

MANDIBULAR MORPHOLOGY OF SOME FLORIDIAN GRASSHOPPERS (ORTHOPTERA: ACRIDIDAE)

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The relationship between mouthpart structure and diet has been known for years. This connection between mouthpart morphology and specific food types is incredibly pronounced in the class Insecta (Snodgrass 1935). As insects have evolved and adapted to new food sources, their mouthparts have changed accordingly. This is an extremely important trait for evolutionary biologists (Brues 1939) as well as systematists (Mulkern 1967).

Isley (1944) was one of the first to study grasshopper mouthparts in detail. He described three groups of mandibles according to general structure and characteristic diet. These three groups, still used today, were graminivorous (grass-feeding type) with grinding molars and incisors typically fused into a scythe-like cutting edge, 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 herbivorous (mixed-feeding type) that have characteristics of both of the aforementioned groups. The original findings by Isley (1944) have since been proven to be widespread in grasshoppers. Additional studies have been conducted by Snodgrass (1928), Gangwere (1965, 1966), Gangwere et al. (1976), and Patterson (1984) in North America; Lieberman (1968) and Gangwere & Rondros (1975) in South America; Williams (1954), Kaufmann (1965), and 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.

The relationship between grasshopper mouthparts and food is far from precise. Mulkern (1967) was convinced that only the grossest determinations could be made between mandibular structure and diet (i.e., graminivorous, forbivorous, and herbivorous). 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 grasshoppers, especially for the many rare or non-economic species that are unlikely to be studied in detail. Thus, the morphological characteristics and structural adaptations of the mouthparts of 36 of the 71 grasshoppers occurring in Florida were examined.

Grasshoppers were collected from various habitats throughout north-central Florida in 2001 and 2002. Thirty-six of the most common Floridian grasshopper species were identified with the taxonomic key found in Smith et al. (2004) and fro-

zen until examination. Mandibles were removed from thawed specimens by lifting the labrum and pulling out each mandible separately with forceps. Only young adults were used in an effort to avoid confusion of mandible type due to mandible erosion (Chapman 1964; Uvarov 1977). An example of moderate erosion can be seen in Figure 1 (I). This process was replicated with 10 individuals from each species. After air-drying, each mandible was glued to the head of a #3 or #2 insect pin, depending on its size, for easier manipulation, and examined microscopically.

We used Isley's (1944) description of mandible types and their adaptive functions to divide the mandibles into 3 major categories: forbivorous (forb-feeding), graminivorous (grass-feeding), and herbivorous (mixed-feeding).

Mandibles were lightly brushed with 80 percent ETOH and distilled water in an effort to remove most of the sand and debris adhering to the mouthparts. Photographs were taken with the Syncroscopy Auto-Montage system (University of Florida, Entomology and Nematology Dept.).

The mandible structure of 36 species of grasshopper, from five subfamilies (Acridinae, Cyrtacanthacridinae, Gomphocerinae, Oedipodinae, and Romaleinae), found in Florida was microscopically examined. These grasshoppers were collected from a variety of habitats including disturbed freshwater marsh, high pine, swamp, and oak hammocks. All grasshoppers had distinctive mouthparts that could be described as forbivorous (forb-feeding type), herbivorous (mixed-feeding type), or graminivorous (grass-feeding type) (Fig. 1, A-L). A list of each species studied and the mandible type is given in Table 1.

Of the subfamilies examined, the Cyrtacanthacridinae demonstrated the most diversity in mandible type; however, most of them displayed either herbivorous or forbivorous mandibles, indicating a tendency toward forb-feeding. These grasshoppers can be found in a wide range of habitats, usually in dense vegetation or woodland areas, and are quite active in both walking and flying. It is interesting to note that both the grasshoppers in this subfamily that did display graminivorous type mandibles (*L. marginicollis* and *S. vitreipennis*) also have extremely slender, elongated bodies and can be found on the edges of ponds or in freshwater marshes (Isley 1944; Squitieri & Capinera 2002b; 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.

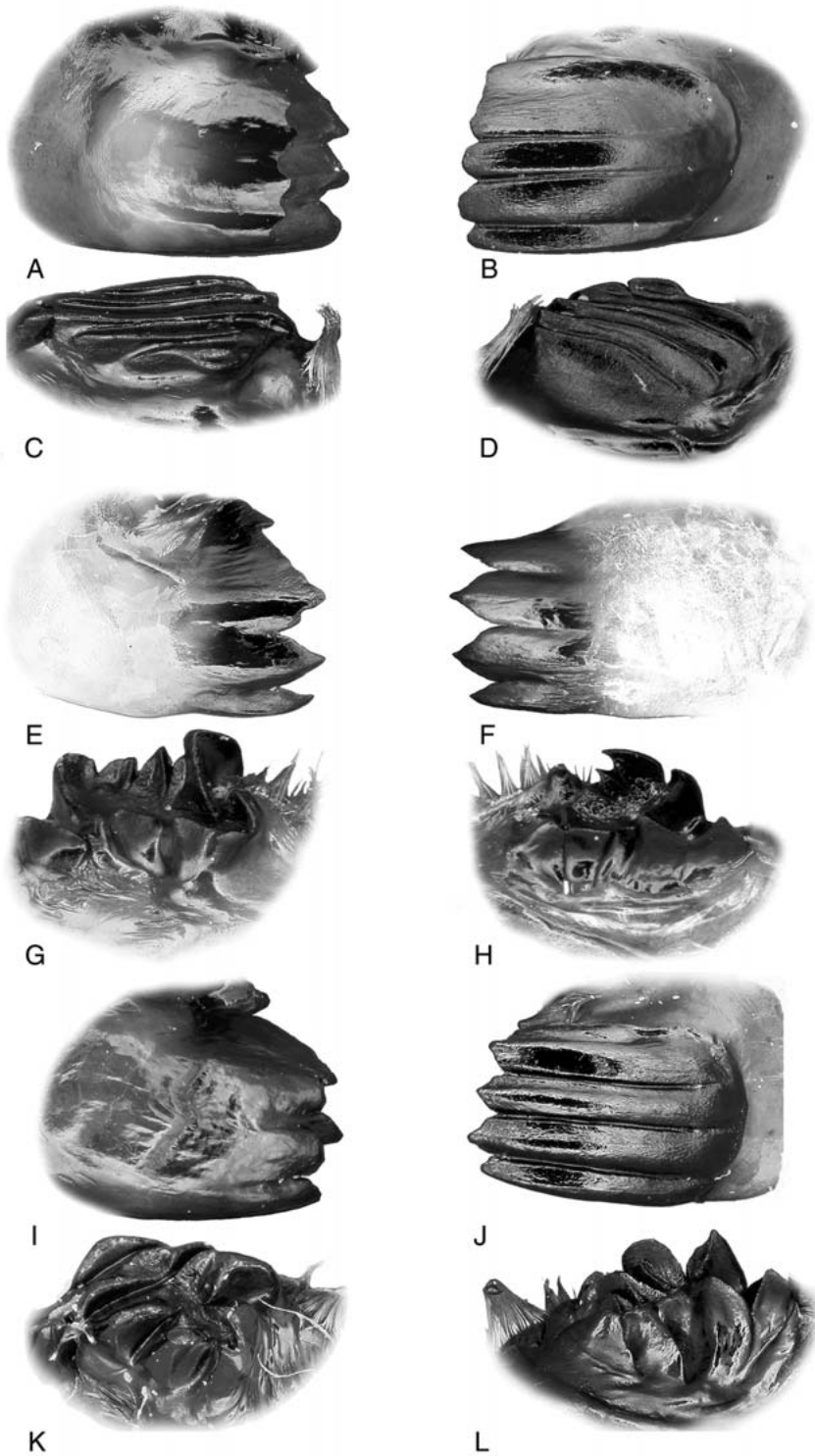


Fig. 1. Mandibles of *Amblytropidia mysteca*, a representative graminivorous species: right incisor region (A), left incisor region (B), right molar region (C), and left molar region (D); *Schistocerca ceratiola*, a representative forbivorous species: right incisor region (E), left incisor region (F), right molar region (G), and left molar region (H); and *Spharagemon cristatum*, a representative herbivorous species: right incisor region (I), left incisor region (J), right molar region (K), and left molar region (L).

TABLE 1. ACRIDID SPECIES EXAMINED AND THEIR MOUTHPART MORPHOLOGY.

| Graminivorous type mandibles | Herbivorous type mandibles | Forbivorous type mandibles |
|--|---|--|
| Acridinae | Cyrtacanthacridinae | Cyrtacanthacridinae |
| <i>Metaleptea brevicornis</i> (Johannson) | <i>Gymnoscirtetes pusillus</i> Scudder | <i>Aptenopedes aptera</i> Scudder |
| | <i>Melanoplus bispinosus</i> Scudder | <i>Aptenopedes sphenarioides</i> Scudder |
| Cyrtacanthacridinae | <i>Melanoplus sanguinipes</i> (Fabricius) | <i>Melanoplus keeleri</i> (Thomas) |
| <i>Leptysmia marginicollis</i> (Serville) | <i>Schistocerca alutacea</i> (Harris) | <i>Melanoplus ordwayae</i> Deyrup |
| <i>Stenacris vitreipennis</i> (Marschall) | <i>Schistocerca americana</i> (Drury) | <i>Melanoplus propinquus</i> Scudder |
| | <i>Schistocerca obscura</i> (Fabricius) | <i>Melanoplus punctulatus</i> Scudder |
| Gomphocerinae | <i>Schistocerca rubiginosa</i> (Scudder) | <i>Melanoplus querneus</i> Rehn & Hebard |
| <i>Achurum carinatum</i> (F. Walker) | | <i>Melanoplus rotundipennis</i> Scudder |
| <i>Amblytropidia mysteca</i> (Saussure) | Oedipodinae | <i>Melanoplus atlantica</i> Scudder |
| <i>Dichromorpha viridis</i> (Scudder) | <i>Chortophaga australior</i> (Rehn & Hebard) | <i>Paroxya clavuliger</i> (Serville) |
| <i>Eritettix obscurus</i> (Scudder) | <i>Spharagemon crepitans</i> (Saussure) | <i>Schistocerca ceratiola</i> Hubbell & Walker |
| <i>Mermiria intertexta</i> Scudder | <i>Spharagemon cristatum</i> (Scudder) | <i>Schistocerca damnifica</i> (Saussure) |
| <i>Orphulella pelidna</i> (Burmeister) | | |
| <i>Syrbula admirabilis</i> (Uhler) | | Romaleinae |
| | | <i>Romalea microptera</i> (Beauvois) |
| Oedipodinae | | |
| <i>Arphia granulata</i> (Saussure) | | |
| <i>Hippiscus ocelote</i> (Saussure) | | |
| <i>Pardalophora phoenicoptera</i> (Burmeister) | | |

However, the overwhelming majority of these grasshoppers display either herbivorous or forbivorous mandibles (Isley 1944; Gangwere 1965, 1966; Squitier & Capinera 2002a).

The Oedipodinae were split between two mandible types: graminivorous and herbivorous. 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 most mandible diversity of all the grasshopper subfamilies. Isley (1944), Gangwere (1966), and Kang et al. (1999) found a fairly even distribution of the three mouthpart types in this group.

The gomphocerinae all had graminivorous mandibles, indicating a consistent diet of grasses. These findings are reinforced by the preferred habitats of this subfamily, usually open grassy fields and pastures. Virtually all Gomphocerinae are graminivorous (Lockwood et al. 1994), or at least have graminivorous type mandibles. Occasionally a gomphocerine will display graminivorous type mandibles but feed entirely on forbs (Gangwere & Morales 1973); however, these are rare exceptions. In almost every study carried out on orthopteran mouthpart morphology, the Gomphocerinae display graminivorous type mandibles (Isley 1944; Gangwere 1965, 1966; Lockwood et al. 1994; Kang et al. 1999).

Due to only one representative species from both the subfamilies Acridinae and Romaleinae, determination of the mandibular morphology of

these subfamilies was limited. The Acridinae are typically considered to be grass-feeders, displaying the classic graminivorous type mandibles (Chapman 1964; Isley 1944). Very rarely a species in this subfamily will display herbivorous type mandibles (Chapman 1964). The Romaleinae are always forb feeders and always display forbivorous type mandibles (Isley 1944; Squitier & Capinera 2002a; Smith & Capinera 2005).

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SUMMARY

Mouthpart consistency within subfamilies indicates that evolution is just as important as ecological factors in determining food plants; for most subfamilies there is a strong association with a particular form of vegetation. It is evident that the ability, or tendency, of grasshoppers to change hosts is partly limited by the structure of their mandibles. However, because there are exceptions to the strong association of cyrtacanthacridines with forbs, and gomphocerines with grasses, we see evidence that behavioral plasticity or ecological opportunism is present even in relatively primitive taxa such as Orthoptera.

REFERENCES CITED

- BRUES, C. T. 1939. Food, drink, and evolution. *Science* 90: 145-149.

- CHAPMAN, R. F. 1964. The structure and wear of the mandibles in some African grasshoppers. *Proc. Zool. Soc. London* 142: 107-121.
- CHAPMAN, R. F. 1966. The mouthparts of *Xenocheila zarudnyi*. *J. Zool.* 148: 277-288.
- FEROZ, M., AND M. A. CHAUDHRY. 1975. Studies on mandibles of some grasshoppers of Lahore. *Biologia (Lahore)* 21: 211-225.
- GANGWERE, S. K. 1965. Food selection in the Oediponidae grasshopper *Arphia sulphurea*. *American Midl. Nat.* 74: 67-75.
- GANGWERE, S. K. 1966. Relationships between mandibles, feeding behavior and damage inflicted on plants by the feeding of certain acridids (Orthoptera). *Michigan Entomol.* 1:13-16.
- GANGWERE, S. K., F. C. EVANS, AND M. L. NELSON. 1976. The food habits and Biology of Acrididae in an old-field community in Southeastern Michigan. *Great Lakes Entomol.* 9: 83-123.
- GANGWERE, S. K., J. C. MCKINNEY, M. A. ERNEMANN, AND R. G. BLAND. 1998. Food selection and feeding behavior in selected Acridoidea (Insecta: Orthoptera) of the Canary Islands, Spain. *J. Orth. Res.* 7: 1-21.
- GANGWERE, S. K., AND A. MORALES. 1973. Food selection and feeding behaviour in Iberian Orthopteroidea. *An. Inst. Nac. Invest. Agrar., Ser. Prot. Veg. Num.* 3: 251-337.
- GANGWERE, S. K., AND R. A. RONDEROS. 1975. A synopsis of food selection in Argentine Acridoidea. *Acrida* 4: 173-194.
- GANGWERE, S. K., AND D. O. SPILLER. 1995. Food selection and feeding behavior in selected Orthoptera sen. lat. of the Balearic Islands, Spain. *J. Orth. Res.* 4: 147-160.
- GAPUD, V. P. 1968. The external morphology of the head and mouthparts of some Philippine Orthoptera. *Philippine Entomol.* 1: 11-32.
- ISLEY, F. B. 1944. Correlation between mandibular morphology and food specificity in grasshoppers. *Ann. Entomol. Soc. Am.* 37: 47-67.
- KANG, L., Y. GAN, AND S. L. LI. 1999. The structural adaptation of mandibles and food specificity in grasshoppers on Inner Mongolian grasslands. *J. Orth. Res.* 8: 257-269.
- KAUFMANN, T. 1965. Biological studies on some Bavarian Acridoidea (Orthoptera), with special reference to their feeding habits. *Ann. Entomol. Soc. Am.* 58: 791-801.
- LIEBERMANN, J. 1968. The mandibles of grasshoppers of the subfamily Chilacridinae. *Rev. Invest. Agropecu., Patol. Veg. Ser.* 5: 53-62.
- LOCKWOOD, J. A., H. C. LI, J. L. DODD, AND S. E. WILLIAM. 1994. Comparison of grasshopper (Orthoptera: Acrididae) ecology on the grasslands of the Asia steppe in Inner Mongolia and the Great Plains of North America. *J. Orth. Res.* 2: 4-14.
- MULKERN, G. B. 1967. Food selection by grasshoppers. *Annu. Rev. Entomol.* 12: 59-78.
- PATTERSON, B. D. 1984. Correlation between mandibular morphology and specific diet of some desert grassland Acrididae (Orthoptera). *American Midl. Nat.* 111: 296-303.
- SMITH, T. R., J. G. FROEBA, AND J. L. CAPINERA. 2004. Key to the grasshoppers (Orthoptera: Acrididae) of Florida. *Florida Entomol.* 87: 537-550.
- SMITH, T. R., AND J. L. CAPINERA. 2005. Host preferences and habitat associations of some Florida grasshoppers (Orthoptera: Acrididae). *Environ. Entomol.* 34: 210-224.
- SNODGRASS, R. E. 1928. Morphology and evolution of the insect head and its appendages. *Smithsonian Misc. Coll.* 81: 1-158.
- SNODGRASS, R. E. 1935. *Principles of Insect Morphology*. McGraw-Hill. New York. 667 pp.
- SQUITIER, J. M., AND J. L. CAPINERA. 2002a. Host selection by grasshoppers (Orthoptera: Acrididae) inhabiting semi-aquatic environments. *Florida Entomol.* 85: 336-340.
- SQUITIER, J. M., AND J. L. CAPINERA. 2002b. Habitat associations of Florida grasshoppers (Orthoptera: Acrididae). *Florida Entomol.* 85: 235-244.
- UVAROV, B. 1977. Grasshoppers and locusts. *A Handbook of General Acridology*, Vol. 2, Cambridge, United Kingdom. 613 pp.
- WILLIAMS, L. H. 1954. The feeding habits and food preferences of Acridinae and the factors which determine them. *Trans. R. Entomol. Soc. London* 105: 423-454.