THE LORAL PLATES AND THE HYPOPHARYNX OF HEMIPTERA.

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After many years of investigation and discussion on the morphology of the hemipterous head and mouth parts, two features have remained without a satisfactory explanation. It must be understood, of course, that a "satisfactory explanation" in this case is one that shows how the parts in question correspond with generalized structures in the head of orthopteroid insects. One of the problematical points in the morphology of the hemipterous head is the nature of the sclerites lying at the sides of the clypeus, known as the lora, juga, paraclypeal lobes, or mandibular plates, on which the protractor muscles of the mandibles are attached; the other is the homology of these muscles themselves. The lora, as the plates in question are termed by homopterists, have been referred by different writers to the mandibles, to the genae, and to the clypeus. Two recent papers appearing almost at the same time, one by Spooner (April, 1938), the other by Evans (May, 1938), take up the question of the nature of the lora, and, by a further coincidence, the two authors arrive independently at the same conclusion, namely, that the lora are secondarily detached parts of the postclypeus. Neither writer, however, gives due consideration to the facts that the lower ends of the lora are directly continuous beneath the anteclypeus with the body of the hypopharynx, and that their lateral areas give attachment to the protractor muscles of the mandibles. These two constant features of the lora constitute an anatomical condition quite incompatible with the idea that the loral plates are primarily parts of the clypeus. Though sclerites on which mandibular muscles are normally attached may be supposed to have united secondarily with the clypeal margins, there is no precedent in insect anatomy for the origin of mandibular muscles on any part of the clypeus. Sclerites having the anatomical relations of the hemipterous lora, excepting the clypeal connections, are to be found among insects with biting mouth parts only in the lateral sclerites of the hypopharynx itself that give attachment to the hypopharyngeal muscles of the mandibles.

The basic structure of the hemipterous head is best exemplified in the hypognathous, or auchenorrhynchous, Homoptera (Pl. 22, A, B, C). The clypeus in this group is usually subdivided into a large, protuberant postclypeus (A, *Plcp*), on which the dilator muscles of the sucking pump take their origin, and into a smaller anteclypeus, or clypeolus (*Aclp*), which supports the Labrum (*Lm*), and bears on its inner, or epipharyngeal,

surface the plunger of the pump (H, I, *i*). In some forms, as in the Fulgoridae (B, C), the clypeus is a smaller, more ventral plate, and is not distinctly divided between its postclypeal and anteclypeal areas. Lying immediately laterad of the clypeal margins are the lora (A, B, *Lor*), and behind the lora are the so-called maxillary plates (*MxPl*). Deeply inflected between the lorum and the maxillary plate on each side is the protractor arm of the mandible (E, K, *pa*), which articulates dorsally with the posterior lateral margin of the lorum (*k*), and gives insertion to the protractor muscles of the mandible (*mdpr*) arising on the inner face of the lorum (*Lor*). The retractor arm of the mandible (*ra*) extends up the lateral wall of the bristle pouch and gives attachment to retractor muscles (*mdr*) arising on the vertex.

The loral plates, when fully exposed by removing the anteclypeus from the head, are seen to be directly continuous ventrally with the sides of the hypopharynx (E, F, *Lor*). Their upper parts are always attached anteriorly to the lateral margins of the postclypeus, and usually the lines of attachment are evident as grooves formed by the inflected clypeal margins (E, F, *g*). In some forms, however, as in certain Fulgoridae among the Homoptera (C), the Peloridiidae (D), and in all Heteroptera, the upper parts of the lora are entirely fused with the postclypeus, so that the exposed areas of the loral plates (*Lor*) appear as lateral lobes of the postclypeus. The condition of continuity between the postclypeus and the lora is taken by Spooner (1938) and by Evans (1938) to represent the more generalized structure, and is given as evidence that the lora have been derived by a secondary separation from the postclypeus. This conclusion involves the assumption that the protractor muscles of the mandibles primarily had their mesal attachments on lateral lobes of the clypeus (C, *mdpr*), and it is further burdened with the necessity of explaining how the lower ends of the lora acquired a continuity with the hypopharynx before they separated from the clypeus.

The simplest and most satisfactory explanation that can be given of the nature of the hemipterous lora is the assumption that the loral plates are morphologically, as well as anatomically, lateral expansions of the parts of the hypopharynx on which the hypopharyngeal muscles of the mandibles take their origin (J, *mdh*). Heymons (1899), in his study of the embryonic development of the Hemiptera, says (p. 440) that the lora (laminae mandibulares) are derived from "Bestandtheilen des Mandibularsegmentes," though in describing the cicada (p. 422) he ascribes them to both the mandibular and the antennal segment, and in Heteroptera (p. 370) to the antennal segment alone. The attachment of mandibular muscles on the loral plates, however, is presumptive evidence that the lora themselves are derived from the mandibular somite, and there is no

question that the anterior part of the hypopharynx is formed from the venter of this somite.

The mandibular muscles attached on the sides of the base of the hypopharynx in orthopteroid insects are undoubtedly remnants of the primary ventral adductors of the mandibular appendages, though in modern biting insects it is questionable whether their contraction adducts the jaws or flattens the base of the hypopharynx. In orthopteroid and other insects with biting mouth parts in which these muscles occur (J, *mdh*), the muscles are attached mesally either directly on the base of the hypopharynx or on mandibular arms (*x*) of the suspensorial sclerites (*sus*) of the hypopharynx, and laterally on the inner surfaces of the lateral walls of the mandibles. The protractor arms of the hemipterous mandibles, on which the loral muscles are attached (E, K, *pa*), are not true apodemes but are proximal extensions of the lateral walls of the mandibular bases, and hence represent the same areas of the mandibles as those of biting insects (J) on which the hypopharyngeal muscles are attached. In the Hemiptera both of the primary articulations of the mandible on the subgenal margin of the cranium have been suppressed in order to give freedom of movement to the mandibular base; the articulation with the lorum (E, K, *k*) represents the mesal point of contact between the mandibular base and the base of the hypopharynx. The retractor muscle of the hemipterous mandible arising on the vertex (K, *1mdr*) is evidently the adductor muscle of the biting jaw; in the cicada the primitive cranial abductor appears to be represented by a second retractor muscle (K, *2mdr*) arising on the gena and inserted laterally on the mandibular base. The reduction in size of the mandibular bases in hemiptera has exposed the lateral parts of the hypopharynx on the sides of the head, and the retraction of the mandibles has converted the primitively adductor hypopharyngeal muscles of the mandibles into protractor muscles. The connection of the hypopharyngeal loral plates with the postclypeus, therefore, is a secondary union, which in some forms has progressed to a complete fusion by an obliteration of the clypeoloral sutures.

A morphological interpretation can not be fully acceptable unless it is consistent in all its implications. If the loral plates of the hemipterous head are lateral expansions of the base of the hypopharynx, we should find an entire conformity in the structture of the hypopharynx in Hemiptera with the structure of the hypopharynx in more generalized insects.

The removal of the anteclypeus and labrum of an homopterous insect, including the epipharyngeal wall of the anteclypeus, not only exposes the continuity of the lower ends of the loral plates with the median body of the hypopharynx (E, F), but reveals

also, on the base of the hypopharynx, a median, oval or elongate, basinlike cavity (*f*) with strongly sclerotic walls and well-defined marginal ridges. This cavity is the floor of the sucking pump (I, *f*). On the epipharyngeal surface of the removed anteclypeus (H) is the piston, or plunger, of the pump (*i*), which projects as an oval or elongate elastic fold from an epipharyngeal cavity with marginal ridges that normally fit tightly upon the marginal ridges of the hypopharyngeal pump floor. The relations of the epipharyngeal and hypopharyngeal parts of the pump are readily seen in a cicada if the "mouth" is forcibly opened by depressing the hypopharynx (I). The "orthopteroid" structure of the parts exposed at once becomes evident. The free terminal hypopharyngeal lobe (*d*) is only the apical part of the hypopharynx (*Hphy*), since the anterior surface of the latter continues upward to the mouth (*Mth*), includes the basinlike floor of the sucking pump (*f*), and gives off laterally the large loral plates (*Lor*). In addition, moreover, the hemipterous hypopharynx includes a pair of posterior plates (G, *h*, *h*) that arise from the base of the apical lobe and extend dorsally in the mesal and posterior walls of the invaginations that form the bristle pouches. The upper ends of these plates in Homoptera are generally united with the posterior arms of the tentorium (*PT*), and their haemocoelic surfaces give attachment to the dilator muscles of the salivary syringe. The hemipterous hypopharynx is thus seen to be a highly developed and complex structure forming many important elements of the feeding apparatus.

In order to understand the modifications that have produced the complex structure of the hypopharynx in Hemiptera, some attention should be given to the generalized structure of the organ shown in Orthoptera. In the hypognathous position, which may be taken as basic for descriptive orientation, the typical orthopterous hypopharynx hangs between the mandibles from the ventral wall of the head (J, *Hphy*). Its long anterior surface continues upward to the mouth (*Mth*); its relatively short posterior surface is reflected into the anterior wall of the labium at the base of the prementum, where is situated the orifice of the salivary duct.

The upper part of the anterior surface of the orthopteroid hypopharynx is always, and usually very distinctly, differentiated from the ventral part of the organ that forms the free tongue-like hypopharyngeal lobe (J, *d*), which may be termed specifically the *lingua*. The adoral supralingual area is generally depressed, and is flanked by a pair of sclerites (*sus*) from which two slender arms (*y*) extend upward into the angles of the mouth, where they enter the stomodaeal wall and give insertion to a pair of retractor muscles (*hf*) arising on the frons. This upper adoral hypopharyngeal structure serves in biting and chewing insects

as a receptacle for the masticated food passed back from the mandibles, and also, by the contraction of the frontal muscles inserted on its suspensorial sclerites, as a conveyor of the food to the mouth. In orthopteroid insects it often resembles a basket, but since in other insects it takes on various forms, it may be termed the *sitophore*, or "food carrier." To the sides of the suspensorial sclerites, usually on a pair of lateral arms (J, *x*), are attached the hypopharyngeal muscles of the mandibles.

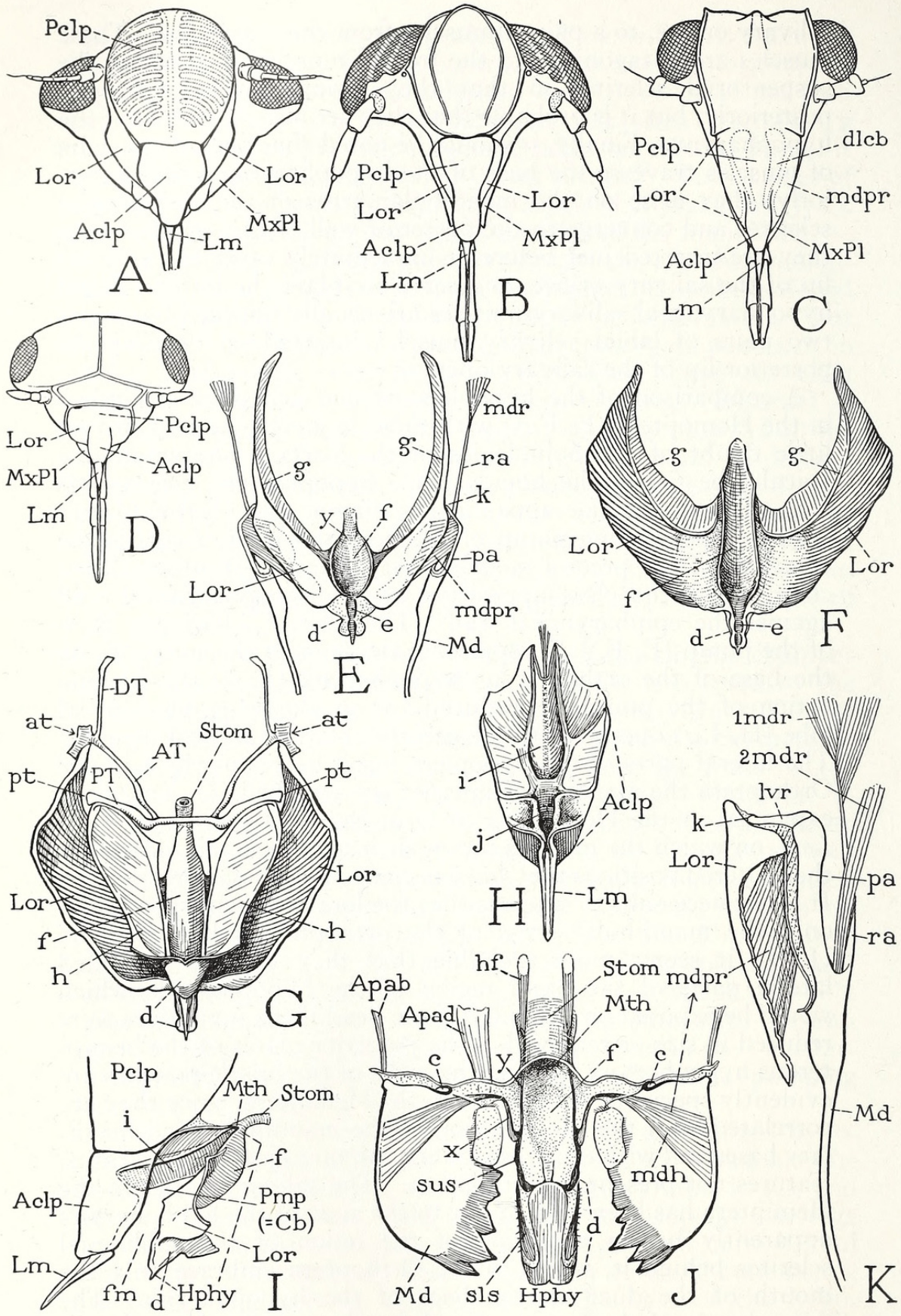
The sitophore of the hypopharynx, with the attached mandibular muscles, is characteristic of Orthoptera, is well developed in Dermaptera, and is typically present in Lepismatidae, but apparently it has no prototype in other apterygote insects or in other arthropods. Its suspensory sclerites have no clear relation to the premandibular suspensory plates (fulturae) of Chilopoda and Diplopoda that support the hypopharynx on the lateral margins of the cranium, and at most could be derived from only the mesal ends of these plates. In an earlier discussion of the insect hypopharynx the writer suggested that the food-carrying part of the organ may represent the venter of the tritocerebral somite, but the attachment of mandibular muscles on it would indicate that it belongs specifically to the somite of the mandibles.

The floor of the sitophore is the floor of the cibarial chamber of the preoral mouth cavity, which normally is covered by the inner, or epipharyngeal, wall of the clypeus. In the more generalized insects, as above noted, the sitophore is characteristically a basketlike structure suspended from the frons by the frontal muscles attached on its lateral arms. However, in coleopterous larvae it forms the large retractile preoral sclerite situated on the base of the hypopharynx, in Corrodentia and Mallophaga it becomes the curious mortarlike hypopharyngeal sclerite with thick basal arms on which the frontal muscles are inserted, and in Thysanoptera, Hemiptera, and Diptera it is the sclerotic basin of the sucking pump. The epipharyngeal dilator muscles of the cibarium arising on the clypeus probably play only a minor part in the process of ingestion with Orthoptera, but they become highly important elements of the "mortar-and-pestle" apparatus of Corrodentia, and of the pumping mechanism of sucking insects.

The free lobe, or true lingua (J, *d*), of the generalized hypopharynx has a pair of lateroventral sclerites (*sls*), which may be designated the *sublingual sclerites*. Though variable in size and shape, these sclerites, when typically developed, converge proximally in the posterior wall of the lingua and unite behind the orifice of the salivary duct. Contrary to usual statements, therefore, the salivary opening is on the base of the hypopharynx, and not literally between the hypopharynx and the labium. The sublingual sclerites give attachment, laterad of the

salivary orifice, to a pair of muscles from the tentorium. These muscles are antagonistic to the frontal muscles inserted on the suspensorial sclerites in that they swing the hypopharynx posteriorly, but it is probable that they are also retractors of the hypopharynx. Finally, it should be noted that one or two pairs of muscles traverse the base of the hypopharynx anteroposteriorly; they arise on the mandibular arms of the suspensorial sclerites and converge to the posterior wall of the lingua, where they are inserted just before or immediately upon the anterior lip of the salivary orifice, and serve to dilate the latter. These hypopharyngeal salivary muscles are usually opposed by one or two pairs of labial salivary muscles inserted on or near the posterior lip of the salivary opening.

A comparison of the hypopharynx and accessory structures in the Homoptera (E, F, I) with those in a cockroach (J) leaves little doubt of the homologies of the parts. The small free apical lobe (*d*) of the homopterous hypopharynx corresponds with the tongue-like appendicular lingua (*d*) of the blattid organ. The sucking pump of the hemipteron (I, *Pmp*) is the cibarium of the preoral mouth cavity, converted into a closed chamber by the close apposition of the hypopharyngeal wall against the epipharyngeal wall. The sclerotic, basinlike floor of the pump (E, F, I, *f*) represents the floor of the sitophore on the base of the orthopterous hypopharynx (J, *f*); the sucking action of the pump is produced by an elastic epipharyngeal lobe (H, I, *i*) operated by the greatly enlarged clypeal muscles. The lateral parts of the hypopharyngeal base, on which in the Orthoptera the mandibular muscles are attached (J), have been expanded in the Hemiptera to form the loral plates (E, F, I, *Lor*), on which the muscles retain their attachments, though by their altered positions they have become mandibular protractors. It is not necessary to suppose that the lora represent specifically only the mandibular arms of the orthopterous hypopharynx (J, *x*); it seems more probable that they are the expanded lateral parts of the basal region of the hypopharynx, which would be exposed on the sides of the head if the mandibles were reduced in size or removed. The posterior plates of the hemipterous hypopharynx forming the walls of the bristle pouches are evidently special developments in the Hemiptera, since they are correlated with the invagination of the mandibular and maxillary bases and with the presence of a salivary ejection apparatus, features not present in Orthoptera. The salivary outlet in the Hemiptera has been carried out to the apex of the hypopharynx apparently by an extension of the union of the sublingual sclerites behind it, which in the Orthoptera embrace only the mouth of the duct on the base of the hypopharynx. The musculature of the hemipterous hypopharynx has been simpli-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fied because the organ is an immovable part of the feeding apparatus. The frontal and tentorial muscles appear to be absent, though the former may be represented by the first pair of stomodaeal dilators, which arise on the frons. The mandibular and salivary muscles, on the other hand, are highly developed, the first attached on the lateral loral plates, the second arising on the plates of the bristle pouches.

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Explanation of Plate.

A, *Cephisus siccifolius* Walk. (Cercopidae), head of nymph, showing usual relation of facial sclerites in auchenorrhynchous Homoptera.

B, *Pentagramma vittatifrons* (Uhl.), adult head, illustrating relatively small size of postclypeus in Fulgoridae, and lack of separation between postclypeus and anteclypeus.

C, *Ormenis pruinosa* (Say), example of a fulgorid having the lora (*Lor*) united with the postclypeus, as shown by origins of protractor muscles of mandibles (*mdpr*).

D, *Hemiodoecus fidelis* Evans (Peloridiidae), lora united with postclypeus as in the fulgorid *Ormenis* (C).

E, *Cephisus siccifolius*, nymph, hypopharynx and bases of mandibles, anterior view, exposed by removal of clypeus, showing continuity of the loral plates (*Lor*) with base of hypopharynx.

F, *Magicicada septendecim* (L.), hypopharynx and its loral expansions exposed by removal of clypeus.

G, same, hypopharynx and tentorium, posterior aspect.

H, same, posterior (epipharyngeal) surface of anteclypeus and labrum.

I, same, lateral view of preoral mouth cavity opened by depression of hypopharynx, showing chamber of sucking pump (*Pmp*) to be the cibarial cavity of orthopterous insects between base of hypopharynx and epipharyngeal wall of anteclypeus.

J, *Periplaneta americana*, mandibles and hypopharynx, anterior surface, showing tentorial mandibular muscles (*mdh*) attached on base of hypopharynx.

K, *Magicicada septendecim*, right mandible and muscles, showing homology of protractor muscle (*mdpr*) with hypopharyngeal muscle of mandible of *Periplaneta* (J, *mdh*).

Acip, anteclypeus (clypeolus); *Apab*, abductor apodeme of mandible; *Apad*, adductor apodeme of mandible; *AT*, anterior tentorial arm; *at*, anterior tentorial pit; *c*, anterior articulation of mandible; *d*, free lobe (lingua) of hypopharynx; *dlcb*, attachment of dilator muscles of sucking pump on postclypeus; *DT*, dorsal tentorial arm; *e*, median groove of hypopharynx; *f*, floor of sucking pump, or of food receptacle (sitophore), on base of hypopharynx; *fm*, food meatus; *g*, line of attachment of lorum with postclypeus; *h*, posterior plates of hypopharynx in walls of bristle pouches; *hf*, musculus hypopharyngis frontalis; *Hphy*, hypopharynx; *i*, epipharyngeal plunger of sucking pump; *j*, epipharyngeal depression receiving terminal lobe (*d*) of hypopharynx; *k*, articulation of protractor arm of mandible with lorum; *Lor*, lorum; *Lm*, labrum; *lvr*, lever of protractor arm of mandible; *Md*, mandible; *mdh*, musculus mandibuli hypopharyngealis; *mdpr*, musculus mandibuli protractor; *mdr*, musculi mandibuli retractores (*1mdr* arising on vertex, *2mdr* arising on gena); *Mth*, mouth; *MxPl*, maxillary plate; *pa*, protractor arm of mandible; *Pclp*, postclypeus; *Pmp*, chamber of sucking pump (preoral cibarial cavity, *Cb*); *PT*, posterior tentorial arm; *pt*, posterior tentorial pit; *ra*, retractor arm of mandible; *sls*, sublingual sclerite; *Stom*, stomodaeum; *sus*, suspensorial sclerite of hypopharynx; *x*, mandibular arm of suspensorial sclerite; *y*, oral arm of suspensorial sclerite.

SOME PSAMMOCHARIDAE FROM SINGAPORE.

By NATHAN BANKS.

During a visit of some months to Singapore, the late C. F. Baker collected a number of Psammocharidae there and on the island of Penang. These were sent to me by the National Museum in shipping the Baker Philippine Psammocharidae for my study. I have therefore made a report on these Singapore species. The collection is particularly interesting because of the number of Pseudagenini. Frederick Smith described a few species from Singapore, and Cameron and one or two others have added a few; but much of the fauna is still unknown. Many of the species are the same as occur in the lowland areas of Borneo, Celebes, and the Philippines, and doubtless other parts of the Insulinde. Of a number of old species I have added some descriptive matter, omitted from the originals. The classification is explained in my paper on the Philippine forms.

The holotypes and uniques of the material herein discussed are in the U. S. National Museum and some paratypes are in the Museum of Comparative Zoology at Cambridge, Mass.