

AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N.Y. 10024
Number 2977, 40 pp., 100 figs., 2 tables June 28, 1990

On the Central and East Asian Milliped Family Diplomaragnidae (Diplopoda, Chordeumatida, Diplomaragnoidea)

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ABSTRACT

The Diplomaragnidae, a family of litter and soil-dwelling millipeds from Mongolia, Siberia, Korea, and Japan, is reviewed and 19 new species are described and illustrated (*Diplomaragna sardyk, ryvkini, longibrachiata, ulykpani, feynmani, mikhajlovae, kemerovo, bakurovi, golovatchi, shilenkovi, coxalis, yakovlevka, anuchino, tsurusakii, lysaya, picea, reducta, korsosi, and ronkayi*). The family names Ancestreumatidae, Syntelopodeumatidae, Tokyosomatidae, and Sakhalineumati-

dae are treated as synonyms of Diplomaragnidae; the generic names *Ancestreuma, Syntelopodeuma, Tokyosoma, Niponiothauma, Pterygostegia, Altajosoma*, and *Sakhalineuma* are treated as synonyms of *Diplomaragna*. Many new records and new anatomical observations of previously described species are given. The evolutionary relationships and biogeography of the family are briefly discussed.

INTRODUCTION

When I revised the large, North American milliped family Cleidogonidae in 1972, a classic pattern in the history of the taxonomy of any group of organisms came to light. Initial publications on the animals establish clear-cut genera and family-level groups. Continued interest by taxonomists doing largely faunistic, not revisionary, work results in the multiplication not only of species

names, but also of generic and family-level names. As more comprehensive collections accumulate, the situation becomes less and less satisfactory, since it becomes obvious that many of the names which at first seemed well-justified are in fact redundant. A second level is reached with a first revision, in which most of the synonyms are recognized, many more new species are described, and a start can be

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made on understanding the biogeography and evolution of the whole group. The following notes on the fascinating millipeds of the family Diplomaragnidae bring their taxonomy to this second level. It is to be hoped that further collection and study will reveal more about their distribution and relationships.

HISTORICAL OVERVIEW: Gerstfeldt (1859) described the first chordeumatid millipeds from Siberia, as *Julus armatus* (Irkutsk) and *J. dahuricum* (Baron Island, Shilka River delta). Haase (1880) transferred both of these species to *Craspedosoma*, which at that time was extremely heterogeneous (just as *Julus* was at first used for any cylindrical diplopod, *Craspedosoma* later included most chordeumatids). While some of Gerstfeldt's types are still in existence in the Leningrad Museum, these two species are missing (S. I. Golovatch, personal commun.). It is possible that they represent diplomaragnids, but this cannot be established at present. The names will continue to cloud the picture until topotypical material or the types themselves can be studied.

Anton Stuxberg (1876) worked up a small collection of Siberian millipeds from the Nordenskiöld Expedition of 1875. Among his new species was *Craspedosoma deplanatum*, described, like the others in the collection, in a few lines of Latin, without reference to the gonopod characters so important in modern diplopod taxonomy. However, the combination of strongly produced lateral shoulders on the metazonites and the presence of 32 trunk segments, together with the collection data, indicated to my colleague Richard Hoffman that *deplanatum* was in fact a diplomaragnid, which he verified by examining the male holotype in the British Museum (Natural History).

The first immediately recognizable diplomaragnid millipede was described from Vladivostok by Attems (1899). He provided good illustrations of the gonopods and named his species *Placodes terricolor*. Eight years later, realizing that the generic name *Placodes* was preoccupied, Attems (1907) replaced it with *Diplomaragna*, and also took the opportunity to establish a subfamily Diplomaragninae, under his commodious Heterochordeumidae. Numerous authors (see Shear, 1987)

have recounted the subsequent dismemberment of this large family, and that story will not be retold here.

In 1914, Karl Verhoeff described *Syntelopodeuma gracilipes* from Hokkaido, Japan, and compared his new genus in detail with *Diplomaragna*, also giving Diplomaragninae full family status. Two additional species of *Syntelopodeuma* would follow: *formosanum* (Formosa; Verhoeff, 1936) and *hokkaidense* (Hokkaido; Verhoeff, 1939). *Syntelopodeuma formosanum* remains the most southerly (and questionable) record of a diplomaragnid. Verhoeff also named two additional species, each placed in its own monotypic genus, despite strong similarities to *Syntelopodeuma*. *Tokyosoma takakuwai* Verhoeff (1932) was placed in a new subfamily, Tokyosominae (recte: Tokyosomatinae). Verhoeff's description contained errors that were corrected by Takakuwa (1954) and Miyosi (1959); a redescription from new material was published by Murakami (1971). *Niponothauma inflatum* Verhoeff was described in 1942; the gonopod illustrations Verhoeff provided were sketchy and he misinterpreted the gonopod anatomy (see the discussion of this species below).

Yasunori Miyosi has worked intensively with the complex cave fauna of Japan. Among his discoveries is an extraordinary diplomaragnid, *Pterygostegia kuroiwadensis* Miyosi, remarkable for having broad, thin, polydesmid-like paranota on each diplosegment (Miyosi, 1958), rivaled only by those of *Heterochordeuma* of Sumatra and Burma or of the North American *Urochordeuma*. Murakami and Kawasawa (1975, 1976) added three more species, also from caves in Shikoku, Japan, including *P. anops*, the only known eyeless diplomaragnid.

In 1972 the focus shifted to central Asia. Jan Gulicka (1972) named a new genus *Altajosoma*, with three species. Though Gulicka failed to make a family assignment, miscounted segments, and presented only very rudimentary illustrations, it is clear his species are diplomaragnids. The exact identity of Gulicka's species, however, cannot be settled, since the badly broken types he returned to the Leningrad Museum did not have gonopods (Golovatch, in litt.) and his drawings

lack the detail required to match them to subsequently collected specimens.

The most prolific recent author trying to work out the diplomaragnid puzzle has been Sergei Golovatch, of Moscow. He began his interest in this group by first describing an unusual new species from Sakhalin Island as *Sakhalineuma molodovae* (Golovatch, 1976), which he recognized as a possibly aberrant diplomaragnid. In 1977, Golovatch added yet another new generic name, *Ancestreuma*, which he made the type of a family Ancestreumatidae. Comparing the gonopod anatomy of a number of Asian and North American chordeumatid families, he recognized that the superfamily Heterochoreumatoidea that I proposed in 1972 was heterogeneous. Therefore, Golovatch proposed removing Diplomaragnidae (*Diplomaragna*, *Sakhalineuma*), Ancestreumatidae (*Ancestreuma*, *Altajosoma*), and a newly minted family Syntelopodeumatidae (*Syntelopodeuma*, *Tokyosoma*, *Niponiothauma*, *Pterygostegia*) to a superfamily which he called Ancestreumatoidea. But since the new superfamily included Diplomaragnidae, the name Ancestreumatoidea Golovatch 1977 became an automatic synonym of Diplomaragnoidea Attems 1907, a coordinate name, and for the same reason Syntelopodeumatidae Golovatch 1977 became an immediate synonym of Tokyosomatidae Verhoeff 1932. Golovatch (1979b) corrected these errors by sinking Syntelopodeumatidae (and by implication Tokyosomatidae) under Diplomaragnidae and recognizing the synonymy of the superfamilial names, but at the same time, he created a family Sakhalineumatidae for *Sakhalineuma*.

Thus the taxonomic history of this family of millipeds has, as usual, engendered confusion. However, large numbers of specimens of the family had accumulated in the Soviet Union and Golovatch generously offered to send me this material as he sorted it from collections. Using these new specimens I was, for the first time, able to see a full range of species and study systematically the distribution of characters among them. The results, which follow, are not unlike those in my 1972 cleidogonid revision—while the number of species in the family is greatly

increased, many old family and genus names become synonyms.

ACKNOWLEDGMENTS

This study could not have been carried out without the cooperation of Dr. Sergei Golovatch, Institute of Evolutionary Animal Morphology and Ecology, Moscow. Most of the specimens used were loaned by him, including paratypes and topotypes, and he helped as well with sorting out gonopod anatomy, locating literature, and checking the English transliteration of Russian place names. Dr. Zoltan Korsós, Budapest, loaned Korean specimens which turned out to contain two important new species, and a gift of specimens from Dr. Nobuo Tsurusaki, Sapporo, added a new species to the Japanese list. Dr. T. Tanabe, Hokkaido University, loaned a newly collected specimen of *D. inflata*. Type material from the Verhoeff collection was loaned by Dr. Hubert Fechter, Zoologisches Staatssammlung in München, and Attems types were loaned by Dr. Jürgen Gruber, Naturhistorisches Museum, Vienna.

Dr. Richard Hoffman, Virginia Museum of Natural History, Martinsville, kindly gave me drawings he had made of *D. deplanata* in the British Museum, and Dr. Paul Jagasich, Hampden-Sydney, provided translations of some papers in Russian.

Measurements in Descriptions are in millimeters.

DEPOSITION OF MATERIAL: Unless otherwise noted, all material is in the Zoological Museum of the University of Moscow (ZMUM). Type material has also been deposited in the American Museum of Natural History (AMNH), the Senckenberg Museum, Hamburg (SMF), the Zoological Museum of the University of Copenhagen (ZMUC), the Natural History Museum, Tokyo (NHMT), and the Hungarian Natural History Museum, Budapest (HNHM). Some none-type material has been temporarily retained in my own collection (WASC); these specimens will eventually be deposited in the AMNH.

GONOPOD ANATOMY

The gonopods of diplomaragnid millipeds are complex and highly modified. The key

development, which defines the family, is the positioning of the telopodites of the anterior gonopods in sheathing grooves on the *posterior* surfaces of the posterior gonopod colpocoxites. This is possible because of the division of the posterior gonopod sternum into small plaques on the left and right sides, while the middle part has become more or less membranous and has been pushed posterior. The anterior gonopod sternum has fused with the coxae of the gonopods (which have also fused in the midline) and rotated posteriorly around its transverse axis. The long, t-shaped coxal part then extends between (and dorsal to) the left and right posterior gonopod sternal elements, so that the sharply recurved anterior gonopod telopodites are erected against the posterior surfaces of the posterior gonopod colpocoxites. Only careful dissection can work this out, and various misinterpretations have been in the literature since 1907, most commonly mistaking the posterior gonopod colpocoxites for "syntelopodites" of the anterior gonopods. By tracing muscle insertions and studying specimens thoroughly digested in trypsin, I was able to confirm many details seen by Golovatch (1979b) and discovered some new ones. Also, the range of species available allowed me to follow some evolutionary trends in gonopod development heretofore obscured.

What remains is for a study to be made on living animals, killed while mating, in order to understand how these gonopods function. A level of complexity that can only be described as baroque is reached in the gonopods of some species.

There is little variation from species to species in the far less complex corresponding female organs, the cyphopods. These latter structures must be studied closely to detect species differences. Kurnik (1988), in an elegant work, has shown that the female genitalia are far more useful to systematists in chordeumatids than heretofore suspected; subsequent taxonomic work should include drawings of the vulvae.

Comparatively simple, the anterior gonopods of diplomaragnids nonetheless show extensive variation. The shape of the coxosternum is more or less uniform, but the telopodites may be one- or two-segmented (the basal segment is always small and trap-

ezoidal), heavy and robust or thin and stylose, and may have a few apical elaborations. In some of the species with very robust telopodites, the distal segment appears to be filled with a glandular tissue of some kind, and a distinct pore appears proximally on the anterior face; the basal segment would seem to be incomplete anteriorly, and muscles (?) cross its anterior face to insert on the base of the distal segment. In other species, the two segments are fused and the whole telopodite is reduced in size, becoming somewhat flagelliform. In species with large telopodites, the telopodite simply lies in a curved receptacle made up of almost the whole posterior gonopod colpocoxite, but in species with flagelliform telopodites, the sheath is narrowed to a groove that in a few cases may actually be closed.

The posterior gonopod sternum is divided into right and left halves and reduced, appearing only on the anterior side of the gonopod complex. In contrast, the wall of the coxa (angiocoxite) is posteriorly bulbous, protruding, and well sclerotized. The anterior face of the angiocoxite is subject to modification. The mesodistal angle may be drawn out to a distinct triangular point or a short, acute rod, but in species from the Pacific coast of Siberia, and from Korea and Japan, the front face of the angiocoxite is depressed, with a distinct rim; from this rim on the mesal surface arises a process which first curves dorsally, then ventroposteriorly, so that the angiocoxite itself appears sigmoid. The process passes mesal to the colpocoxite on each side, either through notches in the mesal edges of the colpocoxites or through a completely enclosed hole in each colpocoxite. In one set of species, the hole runs lengthwise in the coxite, creating a sheath from which the angiocoxal branch may or may not emerge on the posterior surface. In these species, the anterior gonopod telopodite is usually the most reduced and may be completely enclosed in its own sheath. Posteriorly the angiocoxite may bear a process which appears to be movable and is often quite complex, appearing as a grapplelike device with an array of teeth and hooks. This process is socketed on the posterior side of the coxite but I was not able to find any muscle or tendon attachments; it may be movable by changes in hemolymph

pressure. In the more complex situations, there is a mesal arm from this apparatus that meets its counterpart and firmly locks both into place.

The colpocoxites of the posterior gonopods are the sclerotized derivatives of the coxal glands of these appendages. In diplomaragnids (except for *molodovae*) they are fused at least basally and can properly be called a syncolpocoxite. In species in which an angiocoxal process is involved with the syncolpocoxite, two articular knobs extend ventrally from the bases of the syncolpocoxite and articulate on each side with the angiocoxites, the articulation resting in a shallow depression on the anterior gonopod coxosternum. The colpocoxites are usually strongly curved posteriorly. The posterior sheath for the anterior gonopod telopodite may bear both lateral and mesal processes, and the former are sometimes highly exaggerated. Near the colpocoxite apex may appear a variety of small elaborations and patches of velvety cuticular fimbriae.

The telopodites of the posterior gonopods are two-articled. The basal article, probably a trochanteroprefemur, is clavate. Where telopodite reduction has occurred, the thin "stem" of this segment is exaggerated. The distal segment is turned dorsally, and is large and bean-shaped in most species. The nature of the articulation suggests it is the femur alone, a hypothesis reinforced by the relatively frequent observation of tiny, reduced additional articles attached to the end of it; this suggests that more distal articles are reduced and lost, not incorporated. This distal article can become quite small in those cases where the posterior gonopod telopodites are reduced.

ONOPOD ONTOGENY: The gonopods of some milliped orders develop gradually over several instars, before reaching their final form in the adult males, while in other orders there is an almost metamorphosis-like change, with the gonopods appearing only after the last molt. In these latter cases, the legs that are to be transformed into gonopods may be represented in earlier instars only by small bumps. The case in most chordeumatids is intermediate, and in penultimate instar males the rough form of the gonopods can be made out, sometimes in enough detail so that new

taxa have been erected on juveniles of common species (see especially Loomis and Schmitt, 1971).

In *Diplomaragna longibrachiata*, for example, penultimate males have leg pair 8 already reduced to a bandlike sternum, with nothing extending posteriorly between the colpocoxites of leg pair 9. Leg pair 9 has the telopodites on each side as two segments which closely resemble the final form, with the distal article turned sharply dorsally, though the individual articles are noticeably smaller than in adult males. The coxae of leg pair 9 are greatly enlarged, but show no details. Leg pairs 3–7 are already encrassate in penultimate males.

OTHER LEG MODIFICATIONS: In the central Asian species, the anterior legs of males are very much modified, so encrassate and incurved that it is probable they are not of much use in walking. Analogous observations in other families suggest that these legs are used to clasp the female during mating. However, in some species this modification has been reversed, and the legs are of normal size. In *D. lysaya*, but not in any other species, there is an additional modification. The fourth legs have bare patches ventrodistal on the femora that are delimited by brushes of setae; there are corresponding bare spots on the tarsi.

Behind the gonopods, both the tenth and eleventh coxae bear glands and may be slightly modified, with lobes, depressions, etc. The telopodites of these legs are somewhat reduced, and at least in preserved males, appear to be held up out of the way and not used in walking. In one species, *D. coxalis*, the coxae of legs 12–14 are also modified, suggesting again that there might have been an extensive series of coxal glands in some remote ancestor. However, I could not find actual glands on these legs. The eversible coxal glands behind the gonopods form spermatophores. Prior to mating, the males arch their bodies so that the penes in the second coxae are inserted into these glands, and sperm is ejaculated. The spermatophores are produced when the posterior glands are everted, and picked up on the gonopods. In various specimens of diplomaragnids, spermatophores have been observed on the tips of the posterior gonopod colpocoxites (where they could be pushed off by sliding the anterior gonopod telopodites

in their sheaths) and held between the handle-like posterior angiocoxal processes.

CLADISTIC ANALYSIS

The monophyly of the diplomaragnids is established on the peculiar relationship, discussed above, of the anterior and posterior gonopods. No other milliped family has this structure and all diplomaragnids possess it. Members of the superfamily Conotyloidea were considered as the outgroup. These relationships will be further explored in an analysis now in progress, of the evolution and biogeography of related circum-Pacific milliped families.

Using the program MacClade 2.1, the shortest and most consistent cladograms that could be found (i.e., fig. 1) are 44 steps long and have consistency indices (C.I.) of 0.70. Some of the less robust characters are discussed at length below and highlight the preliminary nature of the analysis. I suspect that the collection and description of more species will help to resolve some of the puzzles of the unusual distributions of characters in the genus. For the time being, however, it is encouraging that the cladistic analysis confirmed my subjective arrangement of the species into groups on the basis of general similarity, and also is congruent with the hypothesis of an origin for the group in Mongolia, spreading northward and eastward with ever more evolved species, culminating in the highly specialized forms in Japan.

This same material is discussed again briefly and from a different viewpoint under each of the species groups. Table 1 lists the characters used, their states, and the numerical codes used for each state; table 2 gives the data matrix on which the cladograms were based.

1. Form of the anterior gonopod telopodites. Broad telopodites with complex apices are considered to be plesiomorphic on grounds of their greater resemblance to legs and to conotyloid gonopods, and their obviously greater role in sperm transfer (having assumed that, as in conotyloids, sperm transfer is progressively taken over by the colpocoxites of the posterior gonopods). Two apomorphic states (probably ordered, but not coded as such in the data used here) have the

telopodites first reduced in size but retaining some apical complexities, then becoming simply flagelliform. The character is somewhat complicated by a few species in the *Principalis* group in which the telopodite is not as strikingly reduced but is of a simple form. These were arbitrarily coded as broad telopodites, but may be a separate specialization. As can be seen on the cladogram, the *Kemerovo* group is defined by the first apomorphic state, and a clade containing the *Coxalis*, *Terricolor*, and *Inflata* groups by the second.

2. Posterior gonopod telopodites. Further reduction of these telopodites is apomorphic. The character is difficult to code because in a few species (i.e., *lysaya*) the telopodite looks different but perhaps not obviously reduced. More or less subjective judgment was used; telopodites that are less than half the size of the largest ones observed were considered reduced. The trend reaches its greatest expression in the troglobitic Japanese species, where the structure is only a small button. In the shortest and most consistent cladograms, telopodite reduction appears three times independently; in *molodovae*, in the Japanese members of the *Terricolor* group, and in the *Inflata* group.

3. Division of the posterior gonopod colpocoxites into lateral and median branches was considered an apomorphy on the grounds of greater complexity. It defines a unit within the *Inflata* group which excludes *picea* and *reducta*; *korsosi* also appears not to have divided coxites. However, in the case of *korsosi*, which has rather simplified gonopods, the lateral branch may have been lost and is now seen only as an acute lateral corner of each coxite. Assuming this as an autapomorphy of this species would increase the C.I. of this character from 0.50 to 1.00 and therefore shorten the cladogram.

4. Anterior gonopod telopodites sheathed in posterior gonopod colpocoxites. This is apomorphic on the grounds of correlation with other apomorphies and a shift in function from the anterior to the posterior gonopods. It defines a unit including all groups but the *Principalis* group, and correlates negatively with the presence of the largest anterior gonopod telopodites.

5. Form and position of the mesal sheath

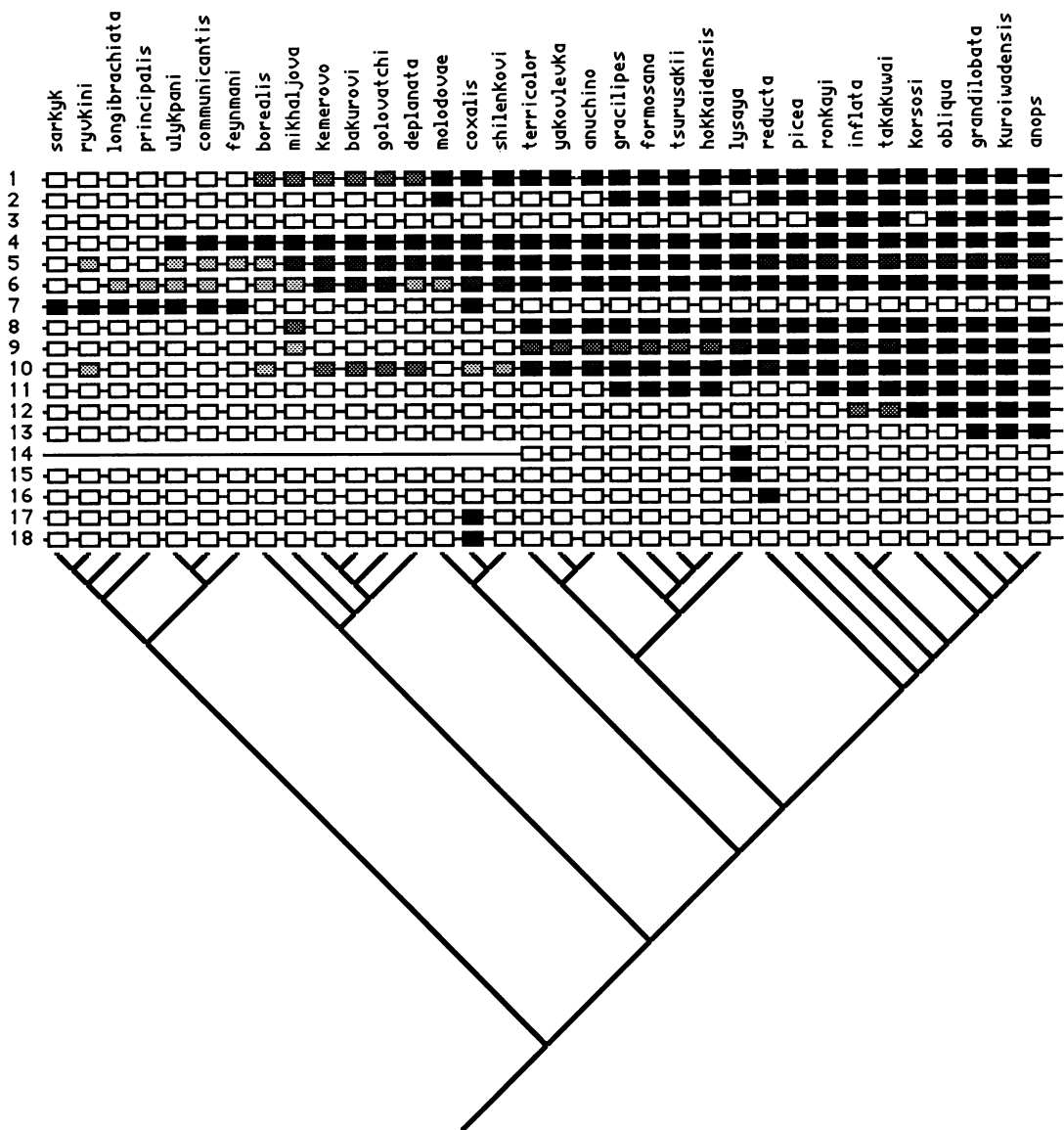


Fig. 1. Cladogram of species of *Diplomaragna*. Characters with multiple apomorphic states coded by progressively darker shading; black indicates highest code number for that character. See text and tables 1 and 2 for explanation.

process of the posterior gonopod colpocoxites. Absence of the process is plesiomorphic, and there are three apomorphic states: present and unfused to its counterpart, fused in the gonopod midline, and lost. The analysis suggests that the process may have developed at least twice independently: once in *ryvkini*, and again in the ancestor of all members of the genus except for those in the *Principalis*

group. Since the telopodites of the anterior gonopods are not sheathed in *ryvkini*, it is possible that the structure I call the mesal sheath process in this species is an unrelated autapomorphy. Fusion in all members of the Kemerovo group, except for *borealis*, suggests that this species is the plesiomorphic sister of all the others. In the *Inflata* group, fusion takes a different form and the fused

TABLE 1
Characters, Character States, and Codes for Cladistic Analysis of Species of *Diplomaragna*
 (See text for discussion)

Character name and number	Character codes				
	0	1	2	3	4
1. anterior gp telos	broad	narrow, w. elaborate tip	flagelliform		
2. posterior gp telos	large	reduced			
3. pgp cc form	entire	divided			
4. agp telo vs pgp cc	not sheathed	sheathed			
5. mesal sheath process	absent	present	fused	lost	
6. lateral sheath process	absent	basal	distal	lost	
7. posterior agcx mesal corner	rounded	angular, projecting			
8. anterior agcx process	absent	short rod	pseudoflagellum		
9. pcc recieves agcx process	no	in groove	in notch	in hole	in sheath
10. posterior agcx process	absent	small, not movable	large, complex, movable	with 2 divisions	reduced or lost
11. anterior legs	enlarged	like posterior legs			
12. paranota	normal	reduced	exaggerated		
13. eyes	present	reduced or lost			
14. post cc hole	mesal	lateral			
15. legs 4	normal	modified			
16. segment #	32	30			
17. Coxae 12	normal	modified			
18. Segment 7	normal	modified			

Abbreviations: gp, gonopod; telo, telopodite; agp, anterior gonopod; pgp, posterior gonopod; cc, colpocoxite; agcx, angiocoxite.

processes become very large and posteriorly projecting; this might be coded as a different state, but the evidence is not conclusive. To do so would improve the C.I. of the cladogram only slightly. The analysis shows that fusion does not necessarily precede loss; if coded as ordered, the C.I. of the character falls substantially.

6. Form and position of the lateral sheath process of the posterior gonopod colpocoxites. Absence of the process is considered plesiomorphic; apomorphic states are presence of the process in a basal position, a distal position, and its loss. The species *ryvkini* and *sardyk* probably lack the process primitively; its absence in *feynmani* may be a loss. Likewise the distal position seems to have developed twice independently—in the ances-

tor of *coxalis* and *shilenkovi*, and in the ancestor of *kemerovo*, *bakurovi*, and *golovatchi*. Loss of this process is difficult to observe; components may merge with the fused and hypertrophied median processes in members of the Inflata group.

7. Mesal corner of the posterior gonopod colpocoxites acute or drawn out into an angle. This is an apomorphy because it differs from the usual rounded form of the homologous leg coxae; it defines the Principalis group. The appearance of the character in *coxalis* seems to be a parallelism, though structurally it looks the same.

8. Anterior angiocoxal process of the posterior gonopods. Presence of such a process is apomorphic by comparison with unmodified leg coxae; the usual form of the process

is as a pseudoflagellum with a sigmoid base, which defines a unit consisting of the Terricolor and Inflata groups. In *mikhaljova*, however, the sagittate rod in this position appears to be an autapomorphy of that species, which does not come out close to the Terricolor and Inflata groups. There are some additional autapomorphic forms of the process in other species as well. For example, it is bifid in *lysaya* and has an expanded tip in *inflata*, but these species fall in the Terricolor and Inflata groups, respectively.

9. Mode of interaction of anterior angiocoxal process and posterior gonopod colpocoxites. Again, this interaction suggests a separate origin of a similar adaptation in *mikhaljovae*. Here the angiocoxal process lies in a groove in the anterior face of the coxite, and the distal margin of the groove is itself drawn out into a short rod. In the Terricolor and Inflata groups, however, there appears at first glance to be a transformation series in which the angiocoxal processes first pass mesal to the coxites in well-defined notches, then through complete foramina, and finally lie in sheaths, though this latter observation requires confirmation in the Japanese troglobites and there obviously could be a continuum between a foramen and sheath. Thus, sheathing may have developed only in a few Soviet Far East and Korean species, and the Japanese species previously assigned to *Pterygostegia* may in fact be more like *inflata* in their gonopods. This outcome would shorten the cladogram and improve its C.I.

10. Presence and form of posterior angiocoxal process of posterior gonopods. Presence of this process as a small and immovable structure is apomorphic compared to its absence. In the Kemerovo group the process becomes larger and more complex and is movable. In Terricolor and Inflata group species, it would appear that the process is at first hypertrophied, with a division into two parts, the mesal of which meets its counterpart from the other side in the gonopod midline. But in a number of these species, the process is reduced or disappears altogether, perhaps to be functionally replaced by the fused median sheath processes. The low C.I. of this individual character (0.57) is vexing because initially it appeared that it would clearly define the more evolved species groups

TABLE 2
Data Matrix for Cladistic Analysis of Species of
Diplomaragna

Species	Characters 1–18, codes			
<i>ryvkini</i>	00001	01001	000?0	000
<i>sardyk</i>	00000	01000	000?0	000
<i>feynmani</i>	00011	01000	000?0	000
<i>longibrachiata</i>	00000	11000	000?0	000
<i>ulykpani</i>	00011	11000	000?0	000
<i>communicantis</i>	00011	11000	000?0	000
<i>principalis</i>	00000	11000	000?0	000
<i>kemerovo</i>	10012	20002	000?0	000
<i>bakurovi</i>	10012	20002	000?0	000
<i>deplanata</i>	10012	10002	000?0	000
<i>golovatchi</i>	10012	20002	000?0	000
<i>coxalis</i>	20013	21001	000?0	011
<i>shilenkovi</i>	20013	20001	000?0	000
<i>borealis</i>	10011	10001	000?0	000
<i>terricolor</i>	20013	30223	00000	000
<i>yakovlevka</i>	00133	30223	00000	000
<i>anuchino</i>	20013	30223	00000	000
<i>gracilipes</i>	21013	30224	10000	000
<i>formosana</i>	21013	30224	10000	000
<i>tsurusakii</i>	21013	30224	10000	000
<i>hokkaidensis</i>	21013	30224	10000	000
<i>mikhaljova</i>	10012	10110	000?0	000
<i>molodovae</i>	21013	10000	000?0	000
<i>picea</i>	21012	30244	00000	000
<i>reducta</i>	21012	30243	00000	000
<i>takakuwai</i>	21112	30234	11000	000
<i>inflata</i>	21112	30234	11000	000
<i>lysaya</i>	20013	30234	00011	000
<i>korsosi</i>	21012	30244	12000	000
<i>ronkayi</i>	21112	30244	10000	000
<i>obliqua</i>	21112	30244	12000	000
<i>kuroiwadensis</i>	21112	30244	12100	000
<i>anops</i>	21112	30244	12100	000
<i>grandilobata</i>	21112	30244	12100	000

and seemed to correspond to the hypothetical west-to-east evolutionary cline in gonopod specialization. However, the cladistic analysis shows an erratic distribution of the first apomorphic state (which appears three times) and seems to suggest at least two separate reductions.

11. Reduction of the originally very crasate pregonopodal legs of males is considered apomorphic. Again, this takes place on a continuum; the cutoff for coding the character as apomorphic was a reduction in size of the pregonopodal legs to about 20 percent larger or less when compared to the postgonopodal legs. This seems to have happened twice, once

in the ancestor of the species of the Japanese members of the Terricolor group, and again in the ancestor of the Korean/Japanese members of the Inflata group.

12. Paranota. The presence of significant paranota on the metazonites is probably synapomorphic for the genus *Diplomaragna*. In *korsosi* and the Japanese troglobites, the exaggeration of the paranota is extreme and the animals look like polydesmids or even platydesmids. But in *inflata* and *takakuwai* (probably sister species) the paranota found in other species have been reduced to low shoulders.

13. Eye reduction, obviously apomorphic, has taken place in three Japanese troglobites, *kuroiwadensis*, *grandilobata*, and *anops* (this last one is eyeless). Probably this should not be regarded as a synapomorphy since it is likely that the eyed ancestors of each species invaded caves independently.

14–18. The remaining characters (table 1) are autapomorphies of single species.

BIOGEOGRAPHY

The species groups detected by cladistic analysis have coherent distributions. The Principalis group is found in a roughly triangular area, with the wide base of the triangle including most of north-central Mongolia, and the apex of the triangle at the northern end of Lake Baikal. The western extreme of the pattern is given by the type locality of *feynmani* in Tannu Tuva. The Kemerovo group has a distribution that is geographically wider and to the west, overlapping slightly with that of the foregoing. The center of diversity, with four species sympatric or nearly so, is in the area of Novosibirsk, Krasnoyarsk, and the Salair Mountains. This may be to some extent an artifact of more intensive collecting around Novosibirsk. The most northerly point is the type locality of *borealis*, near Mirnoye. It is surprising that the group's distribution extends west to the Urals, with localities of *golovatchi* known from the Bashkirian SSR, the vicinity of Sverdlovsk, and from Krasnoyarsk, making this species the most widely distributed diplomaragnid and, assuming there has been no help from man, it has one of the most extensive distributions among milliped species. The Kemerovo group may be linked to the Terricolor group by *mikhail-*

jovae, found far to the east, some distance north of Vladivostok.

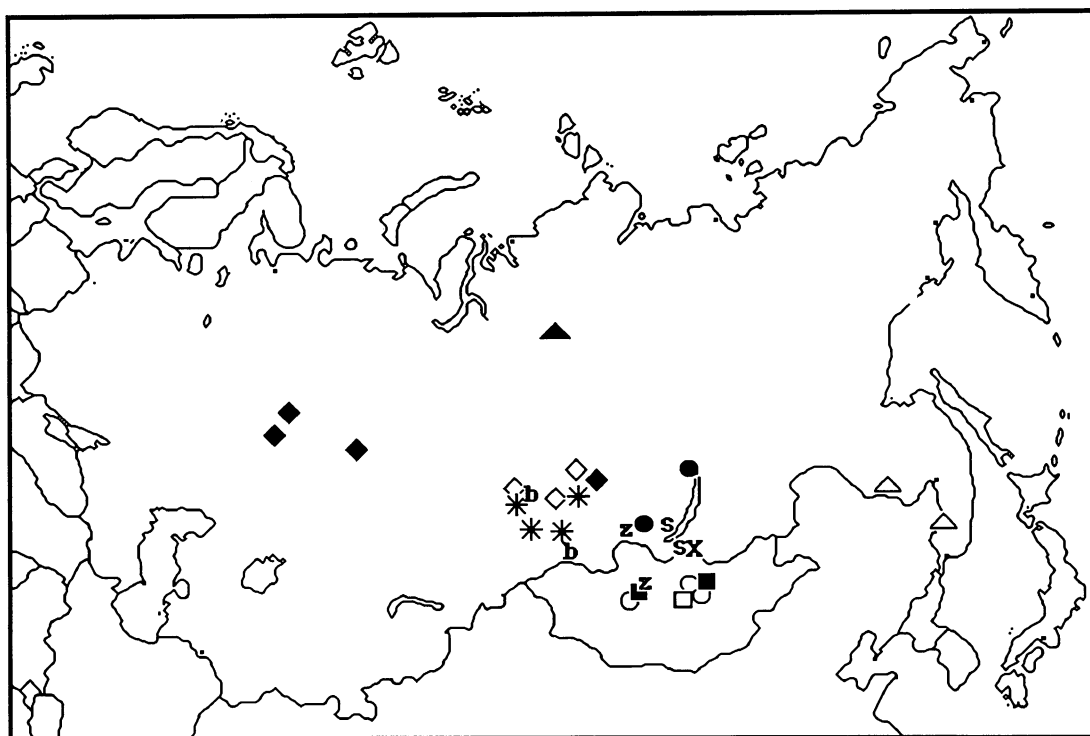
In Eastern Siberia, Korea, and Japan, the Terricolor and Inflata groups again present a pattern congruent with the observed distributions of other animals and plants. The Terricolor group divides into the species of the USSR Maritime Province (Vladivostok region) and those of Japan, which appear to be limited to Hokkaido. The Inflata group is found in the Maritime Province, Korea, and Japan. The Japanese species in this group are, for the most part, moderately to strongly modified for troglitic life, and *anops*, eyeless, with astonishingly broad paranota and highly apomorphic gonopods, is the most evolved diplomaragnid known. The far southern record for the entire family, on Taiwan, needs to be confirmed.

The distributional picture is congruent with a hypothesis of origin in Central Asia, in the borderlands of Mongolia and the USSR. The most plesiomorphic species occur here, and it appears likewise to be a center of diversity. A second center of diversity for the family is certainly in the Maritime Province, and this center probably included Korea and Japan at times of lower sea levels. Unfortunately, nothing is known of the diplomaragnids of northern China and the adjacent USSR, which in all likelihood exist and which would shed light on the origins of the species of the Terricolor group.

The following more detailed notes are taken from a long critique of the manuscript of this paper by S. I. Golovatch, and I am indebted to him for permission to quote them here:

Several diversification centers are obvious [from previous studies]: a Manchurio-Japanese faunogenetic center, from whence come the majority of Japanese and Korean genera of millipeds, with some elements present in eastern Siberia as well. These include *Epanerchodus*, *Cawjeekelia*, *Anaulaciulus*, *Skleroprotopus*, *Kopidiulus*, *Ussuriulus*, *Levizonus*, etc. The Middle Asian center was part of the ancient Mediterranean (presence of *Tianella*, *Turanodesmus*, *Usbekodesmus*, *Peltopodoiulus*, various anthroleucosomatids, etc.), with some Siberian influences via the Djungarsky Alatau, Tarbagatai, and the western Altai Mountains, which served as "stepping stones."

A Central Asian center is dominated by xerophilous forms as well as taiga species, and from here it seems to me the Diplomaragnidae spread outward. The



- ulykpani ● ryvkini □ communicantis, principalis ■ feynmani
 ◆ golovatchi ◇ deplanata * kemerovo b bakurovi ▲ borealis
 s shilenkovi x coxalis z longibrachiata △ mikhailjovae

Map 1. Soviet Union, showing record of selected species of *Diplomaragna*. Additional species occur in the area of Vladivostok, in North Korea, and on Sakhalin Island, Hokkaido, Honshu, Shikoku, and Taiwan.

Mongolian mountains and the various ranges of eastern Siberia are thought to have served as the motherland of the taiga forests, dominated by *Larix* and *Pinus sibiricus*; the paleontological record confirms this to have happened in the Oligocene. From Mongolia, the diplomaragnid stock could have followed the spread of these forests both east and west. The derivative species groups of the east must have originated before the Pleistocene, when the rising sea levels separated Siberia and Korea from Japan. Penetration north into Siberia (Altai, Salair Mountains) has not gone so far, but has almost reached Turukhansk on the Yenissei River, which river is known as a barrier for many plant and animal groups.

The distribution of *golovatchi* reminds one of that of *Schizoturanus dmitriewi*, endemic in the forest-steppe belt of the Russian Plain, and which represents an otherwise Siberian genus. There is evidence from insects, plants, and mammals (*Eotamias sibiricus*) that taiga elements penetrated eastern Europe in the Late

Pleistocene, as a continuous northern zone stretching up into Scandinavia. *Diplomaragna golovatchi* may be a late-comer in this process, its distribution to the east being restricted by available time.

The move to the east has not resulted in a trans-Beringian pattern for the diplomaragnids, such as that found in *Polyzonium*, *Underwoodia*, *Ornisobates*, etc. But we should remember that the source areas for trans-Beringian millipeds seems to have been North America, not Asia, an unusual situation in regard to some other plant and animal groups (including man!). [Golovatch, in litt.]

One outcome of this detailed study of the diplomaragnids has been to convince me that, while they seem quite isolated from other families of chordeumatid millipeds, it is reasonable to think of them as the plesiomorphic sister group of the Heterochordeumatoidea (as I grouped that superfamily in 1972). The diagnostic synapomorphy is

the swollen, dorsally reflexed telopodite of the posterior gonopods. The meaning of this idea for biogeography will be explored in a forthcoming analysis of this entire group of Asian/North American/circum-Pacific millipeds.

SUPERFAMILY

DIPLOMARAGNOIDEA ATTEMS

FAMILY

DIPLOMARAGNIDAE ATTEMS 1907

Diplomaragninae Attems 1907, 24: 122.

Diplomaragnidae, Verhoeff, 1914, 48: 362. Miyosi, 1959, 34: 125. Golovatch, 1977, 56: 722; 1979b, 84: 90. Mauriès, 1978, 351: 63; 1988, 95: 23. Shear, 1979, 60: 120.

Tokysomatinae Verhoeff, 1929, 5: 1481; 1932, 62: 510.

Syntelopodeumatidae Golovatch, 1977, 56: 722; 1979b, 84: 90. Shear, 1979, 60: 120.

Ancestreumatidae Golovatch, 1977, 56: 722. Shear, 1979, 60: 120.

Ancestreumatinae, Mauriès, 1988, 95: 23.

Sakhalineumatidae Golovatch, 1979b, 84: 90. NEW SYNONYMY.

DIAGNOSIS: There would appear to be no closely related families, so the superfamily is coextensive with the family. The relationship of the anterior and posterior gonopods is unique, in that the anterior gonopod coxosternum passes through the divided posterior gonopod sternum mesally, and the anterior gonopod telopodites are enclosed in a sheath formed by the posterior surfaces of the posterior gonopod colpocoxites. Some relationship to families included in *Heterochordeumatoida* is suggested by the form of the posterior gonopod telopodites, but, in the members of that superfamily, the anterior gonopod telopodites (when they interlock with the posterior gonopod colpocoxites) pass lateral to them, between the colpocoxites and the first article of the telopodite. There are coxal glands on leg pairs 10 and 11 of diplomaragnids, whereas in most (but not all) heterochordeumatoids these glands appear only on the tenth coxae. Having more coxal glands is a primitive character. In the *Lankasomatidae* (Mauriès, 1981), the peculiar anterior gonopods are in the form of a fused rectangular plate with various processes, including two flagella, which are inserted in sheaths on the anterior surfaces of the posterior gonopod colpocoxites. These flagella do not appear to be the homologs of the telopodites of diplo-

maragnids, but it is possible. If this is the case, then the two families might be regarded as sister groups. There are biogeographical difficulties; *Lankasomatidae* is known only from Sri Lanka and is thus clearly of Gondwanan origin.

INCLUDED GENUS: *Diplomaragna* Attems.

DESCRIPTION: Thirty-two or 30 segments in males, 32 segments in all known females. Length 7–22. Mentum not divided. Metazonites with more or less prominent paranota, exaggerated in some species to nearly equal $\frac{1}{2}$ ring diameter. Leg pairs 3–7 of males usually enlarged, sometimes strikingly so; coxal glands on leg pairs 10, 11; coxae sometimes slightly modified, telopodites somewhat reduced. Anterior gonopods with T-shaped coxosternum extending between right and left halves of divided posterior gonopod sternum, one- or two-segmented telopodites of various forms, never branched. Posterior gonopods with divided and reduced sternum, large angiocoxites often depressed on anterior faces, posteriorly bulbous, sometimes with long, flagelliform anterior processes and/or movable posterior processes; colpocoxites fused, at least basally, sometimes with median notches or closed foramina receiving processes of angiocoxites, posteriorly forming sheath around anterior gonopod telopodites; telopodites two-segmented, first segment more or less strongly clavate, second elongate-ovoid, strongly curved dorsally, or reduced in size.

DISTRIBUTION: Southern Ural Mountains; Altai Mountains in Central Asia east to the Pacific coast; Sakhalin Island; Korea; Hokkaido, Honshû, Kyûshû, and Shikoku, Japan; Formosa (?).

Diplomaragna Attems 1907

Placodes Attems 1899, 12: 320 (type species *Placodes terricolor* Attems, Vladivostok), name preoccupied by *Placodes* Erichson 1834 (Coleoptera).

Diplomaragna Attems 1907, 24: 123 (proposed to replace *Placodes* Attems 1899). Golovatch, 1979b: 88–90.

Syntelopodeuma Verhoeff 1914, 48: 364 (type species *Syntelopodeuma gracilipes* Verhoeff, Hokkaido). NEW SYNONYMY.

Tokysoma Verhoeff 1932, 64: 515 (type species

Tokyosoma takakuwai Verhoeff, Shikoku). NEW SYNONYMY.

Niponiothauma Verhoeff, 1942: 137: 204 (type species *Niponiothauma inflatum* Verhoeff, Japan). NEW SYNONYMY.

Pteryogstegia Miyosi 1958, 67: 180 (type species *Pteryogstegia kuroiwadensis* Miyosi, Shikoku). Murakami and Kawasawa, 1976, 2: 115. NEW SYNONYMY.

Altajosoma Gulicka 1972, 51: 37 (type species *Altajosoma pinetorum* Gulicka, Altai Mtns., USSR). NEW SYNONYMY.

Ancestreuma Golovatch 1977, 56: 715 (type species *Ancestreuma principale* Golovatch, Mongolia). *Sakhalineuma* Golovatch 1976, 227: 1489 (type species *Sakhalineuma molodovae* Golovatch, Sakhalin Island). NEW SYNONYMY.

DISCUSSION: The diagnosis, description, and distribution of the genus are the same as for the family.

Perusal of the descriptions of species and of the accompanying figures will abundantly justify the generic synonymies above, and these genera carry with them into synonymy the names of their accompanying monobasic families, though a number of these familial synonymies had already been recognized. The essentials of the argument: what once appeared to be a series of related but distinct gonopod plans and body forms now appear to be connected in almost every case by a spectrum of intermediate species occupying a coherent geographical range. Therefore it seems more realistic and practical to recognize species groups rather than genera or subgenera.

PRINCIPALIS GROUP

In this group of species, the most primitive type of gonopod organization occurs. The anterior gonopod telopodites are very large and broad, in some species nearly the size of the posterior gonopod colpocoxites, though a tendency for the telopodites to become more gracile is seen in the more apomorphic species. A synapomorphy uniting members of the group is the prominent angled corner of the posterior gonopod angiocoxite, which also occurs in *coxalis*, a member of another group on other grounds (see discussion of character 7 under Cladistic Analysis). Members of the group are distributed in northern Mongolia and in the adjacent regions of the USSR.

Diplomaragna sardyk, new species

Figures 2–5

TYPES: Male holotype (ZMUM), many male and female paratypes (ZMUM, AMNH, SMF, ZMUC) from *Larix* forest and tundra, elev. 2300–2700 m, Munkhu-Sardyk Mountains, Kankh Somon, Khubsugul Aimak, Mongolia, collected July–August, 1986, by K. Ulykpan.

ETYMOLOGY: The species name, a noun in apposition, refers to the type locality.

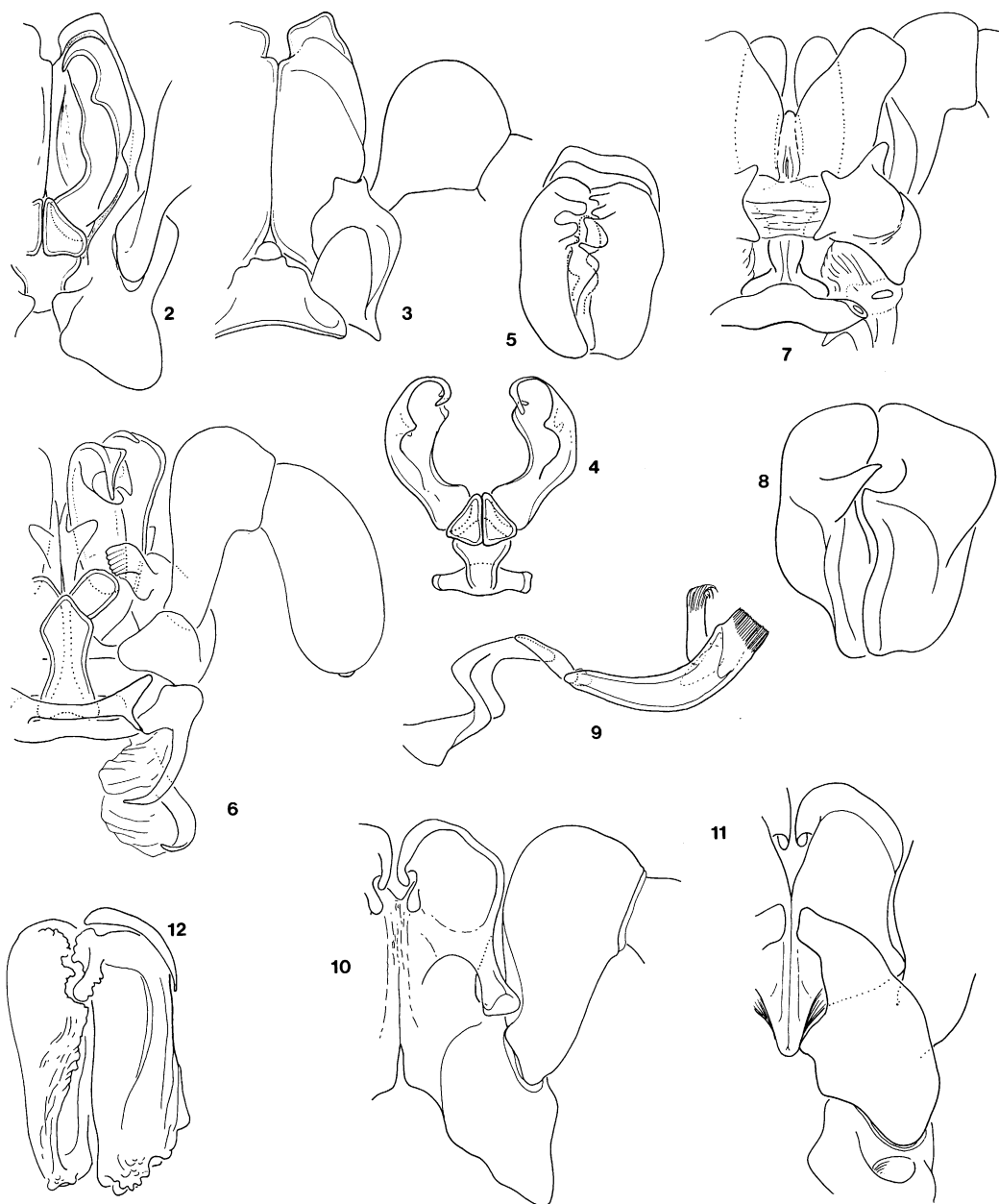
DIAGNOSIS: Differing from related species in the Mongolian group (except for *principalis*) in the extraordinary size and breadth of the anterior gonopod telopodites (fig. 4) and in the lack of posterior gonopod colpocoxite sheath processes. *Diplomaragna principalis* is a much larger species (18–20 mm long) with more complex anterior gonopod telopodites.

MALE: Thirty-two segments. Length, about 10 mm, width at sixth metazonite, 1.43. Antennal segment-3 0.55 long. Ocelli 29–30, well pigmented, in triangular eyepatch. Paranota beginning on segment 2, strongest on segments 9–22, at first planar, then becoming angled dorsad, thinner, longer; reduced on segments 26, 27, absent from segments 28–31. Segmental setae acute, thin, about 0.25 mm long. Pigmentation tan, mottled darker purplish brown on antennae, legs. Anterior leg pairs 3–7 enlarged, crassate, pairs 5–7 much larger, femora swollen and curved.

Anterior gonopods very large, broad, telopodites two-segmented, curved mesoposteriad, with several lateral and mesal lamellae (fig. 4). Posterior gonopods in anterior view (fig. 3) with angiocoxites relatively small; mesodistal angles only slightly extended; colpocoxites for most of their length gently curved posteriorly. In posterior view (fig. 2), sheath occupying most of posterior surface, lateral and mesal processes absent. Telopodite segments large. Leg pair coxae 10, 11 with glands.

FEMALE: Thirty-two segments. Length, about 12–14, width at sixth metazonite, 1.5. Antennal segment-3 0.55 long. Ocelli 29–30. Nonsexual characters as in male. Cyphopods as in figure 5.

DISTRIBUTION: MONGOLIA: Type locality, August 5, 1982, K. Ulykpan, 2♂, 6♀;



Figs. 2-12. 2-5. *Diplomaragna sardykh*, new species. 2. Gonopods, left side, posterior view. 3. Gonopods, right side, anterior view. 4. Anterior gonopods, posterior view. 5. Left cyphopod, ventral view. 6-8. *D. ryvkini*, new species. 6. Gonopods, left side, posterior view. 7. Gonopods, right side, anterior view. 8. Left cyphopod, ventral view. 9-12. *D. longibrachiata*, new species. 9. Left anterior gonopod, lateral view. 10. Posterior gonopods, left side, posterior view. 11. Posterior gonopods, right side, anterior view. 12. Left cyphopod, ventral view.

Uburkhangai Aimak, Bat-Ulziy Somon, Ulaantsugalan Waterfalls, under moss and logs, July 30-August 1, 1986, K. Ulykpan, male.

DISCUSSION: This species and *D. principalis* (Golovatch) would appear to have the most primitive (=simplest) gonopod organization of any species of any *Diplomaragna*. Both the

anterior gonopod telopodites and the posterior gonopod colpocoxites are relatively unmodified; the former are only slightly smaller than the latter. The posterior gonopod angiocoxites show little indication of the unusual elaborations present in the highly derived species from the Soviet Far East, Korea, and Japan.

The large collection of type material contained well over 100 specimens of either sex, but only a half dozen males and about 10 females were intact, the majority of specimens being broken into at least three pieces so that in the jumble of trunks there was no hope of associating parts. Intact specimens were chosen as primary types and the broken ones are all together in a large vial labeled as paratypes (ZMUM).

The Ulaansutgalan Waterfalls record may not be correct and should be confirmed. The single male of *sardyk* was in a vial containing a large collection of *ulykpani*. Since the two species were in the same shipment from Moscow and were studied in tandem in my laboratory, an accidental transfer might have been made in either place.

***Diplomaragna ryvkini*, new species**

Figures 6–8

TYPES: Male holotype (ZMUM) and male and female (AMNH, SMF) paratypes from mixed forest along Gaudjigit River, 15 km W of Severobaikalsk, Buryat ASSR, collected 20–21 August, 1984, by A. Ryvkin.

ETYMOLOGY: The species name honors the collector.

DIAGNOSIS: Closest to *D. principalis*, but differing in the more complex sheath of the posterior gonopod colpocoxites, and other details of the gonopods (figs. 6, 7).

MALE: Thirty-two segments. Length, about 13, width at sixth metazonite, 1.56. Antennal segment-3 0.63 mm long. Ocelli 27–30, pigmented, in triangular eyepatch. Paranota beginning on segment 2, strongest on segments 9–25, then gradually smaller, absent from segments 27–32. Segmental setae acute, thin, about 0.4 long. Pigmentation even medium brown, faintly mottled brownish purple on posterior parts of metazonites, antennae, and anterior legs. Anterior leg pairs 3–7 enlarged, crassate, pairs 5–7 much larger, femora swollen and curved.

Anterior gonopods (fig. 6) large, broad; telopodites distinctly two-segmented, strongly curved posteriad, tip of second article relatively complex. Posterior gonopods in anterior view (fig. 7) with angiocoxite subglobose, with small, subtriangular mesal process; colpocoxites fused at base, apically diverging, blunt. In posterior view (fig. 6), angiocoxal process and mesal process of colpocoxite clasp anterior gonopod telopodite; angiocoxal process apically ribbed, colpocoxite process subtriangular. Colpocoxite has small apical extension. Telopodite segments large. Leg pair coxae 10, 11 with glands, not modified.

FEMALE: Thirty-two segments. Length, about 15, width at sixth metazonite, 1.96. Antennal segment-3 0.65 long. Ocelli 27–30. Nonsexual characters as in male. Cyphopods (fig. 8) with valves each having two depressed areas separated by distinct lamellae.

DISTRIBUTION: USSR: Siberia, Irkutsk area, Kazachinsk-Lenskiy District, 9 km S of Magistralnyi, *Larix*, *Picea*, *Betula* forest, July 17, 1984, A. Ryvkin, 2♂. MONGOLIA: Khubsugul Lake, River Ongolich, pitfall traps in *Larix* forest, August 3, 1977, V. G. Shilenkov, ♂.

***Diplomaragna longibrachiata*,**

new species

Figures 9–12

TYPES: Male holotype (ZMUM) and male and four female paratypes (ZMUM, AMNH) from mixed forest along a stream at kilometer 151 between Kyzyl and Abakan, on the River Us, Krasnoyarsk Province, Siberia, USSR, collected 15 August 1984, by A. Ryvkin.

ETYMOLOGY: The species name refers to the "long arm" of the posterior gonopod lateral sheath process, and is a noun in apposition.

DIAGNOSIS: The anterior gonopod telopodites are of the thick type, but have a posterior subapical extension.

MALE: Thirty-two segments. Length, about 15, width at sixth metazonite, 2.13. Antennal segment-3 0.60 long. Ocelli 30–33, pigmented, in triangular eyepatch. Paranota large, angled strongly dorsad, beginning on segment 2, strongest on segments 9–26, somewhat reduced on segment 27, absent from segments 28–32. Segmental setae acute, thin, about 0.4 mm long. Pigmentation even medium brown,

mottled brownish purple on posterior parts of metazonites, antennae, and anterior legs. Anterior leg pairs 3–7 enlarged, crassate, pairs 5–7 much larger, femora swollen and curved.

Anterior gonopods (fig. 9) large, broad; telopodites distinctly two-segmented, strongly curved posteriad, tip of second article not complex, with thinned, subfimbriate cuticle, long subapical branch present, tip incurved, fimbriate. Posterior gonopods in anterior view (fig. 11) with angiocoxite strongly produced ventromesally, ending in quadrate tip; colpocoxites fused at base, apically diverging, then converging, strongly curved, blunt. In posterior view (fig. 10), mesal process of colpocoxite well distal of midlength; lateral process of colpocoxite very long, subspatulate. Telopodite segments large. Leg pair 10 and 11 coxae with glands, coxae 10 with knobs distal to gland, small mesal knob on trochanter.

FEMALE: Thirty-two segments. Length, about 15, width at sixth metazonite, 2.21. Antennal segment-3 0.65 long. Ocelli 25–28. Nonsexual characters as in male. Cyphopods (fig. 12) strongly elongated in anterior-posterior axis, without convex areas, lacking prominent lamellae.

DISTRIBUTION: MONGOLIA: Khubsugul Lake, River Ongolich, pitfall traps in *Larix* forest, August 3, 1977, V. G. Shilenkov, male (ZMUM).

DISCUSSION: At the Mongolian locality, syntopic with *D. ryvkini*; the present species is the larger of the two, though the size separation is not as great as in some other paired syntopic species. The Mongolian male shows slight differences, perhaps only an expression of individual variation. The anterior telopodite process is somewhat shorter and broader at the base, and the distal telopodite segment of the posterior gonopod has a small “nipple,” vestige of the more distal leg segments. On one side, there is a tiny, twisted claw at the end of the vestige.

Diplomaragna principalis (Golovatch),
new combination

Figure 13

Ancestreuma principalis Golovatch, 1977: 715, figs. 1, 2 (male holotype from Tsetserleg River, Tevshruulekh Somon, Ara-Khangai Aimak, Mongolia, in ZMUM, not examined).

DISCUSSION: Dr. Golovatch sent me toptypical material of this species (WASC), and a new illustration of the gonopods (fig. 13) appears here for comparative purposes. Unfortunately the collection contained no females. The simple organization of the gonopods has already been alluded to under the description (above) of the related species, *sardyk*. This species and *communicantis* are syntopic, providing an example of a case in which two sympatric species differ greatly in size, *principalis* being only a little less than twice as large as *communicantis*. Unfortunately, too little is known of their ecology to indicate how they share the habitat.

Diplomaragna ulykpani, new species

Figure 14–17

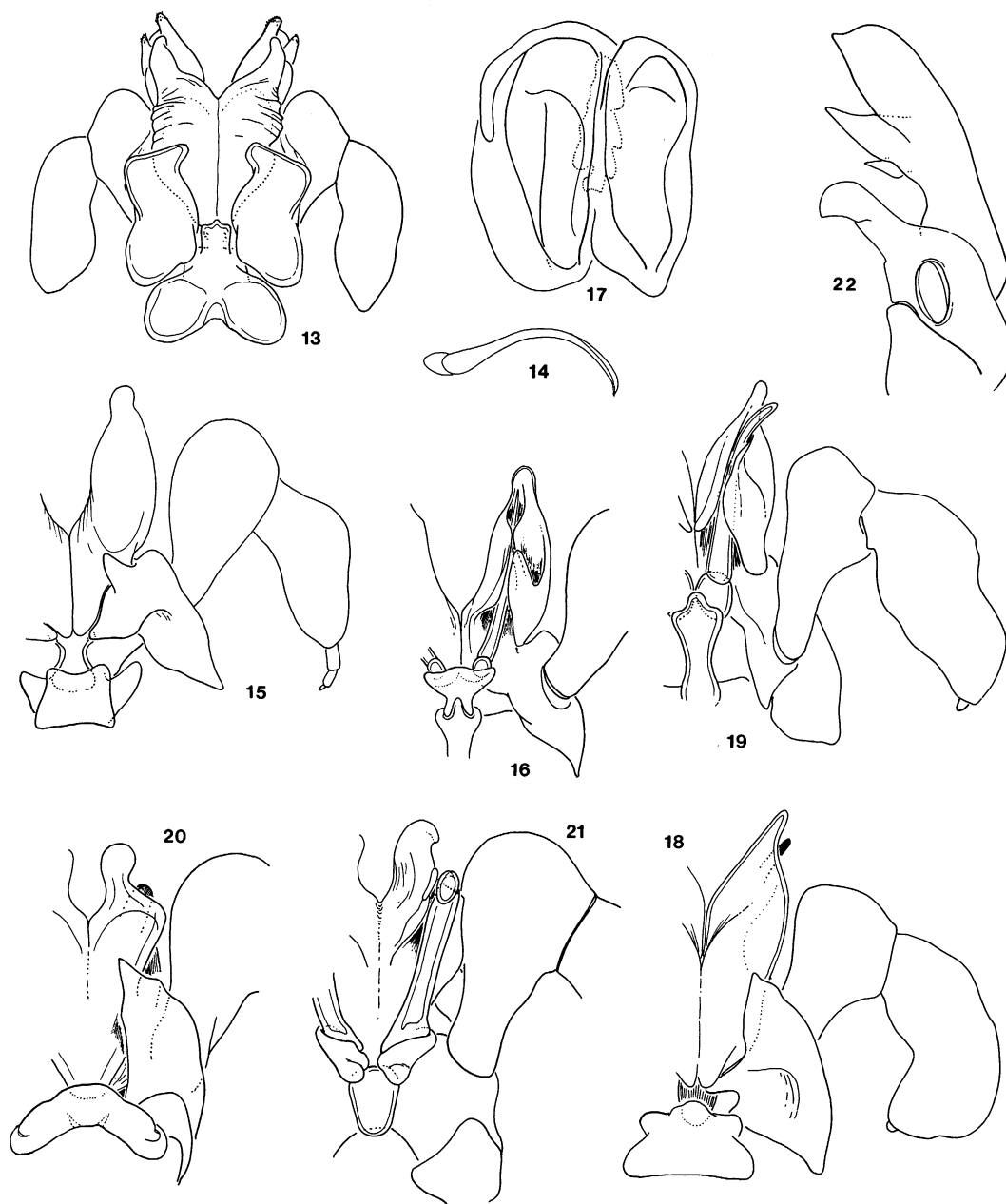
TYPES: Male holotype (ZMUM), many male and female paratypes (ZMUM, AMNH, SMF) from under moss and logs, Ulaantsugalan Waterfalls, Bat-Ulziy Somon, Uburkhangai Aimak, Mongolia, collected July 30–August 1, 1986, by K. Ulykpan.

ETYMOLOGY: The species name honors the collector.

DIAGNOSIS: Very closely related to *communicantis* (Golovatch), but differing in details of the gonopods; the anterior gonopods are more slender, the angiocoxites of the posterior gonopods have pronounced mesal corners, the lateral sheath process of the colpocoxites is free from the colpocoxite for its distal half, and the coxites themselves are apically more narrow.

MALE: Thirty-two segments. Length, about 11–12, width at sixth metazonite, 1.48. Antennal segment-3 0.52 long. Ocelli 29–30, well pigmented, in triangular eyepatch. Paranota beginning on segment 2, relatively low on 3–5, strongest on segments 9–22, at first planar, then becoming angled dorsad, thinner, longer; reduced on segments 26, 27, absent from segments 28–31. Segmental setae acute, thin, about 0.25 long. Pigmentation tan, mottled darker purplish brown on antennae, legs. Anterior leg pairs 3–7 enlarged, crassate, pairs 5–7 much larger, femora swollen and curved.

Anterior gonopods relatively broad at base, but strongly acuminate, two-segmented (fig. 14). Posterior gonopods in anterior view (fig. 15) with angiocoxites mesodistal angles extended; colpocoxites basally fused, strongly



Figs. 13–22. 13. Gonopods of *Diplomaragna principalis* (Golovatch), anterior view. 14–17. *D. ulykpani*, new species. 14. Right anterior gonopod, lateral view. 15. Gonopods, right side, anterior view. 16. Gonopods, left side, posterior view. 17. Right cyphopod, ventral view. 18, 19. *D. communicantis* (Golovatch). 18. Gonopods, right side, anterior view. 19. Gonopods, left side, posterior view. 20, 21. *D. feynmani*, new species. 22. Left posterior gonopod colpocoxite of *D. borealis* (Golovatch), lateral view.

curved posteriorly in distal two-thirds, apex abruptly narrowed. In posterior view (fig. 16), sheath occupying most of posterior surface, mesal processes obsolete, lateral processes

large, mostly free from sheath. Telopodite segments large. Leg pair coxae 10, 11 with glands.

FEMALE: Thirty-two segments. Length,

about 12–14, width at sixth metazonite, 1.5. Antennal segment-3 0.55 long. Ocelli 29–30. Nonsexual characters as in male. Cyphopods as in figure 17.

DISTRIBUTION: MONGOLIA: Ulan Bator, rosarium in hothouse, March–April 1984, K. Ulykpan, 1♂, 9♀.

DISCUSSION: This species and *communicantis* are very close, but the consistent differences are obvious in a side-by-side comparison (see Diagnosis above). The Ulan Bator record is probably an importation from a place near the type locality.

Diplomaragna communicantis (Golovatch),
new combination
Figures 18, 19

Ancestreuma communicantis Golovatch, 1977: 717
(male holotype from Tsetserleg River, Tevshrulekh Somon, Ara-Khangai Aimak, Mongolia, in ZMUM, not examined).

DISCUSSION: Through the courtesy of Dr. Golovatch, I was able to examine topotypes of this species (WASC) and found I could not improve on his description, except to make a drawing of the cyphopods. Some new figures of the gonopods (figs. 18, 19) are also presented here in order that more direct comparisons with related species can be made.

Diplomaragna feynmani, new species
Figures 20, 21

TYPES: Male holotype (ZMUM) from *Larix-Picea* forest 25 km S of Turan, near Pass Vesolyi, Tuva ASSR, collected August 10, 1984, by A. Ryvkin.

ETYMOLOGY: The species name honors Richard P. Feynman, physicist, teacher, artist, musician, raconteur, and personal hero of the author, whose untimely death prevented him from realizing his ambition to visit Tannu Tuva, now the Tuva ASSR.

DIAGNOSIS: Closest to *D. communicantis*, but differing in details of the gonopods, especially the tips of the posterior gonopod colpocoxites (figs. 20, 21).

MALE: Thirty-two segments. Length, about 15, width at sixth metazonite, 2.08. Antennal segment 3, ocelli destroyed in holotype and only specimen. Paranota very pronounced, beginning on segment 2, strongest on segments 9–26, slightly reduced on segment 27,

absent from segments 28–32. Segmental setae acute, thin, about 0.54 long. Pigmentation light brown. Anterior leg pairs badly damaged, but at least some extremely crassate, femora much swollen, nearly C-shaped. Leg pairs 10, 11 with coxal glands, coxae 10 with short, conelike, setose projection posterior to gland.

Anterior gonopods (fig. 21) relatively short, slightly curved, thick, 2-segmented, tips of telopodites simple. Posterior gonopods in anterior view (fig. 20) with large angiocoxite bearing strong triangular mesal projection; posterior process absent. Colpocoxites erect, only slightly curved, with distinct swelling midlength, tip abruptly narrowed, then club-like. In posterior view (fig. 21), lateral colpocoxite process absent, mesal process shifted laterally, lying in situ against tip of anterior gonopod telopodite.

Females not collected.

DISCUSSION: The anterior end of the male holotype is, unfortunately, badly crushed.

KEMEROVO GROUP

This is a group of closely related species that is geographically compact, all being found in the Krasnoyarsk–Irkutsk–Lake Baikal triangle. They are distinguished from the foregoing by having very well-developed sheath processes, especially the lateral, by the appearance of the movable, toothed process posterior on the angiocoxites, and especially by the reduced anterior gonopod telopodites which still retain some apical complexity. Lacking a mesal sheath process, *borealis* appears to be the plesiomorphic sister to all the other species.

The evident close relationships of the species, and the fact that, during the early stages of this study, I designated several more species of the group than I eventually decided to name here, suggests a fruitful field for work on the distribution of sibling species, geographic variation, and ecological partitioning.

Diplomaragna borealis (Golovatch),
new combination
Figures 22–24

Ancestreuma boreale Golovatch, 1979a: 336 (male holotype from Mirnoye, Krasnoyarsk Province, Siberia, USSR, in ZMUM, not examined).

DISCUSSION: Golovatch (1979a) provided a good description of this species, paying particular attention to details of the trunk and head. Because my impressions of the gonopods differs somewhat from that conveyed by his illustrations, I present some new ones (figs. 22–24), made from topotypes (WASC) kindly sent by Golovatch. This species seems somewhat peripheral to the Kemerovo group, mostly because the posterior process of the colpocoxites is either reduced or incompletely developed. In this respect, there is some resemblance to *longibrachiata*, which seems to combine some characters of both the Kemerovo and Principalis groups. However, in *longibrachiata* the lateral sheath process is developed as a long, posteriorly projecting rod, while in *borealis* it appears as a large, lamellar shelf (fig. 22).

Diplomaragna mikhailjovae,
new species
Figures 25–28

TYPES: Male holotype (ZMUM), and male (AMNH) and female paratype (ZMUM) from *Abies* forest litter, Ussuri State Reserve, Maritime Province, USSR Far East, collected August 28, 1979, by E. V. Mikhailjova.

ETYMOLOGY: The species name honors the collector.

DIAGNOSIS: Differing from all other species in the Kemerovo group in the very short, blunt angiocoxal process, which articulates with a groove in the colopocoxite but does not pass mesal to it (fig. 27).

MALE: Thirty-two segments. Length, about 20–22, width at sixth metazonite, 2.86. Antennal segment-3 1.04 long. Ocelli 25–27, well pigmented, in triangular eyepatch. Paranota beginning on collum, strongest on segments 9–22, at first planar, then becoming angled dorsad, thinner, longer; abruptly smaller on segment 27, absent from segments 28–31. Segmental setae acute, thin, about 0.65 long. Pigmentation light brown, mottled darker purplish brown on antennae, legs. Anterior leg pairs 3–7 enlarged, crassate, pairs 5–7 much larger, femora swollen and curved.

Anterior gonopods subflagelliform, telopodites 2-segmented, curved posteriad, tip of telopodite slightly swollen (fig. 25). Posterior gonopods in anterior view (fig. 27) with an-

giocoxites strongly depressed on anterior face; mesodistal angles drawn out into rather blunt, angular processes fitting into grooves on colpocoxites; colpocoxites fused at base, processes from base articulate with angiocoxites; large frontal processes extend laterally to meet in anterior angiocoxal processes; colpocoxite tips with deep groove setting off caplike apex. In posterior view (fig. 26), posterior angiocoxal process absent. Colpocoxite sheath with anterior processes fused and projecting strongly dorsally; lateral processes very large, broad, and membranous at base, drawn out to sclerotized knob projecting posteriodorsally. Telopodite segments large. Leg pair coxae 10, 11 with glands.

FEMALE: Thirty-two segments. Length, about 22, width at sixth metazonite, 2.7. Antennal segment-3 1.00 long. Ocelli 26–28. Nonsexual characters as in male. Cyphopods as in figure 28.

DISTRIBUTION: USSR: Far East, Maritime Province, nl-R7 *Picea* stand, August 27, 1977, R. G. Fedorova, 1♂ (AMNH); Amursk area, Khingan State Reserve, Khingan Forestry, near Karaga, *Quercus* forest on hill, litter, August 21, 1983, Yu. Marusik, 1♂ (ZMUM).

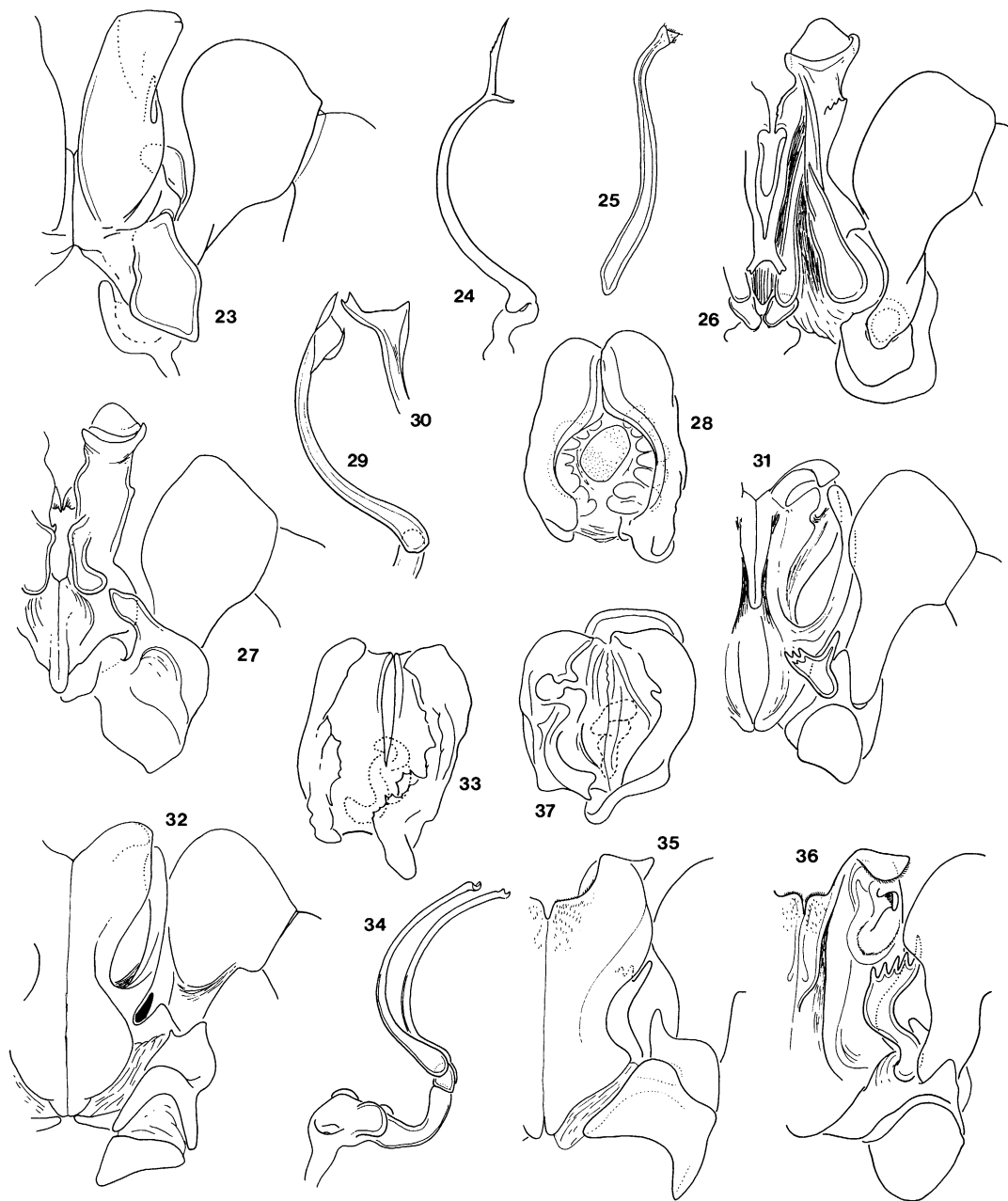
DISCUSSION: This species, for all its unique characters, may link the Kemerovo and Tetricolor species groups. Like the former, it has both lateral and mesal colpocoxite sheath processes on the posterior gonopods, and two-segmented anterior gonopod telopodites. But as in the latter, it occurs in the Far East, and the drawn-out lateral mesodistal angle of the angiocoxite of the posterior gonopod suggests the origin of, and an intermediate step toward, the flagelliform processes of the Tetricolor group. However, the cladistic analysis (see above) suggests that this is probably a separate development.

The Ussuri Reserve is also home to *yakovlevka*, but the two do not seem to be exactly syntopic.

Diplomaragna deplanata (Stuxberg),
new combination
Figures 29–33

Craspedosoma deplanatum Stuxberg, 1876, 33: 34.

TYPES: Male syntype? (BMNH), from between Atschinsk and Mariinsk, Siberia,



Figs. 23–37. 23, 24. *Diplomaragna borealis* (Golovatch). 23. Posterior gonopods, right side, anterior view. 24. Right anterior gonopod telopodite, lateral view. 25–28. *D. mikhajovae*, new species. 25. Right anterior gonopod telopodite, lateral view. 26. Gonopods, left side, posterior view. 27. Posterior gonopods, right side, anterior view. 28. Left cyphopod, ventral view. 29–33. *D. deplanta* (Stuxberg). 29. Right anterior gonopod telopodite, lateral view. 30. Tip of same, posterior view. 31. Posterior gonopods, left side, posterior view. 32. Posterior gonopods, right side, anterior view. 33. Left cyphopod, ventral view. 34–37. *D. kemerovo*, new species. 34. Anterior gonopods, lateral view. 35. Posterior gonopods, right side, anterior view. 36. Posterior gonopods, left side, posterior view. 37. Left cyphopod, ventral view.

USSR, collected in 1875 by the Nordenskiöld Expedition, not seen, examined by Richard Hoffman.

DIAGNOSIS: Lateral colpocoxite process is very long, erect, instead of extending posteriorly; its origin is near the colpocoxite base, visible in anterior view (fig. 32).

MALE FROM SALAIR MOUNTAINS: Thirty-two segments. Length, about 13.5, width at sixth metazonite, 1.53. Antennal segment-3 0.78 long. Ocelli 29, well pigmented, in triangular eyepatch. Paranota beginning on segment 2, strongest on segments 9–26, somewhat reduced on 27, 28, absent from segments 29–32. Segmental setae acute, thin, about 0.4 long. Pigmentation tan, with light mottling of purplish brown along posterior margins of metazonites, on antennae and anterior legs. Leg pairs 3–7 enlarged, crassate, pairs 5–7 much larger, femora swollen and curved.

Anterior gonopods (figs. 29, 30) narrowed, telopodites single-segmented, evenly curved posteriad, tip expanded, with long mesal extension seen in posterior view (fig. 30). In situ, tips of anterior gonopods project prominently from colpocoxite sheath of posterior gonopods. Posterior gonopods in anterior view (fig. 32) with angiocoxite reduced, lacking mesal process; colpocoxites fused for most of their length, apically diverging, blunt; lateral colpocoxite process visible from anterior, appearing to originate near colpocoxite base, nearly as long as main body of coxite. In posterior view (fig. 31), angiocoxal process large, movable, curved, with large lateral and 3 smaller mesal teeth. Mesal process of colpocoxite absent; lateral process very long, erect, rodlike, slightly club shaped at tip. Posterior gonopod telopodite segments large. Anterior gonopod telopodites inserted in tight-fitting groove which completely covers tip. Leg pair 10 and 11 coxae with glands, not modified.

FEMALE FROM SALAIR MOUNTAINS: Thirty-two segments. Length, about 11 (specimen strongly contracted), width at sixth metazonite, 1.61. Antennal segment-3 0.57 long. Ocelli 27–30. Nonsexual characters as in male. Cyphopods as in figure 33.

DISTRIBUTION: USSR: Siberia, Kemerovo area, Salair Mountains, *Picea-Populus tremulans-Betula* taiga, September, 1969, V. Korsunov, 1♂, 1♀ (SMF); environs of Mo-

khovo and Belovo, steppe, June 5, 1981, S. K. Stebaeva, male (ZMUC); Novosibirsk area, Toguchin District, Mirnyi, *Abies, Populus* forest, August 22–September 3, 1984, V. Bakurov, 1♂. Khakassian ASSR, Shera District, Malaya Syya, 650 m elevation, hedge in *Larix* forest, July 20, 1987, V. Kollegova, 2♂, 1♀.

DISCUSSION: The description given by Stuxberg (1876) suggests *Diplomaragna*, but is not adequate to recognize this species from among the several related ones (*deplanata, kemerovo, bakurovi, golovatchi*) that are sympatric in the Kemerovo region. Fortunately, a type specimen is still in existence and was examined and drawn by my colleague, Richard Hoffman, during a visit to the British Museum. His drawings matched well with the gonopods of males from several recent Soviet collections.

That these closely related, similar species occur together is contrary to the expected pattern in which sympatric (syntopic?) congeneric milliped species are strikingly different, especially in size. Perhaps more detailed collecting in the Kemerovo area will reveal ecological exclusion among the three.

Diplomaragna kemerovo,

new species

Figures 34–37

TYPES: Male holotype (ZMUM), 2♂, 4♀ paratypes (ZMUM, AMNH, SMF) from taiga in Kemerovo area, Prokopievsk District, Salair Mountains, Siberia, USSR, collected August 1966 by Y. B. Byzova and Z. V. Chadaeva.

ETYMOLOGY: The species name refers to the type locality.

DIAGNOSIS: Near *bakurovi*, but with much smaller lateral colpocoxite process, quite different posterior angiocoxal process (fig. 36).

MALE: Thirty-two segments. Length, about 12, width at sixth metazonite, 1.3. Antennal segment-3 0.65 long. Ocelli 26–28, poorly pigmented, in triangular eyepatch. Paranota beginning on segment 2, strongest on segments 9–26, somewhat reduced on 27, absent from segments 28–32. Segmental setae acute, thin, about 0.4 mm long. Pigmentation creamy tan after long preservation. Leg pairs 3–7 enlarged, crassate, pairs 5–7 much larger, femora swollen and curved.

Anterior gonopods (fig. 34) narrowed, telopodites distinctly 2-segmented, strongly curved posteriad, tip of second article with short, sinuous region. Posterior gonopods in anterior view (fig. 35) with angiocoxite reduced, with small, subtriangular mesal process; colpocoxites fused for much of their length, apically diverging, blunt. In posterior view (fig. 36), angiocoxal process large, movable, curved, with five apical teeth. Mesal process of colpocoxite much reduced; lateral process enlarged, complex, with laterally cupped lamella, long, thin, posteriorly extending arm. Posterior gonopod telopodite segments large. Anterior gonopod telopodites inserted in tight-fitting groove which completely covers tip. Leg pair 10 and 11 coxae with glands, not modified.

FEMALE: Thirty-two segments. Length, about 14, width at sixth metazonite, 1.82. Antennal segment-3 0.65 long. Ocelli 27–30. Nonsexual characters as in male. Cyphopods as in figure 37.

DISTRIBUTION: USSR: Siberia, Novosibirsk area, Toguchin District, Mirnyi, *Abies* and *Populus* forest, 22 August–3 September 1984, V. Bakurov, 4♂; Salair Mountains near Prokopyevsk, *Abies* and *Populus tremulans* taiga, August 1, 1966, Z. V. Chadaeva, 1♂, 4♀ (paratypes, ZMUC); Krasnoyarsk Prov., West Sayan Mountains, Research Station of Institute of Forestry and Timber, *Populus tremulans* litter, "autumn," 1981, V. K. Dmitrienko, 1♂.

DISCUSSION: The Mirnyi males are very dark brown without markings; their ocelli appear more regular and are more heavily pigmented than in the type collection. Perhaps long preservation dissolved pigment, including that of the ocelli, from the types; alternatively the dark color of the Mirnyi specimens may be due to staining by leachates from conifer needles, if the specimens were preserved for long with a Berlese residue. Sympatric at Mirnyi with *bakurovi* and *deplanata*.

***Diplomaragna bakurovi*,
new species
Figures 38–41**

TYPES: Male holotype (ZMUM), 3♂, 5♀ paratypes (ZMUM, AMNH, SMF) from *Abies*

and *Populus* forest, Mirnyi, Toguchin District, Novosibirsk area, Siberia, USSR, collected 22 August to 3 September, 1984, by V. Bakurov.

ETYMOLOGY: The species name honors the collector of the type series.

DIAGNOSIS: Closely related to *kemerovo*, but differing in the much larger lateral colpocoxite process and the different form of the movable angiocoxite process (see figs. 36 and 38).

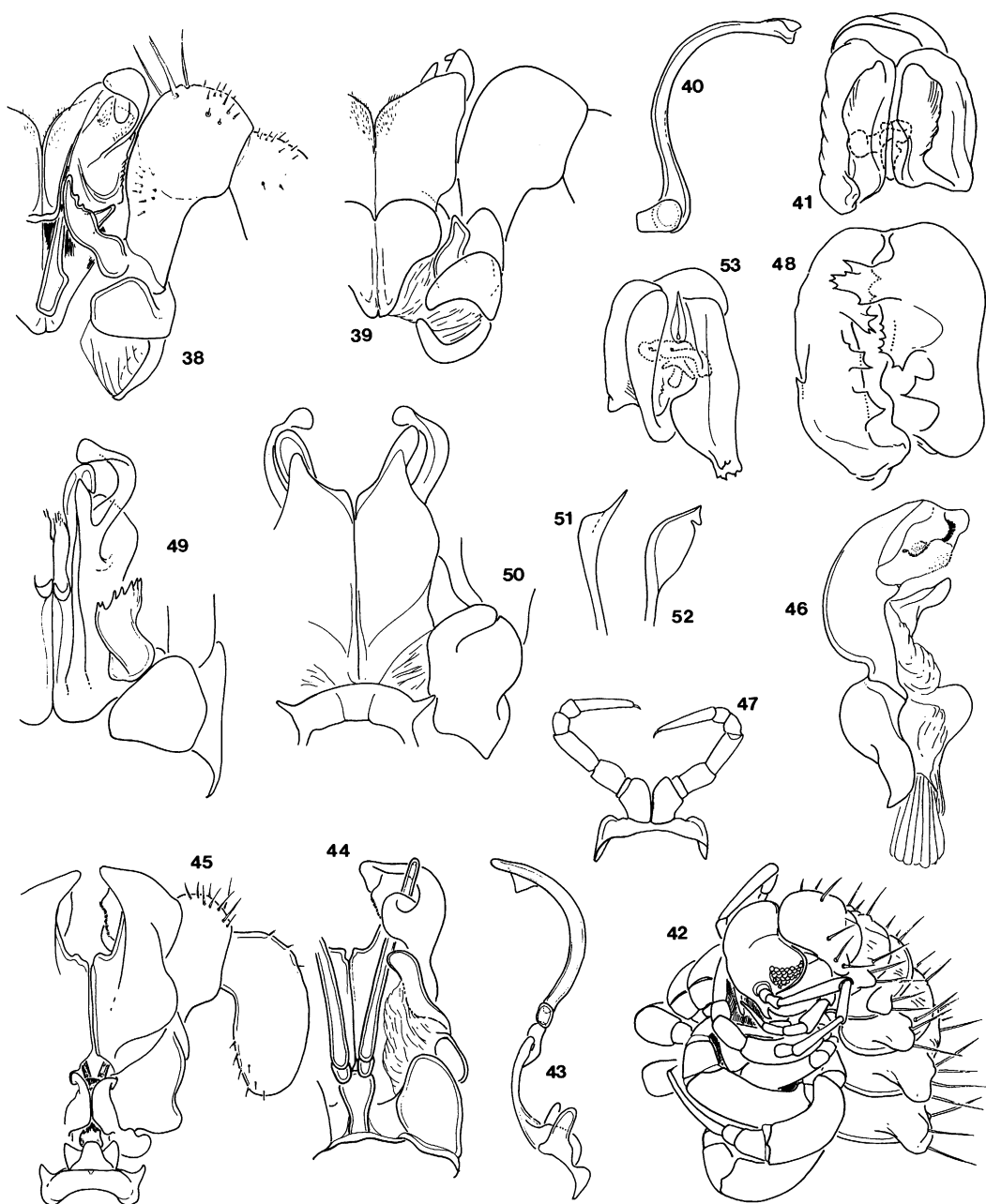
MALE: Thirty-two segments. Length, about 12, width at sixth metazonite, 1.2. Antennal segment-3 0.52 long. Ocelli 26–28, well pigmented, in triangular eyepatch. Paranota relatively low, beginning on segment 2, strongest on segments 9–22, progressively reduced on segments 23–25, absent from segments 26–32. Segmental setae acute, thin, about 0.4 mm long. Pigmentation dark brown, but animals poorly preserved, perhaps stained. Leg pairs 3–7 enlarged, crassate, pairs 5–7 much larger, femora swollen and curved. Leg pairs 10, 11 with coxal glands, coxae 10 with short, conical projection posterior to gland.

Anterior gonopods (fig. 40) narrowed, telopodites distinctly 2-segmented, strongly curved posteriad, tip of second article with short, sinuous region. Posterior gonopods in anterior view (fig. 39) with angiocoxite reduced, with small, subtriangular mesal process; colpocoxites fused for much of their length, apically diverging, blunt. In posterior view (fig. 38), angiocoxal process large, movable, curved, with five apical teeth. Mesal process of colpocoxite much reduced; lateral process enlarged, complex, with laterally cupped lamella, long, thin, posteriorly extending arm. Posterior gonopod telopodite segments large. Anterior gonopod telopodites inserted in tight-fitting groove which completely covers tip.

FEMALE: Thirty-two segments. Length about 12, width at sixth metazonite, 1.44. Antennal segment-3 0.62 long. Ocelli 27–30. Nonsexual characters as in male. Cyphopods as in figure 41.

DISTRIBUTION: USSR: Siberia, Krasnoyarsk Prov., 3.5 km N of Ermakovskoye, *Betula*, *Pinus*, *Crataegus*, *Alnus*, *Salix*, etc., forest near River Oya, 20 August 1984, A. Ryvkin, 2♂, 1♀.

DISCUSSION: At the type locality, this species is sympatric with *kemerovo* and *deplanata*.



Figs. 38–53. 38–41. *Diplomaragna bakurovi*, new species. 38. Posterior gonopods, left side (left anterior gonopod telopodite attached), posterior view. 39. Posterior gonopods, right side, anterior view. 40. Left anterior gonopod telopodite, mesal view. 41. Right cyphopod, ventral view. 42–48. *D. shilenkovi*, new species. 42. Anterior end of body of male, anteriolateral view. 43. Anterior gonopods, lateral view. 44. Gonopods, left side, posterior view. 45. Gonopods, right side, anterior view. 46. Right posterior gonopod coxae, mesal view. 47. Leg pair 3 of female, posterior view. 48. Right cyphopod, ventral view. 49–53. *D. golovatchi*, new species. 49. Posterior gonopods, left side, posterior view. 50. Posterior gonopods, right side, anterior view. 51. Tip of anterior gonopod telopodite, posterior view. 52. Same, lateral view. 53. Left cyphopod, ventral view.

***Diplomaragna golovatchi*,**

new species

Figures 49–53

TYPES: Male holotype (ZMUM), 8♂ and 14♀ paratypes (ZMUM, AMNH, SMF) from *Pinus*, *Betula*, and *Ulmus* litter along stream at 550–600 m elevation, Bashkirian State Reserve, Saragaya, 150 km east of Sterlitamak, Bashkirian ASSR, USSR, collected August 11, 1988, by S. I. Golovatch.

ETYMOLOGY: The species name honors the collector of the type series, a noted Soviet zoologist.

DIAGNOSIS: Similar to species from the Krasnoyarsk region, but differing in that the lateral posterior process of the posterior gonopod colpocoxite originates apically, projects strongly, is visible for most of its length in anterior view, and is swollen at the tip.

MALE: Thirty-two segments. Length, about 11–12, width at sixth metazonite, 1.3. Antennal segment-3 0.60 long. Ocelli 30, pigmented, in triangular eyepatch. Paranota beginning on collum. Strongest on segments 9–25, somewhat reduced on 26, 27, absent from 28–31. Segmental setae acute, thin, about 0.4 mm long. Pigmentation even medium brown, faintly mottled brownish purple on antennae, legs, posterior parts of metazonites. Anterior leg pairs 3–7 enlarged, crassate, pairs 5–7 much larger, femora swollen and curved.

Anterior gonopods subflagelliform, telopodites single-segmented, curved posteriad, tip of telopodite in lateral view with broad posterior lamella (figs. 51, 52). Posterior gonopods in anterior view (fig. 50) with angiocoxite subglobose, somewhat depressed on anterior face; colpocoxites fused at base, sharply angled posteriorly about $\frac{2}{3}$ length, coxite tip and posterior process visible, posterior process appearing longer, strongly incurved, tip swollen. In posterior view (fig. 49), posterior angiocoxal process large, movable with about 7 irregular teeth. Mesal colpocoxite process in normal position, but lateral process much enlarged, originating near apex of coxite, strongly projecting, curved. Telopodite segments large. Leg pair coxae 10, 11 with glands, not modified.

FEMALE: Thirty-two segments. Length, about 12, width at sixth metazonite, 1.35.

Antennal segment-3 0.60 long. Ocelli 30. Nonsexual characters as in male. Cyphopods as in figure 53.

DISTRIBUTION: USSR: Bashkirian ASSR, Shulgan-Tash State Reserve, 35 km WSW Burzian (=Starosubkhanguovo), Gadilgareevo, mixed deciduous forest litter, 500–550 m elevation, August 12–15, 1988, S. Golovatch, 1♂, 2♀; Visim State Reserve, near Nizhniy Tagil, in taiga, "summer," 1984, N. Postnikova, 3♂. Siberia, 40 km S Krasnoyarsk, Pinus, Betula forest near Yemelyanovo Airport, August 31, 1982, K. Eskov, 2♂, 3♀ (paratypes, ZMUC).

DISCUSSION: These records from the Urals are confusing. Aside from this species, diplomaragnids have not been recorded west of the region of Novosibirsk, some 800 air miles east of Sverdlovsk and the localities in the Bashkirian ASSR. The Krasnoyarsk locality of *golovatchi* is about 1300 air miles east of Sverdlovsk! *D. golovatchi* is clearly a member of the group of related species in the Krasnoyarsk area, and when I had seen only the Krasnoyarsk and Sverdlovsk collections, the logical assumption seemed to be that the Sverdlovsk data were in error. However, the appearance of two collections of numbers of males and females from different localities in Bashkiria, not far south of Sverdlovsk, makes the situation much more ambiguous. Now it seems possible that the Krasnoyarsk collection is mislabeled, but *D. golovatchi* has a clear relationship to species from that area.

COXALIS GROUP

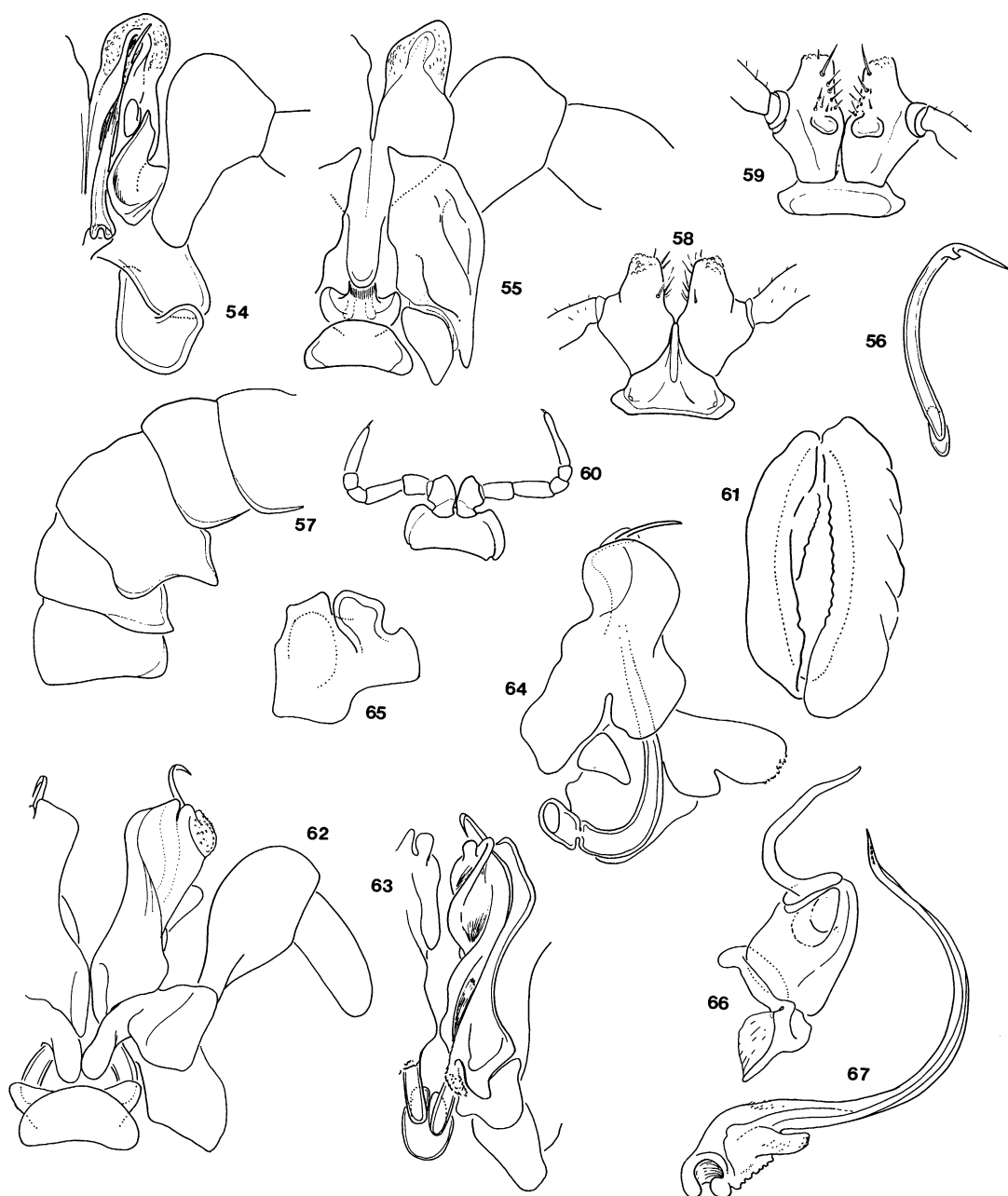
This small group of three species seems heterogeneous, but they persistently cluster near one another in the cladistic analysis. While a case can be made for the relationship of *coxalis* and *shilenkovi* (see below; also discussion of characters 6 and 10 under Cladistic Analysis above), *molodovae* looks quite different and occurs far to the east.

***Diplomaragna shilenkovi*,**

new species

Figures 42–48

TYPES: Male holotype (ZMUM), 7♂, 2♀ paratypes (ZMUM, AMNH) from pitfall traps



Figs. 54–67. 54–61. *Diplomaragna coxalis*, new species. 54. Gonopods, left side, posterior view. 55. Gonopods, right side, anterior view. 56. Anterior gonopod telopodite, lateral view. 57. Diplosegments 5–9, lateral view (anterior to the right). 58. Coxae 12, anterior view. 59. Same, posterior view. 60. Leg pair 3 of female, posterior view. 61. Left cyphopod, ventral view. 62–64. *D. molodovae* (Golovatch). 62. Gonopods, right side, anterior view. 63. Gonopods, left side, posterior view. 64. Right posterior gonopod colpocoxite and anterior gonopod telopodite, mesal view. 65–67. *D. terricolor* (Attems). 65. Right coxae 10, posterior view. 66. Right posterior gonopod angiocoxite, anterior view. 67. Right anterior gonopod telopodite, mesal view.

in taiga, River Solzan valley, Khamar-Daban Mountains, Irkutsk area, Siberia, USSR, collected August 22, 1978, by V. G. Shilenkov.

ETYMOLOGY: The species name honors the collector of the type series.

DIAGNOSIS: The very large, protruding gonopods distinguish this species from all others.

MALE: Thirty-two segments. Length about 16, width at sixth metazonite, 2.34. Antennal segment-3 0.86 long. Ocelli 29, well pigmented, in triangular eyepatch. Paranota prominent, beginning on collum, strongest on segments 9–22, reduced on 28, absent from segments 29–32. Segment 7 greatly enlarged, paranota lower on sides, larger, more rounded. Segmental setae acute, thin, about 0.55 mm long. Pigmentation uniform light brown leg pairs 3–7 enlarged, crassate, pairs 5–7 much larger, femora swollen and curved (fig. 42). Leg pairs 10, 11 with coxal glands, coxae 10 with prominent conelike projection posterior to gland.

Gonopods enormous, strongly projecting from segment 7. Anterior gonopods (fig. 43) rodlike, telopodites distinctly 2-segmented, strongly curved posteriad, tip of second article with subapical triangular lamella. Posterior gonopods in anterior view (fig. 45) with angiocoxite large; colpocoxites tightly appressed (but not fused) for much of their length, apically diverging, blunt. In posterior view (fig. 44), angiocoxal process large, evidently with limited motility, rounded at tip, lacking teeth. Mesal and lateral colpocoxite processes near apex, complexly embracing anterior gonopod telopodite, which projects apically.

FEMALE: Thirty-two segments. Length about 15, width at sixth metazonite 2.08. Antennal segment-3 0.63 long. Ocelli 28–30. Nonsexual characters as in male. Cyphopods as in figure 48.

DISTRIBUTION: (all collections by V. G. Shilenkov): USSR: Siberia, Irkutsk area, Khamar-Daban Mountains, Bezmyannyi Valley, pitfall traps, August 17, 1979, 34♂, 29♀ (paratypes, SMF); type locality, 15 July 1979, 1♂, 3♀; *Larix* taiga on banks of Lake Baikal near Irkutsk, August 1964, collector unknown., 2♂ (paratypes, ZMUC).

DISCUSSION: At the Bezmyannyi Valley locality, this species is syntopic with *coxalis*,

both having been taken in the same pitfall traps in large numbers. However, the males are very distinct. *D. shilenkovi* males are somewhat more robust, with huge protruding gonopods; segment 7 is larger than the others but its lateral margins are not modified. Coxae 12 are not modified. *D. coxalis* males are more slender, with small gonopods that are not strongly protruding; segment 7 is very much enlarged and its posterior lateral margins bear prominent lobes. Coxae 12 are strongly modified (figs. 58, 59).

The females are not so easy to separate, but fortunately at the type locality females could definitely be associated with males of *shilenkovi*, allowing comparative distinctions to be made in the mixed collections from the Bezmyannyi Valley. *D. shilenkovi* females are slightly more robust and slightly darker in color (the color distinction is best observed without a microscope). The cyphopods (fig. 48) are not as long in comparison to their width and have prominent lamellae at the anterior margin of valves and the intravalvular region is depressed; the coxae of the third pair of legs (fig. 47) appear very similar to those of the fourth and the sternum is narrow. In *coxalis* females, the cyphopods (fig. 61) are long, lack prominent lamellae, and are not prominently depressed; the third coxae (fig. 60) bear ventral lobes, and the sternum is broad. Finally, the lateral angles of the collum are more acute in *shilenkovi* and the anterior paranota more prominent. Despite these differences, I would still feel uneasy assigning females not associated with males, since the distinctions are easy to detect only in direct comparisons.

***Diplomaragna coxalis*, new species**

Figures 54–61

TYPES: Male holotype (ZMUM), 24♂ and 25♀ paratypes (ZMUM, AMNH, SMF) from pitfall traps in taiga, Bezmyannyi Valley, Khamar-Daban Range, Irkutsk area, Siberia, USSR, collected 17 August 1979 by V. G. Shilenkov.

ETYMOLOGY: The species name refers to the modifications of the twelfth coxae, not present in any other *Diplomaragna*.

DIAGNOSIS: The modifications of coxae 12 and of the seventh segment will serve to separate this species from any other.

MALE: Thirty-two segments. Length about 15–16, width at sixth metazonite 1.92. Antennal segment-3 0.73 long. Ocelli 28, well pigmented, in triangular eyepatch. Paranota prominent, beginning on collum, strongest on segments 9–22, reduced on 28, absent from segments 29–32. Segment 7 greatly enlarged, paranota lower on sides, larger, more rounded; lateral ventral margins with acute anterior and arcuate posterior lobes (fig. 57). Segment 8 larger than 9, with slight posteroventral marginal lobe (fig. 57). Bodies of preserved specimens often with characteristic sharp flexure between segments 7 and 8. Segmental setae acute, thin, about 0.55 long. Pigmentation uniform creamy tan. Leg pairs 3–7 enlarged, crassate, pairs 5–7 much larger, femora swollen and curved. Leg pairs 10, 11 with coxal glands, coxae 10 with prominent cone-like projection posterior to gland, coxae 11 similar. Coxae 12 much enlarged, trapezoidal, with small cones on posterior faces (figs. 58, 59); small apical cones present on coxae of 13, 14, in few individuals possibly on 15.

Anterior gonopods (fig. 56) rodlike, telopodites distinctly 2-segmented, strongly curved posteriad, tip of second article abruptly narrowed, with small subapical process. Posterior gonopods in anterior view (fig. 55) with angiocoxite large, bearing acute mesal process; colpocoxites fused for much of their length, apically diverging, blunt, flattened, translucent cuticle of tip has definite "pebbly" texture. In posterior view (fig. 54), angiocoxal process large, evidently with limited motility, lamellate, lacking teeth. Mesal colpocoxite process not present, lateral process as short, blunt, curved arm. Telopodite segments large.

FEMALE: Thirty-two segments. Length about 15, width at sixth metazonite, 2.08. Antennal segment-3 0.63 long. Ocelli 28–30. Nonsexual characters as in male. Cyphopods as in figure 61.

DISTRIBUTION: Known only from the type locality.

DISCUSSION: At the Bezmyannyi Valley locality, this species is syntopic with *shilenkovi*, both having been taken in the same pit-

fall traps in large numbers. Distinctions between the two species are discussed under *shilenkovi*.

Diplomaragna molodovae (Golovatch),
new combination
figures 62–64

Sakhalineuma molodovae Golovatch 1976, 227: 1491.

The type material of this species is from Mt. Chekhova, Yuzhna-Sakhalinsk, Sakhalin Island. I studied paratypes kindly donated by S. I. Golovatch (AMNH), and present some new figures.

DISCUSSION: The anterior gonopods are very long, and in undissected examples often extend far beyond the sheath of the posterior gonopod colpocoxites (fig. 63). The angiocoxites of the posterior gonopods are unmodified, except for a mesal interior process that extends mesodorsally to meet its counterpart and rest on the anterior gonopod coxosternum (fig. 62). There is no anterior process of any kind, nor is there a posterior movable process. The colpocoxites are well developed, and there is a large, basal knob that reaches far out posteriorly (fig. 64); this may be a homolog of the lateral sheath process in other species, but it appears very different from that of *longibrachiata* or of *deplanata*, in which species it is largest. The sheath appears to be completely closed posteriorly. The telopodite segments of the posterior gonopod are somewhat reduced.

TERRICOLOR GROUP

The species of the Terricolor group are united by having the anterior angiocoxal process pass mesally between the colpocoxites, through symmetrical grooves or notches on each side. In the members of the group from mainland Asia, the process is thin, while in the Japanese (Hokkaido) species, it is quite robust. The large to very large posterior movable angiocoxal processes are bipartite, with a posterior branch going back into the cavity formed by the colpocoxite walls, and an anterior branch extending mesally to meet its counterpart in the midline (frequently the tips of these branches are enlarged to form pads

that are pressed tightly against each other). Because they were originally described in *Syntelopodeuma*, a genus wholly subsumed in this species group, *formosanum* and *hokkaidensis* are included here. The original illustrations seem to show a complete foramen in the colpocoxites, as in the *Inflatum* group, but as at least *hokkaidensis* is closely related to *tsurusakii* and *gracilipes*, which do not have the foramen, I suspect previous illustrations of *hokkaidensis* and *formosanum* were incorrect.

Diplomaragna terricolor (Attems)

Figures 65–72

Placodes terricolor Attems, 1899, 12: 320 (holotype male from Vladivostok, in NMW, examined); Golovatch, 1979b, 84: 88.

MALE: (from Kedrovaya Pad State Reserve): Thirty-two segments. Length about 20–22, width at sixth metazonite 2.6. Antennal segment-3 1.19 long. Ocelli 27–30, well pigmented, in triangular eyepatch. Paranota beginning on segment 2, strongest on segments 9–25, reduced on 28, absent from 29–31. Segmental setae acute, thin, about 0.6 long. Pigmentation light cream brown, mottled darker purplish brown on head, antennae, and distal leg segments. Anterior leg pairs 3–7 enlarged, crassate, pairs 5–7 much larger, femora swollen and curved.

Anterior gonopods subflagelliform, telopodites 1-segmented, curved posteriad, tip of telopodite acute (fig. 67). Posterior gonopods in anterior view (fig. 69) with angiocoxites subglobose, strongly depressed on anterior surface, anterior processes (fig. 66) long, flagelliform, passing between colpocoxites in incomplete fossa formed by median notch on each side. In posterior view (fig. 68), posterior angiocoxal process very large, movable, complex, with dorsal arms meeting in midline (figs. 70, 71). Colpocoxite sheath without processes. Telopodite segments reduced. Leg pair coxae 10, 11 with glands, coxa 10 (fig. 65) enlarged, with small process distal to gland.

FEMALE: Thirty-two segments. Length about 20, width at sixth metazonite, 2.6. Antennal segment-3 1.07 long. Ocelli 26–28. Nonsexual characters as in male. Cyphopods as in figure 72.

DISTRIBUTION: USSR Far East, Maritime Province, Ussuri State Reserve, rotten wood, May 22, 1972, G. F. Kurcheva, 1♂, 1♀; Kedrovaya Pad State Reserve, under bark, September, 1964, B. Mamaev, 1♂ (ZMUC), 22 August 1985, A. Kompantsev, 3♂, 1♀ (AMNH); Vladivostok, Okeanskaya Park on outskirts of city, forest litter, rotted birch log, May 8, 1979, E. Mikhajlova, 2♂, Yakovlevka District, near Chernyshevka, Sinegorye Mountains, forest, October 6–14, 1979, V. Bakurov, 1♂ (SMF), pitfall traps, August 15–18, 1978, V. Bakurov, 1♂.

Diplomaragna yakovlevka,

new species

Figures 73, 74

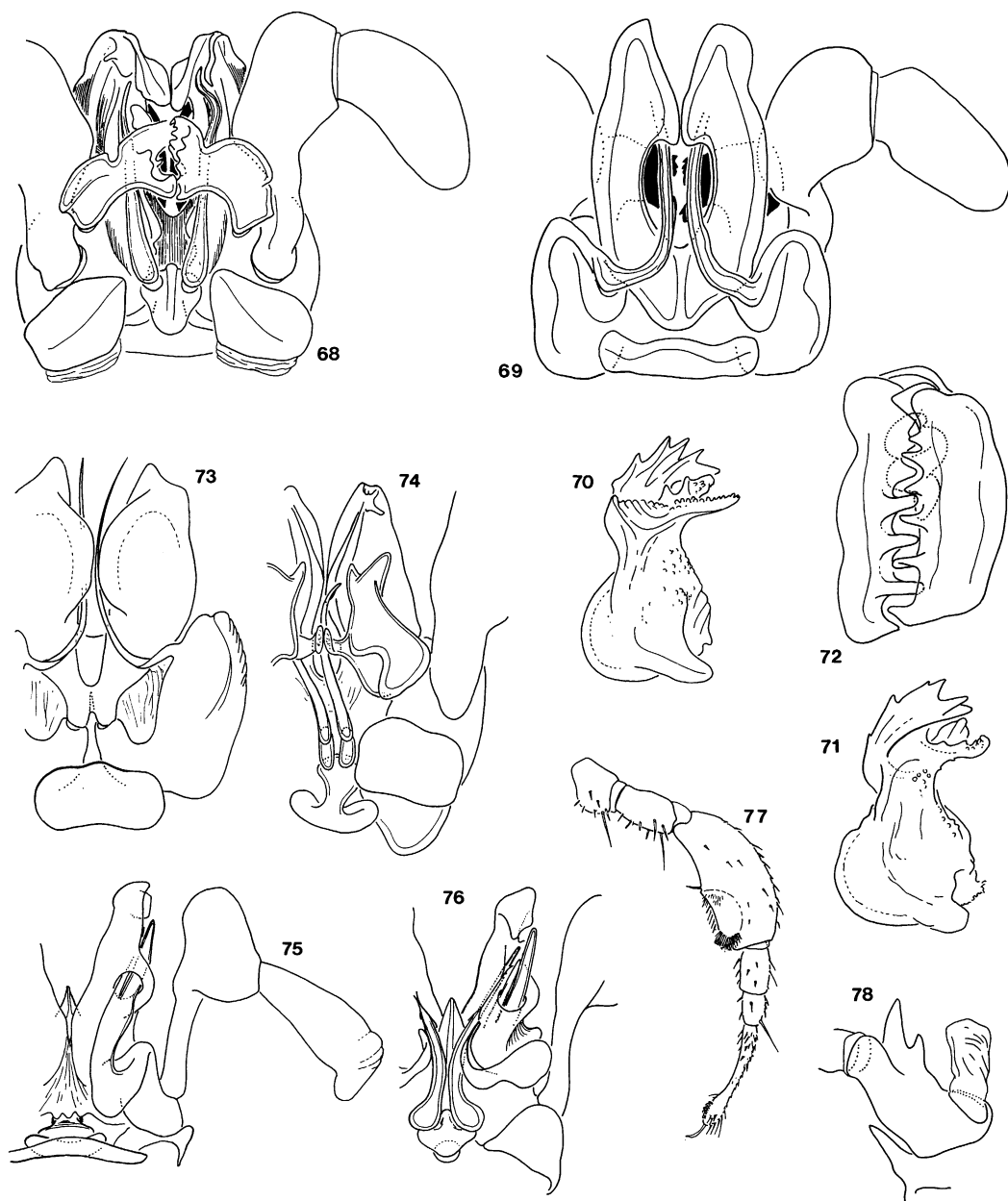
TYPES: Male holotype (ZMUM), 3♂ paratypes (ZMUM, AMNH) from Varfolomeevka, Yakovlevka District, Maritime Province, USSR Far East, collected 25 September 1956, by I. Lokshina and Y. Starobogatov.

ETYMOLOGY: The species name, a noun in apposition, refers to the type locality.

DIAGNOSIS: Differs from related species in the *Terricolor* group in the long, thin, flagelliform, anterior angiocoxal processes of the posterior gonopods, which pass between the colpocoxites in an indistinct notch (fig. 73).

MALE: Thirty-two segments. Length about 15, width at sixth metazonite, 1.46. Antennal segment-3 0.60 long. Ocelli 26, lightly pigmented, in triangular eyepatch. Paranota beginning on segment 2, strongest on segments 9–22, somewhat reduced on 23–26, absent from 27–31. Segmental setae acute, thin, about 0.4 long. Pigmentation light cream brown. Anterior leg pairs 3–7 enlarged, crassate, pairs 5–7 much larger, femora swollen and curved.

Anterior gonopods subflagelliform, telopodites 2-segmented, curved posteriad, tip of telopodite with small posterior lamella (fig. 74). Posterior gonopods in anterior view (fig. 73) with angiocoxites strongly depressed on anterior face; mesodistal angles drawn out into long, curved flagelliform processes passing between colpocoxites in vaguely indicated groove; colpocoxites fused at base, processes from base articulate with angiocoxites; broadly expanded above point traversed by angiocoxal flagella. In posterior view (fig. 74),



Figs. 68–78. 68–72. *Diplomaragna terricolor* (Attems). 68. Gonopods, posterior view. 69. Gonopods, anterior view. 70. Right posterior gonopod posterior angiocoxal process, dorsoposterior view. 71. Same, anterior view. 72. Left cyphopod, ventral view. 73, 74. *D. yakovlevka*, new species. 73. Gonopods, right side, anterior view. 74. Gonopods, left side, posterior view. 75–77. *D. lysaya*, new species. 75. Gonopods, right side, anterior view. 76. Gonopods, left side, posterior view. 77. Right leg 4 of male, posterior view. 78. Left coxa 11 of male *D. tsurusakii*, new species, anterior view.

posterior angiocoxal process very large, movable, without teeth, mesal arms meeting in midline. Colpocoxite sheath without pro-

cesses. Telopodite segments large. Leg pair coxae 10, 11 with glands, coxa 10 enlarged.

DISTRIBUTION: USSR: Far East, Maritime

Province, from rotten wood, Ussuri State Reserve, May 22, 1972, G. F. Kurcheva, 1♂ (paratype, SMF); *Fraxinus* litter in valley, November 2, 1978, E. V. Mikhajlova, 11♂, Vladivostok, Popova Island, forest litter, October 9, 1979, E. V. Mikhajlova, 1♂ (paratype, ZMUC).

DISCUSSION: This species occurs with *mikhajlovae* and *terricolor* in the Ussuri Reserve, and with *terricolor* in the Vladivostok region. A *terricolor* male was in the same vial with the Kurcheva collection from the Ussuri Reserve, suggesting syntopy.

***Diplomaragna lysaya*, new species**

Figures 75–77

TYPES: Male holotype (ZMUM) from upper reaches of Chashevityi Stream, Mt. Lysaya, Lazovsky State Reserve, Maritime Province, USSR Far East, collected July 16, 1979, by T. S. Vshivkova.

ETYMOLOGY: The species name, a noun in apposition, refers to the type locality.

DIAGNOSIS: Differs from all other species in the lateral position of the anterior angiocoxal processes, which are distally bifid (fig. 75).

MALE: Thirty-two segments (head, collum, and second segment missing in holotype). Length about 12, width at sixth metazonite, 1.74. Paranota prominent, horizontal on 3–5, strongest on segments 9–26, slightly reduced on 27, 28, absent on 29–32. Pigmentation tan, very lightly mottled darker purplish brown on antennae, legs. Anterior leg pairs 3–7 enlarged, crassate, legs 4 (fig. 77) with femora clavate, depressed glabrous area posterodistally, framed by eyelashlike group of setae, tarsus with mesally depressed, glabrous area; pairs 5–7 slightly larger than 4, femora swollen and curved, lacking modifications present on 4.

Anterior gonopods not dissected free from posteriors, coxosternum typical, telopodites 1-segmented, simple, acute, sheathed by colpocoxites of posterior gonopods (fig. 76). Posterior gonopods in anterior view (fig. 75) with angiocoxites sigmoid, dominated by anterior processes, which pass through lateral foramina in colpocoxites. Colpocoxites basally

fused, distally diverging, slightly and smoothly curved posteriorly. In posterior view (fig. 76), movable posterior angiocoxal processes relatively small, laminate, curved in semicircle; anterior process clearly visible penetrating foramen. First telopodite segment with very thin stem, clavate distal portion; second segment elongate, some indication of segmentation distally. Leg pair coxae 10, 11 with glands.

Female not collected.

DISTRIBUTION: Known only from the type locality.

DISCUSSION: This species and *anuchino* are both from the Lazovsky Reserve, but that species is very different.

The gonopods of this species are unusual in that the foramen receiving the angiocoxal processes is lateral, not mesal as in the several species from Hokkaido, its possible closest relatives. Assuming that the foramina developed from the notches seen in the mesal surface of the colpocoxites in members of the Terricolor group, its movement to the lateral position is a significant autapomorphy of this species.

***Diplomaragna tsurusakii*,**

new species

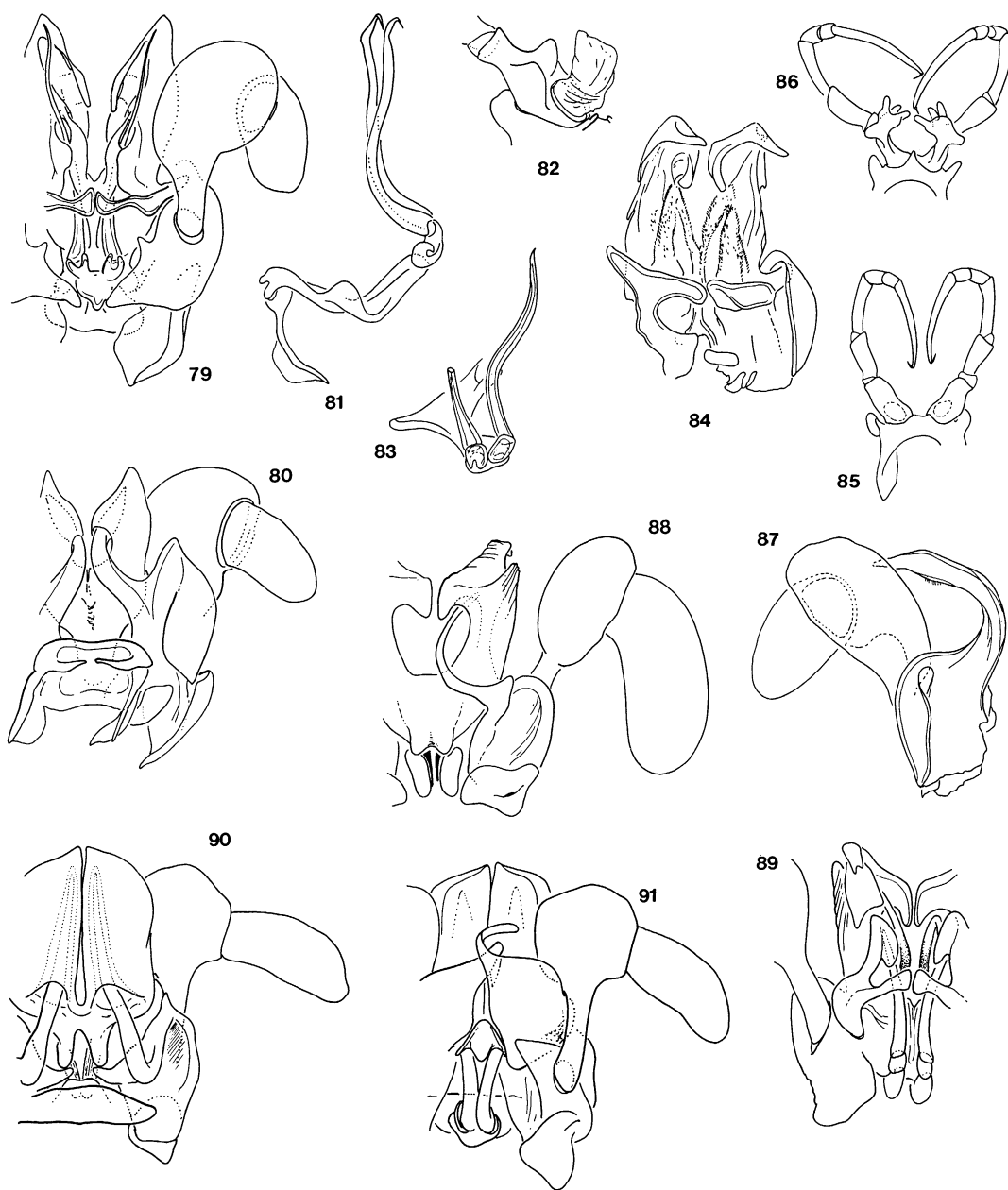
Figures 78–82

TYPES: Male holotype (AMNH) and 2♂ paratypes (ZMUM, NHMT) from Nishioka-Suigenshi, Sapporo, Hokkaido, Japan, collected September 29, 1986, by Nobuo Tsurusaki.

ETYMOLOGY: The species name honors the collector, an outstanding Japanese arachnologist.

DIAGNOSIS: Related to *hokkaidensis* and *gracilipes*, but the anterior angiocoxal processes are more robust in this species than in *hokkaidensis*, and the colpocoxites are differently formed than in *gracilipes* (figs. 80, 84).

MALE: Thirty-two segments. Length about 15, width at sixth metazonite, 1.7. Antennal segment 3 0.7 long. Ocelli 27, well pigmented in triangular eyepatch. Paranota beginning on segment 2, blunt, squarish, level with dor-



Figs. 79–91. 79–82. *Diplomaragna tsurusakii*, new species. 79. Gonopods, left side, posterior view. 80. Gonopods, right side, anterior view. 81. Anterior gonopods, right lateral view. 82. Left coxa 10 of male, anterior view. 83–87. *D. gracilipes* (Verhoeff), from holotype slides. 83. Anterior gonopods, ventroposterior view. 84. Posterior gonopod colpocoxites, posterior view. 85. Legs 10 of male, posterior view. 86. Legs 11 of male, posterior view. 87. Left posterior gonopod angiocoxite and telopodite, anterior view. 88, 89. *D. anuchino*, new species. 88. Gonopods, right side, anterior view. 89. Gonopods, right side, posterior view. 90, 91. *D. picea*, new species. 90. Gonopods, right side, anterior view. 91. Gonopods, left side, posterior view.

sum; those of segment 7 laterally enlarged and bulbous; slightly reduced on 25–27, absent on 28–32. Pigmentation light brown, mottled with darker purplish brown. Anterior leg pairs 3–7 only slightly larger than postgonopodal pairs.

Anterior gonopods (fig. 81) with very long coxosternum, telopodites slender, singly-segmented, sinuously curved, hooked at tips. Posterior gonopods in anterior view (fig. 80) with angiocoxite robust, centrally depressed, distally acuminate; anterior broad, curved, passing between colpocoxites in bilateral notch on each side. Colpocoxites basally fused, undivided, relatively broad, sharply curved posteriorly in distal third. In posterior view (fig. 79), colpocoxites distally sheathing tips of anterior process of angiocoxites; proximally, telopodites of anterior gonopods tightly sheathed between basal swellings. Angiocoxae with posterior processes reduced to single narrow branches meeting in midline. Posterior gonopod telopodite segments somewhat reduced, distal segment more so. Leg pair coxae 10, 11 with glands, modified as shown in figures 78 and 82, respectively.

Females not collected.

DISTRIBUTION: JAPAN: Hokkaido, *Betula ermanni* forest, 1500–1800 m elevation, Mt. Kurodoke, Daisetsuzan Mountains, September 14, 1987, Nobuki Yasuda, 1♂ 3 juveniles (NHMT).

DISCUSSION: The Hokkaido species of *Diplomaragna* seem closely related. Unfortunately there are no definite localities aside from “Hokkaido” for *gracilipes*.

Diplomaragna gracilipes (Verhoeff),
new combination

Figures 83–87

Syntelopodeuma gracilipes Verhoeff, 1914: 364 (male holotype from “Hokkaido,” in Zoologische Staatssammlung, Munich, examined); Miyosi, 1959: 126.

DISCUSSION: Verhoeff’s 1914 description of the nonsexual characters of the species is detailed, and his gonopod drawings accurate, but he misinterpreted their structure and relationships. These errors have been discussed and rectified by Golovatch (1979b) for the related *D. terricolor*.

The type material consists of four microscope slides on which are mounted (1) the

head of a male and leg pairs 1–4, (2) gonopods (figs. 83, 84, 87), leg pairs 5 and 6, and fragments of tergites, (3) leg pairs 7–12 (fig. 85 shows leg pair 10; fig. 86 leg pair 11) and fragments of tergites, and (4) the head of a female, leg pairs 1–6, and tergite fragments. Verhoeff customarily simply pulled apart specimens in a small dish under a low-power magnifier and then mounted the fragments for examination under a compound microscope. The gonopods of the type are badly broken and dissociated as a result. The illustrations presented here were made with a drawing tube.

Diplomaragna hokkaidensis (Verhoeff),
new combination

Syntelopodeuma hokkaidensis Verhoeff, 1939: 113 (male holotype from “Rumoe, Hakkaido,” not seen); Miyosi, 1959: 126.

DISCUSSION: Judging from Verhoeff’s 1939 description and illustrations, this species is close in general structure and size (about 15 mm long) to the others but has a more slender anterior angiocoxal process. Rumoi (as it is now spelled) is a town on the northwest coast of the island.

Diplomaragna formosanum (Verhoeff),
new combination

Syntelopodeuma formosanum Verhoeff, 1936: 168 (male holotype from “Insel Formosa,” not seen).

DISCUSSION: Evidently a large species (20 mm long). According to Verhoeff’s (1936) description and sketchy illustrations of parts of the gonopods, the anterior angiocoxal process is distally bifid.

This record is the southernmost one for the family, more than 1000 mi southwest of the distribution of the *Pterygostegia* group in caves on Shikoku. While such a distribution is possible, due to “stepping-stone” islands between the two areas, it should be checked. Verhoeff himself (1936) expressed some reservations about the accuracy of the locality label.

Diplomaragna anuchino, new species
Figures 88, 89

TYPES: Male holotype (ZMUM) and male paratypes (AMUM, AMNH, SMF) from

USSR Far East, Maritime Province, Anuchino District, near Chernyshvka, Sinegorye Mountain range, collected June 13–19, 1979, by V. Bakurov.

ETYMOLOGY: The species name, a noun in apposition, refers to the type locality.

DIAGNOSIS: A member of the Terricolor group unique in the form of posterior gonopod posterior angiocoxal processes (fig. 89).

MALE: Thirty-two segments. Length about 12–13. Width at sixth metazonite, 1.48. Antennal segment-3 0.68 long. Ocelli 29–30, well pigmented, in triangular eyepatch. Paranota beginning on segment 2, relatively low on 3–5, strongest on segments 9–17. Segmental setae acute, thin, about 0.35 long. Pigmentation tan, very lightly mottled darker purplish brown on antennae, legs. Anterior leg pairs 3–7 enlarged, crassate, pairs 5–7 much larger, femora swollen and curved.

Anterior gonopods not dissected free from posteriors, coxosternum broken off, but telopodites evidently acute, thin (fig. 89). Posterior gonopods in anterior view (fig. 88) with angiocoxite deeply depressed, anterior process very long, thin, curving mesally to pass through opening formed by fusion of colpocoxites proximally, two mesal knobs distally that butt against one another. Colpocoxites basally fused, articulating with processes from angiocoxites (this normally hidden behind anterior gonopod coxosternum), deeply excavate on each side above fusion, then with blunt mesal processes that meet in midline. Above these, coxites angle at nearly 90° posteriorly, terminating in small hook. In posterior view, movable posterior angiocoxal processes with two arms, mesal ones meeting in midline, lateral ones extending back against posterior surfaces of colpocoxites. First telopodite segment with very thin stem, clavate distal portion; second segment relatively small. Leg pair coxae 10, 11 with glands.

Female not collected.

DISTRIBUTION: USSR Far East, Maritime Province, Anuchino District, near Chernyshvka, Sinegorye Mountain range, June 5–7, 1979, 1♂, August 31–September 2, 1♂, September 5–11, 1979, 1♂, October 6, 1979, 1♂, October 23–November 1, 1979, ♂ all collections by V. Bakurov; Lazovsky State Reserve, Sokolovka post no. 4, 3–3.5 km along path from pass to post, July 11, 1979, E. Mikhailova, 1♂.

DISCUSSION: This species and *lysaya* are both from the Lazovsky Reserve, but that species is very different (see figs. 75–77). In the Sinegorye Mountains, *anuchino* co-occurs with *reducta*, which has only 30 segments, and with the much larger *terricolor*.

INFLATA GROUP

This large group of 10 species shares the apomorphic character of large median sheath processes fused in the midline. The anterior angiocoxal process passes through a complete foramen in the colpocoxite or is accommodated in a sheath (see Cladistic Analysis, above, for a more complete discussion of this character complex). Two species, *reducta* and *picea*, occur in the Soviet Far East and seem to be related, though *reducta* is the only species known with 30-segmented males. Both retain large posterior angiocoxal processes. The anterior angiocoxal processes in these two species are sheathed, as they are in the two Korean species, but the latter have strongly exaggerated paranota, like the troglomorphic or troglobitic Japanese forms originally described in *Pterygostegia*. Paradoxically, the two Japanese surface-dwelling species of the group (*inflata*, *takakuwai*) actually have reduced paranota.

This group includes species once considered members of the genus *Pterygostegia* Miyosi. Were it not for the continuity with other groups in gonopod form, very important in milliped systematics, the name could have been allowed to stand. The group is perhaps the most apomorphic of the genus, certainly in body form, with extraordinary broad paranota in some species that make them look more like polydesmids or platydesmids than chordeumatids. The segmental setae are often short and clavate, rather than long and acute as in other species. The pregonopodal legs of the males differ little from the postgonopodal legs; this is probably a reduction, since an intermediate condition exists in the *Picea* group. The eleventh legs of males have also lost their coxal glands (Murakami and Kawasawa, 1976), except in *ronkayi* and *korsosi*. The gonopods are relatively small and retracted into the body. Surprisingly, at least in *korsosi* and *ronkayi*, the anterior gonopod telopodites are very clearly two-segmented, a primitive character. The anterior processes

of the posterior gonopod angiocoxites are strongly developed, as in the *Terricolor*, *Picea*, and *Inflata* groups, and are entirely sheathed in the fused colpocoxites, from the anterior side. As in the *Inflata* group, the colpocoxites have a deep division on each side, except in *korsosi* and *grandilobata*. This makes them look like those of *deplanata*, but in that case the lateral part is really the enlarged lateral sheath process, originating basally. The group includes the only troglobites of the family, and at least one of these, *obliqua*, may be extinct as the type and the only known locality was destroyed by quarrying limestone for cement (Murakami and Kawasawa, 1975). The Japanese species were revised and redescribed by Murakami and Kawasawa (1976) with good illustrations, especially of the body form, so they are simply listed below and the reader is referred to the revision.

***Diplomaragna picea*, new species**

Figures 90, 91

TYPES: Male holotype (ZMUM) from *Picea* stand no. 1, Ussuri State Reserve, Maritime Province, USSR Far East, collected October 29, 1977, by R. G. Fedorova.

ETYMOLOGY: The species name is a noun in apposition, referring to the trees among which the type specimen was found.

DIAGNOSIS: Related to *reducta*, but this species has 32 trunk segments in males; the posterior angiocoxal processes are of a different form (figs. 90–91).

MALE: Thirty-two segments. Length about 9–10, width at sixth metazonite, 1.2. Antennal segment-3 0.4 long. Ocelli 25 (?), difficult to count because of complete lack of pigment. Paranota beginning on segment 2, prominent, horizontal on 3–5, strongest, squarish, horizontal on segments 3–23, slightly reduced on 25–27, absent on 28–32. Pigmentation light cream-tan, antennae white. Anterior leg pairs 3–7 enlarged, crassate, but less so than in other species.

Anterior gonopods not dissected free from posteriors; coxosternum very broad, telopodites one-segmented, simple, acute, strongly curved, sheathed by colpocoxites of posterior gonopods. Posterior gonopods in anterior

view (fig. 90) with angiocoxite sigmoid, centrally depressed, anterior process long, slender, sheathed in anterior surface of colpocoxite. Colpocoxites basally fused, undivided, relatively broad, sharply curved posteriorly in distal third; knobs from fused bases articulated with similar knobs extending mesally from inner surfaces of angiocoxae. In posterior view (fig. 91), colpocoxites very deeply cupped; movable posterior angiocoxal processes large, curving first mesally, then dorsally, broad, bladelike, distally attenuate, with attenuated part curving far back into colpocoxites. Sheaths for telopodites of anterior gonopods with basal mesal and lateral swellings, tightly clasping anterior gonopods. Posterior gonopod telopodite segments both substantially reduced, proximal segments with distinct stem. Leg pair coxae 10, 11 with glands.

Females not collected.

DISTRIBUTION: Known only from the type locality.

***Diplomaragna reducta*,**

new species

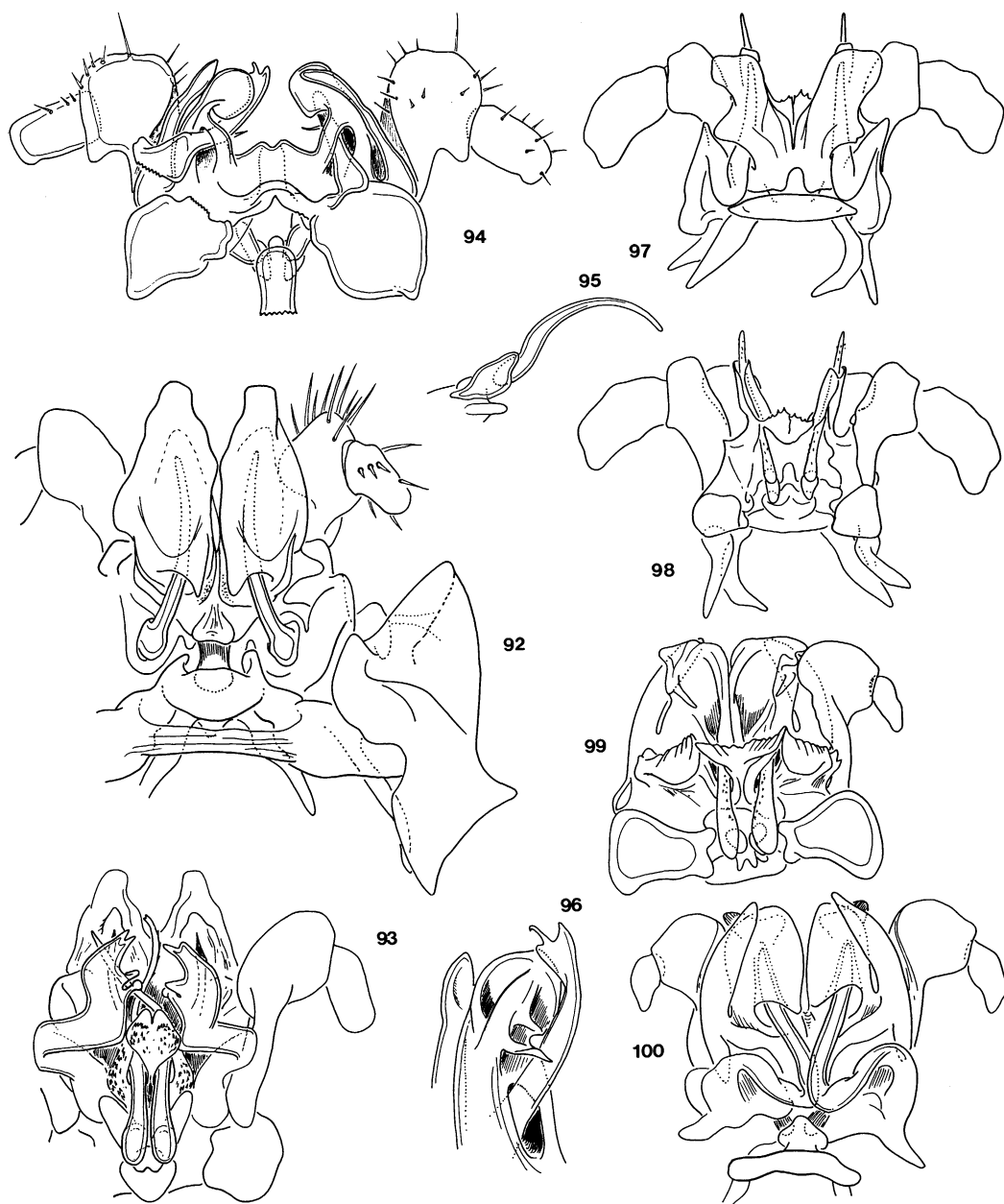
Figures 92, 93

TYPES: Male holotype (ZMUM) and male paratype (AMNH) from forest near Chernyshevka, Sinegorye Mountains, Yakovlevka District, Maritime Province, USSR, collected 5–8 June, 1979, by V. Bakurov; additional male paratype from *Pinus sibiricus* forest, Upper Ussuri Station, Chuguevka District, Maritime Province, USSR, collected September 9, 1974, by G. Kurcheva.

ETYMOLOGY: The species name refers to the reduced number of trunk segments in at least the males of this species.

DIAGNOSIS: Differing from all other species in having only 30 trunk segments, at least in males.

MALE: Thirty segments. Length about 10, width at sixth metazonite, 1.2. Antennal segment-3 0.9 long. Paranota beginning on column, prominent, horizontal on 3–5, strongest, squarish, horizontal on segments 9–23, slightly reduced on 24–26, absent on 27–30. Pigmentation light cream-tan, antennae white. Anterior leg pairs 3–7 enlarged, crassate, but not so much as in other species.



Figs. 92–100. 92, 93. *Diplomaragna reducta*, new species. 92. Gonopods, anterior view, with part of diplosegment 7 attached. 93. Gonopods, posterior view. 94–96. *D. inflata* (Verhoeff), from holotype slides. 94. Gonopods, anterior view; sternite of anterior gonopods broken off. 95. Left anterior gonopod, posterior view. 96. Tip of right posterior gonopod colpocoxite, posterior view. 97, 98. *D. korsosi*, new species. 97. Gonopods, anterior view. 98. Gonopods, posterior view. 99, 100. *D. ronkayi*, new species. 99. Gonopods, posterior view. 100. Gonopods, anterior view.

Anterior gonopods not dissected free from posteriors, coxosternum very broad, telopodites one-segmented, simple, acute, sheathed

by colpocoxites of posterior gonopods. Posterior gonopods in anterior view (fig. 92) with angiocoxite sigmoid, reduced, anterior pro-

cess appearing to be set in membranous socket, long, slender, sheathed in anterior surface of colpocoxite. Colpocoxites basally fused, undivided, relatively broad, sharply curved posteriorly in distal third. In posterior view (fig. 93), movable posterior angiocoxal processes large, curving first mesally, then ventrally, with small mesal knobs probably in contact in midline in undissected specimens, larger toothed lamella with more proximal tooth separated from others. Sheaths for telopodites of anterior gonopods with basal mesal and lateral swellings, tightly clasping anterior gonopods. Posterior gonopod telopodite segments both substantially reduced, proximal segments with distinct stem. Leg pair coxae 10, 11 with glands; coxae 10 with small posteroventral knobs.

Females not collected.

DISTRIBUTION: Known only from the type localities.

DISCUSSION: This species is unique among the known diplomaragnids in having only 30 trunk segments in males (females are unknown). The count was verified in three intact specimens. Reduction in segment number in chordeumatid millipeds is often correlated with unusually small size, but this species is as large as or larger than some having 32 segments.

Diplomaragna inflata (Verhoeff),
new combination

Figures 94–96

Niponiothauma inflatum Verhoeff, 1942: 207 (male holotype from Kuringawa, Japan, in Zoologische Staatssammlung in München, Munich, examined); Miyosi, 1959: 128.

DISCUSSION: The type material consists of two microscope slides, one with fragments of the gonopods (figs. 94–96) and leg pairs 3–8 of a male, the second with leg pairs 1, 2, 10, and 11, probably of the same male. The illustrations presented here were made with a drawing tube but are partial reconstructions.

NEW RECORD: JAPAN: Kyûshû, Kumamoto Pref., Kikuchi-keikoku, Kikuchi-shi, January 3, 1985, T. Moroto, 1♂, 1♀.

Though I could find no information on Kurinagawa in any atlas of Japan available to me, this new record (from specimens sent by T. Tanabe of Hokkaido University; these

specimens will be returned to him) strongly suggests that *D. inflata* was described from Kyûshû. Examination of these new specimens allowed me to confirm that my drawings of the holotype were accurate.

Diplomaragna takakuwai (Verhoeff),
new combination

Tokyosoma takakuwai Verhoeff 1932: 515 (male holotype from Imabari, Ehimé Pref., Japan, not seen).—Takakuwa, 1954: 129; Miyosi 1959: 127.—Murakami, 1971, 323 (complete redescription).

DISCUSSION: Murakami (1971) redescribed this species in detail, providing excellent illustrations and drawing attention to some errors in Verhoeff's 1932 description that had been noted earlier, in publications in Japanese, by Miyosi (1959). However, Murakami (1971) interpreted the colpocoxites of the posterior gonopods as syntelopodites of the anterior, and the real telopodites of the anterior as "small pseudo-flagella."

Takakuwa (1954), who had collected the type material, corrected the locality, said by Verhoeff to be "zwei Pärchen aus der Umgebung von Tokyo," to the vicinity of the town of Imabari, over 300 airline miles southwest, on the north coast of the island of Shikoku. The species has been recorded from Mt. Saragamine, and from two lava caves, Ryûkei-dô Cave and Yûki-dô Cave, both on Daikon-Jima Island, Shimané Prefecture, just north of Imabari.

Diplomaragna korsosi,
new species

Figures 97, 98

TYPES: Male holotype and 2 female paratypes (HNHM) from sifted litter in a rocky forest along Isonnam Pathway, Mt. Myohyang-san, North Pyongyang Province, North Korea, collected October 11, 1987, by Z. Korsós and L. Ronkay.

ETYMOLOGY: The species name honors the collector, a noted Hungarian zoologist, curator at the Hungarian Natural History Museum, Budapest.

DIAGNOSIS: The simple gonopods of this species resemble those of two others, both from caves in Japan, *anops* and *grandilobata*. Both of these species are larger (about 12–15

mm long), and have reduced eyes; *anops* is eyeless (Murakami and Kawasawa, 1976).

MALE: Thirty-two segments. Length about 7, width at sixth metazonite, 1.3. Antennal segment-3 0.4 long. Ocelli 17, sparsely pigmented in triangular eyepatch. Paranota beginning on segment 2, blunt, squarish, level with dorsum; beginning with segment 4, paranota extend broadly from dorsum, producing polydesmoid appearance, strongly reduced on 29, absent from 30–32. Segmental setae short, clavate, lateral two setae near lateral margin of paranota, medial seta midway between lateral margin and midline. Pigmentation cream-tan, very lightly mottled with darker purplish brown near anterior end. Anterior leg pairs 3–7 no larger than other walking legs.

Anterior gonopods not dissected free from posteriors, but obviously 2-segmented (fig. 98), long, acuminate, exceeding telopodite sheath. Posterior gonopods in anterior view (fig. 97) with sharply sigmoid angiocoaxes tapering evenly to robust anterior processes entering sheaths of colpocoaxes by basal foramina; colpocoaxes fused basally, short, apically divergent and squared off. In posterior view (fig. 98), posterior angiocoaxal process absent, mesal sheath processes of colpocoaxes fused to form median lamella; telopodite articles small. Leg pair coxae 10, 11 with glands, modified as shown in figs.

FEMALE: Thirty-two segments. Length, about 8, width at sixth metazonite, 1.35. Antennal segment-3 0.4 long. Ocelli 17. Non-sexual characters as in male. Cyphopods simple, small, lobular.

DISTRIBUTION: Known only from the type collection.

DISCUSSION: With the typical body form of "Pterygostegia," this and the following species, as epigeal forms, differ from the Japanese species, which all come from caves in southwestern Shikoku (Ehimé and Kôchi Prefectures), in having more ocelli and being significantly smaller. Simplified gonopods are found in *korososi* and *grandilobata*, the simplifications being in the reduction of the colpocoaxes of the posterior gonopods and the absence of the posterior angiocoaxal process. This latter process appears definitively only in *ronkayi*.

Murakami and Paik (1968) reported and

illustrated a *Diplomaragna* female from Korea, and Golovatch (1980) also mentioned seeing specimens of the genus from the peninsula, so this species and *ronkayi* are not the first reports of diplomaragnids from Korea.

Diplomaragna ronkayi,

new species

Figures 99, 100

TYPES: Male holotype (HNHM) from forest above the Hotel Kumgang-san, T. Kumgang-san, Onjong-ri, Kangwan Province, North Korea, collected 20 October, 1987, by Z. Korsós and L. Ronkay.

ETYMOLOGY: The species name honors the collector.

DIAGNOSIS: While this species has gonopods typical of the *Pterygostegia* group, the paranota of the midbody segments are not so exaggerated, and the pregonopodal legs are noticeably enlarged.

MALE: Thirty-two segments. Length about 8, width at sixth metazonite, 0.83. Antennal segment-3 0.44 long. Ocelli 20, well pigmented in triangular eyepatch. Paranota beginning on segment 2, but low, blunt, squarish, level with dorsum, relatively prominent on segments 4–24, gradually reduced on 25–27, absent from 28–32. Segmental setae long, but many with blunt tips. Pigmentation cream-tan, very lightly mottled with darker purplish brown near anterior end. Anterior leg pairs 3–7 somewhat crassate, but femora not markedly swollen or curved.

Anterior gonopods not dissected free from posteriors, but obviously two-segmented (fig. 99), acuminate, not exceeding telopodite sheath. Posterior gonopods in anterior view (fig. 100) with sharply sigmoid angiocoaxes tapering evenly to robust anterior processes entering sheaths of colpocoaxes by basal foramina; colpocoaxes fused basally, short, not apically divergent, deeply divided on each side into broad median, narrower lateral branches. In posterior view (fig. 99), posterior angiocoaxal process present but reduced, mesal sheath processes of colpocoaxes fused to form median lamella, lateral process possibly present as small hook; telopodite articles small, distal article very much reduced. Leg pair coxae 10, 11 with glands.

Females not collected.

DISCUSSION: In this species' combination of body form and gonopod structure lies the main argument for synonymizing the genus *Pterygostegia* under *Diplomaragna*. The gonopods are very close to those of other members of the *Pterygostegia* group, but show intermediacy in that the posterior colpocoxite process persists, though not in a movable state. The paranota are prominent, but well within the range of other species of *Diplomaragna*, while in *D. korsosi* and the Japanese species of *Pterygostegia*, they are very much exaggerated, making *anops*, for example, look almost like a platydesmid. The gland of the 11th leg pair has also been retained.

Diplomaragna kuroiwadensis (Miyosi),
new combination

Pterygostegia kuroiwadensis Miyosi, 1958: 180 (male holotype from Kuroiwa-dô Cave, Ehimé Pref., Japan); Murakami and Kawasawa, 1976: 113.

DISCUSSION: In addition to the type locality, Murakami and Kawasawa listed 17 other limestone caves where this species has been collected. It appears to be widespread in caves in the region and may turn up on the surface; it has as many ocelli as the epigeal Korean species. At 20 mm in length, it is among the largest known *Diplomaragna* species.

Diplomaragna obliqua
(Murakami and Kawasawa),
new combination

Pterygostegia obliqua Murakami and Kawasawa, 1975: 192 (male holotype from Tengyôki-dô Cave, Kôchi Pref., Japan, deposited in NSMT); Murakami and Kawasawa, 1976: 115.

DISCUSSION: Known from four limestone caves in the valleys of the Monobé-gawa and Kokubu-gawa rivers (Murakami and Kawasawa, 1976).

Diplomaragna anops
(Murakami and Kawasawa),
new combination

Pterygostegia anops Murakami and Kawasawa, 1976: 115 (male holotype from Rakan-ana Cave, Ehimé Pref., Japan, deposited in NSMT).

DISCUSSION: The only eyeless species of the genus, this animal is found in two caves in

high-elevation karst, and is judged by Murakami and Kawasawa (1976) to be the oldest troglobite of the group.

Diplomaragna grandilobata
(Murakami and Kawasawa),
new combination

Pterygostegia grandilobata Murakami and Kawasawa, 1976: 118 (male holotype from Shi-roiwa-dô Cave, Kôchi Pref., Japan, deposited in NSMT).

DISCUSSION: Recorded from three caves about 18 km apart (Murakami and Kawasawa, 1976).

UNGROUPED SPECIES

Three species of *Diplomaragna* described under *Altajosoma* by Gulicka (1972) cannot be definitively placed because of inadequate illustrations and incomplete type material. Golovatch (in litt.) reported that the type specimens were badly broken and that the gonopods of the males were missing.

Diplomaragna pinetorum (Gulicka),
new combination

Altajosoma pinetorum Gulicka, 1972:37 (male holotype from shores of Teletskoye Lake, Kamchinskaya Bay, Altai Mountains, Siberia, deposited in Leningrad Museum, not seen).

DISCUSSION: This species and the two following were briefly described by Gulicka in the same publication. All the gonopod illustrations are lacking in detail, but leave little doubt that the names refer to species of *Diplomaragna*. According to Golovatch (in litt.), the type material arrived in Leningrad in poor condition and without gonopods; for that reason I made no effort to obtain it. The present species is from within the range of *deplanata*, and according to Gulicka's (1972) figures, the colpocoxites of the posterior gonopods are similar; they could be the same species.

Diplomaragna densecava (Gulicka),
new combination

Altajosoma densecavum Gulicka 1972:38 (male holotype from Kurai Basin, Southeast Altai, deposited in Leningrad Museum, not seen).

DISCUSSION: Judging from the figures, this species is similar, if not identical, to *longi-*

brachiata. In case of synonymy, *densecava* would be the correct name.

Diplomaragna sajanica (Gulicka),
new combination

Altajosoma sajanicum Gulicka, 1972, 51: 38 (male holotype from "Academician Obruchev Range, near Miunh-Khol, *Pinus sibericus* taiga, Tuva SSR, deposited in Leningrad Museum, not seen).

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