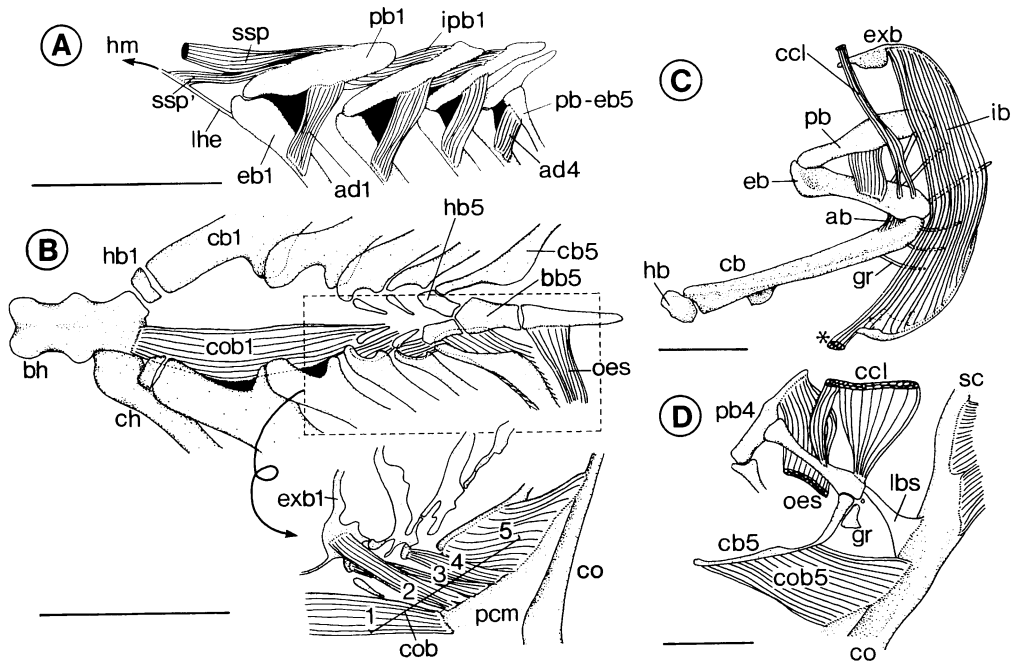
Fig. 3. Skeleton and muscles of branchial arches of *Trigonognathus kabeyai*: (A) dorsal view of dorsal portion of branchial arches; (B) dorsal view of basibranchial copula with the ventral view of same showing coraco-branchiales; (C) lateral view of 1st branchial arch (left side); (D) lateral view of 5th branchial arch. Asterisk in C shows a part of the interbranchialis reaching coraco-branchialis. Scales are 10 mm.

fossa, and three other rectus muscles (rsp, rif, rit) arise from the trunk part of the eye stalk. A muscle slip for the endolymphatic duct is absent.

Viscerocranium (Figs. 2–3)

Skeletons. The mandibular arch (Fig. 2A–B) is considerably elongate, composed of low but thick upper and lower jaw cartilages. The palatoquadrate (pq) has a somewhat long palatine portion with a short orbital process. Its quadrate portion is not strongly elevated to form the otic process (otp), which is composed of two weak anterior and posterior expansions. The mandibula (ma) is about equal to the palatoquadrate in size. The mandibular knob of the mandibula (mk) is moderate in size immediately inside the jaw joint, which is composed of large posterior and supplementary anterior articulations as in other squaloids. The labial cartilages comprise a long lower piece (llc) and a small upper one (alc); these are not connected at the mouth corner. Upper and lower dentitions are similar to each other in shape and arrangement; jaw teeth have a more or less elongate cusp pointed sharply with weak ridges on the lateral and lingual sides, and are arranged quincuncially; the teeth of the anterior tooth file are

much longer than those of the posterior one. The jaw teeth are distributed to near the jaw joint; number of teeth is 10-1-10/10-1-10.

The hyoid arch (Figs. 2A, 3B) comprises three basic components, a long, thick basihyal (bh), low-arched ceratohyal (ch), and strongly elongated hyomandibula (hm). The hyomandibula receives the mandibular knob at its distal end with a tough ligamentous tissue, which covers the articulation between the hyomandibula and ceratohyal. The hyomandibula is composed of a long proximal arm and a short curved distal arm; the proximal arm is depressed anteroposteriorly and has a deeply bifurcated articular condyle for articulation with the neurocranium.

The branchial arches (Fig. 3) are characterized by reduced basibranchial copula, i.e., the loss of hypobranchial and basibranchial in the second arch, and fragile hypobranchials in the third and fourth arches, resulting in an interspace behind the basihyal. The ventral terminus of the ceratobranchials is more or less bifurcated like a mitten. Ceratobranchial 1 (cb 1) is tightly articulated with the basihyal by a minute cartilaginous piece (hb1). Hypobranchial 5 (hb5) is

a paired element articulating with basibranchial 5 (bb5). Epibranchial 5 is neither differentiated from pharyngobranchial 5 (pb-eb5), nor are they unified with pharyngobranchial 4 (pb4). The posterior end of epibranchial 5 is bound to the shoulder girdle by a tough ligament (lbs). Gill rays (gr) are present on the hyoid (Fig. 2A) and branchial arches (Fig. 3C); the last branchial arch has a fragile cartilage that seems to have originated from gill rays (Fig. 3D). Extrabranchial cartilages are developed on the hyoid (exh; Fig. 2A) and the first to fourth branchial arches (exb; Fig. 3C). Ventral extrabranchials on the branchial arches are connected with succeeding ones in order (Fig. 3B). Gill rakers and oropharyngeal denticles are absent.

Musculature. The adductor mandibulae (am; Fig. 2B–C) is moderate in size and covers the posterior portion of the mandibular arch; it is interrupted by a horizontal intersection. The adductor mandibulae superficialis (ams) is a tendinous tissue; it arises from the otic process of the palatoquadrate and is inserted onto the subcutaneous tissue at the posterior end of the eye opening and the dense connective tissue associated with the infraorbital sensory canal. The constrictor dorsalis (cod) covers the dorsolateral surface of the otic region of the neurocranium, and arises from a seam of connective tissue along the middorsal line. This muscle is inserted onto the dorsal margin and internal side of the quadrate portion of the palatoquadrate. The intermandibular muscle (im) is triangular, covering the throat; its posterior portion is inserted directly onto the posterior end of the ceratohyal. The suborbital muscle is absent.

The dorsal and ventral hyoid constrictor muscles (chd, chv; Fig. 2B–C) are continuous with the branchial constrictors (cbs); the anterior extremity of the dorsal muscle is inserted onto the otic process of the palatoquadrate. The hyoid and branchial constrictors support the external surface of the branchial units. The interbranchialis (ib; Fig. 3C) covers the interbranchial septum on branchial arches 1–4, and passes from the dorsal extrabranchial cartilage to the ventral extrabranchial cartilage. The most internal portion of the interbranchial muscle extends beyond the ventral extrabranchial cartilage and is inserted onto the coraco-branchial muscles (cob) or the pericardial membrane (pcm) (asterisk in Fig. 3C). The adductor arcuum branchialium (ab) is present in branchial arches 1–4. The arcualis dorsalis (ad; Fig. 3A) is simple, binding the medial margins of the epibranchial and pharyngobranchial in the branchial arches 1–3; it has no branch to the epibranchial of the succeeding arch (see Fig. 7A). The arcualis dorsalis 4 (ad4) is not associated with pharyngobranchial 4, binding epibranchials 4 and 5.

The subspinalis (ssp; Fig. 3A) is weak with another slip (ssp') running with the ordinal one; the latter arises from the ligament between the hyomandibula and epibranchial 1 (lhe) and is inserted onto pharyngobranchial 1. The interpharyngobranchialis (ipb) forms a connection between the anterior and succeeding pharyngobranchials, but a third slip between pharyngobranchials 3 and 4 is absent.

The genio-coracoideus (gco; Fig. 2C) is an unpaired, slender muscle slip, originating directly from the coracoid symphysis. The rectus cervicis, comprising the coraco-hyoideus (coh) and coraco-arcuales (coa), is moderately developed. The coraco-branchial muscles (Fig. 3B) are composed of five separate slips, and their insertion points are: the dorsoposterior margin of the basihyal for the first slip (cob1, the most developed); the wide portion of extrabranchial 1 for the second slip (cob2, not reaching to basibranchial copula); the ventral surface of ceratobranchial 3 for the third (cob3) and ceratobranchial 4 for the fourth (cob4); and the ceratobranchial, hypobranchial, and basibranchial of the fifth arch for the fifth slip (cob5).

The cucullaris (ccl; Figs. 2B, 3C–D) is a simple, triangular muscle band, inserted mainly on the scapular cartilage (sc) and epibranchial 5. The most anterior part of this muscle has some elongated branches, which reach near the posterior terminus of the epibranchials (Fig. 3C). The constrictor oesophagi (oes; Fig. 3B, D), a circular throat muscle, is well developed.

Others (Fig. 4)

Vertebrae, caudal fin, and body muscles. The vertebral column (Fig. 4A) of *Trigonognathus* is similar to that of squaloids in lacking a supraneural cartilage, superficial calcification, and secondarily calcified lamellae. The abdominal vertebrae (*AB*) are composed of 41 monospondylous vertebrae. Vertebral ribs (rb) are attached to the basiventral process (bvp) of the third to 38th abdominal vertebrae and extend along the horizontal septum (between the dorsal and lateral longitudinal bundles of body muscles). The precaudal tail vertebrae (*PT*), from the cloaca to the origin of the upper caudal lobe, have an arched basiventral process (haemal arch), composed of two monospondylous and 16 diplospondylous ver-
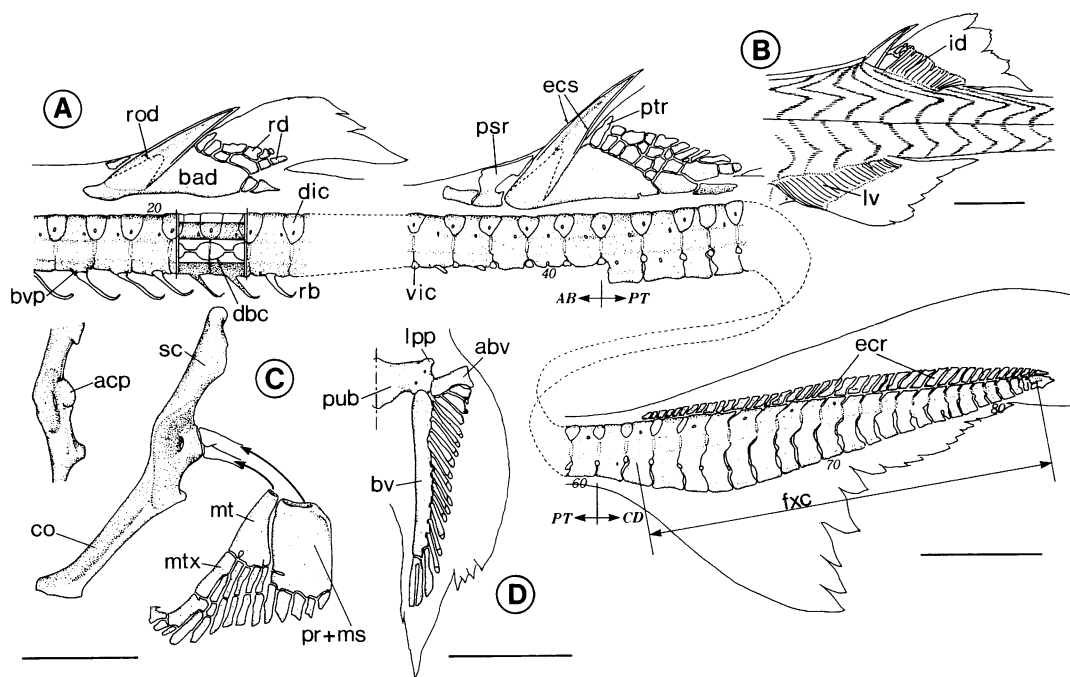
Fig. 4. Vertebral column, fins, and associate muscles of *Trigonognathus kabeyai*: (A) lateral view of vertebral column, dorsal fins, and caudal fin (right lower), with a longitudinal section of 21st and 22nd vertebrae; (B) lateral view of musculature, 2nd dorsal fin and pelvic fin; (C) lateral view of shoulder girdle with two insets, posterolateral view of articular condyle for pectoral fin (left) and dorsal view of pectoral cartilage (right); (D) ventral view of pelvic fin skeleton. Scales are 10 mm.

tebrae. The caudal vertebrae (*CD*) comprise 24 diplospondylous vertebrae. The anterior part of each vertebra has a somewhat elongated haemal process; the ventral margin of caudal haemal process is slightly expanded laterally to accommodate the caudal flexor muscle (fxc). The epichordal radials (ecr) are distributed along the almost entire dorsal margin of the caudal vertebrae. Dorsal intercalary plates (dic) are absent from almost all the caudal vertebrae, and ventral intercalary plates (vic) are restricted to the posterior part of the vertebral column, viz., the anteriormost plate is between the 35th and 36th abdominal vertebrae, and the hindmost one is between the fifth and sixth caudal vertebrae.

Body muscles are normally developed; the body cavity is guarded by somewhat thick, ventral bundles (vb; Fig. 2B). The caudal flexor muscle (Fig. 4A) is moderately developed, and is not anteriorly elongated beyond the origin of the lower caudal lobe.

Dorsal fins. Dorsal fins (Fig. 4A) are somewhat small, being preceded by a short, strongly inclined spine. The dorsal fin skeleton is fully separated from

the vertebral column, and is composed of many pieces of radials (rd) and a triangular basal (bad) fused with a rod (rod) bearing the spine; the postspinal ray (ptr) is weak. Prespinal radials (psr) are present in both fins, those of the second dorsal fin being larger. The fin spine has a tripodal enamelled cap (ecs) and a distinct lateral groove.

The dorsal fin muscle (Fig. 4B) is simple, comprising the inclinator dorsalis (id). It arises from the ventral margin of the tribasal and the surface of the body muscle, and is inserted on the ceratotrichia.

Girdles, paired fins, and associated muscles. The shoulder girdle (Figs. 2B–C, 4C) is a simple and tipically shark-like (U-shaped in frontal view). The coracoid (co) is not elongated anteromedially and is completely fused with its antimere. The articular condyle for the pectoral fin (acp) is single and ovoid in shape. The basal cartilage of the pectoral fin is composed of two elements; the metapterygium (mt) and a fused plate of the propterygium and mesopterygium (pr+ms). The metapterygium carries the metapterygial axis (mtx) and more radials than the
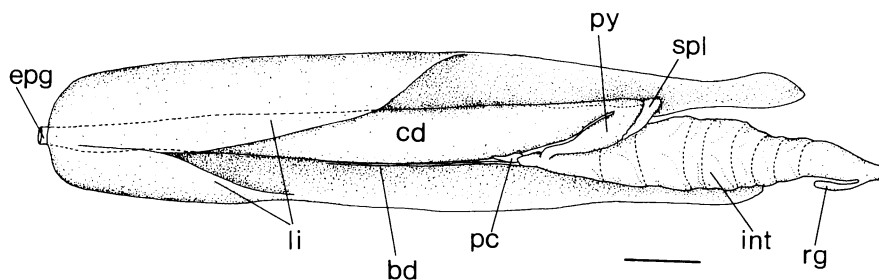
Fig. 5. Ventral view of visceral organs of *Trigonognathus kabeyai* (excretory organ and sexual gland are omitted). Scale is 10 mm.

large fused basal. The musculature of the pectoral fin (Fig. 2B) is typically squaloid, and the levator (lp) and depressor muscles (dp) are moderately developed.

The pelvic girdle (Fig. 4D) is composed of a short, simple transverse puboischiadic bar (pub). Its symphysial portion is somewhat wide, and its terminal portion has two foramina for the pelvic nerves and a small lateral prepelvic process (lpp). The basipterygium (bv) is elongated and supports about 15 radials. The anterior pelvic basal (abv) is directed laterally and somewhat anteriorly with three radials. Each file of the pelvic radial is composed of an elongated proximal and distal piece. Muscles of the pelvic fin are moderately developed, comprising the adductor and depressor on the ventral side of the fin and the levator (lv; Fig. 4B) on the lateral side.

Externals (supplement to the original description). The mouth corner is formed by the lower labial cartilage. The oral pocket (opk; Fig. 2B) is shallow with a short posterior mouth groove (pmg) and no preoral cleft. The labial furrow is absent on both jaws. The lateral sensory canal is mostly closed on the trunk and tail, but the posterior end opens as a groove for half the length of the caudal fin.

Digestive tract (Fig. 5)

The esophagus (epg) is short and surrounded by massive constrictor muscles. The stomach is J-shaped, comprising an appressed shorter portion (py; pyloric) and a very extended portion (cd; cardiac); the latter portion is about three quarters the length of the body cavity. The duodenal and valvular divisions of the intestine (int) are obscure; the intestinal valve begins close to the pyloric end of stomach and comprises eight turns. The bile duct (bd) extends forward from the anterior terminus of the intestine. The liver (li) is large and almost envelops the entire gastrointestinal tract; it comprises two large lobes

connected medially at the anterior portion of the body cavity, and extending to the posterior end of the cavity.

Biological notes

The present specimen is the first female record of *Trigonognathus kabeyai*, which was immature. Comparison with the type specimens (immature males) did not disclose any sexual dimorphism.

The stomach contents included the axial skeleton of a small fish, cycloid fish scales, and eye balls, all which are considerably digested. Of these, the fish vertebrae were not almost destroyed physically.

Discussion

Feeding mechanism

As far as the dentition is concerned, *Trigonognathus kabeyai* is essentially different from most other squaloids, and indicates a different feeding mechanism. Squaloid sharks, except *Aculeola* and *Centroscyllium* (see below), have cutting-type dentition (Cappetta, 1987) characterized by the strong dignathic heterodonty. The lower jaw teeth are flattened in the labio-lingual direction and arranged along the jaw margin to form a saw-like cutting edge, and upper jaw teeth have narrow cusps arranged densely and quincuncially. These species probably seize food items, cutting them with the sharp lower teeth by a twisting of the head, followed by ingestion. The dentition of *Trigonognathus* is characterized by shape (sharp and canine-like; extremely elongated in the anterior files; and dignathic homodonty), number (much fewer than those of other squaloids), and arrangement (quincuncial; somewhat separated from neighbors). These characteristics are recognized not among squaloids but in non-squaloid taxa, for example, *Chlamydoselachus* and *Squatina*, whose dentition is categorized in the clutching-type (Cap-
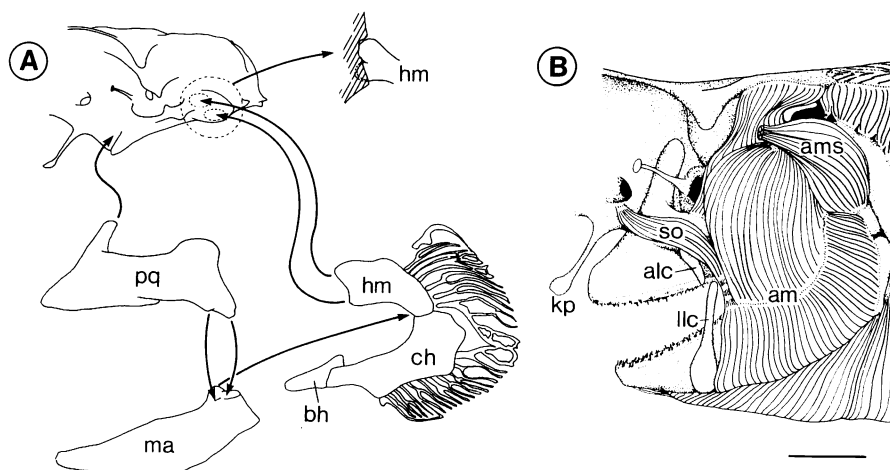
Fig. 6. A, mandibular and hyoid arches of *Centroscyllium* showing jaw suspension, with a diagram showing articulation between hyomandibula and neurocranium (right upper). B, lateral view of superficial cheek musculature of *Centroscyllium excelsum*. Scale is 10 mm.

petta, 1987). These genera might hold prey by the sharp upper and lower teeth and bring it whole to the oesophagus. We can suppose that *Trigonognathus* has a similar feeding manner to these non-squaloids, and several modifications of the head serve this function effectively as discussed below.

Long jaws are one of the common features of clutching-type feeders, although each of them has specialized jaw morphology. In *Trigonognathus* (Fig. 2), the mandibular arch is longer than the length of the neurocranium and slightly curved inward to form a long, narrow, wedge-shaped mouth gape. The orbital articulation is at the posterior end of the orbital region as in other squaloids (Fig. 6), and thus the palatine portion of the palatoquadrate (from the symphysial end to the orbital process) seems to be considerably elongated anteriorly. Among squaloids, *Trigonognathus* alone lacks the suborbital muscle (so; Fig. 6B): the basic function of this muscle is to pull the mandibular arch forward when the jaws are protracted and is probably involved in pursing the lips (Luther, 1909; Edgeworth, 1935). In *Trigonognathus*, the forward protrusion of the mandible is carried out by a swinging of the hyomandibula, and the absence of this muscle would enable a long mouth gape even when the mandibula is lowered.

Trigonognathus has a unique aspect in the articulation between the hyomandibula and neurocranium. In squaloids, the hyomandibula generally has a dual

articular condyle, received by anterodorsal and posteroventral concavities of the hyomandibular fossa, enabling the hyomandibula to be swung anteroventrally (Fig. 6A). While in *Trigonognathus*, the articular condyle of the hyomandibula is more deeply bifurcated, and the hyomandibular fossa is composed of two divided concavities arranged vertically; the ventral concavity continues to the wide surface of the basicranium without a ventral marginal ridge (Fig. 2A). Thus, the hyomandibula of *Trigonognathus* should be able to be lowered more strongly than that of other squaloids. The development of the prootic process suggests that the hyomandibula can be simultaneously swung forward considerably. The swing of the hyomandibula is transmitted to the mandible, causing the jaws to be strongly protruded anteroventrally and the oral cavity to be expanded ventrally and laterally to a large extent. Such functions should serve to effective feeding on large prey. The intermandibularis partly inserted onto the ceratohyal might be related to this function.

Modifications of the branchial arches and associated muscles are noteworthy when considering the feeding functions, although these are also related to respiration, i.e., the reduction of the anterior part of the basibranchial copula (thus, coraco-branchial 2 is inserted ventrally onto extrabranchial 1, not to hypobranchial 2), the discrete hypobranchial 5, and the simple arcualis dorsalis (this muscle generally has
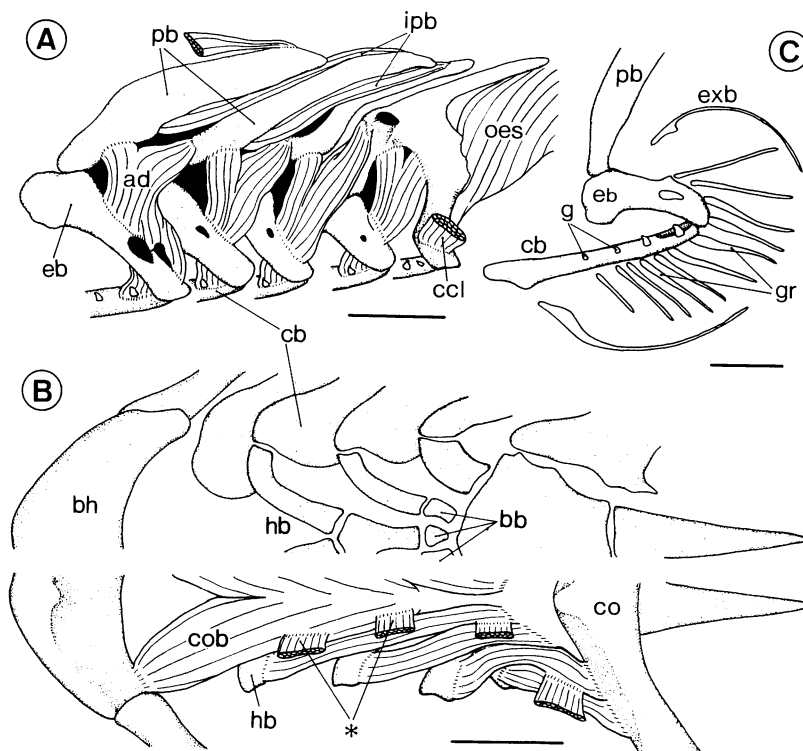
Fig. 7. Skeleton and muscles of branchial arches of *Centroscyllium excelsum*: (A) dorsal view of dorsal portion of branchial arches; (B) basibranchial copula: dorsal view showing skeletal elements (upper) and ventral view showing arrangement of coraco-branchiales; (C) lateral view of 1st branchial arch (left side). Asterisk in B shows a part of the interbranchialis. Scales are 10 mm.

two heads of origin) (Figs. 3, 7). Modifications of the basibranchial copula might be concerned with the expansion of coraco-branchial 1. This muscle should pull the basihyal backward with the rectus cervicis to open the mouth. It might also be involved in closing the mouth, as a singular backward pull of this muscle would cause the basihyal to elevate. Thus, the development of this muscle is related to the opening and closing of an elongate mouth. Modifications of the branchial arches might also be related to the swallowing of food, although exact functional details are obscure, because a similar reduction of the branchial unit is seen in *Isistius* (Shirai, 1991), which is known to swallow large pieces of flesh of fish and cetaceans.

The well-developed constrictor dorsalis is one of the peculiar features of *Trigonognathus*. This muscle is unique among squaloids in having its origin at the seam of connective tissue on the middorsal line (Fig. 2B). The contraction of this muscle will restore the large mandible and hyoid arch with the aid of the

constrictor hyoideus dorsalis and (probably) the coraco-branchialis 1. A large force seems needed to restore them.

Among squaloids, *Aculeola* and *Centroscyllium* species (the Etmopterinae) have clutching-type jaw dentition (Fig. 6B), characterized by many small teeth on both jaws arranged quincuncially as in scyliorhinids. The jaws and associated parts of *Aculeola* and *Centroscyllium* are rather conservative among squaloids, except for their length (Figs. 6–7), and their feeding mechanisms may not be specific. As discussed below, these two genera are probably allied to *Trigonognathus*. Thus, the feeding mechanism of *Trigonognathus* might not have been independently acquired, but would have derived from an ancestor like *Aculeola* and *Centroscyllium*.

Phylogenetic relationships

Two difficulties arise when the relationships of *Trigonognathus* are discussed. One is that squaloid phylogeny is still controversial (Compagno, 1973, 1984; Maisey, 1980; Shirai and Nakaya, 1990); we

have to pay attention to the validity of the closely related group of *Trigonognathus*. The other is that *Trigonognathus* has highly modified conditions especially in the head region compare with those of other suqaloids, viz. the curious profile of the neurocranium (e.g., narrow interorbital wall, considerably expanded trabecular region, and deep hyomandibular fossa with well-developed prootic process), elongated jaws, very long canine-like teeth, and simplified branchial arches and associated muscles (Figs. 6–7; Shirai and Nakaya, 1990, Fig. 2A–D). If the inherent characteristics of *Trigonognathus* and related group are still deposited, we can find the plausible phylogenetic pathway of this shark.

Among the many modifications, we found that *Trigonognathus* shared complete fusion between the pectoral propterygium and mesopterygium (Fig. 4C) with members of the Somniosinae, Dalatiinae, and Oxynotinae. This feature defines the monophyly of these three subfamilies (Shirai, 1991). However, it is doubtful that this character is evidence of monophyly of these subfamilies and *Trigonognathus*, because *Trigonognathus* does not share other derived characters with any species of these subfamilies.

In external structure, *Trigonognathus* is similar to members of the Etmopterinae, comprising four genera, *Aculeola*, *Centroscyllium*, *Etmopterus*, and *Miroscyllium*. We also found some skeletal features in *Trigonognathus*, which represent three of the four synapomorphies of the Etmopterinae (Shirai and Nakaya, 1990), i.e., two separate labial cartilages, no supraotic shelf (Fig. 6B), and a few prespinal radials. Also, the distribution of black markings on the tail will support this hypothesis. Three aggregations of luminous organs at the base of the pelvic fin, the lower caudal origin, and the posterior end of the axial part of the caudal fin are seen in *Trigonognathus* and all of the etmopterine genera, even though they are obscure.

If *Trigonognathus* is a modified etmopterine species, more detailed discussions are possible along the lines of Shirai and Nakaya (1990). One possibility is that *Trigonognathus* has a sister group relationship with the four etmopterine genera. If so, the latter group can be corroborated by the fourth synapomorphy of the Etmopterinae (Shirai and Nakaya, 1990), the presence of a keel-process of the basal cranii (kp; Fig. 6B). This process is immediately in front of the orbital articulation and appears to be the anterior limit of the protrusion of the palatoquadrate. However, in *Trigonognathus*, the anterior portion of the palatoquadrate is extremely elongated, the suborbital region being reasonably fairly modified (deeply notched) to form the roof of the mouth. Thus, we cannot ignore the possibility that the absence of this process in *Trigonognathus* is caused by a secondary loss of this character.

Shirai and Nakaya (1990) proposed two sister groups in the Etmopterinae, *Etmopterus*+*Miroscyllium* and *Aculeola*+*Centroscyllium*, based on the phylogenetic scheme of Compagno (1973, 1977). The second hypothesis that *Trigonognathus* is closely related to *Etmopterus* and *Miroscyllium* is intuitive, because of its slender body form, somewhat conspicuous black markings, and non-spiny, dermal denticles as in *E. pusillus* and *M. sheikoi*. *Etmopterus* and *Miroscyllium* share three synapomorphies, i. e., a short eye stalk without a distal disk (character 8 of Shirai and Nakaya, 1990), lower jaw teeth interlocking (character 9), and several posterior (5 to 9) monospondylous vertebrae with a complete haemal arch (character 14). In *Trigonognathus*, the eye stalk is complete with a distal disk, and interlocking of the teeth does not occur. Regarding the vertebral character, our specimen of *Trigonognathus* has two monospondylous vertebrae with a haemal arch (Fig. 4A). Such arch formation on posterior monospondylous vertebrae in these genera might be homologous, but this character cannot be evidence of the monophyly of them, because the transformation from a monospondylous vertebra to a diplospondylous vertebra does not always correspond with haemal arch formation in other squaloids.

On the other hand, *Trigonognathus* shares one character with another sister group, *Aculeola* and *Centroscyllium*, viz., the genio-coracoideus arising directly from the coracoid bar (character 11; Fig. 2C). However, this character is not persuasive, because *Miroscyllium* also has it. We must consider that this character has been lost secondarily in the lineage of *Etmopterus*. Other similarities among *Trigonognathus*, *Aculeola*, and *Centroscyllium* include jaw dentition (the quincuncial arrangement of jaw teeth and the dignathic homodonty) and the formation of the anterior pelvic basal (directed anterolaterally), but it is dubious as to whether or not they are derived.

Consequently, *Trigonognathus* seems to be a member of the Etmopterinae, but we can only say that this curious shark should have appeared from the early divergence of the Etmopterinae. The three hypotheses discussed above are equally plausible.

Resolution of the phylogenetic relationships of *Trigonognathus* must follow further comprehensive studies of squaloids and related taxa.

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ワニグチツノザメの内部形態，およびその摂餌機能，系統関係に関する一考察

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ワニグチツノザメの内部形態（骨格・筋肉系）を詳細に記載した．摂餌機能に関しては，特殊な顎歯の状態から，本種は餌を上下の顎で捕捉し，これを丸のみするものと考えられる．内臓弓およびこれに関係する筋肉構造には，こうした摂餌機能の向上に関連すると思われるいくつかの特殊な状態が観察された．これらの特殊な状態は，同時に本種の系統的位置の解明をはなはだ困難にしている．しかし，口唇軟骨が2本の離れた要素からなることなど，本種は3つの派生状態をカラスザメ亜科と共有する．カラスザメ亜科全体との姉妹関係，カラスザメ亜科内に想定されている2つの姉妹群（カラスザメ属とハシボソカラスザメ属，および *Aculeola* 属とカスミザメ属）それぞれとの類縁性について考察した．

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