# The problems with Polypedilum Kieffer (Diptera: Chironomidae), with the description of Probolum subgen. n. 

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#### Abstract

A phylogenetic analysis of the genus Polypedilum Kieffer utilizing only species with known larvae, and including one additional species presumed to belong to a new subgenus was performed. The subgenera Tripodura Townes, 1945, Pentapedilum Kieffer, 1913 and Cerobregma Sæther et Sundal, 1999, were all monophyletic, while Uresipedilum Oyewo et Sæxher, 1998 was monophyletic when the new subgenus Probolum was excluded. Polypedilum $s$. str. was never monophyletic even when excluding the atypical $P$. nubifer (Skuse, 1889), but if the relationships between subgenera were unresolved a cladogram as short as the shortest trees could be erected with Polypedilum s. str. as monophyletic.

It is proposed to reestablish the genus Tripedilum Kieffer, 1921a as a subgenus with the type species $P$. (T.) fuscipenne (Kieffer, 1921a) and including P. (T.) nubifer (Skuse); treat Polypedilum Kieffer, 1913 as valid (pending an application to the ICZN to supress Polypedilum Kieffer, 1912); reestablish the subgenus Kribionympha Kieffer, 1921a with the type species Polypedilum (Kribionympha) declivis Kieffer, 1922; give priority to Tripodura Townes, 1945 over senior synonyms; and erect the new subgenus Probolum Andersen et Sæther with Polypedilum (Probolum) marcondesi Pinho et Mendes sp. n. as type species and including at least P. (Probolum) pedatum excelsius Townes sensu Grodhaus et Rotramel, 1980, P. (Probolum) simantokeleum Sasa, Suzuki et Sakai, 1998 and P. (Probolum) bullum Zhang et Wang, 2004.

Short diagnoses for the subgenera of Polypedilum are presented. Polypedilum (Probolum) marcondesi subgen. n., sp. $\mathbf{n}$. is described and figured as male, female, pupa and larva. The two subspecies of $P$. (Uresipedilum) pedatum Townes, 1945 are regarded as full species. The male imago of $P$. (Uresipedilum) excelsius Townes, 1945 and the male and female of $P$. (Uresipedilum) pedatum Townes are redescribed.


Key words: Chironomidae, Polypedilum, Probolum, new subgenus, new species, Brazil

## Introduction

The genus Polypedilum Kieffer is one of the largest chironomid genera containing about 440 described species. The larvae mostly occur in sediments, but several species are associated with phytotelmata and a few mine aquatic plants or co-inhabit pupal retreats of caddis flies (Ashe \& O'Connor 2002; Cranston et al. 1989; Bolton 1991; Kobayashi et al. 2003). Although the triangular, basally constricted eighth tergite combined with the bifid pulvilli readily distinguish the genus among the Chironomini, further division into subgenera has proven problematic. At present the genus is regarded as having five recognized subgenera: Polypedilum s. str. Kieffer, 1912, Pentapedilum Kieffer, 1913, Tripodura Townes, 1945, Uresipedilum Oyewo et Sæther, 1998 and Cerobregma Sæther et Sundal, 1999. The genus Asheum Sublette et Sublette (Sublette \& Sublette 1983) was previously placed in Polypedilum, but as the pulvilli are not bilobed and the eighth abdominal segment of the male is not basally constricted it was reestablished as a separate genus by Oyewo and Sæther (2008).

Several phylogenetic analyses of the genus have been performed during the last decade (Oyewo \& Sæther 1998; Sæther \& Sundal 1999; Bjørlo et al. 2000; Vårdal et al. 2002; Sæther \& Oyewo 2008; Oyewo \& Sæther 2008). What they all have in common, however, is that they attempt to test the monophyly of the separate subgenera rather than analyze the genus as a whole. Pentapedilum, Tripodura, Uresipedilum and Cerobregma all are indicated as being monophyletic by these analyses while the nominal subgenus is often indicated as paraphyletic or polyphyletic even when excluding the unique Polypedilum nubifer (Skuse, 1889).

In spite of the numerous species included in the genus the females and immatures, especially the larvae, are known from a very limited number of species. A major problem with the above mentioned analyses is the unknown character states. Here we attempt to analyze the full genus utilizing only the species with sufficiently known larvae. However, we still lack sufficient female characters to include this stage. In addition to the 53 species in the data matrix the larvae are tentatively or insufficiently known from an additional 3-5 species.

When examining material from Brazil a new species inhabiting phytotelmata, apparently belonging to Uresipedilum, was found. In Brazil 51 Polypedilum species are recorded (Mendes \& Pinho 2008); however, none are from the southern states of Brazil and none belong to Uresipedilum. Most species belong in the subgenera Polypedilum s. str. and Polypedilum (Tripodura) and were described by Bidawid and Fittkau (1995) and Bidawid-Kafka (1996). However, the larva of this new species could not belong to Uresipedilum
as presently defined. It was essentially identical to the larva described as Polypedilum pedatum excelsius Townes by Grodhaus and Rotramel (1980) from tree-holes in California. Sæther and Oyewo (2008: 31) assumed that the drawing of the ventromental plates in Grodhaus and Rotramel (1980), with the median ends of the ventromental plate not in contact with the outer edge of the first pair of lateral teeth of the mentum, but pointing towards each other, was a misrepresentation. However, the new Brazilian species indicates that the drawing in Grodhaus and Rotramel (1980) is correct. Kawai et al. (2006) suggested that Uresipedilum is not monophyletic which now indeed seems to be the case. The males of the new Brazilian species has a basal inner projection of the superior volsella also found in the Japanese $P$. (U.) simantokeleum Sasa, Suzuki et Sakai (Sasa et al. 1998 fig. 12j, k; Sæther \& Oyewo 2008 fig. 8C) as well as in the Chinese P. (U.) bullum Zhang et Wang (Zhang \& Wang 2004 fig. 3; Sæther \& Oyewo 2008 fig. 10 F, G) which is the only known species with spotted wings assigned to Uresipedilum. The Afrotropical Polypedilum longinervis (Kieffer) (Kieffer 1922: 79; Freeman 1958: 290) also appears to belong to the same group.

The basal projection is easily overlooked, especially if the hypopygium is not properly cleared, as it is covered by tergite IX (as shown here in Fig. 10, for the Brazilian species). The hypopygium of $P$. (U.) pedatum Townes, 1945 looks exactly like that of the Brazilian species if the basal part is covered by the caudal portion of tergite IX. However, the immature stages of this taxon, described by Grodhaus and Rotramel (1980), may be incorrectly associated. If the association is correct the male imagines of the new subgenus may not always be possible to separate from those of Uresipedilum.

The material of Grodhaus and Rotramel (1980) has proven impossible to locate. However, two specimens from Marion Lake, British Columbia, obviously belong to Polypedilum pedatum excelsius; these as well as the type material of Polypedilum pedatum pedatum Townes are redescribed below together with the new species from Brazil.

## Material and methods

The general terminology follows Sæther (1980). The specimens were mounted on slides in Canada balsam following the procedure outlined by Sæther (1969). The measurements are given as ranges, followed by the mean when more than three specimens were measured, followed by the number of specimens measured (n) in parenthesis.

The parsimony analyses used PAUP version 4.0 b .10 on a Power Mac G5. The searches were heuristic.
The holotype and most paratypes of Polypedilum (Probolum) marcondesi sp. n. are deposited in the Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo, Brazil; additional paratypes are housed in the Department of Natural History (ZMBN), Bergen Museum, University of Bergen, Norway.

## Systematics

Assessment of the phylogenetic relationship involved compilation of a data matrix for 65 characters in 53 species with known larvae plus $P$. bullum and $P$. simantokeleum, which apparently belong to the same group as the new Brazilian species, with Asheum beckae (Sublette, 1964), Stictochironomus Kieffer, 1919 and Phaenopsectra Kieffer, 1921 as outgroups. The constraint that the genus Polypedilum is monophyletic was used. Otherwise either Asheum or Phaenopsectra plus Stictochironomus often are inside the cladograms.

The data were analyzed under parsimony with PAUP 4.0b. 10 (Swofford 2002) operating on a Macintosh G5, employing 1,000 random addition sequence replicates. Characters 30,40 and 62 were ordered. The characters and states used in the phylogenetic analyses are given below, the data matrix showing the character states in Appendix 1. The data matrix is based on Albu (1980), Beck (1962), Beck and Beck (1964), Boesel (1985), Cranston (1996), Cranston et al. (1989), Epler (2001), Freeman (1958), Grodhaus and Rotramel (1980), Hirvenoja (1962), Kiknadze et al. (1991), Langton and Visser (2003), Lehmann (1979, 1981), Maschwitz and Cook (2000), Niitsuma (1992), Oyewo and Sæther (1998), Pinder and Reiss (1983, 1986),

Roback and Coffman (1983), Rossaro (1985), Sæther and Oyewo (2008), Sæther and Sundal (1999), Sasa (1979, 1985), Sasa and Kikuchi (1995), Sasa and Sublette (1980), Sasa et al. (1998), Soponis and Russell (1982), Soponis and Simpson (1992), Sublette (1964), Vårdal et al. (2002), Zhang and Wang (2004) and material from the collection of the Department of Natural History, Bergen Museum, University of Bergen. Few species are described in full and several of the character alternatives listed in the data matrix remain questionable. The character alternatives for Polypedilum excelsius sensu Grodhaus et Rotramel are scored as if the association with the immatures by Grodhaus and Rotramel (1980) is as in P. excelsius Townes except for the base of the superior volsella. Additional characters such as the shape of the larval eyes probably are useful, but inadequately known for most species.

Characters and states used in the phylogenetic analysis:

## Males

1. Abdomen: (0) uniformly colored; (1) banded.
2. Legs: (0) unicolored or at most with darker shade at some apices; (1) ringed.
3. $A R$ : (0) higher than 1.0; (1) lower than 1.0.
4. Scutellum: (0) with 3-12 setae; (1) with 13 or more setae.
5. Wing membrane: (0) without markings; (1) with dark spots.
6. Wing membrane: (0) without setae; (1) with setae.
7. Wing vein $R_{2+3}$ : (0) relatively well separated from $\mathrm{R}_{1}$; (1) adjacent to $\mathrm{R}_{1}$.
8. Setae on $R_{4+5}:(0)$ less than 41 ; (1) more than 40.
9. Setae on $M$ : (0) present; (1) absent.
10. Antepronotum: (0) without setae; (1) with.
11. Scutal fossal setae: (0) absent; (1) present.
12. Setae on squama: (0) more than 7; (1) 2-7.
13. Fore tibial scale: (0) with apical spur; (1) without spur, but may be sharply pointed.
14. Fore tibial scale: (0) rounded; (1) triangular, pointed.
15. Leg ratio: (0) lower than 2.0 ; (1) 2.0 or higher.
16. Pulvilli: (0) not bifurcate; (1) bifurcate.
17. Tergite VIII: (0) not tapered basally; (1) tapered basally.
18. Superior volsella: (0) with projection; (1) without.
19. Superior volsella: (0) with mostly low base and long apical projection, or large base and no projection; (1) with high and large base and apicomedian projection.
20. Projection of superior volsella: (0) at least as long as base; (1) shorter than base; (2) absent.
21. Projection of superior volsella: (0) not medially directed and straight, often curved at apex; (1) medially directed, straight, at most slightly curved at blunt apex.
22. Projection of superior volsella: (0) not medially directed, straight until abruptly upturned blunt apex; (1) medially directed, straight until abruptly upturned blunt apex.
23. Projection of superior volsella: (0) not medially directed, broad-based, curved; (1) medially directed, broad-based, curved.
24. Projection of superior volsella: (0) not posterior or posteromedially directed, short, broad-based, tapering to acutely pointed apex; (1) posterior or posteromedially directed, short, broad-based, tapering to acutely pointed apex.
25. Projection of superior volsella: (0) not narrow, sickle-shaped, evenly curved and evenly tapering to pointed apex; (1) narrow, sickle-shaped, evenly curved and evenly tapering to pointed apex.
26. Projection of superior volsella: (0) with outer seta; (1) without. (Absence of projection scored as ?).
27. Seta of projection of superior volsella: (0) placed in basal third; (1) placed in middle third; (2) placed in apical third; (3) absent. (Absence of projection scored as ?).
28. Base of superior volsella: (0) without basal inner lobe-like projection; (1) with (only indicated in $P$. excelsius).
29. Base of superior volsella: (0) covered with microtrichia; (1) not completely covered with microtrichia; (2)
completely bare.
30. Base of superior volsella: (0) with 4 or more inner setae; (1) with 3; (2) with 1-2; (3) without.
[The description of $P$. simantokeleum mentions 10 setae on the basal projection while the drawings show 6 . Similarly the description of $P$. bullum mentions 12 setae, while the drawing shows a single seta. The first does not matter for the data matrix, while the second is assumed being a misprint for $1-2$ setae.]
31. Setae of inferior volsella: (0) simple; (1) some split.
32. Median setae of tergite $I X$ : (0) fewer than 10; (1) 10-23; (2) more than 23.
33. Anal tergite bands: (0) absent or weak; (1) not fused basal to median setae; (2) fused basal to median setae.
34. Anal point: (0) not conspicuously broadened; (1) conspicuously broadened.
35. Anal point: (0) without lateral lobes to each side of anal point or on anal point; (1) with.
36. Setae along inner margin of gonostylus: (0) not extremely long; (1) extremely long, simple; (2) extremely long, at least some split.
Pupae
37. Cephalic tubercles: (0) normal to strongly developed; (1) reduced to low humps or absent.
38. Cephalic tubercles: (0) not cone shaped; (1) cone shaped, sometimes fused to form a single structure.
39. Frontal setae: (0) long; (1) short or absent.
40. Thoracic horn: (0) with 3-8 branches; (1) with 9-20; (2) with more than 20.
41. Prealar tubercle: (0) absent; (1) present.
42. Shagreen of tergites: (0) T II without anterior band of spinules; (1) with.
43. Conjunctive III/IV: (0) with spinules; (1) without.
44. Pedes spurii A: (0) present; (1) absent.
45. Pedes spurii B anterior on segment I: (0) absent; (1) weak; (2) well developed.
46. Pedes spurii B on segment II: (0) absent; (1) weak; (2) well developed.
47. Taeniate L-setae on segments V-VIII: (0) as 3:3:4:4 (5); (1) taeniae on V and VI may be reduced in size or number; (2) taeniae on V and sometimes VI absent.
48. Anal spur or comb: (0) single with or without accessory teeth or absent; (1) comb present.
49. Anal spur or comb: (0) with few teeth or absent; (1) with numerous teeth or spinules.
50. Fringe of anal lobe: (0) always more than 20 taeniae; (1) sometimes fewer.
51. Fringe of anal lobe: (0) with 45 or fewer taeniae; (1) with more than 45 taeniae.
52. Dorsal seta of anal lobe: (0) absent; (1) present.

Larvae
53. Anterior margin of frontoclypeal apotome: (0) not straight; (1) straight.
54. Third antennal segment: (0) relatively long, longer than or only slightly shorter than segment 4; (1) shorter, distinctly shorter than segment 4 , or when not, segment 4 also reduced.
55. Lauterborn organs: (0) well developed; (1) small, indistinct or absent.
56. Lauterborn organs: (0) opposite; (1) alternate.
57. Antennal blade: (0) shorter than flagellum; (1) longer.
58. Pecten epipharyngis: (0) median scale with 3-5 teeth; (1) median scale with 1-2 teeth.
59. Mandible: (0) no dorsal tooth or dorsal tooth weak and spine-like; (1) with well developed dorsal tooth.
60. Mola: (0) smooth; (1) serrated.
[Except for in P. (P.) braseniae (Leathers, 1922), the character state ( 0 ) mola smooth is scored based on illustrations. It may be incorrect especially for P. (Pe.) kasumiense (Sasa, 1979) and P. (Pe.) shirokanense Sasa, 1979.]
61. Mentum: (0) first lateral teeth at least as high as median and/or second lateral teeth; (1) first lateral teeth slightly lower than median and/or second lateral teeth; (2) first lateral teeth much lower than median and/ or second lateral teeth.
62. Ventromental plates: (0) without posterior lobes; (1) posterior lobes indicated; (2) lobes well developed.
63. Ventromental plates: (0) less than 3 times as wide as high; (1) at least 3 times as wide as high.
64. Distance between ventromental plates: (0) less than width of 4 median teeth; (1) at least as long as combined width of 4 median teeth.
65. Median ends of ventromental plates: (0) pointing posterior or towards each other or posteriorly or if pointing slightly anteriorly not attached to second lateral teeth; (1) anteriorly produced and in contact with first lateral teeth.

Strict


Strict


FIGURES 1-2. Parsimony analyses of Polypedilum Kieffer with Asheum beckae (Sublette), Stictochironomus Kieffer and Phaenopsectra Kieffer combined as outgroup. 1-strict consensus of shortest trees. 2-strict consensus of shortest trees after successive reweighting according to the rescaled consistency index.


FIGURES 3-4. Parsimony analyses of Polypedilum Kieffer with Asheum beckae (Sublette), Stictochironomus Kieffer and Phaenopsectra Kieffer combined as outgroup and some characters weighted as in text. 1-strict consensus of shortest trees. 2-strict consensus of shortest trees after successive reweighting according to the rescaled consistency index.

Four hundred and sixty-two trees were obtained each with 509 steps, consistency index (CI) of 0.50 , homoplasy index (HI) of 0.84 , retention index (RI) of 0.63 , and a rescaled consistency index (RC) of 0.32 . The strict consensus tree is shown in Figure 1. When the trees were exposed to successive reweighting according to RC, 46 trees each with 516 steps (when the weights were reset to one), CI of $0.56, \mathrm{HI}$ of 0.60 , RI of 0.83 and RC of 0.47 were obtained after two reweightings (Fig. 2).

Giving weight 10 to characters $5,6,7,9,13,18,19,20,25,26,27,28,29,30,34,35,36,38,40,47,48$, $52,54,55,56,59,60,61,62$ and 65 also was attempted. This produced 41,602 trees each with 522 steps (when the weights were reset to one), CI of 0.51 , HI of 0.80 , RI of 0.74 and RC of 0.38 . The strict consensus tree is shown in Figure 3. When the trees were exposed to successive reweighting according to RC, 117 trees each with 518 steps (when the weights were reset to one), CI of 0.52 , HI of 0.65 , RI of 0.81 and RC of 0.42 were obtained after one reweighting (Fig. 4).

The results both before and after successive reweighting as in Figures $1-4$ show the subgenera Cerobregma, Tripodura, Pentapedilum and usually Uresipedilum as monophyletic, except that either $P$. simantokeleum sometimes is retained in Uresipedilum sometimes in the new subgenus while Polypedilum s. str. is never monophyletic even when disregarding $P$. nubifer. The evidence for monophyly of the subgenus Pentapedilum to some extent is based on the wing chaetotaxy. However, as shown by Oyewo and Sæther (2008), even when all characters concerning wing chaetotaxy are deleted the subgenus still forms a monophyletic unit, but only after reweighting and with the exception that $P$. (P.) albicorne (Meigen, 1838) may fall inside the subgenus and $P$. (Pe.) sordens (van der Wulp, 1874) outside the subgenus.

However, if Polypedilum s. str. minus $P$. nubifer is regarded a priori as monophyletic and some of the relationships between subgenera unresolved as shown in Figure 5, the cladogram is 6 steps shorter than in Figure 2 (unweighted after successive reweighting) and 8 steps shorter than the cladogram shown in Figure 4 (weighted and reweighted) as measured in MacClade. (Measured in PAUP, however, the cladogram is longer). The data thus are insufficient to show Polypedilum s. str. minus $P$. nubifer as non-monophyletic. Placing $P$. nubifer at the base of any of the other subgenera or as sister group to all Polypedilum lengthens the tree shown in Figure 5 with 7 to 10 steps. Choosing different outgroups, adding taxa and characters undoubtedly will give better and somewhat different results, but because of the high degree of homoplasies is unlikely to significantly change the outcome. The female genitalia may show diagnostic differences between the different subgenera as indicated by Sæther (1977: 165), but too few females have been studied in sufficient detail. However, all six to seven examined Tripodura have a long parallel-sided dorsomesal lobe clearly overreaching the ventrolateral lobe combined with straight spermathecal ducts; Polypedilum s. str. has nearly straight spermathecal ducts, but shorter dorsomesal lobe; Cerobregma, Uresipedilum, Pentapedilum all have spermathecal ducts with a sharp bend of about 90 degrees; the ventrolateral lobe in the three examined Cerobregma species is reduced or vestigial, the dorsomesal lobe very large; while Uresipedilum and Polypedilum are similar to Polypedilum s. str. in the lobes of gonapophysis VIII.

Geoffrey Morse, University of San Diego, California (personal communication to P. S. Cranston) has shown based on 3 genes that $P$. nubifer apparently is irretrievably embedded in Polypedilum. It thus is not justified to erect a separate genus for $P$. nubifer.

In the parsimony analyses shown here (Figs 1-4) Polypedilum nubifer is sister group to Probolum when the characters are unweighted and not reweighted (Fig. 1), to Tripodura when the characters are reweighted or weighted with the particular weighting scheme chosen (Figs 2-4). It never forms, however, the sister group to all other Polypedilum and is always inside the genus.

It seems clear that the present configuration of subgenera is untenable. Polypedilum nubifer, the type species of Polypedilum s. str. is distinct in all stages and clearly deserves a separate subgenus. Most members of Uresipedilum undoubtedly belong together in a subgenus. However, a separate subgenus for those species which do not possess the characteristic larval characters as in P. marcondesi sp. n. described below and $P$. pedatum excelsius sensu Grodhaus and Rotramel appears warranted.

Polypedilum s. str. with or without $P$. nubifer is never monophyletic. Polypedilum arundineti (Goetghebuer, 1921) may not be correctly scored as the only reasonably complete description is by Sasa (1985 fig. 3E-4) and shows about 17 median setae on tergite IX, while the drawing in Langton and Pinder (2007 fig. 230C) shows about 6 setae. P. nubeculosum (Meigen, 1804) is rather different and may deserve a separate subgenus. Except for the hairy wings in Pentapedilum there are no diagnostic characters separating Pentapedilum from Polypedilum s. str. with or without $P$. nubifer.

Polypedilum s. str. has been divided into species groups by Sasa and Kikuchi (1995), Sæther and Sundal (1999) and Maschwitz and Cook (2000). Sasa and Kikuchi (1995) divided the subgenus into species with a


FIGURE 5. Preferred synapomorphy diagram for Polypedilum Kieffer and included subgenera.
seta on the projection of the superior volsella, the nubeculosum group and species without such a seta, the nubifer group. Except for excluding $P$. nubifer from the nubifer group (defined by Sasa and Kikuchi (1995) as including species without an outer seta on the projection of the superior volsella) the same division was followed by Sæther and Sundal (1999). However, of the species in Pentapedilum and Polypedilum s. str. included here only $P$. nubifer and some $P$. (Pentapedilum) sordens, $P$. (P.) albicorne and $P$. ( $P$.) fallax (Johannsen, 1905) lack a seta on the superior volsella projection. A division based on the presence or absence
of the projection seta clearly is not tenable. Maschwitz and Cook (2000) divide the subgenus into a laetum group, an illinoense group and a fallax group with $P$. (P.) nubeculosum and $P$. (P.) trigonus Townes, 1945 perhaps forming a fourth group. There is some evidence for these groups in the parsimony analyses. A laetum group also including $P$. (P.) albicorne is indicated, an illinoense group excluding $P$. (P.) braseniae and including $P$. (P.) trigonus is found, and a fallax group excluding $P$. (Cerobregma) ontario (Walley, 1926) and including $P$. (P.) braseniae is indicated. Polypedilum (P.) nubeculosum, P. (P.) brunneicorne Kieffer, 1911 and $P$. (P.) arundineti all fall outside these groups.

The larvae and pupae of $P$. braseniae have several unique characters not found in other members of the genus. However, these appear all to be autapomorphies. Polypedilum braseniae is the only member of the genus with two small median teeth on the larval mentum, which, however, often are worn down and not discernible.

Polypedilum nubeculosum may deserve a separate group. It is the only Polypedilum in addition to the subgenus Cerobregma with setae on the antepronotum and the only species with the outer lateral seta of the projection of the superior volsella placed in the apical third. Amongst the species of the enlarged Pentapedilum included in the data matrix, wing membrane with spots is found otherwise only in $P$. laetum (Meigen, 1818). The seta anteriores (S I) of the larva appear to have the apex more filamentously branched than in other species.

Polypedilum declivis (Kieffer, 1922) is the only species other than P. nubifer which has cephalic tubercles (Freeman 1958: 289). The species is the type species of Kribionympha Kieffer. The hypopygium is quite unique and if the species is correctly placed in Polypedilum, Kribionympha deserves subgeneric status.

If the incomplete description is correct Chirocladius Picado, 1913: 288, could belong to Polypedilum s. str., Uresipedilum or to the new subgenus described below. However, no Uresipedilum as redefined here and few Polypedilum s. str. have spotted wings and it is not impossible that Chirocladius could be a senior synonym of the new subgenus as also indicated by the bromeliad biotope. The types are supposed to be in the collection of the US National Museum, Washington, but no specimens could be located in the pinned, slide, or alcohol type collections of Chironomidae. Neither did the computer database contain any listings for the type species (Holly B. Williams, personal communication). Chirocladius and its type species Chirocladius pedipalpus Picado, 1913 thus have to be regarded as nomina dubia.

## Polypedilum subgenus Tripedilum Kieffer

Tripedilum Kieffer, 1921a: 271; 1921c: 28, 47.
Polypedilum Kieffer, 1912; not Kieffer, 1913, (see below).

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Type species
Polypedilum (Tripedilum) fuscipenne (Kieffer)
    Polypedilum fuscipenne Kieffer, 1921a: }98
    Tripedilum armatifrons Kieffer, 1921b: }47
    Polypedilum longiforceps Kieffer, 1921a: }98
    Microtendipes longiventris Kieffer, 1922: }15
Other included species
Polypedilum (Tripedilum) nubifer (Skuse)
    Chironomus nubifer Skuse, 1889: }249
    Chironomus (Prochironomus) triparticus Kieffer, 1910: }231
    Chironomus ceylanicus Kieffer, 1911: }136
    Polypedilum pelostolum Kieffer, 1912: }41
    Polypedilum pharao Kieffer, 1925: }274
    Chironomus (Polypedilum) albiceps Johannsen, 1932: }515
    Polypedilum pruinosum Goetghebuer, 1934: 37.
    Chironomus (Polypedilum) octoguttatum Tokunaga, 1936: 83.
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Diagnostic characters. The male imagines of the subgenus differ from the males of other subgenera primarily by having distinct frontal tubercles and the projection of the superior volsella without any outer seta. The projection of the superior volsella is very long compared to the short base and the gonostylus is broad with a broad, blunt apex.

The pupa has unique well developed cone-shaped cephalic tubercles, numerous branches ( $>20$ ) in the thoracic horn, no pedes spurii A, a well developed comb on the caudolateral margin of segment VIII, and anal lobe with numerous taeniae (about 38-50) and no dorsal setae.

The larva has alternating Lauterborn organs, third antennal segment distinctly longer than fourth, antennal blade shorter than flagellum, mentum with first lateral teeth distinctly lower than second and median teeth and ventromental plates without posterior lobes and with median apices pointing towards each other.

## Key to the males

1. Wing with distinct markings, fore tibial scale rounded without spur. ........................................P. (T.) nubifer (Skuse)

- Wing without distinct markings, fore tibial scale with spur ........................................................................................ 2

2. Anal point slender, $\mathrm{LR}>2.0$, fore tarsus not bearded ......................................................... P. (T.) fuscipenne (Kieffer)

- Anal point stout, LR about 1.1, fore tarsus bearded. P. (T.) lobiferum (Freeman)

Except for the wing markings and the lack of spur on the front tibial scale $P$. (T.) nubifer and $P$. (T.) fuscipenne are essentially identical, while the placement of $P$. (T.) lobiferum is more uncertain.

## Polypedilum subgenus Polypedilum Kieffer

Polypedilum Kieffer, 1913: 15; not Kieffer (1912: 41).
Kribiocharis Kieffer, 1922: 1.
Pentapelma Kieffer, 1921b: 98; 1921c: 33.
Rosenia Kieffer, 1921a: 275; not Waagen and Wentzel (1887: 943).
Propedilum Lenz, 1937: 13.

Type species
Polypedilum (Polypedilum) nubeculosum (Meigen)
Chironomus nubeculosus Meigen, 1804: 18.
Polypedilum emarginatum Kieffer, 1913: 16.

The genus Polypedilum Kieffer was described in 1913 and Polypedilum emarginatum Kieffer, 1913 [=P. nubeculosum (Meigen, 1818)] designated as the type of the genus (Kieffer 1913: 15). As shown by Ashe (1981), however, the type designation was invalid as two species were assigned to the genus Polypedilum in a paper published a year earlier (Kieffer 1912: 41). Of the two species, P. pelostolum Kieffer, 1912 and $P$. ceylanicum (Kieffer, 1912), at least the first according to Freeman (1961) is a synonym of P. nubifer and was selected as the type species. However, Freeman (1961) stated that $P$. nubifer is without frontal tubercles, while the presence of frontal tubercles is one of the most significant features of the species. Two syntypes of $P$. pelostolum from The Natural History Museum in London were examined. The specimens were lacking wings, antennae, hypopygia and most legs, but one head with frontal tubercles intact remained. Accordingly the
synonymy with $P$. nubifer has to be accepted. As shown here $P$. nubifer, however, should be placed in Tripedilum. A case will be made to ICZN for rejecting the type designation of Ashe (1981) and maintaining the type designation of Kieffer (1913).

Diagnostic characters. The male imagines of the subgenus can be distinguished by having no frontal tubercles, bare wing membrane, wing vein $\mathrm{R}_{2+3}$ usually relatively well separated from $\mathrm{R}_{1}$, projection of superior volsella long compared to the short base and nearly always with outer seta and anal point never trifid or with lateral teeth or shoulders to each side of the anal point.

The few female imagines sufficiently described have nearly straight spermathecal ducts and the dorsomesal lobes of gonapophysis VIII are not reaching much caudal of the ventrolateral lobes.

The pupa has no frontal tubercles and no or vestigial cephalic tubercles, less than 20 branches in thoracic horn, single spur on caudolateral margin of segment VIII, taeniae on segments V and VI may be reduced in size or number and anal lobe without dorsal setae.

The larva has opposing Lauterborn organs; third antennal segment distinctly longer to somewhat shorter than fourth; pecten epipharyngis occasionally with less than 3 teeth in median scale, usually $3-5$; mandible occasionally without dorsal tooth, usually with; occasionally mola smooth, usually serrate; mentum usually with first lateral teeth distinctly lower than second and median teeth, but often at least as high as median and/ or second lateral teeth; and ventromental plates without posterior lobes, with median apices pointing towards each other and distance between plates usually at least as long as combined width of 4 median teeth.

Remarks. The pupae of Polypedilum s. str. are not separable from those of Pentapedilum, Uresipedilum and Probolum. Most larvae cannot be distinguished from those of Pentapedilum. Some larvae, however, are separable from other known larvae except P. (Pe.) epleri Oyewo et Jacobsen, 2007, by having first lateral teeth of mentum at least as high as median and/or second lateral teeth. From $P$. (Pe.) epleri they differ by either having mandible with a dorsal tooth, mola without serrations or well developed Lauterborn organs.

## Polypedilum subgenus Pentapedilum Kieffer

Pentapedilum Kieffer, 1913: 25.
Type species
Polypedilum (Pentapedilum) tritum (Walker) Chironomus tritus Walker, 1856: 162.
Tanytarsus unicus Becker, 1908: 77.
Calopsectra longiseta Kieffer, 1913: 29.
Pentapedilum stratiotale Kieffer, 1913: 26.
Tanytarsus praeornatus Santos-Abreu, 1918: 229.
Pentapedilum muscicola Kieffer, 1924: 36.
Polypedilum (Pentapedilum) albulum Townes, 1945: 63.
Not Polypedilum (Pentapedilum) muscicola Oyewo et Sæther, 2008: 79.

Diagnostic characters. The male imagines of the subgenus differ from the males of other subgenera primarily by having setae on the wing membrane and on vein $M$, but no darker markings; wing vein $R_{2+3}$ adjacent to $\mathrm{R}_{1}$; no frontal tubercles; projection of the superior volsella long compared to the short base and with an outer lateral seta on the projection (may be absent in some specimens of some species).

The few female imagines known have spermathecal ducts with a sharp angle and the dorsomesal lobes of gonapophysis VIII not reaching much caudal of the ventrolateral lobes.

The pupae have no frontal tubercles, reduced or absence of cephalic tubercles, less than 20 branches in the thoracic horn, conjunctive III/IV occasionally without spinules, single spur often with numerous lateral spinules on the caudolateral margin of segment VIII and no dorsal setae.

The larvae have third antennal segment usually longer than fourth; antennal blade usually shorter than flagellum; mentum with first lateral teeth as high as, slightly lower than or mostly distinctly lower than second
and median teeth; mandible occasionally without dorsal tooth and ventromental plates without posterior lobes, occasionally at least 3 times as wide as high, distance between plates nearly always greater than the combined width of the four median teeth and with median apices pointing towards each other.

Remarks. The pupae of Pentapedilum are not separable from those of Polypedilum s. str., Uresipedilum and Probolum. Most larvae cannot be distinguished from those of Polypedilum s. str. The larvae of P. (Pe.) leei Freeman, 1961 and $P$. ( $P e$ ) sordens are distinguished by having the ventromental plates more than 3 times as wide as high, first lateral teeth of mentum only slightly lower than median and second lateral teeth and no dorsal tooth of the mandible. Polypedilum (Pe.) epleri also has a mandible without a dorsal tooth, but first lateral teeth of the mentum are as high as median and second lateral teeth.

The revision by Oyewo and Sæther (2008) contains several mistakes. The synonym list of the type species is corrected here. Polypedilum (Pentapedilum) muscicola sensu Oyewo et Sæther is based on a mislabeling of a specimen from Institut Royal des Sciences Naturelles de Belgique in Bruxelles, Belgium (IRSN) and could be given a new name. However, since there is just one specimen without locality we will refrain from naming the species. The type specimen of $P$. (Pe.) tritum Walker, 1856 is listed as lectotype on p .8 , but not designated as such on p. 110. The type specimen of $P$. (Pe.) uncinatum Goetghebuer, 1921 from IRSN is listed as holotype, but should have been listed as syntype or selected as lectotype.

## Polypedilum subgenus Tripodura Townes

Tripodura Townes, 1945: 36.
Kribiotima Kieffer, 1921a: 274.
Kribiophilus Kieffer, 1921c: 30; 1921b: 98; 1922: 43.

## Type species

Polypedilum (Tripodura) simulans Townes
Polypedilum (Tripodura) simulans Townes, 1945: 43.

Diagnostic characters. The male imagines of the subgenus either have a broad and often club-shaped superior volsella without an apical projection, or trifid anal point or lateral teeth or shoulders to each side of the anal point or both. The wings often have dark markings and no setae on the wing membrane except for one Afrotropical and two Neotropical species. The anal point is often broad. The superior volsella is almost always covered with microtrichia and normally has setae on distal parts of the outer and inner margin.

Female imagines can be distinguished by the lobes of gonapophysis VIII, of which the dorsomesal lobe is clearly longer than the ventrolateral and straight spermathecal ducts, usually combined with strong wing markings.

Pupae of the subgenus have dorsal setae on the anal lobe; sometimes numerous branches in the thoracic horn; often well-developed cephalic tubercles; sometimes frontal tubercles present and usually with longitudinal anal combs.

Larvae of the subgenus have a long antennal blade reaching well beyond the flagellum. Antennal segment 3 is at most one-third the length of segment 2 , antennal segments $3-5$ are sometimes all reduced. Normally the first lateral teeth of the mentum are much shorter than the median and second lateral teeth. The ventromental plates sometimes have well developed posterior lobes.

Remarks. A case must be prepared for the ICZN for the priority of Tripodura as a subgeneric name.

## Polypedilum subgenus Uresipedilum Oyewo et Sæther

Polypedilum subgenus Uresipedilum Sasa et Okazawa, 1991: 54, nomen nudum. Polypedilum subgenus Uresipedilum Sasa et Kikuchi, 1995: 119, nomen nudum. Polypedilum subgenus Uresipedilum Oyewo et Sæther, 1998: 317.

Type species
Polypedilum (Uresipedilum) convictum (Walker)
Chironomus convictus Walker, 1856: 161.

Diagnostic characters. The male imagines of the subgenus are distinguished by having the basal portion of the superior volsella much longer than wide, with an apicomedian projection without setae arising from the inner margin of the base and directed medially and without prominent inner projection; wing membrane without markings or setae and fore tibial scale nearly always without spur.

Pupae of the subgenus lack dorsal setae on the anal lobe; have few branches in the thoracic horn; reduced cephalic tubercles and mostly single anal spur with few teeth, but often numerous fine lateral spinules. Conjunctive III/IV is often without spinules and pedes spurii A often absent. The anal lobe is nearly always without dorsal setae.

Larvae of the subgenus are distinguished by having the four median teeth set off from the rest of the mentum and in contact with the anteriorly produced median ends of the ventromental plates and with well developed to at least indicated posterior lobes on the ventromental plates. Antennal segment 3 is very slightly to more distinctly shorter than segment 4 . The mentum has the first lateral teeth much or only slightly lower than median and/or second lateral teeth.

Remarks. The pupae of Uresipedilum are not distinguishable from those of Polypedilum s. str., Pentapedilum and Probolum.

Uresipedilum as previously defined is not monophyletic as it includes the new subgenus Probolum described below. If the association of the immatures described by Grodhaus and Rotramel (1980) with Polypedilum pedatum excelsius Townes is correct not all imagines of Uresipedilum may be separable from Probolum.

## Polypedilum subgenus Cerobregma Sæther et Sundal

Polypedilum subgenus Cerobregma Sæther et Sundal, 1999: 334.
Chironomini genus C Pinder et Reiss, 1986: 362.
Type species
Polypedilum (Cerobregma) ontario (Walley)
Chironomus ontario Walley, 1926: 206.
Chironomus hirtipes Mitchell, 1908: 9 (preoccupied).

Diagnostic characters. The male imagines can be separated from those of other subgenera by having extremely long and strong, split setae along inner margin of gonostylus and gonocoxite with apicolateral bulblike extension with deep lateral incision between bulb and gonostylus.

The pupa is separable from that of other subgenera by the large cone-shaped cephalic tubercles, the large anal comb with numerous toothlets, the usual absence of anterior bands of stronger spinules on tergites and segments V and VI with all or some setae non-taeniate.

The larva is distinguished by the triangularly shaped head, unusually small mouth-parts, indistinct striae on the approximately triangular ventromental plates and median teeth of mentum of about equal height.

## Polypedilum subgenus Kribionympha Kieffer

Kribionympha Kieffer, 1921a: 271; 1921c: 29; 1922: 7.
Type species
Polypedilum (Kribionympha) declivis (Kieffer)
Kribionympha declivis Kieffer, 1922: 7.

Other possibly included species
Polypedilum unigaquartum Sasa
Polypedilum unigaquartum Sasa, 1985: 41.
Diagnostic characters. The male imagines can be separated from those of other subgenera by having frontal tubercles, the superior volsella with an inner lobe nearly as long as the curved lobe and a tapering projection carrying an outer seta, the fore tibial scale triangular with short spur and the wing membrane unmarked without setae.

Remarks. The combination of characters is quite unique within Polypedilum. The superior volsella shows some resemblance with Uresipedilum and the new subgenus described below, but those subgenera do not have any seta on the projection of superior volsella, a dissimilar inner lobe on the base and no frontal tubercles. There also is resemblance with Tripedilum in the presence of frontal tubercles and the stout gonostylus. However, there is some doubt whether the type species as redescribed by Freeman (1958: 289) is identical to the species described by Kieffer. The type material must be considered as lost. However, rather than regard Kribionympha and $P$. (K.) declivis as nomina dubia we here regard the redescription by Freeman as correct in order to retain the subgeneric name.

Polypedilum unigaquartum Sasa, 1985 has frontal tubercles, the superior volsella projection carries an outer seta, the front tibial scale is triangular with spur and the wings unmarked without setae. However, the general shape of the hypopygium is more like most Polypedilum s. str. The species can belong here, to Tripedilum or to Polypedilum s. str.

## Polypedilum subgenus Probolum Andersen et Sæther subgen. n.

Type species
Polypedilum (Probolum) marcondesi Pinho et Mendes sp. n.
Other included species
Polypedilum (Probolum) excelsius Townes sensu Grodhaus et Rotramel
Polypedilum pedatum excelsius Townes sensu Grodhaus et Rotramel, 1980: 70.
Polypedilum (Probolum) simantokeleum Sasa, Suzuki et Sakai
Polypedilum (Uresipedilum) simantokeleum Sasa, Suzuki et Sakai, 1998: 59.
Polypedilum (Uresipedilum) simantokeleum Sasa, Suzuki et Sakai; Sæther and Oyewo (2008: 4).
Polypedilum (Probolum) bullum Zhang et Wang
Polypedilum (Uresipedilum) bullum Zhang et Wang, 2004: 7.
Polypedilum (Uresipedilum) bullum Zhang et Wang; Sæther and Oyewo (2008: 3).
probably Polypedilum longinervis (Kieffer)
Microtendipes longinervis Kieffer, 1922: 10.
Polypedilum (Polypedilum) longinervis (Kieffer); Freeman (1958: 290).
possibly Polypedilum (Uresipedilum) excelsius Townes stat. n.
Polypedilum pedatum excelsius Townes, 1945: 55.
Polypedilum (Uresipedilum) pedatum excelsius Townes; Sæther and Oyewo (2008: 3).

Etymology. From Greek probolos, any projecting or jutting object or prominence, referring to the inner basal projection of the superior volsella. Also Afro-American slang for a problem.

Diagnostic characters. The male imagines of the subgenus differ from the males of other subgenera primarily by having the base of the superior volsella much longer than wide with the apicomedian projection directed inwards, i.e. as in Uresipedilum, but with an additional inner lobe carrying 1-6 (10?) setae (or perhaps sometimes without the inner lobe).

The pupa has thoracic horn with 3-9 branches; lacks well developed frontal warts, but has relatively well developed cephalic tubercles with short frontal setae; often prealar tubercle; well developed pedes spurii A and B; transverse band of shagreen anteriorly on tergites II-V; conjunctives III/IV-V/VI with spinules; segment VIII with 4-5 taeniae and anal lobe without dorsal setae.

The larva has third antennal segment distinctly to slightly shorter than fourth; antennal blade slightly shorter than flagellum; accessory blade less than half as long; premandible bifid, with prominent premandibular brush; mentum with median teeth only slightly higher than first lateral pair and ventromental plates without posterior lobes and with median apices pointing towards each other.

Imago. Moderately sized species, wing length about $1.1-2.7 \mathrm{~mm}$ (or to 3.0 mm if $P$. longinervis is included). Thorax entirely pale or brown with darker markings. Abdomen entirely pale or broadly banded. Legs pale, femora and tibia with or without rings. Wing membrane with or without markings.

Antenna. AR higher than 1 (1.1-1.8 or 2.8 if $P$. longinervis is included).
Head. Eyes bare, frontal tubercles absent. Third palpomere bearing 3-4 lanceolate sensilla clavata. Temporals consisting of inner and outer verticals and few postorbitals.

Thorax. Antepronotum reduced, widely separated, without setae. Scutal tubercle present or possibly absent. Acrostichals long, dorsocentrals uniserial, supraalars absent. Scutellars uniserial.

Wing. Membrane bare, clear or with several darker spots. Brachiolum with 1 seta, $\mathrm{R}, \mathrm{R}_{1}$ and $\mathrm{R}_{4+5}$ each with several setae, other veins bare. Squama with few to several (3-15) setae.

Legs. Fore tibial scale rounded, with or possibly sometimes without apical spur. Mid and hind tibiae with broad, unspurred anterior comb separated from posterior (narrower) comb with elongate spur. Sensilla chaetica absent.

Hypopygium. Anal tergite band well developed, fused basal to median anal tergite setae, several long median anal tergal setae, weaker apical anal tergite setae present lateral to anal point. Anal point narrow, parallel-sided, sometimes slightly spatulate. Superior volsella much longer than wide with apicomedian projection directed inwards, i.e. as in Uresipedilum, but with an additional inner microtrichiose lobe carrying 1-6 (10?) setae; base covered by microtrichia or with median part bare, with long outer seta; projection bare without setae or microtrichia. Inferior volsella slightly broadened subapically or more or less distinctly apically divided, with several sometimes apically split setae, long apical seta arising from tubercle.

Pupa. Small to medium sized, 4-7 mm long. Exuviae pale, marked with brown on margins of cephalothorax and abdomen, anal spur brown.

Cephalothorax. Frontal apotome smooth. Cephalic tubercles comparatively well-developed, frontal tubercles absent, frontal setae short. Prealar tubercle present or absent. Antepronotum with 1 median and 2 lateral antepronotals. Thoracic horn with 3(?)-9 branches. All thoracic setae short. Anterior dorsocentral (Dc ${ }_{1}$ ) close together with $\mathrm{Dc}_{2}, \mathrm{Dc}_{3}$ and $\mathrm{Dc}_{4}$ also close together.

Abdomen. Tergite I and IX without spines and shagreen; T II with broad anterior band of spinules, sometimes divided medially, otherwise with or without shagreen; T III-VI with broad anterior band of strong spinules, central line of sparse and weak to more numerous spinules which may be absent on T III, and posterior band of spinules. T VII and sometimes T VIII with bands of weak anterior spinules, otherwise bare. Sternites VI-VIII with or without weak anterior spinules. Tergite II with caudal hooklets arranged in single row. Spinules on conjunctives III/IV and IV/V in several rows, on conjunctive V/VI medially interrupted and in fewer rows. Pedes spurii A present on segment IV. Pedes spurii B well developed anterior on segment I and posterior on segment II.

Segments II-IV with 3 hair-like L setae; V and VI with 3, VII with 4, VIII with 4-5 taeniae; occasionally the number of taeniae reduced in some specimens. Anal spur single with lateral and basal denticles. Anal lobe well developed with complete fringe of about 20-60 long taeniae, dorsal taenia absent.

Larva. Medium sized larvae. Head capsule yellowish brown with mentum and apex of mandible dark brown and postoccipital margin black.

Antenna. Five segmented, third segment distinctly to slightly shorter than fourth; antennal ratio about 1.0 or slightly higher. Basal antennal segment with ring organ near base, blade slightly shorter than flagellum, accessory blade less than half as long. Style well developed, Lauterborn organs vestigial.

Dorsal surface of head. Frontoclypeal apotome anteriorly broadened into lateral rounded lobes on which S3 is situated, anterior margin straight.

Labro-epipharyngeal area. S I broad, apically plumose; S II very finely plumose on both sides. Labral lamella well developed, with about 50 teeth. Labrum with $2-3$ weak spinulae and $4-5$ weak chaetae. Pecten
epipharyngis distinctly divided into 3 platelets, median with 3-5 teeth, lateral plates with 5-6 teeth. About 67 curved, simple, pointed chaetulae laterales. Premandible bifid, with prominent premandibular brush.

Mandible. With 1 dorsal, 1 apical and 2 inner teeth. Seta subdentalis well developed, long. Seta interna consisting of 4 main branches with secondary numerous branches. Pecten mandibularis of about 6 setae.

Mentum. Median teeth and second laterals subequal in height, both slightly longer than first laterals. Ventromental plates without posterolateral lobes, median apices pointing towards each other.

Abdomen. Body setae inconspicuous. Anal lobe more or less well developed. Claws of posterior parapods all simple. Procercus short, bearing about 9 medium to long anal setae. Supraanal seta well developed, slightly less than half as long as anal setae. Anal tubules short, subequal.

Remarks. The pupae of Probolum are not separable from those of Polypedilum s. str., Pentapedilum and Uresipedilum. The known larvae may be separable by the combination of having mentum with median teeth only slightly higher than first lateral pair, ventromental plates without posterior lobes and mandible with dorsal tooth.

## Polypedilum (Probolum) marcondesi Pinho et Mendes sp. n.

(Figs 6-25)

Polypedilum sp 1 Pinho et al., 2005.

Type material. Holotype male reared from larva (in Canada balsam). Brazil: Santa Catarina State, Florianópolis, Unidade de Conservação Ambiental Desterro (U.C.A.D.), 12.i.2004, in Vriesea vagans (H23), L.C. Pinho \& C.B. Marcondes (MZUSP). Paratypes: 1 male, Santa Catarina State, Florianópolis, Unidade de Conservação Ambiental Desterro (U.C.A.D.), 04-19.ix.2003, emergence trap over Nidularium innocentii, L.C. Pinho (MZUSP); 1 male with larval and pupal exuviae, as previous except 14.xi.2003, (B13) (MZUSP); 1 male with larval and pupal exuviae, as previous except 06.x.2003, (138) (ZMBN); 1 male with larval and pupal exuviae, as previous except 06.iii.2004, (S26) (MZUSP); 1 male with pupal exuviae, as previous except 12.x.2003, (B3) (MZUSP); 1 male with pupal exuviae, as previous except 03.x.2003, (S5) (MZUSP); 1 male with pupal exuviae, as previous except 15.iv.2002, (A16) (ZMBN); 1 male with pupal exuviae, as previous except 05.vi.2002, (AR 44), L.C. Pinho \& C.B. Marcondes (MZUSP); 1 female with larval and pupal exuviae, as previous except 05.iii.2004, (B26) (MZUSP); 1 female with larval and pupal exuviae, as previous except 06.iii.2004, (S27) (ZMBN); 1 female with larval and pupal exuviae, as previous except 29.ii.2004, (B29) (ZMBN).

Etymology. Named for professor Dr. Carlos B. Marcondes, who led the project "Fauna associada a bromélias em Mata Atlântica em Santa Catarina" (CNPq 690143/01-0).

Diagnostic characters. The presence of a scutal tubercle together with the split setae on the inferior volsella and the shape of the superior volsella will separate the male from other P. (Probolum) species. The pupa differs from that of $P$. (Pr.) excelsius sensu Grodhaus et Rotramel by having less extensive shagreen including bare sternites VI-VIII. The larva has an AR of 1.0-1.1 against about 1.4 in P. excelsius and the distance between the ventromental plates is clearly less than the width of the four median teeth combined, while it is about as long as the four median teeth combined in $P$. excelsius.

Male ( $\mathrm{n}=5-6$, except when otherwise stated). Total length $2.55-3.78,3.05 \mathrm{~mm}$. Wing length $1.13-1.81$, 1.64 mm . Total length / wing length 2.04-2.27, 2.11. Wing length / length of profemur 1.67-1.78, 1.73.

Coloration. Thorax brown with darker vittae, postnotum, preepisternum and much of anepisternum. Legs pale with darker rings. Fore femur with brown rings at about $0.10-0.35,0.50-0.65$ and $0.85-0.95$; mid femur with rings at $0.05-0.25,0.35-0.50$ and $0.75-0.90$; hind femur with rings at $0.05-0.25,0.49-0.65$ and $0.80-$ 0.85 . Fore tibia with rings at $0.10-0.50$ and 0.90 to apex; mid tibia with rings at $0.10-0.25,0.50-0.65$ and 0.90 to apex; hind tibia with rings at $0.05-0.25,0.50-0.65$ and 0.90 to apex. Base and apex of $t_{1}$ and apex of $\mathrm{ta}_{2}-$ $\mathrm{ta}_{4}$ brown. Wing with weak dark spots, one anterior and one posterior spot in each of cells $\mathrm{r}_{4+5}, \mathrm{~m}_{1+2}, \mathrm{~m}_{3+4}$ and an. Abdomen broadly banded, darker in anterior two thirds.

Head (Fig. 6). AR $=1.07-1.34$, 1.19. Ultimate flagellomere $364-610,537 \mu \mathrm{~m}$ long. Temporal setae $11-$ 13,11 including $3-4,4$ inner verticals; $3-5,5$ outer verticals and $3-4,3$ postorbitals. Clypeus with $16-27,21$ setae. Tentorium 105-169, $134 \mu \mathrm{~m}$ long; 26-34, $30 \mu \mathrm{~m}$ wide at sieve pore. Stipes $120-150,139 \mu \mathrm{~m}$ long; $38-$ 49, 42 (4) $\mu \mathrm{m}$ wide. Palpomere lengths (in $\mu \mathrm{m}$ ): $19-45,35 ; 30-53,43 ; 86-146,129 ; 90-150,133 ; 135-233$, 190 (4). Third palpomere with 4-6 lanceolate sensilla clavata in small pit; longest 15-19, 18 (4) $\mu \mathrm{m}$ long.


FIGURES 6-12. Polypedilum (Probolum) marcondesi Pinho et Mendes sp. n., male. 6-head. 7-spur of foretibia. 8thorax. 9-wing. 10-hypopygium, dorsal view. 11-hypopygium with tergite IX and anal point removed, dorsal view left, ventral view right. 12-superior volsella.


FIGURES 13-17. Polypedilum (Probolum) marcondesi Pinho et Mendes sp. n., female. 13-genitalia, ventral view. 14tergite IX. 15-dorsomesal lobe. 16-ventrolateral lobe. 17-apodeme lobe.

Thorax (Fig. 8). Acrostichals 10-14, 12; dorsocentrals 13-22, 16; prealars 3-5, 4. Scutellum with 6-12, 9 setae.

Wing (Fig. 9). VR 0.99-1.06, 1.03. $\mathrm{R}_{2+3}$ well separated from $\mathrm{R}_{1} . \mathrm{R}_{4+5}$ strongly curved at apex, ending at wing tip. Brachiolum with $1-2,1$ seta, R with $12-26,21 ; \mathrm{R}_{1}$ with $14-20,17 ; \mathrm{R}_{4+5}$ with $18-31,27$ setae, M bare. Squama with $4-5,4$ setae.

Legs. Scale on fore tibia (Fig. 7) 49-56, $53 \mu \mathrm{~m}$ long; with $4-8,7 \mu \mathrm{~m}$ long apical spur. Spur of mid tibia $41-75,61 \mu \mathrm{~m}$ long including comb; unspurred comb 23-38, $36 \mu \mathrm{~m}$ long. Spur on hind tibia 33-86, $75 \mu \mathrm{~m}$ long including comb; unspurred comb $30-38,33 \mu \mathrm{~m}$ long. Width at apex of fore tibia $38-64,52 \mu \mathrm{~m}$; of mid tibia 41-60, $57 \mu \mathrm{~m}$; of hind tibia 45-71, $64 \mu \mathrm{~m}$. Length and proportions of legs as in Table 1.

Hypopygium (Figs 10-11). Tergite IX with 12-18, 14 strong median setae and 5-7, 6 setae to each side of base of anal point. Anal point 49-64, $57 \mu \mathrm{~m}$ long, nearly parallel-sided medially, with weakly spatulate, 9-11, $10 \mu \mathrm{~m}$ wide apex. Transverse sternapodeme present in 3 specimens, $30-34 \mu \mathrm{~m}$ long, other 3 specimens with completely rounded sternapodeme; phallapodeme 98-120, $108 \mu \mathrm{~m}$ long. Gonocoxite $110-188,174 \mu \mathrm{~m}$ long. Gonostylus 135-180, $164 \mu \mathrm{~m}$ long, with $1-2$ short, stout setae subapically and $6-8$ long setae along inner margin. Superior volsella (Fig. 12) 45-83, $67 \mu \mathrm{~m}$ long; base covered with microtrichia, with 45-86, $68 \mu \mathrm{~m}$ long apicolateral seta; apical projection 26-44, $35 \mu \mathrm{~m}$ long; inner basal protrusion $15-30,23 \mu \mathrm{~m}$ high, $15-26$, $21 \mu \mathrm{~m}$ wide, with $3-4$ setae. Inferior volsella $101-131,120 \mu \mathrm{~m}$ long, nearly parallel-sided with slightly swollen distal one-third, with strong apical setae and 8-13, 11 dorsal, mostly split setae. HR 1.00-1.11, 1.06. HV 1.89-2.18, 2.06.

TABLE 1. Lengths (in $\mu \mathrm{m}$ ) and proportions of legs of Polypedilum (Probolum) marcondesi Pinho et Mendes sp. n., male ( $\mathrm{n}=6$, except 5 for hind tarsi and $3-5$ for BR).

|  | fe | ti | $\mathrm{ta}_{1}$ | $\mathrm{ta}_{2}$ |
| :--- | :--- | :--- | :--- | :--- |
| $\mathrm{p}_{1}$ | $633-1058,955$ | $359-633,560$ | $690-1229,1078$ | $406-794,687$ |
| $\mathrm{p}_{2}$ | $633-1049,953$ | $373-822,732$ | $274-605,533$ | $151-321,271$ |
| $\mathrm{p}_{3}$ | $709-1229,1090$ | $558-936,841$ | $680-813,762$ | $378-454,431$ |
|  | $\mathrm{ta}_{3}$ | $\mathrm{ta}_{4}$ | $227-387,342$ | $90-146,125$ |
| $\mathrm{p}_{1}$ | $302-548,469$ | $66-142,118$ | $47-57,55$ | LR |
| $\mathrm{p}_{2}$ | $132-227,197$ | $194-227,214$ | $57-80,71$ | $1.85-1.98,1.92$ |
| $\mathrm{p}_{3}$ | $293-359,335$ | SV | $0.71-0.74,0.73$ |  |
|  | BV | $1.38-1.48,1.41$ | $0.82-0.87,0.85$ |  |
| $\mathrm{p}_{1}$ | $1.52-1.66,1.60$ | $3.08-3.67,3.20$ | BR |  |
| $\mathrm{p}_{2}$ | $3.23-3.67,3.48$ | $2.38-2.78,2.71$ | $2.4-3.7$ |  |
| $\mathrm{p}_{3}$ | $2.58-2.79,2.69$ |  | $3.8-5.1,4.3$ |  |

Female $(\mathrm{n}=1-3)$. Total length $2.69-2.95 \mathrm{~mm}$. Wing length $1.47-1.73 \mathrm{~mm}$. Total length / wing length 1.76. Wing length / length of profemur 1.63-1.76.

Coloration. As in male except much paler.
Head. AR $=0.28-0.62$. Flagellomere lengths (in $\mu \mathrm{m}$ ): 140-144, 99-101, 94-97, 45-54, 115-151. Longest sensilla chaeticae on ultimate flagellomere $65-72 \mu \mathrm{~m}$ long. Temporal setae $9-11$. Clypeus with $18-20$ setae. Tentorium 141-147 $\mu \mathrm{m}$ long, 18-24 $\mu \mathrm{m}$ wide at sieve pore. Stipes $143 \mu \mathrm{~m}$ long. Palpomere lengths (in $\mu \mathrm{m}$ ): 27, 41-52, 113-137, 109-134, 177-207. Third palpomere with 5-9 lanceolate sensilla clavata in small pit, longest $23-25 \mu \mathrm{~m}$ long.

Thorax. Acrostichals 9-14, dorsocentrals 15-20, prealars 4-7. Scutellum with 9-10 uniserial setae.
Wing. VR 1.06-1.09. $\mathrm{R}_{2+3}$ well separated from $\mathrm{R}_{1}$. Brachiolum with 1 seta, R with $20-26, \mathrm{R}_{1}$ with $14-22$, $\mathrm{R}_{4+5}$ with 34-48 setae. Squama with 5-8 setae.

Legs. Scale on fore tibia $23-38 \mu \mathrm{~m}$ long, with $7-9 \mu \mathrm{~m}$ long spur. Spur of mid tibia $34-48 \mu \mathrm{~m}$ long including comb, unspurred comb $23-27 \mu \mathrm{~m}$ long. Spur on hind tibia 59-64 $\mu \mathrm{m}$ long including comb, unspurred comb 23-34 $\mu \mathrm{m}$ long; one specimen with a $27 \mu \mathrm{~m}$ long spur including comb. Width at apex of fore tibia $45-57 \mu \mathrm{~m}$, of mid tibia $50-59 \mu \mathrm{~m}$, of hind tibia $27-64 \mu \mathrm{~m}$. Length and proportions of legs as in Table 2.

TABLE 2. Lengths (in $\mu \mathrm{m}$ ) and proportions of legs of Polypedilum (Probolum) marcondesi Pinho et Mendes sp. n., female ( $\mathrm{n}=1-3$ ).

|  | fe | ti | $\mathrm{ta}_{1}$ | $\mathrm{ta}_{2}$ | $\mathrm{ta}_{3}$ | $\mathrm{ta}_{4}$ |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| $\mathrm{p}_{1}$ | $903-985$ | $497-589$ | $884-1041$ | $580-723$ | $393-484$ | $258-341$ |
| $\mathrm{p}_{2}$ | $866-995$ | $663-774$ | $451-549$ | $212-258$ | $129-166$ | $92-101$ |
| $\mathrm{p}_{3}$ | $1022-1124$ | $709-866$ | 626 | 318 | 267 | 147 |
|  | $\mathrm{ta}_{5}$ | LR | BV | SV | BR |  |
| $\mathrm{p}_{1}$ | $92-138$ | $1.77-1.84$ | $1.56-1.73$ | $1.50-1.58$ | $3.0-3.3$ |  |
| $\mathrm{p}_{2}$ | $37-46$ | $0.68-0.71$ | $4.03-4.16$ | $3.23-3.39$ | $3.0-3.8$ |  |
| $\mathrm{p}_{3}$ | 55 | 0.88 | 2.99 | 2.76 | 4.5 |  |

Genitalia (Fig. 13). Gonocoxapodeme curved, ending on base of dorsomesal lobe. Gonocoxite IX with 02 setae. Tergite IX (Fig. 14) with 27-42 setae. Segment X with 5-9 setae to each side. Cercus 95-100 $\mu \mathrm{m}$ long. Seminal capsule ovoid, 95-118 $\mu \mathrm{m}$ long, not including 6-9 $\mu \mathrm{m}$ long neck. Notum 143-179 $\mu \mathrm{m}$ long.

Dorsomesal lobe (Fig. 15) 66-71 $\mu \mathrm{m}$ long from base of vagina to apex, 39-41 $\mu \mathrm{m}$ wide near apex. Ventrolateral lobe (Fig. 16) 11-14 $\mu \mathrm{m}$ long, 16-18 $\mu \mathrm{m}$ wide, without microtrichia. Apodeme of apodeme lobe as in Figure 17.


FIGURES 18-25. Polypedilum (Probolum) marcondesi Pinho et Mendes sp. n., pupa (18-21) and larva (22-25). 18tergites. 19-thorax. 20-frontal apotome. 21-anal comb. 22-mentum. 23-pecten epipharyngis. 24-antenna. 25-mandible.

Pupa ( $\mathrm{n}=3$, unless otherwise stated). Total length $3.73-5.10 \mathrm{~mm}$.
Coloration. Exuviae pale brown with margins of wing sheath golden brown, mesal paratergites margins of segments VI-VII and caudal spur brown.

Cephalothorax (Fig. 19). Frontal apotome as in Figure 20, frontal setae 38-56 $\mu \mathrm{m}$ long. Prealar tubercle present in 2 larger specimens, absent in smaller. Thoracic horn apparently with only 3 branches, longest 244$319 \mu \mathrm{~m}$ long, middle 120 (1) $\mu \mathrm{m}$, shortest 98 (1) $\mu \mathrm{m}$ long. Thoracic setae about $40-75 \mu \mathrm{~m}$ long.

Abdomen (Fig. 18). Tergite I, VIII and IX without spines and shagreen. T II with $6-8$ rows of spinules in anterior band, otherwise without shagreen; T III-VI each with 6-8 rows of strong spinules in anterior band, central line of sparse and weak spinules which may be absent on T III and posterior band of spinules. T VII with weak anterior spinules, otherwise bare. Tergite II with 41-70 caudal hooklets in single row. Sternites VIVIII bare. Spinules on conjunctives III/IV and IV/V in 5 rows, on conjunctive V/VI medially interrupted and at most in 4 rows. Pedes spurii A well developed on segment IV. Pedes spurii B well developed anterior on segment I and posterior on segment II. Segment I without lateral setae, S II-IV with 3 hair-like lateral setae; S V-VI with 3 taeniae; S VII with 3-4 taeniae, S VIII with 4-5 taeniae. Anal spur (Fig. 21) single with almost none to several lateral and basal denticles. Anal lobe with 37-58 taeniae, up to $0.6-0.7 \mathrm{~mm}$ long.

Larva ( $\mathrm{n}=3$, unless otherwise stated). Total length not measurable. Head capsule $0.41-0.47 \mathrm{~mm}$ long. Postmentum 168-192 $\mu \mathrm{m}$ long.

Coloration. Mentum and mandible brown, postoccipital margin black.
Head. AR 1.00-1.10. Antenna as in Figure 24; antennal segment lengths (in $\mu \mathrm{m}$ ): 52-57, 19-21, 11-12, $14-17,5-8$. Basal antennal segment $17 \mu \mathrm{~m}$ wide, ring organ about 12 (1) $\mu \mathrm{m}$ from base, blade $40-50 \mu \mathrm{~m}$ long. Pecten epipharyngis as in Figure 23. Premandible 71-78 $\mu \mathrm{m}$ long. Mandible (Fig. 25) $123-135 \mu \mathrm{~m}$ long, seta subdentalis $17-24 \mu \mathrm{~m}$ long, pecten mandibularis of 6 setae. Mentum (Fig. 22) 97-109 $\mu \mathrm{m}$ wide, ventromental plate $109-119 \mu \mathrm{~m}$ wide, distance between plates $12-19 \mu \mathrm{~m}$, about 50 striae. Setae submenti situated just below inner posterior corner of ventromental plates.

Abdomen. Procercus weak, with about 9 anal setae up to 469 (1) $\mu \mathrm{m}$ long. Supraanal seta 206 (1) $\mu \mathrm{m}$ long. Ratio of supraanal setae / anal setae 0.44 (1). Posterior parapods and anal tubules not measurable.

Distribution and biology. Known only from the type locality on Ilha de Santa Catarina, Santa Catarina State, southern Brazil. Adults were taken in a Malaise trap while larvae were collected from leaf-axils of bromeliads (Nidularium innocentii Lemaire and Vriesea vagans L.B. Smith) (see Pinho et al. 2005).

## Polypedilum (Probolum) excelsius Townes sensu Grodhaus et Rotramel

Polypedilum pedatum excelsius Townes sensu Grodhaus et Rotramel, 1980: 70.

Diagnostic characters. The pupa differs from that of $P$. (Pr.) marcondesi by having more extensive shagreen including shagreen spinules anterior on tergite VIII and on sternites VI-VIII. The larva has an AR of about 1.4 against 1.0-1.1 in P. (Pr.) marcondesi and the distance between the ventromental plates is about as long as the four median teeth combined, while it is clearly less than the width of the four median teeth combined in $P$. (Pr.) marcondesi.

Description. The immatures are described in detail by Grodhaus and Rotramel (1980).

## Polypedilum (Uresipedilum) excelsius Townes stat. n.

Figs 26-31

Polypedilum pedatum excelsius Townes, 1945: 55.
Material examined. Canada: British Columbia, Marion Lake at dock and on west shore, 2 males, 7 \& 25.v.1965, A.L. Hamilton (ZMBN).

Diagnostic characters. The males apparently differ from P. pedatum by having $\mathrm{R}_{4+5}$ reaching apex of wing, projection of superior volsella clearly longer than base, third palpomere with $2-3$ lanceolate sensilla clavata, squama with about 16 setae and M without setae.

Male ( $\mathrm{n}=2$, except when otherwise stated). Total length $4.39-4.75 \mathrm{~mm}$. Wing length $2.70-3.01 \mathrm{~mm}$. Total length / wing length 1.58-1.63. Wing length / length of profemur 2.47-2.51.


FIGURES 26-31. Polypedilum (Uresipedilum) excelsius Townes, 1945, male. 26-spur of foretibia. 27-thorax. 28-wing. 29-hypopygium, dorsal view. 30-hypopygium with tergite IX and anal point removed, dorsal view left, ventral view right. 31-superior volsella.

Coloration. Thorax brown with darker vittae, postnotum, preepisternum and much of anepisternum; scutellum pale. Legs beyond coxae pale brown. Abdomen brown, gonocoxite and gonostylus pale.

Head. AR 1.04-1.12. Ultimate flagellomere $633-671 \mu \mathrm{~m}$ long. Temporal setae $12-16$ including $3-4$ inner verticals, 3-5 outer verticals and 6-7 postorbitals. Clypeus with 25-26 setae. Tentorium 128-150 $\mu \mathrm{m}$ long, $56-68 \mu \mathrm{~m}$ wide at sieve pore. Stipes $150-165 \mu \mathrm{~m}$ long, $45 \mu \mathrm{~m}$ wide. Palpomere lengths (in $\mu \mathrm{m}$ ): 41-45, 5668, 221-244, 135-165, 229-263. Third palpomere with $2-3$ lanceolate sensilla clavata, longest $23 \mu \mathrm{~m}$ long.

Thorax (Fig. 27). Acrostichals 20 (1); dorsocentrals 17-23, including 2 scutal fossal setae in one specimen; prealars 7-8. Scutellum with 22-24 setae.

Wing (Fig. 28). VR 1.15-1.29. $\mathrm{R}_{2+3}$ well separated from $\mathrm{R}_{1} . \mathrm{R}_{4+5}$ strongly curved at apex, ending at wing tip. Brachiolum with 2 setae, $R$ with $28-31, R_{1}$ with $28-35, R_{4+5}$ with $46-55$ setae, $M$ bare. Squama with 16 setae.

Legs. Scale on fore tibia (Fig. 26) 38-45 $\mu \mathrm{m}$ long, rounded, without spur. Spur of mid tibia 60-64 $\mu \mathrm{m}$ long including comb, unspurred comb $26 \mu \mathrm{~m}$ long. Spur on hind tibia $64-71 \mu \mathrm{~m}$ long including comb, unspurred comb $30-34 \mu \mathrm{~m}$ long. Width at apex of fore tibia $38-45 \mu \mathrm{~m}$, of mid tibia $64-68 \mu \mathrm{~m}$, of hind tibia $71-74 \mu \mathrm{~m}$. Length and proportions of legs as in Table 3.

TABLE 3. Lengths (in $\mu \mathrm{m}$ ) and proportions of legs of Polypedilum (Uresipedilum) excelsius Townes, male ( $\mathrm{n}=2$ ).

|  | fe | ti | $\mathrm{ta}_{1}$ | $\mathrm{ta}_{2}$ | $\mathrm{ta}_{3}$ | $\mathrm{ta}_{4}$ |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| $\mathrm{p}_{1}$ | $1096-1200$ | $945-1096$ | $1106-1171$ | $728-794$ | $614-680$ | $473-491$ |
| $\mathrm{p}_{2}$ | $1229-1436$ | $1087-1200$ | $567-614$ | $378-416$ | $302-321$ | 170 |
| $\mathrm{p}_{3}$ | $1370-1531$ | $1276-1436$ | $879-983$ | $529-586$ | $482-510$ | $279-284$ |
|  | $\mathrm{ta}_{5}$ | LR | BV | SV | BR |  |
| $\mathrm{p}_{1}$ | $189-194$ | $1.07-1.17$ | $1.57-1.61$ | $1.84-1.96$ | $3.6-4.0$ |  |
| $\mathrm{p}_{2}$ | 95 | $0.51-0.52$ | $3.05-3.25$ | $4.08-4.29$ | $4.4-6.7$ |  |
| $\mathrm{p}_{3}$ | $113-132$ | $0.68-0.69$ | $2.52-2.61$ | $3.01-3.02$ | $4.0-6.3$ |  |

Hypopygium (Figs 29-30). Tergite IX with 10-13 strong median setae and altogether $8-10$ setae to each side of base of anal point. Anal point 79-90 $\mu \mathrm{m}$ long, parallel-sided. Transverse sternapodeme $68 \mu \mathrm{~m}$ long, phallapodeme $116 \mu \mathrm{~m}$ long. Gonocoxite $184-214 \mu \mathrm{~m}$ long. Gonostylus $165-191 \mu \mathrm{~m}$ long, with 1 apical seta and 4-6 long setae along inner margin. Base of superior volsella (Fig. 31) sparsely covered with microtrichia, $45-49 \mu \mathrm{~m}$ long; with $75-86 \mu \mathrm{~m}$ long apicolateral seta and and row of 6 baso-ventral, inner setae; apical projection 56-60 $\mu \mathrm{m}$ long, upturned at apex. Inferior volsella 135-143 $\mu \mathrm{m}$ long, tapering, with $14-15$ setae. HR 1.11-1.12. HV 2.49-2.66.

Remarks. Maschwitz and Cook (2000: 106) synonymized the two subspecies of P. pedatum since they found intermediates in the extent of the downturned curvature of the apical part of wing vein $\mathrm{R}_{4+5}$. In our specimens $\mathrm{R}_{4+5}$ reaches the wing tip in P. excelsius, but ends distinctly before the wing tip in P. pedatum. The projection of the superior volsella is distinctly longer than the base in $P$. excelsius, at most as long as base in $P$. pedatum. We found several other differences in measurements making us believe that the two subspecies should be regarded as separate species rather than be synonymized. However, the differences in the number of setae on squama, the number of sensilla clavata on third palpomere, presence or absence of setae on vein M and the other differences in measurements found may not hold up when associated material can be examined.

## Polypedilum (Uresipedilum) pedatum Townes

(Figs 32-43)
Polypedilum pedatum pedatum Townes, 1945: 55.


FIGURES 32-35. Polypedilum (Uresipedilum) pedatum Townes, 1945, male. 32-wing. 33-hypopygium, dorsal view. 34-hypopygium with tergite IX and anal point removed, dorsal view left, ventral view right. 35-superior volsella.

Material examined. USA: New York, Tompkins Co., McLean Bogs Reserve, holotype male, hypopygium on separate slide in Canada balsam (Cornell University, Dept. of Entomology, Type No. 2671). Paratypes: as holotype, 3 males, 2 females (Cornell University, Dept. of Entomology, Types No. 2671.6, 2671.7, 2671.8, 2671.9, 2671.10).

Diagnostic characters. The male imagines apparently differ from P. excelsius by not having $\mathrm{R}_{4+5}$ reaching apex of wing, projection of superior volsella at most as long as base, third palpomere with 4-7 lanceolate sensilla clavata, squama with 6-10 setae and $M$ often with apical seta.

Male ( $\mathrm{n}=3-4$, except when otherwise stated). Total length 3.15-4.01, 3.57 mm . Wing length $1.79-2.21$ mm . Total length / wing length 1.80-1.86. Wing length / length of profemur 2.20-2.48.

Coloration. Thorax brown with darker vittae, postnotum, preepisternum and much of anepisternum; scutellum pale. Legs beyond coxae pale brown. Abdomen brown, gonocoxite and gonostylus pale.

Head. AR 1.07-1.16, 1.11. Ultimate flagellomere 548-614, $578 \mu \mathrm{~m}$ long. Temporal setae $15-20$ including $5-8$ inner verticals; 6 outer verticals and $4-6,5$ postorbitals. Clypeus with 13-19 setae. Tentorium 148-165, $151 \mu \mathrm{~m}$ long; $38-45,42 \mu \mathrm{~m}$ wide at sieve pore. Stipes $135-161 \mu \mathrm{~m}$ long, $38-49 \mu \mathrm{~m}$ wide. Palpomere lengths (in $\mu \mathrm{m}$ ): $41-45,44 ; 53-60,56 ; 135-180,161 ; 131-169,154 ; 191-278,231$. Third palpomere with 4-7 lanceolate sensilla clavata, longest $26 \mu \mathrm{~m}$ long.

Thorax. Acrostichals 16-18, 17; dorsocentrals 16-18, 17, including 1 scutal fossal setae in one specimen; prealars 6-8. Scutellum with $15-17$, 16 biserial setae.

Wing (Fig. 32). VR 1.07-1.25. $\mathrm{R}_{2+3}$ well separated from $\mathrm{R}_{1}$. Apical part of $\mathrm{R}_{4+5}$ curved near apex, ending nearer apex of $\mathrm{M}_{1+2}$ than to wing tip. Brachiolum with 2 setae, R with $19-25, \mathrm{R}_{1}$ with $14-22, \mathrm{R}_{4+5}$ with 26-33, $M$ with $0-1$ setae. Squama with $6-10$ setae.


FIGURES 36-43. Polypedilum (Uresipedilum) pedatum Townes, 1945, female. 36-spur of foretibia. 37-thorax. 38wing. 39-genitalia, ventral view. 40-tergite IX. 41-dorsomesal lobe. 42-ventrolateral lobe. 43-apodeme lobe.

Legs. Scale on fore tibia 30-38, $36 \mu \mathrm{~m}$ long, rounded, without spur. Spur of mid tibia 49-53 $\mu \mathrm{m}$ long including comb, unspurred comb $26-30 \mu \mathrm{~m}$ long. Spur on hind tibia $56 \mu \mathrm{~m}$ long including comb, unspurred comb $30 \mu \mathrm{~m}$ long. Width at apex of fore tibia $41-56,49 \mu \mathrm{~m}$; of mid tibia $49-56 \mu \mathrm{~m}$; of hind tibia $64 \mu \mathrm{~m}$. Length and proportions of legs as in Table 4.

Hypopygium (Figs 33-34). Tergite IX with 6-11, 9 strong median setae and altogether 14-20, 17 setae to each side of base of anal point. Anal point 53-68, $60 \mu \mathrm{~m}$ long, parallel-sided. Transverse sternapodeme $34-$ $49,38 \mu \mathrm{~m}$ long; phallapodeme 101-120, $109 \mu \mathrm{~m}$ long. Gonocoxite $169-210,188 \mu \mathrm{~m}$ long. Gonostylus $128-$ $158,148 \mu \mathrm{~m}$ long, with 1 apical seta and 6-8 long setae along inner margin. Base of superior volsella (Fig. 35) sparsely covered with microtrichia, $34-41,37 \mu \mathrm{~m}$ long; with $53-56,55 \mu \mathrm{~m}$ long apicolateral seta and 2 basal inner setae; apical projection $30-39,34 \mu \mathrm{~m}$ long, upturned at apex. Inferior volsella $113-131,122 \mu \mathrm{~m}$ long, nearly parallel-sided with slightly divided apex, with $14-17,15$ setae. HR 1.17-1.33, 1.28. HV 1.99-2.69, 2.43.

Female ( $\mathrm{n}=1-2$ ). Total length $3.52-3.64 \mathrm{~mm}$. Wing length $2.21-2.34 \mathrm{~mm}$. Total length $/$ wing length 1.55-1.83. Wing length / length of profemur 2.13.

Coloration. Thorax brown with darker vittae, postnotum, preepisternum and much of anepisternum; scutellum pale. Legs beyond coxae pale brown. Abdomen brown, gonocoxite and gonostylus pale.

TABLE 4. Lengths (in $\mu \mathrm{m}$ ) and proportions of legs of Polypedilum (Uresipedilum) pedatum Townes, male ( $\mathrm{n}=2-4$ for fe and ti, 1-3 for ta).

|  | fe | ti | $\mathrm{ta}_{1}$ | $\mathrm{ta}_{2}$ | $\mathrm{ta}_{3}$ | $\mathrm{ta}_{4}$ |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| $\mathrm{p}_{1}$ | $813-1011,917$ | $652-813,754$ | 1068 | 690 | 520 | 345 |
| $\mathrm{p}_{2}$ | $917-1115,1016$ | $869-964,910$ | $473-520$ | $274-312$ | $208-227$ | $118-137$ |
| $\mathrm{p}_{3}$ | $1058-1106$ | $992-1058$ | - | - | - | - |
|  | $\mathrm{ta}_{5}$ | LR | BV | SV | BR |  |
| $\mathrm{p}_{1}$ | 142 | 1.35 | 1.68 | 1.67 | 3.1 |  |
| $\mathrm{p}_{2}$ | $66-85$ | $0.53-0.54$ | $3.27-3.42$ | $4.00-4.06$ | $4.5-5.5$ |  |
| $\mathrm{p}_{3}$ | - | - | - | - | - |  |

Head. AR $=0.38$. Flagellomere lengths (in $\mu \mathrm{m}$ ): 143, 105, 94, 71, 150. Longest sensilla chaeticae on ultimate flagellomere $71 \mu \mathrm{~m}$ long. Temporal setae $18-20$ including 6-9 inner verticals, 6 outer verticals and 5-6 postorbitals. Clypeus with $18-20$ setae. Tentorium $154-184 \mu \mathrm{~m}$ long, $30 \mu \mathrm{~m}$ wide at sieve pore. Stipes $154 \mu \mathrm{~m}$ long, $45 \mu \mathrm{~m}$ wide. Palpomere lengths (in $\mu \mathrm{m}$ ): 45-56, 60-64, 176-184, 158-173, 278-308. Third palpomere with 6-7 lanceolate sensilla clavata, longest $26 \mu \mathrm{~m}$ long.

Thorax (Fig. 37). Acrostichals 20-22; dorsocentrals 25-30, including 5-9 scutal fossal setae; prealars 7. Scutellum with 18-20 biserial setae.

Wing (Fig. 38). VR 1.16-1.19. $\mathrm{R}_{2+3}$ well separated from $\mathrm{R}_{1}$. Brachiolum with 2 setae, R with $28-31$, $\mathrm{R}_{1}$ with $22-28, \mathrm{R}_{4+5}$ with $40-56$, M with $5-7$ setae. Squama with $8-9$ setae.

Legs. Scale on fore tibia (Fig. 36) $38 \mu \mathrm{~m}$ long, rounded, without spur. Spur of mid tibia 49-53 $\mu \mathrm{m}$ long including comb, unspurred comb $23-26 \mu \mathrm{~m}$ long. Spur on hind tibia $49-56 \mu \mathrm{~m}$ long including comb, unspurred comb $23-26 \mu \mathrm{~m}$ long. Width at apex of fore tibia $64 \mu \mathrm{~m}$, of mid- and hind tibia both $71 \mu \mathrm{~m}$. Length and proportions of legs as in Table 5.

TABLE 5. Lengths (in $\mu \mathrm{m}$ ) and proportions of legs of Polypedilum (Uresipedilum) pedatum Townes, female ( $\mathrm{n}=1-2$ ).

|  | fe | ti | $\mathrm{ta}_{1}$ | $\mathrm{ta}_{2}$ | $\mathrm{ta}_{3}$ | $\mathrm{ta}_{4}$ | $\mathrm{ta}_{5}$ | LR | BV | SV | BR |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| $\mathrm{p}_{1}$ | 1040 | 765 | - | - | - | - | - | - | - | - | - |
| $\mathrm{p}_{2}$ | $1002-1106$ | $964-983$ | 501 | 293 | 217 | 151 | 85 | $0.51-0.52$ | 3.47 | $3.92-4.17$ | 4.0 |
| $\mathrm{p}_{3}$ | 1238 | $1096-1125$ | 737 | - | - | - | - | - | - | - | - |

Abdomen. Number of setae on tergites I-VIII as: 46-67, 47-77, 48-70, 35-56, 27-46, 30-46, 42-46, 2936. Number of setae on sternites I-VIII as: 0, 3-4, 10-26, 25-34, 22-33, 26-33, 32-33, 45-69.

Genitalia (Fig. 39). Gonocoxapodeme completely straight to slightly curved, ending on base of dorsomesal lobe. Gonocoxite IX with 3-6 setae. Tergite IX (Fig. 40) with 36-44 setae. Segment X with 4-6 setae to each side. Cercus $124 \mu \mathrm{~m}$ long. Seminal capsule ovoid, $90-101 \mu \mathrm{~m}$ long, $70 \mu \mathrm{~m}$ wide, with $15-19 \mu \mathrm{~m}$ long neck. Notum 139-150 $\mu \mathrm{m}$ long. Dorsomesal lobe (Fig. 41) $98-105 \mu \mathrm{~m}$ long from base of vagina to apex, $53-56 \mu \mathrm{~m}$ wide near apex. Ventrolateral lobe (Fig. 42) 30-38 $\mu \mathrm{m}$ long, $30-38 \mu \mathrm{~m}$ wide. Apodeme of apodeme lobe as in Figure 43.

## Polypedilum spp.

(Figs 44-45)

Material examined. USA: Missouri, Atherton, 2 female paratypes of P. pedatum pedatum, 7.v. 1916 \& 7.v. 1922, C.F. Adams (Cornell University, Dept. of Entomology, Types No. 2671.2, 2671.3); Louisiana, opposite Orange, Sabine River Ferry, 1 female paratype of P. pedatum pedatum, 20.vi.1917, Cornell Biol. Exped. (Cornell University, Dept. of Entomology, Type No. 2671.1).

Three female paratypes from Missouri and Louisiana although belonging to Polypedilum cannot belong to P. pedatum as they have a quite different ventrolateral lobe of gonapophysis VIII. They have $\mathrm{R}_{4+5}$ strongly curved at apex and ending at wing tip and M is bare. Thus according to the description by Townes they should have been listed under $P$. pedatum excelsius and not under $P$. pedatum pedatum. However, all three specimens have a spine on the fore tibial scale and thus do not belong to $P$. excelsius. The three specimens differ from each other both in the genitalia and in the front tibial scale and apparently consist of at least two different species. The genitalia of both are illustrated in Figures 44-45. Both have the highly unusual, rounded ventrolateral lobe with weak or no microtrichia as in P. (Probolum) marcondesi and not the brush-like lobe typical for other Polypedilum. They thus could very well belong to the subgenus Probolum.


FIGURES 44-45. Polypedilum (Uresipedilum) spp., females. 44-genitalia, ventral view of paratype of Polypedilum (Uresipedilum) pedatum Townes, 1945, from Missouri. 45-genitalia, ventral view of paratype of $P$. (U.) pedatum from Louisiana.

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APPENDIX 1. Character states for characters 1-65 in species of Polypedilum Kieffer, and the genera Asheum Sublette et Sublette, Stictochironomus Kieffer and Phaenopsectra Kieffer. Polymorphies: A = 0\&1; B = 0\&1\&2; C=1\&2.

| Characters | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 2 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  |  |  |  |  |  |  |  | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 0 | 1 |
| marcondesi | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 |
| excelsius sensu G \& R | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | A | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 |
| bullum | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | $?$ | 0 | 0 | 1 | 0 | 1 | ? | 0 | 1 | 1 | 0 |
| simantokeleum | 0 | 0 | 0 | 1 | 0 | 0 | 1 | A | 1 | 0 | $?$ | 0 | 1 | 0 | ? | 1 | 1 | 0 | 1 | 1 | 0 |
| P. (U.) aviceps | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 |
| $P$ ( $U$.) convictum | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 |
| P. (U.) cultellatum | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 |
| $P$ ( (U.) dossenudum | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | A | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 |
| P. (U.) flavum | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | A | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 |
| P. (U.) obtusum | 0 | 0 | 0 | 1 | 0 | 0 | A | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 |
| P. (U.) oresitrophum | 0 | 0 | 1 | ? | 0 | 0 | 1 | ? | 1 | 0 | $?$ | ? | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 |
| P. (U.) paraviceps | 0 | 0 | 0 | 1 | 0 | 0 | 1 | ? | 1 | 0 | $?$ | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 |
| $P$ (U.) surugense | 0 | 0 | 0 | 1 | 0 | 0 | 1 | ? | 1 | 0 | $?$ | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 |
| P. (Pe.) convexum | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 |
| P. (Pe.) epleri | 0 | 0 | A | A | 0 | 1 | 1 | 1 | 0 | 0 | 0 | A | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| P. (Pe.) kasumiense | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | $?$ | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| P. (Pe.) leei | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | A | 1 | 1 | 0 | 0 | 0 | 0 |
| P. (Pe.) nodosum | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | ? | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| P.(Pe.) shirokanense | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | $?$ | A | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| P. (Pe.) sordens | A | 0 | 0 | A | 0 | 1 | 1 | 1 | 0 | 0 | A | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | A |
| P. (Pe.) tritum | 0 | 0 | 0 | A | 0 | 1 | 1 | 1 | 0 | 0 | 0 | A | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| $P$. (Pe.) uncinatum | 0 | 0 | 0 | A | 0 | 1 | 1 | 1 | 0 | 0 | 0 | A | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| $P$. (P.) albicorne | 0 | 0 | 0 | A | 0 | 0 | 1 | 0 | 1 | 0 | 1 | A | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| $P$ ( (P.) angulum | 0 | 0 | 0 | A | 0 | 0 | 1 | 0 | 1 | 0 | A | A | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| $P$ ( (P.) arundineti | 1 | 0 | 0 | 0 | 0 | 0 | 0 | ? | 1 | 0 | $?$ | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 |
| P. (P.) bergi | 0 | 0 | 0 | 1 | 0 | 0 | A | A | 1 | 0 | A | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| P. (P.) braseniae | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| P. (P.) brunneicorne | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | A | 0 | 1 | 0 | A | 1 | 1 | 0 | 0 | 0 | 0 |
| $P$ ( P.) falciforme | 0 | 0 | 0 | A | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | A | 1 | 1 | 0 | 0 | 0 | 0 |
| $P$ ( P.) fallax | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| P. (P.) illinoense | 0 | 0 | 0 | 1 | 0 | 0 | 1 | A | 1 | 0 | 1 | 0 | A | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| P. (P.) laetum | 0 | 0 | 0 | 1 | 1 | 0 | 0 | A | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| P. (P.) melanophilum | 0 | 0 | A | 1 | 0 | 0 | 0 | A | 1 | 0 | A | A | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |


| P. (P.) nubeculosum | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | A | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| P. (P.) nubifer | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| $P$ ( (P.) nymphaeorum | 0 | 0 | 0 | A | 0 | 0 | A | 0 | 1 | 0 | A | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| P. (P.) ophoioides | 0 | 0 | 0 | 1 | 0 | 0 | A | 0 | 1 | 0 | A | 0 | 0 | ? | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| $P$ ( (P.) pedestre | 0 | 0 | 0 | 1 | 0 | 0 | 1 | A | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| $P$ ( $P$.) trigonus | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | A | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 |
| $P$. (P.) tuberculum | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| P. (C.) ontario | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 |
| P. (C.) volselligum | 1 | 1 | A | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | ? | 1 | 1 | 0 | 0 | 0 | 1 |
| P. (T.) acifer | 0 | 1 | A | 0 | 0 | 0 | ? | 0 | 1 | 0 | $?$ | 1 | 0 | 1 | A | 1 | 1 | 0 | 0 | 2 | 0 |
| P. (T.) apfelbecki | 0 | 0 | 1 | 0 | 1 | 0 | $?$ | 0 | 1 | 0 | 1 | ? | 0 | ? | 1 | 1 | 1 | 1 | 0 | 2 | 0 |
| P. (T.) bicrenatum | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | $?$ | ? | ? | ? | 0 | 1 | 1 | 1 | 0 | 2 | 1 |
| P. (T.) digitifer | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 2 | 0 |
| P. (T.) griseoguttatum | A | 1 | 0 | A | 1 | 0 | 0 | 0 | 1 | 0 | A | A | A | 1 | A | 1 | 1 | 1 | 0 | 2 | A |
| P. (T.) griseopunctatum | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | ? | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 2 | 0 |
| P. (T.) majis | 0 | 0 | 1 | 1 | 1 | 0 | 0 | ? | 1 | 0 | 0 | 1 | 0 | ? | 0 | 1 | 1 | 1 | 0 | 2 | 0 |
| P. (T.) parascalaeneum | 0 | 1 | 0 | ? | 1 | 0 | 0 | ? | 1 | 0 | 0 | ? | ? | ? | ? | 1 | 1 | 1 | 0 | 2 | 0 |
| P. (T.) scalaeneum | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | A | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 2 | 1 |
| P. (T.) titicacae | 0 | 0 | 1 | 1 | 0 | 0 | ? | ? | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 2 | 0 |
| $P$. (T.) umayo | 0 | 0 | 0 | A | 0 | 0 | $?$ | ? | 1 | 0 | 0 | ? | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 2 | 0 |
| P. (T.) villcanota | 0 | 0 | 1 | 1 | ? | 0 | $?$ | ? | 1 | 0 | 0 | ? | 0 | ? | 0 | 1 | 1 | 1 | 0 | 2 | 0 |
| P. (T.) watsoni | 0 | 0 | 0 | ? | 1 | 0 | 0 | ? | 1 | 0 | ? | ? | ? | ? | 1 | 1 | 1 | 1 | 0 | 2 | 0 |
| Asheum beckae | 1 | 0 | 0 | 1 | 0 | 0 | 0 | ? | 1 | 0 | 1 | 0 | A | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| Stictochironomus | 0 | A | 0 | 1 | A | 0 | 0 | A | 0 | 0 | A | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Phaenopsectra | 0 | 0 | 0 | 1 | 0 | 1 | A | 1 | A | 0 | A | A | A | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

APPENDIX 1. Continued.

| Characters | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 4 | 4 | 4 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 0 | 1 | 2 |
| marcondesi | 0 | 0 | 0 | 0 | 1 | 3 | 1 | 0 | A | 1 | 1 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | A | 1 |
| excelsius sensu G \& R | 0 | 0 | 0 | 0 | 1 | 3 | 1 | 0 | 2 | 0 | 1 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | ? | 1 |
| bullum | 0 | 0 | 0 | 0 | 1 | 3 | 1 | 0 | 2 | 0 | 1 | 2 | 0 | 0 | 1 | ? | ? | ? | ? | ? | ? |
| simantokeleum | 0 | 0 | 0 | 0 | 1 | 3 | 1 | 1 | 0 | 0 | 1 | 2 | 0 | 0 | 1 | ? | ? | ? | ? | ? | ? |
| P. (U.) aviceps | 0 | 1 | 0 | 0 | 1 | 3 | 0 | 1 | 2 | 0 | 1 | 2 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 |
| P. (U.) convictum | 1 | 0 | 0 | 0 | 1 | 3 | 0 | 1 | 1 | 0 | 1 | 2 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 |
| P. (U.) cultellatum | 1 | 0 | 0 | 0 | 1 | 3 | 0 | 0 | C | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 |
| P. (U.) dossenudum | 1 | 0 | 0 | 0 | 1 | 3 | 0 | 1 | 2 | 0 | A | 2 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 |
| P. (U.) flavum | 1 | 0 | 0 | 0 | 1 | 3 | 0 | 1 | 2 | 0 | 1 | 2 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 |
| P. (U.) obtusum | 0 | 1 | 0 | 0 | 1 | 3 | 0 | 1 | 2 | 0 | 1 | 2 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 |
| P. (U.) oresitrophum | 0 | 1 | 0 | 0 | 1 | 3 | 0 | 0 | 1 | 0 | ? | ? | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 |
| P. (U.) paraviceps | 0 | 0 | 0 | 0 | 1 | 3 | 0 | 1 | B | 0 | 0 | 2 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 |
| $P$ ( $U$.) surugense | 0 | 0 | 0 | 0 | 1 | 3 | 0 | 1 | 2 | 0 | 0 | 2 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 |
| P. (Pe.) convexum | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | A | 0 | 1 | 2 | 1 | 0 | 1 | 1 | 0 | 1 | ? | 0 | 1 |
| P. (Pe.) epleri | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | B | 0 | A | 2 | 0 | 0 | 1 | 1 | 0 | 1 | ? | 0 | 1 |
| P. (Pe.) kasumiense | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | A | 0 | 1 | ? | 1 | 0 | 1 | 1 | 0 | ? | 0 | 0 | 1 |
| P. (Pe.) leei | 0 | 0 | 0 | 0 | 0 | C | 0 | 2 | A | 0 | 1 | 2 | 0 | 0 | 1 | 1 | 0 | 1 | ? | 0 | 1 |
| P. (Pe.) nodosum | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 2 | C | 0 | 2 | 2 | 0 | 0 | 1 | 1 | 0 | ? | ? | 0 | 1 |


| P. (Pe.) shirokanense | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| P. (Pe.) sordens | 0 | 0 | 0 | 0 | A | A | 0 | 2 | A | 0 | 1 | 2 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 |
| P. (Pe.) tritum | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | A | 0 | A | 2 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 |
| P. (Pe.) uncinatum | 0 | 0 | 0 | 0 | 0 | A | 0 | 1 | A | 0 | A | 2 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 |
| P. (P.) albicorne | 0 | 0 | 0 | 0 | A | 1 | 0 | 2 | C | 0 | 0 | 2 | 0 | 0 | 1 | 1 | 0 | A | 1 | 0 | 1 |
| $P$ ( (P.) angulum | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | B | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 |
| $P$. (P.) arundineti | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | A | 2 | 0 | 0 | 1 | A | 0 | 1 | 1 | 0 | 1 |
| P. (P.) bergi | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | B | 0 | A | 1 | 0 | 0 | 1 | 1 | 0 | 1 | ? | 1 | 1 |
| P. (P.) braseniae | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | A | 0 | A | 2 | 0 | 0 | 1 | 1 | 0 | 1 | ? | 0 | 1 |
| P. (P.) brunneicorne | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | A | 0 | 1 | 2 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | ? | 1 |
| P. (P.) falciforme | 0 | 0 | 0 | 1 | 0 | A | 0 | 1 | C | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | ? | 1 | 1 |
| P. (P.) fallax | 0 | 0 | 0 | 0 | A | 1 | 0 | 1 | A | 0 | A | 2 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 |
| P. (P.) illinoense | 0 | 0 | 0 | 0 | 0 | A | 0 | 1 | A | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 |
| P. (P.) laetum | 0 | 0 | 0 | 0 | 0 | ? | 0 | 1 | B | 0 | 0 | 2 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 |
| P. (P.) melanophilum | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 2 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | ? | 0 |
| $P$ ( (P.) nubeculosum | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 2 | 0 | 1 | 2 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 |
| $P$ ( (P.) nubifer | 0 | 0 | 0 | 0 | 1 | 3 | 0 | 0 | C | 0 | A | 2 | 0 | 0 | 1 | 0 | 1 | 1 | 2 | 0 | 1 |
| $P$ ( (P.) nymphaeorum | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | A | 0 | A | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 |
| P. (P.) ophoioides | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | A | 0 | 0 | 1 | 0 | 0 | A | 1 | 0 | 1 | 0 | 0 | 1 |
| $P$ ( (P.) pedestre | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | C | 0 | 1 | 2 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 |
| $P$ ( (P.) trigonus | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | B | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 |
| P. (P.) tuberculum | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | C | 0 | 0 | 2 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 |
| P. (C.) ontario | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 2 | 2 | 1 | 0 | 2 | 0 | 1 | 1 | 0 | 0 | 0 |
| P. (C.) volselligum | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 2 | 2 | 0 | 0 | 2 | 0 | 1 | 1 | 0 | 0 | 0 |
| $P$ ( (T.) acifer | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 3 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | ? | 1 |
| P. (T.) apfelbecki | 0 | 0 | 0 | 0 | ? | ? | 0 | 0 | 3 | 0 | 1 | 1 | 0 | A | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| P. (T.) bicrenatum | 0 | 0 | 0 | 0 | ? | ? | 0 | 0 | 3 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| $P$ ( (T.) digitifer | 0 | 0 | 0 | 0 | ? | ? | 0 | 0 | 3 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | ? | ? | 1 |
| P. (T.) griseoguttatum | 0 | 0 | 0 | 0 | ? | ? | 0 | 0 | 3 | 0 | A | 1 | A | 1 | 1 | 0 | 0 | 0 | ? | ? | 1 |
| P. (T.) griseopunctatum | 0 | 0 | 0 | 0 | ? | ? | 0 | 1 | 3 | 0 | 0 | 2 | 1 | 1 | 1 | 0 | 0 | 1 | ? | ? | 1 |
| P. (T.) majis | 0 | 0 | 0 | 0 | ? | ? | 0 | 0 | 2 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | ? | 1 |
| P. (T.) parascalaeneum | 0 | 0 | 0 | 0 | ? | ? | 0 | 0 | 3 | 0 | ? | ? | 1 | 0 | 1 | ? | 0 | ? | ? | ? | 1 |
| P. (T.) scalaeneum | 0 | 0 | 0 | 0 | ? | ? | 0 | 0 | 2 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 |
| P. (T.) titicacae | 0 | 0 | 0 | 0 | ? | ? | 0 | 0 | 3 | 0 | 0 | ? | 1 | 1 | 1 | ? | 0 | ? | 2 | ? | 1 |
| P. (T.) umayo | 0 | 0 | 0 | 0 | $?$ | ? | 0 | 0 | 3 | 0 | 1 | ? | 1 | 1 | 1 | ? | 0 | ? | 2 | ? | 1 |
| P. (T.) villcanota | 0 | 0 | 0 | 0 | $?$ | ? | 0 | 0 | 3 | 0 | 0 | ? | 1 | 0 | 1 | ? | 0 | ? | 0 | ? | 1 |
| P. (T.) watsoni | 0 | 0 | 0 | 0 | $?$ | ? | 0 | 0 | 3 | 0 | ? | ? | 0 | 0 | 1 | 1 | 0 | 0 | ? | ? | 1 |
| Asheum beckae | 0 | 1 | 0 | 0 | 0 | 3 | 0 | 1 | 0 | 0 | A | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 2 | 0 | 1 |
| Stictochironomus | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | A | C | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 1 | 1 |
| Phaenopsectra | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | B | 0 | B | 2 | 0 | 0 | 0 | 0 | 1 | 1 | A | ? | 1 |

APPENDIX 1. Continued.

| Characters | 4 | 4 | 4 | 4 | 4 | 4 | 4 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | 6 | 6 | 6 | 6 | 6 | 6 | 6 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 0 | 1 | 2 | 3 | 4 | 5 |
| marcondesi | 0 | 0 | 2 | 2 | 0 | 0 | A | 0 | A | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 |
| excelsius sensu G \& R | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | A | 0 |



| P. (T.) <br> griseopunctatum | 0 | 0 | 1 | 1 | 0 | 1 | 1 | ? | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 2 | ? | 0 | 1 | 0 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| P. (T.) majis | 0 | ? | $?$ | ? | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 2 | 0 | 0 | 0 | 0 |
| P. (T.) <br> parascalaeneum | 0 | 0 | ? | 1 | 0 | 1 | 0 | A | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 2 | 1 | 0 | 0 | 0 |
| P. (T.) scalaeneum | 0 | 0 | $?$ | 2 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 2 | 1 | 0 | 1 | 0 |
| P. (T.) titicacae | 0 | 0 | ? | 2 | 0 | 1 | 0 | ? | ? | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 2 | ? | 0 | ? | 0 |
| P. (T.) umayo | 0 | 0 | ? | 2 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | A | 1 | 1 | 2 | 1 | 0 | 0 | 0 |
| P. (T.) villcanota | 0 | ? | 2 | 2 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 2 | 1 | 0 | 0 | 0 |
| P. (T.) watsoni | 1 | 1 | 0 | 0 | 2 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 |
| Asheum beckae | 0 | 0 | 0 | 2 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | A | 0 | 1 | A | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 |
| Stictochironomus | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | A | 0 | 0 | 0 | 0 | 0 | A | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 |
| Phaenopsectra | 0 | 0 | 2 | 2 | 0 | 0 | A | 0 | A | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 |

