New species of *Hebecephalus* from British Columbia, Idaho and adjacent states (Rhynchota: Homoptera: Cicadellidae)*

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ABSTRACT

Eight new nearctic leafhoppers of the genus *Hebecephalus* DeLong are described: *H. planaria* from British Columbia; *H. abies* from Utah; *H. chandleri* from Wyoming; and *H. crenulatus, H. ferrumequinum, H. picea, H. pugnus*, and *H. veretillum* from Idaho. All 27 known nearctic species are illustrated and their critical morphological characters are presented in key and tabular form, along with their geographic distribution. Evidence for endemism within southern British Columbia and the Pacific Northwest is noted.

INTRODUCTION

Leafhoppers, the family Cicadellidae, include many species adapted to grasslands. They include a large number of species characteristic of prairies (Ross 1970) and are important organisms in characterizing and monitoring prairie sites (Hamilton 1995). They are likewise an important part of intermontane grassland environments, primarily in Colorado and the southwestern U.S. (Oman 1949). Sampling more northerly areas in recent years has disclosed a rich endemic fauna in the "Pacific Northwest" including southern British Columbia. This paper describes additional endemic species in the genus *Hebecephalus* DeLong.

Leafhoppers of the genus *Hebecephalus* are small, grass-feeding insects, their heads marked with broken dark crossbands, and wing venation outlined in dark brown or black, or with cells checkered or banded in black and white (Figs. 1-4). Females are readily distinguished from those of other genera by the prominent, black-margined median notch or slit on the pregenital sternite (Figs. 5-10). There are two species from Asia (Anufriev and Emeljanov 1988), one Nearctic transboreal species (*H. algidus* DeLong & Davidson) and three more on North American prairies (*H. occidentalis* Beamer & Tuthill, *H. rostratus* Beamer & Tuthill, *H. truncatus* Beamer & Tuthill) but the majority are confined to Cordilleran North America. The montane species occur in grassy valleys of Alaska (AK) and British Columbia (BC) south to the mountains of California (CA), Nevada (NV) and Arizona (AZ)†. The peculiar distribution patterns of these species is analysed here, following the description of new species.

MATERIALS AND METHODS

Species are defined here, as elsewhere in my publications, following the guidelines of Ross (1974). These species definitions, wherever possible, are based on analyses of series: numerous specimens taken at the same time, preferably on a single plant species. Many are based on

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†The Neotropical *Deltocephalus* (*Hebecephalus*) *insularis* Van Duzee (1933) probably does not belong in this genus; Linnavuori (1959) places it tentatively in *Amplicephalus* DeLong.

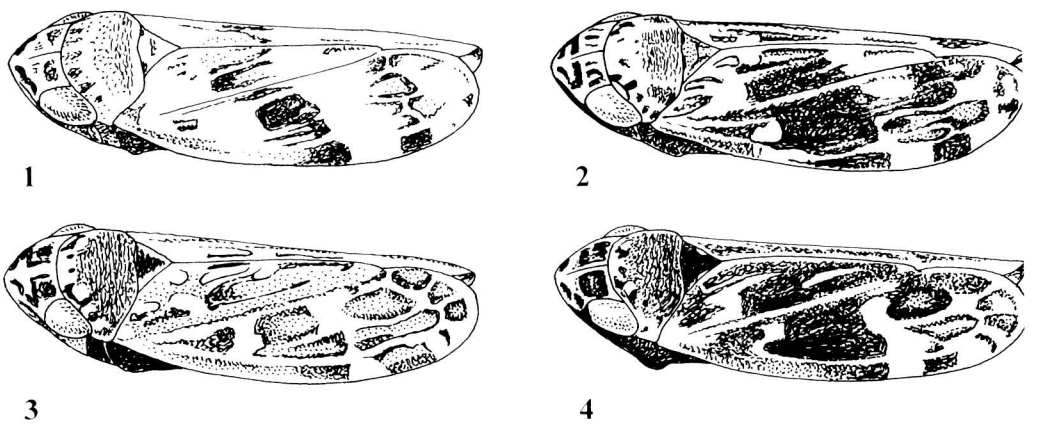
material collected by A.R. Brooks, H.H. Ross and the author, now housed in the Canadian National Collection of Insects (CNCI) in Ottawa and other series collected over the past 20 years by R.F. Whitcomb, USDA-ARS, Beltsville, MD. These collections cover much of the native grasslands of North America, with the exception of those in low elevations of California and regions south of northern Mexico where *Hebecephalus* are rare or unknown. In all, more than 4,500 identifiable specimens of *Hebecephalus* were examined in this study.

This does not pretend to be a complete account of all the species that may occur in North America. Much additional collecting and analysis of material deposited in collections across the continent will be needed before a revision is possible.

Biological data and exact collecting localities are an important aspect of such studies. Label data is supplemented by information taken from collecting notes; this additional information is recorded in square brackets in the text.

Characters of the male genitalia must be examined by maceration in KOH followed by examination of whole structures suspended in glycerin. It is important that these structures not be mounted on microscope slides, as flattening such three-dimensional objects results in distortions that prevent accurate comparisons. For detailed descriptions of technique and body parts of leafhoppers, see Beirne (1956).

All figures of a given structure are drawn to a constant scale, except for the habitus illustrations (Figs. 1-4) which are diagrammatic.



Figures 1-4. Colour variability of *Hebecephalus algidus* DeLong & Davidson from Eagle Plains, Yukon Territory, Canada. 1-2, obliquely banded forms; 3-4, checkered and pale-veined forms.

SYSTEMATICS

The genus has been revised once (Beamer and Tuthill 1935) but various species have been added subsequently (DeLong and Davidson 1935; Beamer 1936; Wittlake and Beamer 1952; Beirne 1954; Hamilton and Ross 1972). Oman (1949) redefined the genus and split off various segregates as additional genera. Their removal left 19 described species, three of which were based on abnormal specimens (Wittlake and Beamer 1952) or variants (Beirne 1954) of previously described species:

(1) *Hebecephalus mornus* Beirne is a variant of *H. occidentalis* (Hamilton and Ross 1972).

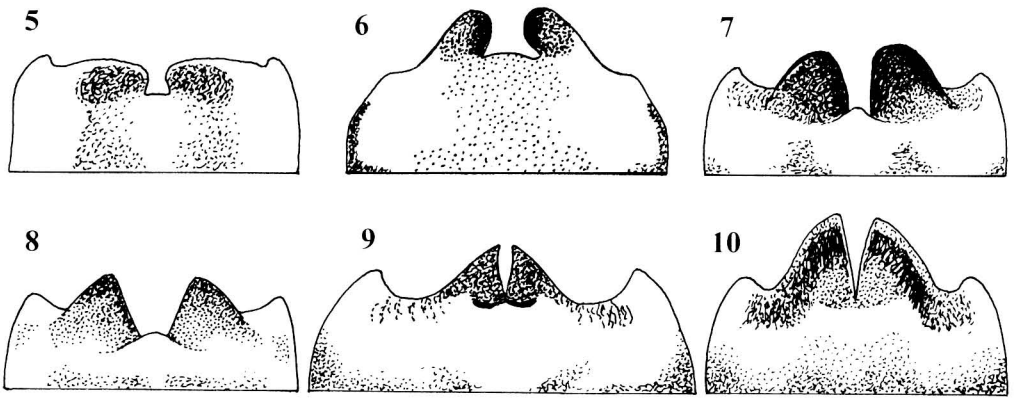
(2) *H. creinus* Beirne appears to fall within the character variation of *H. borealis* DeLong & Davidson, and in fact the types of both species were taken from the same locality and year

(Nordegg, Alta., 1921). Specimens from the type-series of *borealis* have not been examined, so no formal synonymy is offered at present.

(3) *Hebecephalus pedecurtus* Wittlake & Beamer is based on 4 unidentifiable females and a pair of abnormal males. The latter show the incomplete ventral connective, shortened and simplified styles and feminized pygofers characteristic of nematode-parasitized individuals. From the form of the aedeagi, the males are most likely specimens of *H. rostratus*.

Three more species have been described subsequently (Hamilton and Ross 1972). This paper describes an additional eight species, bringing the total to 27 nearctic species.

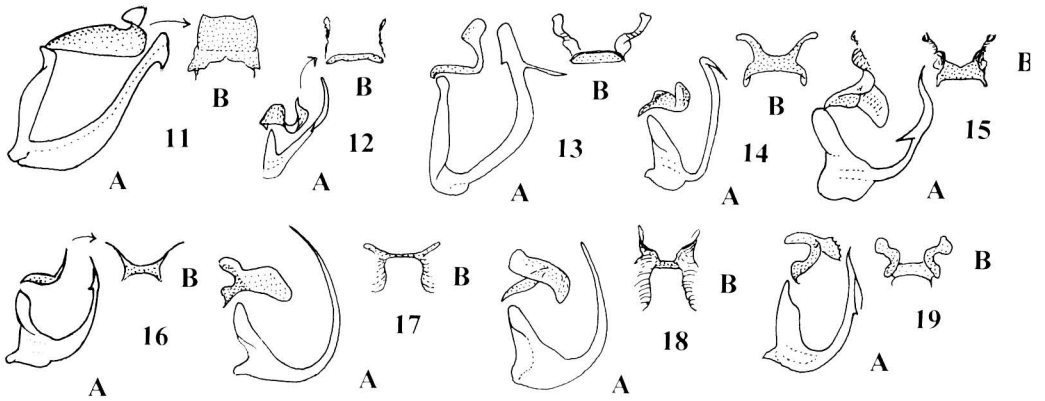
Females of *Hebecephalus* show unique genitalic characters in only two species (Figs. 5, 10). At present, all other females cannot be identified with any degree of certainty in the absence of associated males. Colour patterns, apparently distinctive in some species, are rendered useless by their variability in other species (Figs. 1-4); body size and proportions overlap in many species. Accordingly, the most reliable specific characters are found in male genitalia.



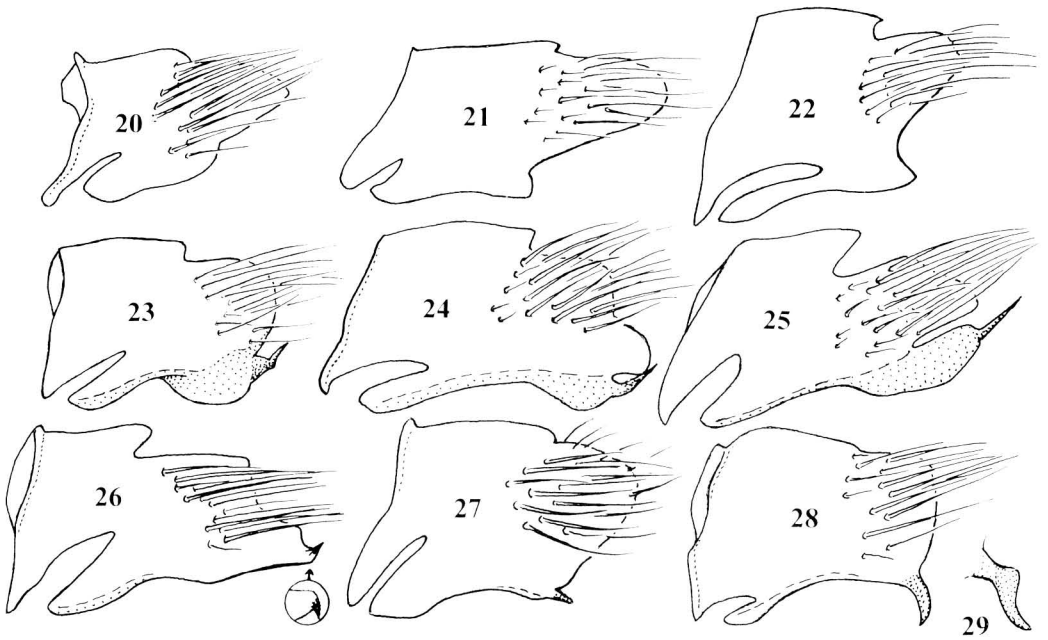
Figures 5-10. Pregenital sternites of *Hebecephalus* females. 5, *H. discessus* Beamer & Tuthill; 6, *H. pugnus* sp.nov.; 7, *H. ferrumequinum* sp.nov.; 8, *H. picea* sp.nov; 9, *H. chandleri* sp.nov.; 10, *H. algidus*.

Males of this genus resemble other grass-feeding Deltocephalini (=Deltocephalina *sensu* Hamilton 1975) in having a loop-shaped "ventral connective" which articulate the claspers ("styles") to the lower edge of the aedeagal base ("atrium"). They may be distinguished from other Deltocephalini by the form of the dorsal connective which articulates the base of the tenth tergite (or "anal tube") to the dorsal arm of the aedeagal base (Figs. 11-19 A). The dorsal connective in other related genera is a pair of ill-defined sclerous strips but in *Hebecephalus* it forms a transverse bar or plate, often with processes at either end (Figs. 11-19 B).

Characters useful at the species level (Table 1) include the outline of the male subgenital plates, armature of the pygofers (Figs. 20-29), shape of the aedeagus and dorsal connective (Figs. 11-19, 30-56) and armature of the style tip (Figs. 57-75). The style tip must be viewed with care as it is more or less twisted from the plane of its base, and appears to vary greatly in shape depending on the angle of study (Figs. 57-61).



Figures 11-19. Aedeagi and dorsal connectives of *Hebecephalus*, lateral aspect (A) and caudoventral aspect of dorsal connective (B). 11, *H. vinculatus* (Ball); 12, *H. veretillum* sp.nov.; 13, *H. chandleri*; 14, *H. pugnus*; 15, *H. borealis* DeLong & Davidson; 16, *H. abies* sp.nov.; 17, *H. ferrumequinum*; 18, *H. crenulatus* sp.nov.; 19, *H. truncatus* Beamer & Tuthill.



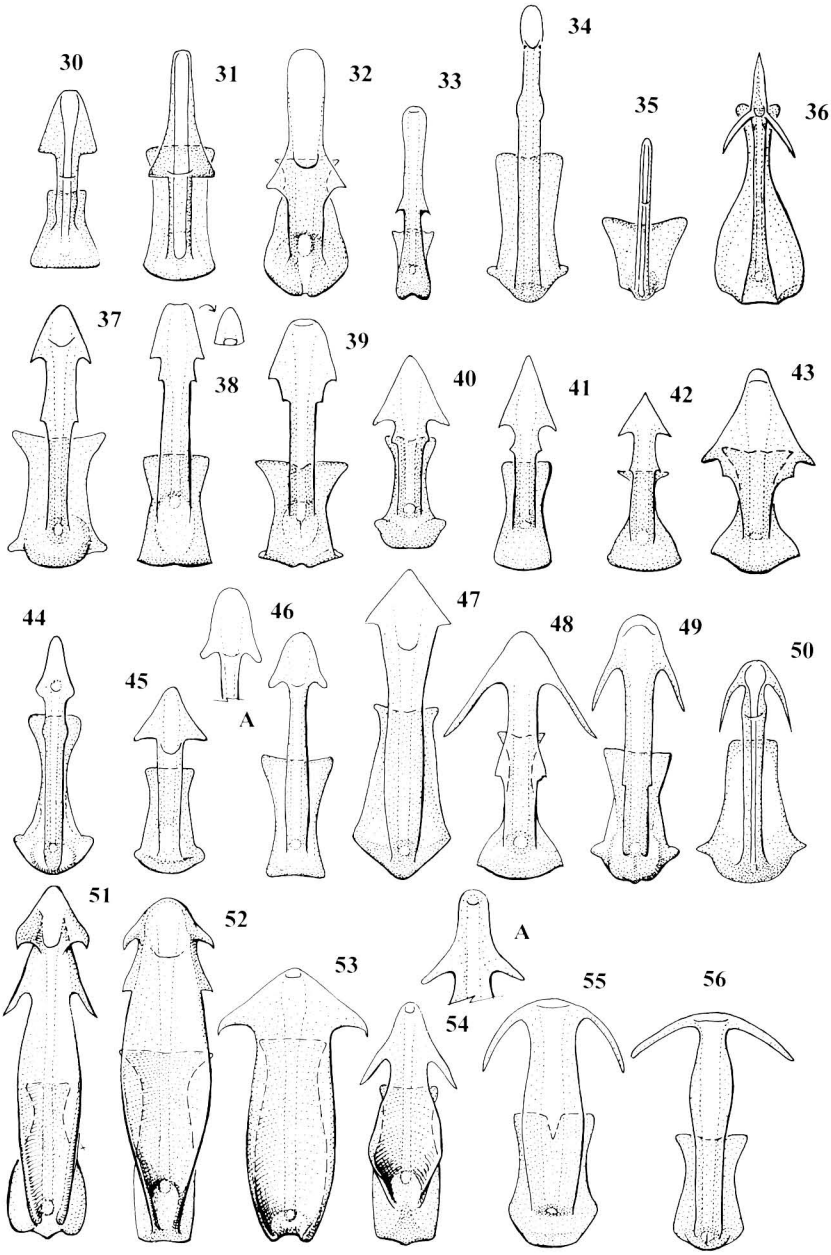
Figures 20-29. Male pygofers of *Hebecephalus*, lateral aspect. 20, *H. veretillum*; 21, *H. algidus*; 22, *H. chandleri*; 23, *H. pugnus*; 24, *H. adversus* Beamer & Tuthill; 25, *H. caecus* Beamer; 26, *H. borealis* (detail: pygofer tip, dorsal aspect); 27, *H. planaria* sp.nov.; 28, *H. crenulatus*; 29, pygofer process of *H. signatifrons* (Van Duzee).

Table 1

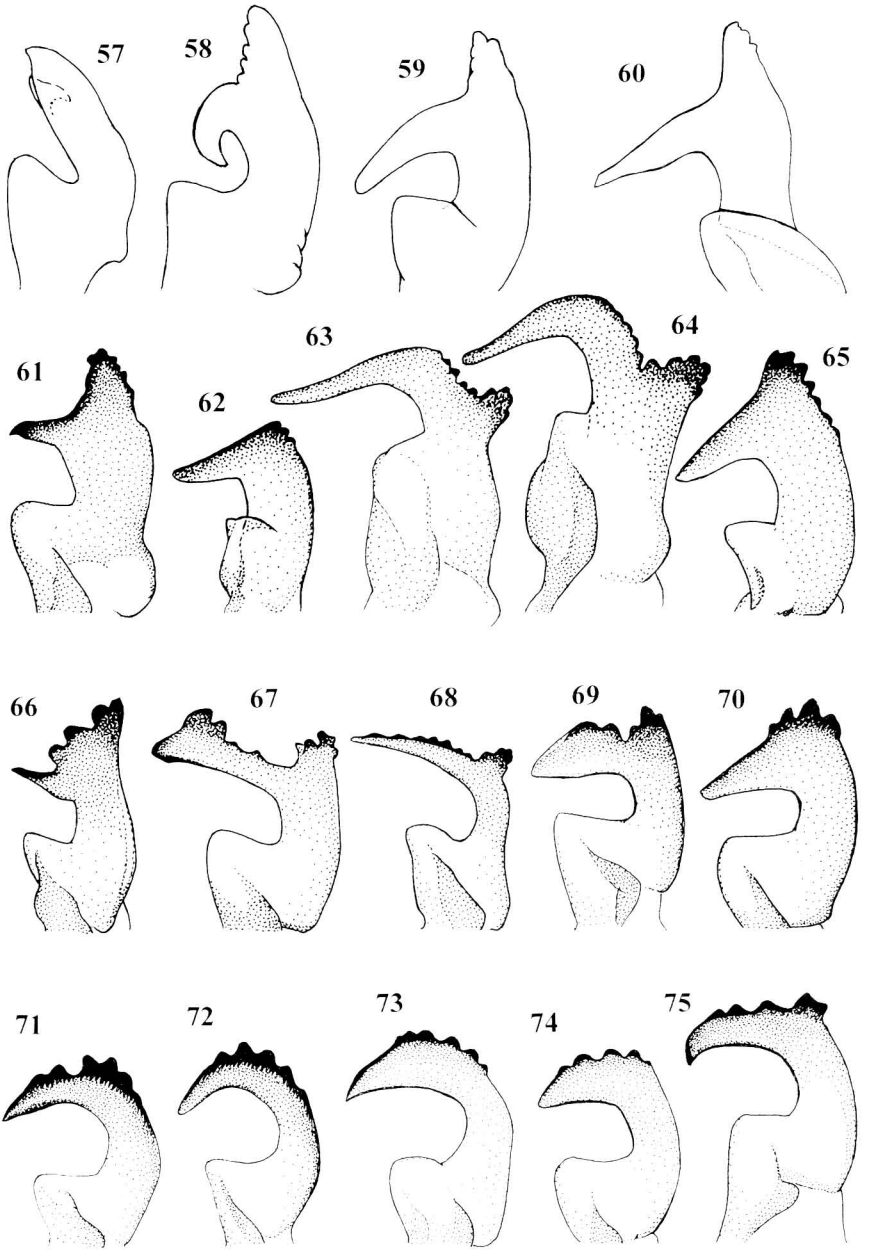
Character states of Nearctic species of *Hebecephalus*, as illustrated. **A**- female pregenital sternite (Figs. 5-10); **B**- aedeagus and dorsal connective, lateral aspect (Figs. 11-19 A and *= fig. 3 in Hamilton and Ross 1972); **C**- dorsal connective, caudoventral aspect (Figs. 11-19 B); **D**- male pygofers (Figs. 20-29 and *= fig. 1 in Hamilton and Ross 1972); **E**- aedeagus, caudoventral aspect (Figs. 30-56); **F**- style tip (Figs. 61-75); **G**- subgenital plates, as follows: figs. 1-2, 4 from Pl. LV (Beamer and Tuthill 1935), fig. 3 from Pl. LXVIII (Beamer 1936), fig. 5 from Pl. LVI (Beamer and Tuthill 1935), fig. 7 from Pl. 7 (DeLong and Davidson 1935) and #6 [not figured] represents elongate, divergent plates. Apomorphies boldfaced.

trivial name	**A**	**B**	**C**	**D**	**E**	**F**	**G**
veretillum sp.nov.	?	12	12	20	33	68	6
discessus Beamer & Tuthill	5	11	14	20	54	62	1
planaria sp.nov.	6	11	14	27	47	73	1
irritus Beamer	6	14	?	24	36	65	1
pugnus sp.nov.	6	14	14	23	49	66	2
filamentus Hamilton & Ross	6	*	14	**28**	35	74	1
callidus (Ball)	6	12	14	**28**	**30**	74	1
circus Hamilton & Ross	?	12	16	*	**31**	72	1
crenulatus sp.nov.	6?	18	18	**28**	44	67	1
sagittatus Beamer & Tuthill	6	16	18	**28**	41	73	1
occidentalis Beamer & Tuthill	6	19	16	**28**	**55**	73	1
rostratus Beamer & Tuthill	6	19	16	**28**	**56**	73	1
signatifrons (Van Duzee)	6	19	14	**29**	37	**75**	1
truncatus Beamer & Tuthill	6	19	19	**28**	48	**75**	4
crassus DeLong	6	12	17	**28**	46	**75**	2
abies sp.nov.	**7**	16	16	**28**	42	**75**	1
ferrumequinum sp.nov.	**7**	17	17	**28**	34	**75**	2
borealis DeLong & Davidson	**7**	**15**	15	26	32	61	7
picea sp.nov.	**8**	**15**	17	**28**	43	70	1
hilaris Beamer	**8**	16	16	**28**	45	**69**	2
beameri Hamilton & Ross	**8**	14	?	**28**	50	**71**	1
adversus Beamer & Tuthill	**8**	16	14	24	39	65	5
caecus Beamer	?	16	14	25	38	65	3
chandleri sp.nov.	**9**	13	13	**22**	36	**64**	3
vinculatus (Ball)	**9**	11	11	**21**	53	**63**	3
firmus Beamer	**9**	11	12	**21**	**52**	**64**	3
algidus DeLong & Davidson	**10**	11	12	**21**	**51**	**64**	3

No phylogeny of the genus can be attempted at present. Genitalic characters, which are all that were discovered to be useful for such an analysis (see derived characters, or apomorphies, in Table 1), show far too much convergence and parallelism (homoplasy) or unique developments (autapomorphy) to be reliable indicators of relationships. For example, the most distinctive aedeagal character (concave posterior face of shaft, Figs. 51-54) correlates well with other genitalic characters in three species related to *H. algidus* (Table 1) but appears to be convergent in the case of *H. discessus* Beamer & Tuthill which in all other characters stands far apart from the *algidus* group. Conversely, *H. chandleri* shares with the *algidus* group its highly characteristic style and female pregenital sternite, but has an aedeagal shape utterly unlike that of any other member of this species group.



Figures 30-56. Aedeagi of *Hebecephalus*, caudoventral (longest) aspect. 30, *H. callidus* (Ball); 31, *H. circus* Hamilton & Ross; 32, *H. borealis*; 33, *H. veretillum*; 34, *H. ferrumequinum*; 35, *H. filamentus* Hamilton & Ross; 36, *H. chandleri*; 37, *H. signatifrons* (Van Duzee); 38, *H. caecus* (detail of tip from gonopore aspect); 39, *H. adversus*; 40-41, *H. sagittatus* Beamer & Tuthill; 42, *H. abies*; 43, *H. picea*; 44, *H. crenulatus*; 45, *H. hilaris* Beamer; 46, *H. crassus* DeLong and var. (A); 47, *H. planaria*; 48, *H. truncatus*; 49, *H. pugnus*; 50, *H. beameri* Hamilton & Ross; 51, *H. algidus*; 52, *H. firmus* Beamer; 53, *H. vinculatus*; 54, *H. discessus* and var. (A); 55, *H. occidentalis* Beamer & Tuthill; 56, *H. rostratus* Beamer & Tuthill.



Figures 57-75. Right style tips of *Hebecephalus*, various angles. 57-61, *H. borealis* (57-60 in laterad rotation; 61 in anteriad rotation); 62, widest aspect of tip of *H. discessus*; 63, same, of *H. vinculatus*; 64, same, of *H. firmus*; 65, same, of *H. caecus*; 66, same, of *H. pugnus*; 67, same, of *H. crenulatus*; 68, same, of *H. veretillum*; 69, same, of *H. hilaris*; 70, same, of *H. picea*; 71, same, of *H. beameri*; 72, same, of *H. circus*; 73, same, of *H. planaria*; 74, same, of *H. truncatus*; 75, same, of *H. crassus*.

Key to males of nearctic *Hebecephalus*

1. Pygofer with process absent (Fig. 20), or lobate, ventral, located approximately halfway between tip of apical lobe and anteroventral angle (Figs. 21-22)..... 22
- Pygofer with process sharp-tipped, apical or ventroapical, located distinctly closer to tip of apical lobe than to anteroventral angle (Figs. 23-29)..... 2
2. Pygofer with process directed caudodorsad or laterad (Figs. 23-26)..... 17
- Pygofer with process directed caudad or ventrad (Figs. 27-29)..... 3
3. Apical processes of aedeagus long and narrow (Figs. 48-50)..... 14
- Apical processes of aedeagus short and thick or absent (Figs. 37-47)..... 4
4. Tip of style with distinct notch between irregular marginal teeth (Figs. 67, 69).... 13
- Tip of style with low, evenly spaced marginal teeth (Figs. 72-75)..... 5
5. Aedeagus slender, without enlarged tip (Figs. 34-35)..... 12
- Tip of aedeagus spatulate to sagittate (Figs. 37-47)..... 6
6. Enlarged tip of aedeagus as long as rest of shaft (Figs. 30, 43)..... 11
- Enlarged tip of aedeagus much shorter than rest of shaft (Figs. 37-42)..... 7
7. Aedeagal shaft short, only about as long as its base (Figs. 40-42)..... 10
- Aedeagal shaft long, nearly twice as long as its base (Figs. 37, 46-47)..... 8
8. Aedeagal shaft robust, tip pointed (Fig. 47)..... *planaria* sp.nov.
- Aedeagal shaft slender, tip rounded (Figs. 37, 46)..... 9
9. Pygofer spine slender, evenly curved (as in Fig. 28)..... *crassus* DeLong
- Pygofer spine wide at angled bend before base (Fig. 29)..*signatifrons* (Van Duzee)
10. Dorsal connective slender, without prominent processes (Fig. 16 B); style with coarse teeth half as deep as style tip between them (as in Fig. 75)..*abies* sp.nov.
- Dorsal connective with broad, elongate lateral processes (as in Fig. 17 B); style with fine teeth a third as deep as style tip between them (as in Fig. 74) ..... *sagittatus* Beamer & Tuthill
11. Aedeagal tip armed with 1 pair of teeth (Fig. 30)..... *callidus* (Ball)
- Aedeagal tip armed with 2 pairs of teeth (Fig. 43)..... *picea* sp.nov.
12. Aedeagal shaft narrow compared to aedeagal base (Fig. 35); style with fine teeth a third as deep as style tip between them (as in Fig. 74) ..... *filamentus* Hamilton & Ross
- Aedeagal shaft broad compared to aedeagal base (Fig. 34); style with coarse teeth half as deep as style tip between them (as in Fig. 75)..... *ferrumequinum* sp.nov
13. Stylar notch much wider than deep (Fig. 67)..... *crenulatus* sp.nov.
- Stylar notch narrow, as wide as deep (Fig. 69)..... *hilaris* Beamer
14. Subgenital plates with outer angles produced, tips thus appearing truncate in ventrolateral aspect; aedeagal processes straight (Fig. 48) ..... *truncatus* Beamer & Tuthill
- Subgenital plates rounded apically; aedeagal processes curved (Figs. 55-56)..... 15
15. Aedeagal processes directed laterad (Fig. 56)..... *rostratus* Beamer & Tuthill
- Aedeagal processes directed ventrad (Figs. 50, 55)..... 16
16. Aedeagal shaft slender (Fig. 50); style tip with irregularly spaced teeth (Fig. 71) ..... *beameri* Hamilton & Ross
- Aedeagal shaft broad (Fig. 55); style tip with evenly spaced teeth (as in Fig. 73) ..... *occidentalis* Beamer & Tuthill
17. Pygofer process directed laterad (Fig. 26); aedeagus in lateral aspect sinuate (Fig. 15 A)..... *borealis* DeLong & Davidson
- Pygofer process directed caudad or caudodorsad (Figs. 27-29); aedeagus in lateral aspect curved evenly dorsad (Figs. 16-19 A)..... 18
18. Lateral process of style short and narrow (Fig. 66)..... *pugnus* sp.nov.

- Lateral process of style long and thick (Fig. 65)..... 19
19. Aedeagus with tip bearing slender processes (as in Fig. 36)..... *irritus* Beamer
- Aedeagus with unarmed tip (Fig. 31) or with short marginal teeth (Figs. 38-39).... 20
20. Aedeagus with elongate, tapered tip beyond marginal teeth (Fig. 31) ..... *circus* Hamilton & Ross
- Aedeagus with short, spatulate tip beyond marginal teeth (Figs. 38-39)..... 21
21. Pygofer process set on small base (Fig. 24)..... *adversus* Beamer & Tuthill
- Pygofer process set on massive base (Fig. 25)..... *caecus* Beamer
22. Aedeagal processes much longer than greatest width of shaft (Fig. 36) ..... *chandleri* sp.nov.
- Aedeagal processes shorter than greatest width of shaft (Figs. 33, 51-54)..... 23
23. Aedeagal shaft slender, caudal surface flat (Fig. 33)..... *veretillum* sp.nov
- Aedeagal shaft broad, caudal surface concave (Figs. 51-54)..... 24
24. Aedeagal shaft with 2 pairs of processes (Figs. 51-52)..... 26
- Aedeagal shaft with 1 pair of processes (Figs. 53-54)..... 25
25. Tip of aedeagal shaft broad, obtuse (Figs. 53) ..... *vinculatus* (Ball)
- Tip of aedeagal shaft narrowed, sagittate (Figs. 54, 54A) ..... *discessus* Beamer & Tuthill
26. Aedeagal shaft slender, with lateral processes longer than preapical ones (Fig. 51); Alaska and northern Canada..... *algidus* DeLong & Davidson
- Aedeagal shaft broad, with lateral processes shorter than preapical ones (Fig. 52); Wyoming..... *firmus* Beamer

Hebecephalus abies sp.nov.

(Figs. 16, 42)

Etymology. Noun in apposition: *abies,* fir tree genus, in reference to the shape of the aedeagus.

Diagnosis. This species is distinguished from its congeners by a combination of genital characters. The female is nearly identical to that of *H. ferrumequinum* sp.nov. (only less angulate in the crown) and structurally similar to that of *H. borealis*, but distinctly smaller (the latter is 3.6-4.0 mm long). The male has a coarsely toothed, nearly straight stylar process like those of *H. crassus* (Fig. 75), *H. ferrumequinum, H. signatifrons* (Van Duzee), and *H. truncatus*. As in *H. signatifrons* and *H. truncatus*, the aedeagal shaft is armed with a pair of teeth near the midlength, but the shaft is scarcely longer than the aedeagal base. It is further distinguished from *H. signatifrons* in having an evenly curved pygofer process (c.f. Figs. 28, 29) and from *H. truncatus* in having rounded subgenital plate apices. The aedeagus of *H. abies* resembles that of *H. sagittatus* but the lateral teeth on the shaft are much farther from the sagittate apex.

Description. Head parabolically produced, crown 0.9x as long as width between eyes. Crown marked with 6 dark spots usual for genus (as in Beirne 1956, figs. 489-494); upper half of face and tip of clypellus black spotted with ivory, lower half ivory with black spots; pronotum with irregular dark brown markings on anterior third separated from paler mottling on posterior third by arcuate paler band; tegmina with veins outlined in dark brown.

Male: length of crown 0.33 mm; width across eyes 0.85 mm; length 2.8-3.0 mm. Pygofer quadrate, concave ventrally, setose, armed with ventroapical process curved ventrad or caudoventrad (as in Fig. 28); subgenital plates short, appressed, tips obtuse, rounded; aedeagal shaft in lateral aspect curved dorsad (Fig. 16 A), in caudoventral aspect shaft short, parallel-margined, half as wide as aedeagal base, as wide as dorsal atrial arm, shaft armed with paired teeth near midlength, tip acute (Fig. 42); style tip nearly straight, coarsely toothed (as in Fig. 75); dorsal connective an X-shaped bar with elongate, slender arms extending to base of anal tube and shorter ones extending to atrial arm (Fig. 16 B).

Female: length of crown 0.4 mm; width across eyes 0.9 mm; length 2.9-3.1 mm. Pregenital sternite with large, black rounded lobes separated by narrow notch extending at least half way to base (as in Fig. 7).

Types. Holotype male, **USA.** *UT*- Tabiona, 11 June 1992 (K.G.A. Hamilton) [in dry tributary of Duchesne River ca. 4 km SE of town; on mixture of *Poa, Distichlis stricta* and other grasses]. Paratypes from **USA.** *UT*- 2 nymphs, 1 male, 4 females, same data as holotype; 2 nymphs, 2 males, 2 females, same data except 41 km SW Duchesne; 3 nymphs, 2 males, 1 female, same data, [2 km N] Mountain Home; 1 male, 1 female, Ouray, 4 Aug. 1986 (R.F. Whitcomb) 002506. All types No. 22377 in CNCI.

Remarks. All sites come from Duchesne and Uintah counties in NE Utah, but occur at a wide variety of elevations, from valley bottom in the Green River canyon at Ouray, 2000 m above sea level (ASL), to 2400m ASL in the Patmos mountains SW of Duchesne.

Hebecephalus chandleri sp.nov.

(Figs. 9, 13, 22, 36)

Etymology. Patronym, named for D.S. Chandler, who collected the type series.

Diagnosis. Males are distinguished from their Nearctic congeners by the narrow aedeagus with long processes; females resemble those of *H. vinculatus* (Ball) and *H. firmus* Beamer. The aedeagus is almost identical to that of *H. atralbus* Emeljanov (c.f. Figs. 13, 36 and Anufriev and Emeljanov 1988, plate 182 Figs. 10-11) from Siberia. The latter differs from the Nearctic species in a much darker wing colour (c.f. Figs. 1, 2) which is consistent in over 60 specimens from four localities (Emeljanov 1976) and a style without produced inner angle, a feature consistently visible (regardless of viewing angle) in four Nearctic species including *chandleri* (Figs. 63-64). The same four species have female pregenital sternites with close-set, pointed lobes (Figs. 9-10), which is probably an apomorphic character showing the close relationship of these species.

Description. Head obtusely pointed, crown 0.75x as long as width between eyes. Crown marked with 2 transverse, broken bars followed by 2-4 longitudinal streaks (as in Fig. 2); upper half of face black spotted with ivory, lower half variable from nearly uniform ivory, to heavily lined with black on sutures and margins; pronotum with pale, irregular dark brown markings on anterior third; tegmina with discal and costal cells black (as in Fig. 1), lying on oblique pale brown bands extending across discal and apical cells.

Male: length of crown 0.35 mm; width across eyes 0.95 mm; length 3.1 mm. Pygofer broad, apex furcate, upper lobe setose, unarmed (Fig. 22); subgenital plates long, appressed, apices obtuse as in *H. algidus*; aedeagus slender, shaft in lateral aspect strongly curved near midlength, bearing long processes directed caudad and toothed on anterior face just before spatulate tip (Fig. 13 A), in caudoventral aspect shaft slender, scarcely wider than strongly tapered atrial arm of bulbous aedeagal base, shaft armed with divergent preapical processes, tip pointed (Fig. 36); style tip bearing long, sinuate, narrow process finely toothed at base, and prominent, coarsely toothed inner angle (as in Fig. 64); dorsal connective a transverse bar with broad, twisted arms extending to base of anal tube (Fig. 13 B).

Female: length of crown 0.4 mm; width across eyes 1.0 mm; length 3.2-3.4 mm. Pregenital sternite with sharp-tipped, black lobes separated by slit extending less than half way to base (Fig. 9).

Type. Holotype male, **USA.** *WY*- Sibley Lake Campground in Bighorn Mountains, Sheridan Co., 22 July 1988 (D.S. Chandler). Paratypes: 6 females, same data as holotype. All types No. 22378 in CNCI.

Remarks. Emeljanov (1976) implied, but did not state, that the pygofers of *H. atralbus* resemble those of *H. algidus*. If so, the short, furcate pygofers of *H. chandleri* are unique.

Hebecephalus crenulatus sp.nov.

(Figs. 18, 28, 44, 67)

Etymology. Adjective: *crenulatus,* battlemented, in reference to the shape of the style.

Diagnosis. This species is based on a single male, but its wide, nearly toothless area on the style tip between prominent teeth is so distinctive that it cannot represent a mere variant of another species. Its exact affinities cannot be ascertained based only on the male characters analysed here. The notched style tip suggests an affinity with *H. hilaris* Beamer.

Description. Head roundedly produced, crown 0.75x as long as width between eyes. Crown marked with six dark spots usual for genus, the posterior pair by far the largest, nearly circular; upper half of face black spotted with ivory, lower half ivory spotted with black; pronotum mottled with brown; tegmina with veins outlined in dark brown.

Male: length of crown 0.3 mm; width across eyes 0.85 mm; length 3.1 mm. Pygofer (Fig. 28) and subgenital plates as in *H. abies*; aedeagal shaft in lateral aspect curved dorsad (Fig. 18 A), in caudoventral aspect shaft slender, scarcely wider than aedeagal base, as wide as dorsal atrial arm near midlength, shaft weakly expanded twice beyond midlength, tip bluntly pointed (Fig. 44); style tip elongate, coarsely toothed either side of wide, nearly toothless area between prominent inner and outer angles (Fig. 67); dorsal connective a short, narrow, transverse bar with large, wrinkled processes extending nearly to aedeagal shaft (Fig. 18 B).

Female [based on non-type material]: length of crown 0.35 mm; width across eyes 0.9 mm; length 3.2-3.3 mm. Pregenital sternite with rounded black lobes separated by narrow notch extending less than half way to base (as in Fig. 6).

Type. Holotype male, **USA.** *ID-* Mud Lake, 19 June 1984 (K.G.A. Hamilton) [silty sand area 2 km W of town; on mixture of *Agropyron, Oryzopsis* and wild oats]; No. 22379 in CNCI.

Remarks. Females taken at other Snake River plain sites (Arco, Howe and Rexbury) all have heads 1.0 mm wide, and are therefore not referable to this species. A series of females from an adjacent valley (Tendoy, ID) have longer, more distinctly produced crowns. Two females taken near the Utah border (15 km W Stone, ID) on 16 June 1992 by the author have the head proportions and colour similar to those of the male type of *H. crenulatus* and are here tentatively associated with this species, though not considered as type material.

Hebecephalus ferrumequinum sp.nov.

(Figs. 7, 17, 34)

Etymology. Noun in apposition: *ferru-,* of iron; *equus,* horse, in reference to the type locality, Railroad Canyon.

Diagnosis. This species is distinguished from its congeners by a combination of genital characters. The female is nearly identical to that of *H. abies* sp.nov. (only more angulate in the crown) and structurally similar to that of *H. borealis*, but distinctly smaller (see Diagnosis of *H. abies*). This species has an aedeagus nearly as strongly curved as that of *H. filamentus* Hamilton & Ross (Hamilton and Ross1972, Fig. 3) but the shaft is much longer and wider in proportion to the aedeagal base (c.f. Figs. 34, 35). From *H. filamentus* it also differs in the straighter, more strongly toothed style process (c.f. Figs. 73, 75).

Description. Head bluntly angled, crown 0.8x as long as width between eyes. Crown marked with six dark spots usual for genus (as in Beirne 1956, figs. 489-494); upper half of face and tip of clypellus black spotted with ivory; pronotum with irregular dark brown markings; tegmina with veins outlined in dark brown.

Male: length of crown 0.33 mm; width across eyes 0.9 mm; length 2.7-3.0 mm. Pygofer as in *H. crenulatus* (Fig. 28); subgenital plates appressed, tips produced, as in *H. crassus* (Beamer and Tuthill 1935, pl. LV Fig. 2); aedeagus slender, shaft in lateral aspect strongly curved anterodorsad (Fig. 17 A), in caudoventral aspect shaft about 2x wider than aedeagal base, shaft armed with tiny paired teeth just below gonopore and low, rounded prominences beyond

midlength, tip rounded (Fig. 34); style tip as in *H. crassus* (Fig. 75); dorsal connective a transverse bar with large, wrinkled processes (Fig. 17 B) extending half way to aedeagal shaft.

Female: length of crown 0.37 mm; width across eyes 0.95 mm; length 2.9-3.2 mm. Pregenital sternite with large, black rounded lobes separated by narrow notch extending at least half way to base (as in Fig. 7).

Types. Holotype male, **USA.** *ID*- Railroad Canyon 2200m ASL, 12 km NE Leadore, 4 June 1992 (K.G.A. Hamilton) [shallow slope alongside road; grasses mainly *Festuca idahoensis* Elmer]. Paratypes: 15 nymphs, 38 males, 19 females, same data as holotype. All types No. 22380 in CNCI.

Remarks. The type locality is the only known site for this species. It is 3 km W of the summit of Bannock Pass on the ID-MT border and lies 300 m lower than the pass.

Hebecephalus picea sp.nov.

(Figs. 8, 43, 70)

Etymology. Noun in apposition: *picea,* spruce tree genus, in reference to the shape of the aedeagus.

Diagnosis. The few females examined fall within the range of variation of *H. hilaris, H. beameri* Hamilton & Ross and *H. adversus*. The male is distinguished by its short, very broad aedeagal shaft which otherwise resembles that of *H. sagittatus*. These two species also differ in the styles: the teeth on the inner angle are more strongly developed in *H. picea*.

Description. Head parabolically produced, crown 0.95x as long as width between eyes. Colour and markings as in *H. abies*, but pronotum without pale band.

Male: length of crown 0.35 mm; width across eyes 0.9 mm; length 2.8-2.9 mm. Pygofer as in *H. abies* (Fig. 28); subgenital plates short, tips rounded; aedeagus short, shaft in lateral aspect weakly sinuate, curved dorsad at tip (as in Fig. 15 A), in caudoventral aspect shaft broadly triangular, wider than aedeagal base and twice as wide as dorsal atrial arm at midlength, shaft armed with two pairs of small teeth near midlength, tip bluntly pointed (Fig. 43); style tip with stout process strongly tapered almost to a point, coarsely toothed on inner angle (Fig. 70); dorsal connective as in *H. ferrumequinum* (Fig. 17 B).

Female: length of crown 0.4 mm; width across eyes 1.0 mm; length 3.1-3.2 mm. Pregenital sternite with large, black pointed lobes separated by V-shaped notch extending at least half way to base (Fig. 8).

Type. Holotype male, **USA.** *ID*- 10 km NW Mackay, 19 June 1984 (K.G.A. Hamilton) [stony plain with scattered clumps of *Oryzopsis hymenoides* (Roem. & Schult.)]. Paratypes: 2 nymphs, 1 male, 2 females, same data as holotype. All types No. 22381 in CNCI.

Remarks. The type locality was revisited on 6 June 1992 but no additional specimens of *Hebecephalus* were found. Unassociated females taken elsewhere in southern Idaho have rounded pregenital lobes separated by a narrower notch and cannot be the same species although their identity cannot be established with certainty (see Remarks under *H. crenulatus*).

Hebecephalus planaria sp.nov.

(Figs. 27, 47, 73)

Etymology. Noun in apposition: *planaria,* flatworm genus, in reference to the shape of the aedeagus.

Diagnosis. Females of this species cannot be distinguished from those of many other *Hebecephalus*. Males have a broad, flat aedeagal shaft that is unique in the genus. The relationship of this species to its congeners is obscure at present.

Description. Head bluntly pointed, crown 0.8x as long as width between eyes. Colour and markings as in *H. abies*, but pronotum without pale band, or this narrow and irregular.

Male: length of crown 0.38 mm; width across eyes 0.9 mm; length 3.3-3.6 mm. Pygofer parallel-margined as far as short ventral spur directed caudad, apex short and bluntly conical, setose (Fig. 27); subgenital plates short, tips rounded; aedeagus large, shaft in lateral aspect nearly straight, curved dorsad near base (as in Fig. 11 A), in caudoventral aspect shaft broad, half as wide as aedeagal base, scarcely narrower than apex of dorsal atrial arm, shaft armed with paired preapical teeth, tip pointed (Fig. 47); style tip strongly curved, finely toothed, inner angle absent (Fig. 73); dorsal connective as in *H. chandleri* (Fig. 13 B).

Female: length of crown 0.4 mm; width across eyes 1.0 mm; length 3.5-3.7 mm. Pregenital sternite with rounded, black lobes separated by narrow notch extending less than half way to base (as in Fig. 6).

Types. Holotype male, **Canada.** *BC*- 10 km NE Douglas Lake, 5 June 1987 (K.G.A. Hamilton) [shallow valley in rangeland; on *Poa pratensis* L.] Paratypes: 6 males, 11 females, same data as holotype. All types No. 22382 in CNCI.

Remarks. Although samples were taken at four other sites in the same extensive ranch area (over a distance of 22 km) no additional populations of this species were found. Unassociated females from other sites in southern BC are too small to be this species.

Hebecephalus pugnus sp.nov.

(Figs. 6, 14, 23, 49, 66)

Etymology. Noun in apposition: *pugnus,* fist, in reference to the shape of the style.

Diagnosis. Females of this species cannot be distinguished from those of many other *Hebecephalus*. Males have an unique style, its tip resembling in outline a fist with thumb extended. The relationship of this species to its congeners is obscure at present.

Description. Head parabolically produced, crown 0.8x as long as width between eyes. Colour and markings as in *H. abies*, but pronotum without pale band.

Male: length of crown 0.35 mm; width across eyes 0.8 mm; length 3.0-3.4 mm. Pygofer weakly tapered, distinctly constricted at midlength, apex with rounded lobes above and below short spine directed caudodorsad, upper lobe setose (Fig. 23); subgenital plates as in *H. ferrumequinum*; aedeagus long, shaft in lateral aspect curved dorsad at base and weakly curved cephalad near tip, nearly straight between (Fig. 14 A), in caudoventral aspect shaft slender, scarcely wider than aedeagal base, shaft armed with low, paired teeth below midlength and spiniform processes a quarter length of shaft on rounded tip of shaft (Fig. 49); style tip short, coarsely toothed, those on inner angle most prominent, that on outer angle slender, resembling an extended thumb on a clenched fist (Fig. 66); dorsal connective a transverse plate with slender, curved arms extending to base of anal tube and shorter ones to atrial arm of aedeagus (Fig. 14 B).

Female: length of crown 0.38 mm; width across eyes 0.9 mm; length 3.0-3.4 mm. Pregenital sternite with rounded, black lobes separated by narrow notch extending less than half way to base (Fig. 6).

Types. Holotype male, **USA.** *ID*- 12 km S Hamer, 19 June 1984 (K.G.A. Hamilton). Paratypes: 3 males, 4 females, same data as holotype; 1 nymph, 2 males, 3 females, Willow Ck. Summit 2350m ASL, SE Challis, 19 June 1984 (K.G.A. Hamilton). All types No. 22383 in CNCI.

Remarks. An unassociated pair of females from the vicinity of the type locality (9 km W Rexburg, ID) was collected on 19 June 1984 by the author.

Hebecephalus veretillum sp.nov.

(Figs. 12, 20, 33, 68)

Etymology. Noun in apposition: *veretillum,* little genitalia.

Diagnosis. This species is based on a single male. Its unarmed pygofer and small, slender aedeagus suggests that it is deformed, but its slender, serrate, blade-like style tip is distinctive and

unlike the lobate style tips of abnormal specimens. Its exact affinities cannot be ascertained based only on the male characters analysed here. Possibly it represents a basal lineage in the genus.

Description. Head parabolically produced, crown 0.95x as long as width between eyes. Crown marked with six dark spots usual for genus (as in Beirne 1956, figs. 489-494); face black spotted with ivory, largely pale on genae; pronotum with irregular dark brown markings on anterior third separated from paler mottling on posterior third by arcuate paler band; tegmina with veins outlined in dark brown, except on basal fifth, on costal cross veins and vein tips, and on oblique pale band extending across bases of anteapical cells.

Male: length of crown 0.32 mm; width across eyes 0.8 mm; length 2.5 mm. Pygofer conical, slightly constricted just beyond midlength, highly setose but otherwise unarmed (Fig. 20); subgenital plates elongate, apically divergent, tips obtuse; aedeagus small, shaft in lateral aspect nearly straight, curved dorsad at tip (Fig. 12 A), in caudoventral aspect shaft slender, scarcely wider than aedeagal base, shaft armed with paired teeth near midlength, tip rounded (Fig. 33); style tip narrow, finely toothed, those on inner angle most prominent (Fig. 68); dorsal connective a transverse bar with slender, twisted arms extending to base of anal tube (Fig. 12 B).

Female unknown.

Type. Holotype male, **USA.** *ID*- Ketcham, 18 June 1992 (K.G.A. Hamilton) [W-facing slope at N edge of town; on mixture of *Poa, Agropyron* and *Elymus*]; No. 22384 in CNCI.

Remarks. A revisit to the type locality on 28 May 1995 failed to find any additional specimens of *Hebecephalus*, possibly because the spring was unusually late that year and the grasses were still quite low.

CONCLUSIONS

Localized populations of *Hebecephalus* are highly regionalized in areas that suffered moderate Pleistocene glaciation. Of the 27 Nearctic species known to date, all but six have been found in or adjacent to Idaho (ID: Table 2), and at least half of the species probably inhabit that one state. British Columbia has the next largest fauna of *Hebecephalus* (nine species), Wyoming has seven, while Utah and Montana have six each. Additional, as yet undiscovered, species are likely to be found in these five political areas plus the adjacent state of Washington, which has four such species. All other states and provinces have five or fewer species of *Hebecephalus* and additional species are not anticipated from these areas.

Endemism is also reflected in the small number of sites where regionalized species were found. Nine species are presently known from only a single site (marked by an asterisk in Table 2). Four of these sites are in Idaho, and four others are in adjacent political areas (BC, NV, WY). Repeated collecting there has yielded additional populations of such regionalized species in only four cases (or possibly five; see *H. crenulatus* sp.nov.)

Conversely, five other species of *Hebecephalus* are among the most widespread of grassland leafhoppers (boldfaced in Table 2), ranging from Utah north to the Yukon, or Alaska east to northern Québec, and from Arizona east to Illinois, with very large gaps between populations. These five widespread species include at least two pairs of closely related species and thus appear to represent cases of divergence in lifestyle. The remaining nine species are usually known from only two or three states or provinces, while *H. callidus* (Ball) is slightly more widespread, being found in southern British Columbia and its three adjacent states: ID, MT, WA. In short, a few of species in this genus are exceptionally good dispersers while the majority have unusually restricted distributions for grassland leafhoppers.

Many species in this genus are found only within certain valleys or passes in the Rocky Mountains where their host grasses are common. Such endemism cannot be attributable to the restricted range of a single host plant. Most species of *Hebecephalus* are generalist feeders on

Table 2

Check list and distribution of Nearctic species of *Hebecephalus*. Boldfaced: widely distributed species. Asterisk (*): known from only one site.

abies sp.nov. - UT
adversus Beamer & Tuthill - MT, NV[1], OR [+*ID?*]
***algidus* DeLong & Davidson - AK; AB, BC, MB, NF, NT[2], QC, YK**
beameri Hamilton & Ross - *AK
borealis DeLong & Davidson - AB, BC, SK
caecus Beamer - ID, OR
callidus (Ball) - ID, MT, WA; BC
chandleri sp.nov. - *WY
circus Hamilton & Ross - CO, UT
crassus DeLong - ID, WY; BC [*YK* = see *sagittatus*]
[*creinus* Beirne: see *borealis, algidus*]
crenulatus sp.nov. - *ID
discessus Beamer & Tuthill - CA
ferrumequinum sp.nov. - *ID
filamentus Hamilton & Ross - UT, WY
firmus Beamer - MT, WA, WY[3] [+ *ID?*]
hilaris Beamer - *WY
irritus Beamer - *NV
[*mornus* Beirne: see *occidentalis*]
***occidentalis* Beamer & Tuthill - AK, AZ, CO, ID, MT, ND, OR, SD, UT, WA, WY; AB, BC, SK, MB, YK**
[*pedecurtus* Wittlake & Beamer: see *rostratus*]
picea sp.nov. - *ID
planaria sp.nov. - *BC
pugnus sp.nov. – ID
***rostratus* Beamer & Tuthill - AZ, CO, ID, IL[4], KS, MT, NM, ND, OR, SD, UT, WA, WY; AB, BC, MB** [+*NE?*[5]; *YK* = see *truncatus*]
***sagittatus* Beamer & Tuthill - ID, OR, UT; BC, YK** [*IL* = see *rostratus*]
signatifrons (Van Duzee) - AZ, CO
***truncatus* Beamer & Tuthill - MT; AB, BC, MB, SK, YK[6]** *[+ID?]*
veretillum sp.nov. - *ID
vinculatus (Ball) - CO [*WY* = see *firmus*]

[1]Incorrectly recorded (Beamer and Tuthill 1935) from "Barclay, Utah"
[2]Incorrectly recorded (Beirne 1956) as *H. creinus*.
[3]Incorrectly recorded (Beamer and Tuthill 1935) as *H. vinculatus*.
[4]Incorrectly recorded (DeLong 1948) as *sagittatus*.
[5]Unverified record by DeLong (1926).
[6]Incorrectly recorded (Hamilton 1997) as H. *rostratus*.

Festuca, Muhlenbergia, Oryzopsis, Poa, Puccinellia, Spartina and *Stipa*. Only one species of *Hebecephalus* is recorded from a single grass host: *H. adversus* Beamer & Tuthill on giant wild rye, *Elymus cinereus* Scribn. & Merr. in Montana. Instead, the members of *Hebecephalus* are usually restricted to areas where mixtures of cool-season grasses are dominant (such leafhoppers are seldom monophagous). Such open grasslands must have been very limited in the Pacific Northwest during the cold and wet era of the Pleistocene, probably restricted to steep, sun-warmed, south-facing slopes in suitable valleys. This suggests that the high degree of endemism in *Hebecephalus* results from highly isolated glacial-age populations.

Unfortunately, detailed patterns of distribution are not yet discernible. Much additional collecting in the Pacific Northwest will be needed to confirm the hypotheses of regional endemism and geographic isolation.

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