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Predominantly Left-Dominant Mandibular Chirality in Coleoptera

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Abstract

Patterns of mandible chirality have been virtually unexplored in beetles, apart from a single study in 2010. Here we present the mandible chirality trends found in 58 beetle species representing the families Carabidae (52 species), Cerambycidae (three species), and Silphidae (three species) that display overlapping mandibles. Mandible chirality was not random in the groups examined, all of which exhibited a dominant trend towards left-superiority. The degree to which each taxonomic group displayed the left-superior trend differed, with tiger beetles showing the greatest dominance (99%) and longhorned beetles the weakest (71%).

Key Words: morphology, mouthparts, mandible, "handedness", dentition, Carabidae, Cerambycidae, Silphidae

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Beetles display enormous diversity in feeding habits, but all possess chewing mouthparts (Triplehorn and Johnson 2005) adapted to different feeding methods. For example, some beetles feed by clipping bits of vegetation. In such cases, mandibles that meet directly are common. Other beetles, particularly predaceous species, often have mandibles that overlap rather than meet directly. In addition to feeding, many male beetles utilize their mandibles to grasp females during mating (Triplehorn and Johnson 2005). Thus, at least two major factors likely affect selection pressure in regard to mandible alignment in beetles.

Despite selection for different mandible orientation, very little research on this exists for insects in general. Crowson (1981) mentions that in most beetles the tip of one mandible overlaps the other, but does not present information about which crosses which. Richardson (2010) showed a strong chirality trend in the tiger beetles *Omus audouini* Reiche and *Omus dejeani* Reiche, both of which usually exhibited left-superiority, *i.e.*, the left mandible crossing over the right mandible. We are not aware of any other published study on this subject in beetles. The benefit of overlapping mandibles in predaceous beetles is unclear. However, the mandibles in such species also tend to be slightly curved inward at the tips, have prominent dentition, or both. The mechanism of mandible crossing also has not been examined in detail, nor has the ability of individuals to control which mandible crosses over the other. Nevertheless, overlap of mandibles may help to minimize wear (Richardson 2010) and improve the maceration efficiency. Mandible overlap may also be important in mating of species such as tiger beetles where males guard mates by grasping the female metathoracic copulatory sulcus with the mandible (Freitag 1974). Sexual dimorphism of tiger beetle mandibles has been documented (*e.g.*, Kritsky and Simon 1995), but mandible overlap was not examined.

Museum specimens allow an opportunity to examine mandible overlap. Preliminary examination of hundreds of specimens within the tiger beetle genus *Cicindela* Linnaeus (*sensu lato*) showed a pattern consistent with the findings of Richardson (2010). Thus, we hypothesized that mandibular chirality in predaceous beetles is not random and is consistent within taxonomic groups.

Material and Methods

Data were gathered from the insect collection at Chadron State College as well as the personal tiger beetle collection of the first author. In larger species and those with large mandibles (*i.e.*, most tiger beetles), mandibular chirality, defined as crossing of the tips of the mandibles, was determined

Table 1. List of taxa examined, including the number of specimens showing left-superiority in mandible chirality (Left) or right-superiority (Right), the total number of each species examined (*n*), and the proportion of each species' cohort showing left-superiority in mandible chirality.

Carabidae: Cicindelinae	**Left**	**Right**	***n***	**Proportion left-dominant**
Amblycheila cylindriformis Say	22	0	22	1.0000
Omus californicus Eschscholtz	35	0	35	1.0000
Omus audouinii Reiche	6	0	6	1.0000
Omus submetallicus G. Horn	2	0	2	1.0000
Omus dejeani Reiche	9	0	9	1.0000
Tetracha virginica (Linnaeus)	51	0	51	1.0000
Tetracha carolina (Linnaeus)	34	0	34	1.0000
Chaetodera regalis (Dejean)	12	0	12	1.0000
Cicindela sylvatica Linnaeus	14	0	14	1.0000
Cicindela granulata Gebler	7	0	7	1.0000
Cicindela soluta Dejean	16	0	16	1.0000
Sophiodela chinenesis DeGeer	7	0	7	1.0000
Cicindela nebraskana Casey, *C. longilabris* Say, and hybrids	330	0	330	1.0000
Cicindela repanda Dejean	683	1	684	0.9985
Cicindela duodecimguttata Dejean	170	0	170	1.0000
Cicindela oregona Dejean	111	0	111	1.0000
Cicindela hirticollis Say	357	0	357	1.0000
Cicindela limbata Say	266	0	266	1.0000
Cicindela bellissima Leng	9	0	9	1.0000
Cicindela formosa Say	1,061	1	1,062	0.9991
Cicindela purpurea Olivier	741	0	741	1.0000
Cicindela splendida Hentz	490	1	491	0.9980
Cicindela denverensis Casey	379	0	379	1.0000
Cicindela limbalis Klug	561	0	561	1.0000
Cicindela decemnotata Say	45	0	45	1.0000
Cicindela sexguttata Fabricius	596	0	596	1.0000
Cicindela denikei Brown	107	0	107	1.0000
Cicindela patruela Dejean	183	0	183	1.0000
Cicindela pulchra Say	168	0	168	1.0000
Cicindela fulgida Say	343	0	343	1.0000
Cicindela parowana Wickham	9	0	9	1.0000
Cicindela scutellaris Say	934	1	935	0.9989
Cicindela tranquebarica (Herbst)	608	0	608	1.0000
Cicindela ancocisconensis (T. W. Harris)	11	0	11	1.0000
Cicindela lengi (Horn)	264	0	264	1.0000
Cicindelidia willistoni (LeConte)	82	0	82	1.0000
Cicindelidia schauppii (G. H. Horn)	9	0	9	1.0000
Cicindelidia punctulata (Olivier)	780	1	781	0.9987
Cicindelidia obsoleta (Say)	24	0	24	1.0000
Cicindelidia ocellata (Klug)	23	0	23	1.0000
Cicindelidia sedecimpunctata (Klug)	15	0	15	1.0000
Habroscelimorpha circumpicta (LaFerté-Sénectère)	148	0	148	1.0000
Cylindera terricola (Say)	116	0	116	1.0000
Ellipsoptera wapleri (LeConte)	10	0	10	1.0000
Ellipsoptera cuprascens (LeConte)	66	0	66	1.0000
Dromochorus pruinina (Casey)	3	0	3	1.0000
Carabidae: non-Cicindelinae				
Pasimachus elongatus LeConte	31	0	31	1.0000
Calosoma luxatum Say	7	1	8	0.8750
Calosoma callidum (Fabricius)	32	12	44	0.7273
Harpalus pennsylvanicus (DeGeer)	5	0	5	1.0000
Chlaenius sp. (purple)	13	3	16	0.8125
Chlaenius sp. (green)	4	0	4	1.0000

Continued on next page

Table 1. Continued.

	Left	Right	*n*	Proportion left-dominant
Silphidae				
Nicrophorus marginatus Fabricius	169	11	180	0.9389
Nicrophorus carolinus (Linnaeus)	229	18	247	0.9271
Nicrophorus obscurus Kirby	5	0	5	1.0000
Cerambycidae				
Tetraopes femoratus LeConte	16	4	20	0.8000
Tetraopes tetraphthalamus (Forster)	37	24	61	0.6066
Tetraopes annulatus LeConte	24	3	27	0.8889

through naked eye observation, otherwise chirality was determined using a dissecting scope. A total of 10,575 specimens representing 58 species in the beetle families Carabidae (52 species, 46 being tiger beetles (subfamily Cicindelinae)), Silphidae (three species of *Nicrophorus* Fabricius), and Cerambycidae (three species of *Tetraopes* Dalman) were examined in this study. For each specimen, the chirality was observed and recorded based on which mandible was superior, thus, each specimen was recorded as either right-superior or left-superior. Specimens with mandibles open were not included.

Results

Mandibular chirality was found to be non-random in all beetle groups examined, with all species and groups exhibiting a strong trend toward left-superior chirality (Table 1). However, the dominance of left-superiority differed among beetle groups. For example, all but five of the 9,922 tiger beetle specimens examined displayed left-superiority; the five specimens not displaying left-superiority each represented a single individual of different species. Thus, 41 of 46 tiger beetle species exhibited 100% left-superiority. In contrast, left-superiority in non-tiger beetle Carabidae averaged 90% (range = 73–100%) (Table 2). Left-superiority in *Nicrophorus* spp. (Silphidae) averaged 96% (range = 93–100%), while in *Tetraopes* spp. (Cerambycidae) it averaged only 77% (range = 61–89%).

Discussion

The trends observed in mandibular chirality in this study suggest that 1) mandibular chirality in beetles with overlapping mandibles is not random and 2) left-superior chirality is dominant but to differing degrees among beetle groups. In tiger beetles, the left-superior state was observed in more than 99% of specimens examined, including more than 9,900 specimens representing 46 species in 11 genera. Left-superiority was also dominant in non-tiger beetle Carabidae (average 90%), Silphidae (average 96%), and Cerambycidae (77%). These three beetle families are distantly related to each other and represent two different suborders, suggesting that left-dominant mandibular chirality may be common throughout the order. Differences in left-superiority could relate to sex, though it was untested in this study and would be expected to result in close to 50:50 ratios. None of the right-superior specimens were noticeably teneral.

The results of our study suggest that mandibular chirality in beetles with overlapping mandibles may be a fixed genetic character that is not controlled by the individual beetle. Additional questions that warrant further investigation include: 1) whether the left-superior trait is a conserved trait that has only evolved once in beetles or has evolved independently more than once; 2) which genes are involved in mandibular chirality and whether they influence other physical traits, most significantly mandibular asymmetry; 3) what other physical modifications are influenced by mandibular chirality, for example, whether one mandible is positioned higher than the other or the head also exhibits asymmetry; 4) if the degree of mandibular dentition or curvature is correlated with degree of mandibular chirality; and 5) what is the interaction in selection pressures on mandible

Table 2. Proportion of specimens per broad taxonomic group showing left-superiority in mandible chirality. *n* = number of specimens examined within each group (n).

Group	Proportion left-dominant	*n*
Carabidae: Cicindelinae	0.9994	9,922
Carabidae: non-Cicindelinae	0.8518	108
Silphidae	0.9329	432
Cerambycidae	0.7130	108

shape for feeding in both sexes versus mate grasping by males.

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References Cited

Crowson, R. A. 1981. The Biology of the Coleoptera. Academic Press, New York, NY.

Freitag, R. 1974. Selection for a non-genitalic mating structure in female tiger beetles of the genus *Cicindela* (Coleoptera: Cicindelidae). The Canadian Entomologist 106: 561–568.

Kritsky, G., and S. Simon. 1995. Mandibular sexual dimorphism in *Cicindela* Linnaeus (Coleoptera: Cicindelidae). The Coleopterists Bulletin 49(2): 143–148.

Richardson, R. K. 2010. Mandibular chirality in tiger beetles. The Coleopterists Bulletin 64(4): 386–387.

Triplehorn, C. A., and N. F. Johnson. 2005. Borror and DeLong's Introduction to the Study of Insects, 7th Edition. Thompson Brooks/Cole, Belmont, CA.

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