



Phylogeny and revision of Diplectanidae Monticelli, 1903 (Platyhelminthes: Monogenoidea)

MARCUS V. DOMINGUES¹ & WALTER A. BOEGER²

¹Laboratório de Helminologia Evolutiva, Instituto de Biociências, Departamento de Zoologia, Universidade de São Paulo, Rua do Matão, trav. 14, n°321, 05508-900 São Paulo, SP, Brasil. E-mail: mydomingues@ib.usp.br

²Curso de Pós Graduação, Zoologia, Laboratório de Parasitologia Evolutiva, Departamento de Zoologia, Universidade Federal do Paraná, Caixa Postal 19073, 81531-980 Curitiba, PR, Brasil. E-mail: wboeger@ufpr.br

Table of contents

Abstract	2
Introduction	2
Material and methods	3
Results and discussion.....	5
Diplectanidae Monticelli, 1903.....	15
Nasobranchitrematinae n. subfam.	15
<i>Nasobranchitrema</i> Yamaguti, 1965	15
Pseudomurraytrematoidinae n. subfam.	16
<i>Pseudomurraytrematoides</i> n. gen.	16
<i>Diplectanocotyla</i> Yamaguti, 1953 sedis mutabilis	16
<i>Lamellodiscinae</i> Oliver, 1969	17
<i>Calydiscoides</i> Young, 1969.....	17
<i>Protolamellodiscus</i> Oliver, 1969.....	17
<i>Lamellodiscus</i> Johnston & Tiegs, 1922	18
<i>Telegamatrix</i> Ramalingam, 1955	19
<i>Furnestinia</i> Euzet & Audouin, 1959.....	19
Diplectaninae Monticelli, 1903	20
<i>Paradiplectanum</i> n. gen.	20
<i>Rhabdosynochus</i> Mizelle & Blatz, 1941	21
<i>Pseudodiplectanum</i> Tripathi, 1957	22
<i>Monoplectanum</i> Young, 1969	22
<i>Latericaecum</i> Young, 1969	23
<i>Acleotrema</i> Johnston & Tiegs, 1922	23
<i>Pseudolamellodiscus</i> Yamaguti, 1953	24
<i>Diplectanum</i> Diesing, 1858.....	24
<i>Lobotrema</i> Tripathi, 1959	26
<i>Murraytrema</i> Price, 1937	26
<i>Lepidotrema</i> Johnston & Tiegs, 1922	27
<i>Spinomatrix</i> Boeger, Fehlaue & Marques, 2006.....	27
<i>Rhamnocercus</i> Monaco, Wood & Mizelle, 1954	28
<i>Rhamnocercoides</i> Luque & Iannaccone, 1991	28
<i>Oliveriplectanum</i> n. gen.	28
<i>Murraytrematoides</i> Yamaguti, 1958	29
<i>Anoplectanum</i> Boeger, Fehlaue & Marques, 2006	29
<i>Laticola</i> Yang, Kritsky, Sun, Jiangying, Shi & Agrawal, 2006	30

<i>Pseudorhabdosynochus</i> Yamaguti, 1958	30
<i>Echinoplectanum</i> Justine & Euzet, 2006	32
Acknowledgments	32
References	33
Appendix 1. Specimens of diplectanid species examined	40

Abstract

A hypothesis on the phylogenetic relationships of diplectanid genera is proposed based on 36 morphological characters using cladistic methods. The analysis supports two subfamilies, Diplectaninae Monticelli, 1903 and Lamellogiscinae Oliver, 1969, and the proposal of two new subfamilies: Nasobranchitrematinae **n. subfam.**, monotypic, composed by *Nasobranchitrema* Yamaguti, 1965; and Pseudomurraytrematoidinae **n. subfam.** comprising *Pseudomurraytrematoides* **n.gen.** *Murraytrematoides pricei* (Caballero, Bravo-Hollis & Grocott, 1955) is transferred to *Pseudomurraytrematoides* as *P. pricei* comb. n. Lamellogiscinae is supported by two synapomorphies and comprises *Calydiscoides*, *Protolamellogiscus*, *Lamellogiscus*, *Telegamatrix* and *Furnestinia*. The analysis indicates that *Lamellogiscus* is polyphyletic. Diplectaninae comprises *Paradiplectanum* **n. gen.**, *Rhabdosynochus*, *Pseudodiplectanum*, *Monoplectanum*, *Latericaecum*, *Pseudolamellogiscus*, *Acleotrema*, *Diplectanum*, *Lobotrema*, *Murraytrema*, *Lepidotrema*, *Spinomatrix*, *Rhamnocercus*, *Rhamnocercoides*, *Oliveriplectanum* **n. gen.**, *Murraytrematoides*, *Anoplectanum*, *Laticola*, *Pseudorhabdosynochus* and *Echinoplectanum*. Rhabdosynochinae Oliver, 1987; Rhamnocercinae Monaco, Wood & Mizelle, 1954; and Murraytrematoidinae Oliver, 1982 are considered junior synonyms of Diplectaninae. *Diplectanum* is restricted to species that present (1) male copulatory organ with nested tubes; (2) accessory copulatory organ; (3) prostatic reservoir separated into three zones; (4) ventral and dorsal squamodiscs. Based on the analysis, *Cornutohaptor* Mendoza-Franco, Violante-González & Vidal-Martinez, 2006 is a junior synonym of *Rhabdosynochus* Mizelle & Blatz, 1941. *Diplectanum cazauxi* Oliver & Paperna, 1984 is transferred to *Latericaecum* as *L. cazauxi* (Oliver & Paperna, 1984) comb. n. *Diplectanocotyla*, Lamellogiscinae and Diplectaninae are considered *sedes mutabilis*.

Key words: Monogeneoidea, Diplectanidae, taxonomy, phylogeny

Introduction

The Diplectanidae Monticelli, 1903 is represented by approximately 250 species occurring primarily on the gills of marine perciforms fishes (Oliver 1987). Five subfamilies are recognized: Diplectaninae Monticelli, 1903, Lamellogiscinae, Oliver, 1969, Murraytrematoidinae Oliver, 1982, Rhabdosynochinae Oliver, 1987 and Rhamnocercinae Monaco, Wood & Mizelle, 1954. This family represents a monophyletic group within Dactylogyrynea (Dactylogyridae (Diplectanidae + Pseudomurraytrematidae) (Kritsky & Boeger 1989, Boeger & Kritsky 1993, 1997, 2001). Diplectanidae is historically diagnosed by the combination of the following characters: (1) accessory adhesive organs (squamodiscs or lamellogiscs); (2) three transversal bars connected to two pairs of anchors (dorsal, ventral); and (3) pretesticular germarium, looping right intestinal caecum.

Despite of its widely accepted monophyly, Diplectanidae has been subject to several taxonomical rearrangements at subfamily and genera levels since it was proposed by Monticelli (1903) (Johnston & Tieggs 1922; Price 1937; Bychowsky 1957; Yamaguti 1963; Oliver 1987). The studies, focusing on the relationships among supraspecific taxa of the family, contain many contradictions (Price 1937; Yamaguti 1953; Yamaguti 1958; Bychowsky 1957; Yamaguti 1963; Yamaguti 1965; Oliver 1968; Young 1968; Bychowsky & Nagibina 1977; Euzet & Dossou 1979; Oliver 1982; Kritsky & Beverley-Burton 1986; Oliver 1987; Rakotofiringa & Oliver 1987; Rakotofiringa *et al.* 1987; Chaves *et al.* 1999; Kritsky *et al.* 2000; Desdevises *et al.* 2001; Kritsky *et al.* 2001; Mendoza-Franco *et al.* 2004; Domingues & Boeger 2006; 2007).

Kritsky *et al.* (2000) suggested that some genera might represent unnatural groups (“catch-all”) by including species with variable features. Yang *et al.* (2006) recognized that one possible solution for the potential unnatural taxa within the Diplectanidae should be synonymy taxa distinguished by apparent secondary char-

acters (e.g. one squamodisc in *Monoplectanum*). While this procedure may resolve problems of unnatural taxa, it can result in reduced resolution of potential relationships within the senior taxon, suggesting that cladistic analyses (i.e., molecular, morphological) is required to support taxonomic decisions within the taxon.

Oliver (1987), using morphological features, performed the first cladistic study addressing the evolutionary relationships among major component groups of Diplectanidae. The resulting phylogeny supports four subfamilies (Murraytrematoidinae, Rhabdosynochinae, Lamellogdiscinae, and Diplectaninae) (fig. 1A). However, this author did not include Rhamnocercinae, *Diplectanocotyla* and *Nasobranchitrema* in the analysis, believing that these taxa were not members of Diplectanidae. Later, Desdevises *et al.* (2001) reevaluated Oliver's hypothesis adding new characters. This most recent hypothesis supports the monophyly of three subfamilies and the apparent paraphyly of Murraytrematoidinae (fig. 1B). Desdevises (2001) also evaluated the taxonomic position of *Furnestinia* and *Lamellogdiscus* based of rDNA 18S (fig. 1C), concluding on the paraphyly of *Lamellogdiscus*. Domingues and Boeger (2006) recognized Rhamnocercinae as a subordinate taxon of Diplectanidae and proposed a cladistic analysis for members of this subfamily. These authors recognized that *Spinomatrix* is closely related to *Rhamnocercus* + *Rhamnocercoides* based on the presence of the peduncular spines and that the absence of squamodiscs in species of *Rhamnocercus* and *Rhamnocercoides* is a likely result of secondary losses (fig. 1D).

Material and methods

The ingroup is composed of valid genera of Diplectanidae as indicated by Oliver (1987) except for *Heteroplectanum* and *Cycloplectanum*, considered junior synonymies of *Acleotrema* and *Pseudorhabdosynochus*, respectively (see Kritsky & Beverley-Burton 1986; Domingues & Boeger 2007). Genera described after Oliver (1987) also are included in the analysis. *Diplectanocotyla* Yamaguti, 1953, *Nasobranchitrema* Yamaguti, 1965 and species of Rhamnocercinae Monaco, Wood & Mizelle, 1954 are included in the analysis as internal taxa to understand their relationships with other diplectanids.

The hypothesis on the evolutionary relationship of the Diplectanidae genera is based on morphological data. The characters were obtained from the literature or directly through the study of type- and/or voucher-specimens deposited at museums (Appendix I). Assignment of character states for each genera were based on a preliminary analysis of available specimens, whenever possible using the type species. Specimens of *Lobotrema*, *Murraytrema*, and *Telegamatrix* were not available for the present study. Thirty-five taxa were used in the cladistic analysis; two are representatives of the outgroup and 33 taxa represent the ingroup.

Thirty-six characters, representing 77 character states, were used in the reconstruction of the phylogenetic relationships. Characters in which the respective derived character represents an autapomorphy of a single ingroup taxon were included and used for generic diagnosis. All characters were unordered, with equal weight, and unambiguous. Coding of polymorphic characters was made by prediction of the respective primitive state for each taxon (see Kornet & Turner 1999). *Pseudomurraytrema* (Pseudomurraytrematidae) and *Euryhaliotrema* (Dactylogyridae) were used as outgroup, based on the phylogenetic relationships of their families to the Diplectanidae as hypothesized by Boeger and Kritsky (1993, 1997, 2001). The phylogenetic hypothesis was developed with the program T.N.T. (Goloboff *et al.* 2003), using heuristic search (hsearch addseq= random; maxtree=10000; nreps=1000; swapping algorithm= TBR; hold trees per replication = 10). Rooting was *a posteriori* as proposed by Nixon and Carpenter (1993). Bremer support values were determined for each proposed branch.

Tests of monophyly of *Diplectanum*, *Lamellogdiscus* and *Murraytrematoides*

To test the monophyly of *Diplectanum* and *Lamellogdiscus*, they were separated into morphological group/types as proposed by Oliver (1987). Morphological groups of *Diplectanum* are based on the morphology of the male copulatory organ and are represented by *D. aequans*, *D. caxauzi*, *D. monticelli*, *D. sillagonum* and *D. priacanthi*. For *Lamellogdiscus*, *L. furcillatus* and *L. mormyri* represent the morphological type of lamellogdiscs.

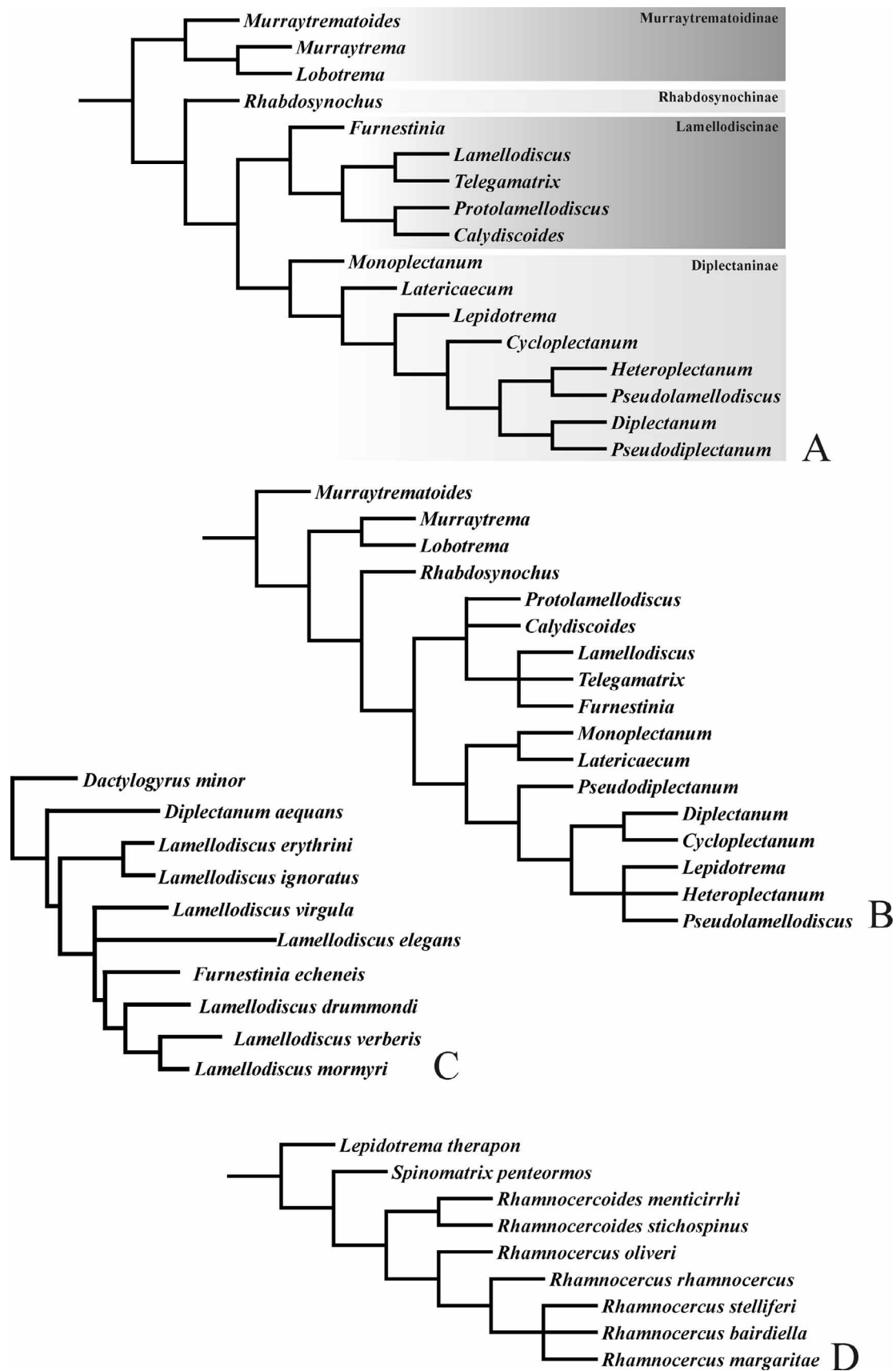


FIGURE 1. Summary of the proposed phylogenetic hypotheses of Diplectanidae. **A.** Hypothesis for genera of Diplectanidae from Oliver (1987); **B.** Hypothesis for genera of Diplectanidae from Desdevises *et al.* (2001); **C.** Hypothesis of several species of *Lamellogiscus* and *Furnestinia echeneis* from Desdevises (2001). **D.** Hypothesis for Rhamnocercinae from Domingues and Boeger (2006).

Similarly, the monophyly of *Murraytrematoides* was tested in the present study. We detected under study of type specimens of *M. ditrematis*, *M. lateolabracis*, and *M. pricei*, that *Murraytrematoides* was likely not monophyletic based on the morphology of the male copulatory organ.

Results and discussion

Character analysis

Characters used in the analysis follow with comments on character-state evolution. Numbers in parentheses preceding a character state refer to the code that the state received in the matrix. Bold numbers in brackets, following the definition of the character-state, refer to the position of the characters in the tree. Character changes are sequentially numbered in the tree, as defined below:

(1)*Accessory adhesive organ*: **(0)** absent [30, 45, 53, 60]; **(1)** present [7].

(2)*Type of accessory adhesive organs (when present)*: **(0)** squamodiscs (fig. 2); **(1)** lamellodiscs (fig. 3) [12]. Oliver (1987) proposed three basic types of accessory adhesive organs derived from the tegumental scales, squamodiscs, lamellodiscs, and placodiscs. Oliver (1993) considered echinodiscs (peduncular spines *sensu* Domingues & Boeger 2006) observed in Rhamnocercinae as homologous to the accessory adhesive organ of the other Diplectanidae. However, Domingues and Boeger (2006) rejected the homology between the peduncular spines, the spines associated with the ventral bar, and accessory adhesive organ based on their morphology and topological position in the haptor. Kritsky *et al.* (2001) refuted the homology between the accessory adhesive organ and the placodiscs observed on some species of *Rhabdosynochus*, as suggested by Hargis (1955) and Oliver (1987). Thus, in this analysis only the squamodiscs and lamellodiscs were considered accessory adhesive organs.

(3)*Number of accessory adhesive organs*: **(0)** two; **(1)** one [24, 34]

(4)*Configuration of the anterior rows of the rodlets of the squamodisc*: **(0)** open rings (fig. 2A); **(1)** closed rings (fig. 2B) [36, 58, 67]; **(2)** divergent rows (fig. 2C) [39]; **(3)** parallel rows (fig. 2D) [41]. The anterior rows of the rodlets type “open ring” is defined by rows of rodlets with extremities not in contact or closed. While, the type “closed ring” is defined by rows of rodlets with extremities in contact or closed.

(5)*Intermediate rows of the rodlets of the squamodiscs*: **(0)** rodlets without anterior lightly sclerotized blunt spinelet (figs. 2B–C); **(1)** rodlets with anterior lightly sclerotized blunt spinelet (fig. 2A) [28, 37, 69]. This character is polymorphic for *Diplectanocotyla*. However, the rodlets without anterior lightly sclerotized blunt spinelet is the plesiomorphic condition for this character, defined by the relationships of this genus with its respective sister groups.

(6)*Intermediate lamellae of the lamellodiscs*: **(0)** fused at midline (fig. 3A); **(1)** superficially incomplete, partially fused at midline (fig. 3B) [19]; **(2)** incomplete, lamellae free at midline (fig. 3C) [18].

(7)*Telescoping lamellae*: **(0)** absent; **(1)** present (e.g., Young 1969: figs. 6a, 6h; Oliver 1984: figs. 1, 3, 7, 11; Thoney 1987: figs. 1, 7–13) [14]. This character seems to be polymorphic for *Protolamellodiscus*. Kritsky *et al.* (2000) observed that *Protolamellodiscus senilobatus* Kritsky, Jiménez-Ruiz & Sey, 2000 presents telescoping lamellae such as those observed in species of *Calydiscoides*. However, the absence of telescoping lamellae is the plesiomorphic condition for this character, defined by the relationships of this genus with its respective sister groups.

(8)*Haptoral suckers*: **(0)** absent; **(1)** present (e.g., Yamaguti 1953: pl. VII, fig. 27; Rakotofiringa & Oliver 1987: figs. 1, 2A; Mendoza-Franco *et al.* 2004: fig. 6; Lim & Gibson 2007: figs. 1h2, 3h, 4h2, 6, 7h2) [8].

(9)*Accessory spines associated with the posterior region of the haptor (closed to ventral bar)*: **(0)** absent; **(1)** present (e.g., Kritsky *et al.* 2000: fig. 16; Domingues & Boeger 2006: fig. 6, 20, 30, 35, 36; Boeger *et al.* 2006: figs. 28, 37–38) [48].

(10)*Peduncular spines*: **(0)** absent; **(1)** present (e.g., Mendoza-Franco *et al.* 2004: fig. 6; Domingues & Boeger 2006: fig. 6; Boeger *et al.* 2006: figs. 28, 37; Lim & Gibson 2007: fig. 10) [9, 52].

- (11)*Haptoral bars*: **(0)** 2 (1 ventral, 1 dorsal); **(1)** 2 (2 dorsal) [46]; **(2)** 3 (1 ventral, 2 dorsal); **(3)** 4 (2 ventral, 2 dorsal) [10].
- (12)*Longitudinal groove on the ventral bar*: **(0)** absent [11]; **(1)** present [1].
- (13)*Ventral bar*: **(0)** with straight ends; **(1)** with recurved ends (e.g., Rakotofiringa & Maillard 1979: figs. 1, 6; Kritsky *et al.* 2000: fig. 34) [42].
- (14)*Posteromedial projection of the ventral bar*: **(0)** absent; **(1)** present (e.g., Domingues & Boeger 2006: figs. 13, 17, 28, 34, 42) [54].
- (15)*Shape of ventral anchor*: **(0)** with elongate roots, evenly curved shaft and point (fig. 4); **(1)** with long deep root, short shaft, straight point (e.g., Nagibina 1977: figs. 2, 5, 7; Oliver 1980b: figs. 1–2; Vala *et al.* 1980: figs. 1–3) [32].
- (16) *Superficial root of the ventral anchor*: **(0)** developed (fig. 4A) [57]; **(1)** reduced or inconspicuous (fig. 4B) [15, 26]. The development of the ventral anchor is defined by the angle formed by an imaginary line that tangency the subsequent margins of the superficial and deep roots, and a line that tangency the deep margin of the deep root and shaft. By convention, a developed superficial root presents angle $\geq 90^\circ$ and a reduced or inconspicuous superficial root presents angle $< 90^\circ$. This character is polymorphic for *Protolamellodiscus* and *Rhabdosynochus*. However, ventral anchor with superficial root conspicuous is the plesiomorphic condition for this character, defined by the relationships of these genera with their respective sister groups.
- (17)*Superficial root of the dorsal anchor*: **(0)** conspicuous (fig. 5A); **(1)** reduced or inconspicuous (fig. 5B) [2]. The definition of the state of development of the dorsal anchor follows that proposed for the ventral anchor (character 16).
- (18)*Male copulatory organ*: **(0)** simple tube; **(1)** nested tubes (e.g., Oliver 1968: figs. 4–5; Oliver 1980a: fig. 3; Oliver & Paperna 1984: figs. 1–2; Domingues & Boeger 2006: figs. 1, 7, 16 [31].
- (19)*External tube of the male copulatory organ (when nested tubes are present)*: **(0)** simple (e.g., Domingues & Boeger 2006: figs. 16, 25, 31, 41) [55]; **(1)** twisted (e.g., Domingues & Boeger 2006: figs. 1, 7) [49].
- (20)*Base of the male copulatory organ*: **(0)** not expanded; **(1)** expanded (e.g., Domingues & Boeger 2003: fig. 2; Justine 2005a: figs. 3A–D, 4B, 5K, 7A, 11A, 12C; Yang *et al.* 2006: figs. 4–5, 12, 19–20; Justine & Euzet 2006: figs. 1B, 2G, 3B, 4J, 5D, 8C) [62].
- (21)*Male copulatory organ with distal tube enclosing eversible cirrus*: **(0)** absent; **(1)** present (e.g., Domingues & Boeger 2003: fig. 2; Justine 2005a: figs. 3A–D, 4B, 5K, 7A, 11A, 12C; Yang *et al.* 2006: figs. 4–5, 12, 19–20; Justine & Euzet 2006: figs. 1B, 2G, 3B, 4J, 5D, 8C) [63].
- (22)*Quadriloculate male copulatory organ*: **(0)** absent; **(1)** present (e.g. Justine 2005a: figs. 3A–D, 4B, 5K, 7A, 11A, 12C) [68].
- (23)*Muscular ridges associated with the base of the male copulatory organ*: **(0)** absent; **(1)** present (e.g., Yang *et al.* 2006: figs. 4–5, 12, 19–20; Justine & Euzet 2006: figs. 1B, 2G, 3B, 4J, 5D, 8C) [64, 70].
- (24)*Spines associated with the distal portion of the copulatory organ*: **(0)** absent; **(1)** present (e.g., Justine & Euzet 2006: figs. 1B, 2G, 3B, 4J, 5D, 8C) [71].
- (25)*Accessory piece*: **(0)** present; **(1)** absent [20, 35].
- (26)*Accessory piece (when present)*: **(0)** single ramus; **(1)** “Y” shape [13].
- (27)*Accessory piece*: **(0)** articulated with male copulatory organ [23]; **(1)** non-articulated with the male copulatory organ [3]. This character is polymorphic for *Calydiscooides*. Oliver (1984, 1987) considered that species of *Calydiscooides* are characterized by presenting articulation between the male copulatory organ and the accessory piece. However, Kritsky *et al.* (2000) observed that there is no connection between these two structures in *Calydiscooides flexuosus*. We also detect the absence of this connection in the analysis of museum specimens of *Calydiscooides difficilis*. For *Calydiscooides*, we consider the non-articulated accessory piece with the male copulatory organ the plesiomorphic condition for this character, defined by the relationships of *Calydiscooides* with its respective sister groups.

(28) *Genital pore opening*: (0) anterior to the male copulatory organ [50, 59]; (1) posterior to the male copulatory organ [4, 27].

(29) *Sexual appendix*. (0) absent; (1) present (e.g., Bychowsky & Nagibina 1976: fig. 1) [21].

(30) *Egg shape*: (0) ovate; (1) tetrahedral [16]. Oliver (1987) characterized tetrahedral egg by the presence of a polar filament and an operculum located in two different apices, not opposed, determining the axis of symmetry of the egg. The polar filament located in opposite position to the operculum characterizes the ovate egg. It was not possible to establish the state of this character for *Nasobranchitrema*, *Telegamatrix*, *Pseudodiplectanum*, *Rhamnocercoides* and *Anoplectanum* for lack of information in the literature and absence of eggs in the examined specimens of museums.

(31) *Vagina*: (0) dextral [22]; (1) sinistral [5].

(32) *Vaginal atrium*: (0) sclerotized [47, 51, 56, 61, 66]; (1) muscular [6, 17, 25, 33].

(33) *Vaginal aperture*: (0) marginal [38]; (1) medial [29, 65].

(34) *Genital atrium*: (0) muscular; (1) sclerotized [40].

(35) *Prostatic reservoir*: (0) uniform; (1) separated into three zones (fig. 6) [43]. Oliver (1968) described in details the prostatic reservoir for *Diplectanum aequans*, recognizing two prostatic reservoirs (anterior and posterior). However, in the present paper, only the anterior prostatic reservoir is homologous to the prostatic reservoir of other monogenoideans, based on the position and association with the male copulatory organ. The posterior prostatic reservoir will be discussed further (character 36). Oliver (1968) observed, for *D. aequans*, the presence of a prostatic reservoir (anterior prostatic *sensu* Oliver 1968) separated into three zones: two terminal areas (located in the extremities of the reservoir), densely stained with carmine and a medium narrow area that does not stain with carmine.

(36) *Accessory copulatory organ*: (0) absent; (1) present (fig. 6) [44]. Oliver (1968) reported the presence of a glandular structure with a sclerotized canal, posterior to the anterior prostatic reservoir (*sensu* Oliver 1968) for *D. aequans* and other species. This author named this structure as “posterior prostatic reservoir”. However, study of species of *D. aequans* and *D. sciaenae* did not detect any connection between this structure and the male copulatory organ, rejecting the hypothesis of homology with the prostatic reservoir. Bychowsky and Nagibina (1977) described a structure associated with genital pore and the male copulatory organ of species of *Lobotrema* and *Murraytrema*, which they named “pear-shape” organ. These authors observed that this structure projects outside of the body through the genital pore, suggesting that it has some function in the copulation of these parasites. We propose abandoning the term “posterior prostatic reservoir” (Oliver 1968; Oliver 1980a; Oliver 1984; Obiekiezie 1988; Williams 1989; Santos *et al.* 2002) due to the erroneous homologization with the true prostatic reservoir. Alternatively, the name “accessory copulatory organ” is suggested here for this structure, because it denotes its most probable function.

Phylogenetic analysis

The phylogenetic hypothesis depicted in figure 7 is one of two most parsimonious trees produced through the program T.N.T. 1.0 using 36 characters (length = 71; C.I. = 57%; R.I. = 76%). In this analysis, the monophyly of the Diplectanidae is supported by three synapomorphies: (1) ventral bar with longitudinal groove; (2) reduced superficial root of the dorsal anchor; (3) absence of articulation of the male copulatory organ with the accessory piece.

Previous hypothesis (Oliver 1987; Desdevises *et al.* 2001) supported the subdivision of Diplectanidae in Rhabdosynochinae, Lamellodiscinae and Diplectaninae. In the present analysis, however, Lamellodiscinae is the only subfamily recognized as monophyletic, supported by two synapomorphies (both with 100% consistency): (1) presence of lamellodiscs and (2) “Y” shaped accessory piece.

The sister group relationships within the Lamellodiscinae presented in the figure 7 differs from the relationship of the other equally parsimonious tree by the relative position of *Lamellodiscus furcillattus*, *Telegamatrix*, *Lamellodiscus mormyri*, and *Furnestinia*. This variation is related apparently to the characters

“accessory piece articulated with the MCO”, “type of the intermediate lamellae of the lamellogdiscs”, and to the presence of missing data (?). In one tree (fig. 7), the character state “incomplete intermediate lamellae of the lamellogdiscs” appear as synapomorphies uniting *Lamellodiscus furcillatus*, *Telegamatrix* and clade “G” assuming the independent origin of the superficially incomplete intermediate lamellae of the lamellogdiscs, partially fused at midline in *Lamellodiscus furcillatus*. In the other tree, the character states “accessory piece articulated with the MCO” and “intermediate lamellae of the lamellogdiscs incomplete” appear as synapomorphies uniting *Telegamatrix*, *Lamellodiscus mormyri*, and *Furnestinia*.

Desdevises (2001) evaluated the taxonomic status of *Furnestinia* and *Lamellodiscus* based of 18S rDNA, concluding on the paraphyly of *Lamellodiscus* and suggesting that these two genera should be synonymized. The present analysis, based on morphological features, corroborates Desdevises (2001)’s hypothesis and the synonymy of *Lamellodiscus* and *Furnestinia* is discussed in the taxonomic section.

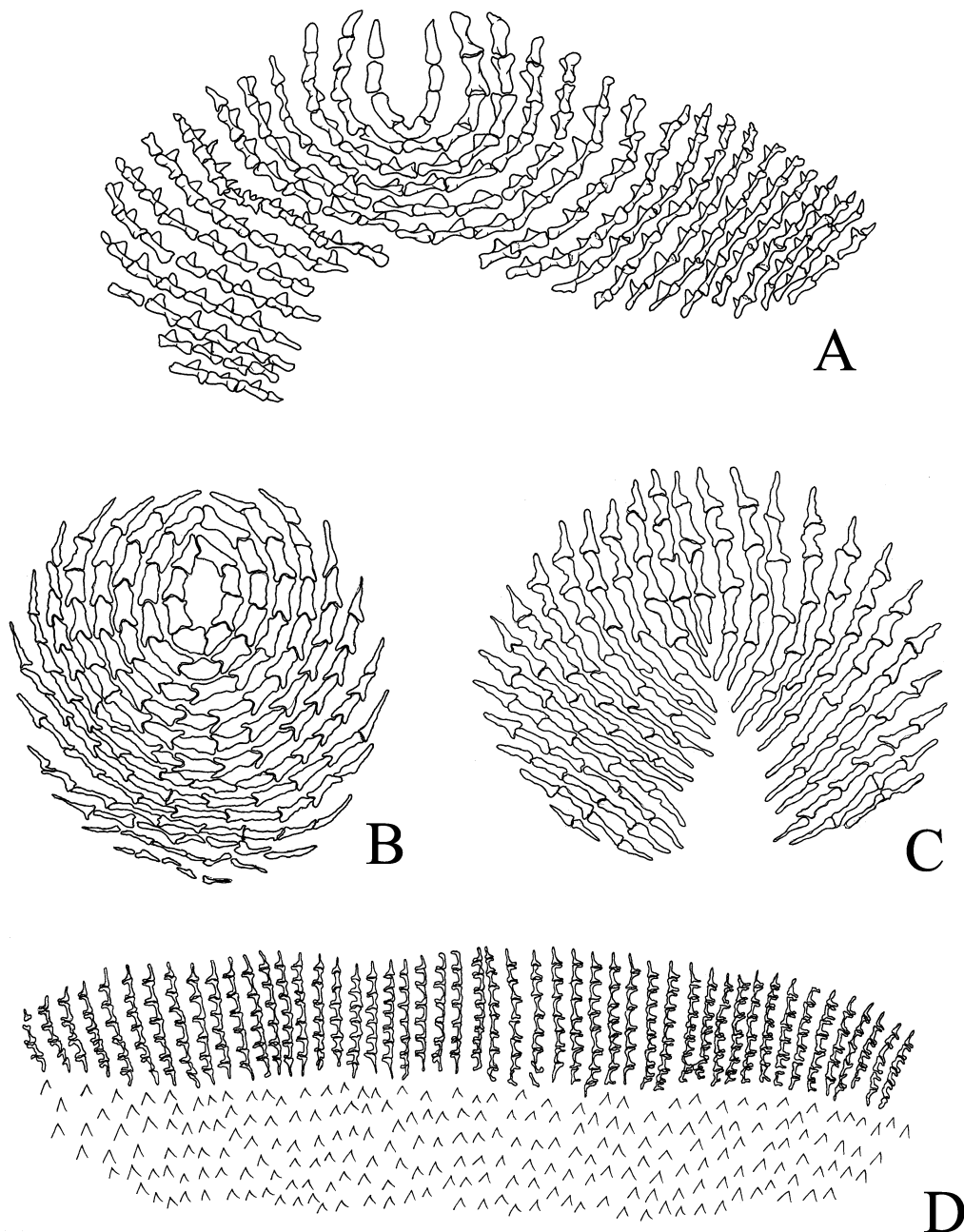


FIGURE 2. Basic types of squamodiscs. **A.** Anterior rows of the rodlet with open rings. **B.** Anterior rows of the rodlet with closed rings. **C.** Anterior rows of the rodlet with divergent rows. **D.** Anterior rows of the rodlet with parallel rows.

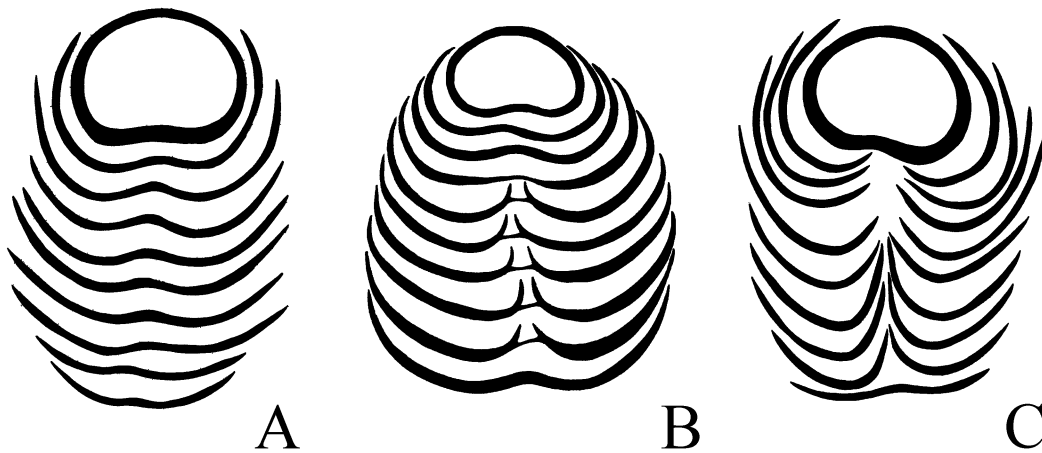


FIGURE 3. Basic types of lamellocdiscs. **A.** Intermediate lamellae fused at midline. **B.** Intermediate lamellae superficially incomplete, partially fused at midline. **C.** Intermediate lamellae incomplete, free at midline.

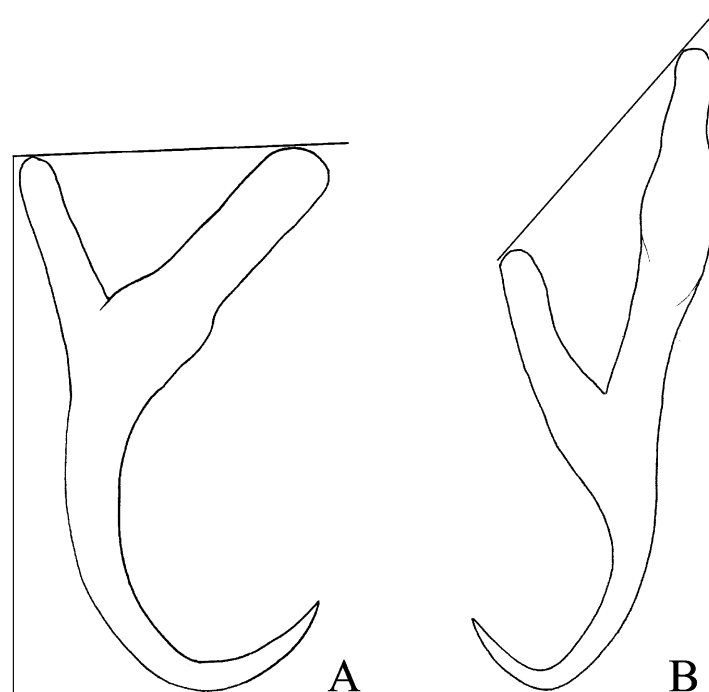


FIGURE 4. Basic types of ventral anchors. **A.** Ventral anchor with developed superficial root. **B.** Ventral anchor with reduced superficial root.

Our hypothesis differs significantly from that proposed by Oliver (1987) and Desdevises *et al.* (2001) on the sister group relationship within the Diplectaninae. While genera traditionally included in this subfamily are supported by the analysis (fig. 7), Rhamnoscercinae, Rhabdosynochinae, *Murraytrematoides ditrematis* and *Murraytrematoides lateolabracis* appear within Diplectaninae (clade “H”). The relationships among some terminal taxa of this subfamily are not completely resolved, as clade “O”, composed by *Pseudolamellodiscus* + *Acleotrema* + clade “P” + clade “R” + clade “U”.

Monophyly of *Diplectanum* is rejected in all equally parsimonious trees. *Diplectanum sillagonum* is basal within the subfamily (clade “H”), while *D. cazauxi* appears as sister group of *Latericaecum* (clade “N”); *D. aequans* represents a sister group of *Lobotrema* + *Murraytrema* (clade “P”); *D. priacanthi* appears in the polytomy of clade “U”; and *D. monticellii* is sister group of *Pseudorhabdosynochus* + *Echinoplectanum* (clade “Y”).

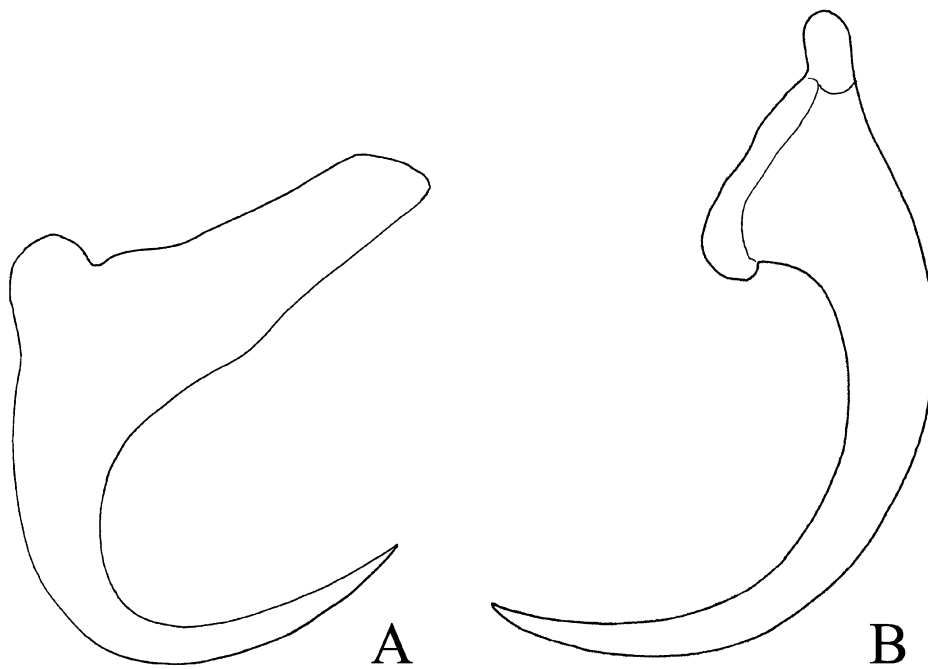


FIGURE 5. Basic types of dorsal anchors. **A.** Dorsal anchor with developed superficial root. **B.** Dorsal anchor with reduced superficial root.

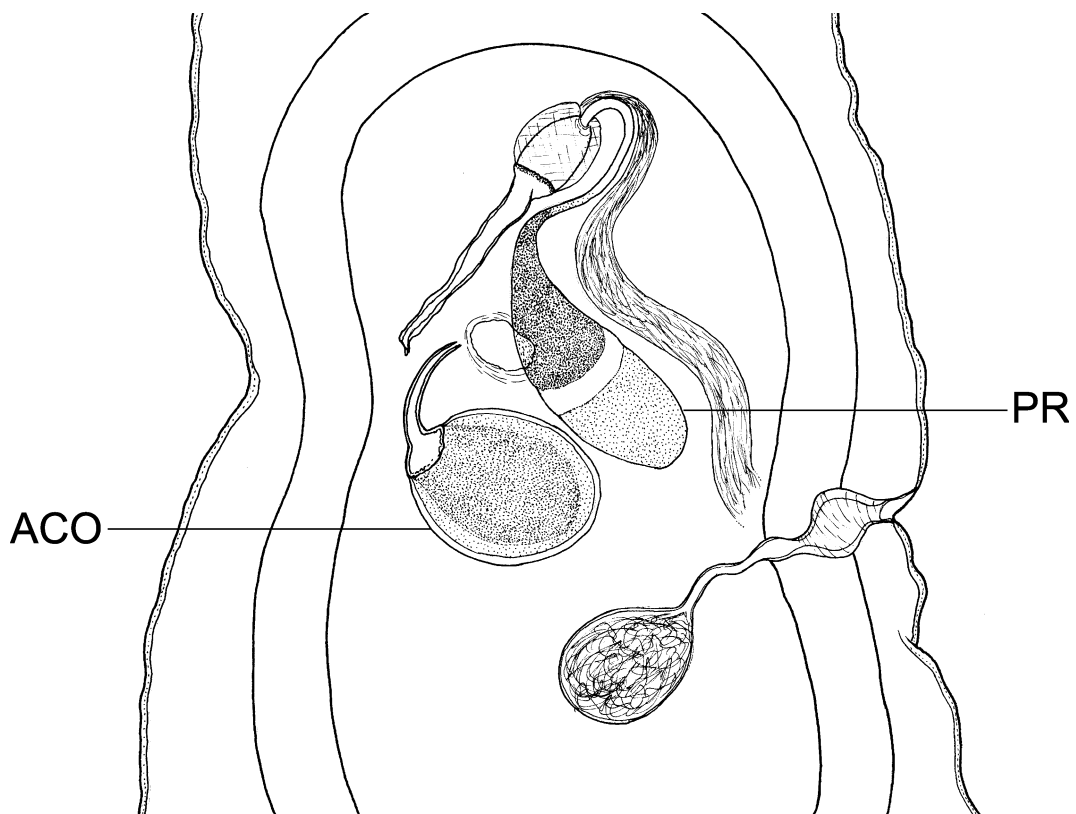


FIGURE 6. Detail of the some reproductive structures of *Diplectanum dollfusi* Oliver, 1980. ACO = accessory copulatory organ; PR = prostatic reservoir.

The phylogenetic hypothesis indicates that the Murraytremaoidea contains both para- and polyphyletic components, as already suggested by Desdevises *et al.* (2001). The polyphyletic status of the subfamily reflects the position of *Lobotrema* + *Murraytrema* as sister group of *Diplectanum aequans* in clade “P” and

the isolated position of species of *Murraytrematoides*. All equally parsimonious trees reject the monophyly of *Murraytrematoides*. *Murraytrematoides pricei* originated early in the evolution of Diplectanidae while *M. diatrematis* and *M. lateolabracis* are more apical, comprising a polytomy with *Anoplectanum* in clade “V”.

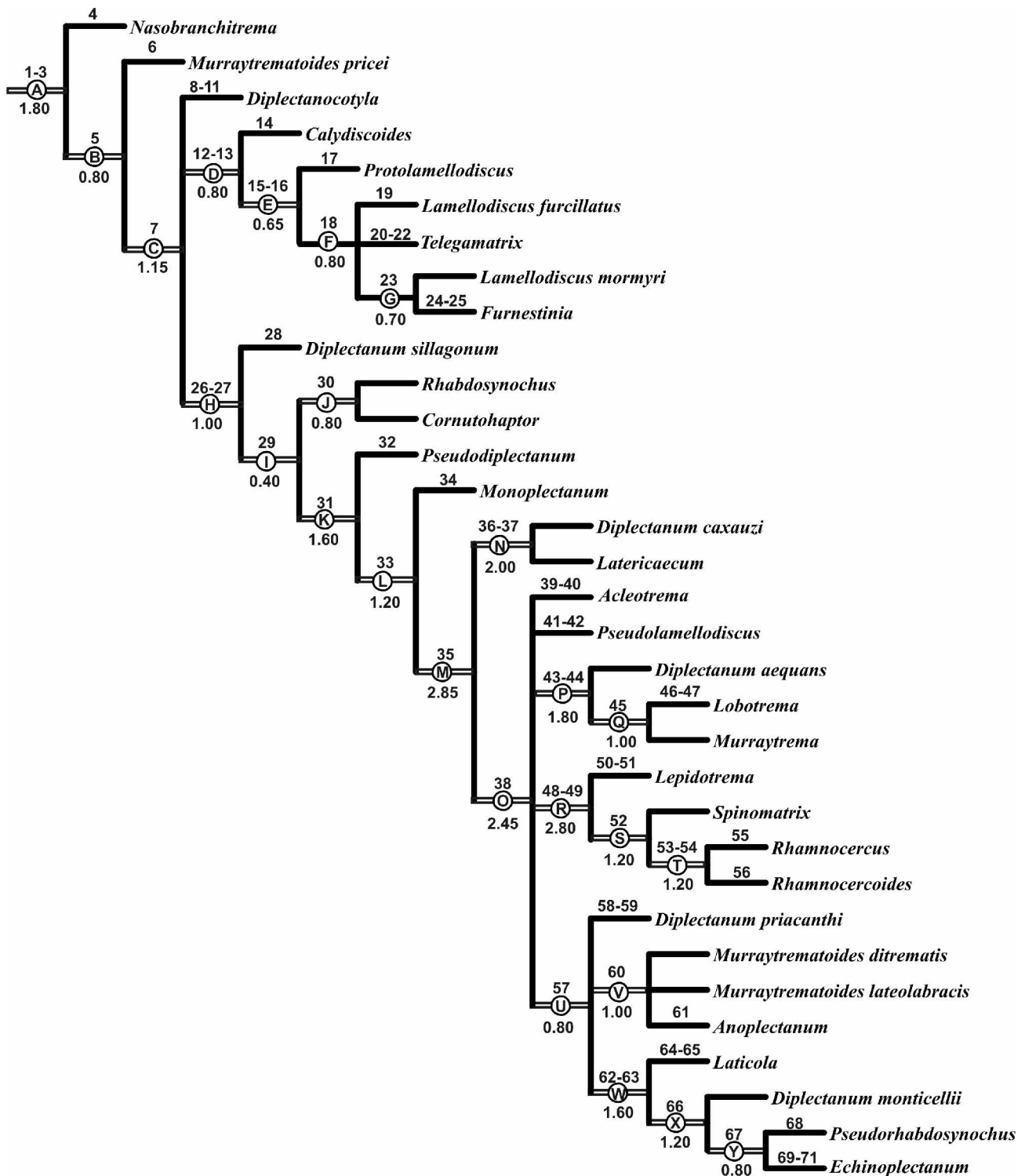


FIGURE 7. Phylogenetic hypothesis based on morphologic data (36 characters) for genera of Diplectanidae and selected species of *Diplectanum*, *Lamellodiscus* and *Murraytrematoides* for monophyly test of *Diplectanum*, *Lamellodiscus* and *Murraytrematoides*, respectively (length = 71; C.I. = 57%; R.I. = 76%). Numbers above respective branches refer to postulated evolutionary changes in character states indicated in the character analysis. Supported branches from strict consensus of the two equally parsimonious trees are indicated by double lines. Numbers below branches indicate respective Bremer supports.

TABLE 1. Matrix of characters used in the cladistic analysis for the Diplectanidae. The sequence of characters follows that in the Character Analysis; (–) represents an inapplicable state; (?) represents an unknown state.

Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36			
<i>Euryhaliotrema</i>	0	–	–	–	–	–	–	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Pseudomurraytrema</i>	0	–	–	–	–	–	–	0	0	0	2	0	0	0	0	–	–	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Nasobranchitrema</i>	0	–	–	–	–	–	–	0	0	0	2	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	?	0	0	0	0	0	0		
<i>Murraytrematoides pricei</i>	0	–	–	–	–	–	–	0	0	0	2	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	
<i>Diplectanocotyla</i>	1	0	0	0	0*	–	–	1	0	0	3	0	0	0	0	0	1	?	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	
<i>Calydiscoides</i>	1	1	0	–	–	0	1	0	0	0	2	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1*	0	0	0	1	0	0	0	0	0	0	
<i>Protolamellodiscus</i>	1	1	0	–	–	0	0*	0	0	0	2	1	0	0	0	1*	1	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1	0	0	0	0	0	0	
<i>Lamellodiscus furcillatus</i>	1	1	0	–	–	1	0	0	0	0	2	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1	0	0	0	0	0	0	
<i>Telegamatrix</i>	1	1	0	–	–	2	0	0	0	0	2	1	0	0	0	1	1	?	0	0	–	0	0	0	0	1	–	–	–	1	?	0	0	0	0	0	?		
<i>Lamellodiscus mormyri</i>	1	1	0	–	–	2	0	0	0	0	2	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	
<i>Furnestinia</i>	1	1	1	–	–	2	0	0	0	0	2	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	
<i>Diplectanum sillagonum</i>	1	0	0	0	1	–	–	0	0	0	2	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0
<i>Rhabdosynochus</i>	0	–	–	–	–	–	–	0	0	0	2	1	0	0	0	1*	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	1	0	0	?	
<i>Cornutohaptor</i>	0	–	–	–	–	–	–	0	0	0	2	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	1	0	0	0	
<i>Pseudodiplectanum</i>	1	0	0	0	–	–	–	0	0	0	2	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	1	1	0	?	1	0	1	0	0	0	0	
<i>Monoplectanum</i>	1	0	1	0	0	–	–	0	0	0	2	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1	?	0	0	0	0	
<i>Diplectanum caxauzi</i>	1	0	0	1	1	–	–	0	0	0	2	1	0	0	0	1	1	1	0	0	0	0	0	0	0	1	–	–	1	0	0	1	1	0	0	0	0	0	
<i>Latericaecum</i>	1	0	0	1	1	–	–	0	0	0	2	1	0	0	0	1	1	1	0	0	0	0	0	0	0	1	–	–	1	0	0	1	1	0	0	0	0	0	
<i>Acleotrema</i>	1	0	2	0	–	–	–	0	0	0	2	1	0	0	0	1	1	1	0	0	0	0	0	0	0	1	–	–	1	0	0	1	1	0	1	0	0	0	
<i>Pseudolamellodiscus</i>	1	0	0	3	0	–	–	0	0	0	2	1	1	0	0	1	1	1	0	0	0	0	0	0	0	1	–	–	1	0	0	1	1	0	0	0	0	0	
<i>Diplectanum aequans</i>	1	0	0	0	–	–	–	0	0	0	2	1	0	0	0	1	1	1	0	0	0	0	0	0	0	1	–	–	1	0	0	1	1	0	0	1	0	1	

Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
<i>Lobotrema</i>	0	--	--	--	--	--	0	0	0	1	--	--	--	0	1	1	1	1	0	0	0	0	0	0	1	--	--	1	0	0	1	0	0	0	1	1
<i>Murraytrema</i>	0	--	--	--	--	--	0	0	0	2	1	0	0	0	1	1	1	1	0	0	0	0	0	0	1	--	--	1	0	0	1	1	0	0	1	1
<i>Lepidotrema</i>	1	0	0	0	--	0	1	0	2	1	0	0	0	0	1	1	1	1	1	0	0	0	0	0	1	--	--	0	0	0	1	0	0	0	0	0
<i>Spinomatrix</i>	1	0	0	0	--	0	1	2	1	2	1	0	0	0	1	1	1	1	1	0	0	0	0	0	1	--	--	1	0	0	1	1	0	0	0	0
<i>Rhamnocercus</i>	0	--	--	--	--	--	0	1	1	2	1	0	1	0	1	1	1	1	0	0	0	0	0	0	1	--	--	1	0	0	1	1	0	0	0	0
<i>Rhamnocercoides</i>	0	--	--	--	--	--	0	1	1	2	1	0	1	0	1	1	1	1	1	0	0	0	0	0	1	--	--	1	0	?	1	0	0	0	0	
<i>Diplectanum priacanthi</i>	1	0	0	1	0	--	0	0	2	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1	--	--	0	0	0	1	1	0	0	0	0
<i>Murraytrema ditrematis</i>	0	--	--	--	--	--	0	0	2	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1	--	--	1	0	0	1	1	0	0	0	0
<i>Murraytrema laticolae</i>	0	--	--	--	--	--	0	0	2	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1	--	--	1	0	0	1	1	0	0	0	0
<i>Anoplectanum</i>	0	--	--	--	--	--	0	0	2	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1	--	--	1	0	?	1	0	0	0	0	0
<i>Diplectanum monticellii</i>	1	0	0	0	--	0	0	2	1	0	0	0	0	0	0	1	1	1	0	1	1	0	0	0	1	--	--	1	0	0	1	0	0	0	0	0
<i>Pseudorhabdosynochus</i>	1	0	0	1*	0	--	0	0	2	1	0	0	0	0	0	1	1	1	0	1	1	1	0	0	1	--	--	1	0	0	1	0	0	0	0	0
<i>Echinoplectanum</i>	1	0	0	1	0	--	0	0	2	1	0	0	0	0	0	1	1	1	0	1	1	0	1	1	1	--	--	1	0	0	1	0	0	0	0	0
<i>Laticola</i>	1	0	0	0	--	0	0	2	1	0	0	0	0	0	0	1	1	1	0	1	1	0	1	0	1	--	--	1	0	0	1	1	0	0	0	0

*The plesiomorphic condition for the indicated characters were predicted by the relationships of these taxa with their respective sister groups according Kornet and Turner (1999).

Taxonomic section

The revised classification of Diplectanidae is coordinated according Wiley (1981) and Amorim (1997). Diagnoses include traditional and cladistic information. Plesiomorphic characters are in bold in the diagnoses as well as, autapomorphic characters for subfamilies and genera. Numbers in brackets refer to the position of the characters in the tree (fig. 7). Taxa that appear in polytomy are treated as *sedis mutabilis* in a same taxonomic level. The terminal taxa of *Diplectanum* and *Lamellodiscus* that appear as independent taxa in the present analysis are treated as *incertae sedis*.

Family Diplectanidae Monticelli, 1903

Subfamily *Nasobranchitreminae*, **n. subfam.**

Nasobranchitrema Yamaguti, 1965

Subfamily *Pseudomurraytrematoidinae*, **n. subfam.**

Pseudomurraytrematoides, **n. gen.**

Diplectanocotyla Yamaguti, 1953, *sedis mutabilis*

Subfamily *Lamellodiscinae* Oliver, 1969, *sedis mutabilis*

Calydiscoides Young, 1969

Protolamellodiscus Oliver, 1969

Lamellodiscus furcillatus Kritsky, Jiménez-Ruiz & Sey, 2000 *incertae sedis*

Telegamatrix Ramalingam, 1955 *incertae sedis*

Lamellodiscus mormyri Euzet & Oliver, 1967 *incertae sedis*

Furnestinia Euzet & Audouin, 1959 *incertae sedis*

Subfamily *Diplectaninae* Monticelli, 1903, *sedis mutabilis*

Paradiplectanum, **n. gen.**

Rhabdosynochus Mizelle & Blatz, 1941

Pseudodiplectanum Tripathi, 1957

Monoplectanum Young, 1969

Latericaecum cazauxi +

Latericaecum cazauxi (Oliver & Paperna, 1984) comb. n.

Latericaecum Young, 1969

Pseudolamellodiscus +, *sedis mutabilis*

Pseudolamellodiscus Yamaguti, 1953, *sedis mutabilis*

Acleotrema Johnston & Tiegs, 1922, *sedis mutabilis*

Diplectanum aequans +, *sedis mutabilis*

Diplectanum aequans (Wagener, 1857) Diesing, 1858

Lobotrema Tripathi, 1959

Murraytrema Price, 1937

Lepidotrema +, *sedis mutabilis*

Lepidotrema Johnston & Tiegs, 1922

Spinomatrix Boeger, Fehlaue & Marques, 2006

Rhamnocercus Monaco, Wood & Mizelle, 1954

Rhamnocercoides Luque & Iannaccone, 1991

Oliveriplectanum **n. gen.** +, *sedis mutabilis*

Oliveriplectanum **n. gen.**, *sedis mutabilis*

Murraytrematoides ditrematis +, *sedis mutabilis*

Murraytrematoides ditrematis Yamaguti, 1958, *sedis mutabilis*

Murraytrematoides lateolabracis (Yamaguti, 1958) Oliver, 1987, *sedis mutabilis*

Anoplectanum Boeger, Fehlaue & Marques, 2006, *sedis mutabilis*
Laticola+, *sedis mutabilis*
Laticola Yang, Kritsky, Sun, Jianying, Suhua & Agrawal, 2006
Pseudorhabdosynochus Yamaguti, 1958
Echinoplectanum Justine & Euzet, 2006

Diplectanidae Monticelli, 1903

Diagnosis: Body fusiform, comprising cephalic region, trunk, peduncle, haptor. Tegument smooth or scaled. Cephalic glands unicellular, lateral or posterolateral to pharynx. Eyes present or absent. Mouth subterminal, midventral. Pharynx muscular, glandular. Intestinal caeca 2, non-confluent posteriorly, usually lacking diverticula (exceptionally present in *Latericaecum pearsoni* Young, 1969). Genital pore midventral near level of caecal bifurcation (exceptionally modified in *Telegamatrix*). Genital atrium muscular or sclerotized. One testis, postgermarian. Male copulatory organ sclerotized; accessory piece present or absent. **Articulation of the male copulatory organ with the accessory piece (when accessory piece present) absent [3]** or present. Vas deferens intercaecal or looping left intestinal caecum. Seminal vesicle an expansion of vas deferens. Germarium saccate, looping right intestinal caecum. Vagina sclerotized or muscular; sinistral or dextral. Seminal receptacle saccate. Egg operculate with polar filament, ovate or tetrahedral. Haptor usually with 3 (1 midventral, 2 laterodorsal) and exceptionally with 2 (*Lobotrema*) or 4 haptoral bars (*Diplectanocotyla*); 14 hooks (8 marginal, 2 central, 4 dorsal); 2 pairs of anchors (1 ventral, 1 dorsal); accessory adhesive organ (squamodiscs, lamellodiscs) present or absent. **Ventral bar with longitudinal groove [1]**. Superficial root of ventral anchor well defined or reduced. **Dorsal anchor with reduced superficial root [2]**. Parasites of marine and freshwater actinopterygians.

Nasobranchitrematinae n. subfam.

Diagnosis: The subfamily is monotypic. Tegument smooth. Eyes present (2 pairs). **Genital pore opening posterior to male copulatory organ (MCO) [4]**. Genital atrium muscular. Vas deferens intercaecal. MCO tubular, simple. Accessory piece present, lacking articulation with MCO. Prostatic reservoir simple. Vagina dextral; vaginal atrium sclerotized. Accessory adhesive organ absent. Superficial root of ventral anchor conspicuous. Parasites of marine fishes (Acanthuridae, Perciformes).

Type genus: *Nasobranchitrema* Yamaguti, 1965

Nasobranchitrema Yamaguti, 1965

Diagnosis: With the characteristics of the subfamily.

Type species: *Nasobranchitrema pacificum* Yamaguti, 1965 from *Naso hexacanthus* (Bleeker) (type host), *Naso lituratus* (Forster), *Naso brevirostris* (Cuvier), and *Naso annulatus* (Quoy & Gaimard) (Acanthuridae).

Remarks: Young (1969) transferred *Nasobranchitrema* from Diplectanidae to Ancyrocephalinae (Dactylogyridae) based on the apparent intercaecal germarium. However, studied specimens clearly show germarium looping right of intestinal caecum. This characteristic is apparently symplesiomorphic for Diplectanidae (see Kritsky & Boeger 1989) and, thus, it does not support Young (1969)'s proposal.

Pseudomurraytrematoidinae n. subfam.

Diagnosis: The subfamily is monotypic. Tegument smooth. Eyes present (2 pairs). Genital pore opening anterior to male copulatory organ (MCO). Genital atrium muscular. Vas deferens looping left intestinal caecum. MCO tubular, simple. Accessory piece present, lacking articulation with MCO. Prostatic reservoir simple. **Vagina sinistral [5]. Genital atrium muscular [6].** Egg ovate. Accessory adhesive organ absent. Superficial root of ventral anchor developed. Parasites of marine fishes (Muraenesocidae, Anguiliformes).

Type genus: *Pseudomurraytrematoides* n. gen.

***Pseudomurraytrematoides* n. gen.**

Synonymy: *Murraytrematoides* Yamaguti, 1963, *partim*.

Diagnosis: With the characteristics of the subfamily.

Type species: *Pseudomurraytrematoides pricei* (Caballero, Bravo-Hollis & Grocott, 1955) n. comb. from *Cynoponticus coniceps* (Jordan & Gilbert) (Muraenesocidae).

Remarks: From the five species of *Murraytrematoides* recognized by Oliver (1987), only *M. ditrematis* (type species), *M. lateolabracis* and *M. pricei* were available for study. The comparative analysis of the reproductive structures and the cladistic analysis suggest that the studied specimens are not congeneric. *Murraytrematoides pricei* shows a simple male copulatory organ (MCO), accessory piece, and genital pore opening posterior to MCO. *Murraytrematoides ditrematis* and *M. lateolabracis* have MCO formed by nested tubes, genital pore opening anterior to the MCO, and the absence of accessory piece. In the cladistic analysis, *M. pricei* appears as basal within Diplectanidae, sister group of clade “C”, while *M. ditrematis* and *M. lateolabracis* appear in a polytomy with *Anoplectanum* (clade “V”). Thus, we propose to accommodate *M. pricei*, as *Pseudomurraytrematoides pricei* n. comb., a member of the new subfamily. The generic name is from Greek (pseud/o = false) and refers to the fact that members of this genus are not congeneric with *Murraytrematoides*, as presented herein.

Diplectanocotyla* Yamaguti, 1953 *sedis mutabilis

Diagnosis: Tegument scaled. Eyes present (2 pairs). Genital pore opening anterior to male copulatory organ (MCO). Genital atrium muscular. Vas deferens looping left intestinal caecum. MCO tubular, simple. Accessory piece present, lacking articulation with MCO. Prostatic reservoir simple. Vagina dextral; vaginal atrium sclerotized. Egg unknown. **Accessory adhesive organ present [7]**, ventral, dorsal squamodiscs; anterior rows of rodlets with open rings. **Peduncular spines [9]**. Superficial root of ventral anchor conspicuous. **Ventral and dorsal haptor suckers, [8]. Two ventral bars [10] each with longitudinal groove [11]**. Parasites of marine fishes (Megalopidae: Elopiformes).

Type species: *D. gracilis* Yamaguti, 1953 from *Megalops cyprinoides* (Broussonet) (Megalopidae)

Other species: *D. langkawiensis* Lim & Gibson, 2007 from *Megalops cyprinoides*; *D. megalopis* Rakotofiringa & Oliver, 1987 from *Megalops atlanticus* Valenciennes, *Megalops cyprinoides*; *D. parva* Lim & Gibson, 2007 from *Megalops cyprinoides*.

Remarks: Rakotofiringa and Oliver (1987) proposed Diplectanocotylidae Rakotofiringa & Oliver, 1987 to allocate *Diplectanocotyla* based on the presence of haptor suckers and four haptor bars (2 ventral, 2 dorsal). However, Mendoza-Franco *et al.* (2004) rejected Diplectanocotylidae returning *Diplectanocotyla* to Diplectanidae as originally proposed by Yamaguti (1963), based on sharing features within Diplectanidae (e.g. germarium looping right of intestinal caecum, accessory adhesive organ).

Lamellodiscinae Oliver, 1969

Diagnosis: Tegument smooth. Eyes present or absent. Genital pore opening anterior to male copulatory organ (MCO). Genital atrium muscular. Vas deferens intercaecal or looping left intestinal caecum. MCO tubular, simple or complex; accessory piece present or absent, when present “**Y**” shape [13]. Articulation of the male copulatory organ with the accessory piece (when accessory piece present) present or absent. Prostatic reservoir simple. Vagina muscular or sclerotized; sinistral. Egg ovate or tetrahedral. Accessory adhesive organ present, **lamellodisc** [12], one or two. Superficial root of ventral anchor developed or reduced. Parasites of marine and estuarine Perciformes (Centranchidae, Lethrinidae, Pomacanthidae, Serranidae, Sparidae) and marine Beloniformes (Hemiramphidae).

Type genus: *Lamellodiscus* Johnston & Tiegs, 1922

Calydiscoides Young, 1969

Synonymy: *Lamellospina* Karyakarte & Das, 1978

Diagnosis: Eyes present (2 pairs). Vas deferens intercaecal. MCO tubular, simple. Accessory piece present, articulated or non-articulated with MCO. Vaginal aperture marginal; vaginal atrium sclerotized. Egg ovate. Lamellodiscs ventral, dorsal; intermediate lamellae fused at midline. **Telescoping lamellae** [14]. Superficial root of ventral anchor developed. Parasites of marine perciform fishes (Lethrinidae, Nemipteridae).

Type species: *C. australis* Young, 1969 from *Lethrinus miniatus* (Forster) (type host), and *Lethrinus* sp. (Lethrinidae).

Other species: *C. conus* Lim, 2003 from *Scolopsis margaritifera* (Cuvier) (Nemipteridae); *C. cymbidoides* Ding & Zhang, 1996 from *Scolopsis taenioptera* (Cuvier); *C. difficilis* (Yamaguti, 1953) Young, 1969 from *Lethrinus harak* (Forsskål), *Lethrinus laticaudis* Alleyne & Macleay, *Lethrinus lentjan* (Lacépède), *Lethrinus miniatus*, *Lethrinus nebulosus* (Forsskål), *Lethrinus obsoletus* (Forsskål), *Lethrinus ravus* Carpenter & Randall, *Lethrinus reticulatus* Valenciennes, and *Lethrinus* sp.; *C. duplicostatus* (Yamaguti, 1953) Young, 1969 from *Lethrinus harak*, *Lethrinus lentjan*, *Lethrinus nebulosus*, and *Lethrinus* sp.; *C. euzeti* Justine, 2007a from *Lethrinus rubrioperculatus* Sato, and *Lethrinus xanthochilus* Klunzinger; *C. flexuosus* (Yamaguti, 1953) Young, 1969 from *Nemipterus bipunctatus* (Valenciennes) (Nemipteridae), *Nemipterus hexodon* (Quoy & Gaimard), *Nemipterus japonicus* (Bloch), and *Nemipterus peronii* (Valenciennes); *C. gussevi* Oliver, 1984 from *Lethrinus miniatus*; *C. indianus* (Karyakarte & Das, 1978) Oliver, 1987 from *Nemipterus japonicus*; *C. japonicus* (Pillai & Pillai, 1976) Thoney, 1989 from *Nemipterus japonicus*; *C. kemamanensis* Lim, 2003 from *Pentapodus setosus* (Valenciennes) (Nemipteridae); *C. monogrammae* Lim, 2003 from *Scolopsis monogramma* (Cuvier); *C. nemipteris* Thoney, 1989 from *Scolopsis temporalis* (Cuvier); *C. rohdei* Oliver, 1984 from *Lethrinus atkinsoni* Seale, and *Lethrinus mahsena* (Forsskål); *C. scolopsidis* Lim, 2003 from *Scolopsis margaritifera*, and *Scolopsis monogramma*; *C. terpsichore* Rascalou & Justine, 2007 from *Lethrinus harak*, and *Lethrinus nebulosus*.

Protolamellodiscus Oliver, 1969

Diagnosis: Eyes present (2 pairs). Vas deferens intercaecal or looping left intestinal caecum. MCO tubular, simple. Accessory piece present, lacking articulation with MCO. Vaginal aperture marginal. **Vaginal atrium muscular** [17]. **Egg tetrahedral** [16]. Lamellodiscs ventral, dorsal; intermediate lamellae fused at midline. Telescoping lamellae present or absent. **Superficial root of ventral anchor reduced** [15]. Parasites of marine perciform fishes (Lethrinidae, Nemipteridae, Serranidae and Sparidae).

Type-species: *P. serranelli* (Euzet & Oliver, 1965) Oliver, 1969 from *Serranus cabrilla* (Linnaeus) (Serranidae) (type host), *Serranus hepatus* (Linnaeus), and *Serranus scriba* (Linnaeus).

Other species: *P. convolutus* (Yamaguti, 1953) Oliver, 1987 from *Lethrinus obsoletus* (Lethrinidae), and *Nemipterus hexodon* (Quoy & Gayard) (Nemipteridae); *P. raibauti* Oliver & Radujkovic, 1987 from *Diplodus annularis* (Linnaeus) (Sparidae); *P. senlobatus* Kritsky, Jiménez-Ruiz & Sey, 2000 from *Argyrops filamentosus* (Valenciennes) (Sparidae), and *Argyrops spinifer* (Forsskål).

Remarks: Kritsky *et al.* (2000) suggested that *Protolamellodiscus* might be a synonym of *Calydiscoides*, since species of both genera possess intermediate lamellae of the lamellodisc fused at midline and by some species of *Protolamellodiscus* presenting telescoping lamellae. However, the present analysis does not support this synonymization, because *Protolamellodiscus* appears as a sister taxon of clade “F”, sharing the presence of tetrahedral egg [16].

Lamellodiscus Johnston & Tiegs, 1922

Diagnosis: Eyes present (2 pairs). Vas deferens intercaecal or looping left intestinal caecum. MCO tubular, simple. Accessory piece present, articulated or non-articulated with MCO. Vaginal aperture marginal. Vaginal atrium sclerotized. Egg tetrahedral. Ventral and dorsal Lamellodiscs; intermediate lamellae incomplete **partially fused [18]** or free at midline. Superficial root of ventral anchor reduced. Parasites of marine and estuarine perciform fishes (Centracanthidae, Pomacanthidae, Serranidae and Sparidae).

Type-species: *L. typicus* Johnston & Tiegs, 1922 from *Acanthopagrus australis* (Günther) (Sparidae).

Other species: *L. acanthopagri* Roubal, 1981 from *Acanthopagrus australis*; *L. baeri* Oliver, 1974 from *Pagrus pagrus* Linnaeus (Sparidae); *L. bidens* Euzet, 1984 from *Diplodus puntazzo* (Cetti) (Sparidae); *L. butcheri* Byrnes, 1987 from *Acanthopagrus australis*, and *Acanthopagrus butcheri* (Munro); *L. caballeroi* Venkatanarsaiah & Kulkarni, 1980 from *Crenidens crenidens* (Forsskål) (Sparidae); *L. cirruspiralis* Byrnes, 1987 from *Acanthopagrus berda* (Forsskål), and *Acanthopagrus latus* (Houttuyn); *L. corallinus* Paperna, 1965 from *Centropyge bispinosa* (Günther) (Pomacanthidae), and *Dascyllus marginatus* (Rüppell) (Sparidae); *L. coronatus* Euzet & Oliver, 1966 from *Diplodus cervinus cervinus* (Lowe); *L. dentexi* Aljoshkina, 1984 from *Dentex macrophthalmus* (Bloch) (Sparidae); *L. drummondi* Euzet & Oliver, 1967 from *Pagellus acarne* (Risso) (Sparidae); *L. elegans* Bychowsky, 1957 from *Acanthopagrus sivicolus* Akazaki, *Diplodus annularis* (Linnaeus), *Diplodus sargus cadenati* de la Paz, Bauchot & Daget, *Diplodus sargus sargus* (Linnaeus), *Diplodus vulgaris* (Geoffroy Saint-Hilaire), *Oblada melanura* (Linnaeus) (Sparidae), and *Spondyliosoma cantharus* (Linnaeus) (Sparidae); *L. epsilon* Yamaguti, 1968 from *Monotaxis* sp. (Lethrinidae); *L. ergensi* Euzet & Oliver, 1966 from *Diplodus annularis*, *Diplodus puntazzo*, *Diplodus sargus cadenati*, *Diplodus sargus sargus*, and *Diplodus vulgaris*; *L. erythrini* Euzet & Oliver, 1967 from *Pagellus erythrinus* (Linnaeus); *L. fraternus* Bychowsky, 1957 from *Diplodus annularis*, and *Diplodus vulgaris*; *L. furcillatus* Kritsky, Jiménez-Ruiz & Sey, 2000 from *Diplodus noct* (Valenciennes); *L. furcosus* Euzet & Oliver, 1966 from *Diplodus annularis*, *Diplodus sargus cadenati*, and *Diplodus sargus sargus*; *L. gracilis* Euzet & Oliver, 1966 from *Diplodus annularis*, *Diplodus sargus cadenati*, *Diplodus sargus sargus*, *Oblada melanura*, and *Spondyliosoma cantharus* (Linnaeus); *L. hilli* Euzet, 1984 from *Diplodus puntazzo*; *L. ignoratus* Palombi, 1943 from *Diplodus annularis*, *Diplodus puntazzo*, *Diplodus sargus cadenati*, *Diplodus sargus sargus*, *Diplodus vulgaris*, *Lithognathus mormyrus* (Linnaeus) (Sparidae), *Sarpa salpa* (Linnaeus) (Sparidae), and *Pagrus caeruleostictus* (Valenciennes); *L. impervius* Euzet, 1984 from *Diplodus puntazzo*; *L. indicus* Tripathi, 1957 from *Rhabdosargus sarba* (Forsskål) (Sparidae); *L. japonicus* Ogawa & Egusa, 1978 from *Acanthopagrus latus* (Houttuyn), and *Acanthopagrus schlegelii schlegelii* (Bleeker); *L. kechemirae* Amine & Euzet, 2005 from *Diplodus sargus sargus*; *L. knoepffleri* Oliver, 1969 from *Spondyliosoma cantharus*, *Spicara maena* (Linnaeus) (Centracanthidae), *Spicara smaris* (Linnaeus); *L. major* Murray, 1931 from *Acanthopagrus australis*, *Acanthopagrus berda*, *Acan-*

thopagrus butcheri, and *Acanthopagrus latus*; *L. mirandus* Euzet & Oliver, 1966 from *Diplodus sargus cadenati*; *L. mormyri* Euzet & Oliver, 1967 from *Lithognathus mormyrus*; *L. niedashui* Li, Yan, Liu & Yu, 1995 from *Acanthopagrus latus*; *L. obeliae* Oliver, 1973 from *Pagellus bogaraveo* (Brünnich); *L. pagrosomi* Murray, 1931 from *Acanthopagrus latus*, *Chrysophrys auratus*, *Epinephelus akaara* (Temminck & Schlegel) (Serranidae), *Epinephelus awoara* (Temminck & Schlegel), *Pagrus major* (Temminck & Schlegel), *Parargyrops edita* Tanaka, and *Sparus aurata* Linnaeus; *L. parisi* Oliver, 1969 from *Sarpa salpa*; *L. rastellus* Neifar, Euzet & Oliver, 2004 from *Pagrus auriga* Valenciennes; *L. sanfilippo* Amine, Neifar & Euzet, 2006 from *Diplodus sargus sargus*; *L. sarculus* Neifar, Euzet & Oliver, 2004 from *Pagrus coeruleostictus*; *L. sigillatus* Neifar, Euzet & Oliver, 2004 from *Pagrus coeruleostictus*; *L. spari* Zhukov, 1970 from *Acanthopagrus australis*, *Acanthopagrus berda*, *Acanthopagrus butcheri*, *Acanthopagrus latus*, and *Acanthopagrus schlegelii*; *L. squamosus* Roubal, 1981 from *Acanthopagrus australis*, *Acanthopagrus berda*, and *Acanthopagrus latus*; *L. takitai* Ogawa & Egusa, 1978 from *Acanthopagrus schlegelii*; *L. tomentosus* Amine & Euzet, 2005 from *Diplodus vulgaris*; *L. vaginalis* Byrnes, 1987 from *Acanthopagrus australis*, and *Acanthopagrus butcheri*; *L. verberis* Euzet & Oliver, 1967 from *Lithognathus mormyrus*; *L. virgula* Euzet & Oliver, 1967 from *Pagellus acarne*.

Remarks: Kritsky *et al.* (2000) questioned the monophyly of *Lamellodiscus* based on the variable morphology of the sclerotized structures, which may not represent generic features, as originally proposed by Oliver (1987). In the molecular phylogeny of Desdevises (2001), *Lamellodiscus* spp. appear in two distinct clades and *Furnestinia* represents an internal taxon closely related to *L. verberis* and *L. mormyri*.

Our cladistic hypothesis was not capable to identify synapomorphies for species of *Lamellodiscus*, as already suggested by Kritsky *et al.* (2000) and Desdevises (2001), and, thus, its monophyly is rejected. *Lamellodiscus furcillatus* shows the most basal position among the fragment of *Lamellodiscus* in the tricotomy with *Telegamatrix* and clade “G”, while *Lamellodiscus mormyri* and *Furnestinia* appear as a sister taxa in clade “G”, supported by the presence of the accessory piece articulated with the MCO.

Despite the non-monophyly of *Lamellodiscus*, we decided to retain all species in the genus, without proposal of new taxonomic categories until a cladistic analysis within *Lamellodiscus* species is performed.

***Telegamatrix* Ramalingam, 1955**

Diagnosis: Eyes present (2 pairs). Vas deferens not observed. MCO tubular, simple. **Accessory piece absent [20]. Vaginal aperture dextral [22]**, marginal. Vaginal atrium sclerotized. Egg tetrahedral. **Sexual appendix present [21]**. Ventral and dorsal lamellodiscs; intermediate lamellae incomplete, free at midline. Superficial root of ventral anchor reduced. Parasites of marine perciform (Leiognathidae) and clupeiform (Clupeidae) fishes.

Type-species: *T. pellona* Ramalingam, 1955 from *Ilisha melastoma* (Bloch & Schneider) (Clupeidae).

Other species: *T. elegans* Bychowsky & Nagibina, 1976 from *Gazza minuta* (Bloch), and *Secutor insidiator* (Bloch) (Leiognathidae); *T. grandis* Bychowsky & Nagibina, 1976 from *Gazza minuta*, and *Secutor insidiator*; *T. ramalingami* Bychowsky & Nagibina, 1976 from *Gazza minuta*, and *Secutor insidiator*.

***Furnestinia* Euzet & Audouin, 1959**

Synonymy: *Dactylogyrus* Wagener, 1857, *partim*, *nec* Diesing, 1858, *partim*

Diagnosis: Eyes present (2 pairs). Vas deferens intercaecal. Accessory piece present, **articulated with MCO [23]. Vaginal atrium muscular [25]**. Vaginal aperture marginal. Egg tetrahedral. Lamellodiscs (one), **ventral**

[24], intermediate lamellae of the lamellogdisc incomplete, free at midline. Superficial root of ventral anchor reduced. Parasites of marine perciform fishes (Sparidae).

Type-species: *Furnestinia echeneis* (Wagener, 1857) Euzet & Audouin, 1959 from *Sparus aurata*.

Remarks: The present hypothesis corroborates the conclusions of Desdevises (2001), in which *Lamello-discus mormyri* appears to be more closely related to *Furnestinia* than to other species of *Lamello-discus*. However, we decided for the maintenance of *Furnestinia* since any taxonomic proposal would be premature before the resolution of the taxa of clade “F”.

Diplectaninae Monticelli, 1903

Synonymy: Lepidotrematinae Johnston & Tiegs, 1922; Murraytrematoidinae Oliver, 1982 *partim*; Rhabdosynochinae Oliver, 1987; Rhamnocercinae Monaco, Wood & Mizelle, 1954

Diagnosis: Tegument smooth or scaled. Eyes present (2 pairs). Genital pore opening **posterior** [27] or anterior to male copulatory organ (MCO). Genital atrium muscular or sclerotized. Vas deferens intercaecal or looping left intestinal caecum. MCO tubular, simple or nested tubes; when nested tubes present, external tube uniform or twisted; accessory piece present or absent; non-articulated with MCO (when accessory piece present). Prostatic reservoir simple or separated into three zones. Accessory copulatory organ present or absent. Vagina muscular or sclerotized; sinistral. Egg ovate. Accessory adhesive organ, squamodiscs, present (one or two) or absent, rodlet dumbbell-shaped. Accessory spines associated with the posterior region of the haptor present or absent. Peduncular spines present or absent. Haptoral bars two or three. Posteromedial projection of the ventral bar present or absent. Superficial root of ventral anchor conspicuous or **reduced** [26]. Parasites of marine and freshwater Teleostei.

Remarks: Rhabdosynochinae and Rhamnocercinae have not received evolutionary support in the present analysis because both subfamilies appear as internal groups within Diplectaninae. *Rhabdosynochus*, originally included in Rhabdosynochinae, appears as sister group of *Cornutohaptor* (within clade “J”), while Rhamnocercinae appears as sister group of *Lepidotrema* (in clade “R”).

The cladistic analysis also indicates that Murraytrematoidinae, which includes *Murraytrema*, *Lobotrema* and *Murraytrematoides*, is polyphyletic. *Murraytrema* and *Lobotrema* (clade “Q”) appear within Diplectaninae as sister group of *Diplectanum aequans* in clade “P”, which is supported by the presence of accessory copulatory organ and prostatic reservoir separated into three zones. Additionally, *Murraytrematoides*, represented by *M. pricei*, *M. ditrematis*, and *M. lateolabracis*, does not constitute a natural group. *Murraytrematoides pricei* is basal, sister group of clade “C”, and *M. ditrematis* and *M. lateolabracis* appear in the tricotomy with *Anoplectanum* in clade “V”.

Two distinct options concerning Rhamnocercinae, Rhabdosynochinae, and Murraytrematoidinae are possible, based on the present analysis. The first option assumes Rhabdosynochinae, Rhamnocercinae, and Murraytrematoidinae as valid subfamilies. In this case, however, Diplectaninae would represent a paraphyletic group being necessary a proposal of new subfamilies for the different clades starting at clade “H”.

The second option, the one chosen in this study, is more conservative and includes recognition of Diplectaninae as a subfamily, including all groups in the cladogram originating at clade “H”. Rhabdosynochinae, Rhamnocercinae, and Murraytrematoidiane are rejected and considered junior synonyms of Diplectaninae.

Paradiplectanum n. gen.

Synonymy: *Diplectanum* Diesing, 1858, *partim*

Diagnosis: Tegument smooth. Genital pore opening posterior to male copulatory organ (MCO). Genital

atrium muscular. Vas deferens not observed. MCO tubular, simple; accessory piece present, non-articulated with the MCO. Prostatic reservoir simple. Accessory copulatory organ absent. Vaginal atrium sclerotized. Vaginal aperture marginal. Squamodiscs ventral, dorsal; anterior rows of rodlets with open rings; **intermediate rows of rodlets with anterior lightly sclerotized blunt spinelet [28]**. Superficial root of ventral anchor reduced. Parasites of marine perciform fishes (Sillaginidae).

Type-species: *Paradiplectanum sillagonum* (Tripathi, 1957) n. comb. from

Sillago attenuata McKay, *Sillago sihama* (Forsskål) (type host), and *Sillago vincenti* McKay.

Other species: *Paradiplectanum blairense* (Gupta & Khanna, 1974) n. comb.

from *Sillago indica* McKay, Dutt & Sujatha, *Sillago japonica* Temminck & Schlegel, and *Sillago sihama*.

Remarks: *Paradiplectanum* is clearly apart of the *Diplectanum* complex (see comments above and *Diplectanum* diagnosis). Including the fact that members of *Paradiplectanum* n. gen. are parasitic on the gills of sillaginid fishes, features distinguishing the genus include the combined presence of (1) squamodiscs (ventral, dorsal) with intermediate rows of rodlets with lightly sclerotized blunt spinelet; (2) MCO not articulated with the accessory piece; and (3) vaginal atrium sclerotized.

There are four other diplectanid species occurring on sillaginid hosts: *Diplectanum blairense* Gupta & Khanna, 1974, *D. puriense* Tripathi, 1957, *Monoplectanum australe* Young, 1969 and *M. youngi* Hayward, 1996. *Paradiplectanum* can be easily distinguished from *Monoplectanum* since species of the later genus possess a vaginal atrium muscular and a single ventral squamodisc. Comparison of *P. sillagonum* with *D. blairense* suggests that these species are congeneric. The transfer of *D. blairense* as a member of *Paradiplectanum* is based on voucher specimens in Hayward's (1996) redescription of this species (type material was not deposited by the senior authors). However, the illustration of the species clearly shows that Hayward (1996) confused the posterior prostatic reservoir with the accessory piece. *Diplectanum blairense* has all the diagnostic features attributed to *Paradiplectanum*. *Diplectanum puriense*, another parasite of a sillagid fish, does not represent a species of *Paradiplectanum* and can be distinguished from members of the new genus by having a male copulatory organ with nested tubes and lacking of accessory piece.

The generic epithet refers to the independent origin of members of this genus within Diplectaninae.

***Rhabdosynochus* Mizelle & Blatz, 1941**

Synonymy: *Cornutohaptor* Mendoza-Franco, Violante-González & Vidal Martínez, 2006

Diagnosis: Tegument scaled. Genital pore opening posterior to male copulatory organ (MCO). Genital atrium muscular. Vas deferens intercaecal or looping left intestinal caecum. MCO tubular, coiled; accessory piece present, complex. Prostatic reservoir simple. Accessory copulatory organ absent. Vaginal atrium sclerotized. **Vaginal aperture medial [29]**. **Accessory adhesive organ absent [30]**. Superficial root of ventral anchor reduced. Parasites of marine perciform fishes (Centropomidae).

Type-species: *R. rhabdosynochus* Mizelle & Blatz, 1941 from *Centropomus undecimalis* (Bloch).

Other species: *R. hargisi* Kritsky, Boeger & Robaldo, 2001 from *Centropomus undecimalis*; *R. hudsoni* Kritsky, Boeger & Robaldo, 2001 from *Centropomus undecimalis*; *R. nigrescens* (Mendoza-Franco, Violante-González & Vidal-Martínez, 2006) n. comb. from *Centropomus nigrescens* Günther.

Remarks: Oliver (1987) and Desdevises *et al.* (2001) considered *Rhabdosynochinae* a sister group of *Lamellodiscinae* and *Diplectaninae* based on the primarily homology of placodiscs and the other accessory adhesive organs (squamodiscs and lamellodiscs). However, Kritsky *et al.* (2001) suggest that these structures do not represent homologous features and considered that species of *Rhabdosynochus*, *Murraytrema* and *Murraytrematoides* share the character "absence of accessory adhesive organ".

Our analysis suggests that the accessory adhesive organ was secondarily lost several times in the evolutionary history of Diplectaninae (character changes 29, 43, 51, 58, in fig. 7), including in the clade formed by *Rhabdosynochus* + *Cornutohaptor*, supporting the non-homology of the placodiscs with the lamellodiscs and squamodiscs. The recognition of Rhabdonynochinae as a junior synonymy of Diplectaninae is supported by the opening of the common genital pore subsequent to MCO [27], and ventral anchor with reduced superficial root [26].

Cornutohaptor is monotypic and consistently emerged as the sister group of *Rhabdosynochus* in clade “J” by sharing the secondary loss of the accessory adhesive organ. *Cornutohaptor* has no autapomorphies, suggesting its single species is congeneric with species of *Rhabdosynochus*. Both genera share the same morphology of the copulatory complex (non-articulated, coiled MCO, complex accessory piece) and hosts (centropomid fishes). *Cornutohaptor nigrescensi* is, thus, transferred to *Rhabdosynochus* as *R. nigrescensi* n. comb.

***Pseudodiplectanum* Tripathi, 1957**

Diagnosis: Tegument smooth or scaled. Genital pore opening posterior to male copulatory organ (MCO). Genital atrium muscular. Vas deferens intercaecal. **MCO tubular, composed of nested tubes [31]**, twisted or sinuous; external tube uniform; accessory piece present (exceptionally absent on *P. caballeroi*). Prostatic reservoir simple. Accessory copulatory organ absent. Vaginal atrium sclerotized. Vaginal aperture medial. Squamodiscs ventral, dorsal; anterior rows of rodlets with open rings. **Ventral anchor probe shape [32]**. Parasites of marine teleostean fishes (Pleuronectiformes and Osteoglossiformes).

Type-species: *P. cynoglossum* Tripathi, 1957 from *Cynoglossus arel* (Bloch & Schneider) (type host), and *Cynoglossus bilineatus* (Lacépède) (Cynoglossidae).

Other species: *P. bychowskii* Nagibina, 1977 from *Cynoglossus bilineatus*; *P. caballeroi* Nagibina, 1977 from *Symphurus orientalis* (Bleeker) (Cynoglossidae); *P. gibsoni* (Oliver, 1980) Oliver, 1987 from *Microchirus variegatus* (Donovan) (Soleidae); *P. kearni* Vala, Lopez-Roman & Boudaoud, 1980 from *Solea solea* (Linnaeus); *P. lucknowensis* Agrawal & Sharma, 1986 from *Chitala chitala* (Hamilton) (Notopteridae, Osteoglossiformes); *P. syrticum* Derbel, Boudaya & Neifar, 2007 from *Synapturichthys kleinii* (Risso) (Soleidae).

Remarks: Oliver (1987) recognized two different morphological types of MCO in *Pseudodiplectanum*: (1) spiraled (*P. bychowskii*, *P. caballeroi*, *P. cynoglossum*) and (2) tubular with accessory piece (*P. gibsoni*, *P. kearni*). Except for *P. caballeroi*, all the other species present accessory piece. However, despite the fact that we could not confirm the presence of accessory piece in the unavailable specimens of *P. caballeroi*, we decided to retain all species in the genus, without proposal of new taxonomic rearrangement until information about this species be available.

***Monoplectanum* Young, 1969**

Diagnosis: Tegument smooth. Genital pore opening posterior to male copulatory organ (MCO). Genital atrium muscular. Vas deferens intercaecal. MCO tubular, composed of 2 nested tubes; external tube uniform. Accessory piece present. Prostatic reservoir simple. Accessory copulatory organ absent. **Vaginal atrium muscular [33]**. Vaginal aperture not observed. Squamodiscs **ventral [34]**; anterior rows of rodlets with open rings. Superficial root of ventral anchor reduced. Parasites of marine perciform fishes (Sillaginidae).

Type-species: *M. australe* Young, 1969 from *Sillago burrus* Richardson, and *Sillago ciliata* Cuvier (type host).

Other species: *M. youngi* Hayward, 1996 from *Sillago analis* Whitley.

Latericaecum Young, 1969

Diagnosis: Tegument smooth. Genital pore opening posterior to male copulatory organ (MCO). Genital atrium muscular. Vas deferens intercaecal. MCO tubular, composed of 2 nested tubes; external tube uniform. **Accessory piece absent [35]**. Prostatic reservoir simple. Accessory copulatory organ absent. Vaginal atrium muscular. Vaginal aperture medial. Squamodiscs ventral, dorsal; **anterior rows of rodlets with closed rings [36]; intermediate rows of rodlets with anterior lightly sclerotized blunt spinelet [37]**. Superficial root of ventral anchor reduced. Parasites of marine perciform fishes (Sphyraenidae).

Type-species: *L. pearsoni* Young, 1969 from *Sphyraena obtusata* Cuvier.

Other species: *L. cazauxi* (Oliver & Paperna, 1984) n. comb. from *Sphyraena flavicauda* Rüppel, *Sphyraena jello* Cuvier, and *Sphyraena obtusata*.

Remarks: Young (1969) reported 12 haptorial hooks and intestinal diverticulae for *Latericaecum pearsoni*. Our study of available specimens confirms the presence of 14 hooks, similar in distribution and morphology to the other diplectanids. However, the intestinal diverticulae were not visible in the specimens limiting its use in the generic diagnosis.

The comparative morphology of male copulatory organ, squamodiscs, and host group suggested that *Diplectanum cazauxi* is congeneric with *L. pearsoni*, as proposed by Kritsky *et al.* (2000). This species is, thus, transferred to *Latericaecum* as *L. cazauxi* n. comb.

Acleotrema Johnston & Tiegs, 1922

Synonymy: *Heteroplectanum* Rakotofiringa, Oliver & Lambert, 1987.

Diagnosis: Tegument smooth or scaled. Genital pore opening posterior to male copulatory organ (MCO). **Genital atrium sclerotized [40]**. Vas deferens intercaecal. MCO tubular, composed of 2 nested tubes; external tube uniform. Accessory piece absent. Prostatic reservoir simple. Accessory copulatory organ absent. Vaginal atrium muscular. **Vaginal aperture marginal [38]**. Squamodiscs, ventral, dorsal; anterior rows of rodlets **forming divergent rows [39]**. Parasites of marine perciform fishes (Carangidae, Kyphosidae, Sparidae and Toxotidae).

Type species: *A. girellae* Johnston & Tiegs, 1922 from *Girella tricuspidata* (Quoy & Gaimard) (type host), *Kyphosus elegans* (Peters), *Kyphosus cinerascens* (Forsskål), and *Kyphosus vaigiensis* (Quoy & Gaimard) (Kyphosidae).

Other species: *A. diplobulbus* (Yamaguti, 1968) Domingues & Boeger, 2007 from *Kyphosus cinerascens*; *Acleotrema flabelliforme* (Lim, 2006) n. comb. from *Toxotes jaculatrix* (Pallas) (Toxotidae); *A. nenue* (Yamaguti, 1968) Domingues & Boeger, 2007 from *Kyphosus elegans*, and *Kyphosus cinerascens*; *A. nenuides* (Rakotofiringa, Oliver & Lambert, 1987) Domingues & Boeger, 2007 from *Rhabdosargus sarba*, and *Polyamblyodon gibbosum* (Pellegrin) (Sparidae); *A. oliveri* (Leòn-Règagnon, León & Garcia-Prieto, 1997) Domingues & Boeger, 2007 from *Kyphosus elegans*; *A. parastromatei* (Rakotofiringa, Oliver & Lambert, 1987) Domingues & Boeger, 2007 from *Parastromateus niger* (Bloch) (Carangidae); *A. serrulopenis* (Rakotofiringa, Oliver & Lambert, 1987) Domingues & Boeger, 2007 from *Rhabdosargus sarba*, and *Polyamblyodon gibbosum*; *A. spiculare* (Yamaguti, 1968) Domingues & Boeger, 2007 from *Kyphosus cinerascens*; *A. tamatavense* (Rakotofiringa, Oliver & Lambert, 1987) Domingues & Boeger, 2007 from *Polyamblyodon gibbosum*; *A. yamagutii* (Oliver, 1983) Domingues & Boeger, 2007 from *Kyphosus cinerascens*.

Remarks: *Acleotrema* was revised by Domingues and Boeger (2007).

Pseudolamellodiscus Yamaguti, 1953

Diagnosis: Tegument smooth. Genital pore opening posterior to male copulatory organ (MCO). Genital atrium muscular. Vas deferens intercaecal. MCO tubular, composed of 2 nested tubes; external tube uniform. Accessory piece absent. Prostatic reservoir simple. Accessory copulatory organ absent. Vaginal atrium muscular. Vaginal aperture marginal. Squamodiscs ventral, dorsal; anterior rows of rodlets **forming parallel rows [41]. Ventral bar with recurved ends [42].** Superficial root of ventral anchor reduced. Parasites of marine perciform fishes (Sphyraenidae and Polynemidae).

Type species: *P. sphyraenae* Yamaguti, 1953 from *Sphyraena barracuda* (Walbaum), and *Sphyraena* sp. (Sphyraenidae) (type host).

Other species: *P. forsterii* Rakotofiringa & Maillard, 1979 from *Sphyraena forsteri* Cuvier; *P. jelloi* Rakotofiringa & Maillard, 1979 from *Sphyraena jelloi*; *P. nossibeii* Euzet & Razarihelisoa, 1959 from *Sphyraena barracuda*; *P. polynemus* Rao & Kulkarni, 1985 from *Polydactylus sexfilis* (Valenciennes) (Polynemidae).

Diplectanum Diesing, 1858

Synonymy: *Dactylogyrus* Wagener, 1857, *partim, nec* 1850; *Lepidotes* Johnston & Tiegs, 1922; *Neodiplectanum* Mizelle & Blatz, 1941; *Lamellodiscoides* Yamaguti, 1963; *Pseudolamellodiscoides* Gupta & Krishna, 1979

Diagnosis: Tegument smooth or scaled. Genital pore opening posterior to male copulatory organ (MCO). Genital atrium muscular. Vas deferens intercaecal or looping left intestinal caecum. MCO tubular, composed of 2 nested tubes; external tube uniform. Accessory piece absent. **Prostatic reservoir separated into three zones [43]. Accessory copulatory organ present [44].** Vaginal atrium muscular. Vaginal aperture marginal. Squamodiscs, ventral, dorsal; anterior rows of rodlets with open rings. Superficial root of ventral anchor reduced. Parasites of freshwater and marine actinopterygian fishes (Perciformes, Siluriformes).

Type species: *D. aequans* (Wagener, 1857) Diesing, 1858 from *Dicentrarchus labrax* (Linnaeus) (type host), *Dicentrarchus punctatus* (Bloch) (Moronidae), and *Bagrus* sp. (Bagridae).

Other species: See comments below.

Remarks: Kritsky *et al.* (2000) questioned the monophyly of *Diplectanum* based on the greatly variable morphology of its species (e.g., presence/absence of accessory piece, MCO morphology). The comparative morphology and cladistic analysis did not support monophyly of *Diplectanum* (see comments above). Thus, *Diplectanum* is presently restricted to species possessing the combination of the following characteristics: (1) male copulatory organ formed by two nested tubes; (2) accessory copulatory organ; (3) prostatic reservoir separated into three zones; (4) two squamodiscs. *Diplectanum stricto sensu* contains the type species, *D. aequans* (Wagener, 1857) Diesing, 1858 from *Dicentrarchus labrax*, *Dicentrarchus punctatus*, and *Bagrus* sp.; *D. aculeatum* Parona & Perugia, 1889 from *Sciaena umbra* Linnaeus, and *Umbrina cirrosa* (Linnaeus) (Sciaenidae); *D. banyulense* Oliver, 1968 from *Umbrina canariensis* Valenciennes; *D. belengeri* (Chauhan, 1945) Chauhan, 1954 from *Johnius belangerii* (Cuvier), *Johnius carutta* Bloch (Sciaenidae), and *Congresox talabonoides* (Bleeker) (Muraenesocidae); *D. bocqueti* Oliver, 1980 from *Argyrosomus regius* (Asso) (Sciaenidae); *D. chabaudi* Oliver, 1980 from *Umbrina cirrosa*; *D. dollfusi* Oliver, 1980 from *Argyrosomus regius*; *D. glandulosum* Williams, 1989 from *Argyrosomus hololepidotus* (Lacépède); *D. jamestownense* Obiekezie, 1988 from *Pseudotolithus typus* Bleeker; *D. labourgi* Oliver, 1974 from *Umbrina canariensis*; *D. minutum* Tripathi, 1957 from *Johnius glaucus* (Day), and *Nibea maculata* (Bloch & Schneider) (Sciaenidae); *D. oliveri* Williams, 1989 from *Argyrosomus hololepidotus*; *D. sciaenae*, van Beneden & Hesse, 1863 from *Argyrosomus regius*; *D. simile* Bychowsky, 1957 from *Sciaena umbra*, and *Argyrosomus regius*. Except for the type species, members of *Diplectanum stricto sensu* were reported from perciform fishes, which seem to represent

their natural hosts group. However, *Diplectanum aequans* has been reported also from *Bagrus* sp. (Bagridae, Siluriformes) (Paperna & Kohn 1964), but this probably represents a misidentification of the parasite species, as already noted by Oliver (1968).

Diplectanum monticellii appears as a sister species of *Pseudorhabdosynochus* and *Echinoplectanum* in clade “X”. However, we decided not to propose a new genus for this taxon based on the absence of autapomorphic characters. Including this species, the present revision does not recognize the generic status of 51 species of *Diplectanum*, based on the redundant morphology of the accessory adhesive organ (i.e., presence of ventral and dorsal squamodiscs). Although the revision of *Diplectanum* is not within the scope of this work, we believe that some characteristics (e.g. morphology of reproductive structures) can be informative in the determination of generic groupings in future studies. Therefore, we consider the following species *incertae sedis*: *D. bauchotae* Oliver & Paperna, 1984 from *Sphyræna flavicauda*, and *Argyrosomus regius*; *D. bilobatus* Hargis, 1955 from *Cynoscion nebulosus* (Cuvier); *D. cayennense* Euzet & Durette-Desset, 1974 from *Plagioscion auratus* (Castelnaud) (Sciaenidae); *D. collinsi* (Muller, 1936) Price, 1937 from *Morone saxatilis* (Waulbaum) (Moronidae); *D. copiosum* Boeger, Fehlaue & Marques, 2006 from *Petilipinnis grunniens* (Jardine & Schomburgk) (Sciaenidae); *D. decorum* Kritsky & Thatcher, 1984 from *Plagioscion squamosissimus* (Heckel); *D. elongatum* Obiekiezie, 1988 from *Pseudotolithus elongatus* (Bowdich) (Sciaenidae); *D. enyenibii* Obiekiezie, 1988 from *Cynoglossus senegalensis* (Kaup) (Cynoglossidae); *D. fluviale* Johnston & Tieg, 1922 from *Macquaria ambigua* (Richardson) (Percichthyidae); *D. fujianensis* Zhang, Liu, & Ding, 1995 from *Argyrosomus amoyensis* (Bleeker), and *Pennahia argentata* (Houttuyn) (Sciaenidae); *D. furcelamellosum* Zhang, Liu, Ding & Chen, 2000 from *Otolithes ruber* (Bloch & Schneider) (Sciaenidae); *D. fusiforme* Oliver & Paperna, 1984 from *Lutjanus kasmira* (Forsskål) (Lutjanidae); *D. grassei* Oliver, 1974 from *Umbrina cirrosa*; *D. grouperi* Bu, Leong, Wong, Woo & Foo, 1999 from *Epinephelus areolatus* (Forsskål), and *Epinephelus coioides* (Hamilton) (Serranidae); *D. gymnopus* Kritsky & Thatcher, 1984 from *Plagioscion squamosissimus*; *D. hilum* Kritsky & Thatcher, 1984 from *Plagioscion squamosissimus*; *D. jaculator* Mizelle & Kritsky, 1969 from *Toxotes jaculatrix* (Toxotiidae); *D. jerbuae* Gupta & Khanna, 1974 from *Terapon jarbua* (Forsskål) (Theraponidae); *D. kuhliae* Yamaguti, 1968 from *Kuhlia sandvicensis* (Steindachner) (Kuhliidae); *D. lacustre* Thurston & Paperna, 1969 from *Lates niloticus* (Linnaeus) (Latidae); *D. laubieri* Lambert & Maillard, 1974 from *Dicentrarchus labrax*, and *Dicentrarchus punctatus*; *D. lichtenfelsi* Oliver & Paperna, 1984 from *Polydactylus sextarius* (Bloch & Schneider) (Polynemidae); *D. maa* Justine & Sigura, 2007 from *Epinephelus malabaricus* (Bloch & Schneider); *D. maculatum* Tripathi, 1957 from *Otolithes ruber*, and *Pterotolithus maculatus* (Cuvier) (Sciaenidae); *D. magnodiscatum* Zambrano, 1997 from *Eugerres plumieri* (Cuvier) (Gerreidae); *D. megacirrus* (Maillard & Vala, 1980) Oliver, 1987 from *Galeoides decadactylus* (Bloch) (Polynemidae); *D. melvillei* Oliver & Paperna, 1984 from *Umbrina cirrosa*; *D. minousi* (Gupta & Khullar, 1967) Oliver, 1987 from *Minous monodactylus* (Bloch & Schneider) (Synanceiidae); *D. monticellii* Domingues & Boeger, 2003 from *Cynoscion leiarchus* (Cuvier); *D. nagibinae* Oliver & Paperna, 1984 from *Umbrina cirrosa*; *D. nanus* Justine, 2007c from *Cephalopholis sonnerati* (Valenciennes); *D. narimeen* Unnithan, 1964 from *Lates calcarifer* (Bloch); *D. orissai* (Gupta & Krishna, 1979) Oliver, 1987 from *Johnius borneensis* (Bleeker); *D. penangi* Seng & Seng, 1991 from *Lates calcarifer*; *D. pescadae* Kritsky & Thatcher, 1984 from *Plagioscion squamosissimus*; *D. piscinarius* Kritsky & Thatcher, 1984 from *Plagioscion squamosissimus*; *D. polynemus* Tripathi, 1957 from *Eleutheronema tetradactylum* (Shaw), and *Leptomelanosoma indicum* (Shaw) (Polynemidae); *D. puriense* Tripathi, 1957 from *Sillaginopsis panijus* (Hamilton), and *Sillago chondropus* Bleeker (Sillaginidae); *D. secundum* (Tripathi, 1957) Yamaguti, 1963 from *Terapon jarbua*; *D. setosum* Nagibina, 1976 from *Psammoperca waigienis* (Cuvier), and *Lates calcarifer*; *D. spinosum* (Maillard & Vala, 1980) Oliver, 1987 from *Galeoides decadactylus*; *D. spirale* Nagibina, 1976 from *Lutjanus fulviflamma* (Forsskål), and *Lutjanus russellii* (Bleeker); *D. squamatum* Santos, Timi & Gibson, 2002 from *Cynoscion guatucupa* (Cuvier); *D. sumpit* Lim, 2006 from *Toxotes jaculatrix*; *D. tangzhongzhangii* Zhang, Liu & Ding, 1995 from *Argyrosomus amoyensis*, *Nibea albiflora* (Richardson), and *Pennahia argentata*; *D. toxotes*

Mizelle & Kritsky, 1969 from *Toxotes jaculatrix*; *D. uitoe* Justine, 2007b from *Epinephelus maculatus* (Bloch); *D. umbrinum* Tripathi, 1957 from *Dendrophysa russelii* (Cuvier) (Sciaenidae), and *Johnius dussumieri* (Valenciennes); *D. undulicirrosum* Zhang, Liu, Ding & Chen, 2000 from *Terapon theraps* Cuvier, and *Pelates quadrilineaus* (Bloch); *D. veropolynemi* Nagibina, 1976 from *Polydactylus plebeius* (Broussonnet), and *Polydactylus sextarius*; *D. wenningeri* (Mizelle & Blatz, 1941) Oliver, 1987 from *Eucinostomus gula* (Quoy & Gaimard), and *Gerres cinereus* (Walbaum) (Gerreidae).

***Lobotrema* Tripathi, 1959**

Synonymy: *Pseudomurraytrema* Yamaguti, 1958 pre-occupied, *Allomurraytrema* Yamaguti, 1963

Diagnosis: Tegument smooth or scaled. Genital pore opening posterior to male copulatory organ (MCO). Genital atrium muscular. Vas deferens intercaecal or looping left intestinal caecum. MCO tubular, composed of 2 nested tubes; external tube uniform. Accessory piece absent. Prostatic reservoir separated into three zones. Accessory copulatory organ present. **Vaginal atrium sclerotized [47]**. Vaginal aperture marginal. **Accessory adhesive organ absent [45]**. **Two haptor bars [46]**. Superficial root of ventral anchor reduced. Parasites of freshwater and marine Perciformes, Cypriniformes and Pleuronectiformes.

Type species: *L. madrasi* Tripathi, 1959 from *Brachirus orientalis* (Bloch & Schneider) (Soleidae).

Other species: *L. argyrosomi* (Bychowsky & Nagibina, 1977) Oliver, 1987 from *Pennahia macrocephalus* (Tang); *L. aspidopariaii* Gupta & Varsha Sachdeva, 1987 from *Aspidoparia morar* (Hamilton) (Cyprinidae); *L. caballeroi* Gupta & Sharma, 1982 from *Cynoglossus arel*; *L. kumari* Oliver, 1987 from *Johnius coitor* (Hamilton); *L. rajendrai* Srivastava & Kumar, 1983 from *Garra gotyla gotyla* (Gray) (Cyprinidae); *L. sciaenae* (Bychowsky & Nagibina, 1977) Oliver, 1987 from *Johnius dussumieri* (Cuvier); *L. spari* (Yamaguti, 1958) Oliver, 1987 from *Acanthopagrus schlegelii schlegelii*, *Acanthopagrus australis*, *Acanthopagrus berda*, *Acanthopagrus butcheri*, and *Acanthopagrus latus*; *L. youngi* Gupta & Sharma, 1982 from *Pseudorhombus triocellatus* (Bloch & Schneider) (Paralichthyidae).

Remarks: *Lobotrema* has occupied different taxonomic positions since it was proposed by Tripathi (1959): in Tetraonchinae (Dactylogyridae) (Tripathi, 1959), Ancyrocephalinae (Dactylogyridae) (Yamaguti, 1963), and Murraytrematoidinae (Oliver, 1982). Yamaguti (1958) proposed *Pseudomurraytrema spari*, posteriorly transferred to *Allomurraytrema* (see Yamaguti, 1963). Bychowsky and Nagibina (1977) considered *Allomurraytrema* as a junior synonymy of *Lobotrema*, a decision corroborated by Oliver (1982, 1987).

In the present cladistic analysis, *Lobotrema* appears as sister species of *Murraytrema* and *Diplectanum aequans*, within Diplectaninae, as indicated by the sharing of accessory copulatory organ [44] and prostatic reservoir separated into three zones [43]. Bychowsky and Nagibina (1977) suggested that these three taxa are closely related, which is corroborated herein. *Lobotrema* can be differentiated from these two genera for the absence of the ventral bar [46].

***Murraytrema* Price, 1937**

Diagnosis: Tegument smooth. Genital pore opening posterior to male copulatory organ (MCO). Genital atrium muscular. Vas deferens intercaecal or looping left intestinal caecum. MCO tubular, composed of 2 nested tubes; external tube uniform. Accessory piece absent. Prostatic reservoir separated into three zones. Accessory copulatory organ present. Vaginal atrium muscular. Vaginal aperture marginal. Accessory adhesive organ absent. Superficial root of ventral anchor reduced. Parasites of marine perciform fishes (Sparidae and Sciaenidae).

Type-species: *M. robustum* (Murray, 1931) Price, 1937 from *Acanthopagrus australis* (Sparidae).

Other species: *M. bychowskyi* (Bychowsky & Nagibina, 1977) Oliver, 1987 from *Nibeia albiflora* (Sciaenidae).

Remarks: *Murraytrema* is closely related to *Lobotrema* by sharing the secondary loss of the accessory adhesive organ [45]. However, species of *Murraytrema* can be differentiated from species of *Lobotrema* by the presence of a muscular vaginal atrium (sclerotized in *Lobotrema*) and three haptoral bars (two in *Lobotrema*).

***Lepidotrema* Johnston & Tiegs, 1922**

Synonymy: *Empleurodiscus* Johnston & Tiegs, 1922; *Flabellodiscus* Johnston & Tiegs, 1922; *Squamodiscus* Yamaguti, 1934.

Diagnosis: Tegument smooth or scaled. **Genital pore opening anterior to male copulatory organ (MCO) [50].** Genital atrium muscular. Vas deferens intercaecal or looping left intestinal caecum. MCO tubular, composed of 2 nested tubes; **external tube twisted [49].** Accessory piece absent. Prostatic reservoir simple. Accessory copulatory organ absent. **Vaginal atrium sclerotized [51].** Vaginal aperture marginal. Squamodiscs, ventral, dorsal; anterior rows of rodlets with open rings. **Accessory spines associated with the posterior region of the haptor [48].** Superficial root of ventral anchor reduced. Parasites of freshwater and marine perciform fishes (Terapontidae).

Type species: *L. therapon* Johnston & Tiegs, 1922 from *Hephaestus carbo* (Ogilby & McCulloch).

Other species: *L. angustum* (Johnston & Tiegs, 1922) Price, 1937 from *Leiopotherapon unicolor* (Günther); *L. bidyana* Murray, 1931 from *Bidyanus bidyanus* (Mitchell); *L. fuliginosum* Johnston & Tiegs, 1922 from *Hephaestus fuliginosus* Macleay; *L. kuwaitensis* Kritsky, Jiménez-Ruiz & Sey, 2000 from *Terapon puta* Cuvier; *L. longipenis* (Yamaguti, 1934) Kritsky, Jiménez-Ruiz & Sey, 2000 from *Rhynchopelates oxyrhynchus* (Temminck & Schlegel); *L. simplex* (Johnston & Tiegs, 1922) Price, 1937 from *Hephaestus fuliginosus*; *L. tenue* Johnston & Tiegs, 1922 from *Scortum hillii* (Castelnaud).

Remarks: Bychowsky (1957) suggested the homology between spines in the peduncle (peduncular spines, *sensu* Domingues & Boeger 2006) of Rhamnocercinae (see comments above) and squamodiscs of members of *Lepidotrema*. Although our analysis did not support the homology between these structures, *Lepidotrema* appears as sister group of *Spinomatrix* + *Rhamnocercus* + *Rhamnocercoides* (in clade “R”) within Diplectaninae, based on the presence of accessory spines associated with the posterior region of the haptor [48] and MCO tubular, composed of 2 nested tubes; external tube twisted [49].

***Spinomatrix* Boeger, Fehlaue & Marques, 2006**

Diagnosis: The genus is monotypic. Tegument smooth. Genital pore opening posterior to male copulatory organ (MCO). Genital atrium muscular. Vas deferens looping left intestinal caecum. MCO tubular, composed of 2 nested tubes; external tube twisted. Accessory piece absent. Prostatic reservoir simple. Accessory copulatory organ absent. Vaginal atrium muscular. Squamodiscs present, ventral, dorsal; anterior rows of rodlets with open rings. Accessory spines associated with the posterior region of the haptor. **Peduncular spines [52].** Superficial root of ventral anchor reduced. Parasites of freshwater perciform fishes (Sciaenidae).

Type species: *Spinomatrix penteormos* Boeger, Fehlaue & Marques, 2006 from *Pachyurus adpersus* Steindachner.

***Rhamnocercus* Monaco, Wood & Mizelle, 1954**

Diagnosis: Tegument smooth or scaled. Genital pore opening posterior to male copulatory organ (MCO). Genital atrium muscular. Vas deferens intercaecal or looping left intestinal caecum. MCO tubular, composed of 2 nested tubes; **external tube uniform** [55]. Accessory piece absent. Prostatic reservoir simple. Accessory copulatory organ absent. Vaginal atrium muscular. Vaginal aperture marginal. **Accessory adhesive organ absent** [53]. Accessory spines associated with the posterior region of the haptor. Peduncular spines. **Potero-medial projection of the ventral bar** [54]. Superficial root of ventral anchor reduced. Parasites of marine perciform fishes (Sciaenidae).

Type species: *R. rhamnocercus* Monaco, Wood & Mizelle, 1954 from *Umbrina roncadora* Jordan & Gilbert.

Other species: *R. bairdiella* Hargis, 1955 from *Bairdiella chrysourea* (Lacépède); *R. margaritae* Zambrano, 1997 from *Bairdiella ronchus* (Cuvier); *R. oliveri* Luque & Iannacone, 1991 from *Stellifer minor* (Tschudi); *R. stelliferi* Luque & Iannacone, 1991 from *Stellifer minor*.

Remarks: *Rhamnocercus* was revised by Domingues and Boeger (2006).

***Rhamnocercoides* Luque & Iannacone, 1991**

Diagnosis: Tegument smooth or scaled. Genital pore opening posterior to male copulatory organ (MCO). Genital atrium muscular. Vas deferens intercaecal or looping left intestinal caecum. MCO tubular, composed of 2 nested tubes; external tube twisted. Accessory piece absent. Prostatic reservoir simple. Accessory copulatory organ absent. **Vaginal atrium sclerotized** [56]. Vaginal aperture marginal. Accessory adhesive organ absent. Accessory spines associated with the posterior region of the haptor. Peduncular spines. posteromedial projection of the ventral bar. Superficial root of ventral anchor reduced. Parasites of marine perciform fishes (Sciaenidae).

Type species: *R. menticirrho* Luque & Iannacone, 1991 from *Menticirrhus ophicephalus* (Jenyns).

Other species: *R. stichospinus* (Seamster & Monaco, 1956) Domingues & Boeger, 2006 from *Menticirrhus littoralis* (Holbrook), *Menticirrhus americanus* (Linnaeus), and *Micropogonias undulatus* (Linnaeus).

Remarks: *Rhamnocercoides* was revised by Domingues and Boeger (2006).

***Oliveripectanum* n. gen.**

Synonymy: *Diplectanum* Diesing, 1858, *partim*

Diagnosis: Tegument smooth. **Genital pore opening anterior to male copulatory organ (MCO)** [59]. Genital atrium muscular. Vas deferens intercaecal or looping left intestinal caecum. MCO tubular, composed of 2 nested tubes; external tube uniform. Accessory piece absent. Prostatic reservoir simple. Accessory copulatory organ absent. Vaginal atrium muscular. Vaginal aperture marginal. Squamodiscs present, ventral, dorsal; **anterior rows of rodlets with closed rings** [58]. **Superficial root of ventral anchor developed** [57]. Parasites of marine perciform fishes (Lutjanidae, Priacanthidae).

Type species: *Oliveripectanum priacanthi* (Yamaguti, 1968) n. comb from *Heteropriacanthus cruentatus* (Lacépède) (Priacanthidae).

Other species: *O. opakapaka* (Yamaguti, 1968) n. comb. from *Pristipomoides filamentosus* (Valenciennes) (Lutjanidae), and *Aphareus rutilans* Cuvier (Lutjanidae); *O. curvivagina* (Yamaguti, 1968) n. comb from *Pristipomoides sieboldii* (Bleeker), and *Pristipomoides auricilla* (Jordan, Evermann & Tanaka).

Remarks: Oliver (1987) transferred *D. priacanthi*, *D. curvivagina*, and *D. opakapaka* to *Cycloplectanum* and included them into a morphologic group based on the presence of an arched male copulatory organ. However, several authors did not accept *Cycloplectanum* as a valid taxon and considered that species belonging to this genus should represent species of *Diplectanum* and *Pseudorhabdosynochus* (Kritsky & Beverley-Burton 1986; Justine & Euzet 2006). Presence of a genital pore opening anterior to male copulatory organ and squamodiscs with anterior rows of rodlets with closed rings distinguish *Oliveriplectanum* **n. gen.** from these later genera. The genus is named after Dr Guy Oliver, in recognition of his valuable work on the Diplectanidae.

***Murraytrematoides* Yamaguti, 1958**

Synonymy: *Geneticoenteron* Yamaguti, 1958

Diagnosis: Tegument smooth. Genital pore opening posterior to male copulatory organ (MCO). Genital atrium muscular. Vas deferens intercaecal or looping left intestinal caecum. MCO tubular, composed of 2 nested tubes; external tube uniform. Accessory piece absent. Prostatic reservoir simple. Accessory copulatory organ absent. Vaginal atrium muscular. Vaginal aperture marginal. **Accessory adhesive organ absent [60].** Superficial root of ventral anchor developed. Parasites of marine perciform fishes (Polynemidae, Embiotocidae, Kuhliidae, Moronidae).

Type species: *M. ditrematis* Yamaguti, 1958 from *Ditrema temminckii* Bleeker (Embiotocidae).

Other species: *M. bychowskii* (Nagibina, 1976) Oliver, 1987 from *Polydactylus plebeius*, and *Polydactylus sextarius* (Polynemidae); *M. kuhliae* Yamaguti, 1968 from *Kuhlia sandvicensis* (Kuhliidae); *M. lateolabracis* (Yamaguti, 1958) Oliver, 1987 from *Lateolabrax japonicus* (Cuvier) (Moronidae).

Remarks: Oliver (1982) proposed Murraytrematoidinae with *Murraytrematoides ditrematis* as type species. The absence of the accessory adhesive organ was considered the main diagnostic characteristic of the subfamily. This same author considered *Geneticoenteron* a junior synonym of *Murraytrematoides* and transferred *Diplectanum bychowskii* Nagibina, 1976 to *Murraytrematoides*, as *M. bychowskii*.

As mentioned previously, the cladistic analysis indicates that the accessory adhesive organ was lost several times in the evolutionary history of Diplectanidae, suggesting that Murraytrematoidinae is not monophyletic. The present analysis also supports the non-monophyly of *Murraytrematoides*, since *M. pricei* appears as sister group of clade “C”, while *M. ditrematis* and *M. lateolabracis* are sister groups in clade “V.” Therefore, we incorporate Murraytrematoidinae in Diplectaninae (see comments above) and recognize *Murraytrematoides* as a valid genus for species that present the following combined characteristics: (1) absence of accessory adhesive organ, (2) male copulatory organ formed by nested tubes, (3) absence of accessory piece, (4) superficial root of the ventral anchor developed, and (5) vaginal atrium muscular.

***Anoplectanum* Boeger, Fehlaue & Marques, 2006**

Diagnosis: Tegument smooth. Genital pore opening posterior to male copulatory organ (MCO). Genital atrium muscular. Vas deferens apparently looping left intestinal caecum. MCO tubular, composed of 2 nested tubes; external tube uniform. Accessory piece absent. Prostatic reservoir simple. Accessory copulatory organ absent. **Vaginal atrium sclerotized [61].** Vaginal aperture marginal. Accessory adhesive organ absent. Superficial root of ventral anchor developed. Parasites of freshwater perciform fishes (Sciaenidae).

Type species: *Anoplectanum haptorodynatum* Boeger, Fehlaue & Marques, 2006 from *Petilipinnis grunniens*.

Other species: *Anoplectanum microsoma* Boeger, Fehlaue & Marques, 2006 from *Pachyurus junki* Soares & Cassati, and *Petilipinnis grunniens*.

Remarks: *Anoplectanum* is sister group of *Murraytrematoides*. Both genera share the secondary loss of accessory adhesive organ. However, *Anoplectanum* differs from *Murraytrematoides* in the comparative morphology of the vaginal atrium (i.e., sclerotized in *Anoplectanum*; muscular in *Murraytrematoides*).

***Laticola* Yang, Kritsky, Sun, Jiangying, Shi & Agrawal, 2006**

Diagnosis: Tegument smooth or scaled. Genital pore opening posterior to male copulatory organ (MCO). Genital atrium muscular. Vas deferens apparently intercaecal. MCO tubular, composed of 2 nested tubes; external tube uniform; **MCO with distal tube enclosing eversible cirrus [63]; base of the male copulatory organ expanded [62]; muscular ridges associated with the base of the MCO [64]**. Accessory piece absent. Prostatic reservoir simple. Accessory copulatory organ absent. Vaginal atrium muscular. **Vaginal aperture medial [65]**. Squamodiscs, ventral, dorsal; anterior rows of rodlets with open rings. Superficial root of ventral anchor developed. Parasites of marine perciform fishes (Latidae, Serranidae).

Type species: *Laticola lingaoensis* Yang, Kritsky, Sun, Jiangying, Shi & Agrawal, 2006 from *Lates calcarifer* (Latidae).

Other species: *L. dae* Journo & Justine, 2006 from *Epinephelus maculatus*; *Laticola latesi* (Tripathi, 1957) Yang, Kritsky, Sun, Zhang, Shi & Agrawal, 2006 from *Lates calcarifer*; *L. paralatesi* (Nagibina, 1976) Yang, Kritsky, Sun, Zhang, Shi & Agrawal, 2006 from *Lates calcarifer*; *L. seabassi* (Wu, Li, Zhu & Xie, 2005) n. comb. from *Lates calcarifer*.

Remarks: Yang *et al.* (2006) observed that species of *Laticola* and *Pseudorhabdosynochus* possess male copulatory organ with some morphological similarity, suggesting that both genera share a common ancestor. The molecular analyses performed by these authors did not support the sister relationship of *Pseudorhabdosynochus* and *Laticola*. Wu *et al.* (2005) proposed *Pseudorhabdosynochus seabassi* Wu, Li, Zhu & Xie, 2005 based on the morphology of the male copulatory organ. These authors also proposed a phylogenetic hypothesis for this species and other diplectanids based on molecular data (ssrDNA and lsrDNA), where *P. seabassi* consistently appears as sister species of *Laticola latesi*. The presence of muscular ridges associated with the male copulatory organ supports the transfer of *Pseudorhabdosynochus seabassi* to *Laticola* Yang, Kritsky, Sun, Jiangying, Shi & Agrawal, 2006 as *Laticola seabassi* (Wu, Li, Zhu & Xie, 2005) n. comb.

In our analysis, *Laticola* consistently emerged as the sister group of *Pseudorhabdosynochus* and *Echinoplectanum*, based on the presence of the male copulatory organ with distal tube enclosing eversible male copulatory organ [63]; and the base of the male copulatory organ expanded [62]. *Laticola* can be differentiated from the latter genera by two autapomorphies: muscular ridges associated with the base of the MCO [64] and medial vaginal aperture [65].

***Pseudorhabdosynochus* Yamaguti, 1958**

Synonymy: *Cycloplectanum* Oliver, 1968.

Diagnosis: Tegument smooth or scaled. Genital pore opening posterior to male copulatory organ (MCO). Genital atrium muscular. Vas deferens apparently intercaecal. MCO tubular, composed of 2 nested tubes; external tube uniform; MCO with distal tube enclosing eversible cirrus; base of the male copulatory organ expanded. **Quadriloculate male copulatory organ [68]**. Accessory piece absent. Prostatic reservoir simple. Accessory copulatory organ absent. **Vaginal atrium sclerotized [66]**. Vaginal aperture marginal. Squamodiscs, ventral, dorsal; **anterior rows of rodlets with closed rings [67]** (exceptionally open rings in *P. vagampullum*). Superficial root of ventral anchor developed. Parasites of marine perciform fishes (Serranidae,

Chaetodontidae, Polyprionidae, Sparidae) and freshwater cyprinodontiform (Rivulidae) and characiforms (Characidae).

Type species: *P. epinepheli* Yamaguti, 1958 from *Epinephelus bruneus* Bloch (Serranidae), *Epinephelus akaara* (type host), and *Epinephelus awoara*.

Other species: *P. americanus* (Price, 1937) Kritsky & Beverley-Burton, 1986 from *Epinephelus aeneus* (Geoffroy Saint-Hilaire), *Epinephelus itajara* (Lichtenstein), *Rivulus hartii* (Boulenger) (Rivulidae), *Astyanax bimaculatus* (Linnaeus) (Characidae), and *Stereolepis gigas* Ayres (Polyprionidae); *P. amplidiscatus* (Bravo-Hollis, 1954) Kritsky & Beverley-Burton, 1986 from *Paralabrax maculatofasciatus* (Steindachner) (Serranidae); *P. argus* Justine, 2007c from *Cephalopholis argus* Bloch & Schneider (Serranidae); *P. auitoe* Justine, 2007b from *Epinephelus maculatus*; *P. bacchus* Sigura, Chauvet & Justine, 2007 from *Epinephelus coeruleopunctatus* (Bloch); *P. beverleyburtonae* (Oliver, 1984) Kritsky & Beverley-Burton, 1986 from *Epinephelus marginatus* (Lowe); *P. bocquetae* (Oliver & Paperna, 1984) Kritsky & Beverley-Burton, 1986 from *Epinephelus adscensionis* (Osbeck); *P. bouaini* Neifar & Euzet, 2007 from *Epinephelus costae* (Steindachner); *P. buitoe* Justine, 2007b from *Epinephelus maculatus*; *P. caballeroi* (Oliver, 1984) Kritsky & Beverley-Burton, 1986 from *Epinephelus marginatus*; *P. calathus* Hinsinger & Justine, 2006b from *Epinephelus rivulatus* (Valenciennes); *P. caledonicus* Justine, 2005a from *Epinephelus fasciatus* (Forsskål); *P. capurroi* Vidal-Martinez & Mendoza-Franco, 1998 from *Mycteroperca bonaci* (Poey) (Serranidae); *P. chinensis* Zhang, Yang & Liu, 2001 from *Epinephelus tauvina* (Forsskål); *P. coioidesis* Bu, Leong, Wong, Woo & Foo, 1999 from *Epinephelus areolatus*, *Epinephelus coioides*, and *Epinephelus malabaricus*; *P. cuitoe* Justine, 2007b from *Epinephelus maculatus*; *P. cupatus* (Young, 1969) Kritsky & Beverley-Burton, 1986 from *Epinephelus merra* Bloch, and *Epinephelus fasciatus*; *P. cyathus* Hinsinger & Justine, 2006b from *Epinephelus howlandi* (Günther); *P. dolicolpos* Neifar & Euzet, 2007 from *Epinephelus costae*; *P. duitoe* Justine, 2007b from *Epinephelus maculatus*; *P. enitsuji* Neifar & Euzet, 2007 from *Epinephelus costae*; *P. euitoe* Justine, 2007b from *Epinephelus maculatus*; *P. fuitoe* Justine, 2007b from *Epinephelus maculatus*; *P. guitoe* Justine, 2007b from *Epinephelus maculatus*; *P. hirundineus* Justine, 2005b from *Variola louti* (Forsskål) (Serranidae), and *Variola albimarginata* Baissac; *P. huitoe* Justine, 2007b from *Epinephelus maculatus*; *P. justinei* Zeng & Yang, 2007 from *Epinephelus quoyanus* (Valenciennes); *P. kritskyi* Dyer, Williams & Bunkley-Williams, 1995 from *Mycteroperca microlepis* (Goode & Bean); *P. lantauensis* (Beverley-Burton & Suriano, 1981) Kritsky & Beverley-Burton, 1986 from *Epinephelus akaara*, *Epinephelus areolatus*, *Epinephelus awoara*, *Epinephelus bruneus*, *Epinephelus coioides*, *Epinephelus longispinis* (Kner), and *Pagrus major* (Sparidae), *P. maaensis* Justine & Sigura, 2007 from *Epinephelus malabaricus*; *P. magni squamodiscum* (Aljoshkina, 1984) Kritsky & Beverley-Burton, 1986 from *Chaetodon hoefleri* Steindachner (Chaetodontidae); *P. malabaricus* Justine & Sigura, 2007 from *Epinephelus malabaricus*; *P. manifestus* Justine & Sigura, 2007 from *Epinephelus malabaricus*; *P. manipulus* Justine & Sigura, 2007 from *Epinephelus malabaricus*; *P. marcellus* Justine & Sigura, 2007 from *Epinephelus malabaricus*; *P. maternus* Justine & Sigura, 2007 from *Epinephelus malabaricus*; *P. melanesiensis* (Laird, 1958) Kritsky & Beverley-Burton, 1986 from *Epinephelus merra*; *P. minutus* Justine, 2007c from *Cephalopholis sonnerati*; *P. monaensis* Dyer, Williams & Bunkley-Williams, 1994 from *Epinephelus adscensionis*; *P. querni* (Yamaguti, 1968) Kritsky & Beverley-Burton, 1986 from *Epinephelus quernus* Seali; *P. riouxi* (Oliver, 1986) Kritsky & Beverley-Burton, 1986 from *Epinephelus marginatus*; *P. serrani* (Yamaguti, 1953) Kritsky & Beverley-Burton, 1986 from *Epinephelus coioides*, and *Serranus* sp.; *P. shenzhenensis* Yang, Zeng & Gibson, 2005 from *Epinephelus coioides*; *P. sinediscus* Neifar & Euzet, 2007 from *Epinephelus costae*; *P. sosia* Neifar & Euzet, 2007 from *Epinephelus costae*; *P. sulamericanus* Santos, Buchmann & Gibson, 2000 from *Epinephelus niveatus* (Valenciennes); *P. summanae* (Young, 1969) Kritsky & Beverley-Burton, 1986 from *Epinephelus summana* (Forsskål); *P. summanoides* Yang, Gibson & Zeng 2005 from *Epinephelus coioides*; *P. vagampullum* (Young, 1969) Kritsky & Beverley-Burton, 1986 from *Epinephelus longispinis*, and *Epinephelus merra*; *P. venus* Hinsinger & Justine, 2006a from *Epinephelus howlandi*; *P. yucatanensis* Vidal-Martinez, Aguirre-Macedo & Mendoza-Franco, 1997 from *Epinephelus morio* (Valenciennes).

Remarks: Ten years after its proposal, *Pseudorhabdosynochus* was synonymized with *Cycloplectanum*. Oliver (1968) considered the presence of squamodiscs with inner rows forming a closed circle a diagnostic feature of *Cycloplectanum* and indicated *C. americanum* as type species. However, Beverley-Burton and Suriano (1981), and Kritsky and Beverley-Burton (1986) did not accept Oliver's (1968) opinion. Kritsky and Beverley-Burton (1986) indicated that the proposal of *Cycloplectanum* represents an erroneous interpretation of the International Code of Zoological Nomenclature (ICZN), because Oliver's (1968) decision did not invalidate the status of *Pseudorhabdosynochus*. Justine and Euzet (2006) also did not accept *Cycloplectanum* and considered that all species attributed by Oliver (1968) to *Cycloplectanum* should be included in *Diplectanum*, *Pseudorhabdosynochus*, or *Echinoplectanum* Justine & Euzet, 2006.

Pseudorhabdosynochus is unique among Diplectanidae by having quadriloculate male copulatory organ and the anterior rows of rodlets with closed rings. However, Neifar and Justine (2007) described *Pseudorhabdosynochus sinediscus* Neifar & Justine, 2007 that is characterized by lacking squamodiscs. Other diplectanid genera also have species in which the AAO are absent (see comments for *Lobotrema*, *Rhabdosynochus*, *Murraytrema*, *Murraytrematoides*, *Rhamnocercus*, *Rhamnocercoides* and *Anoplectanum*). The absence of an AAO within species of *Pseudorhabdosynochus* is, however, likely to be secondary for *P. sinediscus* and represents an independent event within the evolutionary history of the family.

***Echinoplectanum* Justine & Euzet, 2006**

Diagnosis: Tegument smooth. Genital pore opening posterior to male copulatory organ (MCO). Genital atrium muscular. Vas deferens intercaecal. MCO tubular, composed of 2 nested tubes; external tube uniform; MCO with distal tube enclosing eversible cirrus; **spines associated with the distal portion of the copulatory organ [71]**; base of the male copulatory organ expanded; **muscular ridges associated with the base of the MCO [70]** Accessory piece absent. Prostatic reservoir simple. Accessory copulatory organ absent. Vaginal atrium sclerotized. Vaginal aperture marginal. Squamodiscs ventral, dorsal; anterior rows of rodlets with closed rings, **intermediate rows of rodlets with anterior lightly sclerotized blunt spinelet [69]**. Superficial root of ventral anchor well developed. Parasites of marine perciform fishes (Serranidae, Centropomidae,) and freshwater siluriforms (Schilbeidae).

Type species: *E. laeve* Justine & Euzet, 2006 from *Plectropomus laevis* (Lacépède) (Serranidae).

Other species: *E. echinophallus* (Euzet & Oliver, 1965) Justine & Euzet, 2006 from *Epinephelus marginatus*, *Schilbe mystus* (Linnaeus) (Schilbeidae), and *Lates niloticus* (Latidae); *E. plectropomi* (Young, 1969) Justine & Euzet, 2006 from *Plectropomus maculatus* (Bloch); *E. chauverotum* Justine & Euzet, 2006 from *Plectropomus laevis*; *E. leopardi* Justine & Euzet, 2006 from *Plectropomus leopardus* (Lacépède); *E. pudicum* Justine & Euzet, 2006 from *Plectropomus leopardus*; *E. rarum* Justine & Euzet, 2006 from *Plectropomus leopardus*.

Remarks: *Echinoplectanum* is closely related to *Pseudorhabdosynochus* by sharing the following synapomorphies: (1) squamodiscs, with anterior rows of rodlets with closed rings; (2) and vaginal atrium sclerotized. However, *Echinoplectanum* can be differentiated from *Pseudorhabdosynochus* by an autapomorphy: spines associated with the distal portion of the copulatory organ.

Acknowledgments

The authors thank the following individuals and agencies for supporting this study: E. Hoberg and P. Pillit, U.S. National Parasite Collection; L.C.M. Pereira and D. Noronha, Coleção Helminológica do Instituto Oswaldo Cruz (Brazil); J. Carpel, Museo Oceanológico Hno. Benigno Román/Fundación La Salle/ Campus

de Margarita/ Estado Nueva Esparta (Venezuela); I. Franke and L. Sánchez, Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos (Peru); J. Cassone, Muséum National d Histoire Naturelle de Paris; P. Berents, Australian Museum; S. Sterner and F.A. Jiménez, Harold W. Manter Laboratory of Parasitology, University of Nebraska; G.P.P. de Leon, Colección Helminológica Nacional, Universidad Nacional Autónoma de México; M. Bryant, Queensland Museum (Australia), allowed access to specimens under their care; V.M. Bueno (Universidade de São Paulo, Brazil) for the English revision. This study was partially supported by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) and Fundação Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES).

References

- Agrawal, N. & Sharma, R. (1986) *Pseudodiplectanum lucknowensis* n. sp., a new monogenean in *Notopterus chitala* (Ham.) from Lucknow. *Uttar Pradesh Journal of Zoology*, 6, 256–260.
- Aljoshkina, L.D. (1984) New species of the family Diplectanidae (Monogenea) in the south-east Atlantic. *Zoologicheskii Zhurnal*, 63, 1253–1256. (In Russian)
- Amine, F. & Euzet, L. (2005) Deux espèces nouvelles du genre *Lamellodiscus* Johnston & Tiegs, 1922 (Monogenea: Diplectanidae) parasites de Sparidae (Teleostei) des côtes de l'Algérie. *Systematic Parasitology*, 60, 187–196.
- Amine, F., Neifar, L. & Euzet, L. (2006) *Lamellodiscus sanfilippo* n. sp. (Monogenea, Diplectanidae) parasite branchial de *Diplodus sargus* (Teleostei, Sparidae) en Méditerranée. *Parasite*, 13, 45–49.
- Amorim, D.S. (1997) *Elementos Básicos de Sistemática Filogenética*. 2^a ed. Holos Editora e Sociedade Brasileira de Entomologia, Ribeirão Preto, SP, Brasil 276 pp.
- Beverly-Burton, M. & Suriano, D.M. (1981) A revision of *Cycloplectanum* Oliver, 1968 (Monogenea: Diplectanidae) and descriptions of *C. hongkongensis* n. sp. and *C. lantauensis* n. sp. from *Epinephelus* spp. (Serranidae) in the South China Sea. *Canadian Journal of Zoology*, 59, 1276–1285.
- Boeger, W.A. & Kritsky, D.C. (1993) Phylogeny and a revised classification of the Monogenoidea Bychowsky, 1937 (Platyhelminthes). *Systematic Parasitology*, 26, 1–32.
- Boeger, W.A. & Kritsky, D.C. (1997) Coevolution of the Monogenoidea (Platyhelminthes) based on a revised hypothesis of parasite phylogeny. *International Journal for Parasitology*, 27, 1495–1511.
- Boeger, W.A. & Kritsky, D.C. (2001) Interrelationships of the Monogenoidea. In: Littlewood, D.T.J. & R.A. Bray (Eds), *Interrelationships of Platyhelminthes*. The systematics Association Special Volume Series 60. pp. 92–102.
- Boeger, W.A., Fehlauer, K.H. & Marques, E.E. (2006) Neotropical Monogenoidea. 49. Four new species of the Diplectanidae (Dactylogyrinea) from the gills of some pachyurines (Teleostei: Sciaenidae) from the Rio Tocantins and Rio Doce Basins, with the proposal of *Anoplectanum* n. g. and *Spinomatrix* n. g. *Systematic Parasitology*, 64, 57–68.
- Bravo-Hollis, M. (1954) *Diplectanum amplidiscatum* n. sp., Trematódes monogenético des branchies d'un poisson Marin. *Annales de Parasitologie Humaine et Comparée*, 29, 37–41
- Bu, S.S., Leong T.S., Wong, S.Y., Woo & Foo, R.W.T. (1999) Three diplectanid monogeneans from marine finfish (*Epinephelus* spp.) in the far east. *Journal of Heminthology*, 73, 301–312.
- Bychowsky, B.E. (1957) *Monogenetic Trematodes. Their systematic and phylogeny*. Akad. Nauka. USSR. English translation by the American Institute of Biological Science, Washington. 509 pp.
- Bychowsky, B.E. & Nagibina, L.F. (1976) New species of the genus *Telegamatrix* Ramalingam, 1955 (Monogenoidea, Diplectanidae). *Biologiya Morya, Vladivostok*, 2, 10–15. (In Russian).
- Bychowsky, B.E. & Nagibina, L.F. (1977) The systematic position of some representatives of lower monogeneans from marine fish. *Parazitologicheskii. Sbornik*, 27, 7–17. (In Russian).
- Byrnes, T. (1987) Six species of *Lamellodiscus* (Monogenea: Diplectanidae) from Australian bream (*Acanthopagrus* spp.). *Publications of the Seto Marine Biological Laboratory*, 31, 169–190.
- Caballero, E., Bravo-Hollis, M. & Grocott, R.C. (1955) Trematodos monogeneos y Digeneos de peces marinos del Oceano Pacífico del Norte con descripción de nuevas formas. *Anales del Instituto de Biología, Universidad Nacional Autónoma de México*, 26, 117–147.
- Chauhan, B.S. (1945) Trematodes from Indian marine fishes. Part I. On some new Monogenetic Trematodes of the sub-order *Monopisthocotylea* Odhner, 1912, and *Polyopisthocotylea* Odhner, 1912. *Proceedings of the Indian Academy of Sciences*, 21, 129–159.
- Chauhan, B.S. (1954) Studies on the trematode fauna of India. Part I. Subclass Monogenea. *Records of the Indian Museum*, 51, 113–208.
- Chaves, N.N., Luque, J.L. & Cezar, A.D. (1999) Redescription of *Rhamnocercus stichospinus* Seamster and Monaco, 1956 (Monogenea: Diplectanidae), parasitic on *Menticirrhus americanus* (Osteichthyes: Sciaenidae) from the Coastal

- Zone of the State of Rio de Janeiro, Brazil. *Memórias do Instituto Oswaldo Cruz*, 94, 615–618.
- Derbel, H., Boudaya, L. & Neifar, L. (2007) *Pseudodiplectanum syrticum* n. sp. (Monogenea: Diplectanidae), a parasite of *Synapturichthys kleinii* (Teleostei: Soleidae) from off Tunisia. *Systematic Parasitology*, 68, 225–231.
- Desdevises, Y., Morand, S. & Oliver, G. (2001) Linking Specialization to Diversification in the Diplectanidae Bychowsky 1957 (Monogenea, Platyhelminthes). *Parasitology Research*, 87, 223–230.
- Desdevises, Y. (2001) The phylogenetic position of *Furnestinia echeneis* (Monogenea, Diplectanidae) based on molecular data: a case of morphological adaptation? *International Journal for Parasitology*, 31, 205–208.
- Diesing, K.M. (1858) Revision des Myzhelminthen. Abteilung: Trematoden. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften in Wien*, 32, 307–390.
- Ding, X.J. & Zhang, J.Y. (1996) Monogenoidea of Chinese marine fishes VIII. A new species of the genus *Calydiscodes* Young, 1969 (Dactylogyridae: Diplectanidae). *Annual Bulletin of the Society of Parasitology of Guangdong Province*, 18, 57–59. (In Chinese).
- Domingues, M.V. & Boeger, W.A. (2003) Neotropical Monogenoidea. 43. *Diplectanum monticellii* n. sp. (Diplectanidae) from the gills of *Cynoscion leiarchus* (Perciformes: Sciaenidae) in Brazil. *The Journal of Parasitology*, 89, 698–700.
- Domingues, M.V. & Boeger, W.A. (2006) Revision and phylogeny of Rhamnocercian Monogenea, Wood et Mizelle, 1954 (Monogenoidea: Diplectanidae). *Folia Parasitologica*, 53, 107–116.
- Domingues, M.V. & Boeger, W.A. (2007) The status of *Acleotrema* Johnston & Tiegs, 1922 and *Heteroplectanum* Rakotofiringa, Oliver & Lambert, 1987 (Monogenoidea: Diplectanidae), with the redescription of *Acleotrema girellae* Johnston & Tiegs, 1922. *Systematic Parasitology*, 66, 35–41.
- Dyer, W.G., Williams, E.H. Jr & Bunkley-Williams, L. (1994) *Pseudorhabdosynochus monaensis* n. sp. (Monogenea: Diplectanidae) on rock hind from Mona Island, Puerto Rico. *Journal of Aquatic Animal Health*, 6, 59–63.
- Dyer, W.G., Williams, E.H. Jr & Bunkley-Williams, L. (1995) *Pseudorhabdosynochus kritskyi* n. sp. (Monogenea: Diplectanidae) on gag from the Gulf of Mexico. *Journal of Aquatic Animal Health*, 7, 337–340.
- Euzet, L. (1984) Diplectanidae (Monogenea) parasites de poissons des îles Kerkennah (Tunisie). *Archives Institut Pasteur Tunis*, 61, 463–474.
- Euzet, L. & Audouin, J. (1959) Sur un genre nouveau de Monogenoidea parasite de la dorade *Chrysophrys aurata* L. *Revue des Travaux de l'Institut scientifique des Pêches maritimes*, 23, 317–322.
- Euzet, L. & Durrete-Desset, M.C. (1974) *Diplectanum cayennensis* n. sp. (Monogenea) parasite branchial de *Plagioscion auratus* (Castelnau, 1855) (Téléostéen, Sciaenidae) sur les côtes de Guyanne. *Bulletin du Museum National d'Histoire Naturelle de Paris*, 3^e série, 137, Zoologie 101, 789–794.
- Euzet, L. & Razarihelisoa, M. (1959) Sur quelques Monogènes de *Sphyraena commersonii* (Telestei, Sphyraenidae). *Bulletin de la Société Zoologique de France*, 84, 77–85.
- Euzet, L. & Oliver, G. (1965) Diplectanidae (Monogenea) des Téléostéens de la Méditerranée occidentale. II. Parasites d'*Epinephelus gigas* (Brünnich, 1768). *Annales de Parasitologie Humaine et Comparée*, 40, 517–523.
- Euzet, L. & Oliver, G. (1966) Diplectanidae (Monogenea) des Téléostéens de la Méditerranée occidentale. III. Quelques *Lamellodiscus* Johnston et Tiegs, 1922, parasites de poissons du genre *Diplodus* (Sparidae). *Annales de Parasitologie Humaine et Comparée*, 41, 573–598.
- Euzet, L. & Oliver, G. (1967) Diplectanidae (Monogenea) de Téléostéens de la Méditerranée occidentale. IV. Quelques *Lamellodiscus* Johnston et Tiegs, 1922, parasites de poissons du genre *Pagellus* Valenciennes, 1830 (Sparidae). *Annales de Parasitologie Humaine et Comparée*, 42, 407–425.
- Euzet, L. & Doussou, C. (1979) Anatomie et position systématique du Monogène *Heterotesia voltae* Paperna, 1969. *Bulletin de l'Institut Français d'Afrique Noire, Série A, Sciences naturelles*, 41, 505–511.
- Goloboff, P., Farris, J. & Nixon, K. (2003) T.N.T.: Tree Analysis Using New Technology. Program and documentation, available from the authors, and at www.zmuc.dk/public/phylogeny (accessed 6 November 2007).
- Gupta, N.K. & Khanna, M. (1974) On some of the monogenetic trematodes of marine fishes from Port-Blair (Andaman and Nicobar Islands, India) Part 1. *Revista Iberica de Parasitologia*, 34: 257–272.
- Gupta, N.K. & Khullar, M. (1967) On a new monogenetic trematode, *Lamellodiscus minousi* n. sp. (Diplectanidae) from gills of the marine food fish at Bombay (India). *Research Bulletin of the Panjab University, Science*, 18, 429–431.
- Gupta, G.P. & Krishna (1979) On some monogenetic trematodes from marine fishes of Puri, Orissa. *Indian Journal of Helminthology*, 31, 81–110.
- Gupta, S.P. & Sharma, R.K. (1982) On some Monogenetic Trematodes of fishes. *Indian Journal of Helminthology*, 34, 85–105.
- Gupta, P.C. & Varsha Sachdeva (1987) *Neohamatopeduncularia bengalensis* gen. nov., sp. nov. and *Lobotrema aspidopariarii* sp. nov. (Monogenea: Dactylogyridae) from the gills of Indian fishes. *Kanpur University Research Journal (Science)*, 5, 51–55.
- Johnston, T.H. & Tiegs, O.W. (1922) New Gyrodactyloid Trematodes from Australian fishes together with a reclassification of the Super-Family Gyrodactyloidea. *Proceedings of the Linnean Society of New South Wales*, 47, 83–131.
- Journo, C. & Justine, J.-L. (2006) *Laticola dae* n. sp. (Monogenea: Diplectanidae) from *Epinephelus maculatus* (Perciformes: Serranidae) off New Caledonia. *Systematic Parasitology*, 64, 173–180.

- Justine, J.-L. (2005a) Species of *Pseudorhabdosynochus* Yamaguti, 1958 (Monogenea: Diplectanidae) from *Epinephelus fasciatus* and *E. merra* (Perciformes: Serranidae) off New Caledonia and other parts of the Indo-Pacific Ocean, with a comparison of measurements of specimens prepared using different methods, and a description of *P. caledonicus* n. sp. *Systematic Parasitology*, 62, 1–37.
- Justine, J.-L. (2005b) *Pseudorhabdosynochus hirundineus* n. sp. (Monogenea: Diplectanidae) from *Variola louti* (Perciformes: Serranidae) off New Caledonia. *Systematic Parasitology*, 62, 39–45.
- Justine, J.-L. (2007a) Species of *Calydiscoides* Young, 1969 (Monogenea: Diplectanidae) from lethrinid fishes, with the redescription of all of the type specimens and the description of *C. euzeti* n. sp. from *Lethrinus rubrioperculatus* and *L. xanthochilus* off New Caledonia. *Systematic Parasitology*, 67, 187–209.
- Justine, J.-L. (2007b) Parasite biodiversity in a coral reef fish: twelve species of monogeneans on the gills of the grouper *Epinephelus maculatus* (Perciformes: Serranidae) off New Caledonia, with a description of eight new species of *Pseudorhabdosynochus* (Monogenea: Diplectanidae). *Systematic Parasitology*, 66, 81–129.
- Justine, J.-L. (2007c) *Pseudorhabdosynochus argus* n. sp. (Monogenea: Diplectanidae) from *Cephalopholis argus*, *P. minutus* n. sp. and *Diplectanum nanus* n. sp. from *C. sonnerati* and other monogeneans from *Cephalopholis* spp. (Perciformes: Serranidae) off Australia and New Caledonia. *Systematic Parasitology*, 68, 195–215.
- Justine, J.-L. & Euzet, L. (2006) Diplectanids (Monogenea) parasitic on the gills of the coral groupers *Plectropomus laevis* and *P. leopardus* (Perciformes, Serranidae) off New Caledonia, with the description of five new species and the erection of *Echinoplectanum* n. g. *Systematic Parasitology*, 64, 147–172.
- Justine, J.-L. & Sigura, A. (2007) Monogeneans of the malabar grouper *Epinephelus malabaricus* (Perciformes, Serranidae) off New Caledonia, with a description of six new species of *Pseudorhabdosynochus* (Monogenea: Diplectanidae). *Zootaxa*, 1543, 1–44.
- Hargis, W.J. Jr. (1955) Monogenetic Trematodes of Gulf of Mexico Fishes. Part III. The Superfamily Gyrodactyloidea (continued). *Quarterly journal of the Florida Academy of Sciences*, 18, 33–47.
- Hayward, C.J. (1996) Revision of diplectanid monogeneans (Monopisthocotylea, Diplectanidae) in sillaginid fishes, with a description of a new species of *Monoplectanum*. *Zoologica Scripta*, 25, 203–213.
- Hinsinger, D.D., & Justine, J.-L. (2006a) *Pseudorhabdosynochus venus* n. sp. (Monogenea: Diplectanidae) from *Epinephelus howlandi* (Perciformes: Serranidae) off New Caledonia. *Systematic Parasitology*, 63, 155–160.
- Hinsinger, D.D., & Justine, J.-L. (2006b) The '*Pseudorhabdosynochus cupatus* group' (Monogenea, Diplectanidae) in *Epinephelus fasciatus*, *E. howlandi*, *E. rivulatus* and *E. merra* (Perciformes: Serranidae) off New Caledonia, with descriptions of *Pseudorhabdosynochus cyathus* n. sp. and *P. calathus* n. sp. *Systematic Parasitology*, 64, 69–90.
- Karyakarte, P.P., & Das, S.R. (1978) A new monogenetic trematode, *Lamellospina indiana* n. gen., n. sp. (Monopisthocotylea: Diplectanidae) from the marine fish, *Nemipterus japonicus* (Günther) in India. *Rivista di Parassitologia*, 34, 19–22.
- Kornet, D.J. & Turner, H. (1999) Coding polymorphism for phylogeny reconstruction. *Systematic Biology*, 48, 365–379.
- Kritsky, D.C. & Thatcher, V.E. (1984) Neotropical Monogenea. 6. Five new species of *Diplectanum* (Diplectanidae) from freshwater Teleosts *Plagioscion* spp. (Scieanidae), in Brazil. *Proceedings of the Biological Society of Washington*, 97, 425–439.
- Kritsky, D.C. & Beverley-Burton, M. (1986) The status of *Pseudorhabdosynochus* Yamaguti, 1958, and *Cycloplecyanum* Oliver, 1968 (Monogenea: Diplectanidae). *Proceedings of the Biological Society of Washington*, 99, 17–20.
- Kritsky, D.C. & Boeger, W.A. (1989) The phylogenetic status of Ancyrocephalidae Bychowsky, 1937 (Monogenea: Dactylogyroidea). *Journal of Parasitology*, 75, 207–211.
- Kritsky, D.C., Jiménez-Ruiz, F.A. & Sey, O. (2000) Diplectanids (Monogeneoidea: Dactylogyridae) from the gills of marine fishes of the Persian Gulf of Kuwait. *Comparative Parasitology*, 67, 145–164.
- Kritsky, D.C., Boeger, W.A. & Robaldo, R.B. (2001) Neotropical Monogeneoidea. 38. Revision of *Rhabdosynochus* Mizelle and Blatz, 1941 (Polionchoinea: Dactylogyridae: Diplectanidae), with description of two new species from Brazil. *Comparative Parasitology*, 68, 66–75.
- Lambert, A. & Maillard, C. (1974) Parasitisme branchial simultan e par deux esp ces de *Diplectanum* Diesing, 1858 (Monogenea, Monopisthocotylea) chez *Dicentrarchus labrax* (L., 1758) (T leost ens). *Comptes rendus hebdomadaires des seances de l'Academie des sciences, Serie D, Sciences naturelles*, 279, 1345–1347.
- Laird, M. (1958) Parasites of South Pacific Fishes II. *Diplectanum melanesiensis* n. sp., a monogenetic trematode from Fiji and the New Hebrides. *Canadian Journal of Zoology*, 36, 167–173.
- Le n-R gagnon, V., P rez-Ponce de Le n, G. & Garc a-Prieto, L. (1997) Description of *Heteroplectanum oliveri* sp. n. (Monogenea: Diplectanidae) and comments on the helminth fauna of *Kyphosus elegans* (Perciformes: Kyphosidae) from Chamela Bay, M xico. *Proceedings of the Helminthological Society of Washington*, 64, 9–16.
- Li, Z.C., Yan, P.H., Liu, L. & Yu, X.D. (1995) Monogeneoidea of Chinese marine fishes. V. Some monogeneans of the families Diplectanidae and Ancyrocephalidae from sparids and serranids in South China Sea. *Proceedings of the Tenth Anniversary of the Founding of China Parasitological Society* (1985–1995), Beijing: Science Press, 88–92. (In Chinese).
- Lim, L.H.S. (2003) Species of *Calydiscoides* Young, 1969 (Monogenea: Diplectanidae) Bychowsky, 1957: Lamelloglyptid

- nae Oliver, 1969) from the nemipterid fishes off Peninsular Malaysia. *Systematic Parasitology*, 55, 115–126.
- Lim, L.H.S. (2006) Diplectanids (Monogenea) on the archerfish *Toxotes jaculatrix* (Pallas) (Toxotidae) off Peninsular Malaysia. *Systematic Parasitology*, 64, 13–25.
- Lim, L.H.S. & Gibson, D.I. (2007) *Diplectanocotyla* Yamaguti, 1953 (Monogenea: Diplectanoidea) from *Megalops cyprioides* (Broussonet) (Teleostei: Megalopidae) off Peninsular Malaysia. *Systematic Parasitology*, 67, 101–117.
- Luque, J.L. & Iannaccone, J. (1991) Rhamnocercidae (Monogenea: Dactylogyroidea) in Sciaenidae fishes from Perú, with description of *Rhamnocercoides menticirrho* n. gen., n. sp. and two new species of *Rhamnocercus*. *Revista de Biología Tropical*, 39, 193–201.
- Maillard C, & Vala, J-C. (1980) Two new species of Monogenea of the genus *Pseudodiplectanum* Tripathi, 1955, branchial parasites of *Galeoides decadactylus*, a teleostean from the coast of Gabon. *Systematic Parasitology*, 1, 111–116.
- Mendoza-Franco, E.F., Violante-González, J. & Vidal-Martínez, V.M. (2006) A New Diplectanid (Monogenea) Genus and Species from the Gills of the Black Snook, *Centropomus Nigrescens* (Perciformes: Centropomidae) of the Pacific Coast of Mexico. *Journal of Parasitology*, 92, 481–485.
- Mendoza-Franco, E.F., Kritsky, D.C., Vidal-Martínez, V.M., Scholz, T. & Aguirre-Macedo, M.L. (2004) Neotropical Monogenoidea. 45. Revision of *Diplectanocotyla* Yamaguti, 1953 (Diplectanidae) with redescription of *Diplectanocotyla megalopis* Rakotofiringa and Oliver, 1987 on the Atlantic Tarpon, *Megalops atlanticus* Cuvier and Valenciennes, from Nicaragua and Mexico. *Comparative Parasitology*, 71, 158–165.
- Mizelle, J.D. & Blatz, V. (1941) Studies on Monogenetic Trematodes VI. Two new dactylogyrid genera from Florida fishes. *American Midland Naturalist*, 26, 105–109.
- Mizelle, J.D. & Kritsky, D.C. (1969) Studies on Monogenetic Trematodes. XL. New Species from Marine and Freshwater Fishes. *American Midland Naturalist*, 82, 417–428.
- Monaco, H.L., Wood, R.A. & Mizelle, J.D. (1954) Studies on monogenetic trematodes. XVI. Rhamnocercinae new subfamily of Dactylogyridae. *American Midland Naturalist*, 52: 129–132.
- Monticelli, F.C. (1903) Per una nuova classificazione degli “Heterocotylea”. *Monitore Zoologico Italiano*, 14, 334–336.
- Muller, J.F. (1936) New Gyrodactyloid Trematodes from North American Fishes. *Transactions of the American microscopical Society*, 55, 457–464.
- Murray, F.V. (1931) Gill trematodes from some Australian fishes. *Parasitology* 23, 492–506.
- Nagibina, L.F. (1976) New species of the genus *Diplectanum* (Monogenoidea, Diplectanidae). *Trudy Biologo-Pochvennogo Instituta*, 35, 89–96. (In Russian).
- Nagibina, L.F. (1977) New data on the genus *Pseudodiplectanum* Tripathi, 1955 (Monogenoidea, Diplectanidae). In: *Excerta Parasitológica en memoria del Doctor Eduardo Caballero y Caballero*. México. *Instituto de Biología, Publicaciones Especiales*, 4, 85–89.
- Neifar, L., Euzet, L. & Oliver, G. (2004) *Lamellodiscus* (Platyhelminthes, Monogenea, Diplectanidae) nouveaux parasites branchiaux des poissons marins du genre *Pagrus* (Teleostei, Sparidae). *Zoosystema*, 26, 365–376.
- Neifar, L. & Euzet, L. (2007) Five new species of *Pseudorhabdosynochus* (Monogenea: Diplectanidae) from the gills of *Epinephelus costae* (Teleostei: Serranidae). *Folia Parasitologica*, 54, 117–128
- Nixon, K.C. & Carpenter, J.M. (1993) On Outgroup. *Cladistics*, 9, 413–426.
- Obiekezie, A.I. (1988) Some species of *Diplectanum* Diesing, 1858 (Monogenea: Dactylogyroidea) parasites of marine fishes from the Nigerian coast. *Journal of African Zoology*, 102, 133–142.
- Ogawa, K. & Egusa, S. (1978) Three species of *Lamellodiscus* (Monogenea: Diplectanidae) from the gills of the Japanese Black Sea Bream, *Acanthopagrus schlegelii* (Bleeker). *Bulletin of the Japanese Society of Scientific Fisheries*, 44, 607–612.
- Oliver, G. (1968) Recherches sur les Diplectanidae (Monogenea) parasites de Téléostéens du Golfe du Lion. I. Diplectaninae Monticelli 1903. *Vie et Milieu, Serie A, Biologie marine*, 19, 95–138.
- Oliver, G. (1969) Recherches sur les Diplectanidae (Monogenea) parasites de Téléostéens du Golfe du Lion. II. Lamellogiscinae nov. sub. fam. *Vie et Milieu, Serie A, Biologie marine*, 20, 43–72.
- Oliver, G. (1969) Recherches sur les Diplectanidae (Monogenea) parasites de Téléostéens du Golfe du Lion. III. Biologie. *Vie et Milieu, Serie A, Biologie marine*, 20, 397–420.
- Oliver, G. (1973) *Lamellodiscus obeliae* n. sp. une nouvelle espèce de Diplectanidae (Monogenea, Monopisthocotylea) parasite de *Pagellus centrodonatus* (Delaroche, 1809) (Pisces, Sparidae). *Zeitschrift für Parasitenkunde*, 41, 103–108.
- Oliver, G. (1974) Nouveaux aspects du parasitisme des Diplectanidae Bychowsky 1957 (Monogenea, Monopisthocotylea) chez les Téléostéens Perciformes des côtes de France. *Comptes rendus hebdomadaires des séances de l'Académie des sciences de Paris*, 279, série 10, 803–805.
- Oliver, G. (1980a) Les Diplectanidae Bychowsky 1957 (Monogenea, Monopisthocotylea) parasites des Sciaenidae (Pisces, Perciformes) du Golfe de Gascogne. *Bulletin du Museum National d' Histoire Naturelle, Zoologie, Paris*, 4^{ème} série, 2 Sect A, 669–689.
- Oliver, G. (1980b) Description de *Pseudodiplectanum kearni* n. sp. (Monogenea, Diplectanidae), des côtes européennes,

- parasite d'un Poisson Pleuronectiforme. *Bulletin du Museum National d' Histoire Naturelle, Zoologie, Paris*, 4^{ème} série, 2 Sect A, n° 3, 691–695.
- Oliver, G. (1982) Quelques aspects de la spécificité parasitaire chez les Diplectanidae Bychowsky, 1957 (Monogenea, Monopisthocotylea). *Bulletin du Museum National d' Histoire Naturelle, Zoologie, Paris*, série A, 123, 295–301.
- Oliver, G. (1983) *Diplectanum yamagutii* sp. n. (Monogenea, Monopisthocotylea, Diplectanidae), parasite de *Kyphosus cinerascens* (Forsskal) à Hawaii. *Zoologica Scripta*, 12, 91–93.
- Oliver, G. (1984) Quelques espèces du genre *Calydiscooides* Young (Monogenea, Monopisthocotylea, Diplectanidae), parasites de Perciformes du Récif de la Grande Barrière (Australie). *Zoologica Scripta*, 13, 189–193.
- Oliver, G. (1987) *Les Diplectanidae Bychowsky 1957 (Monogenea, Monopisthocotylea, Dactylogyridea). Systématique. Biologie. Ontogénie. Écologie. Essai de phylogénèse. Thèse d'état.* Université des Sciences et Techniques du Languedoc, Montpellier, France, 433 pp.
- Oliver, G. (1993) Les Diplectanidae Bychowsky, 1957 (Monogenea, Monopisthocotylea, Dactylogyridea) marqueurs biologiques, témoins de la biogéographie et de l'évolution de leurs hôtes. *Bulletin de la Société Zoologique de France*, 118, 25–36.
- Oliver, G. & Paperna, I. (1984) Diplectanidae Bychowsky 1957 (Monogenea, Monopisthocotylea) parasites de Perciformes de Méditerranée orientale, de la Mer Rouge et de l'Océan Indien. *Bulletin du Museum National d' Histoire Naturelle, Zoologie, Paris*, 4^{ème} série, 6, Sect A, 49–65.
- Oliver, G. & Radujkovic, B. (1987) *Protolamellodiscus raibauti* n. sp., une nouvelle espèce de Diplectanidae Bychowsky, 1957 (Monogenea, Monopisthocotylea) parasite de *Diplodus annularis* (Linnaeus, 1758) (Sparidae). *Annales de Parasitologie Humaine et Comparée.*, 62, 209–213.
- Palombi, A. (1943) Notizie Elmintologiche. V. *Diplectanum (Dactylogyrus) echeneis* (Wag.) Par. et Per. = *Lamellodiscus ignoratus* n. sp. Diagnosi della specie e suoi opistatori. *Annuario dell' Istituto e Museo di Zoologia dell' Università di Napoli*, 7, 1–5.
- Paperna, I. (1965) Contribution to the knowledge of the Red Sea. No 32. Monogenetic Trematodes from the gills of Red Sea fishes. *Bulletin of the Sea Fisheries Research Station of Israel*, 39, 17–26.
- Paperna, I. & Kohn, A. (1964) Report on Monogenetic Trematodes collected from eastern Mediterranean. *Revista Brasileira de Biologia*, 24, 243–248.
- Pillai, V.S., & Pillai, N.K. (1976) Monogenean parasites of the marine fishes of the Kerala coast. I. *Aquatic Biology*, 1, 85–100.
- Price, E.W. (1937) North American Monogenetic Trematodes. I. The superfamily Gyrodactyloidea. (continued). *Journal of the Washington Academy of Science*, 27, 146–164.
- Rakotofiringa, S. & Maillard, C. (1979) Helminthofaune des Teleostei de Madagascar. Révision du genre *Pseudolamellodiscus* Yamaguti, 1953. *Annales de Parasitologie Humaine et Comparée*, 54, 507–518.
- Rakotofiringa, S. & Oliver, G. (1987) Révision du genre *Diplectanocotyla* Yamaguti, 1953 avec description d'une espèce nouvelle et création de la famille des Diplectanocotylidae nov. fam. (Monogenea, Monopisthocotylea). *Bulletin du Museum National d' Histoire Naturelle*, 4, 333–339.
- Rakotofiringa, S., Oliver, G. & Lambert, A. (1987) *Heteroplectanum* n. gen., un nouveau genre de Diplectanidae Bychowsky, 1957 (Monogenea, Monopisthocotylea) parasite de Téléostéens marins de Madagascar. *Bulletin du Museum National d' Histoire Naturelle, Zoologie, Paris*, 4^{ème} série 9, Sect A (1):145–157.
- Ramalingam, K. (1955) A remarkable organism, *Telegamatrix pellona* gen. and sp. nov. (Monogenea: Diplectaninae) parasitic in an Indian herring. *Proceedings of the Indian Academy of Sciences, Section B, Biological Sciences*, 42, 209–218.
- Rao, G.P. & Kulkarni, T. (1985) *Pseudolamellodiscus polynemus* n. sp. From the gills of *Polynemus sexfilis* of the coast of Bay of Bengal at Kakinada, Andhra Pradesh, India. *Proceedings of the Indian Academy of Parasitology*, 6, 51–54.
- Rascalou, G. & Justine, J-L. (2007) Three species of *Calydiscooides* (Monogenea: Diplectanidae) from five *Lethrinus* spp. (Lethrinidae: Perciformes) off New Caledonia, with a description of *Calydiscooides terpsichore* sp. n. *Folia Parasitologica*, 54, 191–202.
- Roubal, F. (1981) The taxonomy and site specificity of the Metazoan ectoparasites on the Black Bream, *Acanthopagrus australis* (Günther), in Northern New South Wales. *Australian Journal of Zoology, Supplementary Series*, 84, 1–100.
- Santos, C.P., Buchmann, K. & Gibson, D.I. (2000) *Pseudorhabdosynochus* spp. (Monogenea: Diplectanidae) from the gills of *Epinephelus* spp. in Brazilian waters. *Systematic Parasitology*, 45, 145–153.
- Santos, C.P., Timi J.T. & Gibson D.I. (2002) *Diplectanum squamatum* n. sp. (Monogenea: Diplectanidae) from the gills of *Cynoscion guatucupa* (Sciaenidae) in the Southwest Atlantic waters. *Systematic Parasitology*, 52, 199–204.
- Seng, L.K. & Seng, L.T. (1991) A redescription of *Pseudorhabdosynochus latesi* (Tripathi 1955) and description of *Diplectanum penangi* n. sp. (Monogenea: Diplectanidae) from *Lates calcarifer* cultured in floating cages in Malaysia and Thailand. *Journal of Biosciences*, 2, 77–84.
- Sigura, A., Chauvet, C. & Justine, J-L (2007) *Pseudorhabdosynochus bacchus* sp. n. (Monogenea, Diplectanidae) from *Epinephelus coeruleopunctatus* (Perciformes, Serranidae) off New Caledonia. *Acta Parasitologica*, 52, 196–200.

- Srivastava, J.K. & Kumar, R. (1983) On a new monogenetic trematode *Lobotrema rajendrai* n. sp. from the gills of a fresh water fish *Garra gotyla* (Gray). *Indian Journal of Forestry*, 6, 330–331.
- Thoney, D.A. (1989) Morphology of *Calydiscoides nemipteris*, sp. nov. (Monogenea), with a redescription and revision of the Genus. *Australian Journal of Zoology*, 37, 37–43.
- Thurston, J.P. & Paperna, I. (1969) *Diplectanum lacustris* sp. nov. (Dactylogyroidea, Diplectanidae), a monogenetic Trematode from the gills of the Nile Perch. *Proceedings of the Helminthological Society of Washington*, 36, 214–218.
- Tripathi, Y.R. (1957) Studies on parasites of Indian fishes. II. Monogenea, family Dactylogyridae. *Indian Journal of Helminthology*, 7, 5–24.
- Tripathi, Y.R. (1959) Monogenetic Trematodes from fishes of India. *Indian Journal of Helminthology*, 9, 1–149.
- Unnithan, R.V. (1964) Four new polyonchoineans (*Monogenoidea*) parasitic on gills of marine fishes from the Indian seas. *Journal of Parasitology*, 50, 241–247.
- Vala, J.C., Lopez Roman, R. & Boudaoud, K. (1980) *Pseudodiplectanum kearneyi* n. sp. (Monogenea, Diplectanidae) parasite branchial de *Solea vulgaris* Quensel, 1806 en Méditerranée. *Revista Iberica de Parasitologia*, 40, 21–26.
- Van Beneden, P.J. & Hesse, C.E. (1863) Recherches sur Bdelloides et les Trématodes marins. *Memoires, Academie royale de Belgique, Classe des Sciences*, 34, 1–150.
- Vidal-Martinez, V.M. & Mendoza-Franco, E.F. (1998) *Pseudorhabdosynochus capurroi* sp. n. (Monogenea, Diplectanidae) from the gills of *Mycteroperca bonaci* (Pisces, Serranidae) of the Yucatan peninsula, Mexico. *Folia Parasitologica*, 45, 221–224.
- Vidal-Martinez, V.M., Aguirre-Macedo, L. & Mendoza-Franco, E.F. (1997) *Pseudorhabdosynochus yucatanensis* sp. n. (Monogenea, Diplectanidae) from the gills of the red grouper *Epinephelus morio* (pisces, serranidae) of the Yucatan peninsula, Mexico. *Folia Parasitologica* 44, 274–278.
- Venkatanarsaiah, J. & Kultani, T. (1980) On a new monogenetic trematode, *Lamellodiscus caballeroi* n. sp., from the gills of *Crenidens indicus* at Machilipatnam Coast, Andhra Pradesh, India. *Proceedings of the Indian Academy of Parasitology*, 1, 23–26.
- Wu, X.Y, Li, A.X., Zhu, X.Q. & Xie, M.Q. (2005) Description of *Pseudorhabdosynochus seabassi* sp. n. (Monogenea: Diplectanidae) from *Lates calcarifer* and the revision of the phylogenetic position of *Diplectanum grouperi* (Monogenea: Diplectanidae) based on rDNA sequence data. *Folia Parasitologica*, 52, 231–240.
- Wagener, G. (1857) Helminthologische Bemerkungen aus einem Sandsschreibe an C. Th. v. Siebold. *Zeitschrift fur Wissenschaftliche Zoologie*, 9, 73–90.
- Williams, A. (1989) Some monogenean parasites of the genera *Calceostoma* van Beneden, 1852 and *Diplectanum* Diesing, 1858 from *Argyrosomus hololepidotus* (Lacépède, 1802) (Sciaenidae: Teleostei) in Western Australia. *Systematic Parasitology*, 14, 187–201.
- Wiley, E.O. (1981) *Phylogenetics. The theory & practice of phylogenetic systematics*. New York, John Wiley and Sons. 439 pp.
- Yamaguti, S. (1934) Studies of the helminth fauna of Japan. Part 2. Trematodes of fishes. I. *Japanese Journal of Zoology*, 5, 249–541.
- Yamaguti, S. (1953) Parasitic worms mainly from Celebes. Part 2. Monogenetic trematodes of fishes. *Acta Medicinæ Okayama*, 8, 203–256.
- Yamaguti, S. (1958) Studies of the helminth fauna of Japan. Part 53. Trematodes of fishes. XII. *Publications of the Seto Marine Biological Laboratory*, 7, 53–88.
- Yamaguti, S. (1963) *Systema Helmithum IV. Monogenea and Aspidocotylea*. London-New York, Interscience Publishers. 699 pp.
- Yamaguti, S. (1965) New monogenetic trematodes from Hawaiian fishes. I. *Pacific Science*, 19, 55–95.
- Yamaguti, S. (1968) *Monogenetic Trematodes of the Hawaiian Fishes*. University of Hawaii Press. 287 pp.
- Yang, T., Gibson, D.I. & Zeng, B. (2005) *Pseudorhabdosynochus summanooides* n. sp. (Monogenea: Diplectanidae) from *Epinephelus coioides* in Dapeng Bay, South China Sea, with observations on several similar species of *Pseudorhabdosynochus* Yamaguti, 1958. *Systematic Parasitology*, 62, 221–239.
- Yang, T., Zeng, B. & Gibson, D.I. (2005) Description of *Pseudorhabdosynochus shenzhenensis* n.sp. (Monogenea: Diplectanidae) and redescription of *P. serrani* Yamaguti, 1953 from *Epinephelus coioides* off Dapeng Bay, Shenzhen, China. *Journal of Parasitology*, 91, 808–813.
- Yang, T., Kritsky, D.C., Sun, Y, Zhang, J., Shi, S. & Agrawal, N. (2006) Diplectanids infesting the gills of the barramundi *Lates calcarifer* (Bloch) (Perciformes: Centropomidae), with the proposal of *Laticola* n. g. (Monogenoidea: Diplectanidae). *Systematic Parasitology*, 63, 125–139.
- Young, P.C. (1968) The taxonomy of some Dactylogyrid Monogenoidea from Australian fishes. *Zoologischer Anzeiger*, 180, 169–179.
- Young, P.C. (1969) Some monogenoideans of the family Diplectanidae Bychowsky 1957, from Australian Teleost fishes. *Journal of Helminthology*, 43, 223–254.
- Zambrano, J.L.F. (1997) Dos especies nuevas de monogéneos (Diplectanidae) parásitos de peces marinos de la Laguna

- de la Restinga. *Anales del Instituto de Biología, Universidad Nacional Autónoma de México, serie Zoología*, 68: 225–236.
- Zhang, J.Y., Liu, L. & Ding, X.J. (1995) Monogenea of Chinese marine fishes. IV. Two new species of the genus *Diplectanum* Diesing, 1858, from sciaenid fishes in East China Sea (Monogenea: Diplectanidae). *Proceedings of the Tenth Anniversary of the Founding of the China Parasitological Society (1985–1995)*. Beijing: Science and Technology Press, pp. 83–87. (In Chinese).
- Zhang, J.Y., Yang, T.B. & Liu, L. (2001) *Monogeneans of Chinese marine fishes*. Beijing: Agriculture Press, 400 pp. (In Chinese).
- Zhang, J.Y., Liu, L., Ding, X.J. & Chen, Z.B. (2000) Monogenea of Chinese marine fishes. XI. Two new species of the genus *Diplectanum* Diesing, 1858. *Acta Hydrobiologica Sinica*, 24, 150–154. (In Chinese).
- Zeng, B. & Yang, T. (2007) Description of *Pseudorhabdosynochus justinei* n. sp. (Monogenea: Diplectanidae) and redescription of *P. vagampullum* (Young, 1969) Kritsky & Beverley-Burton, 1986 from the gills of the longfin grouper *Epinephelus quoyanus* (Valenciennes) (Perciformes: Serranidae) in Dapeng Bay, South China Sea. *Systematic Parasitology* 66, 223–235.
- Zhukov, E.V. (1970) New species of digeneans and monogeneans of marine fishes of the Bay of Psjet (Sea of Japan). *Parazitologiya*, 4, 321–326. (In Russian).

Appendix 1. Specimens of diplectanid species examined.

1 specimen of *Acleotrema girellae* (AM n° W875); 11 specimens of *Acleotrema kyphosi* (USNPC n° 63663.02 ; USNPC n°63149–63151; QM n°GL 13643–48; CNHE n° 2731); 2 specimens of *Acleotrema nenu* (USNPC n°63659; CNHE n°2730); 9 specimens of *Acleotrema sp.* (QM n° GL 13649–57); 1 specimen of *Calydiscoides australis* (HWML n° 1370); 1 specimen of *Calydiscoides difficilis* (MNHNP n° 186 TC–Tj 126); 1 specimen of *Calydiscoides flexuosus* (HWML n° 15019); 2 specimens of *Calydiscoides nemipteris* (QM n°GL 10099–10100; USNPC n°80293); 1 specimen of *Calydiscoides rohdei* (MNHNP n° 188 TC–Tj 128); 2 specimens of *Cornutohaptor nigrescens* (USNPC n° 97290); 1 specimen of *Cycloplectanum beverleyburtonae* (MNHNP n°249 H–Tc 167bis); 1 specimen of *Cycloplectanum cupatum* (USNPC n°76725); 1 specimen of *Cycloplectanum echinophallus* (USNPC n° 77470); 1 specimen of *Cycloplectanum lantauensis* (USNPC n°76725); 1 specimen of *Cycloplectanum riouxi* (MNHNP n° 27 TF–Tj 145); 1 specimen of *Cycloplectanum vagapullum* (USNPC n°76725); 1 specimen of *Diplectanocotyla gracilis* (USNPC n° 84683); 2 specimens of *Diplectanum aequans* (MNHNP n°246 H–TC 164bis); 1 specimen of *Diplectanum americanum* (USNPC n° 35703.02); 2 specimens of *Diplectanum cayennense* (MNHNP n° 165 TC Ti 180–181); 2 specimens of *Diplectanum cazauxi* (HWML n° 15023); 1 specimens of *Diplectanum cupatum* (HWML n° 1368); 1 specimen of *Diplectanum curvivagina* (USNPC n° 63656); 2 specimens of *Diplectanum dollfusi* (USNPC n° 77466); 2 specimens of *Diplectanum fluviatile* (AM n°8931, W 874; HWML n°1404); 2 specimens of *Diplectanum grassei* (MNHNP n°58 PC–Tj 17–18); 2 specimens of *Diplectanum jaculator* (HWML n°21281); 1 specimen of *Diplectanum magnodiscatum* (EDIMAR i n°596); 2 specimens of *Diplectanum megacirrus* (MNHNP n°194 PE–Tj 31–32); 10 specimens of *Diplectanum monticellii* (CHIOC n°34962–34963 a–c, 34964, 34965; HWML n°17604–17605; W.A.B. Collection); 1 specimen of *Diplectanum opakapaka* (USNPC n° 63660); 1 specimen of *Diplectanum priacanthi* (USNPC n° 63661); 1 specimen of *Diplectanum sciaenae* (USNPC n°76359); 2 specimens of *Diplectanum sillagonum* (HWML n° 15022); 1 specimen of *Diplectanum spiculare* (USNPC n°63663); 2 specimens of *Diplectanum spinosum* (MNHNP n°PE–Tj 33–34); 5 specimens of *Diplectanum squamatum* (CHIOC n° 34538 a–d; W.A.B. collection); 3 specimens of *Diplectanum yamagutii* (USNPC n°63663, n°63657, n°63665); 1 specimen of *Furnestinia echeneis* (MNHNP n° 258 H–Tc 1976); 12 specimens of *Geneticoenteron lateolabracis* (MPM n° 22562); 2 specimens of *Heteroplectanum nenuoides* (MNHNP n°59 H–Ti101–102); 3 specimens of *Heteroplectanum oliveri* (USNPC n°84878); 3 specimens of *Heteroplectanum parastromatei* (MNHNP n°61 HC–Ti 104–105; n°59 H–Ti101); 2 specimens of *Heteroplectanum serrulopenis* (MNHNP n°62 HC–Ti 106–107); 2 specimens of *Heteroplectanum tamatavense* (MNHNP n°60 HC–Ti 103); 1 specimen of *Lamellodiscus acanthopagri* (AM n° W 17054); 1 specimen of *Lamellodiscus butcheri* (AM n° W 198991); 1 specimen of *Lamellodiscus cirruspiralis* (AM n° W 198994); 1 specimen of *Lamellodiscus drummondi* (MNHNP n° 255 H–Tc 173); 1 specimen of *Lamellodiscus furcillatus* (HWML n° 15024); 1 specimen of *Lamellodiscus mormyri* (MNHNP n° 257 H–Tc 175 bis); 1 specimen of *Lamellodiscus pagrosomi* (AM n° W 194646); 1 specimen of *Lamellodiscus squamosus* (AM n° 17056); 1 specimen of *Lamellodiscus vaginalis* (AM n° W 198993); 4 specimen of *Latericaecum pearsoni* (USNPC n°63160; HWML n° 1373); 4 specimens of *Laticola lingaoensis* (USNPC n° 96274); 1 specimen of *Lepidotrema angustum* (HWML n° 174); 1 specimen of *Lepidotrema fuliginosum* (AM n° W 870); 3 specimens of *Lepidotrema kuwaitensis* (HWML n°15025); 1 specimen of *Lepidotrema tenue* (AM n° W 879); 1 specimen of *Lepidotrema terapon* (AM n° W 4525); 1 specimen of *Monoplectanum australis* (HWML n° 1370); 2 specimens of *Murraytrema copulata* (USNPC n°71438–71439); 12 specimens of *Murraytrematoides ditrematis* (MPM n° 22563); 4 specimens of *Murraytrematoides price* (CNHE n° 213–1); 2 specimens of *Nasobranchitrema pacificum* (USNPC n° 61295, 63506); 1 specimen of *Protolamellodiscus raibauti* (MNHNP n° 43 HC–Tj 174); 3 specimens of *Protolamellodiscus senilobatus* (HWML 15021); 1 specimen of *Protolamellodiscus serranelli* (MNHNP n° 161 Z–Tb 122); 1 specimen of *Pseudodiplectanum kearneyi* (MNHNP n°884 TA–Tj 28); 1 specimen of *Pseudolamellodiscus nossibei* (MNHNP n°71 HC–Ti 112); 4 specimens of *Pseudolamellodiscus sphyraenae* (MNHNP n°42 HC–Tj 173; HWML n°15020); 1 specimen of *Pseudomurraytrema alabarrum* (HWML n° 1449); 2 specimens of *Pseudomurraytrema copulata* (HWML n° 23854); 3 specimens of *Pseudomurraytrema rogersi* (USNPC n° 70475); 6 specimens of *Rhabdosynochus rhabdosynochus* (HWML n° 21551; W.A.B. collection); 2 specimens of *Rhabdosynochus hargisi* (W.A.B. collection); 1 specimen of *Rhamnocercoides menticirri* (MHNUNMSM n° 1729); 20 specimens of *Rhamnocercoides stichospinus* (CHIOC n° 33959a–f.; CHMZUSP n° 6138 a–k; IPCR n° M–419); 2 specimens of *Rhamnocercus bardiella* (USNPC n° 49345–49346); 1 specimen of *Rhamnocercus margaritae* (EDIMAR i n° 608); 1 specimen of *Rhamnocercus oliveri* (MHNUNMSM n° 1727); 2 specimens of *Rhamnocercus rhamnocercus* (USNPC n° 49426); 1 specimen of *Rhamnocercus stelliferi* (MHNUNMSM n° 1728).