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ON THE TAXONOMIC STATUS OF *THINDYLA* CHAMBERLIN, 1955, A GENUS OF PERUVIAN CENTIPEDS WITH REMARKABLE STERNAL MODIFICATION (GEOPHILOMORPHA: SCHENDYLIDAE)

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ABSTRACT

Thindyla, a monotypic genus based upon *T. pacifica* Chamberlin, 1955, from the coast of Peru, is removed from synonymy under the polyphyletic genus *Pectiniunguis* on the basis of a deep, large, cylindrical cavity in the sterna of several anterior body segments, not approximated in any other known geophilomorph. Synonymy of *pacifica* with *litoralis* Kraus, 1954, is confirmed, and the species redescribed and figured in detail from type material of both names. Problems associated with the definition of genera in the Schendylidae are discussed; it is recommended that recourse to simple "present" vs. "absent" character states be minimized or discontinued, and that single "loss" characters not be the basis for generic diagnosis.

INTRODUCTION

Chilopods are prominent among the groups of organisms which, owing to a paucity of available character-systems, are the despair of taxonomists. This bad situation is made worse by structural variability – individual, ontogenetic, sexual, and geographic – in what few there are, and a tendency for incongruence in the expression of characters has complicated the definition of genera in particular. Heretofore two general philosophies have dominated the taxonomic literature: the analytic as practiced by R. V. Chamberlin and the synthetic approach espoused by Graf Attems. Chamberlin seized in particular upon "present or absent" polarities as generic criteria and thereby often separated nominal genera by characters far less fundamental than those used to distinguish congeneric species. Attemsian genera were, as is well-known, almost always patently heterogeneous (or polyphyletic) as the result of a more inclusive generic concept.

In the Geophilomorpha, families have been traditionally based upon mouthpart characters, and excepting a few apparently intermediate situations, seem to be reasonably coherent taxa with plausible geographic ranges. There has been, for instance, no investigation of the monophyly of the Schendylidae (after removal of the Ballophilidae), as conceived on the basis of mandibular structure. Within this taxon, organization of species

into higher groups is fraught with problems and uncertainties. Detailed knowledge of structural details is still so inadequate that degrees of relationships cannot confidently be assessed, and without trustworthy generic categories, it is virtually impossible to look for polarity information in sister-groups which have yet to be identified. The problem is obviously circular.

We have alluded to aspects of this difficulty in our revision of Nearctic species of *Escaryus* (1993). Most of the American "genera" of Schendylidae were proposed by R. V. Chamberlin on the basis of present-absent options implicating sternal pores, maxillary palps, and tarsal claws.

Sometimes such characters are expressed in more than one way. Consider the distribution of sternal pores in a group of basically similar species: present on all sterna, present on only the first three sterna, or absent altogether. Is absence more taxonomically significant than extreme reduction or metameric plenitude, or is it simply **easier** for the human mind to make such a distinction? Could not the spectrum just described be justifiably dichotomized as "all sterna with pores" *versus* "pores absent or present only on the first three sterna"?

We have (1993) alluded to the similar problem involving the presence or absence of a true tarsal claw on the last pair of legs in geophilomorphs. In some species this claw resembles those on the preceeding legs, in others it may be reduced to a small rudiment, or perhaps missing entirely. This distinction satisfied the Chamberlinian requirement for generic status, regardless if the species so characterized agreed in every other important trait with obviously related species. Respecting tradition, we continued to separate Chamberlin's schendylid genus *Gosendyla* from *Escaryus* despite the utter triviality of the single "reduction character". It is not easy to reject the very methodological bases by which one learned a particular subscience, yet it seems clear that a more rational approach to generic definition is prerequisite to a realistic classification of geophilomorphs.

Practitioners of phylogenetic systematics insist that monophyly can be assumed only by reference to character-states proven to be derived. Yet even here extreme caution is required, in the sense that every demonstrable "loss character" is *ipso facto* an apomorphy as well as a potential sidetrack into homoplasy. Perhaps the solution for geophilomorphs is to exclude such expressions of characters from diagnostic use and rely strictly upon those reasonably considered to be "acquisition characters." Random parallel evolution may indeed produce very similar effects in different clades, but never so similar as the results of character loss.

In the present state of schendylid classification, and doubtless that of other geophilomorph taxa as well, nearly all nominal genera are defined by arbitrary combinations of traits in both plesiomorphic and apomorphic expressions. Until these polarities can be identified with some confidence, monophyletic taxa will be hard to define. As noted above, it is difficult to use the outgroup comparison method to determine derived states if there is no confirmed monophyletic outgroup available. Cladists who work with taxa already organized over years of repeated revision may not immediately appreciate this problem.

Thindyla litoralis, the subject of this presentation, is a member of a group of species which cluster around the traditional image of *Pectiniunguis*, and in fact has been formally subsumed under that name. We hope, as material and opportunity permit, to develop a new definition of *Pectiniunguis* based solely upon derived acquisition characters of the type species and any others which may share them (in the quaint terminology of a more naive past, splitting up the genus into more natural components). As this project may be a slow one, probably entailing critical examination of all established schendylid genera, we venture at this time to make a positive start by extracting one alien element from *Pectiniunguis* on the basis of a spectacular structural adaptation shared by no other known geophilomorph. By

chance, the generic name *Thindyla* happens to be available to designate this branch-end. Perhaps later we will be able to offer a model phylogram, apomorphically based, that will indicate how the various species currently combined under the broad concept of *Pectiniunguis*, may be related.

TAXONOMY

Family Schendylidae

In our present concept of this family (i.e., with ballophilids removed into separate family status), the Schendylidae encompasses about 40 nominal genera and nearly 230 species. The group is almost cosmopolitan, but with its maximal diversification in the Neotropical Region, and minimal occurrence in the Australian. The presence of several "blocks" of teeth on the mandible appears to be a constant apomorphy for the family, within which other structural characters are distributed rather randomly in terms of their phylogenetic polarity.

Thindyla

Thindyla Chamberlin, 1955, Lunds Univ. Arsskr. (2) 51 (5): 8. Type species: *T. pacifica* Chamberlin, 1955, by original designation.

Diagnosis: Pleurites of second maxillae not fused with the coxosternum; apical claw of second maxillae pectinate on both dorsal and ventral edges. Sterna with pore fields. Some sterna of the anterior region of the body with a deep cylindrical invagination ("*orygma*") originating from a median cleft on the anterior border. Last pair of legs with seven podomeres; praetarsus in form of a small pilose tubercle; coxopleura of the last leg-bearing segment each with two internal coxal organs of compound structure ("heterogeneous coxal glands" *sensu* Brölemann & Ribaut, 1912).

Remarks: This genus is very closely related to *Pectiniunguis* Bollman, 1889 but differs from it (and from the other all known genera of Geophilomorpha) by the presence of a well developed, deep, cylindrical invagination on some sterna of the anterior region of the body (see further commentary under "Remarks" in the species account that follows).

Type species: *Litoschendyla litoralis* Kraus, 1954.

Name: This generic name (presumably neuter) is a neologism composed of the elements *thinos* (Gk., beach, shore, strand) + the last four letters of the generic name *Schendyla*.

Thindyla litoralis (Kraus, 1954), comb. nov.

Figures 1-35

Litoschendyla litoralis Kraus, 1954, Senck. 34: 312. Holotype ♂ (SMF 2170) from near Atico, Dept. Arequipa, Peru; H.-W. Koepcke leg. 16 June 1951.

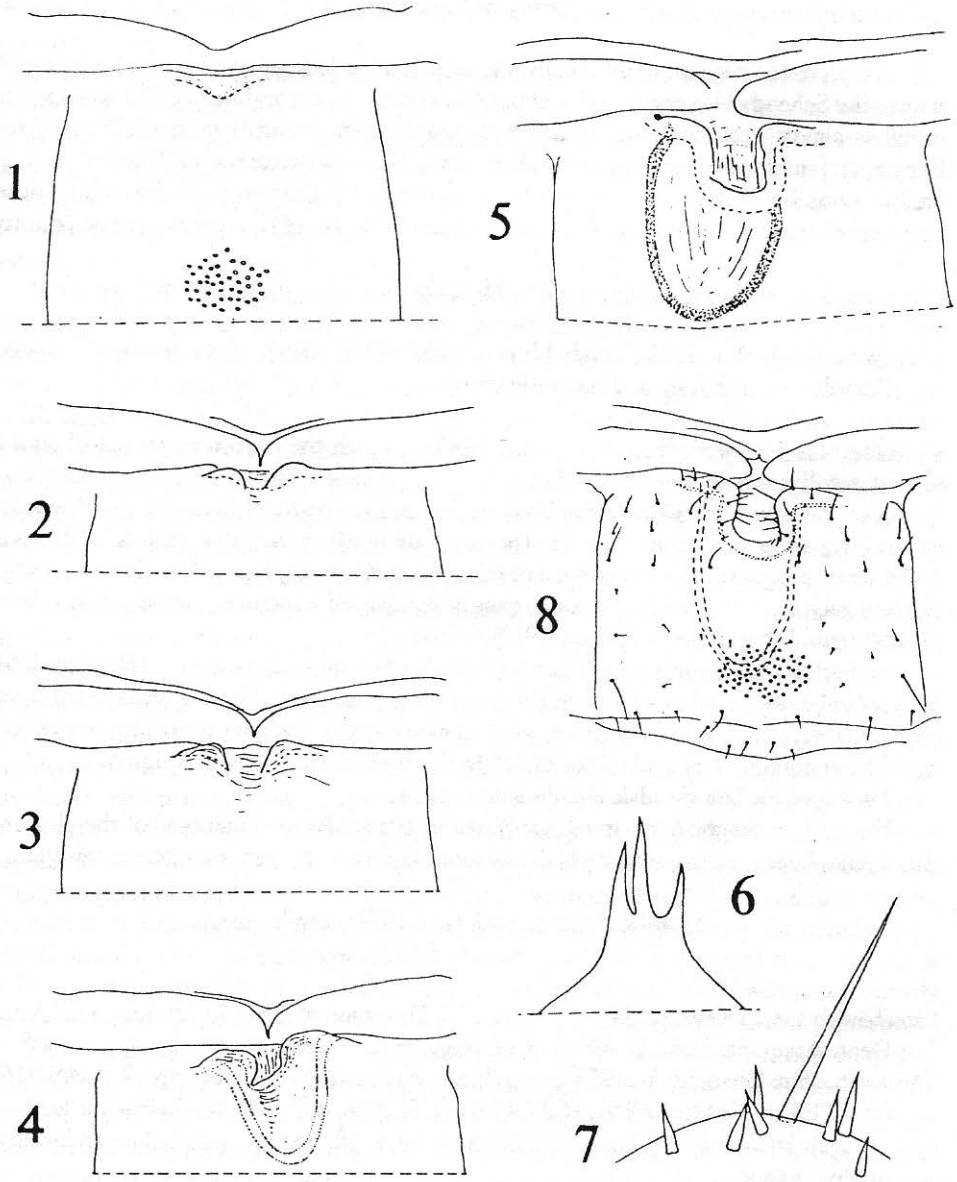
Thindyla pacifica: Chamberlin, 1955, Lunds Univ. Arsskr. (2) 51: 9. Holotype ♀ (CAS 9169) from PERU: LIMA: Callao, 16.XI.1950, E. S. Ross and A. E. Michelbacher leg.

Pectiniunguis littoralis [sic!]: Kraus, 1957, Senck. biol. 38: 361 (Unjustified emendation of original name).

Diagnosis: This species can be distinguished by the presence of a cleft on the anterior border of the sterna 3(4) to 15(16) associated with a cylindrical invagination on sterna 8 (or 9) to 12. The absence of prelabral setae is also diagnostic. The coxal organs of the last leg

pair are unusually well developed, perhaps because of the littoral habitat of this species. Another particularity of this species is the complete lack of pores on the sterna of the posterior quarter of the trunk (varying from the last 8 to 24 sterna in individual specimens).

Type material examined: Holotype ♂ of *Litoschedyla litoralis* from PERU: AREQUIPA: near Atico, 16.VI.1951 Koepcke leg. (SMF 2170). Specimen 21 mm long with 61 pairs of legs on 6 slides: (1) head capsule; (2) labrum; (3) forcipular segment and 1st pedal segment;



Figures 1-8. *Thindyla litoralis* (♂), SMF 2904/8, Specimen A). 1-5. Anterior part of sterna 4, 6, 7, 8, and 9. 6. Detail of distal end of last podomere of right last leg, ventral view. 7. Apex of terminal right antennomere showing specialized setae, ventral view. 8. Sternum 10, ventral view showing gross appearance of orygma as seen through the sternal cuticle.

(4) pedal segments 2 to 59; (5) last 2 pedal segments with postpedal segments; (6) last left leg. Holotype ♀ of *Thindyla pacifica* from PERU: LIMA: Callao, 16.XI.1950, Ross and Michelbacher leg. (CAS 9169). Specimen 60 mm long with 61 pairs of legs (head capsule, mouth parts, last 7 pedal segments and postpedal segments on 1 slide; remaining body parts in one vial). Chamberlin's original holotype label reads "*Thinondyla pacifica*". In his later years he frequently changed either the vial label or name in a manuscript without making the corresponding changes in the other place: a source of curatorial dismay and confusion when not so obvious as in this instance.

Other material examined: (All specimens from PERU, and labeled *Pectiniunguis litoralis*). Isla Don Martin, 1955, Peña leg.: 1 ♀ (65/65) in 1 vial (SMF 2906/1); 2 ♀♀ (25/65, 43/65) in 1 vial (SMF 2907/2); 2 ♂♂ (46/63, 55/63) in 1 vial (SMF 2921/2); 1 ♀ (70/65, specimen "A") and 1 ♂ (38/63) in 1 vial (SMF 2923/2). LIMA, Callao, La Punta, 22.IX.1953, Weyrauch leg.: 1 ♀ (67/65) with head capsule and mouth parts on 1 slide and trunk in 1 vial (SMF 2905/1). ICA: Pisco, near La Puntilla, 7.X.1954, Koepcke leg.: 4 ♀♀ (30/61, 50/65, 51/65, 56/65) and 4 ♂♂ (36/61, 42/61, 46/61 and 46/63, this last designed as specimen "A") in one vial (SMF 2904/8). AREQUIPA, near Atico, 16.VI.1951, Koepcke leg.: 1 ♂ (40/63) in 1 vial (SMF 2922/1); same locality, 9.I.1956, Koepcke leg.: 2 ♀♀ (23/65, 28/65) and 2 ♂♂ (26/61, 26/61) in 1 vial (SMF 2904/3); 2 ♀♀ (28/65, 23/65) 1 ♂ (26/61) and 1 juvenile (15/61, specimen "A") in one vial (SMF 2924/3).

Composite redescription:

Male: maximum body length 55 mm, 59, 61 or 63 pairs of legs.

Color of head capsule a clear orange, remaining body parts yellowish (anterior 1/5 more deeply pigmented).

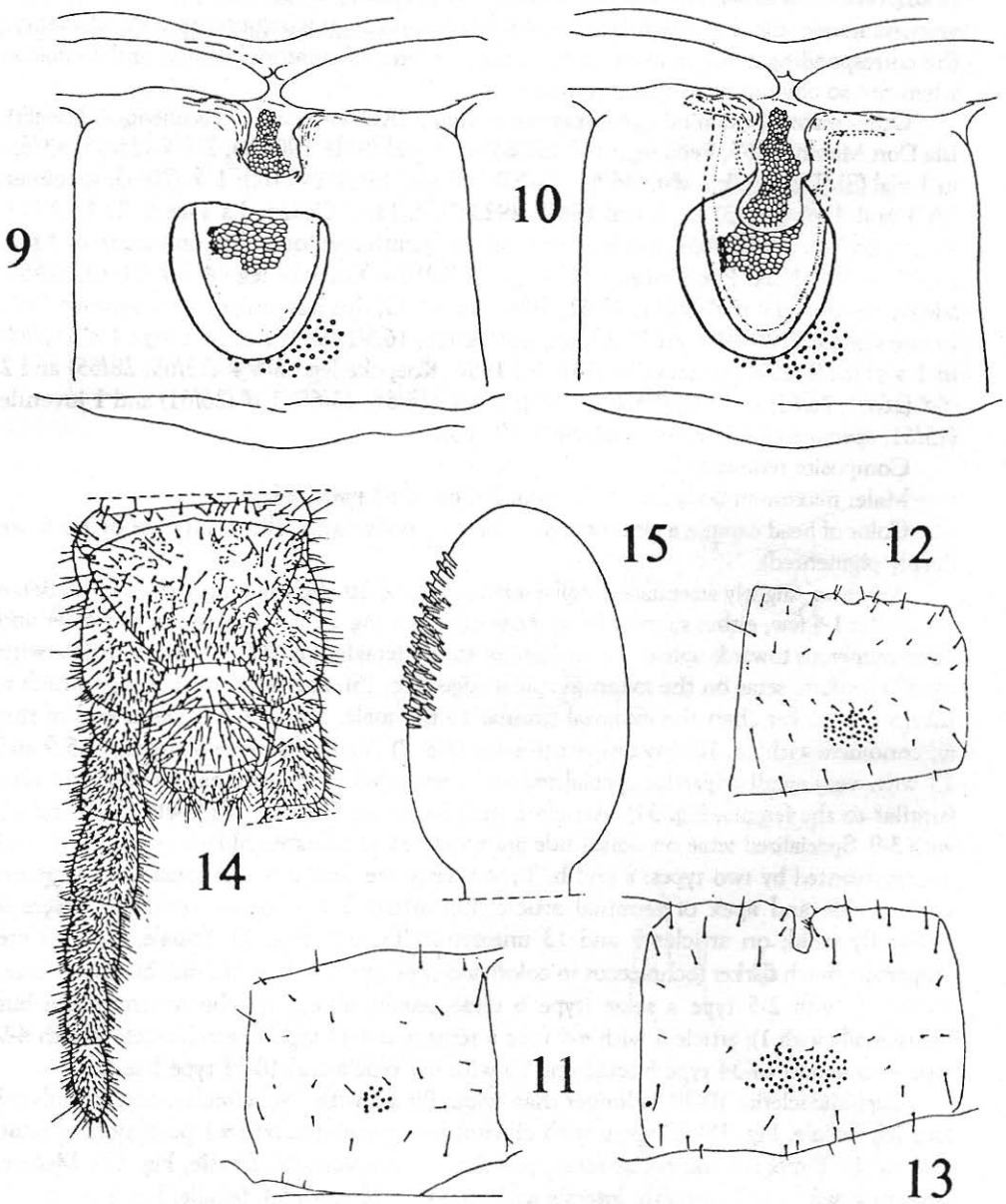
Antennae slightly attenuate distally; articles except 1st slightly longer than wide. Setae on articles 1-4 few, either short or long; those of remaining articles progressively shorter and more numerous towards apical region (similar to the female, Fig. 27). Terminal article with ca. 50 claviform setae on the external apical edge (Fig. 15), absent on medial edge which is internally thicker than the external (similar to the male, Figs. 29-30). Distal end of this antennomere with ca. 10 tiny unipartite setae (Fig. 7). Ventral surface of articles 2,5,9 and 13 with very small tripartite specialized setae restricted to an internal latero-apical area (similar to the female, Fig. 31). Article 2 with 2-6 setae; 5 with 3-10; 9 with 3-10 and 13 with 3-9. Specialized setae on dorsal side are restricted to an external latero-apical area and are represented by two types: **a** and **b**. Type **a** setae are similar to the specialized setae on ventral side and apex of terminal article. On article 2 are equally trifid; on article 5 unequally trifid; on articles 9 and 13 unipartite. Type **b** setae (cf. female, Fig. 28) are unipartite, much darker (ochraceous in color) and sizes vary 1-3 times the size of type **a** setae. Article 2 with 2-5 type **a** setae (type **b** setae usually absent on this antennomere but occasionally with 1); article 5 with 4-9 type **a** setae and 4-11 type **b** setae; article 9 with 4-9 type **a** setae and 14-34 type **b** setae and 13 with 4-7 type **a** and 18-31 type **b** setae.

Cephalic sclerite 10-20 % longer than wide. Pleura with a subcircular, non reticulated area (cf. female, Fig. 18). Clypeus with chaetotaxy represented by 1+1 postantennal setae and ca. 6+8 median transverse setae, prelabral setae absent (cf. female, Fig. 17). Median labromere with ca. 7-10 teeth, laterals with ca. 10 + 10 teeth (cf. female, Fig. 23).

Dentate lamella of mandible divided into three-four blocks with formula 3-2-5; 3-3-3-2; 3-3-4 (cf. female, Figs.21-22); pectinate lamella with ca. 21 hyaline teeth.

Palps present on both coxosternum and telopodites of first maxillae. Coxosternum with ca. 4+3 setae; median projection of coxosternum subtriangular, well developed, provided with ca. 3+3 setae. Distal article of telopodite with ca. 7+8 ventral setae and ca. 11+12 sensory papillae on the dorsal side (cf. female, Fig. 19).

Second maxillae with ca. 12+12 setae on coxosternum distributed according to Figure 19. Apical claw of telopodite well developed and bipectinate, dorsal pectine with ca. 17 teeth and ventral with ca. 19-26 (cf. female, Fig. 20). Shape and chaetotaxy of telopodite cf. female, Fig. 19.



Figures 9-15. *Thindyla litoralis* (♂), SMF 2904/8, Specimen A). 9-10. Sternum 10, showing different details of orygma, shown as though different amounts of sternal cuticle were removed. 11-13. Sterna 2, 6, and 12 respectively. 14. Last pedal segment and postpedal segments, ventral view. 15. Ultimate left antennomere showing claviform setae, dorsal view.

Closed telopodites of prehensors extending forward as far as anterior edge of cephalic sclerite. Basal sclerite with an irregular transverse median row of ca. 11 setae and a few additional on the anterior part. Telopodites with all articles lacking teeth. Calyx of toxicodene cylindrical. Chaetotaxy of coxosternum and telopodites as shown in Fig. 35.

Legs (last pair excepted) with chaetotaxy uniform throughout the body length and represented by few long setae. All three parungues robust, dark, equal in size.

Sterna: first sternum without pores; pore fields begin on sternum 2 and end on sterna 39-51 depending on specimen; completely lacking on remaining ones (and also on some sterna within series). Fields always single, their form changing along trunk from subcircular to subrectangular to irregular. One specimen (63 leg pairs, posterior pore field limit on sternum 49 and lacking pores on 44, 47, 48) with number of pores/sternite number as 11/2, 25/3, 30/14, 20/37, 23/38, 14/39, 17/40, 4/41, 5/42, 3/43, 4/45, 3/46, 1/49. Orygmata (see Remarks) present on sterna 8(9) - 12, largest on sterna 10-11; external and internal surfaces of invagination showing polygonal structure (Figs. 4-5, 8-10). Cleft of anterior border present on sterna 3(4) - 15(16), increasing in size until sterna 10 (11), then decreasing until vestigial on sterna 15 (16).

Last pedal segment: on the majority of the specimens studied, pretergum on both sides not separated from pleurites by sutures, in a few specimens separated only on one side. Presternite not divided sagittally; form and chaetotaxy of sternum as in Fig. 14. Coxopleura slightly protruding on ventro-apical area; vestiture as numerous setae dispersed on all surfaces, more numerous and smaller on the distal ventral half. Two compound ("heterogeneous") and well-developed coxal organs on each coxopleuron with numerous lobes present. Organs open on membrane between coxopleura and sternum covered by the latter. Posterior organs always larger than anterior; organs on largest specimens much more developed and with more lobes than in juveniles (cf. female, Fig. 32, and Figs. 33-34). Podomeres of terminal legs moderately incrassate, vestiture as numerous setae ventrally, covering entire segmental surfaces (Fig. 14); apex of distalmost podomere with a tuberculate pretarsus with 3 or 4 small apical spines (Fig. 6). Form of podomeres and their chaetotaxy as represented on Figure 14.

Posterior border of intermediate postpedal segment slightly concave; posterior border of genital segment I convex medially, slightly concave laterally; basal article of gonopod with ca. 25 setae; distal with ca. 14 (Fig. 14).

Female: Maximum body length 70 mm, leg pairs numbers 61, 63 or 65.

Characters concurring with those of male except for the usual sexual differences in the posteriormost segments.

Last pedal segment: form and chaetotaxy of sternum and tergum as in Figs. 24-25. Coxopleura slightly protruding at their distal ventral ends, with setae more numerous on distal internal edge. Podomeres of terminal legs with shape and chaetotaxy as in Figs. 24-25.

Post pedal segments: intermediate tergum with posterior margin convex; intermediate sternum with posterior border straight; first genital sternum with posterior border concave. Gonopods uniarticulate. Anal valves very developed and pilose (Fig. 24).

Distribution: PERU (Don Martin Island and coasts of the Departments of LIMA, ICA and AREQUIPA).

Habitat: This species seems limited to the littoral zone along coasts. Specimens have been collected under stones, in the driftline, or under carcasses near the tide zone.

Remarks: In his description of the holotype male, Kraus (1954) reported pore fields on sterna 2-30, but in fact pores are present on sterna 2-44, excepting 29, 33, 36, 37, 40 and 41, (this interruption within the series not described by Kraus). Later, Kraus (1957) described the shape of the pore fields as circular, but actually the field shape changes posteriorly from

subcircular to subrectangular to irregular; in addition he stated that pore fields are present to sternum 40 but in fact the posterior limit of the pore fields varies between specimens .

The 1957 redescription of *litoralis* mentioned the sternal origmata for the first time (they were not evident in the poorly preserved original material), but the illustrations represent

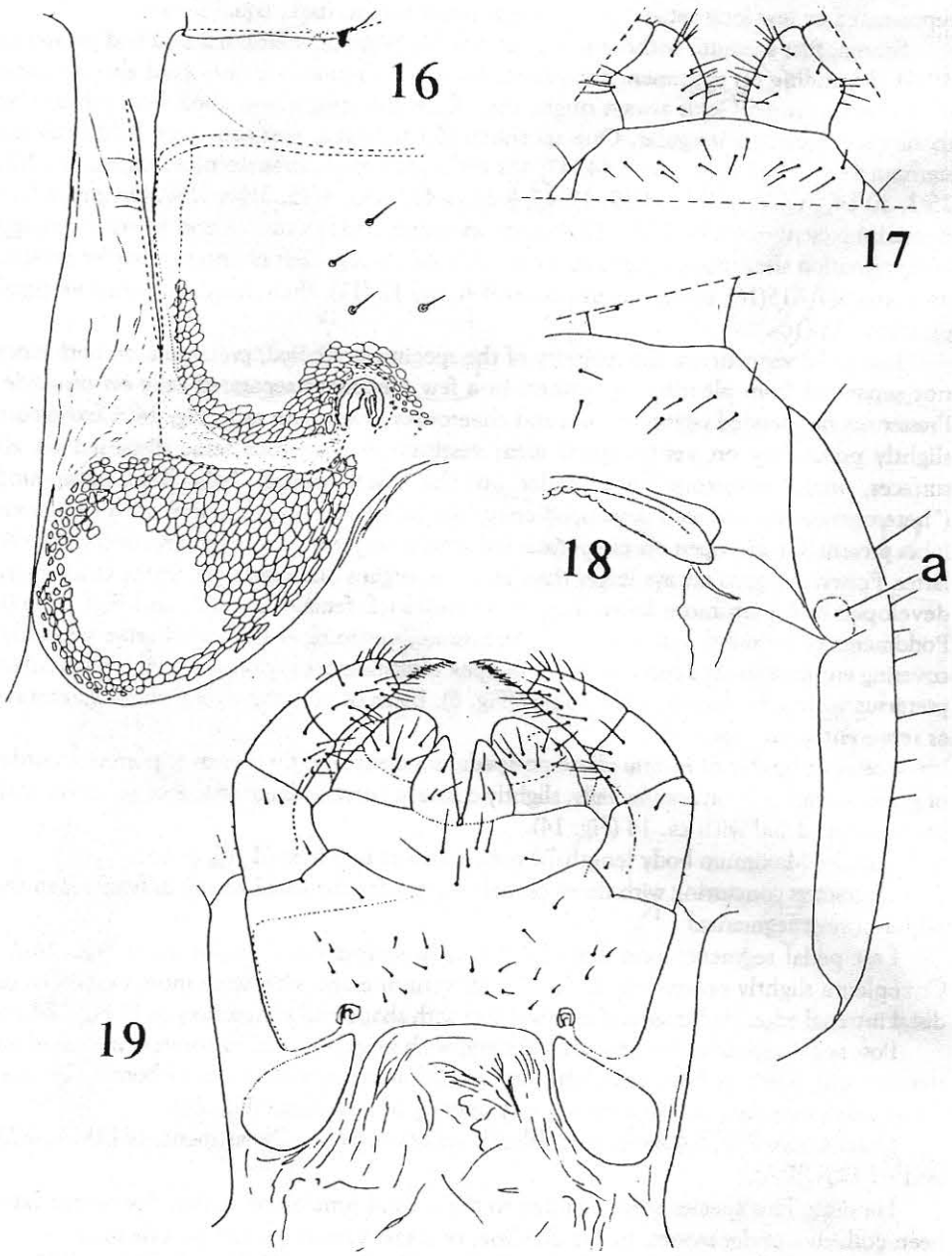
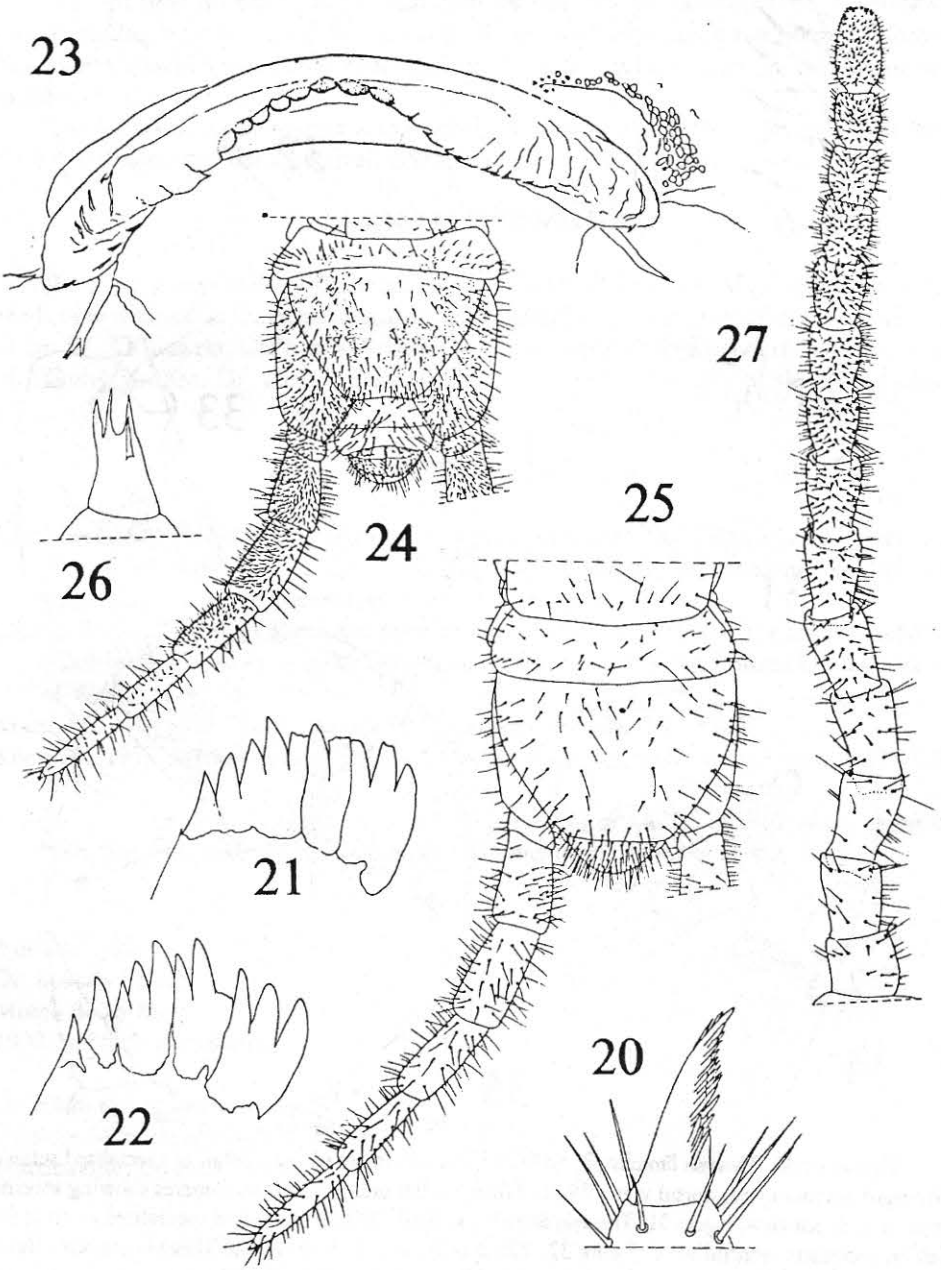
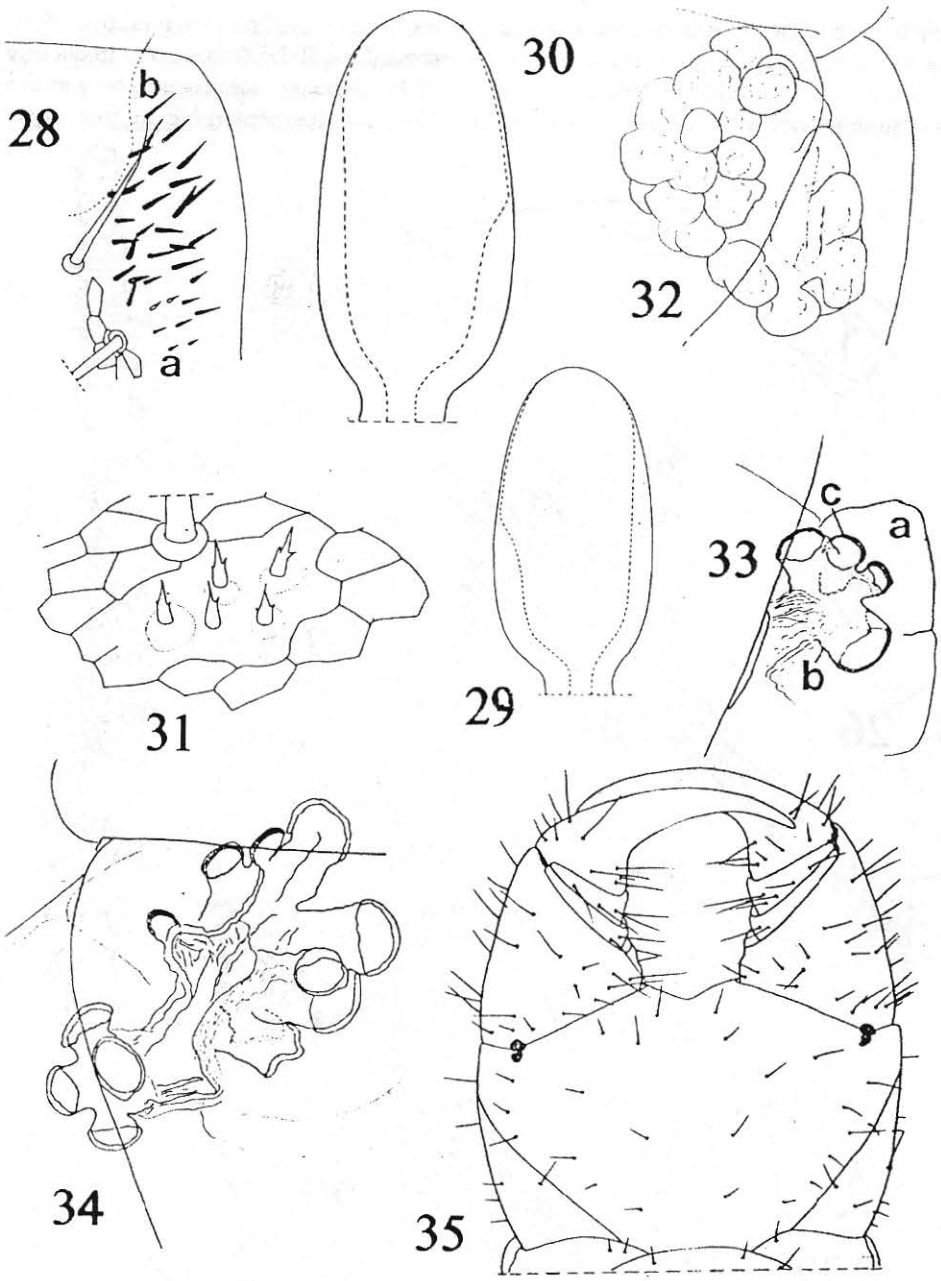


Figure 16. *Thindyla litoralis* (♂) SMF 2904/8, specimen A). Coxosternum and pleurite of right second maxilla, ventral. Figures 17-19. *Thindyla litoralis* (♀), SMF 2905/1). 17. Clypeus and basal antennomeres. 18. Cephalic capsule (left anterolateral portion, ventral view, a, area without reticulation). 19. 1st and 2nd maxillae, ventral view.

them as deep grooves rather than actual invaginations. These remarkable cavities, from their position on the sterna, suggest homology with the *sacculi* (Crabill, 1954) that occur frequently in the family Geophilidae, but their absence from Schendylidae — or presence only in the most rudimentary form — leads us to suspect they are autapomorphic in this single



Figures 20-26. *Thindyla litoralis* (♀, SMF 2905/1). 20. Apex of right telopodite of 2nd maxilla, ventral view. 21-22. Mandibular dentate lamellae. 23. Labrum. 24-25. Last pedal segment and postpedal segments, ventral view. 26. Detail of distal end of last podomere of right last leg, ventral view. Figure 27. *Thindyla litoralis* (♀, SMF 2923/2, specimen A). Right antenna, ventral view.



Figures 28-30. *Thindyla litoralis* (♀, SMF 2923/2, specimen A). 28. Detail of specialized setae of 9th right antennomere, dorsal view. 29-30. Ultimate left and right antennomeres showing internal structure, dorsal view. Figure 31. *Thindyla litoralis* (♀, SMF 2906/1). Detail of specialized setae of 9th left antennomere, ventral view. Figure 32. *Thindyla litoralis* (♀, holotype of *Thindyla pacifica*). Detail of left anterior coxal organ. Figures 33-34. *Thindyla litoralis* (♂, SMF 2924/3, specimen A, juvenile). 33. Detail of portion of left posterior coxal organ, ventral view (a, transport epithelium; b, duct; c, independent area of cuticle of the transport epithelium covered by a mucous layer). 34. Detail of internal structure of right anterior coxal organ. Figure 35. *Thindyla litoralis* (♂, SMF 2922/1). Prehensorial segment, ventral view.

"pectiniunguid" lineage. A very small indentation on the same sterna in *Pectiniunguis halirhytus* could be an early stage in the development of *orygmata*, or the final stage in a reductional trend. Better insights will emerge as more pectiniunguid schendylids become known.

We can offer no functional explanation for the extreme development of a singular sternal structure in this species, the habitat (and life style?) of which is not notably different from that of related forms. Future histological studies may shed some light on this interesting problem.

The suggested name *orygma* is the Greek word meaning "pit" or "cavity"; the plural form is *orygmata*, and the adjectival, *orygmate* (e.g., orygmate sterna).

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