

## EVOLUTION OF CRANIAL STRUCTURE IN ADULT COLEOPTERA<sup>1</sup>

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### Abstract

The variety in the structure of the cranium is due largely to the disproportionate growth of its sclerites. The epifrons may grow anteriorly at the expense of the frons until the latter is almost or completely suppressed and the antennal sockets lie near or against the clypeus. The parietals may also grow laterally and invade the ventral side where they may form a considerable portion of the ventral wall at the expense of the postgenae.

The clypeus may either contract or expand. Its lateral lobes, the anterior condyles of the mandibles, are usually separated from the body of the clypeus by sutures. The anterior tentorial pits retain their primitive position against the clypeus at the level of the mouth.

New evidence is given for the origin of the gula by sclerotization of the neck membrane between ventral extensions of the postoccipital ridge which now form the gular ridges. The gula may be partially or completely suppressed by the mesal growth of the postgenae.

The basal limit of the submentum may be defined by a line drawn through the ends of the postoccipital or gular ridges but, rarely, the mesal growth of the postgenae may crowd out its proximal region and thus a postgenal bridge is interposed between the gula and the definitive submentum.

### Introduction

Much of the very extensive literature on the Coleoptera contains descriptions or illustrations of the cranium, but the interpretation of the regions and sutures is still in an unsatisfactory condition.

The evolution of the insect cranium from the postulated generalized type seldom involves the acquisition of new structures or the migration of organs from one sclerite to another. It is rather the result of differences in the degree and direction of growth of the various sclerites or regions, leading to changes in the form and proportions of these regions. The gula is the only new structure in the cranium of the Coleoptera as compared with the generalized hypognathous head.

The object of this paper is neither to survey the entire order of beetles nor to describe in detail the structure of any individual head, but to select illustrative material to show how changes in the relative proportions of the different sclerites have affected the form and structure of the head.

Ridges, shallow grooves, and other topographical features of no particular morphological significance are omitted or merely indicated in the drawings. Where the specific name of the insect is not given, two or more species of the genus have been examined and found to be in general agreement as to their morphological features.

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in the region distal to the postoccipital ridge. The postocciput was not involved and no gula was formed except, possibly, for a very narrow band between the pits. In other species (Figs. 16, 18, 31) the elongation involves both the region of the pits and that distal to them. The ventral ends of the ridge are produced anteriorly for only a short distance. The gulamentum then consists of a short gular region and a relatively long submental region.

The elongation in many species apparently took place chiefly in the region proximal to the pits. The postoccipital ridge therefore extends far forward (Figs. 27, 38, 41, 45) and the tentorial bridge (*Tb*) is also carried forward, retaining its relation to the ends of the ridge. In these all or most of the mid-ventral wall is formed by the gula.

In still other species the elongation seems to have taken place chiefly in the region of the pits. The tentorial bridge remains in or near its original position but the ridge extends anteriorly beyond the bridge (Figs. 21, 23). Here again all or most of the mid-ventral sclerite is formed by the gula. Those parts of the postoccipital ridge extending beyond the bridge, i.e., the gular ridges, may be interpreted as the expanded bases of the posterior tentorial arms. The entire gular suture would then constitute the posterior tentorial pit.

This is the picture that the definitive ventral wall of the cranium presents and it suggests different lines of evolution from the hypognathous condition. It is at least as probable, however, that the ancestral head had a ventral wall resembling that of *Meloe* (Fig. 7) or *Criocephalus* (Fig. 16) and that the variations described were due to the contraction of the gula as in *Chalcophora* (Fig. 15) or by its anterior expansion in most other species.

It will be seen, if the drawings of the tentorium are consulted, that the base of the submentum is adjacent to the ends of the postoccipital ridge regardless of the position of the pits as indicated by the tentorial bridge. Figures 10, 11, 21, and 24 show this clearly.

### Modification of the Ventral Wall

The ventral wall in the primitive prognathous head consists of the postgenae and the gulamentum (Figs. 3, 7, 18) but, as shown earlier, the parietals usually grow around the sides and invade the ventral region. The occipital suture is usually lacking, therefore the extent of the contribution of the parietals to the ventral wall can seldom be determined precisely. In insects like *Phyllophaga* (Fig. 23), however, the area occupied by the ventral portion of the eye, the size of the hypostoma, and the position of the socket of the mandibular articulation show quite clearly that most of the lateral sclerites of the ventral wall are formed by the parietals and that this has happened at the expense of the postgenae which are greatly reduced while the width of the gula is not affected. In *Podabrus* (Fig. 48) on the other hand it is evident that the encroachment of the parietals occurs at the expense of both the postgenae and the gula.

In extreme cases the encroachment of the parietals may continue until both the gula and the postgenae are completely obliterated throughout most of their length. This seems to have happened in the cranium of *Dendroctonus*



(Fig. 52) in which the gula is lost except for a minute anterior fragment (*Gu*), and the postgenae (*Pgen*) are reduced to narrow transverse sclerites at the anterior edge of the ventral wall. If we assume that the dotted lines *Osf* and *Gsf* represent positions occupied by the occipital and gular sutures at some early stage in the evolution of the cranium, it is evident that, if the regions of the parietals proximal to the eyes were to grow mesally until their edges meet, the greatly reduced postgenae would be forced into the position they now occupy.

The postgenae may grow mesally along with or independently of the parietals. This has the effect of reducing the width of the gula until in many species it is almost or completely suppressed as an external sclerite. A series which shows progressive stages in the suppression of the gula may be seen in *Silpha* (Fig. 36), *Harpalus* (Fig. 28), *Staphylinus* (Fig. 42), *Necrophorus* (Fig. 46), *Dendroctonus* (Fig. 52), and *Cleonus* (Fig. 54). The middle region of the gula is progressively narrowed in the first three. In *Necrophorus* this region is completely suppressed leaving only anterior and posterior remnants of the gula. In *Dendroctonus*, only a very small anterior portion persists, while in *Cleonus* the gula is completely suppressed.

When the postgenae or parietals meet in the middle line the two gular sulci come together and coalesce to form a single mid-ventral gular suture. (The term "midgular suture" sometimes used for it has misleading connotations.) The two gular ridges also unite and when these ridges are high, as they are in most of the species examined, they form a flattened median plate (Figs. 45, 51, 55, *Gr*). Steps leading to the formation of such a plate may be envisaged by comparing the diagrams shown in Figs. 37, 40, and 44. It will be seen that the ridges form a pair of lateral wings to the united structure. If, however, the gular sulci are shallow grooves, when they coalesce an ordinary low ridge is formed. Such a ridge is found in *Podabrus* (Fig. 49, *Gr*) and some other cantharids. The sulci in some cantharids with a normally developed gula are shallow, and if they were to coalesce, the resulting median ridge would be similar to that of *Podabrus*.

The short gular ridges in *Tenebroides* (Fig. 33, *Gr*) meet in the middle line and enclose a small triangular gula (Fig. 34, *Gu*). A faint median suture (Fig. 34, *Mvs*) extends from the apex of the gula to the submentum, which is borne far forward on the head. It might be thought that here also the gula has been suppressed except for its proximal region, but the median suture is very faint and is not associated with extensions of the postoccipital ridge as in the heads just discussed. Apparently therefore it is the proximal region of the submentum, and not the gula, that has been suppressed by the mesal growth of the postgenae. If this head is compared with that of *Criocephalus* (Fig. 16) it will be seen that the gular sutures of the two are very similar but their anterior ends are separated in *Criocephalus*; therefore there is a wide submentum (*Sm*). There can be no reason why the postgenae may not extend mesally in a head of this structure as they do in other heads. If this happened and the two sclerites meet in the middle line most of the submentum would disappear and the resulting structure would resemble that of

*Tenebroides*. Actually the beginning of the mesal growth of the postgenae at the expense of the submentum may be seen in *Chalcophora* (Fig. 14) and *Monochamus* (Fig. 18). The cranium of *Tenebroides* is the only one of those examined in which the base of the submentum has been separated from the postoccipital ridge and the gula by a postgenal bridge.

The hypostoma is invariably present extending along the free edge of the postgena from the posterior articulation of the mandible to the point at which the postgena joins the median sclerite whether this is the gula or the submentum. The hypostomal "suture" is usually a ridge rather than a sulcus because in most species the hypostoma is bent inwards at an angle to the postgena. Because of this it is not always as completely visible from the ventral view as the figures suggest.

The gular sutures also, whether separate or coalesced, are always present as well-defined sulci, but the portion of the hypostomal suture between the submentum and the postgena, when these are united, may be lost. It is very faint in *Criocephalus* (Fig. 16) and completely lost in *Derobrachus* (Fig. 31).

### Conclusions and Summary

This paper probably includes most of the significant changes that have taken place in the cranium of adult Coleoptera but makes no pretense at exhaustive treatment. It should, however, serve as a guide in interpreting the morphology of the head in other species. It is not possible to draw firm phylogenetic conclusions from such a limited survey but it does seem rather surprising to find insects with such differing head structures as found in *Chelymorpha* and *Leptinotarsa* placed in the same family.

It is not certain whether the cranium in all species evolved from a common prognathous type or whether there were several lines of descent from the hypognathous type, but the fact that the ventral wall has essentially the same structure, regardless of the orientation of the head, seems to be strong evidence in favor of the first alternative. Possibly the ancestral head resembled that of *Anisolabis*. The fusion of the gula with the cranium would produce a short ventral wall resembling that of *Chelymorpha* and when the submentum also fused with the cranium the ventral wall would resemble that of *Criocephalus*. Differential growth, resulting in unequal expansion or contraction of the various cranial sclerites, would then be responsible for the variety in the definitive structure of the cranium in the different species.

The text deals largely with the disproportion in the various sclerites as compared with the generalized hypognathous cranium.

The facial sutures which define the sclerites are never complete and frequently are entirely lost. They are best represented in the Cassidinae. The so-called "epicranial suture" of authors consists actually of the midcranial sulcus and other sulci which may differ in different species.

The parietal region is greatly expanded in most species. The epifrons, or median region of the parietals, may grow anteriorly at the expense of the frons until the latter is completely suppressed and the antennae come to lie against



the clypeus. The parietals may also expand laterally, growing around to the ventral side where they may continue to grow mesally at the expense of the postgenae and often of the gula also. In an extreme case their edges meet in the mid-ventral line and both the gula and the postgenae are suppressed as external sclerites.

The clypeus may be greatly enlarged or it may be reduced to a narrow transverse band. The anterior mandibular condyles are formed from lateral lobes of the clypeus and are usually separated from the body of the clypeus by a sulcus. They are not to be equated with the paraclypeal lobes of *Corydalis*.

The anterior tentorial pits retain their primitive position at the level of the mouth and always lie against or in the frontoclypeal suture when this is present.

The gula originated as a sclerotization in the neck membrane between ventral extensions of the postoccipital ridge. Thus the gular sutures and ridges are parts of the postoccipital suture and ridge. The gula may be suppressed by the mesal growth of the postgenae. When this happens the two gular sutures and ridges coalesce to form a median suture and ridge.

The proximal margin of the submentum retains its position adjacent to the ends of the postoccipital ridge regardless of the extent of the ridge. An apparently rare exception occurs when the mesal growth of the postgenae crowds out the proximal region of the submentum and interposes a postgenal bridge between the gula and the definitive submentum.

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## EXPLANATION OF FIGURES

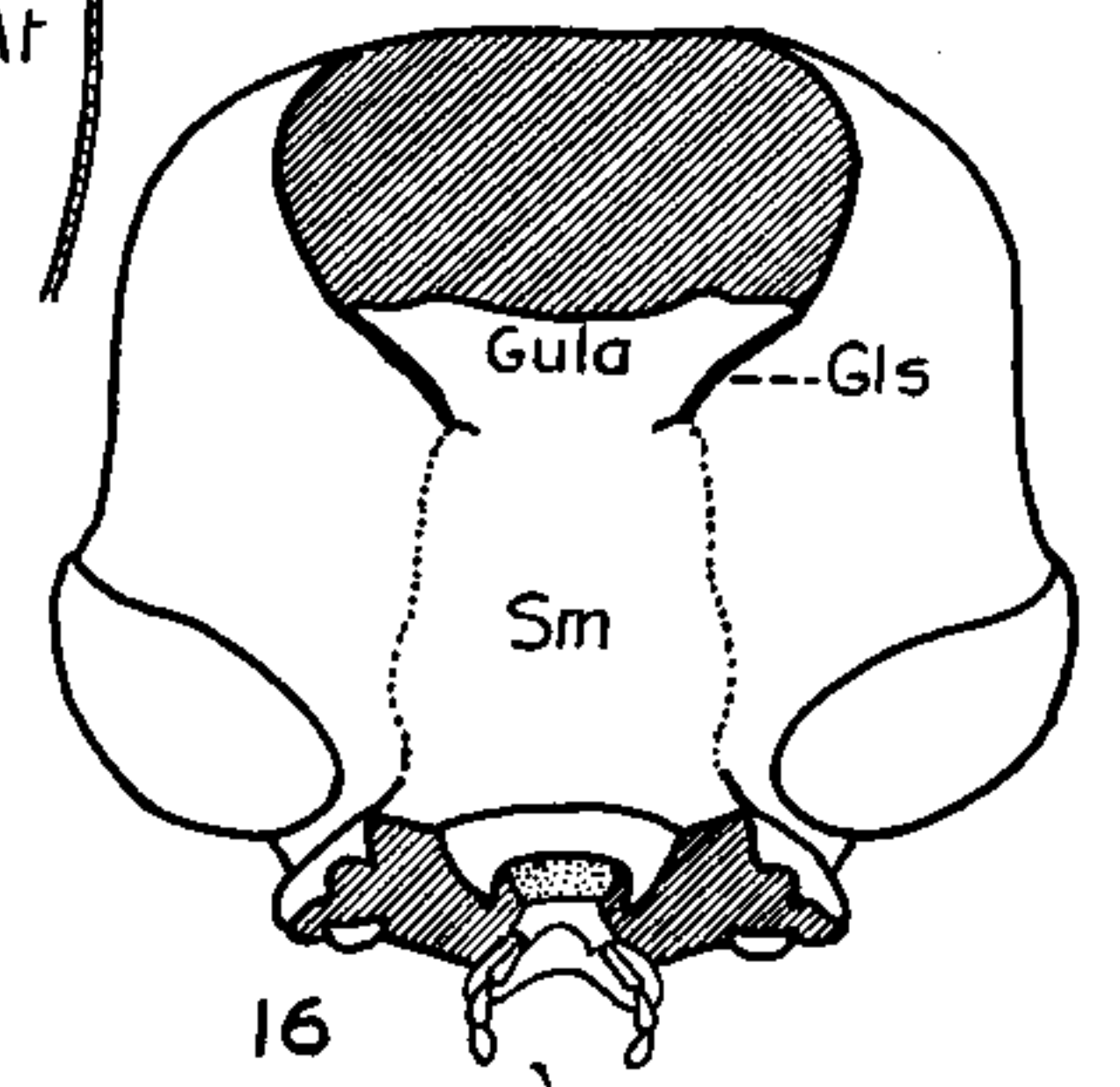
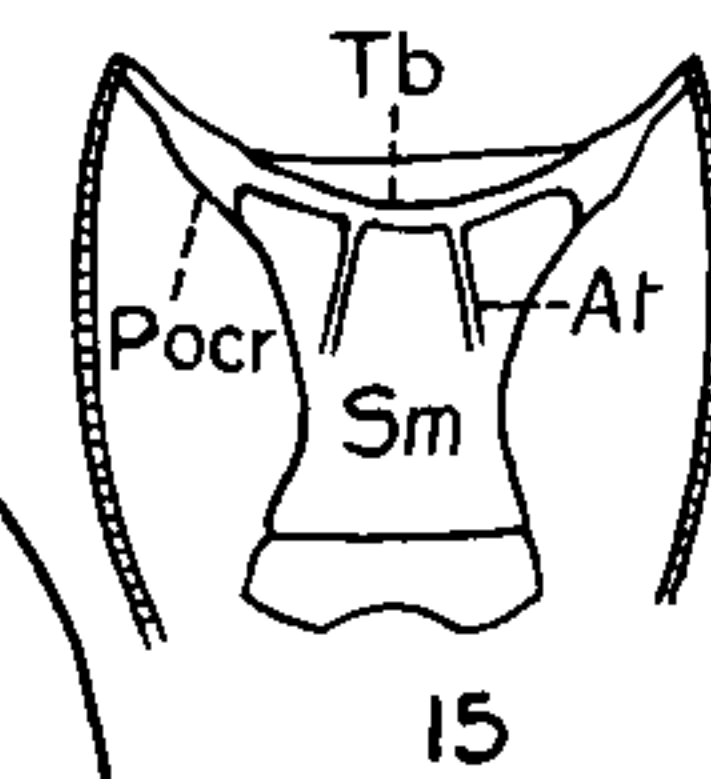
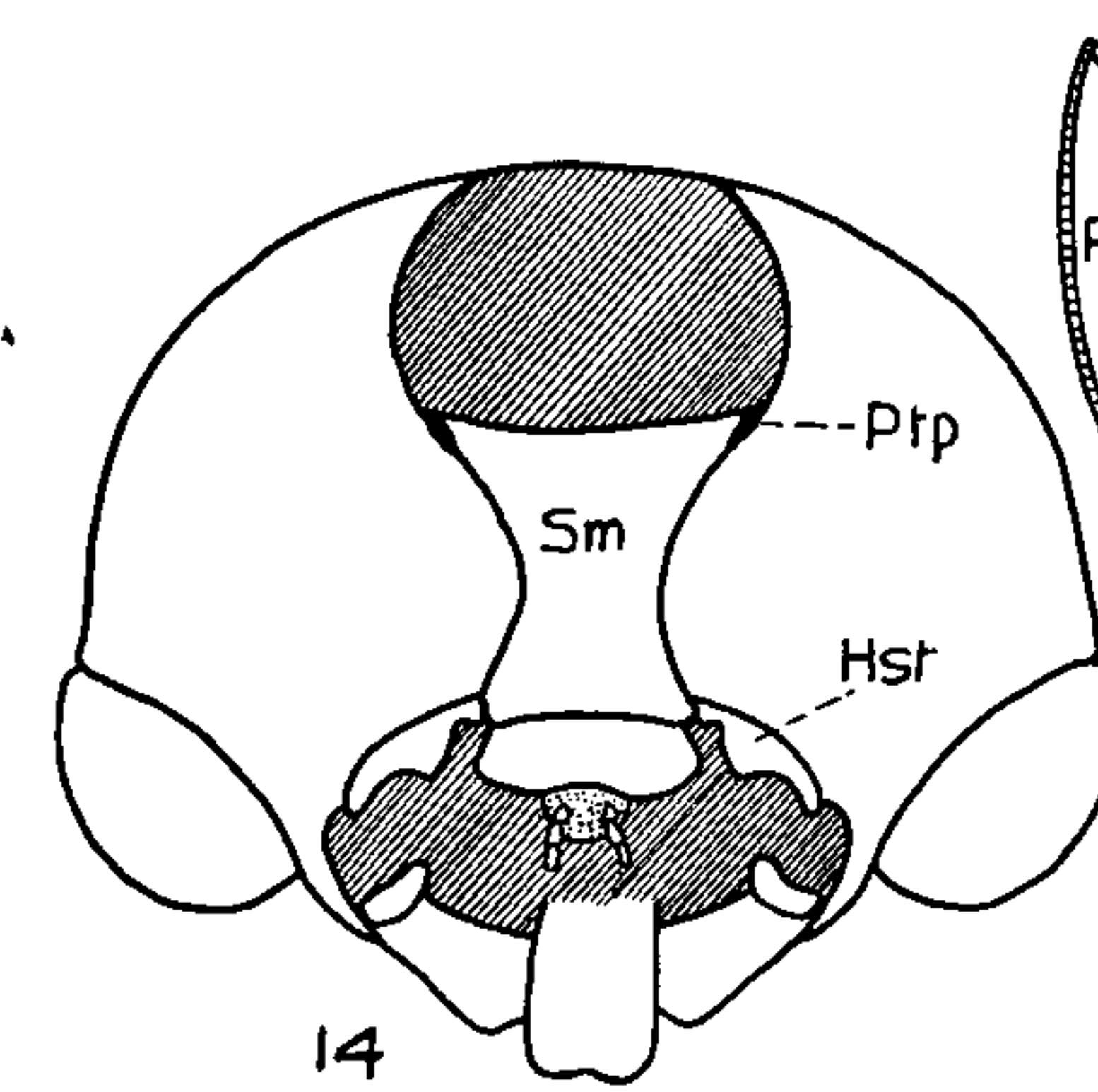
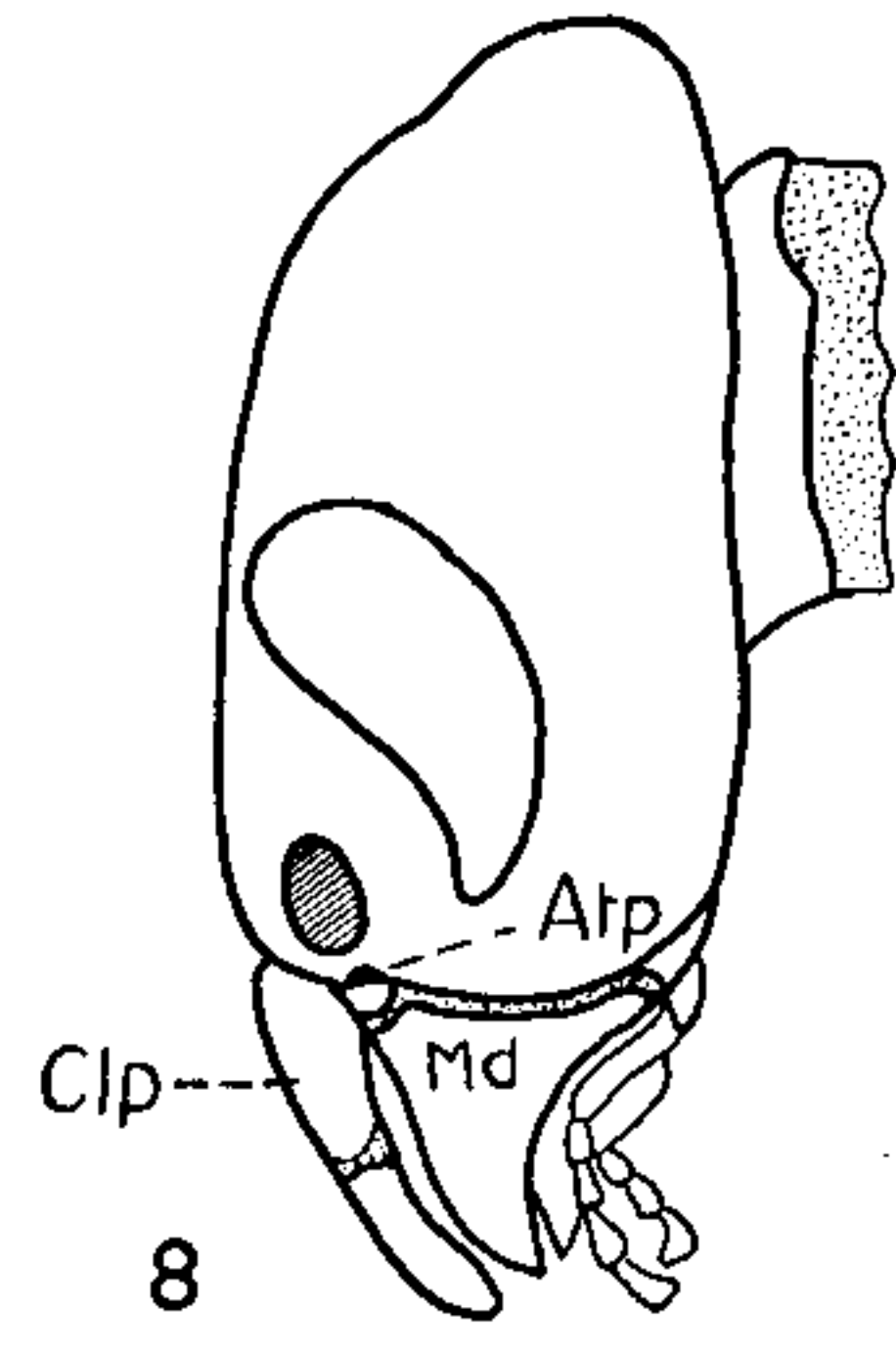
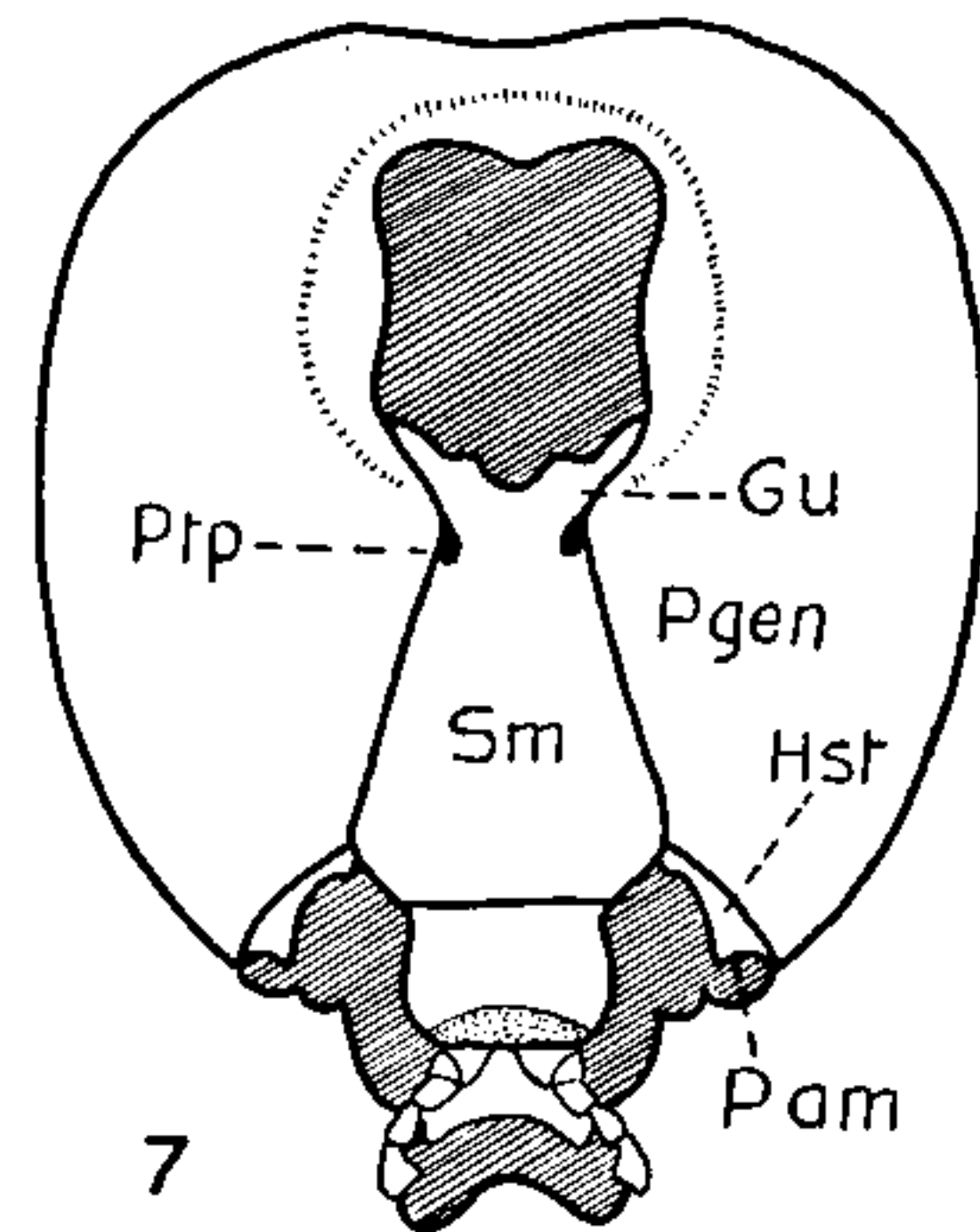
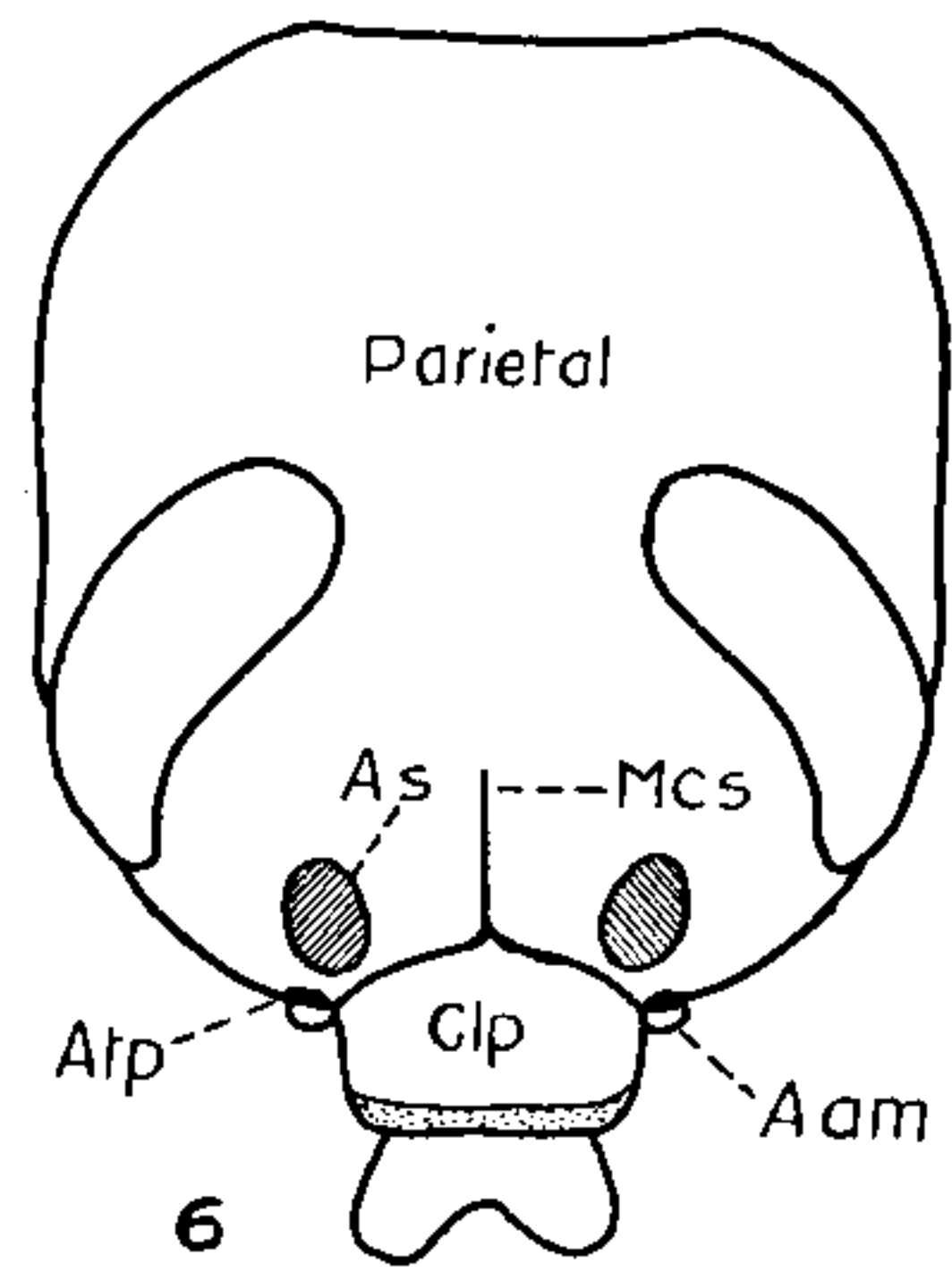
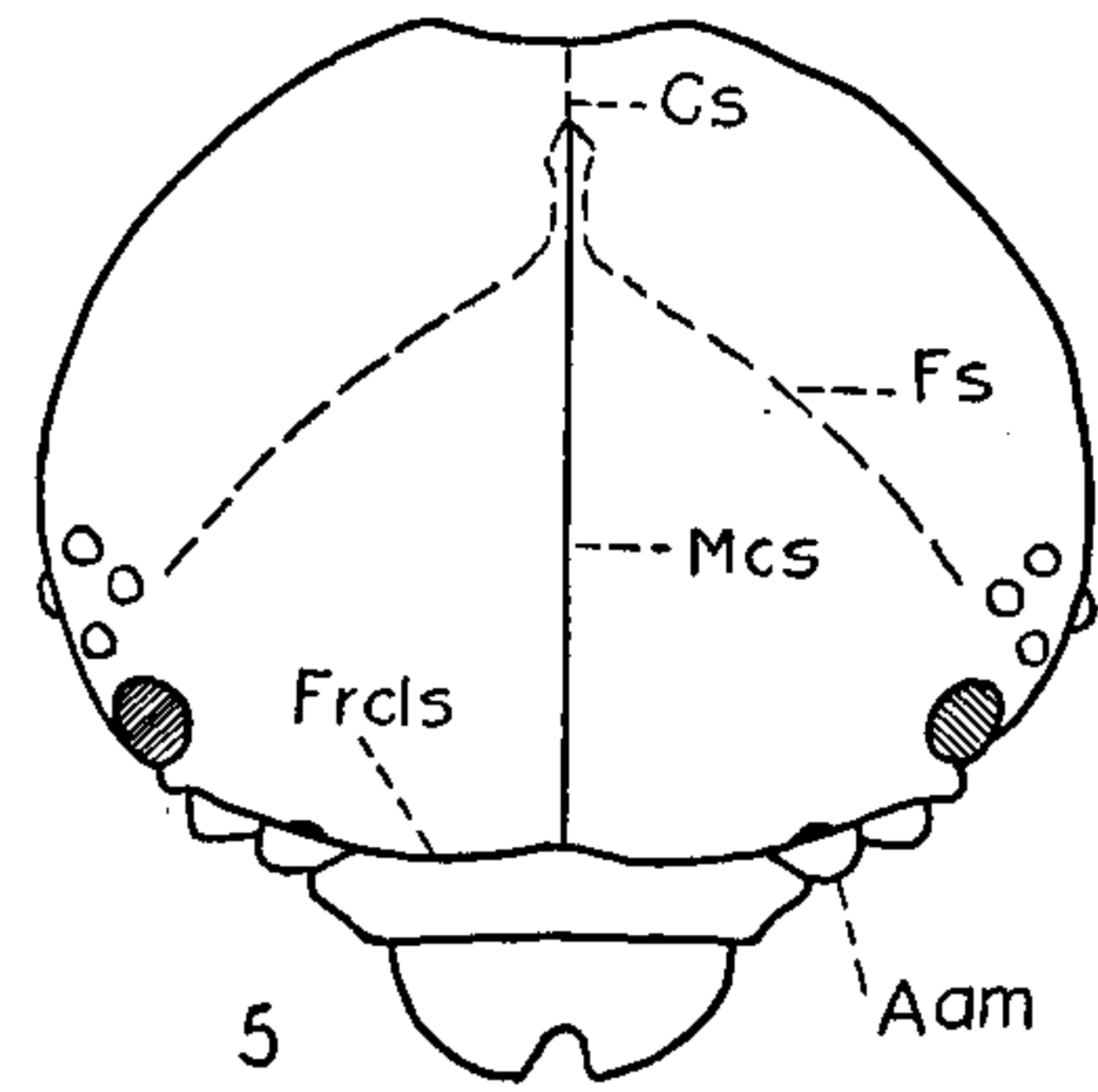
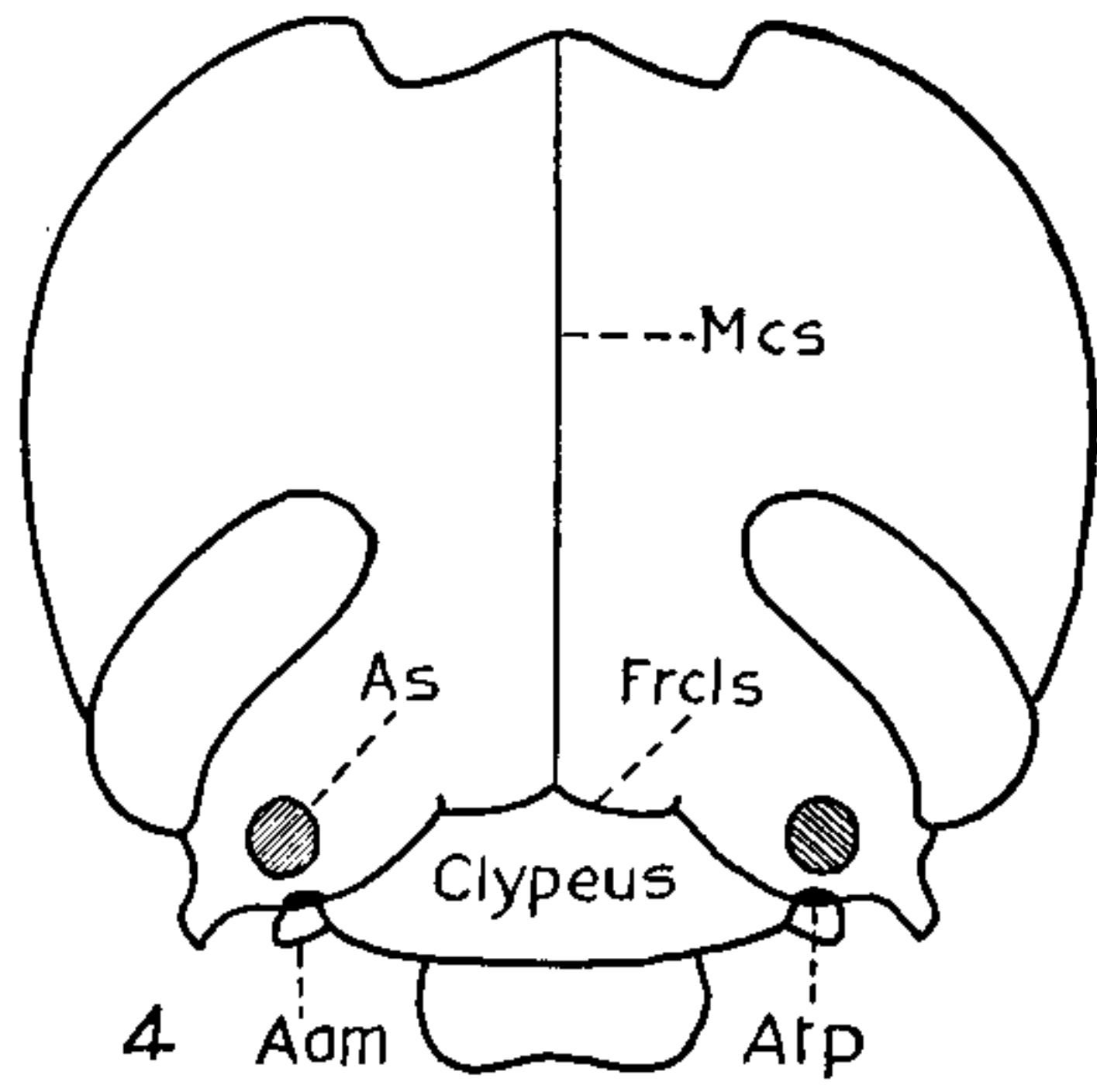
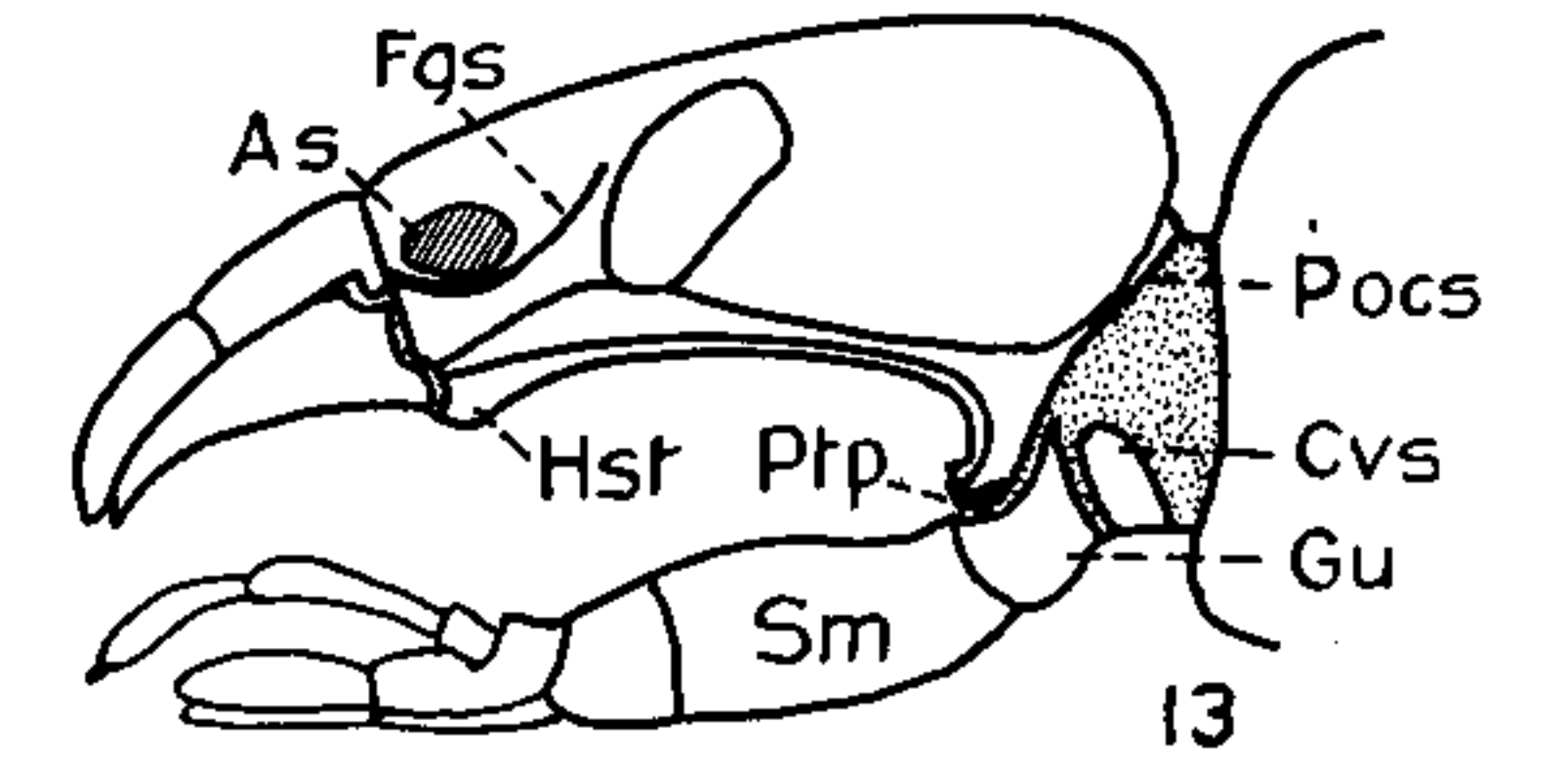
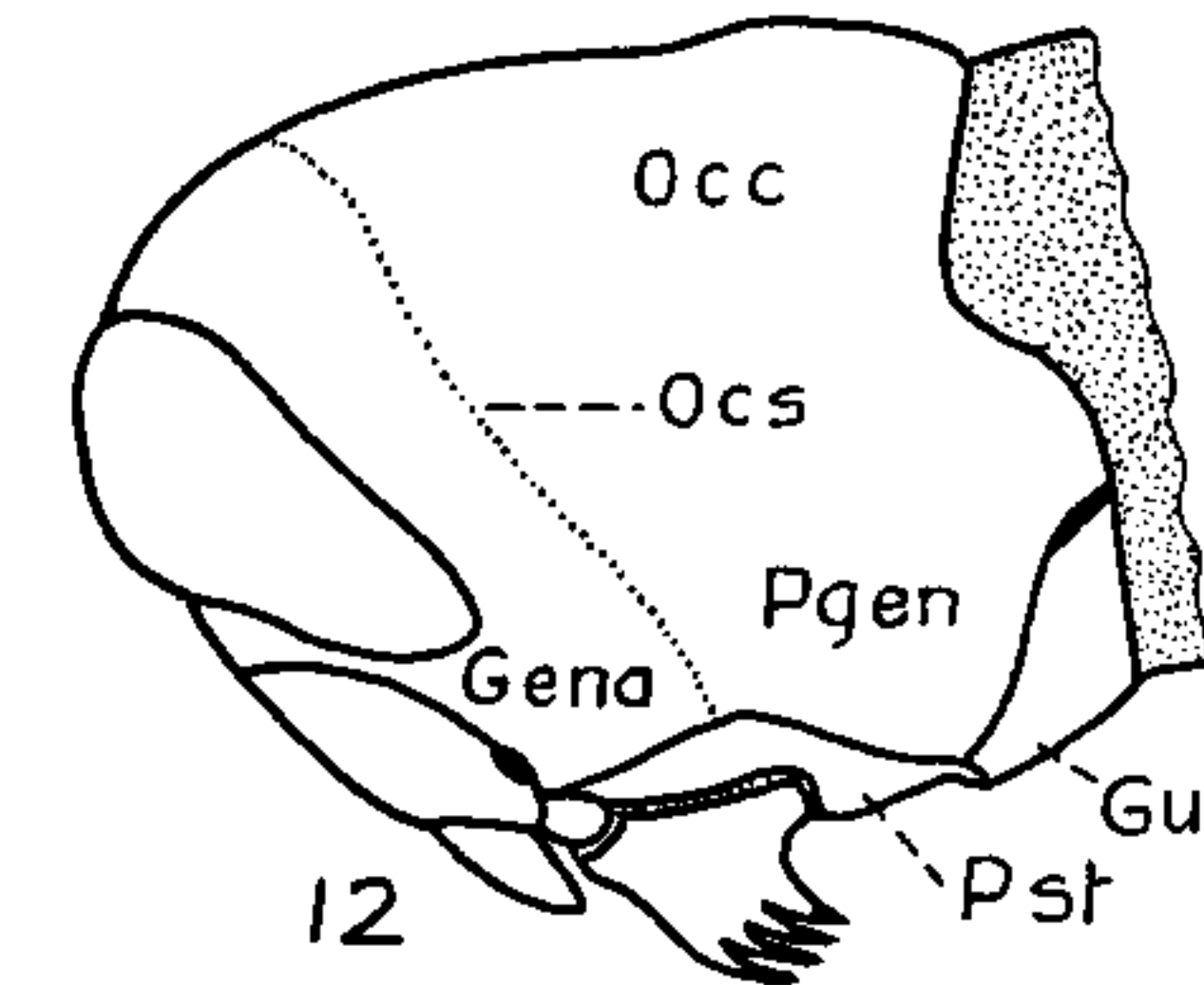
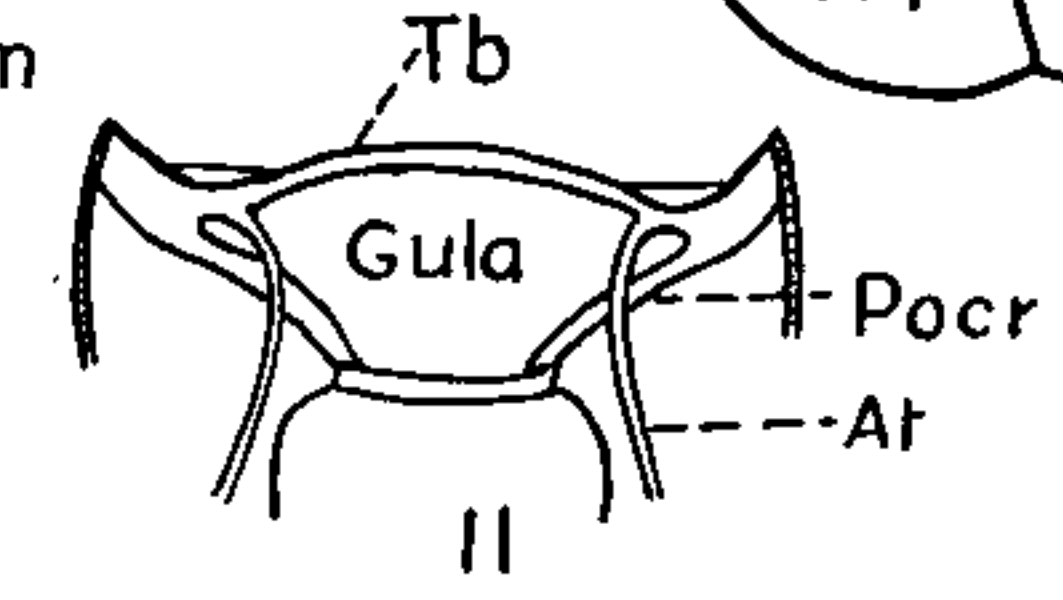
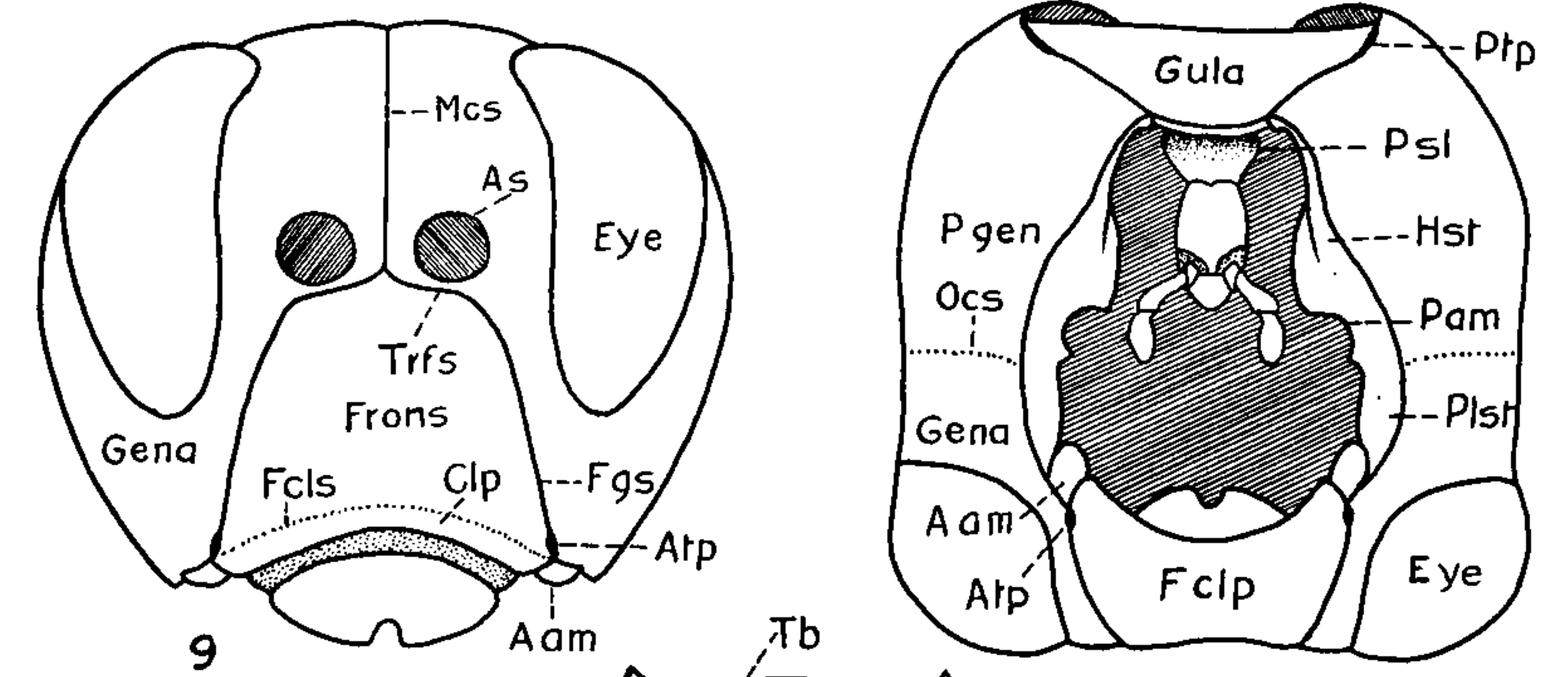
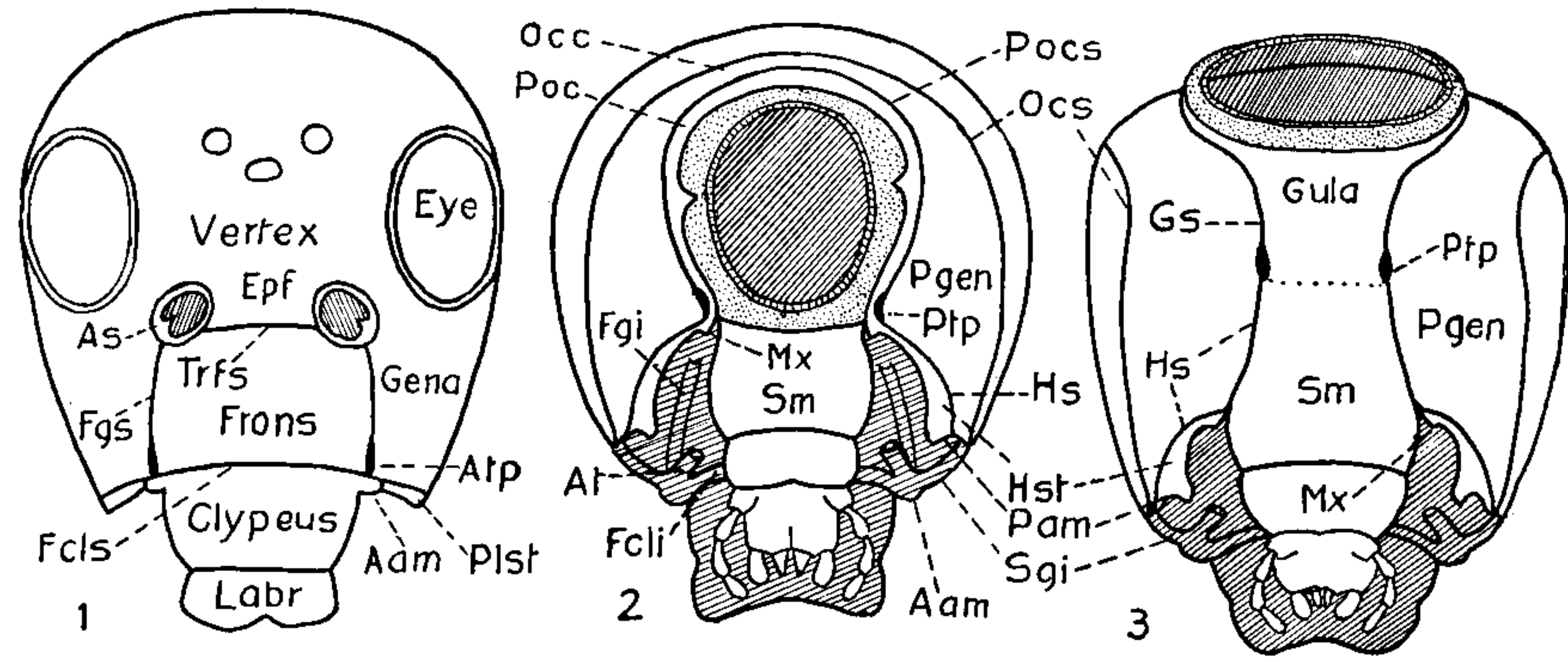
- FIG. 1. The generalized hypognathous head, anterior view.  
FIG. 2. The generalized hypognathous head, posterior view.  
FIG. 3. The generalized prognathous head, ventral view.  
FIG. 4. *Leptinotarsa decemlineata* (Chrysomelidae), larva.  
FIG. 5. *Leptinotarsa decemlineata*, adult.  
FIG. 6. *Meloe angusticollis* (Meloidae), dorsal view.  
FIG. 7. *Meloe angusticollis*, ventral view.  
FIG. 8. *Meloe angusticollis*, lateral view.  
FIG. 9. *Chelymorpha cassidea* (Chrysomelidae), dorsal view.  
FIG. 10. *Chelymorpha cassidea*, ventral view.  
FIG. 11. *Chelymorpha cassidea*, postoccipital or gular ridges and tentorium.  
FIG. 12. *Chelymorpha cassidea*, lateral view.  
FIG. 13. *Anisolabis maritima* (Dermaptera), lateral view.  
FIG. 14. *Chalcophora* (Buprestidae), ventral view.  
FIG. 15. *Chalcophora*, internal view of ventral wall and tentorium.  
FIG. 16. *Criocephalus* (Cerambycidae), ventral view.  
FIG. 17. *Monochamus* (Cerambycidae), dorsal view.  
FIG. 18. *Monochamus*, ventral view.  
FIG. 19. *Monochamus*, tentorium and postoccipital ridge.  
FIG. 20. *Phyllophaga* (Scarabaeidae), dorsal view.  
FIG. 21. *Phyllophaga*, tentorium and gular ridges.  
FIG. 22. *Osmoderma* (Scarabaeidae), dorsal view.  
FIG. 23. *Phyllophaga*, ventral view.  
FIG. 24. *Osmoderma*, tentorium and gular ridges.  
FIG. 25. *Osmoderma*, ventral view.  
FIG. 26. *Harpalus* (Carabidae), dorsal view.  
FIG. 27. *Harpalus*, tentorium and gular ridges.  
FIG. 28. *Harpalus*, ventral view.  
FIG. 29. *Derobrachus brunneus* (Cerambycidae), dorsal view.  
FIG. 30. *Derobrachus brunneus*, tentorium and postoccipital ridge.  
FIG. 31. *Derobrachus brunneus*, ventral view.  
FIG. 32. *Tenebroides mauritanicus* (Ostomidae), dorsal view.  
FIG. 33. *Tenebroides mauritanicus*, tentorium and gular ridges.  
FIG. 34. *Tenebroides mauritanicus*, ventral view.  
FIG. 35. *Silpha* (Silphidae), dorsal view.  
FIG. 36. *Silpha*, ventral view.  
FIG. 37. *Silpha*, diagrammatic cross section of ventral wall.  
FIG. 38. *Silpha*, tentorium and gular ridges.  
FIG. 39. *Staphylinus* (Staphylinidae), dorsal view.  
FIG. 40. *Staphylinus*, diagrammatic cross section of ventral walls.  
FIG. 41. *Staphylinus*, gular ridges and tentorium.  
FIG. 42. *Staphylinus*, ventral view.  
FIG. 43. *Necrophorus* (Silphidae), dorsal view.  
FIG. 44. *Necrophorus*, diagrammatic cross section of ventral wall.  
FIG. 45. *Necrophorus*, gular ridge and tentorium.  
FIG. 46. *Necrophorus*, ventral view.  
FIG. 47. *Podabrus* (Cantharidae), dorsal view.  
FIG. 48. *Podabrus*, ventral view.  
FIG. 49. *Podabrus*, postoccipital or gular ridge and tentorium.  
FIG. 50. *Dendroctonus valens* (Scolytidae), dorsal view.  
FIG. 51. *Dendroctonus valens*, gular ridge and tentorium.  
FIG. 52. *Dendroctonus valens*, ventral view.  
FIG. 53. *Cleonus piger* (Curculionidae), dorsal view.  
FIG. 54. *Cleonus piger*, ventral view.  
FIG. 55. *Cleonus piger*, internal view of ventral wall showing gular ridge.

## ABBREVIATIONS:

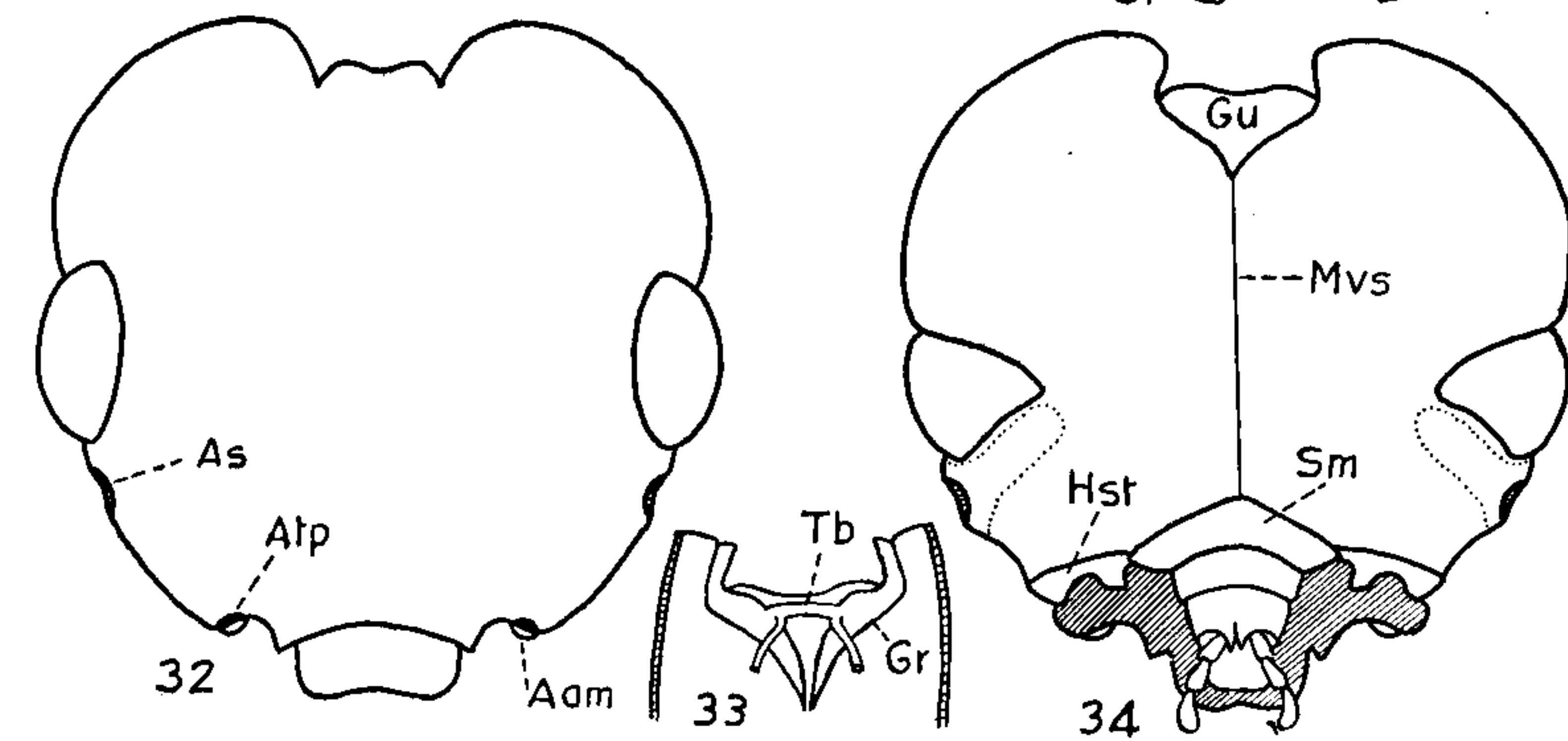
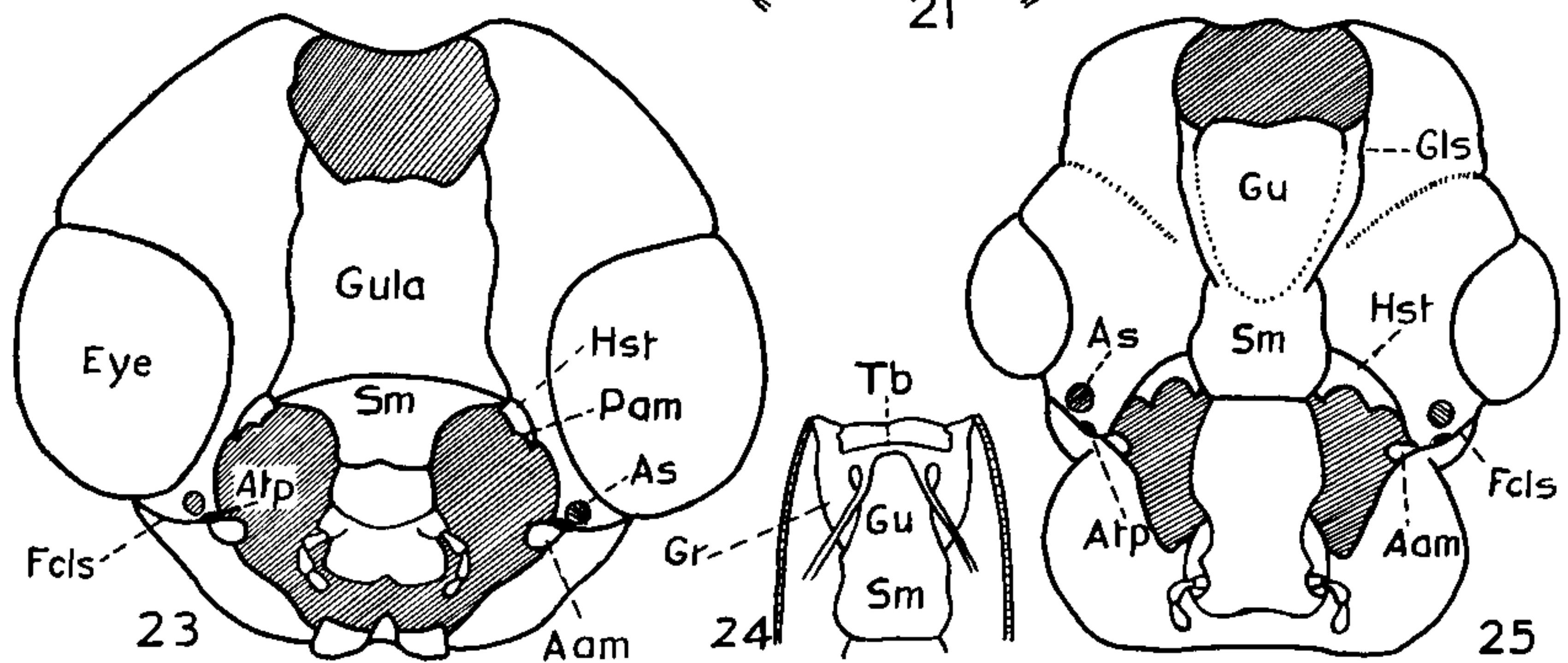
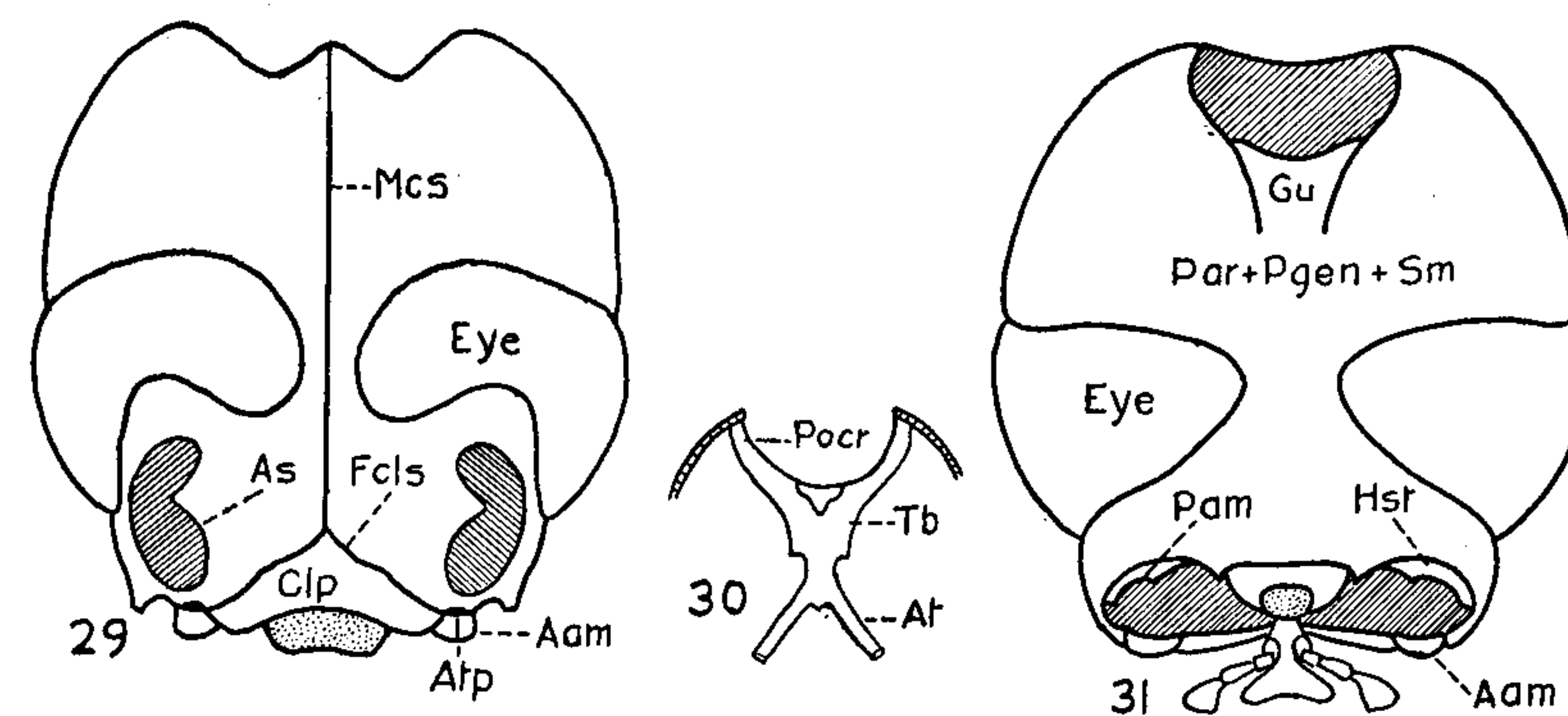
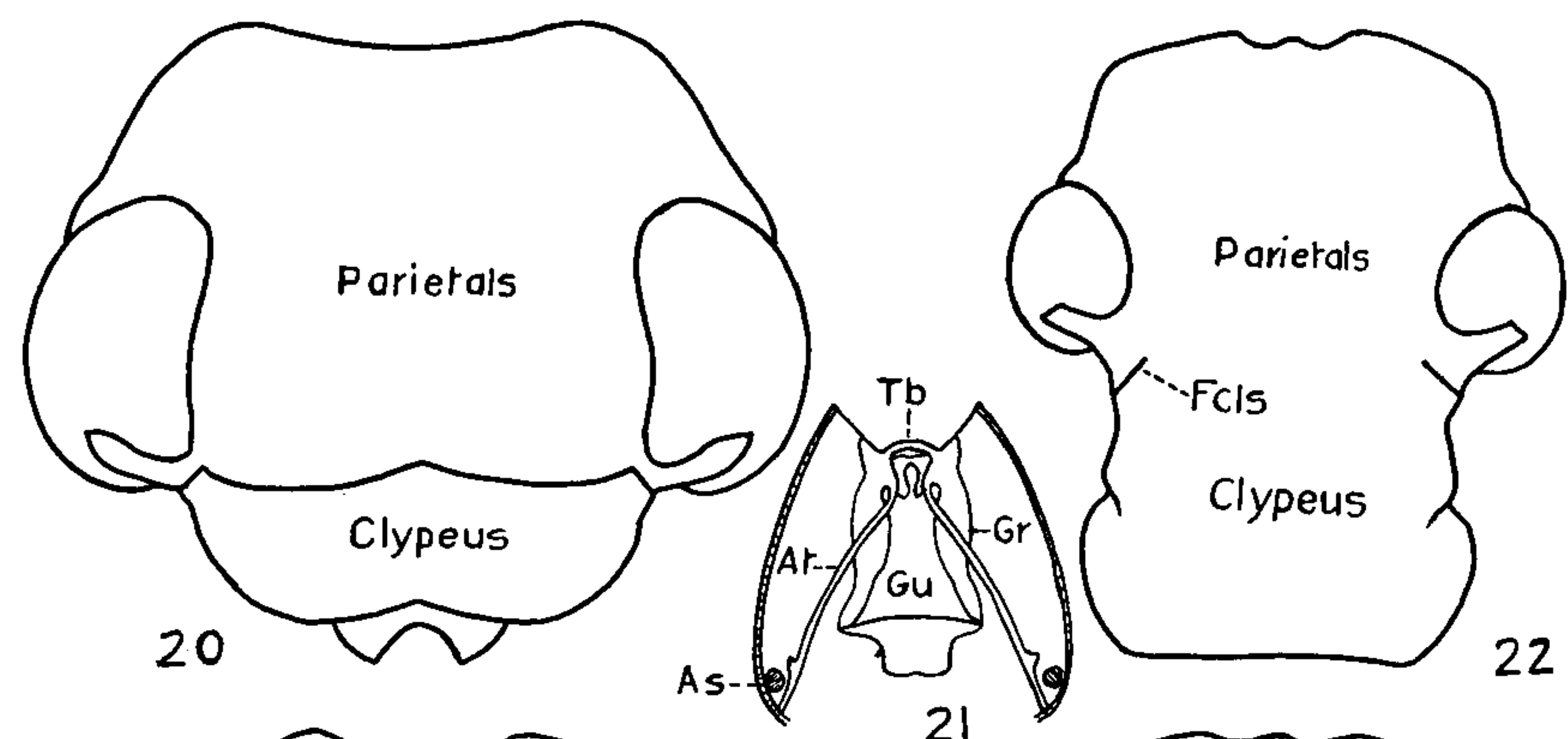
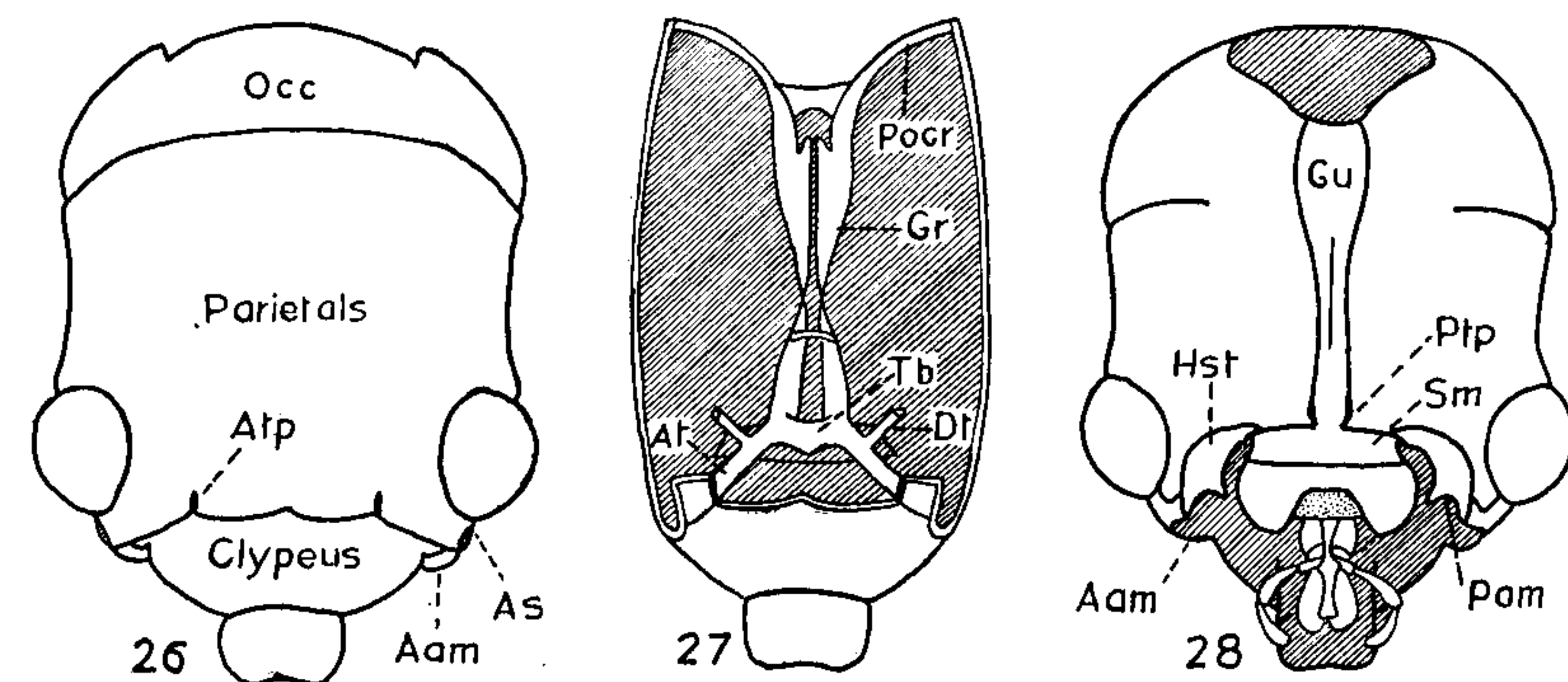
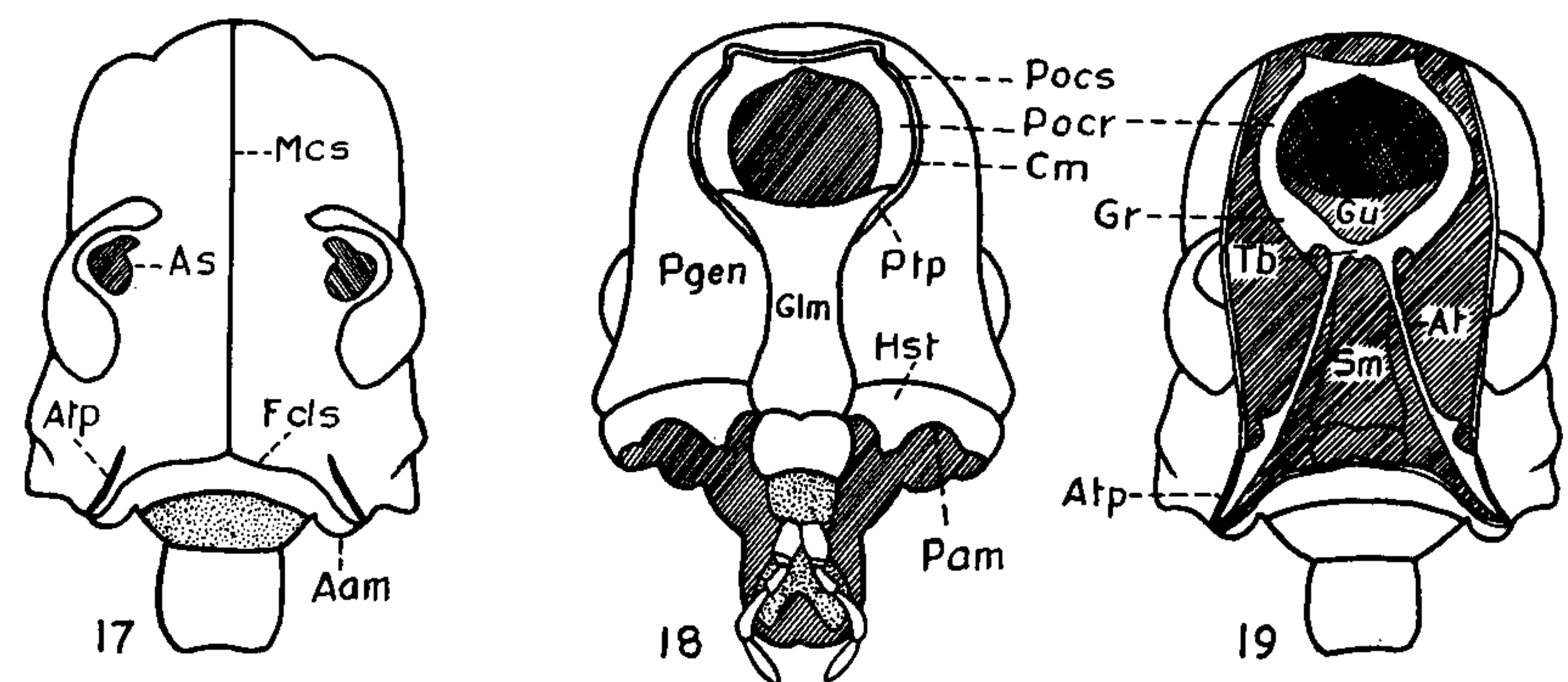
<i>Aam</i> , condyle of the anterior articulation of the mandible	<i>Labr</i> , labrum
<i>As</i> , antennal socket	<i>Mcs</i> , midcranial suture
<i>At</i> , anterior tentorial arm	<i>Md</i> , mandible
<i>Atp</i> , anterior tentorial pit	<i>Mvs</i> , mid-ventral suture
<i>Clgs</i> , clypeogenal suture	<i>Mx</i> , articulation of the maxilla
<i>Clp</i> , clypeus	<i>Occ</i> , occiput
<i>Cm</i> , posterior lip of the postoccipital ridge to which the neck membrane and the gula are attached	<i>Ocs</i> , occipital suture
<i>Cs</i> , coronal suture	<i>Pam</i> , socket of the posterior mandibular articulation
<i>Cvs</i> , cervical sclerite	<i>Par</i> , parietal
<i>Dt</i> , dorsal tentorial arm	<i>Pgen</i> , postgena
<i>Epf</i> , epifrons	<i>Plst</i> , pleurostoma
<i>Fcli</i> , frontoclypeal inflection or ridge	<i>Poc</i> , postocciput
<i>Fclp</i> , frontoclypeus	<i>Pocr</i> , postoccipital ridge (sometimes same as gular ridge)
<i>Fcls</i> , frontoclypeal suture	<i>Pocs</i> , postoccipital suture
<i>Fgi</i> , frontogenal inflection	<i>PSl</i> , postlabium
<i>Fgs</i> , frontogenal suture	<i>Pst</i> , parastoma
<i>Fr</i> , frons	<i>Pt</i> , posterior tentorial arm
<i>Fs</i> , frontal suture	<i>Ptp</i> , posterior tentorial pit
<i>Glm</i> , gulamentum	<i>S</i> , suture between dorsal tentorial arm and frontoclypeal sulcus
<i>Gls</i> , gular suture	<i>Sgi</i> , subgenal inflection
<i>Gr</i> , gular ridge	<i>Sm</i> , submentum
<i>Gu</i> , gula	<i>Tb</i> , tentorial bridge
<i>Hs</i> , hypostomal suture	<i>Trfs</i> , transfrontal suture
<i>Hst</i> , hypostoma	

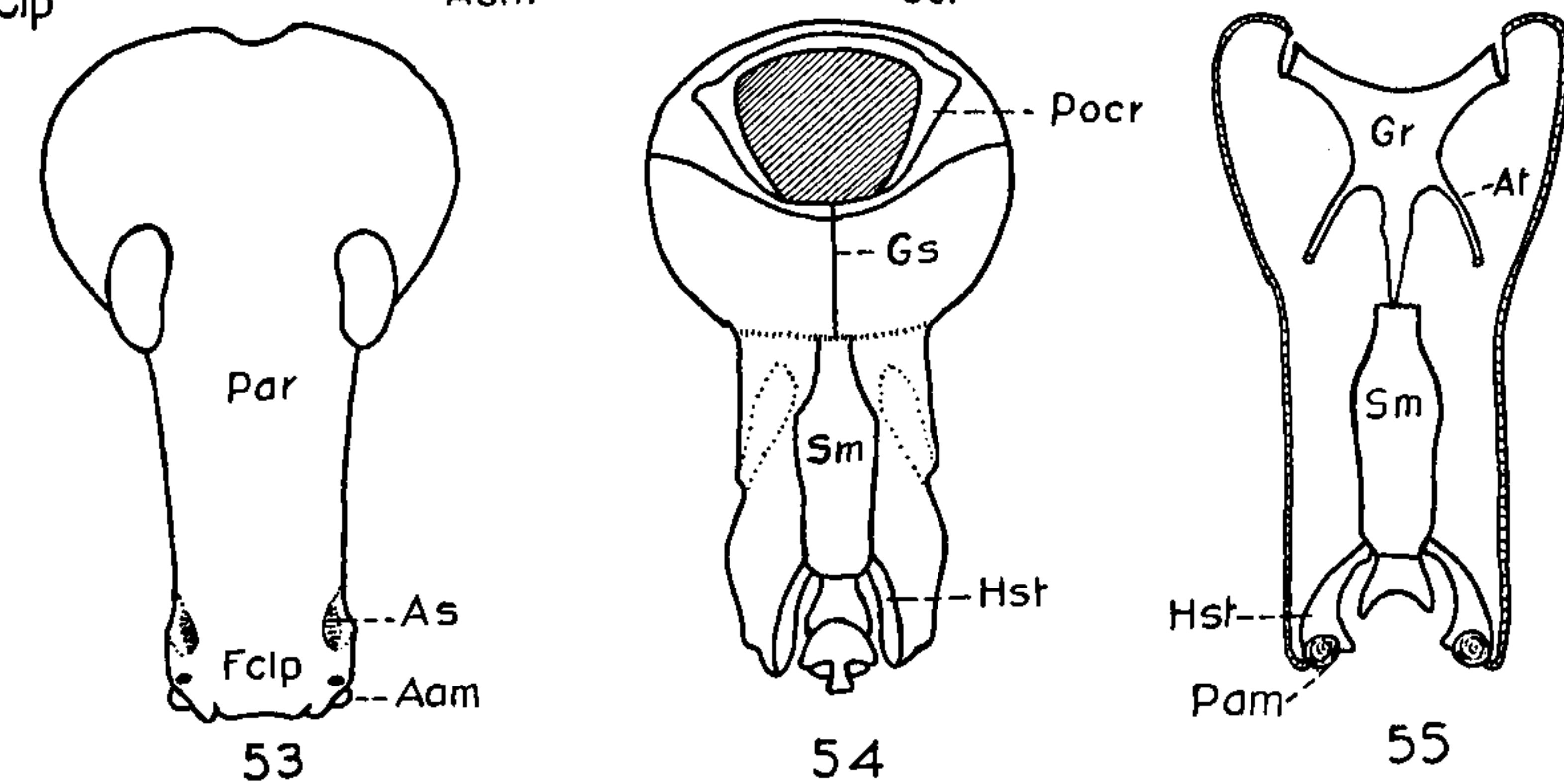
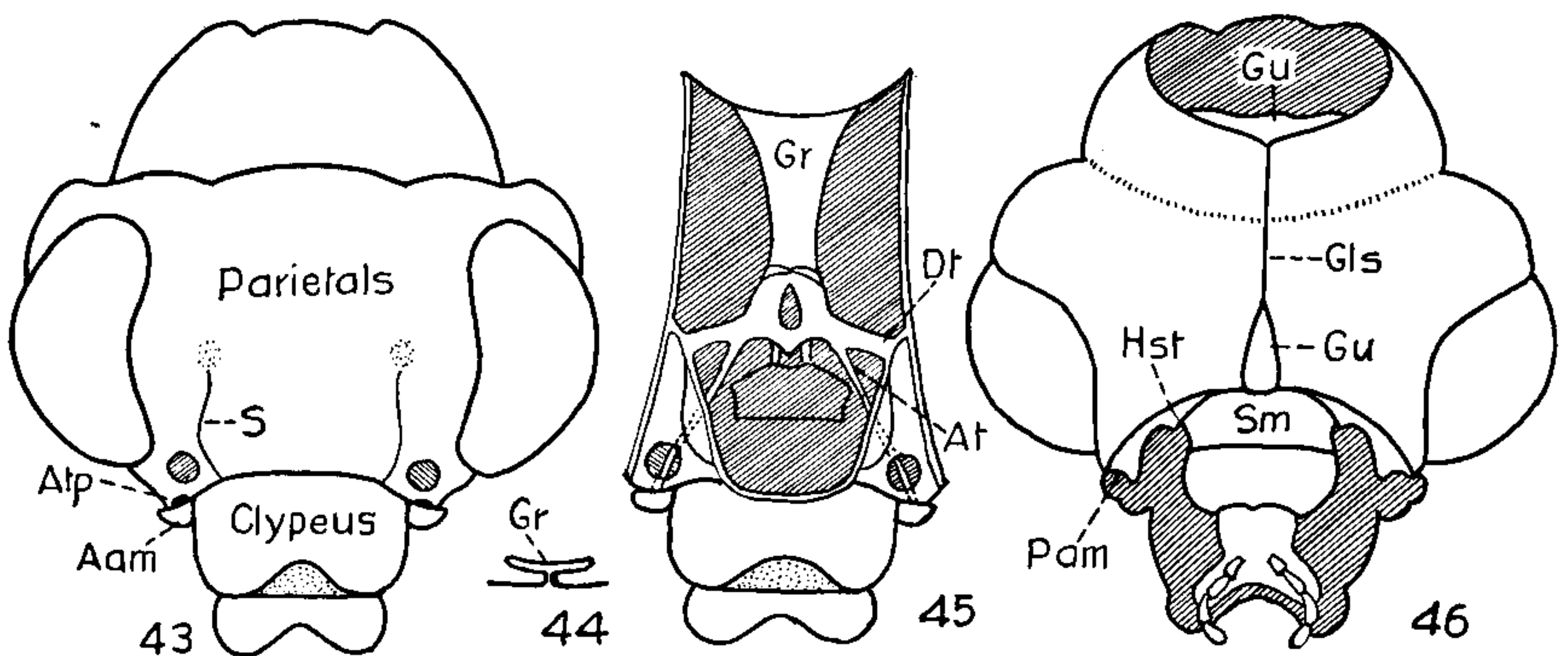
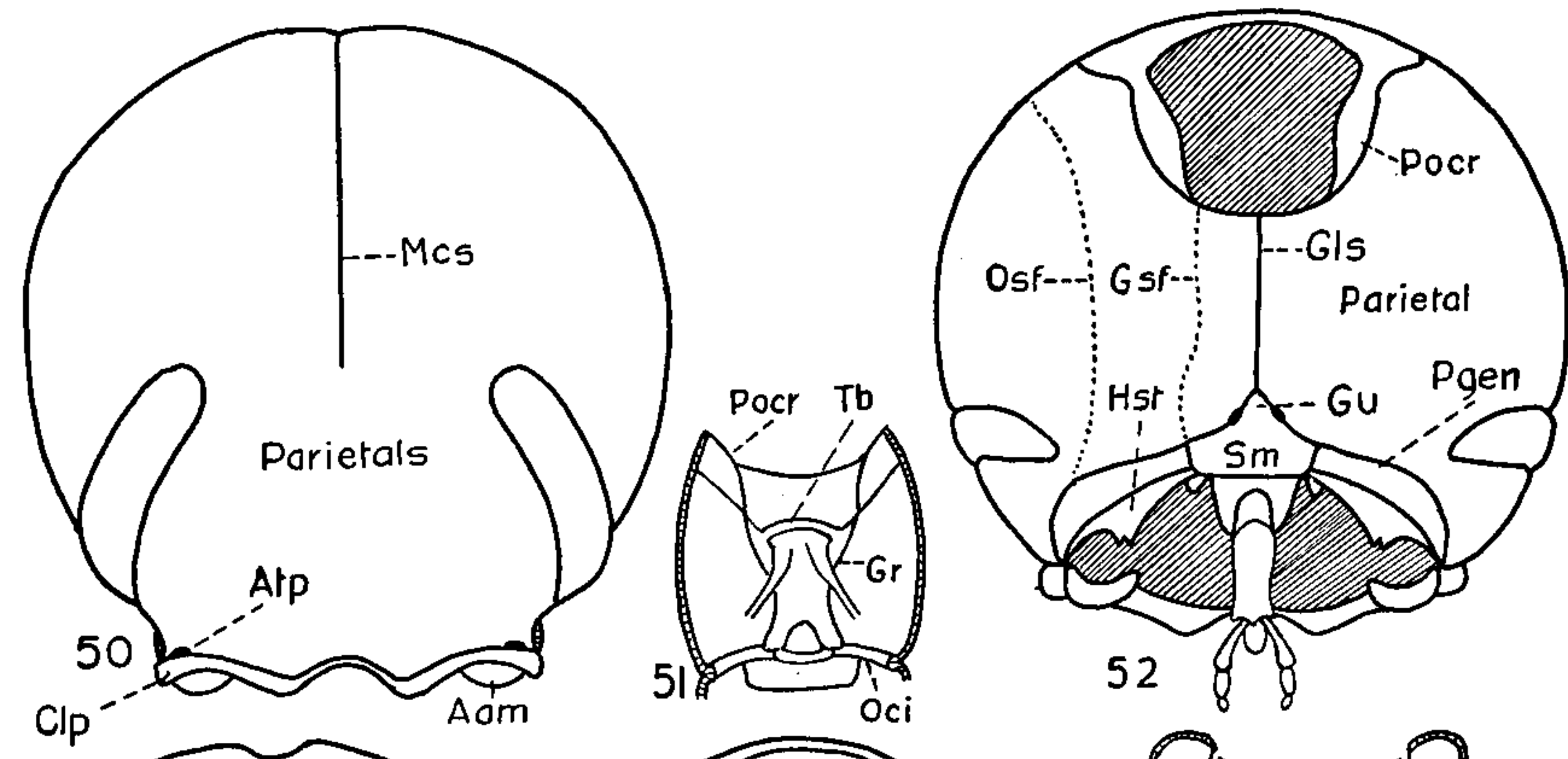
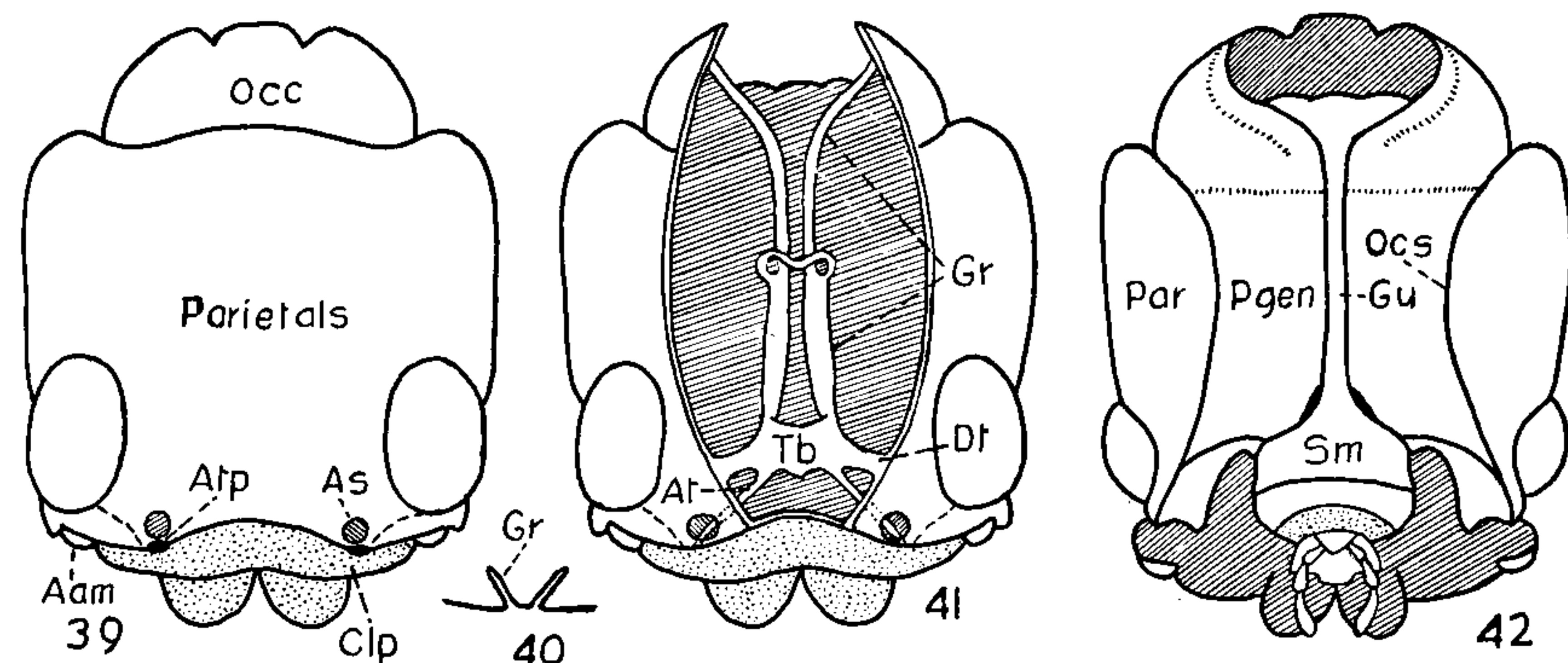
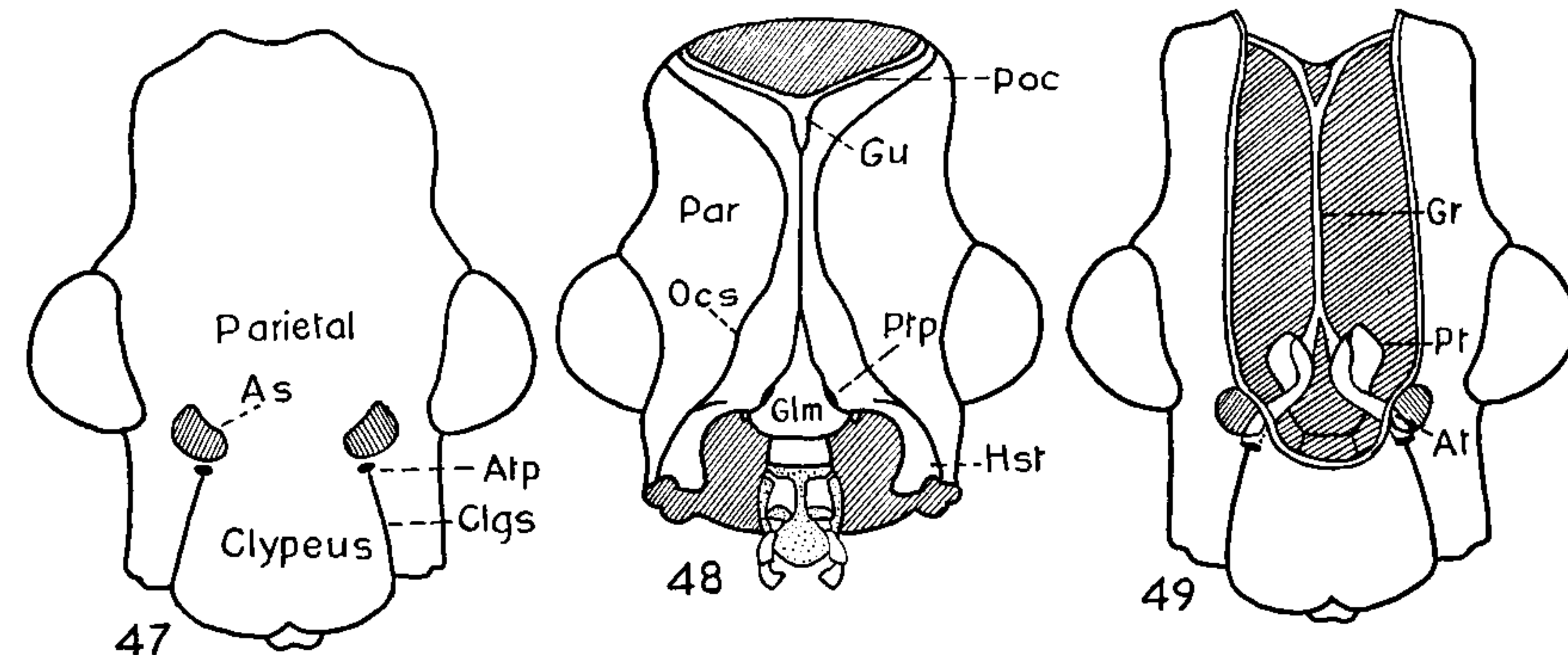
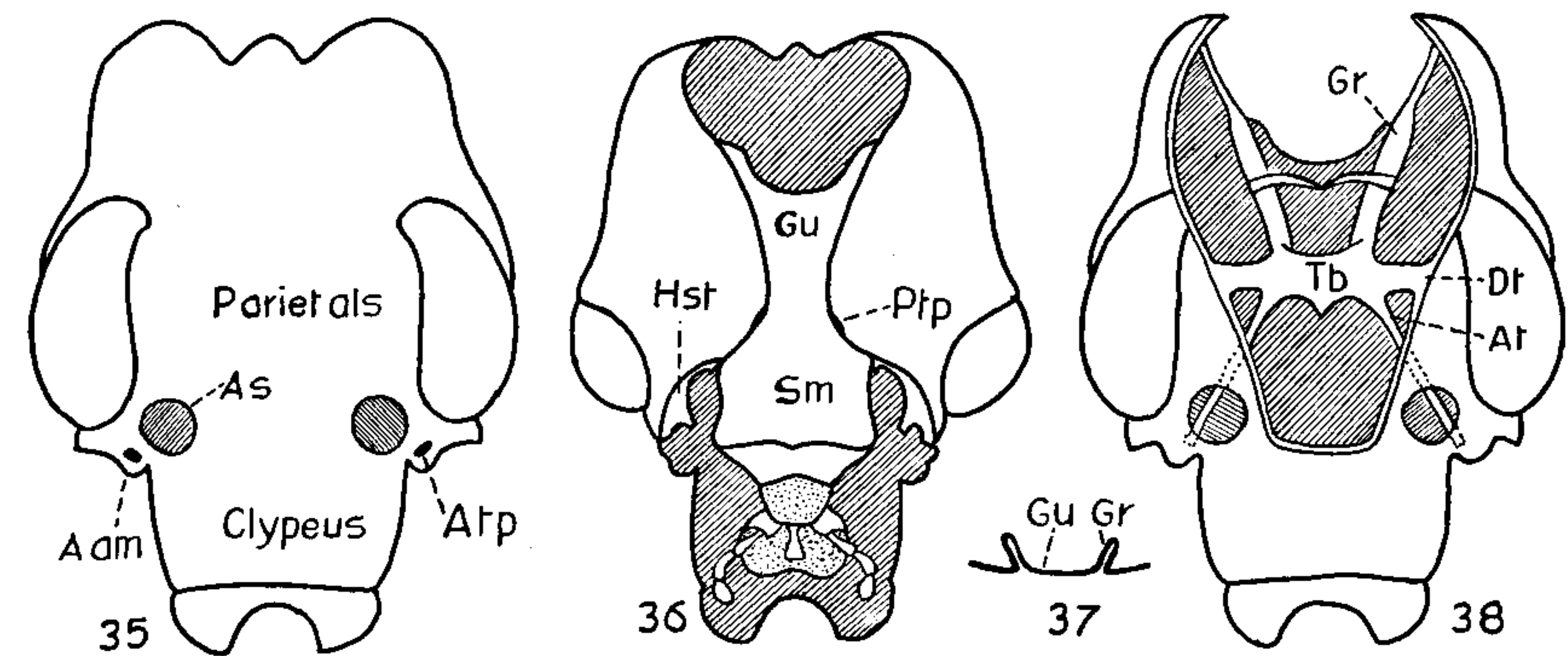
NOTE: Figs. 1-55 follow.













## Criteria for Interpreting the Cranial Structure

In order to interpret the changes which have taken place in the cranium, it is necessary to review certain landmarks in the generalized hypognathous head. If these can be identified in the head of the Coleoptera, it should be possible to trace, with reasonable certainty, the nature of the changes which have taken place.

### *The Facial Region (Fig. 1)*

The face in the generalized head consists of a parietal and a frontoclypeal region (8). The parietal region includes the vertex, which forms the entire dorsal region of the face, and the genae, two lateral lobes that extend to the ventral margin. The frontoclypeus is typically divided by the frontoclypeal sulcus (*Fcls*) into a dorsal frons and a ventral clypeus. The frons lies between the two genae and is separated from them by the frontogenal sulci (*Fgs*) which extend from the antennal sockets to the frontoclypeal sulcus adjacent to the condyles of the anterior mandibular articulation (*Aam*). The dorsal limit of the frons is not generally marked by a suture but in some insects a trans-frontal sulcus (*Trfs*), extending between the antennal sockets, cuts it off from the median region of the vertex. This median region, which bears the antennae, may be called the epifrons (*Epf*) for descriptive purposes.

The anterior tentorial pits (*Atp*) lie in the ventral ends of the frontogenal sulci at their junction with the frontoclypeal sulcus. They therefore lie at the level of the morphological mouth and it has been shown that they tend, in many insects at least, to retain this position regardless of changes in the head structure (1, 7, 9). If the frontoclypeal sulcus is absent a line drawn through the ventral ends of the pits will mark the approximate dorsal limit of the clypeus.

The proximal region of the clypeus extends laterally to form two small rounded lobes (*Aam*) which function as condyles for the anterior articulation of the mandibles.

### *The Occipital Region (Fig. 2)*

The occipital suture (*Ocs*), which extends around the cranium and terminates on each side just anterior to the posterior articulation of the mandible (*Pam*), separates the anterior, facial region from the posterior, occipital region. Another suture, the postoccipital sulcus (*Pocs*), divides the latter into the occipital arch and the postocciput. The postocciput (*Poc*) is the narrow sclerite to which the neck membrane is attached. The occipital arch is a more extensive sclerite in which three regions, the occiput (*Occ*) and two postgenae (*Pgen*), can be distinguished though not separated by sutures and therefore indefinite in their limits.

The postoccipital suture marks the position of an internal, often quite deep, inflection or ridge. The posterior tentorial arms, which unite to form the tentorial bridge, are attached to the postoccipital ridge near its ends; therefore the posterior tentorial pits (*Ptp*) are in the ventral ends of the suture. The proximal border of the submentum (*Sm*) lies between the ends of the postocciput adjacent to the pits.

The hypostomal suture (*Hs*) extends from the posterior articulation of the mandible to the ventral end of the postoccipital suture with which it is continuous. It cuts off a narrow marginal hypostoma (*Hst*) from the edge of the postgena. The socket of the posterior mandibular articulation (*Pam*) is in the ventral end of the hypostoma, and the maxillary articulation (*Mx*) is near its dorsal end. The hypostoma may be continuous with the pleurostoma (Fig. 1, *Plst*), when this is present, and the combined sclerites may be called the parastoma.

### Orientation of the Head in Coleoptera

A diagram of a typical hypognathous head is shown in Fig. 3. The occipital foramen retains its vertical orientation but the head rotates upwards through 90° causing the mouthparts to be directed anteriorly and the face to assume a dorsal instead of an anterior aspect. This is accompanied by the elongation of the postgenae which now form the lateral regions of a ventral wall to the cranium. The median region of the ventral wall is formed by the gulamentum, which is united with the postgenae. The gulamentum is composed of the submentum (*Sm*) and the gula, the latter being a new sclerite interposed between the submentum and the occipital foramen.

The head of Coleoptera is typically prognathous but, if we define prognathism strictly in terms of the orientation of the mouth parts, it shows all conditions from virtual opisthognathism, through hypognathism and various degrees of obliquity to literal prognathism.

The head of *Meloe* (Fig. 8) is definitely hypognathous in orientation. It will be seen from the figure that the mouth parts are directed ventrally and the facial aspect is anterior.

The occiput of the Cassidinae or tortoise beetles is greatly elongated in the dorsal region (Fig. 12, *Occ*) while the postgenae in the ventral region are much shorter. As a consequence the face is bent at an acute angle to the occiput, and the labrum is directed posteriorly. This brings the pleurostoma (Fig. 10, *Plst*) and hypostoma (Fig. 10, *Hst*) into the same plane, the two forming a continuous ventral sclerite, the parastoma (Fig. 12, *Pst*). The boundary between the parietal and occipital regions in *Chelymopha* is shown by the dotted line (Figs. 10 and 12, *Ocs*). There is no actual suture here but there is a sharp division between the light-colored face and the darker occipital arch.

Apart from the actual orientation the cranium in Coleoptera always conforms in structure to that of the prognathous head, therefore terms denoting direction or position will be used uniformly throughout as if the heads were all prognathous. Thus the gular region will be described as ventral regardless of its actual aspect.

### Facial Sutures

Reinforcing ridges, marked externally by sulci, are relatively unimportant in the usually heavily sclerotized and rigid cranium of the Coleoptera, therefore the facial sutures tend to be reduced or lost. They are best represented in *Chelymopha* (Fig. 9) and other tortoise beetles in which the frontogenal (*Fgs*) and transfrontal (*Trfs*) sulci as well as a midcranial sulcus (*Mcs*)



are present. The frontoclypeal sulcus is lost except for the extreme lateral ends which cut off the mandibular condyles (*Aam*). In one specimen, however, I found a faint groove, indicated by the dotted line (*Fcls*), in the position normally occupied by the sulcus.

The frontoclypeal sulcus is the one most frequently present in the facial region, but it is sometimes incomplete (Figs. 22 and 25, *Fcls*) and very frequently completely lacking (Figs. 32, 35, 47, 53). A complete or partial midcranial sulcus (Figs. 4, 6, 9, 17, 29, 50, *Mcs*) is frequently present. The genae in *Podabrus* have grown anteriorly, embracing the clypeus, and a pair of clypeogenal sulci (Fig. 47, *Clgs*), not observed in any other beetle examined, marks the lines of union between the clypeus and genae. In *Necrophorus* also there is a pair of sulci which are lacking in other heads examined. These extend from the frontoclypeal sulcus to the points of attachment of the dorsal tentorial arms to the cranium (Fig. 43, *S*).

There has been much confusion over the so-called "epicranial suture". Comstock and Kochi (2) defined it as "the inverted Y-shaped suture on the dorsal part of the head in the more generalized insects". It is obvious from this definition and from their figures that the term was used for the ecdysial line, which is not found in the head of adult Coleoptera, nor in the heads of most adult insects. Nevertheless several sulci in the cranium of adult Coleoptera have been interpreted as the "epicranial suture". When the midcranial sulcus is present, it is often interpreted as the "epicranial stem", and various other sulci as the "epicranial arms". Stickney (14), for example, thus interprets in different species the frontoclypeal sulcus, the clypeogenal sulci, the frontogenal and transfrontal sulci. Because of this confusion in the interpretation of the "epicranial suture" DuPorte (6) and Snodgrass (13) have suggested that the use of this term be discontinued since the sutures that have been included in it have other and more appropriate names.

The difference between these sulci and the ecdysial line is clearly shown in the adult and larval heads of *Leptinotarsa*. The ecdysial line (Fig. 5, *Cs* and *Fs*) is clearly defined in the larva and in addition there is a midcranial sulcus (*Mcs*) which extends anteriorly to meet the frontoclypeal sulcus (*Fcls*). The ecdysial sulcus is not present in the head of the adult (Fig. 4) but the midcranial sulcus persists, though it is much more weakly developed than in the head of the larva. This combination of midcranial and frontoclypeal sulci, which is found in the head of many species, has frequently been referred to as the "epicranial suture" in the literature.

### The Frontoparietal Region

The typical relation between the frons and the parietals is retained in *Chelymorpha* (Fig. 9) and other tortoise beetles. These are the only heads examined which retain distinct frontogenal and transfrontal sutures but, if the distance between the antennal sockets and the anterior tentorial pits is used as a criterion, it will be seen that some other species such as *Monochamus* (Fig. 17), for example, also retain more or less the primitive relations. Most species, however, do not.

One of the commonest modifications in the frontoparietal region is a progressive reduction in the distance between the antennae and the clypeus, until the antennal sockets in most species lie very close to or actually against the frontoclypeal sulcus. It might be thought that the antennae have migrated independently to the new position but a more likely explanation is that the epifrons has expanded anteriorly at the expense of the frons until the latter is almost or completely suppressed. Apparently the antennae do migrate independently in some insects. This seems to have happened in the dermapteron *Anisolabis* as is indicated by the position of the frontogenal sulci (Fig. 13, *Fgs*) which extend posteriorly far beyond the antennal sockets. The frontogenal sulci are almost always lacking in Coleoptera but the relation between the antennal sockets and the tentorial pits seems to be similar to that in the heads of Hymenoptera. In ichneumonids, for example, the antennae are high on the face, a considerable distance from the pits. In some sawflies, short-tongued bees, and many others the antennae are relatively much nearer the pits, while in the honeybee and vespids the antennal sockets almost touch the pits (1, 8, 9). In all of these, however, the frontogenal ridge terminates dorsally in the antennal ridge, regardless of the position of the latter. This suggests a progressive reduction in the height of the frons accompanied by the ventral expansion of the epifrons.

Examination of Figs. 1 and 9 will show clearly that if the epifrons, carrying the antennae, grows anteriorly until the frons is forced out, the antennae will come to lie adjacent to the frontoclypeal sulcus and the tentorial pit will be between the socket and the mandibular condyle (*Aam*). This is exactly the relation between these three structures when the socket is close to the suture. I have found exceptions to this only in the heads of *Harpalus* (Fig. 26) and *Staphylinus* (Fig. 39). The face in both of these insects is very broad, both the parietals and clypeus being expanded laterally. In *Harpalus* the antennae and mandibular condyles have been carried to the lateral borders of the face, leaving the tentorial pits in their primitive position. In *Staphylinus*, only the mandibular condyles are in the lateral border; the antennae and pits retain their primitive positions.

With the elimination of the frons the region proximal to the clypeus is the parietal region in which the distinction between the vertex and genae is lost. The parietal region tends to expand laterally and to grow around to the ventral side until, in most species, the ventral portion lies in the same plane as the postgenae and may form a very considerable part of the ventral wall of the cranium. As the occipital suture is usually lacking, the parietals and postgenae form a continuous sclerite, but the approximate position of the boundary between them may be ascertained by reference to the position of the socket of the posterior mandibular articulation (cf. Figs. 2 and 3, *Pam*, *Ocs*, with Fig. 23, *Pam*).

The extent to which the parietals encroach on the ventral wall varies widely. There is obviously no such encroachment in *Meloe* (Fig. 7). In *Staphylinus*, which retains the occipital suture (Fig. 42, *Ocs*), there is a slight encroachment,



whereas in *Podabrus*, which also retains the suture (Fig. 48, *Ocs*), the parietals form a considerable portion of the ventral wall. In *Dendroctonus* (Fig. 52) the parietals appear to have met in the mid-ventral line forcing out both the postgenae and the gula.

Another criterion which is sometimes useful in establishing the extent to which the parietals have spread to the ventral wall is the size of the ventral portion of the eye. The eyes are borne on the acronal or prostomial region of the head and it is unlikely that they would extend on to the postgena, which is almost certainly derived from the mandibular and maxillary segments. It is unthinkable, for example, that the ventral eyes of gyrids are borne on the mandibular segment. In insects like *Phyllophaga* (Fig. 23) and *Derobrachus* (Fig. 31) therefore it is evident from the area occupied by the eyes that much of the ventral wall is formed by the parietals.

In the circlionid *Cleonus* (Fig. 53) the anterior region of the parietals beyond the eyes, and the corresponding region of the postgenae, are greatly elongated and attenuated. This is responsible for the beak-like elongation of the head. There are no facial sutures but the position of the antennae and the tentorial pits shows that remnants of the frons and clypeus persist.

### The Occiput

Since the occipital suture is rarely present the occipital region is not clearly defined. The proximal region of the cranium is frequently narrowed (Figs. 39, 43) and an open groove separates it from the larger distal region. It is doubtful if the narrow region ever consists of the occiput only. Examination of the cranium of *Necrophorus* in ventral view (Fig. 46) shows that if this region is the occiput nothing remains of the postgenae but the hypostomae. This is extremely unlikely. It is obvious also that the transverse groove on the ventral side of the cranium of *Staphylinus* (Fig. 42), which retains the occipital suture, does not mark the limit of the occiput and it is doubtful whether the groove on the dorsal side is a continuation of the occipital suture.

### The Clypeus

The clypeus sometimes resembles that of the generalized cranium in that it projects beyond the anterior edge of the parietals and its lateral edges are free (Figs. 6, 26, 43), but in many species there is little or no such projection and it is reduced in size, being often little more than a narrow transverse band (Figs. 9, 39, 50). The clypeus is greatly enlarged in some species, notably in the scarabaeids, that of *Osmoderma* (Fig. 22), including its inflected border, being considerably longer than the remainder of the cranium. In these scarabaeids the entire border of the clypeus is inflected, carrying the mandibular condyles to the ventral side, but the adjoining regions of the parietals are also inflected and the antennae are carried to the ventral side. Therefore the antennae, tentorial pits, and mandibular condyles retain their normal relations to each other (Figs. 23, 25).

The labium is usually joined to the clypeus by a membranous strip which varies in width in different species. In some (Fig. 17) it appears to be a desclerotized region of the clypeus and in the literature it is known as the anteclypeus.

The basal region of the clypeus of the generalized orthopteroid insect extends laterally as two small rounded lobes which form the condyles for the anterior articulation of the mandibles (Fig. 1, *Aam*). Internally the thick ridges of the lobes form part of the junction between the anterior tentorial arms and the frontogenal, frontoclypeal, and subgenal ridges (Fig. 2, *At*, *Fgi*, *Fcli*, *Sgi*). I have interpreted the articulatory ridges as the ventral ends of the frontogenal inflections because in *Lepisma* the secondary articulation of the mandible is made at the ventral edge of the laterofacial inflection which, in Pterygota, becomes the frontogenal inflection (6). The anterior tentorial pits lie in the frontogenal sulci immediately above the condyles.

A similar lateral lobe of the clypeus forms the mandibular condyle in Coleoptera. It is heavily sclerotized even if, as in *Staphylinus* (Fig. 39), the body of the clypeus is membranous. The condyle in some species (Figs. 17 and 35, *Aam*) is continuous with the body of the clypeus, but in most species it is separated by a suture. In all of the heads examined, except those of *Harpalus* and *Staphylinus*, the tentorial pits are immediately posterior to the condyles. In the cranium of *Podabrus* or any other in which the genae have grown anteriorly and united with the clypeus the mandibles are of necessity articulated in another position.

There has been considerable confusion in the interpretation of these articulatory lobes. The frontal suture in the larva of *Corydalis* and some related neuropteroids cuts through the clypeus and divides it into a median and two lateral sclerites. Comstock and Kochi (2), believing that the lateral sclerites are the equivalent of the articulatory lobes in the cricket and that they are both detached fragments of the mandibular segment, called them the antecoxal pieces of the mandibles. Crampton (4) recognized that the lateral sclerites of *Corydalis* are parts of the clypeus and called them the lateroclypeal or paraclypeal lobes. MacGillivray (11) believed that the clypeus is formed by the fusion of four primary sclerites, two of which are represented by the paraclypeal lobes of *Corydalis*. He called these lobes the clypealia and the condyles, which of course are borne on them, the clypanguli. Stickney (14), accepting MacGillivray's interpretation, interpreted the condyles in the Coleoptera as clypealia, presumably because they are usually separated from the body of the clypeus by sutures. Ferris (10), confusing the frontal suture with the frontoclypeal, claimed that the paraclypeal lobes are not parts of the clypeus, but belong to the "antennal segment". He believed them to be basic components of the head with which the anterior articulation of the mandible is made. Cook (3) accepted Ferris's interpretation and identified the condyles in Coleoptera with the paraclypeal lobes of *Corydalis* and tried to show how they become reduced in these insects and, in some species, secondarily united with the clypeus.



The condyles cannot possibly be the same as the paraclypeal lobes. These are formed as the result of the extension of the frontal sutures through the clypeus of the larva and are not present in the adult *Corydalis*. There is no frontal suture in adult Coleoptera and the suture which cuts off the condyles from the clypeus is a sulcus and not a line suture. The frontal sutures in the larva of *Leptinotarsa* (Fig. 5, *Fs*) terminate far distant from the condyles (*Aam*), which are nevertheless cut off from the clypeus.

### The Gula and Submentum

MacGillivray (11) believed that the gula is formed as a result of the mesal growth and union of the two postgenae. Stickney (14), who held the same view, claimed further that the gular sutures mark the path of migration of the posterior tentorial arms. If the gula originated in this way we should expect to find some evidence of its origin in the occasional presence of a median suture marking the line of union of the postgenae. Such evidence is found in some Lepidoptera and Hymenoptera in which the subforaminal bridge is formed by the mesal growth of the hypostomae. When there is a mid-ventral suture in the Coleoptera its presence is susceptible of another and more plausible explanation.

Crampton (5) adopted Holmgren's interpretation of the origin of the submentum as a sclerite in the membrane between the labial and prothoracic segments. He regards it as part of the sternum of the labial segment and claims that in some insects, including the Coleoptera, the plate, which Holmgren calls the submentum in the embryonic termite, gives rise to the gula, the submentum, and the mentum. He believes therefore that the gula-mentum is primary and the separation into gula and submentum secondary. In other words the gula in Coleoptera is a proximal region of the submentum as the latter exists in the generalized cranium. Ferris (10) takes essentially the same view. The sclerite which in some species (Fig. 14, *Sm*) is often called the gula is the submentum or gulamentum, but there is no evidence that the sclerite here interpreted as the gula is a subdivision of the submentum and much against it.

Other workers have given a more acceptable interpretation of the gula. Snodgrass (12) states, in effect, that with the rotation of the head and the elongation of the ventral region the posterior tentorial pits are carried anteriorly and that the submentum, retaining its relation to the pits, is also carried forward. Thus a space is formed between the submentum and the occipital foramen and this space is filled with an extension of the neck membrane which becomes sclerotized to form the gula. Thus the position of the pits defines the boundary between the gula and the submentum.

It is preferable, however, to relate the gula to the postoccipital sulcus and ridge rather than the tentorial pits. It can then be defined as the sclerite lying between the anterior extensions of the postoccipital ridge. If the figures which show the tentorium are examined and compared with the ventral view of the corresponding heads, this relation between the postoccipital ridge, the gula, and the submentum should be clear.

The head of the dermapteron *Anisolabis* (Fig. 13) provides a clue to the probable origin of the gula. Except for the elongation of the postgenae the ventral aspect of the cranium resembles the posterior aspect of the generalized hypognathous head (Fig. 2) very closely, but the head of *Anisolabis* is tilted upwards into the prognathous position. As a result the occipital foramen, as indicated by the postoccipital sulcus (*Pocs*), is oblique and the submentum (*Sm*) is carried forward but retains its basal connections with the ends of the postocciput adjacent to the tentorial pits. The obliquity of the foramen is compensated for by the development of two sclerites in what would otherwise have been a ventral extension of the neck membrane. The posterior sclerite (*Cvs*) is free in the neck membrane but the anterior one, the gula, is united with the submentum. Neither the gula nor the submentum is united with the cranial wall but if they were, the ventral wall of the head would be essentially like that of *Criocephalus* (Fig. 16).

The ventral region of the head of the embiid *Enveja* is almost exactly like that of *Anisolabis* except that the gula (but not the submentum) is united with the cranium. The cranium of *Chelymorpha* (Fig. 10) is, in this respect, quite similar to that of *Enveja*.

Further evidence of the origin of the gula from the cervical membrane is given by Snodgrass (12) in his figure of the larval head of *Melanodrya* in which the region which in other species is occupied by the gula is simply an extension of the cervical membrane.

It is obvious that the gular sutures and gular ridges are ventral extensions of the postoccipital suture and postoccipital ridge and can legitimately be referred to as such. This is clearly shown in *Monochamus* (Figs. 18 and 19) and in most of the internal views of the cranium.

The gula and submentum, having united with the cranium, may now increase or diminish in either dimension as do the other cranial sclerites.

It might be asserted that if the gula is a sclerotization between the two anterior extensions of the postocciput it is tripartite in origin and that some evidence of this might be expected to persist in the form of sutures between the three components. That such evidence is not found, except in some doubtful cases (Fig. 25), is not really surprising because in most species there is no external postoccipital sclerite, the postocciput being represented only by the posterior lamina of the postoccipital ridge. If this ridge is carried forward by the tilting of the head or the elongation of the postgenae the gula when formed will extend between the posterior lips of the ridge and will not include any external portion of the postocciput. These relations are shown in the cranium of *Monochamus* (Fig. 18) in which the line *Cm* represents the posterior lip of the ridge to which both the cervical membrane and the gula are attached.

The variation in the length of the gula and the position of the tentorial bridge suggests that when the head rotated, the region of the postgenae which increased in length was not the same in all species. In *Chalcophora* (Figs. 14 and 15) there is no elongation of the postoccipital ridge, and the tentorial pits remain in their original position. Elongation took place therefore