

## Review of the millipede genus *Poratia* Cook & Cook, 1894 (Diplopoda: Polydesmida: Pyrgodesmidae)

### Обзор двупарноногих многоножек рода *Poratia* Cook & Cook, 1894 (Diplopoda: Polydesmida: Pyrgodesmidae)

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КЛЮЧЕВЫЕ СЛОВА: Diplopoda, Pyrgodesmidae, *Poratia*, таксономия, новый вид, синонимика, партеногенез, Неотропики.

ABSTRACT: The millipede genus *Poratia* Cook & Cook, 1894 is redefined and shown to be Neotropical (Central and northern South America), with the following junior subjective synonyms: *Dominicodesmus* Chamberlin, 1923; *Tidopterus* Chamberlin, 1923; *Kapyrodesmus* Attems, 1940, syn.n.; *Muyudesmus* Kraus, 1960, syn.n.; and *Poratioides* Loomis, 1970, syn.n. The following seven valid species are currently assigned to *Poratia*: (1) *P. digitata* (Porat, 1889) (= the type species *Scytonotus digitatus* Porat, 1889; = *Poratia heterotuberculata* Carl, 1902; = ?*Dominicodesmus panamicus* Chamberlin, 1940; = *Poratioides virginalis* Loomis, 1970, syn.n.; = *Poratioides disparatus* Loomis, 1973, syn.n.); (2) *P. mulegensis* (Chamberlin, 1923) (= *Xerodesmus mulegensis* Chamberlin, 1923; = *Dominicodesmus geophilus* Chamberlin, 1923); (3) *P. sequens* (Chamberlin, 1923) (= *Tidopterus sequens* Chamberlin, 1923); (4) *P. insularis* (Kraus, 1960) (= *Muyudesmus insularis* Kraus, 1960); (5) *P. obliterated* (Kraus, 1960) (= *Muyudesmus obliterated* Kraus, 1960); (6) *Poratia fossata* Loomis, 1964; and (7) *Poratia salvator* sp.n. *Treseolobus granulofrons* Chamberlin, 1918 is transferred to *Docodesmus* Cook, 1896, comb.n. *Poratia digitata*, as a strictly parthenogenetic form, occurs commonly in European green houses, also known from open habitats in Java and the southern U.S.A. and is recorded here from North American green houses for the first time. *P. obliterated* is bisexual throughout Amazonia as well as in Costa Rica and perhaps Panama, but distinctly parthenogenetic in a few European hothouses. Parthenogenesis is likewise characteristic of *P. mulegensis*, at least so in the Caribbean. A character table and a key to *Poratia* species have been compiled.

РЕЗЮМЕ: Диплоподам рода *Poratia* Cook & Cook, 1894 дан новый диагноз. Показано, что этот род исконно неотропический (Центральная и север-

ная часть Южной Америки) и насчитывает следующие младшие субъективные синонимы: *Dominicodesmus* Chamberlin, 1923; *Tidopterus* Chamberlin, 1923; *Kapyrodesmus* Attems, 1940, syn.n.; *Muyudesmus* Kraus, 1960, syn.n.; и *Poratioides* Loomis, 1970, syn.n. Следующие семь валидных видов ныне отнесены к *Poratia*: (1) *P. digitata* (Porat, 1889) (= типовой вид *Scytonotus digitatus* Porat, 1889; = *Poratia heterotuberculata* Carl, 1902; = ?*Dominicodesmus panamicus* Chamberlin, 1940; = *Poratioides virginalis* Loomis, 1970, syn.n.; = *Poratioides disparatus* Loomis, 1973, syn.n.); (2) *P. mulegensis* (Chamberlin, 1923), comb.n. (= *Xerodesmus mulegensis* Chamberlin, 1923; = ?*Dominicodesmus geophilus* Chamberlin, 1923); (3) *P. sequens* (Chamberlin, 1923) (= *Tidopterus sequens* Chamberlin, 1923); (4) *P. insularis* (Kraus, 1960), comb.n. (= *Muyudesmus insularis* Kraus, 1960); (5) *P. obliterated* (Kraus, 1960), comb.n. (= *Muyudesmus obliterated* Kraus, 1960); (6) *Poratia fossata* Loomis, 1964; and (7) *Poratia salvator* sp.n. *Treseolobus granulofrons* Chamberlin, 1918 переведен в род *Docodesmus* Cook, 1896, comb.n. Вид *Poratia digitata* в качестве строго партеногенетической формы обычен в европейских оранжереях, также известен на открытых грунтах на Яве и юге США. и ныне впервые отмечается в теплице в Северной Америке. Вид *P. obliterated* с обоими полами по всей Амазонии, в Коста-Рике и, возможно, в Панаме, но явственно партеногенетический в нескольких европейских оранжереях. Партеногенез характерен и для *P. mulegensis* по крайней мере в Карибском бассейне. Составлены таблица признаков и ключ для определения видов рода *Poratia*.

### Introduction

The taxonomy of the worldwide, predominantly tropical diplopod family Pyrgodesmidae has long been con-

sidered highly problematic [e.g., Hoffman, 1980: 149]. With currently 173 nominal genera assigned, the Pyrgodesmidae represents one of the largest families within the Diplopoda. The bulk of them, 131 genera, are monotypic, most of the remainder are oligobasic and approximately half of the species are only known from females and/or juveniles [cf. Golovatch, 1996: 110]. Pyrgodesmids are small animals, ranging in size mostly between 6 and 10 mm, often cryptic in both habits and colouration. The collum is usually flabellate, lobulated anteriorly and richly ornamented dorsally, the tergites are virtually always strongly declivous (sloping downward), and usually conspicuously tuberculate and/or lobulate, often dirt-coated and/or pilose. The pore formula is variable among the taxa, only relatively seldom being normal, i.e. comprising ozopores on the rings 5, 7, 9, 10, 12, 13, and 15 to 18(19) as known in most of the Polydesmida, usually bearing partial sets thereof. In a substantial number of genera some or nearly all ozopores may be placed on highly distinctive stalks, or porosteles. Some species lack ozopores altogether. Such a great variety of peripheral features is outstanding, even compared to other Polydesmida, and may account for the disproportionately high number of monotypic and oligobasic pyrgodesmid genera and species described without any account of gonopod structure and/or based on females and/or juveniles alone.

The genus *Poratia* Cook & Cook, 1894 is no exception both with regard to its typical pyrgodesmid traits (e.g., small body size, some of the ozopores on stalks) and confused taxonomy. Ever since its erection, the identity of the type species *P. digitata* (Porat, 1889) was shrouded by uncertainty [see Kraus, 1960: 251; Hoffman, 1980: 150], because the type series contained only females derived from a Swedish hothouse [Porat, 1889]. The recent discovery of topotypic (= European hothouse) male material clarified the identity of this species, and the identity of its respective genus [cf. Adis et al., 2001]. Moreover, the first biological observations were made of this apparently parthenogenetic species.

The present paper focuses on taxonomic issues concerning *P. digitata* and its presumed congeners. This genus is now seen as originally Neotropical, viz., Central and northern South American, comprising no fewer than seven species. One of these, from El Salvador, is new, another one seems relatively widespread in the Caribbean, while among the rest one is apparently pan-tropical, and one more Amazonian and Central American, though both latter also appear quite common as parthenogenetic introductions in European hothouses as well as occur in the open at least in the southern U.S.A. In addition, a number of new synonyms are here established or formalized.

## Historical

The taxonomy of the genus *Poratia* was reviewed recently [Hoffman, 1999: 496; Adis et al., 2001: 150]. *Poratia* Cook & Cook, 1894 is based on *Scytonotus digitatus* Porat, 1889 [see Cook & Cook, 1894], a parthe-

nogenetic, all-female (= thelytokous) species currently known to being quite widespread in European hothouses (Gothenburg, Paris, Kew, Kiel, Berlin, Düsseldorf) [Schubart, 1934, 1947b; Blower & Rundle, 1986; Adis et al., 2001] as well as both in open habitats in the southern U.S.A. [Shelley & Golovatch, 2001] and in a green house in the northern U.S.A. The types of *P. digitata*, now in Swedish Royal Natural History Museum, Stockholm, have thereby been relocated and revised [Adis et al., 2001]. Also, *P. digitata* has formally been recorded in Panama [Loomis, 1961, 1964], with *Dominicodesmus panamicus* Chamberlin, 1940, described from a single female taken from Panama [Chamberlin, 1940], serving as its junior synonym [Loomis, 1961]. In addition, this species has also been reported from Costa Rica [Hoffman, 1999]. However, at least some of the Costa Rican and Panamanian material referred to by Hoffman [1999] as well as all samples from Brazil erroneously attributed to *P. digitata* by Silvestri [1923], Schubart [1934, 1947a, 1947b] and Attems [1940] appear to actually represent *Muyudesmus obliterated* Kraus, 1960, a species only represented by bisexual populations throughout Amazonia [Kraus, 1960; Adis et al., 2001] as well as in Costa Rica and possibly Panama [Shelley & Golovatch, 2001] whence it must have been introduced to Europe as a parthenogenetic form, i.e. hothouses in the botanic gardens of Kiel, Germany and Paris, France [Adis et al., 2001; Adis & Golovatch, unpublished].

Four further nominal congeners have since been added to *Poratia*. *P. heterotuberculata* Carl, 1902, based on 16 females collected in a sugar cane plantation on Java, Indonesia [Carl, 1902], was synonymized under *P. digitata* by Silvestri [1923]. This synonymy had been generally accepted [e.g., Attems, 1940; Loomis, 1961, 1964] until Hoffman [1999] questioned it. However, a revision of pertinent type material (now in the Geneva Museum) has unequivocally shown that both names are indeed synonyms [Adis et al., 2001].

*Treseolobus granulofrons* Chamberlin, 1918, was originally described from a few females taken in Haiti. Later, Loomis [1934], based on his examination of some paratypes, assumed *granulofrons* to be a subjective senior synonym of *Dominicodesmus geophilus* Chamberlin, 1923, the latter taxon based on a single (sub)adult female (with 19 body segments) from the Dominican Republic [Chamberlin, 1923b]. Loomis [1934] recorded *granulofrons* in Haiti, St. Eustatius, Guadeloupe, St. Kitts, Antigua, and Trinidad and he was also the first to transfer this species first to *Psochodesmus* Cook, 1896 and then [1961, 1964] to *Poratia*. Finally, Loomis [1961, 1964] recorded *granulofrons* in Panama and synonymized both *Dominicodesmus* Chamberlin, 1923 and *Tidopterus* Chamberlin, 1923 under *Poratia*. Mauriès [1981] reported, with some reservations, the first male of what he presumed to represent *Poratia granulofrons* taken among rich material (altogether 52 specimens, mainly female and/or juvenile) in Guadeloupe.

Due to the above synonymization by Loomis [1961], *Tidopterus sequens* Chamberlin, 1923, originally described from a single male from Guyana (= formerly

British Guiana) [Chamberlin, 1923c], became the next species to be formally assigned to *Poratia*.

Ultimately, *P. fossata* Loomis, 1964, was described based on an adult and a juvenile (18-segmented) male taken from Panama [Loomis, 1964]. As a result, only four *Poratia* species have heretofore been considered as valid: *P. digitata*, *P. granulofrons*, *P. sequens*, and *P. fossata*. However, a few more species have long been described that, though never formally assigned to *Poratia*, do display very close affinities to the above four.

## Material and methods

The available type material of all species and synonyms was examined for the present study. In addition, material of a new species has been located at FSCA, described below.

The pattern of metatergal tuberculation follows the formula developed by Hoffman [1976], with **PM** and **DL** standing for large paramedian and dorsolateral tubercles on the metaterga. If there are more than one **PM** or **DL**, these are numbered, starting from the median, e.g., **PM1**, **PM2** etc. The terms antemarginal, lateromarginal and posteromarginal denote the lobulations at the anterior, lateral and posterior margins of the paraterga, respectively.

The following acronyms for the repositories are being used here: California Academy of Sciences, San Francisco, California (CAS), Florida State Collection of Arthropods, Gainesville (FSCA), Forschungsinstitut und Natur-Museum Senckenberg, Frankfurt a.M. (SMF), Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (MCZ), Muséum d'histoire naturelle, Geneva (MHNG), Muséum national d'Histoire naturelle, Paris (MNHP), and National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM).

## Taxonomic part

### GENUS *PORATIA* COOK & COOK, 1894

*Poratia* Cook & Cook, 1894: 238. Type species: *Scytonotus digitatus* Porat, 1889, by original designation.

*Dominicodesmus* Chamberlin, 1923b: 189. Type species: *D. geophilus* Chamberlin, 1923, by original designation. Synonymized with *Psochodesmus* Cook, 1896, by Loomis [1934: 53]. Removed from the synonymy of *Psochodesmus* and placed in the synonymy of *Poratia* by Loomis [1961: 97].

*Tidopterus* Chamberlin, 1923c: 420. Type species: *T. sequens* Chamberlin, 1923, by original designation. Synonymized with *Psochodesmus* by Loomis [1934: 53]. Removed from the synonymy of *Psochodesmus* and placed in the synonymy with *Poratia* by Loomis [1961: 97].

*Kapyrodesmus* Attems, 1940: 322, **syn.n.** Type species: *Xerodesmus mulegensis* Chamberlin, 1923, by subsequent designation by Attems [1940: 323].

*Muyudesmus* Kraus, 1960: 250, **syn.n.** Type species: *M. insularis* Kraus, 1960, by original designation.

*Poratioides* Loomis, 1970: 131, **syn.n.** Type species: *P. virginialis* Loomis, 1970, by original designation.

NOTE: Loomis [1961: 98] examined the gonopods of *Psochodesmus crescentis* Cook, 1896 (male holotype from Florida, deposited in USNM 2407, also re-examined here), the type species of *Psochodesmus* Cook, 1896, and concluded that the genus is distinct from *Poratia*.

DIAGNOSIS: Members of the genus *Poratia* are characterized by the following combination of characters: collum flabel-

late, covering most of the head from above, with (4)5+(4)5 deeply incised and somewhat upright lobulations, or scallops, at anterior margin (occasionally lateralmost scallops less deeply incised); paraterga with three lateral marginal lobulations on body rings 3–15, lacking antemarginal lobulations and not exceeding 2 posteromarginals; all porostele-bearing segments laterally with one lobule in front of porostele; body strongly convex, paraterga pointing ventrolaterad, giving the appearance of being short. Gonopods either with a solenomerite splitting off quite distally from the telopodite or solenomerite absent.

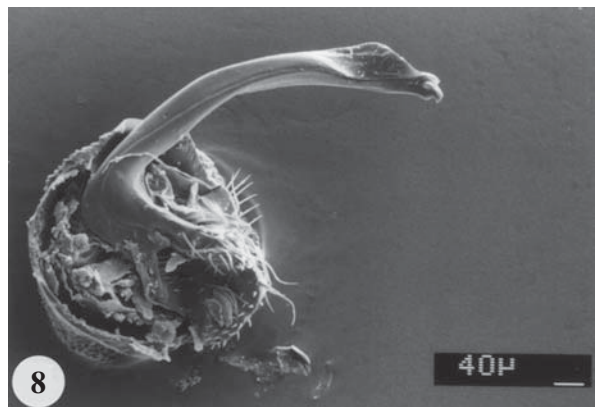
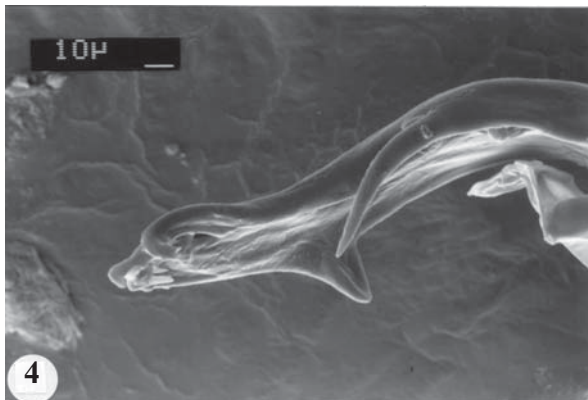
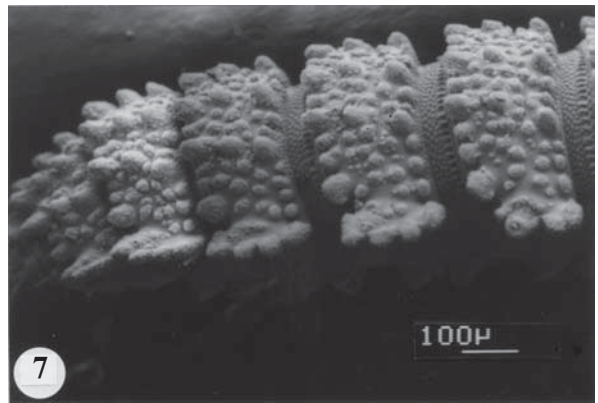
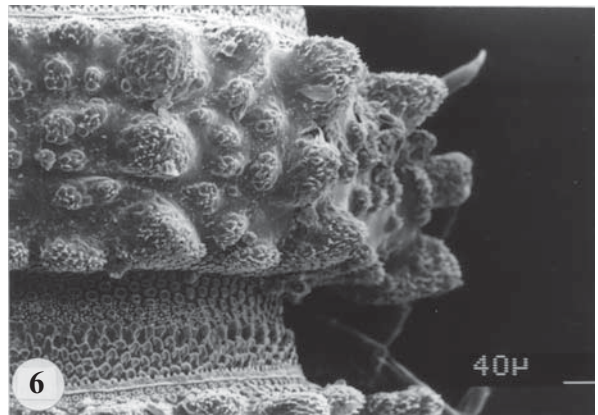
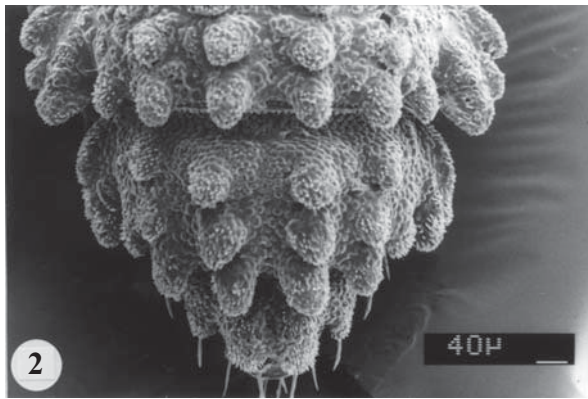
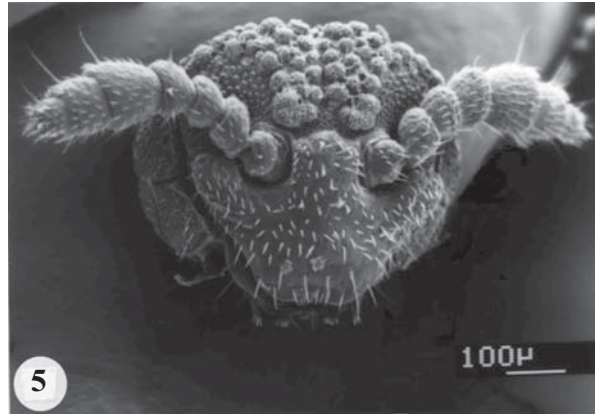
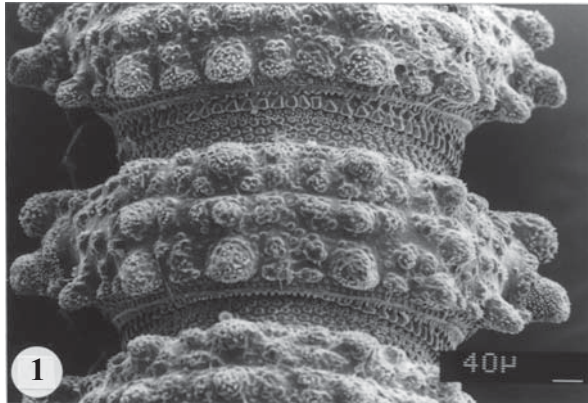
*Poratia* can be confused first of all with the pyrgodesmid genera *Psochodesmus* Cook, 1896 and *Pseudoporatia* Golovatch, 2000. *Psochodesmus* can be distinguished from *Poratia* by the somewhat less strongly incised and upright scallops at the anterior margin of the collum and, above all, by the mostly two lateral lobulations in front of the porostele (only the 5<sup>th</sup> segment with a single lobulation anterior to the porostele) and with all its porosteles being placed at the caudolateral corner of the paraterga [Loomis, 1934: 54, fig. 27; Shelley & Golovatch, 2001, see fig. 3]. *Poratia* differs from *Pseudoporatia* in having two, not three posteromarginals and, above all, the much less complex gonopods never nearly fully concealed inside the gonocoel [Golovatch, 2000: 228, figs 30, 31].

DESCRIPTION: Small, rather pallid to brown-pinkish pyrgodesmids less than 1 cm long, with 19 or 20 body segments in adults. Head roughly granulate all over vertex, clypeolabrum densely pilose/setose, set off from vertex by a rather distinct sulcus (Fig. 5). Collum flabellate, barely, inverted subtrapeziform in shape, covering most of the head from above but not in side view, with (4)5+(4)5 deeply incised, somewhat upright lobulations, anterior margin slightly rounded in outline and with a tuberculate/granulate dorsal surface (Figs 13, 20, 32, 40). Antennomere 5 always longer and wider than 6<sup>th</sup> (Figs 5 & 13). Metatergal tuberculation pattern usual, with 2+2 longitudinal rows of larger paramedian (**PM**) and dorsolateral (**DL**) tubercles tending to grow higher toward caudal body end (Figs 2, 7, 15, 23, 29, 34, 42), antemarginals (almost) absent, posteromarginals virtually never exceeding 2 in number; lateral marginals 3, on segments subsequent to 15<sup>th</sup> usually 4, seldom 3. Paraterga of 2<sup>nd</sup> segment much longer than remaining paraterga. Pore formula normal (5, 7, 9, 10, 12, 13, 15 to 18(19)); ozopores on distinct porosteles, porosteles replacing middle lateral marginal lobule until segment 15 (Figs 1, 6, 14, 21, 33, 38, 41), onward ozopores barely traceable but present (Fig. 25). Metatergal trichome wanting. Preanal ring at least partly visible from above. Legs and sterna usual, without modifications.

Gonopod coxae globose, almost as wide combined as male metatergum 7 from below, anterodistally each coxite with two strong setae (Fig. 9, 39). Telopodites crossing in situ, not very elaborate, strongly exposed, subfalcate, each usually with a caudo-parabasal bulge or two and 1–2 branches distally on the femorite, one of the branches, if any, being a more or less subflagelliform solenomerite.

Epigynal ridge behind female coxae 2 very low, inconspicuous. Vulvae relatively elaborate and particularly densely setose.

REMARKS: The species previously assigned to the nominal genera *Kapyrodesmus*, *Muyudesmus*, and *Poratioides* all share the genus-typical characters as listed in the diagnosis. These form the basis for our delineation of the genus *Poratia*. This approach broadens the previous diagnosis of the genus *Poratia* and allied nominal genera, which are here considered subjective junior synonyms. Shear's [1973, 1977] revisionary work on the Central American pyrgodesmid genus *Myrmecodesmus* Silvestri, 1910 resulted in a comparable number of junior subjective generic synonyms.



As Loomis [1970] admitted, his *Poratioides* was defined versus Silvestri's [1923] concept of *Poratia*. However, as we know this now, Silvestri erred and his *Poratia* was exactly what Kraus [1960] formalized later as *Muyudesmus*, something that Loomis overlooked. So there is no diagnostic difference between *Poratioides* and *Muyudesmus*, while the gap between these two nominal genera and *Poratia* is apparently too minor (mainly the number of body segments and that of lateral lobulations on a few posteriormost paraterga) to keep the trio separate [cf. Adis et al., 2001].

Although the holotype of *Dominicodesmus geophilus* Chamberlin, 1923 could no longer be found at MCZ (presumably lost since the respective vial is empty), we are inclined to follow Loomis [1961, 1964] and Hoffman [1999] in treating *Dominicodesmus* as a subjective junior synonym of *Poratia*.

*Xerodesmus mulegensis*, the type, and only, species of *Kapyrgodesmus*, was described with two misleading mistakes [Chamberlin, 1923a]: (1) the body of the holotype was said to be composed of 20 segments, and (2) the ten lobulations at the anterior edge of the collum were depicted as relatively poorly incised. Had these characters been properly described or illustrated, there would have hardly been any grounds already for Attems [1940] to keep *Kapyrgodesmus* separate from *Poratia*. Also, Attems might have even considered a substitute name superfluous in the first place (see below).

Certain *Poratia* species readily form parthenogenetic populations. *P. digitata* has become introduced to Europe, always as a hothouse millipede, the United States (a green house in Chicago, IL; open habitats in Florida and U.S. Virgin Islands), and to Java as a free-living though strictly parthenogenetic and apparently anthropochoric form, with Central America likely to represent the source area. As at least some of the Costa Rican and Panamanian records of *P. digitata* by Hoffman [1999] prove to actually be referred to *P. oblitterata*, it still remains open to question if *P. digitata* indeed occurs in these countries. Similarly, *P. oblitterata* is a species possibly rooting in the Andes but widespread all over Amazonia as well as in Panama and Costa Rica (see above) where it is always represented by bisexual populations; yet a couple of parthenogenetic populations have been discovered in European hothouses, i.e. Kiel [Adis et al., 2001] and Paris [Adis & Golovatch, unpublished]. Finally, the strong bias toward females in *P. mulegensis* seems to be evidence of still another case of thelytoky in *Poratia*, a fact that would make the relatively vast distribution of this species in the Caribbean, in the Lesser Antilles in particular, far more easy to account for.

*Poratia digitata* (Porat, 1889)  
Figs 1–4, 9–12.

*Scytonotus digitatus* Porat, 1889: 59. Several female syntypes (of which 5 were located and examined by the senior author, and a lectotype selected) from a green house in Gothenburg (= Göteborg), deposited in the Stockholm Museum; see also Adis et al., 2001.

*Poratia digitata* — Cook & Cook, 1894; Adis et al., 2001; Shelley & Golovatch, 2001.

*Poratia heterotuberculata* Carl, 1902: 667. 16 female syntypes (of which 10 were relocated and examined by the senior author, and a lectotype selected) from a sugar plantation in Java, Indonesia, deposited in MHNG, synonymized by Silvestri [1923]; see Adis et al., 2001.

(?) *Dominicodesmus panamicus* Chamberlin, 1940: 6 (synonymized by Loomis [1961: 98]). Female holotype from Barro Colorado Island, Panama, deposited at USNM, specimen could not be found in the USNM type collection.

*Poratioides virginalis* Loomis, 1970: 132, **syn.n.** Female holotype from U.S. Virgin Islands, deposited in USNM # 3495, examined; female paratypes deposited in FSCA, examined.

*Poratioides disparatus* Loomis, 1973: 322, **syn.n.** Male holotype from Dade County, Florida, numerous paratypes, in FSCA, examined.

(?) *Poratia digitata* — Loomis, 1961, 1964; Hoffman, 1999.

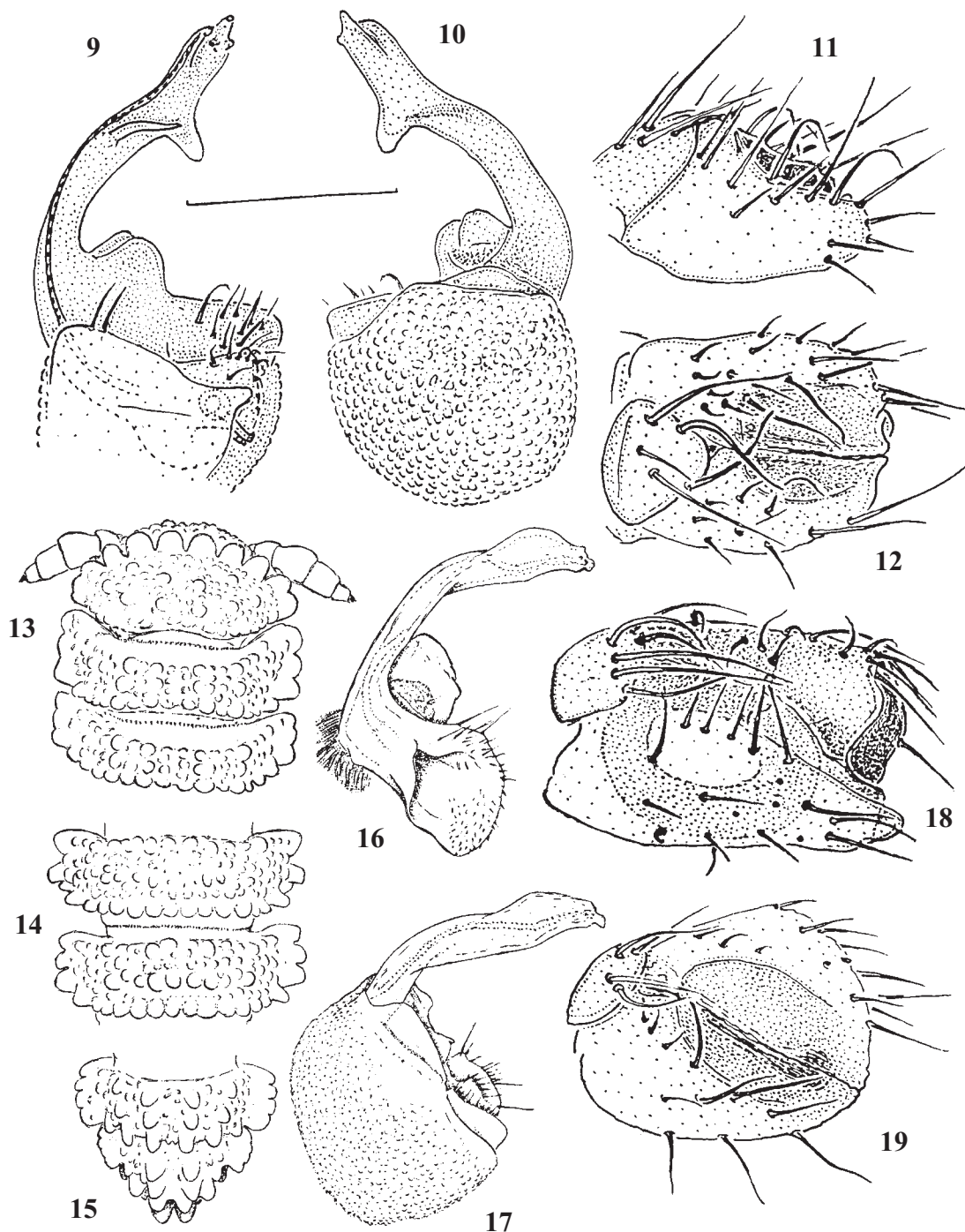
REMARKS: This species has already been defined quite well using both male and female material deriving from European hothouses and Java [Adis et al., 2001]. The records of *P. digitata* in Panama [Loomis, 1961, 1964] and Costa Rica [Hoffman, 1999] require confirmation as at least some of them seem to represent misidentifications (cf. below under *P. oblitterata*).

*Poratia heterotuberculata* Carl, 1902, based on 16 females collected in a sugar cane plantation on Java, Indonesia [Carl, 1902], was synonymized under *P. digitata* by Silvestri [1923]. This synonymy had been generally accepted [e.g., Attems, 1940; Loomis, 1961, 1964] until Hoffman [1999] questioned it. However, a revision of pertinent type material (now in the Geneva Museum) has unequivocally shown that both names are indeed synonyms [Adis et al., 2001]. The synonymization with *Dominicodesmus panamicus* by Loomis [1961] cannot be re-examined since the type material of *panamicus* is lost, but we tend to trust Loomis in this case (see above). The synonymization with *disparatus* is confirmed by a direct re-examination of both the type series and topotypes (three males and hundreds of females), though the synonymy would become apparent if one simply compares the gonopod conformation as depicted by Loomis [1973] and herein (Figs 3, 4, 9, 10). In addition, we have no doubts to formally synonymize *Poratioides virginalis* Loomis, 1970 (holotype female, USNM # 3495, re-examined). Loomis [1973] did emphasize the extremely close resemblance both of his *Poratioides* species appeared to display, yet he preferred to wait until male-containing material be taken from U.S. Virgin Islands. The samples from Brazil erroneously attributed to *P. digitata* by Silvestri [1923], Schubart [1934, 1947a, 1947b] and Attems [1940] appear to actually represent *P. oblitterata* (see below). The same can be said as regards at least some of the samples from Costa Rica referred to by Hoffman [1999].

DIAGNOSIS: *Poratia digitata* can be distinguished from all other *Poratia* species by the following combination of characters: body with 19 segments, three (rarely four) latero-marginals on paraterga 16–18, a single posteromarginal; midbody **PM** and **DL** tubercles well developed and round (Fig. 1), **PM1** and **PM2** on penultimate segment clearly separated medially (Fig. 2); gonopods relatively elaborate,

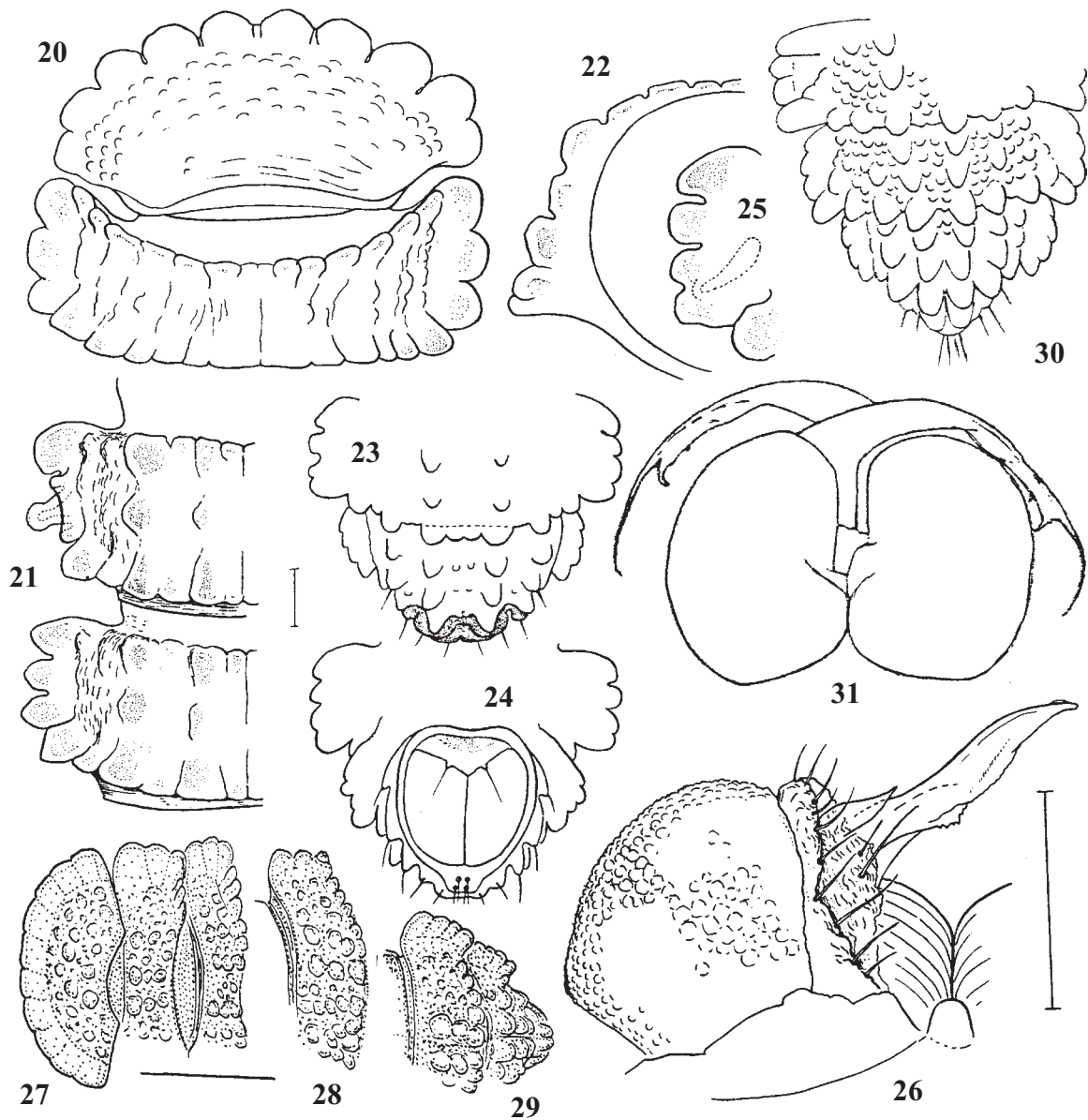
Figs 1–8. Scanning micrographs of *Poratia digitata* (Porat, 1889) (1–4), males (1, 3, 4) and a female (2) from Kiel Botanic Garden, Germany, and *P. oblitterata* (Kraus, 1960) (5–8), males (5, 6, 8) from several places in Amazonia and a female (7) from Kiel Botanic Garden. 1 — midbody segments, dorsal view; 2 — caudal body end, dorsal view; 3 & 4 — right gonopod, submesal view; 5 — head, front view; 6 — right half of a poriferous midbody segment, dorsal view; 7 — caudal body portion, lateral view; 8 — left gonopod, mesal view. Scale bars in micrometers. After Adis et al. [2001].

Рис. 1–8. Электронные микрофотографии *Poratia digitata* (Porat, 1889) (1–4), самцы (1, 3, 4) и самка (2) из ботанического сада в Киле (ФРГ), и *P. oblitterata* (Kraus, 1960) (5–8), самцы (5, 6, 8) из разных мест в Амазонии и самка (7) из ботанического сада в Киле. 1 — среднетуловищные сегменты, сверху; 2 — задний конец тела, сверху; 3 и 4 — правый гоноподий, почти изнутри; 5 — голова, спереди; 6 — правая половина несущего поры защитных желез среднетуловищного сегмента, сверху; 7 — задняя часть тела, сбоку; 8 — левый гоноподий, изнутри. Масштаб в микрометрах. По: Adis et al. [2001].



Figs 9–19. *Porattia digitata* (Porat, 1889) (9–12), a male (9 & 10) and a female (11 & 12) from Kiel Botanic Garden, and *P. obliterated* (Kraus, 1960) (13–19), male paratypes (13–17) from near Iquitos, Peru, a female (18) from near Manaus, Brazil, and a female (19) from Kiel Botanic Garden. 9, 10, 16 — left gonopod, mesal, lateral, and mesal views, respectively; 11, 12, 18, 19 — vulva, sublateral, ventral, ventral, and ventral views, respectively; 13 — anterior body portion, dorsal view; 14 — segments 10 and 11, dorsal view; 15 — caudal body end, dorsal view; 17 — right gonopod, lateral view. Scale bar 0.1 mm (9–12, 18 & 19), others drawn not to scale. After Kraus [1960] and Adis et al. [2001].

Рис. 9–19. *Porattia digitata* (Porat, 1889) (9–12), самец (9 и 10) и самка (11 и 12) из ботанического сада в Киле, и *P. obliterated* (Kraus, 1960) (13–19), самцы-паратипы (13–17) из окрестностей Икитоса (Перу), самка (18) из-под Манауса (Бразилия) и самка (19) из ботанического сада в Киле. 9, 10, 16 — левый гоноподий, соответственно изнутри, сбоку и изнутри; 11, 12, 18, 19 — вульва, соответственно примерно сбоку, снизу, снизу и снизу; 13 — передний конец тела, сверху; 14 — 10-й и 11-й сегменты тела, сверху; 15 — задний конец тела, сверху; 17 — правый гоноподий, сбоку. Масштаб 0,1 мм (9–12, 18 & 19), прочие без масштаба. По: Kraus [1960] и Adis et al. [2001].



Figs 20–31. *Poratia mulegensis* (Chamberlin, 1923) (20–26), a male from Guadeloupe, *Docodesmus granulofrons* (Chamberlin, 1918) (27–29), female holotype from Haiti (orig.), and *Poratia sequens* (Chamberlin, 1923) (30 & 31), male holotype from Guyana. 20 & 27 — anterior body portion, dorsal view; 21 — segments 10 and 11, dorsal view; 22 — midbody segment, caudal view; 23, 24, 29 & 30 — caudal body end, dorsal, ventral, dorsal, and dorsal views, respectively; 25 — paratergite 16, ventral view; 28 — segment 10, dorsal view; 26 — right gonopod, caudal view; 31 — gonopods, front view. Scale bars 0.1 mm (20–26) and 1.0 mm (27–29), others drawn not to scale. After Chamberlin [1923c] and Maurius [1981], and original.

Рис. 20–31. *Poratia mulegensis* (Chamberlin, 1923) (20–26), самец из Гваделупы, *Docodesmus granulofrons* (Chamberlin, 1918) (27–29), голотип-самка из Гаити (ориг.) и *Poratia sequens* (Chamberlin, 1923) (30 & 31), голотип-самец из Гайаны. 20 и 27 — передняя часть тела, сверху; 21 — 10-й и 11-й сегменты тела, сверху; 22 — среднетеловишный сегмент, сзади; 23, 24, 29 и 30 — задний конец тела, соответственно сверху, снизу, снизу и сверху; 25 — 16-й паратергит, снизу; 28 — 10-й сегмент тела, сверху; 26 — правый гоноподий, сзади; 31 — гоноподии, спереди. Масштаб 0,1 (20–26) и 1,0 мм (27–29), прочие без масштаба. По Chamberlin [1923c] и Maurius [1981], прочие — оригинальные рисунки.

bifid terminally (one of the branches being an inconspicuous solenomerite), at midway with a median spiniform process and a lateral lobe (Figs 3, 4, 9, 10). Vulva roundish, apparently reduced due to thelytoky (Figs 11 & 12) [Adis et al., 1981]. Body 4.5–6 mm long, 0.5–0.8 mm wide, usually females a little larger than males.

RANGE: Obligatory hothouse-dweller in Western Europe (parthenogenetic), but free-living at least in the southern U.S.A., U.S. Virgin Islands and Java, maybe also in Panama and Costa Rica. Female specimens have been collected from a North American hothouse, i.e. Lincoln Conservatory, Cook County, Chicago, Illinois, U.S.A.

*Poratia mulegensis* (Chamberlin, 1923), **comb.n.**  
Figs 20–26.

*Treseolobus granulofrons* Chamberlin, 1918 (partim!): 221. Female holotype from Jacmel, Haiti, deposited at MCZ 4477 (= *Docodesmus granulofrons* (Chamberlin, 1918), **comb.n.**). Paratypes from the same locality, deposited in MCZ 4478, but apparently lost.

*Xerodesmus mulegensis* Chamberlin, 1923a: 403, **comb.n.** Female holotype from Baja California, Mexico, deposited at CAS, examined.

*Dominicodesmus geophilus* Chamberlin, 1923b: 189. Female holotype, subadult from the Dominican Republic, deposited at the MCZ 5215, apparently lost, respective vial at MCZ is empty. Loomis [1934: 54] erroneously synonymized *D. geophilus* with *Treseolobus granulofrons*, based on the examination of female paratype specimens of *granulofrons* and placed it in *Psochodesmus*.

*Psochodesmus granulofrons* — Loomis, 1934.

*Kapyrodesmus mulegensis* — Attems, 1940. Nomen novum for *Xerodesmus*, preoccupied by *Xerodesmus* Cook, 1896.

*Poratia granulofrons* — Loomis, 1961, 1964; Hoffman, 1999.

*Poratia* (?) *granulofrons* (sic!) — Mauriès, 1981.

REMARKS: The female holotype of *Treseolobus granulofrons* is not misplaced, as erroneously stated by Loomis [1934: 55], and is still available at MCZ. Furthermore, this specimen is by no means a *Poratia* but it seems to actually belong to *Docodesmus* Cook, 1896, a genus particularly prolific in the Caribbean and widespread throughout the Neotropics [Golovatch, 1997, 1999]. Figures 27–29 are provided to substantiate this allocation: *Docodesmus granulofrons* (Chamberlin, 1918), **comb.n.** Apparently, the type series of *granulofrons* contained at least two genera and two species, with (some of) the now lost paratypes re-examined by Loomis [1934] obviously representing a *Poratia*. To avoid nomenclatural confusion and to properly allocate the *Poratia* species involved, the specific epithet *geophilus* could be resurrected from synonymy if it were not for still another older synonym available: *Xerodesmus mulegensis* Chamberlin, 1923. Indeed, whereas the name *mulegensis* dates July 1923, that of *geophilus* is of December 1923.

*Xerodesmus mulegensis* was described as the type of *Xerodesmus* Chamberlin, 1923 but, as the latter genus is a junior homonym of *Xerodesmus* Cook, 1896, a replacement name, *Kapyrodesmus*, was proposed [Attems, 1940].

DIAGNOSIS: *Poratia mulegensis* can be distinguished from all other congeners by a body composed of 19 segments, paraterga very short; distinctly flattened midbody **PM** and **DL**, only a single posteromarginal lobulation, four weak lateromarginals on the paraterga 16–18; and gonopods (Fig. 26) simple, uniramous, with a minor hyaline fringe at midway but without solenomerite branch.

Body ca. 4–5 mm long, in male 0.6 mm wide, females apparently a little larger than males; body with 19 segments, four lateral lobulations on paraterga 16–18 (Figs 23–25), midbody **PM** and **DL** relatively poorly developed, (sub-) truncate (Figs 21 & 22), not only **PM1** and **PM2** but also **PM3** on penultimate segment more or less distinctly separated medially (Fig. 23); gonopods simple, uniramous, with a minor hyaline fringe at midway but without solenomerite branch (Fig. 26) [Mauriès, 1981].

COMMENTS: The female holotype of *mulegensis* is in poor condition, partly deformed, broken into three pieces. Altogether, body with 19 segments, not 20 as stated in the original description [Chamberlin, 1923a]. Chamberlin must have miscounted the segments, as revealed by a complete, normal pore formula. Despite the poor condition, the holotype of *mulegensis* proves to bear all the main traits characteristic of a *Poratia*, viz., the ten deeply incised and somewhat

elevated lobulations at the front edge of the collum, the three lobulations each on the paraterga 2–15, and four poorly developed lobulations on paraterga 16–18. The midbody **PM** and **DL** tubercles are quite flattened dorsally, far better developed and higher on segments 17 and 18, but generally somewhat higher than depicted in Figs 20–23, with **PM3** on penultimate metatergite separated, though not as strongly as is shown in Fig. 23.

This diagnosis matches pretty well that of what Loomis [1934, 1961, 1964] believed to be characteristic of *granulofrons* (see also Table below). Whereas the original description of *granulofrons* as given by Chamberlin [1918] is obviously a composite (since the type series may have contained two different species and genera), Loomis' [1934, 1961, 1964] records of and brief diagnostic notes on *mulegensis* referred to as *granulofrons* in the Caribbean and Panama seem reliable.

The same concerns the first description of the male sex by Mauriès [1981]. Both Loomis [1934] and Mauriès [1981] only reported on material of a single species of *Poratia* occurring on Guadeloupe. Mauriès' paper presents a thorough survey of the millipede fauna of Guadeloupe, and that the *Poratia* material he had at hand amounted to over 50 specimens, it would seem more than likely that only *P. mulegensis* lives on that island.

RANGE: Mexico (Baja California), ?Panama, Haiti, St. Eustatius, Guadeloupe, St. Kitts, Antigua and Trinidad.

*Poratia sequens* (Chamberlin, 1923)  
Figs 30 & 31.

*Tidopterus sequens* Chamberlin, 1923c: 420. Male holotype from British Guiana, type specimen presently neither at AMNH nor USNM, not examined.

*Psochodesmus sequens* — Loomis, 1934.

REMARKS: Loomis [1934: 53] first synonymized *Tidopterus* under *Psochodesmus*, and discussed similarities between *sequens* and *Psochodesmus crescentis*, basing his remarks on illustrations and description by Chamberlin, not on the examination of specimens [Loomis, 1934: 55]. Later [Loomis, 1961: 97], he synonymized *Tidopterus* under *Poratia*, but made no comments regarding the identity of the only species in this genus, *Tidopterus sequens*.

DIAGNOSIS: Body with 20 segments, four lateral lobulations on paraterga 16–19, **PM1** and **PM2** on penultimate segment fused basally (Fig. 30); gonopod telopodite branching distally into a long flagelliform solenomerite and a shorter process (Fig. 31) [Chamberlin, 1923c]. The holotype male is about 6 mm long. Number of posteromarginals unknown.

RANGE: Known only from Guyana.

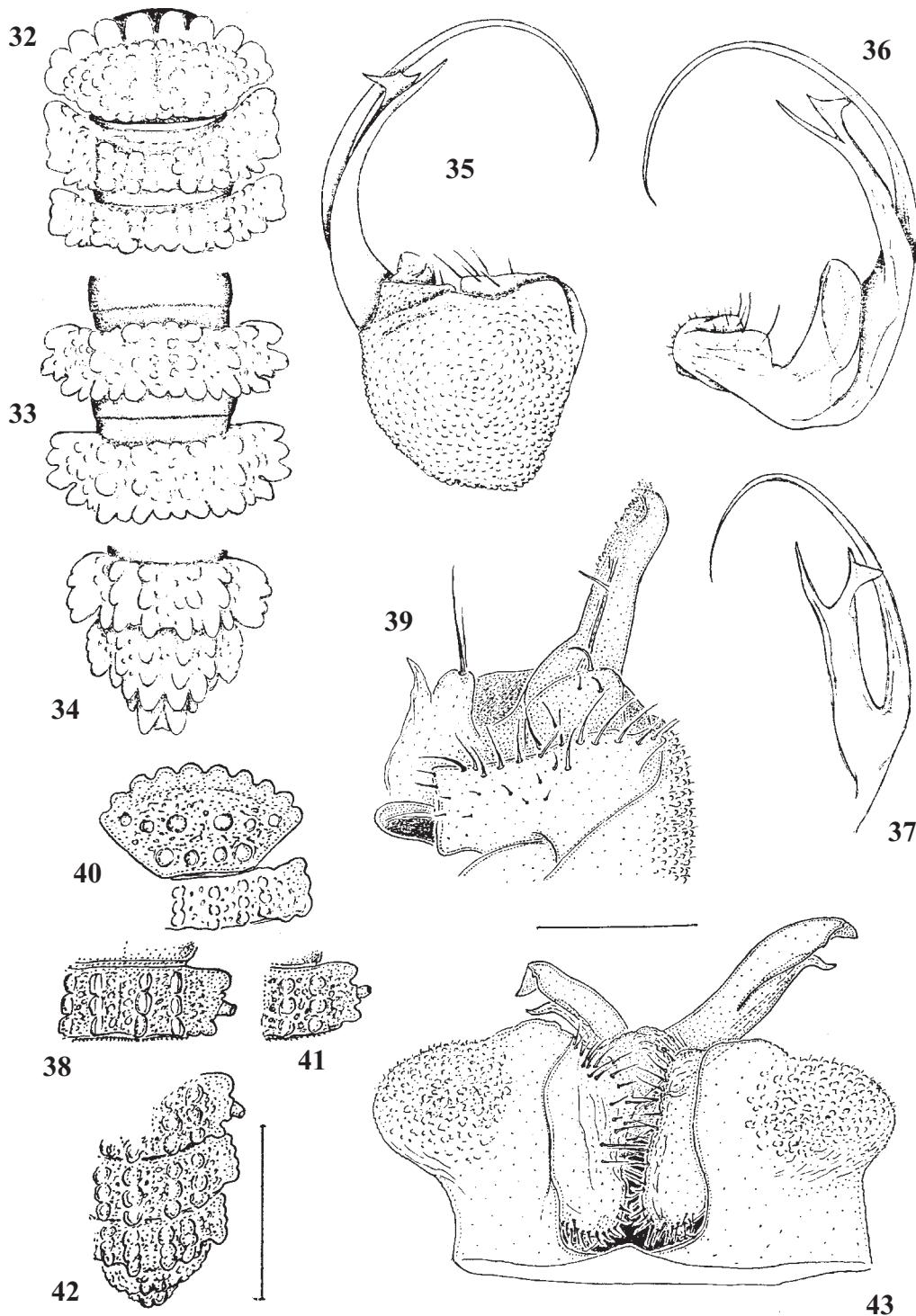
*Poratia insularis* (Kraus, 1960), **comb.n.**  
Figs 32–37.

*Muyudesmus insularis* Kraus, 1960: 251. Male holotype from Peru, deposited at SMF 3809; 1 male, 4 female paratypes, SMF 3811–2, examined by the senior author; 6 males paratypes Museum Braunschweig, not examined.

REMARKS: This species remains only known from Muyu Island in Amazon River near Iquitos, Peru, basically an area where *P. obliterated* appears to be the most common and widespread congener [Adis et al., 2001]. Furthermore, both *P. insularis* and *P. obliterated* co-occur on Muyu Island [Kraus, 1960].

DIAGNOSIS: *Poratia insularis* can be distinguished from all other congeners by the combination of the following





Figs 32–43. *Poratia insularis* (Kraus, 1960) (32–37), male paratype from near Iquitos, Peru, *P. fossata* Loomis, 1964, male holotype from Panama (orig.) (38 & 39), and *P. salvator* sp.n., male holotype from El Salvador (orig.) (40–43). 32 & 40 — anterior body portion, dorsal view; 33 — segments 10 and 11, dorsal view; 34 & 42 — caudal body portion, dorsal view; 38 & 41 — right half of segment 10, dorsal view; 35 — right gonopod, lateral view; 36, 37 & 39 — left gonopod, mesal, sublateral and subcaudal views, respectively; 43 — gonopods, front view. Scale bars 0.1 mm (38, 40–42) and 1.0 mm (39 & 43), others drawn not to scale. After Kraus [1960] and original.

Рис. 32–43. *Poratia insularis* (Краус, 1960) (32–37), паратип-самец из-под Икитоса (Перу), *P. fossata* Лумис, 1964, голотип-самец из Панама (ориг.) (38 и 39), и *P. salvator* sp.n., голотип-самец из Сальвадора (ориг.) (40–43). 32 и 40 — передняя часть тела, сверху; 33 — 10-й и 11-й сегменты тела, сверху; 34 и 42 — задняя часть тела, сверху; 38 и 41 — правая половина 10-го сегмента тела, сверху; 35 — правый гоноподий, сбоку; 36, 37 и 39 — левый гоноподий, соответственно изнутри, примерно сбоку и почти сзади; 43 — гоноподии, спереди. Масштаб 0,1 (38, 40–42) и 1,0 мм (39 & 43), прочие без масштаба. По: Краус [1960], прочие — ориг. рисунки.

Table 1. Morphological characters of *Poratia* species.  
Таблица 1. Морфологические признаки видов *Poratia*.

Species/ Characters	Body segments	Lateral lobulations on paraterga 16–18(19)	PM1 and PM2 on penultimate segment medially at base	PM and DL	Gonopod telopodite
1. <i>digitata</i>	19	3(4)	separated	rounded	rather elaborate, solenomerite inconspicuous
2. <i>fossata</i>	20	4	separated, even PM3 separated	ridge-like	rather simple, bifid, hyaline fringe long, solenomerite absent
3. <i>mulegensis</i>	19	4	separated, even PM3 separated	strongly flattened	simple, an abbreviated hyaline fringe at midway, solenomerite absent
4. <i>insularis</i>	19	4	separated	rounded	rather simple, divided distally into a very long solenomerite and a shorter bifid process
5. <i>obliterata</i>	20	4	separated	rounded	simple, solenomerite absent
6. <i>salvator</i>	19	4	separated	rounded	rather simple, divided distally into a shorter solenomerite and a longer larger process
7. <i>sequens</i>	20	4	in touch	rounded	rather simple, divided distally into a very long solenomerite and a short process

characters: body with 19 segments, four lateral lobulations on paraterga 16–18 (Fig. 34), two posteromarginals (Figs 32, 33), **PM** and **DL** rather distinct throughout (Figs 32–34), **PM1** and **PM2** on penultimate segment distinctly separated, only **PM3** in touch at base medially (Fig. 34); gonopods with a long flagelliform solenomerite and a bifid terminal process (Figs 35–37). Male about 5 mm long and 0.7 mm wide [Kraus, 1960].

RANGE: Only known from the type locality.

*Poratia obliterata* (Kraus, 1960), **comb.n.**  
Figs 5–8, 13–19.

*Muyudesmus obliteratus* Kraus, 1960: 253. Male holotype from Muyu Island near Iquitos, Peru, deposited in SMF 3813; 2 male paratypes, same locality, deposited in SMF 3814, 9 males paratypes, same locality, deposited in SMF 3815, examined by the senior author. 25 male and female paratypes, same locality, Museum Braunschweig, not examined.

*Poratia digitata* — Silvestri, 1923; Schubart, 1934 (partim?), 1947a, 1947b; Attems, 1940.

*Muyudesmus obliteratus* — Adis et al., 2001.

*Poratia obliterata* — Shelley & Golovatch, 2001.

REMARKS: This species has just been shown to only comprise bisexual populations throughout Amazonia (Peru, Colombia and Brazil) and in Costa Rica [Adis et al., 2001; Shelley & Golovatch, 2001] but it also has a parthenogenetic form introduced at least to a couple of European hothouses [Adis et al., 2001]. In the hothouse of Kiel Botanic Garden, Germany as well as in the hothouse (= Serre) of the Jardin des Plantes, Muséum national d'Histoire naturelle in Paris, France, both *P. obliterata* and *P. digitata* appear to be coexisting. Near Iquitos, *P. obliterata* co-occurs with *P. insularis* [Kraus, 1960]. The status of the form recently reported from an open habitat in Georgia, southern U.S.A. remains to be clarified but one could rather expect its being parthenogenetic [Shelley & Golovatch, 2001].

DIAGNOSIS: Body with 20 segments, four lateral lobulations on paraterga 16–19 (Figs 7 & 15), two subequal

posteromarginals, midbody **PM** and **DL** rather inconspicuous (Fig. 14), more distinct both in anterior and caudal body parts (Figs 7 & 13), **PM1** and **PM2** on penultimate segment distinctly separated, only **PM3** in touch at base medially (Fig. 15); gonopod telopodite like a rather long, slender, flattened shaft without a solenomerite branch (Figs 8, 16, 17).

Body 5–7 mm long, parthenogenetic females tending to be larger than bisexual ones. Width of adult males 0.63–0.70 mm, of adult females 0.67–0.77 mm. [Kraus, 1960; Adis et al., 2001]. Vulva quite elaborate in bisexual populations (Fig. 18) and strongly reduced in thelytokous ones (Fig. 19) [Adis et al., 2001].

RANGE: Amazon region in Peru, Brazil and Colombia, also Costa Rica and Panama; hothouses in Germany (Kiel) [Adis et al., 2001] and France (Paris) [Adis & Golovatch, unpublished].

MATERIAL examined: Brazil, Pará (Schubart's [1947a] specimens; Museo de Zoologia, Universidade de São Paulo). Numerous specimens (kept in the laboratory) from near Tabatinga and Manaus, Brazil as well as at Nauta, Peru, deposited in the Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil; Museo Nacional de Historia Natural, Lima, Peru, MHNG; Zoological Museum of the Moscow University, Russia; Zoologisk Museum, University of Copenhagen, Denmark, and SMF. Virginia Museum of Natural History: Costa Rica: Cairo, Dec. 7, 1937, H. Loomis — 2 ♂♂, 5 ♀♀, 2–3 juv. and fragments; det. Loomis as *Poratia digitata*. Cairo, Dec. 5, 1937, H.F. Loomis — 1 ♂, 1 ♀; det. Loomis as *Poratia digitata*. Gamboa, Apr. 13, 1925, no collector's name — 3 ♂♂, 2 ♀♀, 1 juv. det. Loomis as *Poratia digitata*. Panama, Taboga Island, 7-15-1923, O.F. Cook & H.F. Loomis — 1 subad.♀ (with 19 segments), labeled "Psochodesmus geophilus (Chamb.)" det. Loomis.

*Poratia fossata* Loomis, 1964  
Figs 38 & 39.

*Poratia fossata* Loomis, 1964: 74. Male holotype from Panama and juvenile paratype, deposited FMNH; examined.

DIAGNOSIS: Body with 20 segments, four lateral lobulations on paraterga 16–19, **PM1** and **PM2** on penultimate

segment clearly separated, only **PM3** in touch at base medially, both **PM** and **DL** distinctly elevated and comb-like due to strong lateral compression (Fig. 38); one posteromarginal, gonopod telopodite like a relatively long, slender, simple, flattened shaft with a caudal spine-like process at midway but without a solenomerite, indistinctly bifid distally and with a hyaline fringe on caudal side (Fig. 39).

Male: about 4.5 mm long and 0.6 mm wide. Head: see Fig. 5 [cf. Loomis, 1964].

RANGE: Known only from Panama.

*Poratia salvator* sp.n.

Figs 40–43.

Holotype: ♂ (deposited in FSCA), El Salvador, 1 km N Quenzaltepeque, dirt under a coffee tree, 1.08.1961; leg. Irwin-Berkeley.

Paratype: ♀ (deposited in FSCA), same locality, together with holotype.

DIAGNOSIS: Differs from congeners by probably the smallest body size and its peculiar gonopod traits (see also Table 1 and Key below).

NAME: Derives from the terra typica.

DIAGNOSIS: Body with 19 segments, dorsal surface sculpture similar to *P. digitata* (Figs 40–42), but tubercles not as high. Four weakly developed lateromarginals on the short paraterga 16–18 instead of three (Fig. 42), lateromarginals much deeper incised than in *P. digitata*; a single posteromarginal.

Gonopods (Fig. 43) relatively simple, telopodite branching distally into a relatively stout, subflagelliform solenomerite and a larger and somewhat longer terminal process.

Length ca. 3.5 mm, width 0.5 mm both in holo- and paratype. Color uniform yellow-brownish, rather flavous. Body with 19 segments (holotype, complete), while paratype fragmented, apparently incomplete, with 18 body segments.

RANGE: Only known from type material.

KEY TO *PORATIA* SPECIES:

- 1(2) Adults with 19 body segments ..... 3.  
 2(1) Adults with 20 body segments ..... 9.  
 3(4) Usually 3 lateral lobulations on paraterga 16–18, 4 occasionally at individual paraterga. Gonopod with 2 subterminal projections, one of the branches being a minute solenomerite (Figs 3, 4, 9, 10) ..... *P. digitata*  
 4(3) Always 4 lateral lobulations on paraterga 16–18. Solenomerite either conspicuous or wanting ..... 5.  
 5(6) Larger dorsal tubercles on metaterga (**PM** and **DL**) considerably flattened, subtruncate (Figs 20–22). Even **PM3** on penultimate metatergite rather clearly separated. Solenomerite wanting, gonopod telopodite subacuminate (Fig. 26) ..... *P. mulegensis*  
 6(5) **PM** and **DL** always rounded, convex, easily traceable. **PM3** on penultimate metatergite in touch at base. Solenomerite branch conspicuous, gonopod telopodite bifid/biramous ..... 7.  
 7(8) Solenomerite flagelliform, much longer than terminal process of gonopod telopodite. Peru (35–37) .....  
 ..... *P. insularis*  
 8(7) Solenomerite subflagelliform, somewhat shorter than terminal process of gonopod telopodite. El Salvador (Fig. 43) ..... *P. salvator*  
 9(10) **PM** and **DL** unusually strongly compressed on sides, high (Fig. 38). Gonopod with a stout telopodite, tip poorly bifid, hyaline caudal fringe conspicuous (Fig. 39). Panama ..... *P. fossata*

- 10(9) **PM** and **DL** usual, rounded, more or less convex, not so high, sometimes rather inconspicuous on midbody metaterga. Gonopod relatively slender and complex, then branching at midway, or very simple, a little enlarged distally, uniramous ..... 11.  
 11(12) Even **PM1** and **PM2** on penultimate metatergite in touch medially. Gonopod telopodite branching distally, with solenomerite far longer than terminal process (Fig. 31). Guyana ..... *P. sequens*  
 12(11) **PM1** and **PM2** clearly separated at base medially. Gonopod telopodite unipartite, solenomerite branch wanting (Figs 8, 16, 17). Bisexual in Amazonia, ?Panama and Costa Rica; thelytokous in European hothouses and likely also in southern U.S.A ..... *P. obliterated*

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