



Mandibular structure, gut contents analysis and feeding group of orthopteran species collected from different habitats of Satoyama area within Kanazawa City, Japan

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Abstract: In a survey of orthopteran assemblages from different habitats of Satoyama area, Kanazawa City, Ishikawa Prefecture, Japan, 50 different species belonging to 10 families representing 17 subfamilies and 27 tribes were recorded. Seven feeding groups were proposed based on stereo microscopic examination of mandibular morphology and analysis of gut contents. Among the examined subfamilies, family Tettigonidae proved to be the most diverse in term of mandible types, with four feeding groups. This was followed by family Acrididae, which also possessed a variety of mandibular structures with three feeding groups. Other families contained only single feeding groups. It was noted that only five species were graminivorous, all were from the family Acrididae, with mandibles characterized by very short incisors and relatively wide molar regions. The gut contents of these five species contained more than 80% monocotyledonous plant species.

Keywords: Orthoptera, mandibular adaptations, gut contents analysis, feeding group, Satoyama area

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INTRODUCTION

The strong relationship with diet makes mouthpart morphology (Snodgrass 1935) an important trait for insect evolutionary biologists (Brues 1939) and systematists (Mulkern 1967). Isley (1944) was one of the first to study mouthparts in detail and correlate morphological characteristics with feeding habits. He described three groups of mandibles according to general structure and characteristic diet: (i) graminivorous (grass-feeding type) with grinding molars and incisors typically fused into a scythe-like cutting edge, (ii) forbivorous (forb or broadleaf plant-feeding type) which have a molar region consisting of a depression surrounded by raised teeth and sharp interlocking incisor teeth, and (iii) herbivorous (mixed feeding type) that have characteristics of both of the aforementioned groups.

The original findings on mandible groups by Isley (1944) have since proven to be widespread in grasshoppers and other insect taxa. Further studies have been conducted by many authors in different localities, significant among them are Snodgrass (1928), Gangwere (1965, 1966), Gangwere et al. (1976) and Patterson (1984) in North America; Liebermann (1968) and Gangwere & Ronderos (1975) in South America; Williams (1954), Kaufmann (1965), Gangwere & Morales (1973) in Europe; Gangwere & Spiller (1995) and Gangwere et al. (1998) in the Mediterranean islands; Feroz & Chaudhry (1975), Gapud (1968) and Kang et al. (1999) in Asia; and Chapman (1964) in Africa. A general method for determining the diet of an insect species begins with an examination of the morphology of the mandibular structure (Isely 1944; Mulkern 1967; Patterson 1984). The morphological characters of the mandibles, incisor and molar surfaces in particular, are useful in labeling species as grass- or forb-feeders (Chapman 1964; Bernays & Barbehenn 1987; Kang et al. 1999). Although most species with forb feeding mandibles feed on a mixture of grasses and forbs; determination of the diet of an insect should be followed by gut contents analysis for more confirmations (ElSayed 2005; ElShazly & ElSayed 2006).

Although often viewed as polyphagous herbivores, most orthopteran



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species, especially grasshoppers, are selective to some degree, exhibiting specific food preferences (Mulkern 1967). Occasionally, grasshoppers with forb-feeding mandibles regularly feed on grasses or vice versa (Chapman 1964). Nevertheless, there is some value in assessing mouthpart structure relative to predicting diet and habitat of the orthopteran species, especially for the many rare or non-economic species that are unlikely to be studied in details. Information concerning the feeding habits and mouthparts of different orthopteran species in Satoyama area, Kanazawa City, Ishikawa Prefecture, Japan are fragmentary (Ichikawa et al. 2006; ElSayed 2010) and there is a shortage of knowledge concerning the mandibular morphology of many orthopteran species inhabiting Satoyama. Thus, in this paper the morphological characteristics and structural adaptations of the mouthparts of 50 different orthopteran species co-occurring in Satoyama area and covering different habitat types were examined and tabulated.

MATERIALS AND METHODS

Study Area: The survey of orthopteran fauna was conducted among four sampling sites within Satoyama area of Kanazawa City, Ishikawa Prefecture, Japan (Image 1). Satoyama covers an area of ca. 74ha and is located at 150m altitude, 5km southeast from the

city center. The area comprises various habitat types ranging from secondary forests dominated by Konara (*Quercus serrata*), Abemaki (*Q. variabilis*), Moso Bamboo (*Phyllostachys pubescens*) and Japanese Cedar (*Cryptomeria japonica*) to grasslands dominated by the Bermuda Grass (*Cynodon dactylon*) and artificial ecosystems such as ponds, paddy fields and farmlands.

Collecting: The entomological sweep net sampling method was used for sampling orthopteran species from various habitats during different seasons. Sampling was done between 1000 and 1400 hr. Collected specimens were immediately killed and preserved in 70% ethanol in a 1l container secured with a rubber stopper. They were later identified, counted, sorted and kept in individual labeled glass vials in the laboratory. These vials could be stored in freezer for a year with no apparent damage to the specimens (Mulkern & Anderson 1959; Brusven & Mulkern 1960; ElSayed 2005).

Orthopteran species were identified following the taxonomic key offered by Ichikawa et al. (2006), specimens were also compared with known museum specimens in Kanazawa University for further confirmation.

Mandibular structure: Mandibles were removed from the specimens by lifting the labrum and pulling out each mandible separately with forceps. Only young adults were used in order to avoid confusion of mandible type due to mandible erosion (Chapman 1964; Uvarov 1977). This process was replicated with three individuals

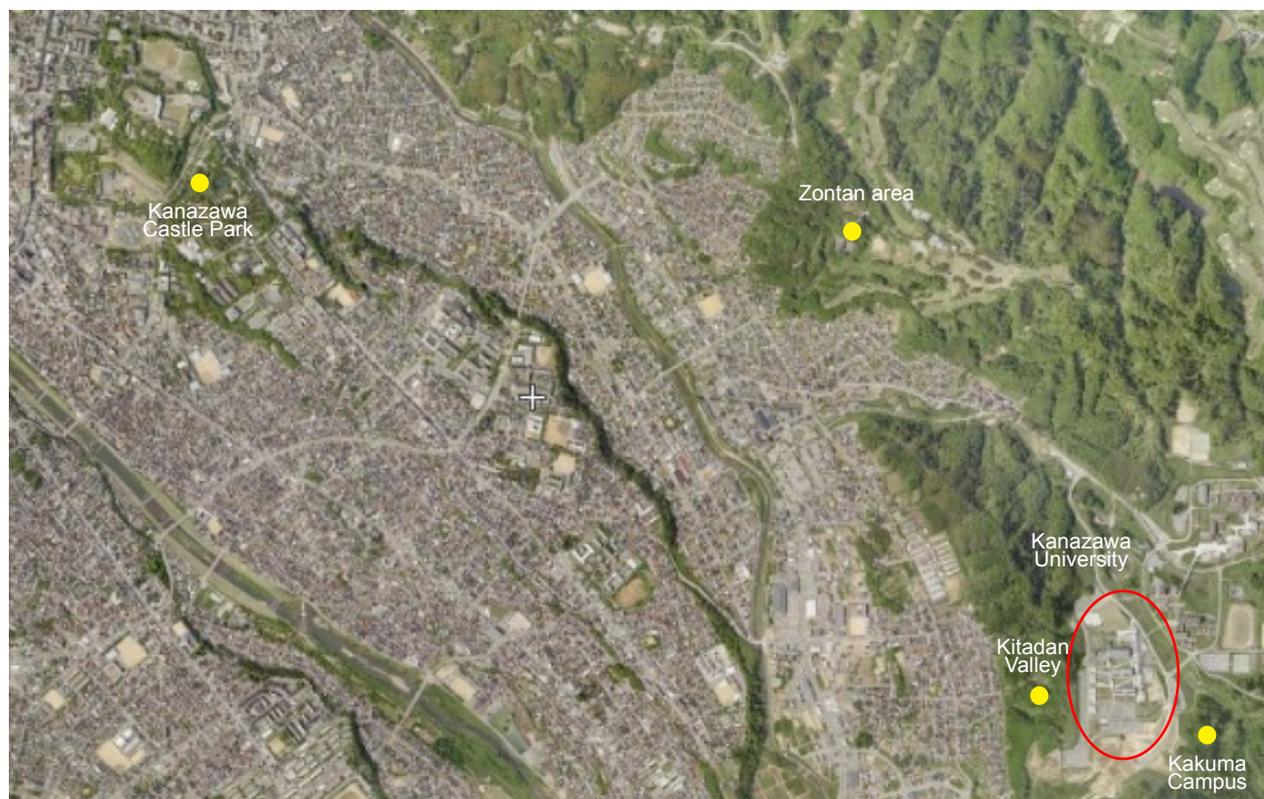


Image 1. Map of the study locations showing the four sampling sites in Satoyama. Area in red oval line is Kanazawa University

from each species. Mandibles were lightly brushed with 80% ethanol and distilled water to remove adherent sand and debris. After air-drying, each mandible was glued to the head of a #3 or #2 insect pin, depending on its size, for easier manipulation. The mandibular structure (with both ventral and dorsal sides) of 50 species of Orthoptera from 10 families (Acrididae, Eneopteridae, Gryllidae, Mecopodidae, Phaneropteridae, Pyrgomorphidae, Mantidae, Tetrigidae, Tettigoniidae and Trigonidae) was examined under a stereo fluorescence microscope (Nikon® SMZ800 series) equipped with digital camera and TFT LCD Nikon® monitor. Illumination source was provided by a double gooseneck Olympus® HLL-301 device. Photographs were taken with the Syncrosopy Auto-Montage system (Kanazawa University, Laboratory of Biodiversity).

We adopted Isley's (1944) description of mandible types and their adaptive functions, with the gut analysis technique, to divide the mandibles into seven major categories: Forbivorous (F), Herbivorous or Mixed-feeders (H), Graminivorous (G), Scavengers (S), Herbivorous with observed scavenging behavior (H_s), Forbivorous with scavenging behavior (F_s) and Predators (P). Detailed explanations of these groups are given hereafter in the methodology.

Field cages experiment: Live specimens were kept in wooden cages under natural environmental conditions and were provided with almost all available plant species recorded from the field to minimize the hunger-effect. Continual observations of feeding behavior were made for 3hr in three replicate field cages in each season of the year. Results from field cages were compared with those from mandibular morphology for confirmation concerning feeding group assignments.

Gut contents analysis and feeding groups: Gut contents analysis was performed to compare results with mandibular morphological features in an attempt to deduce the feeding group of each collected orthopteran species. Gut analysis technique was applied according to Mulkern & Anderson (1959), Ohabuiké (1979), Le Gall et al. (1998, 2003) ElSayed (2005), and ElShazly & ElSayed (2006) with slight modifications. Individuals were dissected and their midgut contents transferred to clean test tubes. The contents were digested by adding about 3ml of freshly prepared bleaching agent (1% W/V of sodium hypochlorate and 16.5% W/V of sodium chloride) for a period of 30 minutes (Ohabuiké 1979; ElSayed 2005). The solution discolored the chlorophyll and other ingested chitinous parts; distilled water was added after digestion to stop further bleaching action. The digested contents were transferred by pipette to petri dishes for microscopic examination of fragments, for which estimates were made of the proportions of different plant species, arthropod parts or other ingested particles. Characteristic features of fragments included hair, spines, serration, epidermal characteristics, orientation of the cells

and stomata. Qualitative records were made following ElSayed (2005). The proportions of four main categories (monocotyledonous plant species, dicotyledonous species, orthopteran or animal parts, and scavenging observations in caged species) were adopted to classify each orthopteran species into one of the proposed seven feeding group. These seven feeding groups are:

1. Herbivorous (H): in which the number of fragments of dicotyledonous plant is almost equal to the number of fragments of monocotyledonous species.

2. Herbivorous with scavenging behavior (H_s): the same as herbivorous group with some scavenging actions were recorded in laboratory caged species.

3. Graminivorous (G): The number of fragments of monocotyledonous species is more than 75% of the gut contents.

4. Forbivorous (F): the number of fragments of dicotyledonous plant species is more than 75% of the gut contents.

5. Forbivorous with scavenging behavior (F_s): the same as forbivorous group with some scavenging actions were recorded in laboratory caged species.

6. Scavengers (S): plants species (especially roots or tubers) and dead orthopteran and/or oligochaetan parts were encountered in almost equal proportions.

7. Predators (P): all contents of the gut were insect or other orthopteran body parts with no occurrence of plant fragments.

Collected orthopteran specimens were deposited in a catalogued repository in Kanazawa University in special boxes containing small sachets enclosing naphthalene coated tablets for further specimen protection against moths and other destructive pests.

RESULTS AND DISCUSSION

The mandibular structures of 50 orthopteran species, belonging to 10 families representing 17 subfamilies and 27 tribes, collected from different habitats of Satoyama area were stereomicroscopically examined. Species were sampled from different habitats including open grasslands, forest margins, ponds and paddy fields, and belonged to seven major feeding groups, with the results listed in Table 1. Among the examined subfamilies, family Tettigoniidae proved to be the most diverse in term of mandible types (four feeding groups). This was followed by family Acrididae which also possessed a variety of mandibular structures (three feeding groups). Other families contained only single feeding group (Table 2).

Species from the family Acrididae (Short-horned Grasshoppers) and family Tettigoniidae (Long-horned Grasshoppers) can be found in a wide range of habitats, usually in dense vegetation like open grasslands and around paddy fields or pond areas. They are quite active in both walking and flying. It is interesting to note that

Table 1. Check-list of orthopteran species inhabiting different habitats of Satoyama area with their family, subfamily, tribe and feeding group.

Family	Subfamily	Tribe	Acridid Species	Feeding group
Acrididae	Acridinae	Acridini	<i>Acrida cinerea</i>	G
		Parapleurini	<i>Stethophyma magister</i>	G
	Melanopilinae	Podismini	<i>Parapodisma mikado</i>	F
	Oedipodinae	Aiolopini	<i>Aiolopus thalassinus tamulus</i>	H
		Oedopodini	<i>Eusphingonotus japonicas</i>	F
		Locustini	<i>Oedaleus infernalis</i>	G
		Trilophidiini	<i>Trilophidia annulata</i>	G
Oxyinae	Oxyini	<i>Oxya yezoensis</i>	G	
Eneopteridae	Oecanthinae	Oecanthini	<i>Oecanthus simulator ichikawa</i>	F
Gryllidae	Gryllinae	Gryllini	<i>Acheta domesticus</i>	S
			<i>Loxoblemmus equestris</i>	S
			<i>Loxoblemmus sylvestris</i>	S
			<i>Loxoblemmus tsushimensis ichikawa</i>	S
			<i>Stethophyma magister</i>	S
			<i>Teleogryllus occipitalis</i>	S
			<i>Teleogryllus emma</i>	S
			<i>Velarifictorus asperses</i>	S
			<i>Velarifictorus mikado</i>	S
			<i>Velarifictorus ornatus</i>	S
		Modicogryllini	<i>Modicogryllus siamensis</i>	S
	Sclerogryllinae	Sclerogryllini	<i>Sclerogryllus punctatus</i>	S
Mecopodidae	Mecopodinae	Mecopodini	<i>Mecopoda niponensis</i>	F _s
Phaneropteridae	Phaneropterinae	Ducetini	<i>Ducetia japonica</i>	F _s
		Phaneropterini	<i>Phaneroptera falcate</i>	F _s
			<i>Phaneroptera nigroantennata</i>	F _s
Pyrgomorphidae	Pyrgomorphinae	Atractomorphi	<i>Atractomorpha lata</i>	F
Mantidae	Mantinae	Mantini	<i>Tenodera angustipennis</i>	P
			<i>Tenodera aridifolia</i>	P

Tetrigidae	Scelimeninae	Criotettigini	<i>Criotettix japonicas</i>	F
	Tetrigidae	Tetrigini	<i>Euparatettix tricarinatus</i>	F
			<i>Tetrix japonica</i>	F
			<i>Tetrix macilenta</i>	F
			<i>Tetrix minor ichikawa</i>	F
			<i>Tetrix nikkoensis</i>	F
			<i>Tetrix silvicultrix ichikawa</i>	F
Tettigoniidae	Conocephalinae	Conocephalini	<i>Conocephalus japonica</i>	F _s
			<i>Conocephalus melaenus</i>	F
		Copiphorini	<i>Euconocephalus varius</i>	F
			<i>Ruspolia dubia</i>	F _s
	Tettigoniinae	Decticini	<i>Chizuella bonneti</i>	F _s
			<i>Eobiana gradiella ishikawa</i>	H
			<i>Eobiana engelhardti subtropica</i>	F _s
		Gampsocleidini	<i>Gampsocleis Mikado</i>	H _s
	Hexacentrinae	<i>Hexacentrus japonicas</i>	H _s	
	Tettigoniinae	Tettigoniini	<i>Tettigonia orientalis</i>	F
<i>Tettigonia sp 6</i> ^{**}			F	
<i>Tettigonia sp 8</i>			F	
Trigonididae	Nemobiinae	Pteronemobiini	<i>Dianemobius furumagiensis</i>	S
			<i>Pteronemobius fascipes</i>	S
	Trigonidinae	Trigonidini	<i>Trigonidium pallipes</i>	S

*F - Forbivorous (Forb-feeder); H - Herbivorous (Mixed-feeder); G - Graminivorous (Grass-feeder); S - Scavengers; H_s - Herbivorous with observed scavenging behavior; F_s - Forbivorous with observed scavenging behavior; P - Predator; ** - Species 6 and 8 according to Ichikawa et al. (2006)

species belonging to these subfamilies, with graminivorous type mandibles, were characterized by extremely slender and elongated bodies and were encountered on the edges of ponds. This was in accordance with the findings of other authors (Isley 1944; Squitier & Capinera 2002; Smith & Capinera 2005). These grasshoppers typically grasp the stems of emergent grass or grass-like vegetation such as sedges or cattails, blending in almost perfectly. The Oedipodinae were split into three mandible types: graminivorous, forbivorous and herbivorous as stated by Capinera (2005). This signifies a more grass-dominated diet. However, these grasshoppers are much more divergent and some may be completely graminivorous or forbivorous. Most of the species in this subfamily were found on the ground in open areas on

bare soil, rarely on plants or grasses. As a general rule, the Oedipodinae show the greatest mandible diversity of among orthopteran subfamilies (Capinera 2005). Isley (1944), Gangwere (1966), and Kang et al. (1999) found a fairly even distribution of the three mouthpart types in this group.

Mantidae, on the other hand, were represented by only two tenoderan species (*Tenodera angustipennis* and *T. aridifloia*). These two species were completely predacious in their feeding habit, with mandibles characterized by sharp incisor points used to pierce and capture prey, and a long terebral ridge used to kill and slice prey into pieces. Gut contents analysis revealed fragments of chitinous arthropod exoskeleton and other body parts including wings, legs and antennae, confirming their zoophagous

Table 2. Number of families, subfamilies, tribes, species and feeding group of orthopteran species co-occurring in different habitats of Satoyama area.

Family	Number			
	Subfamilies	Tribes	Observed species	Feeding group
Acrididae	4	8	8	3
Eneopteridae	1	1	1	1
Gryllidae	2	3	12	1
Mecopodidae	1	1	1	1
Phaneropteridae	1	2	3	1
Pyrgomorphidae	1	1	1	1
Mantidae	1	1	2	1
Tetrigidae	2	2	7	1
Tettigoniidae	2	6	12	4
Trigonididae	2	2	3	1
Total	17	27	50	7

feeding behavior.

It was interesting to note that only five out of the 50 collected orthopteran species were graminivorous, all were from the family Acrididae. The mandibles of these 5 species were characterized by very short incisors and relatively wide molar region (Image 2). The molar area of some individuals of *Oxya yezoensis* (one of these five species), an example of severe erosion could be observed (Image 2). It has to be mentioned that, feeding on grasses could be one avenue by which grasshoppers may avoid toxic chemicals (Bernays & Chapman 1978; ElSayed 2005; ElShazly & ElSayed 2006). In this process, little or no energy, or other resources, would need to be spent on the detoxification process (Joern 1983). During the gut content analysis of these five graminivorous species silica particles were recorded in minor amounts. These silica particles could be ingested accidentally during feeding and accelerate the erosion of the molar area especially in old individuals.

The gut contents of these five species contained more than 80% monocotyledonous plant species. However, in the graminivorous species, *Acrida cinerea*, small amounts of dicotyledons (less than 12%) were also encountered. Hafez & Ibrahim (1958 a,b), ElSayed (2005) and ElShazly & ElSayed (2006) in their field and laboratory works on a related acridid, *Acrida pellucid*, found that this species may select non-graminous plants for enhancing its reproductive potential since some non-graminous plant species showed a pronounced effect on both fecundity and development in laboratory rearing and food-choice tests. It could be assumed that *Acrida cinerea* may utilize some dicotyledonous plant species for enhancing certain biological and physiological processes. In this study, the acridid species with the subfamily Acridinae are typically

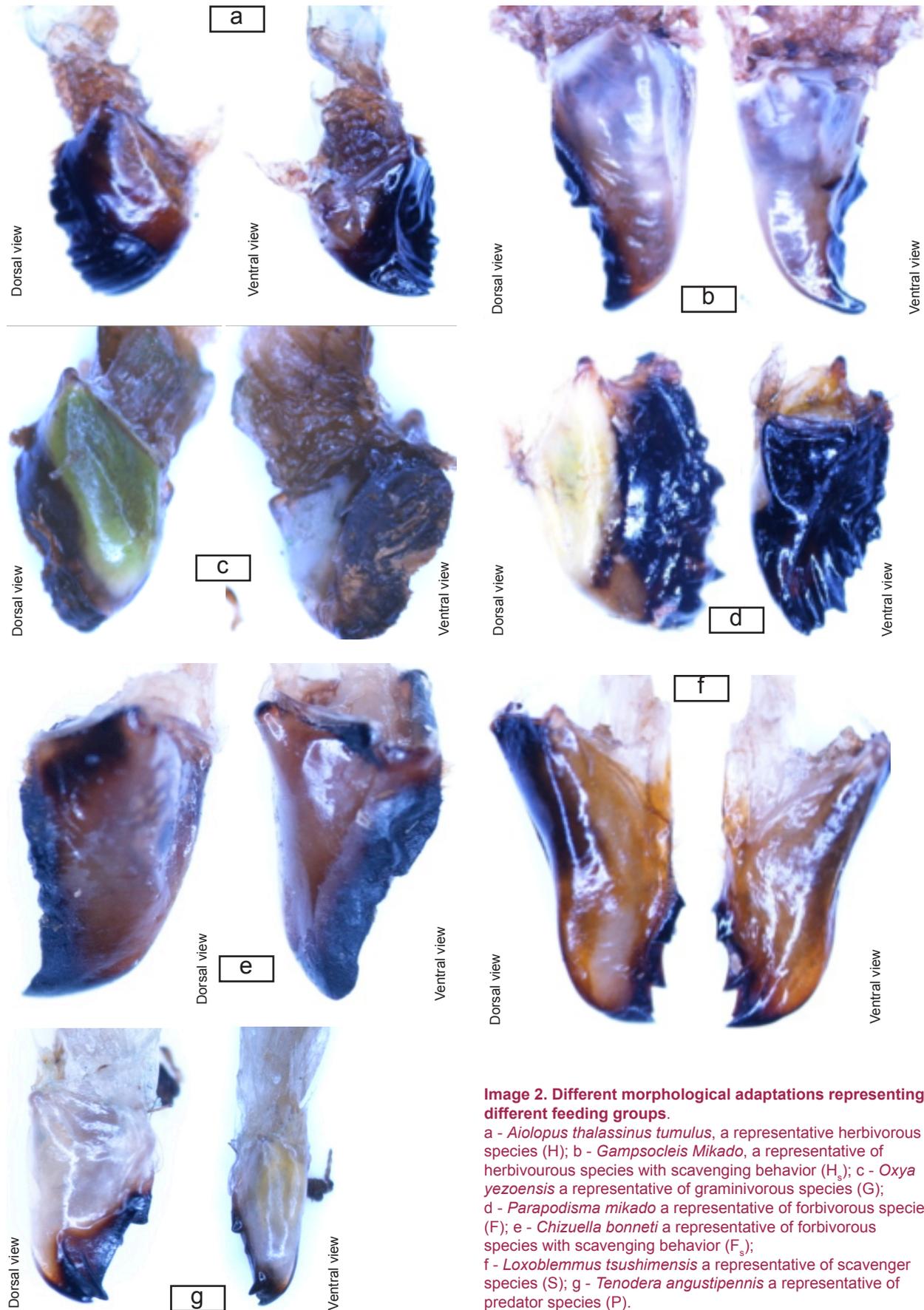
considered to be grass-feeders, displaying the classic graminivorous type mandibles (Isley 1944; Chapman 1964; ElSayed 2005).

Family Gryllidae, with 12 gryllid species, showed mandibles with sharp incisors and comparatively long knife-shape terebral ridge. These mandibular morphological modifications could delineate a predacious feeding habit, but the gut content analysis of these 12 species showed that parts from plant roots, tubers or even debris (38%) and subterranean arthropod species including amphipod and isopod species (62%) were collected from different gryllid species. As a consequence, the feeding group of these 12 gryllid species could be confined to the scavenging feeding habit.

The seven species of Tetrigidae were mainly forbivorous (F_m). Their mandibles were characterized by pointed and sharp incisor points and relatively small molar region (Image 2). The gut contents contained only dicotyledonous plan species.

Due to only one representative species from the subfamilies Eneopteridae, Mecopodidae and Pyrgomorphidae, determination of the mandibular morphology of these families was limited (Table 1). However, the major mandible type and in turn the feeding group was mostly confined to the forbivorous type where more dicotyledonous plants (79%) were consumed in much greater amount than monocotyledonous species as confirmed by gut contents analysis.

At the family level, it has to be mentioned that the family Tettigoniidae (12 species) was the most diverse for mandibular type and feeding group (four feeding groups). This was followed by family Acrididae (eight species) which harbor three feeding groups (Table 2). Other families possessed only a single feeding group



irrespective to the number of species (Table 2). From Table 2, it can be observed that both family Gryllidae and family Tetrigidae (12 and seven species, respectively) possessed only one type of mandible and a single feeding group for each family.

Cates (1980) proposed the following criteria to delineate the degree of diet specialization: (1) monophagy: one or more species within a genus; (2) oligophagy: two or more closely related genera, and (3) polyphagy: two or more plant families. However, none of the orthopteran species considered in this study can be considered either monophagy or oligophagy. In all cases, a range of food of plant and/or animal origin was used, even though some were used infrequently. Thus these orthopteran species inhabiting different habitats in Stoyama area could be considered polyphagous.

In conclusion, the relationship between orthopteran mouthparts and food is far from precise. Mulkern (1967) was convinced that only the grossest associations could be made between mandibular structure and diet (i.e., graminivorous, forbivorous, and herbivorous). Occasionally some orthopteran species, in particular grasshoppers with forb-feeding mandibles, regularly feed on grasses or vice versa (Chapman 1964; Elsayed 2005). Nevertheless, there is some value in assessing mouthpart structure as predictive of diet and habitat in orthopteran species, especially for the many rare or non-economic species that are unlikely to be studied in detail. Thus, the gut content analysis together with laboratory observations on feeding behavior were used either as a confirmation cues for the mandibular structural adaptations or add to our knowledge some hidden aspects that could not deduced from the morphological characters of the mandibles if they were treated alone.

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