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A SYNOPSIS OF THE ATOPETHOLIDAE, A FAMILY OF SPIROBOLOID MILLIPEDS

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Introduction

The Sonoran region of Mexico and southwestern United States is inhabited by species of the milliped family Atopetholidae, a small group of the order Spirobolida apparently endemic to North America. Despite its relatively limited extent, the family has fallen over the years into a state of progressively increasing confusion, which seems to be the normal course of events in this class of arthropods. Since the family Atopetholidae was defined in 1918, some of its genera have frequently been listed in the Spirobolidae (a completely dissimilar family), while perfectly typical genera of the latter group have simultaneously been considered atopetholids. No serious attempt has been made to study the male gonopods of any atopetholid species; hence the systematic position of the family has never been established. Still worse, several genera were so poorly proposed that they have remained unidentifiable up to the present time, and have provoked considerable confusion and synonymy. The value of the various taxonomic characters normally used has never been critically considered.

At this time a complete and satisfactory revision of the family Atopetholidae cannot be undertaken. Many of the species are known

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only from type specimens which are now lost or otherwise inaccessible. Obviously, a large number of species and probably additional genera remain to be discovered and integrated into the existing system, which thus stands vulnerable to future modification and expansion. The geographic range of no single species can presently be mapped with any sort of precision.

These facts might suggest that the present synopsis is founded upon an undue measure of presumption. Actually, there is every justification for immediate attention to whatever problems can be solved or even defined with the material at hand, for it is essential that the confusion be resolved and the classification stabilized as soon as possible before additional knowledge is superimposed on the currently shaky framework.

In this paper we have endeavored to phrase some tangible definitions for the family as well as for subfamily and generic categories, to clarify gonopod structure and thus establish a basis for future studies of comparative morphology, and to evaluate some of the structural variables which have been used to recognize species. Where material has permitted, we have redescribed both species and genera in detail, and have emphasized some characters normally overlooked. The level of thoroughness of this phase is noticeably uneven, for, lacking specimens, almost nothing could be done with the subfamily Atopetholinae. Nonetheless, this paper lays some claim to distinction in being the only one of its kind yet essayed for a family of millipeds.[3] We trust that our paper will be useful to those interested in describing and collating our native milliped fauna, one of the most diverse in the world, and will constitute a first step toward an eventual monograph of the great order Spirobolida.

Materials and Acknowledgments

Although the quantity of specimens that we have examined is not great, it nonetheless is quite diverse and gives a fair cross section of the family. We have studied 9 species representing 7 of the 11 known genera and all of the 4 subfamilies here recognized, and as a result have been able to utilize accounts in the literature of other genera with some degree of confidence. The validity of specific concepts has been enhanced by the abundance of typical material, one of the species being represented by a topotype, three others by paratypes, and two more—here described as new—by the holotypes. All of these type specimens as well as material of the other species are in the collection of the U.S. National Museum.

[3] A detailed study of the family Spirobolidae, by Dr. William T. Keeton, is now being prepared for publication.

We wish to acknowledge the cooperation in the loan of material by Dr. H. W. Levi of the Museum of Comparative Zoology and by H. S. Dybas and R. L. Wenzel of the Chicago Natural History Museum. Dr. Ralph Crabill deserves our thanks for the loan of paratypes from the U.S. National Museum and for the gift of atopetholids that previously came into his hands. Dr. R. V. Chamberlin very kindly examined some type specimens in his collection in response to several appeals for information on structural details. Our colleague H. F. Loomis, the describer of several atopetholids, kindly gave valuable comparative material and advice concerning some phases of the project. Finally, that the subfamily Eurelinae is now the best known atopetholid group is attributable to the interest and cooperation of Leslie Hubricht, whose collections provided the initial stimulus for undertaking the project.

Review of the Literature

Apparently the first member of the Atopetholidae to be described was the small Mexican species named *Iulus nietanus* by Saussure in 1860. Owing to a lack of information on its sexual characters, this species was subsequently placed first in the genus *Spirobolus*, then into *Cyclothyrophorus*, and finally, after a study of the type specimens, was made the type of the genus *Saussurobolus* by Carl in 1919.

The first generic name based upon an atopetholid is *Onychelus* Cook, proposed in 1904 for a small spiroboloid from southern California. Cook included *Onychelus* in the Spirobolidae, which he considered at that time to be the only family in the order Spirobolida. The description of the genus and its type species, *O. obustus*, was fairly detailed, but most unfortunately lacked illustrations and presented a very vague description of the gonopods, conditions that subsequently gave rise to considerable confusion. In a later paper (1911), Cook described several additional genera and species, including *Eurelus soleatus*, *Centrelus falcatus*, *Onychelus dentatus*, *O. hospes*, and *O. suturatus*, the last three being species of the genus now known as *Arinolus*. In this paper Cook also neglected to provide illustrations of the genitalia, and considerable synonymy has resulted from subsequent inability to recognize his species with any degree of certainty. One generic and two specific names must now be rejected as junior synonyms because of the shortcomings of Cook's work, although the verbal descriptions of body form are as detailed and accurate as one might wish.

The family Atopetholidae was erected in 1918 by R.V. Chamberlin to include the new genera *Atopetholus* and *Hesperolus*, and also "*Onychelus*, *Eurelus*, and related genera of the southwestern United States and Mexico." In defining the family limits, Chamberlin relied

chiefly upon the characters of the typical genus, and some of the original criteria must now be modified or restricted. However, at least one statement still holds true for the family as now known: "Posterior gonopods with telopodite simple and mostly bladelike with no separate inner piece; basal region often more or less extended mesad at an angle suggestive of condition in the Trigoniulidae." It was also remarked that the shape of the collum distinguishes atopetholids from the true Spirobolidae of North America, but this character is not exclusive to the Atopetholidae. Most regrettably, the paper contained no figures of the gonopods, the reason being given that "Preliminary accounts of these and three other new forms . . . are given below in order that the names may be validated for early use." But nearly 40 years passed before any of the species were ever mentioned again, even nominally, in the literature.

In the following year (1919) appeared a paper by Johann Carl, redescribing some of the type specimens of Saussurean species, which were still unknown with respect to their important characters. Carl, who found that actually two species had been originally included in *Julus nietanus*, described the second species under the name *neglectus*, and proposed the new genus *Saussurobolus* for the two. He also presented clear and useful illustrations. He remarked on the similarity of the gonopods to those of typical trigoniulids, a comment that influenced most of his successors.

A few years later Chamberlin described two additional atopetholids, *Atopetholus angelus* in 1920 and *Onychelus nigrescens* in 1923. The latter species was illustrated, and the figures give a fair impression of the gonopod characters.

By 1926, the family was still virtually unknown, as it was then impossible to associate *Saussurobolus* with the typical genus; it is small wonder that Attems could only note the existence of the name Atopetholidae, with its originally included genera, in the "Handbuch der Zoologie." Following the statement by Carl, Attems placed *Saussurobolus* in the family Trigoniulidae, where it has remained to this day.

With the description of *Piedolus utus* by Chamberlin in 1930, another form was added to the atopetholid roster, but unfortunately this name fell into obscurity and was not mentioned in several subsequent lists of genera until its inclusion in the checklist of Chamberlin and Hoffman in 1958. Subsequent to *Piedolus*, no other atopetholids were described until 1938, when Karl W. Verhoeff, publishing on material received from southern California, named *Onychelus michelbacheri* as a new species, erected a family Onychelidae on the basis of the single form, and stated that the name Atopetholidae was a nomen nudum. He obviously had not seen Chamberlin's 1918 paper.

Since 1940 a steady flow of publications has swollen the ranks of the family. Most of these papers have been concerned solely with the description of new species and genera, and need not be summarized in detail. It may be added, however, that no consistency has been obtained as regards the systematic position of many genera. In a contribution appearing in 1941, Chamberlin (1941a) included the genera *Hiltonius* and *Messicobolus* in the Atopetholidae although both belong elsewhere. In the previous year, the new genus *Arinolus* had been compared in the generic diagnosis only with *Tylobolus*, *Hiltonius*, and *Spirobolus*, of which all belong to the Spirobolidae. In 1943, he (1943a) treated five genera as atopetholids—*Hiltonius*, *Tarascolus*, *Toltecolus*, *Messicobolus*, and *Aztecolus*—and of these only the second and third actually belong to the family.

In 1949, a short paper by Dr. Chamberlin reviewing the genera of both families restated the main differences between the two and corrected the previous erroneous allocations. Yet, even in this work, with three new atopetholid generic names proposed, the established genera *Arinolus* and *Piedolus* were completely omitted.

The recently published "Checklist of the Millipeds of North America" (Chamberlin and Hoffman, 1958) lists all the known genera and species occurring within the United States, but, being largely a compilation from the literature, it perpetuates a number of errors, which we discuss fully in the following systematic account. We earnestly hope that with the publication of the present work, the misunderstood and abused Atopetholidae will at last become an intelligible group upon which future systematic work can be based with a considerable degree of confidence. This synopsis claims only to be the rough foundation upon which a handsome systematic edifice may someday be erected.

Taxonomic Characters

In preparing descriptions, we have devoted attention to all of the structural features of atopetholids hitherto utilized for diagnostic purposes, as well as to numerous others that were entirely neglected in the general preoccupation with those characters easiest to observe and mention. Many characters in this last category have been found worthless for taxonomic purposes. An attempt to study variation, whenever adequate series permitted, has been moderately successful. We have also determined that it is possible in many cases to identify female specimens at least to genus, although our knowledge of the family is still too meager to warrant the description of new species from female specimens. When sufficient material has accumulated to permit careful revision of genera and actual comparison of known females is possible, it seems quite likely that determinations can be

made on specimens of either sex by the use of qualitative external characters as pronounced as those utilized to distinguish species in Coleoptera, Orthoptera, and other insect groups.

CRANIUM: In nearly all of the species examined, the head is completely smooth and polished except for the normally concealed surface of the vertex, which tends to be finely rugose. The eurelines, however, often develop faint sculpture on the lower part of the head, the sculpture being well developed as genal striation in *Centrelus* and thus providing a means for distinguishing this genus from the closely related *Eurelus*.

CLYPEAL FOVEOLAE: In all the species of the family, the total range of variation in this character is from 3–3 to 5–5, and this range may be observed in a single species. There is no defensible reason for the erection of species upon slight variation in this character. In nearly every case, comparison was made between a single specimen of an allegedly new species with a single specimen of another. The tacit assumption that the clypeal foveolae do not vary within a species indicates nothing more than unfamiliarity with the group.

OCELLI: In a general way, the number of ocelli tends to be characteristic of the subfamilies although there is some overlap. Species of the Eurelinae usually have 40 to 50 in each ocellarium (a new term to replace the incorrect "eye" and the awkward "ocellus patch"), and those of the Arinolinae have from 30 to 40, but the variation in a single species is usually as great as for the entire subfamily. We have detected no significant variation in size, shape, or arrangement of the ocelli in species or genera. As a rule, the ocelli are difficult to count with accuracy. We have found that the only way to be absolutely sure of the number is to boil the cranium in strong KOH or NaOH until the exoskeleton is rendered colorless and the ocelli become very sharply defined. As a rule, the smaller species have smaller ocellaria, which are correspondingly more widely separated, and it may be entirely possible to take accurate measurements and work out ratios that would be of diagnostic importance. Such refinements, it seems, may profitably be postponed until an adequate volume of material is available for analysis.

ANTENNAE: The antennal articles are generally similar in size, proportion, and vestiture throughout the family, with the second normally the largest, followed by the sixth, third, fourth, fifth, seventh, and first. In the Eurelinae the antennae are shortest in proportion to the size of the animal, and usually do not reach beyond the caudal edge of the collum when straightened and extended caudad. The smaller species, such as those of *Arinolus* and *Onychelus*, have much longer antennae; these extend back to the third segment, and the individual articles are much longer in proportion to their width. The

second article in such forms usually extends distad beyond the rounded apex of the genae. There seems to be no significant variation with respect to the size and distribution of setae and pubescence on the antennae, and all known species have four terminal sensory cones. No other sensory structures or areas have been detected.

Mandibles: The basal joint of the mandibles is somewhat enlarged on the outer surface and appears elongated in the dorsoventral direction; the collum is correspondingly cut away on the anterior edge to accommodate this convexity. There is therefore no provision for an antennal groove such as occurs in the Spirobolidae, the antennae being held instead in a shallow depression on the outer face of the stipital joint of the mandible. This surface may be either smooth or moderately transversely striate and may be shown by future studies to be useful in the recognition of species, although the surface seems to vary within the limits of a genus. The free ventral edge may or may not be set off by a fine marginal ridge.

Gnathochilarium: The appearance of the gnathochilarium is essentially the same in all genera of the family and seems not to differ from that in most spiroboloid families. It may be noted in passing, however, that the base of the mentum is produced on each side into a distinct lobe possibly homologous to the cardine, which is said by Attems to be missing in the Spirobolida. This development is readily seen in *Eurelus soleatus* (see fig. 1,*a*).

Hypopharynx: The shape of the hypopharynx was not investigated by previous workers for its possible utility in classification. In the belief that some differences may exist in the structure at least at the family level, we introduce a drawing (fig. 1,*b*) of the hypopharynx in *Eurelus soleatus* for comparison with species in other families.

Collum: In general appearance the collum is similar in all members of the family in being smooth, evenly acuminate laterad, and with the anterior margin excavated, but there is considerable minor variation reflecting specific differentiation. Particular reference is made to the shape of the lateral ends of the collum, and the submarginal anterior groove on each side. In *Centrelus kerrensis* (fig. 5,*c*), for instance, the groove is very deep and distinct and sets off the edge as a sort of swollen ridge, which is extended ventrad into a rounded projection more pronounced than in any other atopetholid. In *Arinolus torynophor* (fig. 10,*b*) the caudal edge is somewhat concave just before the end so that the extreme tip seems to be produced caudoventrad, a peculiarity not observed in *A. apachellus* or *A. citrinus*. In species of *Watichelus* the condition is even more accentuated and thus provides a means of separating them from the closely related species of *Atopetholus*. In some forms the submarginal groove is nearly parallel to the anterior edge; in others (fig. 7,*d*) the groove becomes more remote

in going upward. The extreme lateral ends may be turned outward, as for instance in *Scobinomus*, and are readily visible from above.

Body segments: A close scrutiny of the body segments in our material has revealed some interesting information of a broad morphological nature. It seems pertinent to preface a consideration of segmental sculpture with some remarks on the composition of segments in the Spirobolida.

For many years the segments of spiroboloid millipeds were generally considered to be composed of a sternite and a completely coalesced

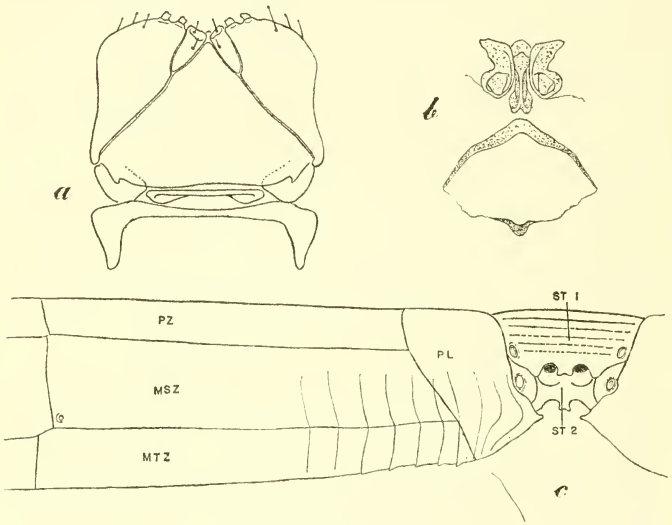

Figure 1.—Structural details of *Eurelus soleatus: a*, Gnathochilarium; *b*, hypopharynx; *c*, semidiagrammatic sketch of a midbody segment showing the two fused sternites, and the pleurite and lower tergal elements of the left side. Abbreviations; PL, pleurite: PZ, prozonite; MSZ, mesozonite; MTZ, metazonite; ST 1, anterior sternite; ST 2, posterior sternite.

"pleurotergite" often divided by a transverse suture into a prozonite and a metazonite, the latter occasionally with a faintly defined longitudinal suture behind the ozopore. In numerous publications by two such celebrated authorities as Attems and Verhoeff, suprageneric groupings were often based on the location of the pore in front of or behind the transverse suture. That the traditional dichotomy of "prozonite" and "metazonite" is untenable was first established by Cook (1896), who discovered that the spiroboloid segment is composed of a double sternite, a distinct pleurite on each side, and a dorsal

tergite subdivided into 12 smaller sclerites in 3 transverse series of 4 each.

Cook's observations were made upon specimens of *Pachybolus*, an African genus belonging to the same suborder as the Atopetholidae, and a newly moulted specimen of *Narceus*, a genus of the suborder Spirobolidea. We can confirm his account with the notice of identical segmentation in a newly moulted specimen of *Eurhinocricus* (Rhinocricidae) from Jamaica, and in several adult and hardened specimens of *Arinolus* and *Centrelus* in the Atopetholidae. In brief, there is a small elongate pleurite on each side, slightly narrower than the sternite, above which the tergite is divided into three transverse belts by two sutures. There is furthermore a median dorsal suture across all three transverse belts, and one such suture on each side at the level of the pores. If the familiar usage of prozonite and metazonite is to be preserved, it must be corrected and amended by the addition of the intermediate belt, which can be designated as the mesozonite (new term). It will now be into the mesozonite that the pore opens when it is in front of the second suture, not into the prozonite. A diagram (fig. 1,*c*) is provided to indicate segmental composition, which is shown as a flattened strip with the segment broken on one side at the pleurosternal suture.

In the Trigoniulidea, apparently the more primitive of the two suborders on the basis of this segmental composition as well as gonopod characters, much of the subsegmentation is visible in normal adult specimens, particularly in *Centrelus* and in *Arinolus*. In the more specialized Spirobolidae, the sutures are obliterated in adults, and evident only in specimens not completely calcified. The presence in spiroboloids of a distinct middorsal suture is a corroboration of the primitive nature of the order as already indicated by the retention of posterior gonopods and the presence of an eversible "penis" terminating the vasa deferentia.

Typically the surface of the pleurotergites is smooth and polished, usually with a scattering of very fine punctations. In some forms, such as the species of *Onychelus* and *Arinolus*, the surface of the metazonites is somewhat inflated and raised above the preceding subsegment, and may differ from it in microsculpture. In most cases the prozonite is provided with a number of fine encircling striae, as is normal for spiroboloids. The lower ends of both prozonites and metazonites, and often also the pleurites, are ornamented with a very fine reticulum of beaded striae enclosing polygonal areas that become elongated higher up on the sides and gradually merge into the transverse striae. In nearly all forms the lower sides of the metazonites are provided with short longitudinal striae or the ventral edges of impressed grooves; in several species these elevated areas

are strongly developed and may be carried out beyond the caudal edge of the metazonite in the form of acute, upturned spinules. Whether such modification is generic or only specific in value remains to be determined; it recurs in various other spiroboloid families in Central America and elsewhere.

With few exceptions, the ozopores open just in front of the second segmental suture, and slightly below the level of the lateral longitudinal suture. Species of the subfamily Arinolinae, so far as is known, differ in that the pore is on the caudal side of the suture and thus opens in the metazonite. This modification is almost certainly an evolutionary specialization, as it seems to occur only in forms that are specialized in other respects as well.

Male gonopods: The conformation of the male genitalia is basically uniform in most of the genera. Most diagnostic for the family are the combined features of a small transverse sternite and elongated coxal apodemes of the anterior gonopods, and the somewhat diminutive, two-jointed posterior gonopods. On the basis of the material studied in this as well as other spiroboloid families, the musculature of the gonopods appears also to be characteristic of the group.

Details of the sclerotized parts of the gonopods can be appreciated only from material that has been cleaned of muscle tissue after removal from the body of the specimen. Strong caustic solutions, with heating, quickly macerate the tissue, which then can be picked off with fine-tipped forceps. The importance of examining the gonopods in this way cannot be overemphasized.

The sternite of the anterior gonopods is represented in all the genera, usually as a narrow, subtransverse sclerite that is more or less arched at the middle, presumably to facilitate passage of the coelomic cavity. At the lateral ends the sternite is produced proximally into elongate sternal apodemes, the homologs of the functional tracheal apodemes of the typical generalized diplopod sternite. The gonopod apodemes, however, are closed tubes, and function only for muscle attachment; they tend to be short and slender, normally curving slightly mesiad. Beyond the origin of the apodemes, the sternite is curved caudolaterad around the base of the coxite and is usually coalescent with it. In *Comanchelus hubrichti* (fig. 6,*b*) this fusion is incomplete; the tip of the sternal extension remains free of the coxite margin, probably reflecting a primitive condition.

In general, the coxites are firmly attached to the lateral extremity of the sternite, leaving a more or less membranous, unconsolidated area along the middle of the gonopod. This condition is characteristic of the subfamily Eurelinae, where a distinct intercalary thickening of the membrane between the coxites has taken place—a development here referred to as the vinculum (Lat., a buckle)—and clearly

serves the function of providing rigidity to the entire structure. Species of the Atopetholinae have increased the size and efficiency of the vinculum, which takes up much of the intercoxal space, and is prolonged caudad between the coxites, terminating in a ligament that extends laterad on each side to insert on the caudad side of the sternal apodeme (fig. 2,*c*, No. 5). The greatest development of the sternite is found in the subfamily Onychelinae, where it is prolonged distad into a triangular process very similar to the sternite of species of the Rhinocricidae (see fig. 8,*a*). Here there is no spacer between the coxites, rigidity of form apparently being accomplished by a certain amount of fusion of coxites to the sternite.

The coxites are somewhat variable in form throughout the group, but are similar to the typical spiroboloid form in being produced into a slight apex on the mesial surface, this character reaching its greatest extreme in *Arinolus* (fig. 11,*a*), which is apparently the most specialized genus in the family. In all genera, the coxites are produced proximad into slender, acute coxal apodemes that serve for muscle attachment. As seen in caudal aspect (figs. 2,*a*; 4,*b*; 8,*b*), the mesial edge of the coxite is drawn out gradually to form the apodeme, which may be either flat and simple (fig. 8,*b*) or rolled to form a concavity (fig. 4,*b*) with the free caudal edge joining the coxite near its caudomesial end. In all cases, the coxite forms a gonocoel cavity in which the posterior gonopod is carried.

The telopodite joint is normally rather small and unmodified. Usually it is produced into a blunt, laterally directed tip, with a departure from this plan occurring only in *Atopetholus*. Species of that genus are characterized by an additional accessory process that has been referred to in the literature as "posterior apophysis," "digitiform process," and "posterior finger" by Chamberlin and that appears to be possibly homologous to similar processes described by Verhoeff (1924) for some Australian spirobolellid genera. There is a membranous, flexible articulation between the coxite and telopodite, but within the gonopod no major muscles have been detected that might activate the distal joint. Apparently there is an evolutionary tendency for the size of the telopodite to increase, it being smallest in *Comanchelus* and largest in *Arinolus*, genera that are phylogenetically opposed in numerous other characters as well.

The posterior gonopods lie concealed within the anterior pair, their coxites exposed and directed toward the median line, often with their ends in contact. There is, however, no trace of a sternal connection, and it will be recalled that in the Trigoniulidae, where such a sternite persists, the coxites are directed caudad in line with the major body axis. There is a large apodeme, inferentially homologous with the sternal apodeme of the anterior gonopods, attached near the mesial

end of each gonopod by a loose, flexible pivot joint. The shape of the apodeme varies somewhat, it being long and slender in the larger bodied, primitive forms (Eurelinae, Atopetholinae), and becoming shorter in the smaller forms, where it may also (as in Onychelinae) be distally expanded. The relatively larger size of the posterior gonopod in this subfamily presumably requires, within the confines of a smaller available space, a greater surface for attachment of the muscles. In two of the subfamilies, Eurelinae and Atopetholinae, the distal joint of the posterior gonopod is undifferentiated; there is no perceptable articulation between, or remaining evidence of, coxal and postcoxal elements. That the gonopod is actually 2-jointed, however, is shown in the Onychelinae and Arinolinae, where an acute angle is formed, with a flexible articulation at the apex (figs. 8,*c–e*; 10,*c*). In no case, however, are there remnants of intersegmental muscles in the posterior gonopods of atopetholids or any other group known to us. It is curious that this primitive leg condition would be preserved in members of what, in all other respects, are specialized atopetholids, and emphasizes the point that no existing spiroboloid species has retained ancestral characters in all of its structural features, the parts apparently evolving at different rates and somewhat independently of each other in this respect.

In general appearance the posterior gonopod is short and bent somewhat mesiad. In the Eurelinae it tends to develop a large hyaline flange on the median side, as in *Comanchelus hubrichti* (fig. 6,*c*). In the Atopetholinae this gonopod is longer, more slender, and somewhat arcuate, with a thin expansion on the caudal edge in *Atopetholus* and a distinct projecting branch there in *Watichelus*. In the Arinolinae there is a distinct submarginal groove from the coxal attachment distad to a short solenomerite (*Arinolus*, fig. 10,*d*) or a longer one which actually extends distad beyond the tip of the gonopod (*Piedolus*). In this subfamily, also, the gonopod terminates in an expanded, laminate or subglobose area (figs. 10,*a,c*; 11,*c*) which is herein tentatively referred to as the calyx. The occurrence of the groove, presumably homologous to the seminal groove of many other diplopods, is obviously an evolutionary specialty not found in the other three subfamilies.

Gonopod musculature: It is felt that a satisfactory concept of phylogeny and classification of the Spirobolida can be achieved only by a detailed consideration of comparative morphology of the various groups. Studies of the hard parts are undoubtedly a step in the right direction, but lack real significance until the physiological functions of the various modifications are established. These functions are to a certain extent reflected by the nature of the musculature, and as a contribution toward this end we include a brief account of the gonopod muscles in *Atopetholus angelus*, a species of the typical genus of the

family. Unfortunately, none of the available material of the other species was preserved in a way to keep the internal tissues in good condition, but in the Eurelinae, at least, the gonopod muscles appear to be much the same as here described. The similarity in skeletal parts of the other groups permits the inference of essential muscular correspondence. The only previous notice of musculature in an atopetholid is in the paper on *Atopetholus michelbacheri* by Verhoeff (1938), but his drawings are so diagrammatic and vague as to be totally useless. In the absence of detailed studies on species in other families, and in anticipation of much variation in arrangement, we refrain from submitting any tentative nomenclature at this time and use a numerical symbolism in designating the different muscles and describing their functions.

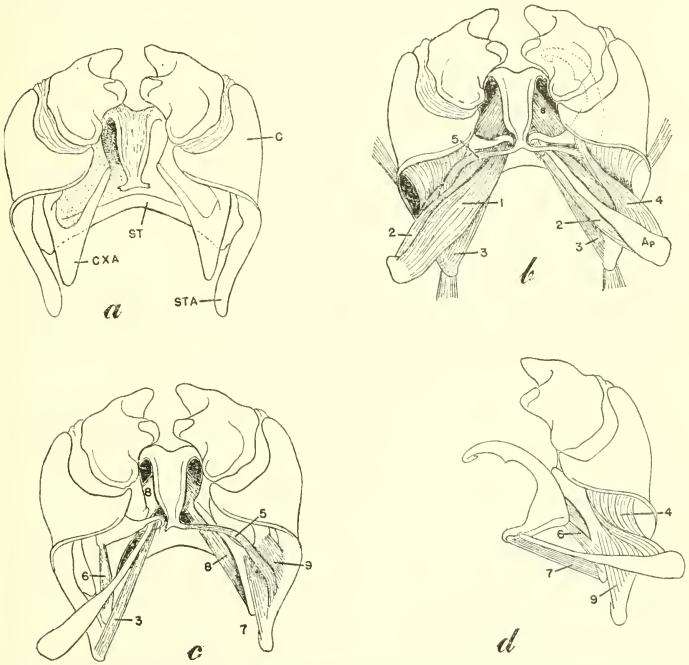

FIGURE 2.—Male gonopods of *Atopetholus angelus* in caudal aspect: *a*, anterior gonopods with all muscle tissue removed to show internal structure characteristic of the family; *b*, *c*, two views of the gonopods with various muscles removed in *c* to show underlying details; *d*, left side of gonopods with posterior gonopod withdrawn from the gonocoel, showing its exclusive muscles. Abbreviations: C, coxite; CXA, coxal apodeme; ST, sternite; STA, sternal apodeme. Numerical muscle designations are discussed in the text, p. 108.

The entire gonopod structure can be protruded from the body by the contraction of a pair of muscles that originate near the ventral ends of the pleurotergite of segment 7 and insert on the gonopod at the ends of the sternite (fig. 2,*b*). Retraction of the genital apparatus into the body cavity is accomplished by large muscles that originate on the dorsal side of the pleurotergite and insert on the distad ends of the sternal apodemes. These two sets of muscles appear to be common to the gonopods of many helminthomorphous diplopods, and seem to be homologous to similar muscles motivating the free sternites of such orders as the Chordeumida.

The muscles that originate on the gonopod apparatus itself are not numerous but provide for a great degree of activity. They are most easily seen in caudal aspect, the accompanying figures (fig. 2,*b–d*) showing several successive stages of dissection as well as a cleaned gonopod for easy reference to hard parts.

The following list designates the muscles and describes their functions:

1. A large, fusiform muscle originating on the caudal side of the posterior apodeme and inserting on the base of the posterior gonopod just mesiad to the pivot joint. Contraction causes the distal end of the gonopod to swing proximomesiad.

2. Similar to 1 but originating on the anterior side of the apodeme. Function is the same.

3. A long slender muscle originating at the tip of the anterior sternal apodeme and inserting on the base of the posterior gonopod near its mesial end. Its contraction would provide extra power in support of muscles 1 and 2, and likewise prevent uncontrolled protrusion of the posterior gonopod by the contraction of 4.

4. A large, flat, twisted muscle, originating along the caudal edge of the anterior coxite, and inserting on the anterior face of the posterior apodeme. Contraction would result in extrusion of the entire posterior gonopod apparatus, the twisting presumably turning the gonopod into a position to facilitate its escape from the gonocoel.

5. A long slender ligamentous-type muscle originating on the anterior sternal apodemes and extending mesiad over 4 to join the caudal extension of the vinculum. The function of 5 is to provide stability for the caudal extension as well as to hold twisted muscle 4 in correct position during its contraction.

6. A small, short muscle originating on the tip of the coxal apodeme and inserting on the outer end of the base of the posterior gonopod (fig. 2,*d*). The muscle would retract the gonopod to get it back into the gonocoel.

7. A small slender muscle running from the anterior side of the coxal apodeme to the mesial end of the posterior gonopod and serving the same function as 1 and 2, but, judging from its origin on the coxal

apodeme, doubtless aiding in drawing the gonopod down and mesiad, and freeing it from the gonocoel.

8. A large thick muscle originating on the anterior sternal apodeme and inserting on the septum on the inner side of the vinculum. The homologs of this muscle may be found in the sternal areas of platydesmoid and chordeumoid millipeds, where the median septum is reflected externally by a median sternal ridge or knob.

9. A short band of muscle from the anterior sternal apodeme to the caudal side of the coxal apodeme. The muscle serves to swing the coxite slightly mesiad in contraction, in opposition to the action of 8.

It should be noted that the sum effect of the motor activities of the gonopods is that of a clasping organ. A hypothetical reconstruction of the procedure is submitted at this time to invoke the interest of other investigators. So far nothing has been published on the mechanics of copulation in this order, and direct observations are needed to establish the function of the gonopods.

Initially, the entire gonopod apparatus is at least partially extruded by the protractor muscles. The coxites are then spread slightly laterad by contraction of 8. Muscles 6 and 7 can then pull the posterior gonopod out of the gonocoel. This done, they relax, and the entire posterior gonopod is exserted by the contraction of 4 until the appendage is exposed and probably directed toward the head of the animal. At this point muscles 1 and 2 pull the gonopod so that the distal end swings down toward the bases of the walking legs, a position enhancing contact with the female cyphopods. Retraction is made by muscles 3, 6, and 7, with 6 and 4 then cooperating to return the appendage into the gonocoel.

Sympleurite of seventh segment: In spiroboloid diplopods, the two pairs of appendages of the seventh segment are modified as gonopods and withdrawn into the body cavity, and thus remove the two sternal elements from the normal segmental ring. The pleurites of the segment project mesiad to fuse at the midventral line and maintain segmental rigidity. In some families, such as the Rhinocricidae, there is no visible midline suture, and the combined pleurites are modified into an elevated thin flange that projects somewhat caudad and protects the exposed tips of the posterior gonopods. Most of the atopetholids, however, retain the median suture and the modified pleurites—herein designated as sympleurite—form a simple transverse bar. An exception occurs in the subfamily Arinolinae, where the sympleurite is medially enlarged and variously lobed cephalad, as shown in figure 11,*d*. Although no good comparative study could be made in this connection, it appears that each species may differ somewhat in the shape of the sympleurite at least in the genus *Arinolus*.

Legs: In most instances the leg joints maintain a uniform proportion and appearance, the order of decreasing length usually 3, 6, 2, 4, 5,

1, any variations almost always affecting the sequence of the last two or three. Modifications of taxonomic value involving leg characters are those of the ventral macrosetae or spurs, and the shape of the anterior male legs and their tarsal claws.

The occurrence of large regular spurs on the ventral apices of the leg joints is to be noted in most spiroboloids, although in the majority of groups the number and stability is greatly reduced. Atopetholids show perhaps the primitive condition in that a definite spur formula holds for each species, with only occasional variations. The coxal joint always bears a single seta, although in old specimens it may be broken off. The number increases in going distad on the leg, and the maximum number is found on the tarsal joint. Although the formula is constant for a species, the formula does not follow a phylogenetic arrangement, and one set of values may recur in several different genera. Three different formulae are given here, to indicate their occurrence: 1–1–2–2–2–6: *Centrelus kerrensis* (Chamberlin & Mulaik), *Comanchelus hubrichti*, new species, and *Arinolus torynophor* Chamberlin; 1–1–3–3–3–6: *Atopetholus angelus* Chamberlain; and 1–1–2–2–2–8: *Eurelus soleatus* Cook.

In nearly all the species examined for the character, the tarsal joint bears a few short setae on the caudal side and usually one on the cephalic face. In *Onychelus obustus*, however, these lateral setae are much more numerous and very elongated, and form a sort of fringe on each side of the leg. Conceivably this may be an aid to locomotion in dry, loose sand, *Onychelus* being known to occur in desert regions.

In many species, the coxae of the anterior male legs are produced into variously shaped lobes, the lobes of the third leg pair usually being most modified. These elaborated coxal lobes seem to characterize species rather than genera for the most part, and although probably a specialization of a sort, do not occur in obviously specialized genera such as *Arinolus*. The pinnacle of coxal development is reached in *Eurelus soleatus*, where the lobes of the third legs are elongated and deeply notched just before the end, the notches being engaged by the coxal lobes of the fourth pair with a nice interlocking mechanism, the advantage of which is difficult to imagine. In the related species *Comanchelus hubrichti*, none of the anterior male legs are lobed. In *Atopetholus angelus* the coxae are produced into small blunt cones, which reverse the normal sequence by increasing slightly from the third to the seventh leg pairs.

The large coxal lobes of *Eurelus* are accompanied by a marked reduction in the size of the tarsal claws to mere uncate remnants (figs. 4,*d–f*). These claws are likewise reduced in *Centrelus*, but are normal in size in *Comanchelus* of the same subfamily, and in most other

atopetholids are actually somewhat larger and longer than the claws of the normal postgenital limbs. It seems safe to infer that the legs of atopetholids have been variously modified or specialized in different genera to serve functional and less obvious needs, although the modifications have not taken the same direction of evolution as seen in other parts of the animals, particularly the gonopods. Taxonomically, however, the legs afford useful recognition characters, particularly in areas where two otherwise superficially similar species may occur together.

Systematic Status

Determination of the systematic position of the Atopetholidae is a matter fraught with great difficulty. Despite useful treatments by Brolemann (1914) and Attems (1926), the classification of the Spirobolida is still very unsatisfactory chiefly because no careful morphological studies have been made to determine the structural details of the male gonopods, upon which family groupings must largely be founded. Brolemann's early study provided a fairly satisfactory arrangement for its time, but since then the number of genera has increased enormously, and in few instances have the new groups been sufficiently diagnosed to enable their placement in his system. Even Attems' treatment in 1926 is objectionable because of the author's reluctance to recognize small genera or families. The genera that he placed in the "Spirobolidae" could obviously be dispersed among three or four families. These families would be small groups, of course, but it must be remembered that so far only a start has been made in the discovery and classification of the Diplopoda. Since 1926, as already remarked, the situation has become even more acute, as evidenced by the way genera have been successively interchanged from the Atopetholidae to the Spirobolidae, and vice versa, as well as the recent and lamentable redescription of one of the best-known trigoniulid species as a new genus in the Spirobolidae. The main reason for the prevailing confusion lies in the fact that few workers have taken the trouble to remove the gonopods from their specimens, and actually study them with respect to their total structure, even though Carl inveighed against this carelessness as far back as 1919.

As the record now stands, the Atopetholidae is the only spiroboloid family whose characters are well enough known to provide a basis for understanding. Comparison with other established groups is therefore somewhat premature, yet it will be useful to point out a few obvious lines of affinity. Attems and Brolemann established a primary subordinal dichotomy in recognizing one group in which the posterior gonopods are connected by a sternal remnant, and another in which they are completely independent, the groups being recognized first as

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families and then as suborders. There is now some doubt that this arrangement can go unchallenged.

That the Atopetholidae occupies a somewhat intermediate position is evidenced by the fact that Attems placed *Saussurobolus* in the Trigoniulidae despite its lack of a gonopod sternite; presumably he was influenced by the overall similarity in other respects. Yet Verhoeff considered the closely related *Orthichelus* to belong to the other suborder, and made it the type of a new family allied to the Rhinocricidae. It seems possible that both were not far from the truth, and that a division into suborders may have to be drawn along lines other than those now in use.

The group that most resembles the Atopetholidae as far as gonopod structure goes is the group typified by the East Asian *Spirobolellus*. The species of this group have the peculiar coxal apodemes, and the posterior gonopods are not strikingly different from those of the atopetholids. Another group in which coxal apodemes occur is the Rhinocricidae, which is pretty clearly a well specialized ensemble and has a distinct solenomerite on the posterior gonopods as well as a vesicle in the base of the telopodite. Stabilization of the clypeal foveolae at a constant number of four and the development of scobinae are likewise to be considered specializations.

The rhinocricid posterior gonopod preserves the same number of segments as are found in the atopetholids, but differs in that the coxae are vertical instead of transverse. It is easy to see the similarity of this appendage in *Piedolus* and *Eurhinocricus*. At the present, it seems reasonable to regard the Atopetholidae as a very primitive family whose progenitors doubtless gave rise to the existing families Rhinocricidae and Spirobolellidae as well as, perhaps, to the Trigoniulidae. There are, unfortunately, no species of spiroboloids which have retained most of the primitive characters. We can assume that the most primitive gonopods are those that most nearly approximate the original walking-leg structure, and on this basis the anterior gonopods of *Comanchelus* are those that are least modified. Retention of a sternite remnant between the posterior gonopods—obviously a primitive character—is known only in the Trigoniulidae, but in this group the gonopods are strongly specialized by the presence of coxal vesicles and associated seminal groove and solenomerite. It therefore seems safe to assume *Comanchelus* to be, probably, the most primitive of existing spiroboloids as its gonopod structure could not be any more generalized without the subdivision of the telopodite into several segments.

Within the family, then, the least specialized group is the Eurelinae, followed closely by the Atopetholinae. *Onychelus*, which is in a subfamily of its own, is somewhat aberrant and out of the main line of

evolution, it having developed a rhinocricid-type anterior gonopod and several modifications for desert life while remaining unspecialized in other respects. In the Arinolinae we reach the apex of atopetholid evolution, with numerous localized species, the appearance of rudimentary scobinae, and development of a distinct solenomerite on the posterior gonopod, as well as a fundamental change in the location of the ozopores and a loss of the original primitive segmental sutures.

Genera Incorrectly Referred to the Atopetholidae

At various times in the past certain genera have been either listed in the family Atopetholidae or associated otherwise with genuine atopetholid genera. Aside from inadvertant or careless listings, the following names warrant comment:

Anelus Cook, 1911, p. 160.

Type species: *Anelus reduncus* Cook, by original designation.

Unfortunately, the type specimen of this genus and species has been misplaced and is not available for study. On the basis of Cook's description, and that of the related *A. richardsoni* (Pocock), as well as the examination of a female *reduncus* taken near the type locality, it seems that the genus departs sufficiently from normal atopetholid structure to warrant exclusion from the family. Cook's paper, published before the Atopetholidae was proposed, considered *Anelus* to be a close relative of *Eurelus* and *Onychelus*, but *Anelus* probably belongs to a presently undefined Neotropical family.

Banosolus Wang, 1951, p. 28.

Type species: *Banosolus phillippinus* Wang, by original designation.

This genus was originally proposed as a member of the Atopetholidae, an allocation that needs verification by restudy of the type specimen. The original illustrations leave much to be desired, and the locality involved makes it seem possible that the genus may actually belong to the related family Spirobolellidae, which is well represented in the Indo-Australian region.

Cyclothyrophorus Pocock, 1910, p. 83.

Type species: *Cyclothyrophorus salvini* Pocock, by original designation.

The remarks made for *Anelus* apply equally well in this case. Details of gonopod structure are as yet virtually unknown, but the weight of evidence suggests exclusion of this genus from the Atopetholidae. Possibly, however, some of the species which Pocock tentatively associated with *C. salvini* may prove to be atopetholids, as we know to be true of *Julus nietanus* Saussure, which was listed in this genus by Pocock (1910). If *salvini* upon restudy proves to be an atope-

tholid, it almost certainly will be necessary to recognize an additional subfamily for *Cyclothyrophorus*.

Messicobolus Brolemann, 1914, p. 32.

Type species: *Spirobolus godmani* Pocock, by original designation.

This genus of large robust spiroboloids has been referred to the Atopetholidae in recent papers by R. V. Chamberlin, but the good figures of the gonopods published by Carl indicate clearly that *Messicobolus* and the possibly synonymous *Oxobolus* constitute a distinct taxonomic group well differentiated from other presently recognized spiroboloid families.

Atopetholid Genera of Uncertain Position

The following generic names appear to be based on species of the Atopetholidae, but are so poorly described that it is impossible to refer them to a subfamily with any degree of confidence.

Hesperolus Chamberlin, 1918, p. 170.

Type species: *Hesperolus wheeleri* Chamberlin, by original designation.

The original description of *H. wheeleri* included no illustrations, and it is difficult to visualize the gonopodal structure from the description. The tiny species was collected in the Santa Ynez Mountains near Santa Barbara, California, and it is hoped that topotypes can eventually be obtained and studied for a correct placement of the genus.

Tidolus Chamberlin, 1949, p. 169.

Type species: *Atopetholus parvus* Chamberlin, by original designation.

The type species was described as an *Atopetholus*, and the diagnosis of *Tidolus* is largely a comparison with that genus. Here again, however, the type species is not illustrated, and the brief description of its gonopods is not sufficient to provide a good idea of their form. Since *parvus* was collected at Claremont, California, it should not be difficult for some collector to eventually secure topotypical specimens.

Family Atopetholidae Chamberlin

Atopetholidae Chamberlin, 1918, p. 167; 1949, p. 168.—Chamberlin and Hoffman, 1958, p. 152.

Onychelidae Verhoeff, 1938, p. 273.

Small to medium sized spiroboloids, characterized by the structure of the male gonopods. The anterior pair consists of a transverse or moderately arched sternite, with the usual sternal apodemes; coxae of normal configuration, separated by a median thickening of the

intersegmental membrane or held apart by a median distal projection of the sternite, produced proximally into conspicuous coxal apodemes; telopodite typically small and largely concealed behind the coxites in anterior aspect. Posterior gonopods rather small, concealed within a gonocoel formed by the anterior pair; their apodemes long and slender, reaching dorsal side of pleurotergite, loosely jointed with the transverse basal coxal element; telopodite usually fused with the latter at a right angle. Posterior gonopods set transverse to the longitudinal body axis, but not connected by a sternal remnant.

Head small, clypeal foveolae 3–3 to 5–5, varying within a species; ocellaria of normal size, ovoid to rounded, with 30 to 50 ocelli in each; antennae variable in length, held in a depression in the face of the mandibular stipe, with 4 terminal sensory cones.

Collum wider than head, laterally acuminate, the anterior lateral edge set off by a distinct groove. Second segment usually about as long as collum but not produced forward under its tip, the pleural element produced mesiad, its anterior edge usually elevated as a distinct flared margin. Surface of tergites smooth or very finely punctate in most species; in some species the lower sides are adorned with longitudinal striations that may be produced beyond the caudal edge of the segments in the form of acute spinulae. Tergites with two transverse sutures, a median dorsal suture, and a lateral suture on each side at level of the ozopores, the ozopores opening in the mesozonites except in the subfamily Arinolinae. Rudimentary scobinae occur in at least one genus (*Scobinomus*). Anal tergite blunt, rounded, shorter than valves; latter inflated, their inner margins meeting at a reentrant angle and provided with a comb of fine, closely set bristles, otherwise glabrous. Preanal scale usually broadly ellipsoid, nearly flat, but occasionally modified slightly (*Centrelus*). Legs moderate in length, the sixth joint longest, ventral macrosetae of legs apparently constant within a genus, varying from 1–2–2–2–2–6 to 1–1–3–3–3–8. Sternites rectangular to trapezoidal, usually widest in front, with 6 to 12 or more transverse ridges or striae. Coxal lobes of anterior legs variable, from small conical productions to elongate and specialized structures, those of the third pair usually largest, extending caudad over or between those of the following pair. Tarsal claws of the third to sixth legs may be normal, rudimentary, or hypertrophied, their form a specific rather than generic character.

The genera that we have been able to recognize fall into four natural groups probably worthy of subfamily rank although some appear to be much more differentiated than others. These groups may be characterized by the following key:

Key to the subfamilies of Atopetholidae

1. Ozopores opening in the metazonite. Posterior gonopods with distinct solenomerite of varying size and shape. Coxites of anterior gonopods with well-defined oblique grooves setting off the lateral surface
   ARINOLINAE (p. 147)

   Ozopores opening in the mesozonite. Posterior gonopods without solenomerite or seminal groove. Coxites of anterior gonopods entire, without oblique grooves 2
2. Sternite of anterior gonopods strongly arched mesially, the suprasternal membrane sclerotized and fused with it to form a flat subtriangular pseudosternite; sternal apodemes of anterior gonopods curved inward distally, those of posterior gonopods greatly expanded at the end. Legs with numerous long bristles on the sides in addition to the normal short ventral setae . . . . . ONYCHELINAE (p. 147)

   Sternite of anterior gonopod transverse or moderately arched; intersegmental membrane sclerotized an as intercoxal vinculum of various shape but never as a flat triangular plate fused with the sternite. Legs without long lateral setae. Apodemes of posterior gonopod not strongly expanded distally 3
3. Segments with one distinct transverse suture. Vinculum broad and heavily sclerotized with a median groove or depression extending caudad between the coxae and more or less in contact with the sternite
   ATOPETHOLINAE (p. 132)

   Segments with two distinct transverse sutures. Vinculum small and separated from the sternite by a large expanse of thin connective tissue
   EURELINAE (p. 117)

Eurelinae, new subfamily

The atopetholids assigned to this distinct and homogeneous subfamily are all fairly large in size and include the largest known representatives of the family. In general form the species tend to be robust and heavy-set, abruptly tapering at both ends of the body, and with the head and column distinctly smaller than the second and succeeding segments. The ocellaria are well-developed, each with 30 to 50 or more ocelli. Normally the pleurotergites are smooth and without distinct punctations. The color in life appears to be, usually, some uniform shade of gray or olivaceous; in preservation the segments may develop annulations of darker color. There is considerable variation in secondary sexual characters of the males: Coxal lobes and claws of the anterior legs may be absent, normal, or hypertrophied, the variation in general tending to reflect specific rather than generic differentiation. The gonopods are basically similar, and are characterized by the considerable amount of sclerotized membrane between the true sternite and the coxae. There is a more heavily sclerotized midpiece, the vinculum, occupying a rather isolated position between the coxites, and presumably serves as a

spacer to maintain rigidity of form in lieu of the sternite, which usually assumes this function in spiroboloids.

The distribution of the Eurelinae (fig. 3) is distinctly Texan—all the three known genera and three of the six species occurring in this State. The others are recorded from the Mexican States of Chihuahua, Nuevo León, and Guanajuato—all on the eastern side of the Mexican Plateau. One species, *Eurelus mulaiki* from New Mexico, is unknown to us. From the drawings of its gonopods, as well as the disjunct distribution, it seems possible that *mulaiki* may represent another generic type within the limits of this subfamily. Those of which we have examined material may be distinguished by the characters selected for the following key:

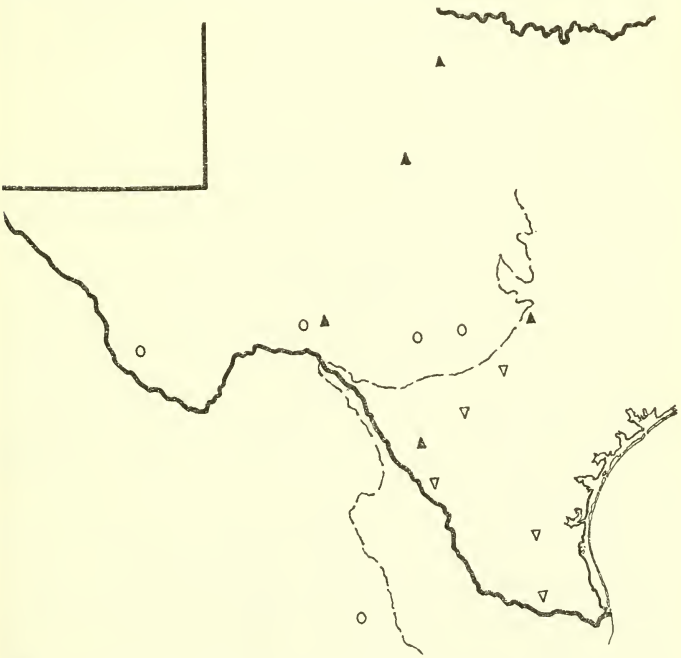

FIGURE 3.—Map showing the known localities for three species of the Eurelinae in Texas and Nuevo León: ▲ *Comanchelus hubrichti;* ○ *Centrelus kerrensis;* ▽ *Eurelus soleatus.* The broken line approximates the 1,000-foot contour, which apparently separates the ranges of *soleatus* and *kerrensis.*

Key to the genera of the subfamily Eurelinae

1. Lower portion of the pleurotergites with a series of 6 to 10 sharp recurved spines on the caudal margin just above the legs; collum of male with the anterior margin set off by a distinct deep groove, and prolonged ventrad into a rounded lobe extending below the level of the second tergite (fig. 5*c*); apex of coxite of anterior gonopod with a fleshy membranous lobe (fig. 5*a*), otherwise quite similar to that of *Eurelus;* coxal lobes of anterior legs well developed . . . . . **Centrelus** Cook

   Lower portion of pleurotergites not produced into spinules on the caudal margin; collum of male with anterior edge set off by a moderate groove and not, or but slightly, produced ventrad as a rounded lobe; coxites of anterior gonopods without trace of membranous lobes (figs. 4*a*, 6*a*). 2

2. Sternite of anterior gonopods nearly straight across; tarsal claws of legs 4–7 of males normal in size and shape; coxal lobes of these legs very small; ventral setae of legs 1–1–2–2–2–6 . . . . . **Comanchelus,** new genus

   Sternite of anterior gonopods of male distinctly arched; tarsal claws of legs 4–7 of males reduced to tiny vestiges; coxal lobes of anterior legs very large and elaborated; ventral setae of legs 1–1–2–2–2–8 . . . **Eurelus** Cook

Genus *Eurelus* Cook

Eurelus Cook, 1911, p. 161.

Type species: *Eurelus soleatus* Cook, by original designation.

Diagnosis: A genus of stout-bodied eurelines in which the anterior tarsal claws of males are reduced to mere vestiges while the coxal lobes are greatly enlarged. The caudal edges of the pleurotergites are not provided with upturned spinules.

Discussion: Although both the generic name and its only included species were described at great length by Cook, he provided no illustrations of the gonopods or other structures, and it is therefore not surprising that *Eurelus* has become something of a pitfall to later workers. The recent acquisition of material clearly referable to *E. soleatus* makes it possible to clear up the mystery satisfactorily.

Subsequent to Cook's 1911 paper, the first reference to the genus appeared in an article on Texan millipeds by Chamberlin and Mulaik (1941), in which two new names, *proximus* and *kerrensis*, were proposed in *Eurelus*. Unfortunately these authors followed Cook's precedent and presented no drawings of the new forms and thus compounded the difficulties. Most of their descriptions consisted of comparisons with that of *soleatus*, and dealt only with very variable structural details. Two years later (1943b), Chamberlin described a third new form, *Eurelus mulaiki*, from New Mexico. We now believe that *proximus* is a synonym of *soleatus*, that *kerrensis* belongs to a different genus, and that *mulaiki* is for the present a sort of species inquirendum.

In 1949 Hoffman described, under the name *Toltecolus parvunguis*, a specimen of what is almost certainly *E. soleatus*. Comparison was made solely with the published descriptions of *Toltecolus garcianus*

and *T. chihuanus*—both now placed in other genera—and the description of *soleatus* overlooked entirely.

At the beginning of the present study, therefore, four names had been proposed in *Eurelus*, and still another had been set up in a related genus although actually based upon *soleatus*. On the basis of all available information, we propose to consider *Eurelus* as monotypic, considering two of the later names as junior synonyms of *soleatus* and transfering another to *Centrelus*. The remaining name, *mulaiki*, is almost surely not congeneric with *soleatus*.

Eurelus soleatus Cook

FIGURES 1, 3, 4

Eurelus soleatus Cook, 1911, p. 153.

Eurelus proximus Chamberlin and Mulaik, 1941, p. 62 (male holotype from Edinburg, Texas, in the collection of R. V. Chamberlin, collected by Stanley Mulaik, 1938).

Toltecolus parvunguis Hoffman, 1949, p. 1, figs. A, B (male holotype from Frio County, Texas, USNM 1853, collected by G. E. Ball, April 8, 1948).

HOLOTYPE: Male, USNM 801, from Falfurrias, Brooks County, Texas, collected in August 1906, by O. F. Cook.[4]

DIAGNOSIS: A large smooth-bodied atopetholid, 60 to 70 mm. in length and up to 8.0 mm. in diameter, with 46 to 49 segments. 40 to 50 ocelli in each rounded ocellarium. Tarsal claws of fourth–seventh legs of male greatly reduced; coxal lobes of third legs (fig. 4*d*) elongated and produced caudad, notched about their midlength and embraced by coxal lobes of fourth leg pair. Sternite of male gonopods distinctly arched medially, separated from the coxites by a considerable area of thin sclerotized membrane. Apices of coxites conically acute, finely punctate. Posterior gonopods robust, telopodite produced distally into a short truncate lobe and an opposed laminate terminally expanded process.

DESCRIPTION: The very detailed description published by Cook cannot be improved upon except with respect to the genitalia, which are now illustrated in detail for the first time.

From the anterior aspect, the anterior gonopods are dominated by the laterally arched coxites, which contact the sternite only slightly at its lateral ends. Mesially the coxites are separated by the intercalary vinculum, formed by thickening and sclerotization of the connective tissue between them and the sternite. The sternite is distinct and subtransverse, but narrower and somewhat arched near the median line. Laterally the sternite becomes broader and gives

[4] This specimen was misplaced by Cook in the main body of the Museum's diplopod collection, and has not yet been recovered for segregation in the type series.

rise to the elongate, slender sternal apodemes. On the caudal side the sternite becomes attenuated and merges with the base of the coxites. The coxites are rather massive and laterally arched, divided on the anterior face into two subsegments by a distinct suture, which, in passing around to the caudal side, broadens into an articulation. Both of the subdivisions of the coxae contribute to the elongate coxal apodeme (fig. 4,*b*), which extends ventrad from both the cephalic and caudal apices of the coxae, and represents a prolongation of the gonocoel formed by each coxa for the accommodation of the posterior gonopods. Superficially the caudal edge of the coxal apodeme appears to be continuous with the mesial margin of the telopodite, but there is actually no connection, and the telopodite is attached to the coxite by a movable articulation.

The posterior gonopods are rather short and robust, and the coxal apodeme is half again as long as the coxotelopodite. The latter has a subtriangular base resulting from consolidation of the acutely angular space formed by the telopodite and coxite in such genera as *Arinolus* and *Onychelus*. Distally the telopodite ends in two lobes—one a subterminal, truncate, marginally fimbriate lobe on the caudal side, and the other an obtusely rounded spatulate terminal lobe. The apodeme is attached a short distance from the mesial end of the coxotelopodite.

The coxal lobes of the anterior male legs are illustrated in figure 4,*d–f*. When in place, the distal third of the processes of the third coxae are clasped by those of the fourth, the interlocking facilitated by a subterminal notch on each of the former. In the drawing, made from a slide mount, the terminal portion distad of this notch is shown as bent somewhat laterad; normally it is directed caudomesiad and in line with the rest of the process. The coxal lobes of the fourth and fifth legs are flat and laminate, the distomesiad corner of each bent caudad and then laterad to form a slight hook. Prefemora of anterior legs unmodified, but femora of each with a distinct rounded projecting lobe at the base. Tarsal joints definitely flattened or depressed on the dorsal surface.

Discussion: Variation: On the basis of our moderate series of mature specimens from a single locality, it is possible to determine something of the individual variability in this species. Heretofore, some authors have assumed that all individuals of a population must be identical, and have made the slightest deviation from a known standard (even from a single specimen) the basis of creation of new species. We have investigated variability in several characters frequently thus misused in spiroboloids.

Segment number: Cook found that 4 of his specimens had 48 segments and 1 had 47. In 12 specimens at hand, we observed the

following frequency distribution: 46 segments in 2 specimens, 47 in 2, 48 in 5, and 49 in 3. The statistical mean for this series is 47.7, with a standard deviation of 1.06. Although the series is not large, a spread of 6 standard deviations should include about 99 percent of the total variability to be expected for an unlimited series from the locality sampled. Numerically this yields an expected range in segment number of 44 to 51, actually not much greater than the observed range in the material studied.

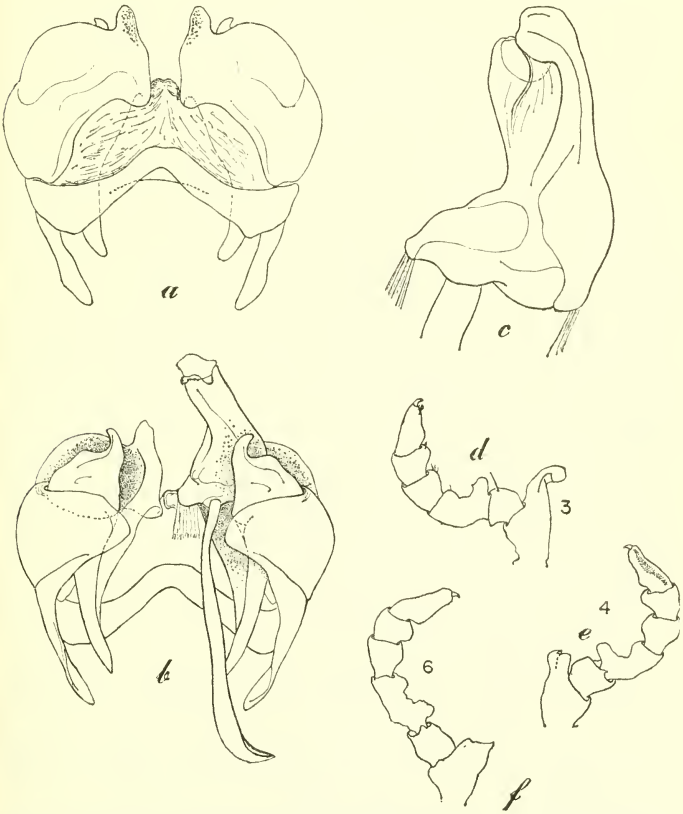

FIGURE 4.—*Eurelus soleatus* Cook, male specimen from Webb County, Texas: *a*, anterior gonopods, cephalic aspect; *b*, anterior and left posterior gonopods, caudal aspect; *c*, right posterior gonopod, cephalic aspect, enlarged; *d*, 3rd leg; *e*, 4th leg; *f*, 6th leg.

Clypeal foveolae: Some taxonomists attach considerable importance to the number of these supralabial pits, and even go so far as to establish species and genera on slight variations in the total number. In some groups, such as the Rhinocricidae, the number may be fixed and constant, in others, including the Atopetholidae, there is considerable variation within a species. Our series of *E. soleatus* yielded the following counts: 3–3 in 4 specimens, 3–4 in 1, 3–5 in 2, 4–4 in 4, and 4–5 in 1. Cook found "five clypeal foveolae on each side, sometimes only four." Apparently the number ranges from 3–3 to 5–5, with 4–4 occurring most frequently. The foveolae appear to afford a very weak basis for the establishment of any grade of taxonomic category, particularly when it is based on a single specimen.

Number of ocelli: Cook gave ocellus counts for one of his types, 43 on one side and 44 on the other. We have made counts from 4 specimens taken at random, and find considerable variation: 49–51; 49–45; 40–41; 44–46. So few numbers cannot be satisfactorily analyzed statistically, yet it should be obvious that the number of ocelli varies at least from 40 to 50 in each ocellarium, and the probability is that the expected range will be slightly greater. Here again is another character which should be used with the greatest caution, if at all, for the discrimination of species.

It should be stated, moreover, that we anticipate the establishment of geographic variational clines in many structural characters of millipeds. If this proves to be the case, the total ranges of variation within a species—particularly a widely distributed form—will doubtless prove to be much greater than we have indicated for material from a single locality.

Synonymy: Upon consideration of the known variability of *Eurelus soleatus*, we can find nothing in the description of *E. proximus* to warrant its recognition as a valid species or subspecies. The statement was made that *proximus* is closely related to *soleatus*, but differs in being slightly smaller, with 45 segments instead of 48 ("apparently the normal and nearly constant number in *soleatus*"), and in having the first segment dark instead of light, as mentioned in Cook's description. Another point of difference drawn from the single type specimen was that the posterior gonopod was extruded.

The figures cited for both size and segment number in *proximus* are included in the known range of variation in *soleatus*. The ostensible difference in coloration is very unreliable inasmuch as the color of preserved material is known to vary with both the method and duration of preservation. The exposure of the posterior gonopod in the type of *proximus* is of course meaningless, since these appendages are extrusible in all spiroboloids; whether they happen to be protruded at the time of preservation is entirely accidental, and does not so far

as is known reflect a peculiarity of any rank of taxonomic group. In our series of 12 male *soleatus*, 3 or 4 have one or the other of the posterior gonopods protruded for various distances.

There is no reason for maintaining *Toltecolus parvunguis* as a separate species. The name was proposed in ignorance of Cook's 1911 paper, and was set up as a new species on the basis of contrast with the Mexican *Toltecolus garcianus* Chamberlin (=*Centrelus kerrensis*). The description agrees in every particular with the material that we have identified with Cook's *E. soleatus*.

Distribution: The Coastal Plain of southern Texas, between the Rio Grande and Colorado Rivers. The type specimens were taken by Cook at Falfurrias, Brooks County, and he had additional specimens from San Antonio, Bexar County, and Moore, Frio County. The type of *E. proximus* is from Edinburg, Hidalgo County, and that of *T. parvunguis* from Frio State Park, Frio County. The series of millipeds at hand was collected along the highway 35.5 miles northwest of Laredo, Webb County, May 29, 1955, by Leslie Hubricht. This locality in the Rio Grande Valley is the westernmost now known for the species. The occurrence of *soleatus* in adjacent parts of Mexico, however, is certainly to be expected.

Genus *Centrelus* Cook

Centrelus Cook, 1911, p. 154.
Toltecolus Chamberlin, 1943a, p. 27 (type species: *Toltecolus garcianus* Chamberlin).

Type species: *Centrelus falcatus* Cook, by original designation.

Diagnosis: A eureline genus similar to *Eurelus*, from which it differs conspicuously in the presence of distinct upcurved spines on the lower caudal edge of the pleurotergites. In the male sex the anterior tarsal claws are reduced, and the coxal lobes well developed; coxites of the anterior gonopods with a large fleshy membranous lobe near the apex on the anterior side.

Discussion: The original generic diagnosis itemized external structural details at some length but touched only briefly on the genitalia, and gave no illustrations of these appendages. *Centrelus* thereupon slipped into a justifiable obscurity, and the name has not appeared again in the literature.

Texan material received from Leslie Hubricht agrees so closely with the description of *Centrelus* that we have no doubt it is at least congeneric with the type species. On this basis we have illustrated the pecularities of the gonopods, and herewith suggest the identity of *Toltecolus* with *Centrelus*, as well as some specific synonymy to be discussed in a following paragraph. The type species *C. falcatus* Cook, is from the State of Guanajuato; the other known species, *C. kerrensis*, is known to occur in Nuevo León and in western Texas, and suggests

a generic range along the Sierra Madre Oriental, with additional species probably remaining to be discovered.

Centrelus falcatus Cook

Centrelus falcatus Cook, 1911, p. 156.

HOLOTYPE: Male, USNM 800, from Guanajuato, Mexico, probably collected by A. Duges.[5]

DIAGNOSIS: A small species of *Centrelus* about half the size of *C. kerrensis*, and with only 3 or 4 lateral spines on each segment instead of 6 to 10 as in that species.

DESCRIPTION (FROM COOK): Length of male about 38 mm., width about 3.0 mm.; female about 42 mm. by 4.5 mm.

Clypeal foveolae 4–4; surface of vertex and clypeus smooth; ocellaria oval or trapezoidal, each with about 40 ocelli in 7 or 8 rows.

Marginal ridge of the collum broad, and the lateral angle rather rounded, not projecting below the second segment as in *Eurelus*. Second segment with the anterior margin decurved.

Surface of segments nearly smooth, very finely and indistinctly punctate and longitudinally striate above; lateral and ventral striations very short, confined to the metazonite, surface below each striation smooth. Segments behind middle of the body with the striations well separated, only three or four on each side, and produced into distinct sharp spines curving obliquely upward.

Last segment smooth, the apex very broadly triangular-rounded, distinctly exceeded by the strongly convex, smooth, anal valves. Preanal scale very broadly rounded.

Centrelus kerrensis (Chamberlin and Mulaik), new combination

FIGURES 3, 5

Eurelus kerrensis Chamberlin and Mulaik, 1941, p. 61.—Chamberlin and Hoffman, 1958, p. 156.

Toltecolus garcianus Chamberlin, 1943a, p. 27 (male holotype from Garcia, Nuevo León, Mexico, in the collection of R. V. Chamberlin, collected by C. Bolivar and F. Bonet, July 14, 1942.)

HOLOTYPE: Male, collection of R. V. Chamberlin, from Raven Ranch, Kerr County, Texas; collected in July 1939 by Stanley and Dorothea Mulaik.

DIAGNOSIS: A moderate to large sized eureline characterized by the number of segments (50–53) and ocelli (35–45), differing from *C. falcatus* as well as other eurelines in having as many as 8 to 10 stout marginal spines on the lower sides of the metazonites.

DESCRIPTION (male from Real County, Texas): Body 65.0 mm. long and 6.5 mm. in diameter, with 51 segments.

[5] This specimen was misplaced by Cook in the main body of the Museum's diplopod collection, and has not yet been recovered for segregation in the type series.

Color of preserved specimen nearly uniform black, the extreme caudal edges of the metazonites silvery white to gray, possibly due to color change in alcohol.

Front of head smooth and polished except for several distinct transverse grooves in the clypeal region; epipharangeal groove distinct up to interantennal space; genae with about 12 distinct short striations extending to the margin of the head. Ocellaria small and nearly circular, ocelli all nearly equal in size and shape, arranged in 7 rows as follows: 4, 5, 6, 6, 6, 6, 5—a total of 38; interocular space almost 4 times the diameter of an ocellarium. Antennae small and short,

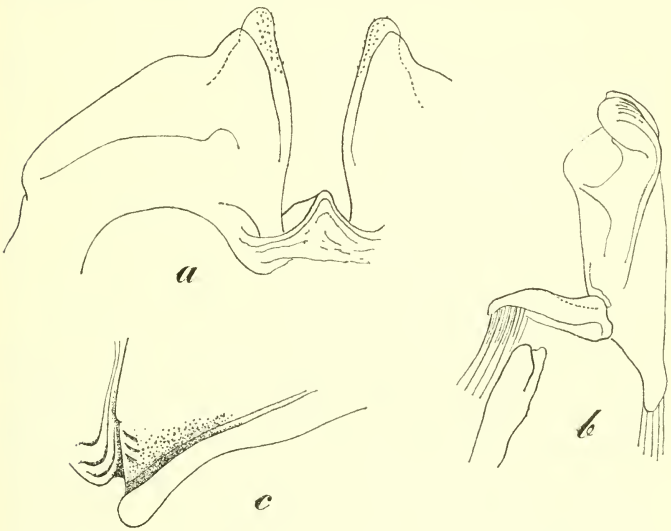

FIGURE 5.—*Centrelus kerrensis* (Chamberlin and Mulaik), male specimen from Real County Texas: *a*, distal half of anterior gonopods to show the membranous lobe in front of the coxal apex; *b*, right posterior gonopod, cephalic aspect; *c*, lower end of collum of left side.

the first three articles glabrous, distal four finely setose; second article longest, third through sixth slightly smaller and all subequal, all articles about the same width.

Collum somewhat wider than head but narrower than following segments, its surface smooth and polished; lateral ends as shown in figure 5*c*; second segment with about five distinct ridges behind end of collum, the lowest of which is actually knobby in contour; pleural lobe with a moderately elevated anterior ridge. Following segments similar to second but with ridges less prominent. Near middle of body the ridges become gradually more produced and project beyond

margin of segments as a series of 6 to 10 sharp upcurved spines. Ventral surface of mesozonites in front of the ridges with a distinct reticulate pattern of fine striae, the striae merging dorsally into transverse parallel ridges that fade out near the level of the ozopores. Transverse sutures very distinct; metazonites slightly elevated.

Three segments in front of the telson strongly telescoped. Telson bluntly acuminate, equalling but not surpassing the anal valves, latter smooth and evenly convex, with their ventrolateral corners depressed and wrinkled. Preanal scale broad, divided by a transverse furrow into two heavily striated portions, the basal part strongly depressed at the lateral ends, the distal half noticeably inflated or convex.

Sternites trapezoidal, with 12 to 16 transverse parallel ridges; stigmata entirely enclosed within the sternites. Legs rather long and slender, the two distal joints visible from above body, all joints smooth and polished, their decreasing order of length: 3, 6, 2, 1, 4, 5. Ventral setal formula: 1, 1, 2, 2, 2, 6.

First two pairs of legs crassate, with long robust claws; legs 3–7 of normal size and shape; third legs with claws of normal size, the others back through the seventh with claws reduced to a tiny vestige, the tarsi of these legs strongly depressed on the dorsal surface. Coxal lobes of third legs erect, slender, and membranous, their tips bent slightly cephalad and then caudad as seen in lateral aspect; lobes of legs 4–7 flat, simple, wedge-shaped, becoming smaller posteriorly.

Sympleurites of seventh segment broadly in contact at the median line with a distinct suture evident; the anterior edge continuing the curve of the segment, the posterior edge elevated and overhanging.

Anterior gonopods very similar to those of *Eurelus soleatus* but differing in the presence of a distinct membranous lobe on the anterior side of the coxal apex (figure 5,*a*). Posterior gonopods rather robust and straight, the telopodite ending in two distal lobes as shown in figure 5,*b*. No trace of a seminal groove can be detected.

Discussion: Variation: In most structural details this species is quite stable over its considerable range. The gonopods of our male from Real County, Texas, match perfectly with the illustrations of the type specimen of *T. garcianus*.

Combining counts from specimens at hand and published information, we have nine counts of segment number, ranging from 50 to 53 with a mean of 51.4. The standard deviation for this series is 1.33. There is a slight indication that the number increases in going north, but this gradient is probably too slight and gradual to be of much significance. Throughout the area occupied by the two species jointly, there is very little overlap in segment count in *C. kerrensis* and *E. soleatus*.

Six ocellus counts are as follows: 33, 35, 37, 37, 39, and 42. Here there seems to be neither sexual nor geographic variation, but the series is too short to be of particular value.

The size appears to vary considerably. The largest known specimen is a female from Garcia, Neuvo León, 75 mm. long and 8.0 mm. wide; the smallest is a female from Pandale, Texas, about 40 mm. long and 5.0 mm. wide. The small specimens appear to be structurally identical with larger ones.

Clypeal foveolae vary from 4–4 to 5–5, and are somewhat more constant than in *E. soleatus*, in which counts of 3–3 are noted as well.

Synonymy: The synonymy of *Eurelus kerrensis* and *Toltecolus garcianus* was established in the following manner. The adult male from Real County, Texas, was found to agree perfectly with the drawings given for *garcianus* as well as with the description, as far as it goes. This specimen also matched the original diagnosis of *Centrelus* very closely, leaving little doubt that it is congeneric with *C. falcatus*, and on this basis we determined two collections from Texas as *Centrelus garcianus*. However, when a map of the known records of the Eurelinae was prepared, it was observed that Real County is geographically adjacent to Kerr County, whence came the type series of *E. kerrensis*. Comparison of our material with the description of that species, moreover, showed a remarkable concordance in every particular except that metazonite spines were not mentioned for *kerrensis*. On the chance that they may have been overlooked, we requested Chamberlin to examine the types for this character. He very kindly did and reported (in a letter dated May 30, 1957) that small but distinct and upturned spines are actually present. This discovery removed the last obstacle for presuming that *kerrensis* is the older of two names applied to a spiroboloid population which occurs in the plateau country of Texas and adjacent Nuevo León. Although we have been unable to study the type specimens of either name, we feel that the available evidence as outlined above makes the likelihood of error quite remote.

Distribution: *Centrelus kerrensis* is now known to have a fairly wide range over much of western Texas and adjacent Nuevo León. From the existing records and the fact that it has not so far been found in the Rio Grande Valley, we assume that it is an upland form. The type locality was Raven Ranch, in Kerr County, Texas (Chamberlin and Mulaik, 1941), and the species was subsequently recorded (under the name *Toltecolus garcianus*) from Garcia, near Monterey, Nuevo León (Chamberlin, 1943a). Material has been seen from the following new localities:

Texas: Real County: 10 miles north of Leakey, June 10; 1955, Leslie Hubricht (R. L. Hoffman). Presidio County: Near Porvenir, September 28, 29, 1946, Bryan

Patterson and J. M. Schmidt (Chicago Nat. Hist. Mus.). Val Verde County: 3.3 miles northeast of Pandale, June 11, 1955, Leslie Hubricht (USNM).

Comanchelus, new genus

TYPE SPECIES: *Comanchelus hubrichti*, new species.

DIAGNOSIS: A eureline genus in which the tarsal claws of the anterior legs are not reduced, and the coxal lobes, if present, are simple with usually only those of the third leg pair enlarged. Sternite of the anterior gonopods nearly transverse; sternal apodemes not completely fused to the coxites on the caudal side (fig. 6,*b*).

DISCUSSION: This genus is proposed for two species which although generally similar to *Eurelus soleatus* appear to diverge enough to justify their recognition as a separate group. The number of segments is about the same as in *soleatus* (45 to 52), but the species appear to average somewhat smaller in size. Probably the most reliable means of recognizing the genus will be found in gonopod characters.

In addition to the type species, we tentatively refer here the form named *Toltecolus chihuanus* by Dr. Chamberlin (1947a). As far as can be ascertained from the original description and illustrations, the species appears to be closely related to *C. hubrichti*, but a careful study of the gonopods of *chihuanus* is needed for a final confirmation of its systematic position.

Comanchelus chihuanus (Chamberlin), new combination

Toltecolus chihuanus Chamberlin, 1947a, p. 10, figs. 5–7.

HOLOTYPE: Male, collection of R. V. Chamberlin, from Chihuahua City, Chihuahua, Mexico, collected on July 23, 1944, by V. E. Shelford.

DIAGNOSIS: The coxae of the third leg pair are produced into elongated, cylindrical lobes. Posterior gonopods with a rounded subterminal lobe on the caudomesial margin instead of a laminate, acutely projecting blade as in *C. hubrichti*.

DESCRIPTION (FROM CHAMBERLIN):

Color a dark, olive gray, with dark annuli about caudal borders of metazonites. Legs dark chestnut.

Clypeal foveolae 5+5. Eyes very widely separated; ocelli arranged in 8 longitudinal series and the same number of transverse series.

Collum strongly narrowed down each side as usual, with the anterior margin conspicuously incurved at lower end, the elevation decreasing dorsad, the elevated border set off by a sulcus (fig. 5).

Segments smooth above. A true segmental sulcus absent above, though below indicated by a faint line which bends forward angularly at level of pore which it touches. Segments strongly striate below. Anal tergite rounded behind, the surface over caudal portion irregularly rugose.

In the male the first two pairs of legs are thickened and have the claws strongly enlarged. The claws of the following three pairs of legs also have enlarged claws but these decreasing from third pair to fifth.

Coxal processes of third legs of male extending back over bases of fourth legs, subcylindrical but with ventral face flattened or concave, the distal ends abruptly uncate.

The gonopods are as shown in the figures. Anterior sternite subquadrate; firmly seated in the shallow excavation on anterior face of gonopods.

Number of segments in the male holotype, 51.

Diameter, 4.8 mm.

RANGE: This species is known so far only from the type locality.

***Comanchelus hubrichti*, new species**

FIGURES 3, 6

HOLOTYPE: Male, USNM 2507, and paratypes of both sexes, from 3.3 miles northeast of Pandale, Val Verde County, Texas, collected on June 11, 1955, by Leslie Hubricht.

DIAGNOSIS: A species in which the anterior coxae of males are not produced into lobes or processes, and in which the posterior gonopod is produced mesially into a thin, acutely angled lamina, its apex distally exceeding the main body of the appendage.

DESCRIPTION (PARATYPE MALE): A stout bodied atopetholid, nearly parallel-sided, with the head and collum narrower than the following segments; last four or five segments much smaller than their predecessors and distinctly telescoped. Color uniform olive-gray.

Head ovoid, slightly flattened frontally, surface smooth and polished, sunk in collum to edge of the ocellaria. Labral sinus deep and acute; clypeal foveolae 4–4, those nearest the midline set closer together. Geneae short and unmargined, exceeded by the second antennal article. Ocellaria rounded-ovoid, separated by about 2.7 times the diameter of each, ocelli variable in size and number, those nearest the mandibular suture much the largest, those near the front of head small and unpigmented, and easily overlooked, 41 on one side, 42 on the other.

Antennae short and slender, not reaching caudal edge of collum; second article largest and longest, the others decreasing in size distally; articles with scattered setae except sixth and seventh, which are fairly thickly clothed with recumbent setae. Outer face of mandibular stipe with a somewhat elevated caudal margin, the discal depression terraced around its periphery and ornamented medially with numerous very fine irregular ridges.

Collum small and rather obtusely triangular laterad, the anterior marginal groove distinct as far as middle of ocellaria, not completely parallel to the edge, and not reaching caudal margin of the collum at the ends. Surface of collum smooth and flat, without punctations or striae. Anterior edge of pleurotergites of second segment turned up into a large marginal flange, the area behind it coarsely striate (fig. 6,*d*).

Body segments finely coriaceous under magnification, without punctations. Segmental sulcus distinct entirely around body, anterior portion of prozonite with fine transverse striae. Pores very small but distinctly in the mesozonite, below level of the lateral longitudinal suture. Lower sides with a few longitudinal ridges, not produced into marginal spines; ventrolateral areas of prozonites and mesozonites ornamented with very fine ridges forming elongate polygons that merge dorsally into the transverse striae.

Telson broad and bluntly angular, not concealing valves in dorsal aspect; the latter typical for the subfamily in appearance; preanal scale broadly transverse, entirely smooth and lacking modifications such as occur in *Centrelus kerrensis*.

Sternites subrectangular, only slightly narrowing caudad, with about six to eight fine transverse striae laterally turned caudad. Stigmata contained entirely with the sternal sclerite. Legs smooth and polished, the tarsal claw very long and slender, more than half as long as tarsal joint; ventral setal formula 1–1–2–2–2–6; tarsi with two or three small setae on caudal side and one on the cephalic.

First two leg pairs of the male reduced in size and strongly incrassate, especially the basal two joints. Tarsal claws of first three leg pairs very long, becoming shorter on the next pairs. Coxae of anterior legs not produced or lobed although membranous areas, possibly extrusible to some extent, can be detected when the legs are dry.

Sympleurite of seventh segment nearly parallel-sided and slender, the median suture visible. Gonopods (figure 6,*a*,*b*) with sternite of anterior pair slender, nearly straight across and, on the caudal side of the gonopods, not entirely fused to the coxite, a distal portion being free and somewhat projecting. Coxites somewhat crescentic in shape, in contact with the sternite, and arching mesially, separated by a small slender vinculum, apices of coxites set with areas of fine denticles. Telopodites quite small, with caudolaterally directed apices, the latter not or but slightly visible in anterior aspect. Posterior gonopod with very long and slender apodeme; distal elements not distinctly divided into coxite and telopodite, the caudal margin of the joint produced into a large thin lamina, drawn out distally into an acute hyaline angle.

Discussion: Variation: The number of segments in four specimens from the type locality ranges from 45 to 48; two males from Baylor County, Texas, have 44 each. However, four specimens from the vicinity of Abilene, Texas, have counts ranging from 48 to 52 and suggest that there may be an east-to-west decrease in segment number. In all of the material examined, the clypeal foveolae vary from 4–4 to 5–5. There is considerable variation in size, specimens from the western extremity of the range being smaller but otherwise similar to the larger eastern individuals.

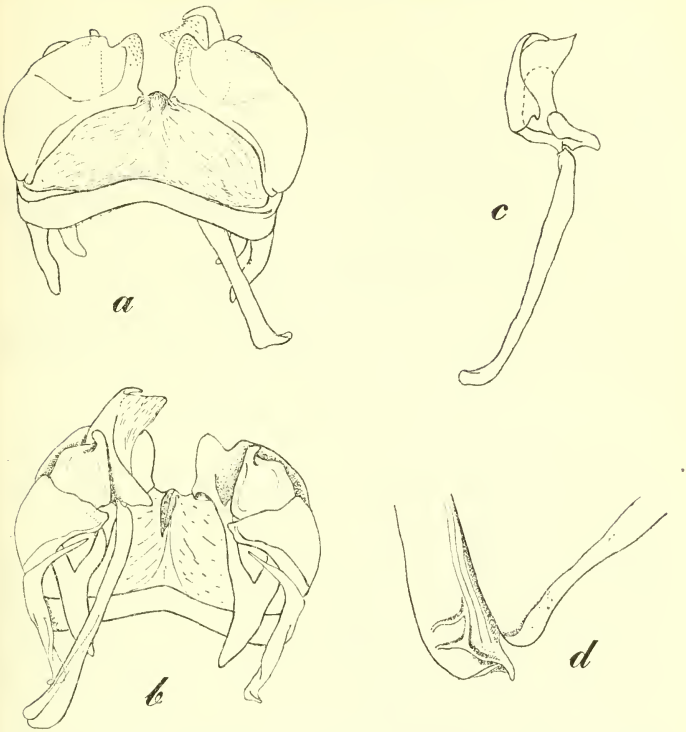

FIGURE 6.—*Comanchelus hubrichti*, new species, male paratype from Val Verde County, Texas: *a*, anterior gonopods and right posterior gonopod, cephalic aspect; *b*, same, caudal aspect; *c*, posterior gonopod, caudal aspect; *d*, lower end of collum and adjacent part of 2nd segment, left side.

DISTRIBUTION: *Comanchelus hubrichti* is apparently rather widespread over much of western Texas despite having been taken at only a few localities. Material has been examined from the following localities:

TEXAS: Baylor County: 5 miles south of Seymour, April 20. 1947, K. P. Schmidt (Chicago Nat. Hist. Mus.). Dimmitt County: Carrizo Springs, October 16, 1954, Leslie Hubricht (R. L. Hoffman). Hays County: Southeast of San Marcos, May 3, 1955, Leslie Hubricht (R. L. Hoffman). Taylor County: 25 miles south of Abilene, March 18, 1948, H. S. Dybas (Chicago Nat. Hist. Mus.). Val Verde County: 3.3 miles northeast of Pandale, June 11, 1955, Leslie Hubricht (USNM).

Eurelinae of uncertain generic position

Eurelus mulaiki Chamberlin, 1943b, p. 147, figs. 7–11.

HOLOTYPE: Male, collection of R. V. Chamberlin, from north of Glencoe, Lincoln County, New Mexico, collected on May 31, 1941, by Stanley and Dorothea Mulaik.

DISCUSSION: The drawings of the gonopods of this form are extremely diagrammatic and show little of specific importance; nor is it possible to determine to what genus the species should be referred. Possibly the closest relationships are with the species of *Comanchelus*, as suggested by the normal tarsal claws and small coxal lobes. Unfortunately, we have been unable to secure material for study.

RANGE: The species, having been reported in the original description from several localities in Lincoln and Torrance Counties, apparently enjoys a wide distribution in central New Mexico.

Atopetholinae, new subfamily

Species of this group are small- to moderate-sized atopetholids, averaging slightly smaller than the species of Eurelinae, which they superficially resemble. Owing to the scarcity of material and to the shortcomings of published descriptions, no satisfactory account of external structure can be essayed beyond an account of details in *Atopetholus angelus*, a member of the type genus. The antennae tend to be of considerable length, extending back to the second segment, and are therefore much longer than in the Eurelinae. In *Atopetholus* the collum is evenly acuminate toward the lateral ends, which in *Watichelus*, however, are bent somewhat caudoventrad. The body segments are smooth and polished, the ozopore opening in the mesozonites, and in *Atopetholus*, at least, the suture between prozonite and mesozonite is very poorly defined or invisible.

In the male, the claws of the anterior legs are not reduced in size, and the coxae are provided only with modest, low subtriangular lobes, which increase slightly in size from the third to seventh leg pair.

Male gonopods are rather similar in both of the genera, particularly the anterior pair. The sternite is slightly arched mesially, and is surmounted by a large subtriangular vinculum that widely separates the coxites, but that becomes hyaline and membranous proximally and is not continuously rigid with the sternite.

The coxites are moderate in size, their mesial corners produced distally as usual but to a lesser extent than normal for the family. The telopodites are large and flattened, the apex being broad and blunt, and in *Atopetholus*, at least, subtended on the caudal side by an additional acuminate process that projects caudad and slightly

laterad or else distinctly distad. The base of the telopodite is set off by a marginal rim which projects slightly out beyond the end of the coxite toward the opposite side.

The posterior gonopods tend to be quite simple, the coxite and telopodite merging into a broad consolidated subtriangular region with no remaining trace of a joint at the point of the union. No traces of a seminal groove have been detected, and nothing that might be considered a solenomerite. The end of the telopodite may be simple and laminate or strongly recurved, and a large subterminal branch is present in *Watichelus*.

There is some doubt attending our disposition of genera in this subfamily. The generic name *Orthichelus* has been proposed for species which differ only slightly from typical *Atopetholus*, and we have therefore united the two names largely on the basis of the "quality level" of degree of differentiation. Final resolution of the matter awaits the attention of someone able to collect material from numerous localities in southern California. The poorly known genera *Tidolus* and *Hesperolus* may prove to be referable to this subfamily when their type species are finally rediscovered and studied.

Genus *Atopetholus* Chamberlin

Atopetholus Chamberlin, 1918, p. 168.

Onychelus (not of Cook) Verhoeff, 1938, p. 274.—Chamberlin, 1949, p. 169 (in part).

Orthichelus Chamberlin and Hoffman, 1950, p. 7 (type species: *Onychelus phanus* Chamberlin).

Type species: *Atopetholus californicus* Chamberlin, by original designation.

Diagnosis: An atopetholid genus characterized by the occurrence of large accessory projections on the telopodite of the anterior gonopods just behind and below the apex of the joint. The absence of a subterminal projection on the caudal margin of the posterior gonopod distinguishes the genus from the related *Watichelus*. The lateral ends of the collum are nearly symmetrically acuminate, in contrast to their being bent caudally in *Watichelus*.

Discussion: The taxonomic history of the group of species assembled under this generic name has been unnecessarily complicated and confusing owing chiefly to the failure of both Cook and Chamberlin to document adequately the descriptions of some of their new forms. The difficulty began with the proposal of *Onychelus obustus* in 1904, when Cook briefly remarked that the posterior gonopods of the species are "concealed, simple, slender, falcate." No illustrations were given for the species, and its really diagnostic characters have remained unknown for almost half a century. In 1923 Chamberlin

described under the name *Onychelus nigrescens* an atopetholid from Coronado Island, Gulf of California, in which the gonopod was much like that described by Cook. His example was followed by Verhoeff (1938) in naming *O. michelbacheri* from southern California, and finally Chamberlin added another related species, *O. phanus*, from the same general area.

The history of *Atopetholus* developed simultaneously with but independently of that of *Onychelus*. Proposed in 1918, *Atopetholus* included species in which the posterior gonopod is slender and falcate, with a recurved tip, and in which the telopodite of the anterior gonopod is provided with an accessory process. Apparently Verhoeff was unaware of this paper for his knowledge of the name Atopetholidae seemed limited to its use as a heading in Chamberlin's 1923 contribution. He thereupon rejected it as a nomen nudum and proposed the new name Onychelidae, a name unfortunately based upon a milliped not even in the same subfamily with the true *Onychelus* of Cook. His species *Onychelus michelbacheri*, indifferently described and illustrated, appears to be a fairly typical form of *Atopetholus* in the sense here adopted.

Onychelus continued to be used for quite a variety of millipeds until 1949, when Chamberlin restricted it to *obustus*, *michelbacheri*, *phanus*, and *nigrescens* and proposed the new names *Gosichelus* and *Watichelus* for species that had been previously described as forms of *Onychelus*. At the same time, however, the long-lost type material of *O. obustus* was found among Cook's effects and returned to the U.S. National Museum. An examination of the gonopods showed at once that Cook's description was quite inaccurate, as the posterior elements are actually arcuate and distally bifid and both these and the anterior gonopods are totally different from those of the other three species mentioned above. Actually, two other millipeds had been described that are very close to *obustus*, although Chamberlin (misled by Cook's description) placed them in the new genus *Gosichelus*. This discovery led to the subsequent relegation of *Gosichelus* to the synonymy of *Onychelus* and the proposal (Chamberlin and Hoffman, 1950) of the new generic name *Orthichelus* to include *phanus*, *michelbacheri*, and *nigrescens*.

The question that we have had to consider is whether the variation in the posterior gonopod justifies retention of *Orthichelus* as a valid genus. Upon weighing all of the available information, we cannot find any support for this course. Whether or not the extreme tip of the gonopod is recurved to form a terminal hook appears to be a very weak basis for a generic name, particularly when all other characters appear to be the same in typical species of *Atopetholus* and *Orthichelus*. There seems to be some variation in the development of the terminal

hook, and, furthermore, the recent description of *Atopetholus barbaranus* states that the species differs from all others "in having the distal end of the posterior gonopods with its border straight, not rolled in or recurved."

For the present, at least, the most reasonable course seems to be the combination of the two names, with the recommendation that the question be reopened someday by an investigator having an abundance of material of all the species concerned.

Atopetholus angelus Chamberlin

FIGURES 2, 7

Atopetholus angelus Chamberlin, 1920, p. 101; 1953, p. 138.—Chamberlin and Hoffman, 1958, p. 155.

HOLOTYPE: Male, Mus. Comp. Zool., from Edendale suburb, Los Angeles, Los Angeles County, California, collected by Gordon Grant on December 30–31.

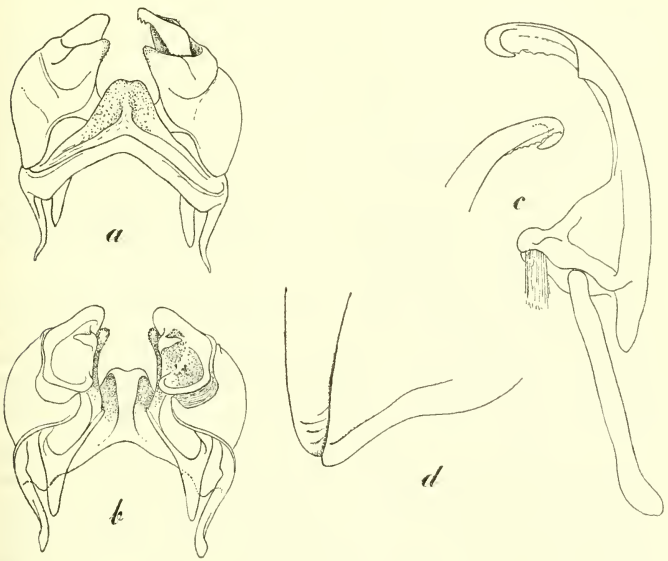

FIGURE 7.—*Atopetholus angelus* Chamberlin, male paratype from Los Angeles County, California: *a*, anterior gonopods, cephalic aspect; *b*, same, caudal aspect; *c*, left posterior gonopod in caudal aspect, with the terminal part shown from cephalic aspect; *d*, lower end of collum, left side.

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DIAGNOSIS: A large species of *Atopetholus* in which the accessory process of the anterior telopodite is rather small and directed caudolaterad instead of distad as in most other species, and in which the tip of the posterior gonopod is recurved proximad, the lower edge of the telopodite being subterminally serrate and the upper edge produced mesiad into an acute lobe at about the midlength.

DESCRIPTION (MALE PARATYPE): Front of head smooth and polished, with several transverse (about 12) grooves between the antennae; genae smooth; labral teeth very low and broad, almost obliterated; labral pores 5–5; ocellaria nearly round, the intervening space almost four times the diameter of an ocellarium; antennae moderately long, extending back to second segment, the first 3 articles glabrous, second article longest, third through seventh gradually decreasing in size. Exposed surface of mandible flat and subcircular, with a distinct marginal ridge.

Collum smooth and polished, somewhat flattened dorsally; second tergite with about six shallow grooves on each side behind ends of collum, the pleural lobe merely depressed without a distinct anterior flared rim.

Body segments smooth and shining, with only one distinct transverse suture passing well behind the ozopore; the lower sides of tergites with small, poorly defined longitudinal striations. Last three segments strongly telescoped; telson very short and blunt, not concealing the anal valves in dorsal aspect, the valves evenly convex, smooth and polished, the preanal scale small and flat. Sternites trapezoidal, with about six to eight fine transverse ridges; adjacent surface of pleurites flat and smooth. Legs moderately long and slender, lengths of joints in order of decreasing length 6, 3, 2, 1, 4, 5; tarsal claw long and slender. Ventral setal formula: 1–1–3–3–3–6.

First two pairs of legs crassate, with a large robust claw; legs 3–7 normal in size and shape, their tarsal claws not reduced, the tarsi not depressed or modified. Coxal lobes subtriangular, moderate in size, increasing slightly from third to seventh; pleurites of seventh segment forming a high transverse crest, fused mesially and slightly overhanging caudally.

Male gonopods are discussed briefly with respect to general form and the musculature on page 107. In the lack of comparative material, it is difficult to single out what might be specifically diagnostic in the gonopod structure, although some presumably diagnostic features have been listed in the foregoing diagnosis of the species. The anterior sternite is rather massive and somewhat pitted over its surface, particularly the intercoxal vincular portion. The base of the posterior telopodite is produced proximally into an elongate lobe for the attachment of retractor muscle "6."

Color (from original description):

General color typically shining black with a narrow, typically ferruginous but sometimes nearly white, pale line along caudal border of each segment, the collum having an anterior ferruginous border as well. Legs from dark brown to fuscous or black.

Discussion: This species appears to be sympatric with *A. californicus*, both having been recorded by Chamberlin (1953) from Los Angeles. The following statement from the original description of *A. angelus* indicates a way of distinguishing males of the two species:

Posterior apophysis of telopodite of anterior gonopods [of *angelus*] in ventral view longer and more slender [than in *californicus*], not expanded distally; the distomesial angle of telopodite more prominent, often meeting its mate in the middle line. Telopodite of posterior gonopods distally more strongly uncate.

The term "posterior apophysis" is referred to in this paper as the accessory process of the anterior telopodite.

Distribution: Known thus far only from Los Angeles County, California. It has been reported in the literature from Edendale suburb and from Reservoir Hill, both at Los Angeles. An additional collection has been studied consisting of a male with 40 segments from the San Juan Hills, 2 miles west of Spadra, Los Angeles County, California, collected in June–July 1943 by D. D. Davis (Chicago Nat. Hist. Mus.).

Atopetholus barbaranus Chamberlin

Atopetholus barbaranus Chamberlin, 1949, p. 168 (male holotype in the Chamberlin collection, from Orcutt, Santa Barbara County, California, date and collector not stipulated).

The original description states:

The species may be readily distinguished from the others thus far known in having the distal end of the posterior gonopods with its posterior border straight, not rolled in or recurved. The two fingers of the anterior gonopods are characteristically long, slender, and divergent. The coxites of the anterior gonopods moderately extending beyond the sternite.

The holotype is said to have 48 segments, with a length of 40 mm. and a diameter of 5 mm. The following remark is also made: "Sternite of the third gonopod with the usual process." What is meant by this remark, we cannot imagine.

Atopetholus californicus Chamberlin

Atopetholus californicus Chamberlin, 1918, p. 168; 1940, p. 82, fig. F; 1953, p. 138 (male holotype, Mus. Comp. Zool., from Claremont, California, collected by W. A. Hilton).

This species is still poorly known and unfortunately the type specimen can no longer be found at the Museum of Comparative Zoology. The original description describes only the external features of the species; a subsequent reference contains a small sketch of a gonopod

telopodite, but this sketch is not useful for comparative purposes. As *Atopetholus californicus* is the type species of the genus, a good description of it is much to be desired.

Atopetholus carmelitus Chamberlin

Atopetholus carmelitus Chamberlin, 1940, p. 81, figs. c–e; 1941a, pp. 30–31, figs. 3, 4 (male holotype in the Chamberlin collection, from the Hastings Reservation, Monterrey County, California, collected on February 1, 1940, by J. M. Linsdale).

The description of this species includes the remark that it is one—

much resembling *A. californicus* but differing in the gonopods of the male. An easily noted difference is in the telopodite of the anterior gonopods; this at the distal end is extended into a curved acute process which lies in front of the base of the digitiform process whereas in *californicus* the corresponding process is short and blunt with its distal margin concave.

Atopetholus fraternus Chamberlin

Atopetholus fraternus Chamberlin, 1918, p. 169 (male holotype, Mus. Comp. Zool. from Friant, Fresno County, California, collected by R. V. Chamberlin).

This species has not, apparently, been reported since its description, and the types cannot at present be found in the Museum of Comparative Zoology. According to the original diagnosis, *Atopetholus fraternus* is:

Easily separable from the two preceding species [*A. californicus* and *A. parvus*] in the form of the male gonopods. The telopodite of the anterior gonopods is bent convexly forward at the side where it bears at the anterodistal angle a straight, simple, process additional to the caudally directed one arising from the distomesal edge behind, this feature at once separating it from the preceding species.

Atopetholus michelbacheri (Verhoeff), new combination

Onychelus michelbacheri Verhoeff, 1938, p. 276, figs. 1–3 (male holotype in the Verhoeff collection now in the Zoologische Staatsammlung, Munich, from Walker's Pass, Kern County, California, collected by A. E. Michelbacher).
Onychelus phanus Chamberlin, 1941b, p. 6, figs. 6, 7 (male holotype in the Chamberlin collection, from 6 miles west of Freeman, Kern County, California, collected on March 17, 1941, by Stanley and Dorothea Mulaik); 1949, p. 169.
Orthichelus phanus Chamberlin and Hoffman, 1950, p. 8.

Onychelus phanus was named insofar as one can deduce from its original description chiefly because of its being found in southern California whereas the admittedly very similar *O. michelbacheri* was stated to have come from "Nordcalifornien, am Walkerpass." [6]

[6] Actually, however, this information was elaborated on in a footnote stating "liegt der Walkerpass in einer sehr trockenen Gegend und befindet sich 100 Eng. Meilen nordlich von Los Angeles, etwa 50 Eng. Meilen südwestlich vom Death Valley Nat. Monument." These directions clearly refer to the Walker Pass that is located in the northeast corner of Kern County, about 4 or 5 miles west of the town of Freeman. There can be no doubt that the types of Verhoeff and Chamberlin actually came from the same locality and the major diagnostic character of *phanus* is thereby demolished.

The only structural difference stipulated for *phanus* was that the telopodite of the posterior gonopods appeared to be broader than illustrated for *michelbacheri*, but this difference is probably due to the fact that Chamberlin's drawing was made from a caudal aspect while Verhoeff's was made from the lateral aspect, which naturally shows the narrower dimension of the gonopod. Unless subsequent collections show that two sympatric sibling species occur at Walker's Pass and can be recognized by other constant differences, it seems that *phanus* must be considered a junior subjective synonym of *michelbacheri*.

***Atopetholus nigrescens* (Chamberlin), new combination**

Onychelus nigrescens Chamberlin, 1923, pp. 406, 407, fig. 46 (male holotype in the California Academy collection, from Coronado Island, Gulf of California, collected by J. C. Chamberlin).

The original account of this species is not as detailed as it should be, and the present generic allocation must be regarded as tentative.

***Atopetholus pearcei* Chamberlin**

Atopetholus pearcei Chamberlin, 1950, p. 6, fig. 3 (male holotype in the Chamberlin collection, from Oildale, Kern County, California, collected by W. M. Pearce on January 19, 1950).

The description of this species compares it only with *A. fraternus*, from which it differs in shape of the posterior gonopod—

such as in the smaller, almost obliterated anterior marginal lobe and in the tooth at proximal end of the posterior marginal lobe, this being acute and directed nearly at right angles to the long axis of the telopodite instead of being blunt and directed proximad parallel with the axis.

Genus *Watichelus* Chamberlin

Watichelus Chamberlin, 1949, p. 169.—Loomis, 1949, p. 241.

Type species: *Onychelus smithi* Chamberlin, by original designation.

Diagnosis: An atopetholid genus characterized by the presence of a distinct mesially directed branch or process on the telopodite of the posterior gonopod, and by the absence of a secondary process from the telopodite of the anterior gonopods. In other respects the genus is quite similar to *Atopetholus*, so far as can be determined from published accounts. Loomis (1949) mentioned that the lateral ends of the collum tend to be bent caudoventrad in species of *Watichelus*, and this condition may also be found to be a diagnostic character when all the species of *Atopetholus* are inspected for this particular detail. In *A. angelus* at least (fig. 2,*d*), the end of the collum is nearly symmetrical and directed ventrad.

Discussion: The distribution of this genus appears to be centered around the Colorado Desert of southern California and the arid region of adjacent Baja California. Doubtless numerous species remain to be discovered. One interesting inference to be made from the recent contribution by Loomis is that several species may occur at a single locality, a form of sympatry apparently not developed in other atopetholid genera. Not having material for personal examination, we merely subjoin a list of the known species, most of which are well described and nicely illustrated in Loomis' paper.

***Watichelus edentatus* Loomis**

Watichelus edentatus Loomis, 1949, p. 241, figs. 1, 2 (male holotype, USNM 2514, from between San Diego and El Centro, San Diego County, California, collected on January 29, 1921, by O. F. Cook).

***Watichelus emarginatus* Loomis**

Watichelus emarginatus Loomis, 1949, p. 243, figs. 7, 8 (male holotype, USNM 2515, from 8 miles south of Tia Juana, Baja California, Mexico, collected on January 1, 1925, by O. F. Cook).

***Watichelus cooki* Loomis**

Watichelus cooki Loomis, 1949, p. 243, figs. 5, 6 (male holotype, USNM 2516, from Descanso, Baja California, Mexico, collected on January 1, 1931, by O. F. Cook).

***Watichelus parallelus* Loomis**

Watichelus parallelus Loomis, 1949, p. 244, figs. 9, 10 (male holotype, USNM 2513, from Chula Vista, San Diego County, California, collected in December 1921, by C. G. Marshall).

***Watichelus robustus* Loomis**

Watichelus robustus Loomis, 1949, p. 241, figs. 3, 4 (male holotype, USNM 2512, from Chula Vista, San Diego County, California, collected on January 23, 1921, by O. F. Cook).

***Watichelus smithi* (Chamberlin)**

Onychelus smithi Chamberlin, 1947b, p. 49, figs. 52, 53 (male holotype, Acad. Nat. Sci. Philadelphia 9971, from Murray Canyon, Colorado Desert, 3 miles north of Palm Springs, Riverside County, California, collected in November 1946 by Lloyd M. Smith).

Watichelus smithi Chamberlin, 1949, p. 169.—Loomis, 1949, p. 244.—Chamberlin and Hoffman, 1958, p. 159.

Atopetholinae of uncertain generic position

Atopetholus paroicus Chamberlin, 1941a, p. 7, fig. 5.

Holotype: Female, collection of R. V. Chamberlin, from Mountain Spring, San Diego County, California, collected on January 8, 1941, by Stanley and Dorothea Mulaik.

Discussion: This species is known only from females and may well be, as Loomis (1949) suggested, actually referable to the related genus *Watichelus*, which occurs in the same area. The lateral end of the collum is strongly bent caudoventrad. Final allocation must await the study of conspecific males from Mountain Spring.

Onychelinae, new subfamily

As presently known, this group consists of two small genera that occupy rather distant regions: *Onychelus* in southern California and adjacent Arizona, and *Saussurobolus* in the southern end of the Mexican Plateau. The diagnostic characters of the subfamily are set forth in the preceding key, to which may be added the general remarks that the group appears to be a rather disjunct one, particularly in the form of the anterior gonopods. Very little is known about the structural details of the Mexican species, but *Onychelus* at least appears to be modified for an arenaceous habitat because of having more and longer setae on the sides of the legs than the other known genera of the family—in effect a fringe that is conceivably an aid in locomotion under loose soil. The marginal setae of the anal valves are also longer and more closely set than in the other species.

In *Onychelus* the anterior legs of the males are provided with long slender claws, and the coxal lobes are but weakly produced. Unfortunately, nothing is known about the tarsal claws in the genus *Saussurobolus*, but the coxal lobes of the third leg pair in that genus are rather long and conspicuous. The similarity of the two genera is best noted by comparing the basal structure of the gonopods, particularly the distinctly incurved sternal apodemes. The sternite itself is much more strongly produced distad than in any other atopetholid genus, approximating the type characteristic of most Rhinocricidae. The apodemes of the posterior gonopods are short and strongly expanded distally in both genera, the telopodites taking the form of a falciform blade, longer and more slender in *Onychelus*.

The very great distance between the two regions inhabited by species of this subfamily indicates that the intervening area has not been explored for its milliped fauna and that a large number of onychelids surely remains to be discovered in northern and central Mexico. Partly on the basis of geographic probability, we refer the inadequately described *Arinolus zacatecus* (Chamberlin, 1947b) to this group of genera, although it is clear enough that the species is not a member of the Arinolinae.

Genus *Onychelus* Cook

Onychelus Cook, 1904, p. 67.
Gosichelus Chamberlin, 1949, p. 168 (type species: *Onychelus medolus* Chamberlin, by original designation).

TYPE SPECIES: *Onychelus obustus* Cook, by original designation and monotypy.

DIAGNOSIS: A group of small atopetholids characterized by the opening of the ozopores in the mesozonites; the extensive development of lateral macrosetae on the legs; the production of the anterior gonopod sternite into a median subtriangular projection nearly as long as the coxal apices; and the posterior gonopod having the coxal and telopodital elements distinct and separate but connected by a flexible articulation, the telopodite being slender, falciform, and distally notched or bifid in all the known forms.

DISCUSSION: The original diagnosis of this genus and its only included species was fairly detailed with respect to body form but virtually ignored the genitalia and provided no drawings of those structures. This neglect gave rise to a considerable volume of confusion, most of which has been outlined in the discussion of *Atopetholus* on page 134. When the type series of *O. obustus* was finally discovered and studied in 1949, it was found that Cook's reference to the form of the posterior gonopods was badly in error, and had misled Chamberlin into using the name *Onychelus* for a group of species that we have referred to *Atopetholus*. For several small Sonoran species that he had previously named in *Onychelus*, Chamberlin recently provided the name *Gosichelus*. But since the type of that generic name, *medolus* Chamberlin, has been found to be congeneric with *obustus*, we herewith establish the synonymy of the two, and hope that with the publication of the accompanying drawing the case of the enigmatic *Onychelus* has been brought to a close.

Onychelus obustus Cook

FIGURE 8

Onychelus obustus Cook, 1904, p. 68.—Chamberlin and Hoffman, 1958, p. 157.

HOLOTYPE: Male (and numerous paratypes), USNM 797, from the Colorado Desert, Riverside County, California, collected by C. R. Orcutt.

DIAGNOSIS: Differing from *O. jaegeri* and *O. medolus* by slight qualitative differences in the form of the male gonopods that may or may not be worthy of specific recognition. No tangible separation of these three entities can be made without reference to illustrations.

DESCRIPTION: From the original generic description the following is taken:

Segments with a distinct transverse constriction, the posterior subsegment distinctly thicker and more convex than the anterior; repugnatorial pores located in front of the constriction; pores followed on posterior subsegments by a very distinct longitudinal sulcus. . . .

Anterior legs of male with claws very large, as long as distal joint; first two pairs strongly crassate; legs 3 to 7 with coxae only slightly produced; second joints with a rounded prominence below distad; other joints normal.

From the original species description, the following is taken:

Length of male 38 mm., width 3.8 mm.; female 39 mm. by 4.2 mm.

Colors in alcohol black and dull yellow or clay-color. Segments in front of posterior suture dull black to below the pores; posterior zone reddish above, the ventral surface, legs, and antennae clay-color.

Clypeal foveolae five on each side; some distance above the foveolae two oblique rows of small irregular depressions, the rows converging upward.

First segment with a very distinctly raised anterior margin extending from the lateral corners to near the eyes where the limiting groove bends inward and is suddenly obliterated. The edge is concave along the raised margin, to accommodate the inflated angle of the head, and the lateral corner is rather pointed.

Segments nearly smooth above; in front of the constriction they are quite even, but the black surface does not shine. Behind they are abruptly thicker and distinctly covex; the surface shines though it is less even, being marked by indistinct and irregular longitudinal shallow grooves or depressions. The suture of the median line is marked by a fine sulcus, and that behind the pore is deep and distinct. The longitudinal grooves become more distinct below the pores, and pass gradually into the normal striations more than halfway down to the legs. Pleural sutures distinct but less so than the others. The surface of the anterior part of each segment below is ornamented with a delicate network which takes the place of the concentric striations.

Last segment very broadly and evenly rounded, the surface inflated and convex, both above and on the sides. Anal valves evenly convex, polished, and shining.

Gonopods of male as in figure 8,*a*,*b*. Sternite of the anterior gonopods strongly produced mesiad into a subtriangular distally notched process extending distad almost to the ends of the coxal apices. Proximal margin of sternite with a deep median notch; sternal apodemes long and slender, only slightly expanded distally, bent somewhat mesiad, imperceptibly fused with the caudal side of the coxite. The latter elongated and rather slender, the distal end spatulate and slightly concave on the caudal side, the coxal apodeme short and distinctly set off from the rest of the joint. Telopodite moderately large, flattened, its apical lobe recurved caudolaterad. Posterior gonopod with a stout short apodeme, the distal end strongly expanded (fig. 8*c*). Coxite composed of two pieces diverging from a common base; the telopodite attached by a movable joint, slender, arcuate, the caudal edge produced into a broad flange that distally is enlarged into a triangular lobe just before merging with the main body of the telopodite; extreme terminal end strongly recurved, bifid or with a small subapical dentation.

Discussion: Comparison of the drawings of this species with those published by Chamberlin for *Onychelus jaegeri* and *O. medolus* shows

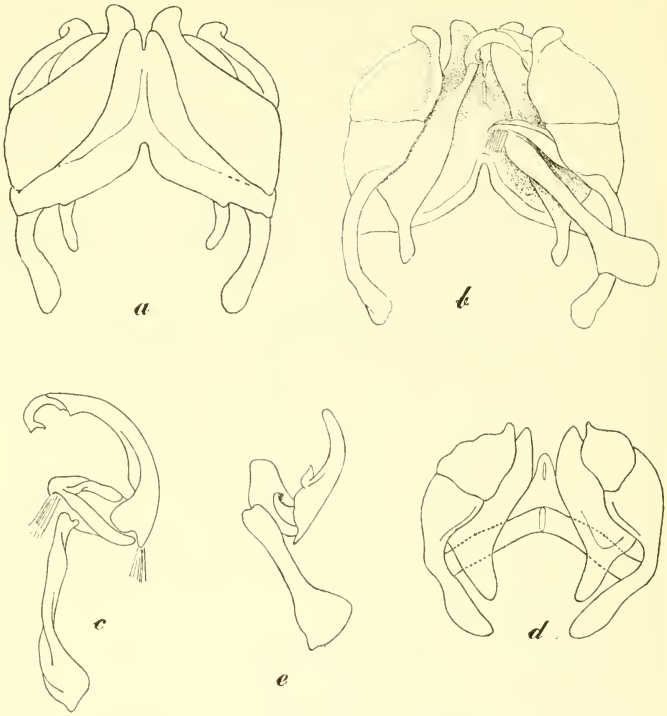

FIGURE 8.—*Onychelus obustus* Cook, male paratype from Riverside County, California: *a*, anterior gonopods, cephalic aspect; *b*, same, with left posterior gonopod in the gonocoel, caudal aspect; *c*, left posterior gonopod, caudal aspect. *Saussurobolus neglectus* Carl, male holotype from Cuernavaca, Mexico: *d*, anterior gonopods, caudal aspect; *e*, left posterior gonopod, caudal aspect (from Carl, 1919).

great similarity, and it seems entirely possible that the last two may not be specifically distinct from *O. obustus*. The final determination concerning this matter we leave to someone having the opportunity to study the genus in detail with large quantities of fresh material from numerous localities. At present, each of the nominal forms is known only from its type locality.

Onychelus medolus Chamberlin

Onychelus medolus Chamberlin, 1941a, p. 13, figs. 17, 18 (male holotype in the Chamberlin collection, from Olberg, Pinal County, Arizona, collected on December 27, 1940, by Stanley and Dorothea Mulaik).

Gosichelus medolus Chamberlin, 1949, p. 168

Onychelus jaegeri Chamberlin

Onychelus jaegeri Chamberlin, 1947b, p. 50, figs. 54, 55 (male holotype, Acad. Nat. Sci. Philadelphia 9972, from the Indio Mudhills, 10 miles northeast of Palm Springs, Riverside County, California, collected in November 1946, by Smith and Jaeger).

Gosichelus jaegeri Chamberlin, 1949, p. 168.

Genus *Saussurobolus* Carl

Saussurobolus Carl, 1919, p. 389.

Type species: *Julus nietanus* Saussure, by original designation.

Diagnosis: A genus of small atopetholids most closely related to *Onychelus*, from which it differs in the presence of elongated coxal processes from the third legs of the males, in the much less produced sternite of the anterior gonopods, and in the shorter and simpler telopodite of the posterior gonopods.

Discussion: The type species of this genus was first described in *Julus*, and was later tentatively placed by Pocock (1910) in his genus *Cyclothyrophorus*. At that time only a single family of spiroboloids was recognized, and the first consideration of the species subsequent to Brolemann's 1914 essay on the classification of the order was given by Johann Carl, who restudied Saussure's types and established the genus *Saussurobolus*. Concerning its systematic position, he wrote (1919, p. 390):

> En dépit de l'absence, réele ou apparente, de l'ampoule et de la rainure séminales [of the posterior gonopod], je crois devoir classer *Saussurobolus* dans la familie des *Trigoniulidae*, où il occupe cependant une place isolée à cause de la structure du coxite, de la position et de la forme des poches trachéennes. Le nombre des fossettes labiales et la forme des valves anales constituent des caractères génériques de second ordre.

In his classification Attems (1926) accepted Carl's disposition of the genus, and placed it with other trigoniulid genera. To the best of our knowledge, *Saussurobolus* has not been subsequently mentioned in the literature.

There now seems to be little or no basis for considering the genus to be related to the highly specialized trigoniulids any more so than to any of the other spiroboloid families.

Occurring at the southern extremity of the Mexican Plateau, the species of *Saussurobolus* are the southernmost known representatives of the family, and may prove to be very numerous when that region has been thoroughly collected. Two species are known with assurance, and a third, originally described in *Arinolus*, appears to be congeneric with *S. nietanus* in structural details. Likewise known from southern Mexico, the species is here tentatively referred to the present genus.

Saussurobolus nietanus (Saussure)

Julus nietanus Saussure, 1860, p. 565, pl. 5, fig. 33, *a–d* (male holotype, Mus. Hist. Nat. Genève, from Cuernavaca, Morelos, Mexico, collected by H. Saussure).
Spirobolus nietanus Saussure and Humbert, 1872, p. 89.
Cyclothyrophorus nietanus Pocock, 1910, p. 84.
Saussurobolus nietanus Carl, 1919, p. 390, fig. 16.

The following description is from Pocock (1910):

Small, cylindrical, with the seventh and eighth segments dilated. *Head* polished, punctured below, with 5+5 or 4+4 labral pores. *First tergal plate* with its antero-lateral border widely emarginate, its inferior angle very acute and extending slightly below the level of the second, which is not produced inferiorly below the level of the third. The remaining segments smooth and shining; the normal transverse sulcus complete and preceded by an additional complete sulcus; a well-marked longitudinal sulcus in front of and behind pore. The lateral sulci or striae strongly defined. *Anal segment* with tergal plate obtusely rounded, marked with a transverse rugulose groove; valves scarcely surpassing the tergal plate, strongly punctured, convex, and not compressed marginally; sternal plate rounded.

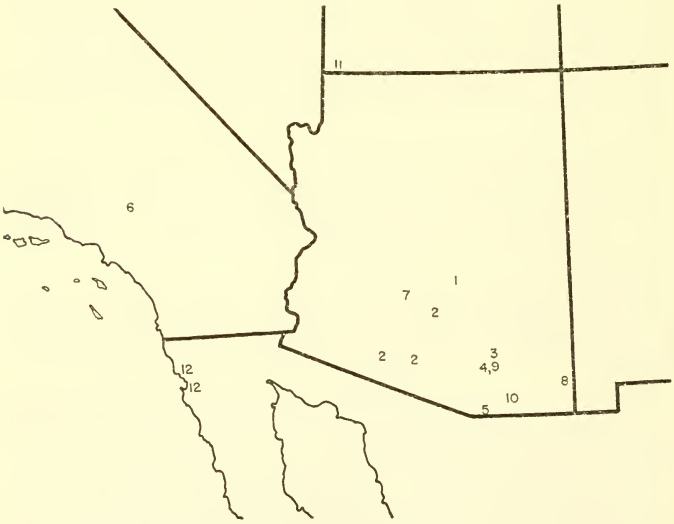

FIGURE 9.—Distribution of species of the subfamily Arinolinae in the southwestern United States and Baja California: 1, *Arinolus torynophor;* 2, *A. apachellus;* 3, *A. citrinus;* 4, *A. hopinus;* 5, *A. nogalanus;* 6, *A. latus;* 7, *A. pimus;* 8, *A. chiricahuanus;* 9, *A. hospes;* 10, *A, dentatus;* 11, *Piedolus utus;* 12, *Scobinomus serratus.*

♂. Sixth and seventh segments with their lower surfaces thickened and extending inferiorly. *Coxae of second leg* large; that of the third leg bearing a long, slender, pointed process; coxae of fourth, fifth, and sixth with a wide, somewhat triangular apophysis.

Number of segments 44. Length, 32 mm.

Saussurobolus neglectus Carl

Spirobolus nietanus Saussure and Humbert, 1872, p. 89.

Saussurobolus neglectus Carl, 1919, p. 391, figs. 17–22 (male holotype, Mus. Hist. Nat. Genève, from Cuernavaca, Morelos, Mexico).

Saussure and Humbert reported specimens from Cuernavaca that they thought to be conspecific with the species *nietanus*, which Saussure had previously described from the same locality. These specimens were, however, much larger than the original types, and with more segments, and on this basis Pocock suggested (1910) that perhaps two species were involved. This possibility was explored by Carl, who restudied the gonopods of the specimens concerned, and found differences in the posterior pair. He thereupon proposed the appropriate name *neglectus* for the larger species, and illustrated the genitalia of both in useful detail. Some of his drawings are introduced here for comparison with *Onychelus* (fig. 8,*d*,*e*).

Saussurobolus zacatecus (Chamberlin), new combination

Arinolus zacatecus Chamberlin, 1947b, p. 51, figs. 59, 60 (male holotype, Acad. Nat. Sci. Philadelphia 9974, from the Sierra Temperoso del Oro, Zacatecas, Mexico, collected in June, 1934, by H. A. Pilsbry).

Arinolinae, new subfamily

The four genera of this group include small-bodied atopetholids with numerous structural peculiarities. The body form is subparallel except for the enlarged sixth and seventh segments, and the slightly constricted segments just behind the collum. The telescoping of the caudal-most segments is limited to the last two or three, and there not to the extent found in the Eurelinae. The ocellaria are small and rounded, each with 25 to 40 ocelli, and are separated by a distance about equal to 2½ to 3 times the diameter of an ocellarium. In contrast to the antennae of the Eurelinae, those of the Arinolinae are considerably larger and longer, and reach back past the collum, in some cases as far back as the fourth segment. Although there are fewer body segments (from 35 to 45), the visible part of each segment is considerably more extensive than in larger members of the family, and preserves the normal ratio of body length to width. In the material studied for this character, there is a distinct remnant of a middorsal longitudinal suture on the metazonites. Transverse sutures

cannot be observed with accuracy, but it appears that the ozopores open in the metazonites, in contrast to most other genera of the family.

The anterior gonopods are curious in having the membranous tissue between sternite and coxites thrown into folds and rather heavily sclerotized; mesially this tissue is either produced in the form of a subtriangular vinculum or extends up between the coxae as two closely appressed lobes that superficially appear to be a single median process. The coxites appear to be subdivided by lateral sutures into two or more sclerites and have occasionally been so illustrated, but this condition is an illusion caused actually by rather pronounced grooving of the surface. The internal effect of this condition is to compartmentalize the inner surface of the coxites as far as the insertion and origin of the coxal muscles are concerned. Distally the coxites are drawn out into rather elongate and distinctly laminate processes of which mostly the narrow dimension is visible in anterior aspect, the elongations being much more pronounced than in other subfamilies of the Atopetholidae. On the caudal side, the sternal apodemes do not extend mesiad as far as usual, but the coxal apodemes are similar to those of other members of the family in having one edge continuous with the mesial anterior edge of the coxite and the other edge extending up to the mesially infolded caudal portion of the coxite. The telopodite is relatively large, and its distal end is likewise drawn out into a slender apex, which, in *Arinolus* at least, is rather laminate and bent distinctly caudolaterad and lies, when in situ, in the paramedian notch of the sympleurite of the seventh segment. Details on this point are unfortunately lacking for the other genera referred to here.

The coxites of the posterior gonopods are large and somewhat variable in shape. The telopodite is attached as usual at the extreme lateral end of a coxite, and the two conjointly form an acute angle with a visible joint at the apex. In *Arinolus* this joint seems to have some flexibility, but in *Scobinomus* and, presumably, *Tarascolus* as well, the two elements of the gonopod are extensively consolidated much as in *Atopetholus*, and the structure is more unified. The telopodite in all genera of this group is thin and flattened, with a basal peduncular portion that merges distally into an expanded laminate, subconchoidal portion subtended on the caudal margin by a solenomerite of variable size and shape. This latter structure is one of the diagnostic features of the Arinolinae, and ranges in appearance from a short, probably nonfunctional knob in some *Arinolus* to a long blade in *Piedolus* that exceeds the tip of the main branch and that is seen to carry a seminal groove. The posterior gonopod in *Scobinomus* is unusually short and heavy, chiefly because of a shortening of the telopodite peduncle and enlargement of the terminal calyx.

The distribution of this subfamily is confined to the Sonoran region of southwestern United States and the Mexican Plateau, centering around Arizona and southern California. Certainly a great number of species remain to be found not only in the areas mentioned but also in the States of New Mexico, Sonora, and Chihuahua, the mountains of which have never been explored for their milliped fauna (fig. 9).

At present we refer four genera to this subfamily, although with considerable reservation concerning the status of one of them. This matter is discussed at length in connection with the genus *Scobinomus*, and the diagnostic contrasts made in the second couplet of the following key to genera must be considered entirely provisional.

Key to the genera of the subfamily Arinolinae

1. Coxites of anterior gonopods produced mesially toward the sternite and separated by two elongate and closely appressed projections of the intersegmental membrane to form a ligulate process with little or no sclerotization; posterior gonopods short and robust, the coxite and telopodite more or less consolidated and immovable 2
   Coxites of anterior gonopods not produced mesially toward the sternite, separated by a broadly triangular projection of sclerotized intersegmental membrane; posterior gonopods long and slender, the coxite and telopodite forming a flexible joint 3
2. Tergites with rudimentary scobinae and with the caudal margins bisinuate; ventrolateral striations of the metazonites produced beyond the edge of the segment into short acute spinules; ends of collum somewhat obliquely flared laterad and readily visible from above . . . . . **Scobinomus** Loomis
   Tergites without scobinae and their caudal margins straight; ventrolateral striations of metazonites not produced into distinct spines; ends of collum not turned outward . . . . . **Tarascolus** Chamberlin
3. Solenomerite of posterior gonopod very long, extending distad well beyond the laminate tip of the telopodite; coxal lobes of third leg pair of males elongated, extending back over the coxae of fourth legs; coxal apices of anterior gonopods only moderately produced distad . . **Piedolus** Chamberlin
   Solenomerite of posterior gonopod small and short, less than half as long as conchoidal portion of telopodite; coxal lobes of third legs of males small, not produced distally; coxal apices of anterior gonopods conspicuously produced and elongated . . . . . **Arinolus** Chamberlin

Genus *Arinolus* Chamberlin

Arinolus Chamberlin, 1940, p. 81.—Loomis, 1950, p. 164.

TYPE SPECIES: *Arinolus torynophor* Chamberlin, by original designation.

DIAGNOSIS: Small- to moderate-sized atopetholids with the sixth and seventh segments noticeably enlarged; antennae rather slender and reaching back beyond the collum, the second article equaling or exceeding genal apex; males with tarsal claws of anterior legs of normal size or slightly enlarged, coxal lobes small and bluntly rounded; sympleurites of seventh segment strongly modified into a rather large

median lobe with a deep notch on either side; anterior gonopods with well developed triangular median projection of the sternite; posterior gonopods distally expanded into a conchoidal or strongly clavate region, with a short slender or spurlike solenomerite remnant.

DISCUSSION: Although its first species was described by Cook in 1911, *Arinolus* was not recognized as a generic entity until 1940, when Chamberlin named the type species and diagnosed the genus as follows:

> Differing from *Tylobolus* and *Hiltonius* in having a free inner piece to the posterior gonopods as in *Spirobolus*. The posterior gonopods expanded at distal end into a spoonlike lamella. Anterior gonopods with both coxal plate and telopodite extended into processes at mesodistal corners. Anterior sternite proportionately very broad. Collum acutely narrowed below at each lateral end, margined in front. Claws of two first pairs of legs in the male conspicuously enlarged, those immediately following more slender and somewhat intermediate in length. Coxae of legs III to VII in the male bearing conspicuous, more or less lamelliform, processes. Anal valves not compressed, somewhat re-entrant at median margin.

Although this diagnosis is fairly accurate and inclusive, there is some doubt concerning what is implied by the term "free inner piece" of the posterior gonopod. The small spur that occurs on the telopodite in *Arinolus* is clearly not homologous with the long processes that originate from the base of the telopodite in species of the Spirobolidae. In general, the diagnosis of *Arinolus* would have been much more improved and manifestly much more meaningful had comparison been made with other atopetholids (particularly *Piedolus*) rather than with genera belonging to a different suborder.

Subsequent papers by Chamberlin (1940, 1941a, and 1947b) included the descriptions of several new species, so that the genus contained six nominal species by 1950. In that year appeared the first and only published discussion of taxonomy in the group, by H. F. Loomis, in which he dealt with the 1911 *Onychelus* species of Cook, and suggested the synonymy of several Chamberlin names. His proposals may be summarized as follows: *Arinolus apachellus* Chamberlin (1941a) = *A. torynophor* Chamberlin (1940); *Arinolus hopinus* Chamberlin (1941a) = *Onychelus hospes* Cook (1911); *Onychelus suturatus* Cook (1911) = *O. dentatus* Cook (1911).

The last two are in all probability correctly evaluated since the type localities of the species involved are the same, and since the forms of *Arinolus* are largely allopatric. There is, however, reason to challenge the synonymy of *A. apachellus* under *A. torynophor*, an association made chiefly on the basis of gonopod similarity. Loomis has kindly loaned the material upon which his opinion was based, a male topotype of *torynophor* and several specimens from the San Tan Mountains near Sacaton, Arizona, that he took to represent the

same species. On the basis of close comparison of this material, we find sufficient differences in body form as well as in gonopod structure to warrant recognition of *apachellus* as a valid form.

At the present, we consider 8 of the 11 names based on specimens of this genus to be valid, and an additional one is herewith proposed. The locality of the genus appears to be southern Arizona, with a single species known to be from southern California. So far none has been taken in New Mexico or in Arizona north of the Salt River, although this situation may be attributed to the general lack of collecting in the areas mentioned. There is a definite indication that at least several of the named forms are merely allopatric populations of a widespread species, but a satisfactory resolution of their status remains a problem for consideration when ample material has been accumulated for a good revision of the genus.

The species of *Arinolus* are among the smallest atopetholids, and are superficially similar under low magnification. In the limited material studied, however, we find that specific differences may be well marked when the animals are closely examined. The characters by which *torynophor* differs from the other two species treated here are almost generic in nature in comparison with the degree of specific differentiation manifested in other atopetholid groups.

The anterior gonopods are rather similar in all the known forms, but the posterior gonopods differ in various small qualitative ways and afford the most tangible recognition characters in the presently very imperfect state of our knowledge of the group. The division between coxite and telopodite is most conspicuous in this genus, there being a flexible joint at the apex of the angle that they form. Distally the telopodite is expanded into a suboval, laminate, somewhat conchoidal development from near the base of which there is a small styliform solenomerite remnant extending medially from one edge of the telopodite. In some forms there is an indication of a groove or duct passing along the base of the telopodite and up onto the base of the solenomerite remnant. This projection is rather clearly homologous with the solenomerite, which is usually quite well developed in the Trigoniulidae. In general, the posterior gonopods of *Arinolus* are the closest approach to the typical trigoniulid form, and exemplify a primitive condition from which other generic types have evolved by various patterns of simplification or elaboration. The anterior gonopods, however, depart considerably from the presumably primitive type characteristic of the Eurelinae.

One name, *Arinolus zacatecus* Chamberlin (1947b), was proposed for a specimen collected in Zacatecas, Mexico. As is clearly shown by the drawing of the anterior gonopod, this species has the sternite of the Onycheline type, and is obviously not congeneric with *A.*

torynophor. We tentatively refer the species to *Saussurobolus*, a genus of the Onychelinae, with the two other species from the highlands of central Mexico.

The original description of *Arinolus torynophor* is not detailed with respect to the external characters, and the drawings of the gonopods are quite small. We take this opportunity to publish a thorough description of the species, and to provide a larger and more detailed illustration of a posterior gonopod. For the other two species treated here, we limit the description to points of difference from the type species.

Arinolus torynophor Chamberlin

FIGURE 10,*a,b*

Arinolus torynophor Chamberlin, 1940, p. 81, figs. A–C.—Loomis, 1950, p. 165.

HOLOTYPE: Male, collection of R. V. Chamberlin, from Fish Creek, 10 miles east of Tortilla Flat, Maricopa County, Arizona (date and collector unknown).

DIAGNOSIS: A large arinolid, up to 40 mm. in length and 3.5 mm. in width in which the lateral ends of the collum are produced caudoventrad and extend below the level of second segment; the pleural lobe of the second segment without distinct anterior marginal ridge; sternites strongly trapezoidal in shape and with curved transverse striae; mandibular stipes excavated for reception of antennae, the ventral margin rounded but without marginal ridge; terminal division of telopodite of posterior gonopod large and elongate-oval, with a very small solenomerite.

DESCRIPTION (FROM TOPOTYPE): Male, about 38 mm. long and 3.4 mm. in diameter, with 44 segments.

Color of preserved specimen light chestnut brown with the metazonites dark brown across dorsum; head, antennae, collum, legs, and anal valves yellowish brown.

Body slender and parallel sided back to last four or five segments, which abruptly decrease in size. Collum and second segment slightly wider than third to fifth, the sixth, and seventh segments also enlarged slightly over normal body dimension.

Head relatively large, width across mandibles as great as width of collum, front slightly convex, very smooth and polished without trace of transverse striations or genal grooves. Labral notch short and rather deep; clypeal groove sharply defined and almost continuous with the distinct occipital groove. Clypeal foveolae 4–4, irregularly shaped and spaced. Antennae relatively long, extending back to middle of second segment, the second article exceeding apex of gena. Articles in decreasing order of length: 2, 3, 4, 5, 6, 1, 7, all slightly compressed and becoming increasingly setose distally, the first three articles glabrous. Mandibular antennal depression very

shallow, striate, the ventral edge rounded and not distinctly margined. Ocellaria small, rounded, separated by a space about 2½–3 times the diameter of an ocellarium, with 25 ocelli in each.

Collum slightly wider than width of head, smooth and polished but with microscopic striations, its anterior lateral marginal ridge distinct and parellel sided throughout its length; the caudal edge emarginate near the end, which is produced distinctly caudoventrad and extends below the level of the second segment.

Pleural lobe of second segment without trace of anterior raised marginal ridge, the segment with four or five small ridges behind the end of the collum.

Body segments completely smooth, dorsally without trace of striae or punctations. Caudal third of segments slightly elevated; the lower surfaces of the metazonites provided with numerous short well defined ridges that do not extend caudad as spinules on the margin. No traces of a transverse segmental constriction remain across the dorsum, but the furrow is very pronounced near the sternite, as a deep depression dividing the segment into two subequal parts. Transverse sutures are not evident, but a lateral suture is distinct behind each ozopore. The last four or five segments decrease abruptly in diameter, but only the last two are telescoped, and these not to the extent found in the Eurelinae.

Anal segment rather small, its apex completely smooth and the margin broadly rounded or slightly truncate, the swollen anal valves conspicuously exposed in dorsal aspect. Valves smooth, strongly inflated, their mesial reentrant edges provided with a long series of short, stiff, interdigitating bristles. Preanal scale very broad and distally subtruncate, without tubercules or setae.

Sternites strongly trapezoidal, almost twice as wide in front as behind, with 6 to 10 transverse striations which curve forward mesially, and set off from the pleurites only by a fine suture. Anterior stigmal depression shared by both sternite and pleurite, posterior depression not set off by an oblique suture.

Legs relatively long and slender, reaching nearly to level of ozopores; the joints in order of decreasing length 3, 6, 2, 4, 5, 1. Ventral setae normally 1, 1, 2, 2, 2, 6, the tarsal joints with an accessory dorsolateral row of four or five long setae on the caudal side. Tarsal claw well developed, about a third to half the length of tarsus. First two pairs of legs strongly crassate and distinctly reduced in size, legs 3–7 normal in size and shape with long claws and low, apically rounded coxal lobes. Claws of legs 3–5 slightly longer than those following.

Sympleurite of seventh segment produced mesially into an anteriorly directed crassate lobe, without trace of median suture.

Anterior gonopods similar to those of *A. citrinus;* the posterior gonopods with the distal enlargement somewhat triangularly-ovoid in

caudal aspect, set off by a much deeper constriction than in the other known species of the genus (fig. 10,*a*).

Discussion: This species ranks among the largest forms of the genus and is very distinct from its smaller congeners in numerous structural characters. No contribution can be made at this time to the knowl-

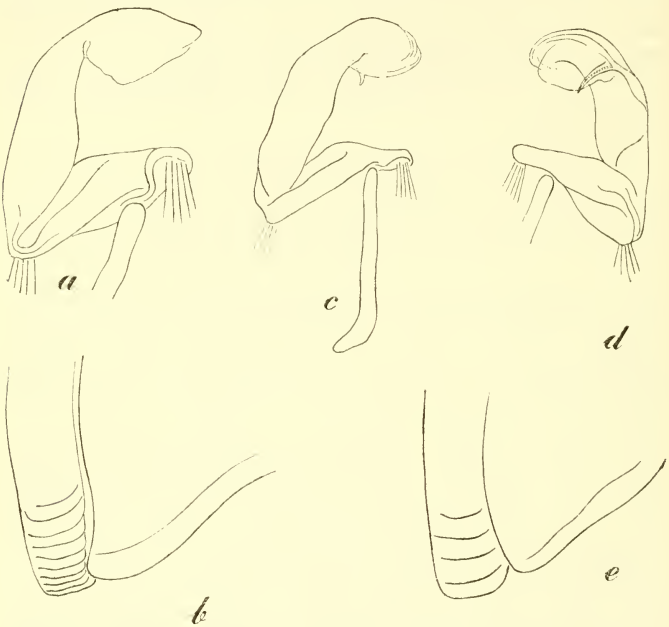

Figure 10.—*Arinolus torynophor*, male topotype from Fish Creek, Arizona: *a*, right posterior gonopod, caudal aspect; *b*, lower end of collum, left side. *Arinolus apachellus*, male specimen from Sacaton, Arizona: *c*, right posterior gonopod, caudal aspect; *d*, same, cephalomesial aspect; *e*, lower end of collum, left side.

edge of variability or of distribution as only two specimens are known, the holotype and a topotype, collected at Fish Creek by Loomis in 1924. Possibly *A. torynophor* will be eventually found to be endemic to the Superstition Mountains of eastern Arizona.

Arinolus apachellus Chamberlin

Figure 10,*c–e*

Arinolus apachellus Chamberlin, 1941a, p. 10, figs. 12–14.

Holotype: Male, collection of R. V. Chamberlin, from Covered Wells (now called Quijotoa), Pima County, Arizona, collected on

January 3, 1941, by Stanley and Dorothea Mulaik.

DIAGNOSIS: A medium-sized species of *Arinolus*, differing from the preceeding species, with which it has been combined, in the shape of the collum, in having longer antennae, in the presence of a flared rim on the front edge of the pleural lobe of the second segment, and in the shape of the telopodite of the posterior gonopod, which likewise distinguishes it from all of the other species in which the male is known.

DESCRIPTION: Based upon a male (USNM, Loomis coll.) from Sacaton, Arizona, about 3.0 mm. in diameter, length undeterminable due to extensive breakage.

Front of head smooth and polished, without transverse wrinkles. Clypeal foveolae 3–3. Antennae rather long and slender, reaching back to the fourth segment, most of the articles more than twice as long as broad. Lower edge of mandibular stipe with a well defined marginal groove, the antennal depression smooth. Ocelli 28 on one side and 27 on the other.

Surface of collum smooth and polished, the anterior marginal ridge widest dorsally and becoming narrower toward the ends, the latter evenly subtriangular and not produced somewhat caudoventrad.

Pleural lobe of the second segment with a low but distinct raised rim along the anterior margin. Body segments without punctation or striation except on lower sides of the metazonites. The median longitudinal dorsal suture is evident on most segments.

The posterior gonopods (fig. 10,*c*,*d*) are of the typical *Arinolus* form, but differ from those of *A. torynophor* in having a larger solenomerite and a more evenly oval terminal calyx.

DISTRIBUTION: This species was originally recorded from Quijotoa, 10 miles south of Ajo, and Congress Station, Arizona. In subsequently synonymizing *Arinolus apachellus* with the earlier name *A. torynophor*, Loomis gave several additional localities that may apply in part to this species, but we can be sure of only one. The male upon which the preceeding account is based, from the San Tan Mountains north of Sacaton, Pinal County, Arizona, provides the fourth definitely known locality for *apachellus*. The range appears to coincide with the plateau country of southwestern Arizona south of the Gila River valley, and probably extends as far east as Tucson. It is entirely probable that this species extends likewise into Mexico.

Arinolus citrinus, new species

FIGURE 11

HOLOTYPE: Male (and male and female paratypes), USNM 2508, from Bear Canyon, 6,000 ft., Mount Lemmon, Santa Catalina Mountains, Pima County, Arizona, collected March 19, 1953, by Henry and Alice Dietrich.

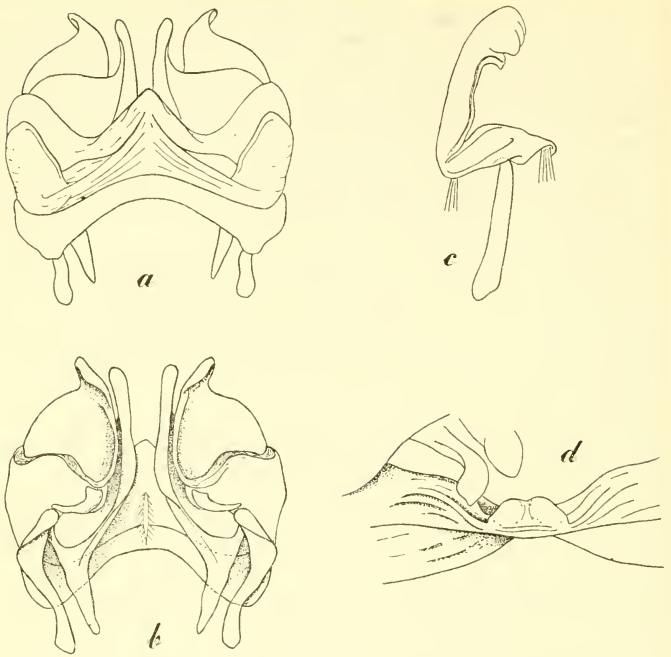

FIGURE 11.—*Arinolus citrinus*, new species, male paratype from Santa Catalina Mountains, Arizona: *a*, anterior gonopods, cephalic aspect; *b*, same, caudal aspect; *c*, left posterior gonopod, cephalic aspect; *d*, sympleurite of 8th segment, showing median process, with tips of gonopods of right side indicated.

DIAGNOSIS: A small arinolid characterized by the somewhat rudimentary calyx of the posterior gonopod, which is not set off by a constriction as in the other species treated here.

DESCRIPTION (FROM HOLOTYPE): Body small and parallel-sided except for the enlarged sixth and seventh and reduced third and fourth segments. Length undeterminable; maximum diameter about 2.8 mm.

Color uniform medium to dark brown, legs and antennae light brown.

Front of head smooth and convex, with several fine transverse striations; occipital groove very faint. Clypeal foveolae 4–3. Labral teeth much larger and better defined than in *A. torynophor*. Mandible without a true antennae groove, the outer surface merely depressed and smooth, the lower edge with a well defined marginal ridge.

Surface of collum smooth and polished with a few fine punctations; the lateral ends not produced caudoventrad and not extending below the level of second segment. Pleural lobe of second segment with a low but distinct anterior marginal rim. Pleurotergites generally smooth but with small scattered punctations, otherwise similar to those of *torynophor*.

Anal segment smooth with tiny punctations; anal valves with several small transverse grooves and striae.

Sternites more nearly rectangular than in *torynophor*, only slightly wider in front than behind.

Sympleurite of seventh segment (figure 11,*d*) strongly produced, with a distinct median notch and longitudinal depression.

Anterior gonopods (figure 11,*a*,*b*) with the sternite distinctly arched; shape of the coxites obscured by the heavily folded intersegmental membrane, which is produced mesially into a sort of "pseudosternite." Coxites impressed near the lateral margin by a deep vertical groove, giving the impression of distinct accessory lateral pieces. Apices of coxites strongly produced distad, and slightly curved laterally, the tips rounded. Telopodites visible in anterior aspect, their apices likewise drawn out and directed laterally, only slightly exceeding the level of the coxal projections. Posterior gonopods rather small and short, the telopodite in particular much less enlarged distally than normal for the genus (figure 11,*c*).

Discussion: Variation: The segment number in three males is 40, 41, and 42; in the female, 44. Clypeal foveolae range from 3–3 to 4–4. The ocelli in two males are 26–27 and 27–28; in the female, 37–39. There is some reason to suspect, therefore, that either the female belongs to a different species (despite having identical external characters), or that sexual dimorphism is more pronounced in this group than in the Eurelinae. This latter alternative is probably the correct one, as sexual differences are usually more pronounced in more specialized or evolutionarily advanced forms.

Distribution: Known only from the type locality, and possibly endemic to the Santa Catalina Mountains.

Arinolus hopinus Chamberlin

Arinolus hopinus Chamberlin, 1941a, p. 12, fig. 16 (male holotype in the Chamberlin collection, from 16 miles east of Tucson, Pima County, Arizona, collected on December 28, 1941, by Stanley and Dorothea Mulaik).

This name was placed by Loomis in the synonymy of *A. hospes* (Cook), a disposition that may be entirely correct. Yet until the Tucson region has been so thoroughly studied that it is certain only one *Arinolus* occurs there, we think it safer to avoid premature rejection of Chamberlin's name.

Arinolus nogalanus **Chamberlin**

Arinolus nogalanus Chamberlin, 1941a, p. 11, fig. 15 (male holotype in the Chamberlin collection, from Nogales, Santa Cruz County, Arizona, collected on December 30, 1941, by Stanley and Dorothea Mulaik).

Arinolus latus **Loomis**

Arinolus latus Loomis, 1953, p. 418, figs. 10–12 (male holotype, USNM 2090, from Antelope Valley, between Lancaster and Palmdale, Los Angeles County, California, collected on January 8, 1928, by O. F. Cook).

Arinolus pimus **Chamberlin**

Arinolus pimus Chamberlin, 1941a, p. 12 (female holotype in the Chamberlin collection, from Litchfield Park, Maricopa County, Arizona, collected on December 26, 1940, by Stanley and Dorothea Mulaik).

Arinolus chiricahuanus **Chamberlin**

Arinolus chiricahuanus Chamberlin, 1947b, p. 50, figs. 56–58 (male holotype, Acad. Nat. Sci. Philadelphia 9973, from White Tail Canyon, Chiricahua Mountains, Cochise County, Arizona, collected in 1906 by H. A. Pilsbry and S. H. Ferris).

Arinolus hospes **(Cook)**

Onychelus hospes Cook, 1911, p. 157 (holotype, a possibly immature female, USNM 803, from Tucson, Pima County, Arizona, collected on December 23, 1896, by H. G. Hubbard).
Arinolus hospes Loomis, 1950, p. 164.

Loomis suggested that *O. hospes* is a senior synonym of *A. hopinus* Chamberlin, which was also based on material from Tucson. In view of the external similarity of arinolines and the fact that two species can occur together, it seems best to keep the two names separate for the time being.

Arinolus dentatus **(Cook)**

Onychelus dentatus Cook, 1911, p. 158 (female holotype, USNM 804, from Fort Huachuca, Cochise County, Arizona, collected by T. E. Wilcox).
Onychelus suturatus Cook, 1911, p. 159 (female holotype, USNM 805, with the same type locality and collector as the preceding).
Arinolus dentatus Loomis, 1950, p. 164.

These two names are probably based upon the same species, the differences stipulated by Cook apparently due to either age or recent moulting by the type of *suturatus*.

Genus *Piedolus* Chamberlin

Piedolus Chamberlin, 1930, p. 117.

Type species: *Piedolus utus* Chamberlin, by original designation.

Diagnosis: An arinoline genus characterized chiefly by the solenomerite of the posterior gonopods, which is very long and slender,

exceeding the tip of the laminate tibiotarsus; by the elongated coxal lobes of the third legs of males; and by the coxal apices of the anterior gonopods, which are not produced distad nearly to the extent seen in *Arinolus*. In other characters the two genera appear to be very similar, although we have not been able to study material of *Piedolus*.

Discussion: Subsequent to its original description, *Piedolus* fell into complete obscurity to the extent that even its author failed to notice the name when subsequently erecting the closely related genus *Arinolus* in 1940 and when listing the known atopetholid genera in 1949. The original generic diagnosis compared the genus only with *Atopetholus;* aside from the differences noted, most of what is said applies to all atopetholids, and the most useful generic characters are to be found in the illustrations of the gonopods.

Piedolus utus Chamberlin

Piedolus utus Chamberlin, 1930, p. 118, 2 figs.

Holotype: Male, collection of R. V. Chamberlin, from St. George, Washington County, Utah, collected on April 3, 1929, by Lowell Woodbury.

Diagnosis: With the characters of the genus.

Description (data taken from the original description): Male 30 mm. long and 3.0 mm. in diameter, with 44 segments.

Color in general deep brown or almost black, the segments lighter beneath; head and anal segment uniform in color except a median pale line above clypeal incision; legs and antennae concolorous with body.

Clypeal foveolae 5–5.

Lateral ends of collum acute, anterior lateral edge concave adjacent to level of eye.

Sternite of anterior gonopod broad and slightly arched mesially, an accessory sclerite present at base of coxite on each side as in most forms of *Arinolus*, the coxites narrowing mesiad, and separated by what appears to be a vinculum formed from sclerotized membrane from the sternite. Details of the basal structure of both gonopods not shown but presumably as in *Arinolus*. Telopodite of posterior gonopod with the distal half set off by a constriction, becoming very broad, laminate, and subovoid in shape. Proximad of the constriction, on the caudal side, originates the long, slender, slightly sinuous solenomerite, which carries a visible groove.

Genus *Tarascolus* Chamberlin

Tarascolus Chamberlin, 1943a, p. 25.

Type species: *Tarascolus bolivari* Chamberlin, by original designation.

DIAGNOSIS: A genus of the Arinolinae with several very distinctive features, most outstanding of which is the shape of the anterior gonopods. These gonopods are in general similar to those of *Arinolus* except that the coxites are more approximate mesially and are separated by an elongate ligulate process formed by two appressed flattened folds of membranous intersegmental sclerotized tissue. The anterior face of the coxites is superficially divided by distinct lateral grooves as in *Arinolus*. The posterior gonopods are rather heavy and short, the telopodite distally modified into a thin membranous calyx, which is subtended by a long slender acuminate solenomerite. Body form slender and parallel except for the enlarged sixth and seventh segments. Collum less narrowed at sides than normal for the family, the anterior margin concave and with a slight marginal ridge, the caudal margin convex and with a few subterminal striae. Metazonites distinctly punctate. Claws of first two pairs of legs of males enlarged, those of following legs somewhat reduced in size. Coxal lobes of third leg pair prolonged and extending back over those of fourth, which are erect and subtriangular processes.

DISCUSSION: This genus was originally compared only with *Messicobolus* and *Eurelus*, neither of which are very closely related to it, while the obvious affinity with *Arinolus* was overlooked.

As presently treated, this genus is known only from two species collected at the southern end of the Mexican Plateau, from which region, however, a number of additional forms are to be expected. *Tarascolus* is discussed at greater length in connection with *Scobinomus*, the genus that follows below.

Tarascolus bolivari Chamberlin

Tarascolus bolivari Chamberlin, 1943a, p. 26, figs. 46–50 (male holotype in the Chamberlin collection, from Zitacuaro, 1,900 m., Michoacán, Mexico, collected on July 13, 1941, by C. Bolivar).

In Chamberlin's paper, figure 46 is stated to represent the right posterior gonopod of *Messicobolus totonacus*. However, this figure bears little resemblance to figure 45, which is also said to be of the posterior gonopod of the same species, and since the figure is almost identical with the corresponding gonopod of the closely related *Scobinomus serratus* (see fig. 12,*c*), it seems reasonable to assume that some mixup in numbering occurred and that figure 46 actually represents the posterior gonopod of *T. bolivari*, which is not otherwise illustrated although stated in the text description to be shown.

Tarascolus clarus Chamberlin

Tarascolus clarus Chamberlin, 1943a, p. 26, fig. 51 (male holotype in the Chamberlin collection, from Santa Rosa, Distrito Federal, Mexico, collected on June 28, 1942, by M. Cardenas).

Genus *Scobinomus* Loomis

Scobinomus Loomis, 1953, p. 420.

TYPE SPECIES: *Scobinomus serratus* Loomis, by original designation.

DIAGNOSIS: A monotypic arinoline genus closely related to *Tarascolus*, from which it differs chiefly in the characters mentioned in the key to genera of the subfamily and discussed in the following paragraph.

DISCUSSION: This generic name was proposed for a milliped that differed from all the atopetholids known to its author by the presence of scobinae on the body segments, as well as the presence of acute spinules on the lower edge of the metazonites. The validity of the name is not beyond challenge, however, for the following reasons. To begin with, the fact that scobinae are not mentioned in the diagnosis of *Tarascolus* does not mean that they are not present; in the paratypes of *S. serratus* examined, they are quite small and rudimentary and could easily be overlooked. Also, the published information on the species of *Tarascolus* is by no means as detailed as might be desired.

Second, there is some doubt that the presence or absence of rudimentary scobinae is a character of generic value. In the genus *Chersastus* of South Africa, they occur in some species but not in others, a condition duplicated in *Eurhinocricus* of Jamaica. Finally, in at least one known Jamaican rhinocricid, scobinae are present in one sex but not in the other. Assuming that scobinae do not occur in *Tarascolus*, the overall general similarity of its species with *S. serratus* is such as to indicate a very close relationship.

Finally, it is stated that "The gonopods bear some resemblence to those of *Tarascolus* Chamb., but the anteriorly exposed coxal joints of the posterior lobes and differently shaped inner [i.e., posterior] gonopods are distinctive characters in addition to the external ones." We believe that the difference in the posterior gonopods is more apparent than real, and is explainable in light of the fact that the gonopod of *Tarascolus bolivari* appears to have been credited to another species in the original drawings. Furthermore, the illustration given by Loomis shows this organ in anterior aspect, in contrast to the posterior views in Chamberlin's paper. The drawing that is here presented was made from a male paratype, the gonopod of which was removed and studied as a microscopic preparation. The drawing is so similar to figure 46 in Chamberlin's paper that the two objects might have come from the same species.

Scobinomus is retained here on the chance that all the characters taken in combination are actual differences, a matter that can be settled by future examination of typical material of *Tarascolus bolivari*.

Scobinomus serratus Loomis

FIGURE 12

Scobinomus serratus Loomis, 1953, p. 420, figs. 13–17.

HOLOTYPE: Male, USNM 2091, from 14 miles north of Ensenada, Baja California, Mexico, collected on January 7, 1925, by O. F. Cook.

DIAGNOSIS: A small arinolid having the characters of the genus as discussed above, and specifically identifiable by the shape of the male gonopods.

DESCRIPTION: The detailed original description given by Loomis cannot be improved upon except as regards the formation of the gonopods. Study of a male paratype has provided the information following, and it should be mentioned at this point that the gonopods were cleaned of all adherent muscle tissue and mounted in glycerine to facilitate examination with considerable magnification. This technique, we feel, provides a more detailed picture of structure than can be gained from the study of untreated parts.

Anterior gonopods in this form (fig. 12*a*) are similar to those of the species of *Arinolus* in most respects. The sternite is nearly transverse, and is enlarged laterally near the origin of the sternal apodemes. On the caudal side the sternal extension reaches only about halfway to the mesial end of the coxite, a detail that is apparently constant in the subfamily. The coxites are large, and mesially are produced toward the sternite, a matter of structural necessity since there is no median vinculum to keep them separate. Each coxite is impressed on its anterior surface with a distinct oblique vertical groove that merges distally into several shorter perpendicular grooves.

Owing to the form of the coxites, there is little intersegmental membrane in the make-up of the anterior gonopods; what is present is largely in the form of a pair of ligulate processes extending distad between the coxites. In untreated material these processes are so closely appressed as to appear as a single structure. There is some membrane in the form of transverse folds along the upper edge of the sternite, the material forming an enlargement near the middle of the basal edge of each coxite. In caudal aspect (fig. 12,*b*) there is little of particular interest to be seen except for a small internally projecting process near the base of the sternal apodeme, a development not observed in any other species.

The posterior gonopod (fig. 12,*c*) as seen in caudal aspect has the usual long apodeme connected about a third of the length from the mesial end of the coxite. The latter takes the form of a slender rod, near the lateral end, enlarging mesially and then reflexed laterad and extending behind the telopodite. There is considerable consolidation of the gonopod, with little indication of the two distinct elements

joined at a flexible joint as in *Arinolus*. The telopodite is short and stout with a slender mesially projecting solenomerite, immediately distad of which the joint is flared into a distinct hyaline cuplike structure obviously homologous to the much smaller distal expansion of *Arinolus*, and for which the name *calyx* is suggested. No trace of a seminal groove could be detected.

The illustration of the posterior gonopod published by Loomis is made from the anterior aspect and presumably from a low magnifi-

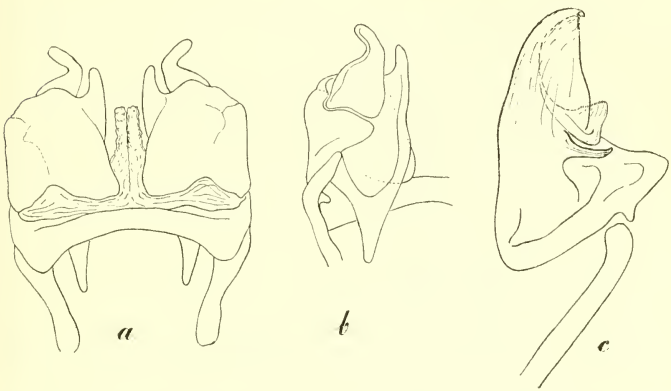

FIGURE 12.—*Scobinomus serratus* Loomis, male paratype from Ensenada, Baja California: *a*, anterior gonopods, cephalic aspect; *b*, right side of anterior gonopods, caudal aspect; *c*, left posterior gonopod, caudal aspect.

cation. Consequently, the solenomerite was not shown, and the similarity to the gonopod of *Tarascolus* was scarcely apparent.

DISTRIBUTION: The two known localities for this species are on the Pacific coast of Baja California, not far south of the international boundary. It is a matter of some interest that this form, obviously a close relative of *Tarascolus* of the southern part of the Mexican Plateau, should occur in such a geographically isolated region. Possibly future collections in the mountains of Sonora and Sinaloa will disclose the presence of additional related forms and thus bridge the present gap. As it stands, this discontinuity is another small but valid reason for retaining *Scobinomus* as a separate genus, as such a magnitude of geographic isolation in Sonoran millipeds usually carries corresponding structural diversification.

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