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LARVAL TAXONOMY, PHYLOGENY AND  
HISTORICAL BIOGEOGRAPHY OF THE  
GENUS CHEUMATOPSYCHE  
(TRICHOPTERA: HYDROPSYCHIDAE) IN  
NORTH AMERICA

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LARVAL TAXONOMY, PHYLOGENY AND HISTORICAL BIOGEOGRAPHY OF  
THE GENUS *CHEUMATOPSYCHE* (TRICHOPTERA: HYDROPSYCHIDAE) IN  
NORTH AMERICA

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A Thesis  
Presented to  
the Graduate School of  
Clemson University

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In Partial Fulfillment  
of the Requirements for the Degree  
Master of Science  
Entomology

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by  
Zachary Louis Burington  
May 2011

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Accepted by  
John C. Morse, Committee Chair  
Peter H. Adler  
Bryan L. Brown

## ABSTRACT

Larvae of the genus *Cheumatopsyche* (Trichoptera:Hydropsychidae) are a abundant and probably significant ecological component of freshwater lotic ecosystems worldwide, with many species inhabiting streams with elevated organic pollution. The varying tolerance levels among these species necessitate species-level identification for accurate water-quality assessment. However, past workers have had difficulty separating the Nearctic species in the larval stage. This research presents progress on the goal towards identification of larval *Cheumatopsyche*. Chaetotaxal and cuticular characters are delimited for 7 larval morphotypes, all of which have been putatively associated with adults. The Nearctic phylogeny of *Cheumatopsyche* is revised, including 5 species described after 1987. The distribution of larval characters is hypothesized with reference to the phylogeny, including 3 main species groups. Biogeographic relationships for Nearctic areas of endemism are inferred cladistically.

## ACKNOWLEDGEMENTS

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## I. INTRODUCTION

The family Hydropsychidae is a cosmopolitan and speciose group of Trichoptera, inhabiting all faunal regions except Antarctica. Larvae of this family build retreats in streams and rivers, with silken seine-like nets for collection of suspended fine particulate organic matter (FPOM) or invertebrates drifting in the current (Wiggins 2004). Like most Trichoptera larvae, hydropsychids are sensitive to changes in dissolved oxygen levels and organic pollution. However, a single genus such as *Hydropsyche* contains species with a wide range of tolerances (Barbour et al. 1999). Hydropsychid caddisflies have been extensively used in biomonitoring through indices of water quality such as the EPT index (Lenat 1988), and Hilsenhoff's Biotic Index (Hilsenhoff 1982). Hydropsychid caddisflies are also important organisms in freshwater ecology due to their density in some streams (Oswood 1979), serving as a primary source of food for fish.

Among the most ubiquitous of these organisms are species of the genus *Cheumatopsyche*. First described by Wallengren (1892), the genus is found in all faunal regions except the Neotropics and Antarctica. Presently, there are 341 described species of *Cheumatopsyche* in the world, 45 species of the genus in North America north of Mexico, and 21 in the Carolinas (Morse 1997, 2011). Larvae of *Cheumatopsyche* are found in streams and rivers throughout North America below the treeline (Morse 1993). While these species have a wide range of tolerances, the most common species are more tolerant than most other hydropsychid caddisflies (Wiggins 1996). *Cheumatopsyche* larvae can often be successful in polluted streams where other caddisflies are absent (Ross 1944). While the genus *Hydropsyche* has more species, *Cheumatopsyche* is the dominant Trichoptera group worldwide with larval densities sometimes exceeding 200,000 m<sup>2</sup> (Gibbs 1973). In the Nearctic faunal region, all *Cheumatopsyche* larvae are distinct from larvae of other hydropsychids by the following combination of characters:



The bifid foretrochantins, a notch in the posterior margin of each of the sternal plates on abdominal segment IX, an anterior and tiny posterior ventral apotome not completely separating the 2 parietal sclerites, absence of a tubercle on the anterior ventral apotome (Pescador et al. 1995), and the presence of either a pair of minute sclerites posterior to the prosternal plate or a pair of larger prosternal sclerites with a notch on the anterior margin of the frontoclypeus (Wiggins 1996).

Water-quality assessment requires accurate identification of organisms to the lowest taxonomic level possible; this is because species within a more-inclusive group may have a wide range of tolerances to organic pollution (Lenat 1993, Lenat & Resh 2001, Bailey et al. 2001, Jones 2008). Earlier workers (Schuster & Etnier 1978, Scheffer & Wiggins 1986) have found characters to diagnose the larvae of most hydropsyhid genera in the Nearctic region, including the large genus *Hydropsyche*. However, taxonomists have struggled to find any means of separating *Cheumatopsyche* larvae to the species level (Ross 1944, Wiggins 1996). In other faunal regions, differences are often distinct, and consistent characters have been found to separate these (Statzner 1984). Gordon (1974) has covered the taxonomy and phylogeny of Nearctic *Cheumatopsyche* adults in detail, excluding 5 more-recently described species (Lago & Harris 1983, Gordon et al. 1986, Moulton & Stewart 1996).

Although Nearctic *Cheumatopsyche* larvae are undiagnosed at the species level currently, some possible characters for diagnosis have been investigated. Herbert Ross (1944) was the first person to note differences in the size and shape of the frontoclypeal notch. The size and shape of this notch has also been shown to vary consistently among some species (Smith 1984), and from initial investigations there also seems to be some variation in the adjacent scalloping and ridges of the frontoclypeal margin. Scheffer and Wiggins (1987) demonstrated with previously associated specimens that the presence or

absence of the notch is consistent between the *C. sordida* and *C. gracilis* Species Complexes proposed by Gordon (1974), being present in the latter and absent in the former. Schefter and Wiggins (1987) also showed consistent variation in the distribution of hairlike setae, brushlike setae and minute spines on the head, thorax and abdomen, and were able to diagnose 10 of the 14 available associated species through these characters alone (Schefter, pers. com.). Thus, chaetotaxy and the emargination and scalloping of the frontoclypeus are currently the most promising character sets for diagnosis.

Morphometric characters, including head capsule width-to-length ratio, have been used to separate 2 species at their various instars (Mackay 1978). While the size of the post prosternal plate sclerites of most *Cheumatopsyche* larvae are characteristically small, in *C. etrona* (and possibly related species) they are larger and similar to those of *Hydropsyche* species (Wiggins 1996). Statzner (1984) comprehensively covered a large number of both morphometric and chaetotaxal characters for diagnosis of Afrotropical *Cheumatopsyche* larvae. While the African fauna comprises different species, some of the characters (e.g., the extensively photographed and measured stridulatory ridges) may be still useful for diagnosing North American species. Keys for *Cheumatopsyche* larvae of the Ivory Coast were produced by Statzner (1984) and were the primary impulse for later investigation of setal characters in Nearctic species. Dean (1999) created a larval key based upon 18 morphotypes of Australian *Cheumatopsyche* species, 6 of which were later confirmed to be genetically distinct (Baker et al. 2003).

One of the difficulties with larval diagnosis is the initial adult-larvae species association. Classical techniques include rearing and the Metamorphotype Method (Milne 1938). These are often time consuming, requiring an elaborate aquarium and flow and filter setup or extensive field collecting. Recently, several molecular-based alternatives have been investigated (e.g., Zhou et al. 2007). In addition, Nishimoto et al. (2002) found

cuticular hydrocarbons to be characteristic at the species level and useful for making larval-adult association. Enzymes also are diagnostic in the adults of several Japanese *Cheumatopsyche* species (Hayashi 1998) and subsequently been used in adult-larvae associations (Hayashi & Yun 1999).

The most promising method of association is the use of mitochondrial Cytochrome *c* Oxidase I (mtCOI) gene. COI is a gene found in all animal mitochondrial DNA and mutates rapidly enough to differ among most species (Hebert et al. 2003). Adult-larval associations through COI gene sequencing and comparison have been successful in Coleoptera (Caterino & Tishechkin 2006, Miller et al. 2005). Zhou et al. (2007) demonstrated the utility of this method in associating Chinese hydropsychid larvae. They also described factors that contribute to successful adult-larva association, including adequate numbers of sequenced adults, preservation methods, the necessity of collecting adults in close temporal-spatial proximity, and criteria of COI gene sequences indicating levels of association. Currently there is a worldwide Trichoptera 'barcoding' initiative to sequence adults of all described species of Trichoptera in all faunal regions. The Trichoptera Barcode of Life database already has sequences for some Nearctic *Cheumatopsyche* species (Trichoptera Barcode of Life 2008). However, the sequence divergence between species is slight or not apparent in most complexes of Nearctic *Cheumatopsyche* species (Xin Zhou, pers. comm.), so using this method for association is not possible for those groups.

The purpose of my research is to resolve in part the larval taxonomy of Nearctic *Cheumatopsyche* by distinguishing and associating larval morphotypes with species and species groups. Additionally, recent evidence allows for presentation of a revised phylogeny with hypotheses of larval character distribution, and a biogeographic analysis of Nearctic areas of endemism.

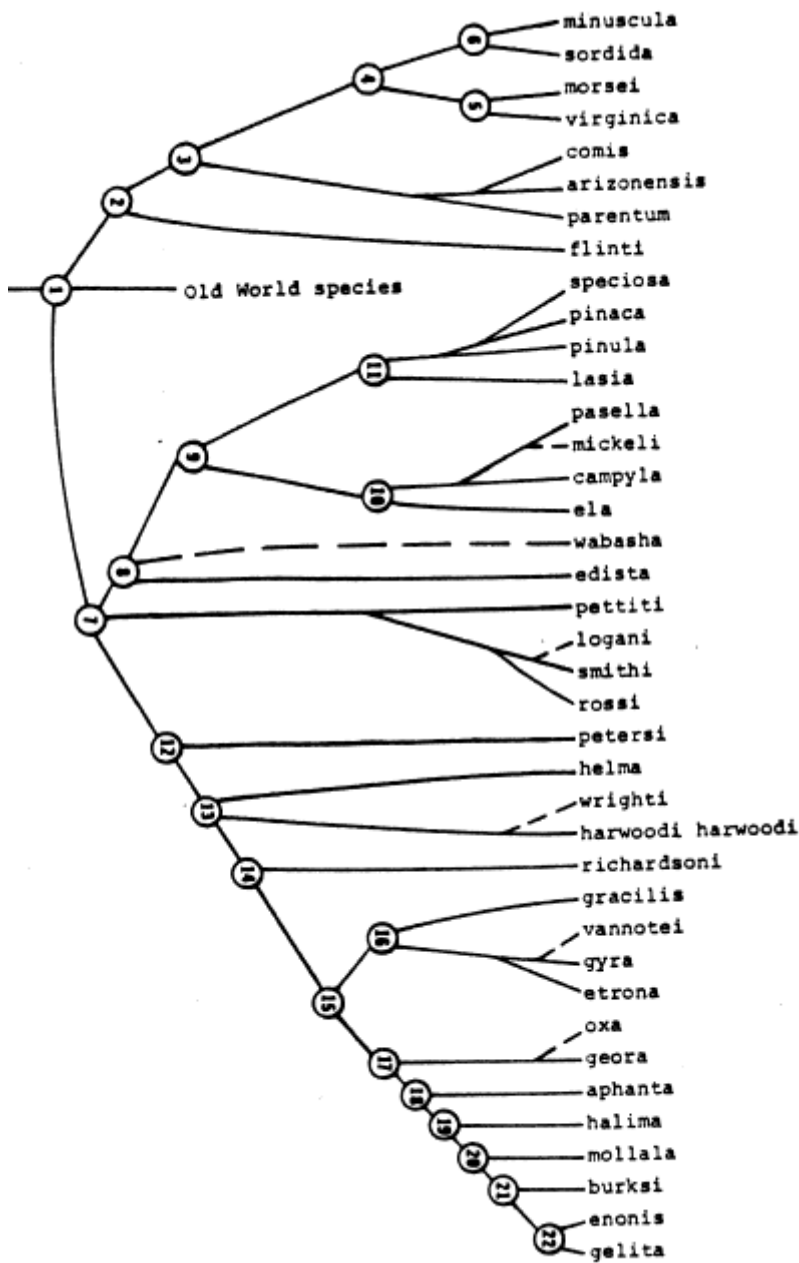


Figure 1. Phylogeny of Nearctic *Cheumatopsyche* species, excerpted from the work of Gordon (1974). Numbers at nodes represent character transformations as mentioned in the previous study. Dashed lines represent Gordon's tentative placements.

## II. METHODS AND MATERIALS

Approximately 200 specimens were studied in detail; the majority of these were museum specimens from the Royal Ontario Museum, Toronto, Ontario, Canada, and the Clemson University Arthropod Collection, Clemson, South Carolina, USA. Adult-associated specimens (via rearing) were studied when possible. While the larval instar (1-5) of studied specimens was unknown, the largest specimens were chosen for detailed study. Individual specimens were cleaned with a fine paintbrush, and severed between the 1st and 2nd abdominal segments. The specimens were then boiled in 10% potassium hydroxide (KOH) or lactic acid to clear the internal tissue. Lactic acid was favored over KOH as it does not attack the cuticle, regardless of the time spent clearing, though it does tend to make tissues expand and can crack the cuticle. Clear specimens were placed in glycerine on a well depression slide and viewed at 200x under a Wild M5 dissecting microscope, and up to 400x under a compound microscope. Drawings were made with the aid of a gridded eyepiece. Heads were sometimes removed and positioned with an insect pin for dorsal orientation. Some specimens were subsequently mounted permanently in Canadian balsam. Comparisons were made and individuals were separated into morphotypes. Adult-associated larvae were assigned species identifications. Identities of other specimens were established by distributional records when possible.

Gordon's (1978) phylogenetic inferences were investigated and, with aid of her morphological notes, informative characters were reconstructed and cataloged. Plesiomorphies were determined by reference to the outgroup *Hydropsyche elissoma*. Individual characters were cataloged as plesiomorphic (0), apomorphic (1) or missing or unavailable (-) for each species previously included in the phylogeny, as well as for *C. robisoni*, *C. gordonae*, *C. kinlockensis*, *C. cahaba*, and *C. bibbensis*, which were

described since Gordon's (1978) work. A complete list of characters and the finished matrix are included in the appendices. A heuristic analysis was run in NONA 2.0 via WinClada 1.00.08 with a Multiple TBR + TBR (multi\*max\*) search strategy and the following options: maximum number of trees to hold=100, number of replications=1, starting trees per replication=1, random seed=0, and unconstrained search. The resulting tree was collapsed by majority rule consensus. Species groupings were compared with those of Gordon (1974) (Fig. 1), and the more-recently described taxa were included. Larval characters were mapped to the updated phylogeny by their known distribution among species.

Areas of endemism for North America were determined by parsimony analysis of endemism (PAE) (Crisci et al. 2003). States and provinces were coded as taxa, and species coded as characters. Each state or province was coded as absent (0) or present (1) for each species-character. An imaginary outgroup area was coded with all characters as absent (0) for polarization purposes. A heuristic analysis was completed as above. Following the initial analysis, cosmopolitan species occupying 10 or more states or provinces were removed to eliminate non-pattern, and the heuristic analysis was repeated. The most contiguous clusters of states were collapsed under a temporary name, cosmopolitan species occupying 5 or more states were removed, and heuristic analysis was repeated. The remaining contiguous clusters of states were considered as endemic area hypotheses. The original matrix and distributional catalog of species are included in Appendix III and IV. Areas of endemism were mapped to the majority consensus cladogram as replacements for species names, and the tree was stripped of polytomy so that only unresolved subtrees remained. Branches containing all areas of endemism were removed and the subtrees were collapsed, yielding reduced, congruent subtrees which were combined into a single areagram of endemic area relationships.

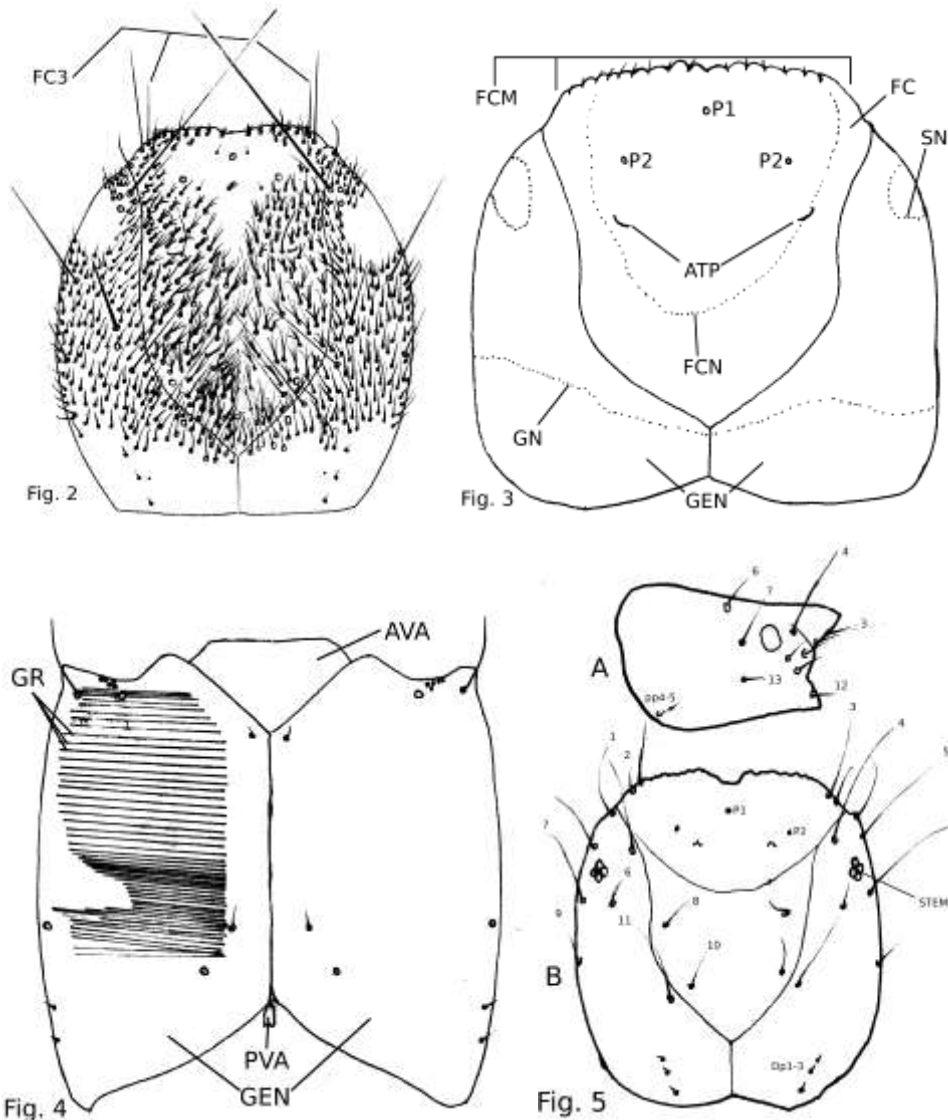
### III. RESULTS

#### A. Taxonomy

***Morphology and Chaetotaxy.*** General larval caddisfly morphology has been previously covered in detail (Wiggins 1996, 2004). Naming conventions for primary setae are *sensu* Mathis (1992, 1997). As the following is a concise summary, only closely examined characters will be discussed.

Head capsules of Nearctic *Cheumatopsyche* are composed of 5 sclerites: the anterodorsal frontoclypeus; the 2 dorsolateral genae, which attach to the frontoclypeus at the coronal lines and curve laterally around the head ending ventrally at the ventral ecdysial line; and 2 small plates, the anterior and posterior ventral apotomes, which lie at the ends of the ventral ecdysial line between the genae. Anterior to the head sclerites, the labrum is attached to the frontoclypeus, the mandibles articulate with the genae, and the lower lip complex (a combination of maxillae and labium) are attached ventrally to the anterior ventral apotome (Figs. 1 and 2).

In Nearctic *Cheumatopsyche* species, the anterior margin of the frontoclypeus is sculpted in a series of crenulations or scallops. These scallops either span the entire length of the frontoclypeal margin (Fig. 6), or are interrupted midway in a flattened or angled notch (Figs. 7-9, 11). Between each scallop arises a stiff, brush-like (*bl*) secondary seta (Fig. 12H) that projects beyond the margin. Medial to lateral, the scallops become less pronounced and the *bl* setae closer together, until primary head seta 3 where the margin becomes smooth and the *bl* setae stop. The presence, depth and shape of the



**Figures 2-5. Features of *Cheumatopsyche* head capsule** (mouthparts not shown). 2, Morphotype D (*C. analis*), dorsal view, with primary setae, secondary setae, and sensory pits; 3, Morphotype D (*C. probably richardsoni*), dorsal view, with setae other than those on the frontoclypeal margin not shown. 4, Morphotype D (*C. analis*), ventral view, with genal ridges shown on only one side. 5, Primary setation of a first instar *Cheumatopsyche* larva with primary setae numbered 1-13, anterodorsal to posteroventral: A, right lateral view; B, dorsal view. ATP=anterior tentorial pits, AVA=anterior ventral apotome, Dp1-3=dorsal prioreceptors, FC=frontoclypeus, FC3=head setae three, FCM=frontoclypeal margin, FCN=frontoclypeal nodus, GEN=genae, GN=genal nodus, GR=genal ridges, P1-P2=sensory pits, pp4-5=ventral prioreceptors, PVA=posterior ventral apotome SN=stemmatal nodus,



frontoclypeal notch and the position of marginal *bl* setae in relation to the notch are diagnostic for some morphotypes.

The dorsum of the head is covered in a number of secondary setal types (Fig. 2) and, while not yet found to be diagnostic, they may be useful in separating morphotypes not yet examined. Posterolateral of the frontoclypeal margin and anterior of the stemmata on the frontoclypeus is another series of short, stout brush-like (*bl*) setae. Anterior to posterior on the frontoclypeus, the setae increase in length and are bifid (*bf*) and multiply branched (*mb*) (Fig. 12G). These *bf* and *mb* setae continue to the occiput where the coronal lines meet the short, dorsal ecdysial line. Often along this corner margin and posterior of it on the genae, there are long, fine hair-like (*lhl*) setae (Fig. 12E), which taper gradually and are of relatively equal width from their base to the middle of their length. Laterally on the genae, the setae become short and hair-like (*shl*), and taper strongly from the base, with the diameter at midlength half that of the base (Fig. 12A). These setae also sometimes have an elongate flagellate portion toward the tip, but are never as long as *lhl* setae. The above secondary setal types extend posteriorly to a genal nodus, a line past which the secondary setae are not found. The genal nodus continues ventrolaterally and ends at the anterolateral edges of the genae. Three other areas on the head capsule are consistently bare of secondary setae and defined by a clear nodus: the anterior portion of the frontoclypeus, often T-shaped, extending posteriorly to the anterior tentorial pits and laterally to the non-marginal *bl* setae, and a circular region surrounding each group of stemma (“eye”) (Figs. 3 and 11). Within the former region are 3 round sensory pits, 1 just posterior of the frontoclypeal margin medially (P1), and 2 others in a sagittal line with the anterior tentorial pits (P2). The 3 sensory pits form an oblique triangle (Fig. 3), and while not yet known to have any morphometric use for diagnosis, are helpful in orienting the head as landmarks on the frontoclypeus. The nodi around the

stemmata are useful for determining the eyes' positions after clearing removes the optical tissue.

The thorax of *Cheumatopsyche* is covered dorsally with 3 separate sclerites, 1 for each thoracic segment: the pronotum, mesonotum and metanotum. The anterior margin of each notum possesses a line of secondary setae. On the pronotum, the setal type may transition along the margin, with *shl* setae laterally and *lhl* setae medially. Long hair-like setae on the prothorax sometimes extend one-quarter the length of the head capsule, and are usually covered with a light-colored flocculent material, as are the posterior setae of the head. Careful cleaning is necessary to determine the length accurately. The *lhl* setae also often become tangled in glycerine, but this usually does not hinder the determination of length if the setae are completely submerged. The anterior margins of the mesonotum and metanotum usually have *shl* setae, except in one morphotype where these margins bear crochet-like (*chl*) setae (Fig. 12F). These resemble the crochet hooks of Lepidopteran prolegs, as *chl* setae are short and curved, with a rounded base and a laterally flattened, pointed tip.

The non-marginal areas of the thoracic nota are covered with *shl* setae arranged randomly in rows. Near the anterior margin of the pronotum there are often 1 or 2 *bf* setae. Although the number of *bf* setae is not consistent, there are, in general, more prothoracic *bf* setae in those morphotypes lacking a frontoclypeal notch. In addition to setae, the dorsum of the larval thorax and abdomen are armed with variously organized rows of microscopic spines (*ms*). These cuticular armaments vary in size and shape from rounded and rivet-like to pointed, although fine points are often broken or missing (Figs. 12B-D, 13-14). On the mesonotum and metanotum, *ms* are arranged, if present, in straight lines or close together in wavy rows, respectively. Mesonotal *ms* are often faint

and apparent only near the medial posterior margin, while metanotal *ms* are usually distinct throughout the sclerite. Microspines have been found on the pronotum of only 1 specimen; as the morphotype has not been replicated it is not defined below. Abdominal *ms* are found on the first 3-5 terga and directed posteriorly and, unlike the thoracic *ms*, can be found in multiple sizes on a single segment. The presence or absence of larger (>15  $\mu\text{m}$ ) abdominal *ms* is useful for separating some morphotypes.

In total, specimens examined have been consistently separated into 7 morphotypes by the characters described above.



Fig. 6



Fig. 7

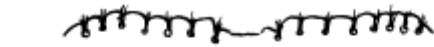


Fig. 8

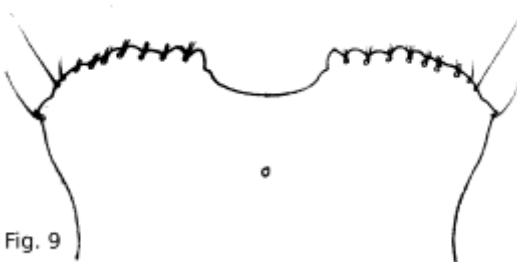


Fig. 9

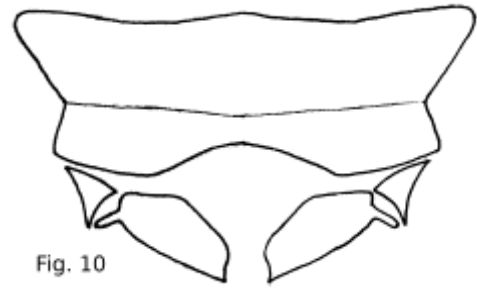


Fig. 10

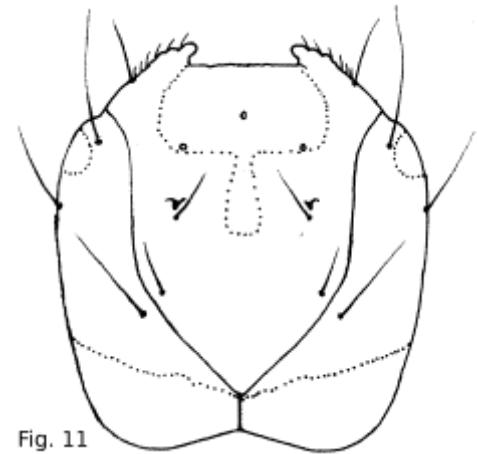


Fig. 11

**Figures 6-9. Frontoclypeal margin, dorsal view.**

6. Morphotype B (*C. probably virginica*), 7. Morphotype G (*C. campyla*), 8. Morphotype D (*C. analis*), 9. Morphotype E (*C. probably etrona*). **Figure 10. Prosternal plates of Morphotype E (*C. probably etrona*).** **Figure 11. Head capsule of Morphotype F, dorsal view.** Nodi are figured as dotted lines.

***Key to the known morphotypes of Nearctic Cheumatopsyche larvae.***

1. Frontoclypeus lacking notch; marginal *bl* setae and scallops uninterrupted between 3rd primary head setae (Fig. 6).....2
- 1'. Frontoclypeus with notch; marginal *bl* setae and scallops interrupted medially on frontoclypeal margin (Figs. 7-9, 11).....4
- 2(1). At least some abdominal *ms* greater than 15  $\mu\text{m}$  in length (Fig. 14).....3
- 2'. All abdominal *ms* less than 15  $\mu\text{m}$  in length (Fig. 13).....Morphotype A
- 3(2). Pronotal *lhl* setae longer than  $\frac{1}{4}$  length of pronotum.....Morphotype B
- 3'. Pronotal margin with *shl* setae shorter than  $\frac{1}{4}$  length of pronotum ..Morphotype C
- 4(1') Frontoclypeal notch shallow and narrow, with annuli of the most medial *bl* setae at or posterior to level of notch (Fig. 8); pronotal margin with *lhl* setae (Fig. 12E).....Morphotype D
- 4'. Frontoclypeal notch deep and square, rounded or acute, with annuli of the most medial *bl* setae anterior to base of notch (Figs. 7, 9, and 11); pronotal margin with or without *lhl* setae.....5
- 5(4'). Frontoclypeal notch various, but usually as in Fig. 9; prosternum with 2 pairs of detached sclerites, 1 large and 1 minute (Fig. 10) ..... Morphotype E
- 5'. Frontoclypeal notch with base and sides at right angles or overhanging (Fig. 7, 12); prosternum with single pair of detached, minute sclerites .....6
- 6(5'). Frontoclypeal notch with sides at acute angle with base, the most medial scallops overhanging the notch (Fig. 12); total notch width at least one-third width of

Fig. 12

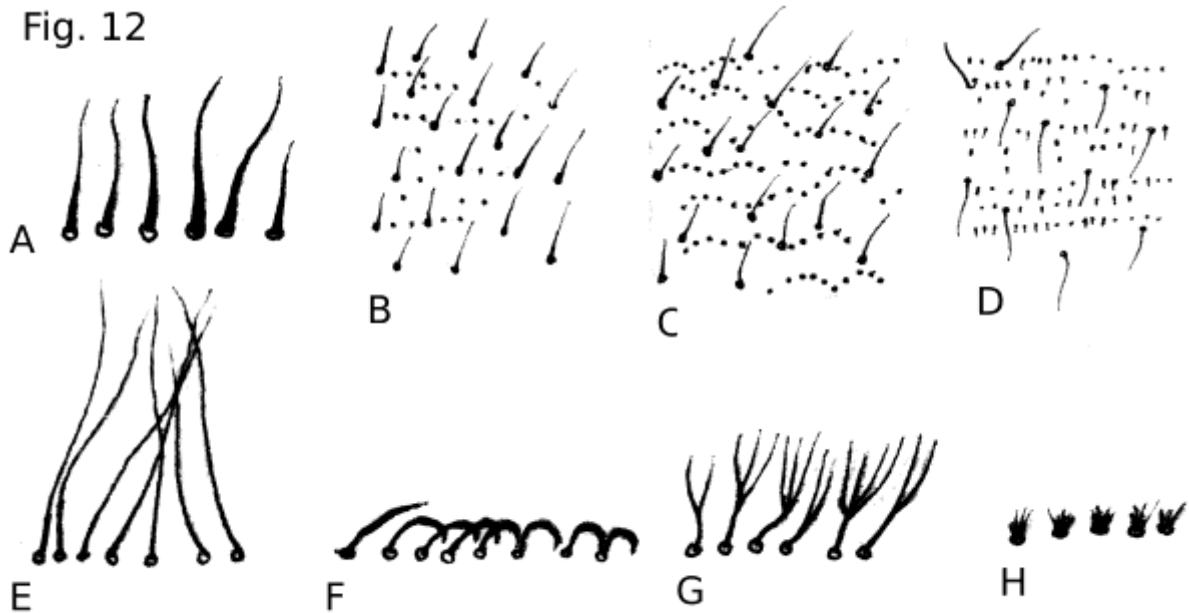


Fig. 13

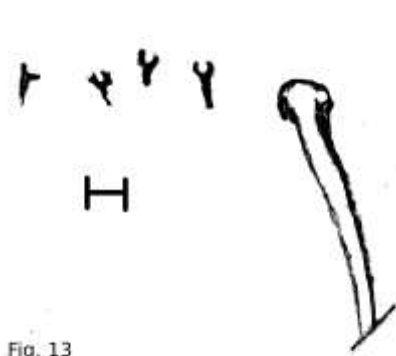


Fig. 14



**Figure 12-14. Chaetotaxy of the Nearctic *Cheumatopsyche* larvae.** 12. Setal types and organizations. A. Short, hairlike (*shl*), B. *shl* setae and microspines (*ms*) on the mesothoracic notum, C. *shl* setae and *ms* on the metathoracic notum, D. Setae and *ms* on the first abdominal tergum, E. Long, hairlike (*lhl*) setae, F. Crochet-like (*chl*) G. Multiply-branched (*mb*) setae, H. Brushlike (*bf*) setae. 13. Magnified image of seta and small *ms* on the first abdominal tergum. Bar= 9  $\mu$ m. Seta truncated for purposes of space. 1000x. 14. Enlarged *ms* and setae on first abdominal tergum of Morphotype D (*C. harwoodi*). Spines ~15-20  $\mu$ m long. 400x.

- frontoclypeal margin; *chl* setae on anterior margin of mesonotum and metanotum (Fig. 12F) .....Morphotype F
- 6'. Frontoclypeal notch with base and sides not at acute angle, never overhanging notch (Fig. 7); total notch width less than one-third width of frontoclypeal margin; mesonotal and metanotal anterior margins with *shl* setae (Fig. 12A). Morphotype G

***Morphotype A***

Diagnosis: Frontoclypeal margin without notch, having uninterrupted scalloping and *bl* along entire length. Pronotal margin with *lhl* setae 1/2 length of pronotum. Mesonotal and metanotal *ms* present. Abdominal *ms* small, less than 15 microns in length.

Material Examined: ONTARIO: Hastings Co., Moira R., 3.vii.1979; Muskoka Dist., Lake of Bays, Oxtongue R., v.1959; Nipissing Dist., South Algonquin, Madawaska R., 23-31.v.1972.

Associated species: *C. minuscula* (reared).

***Morphotype B***

Diagnosis: Frontoclypeal margin without notch, having uninterrupted scalloping and *bl* along entire length. Pronotal margin with *lhl* setae one-half to one-fourth length of pronotum. Some abdominal *ms* greater than 15 microns in length.

Material Examined: NEW JERSEY: Ocean Co, Lakehurst stream, 21.v.1984; SOUTH CAROLINA: Aiken Co., Savannah River Site, Fish Lake outfall, 3.vi.1981.

Associated species: *C. virginica* (reared and sympatry).

### ***Morphotype C.***

Diagnosis: Frontoclypeal margin without notch, having uninterrupted scalloping and *bl* along entire length. Pronotal margin with *shl* setae. Some abdominal *ms* greater than 15 microns in length.

Material Examined: TEXAS: Hays Co., Cypress Cr., 25.v.1978.

Associated species: *C. sordida* (reared).

### ***Morphotype D***

Diagnosis: Frontoclypeal margin with shallow, narrow notch. Annuli of most medial *bl* setae at or below level of notch base. Pronotum with *lhl* setae on anterior margin.

Abdomen with some *ms* greater than 15 microns in length.

Material Examined: ARKANSAS: Madison Co., Withrow Spring, 6.iv.1978; Newton Co., L. Buffalo R., 7.iv.1978; Scott Co., Ceader Cr., 1.iv.1978. LOUISIANA: Ouachita Par., 4 mi. S. of Calhoun, 25.iii.1978. ONTARIO: Huron Co., Maitland R., 20.v.1976; Kent Co., E of Palmyra, small stream @ Hwy. 3, 19.v.1976. SOUTH CAROLINA: Pickens Co., Wildcat Cr., iii-iv.1968; 27.vii.1979; 11.i.1995; Sixmile Cr. @ Hwy 291, 6.xi.1965; 1.ii.1995; Tributary of Camp Cr., 16.vi.1969; 12 Mile Cr. @ S-39-273, 28.viii.1981; 6.ix.1983; Clemson LaMaster Dairy Farm, 31.viii.1999; Willard Pond, 30.i.1987; 4.ii.1993; Brushy Cr., 2.vii.1991; L. Issaqueena, 20.ii.1987; Aiken Co., Savannah River Site, Upper Three Runs Cr. @ SRP 8-1, 22.vii.1977. TENNESSEE: Dickson Co., Montgomery Bell SP, 11.iv.1978; Robertson Co., 3.3 mi. E of Springfield; stream @ Hwy. 49 and 76, 12.iv.1978; Sevier Co., Dudley Cr., 15.iv.1978. TEXAS: Caldwell Co., Marcos R., 26.v.1978.



Associated species: *C. analis* (reared), *C. harwoodi* (reared), *C. enigma* (sympatry), *C. richardsoni* (sympatry).

#### ***Morphotype E***

Diagnosis: Frontoclypeal margin with deep rounded, angular, or square notch.

Prosternum with pair of minute, detached plates and pair of larger, tetrahedral plates, the 2 pairs sometimes fused into 1 pair. Pronotal margin with *shl* setae.

Material Examined: GEORGIA/SOUTH CAROLINA: Tugaloo R., 27.ix.1974. NORTH CAROLINA: Durham Co., Eno River, 10.vi.2008.

Associated species: *C. etrona* (reared).

#### ***Morphotype F***

Diagnosis: Frontoclypeal margin with an angular, flat-bottomed notch, the most medial scallops often overhanging. Width of frontoclypeal notch at least 1/3 width of frontoclypeal margin. Pronotal margin with *shl* setae, mesonotal and metanotal margins with *chl* setae (Fig. 12F)

Material Examined: FLORIDA: Bay Co., Ecofina Cr. @ 388, 30.xi.2010. SOUTH CAROLINA: Aiken Co., Savannah River Site, Tinker Cr. @ SRP 8-1, 29.vi.1977.

Associated Species: *C. edista* (sympatry).

#### ***Morphotype G***

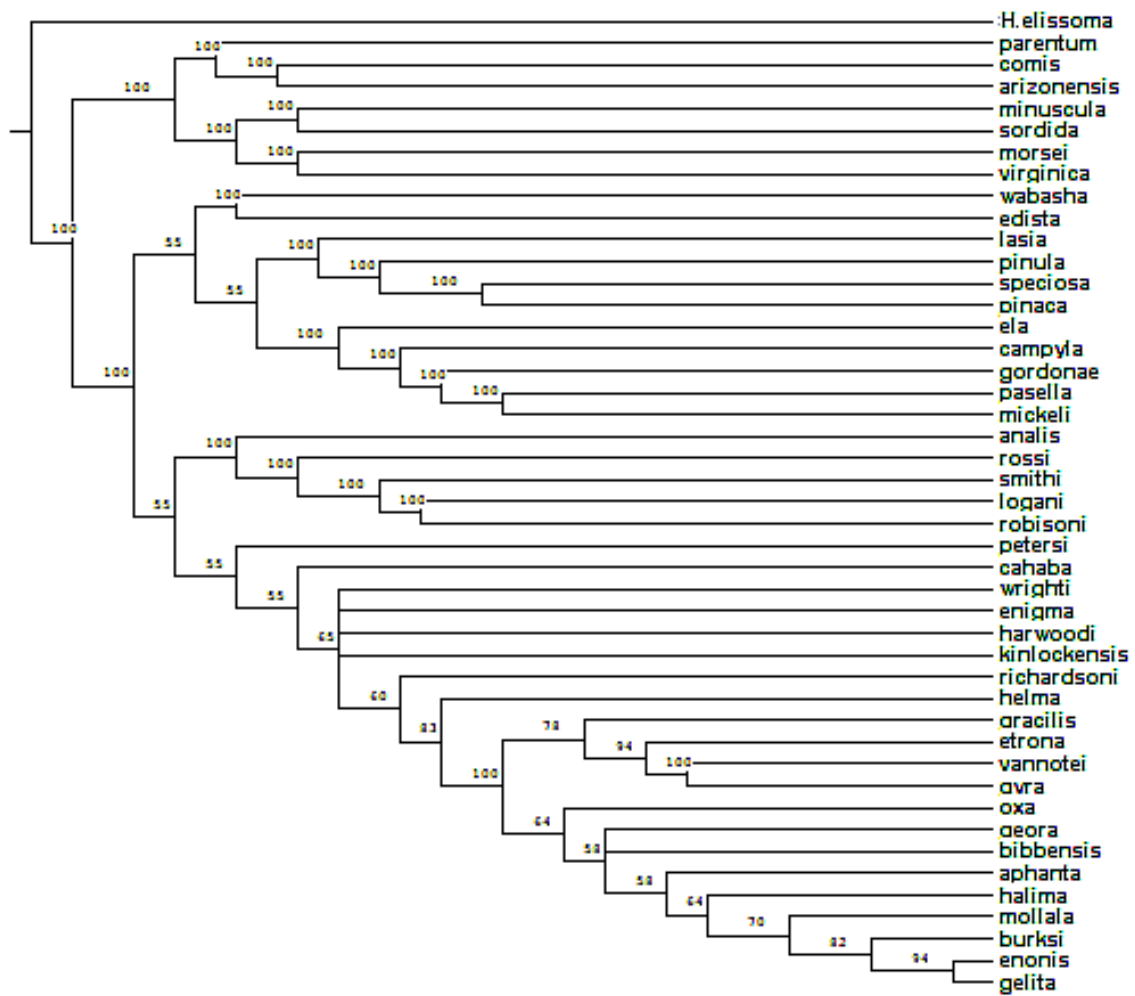
Diagnosis: Frontoclypeal margin with a square, flat-bottomed notch, the most medial scallops not overhanging. Most medial *bl* setae above level of notch base. Width of notch less than 1/3 width of frontoclypeal margin. Thoracic notal margins with *shl* setae.

Material Examined: ARKANSAS: Pike Co., Missouri R., 29.iii.1978; ONTARIO: Peel Co., Credit R., 31.v.1978; Timiskaming Dist., Montreal R. @ Rt. 11, 27.vi.1971; SOUTH CAROLINA: Pickens Co., Reedy Cove Cr., 6.ix.1979; Wildcat Cr., iii-iv.1968; 28.iii.1973; 22.ix.1978; 27.vii.1979; 13.iv.1981; 7.i.1993; 11.i.1995; 10.i.2001.

Associated species: *C. campyla* (reared), *C. pinaca* (sympatry).

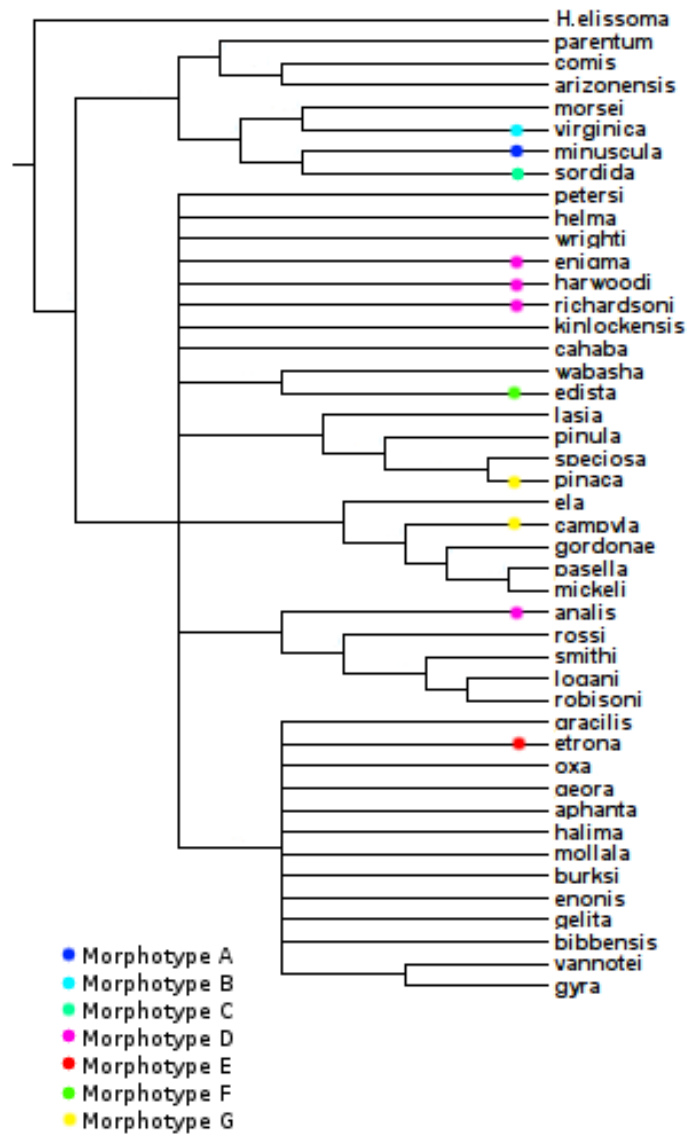
### **B. Phylogeny and character distribution**

The heuristic analysis generated 100 most parsimonious trees (L=45, Ci=84, Ri=86), from which a majority consensus tree of 46 steps was generated (Fig. 15). The following species newly included in this study are inferred to have the following relationships: *C. gordonae* is placed within the *C. campyla* Group; *C. robisoni* is placed within the *C. rossi* Group; *C. kinlockensis* is in a polytomy with *C. wrighti*, *C. enigma* and *C. harwoodi* within the paraphyletic *C. helma* Group; *C. cahaba* is placed as sister to the rest of the paraphyletic *C. helma* Group; *C. bibbensis* is placed within the *C. aphanta* Group. The following groups *sensu* Gordon (1974) are retained in a strict consensus tree (Figure 16): *C. sordida* Complex (*C. comis* Group, *C. sordida* Group), *C. gracilis* Complex (*C. rossi* Group, *C. wabasha* Group, *C. campyla* Group, *C. speciosa* Group). All of Gordon's other groupings collapse to polytomies. Morphotype distributions on the strict consensus tree are as shown in Figure 16. Morphotypes A-C are confined to the *C. sordida* Complex. Morphotype E is confined to the “*C. gracilis* Polytomy.” Morphotype F is confined to the *C. wabasha* Group. Morphotype G is confined to the *C. campyla* and *C. speciosa* Groups. Morphotype D is within the *C. gracilis* Complex but is not confined within any particular species group.



**Figure 15. Majority consensus cladogram of the Nearctic *Cheumatopsyche* species.**

L= 46; Ci=84; Ri=86. Branch support is shown on each clade as a percentage in gray letters. Majority rule is 50%.



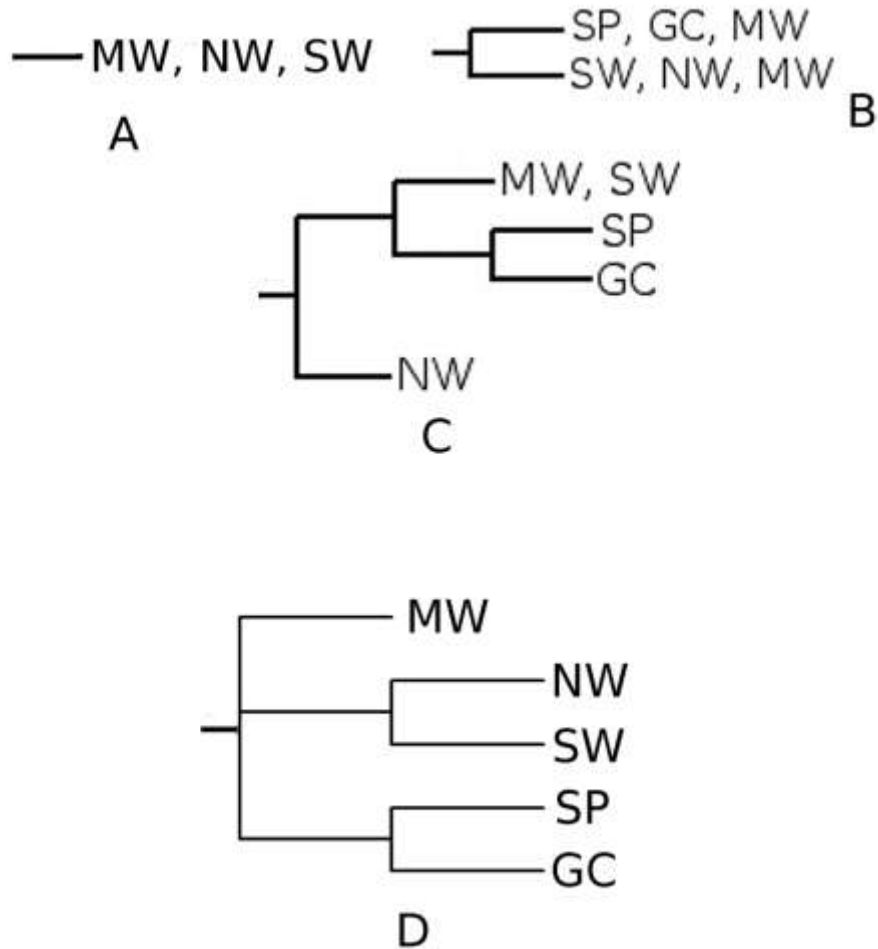
**Figure 16.** Strict consensus cladogram of the Nearctic *Cheumatopsyche*. The distribution of larval morphotypes is mapped to the tree as colored dots.

### **C. Historical biogeography**

PAE analysis yielded 5 Nearctic areas of endemism, containing only 25 of the original 59 “quadrants” due to many instances of cosmopolitan taxa. The final combined areas are as follows:

- Southern Appalachians (SP): NC, TN, GA, SC, PA, WV
- Gulf Coast (GC): MS, AL, FL, LA
- Southwest (SW): NV, AZ, NM, UT, WY
- Northwest (NW): CA, ID, OR, WA
- Midwest (MW): MO, AR, TX, OK, IL, IN

Cladistic analysis of the areas of endemism inferred 3 resolved subtrees (Fig. 17A-C) and one combined areogram (Fig. 17D). The relationships consist of a polytomy whereas the western areas are inferred to be more closely related to each other than to either the MW or western areas, and *vice versa* for the eastern areas.



**Figure 17. Areagrams resulting from PAE analysis and historical biogeography of the Nearctic *Cheumatopsyche* species. A-C: Three resolved subtrees. 17-A is . D: Final combined areagram. Note that the western and eastern areas are intrinsically more closely related than they are to each other or to the Midwest. MW=Midwest, NW=Northwest, SW=Southwest, SP=Southern Appalachians, GC=Gulf Coast.**

#### IV. DISCUSSION

The 7 morphotypes described above are significant progress in the taxonomy of Nearctic *Cheumatopsyche*. While currently we have few species associated with the morphotypes, the strict consensus phylogeny provides several hypotheses as to which not-yet-associated species share these new morphotypes.

Morphotypes A-C are within Gordon's *C. sordida* Complex, a group that seems to share the more general character of lacking a frontoclypeal notch with *Hydropsyche* species. Likewise, those members of the *C. sordida* complex seem to have more visible characters for separating the species than the *C. gracilis* Complex. As it is a small group (7 species), adult-associated specimens for all species might resolve the larval taxonomy of that group completely.

Conversely, Morphotype D has been found in several different groups within the *C. gracilis* complex. While the adults are divergent and separated in their characters, as shown by the phylogeny, the larval species such as *C. harwoodi* and *C. analis* are identical for the larval characters addressed in this research. However, the characters addressed were of a restricted scope. Differences in setal types and arrangements on the thoracic legs, for example, have not yet been investigated. Future work should address these unexplored regions. New techniques of mounting and staining may be needed to take full advantage of internal morphological differences, such as the armament of the gastric mill, or the placement and number of Malpighian tubules. While these methods are more time-intensive, the ultimate payoff will be great knowledge about an important group of aquatic organisms.

Morphotype F has been putatively associated with *C. edista* by distributional records, which Gordon placed in a small species group with *C. wabasha*. As this group is

retained in the strict consensus tree, my analysis suggests that *C. wabasha* may share the enlarged overhanging notch and other characters of Morphotype F. Morphotype G has been associated with 2 species thus far, *C. campyla* and *C. pinaca*, in the *C. campyla* and *C. speciosa* Groups, respectively. Although we have no other associated specimens within either of these groups, parsimony suggests the shared character of the deeper, more square notch may have arisen in the common ancestor of both groups and be a joint synapomorphy. Further associations are needed to clarify the relationships.

Morphotype E is currently associated with only 1 species, *C. etrona*, nested within the large “*C. gracilis* Polytomy” within the *C. gracilis* Complex. The enlarged prothoracic plates, usually associated with Nearctic *Hydropsyche* larvae, have not been found in associated specimens of any other Nearctic *Cheumatopsyche* species to date. However, given the poorly described nature of the larvae, I would not be surprised if more species in the *C. gracilis* Complex were found to share this character.

The combined areogram for the relationships between Nearctic areas of endemism provided by *Cheumatopsyche* distribution records infers no clear event of vicariance within the period these species evolved or colonized North America. The areas show a relationship based in proximity, with what seems to be a mixing region between the western and eastern faunas in the Midwest. This follows roughly the “Eastern Nearctic” and “Western Nearctic” areas of endemism often seen in the literature. The other reason *Cheumatopsyche* species do not suggest a clear vicariance event during their evolution is the large number of cosmopolitan species, especially *C. analis*, *C. campyla*, *C. gracilis*, and *C. speciosa*. While there are some regions with higher amounts of endemism, such as the southeastern United States, most of the Nearctic is inhabited by widely ranging species such as those listed above.



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## **APPENDICES**

## **APPENDIX I: Characters for phylogenetic analysis**

1. Clasper receptacle chimneys: small (0), very small (1)
2. Clasper receptacle inner openings: present (0), absent (1)
3. Clasper receptacle: not dorsal (0), dorsal (1)
4. Ventral margin of clasper receptacle: wide (0), narrow (1)
5. Clasper receptacle chimney: large (0), small (1)
6. Median plate scoop areas pouch like projections: present (0), absent (1)
7. Ventral margin large and: rounded (0), v-shaped (1)
8. Ventral margin of clasper: small and not very rounded (0), large and very rounded (1)
9. Apex of tongue of median plate: not heart-shaped (0), heart-shaped (1)
10. Median plate elaborate membranous folding: absent (0), present (1)
11. Dorsal sclerite of median plate: present (0), absent (1)
12. Tenth tergum apical lobes: rising above the apex (0), flush against the apex (1)
13. Clasper receptacle with ventral margin: unbowed (0), bowed (1)
14. Phallothecal base: normal (0), enlarged (1)
15. Clasper receptacle: linear (0), angular lobate (1)
16. Tenth tergum apical lobes: moderately reflexed (0), strongly reflexed (1)
17. Tenth tergum apical lobes: slightly reflexed (0), moderately reflexed (1)
18. Apical ridge at the posterior end of the tenth tergum: absent (0), present (1)
19. Digitate projection near the dorso-posterior corner of the female eighth sternum: absent (0), present (1)
20. Tenth tergum apical lobes: not reflexed (0), reflexed (1)

21. Ventral margin of clasper receptacle: sometimes incised (0), always incised (1)
22. Ventral margin of clasper: always linear (0), sometimes incised (1)
23. Base of apical lobes: not wide (0), wide (1)
24. Apical lobes: elongate and not widened at base (0) very elongate or widened at base (1)
25. Apical lobes: short (0), elongate (1)
26. Apicolateral angle on the ninth segment: narrow (0), wide (1)
27. Apex of male coxopodite: not bulbous (0), bulbous (1)
28. Tenth tergum apical lobes: short and circular (0), large and disk-like (1)
29. Tenth tergum apical lobes: not circular (0), circular (1)
30. Harpago: elongate (0), flush against the coxopodite (1)
31. Membraneous phallothecal lobes: present (0), absent (1)
32. Female median plate: simple (0), elaborate with a dorsal sclerite (1)
33. Female clasper receptacle: well developed (0), small (1)
34. Male claspers: slender (0), massive (1)
35. Clasper receptacle: pouch-like (0), shallow overhang (1)
36. Median ventral projection on male tenth tergum: absent (0), present (1)
37. Reduced female clasper receptacle: digitate (0), blunt triangular (1)
38. Cerci: poorly defined setose areas (0); raised, well defined (1)

## APPENDIX II: Character matrix

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38
<i>H. ellissoma</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0
<i>minusucula</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	1	0	1
<i>sordida</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	1	0	1
<i>morsei</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1	0	1
<i>virginica</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1	0	1
<i>comis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	1	1	1
<i>arizonensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	1	1	1
<i>parentum</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	1	0	1
<i>speciosa</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0
<i>pinaca</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	1	1	0	0	0	0	0	1	1	0	0	0	0	0	1
<i>pinula</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	1	0	0	0	0	0	1	1	0	0	0	0	0	1
<i>lasia</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	1	1	0	0	0	0	0	1
<i>pasella</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	1	1	0	0	0	0	0	1
<i>mickeli</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	1	1	0	0	0	0	0	1
<i>campyla</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	1	1	0	0	0	0	0	1
<i>ela</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	1	1	0	0	0	0	0	1
<i>wabasha</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	1
<i>edista</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	1
<i>analis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	1
<i>logani</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	1	0	0	0	0	0	1
<i>smithi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	1	0	0	0	0	0	1
<i>rossi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	0	0	0	0	1
<i>petersi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1
<i>helma</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1
<i>wrighti</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1
<i>enigma</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1
<i>harwoodi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1
<i>richardsoni</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1
<i>gracilis</i>	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1
<i>vannatei</i>	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1
<i>gyra</i>	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1
<i>etrona</i>	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1
<i>oxa</i>	0	0	0	0	0	0	0	1	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1
<i>geora</i>	0	0	0	0	0	0	0	1	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1
<i>aphanta</i>	0	0	0	0	0	0	1	1	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1
<i>halima</i>	0	0	0	0	0	0	1	1	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1
<i>mollala</i>	0	0	0	0	1	1	1	1	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1
<i>burksi</i>	0	0	1	1	1	1	1	1	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1
<i>enonis</i>	1	1	1	1	1	1	1	1	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1
<i>gelita</i>	1	1	1	1	1	1	1	1	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1
<i>bibbensis</i>	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	0	0	0	-	0	-	-	0	0	0	0	0	0	0	0	1	-	-	0	-	0	-	1
<i>gordonae</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	1	1	0	0	0	0	0	1
<i>kinlockensis</i>	-	-	-	-	-	-	-	-	-	-	-	0	-	1	-	0	0	0	-	0	-	-	0	0	0	1	0	0	0	0	1	-	-	0	-	0	-	1
<i>cahaba</i>	-	-	-	-	-	-	-	-	-	-	-	0	-	1	1	0	0	0	-	0	0	0	0	1	1	0	1	0	0	0	1	-	-	0	-	0	-	1
<i>robisoni</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	1	0





#### APPENDIX IV: Distribution Records for Nearctic *Cheumatopsyche* species

1. *Cheumatopsyche analis* (Banks, 1903): AB, AL, AR, BC, CO, CT, DE, FL, GA, HI, ID, IL, IN, KS, KY, LA, MA, MB, MD, ME, MI, MN, MO, MS, MT, NB, NC, ND, NE, NF, NH, NJ, NS, NY, OH, OK, ON, PA, PE, PQ, SC, SD, SK, TN, TX, UT, VA, VT, WA, WI, WV, WY.
2. *Cheumatopsyche aphantia* Ross, 1938: AR, IL, IN, KS, KY, MI, MN, MO, NB, ND, NH, NY, OH, OK, PA, PQ, TN, TX, VT, WI.
3. *Cheumatopsyche arizonensis* (Ling, 1938): AZ, CA, NM, NV, TX, UT, WY.
4. *Cheumatopsyche bibbensis* Gordon, Harris, & Lago, 1986: AL.
5. *Cheumatopsyche burksi* Ross, 1941: AL, AR, CT, FL, IL, IN, KY, LA, MS, NY, OK, TN, TX, VA, VT.
6. *Cheumatopsyche cahaba* Gordon, Harris, & Lago, 1986: AL
7. *Cheumatopsyche campyla* Ross, 1938: AB, AL, AR, AZ, BC, CA, CO, CT, DE, FL, GA, IA, ID, IL, IN, KS, KY, LB, MA, MB, ME, MI, MN, MO, MS, MT, NC, ND, NE, NF, NH, NJ, NM, NS, NY, OH, OK, ON, OR, PA, PQ, SC, SK, TN, TX, UT, VA, VT, WA, WI, WV, WY, YT.
8. *Cheumatopsyche comis* Edwards and Arnold, 1961: NM, OK, TX.
9. *Cheumatopsyche edista* Gordon, 1974: AL, FL, GA, NC, SC.
10. *Cheumatopsyche ela* Denning, 1942: AL, DC, DE, GA, ME, NC, NY, ON, PA, PQ, SC, TN, VA, WV.
11. *Cheumatopsyche enigma* Ross, Morse, and Gordon, 1971: AR, GA, MO, NC, PA, SC, VA.
12. *Cheumatopsyche enonis* Ross, 1938: AZ, CO, ID, MT, NM, NV, OR, UT, WY.
13. *Cheumatopsyche etrona* Ross, 1941: GA, NC, SC, TN, VA.
14. *Cheumatopsyche gelita* Denning, 1952: AZ
15. *Cheumatopsyche geora* Denning, 1948: AL, CT, DE, GA, KY, MS, NC, PA, SC, TN, VA.
16. *Cheumatopsyche gordonae* Lago & Harris, 1983: FL.
17. *Cheumatopsyche gracilis* (Banks, 1899): AB, AL, AR, BC, CO, CT, KS, LB, MA, MB, ME, MI, MN, MO, MT, NC, ND, NF, NJ, NS, NY, OH, OK, ON, PA, PQ, SC, TN, UT, VA, VT, WI, WV, WY.

18. *Cheumatopsyche gyra* Ross, 1938: GA, ME, NC, PA, SC, VA, WV.
19. *Cheumatopsyche halima* Denning, 1948: AR, MA, ME, NB, OH, PA, PQ, SC, VA, WV.
20. *Cheumatopsyche harwoodi* Denning, 1949: AL, CT, GA, IN, KY, ME, NC, NS, NY, OH, ON, PA, PE, RI, SC, TN, VA, WV.
21. *Cheumatopsyche helma* Ross, 1939: AL, AR, KY, ME, PA, TN, WV.
22. *Cheumatopsyche kinlockensis* Gordon, Harris, & Lago, 1986: AL.
23. *Cheumatopsyche lasia* Ross, 1938: AB, AR, AZ, IA, IL, IN, KS, MN, MO, MT, ND, NE, NM, OK, PA, SK, TX, WY.
24. *Cheumatopsyche logani* Gordon and Smith, 1974: ID, MT, WA.
25. *Cheumatopsyche mickeli* Denning, 1942: CA, ID, OR, WY.
26. *Cheumatopsyche minuscula* (Banks, 1907): AL, AR, CT, DC, GA, KS, KY, MA, MB, MD, ME, MN, MO, NC, ND, NH, NY, OH, OK, ON, PA, PQ, SC, TN, VA, VT, WI, WV.
27. *Cheumatopsyche mollala* Ross, 1941: AR, CA, ID, ON, OR.
28. *Cheumatopsyche morsei* Gordon, 1974: LA.
29. *Cheumatopsyche oxa* Ross, 1938: AB, AL, AR, BC, CT, GA, IL, IN, KS, KY, MB, ME, MI, MN, MO, MT, NC, NH, NY, OH, OK, ON, PA, PQ, SC, SD, SK, TN, VA, VT, WI, WV, WY.
30. *Cheumatopsyche parentum* Gordon, 1974: MD, VA.
31. *Cheumatopsyche pasella* Ross, 1941: AL, AR, CT, DE, FL, GA, IL, IN, KY, LA, MA, MD, ME, MN, MS, MT, NC, ND, NH, NJ, OH, OK, ON, OR, PA, PQ, RI, SC, TN, TX, VA, WA, WI, WV.
32. *Cheumatopsyche petersi* Ross, Morse, and Gordon, 1971: AL, FL, MS.
33. *Cheumatopsyche pinaca* Ross, 1941: AL, DE, FL, GA, LA, MA, ME, MS, NC, NH, NJ, PA, RI, SC, TN, VA.
34. *Cheumatopsyche pinula* Denning, 1952: AZ, NM.
35. *Cheumatopsyche richardsoni* Gordon, 1974: NC, SC.
36. *Cheumatopsyche robisoni* Moulton & Stewart, 1996: AR.
37. *Cheumatopsyche rossi* Gordon, 1974: AR, KS, MO, OK.

38. *Cheumatopsyche smithi* Gordon, 1974: AB, BC, MB, MT, ND, ON, OK, SK, WA, UT.
39. *Cheumatopsyche sordida* (Hagen, 1861): AL, AR, CT, DC, FL, GA, IL, IN, KY, LA, MB, MD, ME, MI, MN, MO, MS, NB, NC, NH, NJ, NY, OK, ON, PA, PQ, SC, TN, TX, VA, WI, WV,
40. *Cheumatopsyche speciosa* (Banks, 1904): AB, AR, CO, CT, DE, IL, IN, KY, LB, MB, MD, MI, MN, MO, MT, NC, ND, NY, OH, OK, ON, PA, PQ, SK, TN, VA, WI.
41. *Cheumatopsyche vannotei* Gordon, 1974: PA
42. *Cheumatopsyche virginica* Denning, 1949: AL, DE, FL, GA, LA, MS, NC, NJ, SC, VA.
43. *Cheumatopsyche wabasha* Denning, 1947: CO, DE, MN, OH, OR, WI.
44. *Cheumatopsyche wrighti* Ross, 1947: MA, ME, NS, PA, PE, TN, VA, WV.