RESEARCH ARTICLE

Stiff upper lip: Labrum deformity and functionality in bees (Hymenoptera, Apoidea)

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Abstract

In hyper-diverse groups such as Hymenoptera, a variety of structures with different, complementary functions are used for feeding. Although the function of the parts such as the mandibles is obvious, the use of others, like the labrum, are more difficult to discern. Here, we discuss the labrum's function in bees, as well as the implications of deformities to this and associated characteristics.

Introduction

As one of the oldest groups of terrestrial organisms, invertebrates employ an exceptional diversity of feeding and sensory strategies (Grimaldi and Engel 2005). The structures related to the sensation and manipulation of food are most often found on the head (Chapman 1998; Chapman and de Boer 1995; Snodgrass 1993). Although the evolutionary origins of some parts of the insect head remain contested, it is clear that each major component plays a role in the overall functioning of the head and, therefore, the survival of the organism (Frase and Richter 2013; Ortega-Hernández and Budd 2016; Posnien et al. 2009; Smith et al. 2014; Smith and Goldstein In press).

The primary uses of many of the parts of the head are generally obvious (e.g., eyes or mandibles), but those of others, such as the labrum, are more obscure. This is in part due to the frequent conflation of the labrum with the associated epipharynx (Dellacasa et al. 2010; Snodgrass 1993). Although these two components function in tandem, it is important to differentiate between them because failure to do so may obscure the individual functions of each of these structures.

The insect labrum is typically a sclerotized plate found below the clypeus, either articulated there or fused to it, and it is generally innervated and connected to frons musculature (Chapman 1998; Snodgrass 1985; 1993). Often referred to as the "upper lip" based on the Latin origin of the term, it is considered an important element of insect food manipulation (Rebora et al. 2014; Snodgrass 1985). The labrum is also a site of attachment for the epipharyngeal wall, a soft membrane found on the inner face of the labrum that often has a medial projection called the epipharynx (the epipharyngeal wall is also called the membranous inner face of the labrum or similar terms, we will generally consider the epipharynx as a specific part of the epipharyngeal wall (Chapman 1998; Dellacasa et al. 2010; Snodgrass 1993; Vilhelmsen 1996). The epipharyngeal wall is more generally associated with sensory functions, especially chemo- and mechano-sensation, likely because it often continues internally from the labrum, along the inner face of the clypeus, to the mouth (Snodgrass 1985; 1993). Together, the labrum and epipharyngeal wall form a functional unit that assists insect feeding in many different ways.

Interestingly, the labrum appears to be more frequently modified for secondary, non-feeding purposes than the epipharyngeal wall. This may be either a consequence of observer effort, given the fact that the epipharyngeal wall is typically hidden and overlooked in favor of the readily apparent labrum, or simply because the labrum is exposed and can more easily interface with the external environment. Regardless, insects use the labrum in many novel ways. For example, labral sensillae commonly used for more benign purposes are now part of the trigger and lock mechanism used by some trap-jaw ants to spring their powerful mandibles (Larabee and Suarez, 2014). Not all uses of the labrum are tied to such exceptional behaviors, however, as the labrum has many forms and functions across insects and even within orders such as Hymenoptera, making definitive identification of labrum function a surprisingly challenging task.

Even in some economically important groups like bees, the labrum's general role is relatively poorly understood. Similar to insects at large, there is also a great diversity of bee labrum forms (Fig. 1; Michener 1944; Michener 2007), but the function of only relatively few of these forms has been investigated, and labral use remains obscure even in closely-studied groups (Walker 1995). Even the most dramatic labral modifications in the bees, such as the elaborate keels seen in many female Halictidae, have unknown functionality, though they are absent in males and much reduced in parasitic members of the family (Michener 1978; Michener 2007; Walker 1995; Fig. 1A). Conversely, many of the apid bees which have unusually long labrums are cleptoparasitic, though the functionality of this trait is again unknown, these structures are perhaps related to nest cell penetration or protection of the mouthparts (Michener 2007; Fig. 1B).
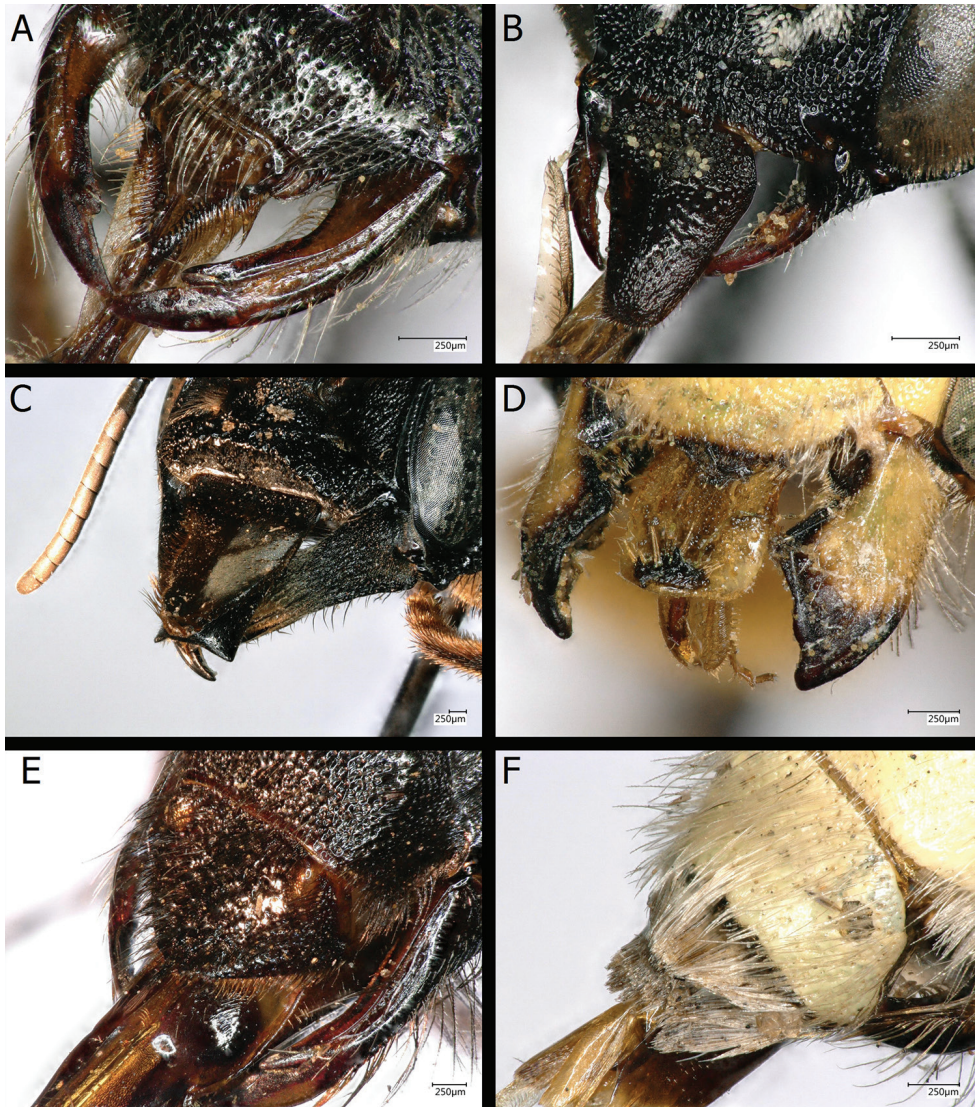
Figure 1. Labrum form diversity in bees. **A** *Halictus ligatus* Say 1837 female (NPIC:87530) **B** *Holcopasites insoletus* (Linsley, 1942) male (NPIC:BBSL211611) **C** *Megachile sculpturalis* Smith 1853 female (NPIC:BBSL1030971) **D** *Trachusa larreae* (Cockerell, 1897) female (NPIC:94880) **E** *Habropoda laboriosa* (Fabricius, 1804) female (NPIC:BBSL253733) **F** *Anthophora abrupta* Say, 1838 male (NPIC:BBSL231004). Scale bars indicate 250µm for each image independently.

However, long labrums are linked to resource transport in some nest-building species. For example, the largest bee in the world (*Megachile pluto* Smith, 1860) and some of its relatives (Fig. 1C) are known to carry nesting materials (resin, wood) between their mandibles and labrum (Messer 1984). Similarly, *Trachusa larreae* females (Fig. 1D) have a shock of setae on the labral apex that facilitates resin collection (Cane 1996),

and *Habropoda laboriosa* females (Fig. 1E) may use labral setae to aide in pollen collection (Cane and Payne 1988; Thorp 2000). Rather more fascinating, *Anthophora abrupta* males (Fig. 1F) are known to use a labral "moustache" to paint floral fragrances onto mating areas to attract females (Lee 1998; Norden and Batra 1985; Whitten et al. 1989). However, relatively few bee species are known to use the labrum in these particular ways, and it appears safe to assume that such non-feeding related functions are secondary.

It is reasonable to state that the labrum serves some broader function in bees, given that it is obviously articulated and connected to both musculature and nerves (Ellis and Hepburn 2006; Erickson Jr et al. 1986; Snodgrass 1985). Reports of bee lice (Braulidae) tickling the labrum of honey bees to induce regurgitation, and the presence of sensillae there, clearly suggest mechano-sensory function at a minimum (Grimaldi and Underwood 1986), although the existence of chemo-sensory labral or epipharyngeal sensillae in bees is debated (de Brito Sanchez 2011; Mitchell et al. 1999; Sandoz et al. 2002; Whitehead and Larsen 1976). The labrum is also apparently used to press the epipharyngeal wall against the proboscis to create an airtight seal during ingestion, giving it an additional function beyond mere sensation (Carreck et al. 2013). Interestingly, the epipharyngeal wall has apparently lost the gustatory functions seen in many other insects, such tasks are instead thought to be managed by bees with the antennae, other mouthparts, and forelegs (de Brito Sanchez 2011; Mitchell et al. 1999). This makes sense when considering that the epipharyngeal wall is less likely to directly touch food that bees are initially handling, in comparison to groups with gustatory labral sensillae (*e.g.*, Orthoptera: Cook 1972; Zaim et al. 2013).

The larval labrum's function also appears to be linked to sensation and feeding, as many bees and other Hymenoptera have conspicuous setae there (Murao and Tadauchi 2005; O'Donnell 1989; Pitts and Matthews 2000; Rozen 2001). However, complications arise in that sensillae can change form, and possibly even function, between instars (Garófalo and Rozen Jr 2001), and the distribution of sensillae is highly variable both across and within groups (Rozen 2001; Rozen Jr and Kamel 2006). Cleptoparasitic larvae are especially interesting, often featuring high numbers of labral sensillae and unusual integumental modifications (e.g., sharp apical tubercles, setae-derived spines; Rozen Jr and Kamel 2006; Straka and Bogusch 2007). It may be that cleptoparasites use their sensillae to locate hosts and competitors, and the broadly flattened labral form of some instars also appears to be used to create a seal on host eggs during feeding (Alves-dos-Santos et al. 2002). Rozen Jr and Kamel (2006) suggest that such enlarged forms are also used in conjunction with the mandibles to crush their opponents. These seemingly antagonistic forms revert to the unmodified type seen in most non-cleptoparasites, supporting the idea that they are likely involved with the belligerent life history typical of early-instar cleptoparasites (Baker 1971). Whatever primary and secondary functions the labrum may serve, it clearly serves purposes in both adults and larvae.

In light of the functional importance of the labrum and epipharyngeal wall, selection should strictly regulate their presence and form. Even if these components do

not serve chemo-sensory functions, the loss of mechano-sensory function could easily hinder food manipulation (Carreck et al. 2013). The discovery of a deformed adult bee without a functional labrum was, then, a surprise. Here, we describe an aberrant specimen of *Anthophora* (*Heliophila*) *petrophila* Cockerell, 1905, compare it to typical specimens of the genus, and discuss the implications of its labral reduction.

Methods

A single bee specimen with an aberrant labrum was found among the >30,000 *Anthophora* that the first author has passed under a microscope. This specimen belongs to *A. petrophila*, a xeric bee that is found commonly throughout much of the western United States. It was collected by P.H. Timberlake at Olancha, California on May 2nd, 1927 off of *Salix exigua* Nuttall 1842, and is held in the University of California, Riverside's Entomology Research Museum (UCRCENT407176). Many typical specimens of *A. petrophila* have also been examined during the first author's studies (n>3000), and the epipharyngeal wall's morphology when dried was also observed in five specimens (NPIC: BBSL482833, BBSL510382, BBSL510415, BBSL516410, BBSL918735 from NPIC). Images were taken with a VHX-5000 Digital Microscope. Terminology follows Michener (2007).

Results

Examination of typical specimens of *Anthophora petrophila* versus the aberrant specimen enabled confirmation of labral reduction, rather than absence (Fig. 2). The darkened clypeal border seen in typical *A. petrophila* is clearly present in the aberrant specimen, surrounding the nozzle-like sclerite which we assert is the reduced labrum. The absence of other sclerites in this area further supports the homology of this sclerite with the labrum of typical *A. petrophila*. The clypeus is correspondingly enlarged, descending and encircling the labrum as it normally does to a lesser extent, which suggests that the growth of these two areas may be linked in some way. Notably, in comparison to normal specimens, this also reduces the protuberance of the deviant's clypeal rim, and the deformed labrum is entirely bare of setae.

Upon further examination, it was determined that the epipharyngeal wall was also greatly reduced. As the aberrant specimen was collected in 1927, it was decided that internal features would not be examined through dissection, in order to avoid unnecessary damage to this apparently unique specimen. Nonetheless, examination of the inner face of the labrum in five normal, pinned specimens of *Anthophora petrophila* confirmed that the epipharyngeal wall would have been distinguishable in the deviant specimen if it were unmodified.

No additional abnormalities were evident in this specimen, and its body size is about average for this species, not visibly larger or smaller than other specimens ob-
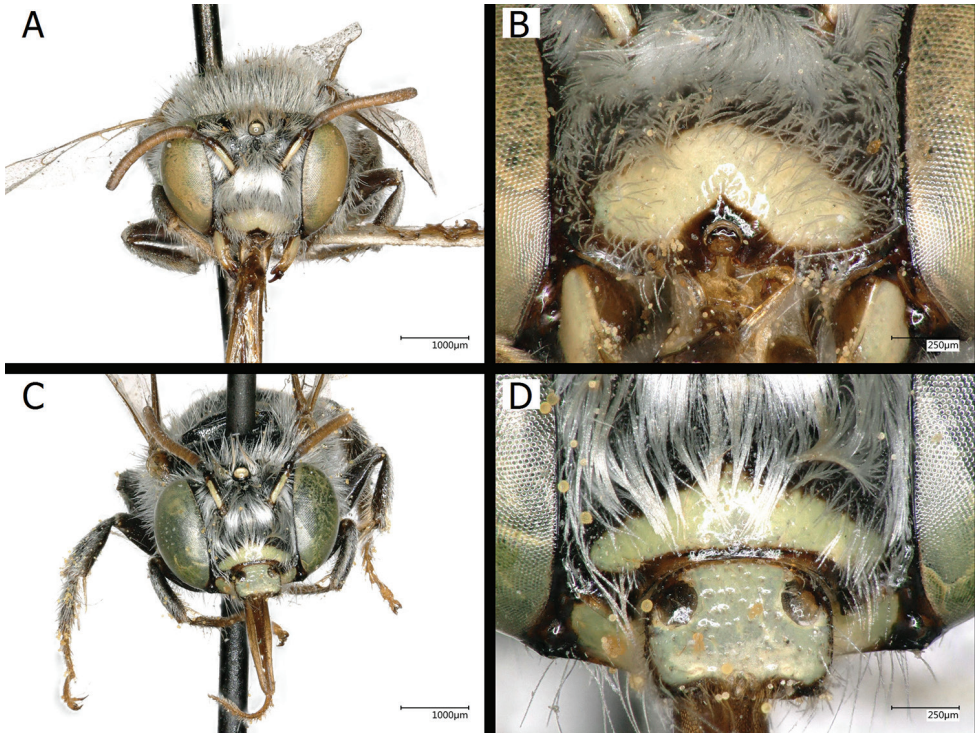
Figure 2. The deviant (UCRCENT407176) and normal (NPIC:BBSL506171) labral forms of *Anthophora petrophila*: **A** deviant, 50× magnification **B** deviant, 200× magnification **C** normal, 50× magnification **D** normal, 200× magnification. Scale bars indicate 1000μM (**A, C**) or 250μm (**B, D**).

served. Consequently, malnutrition during development appears to be an unlikely cause of this labral deformity. No Strepsiptera or other parasites were evident, suggesting the malformed labrum is also not a result of parasitic growth inhibition (Borowiec and Salata 2015; Salt 1927).

It is notable that the wings of the specimen are completely intact. Wing wear is a widely-accepted metric of adult age in bees, based upon activity, and the exceptionally rapid wingbeats and skillful flight of *Anthophora* (*Heliophila*) make this feature especially useful in this group (Foster and Cartar 2011; Kemp 2000; Michener et al. 1955; Packer and Knerer 1986). As the specimen was collected on a flower, this cannot be explained by reduction of musculature or other internal factors that would lead to an inability to fly and, thereby, preservation of the wings.

Discussion

This deformity is quite rare, as it was only seen in one of >30,000 *Anthophora* examined. This could reflect the rarity of labral deformities or suggest that such deformi-

ties are deleterious. Given the apparent use of the epipharyngeal wall as a seal on the proboscis, the wall's reduction should dampen the suction efficiency of the proboscis (Carreck et al. 2013). Another possibility is that the sensillae present on the labrum are involved in initiating or modifying food responses, and setal absence could influence feeding behaviors. It may be that the deviant specimen was unable to feed, or very inefficient at doing so.

Although the direct effects of this deformity are unclear, the lack of wing wear corroborates potential reduced feeding ability, as the bee must have either emerged recently or been discouraged from flying by the futility of attempts to eat. The effects of labrum and epipharyngeal wall reduction could be tested in future studies by using knockout methods to target genes involved in labrum development and then conducting comparative observations on the eating behaviors of normal versus deformed bees (Siemanowski et al. 2015).

Although rarely reported, deviant phenotypes can be useful for exploring developmental pathways, embryology, and potential evolutionary pathways. Changes to developmental pathways can result in new phenotypes that have selective advantages. For example, the facultative polyphenism seen in termite castes is achieved through manipulations of gene regulation in response to socio-environmental characteristics, such as the state of the colony (Korb and Hartfelder 2008). In bees, the developmental fluidity of sex-based characters provides the raw materials on which selective forces can act. Deviant phenotypes often trade female characters, such as pollen-gathering scopae and nest-constructing mandibles, for male characters, such as hairlessness and simple mandibles (Wcislo et al. 2004). Fertile individuals which lack the proper tools to build and provision their own nests may instead opt for a cleptoparasitic lifestyle and usurp others' nests, in lieu of not reproducing. If heritable, such traits could then be passed to future generations.

Abnormalities in insects are thought to arise from one of four teratogenic processes: genetic mutation, malnutrition, disruption of typical developmental pathways by external, abiotic forces (e.g., temperature changes, chemicals, radiation) or parasitism (Wcislo et al. 2004). Given the absence of evidence for malnutrition, parasitism, and the fact that bee larval environments are well-shielded from most abiotic factors, it seems plausible that this aberration is a consequence of mutation. Studies investigating the heritability of deformities are rare outside of model systems like *Drosophila*, but have also been suggested in some studies of ant gyandromorphism and intercastes (Wheeler 1937), as well as deformities of *Tenebrio molitor* L. beetles (Steinhaus and Zeikus 1968). Unfortunately, the rarity of deformed bees makes study of mutation in the group more difficult.

It is initially surprising that this anomalous specimen survived and successfully emerged as an adult. This suggests either that the labrum was functional during its larval stage or that the larva could develop and attain a normal adult body size without its function. If the labrum were also non-functional in the larva, then this suggests that the labrum is not necessary for successful larval development in non-parasitic bees. This may be due to the relatively high effort female bees exert in provisioning their

nests. As females choose and prepare the entire larval food mass, it may be that larval decision-making is of negligible importance, and that if there are contaminants (e.g., fungi) then the larvae are doomed regardless of labral and epipharyngeal functionality. However, as we cannot be certain of the developmental stage in which the deformity arose or the cause of the deformity, our inferences remain limited.

The fact that this specimen is male raises an interesting possibility. If it were female, and the labrum is indeed needed for successful foraging, it is unlikely that such a female would have been able to provision her offspring as well as a normal female could. The energetic costs of foraging and excavation of even a single cell could be too high for a deformed female, because typical members of this subgenus appear to construct a single cell over the course of a day, each in cell its own nest (Torchio and Youssef 1968; Torchio 1971; Orr unpublished nest records). As a result, the mutation would not likely be passed down by a female (if it is indeed genetic). In contrast, a lucky male may mate quite soon after it has emerged. The sex-biased inheritance patterns that this and other abnormalities may exhibit could prove to be an interesting area for future research in bees.

Conclusions

This study describes the novel morphological anomaly of bee labral reduction, while also reviewing the diversity of labral functions across bees overall. The potential implications of this aberration are also discussed, including how labrum reduction might impact feeding ability and whether fitness effects thereof affect life stages and sexes differently. Although many studies have focused on gynandromorphism in bees (Michez et al. 2009, and many others), this is one of relatively few to explore other deformities. Notably, prior papers have focused primarily on visual or antennal deformities, rather than aberrations that could impact feeding ability (Alfonsus 1931 [one central compound eye]; Engel et al. 2014 [extra ocelli]; Gibbs 2010 [ocelli reduction and slight translocation, compound eye enlargement]; Hopwood 2007 [compound eye fusion, "cyclops"]; Knerer and Atwood 1964 [metanotal anomalies]; Rodeck 1943 [one antenna lost]; Sivik 1962 [antennal segment deformation]).

Descriptive studies such as this are fundamental to bettering our knowledge of life on Earth. However, such studies seem to have gradually lost their luster in recent memory (Grimaldi and Engel 2007). It is, nonetheless, vital that we persist in describing the diversity of life and those aberrant variants which we encounter, as these lines of inquiry can uncover fundamental processes, developmental pathways, and mechanistic functions that would otherwise remain obscure. Although new methods will inevitably arise, descriptive studies and the life history information that they reveal will always valuable for both directing future research and putting the results of newer methods in a proper biological context.

Acknowledgements

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