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DOMANIBDELLA GEN. NOV., A DUOGNATHOUS 5-ANNULATE LAND LEECH GENUS IN NEW GUINEA (HIRUDINOIDEA: HAEMADIPSIDAE S.L.), WITH A DISCUSSION ON GENERAL SOMITAL ANNULATION[1]

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1. A study conducted under an award from the Australian Research Grants Committee for researches on Australian aquatic and terrestrial leeches.
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Abstract

Comparison with the duognathous 5-annulate land leeches of E. Australia enables separation of *Domanibdella* as having vii incomplete and viii complete 5-annulate, xxiv complete 3- or 2-annulate, genital pores xi b_5/b_6 (b_6) and xii b_5/b_6 (b_6), auricles large and the ventral margin straight not lobate, lambertian organs present and posterior. The discussion on general somital annulation supports separation in this manner at the generic level. *Geobdella tristriata* Goddard 1909 is the type species for the new genus. *Haemadipsa noxia* Blanchard 1917 is placed in *Domanibdella*.

The presence of land leeches in New Guinea has long been known, but zoological knowledge is scanty. In addition to the leeches dealt with below, Soos (1967) records for New Guinea one 4-annulate species, provisionally referred to *Philaemon grandidieri* (a species based on and known otherwise only in material from Madagascar), and two 6-annulate species, *Phytobdella maculata* and *Phytobdella lineata*, both described by Moore (1944).

This paper is concerned with the generic nature of *Geobdella tristriata* Goddard 1909, a 5-annulate land leech described very incompletely by Goddard from a single poor specimen from Fife Bay, Papua, loaned to Goddard by Mr. T. Steel.

Two 5-annulate species described by Blanchard in 1917 were reduced to synonymy under *tristriata* by Augener (1931). Augener also referred specimens he studied to this species, so that *tristriata* has become the only 5-annulate species recognized for New Guinea (Soos 1967). Augener found his specimens were duognathous, and transferred *tristriata* to *Chtonobdella* Grube 1866, a genus based on a 5-annulate land leech from near Sydney.

There is no knowledge of the survival of the type specimen studied by Goddard. Evidence is given below which associates a specimen in the collections of the National Museum of Victoria, Melbourne, with the specimen described by Goddard, and to such degree that I can only accept both as taken by the one collector in the one area. This was most probably the Rev. H. P. Schlencker of the London Missionary Society, who sent many specimens from Fife Bay to Mr T. Steel.

A description of the general somital annulation of this second specimen is given below. The data contained in the brief descriptions of the two species described by Blanchard are revised by diagrammatic analysis. This shows one of Blanchard's species has full similarity with the general somital annulation in the second specimen.

Recently collected specimens sent to me by Dr. W. Ewers of the University of Papua and New Guinea include a few 5-annulate land leeches. Some of these have the ventral and dorsal pattern as described by Goddard for *tristriata*, and all have the distinctive general somital annulation of the second specimen from Fife Bay.

These have vii incomplete 5-annulate, viii to xxii complete 5-annulate, xxiii complete or incomplete 5-annulate, xxiv complete 3- or 2-annulate.

Departure of this nature from the usual form of general somital annulation was given

Fig. 1—*Domanibdella* gen. nov. a, ventral and b, dorsal aspects of specimen 5(a), 12 mm, Brown River, Port Moresby, showing general facies and pattern.

previously as an item in description, aceepted as a simple variation, or taken as no more than speeific in nature.

Following the aecount of the New Guinea leeehes, I review the nature of genera as previously reeognized for haemadipsine leeehes, review the general somital annulation in hirudiniform leeehes, and from the latter show that unusual levels of annulation in vii, viii, xxiv and xxv, as also others, must now be aeeepted as generic in status.

In the deseriptions below, I give a total of the number of annuli on the dorsum between xxiii a_2 and the anus. I do this beeause it is often diffieult to determine with full eonfidenee the annulation of xxiii, xxiv and xxv, sinee there are rarely reeognizable somital organs on xxiv. Annulus xxiii a_2 is recognizable by its somital sense organs, and/or by the nephropores lateral on b_2, immediately anterior to a_2.

It is only with further specimens from Fife Bay that we can be fully eonfident of the nature of *tristriata* as a speeies, but the following assembly of information demonstrates the nature of a genus in New Guinea whieh is distinet from the Australian *Chtonobdella* and other genera provided for 5-annulate land-leeches.

1. *Geobdella tristriata* Goddard 1909.

The species is deseribed and figured from a single strongly contraeted preserved specimen, 16 mm long, collected at Fife Bay, British New Guinea. Goddard thanks Mr. T. Steel for the opportunity to study the speeimen, and reeords 'Domani' as the native name for the leeeh at Fife Bay.

The deseription is brief and generalized, while the figure is poor; both essentially of no zoological value other than establishing the leech as of moderate size, the oeular areh haemadipsine, 5-annulate, light brown, pattern of two paramedian dark bands defining a median dorsal stripe and three longitudinal bands on the venter. The loeation of the genital pores was not determined.

Fife Bay is on the E. end of the S. eoast of Papua, near Isuisu, on longitude 150°E.

2. *Haemadipsa noxia* and *Haemadipsa papuensis.*

These are described and named by Blanchard (1917) in his monograph on the haemadipsine leeehes. They are of moderate size, the largest speeimens being 24 and 25 mm long. Both are based on speeimens from Moroko, inland from Port Moresby, 9°25′ S., 147°45′ E., altitude 1,300 m.

The deseriptions are brief, restricted to the annulation of somites based on the somital limits of Whitman, and the location of the genital pores. The annulation given below has been eonverted to the somital limits of Moore by diagrammatic analysis. The speeies are not figured.

Haemadipsa noxia is deseribed from seven specimens. The colour is given as greyish yellow; the pattern, some small blaek patches on the back. The somital annulation on the dorsum is v 2-annulate, vi 3-annulate, vii 5-annulate ($b_1 + b_2$),a_2,b_5,b_6—the 1st annulus described as "étant parfois dédoublé à la faee dorsale" can be taken as a_3 below and vii 4-annulate below, viii to xxii eomplete 5-annulate, xxiii incomplete 5-annulate b_1,b_2,a_2,($b_5 + b_6$) above and a_3 below, xxiv 3-annulate, xxv to xxvii uniannulate, 8 annuli on the dorsum behind xxiii a_2. Genital pores xi b_6 and xii b_6.

Haemadipsa papuensis, deseribed from 3 specimens; no reference to colour or pattern. Somital annulation v 2-annulate above, vi 3-annulate, vii 3-annulate, viii to xxii complete 5-annulate, xxiii 4-annulate, xxiv 3- or 2-annulate ($a_1 + a_2$) or a_1a_2, xxv to xxvii uni-annulate, 7 annuli on the dorsum posterior to xxiii a_2. Genital pores xi b_6 and xii/xiii (xiii b_1).

Blanehard plaeed all 5-annulate leeehes with an haemadipsine ocular areh in the g. *Haemadipsa* based on the trignathous *H. zeylanica* of S. India and Ceylon.

3. "*Chtonobdella tristriata* Goddard".

Augener (1931) identified land-leeehes from Vogelkop at the far W. end of New Guinea as *tristriata*, and finding them to be duognathous, transferred *tristriata* to the g.

Chtonobdella.

The colour is given as (preserved) dorsum generally greyish yellow; the venter paler, whiter, immaculate; the pattern on the dorsum two paramedian longitudinal brown bands, each more or less interrupted and poorly represented posteriorly; a narrow dorsomedian stripe in one specimen, broken in another; dark brown supramarginal bands widening segmentally to enclose a patch of the background colour.

The annulation is based on a recurring elongate annulus, the fifth in each complete somite, and only the number of annuli between the genital pores. There is no way in which the general somital annulation can be derived from this data.

As described by Augener, the specimens cannot be recognized as any more than duognathous 5-annulate land leeches of moderate size, up to 25 mm long, with 4·5 annuli between the genital pores. The record has value in demonstrating the wide range of 5-annulate land leeches in New Guinea.

4. *National Museum of Victoria G834*

A single specimen of 5-annulate land leech, 22 mm long. There is a label reading "Fife Bay, British New Guinea. Bush leech. Native name—Domani".

The label carries the proposal of a new generic name, with 'steeli' as a proposed specific name, and the date of April 1902. No account of this specimen has been published. The proposed generic and specific names have not been used. The geographic origin, the data on the label including the name Domani, and the use of the name of Mr. Steel, can only be taken as associating this specimen with the one described by Goddard.

G834 is generally dark brownish in colour with no remains of other colour or pattern. Preserved in alcohol, it is hardened and unsuitable for the study of the auricles, jaws, etc., or for dissection.

It is moderately contracted to be heavy bodied, the dorsum transversely convex, margins obtusely rounded, venter low convex. The velum is thick, its margins continuous with the margins of the body which widens rapidly initially, the margins then parallel along the greater length of the body, narrowing slightly to the base of the posterior sucker which is 4 mm wide, wider than long, and slightly wider than the maximum width of the body.

Interannular and intersomital grooves equivalent, somital limits not directly recognizable, annuli strongly areolate and so strongly contracted that the relative lengths are not generally assessable, somital sense organs erratically detectable, nephropores on ix to xxiii obvious as small open pits on b_2.

The velum folded, concealing somites i to iii, iv uniannulate with the 1st nephropore lateral to the ocular areola, v 2-annulate above with the 4th eyes on $a_1a_2 > a_3$ and uniannulate below, vi 3-annulate above $a_1 > a_2 < a_3$ with the 5th eyes on a_2 (and possibly 3-annulate below), vi a_2 and ix a_2 separated on the dorsum by 13 annuli, vii 5-annulate above $(b_1 + b_2),a_2,b_5,b_6$ (? 4-annulate below), viii to xxii complete 5-annulate, xxiii distinctly 5-annulate on the dorsum $b_1,b_2,a_2,(b_5 + b_6)$ and can only be interpreted as 4-annulate below $b_1 + b_2 + a_2 + a_3$, 9 annuli on the dorsum between xxiii a_2 and the anus, xxiv 3-annulate a_1,a_2,a_3, and a_3 the last annulus complete across the venter, xxv 2-annulate, xxvi and xxvii uniannulate, anus at the posterior edge of xxvii, auricles elongate, lateral to xxiv a_3 to xxvii, ventral margin continuous without distinct lobes.

Dorsum of the posterior sucker strongly areolate, the venter with a large central disc (2 mm wide) which is strongly papillate, and extending from this, strongly developed muscular ridges dividing to a total of about 80 at the edge of the sucker, clamp small and including only 5 ridges.

Genital pores xi and xii b_6.

5. *Rain forest, Brown River, Port Moresby. Two collections Dr. W. Ewers.*

(a) 12/10/71. A single specimen 12 mm long. Figs. 1-2c-e.

Pattern. On the venter longitudinal bands of closely approximated large maculae, a median band and a single pair well spaced from the median, the three about equal in width; the laterals longer than the median.

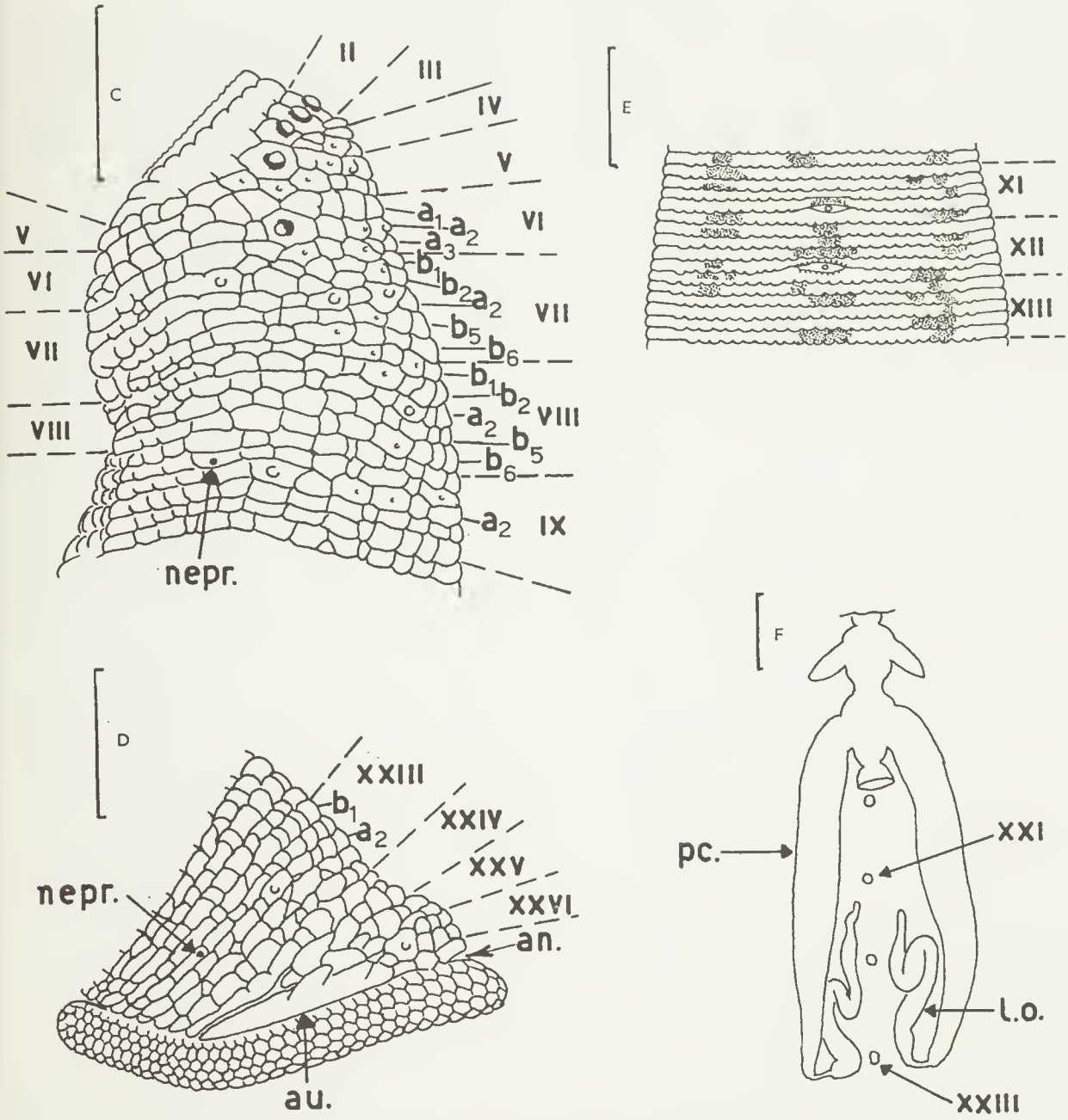

Fig. 2—*Domanibdella* gen. nov. Left lateral views of specimen 5(a), showing somital annulation; c of somites i to ix. d, of somites xxiii to xxvii, the auricle and posterior sucker. e, ventral aspect of somites xi to xiii of specimen 5(a) showing the location of the genital pores. f, the crop showing caecation on somites xviii and xix, postcaeca, and lambertian organs in 5(b)4.

Somital ganglia and somites indicated by roman numerals, somital limits by broken lines, annuli 'a_2' etc., somital ganglia represented at relative size. Scales equal 1 mm.

Abbreviations: an. = anus, au. = auricle, l.o. = lambertian organ, nepr. = nephropore, p.c. = postcaecum.

On the dorsum a median dorsal light stripe from in the ocular area posteriorly into xxv, occupying the median field and defined by a narrow dark band along each of the lines of the paramedian sense organs; these bands (possibly more complete in life) here much broken with the median stripe continuous into the adjacent fields which otherwise appear to be erratically reticulate. Towards the posterior end of the body, the pattern breaks for a few somites into transverse rows of maculae, 3 maculae on each side, suggestive of a possible pattern on the dorsum based on 6 longitudinal dark bands, converging and diverging to provide the reticulations which might extend to the line of the supramarginal sense organs on each side.

Marginal field clear, light.

Although small, there are no distinct couplets or triplets of annuli as seen in juveniles. Somite iv incomplete 2-annulate, v 2-annulate above a_1a_2 with the 4th pair of eyes $>$ a_3, uniannulate below, vi 3-annulate above $a_1 = a_2$ with the 5th pair of eyes $>$ a_3 2-annulate below, vii incomplete 5-annulate above ($b_1 + b_2$), a_2,b_5,b_6 4-annulate below with a_1,a_2,b_5,b_6 the furrow b_1/b_2 reaching to the intermediate line of sense organs, viii to xxiii complete 5-annulate, xxiv briefly 3-annulate across the dorsum, then 2-annulate on the lateral and ventral aspects, xxv and xxvi incomplete 2-annulate, xxvii uniannulate, anus at the posterior margin of xxvii.

Auricles formed by the lateral margins of xxv to xxvii, very large, the lateral face and the ventral margin smooth with no indication of division into marginal lobes, no cavern but only a deep groove between the ventral face of the auricle and the dorsum of the sucker, no indication of a papilla concealed by the auricle.

Dorsum of the posterior sucker strongly areolate as five or six concentric rows, ventral face with a wide coarsely tuberculate central area, and about 80 muscular rays terminating on the margin.

Genital pores xi and xii b_5/b_6.

(b) 8/10/71. Four faded specimens preserved in alcohol.

Specimen 1. Length 15 mm, grossly contracted, unsuitable for general study. Dorsum a clear median longitudinal stripe, openly reticulated lateral to this, margins plain, venter a median band of maculae from in vi and vii to about xxi, and one pair of wide spaced bands of small maculae, each macula centred on a ventral intermediate sense organ from in vii back into about xxii—the bands broken irregularly over one or more somites.

Somite vii distinctly 5-annulate above ($b_1 + b_2$) a_2,b_5,b_6, the furrow b_1/b_2 lacking in the marginal fields and vii 4-annulate below, xxiii b_1,b_2,a_2 ($b_5 + b_6$) above, b_5/b_6 extends into the submarginal fields and a_3 across the venter.

Ventral surface of the posterior sucker coarsely tuberculate across the middle third, about 80 muscular rays terminating on the margin of the sucker.

Genital pores xi and xii b_5/b_6.

Duognathous, teeth minute, close.

Specimen 2. Length 15 mm, moderately extended, twisted along its length. Unsuitable for general study.

Dorsum a light stripe filling the median field from in the ocular arch to xxiv/xxv, on either side of this three longitudinal narrow broken bands which are separate, converge on each second somite, providing a poorly defined elongate reticular pattern. Margins clear, venter with three short longitudinal rows of maculae, the median from x/xi to about xviii, the laterals from in viii to xv (left) and xvi (right).

Annulation of vii, viii, xxiii obscure. Auricles and posterior sucker as in Specimen 1. Clamp minute.

Genital pores central in xi b_6 and xii b_6.

Specimen 3. Length 14 mm. Pattern greatly diminished.

Dorsal median stripe very poorly defined behind ix, inner paired bands along the lines of the paramedian sense organs broken into lengths shorter than a somite with a sense organ central in each length, a similar band parallel and lateral to and narrowly spaced from the inner band is of the same form and extent, and an outer short band is wider spaced from the middle band.

The dark bands being parallel, there is nothing of a reticular pattern on the dorsum.

The dorsal pattern is possibly a late form of a simple juvenile pattern.

Margins plain, light. Venter with no indication of a median row of maculae, lateral rows of maculae from in ix back into xxiii.

Ventral face of posterior sucker as in Specimen 1.

Somite vii ($b_1 + b_2$), a_2,b_5,b_6 above, b_1/b_2 ends in the marginal field and a_1 across the venter, xxiii incomplete 5-annulate.

Genital pores central in xi and xii b_6.

Specimen 4. Length 22 mm, dissected. Fig. 2f.

Yellowish across the dorsum, margins and venter white.

The median light stripe on the dorsum begins in the ocular area, expands to the left in vi and vii, terminates in x, broken to xiii, and then continues from in xiii to enter xxiv; dark bands poorly defined, erratically much broken; a reticular pattern indicated, but very incomplete; margins light, venter with a median and a pair of strongly marked maculate rows, the median from about x to xx, the laterals from viii/ix to xxiv.

Somite vii ($b_1 + b_2$), a_2,b_5,b_6 above, the furrow b_1/b_2 extends into the margins, a_1 across the venter, viii to xxii complete 5-annulate, xxiii incomplete 5-annulate, b_1,b_2,a_2, ($b_5 + b_6$) above a_3 below, xxiv 2-annulate a_3 complete across the venter as a thin ridge, 9 annuli on the dorsum posterior to xxiii a_2.

Ventral face of the posterior sucker as in Specimen 1.

Genital pores xi b_5/b_6 and central in xii b_6.

Duognathous, teeth minute, entrance to the pharynx at vi/vii or just in vii, pharynx short and very thin walled, terminating at viii/ix, crop compartments each with one pair of caeca originating from the middle third of the compartment, as also the postcaeca on xix. Postcaeca terminating in xxiii in the paramedian chambers, each continuing as a short narrow lambertan duct, the length a little more than the width of the lambertian organ which it joins. Lambertian organ elongate, cylindrical, ventral to the posteaeeum, extending anteriorly, folded in the middle of its length in an s-shape, relatively much longer than seen in other land-leeches.

Reproductive systems poorly preserved, typically haemadipsine (v. Richardson 1969b), testes simple saccular with the most anterior at xiii/xiv, vas deferens extending along the paramedian chamber, entering the median chamber at xi/xii, the anterior region of the paired male duct formed on a posteriorly directed primary loop in the median chamber, epididymis on the recurrent limb. A wider sperm duct on the procurrent limb terminating in a small muscular ejaculatory bulb lateral to ganglion xi, short ejaculatory duct connecting directly to the male atrium in the posterior half of xi, the atrium ventral to the nerve cord and concealed by prostate glands, the loops on the anterior region of the male paired ducts in tandem, the left anterior to the right.

Saccular ovaries, obtusely ovate, situated in the posterior half of xii. Oviducts very short, joining without forming an obvious atrium. The female median region formed on a posteriorly directed primary loop, reflecting at the level of ganglion xiii, the posterior face of the elbow of the loop expanded into a thin-walled glandular sac terminating at ganglion xv; the recurrent, initial limb of the loop, thick-walled, about 0·5 the diameter of the strongly muscular thick-walled procurrent limb which terminates at the genital pore.

I could not detect longitudinal internal muscles terminating in the base of the posterior sucker; the paramedian palisades were not obviously thickened in the posterior somites of the body.

Summary. Section 1 shows *tristriata* as a small 5-annulate land leech with three longitudinal dark bands on the venter with broken paramedian bands on the dorsum.

Section 4 provides a somital annulation in which vii is incomplete 5-annulate, viii to xxii complete 5-annulate, xxiii incomplete 5-annulate with 9 annuli on the dorsum posterior to xxiii a_2, the genital pores at xi and xii b_6.

Section 5 contains some specimens with the ventral pattern of 1, and also a poorly formed reticular pattern based on longitudinal bands on the dorsum, vii incomplete 5-annulate, viii to xxii complete 5-annulate, xxiii incomplete 5-annulate with 9 annuli posterior to xxiii a_2

or (a_1) complete 5-annulate with 10 annuli posterior to xxiii a_2, the genital pores, xi and xii b_5/b_6 in two, xi b_6 and xii b_6 in two, and xi b_5/b_6 and xii b_6 in one.

My collection of duognathous 5-annulate land leeches from eastern Australia includes specimens from Cairns, N. Queensland to S. of Sydney, N.S.W.

None of this material has the somital annulation shown in Sections 4–5. In all these specimens, as also in the type specimens of *Chtonobdella limbata* which I have now examined, vii is complete 3-annulate, viii complete 4-annulate, ix to xxiii 5-annulate; 7 (rarely 6) annuli on the dorsum posterior to xxiii a_2, genital pores xi b_5/b_6 (b_5) and xiii b_1/b_2 (b_2,b_2/a_2).

The only other duognathous 5-annulate genus is *Idiobdella* Harding 1913 of the Seychelles: vii 3-annulate, viii 4-annulate, ix to xxiii 5-annulate, 7 annuli posterior to xxiii a_2, genital pores xi b_1/b_2 and xiii a_2. The genus is monotypic. In the type, the anterior region of the male paired duct is thrown into a secondary (not primary) loop during development, reflecting briefly from the middle of xiii into xiv, an epididymis (if present) short and poorly formed, a sperm duct occupying the greater part of the length of the anterior region which terminates with a narrow duct without an ejaculatory bulb (v. Harding 1913, pl. 6, fig. 6).

Although we will not know the precise specific nature of Goddard's *tristriata* until suitable specimens have been obtained from the type locality, it is now fully clear in the above that *tristriata* as also *noxia*, and the leeches in Section 5 from the Brown River, are congeneric and members of a genus distinct from *Chtonobdella* and *Idiobdella*.

The small amount of variation seen in the annulation of the posterior somites of the body is of the same order as was found in the 4-annulate *Neoterrabdella australis* Richardson 1969, a leech in which these somites also exhibit a higher level of annulation than in other 4-annulates.

It is proper now to provide a new genus based on the above assembly, to select *tristriata* as the type species of the new genus, and to indicate the specimen 5a—12/10/71 as the specimen before me in the proposal of this genus.

Domanibdella gen. nov.

Derivation: Domani, native name for a land-leech in the Fife Bay area, Papua, + bdella = a leech, f.

Duognathous, teeth minute and numerous, somites viii to xxii complete 5-annulate, vii incomplete 5-annulate, xxiii complete (or incomplete) 5-annulate, 10 (9) annuli on the dorsum following xxiii a_2, xxiv complete 3- or 2-annulate, genital pores xi b_5/b_6 (b_6) and xii b_5/b_6 (b_6), auricles large and restricted to the lateral ends of xxv, xxvi and xxvii, the ventral margin straight not lobate, pharynx thin-walled terminating at viii/ix, crop compartments each with a pair of primary caeca median in the length of the compartment, postcaeca terminating as a short lambertian duct connecting to an elongate lambertian organ beneath the posterior portion of the postcaecum, reproductive systems haemadipsoid: testes saccular, vasa deferentia entering the median chamber at xi/xii, anterior region of the male paired duct reflected as a posteriorly directed primary loop in the paramedian chamber, an epididymis on the recurrent limb, sperm duct on the procurrent limb which terminates in a small muscular ejaculatory bulb, ejaculatory ducts very short, male median region micromorphic, a thin-walled amyomeric atrium entirely ventral to the nerve cord; female reproductive system mesomorphic and myomeric, saccular ovaries posterior in xii, oviducts very short joining without a defined atrium, median region formed on a posteriorly directed primary loop, recurrent limb, thick walled, narrower than the strongly muscular procurrent limb; glandular sac formed as a posteriorly directed expansion of the posterior face of the elbow of the primary loop.

Pattern: Longitudinal dark bands, simple to reticulate on the dorsum; simple longitudinal bands (maculate) on the venter.

Terrestrial, sanguivorous. Australian Region, Papuan.

Type species: *Geobdella tristriata* Goddard 1909.

The Brown River leeches and Blanchard's *Haemadipsa uoxia* have the general somital annulation of *Domanibdella*.

The Brown River leeches have the ventral pattern described for *tristriata* by Goddard, b_3 differing in lacking the median band. I can see no reason at this time to separate the Brown River leeches from *tristriata*.

Blanchard's *uoxia* has 8 annuli posterior to xxiii a_2, the genital pores in xi b_6 and xii b_6, and differ in having a pattern of black patches on the dorsum. The pattern can only be taken at this time as separating *uoxia* from *tristriata*.

Blanchard's *papuensis* differs in having vii 3-annulate, xxiii 4-annulate, 7 annuli behind xxiii a_2, xxiv incomplete 3-annulate, genital pores xi b_5/b_6 and xii/xiii (xiii b_1). If valid, these differences set *papuensis* apart from *uoxia* and *tristriata*, and leave some small doubt that *papuensis* can be admitted to *Domanibdella* other than provisionally. Certainly it cannot remain in *Haemadipsa* or *Chtonobdella*.

Dispersal of study material

5. Rain forest, Brown River, Port Moresby. Coll. Dr. W. Ewers, University of Papua and New Guinea.

5(a). 12/10/71. Single specimen 12 mm, National Museum of Victoria G2276.

5(b)4. 8/10/71. Single specimen 22 mm, dissected. National Museum of Victoria G2277.

5(b)1,3. 8/10/71. Two specimens 15 and 14 mm, Papua and New Guinea Public Museum and Art Gallery, Port Moresby.

5(b)2. 8/10/71. Single specimen 15 mm, Australian Museum, Sydney W4302.

Systematic values in general somital annulation

This discussion is concerned with the nature of the general somital annulation in those leeches which can be referred to now as 'hirudiniform', i.e. having the eyes arranged in an ocular arch, typically five pairs, the lateral and ventral margins of the anterior sucker formed by somite v, the pharynx euthylaematous with a dorsomedian and a pair of ventrolateral primary internal muscular ridges, in most each ridge subdivided lengthwise.

This is a diverse group including terrestrial, terricolous, amphibious, aquatic, sanguivorous and macrophagous leeches. The group exhibits a range in the annulation of complete fully annulate somites from 3-annulate to 9-annulate and more.

The first descriptions of leeches included the total number of annuli. In 1886 Whitman showed the body to be divided into 'somites'; the division of the 'somites' into a middle series in which all 'somites' have the annuli always complete on all aspects, and the same number of annuli in all; and an anterior and a posterior series in which there is progressive reduction in the number and completeness of the annuli from the 'somite' contiguous with the middle series, to the end of the body. Whitman made the number of 'somites' in the middle series a primary generic characteristic, but it must be recognized that Whitman combined this feature with others (number of annuli between the genital pores, jaws, dentition, nature of the pharynx, etc.) in his definition of genera. In terms of the true morphological limits of the somites as established by Moore, Whitman's series are: anterior i to viii, middle ix to xxiii, posterior xxiv to xxvii.

The development of the concept of 'genus' in the hirudiniform leeches followed a common pattern which can be briefly reviewed in the haemadipsine leeches.

In 1859 Tennent recognized that a land leech from Ceylon had annuli grouped in fives, 3 jaws, 5 pairs of eyes arranged in an ocular arch, all as in *Hirudo medicinalis*, but differed in having the 3rd and 4th pairs of eyes on contiguous annuli. On this difference, Tennent established the g. *Haemadipsa*. This arrangement of eyes became recognized as the 'haemadipsine ocular arch', and all leeches with this arch were subsequently accepted as 'haemadipsine'. *Haemadipsa zeylanica* was shown to have 5 annuli between the genital pores, as in *medicinalis*, but a lower total number of annuli.

Further genera were defined on:

(a) the number of annuli between the genital

pores—*Chtonobdella* Grube 1866 (Australian, near Sydney, 5-annulate, 7·5 annuli between the genital pores), (also *Geobdella* Whitman 1886, specimens sent Whitman by Haswell, *Geobdella* abandoned as preoccupied).
(b) the number of annuli in a somite in the middle series of somites—*Mesobdella* Blanchard 1893 (Neotropical, 3-annulate), *Phytobdella* Blanchard 1894 (Oriental, 6-annulate), *Planobdella* Blanchard 1894 (Oriental, 7-annulate), *Philaemon* Blanchard 1897 (Australian/Oriental, 4-annulate).

Blanchard, Moore and others, followed Whitman in placing generic values on the number of somites in the middle series in aquatic hirudiniform leeches where this ranges from 14 to 17, but Blanchard (1917) in his monograph of leeches assembled as having the haemadipsine ocular arch, adhered to a separation of genera as in (b) above.

In this way Blanchard assembled 2-jawed and 3-jawed 5-annulate land-leeches in the g. *Haemadipsa*, separating species in this (as in other genera) on the number of annuli between the genital pores, the somital location of these and other external landmarks, and differences in the annulation of somites such as viii and xxiii. Colour and pattern were regarded as most highly variable, included briefly as items in specific descriptions, and given no particular value.

Blanchard did not make use of the important earlier discoveries by Miss A. M. Lambert in her excellent studies on Australian land leeches. In two papers (1898, 1899) Miss Lambert showed *Philaemon* and '*Geobdella*' were similar in being duognathous (lacking a dorsomedian jaw), and having the postcaeca each ending in a duct leading to a saccular blind organ (now the lambertian organ).

These discoveries provided a departure from the 'genus' of Blanchard. The g. *Idiobdella* Harding 1913 was based on a 5-annulate land leech from the Seychelles, duognathous, 11·5 annuli between the genital pores, and lacking lambertian organs; the g. *Tritetrabdella* Moore 1938, a 4-annulate land-leech from Malaya, trignathous, and lacking lambertian organs; the g. *Nesophilaemon* Nybelin 1943, a 4-annulate from Juan Fernandez Islands, duognathous and lacking lambertian organs.

Soos (1967) reviews all too briefly the major zoological problems he encountered in constructing a key to the genera of land-leeches, problems stemming essentially from the zoological inadequacy of Blanchard's genera as demonstrated by Lambert, Harding, and Moore.

Following the latter workers, I had no hesitation in establishing (1969b) *Neoterrabdella* for an Australian duognathous land leech, 4-annulate, lacking lambertian organs. This has other novelty: elongate auricles bordering not only xxv, xxvi, and xxvii as is usual, but also xxiv, and an unusually high level of annulation on the somites in the posterior series. I demonstrated a distinctive morphology for the reproductive systems common to all auriculate land leeches as so far known. On the basis of the morphology of the reproductive systems, etc., I removed *Nesophilaemon* and later (1971) *Mesobdella*, both with an 'haemadipsine ocular arch' from the Haemadipsidae and associated them with the neotropical fauna. They are now in the Mesobdellidae Ringulet 1972.

I have shown (1969a) that genera are characterized for aquatic sanguivorous and macrophagous hirudiniform leeches in the morphology of the pharynx and associated structures, combined with the distinctive morphology and morphological relationships of organs on the anterior region of the male paired duct, as also the diversity of distinctive morphological forms of the male and female median regions. This divided some earlier genera and provided additional genera, many having a common general somital annulation. This has led to the demonstration of systematic values in the topography of pattern, and shown pattern may be similar in related genera Richardson 1970, 1972b).

As I extend my experience of the auriculate 5-annulate leeches in E. Australia, I find these to be similar, monotonous in general somital annulation, essentially constant in the number of somites in the middle series, and the anterior and posterior series each reducing in the one

manner; a similar somital annulation for the genital pores, as also the auricles, etc. So far I have seen in them no significant variation in the nature of the pharynx and associated structures, or in the morphology of the reproductive systems. There is variety in the form of the lambertian organs, but this has not yet been adequately studied.

With Blanchard and others all would be one species in a single genus, as also a single genus in terms of the principles I have provided for genera in other hirudiniform leeches.

All have a pattern of longitudinal contrast stripes dividing the dorsum into bands. Some of the 5-annulates separate as having distinctive patterns, differences in pattern as distinctive as separate groups of genera in the aquatic sanguivores in the Richardsonianidae. Others have superficially similar patterns but separate in terms of distinctive differences in details of the topography of the patterns.

Pattern provides indications for generic separations of the E. Australian auriculate 5-annulates equivalent to the generic separations now established for the Australian aquatic jawed sanguivores. Such auriculate 'genera' cannot be substantiated in the combination of the characteristics employed with the latter, at least not so far as I have gone.

Experience with *Neoterrabdella* and also the Australian aquatic jawed sanguivorous g. *Habeobdella* directs attention to the need for an examination of the nature of the general somital annulation other than in Whitman's use of only the number of somites in the middle series as a systematic characteristic. In doing this, it is found that we can divide the hirudiniform genera into two major groups, each group diverse in content and not in itself of systematic status.

Mesobdella (Mesobdellidae, Neotropical) is the only hirudiniform genus with a 3-annulate condition in the middle series, and this series consists of vii to xxiii, with the posterior series having xxiv incomplete 3-annulate, xxv and xxvi 2-annulate (Richardson 1971).

A 4-annulate condition in the middle series in hirudiniform leeches is known only in the Haemadipsidae (Australian/Oriental) and the Mesobdellidae (Neotropical). In the majority of these genera the middle series is viii to xxiii (in some xxiii incomplete), and the posterior series (incomplete xxiii) xxiv 2- or uniannulate, xxv to xxvii uniannulate and incomplete.

In the great majority of 5-annulate genera of hirudiniform leeches (Haemadipsidae, aquatic sanguivores and macrophages) the middle series is ix to xxiii or ix to xxiv, and rarely (*Aetheobdella,* Ornithobdellidae, Australian; *Whitmania* 1 sp., F?, Oriental; *Semiscolex* 1 sp., Semiscolecidae, Neotropical) viii to xxiv.

In terms of general somital annulation, the above forms a hirudiniform group in which with few exceptions vii is complete 3-annulate (exceptionally incomplete 4-annulate), vi incomplete 3-annulate (exceptionally complete 3-annulate), v incomplete 2-annulate (exceptionally complete 2-annulate), iv to i not formed ventrally with iv 2- or uniannulate, iii to i uniannulate.

In this group with the exception of *Mesobdella,* viii is 4-annulate in the great majority, exceptionally incomplete 5 - annulate, and rarely complete 5-annulate.

The second group includes a relatively small number of hirudiniform genera in which the annulation of the middle series is 6- 7- 8- or 9-annulate. I lack data on a 12-annulate still in the g. *Diestecostoma.*

In the 6-annulate *Phytobdella* (Haemadipsidae, Oriental/Australian) vi is 3- to 5-annulate, vii 5- or 4-annulate, viii 6- or 5-annulate, ix to xxiii 6-annulate, xxiv 2-annulate, xxv to xxvii uniannulate (v. Moore 1944).

In the 6-annulate species of *Gastrostomobdella* (Gastrostomobdellidae, Oriental) v is 2-annulate or incomplete 3-annulate, vi 2-annulate or incomplete 3-annulate, vii complete 4-annulate, viii 5- or 6-annulate, ix to xxiii 6-annulate, xxiv 4-annulate, xxv 3-annulate, xxvi 2-annulate, xxvii uniannulate (v. Moore 1929).

The 7-annulate g. *Planobdella* (Haemadipsidae, Oriental) is known only in Blanchard's descriptions (1917). From this the somital annulation appears to be: vi 5- (? complete) annulate, vii incomplete 6-annulate, viii to xxii (possibly also xxiii) 7-annulate, xxiv ?

The 8-annulate g. *Kumabdella* (Gastrostomobdellidae, Oriental) has: v 2-annulate,

vi 6-annulate above 4-annulate below, vii 5-annulate above 4-annulate below, viii to xxv 8-annulate, xxvi complete 5-annulate, xxvii incomplete 2-annulate (Richardson 1972a).

The terrestrial 8-annulate g. *Diestecostoma* (Diestecostomidae, Neotropical) can be included as most certainly hirudiniform. In this v is incomplete 2-annulate, vi 3-annulate, vii 3-annulate (incomplete 4-annulate), viii 4-annulate, ix, x, xi each 5-annulate, xii 7-annulate, xiii to xxii 8-annulate, xxiii 7-annulate, xxiv 6-annulate, xxv 3-annulate, xxvi and xxvii (?) 2-annulate (v. Moore 1946).

The 9-annulate *Diestecostoma* (Diestecostomidae) has: v 2-annulate above (?) below, vi complete 3-annulate, vii 5-annulate above and 3-annulate below, viii 5-annulate above 4-annulate below, ix 6-annulate, x 7-annulate above 6-annulate below, xi to xxiii 9-annulate, xxiv (?) 9-annulate (v. Ringuelet 1944).

It is possible that I have omitted other examples of significant general somital annulation in hirudiniform leeches. The above is sufficient to demonstrate the need to consider the status of all three series, and not solely the number of somites in the middle series, in formulating the nature of genus in hirudiniform leeches.

Some general principles can be taken from both groups. Only in the 3-annulate *Mesobdella* does vii have the same annulation as viii and the somites of the middle series, giving the impression that vii has shifted from the anterior to the middle series, but here vii has the same annulation as in 4- and 5-annulates of the first group and in the 8-annulate *Diestecostoma*. Somite vi is essentially incomplete 3-annulate in the first group, of this form in the 6-annulate *Gastrostomobdella*, the 8- and 9-annulate *Diestecostoma*; v essentially incomplete 2-annulate in the first group, and of this form in *Gastrostomobdella*, and 2-annulate in the 8-annulate *Kumabdella*.

In the posterior series, xxvii is most commonly uniannulate in both groups, xxvi essentially 2-annulate in the first group, as also in *Gastrostomobdella* and *Diestecostoma* in the second group, xxv 3- or 4-annulate in the first group (excepting most haemadipsines, uniannulate as also xxvi) and 3-annulate in *Gastrostomobdella* and *Diestecostoma*.

Somites viii and xxiv exhibit changes in form, but only in some increasing to the level of the annulation in the middle series. There is the clear expression of conservatism in form in both the anterior and posterior series, and to a degree which is significant.

Such conservatism in *Diestecostoma* is expressed in two genera of the second group in which the anterior limit of the middle series is xiii and xi, in contrast to ix as the general anterior somite in this series.

The great majority of aquatic hirudiniform leeches have a 5-annulate condition in the middle series. Terrestrial and terricolous genera exhibit also higher and lower levels of annulation in this series.

It can be proposed from the above that the general somital annulation is the result of two differing and independent processes:
(a) Cotylization, processes controlling the formation of the anterior and posterior suckers involving stabilization in progressive morphological reduction of the somites in the anterior and posterior series of somites, and
(b) A process leading to a uniformity of complete annulation in the somites of the middle series which constitute the greater length of the body.

Interaction between these processes can be seen in the second group where, in some, a higher level of annulation is imposed on the somites in the anterior and posterior series, but even in these the somites otherwise exhibit the conservative trends seen in these series in the first group.

The result is irregular and cannot be reduced to a single simple pattern, as can be seen in the variety of annulation on the anterior and posterior series in the 6- and 8-annulate genera.

The essential stability of form in these series in the first group of genera, and the limited number of departures from this form, can be taken in combination as demonstrating that such departures are not simply random or erratic, and are to be recognized as an essential change in the processes controlling the formation of the general somital annulation.

Such departure from the common pattern of general somital annulation in the first group is to be given systematic value at the generic level, as has been demonstrated where genera have been characterized on other grounds: *Aetheobdella* viii 5-annulate, *Domanibdella* viii 5-annulate, vii incomplete 5-annulate, etc., *Neoterrabdella* xxiv 3-annulate, *Habeobdella* xxv 5-annulate, etc.

This review illustrates the traditional contradiction in practice which, early with Whitman and since then, has accepted the level of annulation of xxiv and viii as generic in value in aquatic and other hirudiniform leeches, but not in the haemadipsines in which these features have been allowed no value or only specific value at best.

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