Contributions to Zoology, 65 (4) 233-243 (1995)
SPB Academic Publishing bv, Amsterdam

Phylogeny and biogeography of the Ergasilidae (Copepoda, Poecilostomatoida), with reconsideration of the taxonomic status of the Vaigamidae

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Keywords: Phylogenetic analysis, biogeography, Copepoda, Poecilostomatoida, Ergasilidae, Vaigamidae, *Pseudovaigamus* gen. n.

Abstract

Nineteen genera are currently considered valid in the Ergasilidae. A cladistic analysis was conducted on these genera and the five genera composing the closely allied Vaigamidae. Nineteen morphological characters were selected and polarized using *Anthessius* (Anthessiidae) as the outgroup. The most parsimonious cladogram (tree length = 60, Consistency Index = 0.50, Retention Index = 0.71), obtained through the use of the BB command in Hennig 86, is composed of eight major clades, with the five vaigamid genera composing the most derived clade. Based on Wiley's (1981) "sequencing" convention, the five vaigamid genera cannot be placed in a family separate from the Ergasilidae. The biogeography of the ergasilid genera is discussed. *Vaigamus spinicephalus* is placed separately in a new genus, *Pseudovaigamus*.

Résumé

Actuellement dix-neuf genres d'Ergasilidae sont considérés comme valides. Une analyse cladistique a été réalisée pour ces genres, ainsi que pour cinq genres de la famille étroitement apparentée Vaigamidae. Dix-neuf caractères morphologiques ont été choisis et polarisés en utilisant *Anthessius* (Anthessiidae) comme outgroup. Le cladogramme le plus parcimonieux (longueur de l'arbre = 60; index de consistence = 0.50; index de retention = 0.71), obtenu par utilisation de la commande BB dans Hennig 86, se compose de huit clades principaux, les cinq genres de Vaigamidae formant le clade le plus dérivé. Si l'on se base sur la séquence conventionnelle de Wiley (1981) il n'y a pas de raison de séparer dans une famille indépendante des Ergasilidae les cinq genres actuellement placés dans la famille Vaigamidae. La biogéographie des genres d'Ergasilidae est discutée. *Vaigamus spinicephalus* est séparé dans un nouveau genre *Pseudovaigamus*.

Introduction

Copepods of the family Ergasilidae (Poecilostomatoida) are found mostly in fresh water and sometimes in estuarine and shallow coastal waters. While larval stages and male adults are planktonic, adult female ergasilids are parasitic on teleosts, with the exception of *Teredophilus* spp., which live in bivalve molluscs.

In this paper we attempt to reconstruct the phylogeny of the Ergasilidae using the cladistic approach. In order to determine relations between Vaigamidae and Ergasilidae, we included four vaigamid genera (*Gamidactylus*, *Gamispinus*, *Gamispatulus*, and *Vaigamus*) in the analysis. *Amazonicopeus* Thatcher, 1986, the sole representative of the Amazonicopeidae, was excluded from the performed analysis because it was found to be synonymous with *Therodamas* Krøyer, 1863, by Amado (1992) and Abdelhalim et al. (1993).

According to Ho (1991), the family Gastrodelphyidae is the sister taxon of this study's ingroup (Ergasilidae–Vaigamidae). However, being parasitic on polychaetes and being highly modified, no gastrodelphyid genus serves very well as an outgroup to assist in character state polarization for Ergasilidae and Vaigamidae. The closest sister taxon with the least specialized state of morphology are Anthessiidae (Ho, 1991); therefore, the type-genus (*Anthessius* Della Valle, 1880) was selected as the outgroup for this analysis.

Material and methods

Type-materials of 20 genera were examined in order to verify character states to be used in the phylogenetic analysis. The materials and the respective institutions where the specimens are kept are listed below. The names of the institutions are abbreviated as follows: INPA = Instituto Nacional de Pesquisas de Amazonia, Manaus, Brazil; MZUSP = Museu de Zoologia da Universidade de São Paulo, Brazil; NHM = Natural History Museum, London; and NMNH = National Museum of Natural History, Washington DC.

– *Abergasilus amplexus* Hewitt, 1978. Holotype female. New Zealand, Ellesmere Lake (NHM-419).
– *Acusicola lycengraulidis* Thatcher & Boeger, 1983. Paratype female. Brazil, State of Pará, Tocantins River (MZUSP-8166).
– *Acusicola pelonidis* Thatcher & Boeger, 1983. Paratype female. Brazil, State of Amazonas, Amazonas River (MZUSP-8167).
– *Acusicola tenax* Cressey, 1970. Holotype and paratype females. Guatemala, Pasion River (NMNH-180760, 125685, 125686).
– *Acusicola tucunarensis* Thatcher, 1984. Paratype female. Brazil, State of Amazonas, Amazonas River (MZUSP-8165).
– *Amazonicopeus elongatus* Thatcher, 1986. Paratype female. Brazil, State of Amazonas, Amazonas River (MZUSP-8173). Syn. *Therodamas*.
– *Amplexibranchius bryconis* Thatcher & Paredes, 1985. Holotype female. Perú, Iquitos (MZUSP-8172).
– *Brasergasilus anodus* Thatcher & Boeger, 1983. Paratype female. Brazil, State of Pará, Tocantins River (MZUSP-8164).
– *Brasergasilus jaraquensis* Thatcher & Boeger, 1983. Paratype female. Brazil, State of Amazonas, Amazonas River (MZUSP-8162).
– *Brasergasilus oranus* Thatcher & Boeger, 1984. Paratype female. Brazil, State of Amazonas, Amazonas River (MZUSP-8163).
– *Dermoergasilus amplectens* Ho & Do, 1982. Holotype and paratype females. Russia, Tumen-ul River (NHM-489, 498).
– *Diergasilus kasaharai* Do, 1981. Holotype and paratype females. Japan, Okayama, Kojima Bay (NMNH-184160, 184161).
– *Ergasilus bryconis* Thatcher, 1981. Paratype female. Brazil, State of Amazonas, Amazonas River (MZUSP-8155).
– *Ergasilus callophysus* Thatcher & Boeger, 1984. Paratype female. Brazil, State of Amazonas, Amazonas River (MZUSP-8161).
– *Ergasilus coleus* Cressey, 1970. Holotype and paratype females. Philippines (NMNH-12679, 125680). Syn. *Dermoergasilus*.
– *Ergasilus colomesus* Thatcher & Boeger, 1983. Paratype female. Brazil, State of Amazonas, Amazonas River (MZUSP-8157).
– *Ergasilus holobryconis* Malta & Varella, 1986. Holotype female. Brazil, State of Amazonas, Amazonas River (MZUSP-7011).
– *Ergasilus hydrolycus* Thatcher, Boeger & Robertson, 1984. Paratype female. Brazil, State of Amazonas, Amazonas River (MZUSP-8158).
– *Ergasilus jaraquensis* Thatcher & Robertson, 1981. Paratype female. Brazil, State of Amazonas, Amazonas River (MZUSP-8159).
– *Ergasilus leporinidis* Thatcher, 1981. Paratype female. Brazil, State of Amazonas, Amazonas River (MZUSP-8156).
– *Ergasilus semicoleus* Cressey, 1970. Holotype and paratype females. Australia (NMNH-125681, 125682). Syn. *Dermoergasilus*.
– *Ergasiluxulus infaltus* (Rancurell, 1954). Paratype female. Africa, West Lake (NHM-976). Syn. *Teredophilus*.
– *Gamidactylus jaraquensis* Thatcher & Boeger, 1984. Paratype female. Brazil, State of Amazonas, Amazonas River (MZUSP-8170).
– *Gamispatulus schizodontis* Thatcher & Boeger, 1984. Paratype female. Brazil, State of Amazonas, Amazonas River (MZUSP-8174).
– *Gamispinus diabolicus* Thatcher & Boeger, 1984. Paratype female. Brazil, State of Amazonas, Amazonas River (MZUSP-8171).
– *Mugilicola australiensis* Boxshall, 1986. Holotype female. Australia, P. Arrawara (NHM-189).
– *Neoergasilus japonicus* (Harada, 1930) Yin, 1956. Holotype female. Japan, Jetsugetsutan Lake (NHM-111).
– *Paraergasilus remulus* Cressey, 1970. Holotype and paratype females. Cambodja (NMNH-125689, 125690).
– *Prehendorastrus bidentatus* Boeger & Thatcher, 1990. Paratype female. Brazil, State of Amazonas, Furo do Catalão (INPA-191a).
– *Rhinergasilus piranus* Boeger & Thatcher, 1988. Holotype female. Brazil, State of Amazonas, Machantaria Island (INPA CR 476).
– *Thersitina gasterostei* (Pagenstecher, 1861). Paratype female. Locality not known (NHM-727).
– *Vaigamus retrobarbatus* Thatcher & Robertson, 1984. Paratype female. Brazil, State of Amazonas, Machantaria Island (MZUSP-8168).
– *Vaigamus spinicephalus* Thatcher & Robertson, 1984. Paratype female. Brazil, State of Pará, Tocantins River (MZUSP-8169). Syn. *Pseudovaigamus* gen. nov.

We were not able to obtain specimens of *Sinergasilus*, *Nipergasilus*, *Pseudergasilus*, and *Paeonodes* for examination. Information on these genera was taken from their original descriptions.

In conducting the character analysis only adult female characters were considered. The direction of character transformation was made mainly by outgroup comparison, but Huys & Boxshall's (1991) contention that copepod evolution commonly is associated with oligomerization is also taken into consideration.

To avoid confusion, the character states found in the type-species were used to represent each genus. For example, the endopodite of leg 1 is considered 3-segmented for *Ergasilus* (with more than 130 species known), because this is the situation found in the type-species, *E. sieboldi*, even though there are, at

least, 16 species with 2-segmented endopodite forming leg 1. By convention, ancestral (i.e., plesiomorphic) states were coded "0" and derived (i.e., apomorphic) states were coded "1", "2", or "3". Higher codes represent further derived states (i.e. "2" more derived than "1" and "3" more derived than "1" and "2").

The phylogenetic computer package Hennig 86 Version 1.5 (James S. Farris, 1988) was used to analyze the data summarized in Table I. Two algorithms were employed, M HENNIG that constructs cladograms (trees) by adding the terminals in several different sequences and retains the shortest trees found, and BB (branch-breaking) which extends branch-swapping to the trees to produce a new file.

Characters used in the character analysis

1. Cephalothorax not inflated (0), or inflated (1). The apomorphic state appears in *Teredophilus* and *Thersitina*, where the fused cephalothorax is tremendously enlarged.
2. Metasomal somites well defined (0), or fused (1). The apomorphic state is found in *Mugilicola*, *Paeonodes*, *Pseudergasilus*, and *Sinergasilus*, although traces of segmentation appear as lateral furrows in the last genus.
3. Anterior portion of the cephalosome not inserted into host tissue (0), or inserted into host tissue (1). The apomorphic state is found in *Mugilicola*, *Therodamas*, and *Paeonodes*.
4. Area between head and first pediger not elongated (0), or elongated (1). The latter state is shared by *Mugilicola* and *Paeonodes*.
5. Rostral spine absent (0), or present (1). The apomorphic state is found in *Gamispatulus*, *Vaigamus*, and *Pseudovaigamus*.
6. Posterolateral corners of cephalosome rounded (0), or bearing a spiniform posterolateral protrusion ("retrostylets") (1). The derived state of this character was considered by Thatcher (1991) as the major defining characteristic of the vaigamid genera. However, according to Chernysheva & Purasjoki's (1991) recent account, this pair of "retrostylets" is not unique to the vaigamids. It is also present in *Paraergasilus*. Amado's (1992) reexamination of the type-materials of vaigamids showed that structural details of the "retrostylets" in *Gamidactylus*, *Gamispinus*, and *Gamispatulus* are different from those found in *Vaigamus* and *Pseudovaigamus*. The "retrostylets" in *Paraergasilus* are similar to those found in the latter two vaigamid genera.
7. Abdominal somites free (0), or fused (1). Three somites are known for both ergasilids and vaigamids, but in *Mugilicola*, *Paeonodes*, and *Therodamas* they are fused into a unit behind the genital double somite.
8. Antennule 7-segmented (0), or 6-segmented (1), or 5-segmented (2). According to current knowledge on the development of certain species of *Ergasilus* (Yin, 1956; Ben Hassine, 1983; Varella, 1985; Abdelhalim et al., 1991) and *Neoergasilus* (Urawa et al., 1980) the formation of a 5-segmented antennule is due to a failure in division of the second segment towards the later stages of larval development. Twelve genera exhibit 5-segmented antennules (*Acusicola*, *Amplexibranchius*, *Diergasilus*, *Gamispatulus*, *Gamispinus*, *Mugilicola*, *Paeonodes*, *Paraergasilus*, *Prehendorastrus*, *Teredophilus*, *Therodamas*, and *Thersitina*).
9. Antenna tipped with 4 claws (0), 3 claws (1), 2 claws (2), or 1 claw (3). The terminal armature of the antenna has been variously referred to as spines or accessory spines. The heaviest armature of 3 claws is found only in one genus, viz. *Paraergasilus*. Five genera (*Diergasilus*, *Gamispinus*, *Gamidactylus*, *Gamispatulus*, and *Thersitina*) carry 2 claws and the remaining 18 genera each have a single claw.
10. Antenna prehensile (0), or chelate (1). The development of chelate antennae is rather rare for parasitic copepods. In ergasilids, it is only found in *Abergasilus* and *Prehendorastrus*. In these two genera, the medial surface of the second segment bears a large, basal, spiniform protrusion that opposes the tip of the terminal claw.
11. Antennal segments naked (0), or enveloped with a cuticular membrane (1). The derived state is found in only three genera: *Acusicola*, *Amplexibranchius*, and *Dermoergasilus*.
12. Third antennal segment smooth (0), or bearing a "socket" (1). Most gill-parasitizing ergasilids and vaigamids attach to their host by embracing the gill filament or by piercing the host tissue with the terminal claw. However, in *Acusicola* and *Amplexibranchius* there is a "socket" on the third segment to receive the terminal claw of the opposite appendage so as to form a firm, interlocking grasp.
13. Leg 1 endopodite 3-segmented (0), or 2-segmented (1). Ten ergasilid genera (*Acusicola*, *Amplexibranchius*, *Brasergasilus*, *Gamidactylus*, *Gamispatulus*, *Gamispinus*, *Prehendorastrus*, *Rhinergasilus*, *Vaigamus*, and *Pseudovaigamus*) exhibit this oligomerization in leg 1.
14. Third segment of leg 1 exopodite with 8 elements (0), or with 7 elements (1), or with 6 elements (2). Only two genera (*Mugilicola* and *Paeonodes*) bear 6 elements (spines and setae), all the other have 7 elements.
15. Second segment of leg 2 endopodite with 2 setae (0), or with 1 seta (1). As above, only two genera (*Abergasilus* and *Dermoergasilus*) exhibit the derived character state.
16. Leg 4 biramous (0), or represented by a seta (1), or leg 4 completely absent (2). Most ergasilids and vaigamids have biramous fourth legs. However, in *Abergasilus* and *Rhinergasilus* leg 4 is reduced to a seta and in *Brasergasilus* and *Mugilicola* it is entirely lost.
17. Leg 4 exopodite 3-segmented (0), or 2-segmented (1), or 1-segmented (2), or absent (3). Most ergasilids have fourth legs with 2-segmented exopodite, except for the four genera mentioned above that lack leg 4 and *Neoergasilus* and *Paeonodes* where there is a single segment. Most vaigamids are distinctive in having fourth legs with 1-segmented exopodite but *Pseudovaigamus* has two segments as the majority of ergasilids.
18. Leg 4 endopodite 3-segmented (0), or 2-segmented (1), or 1-segmented (2), or basent (3). The four ergasilid genera

Table I. Character matrix.

	Characters																		
Genera	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Abergasilus	0	0	0	0	0	0	0	1	3	1	0	0	0	1	1	1	3	3	2
Acusicola	0	0	0	0	0	0	0	2	3	0	1	1	1	1	0	0	1	0	1
Amplexibranchius	0	0	0	0	0	0	0	2	3	0	1	1	1	1	0	0	1	0	1
Brasergasilus	0	0	0	0	0	0	0	1	3	0	0	0	1	1	0	2	3	3	3
Dermoergasilus	0	0	0	0	0	0	0	1	3	0	1	0	0	1	1	0	1	0	0
Diergasilus	0	0	0	0	0	0	0	2	2	0	0	0	0	1	0	0	1	0	1
Ergasilus	0	0	0	0	0	0	0	1	3	0	0	0	0	1	0	0	1	0	0
Gamidactylus	0	0	0	0	0	1	0	1	2	0	0	0	1	1	0	0	2	1	1
Gamispatulus	0	0	0	0	1	1	0	2	2	0	0	0	1	1	0	0	2	1	1
Gamispinus	0	0	0	0	0	1	0	2	2	0	0	0	1	1	0	0	2	1	2
Mugilicola	0	1	1	1	0	0	1	2	3	0	0	0	0	2	0	2	3	3	3
Neoergasilus	0	0	0	0	0	0	0	1	3	0	0	0	0	1	0	0	2	2	0
Nipergasilus	0	0	0	0	0	0	0	1	3	0	0	0	0	1	0	0	1	1	0
Paeonodes	0	1	1	1	0	0	1	2	3	0	0	0	0	2	0	0	2	2	3
Paraergasilus	0	0	0	0	0	1	0	2	1	0	0	0	0	1	0	0	1	0	0
Prehendorastrus	0	0	0	0	0	0	0	2	3	1	0	0	1	1	0	0	1	0	1
Pseudergasilus	0	1	0	0	0	0	0	1	3	0	0	0	0	1	0	0	1	0	2
Rhinergasilus	0	0	0	0	0	0	0	1	3	0	0	0	1	1	0	1	3	3	2
Sinergasilus	0	1	0	0	0	0	0	1	3	0	0	0	0	1	0	0	1	0	0
Teredophilus	1	0	0	0	0	0	0	2	3	0	0	0	0	1	0	0	1	0	3
Therodamas	0	0	1	0	0	0	1	2	3	0	0	0	0	1	0	0	1	0	3
Thersitina	1	0	0	0	0	0	0	2	2	0	0	0	0	1	0	0	1	0	2
Vaigamus	0	0	0	0	1	1	0	1	3	0	0	0	1	1	0	0	2	1	1
Pseudovaigamus	0	0	0	0	1	1	0	1	3	0	0	0	1	1	0	0	1	0	1
Anthessius	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Note: *Amplexibranchius* and *Acusicola* are different from each other in the structure of the antenna and leg 1 through leg 4. These autapomorphies are not used in the cladistic analysis.

mentioned above with the most derived state of character 17 also exhibit the most derived state for this character. Unlike most of the vaigamids with a 2-segmented endopodite, the new vaigamid genus *Pseudovaigamus* has a 3-segmented endopodite.

19. Free segment of leg 5 well-developed (0), or reduced (1), or represented by a seta (2), or absent (3). As shown in Table I, the four states of this character are somewhat evenly distributed among the 24 genera studied. Again, as in the other characters, the most transformed genera (*Mugilicola*, *Paeonodes*, and *Therodamas*) also have the most derived state of this character.

Results and discussion

Eight trees were obtained initially, with a length equal to 60, a Consistency Index of 0.50 and a Retention Index of 0.70. Later, on a second approach, BB was used and four most parsimonious trees were obtained (trees 0, 1, 2, and 3) with the same Consistency Index and a Retention Index of 0.71.

Of these four cladograms, two (trees 0 and 2) presented a pentatomy and were considered least acceptable. Trees 1 and 3 were selected for further consideration because they are better resolved. Out of these trees, one was chosen to represent the hypothesis of the family phylogeny based on the relative positions of *Gamidactylus* and *Gamispatulus* to *Gamispinus*. In tree 1, these three genera together form a monophyletic group and this reflects the current view of their relationships (Thatcher, 1991). This cladogram (tree 1) is reproduced in Fig. 1 along with the other three cladograms.

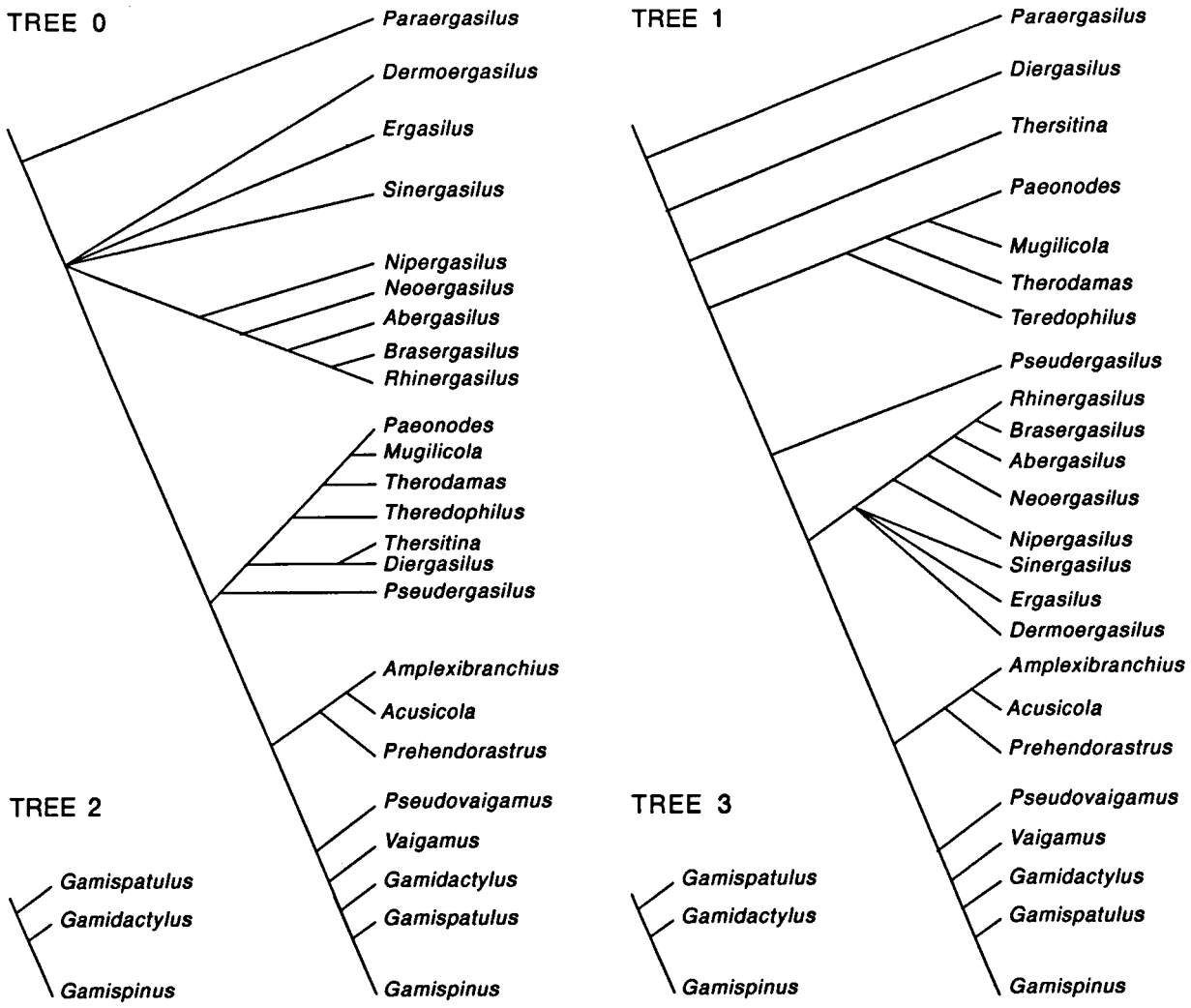

Fig. 1. The most parsimonious cladograms obtained through the use of the BB* command in Hennig 86. Tree 2 shows only the part different from tree 0, and tree 3 only the part different from tree 1.

Establishment of *Pseudovaigamus* gen. nov.

In conducting the character analysis of the vaigamid genera, it was discovered that *Vaigamus spinicephalus* Thatcher & Robertson, 1984 differs so much from the type-species of *Vaigamus* (*V. retrobarbatus* Thatcher & Robertson, 1984) that it must be placed in a separate genus. Accordingly, *Pseudovaigamus* is erected here to facilitate this transfer.

Genus definition. – Ergasilidae. Female: Cephalosome partly fused with first pediger forming a bullet-shaped cephalothorax. Retrostylets slender and curved on posterolateral corner of cephalosome. Rostrum elongated and bearing a thin spine, dilated near base. Four free pedigers decreasing in width posteriorly. Genital double-somite hexagonal. Three free abdominal somites. Anal somite with median notch. Caudal rami longer than wide with a notch on outer lateral border, where there is a seta; terminally with two long setae and two lobules; innermost element spinulose on ventral surface, and outermost element smooth on dorsal

surface. Antennule 6-segmented. Antenna 3-segmented (coxobase and endopodite bi-segmented) with a curved claw, and first segment bearing a seta. Maxillule without setae. Legs 1 to 4 biramous. Leg 1 with 2-segmented endopodite. Legs 2 and 3 with both rami 3-segmented. Leg 4 with 2-segmented exopodite and 3-segmented endopodite. Leg 5 reduced to two setae. Egg sacs short with few eggs in a single row. Ovigerous female free in plankton.

Male: Shape of body similar to female, without retrostylets or rostral spine. Genital somite sub-rectangular, with a median notch. Four abdominal somites. Pre-anal somite bearing a spine on each posterior corner. Anal somite also bearing a spine at same place as in latter and with one median notch. Maxilliped 4-segmented; terminal segment thin and straight. Leg 5 with same structure as in female. Leg 6 reduced to one seta projecting posterolaterally from genital somite. Free in plankton.

Type-species. – *Pseudovaigamus spinicephalus* (Thatcher & Robertson, 1984). By present designation.

Etymology. – The new genus name refers to its similarity with *Vaigamus* Thatcher & Robertson, 1984; "*pseudo*" is Greek for "false".

Remarks. – The new genus differs from *Vaigamus* chiefly in the segmentation of leg 4. In *Vaigamus* this pair of legs has a 1-segmented exopodite and a 2-segmented endopodite, but in the new genus, the plesiomorphic state remains (2-segmented exopodite and 3-segmented endopodite). Additionally *Pseudovaigamus* possesses unusual caudal rami with the mediodistal corner protruded into a spinulose lobe.

Pseudovaigamus differs from all other genera by the presence of a rostral spine in the ventral face of the cephalosome with a dilated basis and oriented to the posterior part of the body, and by caudal rami with terminal lobules. These differences were detected by examination of the paratype MZUSP 8169 B, deposited in the Museu de Zoologia da Universidade de São Paulo, Brazil.

Phylogeny and classification

The phylogenetic tree illustrates that the five genera of Vaigamidae (clade VIII of Fig. 2) are monophyletic, sharing the apomorphic states of character 5 (rostral spine present) and character 6 ("retrostylet" on cephalosome). However, based on Wiley's (1981) "sequencing" convention, the five vaigamid genera (*Gamidactylus*, *Gamispatulus*, *Gamispinus*, *Vaigamus*, and *Pseudovaigamus*) cannot be treated as a family separate from the Ergasilidae. If they are given a familial status, the 19 ergasilid genera will have to be classified into seven separate families or else these would be left as a paraphyletic taxon. Since such splitting of the Ergasilidae would create much taxonomic problems, we propose to follow the phylogeny inferred in Fig. 1 and consider the five vaigamid genera as the most derived members of the Ergasilidae.

In Fig. 2, the branches that lead to *Paraergasilus*, *Diergasilus*, *Thersitina*, and *Pseudergasilus* each form a cluster of their own, but the remaining 20 genera form four generic clusters (clades), each with at least one unifying character (synapomorphy). The largest of these four clades (clade VI) is composed of eight genera, including the genus *Ergasilus* which alone contains about 75% of all known ergasilid species. The three genera of clade VII are unified by having a 5-segmented antennule (the most derived state of character 8). *Mugilicola*, *Paeonodes*, *Teredophilus*, and *Therodamas* are united together in clade IV only by the loss of leg 5 (the most derived state of character 19). This last clade is also the one containing the most transformed ergasilids.

Based on Wiley's (1981) "sequencing" convention, the eight clades in Fig. 2 are to be called eight subfamilies of the Ergasilidae. However, considering that many freshwater and coastal fishes of South America are yet to be examined for their ergasilid copepods and that more new taxa are yet to be established, we think it is still premature to designate formally the subfamilial status of the eight clades.

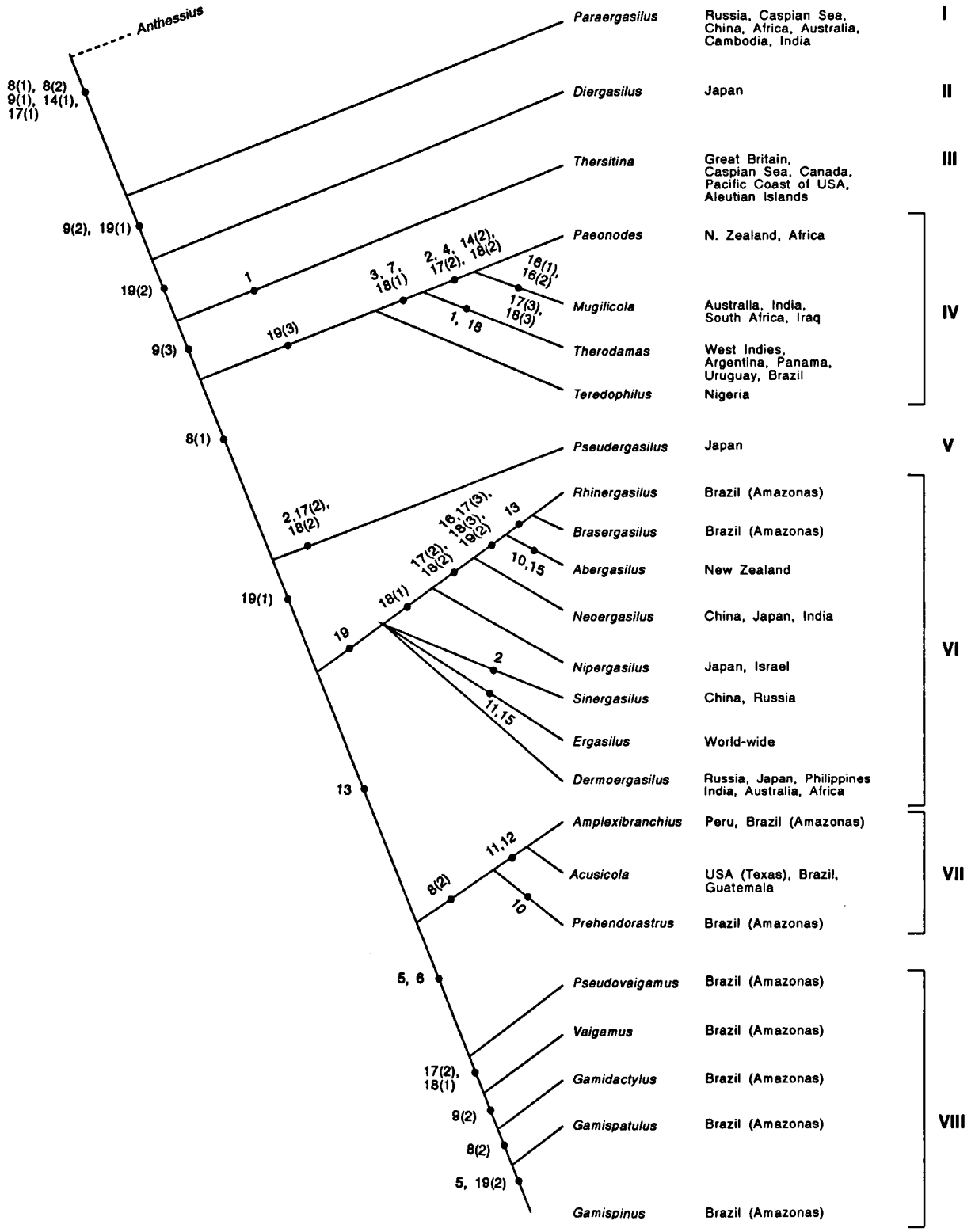

Fig. 2. Cladogram of the Ergasilidae. The Roman numerals refer to the clades discussed in the text.

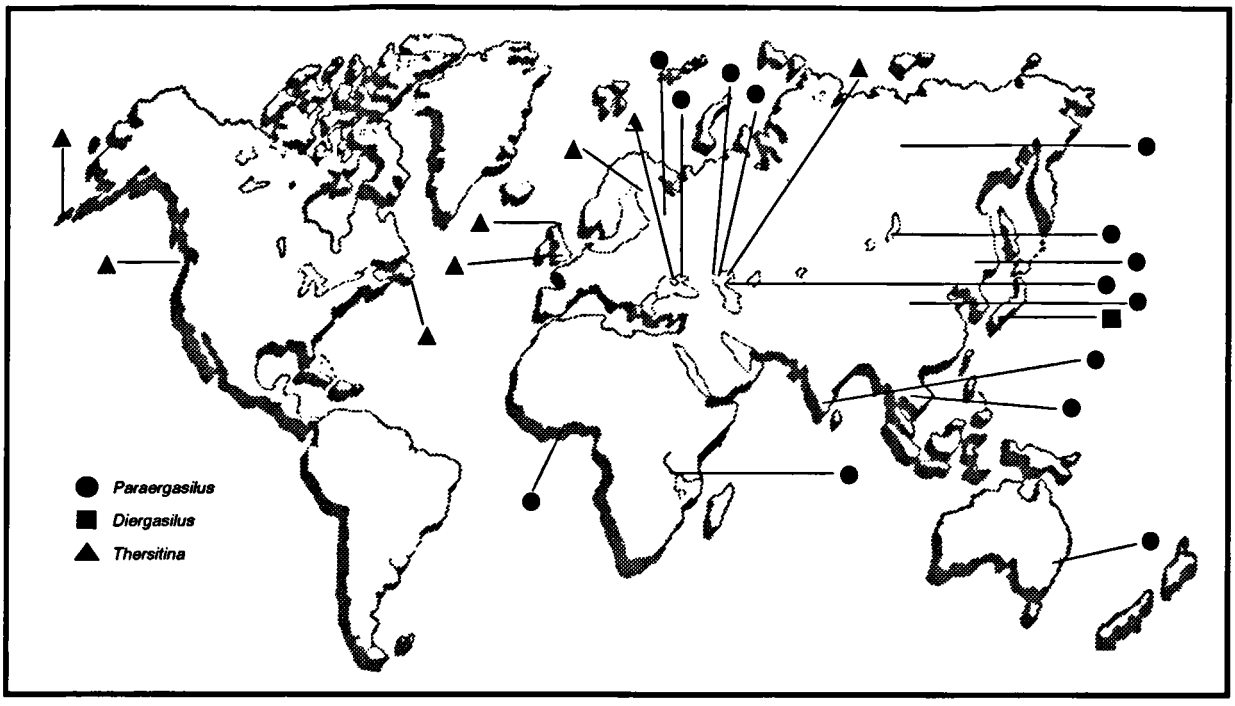

Fig. 3. Distribution of *Paraergasilus* (clade I), *Diergasilus* (clade II), and *Thersitina* (clade III).

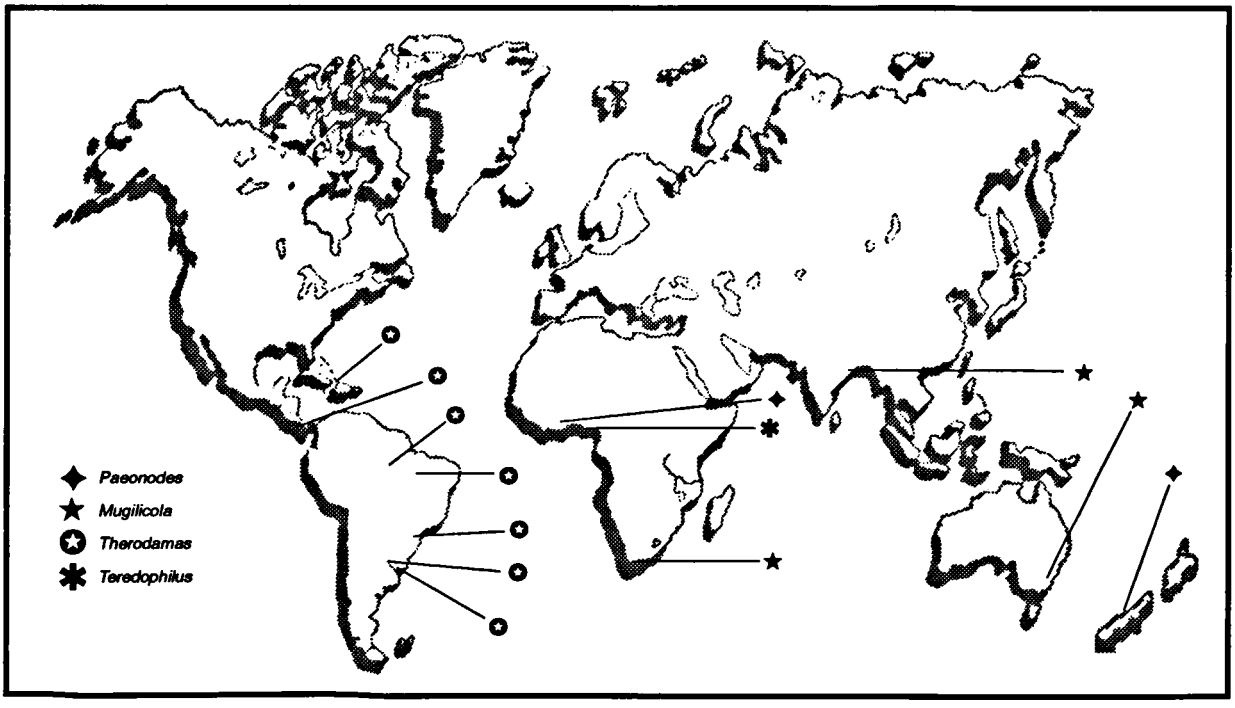

Fig. 4. Distribution of *Paeonodes*, *Mugilicola*, *Therodamas*, and *Teredophilus* (clade IV).

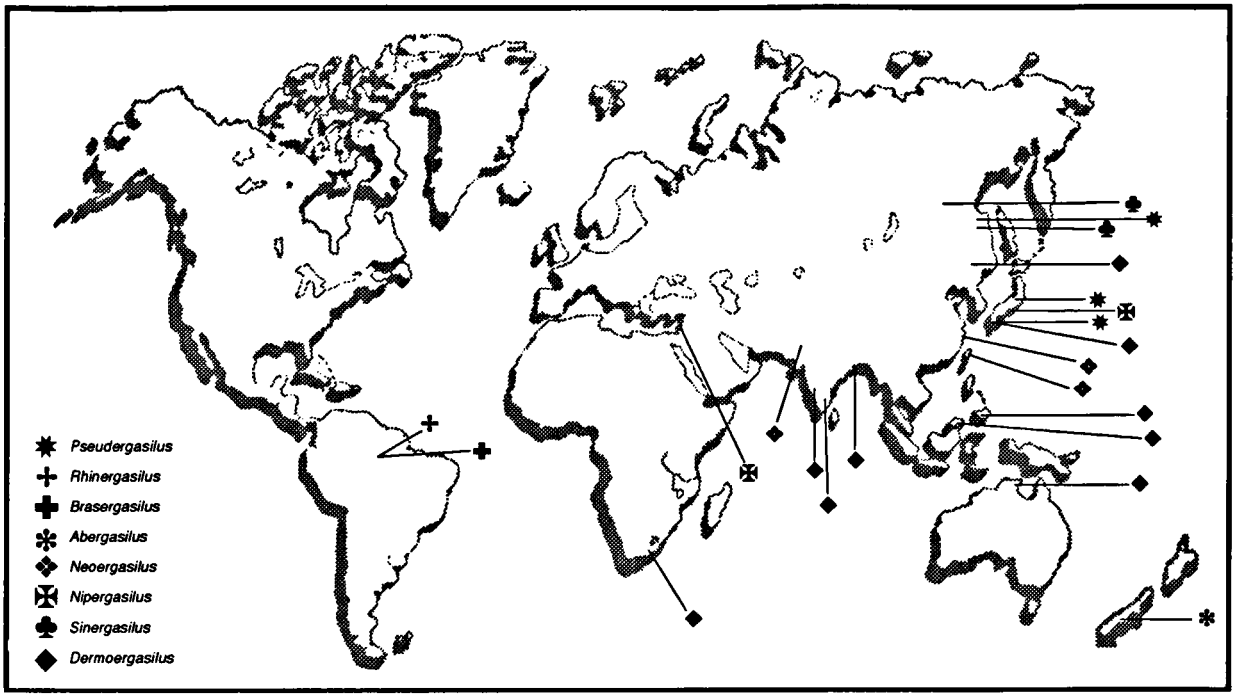

Fig. 5. Distribution of *Pseudergasilus* from clade V and *Rhinergasilus*, *Brasergasilus*, *Abergasilus*, *Neoergasilus*, *Nipergasilus*, *Sinergasilus*, and *Dermoergasilus* from clade VI. *Ergasilus* from clade VI is world-wide in distribution and omitted from this map.

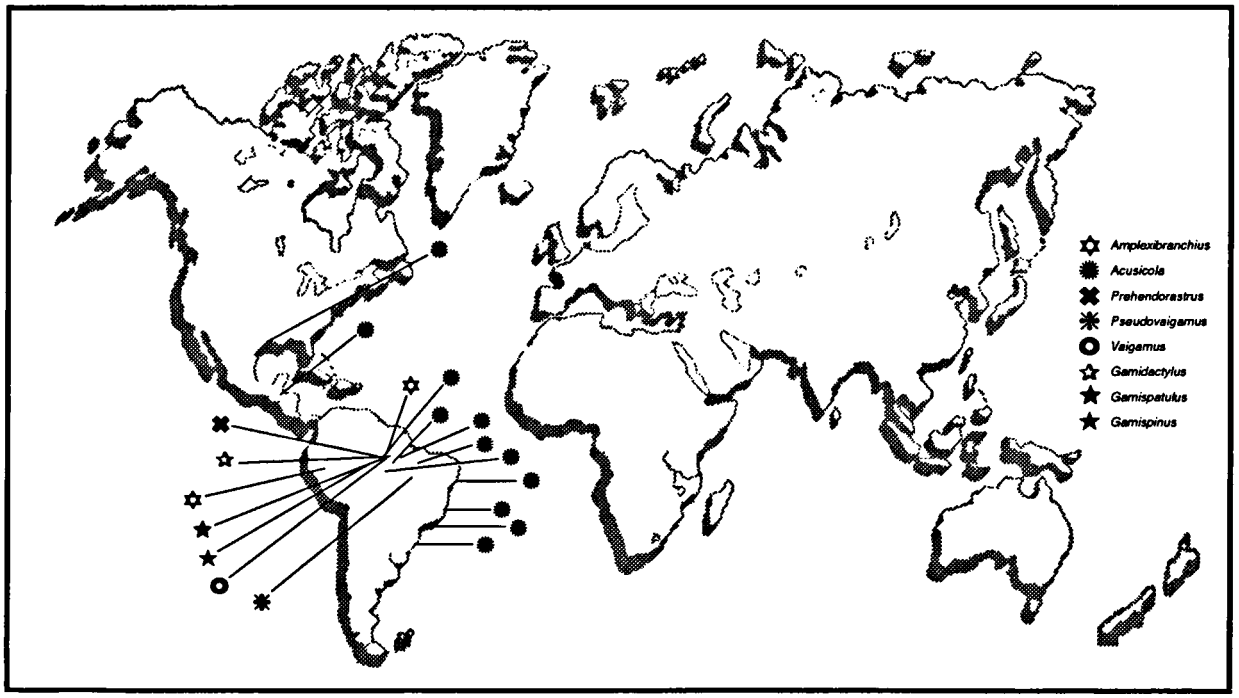

Fig. 6. Distribution of *Amplexibranchius*, *Acusicola*, and *Prehendorastrus* from clade VII and *Pseudovaigamus*, *Vaigamus*, *Gamispatulus*, *Gamidactylus*, and *Gamispinus* from clade VIII.

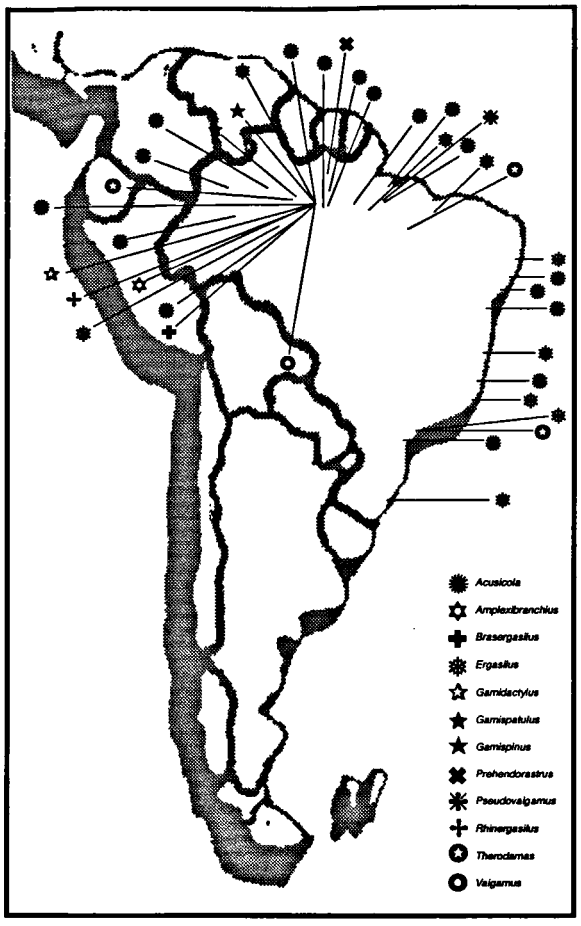

Fig. 7. Distribution of ergasilid genera in Brazil.

Biogeography

An hypothesis on historical biogeography can sometimes be deduced from a cladogram. From these phylogenetic studies, some patterns of ergasilid distribution are apparent. *Paraergasilus* is found in Eurasia, Africa, and Australia (Fig. 3). Its absence from the New World suggests that this new genus evolved after the widening of the Atlantic Ocean. On the contrary, the amphi-Atlantic distribution of *Thersitina* would indicate that it evolved before the birth of this ocean. The genus is host-specific to sticklebacks (Pisces, Gasterosteidae).

The distribution pattern of the most transformed ergasilids (clade IV, see Fig. 4) seems to suggest that these genera originated in Gondwana. The wide distribution of the members of this clade is thought to be a result of their utilization of wide spreading coastal fish such as needlefish and mullet. A similar pattern is found in *Dermoergasilus* and *Neoergasilus* (clade VI, see Fig. 5). The remaining members of the last-mentioned clade, with the exception of *Ergasilus*, are rather restricted in their distribution, possibly due to their utilization of narrowly distributed freshwater hosts. The members of clades VII and VIII are essentially confined to South America, particularly the Amazon Basin (Fig. 6). *Acusicola* is the only exception, with some of its members reaching as far as Texas to the North. As in the case of *Dermoergasilus* and *Neoergasilus*, this distribution pattern may be due to the utilization of coastal euryhaline fishes as hosts.

Twelve genera of ergasilids are known from Brazil (Fig. 7). They include all members of the most derived genera (cf. Fig. 2), from clade VII and clade VIII, plus three genera (*Ergasilus*, *Brasergasilus*, and *Rhinergasilus*) from clade VI and one genus (*Therodamas*) from clade IV. Aside from *Ergasilus*, which is cosmopolitan, these Brazilian ergasilids are essentially confined to the Amazon Basin. This high diversity (12/24 or 50% of the known genera from the Amazon Basin) suggests that ergasilids may have gone through an explosive cladogenesis in the Amazon Basin, probably in association with a similar radiation of their fish hosts. Given these patterns, we feel confident that many ergasilids are yet to be discovered on Amazon fishes.

Acknowledgements

This work was supported by a grant from the Brazilian Ministry of Education and CAPES to the first author (M.A.P. da M. Amado). The authors gratefully acknowledge the help and the favourable research facilities offered by the Department of Biology of California State University, Long Beach, USA, and by the Departamento de Zoologia and Museu de Zoologia da Universidade de São Paulo, Brazil. They also thank the Natural History Museum, London, in the person of Dr. Geoff Boxshall, the Smithsonian Institution, Washington, USA, particularly Dr. Janet Reid, and the Instituto Nacional de Pesquisas da Amazonia, Amazonas, Brazil, for help in obtaining the type materials of the ergasilids and vaigamids deposited in these Institutions.

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Received: 28 October 1994
Revised: 1 September 1995