

# The dipnoan species, *Sorbitorhynchus deleaskitus*, from the Lower Devonian of Guangxi, China

WANG SHITAO<sup>1</sup>, V. DRAPALA<sup>2</sup>, R. E. BARWICK<sup>3</sup> AND K. S. W. CAMPBELL<sup>2</sup>

<sup>1</sup>Academy of Geological Sciences, Baiwanzhuang Road, Beijing, China

<sup>2</sup>Geology Department, and <sup>3</sup>Division of Botany and Zoology, Australian National University, GPO Box 4, Canberra ACT 2601, Australia

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## SUMMARY

A dipnoan species from the Emsian of Guangxi, China, *Sorbitorhynchus deleaskitus*, which has previously been diagnosed in the appendix to a more general paper on dipnoan phylogeny (Campbell & Barwick 1990), is described in detail. The head is large and heavily ossified, with cosmine on the external dermal bones. The dental plates are thick and have few poorly defined large tuberosities towards their anterolateral edges. It is the only Early Devonian dipnoan for which the full hyoid arch, gular, basibranchial, and submandibular plates are preserved, and in which the parasphenoid is clearly defined. In many features the genus is more advanced than *Dipnorhynchus*, but in none is it more advanced than *Dipterus*, apart from the loss of the buccohypophysial foramen. It gives a new perspective on late Emsian evolution of the group, and reinforces our concept of an independently developing dentine-plated line contemporaneous with a true tooth-plated line.

## 1. INTRODUCTION

The discovery of a large and well-ossified head of a dipnoan in the late Emsian rocks of Guangxi adds considerable new information to our knowledge of the early evolution of the group in an area where the Early Devonian fish fauna is regarded as very provincial (Young 1981, 1990). The specimen, consisting of the skull, mandible, branchial and sub-branchial elements, clearly belongs to the same group as the Australian *Dipnorhynchus*. It has some features that allow us to interpret that genus more accurately, and

gives us new light on the biogeography of early fishes.

The specimen comes from a marine unit in which it is associated with marine invertebrates. Its preservation with the mandible, the gulars and submandibulars still in position beneath the skull, shows that it has not been transported after decomposition of the soft tissues or moved around on the bottom before burial. This supports our view that the habitat of the early dipnoans was marine rather than freshwater (Campbell & Barwick 1987, 1988). Also its very heavy ossification and its preservation, indicate that the animal lived close to the bottom in water that was

sufficiently deep to prevent reworking by storm action. This, in association with the preservation of gill arches showing the grooves for the branchial arteries and the branches therefrom, supports our view that the early dipnoans were not air breathers.

The specimen was brought to Australia for study by Wang Shitao of the Academy of Geological Sciences in Beijing, and it was prepared for study by Vicki Drapala. The rock matrix was a muddy carbonate which etched very slowly and this caused some problems in that the specimen was exposed to acid for long periods. Consequently extra care had to be taken to ensure that all exposed bone was quickly covered with plastic. In addition, some of the bone had been badly fractured during preservation. For this reason also, extreme care had to be taken as new bone became exposed. The skull roof in particular had been

badly shattered by compaction after burial, with the result that we had to work with small pieces that could not be interpreted without X-rays. Even then bone boundaries were difficult to recognize. Some fragments were lost, but most were held together to make a relatively robust preparation.

The pencil sketches were made using selected measurements of a number of features, some of which, being of special significance, were slightly emphasized.

## 2. STRATIGRAPHY

Devonian rocks are widespread in Guangxi, especially in Xiangzhou County where the type benthic facies for China has been described. In fact this facies is known as the Xiangzhou type. The typical section is at Dale, and this has been described in detail by Hou

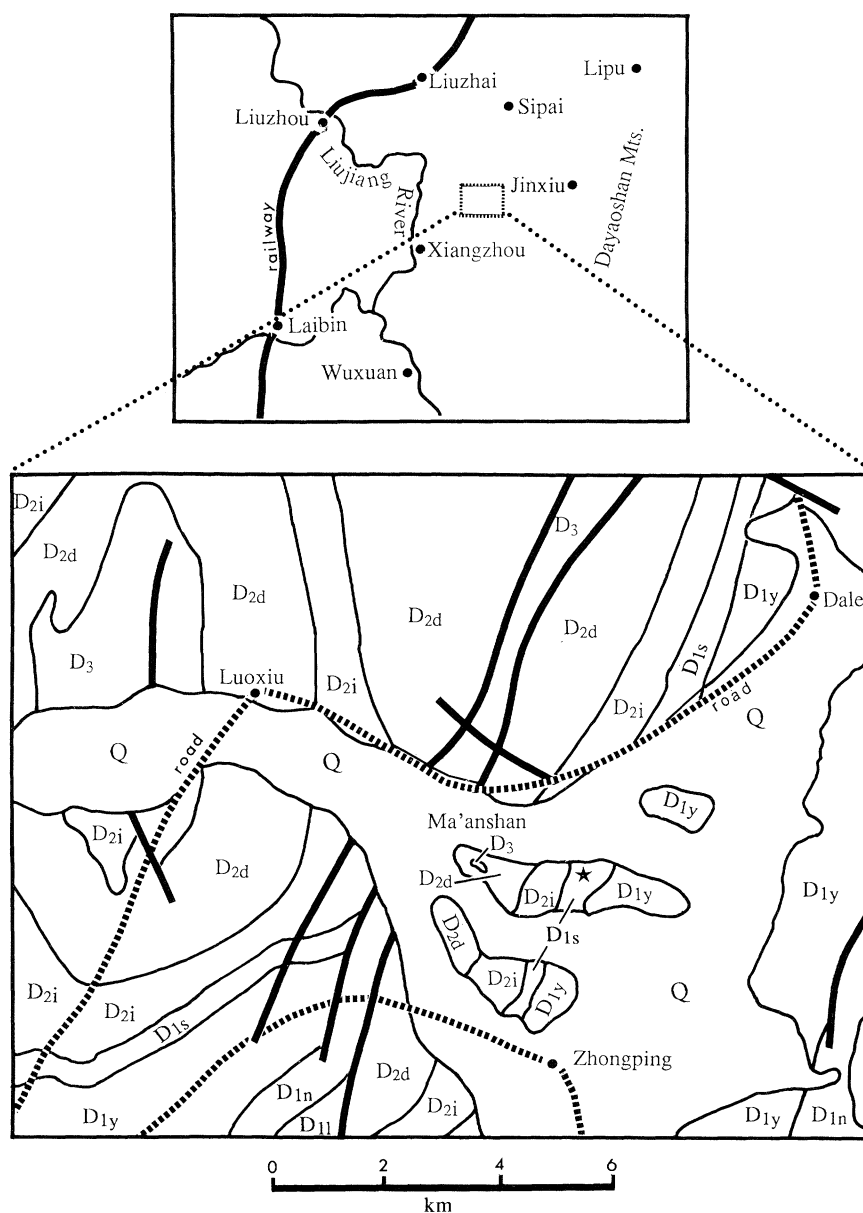


Figure 1. Geological map of the Dale-Luoxiu-Zhongping district showing the stratigraphy and location of the specimen described in this article. (Modified from Hou *et al.* (1986).) D<sub>3</sub> = Upper Devonian; D<sub>2d</sub> = Dongganglingian; D<sub>2i</sub> = Yingtangian; D<sub>1s</sub> = Sipaian; D<sub>1y</sub> = Yujiangian; D<sub>1n</sub> = Nagaolingian; D<sub>1l</sub> = Lianghuashangian. Star = fossil locality.

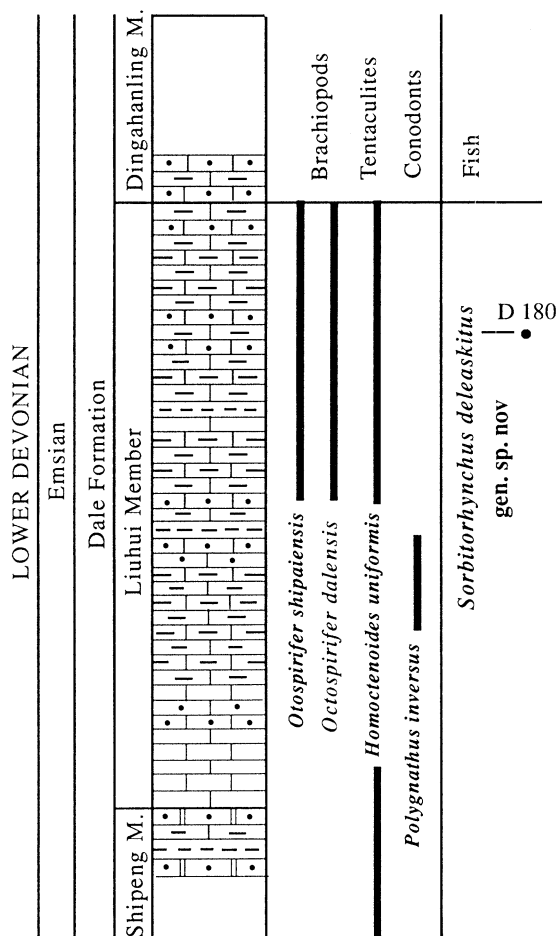


Figure 2. Stratigraphic column taken from the fossil locality. (Modified from Hou *et al.* (1986).)

Hongfei *et al.* (1988). Details are given in Figures 1 and 2 (Hou Hongfei *et al.* 1986). From a palaeogeographical point of view, the sedimentary basin lies on the southeastern side of the Upper Yangtse Massif and the southeastern side of the Dayaoshan Massif (Hou Hongfei & Wang Shitao 1985; Pan & Dineley 1988). The Early Devonian sediments in this area consist of red to purple sandy and muddy clastics interbedded with limestones and muddy limestones. They are considered to be littoral in origin. Plants, brachiopods and fish are found at several horizons. For example, the antiarchs *Liujiangolepis suni* (Wang Shitao 1987) and *Tridenspis magnaculus* (Liu Shifan 1986), and the brachiopod *Orientospirifer sp.* occur in the Xiaoshan Formation (Jia Huizhen *et al.* 1993).

The lungfish described in this paper was collected from the middle part of the Dale Formation, known as the Liuhui Member, which is composed of yellowish grey muddy limestone. The collecting was done by Yang Deli and associates during the mapping by Jia Huizhen and party which is referred to above. Associated with the lungfish are the brachiopods *Otospirifer shipaiensis* Hou & Xian and *O. dalensis* Hou & Xian, the tentaculitid *Homoctenoides uniformis*, and the trilobite *Shipaia hexaspira*. Studies of conodonts

show that the Dale Formation covers the *Polygnathus inversus* and *Polygnathus serotinus* Zones. The age of the lungfish is therefore considered to be late Emsian, and slightly younger than any known *Dipnorhynchus* species.

## SYSTEMATIC PALAEOONTOLOGY

Genus *Sorbitorhynchus* Wang, Drapala, Barwick & Campbell, 1990.

### (a) Type Species

*S. deleaskitus* Wang, Drapala, Barwick & Campbell, 1990 (in Campbell & Barwick 1990) from the late Emsian Dale Formation (Liuhui Member) near Zhongping Village, Xiangzhou County, Guangxi Zhuang Autonomous Region, China.

### (b) Diagnosis

(Amended from Wang *et al.* 1990) Skull large and heavily ossified; palate massive and with thick pterygoid dental plates separated by a median suture; tuberosities restricted to the anterior and anterolateral plate margins; most of the plate surface smooth and covered with hypermineralized dentine, but undulose margins with intergrown dentine and bone; parasphenoid short anteriorly, with a ploughshare shape and short stem as in *Chirodipterus australis*; surface of parasphenoid without dentine; no buccohypophysial opening; jaw articulation of the restricted type, consisting of a narrow, deeply grooved cartilage-covered surface on the quadrate and the adjacent pterygoid. Mandible massively ossified; dental plates like those of the palate but separated by a deep lingual groove; anterior part of lingual groove with a depression covered by irregular patches of dentine and intergrown bone and dentine with resorption patches; external surface with only three dermal bones; surangular high and with a large vertical blade against the prearticular process; glenoid fossa C-shaped in lateral profile, and grooved to fit the quadrate articulation fairly closely; articular strong and extended forwards to form a large and high preglenoid process; supra-meckelian fossa very small; surface of external dermal bones with cosmine.

*Sorbitorhynchus deleaskitus* Wang, Drapala, Barwick & Campbell, 1990.

### (c) Holotype

A single individual consisting of a broken skull and an uncrushed mandible, still articulated, but both lacking the rostral region. Field Number D'180; Museum of Geology (Beijing), Number V2034.

### (d) Diagnosis

As for the genus.

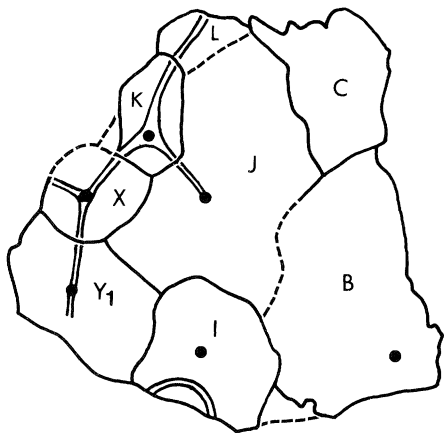


Figure 3. Restoration of part of the posterior of the skull of the holotype of *Sorbitorhynchus deleaskitus* based on X-radiographs. Solid lines represent the observed shapes, and broken lines represent hypothetical limits of plates.

#### (e) Description

This is a large species with a heavily ossified skull and mandible, comparable in these respects with *Dipnorhynchus kurikae*. The snout was naturally eroded prior to collection, and the roof and posterior wall of the skull were badly crushed by compaction during preservation. This has meant that we have been unable to make complete comparisons with other genera, but sufficient data are available to distinguish the new genus unambiguously from all those previously described.

##### (i) Skull roof

(Bone nomenclature follows Thomson & Campbell (1971) and Campbell & Barwick (1982).) The skull roof is badly crushed and incomplete. Moreover the cosmine has been irregularly resorbed, so that it has not been possible to use Westoll lines to determine the approximate shapes of the bones. The left posterior part of the skull was in a single piece, though badly crushed. Without loss of information, it could be removed from the braincase, against which it had been compressed. This was done and the isolated piece of roof was X-rayed. Though crushing has destroyed some structures, this preparation has provided some useful information about the roof, and has also allowed us to examine some aspects of the neurocranium that were not otherwise accessible (figure 3).

Bone 'B' is a long and transverse bone with its radiation centre situated well towards the rear. Its posterior edge has a slight overlap on bone 'A' which is not preserved in position. Bone 'B' contains no lateral line. Bone 'I' is small and does not meet its counterpart behind 'B'. Its radiation centre is also well back on the bone, and there is some evidence that a short loop of the occipital commissure of the lateral line passes through it. Bone 'J' is the largest of the bones in the skull. X-rays show that it contains a lateral line canal that joins the supraorbital canal in

'K', which is a small bone lying in the 'X'-'L' series in the manner of *Dipterus* rather than *Dipnorhynchus*. Bones 'X', 'Y<sub>1</sub>' and 'Y<sub>2</sub>' are relatively small and are difficult to outline on the X-rays, but their presence is determined from the identification of radiation centres. A broken bone 'C' is present on one side only and its full extent cannot be determined.

A number of small bones lay in front of 'C' and 'L', but they are too poorly preserved to permit us to define any pattern. Only the posterior part of the snout remains, and the cheeks have been completely lost.

Preserved intermingled with the gill arches were two thin bones that have patches of cosmine on their surfaces, and which are traversed by buried lateral line canals (figures 19*b-e*). One is triangular in outline and has bevelled edges along two sides and sutural edge on the other. A loop of lateral line passes through the sutured edge, and gives rise to a branch that passes out of the inner surface of the bone before reaching the posterior edge. We consider this to be the left bone 'Z'. It is transverse, with a width:length ratio of 1.75:1.0, and it would have reached from the outer edge of 'Y' less than half way across 'I'. The second bone is not so well preserved, and appears to be asymmetrical, probably because its left side has been lost. It also has a loop of lateral line canal on one side, but no branches within the bone. The opposite edge is bevelled. All this is consistent with the bone being an 'A'. Together with the 'Z', the restored 'A' is not sufficiently wide to cover the whole width of the very wide skull. Nevertheless this evidence, together with the reconstructed widths of 'Z' in *Uranolophus* and *Speonesydrion*, suggest that it was primitively a transverse bone, and that its reconstruction in *Dipnorhynchus* as a relatively narrow entity by Thomson & Campbell (1971) may be incorrect.

##### (ii) Palate

The front of the palate is missing, and although it is not possible to say if dermopalatines were present, it is clear that they were not fused to the pterygoids as in *Dipnorhynchus*.

The pterygoids are massive bones clearly sutured (rather than fused) in the midline. In longitudinal profile they are gently concave and in lateral profile they are even more gently concave except at the posterior end where they turn down abruptly to the articulation. On the posterior surface they are abruptly upturned to join the quadrate. Unlike those of *Dipnorhynchus* the pterygoids do not carry a lateral palatal process that protrudes up behind the orbital chamber (figures 7-9).

Most of the buccal surface of the pterygoid is dentine-covered to form a dental plate. The two dental plates are sutured in the midline, and are clearly separated by a narrow furrow that runs their whole length. They extend back to the level of the articulation. Each plate is divided into two distinct parts by a shallow groove lying 5-7 mm in from the anterior and anterolateral margins, the groove being deepest mesially. The main part of the plate, which

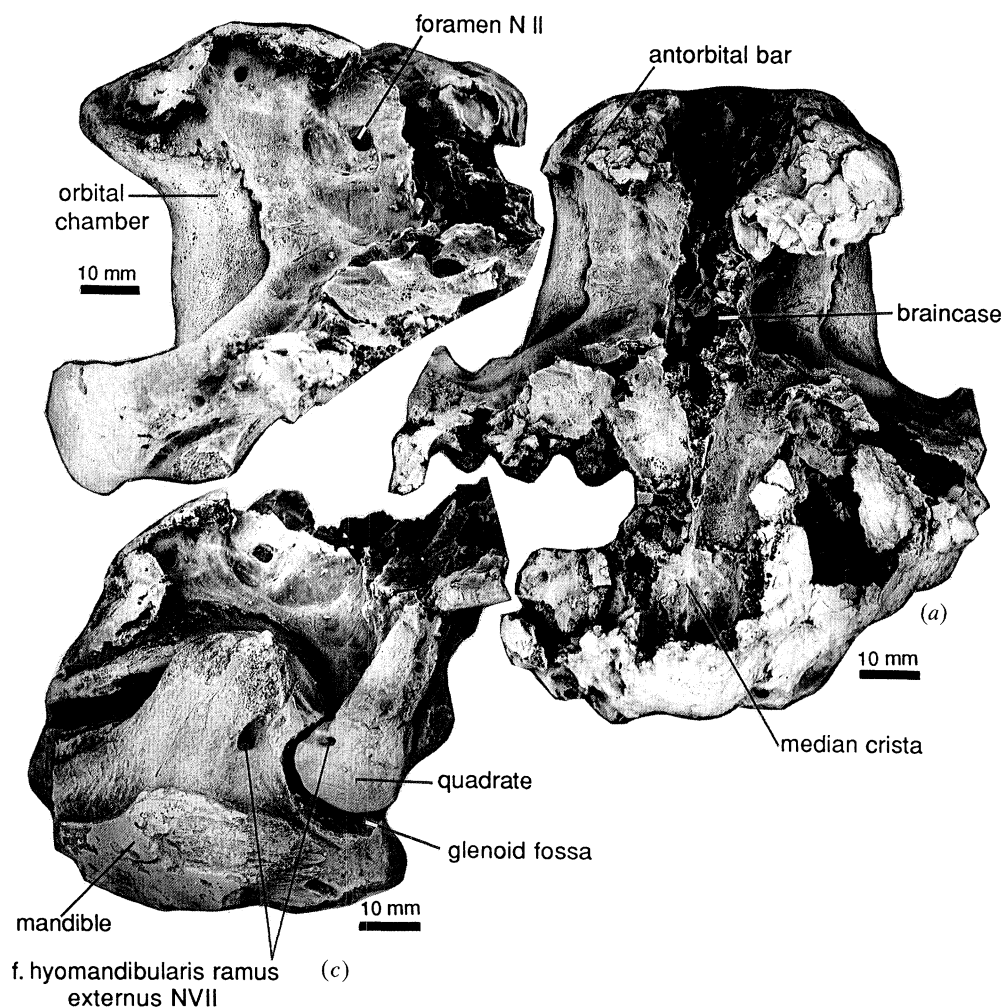


Figure 4. (a) Dorsal view of the holotype of *Sorbitorhynchus deleaskitus*. (b) Dorsolateral view of the left side of the orbital chamber of same to show form and foramina. (c) Left lateral view of the quadrate region and articulated mandible of same.

lies inside the groove, consists of smooth hypermineralized dentine, and carries a slight ridge close to its mesial edge. Outside the groove the plate carries a slight ridge whose surface is rough and tuberoso. The roughness is probably caused by the mixed nature of the tissue. Although the specimen cannot be sacrificed to cut sections, it is almost certain that the texture results from the intergrowth of bone by hypermineralized dentine. This is entirely comparable with the tissue between the ridges around the margins of the plates in *Chirodipterus australis*. In addition to the textural features, this marginal ridge carries three or four weak, rounded tuberosities, the mesial one being the largest on each plate. These relatively minor features provide the only sculpture.

The lateral and posterior margins of the plate are slightly irregular, but in only one or two places is there evidence that a slight platform of bone was built out to provide a base for selective resorption and penetrative intergrowth by dentine. Although the preservation is good, no evidence of enamel is to be seen along these edges. Mesially the dentine edge stops short of the suture, which is bounded on either side by bone. The dentine edge is ragged, but again it is devoid of

enamel. Posteromesially, small isolated patches of dentine lie on either side of the suture. These are at a lower level than the adjacent dental plate.

Growth of the plates may be compared most fruitfully with that of *Dipnorhynchus*, but discussion of this topic will be deferred until the mandibular plates have been described.

### (iii) Parasphenoid

This bone is well defined except on its left anterolateral edge (figures 7–9). Its anterior edges are broadly convex and they must have met in the midline to form an obtuse angle. The length in front of the line of maximum width is half of the length behind. Most of the sutural boundaries can be distinguished. On the right side behind the alignment of the pterygoids, the stalk of the parasphenoid (i.e. that part of the bone that tapers towards the posterior end, and lies behind the dentine-bearing surface of the pterygoids) has a rounded lateral projection that has no equivalent in any other Devonian genus. A similar outline is present on the other side though it is not so clear. Through fractures, the great height of the bone can be seen, and it seems to rise to form a ploughshare-like front wall

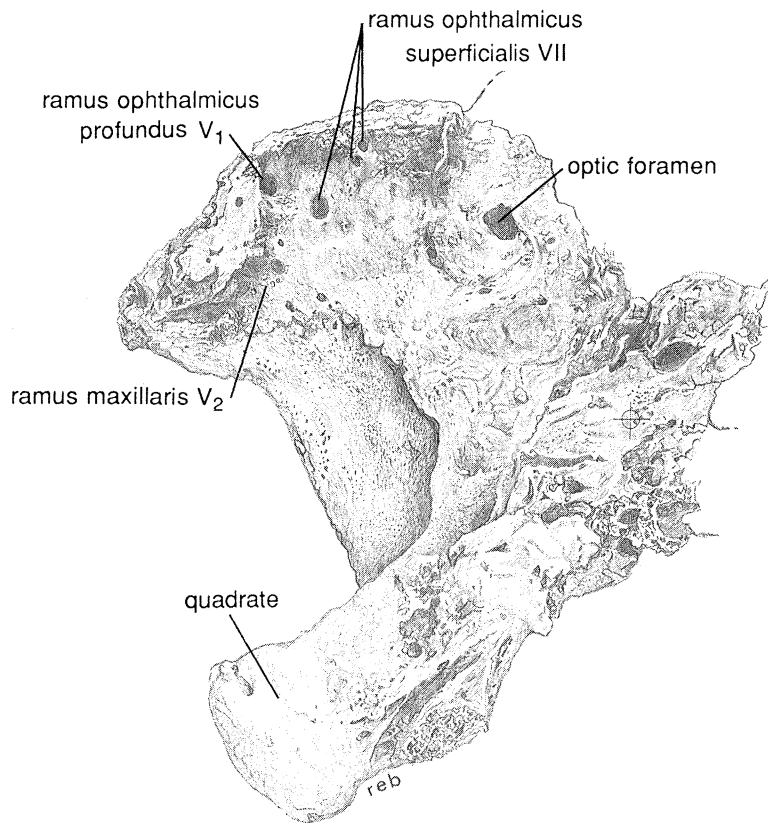


Figure 5. Drawing of the orbital chamber of the left side of the holotype of *Sorbitorhynchus deleaskitus* based on figure 4b.

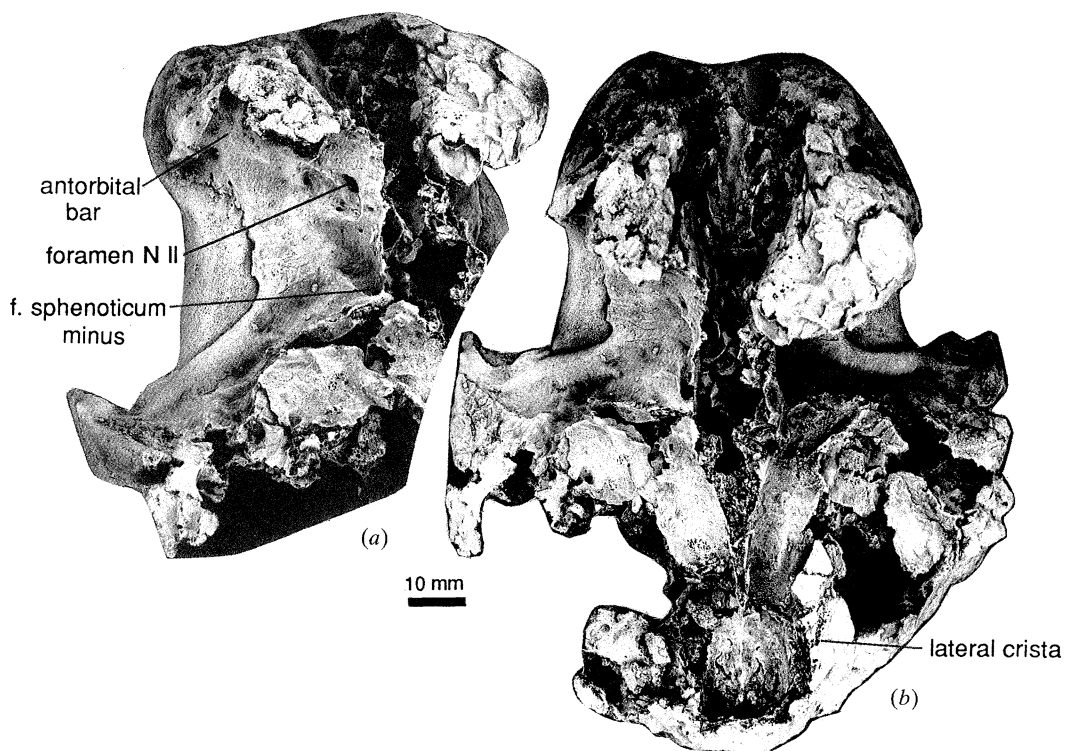


Figure 6. (a) Anterodorsal view of the skull of *Sorbitorhynchus deleaskitus* with the remnants of the roof removed. (b) Anterodorsal view of the left side of the orbital chamber of same showing the position of the nerve foramina.

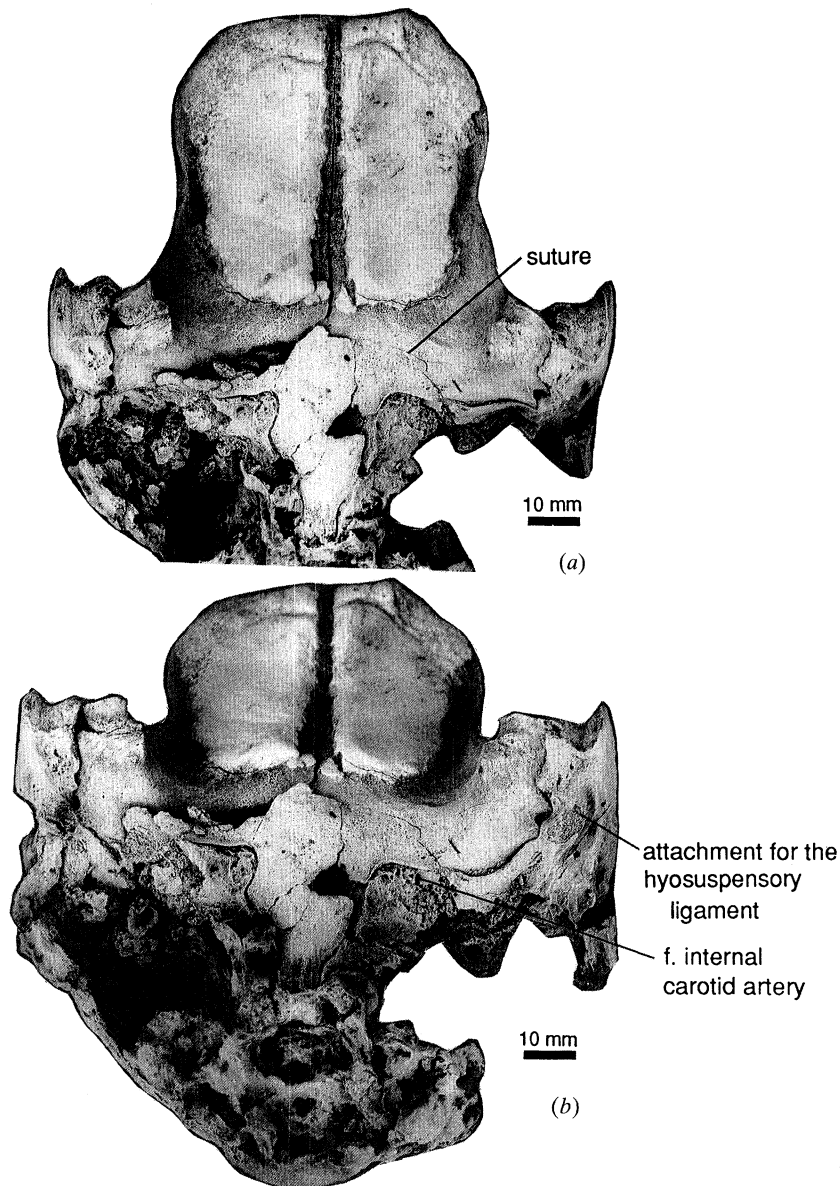


Figure 7. (a) Palatal view of the holotype of *Sorbitorhynchus deleaskitus*. (b) Posteroventral view of same showing the foramina and grooves on the back of the endocranium and the quadrate, with much of the endocranium destroyed by crushing.

similar to that of *Chirodipterus australis* (Campbell & Barwick 1982). This peculiar shape is probably present in all early dental-plated dipnoans because the pterygoid plates carry thick ridges on the quadrate rami and meet in the midline. The parasphenoid has to butt up against a thick mass of bone and dentine, and hence it thickens anteriorly though it remains a lightly ossified structure itself. We return to this matter in the discussion of the phylogenetic position of the genus. No dentine is present on its ventral face, which in ventral view is depressed below the level of the dental plates.

This discovery is important in that it is the first Early Devonian dipnoan species in which the parasphenoid can be clearly shown to be short and not extended forwards almost to the anterior end of the pterygoids (Schultze 1987). In *Speonesydrion* and *Dip-*

*norhynchus* the parasphenoid is fused to the pterygoids making the definition of boundaries difficult, and in *Uranolophus* there is contention about what is suture and what is cracking as a result of compression during preservation.

(iv) *Quadrate*

This bone is well preserved on the left side of the specimen where it is clearly sutured against the pterygoid. Its upper edge is not preserved. Its anterior face, the upper part of which has a rugose surface that appears to have been for muscle attachment, merges with the lateral wing of the neurocranium with no sign of a suture. Along the suture between the quadrate and the adjacent neurocranium with the pterygoid is a thick roll of bone that becomes less prominent mesially (figures 4b and 5).

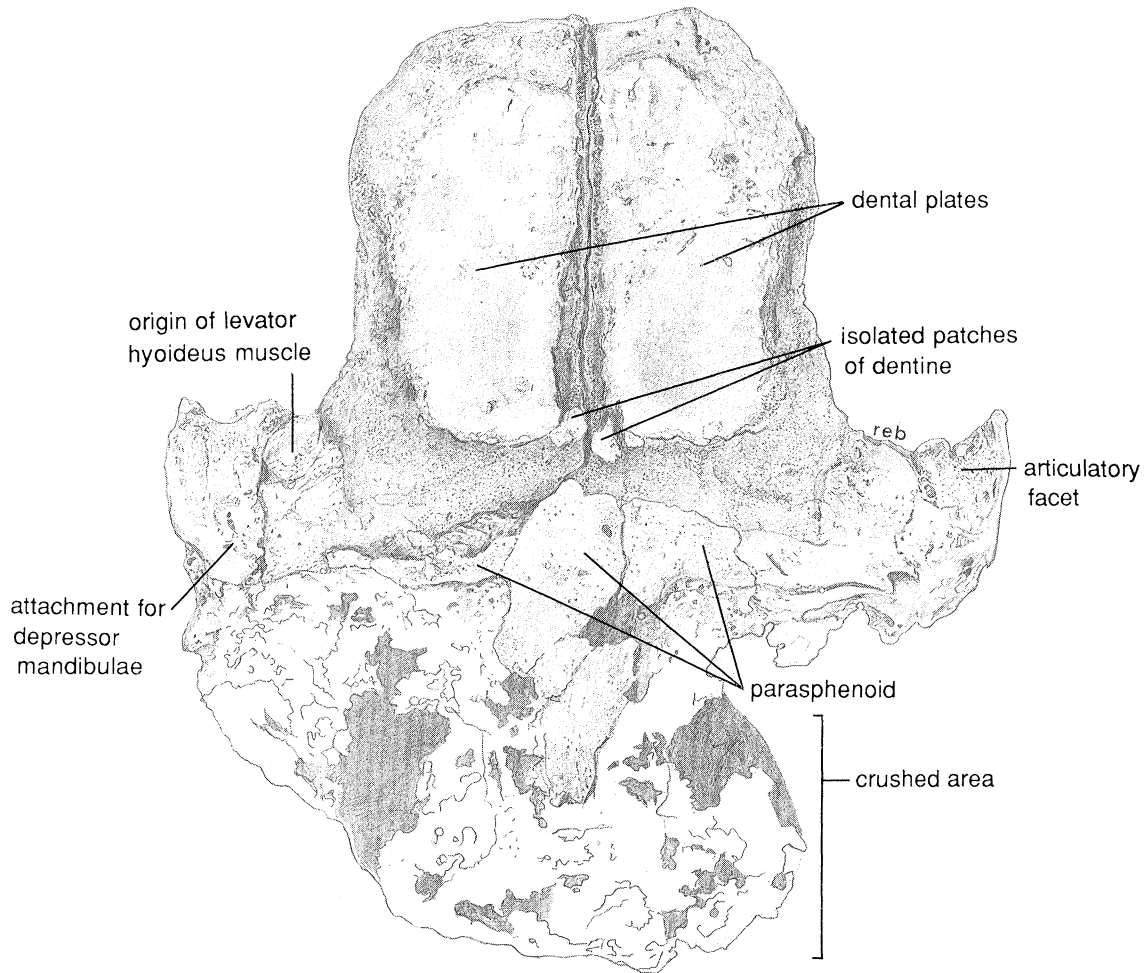


Figure 8. Drawing of the ventral aspect of the palate and articular surfaces of the holotype of *Sorbitorhynchus deleaskitus*.

The attachment areas for the dorsal end of the hyomandibular are not preserved. On the posterior face, a short distance above the articulation, there is a knob with a surface of finely textured endochondral bone (figures 7*b*, 9 and 18*b*) which is roughly divided into two parts. The upper part was probably for the attachment of the ventral end of the hyomandibular and the lower part for the attachment of the ceratohyal by the hyosuspensory ligament. A broad deep groove runs down on to the dorsal edge of this knob (figures 7*b* and 18*b*). Around its outer edge a narrow groove, whose connections are not clear, runs down and off the bone behind the articulation. This is in precisely the same position as the groove that runs out from the spiracular recess in *Dipnorhynchus sussmilchi* and has been interpreted as carrying the *ramus mentalis externus VII posterior* by Campbell & Barwick (1985, figure 7*a*). Lateral to this groove is another one which enters a foramen that connects with the foramen on the front of the quadrate just above the articulation (figure 18*b*). This carried the *ramus mentalis externus VII* as in all other Devonian dipnoans, and probably also received the anterior edge of the hyomandibular bone. The nerve must have been deep in the floor of the furrow beneath the edge of the hyomandibular.

The bone forming the mandibular articulation surface on the quadrate carries a deep longitudinal groove which receives a corresponding ridge from the articular. The articulation extended mesially onto a blade-like edge of the pterygoid that forms a projection down onto a flange on the inside edge of the prearticular (figures 7*a,b*; 9 and 18*b*). This surface of the pterygoid is almost smooth but it clearly must have been covered by a thin sheet of cartilage. The whole of the articulating surface of the quadrate is composed of fine spongy bone (figure 7*a,b*) unlike the very coarse blisters found in *Dipnorhynchus* and *Speonesydrion* (Campbell & Barwick 1984, 1985). It is clear that the articulation extended mesially. The fit between the articulatory surfaces of the quadrate and the mandible is so good that there is no doubt that only a thin articular cartilage was present in life (figures 4*c* and 18*b*).

The flange on the outer edge of the quadrate, the deep furrow and matching groove in the articular surface, and the containment of the pterygoid flange by the prearticular, all restrict the mandible to up-and-down movements. Lateral slippage as the jaw closed in the final stages of the bite would have been very limited or impossible, a view that may be tested



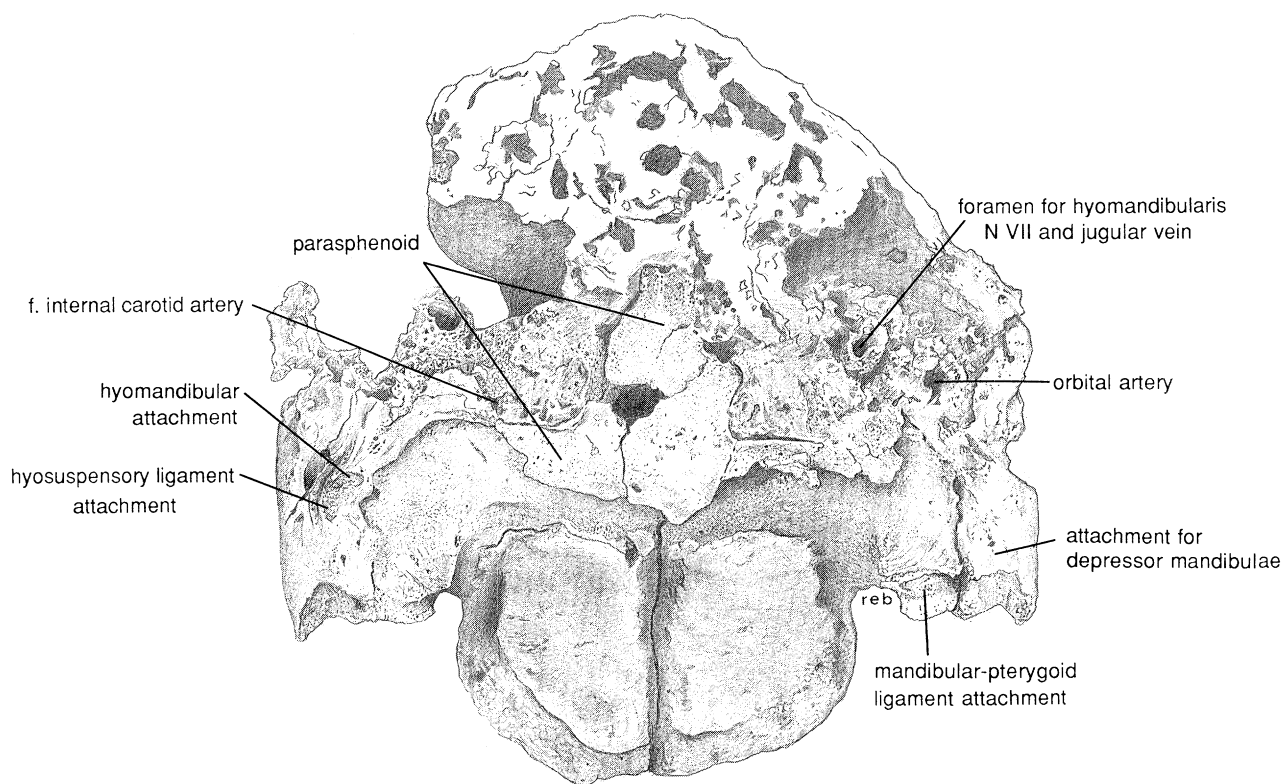


Figure 9. Drawing of the skull of the holotype of *Sorbitorhynchus deleaskitus* in posteroventral view.

by actual reassembly of the specimen. This is most unusual for an ancient member of the crushing lineage. A similar type of structure occurs in the extant lepidosirenids (Bemis 1987a), which also retain a limited amount of lateral slippage.

(v) *Neurocranium*

Most of the braincase is crushed and it cannot be described in detail. It is possible, however, to comment effectively on a number of significant features.

The braincase is suspended from the dermal skull roof by a median and two dorsolateral cristae (figures 4a and 6a). The median crista is sufficiently well preserved to show that it is present almost to the posterior of the skull, but it is not continuous. It has two short breaks beneath the posterior half of bone 'B', and it splits into two divergent parts well behind the anterior end of that bone. It is a delicate structure as is normal for early Devonian dipnoans. The dorsolateral cristae (figure 6a) are continuous, unlike those of *Chirodipterus australis*. They diverge only slightly in their posterior courses, but when they reach the vertical plane where the median crista divides they turn abruptly laterally making an angle of about 20° with the midline.

The postnasal-antorbital bar is very strong and has resisted crushing during preservation. In other Devonian genera this bar is mostly hollow, and contains a few struts of endochondral bone joining the well-developed perichondral layers. In *Sorbitorhynchus* it is made of finely vesicular bone with a smooth perichondral layer on its anterior, ventral and posterior faces (figures 4a, 5 and 6b). The bar has a similar form to

that of other Devonian dipnoans, though it is more extensively flared as it approaches the skull roof, with which it makes a very strong buttress. Ventrally it is closely applied to the pterygoid, the suture between them being much less clear than the suture between the neurocranium and the pterygoid in a more posterior position. The foramina and grooves on and through the bar are well defined (figures 4b; 5 and 6b). On each side of the animal the largest foramen lies immediately beneath the dermal bone, runs through the bar in a perichondrially lined tube, and presumably entered the tubule system above the nasal capsules. Details are not preserved anterior to the exit of this canal from the bar. This was presumably for the *ramus ophthalmicus profundus V*. Low on the posterior wall is a large foramen that enters a mesially directed tube. It is probable that this carried the *ramus maxillaris V*. Three other foramina penetrate the higher part of the posterior wall of the bar. They are directed mesially, and although the preservation is not good enough to be certain, they seem to have emerged into the open ethmoid space that surrounds the olfactory tubes. This would allow them to connect with the rostral tubules. They are interpreted as branches of the *ramus ophthalmicus superficialis VII*. Another large canal runs between the bar and the pterygoid at its lateral margin. We have previously interpreted the foramen in this position as being for the subnasal vein (Campbell & Barwick 1982).

The optic nerve foramen is small for a specimen of this size, and is situated close up to the antorbital bar (figures 4a,b and 6a,b). In the wall of the neurocranium behind it there are two or three foramina whose



Figure 10. (a) Dorsal view of the reassembled hyoid arch of the holotype of *Sorbitorhynchus deleaskitus*. The posterior part of the basihyal is not preserved. (b) The same in left dorsolateral view.

identity we cannot determine. The surrounding surface is dimpled in the usual manner, presumably indicating attachment areas for the eye muscles.

The deep pit in *Dipnorhynchus*, considered by Thomson & Campbell (1971) to be the spiracular recess, and subsequently shown by Campbell & Barwick (1982) to be also for a branch of the *ramus mentalis externus* of *hyomandibularis VII* is not present in this new species.

The foramen for the orbital artery is well preserved in the lateral wing of the braincase on each side of the specimen (figures 7b and 9). It enters a completely lined canal that passes directly through to the orbital chamber. On the posterior wall below the orbital artery foramen is a smaller opening that can be traced into a canal that enters the canal for the jugular and

*hyomandibularis VII* (figure 9). We conclude therefore that it carried a branch of the VIIth nerve. The bone around the orbital canal is not well preserved, but on the left side of the specimen enough remains to show that mesial to the orbital artery foramen is a separate foramen that opens anteromesially into a canal that runs down to the *foramen sphenoticum minus*, situated well forward on the lateral wall of the braincase (figures 4b and 6b). This canal is for the jugular vein. In its posterior course it also contains the hyomandibular branch of the VIIth nerve. The arrangement is very similar to that in *Dipnorhynchus* (Campbell & Barwick 1982, figures 15, 16 and 20), but in that genus the two foramina are combined on the posterior face to form a *foramen prooticum basicraniale*.

On the right side the *foramen sphenoticum minus* is

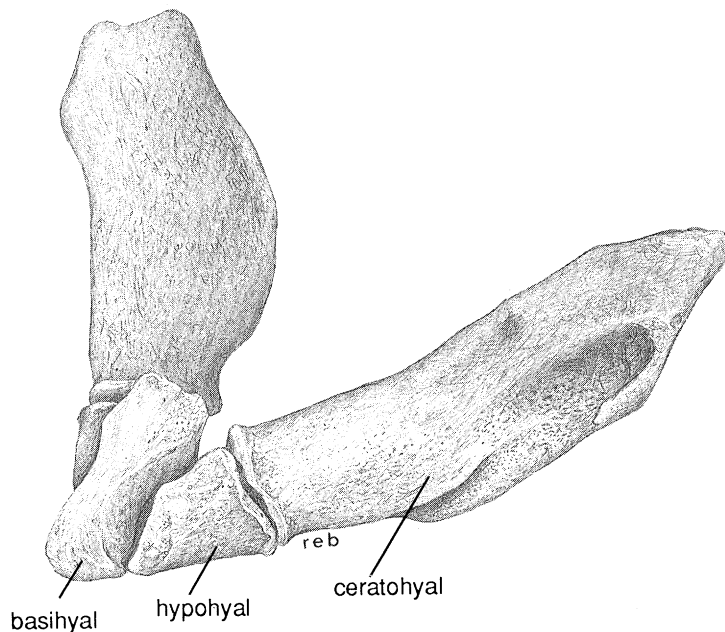


Figure 11. Drawing showing a restoration of the hyoid arch of *Sorbitorhynchus deleaskitus* in dorsolateral view as shown in figure 10*b*.

better preserved than on the left, and it retains part of the canal for the pituitary vein that can be seen opening into the inner wall of the braincase lateral to the hypophysis. No hypophysial stalk has been observed.

The left side preserves the region of the *foramen sphenoticum majus* better than the right. Two large canals open into it from a mesial direction. These are the conjoined second and third branches of the trigeminal nerve and the branch of the facialis nerve into the orbital chamber. One of them may also carry the middle cerebral vein. Opening from a posterior direction lateral to these foramina is a much smaller canal whose connections cannot be traced.

As is normal for dipnoans, the foramen for the entry of the internal carotid artery is placed just above the junction between the pterygoids and the neurocranium and lateral to the extremity of the parasphenoid (figures 7*b* and 9). The artery entered this foramen from a posterolateral direction.

A peculiar slit-like opening lies at the junction of the quadrate and the pterygoid mesial to the hyosuspensory ligament attachment. A short groove enters this opening from a posterior direction, as is especially clear on the right side (figures 7*a,b*). This suggests that it may have carried a nerve, but its identity remains in doubt. Its presence on both sides of the specimen indicates that this is probably of significance, as we have been unable to find a similar opening in other Devonian dipnoans.

(vi) *Hyoid arch*

Almost the entire arch on each side has been preserved (figures 10 and 11). This consists of a robust ceratohyal, a small hypohyal and a weak basihyal. These will be described in order.

The ceratohyal is a 'chunky' bone that was made of a relatively thin perichondral layer over cartilage through which passed several supporting struts of bone (figures 12 and 13). The mesial surface is broad and smooth as is normal for dipnoans. It carries a tracery of fine furrows that record the positions of the circulatory system as in *Griphognathus whitei* (Campbell & Barwick 1987). The outer surface bears a long, high flange just below its mid-height. This forms the upper edge to the deeply concave *interhyoideus* muscle attachment. The flange is high and thin over most of its length, but thickens posteriorly for the attachment of the *depressor mandibulae* muscles. Above the ridge there is a large depression that seems to have been occupied mainly by the *levator hyoideus* muscle, though the anterior outline of this scar is not clearly defined. At the posterior end of this scar is a pit with its anterior edge clearly ridged and its posterior marked by a smooth notch in the bounding ridge, giving the impression of soft tissue passing posteriorly out of the pit. Such a structure occurs in *Chirodipterus australis*, where it is not so strongly developed, but it is not present in *Griphognathus whitei*. We are at a loss to understand its significance. There is a strong posterior projection for the attachment of the *sternohyoideus* muscle, and an incomplete posterodorsal termination for the ligament attaching the ceratohyal to the neurocranium. On the dorsal side of the lateral flange below the *levator hyoideus* attachment is a pronounced groove that runs off the ventral edge of the bone at the anterior end of the flange (figures 11 and 12*g*). This is too large for a nerve, and the only vessel in this region in *Neoceratodus* is the posterior branch of the efferent epibranchial artery.

The anterior end of the ceratohyal is expanded to form a slight flange that runs around the entire end of

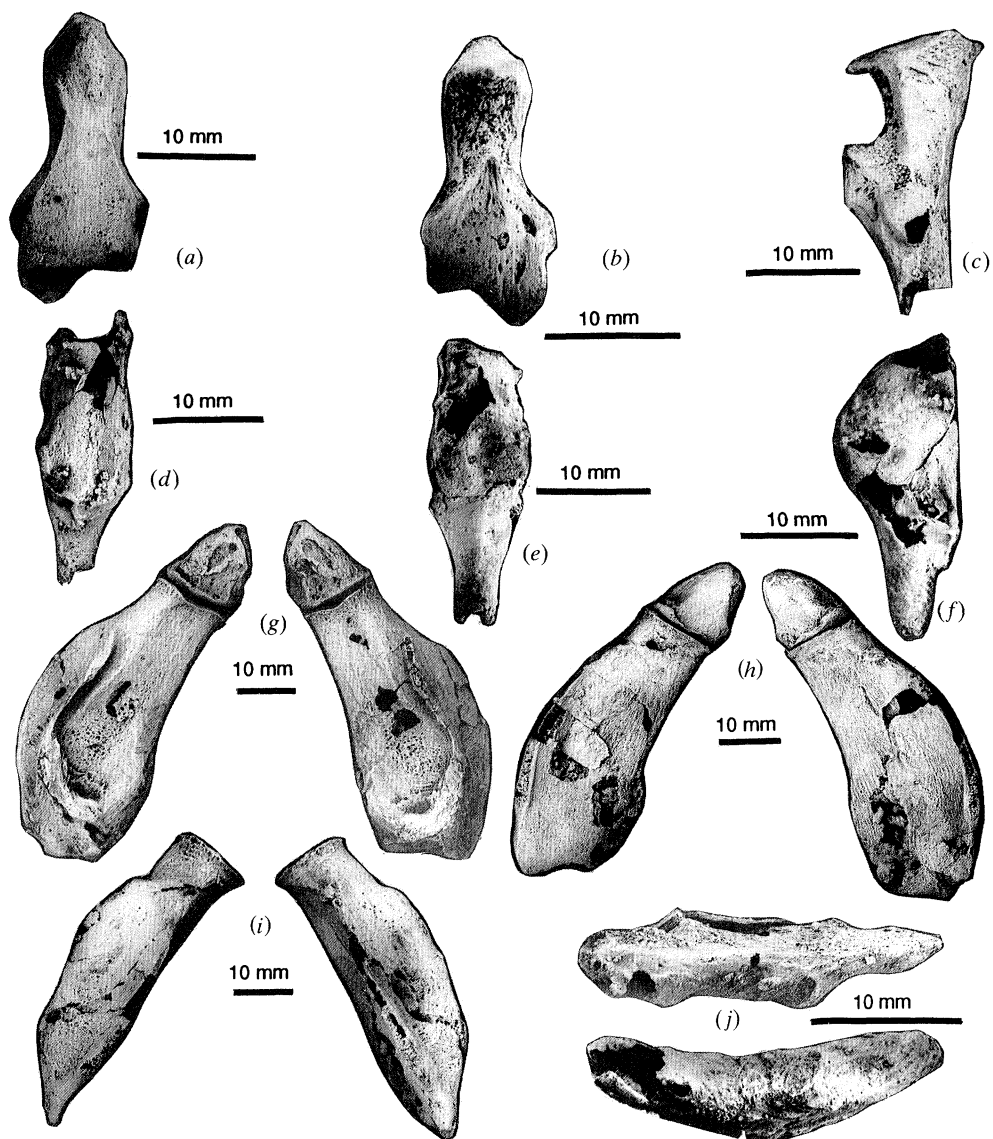


Figure 12. (a–c) Dorsal, ventral and left lateral views of the broken basihyal of *Sorbitorhynchus deleaskitus*. (d–f) Dorsal, ventral and left lateral views of the posterior basibranchial. (g) Ventrolateral views of the left and right ceratohyals and attached hypohyals. These specimens have been rotated so that the ventrolateral surfaces lie in the one plane. (h) Mesial surfaces of same rotated outwards so that these surfaces lie in the one plane. (i) Left and right ceratohyals in ventral view. (j) Urohyal in dorsal and ventral views.

the bone. The perichondral bone laps around the edge of this rim on to the articulatory face with the hypohyal. This articulatory face is slightly concave, and its medial part is occupied by fine vesicular bone where the cartilage of the articulation was embedded.

The hypohyal (figures 10–13) is a cuneiform bone with strong perichondral ossification. Its articulatory surface against the ceratohyal has a similar texture to the articulatory surface of that bone, and has a thickened rim. At its anteromedial end is a tear-shaped surface with vesicular bone which served for the attachment of the cartilage making the join with the basihyal. Posteroventral to this surface is an elliptical depression (figure 12g) which lies opposed to a similar one on the other hypohyal. Its floor is covered with perichondral bone. We consider that it housed a ligament or muscle that passed ventral to the

basihyal and pulled the hypohyals together, thus making their attachment to the basihyal more secure. A similar structure is seen on *Chirodipterus australis* and *Pillararhynchus longi*, but not on *Griphognathus whitei*.

Only the anterior part of the basihyal + anterior basibranchial is preserved (figures 10–12). This consists of a short perichondrially ossified unit with an anterior end shaped like a ship's prow. Its ventral surface carries the articulatory surfaces for the hypohyals. These surfaces are in contact on their ventral edges. Behind them the basal element expands and produces small rounded processes that articulate with small rounded depressions in the upper surface of the hypohyals (figure 12c). These are not appropriately placed to have served for the articulation of the first ceratobranchial. The posterior part of the element has been lost through breakage.

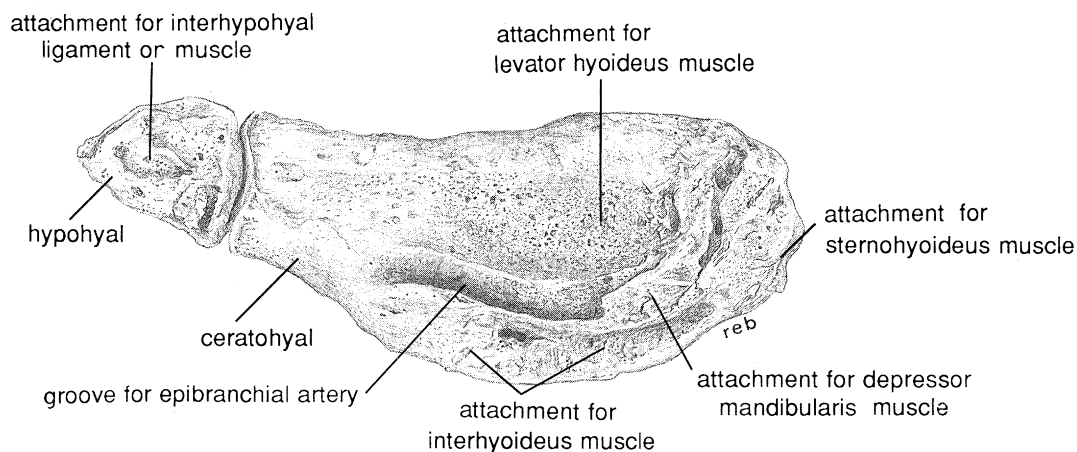


Figure 13. Restoration of left ceratohyal and hypohyal of *Sorbitorhynchus deleaskitus* in ventrolateral view to show the muscle attachments and the foramina.

A well-ossified median element, probably the urohyal, is also preserved (figure 12j). It is shorter and more robust than that of *G. whitei*. It is not quite symmetrical, but has slight embayments on its flanks presumably for the attachment of soft tissues. In lateral view it has a curved fusiform shape.

(vii) Gill arches

These are all fragmentary and we cannot place them in sequence. A couple of points are obvious however. At least some of the ceratobranchials have expanded ventral articularity ends like those of *Griphognathus whitei*. They have slight projections so that adjacent elements are able to articulate, but we see no evidence of the small bones like those that acted as spacers in *G. whitei*. A pronounced blade-like process is present on the posteroventral edge like those known in both *Griphognathus whitei* and *Chirodipterus australis* (Miles 1977). Other details of this end of the ceratobranchial are not preserved. Several ceratobranchials show furrows for the branchial arteries and their branches to the gill filaments (figure 19j).

A well-developed posterior basibranchial is preserved (figures 12d–f). It is a bulkier structure than that of *G. whitei*, and is more like that of *C. australis* in shape having a more or less straight dorsal edge in lateral profile, and the attachment for one pair of ceratobranchials on swellings at the anterodorsal corners of the bone and another on its flanks. Its posterior end tapers rapidly but the extremity is not preserved.

(viii) Mandible

External dermal bones

The mandible is massively ossified (figures 14–16) making a very robust structure that has withstood crushing almost completely.

The external dermal bones have been eroded from the anterior, and the dentary has been completely removed. By projecting the curvature of the remaining bones forwards we conclude that the leading edge of the mandible would have been about 1.5 cm in front

of the preserved bone, allowing room for a dentary as well as an anterior furrow. On the left side of the specimen most of the dermal bone remains. Only three infradentaries are present; they will be described and then their homologies discussed. The three include one unusually wide mesial and one lateromesial bone, the preserved parts of which are cosmine-covered, together with a lateral bone. This lateral bone has a small cosmine-covered part which has a pointed posterior end, a much larger naked dorsal blade forming the high flank of the jaw, and a naked posteroventral part where it is plastered against the articular (figures 14d,e). The upper edge of the cosmine is distinctly flexed, the posterior part indicating the extent of the overlap by the cheek bones when the jaw was fully closed. This is normal for cosmine-bearing species such as *C. australis* (Campbell & Barwick 1987, figure 15). Anterior to this, the bone is inflected slightly mesially to form the floor of the labial furrow. This inflection is unusually narrow in comparison with those of *Dipnorhynchus* and *Speonesydrion*, and its vertical extent is unusually large. These features are correlated with the absence of a large suprameckelian vacuity and the presence of a high preglenoid process for the attachment of the *adductores mandibulae*.

The lateral line canals are deeply buried, and can be traced only by the indistinct rows of their pores and by their entry and exit points (figure 17). The mandibular canal enters the lateromesial bone near its posteroventral corner and can be traced in a broad arc across the commissure to join its fellow of the other side. Within the mesial bone it forms a branch that runs approximately through the middle of that bone. In most other Devonian genera this branch is in the postsplenial. This fact, together with the great width of the mesial bone indicates that the splenial and postsplenial bone spaces are occupied by a single bone. We regard this bone as splenial–postsplenial, and the other two as angular and surangular.

Like the cosmine on the roof, the cosmine on these bones shows irregular resorption. In addition the

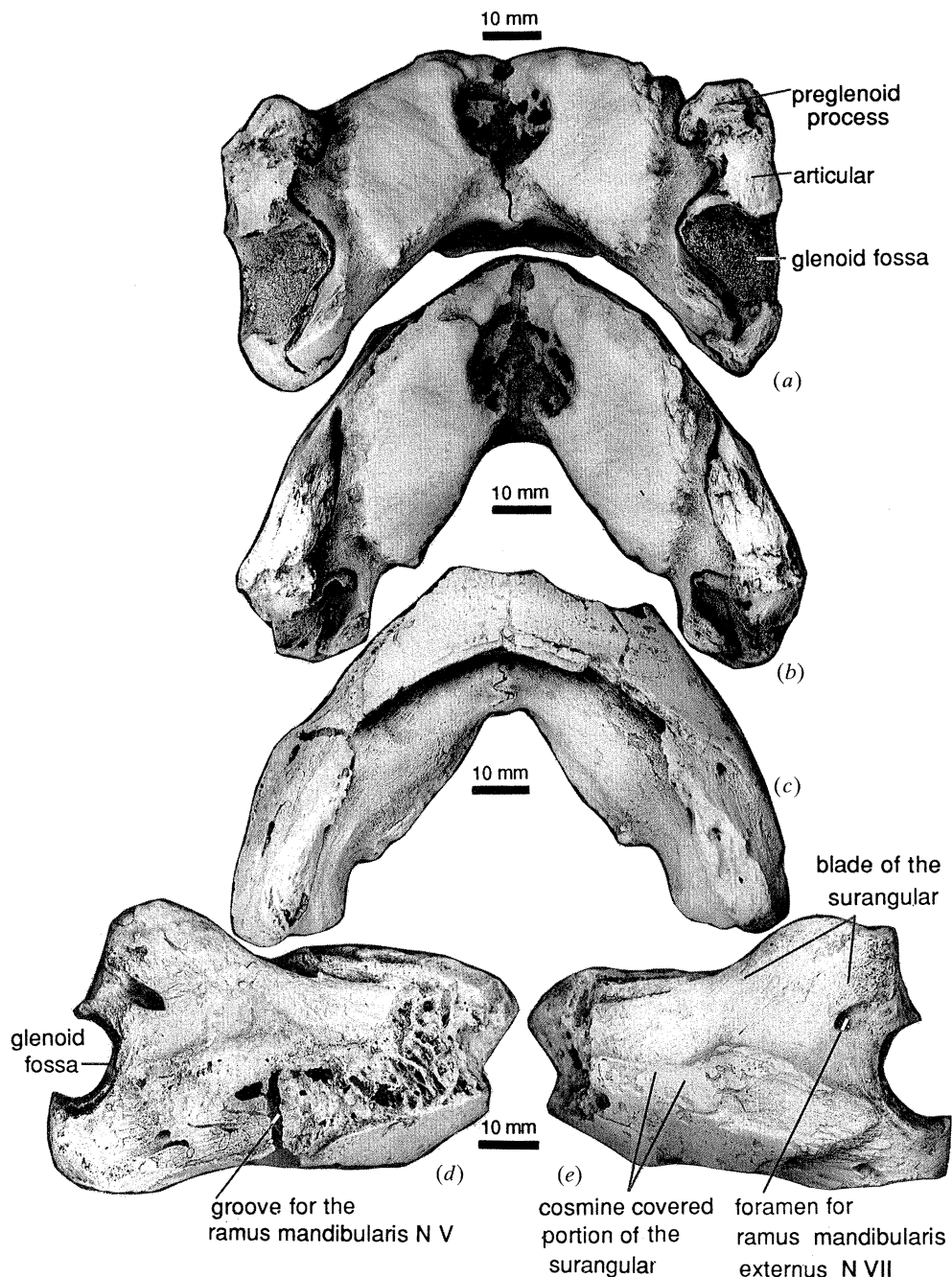


Figure 14. (a) Posterior view of the mandible of the holotype of *Sorbitorhynchus deleaskitus* showing the massive structure of all the bones. (b) Full dorsal view of the mandible showing the dental plates, the massive preglenoid process and the structure in the lingual furrow. (c–e) Ventral, right and left lateral views of the mandible.

splenic–postsplenic shows numerous longitudinal resorption lines. These are unlike any other structures we have observed in dipnoans.

#### Internal dermal bones

As usual the prearticular is the main internal dermal bone. An adsymphysial may have been present, but it could not have been preserved as that part of the specimen has been removed. The prearticular is a massive bone also, with a thick posterior wall and a lamina running up the inner face of the preglenoid process. The two prearticulars are clearly sutured in

the midline, the suture having a strongly zig-zag shape on the posterior face, but it is only slightly sinuous in the floor of the lingual furrow. A knob-like process is present on the posterior face in the midline.

The dental plates are comparable with those of the palate, but they are not complementary. For example, they touch at only one point on each side at full occlusion. The main part of the plate consists of smooth hypermineralized dentine, but the anterior and anterolateral edges are clearly demarcated by changes in slope and in composition. They are turned down slightly and are composed of a mixture of bone

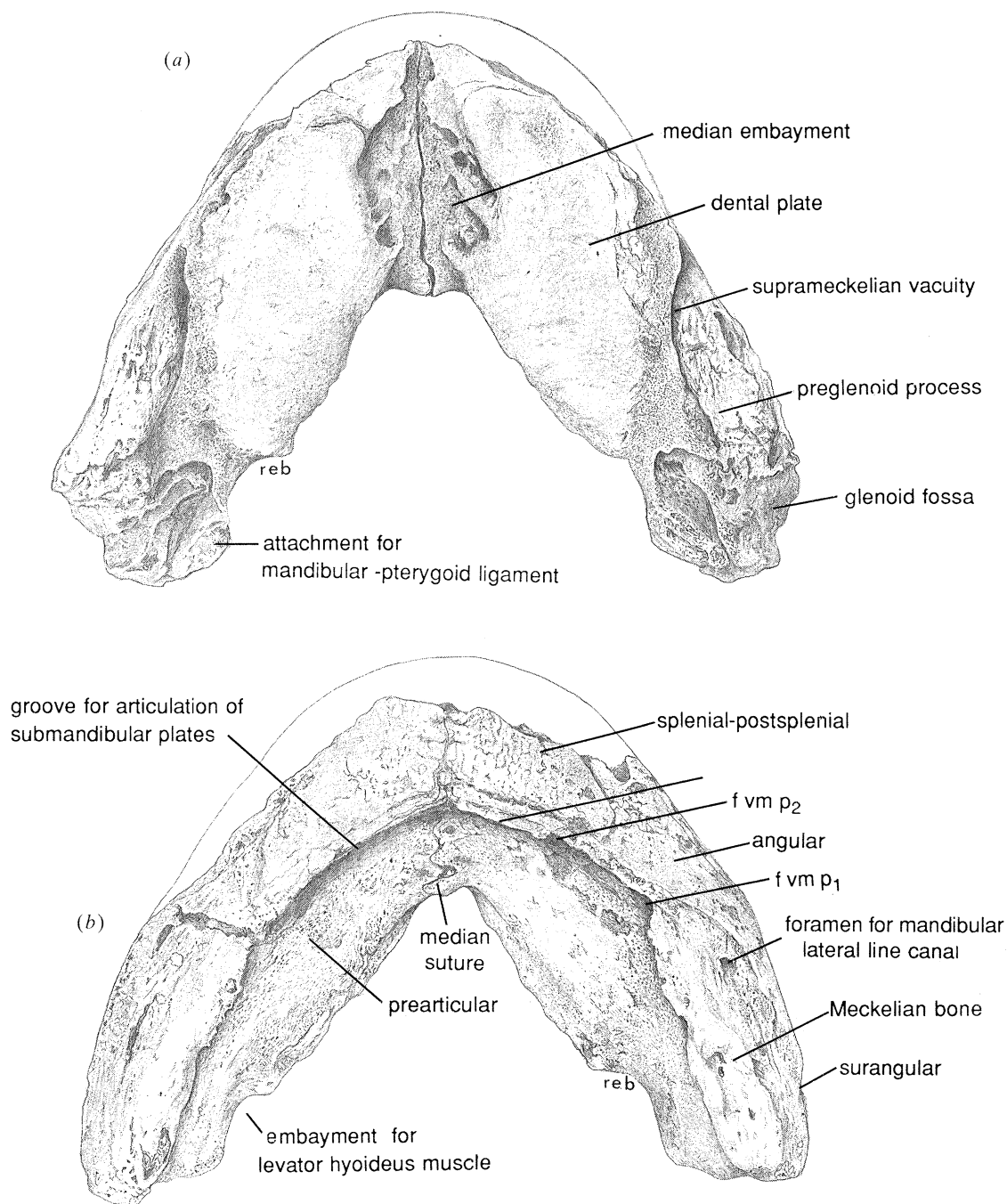


Figure 15. (a,b) Reconstructions of the mandible of *Sorbitorhynchus deleaskitus* in dorsal and ventral views.

and intergrowing dentine. They are also slightly undulose. Towards the midline on each side this zone has a rounded tuberosity formed of hypermineralized dentine, the one on the left being larger than the one on the right. On the right side, the outermost extremity of the anterolateral margins carries four or five small enamel-covered blisters like those that occur in *Chirodipterus australis*. Presumably such blisters have been eroded from much of this edge and all of the corresponding edge on the left side. The lateral and posteromesial edges of the plates are like those of similar parts of the palatal plates.

Each plate has an ovate, deep, rimmed embayment formed within the lingual furrow (figures 14a,b and

15a). This embayment is floored by intergrown bone and dentine within which lie a number of ragged resorption patches of different sizes. These patches are floored by bone without dentine. The rim of the embayment is slightly raised and well-rounded. The embayment opens posteriorly into a deep triangular space floored with bone which slopes downwards posteriorly. This relatively confined posterior space would have accommodated the end of the basihyal-hypohyal complex, which would have had little room for lateral movement or anterior protrusion.

The edge of the prearticular mesial to the glenoid fossa carries a striated lenticular flange for the attachment of the mandibular-ptyergoid ligament. Towards

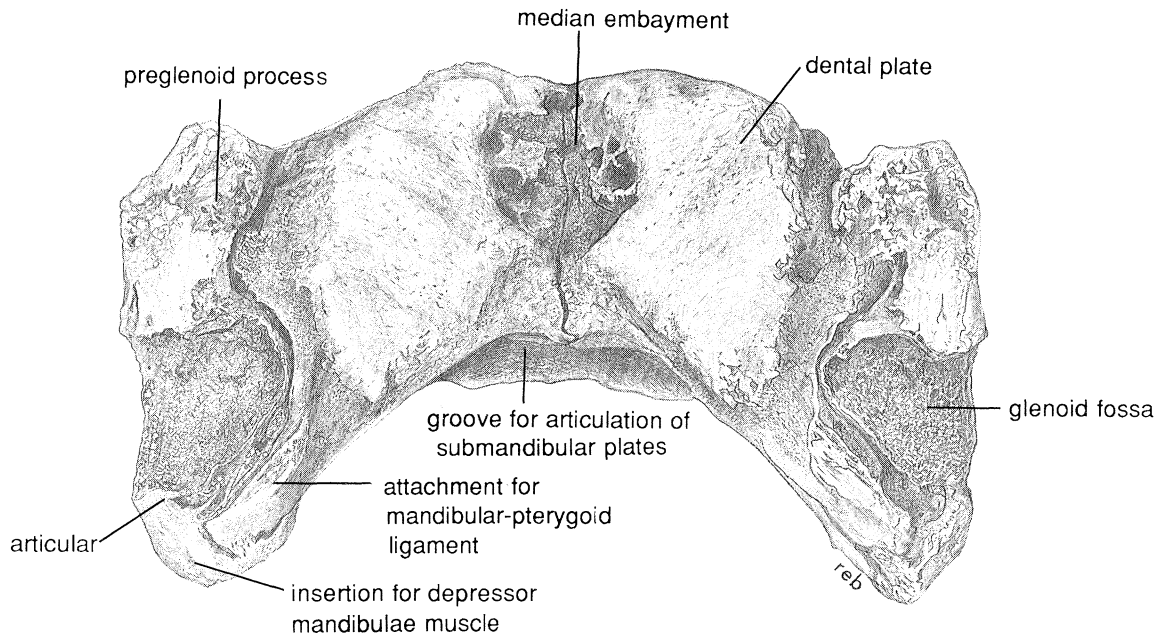


Figure 16. Reconstruction of the mandible of *Sorbitorhynchus deleaskitus* in posterior view.

the glenoid fossa the bone slopes down on a smooth surface that takes the flange on the inside of the articular process that is formed by the pterygoid.

The rounded embayment in the margin of the prearticulars between the back of the dental plate and the mandibular-ptyergoid ligament attachment is short as in *Dipnorhynchus*, *Chirodipterus australis* and *Pilliarhynchus*. Reassembly of the specimen shows that the *levator hyoideus* would have been in this position, passing from the ceratohyal to the pterygoid. It would originate on the pterygoid posterolateral to the edge of the dental plate (figure 8), and insert in the large pit on the ceratohyal. In the primitive tooth-plated genus *Speonesydrion*, the space for the passage of this muscle across the back of the mandible is much larger. It is not known if this is because the muscle was larger or because the dental plates did not extend so far back. Regardless of its functional significance, present evidence suggests that the size of this embayment in the mandible may be another useful feature for dis-

tinguishing members of the tooth-plated and dentine-plated groups.

#### Articular and Meckelian bones

The articular is a large bone which forms a high preglenoid process that is rugged on its dorsal surface, but smooth on its posterior (figures 14a,b). The glenoid fossa is narrow in comparison with those of other crushing dipnoans from the Devonian. It is in two parts, a very narrow outer band separated from the broader inner band by a gentle ridge. The outer part is overlapped by the outer edge of the quadrate articulation. The articular surface is covered by fine bone that was obviously the seat of the articular cartilage. In lateral profile the fossa is C-shaped. This also is unusual in a dipnoan with crushing dentition.

Below the glenoid the articular makes a small posterior projection and then turns around to become a wedge-shaped Meckelian bone that is exposed posteriorly only half way to the midline (figures 14c and 15b). Mesial to this the external dermal bones are in direct contact with the prearticular but along their junction is a deep furrow of a kind not seen on any other Devonian dipnoan. The surface of the Meckelian bone is not striated as it is in many other Devonian dipnoans, but it is irregularly rough.

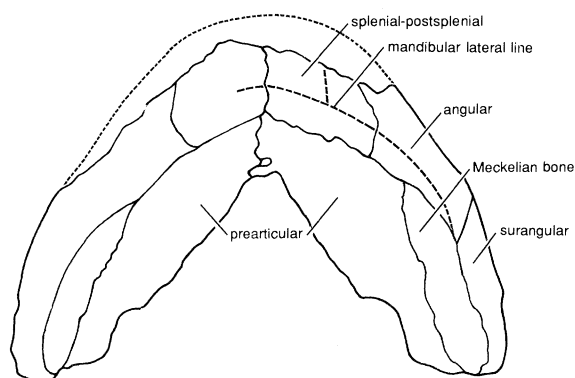


Figure 17. Outline drawing of the mandible with the position of the lateral line canals inferred from entry and exit openings and lateral line pores.

#### Foramina and grooves

The foramen for the *ramus mentalis externus* of the *hyomandibularis VII* is on the blade of the surangular at about the level of the top of the glenoid fossa. It is entered from a posterodorsal direction by a single shallow groove (figure 4c). The supra-meckelian vacuity is greatly reduced in comparison with other early dipnoans, and it is little more than a pit. It is slightly overhung by the dental plate so that there is no prospect of entry by the mass of the *adductores*



*mandibulae*. On the left side particularly, there is a groove down the anterior face of the preglenoid process and this is directed towards the supra-meckelian pit; this seems a possible entry point for the *ramus mandibularis*, though it is a little too far forwards. The alternative would be to pass this nerve into the mandible through the same foramen as the *ramus mentalis externus VII*.

Along the junction between the dermal and the prearticular or Meckelian bones, or close to it, is a series of foramina that compares closely with other Devonian genera (figures 14c and 15b). The *ramus mandibularis VII* leaves a large foramen ventral to the anterior end of the glenoid, passes along a posteriorly directed groove and then off the bone. On the right side of the specimen where much of the dermal bone has been removed, the mandibular lateral line canal is closely connected with the intermandibularis groove, but on the left the two are quite separate. A large foramen, homologous with the *f vm p 1* of *Speonesydrion iani* (Campbell & Barwick 1984) lies at the end of the Meckelian bone wedge and opens into a vertically oriented canal that runs up through the Meckelian bone plastered on the inside of the dermal bone. Its upper end is not seen, but tends to turn forwards along the inner face of the external dermal bone. Towards the midline on each side there are two more foramina that have been interpreted as the homologues of *f vm p 2* and *f ma* of *S. iani*. (Campbell & Barwick 1984, figure 21b). Apart from the fact that these are entered from a posterior direction, nothing is known about the courses of the nerves or vessels they carried. Finally, about half way along the posterior edge of the junction between the Meckelian bone and the prearticular is a small foramen that is homologous with *f pd* in *S. iani*.

In summary, there is a remarkable concordance in the patterns of the foramina in the early Devonian genera *Dipnorhynchus*, *Speonesydrion* and *Sorbitorhynchus*, as well as the late Devonian *Chirodipterus australis*. They differ mainly in the orientation of the canals associated with the foramina, but that is to be expected if the overall shapes of the jaws are taken into account.

(ix) *Growth of the dental plates*

This is best understood by reference to the mandibular plates. The maximum rate of growth was in an anterolateral direction. As in *Chirodipterus australis* the growing edge carries a number of enamel-covered dentine blisters. This edge is crudely undulose, and additions following this pattern result in radial ridges. Behind the growing edge, bone was formed in the depressions and a mixture of bone and dentine was formed in the ridges. As growth proceeded outwards, the bone in the ridges resorbed in patches and the resorbed spaces filled with hypermineralized pleromic dentine. (The terms are used in the sense defined in the glossary provided by Campbell & Smith (1987).) These patches are not continuous along the ridges, but are concentrated in the first instance in discrete areas thus forming tubercles that can be seen even in the differentiated marginal strip of bone + dentine.

Gradually the intervening spaces were also intergrown by pleromic dentine and the whole surface became hard and uniform. This accounts for the increasing smoothness of the plate away from the growing margin.

The lateral posterior and mesial edges were not sites of much growth (figures 7a,b, 8, 9 and 14a,b). They rarely show any marginal dentine blisters. In fact, as the plate increased in size by anterolateral growth, the other edges were remodelled by resorption. This has been described for *Chirodipterus australis* particularly, but *Sorbitorhynchus* does not show the reparative dentine blisters recorded in that species. Instead it merely shows ragged edges where resorption has taken place.

(x) *Gulars and submandibulars*

These are well preserved, most of the bones still being in position on the specimen before etching (figure 18a). The mandible also shows areas of overlap by the submandibular bones, particularly on the right side, and this has helped to make the reconstructions accurate. This is the most complete series of sub-branchial bones known for any Early Devonian species. *Speonesydrion* has the gular and a few other fragments preserved, but the main part of the reconstruction given by Campbell & Barwick (1984) is based on embayments in the margins of the mandible. Consequently, the value of this new specimen for checking such a reconstruction, is considerable.

The *principal gulars* are large, and in outline they are as wide as long. This could have been predicted from the shape of the mandible (figure 18a). The surfaces of both plates carry well-developed concentric Westoll lines, which were partially destroyed on the left one during preservation. On the surface is a weak, short pit line. The anterolateral edge of the principal gular has a wide overlap area that is covered in part by the *principal submandibular* and the adjacent *postmandibular* (see Campbell & Barwick 1984, figure 26). A small *median gular* has a tiny central area with cosmine, and this is completely surrounded by wide overlap areas which are covered by the gulars behind and the principal submandibulars in front. These latter bones are irregularly polygonal in shape, and are also covered with cosmine showing concentric Westoll lines. Medially, between the principal submandibulars and the edge of the mandible, is a *median submandibular* of moderate size. This bone carries concentric Westoll lines and laterally overlaps the two principal submandibulars. Its anterior edge has a narrow flange that is not covered with cosmine, and this abuts a similar edge on the mandible. The principal submandibular itself is in contact with the mandible for a great part of its length, but near its posterior end it is overlapped by two much smaller bones, the anterior one being the *lateral submandibular* and the posterior one the *postmandibular*. The more anterior one is not preserved on either side but, judging from the overlaps and the adjacent margin of the mandible, it must have been a more or less triangular structure as reconstructed on figure 18a. The more posterior bone is preserved and has a distorted quadrangular outline, and it also makes an embayment in the edge of the mandible. Its

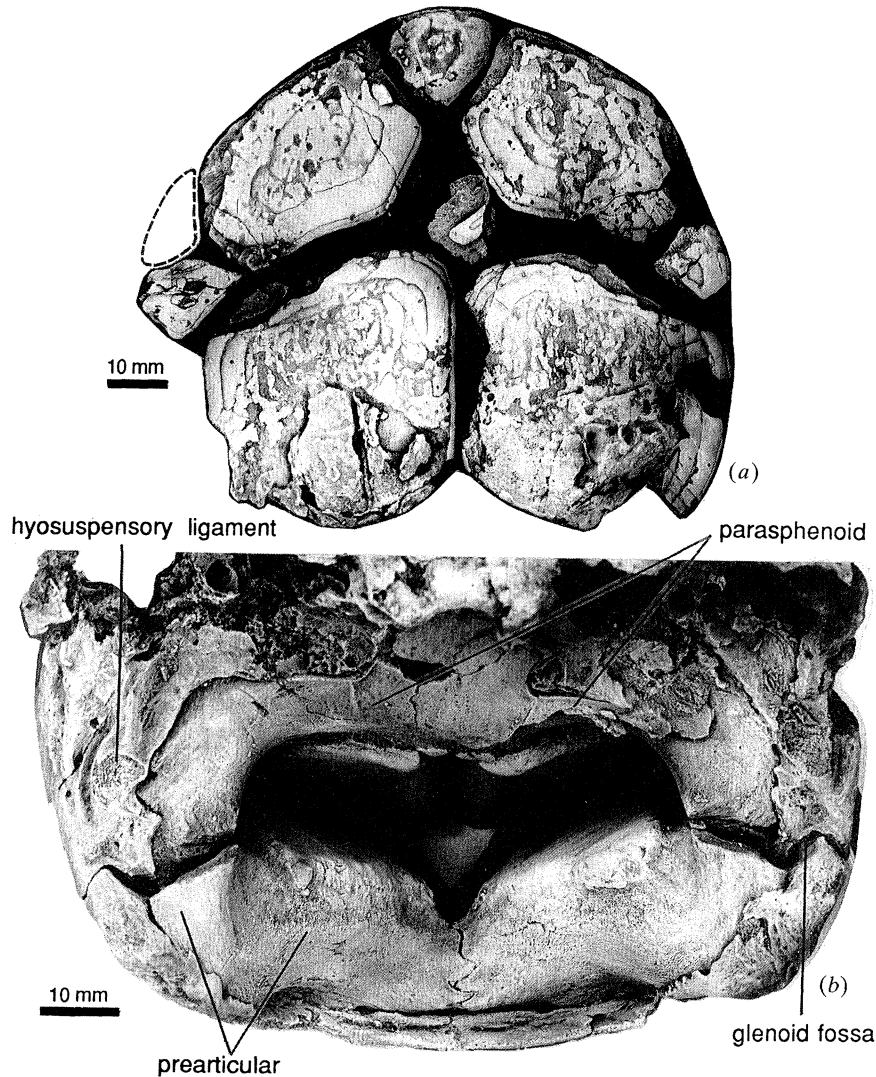


Figure 18. (a) Reassembled gular and submandibular bones of the holotype of *Sorbitorhynchus deleaskitus*. The outline of the missing lateral submandibular is drawn in on the right side of the specimen. (b) Posterior view of part of the articulated skull and mandible of same.

surface is covered with cosmine that carries concentric Westoll lines.

Whereas the Early Devonian genera *Speonesydrion* and *Sorbitorhynchus* both had lateral and posterior submandibulars, only one of the Middle or Late Devonian genera in which the sub-branchial plates are known, namely *Dipterus*, *Iowadipterus*, *Scaumenacia*, *Chirodipterus* or *Griphognathus*, has both these plates. That is the Givetian (late Middle Devonian) genus *Iowadipterus* Schultze (1992). It is probable, therefore, that the joint occurrence of these plates is a primitive dipnoan character.

Between the gular and the clavicle are a couple of small plates that were preserved on the right side. A number of small cosmine-covered plates were also found associated with the posterolateral part of the mandible. All are cosmine-covered and some of them carry a lateral line. They must have been some of the series that covered the naked part of the mandible and carried the mandibular lateral line down from the

cheek, as is normal for Devonian dipnoans (Miles 1977, figures 112 and 117).

(xi) *Pectoral girdle*

The cleithrum of the right side of the specimen is partly preserved, along with an incomplete anocleithrum and the almost complete interclavicle (figure 19*f-i,k*).

The cleithrum has a gently concave outer surface, most of which has been destroyed. Apart from a small patch of cosmine on the posterodorsal edge, the remainder of the preserved surface is formed of dense bone with numerous more or less equidimensional perforations. The inner surface is composed of dense imperforate bone. Between the two layers there are numerous struts that have the superficial appearance of endochondral rather than dermal bone. Presumably the space was occupied by very coarse bone vesicles. Too small a part of the branchial lamina is preserved to permit any useful statements to be made.

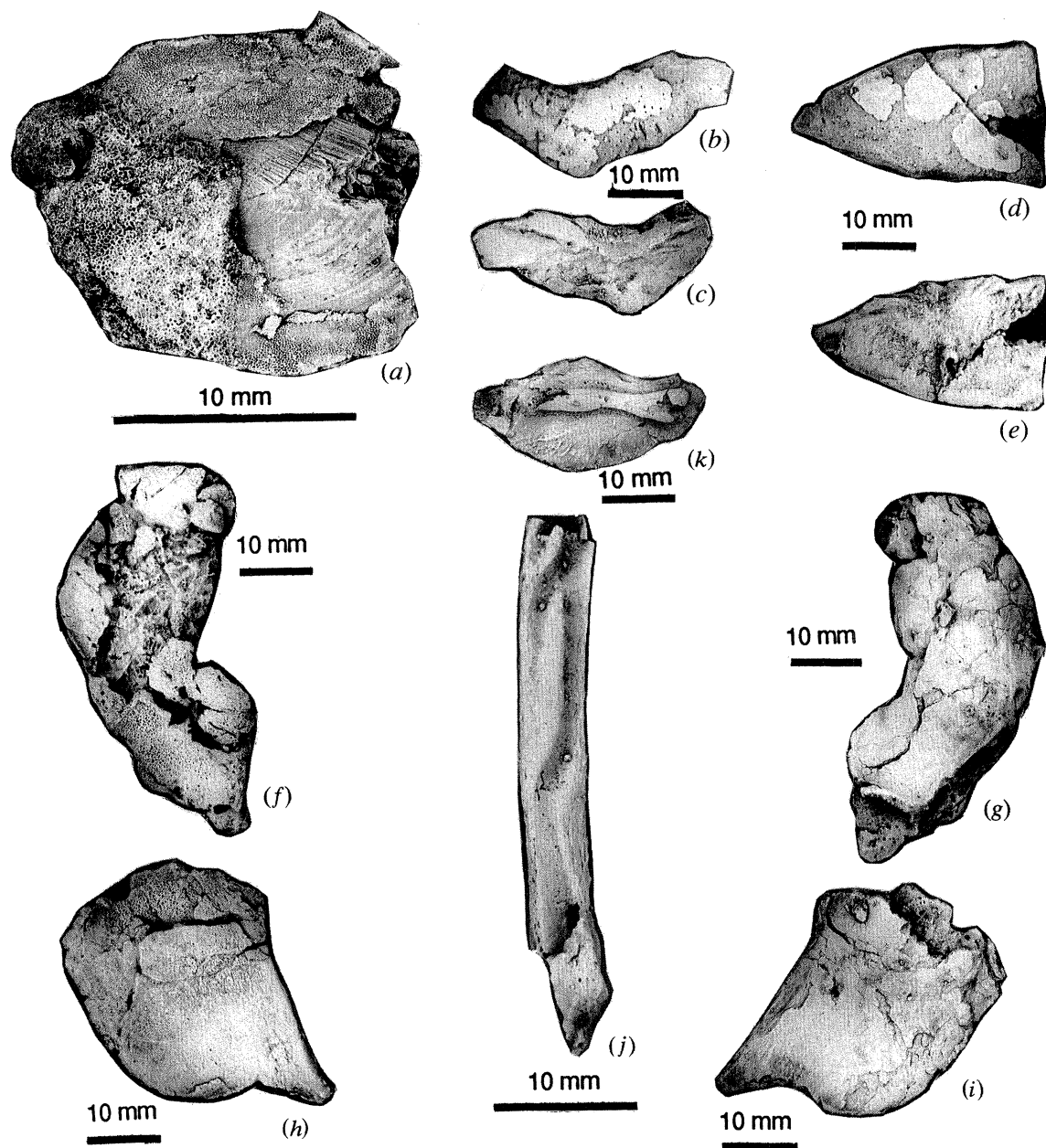


Figure 19. (a) Scale of *Sorbitorhynchus deleaskitus* to show the fine bone overlying denser bone with growth laminae. (b-c) Dorsal and ventral views of an incomplete bone 'A'. (d-e) Dorsal and ventral views of bone 'Z'. (f-g) External and internal views of an incomplete right cleithrum. (h-i) External and internal views of the anterior end of an incomplete anocleithrum or possibly the ventral end of the clavicle. (j) Fragment of a ceratobranchial showing grooves for the vascular vessels. (k) Interclavicle in ventral view.

What is taken to be the anterior end of the anocleithrum is preserved, and even that is broken around the edges. At first we thought that this fragment was part of the clavicle, but the absence of a clearly defined branchial lamina, and its size relative to the cleithrum, gave us pause. The material is too poor to warrant detailed description. As the figure shows there is a broad body with a short triangular process at one end.

The interclavicle (figure 19k) consists of solid bone and shows overlaps all round. Along its axis is a ridge of fine spongy bone covered with cosmine. The spongy bone extends almost to each end of the element, and

the cosmine may have had a similar extent before weathering. Most of the element including all the overlaps, is made of dense bone. There is no coarse vesicular core as in the other girdle bones.

(xii) Scales

Five or six imperfect scales up to 25 mm in diameter have been preserved (figure 6a). These must all come from the front part of the body, but it is not known if they are dorsal, ventral or lateral. In form they are cycloid rather than rhombic, and there is no articulatory peg. A large part consists of overlap; the exposed part is small and rhombic in outline, and consists of a

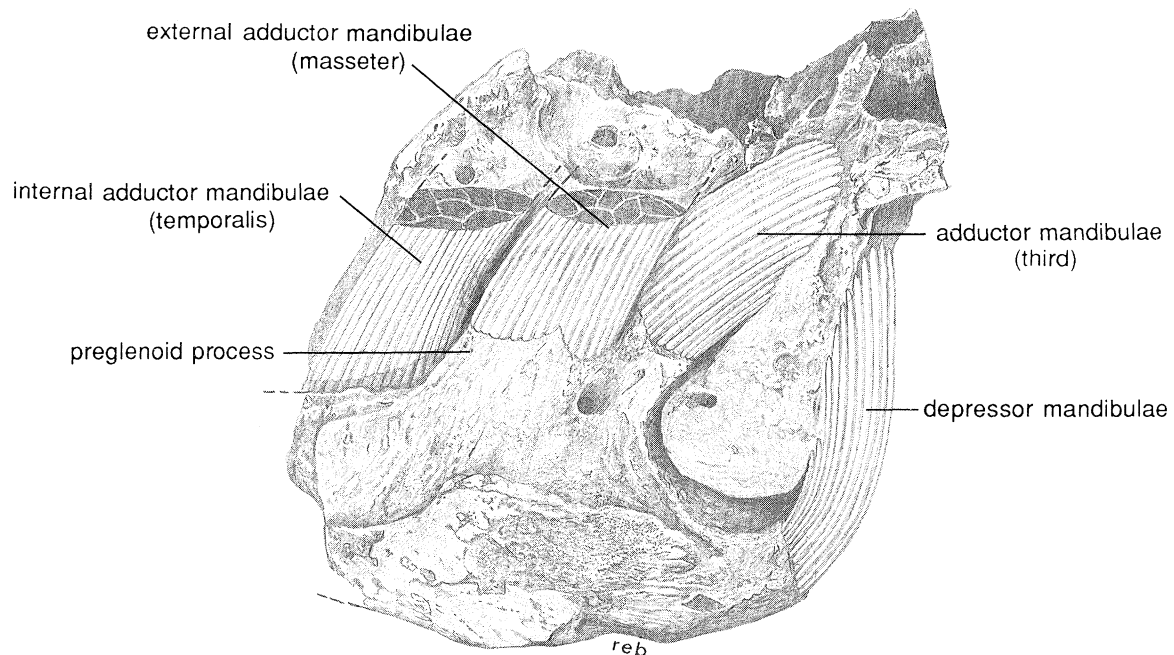


Figure 20. Inferred positions of the short adductor mandibulae and depressor mandibulae muscles anterior and posterior to the jaw articulation, represented in left lateral view.

thick layer of fine spongy bone on which cosmine is in places developed. The overlapped areas have a thin layer of finer spongy bone which is easily removed from the underlying dense bone.

The inner surface shows concentric rings on hard, dense tissue. Growth has taken place by marginal addition of layers of tissue, and one has the impression that successive layers do not underlie the previous ones to any great extent.

#### 4. FUNCTIONAL ASPECTS

##### (a) Feeding

This species shows several features that are interpreted in terms of unusual feeding methods. The first is the large cavity which, for reasons given below, Drapala, Barwick and Campbell (but not Wang) interpret as being for a soft pad, in the front of the lingual groove. They have considered the possibility that this is pathological because dental caries are known from other Palaeozoic dipnoans (Kemp 1991), but have decided against this interpretation because the margins show signs of being finished, rather than destructive, and the cavity is more or less symmetrical around the midline. No such structure is known in any other dipnoan, fossil or extant, and consequently we cannot assert that it is a normal dipnoan feature. Hence it is not possible to use that type of evidence to exclude the possibility that it is pathological. It has been suggested to us that it represents a deformity initiated early in the development of the individual, and this remains to be tested. The matter will be resolved only by the discovery of another specimen of this species.

As indicated previously, behind this cavity lies a triangular gap which forms the posterior part of the

lingual groove. This gap received the ends of the basihyal and hypohyals. The anchoring system of the hyoid arch, and the confinement of its front end by the wall of this space, preclude the possibility that the hyoid bones were protrusible into the anterior space. This suggests that a protrusible fleshy tongue pad did not occupy the space. If not, then a pad of soft tissue anchored to the floor seems to be a possible explanation. We speculate that, *inter alia*, such a pad could have been a chemosensory organ, an electric stunning organ, or a lure to attract vagile prey. Judging from the associated fauna such prey was present in the form of conodont animals and trilobites. We accept that there seems to be no way at present to choose between the above possibilities, but this scarcely matters. The real point is that all these options offer sophisticated means for getting prey into a position in front of the mouth, and that this occurs in an early Devonian dipnoan. Once the prey was so organized, it would have been sucked into the mouth by rapidly dropping the mandible and the hyoid arch. This matter is discussed in the following section.

The jaw articulation is quite remarkable for a primitive dental-plated form in that the mandible was capable of up-and-down movement only: that is, it was 'restrictive' in the sense of Bemis (1987*a,b*). This can be demonstrated by the specimen itself because the fit of the mandible to the skull is almost perfect. Such an arrangement means that the dental plates, which were in contact at only a couple of points around the margins even at full occlusion, were able to do little more than crush large prey in the crudest manner. Unlike even the most primitive tooth-plated genera, such as *Speonesydrion*, which were 'unrestrictive', it was incapable of more refined reduction of food by passing it across the short tooth rows around

the plate edges where the teeth could slip down the sides of the teeth on the opposing plates and into adjacent pits, thus cutting and grinding food more finely. A variety of jaw movements and a variety of outcomes for reducing food are apparent even in advanced ceratodont forms such as the extant *Neoceratodus* (Kemp 1987), but these depend on the presence of the bladed distal tooth rows as well as the flat plated proximal surfaces of such teeth. In this respect *Sorbitorhynchus* is like *Dipnorhynchus*. The animal would have been able to cope with hard-shelled invertebrates as well as softer material such as infaunal worms and such relatively soft forms as trilobites. With brachiopods and molluscs, the edible parts would have been extracted by suction after crushing, and the indigestible parts ejected.

As figures 4a and 6a show, the dorsolateral cristae of the neurocranium are aligned in such a way as to suggest that the *adductores mandibulae* did not occupy the whole of the *temporalis* chamber. This is not surprising in view of the peculiar orientation of the neurocranium in that region, and the large size of the *masseter* chamber. In this genus the orientation of the jaw articulation with respect to the posterior wall of the neurocranium is such that the masseter chamber must be enlarged with respect to the *temporalis*. (Note that, following Miles (1977, p. 72), we use the terms *masseter* and *temporalis fossae* for the chambers into which the external and internal adductor muscles were attached respectively. We do not imply homology with mammalian muscles.)

We also draw attention to the fact that muscles attached to the back of the preglenoid process and the front of the quadrate were apparently well-developed. They were clearly present in *Pillararhynchus*, which also has a strong preglenoid process. Such short muscles would have exerted a powerful force as the mandible approached closure, and this supports our view that the genus had an unusually strong crushing bite. These muscle insertions have not been recorded in other Devonian genera without a large process, but our examination of *Chirodipterus australis*, *Dipnorhynchus sussmilchi* and *D. kurikae*, shows that muscle scars are also apparently present in the same position on their quadrates. Two of our specimens of *C. australis* have unusually well-developed preglenoid processes and on them the muscle scars are obvious. Presumably muscles were attached to the preglenoid processes of all the dentine-plated genera, even if the area available was very small. This implies that these muscles were a primitive feature, either of the Dipnoi or of the group with crushing dental plates, a point that does not seem to have been recognised previously. Bemis & Lauder (1986) and Bemis (1987a) have recorded the presence of powerful *retractor angularis oris* muscles, both *superficialis* and *profundus*, that insert on the posterior face of the preglenoid process in the extant *Protopterus aethiopicus* and *Lepidosiren paradoxa*, but not in *Neoceratodus forsteri*. In those species these muscles are long relative to the size of the head of the animal, and they exert a powerful force on the closing mandible during the early phase of the bite. The inferred shortness of the muscles attached to the back

of the preglenoid process in *Sorbitorhynchus* suggests that they would have exerted maximum force only as the mandible approached closure, i.e. late in the bite. As the retractor *angularis oris* muscles are not present in *Neoceratodus* (Bemis 1987a), the most primitive of the extant genera, it seems likely that they originated in the *Protopterus-Lepidosiren* lineage. In these circumstances, the muscles in this position in *Sorbitorhynchus* would not be the homologues of the *retractor angularis oris* but rather a third set of *adductores mandibulae*.

Finally, we note the importance of the area of muscle attachment on the posterior surface of the quadrate immediately above the articulation (figures 5 and 7b). This is interpreted as being the origin of a short muscle that inserted on the short retroarticular process of the mandible, and served as a *depressor mandibulae*. Such an arrangement is not recorded in any other Devonian dipnoan so far as we know, though members of the *Griphognathus-Soederberghia* group have a long retroarticular process and *Griphognathus whitei* shows a slight depression on the back of the quadrate that could indicate the presence of a muscle in that position. These genera are not closely related to *Sorbitorhynchus* but they share the same kind of jaw articulation. Examination of well-preserved specimens of *Chirodipterus australis* indicates that depressions are present in appropriate places on both the back of the quadrate and the articular suggesting that the postulated muscle was a normal feature in primitive dipnoans. In the extant *Lepidosiren paradoxa* and *Protopterus aethiopicus*, Bemis & Lauder (1986) have observed a muscle, referred to as a *depressor mandibulae*, inserted on the retroarticular process, but originating on the mesial face of the opercular. This muscle is not present in *Neoceratodus*, which is regarded as the most primitive of the extant genera. In view of its different origin, and its absence from *Neoceratodus*, it is unlikely that the muscle in the Devonian genera is the homologue of the *depressor mandibulae* in the extant genera.

#### (b) Suction

The negative pressure in the buccal cavity of living lungfishes is produced by movements of the hyoid arch, the pectoral girdles, and the operculars (Bishop & Foxon 1968; Bemis & Lauder 1986; Bemis 1987a). In *Sorbitorhynchus* the hyoid arch forms a well-ossified and well-articulated system moved by a set of strong muscles, judging from the strength of their attachment to the bones. The short, stubby basihyal shows no sign of denticulate plates on its buccal surface, and the preservation is good enough to reveal them if they had been present. Moreover, the absence of denticulation on the palate indicates that such plates would not have been present. As noted above, the hypohyals were not only well articulated with the basihyal; they also had a ligament or a muscle attachment on the ventral side holding them together and firmly clamping them to the side of the basihyal. As indicated above no such structure has been observed on *Griphognathus*, in which all these bones are well preserved, although it is present in a less well-developed form in

*C. australis* and *Pilliararhynchus longi*. Thus we conclude that it is related to some distinctive function of forms with crushing dentition.

From these details we have concluded that the hyoid arch was subjected to rapid and strong muscle contractions, and that these may have been associated with food capture. Bemis (1987*a,b*) and Bemis & Lauder (1986) have studied the roles of the various muscle systems used to raise and lower the hyoid arch in the extant dipnoan genera. These fall into the following groups:

hyoid raising:	<i>intermandibularis</i> <i>interhyoideus</i> & <i>constrictor hyoideus</i> <i>levator hyoideus</i>
hyoid depressing:	<i>rectus cervicus</i> ( <i>sternohyoideus</i> ) Other hypaxials.

Of these the *intermandibularis* muscles and the hypaxials are not directly attached to the hyoid arch, but function indirectly by constricting the surrounding tissues.

In the living dipnoans the ceratohyal and the mandible are coupled by the mandibulohyoid ligament which runs from the posterior part of the ceratohyal to the posterior process of the mandible. Dropping of the hyoid arch produces a backwards pull on the mandible which is thus depressed (Bemis & Lauder 1986; Bemis 1987*a*). In *Sorbitorhynchus* this mechanism would have been minimally effective for two reasons.

1. No scar on the ceratohyal is in a position to permit the attachment of a ligament to the posterior process of the mandible. The scar that could possibly be for a mandibulohyoid ligament is on the ridge below the *levator hyoideus* scar, and is placed so that the ligament would have attached to the mandible below the articulation thus giving it poor leverage.

2. Of greater significance is the fact that the mandible is such a massive structure that its moment of inertia would have prevented the effective operation of such a ligament in functioning to open the mandible.

The second of these objections applies equally well to such genera as *Dipnorhynchus* and *Speonesydrion*, but the ceratohyal in these genera remains unknown. Consequently we do not accept the view that this ligament was an effective structure operating during the early phases of jaw opening in all teleostomes, including the dipnoans (Lauder 1980).

For the hyoid arch to be dropped rapidly to produce suction the basihyal would have to be pulled backwards so that its anterior end was clear of the mandible. The ceratohyal has large attachment surfaces for *sternohyoideus* muscles which would have been the main ones involved in this process. The return of the hyoid arch to its resting position would still require considerable force. This would have been partly accomplished by the contraction of the *intermandibularis* and *interhyoideus* muscles, but also by the *levator hyoideus* which, as we have seen, were all well developed. Rotational movements as well as others in

a vertical plane must have taken place with great speed if the action was to be effective, and great stress would have been placed on the ceratohyal–hypohyal–basihyal junctions. Hence it is not surprising that these were somewhat expanded and rimmed with thickened bone, and that a special ligament or muscle was present binding the two hypohyals together below the anterior end of the basihyal.

## 5. PHYLOGENETIC POSITION OF THE GENUS

We have previously attempted (Campbell & Barwick 1990) to outline a non-cladistic approach to the phylogeny of Palaeozoic dipnoans, using functional morphological complexes to define evolving lineages. Such a method produces a division in the group from the time it first appeared in the Early Devonian. The two groups are recognized primarily by the nature of their dentition, the structure of the hyoid arch, and the form of the pectoral girdle. The group to which *Sorbitorhynchus* belongs is the one that crushed its food between thick dental plates. Within that group it is a member of the subgroup that made its dental plates by marginal addition of dentine blisters rather than well-formed teeth (Smith & Campbell 1987). This subgroup was referred to as dentine plated rather than tooth plated. Given this background, we consider that *Sorbitorhynchus* shows a unique mixture of primitive and advanced characters.

The following are regarded as primitive for the Dipnoi as a whole: (i) the great breadth of the skull posteriorly, similar to that of *Dipnorhynchus* and *Uranolophus*; (ii) the large bone 'J' with a strong lateral line canal; (iii) the number of small bones in the snout; (iv) cosmine on the external dermal bones; (v) the massive ossification of the whole skull; and (vi) the presence of both lateral submandibular and postmandibular bones.

The following are regarded as primitive for the dentine plated group: (vii) the thick relatively undifferentiated dental plates; (viii) the long medial symphysis of the mandible; (ix) the thick mandibular ramus; and (x) the ploughshare shape of the parasphenoid. †

† As indicated above, the ploughshare shape of the parasphenoid is present in early members of the dentine- and tooth-plated lineages because the bone is butted against the thickened ridge of the quadrate ramus of the pterygoid plates. All known members of the dentine-plated lineage have pterygoid ridges of this kind. Primitive tooth-plated forms also have the tooth-bearing parts of their plates close to the midline, and hence the parasphenoid is thick anteriorly. Although isolated parasphenoids of this kind are hard to find, an excellent example has been illustrated for the Upper Devonian *Andreyevichthys* by Krupina (1987, figure 2). With further evolution the tooth-bearing parts of the plates move laterally, and the parasphenoid articulates with the thin bone of the pterygoids. This condition is present in all three extant genera and is seen as far back as the early Carboniferous *Sagenodus* (personal observation). *Uranolophus*, *Griphognathus* and *Soederberghia*, members of the denticulated lineage, all had thin pterygoids and hence their parasphenoids are thin from the beginning. Only in *Holodipterus*, which secondarily developed a marginal bite, did the parasphenoid become thick in front to meet the ridge on the quadrate ramus of the pterygoid, and even then the mode of thickening is distinctive as we will show in a forthcoming paper.

The following are regarded as advanced relative to other Devonian dipnoans: (xi) the lack of contact of 'P' bones behind 'B'; (xii) the position of 'K' in the 'X'-'L' series; (xiii) the reduction of the external dermal bones on the mandible from four to three; (xiv) the reduction of the suprameckelian vacuity; (xv) the development of a strong preglenoid process; (xvi) the shape and structure of the scales; and (xvii) the suture between the pterygoidal dental plates.

The following are considered to be advanced relative to other members of the dentine-plated group: (xviii) the absence of the buccohypophysial foramen; (xix) the absence of dermopalatines fused to the pterygoids; (xx) the absence of the spiracular recess; (xxi) the definition of the dental plates against the lingual furrow and the failure of the dentine to make a continuous sheet across the furrow; (xxii) the absence of a dorsal process (lateral palatal process) on the pterygoids; and (xxiii) the space for the soft body in the bone of the lingual furrow.

One character that is difficult to polarize at present is the scar on the hypohyal for the muscle or ligament that ran beneath the basihyal to bind the left and right hypohyals together. Hypohyals are not well known in any other Early Devonian genus, but we know that scars of the type described are present on the dentine plated *Chirodipterus australis* and *Pillarrhynchus longi* from the Upper Devonian at Gogo. Either they were primitive for dipnoans and have not been observed on members of the other lineages, or they were developed first in the early stages of the dentine plated lineage, for which they would therefore be primitive. An answer will be forthcoming only when the hypohyals of other Early Devonian dipnoans are discovered.

We place *Sorbitorhynchus* with the dentine-plated lineage because of its dental structure, the massive nature of the bones, and the shape of the space behind the dental plates of the mandible for the passage of the *levator hyoideus* muscles. It shares many features with *Pillarrhynchus* and *Chirodipterus*, including large flat areas of the dental plates without tuberosities, dermopalatines and anterior median plate not fused to the pterygoids, and strong grooves on the ceratohyal for the transmission of the efferent epibranchial artery, a feature not observed on any other Devonian groups (Campbell & Barwick 1990). With *Pillarrhynchus* it shares an almost occluded suprimeckelian vacuity, a long and high preglenoid process, a reduced number of infradentaries, and a glenoid fossa that restricts the lateral movement of the mandible. *Sorbitorhynchus* had already become more advanced than the much younger *Chirodipterus australis* in a number of features including the reduction of the number of dermal bones in the mandible, the reduction of the suprimeckelian vacuity, and the development of the large preglenoid process, all of which characters indicate that *Sorbitorhynchus* had not begun to evolve towards *Chirodipterus*, but along a line that led to *Pillarrhynchus*. It is more primitive than *Pillarrhynchus* in characters (i), (ii), (iv), (v) and (ix) above, and it is not more advanced in any known character. These two genera therefore fit comfortably in a small group

derived from a *Dipnorhynchus* - like form that evolved away from the *C. australis* line (Campbell & Barwick 1990). *Sorbitorhynchus* is the older and more primitive of the two.

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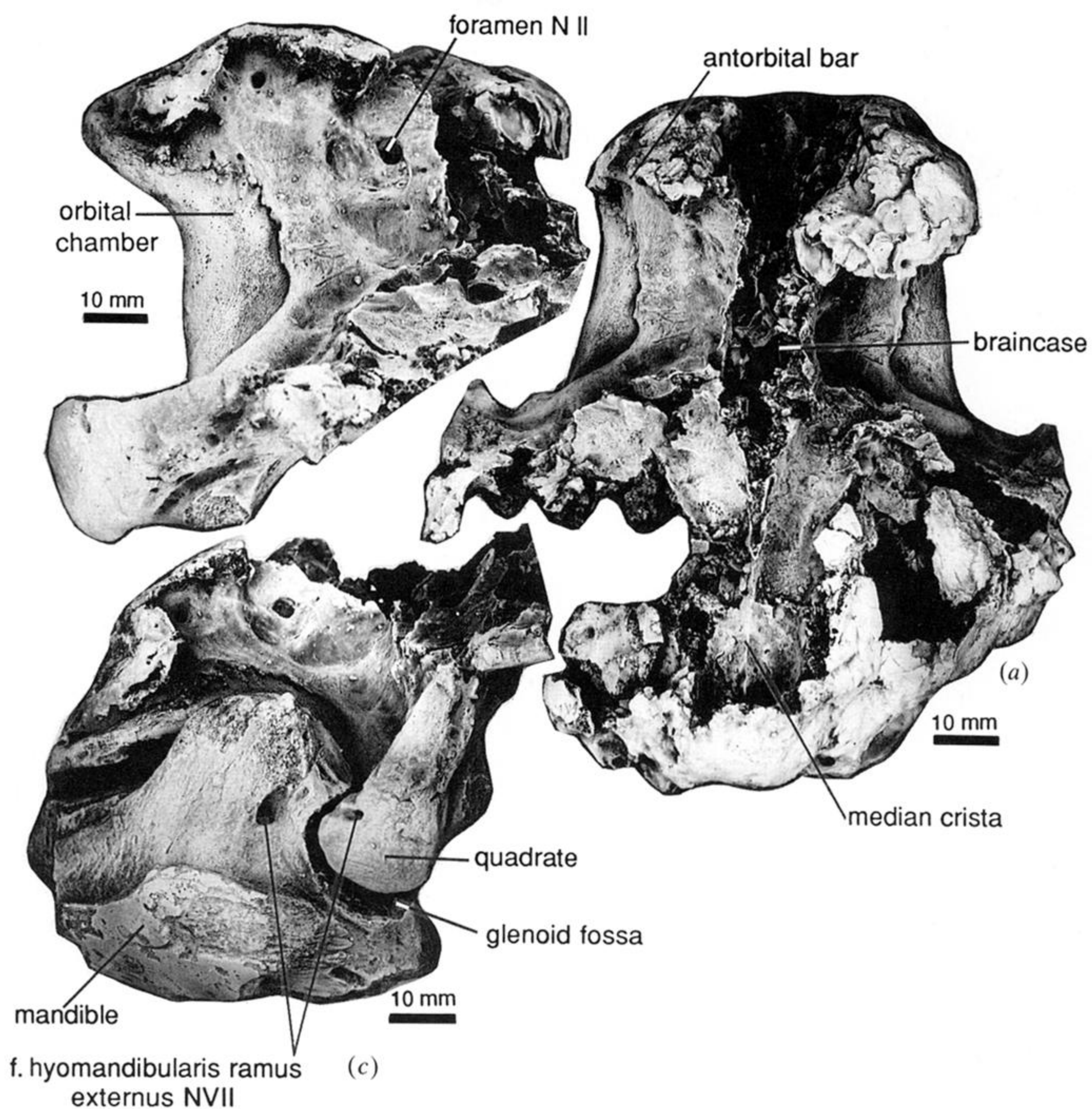


Figure 4. (a) Dorsal view of the holotype of *Sorbitorhynchus deleaskitus*. (b) Dorsolateral view of the left side of the orbital chamber of same to show form and foramina. (c) Left lateral view of the quadrate region and articulated mandible of same.

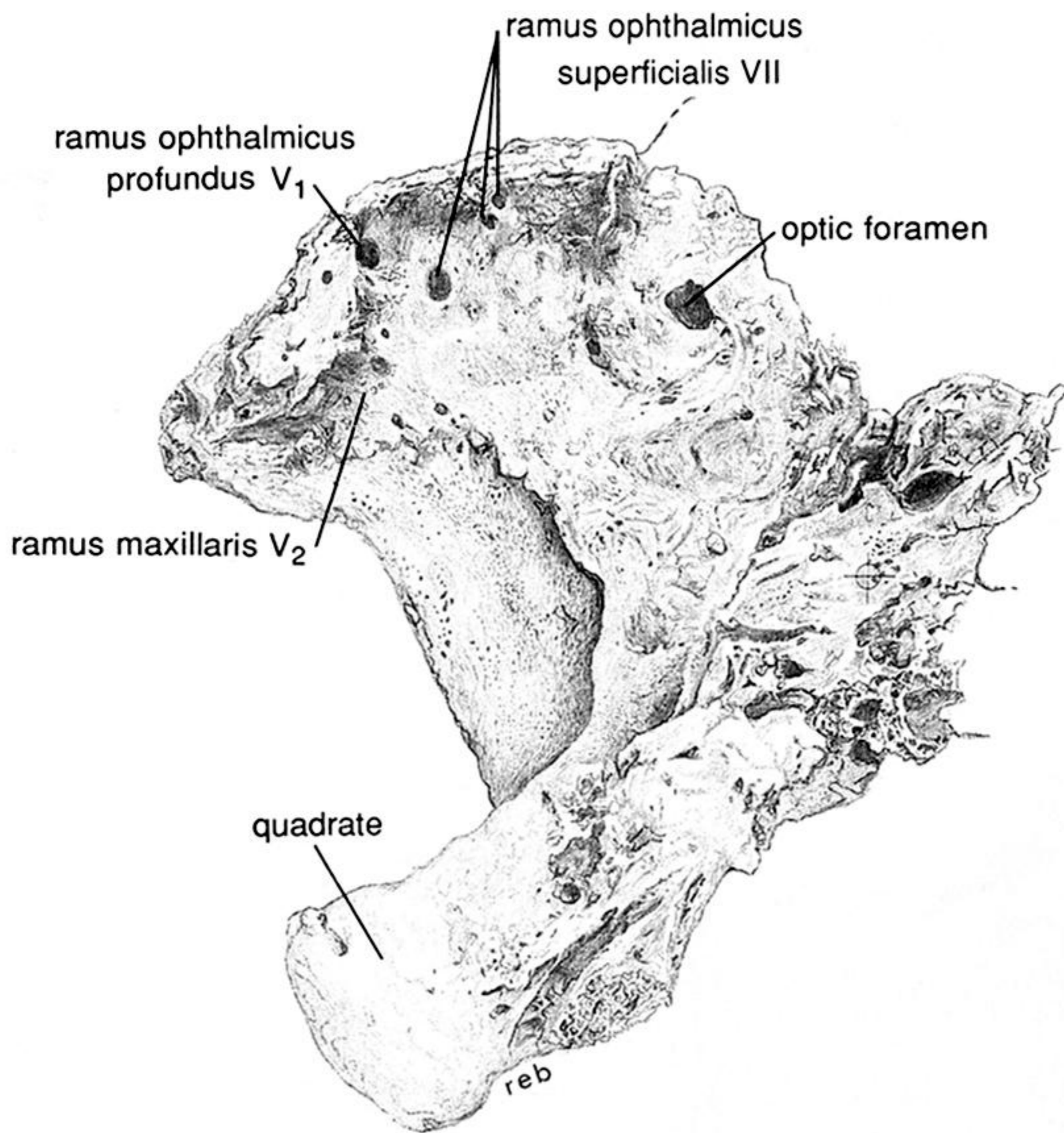


Figure 5. Drawing of the orbital chamber of the left side of the holotype of *Sorbitorhynchus deleaskitus* based on figure 4b.

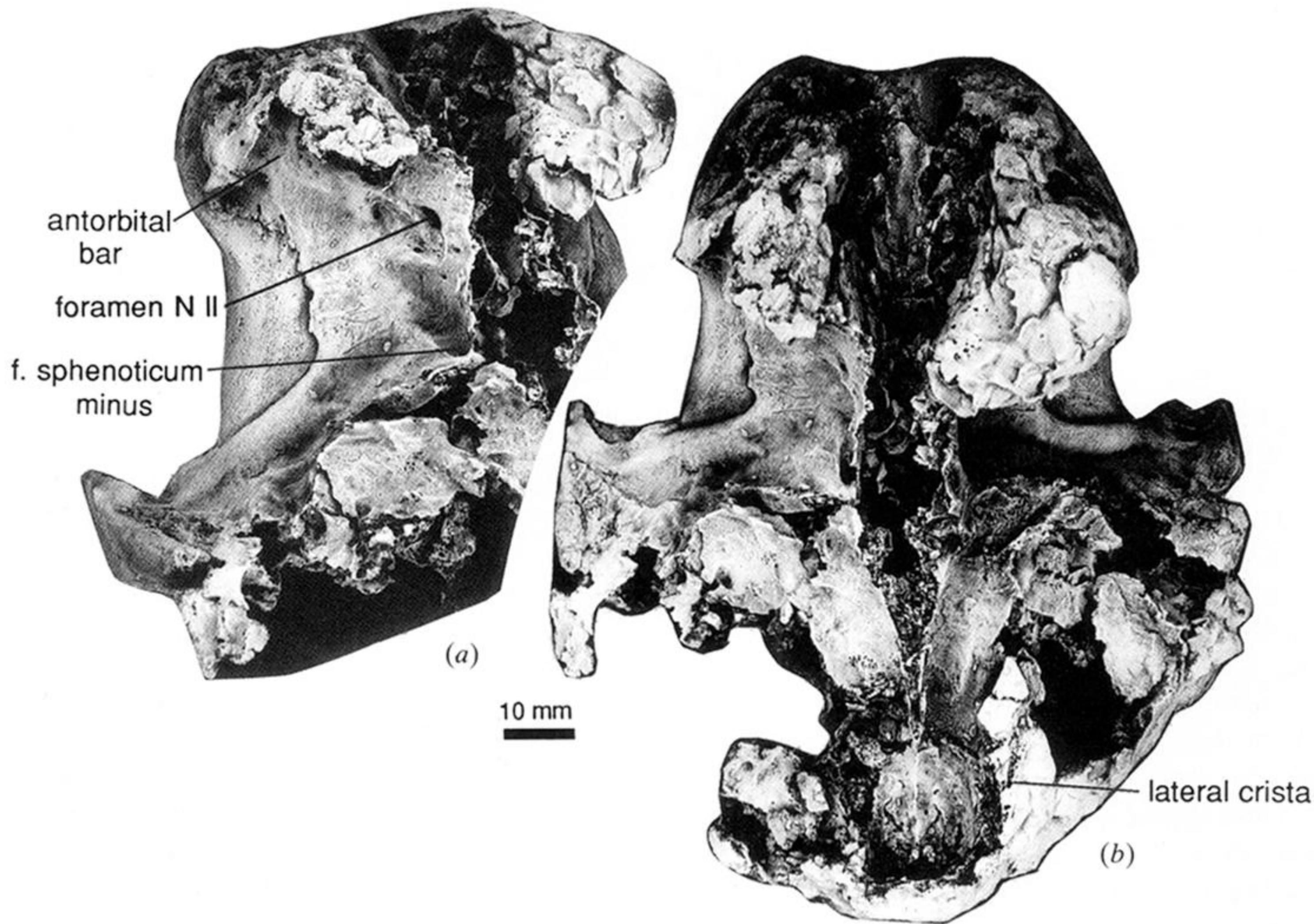


Figure 6. (a) Anterodorsal view of the skull of *Sorbitorhynchus deleaskitus* with the remnants of the roof removed. (b) Anterodorsal view of the left side of the orbital chamber of same showing the position of the nerve foramina.

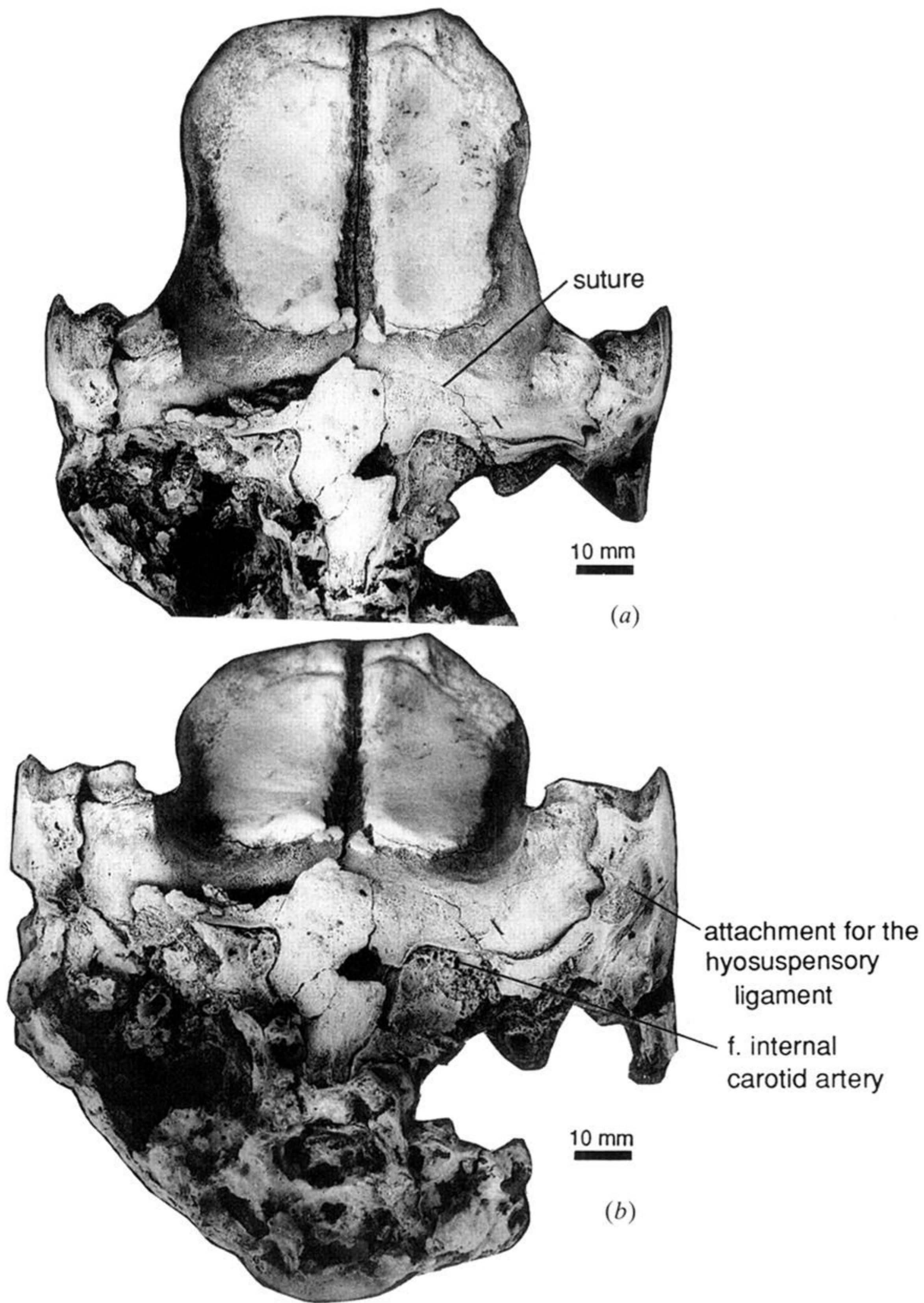


Figure 7. (a) Palatal view of the holotype of *Sorbitorhynchus deleaskitus*. (b) Posteroventral view of same showing the foramina and grooves on the back of the endocranium and the quadrate, with much of the endocranium destroyed by crushing.

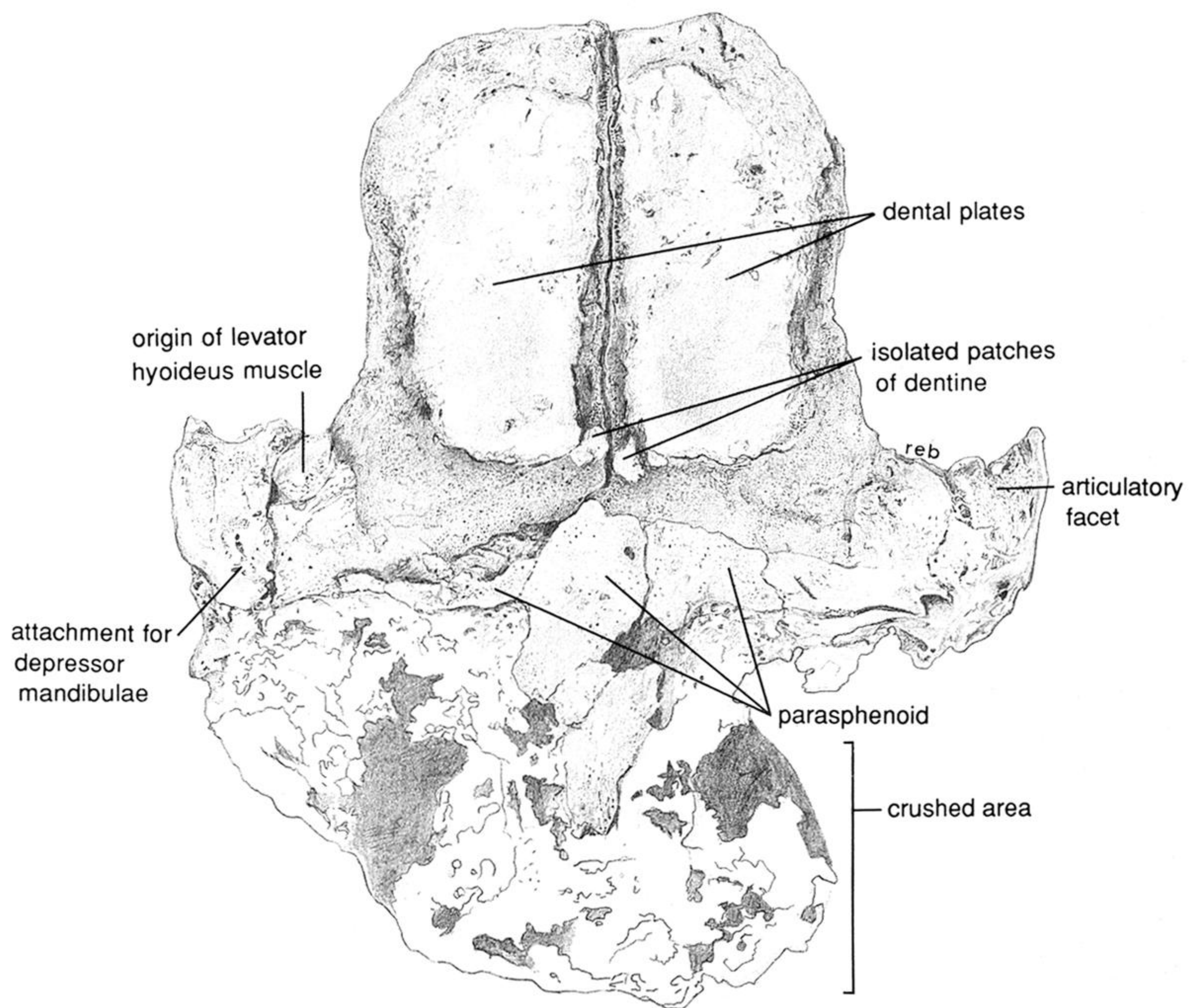


Figure 8. Drawing of the ventral aspect of the palate and articular surfaces of the holotype of *Sorbitorhynchus deleaskitus*.

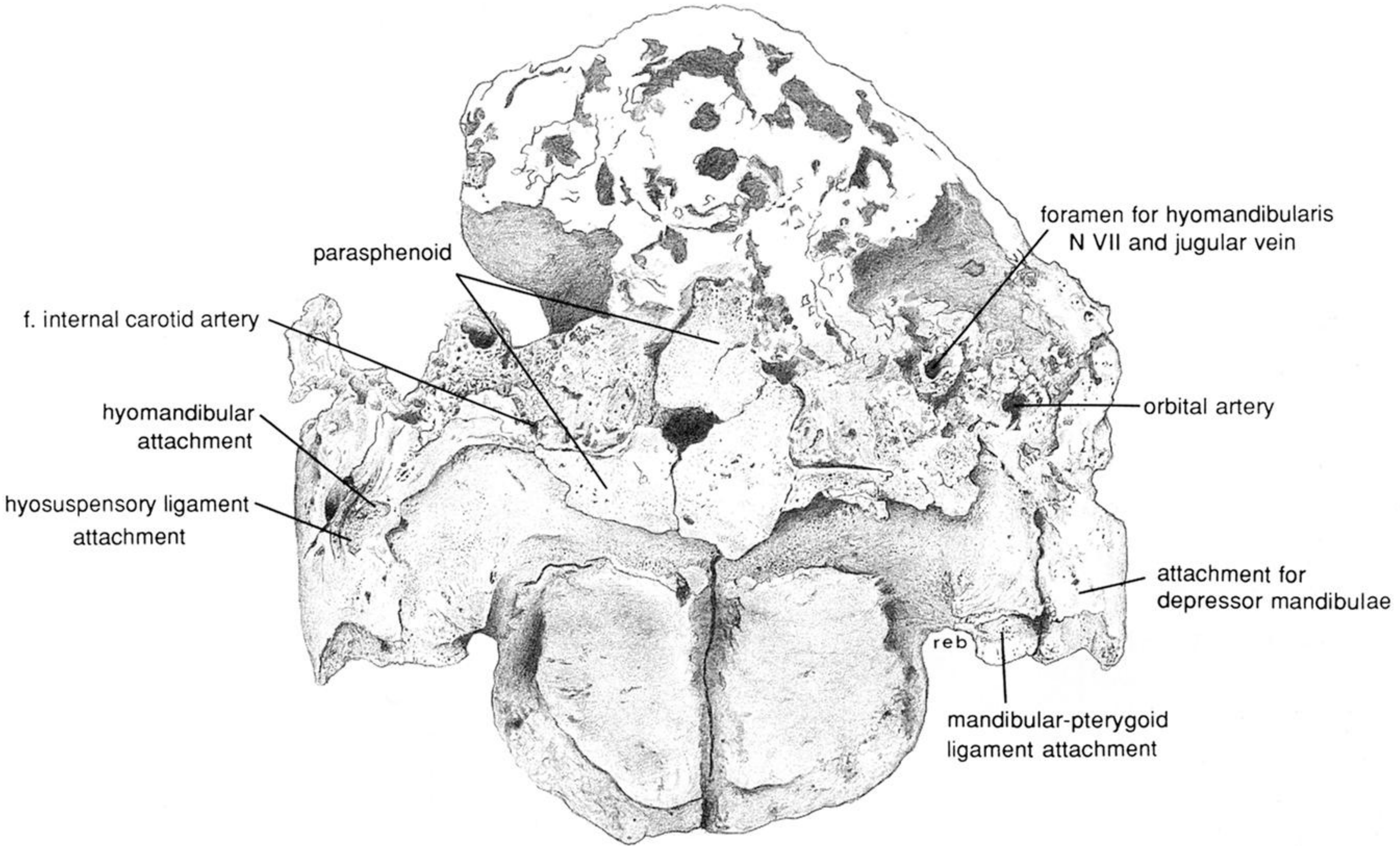


Figure 9. Drawing of the skull of the holotype of *Sorbitorhynchus deleaskitus* in posteroventral view.



Figure 10. (a) Dorsal view of the reassembled hyoid arch of the holotype of *Sorbitorhynchus deleaskitus*. The posterior part of the basihyal is not preserved. (b) The same in left dorsolateral view.

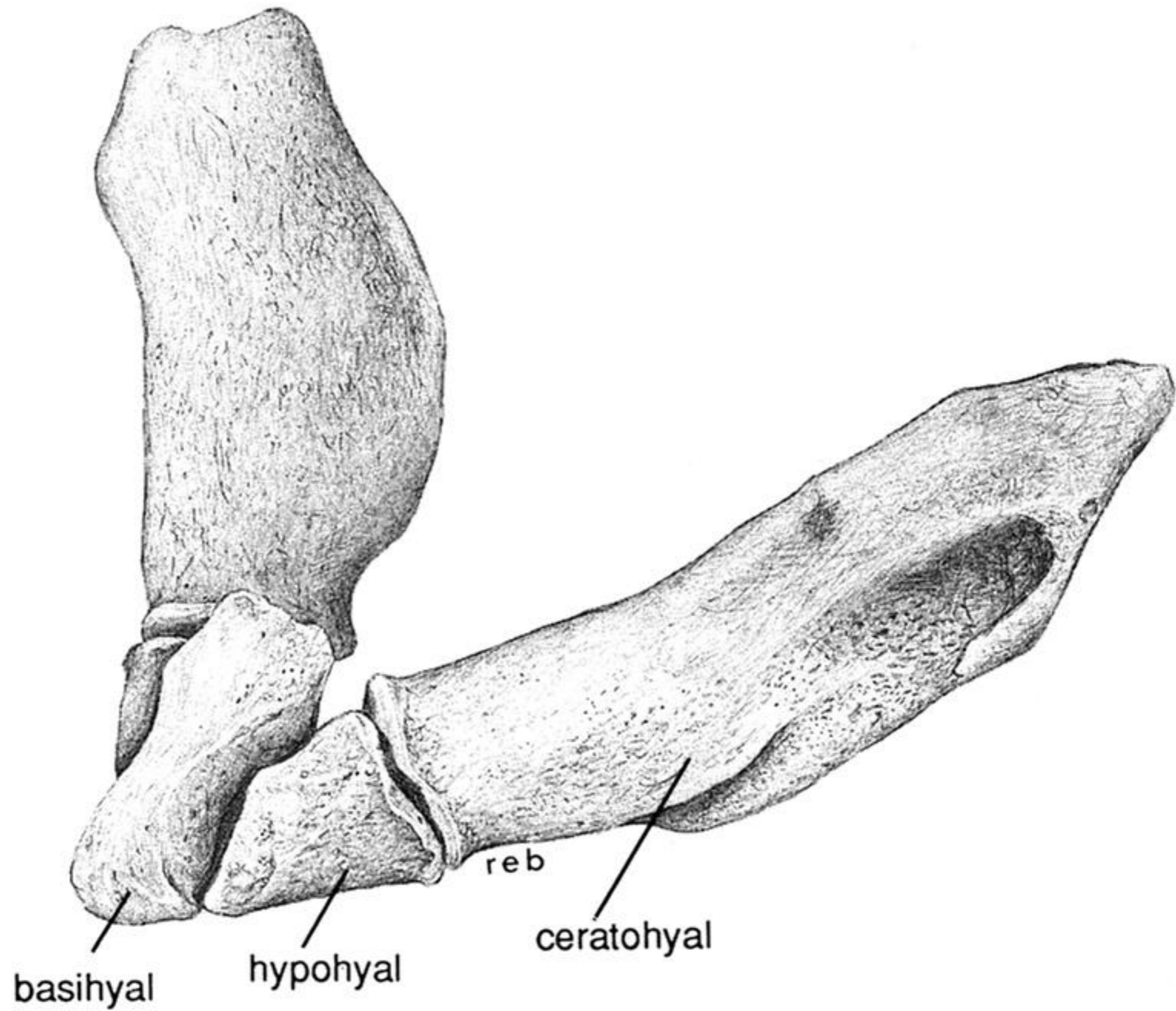


Figure 11. Drawing showing a restoration of the hyoid arch of *Sorbitorhynchus deleaskitus* in dorsolateral view as shown in figure 10*b*.



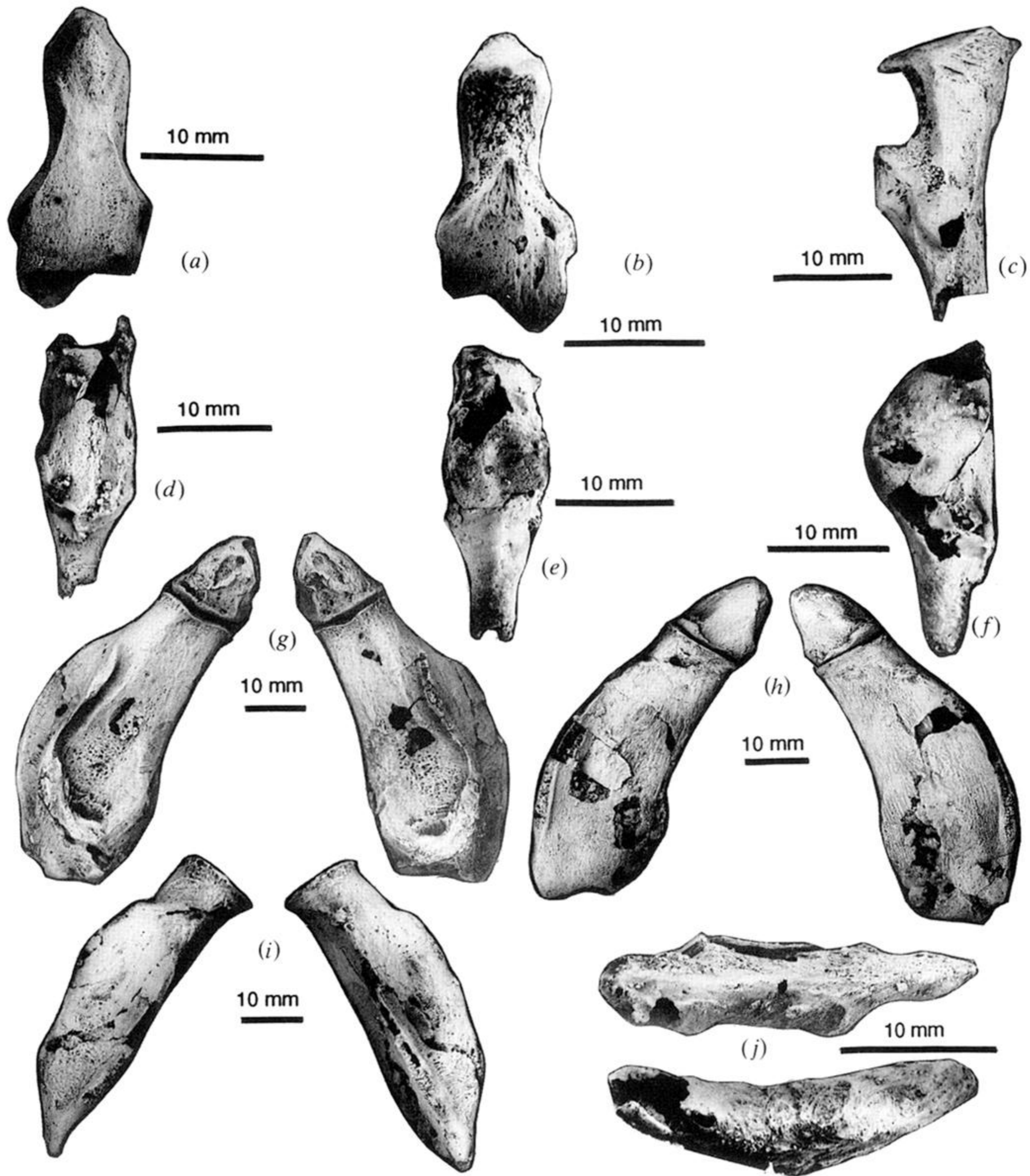


Figure 12. (a-c) Dorsal, ventral and left lateral views of the broken basihyal of *Sorbitorhynchus deleaskitus*. (d-f) Dorsal, ventral and left lateral views of the posterior basibranchial. (g) Ventrolateral views of the left and right ceratohyals and attached hypohyals. These specimens have been rotated so that the ventrolateral surfaces lie in the one plane. (h) Mesial surfaces of same rotated outwards so that these surfaces lie in the one plane. (i) Left and right ceratohyals in ventral view. (j) Urohyal in dorsal and ventral views.

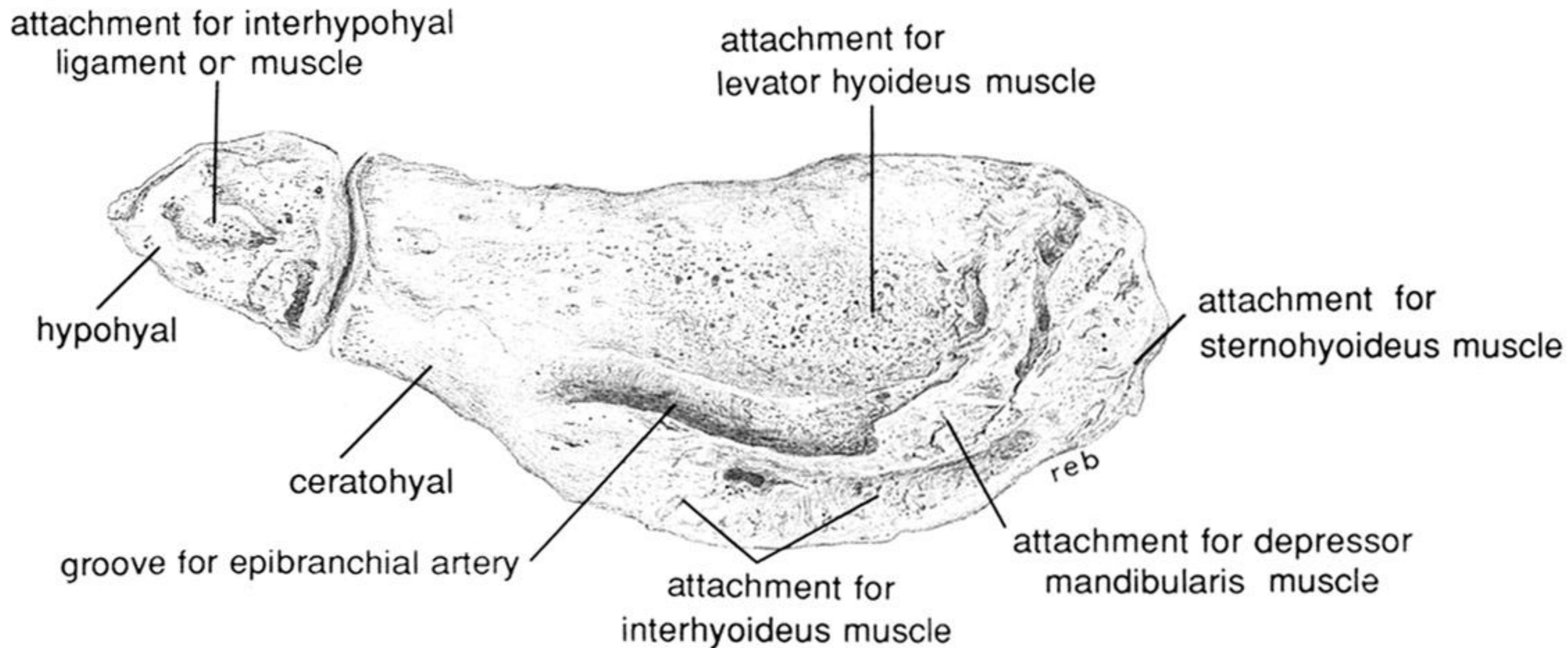


Figure 13. Restoration of left ceratohyal and hypohyal of *Sorbitorhynchus deleaskitus* in ventrolateral view to show the muscle attachments and the foramina.

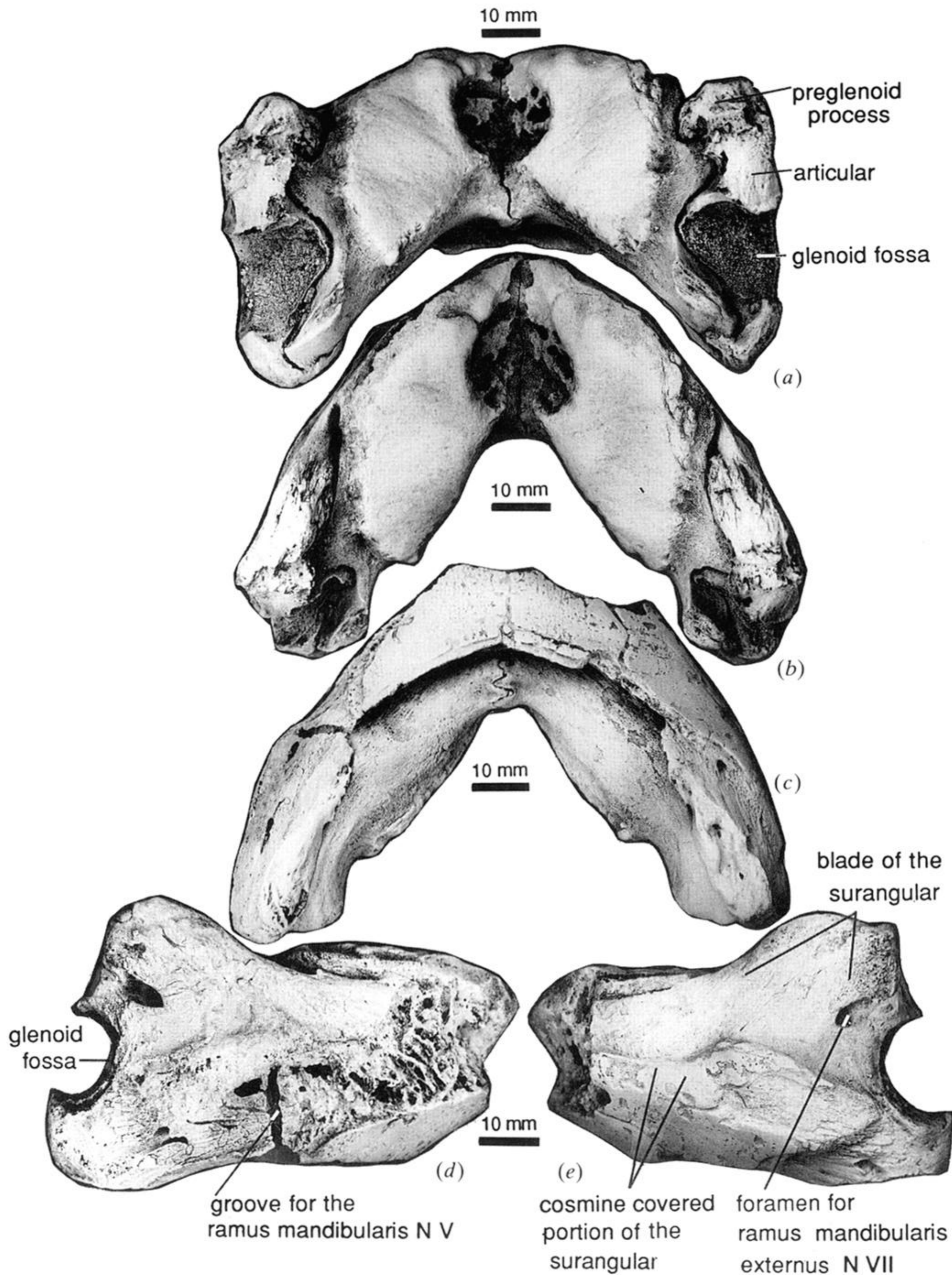


Figure 14. (a) Posterior view of the mandible of the holotype of *Sorbitorhynchus deleaskitus* showing the massive structure of all the bones. (b) Full dorsal view of the mandible showing the dental plates, the massive preglenoid process and the structure in the lingual furrow. (c–e) Ventral, right and left lateral views of the mandible.

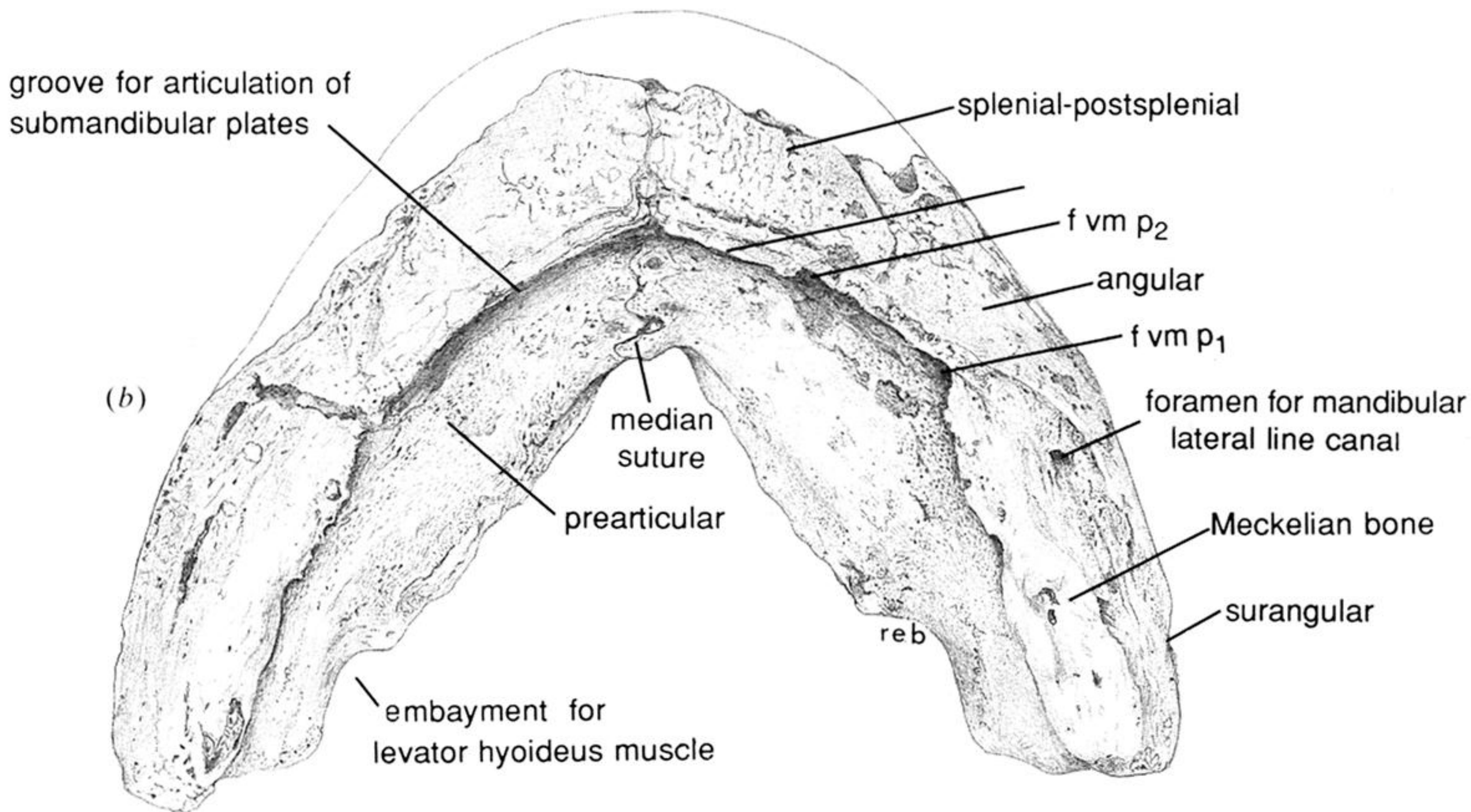
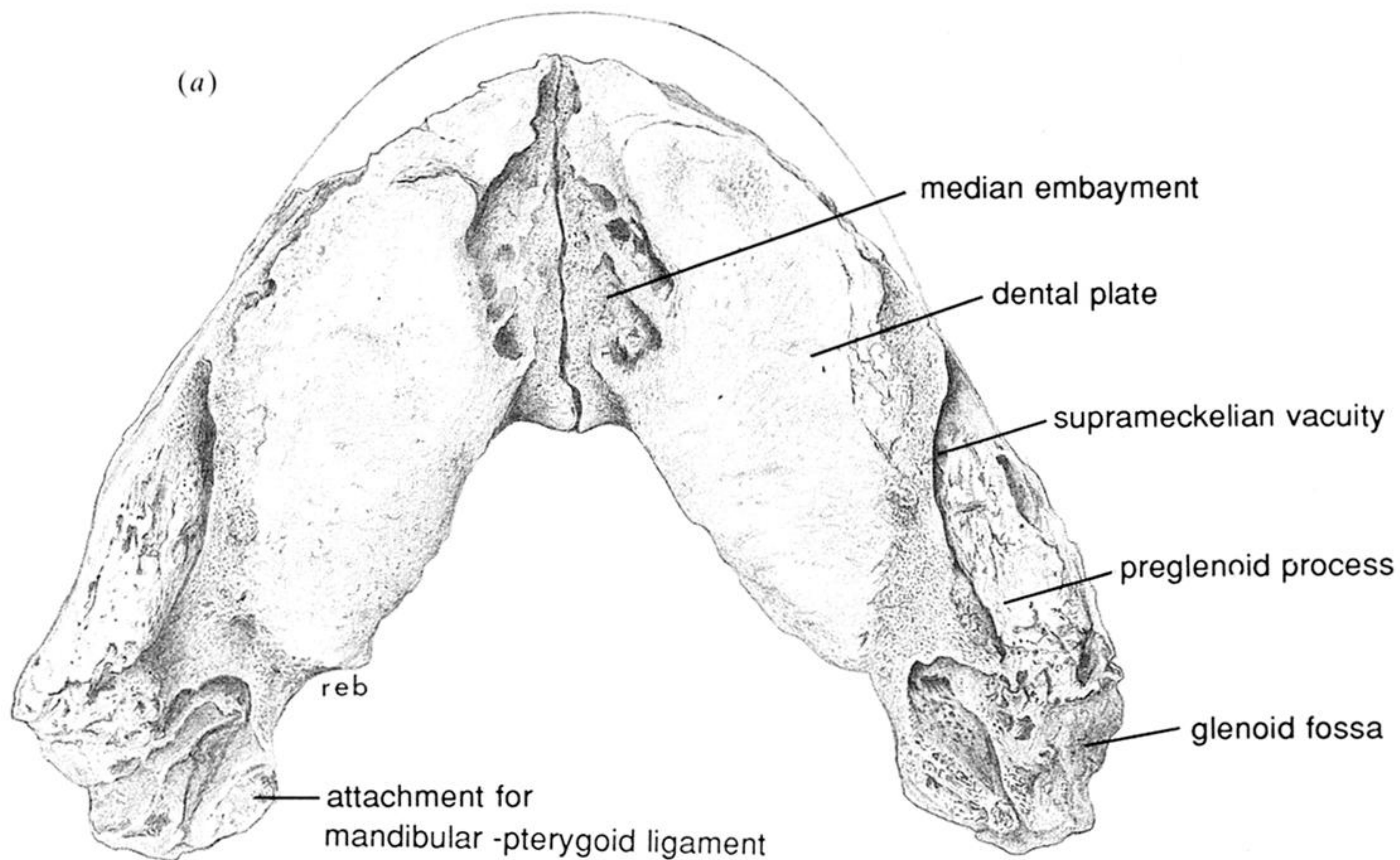


Figure 15. (a,b) Reconstructions of the mandible of *Sorbitorhynchus deleaskitus* in dorsal and ventral views.

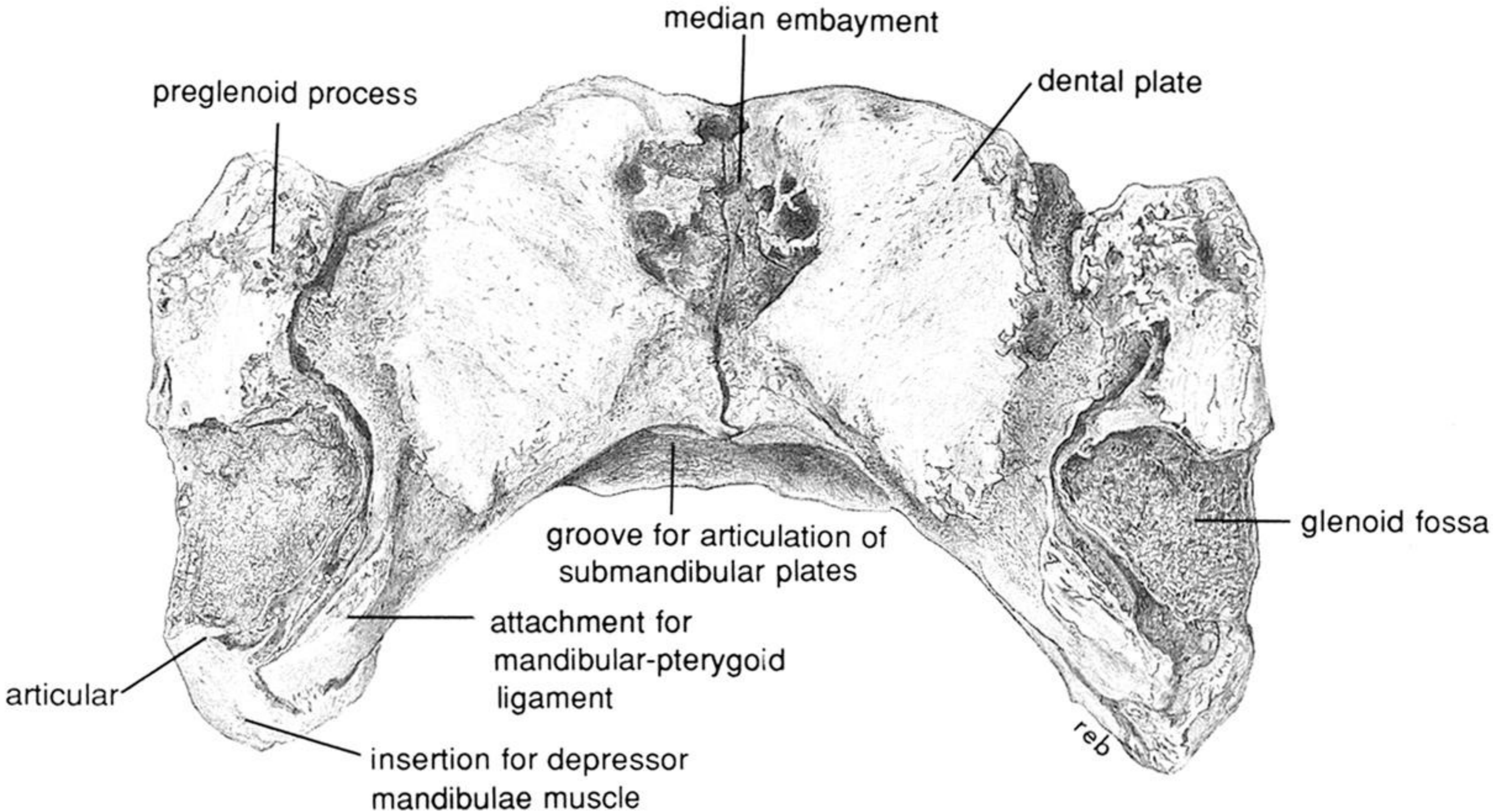


Figure 16. Reconstruction of the mandible of *Sorbitorhynchus deleaskitus* in posterior view.

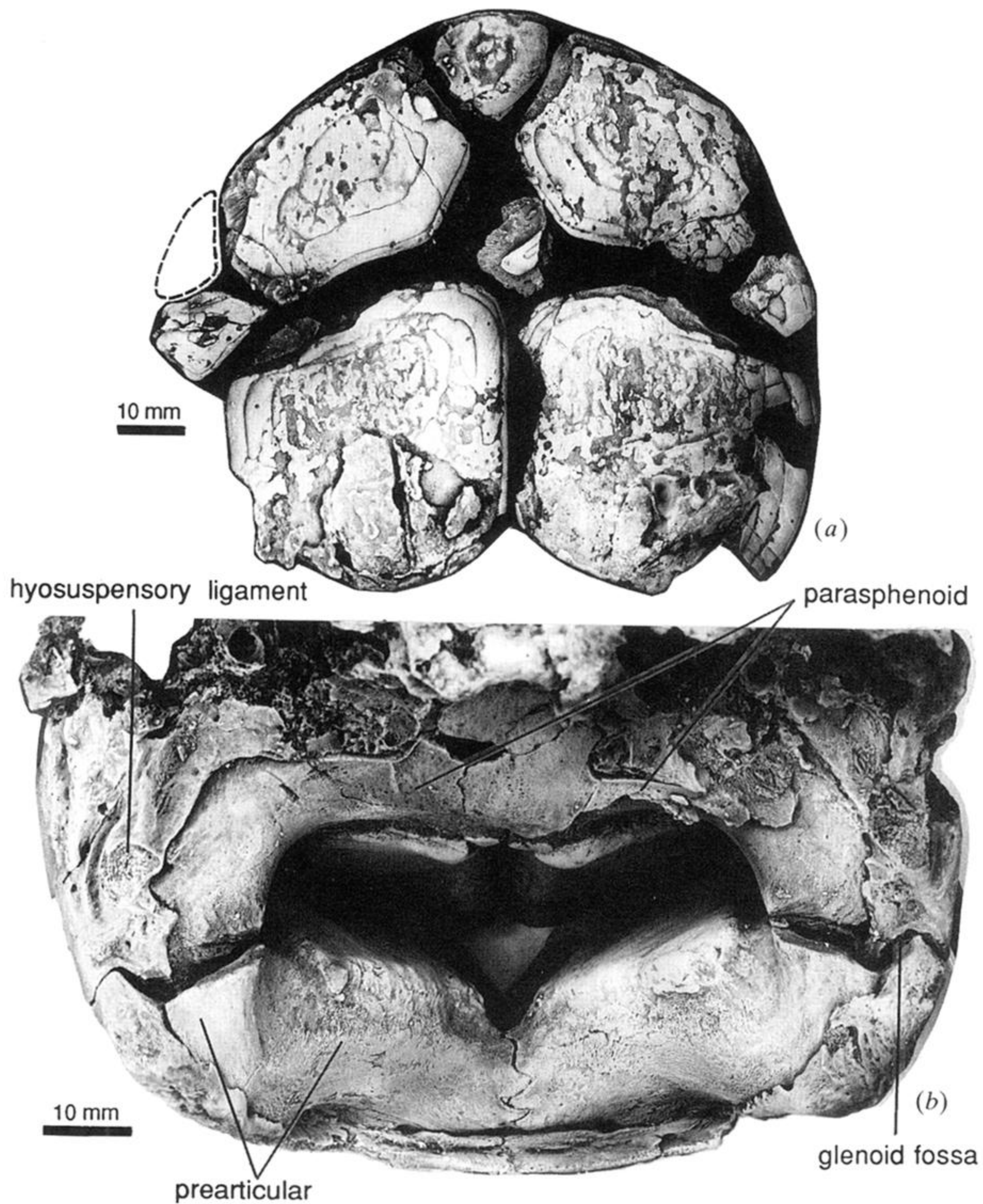


Figure 18. (a) Reassembled gular and submandibular bones of the holotype of *Sorbitorhynchus deleaskitus*. The outline of the missing lateral submandibular is drawn in on the right side of the specimen. (b) Posterior view of part of the articulated skull and mandible of same.

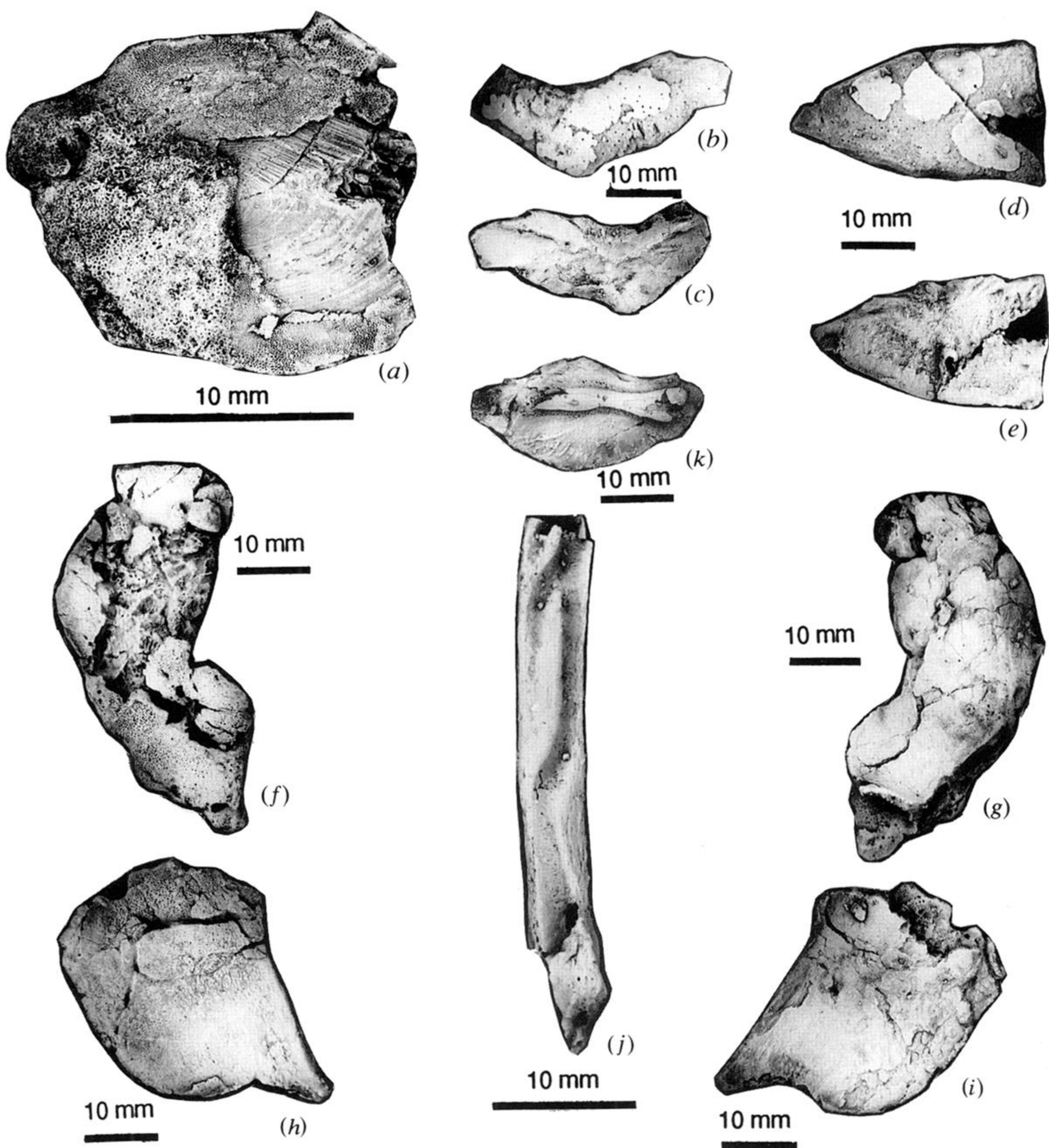


Figure 19. (a) Scale of *Sorbitorhynchus deleaskitus* to show the fine bone overlying denser bone with growth laminae. (b-c) Dorsal and ventral views of an incomplete bone 'A'. (d-e) Dorsal and ventral views of bone 'Z'. (f-g) External and internal views of an incomplete right cleithrum. (h-i) External and internal views of the anterior end of an incomplete anocleithrum or possibly the ventral end of the clavicle. (j) Fragment of a ceratobranchial showing grooves for the vascular vessels. (k) Interclavicle in ventral view.

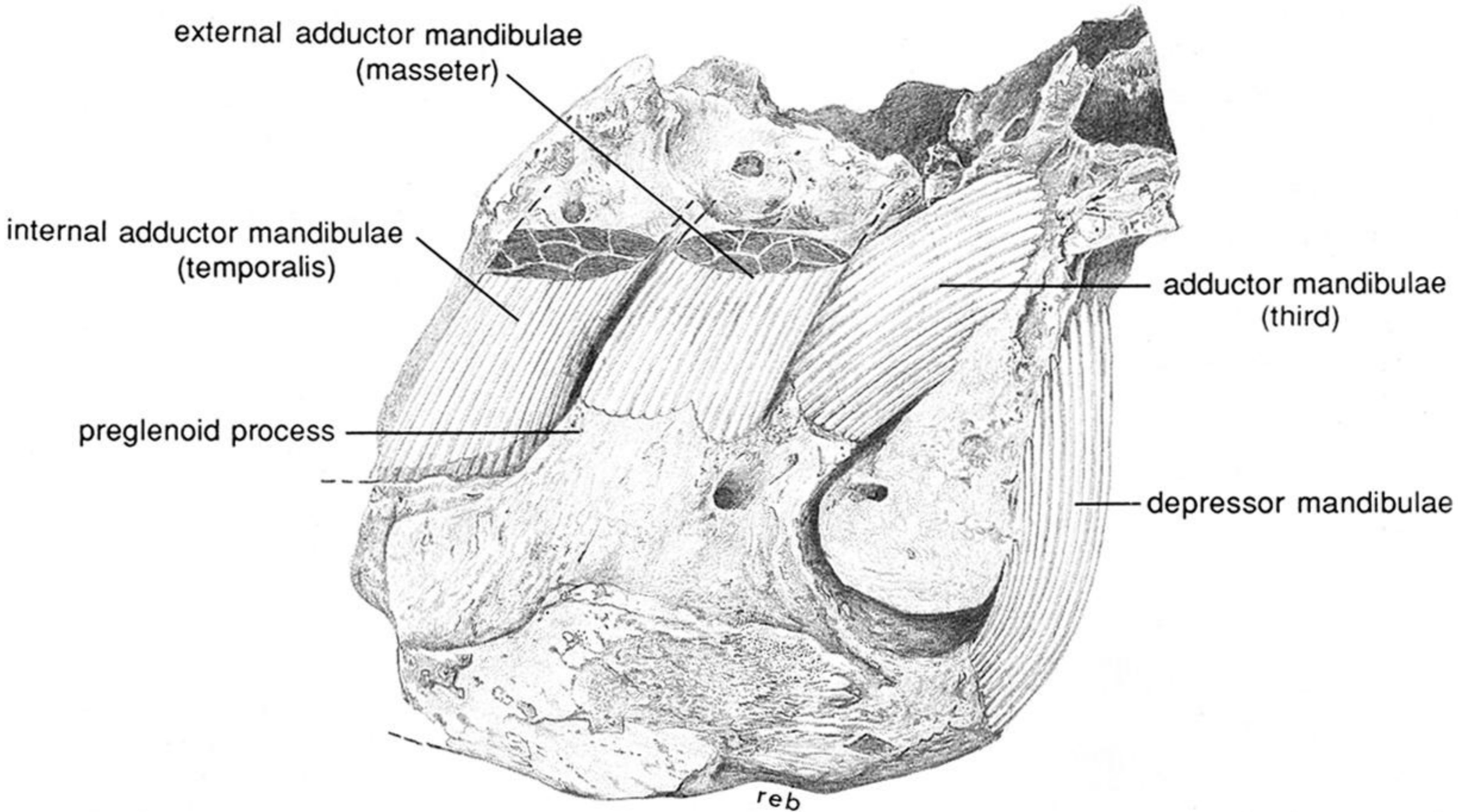


Figure 20. Inferred positions of the short adductor mandibulae and depressor mandibulae muscles anterior and posterior to the jaw articulation, represented in left lateral view.