Maxillae of Fourth Stage Mosquito Larvae (Diptera: Culicidae)

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ABSTRACT. The maxillae of fourth stage mosquito larvae, representing all but 2 of the known genera, have been examined with the light microscope. A general description of the maxilla is given and the dorsal and ventral surfaces of the maxillae examined are illustrated. In addition, representatives of the families Dixidae and Chaoboridae are included.

Introduction

In Part XI of "A Mosquito Taxonomic Glossary" (Harbach and Knight 1977), we adopted a single terminology for the substructures of the larval culicid maxilla based upon an examination of fourth instars of the genera listed by Knight and Stone (1977) except *Ficalbia* and *Galindomyia*. The maxillae depicted in Part XI, however, were only those necessary to illustrate each named structure. The mophological diversity of the maxilla offers additional taxonomic characters for systematists, therefore, all of the maxillae examined to complete Part XI are portrayed herein, including representative species from the Dixidae and Chaoboridae. Also included is a composite description of the fourth stage larval maxilla to complement the list of definitions for maxillary substructures given in Part XI. For previous important contributions on the morphology of the maxillae of culicid and other nematocerous larvae, consult the references cited by Harbach and Knight (1977).

Materials and Methods

Alcohol-preserved larvae used in this investigation were accrued over a period of many years by the senior author. For slide preparations, heads were removed from the larvae, cleared in 10% potassium hydroxide, and transferred to a mixture of phenol-balsam (Wirth 1961) where the maxillae were dissected out. The maxillae were subsequently mounted on glass slides using Knight's (1971) modification of Wirth's procedure. One or more specimens were prepared for each species examined.

The terminology and the system of abbreviations developed by Harbach and Knight (1977) are used throughout the manuscript. With respect to the figures, 2 drawings for each species are arranged with the dorsal aspect of the left maxilla on the left and the ventral aspect of the right maxilla on the right. The sequence of the taxa has no phylogenetic significance, but in some instances related genera are placed together.

The Maxilla

The head of the culicid larva is basically prognathous. The mouthparts, therefore, are considered as anterior appendages with the maxillae borne obliquely on the transverse margin of the lateralia where they lie ventral to the mandibles. For simplicity, the surface of each maxilla adjacent to a mandible is considered as the dorsal surface. This means that the margin bearing the maxillary palpus is the lateral margin, the ventral surface lies parallel to the plane of the lateralia, and the mesal margin is that border near the midline of the head.

1. Cardo, stipital arm, and cardostipital arm.

Located mesally below the base of the maxilla in dixid (Fig. 1a) and anopheline larvae is an inward projection of the head, the *paracoila* (Pla). Articulated with the paracoila is a rod-like structure which represents a reduced and modified *cardo* (Cd) (Figs. 1a,f; 2a,c). Distally the cardo articulates with the ventral end of an apodematous ridge, the *stipital arm* (SAr), which is borne along the mesobasal edge of the maxillary body. In culicine and toxorhynchitine larvae the cardo is absent, but in many culicines the apodematous ridge is well developed. In some culicines, e.g., *Armigeres* (Fig. 10e), the ridge articulates with a distinct paracoila (Fig. 10f). This ridge, which probably represents the fused cardo and stipital arms of dixids and anophelines, is referred to as the *cardostipital arm* (CAr). The stipital adductor, which originates on the posterior tentorial arm in *Armigeres, Eretmapodites,* and *Zeugnomyia,* usually has its insertion on the dorsal end of the stipital or cardostipital arm.

2. Maxillary palpus and merostipes.

In dixid larvae (Fig. 1a,b) the *maxillary palpus* (MPlp) is borne on a lateral extension of the maxillary body. This extension evidently represents a lateral part of the stipes, the *merostipes* (mSt). The merostipes articulates with the base and/or postartis of the mandible. In the generalized culicine genera *Opifex* (Fig. 10b), *Eretmapodites* (Fig. 10d), and *Armigeres* (Fig. 10f), a small sclerite located below the base of the palpus also articulates with the mandible. Since this structure is believed to be homologous with the merostipes, it has been named the *merostipital sclerite* (mSS). Similarly, a small band of cuticle which also articulates with the mandible but is directly attached to the base of the palpus in a number of other culicines (e.g., see *Deinocerites*, Fig. 4a,b) has been named the *merostipital process* (mSP).

The merostipes has been incorporated into the maxillary palpus in anophelines (Figs. 1e,f; 2a-d), toxorhynchitines (Fig. 16e,f), and some culicine larvae. Evidence for this is twofold: 1) the base of the maxillary palpus articulates directly with the mandible and 2) the seta borne laterally on the merostipes of dixids (Fig. 1b) appears to be homologous with *seta 7-MP* (7) which is borne laterally on the maxillary palpus of *Mimomyia* (Fig. 5c,d) and the anophelines (Figs. 1e,f; 2a-d). Rather than apply a new term to the merostipes-palpus complex in these cases, it is referred to simply as the *maxillary palpus* (MPlp).

Small spine-like cuticular projections, the *maxillary palpal spiculi* (MPS), occur on the maxillary palpus in some species. These are located over most of its surface in dixids (Fig. 1a,b), primarily the dorsal surface in anophelines (Figs. 1e; 2a,c), near its apex in toxorhynchitines (Fig. 16e), and occupy various positions in certain culicines, e.g., *Udaya* (Fig. 12d).

Located at the apex of the maxillary palpus are as many as 7 innervated cuticular structures, the *maxillary palpal sensoria* (MS). These are typically peg-like although 3 are usually scalelike in anophelines. They are numbered 1 through 7. In order to number homologous sensoria in various taxa, consult Harbach and Knight (1977).

3. Maxillary body.

The main part of the maxilla, the *maxillary body* (MxBo), lies mesal to the maxillary palpus. In many culicines, the maxillary body has distinct lateral and mesal lobes which are demarcated dorsally by a *dorsal maxillary suture* (DMxS) and ventrally by a *ventral maxillary suture* (VMxS) (Figs. 6, 10a-d, 11a,b). The mesal lobe, the *laciniastipes* (LSt) is believed to represent the fused lacinia and stipes because: 1) it has a muscle inserted dorsally which is probably homologous with the cranial flexor of the lacinia, 2) it bears rows of setae laterally which are similar to those borne on the lacinia of generalized insects, and 3) it bears the stipital or cardostipital arm basally. In dixids (Fig. 1b), that portion of the maxillary body corresponding to the lateral lobe is separated from the merostipes by a wedge of translucent cuticle, the *galeastipital fissure* (GSF). Because of this, the lateral lobe of the culicine maxilla is thought to represent the fused galea and stipes, the *galeastipes* (GSt). In those genera where the laciniastipes and galeastipes are readily distinguishable, e.g., *Haemagogus* (Fig. 6d) and *Opifex* (Fig. 10b), a slender mesoventral extension of the galeastipes, the *galeastipital stem* (GSS), is usually separated from the laciniastipes by a small gap or slit, the *basal notch* (BN). Where the laciniastipes and galeastipes are indistinct, the ventral maxillary suture is absent. The dorsal maxillary suture is almost always present except in certain predatory species, e.g., *Aedes (Mucidus)* (Fig. 9c), and in some species where the maxillary palpus and maxillary body are fused, e.g., *Chaoborus* (Fig. 1c), *Malaya* (Fig. 13c), and *Sabethes* (Fig. 16a).

In many culicid larvae a dorsally located, often poorly developed, basal expansion of the laciniastipes, the *laciniastipital expansion* (LSE) (Figs. 2a, c; 10a,e), extends laterally from a point where the cardostipital or stipital arm and the dorsal maxillary suture merge. The expansion usually bears the insertion of the cranial flexor of the lacinia, but the stipital adductor is sometimes attached to it as well.

Borne on the mesodorsal surface of the maxillary body, or the laciniastipes when distinguishable, are 3 rows of variously developed setae, the *laciniarastra* (LR). *Laciniarastrum 1* (LR_1) is the most mesal of the laciniarastra. It usually consists of stout or long hair-like setae, but other forms are not uncommon, e.g., it may consist of scale-like elements as in *Opifex* (Fig. 10b), *Eretmapodites* (Fig. 10d), and *Armigeres* (Fig. 10f) or tooth-like processes as in *Limatus* (Fig. 14b), *Sabethes* (Fig. 16b), and *Trichoprosopon* (Fig. 16d). *Laciniarastra 2* and *3* (LR_2, LR_3) generally consist of slender, hair-like setae (see e.g., Fig. 3a). Those of laciniarastrum 3 are often grouped rather than linearly arranged. *Seta 3-MP* (3) is usually situated between laciniarastra 2 and 3.

Arising distally from the maxillary body, or the galeastipes when distinguishable, is a collection of variously modified setae, the *maxillary brush* (MxB). Usually, the maxillary brush of a given species is composed of more than one type of *maxillary brush setae*. The setae are usually spinelike in predaceous species (Figs. 3c, 16e), typically lamellate in anophelines and dixids (see Harbach and Knight 1977, Figs. 61, 62), and hairlike in most other species.

As many as 3 alveolus-borne setae may arise near the maxillary brush. *Seta 6-MP* (6) (not to be confused with 6-MP of previous authors), when present, is a small seta located mesally, sometimes ventrally, at the base of the brush. *Seta 4-MP* (4) is usually borne dorsal and lateral to the brush and *seta 5-MP* (5) is usually situated ventral and lateral to it. Seta 5-MP is variable in form. It is sometimes bristlelike (Figs. 4c,d; 5, 7, 16a,b) and branched as in *Phoniomyia* (Fig. 12a,b) and *Malaya* (Fig. 13c,d) species. This seta is borne much more ventrally in dixid, chaoborid, anopheline, and *Uranotaenia* species (Figs. 1, 2) as well as *Heizmania* larvae (Fig. 8c,d). The maxillae of these larvae are generally of similar form.

A pair of innervated, often pedicel-borne, peg-like cuticular structures, the *galeal sensoria* (GS), arise dorsally on the maxillary body, or the galeastipes when distinguishable. These are usually located near the dorsal maxillary suture, but in some cases they are borne apically, extremely so in *Uranotaenia* (Fig. 2e,f), *Heizmania* (Fig. 8c,d), and *Trichoprosopon* (Fig. 16c,d) larvae. Sometimes only one galeal sensorium is present, e.g., in the *Orthopodomyia* (Fig. 8a), *Psorophora* (Fig. 11c), and *Phoniomyia* (Fig. 12a) species illustrated herein. In species of *Aedes (Mucidus)* (Fig. 9c), *Opifex* (Fig. 10a), and *Limatus* (Fig. 14a), the pair of sensoria are fused.

The membranous dorsal surface of the maxillary body lateral to the dorsal maxillary suture is usually covered, at least in part, by a grouping of fine hair-like cuticular filaments, the *maxillary pilose area* (MxPA). The filaments cover most of the dorsal surface in anophelines and dixids (Figs. 1, 2). They are probably absent in all or most toxorhynchitines (Fig. 16e).

In many *Culex* (Fig. 3a) and *Aedes* (Fig. 9a) species, as well as in *Maorigoeldia argyropus* (Fig. 15a,b), a grouping of minute spine-like projections, the *maxillary spiculose area* (MSpA), is located on the lateral surface of the maxillary body, or the galeastipes when distinguishable. In the *Topomyia* and *Malaya* larvae examined (Fig. 13), this area is set with nodules.

4. Articulation.

As in generalized insects, the *primary maxillary articulation* (PMxA) of anophelines and dixids (Fig. 1a) is the junction line along which the cardo and the paracoila come into contact during maxillary movements. In most culicine and toxorhynchitine larvae, this articulation lies between a point at the ventral end of the cardostipital arm, the *parartis* (Pat), and a poorly developed paracoila (see e.g., Fig. 15d). In those species where a galeastipital stem is developed (Figs. 6d, 9b, 10b, 11b, 12d), the stem is more directly articulated with the head than is the true parartis. In fact, the stem is sometimes narrowly fused to the hypostomal ridge. In some species where the stem is undeveloped, this area of the maxillary body, or galeastipes, is contiguous with the parartis and articulates with the paracoila, e.g., in *Eretmapodites* (Fig. 10d).

In all culicid and most other nematocerous larvae, a *secondary maxillary articulation* has formed between the maxilla and mandible basally. Specifically, it lies between a point at the base and/or postartis of the mandible and a lateral part or remnant of the stipes, the merostipes or homologous structure.

In some *Uranotaenia* larvae (Fig. 2f), a lightly sclerotized setose sclerite, the *submaxillary sclerite* (SSc), is located between the maxillary body and the ventral margin of the cranium. In is embedded in the membrane which connects the base of the maxilla and the hypostomal ridge.

The Hypostomal Sclerite

Closely associated with the base of the maxilla is a small triangular sclerite, the *hypostomal sclerite* (HSc), which is believed to be a fragment of the cranium, specifically a part of the lateralia and the hypostomal ridge (HR) (see Harbach and Knight 1977). In most species, the sclerite exists as a separate structure between the base of the maxillary palpus and the hypostomal ridge, but the following variations are common within the family: 1) in some larvae, e.g., *Armigeres* (Fig. 10f) and toxorhynchitines, *seta 20-C* (20) (bmh and 6-MP of previous authors), which is normally borne on the sclerite, is borne on the anteroventral margin of the head indicating that the sclerite has been retained as part of the lateralia; 2) in certain other larvae, including species of the genera *Culex* (Fig. 3b), *Deinocerites* (Fig. 4b), *Aedes* (Fig. 9b), *Opifex* (Fig. 10b), and others, the sclerite is attached to the cranium via the hypostomal ridge; 3) in *Hodgesia* (Fig. 5b), *Tripteroides* (Fig. 15d), and *Trichoprosopon* (Fig. 16d) larvae, perhaps others as well, the sclerite is fused with the base of the maxillary palpus; and 4) in still other larvae, including chaoborids (Fig. 1d), the sclerite has completely fused with the maxillary body and palpus to form a single compound unit. The latter modification is found in species of the genera *Culex (Lutzia)* (Fig. 3d), *Malaya* (Fig. 13d), *Limatus* (Fig. 14b), *Wyeomyia* (Fig. 14d), and *Sabethes* (Fig. 16b).

Fig. 1

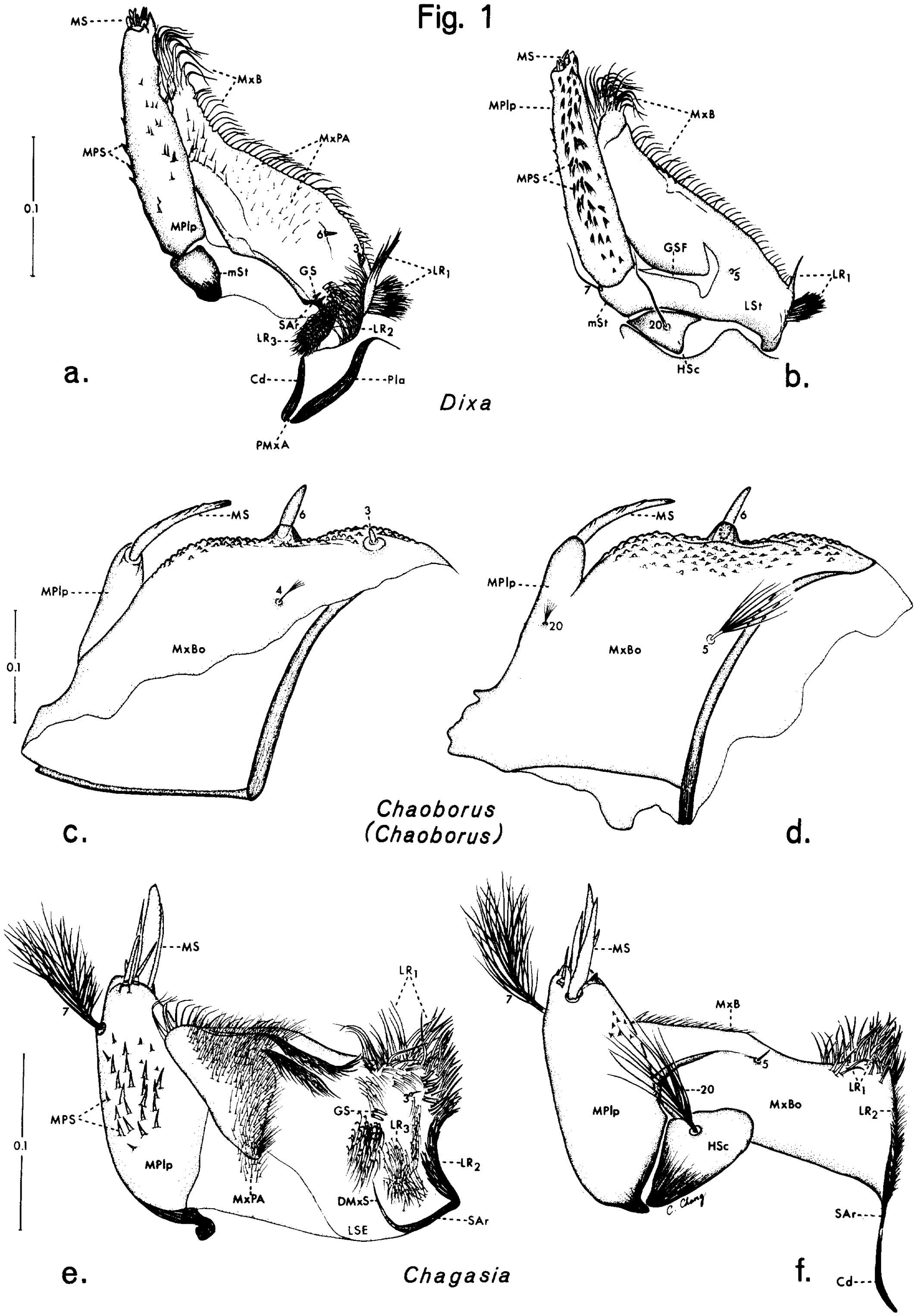

Fig. 1. (The collection from which each specimen came is shown in parenthesis.) (a,b) *Dixa* sp. California, Crater Camp, Los Angeles Co. 22.IV.1953. (J. N. Belkin) Dixidae. (c,d) *Chaoborus (Chaoborus) flavicans* (Meigen). Iowa. (Iowa State University) Chaoboridae. (e,f) *Chagasia bathana* (Dyar). (J. N. Belkin).

Fig. 2

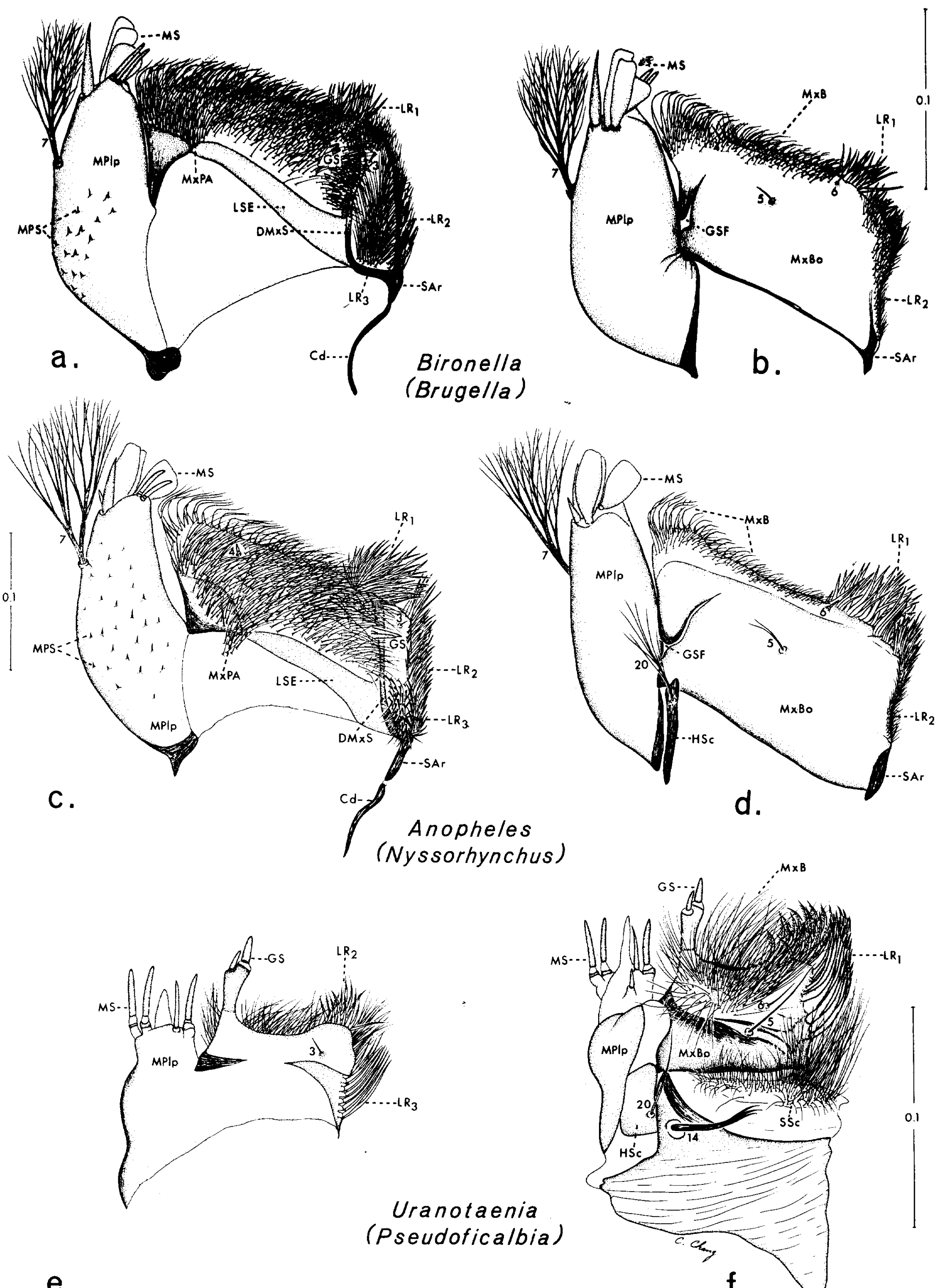

Fig. 2. (a,b) *Bironella (Brugella) hollandi* Taylor. Solomon Islands, Guadalcanal. 1944. (J. N. Belkin). (c,d) *Anopheles (Nyssorhynchus) albimanus* Wiedemann. Canal Zone, Gamboa. 15.11.1949. (J. N. Belkin). (e,f) *Uranotaenia (Pseudoficalbia) lagunensi* Baisas. Philippines, Luzon. 1969. Peyton. (U.S.N.M.).

Fig. 3

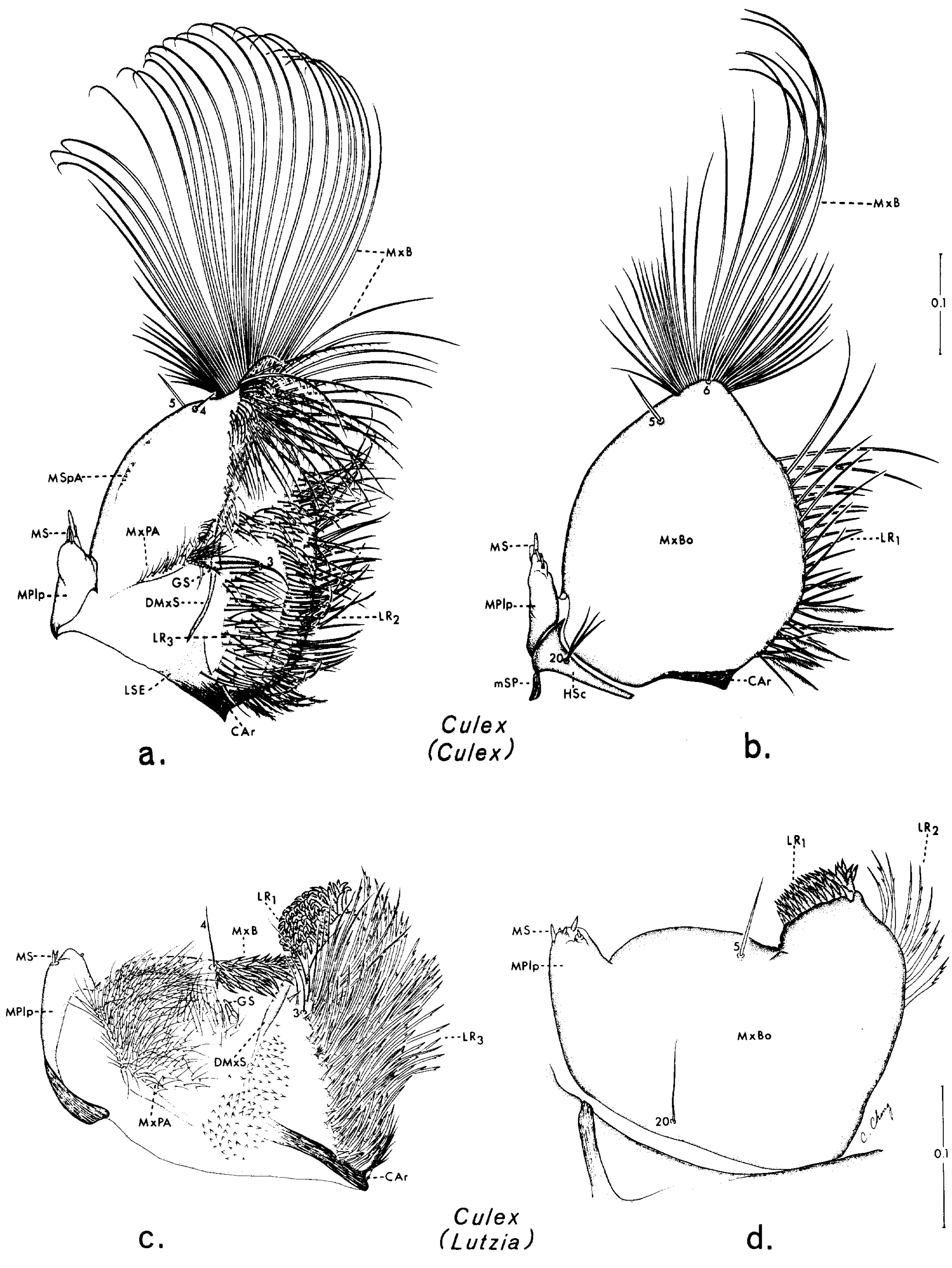

Fig. 3. (a,b) *Culex (Culex) nigripalpus* Theobald. Florida, Vero Beach, Labr. Colony. XII.1969. (J. S. Haeger). (c,d) *Culex (Lutzia) allostigma* (Howard, Dyar, and Knab). Panama, Cativa. 16.11.1949. (K. L. Knight).

Fig. 4

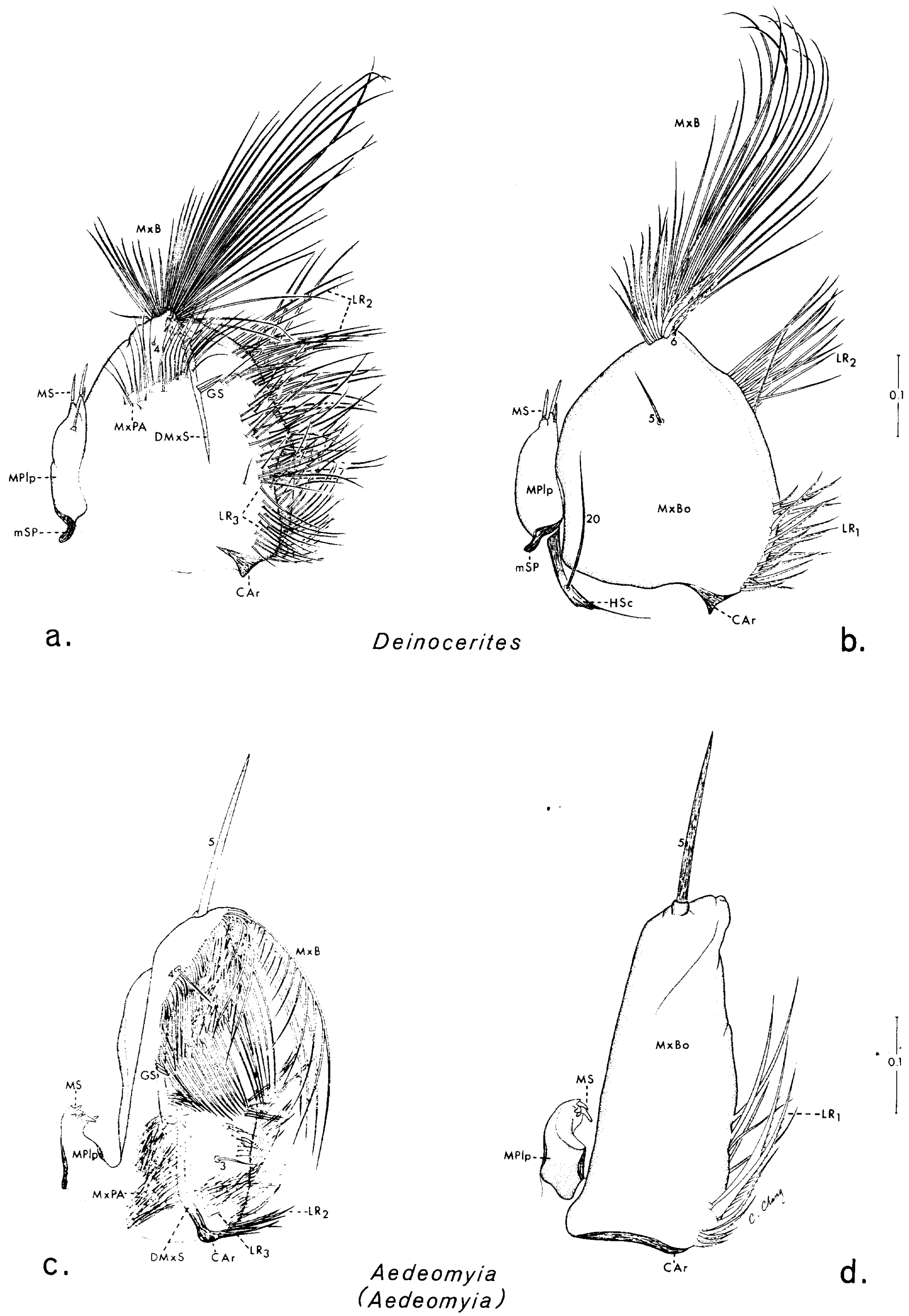

Fig. 4. (a,b) *Deinocerites pseudes* Dyar and Knab. LCBA 167. Hogue & Bright. (C. L. Hogue). (c,d) *Aedeomyia (Aedeomyia) catasticta* Knab. #249. Caroline Islands, Yap. 14.11.1946. D. G. Frey. (U.S.N.M.).

Fig. 5

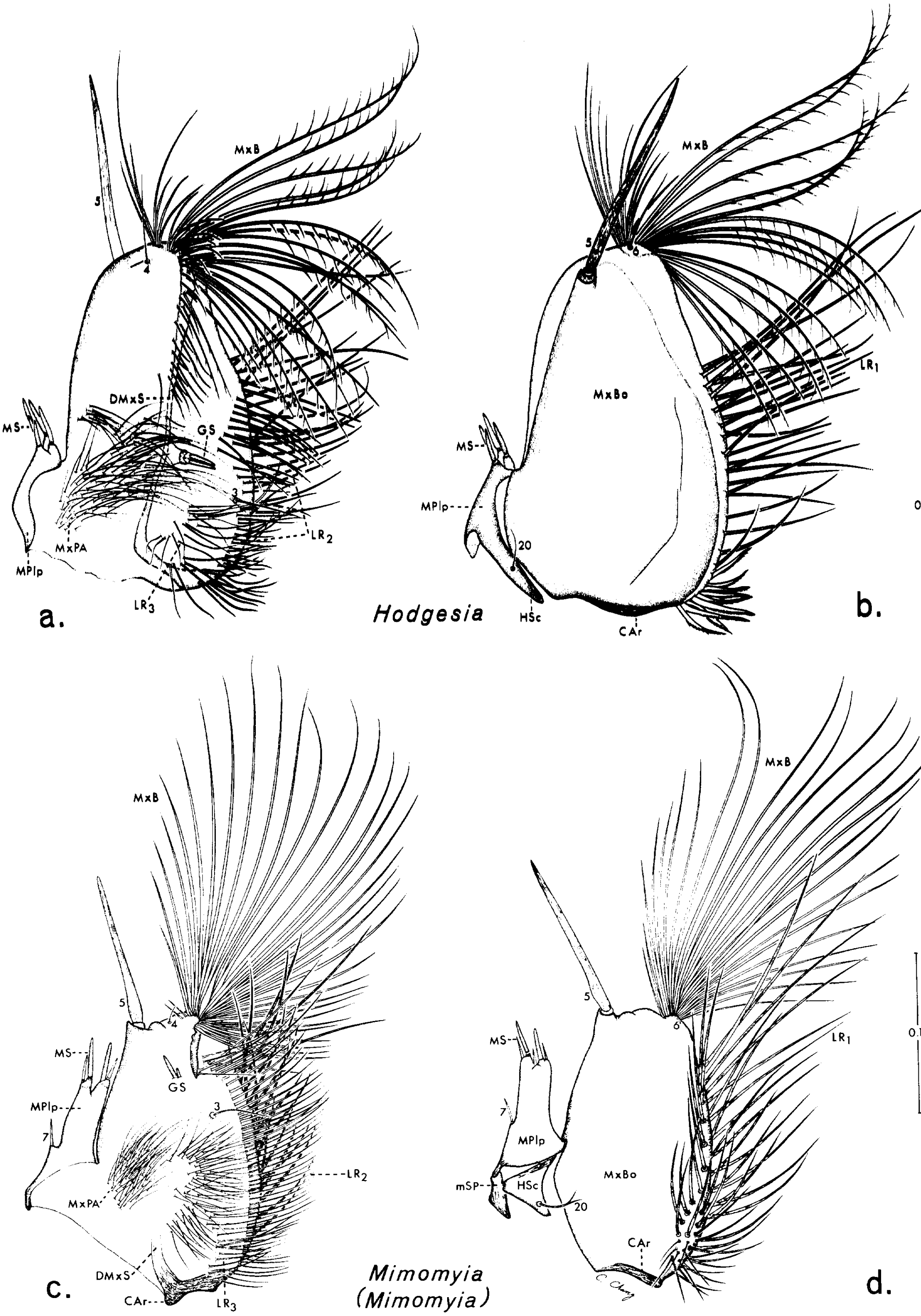

Fig. 5. (a,b) *Hodgesia solomonis* Belkin. #386. Solomon Islands, Bougainville. 22.V.1944. A. B. Gurney. (U.S.N.M.). (c,d) *Mimomyia (Mimomyia) chamberlaini* Ludlow. Philippines. In ditch. 26.IV.1945. D. Bray. (U.S.N.M.).

Fig. 6

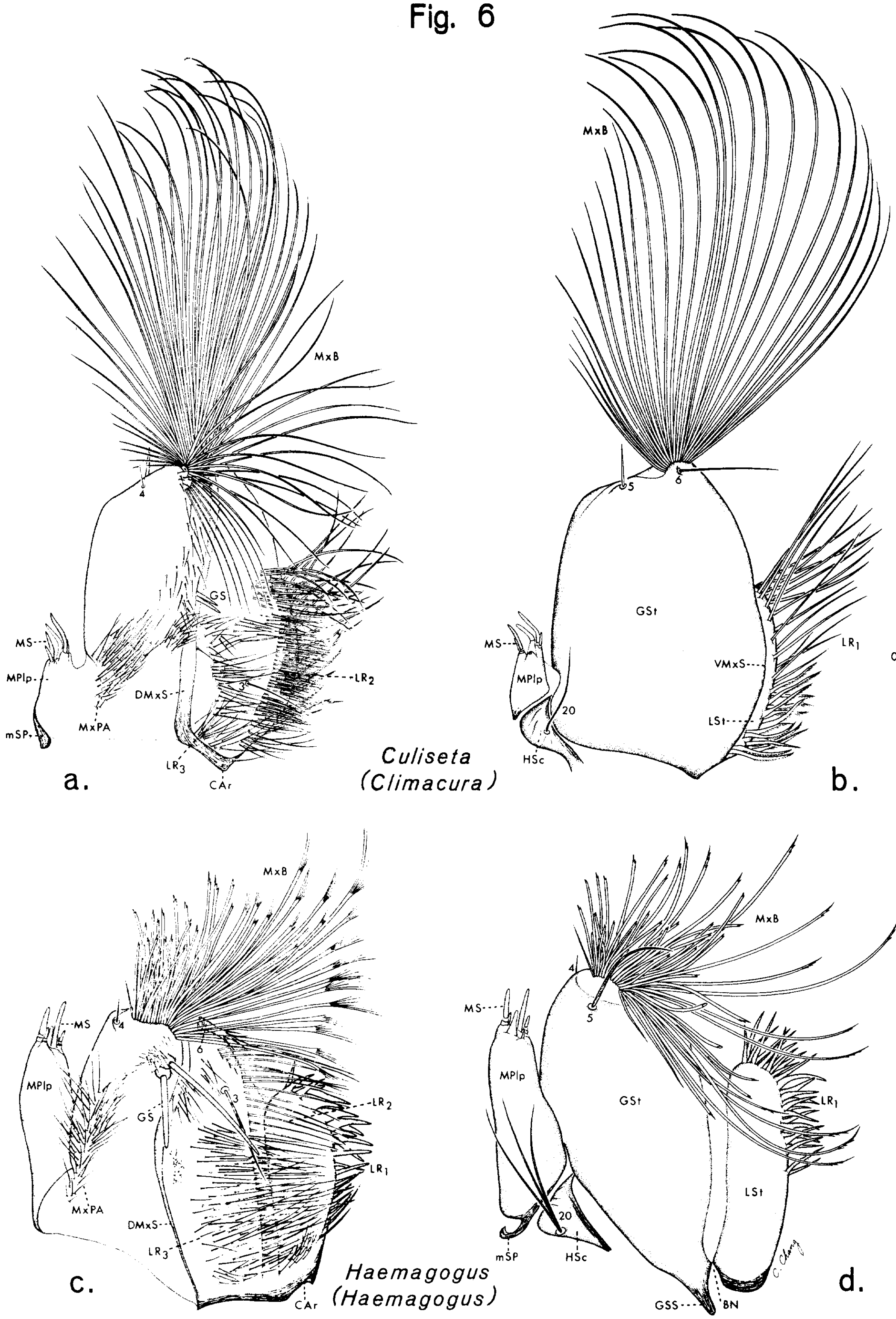

Fig. 6. (a,b) *Culiseta (Climacura) melanura* (Coquillett). Florida, Vero Beach, Labr. Colony. XII. 1969. (J. S. Haeger). (c,d) *Haemagogus (Haemagogus) panarchys* Dyar. Ecuador, Guayas. Levi-Castillo. (U.S.N.M.)

Fig. 7

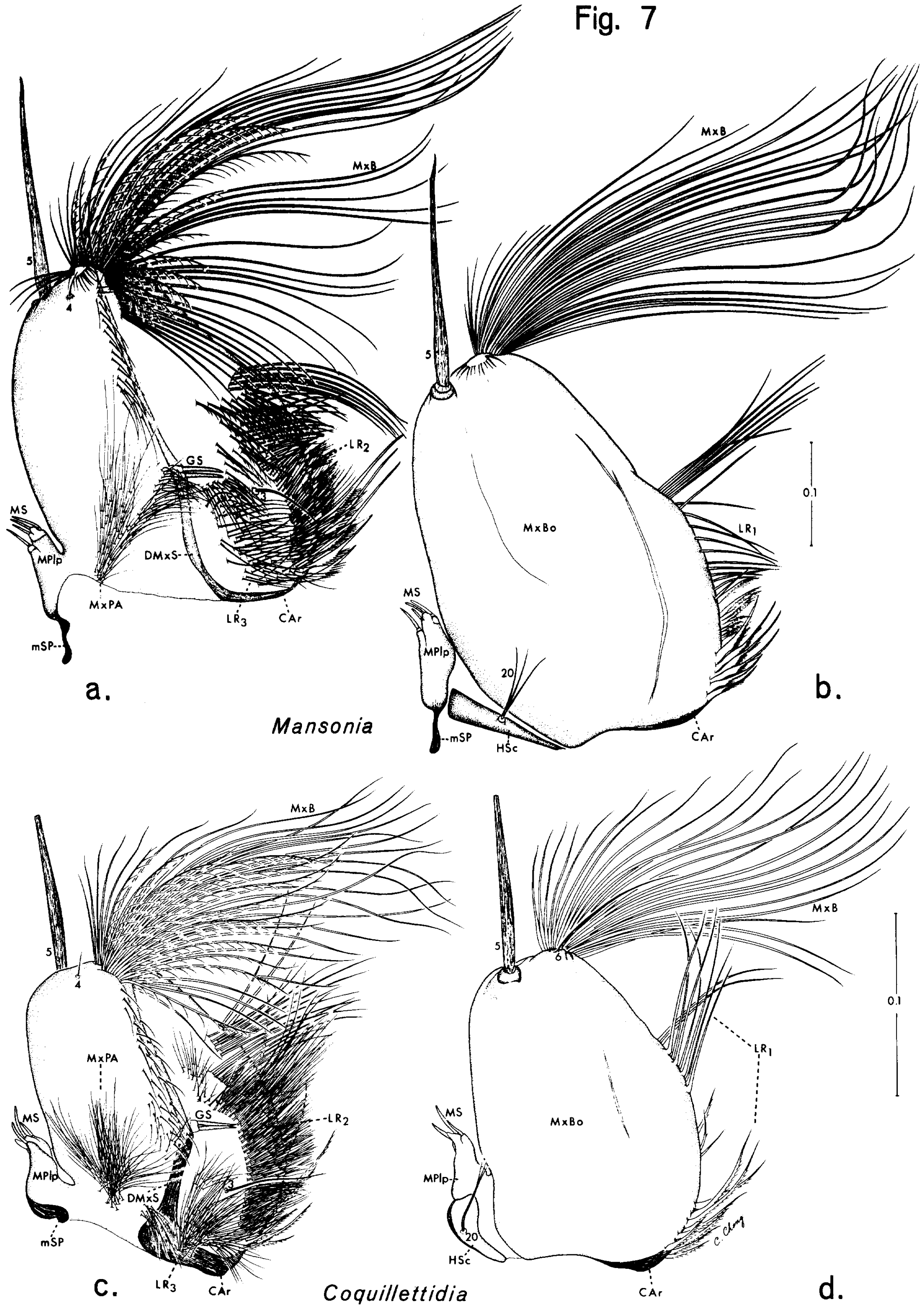

Fig. 7. (a,b) *Mansonia* sp. Philippines, Dakuan, Mindanao. 17.V.1945. R. Staples. (U.S.N.M.). (c,d) *Coquillettidia (Coquillettidia) perturbans* (Walker). Oregon, Roseburg, (U.S.N.M.).

Fig. 8

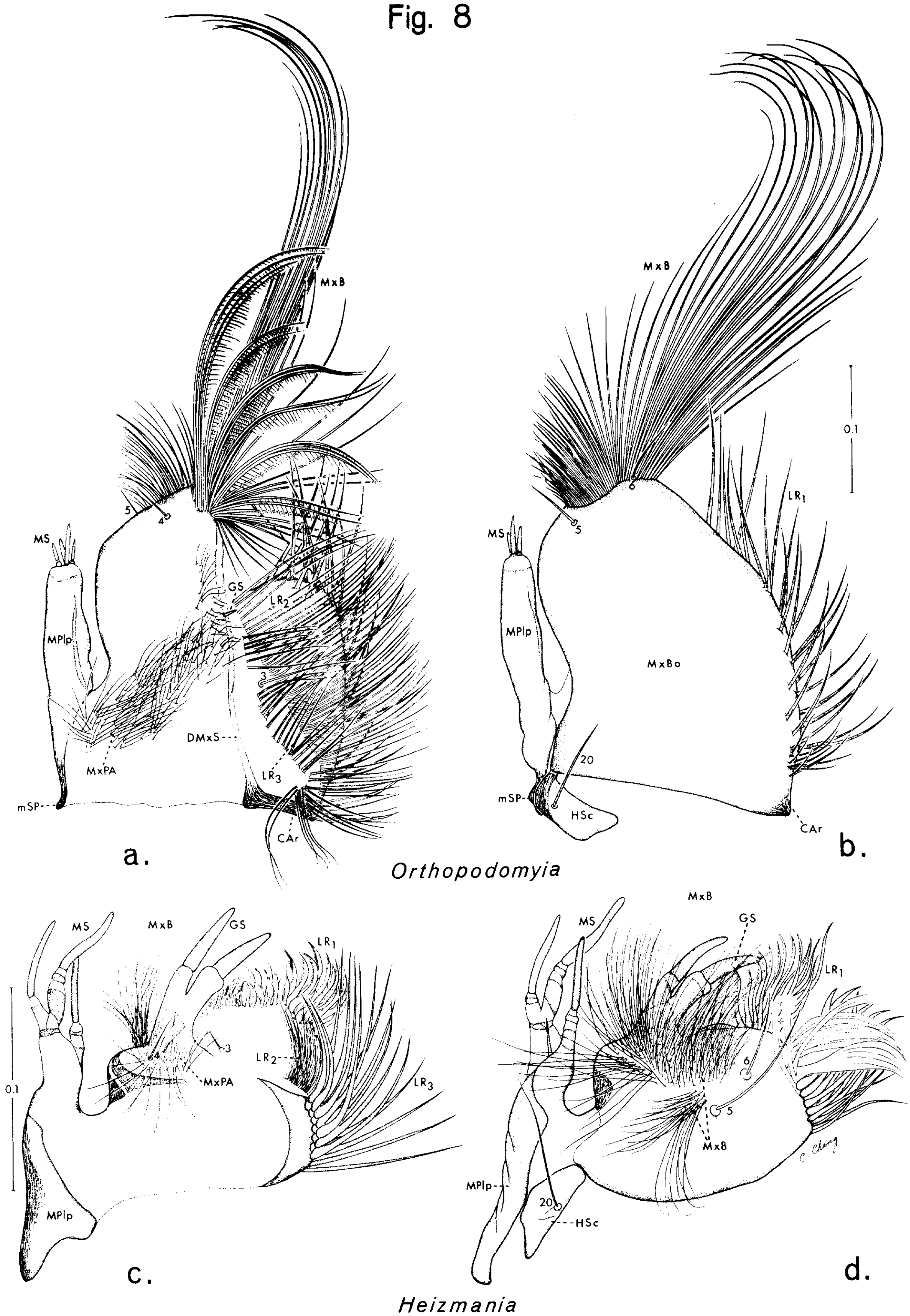

Fig. 8. (a,b) *Orthopodomyia signifera* (Coquillett). #1042. Georgia, Athens, Clarke Co. 1.XII.1967. (K. L. Knight). (c,d) *Heizmania* sp. #748. Malaya, Ulu Gombak, Selangor. (S. Ramalingam).

Fig. 9

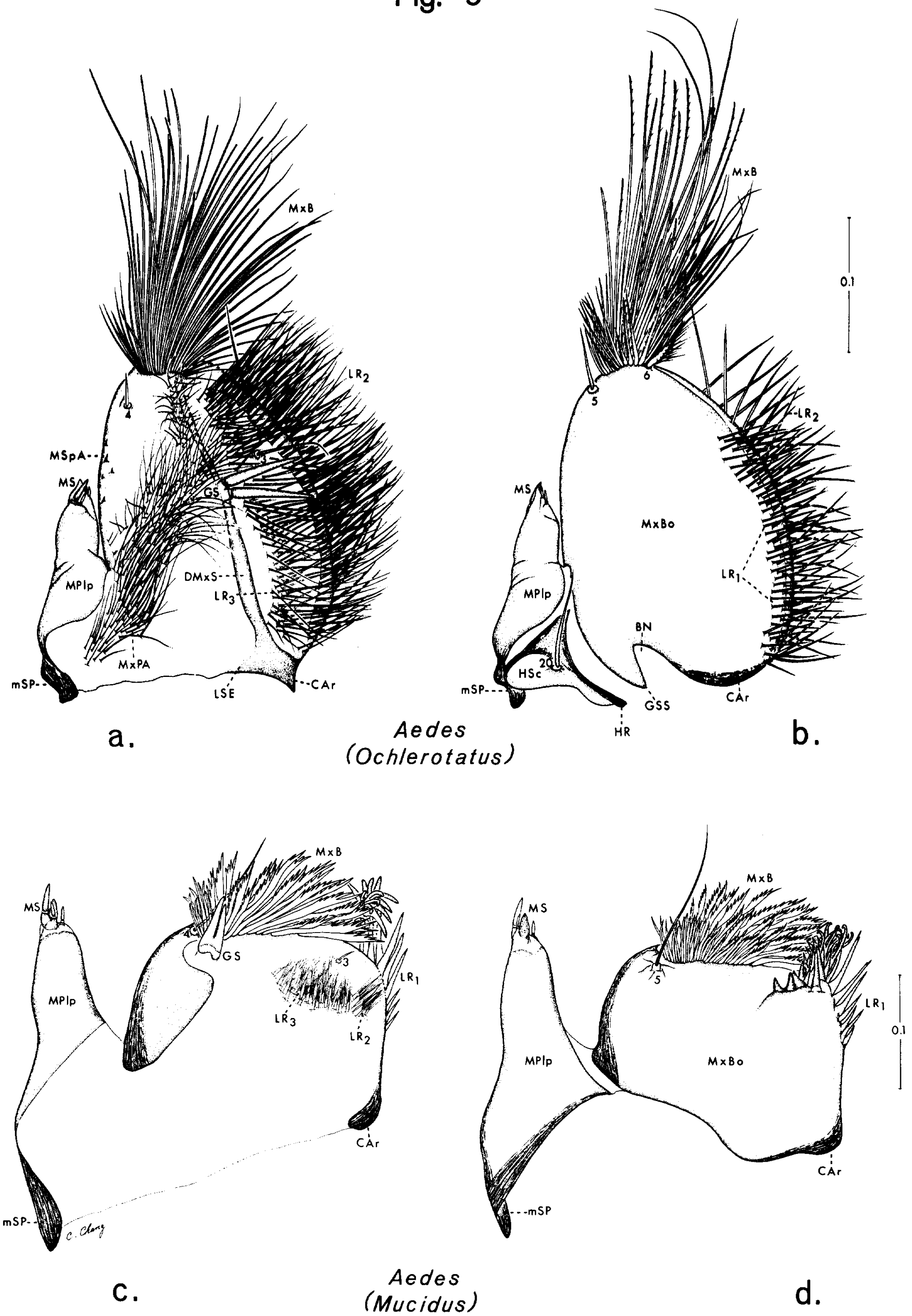

Fig. 9. (a,b) *Aedes (Ochlerotatus) canadensis* (Theobald). Iowa, Ames, Story Co. 5.V.1963. (K. L. Knight). (c,d) *Aedes (Mucidus) alternans* (Westwood). Sandgate. 28.V.1942. (J. N. Belkin).

Fig. 10

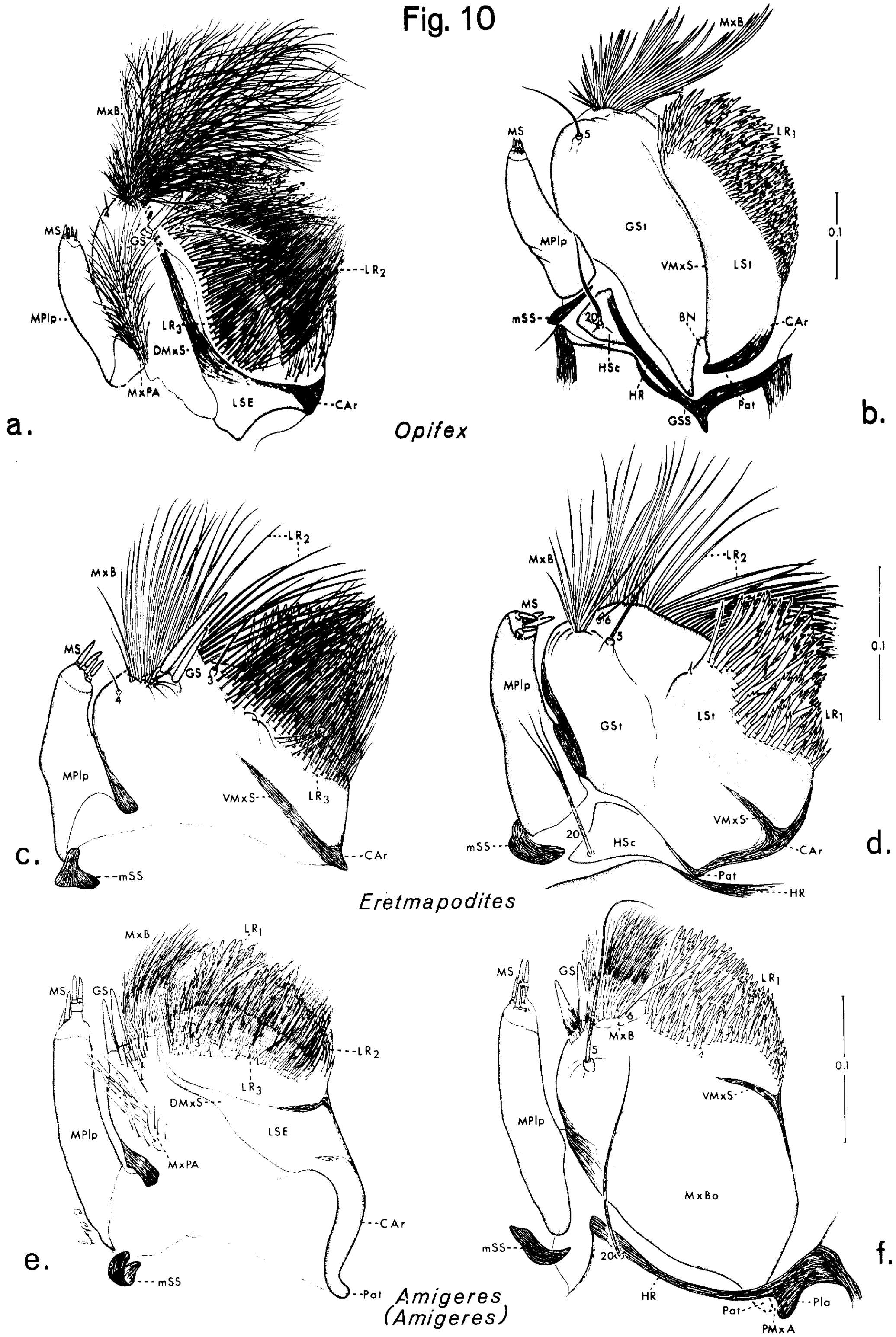

Fig. 10. (a,b) *Opifex fuscus* Hutton. New Zealand, Wellington. 1921. G. Hudson. (B.M.). (c,d) *Eretmapodites chrysogaster* Graham. Conn., New Haven, Yale Arbovirus Research Unit, Labr. Colony. 22.V.1970. (R. C. Wallis). (e,f) *Armigeres (Armigeres) subalbatus* (Coquillett). Okinawa, Chihana. Artificial container. 9.V.1945. A. J. Rogers. (U.S.N.M.).

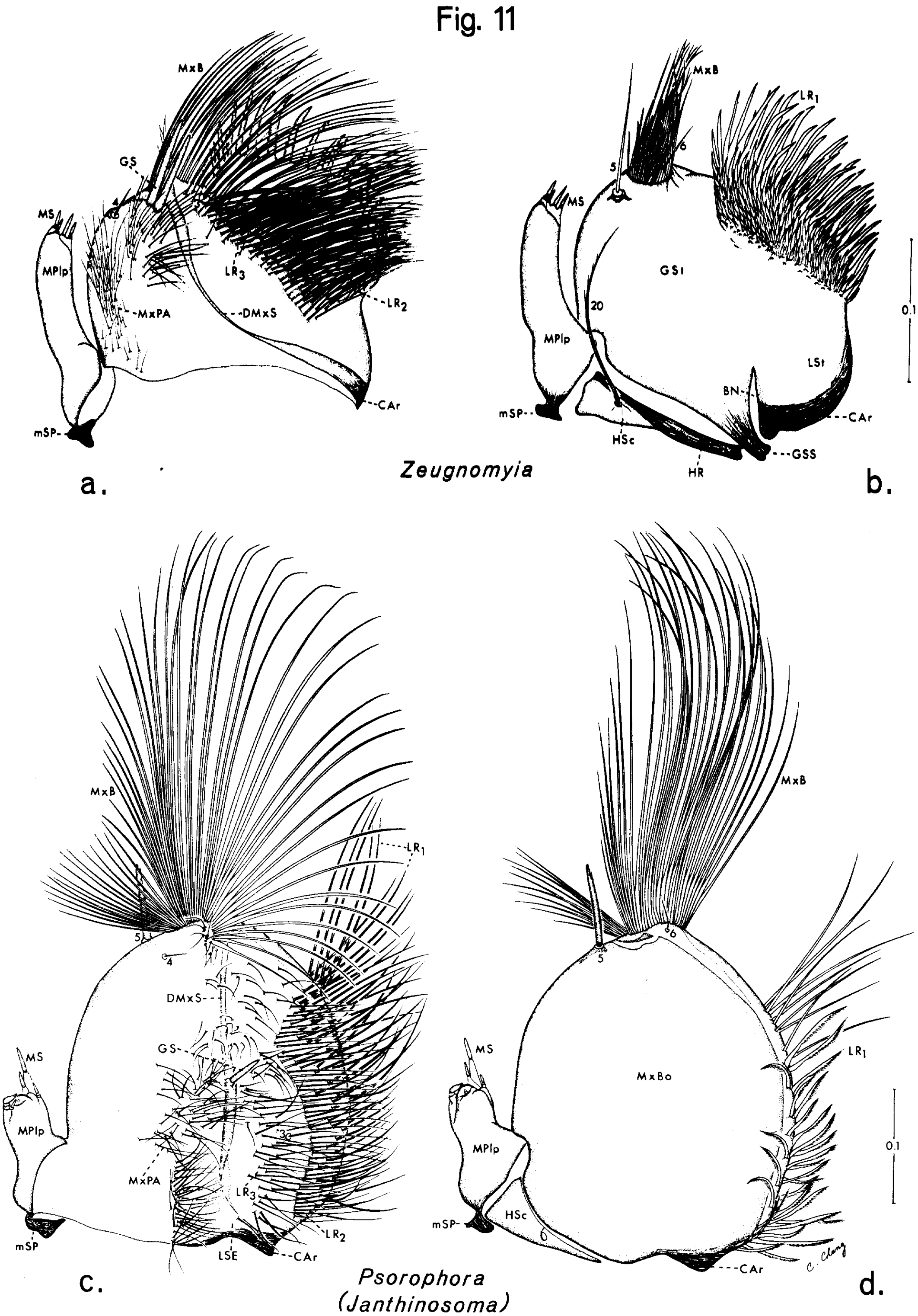

Fig. 11. (a,b) *Zeugnomyia* sp. #1079. Malaya, Banting, Selangor. (S. Ramalingam). (c,d) *Psorophora (Janthinosoma) mathesoni* Belkin and Heinemann. #1061E. Louisiana, Lake Charles. 31.III.1968. (H. C. Chapman).

Fig. 12

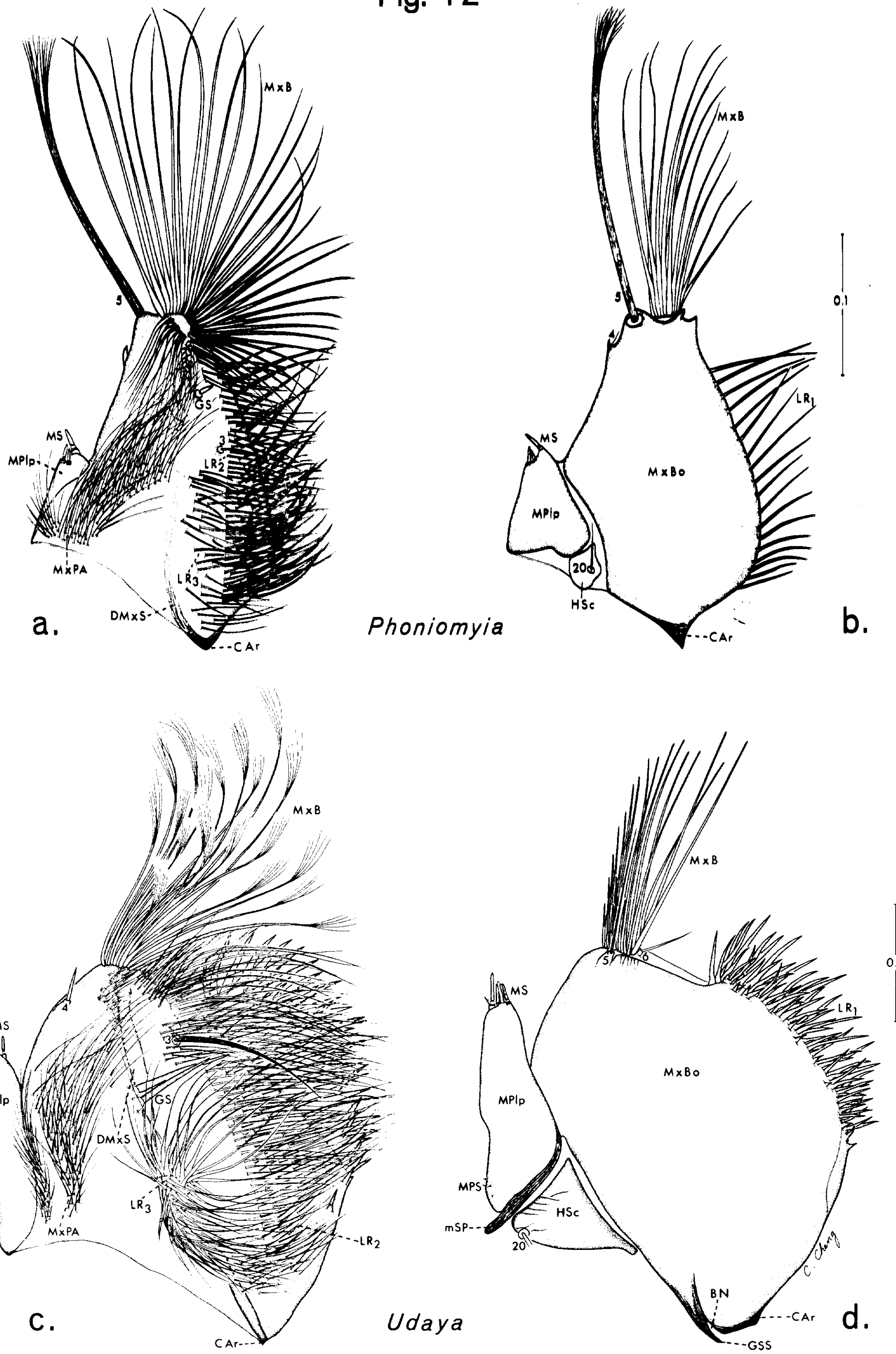

Fig. 12. (a,b) *Phoniomyia splendida* (Bonne-Wepster & Bonne). #SUR 254-3. Surinam. 1967. (J. N. Belkin). (c,d) *Udaya argyrurus* (Edwards). #268. Malaya, K-Kubu Gap Rd., Selangor. (S. Ramalingam).

Fig. 13

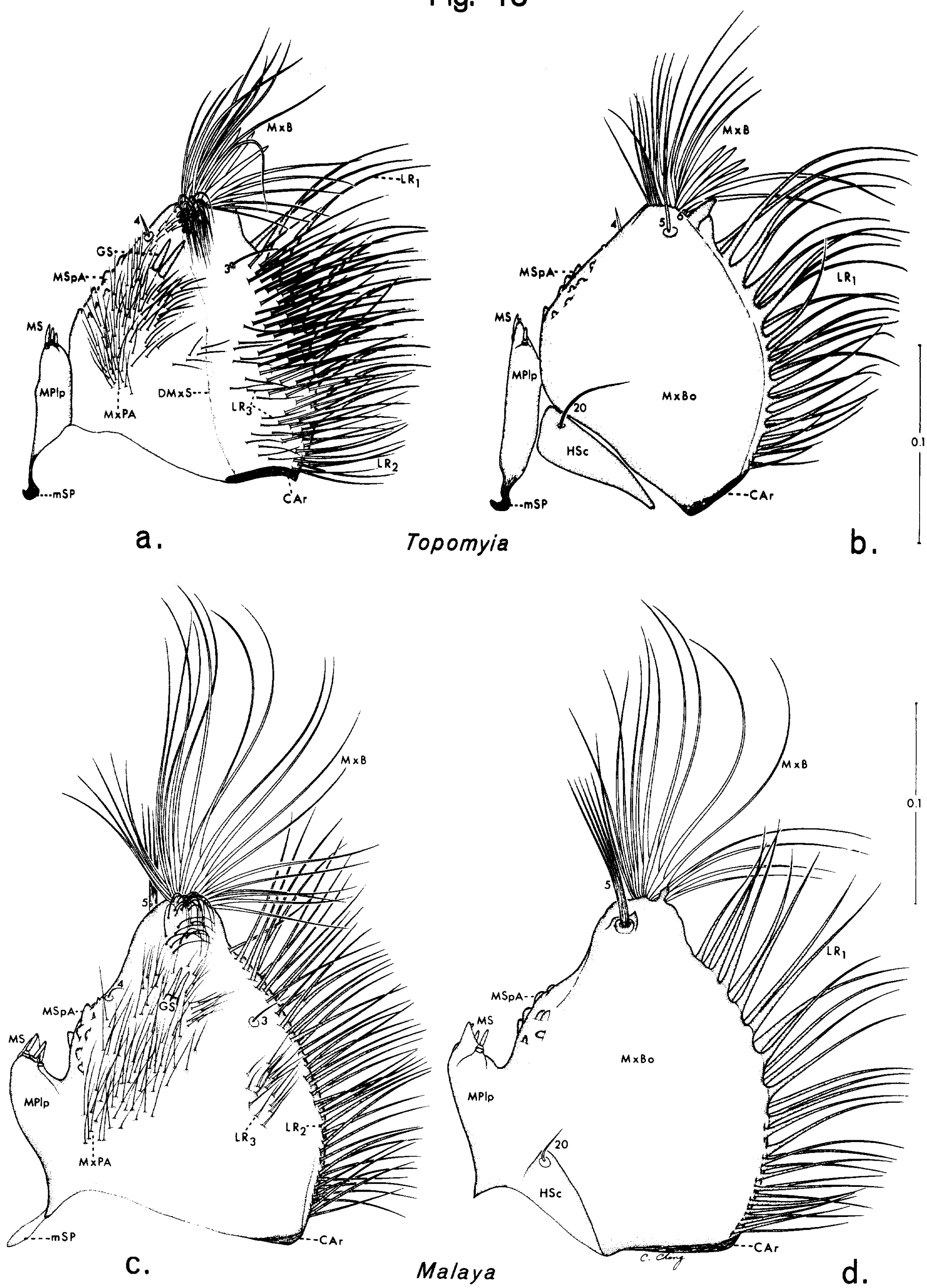

Fig. 13. (a,b) *Topomyia* sp. Philippines, San Jose, Mindoro. Climbing pandanus. 5.11.1945. E. S. Ross. (U.S.N.M.). (c,d) *Malaya* sp. Philippines, Alangalang, Leyte. II.XI.1944. E. S. Ross. (U.S.N.M.)

Fig. 14

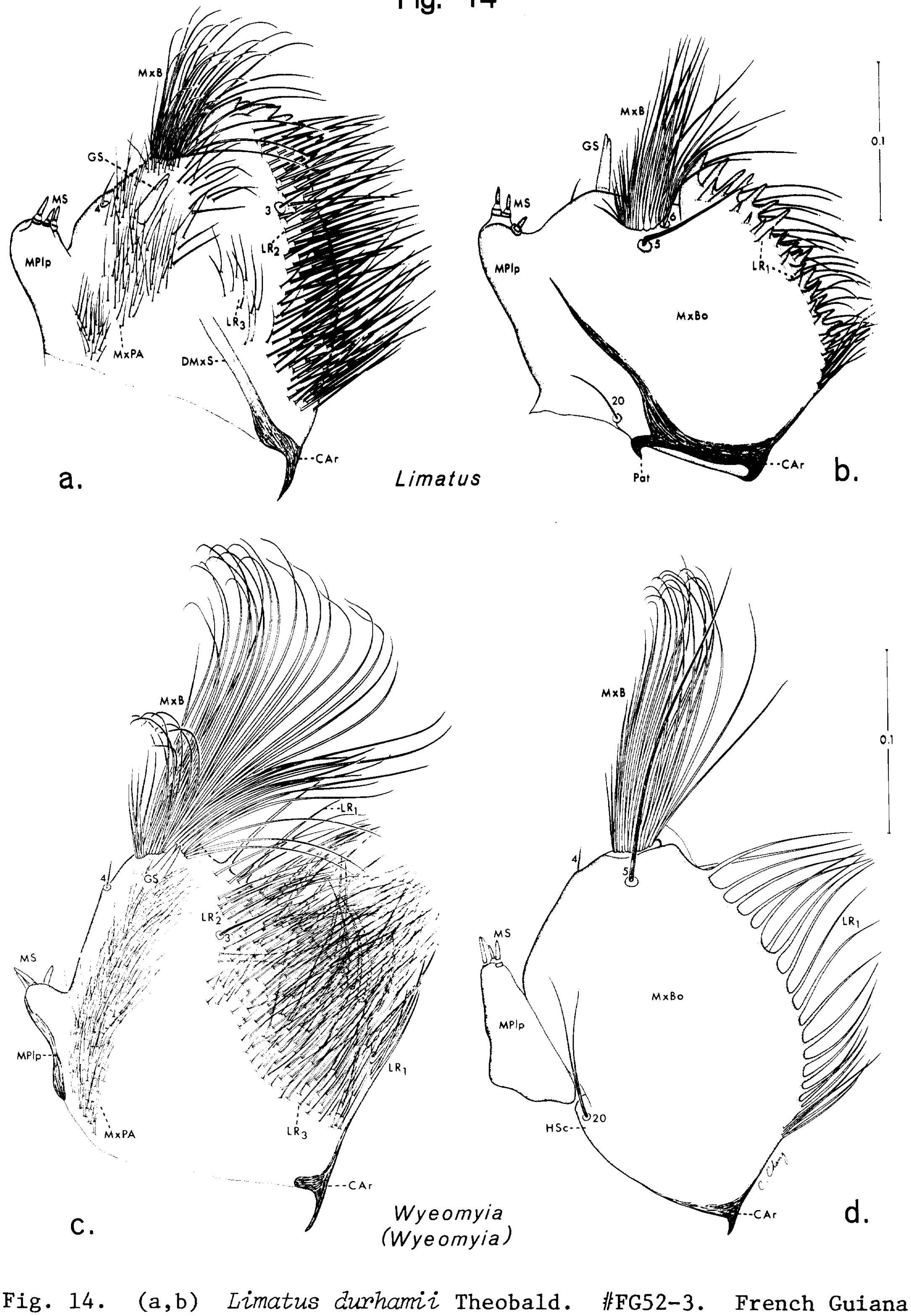

Fig. 14. (a,b) *Limatus durhamii* Theobald. #FG52-3. French Guiana. 1965. (J. N. Belkin). (c,d) *Wyeomyia (Wyeomyia) grayii* Theobald. St. Lucia. LU-17-1. (J. N. Belkin).

Fig. 15

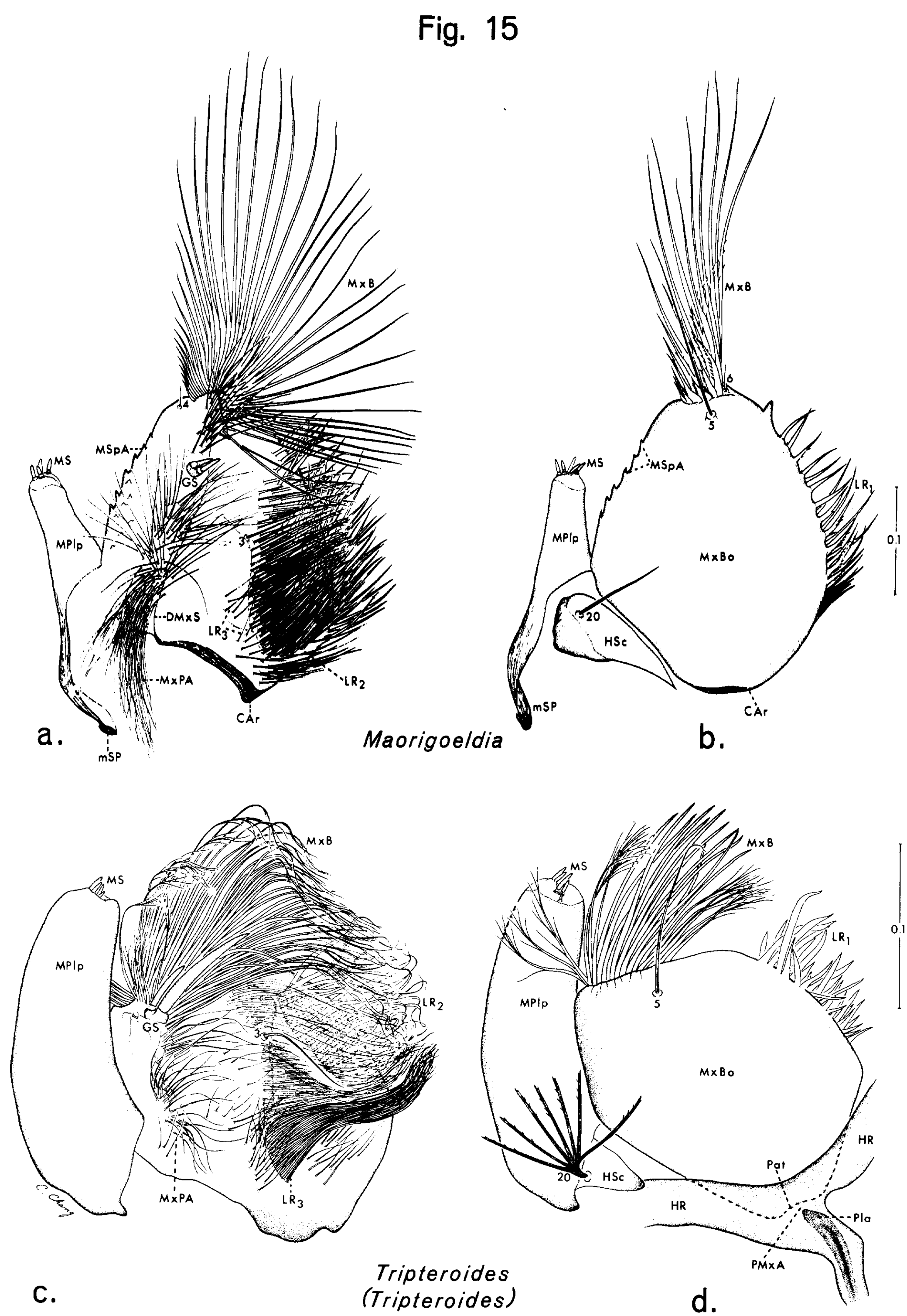

Fig. 15. (a,b) *Maorigoeldia argyropus* (Walker). NZ143. New Zealand. 1958. Belkin/Schroeder. (Smithsonian Institution). (c,d) *Tripteroides (Tripteroides) nepenthis* Edwards. Borneo, Tarakan. Pitcher plant. 20.VI. 1945. A. G. Humes. (U.S.N.M.)

Fig. 16

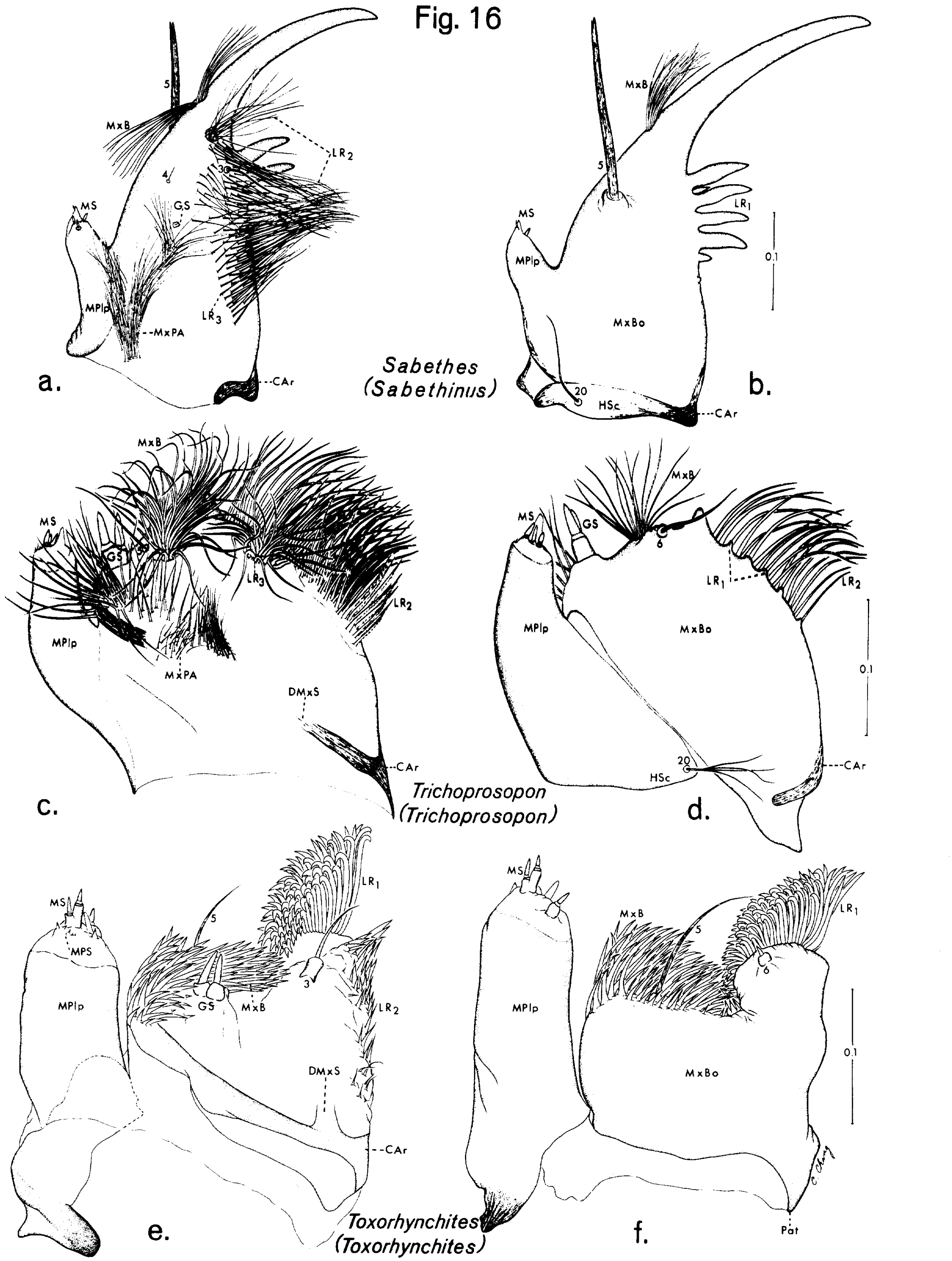

Fig. 16. (a,b) *Sabethes (Sabethinus) undosus* (Coquillett). #9. (U.S.N.M.). (c,d) *Trichoprosopon (Trichoprosopon) digitatum* (Rondani). Panama, GatunCillo. 5.X.1948. (K. L. Knight). (e,f) *Toxorhynchites (Toxorhynchites) brevipalpis* Theobald. Illinois, Urbana. University of Illinois, Labr. Colony. X.1976. (J. R. Larsen).

ABBREVIATIONS USED IN FIGURES

3	= seta 3-MP	LR_3	= laciniarastrum 3
4	= seta 4-MP	LSE	= laciniastipital expansion
5	= seta 5-MP	LSt	= laciniastipes
6	= seta 6-MP	MPlp	= maxillary palpus
7	= seta 7-MP	MPS	= maxillary palpal spiculi
14	= seta 14-C	MS	= maxillary palpal sensoria
20	= seta 20-C	mSP	= merostipital process
BN	= basal notch	MSpA	= maxillary spiculose area
CAr	= cardostipital arm	mSS	= merostipital sclerite
Cd	= cardo	mSt	= merostipes
DMxS	= dorsal maxillary suture	MxB	= maxillary brush
GS	= galeal sensoria	MxBo	= maxillary body
GSF	= galeastipital fissure	MxPA	= maxillary pilose area
GSS	= galeastipital stem	Pat	= parartis
GSt	= galeastipes	Pla	= paracoila
HR	= hypostomal ridge	PMxA	= primary maxillary articulation
HSc	= hypostomal sclerite	SAr	= stipital arm
LR_1	= laciniarastrum 1	SSc	= submaxillary sclerite
LR_2	= laciniarastrum 2	VMxS	= ventral maxillary suture

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