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GEOGRAPHICAL DISTRIBUTION AND BIOLOGICAL  
OBSERVATIONS OF *CYPHODERRIS*  
(ORTHOPTERA: HAGLIDAE)  
WITH A DESCRIPTION OF A NEW SPECIES

BY GLENN K. MORRIS<sup>1</sup> AND DARRYL T. GWYNNE<sup>2</sup>

## INTRODUCTION

With the exception of *Prophalangopsis obscura* (F. Walker) from India, *Cyphoderris* are sole survivors of a primitive orthopteran family, the Haglidae, abundant in the Triassic and ancestral to modern Ensifera (Zeuner, 1939; Ander, 1939; Ragge, 1955; Sharov, 1968).

There are presently two recognized species of *Cyphoderris*: *C. monstrosa* Uhler and *C. buckelli* Hebard. Their most dramatic distinguishing feature is the presence in *C. monstrosa*, and the absence in *C. buckelli*, of a prominent ventrally-directed sternal process, shaped like the claw of a hammer and located on the IXth sternum (Hebard, 1934). Specimens of both species have been extensively collected from mountainous areas of the North American northwest.

When Uhler established *Cyphoderris* in 1864 he had before him two adult male specimens. He published body measurements for both of these and there is a substantial size difference e.g. body length 22 mm for one specimen and only 16 mm for the other. These specimens are in the Museum of Comparative Zoology, Harvard University and we have examined them. The larger has a prominent

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<sup>1</sup>Erindale College and Department of Zoology, University of Toronto, Mississauga, Ontario, L5L 1C6, Canada.

<sup>2</sup>Department of Zoology and Entomology, Colorado State University, Fort Collins, Colorado, 80523, U.S.A.

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sternal process and is *C. monstrosa* of present usage; the smaller specimen lacks the process and is *C. buckelli* of Hebard. It is the *C. buckelli* specimen which bears a red 'Type 792' label. Uhler's description concentrates on the larger specimen. Thus *monstrosa* is said to have a "pointed keel-like elevation, projected backwards upon the segment, grooved and emarginated at tip", i.e. a sternal process. He does not indicate that such a structure is absent from the other specimen.

Caudell (1904) described a variety of *C. monstrosa* which he called *Cyphoderris monstrosa piperi*. His types, which we have seen, are a male and a female from Mt. Rainier, Washington, housed in the U.S. National Museum. The male has a sternal process identical with that of Uhler's larger specimen and the female has Ander's organs (see below).

In 1922 Fulton collected a series of males in Oregon about 30 mi. southwest of Crater Lake (Fulton, 1930). He compared these with specimens furnished him by E. R. Buckell from southern British Columbia and found that Buckell's specimens lacked a genitalic process. Drawings were sent to Nathan Banks and to Caudell who compared them with the types of *monstrosa* and *piperi*.

It might now have become apparent that Uhler's types differed in their genitalia and that only the larger was of the same species as *piperi*. Since the published description applied substantially to the larger specimen one would then have expected it to be designated as *monstrosa*. But for some reason *piperi* was given specific status by Fulton and applied to the taxon with the sternal process while Uhler's name was conferred upon the smaller of Uhler's two species. Probably it was at this point that the red type label was appended at Harvard.

Hebard (1934), responding to Uhler's published description, recognized *piperi* as a synonym of *monstrosa* and gave the name *buckelli* to the species without the sternal process. It is clear that he did not examine Uhler's types and was unaware that one of these was his new species. Uhler did not designate a holotype and so in accordance with Article 74 of the code and in the interest of taxonomic stability, we here designate as lectotype the larger of the two specimens in his type series, that possessing the sternal process. This ensures that application of the name *monstrosa* continues in conformity with present custom.

A third species of *Cyphoderris*, *C. strepitans*, is described here. Its distribution lies southeast of both *monstrosa* and *buckelli* (Figure 5), populations of *strepitans* being originally considered as southern range extensions of *monstrosa* (Alexander, 1935; Willey and Willey, 1963). *C. strepitans* appears to be most similar in morphology and calling song to *buckelli* but is readily distinguished from the latter species by the structure of the male terminalia.

We have made use of the following abbreviations: ROM/ Royal Ontario Museum, Toronto, Canada; UMMZ/ University of Michigan, Museum of Zoology, Ann Arbor; ANSP/ Academy of Natural Sciences, Philadelphia; CNC/ Canadian National Collection, Ottawa, Canada; MCZ/ Museum of Comparative Zoology, Harvard University; USNM/ National Museum of Natural History, Smithsonian, Washington, D.C.

### ***Cyphoderris strepitans* new species**

Figures 1 and 2

The specific name refers to the calling song: *strepitans* (Latin) 'making a great noise'.

#### SYNONYMY:

*Cyphoderris monstrosus*, Thomas (not Uhler), 1876. Proc. Davenp. Acad. Nat. Sci. 1, p. 263. Wind River, Wyo.

*Cyphoderris monstrosa*, Hebard (in part not Uhler), 1934. Trans. Am. ent. Soc. 59, p. 374. Pearl, Col.

*Cyphoderris monstrosa*, G. Alexander (not Uhler) 1935. Ent. News 46, p. 30. Park Range (Pearl) Col.; *ibid* 1941. Univ. Col. Studies 1, p. 136.

*Cyphoderris monstrosa*, Willey & Willey (not Uhler) 1963. Ent. News 74, p. 200. Los Pinos Pass, Col.

*Cyphoderris monstrosa*, Evans (not Uhler) 1970. Bull. Mus. Comp. Zool. Harv. 140, p. 484. Jackson Hole, Wyo.

**HOLOTYPE.** Adult o. Park Range 24.7 mi. west of Cowdrey via Pearl, nr Big Creek Lakes, Jackson Co., Col., U.S.A.; 19 June 1976; Coll. G. K. Morris & D. T. Gwynne (Deposited ROM).

**DESCRIPTION OF MALE TYPE.** Body length (fastigium to paraprocts in dorsal view) 18.6 mm; pronotum mid-line length 7.2 mm; caudal pronotum width 7.8 mm; maximum exposed tegminal length in dorsal view 8.2 mm; length in lateral view of left metathoracic femur 8.3 mm.

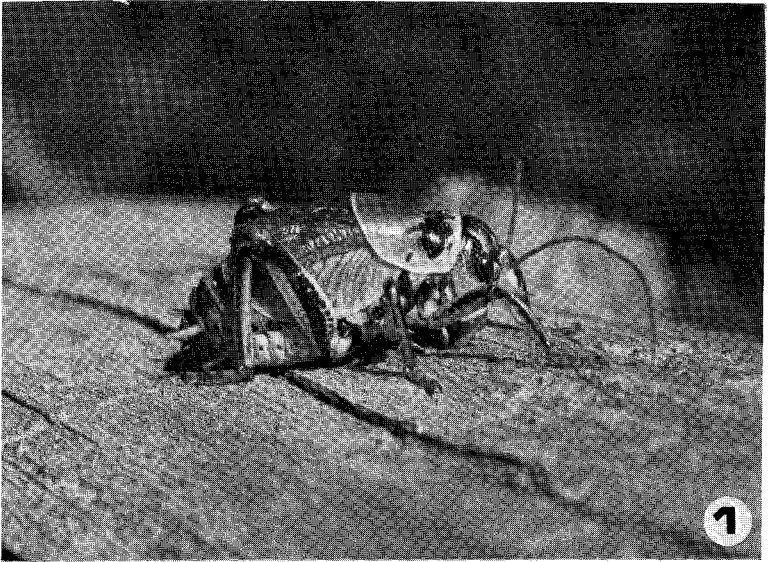


Figure 1. Adult male *C. strepitans*.



Figure 2. Adult female *C. strepitans* (both antennae broken).

ALLOTYPE. Adult ♂. Los Pinos Pass, Saguache Co., Col., U.S.A.; 17 June 1977; Coll. D. T. Gwynne (Deposited ROM).

DESCRIPTION OF FEMALE ALLOTYPE. Body length (fastigium to extremity of epiproct in dorsal view) 21.5 mm; pronotum mid-line length 5.9 mm; caudal pronotum width 5.4 mm; length of ovipositor 2.0 mm; length in lateral view of left metathoracic femur 9.6 mm.

DIAGNOSIS. Adult males of *strepitans* are similar in size and coloration to *buckelli*, but readily distinguished by the presence of the sternal process (Figures 3 & 4). Males of both *strepitans* and *buckelli* are generally smaller than males of *monstrosa*. In life they usually lack the vivid pink coloration of *monstrosa*'s venter, their venters being instead cream white. The styli of the IXth sternum are strongly depressed in *monstrosa*; viewed from above each stylus is sublanceolate and broadest at its base; they are inserted on the lamellate dorsal projection of the IXth sternum at a distance slightly greater than the stylus length. By contrast the styli of *strepitans* are distally dilated and broadly rounded (mitten-like), gently arcuate and tapering slightly to the base; they are inserted close together immediately adjacent to the mid-line with less than one stylus length between their bases.

The sternal process of *monstrosa*, viewed in lateral outline, follows a broadly concave arc beyond the base of the styli to where it turns abruptly downward; in *strepitans* this arc is shorter and much shallower. From the end of the arc the process of *monstrosa* is more strongly reflexed than in *strepitans* and is often bent sharply forward at its extremity.

We are unable at present to distinguish between females of *buckelli* and *strepitans* but both of these species may be separated from *monstrosa* by their lack of the 'stridulatory' organs of Ander (1938). In *C. monstrosa* these structures are located dorsolaterally at the junction of abdomen and thorax (Ander, 1938; Kevan, 1954; Dumortier, 1963). Each organ consists of a row of robust posteriorly-directed recurved teeth on the slightly swollen posterolateral edge of the metanotum. The teeth contact a patch of transverse ridges on the first abdominal tergite during telescoping of the abdominal segment. Ander's organs are present in both sexes and are readily seen in later stadia of immatures. While *buckelli* sometimes possesses weak thoracic teeth, it never exhibits the ridged

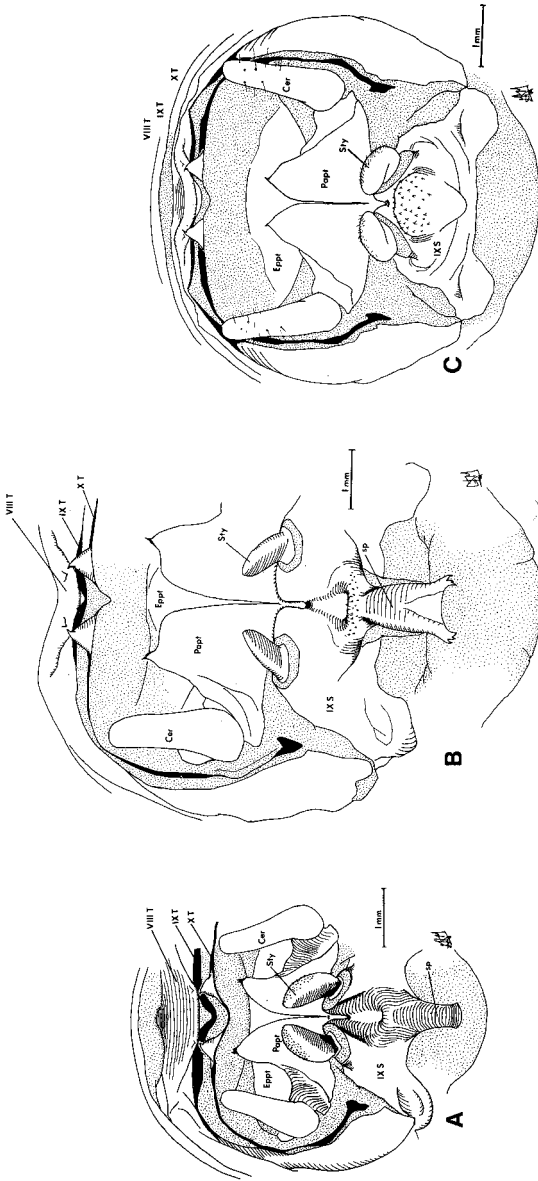


Figure 3. Posterior views of terminalia, A) *C. strepitans*, B) *C. monstrosa*, and C) *C. buckelli*. Symbols: VIII T, 8th tergum; IX T, 9th tergum; XT, 10th tergum; Cer, cercus; Eppt, epiproct; Papt, paraproct; Sty, stylus; IX S, 9th sternum; sp, sternal process.

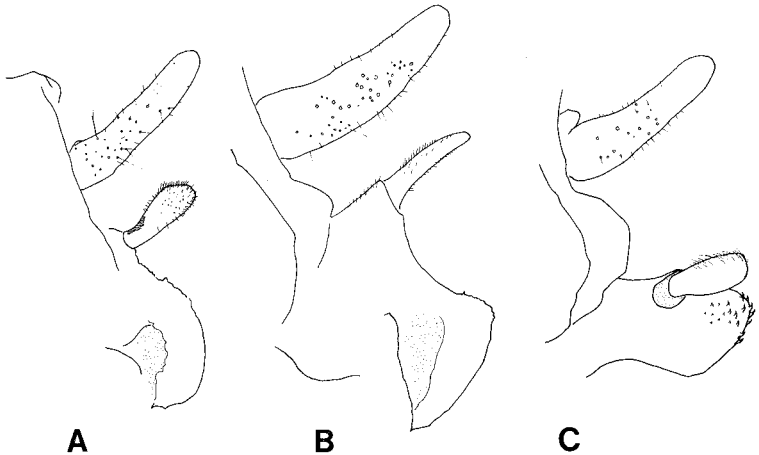


Figure 4. Lateral view of IXth sternum, A) *C. strepitans*, B) *C. monstrosa*, and C) *C. buckelli*.

patch. No stridulatory function has been established for these structures.

*Paratypes.* 9 adult ♂♂, same data as holotype (ROM, MCZ, & UMMZ); 1 adult ♀, same data as holotype (ROM); 4 adult ♂♂, Cowdrey, 8.8 mi. west on road to Pearl, 4 June 1978 (G. K. Morris & D. T. Gwynne) (ROM & Colorado State Univ., Ft. Collins); 1 adult ♂, Park Range nr Pearl, Col., 17 Aug. 1932 (G. Alexander) (ANSP); 1 adult ♂, Pearl, Col., 17 Aug. 1932 (G. Alexander) (Museum of University of Colorado, Boulder, Col.); 7 adult ♂♂, Los Pinos Pass, Col., 17 June 1977 (D. T. Gwynne) (USNM & CNC); 1 imm. ♂, Los Pinos Pass, Col., 17 June 1977 (D. T. Gwynne) (ROM); 1 adult ♂, Dunraven Pass, Yellowstone Nat. Pk, Wyo., 25 June 1930 (E. C. Van Dyke) (UMMZ); 1 adult ♀, Jackson Hole Res. Stn, Grand Teton Nat. Pk, Wyo., Aug. 1967 (H. E. & M. A. Evans) (USNM); 1 imm. ♂, Jackson Hole Res. Stn, Grand Teton Nat. Pk, Wyo. (H. E. & M. A. Evans) (USNM); 1 adult ♀, Stratton Exp. Watershed, nr Saratoga, Wyo. (J. M. Schmid) (USNM).

Key to *Cyphoderris* Species  
(Males only)

1. Subgenital plate (IXth sternum) with prominent ventrally-directed process (Figures 4a, b) ..... 2  
    Sternal process absent (Figure 4c) ..... *C. buckelli* Hebard
2. IXth sternum strongly produced posteriorly; sternal process with an angularly forward-bent tip, often appearing terminally cleft and toothed; styli of IXth sternum depressed, sublanceolate (Figure 3b); Ander's organ ridge-patch present and thoracic teeth robust; fastigium often weakly rugose .....  
    ..... *C. monstrosa* Uhler  
    Posterior of sternal process not angular but rounded, never terminally cleft and toothed (Figure 3a); Ander's organ absent or if present, only as weak thoracic teeth; styli of IXth sternum mitten-like; fastigium smooth ... *C. strepitans* new species

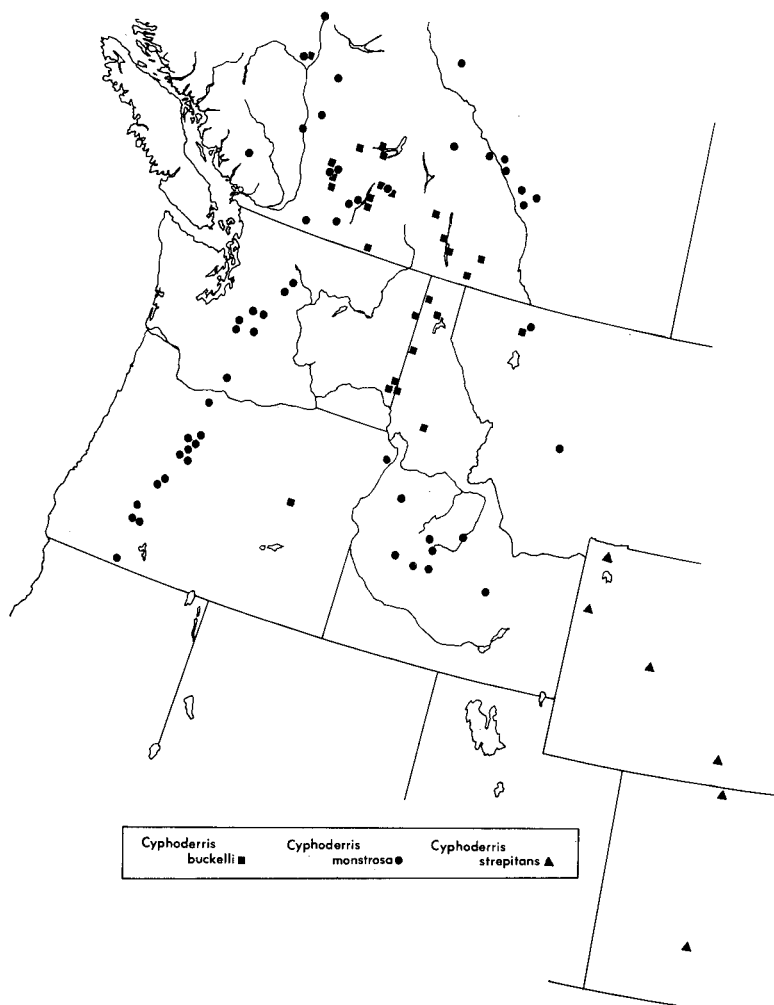
GEOGRAPHICAL DISTRIBUTION

*C. strepitans*, as presently known, is confined to the mountains of Colorado and Wyoming (Figure 5). Its distribution is disjunct from that of *buckelli* and *monstrosa*. The broad valley of the Snake River isolates it on the northwest from the most southerly populations of Idaho *monstrosa*; if overlap occurs it must be north of Yellowstone in southern Montana.

*C. monstrosa* is found from the Canadian Rockies in the southwest corner of Alberta, west through southern British Columbia. It reaches much farther north than *buckelli*, to Quesnel and to Smithers B.C. (This latter record exceeds the northern extent of our map and could not be plotted; Smithers is about 700 miles north of the Canada/U.S. border.) A western arm of *monstrosa* extends down the Cascades, reaching almost to northern California. A less documented eastern arm crosses western Montana to a cluster of localities in the Salmon River Mts of central Idaho.

*C. buckelli* has a more restricted range. It lies between these arms, overlapping broadly with *monstrosa* in southern B.C. and extending south through northern Idaho. There are interesting isolated records from Columbia Falls, Montana and from near Seneca in east central Oregon. Though their distributions overlap substantially we have not found *monstrosa* and *buckelli* together at the demic level.



Figure 5. Geographical distribution of *Cyphoderris*.

However Buckell (1924) states that both species have been seen at Nicola, B.C. "in large numbers during late May feeding together upon flowers of *Amelanchier* . . .".

We have examined about 300 specimens of *monstrosa* and 200 of *buckelli*. In addition to the type, allotype and paratypes of *strepitans*, we have seen 20 or so alcoholic specimens supplied by Dr. R. Willey of the Univ. of Chicago. Dr. Willey's material is from Los Pinos Pass, Col., a locality which he discovered in 1962 (Willey & Willey, 1963).

All plotted localities are based upon actual examination of specimens excepting Wind River, Wyo. This record is taken from Thomas (1876) on the strength of his illustration of an adult male. Though the drawing is small the shape of the sternal process is apparent and marks the specimen as *strepitans*. A listing of localities is given below for each species.

*C. strepitans*: WYOMING: Dunraven Pass, Yellowstone N. Pk; Jackson Hole, Grand Teton N. Pk.; Wind River, Fremont Co.; Stratton Exp. Watershed, nr Saratoga, Carbon Co. COLORADO: Park Range, nr Big Creek Lks, Jackson Co.; Cowdrey, 8.8 mi. west, Jackson Co.; Los Pinos Pass, Saguache Co.

*C. monstrosa*: BRITISH COLUMBIA: Smithers; Quesnel; Chilcotin nr Williams Lk; Lac La Hache; Clinton; Lillooet; Whistler Mt., Garibaldi Prov. Pk; Salmon Arm; Field, Yoho N. Pk; Glacier N. Pk; Monck Prov. Pk; Merritt; Lumby; Peachland; Fish Lk, nr Summerland; Manning Prov. Pk; Hedley. ALBERTA: Jasper N. Pk; Mt. Eisenhower Cpgrd, Banff N. Pk; Sulphur Mt., Banff N. Pk; Bragg Creek, w. of Calgary; Barrier Lk, Kananaskis Valley; Kananaskis Lks, Kananaskis Valley. MONTANA: Belton, Flathead Co.; 2 mi. s. Elliston, Powell Co. IDAHO: McCall, Valley Co.; Challis, Custer Co.; Beach Cr., nr Bull Trout Lk, Custer Co.; Red Fish Lk, Custer Co.; Centerville, Boise Co.; 22 mi. ne. Idaho City, n. fork Boise R., Boise Co.; Camas Co.; Arco, Butte Co. WASHINGTON: Lk. Wenatchee St. Pk, Chelan Co.; Entiat R. Trail, Chelan Co.; 2 mi. se. Easton, Kittitas Co.; Stampede, King Co.; Paradise Valley, Mt. Rainier N. Pk.; Berkeley Park, Mt. Rainier N. Pk; Gooseprairie, Yakima Co.; Trout Lk Cpgrd, Klickitat Co. OREGON: Mt. Hood, Hood R. Co.; Hat Point, Wallowa Co.; Middle Sister, Lane Co. & Deschutes Co.; McKenzie Pass, Lane Co. & Deschutes Co.; Salt Creek Falls, Lane Co.; Waldo Lk, Lane Co.; Lost Lk, Willamette Nat. For., Linn Co.; North Santiam R., Linn Co.; Pinehurst,

Jackson Co.; Union Creek, Jackson Co.; Crater Lk N. Pk, Klamath Co.; Douglas Co.; Olallie Lk, Marion Co.; Mt. Jefferson, Jefferson Co.

*C. buckelli*: BRITISH COLUMBIA: Chilcotin; Paul Lk Prov. Pk; Squilax; Salmon Arm; Nicola Lk; 2 mi. s. Merritt; Aspen Grove; Vernon; Lumby; Kelowna, nr airport; 3 mi. se. Rutland; Okanagan Falls; Rock Creek; Yahk; Ainsworth; Rosebery Prov. Pk; Cranbrook; Boswell, Kootenay Lk. IDAHO: Reeder Bay, Priest Lk, Bonner Co.; Sandpoint, Bonner Co.; 10 mi. s. Coeur d'Alene, Kootenai Co.; Moscow Mt., Latah Co.; Moscow, Latah Co.; Kamiah, Lewis Co. WASHINGTON: Newport, Pend Oreille Co.; Palouse, Whitman Co.; Pullman, Whitman Co. MONTANA: Columbia Falls, Flathead Co. OREGON: 3 mi. e. Seneca, Grant Co.

#### HABITAT AND FEEDING BEHAVIOR

The distribution of *Cyphoderris* corresponds roughly with the Cordilleran forest province (Gleason & Cronquist, 1964). In southern British Columbia *C. buckelli* occurs in the Dry Forest biotic area (Cowan & Guiguet, 1965) characterized by yellow pine (*Pinus ponderosa*) and at higher elevations, by interior Douglas fir (*Pseudotsuga menziesii*). *Amelanchier* (serviceberry), *Balsamorhiza* (arrow-leaf balsam-root) and *Berberis* (tall Oregon grape) are common understory plants in this association. In spring the nymphs and adult females of *C. buckelli* feed upon the flowers of these plants; night collecting at blooms is a good way to obtain specimens.

*C. buckelli* is also found in the Columbia Forest biotic area, the so-called interior wet belt of British Columbia. In 1977 we located large populations adjacent to Kootenay Lake near Boswell and at Rosebery on Slocan Lake.

*C. monstrosa* does occur in Dry Forest e.g. at Monck Prov. Park in southern British Columbia, but it is typically encountered in Sub-alpine Forest. Lodgepole pine (*Pinus contorta*) and Englemann spruce (*Picea engelmannii*) are characteristic of the Sub-alpine biotic area. In the Kananaskis Valley of southern Alberta we observed nymphs and adults to feed upon staminate cones of lodgepole pine (this before the cones reach a 'loose pollen' stage). Consumption was established by identifying cone bracts in the feces of field-caught specimens. Also caged insects were given cones and in most cases overnight they ate large portions.

It is presumably to feed upon staminate cones that *C. monstrosa* nymphs and adult females are observed at dusk climbing high into the trees. A useful method of collection is to search tree trunks with a flashlight just after sunset. The insects are always discovered oriented head upward. More often than not they occur in groups of 2 to 4 on the same trunk, which suggests that they may aggregate during their daytime stay in the leaf litter of the forest floor.

David Lightfoot of Oregon State University has studied *C. monstrosa* at Three Sisters in the central Oregon Cascades. He found this species abundant there in drier, more open stands of lodgepole pine and mountain hemlock (*Tsuga mertensiana*) above 5000' elevation. In contrast to our observations of ascent as the evening progresses Lightfoot notes that the singers begin high in the trees (about 6 m) and gradually occupy lower and lower perches until singing at ground level.

*C. strepitans* is found in both subalpine forest and high altitude sagebrush prairie. The holotypic site near Big Creek Lakes is an open forest of subalpine fir (*Abies concolor*) and lodgepole pine at an altitude of 8800'. At Los Pinos Pass, Colorado, *strepitans* is found in aspen woods adjacent to open areas of prairie. The mature aspen (*Populus tremuloides*) has an understory of subalpine fir and englemann spruce (altitude 10,200'). Two predominant ground cover plants at both sites are kinnikinnick (*Arctostaphylos* spp.) and a shrubby juniper (*Juniperus communis*). In the high altitude (8400') sagebrush (*Artemesia tridentata*) prairie of North Park, Colorado, the density of singing males appeared to be much greater than in the nearby pine forest of the holotypic site to the east. *C. strepitans* is also very numerous in the sagebrush areas (altitude 6700') of Grand Teton National Park, Wyoming. In late June, 1978, aggregations of singing males were easily heard while we drove along park roads at night. Thus, *C. strepitans* may be considered a predominantly sagebrush species although occurring in open forest habitats in the vicinity of sagebrush prairie.

#### ACOUSTIC BEHAVIOR

Males of all three species produce a succession of short musical trills, beginning in late evening and continuing well past midnight if weather permits. *C. buckelli* invariably sing near the ground from low shrubs (knee-height), the bases of tree trunks or on the forest

floor itself. The same is true of *C. strepitans*. Only *C. monstrosa* climb high into the trees as the night's signalling progresses. At Monck Park singing heights in excess of 5 m were common and an hour after sunset collection without climbing trees becomes impossible.

The calling songs are generated by tegminal stridulation. As in Gryllidae the tegmina are morphological mirror-images, both left and right bearing a functional file and scraper. Unlike gryllids however, which maintain a characteristic 'right above' forewing overlap, the overlap of a *Cyphoderris* male may change during his lifetime and both files take part in his stridulation.

Certain Tettigoniidae also have mirror-image tegmina and two functional files: *Megatympanon speculatum* Piza (Listroscolinae) (Riek, 1976), *Neduba macneilli* Rentz & Birchim, *Neduba sierranus* Rehn & Hebard (Decticinae) (Morris et al., 1975). Most tettigoniids have structurally distinct left and right forewings and overlap them 'left above'. In the *Neduba* species some individuals show left above, some right above. Unlike *Cyphoderris* they appear to maintain their particular overlap as individuals through life. Both overlaps were represented by Riek's two (pinned) specimens of *M. speculatum*.

Spooner (1973) analysed the calling song of *C. monstrosa* and describes it as a trill of grylloid (sinusoidal) pulses at a carrier frequency of 13 kHz. He noted substantial variation in the intensity and frequency of pulses and suggested that these changes "reflect irregular switching of tegmina from top to bottom position". He refers to this habit as "switch-wing singing" and regards it as occurring several to many times in the course of a single trill.

Overlap at rest (i.e. between singing bouts) is very infrequently changed in *C. buckelli*. The overlap of 16 individually-caged males was monitored by examining them once a day during almost 2 weeks. Of 141 checks, only 4 reversals from the immediately previous overlap were observed; the incidence of resting overlap reversal was less than 3%. Thirteen of these males never showed an overlap reversal.

Four *C. monstrosa* males checked over 5 days, gave similar results: two were never found with reversed overlap (checked respectively 5 and 6 times), one was reversed once in 5 checks and one twice in 6 checks. If *Cyphoderris* alter overlap several times within a single trill, it is strange that individuals end up so consistently at the same overlap with which they began.

We recorded the calling song of a *C. monstrosa* specimen (Figure 6, 75-6) before and after damaging with a scalpel, several teeth in the central region of his right tegmen file. In oscillograms of post-mutilation recorded song, his use of the damaged file (i.e. right above overlap) was apparent as a drastic mid-pulse drop in amplitude. In one oscillogram, a portion of which makes up Figure 6 (second trace from bottom), 20 pulses in succession were 'right above'.

Switch-wing singing as suggested by distinctive pulse envelopes within the same trill was only evident in our records on one occasion. A male of *C. monstrosa* had been released in the immediate vicinity (i.e. within antennal range) of a mature female on the observer's hand. He began to sing while walking about on the hand and directing his attention toward the female. His song was recorded and on analysis found to be a trill in which every other pulse was identical in envelope and distinctly different from the intervening pulse i.e. there were two pulse types occurring in alternation without break in the sequence of the trill (Figure 6, bottom trace). This was apparently a courtship song.

It is clear that pulse envelopes are highly variable in the genus, though usually quite consistent for a particular recording session of a particular individual. Switch-wing stridulation is probably not an everyday feature of *C. monstrosa* calling song but it may occur under special circumstances such as courtship.

Oscillograms of normal calling songs are given in Figure 6. The pulses of *C. strepitans* and *C. buckelli* are apparently indistinguishable. They are usually wedge-shaped: each begins with a steep rise to maximum amplitude, then falls steadily to the pulse's end. The pulses of *C. monstrosa* also have a steep onset but are usually of longer duration. They are drawn out in an uneven envelope near their maximum amplitude before dropping away to silence.

Carrier frequency spectra of all three species are highly similar. Specimens were analysed 'live' (i.e. without tape-recording) by directing the output of a Bruel & Kjaer sound level meter (2204) fitted with a  $\frac{1}{4}$ " microphone (4135) into a Tektronix 3L5 spectrum analyser. This system will detect ultrasonic frequencies up to 100 kHz. No substantial sound energy exists in the ultrasonic range for any of the *Cyphoderris* species. The sinusoidal nature of the waveform is apparent in the narrowness of the dominant frequency

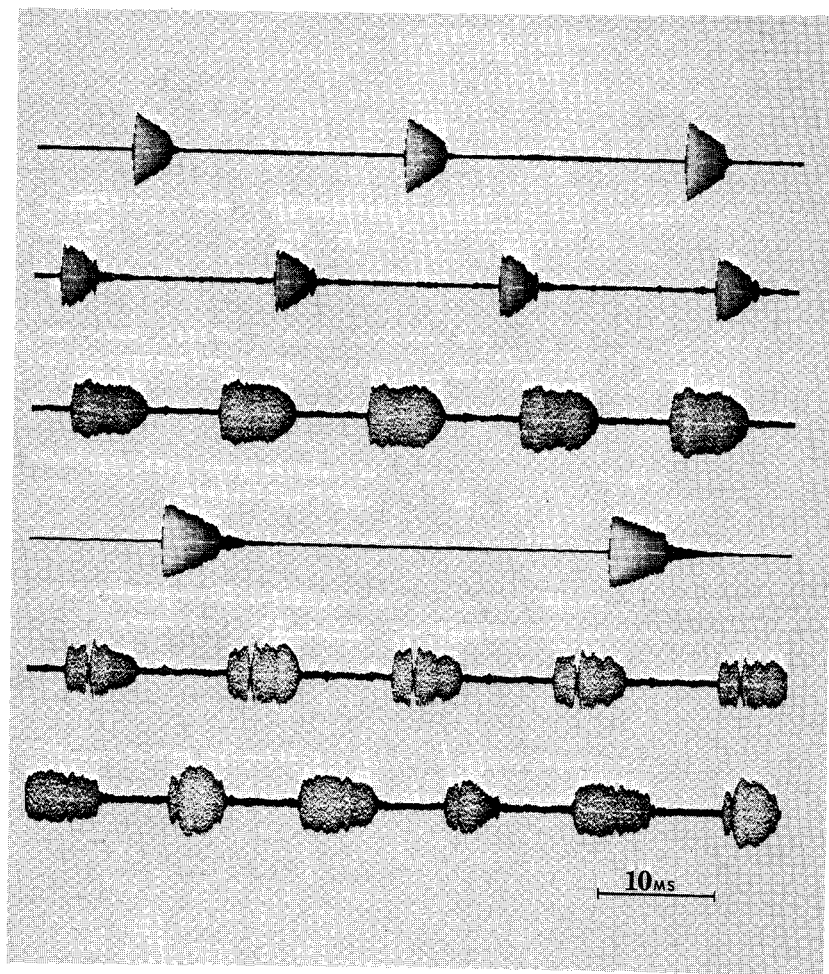


Figure 6. Oscillograms of *Cyphoderris* calling song. From top trace downward: *C. strepitans* 76-8, 17.8°C; *C. buckelli* 76-14, 25.0°C; *C. monstrosa* 75-6, 24.5°C, intact file; *C. monstrosa* 76-2, 8.7°C, field-recorded, Monck Prov. Pk B.C.; *C. monstrosa* 75-6, 24.0°C, file teeth of right forewing damaged; *C. monstrosa* 75-10, 23.1°C, male recorded singing in immediate presence of female.

peak, suggesting the operation of a sharply-tuned (high Q) tegminal resonator (Sales & Pye, 1974).

In the figured *C. strepitans* male (Figure 7), the dominant peak centers on 12.7 kHz and there are very weak second and third harmonics near 25 and 38 respectively. The *C. buckelli* specimen has its principal peak near 13.3 kHz and a lesser peak occupies the range 28–30 kHz. Like Spooner (1973) we obtained 13 kHz as the dominant carrier frequency of *C. monstrosa*.

Sound level measurements were obtained with the ¼" microphone and the 2204 meter, the latter on 'linear, fast' setting. At 5 cm dorsal aspect, the sound level of *C. strepitans* (76-7) was between 100.5 and 101.0 dB. A specimen of *C. buckelli* (76-3) was  $102 \pm 2$  dB at 6.5 cm dorsal.

Pulse rate varies linearly with temperature (Figure 8) as in other acoustic Ensifera (Walker 1962, 1975). Both field and laboratory recordings of calling song contributed to the regression lines. One *C. monstrosa* plotted point is from Spooner (1973) (S in Figure 8); 5

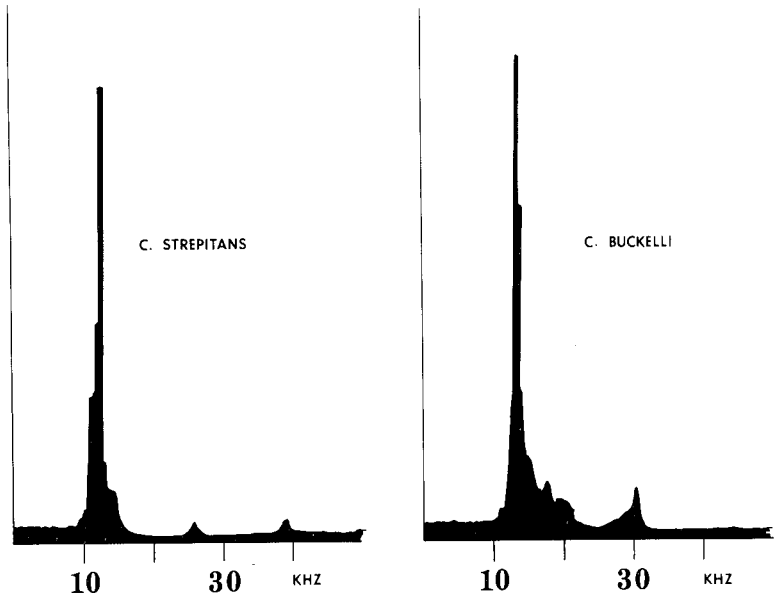


Figure 7. Calling song frequency spectrograms traced from photographs.



different males provide the other 6 points. *C. buckelli*'s regression is based on 12 different individuals, 3 at two different temperatures each. Each of the 13 *C. strepitans* pulse rates derives from a different individual; all those at temperatures of 8°C and below are field recordings. Pulse rates were calculated from an oscilloscope display in which a single beam sweep embraced 3–13 pulses. Successive, single-sweep samples (3–6), were averaged to obtain each plotted value. The coefficients of determination indicate a very good fit to the calculated regression lines. Although the *C. monstrosa* regression line is different from the *strepitans* and *buckelli* lines the slopes and Y intercepts of the latter two species are not significantly different.

*C. strepitans* males stridulate at very low temperatures. Previous reports cite minimal singing temperatures for acoustic Orthoptera of about 7°C [e.g. Fulton (1925) for the tree cricket *Oecanthus fultoni* (under the name of *O. niveus*) and Frings and Frings (1957) for the katydid *Neoconocephalus ensiger*]. On May 17, 1977, at the holotypic site, one of us (D.T.G.) heard three of four males singing from branches and logs near the ground when the air temperature at waist level was -0.5°C. On June 4 and 5, 1978, tape recordings were made of males singing at temperatures as low as 2°C (see Figure 8). Following the recording the thermometer bulb was placed close to the singing male's perch. There is a suggestion in the plotted rates in Figure 8 of a departure from linearity at very low temperatures.

In conclusion, the song of *C. monstrosa* differs from the other two species in both the shape of the pulse amplitude envelope and in pulse rate, both these parameters being useful diagnostic features. *C. buckelli* and *C. strepitans*, however, have virtually identical calling songs: song intensities, carrier frequencies, and pulse amplitude envelopes provide no basis for human discrimination; the pulse rates, especially, are indistinguishable at any given temperature.

It is interesting to note that Alexander (1969) has questioned the traditional interpretation that reproductive isolating mechanisms evolved to prevent "mating mistakes" between species. He suggested (citing evidence from acoustical insects) that species differences have most likely arisen as a result of the different selection pressures operating on populations while they are in allopatry. He reasoned that if this is so, among other things, we should rarely find identical pair forming signals among allopatric or allochronic species. *C. strepitans* and *C. buckelli* are allopatric (Figure 5) and by the above

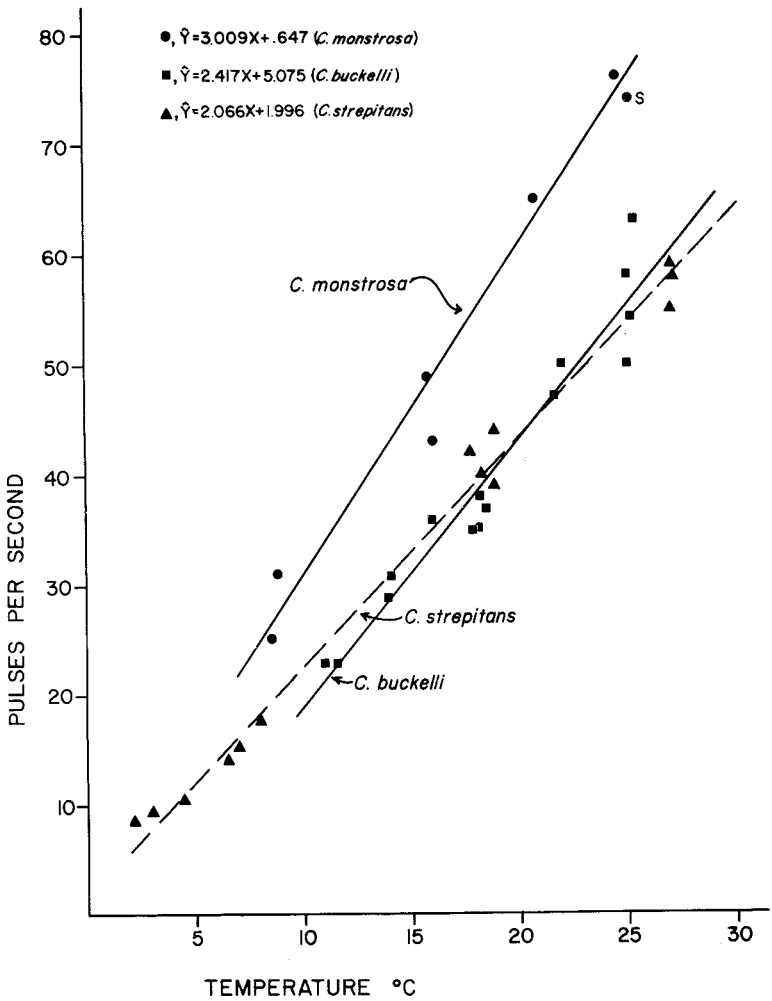


Figure 8. Relation of pulse rate and temperature in *Cyphoderris* calling song (S is from Spooner, 1973).

reasoning their songs should have diverged yet this is not the case. Any difference between these two species (including the above mentioned habitat differences) apparently have not affected their pair forming signals.

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