A REVIEW OF THE ARHYTHMACANTHIDAE (ACANTHOCEPHALA) WITH A DESCRIPTION OF *HETEROSENTIS HIRSUTUS* N. SP. FROM *CNIDOGLANIS MACROCEPHALA* (PLOTOSIDAE) IN AUSTRALIA

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Summary :

Heterosentis hirsutus n. sp. is described from *Cnidoglanis macrocephala* (Siluriformes: Plotosidae) from the Swan Estuary, Western Australia. It is distinguished by having 14 longitudinal rows of 6-7 hooks per row on the proboscis, a trunk armed anteriorly and posteriorly (=genital spines) with minute spines and lemnisci that may extend to the posterior margin of the proboscis receptacle. The new species also has prominent fragmented nuclei in its trunk wall. New information is given for *Heterosentis plotosi* Yamaguti, 1935 from *Plotosus lineatus* (Siluriformes: Plotosidae) and *H. paraplusiarum* (Nickol, 1972) Amin, 1985 from *Paraplusius guttata* (Pleuronectiformes: Cynoglossidae), both from Queensland. A key to the species of *Heterosentis* Van Cleave, 1931 is provided. The Arhythmacanthidae subfamilies are reviewed: there is little utility in the recognition of these taxa because of the small number of genera involved and the validity of the characters on which they are based is in doubt, particularly whether trunk spines are present or absent. Only *Acanthocephaloides* Meyer, 1932, *Breizacanthus* Golvan, 1969, *Euzetacanthus* Golvan & Houin, 1964, *Heterosentis*, *Hypoechinorhynchus* Yamaguti, 1939 and *Paracanthocephaloides* Golvan, 1969 of the Arhythmacanthidae are considered valid. A key to these genera is provided. The monotypic genus *Neoacanthocephaloides* Cable & Quick, 1954 is considered a new synonym of *Acanthocephaloides* thus creating *Acanthocephaloides spinicaudatus* (Cable & Quick, 1954) n. comb. *Arhythmacanthus* Yamaguti, 1935 is maintained as a synonym of *Heterosentis* because the distinction between two and three hook types is made equivocal when the transition between the apical and subapical hooks is gradual.

KEY WORDS : Arhythmacanthidae, Acanthocephala, *Heterosentis*, taxonomy, fish, Plotosidae, new species, Australia.

MOTS CLÉS : Arhythmacanthidae, Acanthocephala, *Heterosentis*, taxonomie, poisson, Plotosidae, nouvelle espèce, Australie.

Résumé : UNE RÉVISION DE LA FAMILLE ARHYTHMACANTHIDAE (ACANTHOCEPHALA) ET UNE DESCRIPTION D'UNE ESPÈCE NOUVELLE DE *CNIDOGLANIS MACROCEPHALA* (PLOTOSIDAE) EN AUSTRALIE

Heterosentis hirsutus n. sp. est décrite de *Cnidoglanis macrocephala* (Siluriformes: Plotosidae) du Swan Estuary, Australie occidentale. L'espèce est distinguée par la présence de 14 files longitudinales de 6-7 crochets chacune sur le proboscis, un tronc portant des épines cuticulaires de petite taille sur la partie antérieure et autour de l'orifice génital, et de lemnisques qui ne sont pas plus longs que le réceptacle. Le tégument de l'espèce nouvelle contient des fragments de noyaux géants. Des données nouvelles sur *Heterosentis plotosi* Yamaguti, 1935 récoltée chez *Plotosus lineatus* (Siluriformes: Plotosidae) et sur *H. paraplusiarum* (Nickol, 1972) Amin, 1985 récoltée chez *Paraplusius guttata* (Pleuronectiformes: Cynoglossidae) sont présentées. Une clé de détermination est établie pour les espèces d'*Heterosentis* Van Cleave, 1931. Les sous-familles d'Arhythmacanthidae sont réexaminées: il nous semble que ces sous-familles sont de peu d'importance à cause du petit nombre de genres et que les caractères taxonomiques sont douteux, surtout la présence ou l'absence d'épines sur le tronc. Seule *Acanthocephaloides* Meyer, 1932, *Breizacanthus* Golvan, 1969, *Euzetacanthus* Golvan & Houin, 1964, *Heterosentis*, *Hypoechinorhynchus* Yamaguti, 1939 et *Paracanthocephaloides* Golvan, 1969 sont valides. Une clé de détermination pour ces genres est donnée. Le genre *Neoacanthocephaloides* est considéré comme un synonyme de *Acanthocephaloides*; donc la seule espèce du genre *Neoacanthocephaloides* Cable & Quick, 1954 devient *Acanthocephaloides spinicaudatus* (Cable & Quick, 1954) n. comb. Le genre *Arhythmacanthus* Yamaguti, 1935 reste un synonyme d'*Heterosentis* car la différence entre les types de crochets apicaux et sous-apicaux n'est pas évidente. En effet, lorsque la transition entre ces crochets se fait de manière graduelle, il devient difficile de distinguer précisément entre deux ou trois types de crochets.

INTRODUCTION

There are about fifty species of acanthocephalans known from Australian hosts (Edmonds, 1989). A recent investigation into the parasitic

fauna of some Western Australian and Queensland fish yielded specimens of acanthocephalans. These appeared to belong to the Arhythmacanthidae Van Cleave, 1931 because they possessed six cement glands and an abrupt transition on the proboscis from the small basal hooks (= spines) without roots to larger subapical or apical hooks with roots. The only arhythmacanthids recorded from Australian hosts are *Heterosentis paraplusiarum* (Nickol, 1972) Amin, 1985 from *Paraplusius guttata* (Cynoglossidae) in Moreton Bay, Queensland (Nickol, 1972), *Hypoechinorhynchus*

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alaeopis Yamaguti, 1939 from *Callionymus calauro-pomus* (Callionymidae) and *Notolabrus tetricus* (as *Pseudolabrus tetricus*) (Labridae) in southern Australian waters (Johnston & Edmonds, 1947; Edmonds, 1989) and *Hypoechinorhynchus robustus* Pichelin, 1999 from *Notolabrus parilus* (Labridae) from Western Australia (Pichelin, 1999).

Collection of three species of arhythmacanthids in Australian waters created the opportunity to review the taxonomy within the family.

MATERIALS AND METHODS

Arthrocephalans were removed from the intestines of fish, washed in 0.85 % saline, fixed in Berland's fluid (95 % glacial acetic acid and 5 % formalin) and stored in 70 % ethanol. Specimens were stained with Mayer's haematoxylin, dehydrated through a graded series of alcohols, cleared with methyl salicylate and mounted in Canada balsam. Drawings were made with the aid of a camera lucida and added to by hand. Measurements, presented as the

range with the mean in parenthesis, are given in micrometres. Abbreviations used: AHC – Australian Helminthological Collection, South Australian Museum, Adelaide, Australia; QM – Queensland Museum, Queensland, Australia.

RESULTS

HETEROSENTIS HIRSUTUS N. SP.

(Fig. 1; Table I)

Type host: *Cnidoglanis macrocephala* (Plotosidae)

Type locality: Swan Estuary, Western Australia

Site in host: intestine

Specimens deposited: QM G 217389 (holotype), QM G 217390-217404 (paratypes), AHC 28131-28135 (paratypes).

Description

Arhythmacanthidae. Arhythmacanthinae. Sexual dimorphism not pronounced but females larger than males. Proboscis cylindrical, armed with 14 longitudinal rows:

	<i>H. hirsutus</i> n. sp. males	<i>H. hirsutus</i> n. sp. females	<i>H. plotosi</i> males	<i>H. plotosi</i> females
Proboscis apical hook	46-58 (51) n = 8	45-68 (55) n = 6	33-48 (39) n = 13	38-53 (43) n = 6
Proboscis subapical hook	63-86 (73) n = 11	68-92 (82) n = 11	68-79 (74) n = 12	74-84 (81) n = 6
Proboscis basal hook 1	18-28 (23) n = 9	25-33 (28) n = 14	18-25 (22) n = 11	22-28 (24) n = 5
Proboscis basal hook 2	18-25 (22) n = 10	20-28 (24) n = 13	17-22 (18) n = 11	17-23 (20) n = 5
Proboscis basal hook 3	17-23 (19) n = 10	17-25 (21) n = 14	12-19 (16) n = 11	15-20 (18) n = 5
Proboscis basal hook 4	13-18 (17) n = 10	17-20 (18) n = 14	10-17 (13) n = 4	13-15 (14) n = 2
Proboscis basal hook 5 (most basal)	13-17 (15) n = 6	13-17 (15) n = 5	–	–
Trunk length	1657-3233 (2508) n = 11	1641-4070 (2896) n = 11	1001-4103 (2673) n = 11	3873-6400 (4859) n = 9
Trunk width	377-722 (533) n = 11	263-788 (540) n = 11	312-656 (555) n = 11	656-1083 (824) n = 9
Proboscis length	197-270 (245) n = 5	194-283 (236) n = 4	139-191 (167) n = 10	132-224 (183) n = 7
Proboscis width	72-138 (120) n = 5	113-145 (129) n = 4	87-118 (100) n = 10	103-250 (137) n = 7
Proboscis receptacle length	237-474 (387) n = 9	258-474 (402) n = 8	297-507 (411) n = 11	434-559 (503) n = 8
Proboscis receptacle width	112-138 (126) n = 7	103-151 (126) n = 8	92-178 (130) n = 11	132-204 (163) n = 8
Proboscis length: trunk length	1:10	1:12	1:16	1:27
Trunk spines extending posteriorly from anterior end of trunk	258-340 (307) n = 3	245-446 (307) n = 4	362-658 (490) n = 4	–
Trunk spines extending ante- riorly from posterior end of trunk	136-310 (212) n = 7	113 n = 1	not present	not present
Lemnisci length	217-494 (312) n = 13	281-592 (404) n = 8	197-651 (447) n = 11	625 n = 1
Lemnisci width	53-151 (96) n = 11	74-126 (94) n = 4	33-89 (58) n = 8	118 n = 1
Anterior testis length	252-461 (352) n = 10	–	129-591 (374) n = 11	–
Anterior testis width	171-283 (223) n = 9	–	162-279 (217) n = 11	–
Posterior testis length	204-441 (312) n = 10	–	171-525 (362) n = 11	–
Posterior testis width	132-329 (219) n = 9	–	139-295 (216) n = 11	–
Säffigen's pouch length	320 n = 1	–	–	–
Säffigen's pouch width	118-155 (137) n = 8	–	97-158 (137) n = 10	–
Cement glands width	58-136 (91) n = 30	–	48-145 (100) n = 26	–
Bursa (everted) length	230 n = 1	–	165-197 (181) n = 2	–
Bursa (everted) width	243 n = 1	–	145-184 (165) n = 3	–
Egg length	–	56.1-66.0 (61.3) n = 25	–	49.5-54.5 (51.0) n = 10
Egg width	–	13.2-15.8 (14.7) n = 25	–	10.7-11.6 (11.4) n = 10

Table I. – Measurements of specimens of *Heterosentis hirsutus* n. sp. and of new specimens of *H. plotosi* from Australian hosts.

Fig. 1. – *Heterosentis birsutus* n. sp. a) male specimen (holotype). b) female specimen (paratype). c) armature of proboscis showing abrupt transition from small rootless hooks (= spines) to larger hooks with roots. d) egg with filaments. Scale bars: a & b= 500; c = 50; d = 25.

each row consists of 1 medium apical hook 45-68 (53) $n = 14$ with root 20-36 (29) $n = 12$, 1 larger subapical hook 63-92 (77) $n = 22$ with root 30-50 (40) $n = 15$ and 4-5 small, basal, curved, rootless hooks 13-33 (21) $n = 105$. Neck present, unarmed. Trunk fusiform, armed with minute posteriorly-pointing spines, extending from anterior end of trunk to just beyond posterior margin of lemnisci in a wedge or v-shape; trunk also armed with minute spines near genital pore at dorso-posterior end. Fragmented nuclei present in mid-trunk wall. Proboscis receptacle double-walled with cephalic ganglion at base. Lemnisci roughly equal in length, extend to about posterior margin of proboscis receptacle. Testes roughly oval, tandem, in mid to posterior part of trunk. Cement glands 6, pyriform; some glands contiguous with margin of posterior testis. Säftigen's pouch tubular to pyriform. Seminal vesicle partially obscured by cement glands and their ducts. Copulatory bursa with digital rays. Male genital pore terminal. Eggs elongated, ovoid with polar extension of fertilization membrane; filaments present. Female genital pore terminal.

Comparison

Heterosentis hirsutus n. sp. is distinguished from the other 11 species of the genus by having a combination of the following characters: 14 longitudinal rows of hooks on the proboscis consisting of 2 large apical hooks and 4-5 small basal hooks, a trunk armed with minute spines at its anterior and posterior ends, and lemnisci that extend to about the posterior margin of the proboscis receptacle.

H. hirsutus differs from *H. overstreeti* Schmidt & Paperna, 1978 by having spines restricted to the anterior and posterior regions of the trunk. *H. overstreeti* has spines covering the entire trunk (Schmidt & Paperna, 1978). *H. parasiluri* Yin & Wu, 1984 also has spines on its posterior end (Yu & Wu, 1989) but has fewer small basal hooks ($n = 2$) and more large apical hooks ($n = 3$) per longitudinal row on the proboscis (Yin & Wu, 1984) than *H. hirsutus*.

This new species resembles a few species of *Heterosentis* Van Cleave, 1931 that lack spines on the posterior part of the trunk. *H. paraplagueiarum* and *H. fusiformis* Yamaguti, 1935 have longer hooks than *H. hirsutus*: the longest hooks of *H. paraplagueiarum* (Nickol, 1972) are 113-132 long (Nickol, 1972) and those of *H. fusiformis* are 188-210 long (Yamaguti, 1935) whereas the longest hooks of *H. hirsutus* are only 63-92 long. It is not clear whether *H. pseudobagri* (Wang & Zhang, 1987) has posterior trunk spines but it differs from *H. hirsutus* by having fewer longitudinal rows ($n = 12$), fewer small basal hooks ($n = 2$) and more large apical hooks ($n = 3$) per longitudinal row on the proboscis (see Wang & Zhang, 1987). *H. heteracanthus* (Linstow, 1896) as redescribed by Zdzitowiecki (1984) has 10 rows of 3-5 pro-

boscis hooks whereas *H. hirsutus* has 14 rows of 6-7; *H. heteracanthus* also has lemnisci longer than its proboscis receptacle and the trunk spines extend further down the trunk. *H. hirsutus* differs from *H. thapari* (Gupta & Fatma, 1979) by having more than the 10-12 longitudinal rows and fewer than the 7-8 hooks per row described by Gupta & Fatma (1979); the hooks of *H. hirsutus* are also considerably longer. *H. septacanthus* (Sita in Golvan, 1969) has smaller apical proboscis hooks and lemnisci twice as long as the proboscis receptacle (see Golvan, 1969). The eggs of *H. zdzitowieckii* (Kumar, 1992) are smaller, 50-52 long, (Kumar, 1992) than those of *H. hirsutus*. *H. caballeror** Gupta & Fatma, 1985 has only 10 rows of hooks (Gupta & Fatma, 1985) as opposed to the 14 in *H. hirsutus*. *H. plotosi* Yamaguti, 1935 has a higher proboscis length to trunk length ratio than *H. hirsutus*: Yamaguti's (1935; 1939) specimens have a ratio of 1:12 for his sole male specimen and 1:19 for females; see also Table I. Also the four giant muscle cells described for *H. plotosi* by Yamaguti (1935) were not seen in *H. hirsutus*. Conversely, the scattered nuclei seen in *H. hirsutus* are absent in Yamaguti's (1935) *H. plotosi*.

HETEROSENTIS PLOTOSI YAMAGUTI, 1935 (Fig. 2; Table I)

Type host: *Plotosus lineatus* (as syn. *P. anguillaris*) (Plotosidae)

Type locality: Pacific coast of Wakayama Prefecture, Japan

Site in host: intestine

New specimens examined: QM G 217405-217414 (vouchers) - all from *Plotosus lineatus*, Moreton Bay, Qld, Australia.

Description

Sexual dimorphism present; females larger than males. Proboscis short, globular, armed with 13-14 longitudinal rows: each row consists of 1 apical hook 33-53 (40) $n = 19$ with root 18-25 (22) $n = 2$, 1 larger subapical hook 68-84 (76) $n = 18$ with root 26-41 (34) $n = 5$ and 3-4 small basal curved rootless hooks 10-28 (19) $n = 54$. Trunk fusiform, armed anteriorly with minute posteriorly-pointing spines, extending ventrally and posteriorly in v-shape; fragmented nuclei not seen in trunk wall. Proboscis receptacle double-walled, with cephalic ganglion at base. Large muscle cells 2, near base of proboscis receptacle. Lemnisci equal, extend beyond posterior margin of proboscis receptacle. Cement glands 6, pyriform. Testes oval, in mid to posterior part of trunk. Säftigen's pouch partially obscured by cement glands and ducts. Seminal vesicle oval. Genital pore terminal in males and females. Eggs elongated, ovoid with polar extensions of fertilization membrane.

Remarks

The eggs of the specimens of *H. plotosi* from Moreton Bay (50-55 (51) × 11-12 (11)) are slightly smaller than those recorded for the Japanese specimens (51-60 × 13-15) by Yamaguti (1939). However, the remainder of the measurements given by Yamaguti (1935; 1939) are sufficiently similar to those of the present study (Table I) that we believe our specimens to be conspecific with *H. plotosi*.

HETEROSENTIS PARAPLAGUSIARUM (NICKOL, 1972)
AMIN, 1985

Type host: *Paraplagusia guttata* (Cynoglossidae)

Type locality: Moreton Bay, Qld, Australia

Site in host: intestine

Museum specimens examined: USNM 72254 (allotype), USNM 72255 (paratype)

New specimens examined: QM G 217415-217428 (vouchers) - all from *Paraplagusia guttata*, Moreton Bay, Qld.

Description

Sexual dimorphism not pronounced; females only slightly larger than males. Proboscis globular to clavi-form, armed with 13-15 longitudinal rows: each row consists of 1 slender apical hook 31-59 (43) $n = 7$, 1 large thick hook 68-92 (77) $n = 20$ with root and 3-4 small basal curved rootless hooks 13-18 (14) $n = 19$. Trunk fusiform, armed anteriorly with large posteriorly-pointing spines, extending ventrally and posteriorly in v-shape; spines become smaller posteriorly; fragmented nuclei in trunk wall absent. Proboscis receptacle double-walled, with cephalic ganglion at base. Lemnisci equal, extend beyond posterior margin of proboscis receptacle. Cement glands 6, pyriform. Testes round to oval, in mid to posterior part of trunk. Säftigen's pouch and seminal vesicle partially obscured by cement glands and ducts. Eggs elongated, ovoid with polar extensions of fertilization membrane.

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Fig. 2. - Male specimen of *Heterosentis plotosi* Yamaguti, 1935. Scale bar: 500.

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Fig. 3. - Male specimen of *Heterosentis paraplagusiarum* (Nickol, 1972) Amin, 1985. Scale bar: 250.

	Nickol (1972)		Present study	
	males	females	males	females
Proboscis apical hook	31-36 (35)	31-36 (35)	48-51 (50) n = 2	31-59 (41) n = 5
Proboscis subapical hook I	60-72 (68)	60-72 (68)	—	—
Proboscis subapical hook II	113-120 (116)	120-132 (127)	68-74 (71) n = 7	69-92 (80) n = 13
Proboscis basal hooks	12-17 (14)	22-26 (23)	13-18 (15) n = 4	13-17 (14) n = 15
Trunk length	2500-3300	2500-3300	952-1969 (1358) n = 8	1182-2872 (1818) n = 4
Trunk width	520-660	520-660	213-377 (288) n = 8	187-295 (245) n = 4
Proboscis length	182-206 (196)	202-221 (212)	151-197 (179) n = 5	165-184 (171) n = 3
Proboscis width	139-149 (145)	168-187 (178)	81-125 (104) n = 5	110-118 (115) n = 3
Proboscis receptacle length	—	—	138-296 (228) n = 8	178-342 (265) n = 4
Proboscis receptacle width	—	—	61-112 (80) n = 7	82-112 (92) n = 4
Trunk spines extending posteriorly from anterior end of trunk	425	425	203 n = 1	n/a
Trunk length: spines distance	1:0.15	1:0.15	1:0.14	n/a
Lemnisci length	499-586 (528)	—	n/a	191-226 (211) n = 4
Lemnisci width	58-62 (60)	—	n/a	29 n = 2
Anterior testis length	336-422 (370)	—	116-224 (160) n = 7	—
Anterior testis width	202-269 (232)	—	94-158 (122) n = 7	—
Posterior testis length	336-422 (370)	—	113-224 (152) n = 7	—
Posterior testis width	202-269 (232)	—	97-158 (119) n = 7	—
Säfftigen's pouch length	—	—	—	—
Säfftigen's pouch width	—	—	53-138 (86) n = 8	—
Cement glands width	106-144 (125)	—	—	—
Bursa (everted) length	—	—	84-138 (111) n = 2	—
Bursa (everted) width	—	—	116-138 (127) n = 2	—

Table II. — Measurements of specimens of *Heterosentis paraplusiarum* collected during the present study compared with those published by Nickol (1972).

Remarks

The measurements of the new specimens (Table II) are generally smaller than those given by Nickol (1972), particularly in the length of the largest hooks on the proboscis. However, since our specimens appear to be similar in most other respects (e.g. proboscis armature, ratio of trunk length to extent of trunk spines) we consider them tentatively to be *Heterosentis paraplusiarum*. Our specimens are also from the type host and locality.

KEY TO SPECIES OF THE *HETEROSENTIS*

This key is based on information contained in the descriptions for *Heterosentis caballeroi** by Gupta & Fatma (1985), for *H. fusiformis* by Yamaguti (1935), for *H. heteracanthus* by Zdzitowiecki (1984), for *H. overstreeti* by Schmidt & Paperna (1978), for *H. paraplusiarum* by Nickol (1972), for *H. parasiluri* by Yin & Wu (1984) and Yu & Wu (1989), for *H. plotosi* by Yamaguti (1935, 1939), for *H. pseudobagri* by Wang & Zhang (1987), for *H. septacanthus* by Golvan (1969), for *H. thapari* by Gupta & Fatma (1979), for *H. zdzitowieckii* by Kumar (1992) and for *H. hirsutus* n. sp. from the present study.

* The original spelling "*cabelleroi*" by Gupta & Fatma (1985) was a mistake since they dedicated their new species in honour of Dr Caballero.

- 1(0). Up to 12 longitudinal rows of hooks on proboscis...2
- 13 or more longitudinal rows8
- 2(1). Apicalmost hook up to 30 µm long..*H. thapari*
- Apicalmost hook longer than 30 µm3
- 3(2). Trunk spines extend well past receptacle but not to trunk end*H. heteracanthus*
- Trunk spines cover entire body*H. overstreeti*
- Trunk spines other than above4
- 4(3). 3 or more small basal hooks on proboscis*H. caballeroi*
- Fewer than 3 small basal hooks.....*H. pseudobagri*
- 8(1). Lemnisci not twice as long as proboscis receptacle..9
- Lemnisci twice as long as proboscis receptacle13
- 9(8). No spines on posterior end of trunk10
- Spines present on posterior end of trunk12
- 10(9). Lemnisci equal in length.....11
- Lemnisci unequal.....*H. zdzitowieckii*
- 11(9). Longest proboscis hook less than 100 µm long*H. plotosi*
- Longest proboscis hook 100 µm or longer.....*H. paraplusiarum*
- 12(9). 3 large apical (incl. subapical) hooks or fewer on proboscis*H. hirsutus*
- More than 3 apical hooks on proboscis..*H. parasiluri*
- 13(8). Anterior testis less than 500 µm long.....*H. septacanthus*
- Anterior testis 500 µm or longer*H. fusiformis*

DISCUSSION

The diagnosis of the Arhythmacanthidae Yamaguti, 1935 as amended by Golvan (1969) distinguishes this family from other acanthocephalan families. The two most characteristic features of the family is the abrupt transition from small basal hooks (spines) without roots to larger apical (or subapical if present) hooks with roots on the proboscis and the possession of six cement glands.

SUBFAMILIES

Golvan (1969) used the presence and absence of trunk spines and their distribution to recognise three subfamilies in the Arhythmacanthidae. He suggested that the Arhythmacanthinae Yamaguti, 1935 are distinguished by having spines only on the anterior part of the trunk and a tendency for the proboscis to be spherical; the Neoacanthocephaloidinae Golvan, 1960 are distinguished by having spines on the anterior part of the trunk and genital spines (= posterior trunk spines); and the Paracanthocephaloidinae Golvan, 1969 are distinguished by having no trunk spines and a short and cylindrical proboscis. Recent discoveries of spines on the posterior end of the trunk of species of Arhythmacanthinae (Yu & Wu, 1989; present study) and the placement by Schmidt & Paperna (1978) of their new species which has spines over the entire body into *Arhythmacanthus* Yamaguti, 1935 has made these distinctions of equivocal value.

Arhythmacanthinae Yamaguti, 1935

This subfamily is currently represented by *Heterosentis* and *Hypoechinorhynchus* (see Pichelin, 1999). The subfamily also previously contained *Arhythmacanthus* but this genus was synonymised with *Heterosentis* and all species of *Arhythmacanthus* were transferred to *Heterosentis* (see Amin, 1985). Kumar (1992) disagreed with this move, stating that species of *Arhythmacanthus* had three types of hooks and species of *Heterosentis* only two. The distinction between two and three types of hooks is not clear. For example, *H. plotosi* was described by Yamaguti (1935) as having two kinds of hooks and was put into *Heterosentis*. Schmidt & Paperna (1978), however, transferred *H. plotosi* to *Arhythmacanthus*, presumably because they considered the slender apical hooks distinct from the subapical hooks and small basal hooks. The transition from small basal spines to large apical (or subapical if present) hooks is abrupt in all arhythmacanthids (except *A. cyrusi*) but the transition from apical to subapical hooks, if it exists, is less evident and clearly gradual in some species. For this reason it can be difficult to decide whether there are two or three types of hooks. It is proposed here that *Arhythmacanthus*

should remain a junior synonym of *Heterosentis* since the distinction between two and three hook types cannot be made reliably and consistently. This synonymy requires the new combinations *H. zdzitowieckii* (Kumar, 1992) n. comb. and *H. pseudobagri* (Wang & Zhang, 1987) n. comb. These new combinations, *Heterosentis hirsutus* n. sp., *H. parasiluri* Yin & Wu, 1984 and *H. caballeroi* Gupta & Fatma, 1985 have been described since Amin's (1985) classification. Thus, there appear to be 12 species of *Heterosentis* (including *H. hirsutus*) and four species of *Hypoechinorhynchus* (*H. alaeopis* Yamaguti, 1939, *H. magellanicus* Szidat, 1950, *H. thermaceri* de Buron, 1988 and *H. robustus* Pichelin, 1999). A key to the species of *Heterosentis* is provided above.

Diagnosis: Arhythmacanthidae. Trunk spines always present; spines may be restricted to the anterior end of the trunk, may be present on anterior and posterior ends or may cover entire trunk. Proboscis short, globular or claviform with a tendency to have either about the same number of large apical hooks as small basal hooks or fewer large hooks than small hooks. Included genera: *Heterosentis* Van Cleave, 1931 and *Hypoechinorhynchus* Yamaguti, 1939.

Neoacanthocephaloidinae Golvan, 1960

This subfamily is distinguished by the presence of posterior trunk (= genital) spines (Golvan, 1969) and is represented by two genera, *Acanthocephaloides* and *Neoacanthocephaloides* (see Amin, 1985).

Species of *Acanthocephaloides* were considered to be devoid of trunk spines until Golvan (1960) discovered spines along the entire length of the trunk of the type species, *A. propinquus* (Dujardin, 1945) Meyer, 1932. He amended the generic diagnosis and considered the genus to contain provisionally *A. propinquus*, *A. distinctus* Golvan, 1969, *A. incrassatus* (Molin, 1858) Meyer, 1932, *A. kostylewi* Meyer, 1932 and *A. soleae* (Porta, 1905) Petrotschenko, 1956. Golvan (1969) assigned *Acanthocephaloides rhinoplagusiae* Yamaguti, 1935 and *A. neobythitis* Yamaguti, 1939 to *Yamaguti-sentis* Golvan, 1969 in the Echinorhynchidae because he considered the hooks on the proboscis to be simply diminishing in size from anterior to posterior rather than being of two distinct types.

Paggi & Orecchia (1983) transferred *Acanthocephaloides soleae* to *Paracanthocephaloides* Golvan, 1969 because it lacked trunk spines. De Buron & Maillard (1985) created *Solearhynchus* in the Echinorhynchidae to accommodate this species principally because it lacked trunk spines and had only one type of hook on the proboscis.

Araki & Machida (1987) described two new species, *Acanthocephaloides ichiharai* Araki & Machida, 1987 and *Acanthocephaloides claviformis* Araki & Machida,

1987. They synonymised *Yamagutisensis* with *Acanthocephaloides* because they considered the presence or absence of trunk spines to be unreliable at the generic level. Thus *Y. rhinoplagusiae* and *Y. neobythitis* were returned to *Acanthocephaloides*. As a result of this action, the genus *Acanthocephaloides* now contains species with trunk spines that either are confined to the anterior region of the trunk or cover the trunk entirely.

Bray, Spencer Jones & Lewis (1988) described *Acanthocephaloides cyrusi* Bray, Spencer Jones & Lewis, 1988. They suggested that *A. incrassatus* and *A. kostylewi* should be placed in *Paracanthocephaloides* because descriptions of these species failed to report spines on the trunk. *A. cyrusi* possesses hooks that gradually increase in size towards the anterior end of the proboscis (Bray, Spencer Jones & Lewis, 1988). This feature is more characteristic of the rhadinorhynchid genus *Micracanthorhynchina* than of any arhythmacanthid genus. However, specimens of *A. cyrusi* have six cement glands (Bray, Spencer Jones & Lewis, 1988) whereas *Micracanthorhynchina* is characterised as having only four (Golvan, 1969). It may be that *A. cyrusi* requires a new genus.

Cable & Quick (1954) created a monotypic genus, *Neoacanthocephaloides*, within the Echinorhynchidae on the basis of differences in proboscis armature, relative lengths of lemnisci and proboscis receptacle, size and shape of trunk, the distribution of trunk spines and having anterior trunk spines directed posteriorly and posterior trunk spines directed anteriorly. These differences no longer warrant the recognition of *Neoacanthocephaloides* particularly since Golvan (1960) placed it in the Arhythmacanthidae. The proboscis armature of *N. spinicaudatus* is similar to that of *Acanthocephaloides ichibarae* Araki & Machida, 1987: *N. spinicaudatus* has 10 rows of 13 hooks (Cable & Quick, 1954) and *A. ichibarae* has 12-16 rows of 10-13 hooks (Araki & Machida, 1987). The lengths of the lemnisci of species of *Acanthocephaloides* range from nearly as long as the proboscis receptacle as in *A. rhinoplagusiae* Yamaguti, 1935 (see Yamaguti, 1935) to nearly twice as long as the receptacle as in *A. claviformis* Araki & Machida, 1987 (see Araki & Machida, 1987). Thus, the relative length of the lemnisci to proboscis receptacle length is not useful for distinguishing between the two genera. The posteriorly directed spines of *N. spinicaudatus* are also no longer unique. This condition has been shown for *Acanthocephaloides propinquus* by Golvan (1969, Fig. 120) and has been noted by us using SEM (personal observations) also for *A. propinquus*. The description by Cable & Quick (1954) of *N. spinicaudatus* is based on a single male specimen. They noted that the trunk tapered towards each end from a prominent enlargement which they considered

a thickening of the body wall. Such enlargements or deformities are quite common among acanthocephalans and sometimes are the result of the method used to fix the worms. The size of the trunk and its tapering ends (= fusiform) are also not unusual in arhythmacanthids (see descriptions above). We therefore propose *Neoacanthocephaloides* as a junior synonym of *Acanthocephaloides* and the new combination *A. spinicaudatus* (Cable & Quick, 1954) n. comb. The *Neoacanthocephaloidinae* is thus restricted to a single genus, *Acanthocephaloides*.

The proboscis of neoacanthocephaloidines tends to be elongate rather than spherical and also tends to have a greater number of large apical hooks than small basal hooks. As opposed to the arhythmacanthines which have either fewer or about the same number of large apical (including subapical) hooks as small basal hooks on the proboscis. Both subfamilies appear to have species with trunk spines confined to the anterior end of the trunk (e.g. *Heterosentis heteracanthus*, *Acanthocephaloides rhinoplagusiae*), have spines on the anterior and posterior ends (e.g. *H. hirsutus*, *A. spinicaudatus*), have their trunks covered with spines (*H. overstreeti*, *A. propinquus*). Thus the main distinctions between arhythmacanthines and neoacanthocephaloidines are the shape and armature of the proboscis, not the distribution of spines on the trunk.

This subfamily therefore contains *A. propinquus*, *A. distinctus*, *A. geneticus* de Buron, Renaud & Euzet, 1986, *A. claviformis*, *A. ichibarae*, *A. rhinoplagusiae*, *A. neobythitis*, *A. cyrusi* and *A. spinicaudatus* n. comb.

Diagnosis: Arhythmacanthidae. Trunk spines always present; spines may be restricted to the anterior end of the trunk or may be present on anterior and posterior ends or may cover the entire trunk. Proboscis long, cylindrical with a tendency to have a greater number of large apical proboscis hooks than small basal hooks. Included genera: *Acanthocephaloides* Meyer, 1932 (new syn. *Neoacanthocephaloides* Cable & Quick, 1954).

Paracanthocephaloidinae Golvan, 1969

The Paracanthocephaloidinae presently contains *Paracanthocephaloides*, *Euzetacanthus* and *Breizacanthus* (see Amin, 1985) and is distinguished from the other subfamilies by the complete absence of trunk spines (Golvan, 1969). It is possible that trunk spines will be found on new specimens of these species because these spines are often small and difficult to see or, possibly, lost. This difficulty has been discussed by Golvan (1969) who found spines on the type species of *Acanthocephaloides* which was thought previously to be without spines. It is also exemplified by the recent discovery of small spines on the posterior region of the

trunk of *H. parasiluri* by Yu & Wu (1989) and *H. birsutus* (present study). *Euzetacanthus* and *Breizacanthus* are also very similar to each other with few morphological characters to separate them (see Golvan (1969) for generic diagnoses). Conceivably some of the paracanthocephaloidine genera and perhaps the entire subfamily will fall into synonymy. Until then, we consider that the three genera should be retained despite the similarities in the proboscis hooks between species with trunk spines and those without. The following five species have been described or transferred to this subfamily and are considered to belong to this subfamily in addition to the six species listed in Amin (1985): *Breizacanthus golvani* Gaevskaja & Shukgaltor, 1984, *Euzetacanthus golvani* Gupta & Fatma, 1985, *Euzetacanthus chorinemusi* Gupta & Naqvi, 1984, *Paracanthocephaloides kostylewi* (Meyer, 1932) Bray, Spencer Jones & Lewis, 1988, *Paracanthocephaloides incrassatus* (Molin, 1858) Bray, Spencer Jones & Lewis, 1988.

Diagnosis: Arhythmacanthidae. Trunk spines always absent. Included genera: *Breizacanthus* Golvan, 1969, *Euzetacanthus* Golvan & Houin, 1964 and *Paracanthocephaloides* Golvan, 1969.

SUMMARY

At present it seems reasonable to recognise just six genera within the Arhythmacanthidae: *Heterosentis*, *Hypoechinorhynchus*, *Acanthocephaloides*, *Breizacanthus*, *Euzetacanthus* and *Paracanthocephaloides*. Given this small number of genera, we argue that there is little utility in the recognition of subfamilies. Further, absolute validity of the characters on which they are based is in doubt (spines may not be genuinely lacking from the trunk of some paracanthocephaloidines) and may in any case be a poor reflection of evolution within the family. We suggest a de-emphasising of subfamilies within the family and the distinction of genera as per the following key.

KEY TO GENERA OF THE ARHYTHMACANTHIDAE

- 1(0). Proboscis globular or claviform.....2
- Proboscis cylindrical4
- 2(1). Trunk with spines.....3
- Trunk without spines.....*Paracanthocephaloides*
- 3(2). Trunk with antero-dorsal curvature.....
-*Hypoechinorhynchus*
- No trunk curvature *Heterosentis*
- 4(1). Trunk with spines.....*Acanthocephaloides*
- Trunk without spines.....5
- 5(4). Only anterior end of trunk dilated, lemnisci longer than receptacle*Breizacanthus*
- Anterior and posterior ends of trunk dilated, lemnisci not longer than receptacle*Euzetacanthus*

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