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Abstract. Ptyoiulus Cook 1895, the dominant parajulid diplopod genus in the eastern United States (US), comprises two species – P. impressus (Say 1821), with a slanted, flared, circumferentially entire, and marginally serrate apical calyx on the anterior gonopod coxal process, and P. montanus (Cope 1869), n. comb., with a smooth, upright, cupulate calyx that is open caudad and coaxial with the process' stem. The genus occupies a broad area between the Mississippi River and Atlantic Ocean extending from southern New England, Ontario, and Michigan to the Florida Panhandle and four small disjunct ones – from Montreal, Québec, to northern Vermont, along southwestern Lake Michigan in Wisconsin and Illinois; northeastern/eastcentral Arkansas, primarily in Crowley’s Ridge physiographic feature and beside the “booth” of Misouri; and a point locality in northeastern Louisiana just south of the Arkansas line. A male from Chester County (Co.), Pennsylvania, is designated as the neotype of Julus impressus, as is one from Durham Co., North Carolina, for J. montanus. As both species inhabit Montgomery Co., Virginia, the type locality of J. montanus, we exercise the right of first reviser, conserve the latter name, and assign it to the species with the smooth, cupulate, and coaxial calyx. We also exercise first reviser rights and assign Parajulus ectenes Bollman 1887 to this form, thereby relegating it to synonymy under Ptyoiulus montanus. Other new synonymies include Ptyoiulus georgiensis Chamberlin 1943 under P. impressus and P. coveanus Chamberlin 1943 under P. montanus. Both Ptyoiulus and P. impressus are projected for Delaware and Rhode Island and newly reported from Québec, Connecticut, District of Columbia, Maryland, Mississippi, South Carolina, Vermont, West Virginia, and Wisconsin, and the genus and species, respectively, are newly documented from Louisville and Arkansas; P. montanus is newly cited from Alabama, Arkansas, Georgia, Mississippi, and South Carolina. Ptyoiulus impressus occupies every state except perhaps Louisiana and is the only species in areas that were inundated during the Cretaceous and glaciated during the Pleistocene; by contrast, P. montanus inhabits a relatively narrow east/west transect through the center of the generic range. Their distribution patterns suggest an old species, montanus, being actively displaced by the younger and more successful impressus. The decurvature of the epiproct in uroblaniulinines appears to increase with age and developmental stage. A key is presented to parajulid family-group taxa in the US and Canada east of the Rocky Mountains.

Key Words. Aniulini, Bollmaniulini/Bollmaniulus, calyx, ectenes, Florida, North Carolina, Parajulus, Tennessee, Uroblaniulinini

Introduction

Parajulid millipeds occur along the Atlantic Coast of North America from James Bay, Ontario, southern Québec, and New Brunswick, Canada, to the southern tip of peninsular Florida, United States (US) (Causey 1974; Hoffman 1999; Shelley 2000a, 2008; Shelley and Golovatch 2011). Three family-group taxa are represented – Aniulini, Uroblaniulinini, and Ptyoiulinae – the last dominant in the northern/northeastern US, with a single component genus, Ptyoiulus Cook 1895, and known or projected for every state from Vermont southward. A few mostly general records exist for Ontario, Canada, that apparently lack vouchers; we question their authenticities but report two new Ontario localities and the first from Québec. More Canadian samples should seemingly be available given the amount of sampling in the projected area in Ontario (Fig. 4, 14).
Ptyoiulus is readily distinguished by the pilose caudal rings and paraprocts and by the straight, spiniform epiproct that overhangs and clearly extends beyond the caudal paraproctal margins (Fig. 1–3; Blake 1931, Fig. 2 in part). Aniulini and Uroblaniulini have at most only scattered tergal setae; the

Figure 1–3. Pilosity and epiproct variation on caudalmost rings of Ptyoiulus impressus. 1) Specimen from Morgan Co., Ohio. 2) Specimen from Allen Co., Kentucky. 3) Specimen from Leon Co., Florida. e, epiproct; h, hypoproct; lp, left paraproct.

Figure 4. Distributions of Ptyoiulus/Ptyoiulinae plotted against the maximal extent of the Western Interior Seaway during the Cretaceous Period, Mesozoic Era. All land areas shown are in the eastern land mass, Appalachia, which was separated from western Laramidia by the vertical, latitudinal arm of the Seaway (not shown), which segregated Ptyoiulus from bollmaniulines in Laramidia but is irrelevant to Ptyoiulus itself. The Seaway spread eastward south of Appalachia and when it receded, P. impressus spread southward into the formerly inundated area. 1, large, contiguous main range area. 2, small, disjunct northernmost population extending from Montreal, Québec, to northern Vermont. 3, disjunct population along the southwestern coast of Lake Michigan. 4, disjunct area in northeastern/eastcentral Arkansas. 5, point locality in northeastern Louisiana vouchered by females. The transect denoted by the red lines near the center of the distribution is the band occupied by both P. montanus and P. impressus; the latter occurs alone to the north and south.
epiproct in the former is usually shorter than or only barely overhangs the paraprocts; and the structure is a strongly decurved hook in adult uroblaniulinines (Blake 1931, Fig. 2 in part) and slants gently ventrad, particularly apically, in juveniles. From RMS' sampling and field observations, the degree of epiproctal slanting and/or falcateness in uroblaniulinines increases with age and developmental stage. A parajulid in eastern North America with a seemingly linear epiproct and only scattered segmental hairs is an immature uroblaniuline, not a Ptyoiulus, whose caudal rings are noticeably pilose in even early instars.

Long, dark, and cylindrical, Ptyoiulus is common in the aforementioned area between the Atlantic Coast and Mississippi River, and it spreads discontinuously westward to southeastern Wisconsin, the Mississippi River from southern Illinois to southern Tennessee, and northeastern Arkansas, with a point locality in northeastern Louisiana near the Arkansas border represented by females (Fig. 4). Causey (1974) proposed a familial taxonomy, but Hoffman (1980) noted that the subfamily Ptyoiulinae seemed superfluous with only one component tribe, Ptyoiulini, that clearly is such. We recognize only two species in the genus: Ptyoiulus impressus (Say 1821) and Ptyoiulus montanus (Cope 1869) n. comb., originally assigned to Julius L. These species are distinguished primarily by the configuration and orientation of the laminate apical calyx on the anterior gonopod coxal process, which is best viewed in caudal aspect. The structure slants laterad, is discontinuous with the stem of the process, circumferentially entire, flared, and usually marginally serrate in the dominant form, for which impressus is the oldest available name, and is upright, coaxial with the stem, cupulate, open caudad, and marginally smooth in the form to which we assign montanus (Fig. 5–6). Proposed 195 and 147 years ago, the types of J. impressus and J. montanus, respectively, have long been lost, and neotype designations are necessary. According to Say's original account, the type specimen of J. impressus was in his “cabinet,” but he sent some types to William Leach in London, and some of these are now in the Natural History Museum (Beccaloni 2012). RMS visited this institution in 1997, searched for Say’s types, and that of J. impressus was not there, nor is it cited in the museum’s on-line Arachnida and Myriapoda database. Consequently, in accord with Chamberlin and Hoffman (1958) and Hoffman (1999), we designate as Neotype a male in the ANSP (acronyms below) from Chester County (Co.), Pennsylvania, adjacent to Philadelphia, where Say spent much of his adult life. Appropriately, the specimen was collected by H. C. Wood, the first US author to publish comprehensively on diplopods.

The situation with Julius montanus Cope 1869 is not so easily resolved. The type was taken at an unknown site in Montgomery Co., Virginia, which today harbors both species of Ptyoiulus. Lacking both a gonopod illustration and a meaningful description, it is impossible to determine which species Cope had, but to credit him and conserve his name, we exercise the right of first reviser and designate as Neotype a male in the FSCA from Durham Co., North Carolina, with the cupulate, coaxial calyx, since
the Montgomery Co. male, illustrated in fig. 15, 22, was misplaced and cannot now be located. Such action also allows us to synonymize the second oldest name for this form, Parajulus euctenes Bollman (1887a), and remove it from nomenclature. Lacking labels and statements of typification, the original male and female are necessarily syntypes, but the former individual is also lost. They were from Chapel Hill, Orange Co., North Carolina, and the cupulate, coaxial form is the only species in central North Carolina. In comparing it to Pt. impressus, Bollman noted the “much more slender” body form and that the epiproct does not pass “beyond (the) anal valves” or paraprocts, suggesting an aniuuline. However, he also stated that the paraprocts “are pilose,” the condition in Ptyoiulus. Though citing it as a parajulid of “uncertain generic position or validity,” Hoffman (1980, 1999) speculated that Pa. euctenes may be a senior synonym of the sympatric aniuuline, Aniusius orientalis Causey 1952, based on the body form characterization and the fact that its epiproct does not extend beyond its lightly hirsute paraprocts. However, two aniuulines inhabit central North Carolina, the other being Oriulus venustus Wood 1864 (=Aniusius carolinensis Shelley 2001) (Shelley 2000b, 2001, 2002), so if Pa. euctenes does refer to an aniuuline, there is no way to infer which species from Bollman’s (1887a) description. Hoffman (1980, 1999) did not mention it, but Bollman could also have been correct; he could have had the ptyoiuline in central North Carolina, which is far more abundant than either aniuuline, because he did mention pilose paraprocts. Bollman’s (1887a) description is thus ambiguous, citing features more characteristic of an aniuuline than Ptyoiulus and vice versa, but Hoffman selectively latched onto the subjective comment about “much more slender body form” and ignored the objective one about pilose paraprocts. We think he overemphasized what could have been an off-hand comment to the exclusion of the rest of the account, but without gonopod illustrations and the male syntype, it is impossible to determine the identity of Pa. euctenes with certainty, and we cannot designate a neotype because the female syntype still exists at the NMNH (see following list of acronyms). Additionally, there is no way of determining whether the male and female syntypes truly were conspecific; they could have represented two of the parajulids in central North Carolina with the existing female syntype differing from the lost male! The identity of Pa. euctenes is thus an unsolvable problem, but after 129 years, it is time to act decisively rather than carry the enigma even longer. Consequently, we again exercise first reviser rights, assume Bollman was correct because he did compare Pa. euctenes to Pt. impressus and did note pilose paraprocts, and formally assign Pa. euctenes to the Ptyoiulus in central North Carolina to which we just assigned Pt. montanus, which holds priority by 18 years. Parajulus euctenes therefore falls in synonymy under Ptyoiulus montanus, n. comb, and disappears from nomenclature.

Causey (1974) placed Ptyoiulus in its own subfamily thereby opposing it to all other parajulid genera. Hoffman (1980, 1999) noted a technical error, but otherwise we tentatively accept her taxonomy, not being competent now to effect changes. We have not yet studied the multitude of western taxa, many species of which are assignable to Bollmaniulus Verhoeff 1926 and the tribe Bollmaniulini (Hoffman 1999). Nonetheless, we think Causey’s action was unjustified because the gonopods of Ptyoiulus and Bollmaniulus exhibit similar configurations, and we interpret the former as the eastern representative that became detached when the Cretaceous Western Interior Seaway segregated it in Appalachia around 100 mya (Fig. 4). Ptyoiulus appears to us to be a bollmaniulinine with a calyx atop the anterior gonopod coxal process, but we defer formal action to our study of Bollmaniulus and other western parajulids, the next project in this series.

In the ensuing accounts, “MM”, “FF”, and/or “juvs.” mean too many individuals to count, and the abbreviation “GSMNP” signifies the Great Smoky Mountains National Park, which straddles the southwestern border between North Carolina and Tennessee. Missing data in locality listings was not provided on vial labels. Because it is less abundant, we provide full locality data for P. montanus; excepting North Carolina and the easternmost counties of Tennessee in/near GSMNP, we provide detailed localities for P. impressus in states where it occurs in six or fewer counties and list the latter for states where it occupies seven or more counties. Because both species seemingly occur side-by-side in western North Carolina and eastern Tennessee, we provide locality citations for all counties in these areas. Repository acronyms are AMNH, American Museum of Natural History, New York, New York; ANSP, Academy of Natural Sciences of Drexel University, Philadelphia, Pennsylvania; CMN, Canadian Museum of Nature, Ottawa, Ontario, Canada; CMNH, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; DAH, private collection of D. A. Hennen, Blacksburg, Virginia; FEM, Frost Entomological Museum, Pennsylvania State University, State College; FMNH, Field Museum of

### Taxonomy

**Order Julida Brandt 1833**

**Family Parajulidae Bollman 1893**

Key to US and Canadian parajulid family-group taxa occurring east of the Rocky Mountains

1. Epiproct short and blunt, not, or only barely, overhanging paraprocts; anterior gonopods with lateral syncoxal processes ................................................................. 2
   — Epiproct moderately long to long, clearly overhanging and extending beyond level of paraproctal margins, apically acuminate; anterior gonopods without lateral syncoxal processes ........ 3

2. Small-bodied to minute parajulids, posterior gonopods with three ventrally directed projections (two in the Mexican genus), solenomere longest; central Colorado to northwestern Arizona, east central Texas, and Nuevo León, Mexico (Shelley and Smith 2016) ................................................................. **Gosiulini Causey 1974**
   — Small-bodied to moderately large parajulids; posterior gonopods usually with two ventrally directed projections, solenomere usually longer; anteromedial margins of 8th male sterna with anteriorly-directed lobes protruding over aperture and usually between gonopods; Alberta and Québec to southern peninsular Florida, the Rio Grande in Texas, southern New Mexico, and southwestern Arizona ............................................. **Aniulini Causey 1974**

3. Caudal rings, paraprocts, and epiproct heavily setose; latter extending directly caudad; Québec and northern Vermont to northern Florida, westward to southeastern Wisconsin, the Mississippi River from southern Illinois to southern Tennessee and northeastern Arkansas ................................................................. **Ptyoiulinae Causey 1974**
   — Caudal rings, paraprocts, and epiproct glabrous or with at most only scattered setae; epiproct either angling slightly ventrad distally (juveniles) or strongly decurved and falcate (late instars and adults); James Bay, Ontario, southern Québec, and western New Brunswick to central Georgia, westward to Illinois ........................................................................... **Uroblaniulini Causey 1974**

**Subfamily Ptyoiulinae Causey 1974**


**Genus Ptyoiulus Cook 1895**

Type species. *Julus (Julus) pensylvanicus* (recte: *pennsylvanicus*) Brandt 1841, by original designation. Gervais (1847, 1859) repeated the original spelling, but Wood (1865) and nearly all subsequent authors (see synonymies under *Ptyoiulus impressus*) have employed the “two n” spelling. The earliest editions of the International Code of Zoological Nomenclature did not allow such corrections even for unequivocal misspellings; Pennsylvania, after all, is named for William Penn, with the two “n” spelling. However, the fourth edition of the Code, whose provisions took effect on 1 January 2000 and supersede those in previous editions, allows such corrections. Article 33.2.3.1 states “when an unjustified emendation is in prevailing usage and is attributed to the original author and date it is deemed to be a justified emendation,” and article 33.3.1 states “when an incorrect subsequent spelling is in prevailing usage and is attributed to the publication of the original spelling, the subsequent spelling and attribution are to be preserved and the spelling is deemed to be a correct original spelling.” Consequently, “*pennsylvanicus*” is now a justified emendation and the correct spelling for the specific name of the type-species (Shelley and Golovatch 2015).

Descriptive notes. Adults long-bodied, upwards of 65 rings including collum and epiproct. Anterior rings lightly setose, gradually or abruptly becoming more setose and distinctly more so on caudal rings, epiproct, and paraprocts. Epiproct setose and spiniform, overhanging paraprocts and extending varying lengths beyond their caudal margins. Male first legs greatly enlarged, strongly forcipulate (Blake 1931, fig. 2 in part), clearly more so than in other eastern family-group taxa. Telopodites of both pairs of gonopods lying entirely outside of aperture *in situ*, angling caudal over body and extending between leg pairs to level of rings 9–10. Anterior gonopod (Fig. 5–6) comprising long, clavate, and distally hirsute telopodite and longer, glabrous coxal process terminating in laminate apical calyx, latter either slanting laterad, circumferentially entire, and marginally serrate or coaxial with stem of process, marginally smooth and cupulate on medial, lateral, and anterior surfaces (open caudad) (Fig. 5–6); lateral syncoxal process absent. Posterior gonopod subacicular, inconspicuous, closely appressed to medial surface of stem of anterior gonopod coxal process, comprising two branches -- a long, slender major branch and shorter, spiniform, secondary branch arising at 1/4–1/3 of length of former; major branch curving basally then narrowing smoothly and continuously to scoop-like flange around 7/8 length, curving to acuminate tip distal to flange.

Distribution. The distributions of Ptyoiulinae and *Ptyoiulus* are the same, but we place our commentary with the genus because of doubts as to the merits of the subfamily. Past range descriptions include “Appalachian region from New York southward to Georgia, west to Illinois” (Chamberlin and Hoffman 1958), “centered in the Appalachian Mountains, extending north into southern Ontario, west to Arkansas, and south to Florida” (Causey 1974, for the redundant Ptyoiulini), and “Eastern North America” (Hoffman 1999).

*Ptyoiulus* occupies five areas (Fig. 4, 14) -- a large one covering most of the US east of the Mississippi River, and four small, detached areas, two east and two west of this watercourse, one of the latter being a point locality. Overall, the known and projected generic range extends, north-south, from Montreal, Québec, to northern Florida and the Gulf Coast of the Panhandle; east-west, it spreads from Plymouth Co., Massachusetts, Currituck and Wilmington, North Carolina, Charleston, South Carolina, and Savannah, Georgia, to the southwestern shoreline of Lake Michigan, northeastern/eastcentral Arkansas, and the northeastern periphery of Louisiana. The known and projected range encompasses parts of two Canadian provinces, Ontario and Québec, and 27 US states and the District of Columbia, including all or essentially all of the following 16 listed from north to south: Rhode Island (projected), Connecticut, New Jersey, Pennsylvania, Ohio, Indiana, Delaware (projected), Maryland, West Virginia, Kentucky, Virginia, North Carolina, Tennessee, South Carolina, Georgia, and Alabama. The only states east of the Mississippi for which *Ptyoiulus* is neither known nor projected are Maine and New Hampshire; the only states west of the Mississippi where the genus either occurs or is projected are Missouri (projected for the “bootheel”), Arkansas, and Louisiana. *Ptyoiulus* is dominant in the southern Appalachian Mountains.

In Fig. 4, the main area is number “1” and the detached ones are numbers 2–5. The first extends, north - south, from Boston, Massachusetts, Lake Ontario and the vicinities of Orillia, Ontario, and Flint, Michigan, to the Florida Panhandle; east - west, it extends from the Atlantic Ocean from Boston...
to Savannah to northwestern Indiana, the Mississippi River from southern Illinois to southern Tennessee, and 2/3 of the breadth of Mississippi. Maximal dimensions, both north/south and east/west, are around 1,508.0 km (942.5 mi). The detached areas are as follows:

(2). Montreal, Québec, to Franklin/Chittenden cos. in northern Vermont; length around 136.0 km (85.0 mi). We combine Montreal with the northernmost US sites for both the genus and *P. impressus* because the city is closer to them than to the nearest Canadian locality, Orillia, Ontario.

(3). Along the southwestern margin of Lake Michigan from Milwaukee, Wisconsin, to Lake Co., Illinois, north of Chicago, a distance of some 83.0 km (50.0 mi). We do not know how far inland this area extends.

(4). From the northeastern corner of Arkansas, and doubtlessly in the adjacent Missouri “booteel,” to Cleburne Co., eastcentral Arkansas, a distance of 193.3 km (120.8 mi). The sites in Clay and Greene cos., adjacent to the “booteel,” are in Crowley’s Ridge physiographic feature, which may have originated as an island between the Mississippi and Ohio Rivers that became a ridge of low hills on the west side of the former after their courses changed (Shelley et al. 2012). Consequently, these populations of both species lie west of the Mississippi River and are detached from the rest of the generic range located east of the watercourse. The Cleburne Co. locality, the westernmost for the genus and *P. impressus*, is detached to the west-southwest and in the eastern Ozarks, suggesting more widespread occurrence in this region of the state.

(5). A point locality in Morehouse Co., Louisiana, just south of the Arkansas state line, represented only by females. Latitudinally equivalent records in Mississippi, Alabama, Georgia, and Florida suggest that the species is *P. impressus*.

**Remarks.** In general, the species are anatomically stable with insignificant variation, the antithesis of *Gosiulus conformatus* Chamberlin 1940 (Gosiulini), in which the gonopods of every male differ (Shelley and Smith 2016). Such stability reflects age, and *Ptyoiulus* is clearly an old taxon that has occupied today’s North American land mass for a long time, perhaps since ancestral diplopods penetrated Euramerica after Baltica + Avalonia merged with Laurentia in the early Silurian Period, Paleozoic Era, 440 mya (Shelley and Golovatch 2011). *Gosiulus conformatus*, however, is a young species that could not have arisen until after the Western Interior Seaway receded and the Texas lowlands became available for occupation. Insufficient time has passed since it arose for the gonopodal structure to stabilize.

The species of *Ptyoiulus* intermingle in the narrow east-west band of the generic range where *P. montanus* occurs (Fig. 4, red lines; 14). This distribution pattern suggests an old species, *P. montanus*, being displaced by the younger, more adaptable, and ecologically superior *P. impressus*. Sizeable populations of apparently pure *P. montanus* still exist, particularly in the central Carolinas and northeastern Mississippi, and both species seem to be abundant in the GSMNP and the Blue Ridge Mountains of southwestern North Carolina, where they tend to occur side-by-side. Otherwise, only small, isolated, and even point populations of *P. montanus* exist, some surrounded by primarily or exclusively *P. impressus*. The northernmost locality of the former is in Gallatin Co., Illinois, and a moderate-size population of the species occurs along the Ohio River in the southeast of this state. The northernmost population of *P. montanus* in the east is in Montgomery/Giles Cos., Virginia (Fig. 14); *P. impressus* alone occurs from there northward, in formerly glaciated territory and in the following states with definite records plus the District of Columbia: Vermont, Massachusetts, Connecticut, New York, New Jersey, Pennsylvania, Ohio, Indiana, Michigan, Wisconsin, Maryland, West Virginia, and Kentucky although records of *P. montanus* exist in Illinois and Tennessee that border Kentucky. *Ptyoiulus impressus* is also the only species in Florida and the southern halves of Georgia, Alabama, and Mississippi, which were inundated by the Western Interior Seaway in the late Cretaceous, approximately 60–80 mya. That *impressus* alone dispersed that far from refugia to the north testifies to its greater motility and adaptability. It is a substantially more successful species than *P. montanus*, whose populations are gradually dwindling and apparently relictual or nearly so in Virginia, Georgia, and Alabama.
Figures 7–13. Gonopodal variation in *P. impressus*. 7) Distal extremity of right anterior gonopod of neotype, caudal view. 8) The same of male from Rabun Co., Georgia. 9) The same of male from Liberty Co., Florida. 10) The same of male from Leon Co., Florida. 11) The same of male from Greene Co., Arkansas. 12) Right posterior gonopod of male from Rabun Co., Georgia, lateral view. 13) The same of male from Greene Co., Arkansas. Abbreviations as in Fig. 5–6.

*Ptyoiulus impressus* (Say 1821)
Fig. 1–3, 5, 7–13.


*Julus (Julus) pensylvanicus* (Recte: *pennsylvanicus*) Brandt 1841: 102–103.


*Iulus pilosiscutis* Wood 1864: 11.


*Iulus pennsylvanicus*: Wood 1865: 201, fig. 34.

*Julus pensylvanicus*: Preudhomme de Borre 1884: 59.

*Julus pilosiscuta*: Preudhomme de Borre 1884: 59.


Parajulus pilosiscutis: Brölemann 1896: 45, 69 (list, account).


Parajulus pilosiscutus: Bollman 1887b: 44 (list).


Ptyoiulus pennsylvanicus: Chamberlin 1940a: 15, pl. 8, fig. 71–73. Wray 1967: 153.


Type specimens. Male neotype and numerous male, female, and juvenile paraneotypes (ANSP) collected by H. C. Wood on an unknown date at an unspecified locality in Chester Co., Pennsylvania. One female paraneotype (FSCA) collected by J. Oughton. 31 October 1934, in Philadelphia (Fairmont Park), Philadelphia Co., Pennsylvania.

Diagnosis. Calyx of anterior gonopod coxal process (Fig. 5, 7–11) slanting laterad, not coaxial with stem, lamellae flared and circumferentially entire, margins usually irregularly serrate to jagged, occasionally smooth or nearly so.

Color in life. Usually a mottled, subuniform dark brown, gray, or black. According to the vial label, the decapitated female from Wayne Co., Kentucky, exhibited a yellow circumferential band on most rings.

Variation. So many adult males of P. impressus reside in preserved repositories that no human could begin to measure a significant sample, particularly as part of an initial, broad, generic overview with time a factor. In the few individuals with fully-developed gonopods that we did measure, lengths varied from 28.9 to 57.9 mm, and the number of rings, including the collum and epiproct, ranged from 57 to 65. From the caudal end, heavily setose rings extend anteriad for at least 15 rings and even to around midbody, and the change to denser pilosity can be abrupt and noticeable or gradual, with denser and sparser pilosities blending together over a number of rings without a detectable change. Additionally, the denser pilosities may be random, subuniform, patchy, or in sublinear, circumferential rows (Fig. 1–3; Blake 1931, fig. 2 in part). The epiproct is always apically acuminate and always overhangs and extends beyond the caudal paraproctal margins, but this too varies. The structure can be relatively short and narrow, as in fig. 1 of a male from Morgan Co., Ohio; long and spiniform as in fig. 2 of one from Allen Co., Kentucky; or short and stubby, as in fig. 3 of an individual from Leon Co., Florida, and Blake (1931, fig. 2 in part) of a New England male. Gonopodal variation is minimal, subtle, and primarily involves the calyx on the anterior gonopod coxal process (Fig. 5, 7–11), which always slants laterad. However, the angle of the slant varies slightly (compare those of the neotype, Fig. 7, and the male from Greene Co., Arkansas, fig. 11) and some calyces also lean or tilt caudad such that in caudal view one can see slightly inside the structure (Fig. 10 of a male from Leon Co., Florida). In some individuals the caudal flange of the calyx is shorter than the anterior one, so again one can view inside the calyx in caudal aspect (Fig. 9 of a male from Liberty Co., Florida). The degree of serration and the jaggedness of the margins vary dramatically; from lightly and shallowly wavy or nearly smooth (Fig. 8 of a male from Rabun Co., Georgia), to a host of continuous and irregular serrations, as in most individuals that we examined (Fig. 10–11 of males from Leon Co., Florida, and Greene Co., Arkansas, respectively). Posterior gonopods (Fig. 12–13) are subuniform. Relative lengths of the two branches vary slightly as do the lengths and degrees of curvatures of the main projections, the sizes of the subterminal flanges, and the lengths and degree of curvatures of the apices distal to the latter. All these variations are trivial and clearly intraspecific.
Ecology. Say (1821) characterized the habitats as “under stones and in humid situations.” An adult female that we examined from Wayne Co., Kentucky, was decapitated and dead on a trail. Habitat notations on vial labels include “under small pieces of 2x4s in oak litter,” “yellow pan trap,” “under stove in woods,” “fungus & under rock,” “upland forest,” “ground cover in woods,” “in woods near cave,” “pitfall trap in mixed mesic forest ravine,” “pitfall in deciduous woods,” “upland (oak) woods,” “litter around cotton,” “in junk pile,” “in house,” “mammal burrow,” “moist leaf mold in rotting logs in mixed mesophytic forest,” “in leaf litter and moist very rotten logs on ground in mixed mesophytic woods,” “beech woods,” “under bark of rotting pine log,” “west side of hill, open woods, under rock, leaf litter, & rotten wood,” and “around pines, hardwoods.”

Distribution (Fig. 4, 14). Southern Québec, northern Vermont, southern Alabama and Mississippi, east central/ northeastern Arkansas, and probably the northeastern periphery of Louisiana, presently documented only for the genus. With this possible exception, *P. impressus* inhabits every state documented for the genus and is anticipated in Rhode Island and Delaware, where *Ptyoiulus* is projected. Dimensions of the areas occupied by *P. impressus* are the same as those of the genus, and it alone inhabits detached areas 2 and 3. As only *P. impressus* has dispersed southward into areas inundated in the Cretaceous, we suspect that the unassigned records in southern Alabama and Mississippi (Fig. 14, blue dots) also are this species.


**Deletions:** Iowa, Kansas, Minnesota, Nebraska, and Durham and Wake Cos., North Carolina. Gonopod illustrations were not published for records from the first four states, and RMS has not found vouchers in any repository. All are also well outside the ranges we document (Fig. 4, 14) for the genus and species, so we consider them misidentifications of other parajulids, probably anulimines. Likewise, Durham and Wake Cos., in central North Carolina where *P. montanus* is common, are also outside the range of *P. impressus* (Fig. 14), and we do not believe the latter occurs in this part of the state.

**Figure 14.** Distributions of species of *Ptyoiulus*. Black dots, *P. impressus*. Open black circle in southeastern Pennsylvania, denoted by the black arrow, is the neotype locality. Red dots, *P. montanus*. Open red circle in central North Carolina, denoted by the red arrow, is the neotype locality. Blue dots, geographically significant samples lacking adult males and presently unidentifiable to species.

**Material examined**

**CANADA:**


**Québec:** Montreal, 3F (LEM). New Provincial Record for the Genus and Species.

**USA:**


**Arkansas:** Clay Co., Chalk Bluff Natural Area, M, 19 November 2010, C. T. McAllister, H. W.


**District of Columbia:** Washington, M, Schumacher (NMNH) and M, 30 March 1908, J. V. Nichols (AMNH); Catholic University, juvs., June 1892 (NMNH); Georgetown, F (NMNH).


**Georgia:** *Butts, Chatham, Dade, Dawson, DeKalb, Effingham, Fayette, Floyd, Fulton, Gwinnett, Lumpkin, Meriwether, Muskogee, Rabun, Screven, Stephens, Thomas, and Towns Cos.* (FSCA, MCZ, MPM, NCSM, NMNH, VMNH).


**Kentucky:** *Allen, Bell, Boyle, Edmonson, Estill, Greenup, Letcher, Menifee, Morgan, Nicholas, Rockcastle, Wayne, Whitley, and Wolfe Cos.* (AMNH, FSCA, NCSM, NMNH, VMNH).

**Maryland:** *Anne Arundel, Baltimore, Calvert, Caroline, Cecil, Charles, Frederick, Garrett, Montgomery, Prince Georges, St. Marys, and Talbot Cos.* (AMNH, ANSP, NCSM, NMNH, UTIC, VMNH). **New State Record for the Genus and Species.**


**New Jersey:** *Bergen, Camden, Essex, Monmouth, Morris, Passaic, Somerset, Sussex, and Union Cos.* (AMNH, FSCA, NMNH, PMNH).

**New York:** *Bronx, Cattaraugus, Columbia, Greene, Kings, Madison, Monroe, New York, Oneida, Onondaga, Putnam, Queens, Rensselaer, Suffolk, Tompkins, Ulster, and Westchester Cos.* (AMNH, FSCA, MCZ, MNHP, NCSM, NMNH, PMNH, UMMZ, VMNH).


Remarks. Without adult males, Hoffman (1950) declined to provide a species for the form he found to be abundant at Highlands, Macon Co., North Carolina, calling it “Ptyoiulus, species incertis.” As the only mature males known from there today are *P. impressus*, we assign Hoffman’s moniker to this species.

As shown by their key and gonopod figures, Williams and Hefner (1928) assigned *Parajulus impressus* to an anioluline that we do not recognize and recorded true *Ptyoiulus impressus* as *Parajulus pennsylvanicus*. Their fig. 19A shows the unmistakable gonopods of *P. impressus* with the slanted calyx, and its key characteristic is “anal valves (paraprocts) and posterior segments densely pilose.” They report the species as “general but not abundant” throughout Ohio; we suspect it occurs statewide.

Morse (1903), in the Zoology Department, Ohio State University, Columbus, reported a mass aggregation of *P. impressus* on the campus. Individuals covered sidewalks, terraces, and even entered buildings, making it virtually impossible to avoid crushing numbers of millipeds at every step.

**Figures 15–22.** Gonopodal variation in *P. montanus*. 15) Distal extremity of right anterior gonopod of male from Montgomery Co., Virginia, caudal view. 16) The same of male from Tishomingo Co., Mississippi. 17) The same of male from DeKalb Co., Georgia. 18) The same of male from Craighead Co., Arkansas. 19) The same of male from Clay Co., Arkansas. 20) Right posterior gonopod of male from Mason Co., Tennessee, lateral view. 21) The same of male from Tishomingo Co., Mississippi. 22) The same of male from Montgomery Co., Virginia. Abbreviations as in Fig. 5–6.
Chamberlin and Hoffman (1958) assigned *Julus montanus* Cope to synonymy under *Ptyoiulus impressus*, where it was retained by Hoffman (1999). As first reviser, we resurrect *montanus* as the name of the other species.

Hefner (1929a, b) conducted two non-taxonomic studies on, purportedly, *Ptyoiulus impressus*. The first concerned genitalic development, and judging from the gonopod drawings (pl. 2, fig. 7–9), the parajulid actually was *Aniulus garius* (Chamberlin) (Aniulini). Without gonopod drawings, the true identity of the species in the second study cannot be determined.

**Ptyoiulus montanus** (Cope 1869), New Combination

Fig. 6, 15–22.

*Julus montanus* Cope 1869: 181.


*Ptyoiulus ectenes*: Filka and Shelley 1980: 12–13, fig. 5.


*Ptyoiulus* sp.: Shelley 1978: 43, 48, fig. 8–9 (list, account).

**Type specimen.** Male neotype and numerous male and female paraneotypes (FSCA) taken by A. S. Pearse, 24 September 1952, in Duke Forest, Durham Co., North Carolina.

**Diagnosis.** Calyx of anterior gonopod coxal process (Fig. 6, 15–19) three-sided, open caudad, upright and cupulate, coaxial with stem, lateral and medial lamellae joined by smaller one anteriorly, margins usually smooth.

**Variation.** Somatic features vary as in *P. impressus*. On the anterior gonopods (Fig. 15–19), the calyx is subcontinuous anteriad, with a gap in the lamina that varies from deep to shallow. The thicknesses of the lateral and medial lamellae vary (compare fig. 15–16, of the males from Montgomery Co., Virginia, and Tishomingo Co., Mississippi, respectively) as do the terminal configurations, particularly that of the latter. The calyx tilts slightly laterad in a male from Craighead Co., Arkansas (Fig. 18). The posterior gonopods (Fig. 20–22) also vary as in *P. impressus* but form longer and narrower arcs, and the tip is prolonged in the male from Montgomery Co., Virginia (Fig. 22), which also has a longer, broader, and lobe-like flange.

**Ecology.** Labels with samples carry the following habitat characterizations: “bottomland hardwoods,” “under decaying pine tree bark,” “woods, pitfall traps,” “large aggregation near light on carport,” “pitfall traps in oaks,” “under dead pig,” “wooded hillside,” “in ravine,” “oak-maple litter,” and “under bark of decaying pine tree.”

**Distribution.** All localities fall roughly between 37°42' and 33°46' N, a mere four latitudinal degrees; by contrast, the distribution of *P. impressus* covers around 15° of latitude. *Ptyoiulus montanus* extends, north/south, from southeastern Illinois and western Virginia to east-central South Carolina, north-central Georgia, northwestern Alabama, and northeastern Mississippi and Arkansas, an area of some 584.0 km (365.0 mi) north-south, and 1,160.0 km (725.0 mi), east-west. Longitudinally, *P. montanus* ranges from the Atlantic Ocean along southeastern North Carolina to west of the Mississippi River in northeastern Arkansas adjacent to the Missouri “boothed.” An older species that is apparently being displaced by a younger and more successful conger, *P. montanus* seems to have already been reduced to a host of relictual populations in Virginia, central Tennessee, and Georgia. The one Alabama record is a logical extension of the moderate-sized population in northeastern Mississippi, and minute, point populations survive in southeastern Illinois and northeastern Arkansas.

The largest population of purely *P. montanus* occupies the central Carolinas and extends to the coast in southeastern North Carolina; no authentic males of *P. impressus* have been taken within this
area. The second largest is in northcentral/northeastern Mississippi and northwestern Alabama, and if the female samples from Chickasaw and Obion Cos., Tennessee, are *P. montanus*, they would tend to connect the Mississippi population to that along the Ohio River in southeastern Illinois, where *P. impressus* also occurs.

A sizeable population inhabits the Great Smoky and Blue Ridge Mountains of western North Carolina, extending from easternmost Tennessee to westernmost South Carolina, which intermingles tightly with an equally large one of *P. impressus*. While the Gatlinburg area and the Visitor’s Center and administrative offices of the GSMNP seem to be in primarily *P. montanus* territory, the two species otherwise occur sympatrically and essentially side-by-side along the North Carolina/Tennessee border from the southern GSMNP to the Black Mountains in Mitchell and Yancey cos., North Carolina. We interpret this mutual occurrence as an area of active displacement, and one must examine every individual male for reliable determinations.

**Published records. Illinois:** Illinois in general (Chamberlin and Hoffman 1958, Hoffman 1999).

- Gallatin Co. (Causey 1952a).
- Hardin Co. (Causey 1952a).
- Pope Co. (Causey 1952a).
- *P. montanus*.
- *P. impressus*.

**North Carolina:** North Carolina in general (Bollman 1893, Hoffman 1999).

- Benton Co., 1.6 km (1.0 mi) W Canaan, M, 27 February 1961, L. Hubricht (VMNH).
- Benton Co., 1.6 km (1.0 mi) W Canaan, M, 27 February 1961, L. Hubricht (VMNH).
- Pontotoc Co., 32.0 km (20.0 mi) SW Asheville, foothills of Mt. Pisgah, M, 18 October 1965, J. and W. Ivie (AMNH); and 10.9 km (6.9 mi) SW Asheville, Bent Creek Forest Exper. Sta., M, 20 October 1974, R. M. Shelley (NCSM).
- *P. montanus*.
- *P. impressus*.

**Arkansas:** Clay Co., Chalk Bluff Natural Area, M, 19 November 2010, C. T. McAllister, H. W. Robison (NCSM).


**Illinois:** Illinois in general (Chamberlin and Hoffman 1958, Hoffman 1999).

- DeKalb Co., Atlanta, MM, FF, 7 July 1960, R. Davidson (FSCA).
- Fulton Co., Atlanta, MM, FF, juvs., 6 December 1960 (FSCA).
- *P. montanus*.
- *P. impressus*.

**Mississippi:** Alcorn Co., 11.2 km (7.0 mi) W Corinth, 3M, FF, 27 February 1961, L. Hubricht (VMNH).

**New State Record for the Species.**

- Benton Co., 1.6 km (1.0 mi) W Canaan, M, 27 February 1961, L. Hubricht (VMNH).
- Pontotoc Co., 32.0 km (20.0 mi) SW Asheville, foothills of Mt. Pisgah, M, 18 October 1965, J. and W. Ivie (AMNH); and 10.9 km (6.9 mi) SW Asheville, Bent Creek Forest Exper. Sta., M, 20 October 1974, R. M. Shelley (NCSM).

**Material examined**

- Georgia: DeKalb Co., Atlanta, MM, FF, 7 July 1960, R. Davidson (FSCA). *New State Record for the Species.*
- Benton Co., 1.6 km (1.0 mi) W Canaan, M, 27 February 1961, L. Hubricht (VMNH).
- Pontotoc Co., 32.0 km (20.0 mi) SW Asheville, foothills of Mt. Pisgah, M, 18 October 1965, J. and W. Ivie (AMNH); and 10.9 km (6.9 mi) SW Asheville, Bent Creek Forest Exper. Sta., M, 20 October 1974, R. M. Shelley (NCSM). *New State Record for the Species.*

April 1974, R. M. Shelley (NCSM).

the Neuse St. Pk., M, 8 October 1974, R. M. Shelley (NCSM).

and 17.8 km (11.1 mi) S Smith field, MM, FF, juvs., J. Laerm (GMNH).


Remarks. Shelley (1978, fig. 8-9) declined to assign a specific name to what was clearly *P. ectenes* (=*montanus*), as shown by his gonopod illustrations, in deference to studies then being conducted by N. B. Causey. She died a year later without publishing on this matter. Cope (1869) admitted that this species is closely similar to *Julus pennsylvanicus* of Wood, but he distinguished it on a slightly higher number of rings (69 vs. 63) with the medial parts smooth and the ventral parts striate (“closely many grooved”). The name may have indeed been proposed for an individual of *P. impressus*, but since both species occupy Montgomery Co., Virginia, one of the two counties Cope listed, we conserve *montanus* as the senior name for the second species of *Ptyoiulus*.

*Ptyoiulus* sp.

For completion and to delineate the entire generic and subfamilial ranges, we cite here samples, 10 with specific localities, without adult males and mostly from counties where males have not been collected. Judging from other records at the general latitudes of the Alabama and Louisiana record, the species there is probably *P. impressus*.

Alabama: Perry Co., 9.6 km (6.0 mi) NNW Marion, FF, juvs., 6 January 1954, N. B. Causey (FSCA).

Louisiana: Morehouse Par., along LA hwy. 142, 3.2 km (2.0 mi) S AR state line (NCSM). New State Record for the Genus.

North Carolina: Alexander, Ashe, Caldwell, Clay, Currituck [3.2 km (2.0 mi) N Poplar Branch, along US hwy. 158, 1.9 km (1.2 mi) S jct. SR 1140], Gates [4.8 km (3.0 mi) WNW Eure, along SR 1200, 1.2 km (0.7 mi) E jct. SR 1201], Guilford, Iredell, Madison, New Hanover [along US hwy. 421, 15.2 km (9.5 mi) S Wilmington], and Stokes Cos. (AMNH, NCSM).


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