A new genus and species of mesoparasitic ergasilid (Copepoda: Cyclopoida) from brackish water pufferfishes collected in northern Australian waters

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Abstract A new mesoparasitic ergasilid copepod, *Majalincola buthi* n. g., n. sp., is described based on material collected from the gills of *Marilyna darwinii* (Castelnau) and *M. meraukensis* (de Beaufort) (Tetraodontidae) captured in brackish waters in northern Australia. The new genus is characterised by the presence in the fully-transformed adult female of: four tagmata (antennary, neck, postantennary cephalothoracic region and trunk region); a 5-segmented antennule; a trimerous leg 1 endopod; and a free exopod segment armed with two setae on the fifth leg. The establishment of the new genus is supported by the results of a cladistic analysis of *Majalincola* and members of its sister taxon.

Introduction

The copepod family Ergasilidae von Nordmann, 1832 currently contains 25 genera and over 260 species, many of which are found in fresh water and some in

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brackish or coastal environments (Lin & Ho, 1998; Boxshall & Halsey, 2004). Post-mated adult females from 22 of these 25 genera parasitise fishes, whilst those of the monotypic *Teredophilus* Rancurel, 1954 infect solely brackish water bivalve molluscs, and those in the monotypic *Vaigamus* Thatcher & Robertson, 1984 and *Pseudovaigamus* Amado, Ho & Rocha, 1995 have been collected thus far from the plankton (Harding, 1964; Thatcher & Robertson, 1984). Of these 22 fish-inhabiting genera, 19 are ectoparasitic, using their modified prehensile antennae to attach to the gills, fins and nasal cavities of their hosts (El-Rashidy & Boxshall, 1999). The remaining three fish-parasitic genera (i.e. *Therodamas* Krøyer, 1864, *Paeonodes* C. B. Wilson, 1944 and *Mugilicola* Tripathi, 1960) are mesoparasites, living with their anterior ends buried in the host and their posterior ends protruding from the host tissue (Boxshall & Montú, 1997). These three genera utilise a broad range of host families, with *Therodamas* reported from the Carangidae, Characidae, Dactyloscopidae, Mugilidae, Sciaenidae and Serranidae, *Paeonodes* occurring on the Cichlidae, Mugilidae, Salmonidae and Verillidae and *Mugilicola* recorded from the Anguillidae, Mugilidae and Sillaginidae (El-Rashidy & Boxshall, 2001). Furthermore, these mesoparasitic genera exhibit collectively a Gondwana distribution: *Therodamas* has been reported from the Neotropical region only; *Paeonodes* occurs in the Ethiopian and Australasian regions; and *Mugilicola* is distributed in the Ethiopian, Oriental

and Australasian regions (El-Rashidy & Boxshall, 2001). The current paper describes a new mesoparasitic ergasilid genus collected from two brackish water pufferfish species captured in northern Australian waters. The results of the cladistic analyses of the ergasilid genera, as well as between the new taxon and members of its sister taxon, are also presented to support the establishment of the new genus.

Materials and methods

Preserved *Marilyna darwinii* (Castelnau) and *M. meraukensis* (de Beaufort) specimens deposited at the Museum and Art Gallery of the Northern Territory (MAGNT), Darwin, Australia and the Western Australian Museum (WAM), Perth, Australia, respectively, were examined during June, 2003 for parasitic copepods. Gills containing attached copepods were excised from the fish hosts and subsequently stored in 70% ethanol. Copepods were dissected from the gills by using fine forceps and probes to carefully tease away the epithelial tissue ensheathing the anterior portion of the copepods' body. Copepods were then soaked in lactic acid, into which several lignin pink crystals had been dissolved, for a minimum of 24 h prior to examination using an Olympus BX-50 compound microscope. Selected specimens were measured using a calibrated eyepiece micrometer, dissected and examined according to the wooden slide procedure of Humes & Gooding (1964). Drawings were made with the aid of a camera lucida. Anatomical terminology follows El-Rashidy & Boxshall (2001).

Majalincola n. g.

Diagnosis
Late metamorphic female. Antennules and antennae separated from oral area by elongated neck. Oral area fused with first pedigerous somite forming globose postantennary cephalothoracic region; tagma wider than antennary region. Second to fourth pedigerous somites and urosomites free, decrease in width posteriorly, form narrow trunk region. Genital double-somite suborbicular. Egg-sacs paired, multiseriate. Three free abdominal somites present.

Caudal ramus armed with 4 setae. Antennule 5-segmented. Antenna 4-segmented, compact. Mandible armed with 3 blades. Maxillule lobate, bears 2 setae and spinous process. Maxilla 2-segmented, armed with spinules on distal segment. Maxilliped absent. Legs 1 to 3 biramous and trimerous. Leg 4 with bimerous exopod and trimerous endopod. Free segment of leg 5 armed with 2 setae. Mesoparasites of pufferfishes.

Pre-metamorphic female. Similar to late metamorphic female, except antennules and antennae separated from oral area by short incipient neck and postantennary cephalothoracic region not expanded, narrower than antennary region.

Early metamorphic female. Similar to late metamorphic female, except antennules and antennae separated from oral area by shorter neck and postantennary cephalothoracic region slightly inflated, as wide as antennary region.

Male: Unknown.

Type-species: *M. buthi* n. sp.

Etymology: The generic name is an amalgamation of *majalin* (= a term used by the Wagiman Aboriginal tribe of the Northern Territory for fish) and the Latin *incola* (= an inhabitant), referring to the copepod's lifestyle.

Majalincola buthi n. sp.

Type-host: *Marilyna meraukensis* (de Beaufort) (Tetraodontiformes: Tetraodontidae), fish specimen in WAM fish collection (WAM P.25038.003), collected 31 August, 1974.

Other host: *Marilyna darwinii* (Castelnau) (Tetraodontiformes: Tetraodontidae), fish specimens in MAGNT fish collection (MAGNT S.11360-005), collected 23 July, 1984.

Type-locality: Prince Regent River, Western Australia, Australia (15°38′S, 125°19′E).

Other localities: Joseph Bonaparte Gulf, Western Australia, Australia (14°35′S, 128°23′E), ex *M. meraukensis* (WAM P.29104.001), collected February 1968; Darbilla Creek, Northern Territory, Australia (12°16′S, 135°32′E), ex *M. darwinii* (MAGNT S.11360-005).

Attachment site: Late metamorphic females were nestled between the base of two gill filaments, with the postantennary and neck regions embedded into

the gill arch; pre-metamorphic and early metamorphic females were attached to the secondary gill lamellae.

Type-material: Holotype: late metamorphic ♀ in alcohol (WAM C38272). Paratypes: 35 ♀♀ (1 pre-metamorphic, 3 early metamorphic and 31 late metamorphic) in alcohol (WAM C38273); 3 late metamorphic ♀♀ dissected and mounted on glass slide (WAM C38274).

Other material deposited: One late metamorphic ♀ in alcohol (WAM C38275), ex *M. meraukensis*; 10 late metamorphic ♀♀ (6 whole and 4 damaged) in alcohol (MAGNT Cr15333–15335) and 1 damaged late metamorphic ♀ dissected and mounted on glass slide (MAGNT Cr15334), ex *M. darwinii*.

Etymology: The species is named for Dr Donald G. Buth (University of California, Los Angeles), an expert in phylogenetic systematics.

Description of late metamorphic female
(Figs. 1A–3B)

Body (Fig. 1A,B) composed of 4 regions: antennary, neck, postantennary cephalothoracic and trunk. Mean body length 1.34 mm (n = 4). Antennary region relatively small, without lobes, bears antennules and antennae. Neck region long, comprises about half of total body length, separates antennary region from postantennary cephalothoracic region. Neck contracted in specimens collected from Darbilla Creek, Northern Territory. Postantennary cephalothoracic region highly swollen, globose, comprises somites bearing oral appendages and first pair of swimming legs, about twice width of antennary region. Trunk region composed of second to fourth pedigerous somites and urosome, considerably narrower than preceding body region. Second to fourth pedigerous somites free, well defined, decrease in width posteriorly. Urosome flexed ventrally, composed of fifth pedigerous somite, genital double-somite and three free abdominal somites. Fifth pedigerous somite very short, indiscernible in dorsal aspect. Genital double-somite (Fig. 1C) suborbicular, with several transverse rows of spinules on ventral surface; genital apertures paired, each located dorsolaterally. Each abdominal somite (Fig. 1C) furnished with discontinuous row of spinules posteroventrally. Caudal ramus (Fig. 1C)

rectangular, bears spinules posteroventrally and 4 apical setae. Egg-sac (Fig. 1A) about two-thirds of total body length, multiseriate.

Antennule (Fig. 1D) 5-segmented, with setal formula of 12, 4, 3, 2 + aesthetasc and 5 [this formula is most likely incomplete due to the extreme fragility of the setal elements]. Antenna (Fig. 1E) 4-segmented; coxobasis squat, armed with inner seta; first endopodal segment robust, bears short medial seta and distomedial tooth-like process; second endopodal segment robust, recurved and unarmed; third endopodal segment short, bears minute seta on anterior surface; claw robust, with fine striations on anterior surface. Labrum (Fig. 1F) subquadrangular, notched along posterior margin. Mandible (Fig. 1G) armed with anterior, middle and posterior blades. Anterior blade with small teeth on both margins; middle blade armed with large teeth posteriorly; posterior blade with small teeth on anterior margin. Maxillule (Fig. 1H) lobate, bears 2 unequal distolateral setae and inner spinous process. Maxilla (Fig. 1I) 2-segmented; syncoxa large, tapers distally, armed with minute distal seta; basis armed with basal seta and numerous spinules distally. Maxilliped absent.

Legs 1 to 4 (Figs. 2A–3A) biramous and 3-segmented, except for 2-segmented exopod of leg 4. Spine and setal formula as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1	0-0	1-0	I-0; 0-1; II, 5	0-1; 0-1; II, 4
Leg 2	0-0	1-0	I-0; 0-1; 6	0-1; 0-2; I, 4
Leg 3	0-0	1-0	I-0; 0-1; 6	0-1; 0-2; I, 4
Leg 4	0-0	1-0	I-0; 5	0-1; 0-2; I, 3

Leg 1 (Fig. 2A) with inner row of setules on first exopodal segment; outer margin of endopodal segments ornamented with row of setules and spinules; invariably reflexed anteriorly. Intercoxal sclerite of leg 1 overlapped by posterior end of post-oral sternite (Fig. 2B). First interpodal sternite (Fig. 2C) furnished with discontinuous row of spinules along posterior margin; second and third interpodal sternites (not figured) unornamented. Legs 2 to 4 (Figs. 2D–3A) ornamented as follows: with inner row of setules on first exopodal segment; with outer row of setules on all endopodal segments; with few spinules along
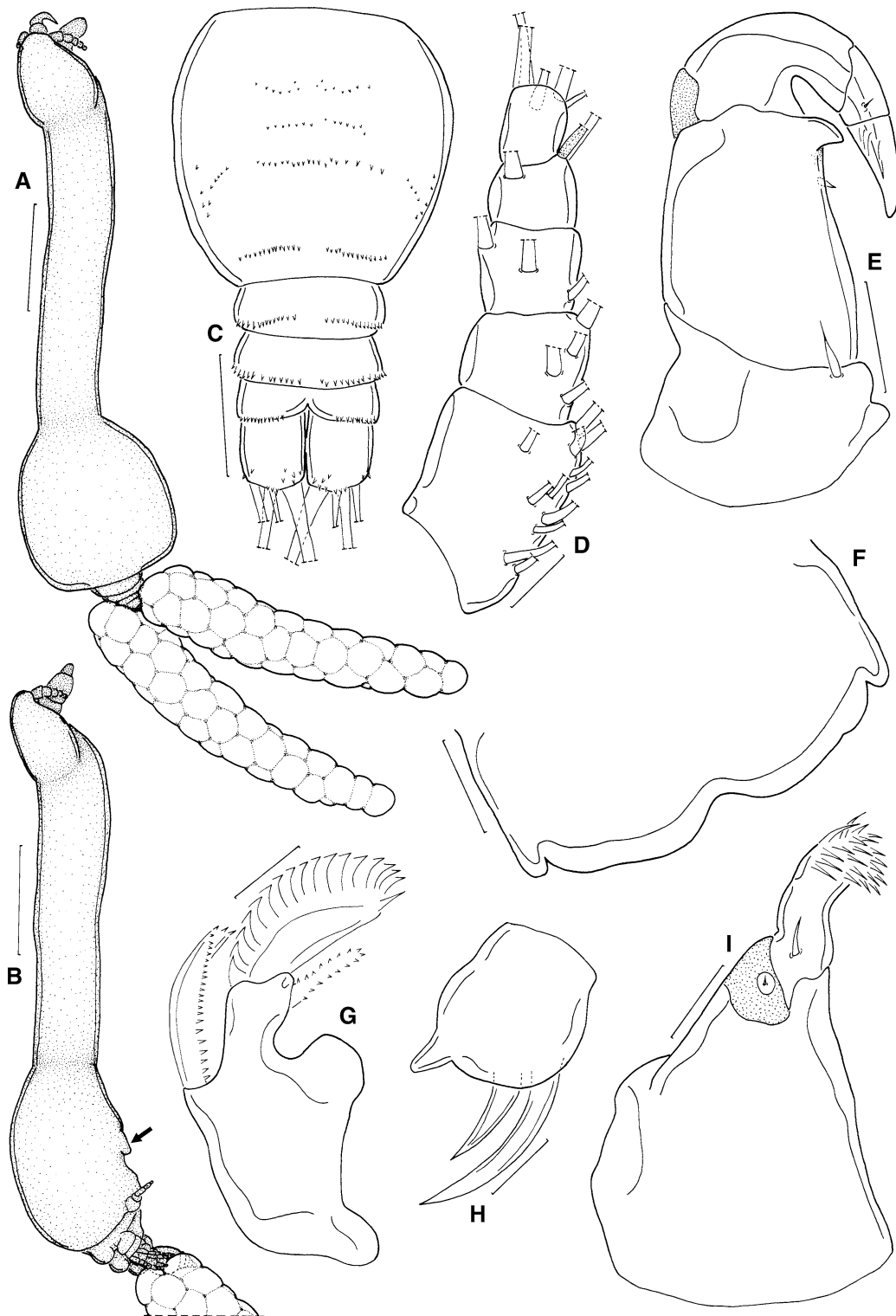
Fig. 1 *Majalincola buthi* n. g., n. sp., late metamorphic female. A, habitus, dorsal; B, same (arrow indicates oral area), lateral; C, urosomites 2–5 and caudal rami, ventral; D, antennule, ventral; E, antenna, anterior; F, labrum, ventral; G, mandible, ventral; H, maxillule, ventral; I, maxilla, ventral. *Scale-bars*: A,B, 0.20 mm; C,E, 25 μm; D,F,I, 12.5 μm; G,H, 6.25 μm
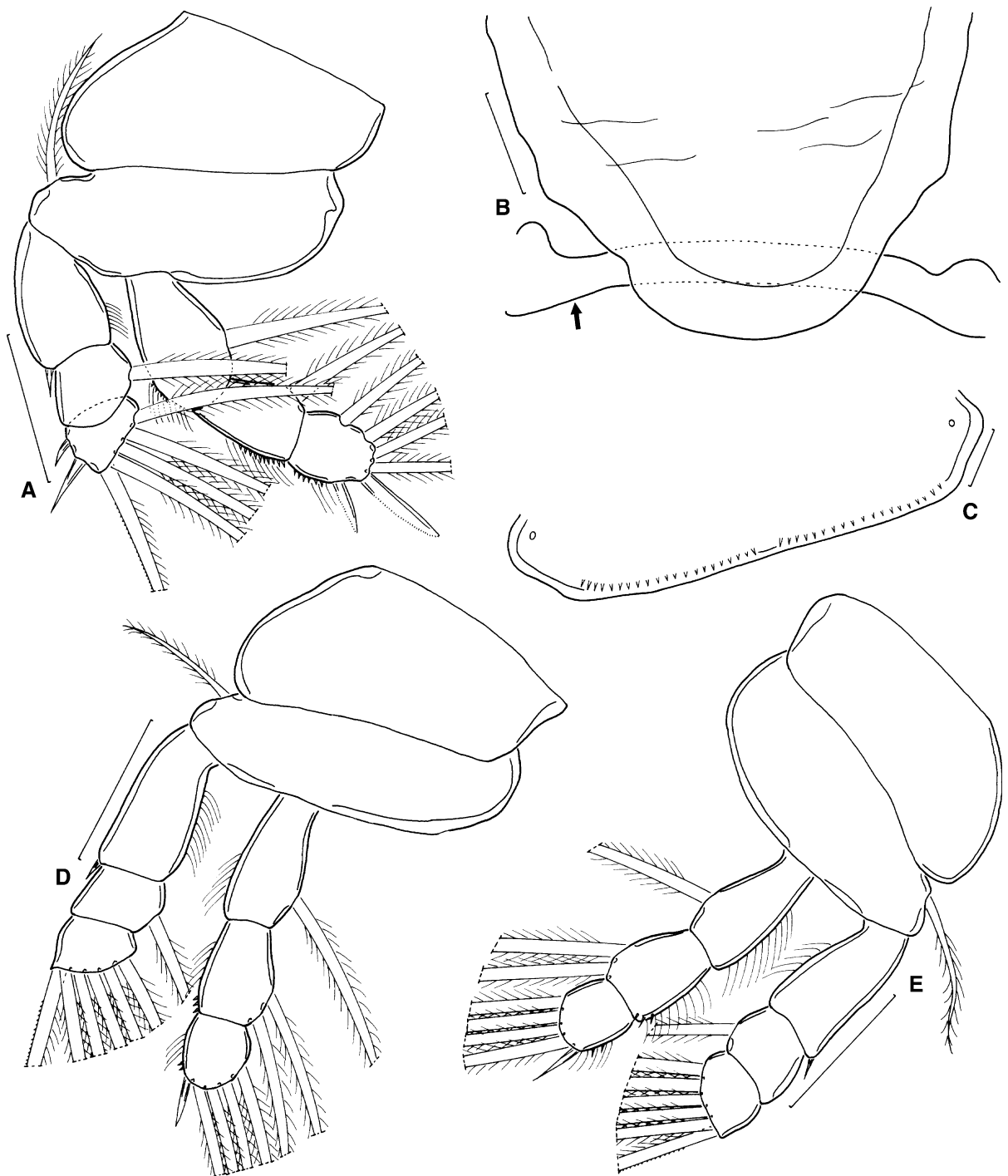
Fig. 2 *Majalincola buthi* n. g., n. sp., late metamorphic female. A, leg 1, anterior; B, post-oral sternite (arrow indicates leg 1 intercoxal sclerite), ventral; C, first interpodal sternite, ventral; D, leg 2, anterior; E, leg 3, anterior. *Scale-bars*: A,D,E, 25 μm; B, 12.5 μm; C, 6.25 μm

outer margin of second and third endopodal segments. Leg 5 (Fig. 3B) with protopodal segment incorporated into somite, represented by outer naked seta carried on papilla; free exopodal segment armed with 2 unequal setae (inner seta sparsely pinnate; outer seta naked).

Remarks

This new copepod species is placed in the Ergasilidae based on the absence of maxillipeds and the presence of an unsegmented mandible bearing three spinulate blades, a lobate maxillule armed with two setae and a medial process, a 2-segmented maxilla with the distal segment furnished with spinules and a 2-segmented leg 4 exopod in the adult female. This new species differs from all ergasilid species except those of *Therodamas* in its possession of a pre-oral neck. Nonetheless, it cannot be included as a member of *Therodamas* due to its retention of free abdominal somites (rather than incorporated with the genital-double somite into a single unit), a 3-segmented (rather than 2-segmented) leg 1 endopod and a 1-segmented exopod (rather than absent, represented by a seta) on leg 5.

This new species further differs from *Therodamas* in the developmental (metamorphic) pattern of the adult female, resulting in dissimilar tagmosis between the two taxa. For instance, morphological changes occur only in the neck length and shape and size of the postantennary cephalothoracic region between the

pre-metamorphic (Fig. 3C), early metamorphic (Fig. 3D) and late metamorphic stages (Fig. 1A) of the new species. This developmental pathway leads to the formation of a large, globose postantennary cephalothoracic region and narrow trunk region that are separated from the antennary region by a long neck in the fully-transformed female. In sharp contrast, for species of *Therodamas* where the developmental stages are known, a different set of allometric alterations occur between the early meta-morphic stages and the egg-bearing female. For example, the early metamorphic stage of *T. fluviatilis* Paggi, 1976 and pre-metamorphic stage of *T. serrani* Krøyer, 1863 retain distinct boundaries between the pedigerous somites and urosomites (Paggi, 1976; Araujo & Boxshall, 2001). However, as the adult female approaches the ovigerous state in both species, these somites expand considerably so that the boundaries between them are ill-defined or no longer discernible, which results in a fully-trans-formed female having a large, fleshy trunk that is separated from the anterior cephalic appendages by a long neck (Paggi, 1976; El-Rashidy & Boxshall,
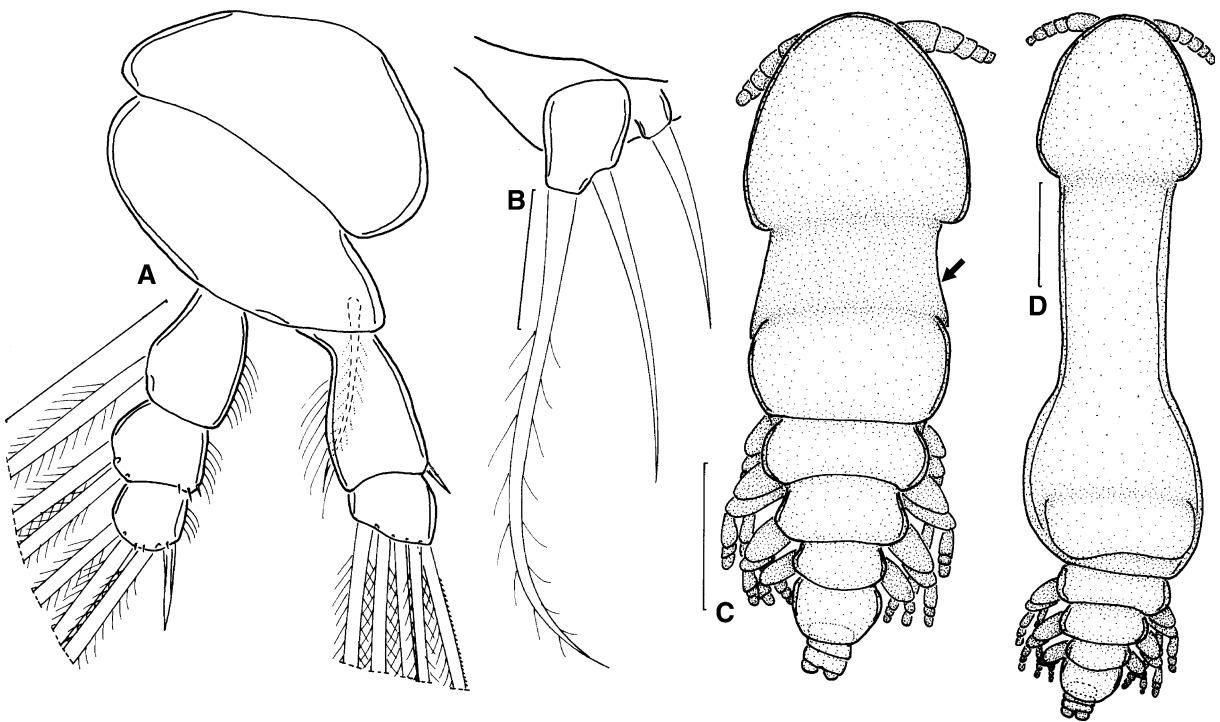
Fig. 3 *Majalincola buthi* n. g., n. sp., late metamorphic female (A,B), pre-metamorphic female (C), early metamorphic female (D). A, leg 4, anterior; B, leg 5, lateral; C, habitus (arrow indicates incipient neck), dorsal; D, habitus, dorsal. *Scale-bars*: A, 25 μm; B, 12.5 μm; C,D, 0.10 mm

2001). The metamorphosis of the adult females in the other four *Therodamas* species (i.e. *T. sphyricephalus* Thomsen, 1949, *T. dawsoni* Cressey, 1972, *T. elongatus* (Thatcher, 1986) and *T. frontalis* El-Rashidy & Boxshall, 2001) most likely follows that of *T. fluviatilis* and *T. serrani*, as the body of the egg-bearing female for each species is similarly arranged (Thomsen, 1949; Cressey, 1972; Motta Amado & Rocha, 1996; El-Rashidy & Boxshall, 2001).

Unable to place this new species in any known ergasilid genus based on the morphological and ontogenetic differences provided above, we propose a new genus, *Majalincola*, to accommodate this highly modified ergasilid species. *Majalincola* can be distinguished from other ergasilid genera by the presence in the fully-transformed adult female of a relatively long neck separating the antennary region from the globose postantennary cephalothoracic and narrow trunk regions, well-defined leg-bearing somites 2–4 and urosomites, a 5-segmented antennule, a 3-segmented leg 1 endopod and a 1-segmented exopod armed with two setae on leg 5.

Systematics

The phylogenetic relationships between the new taxon and other ergasilid genera were first explored by carrying out both ordered and unordered cladistic analyses using the Heuristic Search option in PAUP* 4.0b10 (Swofford, 2002) to find all most parsimonious trees (MPTs). These analyses were based on a character matrix (Table 1) and a morphological

Table 1 Character matrix for 20 morphological characters used in the cladistic analysis of the genera of the Ergasilidae

Taxa	Characters																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Anthessius	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Abergasilus	0	0	0	0	0	0	0	1	3	1	0	0	0	1	1	1	3	3	2	0
Acusicola	0	0	0	0	0	0	0	2	3	0	1	1	1	1	0	0	1	0	1	0
Amplexibranchius	0	0	0	0	0	0	0	2	3	0	1	1	1	1	0	0	1	0	1	0
Brasergasilus	0	0	0	0	0	0	0	1	3	0	0	0	1	1	0	2	3	3	3	0
Dermoergasilus	0	0	0	0	0	0	0	1	3	0	1	0	0	1	1	0	1	0	0	0
Ergasilus	0	0	0	0	0	0	0	1	3	0	0	0	0	1	0	0	1	0	0	0
Gamidactylus	0	0	0	0	0	1	0	1	2	0	0	0	1	1	0	0	2	1	1	0
Gamispatulus	0	0	0	0	1	1	0	2	2	0	0	0	1	1	0	0	2	1	1	0
Gamispinus	0	0	0	0	0	1	0	2	2	0	0	0	1	1	0	0	2	1	2	0
Gauchergasilus	0	0	0	0	0	0	0	2	3	0	0	0	1	1	0	0	1	0	2	0
Miracetyma	0	0	0	0	0	0	0	2	3	0	1	1	1	2	0	0	1	0	2	0
Mugilicola	0	1	1	1	0	0	0	2	3	0	0	0	0	2	0	2	3	3	2	0
Neoergasilus	0	0	0	0	0	0	0	1	3	0	0	0	0	1	0	0	2	2	0	0
Nipergasilus	0	0	0	0	0	0	0	1	3	0	0	0	0	1	0	0	1	1	0	0
Paeonodes	0	1	1	1	0	0	1	2	3	0	0	0	0	2	0	0	2	2	2	0
Paraergasilus	0	0	0	0	0	1	0	2	1	0	0	0	0	1	0	0	1	0	0	0
Pindapixara	0	0	0	0	0	0	0	1	3	0	0	0	1	1	0	0	1	1	2	0
Prehendorastrus	0	0	0	0	0	0	0	2	3	1	0	0	1	1	0	0	1	0	1	0
Pseudovaigamus	0	0	0	0	1	1	0	1	3	0	0	0	1	1	0	0	1	0	1	0
Rhinergasilus	0	0	0	0	0	0	0	1	3	0	0	0	1	1	0	1	3	3	2	0
Sinergasilus	0	1	0	0	0	0	0	1	3	0	0	0	0	1	0	0	1	0	0	0
Teredophilus	1	0	0	0	0	0	0	2	3	0	0	0	0	1	0	0	1	0	2	0
Therodamas	0	0	1	0	0	0	1	2	3	0	0	0	1	2	0	0	1	0	2	1
Thersitina	1	0	0	0	0	0	0	2	2	0	0	0	0	1	0	0	1	0	2	0
Vaigamus	0	0	0	0	1	1	0	1	3	0	0	0	1	1	0	0	2	1	1	0
Majalincola n. g.	0	0	1	0	0	0	0	2	3	0	0	0	0	1	0	0	1	0	1	1

Table 2 Characters and character states used in the cladistic analysis of the genera of the Ergasilidae. Numbers in parentheses indicate the score given for that particular transformation of the character

No.	Character
1	Cephalothorax not inflated (0), or inflated (1)
2	Metasomal somites well defined (0), or fused (1)
3	Anterior portion of cephalosome not inserted into host tissue (0), or inserted into host tissue (1)
4	Post-oral neck absent (0), or present (1)
5	Rostral spine absent (0), or present (1)
6	Posterolateral corners of cephalosome rounded (0), or bearing retrostylets (1)
7	Abdominal somites free (0), or fused (1)
8	Antennule 7-segmented (0), 6-segmented (1), or 5-segmented (2)
9	Antenna tipped with 4 claws (0), 3 claws (1), 2 claws (2), or 1 claw (3)
10	Antenna prehensile (0), or chelate (1)
11	Antennal segments naked (0), or enveloped with cuticular membrane (1)
12	Third antennal segment smooth (0), or bearing a 'socket' (1)
13	Leg 1 endopod 3-segmented (0), or 2-segmented (1)
14	Leg 1 exopod, terminal segment with 8 elements (0), 7 elements (1), or 6 elements (2)
15	Leg 2 endopod, middle segment with 2 setae (0), or 1 seta (1)
16	Leg 4 biramous (0), represented by a seta (1), or absent (2)
17	Leg 4 exopod 3-segmented (0), 2-segmented (1), 1-segmented (2), or absent (3)
18	Leg 4 endopod 3-segmented (0), 2-segmented (1), 1-segmented (2), or absent (3)
19	Leg 5 well developed (0), reduced (1), represented by a seta (2), or absent (3)
20	Pre-oral neck absent (0), or present (1)

character set (Table 2) modified from Motta Amado et al. (1995) as follows: (1) *Diergasilus* Do, 1981 and *Pseudergasilus* Yamaguti, 1936 were omitted as these genera were considered synonyms of *Thersitina* Norman, 1905 and *Ergasilus* von Nordmann, 1832 by Ohtsuka et al. (2004) and Boxshall & Halsey (2004), respectively; (2) three additional ergasilid genera were included (*Miracetyma* Malta, 1993, *Pindapix-ara* Malta, 1993 and *Gauchergasilus* Montú & Boxshall, 2002); (3) the character state of Character 7 for *Mugilicola* was changed from 1 (abdominal somites fused) to 0 (abdominal somites free) based on the redescription of the type-species by El-Rashidy & Boxshall (2001); (4) the character state of Character 13 for *Therodamas* was changed from 0 (leg 1 endopod 3-segmented) to 1 (leg 1 endopod 2-segmented) based on the redescription of *T. serrani* syntype material by El-Rashidy & Boxshall (2001); (5) the character state of Character 14 for *Therodamas* was changed from 1 (third segment of leg 1 exopod with 7 elements) to 2 (third segment of leg 1 exopod with 6 elements) based on the redescription of *T. serrani* syntype material by El-Rashidy &

Boxshall (2001); (6) the character state of Character 19 for *Mugilicola, Paeonodes* and *Therodamas* were each changed from 3 (free segment of leg 5 absent) to 2 (free segment of leg represented by a seta) based on species (re)descriptions from each of these genera by El-Rashidy & Boxshall (2001); (7) the character state of Character 19 for *Teredophilus* was changed from 3 (free segment of leg 5 absent) to 2 (free segment of leg represented by a seta) based on the redescription of the type species by Harding (1964); and (8) one new character (Character 20) was added (pre-oral neck: absent (0), or present (1)). A 50% majority-rule consensus tree was constructed for each analysis using PAUP* to combine all MPTs into a single tree showing their common components.

The resultant consensus trees differ markedly, with the unordered consensus tree (Fig. 4) being much less resolved than the ordered consensus tree (Fig. 5). Both consensus trees, however, depict *Majalincola* and *Therodamas* as sister taxa. This clade is defined in 76% of the unordered MPTs by three synapomorphies, the presence of a 5-segmented antennule (Character 8), the anterior portion of cephalosome
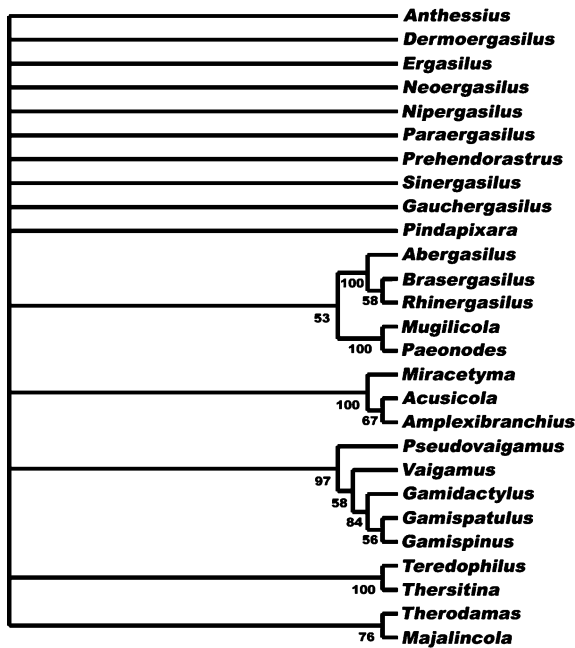
Fig. 4 The majority-rule consensus tree of 11,362 equally parsimonious trees (TL = 58; CI = 0.53; RI = 0.68) for the Ergasilidae based on an unordered analysis (numbers below branches indicate the percentage of equally parsimonious trees that show that particular topology)
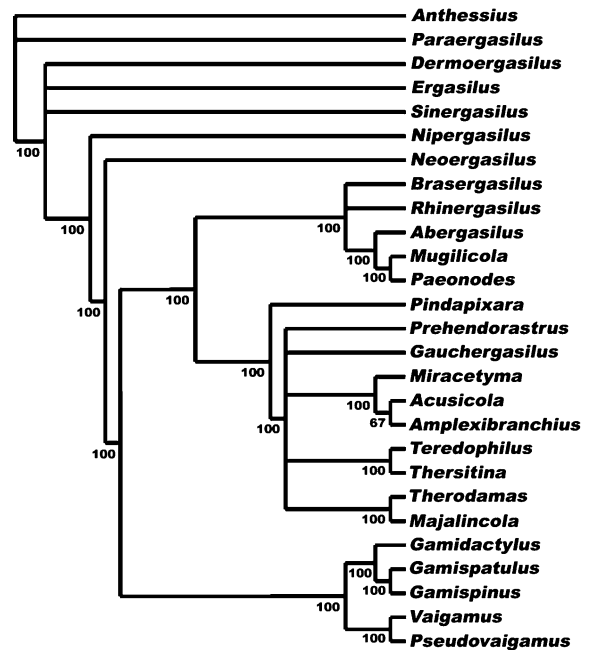
Fig. 5 The majority-rule consensus tree of 12 equally parsimonious trees (TL = 62; CI = 0.50; RI = 0.71) for the Ergasilidae based on an ordered analysis (numbers below branches indicate the percentage of equally parsimonious trees that show that particular topology)

inserted into host tissue (Character 3) and a pre-oral neck (Character 20), whilst it is united in all ordered MPTs by the possession of the latter two derived character states. Interestingly, both consensus trees also indicate that mesoparasitism independently evolved twice during the course of ergasilid evolution, namely once in the *Mugilicola–Paeonodes* clade and the other involving the *Therodamas–Majalincola* group.

The phylogenetic relationships between the new species and the six nominal species of *Therodamas* were subsequently examined using the Branch and Bound search option in PAUP*, with *Paraergasilus rylovi* Markevich, 1937 (see Chernysheva & Purasjoki, 1991) serving as the outgroup and all characters treated as unordered, as the previous generic analyses equally established the sister taxon relationship of *Majalincola* and *Therodamas*. This analysis, which was based on a character matrix (Table 3) comprising six characters (Table 4) modified from El-Rashidy & Boxshall (2001), generated a single tree (Fig. 6) (TL = 8, CI = 1.00 and RI = 1.00). This tree indicates that members of *Therodamas* form a lineage
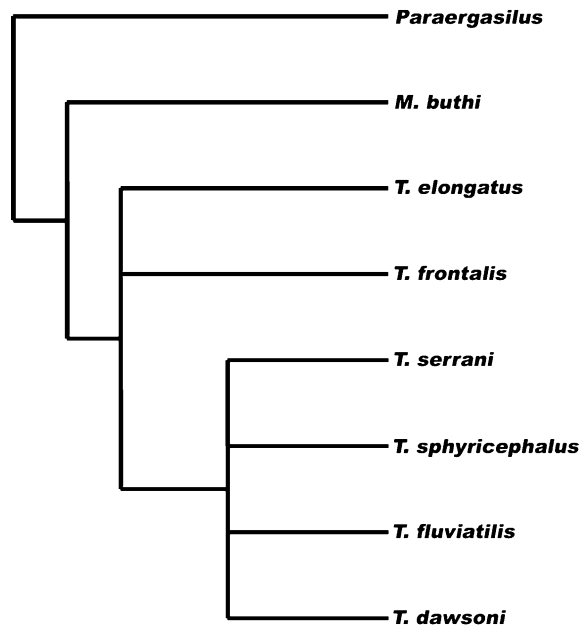
Table 3 Character matrix for six morphological characters used in the cladistic analysis of species of *Therodamas* and *Majalincola* n. g.

Taxa	Characters					
	1	2	3	4	5	6
Paraergasilus	0	0	0	0	0	0
T. serrani	1	1	1	1	2	2
T. sphyricephalus	1	1	1	1	2	2
T. fluviatilis	1	1	1	1	2	2
T. dawsoni	1	1	1	1	1	2
T. elongatus	1	0	1	1	2	2
T. frontalis	1	0	1	1	2	2
M. buthi n. sp.	1	0	0	0	0	1

distinct from the new species and defined by the presence of the following apomorphies: fused abdominal somites, one outer spine on the terminal exopodal segment of leg 1, a 2-segmented leg 1 endopod and leg 5 exopod represented by a seta. These phylogenetic results, therefore, further support the establishment of a new ergasilid genus.

Table 4 Characters and character states used in the cladistic analysis of species of *Therodamas* and *Majalincola* n. g. Numbers in parentheses indicate the score given for that particular transformation of the character

No.	Character
1	Pre-oral neck absent (0), or present (1)
2	Posterior margin of antennary region of cephalothorax without lobes (0), or with posteriorly-directed lobes (1)
3	Abdominal somites free (0), or fused dorsally and ventrally to form a unit (1)
4	Articulation between second and third endopodal segments of leg 1 expressed (0), or not expressed (1)
5	Armature of leg 1 exopod terminal segment II, 5 (0), I, 6 (1), or I, 5 (2)
6	Leg 5 exopod 1-segmented, armed with 3 setae (0), 1-segmented, armed with 2 setae (1), or absent, represented by a seta (2)

Fig. 6 Cladogram of *Majalincola* and *Therodamas* species based on an unordered analysis

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