

# Comparative morphology of the labrum in Hymenoptera: the digitate labrum of Perilampidae and Eucharitidae (Chalcidoidea)<sup>1</sup>

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The ground plan structure of the labrum of the Apocrita and Chalcidoidea was characterized by reference to the structure of the labrum in Symphyta. The ground plan configuration in Chalcidoidea is regarded as flaplike, with many evenly distributed setae and a lobate epipharynx. Within Chalcidoidea, the structure of the labrum was compared in exemplars of Eucharitidae, Perilampidae, and most of the subfamilies currently referred to the Pteromalidae. The digitate labrum of Perilampidae and Eucharitidae is regarded as the first synapomorphy of the two families from the adult stage. The digits of the labrum intermesh with setae of the labiomaxillary complex to form a sievelike apparatus that may exclude pollen and are hypothesized as an adaptation for nectar feeding. The digitate labrum and the flaplike labrum with marginal setae of Chrysolampinae share derived characters: stout setae, reinforced setal bases, and distinct sockets. A transformation series is proposed that derives the digitate labrum from the chrysolampine labrum by the extension of processes from the margin. A survey of the structure of the labrum in Pteromalidae failed to refute this hypothesis of synapomorphy; the labrum of Eutrichosomatinae is similar in many regards but is regarded as independently derived. Three distinct configurations of the labrum are shared by subfamilies and tribes of Pteromalidae: (i) Cleonyminae, Chalcedectinae, Brachyscelidiphaginae, Cerocephalinae, and Macromesinae; (ii) Spalangiinae, Asaphinae, Ceinae, and Miscogasterinae (Ormocerini); and (iii) Miscogasterinae (Sphegigasterini, Miscogasterini) and Pteromalinae. The following subfamilies have unique configurations of the labrum: Chrysolampinae, Diparinae, Eutrichosomatinae, Cratominae, Colotrechninae, and Eunotinae. Hypotheses of transformation of the labrum were suggested for the following: Eutrichosomatinae to Miscogasterinae (Sphegigasterini, Miscogasterini), Pteromalinae; Diparinae to Miscogasterinae (Sphegigasterini, Miscogasterini), Pteromalinae; and Diparinae to Cratominae. The analysis makes explicit use of *a priori* rules of character transformation as a basis for testable hypotheses of relationships. This method is considered the most appropriate for evaluating complex morphological data sets and should allow progress toward a natural classification in groups, such as the Chalcidoidea, that do not have an explicit phylogenetic hypothesis as a point of departure.

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La structure de base du labre, chez les Apocrites et les Chalcidoidea, est caractérisée en fonction de la structure du labre des Symphytes. La configuration de base du labre chez les Chalcidoidea inclut un clapet muni de soies à répartition uniforme et un épipharynx lobé. Au sein des Chalcidoidea, la structure du labre a été comparée chez les Eucharitidae, les Perilampidae et chez la majorité des sous-familles actuellement classifiées parmi les Pteromalidae. Le labre digité des Perilampidae et des Eucharitidae est considéré comme la première caractéristique synapomorphe des deux familles au stade adulte. Les prolongements digités du labre s'entremêlent aux soies du complexe labio-maxillaire pour former un appareil filtreur qui peut exclure le pollen et qui est probablement une adaptation à la consommation de nectar. Le labre digité et le labre en clapet à soies marginales des Chrysolampinae ont en commun des caractéristiques dérivées : soies robustes, bases des soies renforcées en réceptacles des soies distincts. On trouvera ici la description d'un série de transformations hypothétiques qui pourraient expliquer comment le labre des Chrysolampinae a pu devenir digité par prolongement des structures marginales. L'examen des structures du labre chez les Pteromalidae n'a pas permis de contredire cette hypothèse de synapomorphie; le labre des Eutrichosomatinae est semblable par plusieurs points, mais s'est probablement développé indépendamment. Trois configurations distinctes du labre se retrouvent chez certaines sous-familles et tribus de Pteromalidae : (i) Cleonyminae, Chalcedectinae, Brachyscelidiphaginae, Cerocephalinae et Macromesinae, (ii) Spalangiinae, Asaphinae, Ceinae et Miscogasterinae (Ormocerini) et (iii) Miscogasterinae (Sphegigasterini, Miscogasterini) et Pteromalinae. Les sous-familles suivantes ont un labre de configuration distinctive : Chrysolampinae, Diparinae, Eutrichosomatinae, Cratominae, Colotrechninae et Eunotinae. Des hypothèses de transformation du labre sont proposées : des Eutrichosomatinae aux Miscogasterinae (Sphegigasterini, Miscogasterini), Pteromalinae, des Diparinae aux Miscogasterinae (Sphegigasterini, Miscogasterini), Pteromalinae, et des Diparinae aux Cratominae. L'analyse utilisée obéit à des règles *a priori* de transformation de caractéristiques, ce qui permet de poser les bases d'hypothèses de liens de parenté qui soient vérifiables. Il s'agit là de la méthode la plus appropriée pour évaluer des séries de données morphologiques complexes; cette méthode devrait en outre permettre d'aboutir à une classification naturelle au sein de groupes, tels les Chalcidoidea, pour lesquels il n'existe pas d'hypothèse phylogénétique explicite comme point de départ.

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## Introduction

Much of the uncertainty and instability in the higher classification of Chalcidoidea is due to a lack of comparative

morphological studies. Morphological investigations usually develop as adjuncts to taxonomic studies and are restricted in scope, stressing the terms for external structures. There have been very few comparative studies that consider modifications of a particular morphological structure throughout the Chalcidoidea and, in these few cases, only a smattering of taxa have been considered. Examples include a study of wing venation

<sup>1</sup>This paper is dedicated to Dr. William L. Brown, Jr., of Cornell University in commemoration of his 65th birthday.

(Burks 1938) and a series of papers on the female reproductive system (Copland 1976; Copland and King 1971a, 1971b, 1972a, 1972c; Copland *et al.* 1973; King 1962; King and Copland 1969). The major contributions in comparative morphology of Chalcidoidea are detailed studies by Domenichini (1953, 1969, 1978).

Previous morphological studies have been primarily descriptive summaries of the diversity and similarity of structure, and lack information on character evolution. Phylogenetic inferences from these studies are hampered by the lack of information concerning character polarity, i.e., distinguishing plesiomorphic (ancestral or primitive) from apomorphic (derived or advanced) similarities. This information is essential if morphological data are to be used to propose phylogenetic relationships. Morphologists can provide extremely valuable phylogenetic information by first characterizing the ground plan of a morphological structure by reference to the hypothesized sister group and to more distantly related taxa (outgroup or parsimony methods; Watrous and Wheeler 1981; Farris 1982; Maddison *et al.* 1984) and then interpreting the diversity of forms as modifications of this ground plan.

A major source of confusion in the higher classification of the Chalcidoidea is the composition of the family Pteromalidae. It is generally accepted that the Pteromalidae is not a monophyletic group in a phylogenetic system, but is rather a paraphyletic or polyphyletic assemblage characterized by plesiomorphic meristic characters, e.g., 5-segmented tarsi, 13-segmented antennae. The "pteromalid problem" is exacerbated by the inclusion of putatively monophyletic taxa as subfamilies (e.g., Perilampinae, Eucharitinae, Eutrichosomatinae, Ormyrinae, Cleonyminae, Chalcedectinae) for unstated or unconvincing reasons. The challenge is to subdivide this assemblage into monophyletic taxa while retaining the heuristic quality of efficient information retrieval in the resultant classification. The simplistic approach, but perhaps the best interim solution, is to elevate these taxa to the same categorical rank as Pteromalidae. The result is the "top-heavy" traditional classifications (e.g., Nikol'skaya 1952; Peck 1963). Subsequent phylogenetic work can address the amalgamation of the monophyletic unit taxa.

General problems related to the classification of Pteromalidae can be illustrated by a consideration of *Perilampus* Latreille and allies and *Eucharis* Latreille and allies. Both assemblages are traditionally regarded as monophyletic and are recognized either as subfamilies of Pteromalidae (Perilampinae, Eucharitinae; Riek 1970) or as separate families (Perilampidae, Eucharitidae; Graham 1969). More importantly, these two groups are generally considered to be closely related (Bouček 1956a). The insight of Graham (1969), that a "more mature classification" could result from uniting Perilampidae and Eucharitidae, may eventually be supported as phylogenetic studies proceed. My provisional approach is to follow the family-level classification of Graham (1969).

The strongest evidence of a relationship between perilampids and eucharitids centres on the life history and morphology of first-instar larvae. Females deposit eggs away from the host, in or on leaves, fruits, or buds, and the first-instar larvae are active planidia (Smith 1917; Clausen 1940; Askew 1971, 1979). Development is hypermetamorphic: the second and subsequent larval instars are typically hymenopteriform (see Parker 1924). A comparative study of the eggs and planidia of Eucharitidae and Perilampidae (Heraty and Darling 1984) resulted in nine putative synapomorphies

uniting the two families as monophyletic. Larval characters are not available to document the monophyly of Perilampidae; larvae are known for only the genus *Perilampus*. To date, it has been difficult to justify relationships between the families on the basis of adult characters; there are similarities but these are neither universal, precise, nor thought to represent apomorphies.

A sister group relationship has been proposed for Chrysolampinae and Perilampidae + Eucharitidae based on synapomorphies of the larvae (Heraty and Darling 1984) and adults (Darling 1986). Life history information is consistent with this hypothesis: females of *Chrysolampus sisymbrii* (Ashmead) oviposit in developing seedpods of *Astragalus* (Leguminosae), the food plant of the host weevil (*Tychius*, Coleoptera: Curculionidae), and the first-instar larvae actively locate the host larvae (T. D. Miller, personal communication). These behaviours are similar to those of perilampid and eucharitid planidia (Heraty and Darling 1984, and references therein). This sister group relationship facilitates the critical examination of morphological attributes of adults of Perilampidae and Eucharitidae for evidence of monophyly.

The purpose of this paper is to present a phylogenetic interpretation of the structure of the labrum in adult Perilampidae and Eucharitidae and in the hypothesized sister group, the Chrysolampinae. The ground plan labrum in Chalcidoidea is developed based on published accounts and a comparative study of the labrum in Hymenoptera. I review the structure of the labrum, propose synapomorphic similarities between labra of Eucharitidae and Perilampidae, and discuss the possible function of the derived digitate labrum. In addition, I describe labra for exemplars of most of the subfamilies currently referred to Pteromalidae and discuss the implications for the higher classification of Chalcidoidea.

## Methods

### Techniques

The labrum is an integral component of the mouthparts of Hymenoptera and is attached to both the labiomaxillary complex and the inner surface of the clypeus. Mouthparts were prepared by removing the head and clearing it overnight, at room temperature, in Nesbitt's solution or for 2–4 h in warm lactophenol. This treatment allowed the mandibles to be played and provided access to the inner mouthparts. In large specimens, the labrum could then be detached and the head and labiomaxillary complex remounted with the specimen. In smaller specimens or in species with reduced labra, the mouthparts were removed intact by splaying (retracting or abducting) the mandibles and then gently pulling on the labiomaxillary complex with a fine pin or minuten nadeln. With this technique, care must be taken that the labrum does not remain attached to the inner surface of the clypeus. In some species side mounts were made of the entire head in a manner similar to the technique developed by A. A. Girault (see Dahms 1986, cover illustration). Slides were routinely prepared using Hoyer's solution as a mounting medium; in cases of rare or undescribed species, mouthparts were remounted in Canada balsam. Hoyer's mounting medium is optically superior for phase-contrast microscopy, which is necessary to discern the shape of labral setae. In addition, labral setae are often distorted in slides prepared with balsam and it is now impossible to discern the shape of setae in slide preparations that were the basis for descriptions and drawings in Waterston (1922).

Labra were examined and drawn using a compound microscope and camera-lucida (drawing tube) attachment. The descriptions and drawings were based on slide-mounted material. In most cases drawings are based on single specimens, but occasionally composite drawings are provided, as noted in the figure legends. Scanning electron micro-

scopy (SEM), photomicrography, and macrophotography supplemented the analysis.

### Terms

The generalized insectan labrum (s.l.) is a broad, transverse flap that articulates with the ventral or apical margin of the clypeus (Snodgrass 1935; Matsuda 1965). The outer (dorsal or aboral) surface is heavily sclerotized and covered with strong setae and is here referred to as the *labrum* (s.s.). In slide preparations of the labrum a pair of circular translucent areas are often apparent (e.g., Fig. 13) that are not visible externally with SEM (Fig. 7). These structures are broadly distributed in the Chalcidoidea, as indicated by published illustrations (see Domenichini 1969) and my unpublished observations. They may represent subcuticular sensilla (proprioceptors) or glandular pores. Histological work will be necessary to address the homology and phylogenetic significance of these structures. The inner (ventral or oral) surface of the labrum forms the epipharyngeal wall of the preoral cavity and is contiguous with the dorsal surface of the *pharyngeal plate*. If the epipharyngeal surface is differentiated as a distinct lobe it is referred to as the *epipharynx*. The epipharynx of Chalcidoidea usually has paired and differentiated stout setae on the inner surface that project into the buccal cavity; these are here referred to as *epipharyngeal setae* (Figs. 12–14). Small sclerites, *tormae*, are situated laterally on the epipharyngeal surface, near the articulation of the clypeus and labrum and are sites for muscle attachment (Figs. 12–14).

It is often difficult to determine the shape of individual labral setae because of artifacts produced by clearing and slide preparation. Setae are therefore described in rather general terms as either *spatulate*, if broader in the middle than at the base and apex (e.g., Fig. 17), or *tapered*, if gradually narrowed from base to apex (e.g., Fig. 15). Finer distinctions are usually not possible with any degree of certainty. There is also a persistent problem of spatulate setae that appear tapered when examined in lateral view. Symmetry was used to resolve apparent conflicts in resolving setal shape and also to add missing or damaged digits and setae to the illustrations.

### Material examined

The Chalcidoidea examined are listed in Table 1. There is the possibility of confusion because of differing usage of various generic names, uncertainty in species determinations, and the inclusion of undescribed or undetermined species. Voucher specimens are associated with the authors' slide catalog numbers; both the slides and pinned or alcohol-preserved specimens have corresponding numbers. The repositories are listed in Table 1, unless the voucher specimens and associated slides are in the author's collection, currently housed at the Royal Ontario Museum.

### Character analysis

A justification may be necessary for basing phylogenetic decisions on information from a single morphological structure, in this case the labrum. The simplest argument is that only one reliable character is necessary to indicate a lineage (Hecht and Edwards 1977). However, it is often difficult to decide that a character is "reliable," given the frequent occurrence of homoplasy (convergence and parallelism). There are two classes of solutions to this dilemma. One is to consider as many unweighted characters as possible and to use parsimony to decide the issue (e.g., Kluge and Farris 1969; Farris 1983; but see Panchen (1982) for a differing viewpoint on parsimony criteria). The alternative approach, and the one I favour, is to base phylogenetic hypotheses on a few well-analyzed and understood character systems (Hecht and Edwards 1977; Gaffney 1979). If it is understood that hypotheses are being suggested, rather than theories being proven, then single-character systems can be extremely valuable in stimulating additional refinement, if not refutation in whole or in part. A further advantage of this approach is that information on character evolution allows a critical discussion of adaptive significance of traits. A phylogeny provides the only rational means for determining at which level characters represent evolutionary novelties, and therefore the only means by which influences of shared ancestry and current

selective pressures can be untangled.

Any attempt to extract phylogenetically relevant information from a comparative morphological study quickly encounters the vexing problem of the treatment of suites of homologous character states that constitute a morphological transformation series (Hecht and Edwards 1977) or morphocline (Maslin 1952). Two aspects of character evolution are best treated as independent (Meacham 1984): polarity or direction (determining the ancestral state) and order (interrelationship of the various states). With binary (two-state) characters, both polarity and order are determined simultaneously by reference to the outgroup(s) (Watrous and Wheeler 1981; Maddison *et al.* 1984).

Most detailed comparative morphological studies result in multiple character states, but outgroup methods will only fully resolve a multistate transformation series after the order of various states is determined by some other means: "a general method of character analysis would have to include some means of inferring transformation series" (Farris 1982, p. 332). Various solutions have been proposed. All characters can be treated as binary, which either results in the loss of considerable character information or sets up arbitrary dichotomies (e.g., labrum digitate versus labrum not digitate, actually many configurations). Another solution is to assume that any transformation between different states is possible, and to resort to strict parsimony to adjudicate. Michevich (1982) discusses many of the problems with various approaches to the problem of multistate characters and proposes an analytical solution called transformation series analysis (TSA). TSA involves parsimonious interpretation of character change from iterations of the cladogram until a stable point is reached. But what if there is insufficient phylogenetic information to construct an initial cladogram or if previous phylogenetic work has not been done on the group under consideration?

Another alternative is to initially order states based on general theories of character transformation as *a priori* hypotheses. This is the approach I think best suited to most morphological studies and is implicit in many synthetic evolutionary studies (e.g., dacetine ants, Brown and Wilson 1959). The method has been denigrated as a reliance on "what were called in a more naive era, Rules of Evolution" (Michevich 1982, p. 461). But as eloquently argued by Nelson (1970):

It is not now fashionable, and perhaps it never again will be, to speak of "laws" of comparative biology. One gets the impression that such "laws" belong to a remote period of naive heroism in the development of the discipline. To mind come phenomena such as the "biogenetic law," "Dollo's law," "Williston's law" and similar generalizations, for which some biologists, with subdued glee, have always been willing and able to point out exception. Nevertheless, there are comparative theories, or parts of them, which after repeated and independent confirmation, have achieved an order of "probability" (i.e., maximum generality and parsimony) approaching that of any of the "laws" of other sciences. Biologists who, from embarrassment of past excesses, choose not to call them "laws," should suggest another name for them.

Transformation series of the labrum were initially ordered by application of Dollo's law, the law of irreversibility, which suggests that when a complex structure is lost during evolution it does not reappear in the same form, and the rule of evolution reduction (Brown 1965), which suggests that for meristic characters in general, a phylogenetic change in number much more frequently results in a decrease rather than an increase. In many cases alternative transformation series are possible and these represent alternative testable hypotheses. If sufficient additional phylogenetic information is available to construct a cladogram, these alternatives can be evaluated by parsimony methods. If a cladogram cannot be resolved for the group under study then the hypotheses can either be evaluated in terms of traditional classification or can stand alone as a character phylogeny. Future work will serve to refine or reject the working hypothesis.

The specific methodological rule used in this analysis is that the number of setae on the labrum and epipharynx is expected to transform from large, indeterminate numbers to small, determinate

TABLE 1. List of species of Chalcidoidea studied

	Locality	Remarks (repositories)
Chalcididae		
Haltichellinae		
<i>Hockeria</i> sp.	U.S.A.	♂, DCD slide 255
Brachymerinae		
<i>Brachymeria intermedia</i> (Nees)	U.S.A.	♀, DCD slide 254
<i>Brachymeria</i> sp.	Panama	♂, ♀, DCD slides 499, 253
<i>Phasgonophora sulcata</i> Westwood	Canada	♀, DCD slide 649
Dihirinae		
<i>Dihirinus</i> sp.	U.S.A.	♂, DCD slide 258
Chalcidinae		
<i>Spilochalcis mariae</i> (Riley)	U.S.A.	♀, DCD slide 257
<i>Spilochalcis</i> sp.	Mexico	♀, DCD slide 259
Eupelmidae		
<i>Metapelma spectabile</i> Westwood	U.S.A.	♀, DCD slide 276
<i>Phlebotopos</i> sp.	Trinidad	♀, DCD slide 105
Eucharitidae		
Eucharitinae		
<i>Pseudochalcura gibbosa</i> (Provancher)*	U.S.A.	♀, DCD slide 506
<i>Eucharis adscendens</i> Fabricius*	Europe	♂, 2 ♀♀, DCD slides 515, 405, 483
<i>Mateucharis glabra</i> Bouček and Watsham*	South Africa	2 ♂♂, ♀, paratypes, DCD slides 485, 516, 517, 518 (BMNH)
<i>Pseudometagea schwarzii</i> (Ashmead)*	U.S.A.	♂, ♀, DCD slides 291, 510
<i>Pseudometagea montana</i> (Ashmead)	Canada	♀, DCD slide 406
<i>Schizaspidia</i> sp. 1	Malaysia	♂, DCD slide 416 (CNC)
<i>Dilocantha</i> sp.	Trinidad	♂, DCD slide 418 (CNC)
<i>Stilbula</i> sp.	Yugoslavia	2 ♂♂, DCD slides 420, 568 (CNC)
<i>Obeza floridana</i> (Ashmead)*	U.S.A.	♂, DCD slide 407
<i>Rhipipallus</i> sp. 1	Australia	♀, DCD slide 411
<i>Rhipipallus</i> sp. 2	Australia	♀, DCD slide 434
<i>Lophyrocera apicalis</i> (Ashmead)*	U.S.A.	♀, DCD slide 409
<i>Chalcura</i> sp.	New Hebrides	♂, DCD slide 404
<i>Kapala floridana</i> (Ashmead)	U.S.A.	♂, ♀, DCD slides 507, 292
<i>Kapala</i> sp.	Columbia	♂, DCD slide 97
<i>Galearia bruchi</i> (Gemignani)	Argentina	♀, DCD slide 513 (FML)
Oraseminae		
<i>Orasema</i> sp. 1	U.S.A.	♂, ♀, DCD slides 527, 530
<i>Orasema</i> sp. 2	Mexico	♂, ♀, DCD slides 511, 414
<i>Losbanus</i> nr. <i>laeviceps</i> Gahan	Nepal	♂, DCD slide 422 (CNC)
Eucharitidae?		
<i>Akapala</i> sp.	Australia	♂, DCD slide 298 (AEI)
Perilampidae		
<i>Monacon productum</i> Waterston*	Bengal	♀, paratype (BMNH); ♂, paratype, DCD slide 626 (BMNH)
<i>Monacon latispina</i> Bouček	Cameroon	♀, DCD slide 442
<i>Steffanolampus salicetum</i> (Steffan)*	U.S.A.	2 ♂♂, 2 ♀♀, DCD slides 164, 570, 87, 572
<i>Burksilampus anobii</i> (Burks)*	U.S.A.	♂, DCD slide 439
<i>Perilampus hyalinus</i> Say	U.S.A.	4 ♀♀, DCD slides 250, 505, 576, 578
<i>Perilampus auratus</i> Panzer	U.S.A.	♀, DCD slide 551
<i>Euperilampus scutellatus</i> (Girault)	Philippines	♂, ♀, DCD slides 158, 593
<i>Krombeinius eumenidarum</i> Bouček*	India	♂, DCD slide 161
Pteromalidae		
Cleonyminae		
<i>Epistenia</i> sp.	U.S.A., Canada	2 ♀♀, ♂, DCD slides 91, 642, 763
<i>Heydenia unica</i> Cook and Davis	U.S.A.	2 ♂♂, 3 ♀♀, DCD slides 633-637
Chalcedectinae		
<i>Chalcedectes</i> sp.	U.S.A.	♀, DCD slide 646
<i>Euchrysia hyalinipennis</i> Ashmead	Canada	♀, DCD slide 766
Brachyscelidiphaginae		
<i>Hemadas nubilipennis</i> (Ashmead)	Canada	♀, DCD slide 632
Cerocephalinae		
<i>Gahanisca</i> sp.	Brazil	♀, DCD slide 683 (CNC)
<i>Neocalosoter</i> sp.	Brazil	♀, DCD slide 698 (CNC)
Macromesinae		
<i>Macromesus</i> sp.	U.S.A.	♀, DCD slide 867

TABLE 1 (concluded)

	Locality	Remarks (repositories)
<b>Pteromalidae (continued)</b>		
<b>Spalangiinae</b>		
<i>Spalangia cameroni</i> Perkins	U.S.A.	♂, ♀, DCD slides 611, 363
<b>Asaphinae</b>		
<i>Asaphes</i> sp.	England, U.S.A.	2 ♀♀, DCD slides 24, 30
<b>Ceinae</b>		
<i>Spalangiopelta felonia</i> Darling and Hanson	U.S.A.	♀, paratype, DCD slide 355
<i>Cea</i> sp.	U.S.A.	♂, DCD slide 380
<b>Miscogasterinae</b>		
<b>Ormocerini</b>		
<i>Gastrancistrus salicis</i> (Nees)	Europe	2 ♀♀, DCD slides 321, 666
<i>Gastrancistrus</i> sp.	Mexico	♂, DCD slide 106
<b>Sphegigasterini</b>		
<i>Sphegigaster pallicornis</i> (Spinola)*	Europe	♀, DCD slide 325
<b>Miscogasterini</b>		
<i>Halticoptera circulus</i> (Walker)	U.S.A.	♂, DCD slide 323a
<i>Halticoptera</i> sp.	U.S.A.	♀, DCD slide 296
<i>Lamprotatus splendens</i> Westwood*	Norway	♀, DCD slide 197
<b>Pteromalinae</b>		
<i>Dinotiscus thompsoni</i> (Crawford)	U.S.A.	♀, DCD slide 774
<i>Rhopalicus pulchripennis</i> (Crawford)	Canada	2 ♀♀, DCD slides 678, 777
<i>Pteromalus puparum</i> (L.)*	U.S.A.	3 ♂♂, 2 ♀♀, DCD slides 101, 287, 290
<i>Perilampidea syrphi</i> Crawford	Venezuela	♀, DCD slide 614
<i>Psychophagus</i> sp.	U.S.A.	♂, DCD slide 92
<i>Muscidifurax raptor</i> Girault and Saunders*	U.S.A.	♂, ♀, DCD slides 619, 621
<i>Nasonia vitripennis</i> (Walker)*	U.S.A.	♂, ♀, DCD slides 622, 624
<b>Cratominae</b>		
<i>Cratomus megacephalus</i> (Fabricius)	Canada	♀, DCD slide 671
<b>Diparinae</b>		
<i>Lelaps</i> sp.	Bolivia	♀, DCD slide 609
<b>Eutrichosomatinae</b>		
<i>Eutrichosoma mirabile</i> Ashmead*	U.S.A.	2 ♀♀, DCD slides 283, 301
<b>Colotrechninae</b>		
<i>Colotrechnus ignotus</i> Burks	U.S.A.	♀, DCD slide 652
<b>Eunotinae</b>		
<i>Scutellista cyanea</i> Motschulsky	U.S.A.	3 ♀♀, DCD slides 674, 771, 779
<b>Chrysolampinae</b>		
<i>Brachyelatus viridis</i> Hoffer and Nowicky*	Czechoslovakia	♀, DCD slide 333
<i>Chrysomalla roseri</i> Förster*	Azerbaijan S.S.R.	♀, DCD slide 331
<i>Chrysolampus splendidulus</i> (Spinola)*	Italy	♀, DCD slide 302 (USNM)
<i>Chrysolampus schwarzi</i> Crawford	U.S.A.	♂, 3 ♀♀, DCD slides 598, 90, 299, 605
<i>Chrysolampus sisymbrii</i> (Ashmead)	Canada, U.S.A.	♂, ♀, DCD slides 337, 599
<i>Chrysolampus improcerus</i> Darling	U.S.A.	♀, paratype; DCD slide 342
<b>Family placement uncertain</b>		
<b>Philomidinae</b>		
<i>Aperilampus discolor</i> (Walker)*	Kenya	♀, DCD slide 260
<i>Philomides</i> sp.	Egypt	♀, DCD slide 665 (USNM)
<b>Torymidae?</b>		
<i>Echthrodape africana</i> Burks	Kenya	♂, paratype; DCD slide 628 (USNM)

NOTE: DCD, author's slide numbers; AEI, American Entomological Institute, Gainesville; BMNH, British Museum (Natural History), London; CNC, Canadian National Collection, Ottawa; FML, Fundacion Miguel Lillo, Tucumán; USNM, U.S. National Museum, Washington.

\*The type species of the genus or the senior synonym or present combination of the type species.

numbers. The tendency towards reduction recurs in the insects, as reviewed by Brown (1965).

### Phylogenetic analysis of the structure of the labrum

#### Hymenoptera

##### Ground plan structure

Flaplike, with contiguous labral and epipharyngeal surfaces (Fig. 3); labrum heavily sclerotized, covered with long, stout setae, epipharynx membranous, densely covered with smaller setae, arranged in a whorled pattern (Figs. 1, 2); labrum

broadly contiguous with apical margin of clypeus, not internalized; torxae distinct sclerites.

#### Rationale

The generalized configuration of the insectan labrum is present in primitively wingless insects (e.g., Thysanura, Chaudonneret 1950), in Orthoptera (Snodgrass 1928) and Dictyoptera (e.g., Blattodea, Snodgrass 1935), and in the plesiomorphic suborder of Hymenoptera, the Symphyta (sawflies). Two main groups of sawflies are generally recognized, the Orthandria and Strophandria (Ross 1937; Benson

1938). Basal families in each have the plesiomorphic labrum: (i) Xyeloidea: Xyelidae, both Xyelinae and Macroxyelinae (Figs. 1–3); (ii) Tenthredinoidea: all families (D. C. Darling, unpublished data), e.g., Tenthredinidae, Nematinae, *Hoplomampa halycon* (Fig. 7 in Bird 1926), *Nematus ribesii* (Figs. 1, 8, 9, 14, 15 in Taylor 1931, as *Pteronidea ribesii*); Tenthredinidae, Tenthredininae, *Filacus pluricinctus* (Plates IB, C in Matsuda 1957, as *Macrophya pluricincta*); Pergidae, Perginae, *Perga affinis* (Fig. 1A in Tait 1962). This configuration is here regarded as the plesiomorphic configuration in Hymenoptera (for a similar viewpoint, see Richards 1977). There is considerable variation in the structure of the labrum in Symphyta (see Ross 1937) and I am currently analyzing this variation to test various theories concerning the origin of Apocrita (for discussion of various theories, see Gibson 1985).

### Apocrita

#### Ground plan structure

Bilobed, labrum and epipharyngeal surfaces split to form distinct epipharynx (Figs. 5, 6); labrum heavily sclerotized, covered with long, stout setae, epipharynx membranous, densely covered with smaller setae, arranged in a whorled pattern; labrum broadly contiguous with apical margin of clypeus, not internalized; tormae distinct sclerites.

#### Rationale

Two major groups of apocritans are traditionally recognized, the Terebrantes, or parasitic Hymenoptera, and the Aculeata, the stinging wasps. The Aculeata are demonstrably monophyletic (Brothers 1975) but it is unclear if the Terebrantes are monophyletic.

Published information indicates that in aculeates a distinct epipharynx is formed by the splitting of the labral lobe and epipharyngeal surface of the labrum (Kirmayer 1909). A distinct and separate epipharynx is reported in Sphecidae (Ulrich 1924), Vespidae (Kirmayer 1909; Duncan 1939), and Apidae (Michener 1944; Snodgrass 1956; Eickwort 1969). A distinct epipharynx also occurs in many families of Chrysoidea (viz., Chrysididae, Bethyloidea, Scolebythidae; D. C. Darling, unpublished data), the most basal lineage of Aculeata (Brothers 1975), and more significantly in Plumariidae (D. C. Darling, unpublished data), the proposed sister group of the remaining families of Chrysoidea (Carpenter 1986). The labrum is often somewhat elongate in chrysidoids (cf. transverse in Hymenoptera ground plan) but does have stout setae covering the anterior surface.

The comparative morphology of the labrum in Hymenoptera has not been previously investigated and therefore the distribution of a distinct epipharynx in Terebrantes is not known. I have undertaken such a study, the results and phylogenetic implications of which will be published separately. I offer a summary at this time to allow characterization of the ground plan structure of the labrum in Chalcidoidea. The heavily sclerotized flaplike labrum with a distinct epipharynx is broadly distributed in the major groups of Terebrantes, including many putatively basal or "primitive" extant taxa (e.g., Braconidae (Doryctinae), Ichneumonidae (Xoridinae), Megaspilidae, Pelecinidae, and Megalyridae; D. C. Darling, unpublished data), and in Stephanidae (Figs. 4–6). The Stephanidae retain a large number of plesiomorphic features and are a plausible sister group to the rest of the Apocrita (Rasnitsyn 1980; Gibson 1985).

#### Phylogenetic implications

It is unclear if the presence of a distinct epipharynx can be

considered a synapomorphy of Apocrita because the occurrence of a homologous epipharynx in Symphyta is uncertain at the present time. This has no bearing on the determination of the plesiomorphic condition of the labrum in Apocrita, but could provide valuable information concerning the origin and monophyly of Apocrita.

### Chalcidoidea

#### Ground plan structure

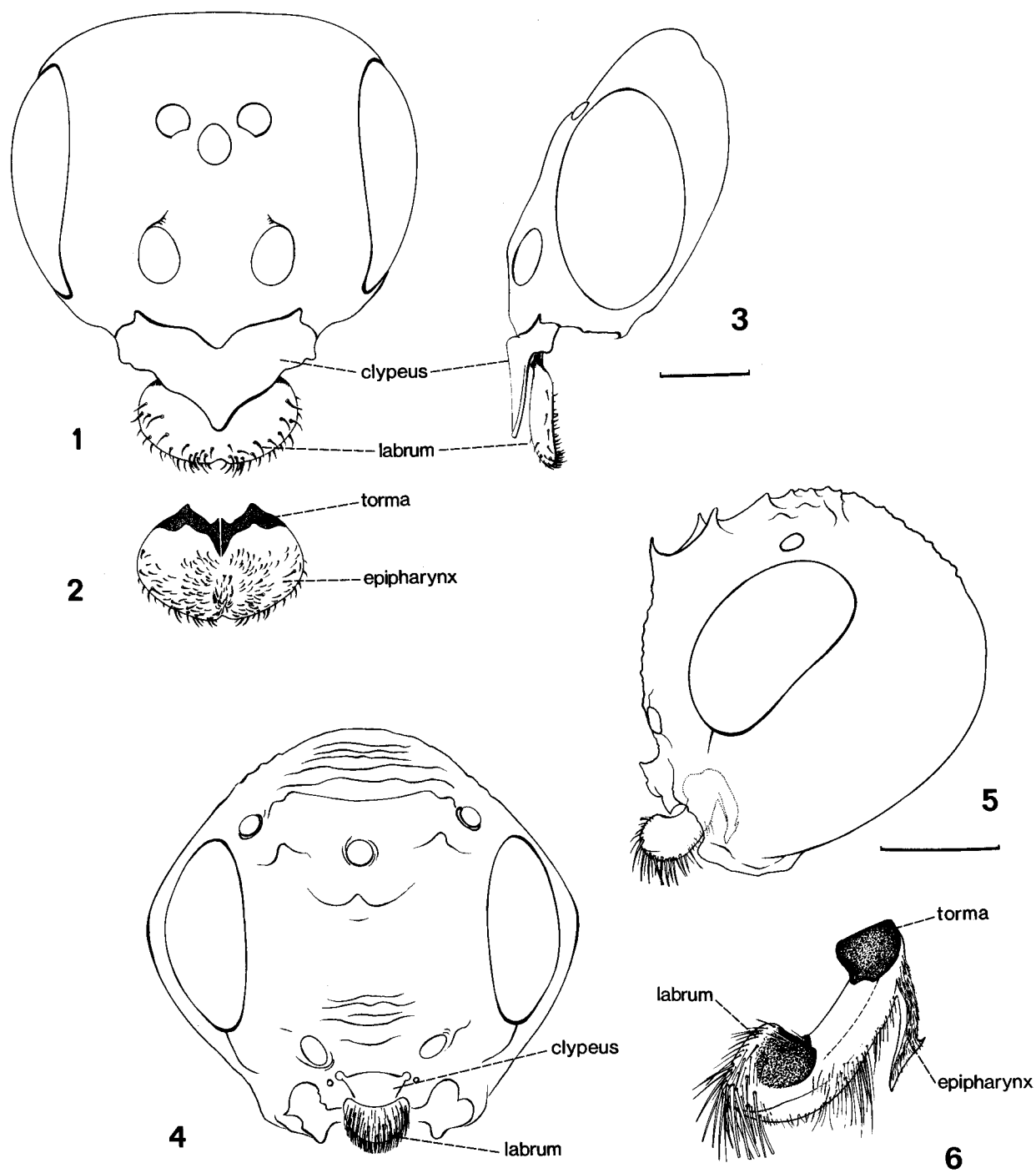
Bilobed, labrum and epipharyngeal surface split to form distinct epipharynx (Fig. 58); labrum heavily sclerotized, covered with long, stout setae, epipharynx membranous, densely covered with smaller setae, arranged in a whorled pattern (Figs. 7, 11–14); inner and outer surfaces of labrum separate, not appressed to form single narrow flap (Fig. 20); inner or oral surface of epipharynx with differentiated, stout epipharyngeal setae (Figs. 12, 14, 16, 18, 58); labrum broadly contiguous with apical margin of clypeus, not internalized; tormae distinct sclerites.

#### Rationale

A highly corroborated sister group relationship is the best source of information concerning the plesiomorphic state of characters in Chalcidoidea. Unfortunately, there are few satisfactory phylogenetic hypotheses for Terebrantes. The most explicit discussion is that of Königsmann (1978), who suggested the following relationships: Evanioidea + (Chalcidoidea + Cynipoidea). Gibson (1986) questioned all of the putative synapomorphies supporting the above relationships and proposed a sister group relationship for Mymaromatidae + Chalcidoidea. The traditional viewpoint of the monophyly of Cynipoidea + Chalcidoidea was seriously questioned but, unfortunately, no more inclusive hypotheses were proposed. Gibson (1986) also presented the interesting hypothesis that the Chalcidoidea is a very early clade in the evolution of the Terebrantes and that the "probable sister group... is some combination of several higher taxa of Terebrantes and not just one family, or one superfamily" (p. 231). The implications of Gibson's hypothesis for determining the ground plan structure for any morphological structure in Chalcidoidea are significant and disconcerting. The most logical outgroup is Mymaromatidae, a highly apomorphic lineage. The only alternatives are either to survey Terebrantes in general and base the hypothesis of plesiomorphy on the commonality principle, the primitive state being widely distributed in the more inclusive group, or to base the decision of plesiomorphy on ingroup criteria. The latter requires a hypothesis of the phylogeny of Chalcidoidea. Neither is an optimal solution but a methodological rule is necessary if the analysis of data is to proceed.

It is virtually impossible to determine with any certainty which are the plesiomorphic taxa in Chalcidoidea. The ground plan undoubtedly includes 5 tarsomeres, a distinct calcar on the foretibia, and 13 antennomeres. Königsmann (1978) further suggested that metallic colouration is a ground plan character of the Chalcidoidea. The traditional viewpoint holds that primitive chalcidoids are characterized by large size and rather coarse, umbilicate sculpture (Bouček 1971). Suggestions for primitive lineages include Eurytomidae (Malyshev 1966), Torymidae (Handlirsch 1925), Cleonymidae (Hedqvist 1961), and Chalcididae (Nikol'skaya 1960, cited in Königsmann 1978).

The family Chalcididae has been regarded as a primitive element of Chalcidoidea on the basis of complete wing venation (Burks 1938) and other plesiomorphic characters (Bouček



FIGS. 1-6. Heads, with mandibles and labiomaxillary complex removed. FIGS. 1-3. *Megaxyela tricolor* (Norton). FIG. 1. Anterior view. FIG. 2. Posterior view of labrum. FIG. 3. Lateral view. FIGS. 4-6. *Schlettererius cinctipes* (Cresson). FIG. 4. Anterior view. FIG. 5. Lateral view. FIG. 6. Detail of labrum and epipharynx. Scale bars = 0.5 mm.

1978). The labrum was examined in representatives of four of the six subfamilies of Chalcididae (Table 1) and was previously illustrated for representatives of the remaining subfamilies, Epitraninae (Fig. 90 in Bouček 1982) and Smicromorphinae (Fig. 9 in Naumann 1986). The labrum is remarkably uniform and is similar to that hypothesized as the ground plan for Apocrita. The labrum is heavily sclerotized and contiguous with the margin of the clypeus (Fig. 7). The dorsal surface has long, stout, tapered setae which arise from distinct sockets, and there is a single pair of epipharyngeal setae. The tormae of all Chalcididae examined are fused to the pharyngeal

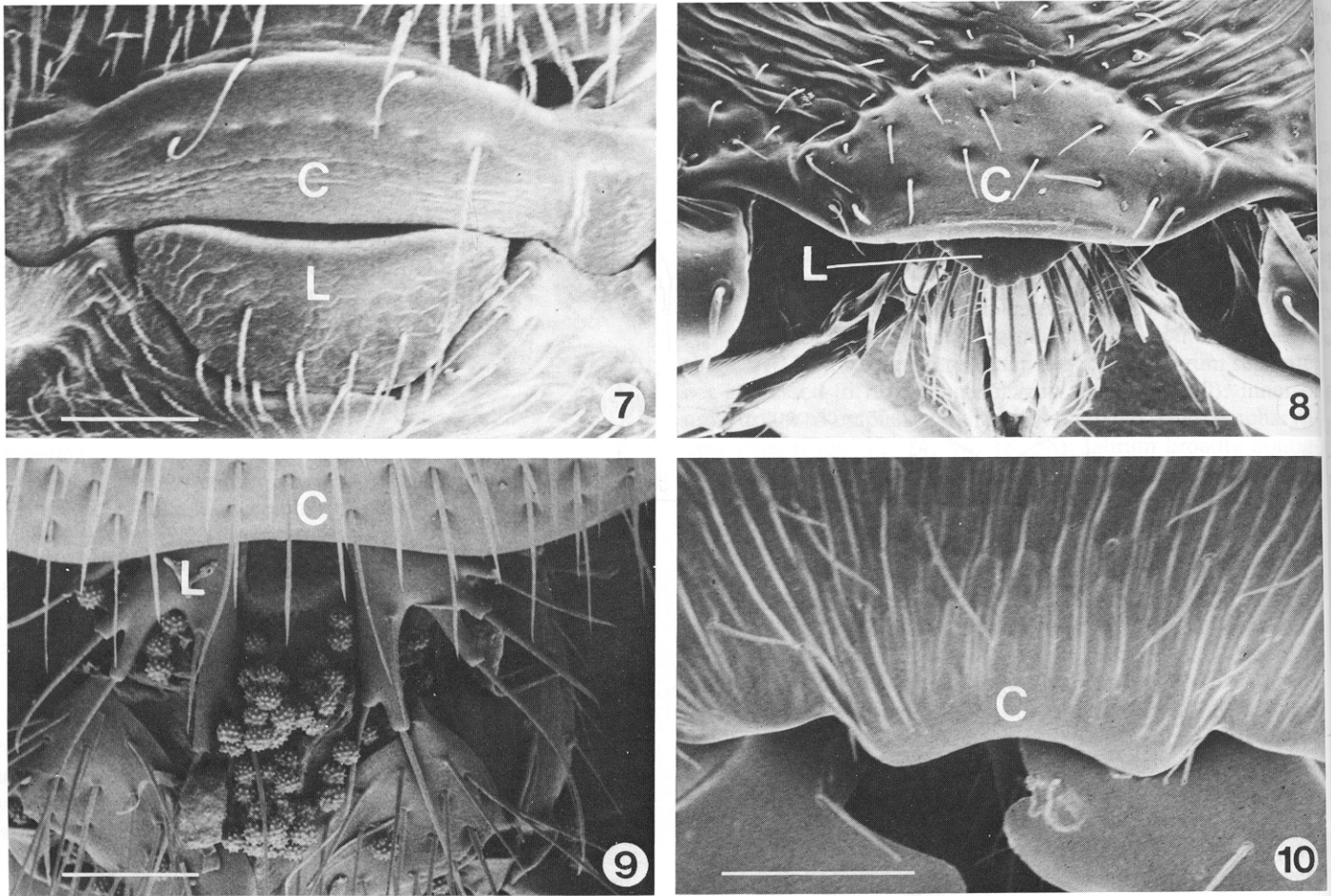
plate; distinct sclerites are not present (Fig. 14). I regard the fusion of the tormae as apomorphic in Chalcidoidea.

For the purpose of determining derived configurations of the labrum and epipharynx within Chalcidoidea it is sufficient to conclude that on the basis of outgroup analysis with Symphyta and a diversity of Terebrantes, a flaplike labrum, with many evenly distributed setae, and a distinct lobate epipharynx are plesiomorphic.

#### Phylogenetic implications

Stout, differentiated epipharyngeal setae have not been





FIGS. 7–10. Scanning electron micrographs of anterior views of oral region. Fig. 7. *Brachymeria* sp. (Chalcididae). Fig. 8. *Chrysolampus schwarzi* (Chrysolampinae). Fig. 9. *Euperilampus triangularis* (Perilampidae). Scale bars, Figs. 7–9 = 0.1 mm. Fig. 10. *Pteromalus puparum* (Pteromalinae). Scale bar = 0.05 mm. C, clypeus; L, labrum.

found to date in any other superfamily of Terebrantes or in the Aculeata (D. C. Darling, unpublished data). Such setae have been found in all chalcidoids examined but the survey is incomplete and has concentrated on plesiomorphic families with pentamerous tarsi. Mymaridae have not been examined. These preliminary results are consistent with the hypothesis that epipharyngeal setae are synapomorphic for Chalcidoidea. It is unclear if a single pair of epipharyngeal setae is in the ground plan of Chalcidoidea. This is certainly the most common configuration; the only known exceptions are *Aperilampus* (Fig. 12) and Chrysolampinae (Fig. 18). The labrum (s.s.) of *Aperilampus* has the ground plan character states for Chalcidoidea, indicating that multiple setae could be plesiomorphic. Derived character states are herein proposed for the labrum (s.s.) of Chrysolampinae, but this does not refute the hypothesis that multiple epipharyngeal setae are plesiomorphic for Chalcidoidea. This hypothesis is also consistent with the reduction rule and prevents proposing convergent reversals to multiple pairs of epipharyngeal setae. Clearly, epipharyngeal setae warrant further study in Apocrita and in Chalcidoidea.

#### *Pteromalidae*

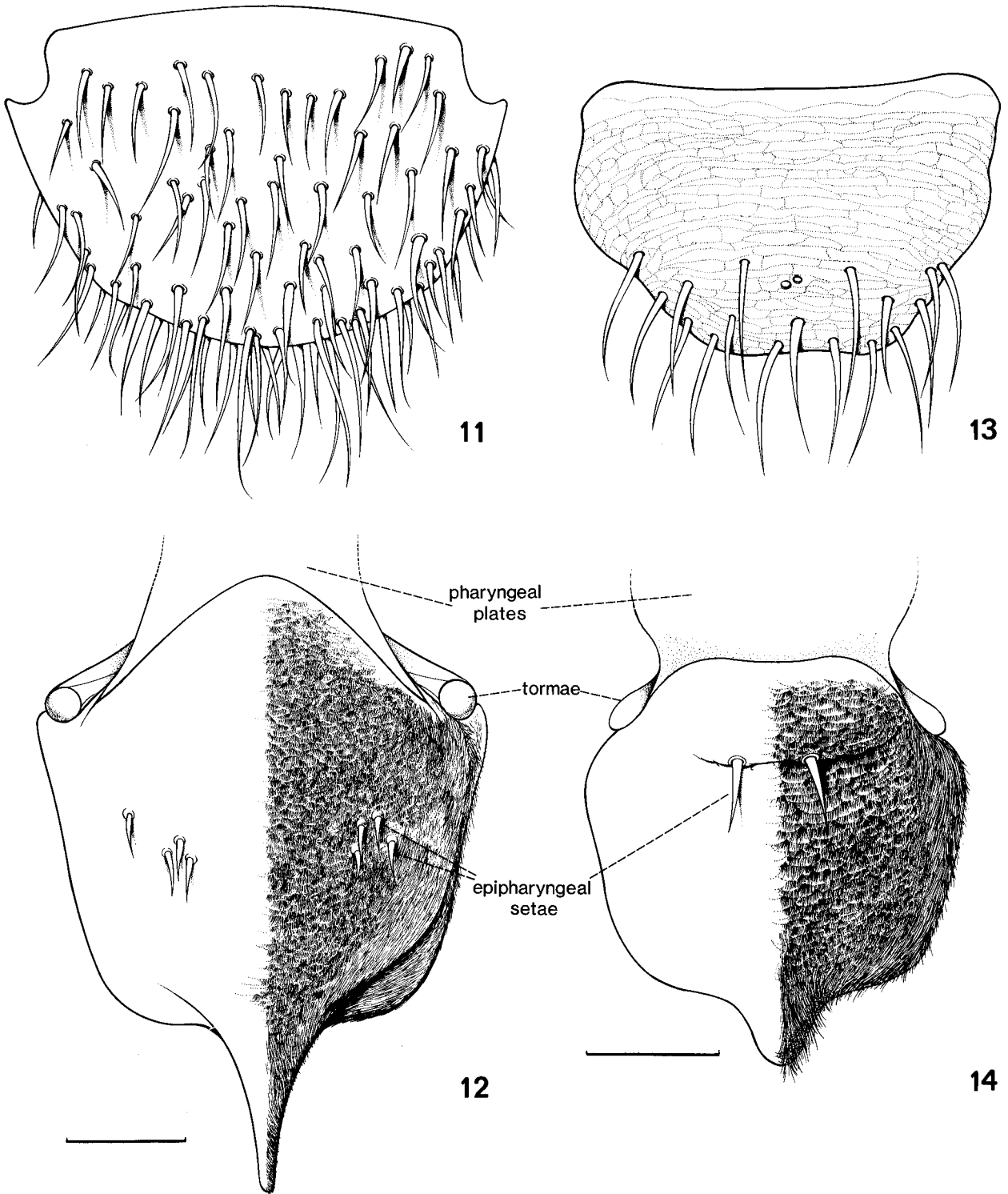
Various genera currently classified in the "Pteromalidae" were examined to determine the structure of the labrum. This analysis is far from comprehensive but special effort was made to examine exemplars of recognized subfamilies (*sensu*

Graham 1969) with particular attention to taxa thought to represent plesiomorphic elements and taxa reported to have a conspicuous labrum (Table 1). Domenichini (1969) illustrated the labrum for a representative of the subfamily Cerocephalinae, *Choetospila elegans* Westwood (his Fig. V-1) and for three genera of Pteromalinae (his Table V): *Anisopteromalus calandrae* (his Fig. 3), *Dinarmus laticeps* (his Fig. 2), and *Habrocystus fenomenalis* (his Fig. 4). Information on the structure of the labrum is currently available for 17 subfamilies.

#### *Distribution of plesiomorphic labrum*

The subfamilies Cleonyminae and Chalcedectinae are closely related and are generally regarded as plesiomorphic elements of Chalcidoidea (Bouček 1971). Hedqvist (1961) goes so far as to suggest that we must search for ancestors of many groups of Chalcidoidea in the cleonymine tribe Heydenini. Many cleonymines and chalcedectines are parasitoids of xylophagous beetles, a host association that recurs in many basal lineages of Terebrantes. The labrum in members of these two subfamilies is often visible beyond the clypeus and is referred to as a "free" labrum. A free labrum has been reported in the following species of Cleonyminae: *Cleonymus albomaculatus* Hedqvist (Fig. 1 in Hedqvist 1960), *Cleonymus depressus* Fabricius (Fig. 3 in Kerrich and Graham 1957), *Leptofoenus peleciniiformis* Smith (Fig. 3 in LaSalle and Stage 1985), *Heydenia pretiosa* Förster (Fig. 24b in Hedqvist 1963;



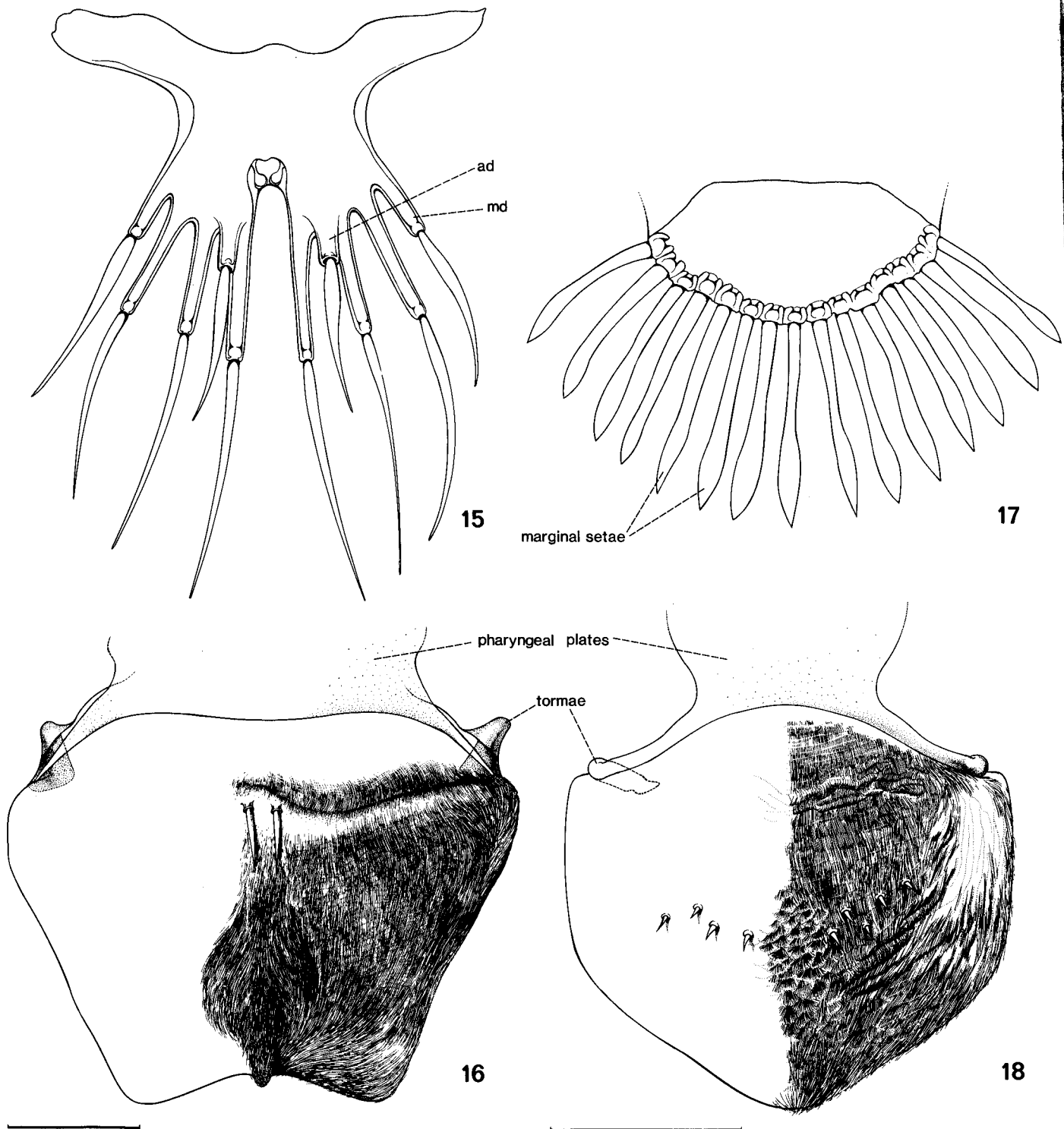


Figs. 11–14. Labrum and epipharynx, anterior (Figs. 11, 13) and posterior (Figs. 12, 14) views. Figs. 11 and 12. *Aperilampus discolor* (DCD slide 260). Figs. 13 and 14. *Brachymeria* sp. (DCD slide 253). Scale bars = 0.1 mm.

Fig. 99 in Russo 1939, as *Lycisca silvestrii*) and *Oodera formosa* Giraud (Fig. III-1 in Domenichini 1969), which is classified in either Cleonyminae or Eupelmidae (see Graham 1969, p. 35).

In *Epistenia* the labrum is partially retracted into the buccal cavity and only the exposed apical portion has stout setae (Fig. 19). In *Heydenia* the labrum is reduced in size and more retractile, with a pair of very long setae in addition to numer-

ous shorter setae. In *Chalcedectes* (Fig. 20) and *Euchrysia* (Chalcedectinae) the labrum is a heavily sclerotized semi-circular flap that articulates near the ventral margin of the clypeus. In both subfamilies there are many labral setae and these are rather evenly distributed on the exposed outer surface of the labrum, not restricted to the apical margin. In Cleonyminae and Chalcedectinae the tormae are distinct sclerites that are closely associated with the pharyngeal plate; there is a



Figs. 15–18. Labrum and epipharynx, anterior (Figs. 15, 17) and posterior (Figs. 16, 18) views. Figs. 15 and 16. *Perilampus hyalinus* (DCD slide 250). Figs. 17 and 18. *Chrysolampus schwarzi* (DCD slide 598). *ad*, aboral digit; *md*, marginal digit. Scale bars = 0.1 mm.

single pair of epipharyngeal setae.

The labra of Brachyscelidiphaginae (*Hemadas*, Fig. 21), Cerocephalinae (*Neocalosoter*, Fig. 22; *Choetospila*, *Gahanisca*), and Macromesinae (*Macromesus*) are similar in many regards to those of Cleonyminae and Chalcedectinae. There are a large number of setae which are distributed over the entire surface of the labrum and are not restricted to the apical margin.

A heavily sclerotized and flaplike labrum is also found in the subfamilies Spalangiinae and Asaphinae. The setae are all tapered and are concentrated at the apical margin of the labrum. Only 8–10 setae occur and the medium setae are very long. In *Spalangia* (Fig. 23) and *Platyspalangia* (Figs. 1, 3 in Yoshimoto 1976) the setae are not restricted to the margin. In *Asaphes* (Fig. 26) the setae originate on the apex of the labrum. A flaplike labrum, similar to that of *Asaphes*, has been

illustrated for the subfamily Panstenoninae (Figs. 62, 64 in Yoshimoto 1984).

#### Apomorphic configurations of the labrum

The labrum is distinctly transverse, much wider than the length along the midline, and emarginate in Ceinae (*Spalangiopecta*, Fig. 27) and in Miscogasterinae (Ormocerini, *Gastrancistrus*, Fig. 25). This type of labrum is slightly sclerotized and usually concealed beneath the clypeus. In both species of *Gastrancistrus* examined 11 tapered setae are arranged in an irregular row with all but the outermost setae offset from the anterior margin of the labrum. There are fewer setae in Ceinae (four in *Cea* and five in *Spalangiopecta*).

The labrum is more or less quadrate or triangular with only four setae in the Miscogasterinae (*Sphegigasterini*, *Miscogasterini*) and in most genera of Pteromalinae examined (Figs. 30–38). The median pair of labral setae are either tapered or spatulate but the lateral setae are always tapered. The labra have distinct lateral lobes, which may be either rounded or acuminate. In both *Halticoptera* species (Fig. 38), the median setae are located on an elongate process which extends beyond the lateral lobes, and the lateral setae are situated in notches between the median process and the lateral lobes. The labra of *Anisopteromalus*, *Dinotiscus*, *Habrocytus*, *Nasonia*, *Pteromalus* (Fig. 31), and *Rhopalicus* (Fig. 30) are very similar. The most obvious difference concerns the form of the median setae: spatulate in *Anisopteromalus*, *Habrocytus*, *Halticoptera*, and *Pteromalus*, and tapered in *Dinotiscus*, *Nasonia*, and *Rhopalicus*. In *Lamprotatus* (Fig. 32) and *Sphegigaster* (Fig. 37) the median area is more heavily sclerotized than the lateral margins and the lateral setae originate on the pigmented median area, not between the lateral lobes and median process. In *Lamprotatus* the median process is short and the median setae are longer than the lateral setae. In *Sphegigaster* the median setae are each inserted on short processes and the tapered median setae are subequal in length to the lateral setae. The labrum of *Psychophagus* is essentially identical with that of *Sphegigaster* (Fig. 37) except that the labrum is uniformly pigmented and the setae are longer. The labrum in *Muscidifurax* (Fig. 34) is more transverse than in other pteromaline genera and the lateral lobes are small and pointed with four tapered setae inserted on short processes along the margin. Circular translucent areas are present in *Anisopteromalus*, *Dinarmus*, *Lamprotatus*, *Psychophagus*, and *Sphegigaster*, and absent in *Dinotiscus*, *Habrocytus*, *Halticoptera*, *Muscidifurax*, *Pteromalus*, and *Rhopalicus*.

A more transverse labrum with distinctly rounded lateral lobes is found in the genus *Perilampidea* (Fig. 35), currently referred to the Pteromalinae, and *Colotrechnus* (Fig. 29; Colotrechninae). In *Perilampidea* there are six tapered setae and very prominent lateral lobes. The four marginal setae are distributed on a slightly produced median area; there is also a pair of setae on the aboral surface. In *Colotrechnus* there are four tapered setae, paired marginal setae and a pair on the aboral surface. Circular translucent areas are present in both genera.

Six tapered labral setae are also found in *Lelaps* (Fig. 33; Diparinae): two pairs of marginal setae on short processes and a pair originating on the aboral surface. Paired translucent areas are present. The labrum of *Lelaps* is remarkably similar to that of *Cratomus* (Fig. 36). The latter is usually referred to the subfamily Cratominae, but close affinities with the Pteromalinae are usually advanced (E. E. Grissell, *in litt.*). The

labrum is characterized by an extremely long medial process with paired spatulate setae and tapered lateral setae. The lateral setae arise on short processes, as in *Lelaps*, not on the aboral surface of the labrum or between the lateral lobes and median process as found in the Pteromalinae.

The labrum of *Eutrichosoma mirabile* (Eutrichosomatinae, Fig. 24; Fig. 7 in Bouček 1974) extends beyond the margin of the clypeus and has eight setae. Six setae are spatulate and arranged on short digits along the margin of the labrum. There is also a single pair of tapered setae. The tormae are elongate and fused to form a narrow band that articulates with a sclerotized process on the inner surface of the labrum. A similar sclerotized process has been found only in Colotrechninae (Fig. 29). In other regards the labra are dissimilar.

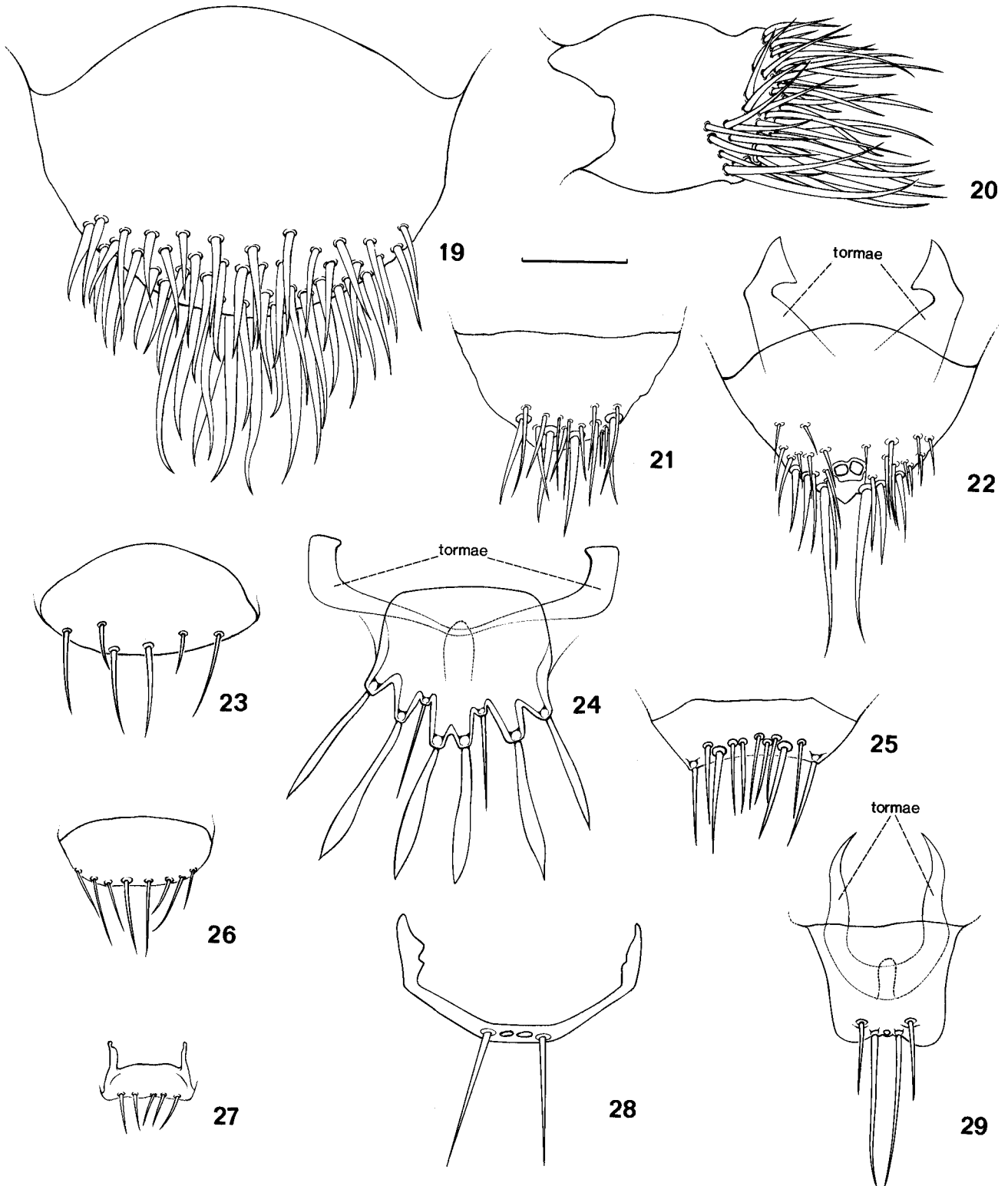
The labrum is very highly modified in the subfamily Eunotinae. The base of the labrum is very narrow and there is a single pair of stout setae on the margin (Fig. 28).

The subfamily Chrysolampinae is a very distinctive and readily diagnosed assemblage of Chalcidoidea. It is more difficult to document the monophyly of this group on the basis of shared derived characters (for discussion, see Darling 1986). Five genera are currently referred to this subfamily and the labrum has been examined in representatives of three of them (Table 1).

The labrum of Chrysolampinae is a very thin semicircular flap that can be extended beyond the margin of the clypeus (Figs. 17, 39–41). The inner and outer surfaces are appressed and the labrum is uniformly sclerotized. The line of attachment of the labrum and clypeus has moved upwards on the inner side of the clypeus so that much of the labrum is hidden (Fig. 8). The tormae are fused with elongate extensions of the pharyngeal plate (Fig. 18) and articulate with the base of the labrum. Stout setae are arranged in a series along the margin of the labrum and each seta originates from a distinct socket. There are no fingerlike processes or digits and no setae originate on the dorsal surface. In *Brachyelatus* (Fig. 40) the labrum is much narrower than in the other genera. There are 13 tapered setae that decrease in length laterad. Eleven setae are present in *Chrysomalla* (Fig. 39) and these setae are very broadly spatulate and oar-like. All species of *Chrysolampus* examined have spatulate setae but the number of setae is quite variable within and between species (*C. splendidulus*, 10; *C. improcerus*, 7; *C. sisymbrii*, 8, 12; *C. schwarzi*, 10, 12, 14, 15, 16). I consider that the number of labral setae in the chrysolampine ground plan is 13, based on *Brachyelatus* as the most plesiomorphic genus of Chrysolampinae (Darling 1986). A reduction in the number of setae occurs in *Chrysomalla* and in most species of *Chrysolampus*. The number of setae is related to the absolute size of the labrum, larger specimens of *Chrysolampus schwarzi* typically having a greater number of setae, and this accounts for the increase in number of setae compared with the ground plan. Multiple epipharyngeal setae were found in all species examined and the setae are similar in size and number to those found in *Aperilampus* (Fig. 18, cf. Fig. 12). In *Chrysolampus* there are two to five setae on each side of the epipharynx and the numbers of setae are symmetrical in *Chrysomalla* and *Brachyelatus*, two and three per side, respectively.

#### Eucharitidae and Perilampidae

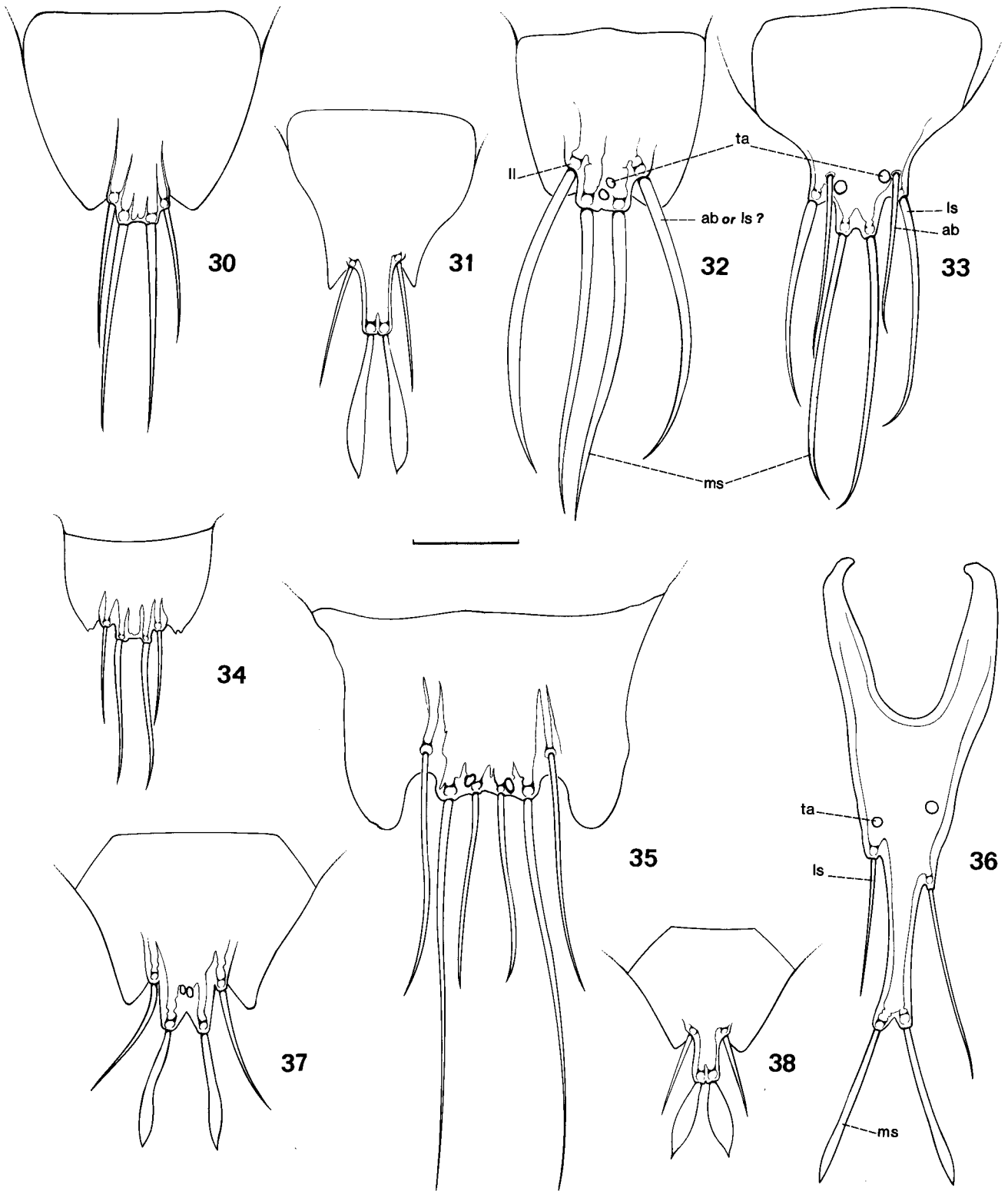
In Eucharitidae and Perilampidae the line of attachment of the labrum and clypeus has moved dorsad on the inner surface of the clypeus so that much of the labrum and the epipharynx is



FIGS. 19–29. Labra of Pteromalidae, anterior view, except where noted. Fig. 19. *Epistenia* sp. (DCD slide 642). Fig. 20. *Chalcedectes* sp., lateral view (DCD slide 646). Fig. 21. *Hemadas nubilipennis* (DCD slide 632). Fig. 22. *Neocalosoter* sp. (DCD slide 698). Fig. 23. *Spalangia cameroni* (DCD slide 611). Fig. 24. *Eutrichosoma mirabile* (composite; DCD slide 283, 301). Fig. 25. *Gastrancistrus* sp. (DCD slide 106). Fig. 26. *Asaphes* sp. (DCD slide 30). Fig. 27. *Spalangiopelta felonia* (DCD slide 355). Fig. 28. *Scutellista cyanea* (composite; DCD slides 674, 771). Fig. 29. *Colotrechnus ignotus* (DCD slide 652). All drawn to same scale, scale bar = 0.05 mm.

generally hidden from view (Fig. 9). The epipharynx in both families is a distinct lobe with a single pair of stout epipharyngeal setae (as in Fig. 14). The labrum is characterized by having the apical margin produced as fingerlike lobes or digits

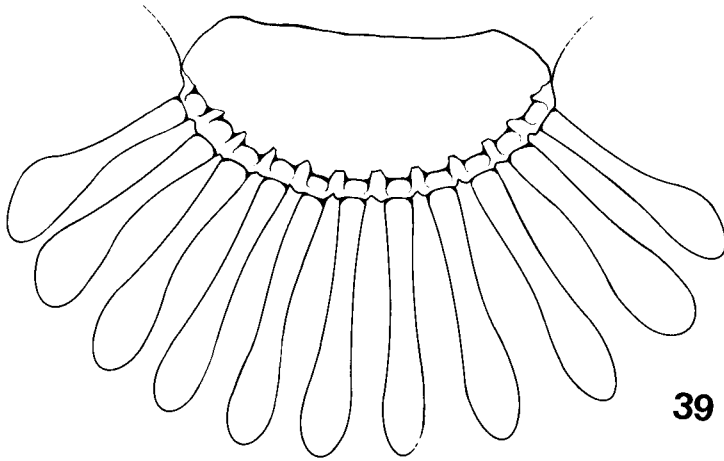
(Figs. 42–65). Digits either are arranged along the margin of the labrum (marginal digits, *md*; Figs. 15, 58, 59) or arise from the anterior or aboral surface of the labrum and project outward (aboral digits, *ad*; Figs. 15, 58, 59). Each digit bears



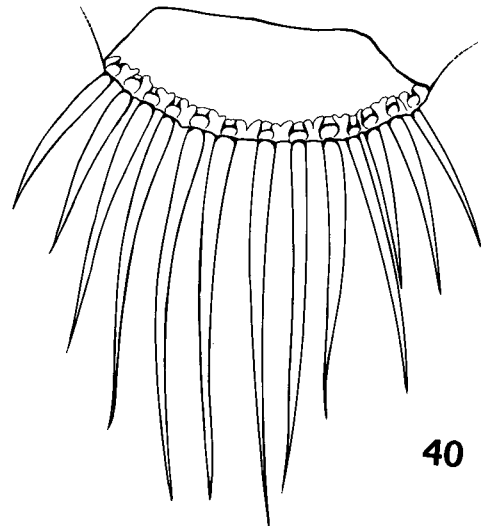
FIGS. 30–38. Labrum of Pteromalidae, anterior view. Fig. 30. *Rhopalicus pulchripennis* (DCD slide 777). Fig. 31. *Pteromalus puparum* (DCD slide 290). Fig. 32. *Lamprotatus splendens* (DCD slide 197). Fig. 33. *Lelaps* sp. (DCD slide 609). Fig. 34. *Muscidifurax raptor* (DCD slide 619). Fig. 35. *Perilampidea syrphi* (DCD slide 614). Fig. 36. *Cratomus megacephalus* (DCD slide 671). Fig. 37. *Sphegigaster pallicornis* (DCD slide 325). Fig. 38. *Halticoptera circulus* (DCD slide 323). *ab*, aboral seta; *ll*, lateral lobe; *ls*, lateral seta; *ms*, median seta; *ta*, translucent area. All drawn to same scale, scale bar = 0.05 mm.

a terminal seta, which may be either spatulate or tapered toward the apex. There is frequently evidence of reduction in the number of digits and setae. The only clear exception to a digitate labrum in either family is that of *Timioderus refringens*

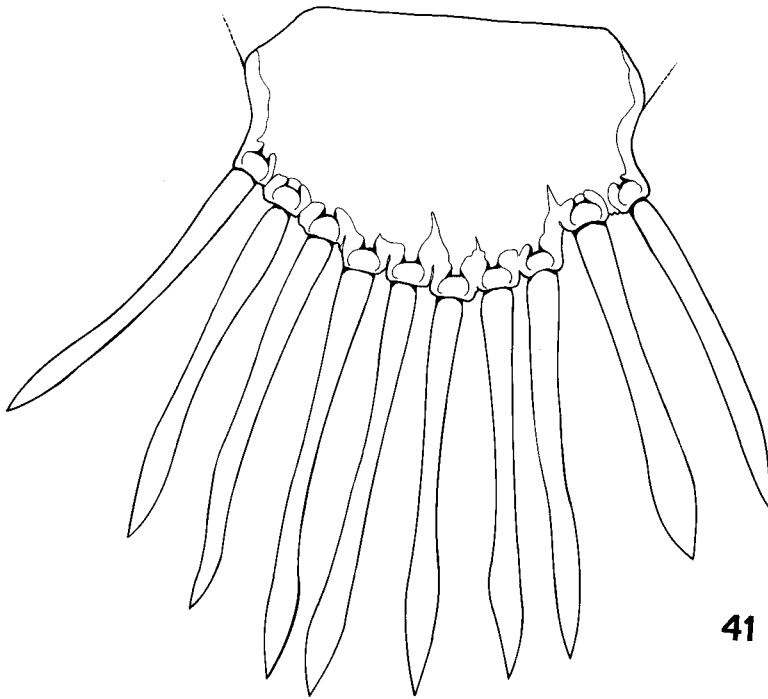
Waterston. As illustrated in Waterston (1916, his Fig. 1*b*), the labrum is elongate with seven long tapered setae and no indication of digits. The assignment of this species to either Eucharitidae or Perilampidae is problematic; the habitus and



39



40



41

Figs. 39–41. Labra of Pteromalidae, Chrysolampinae, anterior view. Fig. 39. *Chrysomalla roseri* (DCD slide 331). Fig. 40. *Brachyelatus viridis* (DCD slide 333). Fig. 41. *Chrysolampus splendidulus* (DCD slide 302). Scale bar = 0.05 mm.

ovipositor are typical of Oraseminae (Eucharitidae) but the mandibles are not falcate and have two teeth, as is typical of the Chrysolampinae.

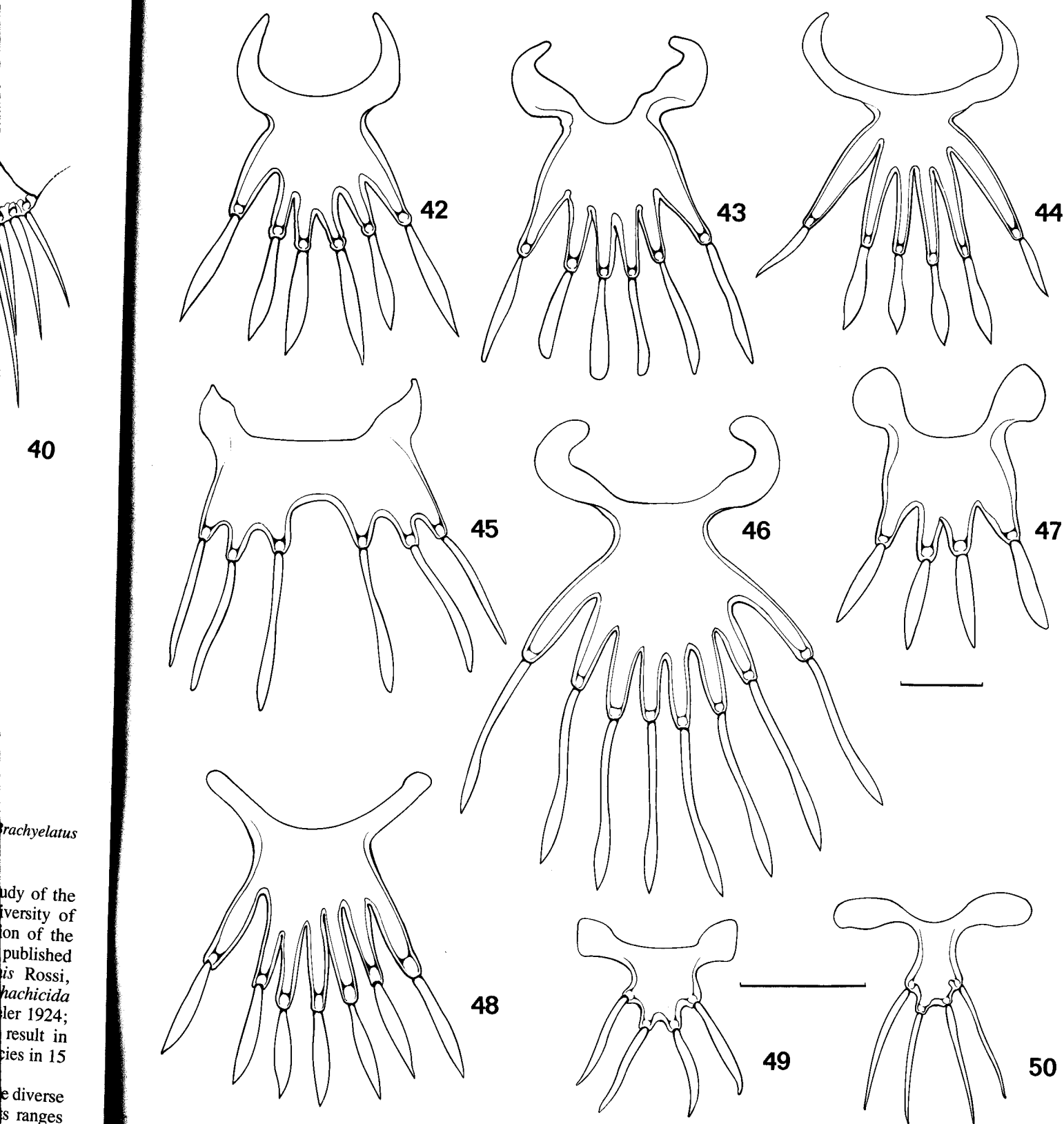
#### *Eucharitidae*

The Eucharitidae are a poorly known group of primary parasitoids of ants (Hymenoptera: Formicidae) with 332 species recognized and classified in 44 genera (Heraty 1985). The morphological diversity is extreme, often approaching the bizarre. Their distribution is worldwide and they are particularly well represented in tropical regions. The higher classification recognizes two subfamilies, Oraseminae and Eucharitinae. Generic limits are actively being redefined with the nomenclature in a state of transition. This is not too surprising when it is realized that the only comprehensive treatments of the entire family are outdated (Ashmead 1904; Schmiedeknecht 1909).

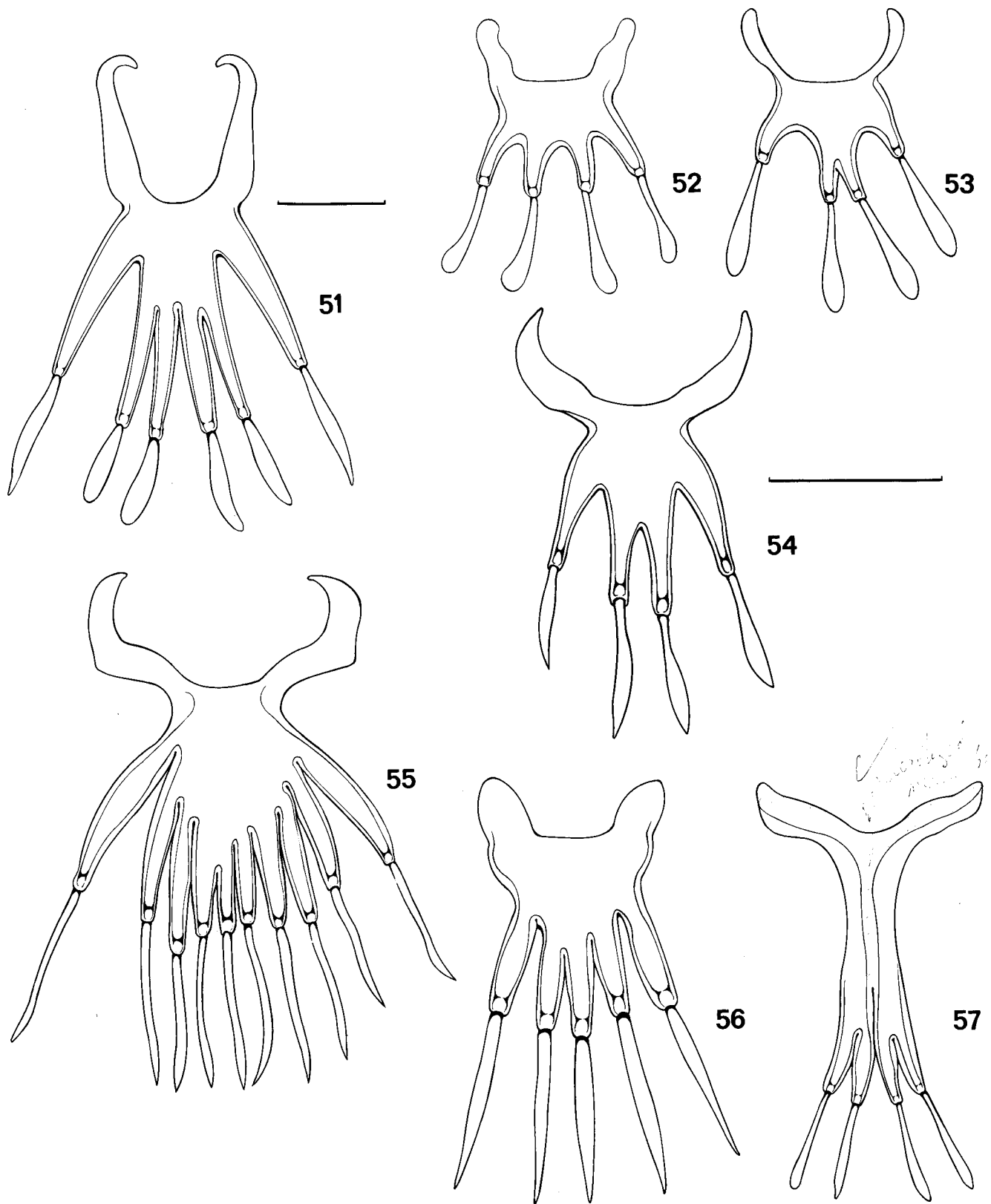
My purpose here is not to present a complete study of the labrum in Eucharitidae but rather to survey the diversity of structure to determine the ground plan configuration of the labrum. The material examined (Table 1) and published figures of additional species (*Stilbula cynipiformis* Rossi, Fig. 6 in Domenichini 1969; *Schizaspidia polyrhachicida* Wheeler and Wheeler, Fig. 1 in Wheeler and Wheeler 1924; various New World species (Heraty 1985, 1986)) result in information on the structure of the labrum for 36 species in 15 genera, representing both subfamilies.

The labra of eucharitids are remarkably similar in the diverse genera studied (Figs. 42–57). The number of digits ranges from 4 to 15. All digits are in the same plane and aboral digits are absent (cf. Perilampidae). The digits are usually arranged in a fanlike configuration, with digits and setae projecting beyond the clypeus. *Lophyrocera apicalis* is a notable exception; the labrum is bilaterally symmetrical with three short

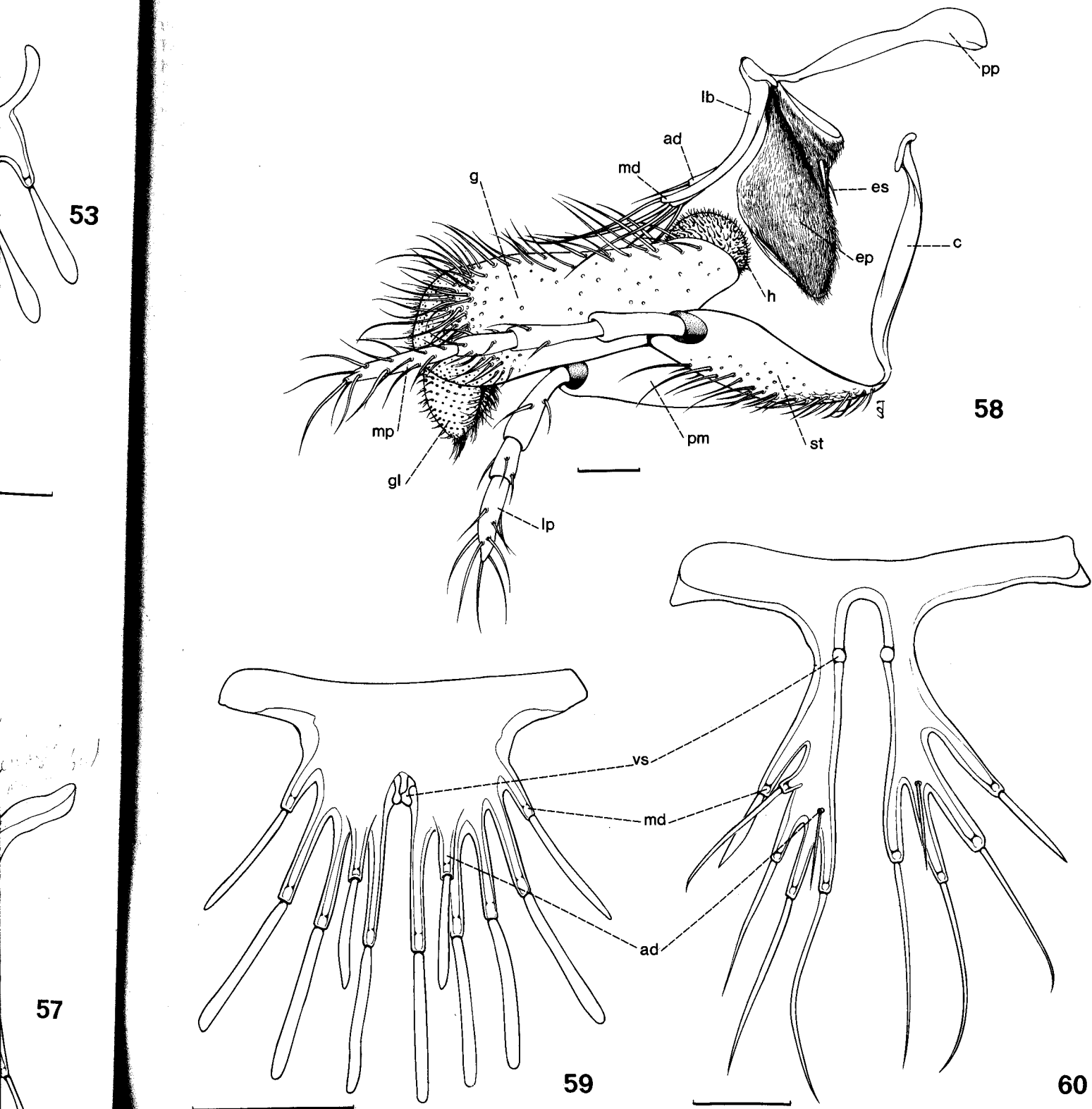




Figs. 42–50. Labra of Eucharitidae, Eucharitinae, anterior view. Fig. 42. *Galearia bruchi* (DCD slide 513). Fig. 43. *Dilocantha* sp. (DCD slide 418). Fig. 44. *Rhipipallus* sp. 1 (DCD slide 411). Fig. 45. *Lophyrocera apicalis* (DCD slide 409). Fig. 46. *Chalcura* sp. (DCD slide 404). Fig. 47. *Pseudochalcura gibbosa* (DCD slide 506). Fig. 48. *Kapala floridana* (DCD slide 507). Fig. 49. *Pseudometagea montana* (DCD slide 406). Fig. 50. *Pseudometagea schwarzii* (DCD slide 291). Figs. 42–48 and Figs. 49 and 50 drawn to same scale. Scale bars = 0.05 mm.



FIGS. 51–57. Labra of Eucharitidae, anterior view. Figs. 51–54. Oraseminae. Fig. 51. *Orasema* sp. 2 (DCD slide 511). Fig. 52. *Orasema* sp. 1 (DCD slide 530). Fig. 53. *Orasmea* sp. 1 (DCD slide 527). Fig. 54. *Losbanus* nr. *laeviceps* (DCD slide 422). Figs. 55 and 56. Eucharitinae. Fig. 55. *Schizaspidia* sp. 1 (DCD slide 416). Fig. 56. *Stilbula* sp. (DCD slide 420). Fig. 57. *Akapala* sp. (DCD slide 298). Figs. 52–57 drawn to same scale. Scale bars = 0.1 mm.

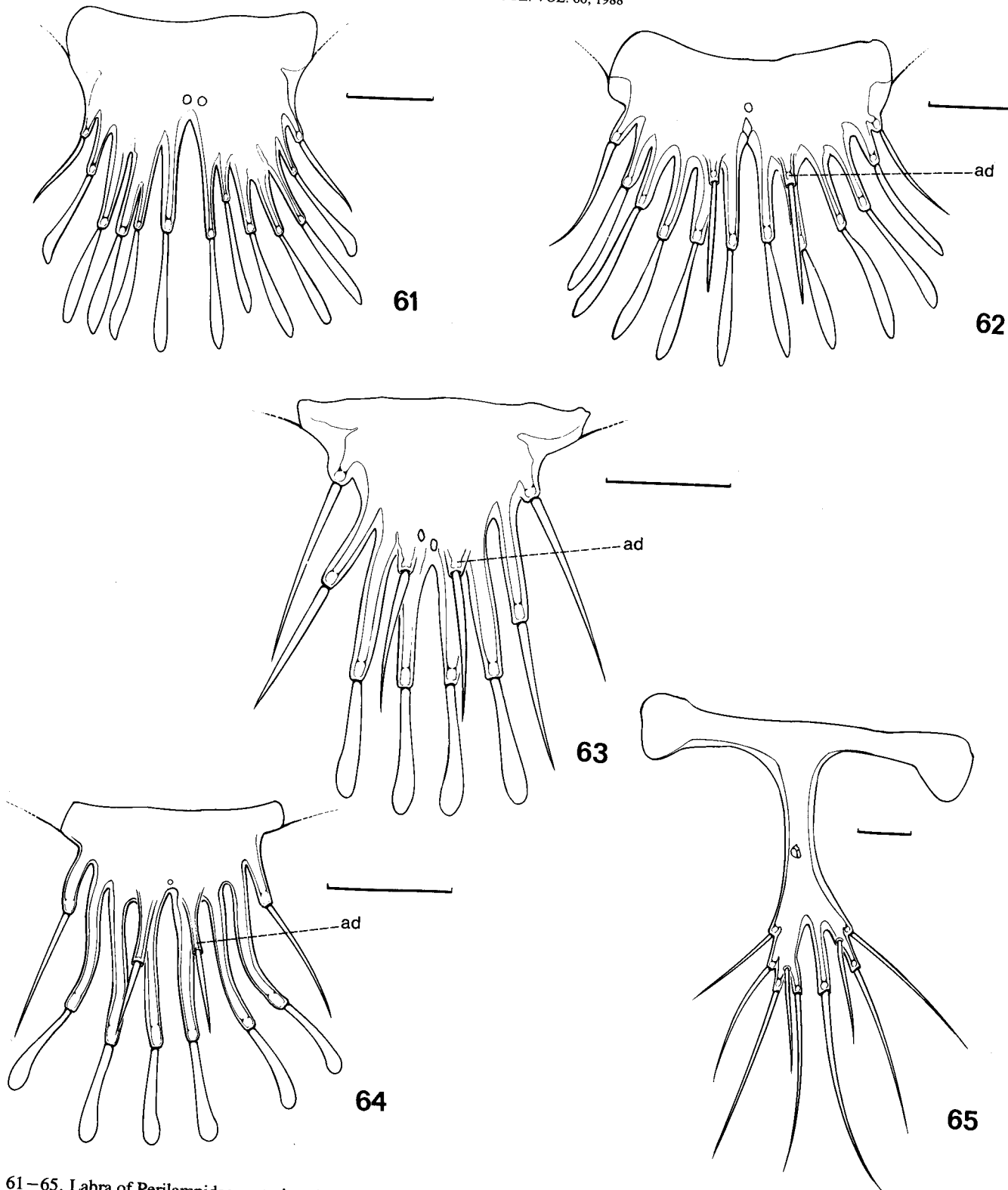


FIGS. 58-60. Mouthparts and labra of Perilampidae. Fig. 58. Lateral view of mouthparts of *Perilampus hyalinus* (DCD slide 505). Fig. 59. *Perilampus auratus* (DCD slide 551), anterior view. Fig. 60. *Euperilampus scutellatus* (DCD slide 593), anterior view. *ad*, aboral digit; *c*, cardo; *ep*, epipharynx; *es*, epipharyngeal seta; *g*, galea; *gl*, glossa; *h*, hypopharynx; *lb*, labrum; *lp*, labial palp; *md*, marginal digit; *mp*, maxillary palp; *pm*, prementum; *pp*, pharyngeal plate; *st*, stipes; *vs*, vestigial sockets. Scale bars = 0.1 mm.

52. *Orasema*  
56. *Euchari-*  
Figs. 52-57

digits on each side of a broad median excision (Fig. 45). This is the only indication of a bilaterally arranged labrum in the Eucharitidae. Within various genera some species have reduced digits, the setae appearing almost sessile. In *Pseudo-*

*metagea*, the total number of digits is small (three or four); the labrum has short digits in *P. montana* (Fig. 49), but the setae are almost sessile in *P. schwarzii* (Fig. 50). Similar intra-generic variation is found in *Pseudochalcura* (Heraty 1986);



Figs. 61–65. Labra of Perilampidae, anterior view. Fig. 61. *Monacon productum* (DCD slide 626). Figs. 62. *Monacon latispina* (DCD slide 442). Fig. 63. *Steffanolampus salicetum* (DCD slide 87). Fig. 64. *Burksilampus anobii* (DCD slide 439). Fig. 65. *Krombeinius eumenidarum* (DCD slide 161). *ad*, aboral digit. Scale bars = 0.05 mm.

the labrum has long digits in seven species (as in *P. gibbosa*, Fig. 47) and reduced digits in two species (as in *P. nigrocyanea* Ashmead, Fig. 32 in Heraty 1986). The labral setae are usually distinctly spatulate. The only clear exception is *Pseudometagea schwarzii* in which the setae are elongate and distinctly tapered (Fig. 50). In its congener, *P. montana*, the

setae are spatulate (Fig. 49). Rudimentary mouthparts are characteristic of *Eucharis* and the closely related genus *Mateucharis* (Bouček and Watsham 1982). The adults do not feed and the labiomaxillary complex is virtually absent (Bouček 1956b) and therefore it is not unexpected that the labrum and epipharynx are extremely reduced and unsclero-

tized. This is here regarded as a derived configuration in the Eucharitidae. The eucharitid labrum is further characterized by basal processes that are often elongate and arched (Figs. 42–57). The absence of tormae suggests that these basal labral processes are in fact fused tormae.

*Akapala* was originally placed in the Eucharitidae, but with the notation that the antennae were "as in *Perilampus*" (Girault 1934). This rare Australian genus has the eucharitid habitus with very narrow falcate mandibles, a triangular head that is abruptly narrowed below the eyes, and a strongly vaulted scutellum extended over the metasoma. Eucharitidae and Perilampidae are traditionally distinguished by the structure of the pronotum. The eucharitid pronotum is very reduced and virtually invisible in dorsal view and not overlapping the mesoscutum medially (Heraty 1985); in all Perilampidae the pronotum is clearly evident in dorsal view. The pronotum is about 0.20 times the length of the mesoscutum in *Akapala*. However, a distinct pronotum is a plesiomorphic character in the Chalcidoidea and may have no phylogenetic significance. The labrum of *Akapala* is clearly digitate (Fig. 57) and is characterized by an elongate central stalk and four spatulate setae. A labrum with a central stalk is hypothesized as a synapomorphy of the species of *Krombeinius* (Darling 1982, 1988) but no species of *Krombeinius* has such a reduced number of setae or spatulate setae. There is also no evidence of aboral digits or setae in *Akapala*, whereas these are clearly evident in *Krombeinius* (Fig. 65). The phylogenetic affinities of *Akapala* remain problematic but I tentatively regard the genus as a highly derived relict species of Eucharitidae. Another possibility is that *Akapala* belongs to the lineage that gave rise to the extant members of Eucharitidae and (or) Perilampidae.

The number of digits in the ground plan eucharitid labrum is difficult to determine because of uncertainty in the relative apomorphy (and monophyly) of the subfamilies. The orasemines studied all have a small number of digits (four to six) (Figs. 51–54). Eucharitines display a much greater diversity, but this is to be expected; only 3 or 4 of the 44 genera are currently referred to Oraseminae (Heraty 1985). The number of labral digits in Eucharitinae ranges from 4 to 15. Few digits occur in independent monophyletic groups of Eucharitinae based on the discussion in Heraty (1985, 1986). Strict outgroup comparison with Oraseminae would indicate that four to six digits is the plesiomorphic condition in the Eucharitinae but I suggest that independent reductions have occurred, based on more distant outgroup comparison with Perilampidae. As a working hypothesis, a labrum with 13 digits, each with a spatulate seta, is proposed for the eucharitid ground plan, based on outgroup comparisons with Chrysolampinae and Perilampidae.

In comparison with Perilampidae, the structure of the labrum in the Eucharitidae is rather conservative although the number of digits is extremely variable, even within a single species. Heraty (1985) reports 9–15 digits in *Obeza septentrionalis* (Brues). There is, however, no variation in the orientation of the digits, all being arranged along the margin, and there is no amalgamation of the digits and setae into a more complex functional unit. A conclusion of morphological conservation in eucharitids was also reached after a comparison of the planidial larva of the Eucharitidae and Perilampidae (Heraty and Darling 1984).

#### Perilampidae

The Perilampidae contains six recognized genera (Bouček 1978), all of which have been recently revised on a world basis

except for the cosmopolitan genus *Perilampus*. It is uncertain which of the six genera represent the basal lineage but *Steffanolampus* is probably the best choice. *Steffanolampus salicetum* (Steffan) is the only species of Perilampidae in which the prepectus is not fused to the pronotum. The fused prepectus is regarded as an apomorphic character state based on outgroup analysis with orasemine Eucharitidae and Chrysolampinae. The single described species is probably a parasitoid of xylophagous beetles, probably Anobiidae (Peck 1974), but this host association needs confirmation.

The labrum was examined extensively in representatives of all genera and many species groups of Perilampidae, data that will be presented in detail in a separate publication. The following summary is based on dissections of 55 species, distributed as follows: *Steffanolampus*, 1; *Monacon*, 13; *Perilampus*, 31; *Burksilampus*, 3; *Euperilampus*, 5; *Krombeinius*, 2.

The labra of perilampids exhibit considerable morphological variation (Figs. 59–65), much of which can be interpreted as a reduction in the number and length of various digits and the subsequent loss of setae. The number of digits varies from 8 to 18. In some *Monacon* species all of the digits are in the same plane and are arranged in a fanlike configuration similar to the Eucharitidae (Fig. 61). Aboral setae are found in other species of *Monacon* (Fig. 62) and in all species of *Perilampus* (Figs. 15, 58, 59), *Steffanolampus* (Fig. 63), and *Burksilampus* (Fig. 64). The aboral digits are reduced and these setae are sessile in all species of *Euperilampus* (Fig. 60) and *Krombeinius* (Fig. 65). Structures interpreted as vestigial sockets are present along the midline of the labrum in most species (*vs.*, Figs. 59, 60). These are always associated with the absence of the innermost pair of digits, resulting in a bilaterally arranged labrum. The labral setae are either distinctly spatulate or tapered. Distinct tormae, closely associated with the epipharynx, are present in all species examined (Fig. 16).

Based on outgroup comparison with the Eucharitidae, the ground plan configuration in the Perilampidae is the fanlike labrum with all digits arranged along the margin, each with a spatulate seta. This type of labrum is very similar to that of certain species of *Monacon* (Fig. 61). However, this hypothesis is inconsistent with ingroup relationships (i.e., *Steffanolampus* as the most plesiomorphic perilampid lineage) and with the intrageneric relationships of *Monacon* proposed by Bouček (1980). Alternatively, aboral digits may be a ground plan character of the Perilampidae. These competing hypotheses will be evaluated in detail in a subsequent publication.

#### Unplaced taxa

Discussed here are a number of taxa of uncertain family placement that have on occasion been referred to either Eucharitidae or Perilampidae (Table 1).

#### Philomidinae

This subfamily has been transferred back and forth between the Perilampidae (e.g., Ashmead 1904) and the Eucharitidae (Bouček 1978), usually as a matter of convenience and with little justification. The structure of the labrum offers no support for considering either *Philomides* or *Aperilampus* as related to Eucharitidae or Perilampidae. The labrum and epipharynx of Philomidinae are among the most plesiomorphic observed in Chalcidoidea. The labrum has many long, stout, and tapered setae dispersed on the outer surface (Fig. 11) and there are multiple stout epipharyngeal setae (Fig. 12). There is no indication of a digitate labrum and Philomidinae is best left

unplaced as a plesiomorphic element of the Chalcidoidea. Although there are a number of similarities with Chalcididae, both in the labrum and other characters, I interpret these all as plesiomorphies.

#### *Echthrodape* Burks

This genus was originally referred to Perilampidae although in the original description it was noted that it could as well be placed in Torymidae or Pteromalidae. The placement of the genus was decided by a "slight preponderance of perilampid characters" (Burks 1963) and the rejected concept that *Chrysolampus* is a member of the Perilampidae (see Darling 1986). The labrum is very reduced, with a single long apical seta, and is not digitate. I regard *Echthrodape* as most closely related to the Torymidae (Mondontomerinae), a hypothesis consistent with the known host associations, viz., parasites of bees, and with the structure of the labrum and the enlarged hind coxae.

### Discussion

#### *The phylogenetic significance of the digitate labrum*

The digitate labrum is here regarded as a synapomorphy of Perilampidae and Eucharitidae, based on outgroup comparison with Chrysolampinae and the chalcidoid ground plan. This is the first synapomorphy proposed for the adults and corroborates relationships posited on the morphology of the first-instar (planidial) larvae (Heraty and Darling 1984). The digitate labrum can be readily derived from the labrum of *Chrysolampus* (Fig. 17) either by excising the margin of the labrum and isolating the marginal setae on fingerlike processes or by the extension of fingerlike processes from the margin of the labrum (Fig. 66). The latter hypothesis would extend the labral setae farther beyond the ventral margin of the clypeus and is supported by consideration of the relative proportions of the basal region of the labrum in *Chrysolampus*, Eucharitidae, and Perilampidae. Domenichini (1969) was the only previous worker to note the distribution and significance of the digitate labrum and proposed a scenario that derived the digitate labrum directly from the flaplike labrum of Chalcididae. His study included *Perilampus* as the only exemplar of Perilampidae and the conclusions are inconsistent with the morphological data from additional perilampid genera and from Chrysolampinae presented herein. Distinct and separated tormae are plesiomorphic in Chalcidoidea and are also characteristic of Perilampidae. The tormae in Chrysolampinae and Eucharitidae are more closely associated with the labrum than with the epipharynx. The fusion is complete in eucharitids; the tormae constitute the base of the labrum. A reasonable transformation from the plesiomorphic condition to the elongate tormae of chrysolampines to the fused tormae of eucharitids could be postulated, but not without requiring that the digitate labrum and characters of the planidial larvae be due to convergence. I therefore regard the apomorphic conditions of the modified tormae as independently derived in Chrysolampinae and Eucharitidae.

The eutrichosomatine labrum is the closest approximation to the digitate labrum of Perilampidae and Eucharitidae; distinct but very short digits are present in *Eutrichosoma*. As discussed above, I regard the digitate labrum as a further modification of the narrow flaplike chrysolampine labrum in which the inner and outer surfaces are appressed. The absence of this derived character state in *Eutrichosoma* suggests either that the labrum was derived independently of Chrysolampinae and therefore is

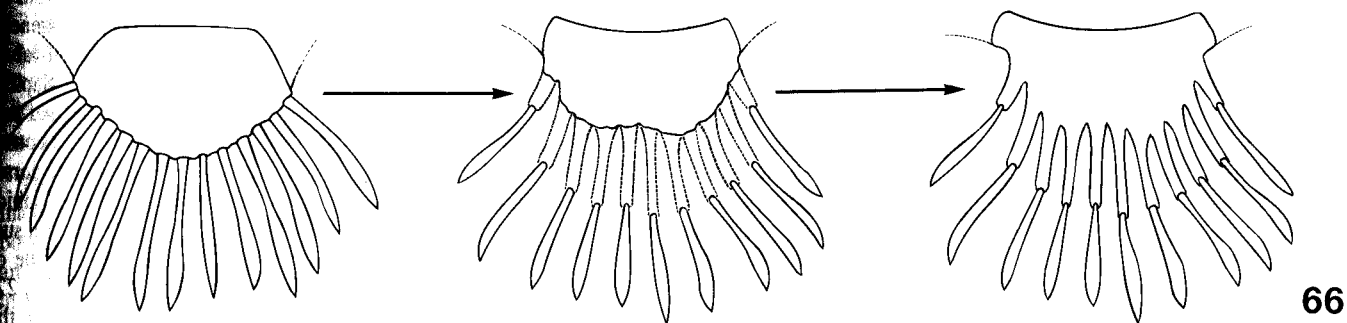
nonhomologous to the labrum of Perilampidae + Eucharitidae or that there was a reversal in eutrichosomatines to the plesiomorphic condition in the Chalcidoidea. I regard the former as more probable. In addition, there are a number of differences in morphology between the labrum of *Eutrichosoma* and the digitate labrum of Eucharitidae and Perilampidae. In *Eutrichosoma* (Fig. 24) only some of the setae are digitate; there are sessile marginal setae. Sessile setae are nearly absent in Eucharitidae and are restricted to the aboral surface in Perilampidae (synapomorphic in *Euperilampus* and *Krombeinius*, not in perilampid ground plan). Sessile marginal setae, however, are common throughout Pteromalidae (Figs. 29, 30, 32, 34, 35). In addition, the labrum of *Eutrichosoma* has differentiated inner and outer surfaces with a sclerotized structure on the inner surface that articulates with the fused tormae. In summary, I regard the labrum of Eutrichosomatinae as independently derived from Eucharitidae and Perilampidae based primarily on the proposed transformation series from the chrysolampine labrum to the digitate labrum, a hypothesis of relationship that is corroborated by both larval morphology and life history.

#### *The digitate labrum as an adaptation for nectar feeding*

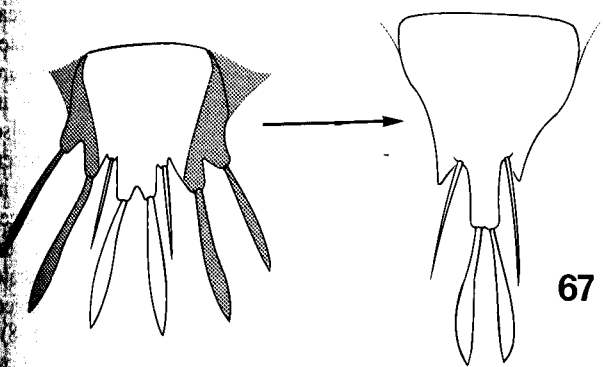
As a synapomorphy at this level of analysis, it is appropriate to consider the possible adaptive significance of the origin of the digitate labrum. I regard the digitate labrum as an adaptation for nectar feeding. As in most Hymenoptera, the mandibles, labrum-epipharynx, and labiomaxillary complex are interconnected by membrane. The digitate labrum and epipharynx are extended beyond the clypeus when the mandibles are retracted (abducted) and the labiomaxillary complex is extended. The labral setae often intermesh with long setae on the labiomaxillary complex (fused galea-lacinea of the maxillae) to form a sievelike apparatus (Fig. 58). Pollen grains are commonly found attached to these setae in museum specimens of Perilampidae (Fig. 9). I suggest that the mouthparts function to exclude pollen while nectar is being collected. Eucharitids and perilampids are often collected on flowers, will take sugar water readily in the laboratory, and undoubtedly use nectar as their primary energy source. Pollen, which is metabolically more difficult to digest, is excluded by the digitate labrum, a process analogous to that in honeybees and some ants, in which pollen and nectar are separated in the digestive system by the action of the proventriculus (Bailey 1952). Chrysolampines also frequent flowers and the modified features of the labrum (viz., stout setae, contiguous setal bases, and modified sockets) are considered adaptations to similar selection pressures. The digitate labrum is a further development in the trend to orient the sievelike structures, be they setae or digits, beyond the clypeus and into a position to exclude pollen from the buccal cavity. Similar selection pressures may have been responsible for the development of digits on the labrum of Eutrichosomatinae.

Many of these generalizations may not be relevant to extant representatives of Eucharitidae and Perilampidae. J. M. Heraty (*in litt.*) has noted a number of apparent contradictions with respect to Eucharitidae, including short adult life-spans, species with reduced labiomaxillary complexes but distinctly digitate labra, and species with reduced labra and greatly swollen labiomaxillary complexes. Such inductive arguments are largely irrelevant to a discussion of the possible selective pressures behind the origin of the digitate labrum; they are, however, extremely relevant to understanding the maintenance

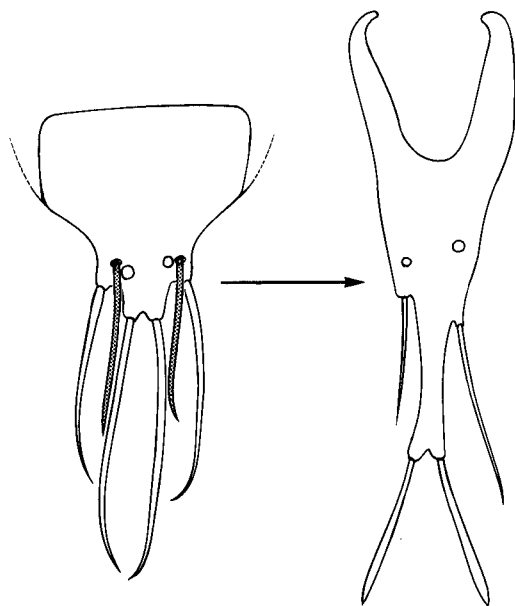




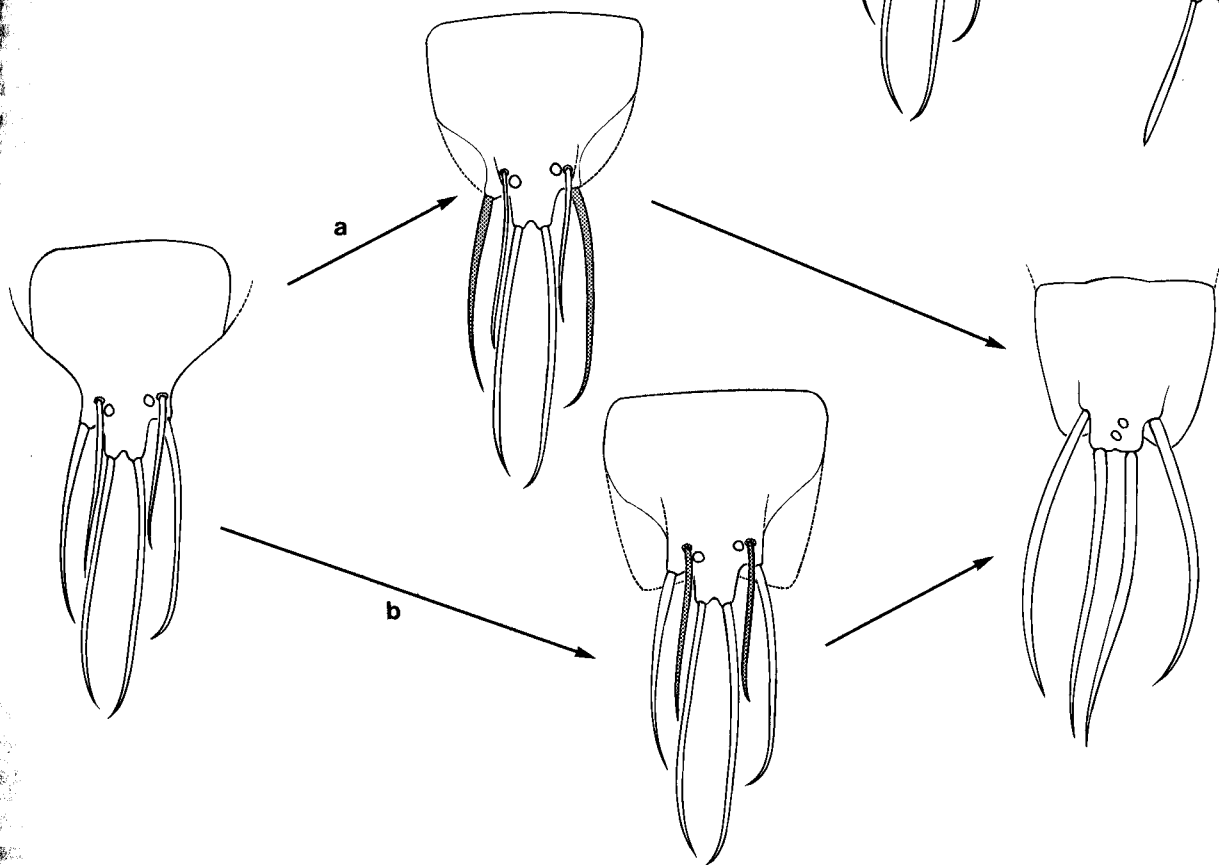
66



67



68



69

Figs. 66-69. Possible transformation series of the labrum. Fig. 66. *Chrysolampus* to *Monacon*. Fig. 67. *Eurichosma* to *Pteromalus*. Fig. 68. *Lelaps* to *Cratomus*. Fig. 69. *Lelaps* to *Lamprotatus*, alternative scenarios. Stippled areas, reductions; broken lines, additions.

of the digitate labrum. It is not unexpected that there have been various modifications of the structure of the mouthparts in Eucharitidae and that these may be associated with derived life history attributes such as short adult life-spans. In most regards eucharitids are the apomorphic representatives of the clade Eucharitidae + Perilampidae, based on morphology, behaviour, and ecology. My hypothesis is historically constrained and does not seek to explain the functional significance of the digitate labrum in all members of the clade. In its simplest form, I am suggesting that the digitate labrum facilitated nectar feeding by acting as a pollen sieve in the common ancestor of Eucharitidae and Perilampidae. The attributes of extant and highly apomorphic representatives can be very misleading in any discussion of the origin of adaptations. Attention must be focused at the level at which the attribute appeared as a derived character (synapomorphy), which is the reason why a credible discussion of the adaptive significance of character states cannot be divorced from phylogenetic studies.

#### *The labrum of Pteromalidae*

The plesiomorphic heavily sclerotized, flaplike labrum with a large number of evenly distributed setae has been modified in the vast majority of Chalcidoidea. The line of attachment of clypeus and labrum has moved dorsad on the inner surface of the clypeus and the labrum is situated within the buccal cavity. Richards (1977, p. 4) notes that "in every group [of Hymenoptera] there is a tendency for the line of attachment to move upwards on the under (or inner) side of the clypeus so that much or all of the labrum is hidden." Convergence has no doubt occurred and this orientation of the labrum offers little phylogenetically useful information. Of more interest is the reduction in the number of labral and epipharyngeal setae and the restriction of setae to the margin of the labrum, modifications that are thought to represent evolutionary novelties.

Considerable attention and significance has been given to the occurrence of the "free" labrum in various pteromalids. For example, Graham (1957) noted a number of characteristics of *Micradelus* Walker that suggested affinities to Cleonyminae, including the presence of a free labrum. Graham (1969) referred the genus to Miscogasterinae as a separate tribe and the only included genus with a free labrum. This classification presents no problems when it is realized that the free labrum is regarded as the ground plan labrum of Chalcidoidea and that phylogenetic relationships cannot be supported by shared plesiomorphic characters. In fact, a very similar type of labrum is found in the Brachyscelidiphaginae (Fig. 21), Cerocephalinae (Fig. 22), *Metapelma* and *Phlebopenes* (Eupelmidae), *Ormyrus* (Fig. IV-4 in Domenichini 1969), which is classified either in the Pteromalidae or Torymidae, and *Torymus* (Torymidae; Fig. IV-2 in Domenichini 1969).

Many of the species with a free labrum are known to be parasites of wood-boring beetles, suggesting the possibility of convergence as a result of functional constraints. Perhaps the flaplike labrum prevents damage to the labiomaxillary complex when the adult wasps are emerging from the galleries of the host. To test this hypothesis, the labra were examined in other pteromalid parasites of xylophagous beetles: *Rhopalicus* and *Dinotiscus*, two closely related species of Pteromalinae (Grissell 1983), and *Cratomus* (Cratominae). The labra of these taxa (Figs. 30, 36) bear no resemblance to a free labrum, suggesting plesiomorphy as the best explanation for the wide occurrence of a free labrum in many distantly related groups of Chalcidoidea. Consistent with this hypothesis is the similarity of the labra of *Chalcedectes* (Fig. 20) and Stephanidae (Figs.

6, 20). A number of derived configurations of the labrum do occur in Pteromalidae and these may provide phylogenetic insights. There has been a reduction in the number of labral setae in Spalangiinae and Asaphinae, resulting in a flaplike labrum with a row of marginal setae. It could be argued that the restriction of setae to the margin of the labrum is a consequence of the internalization of the labrum; setae on the dorsal surface would hinder the movement of the labrum and labiomaxillary complex. However, setae do occur on the dorsal surface of the labrum in many chalcidoids in which the line of articulation with the clypeus has moved dorsad (Figs. 21, 22, 25). This functional constraint cannot be used to question the phylogenetic significance of marginal setae.

The Chrysolampinae and Philomidinae are the only two groups that have multiple and indeterminate epipharyngeal setae. This is tentatively regarded as a plesiomorphic character in Chalcidoidea based on the reduction rule and analyses are underway to determine the number of epipharyngeal setae in various Terebrantes and Aculeata. The Chrysolampinae also have a relatively large number of marginal setae. Thirteen tapered setae are present in *Brachyelatus* (Fig. 40, cf. 8–10 in Spalangiinae and Asaphinae), and the setae are much longer and stouter than in Asaphinae (Fig. 26). The setal sockets are contiguous along the margin of the labrum and incorporate internal cuticular processes which perhaps support the enlarged setae as rigid structures when the labrum is extended (Fig. 8). Spatulate setae occur in all species of *Chrysomalla* and *Chrysolampus*, and this could be a further modification to increase the surface area of setae exposed beyond the clypeus. I propose that stout setae with reinforced setal bases and distinct sockets are synapomorphies of the Chrysolampinae, Eucharitidae, and Perilampidae.

Plausible morphological transformations of the labrum can be proposed between various subfamilies of Pteromalidae based on both a tendency for the reduction of the number of setae and other apomorphic modifications. These are presented at this time as testable hypotheses to stimulate additional research. The following characters exhibit a variety of configurations within Pteromalidae and may provide phylogenetic insights.

#### *Form of setae*

Tapered setae are regarded as plesiomorphic in Pteromalidae based on outgroup comparison with the ground plan labrum of Chalcidoidea. Spatulate setae have been found only in Chrysolampinae, Eutrichosomatinae, Miscogasterinae, and Pteromalinae. Spatulate aboral setae have not been found.

#### *Orientation of setae*

There are two distinct orientations of setae on the labrum of Pteromalidae. Marginal setae project forward, parallel to the axis of the labrum, whereas aboral setae arise on the upper surface of the labrum. Both types of setae are present in *Lelaps* (Fig. 33) and *Perilampidea* (Fig. 35) but only marginal setae are present in *Eutrichosoma* (Fig. 24) and *Cratomus* (Fig. 36). Recognition of these differing orientations may assist in determining setal homologies. Tapered aboral setae are regarded as plesiomorphic in Pteromalidae.

#### *Lateral lobes*

Distinct lateral lobes, lacking setae, are present in only Miscogasterinae, Pteromalinae, and Colotrechninae. This is regarded as an apomorphic character state based on comparison with the chalcidoid ground plan.

### Translucent circular areas

These are broadly distributed in Chalcidoidea, present in Pteromalidae (Fig. 13), and here regarded as plesiomorphic in Pteromalidae. These structures have not been observed in Pteromalinae or Chalcedectinae but are present in Cerocephalinae (Fig. 22).

The transverse labrum of Ormocerini is of considerable interest (Fig. 25). There is a large number of setae, all tapered, both marginal and aboral setae are present, and lateral lobes are lacking. I regarded this as the most plesiomorphic labrum in Miscogasterinae or Pteromalinae. The labrum of Diparinae and Cratominae are also of interest. Lateral lobes are also absent in both subfamilies and the four marginal setae are positioned on short processes. The six-digitate labrum of *Lelaps* can be readily transformed into the four-digitate labrum of *Cratomus* by the simple loss of aboral setae (Fig. 68). However, it should be noted that the median setae are spatulate in *Cratomus*. The majority of pteromaline and miscogasterine genera examined have distinct lateral lobes and setae arising on the surface of the labrum that project forward and are oriented as marginal setae (Figs. 30–32, 34, 35, 37, 38). These setae are often inserted on a raised median area which is often more pigmented than the lateral lobes of the labrum. There are at least two plausible transformation series that would result in derived labra with this configuration. The lateral setae of these genera may be homologous to the aboral setae of *Lelaps* and *Perilampidea*, i.e., the lateral setae are lost and the labrum is expanded laterad (Fig. 69a). Alternatively, the lateral setae may be homologous to the lateral setae of *Lelaps* and *Cratomus*, i.e., the aboral digits are lost and the lateral lobes are developed with the lateral setae moving to the aboral surface (Fig. 69b).

Bouček (1974) has suggested that Eutrichosomatinae represent a remnant of one of the plesiomorphic branches related to the pteromaloid Chalcidoidea. The labrum, however, exhibits numerous derived character states and the size and number of setae are intermediate between the configuration of Spalanginae, Asaphinae, Miscogasterinae (Ormocerini), and the more derived labra of Miscogasterinae and Pteromalinae. In fact, the labrum of *Eutrichosoma mirabile* can be readily transformed into a typical four setae labrum by deleting the lateral two pairs of setae (Fig. 67).

### Summary

It is premature to suggest the phylogenetic and therefore the classificatory implications of these preliminary results for Pteromalidae. Clearly, additional species must be examined to evaluate other equally plausible scenarios for the evolution of the labrum. It is important to note that additional dissections are not a panacea; there would still be uncertainty if we knew the structure of the labrum for every species of Chalcidoidea. The step from the analysis of a single-character system to a hypothesis of phylogeny requires dealing with the distribution of homoplasy in individual character phylogenies. Homoplasy is present in all data sets and the goal is not to find a character system that is free of homoplasy, but rather to be able to identify where homoplasy is distributed in a particular data set. A monothetic approach will not work; what is needed is the accumulation of morphological data sets from different life history stages and disparate regions of the body. The reciprocal illumination provided by multiple character systems will ultimately result in a clearer understanding of evolutionary relationships. The structure of the labrum is grist for the mill.

### Conclusions

The basic conclusion of this paper is that the digitate labrum is synapomorphic in Eucharitidae and Perilampidae. The path to justifying this traditional conclusion was rather circuitous and required considerable additional dissections and study because of the regress of phylogenetic analysis. Two points require emphasis. First, the structure of the labrum exhibits considerable morphological variation and should be a source of phylogenetically useful information concerning the phylogeny of the Chalcidoidea. Second, comparative morphology is the only hope for the maturation of a classification for the Chalcidoidea. Studying additional character systems and integrating the results is perhaps the only effective means for progress towards the ultimate goal, a stable and informative classification. There seems to be a naive hope that after the descriptive taxonomic work is completed for the world fauna of Chalcidoidea the phylogeny, hence classification, will be revealed. Clearly, such alpha-taxonomic work must proceed, and at an ever increasing rate given the ongoing transgressions against nature. But phylogenetic studies must keep pace and suggest priorities for future taxonomic studies. Regrettably, species will be lost that will never be known to science but improvements in the general reference system of biology cannot be predicated on the Sisyphean task of a comprehensive biological inventory.

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