

**New species of Acanthodrilinae and a new genus
of Perionychini (Oligochaeta, Megascolecidae)
from New Caledonia, their phylogeny and zoogeography**

by B. G. M. JAMIESON and J. D. BENNETT *

Abstract. — Seven new and two previously known species of *Acanthodrilus* from New Caledonia are described : *A. chabaudi*, *A. chevalieri*, *A. fabresi*, *A. koghis*, *A. longicystis*, *A. paripapillatus* and *A. ruber* spp. nov., *A. cavaticus* and *A. paniensis* Michaelsen, 1913. The genus *Acanthodrilus* is redefined and its close relationship with the Australian *Diploctrema* and North American *Diplocardia* discussed. A former Gondwanan or Pangean distribution of acanthodriles is suggested. *Plutellus* (*Diploctrema*) *sarasini* Michaelsen is redescribed from new material and is made the type-species of the new genus *Eudiploctrema* to which the other four New Caledonian species attributed to *Diploctrema* by MICHAELSEN are assigned. *Plutellus pygmaeus* Michaelsen is transferred to *Diporochoeta*. The phylogeny of *Eudiploctrema* in relation to *Diporochoeta*, *Graliophilus* and *Simsia* is investigated and it is concluded that these genera evolved before the Cretaceous separation of New Caledonia from Australia and that *Diporochoeta* originated after the Triassic separation of Africa from Gondwanaland but before rifting of India.

Résumé. — Deux espèces déjà connues et sept nouvelles d'*Acanthodrilus* de Nouvelle-Calédonie sont décrites : *A. chabaudi*, *A. chevalieri*, *A. fabresi*, *A. koghis*, *A. longicystis*, *A. paripapillatus* et *A. ruber* n. spp., *A. cavaticus* et *A. paniensis* Michaelsen, 1913. Le genre *Acanthodrilus* est redéfini et son étroite parenté avec le genre australien *Diploctrema* et le genre nord-américain *Diplocardia* est discutée. Une distribution gondwanienne ou pangéenne est suggérée pour les Acanthodriles. *Plutellus* (*Diploctrema*) *sarasini* Michaelsen est redécrite à partir d'un nouveau matériel et devient l'espèce-type du nouveau genre *Eudiploctrema* ; les quatre autres espèces de Nouvelle-Calédonie attribuées à *Diploctrema* par MICHAELSEN sont transférées dans ce nouveau genre. *Plutellus pygmaeus* Michaelsen est transférée dans le genre *Diporochoeta*. Les relations phylogéniques d'*Eudiploctrema* avec *Diporochoeta*, *Graliophilus* et *Simsia* sont étudiées ; la conclusion est que ces genres ont évolué avant la séparation crétacée entre Nouvelle-Calédonie et Australie et que les *Diporochoeta* se sont formés après la séparation triasique entre Afrique et Gondwana mais avant la séparation de l'Inde.

INTRODUCTION

New Caledonia is a large island, approximately 235 km long and 42 km wide, lying between the Tropic of Capricorn and latitude 20° South and straddling longitude 165° East, about 1365 km from the East coast of Australia. At 90 million years before the present New Caledonia, as part of the Norfolk Ridge, was juxtaposed to the Lord Howe Rise which in turn was in contact with the East coast of Australia. Separation of New Caledonia

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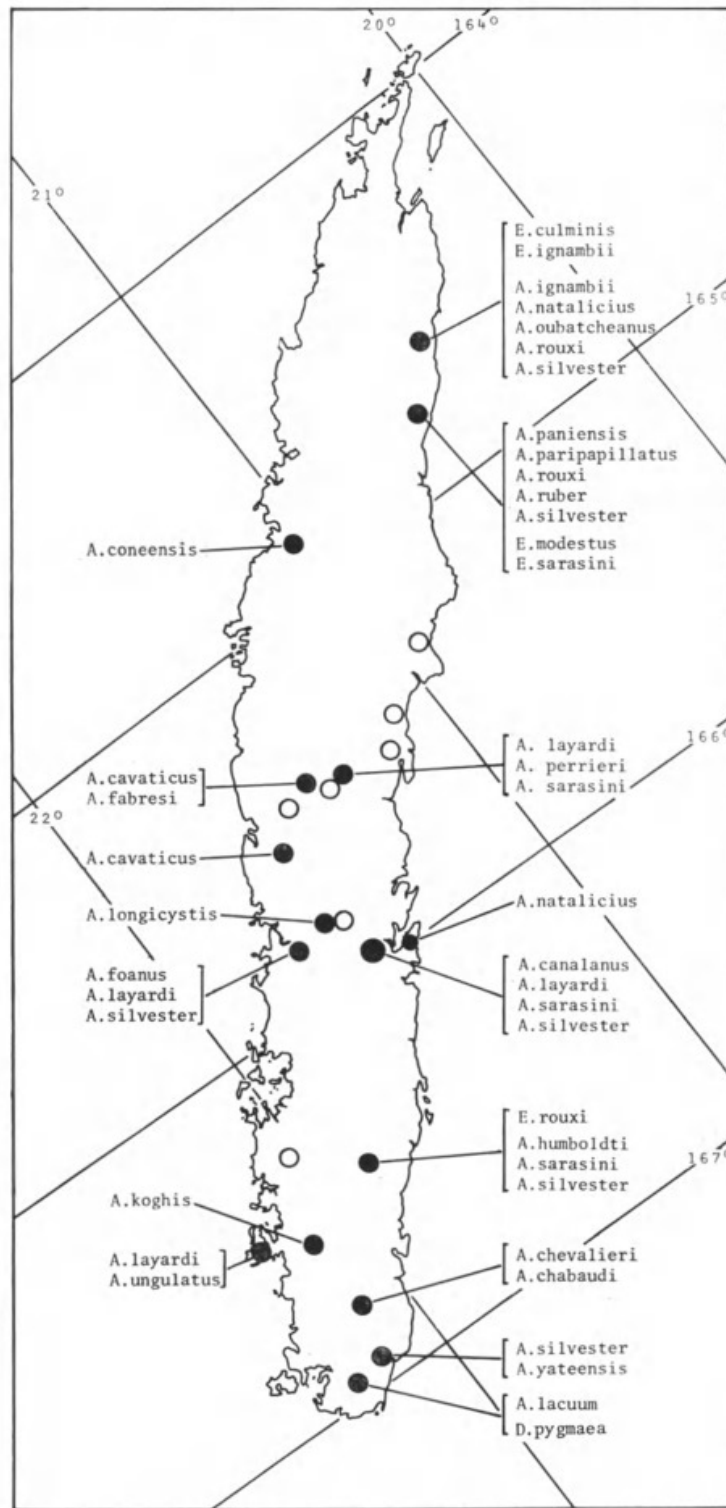


FIG. 1. — All records of *Acanthodrilus*, *Eudiploctrema* and *Diporochaeta* for New Caledonia (Black circles). Open circles are sites which yielded earthworms in other genera only.

from these masses by rifting is dated shortly after 80 million years ago (GRIFFITHS, 1971 ; GRIFFITHS and VARNE, 1972 ; GRIFFITHS, 1974). Separation of Australia from Antarctica occurred later, being dated by these workers at 50 million years ago, or 43 million years

ago in the estimate of JARDINE and MCKENZIE (1973). The fauna and flora of New Caledonia may thus be deduced to be partly relictual from that of Cretaceous Australia and ultimately of Gondwanaland. The earthworm fauna, listed by MICHAELSEN (1913), consists of Megascolecidae assigned to the genera *Acanthodrilus*, *Plutellus*, *Pontodrilus*, *Megascolex*, *Pheretima* and *Dichogaster*; Ocnerodrilidae, represented by a species of *Eukerria*; Eudrilidae; Glossoscolecidae and Lumbricidae. Of these, only *Acanthodrilus*, *Plutellus* and possibly the single species of *Megascolex* are endemic, the others being widely distributed, peregrine forms.

The relevance of the relictual endemic fauna to Australian studies, morphological similarity of *Acanthodrilus* to the Australian *Diplotrema* and the phylogenetically very significant position of the New Caledonian plutelli, prompted the authors to collect in New Caledonia in February 1977.

HISTORIC

Acanthodrilus

The confused taxonomic history of *Acanthodrilus* leading to the modern concept of this genus is discussed by PICKFORD (1937) and JAMIESON and DYNE (1976) and only a brief summary is necessary here. *Acanthodrilus* was erected by PERRIER (1872) for three species first described in the same work, *A. obtusus* and *A. unguatus*, from New Caledonia, and *A. verticillatus*, from Madagascar. *A. verticillatus* was subsequently transferred to the glossoscolecoid genus *Kynotus* (MICHAELSEN, 1897). *A. obtusus* was transferred to the Acanthodriline genus *Notiodrilus* by MICHAELSEN, 1899, *Notiodrilus* being distinguished from *Acanthodrilus* by free testes and funnels and from *Microscolex* by retention of both pairs of prostates, only the anterior pair being retained in *Microscolex*. *Acanthodrilus* was thereby restricted to the single species *A. unguatus*. *A. layardi* Beddard, 1886, was regarded as a junior synonym of *A. unguatus* but was later reinstated as a distinct species (MICHAELSEN, 1913).

Notiodrilus was later suppressed in *Microscolex* on demonstration of variation in closely related species from the acanthodrilin condition seen in *Notiodrilus* to the microscolecoid condition previously diagnostic of *Microscolex* (MICHAELSEN, 1905). PICKFORD (1932) confirmed this decision, noting that this variation also occurred intraspecifically. However, on erection of *Eodrilus* (MICHAELSEN, 1907), *Microscolex* was retained only for species in which the gizzard was reduced or absent, while the large residue was assigned to *Eodrilus*. The type-species of *Notiodrilus* (*N. georgianus*) remained in *Microscolex*.

Acanthodrilus remained monotypic in Das Tierreich (MICHAELSEN, 1900) but MICHAELSEN (1913) added 16 New Caledonian and Loyalty Island species and merged *Eodrilus* with it on the grounds that in many of the new species the testis-sacs were in a very incomplete state of development and that generic significance could therefore no longer be attached to the presence or absence of these sacs. He noted also that the New Caledonian species of *Acanthodrilus* had well developed nephridial vesicles, a character which he had previously considered to be peculiar to *Microscolex*. Demonstration by JAMIESON (1971a)

that *Diplootrema* Spencer, 1900, has acanthodrilin male pores necessitated placing the type species of *Eodrilus*, *E. cornigravei* Michaelsen, 1907, and some other Australian species of *Eodrilus*, in *Diplootrema*. The congeneric position of the two type species was emphasized by mutual possession of modified, genital setae in the vicinity of the spermathecal pores. PICKFORD (1932) had reinstated *Eodrilus* for acanthodrilin worms lacking nephridial vesicles while *Microscolex* and *Acanthodrilus* were characterized by these structures. In *Acanthodrilus* they were widened J-shaped tubes, while in *Microscolex* they were ovoid or pear-shaped.

The residue of *Eodrilus*, not assignable to *Diplootrema* and lacking the J-shaped vesicles of *Acanthodrilus*, was placed by JAMIESON (1971b) in *Notiodrilus*. Reexamination (JAMIESON, 1974b) of the type-species of *Notiodrilus*, *Acanthodrilus georgianus* Michaelsen, 1888, indicated that, notwithstanding the variation from acanthodrilin to microscolecin terminalia noted by MICHAELSEN and PICKFORD in other species, this species differed sufficiently from the type-species of *Microscolex* to justify retention of *Notiodrilus* though only as a subgenus of *Microscolex*. *Diplootrema* was included in *Microscolex* as a third subgenus. The subgenus *Microscolex* included only three (microscolecin) species, all with nephridial bladders; *Notiodrilus* was a large, heterogeneous group, containing vesiculate and avesciculate species, while the sole unique feature of five species assigned to the avesciculate subgenus *Diplootrema* was the invariable presence of spermathecal genital setae. JAMIESON and DYNE (1976) added new species to the formerly monotypic *Diplootrema* which absorbed all Australian *Notiodrilus* species and became polythetic in containing forms with or without spermathecal genital setae. Attention was drawn to the need for resolution of the problem posed by the residue of *Notiodrilus*.

The presence in *Acanthodrilus* of spermathecal genital setae which are often indistinguishable from those of *Diplootrema* underlines the desirability of comparison with *Diplootrema*. The two entities are undoubtedly closely related, and, as a whole, *Acanthodrilus* is distinguished only by presence of nephridial vesicles. Similar setae occur in the digastric North American genus *Diplocardia* which JAMIESON and DYNE (1976) maintain is also closely related to *Diplootrema*, despite assertions of GATES (1977) to the contrary.

Acanthodrilus takes priority over *Microscolex*, *Notiodrilus* and *Diplootrema* respectively and, as *Diplootrema* appears morphologically and phylogenetically closer to it than to *Microscolex*, it might be argued that these four entities, and even *Diplocardia*, should be grouped as subgenera in the genus *Acanthodrilus*. The four groups represent geographically distinct portions of a Gondwanan acanthodriline fauna and *Diplocardia* may indicate a Mesozoic incursion into Laurasia. Until *Notiodrilus* and other acanthodriline genera such as *Yagansia* are revised, their status must remain uncertain. The present study is directed to providing a thorough characterization of *Acanthodrilus* which in conjunction with the revision of *Diplootrema* by JAMIESON and DYNE (1976) and of *Diplocardia* by GATES (1977) will lay a firmer foundation for future revisionary studies on the Acanthodrilinae.

New Caledonian Plutelli

With the exception of the single species of *Pontodrilus*, MICHAELSEN (1913) placed the New Caledonian plutelloid worms (those with holonephridia, eight setae per segment and

tubular prostates) in the genus *Plutellus*. One was referred to the subgenus *Plutellus* and the remaining six to the subgenus *Diploptrema*. MICHAELSEN placed the hitherto monotypic Australian *Diploptrema* in *Plutellus* because he had demonstrated in the New Caledonian specimens that the male pores opened separately from the prostate pores on XVIII, a condition described by SPENCER (1900) for the type-species of *Diploptrema*, *D. fragilis*. This condition prompted STEPHENSON (1930) to regard *Diploptrema* as the ancestral genus of the Megascolecinae, the normal megascolecine condition in which male and prostate pores are combined, being derivable from it. It has been shown, however, (JAMIESON, 1971b) that the type-species of *Diploptrema* was incorrectly described by SPENCER and that its male terminalia showed the acanthodrilin arrangement, male pores on XVIII and two pairs of prostate pores, on XVII and XIX. As stated by JAMIESON and DYNE (1976), this condition, with the holonephric condition of the excretory system, necessitated placing this species, and therefore its genus, in the subfamily Acanthodrilinae. It was pointed out that if MICHAELSEN's observation of discrete male and prostatic pores in the five New Caledonian species were correct this would appear to warrant erection of a new plutelloid genus. They cannot be accommodated in *Plutellus* as restricted by JAMIESON (1971c). It will be seen below that the name *Eudiploptrema* is proposed to receive these species. The single New Caledonian plutelloid with fused male and prostatic pores, *P. pygmaeus*, can be accommodated neither in *Eudiploptrema* nor *Plutellus* and its affinities will be considered in the Discussion. The *Eudiploptrema* condition of the male terminalia remains the most primitive in the Megascolecinae. Its restriction to New Caledonia seems compatible with the view of this island as a refuge of early Gondwanan forms.

DESCRIPTIVE FORMAT AND ABBREVIATIONS

The characters employed and their sequence in the generic and specific descriptions conform with the senior author's previous works.

Abbreviations in the illustrations are : b.v., blood vessel ; bl, bladder ; cae, caecum of intestine ; d.b.v., dorsal blood vessel ; ♀, female pore ; g.m, accessory genital marking ; g.s, genital seta ; gl.m.st, glandular and muscular stroma ; lep, lining epithelium ; ♂, male pore ; nk, neck ; np, nephropore ; ns, nephrostome ; pr.d, prostate duct ; pr.g, glandular part of prostate ; pr.p, prostate pore ; pr.po, prostate porophore ; ps. f, penisetal follicle ; s.tum, setal tumescence ; sem.ch, seminal chamber ; sem. gr, seminal groove ; sp.amp, spermathecal ampulla ; sp.div, spermathecal diverticulum ; sp.p, spermathecal pore ; tu, tuft of nephridium.

In the text, abbreviations for specimens are : H, holotype ; P, paratype ; S, specimen ; registration numbers for institutions commence with AH, National Museum of Natural History, Paris ; BJ, Jamieson Collection ; BMNH, British Museum (Natural History) ; QM, Queensland Museum. All specimens were collected by B.G.M. JAMIESON and J. D. BENNETT.

SYSTEMATIC DESCRIPTIONS

Genus **ACANTHODRILUS** Perrier, 1872

Acanthodrilus (part.) ; PERRIER, 1872 : 85 (excluding *A. verticillatus*).

Acanthodrilus (part.) ; MICHAELSEN, 1899 : 237 ; 1900 : 127 ; 1913 : 188 ; STEPHENSON, 1930 : 824.

Notiodrilus (part.) ; MICHAELSEN, 1899 : 239 ; 1900 : 128.

Eodrilus (part.) ; MICHAELSEN, 1907 : 141.
Acanthodrilus ; PICKFORD, 1937 : 589 ; LEE, 1959 : 37.

DIAGNOSIS : (Setae lumbricinae. Dorsal pores present). Prostate pores 2 pairs in XVII and XIX with male pores in XVIII or all pores transposed 1-3 segments posteriorly. Holonephric ; nephridia with elongate, caudally usually J-shaped, bladders. Prostates tubular (extending through several segments). Spermathecae 2 pairs (diverticulum usually with multiple sperm chambers ; usually with genital setae in their vicinity).

DESCRIPTION

Prostomium tanylobous or exceptionally (*yateensis*) epilobous. With or without parietal pigmentation. Perforate dorsal pores commencing in 11/12 — 13/14 or behind the clitellum. Ventral setal couples in the vicinity of the spermathecal pores frequently enlarged and sculptured as genital setae and on glandular protuberances ; those at the prostate pores modified as penial setae. Somatic setae in 8 regular longitudinal rows throughout ; very closely paired, the dorsolateral pair (*cd*) slightly wider to narrower than the ventrolateral pair (*ab*). Nephropores commencing near the anterior extremity, in a single, straight series on each side in *cd* but when present at the anterior limit of II well dorsal to *d* (excepting *kermadecensis*). Clitellum annular, except where interrupted by the male genital field, exceptionally (*kermadecensis*) saddle-shaped ; including the segment of the female pores. Prostate pores 2 pairs, in XVII and XIX ; male pores near the equator of XVIII ; or all pores displaced 1-3 segments further posteriorly ; seminal grooves (always ?) present, placing the male pores in communication with the prostate pores. Female pores, a minute pair in XIV, anterior to the setal arc. Spermathecal pores 2 pairs, at the anterior margins of VIII and IX, in *ab* lines. Accessory genital markings frequently present ; eyelike or transverse pads.

Dorsal blood vessel single, rarely in places segmentally doubled, continuous onto the pharynx. Last hearts in XIII ; those in X-XIII latero-oesophageal, each receiving a connective from the dorsal vessel and one from the supra-oesophageal vessel ; preceded by dorso-ventral commissurals. A pair of latero-oesophageal vessels, median to the hearts ; extending far anteriorly. Supra-oesophageal vessel oesophageal only. Subneural vessel absent. Gizzard single, strongly muscular, anterior to septum 7/8 or 8/9, usually in VI, never wholly in V. Oesophagus lacking extramural calciferous glands. Intestine (always ?) commencing in or behind XVII ; dorsal typhlosole unilaminar, bilaminar or absent ; muscular thickening absent ; a pair of short intestinal caeca rarely present (in XXVI). Nephridia : vesiculate holonephridia ; anterior pairs tufted (excepting *kermadecensis*), with straight, hooked, tortuous or V-shaped bladderlike ducts ; those in intestinal segments simple, bladder V-shaped or, usually, with the ectal limb shorter than the ental, (i.e. J-shaped) but sometimes passing straight laterally and slightly diverticulate lateral to the pore ; intestinal (and more anterior ?) nephridia each with preseptal funnel. Testes in X and XI, free or in testis-sacs ; seminal vesicles in IX and XII, less commonly in XI and XII, rarely otherwise disposed. Prostates 2 pairs ; tubular, though often depressed. Penial setae (always ?) present, associated with the prostate pores. Ovaries, in XIII, fan-shaped, with several

egg strings ; ovisacs present or absent. Spermathecae 2 pairs, in VIII and IX, diverticulum sessile, simple, bi-or multilobed, usually with numerous sperm chambers in its walls, exceptionally (*kermadecensis*) clavate.

TYPE-SPECIES : *Acanthodrilus ungulatus* Perrier, 1872.

DISTRIBUTION : New Caledonia and the Loyalty Islands. One species, questionably congeneric, on Raoul (Sunday) Island in the Kermadec group.

LIST OF SPECIES

New Caledonia

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|---|---|
| 1. <i>A. canalanus</i> Michaelsen, 1913 | 14. <i>A. natalicius</i> Michaelsen, 1913 |
| 2. <i>A. cavaticus</i> Michaelsen, 1913 | 15. <i>A. oubatcheanus</i> Michaelsen, 1913 |
| 3. <i>A. chabaudi</i> sp. nov. | 16. <i>A. obtusus</i> Perrier, 1872 |
| 4. <i>A. chevalieri</i> sp. nov. | 17. <i>A. paniensis</i> Michaelsen, 1913 |
| 5. <i>A. coneensis</i> Michaelsen, 1913 | 18. <i>A. paripapillatus</i> sp. nov. |
| 6. <i>A. fabresi</i> sp. nov. | 19. <i>A. perrieri</i> Michaelsen, 1913 |
| 7. <i>A. foanus</i> Michaelsen, 1913 | 20. <i>A. rouxi</i> Michaelsen, 1913 |
| 8. <i>A. humboldti</i> Michaelsen, 1913 | 21. <i>A. ruber</i> sp. nov. |
| 9. <i>A. ignambii</i> Michaelsen, 1913 | 22. <i>A. sarasini</i> Michaelsen, 1913 |
| 10. <i>A. koghis</i> sp. nov. | 23. <i>A. silvester</i> Michaelsen, 1913 |
| 11. <i>A. lacuum</i> Michaelsen, 1913 | 24. <i>A. ungulatus</i> Perrier, 1872 |
| 12. <i>A. layardi</i> Beddard, 1886 | 25. <i>A. yateensis</i> Michaelsen, 1913 |
| 13. <i>A. longicystis</i> sp. nov. | |

Loyalty Islands (Mare)

26. *A. mareensis* Michaelsen, 1913

Kermadec Islands (Raoul Island)

27. *A. kermadecensis* Lee, 1953

***Acanthodrilus cavaticus* Michaelsen, 1913**
(Fig. 1, 6A, 7A, 8A, B, 9A, G ; Pl. IV, 30-35)

Acanthodrilus cavaticus Michaelsen, 1913 : 215-217, Pl. VII, fig. 23-26.

Length 46-60 mm (mean of 5 = 51.4 mm ; specimens 4 and 8 are posterior amputees), width (XV) 3.7 (S8), range 2.8-3.7 mm (mean of 7 = 3.5 mm), segments 126-140 (mean of 5 = 136). Form moderately stout, approximately circular in cross section with tendency to dorsoventral depression ; a narrow dorsal groove (canalicula) in the posterior segments

leads to the anus which forms a vertical terminal cleft at the pointed posterior end. Traces of reddish dorsal pigmentation present in alcohol. Peristomium rudimentary, reduced to about one fourth the length of most segments of the forebody; prostomium indicated by a pair of parallel clefts separated by about one third the width of the peristomium; tanylobous. First dorsal pore 12/13 (S3, 8). Glandular protuberance around the ventral setal couple of VII (S2, left only), VIII (S7, left only) or IX (S4, 7, 8, right only; S1, left only); or not externally evident. Dorsal and some or all of the ventral setae present on XVIII; in XII, $aa:ab:bc:cd:dd = 8.4:1.0:8.6:1.1:28.1$; $dd:u = 0.49$ (mean of 7). Nephropores small but distinct, visible throughout the body from V, in cd , nearer or in d , near the anterior borders of their segments. Clitellum annular, weakly developed, in the vicinity of XIV-XVII but limits not determinable. Prostate pores equatorial in XVII and XIX, in mid ab , each with narrow raised lips which constitute a small porophore; an elliptical area around each porophore somewhat elevated; broad seminal grooves with sharply demarcated median margins forming parentheses, the greater length almost straight at about 1.5 ab lateral of b . Prostate pores of XVII 0.9 mm (S8), 0.09 body circumference, apart. The male field depressed (insunk) between the seminal grooves (S4, 5, 7, 8; male field weakly developed in S1-3, 6). Female pores distinctly visible, each minute but with narrow, whitish lips, immediately anterior to the setal arc in ab of XIV (S1-3, 8). Spermathecal pores 2 pairs, at the anterior margins of VIII and IX, small slits with firm white lips, in b lines, preceded by a corresponding embayment of the anterior segment (S1-3, 8); the posterior pair 2.12 mm, 0.25 body circumference, apart (S8). Accessory genital markings in the form of whitish approximately equatorial, circular to elliptical glandular pads: a hemispheroidal pair in XI including setae a in their lateral borders (S2, 4, 6, 7); a small marking in XIV, double (S8) or single (S4, 7); one to the right of the ventral midline in XV (S8); one midventral in XVI (S2, 8) bearing in S2 a double glandular porelike marking; one midventral in XXI (S4, 7, 8); or in XXII (S2, 7) bearing in S2 a double pore-like marking.

Thickest septa 10/11-12/13, strongly thickened. Last hearts in XIII. Supra-oesophageal vessel in IX (and further anteriorly?) - XIII. A large latero-oesophageal vessel on each side, free from the oesophagus, originating below the oesophagus in VIII and passing forward to the buccal region.

Gizzard large, subspheroidal, strongly muscular, in VI, septa 6/7 exceedingly, and 7/8 very thin; preceded by a longer region of the oesophagus which, though thinner walled, is almost as wide. Oesophagus segmentally dilated, without demonstrable specialization; calciferous glands absent. Intestine commencing at 1/2 XVII and reaching full width by XVIII; a fairly deep, thick, unilaminar dorsal typhlosole commencing in XXIV but absent from posterior caudal segments; caeca absent. Nephridia: a pair of very large tufts in V by external segmentation sends a pair of widely tubular, tortuous, bladder-like ducts forwards to enter the body-wall anteriorly in II well dorsal of d . Tufting continuing but diminishing to the posterior end of the oesophagus; bladder in III short and straight, in IV short but entally hooked, in V to the posterior end of the oesophagus variable, slightly tortuous, sinuous or V-shaped; in the intestinal region J-shaped insofar as the ectal limb is much shorter than the ental limb but the ectal limb itself is bent down to the pore. Funnels not demonstrated but the nephridia have postseptal necks. Large, iridescent, free sperm funnel in X and XI; large racemose seminal vesicles in XI and XII. Prostates

basically tubular but strongly flattened tangentially to the body wall ; winding irregularly, the anterior pair for 6-8, the posterior pair for 6 or 7 segments (S1, 8) ; each with slender moderately long sinuous duct the ental half of which is weakly, the ectal half strongly, muscular ; a muscular hemispheroidal swelling corresponding with the external porophore ; the posterior prostates sometimes reduced to approximately half the width of the anterior pair. Penial setae (S1, 2, 6) slender with a curved, obtusely pointed tip ; ectally directed teeth 3-8 μm long, singly or in groups of two to several, densely clothing the ectal region of the shaft and ventrally extending up to the curvature ; dorsally devoid of teeth over, and shortly ental to, the curved region ; length of a mature seta (S6) 1.82 mm, midshaft width (ectal to which it swells locally) 53 μm . *a* and *b* follicles strongly muscular, separate ectally, uniting entally, extending through two segments and attached by a strong ligament to the body wall in the segment next posterior to these. Genital setae (examined in VII, S2, 6) moderately slender, slightly curving (almost straight) to a sharply pointed laterally keeled tip ; the ectal 343 μm , except the tapered tip, with four or more rows of deep scallops (notches) which are staggered so that those of adjacent rows are not in the same transverse line ; the posterior lip of each notch forming a smooth crescent or with one or more small tooth like projections ; the arrangement breaking up into less regularly disposed pits at the ectal limit of sculpturing ; length mature seta 0.74 mm, midshaft width 32 μm . Large palmate bodies smaller than but resembling seminal vesicles, in XIII and XIV may be the ovaries and ovisacs respectively. Spermathecae 2 pairs discharging anteriorly in VIII and IX, the ampulla often deflected into the preceding segment excepting the ectal end of the duct ; each with wide, entally narrowing ovoid ampulla and stout well demarcated cylindrical duct ; a large, bilobed, cushion-like diverticulum sessile dorsally at junction of ampulla and duct, with numerous small sperm masses visible through its walls ; sections through the spermatheca (S7) reveal numerous ovoidal sperm chambers deeply embedded in the thick, irregular epithelium which lines, and much constricts, the lumen of the diverticula ; the anterior spermathecae sometimes appreciably reduced ; length right spermatheca of IX 1.92 mm (H) ; ratio total length : length duct 2.42 ; ratio length : length diverticulum 3.29.

MATERIAL EXAMINED : 165°27' E. 21°24' S. Col des Roussettes, in clay soil on a bank in rainforest, near road, 15 Feb. 1977 — specimens (S) 1,2 and 8 (AH 577-579), specimens 3, 6 and 7 (BJ 1977. 9.2, 3, 8), specimen 4 (QMG 8888), specimen 5 (BMNH 1978.1.7).

REMARKS : The type-locality of *A. cavaticus* is the grotto of Ouaoué near Bourail. The new material, from Col des Roussettes, agrees in important respects, notably the bilobed spermathecal diverticula, the densely crowded minute teeth on the penial setae (the form of these setae corresponding sufficiently for identification), the general form of the genital setae (though scalloping of these is more frequent in the seta illustrated by MICHAELSEN) and the midventral genital marking in XXI. Differences in the accessory genital field are within the range acceptable as intraspecific variation.

***Acanthodrilus chabaudi* sp. nov.¹**

(Fig. 1, 2A, 7B, C, D, 8C, D ; Pl. II 16-18, 19, 20)

Length 50-58 mm (P1, 2) ; width (midclitellar) 3.1 mm (H), range 2.5-3.6 mm (mean of 5 = 3.0 mm). Segments 154-165 (P1, 2). Form moderately slender, circular tending to depressed in cross section. Pigmentless excepting the yellowish clitellum in alcohol. Tanylobous, dorsal tongue narrowing posteriorly, with a transverse furrow behind its mid-length. First dorsal pore 11/12. Epidermal modification around genital setae not recognizable (H, P3) or slight at *ab* of VIII and IX (P1, 2, 4). All setae present in XVIII ; in XII, $aa:ab:bc:cd:dd = 9.0:1.0:9.2:1.1:27.2$; $dd:u = 0.46$ (mean of 5). Nephropores small, visible behind the clitellum in *cd*. Clitellum annular, narrower than adjacent regions though well developed, in XIV-XVII but least developed in XVII in which it is possibly interrupted between the seminal grooves. Prostate pores in *b* lines of XVII and XIX on small but distinct elliptical papillae ; male pores minute, almost as far forward as midway between the setal arc and anterior border of XVIII, lateral of *b* a distance equal to *ab* ; seminal grooves indistinct, laterally convex parentheses, bounded laterally by a thick tumid band, this band continuing to the anterior margin of XVII and posterior margin of XX so as to clearly circumscribe the male field. Prostate pores of XVII (H) 1.39 mm, 0.17 body circumference, apart. Female pores minute, shortly anterior to setae *a* of XIV. Spermathecal pores in *ab*, nearer *b*, at the anterior borders of VIII and IX, on small papillae ; the posterior pair (H) 1.75-1.88 mm (H, P1-3), 0.19-0.2 body circumference, apart. Accessory genital markings : a pair of approximately elliptical pads with a transverse line of cicatrizing in *ab* in each of intersegments 17/18, 18/19 and 19/20 (H, P1-4) and also in 16/17 (P1, 3). Midventral tumescence equatorially in some or all of XVII-XX : an elliptical pad with paired pore-like markings in XVII (H, P3), a similar somewhat more extensive marking in XVIII (P3), and thin cicatrized ridges in XIX (H, P3) and XX (P3) ; or midventral markings absent (P4).

Thickest septa 9/10-12/13, fairly strongly thickened. Last hearts in XIII. Commisural vessels in VII-IX dorsoventral, only, though still valvular, and each giving a branch to the body wall. Supra-oesophageal vessel traceable in VIII-1/2 XIV. A large latero-oesophageal vessel on each side free from the oesophagus seen in VIII and IX.

Gizzard relatively very large, narrowly cylindroid, very strongly muscular, in VI ; septum 6/7 delicate and funnel-shaped but not adherent to it. Oesophagus virtually suppressed in VII by backward extension of the gizzard ; segmentally somewhat dilated in VIII and IX ; in XI-XIII strongly pouched laterally and darkly vascularized, and less so in X and XIV, but extramural calciferous glands absent ; narrow and not especially vascular in XV-XVII (H, P2). Intestine commencing in 1/2 XVII but not reaching full width until XXII. Dorsal typhlosole commencing in XXIII ; consisting of two laminae with free margins directed ventrolaterally so that its form is λ -shaped with negligible vertical limb but absent from posterior caudal segments ; caeca absent. Nephridia : the most

1. Named for Professor A. G. CHABAUD, Laboratoire de Zoologie (Vers), Muséum national d'Histoire naturelle, for his kind encouragement of our work.

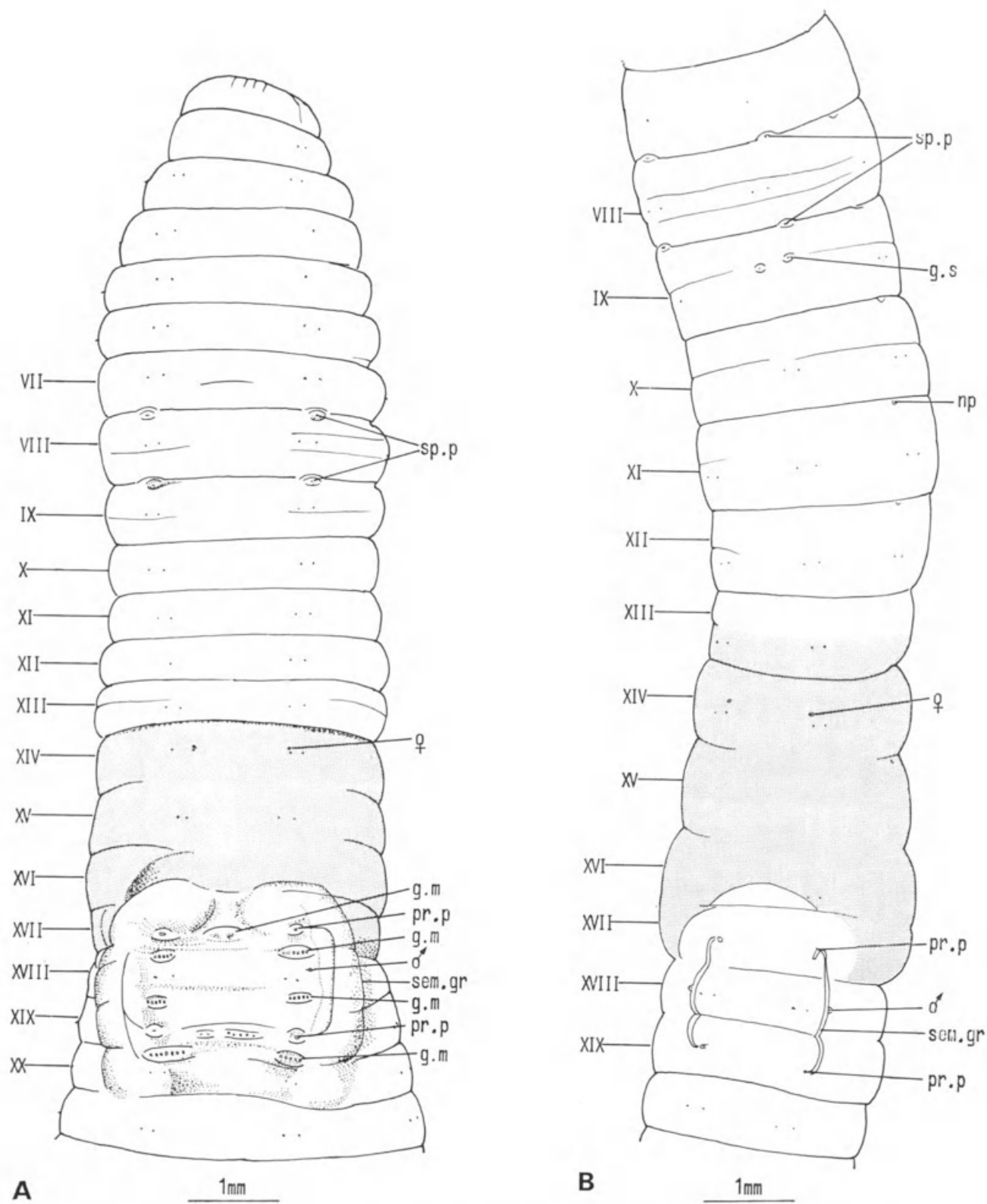


FIG. 2. — Genital fields. A, *Acanthodrilus chabaudi*, holotype, AH 580 ; B, *A. chevalieri*, holotype, AH 582.

anterior is a pair of very large compact tufts with a wide, anterolaterally directed straight, broadly tubular bladder-like duct which discharges at the anterior margin of III near the middorsum. Tufts decrease in size posteriorly but the duct of the nephridium discharging anteriorly in IV is already an elongate bladder with > -shaped lateral bend, discharging anterior to *cd*. Tufting continues to IX; at least some of the tufts display a postseptal neck and probably each, therefore, has a preseptal funnel. Very slender necks are visible on nephridia of the intestinal region but funnels are not demonstrable and are presumably unusually small. By the intestinal region the bladder is J-shaped insofar as the ectal limb is shorter than the ental limb but the ectal limb is itself bent down prior to entering the body wall (H, P2). Caudally bladders each an elongate somewhat tortuous wide tube passing laterally as far as the pore over which it dilates slightly before narrowing to the body wall (P2). Iridescent free sperm funnels in X and XI; moderately large racemose seminal vesicles in IX and XII. Prostates slenderly tubular, very strongly and compactly convoluted, the loops closely contiguous and deformed in cross section by mutual contact; each with long slender strongly muscular duct which does not widen ectally and is mostly concealed by the corresponding *a* and *b* penisetal follicles; glands of XVII extending into XVIII or XIX, those of XIX into XXI; approximately equal in size (H, P2). Penial setae (P2) slender, slightly curved, the ectal tip hollowed out or spatulate; ectally with a moderately dense scattering of short (approx. 3-4 μ m long) ectally directed groups of 2-4, sometimes more, pointed spines; entally spines forming incompletely encircling serrated bands with each spine entally continuous to the next band as a ridge, giving a corrugated appearance; length mature seta 2.1 mm, midshaft width 31 μ m. Genital setae (examined in IX, P2) stout, gently curving to a moderately pointed unsculptured tip; ectally in profile with some eight diagonal rows of three or four shallow scallops, the posterior lip of each scallop jagged with some indistinct teeth; the rows approx. 10 μ m apart; length mature seta 0.72 mm; midshaft width 21 μ m. Ovaries, tufts of numerous strings of moderately large oocytes, and funnels in XIII; ovisacs absent. Spermathecae 2 uniform pairs, discharging anteriorly in VIII and IX though all but the ectal end of the duct is reflected into the preceding segment on the right side (H) or both sides (P2); each with ovoid, entally narrowed, ampulla and well demarcated stout duct; a large cushion-like diverticulum sessile dorsally at junction of ampulla and duct with iridescent sperm masses visible at its ental margins. Length left spermatheca of VIII 1.6 mm, ratio of total length : length duct 2.3; ratio length : length diverticulum 3.2.

MATERIAL EXAMINED : 166°45' E. 22°07' S. Rivière Bleue, in clay soil under a giant Kaori tree (*Agathis*) in rainforest, 17 Feb. 1977 — holotype, paratype 2 (AH 580, 581), paratype 1 (QMG 8889), paratype 3 (BMNH 1978.1.8), paratype 4 (BJ 1977.9.4).

REMARKS : *A. chabaudi* differs from all other species of *Acanthodrilus* in the form and ornamentation of the penial setae. Of the species described in this paper, *A. paripapillatus* and *A. ruber* agree with it in origin of the typhlosome in XXIII and in its bilaminar form, but these differ from it in the more posterior origin of the intestine and in other respects.

***Acanthodrilus chevalieri* sp. nov.¹**

(Fig. 1, 2B, 8E, F, 9D; Pl. V, 41-45)

Length $> 36, 44, 29$ mm, width 2.3-2.8 mm, segments ? (H, P1, 2, posterior amputees). Form slender, approximately circular in cross section though tending to be flattened ventrally, notably at the male field. Traces of reddish dorsal pigmentation in alcohol. Prostomium tanylobous, about $1/3$ the width of the peristomium but dorsal tongue narrowing slightly posteriad, distinctly demarcated. First dorsal pore 12/13 (H, P2). Glandular modification indicative of genital setae visible only in the holotype as two pore-like markings in the vicinity of the left *ab* locus of IX. All setae present on XVIII; in XII, *aa:ab:bc:cd:dd* = 5.5:1.0:6.7:0.9:19.5; *dd:u* = 0.46 (mean of 3). Nephropores visible throughout from III, small pores in *cd* at the anterior margins of their segments; a pair of minute marks anteriorly in II shortly below the prostomium, well dorsal of *d* lines are probably the nephropores. Clitellum annular, well developed and posteriorly slightly wider than adjacent segments, $1/2$ XIII-XVII but interrupted by the male field in XVII and, as a postsetal embayment, in XVI; intersegmental furrows, nephropores and dorsal pores visible though somewhat obscured. Prostate pores in *b* lines (relative to adjacent segments) of XVII and XIX, each indicated by a protruding penial seta in a transverse slit or depression; porophores absent; seminal grooves narrow but distinct, almost straight but deflected medially at intersegments 17/18 and 18/19, lateral of *b* by less than the width of a setal couple except at the prostate pores which they join by curving medially; prostate pores of XVII 0.92 mm (H, P1), 0.17-0.18 body circumference, apart. Female pores shortly anterior to setae *a* of XIV (3 specimens). Spermathecal pores in 7/8 and 8/9, each with crescentic anterior lip, immediately lateral of *b* (3 specimens); the posterior pair 1.1-1.4 mm (H, P1), 0.22 body circumference, apart. Accessory genital markings not developed.

Thickest septa 11/12 and 12/13, fairly strongly thickened. Last hearts in XIII; commissurals in IX (and further anteriorly?) dorsoventral only, though valvular, and, unlike the hearts, each giving a branch to the body wall. Supra-oesophageal vessel traceable in X (and anteriorly?) - XVIII, weak in X-XIII; well developed in XIV-XVIII. A large latero-oesophageal vessel on each side, free from the oesophagus, originating beneath the latter in IX and passing forward to the buccal region, giving branches to the body wall in front of the spermathecal region.

Gizzard large, ellipsoidal, almost cylindroid, strongly muscular, anterior to the very delicate septum 8/9 but segmental location not determinable as septa 6/7 and 7/8 are not certainly demonstrable; posterior end of gizzard in XI relative to external segmentation; unmodified oesophagus anterior to the gizzard approaching the latter in length and suggesting posterior displacement of the gizzard (into VIII). Oesophagus segmentally dilated and darkly vascularized in XII, XIII-XVI, narrow in XVII to $1/2$ XIX. Intestine commencing at $1/2$ XIX but not reaching full width until XXII or XXIII (H, P1), a large dorsal typhlosole which consists of a single straight or slightly tortuous vertical lamina, commencing in XXIV (H), XXV (P1); muscular thickening and caeca absent. Nephridia:

1. Named for Mr. L. CHEVALIER, Conservateur du Musée Néo-Calédonien, Directeur du Centre Lapidaire, whose helpful advice led to our visiting Rivière Bleue.

large paired tufts discharge by straight, anterolaterally directed, tubular bladder-like ducts anteriorly in II (dorsal to *d* ?) and in III-IV (in *cd* lines); tufts discharging anteriorly in V-IX in *cd* have long V-shaped bladders, the median limb of which in segment V is only about one third of the length of the lateral limb, and becomes progressively shorter in VI-IX; the latter condition persisting in the posterior oesophageal region in which some tufting persists; a preseptal funnel demonstrated in postcardiac oesophageal and intestinal regions but nephrostomes possibly present in the anterior segments. In intestinal segments nephridia are simple and the bladders are sharply bent, with the ectal limb shorter than the ental limb but not so short as to give a J-shaped appearance, i.e. they are intermediate between V-shaped and J-shaped vesicles. Large, iridescent, free sperm funnels in X and XI; large racemose seminal vesicles in XI and XII. Prostates tubular, zig-zagged with adjacent bends closely contiguous and deformed in cross section by contact; each gland significantly depressed tangentially to the body wall and consequently almost leaf-like; those of XVII extending into anterior XX (H) or XIX (P1); those of XIX into XXI; each gland with moderately stout, muscular duct which is slightly sinuous but not tortuous and expands very slightly at the pore. Penial setae: *a* and *b* follicles separate though contiguous, not concealing the prostate glands nor all but the median part of the ducts; those of XVII extending into XIX, those of XIX into XX (H) or XXI (P1) (ignoring a terminal tendon-like extension). Penial setae (P1) slender with a curved obtusely pointed to blunt tip; irregularly alternating bands of ectally directed bract-like teeth, approximately 5 μ m long, occur on the ectal tenth, excepting the extreme tip, and further entally join to form irregular serrated bands partly or wholly encircling the shaft at approximately 18 μ m intervals; a shallow ventral gutter extending entally from the tip; length of a mature seta 1.53 mm; midshaft width 34 μ m. Ovaries, tufts of several conjoined strings of large oocytes, and funnels in XIII; ovisacs possibly represented by small (empty) sacs on each side in XIV well above the location of the corresponding funnels; such sacs not present in other segments. Spermathecae 2 pairs discharging anteriorly in VIII and IX, each with a rounded ovoid ampulla and stout downwardly directed duct at right angles to it; a cushion-like diverticulum sessile dorsally at junction of ampulla and duct with sperm masses visible through its walls. Length right spermatheca of IX 1.67 mm; ratio total length : length duct 1.9; ratio length : length diverticulum 4.0.

MATERIAL EXAMINED : 166°45' E. 22°07' S. Rivière Bleue, in clay soil under a giant Kaori tree (*Agathis*) in rainforest, 17 Feb. 1977 — holotype (AH 582), paratype 1 (BMNH 1978.1.9), paratype 2 (BJ 1977.9.5).

REMARKS : *A. chevalieri* resembles only *A. koghisi* in the palisade-like arrangement of long blunt spines partly encircling the penial setae, and, in some setae, in the terminal dimpling of the tip. It further resembles that species in the relatively uncommon location of seminal vesicles in XI and XII. Noteworthy differences from *A. koghisi* are the much smaller body length, the (constant ?) absence of accessory genital markings and the presence of a typhlosole. *A. chabaudi*, also from Rivière Bleue, has similar but less circumferentially extensive spination of the penial setae but differs in having a bilaminar, not unilaminar typhlosole, origin of the intestine in 1/2 XVII, seminal vesicles in XI and XII and in other respects.

Acanthodrilus fabresi sp. nov.¹
(Fig. 1, 3B, 8G, H, 9B; Pl. II, 13-15)

Length 45 mm, width (XV) 1.9 mm, segments 138. Form moderately slender, circular in cross section; posterior end somewhat clubbed. Pigmentless in alcohol. Tanylobous, dorsal tongue broad and parallel-sided, with faint transverse furrow at midlength. First dorsal pore 11/12. Setae *ab* of VIII on slight glandular prominences. All setae present on XVIII; in XII, $aa:ab:bc:cd:dd = 4.0:1.0:6.9:1.1:17.7$; $dd:u = 0.47$. Nephropores visible in the forebody as inconspicuous orifices anteriorly in their segments in *cd* lines but nearer *c*, behind the clitellum nearer *d*, but apparently represented in II by a minute mark shortly behind the lateral limit of the prostomium, well dorsal to *d*. Clitellum not developed. Prostate pores in *ab* slightly median of *a* lines, approximately equatorial, in XVII and XIX, each on an inconspicuous, minute papilla (specimen incompletely mature but, as inseminated, post-sexual); seminal grooves broad parenthetical tracts with narrow groove bounding the median edge of each, very strongly convex laterally. Prostate pores of XVII 0.67 mm (H), 0.1 body circumference, apart. Male pores on minute papillae, in the seminal tracts equatorially in XVIII almost 2 *ab* lateral of *b*. Female pores minute, shortly anteromedian of setae *a* of XIV. Spermathecal pores on small but distinct papillae in *ab* of 7/8 and 8/9, projecting into the anterior segment; the posterior pair 0.87 mm, 0.15 body circumference, apart. Accessory genital markings not developed.

Thickest septa 9/10-11/12, strongly thickened. Last hearts in XIII; commissural vessels in VII-IX dorsoventral only, though still valvular, and each giving a branch to the body wall. Supra-oesophageal vessel traceable in VIII-XVI, weakly developed. A large latero-oesophageal vessel on each side free from the oesophagus running from its connection beneath the oesophagus in VI through anterior segments.

Gizzard moderately large, globose, strongly muscular, in VI, preceded by a wider and equally long portion of unmodified oesophagus; septum 6/7 funnel-shaped but not adherent to it. Oesophagus virtually suppressed in VII; segmentally dilated and with circumferential vascular striae in VIII-XV; less so in XVI; narrow and not especially vascular in XVII-1/2 XIX; calciferous glands absent. Intestine commencing in 1/2 XIX but not reaching full width until XXIII; a well-developed dorsal typhlosole beginning gradually in XXI, single for a few segments and thereafter consisting of 2 parallel contiguous, thick, vertical laminae; caeca absent. Nephridia: a pair of large tufts in V send a tortuous tubular bladder-like duct on each side anterolaterally to discharge anteriorly (in III), the bladder being preceded in II by a smaller bladder discharging well dorsally of *d* which appears to belong to a smaller pair of tufts; nephridia still slightly tufted in VIII with tortuous, tubular bladder. By XII the bladder is wide and V-shaped with longer ectal limb but in XIII and XIV the limbs are approximately equal. In the intestinal region the bladders are wide, almost straight, passing laterally as far as the pore, are composed of 2 irregular dilatations or are less distinctly, or not, subdivided, and turn down to the pore with or without a very small diverticulum-like projection laterally; i.e. bladders are not J-shaped. Preseptal funnels

1. Named for Dr. Gérard FABRES of ORSTOM, Noumea, who greatly facilitated collecting in New Caledonia.

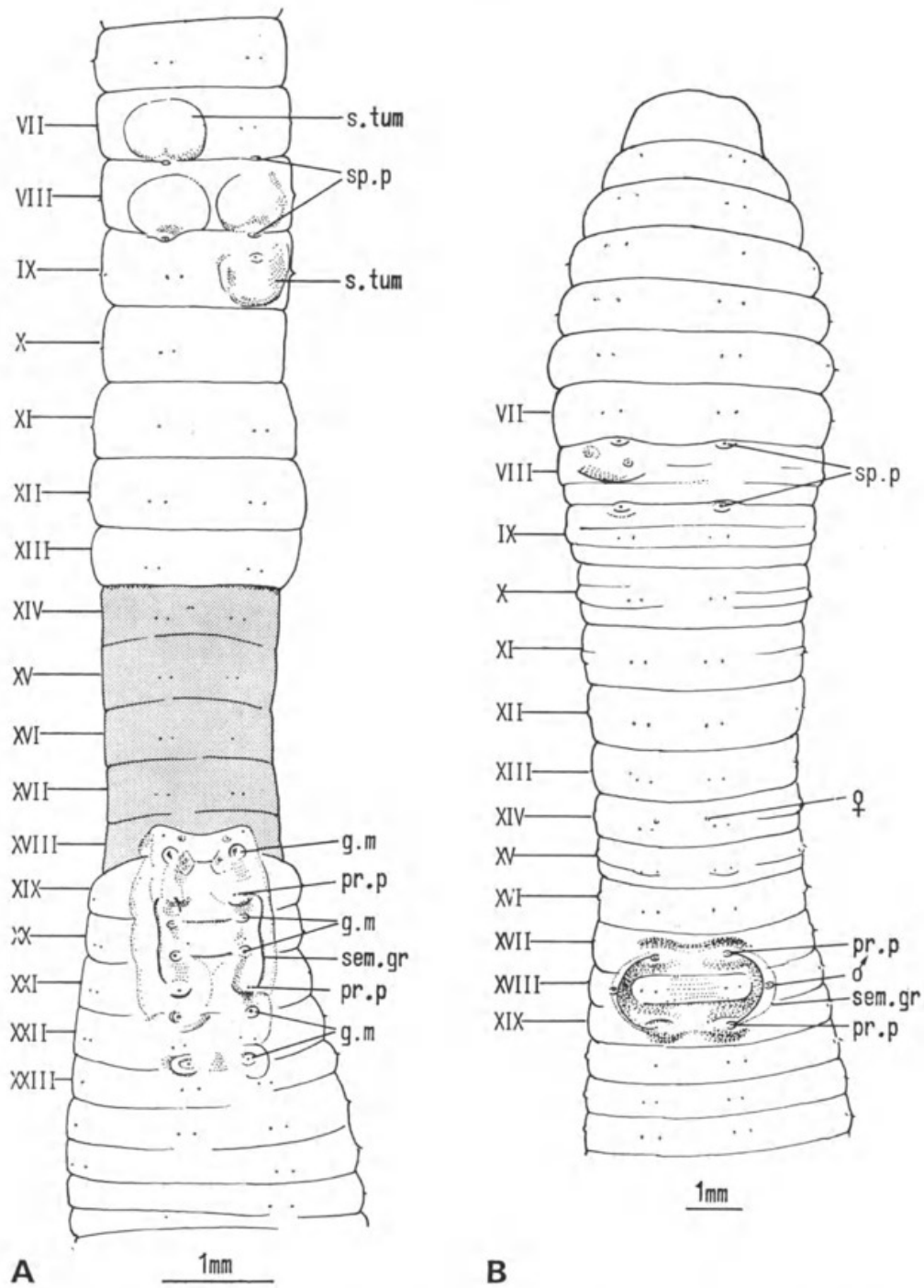


FIG. 3. — Genital fields. A, *Acanthodrilus paripapillatus*, holotype, AH 587; B, *A. fabresi*, holotype, AH 583.

demonstrated for intestinal nephridia. Large iridescent sperm funnels in X and XI; sperm masses apparently united beneath the gut in a delicate membrane which is continuous with the funnels, in each segment; small racemose seminal vesicles in IX and XII. Prostates moderately long, slenderly tubular, convoluted; approximately uniform; adpressed loops not greatly deformed by contact; those of XVII extending into XXI, those of XIX into XXII; each with fairly long tortuous muscular duct which ectally widens slightly;

duct (but not the gland) almost concealed by two entally conjoined approximately equal penisetal follicles; the follicles of XVII and XIX extending into XVIII and XX respectively, each with a ligament to the body wall. Penial seta (H) slightly sinuous ectally the tip hollowed out or grooved and strongly spatulate with strongly rolled, roughly parallel sides; the groove open at the blunt ectal extremity, and with incomplete encircling serrations at approx. 5 μ m intervals; further entally serrations breaking up into individual ectally directed sharply pointed teeth (2.5 μ m long) which densely clothe the shaft. Ornamentation on the shaft ceases 200 μ m from the tip, leaving the shaft further entally devoid of teeth. Length mature seta 1.1 mm, midshaft width 18 μ m. Genital setae in VIII only; slender, gently curving to a pointed, unsculptured tip; the ectal 470 μ m in profile with some 2-3 rows of scallops (notches) which are staggered so that those of adjacent rows are not in the same transverse line. Entally, the posterior lip of each notch forming a smooth or slightly irregular crescent; the rows approx. 60-70 μ m apart. Ectally the scallops are gradually replaced by less regularly disposed partially encircling serrations at 18 μ m intervals. Length mature seta 0.8 mm; midshaft width 33 μ m. Ovaries, several strings of large oocytes, and funnels in XIII; small sacs in XIV possibly ovisacs. Spermathecae 2 approximately uniform pairs discharging anteriorly in VIII and IX but the ampullae and much of the duct reflexed into the preceding segment; each with ovoid-sacciform ampulla and moderately slender duct; the whole approximately retort-shaped; a wide cushion-like diverticulum sessile at junction of ampulla and duct with many iridescent sperm chambers visible through its walls. Length right spermatheca of IX 1.46 mm, ratio of total length : length duct 1.75; ratio length : length diverticulum 3.5

MATERIAL EXAMINED : 165°27' E. 21°24' S. Col des Roussettes, in gully in dense rainforest near road, 12 Feb. 1977 — Holotype (AH 583).

REMARKS : *A. fabresi* differs from all species of *Acanthodrilus* excepting *A. paniensis* in the inrolled form of the ectal region of the penial setae but differs from *paniensis* in having the more usual pointed, scalloped genital setae, in origin of the typhlosome in XXI (not XXVII) and its double lamina and in other respects.

***Acanthodrilus koghisi* sp. nov.**

(Fig. 1, 4B, 7G, 8P; Pl. V, 36-40)

Length 255-300 mm (P1-3), width (midclitellar) 5.3 (H) range 4.6-6.9 (mean of four = 5.5 mm), segments 382, 368 (P1, 3). Form slender, circular in cross section, but ventrally flattened in the vicinity of the male genital field. Pigmentless, tanylobous, dorsal tongue broad, parallel sided. First dorsal pore 11/12 (imperforate?), 12/13 perforate. Large paired genital seta tumescences, from which in life long stout genital setae were seen to conspicuously protrude, centered on *ab* of IX-XI (P1), XIII (H). All setae present in XVIII; in XII, *aa:ab:bc:cd:dd* = 9.3:1.0:9.2:0.7:24.4; *dd:u* = 0.44 (mean of 4). Nephropores small, in *cd* throughout, excepting those anteriorly in II, which are well dorsal of *d* lines. Clitellum well developed but limits uncertain, including 1/2 XII-XVII (XVIII?) (P1), annular but possibly interrupted ventrally in XVII between the seminal grooves. Prostate pores in

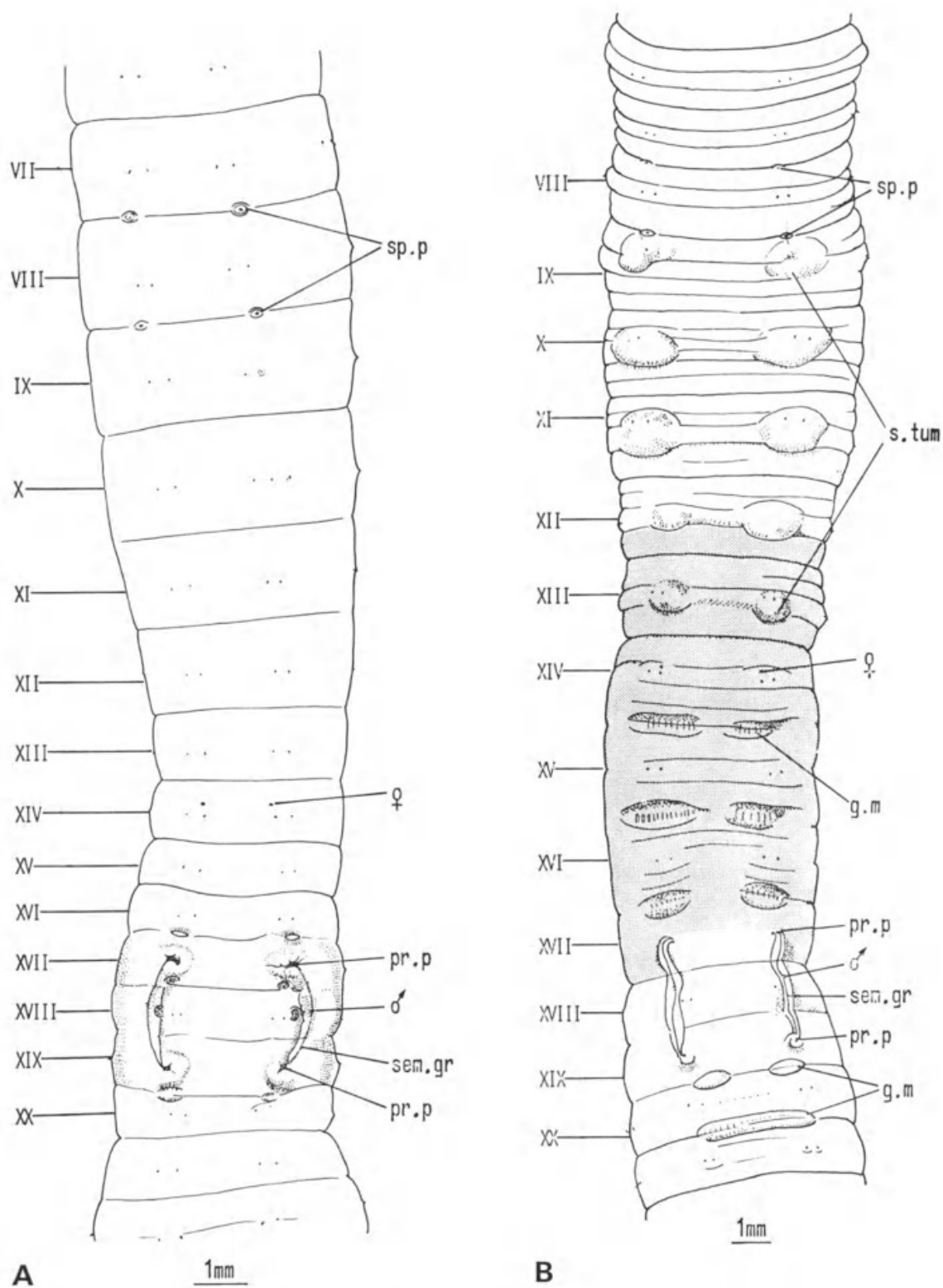


FIG. 4. — Genital fields. A, *Acanthodrilus paniensis*, specimen 1, AH 586; B, *A. koghii*, holotype, AH 584.

ab of XVII and XIX on small hemispheroidal porophores ; male pores minute, midway between the setal arc and anterior border of XVIII, slightly lateral of *b* lines ; seminal grooves thin and indistinct but with conspicuous margins which form slender strongly raised longitudinal bands which connect the outer edges of the prostate porophores with the male pores ; these bands therefore very slightly convex laterally though indented medially at intersegments 17/18 and 18/19 (H). Prostate pores of XVII (H) 2.5 mm, 0.20 body circumference, apart. Female pores in *a* lines, nearer the setal arc than the anterior margin of XIV. Spermathecal pores in *ab*, in 7/8 and 8/9, on small papillae ; the posterior pair (H) 3.5 mm, 0.16 body circumference, apart. Accessory genital markings : apart from the genital seta tumescences, there are 3 pairs of transversely elliptical depressions, of which the middle pair is medianly conjoined, in and extending beyond *ab* of 14/15, 15/16, and 16/17 ; their surfaces with longitudinal striations or punctae indicative of orifices of glands. A pair of transversely elongate pads in 19/20, and a similar conjoined pad in 20/21, with lateral margins in *b* lines.

Thickest septa 10/11-13/14, very strongly thickened. Last hearts in XIII. Commissural vessels in VII-IX dorsoventral only and each giving a branch to the body wall. Supra-oesophageal vessel in VIII-XV. A large latero-oesophageal vessel on each side free from the oesophagus but median to the dorsoventral commissurals in IX where it originates from the lateral wall of the oesophagus ; continuing to the pharynx.

Gizzard very large, subspheroidal in VI ; septum 6/7 very delicate and ensheathing it. Oesophagus virtually suppressed in VII and VIII by backward extension of the gizzard ; segmentally dilated in IX, and also darkly vascularised in X-XVI, narrower, and little vascularised in XVII and XVIII. Intestine commencing with abrupt expansion in XIX ; caeca and typhlosole absent. Nephridia commencing in II forming a pair of large tufts with very numerous twisted loops, the long tubular, slightly fusiform bladder running antero-laterally to enter the body wall immediately behind intersegment 1/2 well above *d* line ; nephridia in III-IX also tufted, but smaller though still large, with slenderly fusiform bladders discharging anteriorly in their respective segments in *cd* ; at least some of them displaying a postseptal neck and probably each with a preseptal funnel ; still strongly tufted to XVII ; transitional to non-tufted in XVIII and XIX after which they are simple ; large single nephrostomal funnels demonstrated in the intestinal region. Elongate iridescent free sperm funnels in X and XI ; large racemose seminal vesicles in XI and XII. Prostates slenderly tubular, and very strongly convoluted, the loops closely contiguous, and modifying the cross section of adjacent loops but not fused with them ; the entire gland dorso-ventrally depressed to form an irregular lobed mass ; each with a slender, once-coiled muscular duct dilating appreciably near the body wall and entering a small muscular internal swelling (bursa) corresponding with the prostate pore ; glands of XVII extending into XX ; those of XIX into XXII ; the anterior pair a little if at all larger than the posterior pair ; each duct overlain by a stout penisetal follicle which entally terminates in the succeeding segment. Double vasa deferentia traced to each male pore ; slightly but not significantly widened near the pore. Penial seta slender with a strongly curved ectal tip ; excepting the smooth apical 140 μ m, ectally with pointed apically directed teeth, approx. 3 μ m long, forming bands at approx. 6-10 μ m intervals longitudinally and apically breaking up into short staggered or alternating sections while entally tending to form complete rings ; length of mature seta 2.0 mm, midshaft width 32 μ m. Genital setae (examined in XI and XII,

P1) moderately stout, virtually straight, tapering to a sharply pointed tip by stronger curvature of one, the "upper" surface; the ectal region, excepting the 45 μ m tip, with diagonally arranged jagged scallops which ectally become incomplete encircling serrations; the scallops forming 3 or 4 longitudinal rows in profile, those of each row 10-15 μ m apart; length 2 mature setae 0.83 and 0.94 mm, midshaft width 21 μ m. Ovaries, tufts of numerous strings of small oocytes, and funnels in XIII; ovisacs absent. Spermathecae 2 uniform pairs discharging anteriorly into VIII and IX, each with firm subspherical ampulla and well demarcated moderately slender duct, the ampullae reflected into VII and VIII; a small spherical inseminated diverticulum with several internal sperm masses sessile on the ental end of the duct. Length right spermatheca of VIII (H) 2.3 mm; ratio of total length : length duct 1.8; ratio length : length diverticulum 4.6.

MATERIAL EXAMINED : 166°33' E. 22°10' S. Mt. Koghis, 11 km. north of Noumea, in clay soil in rainforest at approximately 1000 metres, 16 Feb. 1977 — holotype (AH 584), paratype 1 and 3 (QMG 8886-8887), paratype 2 (BMNH 1978.1.6), paratype 4 (BJ 1977.9.1).

REMARKS : The regular, palisade-like circlets of spines on the penial setae of *A. koghis* distinguish this large species from all others of the genus though the condition is approached by *A. chevalieri*. The latter species differs notably from it, as do all other species described in this paper, in possessing a typhlosole. The configuration of the accessory genital markings in *A. koghis* is also distinctive.

***Acanthodrilus longicystis* sp. nov.**
(Fig. 1, 5B, 8K, L, 9E; Pl. I, 8-9, 10-12)

Length 70 mm, width (XV) 3.2 mm, segments 160. Form moderately slender, circular in cross section; posterior end clubbed. Pigmentless but clitellar region faintly yellow. Tanylobous, dorsal tongue broad and parallel-sided. First dorsal pore 12/13. Setae *a* and *b* of VIII on slight glandular prominences. All setae present on XVIII; in XII, *aa:ab:bc:cd:dd* = 5.4:1.0:8.2:0.8:20.5; *dd:u* = 0.45. Nephropores visible in the forebody as conspicuous white points anteriorly in their segments in *d* lines but represented in segment II by a minute pore shortly behind the lateral limit of the prostomium, well dorsal to *d*. Clitellum scarcely developed, limits indeterminable. Prostate pores slightly median of *a* lines, approximately equatorial, in XVII and XIX, each with a conspicuous white margin on a low mound which almost fills the segment longitudinally; seminal grooves narrow but very distinct, very strongly convex laterally. Prostate pores of XVII 0.96 mm, 0.09 body circumference, apart. Male pores on minute papillae, in the seminal grooves in the anterior half of XVIII approximately a distance *ab* lateral of *b*. Female pores minute, midway between the setal arc and anterior margin of XIV, in *ab* nearer *b*. Spermathecal pores on small but distinct papillae in *a* or *ab* of 7/8 and 8/9; the posterior pair 1.5 mm. 0.15 body circumference, apart. Accessory genital markings not developed.

Thickest septa 10/11-12/13, strongly thickened. Dorsal blood vessel segmentally doubled, though intersegmentally single, on the intestine; single anteriorly to this and continuous onto the pharynx; last hearts in XIII; commissural vessels in VII (and further

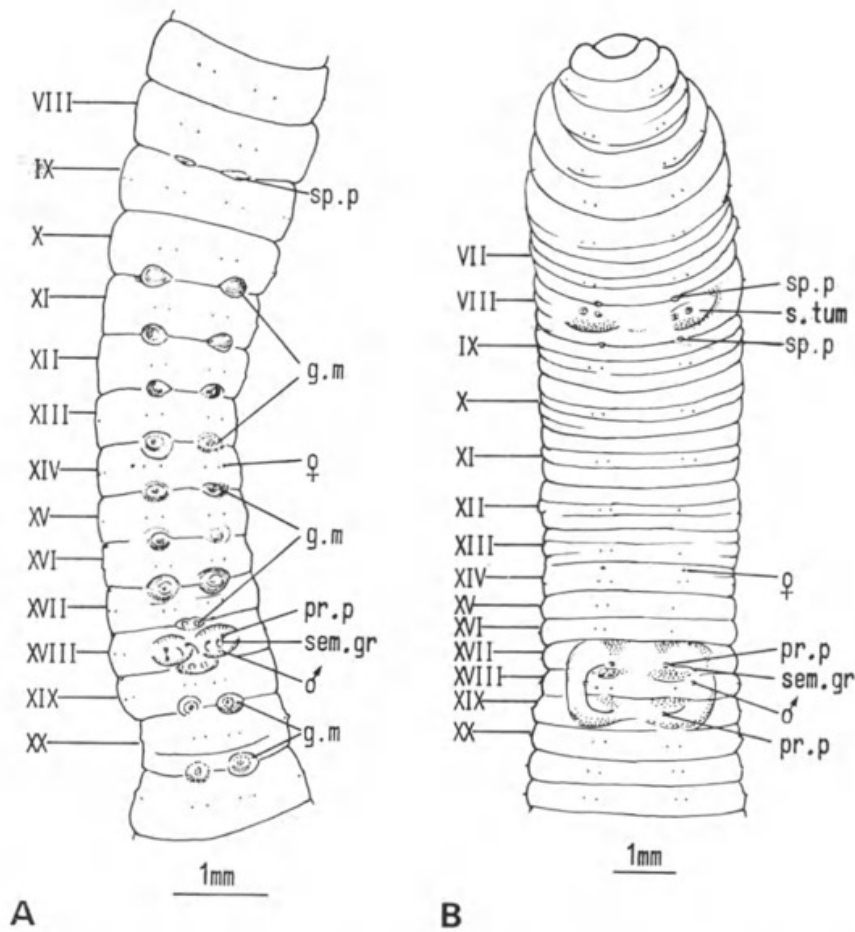


FIG. 5. — Genital fields. A, *Eudiplostrema sarasini*, AH 589 ; B, *A. longicystis*, holotype, AH 585.

anteriorly ?) - IX dorsoventral only, though still valvular, and each giving a branch to the body wall. Supra-oesophageal vessel traceable in X (and further anteriorly)-XVI, well developed. A large latero-oesophageal vessel on each side free from the oesophagus running from its connection beneath oesophagus in VIII through anterior segments.

Gizzard very large, globose, strongly muscular ; anterior to septum 7/8 but whether in VI or VII indeterminable. Oesophagus dilated in VIII-X ; more slender and not as evidently vascular in XI-XVII ; calciferous glands absent. Intestine commencing in XVIII but not widening until XXIII ; the portion in XVIII-XXIII dark in colour, spiral, and forming a distinct region of the alimentary canal ; a well developed bifid laminar dorsal typhlosole commencing in XXX, the two laminae anteriorly with their free edges laterally directed so that the form is \perp -shaped with negligible vertical limb ; caudally λ -shaped ; caeca absent. Nephridia : a pair of very large compact tufts with innumerable spiral loops, in IV relative to external segmentation ; the avesciculate duct of each tuft traced to the anterodorsal region of segment II. Very small tufts almost sessile on the body wall in III and IV ; tufts of V-VII fairly large with tubular, bladderlike ducts which in V are straight, in VI are entally bent and in VII are $>$ -shaped with bend lateral ; tufting decreasing posteriorly and nephridia of IX almost simple, retaining the $>$ -shaped bladder. In the intestinal region the nephridial bladders are J-shaped with the bend lateral and the shorter, ectal,

limb anterior but this ectal limb may be tortuous ; long-stalked preseptal funnel demonstrated in the intestinal region. Small iridescent sperm funnels in X and XI ; small racemose seminal vesicles in IX and XII. Prostates long, slenderly tubular, convoluted ; approximately uniform ; adpressed loops not greatly deformed by contact ; those of XVII extending into XXVII, those of XIX into XXVIII ; each with fairly short, tortuous, muscular duct which ectally widens gradually but strongly ; gland and duct almost concealed by two penisetal follicles of which the median is very long, extending shortly posterior to the corresponding prostate, but the lateral is less than half as long. Penial seta filiform and sinuous, the ectal tip moderately or strongly hooked and spatulate, occasionally with a ventral broad, shallow gutter extending entally from the tip ; the ectal region ornamented as far apically as the curvature of the tip. Ectally with a scattering of single, anteriorly directed, sharply pointed teeth (3-5 μ m) incompletely covering the shaft, usually leaving a bald strip through part of the ornamented region. Further entally teeth adpressed to the shaft. Length mature seta 7.0 mm, midshaft width 19 μ m. Genital seta slender, gently curving to a pointed, unsculptured tip. The ectal 560 μ m, excepting the tapered tip, with four or more longitudinal rows of deep scallops (notches) which are staggered so that those of adjacent rows are not in the same transverse line ; those of each row 40 μ m apart. The posterior lip of each notch forming a smooth, or slightly irregular crescent ; the arrangement breaking up into less regularly disposed pits at the ectal limit of sculpturing. Length mature seta 1.6 mm, midshaft width 20 μ m. Ovaries and funnels not detectable (protandry ?). Spermathecae 2 pairs (the anterior pair slightly the smaller ?), discharging anteriorly in VIII and IX ; each with ovoid, entally narrowed, ampulla and well demarcated, unusually long and slender, sinuous duct ; a large reniform diverticulum sessile near one end at the junction of ampulla and duct, with iridescent sperm masses in a row along its outer margin. Length left spermatheca of IX 3.04 mm, ratio of total length : length duct 1.62 ; ratio length : length diverticulum 4.06.

MATERIAL EXAMINED : 165°49' E. 21°34' S., below Col d'Amieu towards La Foa, in roadside track embankment, in clay soil, 11 Feb. 1977 — holotype (AH 585).

REMARKS : *A. longicystis* resembles *A. ignambii*, *A. layardi* and especially *A. natalicius* and *A. rouxi* Michaelsen, 1913, in the tortuous spermathecal duct. *A. rouxi* differs in location of the prostate pores in XIX and XXI and in the form of the penial setae. *A. layardi* differs notably in its much greater length and the presence of scattered teeth and absence of scalloped sculpturing on the genital setae. *A. ignambii* is again much longer (200 mm), and the penial setae are not ectally expanded. *A. natalicius* is closest to *A. longicystis*, especially in the form of the spermathecae and penial setae (though these are more densely spinose in the former) but differs (significantly ?) in location of the prostate pores in XVIII and XX and possession of accessory genital markings. Further comparison with *A. natalicius* is restricted by omissions in the description of the latter.

***Acanthodrilus paniensis* Michaelsen, 1913**
(Fig. 4A, 7K, 8I, J, 9I; Pl. III, 21-24)

Acanthodrilus paniensis Michaelsen, 1913 : 205-207, Pl. VII, fig. 14-16, 48.

Length 150 mm, width 4.2 mm, segments 176. Form slender; approximately circular in cross section but some flattening between setal couples and caudal extremity dorso-ventrally depressed, tapered, and with distinct dorsal canalicula leading to the vertical, slitlike anus. Pigmented reddish brown dorsally in life. Peristomium equalling segment III in length; prostomium approximately one fourth the width of the peristomium; tanylobous, slightly tapering to a transverse groove shortly behind midlength, dorsal tongue parallel-sided. Segments III and IV forming a helicometamere. First dorsal pore 13/14. Slight glandular modification around the right ventral setal couple of VIII. All setae present in XVIII; in XII, $aa:ab:bc:cd:dd = 4.6:1.0:6.8:0.7:18.4$; $dd:u = 0.46$. Nephropores clearly visible minute, apparently sphinctered apertures demonstrated in V posteriorly, in *cd*, near the anterior border of their segments. Clitellum not recognizable. Prostate pores equatorial in XVII and XIX in or slightly lateral of *b*, gaping apertures with tumid margins constituting porophores; seminal grooves, connecting the pores, broad tracts, moderately convex laterally; male pores a minute transverse slit shortly equatorial in XVIII, in each tract near its lateral border; the posterior prostate pores 2.3 mm, 0.2 body circumference, apart. Female pores minute, slightly less than halfway from the setal arc to the anterior border of XIV, in *a*. Spermathecal pores 2 pairs, distinct small apertures on firm elliptical papillae, 7/8 and 8/9, in *b* lines; the posterior pair 2.2 mm, 0.19 body circumference, apart. Accessory genital markings: a pair of circular pads equatorially in XVIII lateral to *b* and median to the seminal grooves; a pair of eyelike markings in 16/17 in *b* and suggestions of these in 17/18 and 19/20.

Thickest septa 12/13 and 13/14, strongly thickened. Last hearts in XIII. Commisurals in (VII?) VIII and IX dorsoventral only though still valvular and, unlike the hearts, each giving a branch to the body wall. Supra-oesophageal vessel traceable in IX-XIII, well developed. Paired latero-oesophageal vessels originating beneath the oesophagus in VIII, passing forwards to the buccal region.

Gizzard large, depressed barrel-shaped in VII (?), immediately anterior to the commisurals of VII but septum 7/8 not certainly recognizable behind it; 8/9 complete though delicate; preceded by a less though still strongly muscular shorter proventriculus resembling a weak gizzard. Oesophagus dilated and vascularized in X-XVI; more slender in XVII and XVIII. Intestine commencing with abrupt expansion in posterior XVIII but not reaching full width until XXV; a pair of lateral anterolaterally directed shortly conical caeca in XXVI; a deep laminar dorsal typhlosole commencing gradually in XXVII; absent from the last 30 caudal segments. Nephridia: very large tufts in III with V-shaped ducts, the longer, ectal limb of which discharges dorsolaterally at the anterior border of II; smaller tufts in IV with ectal limb very long, discharging anteriorly in III in *cd*; similar tufts in but restricted to each of IV and V; tufts in VI-X with the two limbs almost equal in length contiguous throughout most of their lengths. Nephridia in the remainder of the oesophageal region tufted to the extent of several loops and V-shaped with abrupt

bend posterolateral. Preseptal funnels demonstrated for some anterior tufts and in the intestinal region. Intestinal nephridia simple with J-shaped vesicles, the longer, ental limb passing straight laterally, the shorter limb swollen before turning down to enter the body wall anterior to the dorsal setal couple, the two limbs at the bend discernible but fused. Free, moderately large, iridescent sperm funnels in X and XI; large racemose seminal vesicles in IX and XII. Prostates tubular, somewhat depressed, partly almost straight, partly closely winding, those of XVII extending into XXI, those of XIX into XXII; each with a very muscular, ectally strongly widening duct which has one laterally directed hair-pin bend; the duct and much of the gland concealed by a single large penisetal follicle, extending into XIX and XXI respectively from XVII and XIX. Penial seta slender, gently curving to a rounded ectal tip. The ectal extremity strongly inrolled for a short distance, with a shallow ventral gutter extending as far as a slight transverse annulation 340 μ m from the tip. Ectal to the annulation, individual, anteriorly directed, sharply pointed teeth irregularly clothe the seta to a point 34 μ m from the apex. Shaft ental to the annulation devoid of teeth. Length mature seta 6.8 mm, midshaft width 42 μ m. A long follicle on each side in VIII projects into IX in which it is connected to the body wall by a ligament and a large tongue-shaped gland on each side of the follicle projects far into the coelom of VIII; but setae not appreciably modified as genital setae. Setae of the ventral couples of VIII and IX are periodically notched in profile and have transverse partly encircling serrations but each is sigmoid and has a node. A similar ornamentation and form is seen in ventral somatic setae sampled from XIV and from postclitellar segments; length of a ventral seta of VIII is 0.81 mm (cf. 2.5 mm, MICHAELSEN), compared with 0.63 for a postclitellar seta. Ovaries not seen; funnels posteriorly in XIII; ovisacs absent. Spermathecae (S1) 2 pairs discharging anteriorly in VIII and IX, each with an ovoid ampulla preceded by an almost equally large, subspherical diverticulum, the latter continuous ventrally as a moderately stout duct and apparently communicating with the ampulla; length right spermatheca of VIII (apex of ampulla to pore) 2.1 mm, ratio total length : length duct 2.1; ratio length : length diverticulum 2.6.

MATERIAL EXAMINED : 164°47' E. 20°34' S. Mt. Panié, in dark moist soil in rainforest at approximately 1500 metres, (S1) and 500 metres (S2), 14 Feb. 1977 — specimen 1 (AH 586), specimen 2 (BJ 1977.9.6, immature specimen).

REMARKS : The new material is identified with *A. paniensis* with some hesitation. The above description agrees well with that of MICHAELSEN with the notable exceptions that in the new material accessory genital markings are present, the spermathecal duct is thicker, the genital (?) setae are not terminally flattened, testis-sacs are not demonstrated and seminal vesicles are in IX and XII (not in X and XII). However, MICHAELSEN noted that on one side or the other genital setae were not developed and was uncertain of the position of the anterior seminal vesicles. Very noteworthy similarities with MICHAELSEN's description are the presence of prostate like setal glands in VIII, the form and ornamentation of the setae in this segment, the inrolled terminal region of the penial setae and the large spermathecal diverticula forming a continuation, though here more distinct, of the ampulla.

The new specimen writhed vigorously and was saltatory when exposed.

***Acanthodrilus paripapillatus* sp. nov.**
(Fig. 1, 3A, 8Q, 9H; Pl. I, 1-4)

Length 46 mm, width (midclitellar) 1.5 mm, segments 112. Form slender, circular in cross section in the forebody but in the posterior half of the hind body dorsoventrally depressed and keel-like in *aa* and *cd*. Traces of dorsal pigmentation persisting in alcohol. Prostomium small and narrow, parallel-sided, tanylobous, lateral margins deeply incising the peristomium. First dorsal pore 9/10 but first perforate 11/12. Conspicuous glandular prominences present around the *a* and *b* genital setae of VII (left only), VIII (paired) and IX (right only). All setae present on the segment of the male pores (XX); in XII, *aa:ab:bc.cd:dd* = 5.3:1.0:6.1:0.8:19.4; *dd:u* = 0.48. Nephropores visible in the forebody from III, small pores in *cd* near the anterior borders of their segments. Clitellum annular, very strongly developed but narrower than adjacent regions; in XIV-XVIII but interrupted ventrally in XVIII by the male field; dorsal pores occluded; nephropores visible; intersegmental furrows indistinct. Prostate pores in *ab* of XIX and XXI on small equatorial papillae; male pores not externally visible; seminal grooves very narrow but distinct, almost straight, slightly lateral of *b* lines except at the prostate porophores where they curve medianly towards the pores. Anterior prostate pores 0.5 mm, 0.09 body circumference, apart. Female pores indicated by a pair of indistinct dark areas anterior to and almost imperceptibly median of setae *a* of XIV. Spermathecal pores in 7/8 and 8/9 in *b*, small slits with narrow whitish rims; the posterior pair 0.8 mm, 0.14 body circumference, apart. Accessory genital markings: a pair of eye-like markings in each of the 5 intersegments 18/19-22/23, in *ab*, the anterior four pairs contained within a tumid field which is bounded laterally by ridges which form the lateral borders of the seminal grooves; the markings in 22/23 separate and each divisible into a porelike centre and a wide elliptical border, the anterior markings having the centre but lacking the distinct border.

Thickest septa 11/12 and 12/13, fairly strongly thickened. Last hearts in XIII. Commissural vessels in VIII and IX dorsoventral only, though still valvular, and, unlike the hearts, each giving a branch to the body wall. Supra-oesophageal vessel traceable in XI (and further anteriorly?) to XVIII. A large latero-oesophageal vessel on each side free from the oesophagus originating beneath the oesophagus in IX and passing through anterior segments.

Gizzard very large, elongate cylindroid, strongly muscular, anterior to septum 7/8 which is attenuated, but a delicate film on its surface probably represents septum 6/7, placing the gizzard in VI; an equally wide but shorter, collapsible proventriculus preceding it. Oesophagus virtually suppressed by backward extension of the gizzard in VII-IX, fairly wide and segmentally slightly dilated, and vascularized, in $X - \frac{1}{2}$ XIX; calciferous glands absent.

Intestine commencing at $\frac{1}{2}$ XIX but not reaching full width until XXIII in which the large dorsal typhlosole begins; the latter consisting of two laminae, with free edges directed laterally, lying in the horizontal plane so that the form is J-shaped; the vertical limb negligible anteriorly but moderately developed caudally; caeca absent. Nephridia: a pair

of large tufts in IV relative to external segmentation discharges via an elongate, bladder-like duct on each side anteriorly in II far dorsally of *d* lines, each bladder entally dilated and convoluted but its greater, ectal, length passing straight anteriorly. Smaller tufts in III-VI with V-shaped bladders with longer ectal limb; nephridia in VII-IX almost simple, with progressively longer ectal limb; small preseptal funnel demonstrated for VIII. In the intestinal region the nephridia are simple with J-shaped bladders consisting of a wide, long, dorsoposterior ental limb and shorter, narrower, anteroventral ectal limb which is itself shortly recurved at the pore; a small preseptal funnel is demonstrable with difficulty on the slender neck. Large, iridescent, free sperm funnels in X and XI; small seminal vesicles, minutely loculate, on the anterior septum of XII but none recognizable in IX the posterior septum of which is very delicate. Prostates slenderly tubular, zig-zagged with adjacent bends closely contiguous and deformed in cross section by contact; the anterior prostates significantly larger than the posterior pair, the two pairs extending into XXVI and XXV respectively, each with long, slender, tortuous weakly muscular duct which entally enters a hemispheroidal muscular bursa corresponding with the external porophore. Double vas deferens iridescent and clearly visible throughout its length on each side, entering the body wall, approximately midway between the prostates, in XX, without terminal enlargement. Penial setae: *a* and *b* setae in a single follicle on each side in each of XIX and XXI, concealing the prostate ducts and overlying the glands and extending into XXV. Penial seta slender, gently curving to an obtuse, ectal tip which is sometimes transversely concave ventrally; the ectal extremity usually devoid of ornamentation. Further entally with anteriorly directed, sharply pointed, individual (occasionally conjoined) teeth (1-6 μ m long) densely clothing the tip, with a lateral band lacking teeth in dorsal and ventral view extending entally. Still further entally, teeth sparsely scattered over the entire shaft (occasionally forming 2 regular longitudinal rows viewed ventrally), or grouped to form incomplete, sometimes extensive encircling serrations; length mature seta 2.5 mm, midshaft width 15 μ m. Genital seta slender, gently curving to a pointed, unsculptured tip; ectally with deep scallops (more closely spaced ectally) forming 2-3 indefinite longitudinal rows in profile; the posterior lip of each scallop forming a smooth crescent, or jagged with some indistinct teeth; further entally devoid of sculpturing; length mature seta 0.7 mm, midshaft width 16 μ m. Ovaries, small tufts of a few, mainly conjoined strings of large oocytes, and funnels in XIII; ovisacs probably represented by a small sac on each side in XIV considerably above the location of the corresponding funnel. Spermathecae 2 pairs discharging anteriorly in VIII and IX, each with a dorsoventrally depressed, subspherical ampulla and well demarcated, fairly stout, gently tapering duct; an indistinctly differentiated, cushionlike diverticulum with iridescent sperm clusters, sessile dorsally at junction of duct and ampulla and almost as wide as the duct; the posterior pair considerably the larger. Length right spermatheca of IX 1.26 mm, ratio of total length : length duct 1.88; ratio length : length diverticulum 3.5.

MATERIAL EXAMINED : 164°47' E. 20°34' S. Mt. Panié, in dark moist soil in rainforest at approximately 500 metres, 14 Feb. 1977 — holotype (AH 587).

REMARKS : *A. paripapillatus* approaches *A. coneensis* and *A. rouxi* Michaelsen, 1913, in the form of the penial and genital setae but differs from these in the shorter spermathecal

duct and the presence of postclitellar genital markings. It resembles only *A. rouxi* and *A. obtusus* Perrier, 1872, in location of prostate pores in segments XIX and XXI. *A. obtusus* is a *species inquirendum* (MICHAELSEN, 1913) but differs strikingly from *A. paripapillatus* in its length of 700 mm.

***Acanthodrilus ruber* sp. nov.**

(Fig. 1, 6B, 7E, 8N, O ; Pl. III, 25-27, IV, 28-29)

Length 180 mm, width (midclitellar) 10.6 mm, segments 180. Form moderately stout, ellipsoidal, dorsoventrally depressed in cross section. Vivid reddish plum-coloured in life. Prostomium tanylobous, large, about one third the width of the peristomium, tapering posteriad, dorsal tongue with weak transverse furrow behind midlength. Dorsal pores commencing behind the clitellum (demonstrable with certainty only by expressing alcohol from them when specimen placed in water). Glandular protuberance around each ventral

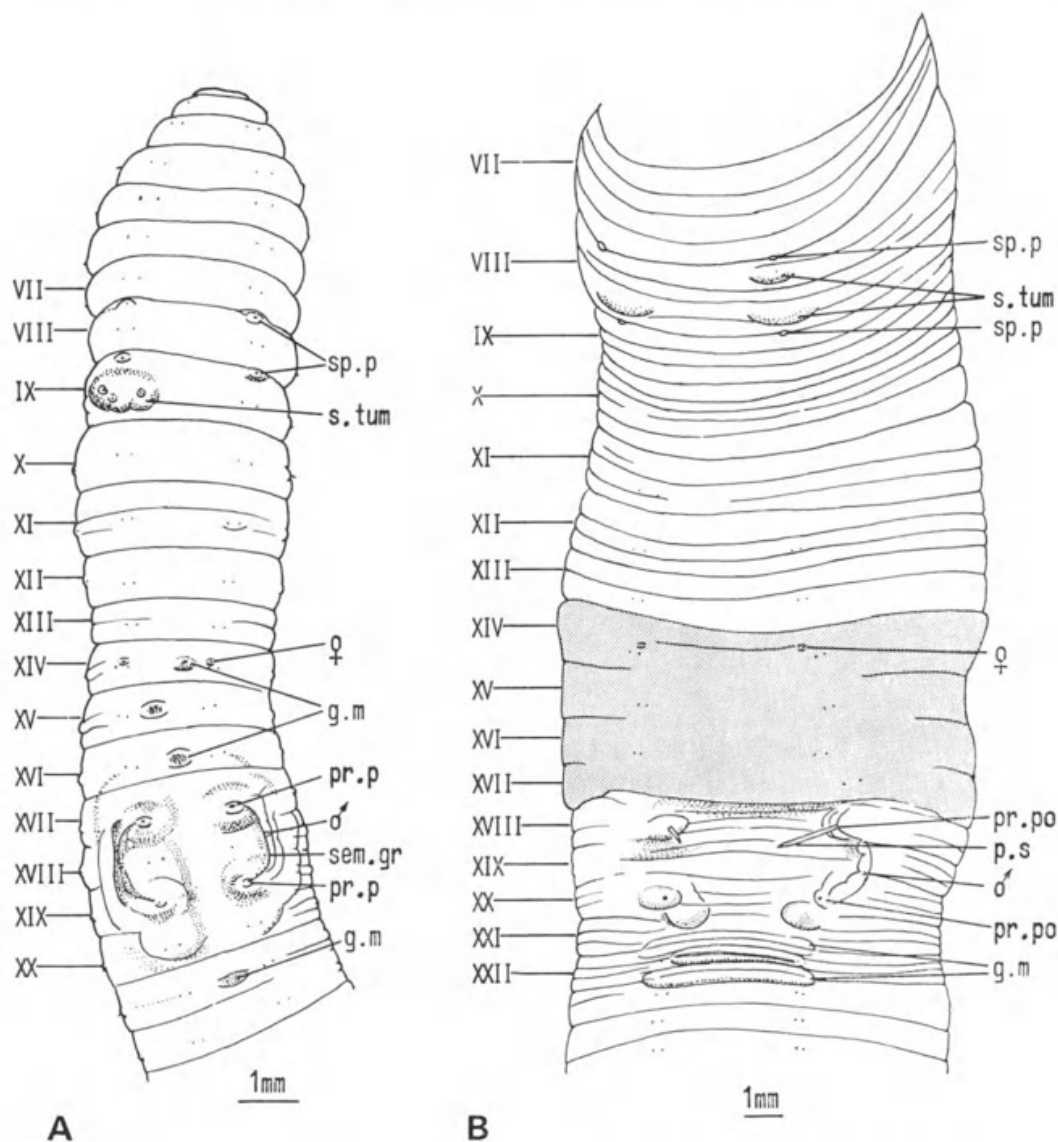


FIG. 6. — Genital fields. A, *Acanthodrilus cavaticus*, specimen 8, AH 579 ; B, *A. ruber*, holotype, AH 588.

setal couple in VIII. All setae present in the segment of the male pores (XIX); slight irregularity in *cd* caudally; in XII, $aa:ab:bc:cd:dd = 5.3:1.0:6.1:0.8:19.4$; $dd:u = 0.43$. Nephropores intermittently visible, commencing in III, throughout the forebody in *cd* and in the midbody in *d*, transverse slits or small circular apertures, apparently sphinctered; not externally visible caudally. Clitellum annular, strongly developed and wider than adjacent segments, sharply delimited at XIV and XVII but the posterior half of XIII possibly with clitellar modification. Prostate pores large gaping orifices, with thick lips constituting porophores, in XVIII and XX in *ab*, penial setae protruding from the anterior pair, the body surface deeply depressed between them as far anteriorly as the clitellum; seminal grooves indistinct glossy bands, strongly convex laterally. Prostate pores of XVIII 4.3 mm, 0.24 body circumference, apart. Male pores minute transverse slits in the bands approximately equatorially in XIX well lateral of *b* lines. Female pores minute, shortly anteromedian of setae *a* of XIV. Spermathecal pores 2 pairs of small lipless apertures almost concealed in intersegmental furrows 7/8 and 8/9, in *ab*; the posterior pair 5 mm, 0.25 body circumference, apart. Accessory genital markings: an indistinct swelling posteromedian to each of the posterior prostate porophores, at 20/21; a narrow transverse pad in XXII filling *aa* midventrally, and longitudinally extending from shortly behind the anterior margin to the posterior third; a similar pad at 22/23 extending laterally beyond *b* lines, contiguous with the pad in XXII and occupying the anterior third of XXIII; each pad bisected transversely by a double line.

Thickest septa 10/11 and 11/12, very strongly thickened. Last hearts in XIII. Commissurals in VII (and further anteriorly?) -IX dorsoventral only. Supra-oesophageal vessel traceable in IX-XV, weakly developed. A large latero-oesophageal vessel (median to the commissurals) originating beneath the oesophagus in VIII and passing anteriorly.

Gizzard very large and strongly muscular, in VI, bulb-shaped with anterior, narrower, end poorly delimited from a strongly though less muscular very tortuous foregut which resembles an elongate, contorted gizzard; the posterior end of the gizzard in X by external segmentation but anterior to septum 6/7. Oesophagus virtually suppressed in VII, elsewhere simple with no notable dilatation or vascularization and lacking extramural calciferous glands. Intestine commencing in XVIII in which it almost attains full width; a very wide, bilaminar dorsal typhlosole, J-shaped with negligible vertical limb, commencing in XXIII but absent in posterior caudal segments; caeca absent. Nephridia with tubular bladder-like ducts, the first three pairs forming conspicuous tufts of which the first pair is by far the largest, discharging respectively at the anterior borders of III (? , pore located but connection of duct not demonstrated), IV and V (followed to pore); the ducts tortuous and by IV <-shaped with bend posterolateral; the first three tufts displaced posteriorly so that the ducts are visible running anterolaterally; tufting continuing to XX but in V posteriorly <-shaped duct restricted to the same segment as the tuft; postseptal necks demonstrated for all but the anterior pair of tufts and preseptal funnels presumably present as demonstrated for IV. In the anterior intestinal region the bladders become transverse and are straight except at the ectal and ental ends at each of which they form a close bend, being therefore J-shaped at each end. Caudally, although some bladders are bent entally, most are simply J-shaped with ectal bend directed medially. Large iridescent free sperm funnels in X and XI. Very large much divided seminal vesicles in XI and XII. Prostates tortuous, tubular though depressed, those of XVIII

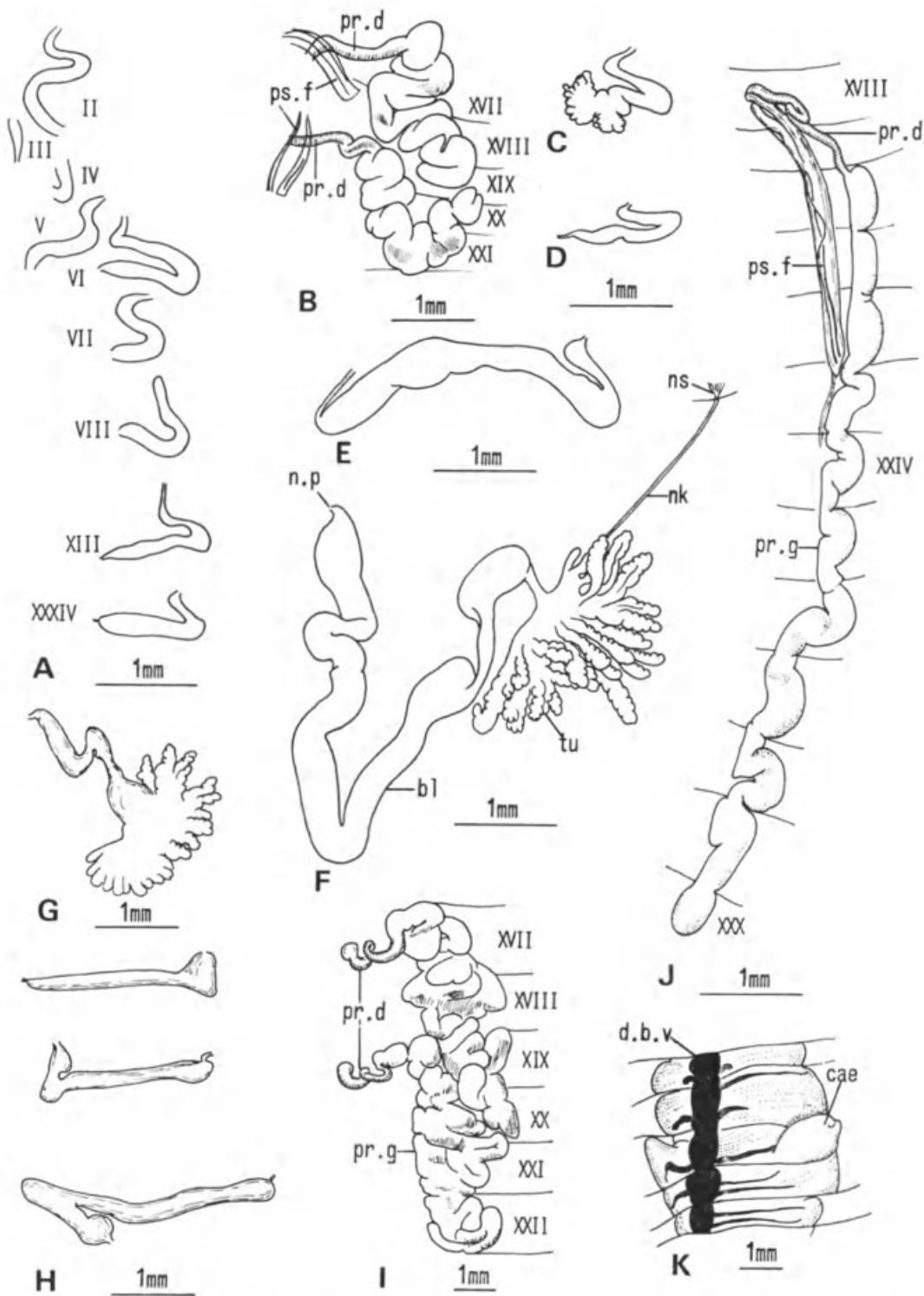


FIG. 7. — A, *Acanthodrilus cavaticus*, nephridia in situ, specimen 8, AH 579. B, *A. chabaudi*, prostates; C, right nephridium of IV; D, intestinal nephridium, holotype, AH 580; E, *A. ruber*, caudal nephridium; F, left nephridium of IV, holotype, AH 588; G, *A. koghis*, right nephridium of VII; H, (Top to bottom) right nephridium of XXV, left nephridium of XXX, right caudal nephridium; I, prostates (penial setae removed), holotype, AH 584; J, *Eudiplotrema sarasini*, prostate gland, AH 589; K, *A. paniensis*, intestinal caecum, specimen 1, AH 586.

and XX extending to posterior XXII; each with a fairly short, narrow slightly sinuous muscular duct which enters a hemispheroidal muscular swelling corresponding with the external porophore; large cushion-like firm intracoelomic glandular masses located at the posterior border of each terminal swelling. Penisetal follicles single, at each prostate duct, those of XVIII extending into XXI, those of XX into XXII, each follicle containing 6 setae of graded sizes. Penial seta moderately stout and elongate, gently curving to a pointed (occasionally blunt) slightly hooked ectal tip; the ectal region more or less depressed dorsoventrally. Single (often more numerous) sharply pointed, ectally directed teeth (5-6 μm long) densely clothing the ectal portion of the shaft; further entally teeth (4-5 μm long) forming irregular serrations; these serrations at approximately 20 μm longitudinal intervals, and numbering 5-6 transversely. A lateral band, lacking teeth in dorsal and ventral view, extends from the tip on each side. Length mature seta 10.5 mm, midshaft width 83 μm . Genital seta stout, slightly curved (almost straight); the tip in profile more strongly convex dorsally than ventrally; keeled laterally and almost parallel sided, thus chisel-like with broadly tapering unsculptured extremity. Ectally in profile with numerous transverse to oblique rows of 3-4 moderately deep scallops; the rows approx. 30-60 μm apart longitudinally; the posterior lip of each scallop with numerous, small, ectally directed, pointed teeth. The arrangement breaking up into less regularly disposed pits at the ectal limit of sculpturing. Length mature seta 3.12 mm, midshaft width 63 μm . Small, apparently immature ovaries and funnels in XIII; no ovisacs demonstrable. Spermathecae 2 pairs, discharging anteriorly in VIII and IX but each reflexed into the preceding segment; each with ovoid-sacciform ampulla and longer, tubular well demarcated duct; a cushion-like diverticulum sessile dorsally on the ectal region of the ampulla where this grades into the duct; length left spermatheca of IX 7.2 mm; ratio total length of spermatheca : length duct 1.7; ratio length : length diverticulum 4.1.

MATERIAL EXAMINED : 164°47' E. 20°34' S. Mt Panié, near surface under moss, in clay soil in rainforest with *Pandanus* locally, at approximately 1000 metres, 13 Feb. 1977 — holotype (AH 588).

REMARKS : *A. ruber* is distinguished from all other species of *Acanthodrilus* by the form of the genital and penial setae and of the male genital field. Location of prostatic pores in XVIII and XX is shared only with *A. coneensis* and *A. natalicius* Michaelsen, 1913, both very much smaller, distinct species. Species resembling it in having the seminal vesicles in XI and XII are relatively few, viz. *A. cavaticus*, *A. foanus*, *A. koghís* and *A. chevalieri*.

Genus **EUDILOTREMA** nov.

Plutellus (*Diplotrema*) (part.) ; MICHAELSEN, 1913 : 241.
(non) *Diplotrema* ; SPENCER, 1900 : 31 ; JAMIESON & DYNE, 1976 : 447.

DIAGNOSIS : (Tanylobous. Setae lumbricine). Dorsal pores absent. Prostate pores 1 pair separate from or uniting in the body wall with the male pores on XVIII. Holonephric; nephridia avesiculate. Prostates tubular, very long (extending through 10 or more segments). Spermathecae 1 pair, diverticulum with multiple sperm chambers.

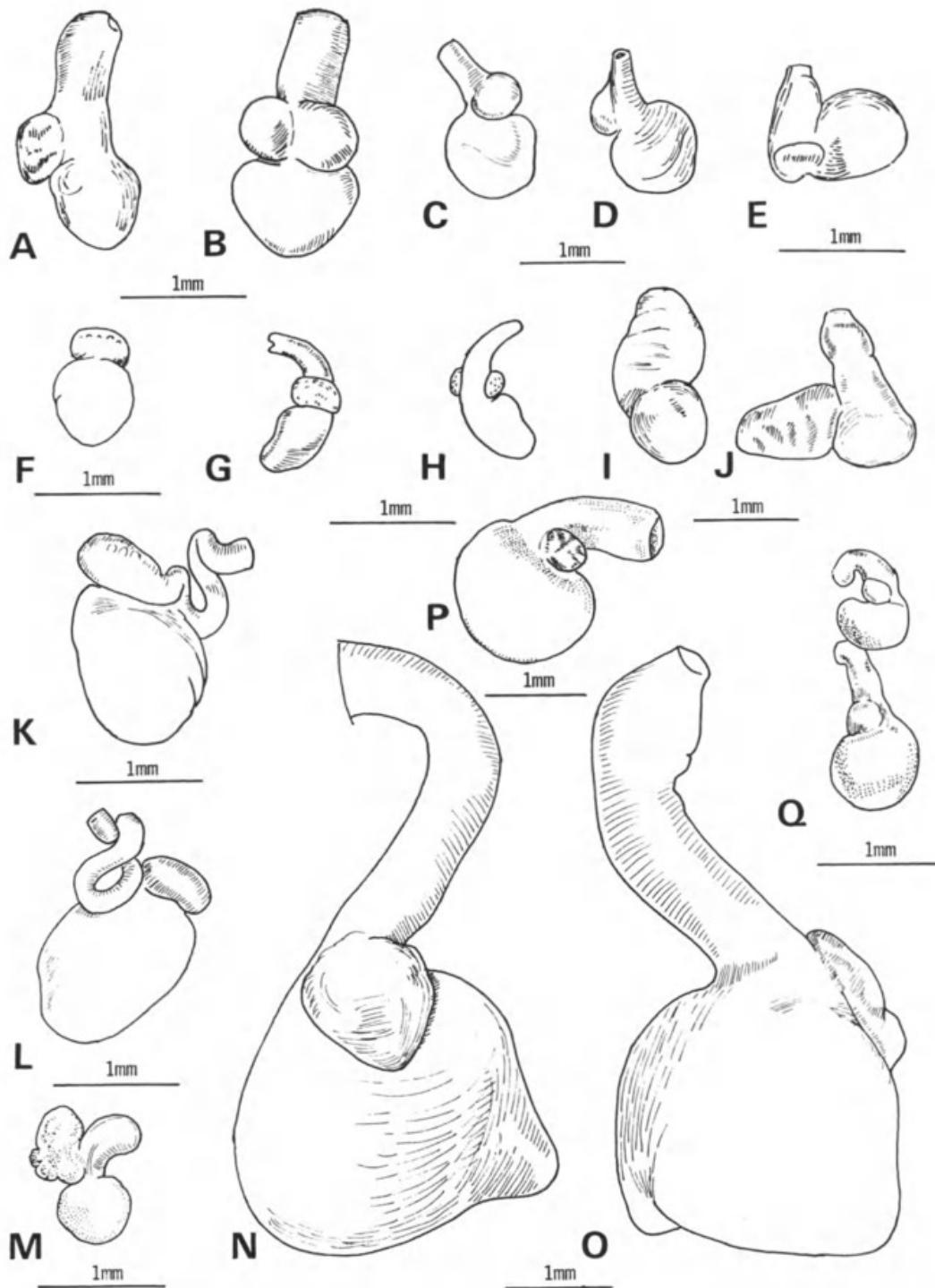


FIG. 8. — Spermathecae. A, B, *Acanthodrilus cavaticus*, specimen 8, R IX, AH 579 : A, lateral, B, dorsal ; C, D, *A. chabaudi*, holotype, L VIII, AH 580 : C, dorsal ; D, ventral ; E, F, *A. chevalieri*, paratype 1, BMNH 1978.1.9 ; E, R IX lateral ; F, R VIII dorsal ; G, H, *A. jabresi*, holotype, R IX, AH 583 : G, dorsal, H, ventral ; I, J, *A. paniensis*, specimen 1, R VIII, AH 586 : I, dorsal, J, lateral ; K, L, *A. longicystis*, holotype, L IX, AH 585 : K, dorsal ; L, ventral ; M, *Eudiploptrema sarasini*, holotype, L IX, AH 589 ; N, O, *A. ruber*, holotype, L IX, AH 588 : N, dorsal ; O, lateral ; P, *A. koghis*, holotype, R VIII AH 584 ; Q, *A. paripapillatus*, holotype, R IX, AH 587.

DESCRIPTION

Prostomium tanylobous. Parietes pigmented. Dorsal pores (always ?) absent. Spermathecal genital setae absent; ventral setal couples at the prostate pores modified as penial setae. Somatic setae in 8 regular longitudinal rows throughout; closely to very widely paired; the dorsolateral pair (*cd*) usually significantly wider than the ventrolateral pair (*ab*). Nephropores typically in *d* lines. Clitellum saddle-shaped, including the segment of the female pores. Prostate pores 1 pair, in XVIII, near the male pores or (*E. rouxi*) uniting with these in the body wall with (typically) or without a seminal groove connecting corresponding prostate and male pores. Female pores a minute pair on XIV, in *a* to lateral of *b*. Spermathecal pores 1 pair anteriorly in IX, in *ab*. Accessory genital markings frequently present; eyelike or transverse pads.

Dorsal blood vessel single or in places double, (always ?) continuous onto the pharynx. Last hearts in XIII; those in X-XIII typically latero-oesophageal and preceded by dorso-ventral commissurals. Supra-oesophageal vessel (always ?) present and oesophageal only. Subneural (always ?) absent. Gizzard moderate to strong in VI. Oesophagus lacking calciferous glands. Intestine (always ?) commencing in XVII; muscular thickening, caeca and typhlosole (always ?) absent. Nephridia holonephridia (always ?) avesciculate with preseptal funnel. Testes free in X and XI; seminal vesicles 2 or 3 pairs, in IX and XII, XI and XII or 3 of these. Prostates tubular, very long, extending through 10 or more segments. Ovaries in XIII, (always ?) fan-shaped. Spermathecae 1 pair, in IX, diverticulum sessile or clavate, (always ?) with one or more sperm chambers.

TYPE-SPECIES : *Plutellus (Diploptrema) sarasini* Michaelsen, 1913.

DISTRIBUTION : New Caledonia. 5 species (MICHAELSEN, 1913).

SPECIES : *Plutellus (Diploptrema) culminis*, *P. (D.) ignambii*, *P. (D.) modestus*, *P. (D.) rouxi*, *P. (D.) sarasini* Michaelsen, 1913.

Eudiploptrema sarasini Michaelsen, 1913
(Fig. 1, 5A, 7J, 8M, 9C; Pl. I, 5-7)

Plutellus (Diploptrema) sarasini Michaelsen, 1913 : 249-251, Pl. VIII, fig. 50, 51, text-fig. II.

Length 62 mm, width 1.6 mm, segments 100. Form slender circular in cross section, lacking significant secondary annulation. Pigmented reddish brown dorsally. Prostomium tanylobous. Dorsal pores absent. Setae large, in 8 regular longitudinal rows, commencing on II; *ab* replaced by penial setae in XVIII; in XII, $aa:ab:bc:cd:dd = 3.4:1.0:4.2:1.0:17.6$; $dd:u = 0.53$. Nephropores (externally visible only in segments in the vicinity of XVIII) at the anterior margins of their segments in *d* lines; small. Clitellum XIII-XVII, but anterior and posterior limits uncertain, largely obliterating the interseg-

ments dorsal to *c* lines and therefore presumably saddle-shaped ; male genital field : a pair of transversely elliptical male porophores in XVIII each bearing two long, projecting penial setae in a transverse line ; shortly lateral to these lies the prostatic pore ; male pore situated behind the lateral of the two penial setae, near the posterior limit of the porophore, in *b* line, and connected to the prostatic pore by a seminal groove. Prostate pores 0.55 mm, 0.01 body circumference, apart. Accessory genital markings subcircular, domed, paired genital markings in *ab*, in intersegments 10/11-16/17 and 19/20-20/21, and a midventral tumescence, each with a pair of depressions, in 17/18-18/19. Female pores an inconspicuous pair in XIV shortly lateral of and almost imperceptibly anterior to seta *b*. Spermathecal pores one pair in 8/9 in *ab*, each a small orifice with elliptical lips of which the anterior is the longer, 0.6 mm, 0.32 body circumference, apart.

Internal anatomy : septa 9/10-11/12 a little stronger than the remainder but only slightly thickened. Dorsal blood vessel continuous onto the pharynx ; single in XIII anteriorly ; double in the posterior 2/3 of each segment in XIV posteriorly. Dorso ventral commissural vessels recognisable in IX to XIII ; those in IX slender dorsoventral only, sending a branch to the parietes before joining the ventral vessel ; those in X-XIII large and heart like, not branching, and in XII and XIII, less certainly in X and XI, with a connective from the dorsal and one from the supra-oesophageal vessel. Supra-oesophageal vessel demonstrable in VIII and XIII only. Subneural blood vessel absent.

Gizzard strong, moderately wide but unusually elongate, in VI but by external segmentation in VII to IX, septa 6/7-8/9 so attenuated as to be almost unrecognizable. Oesophagus in VIII-XIV segmentally swollen and strongly vascularised but extramural calciferous glands absent ; narrower and less vascular in XV-XVI. Intestinal origin indefinite, probably XVII but not strongly widened until XX ; muscular thickening, caeca and typhlosole absent. Nephridia stomate, avesiculate, exonephric holonephridia ; nephridial bodies in III-VIII moderate-sized, considerably coiled with avesiculate duct running antero-laterally to discharge anterior to seta *d* ; progressively less coiled posteriad ; those of II with duct discharging anterior to seta *d* of II but with large much coiled body in IV ; preseptal funnel, one on each side, demonstrated in the intestinal region but nephrostomal necks visible at least as far forward as segment IV ; ectal nephridial ducts at most forming moderately wide straight tubes not warranting designation as bladders. Testes and large much convoluted iridescent sperm funnels 2 pairs, in X and XI ; seminal vesicles 2 pairs, in IX and XII, not much divided ; vasa deferentia not traceable. Ovaries fan shaped with several strings of large oocytes, and small funnels in XIII ; ovisacs absent. Prostates one pair with very tortuous, slender muscular ducts in XVIII and XIX and delicate flattened tubular glandular parts in XX-XXX. In longitudinal sections it is seen that the two vasa deferentia of a side unite at the level of the prostate pore and continue as a single duct to the male pore which is separated by 0.1 mm from the prostate pore. Penisetal follicles 2 on each side entering the body wall median to the prostate ducts ; extending into XXIII but with a ligament attaching the posterior end of the follicle to the body wall in XXIV ; sinuous penial setae visible through their walls. Penial setae filiform, slightly curved ectally, the tip transversely concave ventrally, strongly flattened and almost parallel sided ; the ectal extremity blunt and jagged ; entally a scattering of ectally directed pointed teeth (approx. 2-3.5 μ m long) in groups of two to several. Further ectally teeth are blunt and conjoined into incompletely encircling bands ; the bands at approximately 5 μ m intervals longitudinally ; length of a

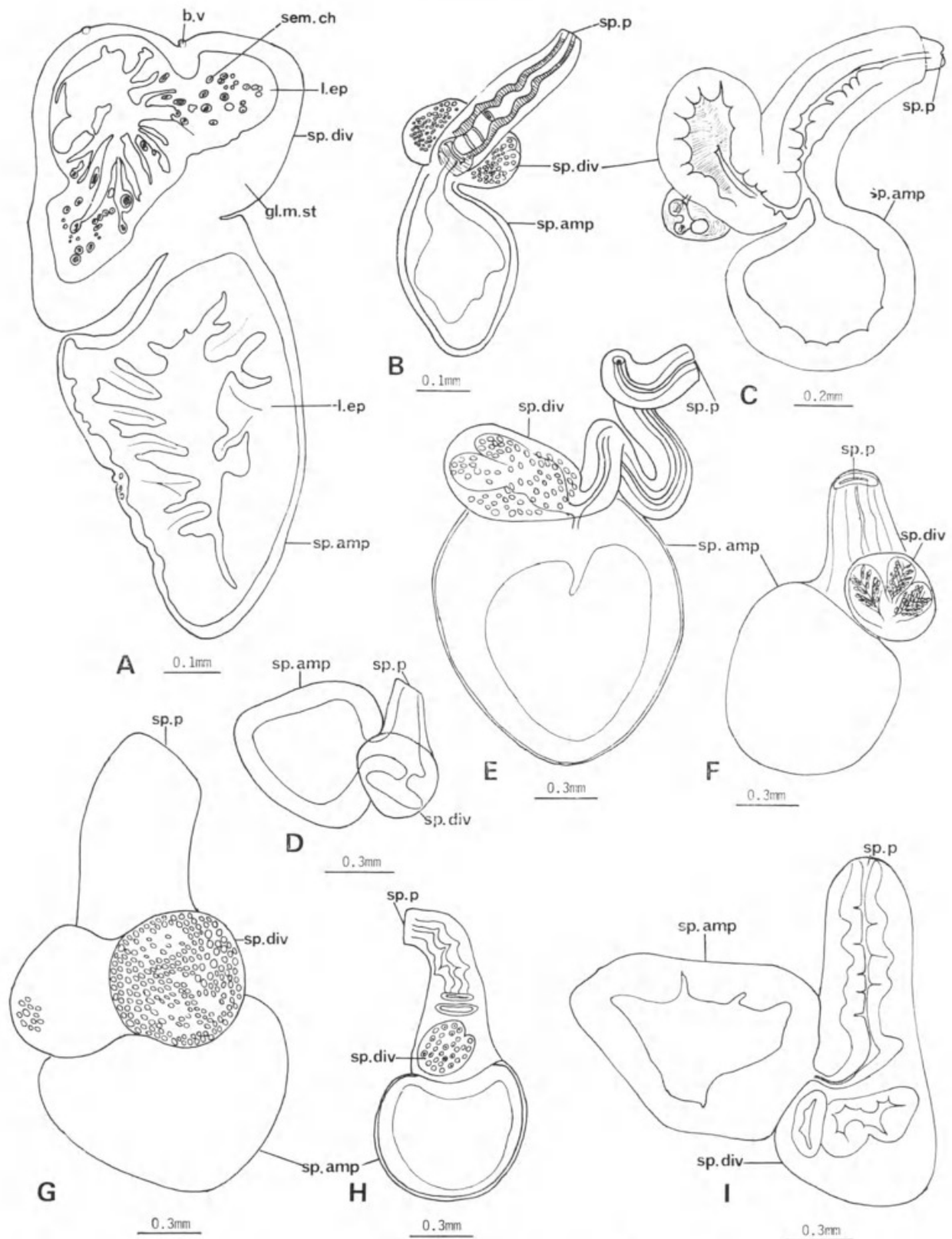


FIG. 9. — Spermathecae. A, *Acanthodrilus cavaticus*, specimen R IX, BJ 1977.9.8 ; B, *A. fabresi*, holotype R IX, AH 583 ; C, *Eudiplotrema sarasini*, holotype L IX, AH 589 ; D, *A. chevalieri*, paratype 1, R IX, BMNH 1978.1.9 ; E, *A. longicystis*, holotype, L IX, AH 585 ; F, *A. chabaudi*, holotype, L VIII, AH 580 ; G, *A. cavaticus*, specimen 8, R IX, AH 579 ; H, *A. paripapillatus*, holotype, R IX, AH 587 ; I, *A. paniensis*, specimen 1, R VIII, AH 586.

TABLE I. -- Intersetal distances in segment XII in *Acanthodrilus* and *Eudiplostrema*.

	Percentage of circumference								U
	<i>aa</i>	<i>ab</i>	<i>bc</i>	<i>cd</i>	<i>dd</i>	<i>dc</i>	<i>cb</i>	<i>ba</i>	
<i>A. cavaticus</i>									
7 specimens									
Min.	12.6	1.2	12.9	1.5	44.8	1.6	13.9	1.5	8.0
Max.	17.1	2.1	15.3	2.2	51.7	2.1	17.4	2.1	10.8
Mean	14.6	1.6	14.3	1.8	48.6	1.9	15.4	1.8	8.9
<i>A. chabaudi</i>									
Holotype	14.1	1.8	16.0	2.4	45.4	2.2	16.5	1.6	
5 specimens									
Min.	14.1	1.4	14.0	1.7	39.6	1.6	14.2	1.5	8.4
Max.	17.4	1.9	18.1	2.4	49.9	2.2	17.8	1.9	9.2
Mean	15.3	1.7	15.4	1.9	46.3	1.9	15.7	1.7	8.9
<i>A. chevalieri</i>									
Holotype	12.7	2.6	15.4	1.7	45.8	1.9	17.6	2.4	7.0
3 specimens									
Min.	12.7	2.5	15.4	1.7	45.5	1.9	14.6	1.9	6.2
Max.	13.8	2.6	16.6	2.3	47.0	2.4	17.6	2.4	7.0
Mean	13.1	2.6	16.0	2.1	46.1	2.1	16.0	2.2	6.5
<i>A. fabresi</i>									
Holotype	9.6	2.4	16.4	2.6	47.3	2.7	16.7	2.4	5.9
<i>A. koghisi</i>									
Holotype	16.2	2.1	15.9	1.3	44.7	1.1	16.7	2.1	16.0
4 specimens									
Min.	15.7	1.4	15.8	1.1	41.9	1.1	16.4	1.5	14.5
Max.	18.9	2.1	17.1	1.4	45.3	1.3	17.1	2.1	16.8
Mean	16.8	1.8	16.4	1.3	44.0	1.2	16.8	1.8	15.5
<i>A. longicystis</i>									
Holotype	11.8	2.1	18.0	1.8	44.6	1.6	17.9	2.2	9.9
<i>A. paniensis</i>									
Spec. 1	11.5	2.5	16.7	1.8	45.9	1.9	17.2	2.5	11.2
<i>A. paripapillatus</i>									
Holotype	13.1	2.2	15.7	2.0	47.9	1.9	14.5	2.7	5.9
<i>A. ruber</i>									
Holotype (Segment 20)	13.1	0.9	19.9	0.7	42.6	0.7	21.3	0.9	28.2
<i>E. sarasini</i>									
Spec. AH 589	10.1	2.9	12.5	3.1	52.8	3.1	12.5	3.1	4.6

U : Circumference in mm.

mature seta 3.8 mm, midshaft width 13 μ m. Spermathecae one pair, opening anteriorly in IX, each with subspherical ampulla, slightly longer, stout duct, and a diverticulum at their junction which forms a narrow depressed sac, about as large as the ampulla, which bears a small lobed protuberance containing three or more sperm masses; length left spermatheca of IX 1.17 mm, ratio total length : length duct 1.86; ratio length : length diverticulum 1.83.

MATERIAL EXAMINED : 164°47' E. 20°34' S. Mt Panié, in dense moist soil in rainforest at approximately 500 metres, 14 Feb. 1977 — 1 specimen (AH 589); serial sections of male terminalia of one side (BJ 1977.9.9).

REMARKS : The above account significantly adds to that of MICHAELSEN.

DISCUSSION

Acanthodrilus

The similarity of the description of the genus *Acanthodrilus* to the characterizations of the Australian genus *Diploptrema* by JAMIESON and DYNE (1976) and of the North American genus *Diplocardia* by GATES (1977) is most striking and indicates their phylogenetic relationship. *Acanthodrilus* is distinguished by the presence of nephridial bladders. *Diplocardia*, as defined, appears to differ from *Diploptrema* only in duplication of the gizzard. There can be little doubt that the three entities are descendants of a Pangean (but chiefly Gondwanan?) acanthodrilid fauna. Restriction of vesiculate species to New Caledonia suggests that the vicariating event which led to division of the Gondwanan stock into *Acanthodrilus* and *Diploptrema* was the rifting of New Caledonia from Australia shortly after 80 million years ago. Alternatively, it is possible that development (or loss?) of nephridial bladders was a later response of the separated stocks to the particular conditions of their locations.

It seems probable as MICHAELSEN (1913) suggested that *A. mareensis* has secondarily dispersed to Maré from New Caledonia. It will be apparent from the generic account that it is questionable that *A. kermadecensis* is closely related to the other species of the genus and its inclusion by LEE (1953, 1959) is followed only because erection of a separate genus for it does not appear warranted in the present state of our knowledge of the wider acanthodrilid fauna.

Eudiploptrema

Tubular prostate glands are regarded as modification of former long series of setal glands which initially had no special relationship with vasa deferentia (JAMIESON, 1971*b*). In the typical acanthodrilid condition the male ducts, opening on segment XVIII, remain discrete from the prostate glands which have pores on XVII and XIX. In all perionychin Megascolecidae, however, with the sole exception of *Eudiploptrema*, the vasa deferentia have united with the prostates or their ducts. Even in *Eudiploptrema rouxi* the first stage in

union occurs with the vasa deferentia joining the prostate ducts within the body wall. New Caledonia thus contains, at least with regard to male terminalia, the most primitive known perionychins. It is tempting to infer evolution of the *Eudiplotrema* condition from the acanthodrilin condition by the megascolecin reduction (loss of posterior prostates and movement of the pores of those of XVII into XVIII, into the vicinity of the male pores) an origin postulated by MICHAELSEN (1903) for the Megascolecinae and accepted by STEPHENSON (1930). MICHAELSEN (1913) rightly points out that retention of only the posterior spermathecal pores in what is now *Eudiplotrema* suggests that it is the anterior pair of prostates which has been retained. This anterior pair would have migrated into XVIII. As the acanthodrilin arrangement may be transposed 1-3 segments posteriorly in New Caledonian acanthodrilids the possibility of retention of anterior prostates in a lineage with the prostate pores on XVIII and XX and movement of the male pores forwards into XVIII from XIX may also be considered. Whether perionychins originated by reduction of the acanthodrilin arrangement or not, an especially close relationship between *Eudiplotrema* and *Acanthodrilus* cannot be proved though there is no strong evidence against it. Shared somatic characters which are sufficiently uncommon for their co-occurrence to have rather low probability without relationship are the tanylobous prostomium, location of last hearts in XIII and perhaps the presence of penial setae which are frequently absent in perionychins. Whether or not *Eudiplotrema* has arisen from an acanthodrilid stock it is not now assignable to the Acanthodrilinae. It is placeable in the Megascolecinae (MICHAELSEN, 1913, JAMIESON and DYNE, 1976) and its taxonomic and phylogenetic status relative to other perionychin genera require discussion.

MICHAELSEN (1913) considered, not surprisingly, that the New Caledonian species which he placed in *Plutellus* (*Diploptrema*), here *Eudiplotrema*, were closest to "*Plutellus*" *pygmaeus*. However, this requires testing and neither entity is assignable to *Plutellus* s. strict. whereas affinity with *Diporochaeta* and related genera, including the junior synonyms *Perionychella* and *Vesiculodrilus*, is suspected. Descriptions of *P. pygmaeus* and of the *Eudiplotrema* species other than that described in the present work are too incomplete to permit a rigorous phylogenetic analysis but some attempt is made here. Fig. 10 shows the phylogenetic affinities of *Eudiplotrema* with the "diporochaetoid" genera as deduced by application of the principles of phylogenetic systematics proposed by HENNIG (1966) but using a necessarily limited set of attributes. *Diporochaeta*, *Perionychella*, *Gratiophilus*, *Simsia* and *Vesiculodrilus*, are represented by their type-species, and the very distinctive South Australian *Diporochaeta inconstans* (JAMIESON, 1974a), and *P. pygmaeus* are also included. The characters employed and their states for the various species are given below (fig. 10) and their states are indicated in the phylogram by the corresponding numbers.

For *P. pygmaeus* the states of three of the seven characters employed are unknown and have been scored as being identical with those in *Eudiplotrema sarasini*. However, it must be stressed that when *pygmaeus* is eliminated from consideration the remaining species have been shown empirically to have the same Hennigian relationships for these seven characters.

The following conclusions are drawn from the phylogram with the reservations expressed. Until a complete revision of *Eudiplotrema* and *P. pygmaeus* is made, and perhaps even then, the phylogeny can only be regarded as heuristic and some discussion of the effects of including additional characters and species accompanies these conclusions.

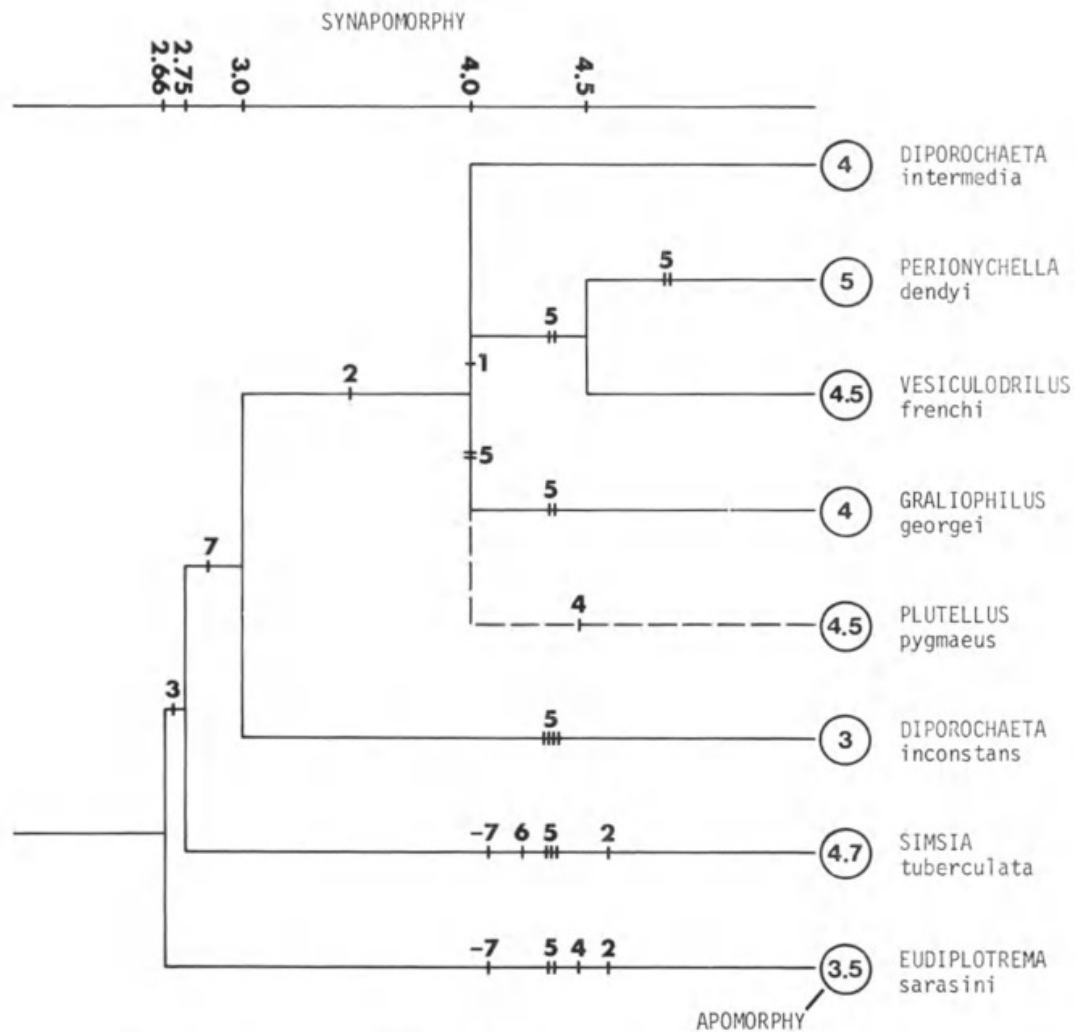


FIG. 10. — Phylogram based on 7 characters, of the genus *Eudiplotrema* (represented by the type-species, *E. sarasini*) relative to other "diporochaetoid" genera. Numerals in circles are the total score of apomorph (advanced) attribute-states for each species. Numbers on the phylogram refer to the character, the number of transverse lines across each lineage indicating the number of steps taken in the character concerned. The number of shared apomorphies (synapomorphies) at each division or dichotomy is indicated in the scale labelled synapomorphy. Characters are : (1) Setae 8 (0) or more (1) per segment ; (2) nephropores ventro- (0) or dorso-lateral (1) ; (3) male and prostate pores separate (0) or fused (1) ; (4) gizzard in V (0) or VI (1) ; (5) intestinal origin XV (0), XVI-XIX (1-4) ; (6) typhlosole absent (0) or present (1) ; (7) spermathecal diverticulum absent (0), multiloculate (-1) or uniloculate (1).

Close relationship of the avesculate *Perionychella* Michaelsen (1907) and vesiculate *Vesiculodrilus* Jamieson (1973), both Australian, and their synonymy in *Diporochaeta* (type-species from New Zealand) which was recently advocated (JAMIESON, 1976) is confirmed. Furthermore, distinction of the Australian *Graliophilus* Jamieson (1970) from *Diporochaeta* which has become increasingly difficult at least for the *G. georgei* group (JAMIESON, 1976) is uncertain. However, in *Graliophilus* the male ducts typically join the prostate ducts much further ectally than in *Diporochaeta* and synonymy of the two cannot be considered proven.

Plutellus pygmaeus, even when three of the seven characters are inferred as identical with those in *Eudiplotrema*, groups with and is taxonomically inseparable from *Diporochaeta*.

Notable differences from *Eudiplotrema* are the epilobous prostomium, the two pairs of spermathecal pores, single (not multiple) seminal chamber in the spermathecal diverticulum, the short prostates and fusion of the male ducts with the ental ends of the prostate ducts. Apparent shared absence of dorsal pores may be a convergence.

The South Australian *Perionychella inconstans* Jamieson (1974a), which differs from other diporochaetoids in having ventrolateral nephropores, is seen to be the plesiomorph sister-group of *Diporochaeta*-through-*Graliophilus*. It may be retained in *Diporochaeta* or assigned to a new genus but such a decision must await description of a second South Australian species with similarly characterized nephropores in our collections. Erection of a new genus would be consistent with the dismemberment of the large and variable genus *Diporochaeta* which would be expected, and desirable, if an Hennigian analysis of a large number of species were undertaken.

The South-east Australian genus *Simsia* is retained as the plesiomorph sister-group of *Diporochaeta*-through-*P. inconstans* (*Diporochaeta* s. lat.).

Eudiplotrema appears to be plesiomorph sister-group of the other computed diporochaetoids and is far removed from the sympatric *Plutellus pygmaeus*. If *E. rouxi* is included in the computation for the same set of characters, it is found to group with *P. pygmaeus* in *Diporochaeta* s. lat. while *E. sarasini* remains distinct. However, the similarities between *E. rouxi*, *E. sarasini* and the other three species here grouped in *Eudiplotrema* are so striking, as summarized in the generic diagnosis, that they are here held to represent a monophyletic group distinct from *P. pygmaeus*.

The phylogram has important zoogeographic implications. If *P. pygmaeus* is correctly placed phylogenetically and if the presence of it and *Eudiplotrema* on New Caledonia is not the result of marine dispersal, the stem-forms which gave rise to them, to the Australian and New Zealand diporochaetas and to *Simsia* must have formerly occurred in the combined New Caledonia-Australia. Furthermore, the occurrence of *Diporochaeta* in India (JAMIESON, 1977) suggests that this genus existed before the much earlier separation of India from Gondwanaland. Absence of perionychins, including *Diporochaeta*, from Africa suggests that they originated in residual Gondwanaland after the very early Triassic separation of Africa. African Megascolecinae are considered by the authors to have probably originated from acanthodrilids, not from perionychins. Absence from South America is less easily explained and raises the possibility that *Diporochaeta* (= *Plutellus*) *peregrina* (Cernosvitov, 1934) may be South American as stated by CERNOSVITOV but questioned by JAMIESON (1975). Alternatively, *Diporochaeta* may not have successfully dispersed via Tertiary Antarctica to South America, or may have been eliminated there by the highly successful Glossoscolecidae.

In conclusion, New Caledonia is seen as the sole refuge of the only perionychin genus with separate male and prostatic pores, the ancestral condition of the tribe and of the Megascolecinae as a whole.

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PLATE I

Scanning electron micrographs of penial and genital setae.

1-2, 4. — Penial setae, *Acanthodrilus paripapillatus* (H).

3. — Genital seta, *A. paripapillatus* (H).

5-7. — Penial setae, *Eudiplostrema sarasini* (H).

8-9. — Genital setae, *A. longicystis* (H).

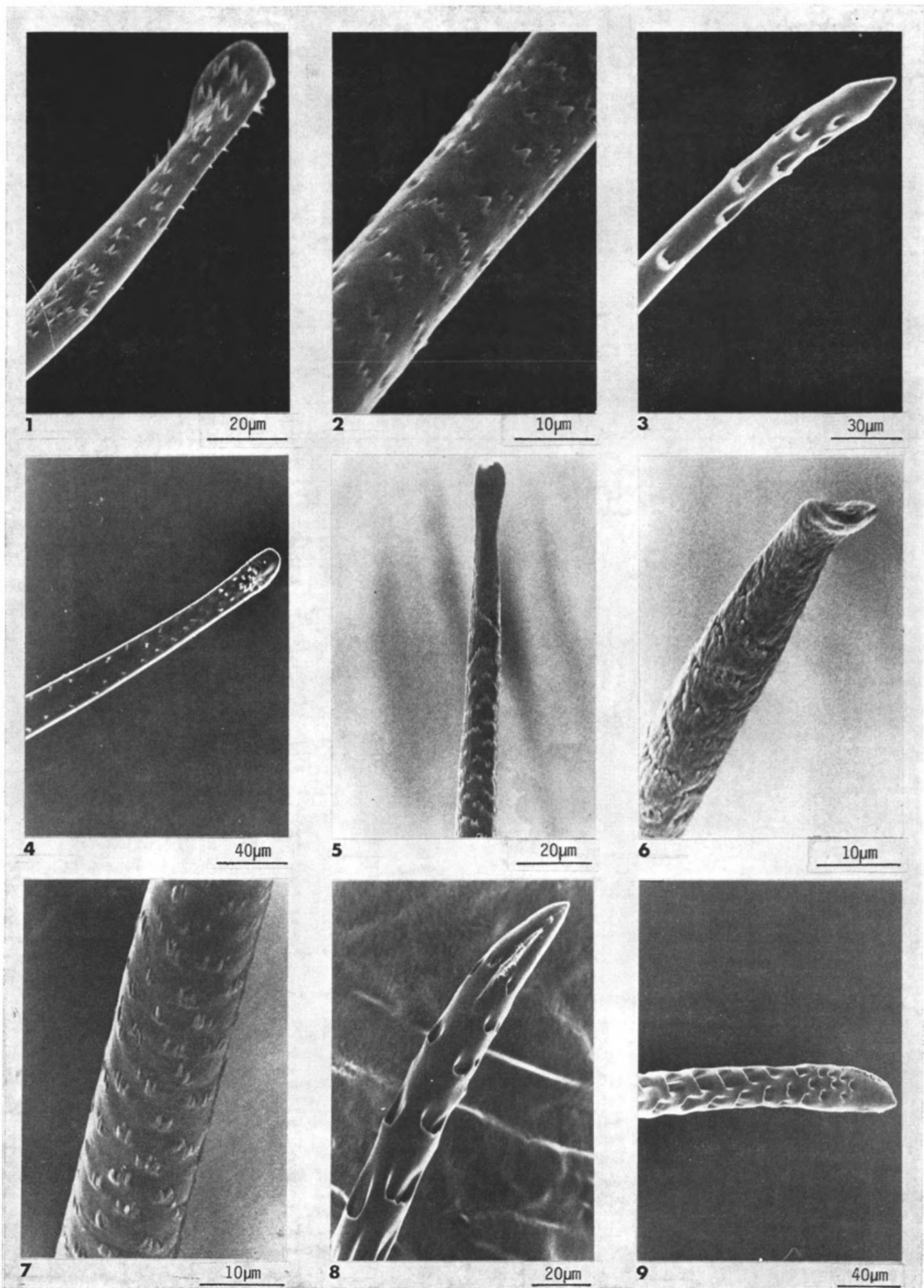


PLATE I

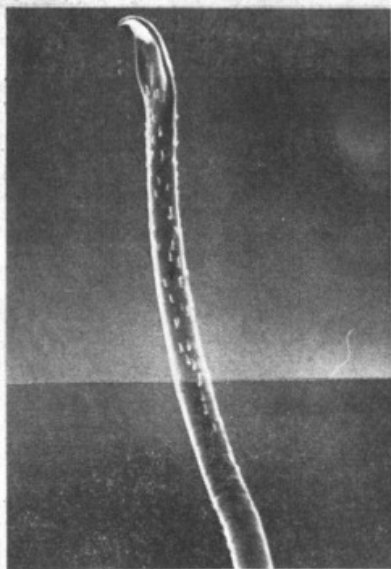
PLATE II

Scanning electron micrographs of penial setae.

10-12. — *Acanthodrilus longicystis* (H).

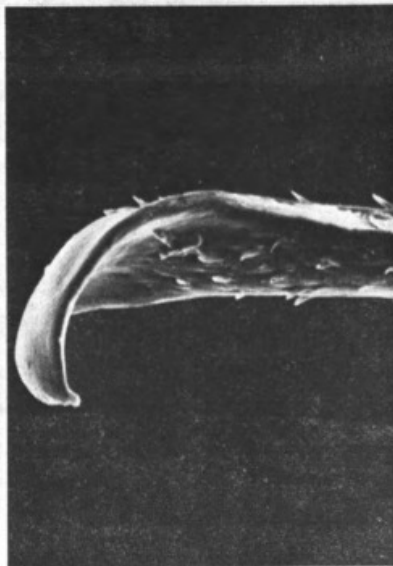
13-15. — *A. jabresi* (H).

16-18. — *A. chabaudi* (P2).



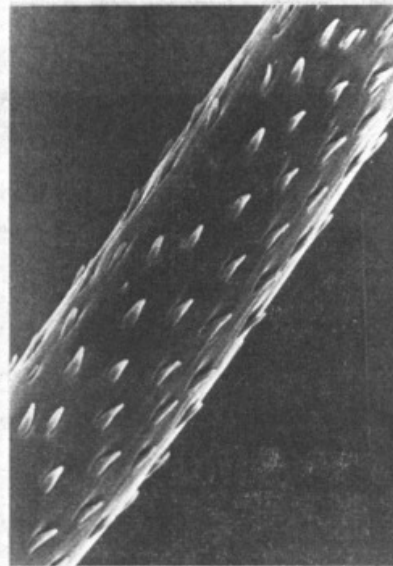
10

40μm



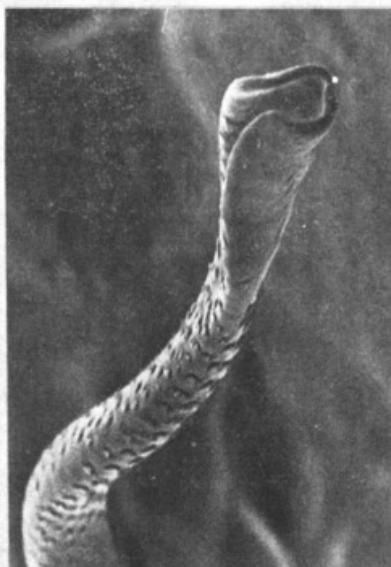
11

20μm



12

10μm



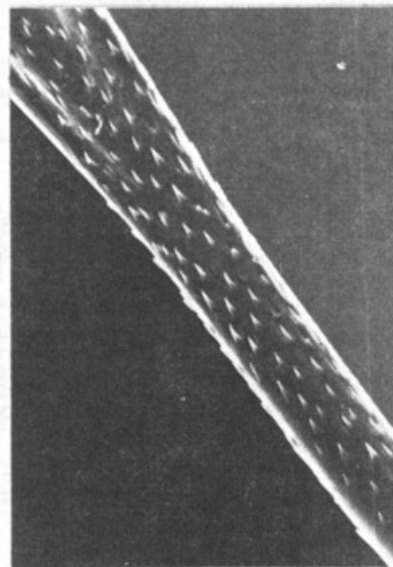
13

20μm



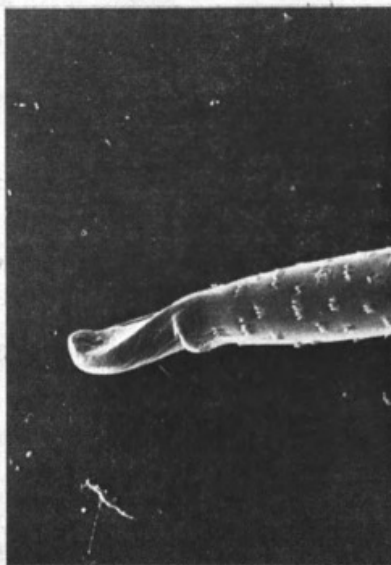
14

20μm



15

20μm



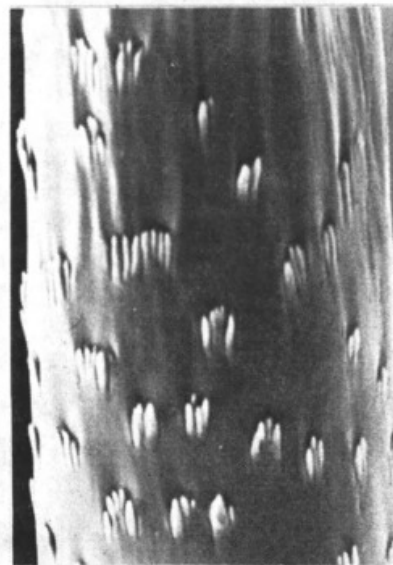
16

40μm



17

40μm



18

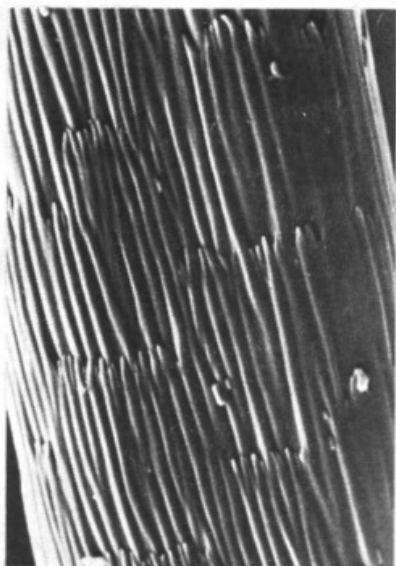
10μm

PLATE II

PLATE III

Scanning electron micrographs of penial and genital setae.

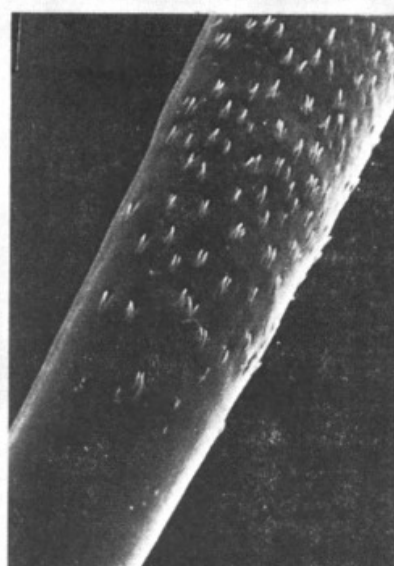
- 19. — Penial seta, *Acanthodrilus chabaudi* (P2).
- 20. — Genital seta, *A. chabaudi* (P2).
- 21-24. — Penial setae, *A. paniensis* (H).
- 25-27. — Penial setae, *A. ruber* (H).



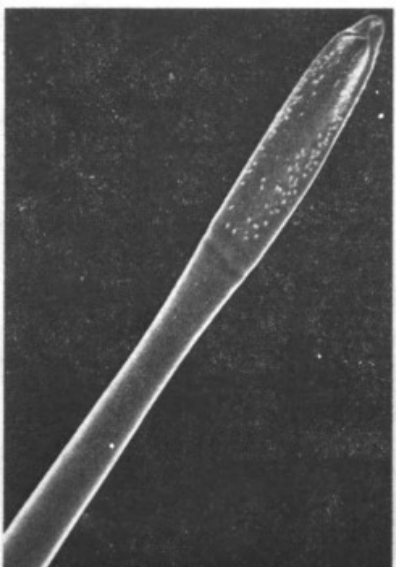
19 10μm



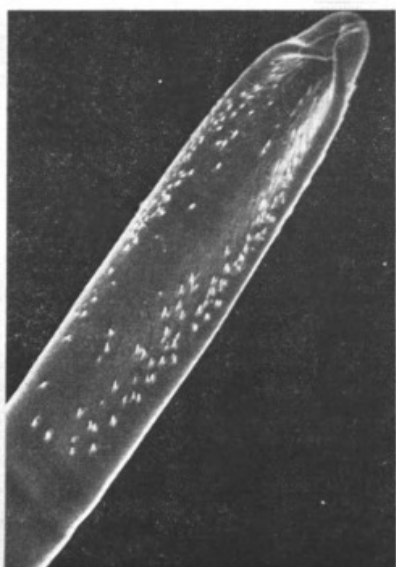
20 20μm



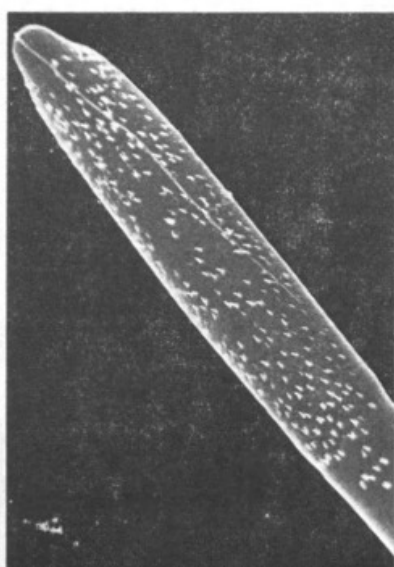
21 20μm



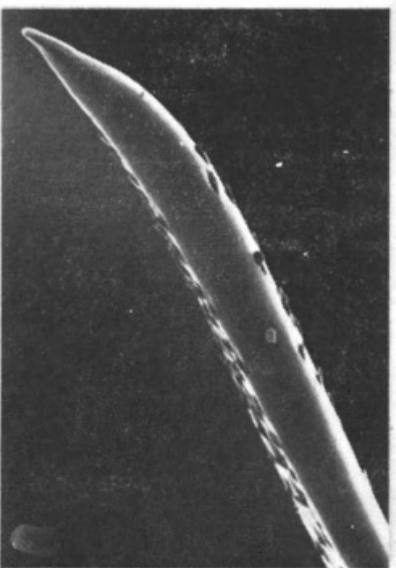
22 100μm



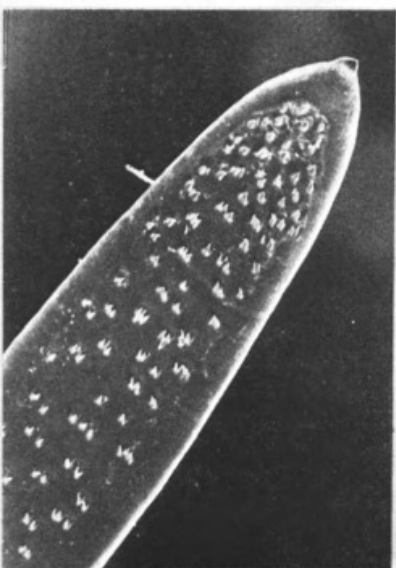
23 60μm



24 80μm



25 40μm



26 40μm

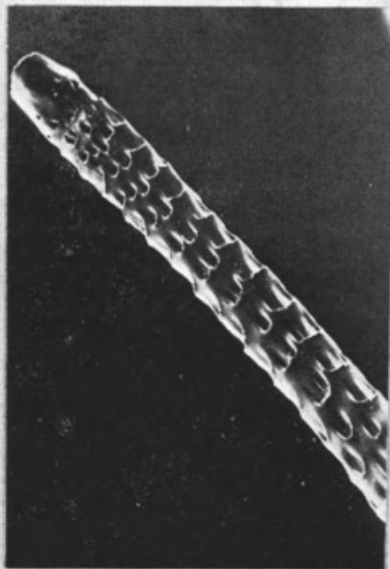


27 20μm

PLATE IV

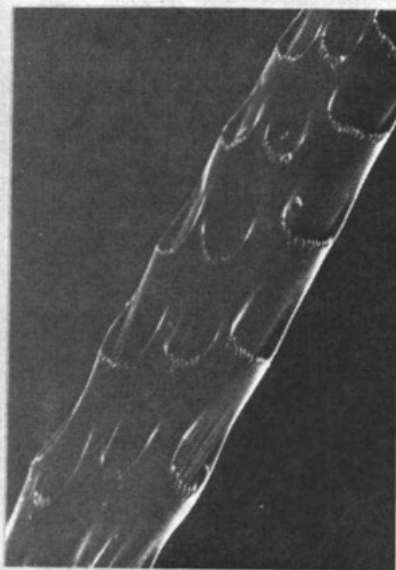
Scanning electron micrographs of penial and genital setae

- 28-29. — Genital setae, *Acanthodrilus ruber* (H).
30-33. — Penial setae, *A. cavaticus* (30-31 S. 2; 32-33 S. 6).
34-35. — Genital setae, *A. cavaticus* (S. 6).
36. — Penial seta, *A. koghisi* (P1).



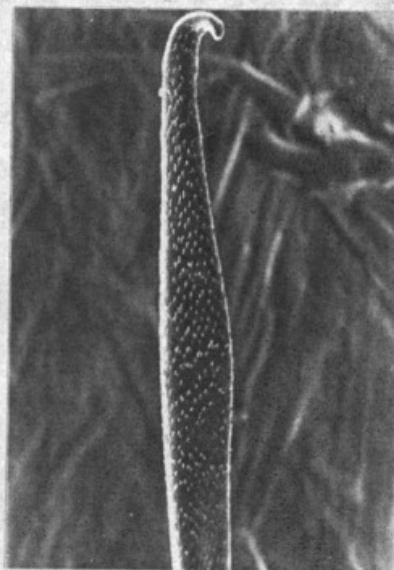
28

100μm



29

40μm



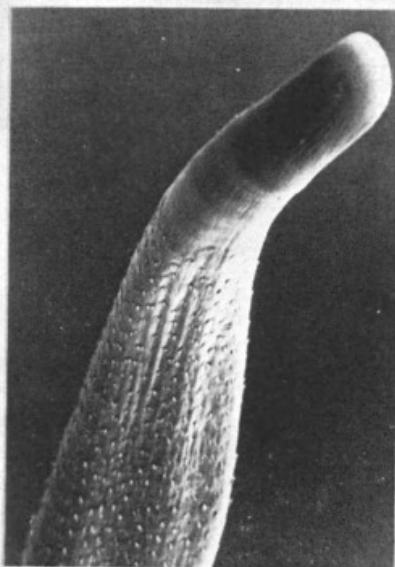
30

100μm



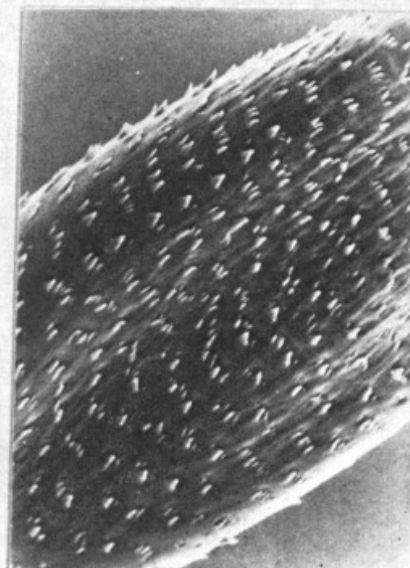
31

20μm



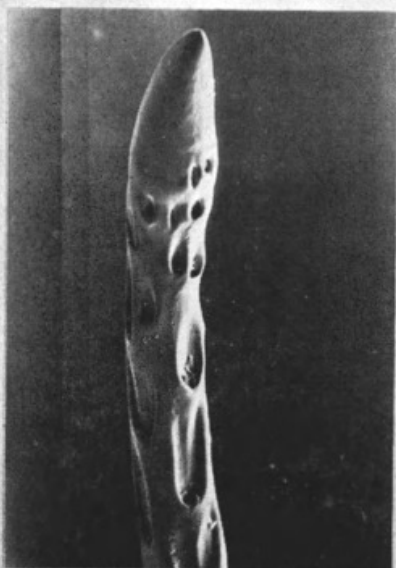
32

40μm



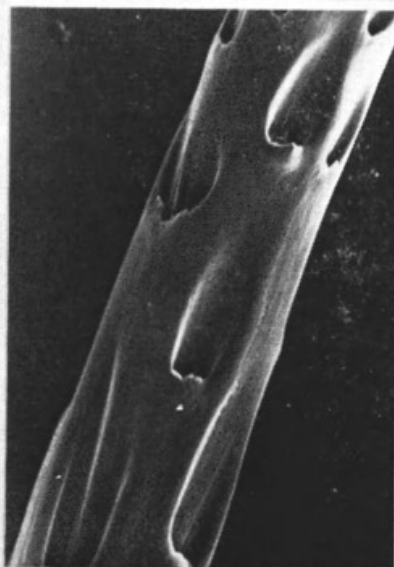
33

20μm



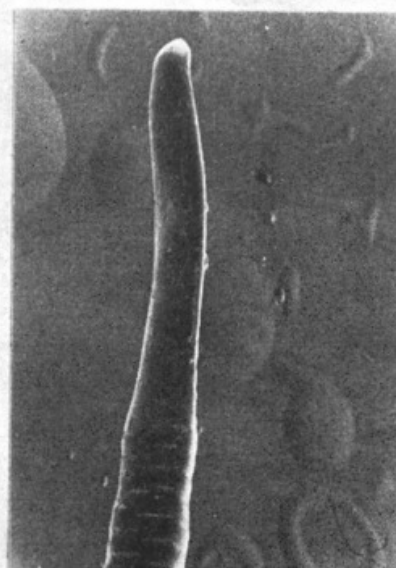
34

40μm



35

20μm



36

40μm

PLATE IV

PLATE V

Scanning electron micrographs of penial and genital setae.

37-38. — Penial setae, *Acanthodrilus koghis* (P1).

39-40. — Genital setae, *A. koghis* (P1).

41-45. — Penial setae, *A. chevalieri* (P1).

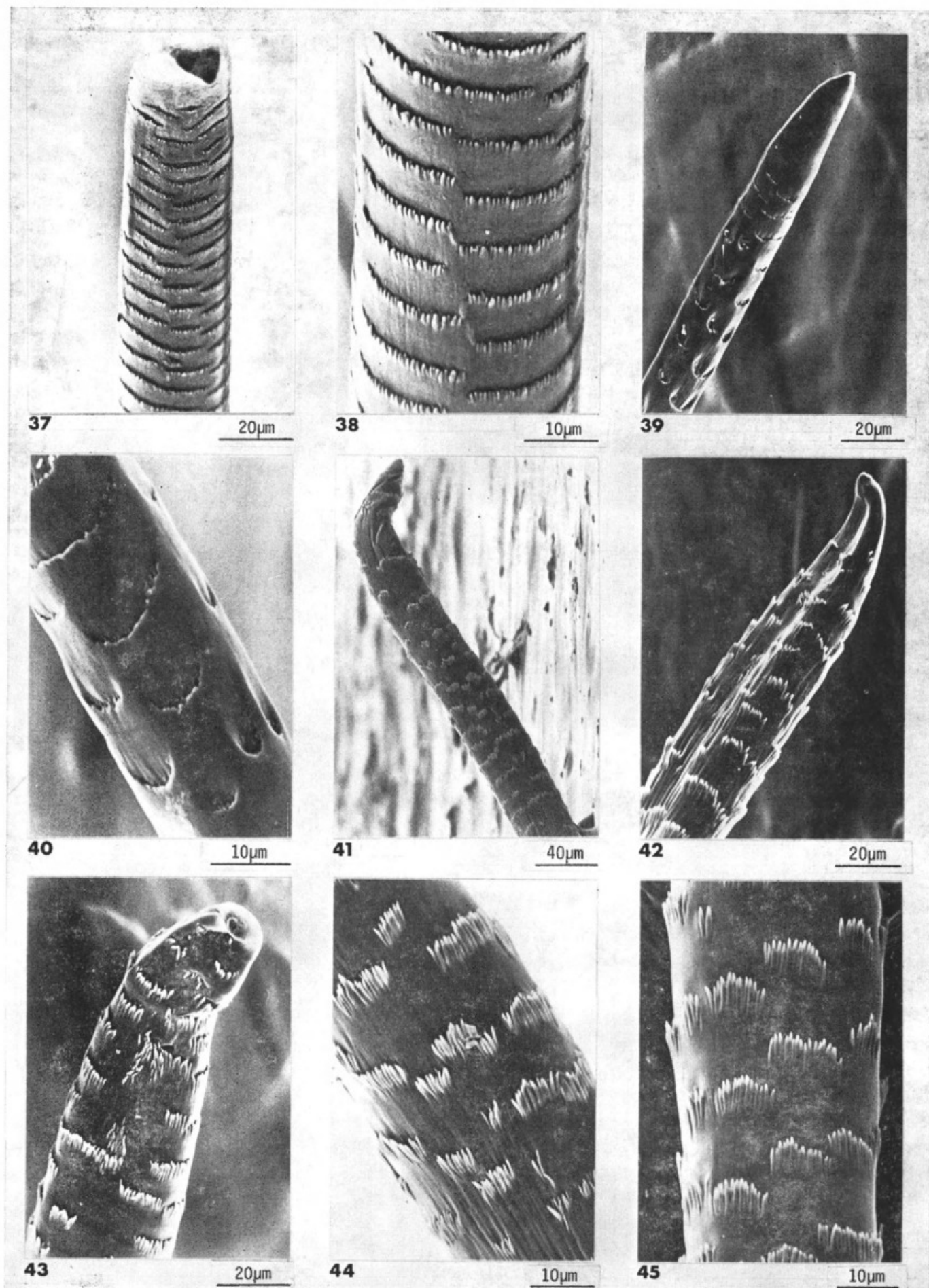


PLATE V



Jamieson, B G M and Bennett, J. D. 1979. "New species of Acanthodrilinae and a new genus of Perionychini (Oligochaeta, Megascolecidae) from New Caledonia, their phylogeny and zoogeography." *Bulletin du Muséum national d'histoire naturelle* 1(2), 353–363. <https://doi.org/10.5962/p.283200>.

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