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Introduction

After publication of Blahnik and Holzenthal (2017), it was noticed that a large portion of the text had been accidentally removed from the “Phylogenetic and evolutionary comments” section during the proofing stage. The beginning of the deleted section completes the sentence on line 6 of page 129, which begins “The species included in the subgenus...”. The Insecta Mundi editorial staff apologizes for this oversight. In order to provide context for the deleted excerpt, the entire “Phylogenetic and evolutionary comments” section is reproduced here, with the deleted text reincorporated. Insecta Mundi has also released a revised version of the Blahnik and Holzenthal (2017) manuscript, with this error corrected. However, the revised version is merely for convenience, and not an official peer-reviewed article. Anyone wishing to reference the findings of Blahnik and Holzenthal (2017) should cite the original 2017 manuscript or this erratum. The references and figure plates cited in this section have also been reproduced here.

Phylogenetic and evolutionary comments

The historical placement of species into the genera *Mortoniella* and *Mexitrichia* was primarily based on the presence or absence of fork V in the hind wing. As pointed out previously (Blahnik and Holzenthal, 2008), one of these character states is undoubtedly plesiomorphic, probably the presence of fork V. Species historically placed in *Mortoniella*, as well as those species listed here as “unplaced to species group” possess fork V in the hind wing. *Mexitrichia* was distinguished by the absence of fork V. Because of the essential morphological similarity of *Mortoniella* and *Mexitrichia*, and absence of evidence that they were reciprocally monophyletic, the two genera were formally synonymized by Blahnik and Holzenthal (2008). Flint (1963) commented that two groups could be recognized among species historically placed in *Mexitrichia*, based on presence or absence of fork III. However, we have determined that this represents a parallel loss in different groups. The species included in the subgenus *Nanotrichia*, in this paper, have lost both forks III and V, and a similar loss has also occurred within the *leroda* group of the subgenus *Mortoniella* (and probably in more than one lineage). Despite this parallel character evolution, the venational loss in *M. (Nanotrichia)*, along with several additional characters similarities, undoubtedly serves as a good indication of the monophyly of the subgenus.

Failure to find support for monophyly of the subgenus *Mortoniella* itself is probably for several reasons, but is consistent with the idea that character loss has played an important role in the evolution

of the subgenus. Many of the species listed as “unplaced to species group,” most newly described in this paper, resemble each other in having an inferior appendage with an elongate and recurved dorsal lobe. Examples are included in Figures 132-134. Many of these species also have elongate, spine-like processes from the mesal pockets of the inferior appendages, a character that is also found in the majority of species in the subgenus *Nanotrichia*, as exemplified in Fig. 130 and 131. Despite the character similarity of the “unplaced species” in the subgenus *Mortoniella*, they are very divergent in overall morphology. An elongate, recurved dorsal process on the inferior appendage also occurs in *M. catherinae*, inferred to be a basal species in the bilineata group (Fig. 135), and also in the akantha subgroup of the leroda group (Fig. 136). The relative distribution of the character states for the two characters discussed (an elongate, reflexed dorsal lobe of the inferior appendages, and elongate spine-like projections from the mesal pockets of the inferior appendages) is included in Fig. 126. It is difficult to make any other inference than that these two apparently very specialized and apomorphic characters have been lost during the course of evolution, and probably in more than one lineage. Parallel character loss of this sort makes phylogeny reconstruction inherently difficult, due to the uneven rate of loss of the character in different lineages, and runs contrary to the usual expectation that complex characters emerge and are elaborated on over the course of evolution. It also begs the question of why this loss should have occurred. What was the original advantage of the complex characters and why were they lost? The following is offered as one potential explanation.

A primary character development defining the *Protoptila-Mortoniella* lineage is the development of the small rod-like appendages from the ventral margin of the phallobase and accompanying mesal pockets of the inferior appendages, with their apical spine-like projections. The origin of the rod-like appendages is difficult to account for, since they do not occur in other genera, but they may represent segmental analogs of the inferior appendages, derived from segment X, which has its sternite degenerate, but nevertheless could have given rise to the appendages as a *de novo* mutation. Regardless of their origin, the function of these appendages appears to be to transmit force from the phallobase to the phallicata and apical portions of the phallic ensemble, countered dorsally in *Mortoniella* by the dorsal phallic spine, which contacts or pushes against the apicomeral invagination of tergum X. It would seem that the original development of using the small basal rods to raise the phallic ensemble from below was inadequate to its function and has been improved on or modified in different ways. In *Protoptila* (Fig. 128) this was accomplished by the extension of the ventral margin of segment VIII beneath the phallic ensemble. This was accompanied by the development of a very enlarged apodeme on the dorsal margin of the phallobase, as an attachment for a muscle, required by the basal transmission of force. We hypothesize that in *Mortoniella*, the apical spine-like projections of the mesal pockets originally served the same function as the enlarged sternum VIII in *Protoptila*, to raise and lift the phallic ensemble from below. They were elongate in the immediate ancestor of extant lineages, directly subtending the phallicata, as in *M. cornuta*, n. sp. of the subgenus *Mortoniella* (Fig. 133), or *M. aequalis* in the subgenus *Nanotrichia* (Fig. 131). In *Protoptila* small spine-like projections are often evident projecting from the mesal pockets. However, due to the development of the elongate sternum VIII, and also to the fusion of the phallobase with the phallicata, it is impossible to say what the ancestral character state was in this taxon, since the spine-like projections are never elongate in surviving members of the genus. In contrast, elongate spine-like projections are found in all of the major lineages of *Mortoniella* (although only a few taxa of the leroda group, where the character, when present, is variably developed and may represent a character reversal). Probably, the support provided by the spine-like projections was relatively weak and various evolutionary modifications evolved to provide additional support, eventually replacing the function of the spines, which subsequently became reduced. In the subgenus *Mortoniella*, an additional method of support was found in the elongate, recurved dorsal lobes of the inferior appendages (Fig. 132-136). Although a plesiomorphic character for the subgenus, it is now relictually found in only a few widely divergent taxa. Its original functional significance is most evidently suggested by species such as *M. akantha* (Fig. 136), in which the lobes engage lateral projections from the dorsal margin of the phallicata. Their current utility is not as evident in other taxa, where they may already be in a process of being lost, as judged, for instance, by the very reduced lobes found in *M. croca* (Fig. 70) of the

argentinica subgroup, whose other species have elongate lobes, as in *M. cornuta* (Fig. 133). Although supplanted by other methods of support in advanced species of both the bilineata and leroda groups, evidence of these recurved lobes is found in individual taxa, such as the shortened, recurved apices of the inferior appendages in *M. guyanensis* of the limona subgroup (Fig. 51), or species of the *M. bolivica* subgroup (Fig. 32-34), or the very tiny recurved apices of the inferior appendages found in several species of the albolineata subgroup (Fig. 12, 17, 18, Blahnik and Holzenthal 2011). Other alternative methods of support were derived in various lineages, and in some cases, themselves subsequently lost or reduced. The closest analogy to the character state in *Protoptila* is found in the elongate spine-like projection from the ventral margin of segment IX in *M. rodmani* of the subgenus *Nanotrichia* (Fig. 129). This represents a unique character development within the genus. In the bilineata group, ancillary support was derived by complementary angular outgrowths from the dorsal margin of the phallicata and ventral margin of the dorsal phallic spine, which are more or less functionally hinged, as exemplified by *M. catherinae* (Fig. 135). However, this probably functions more as a fulcrum to provide leverage than a method of direct support. In the “leroda” subgroup, support was provided by the development of an elongate, asymmetric ventromesal projection on the inferior appendages (Fig. 137). A similar, less apomorphic feature is found in about half the species of the albolineata subgroup, undoubtedly indicating a relationship between the two groups. In both subgroups, the feature is subsequently lost, replaced in the “florica” subgroup of the leroda group *s.l.* by paired extensions from the apices of the inferior appendages. Fusion of the phallobase and phallicata (with each other or the inferior appendages) has probably also played a role in the evolution of a support system, allowing the ventral margin of the phallicata to serve as a kind of direct support, as in the ventral outgrowths of the phallicata in the limona subgroup (Fig. 50), or the elongate, paired ventral sclerites in the bilineata group (Fig. 3). In the flinti subgroup, fusion of the inferior appendages to the phallicata has left the spine-like projections of the mesal pockets freely projecting below the phallicata, rather than providing support, and the spines are variably reduced in the different species of the group, presumably due to their functional obsolescence (Fig. 18-21). Other modifications of this kind can be surmised.

The scenario presented above is a hypothesis and probably not provable in any strict sense. We do not claim that it is the only way that character evolution could be interpreted. It does, however, provide a predictive model for how character evolution of male genitalia progresses in the genus, and an explanation of why character acquisition and character loss may be correlated. As certain structures are replaced by others, the original modification becomes functionally obsolete. The correlation, however, is imperfect, because remnants of the original structure are retained in various lineages, where they are lost multiple times and at various rates. Nevertheless, if the evolutionary hypothesis is correct, the character suite observed in newly described species should more or less make sense. This model of evolution is not particularly parsimonious. Neither does it conform to a Bayesian model in which characters follow a gamma distribution, because the same character may evolve at very different rates at different points in its evolution, depending on its functional utility. Ultimately, molecular data will be useful in testing the hypothesis of relationships presented, or in providing a counter hypothesis, since it evolves under very different constraints than morphological characters. COI sequences, provided by the BOLD initiative, are available for a limited number of taxa, but both the amount of sequence data and its taxonomic coverage are inadequate at this point to make useful comments. Although more sequence data will undoubtedly improve the situation, this will probably have to wait until additional specimens are collected, since many species are based on very old material or only a limited number of specimens. Hopefully, the hypothesis presented will provide a useful framework for interpreting evolution in the genus, once molecular data are available.

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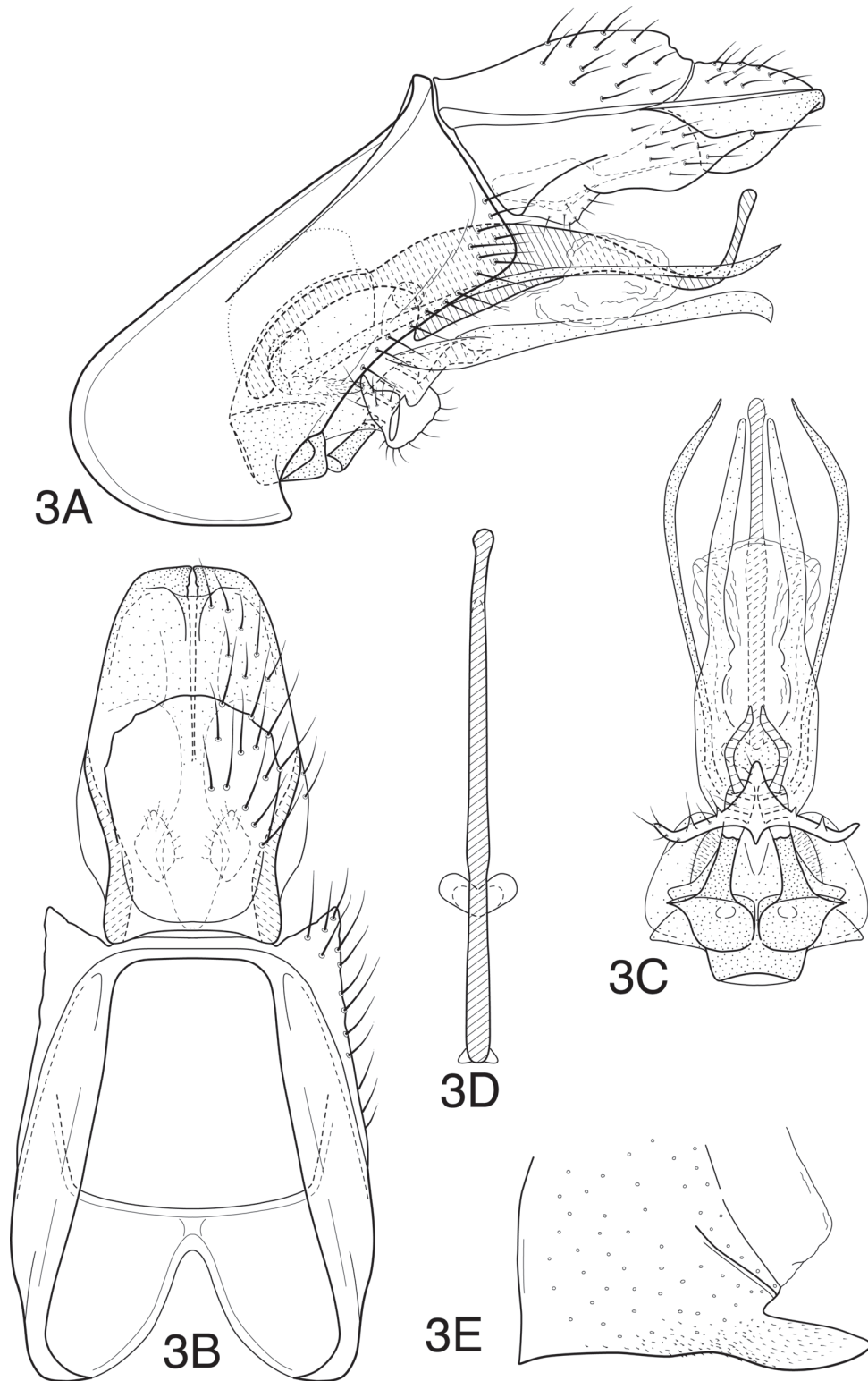


Figure 3. *Mortoniella (Mortoniella) bilineata* Ulmer, male genitalia. **A**—lateral; **B**—segment IX and tergum X, dorsal; **C**—phallic ensemble, ventral; **D**—dorsal phallic spine, dorsal; **E**—ventral process of segment VI, lateral.

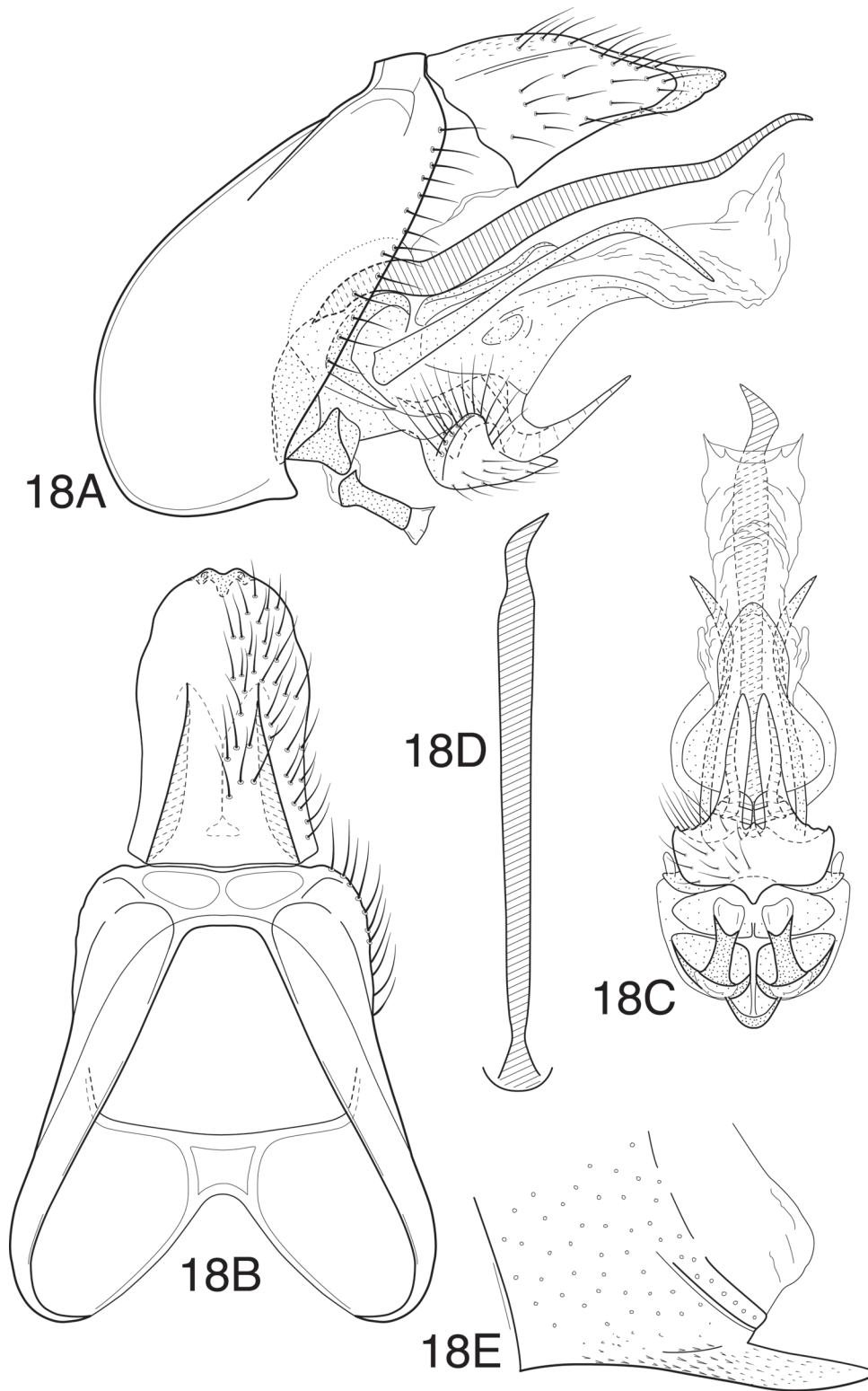


Figure 18. *Mortoniella (Mortoniella) bifurcata* Sykora, male genitalia. **A**—lateral; **B**—segment IX and tergum X, dorsal; **C**—phallic ensemble, ventral; **D**—dorsal phallic spine, dorsal; **E**—ventral process of segment VI, lateral.

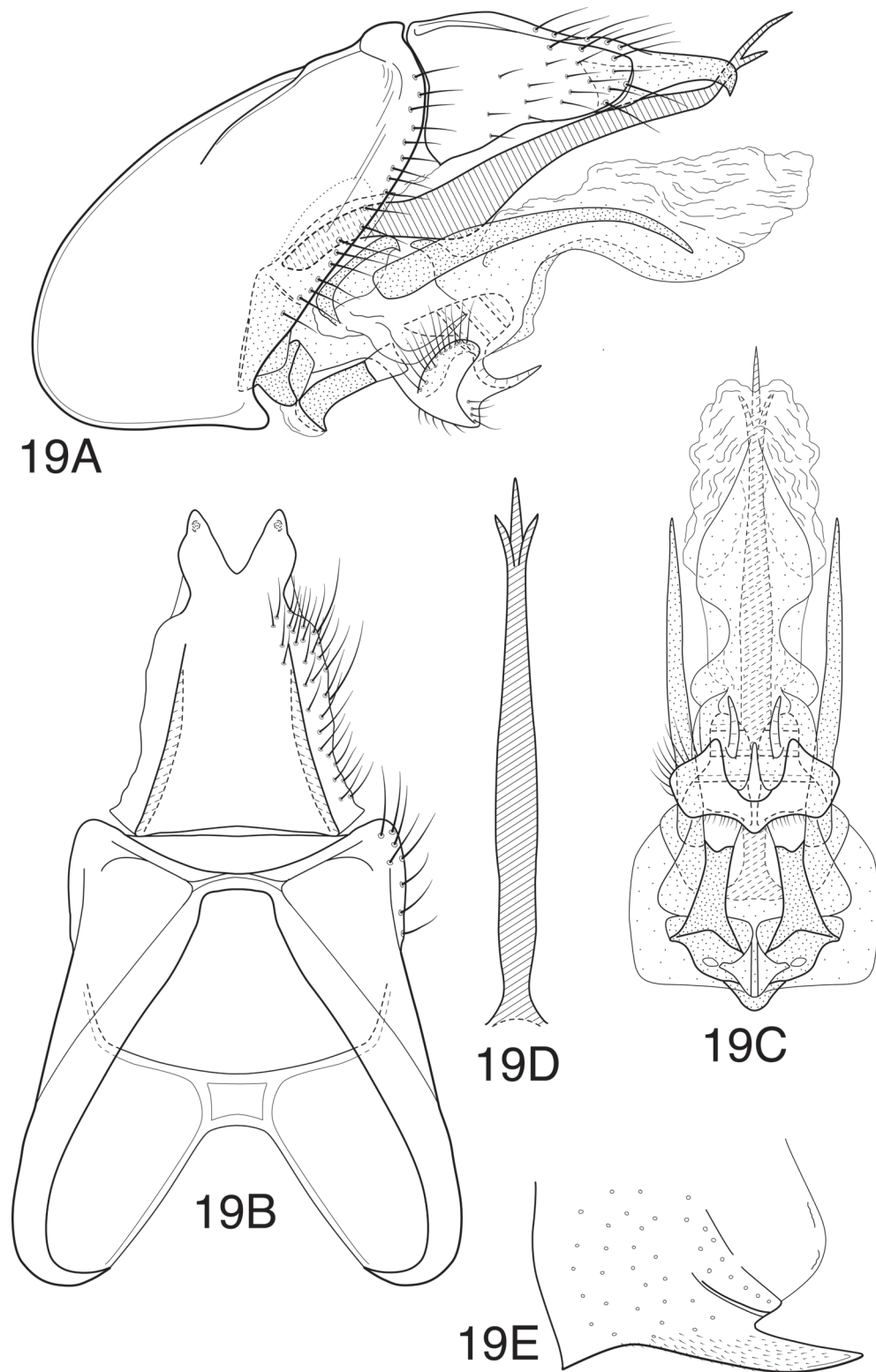


Figure 19. *Mortoniella (Mortoniella) flinti* Sykora, male genitalia. **A**—lateral; **B**—segment IX and tergum X, dorsal; **C**—phallic ensemble, ventral; **D**—dorsal phallic spine, dorsal; **E**—ventral process of segment VI, lateral.

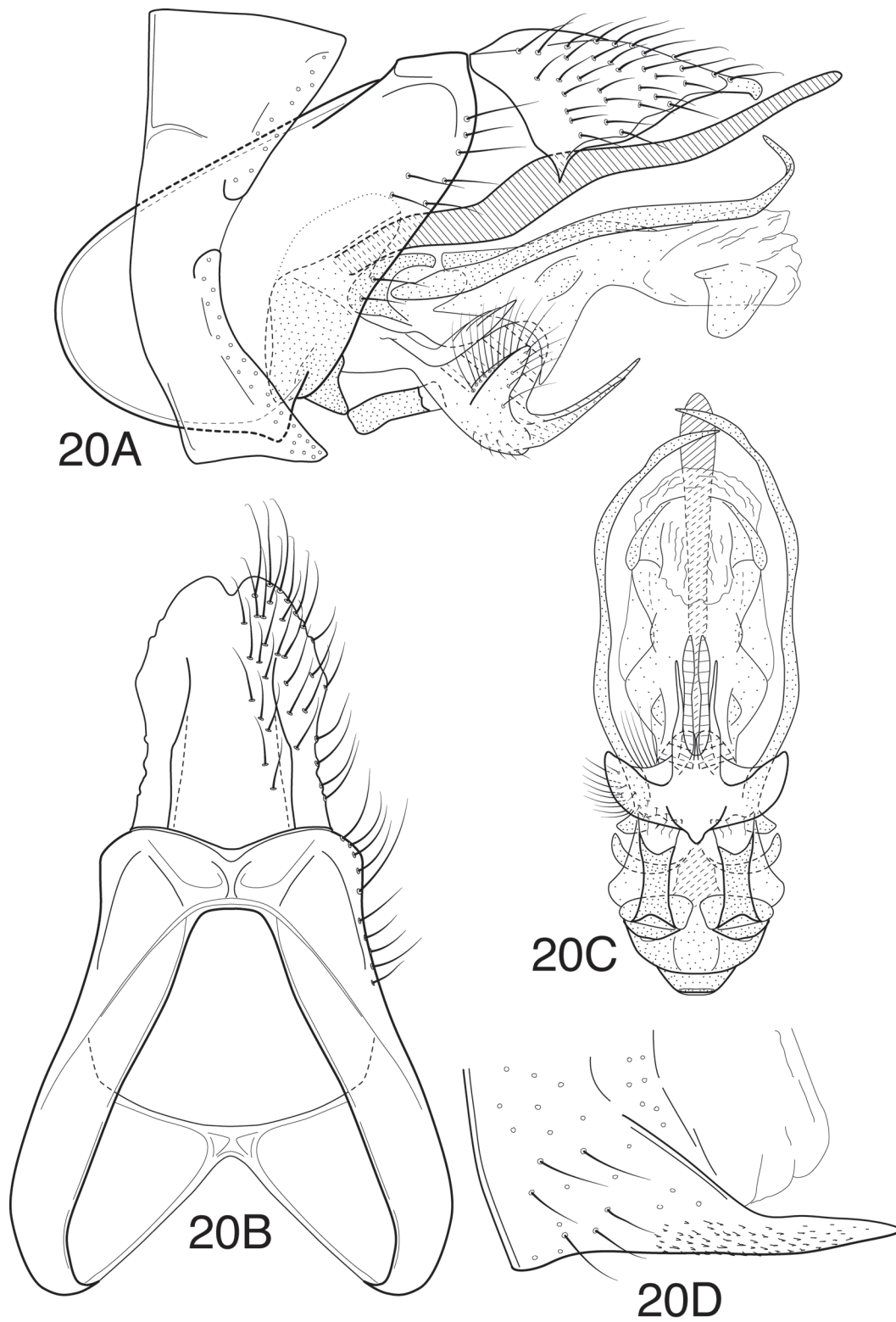


Figure 20. *Mortoniella (Mortoniella) tanyrhabdos*, new species, male genitalia. **A**—lateral; **B**—segment IX and tergum X, dorsal; **C**—phallic ensemble, ventral; **D**—ventral process of segment VI, lateral.

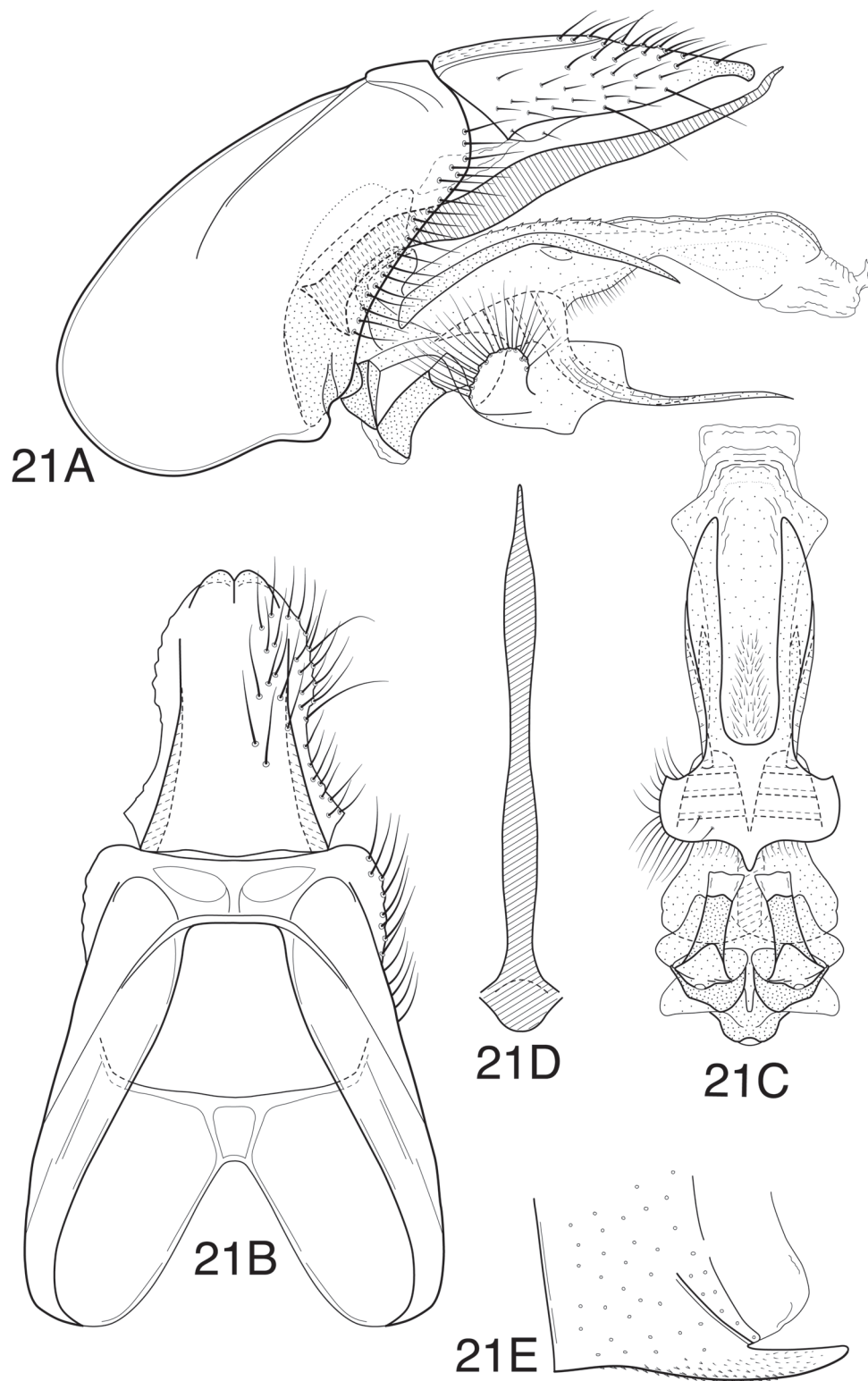


Figure 21. *Mortoniella (Mortoniella) tusci*, new species, male genitalia. **A**—lateral; **B**—segment IX and tergum X, dorsal; **C**—phallic ensemble, ventral; **D**—dorsal phallic spine, dorsal; **E**—ventral process of segment VI, lateral.

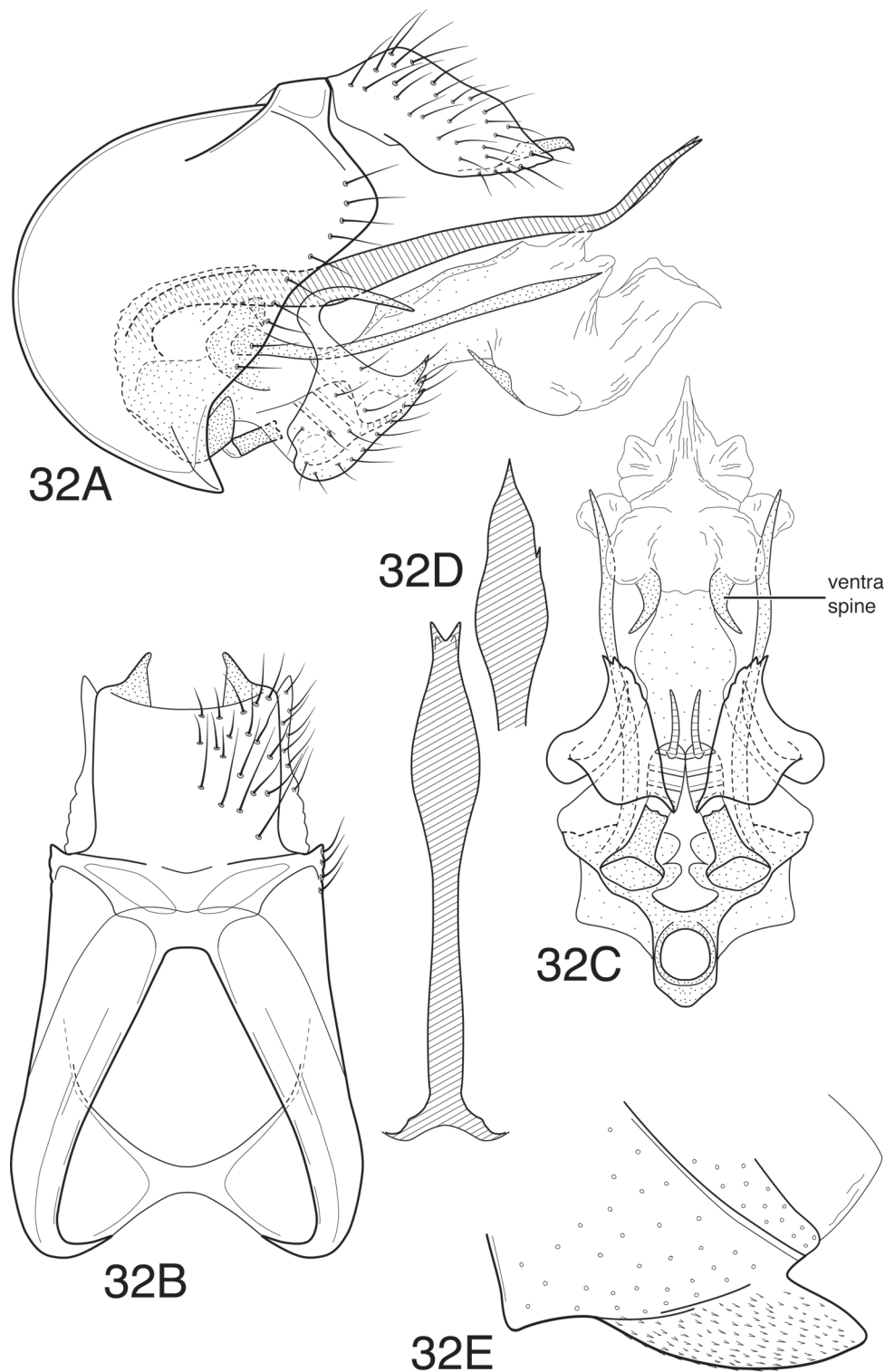


Figure 32. *Mortoniella (Mortoniella) bolivica* (Schmid), male genitalia. **A**—lateral; **B**—segment IX and tergum X, dorsal; **C**—phallic ensemble, ventral; **D**—dorsal phallic spine and apex of variant, dorsal; **E**—ventral process of segment VI, lateral.

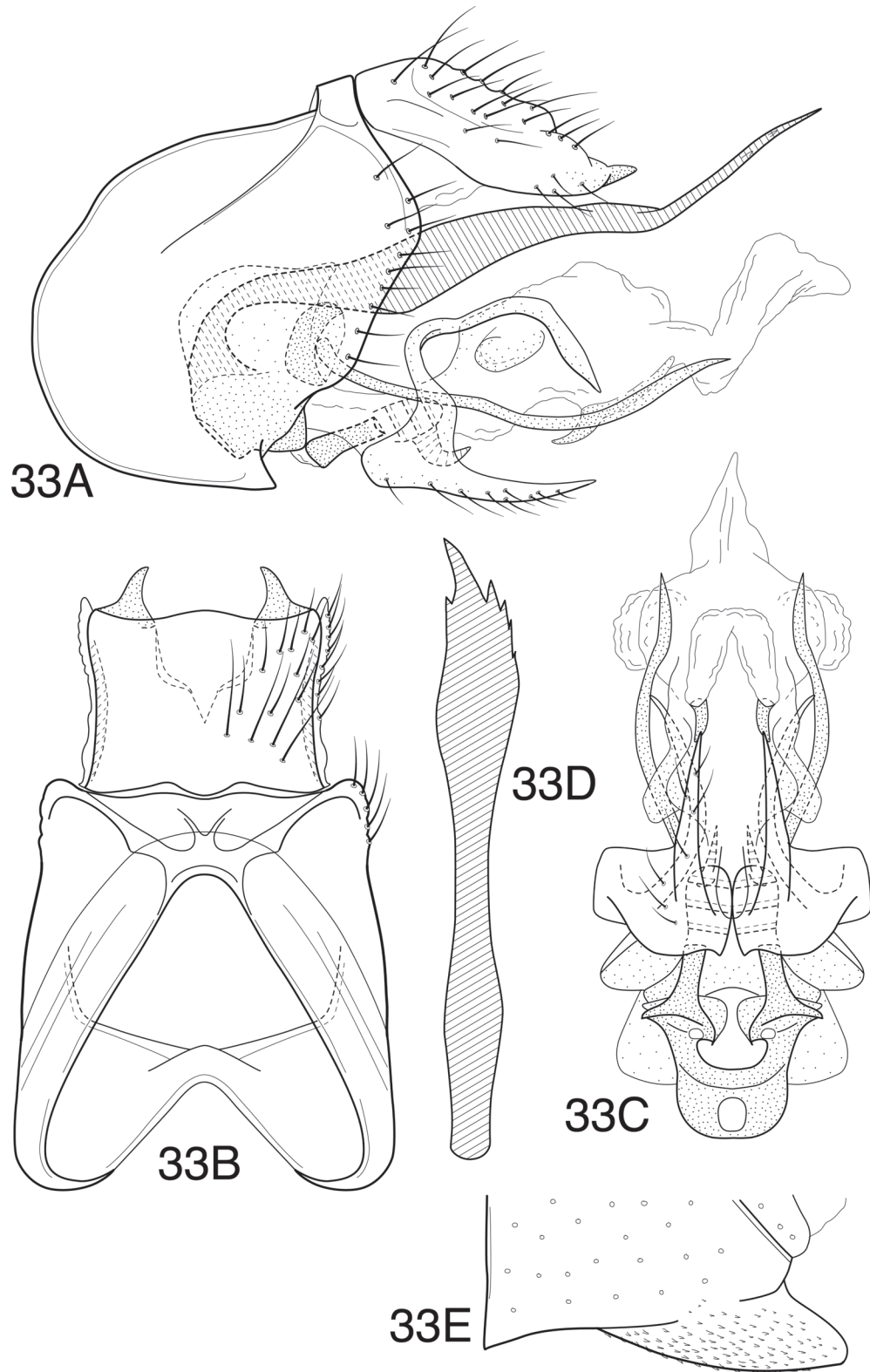


Figure 33. *Mortoniella (Mortoniella) flexuosa*, new species, male genitalia. **A**—lateral; **B**—segment IX and tergum X, dorsal; **C**—phallic ensemble, ventral; **D**—dorsal phallic spine, dorsal; **E**—ventral process of segment VI, lateral.

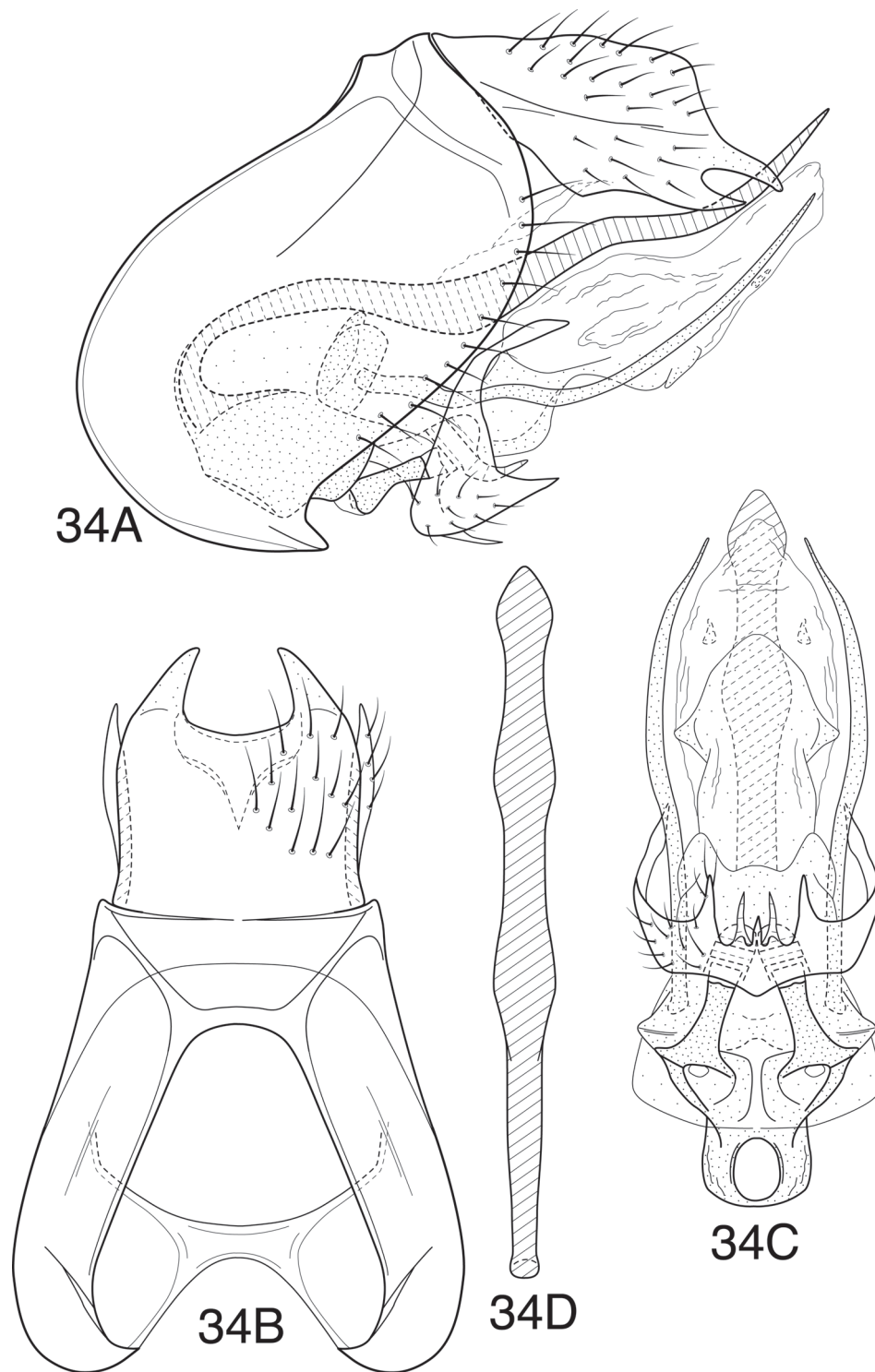


Figure 34. *Mortoniella (Mortoniella) spatulata*, new species, male genitalia. **A**—lateral; **B**—segment IX and tergum X, dorsal; **C**—phallic ensemble, ventral; **D**—dorsal phallic spine, dorsal.

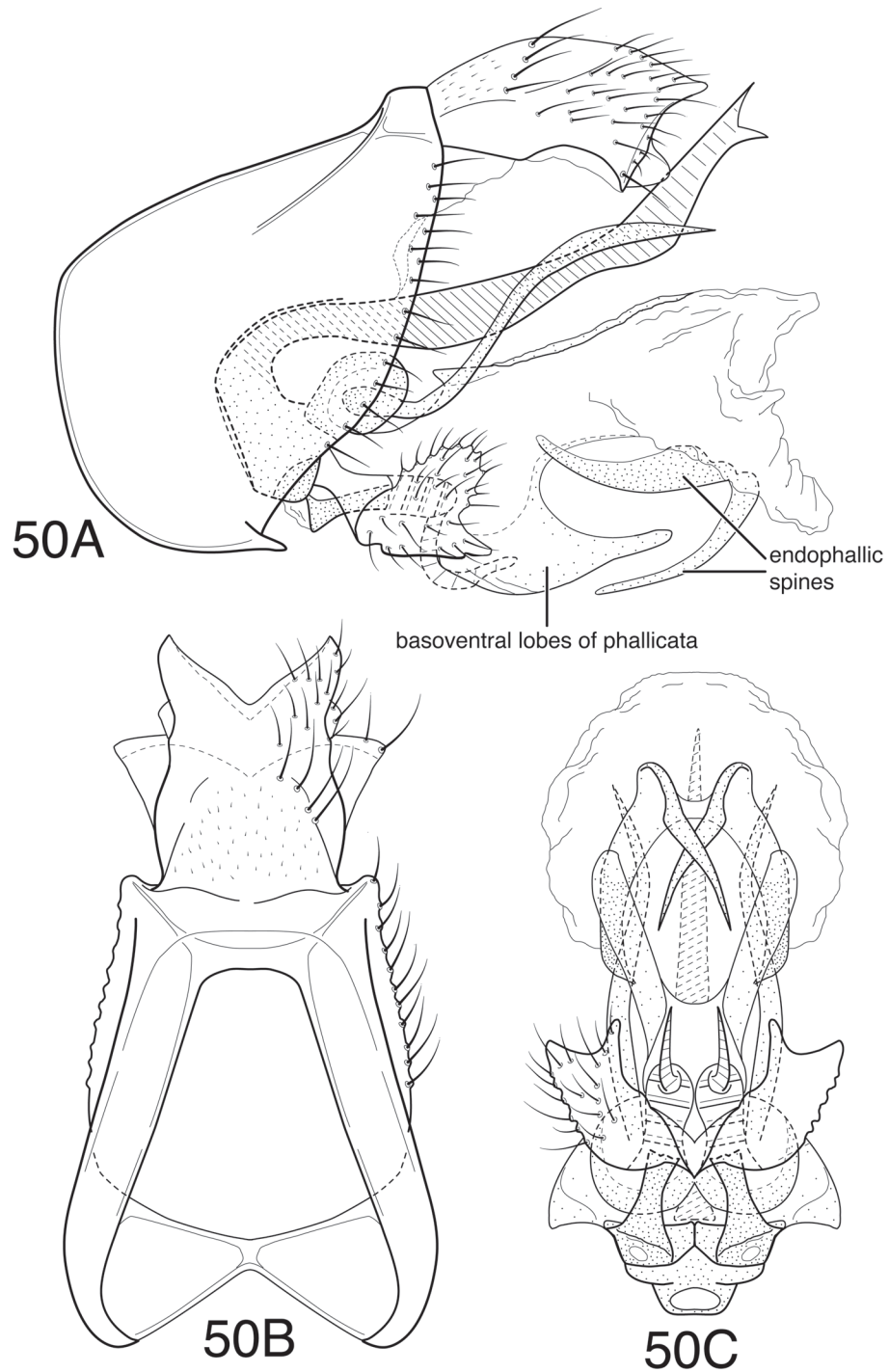


Figure 50. *Mortoniella (Mortoniella) gracilis*, new species, male genitalia. **A**—lateral; **B**—segment IX and tergum X, dorsal; **C**—phallic ensemble, ventral.

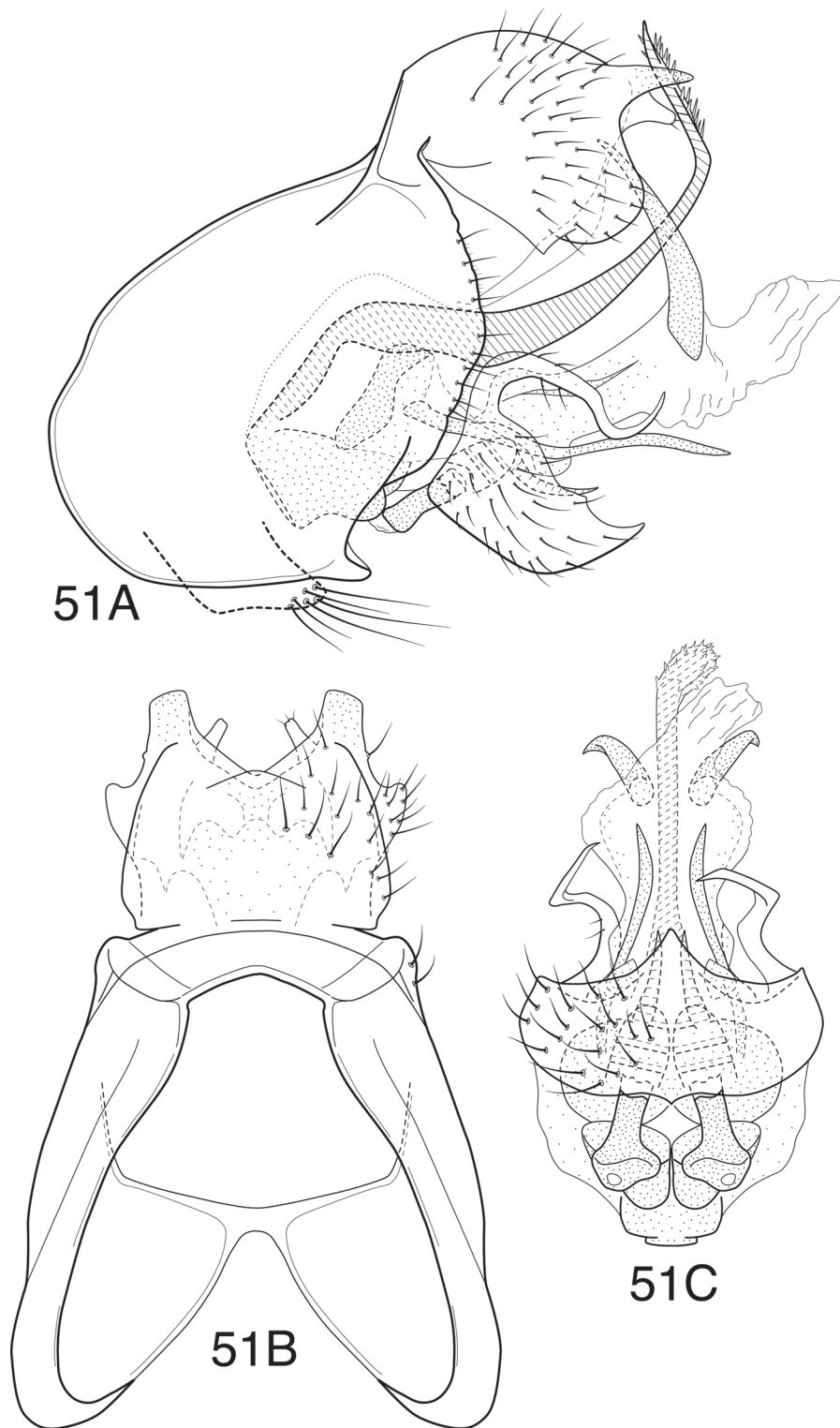


Figure 51. *Mortoniella (Mortoniella) guyanensis*, new species, male genitalia. **A**—lateral; **B**—segment IX and tergum X, dorsal; **C**—phallic ensemble, ventral.

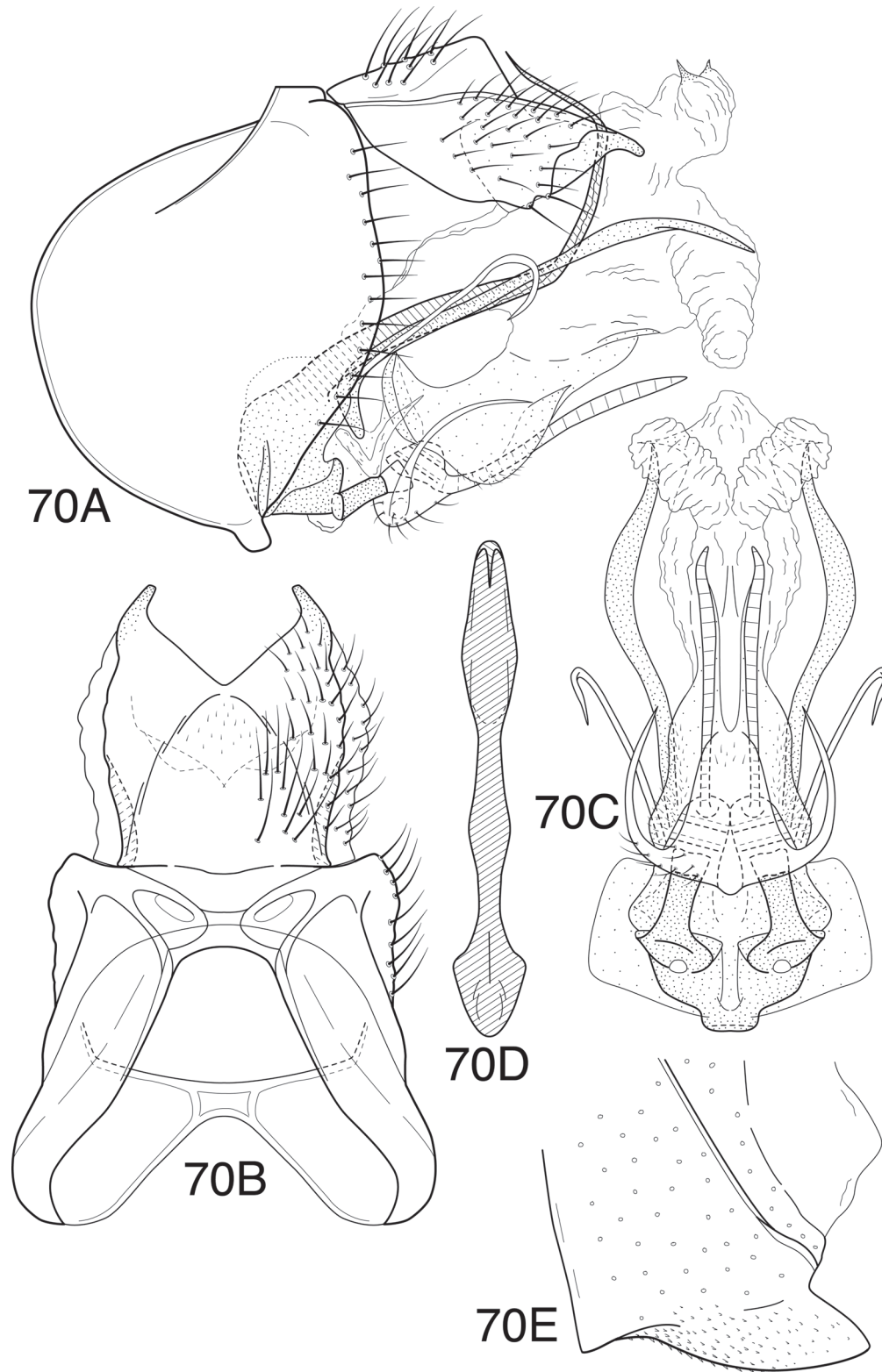


Figure 70. *Mortoniella (Mortoniella) croca*, new species, male genitalia. **A**—lateral; **B**—segment IX and tergum X, dorsal; **C**—phallic ensemble, ventral; **D**—dorsal phallic spine, dorsal; **E**—ventral process of segment VI, lateral.

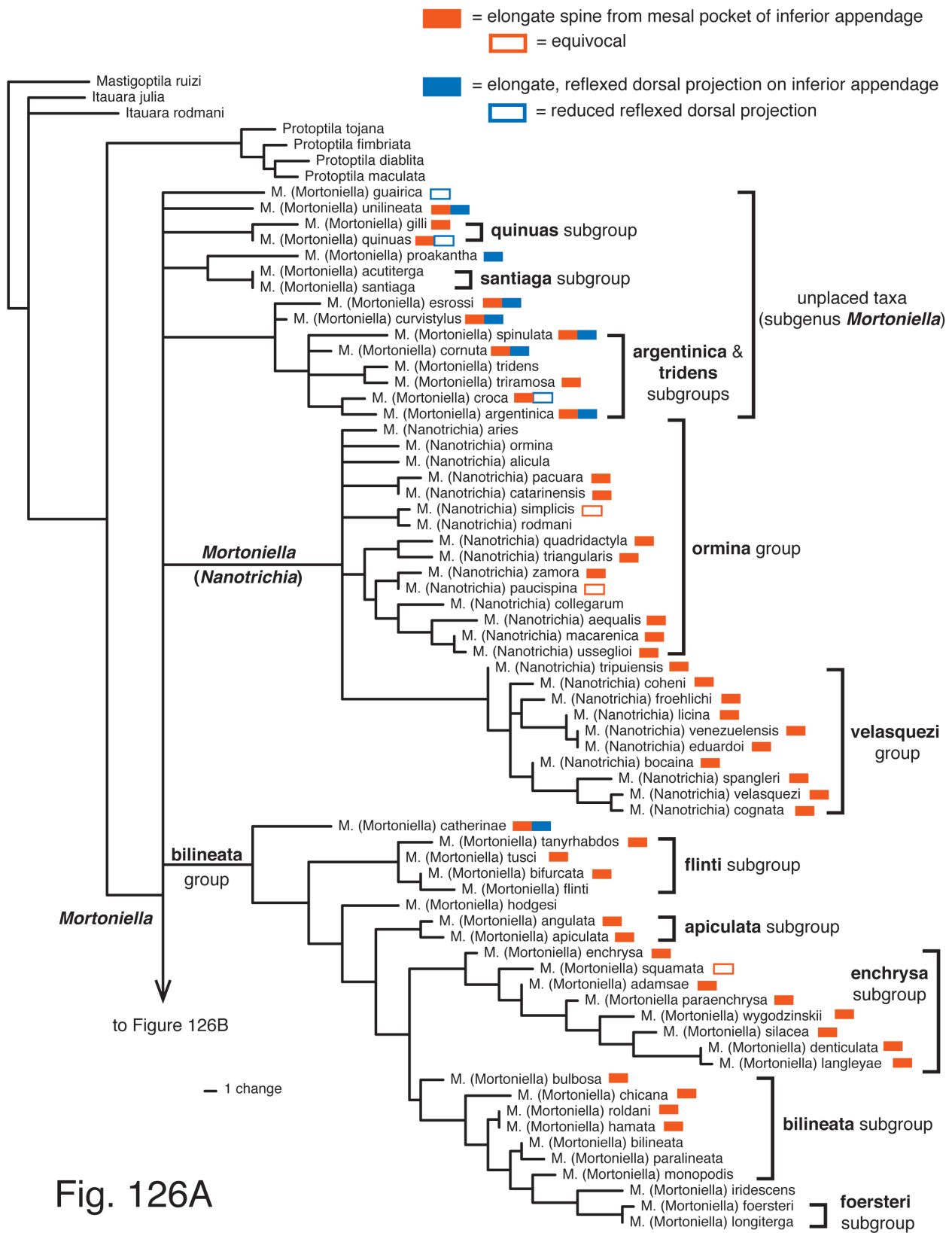


Fig. 126A

Figure 126. Parsimony phylogeny. Part A (above). Part B continues on the next page.

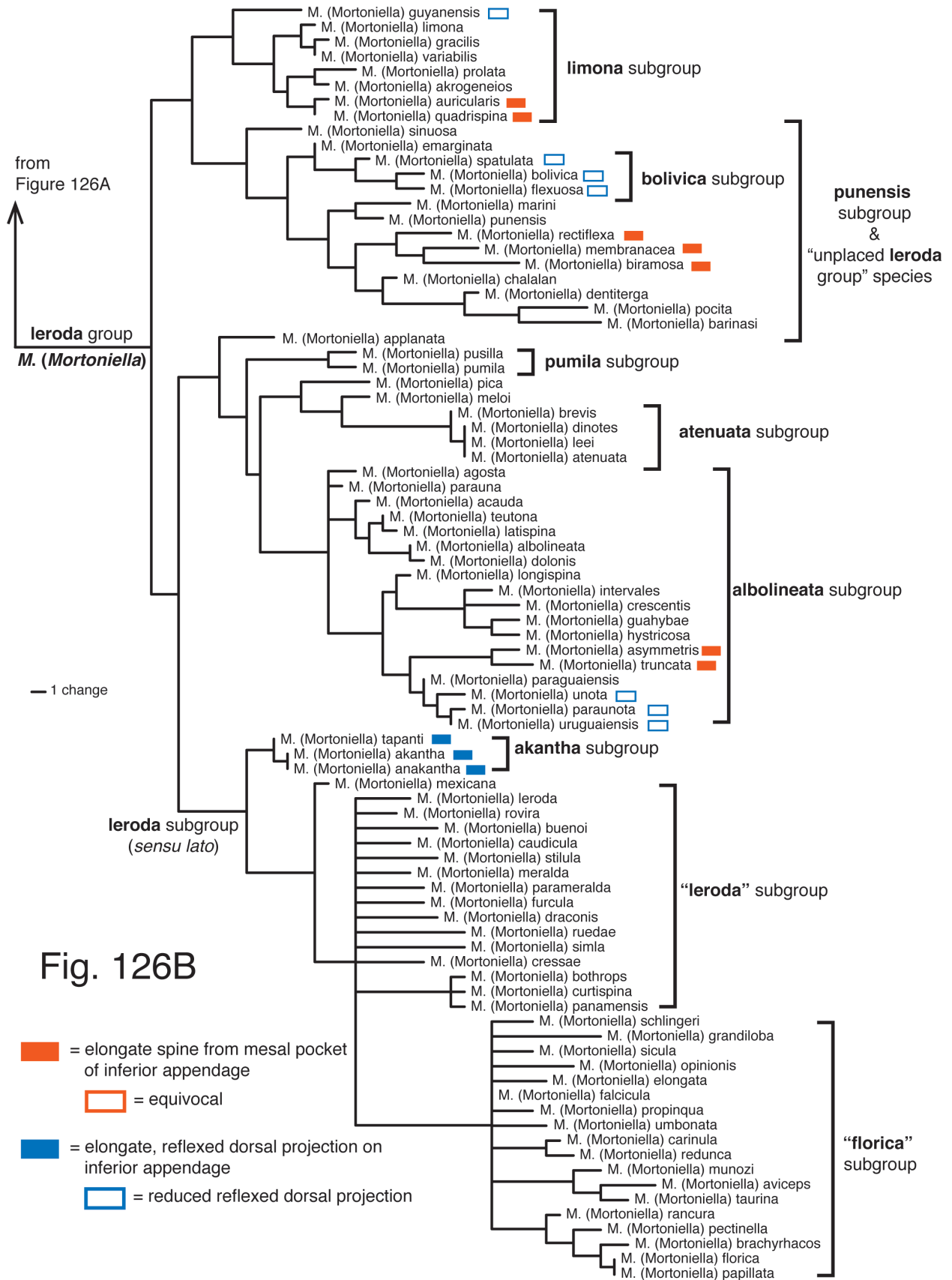
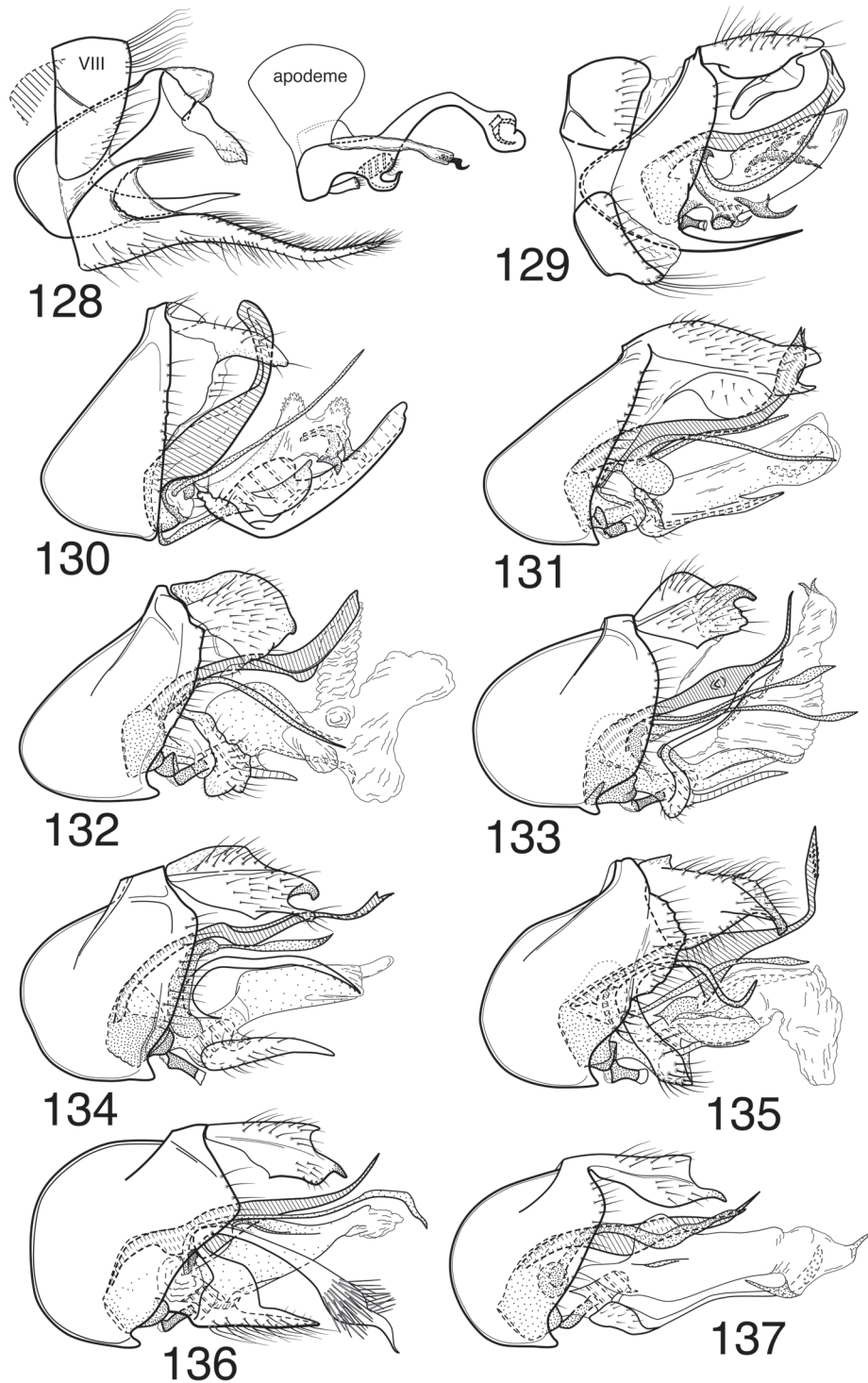


Figure 126. Parsimony phylogeny. Part B (above).



Figures 128-137. Character evolution in *Protoptila/Mortoniella* male genitalia, lateral. **128**—*Protoptila trichoglossa* Blahnik and Holzenthal. **129**—*Mortoniella (Nanotrichia) rodmani* Blahnik and Holzenthal (ormina grp.). **130**—*M. (Nanotrichia) venezuelensis* n. sp. (velasquezi grp.). **131**—*M. (Nanotrichia) macarenica* Flint (ormina grp.). **132**—*M. (Mortoniella) unilineata* Sykora (unplaced to species grp.). **133**—*M. (Mortoniella) cornuta* n. sp. (unplaced to species grp.). **134**—*M. (Mortoniella) proakantha* n. sp. (unplaced to species grp.). **135**—*M. (Mortoniella) catherinae* n. sp. (bilineata grp.). **136**—*M. (Mortoniella) akantha* Blahnik and Holzenthal (leroda grp.). **137**—*M. (Mortoniella) simla* Flint (leroda grp.).