

The genus *Clelandia* Johnston, 1909
and its affinities with *Parvitaenia*
and *Neogryporhynchus* (Cestoda, Dilepididae) (*)

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Résumé.

Le genre *Clelandia* Johnston, 1909, et ses affinités avec *Parvitaenia* et *Neogryporhynchus* (Cestoda, Dilepididae).

La diagnose de *Clelandia* a été modifiée. Discussion de la validité du genre, des caractères utilisés dans la diagnose, et des affinités avec *Parvitaenia* et *Neogryporhynchus*. D'après la morphologie du genre et la spécificité qui s'observe chez les cestodes dilépidides à l'intérieur de l'ordre des Ciconiiformes, il faut croire que l'hôte de *Clelandia* appartient au sous-ordre des Ardeae, et non pas des Ciconiae, et que la diagnose de l'hôte, douteuse dès l'origine, est erronée. *Clelandia* paraît confirmer que le genre *Parvitaenia*, parmi les cestodes des Ciconiiformes, est un centre de radiation évolutive, avec des aspects particuliers dans la Région australienne, et qu'il ne représente pas une unité homogène.

Summary.

The diagnosis of *Clelandia* has been amended. The validity of the genus and its closeness to *Parvitaenia* and *Neogryporhynchus* are discussed. On the basis of its morphology and of the specificity of the dilepidid cestodes within the order Ciconiiformes, one may admit that its host belongs to the suborder Ardeae, and that the original doubtful diagnosis of the host was wrong. *Clelandia* seems to confirm that the genus *Parvitaenia* is a nucleus of evolutionary radiation among cestodes of the Ciconiiformes, with peculiar traits in the Australian region, and that it isn't a homogeneous unit.

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This work must be considered the completion of a recently published monograph on the Dilepididae of Ciconiiformes (Bona, 1975), to which we refer concerning information we need now as a basis for discussion and comparison.

Clelandia parva Johnston, 1909, still presented an old unsolved problem; as the original description left many doubts, we considered *Clelandia* as a « *genus incertum* ». It was hard to fit this monotypical genus into the context of the other genera of Dilepididae parasitizing the Ciconiiformes. The holotype being in good condition, and many data being by now available about the genera to be compared with *Clelandia*, we are enabled to go beyond a mere redescription of this species and to gain a deeper knowledge of relationships between genera within a limited group of hosts.

Material

The holotype, on which our redescription is based, consists of a complete well-preserved specimen, having some hooks in good position, deposited at The Australian Museum, Sydney, and labelled: « *Clelandia parva* Instn, from Jabiru?, *Xenorhynchus asiaticus*, Jervis Bay - Type, 1893, N° W 5; Cestode from Jaby ». The exact scientific name of the bird (Ciconiiformes) should be: *Ephippiorrhynchus asiaticus australis* (Shaw) (syn.: *Xenorhynchus*), subspecies of *asiaticus* Latham, spread from New Guinea to Australia (Kahl, 1972).

All measurements are in micrometers unless otherwise indicated; we state first the length, then the width.

Clelandia parva Johnston, 1909

(Fig. 1, 7-17, 20)

Redescription.

Length: 9 mm, including the first shed proglottis. Anterior part much stretched. Brittleness of strobila is confirmed, but only starting from the first gravid segments. Proglottids craspedote; their front side is much narrower than the posterior one. Adult proglottids wider than longer, 245-275 × 560-602; gravid ones, shed, up to 525 × 917. Strobila of 54 segments (without the shed gravid ones), consisting, after the youngest part, of: 6 segments having well-defined testes and not yet a clear edged small ovary; 5-6 having a visible ovary (of these only 2 are wholly mature); 1 a disgregating ovary and an uterus appearing simultaneously; 2-3 (perhaps up to 4), still fastened to the strobila, having a gravid uterus. The ovary is replaced at once by the uterus.

The scolex, having an everted rostellum, reaches a diameter of 173. Suckers: 74 × 65-72. The rostellum pouch, difficult to see, measures 43 × 64. When the rostellum protrudes, the pouch overlaps slightly the front edge of the suckers. Its wall

is not well-defined and its posterior cap consists of muscular laminar layers. Stubby hook-supporting pad: 35×40 . Its real length may be somewhat greater. A neck is lacking; width of the first segment: 66.

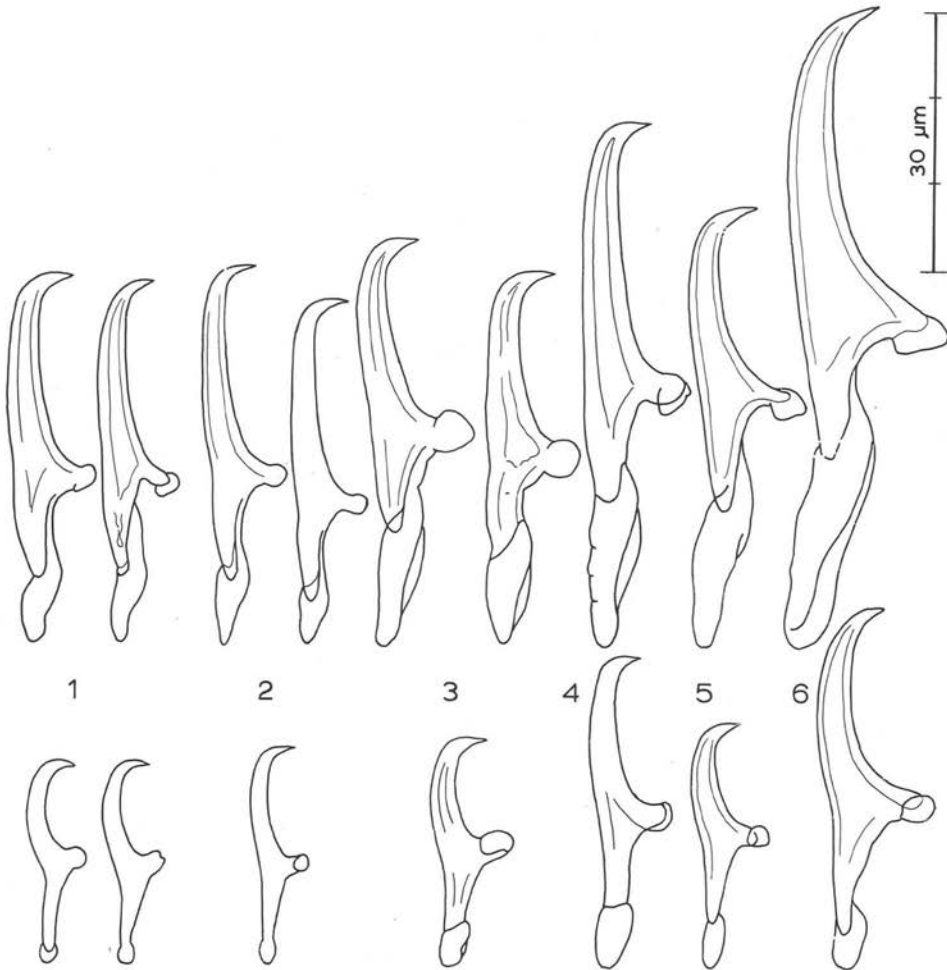


FIG. 1-6. — The hooks of *Clelandia parva* and of other species for comparison. 1: *Clelandia parva* Johnston, 1909, holotype, Australia. The small hooks are not perfectly flat. 2: *Parvitaenia macropeos* (Wedl, 1855) Baer and Bona, 1960, neotype, Italy, cosmopolitan. Hooks of one scolex. 3: *Parvitaenia ardeae* (Johnston, 1911) Baer and Bona, 1960, coll. Johnston, Australia. Large hooks of two scoleces (see Bona, 1975, Pl. 37). 4: *Parvitaenia cochlearii* Coil, 1955, holotype, Mexico. 5: *Neogryporhynchus lasiopeius* Baer and Bona, 1960, syntype, France. 6: *Neogryporhynchus cheilancristotus* (Wedl, 1855) Baer and Bona, 1960, Italy, holarctic.

Hooks : 20 in a double row. Large ones : 41-42.5 (blade : 23 ; handle : 19.5-20.5), small ones : 24-26 (blade : 11 ; handle : 13-14), including the swelling of the handle. Two large hooks alone are in a good position ; as to the small ones only imprecise data can be gathered. In both rows their shape is identical to the hooks of the « typical » set in the genus *Parvitaenia*. The guard ends in a spatula-shaped enlargement which is wider in the large hooks, reduced in the small ones. The handle has a swelling, like a small spatula in the small hooks, fair-sized in the large ones where it extends over the handle ventral side.

Unilateral gonopores on the left side, the vagina lying dorsally to the cirrus pouch. Out of 16 proglottids in which the gonopore position can be detected, only a young one shows the opening on the right side, the vagina lying ventrally to the cirrus pouch (given the immaturity of this segment, the mutual position of pouch and vagina was established by examining the cells destined to form the cirrus pouch and the vagina, the first ones being smaller and crowded).

The excretory vessels are extremely difficult to detect, especially the ventral one, and are seen in few proglottids. The dorsal is superimposed exactly upon the ventral one ; the first measures 5-6.5, the latter 9.5 (in the 28th and 29th segment from the posterior end of the strobila). In adult proglottids the dorsal measures 7-8. The genital ducts pass between the excretory vessels (7th and 8th segment from the end of the strobila, where the dorsal vessel only can be detected, lying on the dorsal face of the sex ducts). According to Yamaguti (1959, p. 241) the sexual ducts are ventral to the excretory ones, but this statement does not seem justified, and anyway Johnston's text does not say so.

The muscle thinness of the strobila and the fact that the cirrus pouch hits against the preceding proglottis account for the brittleness of the strobila rear end.

Testes : 11 to 13. In the ripe proglottids : 52-55 × 41-52. They lie in a single field — posterior and lateral to the ovary — extending on the antiporal side up to the cirrus pouch beyond the ovary lobe and on the poral side up to about the midpoint of the ovary lobe. In the ripe proglottids testes are mostly dorsal to the ovary, covering the posterior and lateral half of the lobes. In the young proglottids (highly stretched) the antiporal testes stand in line — which probably does not occur in normally extended proglottids — and occasionally appear to form an independent anterior cluster of 4-5 units ; in my opinion however, this hint toward a dual primary anlage is an artifact resulting from the excessive stretching of the segment.

The cirrus pouch bears a very large cirrus which forms an « S » or a complete ring when retracted. The pouch extends as far as the antiporal edge of the ripe ovary ; it is oval-shaped, occasionally having some constriction and a contracted proximal end. Its distal end is stubby, given the considerable width of the cirrus base ; its maximum breadth occurs about midway. In a subadult proglottid it attains 183 × 125 ; in the adult ones, with a retracted cirrus, 260-265 × 122-151 and with a partially evaginated cirrus 290 × (73) 131 (the figure in brackets corresponds to constrictions) ; in the gravid ones from 250-290 × 134-143 to a maximum of 355 × 184 in shed ones. To sum up, the normal dimensions in adult and fully extended proglottids



FIG. 7-9. — *Clelandia parva*, holotype. 7: Immature proglottid seen dorsally, the atrium being a still closed cavity. Complete set of testes. 8: Adult proglottid seen dorsally. Part of the testes are not seen clearly in this proglottis. 9: Strobila at low magnification having three shed proglottids; the two more mature ones are seen ventrally. The arrow shows the only proglottid having a gonopore turned towards the right side.

are $260-290 \times 122-151$, leaving aside constrictions when present. The pouch anterior edge, enhancing its gibbosity, is hidden inside the rear portion of the preceding proglottid. When the cirrus is retracted the wall measures 6-7. The powerful cirrus retractor may look like a sliced bowl (29×41). We failed to identify the ejaculatory duct.

The cirrus is armed with large spines; when protruded, even taking into account the still invaginated portion, it should attain 470-540 and 594 in gravid proglottids. The cirrus is subdivided into four ill-demarcated parts. In invaginated cirri the more distal segment bears very large spines with a lozenge-shaped (almost square) base, making up an actual pavement (*fig. 13*). They become abruptly smaller towards the orifice. A second portion, longer and somewhat smaller in diameter follows, in which the spines, retaining nearly the length of the preceding ones, taper gradually. In a third somewhat more dilated tract the spines become thinner and thinner until they are almost invisible setae (this part may look unarmed). Lastly, the sharply demarcated terminal portion, thinning towards its tip, bears very long and slender spines which make up an apical bundle. The inner diameters (at the level of the thorn bases) of the first three portions are 25-28, 14-19 and 23-32 respectively. The tract bearing the invaginated apical bundle may be more or less stretched; its size ranges from $55-61 \times 28-29$ in adult proglottids, to $61-76 \times 32-29$ in gravid ones, up to 87×26 at the maximum stretching observed. In protruded cirri, the diameter of the base measures 65-73 in adult proglottids, (82 in gravid ones), and the tract bearing large spines, slightly dilated, 67-84; then the cirrus becomes progressively narrower: 40 at about 300 from its base (spines are excluded in diameter measurements). The larger spines, occurring in a band extending from 43 to 72 from the cirrus base, are 14-15 along their convexity (averagely the longest face), and 12.5-14.5 along the concavity; their base is 6-8 wide. The finer spines, at about $1/3$ of the cirrus length, are 12.5-14 along the convexity and 10-11.5 along the concavity, with a base of about 4-5.5. In an apical open bundle, the spines should be shorter at its base; the greatest length of a single spine (not of the whole bundle) is about 38 (no open bundle could be observed).

The sperm duct, relatively short and of fairly wide diameter, is just barely perceptible (*fig. 8, 11*). It lies in a transverse antipodal position, pressed between the rear wall of the cirrus pouch and the ovary anterior edge, or the uterus at its earliest appearance. The atrium is deep; in mature proglottids its cavity measures 58-76 in length and 82 in width with protruded cirrus, reaching a maximum of 102×102 in shed proglottids. When the cirrus protrudes a broad papilla is formed, whose anterior face tends to align with the proglottis anterior edge ($26 \times 105-130$ in adult proglottids and $45-60 \times 170-185$ in gravid ones).

The atrium exhibits on its bottom a shallow crescent-shaped groove lined by short, packed cilia (length: 3-4), which surrounds the base of the cirrus ventrally (the vagina lying dorsally) and appears in adult proglottids as a tiny collar, 9-10 wide in its centre, indicating clearly the end of the cilia towards the atrium cavity (*fig. 8, 13-17*). This groove is less clear-cut in its rear part, where it widens, merging into the posterior vaginal folds (*fig. 15, 16*).



FIG. 10-12. — *Clelandia parva*, holotype. 10: Scolex. 11: Dorsal view of sexual organs having a partially evaginated cirrus of an adult proglottis. Sperm duct at the bottom. 12: Thorns of the cirrus at different distances from the base of the cirrus.

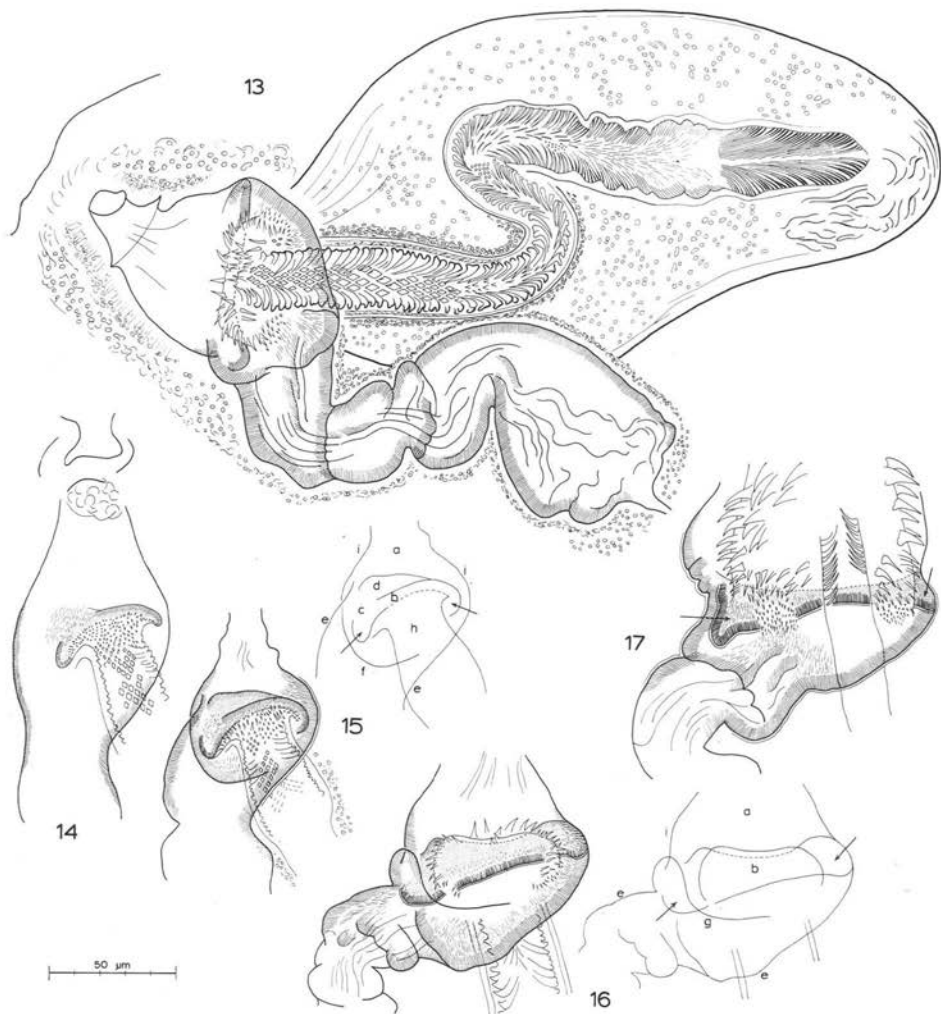


FIG. 13. — *Clelandia parva*, holotype. Invaginated cirrus in an adult proglottis. Dorsal view. FIG. 14-17. — *Clelandia parva*, holotype. Phases in the formation, on the bottom of the atrium, of the crescent-shaped ciliated groove. Dorsal view: from the observer's viewpoint there follow in depth the terminal part of the vagina, the male orifice, the ciliated groove. The fore-part of the proglottis corresponds to the right side of the drawing. Schemes of Fig. 15 and 16: fore and rear ends of ventral groove (arrows); atrium (*a*); ventral ciliated groove (*b*); transition from the groove cilia to the vagina rear ones (*c*); enlarging of the ciliated groove on the rear side (*d*); walls of the vagina (*e*); fold at the end of the ventral part of the vagina (*f*); a vagina dorsal fold (*g*); invaginated cirrus (*h*); posterior cilia of the vagina going up slightly along the atrium wall (*i*). — 14: Young proglottis. Ciliated groove beginning to take shape in close connection with the male orifice. The external edge of this groove seems interrupted in its rear part. 15: Subadult proglottis having invaginated cirrus. The vagina terminal funnel starts forming folds, but the groove at the cirrus base, enlarged in its rear part, assumes its characteristics. 16: Adult proglottis having a cirrus just starting evagination. The cilia of the ventral groove form a fairly wide belt (dashed on the external side). At the fore end (on the right side in the drawing) note groove and vagina cilia overlapping each other. 17: Adult proglottis having a partially evaginated cirrus. The belt made by the groove cilia is narrower, having been stretched by the protruded cirrus. In two areas of the dorsal wall of the cirrus base the transition from the very small thorns of the cirrus to the cilia of the vagina ventral side is shown.

The vagina is wide, and its wall appears thick on account of its being lined by extremely fine and densely packed cilia. It is wrapped in a compact, rather thin, layer of small cells; its wall forms large longitudinal folds; its course is relatively short, exhibiting some narrow, partly overlapping loops; it lies dorsal to the distal end of the cirrus pouch, flanking it posteriorly so as to sometimes cover its rim; it forms a very wide and asymmetrical distal funnel whose opening is as wide as the atrium bottom, embracing the cirrus base dorsally. The funnel is directed backwards, then a first bend causes the wavy course of the vagina to become transverse; the proximal part is again directed diagonally backwards. In its proximal tract (about 1/4 its length) the vagina looks more expansible (*fig. 11, 13*); it may become fusiform and wider than its intermediate part (this tract however is not easily identifiable as a seminal pre-receptacle: see Bona, 1975, p. 218). The vagina terminates into a nearly sharp spike. The female opening, whose outer margin is almost impossible to identify, as difficulties arise in making out exactly where the vagina ends and the atrium proper begins, is 72-87 wide (87-102 in gravid proglottids). The cilia are 16 long at the centre of the funnel, and only 8-10 at its outer border and towards the vagina midlength (approximative values). These cilia, gradually shortening, expand only to the dorsal, anterior and posterior walls of the atrium bottom, whereas in the ventral direction they join with the extremities of the ventral groove at the cirrus base. Anyway, in immature proglottids it was seen (*fig. 14*) that the groove differentiates very early around the male opening; it is a structure which seems related to the male organ, even if later connected to the vaginal ciliated field.

The seminal receptacle leans against the anterior part of the yolk gland. In adult proglottids it is ill-defined and measures 55-73 × 44-49. Yolk gland poorly lobulated, located far backwards; 64-81 × 84-67 in the two adult proglottids. The mature ovary is much extended and bulky, each lobe consisting of a few stumpy lobules close to one another; it has a smaller poral lobe and reaches the rear limit of the segment. When ripe it borders the yolk sides. Maximum width: 306-358. The uterus is saccular, slightly lobulated only superficially. It appears suddenly very extensive. It can be detected simultaneously with the ovary in a single proglottid at most, since the ovary disappears at once. The antiporal half is wider from the beginning and expands into small fan-wise lobules. It has a horse-shoe shape only at first, and contains the seminal receptacle in its posterior infolding; then it tends to flatten posteriorly, resting on the proglottid edge. Mature oncospheres are lacking.

Comparison with Johnston's description.

There are many conflicting points as regards Johnston's description. The rostellar crown is not single, but double, made up of 20 hooks instead of 14. Furthermore, Johnston's *fig. 3, Plate VIII* does not resolve the shape of hooks satisfactorily. The gonopores in the type specimen are left-handed and not right-handed. To assess their position the dorsal and ventral sides of the worm must be defined. The specimen orientation was established by the testes which are decidedly dorsal and by the uterus, which

forms on the opposite side. The fact that Johnston regarded the cirrus as « lying dorsally to the vagina » instead of the reverse, results from his considering the pores as opening rightwards, having confused the dorsal and ventral faces of the worm. The walls of the vagina certainly contain muscle fibres, though no independent muscle bundles occur here and the « longitudinal muscles » mentioned by Johnston are longitudinal folds of the wall. Johnston does not report the dimensions of the cirrus pouch, and the text concerning this organ as well as the cirrus is not clear. Johnston's fig. 5, Pl. VIII, shows a fusiform structure at the base of the cirrus, along the path of the ejaculatory duct, which probably corresponds to what he calls « slight enlargement representing a *vesicula seminalis* » (p. 143). This enlargement should correspond to the still invaginated terminal portion of the cirrus; in fact there is no trace of any inner seminal vesicle. Only 6 (7-8) testes are mentioned by Johnston instead of 11-13 (it is necessary to count them in young proglottids, where they stand out more clearly).

Some differences, such as the number of rostellar crowns, the location of sexual pores and the position of the vagina with respect to the cirrus pouch, justify an emendation of the generic diagnosis.

Clelandia Johnston, 1909 emend.

Dilepidinae. Rostellum with 20 hooks in two rows with a characteristic shape. Unilateral left-hand genital pores. Vagina: dorsal as regards the cirrus pouch (the pores being on the left side). Genital ducts pass between the excretory vessels. Testes: small number, at least more than 4, posterior and on the sides of the ovary, which they partially cover; and extending on the antiporal side beyond its lobe. Uterus saccular, at first lobed and horse-shoe shaped. Parasites of Ciconiiforms. Type species: *Clelandia parva*, Johnston, 1909. Type host: unknown. Type locality: Jervis Bay, N. S. Wales, Australia.

Remarks upon the diagnosis and validity of the genus.

The spreading practice of using the avian order as a generic character is justified when there are sufficient reasons to believe that in a host group a given genus of cestodes is specific. In the case of *C. parva* we consider the specificity for the Ciconiiformes as valid until evidence to the contrary is found (see p. 175). The use of the shape of the hooks as a character in the genus diagnosis proved sometimes to be significant, as in some cestode genera of Ciconiiformes and particularly in the very genera *Parvitaenia* and *Neogryporhynchus* (see Bona, 1975). Sometimes, the same shape of hooks in different genera shows a relationship amongst genera more than many other characters normally do. The hooks of *C. parva*, considered as characteristic in the generic diagnosis, are identical as to shape and size to the very homogeneous hook series of the « typical » *Parvitaenia* (*sensu* Bona, 1975) (fig. 1, 2, 4), and can be defined as « parvitaenioid ».

Clelandia differs from the other genera parasitizing Ciconiiformes having two rows of hooks, unilateral pores and a saccular uterus by means of the left-hand pores combined with a dorsal vagina, the excretory vessels having no antiporal inversion, and the « parvitaenioid » shape of hooks, which only appears in two other genera harboured by Ciconiiformes (*Parvitaenia* and *Neogryporhynchus*) (fig. 1-6).

We have already reported that one proglottis of *C. parva* has a rightward-facing pore. We consider this proglottis to be anomalous; it does not contradict the character of unilaterality used in the genus diagnosis. The position of the pores is a character whose steadiness can slightly vary from species to species and from genera to genera. This statement is needed in order to avoid misunderstandings, since the diagnosis of *Clelandia* differs essentially from that of *Parvitaenia* in the very position of the pores, unilateral in the first, irregularly alternate in the latter.

As to generic characters, it will be necessary in the future to verify: 1) whether also in *Clelandia* specimens with left- as well as right-hand pores occur in the same species, as in *Neogryporhynchus* and in some other genera harboured by Ciconiiformes; and 2) if so, whether in *Clelandia* too the position of the vagina with respect to the cirrus pouch is turned upside-down when pores change position, as it happens in the strobilas of *Neogryporhynchus* and in the proglottids of *Parvitaenia*, the pores being in this genus irregularly alternated.

Anyway, should in the future these two correlated characters not be recognised in *Clelandia*, we would always have « unilateral pores on the left side » and « dorsal vagina », both characters being valid at genus level.

One species only is not sufficient to point out in the diagnosis of *Clelandia* the particular structure of the bottom of the atrium around the cirrus base, as on the contrary we have done (Bona, 1975) in the diagnosis of *Neogryporhynchus*, where atrial modifications are very evident and typical in both the species belonging to this genus (see also p. 168).

Having established the validity of *Clelandia*, we may exclude its synonymy with *Lateriporus* Fuhrmann, 1907, as supposed by Matevosian (1963) and leave out our assumption of its similarity with *Paradilepis* Hsü, 1935, despite its unilateral pores (Bona, 1975, p. 616), as other characters (hook shape, position of the vagina, number of testes) allow us to deny any particular relationship with the last one.

Discussion

Comparisons and affinities with *Parvitaenia* and *Neogryporhynchus*.

Clelandia looks very much like *Parvitaenia* Burt, 1940 and *Neogryporhynchus* Baer and Bona, 1960. This dual similarity is not surprising, seeing that these last two genera are alike in several respects (Bona, 1975, p. 649). We must recognize that Johnston (1909, p. 146), with remarkable intuition, compared *Clelandia* with *Acanthocirrus macropeos* (Wedl) and *A. cheilancristota* (Wedl), species which were just transferred by Baer and Bona (1960), respectively to *Parvitaenia* and *Neogryporhynchus*.

The hooks of *Clelandia* look more similar to those of *Parvitaenia* than those of *Neogryporhynchus* do (fig. 1-6). As in « typical » *Parvitaenia*, characteristically shaped hooks fit in with a markedly smaller number of testes than are found in the « atypical » species and with relatively reduced strobila size. The fairly short rostellum and its pouch are like those of *Parvitaenia* in general.

Worthy of note is the fact that in the holotype of *C. parva* a vagina dorsal to the cirrus pouch corresponds to left-sided pores, as we find in the left *strobilas* of *Neogryporhynchus* and in the left *proglottids* of *Parvitaenia*. Furthermore, the proglottis we detected in an anomalous position, that is with a right-hand pore, whose vagina lies ventrally, exactly as it occurs in the right-hand specimens of *Neogryporhynchus* and proglottis of *Parvitaenia* (see p. 166 and 173), shows that *Clelandia* has maintained a « tendency » towards the inverted position of the vagina as regards the cirrus pouch when the pore position changes. This indicates another link between these three genera, and we should not be surprised to find in *Clelandia parva* too specimens having unilateral right-hand pores and a ventral vagina.

Clelandia differs from *Parvitaenia*: in having unilateral pores and a primary single field of testes, whereas in *Parvitaenia* these may more frequently develop in two distinct fields which subsequently meet on the antiporal side of the ovary of adult proglottids (Bona, 1975, p. 180-82); in lacking a vaginal sphincter, nearly always present in typical *Parvitaenia* (missing in two Brazilian species alone, i.e. *P. microphallica* and *P. macrophallica*) and a cellular muff surrounding the distal part of the sperm duct (as far as we were able to observe), this formation being frequent, though not always ascertained, in *Parvitaenia* species.

The characters shared by *Clelandia* with *Neogryporhynchus* are the shape of hooks, with some restraint, the unilateral pores, the position of the vagina with respect to the cirrus pouch and probably a certain complication of the atrium bottom. In fact, in the narrow groove around the ventral part of the male orifice of *C. parva*, a correspondence might be envisaged with the wide groove, also semicircular and in the same position, lined however with much longer bristles, in *Neogryporhynchus lasiopeius*, and with the field of spines (homologizable to the ciliated groove in *lasiopeius*, Bona, 1975, p. 271) around the base of the cirrus in young proglottids of *N. cheilancristrotus*, before the final formation of the two large pairs of atrial hooks. This suggests the existence of a link between *C. parva* and both the above mentioned species, though we cannot tell so far to what extent (fig. 18, 19, 20). A structure, comparable to the arch of tightly-packed cilia bordering the edge of the vaginal opening of *N. lasiopeius* at the opposite side of the groove, is missing in *C. parva* as well as in *N. cheilancristrotus*. Furthermore, in *Clelandia*, as in *Neogryporhynchus*, the grooves, according to the way they are formed, appear to be linked to the male anlage rather than to the vagina (Bona, 1975, p. 266-67, 271).

Clelandia differs from *Neogryporhynchus* in having a higher number of testes instead of only four and a lesser complexity of the bottom of the atrium. There is also a slight difference in the shape of the hooks, and a completely different structure of the cirrus.

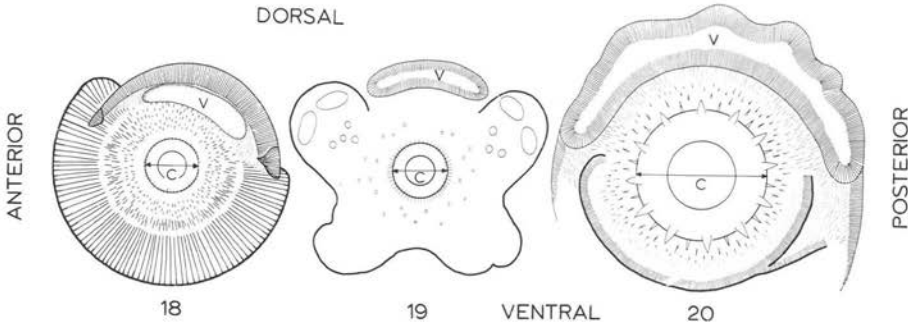


FIG. 18-20. — Schemes of the atrium bottom as seen from the sexual pore, showing the correspondence between *Clelandia* and *Neogryporhynchus*. Left pores, dorsal vagina, without exact relations in size. Transversal arrows show the cirrus diameter. In every design the thicker tract, towards the lower part, shows the limit of the ventral semicircular groove round the cirrus base. 18: *Neogryporhynchus lasiopeius*. Adult proglottis. Note the long bristles of the groove and the crescent-shaped ciliate belt round the dorsal part of the female orifice (to which formation an homologous one is missing in *N. cheilancristrotus* and *C. parva*) (Bona, 1975, fig. 29). 19: *Neogryporhynchus cheilancristrotus*. Immature proglottis, where the loss of the young spinules, the concentration of part of them to form the two pairs of large thorns, and the shifting of these towards the two sides of the vagina have not yet come to an end. The field of spines round the cirrus base is considered as homologous to the field of bristles of *N. lasiopeius* (Bona, 1975, fig. 27, 28). 20: *Clelandia parva*. Adult proglottid. The cirrus diameter and the vagina opening are much bigger than in the two preceding species. The ventral ciliate groove is narrow, not very deep, but clear.

The host of *Clelandia parva*.

Johnston's suspicion that the host of *Clelandia parva* may have been mistakenly identified by the collector (see also Johnston, 1910) affords an interesting opportunity of putting to the test the principle of specificity as to locating the group to which the host belongs, starting from the parasite.

Before its redescription, *C. parva* seemed a rather puzzling species as a parasite of Ciconiiformes, but now, given the morphology of the worm, it seems almost certain that the host belongs to this avian order. Not only this, but the morphology of *Clelandia* being even highly similar to that of cestode genera, as *Parvitaenia* and *Neogryporhynchus*, characteristic, within the order Ciconiiformes, of the suborder Ardeae, and the Dilepididae now known of the suborders Ardeae and Ciconiae being sharply demarcated (Bona, 1974 and 1975), so that species or genera in common are very rare, we are able to regard as it being very likely that the host belongs to the Ardeae and as erroneous the original diagnosis, *Ephippiorhynchus asiaticus australis* (Shaw) belonging to the Ciconiae.

Further collections of *Clelandia* in Australia for assessing the identity of the host and the spectrum of the possible hosts would be interesting.

TABLE I. — Comparison of genus characters.

	<i>Neogryporhynchus</i> Baer and Bona, 1960	<i>Parvitaenia</i> Burt, 1940	<i>Clelandia</i> (type sp.) Johnston, 1909
Crown	double (10 + 10)		
Shape of hooks	as in the typical series of <i>Parvitaenia</i> : slightly modified	characteristic of the genus: « typical » « atypical »	as in the typical series of <i>Parvitaenia</i>
Gonopores	unilateral	irregularly alternating	unilateral
Strobila (in the same species)	left- or righthand gonopores	—————	lefthand gonopores (1)
Vagina with respect to the cirrus pouch	lefthand strobila: dorsal	lefthand proglottis: dorsal	lefthand strobila: dorsal
	righthand strobila: ventral	righthand proglottis: ventral	? (1)
Sex ducts	between the excretory vessels		
Testes	4	few to numerous: « typical » « atypical » 6-15 25-58	few, more than 4
Atrium bottom	well outlined particular structures	normal	hardly outlined particular structures (2)
Uterus	sacciform, horse-shoe shaped at the beginning		
Host group	Ciconiiformes Ardeae	Ciconiiformes Ardeae	Ciconiiformes suborder?

Other data (3)

		« typical »	« atypical » (4)		
Hook length	long ones	48-72	40-60	85-274	41-42,5
	short ones	28-42	25-37	52-204	24-26
worm length (mm)	2,5 - more than 24	1,4-14 (20 ?)	more than 20 - 120		9

(1) It is not known whether specimens having right-hand unilateral pores as in *Neogryporhynchus* exist.

(2) Character not used in the genus diagnosis of *Clelandia*.

(3) Characters which do not appear in generic diagnosis. Data show minima and maxima in each genus or group of species.

(4) Excluded *Parvitaenia ardeae*, which lies between typical and atypical species.

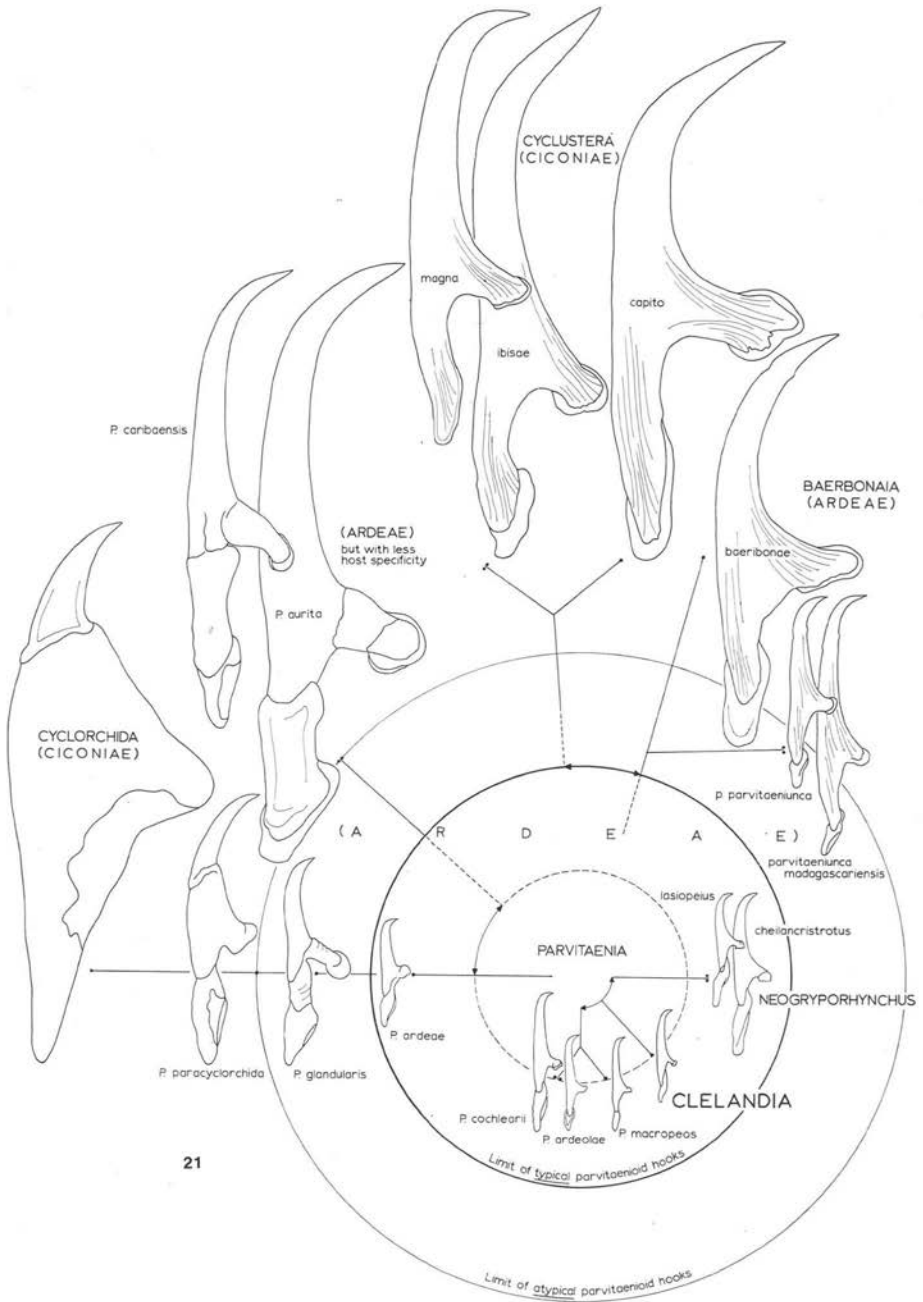
Phylogenetic links of *Parvitaenia* with other genera infesting Ciconiiformes.

The morphology of the species in genus *Parvitaenia* is much diversified. That is: in the genus it is possible to group some species into more homogeneous units; the hooks of some species, while maintaining aspects of a basic shape which I call « parvitaenioid », seem to be the steps of increasing changes towards very different shapes (hence the need to divide the hooks into « typical » and « atypical » according to the degree of their diversity from the shape we consider as characteristic of the genus); important differences in the hooks entail anatomical differences as well (especially as to number and position of the tests) but less clear-cut; in this diversity of species we can see similarities with other genera parasitizing Ciconiiformes. Such similarities are sometimes so clear-cut as to suggest fairly close phylogenetic connections, and to lead to the assumption that the genus *Parvitaenia* could actually be a nucleus of evolutionary radiation (within a host group). The indisputable affinity of *Clelandia* with *Parvitaenia*, which are after all cestodes of the same avian order, provide additional evidence for this hypothesis (fig. 21).

Attention should be given to the fact that some lineages which can be seen in the genus *Parvitaenia* seem to develop, preserving a striking likeness to the group of « typical » species of *Parvitaenia*, within the suborder Ardeae, characteristic hosts of the genus *Parvitaenia* (see *Neogryporhynchus*), while other lineages seem to develop with greater morphological deviations, preserving only a vague likeness with the original group *Parvitaenia*, and connected with its « atypical » species, particularly outside the Ardeae, and precisely in the suborder Ciconiae (Bona, 1975, p. 191, 642 and followings).

The genus *Clelandia* lies, morphologically considered, along an evolutionary line of the first type, quite close to the « typical » *Parvitaenia* and very similar to *Neogryporhynchus*. Considering now its host group as well as its morphology, if *Clelandia* should be, as we believe, a parasite of Ardeae, a further instance would be available of the evolution of related genera, starting from the « typical » species of *Parvitaenia* stem group, within a restricted host group like Ardeae. But if the host of *Clelandia*, contrary to our assumption, should belong to the Ciconiae, we shall encounter here an evolutionary line reaching the Ciconiae (*Parvitaenia-Clelandia*), morphologically very similar to a line observed in Ardeae (*Parvitaenia-Neogryporhynchus*), meaning that we should find in two groups of helminthologically quite different hosts very similar forms and evolutionary lines. It would mean, in opposition to nearly every example we know (Bona, 1975), that the genera of cestodes which appear in each of the two avian suborders need not be morphologically very different. If so: in the Ciconiae, genera of cestodes not only remotely derived from, but even closely related to those of Ardeae, may exist.

Clelandia parva, as we have seen, is a species closely related to the « typical » group of *Parvitaenia*, namely, given its strongly armed cirrus, it seems to lie close to the subgroup *macropeos-macrocoleo*. As the few known Australian *Parvitaenia* belong to the « atypical » group, with *P. ardeae* in an intermediate position (Bona, 1975, p. 183 and 190), from a zoogeographical viewpoint *Clelandia parva* appears more closely



related to a group of *Parvitaenia* not represented for the time being in Australia, than to the species (« atypical » *Parvitaenia*) endemic to that Region.

An anomalous taxonomic situation (see fig. 21) is in fact created by *Clelandia parva*, in which two different genera, *Clelandia* and *Parvitaenia*, resemble one another more, on the basis of their recent generic diagnosis, than some species of the same genus do, e.g. the typical and atypical species of *Parvitaenia*. (Atypical *Parvitaenia* possess all the requisites needed to belong to the genus *Parvitaenia*, while *Clelandia parva*, chiefly with its unilateral gonopores, does not).

The foregoing suggests that the composition of the genus *Parvitaenia* is even less homogeneous than had been supposed, and that the taxonomic relationships between the species groups by which it is composed, as well as between the genus taken as a whole and other genera, are rather complicated. Anyway, a possible rearrangement of *Parvitaenia* would not affect the validity of *Clelandia*.

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FIG. 21. — Diagram of the structure of genus *Parvitaenia* with reference to the similarity amongst its species and between these and related genera, considering the shape of the hooks. Such shape can vary in comparison with the shape considered as characteristic and « typical » of genus *Parvitaenia*, which is at the centre of the diagram. The distance of a species from the centre shows its degree of dissimilarity from the typical *Parvitaenia*. When the shape of the hooks is considerably different from the « typical » one (« atypical » hooks), even the anatomy is different in some details. But the opposite is not true, for there are anatomies quite different from the anatomy of « typical » *Parvitaenia*, combined with hooks maintaining a « typical » shape: see *Clelandia* and *Neogryporhynchus*. The angular distance between some groups (see arrows) refers to a certain similarity to each other. This diagram gives a first frame for an eventual revision of genus *Parvitaenia*. — The figure shows only a few of the typical species of genus *Parvitaenia*, since their hooks have almost the same shape. — Nomenclature: *Cyclustera ibisae* (Schmidt and Bush, 1972) (syn.: *Parvitaenia ibisae* Schmidt and Bush, 1972 and *Parvitaenia eudocimi* Rysavy and Macko, 1973); *Parvitaenia caribaensis* Rysavy and Macko, 1973 (syn.: *Parvitaenia heardi* Schmidt and Courtney, 1973) (see Bona, 1975).

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