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FOUR NEW GENERA OF MONOGENEA (DACTYLOGYRIDAE) FROM THE GILLS OF AUSTRALIAN ATHERINIFORM FRESHWATER FISHES

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To date only 26 monogenean parasite species have been described from Australian freshwater fishes. In this study freshwater fishes of the Atheriniformes, represented in Australia by the Melanotaeniidae, Atherinidae and Pseudomugilidae, were examined for monogenean gill parasites. Nineteen new dactylogyrid monogeneans are described; *Longidigitis auripontiformis* gen. et sp. nov., *L. robustus* sp. nov., *Iliocirrus iliocirrus* gen. et sp. nov., *Helicirrus splendidae* gen. et sp. nov. and *H. megaloanchor* sp. nov. from *Melanotaenia splendida splendida* (Peters, 1876); *L. gracilis* sp. nov. from *M. utcheensis* McGuigan, 2001; *I. mazlini* sp. nov. from *M. eachamensis*; *L. maccullochii* sp. nov. and *H. maccullochii* sp. nov. from *M. maccullochi* Ogilby, 1915; *I. trifasciatae* sp. nov., *H. mcivori* sp. nov. and *L. hopevalensis* sp. nov. from *M. trifasciata* (Rendahl, 1922); *I. ornatusi* sp. nov. from *Rhadinocentrus ornatus* Regan, 1914; *L. utcheei* sp. nov. from *Cairnsichthys rhombosomoides* (Nichols & Raven, 1928); *Recurvatus chelatus* gen. et sp. nov. and *I. rossi* sp. nov. from *Craterocephalus stercusmuscarum stercusmuscarum* (Günther, 1867); *H. marjoriaea* sp. nov. from *Craterocephalus marjoriae* Whitley, 1948; *R. signiferi* sp. nov. from *Pseudomugil signifer* Kner, 1865; and *H. gertrudaea* sp. nov. from *Pseudomugil gertrudae* Weber, 1911. *Longidigitis*, *Iliocirrus*, *Helicirrus* and *Recurvatus* are defined by copulatory apparatus morphology of which 4 types are recognised. Species are recognised on morphological and morphometric variation of haptoral sclerites as well as copulatory apparatus morphology. Multivariate analysis of variance, principal component analysis and discriminant function analysis of morphometric variation are used to assess congruence of genera and species initially distinguished by morphology. Multivariate analysis identified significant differences ($p<0.01$) between species within each genus for 24 measured haptoral sclerite characters. Principal component analysis corroborated the species recognised by morphology, and discriminant function analysis identified morphometric characters that can best identify genera and species. Discriminant function analysis cross-validation classified 97.1% of the 591 measured parasites into their correct genus, and 99.5% were classified correctly into their respective species based on haptoral sclerite morphometric variation alone. ❐ *Melanotaeniidae, Atherinidae, Pseudomugilidae, Monogenea, rainbowfish.*

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There have been very few studies of monogenean parasites from Australian freshwater fishes. Johnston & Tiegs (1922) described 13 species in 6 genera. Since then 9 publications have described Australian freshwater Monogenea (Fletcher & Whittington, 1998). To date 26 species of monogenea have been described from 16 species of native freshwater fishes (Fletcher & Whittington, 1998). With approximately 300 species of freshwater fish known in Australia (Allen et al., 2002), much work remains.

The Atheriniformes comprises 6 families, 49 genera, and approximately 285 species (Dyer & Chernoff, 1996) and its members are found in marine and freshwater environments from tropical and temperate regions. In Australia and New Guinea, Atheriniformes is represented by Melanotaeniidae, Pseudomugilidae and Atherinidae (Allen, 2002). The former 2 are endemic (Dyer & Chernhoff, 1996). Melanotaeniidae includes 69 described species in 7 genera (Allen & Renyaan, 1998; McGuigan, 2001). Of these the Australian mainland has 4 genera with 16 species (McGuigan, 2001). Outside Australia, 5 Atheriniformes, *Hypoatherina temminckii* (Bleeker, 1853), *H. valenciennei* (Bleeker, 1853) (= syn. *Atherina. bleekeri*), *Atherina araea* (Jordan & Gilbert, 1882), *A. stipes* (Müller & Troschel, 1848), *Atherinomorus lacunosus* (Forster, 1801), all marine, have been examined for monogenean parasites. Eight species of dactylogyrid Monogenea, *Diversohamulus tricuspidatus* Bychowsky & Nagibina, 1969, *D. curvionchus*, Zhukov, 1984, *Atherinicus cornutus*

Bychowsky & Nagibina, 1969, *A. subserratus* Zhang et al., 2001, *A. bychowskyi* Zhukov, 1984, *A. cubanus* Zhukov, 1984, *Ancyrocephalus atherinae* Price, 1934 and *Ancyrocephalus littoralis* Paperna & Kohn, 1964 are known from these hosts. Descriptions of monogenean parasites from atheriniform fishes from freshwater or from Australia are lacking.

Two sets of morphological characters are often applied to define genera of Dactylogyridae. Bychowsky & Nagibina, (1978) considered the following morphological characteristics important in separating genera: 1) structure of the central and haptoral hooks; 2) number of chitinous elements in the haptoral armature; 3) position of the testis in relation to the ovary; 4) confluence or non-confluence of distal end of intestinal tract; 5) situation of vas deferens in relation to intestine; and 6) placement of the vaginal pore. These characters have been the main basis for many taxonomic groupings of dactylogyrid mongeneans.

Secondly, copulatory apparatus structure which was not considered important by Bychowsky & Nagibina (1978), is having a greater role in defining genera than previously. It was recognised early in monogenean taxonomy that diagnostically important sexual characters have more taxonomic value than the sporadic occurrence of spines on, or differences in size or shape of certain haptoral parts (e.g. Mizelle & Hughes, 1938). Young, (1968) recognised the importance of minor variations in copulatory apparatus morphology and used these to group species of *Haliotrema.* However, he did not go as far as to separate these groups into different genera. The reclassification of the Nearctic genera of Dactylogyridae used minor variations in copulatory apparatus morphology and identified several types (Beverley-Burton & Suriano, 1980a, b; Suriano & Beverley-Burton, 1982; Beverley-Burton & Klassen, 1990). More recently, copulatory apparatus morphology has been used to classify the groups of *Haliotrema* species from the marine boxfish (Klassen, 1991).

Haptoral, rather than copulatory apparatus, characters tend to be used for defining species. Generally, haptoral characters are more easily identified. However, when morphological characters among different species are not easily distinguished, a statistical approach can be used on the morphometric variation of the characters. Analytical tools such as discriminant function analysis (DFA), principal component analysis (PCA) and multivariate analysis (MANOVA) are used to distinguish species and genera. Such methods have been little used in studies of monogenean species. Klassen (1991) used MANOVA and DFA to define species of *Haliotrema* from boxfish while MANOVA and PCA were used to identify species of *Gyrodactylus* from salmonid hosts (Shinn et al., 2000).

TABLE 1. Host species examined and collection sites.

host	location	longitude	latitude
C. marjoriae	Amamoor Ck	152°40'E	26°21'S
C. rhombosomoides	Utchee Ck	145°56'E	17°37'S
C. rhombosomoides	Behana Ck	145°56'E	17°17'S
C. s. stercusmuscarum	Tungamull Ck.	150°30'E	23°30'S
C. s. stercusmuscarum	Ross R.	146°45'E	19°18'S
M. eachamensis	Dirran Ck	145°06'E	17°27'S
M. maccullochi	McIvor R	145°06'E	15°09'S
M. maccullochi	Corduroy Ck	145°50'E	18°10'S
M. s. splendida	Bluewater Ck	146°45'E	19°18'S
M. s. splendida	Stewart Ck.	145°46'E	19°22'S
M. trifasciata	McIvor R	145°06'E	15°09'S
M. trifasciata	Dulhunty R.	142°14'E	11°53'S
M. utcheensis	Utchee Ck	145°56'E	17°37'S
P. gertrudae	Howard Ck.	130°50'E	12°27'S
P. signifer	Liverpool Ck	145°56'E	17°43'S
P. signifer	S. Mossman R.	145°23'E	16°29'S
R. ornatus	Brunswick Ck	151°60'E	28°70'S
R. ornatus	Bible Ck	150°40'E	28°50'S

The first monogenean parasites from Melanotaeniidae, Atherinidae and Pseudomugilidae from Australian freshwater systems are described and comparison and use of the two approaches to genus-level classification is discussed. An applied statistical approach, using MANOVA, PCA and DFA, will confirm or refute a correlation between haptoral sclerite variation and the genus- and species-level classification based on morphology.

MATERIALS AND METHODS

Identification of hosts is according to Allen (2002) and McGuigan (2001). Host specimens (Table 1), collected by a number of methods (6mm seine net, dip net), were killed by placing them in iced water for thirty seconds. This kills the host but not the monogeneans. The gills were removed from the host using fine needle forceps and placed in a 50mm Petri-dish containing water from the collection site. Monogenean parasites were observed with a ×40 dissecting microscope and removed from the gills using a fine needle. Live parasites were transferred to a 50 × 25mm glass slide using a pipette and covered with a cover slip. Examination of live parasites used ×400 and ×1000, D.I.C. Nomarski optics to determine internal soft tissue morphology. As the slides dried, specimens became compressed which caused body fluids to be exuded. This leaves an outline of the worm's tissue edges

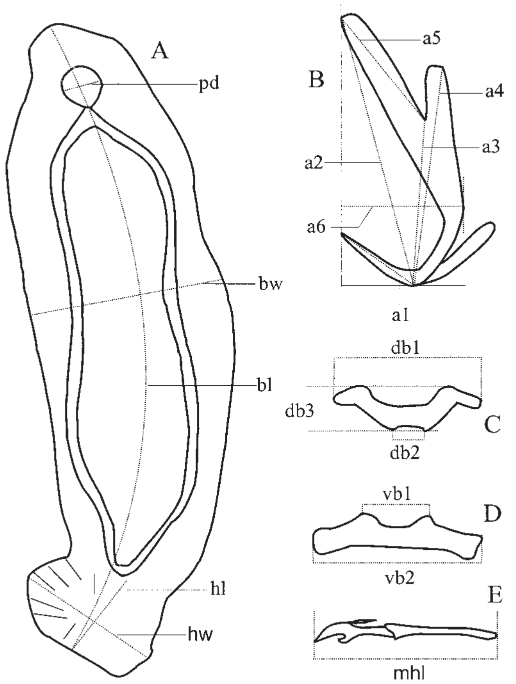

FIG. 1. Parasite measurements. A. Body measurements: bl, body length; bw, body width; hl, haptor length; hw, haptor width; pd, pharynx dia. B. Anchor measurements a 1-5. C. Dorsal bar measurements db1-3. D. Ventral bar, vb1-2. E. Hook length, hl 1-7. Numbers 1-7, hook numbering system.

showing details of all sclerotised morphometric characters and most of the morphological characters. The worms were preserved in this state in glycerol-ammonium-picrate (Malmberg, 1970) by placing a drop at the edge of the cover slip and allowing capillary action to spread the preservative under the cover slip. Nail polish was used to seal the cover slip. This is referred to as technique one. When live specimens could not be examined, gills were preserved in 5% formalin, parasites were extracted and mounted in Grey & Weiss mountant (Humason, 1979) or glycerol-ammonium picrate. This is referred to as technique two. Holotype and paratypes of each species are deposited at the Queensland Museum.

Morphometric variables of 5 soft body and 24 sclerotised variables of the haptoral apparatus were measured (Fig. 1). Where possible, at least 20 parasites of each species were measured. Hook numbering follows that of Mizelle, (1936) (Fig. 2A, B). The haptoral terminology follows Gussev, (1973) and male copulatory apparatus terminology follows Klassen, (1991).

STATISTICAL ANALYSIS. Data were analysed using SPSS for Windows 11 (SPSS Inc.). Descriptive statistics were obtained for the soft body and the haptoral sclerite variables. Formalin preserved specimens were used for measurements as more specimens were available in this state. Means and range are expressed for soft body measurements and means and one standard error are expressed for sclerite variables. Soft body data were not examined further as variation is commonly related to preservation techniques (Klassen, 1991). Examination of sclerite variables used multivariate analysis of variance (MANOVA), principle component analysis (PCA) and discriminant function analysis (DFA). Initial examination of the data for normality and homoscedasticity, graphically using frequency distributions and statistically using Levene's test (with ∝=0.01), indicated a need for transformation. Data for MANOVA were natural-log transformed (ln(1 + x)), while data for PCA and DFA were z-score transformed to approximate multivariate normality, homoscedasticity and to remove the scale factor between variables. Each genus was examined for mean differences in variables between species using MANOVA. Tests were considered significant at the experiment-wise error rate ∝=0.01. A post-hoc analysis (MANOVA) for pair-wise comparisons and range used the Scheffé test. The significance level of the Scheffé test (∝=0.01) is designed to allow all possible linear combinations of group means to be tested, not just pair-wise comparisons. The result is that the Scheffé test is often more conservative than other tests. Tukey's HSD test (unequal group sizes present) was also conducted and results compared with Scheffé test as unequal group sizes were present in the data. The Tukey's HSD test uses a Bayesian approach and uses the harmonic mean of the sample size when the sample sizes are unequal.

For PCA the covariance matrix was used and initially all characters were entered in analyses. Characters were removed from the final set of analyses based on low communality (<0.7). Data were examined at two levels. Firstly, all species together; secondly, each genus was examined separately. Visual examination of scatter plots assessed if separation of parasite species occurred.

Discriminant function analysis identified morphometric sclerite characters having highest correlation with genera and species, recognised

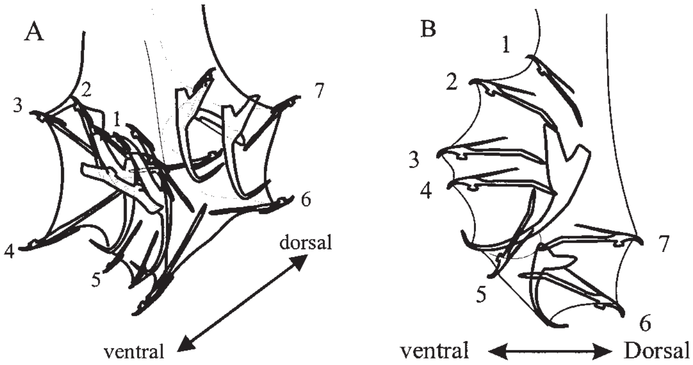

FIG. 2. A, haptoral sclerite relationships and orientation for *Longidigitis*, *Iliocirrus*, *Recurvatus*, and *Helicirrus*: *H. marjoriaea*, *H. mcivori* and *H. gertrudaea* species. 1-7, hook numbering. B, for *H. megaloanchor*, *H. splendidae* and *H. maccullochii*.

by morphology. The analysis used the stepwise approach and the within-group covariance distance matrix (Mahalanobis distances). Probability of F to enter and F to remove were set at (P<0.01) and (P<0.05) respectively. The stepwise method removes uninformative characters from analysis based on the significance levels set. A cross-validation (leave one out classification) assessed the validity of the genera and species, and groups were weighted by sample size. Analyses were conducted at two levels. Firstly, examination of all species together; secondly, each genus was examined separately. Scatter plots were examined to determine if separation of parasite species occurred using the first three functions.

SYSTEMATICS

Order MONOGENOIDEA Bychowsky, 1937
Superfamily DACTYLOGYRIDEA Bychowsky, 1937
Family DACTYLOGYRIDAE Bychowsky, 1933
Subfamily ANCYROCEPHALINAE Bychowsky, 1937

Recurvatus gen. nov.

TYPE-SPECIES AND HOST. *Recurvatus chelatus* sp. nov. from *Craterocephalus stercusmuscarum stercusmuscarum* (Günther, 1876), Ross River, Qld (19°18'S, 146°45'E).

ETYMOLOGY. Latin *re-* back and *curvatus* curved; refers to the copulum shaft shape.

DIAGNOSIS. Body minute (rarely >150μm), divisible into cephalic, trunk, peduncle and haptoral regions. Tegument thin, smooth. Head organs 3 pairs; cephalic lobes, glands present. Eyes rarely 2 pairs, commonly 1 pair, anterior or dorsal to pharynx, when present posterior pair larger than anterior pair, generally compact; granules large, subspherical. Mouth subterminal, midventral; pharynx muscular; intestine bifurcate, caeca united posterior to gonads; diverticula absent. Vitellaria coextensive with intestine, lateral and posterior to crura. Gonads intercaecal; ovary trianguloid, in middle part of body; testis, single, oval to elliptical, smaller than ovary, overlapping ovary dorsally. Vas deferens originating from anterior end of testis, looping around left intestinal crus, joining copulum base dextrally; seminal vesicle formed by dilation of vas deferens, non-sclerotised; prostatic reservoir single, terminating on right side of copulum base. Copulatory apparatus sclerotised, its shaft originating from anterior end of copulum base, consisting of a counter clockwise ring circling copulum base (ventral view, see Kritsky et al., 1985); copulum base bulbate; accessory piece present; spiral filament absent (Type 1 copulatory apparatus Fig. 26A). Vagina sclerotised or not, aperture sclerotised, sinistroventral; seminal receptacle, median, formed by dilation at distal end of vagina, anterior to ovary. Egg with polar filament. Haptor well set off from body, wider than body, subhexagonal. Anchors two pairs, opposed dorsoventrally (Fig. 2A), well-developed inner, outer roots, dorsal pair smaller than ventral pair; shaft, blade present; point well-developed; wing processes present. Transverse bars 2, not articulated; ventral bar arcuate with 2 knobs directed anteriorly 1/3 of length from end; dorsal bar arcuate, often transversely elongate with lateral extensions. Hooks 14, 6 pairs (H2-H7) marginal, 1 pair (H1) more central, 5 pairs ventral (H1-5), 2 pairs dorsal (H6-7), hook H4 longer than anchors; hook shaft and handle equally prominent, handle with expanded demarcation; hook H7 anterior to dorsal anchors. Parasites of freshwater atheriniform fishes.

OTHER SPECIES. *R. signiferi* sp. nov. from *Pseudomugil signifer* Kner, 1865.

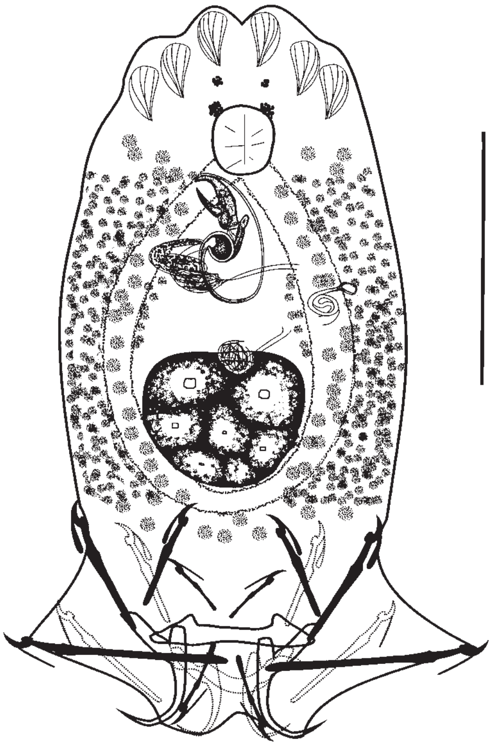

FIG. 3. *Recurvatus chelatus* sp. nov.; composite drawing whole worm, ventral. Scalebar 50µm.

Recurvatus chelatus sp. nov.
(Figs 3-4, Table 2)

MATERIAL. HOLOTYPE. QMG219478 and PARATYPES. QMG219479-219482. All from *Craterocephalus stercusmuscarum stercusmuscarum*, Ross River, Qld, (19°18'S, 146°45'E).

ETYMOLOGY. Latin *chela*, claw; referring to shape of the copulatory apparatus accessory piece.

DESCRIPTION. Eyes 2 pairs, anterior or dorsal to pharynx, anterior eyes usually comprising a few dispersed granules. Anchors with well-developed recurved points. Ventral bar inverted V. Dorsal bar slightly smaller than ventral, in form of deep inverted arch, lateral extensions present. Hooks increase in length from H1 to H4, H2 and H7 of similar size, H3 and H6 of similar size, all similar thickness. Copulatory apparatus well developed; copulum shaft thin; accessory piece large, well sclerotised, chelate. Vagina sclerotised along entire length, consisting of double coil.

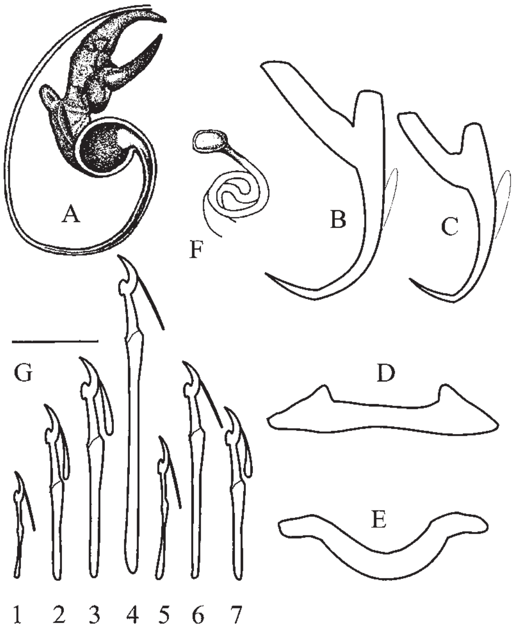

FIG. 4. *Recurvatus chelatus* sp. nov.; A, ♂ copulatory apparatus (dorsal); B, ventral anchor; C, dorsal anchor; D, ventral bar; E, dorsal bar; F, vagina; G, hooks 1-7. Scalebar 10µm.

REMARKS. This species is easily distinguished from *R. signiferi* sp. nov. by the enlarged chelate accessory piece and a coiled sclerotised vagina.

Recurvatus signiferi sp. nov.
(Fig. 5, Table 2)

MATERIAL. HOLOTYPE. QMG218862 and PARATYPES. QMG218863-218866. All from *Pseudomugil signifer*, Liverpool Creek, Qld, (17°43'S, 145°56'E).

ETYMOLOGY. Named after the type host.

DESCRIPTION. Eyes 2 pairs, anterior or dorsal to pharynx. Copulatory apparatus reduced, shaft thin; accessory piece reduced, lightly sclerotised, thumb-shaped, partially encapsulating distal end of copulum shaft. Vagina nonsclerotised, tapered, straight. Anchors with well-developed recurved points; dorsal anchor slightly smaller than ventral. Ventral bar inverted V. Dorsal bar slightly smaller than ventral bar, consisting of a deep inverted arch with lateral extensions. Hooks H2 and H7 of similar size, H3 smaller than H2, H4 handle much thinner than other hooks, H6 smaller than H3.

TABLE 2. Morphometric measurements (µm) of *Recurvatus* species. Means and standard error. ME, number of parasites measured; BL, body length; BW, body width; HW, haptor width; HL, haptor length; PD, pharynx diameter; DA1-6, dorsal anchor; VA1-6, ventral anchor; DB1-3, dorsal bar; VA1-2, ventral bar; H1-7, hook length. ( ) range.

	R. chelatus	*R. signiferi*
ME	28	40
BL	(100-155)	(100-150)
BW	(45-80)	(50-70)
HL	(25-50)	(30-50)
HW	(60-85)	(55-90)
PD	(9-11)	(10-12)
DA1	6.6 ± 0.14	6.8 ± 0.12
DA2	22.9 ± 0.29	22.4 ± 0.24
DA3	17.4 ± 0.24	15.1 ± 0.20
DA4	21.3 ± 0.27	18.6 ± 0.23
DA5	7.7 ± 0.21	8.4 ± 0.18
DA6	10.8 ± 0.22	9.6 ± 0.18
VA1	5.7 ± 0.14	5.0 ± 0.12
VA2	27.5 ± 0.33	27.4 ± 0.28
VA3	20.2 ± 0.26	19.2 ± 0.22
VA4	24.9 ± 0.34	23.4 ± 0.28
VA5	11.6 ± 0.28	12.5 ± 0.23
VA6	13.7 ± 0.26	13.4 ± 0.21
DB1	24.2 ± 0.31	22.4 ± 0.26
DB2	0	0
DB3	7.8 ± 0.15	6.3 ± 0.13
VB1	27.4 ± 0.32	23.9 ± 0.27
VB2	13.2 ± 0.20	12.1 ± 0.17
H1	12.4 ± 0.20	13.5 ± 0.17
H2	20.2 ± 0.30	30.2 ± 0.25
H3	25.0 ± 0.40	27.5 ± 0.34
H4	36.7 ± 0.42	43.6 ± 0.35
H5	16.6 ± 0.22	15.2 ± 0.18
H6	24.0 ± 0.35	25.9 ± 0.29
H7	19.7 ± 0.32	29.0 ± 0.17

Helicirrus gen. nov.

TYPE SPECIES. *Helicirrus splendidae* sp. nov. from *Melanotaenia splendida splendida*, Ross River, Qld, (19°18'S, 146°45'E).

ETYMOLOGY. Latin *heli-*, coiled and *cirrus*, hair; referring to the distal end of copulum shaft.

DIAGNOSIS. Body minute (rarely >150µm), divisible into cephalic, trunk, peduncle, haptoral regions. Tegument thin, smooth. Head organs 3 pairs; cephalic lobes, glands present. Eyes 1or 2 pairs, anterior or dorsal to pharynx, anterior eyes smaller. Mouth subterminal, midventral; pharynx muscular; intestine bifurcate, united posterior to gonads. Gonads intercaecal; ovary ovoid to elliptical, in posterior part of body; testis, single, oval to elliptical, smaller than ovary, overlapping ovary dorsally. Vas deferens originating from anterior end of testis, looping left intestinal crus; seminal vesicle formed by expansion of vas deferens. Copulatory apparatus consisting of a bulbate copulum base; shaft emanating from anterior end of base and recurved sinistro-posteriorly, highly coiled at posterior end with coils posterior to copulum base just anterior to gonads; accessory piece thin elongated spike, attached to right side of base; hair-like filament originating at anterior extremity of shaft (Type II copulatory apparatus, Fig. 25B). Single prostatic reservoir often partially sclerotised. Vagina not observed; seminal receptacle anterior to ovary. Haptor well set off from body, round to hexagonal, equal to body width. Anchors 2 pairs, 1 dorsal, 1 ventral, opposed dorsoventrally (elongated hook haptor form Fig. 2A) or dorsal anchor posterior to ventral anchors (reduced hook haptor form Fig. 2B); ventral anchors larger than dorsal; inner, outer roots distinct; shaft, blade present; wing processes inconspicuous. Two transverse bars not articulated; ventral bar straight, transversely elongate, often much larger than dorsal, with 2 processes 1/3 of length from ends along anterior edge, directed anteriorly. Dorsal bar arched, well-developed or highly reduced. Hooks 14, 6 pairs marginal (H2-H7), pair 1 more central, 5 pairs (H1-5) ventral, 2 pairs dorsal (H6-7); reduced form with kink 1/3 of

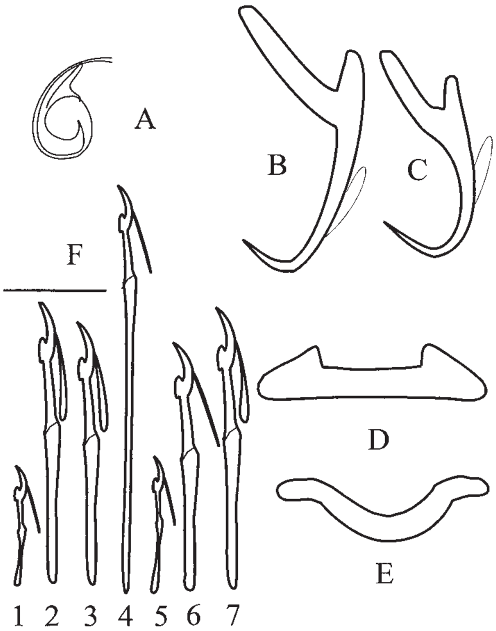

FIG. 5. *Recurvatus signiferi* sp. nov.; A, ♂ copulatory apparatus (dorsal); B, ventral anchor; C, dorsal anchor; D, ventral bar; E, dorsal bar; F, hooks 1-7. Scalebar 10µm.

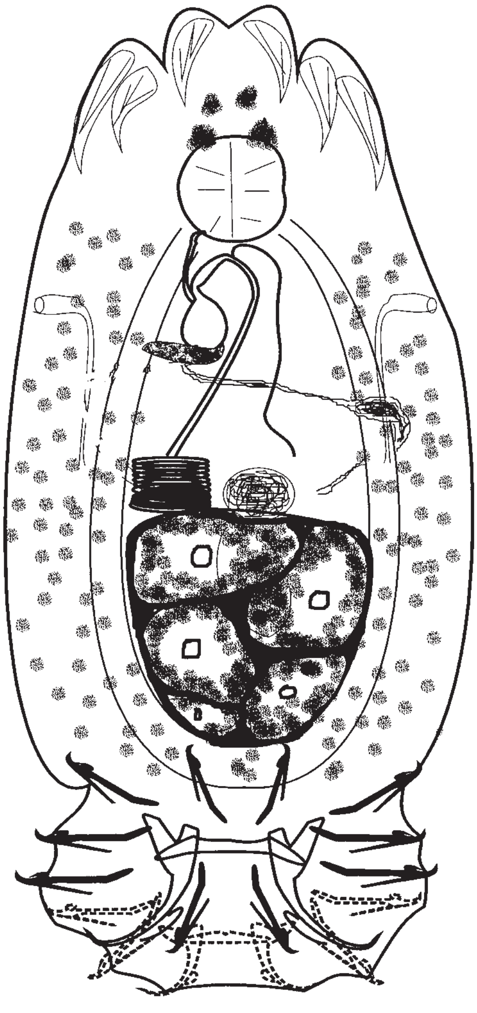

FIG. 6. *Helicirrus splendidae* sp. nov.; composite drawing whole worm, ventral. Scalebar 50µm.

length from end of handle, H7 posterior to ventral anchors, H4 shorter than ventral anchor; elongated form with H4 longer than ventral anchor, H7 anterior to ventral anchors; hook shaft and handle equally prominent, with prominent expanded demarcation; wing processes present. Parasites on gills of freshwater atheriniform fishes.

OTHER SPECIES. *H. megaloanchor* sp. nov. from *M. s. splendida* (Peters, 1866), *H. mcivori* sp. nov. from *M. trifasciata* (Rendahl, 1922), *H. macculochii* sp. nov. from *M. maccullochi* Ogilby, 1915, *H. marjoriaea* sp. nov. from *C. marjoriae.*

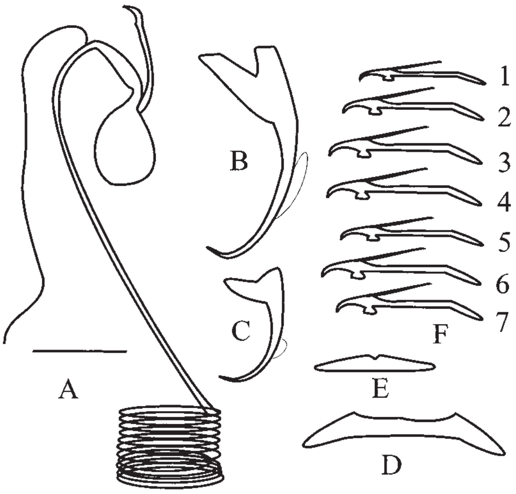

FIG. 7. *Helicirrus splendidae* sp. nov.; A, ♂ copulatory apparatus (dorsal); B, ventral anchor; C, dorsal anchor; D, ventral bar; E, dorsal bar; F, hooks 1-7; Scalebar 10µm.

Helicirrus splendidae sp. nov.
(Figs 6-7, Table3)

MATERIAL. HOLOTYPE QMG218850 and PARATYPES QMG218851-218854. All from *Melanotaenia splendida splendida*, Ross River, Qld, (19°18'S, 146°45'E).

ETYMOLOGY. Named after the type host.

DESCRIPTION. Eyes two pairs, anterior eyes slightly smaller. Haptor with reduced hook orientation (Fig. 2B). Dorsal anchors smaller than ventral, with well-developed inner, reduced outer root; point poorly developed. Ventral anchors with well-developed inner root, reduced outer root; recurved point poorly developed. Dorsal bar much smaller than ventral, inverted arch, thin, weakly developed. Hooks of reduced form and similar size. Copulum shaft with approximately ten coils at posterior end; copulum base single chamber, bulbate, slightly elongate. Accessory piece slightly curved. Seminal vesicle formed by kidney shaped expansion of vas deferens midway between copulum base and loop of intestine. Two excretory pores with cup shaped cavity at body margin, opening at level of copulatory apparatus, ducts extending posteriorly along margin of intestine.

REMARKS. This species is similar to *H. macculochii* sp. nov. by having reduced hooks, dorsal anchors and bar. They differ in the shape of

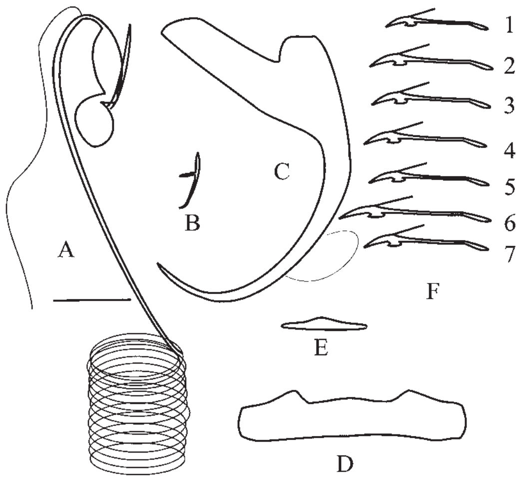

FIG. 8. *Helicirrus megaloanchor* sp. nov.; A, ♂ copulatory apparatus (dorsal); B, dorsal anchor; C, ventral anchor; D, ventral bar; E, dorsal bar; F, hooks 1-7. Scalebar 10µm.

the copulum shaft and ventral anchor inner root length.

Helicirrus megaloanchor sp. nov.
(Fig. 8, Table 3)

MATERIAL. HOLOTYPE QM G219458 and PARATYPES QM G219459-219462. All from *Melanotaenia splendida splendida*, Ross River, Qld, (19°18'S 146°45'E).

ETYMOLOGY. Named after the large size of the ventral anchors.

DESCRIPTION. Eyes two pairs. Haptor with reduced hook sclerite orientation (Fig. 2B). Ventral anchors much larger than dorsal, well-developed inner, reduced outer root; recurved point well-developed. Dorsal anchors with weakly developed inner, outer root, inner root directed toward point; point reduced or absent, often inconspicuous. Dorsal bar slight inverted arch, thin, highly reduced, often inconspicuous, smaller than ventral. Hooks of reduced form and similar size. Copulum shaft expanded proximally posterior to shaft recurve loop, approximately 15 coils at posterior end. Accessory piece thin, directed anteriorly, slightly curved tip. Prostatic reservoir partially sclerotised.

REMARKS. This species is similar to *H. splendidae* sp. nov. and *H. maccullochii* sp. nov. by having reduced hooks, dorsal bar and dorsal anchors. They differ in the size of the ventral anchors.

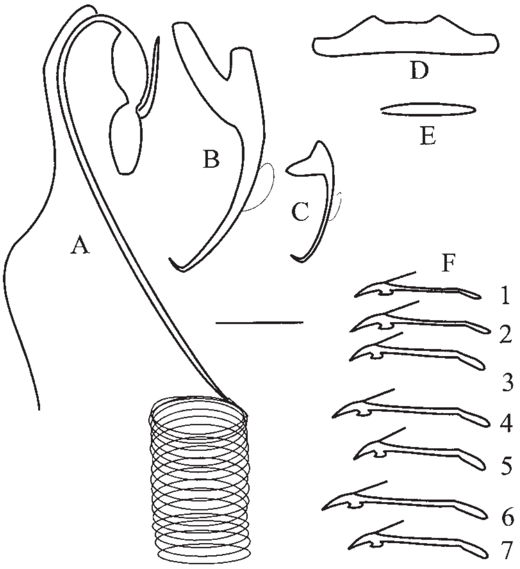

FIG. 9. *Helicirrus maccullochii* sp. nov.; A, ♂ copulatory apparatus (dorsal); B, ventral anchor; C, dorsal anchor; D, ventral bar; E, dorsal bar; F, hooks 1-7. Scalebar 10µm.

Helicirrus maccullochii sp. nov.
(Fig. 9, Table 3)

MATERIAL. HOLOTYPE QM G218823 and PARATYPES QM G218824-218827. All from *Melanotaenia maccullochi*, McIvor River, Qld, (15°03'S 145°26'E).

ETYMOLOGY. Named after the type host.

DESCRIPTION. Eyes one pair. Haptor with reduced hook sclerite orientation (Fig. 2B). Ventral anchors slightly larger than dorsal, well-developed inner, outer roots; recurved point well-developed. Dorsal bar weakly-developed inverted arch, much smaller than ventral. Hooks of reduced form and similar size. Copulum shaft expanded proximally posterior to shaft recurve loop, approximately 35 coils at posterior end; accessory piece thin spike. Prostatic reservoir partially sclerotised.

REMARKS. See remarks for *H. megaloanchor* sp. nov. and *H. splendidae* sp. nov.

Helicirrus mcivori sp. nov.
(Fig. 10, Table 3)

MATERIAL. HOLOTYPE QM G219486 and PARATYPES QM G219487-219489. All from *Melanotaenia trifasciata*, McIvor River, Qld, (15°09'S 145°26'E).

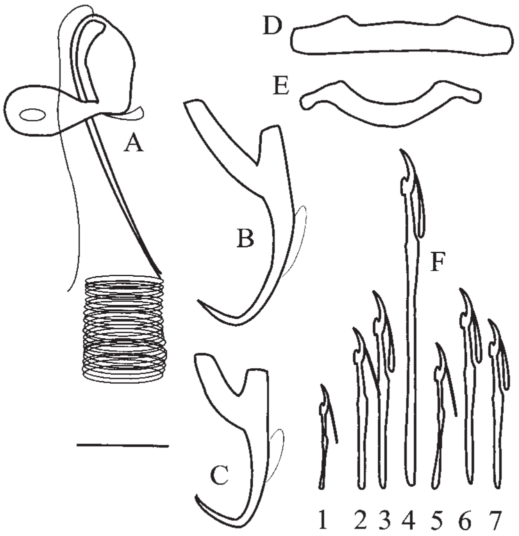

FIG. 10. *Helicirrus mcivori* sp. nov.; A, ♂ copulatory apparatus (dorsal); B, ventral anchor; C, dorsal anchor; D, ventral bar; E, dorsal bar; F, hooks 1-7. Salebar 10µm.

ETYMOLOGY. Named after the type host location.

DESCRIPTION. Eyes one pair. Haptor with elongated hook sclerite orientation (Fig. 2A). Ventral anchors slightly larger than dorsal, well-developed inner, outer roots; recurved point well-developed. Dorsal bar well-developed inverted arch, similar in size to ventral. Hooks elongated form, increasing in handle length from H1 to H4, H4 much longer than other hooks and ventral anchors, H3 and H6 of similar length, H7 anterior to ventral anchors. Copulum base orientated perpendicular and sinistral to shaft; shaft expanded proximal to recurve, approximately 30 coils at posterior end; accessory piece reduced. Seminal vesicle expanded bulb at loop of gut crura.

REMARKS. This species is similar to *H. gertrudaea* sp. nov. and *H. marjoriaea* sp. nov. by having elongated hooks and well-developed dorsal anchors and bar. It differs by having a proximal expansion of the copulum shaft.

Helicirrus gertrudaea sp. nov.
(Fig. 11, Table 3)

MATERIAL. HOLOTYPE QM G218857 and PARATYPES QM G218858-218861. All from *Pseudomugil gertrudaea*, Howard Creek, Northern Territory, (12°27'S 130°50'E).

ETYMOLOGY. Named after the type host.

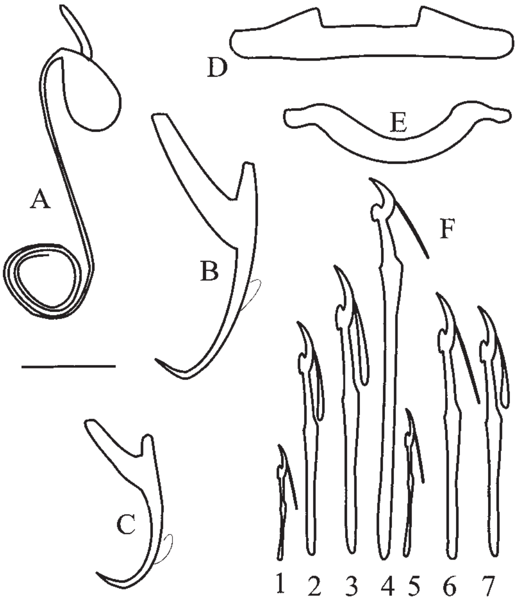

FIG. 11. *Helicirrus gertrudaea* sp. nov.; A, ♂ copulatory apparatus (dorsal); B, ventral anchor; C, dorsal anchor; D, ventral bar; E, dorsal bar; F, hooks 1-7. Scalebar 10µm.

DESCRIPTION. Eyes two pairs, anterior eyes reduced. Haptor with elongated hook sclerite orientation (Fig. 2A). Ventral anchors larger than dorsal, well-developed inner, outer roots; recurved point. Dorsal bar well-developed inverted arch, similar in size to ventral. Hooks elongated form, increasing in handle length from H1 to H4 then decrease in length, H4 longer than ventral anchor, H3 longer than H6, H7 longer than H2. Copulum shaft thin, proximal expansion absent, approximately ten coils at posterior end; copulum base single chamber, oval, elongated; accessory piece elongated spike.

REMARKS. This species is most similar to *H. marjoriaea* sp. nov. by having elongated hooks and well-developed anchors and bars. They differ in the number of coils present in the copulum shaft.

Helicirrus marjoriaea sp. nov.
(Fig. 12, Table 3)

MATERIAL. HOLOTYPES QM G218834 and PARATYPES QM G218835-218838. All from *Craterocephalus marjoriae*, Amamoor Creek, Qld, (26° 21'S 152°40'E).

ETYMOLOGY. Named after the type host.

DESCRIPTION. Eyes one pair. Haptor with elongated hook sclerite orientation (Fig. 2A). Ventral anchor slightly larger than dorsal, well-developed inner, outer roots; recurved point well-developed. Dorsal bar well-developed inverted arch, similar in size to ventral. Hooks elongated form, hook H7 slightly smaller than H2, H3 much longer than H6, H4 longer than anchors. Copulum shaft thin, proximal expansion absent, approximately 30 coils at posterior end; accessory piece elongated spike. Prostatic reservoir partially sclerotised.

REMARKS. See remarks for *H. gertrudaea* sp. nov.

Longidigitis gen. nov.

TYPE SPECIES AND HOST. *Longidigitis auripontiformis* sp. nov. from *M. s. splendida*, Bluewater Creek, Qld, (19°18'S 146°45'E).

ETYMOLOGY. Latin *longus*, long and *digitus*, finger; refers to the hooks.

DIAGNOSIS. Body minute (rarely >150µm), divisible into cephalic, trunk, peduncle and haptoral region. Tegument thin, smooth. Head organs three pairs, cephalic lobes and glands present. Eyes rarely two pairs, commonly one, anterior or dorsal to pharynx, anterior eyes, when present, consisting of scattered granules. Mouth subterminal, midventral; pharynx muscular; intestine bifurcate, united posterior to gonads. Vitellaria coextensive with intestine, lateral and posterior to crura. Gonads intercaecal; ovary trianguloid, in middle part of body; testis single, oval to elliptical, smaller than ovary, overlapping ovary dorsally. Vas deferens originating from anterior end of testis, looping intestinal crus sinistrally, joining dextral side of copulum base posteriorly; seminal vesicle formed by dilation of vas deferens, often partially sclerotised; single prostatic reservoir originating from dextral side of copulum base. Copulatory apparatus consisting of a copulum base; copulum shaft originating from anterior end of copulum base consisting of a single sinistral recurved loop (Type III copulatory apparatus, Fig. 26C) distal end arches anterior to copulum base and is directed at right side of body, terminating dextral to copulum base; base bulbate; accessory piece thumb shaped, directed anteriorly; spiral filament absent. Vagina, non-sclerotised, opening sinistromarginal; seminal receptacle formed by dilation of vagina at distal end, anterior to ovary. Egg with polar filament. Haptor well-set off from body, wider than body, subhexagonal in shape. Anchors two pairs, well-developed, opposed dorsoventrally (Fig. 2A); dorsal anchors smaller than ventral, inner roots well-developed, outer roots reduced; shaft and blade present; point well developed; ventral anchors inner, outer roots; shaft and blade present; point well-developed. Transverse bars two, not articulated; ventral bar with two knobs directed anteriorly third of length from end, usually tapering laterally, rarely with expansions at ends; dorsal bar arcuate, often transversely elongate with lateral extensions, medial notch present or absent on posterior surface, equal in length or slightly smaller than ventral. Hooks 14, six pairs (H2-H7) marginal, pair one more central, five pairs ventral (H1-H5), two pairs dorsal (H6-7); handle length increases from H1 to H4, H4 always longer than the anchors, H7 anterior to ventral anchors; hook shaft and handle equally prominent, handle with expanded demarcation; wing process present. Parasites of freshwater fish (Atheriniformes).

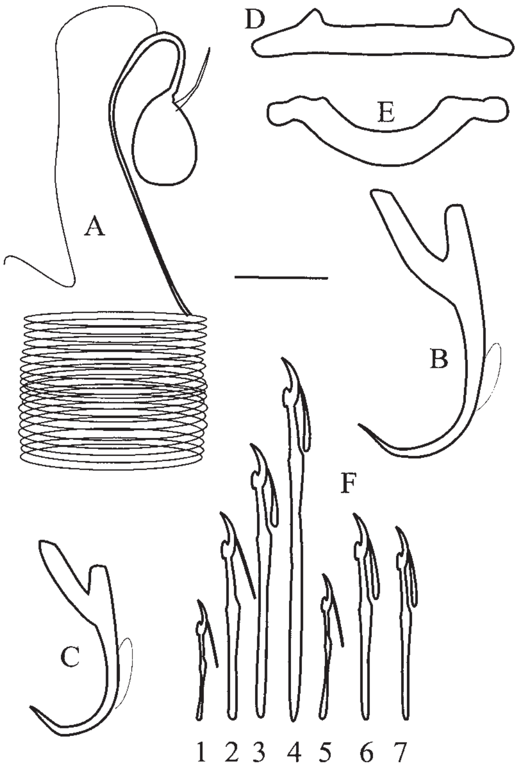

FIG. 12. *Helicirrus marjoriaea* sp. nov.; A, ♂ copulatory apparatus (dorsal); B, ventral anchor; C, dorsal anchor; D, ventral bar; E, dorsal bar; F, hooks 1-7. Scalebar 10µm.

TABLE 3. Morphometric measurements (µm) of *Helicirrus* species. Means and standard error. ME, number of parasites measured; BL, body length; BW, body width; HW, haptor width; HL, haptor length; PD, pharynx diameter; DA1-6, dorsal anchor; VA1-6, ventral anchor; DB1-3, dorsal bar; VA1-2, ventral bar; H1-7, hook length. ( ) range.

	H. splendidae	*H. megaloanchor*	*H. maccullochii*	*H. mcivori*	*H. gertrudaea*	*H. marjoriaea*
ME	28	15	10	17	15	41
BL	(140-200)	(130-170)	(130-200)	(90-160)	(80-100)	(100-150)
BW	(70-140)	(40-80)	(50-90)	(25-50)	(25-40	(50-100)
HL	(25-55)	(35-50)	(25-40)	(25-45)	(20-35)	(25-45)
HW	(50-70)	(50-90)	(50-80)	(40-90)	(50-70)	(60-110)
PD	(15-21)	(10-16)	(17-21)	(7-11)	(8-12)	(9-15)
DA1	2.7 ± 0.17	2.4 ± 0.24	1.80 ± 0.29	4.87 ± 0.26	3.7 ± 0.19	6.07 ± 0.10
DA2	11.3 ± 0.31	9.3 ± 0.47	11.20 ± 0.39	19.4 ± 0.38	18.3 ± 0.32	20.80 ± 0.14
DA3	10.9 ± 0.18	4.7 ± 0.17	12.60 ± 0.31	14.8 ± 0.50	14.2 ± 0.20	15.73 ± 0.12
DA4	12.9 ± 0.26	6.7 ± 0.17	14.10 ± 0.28	17.6 ± 0.68	16.6 ± 0.24	19.43 ± 0.14
DA5	4.2 ± 0.21	2.4 ± 0.18	2.50 ± 0.17	5.1 ± 0.19	7.1 ± 0.28	7.15 ± 0.13
DA6	7.1 ± 0.17	1.9 ± 0.11	5.50 ± 0.22	8.4 ± 0.21	8.6 ± 0.35	10.18 ± 0.16
VA1	2.1 ± 0.16	5.6 ± 0.44	2.10 ± 0.10	4.7 ± 0.17	3.9 ± 0.17	5.78 ± 0.10
VA2	21.6 ± 0.26	38.6 ± 0.44	26.00 ± 0.61	25.6 ± 0.45	27.9 ± 0.34	27.38 ± 0.16
VA3	19.2 ± 0.26	32.0 ± 0.47	23.40 ± 0.45	18.1 ± 0.46	20.4 ± 0.29	21.35 ± 0.13
VA4	22.4 ± 0.26	37.7 ± 0.65	27.40 ± 0.40	21.8 ± 0.48	25.0 ± 0.32	26.30 ± 0.19
VA5	5.9 ± 0.25	13.8 ± 0.52	8.30 ± 0.47	9.8 ± 0.44	11.5 ± 0.27	9.72 ± 0.17
VA6	10.9 ± 0.19	25.6 ± 0.47	13.40 ± 0.40	11.4 ± 0.21	11.9 ± 0.31	13.85 ± 0.14
DB1	12.7 ± 0.33	12.7 ± 0.24	10.50 ± 0.37	19.8 ± 0.32	24.3 ± 0.25	25.68 ± 0.24
DB2	0.00	0.00	.00	0.00	0.00	.00
DB3	2.4 ± 0.13	2.6 ± 0.24	2.30 ± 0.15	5.6 ± 0.18	6.1 ± 0.18	7.50 ± 0.13
VB1	21.9 ± 0.25	31.0 ± 0.58	21.80 ± 0.33	24.5 ± 0.31	24.1 ± 0.35	28.38 ± 0.24
VB2	11.0 ± 0.21	15.3 ± 0.29	7.70 ± 0.30	11.8 ± 0.23	10.9 ± 0.25	15.43 ± 0.22
H1	14.1 ± 0.24	13.9 ± 0.39	13.20 ± 0.42	12.2 ± 0.47	12.2 ± 0.17	13.23 ± 0.17
H2	15.7 ± 0.25	16.9 ± 0.39	16.10 ± 0.23	18.5 ± 0.37	24.5 ± 0.19	22.65 ± 0.18
H3	16.4 ± 0.24	17.1 ± 0.51	16.10 ± 0.23	22.5 ± 0.33	30.3 ± 0.32	30.52 ± 0.29
H4	17.0 ± 0.23	16.2 ± 0.43	16.10 ± 0.18	37.8 ± 0.41	39.3 ± 0.35	41.53 ± 0.28
H5	15.6 ± 0.40	16.6 ± 0.34	13.70 ± 0.37	16.2 ± 0.30	15.9 ± 0.24	17.57 ± 0.19
H6	17.8 ± 0.41	21.1 ± 0.31	17.80 ± 0.39	22.1 ± 0.30	27.5 ± 0.34	22.98 ± 0.23
H7	17.2 ± 0.19	17.1 ± 0.31	16.90 ± 0.43	19.5 ± 0.69	26.8 ± 0.38	21.08 ± 0.19

OTHER SPECIES: *Longidigitis robustus* sp. nov. from *M. s. splendida*, *L. maccullochii* sp. nov. from *M. maccullochi*, *L. hopevalensis* sp. nov. from *M. trifasciata*, *L. gracilis* sp. nov. from *Melanotaenia utcheensis* McGuigan, 2001 and *M. eachamensis*, *L. utcheei* sp. nov. from *Cairnsichthys rhombosomoides* (Nichols & Raven, 1928).

Longidigitis auripontiformis sp. nov.
(Fig. 13-14, Table 4)

MATERIAL. HOLOTYPE QM G218877 and PARATYPES QM G218878-218881. All from *Melanotaenia splendida splendida*, Bluewater Creek, Qld, (19°18'S, 146°45'E).

ETYMOLOGY. Latin *auris*, ear, *pons*, bridge and *forma*, shape; referring to the dorsal bar shape.

DESCRIPTION. Eyes two pairs, rarely one. Dorsal anchors slightly smaller than ventral, with well-developed elongated points, inner roots, slightly reduced outer roots with conspicuous bump on inner curve of shaft; ventral anchor well-developed inner, outer roots. Ventral bar arcuate, not tapering laterally, ends square with protuberance directed anteriorly. Dorsal bar, semi-circular, with lateral extensions, notch absent on posterior edge, thin membranous infill present on anterior edge. Hooks H7 smaller than H2, H6 smaller than H3, H1 and H5 much smaller than H6. Copulum shaft thick; accessory piece well-developed. Vas deferens with partially sclerotised seminal vesicle, extending from copulum to intestinal crus loop. Vagina tubular, usually inconspicuous.

REMARKS. This species is similar to *L. hopevalensis* sp. nov. by having similar shaped anchors and ventral bar. It is distinguished by the thickness of the copulum shaft and the shape of the ventral bar.

Longidigitis hopevalensis sp. nov.
(Fig. 15, Table 4)

MATERIAL. HOLOTYPE QM G219490 and PARATYPES QM G219491-219493. All from *Melanotaenia trifasciata*, McIvor River, Qld, (15°09'S 145°26'E).

ETYMOLOGY. From Hopevale near the sample location.

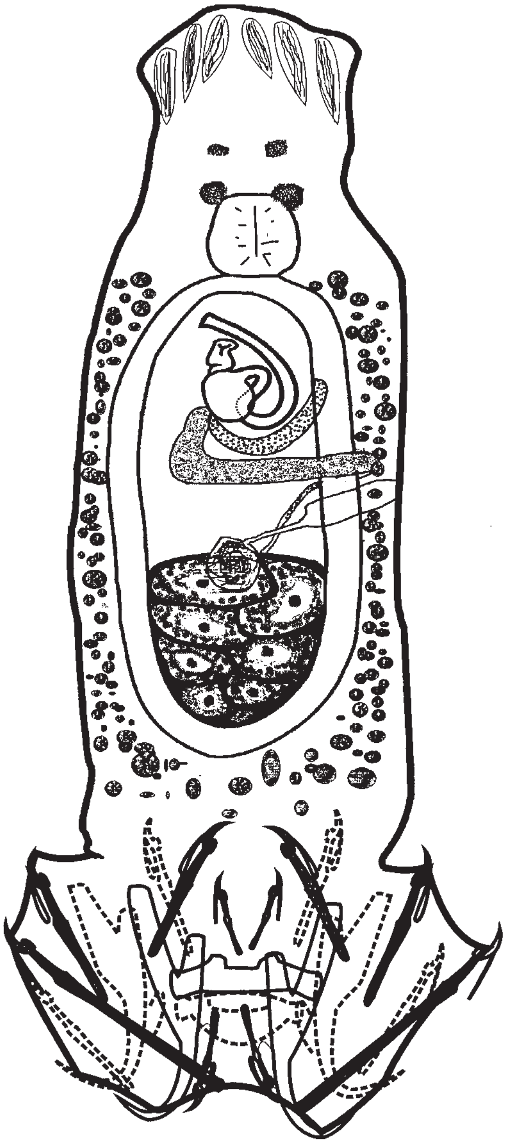

FIG. 13. *Longidigitis auripontiformis* sp. nov.; composite drawing whole worm ventral. Scalebar 50µm.

DESCRIPTION. Eyes two pairs, rarely one. Dorsal anchors slightly smaller than ventral, with well-developed elongated points, inner roots, reduced outer roots with conspicuous bump on inner curve of shaft. Ventral anchor well-developed inner roots, reduced outer roots. Ventral bar arcuate, not tapering laterally, ends square with protuberance directed anteriorly. Dorsal bar, semi-circular, with lateral extensions, posteromedial notch present, thick infill present on anterior edge. Hooks H7 smaller than H2, H6 smaller than H3, H1 and H5 much smaller than H6. Copulum shaft thin; accessory piece well-developed. Vas deferens with partially sclerotised seminal vesicle, extending from copulum to intestinal crus loop. Vagina tubular, usually inconspicuous.

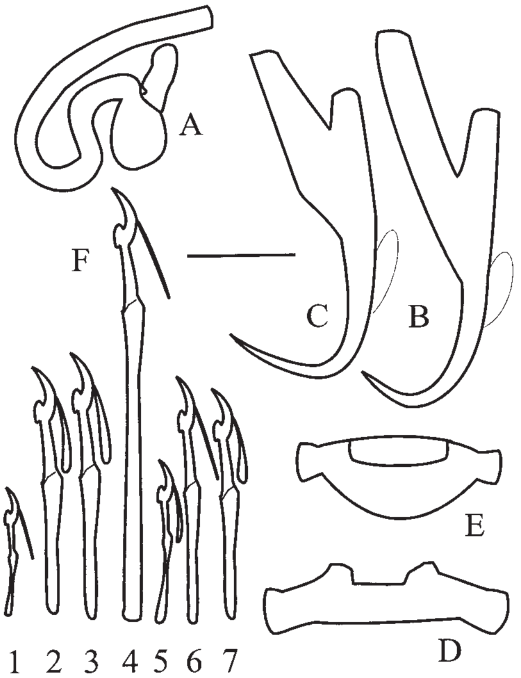

FIG. 14. *Longidigitis auripontiformis* sp. nov; A, ♂ copulatory apparatus (dorsal); B, ventral anchor; C, dorsal anchor; D, ventral bar; E, dorsal bar; F, hooks 1-7. Scalebar 10µm.

REMARKS. See *L. auripontiformis* sp. nov.

Longidigitis robustus sp. nov.
(Fig. 16, Table 4)

MATERIAL HOLOTYPE QM G218882 and PARATYPES QM G219195. All from *Melanotaenia splendida splendida*, Bluewater Creek, Qld, (19°18'S, 146°45'E).

ETYMOLOGY. Named after the robust anchors.

DESCRIPTION. Eyes one pair, rarely two. Dorsal anchors slightly smaller than ventral, with well-developed elongated points, well-developed thickened inner, outer roots, outer roots slightly reduced in length. Ventral bar arcuate, ends

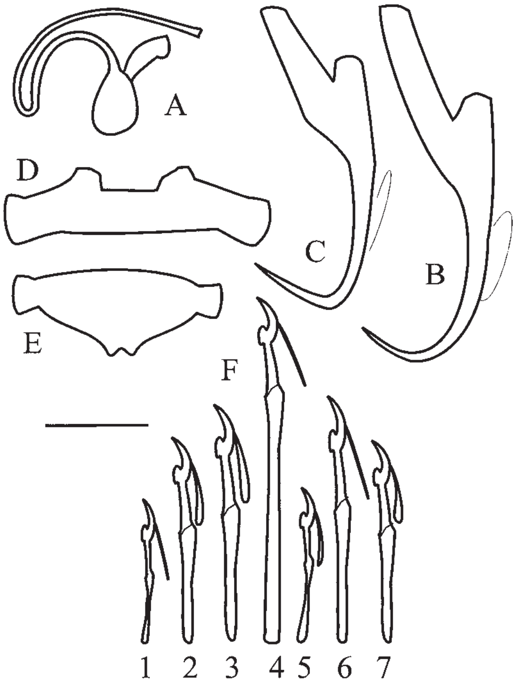

FIG. 15. *Longidigitis hopevalensis* sp. nov; A, ♂ copulatory apparatus (dorsal); B, ventral anchor; C, dorsal anchor; D, ventral bar; E, dorsal bar; F, hooks 1-7. Scalebar 10μm.

square with protuberance directed anteriorly. Dorsal bar expanded medially, tapering laterally, posteromedial notch present, thick membranous infill present on anterior edge. Hooks H7 and H2 of equal length, H6 smaller than H3, H2 slightly smaller than H6. Copulum shaft thin, with highly reduced loop; accessory piece well-developed. Vas deferens inconspicuous. Vagina inconspicuous.

REMARKS. This species is distinguished within the genus by robust anchors and shape of the bars.

Longidigitis maccullochii sp. nov.
(Fig. 17, Table 4)

MATERIAL. HOLOTYPE QM G218828 and PARATYPES QM218829-218833. All from *Melanotaenia maccullochi*, McIvor River, Qld, (15°03'S 145°26'E).

ETYMOLOGY. Named after the type host.

DESCRIPTION. Eyes two pairs. Dorsal anchors slightly smaller than ventral, both with well-developed recurved points, inner, outer roots. Ventral bar triangular, with lateral extremities tapered. Dorsal bar of similar size to ventral, consisting of an inverted arch, transversely elongate with lateral extensions; thin membranous infill absent on anterior edge; posteromedial notch absent. Hooks H2 slightly smaller than H7, H6 smaller than H3, H1 and H5 much smaller than H6. Copulum shaft thin; accessory piece lightly sclerotised, anterior end directed away from inner edge of copulum shaft. Vas deferens not sclerotised; seminal vesicle partially sclerotised, formed by bulbate dilation of vas deferens just posterior to copulum base. Vagina elongate tube.

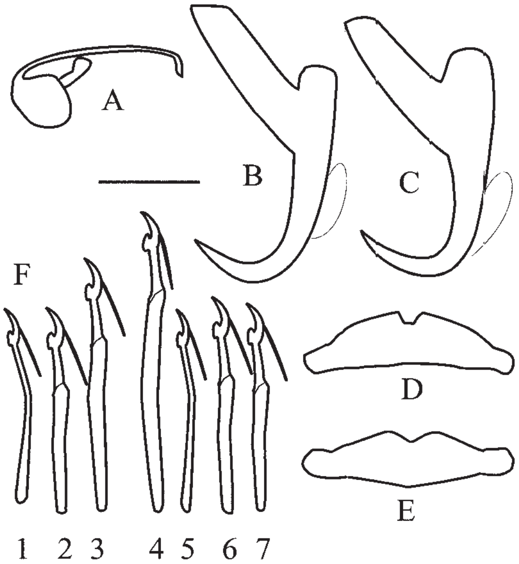

FIG. 16. *Longidigitis robustus* sp. nov.; A, ♂ copulatory apparatus (dorsal); B, ventral anchor; C, dorsal anchor; D, ventral bar; E, dorsal bar; F, hooks 1-7. Scalebar 10μm.

REMARKS. This species is most similar to *L. utcheei* sp. nov. It differs in the size of the copulum shaft and shape of the bar structure.

Longidigitis utcheei sp. nov.
(Fig. 18, Table 4)

MATERIAL. HOLOTYPE QM G219473 and PARATYPES QM G219474-219477. All from *Cairnsichthys rhombosomoides*, Utchee Creek, Qld, (17º37 S 145º56 E).

ETYMOLOGY. Named after the type-host collection site.

DESCRIPTION. Eyes two pairs, anterior or dorsal to pharynx. Anchors with well-developed

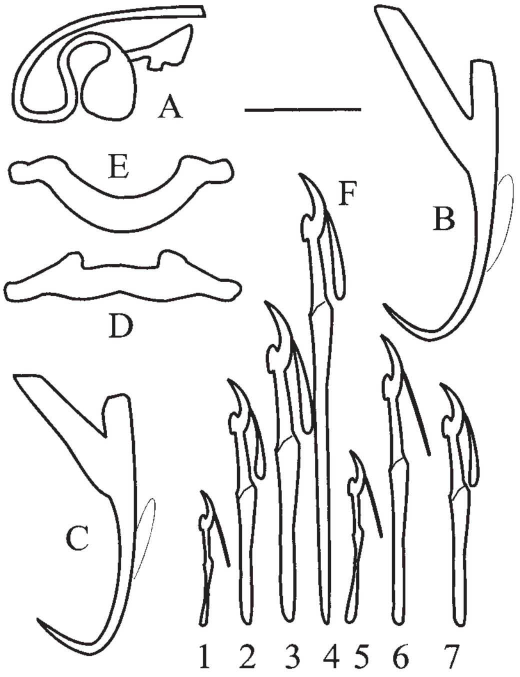

FIG. 17. *Longidigitis maccullochii* sp. nov.; A, ♂ copulatory apparatus (dorsal); B, ventral anchor; C, dorsal anchor; D, ventral bar; E, dorsal bar; F, hooks 1-7. Scalebar 10µm.

recurved points and inner and outer roots; dorsal anchors much smaller than ventral. Ventral bar inverted V, tapering laterally. Dorsal bar slightly smaller than ventral; consisting of a shallow inverted arch, with lateral extensions, thin membranous infill reduced on anterior edge, posteromedial notch absent. Hooks H2 slightly longer than H7, H3 and H6 of similar length, H1 and H5 much smaller than H6. Copulum shaft thick; accessory piece slightly sclerotised. Seminal vesicle non-sclerotised. Vagina inconspicuous.

REMARKS. See remarks for *L. maccullochii* sp. nov.

Longidigitis gracilis sp. nov.

(Fig. 19, Table 4)

MATERIAL. HOLOTYPE QM 218845 and PARATYPES QM G218846-218849. All from *Melanotaenia utcheensis*, Utchee Creek, Qld, (17º37 S 145º56 E).

ETYMOLOGY. Named after the thin copulum shaft.

DESCRIPTION. Eyes two pairs. Dorsal and ventral anchors with well-developed recurved points, inner, outer roots. Dorsal anchors slightly smaller than ventral. Dorsal bar slightly smaller than ventral, consisting of a shallow inverted arch with lateral extensions, thin membranous infill absent on anterior edge, posteromedial notch present. Ventral bar straight, tapering laterally. Hooks H2 and H7 of similar length, H3 and H6 of similar length, H1 and H5 much smaller than H6. Copulum shaft thin; accessory piece thin partially sclerotised. Seminal vesicle non-sclerotised. Vagina tubular, usually inconspicuous.

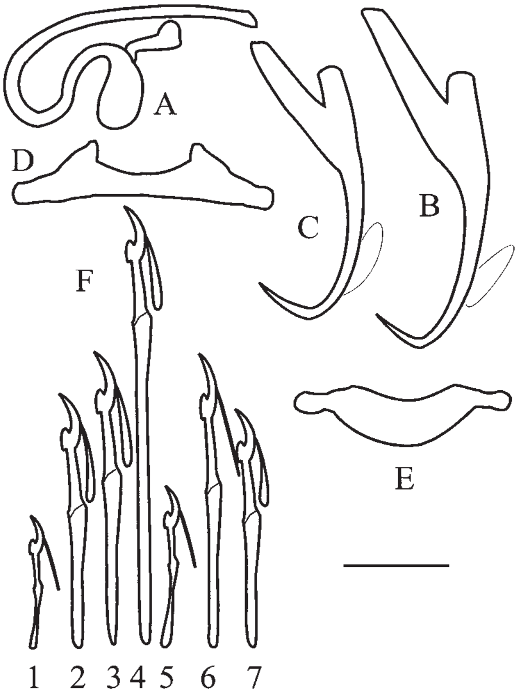

FIG. 18. *Longidigitis utcheei* sp. nov.; A, ♂ copulatory apparatus (dorsal); B, ventral anchor; C, dorsal anchor; D, ventral bar; E, dorsal bar; F, hooks 1-7. Scalebar 10µm.

REMARKS. This species is similar to *L. maccullochii* sp. nov. and *L. utcheei* sp. nov. It differs by having a posteromedial notch on the dorsal bar and the size of the copulum shaft.

Iliocirrus gen. nov.

TYPE SPECIES AND HOST. *I. iliocirrus* sp. nov. from *M. s. splendida*, Bluewater Creek, Qld, (19°18'S 146°45'E).

ETYMOLOGY. Latin *ilios*, twisted and *cirrus*, hair; referring to the form of the copulum shaft.

DIAGNOSIS. Body minute (rarely >150µm), divisible into cephalic, trunk, peduncle, haptoral

TABLE 4. Morphometric measurements (µm) of *Longidigitis* species. Means and standard error. ME, number of parasites measured; BL, body length; BW, body width; HW, haptor width; HL, haptor length; PD, pharynx diameter; DA1-6, dorsal anchor; VA1-6, ventral anchor; DB1-3, dorsal bar; VA1-2, ventral bar; H1-7, hook length. ( ) range.

	L. auripontiformis	*L. hopevalensis*	*L. robustus*	*L. maccullochii*	*L. utcheei*	*L. gracilis*
ME	35	16	20	47	27	31
BL	(120-160)	(110-140)	(130-220)	(90-160)	(120-190)	(110-140)
BW	(35-60)	(40-70)	(50-90)	(40-70)	(50-80)	(50-70)
HL	(25-50)	(20-40)	(30-50)	(25-60)	(30-50)	(25-40)
HW	(60-95)	(50-70)	(50-80)	(50-80)	(55-80)	(50-80)
PD	(9-12)	(9-12)	(13-17)	(9-13)	(11-15)	(9-11)
DA1	9.4 ± 0.14	7.9 ± 0.18	6.4 ± 0.26	5.52 ± 0.09	6.2 ± 0.21	5.0 ± 0.14
DA2	30.7 ± 0.31	29.4 ± 0.26	26.2 ± 0.26	23.00 ± 0.18	27.0 ± 0.49	20.6 ± 0.24
DA3	23.8 ± 0.21	22.0 ± 0.26	19.2 ± 0.28	17.81 ± 0.17	20.8 ± 0.20	15.8 ± 0.20
DA4	27.2 ± 0.23	24.5 ± 0.26	22.4 ± 0.27	20.27 ± 0.19	23.9 ± 0.28	19.0 ± 0.23
DA5	9.7 ± 0.19	10.8 ± 0.40	10.8 ± 0.31	6.96 ± 0.13	7.4 ± 0.28	6.0 ± 0.20
DA6	13.0 ± 0.25	11.9 ± 0.41	12.4 ± 0.48	8.27 ± 0.14	9.9 ± 0.14	8.8 ± 0.24
VA1	5.4 ± 0.13	6.1 ± 0.17	6.3 ± 0.22	4.62 ± 0.08	5.4 ± 0.13	5.1 ± 0.17
VA2	34.7 ± 0.39	34.2 ± 0.26	27.2 ± 0.31	27.65 ± 0.24	31.7 ± 0.36	23.4 ± 0.26
VA3	22.8 ± 0.24	24.1 ± 0.27	18.7 ± 0.35	18.87 ± 0.19	22.1 ± 0.19	16.6 ± 0.18
VA4	28.5 ± 0.20	27.1 ± 0.34	21.9 ± 0.26	22.85 ± 0.22	26.3 ± 0.28	20.4 ± 0.22
VA5	13.5 ± 0.27	12.7 ± 0.21	11.8 ± 0.36	11.13 ± 0.18	11.4 ± 0.33	8.8 ± 0.23
VA6	12.6 ± 0.24	13.1 ± 0.30	13.1 ± 0.30	9.94 ± 0.24	10.9 ± 0.18	10.0 ± 0.23
DB1	19.2 ± 0.27	19.4 ± 0.27	20.7 ± 0.36	17.79 ± 0.15	20.7 ± 0.29	19.3 ± 0.32
DB2	0.00	0.0	0.00	.00	0.00	4.4 ± 0.16
DB3	7.8 ± 0.18	8.6 ± 0.15	5.9 ± 0.19	5.33 ± 0.10	5.4 ± 0.14	5.6 ± 0.20
VB1	22.7 ± 0.25	25.7 ± 0.34	20.4 ± 0.20	19.54 ±0.16	25.0 ± 0.29	23.1 ± 0.31
VB2	8.6 ± 0.15	9.6 ± 0.12	5.2 ± 0.66	8.02 ± 0.13	9.4 ± 0.18	11.2 ± 0.24
H1	13.2 ± 0.17	14.1 ± 0.26	12.4 ± 0.44	11.96 ± 0.13	12.4 ± 0.26	11.0 ± 0.21
H2	22.9 ± 0.27	21.0 ± 0.20	19.2 ± 0.35	20.83 ± 0.20	24.0 ± 0.41	18.8 ± 0.25
H3	24.4 ± 0.24	22.8 ± 0.28	24.0 ± 0.37	26.65 ± 0.27	27.5 ± 0.46	22.7 ± 0.31
H4	41.0 ± 0.32	33.3 ± 0.33	28.8 ± 0.42	36.94 ± 0.27	40.7 ± 0.64	36.7 ± 0.31
H5	16.4 ± 0.21	16.1 ± 0.20	15.9 ± 0.36	14.08 ± 0.12	15.2 ± 0.16	14.3 ± 0.35
H6	23.6 ± 0.24	24.2 ± 0.28	23.6 ± 0.49	24.10 ± 0.20	28.8 ± 0.46	21.6 ± 0.24
H7	22.1 ± 0.26	20.2 ± 0.28	19.6 ± 0.38	21.58 ± 0.22	23.1 ± 0.41	18.4 ± 0.16

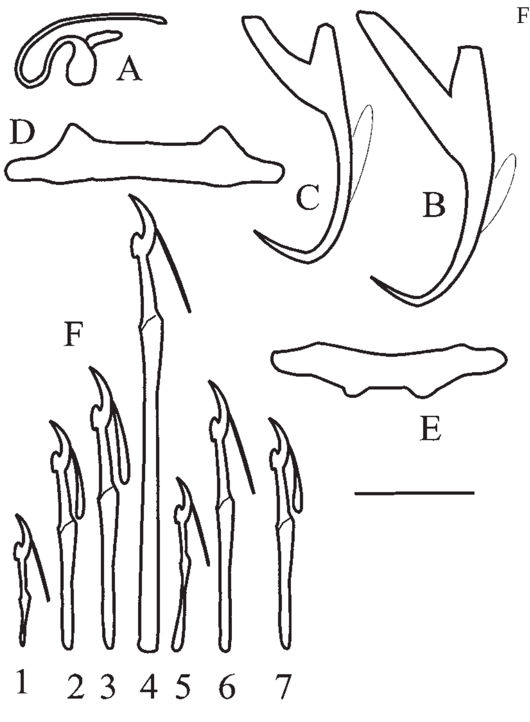

FIG. 19. *Longidigitis gracilis* sp. nov.; A, ♂ copulatory apparatus (dorsal); B, ventral anchor; C, dorsal anchor; D, ventral bar; E, dorsal bar; F, hooks 1-7. Scalebar 10µm.

regions. Tegument thin, smooth. Head organs three pairs; cephalic lobes and glands present. Mouth subterminal, midventral; pharynx muscular; intestine bifurcate, united posterior to gonads. Eyes rarely two pairs, commonly one, anterior or dorsal to pharynx, anterior eyes, when present, consisting of scattered granules. Gonads intercaecal; ovary trianguloid, in middle part of body; testis single, oval to elliptical, smaller than ovary, overlapping ovary dorsally. Vas deferens originating from anterior end of testis, looping intestinal crus sinistrally, joining copulum base posterodextrally; seminal vesicle non-sclerotised, formed by dilation of vas deferens; prostatic reservoir, single terminating dextral to copulum base. Copulum sclerotised, shaft originating from anterior end of copulum base, consisting of a double sinistral recurved loop (Type IV copulatory apparatus, Fig. 26D), distal end arches anterior to copulum base, directed to dextral side of body, terminating

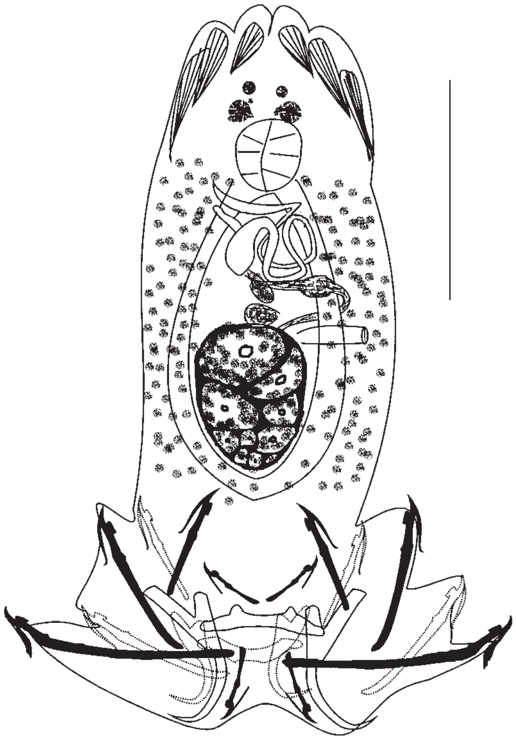

FIG. 20. *Iliocirrus iliocirrus* sp. nov.; composite drawing whole worm, ventral. Scalebar 50µm.

dextral to copulum base; base bulbate; accessory piece thumb shaped, directed anteriorly; spiral filament absent. Vagina, non-sclerotised, opening dextromarginal; seminal receptacle formed by dilation of vagina, at distal end, anterior to ovary. Vitellaria coextensive with intestine, lateral and posterior to crura. Haptor well set off from body, wider than body, sub-hexagonal. Anchors two pairs, well-developed, opposed dorso-ventrally (Fig. 2A); dorsal anchors much smaller than ventral. Transverse bars two, not articulated; ventral bar laterally elongate, two knobs directed anteriorly third of length from end, usually tapering laterally, rarely with expansions at ends; dorsal bar arcuate, with lateral extensions, medial notch present on posterior surface, smaller than ventral. Hooks 14, six pairs (H2-H7) marginal, pair one more central, five pairs ventral, two pairs dorsal (H6-7), H7 anterior to ventral anchors; handle length increases from H1 to H4, H4 always longer than the anchors; hook shaft and handle equally prominent, handle with expanded demarcation; wing process present. Parasites of freshwater atherinform fishes.

OTHER SPECIES: *Iliocirrus trifasciatae* sp. nov. from *M. trifasciata*, *I. mazlini* sp. nov. from *M. eachamensis* and *Melanotaenia utcheensis*, *I. ornatusi* sp. nov. from *Rhadinocentrus ornatus* Regan, 1914, *I. rossi* sp. nov. from *C. s. stercusmuscarum.*

Iliocirrus iliocirrus sp. nov.
(Fig. 20-21, Table 5)

MATERIAL. HOLOTYPE QM G219468 and PARATYPES QM G219469-72. All from *Melanotaenia splendida splendida*, Bluewater Creek, Qld, (19°18'S 146°45'E).

ETYMOLOGY. As for genus.

DESCRIPTION. Eyes one pair, rarely two. Vas deferens, non-sclerotised; seminal vesicle consisting of expanded bulb at point of loop around intestine. Copulum shaft consisting of a thick well-developed double sinistral recurved loop, distal end with pronounced sickle-shape expansion; accessory piece thin lightly sclerotised. Vagina tubular. Anchors with well-developed recurved points, shaft, blade present; ventral anchor with well-developed inner, outer roots; dorsal anchors much smaller than ventral, with reduced inner, outer roots. Dorsal bar shallow inverted arch; ventral bar ends tapering laterally. Hooks H7 slightly smaller than H2, H6 slightly smaller than H3, H1 and H5 much smaller than H6.

REMARKS. This species is most similar to *I. rossi*. sp. nov. It is easily distinguished by morphometric variation and the copulum shaft thickness.

Iliocirrus rossi sp. nov.
(Fig. 22, Table 5)

MATERIAL. HOLOTYPE QM G219463 and PARATYPES QM G219464-219467. All from *Craterocephalus stercusmuscarum stercusmuscarum*, Ross River, Qld, (19°18'S 146°45'E).

ETYMOLOGY. Named after the type host locality.

DESCRIPTION. Eyes one pair, rarely two. Anchors with well-developed recurved points, shaft, blade present; ventral anchors with well developed inner, outer roots; dorsal anchors much smaller than ventral, reduced inner roots, outer roots. Ventral bar with ends tapering laterally; dorsal bar inverted bell curve, with lateral extensions at extremities, slightly smaller than ventral. Hooks H7 slightly smaller than H7, H6 much smaller than H3, H1 and H5 much smaller than H6. Copulum shaft consisting of a thin well-developed double sinistral recurved loop, distal end with sickle-shape expansion; accessory piece thin, lightly sclerotised. Vas deferens, non-sclerotised; seminal vesicle consisting of

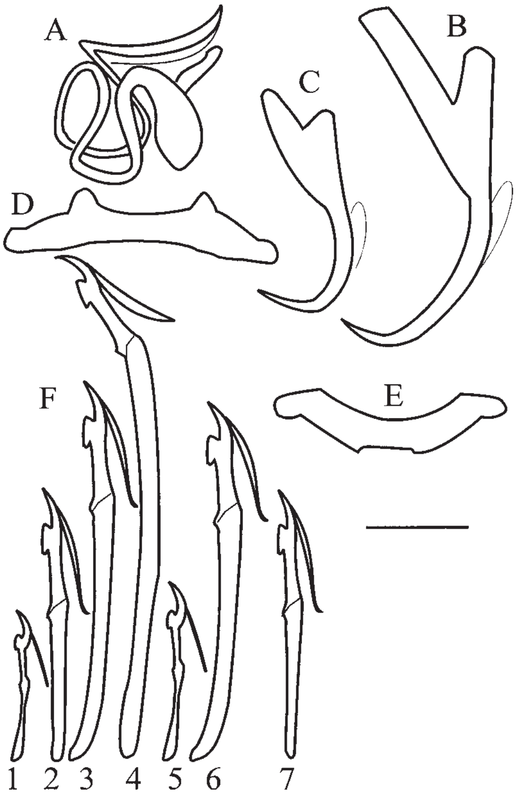

FIG. 21. *Iliocirrus iliocirrus* sp. nov.; A, ♂ copulatory apparatus (dorsal); B, ventral anchor; C, dorsal anchor; D, ventral bar; E, dorsal bar; F, hooks 1-7. Scalebar 10µm.

expanded bulb at point of loop around intestine. Vagina tubular. This species is not visually discernable from *I. iliocirrus*. Morphometric variation used as criteria for species recognition.

REMARKS. See *L. iliocirrus* sp. nov. and morphometric analysis.

Iliocirrus trifasciatae sp. nov.
(Fig. 23, Table 5)

MATERIAL. HOLOTYPE QM G218872 and PARATYPES QM G218873-218876. All from *Melanotaenia trifasciata*, McIvor River, Qld, (15°09'S 145°26'E).

ETYMOLOGY. Named after the type host.

DESCRIPTION. Eyes two pairs, anterior eyes usually a few dispersed granules. Anchors shaft, blade present; point well-developed; dorsal anchors much smaller than ventral; with reduced inner, outer roots. Ventral bar with ends tapering laterally; dorsal bar slightly smaller than ventral, consisting of a deep inverted arch with lateral extensions. Hooks H2 slightly longer than H7, H3 and H6 of similar length, H1 and H5 much smaller than H6. Copulum shaft thin, with loop reduced; accessory piece reduced, lightly sclerotised. Seminal vesicle non-sclerotised. Vagina tubular, usually inconspicuous.

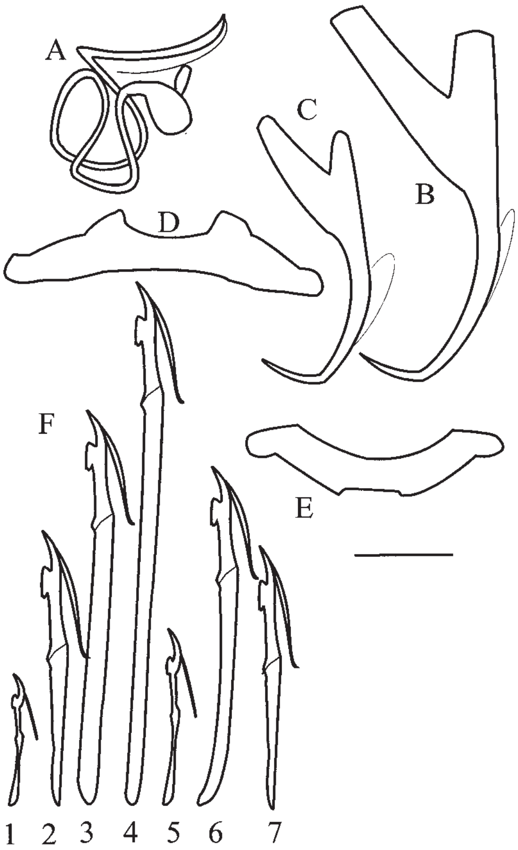

FIG. 22. *Iliocirrus rossi* sp. nov.; A, ♂ copulatory apparatus (dorsal); B, ventral anchor; C, dorsal anchor; D, ventral bar; E, dorsal bar; F, hooks 1-7. Scalebar 10µm.

REMARKS. This species is most similar to *I. iliocirrus* sp. nov. and *I. rossi* sp. nov. in the size and shape of the haptoral sclerites. It differs from these species by the shape of the copulum shaft.

Iliocirrus ornatusi sp. nov.
(Fig. 24, Table 5)

MATERIAL. HOLOTYPE QMG218867 and PARATYPES QMG218868-218871. All from *Rhadinocentrus ornatus*, Brunswick River, New South Wales, (28°70'S, 151°50'E).

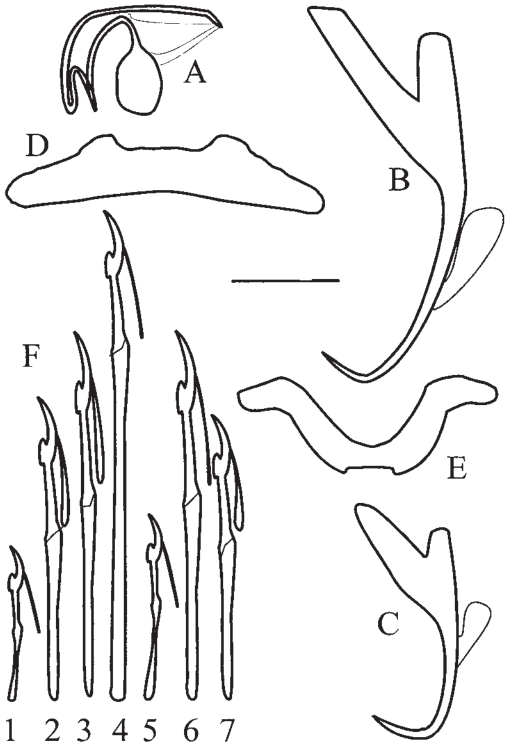

FIG. 23. *Iliocirrus trifasciatae* sp. nov.; A, ♂ copulatory apparatus(dorsal); B, ventral anchor; C, dorsal anchor; D, ventral bar; E, dorsal bar; F, hooks 1-7. Scalebar 10µm.

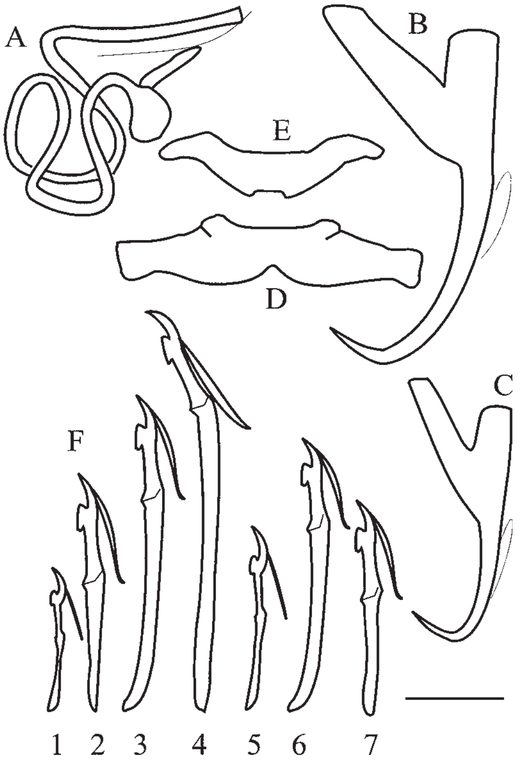

FIG. 24. *Iliocirrus ornatusi* sp. nov.; A, ♂ copulatory apparatus (dorsal); B, ventral anchor; C, dorsal anchor; D, ventral bar; E, dorsal bar; F, hooks 1-7. Scalebar 10µm.

ETYMOLOGY. Named after the type host.

DESCRIPTION. Eyes 2 pairs, anterior or dorsal to pharynx. Anchors shaft, blade present; point well-developed; ventral anchors with well-developed inner, outer roots; dorsal anchors much smaller than ventral, highly reduced inner, outer roots. Ventral bar with ends expanded and square, V-shaped notch present on posteromedial edge; dorsal bar slightly smaller than ventral, deep inverted arch. Hooks H7 smaller than H2, H6 smaller than H3, H1 and H5 much smaller than H6. Copulum shaft thin, distal end straight tube; accessory piece reduced, lightly sclerotised. Seminal vesicle inconspicuous. Vagina tubular, usually inconspicuous.

REMARKS. This species is most similar to *I. mazlini* having similar hook length ratios. It differs in the shape of the ventral bar and ventral anchor.

Iliocirrus mazlini sp. nov.
(Fig. 25, Table 5)

MATERIAL. HOLOTYPE QMG218839 and PARATYPES QMG218840-218844. All from *Melanotaenia eachamensis*, Dirran Creek, Qld, (17º27'S, 145º06'E).

ETYMOLOGY. For Rob Mazlin who helped me with collections and kept me inspired.

DESCRIPTION. Eyes 2 pairs. Anchors shaft, blade present; point well-developed; ventral anchors with well-developed inner, outer roots, distinct bump present on outer curve of blade; dorsal anchors much smaller than ventral, highly reduced inner, outer roots. Ventral bar inverted V, tapering laterally; dorsal bar slightly smaller than ventral, deep inverted arch. Hooks H7 much smaller than H2, H6 smaller than H3, H1 and H5 much smaller than H6. Copulum shaft thin; base elongate; accessory piece elongate, thin, partially sclerotised. Seminal vesicle inconspicuous. Vagina tubular.

REMARKS. See *I. ornatusi* sp. nov.

REMARKS ON MORPHOLOGICAL CHARACTERISTICS

Copulatory Apparatus Structure. Four types are identified (Fig. 26A-D).

Type I. A type I copulatory apparatus identifies species of *Recurvatus* and consists of a ball-shaped base with the shaft emanating from the right-anterior side. The shaft consists of a thin tube forming a counter-clockwise curving single loop (ventral view), which encircles the base. The distal end of the shaft terminates anterior to and to the right of the base. The accessory piece is attached to the anteromedial end of the base, dextral to the copulum shaft.

Type II. A type II copulatory apparatus identifies *Helicirrus* and consists of a single teardrop-shaped base with the shaft emanating from the anteromedial end. The shaft projects anteriorly initially then sharply reverses direction to continue left and posteriorly to the base, ending in a helix anteriorly to gonads. A thin spike-shaped accessory piece projects anteriorly from the right anterior end of the copulum base and to the right of the shaft. A long thin filament arises from near the anterior end of the shaft. This filament was not observed in live specimens or most permanent mounts but was easily discernable when the internal fluids of the parasite were extruded in preserved material using Malmberg's glycerol-ammonium-picrate. This was also the case for the vas deferens.

Type III. A type III copulatory apparatus identifies species of *Longidigitis* and consists of a bulbate base with the shaft emanating from the anterior end. The shaft consists of a tube with a single sinistral loop with distal end anterodextral to the base. The accessory piece is sclerotised; thumb shaped and arises from the anterosinistral side of the shaft.

Type IV. A type IV copulatory apparatus identifies species of *Iliocirrus* and consists of a bulbate base with the shaft arising from the anterior end. The shaft consists of a tube with two sinistral loops. The first loop is posterosinistral and the second loop anterosinistral to base. The copulum shaft distal end is anterior and to the right of the base. The accessory piece is sclerotised; thumb shaped and emanates from the right-anterior side of the copulum.

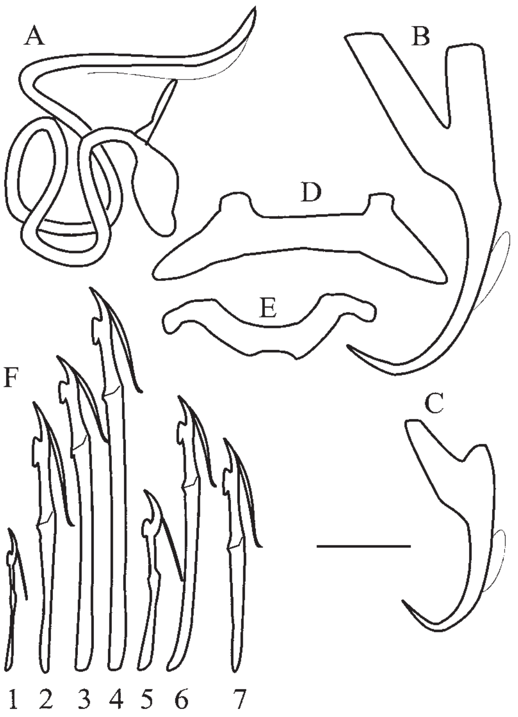

FIG. 25. *Iliocirrus mazlini* sp. nov.; A, ♂ copulatory apparatus (dorsal); B, ventral anchor; C, dorsal anchor; D, ventral bar; E, dorsal bar; F, hooks 1-7. Scalebar 10µm.

Haptoral Structure. The haptoral sclerite morphology can be discussed in three parts, anchors, bars and hooks. In the new genera proposed here, variations of these characters do not clearly reflect generic groupings.

Anchors have a large variation in size and shape although two patterns are recognised. Pattern one has dorsal anchors slightly smaller than ventral, while pattern two has dorsal anchors much smaller than ventral. Pattern one is seen in all species of *Recurvatus* and *Longidigitis*, but also occurs in several species of *Helicirrus*. For *Helicirrus*, pattern one occurs in *H. mcivori*, *H. gertrudaea* and *H. marjoriaea*. Pattern 2 occurs in all species of *Iliocirrus* and three species of *Helicirrus*, *H. splendidae*, *H. megaloanchor* and *H. maccullochii* and is associated with the reduced hook pattern (see below).

The dorsal bar has 3 morphological variants. The simple arch with the anteromedial membrane occurred in *L. auripontiformis*, *L. hopevalensis* and *L. robustus*. The second variant of the dorsal bar possesses a posteromedial notch as in *L.*

gracilis and all species of *Iliocirrus*. The third variant is the highly reduced dorsal bar which is observed as a thin filament and occurs in *H. splendidae*, *H. megaloanchor* and *H. maccullochii*. All species of *Recurvatus* and *L. maccullochii*, *L. utcheei*, *H. mcivori*, *H. marjoriaea* and *H. gertrudaea* have a well-developed arched dorsal bar and lacking both the medial notch and the anteromedial membrane.

Hook lengths show two character patterns that are spread across members of more than one genus. In the first pattern, hooks are of reduced form; all smaller than ventral anchors with the dorsal hooks H6 always longest. This pattern is found *in H. splendidae*, *H. megaloanchor* and *H. maccullochii* and is also associated with highly reduced dorsal anchors and bar. The second pattern, occurring in members of all four genera, consists of elongated hooks and widely differing lengths though generally increasing from H1 to H4. Ventral hook H4 is always the longest and always longer than the ventral anchors.

TABLE 5. Morphometric measurements (µm) of *Iliocirrus* species. Means and standard error. ME, number of parasites measured; BL, body length; BW, body width; HW, haptor width; HL, haptor length; PD, pharynx diameter; DA1-6, dorsal anchor; VA1-6, ventral anchor; DB1-3, dorsal bar; VA1-2, ventral bar; H1-7, hook length. ( ) range.

	I. iliocirrus	*I. trifasciatae*	*I. rossi*	*I. ornatusi*	*I. mazlini*
ME	49	31	33	51	32
BL	(100-160)	(100-170)	(100-160)	(120-180)	(130-220)
BW	(40-90)	(35-80)	(35-60)	(40-90)	(50-140)
HL	(25-50)	(20-40)	(30-60)	(25-60)	(25-50)
HW	(70-110)	(65-120)	(70-110)	(60-100)	(70-110)
PD	(7-13)	(9-13)	(9-13)	(12-18)	(12-21)
DA1	5.7 ± 0.11	5.3 ± 0.16	6.0 ± 0.15	5.5 ± 0.10	5.7 ± 0.13
DA2	22.2 ± 0.22	22.8 ± 0.15	27.4 ± 0.30	24.7 ± 0.21	22.5 ± 0.22
DA3	17.0 ± 0.18	17.1 ± 0.15	20.7 ± 0.21	18.1 ± 0.18	17.8 ± 0.28
DA4	19.8 ± 0.21	19.7 ± 0.25	24.9 ± 0.20	21.9 ± 0.20	20.5 ± 0.19
DA5	7.2 ± 0.16	7.6 ± 0.18	9.1 ± 0.28	8.6 ± 0.16	6.8 ± 0.17
DA6	9.7 ± 0.17	8.8 ± 0.24	10.8 ± 0.17	9.9 ± 0.16	9.5 ± 0.23
VA1	4.9 ± 0.11	4.5 ± 0.13	5.0 ± 0.16	5.2 ± 0.10	5.3 ± 0.13
VA2	32.4 ± 0.25	34.4 ± 0.21	38.1 ± 0.46	34.0 ± 0.25	36.0 ± 0.26
VA3	25.1 ± 0.20	25.3 ± 0.18	28.4 ± 0.27	24.2 ± 0.19	27.0 ± 0.24
VA4	31.0 ± 0.26	32.5 ± 0.24	35.5 ± 0.41	30.4 ± 0.25	34.9 ± 0.34
VA5	12.3 ± 0.21	13.5 ± 0.21	14.2 ± 0.33	12.5 ± 0.20	13.7 ± 0.23
VA6	14.3 ± 0.19	14.7 ± 0.16	15.9 ± 0.22	13.9 ± 0.19	15.6 ± 0.19
DB1	22.4 ± 0.24	24.1 ± 0.38	24.4 ± 0.34	23.6 ± 0.23	23.3 ± 0.34
DB2	3.9 ± 0.07	4.7 ± 0.17	5.9 ± 0.19	3.7 ± 0.07	4.8 ± 0.14
DB3	7.2 ± 0.12	9.1 ± 0.22	7.2 ± 0.18	7.1 ± 0.11	7.4 ± 0.16
VB1	26.5 ± 0.24	29.8 ± 0.27	30.8 ± 0.28	30.7 ± 0.24	30.9 ± 0.49
VB2	11.8 ± 0.16	10.5 ± 0.16	10.8 ± 0.20	12.2 ± 0.15	14.5 ± 0.22
H1	14.1 ± 0.15	14.2 ± 0.15	14.2 ± 0.18	13.4 ± 0.15	14.1 ± 0.13
H2	25.7 ± 0.23	27.6 ± 0.29	27.4 ± 0.29	24.2 ± 0.23	27.7 ± 0.36
H3	36.2 ± 0.30	33.0 ± 0.34	37.8 ± 0.30	30.6 ± 0.30	33.0 ± 0.47
H4	48.5 ± 0.31	44.6 ± 0.57	49.9 ± 0.34	37.9 ± 0.31	39.1 ± 0.39
H5	17.4 ± 0.16	17.4 ± 0.17	17.5 ± 0.20	17.6 ± 0.16	19.4 ± 0.22
H6	33.9 ± 0.27	33.5 ± 0.22	33.0 ± 0.38	27.1 ± 0.26	27.8 ± 0.33
H7	25.4 ± 0.24	25.9 ± 0.25	25.6 ± 0.47	21.5 ± 0.24	21.8 ± 0.24

Several patterns of associated hook lengths are identified in the elongated form. Size differences between H2 and H7 have three patterns: H2 is longer than H7 in *I. ornatusi*, *I. mazlini*, *I. trifasciatae*, *L. auripontiformis*, *L. utcheei*, and *H. marjoriaea*; H2 equals H7 in *R. chelatus*, *R. signiferi*, *I. rossi*, *I. iliocirrus*, *L. gracilis*, *L. maccullochii*, *L. robustus* and *H. mcivori*; and *Helicirrus gertrudaea* has H2 shorter than H7. Generally H3 is noticeably longer than H6; however in *I. trifasciatae* and *L. utcheei*, H3 and H6 are of similar size. Most species have hooks H3 longer than H2, but this is reversed for *R. signiferi*.

Morphometrics. Means and ranges of measured soft body characters, and means and standard error of haptoral sclerite measurements are shown in Tables 2-5. Soft body measurements show large variation and are influenced by preparation method. Slide preparations that used formalin-preserved parasites (technique two) had much smaller soft body dimensions than those prepared by technique one (unpubl. data). This is an important point when considering comparing species from other studies. However, several species show visual size differences in body width. *Helicirrus splendidae*, *H. maccullochii*, *I. mazlini* and *I. ornatusi* have greater body widths than other species examined. *Iliocirrus mazlini* and *I. ornatusi* are easily distinguished from other species of the genus based on this observation.

MULTIVARIATE ANALYSIS. Using Scheffé test between-subjects MANOVA, a significant difference between means was observed among species of *Longidigitis* using Wilks' λ ($F_{(92. 513)}$ =43.2, $p<0.01$), among *Iliocirrus* species using Wilks' λ ($F_{(96, 596)}$=30.5, $p<0.01$), among *Helicirrus* species using Wilks' λ ($F_{(115, 618)}$ =31.0, $p<0.01$) and among *Recurvatus* species using Wilks' λ ($F_{(23, 57)}$=145.7, $p<0.01$). Thus, some species are significantly different within each genus. A between-subjects effect

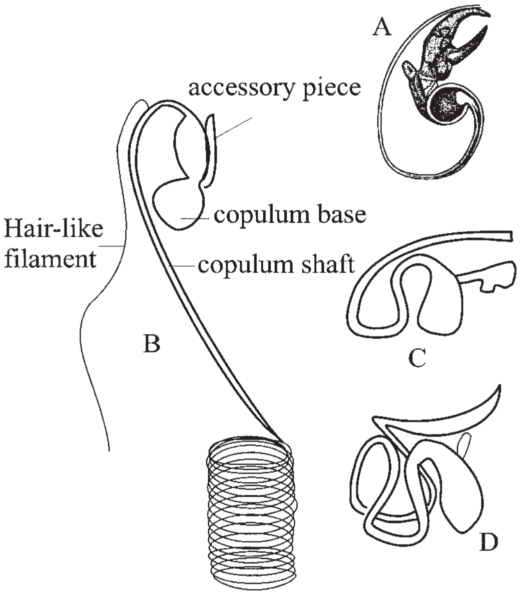

FIG. 26. Copulum types; A, '*Recurvatus*' type I; B, '*Helicirrus*' type II; C, '*Aaripontiformis*' type III; D, '*Iliocirrus*' type IV.

MANOVA showed a significant difference between character means for species of *Longidigitis* (p<0.01). A significant difference (p<0.01) between means for species of *Recurvatus* was observed for all variables except DA5 and DA2, (p<0.01) and DA1, VA6 and VA2 (p>0.05). For *Helicirrus* species a significant difference (p<0.01) between means was observed for all variables. For *Iliocirrus* species a significant difference (p<0.01) between means was observed for all variables except DA1 (p<0.05) and VA6 (p>0.05).

A MANOVA using Scheffé test for pair-wise comparisons of species within each genus (P<0.01) showed the maximum number of significantly different variable means between any two species was 21 of the possible 24 variables measured, while the minimum was seven. The maximum difference of 21 occurred between *L. gracilis* and *L. hopevalensis* (Table 7) and *H. splendidae* and *H. gertrudaea* (Table 7). A minimum of seven significant differences (p<0.01) occurred between *H. gertrudaea* and *H. marjoriaea* (Table 6) and between *L. hopevalensis* and *L. auripontifomis* (Table 7). For *Iliocirrus* species, the maximum was 17 between *I. iliocirrus* and *I. mazlini* (Table 8) and between *I. rossi* and *I. ornatusi* (Table 8). The minimum for *Iliocirrus* species was eight between *I. trifasciatae* and *I. rossi* (Table 8). For the *Recurvatus* species, the difference was 18. A MANOVA using Tukey's HSD test for pairwise comparisons (P<0.01) of species within each genus identified more significant differences. The minimum number of significantly different variable means between any two species was 13; between *H. mcivori* and *H. gertrudaea* (Table 6). A maximum of 22 occurred between species as follows: *H. maccullochii* and *H. marjoriaea*; *H. megaloanchor* and *H. gertrudaea*; *H. gertrudaea* and *H. splendidae*; *H. marjoriaea* and *H. splendidae*; *H. maccullochii* and *H. mcivori*; *L. gracilis* and *L. hopevalensis* and *L. utcheei*; *L. auripontiformis* and *L. gracilis* and *L. macculochi*; *I. rossi* and *I. ornatusi*.

TABLE 6. Species of *Helicirrus* and statistically significant (∝ = 0.01) morphometric character differences using Scheffé pairwise comparisons. ( ) indicates number of significant character differences. *Characters identified as significantly different using Tukey's HSD test.

SPECIES	MINIMUM DIFFERENCE	MAXIMUM DIFFERENCE
H. splendidae	*H. maccullochii* (10) (15)* *H. megaloanchor* (13) (14)* *H. mcivori* (13) (18)*	*H. marjoriaea* (20) (22)* *H. gertrudaea* (17) (20)*
H. maccullochii	*H. splendidae* (10) (15)* *H. megaloanchor* (15) (16)*	*H. marjoriaea* (18) (20)* *H. gertrudaea* (16) (20)* *H. mcivori* (20) ((22)*
H. megaloanchor	*H. gertrudaea* (18) (22)*	*H. marjoriaea* (18) ((20)* *H. mcivori* (19) (21)*
H. mcivori	*H. gertrudaea* (7) (13)* *H. marjoriaea* (13) (21)*	*H. megaloanchor* (19) (21)*
H. gertrudaea	*H. marjoriaea* (11) (17)*	*H. megaloanchor* (18) (22)*
H. marjoriaea	*H. gertrudaea* (11) (17)*	*H. splendidae* (21) (22)*

PRINCIPAL COMPONENT ANALYSIS. Initially all analyses were run to examine communalities between variables and functions. All variables with communalities <0.7 were removed and a final analysis was done. For all species analysed together, PCA extracted four components after the removal of characters DB2, VA1, H1, and H5. The four components accounted for 84.4 % of the explained variance. PC1 accounted for 48.3%, PC2 accounted for 22.3% and PC3 accounted for 7.9% while PC4 accounted for 5.9%. Examination of the scatter plots showed that specimens clearly clustered into their respective genera (Fig. 27). This indicates that haptoral sclerite variation has a close correlation to copulum morphology although two clusters of *Helicirrus* species also separated from the third. These separated clusters represent *H. splendidae*, *H. maccullochii* and *H. megaloanchor* and identify the reduced hook

TABLE 7. Species of *Longidigitis* and statistically significant (∝ = 0.01) morphometric character differences using Scheffé pairwise comparisons. ( ) indicates number of significant character differences. *Characters identified as significantly different using Tukey's HSD test.

SPECIES	MINIMUM DIFFERENCE	MAXIMUM DIFFERENCE
L. auripontiformis	*L. hopevalensis* (7) (18)* *L. robustus* (13) (19)* *L. utcheei* (14) (19)*	*L. gracilis* (19) (22)* *L. maccullochii* (20) (22)*
L. robustus	*L. maccullochii* (11) (20)* *L. hopevalensis* (14) (16)*	*L. gracilis* (17) (21)* *L. utcheei* (15) (18)*
L. maccullochii	*L. utcheei* (16) (19)* *L. gracilis* (17) (20)*	*L. hopevalensis* (20) (21)* *L. auripontiformis* (20) (22)*
L. utcheei	*L. hopevalensis* (14) (20)* *L. robustus* (14) (17)*	*L. gracilis* (19) (22)*
L. hopevalensis	*L. auripontiformis* (7) (18)*	*L. gracilis* (21) (22)*
L. gracilis	*L. maccullochii* (17) (20)*	*L. hopevalensis* (21) (22)*

TABLE 8. Species of *Iliocirrus* and statistically significant (∝ = 0.01) morphometric character differences using Scheffé pairwise comparisons. ( ) indicates number of significant character differences. *Characters identified as significantly different using Tukey's HSD test.

SPECIES	MINIMUM DIFFERENCE	MAXIMUM DIFFERENCE
I. trifasciata	*I. rossi* (8) (16)* *I. mazlini* (9) (17)*	*I. iliocirrus* (14) (17)* *I. ornatusi* (12) (19)*
I. iliocirrus	*I. ornatusi* (12) (19)* *I. rossi* (14) (16)*	*I. mazlini* (17) (21)*
I. rossi	*I. mazlini* (11) (16)*	*I. ornatusi* (17) (22)*
I. ornatusi	*I. trifasciatae* (12) (19)* *I. iliocirrus* (12) (19)*	*I. mazlini* (15) (20)*
I. mazlini	*L. trifasciatae* (9) (17)*	*I. iliocirrus* (17) (21)*

haptor type. The main cluster, which includes all four genera, identifies the elongated hook haptor type. Dorsal anchor and hook characters dominated the first component, while ventral anchor and bar characters dominated PC2 (Table 9).

When *Helicirrus*, *Recurvatus*, *Longidigitis* and *Iliocirrus* were analysed separately, clusters of each species were generally well defined. Principal component analysis identified four components for *Recurvatus*, after the removal of eight characters: DA-6, VA3, VA6, DB1-3, H1 and H5. The four components accounted for 85.8% of the explained variance. PC1 accounted for 39.8%, PC2 accounted for 22.4% and PC3 accounted for 16.4% while PC4 accounted for 7.2% (Table 10). Examination of the scatter plots showed that species clearly separated on the first component (Fig. 28). Hooks H2-4 and H6-7 and dorsal anchor characters DA3-4 dominated the first component, ventral anchor characters VA2 and VA4-5 dominated PC2 and characters DA1 and VB2 dominated the third component (Table 10).

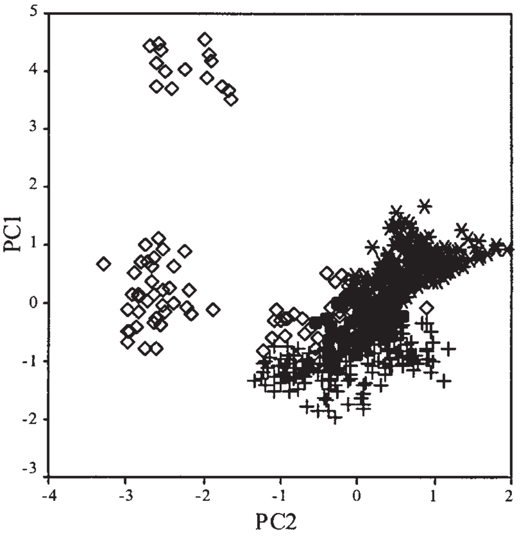

FIG. 27. Scatter plots of first two axes of principal component analysis using 20 natural log/z-score transformed metric variables for generic-level. ● *Recurvatus*; + *Longidigitis*; ✶ *Iliocirrus*; ◇ *Helicirrus*.

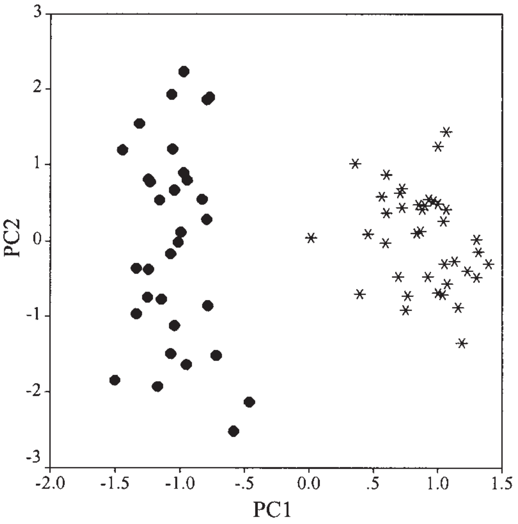

FIG. 28. Scatter plots of first two axes of principal component analysis using 16 natural log/z-score transformed metric variables for *Recurvatus* species. ✶ *R. signiferi*; ● *R. chelatus*.

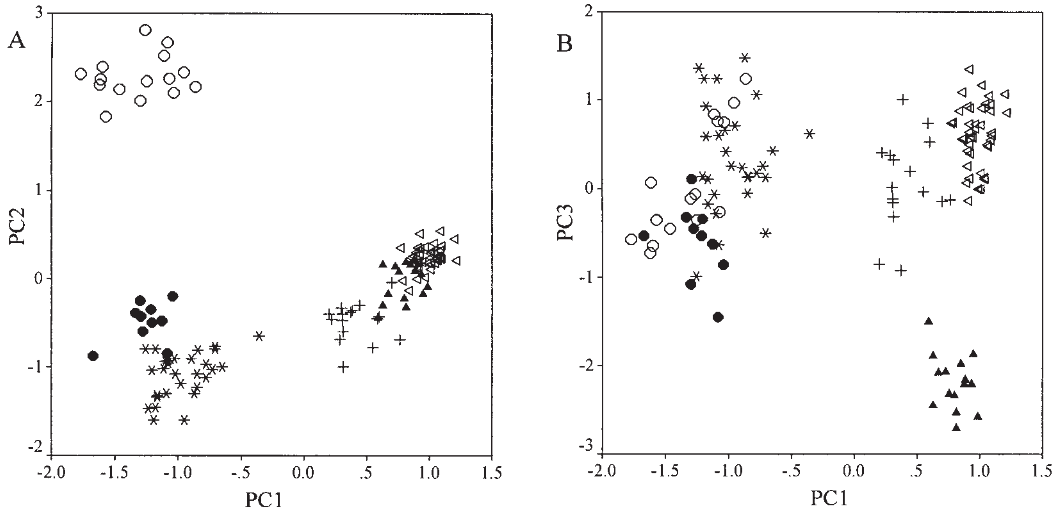

FIG. 29A-B. Scatter plots of first three axes of principal component analysis using 21 natural log/z-score transformed metric variables for *Helicirrus* species. ✶ *H. splendidae*; ○ *H. megaloanchor*; + *H. mcivori*; ◁ *H. marjoriaea*; ● *H. maccullochii*; ▲ *H. gertrudaea*.

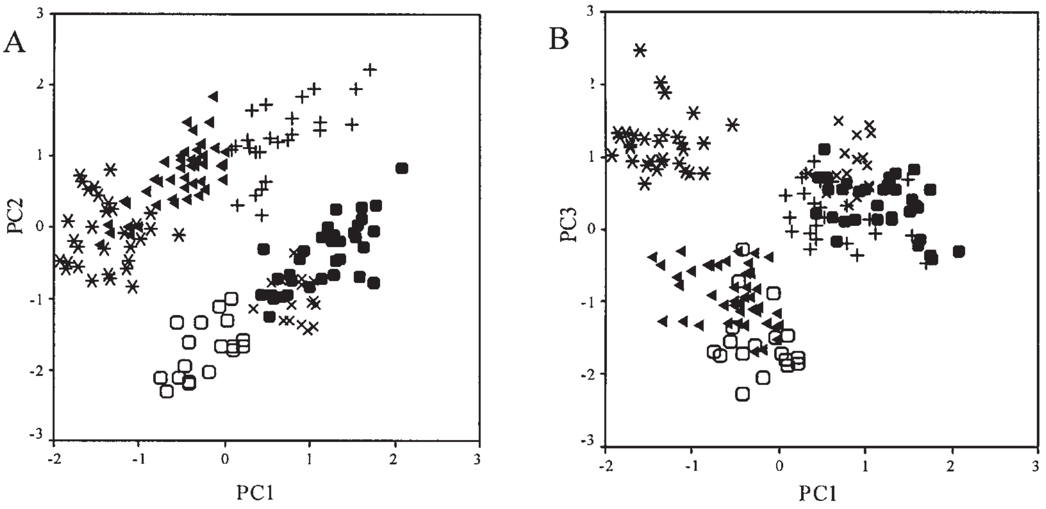

FIG. 30A-B. Scatter plots of first three axes of principal component analysis using 18 natural log/z-score transformed metric variables for *Longidigitis* species. + *L. maccullochii*; ◀ *L. utcheei*; × *L. hopevalensis*; ✶ *L. gracilis*; ○ *L. robustus*; ● *L. auripontiformis*.

Analysis of *Helicirrus* species identified three components, after the removal of three characters: DB2, H1 and H5. The three components accounted for 85.8% of the explained variance. PC1 accounted for 50.8%, PC2 accounted for 29.4% and PC3 accounted for 5.6%. The scatter plot combination of PC1 and PC2 clearly separated *H. megaloanchor*, *H. splendidae* and *H. maccullochii* (Fig. 29A) while the combination of PC1 and PC3 clearly separated *H. marjoriaea*, *H. gertrudaea* and *H. mcivori* (Fig. 29B). Dorsal anchor characters dominated the first component, while ventral anchor measurements dominated the second component and H6-7 and VB2 had highest correlation with PC3 (Table 11).

TABLE 9. Principal component correlation between natural log/z-score transformed variables and principal component functions for all species. Variables ordered by absolute size of correlation within function. DA1-6, dorsal anchor; VA1-6, ventral anchor; DB1-3, dorsal bar; VA1-2, ventral bar; H1-7, hook length. (%) percent total variance accounted for. * Largest absolute correlation between each variable and any principal component.

	Component			
	1	2	3	4
	(48.3%)	(22.3%)	(7.9%)	(5.9%)
H4	*.884	-.154	.305	-.100
H3	*.859	.163	.256	-.149
DB3	*.847	-.164	.119	.230
H2	*.821	.204	.271	-.262
DA2	*.819	-.514	-.118	.072
DB1	*.805	.005	.400	.213
H6	*.805	.247	.113	-.360
DA4	*.797	-.430	-.287	.150
DA5	*.772	-.354	-.112	.121
DA3	*.751	-.455	-.372	.086
DA1	*.718	-.476	-.031	.143
H7	*.698	.096	.321	-.513
VA5	*.680	.292	-.269	-.158
DA6	*.668	-.520	-.029	.260
VA2	*.661	.549	-.440	-.040
VA3	.409	*.782	-.351	.019
VA4	.492	*.763	-.294	.006
VA6	.231	*.737	-.124	.125
VB1	.423	*.732	.116	.400
VB2	.049	*.587	.530	.490

TABLE 10. Principal component correlation between natural log/z-score transformed variables and principal component functions for *Recurvatus* species. Variables ordered by absolute size of correlation within function. DA1-6, dorsal anchor; VA1-6, ventral anchor; DB1-3, dorsal bar; VA1-2, ventral bar; H1-7, hook length. (%) percent total variance accounted for. * Largest absolute correlation between each variable and any principal component.

	Component			
	1	2	3	4
	(39.8%)	(22.4%)	(16.4%)	(7.2%)
H2	* .942	.157	-.034	.000
H7	* .934	.189	-.030	-.003
H4	* .888	.268	.072	.014
VB1	*-.794	.107	.311	.083
DA3	*-.792	.488	.006	.068
DA4	*-.781	.510	.090	.033
H3	* .712	.311	.368	-.059
H6	* .617	.579	.09	-.123
VA1	*-.544	-.078	-.451	-.444
VA2	-.115	*.857	-.076	-.206
DA2	-.346	*.781	-.193	.171
VA5	.399	*.661	.156	-.324
VA4	-.522	*.600	.222	-.312
DA1	-.022	.330	*-.791	.268
VB2	-.370	.040	* .660	.381
DA5	.248	.510	-.153	*.653

Principal component analysis identified four components for the *Longidigitis* species after the removal of six variables: VA1, VA6, DB2-3, H1 and H5. The four components accounted for 83.3% of the explained variance. PC1 accounted for 51.3%, PC2 accounted for 14.5%, PC3 accounted for 10.7% and PC4 accounted for 6.8%. The scatter plot combination of PC1 and PC2 separated *L. maccullochii*, *L. robustus*, *L. auripontiformis* and *L. gracilis*, with *L. utcheei* slightly overlapping *L. gracilis* and *L. hopevalensis* partially overlapping *L. auripontiformis* (Fig. 30A). The combination of PC1 and PC3 clearly separated *L. gracilis*, *L. utcheei* and *L. maccullochii* from each other while *L. auripontiformis*, *L. maccullochii* and *L. hopevalensis* overlapped and *L. utcheei* and *L. robustus* overlapped (Fig 30B). *Longidigitis auripontiformis* and *L. hopevalensis* clearly separated on PC4 (not shown). Dorsal and ventral anchor characters dominated component PC1, while hook measurements dominated PC2. Ventral bar characters dominated PC3 and dorsal bar character DB1 dominated PC4 (Table 12).

Principal component analysis identified four components for the *Iliocirrus* species after the removal of nine variables: DA1, DA6, VA1, VA6, DB1-3, H1 and H5 (Table 13). The four components accounted for 79.3% of the explained variance. PC1 accounted for 37.5%, PC2 accounted for 22.2%, PC3 accounted for 12.5% and PC4 accounted for 7.2%. Examination of scatter plot combination of PC1 and PC2 identified the separation of *I. mazlini*, *I. rossi* and *I. iliocirrus* from each other, while *I. ornatusi* overlapped *I. mazlini* and *I. trifasciatae* and slightly overlapped *I. rossi* and *I. iliocirrus* (Fig. 31A). The combination of PC1 and PC3 clearly separated *I. mazlini* from *I. ornatusi* while *I. trifasciatae* slightly overlapped *I. rossi* and *I. iliocirrus* (Fig. 31B). A combination of dorsal and ventral anchor and hook characters dominated the first

TABLE 11. Principal component correlation between natural log/z-score transformed variables and principal component functions for *Helicirrus* species. Variables ordered by absolute size of correlation within function. DA1-6, dorsal anchor; VA1-6, ventral anchor; DB1-3, dorsal bar; VA1-2, ventral bar; H1-7, hook length. (%) percent total variance accounted for. * Largest absolute correlation between each variable and any principal component.

	Component		
	1	2	3
	(50.8%)	(29.4%)	(5.6%)
H4	*.972	.052	-.042
DB1	*.961	.113	-.039
H3	*.931	.164	-.037
DB3	*.929	.051	.008
DA2	*.910	-.308	.087
H2	*.887	.220	-.234
DA4	*.886	-.185	.181
DA5	*.850	-.065	.136
DA3	*.847	-.279	.129
DA1	*.833	-.114	.231
DA6	*.765	-.471	.207
H7	*.743	.077	-.552
H6	*.726	.322	-.512
VA1	*.612	.602	.234
VA2	.012	*.946	-.095
VA6	-.236	*.922	.104
VA4	-.228	*.893	.005
VA3	-.334	*.883	.006
VB1	.256	*.869	.264
VA5	.272	*.804	-.215
VB2	.362	*.665	.433

TABLE 12. Principal component correlation between log/z-score transformed variables and principal component functions for *Longidigitis* species. Variables ordered by absolute size of correlation within function. DA1-6, dorsal anchor; VA1-6, ventral anchor; DB1-3, dorsal bar; VA1-2, ventral bar; H1-7, hook length. (%) percent total variance explained. * Largest absolute correlation between each variable and any principal component.

	Component			
	1	2	3	4
	(51.3%)	(14.5%)	(10.7%)	(6.8%)
DA2	*.958	-.195	-.033	-.005
VA2	*.950	.013	.003	-.123
DA4	*.943	-.149	.078	-.035
DA3	*.941	-.159	.0265	-.0621
VA4	*.937	.094	.122	-.127
VA3	*.897	.049	.126	-.024
DA1	*.806	-.299	.113	-.242
VA5	*.790	-.158	-.279	-.105
H2	*.750	.494	-.005	.005
DA5	*.699	-.505	-.213	.090
DA6	*.676	-.502	.093	.073
H7	*.643	.521	-.260	-.057
H3	.284	*.704	-.481	.090
H4	.402	*.695	.300	-.252
H6	.496	*.511	-.278	.459
VB2	-.104	.355	*.851	-.087
VB1	.415	.053	*.734	.363
DB1	.289	-.111	.088	*.828

component, while hook characters dominated the second component. Ventral bar character VB2 and dorsal anchor character DA5 correlated highest with PC3.

DISCRIMINANT FUNCTION ANALYSIS. Stepwise analysis of the 4 genera combined with parasite species grouped into genera, identified the 3 characters, DB3 and DA5 and H1, not fitting the selection criteria of F to enter ($p<0.05$) and F to remove ($p<0.01$) and were removed from the final analysis. The first function (F1) accounted for 76.1%, F2 for 18.9% and F3 for 5.0% of total variance. Examination of scatter plot of F1 and F2 separated *Helicirrus*, *Longidigitis* and *Iliocirrus* using F1 characters (Fig. 32A). Characters of F1 and F2 do not separate *Recurvatus* and *Helicirrus*. *Recurvatus* separates from the other 3 genera using F3 characters; however, *Helicirrus*, *Iliocirrus* and *Longidigitis* do not separate from each other (Fig. 32B). All functions were significantly different using Wilks' λ ($p<0.001$). The characters, VA2 and DB2 had the highest correlation with F1, while DA3, VB1-2, VA4, VA6 and DA3-4 had the highest correlation with F2 and F3 had highest correlation with hook characters H2-4, H7, dorsal anchor characters DA1-2, DA6 and ventral anchor characters VA1 and VA5 (see Table 14). The functions were not dominated by a set of variables from any one morphological character i.e. anchors, bars or hooks, but a mixture of variables from each. All functions were significantly different using Wilks' λ ($p<0.001$). All eigenvalues were positive except DA3-4 indicating a size difference in the characters between genera.

Analysis of all 20 species together, identified all variables fitting the selection criteria of F to enter ($p<0.05$) and F to remove ($p<0.01$). The first function accounted for 54.8% of the explained variance and uniquely correlated with DB2. F2 accounted for 22.8% of variance and

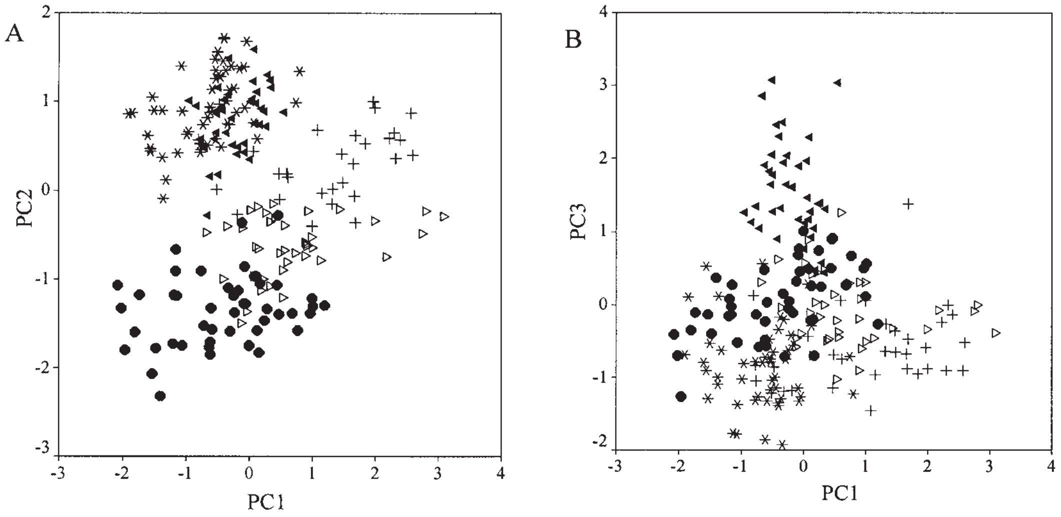

FIG. 31A-B. Scatter plots of first three axes of principal component analysis using 13 natural log/z-score transformed metric variables for *Iliocirrus* species; ▷ *I. trifasciatae*; + *I. rossi*; ✶ *I. ornatusi*; ◀ *I. mazlini*; ● *I. iliocirrus*.

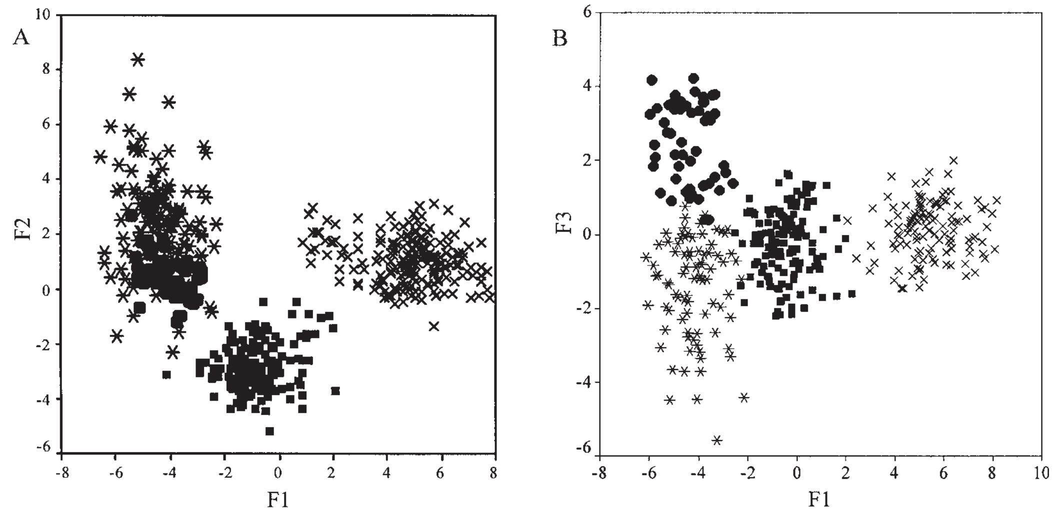

FIG. 32A-B. Scatter plots of first three axes of discriminant analysis for using 21 natural log/z-score transformed variables. Specimens entered as genera; × *Iliocirrus*; ■ *Longidigitis*; ✶*Helicirrus*; ● *Recurvatus*.

characters H4 and DA2 had highest correlation. F3 accounted for 5.5% of variance and correlated highest with ventral and dorsal anchor characters (Table 15). The first 17 functions were significantly different using Wilks' λ ($p<0.001$).

Analysis of *Recurvatus* identified 19 variables not fitting the selection criteria of F to enter ($p<0.05$) and F to remove ($p<0.01$) (Table 16). Most of these rejected variables were anchor and bar measurements. The remaining five variables, hook characters H1, H2, H7, VB1 and VA4, clearly separated *R. signiferi* and *R. chelatus* (not shown). The low number of species in the analysis can explain the low number of characters used.

TABLE 13. Principal component correlation between natural log/z-score transformed variables and principal component functions for *Iliocirrus* species. Variables ordered by absolute size of correlation within function. DA1-6, dorsal anchor; VA1-6, ventral anchor; DB1-3, dorsal bar; VA1-2, ventral bar; H1-7, hook length. (%) percent total variance explained. * Largest absolute correlation between each variable and any principal component

	Component			
	1 (37.5%)	2 (22.2%)	3 (12.5%)	4 (7.2%)
VA2	*.769	.456	.247	.044
VA4	*.709	.211	.475	-.079
H2	*.689	-.148	.456	.113
VA5	*.680	.161	.102	.452
H7	*.666	-.614	-.007	.128
DA4	*.661	.474	-.394	-.258
DA3	*.660	.373	-.264	-.458
H3	*.652	-.587	.073	-.015
DA2	*.649	.445	-.522	-.070
VA3	*.628	.194	.442	-.370
H6	.551	*-.756	-.054	.038
H4	.607	*-.721	-.109	-.040
VB1	.310	* .633	.154	.455
VB2	-.320	.393	* .570	.027
DA5	.408	.236	*-.558	.452

Analysis of species of *Helicirrus* identified 4 variables DA2, DA6, H1, and H5 not fitting the selection criteria of F to enter ($p<0.05$) and F to remove ($p<0.01$). The first 3 functions accounted for 96.6% of the total explained variance. Function F1 accounted for 74.8%, F2 for 21.9% and F3 for 4.0% of the explained variance. Examination of the combined functions F1 and F2 scatter plot shows 3 distinct clusters. Characters of F1 and F2 separate *H. megaloanchor* from all other species, *H. splendidae* and *H. maccullochii* from all other species and *H. mcivori*, *H. gertrudaea* and *H. marjoriaea* from all other species (Fig. 33A). Function F1 and F2 characters do not clearly separate *H. splendidae* from *H. maccullochii* or *H. mcivori*, *H. gertrudaea* and *H. marjoriaea* from each other. Characters of F3 clearly separate *H. splendidae* from *H. maccullochii*, and *H. mcivori*, *H. marjoriaea* and *H. gertrudaea* from each other (Fig. 33B). Dorsal bar characters DB1, DB3 and H4 have highest correlation with F1, F2 correlates highest with ventral anchor characters and F3 correlates highest with characters VA5, VB2, H6 and DA1 (Table 17).

TABLE 14. Pooled within-groups correlations between natural log/z-score transformed variables and standardised canonical discriminant functions for generic level grouping. Specimens entered as genera. Variables ordered by absolute size of correlation within function. DA1-6, dorsal anchor; VA1-6, ventral anchor; DB1-3, dorsal bar; VA1-2, ventral bar; H1-7, hook length. (%) percent total variance explained * Largest absolute correlation between each variable and any discriminant function. # Variable not used in the analysis.

	Function		
	1 (76.1%)	2 (18.9%)	3 (5.0%)
DB2	* .500	.213	.073
VA2	* .205	.028	.040
VB2	-.012	* .440	.193
DA3	.154	*-.410	.177
VB1	.153	* .408	.134
DA4	.144	*-.348	.263
VA6	.075	* .298	.147
VA4	.227	* .267	-.058
H5	.122	* .252	-.012
VA3	.189	* .245	-.113
H1#	.028	* .129	.071
H2	.169	.091	*.605
H7	.101	.049	*.495
DA1	.068	-.280	*.453
H4	.144	-.077	*.411
DB1	.113	.088	*.402
DA5#	.085	-.164	*.389
DA2	.144	-.348	*.385
H6	.264	.050	*.375
VA5	.140	-.064	*.348
DB3#	.112	-.115	*.347
H3	.241	.088	*.309
DA6	.070	-.168	*.269
VA1	.047	-.156	*.231

Analysis of species of *Longidigitis* identified the 3 characters H1, VA5-6 not fitting the selection criteria of F to enter ($p<0.05$) and F to remove ($p<0.01$). The first 3 functions account for 89.2% of the total explained variance. Function F1 accounted for 48.5%, F2 accounted for 28.9% and F3 accounted for 11.8% of the variance. Function F1 characters separate *L. utcheei*, *L. maccullochii* and *L. gracilis* from *L. auripontiformis*, *L. robustus* and *L. hopevalensis* while F2 characters separate *L. auripontiformis*, *L. hopevalensis* and *L. robustus* from each other (Fig. 34A). Function F1 and F2 characters do not clearly separate *L. gracilis*, *L. maccullochii* or *L. utcheei* from each other. Function F3 characters separate *L. gracilis* from *L. utcheei* and *L. maccullochii* (Fig. 34B), while *L. maccullochii* and *L. utcheei* separate by using F4 characters (not shown). Dorsal anchor characters dominate F1, ventral anchor characters dominate F2, hook characters dominate F3, and ventral bar characters dominate F4 (Table 18).

TABLE 15. Pooled within-group correlations between natural log/z-score transformed variables and standardised canonical discriminant functions at species level grouping. Specimens entered as species groups. Variables ordered by absolute size of correlation within function. DA1-6, dorsal anchor; VA1-6, ventral anchor; DB1-3, dorsal bar; VA1-2, ventral bar; H1-7, hook length. Only functions with highest correlations shown. (%) percent total variance explained. * Largest absolute correlation between each variable and any discriminant function.

	Function											
	1	2	4	5	6	7	9	10	11	14	15	17
%	54.8	22.8	5.5	2.9	1.9	1.5	1.2					
DB2	*.93	-.07	-.07	.08	-.10	.11	-.05	-.04	-.01	.01	.06	-.00
H4	.24	*.64	.08	-.23	-.01	-.11	.09	.34	-.02	.05	-.18	-.04
DA2	.08	*.54	.46	.03	.15	.29	-.12	.14	.22	.01	-.21	-.12
VA2	.13	.05	*.68	-.26	-.07	.14	-.14	-.05	-.07	.02	-.03	.12
VA3	.13	-.10	*.50	-.20	.15	.21	-.04	.21	.14	.08	.01	-.14
VA4	.17	-.08	*.50	-.19	.15	.26	.09	.12	-.17	.12	.13	-.08
DA3	.05	.34	*.47	-.05	.03	.19	.02	.23	.06	.10	.34	-.02
DA4	.05	.33	*.43	.02	.01	.16	-.02	.22	.09	.41	.16	-.03
VB2	.06	-.08	-.18	* .49	-.04	.04	-.15	.05	.38	.21	-.06	.08
H7	.06	.19	-.04	*-.36	.14	.33	-.05	.19	-.07	.22	.05	.24
H3	.21	.26	.10	-.27	*.63	-.09	.03	-.03	.00	.19	-.19	.16
H2	.11	.21	.06	-.22	.19	*.56	-.29	.02	.09	.04	.21	-.06
DA6	.02	.25	.14	.16	.25	*.37	.23	.31	-.21	-.04	.04	.21
VB1	.15	-.06	.23	.31	.17	.01	*-.45	.42	-.17	.04	.07	.13
H6	.14	.14	.14	-.40	.30	-.09	-.08	*.53	.09	-.02	.13	.08
VA6	.06	-.10	.27	.03	.06	.01	.32	*.36	-.03	.18	-.17	-.23
VA1	.02	.12	.21	.10	-.13	-.23	-.02	-.07	*.40	-.28	.11	.27
VA5	.06	.10	.34	-.15	-.07	-.04	.03	-.11	-.09	*.45	-.01	-.23
DA5	.02	.20	.24	-.01	.20	.20	.10	.06	.19	*.36	.01	.18
H5	.06	-.03	.15	.07	.19	.08	.14	.04	-.25	-.13	*-.41	.19
DB3	.08	.24	.27	.15	.14	-.05	.34	-.07	.08	-.16	* .38	-.07
DA1	.01	.23	.29	.05	-.16	.21	.30	.13	.28	-.02	.03	* .38
H1	.03	-.05	.09	-.09	.137	.24	.18	.25	.04	-.29	-.15	*-.36
DB1	.10	.23	.06	.18	.39	-.11	-.18	.10	-.24	.07	.22	-.07

TABLE 16. Pooled within-group correlations between natural log/z-score transformed variables and standardised canonical discriminant functions for *Recurvatus* species. Variables ordered by absolute size of correlation within function. DA1-6, dorsal anchor; VA1-6, ventral anchor; DB1-3, dorsal bar; VA1-2, ventral bar; H1-7, hook length. # Variable not used in the analysis.

	Function
	1
H2	.548
H7	.492
H3#	.309
H6#	.284
DB3#	-.243
H4#	.206
VA6#	.202
VA5#	.196
VB1	-.196
DB1#	.166
VA4	-.091
VA3#	-.078
DA6#	.071
VA2#	-.056
H1	.055
VA1#	.046
DA2#	.032
DA3#	.023
VB2#	.009
DA1#	-.006
H5#	-.006
DA4#	.006
DA5#	.003

Analysis of species of *Iliocirrus* identified 12 variables not fitting the selection criteria of F to enter (p<0.05) and F to remove (p<0.01). The first 3 functions account for 91.4% of total explained variance. Function F1 accounted for 58.4%, F2 for 18.5% and F3 for 14.5% of the variance. Examination of characters for F1 and F2 scatter plot clearly separates *I. ornatusi*, *I. mazlini* and *I. iliocirrus* from each other. *Iliocirrus rossi* and *I. trifasciatae* cluster together with partial overlapping of *I. iliocirrus* (Fig. 35A). Function F3 characters separate *I. rossi* from *I. iliocirrus* and *I. trifasciatae* (Fig. 35B), while F4 characters separate *I. trifasciatae* from *I. ross*i and *I. iliocirrus* (Fig. 35C). Hook characters dominate F1; characters VB2, DA5 and H5 dominate F2. Dorsal and ventral bar characters are correlated highest with F3 and characters H1-2 and DB3 correlate highest with F4 (Table 19).

CROSS VALIDATION. Using the within-group covariance matrix and weighted for sample size with parasites entered as genera, cross-validation correctly classified 97.1% of the 591 specimens measured (Table 20). For *Recurvatus*, 10.8% of specimens mis-classified as *Helicirrus*, while for specimens of *Helicirrus* 3.7% classified as *Recurvatus* and 2.2% classified as *Longidigitis*. All specimens of *Longidigitis* and *Iliocirrus* classified correctly. This high level of correctly classified specimens indicates that combinations of haptoral morphometric variables are able to identify the genera defined by copulatory apparatus morphology. When all parasites were analysed together and entered as species, 99.5% of specimens classified into their correct genus. Specimens mis-classified were not identified as species within their own genus but across genera. Two specimens (13.3%) of *H. gertrudaea* classified as *R. signiferi* while one specimen of *H. mcivori* classified as *L. gracilis.*

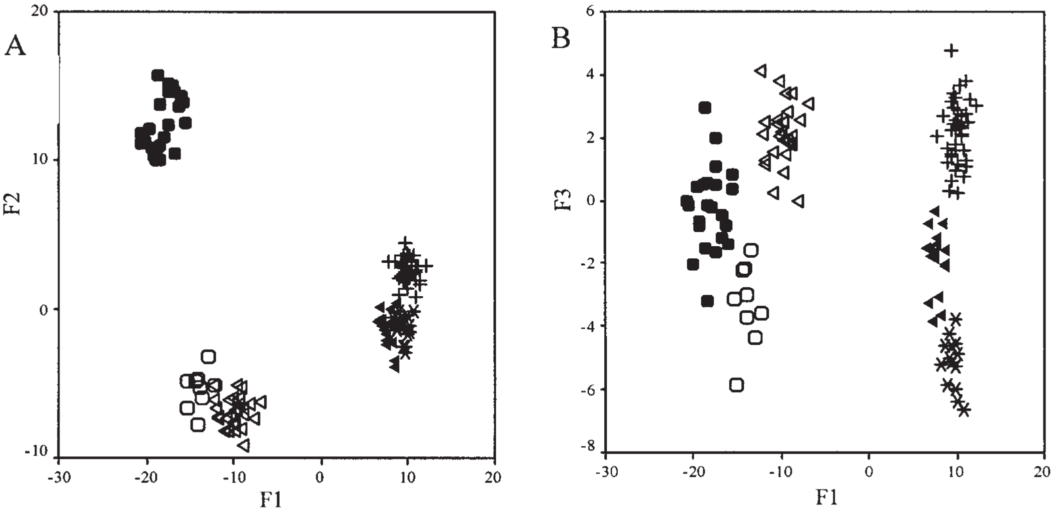

FIG. 33A-B. Scatter plots of first three axes of discriminant functions using 18 natural log/z-score transformed metric variables for *Helicirrus* species. ◁ *H. splendidae*; ● *H. megaloanchor*; ◀ *H. mcivori*; + *H. marjoriaea*; ○ *H. maccullochii*; ✶ *H. gertrudaea*.

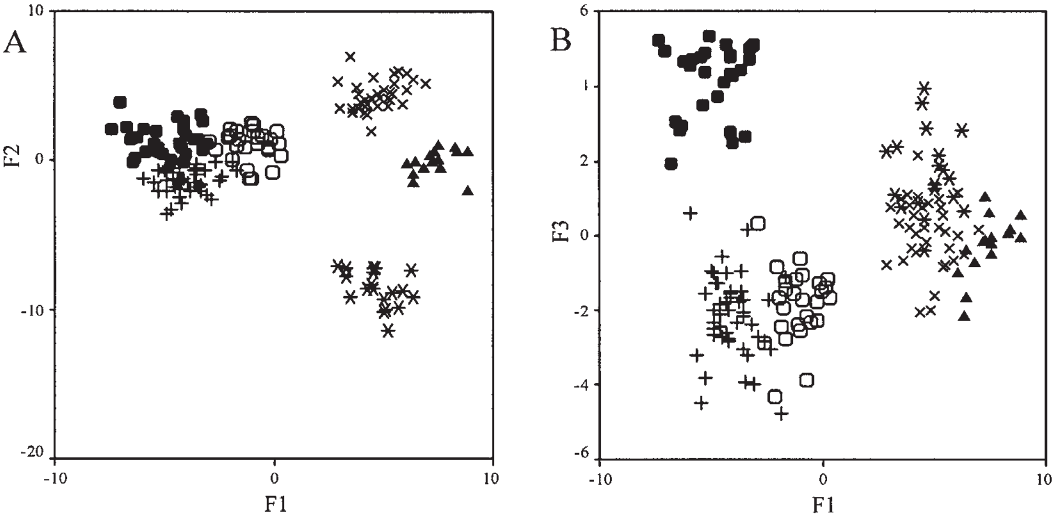

FIG. 34A-B. Scatter plots of first three axes of discriminant functions using 20 natural log/z-score transformed metric variables for *Longidigitis* species. ○ *L. utcheei*; + *L. maccullochii*; ▲ *L. hopevalensis*; ● *L. gracilis*; ✶ *L. robustus*; × *L. aouripontiformis*.

DISCUSSION

Helicirrus species have the greatest haptoral sclerite variation while *Iliocirrus* species have the least. For *Iliocirrus*, *I. trifasciatae* is least discernable from other species of the genus, especially from *I. rossi* and *I. mazlini*, based on haptoral sclerite variation; however, *I. trifasciatae* is the most different from all species of *Iliocirrus*, based on copulatory apparatus morphology. Species of *Longidigitis* could be separated into two groups, *L. gracilis*, *L. maccullochii*, *L. utcheei* and *L. auripontiformis*, *L. hopevalensis* and *L. robustus*, based on haptoral sclerite variation. The '*gracilis*' group shows consistent similarities in haptoral and copulum structures

TABLE 17. Pooled within-groups correlations between natural log/z-score transformed variables and standardised canonical discriminant functions for *Helicirrus* species. Variables ordered by absolute size of correlation within function. DA1-6, dorsal anchor; VA1-6, ventral anchor; DB1-3, dorsal bar; VA1-2, ventral bar; H1-7, hook length. (%) percent total variance explained. * Largest absolute correlation between each variable and any discriminant function. # Variable not used in the analysis.

	Function				
	1	2	3	4	5
	(74.8%)	(17.8%)	(4.0%)	(2.1%)	(1.2%)
H4	*.688	.286	-.129	-.169	.060
DB1	*.316	.175	.073	.244	-.038
DB3	*.233	.110	.053	.004	.196
VA2	-.046	*.552	-.345	.024	.090
VA6	-.121	*.542	-.045	.038	.285
VA3	-.129	*.388	-.117	.159	.383
VB1	.011	*.366	.122	-.013	.013
VA1	.086	*.260	.060	-.132	.004
H5#	-.052	*.258	-.004	-.093	.010
VB2	.044	.340	* .420	.095	-.264
VA5	.026	.305	*-.346	-.038	.061
H6	.124	.137	*-.278	.219	-.168
DA1	.166	.039	* .245	-.108	-.025
DA2#	.181	.038	* .198	-.196	.107
DA6#	.101	.091	* .144	.015	-.031
H7	.150	.052	-.309	* .486	-.132
H2	.196	.144	-.146	* .385	.162
DA5	.135	.026	.095	* .205	-.128
H1#	.046	.124	.081	*-.148	.012
DA3	.167	-.074	.046	-.107	*.385
VA4	-.092	.364	-.079	.230	*.378
DA4	.176	-.030	.092	-.116	*.372
H3	.236	.153	.062	.249	*.274

TABLE 18. Pooled within-groups correlations between natural log/z-score transformed variables and standardised canonical discriminant functions for *Longidigitis* species. Variables ordered by absolute size of correlation within function. DA1-6, dorsal anchor; VA1-6, ventral anchor; DB1-3, dorsal bar; VA1-2, ventral bar; H1-7, hook length. (%) percent total variance explained. * Largest absolute correlation between each variable and any discriminant function. # This variable not used in the analysis.

	Function				
	1	2	3	4	5
	(48.5%)	(28.9%)	(11.8%)	(7.1%)	(3.6%)
DA2	*.452	.167	-.328	.040	-.356
DA3	*.416	.223	-.338	.021	-.389
DA1	*.340	.235	-.124	-.199	-.153
DA5	*.330	-.075	-.075	-.084	-.027
DA6	*.291	.060	.111	-.046	-.268
DB3	*.283	.135	.003	-.057	.275
H4	-.088	*.451	-.266	-.009	-.392
VA2	.399	*.274	-.587	.118	-.174
VA3	.337	*.233	-.504	.314	-.038
VA4	.324	*.322	-.478	.135	-.232
H7	.037	.106	*-.402	-.024	-.281
H3	-.078	-.024	*-.393	.019	-.304
H6	.026	-.041	*-.363	.358	-.357
H1	.171	.021	*-.187	.052	.113
VB1	.143	.239	.140	*.713	.015
VB2	-.118	.357	.200	*.386	.370
DA4	.384	.238	-.244	.044	*-.481
H2#	.029	.175	-.287	.158	*-.292
VA5#	.208	.032	-.119	-.015	*-.287
H5	.214	-.060	.028	-.014	*-.250
VA6#	.120	.102	-.085	-.102	*-.240
DB1	.065	-.032	.096	.120	*-.173
VA1	.148	-.023	.083	.140	*-.150
DA2	.452	.167	-.328	.040	*-.356

and is clustered together in both PCA and DFA analyses. *Longidigitis auripontiformis* and *L. hopevalensis* have similar haptoral sclerite morphologies but are easily distinguished by the differences in copulatory apparatus morphology.

Two haptor morphologies were identified in species of *Helicirrus*. Well-developed dorsal anchors, dorsal bar and elongated hooks are present in *H. mcivori*, *H. gertrudaea* and *H. marjoriaea*. Highly reduced dorsal anchors, dorsal bar and hooks are found in *H. splendidae*, *H. maccullochii* and *H. megaloanchor*. This may be associated with the attachment site on the host. All *Longidigitis*, *Iliocirrus* and *Recurvatus* species attach to the gill filaments while *H. splendidae* and *H. maccullochii* most often attach between the gill raker spines (unpublished data). A similar reduction can be also found in gyrodactylids (pers. obs.). It is not known if this is related to their attachment to a different, more simplified, part of the gill structure. The well-developed haptoral sclerite structures of the *Longidigitis*, *Iliocirrus* and *Recurvatus* species and *Helicirrus mcivori*, *H. gertrudaea* and *H. marjoriae* may be an adaptation to the complexity of the soft gill tissue which may require more developed ventral and dorsal sclerites. *Helicirrus megaloanchor* has reduced hooks and highly reduced dorsal bar and anchors. However this species attaches to the gill filaments and not between the gill raker spines. This species has extremely large ventral anchors, which may be an adaptation for attachment to the soft gill tissue.

Both haptoral and copulum structure are recognised as important in defining the genera, and there is congruence between the two approaches. The parasite species were grouped into genera based on copulatory apparatus morphology. Principal component analysis and DFA clearly identified a number of clusters, recognised *a posteriori* as the parasite genera and species described using morphology. Thus, the

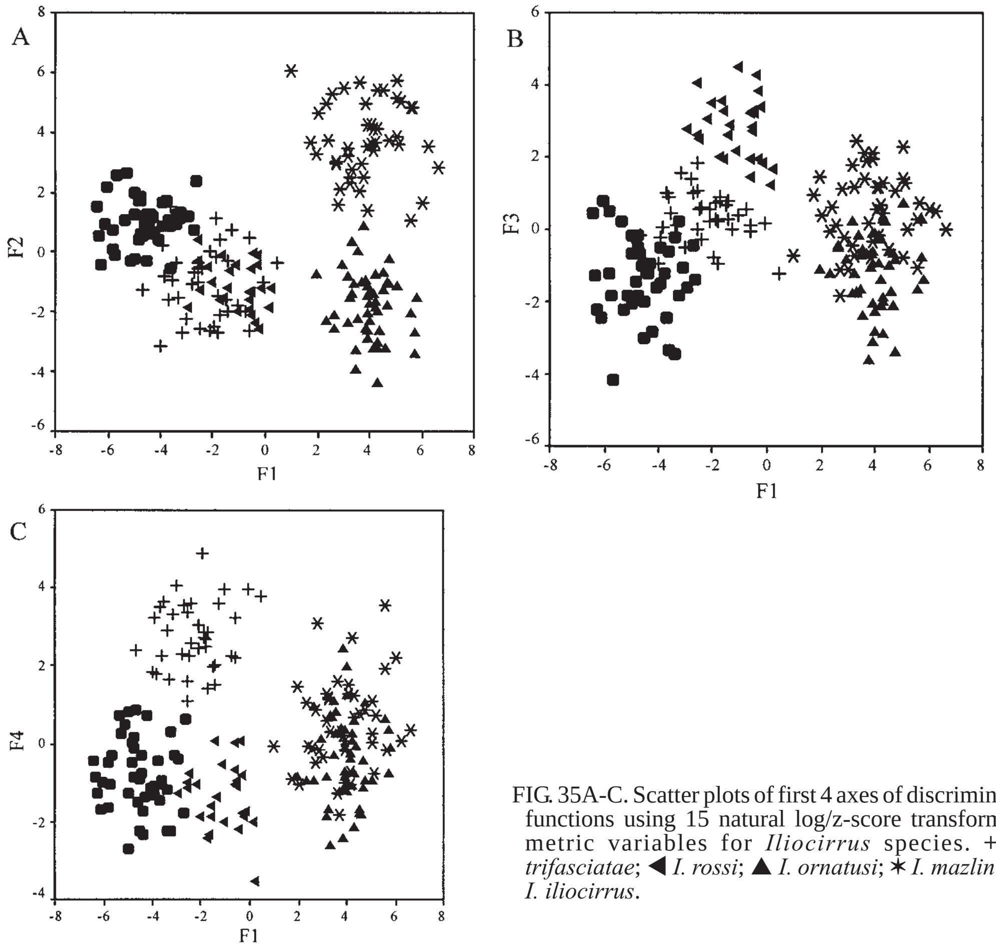

FIG. 35A-C. Scatter plots of first 4 axes of discriminant functions using 15 natural log/z-score transformed metric variables for *Iliocirrus* species. + *I. trifasciatae*; ◀ *I. rossi*; ▲ *I. ornatusi*; ✶ *I. mazlini*; ● *I. iliocirrus*.

genera and species were validated using only morphometric haptoral characters. Reproductive and to a lesser extent haptoral morphology appears the most natural taxonomically for the species assigned to *Helicirrus*, *Recurvatus*, *Iliocirrus* and *Longidigitis*. Haptoral sclerite morphology groupings can also reflect generic groupings based on copulatory apparatus structure. However, no single or set of morphological characters are unique to each genus. Separation of each genus is by a set of broadly recognised morphometric variations between characters defined by PCA and DFA.

Principal component analysis and DFA are used as a means of data reduction by reducing a large number of character variables into a much smaller number of variables called principal components and discriminant functions respectively and are often graphically represented as two or three dimensional scatter plots. These methods also identify which characters have the highest correlation for each new variable. The two, however, use different approaches. Principal component analysis extracts new variables based solely on the correlation within and between variances of characters without any *a priori* grouping of the character variants. Analysis of the 20 species in this study using PCA identified a maximum of five new variables. Discriminant function analysis considers variables to be correlated and is designed to present contrasting (as opposed to independent) patterns of variation. Discriminant function analysis uses *a posteriori* approach to produce a set of new variables that best maximises differences between the predetermined groups using correlation of variances within and between characters. The number of new variables defined for discriminant analysis is (n-1), where

TABLE 19. Pooled within-group correlations between natural log/z-score transformed discriminating variables and standardised canonical discriminant functions for *Iliocirrus* species. Variables ordered by absolute size of correlation within function. DA1-6, dorsal anchor; VA1-6, ventral anchor; DB1-3, dorsal bar; VA1-2, ventral bar; H1-7, hook length. (%) percent total variance explained. * Largest absolute correlation between each variable and any discriminant function. # This variable not used in the analysis.

	Function			
	1 (58.4%)	2 (18.5%)	3 (14.5%)	4 (8.6%)
H4	*-.514	-.050	.299	.056
H6	*-.387	-.021	.011	.234
H3	*-.251	.086	.181	-.023
VA6#	*-.163	-.099	.001	.108
VB2	.201	* .437	-.200	-.252
DA5	.041	*-.338	.133	.025
H5	.093	* .209	-.018	.179
DA6#	-.092	*-.202	.199	.195
DB2	-.033	.110	* .572	.004
VA3	-.009	.197	* .557	.076
VA4	.007	.227	* .456	.206
VA2#	.060	.092	* .424	.153
DA4	.072	-.283	* .417	-.147
DA2	.082	-.378	* .403	-.103
DA3#	-.020	-.123	* .367	-.104
VB1	.255	-.060	* .280	.222
DB1#	-.009	-.062	* .244	.201
VA1#	.008	-.071	*-.142	-.051
DA1#	.069	.022	* .122	-.076
H2	-.070	.166	.318	*.478
DB3	-.023	.019	-.003	*.317
H1	-.082	.059	.105	*.247
H7#	-.165	.049	.212	*.221
VA5#	-.018	.050	.026	*.052

n is the number of predefined groups. Correlation of explained variance is accounted most in the first three discriminant functions and the last few usually produce a non-significant difference in the centroid means of clusters.

Discriminant function analysis differs from PCA in that parasite specimens are assigned *a priori* to groups and then scatter plots are used to assess if these groups are valid. Character variables are also identified which best reflect these *a priori* groups. However, the characters chosen change depending on *a priori* sample grouping. This method was able to identify morphological characters that define the four genera. This is not possible using PCA if clusters are not clearly defined. The advantage of DFA over PCA in taxonomy is that when species have been identified using morphometric variables, measured unknown specimens and especially cryptic species can be identified using cross-validation. Discriminant function analysis identified sets of characters that were not included in the final analysis at the various levels of investigation. These character sets indicate redundancy of information in the data and are not necessary in the analysis. The sets of characters, however, change at the various levels of analysis limiting *a priori* selection of characters for removal. Taxonomists often use alternative methods such as K-cluster or hierarchical cluster analysis for the same purpose (Anderberg, 1973). However, these methods do not identify the most useful characters for the separation of clusters but rely on *a priori* selection, usually obtained by multivariate analysis.

Multivariate analysis identified significant differences within character means between species and the species descriptions use these differences. An example is the length relationships among hooks among and between species. However, different MANOVA methods often identify a varying number of significant differences. This was shown with the comparison of the Scheffé and Tukey's HSD test multiple range tests ($p< 0.01$). For example, for *H. marjoriaea* and *H. mcivori*, 11 significantly different characters were identified using Scheffé test while 17 were identified using Tukey's HSD test. This indicates that Scheffé test is more conservative in identifying significant character differences than the Tukey's HSD test. The true number of differences lies somewhere between these two extremes for $\propto$ =0.05-0.01.

TABLE 20. Generic level grouping cross-validation. Each case is classified by the functions derived from all cases other than that case. Specimens entered as genus groups. 97.1% of cross-validated grouped cases correctly classified.

		Predicted Group Membership				Total
	Genus	*Recurvatus*	*Helicirrus*	*Longidigitis*	*Iliocirrus*	591
Count	*Recurvatus*	66	8	0	0	74
%	*Helicirrus*	5	125	3	0	134
	Longidigitis	0	0	174	0	174
	Iliocirrus	0	0	0	209	209
	Recurvatus	89.2	10.8	.0	.0	100.0
	Helicirrus	3.7	93.3	2.2	.0	100.0
	Longidigitis	.0	.0	100.0	.0	100.0
	Iliocirrus	.0	.0	.0	100.0	100.0

A much better understanding is needed of the diversity of morphological and morphometric variation of the haptoral structures and possible correlations to the genera. The same understanding is also needed for the reproductive system. The species of *Iliocirus* show little easily identifiable copulatory apparatus or haptoral morphological variation and are difficult to recognise visually, but are easily identified, using morphometric analysis of haptoral sclerite variability. This lack of morphological variation also has implications for cladistic studies, which traditionally use morphological characters. Methodologies have been developed for cladistic analysis of morphometric variation (Archie, 1985; Baum, 1988). However, cladistic studies have not been attempted on haptoral variation of monogenean taxa, e.g. Gyrodactylidae, although it is a well studied group.

Comparison of the four monogenean parasites described previously from other atherinid species identified extremely elongated hooks in *Atherinicus cornutus*, *Ancyrocephalus atherinae*, *Diversohamulus tricuspidatus and Ancyrocephalus littoralis*. However, a gonadal bar is present in *A. cornutus*, which is absent in species of the genera *Longidigitis*, *Iliocirrus*, *Recurvatus* and *Helicirrus* as well as all other species of genera infesting atheriniform fishes. *Diversohamulus tricuspidatus* has a haptoral sclerite complex similar to *L. megaloanchor* with similar increase in length of hooks, large ventral anchors and bar and highly reduced dorsal bar and anchors. However the former species (as well as *A. atherinae* and *A. littoralis*) differs from species in the four new genera in the copulatory apparatus structure. The copulatory apparatus of *D. tricuspidatus* does not resemble any of the four types described earlier but consists of a straight tubiform copulum shaft and an accessory piece, which has a few distal ramifications and is attached to the proximal surface of the copulum base. The copulatory apparatus structure of *A. cornutus* has similarities to the Type III form found in *Longidigitis* species consisting of a single recurved loop. However the copulum shaft is directed anteriorly not dextrally and the accessory piece is different. The vaginal opening in *A. cornutus* and *D. tricuspidatus* is ventral and dextral in *A. atherinae* and *A. littoralis* while it is sinistral in species of *Longidigitis* and *Iliocirrus*.

KEY TO MONOGENEAN PARASITE GENERA OF AUSTRALIAN ATHERINIFORM FISHES

1. Copulum shaft coiled at distal end posterior to copulum base . . . . *Helicirrus*
2. Copulum shaft single counter-clockwise coil (ventral view) encircling copulum base . . . . *Recurvatus*
3. Copulum shaft comprises a single sinistral recurved loop . . . . *Longidigitis*
4. Copulum shaft comprises two sinistral recurved loops . . . . *Iliocirrus*

KEY TO SPECIES OF *HELICIRRUS*

1. Hooks reduced, H4 shorter than ventral anchor. 2
   Hooks elongated form, H4 always longer than ventral anchor. 4
2. Copulum shaft proximally expanded to form a chamber. 3
   Copulum shaft not expanded . . . . *H. splendidae*
3. Ventral anchor extremely large dorsal anchor highly reduced. . . . . *H. megaloanchor*
   Ventral anchor slightly larger than dorsal anchor . . . . *H. maccullochii*
4. Copulum shaft not expanded proximally 5
   Copulum shaft expanded proximally . . . . . *H. mcivori*
5. Copulum shaft highly coiled at distal end (30 coils) . . . . *H. marjoriaea*
   Copulum shaft few coils (<10) . . . . . . *H. gertrudaea*

KEY TO SPECIES OF *RECURVATUS*

1. Accessory piece large, claw shaped, hook H4 shaft similar thickness to H3 . . . . *R. chelatus*
   Accessory piece not as above, hook H4 shaft much thinner than H3 . . . . *R. signiferi*

KEY TO SPECIES OF *LONGIDIGITIS*

1. Notch present on posteromedial margin of dorsal bar . 2
   Notch absent on posteromedial margin of dorsal bar . . 4
2. Anchors with thickened roots . . . . *L. robustus*
   Anchor roots not thickened. 3
3. Dorsal bar ear-shaped with membrane infill on anterior edge . . . . *L. hopevalensis*
   Dorsal bar, not ear-shaped, without infill on anterior edge . . . . *L. gracilis*
4. Dorsal bar ear-shaped, membrane infill on anterior edge present . . . . *L. auripontiformis*

Dorsal bar not ear-shaped, without infill on anterior edge. . 5

5. Hooks H2 shorter than H1, H3 and H5 of similar length . . . . *L. utcheei*
   Hooks H2 and H1 similar in length, H3 longer than H5 . . . . *L. maccullochii*

KEY TO SPECIES OF *ILIOCIRRUS*

1. Hooks H1 and H5 similar in length. . . . . . . *I. mazlini*
   Hooks H1 much smaller in length than H5 2
2. Ventral bar with deep V-shaped notch on posterior medial edge . . . . *I. ornatusi*
   Ventral bar without deep V-shaped notch on posterior medial edge 3
3. Hooks H3 and H5 similar size 4
   Hooks H3 longer than H5. . . . . *I. rossi*
4. Copulum shaft thin, recurved loops reduced . *I. trifasciatae*
   Copulum shaft thick, recurved loops well-developed . . . . *I. iliocirrus*

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