RELATING DIET AND MORPHOLOGY OF THE HEAD, MANDIBLES AND PROVENTRICULUS IN ADULT CARABID BEETLES

by

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A Dissertation submitted to the

Graduate School-New Brunswick

Rutgers, The State University of New Jersey

In partial fulfillment of the requirements

for the degree of

Doctor of Philosophy

Graduate Program in Entomology

written under the direction of

Dr. James Lashomb

and approved by

New Brunswick, New Jersey

October, 2014

ABSTRACT OF THE DISSERTATION

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The Carabidae is a large family of beetles with 33,920 valid species world-wide. While the specific diets of many of these species are known, especially among the Carabinae, the feeding preferences of the majority of species are unknown. Attempts to determine the food preferences have been made relying upon morphological characters of the head and mouthparts but not in a quantitative manner. A literature review of morphological characters of the Carabidae in 2002 showed that no consistent morphological character would predict the feeding preferences of all species. In this study, twenty morphological measurements and character conditions from the adults of fourteen species of carabids representing five subfamilies and ten tribes were evaluated to determine whether there is a correlation between the morphology of the mandibles and proventriculus, the gut contents and field observations. Using cluster analysis the measurement means and the presence or absence of structures of all twenty characteristics were evaluated. Five characters were found to provide the most information and provided logical groupings. However, it was apparent that predicting

specific food preferences was not possible. Instead the analysis indicated the type of feeding, that is, fluid feeding with extra-oral digestion, particulate feeding or mixed feeding incorporating both fluid feeding, and particulate feeding.   Fluid and mixed feeding species (*Cicindela punctulata* Oliver and *Calosoma calidum* F., *Paraclivina bipustulata* (F.)) were predaceous while particulate feeders (primarily carnivorous: *Omophron labiatum* F., *Bembidion quadrimaculatum* L., *Poecilus chalcites* (Say), *Stenocrepis duodecimstriata* Chevrolet, *Lebia grandis* Hentz, and *Calathus gregarius* Say; primarily herbivorous: *Harpalus caliginosus* F., *Geopinus incrassatus* Dej., *Stenolophus lineola* F., *Zabrus tenebroides* Goeze, and *Anisodactylus laetus* Dej.) could be both predaceous and herbivorous to varying degrees. Lack of field observations or conflicting evidence of other workers makes some of the designations questionable. Convergent evolution seemed a likely mechanism in unrelated groups in the development of the proventriculus. *Harpalus caliginosus* demonstrated that although the members of the genus *Harpalus* are widely regarded to be seed eaters, *H. caliginosus* is at least a scavenger, if not predator, despite having mandibles appropriate for eating seeds.

ACKNOWLEDGEMENTS

DEDICATION

To my loving wife, Susan Ruth, for believing in me

and keeping me focused.

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INTRODUCTION

The Carabidae is one of the six largest families in the order Coleoptera and largest in the suborder Adephaga, with 33,920 valid species world-wide (Bousquet, 2012). Lawrence (1982) and Larochelle (1990) estimated, that world-wide 30,000 and 40,000 species occur, respectively. Because they occur in a diversity of habitats, can be locally abundant and are often agriculturally relevant, carabids have been extensively collected and studied. The systematic treatment of the Carabidae for this study is based on Bousquet (2012). Bousquet (2012) describes three groups within the family: the basal grade carabids (those groups that diverged early from the main group, Cicindelinae, for example); middle grade lineages (Carabinae); and higher carabids (Harpalinae).

According to this current alignment, six subfamilies, two supertribes, eleven tribes and three subtribes are represented by the fourteen species used in this study (Table 1).

By comparison, using Lindroth's (1969) organization, these 14 species would be included in two subfamilies, nine tribes and three subtribes: Cicindelinae, Carabinae; Carabini, Scaratini, Omophronini, Pterostichini, Lebiini, Oodini, Zabrini, Bembidiini, Harpalini (Harpali, Anisodactyli, and Bradycelli). The differences in the two schemes illustrate that despite well defined groups within the Carabidae, there is still taxonomic uncertainty concerning placement of these groups within the family.

The question of what carabids eat is not new and many researchers have studied their feeding mechanisms and food preferences. While these studies have provided data on feeding habits and dietary preferences of many species of carabids, especially the

Table 1. Species used in this study and their taxonomic position within the Carabidae based upon Bousquet (2012). Except for the Palearctic species, *Zabrus tenebroides*, all species are native to eastern United States.

Subfamily	Supertribe	Tribe	Subtribe	Genus	Species
Cicindelinae		Cicindelini		*Cicindela*	*punctulata* Oliver
Carabinae		Carabini		*Calosoma*	*calidum* F.
Omophroninae		Omophronini		*Omophron*	*labiatum* F.
Scaritinae		Clivinini		*Paraclivina*	*bipustulata* F.
Trechinae		Bembidiini		*Bembidion*	*quadrimaculatum* L.
Harpalinae	Pterostichitae	Pterostichini		*Poecilus*	*chalcites* Say
		Oodini		*Stenocrepis*	*duodecimstriata* Chevrolet
		Zabrini		*Zabrus*	*tenebroides* Goeze
	Harpalitae	Lebiini		*Lebia*	*grandis* Hentz
		Harpalini	Anisodactyla	*Anisodactylus*	*laetus* Dej.
				Geopinus	*incrassatus* Dej.
			Stenolophina	*Stenolophus*	*lineola* F.
			Harpalina	*Harpalus*	*caliginosus* F.
		Sphodrini		*Calathus*	*gregarius* Say

Carabinae and Cicindelinae, there is no current means of predicting dietary preferences for the majority of carabid species. Few quantitative studies of morphological structures associated with catching and processing their food have been conducted. In this work, the objective is to quantify selected (n = 20) characters of the head, mandibles, and proventriculus and correlate these with gut analysis and field observations for predicting dietary preferences.

Based upon feeding observations Forbes (1883) surmised that carabids were herbivorous as well as carnivorous. Other researchers (Webster 1900; Shough 1940; Morrison 1941; Davies 1953; Skuhravy 1959; Johnson and Cameron 1969; Lund and Turpin 1977; Tooley and Brust, 2002; Honek et al, 2005; Honek et al, 2007) have supported these observations well establishing carnivorous, granivorous (= spermaphagous), and herbivorous feeding by carabids. In reviewing the literature up to

1977, Larochelle (1990) determined of the 1054 species referenced, 981 consumed animal matter of which 775 were exclusively carnivores. Eighty-five species were exclusively phytophagous of which 30 species, including *Zabrus tenebroides* Goeze, were particularly noxious to plants and 206 species were omnivorous. Many species have seasonal diets, being carnivorous during part of the year and largely granivorous or herbivorous at other times (Burakowski 1967, Tooley and Brust 2002).

Researchers have determined feeding preferences of other insect groups, especially the Acrididae, using morphological characters. Isley (1944), Chapman (1964), and Feroz and Chaudhry (1975) examined the mandibles of grasshopper species to determine if there were morphological differences according to type of food consumed. Their collective results indicated a clear relationship between mandible morphology and toughness of food, generating three groups: grass feeders, forbs feeders and mixed feeders. Bernays and Hamai (1987) investigated head size and dietary preferences in the Acridoidea and found that grasshoppers feeding on grasses required greater musculature for chewing tougher food than those feeding on forbs. In this study the amount of muscle determined head size so that the dietary preferences of these insects could be determined by their relative head size. Grasshoppers with proportionally larger heads fed on grasses; the smaller head size indicated forbs feeders and intermediate head size mixed feeders.

Paul (2001) found that the nature of mandibular musculature of ants defined their feeding preferences. Species with more muscle mass devoted to short stranded muscle

could close their mandibles more quickly and hence would be more predatory. Ants with more long muscles, exhibited a greater likelihood of granivory.

Evans and Forsythe (1985) considered whether there were important morphological aspects of the carabid head capsule that might bear upon feeding preferences, but aside from a few species, they discounted head characteristics as being important in determining feeding habits.
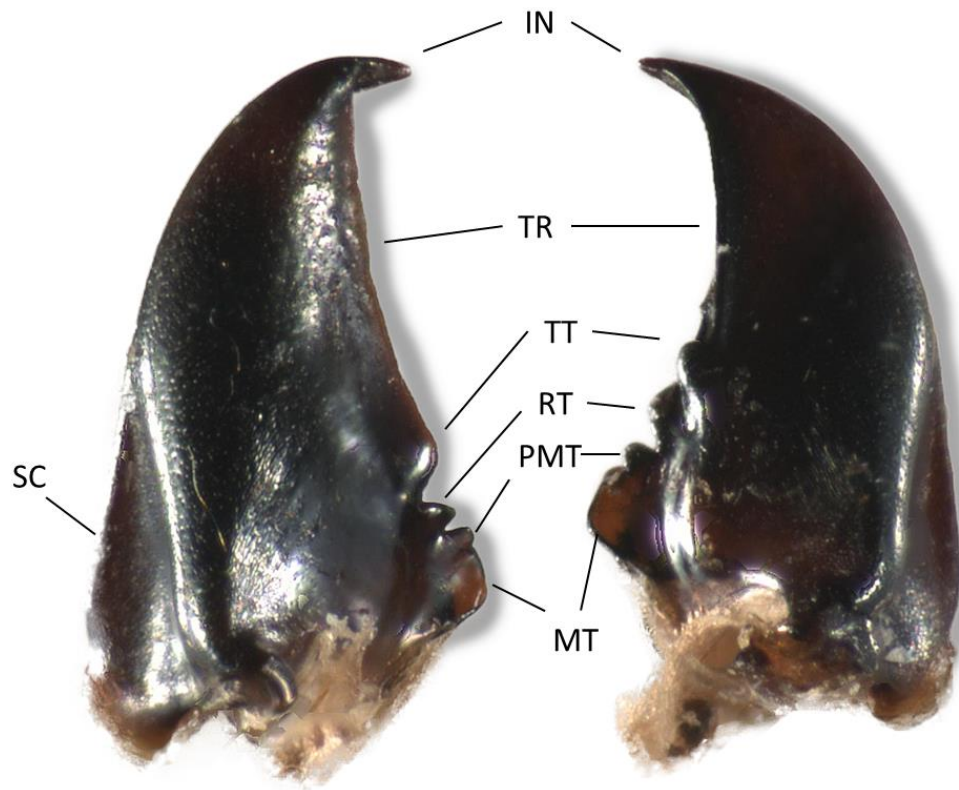
Figure 1. The morphological features of carabid mandibles. Not visible in this view is the retinacular ridge which lies ventral to the terebral ridge culminating posteriorly in the retinacular tooth. IN - incisor; TR – terebral ridge; TT – terebral tooth; RT – retinacular tooth; PMT – premolar tooth; MT – molar tooth; SC – scrobe.

Carabids have two structures for reducing their food to manageable size, the mandibles and the proventriculus. Mandibular form and function have been studied by Jeannel

(1926), Forsythe (1982), Evans and Forsythe (1985), Acorn and Ball (1991), Ball et al (2010), Begum and Islam (1997, 2002).   Generally, carabid mandibles are similar, as noted by Jeannel (1926), who described them as, "three sided pyramids" and first developed the nomenclature for the teeth and ridges (Fig. 1). The terminology was reviewed and expanded by Acorn and Ball (1991) who described the array of teeth and elevations found on the mesal margins of the mandibles as a series of parallel ridges separated by occlusal grooves. The terebral ridges posterior to the incisors shear; the retinacular teeth and ridges, may also shear, or, act as a compacter (Acorn and Ball 1991). The variable basal region may have one or more teeth or ridges for additional reduction of food, or have a flattened basal face. A basal face may or may not support a basal brush. The basal brush of hairs may be extensive, or, confined to a few hairs, that help transfer the food to the mouth.   The left mandible is the dominant mandible generally being longer and sliding over the dorsal side of the right mandible although, within species, there are some exceptions (Ingerson-Mahar, personal observations).

Snodgrass (1935) described in general the alimentary canal of Coleoptera, noting the similarity with orthopteroids and describing the proventriculus as a structure with an intima having major and minor folds forming the surface of the lumen. Longitudinal muscles lie within the major folds and the whole structure is in a sheath of circular muscle, although these muscles are not always attached to the intima but to each other forming a muscular web about the proventriculus.

The function of the proventriculus has been debated. Skuhravy (1959), and Cheeseman and Pritchard (1984a) agreed that the proventriculus of some species serves as a

trituration organ, reducing food particle sizes from the crop to the mesenteron, in contradiction to Brunetti (1931) and Thiel (1936). Smrž (1982) considered that the proventriculus of Geadephaga beetles had four functions: trituration involving crushers, filtration, pumping food to the mesenteron, and mixing food and digestive enzymes. Evans and Forsythe (1985) stated that the proventriculus acted as a pump, filter, and an organ for trituration. Cheeseman and Pritchard (1984b) questioned the filtering aspect of the proventriculus.

Davies (1953) compared proventricular structure to gut contents of British carabids developing different nutritional categories – carnivorous with chewing proventriculus, carnivorous with extraintestinal digestion, temporary carnivores and herbivores. Zhavoronkova (1969) correlated mandibular and proventricular structure with gut contents to discern three feeding categories – obligate zoophages, predominately zoophagous, and predominantly phytophagous. Forsythe (1982) and Evans and Forsythe (1985) developed 3 categories of feeding behaviors based mostly on mandibular form: fluid feeders, fragmentary feeders and mixed feeders (combining both fluid and fragmentary feeding). Davies (1953), Sunderland (1975), Hengeveld (1980a, 1980b), Cheeseman and Pritchard (1984a) and Holopainen and Helenius (1992) conducted gut analysis and characterized food consumed by carabids.

The proventriculus, situated between the crop and mesenteron is highly variable in carabids, nearly indistinguishable from the crop in some species and in others, large and robust. The relative length to width ratio differs among species, as does the amount and arrangement of internal armament. Many researchers have provided cross-

sectional views of the proventriculus but few have delved into the longitudinal appearance of the folds and internal armament (Schaefer 1931, Whittington 1933, Bess 1935, Judd 1947 and 1948, Cheeseman and Pritchard 1984a,b).

Evans and Forsythe (1985) reviewed the morphology of other mouthparts, such as the maxillae, lacinia, and labrum and internal musculature of the cibarial pump and devised feeding categories based upon these structures. Ingerson-Mahar (2002) reviewed the carabid literature to ascertain if any morphological character studied thus far provided consistent clues as to their dietary preferences among carabids and found none Gut dissections, ELISA, laboratory and field observations all help to make a composite picture of carabid dietary preferences but each technique has its limitations (Ingerson-Mahar, 2002).

METHODS

The fourteen species, representing six subfamilies and eleven tribes of the Carabidae, used in this study are all common in the northeastern United States except for the Palearctic *Zabrus tenebroides* Goeze (Table 1). Specimens were collected primarily from blacklight and pitfall traps.   Lindroth (1969) was used for determining species.   All specimens were dissected retaining the head capsule and the stomodeum.   The stomodeum from each specimen was placed in 70% ethanol in a genitalia vial and stored in a larger container of 70% ethanol.   The head capsules were mounted on double-sided tape on trays.   Two digital images (dorsal and lateral views) of each specimen were taken using a Leica MZ 16 stereomicroscope equipped with a Leica DFC 480 digital color camera and illuminated by a Leica KL 1500 LCD.   Image Pro® with the Scope Pro software was used for photography. The head capsules were then dissected retaining the mandibles for further imaging. All head and mandibular images were stored as TIFF files; proventriculi images were stored as jpeg files.   Morphological measurements were taken using Image J 1.45s software (Table 2).

Gut dissections were conducted using a VWR dissecting microscope. Images of the crops and proventriculi were captured with a Nikon Coolpix 4500 digital camera affixed to the ocular tube of a Leica ATC 2000 compound microscope.

Twenty characters were examined and means calculated (Table 2) and characters states (Table 3) noted from the head, mandibles and proventriculus of all fourteen species. Cluster analysis (Proc Cluster and Proc Tree, The SAS system for Windows, Release 9.2., SAS Institute Inc. 2011) was used to analyze the means of character states to determine

groupings of species with similar characteristics. The resulting dendogram groupings were compared, first in terms of logical placement of species. For example, having *Cicindela* and *Anisodactylus* grouped together, even though showing some morphological similarities, would be illogical, whereas a group containing both *Anisodactylus* and *Zabrus* might not be.   Secondly, the groupings were compared by correlating the groupings with gut content data and field observations. Values for each character were analyzed independently and then by groups of characters.

HEAD CAPSULE

Three dimensions were measured – the eye width, head width and head depth. The eye width is the distance between the compound eyes at the widest posterior margin of the compound eye and head (Fig. 2). Head width was measured at the point of the lateral occipital sutures. In species lacking the occipital suture the widest distance behind the eyes was measured. The head depth was measured from the dorsal location of the occipital suture to the greatest distance ventrally, posterior to the eyes. If the occipital suture was absent then the head depth was simply the greatest distance dorsal-ventrally behind the eyes (Fig. 2b).

MANDIBLES

The mandibles were identified as left and right when viewed dorsally with the head facing the top of the page. Two measurements were taken of both mandibles: length and width and compared as ratios (left mandible - Lm/w; right mandible - Rm/w). Mandibular length was from the exterior edge of the dorsal condyle to the farthest point of the incisor. The width was measured from the exterior edge of the dorsal

condyle to the point of attachment for the adductor muscle (Fig. 3a). In *Cicindela punctulata*, the dense basal brush obscured the adductor attachment so the width was measured from the external dorsal condyle to the point of the brush margin at the base of the mandible.
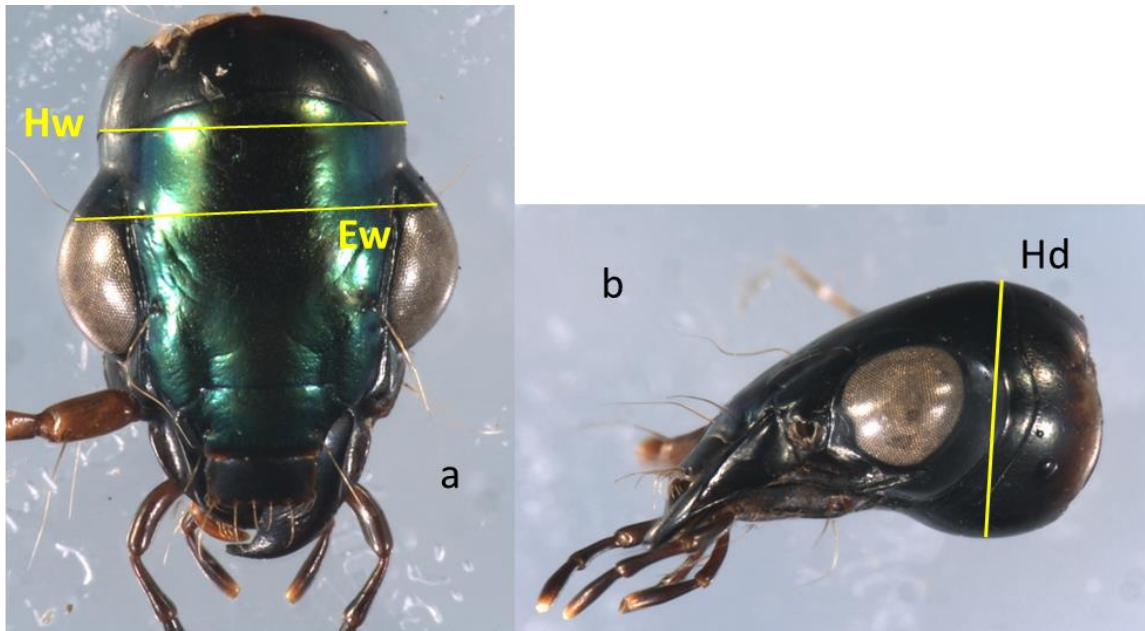
Figure 2. Lines indicate where the head measurements were made: a) head width (Hw) and eye width (Ew), and b) head depth (Hd).

Two additional measurements (Fig. 3b) were taken from only the left mandible: distance from the apical point of the incisor (IN) to the posterior base of the terebral tooth (TT), and the distance from the apical incisor point to the base along the mesal margin (B) of the mandible creating the ratio INT/INB.

Other mandibular characteristics evaluated included the ratio of head width/length of left mandible (Hw/Lm); the ratio of the length of the left mandible/right mandible length (Lm/Rm); the cross-sectional view of the base of the left mandible being rectangular or triangular, either as a scalene, or isosceles triangle (LmX); presence or

absence of a mandibular basal face (BF); and presence or absence of a premolar tooth (PMT).
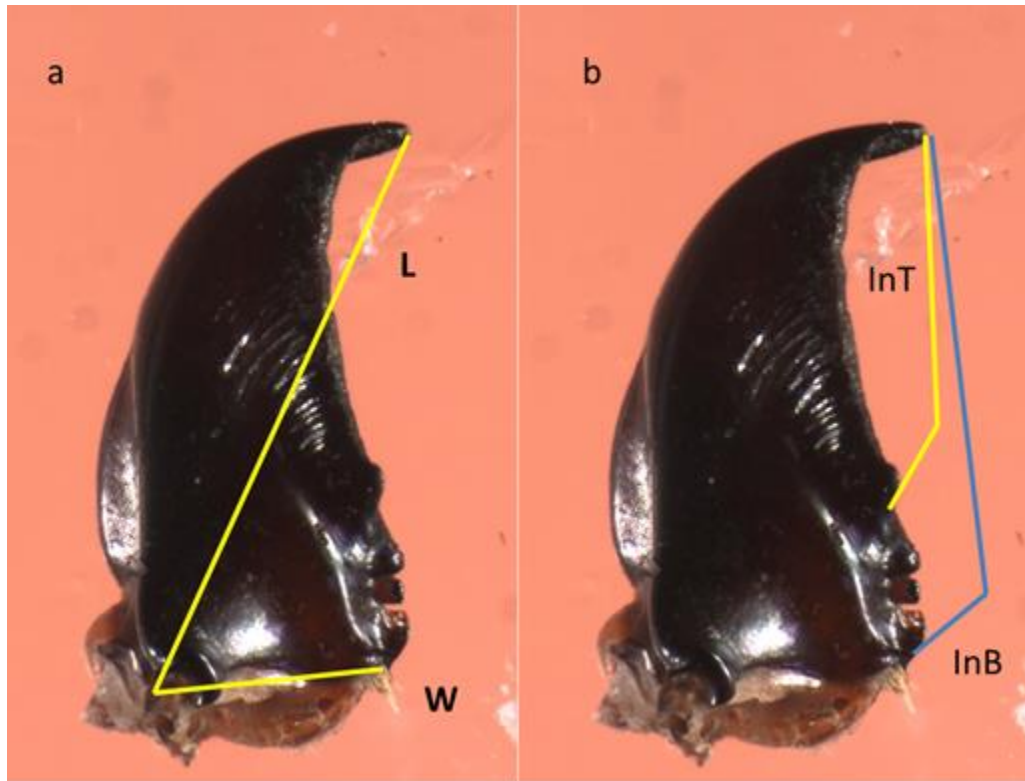
Figure 3. Mandibular measurements: a) The left and right mandible length was measured from the outer edge of the dorsal condyle to the most distant point of the incisor, and the mandible widths were measured from the outer edge of the dorsal condyle to the point of attachment for the adductor muscles. b) The INT distance (yellow line) was measured from the incisor tip to the posterior edge of the terebral tooth. The INB distance (blue line) was measured from the incisor tip to the point of attachment of the adductor muscle.

PROVENTRICULUS

The relative length to width ratio of the entire proventriculus was recorded, as well as, the nature of the interior covering of the lumen and the structures therein.   Specific characters noted were: presence or absence of a neck (neck); presence or absence of anterior teeth (ant t); presence or absence of neck teeth (neck t); presence or absence of posterior nodes with teeth (node t); presence or absence of opposing hairs presence

or absence of cuticular ridges (fl); length of proventriculus (L); width of proventriculus (W); and estimated length to width ratio (L/W).

CATEGORIZING GUT CONTENTS

These were examined using a Leica ATC 2000 binocular microscope by laying out the crop and proventriculus on a microscope slide and examining it under 40x magnification. Crops were recorded as either empty, with little food, half full or mostly full. Food items were determined as best as possible, but moth scales were likely contaminants from specimens taken from blacklights and not included as food items. In addition to identifiable material, two other categories were developed related to the amorphous nature of some food material as blobs (dark oily-appearing clumps) and gruel (non-clumped homogenous material). Initially, iodine was used in an attempt to detect the presence of starch amidst the food material but was deemed an unreliable method. The nature of the gut contents was used in combination with available literature citations of field feeding observations to further substantiate preferred prey items.

RESULTS

MEASUREMENTS OF CHARACTERS

All twenty means and evaluation of character states are summarized in Tables 2 and 3.

THE HEAD CAPSULE

The three measurements were remarkably consistent across species with the exception of *Omophron labiatum* F., which is uncharacteristically wide compared to the majority of carabid species. Otherwise, these measurements collectively show that the area of the head capsule immediately posterior to the eyes is generally spherical, with minimal variation.

THE MANDIBLES

The mandibles were consistent across species in having four regions, incisors, terebral ridges and teeth, retinacular ridges and teeth and a basal region. Variations were observed in all of these areas, but the most variable area was the basal region. Species were divided by having either a basal face, with or without a dense basal brush or having one or more teeth, either poorly developed or broadly expanded. Where the basal tooth was broadly expanded medially, the medial edge was slanted laterally, underneath, so that the medial edge could be used for either shearing or kneading (Fig. 18e).

Under fourth character, the head width/left mandible length ratio (Table 2), three species had mandibles longer than the head width, *Cicindela punctulata* Oliver, *Harpalus caliginosus* F., and *Stenolophus lineola* F. The remaining species had ratios greater than one indicating that the mandible length was shorter than the head width.

Table 2. Ratios of eight morphological characters of the head and mandibles of fourteen carabid species adults. The means of the ratios are listed under obs with the standard deviation listed under std.

Species	n	Hw/Ew		Hw/Hd		Ew/Hd		Hw/LM		LM/w		RM/w		LM/RM		InT/InB	
		obs	std	obs	std	obs	std	obs	std	obs	std	obs	std	obs	std	obs	std
Cicindela punctulata	29	1.01	0.03	1.01	0.02	0.99	0.03	0.85	0.12	5.56	1.01	5.54	0.93	1.01	0.01	0.75	0.02
Calosoma calidum	30	0.93	0.03	1.10	0.04	1.04	0.05	1.25	0.16	2.76	0.26	2.59	0.22	1.05	0.02	0.60	0.05
Omophron labiatum	30	1.00	0.01	1.65	0.09	1.70	0.10	2.37	0.13	2.66	0.02	2.60	0.18	1.09	0.05	0.68	0.05
Geopinus incrassatus	2	0.98	0.00	1.20	0.25	1.24	0.26	1.39	0.02	2.65	0.06	2.43	0.03	1.05	0.02	0.57	0.05
Poecilus chalcites	30	0.85	0.02	1.03	0.04	1.22	0.04	1.49	0.07	2.58	0.10	2.42	0.03	1.02	0.04	0.71	0.02
Stenocrepis duodecimstriata	30	0.90	0.02	1.01	0.02	1.12	0.03	1.58	0.13	2.47	0.20	2.37	0.01	1.05	0.02	0.73	0.02
Calathus gregarius	26	0.86	0.04	1.05	0.03	1.22	0.04	1.48	0.07	2.28	0.15	2.33	0.12	1.03	0.03	0.66	0.03
Lebia grandis	30	0.71	0.01	1.05	0.03	1.46	0.05	1.35	0.05	2.24	0.03	2.19	0.11	1.03	0.03	0.81	0.02
Paraclivina bipustulata	30	0.84	0.03	0.99	0.02	1.20	0.04	1.57	0.11	2.14	0.22	2.40	0.31	0.96	0.04	0.69	0.03
Bembidion quadrimaculatus	30	0.93	0.08	1.02	0.03	1.10	0.04	1.72	0.18	2.04	0.15	2.03	0.20	1.04	0.06	0.68	0.03
Zabrus tenebroides	3	1.00	0.02	1.10	0.04	1.11	0.03	1.81	0.06	2.03	0.05	1.93	0.09	1.01	0.02	0.67	0.02
Stenolophus lineola	30	1.09	0.04	1.09	0.02	1.17	0.03	0.85	0.06	1.85	0.12	1.84	0.08	1.06	0.02	0.64	0.04
Harpalus caliginosus	30	0.93	0.01	1.10	0.03	1.18	0.03	0.75	0.05	1.70	0.13	1.44	0.08	1.17	0.04	0.57	0.01
Anisodactylus laetus	30	0.84	0.01	1.06	0.04	1.27	0.05	1.70	0.06	1.56	0.04	1.55	0.04	1.06	0.02	0.41	0.03

Hw = head width; Ew = eye width; Hd = head depth; Lm = left mandible length; w = width of respective mandible; Rm = right mandible; INT = distance from incisor tip to posterior margin of terebral tooth of left mandible; INB = the distance from incisor tip to the base of left mandible.

Table 3. Character states of morphological characters of adults of fourteen carabid species: the mandibles and proventriculus and estimates of the length and width, in mm, of the proventriculus based upon two to four specimens of each species.

Species	n	Lmx	BF	PMT	Neck	Ant t	Ne t	No t	Opp	Ext f	L	W	L/W
Cicindela punctulata	29	3	1	0	0	0	0	0	1	0	1.0	0.5	2.0
Calosoma calidum	30	2	1	0	0	0	0	0	1	0	1.1	1.0	1.0
Omophron labiatum	30	2	0	0	1	0	0	0	1	0	1.0	0.4	2.5
Geopinus incrassatus	2	1	1	0	1	1	2	0	0	0	2.0	1.0	2.0
Poecilus chalcites	30	2	0	1	1	1	2	0	0	0	1.3	0.7	2.0
Stenocrepis duodecimstriata	30	2	0	1	1	0	2	1	0	0	0.1	0.5	2.0
Calathus gregarius	26	2	0	1	1	1	1	0	0	0	0.9	0.5	2.0
Lebia grandis	30	2	0	0	1	1	1	0	0	0	0.8	0.4	2.0
Paraclivina bipustulata	30	2	0	1	0	1	0	0	1	0	0.6	0.5	1.0
Bembidion quadrimaculatus	30	2	0	1	1	1	0	1	0	0	0.5	0.2	2.5
Zabrus tenebroides	3	1	1	1	1	0	1	0	0	0	1.0	0.4	2.5
Stenolophus lineola	30	1	1	0	1	1	0	1	1	1	0.8	0.8	1.0
Harpalus caliginosus	30	1	1	0	1	1	0	1	0	0	1.6	1.0	1.6
Anisodactylus laetus	30	1	1	0	1	1	0	0	0	0	0.6	0.4	1.5

LmX = left mandible cross-section shape (1=isosceles, 2=scalene, 3=quadrilateral); BF = basal face (1=present, 0=absent); prem = premolar tooth (1=present, 0=absent); neck = posterior region of proventriculus (1=present, 0=absent) ; ant t = anterior teeth on primary fold (1=present, 0=absent); neck t = teeth in neck region of proventriculus (1=present, 0=present); node t = posterior nodes on folds with teeth (1=present, 0=absent); op hairs = opposing hairs in proventriculus (1=present, 0=present); ext fl = external flanges of proventriculus (1=present, 0=absent); L = length of proventriculus in mm; W = width of proventriculus in mm; L/W = ratio of proventriculus length to width.

The list of species in Tables 2 and 3 are in descending order based upon the length to

width ratio of the left mandible (Lm/w), which initially I thought to be a significant

character. The length to width ratio of the right mandible (Rm/w) was very similar to the Lm/w ratio with the exception of *Paraclivina bipustulata* (F.), where the right mandible had a larger Rm/w ratio.

The ratios of the left mandible length/right mandible length (Lm/Rm) showed consistency with values slightly greater than 1.0, with *H. caliginosus* having the largest ratio, 1.17. *P. bipustulata* had the smallest Lm/Rm ratio, 0.96.

Lebia grandis Hentz had the largest INT/INB ratio, 0.81, even larger than *Cicindela punctulata,* at 0.75. Not including *L. grandis,* the remaining species formed two loose groupings consisting of *C. punctulata, Stenocrepis duodecimstriata* Chevrolet, *Poecilus chalcites* (Say), *Omophron labiatum*, *P. bipustulata*, *Bembidion quadrimaculatum* L., *Calathus gregarius* Say and *Zabrus tenebroides* Goeze with values of 0.73 to 0.66. The second group had values of 0.64 to 0.57 included *Calosoma calidum* F., *Geopinus incrassatus* Dej, *Stenolophus lineola*, and *Harpalus caliginosus,* with *Anisodactylus laetus* Dej. having the smallest ratio, at 0.41. .

The cross-sectional shape of the mandibular base also helped separate species into groups: those with a scalene triangular shape (*C. calidum, O. labiatum, P. chalcites, C. gregarius, B. quadrimaculatum, P. bipustulata, L. grandis* and *S. duodecimstriata*) and those with an isosceles-shaped base (*Z. tenebroides*, *G. incrassatus*, *S. lineola*, *H. caliginosus, A. laetus*).   The cross-sectional shape of *C. punctulata* was nearly rectangular.

The last two characters, presence or absence of a basal face and presence or absence of a premolar tooth again split the fourteen species into groups. Those with a basal face

included *C. punctulata*, *C. calidum*, *G. incrassatus*, *Z. tenebroides*, *H. caliginosus*, *A. laetus*, and *S. lineola*. *Lebia grandis*, *B. quadrimaculatum*, *P. chalcites*, *S. duodecimstriata*, *C. gregarius,* and *O. labiatum* lacked a basal face and instead had one or two molar teeth. *Zabrus tenebroides* was the only species that had both a basal face and premolar and molar teeth. Species lacking a premolar tooth included those with a basal face and *L. grandis* which had a molar tooth.

THE STOMODEUM

The crops of all species were thin-walled and translucent but able to unfold or stretch to accommodate food items. There was no delineation between the esophagus and the crop. In all species there appeared to be structural network of thicker cuticular strands within the intima reinforcing the crop wall (Fig. 4). On the surface of the crop lumen sparse, posteriorly directed spines arose from the intima at the intersections of the strands (Fig. 4a). These spines were considerably shorter and thicker than the spines covering the folds of the proventriculus. In *Lebia grandis* the spines were more like fish scales with multiple spines directed posteriorly around the edge of the scale, similar to ctendia illustrated by Smrž (1982). At the juncture of the crop with the proventriculus the density and length of the spines increased in all species.
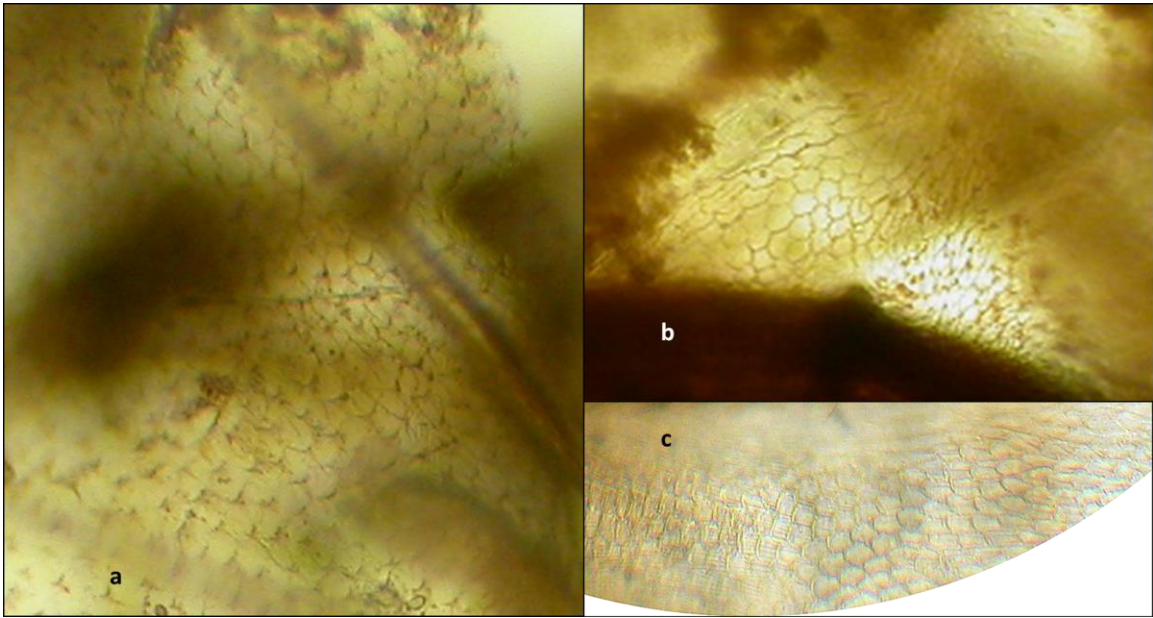
Figure 4. Three views of crops showing the netting structure in the intima. a – typical arrangement of spines are visible on the internal surface of the crop; b – external view of the crop of *Geopinus incrassatus*; c – external view of the crop of *Poecilus chalcites*

The majority of crops contained food, though often in small amounts.

The proventriculus is a discrete organ at the posterior end of the stomodeum that is highly variable in external dimensions and internal armament. It is tetraradially symmetrical with eight invaginations, four primary folds and four secondary folds corresponding, respectively, to the major and minor folds described by Snodgrass (1935). The primary folds arise from the anterior end of the proventriculus and terminate either at the juncture with the mesenteron or at the juncture with the proventricular neck. The secondary folds are either low, non-descript ridges; narrow, heavily armed ridges; or are similar to primary lobes. Long, hair-like spines, sometimes plumose, were present in most areas of the proventriculi. There has been no consensus among researchers for characterizing the spines of the intima, variously referring to them as hairs, setae, spines or variants of spines. At the anterior end of the primary

folds of most species, the spines formed a field that Zhavoronkova (1969) referred to as the radula, where spines were longer and thicker (Fig. 14e; 23d,e). The terminology used here to describe the spines of the proventriculus follows Smrž (1982).

Two types of proventriculi are found in the fourteen species. The first is relatively large and thick (1:1 length/width ratio (*Calosoma calidum* and *Paraclivina bipustulata*)), with the intima covered by dense, long hairs with the posterior end lacking a neck and attaching directly to the mesenteron (Fig. 10d, 11d, 13d). *Cicindela punctulata* had a similar proventriculus except that its length/width ratio was 2. The second type has a region with folds, the body, and a distinct neck (Fig. 14d, 19d), which occurred in the eleven remaining species. The neck intima has short, blunt teeth or knobs in more or less transverse rows, or is smooth, as in *Stenolophus lineola* (Fig. 21d). At the juncture with the mesenteron, the neck forms a broad collar about the opening to the mesenteron.

Eight species had distinct radulae, the enlarged spines of the anterior primary folds. The *B. quadrimaculatum* radula (Fig. 14f) consists of large, thick, posteriorly directed spines. *Paraclivina bipustulata*, *P. chalcites*, *C. gregarius*, *G. incrassatus*, *S. lineola*, and *A. laetus*, have similar types of radulae comprised of shortened stout teeth. *Harpalus caliginosus* had longer teeth-like bristles that projected into the proventricular lumen (Fig. 22d,e). In species where nodes appear at the posterior ends of the folds, the spines are either thickened and anteriorly directed (*H. caliginosus,* Fig. 22f) or are peg-like teeth (*S. duodecimstriata*, Fig. 16d,e; *B. quadrimaculatum* Fig. 14e,f).

FOOD MATERIAL OF THE STOMODEUM

Two hundred and eighty six specimens were dissected and examined for gut contents

(Table 4). Many of the specimens caught by blacklight trap had dried and withered

internal organs thus reducing the number of specimens available for analysis of gut

contents. The dissection data, in concert with literature references and field

observations, provide the correlating factor for the cluster analysis results.

About twenty-six percent of all dissected specimens had empty, or nearly empty, crops

and proventriculi. The most common food material in the crop was a dense, amorphous

gruel-like mass that was probably formed by the mixing of food with digestive enzymes

Table 4. Percentage of food type found in the stomodeum of fourteen species of adult
Carabidae.

Species examined	n	empty	plant	sclerite fragments	hairs/ spines	blobs	gruel	spores	other
Cicindela punctulata	16	13	0	0	0	6	69	6	32
Calosoma calidum	15	7	0	0	0	0	93	0	27
Omophron labiatum	26	38	8	12	8	27	8	8	4
Geopinus incrassatus	1	0	0	0	0	0	100	0	0
Poecilus chalcites	25	72	4	12	8	4	8	0	12
Stenocrepis duodecimstriata	28	43	0	11	3.4	4	21	7	14
Calathus gregarius	30	17	17	23	10	0	63	10	0
Lebia grandis	15	67	0	13	7	13	0	0	7
Paraclivina bipustulata	27	41	0	4	0	33	11	0	8
Bembidion quadrimaculatum	16	6	6	37	19	6	75	19	19
Zabrus tenebroides	3	0	0	0	0	0	100	0	0
Stenolophus lineola	31	35	3	0	3	0	58	0	6
Harpalus caliginosus	22	0	18	36	14	0	68	32	27
Anisodactylus laetus	31	29	3	10	0	3	42	6	19

in the crop. Superficially, the gruel material appeared similar across species and without

biochemical analysis it would be difficult to determine its origin, whether animal or

plant. Several species had more globular lumps but only in *P. bipustulata* did these

lumps take on a dark, oily appearance (blobs, Table 4). Pieces of sclerites were

frequently found including legs, tarsi, head, integument, as well as wings, and occasionally, entire arthropods. Plant material was common in some species as clumps of cellular, sponge-like structures. Fungal spores were commonly found. The crops of some species held unusual items: a specimen of *O. labiatum* had a husk of a plant bud or seed, and a seed, 0.75mm by 0.67mm, was found in a *C. calidum*. Two specimens of *S. duodecimstriata* contained nematodes in their crops. Notably, *C. punctulata* had rectangular crystalline structures of unknown origin present in the gut contents, but other species also had sand-like crystalline structures in their crops. Most of these crystals were less than 0.1 mm, but some were relatively large (Fig. 10d).   These and several other unidentifiable items, including ovoid objects, unusual lumps of unknown material, cuticle-like structures with random holes, were categorized as 'other' (Table 3).

ANALYSIS OF MORPHOLOGICAL CHARACTERS

Using cluster analysis on the morphological means allows for the comparison of traits and the non-taxonomic grouping of species. Table 2 lists the measurement means (Table 2) and character states (Table 3) of the twenty morphological features evaluated by cluster analysis. An analysis incorporating all characters provided a base line against which later analyses would be compared (Fig. 5). Next, each character was reviewed singly and then in groups of characters to remove those deemed redundant or suggesting illogical groupings. Through this process the number of useful characters was reduced to five.   The criteria for selecting these five characters were that they formed logical groupings based upon observed traits of the head, mandibles, and

stomodeum and secondly, the groupings were compared against field observations and gut contents.

Three general groups existed throughout all of the analyses: 1) *C. punctulata*, *C. calidum*, and *P. bipustulata*; 2) *P. chalcites*, *S. duodecimstriata*, *C. gregarius*, *B. quadrimaculatum*, and *L. grandis; 3) S. lineola* and *H. caliginosus*. The remaining four species, *Z. tenebroides*, *G. incrassatus*, *A. laetus* and *O. labiatum* were outliers that shifted from group to group depending upon the traits being examined.

Four mandibular characteristics seemed relevant: the length to width ratio of the left mandible, the ratio INT/INB, cross-section shape of the mandible bases, and the presence of the basal face of the mandibles. The values of these characteristics were plotted (Fig. 6) to provide additional visual representation of the data.

These four mandibular characters were analyzed with cluster analysis resulting in a dendogram (Fig. 7) producing the same groupings as the plot of the means of these characters, and aligns generally with the known feeding habits. Looking at only these
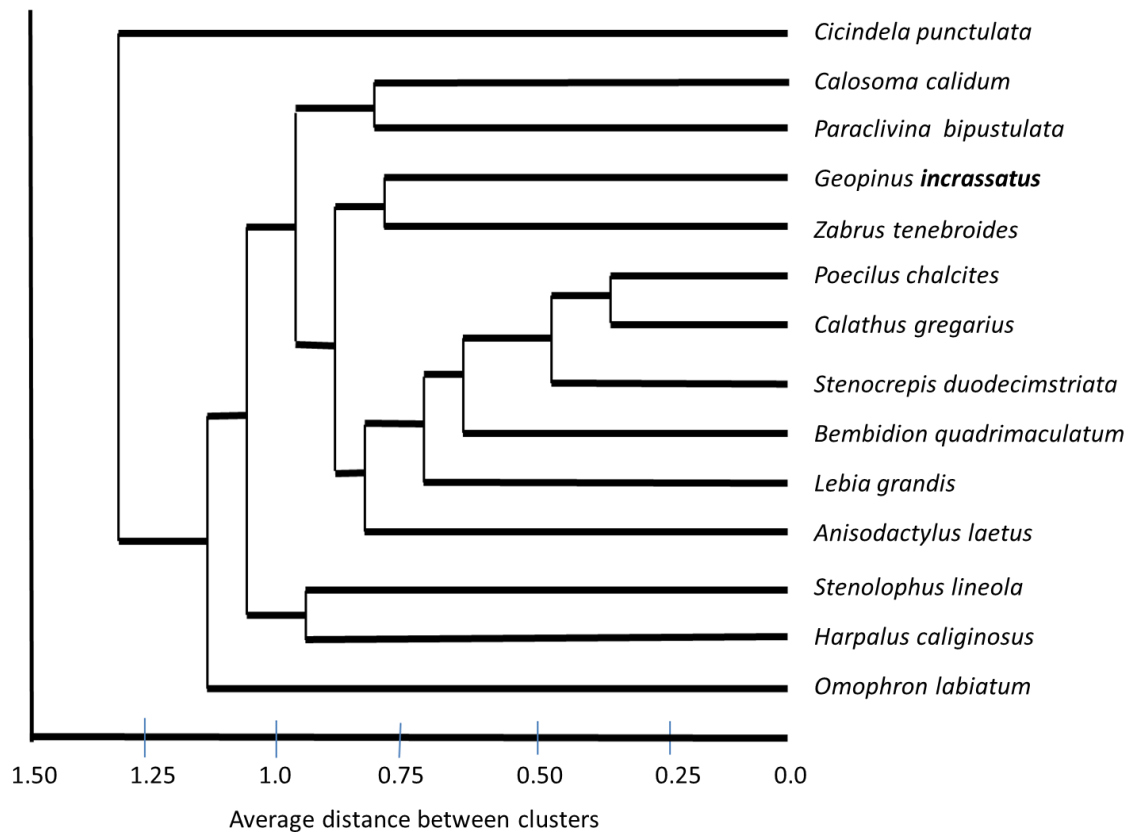
Figure 5. The dendogram of species grouping based on the analysis of twenty morphological characters from the head, mandibles, and proventriculus of fourteen carabid species using cluster analysis.

four characters, *Cicindela* is an outlier because of the derived conditions of its mandibles. The central group (Fig. 6) of *O. labiatum*, *P. chalcites*, *S. duodecimstriata*, *C. gregarius*, *P. bipustulata*, *B. quadrimaculatum* and *L. grandis* forms a tight cluster and *L. grandis* as the outlier in this group, because of its large INT/INB ratio. These four mandibular characters were very important in looking at functional groups of species, but the placement of *C. calidum* in the group of supposed granivores and herbivores is not credible even though both plotting and cluster analysis place it there. Numerous references cite the predatory habit of *C. calidum*. *Paraclivina bipustulata* falls well within the group of largely zoophagous species. The herbivorous group of *G.*

incrassatus, H. caliginosus, S. lineola, Z. tenebroides and *A. laetus* are a close group, with

A. laetus appropriately an outlier here because of its low INT/INB ratio.
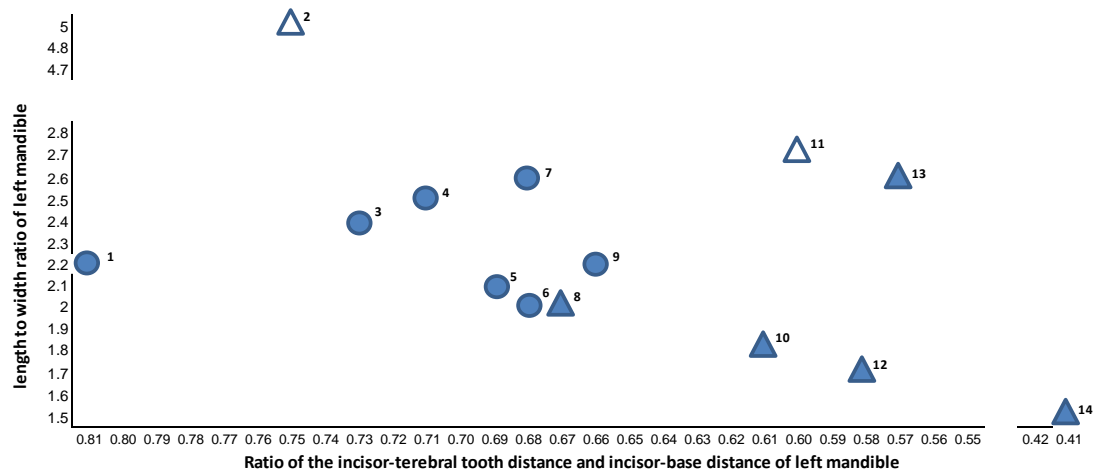
Figure 6. A plot of four mandibular characters: y-axis - length to width ratio of the left mandible; x-axis – ratio of incisor-terebral length and incisor-base length. Open triangles are species with a basal face and non-isosceles mandible base; closed triangles are species with a basal face and isosceles mandible base. Circles are species lacking a basal face and having a scalene mandible base. Superscripts: 1- *Lebia*, 2- *Cicindela*, 3- *Stenocrepis*, 4- *Poecilus*, 5- *Paraclivina*, 6- *Bembidion*, 7- *Omophron*, 8- *Zabrus*, 9- *Calathus*, 10- *Stenolophus*, 11- *Calosoma*, 12- *Harpalus*, 13- *Geopinus*, 14- *Anisodactylus*

These genera are in the Harpalinae, belonging to different tribes and subtribes. While

these groupings are logical, they do not coincide with field observations and gut

contents.

Further evaluation of characters resulted in the use of mandibular characters, length to

width ration of left mandible and INT/INB ratio (Table 2), and presence or absence of a

basal face (Table 3), but dropping the cross-sectional shape of the left mandible; and

adding proventricular characters, presence or absence of a proventricular
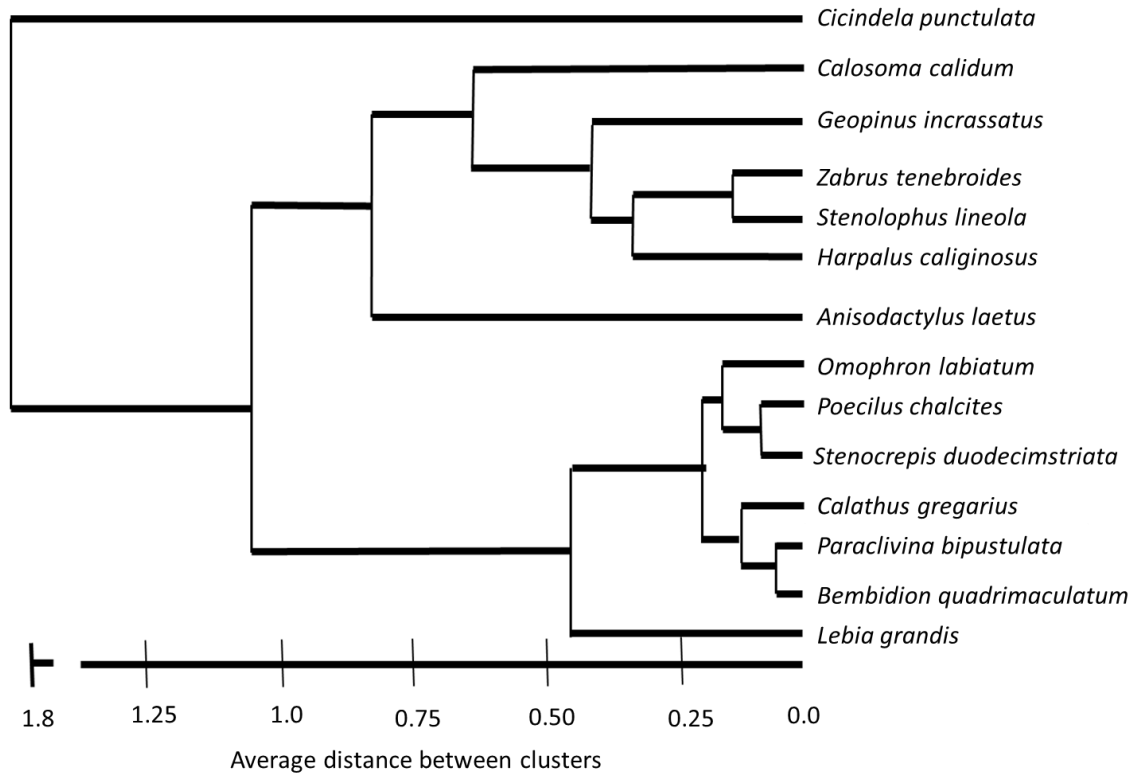
Figure 7. The dendogram of species groupings based on four mandible characters: length to width ratio of left mandible; ratio of incisor-terebral tooth length to incisor-base length; cross-sectional shape of the left mandible; presence or absence of basal face using cluster analysis.

neck and visible external flanges, respectively (Table 3). These characters provided the best fit of morphological characters, feeding observations and gut contents (Fig. 7). Three well defined groups are represented, group 1 (*O. labiatum, P. chalcites, S. duodecimstriata, C. gregarius, B. quadrimaculatum, L. grandis*), group 2, the fluid feeders (*C. punctulata, C. calidum, P. bipustulata*); and group 3, the likely herbivores (*G. incrassatus, H. caliginosus, Z. tenebroides, A. laetus, S. lineola*).

Adding character 17 (external proventricular flanges) to the analysis, the resulting dendogram (Fig. 8) realigns *S. lineola* to be an outlier and altering the grouping of the particulate granivores, so that *A. laetus* still remains an outlier with this grouping. By

setting *S. lineola* apart the analysis emphasizes the uniqueness of its proventriculus, at least amongst these species, but also supports its probable omnivory. The other groups remain unaffected by adding character 17. Now the fluid feeders remain intact with *Cicindela punctulata* being the outlier of that group. Group 1, the carnivorous particulate feeders remain closely affiliated while the herbivorous group is more loosely associated.
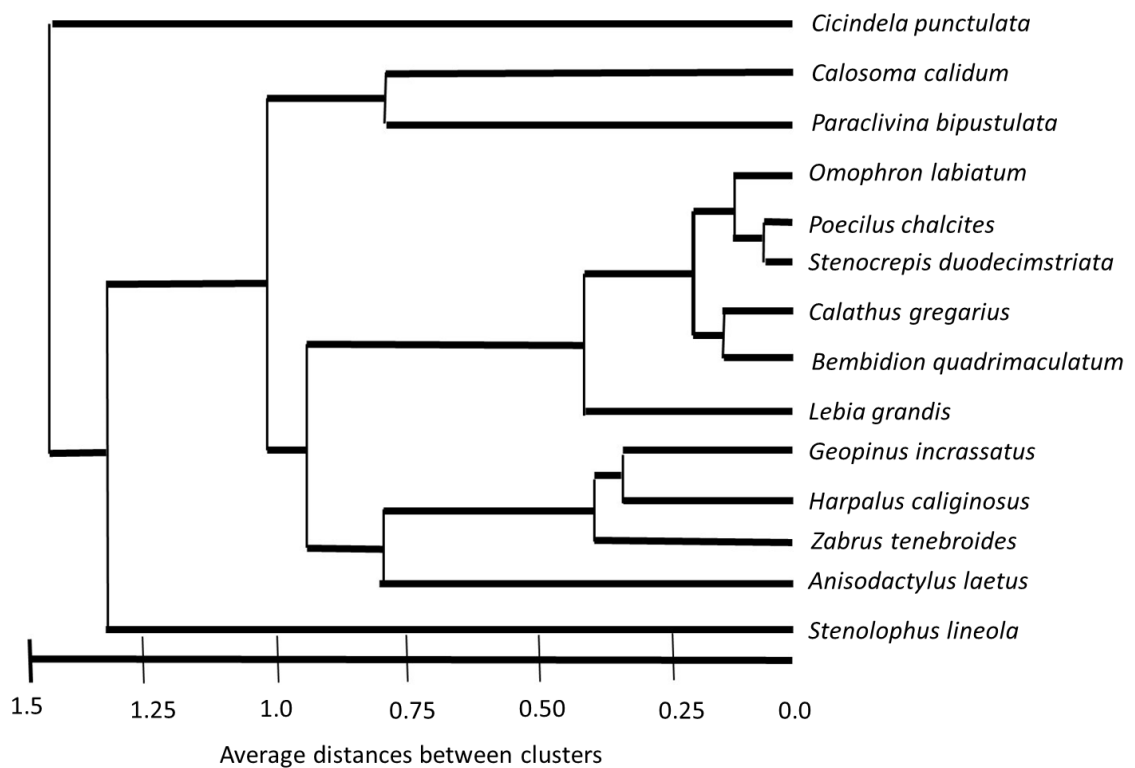
Figure 8. The dendogram of species groupings based on three mandibular characters and two proventricular characters: length to width ratio of left mandible; ratio of length of terebral region to length of mandible; presence or absence of a basal face; presence or absence of a neck; and, presence or absence of externally visible ridges, using cluster analysis.

DISCUSSION

HEAD CAPSULE MORPHOLOGY

Looking at the work done on orthopteroids where relative head size helped to indicate their dietary preferences, the heads of carabids posed problems. A cursory comparison of the relative head size compared to body length did not seem to provide any relevant information for dietary preferences; the head to body length ratio was surprisingly consistent across species. Therefore, the dimensions of the head width, eye width, and head depth were measured.

The head width to head depth ratio of about 1:1 is consistent across species meaning the head capsule is nearly circular in an axial view. This may have greater importance in body form for the wedge pushing ability of carabids (Evans 1986) rather than as a factor in dietary preferences. Only the head capsule of *O. labiatum* and *G. incrassatus* deviated from this ratio (Table 2). In twelve of the fourteen species, the eye width is equal to or greater than the head width producing a larger ratio of the eye width to head depth. Only *C. punctulata* and *S. lineola* have greater head widths than eye widths. These measurements do not provide information on feeding preferences. Analysis of the amount of musculature to operate the mandibles in future studies may yield more meaningful information regarding dietary preferences.

MANDIBULAR MORPHOLOGY

The mandibles of nearly all species examined are approximately triangular in cross section and curve ventrally towards the apices. Jeannel (1929) referred to the three sided nature of mandibles with one edge forming the medial margin bearing the teeth

and the opposing side forming the lateral surface of the mandible. While this was the consistent pattern of structural morphology, another species, not included in this study, *Galerita bicolor* Drury, is exceptional by having dorso-ventrally flattened mandibles attaining the approximate triangular shape only at the base anterior to the condyles suggesting considerable variation in mandible morphology across the family. The mandibles of all species were generally similar, but the goal was to define feeding preferences based upon the variability found among species.

The order of the ridges and teeth were uniform across all species with the exception of *C. punctulata* and *P. bipustulata*. Ball et al (2010) addressed the evolution of tiger beetle mandibles from the more typical carabid mandible. In *P. bipustulata*, the left mandible is inconsistent with the rest of the species in that the terebral ridge of the left mandible does not extend to a medial terebral tooth, which is lacking, but instead diminishes from the base of the incisor towards the dorsal condyle. The retinacular ridge curves dorsally from its ventral position assuming the role of the terebral ridge of other species. The significance of this anomaly is unclear. How this unique characteristic relates to food preferences, if at all, requires more scrutiny.

Acorn and Ball (1991) used the term 'occlusal groove' to denote the existence of grooves that extend diagonally from the dorsal surface of the mandibles antero-ventrally to the ventral side. According to the Ness Visual Dictionary of Dental Technology (Ness, 2011), the term, occlusal groove, would describe a groove on the surface of a tooth or cusp. The grooves on the mandibles of the adult beetles separate the ridges that give rise to the teeth, so it seems inappropriate to use the term occlusal

in this instance. The purpose of the grooves is not clear.   Possibly they allow fluids to move along the ridges or provide strength to the ridges and mandibles.

After a review of the mandibular characters both individually and as a group, certain characters were eliminated from further consideration, such as, the ratio of the head width to the length of the left mandible (This character provided an illogical grouping, both taxonomically, structurally, and observationally, of *C. punctulata* with *H. caliginosus* and *S. lineola.*); the ratio of the length of the right mandible to width was redundant to the left mandible length to width ratio; and the ratio of the length of the left mandible to the right mandible. I expected the latter ratio to be important, because it would show the degree of asymmetry between the mandibles and potentially indicate the degree of granivory. However, it only demonstrated that *H. caliginosus* had the most asymmetrical mandibles.

I thought the most informative mandibular character would be the length to width ratio of the left mandible and theorized that the smaller ratio indicates a shift to herbivory. When the species were listed in descending ratios, it made intuitive sense. Lack of field observations of *G. incrassatus* made it difficult to evaluate this species' placement on the list. In appearance, the mandibles of *G. incrassatus* are intermediate between carnivory and herbivory having neither the acute incisors expected in a predator, nor the crushing surfaces of an herbivore. One character suggesting carnivory for *G. incrassatus* is the strongly produced, acute retinacular tooth of the right mandible.

As for *H. caliginosus*, it had the mandibular structure (quadrate mandibles with broadly rounded incisors and a basal face), and phylogenetic affinities to strongly suggest an

herbivorous diet, but abundant observations show that *H. caliginosus* has carnivorous (or scavenging) tendencies (Larochelle 1990). Thirty-six percent of the *H. caliginosus* specimens dissected for this study contained sclerite fragments, more than any of the other species except *B. quadrimaculatum*.

This study lacked a comparable species to *Loricera pilicornis* (F.) which Forsythe (1987) showed had short mandibles with a length to width ratio of less than 2, but with acute incisors. Field observations supported a carnivorous diet for *L. pilicornis* despite its small length to width mandibular ratio (Forsythe 1987; Larochelle 1990). Species with a length to width ratio less than 2 with rounded incisors tend to be granivores or herbivores. While informative, the left length to width mandibular ratio was not definitive on its own merits.

The cross-section of the mandible at its base was approximately triangular for all species, although in *C. punctulata*, the shape was nearly a quadrilateral. In the remaining species the triangular outline of the base showed that the species that were the most likely to consume a large proportion of plant material had an isosceles shape, that is, *G. incrassatus*, *H. caliginosus*, *A. laetus*, *S. lineola*, and *Z. tenebroides*. The triangular shapes of the remaining species' mandibles were scalene and apparently were associated with carnivorous diets, that is, *C. calidum*, *O. labiatum*, *P. chalcites*, *S. duodecimstriata*, *C. gregarius*, *L. grandis*, *P. bipustulata*, and *B. quadrimaculatum*. These species are not strict carnivores, however. For example, *O. labiatum* has been observed feeding on seedling maize, *Zea mays* L. (Larochelle 1990) and *P. chalcites* had damaged common chickweed seeds, *Stellaria media* (L.) (Lund and Turpin 1977). In the

scalene species, the molar tooth is wedge-shaped when viewed from the proximal end of the mandibles. The dorsal surface projects mesally and recedes ventrally producing a thin edge for either kneading or slicing (Fig. 18e).

The ratio of the distance between the incisor tip and the posterior edge of the terebral tooth to the distance between the incisor tip and the mandible base was informative. This ratio provided a way of discerning the relative proportion of the terebral ridge, a possible indication of carnivory. Again, this made intuitive sense but when ratios were compared between species, a 0.6 ratio for *C. calidum* was very close to the 0.57 ratio of both *G. incrassatus* and *H. caliginosus*. The characterization of *Anisodactylus* sp. by Forsythe (1982) as having short, quadrate, mandibles blunt at the tips and being largely herbivorous fits well with its INT/INB ratio (0.41) as it had the lowest value in this study. Seven species in this study have a basal face (Table 3), a broad, more or less flat area extending from the molar tooth to the adductor muscle attachment. Forsythe (1982) suggested that the dense basal brush in *Carabus problematicus* Herbst aided in the flow of digestive juices to prey and the subsequent ingestion of digested prey fluids. *Cicindela punctulata* and *C. calidum* had dense basal brushes that obscured the area (Figs. 10c, 11c) implying that they also are fluid feeders.

Of the other five species with a basal face, four had a narrow line of hairs on the dorsal-medial edge of the mandible. The basal face of *Z. tenebroides* was glabrous suggesting that it would not likely digest food extra-orally. Therefore, *Z. tenebroides* is probably a particulate feeder as are the four remaining species.

The presence or absence of a premolar tooth indicating feeding habits was suggested by Acorn and Ball (1991), noting that *Euryderus grossus* (Say) lacked a premolar tooth, a characteristic of herbivorous carabids. Alone, this criterion would be misleading. *L. grandis* and *O. labiatum* lack a premolar tooth, but it would be erroneous to surmise that these species are mostly herbivorous. *Zabrus tenebroides*, a notorious granivore has a weakly produced premolar tooth. The premolar character was not considered further.

In those species lacking a basal face the molar area is either produced as a blunt tooth or a thin edge that seems to provide an area for kneading or slicing prey. Mahar (1979) observed a carabid adult, *Cymindis (Pinacodera) limbata* Dej, in the field as it consumed a small geometrid caterpillar. The beetle kneaded the caterpillar's body along its entire length, twice, before rolling it into a ball and consuming it entirely. Examination of the mandibles of *C. limbata* revealed a broadly rounded, flattened molar tooth. Carabid fluid feeders would not knead the prey and those that are known to feed on seeds crush the seeds with their terebral and retinacular ridges and teeth.

Plotting the means of the four most useful mandibular characters the species divide into two primary groups: a tight group comprised of *O. labiatum*, *P. chalcites*, *S. duodecimstriata*, *C. gregarius*, *B. quadrimaculatum*, and *P. bipustulata*, with *L. grandis* as an outlier; and a more loosely defined group of *G. incrassatus*, *Z. tenebroides*, *S. lineola*, *H. caliginosus* and *A. laetus* as an outlier (Fig. 6). *Calosoma calidum* and *C. punctulata* do not seem to fit in either group.

MORPHOLOGY OF THE STOMODEUM

There are obvious differences between species on the size, shape and internal organization of the proventriculus. Yahiro (1990) found the same in 43 Japanese carabid species. Evans and Forsythe (1985) suggested different feeding preferences for the different types of proventriculi found in carabids, for example, fluid feeders and mixed feeders including degrees of fluid and fragmentary food consumption.

The proventriculi of *C. calidum* and *P. bipustulata* are similar in having long, dense, hair-like spines covering the primary and secondary folds. These are directed posteriorly in the anterior portions of the proventriculus, but from approximately mid-length the spines are directed anteriorly, against the flow of food. Where the posteriorly directed spines meet the anteriorly directed spines there is a point of flexion.

It's speculated that the circular muscles in *C. calidum* and *P. bipustulata* constrict the proventriculus about the middle forcing the liquefied food back against the spines in the anterior portion. In transverse views of the proventriculus (Forsythe 1982, 1987) the space around and between the folds is very narrow so that fluids being forced against the spines would be thoroughly mixed. Upon relaxing the muscles fluid material would flow from the crop into the anterior end of the proventriculus. Similarly, when the circular muscles are constricted the fluid food in the posterior part of the proventriculus is mixed a second time by the anteriorly oriented spines as it is forced into the mesenteron. Thus the proventriculus for these two species acts as both a pump and a blender to thoroughly mix the prey fluids with digestive fluids allowing for maximum digestion and absorption (Fig. 9).

a   b

Figure 9. Illustration of supposed proventricular action in a fluid feeder's (e.g. *Calosoma* and *Paraclivina*) proventriculus: a) proventriculus opens drawing in fluids from crop, b) circular muscles about mid-region contract forcing prey fluids and digestive enzymes back against the grain of the long hair-spines further mixing food and enzymes. Fluids in latter half of the proventriculus are pushed into mesenteron.

The organization of the proventriculus of *C. punctulata* is similar to *C. calidum* and *P. bipustulata* in the presence of long, dense hairs covering the folds, but opposing spines occur only in the posterior portion of the primary folds. Based on the pattern of these spines a different type of flexion is occurring since the rods of the secondary folds would prevent medial constrictions. The longitudinal rods may be specific to *C. punctulata* as comparable rods are not mentioned by Judd (1948) for *Cicindela sexguttata* F. The presence of short peg-like spines at the distal end of the folds (Fig. 10g), further complicates the analysis of function of the proventriculus, which needs detailed study. The most critical distinction to separate the fluid feeders from the particulate feeders is the lack of a neck connecting the body of the proventriculus to the mesenteron.

Calosoma calidum, *C. punctulata* and *P. bipustulata* all lack necks of the proventriculus. Both *C. punctulata* and *C. calidum* are known fluid feeders. Since *P. bipustulata* also has this same type of proventriculus it probably is a fluid feeder, even though it lacks the dense, mandibular basal brush of the other two species. Regardless, *P. bipustulata* does retain enlarged spines, the radula, on the anterior end of the primary folds, unlike either *C. calidum* or *C. punctulata*. Perhaps as the four primary folds come together the spines at the anterior ends of the folds mesh together forming both a barrier to food passage and also to help cut through more viscous material. Nearly all food found in the stomodeum of *P. bipustulata* was dark, globular material, unlike the gruel-like material found in the other species, which may be due to either prey selection, or differences in the proteinases for digestion.

The remaining species have necks of varying length connecting to the mesenteron. The opening to the mesenteron of these species seems relatively small in contrast to the opening of the fluid-feeding species. This suggests that the neck serves as a sort of valve to allow only a small amount of food of a specific size to enter the mesenteron. Larger pieces of material that cannot pass through the neck may be forced back into the proventricular body for further trituration.

The presence of a distinctive radula in eight species is difficult to evaluate because its function is unclear and is present in unsuspected species (*P. paraclivina*) and lacking in species where it might be expected (*Z. tenebroides)*. The function of the radula may vary by species, perhaps acting as means to cut through viscous prey material or to regulate the amount of food proceeding to the proventriculus. In *B. quadrimaculatum*,

the spines of the radula are very large and probably help with the trituration of solid food.

The hair-like spines of the intima of particulate feeders are shorter and less dense than those of the fluid feeders suggesting that the mixing of prey fluids and digestive proteins is not as prominent. *Omophron labiatum* and *S. lineola* have opposing spines that would suggest that they also have flexion points in their proventriculi, but these occur caudally near the juncture with the neck.

In *O. labiatum*, *P. chalcites*, *C. gregarius*, *L. grandis*, and *A. laetus*, the intima coating of spines ends abruptly with the primary folds extending into the neck region, the hairs being replaced there with blunt spines or rounded bumps on transverse lines. These modified spines probably further erode or grind solid food before passing into the mesenteron.

Harpalus caliginosus (Fig. 22f), *S. duodecimstriata* (Fig. 16d,f), and *B. quadrimaculatum* (Fig. 14e,f) had swollen areas (nodes) of the most distal portion of the primary folds (and secondary folds in *S. duodecimstriata*), which are covered by spines and teeth directed anteriorly (*H. caliginosus* and *B. quadrimaculatum*) or by short, stout pegs that cover the nodes extending in all directions (*S. duodecimstriata*). It seems obvious that the proventriculus of these three species is designed to scrape or crush solid food particles before passing into the neck and have the ability to stop the flow of food particles, altogether.

The proventriculus of *S. lineola* is distinctly different in structure from the other species examined (Fig. 21). Given the eight externally visible ridges corresponding to each of

the folds and their accompanying musculature, and the highly developed secondary folds as crushing surfaces with appressed lateral teeth, the proventriculus appears to be a food grinding organ. *Nebria obtusa* LeConte (Cheeseman and Pritchard 1984a) and *Nebria gylenhalli* (Schönherr) (Forsythe 1982) may also have this type of proventriculus. Both species have expanded ridges and crushing surfaces similar to *S. lineola*. In species like *S. lineola* and *Nebria* sp., the beetles may be able to ingest food more quickly (Cheeseman and Pritchard, 1984a), letting the proventriculus do the work of masticating particulate food. This may occur where there is either strong competition for food or where prey is quick and elusive. *Stenolophus lineola* occurs in disturbed habitats, such as farm fields, where many species of *Stenolophus* and related genera occur on the soil surface competing for food. Ingesting food items quickly and letting the proventriculus masticate the food might be advantageous. The mandibles of *S. lineola* are transitional in appearance between predatory species and those which consume more vegetative material, suggesting that this species is more of an omnivore able to consume an array of food items.

FOOD PREFERENCES AND FEEDING BEHAVIORS

The original question was, do adult morphological characters of carabid beetles predict their feeding preferences? Not necessarily. Given the mandibular structure of *C. punctulata* it is likely to be a predator as opposed to an omnivore or granivore. The mandibles of *C. calidum* and *S. duodecimstriata* would also suggest predatory diets. But in terms of specific prey preference, there isn't sufficient data from this study to sustain that conclusion. Despite similarities between mandibles across species, excluding *C.*

punctulata, there is no pattern that would definitely indicate a wholly predatory diet or not. Based solely on mandibular structure, *H. caliginosus* would be one of the species that could be assumed to be a seed-eater, yet thirty-six percent of the specimens in this study contained the remains of arthropods. Zhavoronkova (1969) thought that the morphological characters of the mandibles and proventriculus produced three categories of feeding: obligate predators; obligate predators and facultative herbivores; and, facultative predators and obligate herbivores. She indicated that several of her twenty-two species consumed seasonally different foodstuffs varying between plant and animal material. Relying upon this and similar studies (Johnson and Cameron 1969, Lund and Turpin 1977, Sunderland 1975, Tooley and Brust 2002), the results of the gut contents of this study, and feeding observations from the literature, it becomes much more difficult to determine specific feeding preferences of any species, with the possible exception of the fluid feeders.

A second question can be asked, do the morphological characters indicate the type of feeding, that is, fluid or particulate, to which the answer is yes. The structure and armament of the proventriculus largely dictates the type of feeding. Large, robust proventriculi with a dense coating of hair-like, plumose spines and a direct connection to the mesenteron suggest fluid feeding, that is, using extra-oral digestion. Proventriculi with a distinct neck posterior to the folds but anterior to the mesenteron would indicate either particulate feeding or, at least, a mixture of particulate and fluid feeding.

Evans and Forsythe (1985) supported this third type of feeding, a combination of fluid and particulate feeding using *Broscus cephalotes* L as an example, referring to it as

mixed. Examining a single specimen of *B. cephalotes*, the proventriculus is more like a particulate feeder in that it has a 0.5 length to width ratio and has a short neck, while retaining dense, hair-like spines covering of the folds. In this study, *P. bipustulata* may be a mixed feeder because of having a radula on the primary folds and a proventricular structure and vestiture similar to *C. calidum*.

Forsythe (1991) also thought that *O. labiatum* should be included as a mixed feeder. Examination of the *O. labiatum* proventriculus showed that in most respects it had the characteristics associated with particulate feeders, although it did have opposing hairs near the posterior ends of the primary folds.

In Fig. 8 the three species with the fluid feeding type of proventriculus are quickly separated out from the remaining species, which are particulate feeders. *Cicindela punctulata* is further separated from *C. calidum* and *P. bipustulata* by the derived mandibular characteristics.

Another characteristic that was not directly addressed is the amount of musculature associated with the proventriculus. In the three species addressed above, the proventriculus is relatively large and robust having a length to width ratio of 1 for *C. calidum* and *P. bipustulata* and 2 for *C. punctulata*, although Evans and Forsythe (1985) consider the proventricular musculature of *Cicindela* sp. and *Carabus* sp. poorly developed.

For the particulate feeders, it is much more difficult to separate the species into food preference categories because of the overlapping morphological characters. However, five species, which are the most likely to include vegetable matter in their diets, can be

separated because of the presence of a mandibular basal face. *Stenolophus lineola* is quickly separated from the rest of the herbivorous particulate feeders because of its proventricular structure.

Of the four remaining members of this group in Fig. 8, *Z. tenebroides*, *H. caliginosus*, *G. incrassatus* and *A. laetus*, their mandibles share the characteristics of the isosceles-shaped mandible base and the presence of a basal face. These occur in herbivorous and granivorous species where structurally strong mandibles would be an asset. Yet, in overall appearance, the mandibles of these four species are quite dissimilar.

The central group of six species, representing six tribes, possesses overlapping characteristics and includes known predators, but also species that periodically consume plant material. The mandibles are generally similar with differences between species mostly in the area of the retinaculum and basal teeth. The proventriculi of this group are rather simple with four primary folds and four secondary folds, which are often reduced to low ridges, are relatively undifferentiated, and are covered in sparse to dense hair-like spines.

How do these groupings match with literature feeding references and observed food in the stomodeum? In many of the species, particulate matter was found including plant and animal material, and also fungal spores. Most, if not all, animal material appeared to be of arthropod origin. Besides the particulate matter, all species had what was described as 'blob' or 'gruel-like' material. Apparently all food material ingested, whether fluid or particulate produces a thickened gruel when exposed and mixed with digestive enzymes.

The third category offered by Evans and Forsythe (1985) is more generalized where variation of the anterior teeth on the folds, central hairs and posterior teeth would fit particulate feeders having diets including plant and animal material varying in proportions and seasonality.

Based upon the results of this study of fourteen carabid species the following key is suggested to better identify the different feeding categories.

A key to feeding habit modes of Carabid beetles

1 – mandibles with mesally produced, or expanded basal areas; a basal brush (hairs along basal median edge) either lacking or, only a few hairs present _____2

1' – basal area of mandibles not produced or expanded; rather, surface more or less flat with either a narrow line of, or, thick covering of hairs, extending from molar tooth to base of mandible_____3

2 – proventriculus lacking a neck; enlarged (elongated) spines on the anterior end of the primary folds, otherwise interior of proventriculus densely covered by long, hair-like spines _____mixed fluid feeders (*Paraclivina*)

2' – proventriculus with a neck; sparse to dense hair-like spines covering interior of proventriculus body; other characters variable ___primarily zoophagous particulate feeders (*Poecilus*, *Omophron*, *Stenocrepis*, *Bembidion*, *Calathus*, *Lebia*)

3 – cross-sectional shape of mandible base forms an isosceles triangle, or nearly so; proventriculus having a neck; otherwise proventriculus internal structure variable _____omnivorous or herbivorous particulate feeders (*Geopinus*, *Harpalus*, *Anisodactylus*, *Stenolophus*, *Zabrus*)

3' – cross-sectional shape of base may be a scalene triangle or some other shape _____fluid feeders (*Cicindela*, *Calosoma*)

TAXONOMIC CONSIDERATIONS

An important question is, do the selected morphological characters align themselves in a systematic framework that would suggest that feeding preferences are phylogenetically driven, or is there convergent evolution of traits and behaviors?

Four situations can be addressed: 1) *P. bipustulata* being a mixed feeder, 2) the apparent similarity of the proventriculus between *S. lineola* and *Nebria* sp., 3) the similar structural mandibular morphology of *Z. tenebroides* to *S. lineola*; 4) the posterior nodes of *S. duodecimstriata*, *H. caliginosus*, and *B. quadrimaculatum*.

Regarding the fluid or mixed feeding of *P. bipustulata*, from the work of Evans (1965), Evans and Forsythe (1985) and others, it is well known that both the Cicindelinae and the Carabinae are fluid feeders. Additionally, Evans and Forsythe (1985) describe *Scarites* sp. (Scaratini) as fluid feeders. The Scaratini is closely related to the Clivinini in which the genus *Paraclivina* resides. A case can be made for a phylogenetic connection with mode of feeding, if not feeding preferences.

The proventriculus of *S. lineola* is a well-developed grinding organ. The proventriculus of *Nebria gyllenhal* and *N. obtusa* show cuticular ridges and crushing secondary folds similar to *S. lineola* (Cheeseman and Pritchard 1984a, Forsythe 1982, and Yahiro 1990). This is an example of convergent evolution as these species are in separate subfamilies, *Nebria* sp. are in the Trechinae, and *S. lineola* is in the Harpalinae.

Another case of convergent evolution involves *Z. tenebroides,* a well-known seed eater and crop pest in the Palearctic Region. It belongs to the Zabrini, a tribe within the Pterostichitae. Its proventriculus is not much different from the proventriculi of other

particulate feeders, such as *P. chalcites* or *C. gregarius*. However, the mandibles are distinct from the mandibles of *P. chalcites* and share more traits with *S. lineola*, belonging to the Stenolophina of the Harpalitae.

The posterior nodes found in the proventriculi of *S. duodecimstriata*, *H. caliginosus*, and *B. quadrimaculatum* indicate that these species have triturating proventriculi (Evans and Forsythe 1985). *Bembidion quadrimaculatum* belongs in the Bembidiini, within the Trechinae. *Stenocrepis duodecimstriata* and *H. caliginosus* both occur in the same subfamily, Harpalinae, but in different supertribes, Pterostichitae for *S. duodecimstriata* and Harpalitae for *H. caliginosus*. The recurrence of these structures among these taxonomically separated species is a third example of convergent evolution.

Other morphological characters of the mandibles and proventriculus are both more general and also specific. The radula, thickened spines, on the anterior ends of the primary folds is a common feature occurring in ten species and the presence of posterior teeth, spine-like or pegs, in six. It would appear that convergent evolution is a common within the Carabidae.

CONCLUSIONS

The conclusions drawn from this study as well as others that have addressed this problem have been largely based upon the same groups of species, which include only a small percentage of either genera or species of carabids. Some of the difficulty in determining the feeding habits is the lack of field observations for the majority of species. *Anisodactylus laetus* and *Stenocrepis duodecimstriata* are cases in point, in that as far as known there are no published field observations of these species.

From this study and also from conclusions drawn by other researchers, notably Evans and Forsythe (1985) it does not seem possible to determine feeding preferences based solely upon the morphological characters of the head, mandibles or proventriculi. Only in a few species that are specialists on molluscs is it possible to say with certainty what the preferred prey is. Convergent evolution of morphological characters amongst the different groups can complicate their use to determine food preferences. Morphological characters occurring unexpectedly in a particular species forces a reevaluation of the role of the traits.

Many of even the most predaceous species are generalist predators, whether fluid feeders or mixed feeders. But the greatest number of carabid species appears to be particulate feeders, which may include both animal and plant prey, depending upon species, and season. Seasonal availability of different foodstuffs alters diets of many, if not, most carabids. Of Zhavoronkova's three categories of feeding preferences 1) zoophagy, 2) obligate predators/facultative herbivores, and 3) obligate herbivores/facultative predators, the second and third groups are difficult to distinguish

because the degree of carnivory versus herbivory may vary continuously among, or even within taxa. Those who ignore particular species as unimportant in biological control situations because of the phylogenetically perceived diet may be overlooking a key component in the management of a pest species.

Table 5 displays the fourteen species categorized by their most probable type of feeding. Those species with question marks are not fully determined, either because of a lack of feeding observations or conflicting views with other researchers.

Table 5. Classification by feeding type of the fourteen species in this study. Question marks indicate uncertainty of the placement of the species per category, based partly on conflicting views of other researchers and/or lack of observational data.

Fluid/mixed feeders	Particulate	feeders
Carnivores:	**Primarily carnivores:**	**Primarily herbivores:**
Cicindela punctulata	*Omophron labiatum?*	*Anisodactylus laetus*
Calosoma calidum	*Poecilus chalcites*	*Zabrus tenebroides*
Paraclivina bipustulata	*Calathus gregarius*	*Geopinus incrassatus?*
	Lebia grandis	*Harpalus caliginosus?*
	Bembidion quadrimaculatum	*Stenolophus lineola?*
	Stenocrepis duodecimstriata	

Regarding further research, a much broader study of this sort should be done to better understand the diversity of morphology and feeding habits and modes within the Carabidae. The benefits of such a study would aid phylogenetic studies, help in better manipulation of carabids for biological control of pest organisms, including weeds, and understanding interactions between carabid and arthropod and plant communities.

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APPENDIX

ECOLOGICAL INFORMATION AND MORPHOLOGICAL DESCRIPTIONS OF THE MANDIBLES, PROVENTRICULUS AND GUT CONTENTS BY SPECIES

Species: *Cicindela punctulata* Olivier

Size: 11 to 13 mm (Pearson, et al, 2006)

Ecology and field feeding observations: *C. punctulata* prefers dry, upland soils with sparse vegetation, inhabiting open areas as well as sidewalks, lawns, and cultivated fields (Pearson, et al, 2006). While there have been numerous laboratory feeding observations, there are no known field observations of catching prey.

Description of mandibles: The distinctive teeth including the incisor and others are quite different from all other species in this study (Ball et al 2010). The mandibles are much longer than wide, having the largest ratio of all the species studied – 5.56 for the left mandible and 5.54 for the right (Fig. 10c). The cross-sectional shape of the mandibular base, while still having the three point attachment, is of a quadrilateral rather than a triangle. The mandibular base is covered in a dense brush of posteriorly directed hairs (Fig. 10c, arrows).

Description of Proventriculus: The proventriculus (1mm x 0.5mm) appears more or less typical of the other carabids in this study having four primary and four secondary folds. Its structure is complicated by having long cuticular rods arising from the secondary folds extending to the posterior end of the proventriculus (Fig. 10d,f,g). The internal covering of the proventriculus has a series of transverse striations from which the

moderately long setae arise from all surfaces. The anterior ends of the folds are covered in sparse setae that transition to the more dense covering of plumose hairs. In the posterior third of the fold, the fold broadens with a medial fold before tapering to an end in the posterior-most portion of the proventriculus. Towards the posterior end of the folds the covering of hairs give way to shortened peg-like spines, similar to the split spines of Smrž (1982) that jut into the lumen facing anteriorly against the flow of food. The proventriculus lacks a neck connecting to the mesenteron immediately posterior to the folds.

The contents of the crop and proventriculus of all specimens was amorphous, gruel-like material that is most likely the congealed body fluids of prey (Table 4). Occasional mold spores were also found but these are likely to be incidental to the consumption of prey. There were rectangular crystalline bodies present approximately 0.01 mm to 0.1 mm long (Fig. 10d, arrow).
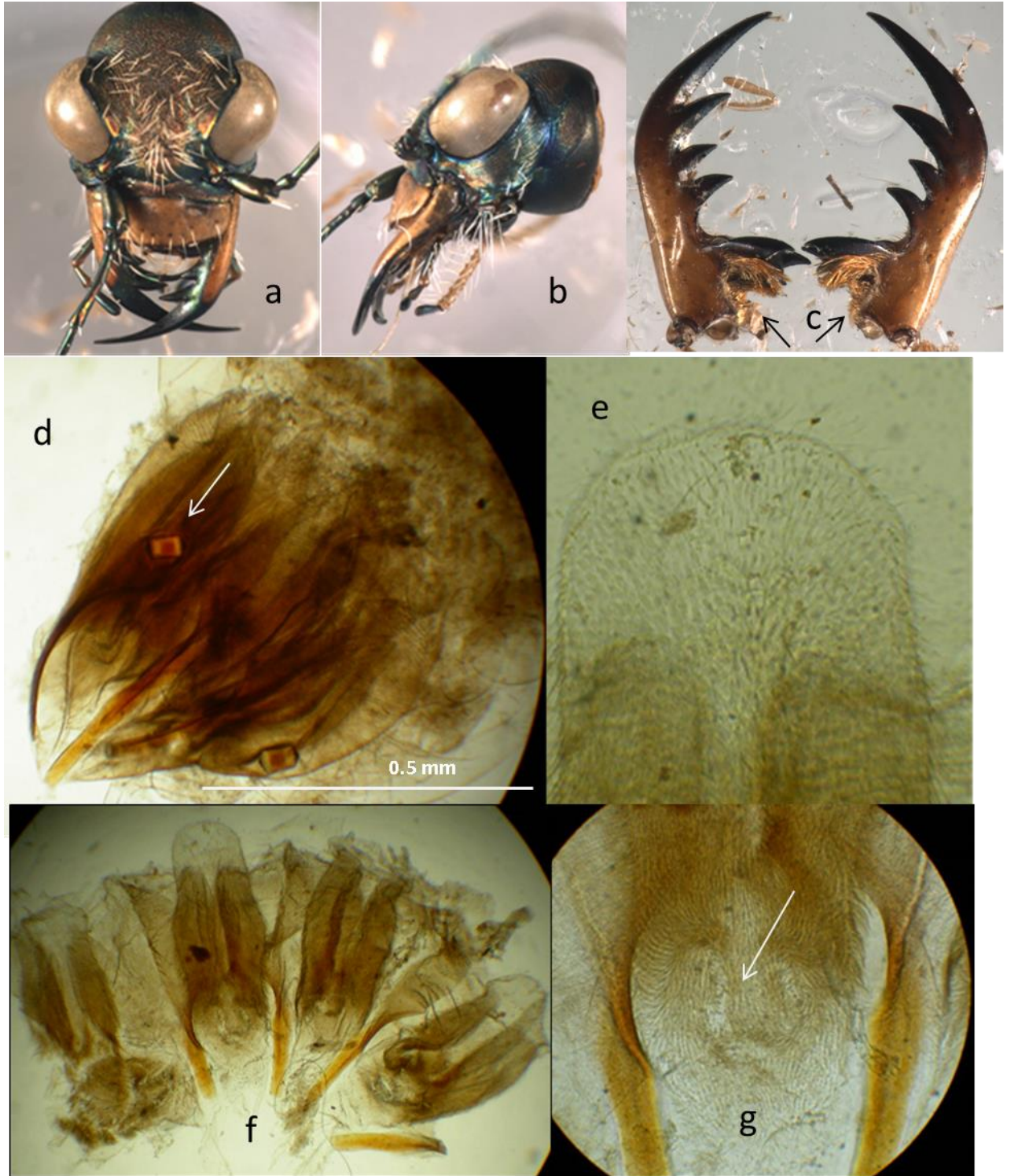
Figure 10. *Cicindela punctulata*: a) dorsal view of head, b) lateral view of head, c) dorsal view mandibles, d) external view of proventriculus, arrow indicating a crystalline body, e) close-up of anterior end of a primary fold, f) internal view of proventriculus, g) close-up of posterior end of a primary fold, arrow indicating an irregular pattern of hairs

Species: *Calosoma calidum* F.

Size: 19 to 25 mm (Lindroth, 1969)

Ecology and field feeding observations: These beetles occur in open ground with moderate cover and cultivated land, such as carrot fields, potatoes and other crops. They prefer dry lighter soils (Larochelle and Laviere, 2003). They have been found to eat caterpillars (various species) and both larval and adult Scarabaeidae in the field (Davis, 1919).

Description of mandibles: Both mandibles are strongly arcuate with the exposed upper surface heavily rugose.   Length to width ratios: left - 2.76 and right - 2.59. The <u>left mandible</u> has an incisor tooth followed by a long terebral blade ending in a groove oriented diagonally, postero-dorsal to antero-ventral.   Posterior and ventral to the groove is a short, broad bidentate retinacular tooth. Posterior to this tooth is a dense brush of hairs on the basal portion of the mandible. There is no evidence of a premolar or molar tooth.   The <u>right mandible</u> has a prominent incisor tooth and a long terebral blade behind it.   The raised terebral blade culminates in a weak terebral tooth that protrudes as a broad, rounded projection, anterior to and dorsad of a more or less conical retinacular tooth, which is bifurcated at its apex in specimens where there is little mandible wear.   Separating the terebral tooth and the retinacular tooth is a broad shallow groove oriented diagonally, postero-dorsal to antero-ventral.   Posterior to the retinacular tooth is a dense brush of hairs on the mandible base.   Dorsal to the basal brush on both mandibles is a second line of hairs, finer and less dense ending at the juncture of the mandible and intersegmental membrane (Fig. 11c).

Description of Proventriculus: The proventriculus of *C. calidum* is approximately as wide as long (1.1mm x 1.0mm). The primary folds are strongly produced, coinciding with invaginations on the external surface of the proventriculus. They extend the length of the proventriculus but at the posterior ends are forked before the proventriculus-mesenteron juncture. The radula is a sparse array of long, thickened spines directed posteriorly. Further along the folds the spines give way to plumose hair-like spines. The secondary folds are as broad as the primary folds though shorter and attenuating to a point, posteriorly. At about two-thirds of way anterior to posterior there is a point of flexion (Fig. 11e, arrow). The primary folds are divided by a constriction and the long hairs covering both parts are oriented in opposing directions; the hairs on the anterior portion are directed posteriorly and the spines on the posterior portion are directed anteriorly. At rest, there is no indication of the constriction but for the juncture of the opposing spines. No such division occurs with the secondary folds but the spines on the secondary folds are oriented the same way as on the primary folds. As in *Cicindela punctulata*, there does not appear to be a distinct neck connecting the proventriculus to the mesenteron.

Gut contents: One hundred percent of specimens examined had some amount of amorphous material within the crop and proventriculus (Table 4). None of the beetles had hard particles or structures that could be associated with prey. One specimen had consumed a rounded pellet, 0.75 mm long, 0.67 mm wide, with a seam, likely a seed, but it is unknown if the beetle would have ingested this structure independently of a prey item.

Figure 11. *Calosoma calidum*: a) dorsal-frontal view of head, b) lateral view of head, c) dorsal view of mandibles, d) exposed internal surface of proventriculus, e) interior view of the line of flexion, arrow indicating where there are opposing hairs on a primary fold.

Species: *Omophron labiatum* F.

Size: 4.8 to 6.3 mm (Lindroth, 1969)

Ecology and literature references to field feeding observations: These beetles prefer bare open ground that is wet as along watercourses or ponds on either sandy or silt soil (Larochelle and Lariviere, 2003). The only field feeding observation is one of this species feeding on young corn plants (Larochelle, 1990).

Description of mandibles: The mandibles are much longer than wide. Length to width ratios: left - 2.66 and right - 2.6. The <u>left mandible</u> is more or less straight with a curving incisor tooth coming to an acute point (Fig. 12c). Posterior to the incisor the terebral blade is long and straight ending with a strongly produced, blunt terebral tooth. Basad to this tooth is a narrow groove and ventral is a retinacular blade ending in a rounded tooth followed by a broad groove and strongly produced molar tooth. The <u>right mandible</u> is more rounded and narrower on the upper surface. The incisor tooth is long followed by a long, curved terebral blade that culminates dorsad of the retinacular tooth. The retinacular tooth is strongly produced. Basad of the tooth the retinacular ridge continues to a shallow groove and a strongly produced molar tooth. Both mandibles lack a basal brush.

Description of Proventriculus: The proventriculus of *O. labiatum* is about twice as long as wide (1mm x 0.4mm), although about half of the length is made up of the neck, which is longer relative to the body of the proventriculus of any of the species examined in this study. The primary folds extend into the neck but lack the covering of long spines. The anterior ends of the primary folds have course spines at the entryway to the

proventriculus. The secondary folds are broader and shorter than the primary folds and attenuate to a point, posteriorly (Fig. 12d), terminating at a line of flexion visible on the primary folds and indicated by the opposing hairs (Fig. 12e, arrows). All of the folds are covered in moderate length hairs. Scale-like ctendia are apparent over almost the entire surface of the intima giving it a striated surface.

Gut contents: Food items found include a partial head capsule of a very small arthropod and a pectinate tarsal claw similar to that seen in Melanotus (Coleoptera: Elateridae). Table 4 lists the percentages of food found in the stomodeum.
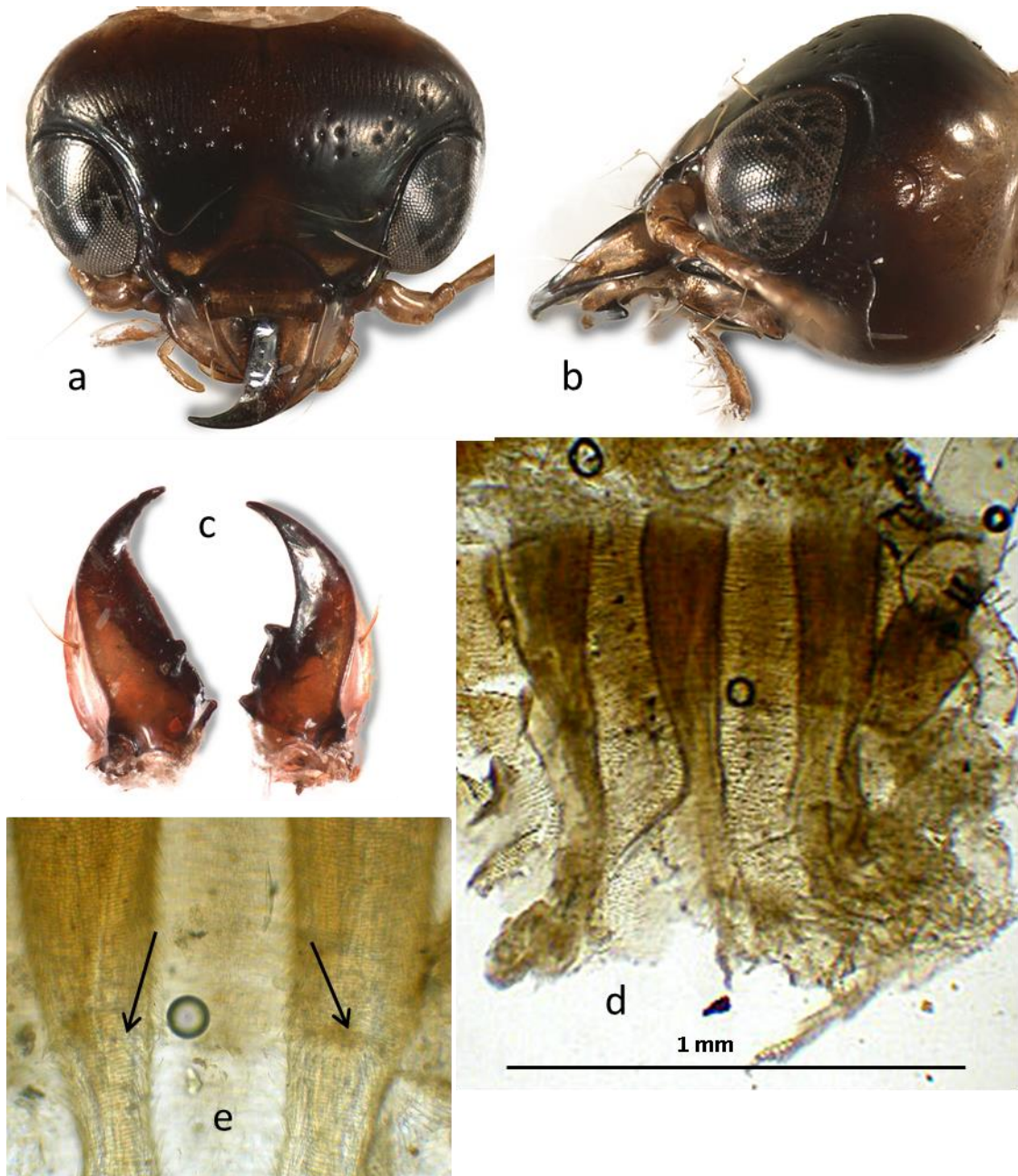
Figure 12. *Omophron labiatum*: a) dorsal view of head, b) lateral view of head, c) dorsal view of mandibles, d) exposed internal surface of proventriculus, e) close-up of flexion line, arrows.

Species: *Paraclivina bipustulata* F.

Size: 5.8 to 7.5 mm (Lindroth, 1969)

Ecology and field feeding observations: *P. bipustulata* prefers open or cultivated ground with some ground cover in wet or damp soil with organic debris (Larochelle and Laviere, 2003).   Kirk (1969) found beetles in trashy areas of woodlots. As far as known there are no field observations of prey consumption.

Description of mandibles: The dorsal and ventral condyles are very large in relation to the overall size of the mandibles and probably reflect the need for firmly attached mandibles for tunneling through the soil. Length to width ratios: left – 2.14 and right – 2.4. The mandibles of *P. bipustulata* are very flat, that is, they do not curve ventrally from condyle to incisor. In relation to the rest of the mandible the incisor teeth are very large.   A strong carina forms the upper and lower outer edge of each mandible (Fig. 13c). Left mandible: The terebral ridge does not produce a terebral tooth and the expanse between the terebral ridge and the medial edge of the mandible is roughened with an alternating pattern of ridges and valleys. A secondary carina develops about where the terebral ridge ends and continues basad towards the dorsal condyle. The dorsal surface between the terebral ridge and the mesal edge is rugose. From the incisor the terebral ridge curves into the interior of the mandible and does not produce a terebral tooth. The retinacular ridge comes from the ventral side of the incisor, continuing dorsally and mesally to produce a weakly pronounced tooth in the normal position for a terebral tooth. A ridge separates the posterior retinacular tooth from the premolar tooth, which in some specimens is bidentate. A second ridge separates the

premolar from the molar tooth, which rounds to the base of the mandible where the adductor muscle attaches. Right mandible: The terebral ridge forms the mesal edge of the right mandible ending with the terebral tooth about midway on the length of the mandible. Below the tooth this ridge then continues to the base of the mandible. The retinacular ridge arises abruptly, producing a flat rounded tooth ventrad of the terebral tooth. Grooves separate the retinacular ridge from the premolar tooth, which is short and rounded and separated from the molar tooth, which is broadly rounded to the base of the mandible.

Description of Proventriculus: The external appearance and organization of the proventriculus is similar to that of *Calosoma calidum* (Fig. 13d), in that the primary folds and secondary folds are covered in long hairs and has a similar point of flexion (Fig. 13e, arrow) with opposing hairs occurring more anteriorly than in *Calosoma calidum*. Both sets of folds taper to the posterior of the proventriculus without additional teeth or grinding surfaces. Unlike *C. calidum*, the anterior portion of the primary folds has a relatively small area of long, thick spines which transition to long hairs. There is no apparent neck connecting the proventriculus to the mesenteron.

Gut contents: The most abundant food item found in the *Paraclivina* stomodeum was dense material appearing as dark, rounded aggregates (blobs). See Table 4 for the percentages of food items found.
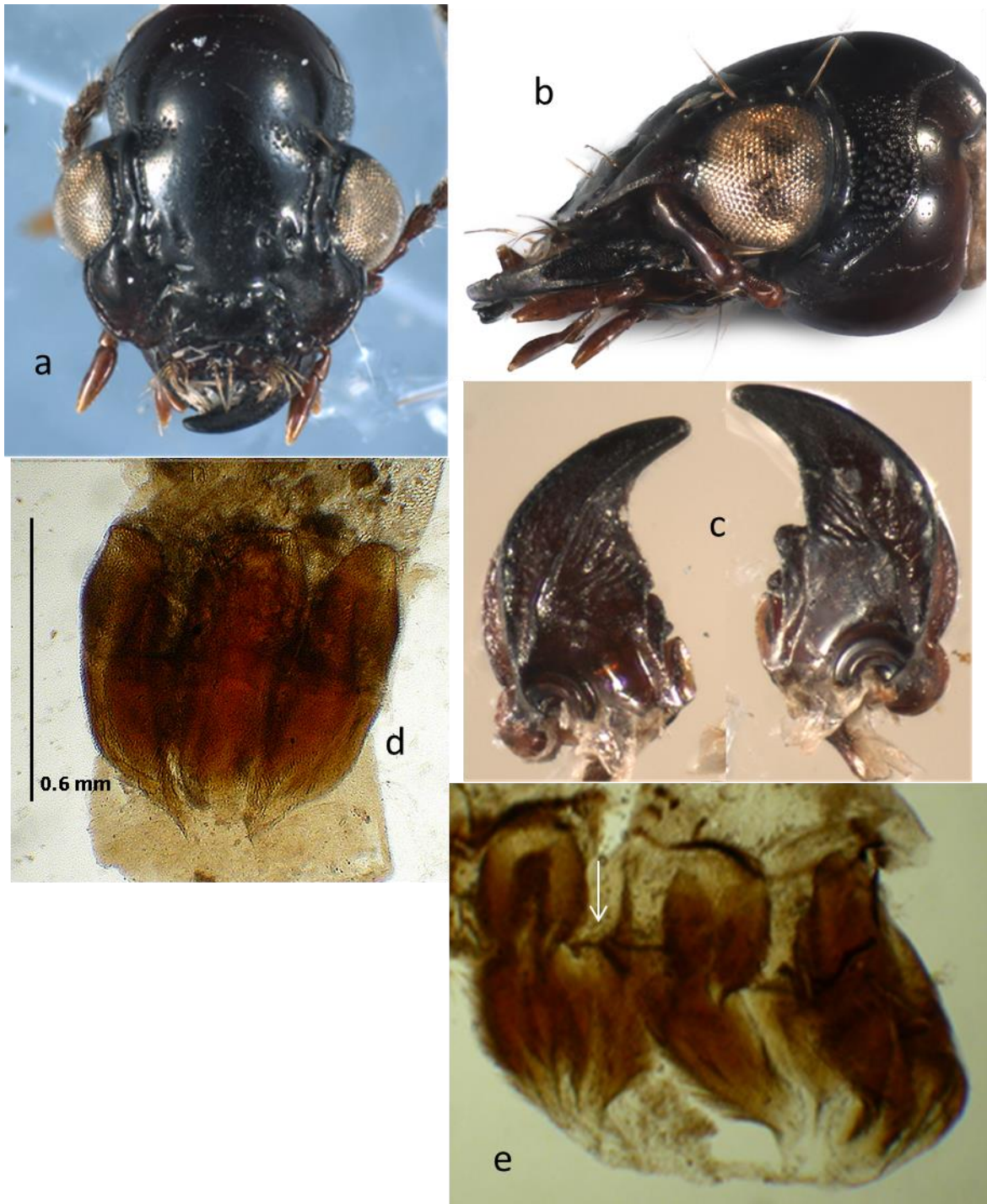
Figure 13. *Paraclivina bipustulata*: a) dorsal view of head, b) lateral view of head, c) dorsal view of mandibles, d) external view of proventriculus, e) exposed internal surface of proventriculus, arrow indicating line of flexion.

Species: *Bembidion quadrimaculatum* L.

Size: 2.8 to 3.7 mm (Lindroth, 1969)

Ecology and field feeding observations: This beetle prefers open ground with cover, like cultivated fields, and lighter, dry soil (Larochelle and Laviere, 2003). They have been observed feeding on insect eggs and small juveniles of many insect species (Larochelle, 1990).

Description of mandibles: The mandibles of *B. quadrimaculatum* are more typical carabid mandibles. Length to width ratios: left – 2.04, and right – 2.03. The greatest difference with other species is in the dorsal external ridge above the scrobe (the lateral indentation towards the mandibular base – see Fig. 1) of each mandible which is broadly indented before reaching the dorsal condyle (Fig. 14c). Left mandible: The terebral ridge extends from the base of the incisor to a weakly produced terebral tooth in the proximal third of the mandible. The retinacular tooth lies ventrad of this tooth. A groove separates the retinacular tooth and the premolar tooth. A second tooth separates the premolar from the molar tooth, which is very large extending into the mesal area between the mandibles as an acute point. The distal portion of this tooth is devoid of melanin and is translucent. Right mandible: The terebral ridge continues from the base of the incisor to the terebral tooth and, although it is weakly produced, is a large raised area just past mid-length of the mandible. The retinacular tooth is anterior to the terebral tooth. A weak groove separates the posterior retinacular ridge from the premolar tooth. A second ridge separates the large molar tooth, which is

similar to its left mandible counterpart in that it is acute and lacking melanin in the distal part of the tooth.

Description of Proventriculus: Externally, the proventriculus has a short, wide body with a neck of equivalent length, which curves before attaching to the mesenteron. Internally, the primary folds are greatly produced, while the secondary folds are flat, roughened surfaces the length of the proventriculus body. The anterior ends of the primary folds are covered with shorter spines but rapidly transition to relatively large, long spines that cover the center surface of the fold to about its middle (Fig. 14e, arrow). The remaining surface of the anterior three-quarters of the fold is covered with fine hairs. At the posterior end, the fold produces a large bulbous node, wider than the rest of the fold, that abruptly rounds off posteriorly before the neck (Fig. 14e). The node is studded with short blunt spines (Fig. 14f) and is analogous to the posterior nodes of *Stenocrepis duodecimstriata* and *Harpalus caliginosus*. The internal surface of the neck has numerous folds and sparse teeth.

Gut contents: While the most abundant material found in the stomodeum of *B. quadrimaculatum* was gruel, there were larger pieces of arthropods and some plant material. See Table 4 for the percentages of materials found.
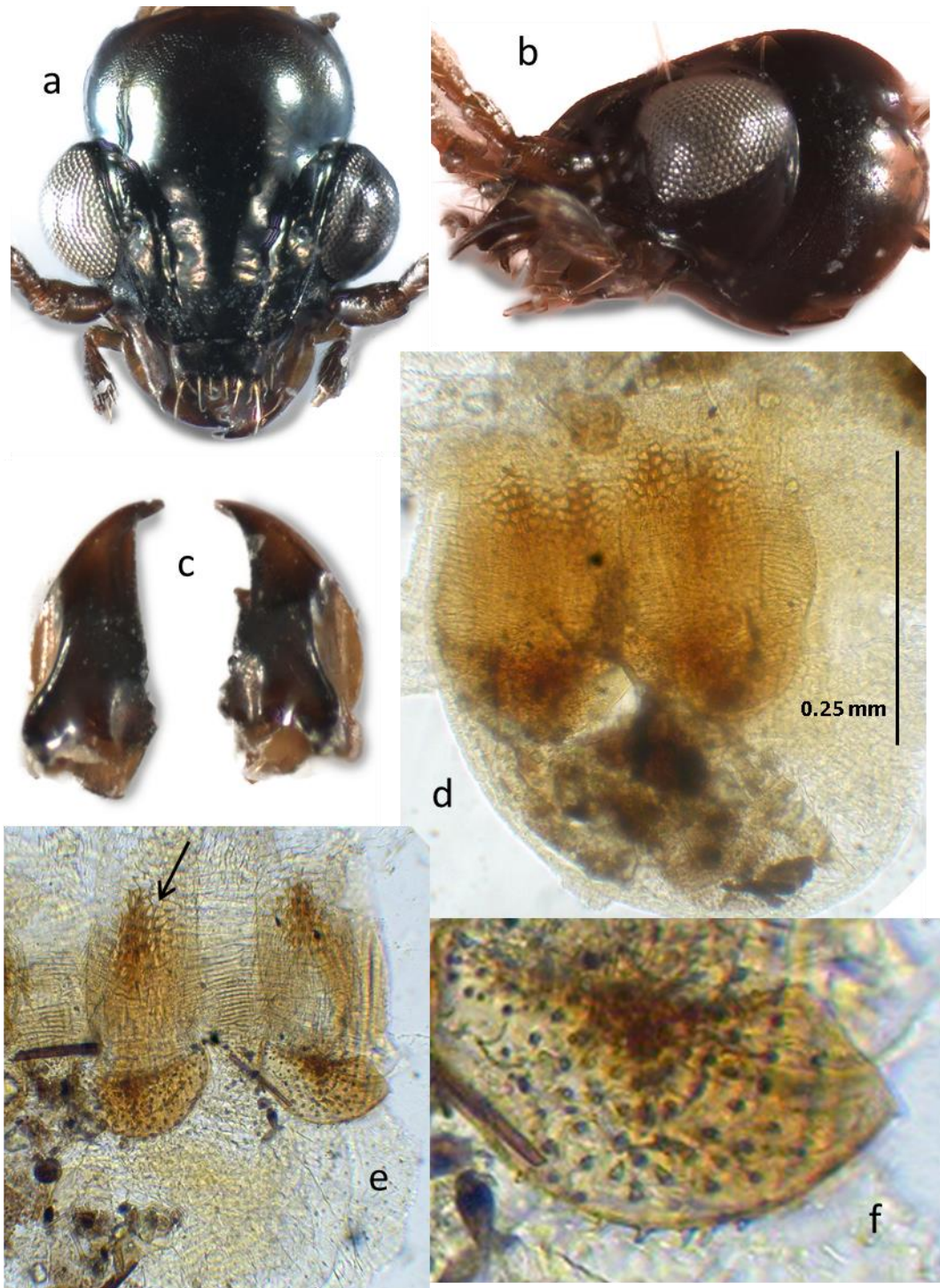
Figure 14. Bembidion *quadrimaculatum*: a) dorsal view of head, b) lateral view of head, c) dorsal view of mandibles, d) external view of proventriculus, e) internal view of proventriculus, arrow indicating field of larger spines, f) close-up of a node with pegs at the posterior end

Species: *Poecilus chalcites* Say

Size: 10.5 to 13 mm (Lindroth, 1969)

Ecology and field feeding observations: *P. chalcites* prefers open ground and is common on cultivated ground; with dry or damp, loam or silt soils (Larochelle and Lariviere, 2003). In the field they have been observed to feed on Hymenoptera and other insects; eggs and larvae of onion maggot and Phyllophaga (Coleoptera: Scarabaeidae) and some vegetative material (Larochelle, 1990).

Description of mandibles: The mandibles of *P. chalcites* are generally similar to *C. gregarius*, but stouter (Fig. 15c) . Both mandibles have a broad carina extending from the base of the molar tooth curving in to the center of the mandible. This carina is quite pronounced behind the retinacular ridge and terebral tooth of the respective mandible. A short basal brush occurs basad of the molar tooth on each mandible. Length to width ratios: left – 2.58 and right – 2.42. Left mandible: The terebral margin of the left mandible is straight ending with the terebral tooth in the proximal third of the mandible. Ventrad of the tooth the retinacular ridge rises. Two grooves separate the posterior retinacular tooth from the premolar tooth and that from the molar tooth. Right mandible: The retinacular ridge curves away from the base of the incisor to the retinacular tooth which is acute and conical. The retinacular ridge extends basad producing the posterior retinacular tooth. Two grooves separate the retinacular tooth from the premolar tooth and that from the molar tooth. The grooves extend, diagonally, from posterior-dorsally to antero-ventrally.

Description of Proventriculus: The proventriculus is about twice as long as wide (1.3mm x 0.7mm) and is comprised of the four primary folds that extend as ridges into the neck. In between the folds are four well-defined ridges that are nearly as long as the folds. The anterior ends of the primary folds have stout posteriorly directed teeth that quickly transition to moderately long hairs on the main body of the fold. The remainder of the folds and ridges are covered with these hairs directed posteriorly. At the transition from the body to the neck the hairs are replaced by narrow transverse ridges lined with blunt teeth (Fig. 15f).

Gut contents: One specimen had two pieces of thin material with holes of different sizes scattered in the pieces. It is unknown whether this was of plant or animal derivation. One specimen had recently consumed an arthropod and the various parts found in the gut suggest that it was a Diptera. Only one specimen had a moderately full crop. See Table 4 for the percentages of food materials.
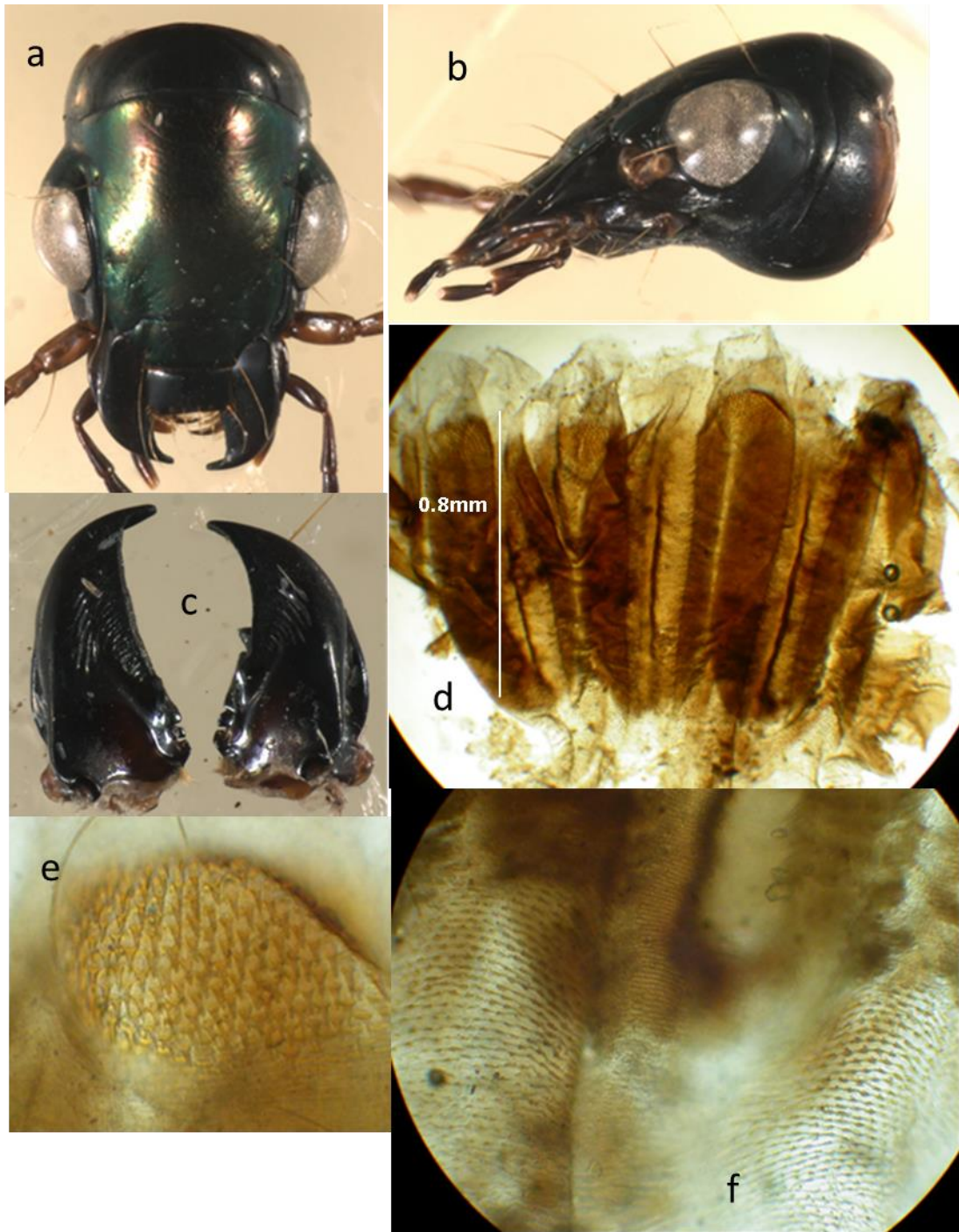
Figure 15. *Poecilus chalcites*: a) dorsal view of head, b) lateral view of head, c) dorsal view of mandibles, d) internal surface of the proventriculus, e) spines at the anterior end of a primary fold, f) blunt teeth in rows in neck region posterior to the ends of the folds.

Species: *Stenocrepis duodecimstriata* (Chevrolat)

Size: 8 to 9mm (personal observations)

Ecology and field feeding observations: *S. duodecimstriata* lives on the borders of semi-aquatic habitats with wet heavy soils, organic debris and vegetation (Larochelle and Lariviere, 2003). As far as is known there is no recorded field observation of prey consumption (Larochelle, 1990).

Description of mandibles: The mandibles are long and straight and more angular at the left incisor in contrast to *Calathus* and *Poecilus*. The molar area is produced and basal brushes are lacking. Length to width ratios: left – 2.47 and right – 2.37 (Fig. 16c). Left mandible: The incisor is acute and relatively long. At its base the terebral ridge extends to the proximal third of the mandible, curving slightly inward, ending in the terebral tooth. The terebral tooth is poorly produced and appears as a rounded protuberance. Ventrad of the tooth the retinacular ridge produces a very small anterior retinacular tooth and extends a short distance before ending at the groove with the premolar tooth. Depending upon the specimen, the posterior retinacular tooth may not be visible from above, giving the appearance of the terebral tooth followed by the groove adjacent to the premolar tooth. The premolar tooth is much smaller than the molar tooth, which is greatly expanded, protruding into the mesal space between the mandibles, being roughly triangular when viewed dorsally. Right mandible: The incisor appears to be relatively longer than in the previous species. The terebral ridge is more or less straight going to the terebral tooth which is narrowly rounded from above. The retinacular tooth is small, acute and conical. The retinacular ridge extends basad

producing a posterior retinacular tooth. Two grooves separate the posterior retinacular

tooth from the premolar and the premolar from the broadly expanded molar tooth.

Description of Proventriculus: The proventriculus is about twice as long as wide

(1.1mm x 0.6mm) and is similar to *P. chalcites* in that besides the primary folds, the four

secondary folds are well defined ridges nearly as long as the primary folds (Fig. 16d).

The anterior ends of the folds have coarse spines that transition to long hairs on the

surface of the intima. At the posterior ends of both folds and ridges there is a narrow,

rounded node covered with stout, blunt teeth just anterior to the transition to the neck

(Fig. 16e).   Within the neck the spines give way to transverse narrow ridges with blunt

teeth and long spines.

Gut contents: One specimen that was regarded as having an empty proventriculus

contained several nematodes of unknown species. One beetle appeared to have

consumed a fly, another had the terminal segment of a palp, and a third beetle

contained an unidentifiable arthropod appendage, flattened with 13 spines around its
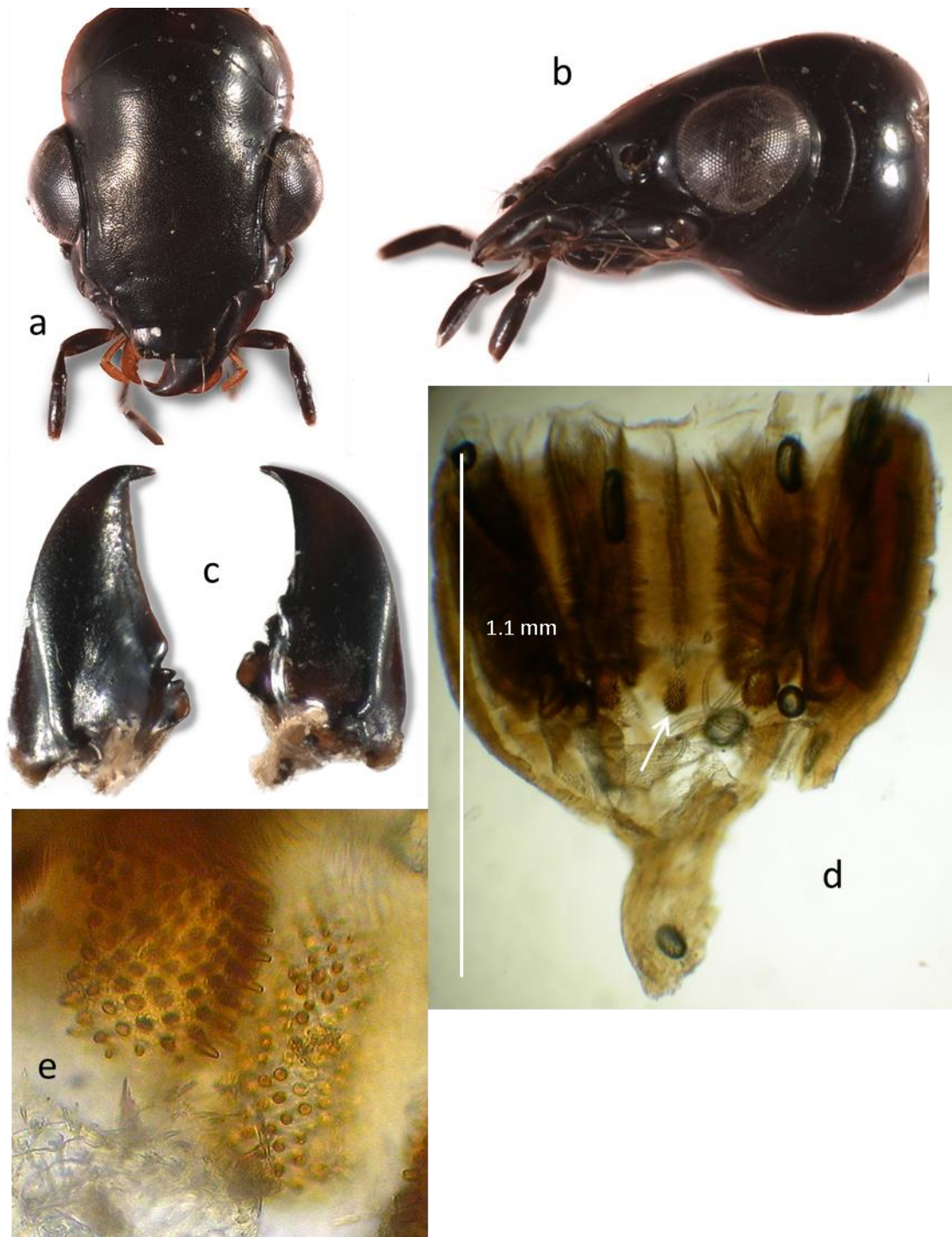
perimeter (Table 4).

Figure 16. *Stenocrepis duodecimstriata*: a) dorsal view of head, b) lateral view of head, c) mandibles, d) exposed internal surface of proventriculus and posterior nodes, arrow e) close-up of nodes with peg-like teeth at posterior ends of all folds.

Species: *Zabrus tenebroides* (Goeze)

Length: 15 mm (multiple internet sources)

Ecology and literature references to field feeding observations: *Zabrus tenebroides* is one of the few carabid species regarded as an agronomic pest (Europe and Asia), which consumes the seeds of small grains and other plants. There is a long record of these beetles consuming grains in the field in Europe (Larochelle, 1990).

Description of mandibles: The mandibles of *Z. tenebroides* are reminiscent of *Stenolophus lineola* in general. Length to width ratios: left - 2.03 and right – 1.93 (Fig. 17c). Left mandible – The incisor tooth is rounded and has a semi-acute tip. The terebral ridge is long and ends with a strongly produced terebral tooth. Vertically, a wide gap exists between the base of the terebral tooth and retinacular tooth and ridge, more or less oval in shape. Posterior to the retinacular ridge is a short ridge, which produces the premolar tooth. A second ridge produces the molar tooth, but both the premolar and molar teeth are small. There is a long basal face, which is glabrous. Right mandible – The incisor tooth is semi-acute and long. The retinacular ridge has two teeth. Both the anterior and posterior retinacular teeth are broadly rounded but flattened dorsal-ventrally. These teeth are widely separated with the posterior tooth lying slightly anterior to the terebral tooth. The premolar and molar teeth are very small. There is a long, glabrous basal face.

Description of Proventriculus: The proventriculus of *Z. tenebroides* is the most simple of all the other species in this study. There are four primary folds that extend into the neck, but the secondary folds are poorly developed. The primary folds lack the typical

long spines at the anterior end as well as lacking terminal teeth at the posterior of the folds (Fig. 17d). A narrow band of long hairs extend from the anterior end to the posterior end of the primary folds and on into the neck region. Otherwise the primary folds are clothed in short sparse hairs. The neck region at the base of the folds has a roughened surface of short rounded teeth (Fig. 17e).

Gut contents: The only material found in the stomodeum of three specimens was gruel-like material (Table 4).
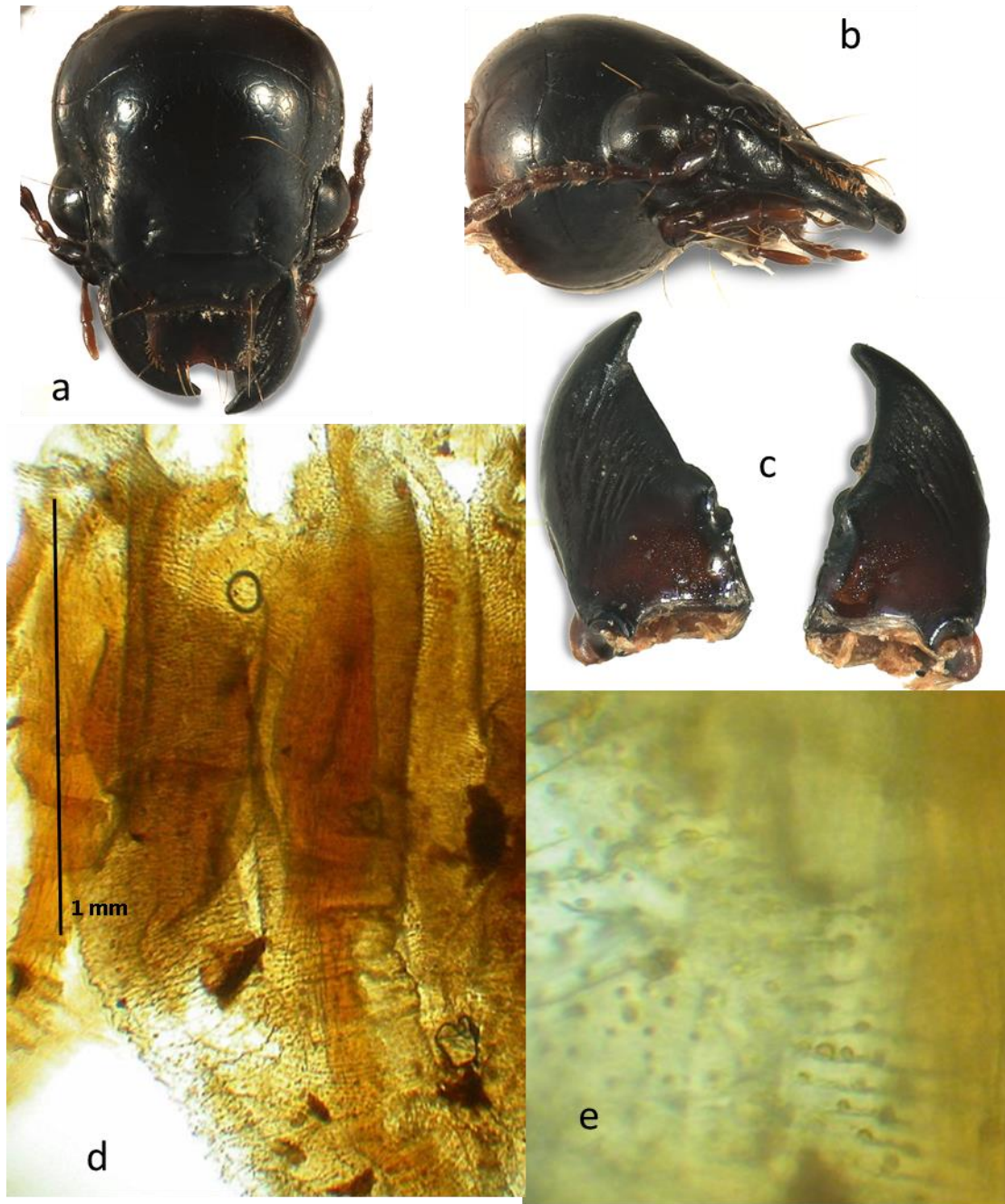
Figure 17. *Zabrus tenebroides*: a) dorsal view of head, b) lateral view of head, c) dorsal view of mandibles, d) internal view of proventriculus, e) close-up view of rounded teeth in the neck.

Species: *Lebia grandis* Hentz

Size: 8.5 to 10.5 mm (Lindroth, 1969)

Ecology and field feeding observations: *L grandis* prefers open ground with cover and dry soils. They are nocturnal staying on plants (Larochelle and Lariviere, 2003) and in the larval stage are ectoparasitic specialists of Colorado potato beetle and related species. Adults feed on all stages of the potato beetle, but also feed on undetermined worms and small insects (Larochelle, 1990).

Description of mandibles: The mandibles are relatively broad at the base. The dorsal surface is smooth and both mandibles have a short, very fine basal brush. The length to width ratios: left – 2.24 and right – 2.19 (Fig. 18c). Left mandible: From the base of the incisor the terebral ridge ends in the terebral tooth in the basal quarter of the mandible. One groove separates the terebral tooth from the molar tooth. The retinacular ridge is nearly lacking, appearing only as a slight raised ridge ventral to the terebral tooth. The groove separating the terebral tooth and the molar tooth has two channels; one is directed ventrally separating the molar from the terebral tooth, and the second channel separates the retinacular ridge from the terebral ridge above it. Right mandible: The terebral ridge curves posteriorly from the incisor and ends with the terebral tooth in the basal third, making it slightly anterior to the corresponding terebral tooth of the left mandible. The retinacular ridge is present but the retinacular tooth is either very small or appears as a roughened surface. The retinacular ridge is short and terminates at the groove that separates the terebral tooth from the molar tooth. From a basal view

looking anteriorly, the basal teeth on both mandibles are wedge shaped, meeting edge on edge mesally (Fig. 18e).

Description of Proventriculus: The proventriculus is twice as long as wide (0.8mm x 0.4mm) (Fig. 18d). It is a delicate organ compared to the proventriculi of other species. The indistinct ridges of the secondary folds lie between the primary folds. The folds are covered with short hairs but at the end of the folds in the neck the hairs are replaced by short, sparse teeth.

Gut contents: Only one specimen, in which the crop was nearly full, had cuticular material in the stomodeum. Most specimens had little or no food in the stomodeum. See Table 4 for percentages of food items.
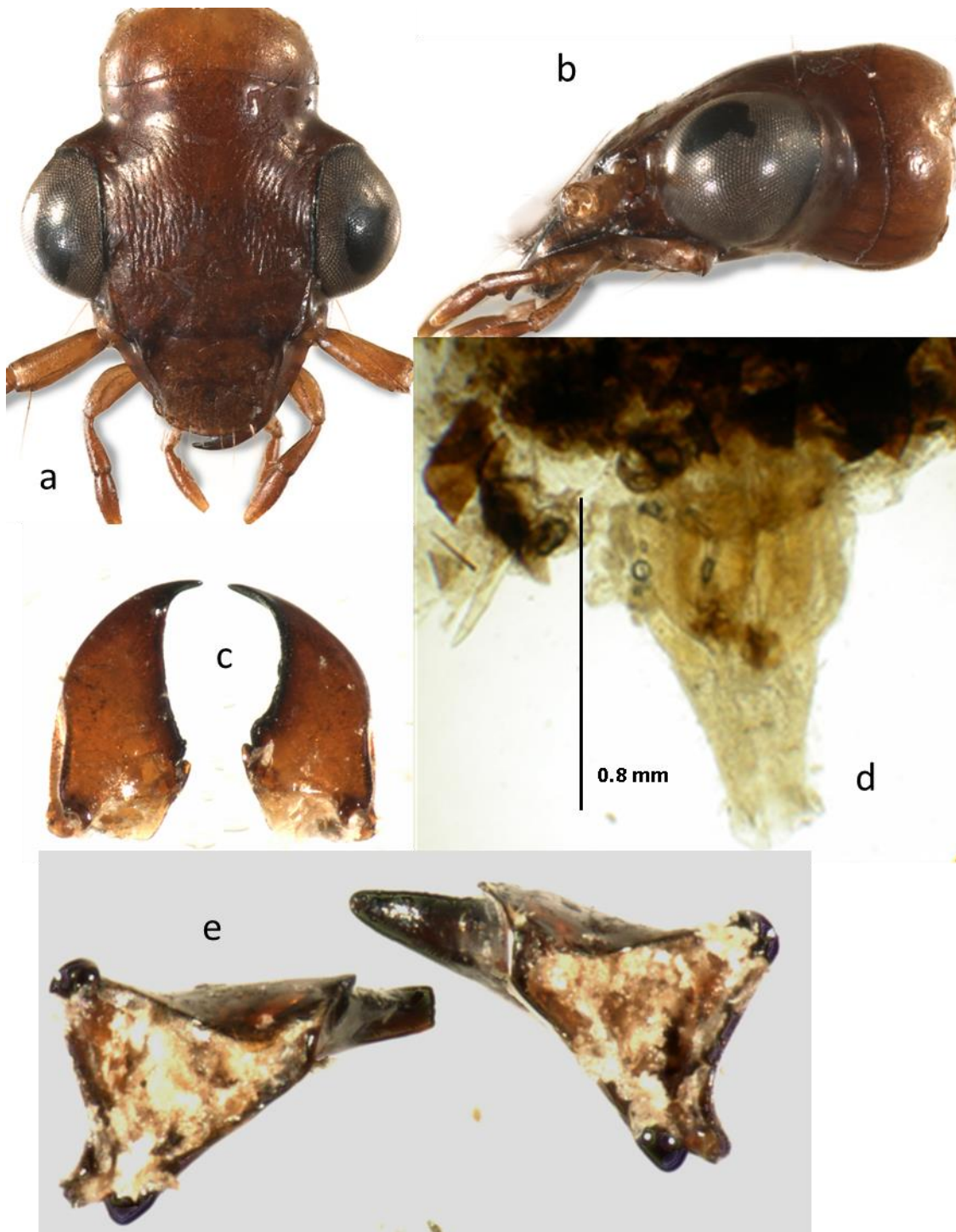
Figure 18. *Lebia grandis*: a) dorsal view of head, b) lateral view of head, c) mandibles, d) external view of proventriculus attached to a full crop, e) basal view of mandibles showing scalene-type base and wedge-shaped molar teeth projecting medially.

Species: *Anisodactylus laetus* Dej.

Size: 8 to 9 mm (Lindroth, 1969)

Ecology and field feeding observations: *A. laetus* prefers open ground; wet, muddy soil w/organic debris (Larochelle and Lariviere, 2003). Beetles have been found in golf greens and in trashy areas of woodlots. As far as known, there are no field observations of prey consumption.

Description of mandibles: The mandibles of *A. laetus* are atypical compared to the other species in the study. The length of the terebral ridge, the distance from the tip of the incisor to the base of the molar tooth, in both mandibles is reduced (Table 2). Each mandible has a long basal face with a dense brush of hairs. The length to width ratios: left – 1.56, and right – 1.55 (Fig. 19c). <u>Left mandible</u>: The incisor is thick, blunt and rounded dorso-ventrally. The short terebral ridge ends in a reduced terebral tooth in the apical third of the mandible. A broad, shallow groove separates the terebral tooth from the retinacular ridge which originates at the base of the incisor and ends in a low rounded tooth in the mid-third of the mandible. Separating the retinacular ridge and tooth from the molar is a narrow groove. The molar tooth is low but at its terminus is a rounded, prominent tooth extending mesally. Immediately below the molar tooth is a long basal face with a brush. <u>Right mandible</u>: Incisor short, thick, broadly rounded at the tip. The terebral ridge is short, ending with the terebral tooth, which is low dorsad and posterior to the retinacular tooth. The retinacular ridge ends with a narrow groove between it and the molar ridge. The molar ridge is short, ending in a prominent tooth that extends mesally.

Description of Proventriculus: The proventriculus is simple, similar to *O. labiatum* and is about one and a half times as long as wide (0.6mm x 0.4mm).   The primary folds have long, flattened spines on their anterior ends with the spines in the center of the fold, forming a more or less triangular field extending approximately one-fifth of the length of the fold (Fig. 19e).   Long hairs cover most of the surface of the primary folds.   The secondary folds are weakly developed and appear as more or less flattened areas between the primary folds.   The surface of the secondary folds appears roughened, especially towards the posterior end.   Distinct teeth are lacking at the posterior of the folds and the internal surface of the neck is smooth but folded.

Gut contents: Several of the 30 specimens examined had more or less spherical structures that may have been fungal spores.   Recognizable arthropod or plant matter was lacking. See Table 4.

Figure 19. *Anisodactylus laetus*: a) dorsal view of head, b) lateral view of head, c) mandibles, d) exposed internal surface of proventriculus, e) anterior end of primary fold showing long spines, arrows, f) cross-section view of left mandible base showing isosceles-type of base.

Species: *Geopinus incrassatus* Dej

Length: 13 to 17mm (Lindroth, 1969)

Ecology and literature references to field feeding observations: *G. incrassatus* prefers sandy or light soil with sparse vegetation and often is found near water where it burrows underground (Lindroth, 1969). In field observations specimens have been found feeding on cutworms and plant seedlings (Larochelle, 1990).

Description of mandibles: The mandibles are thick with long incisors. The cross-sectional shape of the base of the mandibles is isosceles. Both mandibles have rugose dorsal surfaces (Fig. 20c). Length to width ratios: left – 2.65 and right – 2.43. Left mandible – The large incisor tooth draws to an acute tip when viewed from above, but is rounded dorso-ventrally (Fig. 20a). The terebral ridge forms a thin cutting edge from the base of the incisor to the terebral tooth. Ventrally, the mandible is deeply recessed beneath the terebral ridge. The retinacular ridge is anterior to the terebral tooth and has two poorly defined teeth before ending at the groove anterior to a very small molar tooth. There is a long basal face with a brush of hairs. Right mandible – The incisor is relatively long and slender tapering to an acute tip dorsally, but is rounded dorso-ventrally. The terebral ridge is present from the base of the incisor to the terebral tooth, about mid-way of the length of the mandible. The thumb-like retinacular tooth is strongly produced ventral to the terebral ridge. The retinacular ridge is relatively long ending at the groove anterior to the molar tooth. A basal face is present with a brush of long hairs.

Description of Proventriculus: At two millimeters long, the proventriculus (2 mm x 1 m) of *Geopinus incrassatus* is the largest relative to the body size of any of the species examined. In overall structure it is similar to *Poecilus chalcites*. Long spines are present on the anterior end of the four primary folds forming a triangular area extending about one-quarter of length of the folds. The remaining surface of the primary folds is covered in short hairs. The secondary folds are undifferentiated ridges, shorter than the primary folds, covered with hairs. All spines are directed posteriorly. All of the folds end abruptly at the junction with the long neck. In the area immediately posterior to the folds, short spines, directed anteriorly, sparsely cover the internal surface of the neck. Further into the neck, the spines are lacking, but there are many folds in the internal surface.

Gut contents: Only gruel-like material was found in the stomodeum of the single specimen examined. See Table 4.
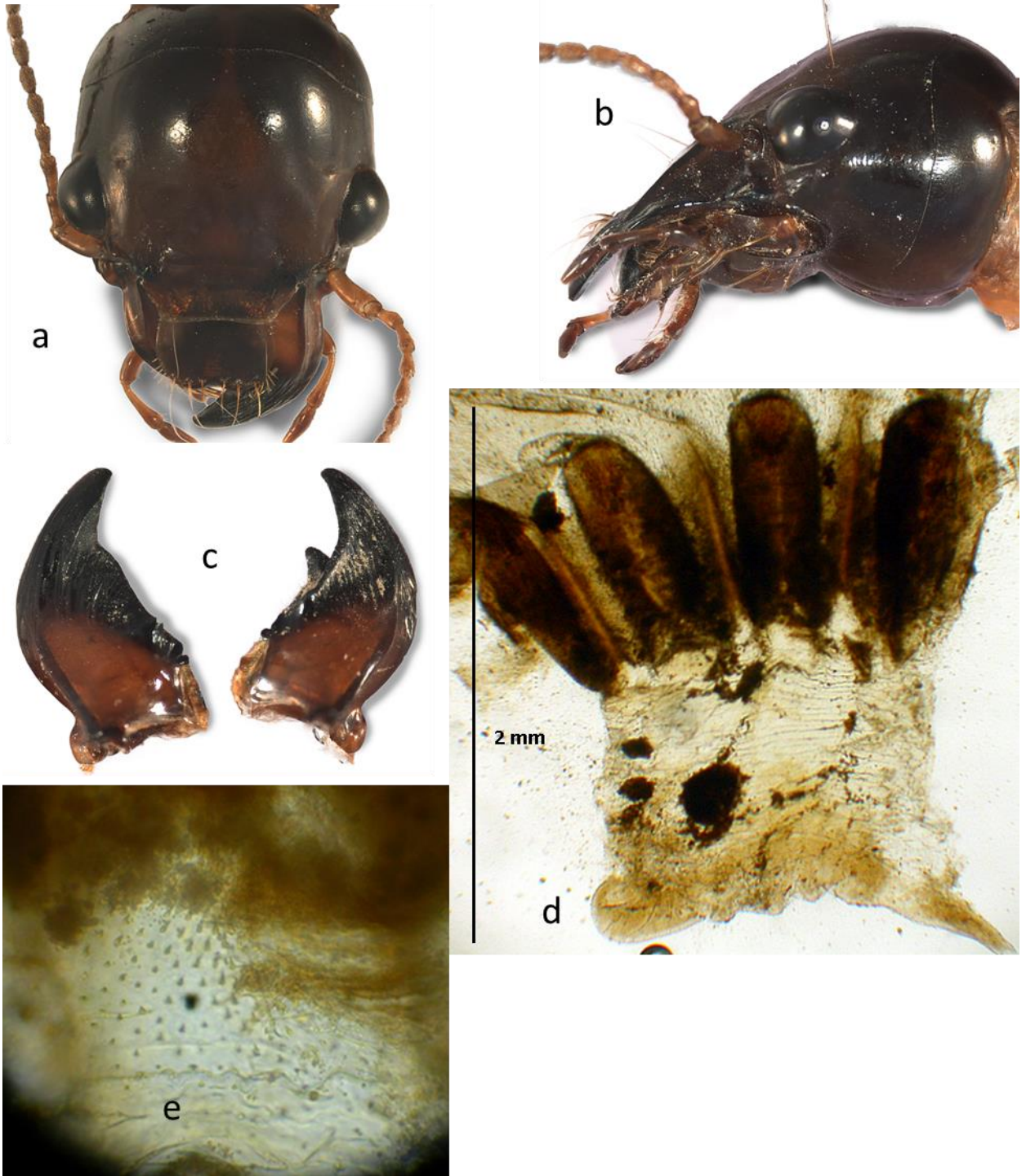
Figure 20. *Geopinus incrassatus*: a) frontal view of head, b) lateral view of head, c) mandibles, d) exposed internal surface of proventriculus including the neck, e) neck area between posterior ends of folds showing short teeth.

Species: *Stenolophus lineola* F.

Size: 7 to 9.1 mm (Lindroth, 1969)

Ecology and field feeding observations: *S. lineola* prefers open ground - moist or dry soil - usually lighter soil with some cover; for example, cultivated ground (Larochelle and Lariviere, 2003) and golf greens (Kirk, 1969). Field feeding observations include corn seed and both live and dead insects (Larochelle, 1990).

Description of mandibles: The mandibles of *S. lineola* are unremarkable. The length to width ratios: left – 1.85, and right – 1.84 (Fig. 21c). Left mandible: The terebral ridge extends from the incisor tooth to the terebral tooth about mid-way along the length of the mandible. The terebral tooth is strongly produced but blunt and rounded, projecting mesally. The retinacular ridge is vestigial. A groove separates the terebral tooth from the retinacular tooth. A second groove separates the retinacular tooth from the molar tooth. There is a thin basal brush of hairs basad of the second retinacular tooth. Right mandible: The terebral ridge extends down to the terebral tooth about midway along the length of the mandible. The blunt and rounded tooth is strongly produced, upwards and mesally. Anterior to and ventrad of the terebral tooth, the retinacular tooth is strongly produced but rounded. The retinacular ridge terminates at the groove separating it from the molar tooth. Basad of this tooth there is a thin basal brush of hairs.

Description of Proventriculus: The proventriculus of *Stenolophus lineola* is the most advanced of all the species examined in this study. Externally, the proventriculus is octagonal in shape due to eight expanded cuticularnous flanges connected by muscle

(Fig. 21d,e). Unlike the proventriculi of other species where the structure is somewhat translucent, the proventriculus of *S. lineola* is opaque because of the increased amount of cuticular structures. The neck is short in relation to the body of the proventriculus. Internally, both the primary and the secondary folds are strongly produced. The primary folds are broad across their anterior ends with a dark clump of long spines in the center of the fold that project medially and posteriorly. The folds narrow towards the posterior ends without the presence of teeth. However, a rounded knob appears medially amongst the hairs in the posterior one-quarter of the primary folds (Fig. 21e Appendix). Immediately posterior to the knob there appears to be a flexion point because of an indentation in the fold on either side. The hairs posterior to the indentations are directed anteriorly. Anterior to the knob, long hairs cover the remaining surface of the primary lobes, directed laterally and posteriorly. The primary folds extend, hairless into the neck region. The secondary folds are poorly developed anteriorly but become ridges that broaden towards the posterior end of the proventriculus. The posterior half of the secondary folds form a cuticularnous ridge that have on either side strongly produced teeth that are appressed to the side of the ridge with their tips pointing posteriorly. The cuticularnous ridge abruptly tapers towards the posterior ending with a cluster of long spines directed medially and anteriorly. Teeth seem to be lacking in the neck region posterior to the folds and ridges.

Gut contents: Sixty percent of the crops contained gruel-like material. No cuticular material was observed (Table 4).
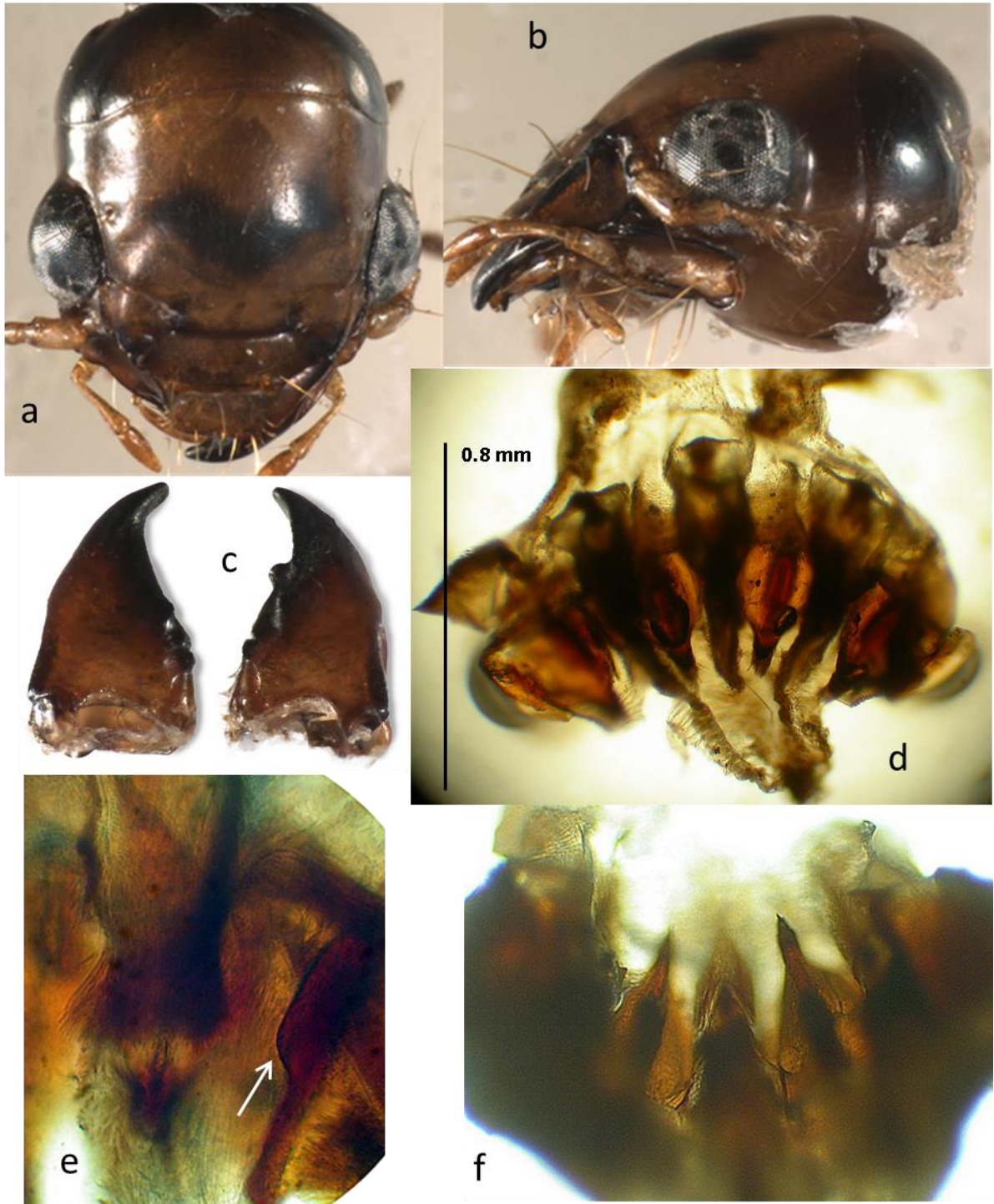
Figure 21. *Stenolophus lineola* a) dorsal view of head, b) lateral view of head, c) mandibles, d) internal view of proventriculus, e) close-up of primary fold (left) and secondary fold ridge, arrow, f) anterior view of folds within proventriculus.

Species: *Harpalus caliginosus* F.

Size: 17.5 to 25.5 mm (Lindroth, 1969)

Ecology and field feeding observations: *H. caliginosus* prefers open or cultivated ground with moderate cover on lighter, dry soils (Larochelle and Lariviere, 2003). Field feeding observations include a mixture of insects and seeds (Larochelle, 1990).

Description of mandibles: The mandibles are noticeably dissimilar (Fig. 22c). Both mandibles have a thick, broadly rounded (dorsal-ventrally) incisor, neither of which comes to an acute point. Length to width ratios: left – 1.70, and right – 1.44. Left mandible: The terebral ridge forms an anterior tooth at the base of the incisor and then extends to a wide blunt posterior terebral tooth. The retinacular ridge arises ventrad of the posterior terebral tooth ending near the base of the terebral tooth so that a large hollow is formed between the two ridges. A small narrow ridge separates the posterior retinacular tooth from the small molar tooth. The basal brush extends from the molar tooth to the point of attachment of the adductor muscle. Right mandible: The incisor is broadly rounded (dorsal-ventrally). The terebral ridge produces a blunt, low terebral tooth in the distal third of the mandible. The anterior retinacular tooth is anterior to the terebral tooth. The retinacular ridge extends to the groove which lies between the retinacular ridge and small molar tooth. A dense basal brush occurs on the basal face.

Description of Proventriculus: The proventriculus is about one and a half times longer than wide with a dense radula of spines in the center of the anterior end of the primary fold that jut into the lumen of the proventriculus (Fig. 22d,e). Otherwise, the primary

folds are covered in moderate length spines. The anterior spines may wear away in older individuals as most of these spines were broken off in one specimen. The posterior ends of the folds are enlarged into a swollen, rounded node that points anteriorly with enlarged spines, directed anteriorly on the anterior face of the node (Fig. 22f, arrow). The spines shorten and are replaced with short blunt teeth on the medial and posterior surface of the bulge. The secondary folds are low ridges without any differentiation covered with thick hairs. Teeth were lacking on the internal surface of the neck.

Gut contents: Thirty-six percent of the specimens examined of *H. caliginosus* contained remnants of arthropod food items. See Table 4.
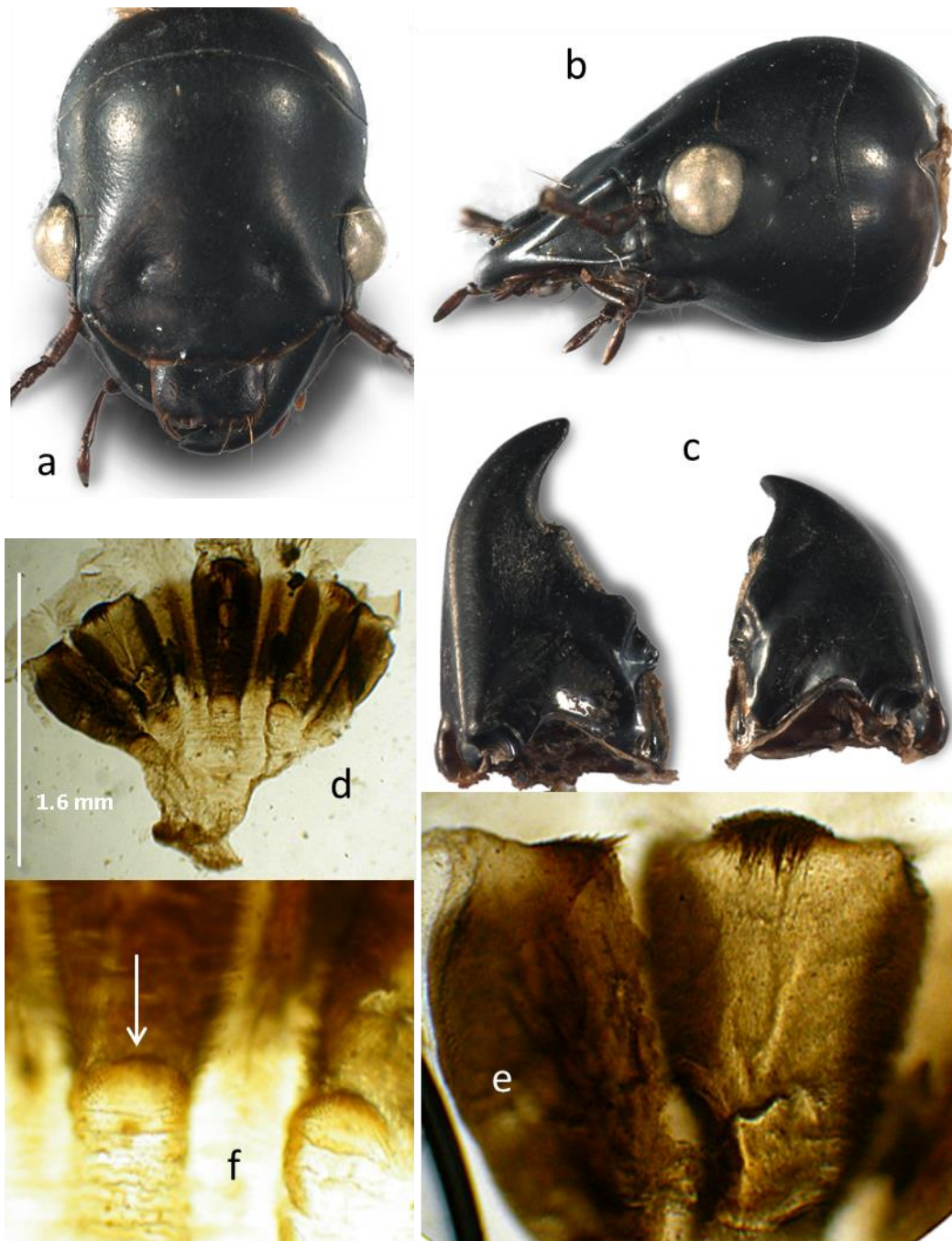
Figure 22. *Harpalus caliginosus*: a) dorsal view of head, b) lateral view of head, c) mandibles, d) exposed internal surface of proventriculus, e) dense patch of spines on anterior end of primary folds, f) swollen nodes with anteriorly pointing spines on posterior end of primary folds, arrow.

Species: *Calathus gregarius* Say

Size: 8.2 to 10.8 mm (Lindroth, 1969)

Ecology and literature references to field feeding observations: *C. gregarius* prefers forested and cultivated ground, with moderate cover and light, dry soils (Larochelle and Laviere, 2003). They are recorded as eating caterpillars and pollen in the field (Larochelle, 1990).

Description of mandibles: The mandibles are more or less straight with the lateral side curving to a relatively small, acute incisor (Fig. 23c). Length to width ratios: left - 2.28 and right – 2.33. <u>Left mandible</u>: From the base of the incisor the terebral ridge curves inward before curving back towards the mesal edge where the ridge ends with a slight terebral tooth adjacent to a narrow groove, about half way down the length of the mandible. Basad of the groove the retinacular ridge continues curving medially towards the molar area. Two diagonal grooves oriented postero-dorsally to antero-ventrally separate three broadly rounded teeth of the retinacular tooth, premolar and molar tooth. Basad of the molar tooth the ridge joins the point of attachment for the adductor muscles. <u>Right mandible</u>: From the base of the short incisor the lateral edge of the terebral ridge ends with a broadly rounded, small terebral tooth. The retinacular ridge produces a short, acute, conical tooth in the distal third of the mandible. The retinacular ridge curves mesally ending at the first groove separating the retinacular tooth from the premolar and the second groove separates the premolar and the molar tooth. The mandibles lack a basal brush.

Description of Proventriculus: The proventriculus is about twice as long as wide (1.1mm x 0.5mm) and comprises the primary folds with slightly raised ridges in-between. The anterior ends of the folds have short blunt, single, bidentate or tridentate teeth, in lieu of spines. These teeth occur across the end of the fold extending down its midline where at about 1/3 of the length of the fold the teeth transition to hairs (Fig, 23f, arrow). The ridges as well as the folds are covered in moderately long hairs that are posteriorly directed. The ridges are shorter than the primary folds. At the transition of the folds from the body to the neck the hairs are replaced by transverse lines of blunt erratic projections.

Gut contents: Most material in the stomodeum was gruel, but there were significant amounts of arthropod pieces, i.e., legs, compound eyes, spines, as well as plant material. See Table 4.

Figure 23. *Calathus gregarius*: a) dorsal view of head, b) lateral view of head, c) mandibles, d) external view of proventriculus, e) exposed internal surface of the proventriculus arrow indicating the field of heavier spines, f) close-up of multi-toothed spines of the anterior end of primary fold