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REPORT ON A FOSSIL PALPIGRADE FROM THE TERTIARY OF ARIZONA, AND A REVIEW OF THE MORPHOLOGY AND SYSTEMATICS OF THE ORDER (ARACHNIDA: PALPIGRADIDA)

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ABSTRACT

Described in Part I is *Paleokoenenia mordax*, new genus and species, an interesting eukoeneniid palpigrade from the late Tertiary of Arizona. Part II includes important morphological descriptions of the Palpigradida, some of which are important to inter- and intraordinal relationships. Part III provides a review of the systematics of the supraspecific taxa, the number of species known, and includes diagnoses of and a key to the two families and seven genera. Also given is a list of the species with their general distribution. Part IV contains the primary bibliographic references for the order.

INTRODUCTION

Arachnid fossils have been known from the Bonner Quarry near Ashfork, Arizona since 1944. In that year the San Diego Natural History Museum sent two onyx marble pen bases from that location to Dr. Alexander Petrunkevitch for study. From these pen bases containing two specimens, Petrunkevitch (1945b) described a new fossil schizomid, *Calcitro fisheri*, and erected the family Calcitronidae in the order Schizomida. In that contribution he reports: "In the same pen base with the paratype three other fossils are present, which I refer to the same species. All three are somewhat smaller and poorly preserved. The one which lies about 25mm. from the paratype at a place corresponding to 1 h. on a clock dial is better visible than the other two and shows at the end of the abdomen a three-jointed tail." Also in the same pen base, he reported long appendages belonging to an arthropod he could not identify.

Later, Pierce (1950, 1951) examined other pen bases from the Bonner Quarry and described two fossil schizomids, *Onychothelyphonus bonneri* (family Calcitronidae) and *Calcoschizomus latisternum* (family Schizomidae). There were additional specimens and fragments he could not identify. Pierce (1951) reports: "In addition to all of these specimens are three tiny ones too deep for exact characterization, but unquestionably pedipalps. They may be young. No division of thorax is evident, nor is any cauda."

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As part of an investigation into the schizomids of the New World the senior author examined a number of these pen bases from the Los Angeles County Museum and the San Diego Natural History Museum. Close examination of the smaller forms mentioned above revealed that they were palpigrades. A total of seventeen specimens were found among this material, affording a variety of anatomical views of this palpigrade. In addition to these anatomical studies, it was suggested by Dr. Robert W. Mitchell that a review of the systematics and morphology of the order itself would greatly enhance the value of this contribution. Here presented, then, is the study outlined above, which was updated, revised, and carried through to publication by the junior author.

PART I. A NEW GENUS AND SPECIES OF FOSSIL PALPIGRADIDA FROM THE TERTIARY OF ARIZONA

Paleokoenenia, new genus

Description.—Prosoma: Carapace with distinct anterodorsal cone projecting somewhat diagonally upward. Opisthosoma: Ninth abdominal segment about equal in width to eleventh segment, about half as wide as eighth segment; pygidium slightly narrowed posteriorly; flagellum longer than opisthosoma, segments long and slender. Pedipalps very long and thin.

Comparisons.—See under species account.

Etymology.—The generic name is taken from the Greek epithet *paleo*, meaning ancient, and *-koenenia*. This name is applied because the sole representative of the genus is a fossil species.

Type species.—The type and only known species of this genus is described as follows:

Paleokoenenia mordax, new species

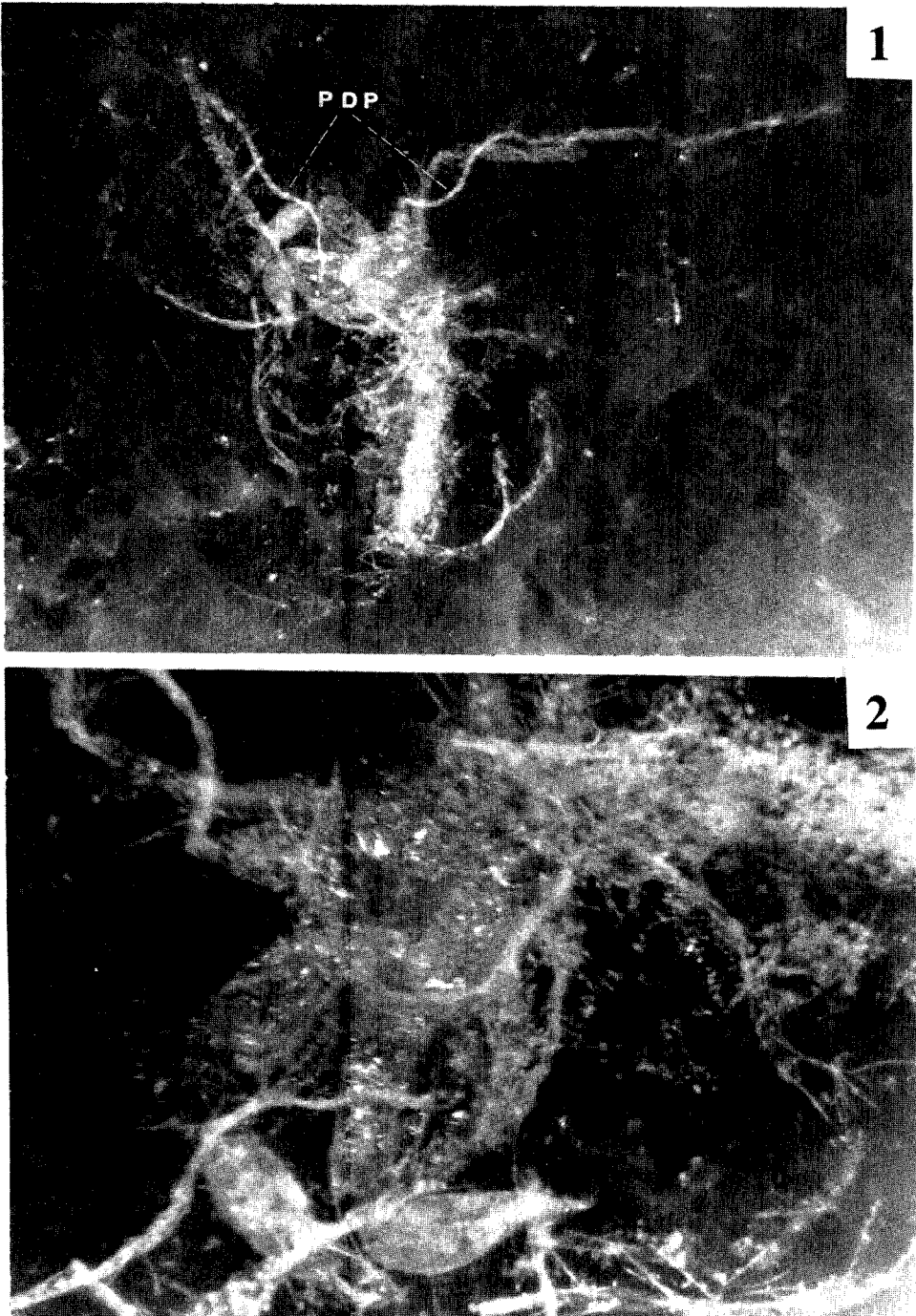
Figs. 1-7

Types.—Holotype (SDSNH Paleo No. 16661), allotype (SDSNH Paleo No. 16662), and fifteen paratypes (SDSNH Paleo Nos. 16663-16677), specimens in calcite pen base mined from Bonner Quarry, 17 mi SW Ashfork, Arizona, NW1/4 of Section 21, Township 20N (southern boundary 35°00'N Lat.), Range 3W (eastern boundary 112°00'W Long.). Altitude 1624 m. Probably Pliocene. Deposited in the Natural History Museum, San Diego Society of Natural History, San Diego, California.

Etymology.—The specific name is taken from the Latin *mordax*, meaning biting, which describes the somewhat formidable chelicerae in this species.

Description.—The following is based on characters selected from wherever possible within the type series. All measurements are in millimeters, and taken from the holotype, except where indicated in parentheses.

Prosoma—Carapace (propeltidium, first prosomal tergum): length 0.54, width 0.23; slightly wider anteriorly than posteriorly, with subapical cone projecting anterodorsally. The anatomy of the ventral surface of the prosoma could not be ascertained, although several coxae of the legs and pedipalps were viewed well enough to enable measurement. The structure of the sterna requires clearing and is difficult to ascertain even in slides of fresh material.



Figs. 1-2.—Dorsal views of the holotype of *Paleokoenia mordax*, new species: 1, whole view with pedipalps indicated (PDP); 2, close up showing, in particular, the propeltidium and chelicerae.

Opisthosoma—Length 1.5 (allotype), width 0.35 (allotype). Terga with several setae, 0.15 (allotype) in length. Tergal lengths: IV, 0.17; V, 0.16; VI, 0.14; VII, 0.13; VIII, 0.09. Pygidium with several setae in circular arrangement, 0.17 (allotype) in length. Pygidial segment lengths and widths: X, 0.07:0.10; XI, 0.16:0.10 (allotype) with four sets of setae spaced about 0.08 (allotype) in length.

Chelicerae—Length 0.85. Cheliceral segment lengths and widths: basal segment 0.38:0.21 (at widest), second segment 0.46:0.18 (at widest), third segment (movable finger) 0.25 in length. Basal segment tapering distally, with several short and a few longer setae present, second segment with several long and short setae, a particularly strong one on ventral surface 0.06 in length, fixed digit with a curved row of seven teeth along inner margin, third segment with a curved row of several teeth along inner margin, a stout seta 0.11 in length about one fourth the way out on the dorsal surface.

Pedipalps—Length about 1.5, thinner than leg I, several long setae 0.20 in length. Coxal length and width 0.16:0.11.

Legs—I at least as long as pedipalps, but total length not measurable; coxal length and width 0.19:0.08. II, total length not measurable; coxal length and width 0.13:0.13, with several long and short setae, the longest 0.24. III, total length not measurable, coxal length and width 0.14:0.11, with a few long setae, the longest 0.26. IV, no measurements possible.

Flagellum—Total length not measurable, first segment 0.28 in length. Each segment with one or more whorls of setae.

Comparisons.—*Paleokoenenia mordax* differs from all other eukoeneniids in having a pronounced conical protuberance anteromedially on the carapace. The pedipalps are much longer than in any other genera, being about equal in length to the opisthosoma. It seems to be most similar to *Eukoenenia*, *Allokoenenia*, and *Koeneniodes* in morphology of the pygidium, which in all is distinctly narrower than the eighth opisthosomal segment. The accompanying key will separate the genera of palpigrades, of which only *Sternarthron* and *Paleokoenenia* are represented by fossils.

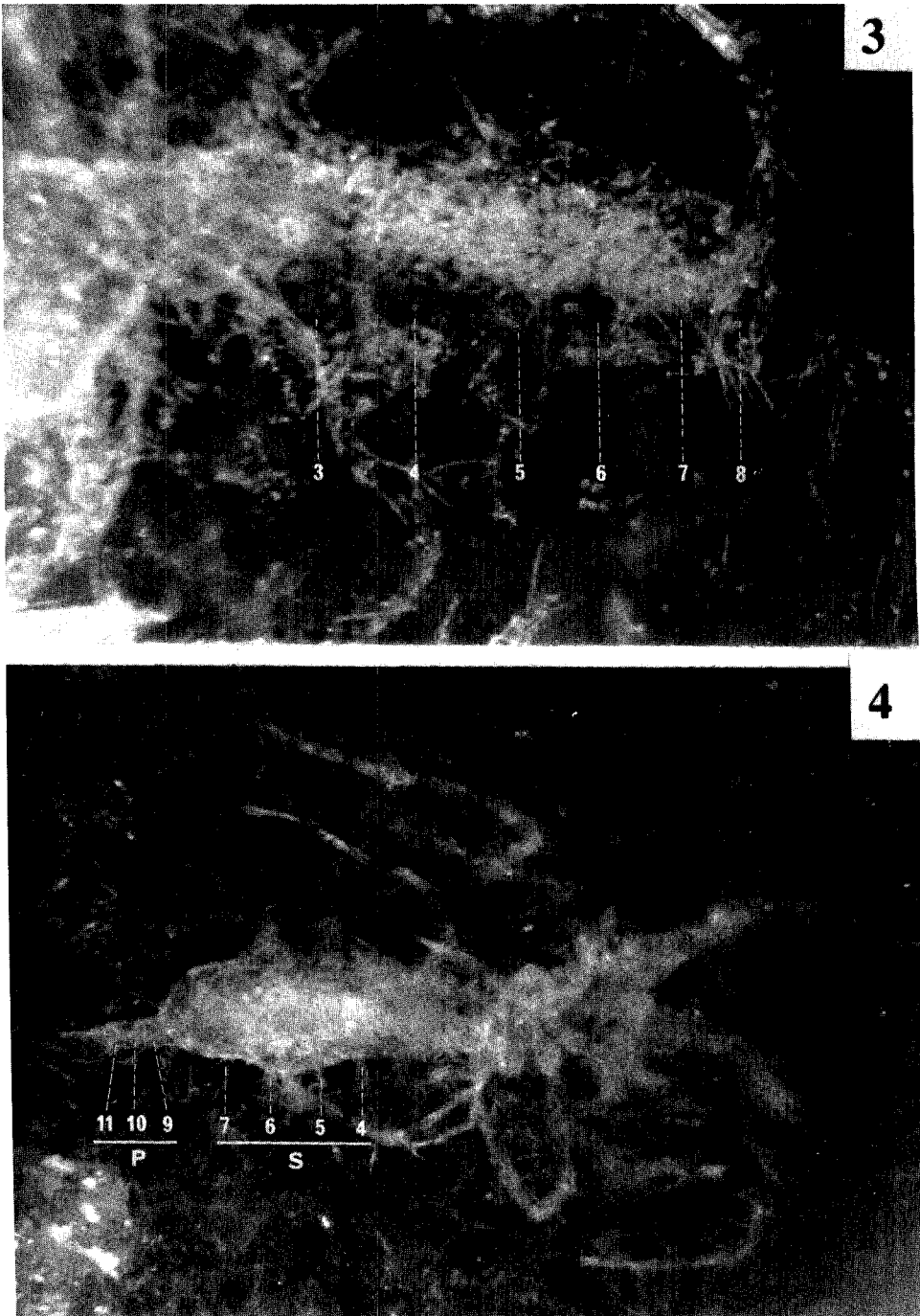
Measurements.—The total length (from anterior margin of prosoma to posterior margin of pygidium) of all measurable specimens 1.7 to 2.4, the holotype and allotype are 1.8 and 2.2, respectively.

Variations.—No variations disproportionate to total length were noticed.

Distribution.—*Paleokoenenia mordax* is known only from onyx deposits at Bonner Quarry, 17 mi SW Ashfork, Arizona.

Age.—The onyx marble containing these specimens was mined from Bonner Quarry by members of the Southwest Onyx and Marble Company from faulted Middle Permian Supai formations on the side of a high angled fault. E. D. McKee was quoted by Petrunkevitch (1945) as stating "The fault passes under and therefore, antedates basalt flows a few miles to the west and these are of a period I consider to be of Pliocene age. The age of the deposit is definitely 'post-faulting' which means since the middle of Cenozoic time, but deposition might have been any time from then to the present." Pierce (1951) gave an age of between 12 and 50 million years. Petrunkevitch (1955) dated other fossils found in this formation as "?Pliocene", which for lack of other information, we will follow here.

Natural History.—The nature of the structure of the onyx formation suggests that it was laid down by subterranean waters in fissures. Petrunkevitch (1945) suggested that the animals in the onyx were probably washed into the fissures from epigeal habitats and became fossilized. Judging by the frail nature of palpigrades it is difficult to imagine



Figs. 3-4.—Views of *Paleokoenenia mordax*, new species: 3, close up of the dorsal aspect of the abdomen of the holotype with the third through the eighth terga labeled; 4, whole view of the ventral aspect of the allotype with the fourth through the seventh sterna (S) and the ninth through the eleventh abdominal segments or pygidium (P) labeled.

specimens being washed in and remaining in the excellent condition of many of the specimens. It is more probable that these animals lived in close proximity to the area of deposition, which suggests that these palpigrades might have been cavernicoles.

The assemblage of fossils present in the onyx is strongly reminiscent of faunas encountered in moist subtropical caves today. Palpigrades are characteristically found only in moist micro-environments, and their occurrence in temperate areas probably indicates a relictual distribution since more pluvial times. The palpigrades from Bonner Quarry may bear witness to the more humid environment attributed to the late Cenozoic of the southwestern United States. Represented in the onyx are three genera of schizomids, three genera of diplurans, two genera of millipedes and two genera of silverfish. Some of these fossils appear to display troglobite facies, such as attenuated appendages, which make it seem even more likely that these animals were cave dwellers.

Remarks.—The minute, primitive arachnids of the order Palpigradida have been of considerable interest since their discovery in Sicily in 1885. Some 50 species have been described and are placed in five extant and two fossil genera. Two families are recognized, one of which is monotypic, based on the Jurassic *Sternarthron zitteli* Haase, 1890.

The discovery of palpigrades in the middle to late Canozoic of Arizona is of some importance. They are quite similar to members of modern genera, however, and will not create the excitement that *S. zitteli* has. The latter fossil has received much attention since its assignment within the Palpigradida. The material was originally identified as *Halometra minor* Oppenheim, 1887, a primitive water-associated insect. The general appearance and size of *S. zitteli* is, in fact, more suggestive of water striders than other palpigrades. A further examination of these fossils, using modern techniques, is needed to add credence to their assignment within or exclusion from the Palpigradida.

The seventeen remarkably preserved specimens of the species described here attest to the high quality of fossils found in onyx. These fossils are perhaps second in quality only to some amber fossils. This material also reveals something of the past distribution of palpigrades and the climatological conditions which probably prevailed.

No significant results have yet been gathered by various efforts to solve basic questions about the mode of life of palpigrades. They appear to prefer humid micro-environments and occur with great regularity in some localities. They have been collected in humus in caves and under rocks, where moist conditions prevail, but members of *Leptokoenenia* live interstitially. Palpigrades possess formidable chelicerae, but otherwise their frail body does not seem built for a predatory existence. Rucker (1903) suggested that they feed on arthropod eggs, but nothing seems to support this idea. It is likely that they feed on small arthropods such as mites, although no evidence is available.

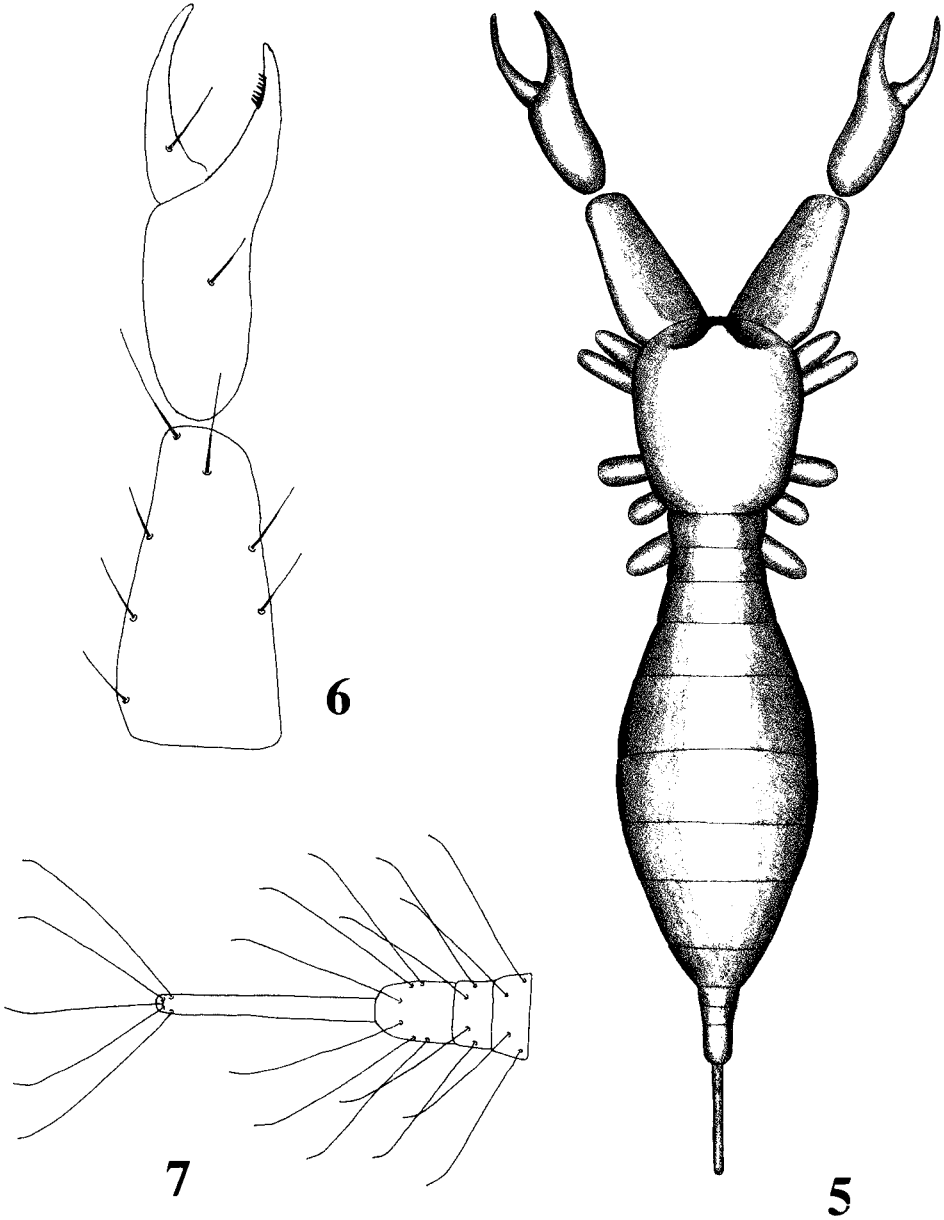
PART II. MORPHOLOGICAL NOTES ON THE PALPIGRADIDA

The following account draws heavily from the works of Börner (1901), Hansen (1901), Hansen and Sørensen (1904), Millot (1943; 1949) Roewer (1934), and Rucker (1901;1903).

The prosoma is segmented into three components, the propeltidium, mesopeltidia, and metapeltidium. Structures of the same names are found in the Solpugida and Schizomida. Because of the difficulty of obtaining embryological date the interordinal relationship of these structures will be difficult to ascertain, but will be of interest.

The prosoma bears the trophic and locomotor appendages, and special sensory organs, but lacks eyes. It is covered for the most part by the propeltidium, which extends from

above the chelicerae to approximately above the third pair of walking legs. Lateral to the posterior margin of the prosoma are two small plates, the mesopeltidia. These are reported to lie just dorsal to the third pair of walking legs, although they could not be found in preparations of *Eukoenenia hanseni* (Silvestri) and *Prokoenenia wheeleri* (Rucker). Directly above and behind the mesopeltidia is the undivided metapeltidium,



Figs. 5-7.—Reconstructions of *Peleokoenenia mordax*: 5, generalized reconstruction, showing only coxae of pedipalps and legs and first flagellar segment; 6, left chelicera; 7, pygidium and first flagellar segment.

which also lies directly above the fourth pair of legs. Situated at the prolateral and promesal aspects of the propeltidium just above the chelicerae and pedipalps are the relatively robust sensory setae which are discussed further below.

The ventral surface of the prosoma is occupied by eight pedal coxae and the five elements of the sterna. These are of special interest because of their primitive number and character, though they are difficult to observe in all but the best microscopical slide preparations. The largest sternal piece is the fused deuto-tritosternum which lies between the pedipalps and first pair of walking legs. Anterior to this sternal piece is the lower lip of the mouth which is generally considered to be the prosternum. Following the deuto-tritosternum and lying between the second, third, and fourth pair of walking legs are the tetrasternum, pentasternum, and metasternum, respectively.

The first pair of appendages, the chelicerae, are composed of three elements. The basal piece articulates with the second piece which reflects posteriorly and articulates with and opposes the third piece. The tips of the chelae rest just below the opening of the mouth. The inner surfaces of these two pieces each have a single row of seven to ten serrated teeth. As regards the naming of the various appendage articles there are some divergent opinions. According to Van der Hammen (1969) in the chelicerae a basal coxal region is followed by the trochanter, which was considered basal before his work. Following the trochanter is the "principal cheliceral segment" formed by the fusion of femur, patella (genu), tibia, and tarsus. The movable chelal digit is named the apotele.

According to classical works the second pair of appendages, the pedipalps, are composed of nine elements. The patella is absent, and the extra number of segments is due to the subdivision of the basitarsus into two and the tarsus into three pieces. There exist two well developed claws and the appendage serves mainly, as far as is known, in locomotion. Van der Hammen (1969) reported having found evidence of a segment basal to what had previously been considered the coxa. He considered this article to be the true coxa and the coxa of other authors he considered the trochanter. From the work of Snodgrass (1948) we must also consider that a pedipalpal patella is present, which he demonstrated convincingly for spiders and the "pedipalpi". Acceptance of the findings of both Van der Hammen and Snodgrass preserves the nominal designation of segments including and distal to the tibia.

The legs possess, from first to fourth, twelve, seven, seven, and eight elements. The basitarsus of leg I is divided into four pieces and the tarsus into three. The basitarsus and tarsus, as well as the other pieces, are simple in legs II and III. In leg IV the tarsus is two segmented. The first leg is reportedly not ambulatory but, as in the "pedipalpi", functions mainly as a tactile organ. The possession of claws on leg I suggests, however, that the leg may serve at least some locomotory role. On all legs and the pedipalps there is a pretarsus with two lateral and a smaller median, or pseudonyctal, claw.

The names and implied serial homologies of the articles of the walking legs have not been the source of much dispute. Certainly the articles proximal to and including the tibia seem to present a fairly clear picture, though Hansen (1931) offered some alternatives to the classical interpretation of articular homologies. Accepted here are Hansen and Sørensen's (1897) interpretation of leg segments. The pedipalp and first walking leg present serious problems in interpreting which of the various subsegments of the appendages distal to the tibia corresponds to the basitarsus (metatarsus) and which corresponds to the tarsus. Hansen and Sørensen (1897) in setting down the interpretation in use today said, ". . . we deviate somewhat from Grassi. . . with regard to the boundary line between metatarsus and tarsus. However, . . . we cannot insist with absolute certainty

on the correctness of our view, as it is only based on a personal estimate." The second and third walking legs are represented by the usual arachnid complement of seven articles. The fourth pair have a divided tarsus according to Millot (1949).

The opisthosoma is usually considered to show evidence of only eleven segments rather than the twelve encountered in some orders. Twelve is considered primitive in the Arachnida. The abdominal terga and sterna are not distinguishable as clearly defined units in palpigrades, rather they are marked by a somewhat thicker pubescence than the intervening pleural regions. The anterior and posterior tergal and sternal borders are, by contrast, sharply delineated by clearly visible sutures. Abdominal segments VIII-XI lack a noticeable reduction in pubescence on the lateral borders, hence in these segments perhaps there is no pleura separating terga and sterna.

The genital organs open to the outside behind the second abdominal sternum as in most other arachnids. Several setational modifications on this sternum and the following one comprise external sexually dimorphic characters. In some species there exist three pairs of sacs, one pair each on sterna four, five, and six. They are purportedly eversible as are the ventral sacs of amblypygids. They are called lung-sacs by those who attribute some respiratory function to them, but no evidence exists as to their function.

The eleventh abdominal segment bears the anus and the flagellum. The flagellum is usually composed of 14-15 units. Evidence exists, however, that each pair of these actually forms a single unit.

The basal flagellar element in at least some, and perhaps all palpigrades is markedly different from the following ones. The setational pattern is much different. There are two dorsal and two larger ventral setae on the basal element, whereas there are one or two whorls of setae on the units following. Furthermore, Monniot (1970) reported that the cuticular pubescence of the surface of the basal piece was structurally very similar to the parts of the body anterior to it, more so than to the rest of the flagellum. This suggests that the basal flagellar piece may in reality be the twelfth abdominal segment. While the position of the anus depreciates this theory, the problem is not insurmountable. It is easy to visualize a gradual shift in position from subterminal to ventral to subproximal. Such a shift would place the anus between the eleventh and twelfth segments. With no hope of embryological studies being done in this order within the near future the nature of this theory must remain speculative, but the morphological evidence is strong. If we assume that the presence of 12 abdominal segments is primitive in arachnids then the 11 encountered in palpigrades is a derived condition. Evidence from the dorsoventral musculature indicates that a coalescence of segments has not occurred, at least anterior to the seventh abdominal segment. It is, if information of Börner (1904) and Roewer (1934) is correct, the same in palpigrades, schizomids, uropygids, and amblypygids.

The cuticle in palpigrades is nearly totally covered by a variable pubescence, but this is absent from the prosomal pleural areas and the apical parts of the chelicerae. Scattered setae are present over much of the body and that of the prosomal sterna and abdominal terga and sterna are put to taxonomic use. Seven trichobothria are present on the first pair of legs. Two occur on the first and second basitarsal segments and one occurs on the patella, the fourth basitarsal segment, and the second tarsal segment. Palpigrades lack lyriform organs.

The digestive system opens from the mouth which is formed by the upper lip (labrum) and lower lip (prosternum). The buccal cavity above the mouth is lined with rows of sclerotized projections which probably sieve the food as it enters. The buccal cavity leads to the pharynx which is supplied dorsally with an extensive musculature. Van der

Hammen (1969) treats the mouthparts of palpigrades in considerable detail. The esophagus leads into the midgut. The midgut has intestinal diverticulae. One pair occurs in the prosoma and six in the opisthosoma. The midgut empties into the rectum, and the anus terminates the intestine.

The excretory system is represented by nephrocytes and coxal glands. The coxal gland tubules, according to Börner (1904), originate in the anterior part of the third opisthosomal segment. They follow a twisting path forward into the prosoma and from there to the level of the coxae of the first pair of legs follow a straight path until turning ventrally to their opening on this coxa.

Constitution of the circulatory and respiratory systems is poorly known. Conflicting reports of the development of the heart range from absence (Rucker, 1903) to one with four ostia (Börner, 1901). Millot (1949) reported a weakly developed heart extending from the second to fifth opisthosomal segment.

The nervous system is composed of a supra- and subesophageal ganglionic mass. From the supraesophageal ganglionic mass the tritocerebrum issues a pair of cheliceral nerves. The subesophageal mass, besides giving off the pedipalpal and pedal nerves, leads to an abdominal ganglionic mass composed of three neuromeres. The sense organs are apparently limited mainly to sensory setae and trichobothria. A single bifurcate seta is located anteromedially and one to four are located anterolaterally on each side of the carapace. One may perhaps be tempted to somehow relate these structures with the eyes of other arachnids, owing to their numbers and position. Van der Hammen (1969), however, homologized the structures with the supracoxal setae of mites, though no such supracoxal setae are found above the chelicerae in mites.

Nearly nothing is known about the reproductive habits of palpigrades. Remy (1949) gave good indication that palpigrades produce spermatophores which he believed he found on females of Madagascan species. Rucker (1903) also mentioned structures in males construed to be spermatophores. Juberthie and Juberthie (1963) uncovered morphological evidence which also points to probable existence of spermatophores.

The works of Rucker (1903), Börner (1904), Millot (1949), and Juberthie and Juberthie (1963) represent nearly all of our knowledge of the reproductive system. The testes are paired, elongate structures in the ventrolateral spaces of the third to eighth abdominal segments. The females have two ovaries and two oviducts which converge in the uterus. The studies of Juberthie and Juberthie (1963) show that females probably produce only one or two eggs at a time. They also point out the great disparity in the relative abundance in the sexes in a few species. In *P. wheeleri* the males are slightly more common than the females; in *E. mirabilis* only two males as opposed to 400 to 500 females have been collected; and in *Eukoenenia austriaca* (Hansen) six females and four males are known.

As pointed out by Van der Hammen (1974) postembryonic developmental data are fragmentary for this order. Rucker (1903) gave evidence of four stages of development; however, these data were gathered from collections of preserved animals and not from life history studies of living animals.

The musculature has been described to some extent by Börner (1904). The major prosomal muscles are associated with the chelicerae, these being the dorsal protractor, interior rotator, exterior rotator, inferior retractor, and dorsal retractor. The musculature of the endosternite was also originally described by Börner (1904). A careful work by Millot (1943), however, appears to be more complete. As Firstman (1973) pointed out, there are six sets of muscles originating from the endosternite. Four sets have a pair of dorsal suspensors, five sets have a pair of lateral suspensors, and all six sets have ventral

suspensors. He concluded that these sets correspond to the six pairs of appendages which is unique in the Arachnida, and may be correct in assuming this to be the primitive condition.

The abdominal musculature consists of dorsal longitudinals, lateral longitudinals, ventral longitudinals, obliques, and dorsoventrals. Reports on the disposition of the abdominal dorsoventral muscles are confusing. Rucker (1901), Hansen (1901) and Firstman (1973) reported five pairs, apparently representing those occurring in segments two through six. Börner (1904) and Roewer (1934) also reported the five pairs occurring in segments two through six, but also found one extending from the first abdominal tergite attaching on the dorsal surface of the endosternite. In the Uropygida, Schizomida, and Amblypygida there exists a pair of dorsoventral muscles attaching the first abdominal tergum to the dorsal surface of the endosternite. Börner (1904) and Roewer (1934) indicated that the posteriormost dorsal muscles of the endosternite were the first pair of dorsoventral muscles. This is not indicated by Millot (1943) or Firstman (1973). Börner correctly interpreted the relationship of this pair of muscles in the Schizomida, Uropygida, and Amblypygida. Firstman also reported that the first abdominal dorsoventral muscles attach to the endosternite in uropygids and amblypygids, but he missed this relationship in the schizomids.

Judging by the close relationship of palpigrades to the previous orders, Börner's and Roewer's interpretation that the posterior pair of dorsal muscles arising on the endosternite connect to the first abdominal tergite, is considered to be correct rather than Millot's observations, repeated by Firstman, that this pair is entirely prosomal.

PART III. SYSTEMATICS OF THE PALPIGRADIDA

Diagnoses of the families and genera and synopsis of the species of the order Palpigradida

FAMILY *STERNARTHRONIDAE* HAASE, 1890

Diagnosis.—Second and third prosomal sterna separate, forming six prosomal sterna in all.

Genus *Sternarthron* Haase, 1890.

Diagnosis.—Same as for the family.

1. *S. zitteli* Haase, 1890. Jurassic of Germany.

FAMILY *EUKOENENIIDAE* PETRUNKEVITCH, 1955

Diagnosis.—Second and third prosomal sterna fused, forming five prosomal sterna in all.

Genus *Eukoenia* Börner, 1901.

Diagnosis.—Without ventral sacs on opisthosoma; ninth abdominal segment about twice as wide as eleventh segment, slightly narrower than eighth segment; pygidium narrower posteriorly; flagellum longer than opisthosoma; fourth and sixth opisthosomal sterna each form a protuberance.

2. *E. angolensis* (Remy), 1956. Angola.
3. *E. angusta* (Hansen), 1901. Thailand.

4. *E. ankaratrensis* Remy, 1961. Madagascar.
5. *E. austriaca* (Hansen), 1926. Austria.
6. *E. bara* (Remy), 1950. Madagascar.
7. *E. berlesei* (Silvestri), 1905. Italy.
8. *E. brolemanni* (Hansen), 1926. France.
9. *E. buxtoni* (Berland), 1914. France.
10. *E. chartoni* (Remy), 1950. Madagascar.
11. *E. deceptrix* Remy, 1961. Madagascar.
12. *E. delfini* (Remy), 1950. Madagascar.
13. *E. depilata* Remy, 1961. Madagascar.
14. *E. draco* (Peyerimhoff), 1906. Mallorca.
15. *E. florenciae* (Rucker), 1903. Texas, U.S.A.
16. *E. fossati* Remy, 1961. Madagascar.
17. *E. grassii* (Hansen), 1901. Paraguay.
18. *E. hanseni* (Silvestri), 1913. Mexico.
19. *E. hesperia* (Remy), 1953. Ivory Coast.
20. *E. hispanica* (Peyerimhoff), 1906. Spain.
21. *E. juberthiei* Condé, 1974. Lebanon.
22. *E. lauteli* (Remy), 1950. Madagascar.
23. *E. lawrencei* Remy, 1957. South Africa.
24. *E. machadoi* (Remy), 1950. Angola.
25. *E. meridiana* Remy, 1961. Madagascar.
26. *E. mirabilis* (Grassi and Calandruccio), 1885. Italy.
27. *E. patrizii* (Condé), 1958. Sardinia.
28. *E. pretneri* Condé, 1977. Yugoslavia.
29. *E. pyrenaica* (Hansen), 1926. France.
30. *E. remyi* Condé, 1974. Yugoslavia.
31. *E. roquetti* (Mello-Leitão and Arlé), 1935. Brazil.
32. *E. sakalava* (Remy), 1950. Madagascar.
33. *E. siamensis* (Hansen), 1901. Thailand.
34. *E. spelaea* (Peyerimhoff), 1902. France.
35. *E. strinatii* Condé, 1976. Italy.
36. *E. subangusta* (Silvestri), 1905. Italy.
37. *E. trehai* Remy, 1961. Madagascar.
38. *E. vagvolgyii* (Szalay), 1956. Hungary.

Genus *Prokoenenia* Börner, 1901.

Diagnosis.—With ventral sacs on opisthosoma; ninth abdominal segment about twice as wide as eleventh segment, slightly narrower than eighth segment; pygidium narrowed posteriorly; flagellum longer than opisthosoma.

39. *P. californica* Silvestri, 1913. California (?), U.S.A.
40. *P. chilensis* Hansen, 1901. Chile.
41. *P. millorum* Remy, 1950. Madagascar.
42. *P. wheeleri* (Rucker), 1901. Texas, U.S.A.

Genus *Koeneniodes* Silvestri, 1913.

Diagnosis.—Without ventral sacs on opisthosoma; ninth abdominal segment about twice as wide as eleventh segment, slightly narrower than eighth segment; pygidium narrowed posteriorly; flagellum longer than opisthosoma; fourth and fifth opisthosomal sterna form single protuberance.

- 43. *K. frondiger* Remy, 1950. Madagascar.
- 44. *K. madecassus* Remy, 1950. Madagascar.
- 45. *K. malagassorum* Remy, 1961. Madagascar.
- 46. *K. notabilis* Silvestri, 1913. French Guinea.

Genus *Allokoenenia* Silvestri, 1913.

Diagnosis—Without ventral sacs on opisthosoma; ninth abdominal segment equal in width to eleventh segment, half as wide as eighth segment; pygidium not greatly narrowed posteriorly; flagellum shorter than opisthosoma.

- 47. *A. afra* Silvestri, 1913. French Guinea.

Genus *Leptokoenenia* Condé, 1965.

Diagnosis—Without ventral sacs on opisthosoma; ninth abdominal segment slightly wider than eleventh segment, about equal in width to eighth segment; pygidium slightly narrowed posteriorly; flagellum shorter than opisthosoma.

- 48. *L. gerlachi* Condé, 1965. Farasan Islands, Saudi Arabia.
- 49. *L. scurra* Monniot, 1966. Zaire.

Genus *Paleokoenenia*, Rowland and Sissom, 1980.

Diagnosis—Presence or absence of ventral sacs on opisthosoma not determined; ninth abdominal segment about equal in width to eleventh segment, about half as wide as eighth segment; pygidium slightly narrowed posteriorly; flagellum longer than opisthosoma; pedipalps extremely long; carapace with an anteromedian cone.

- 50. *P. mordax*, Rowland and Sissom, 1980. ? Pliocene of Arizona, U.S.A.

Key to the families and genera of Palpigradida

- 1. Prosoma with six sterna; Mesozoic Sternarthronidae; *Sternarthron*
 Prosoma with five sterna; Cenozoic Eukoeneniidae 2
- 2. Ninth opisthosomal segment about twice as wide as eleventh segment3
 Ninth opisthosomal segment equal to or only slightly wider than eleventh segment . .5
- 3. Fourth, fifth and sixth opisthosomal segments with ventral sacs *Prokoenenia*
 All opisthosomal segments without ventral sacs4
- 4. Fourth and fifth opisthosomal sterna joined in a midventral protuberance; seventh
 opisthosomal sternum with a pair of long, stout, posteriorly directed setae
 *Koeneniodes*
 Fourth and sixth opisthosomal sterna each forming an independent protuberance;
 seventh opisthosomal sternum without a pair of long, stout, posteriorly directed setae
 *Eukoenenia*
- 5. Ninth opisthosomal segment about half as wide as eighth segment6
 Ninth opisthosomal segment only slightly narrower than eighth segment
 *Leptokoenenia*
- 6. Flagellum longer than opisthosoma; ninth abdominal segment wider than tenth
 segment, and tenth segment wider than eleventh segment; flagellar segments long and
 slender; Pliocene *Paleokoenenia*
 Flagellum shorter than opisthosoma; ninth and eleventh abdominal segments wider
 than tenth segment, ninth and eleventh segments about equal in width; flagellar
 segments moniliform *Allokoenenia*

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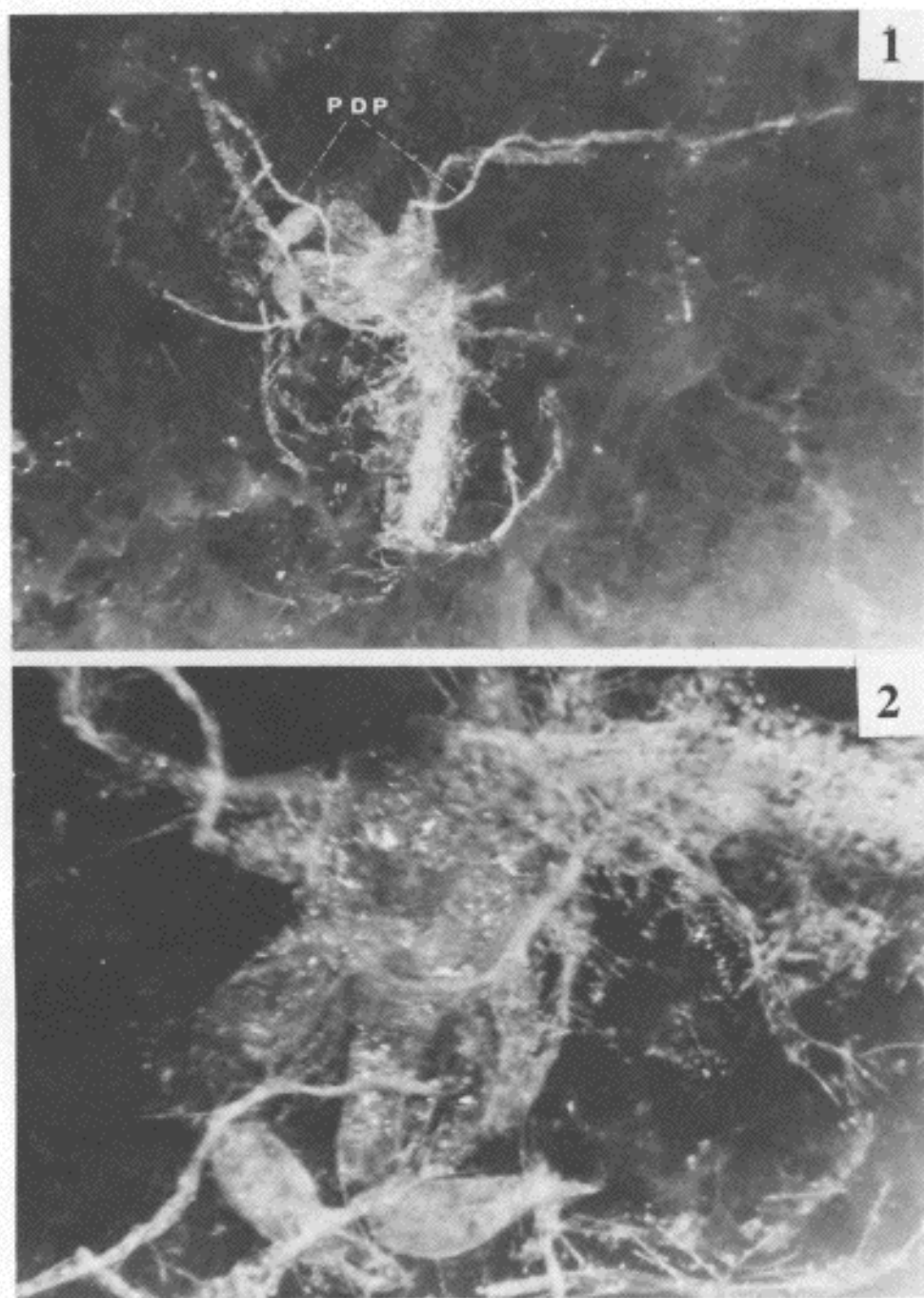
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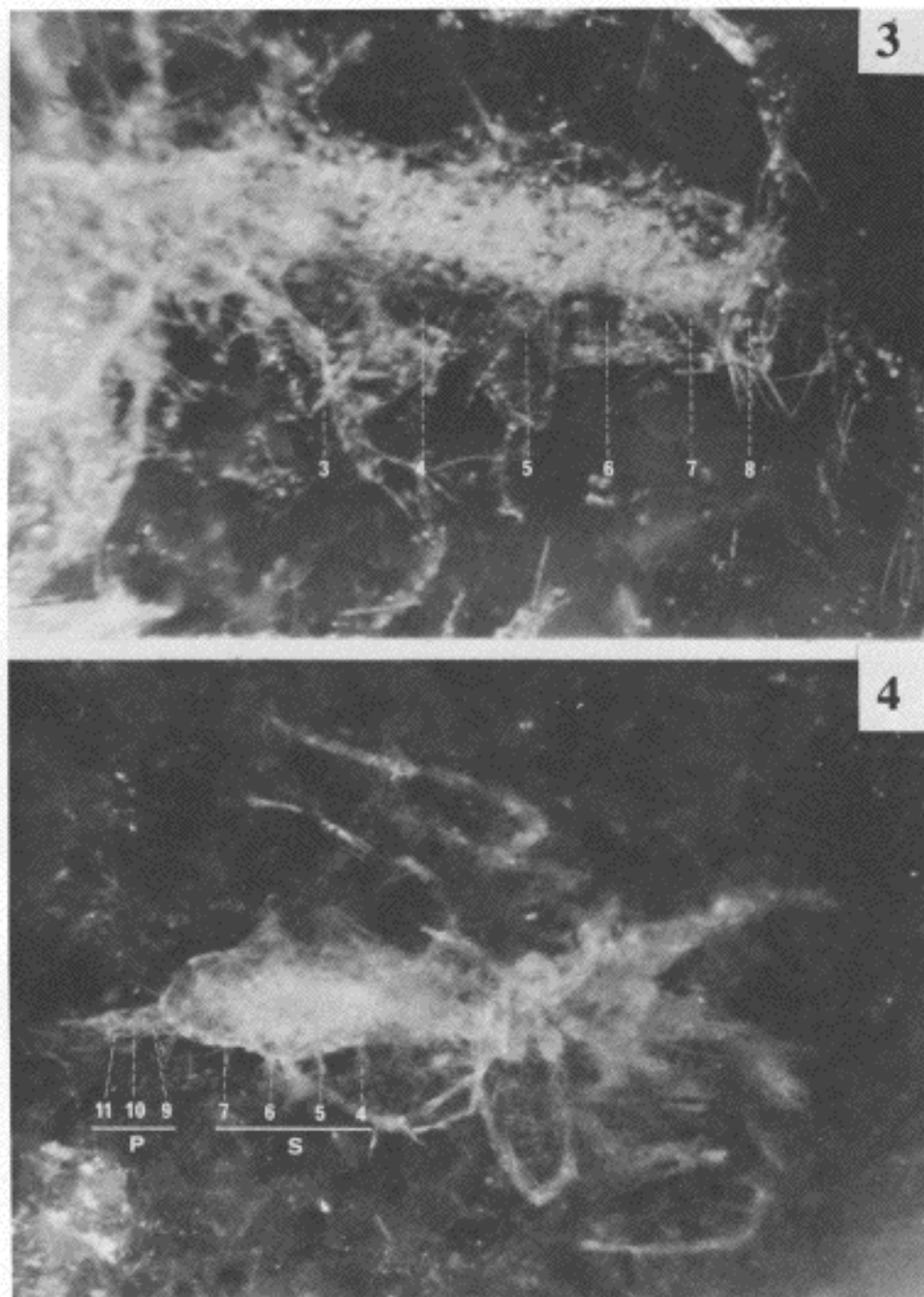
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Figs. 1-2.—Dorsal views of the holotype of *Paleokoenenia mordax*, new species: 1, whole view with pedipalps indicated (PDP); 2, close up showing, in particular, the propeltidium and chelicerae.



Figs. 3-4.—Views of *Paleokoenenia mordax*, new species: 3, close up of the dorsal aspect of the abdomen of the holotype with the third through the eighth terga labeled; 4, whole view of the ventral aspect of the allotype with the fourth through the seventh sterna (S) and the ninth through the eleventh abdominal segments or pygidium (P) labeled.