

GLANDS IN THE HEAD CAPSULE OF COCCINELLID BEETLES WITH A DISCUSSION ON SOME ASPECTS OF GNATHAL GLANDS

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SIX FIGURES

AUTHOR'S ABSTRACT

Glands are classified by structure as multicellular complex acinose, multicellular simple tubular, and unicellular; by position as general, hypodermal, ocular, antennal, intra-mandibular, mandibular, mandibulo-maxillary, maxillary, intra-cardonal ~~glands~~, and labial. Some open outside the extra-oral cavity. They are supposed to be offensive in function. The segmental origin of the gnathal is doubtful.

CONTENTS

Introduction	48
Different types of glands	48
Structure of the glands	49
Multicellular complex acinose glands	49
Multicellular simple tubular glands	54
Unicellular glands	56
Distribution of the glands	56
General hypodermal glands (uni- and multicellular acinose glands)	56
Ocular glands (uni- and multicellular acinose glands)	56
Antennal glands (multicellular acinose glands)	56
Intra-mandibular glands (uni- and multicellular acinose glands)	57
Mandibular glands (tubular glands)	57
Mandibulo-maxillary (maxillular?) gland (tubular glands)	58
Maxillary glands (tubular glands)	58
Intra-cardonal glands (uni- and multicellular acinose glands)	58
Labial glands (multicellular acinose glands)	58
Labral glands (uni- and multicellular acinose)	58
Variations in the size of the glands in the family Coccinellidae	59
Actual openings of the glands	60
Probable functions of the glands	60
Segmental homology of gnathal glands	62
Material and technique	64
Acknowledgments	66

INTRODUCTION

The studies embodied in this paper were initiated by the discovery of well-developed glands associated with the labium in *Coccinella septempunctata* (family Coccinellidae, Coleoptera). This discovery is of special significance in view of the unequivocal statement of Snodgrass ('35) that "labial glands are present in all the principal orders of insects except Coleoptera." I reported the presence of labial glands in Coleoptera with a few preliminary observations (Current Science, vol. 5, May, '37) and am now presenting a detailed description and discussion. Closer examination of the contents of the head capsule in connection with the study of these glands and of the mouth parts of coccinellid beetles revealed the presence of several other glands besides the labial glands, and has also brought to light some facts both of practical and theoretical importance. In the present paper, therefore, I have incorporated not only a description of the labial glands but an account of all the glands found in the head capsule of coccinellid beetles.

A survey of the literature on the subject shows that the glands of the head region in general and those associated with the mouth parts in particular have been very little investigated in Coleoptera. Talking of the insects as a class, we can safely generalize that a pair of glands has been found associated with each pair of head appendages, these glands having been lately named after the mouth appendages with which they are associated. This gap in our knowledge of glands in connection with the mouth parts of Coleoptera is partly attributable to the heavy and densely pigmented sclerotization of the head region of Coleoptera which often defies even the best efforts to obtain successfully proper serial section for study.

DIFFERENT TYPES OF GLANDS

The glands studied can be classified in two ways: 1) on the basis of their structure and 2) on the basis of their distribution.

On the basis of structure they can be classified into three types:

1. Multicellular complex acinose glands
2. Multicellular simple tubular glands
3. Unicellular glands

On the basis of distribution they can be distinguished as follows:

1. General hypodermal glands
2. Ocular glands
3. Antennal glands
4. Intra-mandibular glands
5. Mandibular glands
6. Mandibulo-maxillary (maxillary?) glands
7. Maxillary glands
8. Intra-cardonal¹ glands
9. Labial glands
10. Labral glands

These names simply indicate the position of the glands and not homologies.

STRUCTURE OF THE GLANDS

Multicellular complex acinose glands

The labial glands of *Coccinella septempunctata* (Pradhan, '37) are paired glands closely associated with the labium and situated symmetrically on either side (fig. 1) of the median line. They are comparatively large structures occupying a considerable space in the head capsule, and extending horizontally from the proximal margin of the prelabium in front (fig. 2) to a little distance beneath the sub-oesophageal ganglion (fig. 3) and vertically along the sides of the buccal cavity and the pharynx so as to reach near the top of the supra-oesophageal ganglion. They open separately at the level of the proximal margin of the prelabium, between it and the hypopharynx, the actual openings lying in the salivarium slightly mesially to the basal bars of the suspensorial skeleton of the hypopharynx.

¹ Cardonal, belonging to Cardo.

Each gland consists of a floccular mass of glandular cells with an elaborate system of ducts and ductules. The cells are grouped into lobules of various sizes which look like bunches of grapes under the high power of the microscope. Each lobule is formed of a varying number of cells (fig. 4). If a lobule consists of only two or three cells, each is drawn out

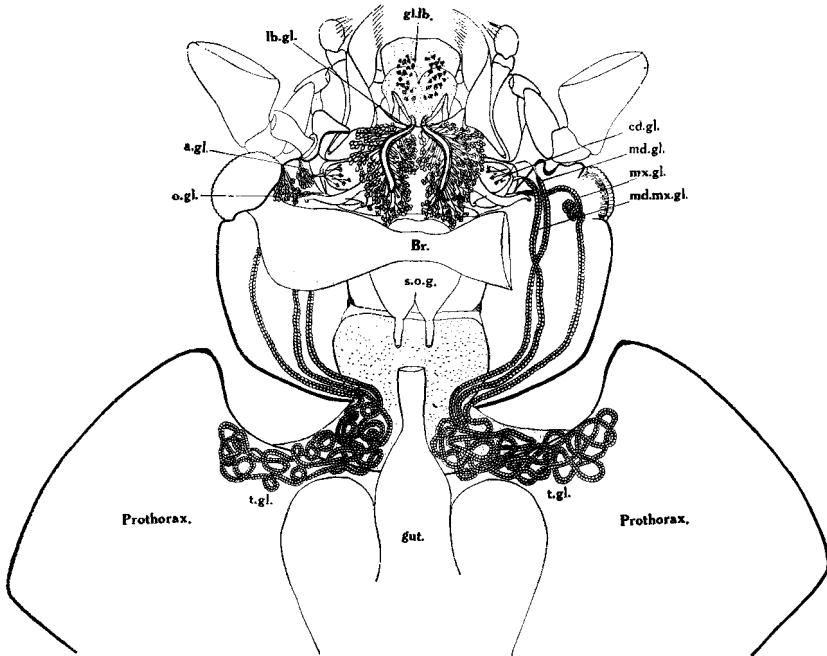


Fig.1 Glands in the head capsule of *C. septempunctata* in situ (slightly diagrammatic). lb.gl., labial gland; a.gl., antennal gland; o.gl., ocular gland; Br., brain; cd.gl., cardonal gland; md.gl., mandibular gland; mx.gl., maxillary gland; md.mx.gl., mandibulo-maxillary (maxillular?) gland; gl.lb., glands within the labium; t.gl., tubular glands (named above).

into a clearer conical process which fuses with similar processes of the other cells and forms a thin chitinous ductule for the whole lobule. On the other hand, if a lobule is formed of a larger number of cells, the ductule is formed by a confluence of fine canaliculi lying in between the adjacent cells. All the cells constituting a lobule are enclosed in a common chitinous covering which forms a kind of basement membrane

to the cells and is continuous with the walls of the ductule of the lobule.

Each gland cell is generally globular in form although the size and shape depend on those of its lobule. Thus the cells of a small lobule look pear-shaped on account of their conical processes, while the cells of a large lobule differ in outline

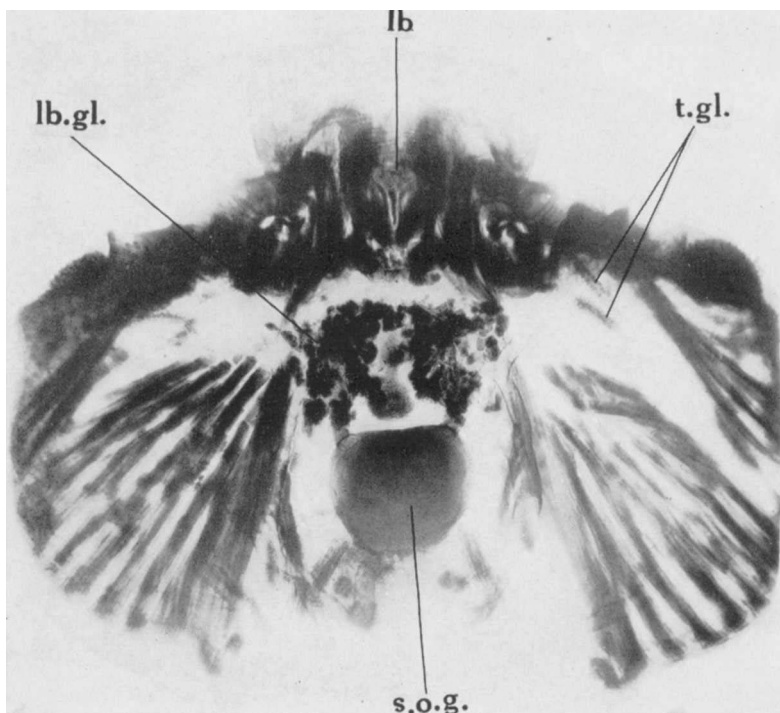


Fig. 2 Photomicrograph of horizontal section of the head capsule of *C. septempunctata* showing labial glands in situ. lb.gl., labial gland; s.o.g., sub-oesophageal ganglion; t.gl., tubular gland; lb., labium.

according to their situation, although all of them are convex on their exposed surfaces. The protoplasm of these cells is finely granular while the outer surfaces are markedly smooth and definite; the nuclei are, however, often irregular in outline and offer much difficulty in differential staining, the chitinous covering of the lobule adding to the difficulty of staining.

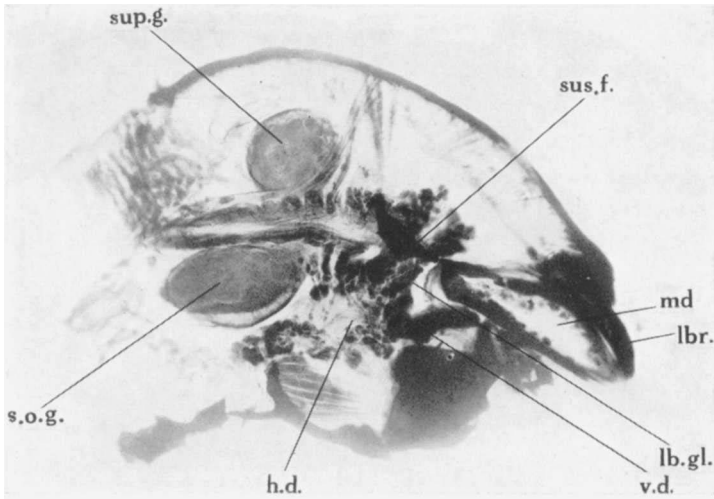


Fig. 3 Photomicrograph of the longitudinal vertical section of the head capsule of *C. septempunctata* showing labial glands in situ. h.d., horizontal duct; v.d., vertical duct; lb.gl., labial gland; md, mandible; lbr., labrum; sup.g., supra-oesophageal ganglion; sus.f., portion of suspensorial fork.

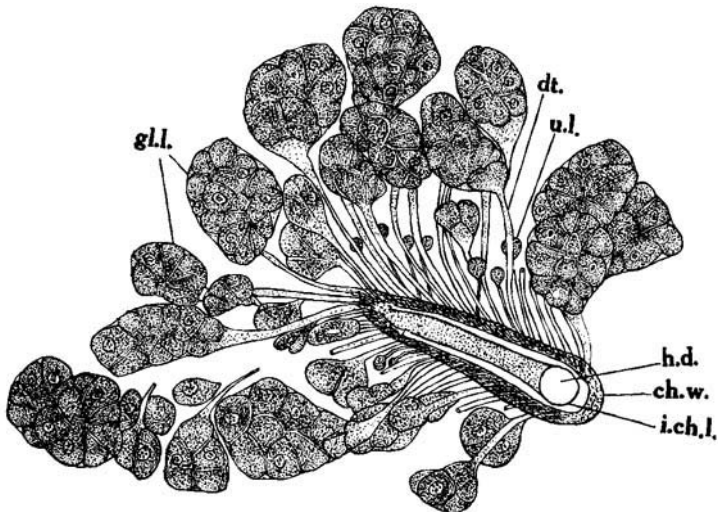


Fig. 4 A portion of the labial gland of *C. septempunctata* drawn under high power (obj. 7; eye.p. 4). dt., duetule; gl.l., glandular lobule; u.l., unicellular lobule; h.d., horizontal duct; ch.w., chitinous wall of the main duct; i.ch.l., internal chitinous layer of the main duct.

The conducting system of the gland is peculiar and elaborate. Each gland has two main ducts: one running horizontally and the other vertically. These two ducts meet together a little proximally to the distal margin of the post-labium, and form a short terminal duct. The terminal ducts of the two glands open separately into the salivarium as already described (p. 49). The horizontal main duct lies more or less in the same plane as the terminal duct, and the two together are S-shaped in a horizontal section of the head (fig. 1). The presence of the vertical main duct is seen in the sagittal section of the head (fig. 3).²

Both the vertical and horizontal main ducts receive along their whole length innumerable fine chitinous ductules from the lobules. These ductules are long and thus the main ducts lie fairly far away from the glandular mass. Generally each of the lobules discharges its secretion into the main duct directly, but some of the lobules at the beginning of the main duct form long chains, and their ductules join with one another before discharging into the main duct.

Beside the glandular lobules described above, there are often a large number of unicellular minute lobules. They form a distinct set of their own, looking different from the multicellular lobules. The ductules of these minute lobules are less than half the length of other ductules. Whether functionally these minute lobules are similar to or different from multicellular lobules, cannot be stated with certainty.

All the component parts of a gland show a wide range of variation, but the following measurements give an idea of their size:

Measurements

	μ
1. The horizontal extent of the gland approximately	486
2. The vertical extent of the gland approximately	720
3. The length of the terminal duct approximately	180
4. The length of the horizontal duct approximately	270
5. The length of the vertical duct approximately	216
6. The diameter of the gland cell approximately up to	20
7. The diameter of the nuclei of a gland cell approximately up to	6

² Also see figure 2, paper III.

Multicellular simple tubular glands

The structure of the tubular glands in different insects has already been described but there is no description of the tubular glands of coccinellid beetles except a short one of those of *Epilachna indica* by myself ('37). It has been known for a very long time that tubular glands exist in *Blaps* (Tenebrionidae) and *Pyrochroa* (Pyrochroidae) while, recently Murray and Teigs ('35) have described a pair of tubular glands in *Calandra oryzae* (Curculionidae), and still more recently R. L. Gupta ('38) has recorded the presence of tubular glands in the families Tenebrionidae, Coccinellidae, Curculionidae and Cerambycidae, with a detailed description of those of Tenebrionidae. It should be noted that in all these

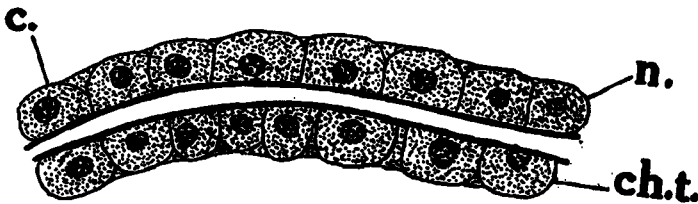


Fig. 5 Optical section of the tubular gland. Magnification same as in figure 4. n., nucleus; c., cell; ch. t., chitinous tube.

beetles, only one pair of glands has been described. Even in Coccinellidae, both Gupta and myself noticed only one pair of these glands. As regards their external opening opinions differ. In *Blaps* no definite place of opening has been described; in *Pyrochroa* the glands unite to form a small median duct which opens into the mouth; in Tenebrionidae Gupta simply writes that they open "in the extra-oral cavity separately on the two sides"; in *Calandra*, Murray and Teigs describe these glands as "opening on to the first maxilla"; in *Epilachna* I described them as opening "separately in the angle between the labium and the maxillae beneath the sides of the hypopharynx." In this case I mistook the extensor apodeme of the cardo for a continuation of the cavity of the underlying gland and thus mistook the site of the opening, which actually lies beneath the tip of the apodeme.

An intensive search for the glands has revealed the presence of three separate pairs of tubular glands in the head capsule of coccinellids. These open in the maxillo-mandibular area (figs. 1 and 6) and either remain confined to the head capsule as in the herbivorous forms (fig. 6) or extend to the prothorax where they remain complexly coiled as in the carnivorous forms (fig. 1). The histological structure is exactly like that

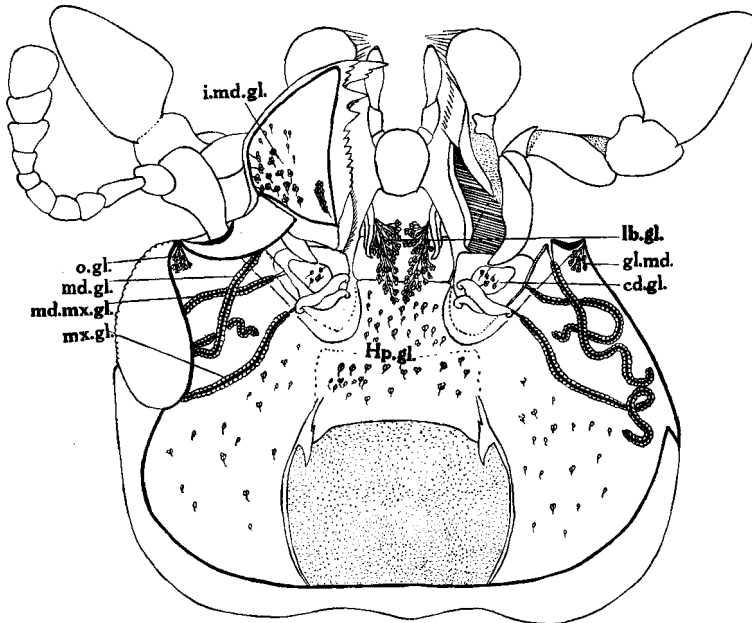


Fig. 6 Glands in the head capsule of *E. indica*. i.md.gl., intra-mandibular gland; lb.gl., labial gland; gl.md., glandular aggregation near mandible; cd.gl., cardonal gland; Hp.gl., hypodermal gland; mx.gl., maxillary gland; md.mx.gl., mandibulo-maxillary gland; md.gl., mandibular gland; o.gl., ocular gland.

of the glands of the Tenebrionidae, a detailed account of which has recently been published by Gupta ('38). Each gland consists of a single layer of cubical cells, surrounding a fine chitinous tube, the wall of which forms the intima of the surrounding cells. The protoplasm of these cells is almost always finely granular and the nuclei are well defined but irregular in outline.

Unicellular glands

These are distributed on the inner surface of the wall of the head capsule, covering almost the whole of the area free from the attachment of muscles (fig. 6). They resemble in structure the unicellular lobules described between the ductules of the labial glands of *C. septempunctata*, but their ductules are comparatively much smaller. It may also be noted that these are not the only glands on the general surface of the cranial wall, but that there are a large number of small multicellular glands also scattered among these unicellular glands.

DISTRIBUTION OF THE GLANDS

General hypodermal glands (uni- and multicellular acinose glands)

These cover the general surface of the cranial wall (fig. 6) and comprise both unicellular and multicellular glandular lobules.

Ocular glands (uni- and multicellular acinose glands)

Seldom if ever has an aggregation of gland cells been described as situated near the eye, but in *C. septempunctata* the ocular gland is too prominent in sections to be overlooked. It looks like a small portion of the labial glands (multicellular complex acinose glands) already described, but the individual cells are comparatively smaller. The gland opens to the exterior through more than one ductule of variable thickness, which open in turn on a very small patch just outside the ocular ridge between the eye and the antenna.

Antennal gland (multicellular acinose gland)

This group is situated nearer the base of the antenna than the eye and opens within the antennal socket. Structurally these are similar to the ocular glands. It may be noted that the antennal glands in the words of Snodgrass "are not of common occurrence in insects."

Intra-mandibular glands (uni- and multicellular acinose glands)

These are of the same general type as the hypodermal glands but the lobules are much larger than those on the cranial wall, and open by minute ductules on the surface of the mandible. As far as I know, glandular structures have never been described within the body of the mandible except those in *Mantis religiosa* by Bordas ('07), which have been described within the base of the mandible. That glands should occur within such strongly sclerotized parts as the mandibles of Coleoptera was quite unexpected.

Mandibular glands (tubular glands)

Glands opening at the bases of the mandibles have been described in various orders of insects including the Coleoptera. Structurally these appear to be fairly constant, showing in most cases a simple tubular structure, although they differ in the actual position of their opening. Thus in *Cossus cossus* (Henseval, 1897), as reproduced in Schroder's 'Handbuch der Entomologie' ('28), the mandibular glands are tubular but branched and have a reservoir before they open into the adductor apodeme of the mandible; in *Pelertes matronula* (Bordas, '09) and in *Acherontia atropos* (Bordas, '10) these glands are unbranched tubules continued into the adductor apodeme. In *Mantis religiosa* (Bordas, '07) the mandibular gland is a peculiar bag opening within the base of the mandible.

In the Coccinellidae, on the other hand, the mandibular glands are not continued into the apodeme but open on the gnathocoria, slightly mesially to the cavity meant to receive the posterior condyle of the mandible. These glands are simple tubular structures of the nature already described, the inner chitinous tube of which appears to be an invagination of the gnathocoria. From the point of opening the tubule travels backward through the muscles and beneath the brain and comes out of the head capsule at the lateral angle of the

foramen magnum. Entering in the mesothorax it forms a complicated coil and lies, as shown in figure 1, in the anterior-most region of the thoracic cavity.

Mandibulo-maxillary (maxillular?) gland (tubular gland)

This opens on the gnathocoria which extends between the bases of the mandible and the maxilla, near the middle of the cardo and then travels backward exactly as the mandibular gland which it crosses as shown in the diagram.

Maxillary glands (tubular glands)

The presence of glands in association with the maxilla has been recorded in several orders of insects including some Coleoptera. In Coccinellidae this gland is a simple tubular structure opening on the gnathocoria near the middle of the extensor apodeme of the maxilla and in whole mounts often appears to be continued into the apodeme itself. From the opening the gland first travels laterally and, after a little coiling near the eye, travels backward like the two preceding glands described above.

Intra-cardonal glands (uni- and multicellular acinose glands)

These glands are small multicellular acinose lobules of the nature of hypodermal glands. They open on the surface of the cardo and also on the membranous connections round about.

Labial glands (multicellular acinose glands)

The structure of these glands has already been described in detail as the type of multicellular complex acinose glands.

Labral glands (uni- and multicellular acinose)

These are also of the nature of the hypodermal glands. There are both unicellular and multicellular lobules opening both on the epipharyngeal and external surfaces of the labrum.

VARIATIONS IN THE SIZE OF THE GLANDS IN THE FAMILY COCCINELLIDAE

The results reported in the present paper are based on a study of seven species of Coccinellidae which were available in sufficient numbers. These are:

- | | | |
|---|---|-------------|
| 1. <i>Coccinella septempunctata</i> , Linn. | } | Carnivorous |
| 2. <i>Chilomenes sexmaculata</i> , Fabr. | | |
| 3. <i>Brumus suturalis</i> , Fabr. | | |
| 4. <i>Chilocorus nigritus</i> , Fabr. | | |
| 5. <i>Synia melanaria</i> , Muls. | } | Herbivorous |
| 6. <i>Epilachna indica</i> , Muls. | | |
| 7. <i>E. vigintioctopunctata</i> , Muls. | | |

The description of the glands applies to *C. septempunctata* in particular and to the next four species in general. The two species of *Epilachna*, however, show remarkable reduction of these glands. Thus the labial glands in *E. indica* do not occupy even the whole of the mental area, and are less than one-tenth the size of those of *C. septempunctata*. The three pairs of tubular glands which form a prominently coiled mass on either side in the prothorax of *C. septempunctata* (fig. 1), are confined in *Epilachna* to the anterolateral corner of the head capsule. The glandular aggregations in connection with the eyes and the antennae are also much smaller in *E. indica* than in *C. septempunctata*. The mandible, however, is more richly supplied with the intramandibular glands in *E. indica*, in which there is also a glandular aggregation at the base of each mandible (gl.md.). The following approximate measurements will give an idea of the differences in proportional size of the glands.

SPECIES	SIZE OF INSECT (ABOUT)	EXTENT OF LABIAL GLANDS (ABOUT)	LENGTH OF TUBULAR GLANDS (ABOUT)	THICKNESS OF TUBULAR GLANDS (ABOUT)
<i>Coccinella septempunctata</i> (carnivorous)	7 × 5 mm.	786 × 720 μ	17 mm.	27 μ
<i>Epilachna indica</i> (herbivorous)	7.5 × 6 mm.	180 × 180 μ	2 mm.	30 μ
Ratio between carnivorous and herbivorous forms	1: 1	10: 1	8: 1	1: 1

ACTUAL OPENINGS OF THE GLANDS

A careful study of the openings of the various glands in coccinellid beetles yields instructive results. For example, the three pairs of the tubular glands associated with the maxillo-mandibular area do not open into the oral or pre-oral cavities; in fact, they do not even reach the inner surfaces of the mouth appendages but open on the intergnathal membranes or the gnathocoriae near the outer edges of their bases. Thus these openings do not lie within the space enclosed by the mouth appendages (pre-oral cavity of Snodgrass) but on the external depression which lodges the cardo. It should not, however, be concluded that the secretion does not reach the pre-oral cavity, because it would be easily carried along the intergnathal grooves from such external depressions to the pre-oral cavity.

In this connection it is interesting to note the development of ideas on this aspect of the subject. All the glands associated with the mouth parts had been indiscriminately described as opening into the mouth, till Snodgrass ('35) made a careful distinction between the oral cavity (morphological mouth) and the pre-oral cavity enclosed by the mouth appendages. It might be expected that the gnathal glands should open, if not into the mouth, at least into the pre-oral cavity but here is a clear case in which the gnathal glands open even outside the pre-oral cavity.

PROBABLE FUNCTIONS OF THE GLANDS

As no physiological work has been done on these glands, ~~and~~ their function remains a matter of conjecture only; but facts of structure afford some clues which are being recorded here.

The main points which emerge from a study of these glands are:

1. All these types are much better developed in the carnivorous than in the herbivorous coccinellids. This is just the opposite of our ordinary expectation if they are salivary in nature in the sense that they act on carbohydrates.

2. There is a regular gradation in the structure of the acinose glands, i.e., there is a series of increasing complexity from the minute simple unicellular hypodermal glands profusely distributed on the wall of the cranial capsule to the well-developed compound labial glands through the various intermediate stages of glandular aggregations of different sizes, e.g., intra-cardonal glands, intra-mandibular glands, ocular glands, antennal glands, etc.

3. The smallest units of the acinose glands, i.e., the hypodermal glands show a strong structural resemblance to the glands described by McIndoo ('16) at the tibio-femoral articulation of *Epilachna borealis*, which are responsible for defensive reflex bleeding.³ On account of these considerations I am inclined to think that the acinose glands described before (even those in connection with the mouth parts) may not be salivary in nature but may be secreting the same kind of liquid as is ejected in reflex bleeding, and that the liquid, instead of being useful as a digestive secretion, may be used as an offensive chemical in paralyzing the prey. This assumption explains why these glands are so well developed in the carnivorous forms while they are merely vestigial in the herbivorous ones.

4. The acinose glands are present not only in connection with the mouth parts but also in connection with eyes and antennae, and on the general cranial wall.

³ It is a fact well known to the entomologists that when disturbed certain coccinellid and meloid beetles fold the antennae and legs against the body, eject small drops of liquid from femoro-tibial articulations and feign death. There has been quite a controversy as to how the liquid is expelled so quickly and as to whether the liquid is blood or glandular secretion. Those who believe that the liquid is blood fail to show how it passes through the articular membrane to the exterior and those who think that the liquid is a glandular secretion do not conclusively prove their view, and they fail to explain how such a large quantity of secretion can be expelled so quickly. The phenomenon of ejecting liquid from the tibio-femoral articulations has been called 'reflex bleeding' (McIndoo, '16).

This author has shown at length "that the phenomenon is a true reflex and that instead of the liquid being blood it is a secretion from hypodermal glands and that it passes to the exterior through innumerable tubes opening near and in the articular membrane."

The identity between these glands of McIndoo and those described in the present paper also strongly supports McIndoo's views.

The tubular glands are also vestigial in herbivorous forms and well-developed in carnivorous ones. It appears therefore that these are also similar in function to the acinose glands, i.e., they are also not salivary in function.

SEGMENTAL HOMOLOGY OF GNATHAL GLANDS

Till very recently all the glandular structures (except the silk glands), having connection with the mouth parts or with the cephalic stomodaeum (including the extra-oral cavity) have been collectively called by the name of salivary glands. Thus Packard ('09), while describing all the differences in position, structure and function of the various glands, divides the whole group into only two categories, namely salivary and silk glands. It appears from his description that he believed in the homology of all the glands included under the common name of salivary glands, because he definitely pointed out the case of lepidopterous larvae wherein he believed the salivary glands to have been modified into silk glands, and the 'so-called salivary glands' to be modified coxal glands of the mandibular segment. Among the more recent writers, Schroder ('28) and Handlirsch ('30) for example, have retained the general name of salivary glands, while others like Imms ('25) and Snodgrass ('35) have discarded this general heading and have named the various glands separately after the appendage or the sclerite with which they are associated. Thus Snodgrass describes antennal glands, mandibular glands, maxillary glands, and labial glands. Imms describes one more gland, namely, the frontal gland in termites. The last two authors seem to have fully realized the absence of any direct homology between these various glands. It has been clear for a long time now that neither are these all salivary in nature nor are they morphologically equivalent.

At present, however, entomologists in general appear to be quite strongly impressed by the segmental recurrence of these glands, so much so that some have begun to think that the gnathal glands are modified nephridial glands of Crustacea, while others, including Snodgrass ('35), think that they are

possibly coxal glands of the gnathal appendages. Thus while the idea that all these glands are modifications of the same original salivary glands seems to have been given up, the idea of segmental homology or serial homology still holds. Since each pair of appendages has been found to have a pair of glands associated with it, their segmental recurrence is very striking and it is extremely tempting to correlate them with some serially homologous organs of the ancestors of insects; and that is why they have been homologized either with coxal or with nephridial glands.

My own studies, however, throw some doubt on this otherwise very plausible proposition. I am therefore, without committing myself to any definite view, simply recording the following considerations in connection with the segmental homology of the gnathal glands:

1. If the gnathal glands of insects are the homologues of the coxal or nephridial glands of Crustacea, we should expect only one ⁴ pair of glands to be associated with each pair of appendages, but in the coccinellids we definitely find three pairs of tubular glands between the bases of the mandibles and those of the maxillae. The presence of this extra pair of glands can be explained only in two ways, i.e., either a) by assuming that the gnathal glands are not segmental in their distribution and are thus not homologous with the coxal or nephridial glands or b) by assuming the presence of a segment corresponding to the supra-linguae or maxillulae between the maxillae and the mandibles. It may be recalled that the presence of a segment between the mandibles and the maxillae has been contended both on embryological and morphological grounds, the strongest advocate of this view being Hansen ('30), although there are equally strong opponents of this view and the whole question is still an open one.

⁴ It may be noted that although in annelids there are often more than one pair of nephridia in each segment, in both Crustacea and Myriopoda (the only sources from which insects can be regarded to have evolved) there is never more than one pair of glands (coxal, nephridial, or excretory) in each segment.

2. In Coccinellidae (specially in *C. septempunctata*) there is a more or less regular gradation from the unicellular hypodermal glands to the multicellular complex labial glands. This gradation strongly suggests that the labial glands are modified hypodermal glands rather than the homologues of coxal or nephridial glands. It may be noted in this connection that at least in two cases quoted by Schroder ('28), i.e., by Mingazzini (1889) and Leydig (1859), the glands in connection with the labium have been interpreted as Häutdrüsen or Integumentaldrüsen.

It may be contended with some force that these glands, which appear to be modified integumental glands, may not be the primary labial glands at all. The primary labial glands of segmental significance might have atrophied and these glands might be secondary in origin. There is hardly any reason at present to deny this proposition, but the labial glands present such an immense variety both in structure and function that it is absolutely impossible to distinguish primary and secondary glands. The fact that a regular gradation from the hypodermal glands to the labial glands has been appreciated in coccinellids, while such a gradation has not yet been noticed in other insects, is certainly no reason for regarding these labial glands as different from the labial glands of other insects. All the same I leave it as an open question, as much more comparative work is needed.

MATERIAL AND TECHNIQUE

The insects used were either brought fresh from the fields or reared in the laboratory, the species which were kept in the laboratory for fairly long periods being *E. indica*, *E. vingintioctopunctata*, *C. septempunctata* and *Chilomenes sexmaculata*. The former two of these species were fed on the solanaceous and cucurbitaceous leaves while the latter two flourished well on every available species of aphids.

The points worthy of mention in the technique employed during these studies are as follows.

Free-hand sections

The strong chitin of the head capsule offers almost insurmountable difficulties in getting microtome sections. In order to get over this difficulty I began trying to cut free-hand sections of the ordinary paraffin blocks which were prepared exactly as if they were to be sectioned with a microtome. After a little practice I could get fairly good sections for anatomical studies. Further treatment of these sections was as in the case of microtome sections, although sometimes they were not fixed to the slide and treated further in a watch glass with much advantage. With these modifications the study of the internal structure of the hard head of these beetles became fairly easy.

Bleaching of chitin

Strongly sclerotized and densely pigmented structures like the mandible ordinarily do not show any of their internal structures. In order to examine their interior I have been bleaching the whole head (after they are well fixed) in hydrogen peroxide. By this treatment the opaque chitin becomes almost transparent and the soft structures inside not only remain absolutely undamaged but also begin to take specially brilliant stain with borax carmine. The intra-mandibular glands for example were revealed by this method.

Stain

Of the various stains that were used, thionin was found to be specially suitable for bringing out labial glands from the surrounding tissue. It stains the glandular lobules blue and the contents of the main duct red. As a matter of fact the labial glands were discovered when once I stained a free-hand section by chance with thionin. The stains used for the histological observations were Delafield haematoxylin, iron haematoxylin, and borax carmine for the nuclei and eosin, orange G, and picro-indigo-carmine for the cytoplasm.

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