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Systematics and Sexual Dimorphism:
Reclassification of the
Crustacean Amphipod Genus
Jassa Leach
(Corophioidea: Ischyroceridae)

by

Kathleen Elizabeth Conlan

B.Sc. . Queen's University, 1972
M.Sc. . University of Victoria, 1977

A thesis submitted to the
Faculty of Graduate Studies and Research
in partial fulfilment of the requirements for the degree of

Doctor of Philosophy

in the
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Carleton University

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We, undersigned, hereby recommend to
the Faculty of Graduate Studies and Research
acceptance of this thesis, submitted by
Eithleen Elizabeth Conlao, B.Sc., A.Sc.
in partial fulfillment of the requirements
for the degree of Doctor of Philosophy

Chairman, Department of Biology

Thesis Supervisor

External Examiner

Urbton University

May 20, 1975

Abstract

Systematic analysis of the crustacean amphipod genus Jassa (Corophioidea: Ischyroceridae) has distinguished twenty-seven species and two subspecies, seventeen of which are new to science. Phenetic analysis indicates that nineteen of these species belong to Jassa, and the other eight species should be transferred to other genera. The resultant reclassification is as follows: Jassa now comprises the type species J. falcata (Montagu, 1808), previously recognized species J. marmorata Holmes, 1903, J. pusilla (Sars, 1894), J. herdmani (Walker, 1893), and J. ingens (Pfeffer, 1888), and the new species J. morinot, J. slatteryi, J. carltoni, J. myersi, J. staudei, J. borowskyae, J. oclairi, J. shawi, J. alonsoae, J. justi, J. gruneri, J. fenwicki, J. thurstoni, and J. hartmannae. Jassa goniamera Walker, 1903 is transferred to Hemijassa Walker, 1907, and Jassa barnardi Stephensen, 1949 is transferred to Ventojassa Barnard, 1970. Pleojassa n.g. is erected for J. wandeli Chevreux, 1906 (type species), J. multidentata multidentata Schellenberg, 1931, J. multidentata orientalis n.subsp., J. lowryi n.sp., and J. moori n.sp. Jassa lilipuna Barnard, 1970 is transferred to Neolschyrocerus n.g., and J. ocia to Plumulojassa n.g. Jassa odontonyx is synonymized with J. pusilla, and J. dentex with Plumulojassa ocia. Jassa pulchella is confirmed as synonymous with J. falcata.

Production of a thumb-like protuberance on the first or second gnathopod at maturity is common in male Corophioidea. However, males of Jassa are unusual in (1) producing the thumb distally to the defining spines, (2) delaying thumb production, and hence functional maturity to

the last molt, and (3) diverging into a minor or major adult form. It is proposed that the two forms have alternative reproductive strategies. Species of Jassa can be categorized into two types according to the size relations and proportions of the adult male forms. It is suggested that type 1 species make the best of a bad situation when small, while type 2 species exhibit a frequency dependent, evolutionarily stable strategy.

On the basis of cladistic analysis it is hypothesized that Jassa originated in the Southern Hemisphere from an ancestor shared with Pleojassa, and twice succeeded in traversing the tropics to then radiate in the Northern Hemisphere. Today Jassa is limited to shallow cold temperate or Antarctic marine coasts, but three species (J. marmorata, J. slatteryi, and J. morinot) have succeeded in traversing the tropics, probably with the aid of man.

This thesis is not intended to constitute publication in order to validate new species names.

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Table of Contents

List of Tables	x
List of Figures	xiv
1. INTRODUCTION	1
1.1. Early taxonomic history	2
1.2. Sexton and Reid's revision.	3
1.3. Taxonomy after Sexton and Reid	5
1.4. Sexual variation in morphology	7
1.5. Sexual behavior	8
1.6 Purpose	10
2. METHODS	11
2.1. Species discrimination	11
2.2. Generic discrimination	20
2.2.1. Phenetic analysis.	21
2.3. Hypotheses of phylogeny	22
2.4. Ecological and behavioral observations	27
3. RESULTS	29
3.1. Morphology and systematics	29
3.1.1. Species discrimination	29
3.1.2. Generic definition	38

3.1.3. Revision of <u>Jassa</u>	49
3.1.4. Sex-and age-related variation in <u>Jassa</u> and comparison with outgroup species	260
3.1.4.1. Sexual development of the second gnathopod	260
3.1.4.1.1. Changes in live <u>Jassa marmorata</u>	260
3.1.4.1.2. Adult male dimorphism	263
3.1.4.1.3. Interspecific differences in morphology . . .	274
3.1.4.1.4. Comparison with changes in outgroup species .	285
3.1.4.1.5. Interspecific differences in development . .	293
3.1.4.2. Sexual development of the second antenna	300
3.1.4.3. Sexual development of the third and fourth peraeopod basis	308
3.2. Behavior	309
3.2.1. Tube building	309
3.2.2. Feeding	311
3.2.3. Locomotion	313
3.3. Ecology	314
3.3.1. Habitat type	314
3.3.2. Algal dwelling amphipod associates	319
3.4. Biogeography	323
3.5. Hypotheses of phylogeny	341
3.5.1. Relationships in the secondary outgroup	344
3.5.2. Relationships within <u>Pleojassa</u>	354
3.5.3. Relationships within <u>Jassa</u>	362
4. DISCUSSION.	369

4.1. The importance of classification	369
4.2. Characteristics of classification	373
4.3. Species: the fundamental unit of evolution.	377
4.4. <u>Jassa</u> : species characteristics	379
4.4.1. Population dynamics, community structure, competition, and predation	379
4.4.2. Sexual dimorphism and reproduction	384
4.4.3. Dispersal	392
4.4.4. Hypotheses of phylogeny	395
 5. CONCLUSIONS	 412
 6. REFERENCES	 416
 7. APPENDIX	 437

List of Tables

1. Acronyms for lending institutions (after Heppner and Lamas, 1982) and the curator of the crustacean collection. 12
2. Private lenders and their institutional association. 14
3. Male specimens of Jassa and outgroups scored for numerical analysis. 30
4. Female specimens of Jassa and outgroups scored for numerical analysis. 34
5. Morphological differences between Pleojassa moori and P. lowryi. 90
6. Nomenclatural disposition of species referred to as Jassa or Jassa falcata by other taxonomists. 113
7. Developmental status of male types of Jassa. 284
8. Comparison of sexual size relationships at maturity for Jassa and outgroup species. A dash indicates insufficient specimens. An asterisk indicates that male growth is indeterminate, thus preventing identification of maturation point. 298

9. Number of individuals of Jassa marmorata and J. slatteryi constructing a tube after isolation in a seawater system with native substrate after twenty-two hours. Total number observed is in parentheses. 310

10. Collection data for Jassa and outgroups. 315

11. Co-occurrence of conspecifics in Jassa (X). Adult male breeding type is given in parentheses. Possibility of hybridization is indicated by an asterisk. Species codes are described in Table 3. 318

12. Survey of algal dwelling amphipods from the exposed rocky intertidal region of Sunset Bay, Coos County, Oregon (stations A-L) and nearby Charleston Harbor (station M). Codes: N, nestler; T, tube dweller; B, borer. The stations are described in Table 13. 320

13. Algal substrate and elevation of collection at Sunset Bay and Charleston Harbor. Sunset Bay collection was from exposed rocky shore. Charleston Harbor collection was from a floating dock. 321

14. Characteristics of the six data subsets for cladistic analysis. 342

15. Characters non-homoplasious for the generic phylogenies produced by Wagner parsimony analysis (Fig. 63) or compatibility analysis

	(Fig. 64) of data set 1. The character states are ordered from plesiomorphic to apomorphic, as polarized by the ischyrocerid, IGE.	351
16.	Species identifications for <u>Jassa</u> in primarily non-taxonomic studies. My identifications, marked by an asterisk, are confirmed (specimens examined); others are likeliest species (assuming correct generic identification).	370
17.	Incidence in the Amphipoda of production of a protuberance or incision of a thumb in the male's sixth segment of gnathopod 2.	391
18.	Characters other than autapomorphies defining the species relations in Fig. 72. The character states are ordered from plesiomorphic to apomorphic, using <u>Ventojassa</u> as the most distant outgroup, <u>Hemijassa</u> as the next-most, and <u>Pleojassa</u> as the sister group. Characters 5 to 100, and 136 to 141 were measured on a male; characters 100 to 129 were measured on a female.	398
19.	Number of trans-equatorial speciation events hypothesized for <u>Jassa</u> by the consensus trees of Figs. 68 and 69, assuming origin in the Southern Hemisphere.	403
20.	Number of trans-North American speciation events hypothesized for Northern Hemisphere lineages of <u>Jassa</u> by the consensus trees of Figs. 68 and 69.	404

- A1. Characters scored for phenetic and cladistic analysis. Codes used in the cladistic analyses are in parenthesis. Characters 1-11, 14-30, 32-52, 54, 57, 58, 60, 62, 64, 65, 67, 68, 70-118 and 138-141 were scored on an adult male, major form; characters 12, 13, 31, 53, 55-56, 59, 61, 63 and 69 on numerous males of various developmental stages; character 66 on a large subadult male; and characters 119-137 on a large adult female.438
- A2. Scores for the 141 characters described in Table 3 on the 27 species of Jassa (OTU's 1-27) and the 5 outgroup species (OTU's 28-32). CHAR: score not transformed and RCHAR: residual. . . . 447

List of Figures

1. Body parts of an amphipod with terminology for their description. A, whole animal; B, upper lip; C, mandible; D, head and antennae; E, gnathopod; F, maxilla 1; G, lower lip; H, maxilla 2; I, maxilliped; J, uropod 3; K, peraeopod 5; L, pleopod 2; M, uropod 1; N, telson. Views A, B, D, G, H, J, M, and N lateral; all other views medial (from Bousfield, 1973).17

2. Phenograms from cluster analysis using UPGMA of all twenty-seven species of Jassa with the five outgroup species (PEL, CLA, CUM, ISP, and IGE). All characters, save those scored as the independent variable for regression. A, mixed quantitative and discrete scores. B, quantitative characters re-scored as discrete.39

3. Plot of the twenty-seven species of Jassa with the five outgroup species (PEL, CLA, CUM, ISP and IGE) on principal coordinates 1 to 3. All characters, as scored for cladistic analysis. The percentage of variation accounted for by each coordinate is shown on the axis. The species are linked by a minimum spanning tree. Species codes are described in Table 3.41

4. Phenograms from cluster analysis using UPGMA of all twenty-seven species of Jassa with the five outgroup species (PEL, CLA, CUM,

- ISP and IGE). Sexually dimorphic characters and independent variables for regression deleted. A, mixed quantitative and discrete scores. B, quantitative characters re-scored as discrete. Species codes are described in Table 3.44
5. Plot of the twenty-seven species of Jassa with the five outgroup species (PEL, CLA, CUM, ISP, and IGE) on principal coordinates 1 to 3, using the non-sexually dimorphic characters as scored for cladistic analysis. The percentage of variation accounted for by each coordinate is shown on the axis. The species are linked by a minimum spanning tree. Species codes are described in Table 3. 46
6. Ischyroceridae. A, Runanga, male; B, Baracuma, male; C, Cerapus, male; D, Ericthonius, male; E, Bogenfelsia, male; F, Bonnierella, male; G, Ventojassa, female; H, Bathyphtis, male. A and E from Barnard (1969); J from Barnard and Drummond (1981); C from Thomas and Heard (1979); D from Bousfield (1973); F from Barnard (1969); G from Barnard (1970); H from Griffiths (1977).52
7. Ischyroceridae. A, Parajassa, male; B, Microjassa, male; C, Pleojassa, male; D, Neoischyrocerus, male; E, Ischyrocerus, female; F, Jassa, male; G, Hemijassa, male. A from Barnard (1970); E from Bousfield (1973). 56
8. Ventojassa. A, whole animal, female; B, antenna 2, male; C, antenna 1, male; D, E, uropod 3, outer ramus; F, G, peraeopod 5;

H, I, peraeopod 7. A, E, H, V. ventosa; B, C, G, I, V. crenulata; D, F, V. frequens. V. crenulata from Ledoyer (1979); V. frequens from Barnard (1972); V. ventosa from Barnard (1970). Scale 0.1 mm.
 64

9. Ventojassa. Gnathopod 2. A-D, adult female; E-G, adult male. A, V. ventosa; B, G, V. frequens; C, E, V. crenulata, D, F, V. barnardi. V. crenulata from Ledoyer (1979); V. frequens from Barnard (1972); V. ventosa from Barnard (1970). Scale 0.1 mm. 66

10. Neoischyrocerus lilipuna. Holotype, adult male, 1.9 mm. Waikiki Aquarium, Oahu, Hawaiian Islands, 11 March 1964. Adult female, 1.5 mm; juvenile male 2, 1.5 mm; adult male 3, 1.8 mm; and adult male 4, 1.9 mm. Fee #1, Waikiki, Oahu, Hawaiian Islands, 25 April 1967. Male 4: new cuticle shown inside; some setae not shown, origins indicated by a small circle. Lateral views: whole body, uropod 3, peraeopods 3,4,6,7 and left mandible; all other views medial. All appendages are of the holotype unless indicated otherwise. Scale 0.1 mm unless indicated otherwise. 76

11. Pleojassa. A, B, antenna 2; C, D, peraeopod 3; E-G, gnathopod 1; H-J, gnathopod 2, adult female; K-N, gnathopod 2, male (K, N, juvenile; L, M, adult). A, P. wandeli; B, P. moori, adult male; C, P. lowryi; D, P. moori; E, P. wandeli; F, P. multidentata multidentata; G, P. moori; H, P. mutidentata orientalis; I, P.

wandeli; J, P. multidentata multidentata; K, P. multidentata multidentata; L, P. wandeli; M, P. lowryi; N, P. multidentata orientalis; Views H, J, K, M, N lateral; all others medial. Views K, M, N, all setae but those at the palmar angle omitted. Scale 0.1 mm.84

12. Pleojassa wandeli. Lectotype, juvenile male, 6.0 mm. Ile Booth-Wandel, Antarctica, 10 December, 1904. Adult, male 1, 9.8 mm; juvenile male 2, 6.3 mm; female, 9.6 mm. Billie Rocks, Signy Island, South Orkney Islands, station no. 10(95), 5 March 1965. Note the thumb cuticle within the juvenile male 2 gnathopod 2. Lateral views: whole body, maxillae 1 and 2; dorsal view: telson; all other views medial. Appendages are of the lectotype unless indicated otherwise. Scale 0.1 mm. 95

13. Jassa. Gnathopod 2, adult male. A, J. staudei; B, J. falcata; C, J. slatteryi; D, J. borowskyae; E, J. oclairi; F, J. morinai; G, J. carltoni; H, J. myersi; I, J. ingens. Views F, G, and I of palmar area, only thumb setae shown. Views A, C, D, F, G, and I lateral, others medial. Scale 0.1 mm.116

14. Jassa. Gnathopod 1. A, J. alonsoae, male; B, J. falcata, male; C, J. borowskyae, female; D, J. shawi, juvenile male; E, J. staudei, female; F, J. slatteryi, female; G, J. thurstoni, male; H, J. pusilla, female. View H lateral, all others medial. Scale 0.1 mm.

-118
15. Jassa. A-D, peraeopod 3; E-G, peraeopod 7; H, I, uropod 1; J, K, uropod 3; L, M, telson. A, J. borowskyae; B, J. myersi; C, J. ingens; D, J. oclairi; E, J. fenwicki; F, J. staudei; G, J. ingens; H, J. falcata; I, J. shawi; J, J. falcata; K, J. borowskyae; L, J. morinoi; M, J. slatteryi. Views F, H, I, J, K, L, M lateral, others medial. Scale 0.1 mm. 120
16. Jassa. Adult female gnathopod 2 palm morphology. A, J. marmorata; B, J. morinoi; C, J. slatteryi; D, J. carltoni; E, J. myersi; F, J. staudei; G, J. oclairi; H, J. borowskyae; I, J. shawi; J, J. pusilla; K, J. falcata; L, J. herdmani; M, J. alonsoae; N, J. justi; O, J. gruneri; P, J. hartmannae; Q, J. thurstoni; R, J. ingens. Setae omitted. All views lateral. Scale 0.1 mm.123
17. Jassa. A-E, antenna 2; F, H, mandible; G, I, maxilla 1. A, J. slatteryi, adult male; B, J. shawi, juvenile male; C, J. falcata, adult male; D, J. pusilla, adult female; E, J. herdmani, adult male; F, J. falcata; H, J. pusilla; G, J. staudei; I, J. ingens. Views B, D, G, H, I lateral; all others medial. Scale 0.1 mm. .126
18. Jassa alonsoae. Adult male, major form. From Sexton and Reid (1951), plates 27-29. x58. 140

19. Jassa staudei. Holotype, adult male, major form, 6.0 mm; allotype, adult female, 5.5 mm; paratypes, adult male 1 minor form, 5.1 mm; adult male 2, minor form, 4.2 mm. Broken Islands, north side of Wouwer Island, Barkley Sound, Vancouver Island, British Columbia, 27 June 1976. Lateral views: whole body, maxilla 1; dorsal view: telson; all other views medial. Appendages are of the holotype unless indicated otherwise. Scale 0.1 mm. 154

20. Jassa staudei. Uropod 3, tip of outer ramus. x1200. 158

21. Jassa marmorata. Adult male, major form, and adult female. Whole body and female gnathopod 2 from Bousfield (1973); all other appendages from Lincoln (1979). 163

22. Jassa marmorata. Telson. A, cusps and associated setae. B, tip of long seta arising proximally to each cusp. x2000. 169

23. Jassa oclairi. Holotype, adult male, minor form, 7.7 mm; allotype, adult female, 7.6 mm; paratypes, juvenile male 1, 7.1 mm; juvenile male 2, 14.1 mm. Square Bay, Amchitka Island, Alaska, 21 September 1969. Adult male, major form, 11.6 mm. Snipe Bay, Alaska, 8 July 1975. Lateral views: whole body, maxilla; dorsal view: telson and uropod 1; other views medial. Scale 0.1 mm. Appendages are of the holotype unless indicated otherwise. . . 173

24. Jassa slatteryi. Holotype, adult male, major form, 5.1 mm; allotype, adult female, 4.1 mm. Moss Landing Harbor, California, 4 July 1986. Intersex 1, 4.6 mm and 5.6 mm, Tanabe Bay, Wakayama Prefecture, Japan, 17 March 1971. Lateral views: whole body, intersex 4.6 mm left gnathopod 2, intersex 5.2 mm right gnathopod 2, and maxilla 1; dorsal view: telson; all other views medial. Scale 0.1 mm unless indicated otherwise. Appendages are of the holotype unless indicated otherwise. 183
25. Jassa slatteryi. Variation in morphology of the antenna 2 and gnathopod 2 with body size. Paratype, juvenile male 1, 2.7 mm; paratype juvenile male 2, 4.5 mm; paratype adult male 3, minor form, 3.5 mm; holotype, adult male 4, major form, 5.1 mm. Moss Landing Harbor, California, 4 July 1986. Medial view: antenna 2; lateral view: gnathopod 2. Scale 0.1 mm. 185
26. Jassa borowskyae. Holotype, adult male, minor form, 4.5 mm; allotype, adult female, 5.0 mm. Brady's Beach, Barkley Sound, Vancouver Island, British Columbia, 26 June 1976. Juvenile male, 4.3 mm; adult male 1, major form, 5.0 mm. Point Grenville, Washington, 22 July 1966. Thumbed new cuticle is shown under the outer cuticle of the juvenile male. Lateral views: whole body, uropod 3, maxillae 1 and 2, maxilliped, right mandible; dorsal view: telson; other views medial. Appendages are of the holotype unless noted otherwise. Scale 0.1 mm. 195

27. Jassa shawi. Holotype, juvenile male, 6.8 mm; allotype, adult female, 5.6 mm. Bamfield, Barkley Sound, Vancouver Island, British Columbia, 24 June 1976. Lateral view: whole body; dorsal view: telson; other views medial. Appendages are of the holotype unless indicated otherwise. Scale 0.1 mm. 209

28. Jassa pusilla. Paralectotype, adult female 1, F.10562 (ZMUO); adult female 2 (length unknown), F.10564; adult male 1, major form (length unknown), F.10563; adult male 2, minor form (length unknown), F.10565. Hammerfest, Norway (date unknown). Adult female 3, 4.7 mm, F. 13359. Risør, Norway (date unknown). Lateral views: whole body, maxilla 1, right and left mandibles; dorsal view: telson; all other views medial. Scale 0.1 mm. 218

29. Jassa pusilla. Male gnathopod 2 palm morphology. Juvenile male, A, 3.3 mm; adult males, minor form, C, 2.8 mm, D, 3.2 mm and E, 3.3 mm; adult males, major form, B, 3.3 mm, F, 3.2 mm, G, 4.0 mm, H, 3.7 mm, I, 4.0 mm and J, 4.1 mm. Risør, Norway (date unknown), catalogue no. F. 13359 (ZMUO). Scale 0.1 mm. 220

30. Jassa falcata. Holotype, adult male, minor form, 6.3 mm. Torcross, South Devon, England (date unknown). Lateral views: whole body, left mandible, left maxilla 1, right uropods 1-3; dorsal view: telson; other views medial. Scale 0.1 mm. 227

31. Jassa falcata. Adult male, major form, 5.7 mm, lectotype 296e of Jassa pulchella. Devon, England (date unknown). The tip of the thumb on gnathopod 2 had been damaged while the animal was alive. Adult male 1, major form, 11.2 mm; juvenile male 2, 7.4 mm; adult male 3, major form, 6.2 mm; juvenile male 4, 4.5 mm; and adult female, 7.0 mm. Stoer Bay, Sutherland, Scotland, 22 October 1937. Developing new cuticle is shown in the gnathopod 2 of the juvenile male 2, not yet at the terminal molt. Lateral view: whole body; all other views medial. Appendages are of the lectotype unless indicated otherwise. Scale 0.1 mm. 229
32. Jassa herdmani. All views of males unless indicated otherwise (from Sexton and Reid, 1951). x58. 237
33. Plumulojassa ocia. Adult male. A, gnathopod 1; B, gnathopod 2; C, peraeopod 4; D, head and gnathopods; E, peraeopod 6. Views A-C, and E from Lincoln (1979). View D from the original description of Podocerus dentex Czerniavski, 1868. 245
34. Plumulojassa ocia. Tip of right uropod 1 inner and outer rami, showing the fringe of cusps on the apex of the outer ramus. x5000. 247
35. Hemijassa goniamera. Lectotype, adult male, 18.3 mm; paralectotypes, juvenile male, 6.1 mm, and adult female, 19.9 mm. Cape Adare, McMurdo Sound, Antarctica, 5 November 1902, Southern

Cross Expedition. Lateral views: whole body, juvenile male, female antenna 2, and left mandible; dorsal view: telson, and uropod 3; other views medial. Appendages are of the adult male unless indicated otherwise. Scale 0.1 mm. 256

36. Jassa marmorata, male. Morphological changes in the second gnathopod upon approaching and reaching adulthood in four individuals of differing size. Figures from Sexton and Reid (1951), as Jassa falcata, Broad Form. From top to bottom row, plate 16 specimen 10, plate 21 specimen 14 (2), plate 15 specimen 9, and plates 13 and 14 specimen 8. All figures x58. 261
37. Male Jassa stauderi (left) and Jassa slatteryi (right). Scatter plot and histogram of thumb position as a function of the second gnathopod's segment 6 length. Jassa stauderi collected at Friday Harbor Marine Lab, 2 October 1984. Jassa slatteryi from various locations. 264
38. Male Jassa stauderi (left) and Jassa slatteryi (right). Scatter plot and histogram of thumb length as a function of body length. Jassa stauderi collected at Friday Harbor Marine Lab over the dates plotted in Fig. 40. Jassa slatteryi from various locations. . 266
39. Male Jassa stauderi (left) and Jassa slatteryi (right). Scatter plot and histogram of the second gnathopod's segment 6 as a function of body length. Jassa stauderi collected at Friday Harbor

- Marine Lab, 2 October 1984. Jassa slatteryi from various locations. 268
40. Jassa staudei, male. Gnathopod 2, segment 6 thumb length. Temporal collections from the east pressure head tank, Friday Harbor Marine Lab, San Juan Island, Washington. Plots show most or all thumbed males and most similarly sized juveniles. . . . 270
41. Jassa staudei, male. Thumb length as a function of body length. Geographic variation. From top to bottom: Barkley Sound, B.C., 27 June 1976, low intertidal; Friday Harbor, Washington, 2 October 1984, east pressure head tank; Point Delgada, California, 5 June 1986, shallow subtidal; Albion Cove, California, 29 June 1978, 20 m depth. 272
42. Jassa. Male gnathopod 2 palm shape in the small juvenile. MAR, J. marmorata; MOR, J. morinoi; SLA, J. slatteryi; CAR, J. carltoni; MYE, J. myersi; STA, J. staudei; OCL, J. oclairi; BOR, J. borowskyae; PUS, J. pusilla; FAL, J. falcata; HER, J. herdmani; ALO, J. alonsoae; JUS, J. justii; GRU, J. gruneri; HAR, J. hartmannae; ING, J. ingens. Small juvenile state unknown for J. shawi (SHA), J. thurstoni (THU), and J. fenwicki (FEN). All setae but those at the defining spines omitted. All views lateral. Scale 0.1 mm. 275

43. Jassa. Male gnathopod 2 palm shape in the minor form adult. Codes as in Fig. 42. State unknown for J. carltoni, J. shawi, J. justii, J. gruneri, and J. fenwicki. All setae but those on the thumb omitted. All views lateral. Scale 0.1 mm.277
44. Jassa. Male gnathopod 2 palm shape in the large juvenile. Individuals of several species have a large thumbed cuticle inside. Codes as in Fig. 42. State unknown for J. gruneri, J. hartmannae, J. thurstoni, and J. fenwicki. All setae but those in the thumb area omitted. All views lateral. Scale 0.1 mm. . . . 279
45. Jassa. Male gnathopod 2 palm shape in the major form adult. Codes as in Fig. 42. State unknown for J. shawi and J. gruneri. All setae but those in the thumb area omitted. All views lateral. Scale 0.1 mm.281
46. Adult female gnathopod 2 palm shape in Pleojassa wandell (WAN), P. m. multidentata (MMU), P. m. orientalis (MOE), P. lowryi (LOW), P. moori (MOO), Hemijassa goniamera (GON), Ventojassa barnardi (BAR), Parajassa pelagica (PEL), Plumulojassa ocia (OCI), and Ishyroceridae n.g. (IGE). All setae omitted. All views lateral. Scale 0.1 mm.286
47. Juvenile male gnathopod 2 palm shape in outgroup species. Codes as in Fig. 46, with the addition of Microjassa cumbrensis (CUM), Neoischyrocerus lilipuna (LIL), Microjassa claustris (CLA), and

- Ischyrocerus sp. All setae but those on the thumb and dactyl omitted. All views lateral. Scale 0.1 mm.288
48. Adult male gnathopod 2 palm shape in outgroup species. Codes as in Figs. 46 and 47. All setae but those on the thumb and dactyl omitted. All views lateral. Scale 0.1 mm. 290
49. Male gnathopod 2, segment 6 thumb length as a function of body length, plotted for the juvenile and adult male of Jassa staudei, J. slatteryi, Pleojassa wandeli, and Hemijassa goniamera. Hemijassa goniamera is not differentiated by maturity because growth is indeterminate. Zero values are not included in the regression calculation. Juveniles with an internal thumbed cuticle visible (i.e., penultimate) are indicated by a half closed circle. Values are standardized on the x axis by range of female maturity; on the y axis by range of thumb length.294
50. Male gnathopod 2, segment 6 length, as a function of body length plotted for the juvenile and adult male of Jassa staudei, J. slatteryi, Pleojassa wandeli, and Hemijassa goniamera. Hemijassa goniamera is not differentiated by maturity because growth is indeterminate. Zero values are not included in the regression calculations. Values standardized on the x axis by range of female maturity; on the y axis by range of thumb length. . . . 296

51.	<u>Jassa staudeli</u> . Antenna 2, tip of flagellum. A, adult female; B, magnification of A, arrow showing the same seta; C, subadult male; D, magnification of C, arrow showing the same seta. A and C x1200; B and D x4700.	.301
52.	<u>Jassa ingens</u> . Antenna 2 segment 5 length as a function of body length at different growth stages in the male and female. . .	.303
53.	<u>Pleojassa wandeli</u> . Antenna 2 segment 5 length as a function of body length in the juvenile and adult male.	.306
54.	Distribution of <u>Jassa</u> , all species combined (map from Lincoln et al., 1982).	.324
55.	Distribution of species <u>Jassa</u> occurring world-wide.	.326
56.	Distribution of species of <u>Jassa</u> restricted to the North Pacific.	.328
57.	Distribution of species of <u>Jassa</u> restricted to the North Atlantic.	.330
58.	Distribution of circum - Antarctic species of <u>Jassa</u>	.332
59.	Distribution of species of <u>Jassa</u> with restricted ranges in the Southern Hemisphere.	.334

60.	Distribution of species of <u>Pleojassa</u>	336
61.	Distribution of the secondary outgroup species, <u>Plumulojassa</u> <u>ocia</u> , <u>Neolschyrocerus</u> <u>lilipuna</u> , <u>Ventojassa</u> <u>barnardi</u> , and <u>Hemijassa</u> <u>gonlamera</u>	338
62.	Consensus trees for data set 1: a single species representative of <u>Jassa</u> (FAL) and <u>Pleojassa</u> (WAN), with LIL, CUM, ISP, GON, OCI, PEL, BAR, and IGE. The outgroup is IGE. Species codes are described in Table 3.	345
63.	Wagner parsimony consensus tree of Fig. 62 with state transitions mapped for non-homoplasious characters. Species codes are described in Table 3.	347
64.	Compatibility consensus tree of Fig. 62 with state transitions mapped for non-homoplasious characters. Species codes are described in Table 3.	349
65.	Consensus trees for data set 2: all primary and secondary outgroup species with <u>J. falcata</u> (FAL). The species were rooted on IGE. Species codes are described in Table 3.	355
66.	Consensus trees for data set 3: five randomly chosen species of <u>Jassa</u> (HER, JUS, MYE, BOR, and THU), and <u>Pleojassa</u> (MMU, WAN, LOW,	

	and MOO) as ingroup, with GON, LIL, and BAR as outgroup. Species codes are described in Table 3.	357
67.	Consensus trees for data set 4: the species of data set 3, with <u>Jassa ingens</u> (ING) added and <u>Neoschyrocerus lilipuna</u> replaced by <u>Plumulojassa ocia</u> (data set 4). The species were rooted on IGE. Species codes are described in Table 3.	359
68.	Consensus trees for data set 5: all characters, for all species of <u>Jassa</u> , rooted on WAN, GON, and BAR. Species codes are described in Table 3.	363
69.	Consensus trees for data set 6: nor.-sexually dimorphic characters for all species of <u>Jassa</u> , rooted on WAN, GON, and BAR. Species codes are described in Table 3.	365
70.	The components of phylogeny (from Stuessy, 1987, Fig. 5). . . .	374
71.	<u>Jassa marmorata</u> , male. Weight of paper outlines of the gnathopod 2, segments 6 and 7, as a function of body length.	386
72.	Wagner parsimony consensus tree of Fig. 68 with state transitions mapped for all synapomorphic characters variable within <u>Jassa</u> . Species codes are described in Table 3.	396

1. INTRODUCTION

Amphipods of the genus Jassa Leach, 1814, are commonly found among algae, sponges, hydroids, and bryozoans on temperate or high latitude marine rocky shores around the world. They inhabit self-constructed tubes spun by secretions from the third and fourth peraeopods, and often form large colonies on boat bottoms, marina docks, rafts, and floats. They breed year round and are early settlers on newly cleared hard substrata. Although primarily a benthic group, individuals have occasionally been found in the plankton. Due to its (1) widespread distribution, (2) penchant for fouling man-made structures, (3) rapid colonizing ability, and (4) availability as fish food, Jassa is frequently encountered and recorded in marine ecological surveys.

1.1. Early taxonomic history

Since the generic description 174 years ago, the name Jassa has appeared in approximately 190 taxonomic studies. Most taxonomists dealt with a few obvious secondary sexual features of the male. However, such characters are highly variable in Jassa, and the consequent taxonomy was never satisfactory. The general sentiment among taxonomists was aptly expressed by Sexton and Reid (1951) when writing of the type species, Jassa falcata (Montagu, 1808):

Cosmopolitan in range, it has been recorded from all parts of the world. It has also the added distinction that, since its establishment by Montagu in 1808, it has caused carcinologists more difficulty in identification than any other amphipod species. This difficulty is mainly due to the diversity of form in the growth-stages of the male, in the posterior antennae and the posterior gnathopods, and most particularly in the shape of the gnathopod hand, a diversity so pronounced as to have led to these stages having been described under thirteen different genera (see p. 47) and about thirty different specific names.

1.2. Sexton and Reid's revision

In 1951 Sexton and Reid synonymized all species of Jassa within Jassa falcata. Their revision was partly based on a study of the live animal, and partly on the literature for the genus. Their live observations were made on a collection of Jassa from a buoy outside the Plymouth Marine Laboratory, England, which was maintained in bowls of seawater in the lab. Although Sexton and Reid considered their live collection to be monospecific, they did note that animals of either sex could be subdivided by consistently different features of the second antennae and gnathopods. These they named the Narrow Form and Broad Form of Jassa falcata. A third form, the Large Polar Form of Jassa falcata, was assigned to specimens of the Antarctic island of South Georgia, because they combined features of the Broad and Narrow Forms.

Observations on the live animals entailed following morphological change through each molt, and assessing the variation produced by crosses of the forms and their variants. It was found that matings within each form produced viable offspring that exhibited the range of variation seen in the parent population. A cross of the two forms produced offspring, but none survived beyond the hatchling stage. However, Sexton and Reid considered this to be evidence that the two forms were a single interbreeding species.

Species other than Jassa falcata were assessed through descriptions and illustrations in the literature. Sexton and Reid found that each species exhibited some or all of the secondary sexual characteristics

seen in the Plymouth population. Accordingly, it was concluded that each species must simply be a variant of the Plymouth Jassa falcata.

There were many faults with Sexton and Reid's work. (1) Although Sexton and Reid knew that Jassa had been found world-wide, they made no attempt to study museum collections, other than to photograph the type species, J. falcata, and to examine the South Georgia Large Polar Form. Instead they relied on descriptions and illustrations, ascribing each previously recognized species to one or the other of their forms. (2) Sexton and Reid focussed their revision on sexually dimorphic characters. They failed to consider the significance of age- and sexually invariant characters to taxonomy, despite having used such characters to differentiate their forms. (3) They failed to recognize that confinement in unnatural conditions could cause unnatural behavior in the captive animals. (4) Although Sexton and Reid claimed to achieve successful crossing of Broad and Narrow Form, they attempted it only once, and none of the offspring lived beyond hatchling age.

1.3. Taxonomy after Sexton and Reid

There are only a handful of taxonomists dealing with a large group such as the Amphipoda (with about 6,500 described species and probably at least that number which are undescribed (Bousfield, pers. comm.)). Revisions tend to be accepted uncritically and stand untested for some time. That Sexton and Reid's (1951) revision was unsatisfactory was made evident by taxonomists' subsequent reluctance to embrace the synonymy. In writing of California specimens, Barnard (1969) differentiated a thin and thick form on primarily non-sexually dimorphic characters, but did not establish a new species. However in 1970, Barnard (1970) found Hawaiian specimens to be so distinct, that he felt obliged to describe them as a new species of Jassa. Although recognizing that the species differed in many non-sexually dimorphic characters, he preferred to use Jassa as the repository for this thumb producing ischyrocerid, as so many taxonomists had done before. Diversity in form of non-sexually dimorphic characters also raised the suspicions of Thurston (1974b), while identifying amphipods from Signy Island (one of the South Orkney Islands). Again, the influence of Sexton and Reid (1951) held, and individuals were separated as forms of J. falcata. Bousfield (1973) was the first taxonomist to run counter to Sexton and Reid (1951), and assigned North American Atlantic specimens of Jassa to J. marmorata Holmes, 1903. Lincoln (1979) followed, and in his analysis of British species, recognized J. oia (Bate, 1862) and J. pusilla (G.O. Sars, 1895) as distinct, and ascribed Sexton and Reid's (1951) Narrow Form to J. falcata and their Broad Form to J. marmorata.

If the response of taxonomists to Sexton and Reid's (1951) massive synonymization was guarded, that of non-taxonomists was of uncritical acceptance. Their species identifications were overwhelmingly J. falcata, despite the specimens coming from regions as distant from Sexton and Reid's study area as Alaska, the Sea of Japan, Macquarie Island, and Antarctica.

1.4. Sexual variation in morphology

As in all gammarid amphipods, the male and female of Jassa are indistinguishable until about one third of the final adult size is attained, wherein the primary sexual structures appear. In the male, these are the penial papillae on sternite 7; in the female, they are the brood plates at the base of the gills. The female's brood plates enlarge through several molts, becoming fringed with long setae at the first maturation molt. The setae intermesh with those from other brood plates, thereby producing a pouch for the eggs. New, setose brood plates are produced at each subsequent molt.

Secondary sexual change is pronounced in Jassa. The male grows to be larger than the female, and its second antennae and second gnathopods enlarge allometrically. The most dramatic change in the male is the production of a thumb-like protuberance from the posterior margin of the second gnathopod palm. This happens at the last molt (Borowsky, 1983). The adult female hardly differs from the juvenile in morphology. It undergoes several molts when mature.

1.5. Sexual behavior

The following observations on sexual behavior are based on laboratory studies by Borowsky (1983, 1985) of Jassa marmorata collected from Jamaica Bay, New York. Since the secondary sex characters of all species of Jassa are very similar, it may be possible to infer that other species behave similarly.

As observed in Gammarus duebeni by Dahl et al. (1970) and in Microdeutopus gryllotalpa by Borowsky (1984), female Jassa may broadcast their sexual receptivity by water-borne secretions. The thumbled male searches for and attends the female until she molts. Soon after molting, the female releases her eggs into her brood pouch, and the male fertilizes the eggs. Subsequently, the male leaves the female's tube to search for another receptive female (Borowsky, 1983). The female remains in her tube, brooding her eggs until hatching. The hatchlings leave the brood pouch soon after, and build their own tubes nearby. The female goes through several cycles of egg production, molting at each.

Thumbless males behave differently from thumbled males in several statistically significant respects (Borowsky, 1983, 1985). (1) Like females, thumbless males tend to stay in their tube. Thumbled males tend to be outside, moving between the tubes of receptive females (Borowsky, 1983). (2) Thumbless males (at later molt stage) are as capable as thumbled males of successfully fertilizing females. In the laboratory they will do so in the absence of a thumbled male (Borowsky, 1985). However, in the presence of a thumbled male, thumbless males act as a juvenile, by searching for a tube, and evicting the occupant if

necessary, even if it is a receptive female. Thumbed males act as an adult; they do not take harbor inside a tube, but instead search for, then attend a receptive female (Borowsky, 1985). (3) Thumbless males lose contests with thumbed males, regardless of size difference. In encounters between thumbed males, however, size is the criterion for victory (Borowsky, 1985).

The thumb does not give its bearer greater purchase on the substrate. Thus the thumb does not function as an aid to navigation. There is some evidence that females treat the two male types differently. Although differences are not statistically significant, females tolerate the proximity of thumbed males more often than they do thumbless males. Thus, the significance of the male's thumb may be demonstrative, to identify intent of reproduction (Borowsky, 1985).

Sand-burrowing amphipods, such as the Phoxocephalidae, Haustoriidae, and Ampeliscidae delay reproduction to the last molt, but here the delay involves both sexes (Bousfield, pers. comm.). Such delay is not known for closer relatives of Jassa (Borowsky, 1983). Many amphipods are very sexually dimorphic, but there is no record in the taxonomic literature of secondary sexual change occurring in a single molt. Borowsky (1985) interprets the delay in male sexual activity in Jassa to be a response to predation pressure, intrasexual competition, and danger of displacement by currents. All three factors would select for minimizing the time spent beyond the protection of the tube.

1.6. Purpose

The purpose of this study is to assess Jassa morphometrically, with a fuller breadth of characters than any taxonomist has used previously, and with a much larger number of specimens from a wider geographical area. In fact, this study is the product of an assessment of about ten thousand specimens - the totality of all that could be located in museums, universities, and field labs throughout the world. The study asks the following questions. (1) Does a larger suite of specimens and characters suggest a similar or different classification from that of Sexton and Reid's? (2) How can the variation seen in the males' secondary sexual characteristics be explained by Jassa's developmental and reproductive biology? (3) What behavioral and life history features explain Jassa's current distribution? (4) What phylogeny can be hypothesized for Jassa? (5) What present and past environmental and geographic features might have effected Jassa's distribution?

2. METHODS

2.1. Species discrimination

For the most part, live animals could not be studied. The species discriminated here are, therefore, morphospecies; that is, "a typological species recognized merely on the basis of morphological difference" (Mayr, 1969). Species were recognized by the following steps:

1. All amphipods classified under Jassa or under genera to which species of Jassa had been ascribed were solicited from museums, universities, private collectors, and field labs. Institutions and private collectors that provided specimens are listed in Tables 1 and 2, respectively.
2. Individuals were separated by sex. The unsexable residue (about 20%) was set aside until age invariant characters had been differentiated from the older animals.
3. Characters were noted as sexually or non-sexually dimorphic. Individuals were sorted by age- and sexually- invariable characters. The variable characters were examined subsequently, to determine whether they supported the groups that the invariant characters differentiated, or suggested additional groups.
4. The groups differentiated by these characters were assigned species or subspecies status. Subspecies status was given if the two groups were allopatric in distribution and were more similar to each other than to the most similar sympatric groups. Groups that included the holotype specimens of previously named species were accorded that name. If the holotype specimens comprised a series of syntypes, then one specimen was

Table 1. Acronyms for lending institutions (after Heppner and Lamas, 1982) and the curator of the crustacean collection.

AM	Australian Museum, Sydney, New South Wales, Australia (Dr. J. K. Lowry)
BCPM	British Columbia Provincial Museum, Victoria, British Columbia, Canada (Mr. P. Lambert)
BMNH	British Museum (Natural History), London, England, UK (Ms. J. Ellis)
BPBM	Bernice P. Bishop Museum, Honolulu, Hawaii, USA (Dr. R. H. Titgen)
CAS	California Academy of Sciences, San Francisco, California, USA (Mr. R. Van Syoc)
LACM	Los Angeles County Natural History Museum, Los Angeles, California USA (formerly The Allan Hancock Foundation) (Dr. R. Brusca)
MHNP	Muséum National d'Histoire Naturelle, Paris, France (Dr. J. Forest)
NMNS	National Museum of Natural Sciences, National Museums Canada, Ottawa, Ontario, Canada (Ms. D. R. Laubitz)
NMNZ	National Museum of New Zealand, Wellington, New Zealand (Dr. G. R. F. Hicks)
NRS	Naturhistoriska Riksmuseet, Stockholm, Sweden (Dr. R. Oleröd)
RSME	Royal Scottish Museum, Edinburgh, Scotland, UK (Ms. S. Chambers)
SAMC	South African Museum, Cape Town, South Africa (Mrs. M. G. van der Merwe)
TAMU	Texas A & M University, College Station, Texas, USA (Dr. L. Pequegnat)
UAM	University of Alaska Museum, Fairbanks, Alaska, USA (Ms. N. R. Foster)
UCT	University of Cape Town, Cape Town, South Africa (Dr. C. Griffiths) (collection currently being transferred to the South African Museum)
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D. C., USA (Dr. J. L. Barnard)
UTM	University of Trondheim Museum, Trondheim, Norway (Dr. T. Stroemgren)

- VIMS Virginia Institute of Marine Science, Gloucester Point, Virginia, USA (Ms. C. H. Hutton)
- ZIL Zoological Institute of the USSR Academy of Sciences, Leningrad, USSR (Dr. Ya. I. Starobogatov)
- ZMHB Zoologisches Museum, Humboldt Universitaet, East Berlin, East Germany. (Dr. H. -E. Gruner)
- ZMUB Zoological Museum, University of Bergen, Bergen, Norway (Dr. E. Willassen)
- ZMUC Zoologisk Museum, Universitets Kjøbenhavn, Kjøbenhavn, Danmark (Dr. J. Just)
- ZMUH Zoologisches Institut und Zoologisches Museum, Universitaet von Hamburg, Hamburg, West Germany (Dr. G. Hartmann)
- ZMUO Zoological Museum, University of Oslo, Oslo, Norway (Dr. N. Langeland and Dr. M. E. Christiansen)

Table 2. Private lenders and their institutional association.

G. M. Alonso	Centro de Investigacion de Biologia Marina, Buenos Aires, Argentina
K. Anger	Meeresstation Helgoland, Biologische Anstalt Helgoland, West Germany
A. Arresti	Universidad del Pais, Vasco Euskal Herriko Unibertsitatea, Bilbao, Spain
D. Bellan-Santini and M. Ledoyer	Station Marine d'Endoume et Centre d'Océanographie, Université d'Aix-Marseille, Marseille, France
G. Diviacco	Istituto di Anatomia Comparata dell'Università di Genova, Genova, Italy
E. Gonzalez	Facultad de Ciencias del Mar, Universidad del Norte, Coquimbo, Chile
J.-S. Hong	Korea Ocean Research and Development Institute, Yeong Dong, Seoul, Korea
S.-I. Ishimaru	Zoological Institute, Faculty of Science, Hokkaido University, Sapporo, Japan
C. Krapp-Schickel	Hoffmannstr. 7a, D-5307 Wachtberg-Adendorf, West Germany
J. C. Marques	Centro de Sistemática e Ecologia, Museu e Laboratório Zoológico, Universidade de Coimbra, Coimbra, Portugal
P. G. Moore	University Marine Biological Station Millport, Isle of Cumbrae, Scotland, UK
H. Morino	Department of Biology, Ibaraki University, Mito, Japan
P. Shaw	Department of Zoology, University of British Columbia, Vancouver, British Columbia, Canada
P. N. Slattery	Moss Landing Marine Laboratories, California State University, Moss Landing, California, USA
C. P. Staude	Friday Harbor Marine Lab, University of Washington, Friday Harbor, San Juan Island, Washington, USA
A. S. Tararam	Instituto Oceanográfico, Universidade de Sao Paulo, Cidade Universitária, Butanta, Sao Paulo, Brazil

R. J. Trott

Department of Pure and Applied Zoology,
University of Reading, Reading, England, UK

selected from the series and designated lectotype. If the type specimens of more than one named species fell within a group, then all members of the group were assigned the oldest name. The other names were synonymized. If the characteristics of the group corresponded to the description of a species for which the type specimens had been lost, and the description (and illustration) was sufficiently clear and extensive to assume that no confusion of designation would arise, then the group was assigned to that species. A new type (neotype) was then selected and designated for that group, from a location as close as possible to the type locality. If no type specimens or type descriptions could be assigned to a group, then that group was assumed to be newly discovered, and a holotype, allotype, and paratype series was established for it. Whenever possible, a large adult male was selected as holotype, and a large adult female was selected as allotype. Paratypes comprised a range of ages for both sexes. Species descriptions encompassed the holotype and allotype if the species were new. If the species had been previously described, the type was described if adult and in good condition; otherwise another specimen was selected for description and phenetic and cladistic analysis. Descending order of preference for selection of lectotype or neotype was large adult male, large adult female, juvenile male, and juvenile female. When species were represented by a large number of collections, the records were summarized by geographic area. Maps of collection sites are presented in the Biogeography Section. Station numbers and associated data can be furnished on request.

The character terminology is that of Bousfield (1973) (Fig. 1). In some of the illustrations the characters are abbreviated as follows: A,

Fig. 1. Body parts of an amphipod with terminology for their description. A, whole animal; B, upper lip; C, mandible; D, head and antennae; E, gnathopod; F, maxilla 1; G, lower lip; H, maxilla 2; I, maxilliped; J, uropod 3; K, peraeopod 5; L, pleopod 2; M, uropod 1; N, telson. Views A, B, D, G, H, J, M, and N lateral; all other views medial (from Bousfield, 1973).

antenna; UL, upper lip; MD, mandible; LL, lower lip; MX, maxilla; MXPD, maxilliped; GN, gnathopod; P, peraeopod; PL, pleopod; U, uropod; T, telson; JV, juvenile; SUBAD, subadult; LFT, left; RT, right; INT, intersex.

To ensure consistency in description, each character was examined across all groups at the same time, from the same, homologous reference points. Measurements were by eyepiece micrometer. Body length is the distance from tip of the rostrum to base of the telson, measured after the animal was uncurled with forceps. Animals observed by scanning electron microscopy were cleaned by sonification, were critical point dried, and then gold coated.

2.2 Generic discrimination

It was soon evident that, although many species were similar to the type for the genus (Jassa falcata), several species were markedly different. This suggested that some species might be assignable to different genera. Therefore the taxonomic literature was searched for genera that resembled Jassa. Four genera were found that seemed close: Microjassa, Parajassa, Ventojassa, and Ischyrocerus. Species for each were borrowed from museums or private collectors and compared with the species of Jassa. An additional species, which seemed to link the Ischyroceridae (of which Jassa is a member) to the ischyrocerid sister family, the Isaeidae (Barnard, 1973), was also included, in order to determine where Jassa stood in relation to other members of the family.

2.2.1 Phenetic analysis

Phenetic analyses were applied to a large character set to determine whether species relationships that had been intuitively derived would be confirmed, and, as well, to determine whether additional species associations could be demonstrated. Since it was impossible to score and analyse all of the 10,000 available specimens, the species were scored on a juvenile male, an adult male, and an adult female. For developmental characters, however, a much larger suite of specimens was scored.

One hundred and forty-one characters were scored either as discrete meristic, multistate coded, or continuous quantitative values. Quantitative characters that were isometric with body size were scored as residuals of regression against size characters. Standardization was by range. Outgroup species (i.e., those from Microjassa, Parajassa, Ventojassa, Ischyrocerus, and an undescribed distant genus of the Ischyroceridae, hereafter termed IGE) were scored only on those characters that varied within the ingroup. All analyses were performed on the University of Ottawa Amdahl 5860 computer. Cluster analysis was by the unweighted pair group method using average linkage (UPGMA) (Sokal and Michener, 1958). Similarity was determined by Gower's (1971) generalized distance (a Manhattan metric). Principal coordinates analysis was applied to assess broad relationships, which cluster analysis tends to distort.

2.3. Hypotheses of phylogeny

Cladistic analysis was applied to generate hypotheses of phylogeny for Jassa. The following procedure was applied.

(1) The species of Microjassa, Parajassa, Ventojassa, Ischyrocerus, and IGE were designated the primary outgroup.

(2) The species of Jassa that had been assigned to new genera as a result of the intuitive and phenetic assessments, were designated the secondary outgroup. All discriminating characteristics of the ingroup (Jassa) and the secondary outgroup were scored (i.e., the species' characteristics were fully resolved). The primary outgroup species were scored on the characters that varied in the ingroup and the secondary outgroup, but were not scored on characters unique to themselves (i.e., the characteristics of the primary outgroup species were not fully resolved).

(3) Due to computer storage and time constraints, the full ingroup could not be analysed with all outgroup species. Thus overlapping subsets of outgroup and ingroup species were analysed in repetitive runs.

(4) Character polarities were derived from the closest outgroup or from a number of outgroup species, using the criterion of parsimony. Parsimony is the principle upon which the outgroup method of Watrous and Wheeler (1981) is based (Farris, 1982). It is now widely accepted by other systematists (Farris, 1982; Maddison et al., 1984; Donoghue and Cantino, 1984; Meacham, 1986; Donoghue and Maddison, 1986; Clark and Curran, 1986). An explicit method for polarity assessment using parsimony has been developed by Maddison et al. (1984) for outgroups

whose relations are well resolved, and by Donoghue and Cantino (1984) for outgroups whose relations are not well known. Since the relationships for Jassa seemed well resolved (i.e., there were several species close to Jassa that could be designated sister species), the approach taken was that of Maddison et al. (1984). As recommended by Farris (1982) and Felsenstein (PHYLIP program documentation), this was achieved by forcing the outgroup species to the bottom of the tree by a dummy weighted character, and then letting all other characters be polarized by parsimony.

All cladistic analyses were run on the PHYLIP version 3.0 package of Felsenstein (Felsenstein, 1985) on the University of Ottawa Amdahl 5860. The same characters used for phenetic analysis were used in cladistic analysis after the necessary reduction of quantitative continuous characters to discrete multistate ones by gap coding. The multistate characters were then reduced to combinations of binary digits by the program FACTOR (copyright 1986, 1987 by C. A. Meacham). Cladistic analysis is highly time-consuming because of the large number of trees that must be generated in search of those that are the most parsimonious. For greater than ten species the amount of computer time required makes a full search impossible. It is necessary, therefore, to use a hill climbing algorithm; that is, a method that searches for a locally optimal solution. By altering the entry order of the species, different optima are reached, and thus there is a better chance of finding the best tree (Felsenstein, 1985). Each data set was accordingly run on ten randomly rearranged species orders. This number seems to be sufficient to assure discovery of the shortest tree (PHYLIP program documentation). Two

different algorithms were applied, the selection being based on matrix size. Program MIX was applied to the large matrices and METRO to the smaller. In the MIX algorithm, a tree is constructed by sequential addition of species in the order of appearance in the input file. The criterion for locating the new species on the tree is maximum parsimony. Local rearrangements of all internal tree segments are made in between each species addition in an effort to improve the tree. In addition, global optimization is applied; that is, each possible subtree is removed and added back in all possible places until no further improvement results. The purpose of global optimization is to reduce the likelihood that a species will be forced into a suboptimal region of the space of all possible trees. The program METRO, which requires about triple the amount of computer time, is a simulated annealing algorithm developed by Metropolis et al. (1953). It involves a quasi-random search, and it does a better job than the addition and search method of MIX (Felsenstein, 1985). A consensus tree was computed for the multiple trees produced by each run. This was effected through the CONSENSE program, which carries out a family of consensus tree methods called the m -sub-1 methods. These include strict or Nelson consensus and majority rule consensus. Bootstrap confidence intervals could not be calculated because of program time constraints.

Two methods of cladistic analysis were applied to each data set: Wagner parsimony (Eck and Dayhoff, 1966; Kluge and Farris, 1969) and compatibility analysis, using the threshold option ($T=2.0$) (Felsenstein, 1981). Under parsimony analysis, the tree is selected that was produced by the least number of character state changes. Under compatibility

analysis, the tree is selected that was produced by the largest number of characters that described that tree. Compatibility is a parsimony method because it counts the number of incompatible characters (i.e., characters that require extra changes of state), and chooses the tree that has the fewest incompatible characters (Felsensten, 1981). Using the threshold method with $T=2.0$, all characters compatible with the tree are accorded a value of 1, and all incompatible characters are accorded a value of 2. The sum for all characters thus reflects the number of incompatible characters. When T is set very large, it becomes irrelevant, because no character will ever require more than T changes of state. In that case, the sum is the total number of character state changes, and the resulting method is the parsimony method.

Both parsimony and compatibility are maximum likelihood methods. Their properties have been discussed by Felsenstein (1973, 1978, 1979, and 1981). Felsenstein (1981) summarizes under what conditions parsimony or compatibility methods are better justified:

"In a statistical framework, parsimony methods gain credibility the lower is the rate of change of the characters over the time-spans involved in the divergence from the common ancestor. The minimization of the number of changes of state then has a very simple and intuitive justification: we prefer that reconstruction of evolutionary history which strains our credulity least, by requiring the smallest amount of change. Furthermore, parsimony will be a robust method, in that it is specified as the preferred estimate whatever the rate of evolution, provided only that that rate is small. We have seen that as the rates of evolution are made small, the weights of the different characters become more equal, and an unweighted parsimony method is approached in the limit. This tends to lend support to the use of these methods.

Compatibility methods gain credibility from their association with variable rates of evolution in different characters. They are best justified when many characters evolve at low rates but a few may be evolving quickly, and we do not know

in advance which characters will evolve at which rates. They are also robust in that small variations of rate of evolution between characters leave our preference for the compatibility method unchanged, as long as they do not move either the high- or the low-rate characters into a category with moderate rates of change."

2.4. Ecological and behavioral observations

Some of the ecological, and much of the behavioral data for Jassa were obtained from living specimens observed on field trips. The first observations were on specimens held in aquaria at Ambleteuse, France. These had been collected nearby from low intertidal rocky shore algae from June 29 to July 3, 1985. The second field collection was at Barren Island Marina, Jamaica Bay Wildlife Refuge, Brooklyn, New York on June 25, 1986. Amphipods and the associated algae and hydroids were gently pulled off the sides of floating docks, and observed at the New York Aquarium with the help of Dr. B. Borowsky. An extensive field collection from northeastern Pacific rocky shores and floating marina docks was made June 25 to July 12, 1986. Live observations were made at Moss Landing Marine Lab, California, and Friday Harbor Marine Lab, Washington. A fall collection from the exposed rocky shore and floating harbor docks at Nahant, Mass., was made on October 29 and 30, 1986. Finally, winter collections were made at various locations in Vancouver, Victoria, Bamfield, Puget Sound, and San Juan Island December 26 - January 9, 1987. Live observations, still photographs, and videos were taken at the University of Victoria, Bamfield Marine Laboratory, and Friday Harbor Marine Laboratory.

During all collections, substrate, temperature, salinity, and exposure were noted. Substrate characterization was precise, (each limited to a single type), so that degree of specificity could be determined. For observation of tube building behavior, specimens and the substrate on

which their tubes were attached, were held in 10 cm culture dishes immersed in running seawater under filtered natural light.

Temporal collections, which were made monthly from 24 September 1984 to 23 February 1987, were from the walls of the east pressure head tank at the University of Washington's Friday Harbor Marine Laboratory on San Juan Island, in Puget Sound. This is a 1.6 cubic meter outdoor tank through which the seawater for the aquarium system moves at rapid pace. The seawater intake is at about 10 m depth.

3. RESULTS

3.1. Morphology and systematics

3.1.1. Species discrimination

Age and sex-invariant characters divided the ten thousand specimens of Jassa into twenty-eight groups of individuals of mixed age and sex. Twenty-seven of these groups were accorded species status. One group was very similar to another. Since it was allopatric, and resembled the other group more than the most similar sympatric species, it was accorded subspecific status. Age- and sex-variable characters suggested additional subdivision. However, since the subgroups were similar in each species, these groups were not accorded taxonomic distinction.

Some groups encompassed the type specimen for species recognized by other taxonomists (eg. J. marmorata Holmes, 1903, J. ingens (Pfeffer, 1888), J. falcata (Montagu, 1808), and J. herdmani (Walker, 1893)). Two groups each held two type species (J. pusilla G. O. Sars, 1895) with J. odontonyx (G. O. Sars, 1895), and J. falcata (Montagu, 1808) with J. pulchella Leach, 1814). Most groups did not encompass a type. The species are listed in Tables 3 and 4. Full descriptions are given in section 3.1.3 following generic analysis. All references to Sars and Barnard are to G. O. Sars and J. L. Barnard, respectively.

Table 3. Male specimens of Jesse and outgroups scored for numerical analysis.

Code	Name	Body		Institute/ Collection	Location	Collector	Collection Date	Reason for Selection	Type
		Length (mm)	Number						
WAR	<u>Jesse</u> <u>marmorata</u> Holmes, 1903	6.7	NMNS 1984-112	New York: Brooklyn: Jamaica Bay	B. Borowsky	early July 1984	neotype	yes	
WAR	<u>Jesse morinoi</u> n.sp.	5.6	H. Morino	Japan: Wakayama Prefecture: Bansho-no-hana Point	H. Morino	17 March 1971	holotype	yes	
WYT	<u>Jesse myersi</u> n.sp.	5.8	LACM stn. 39-H-2	California: Goleta: Coal Oil Point	J. L. Barnard	2 July 1961	holotype	yes	
CLA	<u>Jesse slatteryi</u> n.sp.	5.1	NMNS 1986- 057 stn. C9	California: Moss Landing	K. E. Conlan	4 July 1986	holotype	yes	
WAR	<u>Jesse carltoni</u> n.sp.	2.9	LACM stn. 42-T-5	California: San Luis Obispo County: Hazard Canyon Reef	J. L. Barnard	8-9 December 1961	holotype	yes	
STA	<u>Jesse staudel</u> n.sp.	10.6	NMNS 1984-175	Washington: San Juan Island: Friday Harbor Marine Lab	C. P. Staudel	2 October 1984	largest known	no	
WAR	<u>Jesse borowskyae</u> n.sp.	7.7	P. Shaw	Oregon: Newport	P. Shaw	1 June 1986	largest known	no	
ACL	<u>Jesse oclairi</u> n.sp.	11.8	LAM	Alaska: Baranof Island: Snipe Bay	D. Schamel	8 July 1975	largest known	no	

Code	Name	Body Length (mm)	Institute/Collection Number	Location	Collector	Collection Date	Reason for Selection	Type
SMA	<u>Jassa shawi</u> n.sp.	6.8	NMNS 1976-157 stn.B1	British Columbia: Vancouver Island: Bamfield	E.L.Bousfield	24 June 1976	holotype	yes
PUS	<u>Jassa pusilla</u> (Sars, 1894)	4.1	ZMUC F.13359	Norway: Risør	G.O.Sars	date unknown	holotype damaged	no
FA	<u>Jassa falcata</u> (Montagu, 1808)	8.6	NMNS 1985-093	France: Pas-de-Calais: Andresselles	K.F.Conlan	1 July 1985	holotype damaged	no
HEM	<u>Jassa hardmani</u> (Walker, 1893)	9.5	ZMUC	England: Plymouth	D.M.Reid	14 April 1937	largest known	no
ACC	<u>Jassa alonsoae</u> n.sp.	11.1	ZMUC K-7804	South Georgia	K.v.d.Steinen	16 January 1884	holotype	yes
JUS	<u>Jassa justi</u> n.sp.	8.5	AM Stn. P.34953	Macquarie Island: Garden Bay	J.K.Lowry & D.S.Horning	20 November 1977	holotype	yes
GRU	<u>Jassa gruneri</u> n.sp.	2.1	NMNS 1978-287	Australia: Tasmania: Hobart Harbor	G. Edgar	8 November 1978	holotype	yes
FFN	<u>Jassa fenwicki</u> n.sp.	7.4	AM P.34951	New Zealand: The Snares: Punui Bay	G.D.Fenwick	21 January 1977	holotype	yes

Code	Name	Body Length (mm)	Institute/Collection Number	Location	Collector	Collection Date	Reason for Selection	Type
HAR	<u>Jassa hartmannae</u> 4.5 n.sp.		AM P.34950 Stn. SA-3492	New Zealand: The Snares: Seneclo Pool	G.D.Fanwick	6 January 1977	holotype	yes
THU	<u>Jassa thurstoni</u> 6.0 n.sp.		BMNH 1969:763:1 stn. 52(2085)	South Orkney Islands: Signy Island: Outer Islet: Observation Bluff	M.H.Thurston	14 September 1964	paratype	yes
ENG	<u>Jassa ingens</u> 22.1 (Pfeffer, 1888)		ZMUH K-8017A	South Georgia: Royal Bucht: Moltke-Hafen	G.Pfeffer	16 January 1884	lectotype	yes
GIN	<u>Jassa gonlamera</u> 17.6 Walker, 1903		BMNH 1902:11:5: 6-10	Antarctica: McMurdo Sound: Cape Adare	A.O. Walker	5, 6-10 November 1902	lectotype	yes
WGI	<u>Jassa multi-</u> 8.0 <u>dentata multi-</u> <u>dentata</u> Schellenberg, 1931		ZMUH 22.962	South Georgia	Swedish Antarctic Expedition	unknown	only thumbed male known	no
WGI	<u>Jassa multidentata</u> <u>orientalis</u> n.subsp.		not scored because there is no adult male; the only male known is a juvenile and it is lacking the part of the body that is posterior to segment 4.					
WAN	<u>Jassa wandelli</u> 9.8 Chevreux, 1906		BMNH 1969:735:39 stn. 10(95)	South Orkney Islands: Signy Island: Pillie Rocks	M.H.Thurston	5 March 1965	largest known	no
LIN	<u>Jassa lowryi</u> 5.3 n.sp.		AM P.34948 stn. SA-3417	New Zealand: The Snares: Rime Islet	G.D.Fanwick	21 November 1976	holotype	yes

Code	Name	Body		Collection Number	Location	Collector	Collection Date	Reason for Selection	Type
		Length (mm)	Institute/						
ML	<u>Jasse moori</u> n.sp.	4.0	BMNH	1969:768; ca 430	South Orkney Islands: Signy Island: Billie Rocks	M.H. Thurston	4 March 1965	holotype	yes
LIL	<u>Jasse lilipuna</u> J.L. Bernard, 1970	1.8	BPBM Fee #1		Hawaii Islands: Oahu: Waikiki	J.L. Bernard	25 April 1967	holotype damaged	no
OCI	<u>Jasse ocie</u> (Hate, 1862)	3.5	BMNH 1973:559:3		England: Cornwall: Scilly Isles: St. Agnes: St. Wane's Cove	R. Parston	1 August 1973	neotype	yes
EAR	<u>Jasse</u> <u>bernardi</u> Stephensen, 1949	4.2	ZMIO F.3934 stn. 113		Tristan da Cunha: Nightingale Island	Norwegian Scientific Expedition	8 February 1938	largest known	no
ISP	<u>Ischyrocerus</u> sp.	10.1	MMNS 1987-071		California: Mendocino County: Albion Cove	J.R. Chess	29 June 1978	largest known	no
HFI	<u>Parajasse</u> <u>pelagica</u> (Leach, 1814)	7.5	ZMUR 58706		Norway: Lofoten: Veddøy	W. Vader	unknown	largest known	no
IGI	<u>Ischyroceridae</u> n.q., n.sp.	6.1	MMNS 1976-162		British Columbia: Vancouver Island: Barkley Sound: Bordetals Island	I.D. Lamm	26 June 1976	to be designated holotype	yes
UM	<u>Microjasse</u> <u>cumbrensis</u> (Stebbing and Robertson, 1891)	2.5	BMNH 1984:594:14 (part)		Scotland: Argyll: Loch Riddon	R.J. Lincoln & G.A. Roxshall	unknown	whereabouts of types unknown	no
CLA	<u>Microjasse</u> <u>clausstris</u> J.L. Bernard, 1962	1.9	LACM 624 stn. 45-W-5		California: La Jolla	J.L. Bernard 1962	11-13 November 1962	holotype	yes

Table 4. Female specimens of Jassa and outgroups scored for numerical analysis.

Code	Name	Body		Institute/ Collection Number	Location	Collector	Collection Date	Reason for Selection	Type
		Length (mm)	Weight (g)						
PAR	<u>Jassa</u> <u>marmorata</u> Holmes, 1903	5.3		NMNS 1984-112	New York: Brooklyn: Jamaica Bay	B. Borowsky	early July 1984	part of neotype series	yes
MAH	<u>Jassa morinoi</u> n.sp.	5.8		H. Morino	Japan: Wakayama Prefecture Hansho-no-hana Point	H. Morino	17 March 1971	allotype	yes
SLA	<u>Jassa slatteryi</u> n.sp.	4.1		NMNS 1986- 057 stn. C9	California: Moss Landing	K.E. Conlan	4 July 1986	allotype	yes
PAR	<u>Jassa carltoni</u> n.sp.	2.4		LACM stn. 42-T-5	California: San Louis Obispo County: Hazard Canyon Reef	J.L. Barnard	8-9 December 1961	allotype	yes
MIT	<u>Jassa myersi</u> n.sp.	4.4		LACM stn. 39-H-2	California: Goleta: Coal Oil Point	J.L. Barnard	2 July 1961	allotype	yes
STA	<u>Jassa staudei</u> n.sp.	7.6		NMNS 1984-175	Washington: San Juan Island: Friday Harbor Marine Lab	C.P. Staude	2 October 1984	largest known	no
MAH	<u>Jassa moroskyae</u> n.sp.	5.6		P. Shaw	Oregon: Newport	P. Shaw	1 June 1986	largest known	no

Locality	Spec. Name	Body Length (mm)	Institute/Collection Number	Location	Collector	Collection Date	Reason for Selection	Type
	<u>Jassa oclairi</u> n.sp.	9.8	UAM stn. 11, M13	Alaska: Pribilof Islands; Otter Island	unknown	16 August 1975	largest known	no
SEA	<u>Jassa shawi</u> n.sp.	5.6	NMNS 1976-157 stn. B1	British Columbia: Vancouver Island; Bamfield	E.L. Rousfield	24 June 1976	allotype	yes
PUS	<u>Jassa pusilla</u> (Sars, 1894)	4.7	ZMJO F. 13359	Norway: Risør	G.O. Sars	date unknown	allotype damaged	no
FAL	<u>Jassa falcata</u> (Montagu, 1808)	6.6	NMNS 1985-093	France: Pas-de-Calais: Arras	K.E. Conlan	1 July 1985	largest known	no
HEP	<u>Jassa herdmani</u> (Walker, 1893)	8.1	ZMUC	England: Plymouth	D.M. Reid	14 April 1937	largest known	no
ALG	<u>Jassa alonsoae</u> n.sp.	9.8	ZMNH K-7804	South Georgia	K.V.d. Steinen	16 January 1884	allotype	yes
JIS	<u>Jassa justi</u> n.sp.	6.9	AM P. 34953	Macquarie Island: Garden Bay	J.K. Lowry & D.S. Harning	20 November 1977	allotype	yes
CHI	<u>Jassa gruneri</u> n.sp.	3.2	NMNS 1978-287	Australia: Tasmania: Hobart Harbour	G. Edgar	8 November 1978	allotype	yes
FFN	<u>Jassa fenwicki</u> n.sp.	female unknown						

Code	Name	Body		Institute/ Collection Number	Location	Collector	Collection Date	Reason for Selection	Type
		Length (mm)	Weight (mm)						
MAH	<u>Jasso hartmannae</u> n.sp.	3.6		USNM 149461 stn. E973 (JLR NZ-8)	New Zealand: South Island: Dunedin: Saint Clair	J.L. Barnard	25 January 1968	allotype	yes
TMU	<u>Jasso thurstoni</u> n.sp.	6.5		BMNH 1969:762:3 stn. 50 (AT76)	South Orkney Islands: Signy Island: Bernitsen Pt: Bare Rock	M.M. Thurston	16 October 1964	paratype	yes
INC	<u>Jasso ingens</u> (Pfeffer, 1888)	19.2		BMNH 1969: 723:7 stn. 46 (1929)	South Orkney Islands: Signy Island: Factory Cove: Bernitsen Point	M.M. Thurston	15 April 1884	largest known	no
AMN	<u>Jasso</u> <u>toniamera</u> Walker, 1903	19.6		BMNH 1902:11:5: 6-10	Antarctica: McMurdo Sound: Cape Adare	A.O. Walker	5, 6-10 November 1902	paralectotype	yes
WUJ	<u>Jasso multi-</u> <u>dentata</u> <u>multidentata</u> Schellenberg, 1931	7.7		ZMNH K-402R stn. 7613	South Georgia	K.v.d. Steinen	1883	lectotype	yes
WUE	<u>Jasso multidentata</u> <u>orientalis</u> n. subsp.			Not scored because no male could be scored (female data comprises too small a portion of the character matrix to stand alone)					
MAH	<u>Jasso wandell</u> Chevreux, 1906	9.6		BMNH 1969:735:39 stn. 10 (95)	South Orkney Islands: Signy Island: Rille Rocks	M.M. Thurston	5 March 1965	largest known	no
AMN	<u>Jasso loopyi</u> n.sp.	4.6		AM P. 34948 stn. SA-3417	New Zealand: The Snares: Rima Islet	G.D. Fenwick	21 November 1976	allotype	yes

Code	Name	Body Length (mm)	Institute/Collection Number	Location	Collector	Collection Date	Reason for Selection	Type
WFO	<u>Jassa moorii</u> n.sp.	4.2	BMNH 1969:76P; ca 430	South Orkney Islands: Sidny Island: Billie Rocks	M. M. Thurston	4 March 1965	allotype	yes
LI	<u>Jassa lilipuna</u> J. L. Barnard, 1970	1.6	BMNH 1969:76P; ca 430	Hawaiian Islands: Oahu: Maikiki	J. L. Barnard	25 April 1967	allotype not designated	no
QCI	<u>Jassa ocia</u> (Hate, 1862)	3.5	BMNH Am. 2664	France: Le Croisic	E. Chevreux	unknown	largest known	no
AR	<u>Jassa</u> <u>barnardi</u> Stephensen, 1949	4.5	ZMUO	Tristan da Cunha: Nightingale Island	Norwegian Scientific Expedition	8 February 1938	largest known	no
ISP	<u>Ischyrocerus</u> sp.	7.1	NMNS 1967-071	California: Mendocino County: Albion Cove	J. R. Chess	29 June 1978	largest known	no
PL	<u>Parajassa</u> <u>pelagica</u> (Leach, 1814)	7.7	ZMUR 58706	Norway: Lefoten: Veddy	M. Veder	unknown	largest known	no
IGE	<u>Ischyroceridae</u> n.g., n.sp.	6.6	NMNS 1976-162	British Columbia: Vancouver Island: Barkley Sound: Bordetals Island	I. D. Law	26 June 1976	to be designated allotype	yes
LIW	<u>Microjassa</u> <u>lumbrensis</u> (Stebbing & Robertson, 1891)	2.2	BMNH 1984: 594: 14 (part)	Scotland: Argyll: Loch Riddon	R. J. Lincoln & G. A. Boxshall	unknown	type not sufficiently mature	no
CLA	<u>Microjassa</u> <u>clausstris</u> J. L. Barnard, 1962	1.5	LACM stn. 45-W-5	California: La Jolla	J. L. Barnard	11-13 November	paratype	yes

3.1.2. Generic definition

The 141 characters defined for phenetic and cladistic analysis are described in Appendix Table 1. The characters are drawn from all parts of the body and encompass meristic, size, shape, and developmental differences.

The collection information for each exemplar, its name and code name, is given in Table 3 (male) and Table 4 (female). The scores for cladistic analysis are given in Appendix Table 1; those for phenetic analysis in Appendix Table 2.

Fig. 2A shows the phenogram produced by UPGMA cluster analysis of the mixed quantitative and discrete data of Appendix Table 2. Fig. 2B shows the dendrogram for the discrete values used for cladistics (Appendix Table 1). The mixed data is a more precise evaluation of quantitative relations. Re-scoring the quantitative characters necessarily groups the species and simplifies the information. Despite this, the results are similar, with only some change in the relationship of J. herdmani. A broader picture of species relations is shown by principal coordinates analysis (Fig. 3). The first three coordinates, which accounted for 45.1% of the variation, are plotted for the cladistic data set of Fig. 2B.

Both cluster analysis and principal coordinates analysis show a close relationship among J. marmorata (MAR), J. staudei (STA), J. borowskyae (BOR), J. oclairi (OCL), J. morinoti (MOR), J. slatteryi (SLA), J. myersi (MYE), J. carltoni (CAR), J. shawi (SHA), J. pusilla (PUS), J. justii (JUS), J. gruneri (GRU), J. alonsoae (ALO), J. hartmannae (HAR), J.

Fig. 2. Phenograms from cluster analysis using UPGMA of all twenty-seven species of Jassa with the five outgroup species (PEL, CLA, CUM, ISP, and ICE). All characters, save those scored as the independent variable for regression. A, mixed quantitative and discrete scores. B, quantitative characters re-scored as discrete.

ALL CHARACTERS

A

MAR				
STA	)			
BOR	)			
OCL	)			
MOR	)			
SLA	)			
MYE	)			
CAR	)			
SHA	)			
PUS	)			
JUS	)			
GRU	)			
ALO	)			
HAI	)			
FEN	)			
THU	)			
FAL	)			
HER	)			
ING	)			
MMU	)			
WAN	)			
LOW	)			
MOO	)			
OCT	)			
PEL	)			
GON	)			
LIL	)			
CUM	)			
CLA	)			
ISP	)			
BAR	)			
IGE	)			

ALL CHARACTERS

B

MAR				
STA	)			
BOR	)			
OCL	)			
MOR	)			
SLA	)			
MYE	)			
LAR	)			
SHA	)			
PUS	)			
JUS	)			
HER	)			
GRU	)			
HAR	)			
ALO	)			
FEN	)			
THU	)			
FAL	)			
ING	)			
MMU	)			
WAN	)			
LOW	)			
MOO	)			
OCT	)			
PEL	)			
GON	)			
LIL	)			
CLA	)			
CUM	)			
ISP	)			
BAR	)			
IGE	)			

Fig. 3. Plot of the twenty-seven species of Jassa with the five outgroup species (PEL, CLA, CUM, ISP and IGE) on principal coordinates 1 to 3. All characters, as scored for cladistic analysis. The percentage of variation accounted for by each coordinate is shown on the axis. The species are linked by a minimum spanning tree. Species codes are described in Table 3.

ALL CHARACTERS

fenwicki (FEN), J. thurstoni (THU), and J. herdmani (HER). These cluster around the type species for Jassa, J. falcata. At somewhat greater distance is J. ingens (ING). The remaining seven species of Jassa are considerably more different. J. lilipuna (LIL) shows greater affinity to the primary outgroup species Microjassa cumbrensis (CUM), Microjassa claustris (CLA), and Ischyrocerus sp. (ISP). Jassa ocia (OCI) is closer to the primary outgroup species Parajassa pelagica (PEL), and J. barnardi (BAR) is closer to the un-named ischyrocerid (IGE). The primary outgroup species exhibit less resemblance than suggested here, however. The lack of definition is caused by exclusion of characters invariant for the ingroup. J. multidentata (MUL), J. wandeli (WAN), J. lowyri (LOW), and J. moori (MOO) show as close a range in similarity to each other as does the cluster of species around J. falcata.

Twenty-four percent of the characters in the data vary between the sexes. Figs. 4 and 5 show the phenogram and principal coordinates plot from a re-analysis of the mixed state and discrete state data sets, with sexually dimorphic characters removed. These are characters 5, 10-13, 38-41, 51-60, 62, 64-71, 73, 75, 76, 78, and 140, as numbered in the Appendix Table 1. Although the broad relationships are unchanged, the affinities of some species are affected. Thus J. falcata and J. herdmani are more similar in sexually dimorphic features than in non-sexually dimorphic characters. So too are J. marmorata to J. staudei, and J. oclairi to J. borowskyae. Jassa justi and J. alonsoae resemble each other more on non-sexually dimorphic than on sexually dimorphic characters; so too do the species of the J. multidentata group. The close similarity of J. shawi and J. pusilla may be spurious, since the male

Fig. 4. Phenograms from cluster analysis using UPCMA of all twenty-seven species of Jassa with the five outgroup species (PEL, CLA, CUM, ISP and IGE). Sexually dimorphic characters and independent variables for regression deleted. A, mixed quantitative and discrete scores. B, quantitative characters re-scored as discrete. Species codes are described in Table 3.

NON-SEXUALLY DIMORPHIC CHARACTERS

A

MAR		
STA		}
BOR		} }
OCL		} }
MOR		}
SLA		}
CAR		}
MYE		}
SHA		}
PUS		}
HER		}
ALO		}
JUS		}
GRU		}
THU		}
HAR		}
FEN		}
FAL		}
ING		}
MMU		}
WAN		}
LOW		}
MOO		}
OCI		}
PEL		}
GON		}
LIL		}
CLA		}
ISP		}
CUM		}
BAR		}
IGE		}

NON-SEXUALLY DIMORPHIC CHARACTERS

B

MAR		
STA		}
BOR		} }
OCL		} }
MOR		}
SLA		}
MYE		}
CAR		}
ALO		}
JUS		}
SHA		}
PUS		}
HER		}
GRU		}
HAR		}
FEN		}
FAL		}
THU		}
ING		}
MMU		}
WAN		}
LOW		}
MOO		}
OCI		}
PEL		}
GON		}
LIL		}
CLA		}
ISP		}
CUM		}
BAR		}
IGE		}

Fig. 5. Plot of the twenty-seven species of Jassa with the five outgroup species (PEL, CLA, CUM, ISP, and IGE) on principal coordinates 1 to 3, using the non-sexually dimorphic characters as scored for cladistic analysis. The percentage of variation accounted for by each coordinate is shown on the axis. The species are linked by a minimum spanning tree. Species codes are described in Table 3.

NON-SEXUALLY DIMORPHIC CHARACTERS

adult is unknown for J. shawi. The unstable relationships of J. gruneri, J. thurstoni and J. hartmannae are also due to lack of specimens.

3.1.3. Revision of Jassa

On the basis of the phenetic evidence, the following systematic changes are made to Jassa. (1) Jassa multidentata, J. wandeli, J. lowryi, and J. moori are grouped in a new genus, Pleojassa. (2) The genus Hemijassa Walker, 1907, is resurrected for J. goniamera. Walker (1907) suggested this genus for J. goniamera, should it be transferred out of Jassa. (3) The new genus Neoschyrocerus is established for J. lilipuna. Although this species was shown to have close affinities to Ischyrocerus and the two species of Microjassa, full resolution of these species shows that the relationship is spurious (Conlan, 1988). (4) A new genus, Plumulojassa, is established for J. ocia. Like N. lilipuna, an analysis of the full character variation for the outgroup species would show that P. ocia is not particularly close to any of the species used in this analysis. (5) Jassa barnardi is transferred to Ventojassa Barnard, 1970. This species is strikingly similar to other members of this genus, particularly Ventojassa frequens (Chilton, 1883). (6) Jassa ingens is retained in Jassa, despite its phenetic distance. Jassa ingens is an Antarctic species, and shares with H. goniamera the distinction of being considerably larger than the other species in this analysis. Both differ in certain characters that show little or no size relation in other species (eg., large number of second antennal flagellum segments, mandibular raker spines, pleopod coupling hooks, and maxilla 1 palp setae; short gnathopod thumb; shallow first coxa; pronounced interramal uropod process). Yet J. ingens is considerably different from H. goniamera, but shares many characters that are exclusive to all other

members of Jassa. These are the distinctive medial-lateral-medial spine triplet that define the palm of the first and second gnathopod, the unique mode of thumb production - distal to, rather than at, the position of the defining spines, the sinuous shape of the male's dactyl at adulthood, the dactyl's resting position distal to the defining spines, and finally, the distinctive double cusp and recurved spine arrangement on the third uropod outer ramus. Greater weight should intuitively be given to the common possession of such characters, because the characters are conservative, they have a common form of development, and they come from all parts of the body. It is for this reason that I retain J. ingens within Jassa.

Thus, Jassa will comprise the first nineteen species listed in Tables 3 and 4. The following eight species and two subspecies, which are assigned to the genera listed above, are hereafter termed the secondary outgroup to Jassa. The last five species, which have never been considered by any taxonomist to be members of Jassa, are termed the primary outgroup throughout.

The resultant re-classification is presented following. Descriptions and keys to all members of Jassa and all secondary outgroup species are included.

KEY TO WORLD GENERA OF ISCHYROCERIDAE

(partly after J. L. Barnard, 1973)

- 1a. Uropod 3 with 1 ramus or rami vestigial (not visible under low magnification, 120x) 2
- 1b. Uropod 3 with 2 rami (visible under low magnification, 120x) ... 7

- 2a. Uropod 2 with 1 ramus 3
- 2b. Uropod 2 with 2 rami 6

- 3a. Gnathopod 1, male, carpochele (dactyl apposing segment 5); uropod 3, ramus as long as the peduncle **Chevreuxius** Bonnier, 1896
- 3b. Gnathopod 1, male, subchele (dactyl apposing segment 6); uropod 3, ramus or rami much shorter than the peduncle 4

- 4a. Pleopod 3 with 1 ramus **Runanga** Barnard, 1961 (Fig. 6A)
- 4b. Pleopod 3 with 2 rami 5

- 5a. Peraeopod 5, coxa shallow and distinctly longer than pereon segment 5. Telson, apical cleft less than 1/2 full length
 Baracuma Barnard and Drummond, 1981 (Fig. 6B)
- 5b. Peraeopod 5, coxa deep, hardly longer than pereon segment 5. Telson, apical cleft 1/2 or more of full length... **Cerapus** Say, 1817 (Fig. 6C)

- 6a. Uropods 1 and 2, inner ramus less than 1/2 as long as the outer
 Pseuderichthonyx Schellenberg, 1926

Fig. 6. Ischyroceridae. A, Runanga, male; B, Baracuma, male; C, Cerapus, male; D, Ericthonius, male; E, Bogenfelsia, male; F, Bonnierella, male; G, Ventojassa, female; H, Bathypnotis, male. A and E from Barnard (1969); B from Barnard and Drummond (1981); C from Thomas and Heard (1979); D from Bousfield (1973); F from Barnard (1969); G from Barnard (1970); H from Griffiths (1977).

- 6b. Uropods 1 and 2, rami subequal
Fricthonius Milne Edwards, 1830 (Fig. 6D)
- 7a. Peraeopods 1-7, coxae not overlapping, shallower (dorso-ventrally)
 than wide (antero-laterally).... **Bogenfelsia** Barnard, 1962 (Fig. 6E)
- 7b. Peraeopods 1-7, coxae overlapping, generally deeper than wide
 8
- 8a. Peraeopods 3-7, segment 2 slender, margins parallel; maxilliped
 segment 7 claw-like, longer than segment 6
 Bonnierella Chevreux, 1900 (Fig. 6F)
- 8b. Peraeopods 3-7, segment 2 subovate or broadly rectangular;
 maxilliped segment 7 blunt or subconical, shorter than segment 6
 9
- 9a. Uropod 3, outer ramus with 1-4 setae on the dorsal margin
 1. **Ventojassa** Barnard, 1970 (Fig. 6G)
- 9b. Uropod 3, outer ramus, dorsal margin bare or spinose..... 10
- 10a. Gnathopod 1, segment 5 much longer than segment 6 11
- 10b. Gnathopod 1, segment 5 as long as or shorter than segment 6 ... 12
- 11a. Peraeopod 5, segment 4 twice as wide as on peraeopods 6 and 7.
 Peraeopod 4, coxa posteriorly excavate. Uropod 3, outer ramus not
 hooked at the tip.¹**Bathypotis** Stephensen, 1944 (Fig. 6H)

¹ I concur with Griffiths (1977) that lack of uropod uncination, a synapomorphy of the Ischyroceridae, indicates that the familial status of **Bathypotis** should be re-evaluated. Griffiths (1977) is not correct in

- 11b. Peraeopod 5, segment 4 not markedly wider than that of peraeopods 6 and 7. Peraeopod 4, coxa not posteriorly excavate. Uropod 3, outer ramus with minute hooks at the tip
 Pseudischyrocerus Schellenberg, 1931
- 12a. Antenna 1, accessory flagellum a small scale, 1 segment
 Parajassa Stebbing, 1899 (Fig. 7A)
- 12b. Antenna 1, accessory flagellum 2 segments, the last minute 13
- 13a. Peraeopods 2-4, coxae 1.5-2 times the depth of the body; coxa 4 posteriorly excavate **Microjassa** Stebbing, 1899 (Fig. 7B)
- 13b. Peraeopods 2-4, coxae 1.25 times the depth of the body or less; coxa 4 not posteriorly excavate 14
- 14a. Female gnathopod 2 small and similar in shape to gnathopod 1.
 Peraeopods 3 and 4, segment 6 spinose on the posterior margin.
 Urosome segment 1 without a dorsal pair of erect setae. Uropod 3, peduncle with at least 1 spine mid-dorsally. Telson dorsally spinose 15
- 14b. Female gnathopod 2 markedly larger and different in shape from gnathopod 1. Peraeopods 3 and 4, segment 6 not spinose on the

saying that the coxa 4 excavation is unique within the family; it occurs also in **Microjassa**.

Fig. 7. Ischyroceridae. A, Parajassa, male; B, Microjassa, male; C, Pleojassa, male; D Neoishyrocerus, male; E, Ischyrocerus, female; F, Jassa, male; G, Hemijassa, male. A from Barnard (1970); E from Bousfield (1973).

posterior margin. Urosome segment 1 with a dorsal pair of erect setae. Uropod 3, peduncle spinose only at the origin of the rami.

Telson not dorsally spinose 16

15a. Gnathopod 1 and peraeopods 5-7, dactyl facially striated. Gnathopod 2, male, palmar angle produced into a small protuberance with minute spines at the tip; dactyl, inner margin bearing long..... setae..... **Neoischyrocerus** n.g. (Fig. 7D)

15b. Gnathopod 1 and peraeopods 5-7, dactyl not facially striated. Gnathopod 2, male, palmar angle not produced; dactyl, inner marginal setae minute **Ischyrocerus** Krøyer, 1838 (Fig. 7E)

16a. Gnathopod 1, palm of segment 6 defined by 1 spine. Pleopods short.. 3. **Pleojassa** n.g. (Fig. 7C)

16b. Gnathopod 1, palm of segment 6 defined by 3-4 spines. Pleopods long 17

17a. Gnathopod 2, adult female and juvenile male, segment 6 and dactyl smaller and different in shape to that of the male, without a thumb on the posterior margin; adult male with a thumb distal to the defining spines. Uropod 3, outer ramus tipped by a basally immersed, dorsally recurved spine and a pair of strong cusps... 4. **Jassa** Leach, 1814 (Fig. 7F)

17b. Gnathopod 2, adult female, segment 6 and dactyl similar in shape to that of the adult male, defining spine(s) at the tip or just proximal to the tip of the thumb. Uropod 3, outer ramus with minute

serrations but without additional larger cusps next to the recurved spine 18

- 18a. Gnathopod 2 and peraeopods 3 and 4, both sexes, anterior margin clothed in abundant plumose setae. Gnathopod 2, segment 6 with two narrow teeth, the posterior-most bearing a single defining spine (Figs. 46-48). Peraeopod 5, segment 5 posterodistally spinose. Northern Hemisphere 5. Plumulojassa n.g.
- 18b. Gnathopod 2 and peraeopods 3 and 4, both sexes, anterior margin not clothed in abundant plumose setae. Gnathopod 2, larger male and female, segment 6, palm sinuous, extending at its defining angle into a short thumb with 3-4 minute defining spines at its tip (Figs. 46,48). Peraeopod 5, segment 5 not posterodistally spinose. Southern Hemisphere 6. Hemijassa Walker, 1907 (Fig. 7G)

1. VENTOJASSA Barnard, 1970

Ventojassa Barnard, 1970, p. 204, 205.

ADULT MALE. Body length at maturity 1.5-4.5 mm. Head lobe: dorsal angle acute, ventral margin more broadly rounded. Antenna 1: accessory flagellum 2-4 segments, the last minute, each segment setose. Antenna 2: hardly longer or stouter than antenna 1, filter setae as long as those on antenna 1; flagellum, only distal segments spinose, segment 1 about twice as long as segment 2. Maxilla 1: inner plate bearing abundant fine setae and a single, thicker seta apically. Gnathopod 1: coxa rectangular; segment 6, palm with 1 defining spine, this distal of centre. Gnathopod 2: coxa not deeper posteriorly; segment 2 without filter setae; segment 5 about a third of the length of segment 6; segment 6, hinge tooth small or lacking, thumb small or lacking, defining spines, if present, usually 2 in number and slightly proximal to the palmar angle or thumb tip, thumb setose on both inner and outer margins, not markedly increasing in size at any 1 molt; dactyl shorter than segment 6, tip resting at the palmar angle or thumb tip, dactyl cusps well developed, interspersed with a few short setae. Peraeopods 3 and 4: coxae rectangular; segment 2 not becoming slender at maturity, margins not markedly convex; segment 4 not overlapping segment 5, anterior margin with only a single central seta and a cluster distally; segment 6 not posteriorly spinose. Peraeopods 5-7: segment 2 of at least one of these peraeopods posterodistally produced; segments 4 and 5, posterior margin sometimes spinose; dactyl, posterior (outer) margin not cusped distally, anterior (inner) margin

with a seta only at the junction of the unguis. Urosome: segment 1 bearing a pair of setae dorsally. Uropod 3: peduncle setose mid-ventrally, rarely setose or spinose mid-dorsally, with a lateral and medial cluster of setae (sometimes a few spines additionally) at the junction of the rami; outer ramus bearing 1-3 setae mid-dorsally, tip hooked, sometimes with an accessory cusp and 2 short lateral spine-like setae, but without a basally immersed, dorsally recurved spine. Telson: each corner with 2-3 cusps and accompanying setae (1 long and 1-3 short, plumose), but without spines.

ADULT FEMALE. Size at maturity 2-5 mm. Brood plates narrow, setae well separated. Antenna 2: peduncle, posterior filter setae long, not shortening with age. Gnathopod 2: segment 6 and dactyl much larger than and different in shape from gnathopod 1 but little different in shape from that of the male (only the thumb less pronounced). Peraeopods 3 and 4: segment 2 slender as in the male.

VARIATION: The male's gnathopod 2 shows some change with age, the palm becoming more incised or concave.

TYPE SPECIES: Eurystheus ventosa Barnard, 1962.

INCLUDED SPECIES: Ventojassa frequens (Chilton, 1883), V. barnardi (Stephensen, 1949), V. ventosa (Barnard, 1962), and V. crenulata Ledoyer, 1979.

REMARKS: Ventojassa exhibits much less sexual dimorphism than either Jassa or Hemijassa. It can be quickly differentiated from these species by the longer antenna 1 accessory flagellum, long segment 5 on gnathopod 1, unproduced segment 4 on pereopods 3 and 4, and lack of a long, basally immersed, curved spine on the uropod 3 outer ramus. The species key given here is based on the figures of Barnard (1970) for V. ventosa, Barnard (1972) for V. frequens, Ledoyer (1979) for V. crenulata, and of the type specimens for V. barnardi (herein transferred from Jassa).

The broad distribution of Ventojassa (southern South America, Madagascar, Mauritius, New Zealand, Fiji, Hawaiian Islands, and Baja California makes the taxonomy of the genus suspect, in light of the actual narrow range found for species of Jassa (outside of introductions by man).

KEY TO WORLD SPECIES OF VENTOJASSA

- 1a. Antenna 1 weakly setose (Fig. 8C), accessory flagellum 2 segmented, the last segment minute (Fig. 8C). Peraeopod 5, segment 2, posterior margin broadly expanded (Fig. 8G). Peraeopod 7, segment 2, posterior margin indented at the origin of each seta, giving a crenulated appearance (Fig. 8I). Gnathopod 2, segment 6, female, palm angled obliquely between the 2 defining spines (Fig. 9C); male, palm broadly concave to form an acute tooth or thumb (Fig. 9E).
 V. crenulata Ledoyer, 1979
- 1b. Antenna 1 more strongly setose (Fig. 8A), accessory flagellum 3-4 segmented, the last segment minute (Fig. 8A). Peraeopod 5, segment 2, posterior margin straight or shallowly concave Fig. 8F). Peraeopod 7, segment 2, posterior margin not crenulated (Fig. 8H). Gnathopod 2, segment 6, palm various..... 2
- 2a. Peraeopod 5, segment 4 not noticeably expanded, posterior margin not spinose (Fig. 8C). Uropod 3, outer ramus slightly hooked apically but without a subapical cusp (Fig. 8E). Gnathopod 2, segment 6 not sexually dimorphic, palm oblique, not acutely angled at the defining spines (Fig. 9A)..... **V. ventosa** (Barnard, 1962)
- 2b. Peraeopod 5, segment 4 expanded, posterior margin spinose (Fig. 8F). Uropod 3, outer ramus with a cusp subapical to the terminal hook (Fig. 8D). Gnathopod 2, segment 6 sexually dimorphic, palm quadrate or acutely angled at the defining spines (Figs. 9 B,D,F,G).
 3

Fig. 8. Ventojassa. A whole animal, female; B, antenna 2, male; C, antenna 1, male; D, E, uropod 3, outer ramus; F, G, peraeopod 5; H, I, peraeopod 7. A, E, H, V. ventosa; B, C, G, I, V. crenulata; D, F, V. frequens. V. crenulata from Ledoyer (1979); V. frequens from Barnard (1972); V. ventosa from Barnard (1970). Scale 0.1 mm.

Fig. 9. Ventojassa. Gnathopod 2. A-D, adult female; E-G, adult male. A, V. ventosa; B, G, V. frequens; C, E, V. crenulata, D, F, V. barnardi. V. crenulata from Ledoyer (1979); V. frequens from Barnard (1972); V. ventosa from Barnard (1970). Scale 0.1 mm.

2

Microl

- 3a. Uropod 3, outer ramus with 1 mid-dorsal seta. Gnathopod 2, segment 6, male, palmar defining angle apically transverse (Fig.9G)...
..... V. frequens (Chilton, 1883)
- 3b. Uropod 3, outer ramus with 2-3 mid-dorsal setae. Gnathopod 2, segment 6, male, palmar angle apically acute (Fig.9F).....
..... V. barnardi (Stephensen, 1949)

VENTOJASSA BARNARDI (Stephensen, 1949) new combination

Figs. 9, 46, 47, 48

Jassa barnardi Stephensen, 1949, 50-52, Figs. 21, 22

ADULT MALE. Lectotype (here designated): Length 3.6 mm. Antenna 1: accessory flagellum 4 segments, the last minute; antennae 1 and 2 about equal in length, both bearing long, simple filter setae. Antenna 2: flagellum 8 segments, the last minute, segment 1 28% of full length. Mandible: palp segments 2 and 3 without a dorsal fringe of setae; raker spines in another male, 3.5 mm, 3 right, 4 left. Maxilla 1: palp without setae at the base of segment 1, segment 2 with 1 row of facial setae. Gnathopod 1: coxal margins, anterior 92% of dorsal length, ventral margin convex; segment 2, anterior margin with a short seta distally, ventral margin with a long seta centrally; segment 5, posterior lobe 57% of anterior margin length, anterodistal setal cluster short, 7% of the anterior margin length; segment 6, palm convex, defined by 1 spine; dactyl, inner margin minutely serrated throughout to a single cusp at the junction of the unguis, without facial striations. Gnathopod 2: coxal margins, anterior 75% and posterior 81% of ventral length; ventral margin convex; gill moderately large; segment 2, anterolateral flange without a fringe of filter setae; segment 5, posterior lobe with a long distal seta; segment 6, anterior margin not setose; palm without a hinge tooth, setae more abundant distally, thumb 26% of segment 6 length, distally acute, posterior margin with several clusters of setae, but not changing shape at any cluster, with 2 defining spines subapically, one on either

side of the thumb. Peraeopod 3: coxa, greatest depth at the centre; segment 2, anterior margin straight; segment 4, anterior margin with a single seta centrally and a cluster distally, central seta less than $1/4$ segment width, segment width 75% of length; segment 5 not overlapped by segment 4; segment 6, width 50% of length. Peraeopods 5-7: segment 6 not expanded anteriorly; dactyl without facial serrations. Pleopods: short, each with 2 coupling hooks. Uropod 1: peduncle, posteroventral spinous process underlying 75% of the inner ramus, inner and outer rami with 2 and 3 mid-dorsal spines respectively, not terminating in a fringe of cusps ventral to the apical spine group. Uropod 2: peduncle, posteroventral spinous process underlying 25% of the inner ramus. Uropod 3: outer ramus apically hooked, with an additional cusp immediately proximal and 2 short setae laterally; inner ramus with a single apical spine only. Telson: setose only at the lateral cusps.

CONDITION: Without left peraeopods 5-7.

ADULT FEMALE. (Not type; ZMUC, Nightingale Station 113): Length 4.5 mm. Antenna 2: segment 5 without plumose setae. Gnathopod 1: coxa, ventral margin shallowly convex. Gnathopod 2: coxal margins, anterior 100% and posterior 118% of ventral length; ventral margin shallowly convex; segment 6, thumb hardly produced, distally squared, with 3 medial defining spines (1 on the thumb's inner margin, 2 on the thumb's outer margin); dactyl, inner margin straight, cusps strong, tip approximating the second spine, but not fitting into a depression distal to the defining spines.

CONDITION: Without left peraeopods 3 and 5. Right appendages, left peraeopods 6 and 7, telson, and mouthparts slide mounted. Remaining appendages with the carcass.

VARIATION: Body length at maturity: male to 4.5 mm, female 2.3-4.5 mm. Male gnathopod 2 development with size is like that shown for Il. goniamera (Figs. 49 and 50). The number of setae on the dorsum of the uropod 3 outer ramus varies from 2 in juveniles to 3 in adults.

TYPE MATERIAL: Lectotype, male (ZMUO), reg. no. F3934a, Tristan da Cunha: Nightingale Island, station 114 ($37^{\circ}28'S$, $12^{\circ}32'W$), 8 February 1938, 0m, Norwegian Scientific Expedition 1937-38, E. Sivertsen, collector. Paralectotypes (ZMUO), reg. no. F3934b, same location; also F3897, Tristan da Cunha: Inaccessible Island, station 156 ($37^{\circ}19'S$, $12^{\circ}44'W$), 29 February 1938, 5-8 m, Norwegian Scientific Expedition 1937-38, E. Sivertsen, collector; also F3898, Tristan da Cunha: Inaccessible Island, station 154, 25 February 1938, 40m, Norwegian Scientific Expedition 1937-38, E. Sivertsen, collector.

OTHER MATERIAL: 19 adult males, 37 adult females and 57 juveniles from Tristan da Cunha, 30 December 1939, and Nightingale Island, Station 113, 8 February 1938, E. Sivertsen, collector (ZMUO); 1 adult male and 5 adult females from Lyttelton, New Zealand, 28 March 1928, Charles Chilton, collector (ZMUC); 1 adult male, 1 adult female, and 1 juvenile from Caleta Bruna, Chile, E. Chevreux, collector (MHNP); 1 adult male, 8 adult females, and 2 juveniles from Valparaiso, Chile (NRS).

REMARKS: V. barnardi most closely resembles the V. frequens illustrated by Barnard (1972). Unfortunately I have not been able to locate Chilton's type specimens of V. frequens. Ventojassa barnardi differs from V. frequens (as illustrated by Barnard (1972)) in lacking the grossly expanded peraeopod 6, and in having the male's second gnathopod thumb acutely produced. Specimens (not type) collected by Chilton at Lyttelton, New Zealand and identified by him as V. frequens were V. barnardi, rather than the V. frequens illustrated by Barnard (1972). Should Chilton's type specimens be the same as the Lyttelton morph, however, V. barnardi must be submerged under V. frequens and the specimens illustrated by Barnard (1972) reassigned.

2. NEOISCHYROCERUS n. g.

ADULT MALE. Body length at maturity 1.7-2.0 mm. Head lobe: triangular, anteriorly acute. Antenna 1: accessory flagellum 2 segments, the second minute, both segments setose. Antenna 2: only somewhat stouter and longer than antenna 1, more so in the male, the long filter setae becoming slightly shorter and sparser at maturity, but not developing clusters of brush or plumose setae; flagellum spinose on the last 2 segments, first segment about 1.5 times longer than the second. Maxilla 1: inner plate not setose. Gnathopod 1: coxa oval; segment 6, palm defined by 2 spines (1 lateral, 1 medial), these located midway along the segment. Gnathopod 2: coxa deepest posteriorly; segment 2 without long filter setae; segment 5 about 1/4 the length of segment 6; segment 6, hinge tooth pronounced, bifid, thumb proximal, tipped by 2 minute defining spines, inner margin of thumb not setose, outer margin with a row of finely plumose setae, thumb development seemingly isometric; dactyl as long as segment 6, inner margin shallowly expanded at the hinge tooth, tip resting against the thumb's outer margin, dactyl cusps reduced to small buttons, interspersed with long, finely plumose, lateral setae. Peraeopod 3: coxa deepest centrally; condition of segments 2-7 of peraeopods 3-7 unknown. (Female, 1.5 mm, segment 2, margins shallowly convex; segment 4 hardly overlapping segment 5, anterior margin without setae centrally, 1 cluster distally; segment 6, posterior margin with 2 stout spines. Peraeopods 5-7: at least one segment 2 posterodistally produced; segments 4 and 5, posterior margin not spinose; dactyl, posterior (outer) margin cusped distally, anterior (inner) margin bearing

a seta only at the unguis). Urosome: segment 1 without a pair of erect setae dorsally. Uropod 3: peduncle not setose ventrally, but spinose mid-dorsally, with 1 lateral spine distally but without a lateral cluster of setae; outer ramus not setose mid-dorsally, distally ending in 3-4 small sequential cusps, but without a recurved spine or accessory setae. Telson: each corner with a single cusp, these each accompanied by a spine and short seta.

ADULT FEMALE. Size at maturity 1.4-2.1 mm. Brood plates narrow, setae well separated. Antenna 2: peduncle, posterior filter setae long, not shortening with age. Gnathopod 2: segment 6 hardly larger than and not different in shape from that of gnathopod 1.

TYPE SPECIES: Jassa lilipuna Barnard, 1970 (monotypic).

REMARKS: Neoischyrocerus is closer to Ischyrocerus than to Jassa in the short, stout terminal segment of the mandibular palp, lack of dimorphism in the female gnathopods, non-produced peraeopod 3-4, segment 4, deep coxae 1 and 2 in the male, lack of setal cluster at the junction of the uropod 3 outer ramus and peduncle, and presence of a mid-dorsal spine on the uropod 3 peduncle and spiny telson. The male's gnathopod 2 thumb is not homologous to that of Jassa because it arises at, rather than distal to, the defining spines.

ETYMOLOGY: Referring to the closer relationship of this genus to Ischyrocerus.

NEOISCHYROCERUS LILIPUNA (Barnard, 1970) new combination

Figs. 10, 47, 48

Jassa lilipuna Barnard, 1970, 198-202, Figs. 128-130; 1971, 99.

ADULT MALE. Holotype redescription: Length 1.9 mm. Antenna 1: accessory flagellum 2 segments, the second minute. Antenna 2: overlapped by antenna 1 to part way along the flagellum; segment 5, posterior margin bearing long simple filter setae only, without brush or plumose setae distally; simple setae nearly as long as those of the juvenile; flagellum 5 segments, the last minute, segment 1 37% of full length. Mouthparts lost (male 3, 1.8 mm, mandible: palp segments 2 and 3 without a dorsal fringe of setae; raker spines 3 right, 2 left. Maxilla 1: palp without setae at the base of segment 1; segment 2 with 1 row of facial setae). Gnathopod 1: coxal margins, anterior 100% of dorsal length, ventral margin convex; segment 2, anterior margin with a single seta distally, posterior margin without setae; segment 5, posterior lobe 40% of anterior margin length, anterodistal setal cluster short, 40% of the anterior margin length; segment 6, palm convex, defined by spines; dactyl cusped along the distal part of the posterior margin, with facial striations. Gnathopod 2: coxal margins, anterior 110% and posterior 100% of ventral length; ventral margin broadly convex, anteriorly indented; gill long and slender, as large as that on segment 3; segment 2, anterolateral flange without long filter setae; segment 5, posterior lobe without a distal seta; segment 6, anterior margin without setae; palm, hinge tooth fully bifid, setae confined to the hinge tooth area; thumb 9% of segment 6

Fig. 10. Neoschyrocerus lilipuna. Holotype, adult male, 1.9 mm. Waikiki Aquarium, Oahu, Hawaiian Islands, 11 March 1964. Adult female, 1.5 mm; juvenile male 2, 1.5 mm; adult male 3, 1.8 mm; and adult male 4, 1.9 mm. Egg #1, Waikiki, Oahu, Hawaiian Islands, 25 April 1967. Male 4: new cuticle shown inside; some setae not shown, origins indicated by a small circle. Lateral views: whole body, uropod 3, peraeopods 3,4,6,7 and left mandible; all other views medial. All appendages are of the holotype unless indicated otherwise. Scale 0.1 mm unless indicated otherwise.

length, distally acute, posterior margin straight, bearing 6 well spaced lateral setae, defining spines 2, minute, at the thumb tip; dactyl, inner margin broadly expanded at the location of the hinge tooth. Peraeopod 3: coxa, greatest depth central; segments 2-7 unknown. (Female, 1.5 mm, segment 2, anterior margin convex; segment 4, anterior margin without setae except at the distal corner, segment width 100% of length; segment 5 barely overlapped by segment 4; segment 6 56% of length). Peraeopods 5-7: segment 6 not expanded anteriorly; dactyl with a row of facial striations. Pleopods long, each with 2 coupling hooks. Uropod 1: peduncle, posteroventral spinous process underlying 18% of the inner ramus, inner and outer rami with 0 and 1 mid-dorsal spines respectively, terminating in a fringe of cusps ventral to the apical spine group. Uropod 2: peduncle without a posteroventral spinous process. Uropod 3: outer ramus terminating in 3 cusps but without a dorsally recurved spine, accompanying serrations or setae; inner ramus with only a single apical spine. Telson missing (male 3, 1.8 mm: apex rounded, with a spine at each lateral cusp).

CONDITION: Without left antenna 1, mouthparts, right and left peraeopods 3-7, uropod 3, and telson. Right and left gnathopod 1, left gnathopod 2, and coxa 5 slide mounted.

ADULT FEMALE. Length 1.6 mm. Antenna 2: segment 5 without plumose setae. Gnathopod 1: coxa, ventral margin convex. Gnathopod 2: coxal margins, anterior 100% and posterior 140% of ventral length; ventral

margin broadly convex; segment 6 and dactyl similar in shape to gnathopod 1.

CONDITION: Brooding young. Without right and left peraeopod 5. Right antenna 1, gnathopods 1 and 2, peraeopods 3, 4, 6, and 7, pleopods 1-3, uropods 1 and 3, and telson, and left antenna 2, pleopod 3, and uropods 1-3 slide mounted.

VARIATION: Body length at maturity: male to 2.0 mm, female 1.2-2.1 mm. Gnathopod 2 development in the male resembles that of H. goniamera (Figs. 49 and 50). Like H. goniamera, the defining spines become smaller in the larger thumbed males. The male 4 in Fig. 10 was evidently close to molting as a larger thumb could be seen inside the cuticle. Juvenile male coxae 2 are evenly rounded. The number of spines on segment 6 of peraeopods 3 and 4 varies from 2 to 5. The uropod 3 peduncle may have 1-2 medial spines and the outer ramus 3-4 cusps.

TYPE MATERIAL: Holotype, male (BPBM), catalogue no. S7288, Hawaiian Islands: Oahu: Waikiki (21°17'N, 157°52'W), 25 April 1967, in Ulva seaward of aquarium, J. L. Barnard, collector.

OTHER MATERIAL: 3 males, 9 females, and 7 juveniles from Waikiki and Kaneohe Bay, Oahu (BPBM, USNM).

3. PLEOJASSA n.g.

ADULT MALE. Body length at maturity to 10.8 mm. Head lobe: squared, dorsal angle more acute, lower angle lobe more rounded. Antenna 1: accessory flagellum 2 segments, the second minute, setose only distally. Antenna 2: stouter and longer than antenna 1, setation variable, filter setae shorter and sparser in the adult, flagellum spination variable, first segment considerably longer than following segments. Mandible: palp segments 2 and 3 without a dorsal fringe of setae. Maxilla 1: inner plate bearing a few short, fine setae; palp with 1 row of facial setae. Gnathopod 1: coxa rectangular; segment 6, palm with 1 medial defining spine, this central, or slightly proximal of centre; dactyl facially striated. Gnathopod 2: coxa not deeper posteriorly, without a gill; segment 2 without filter setae; segment 5 a quarter of segment 6 length or less, lobe apically setose; segment 6 without anteroproximal setae, hinge tooth rectangular or triangular, shallowly or deeply bifid, or multiply incised, palm concave to the single medial defining spine, there produced or not into a short "hook" or long thumb, these developed over more than 1 molt; dactyl shorter than segment 6, variably expanded at the hinge tooth, tip apposing the defining spine, or if thumb present, its posterior margin, cusps reduced and interspersed with short setae. Peraeopod 3: coxa deepest centrally or slightly posterior of centre; segment 2 a little slenderer at maturity; segment 4, anterior margin bearing well spaced single or clustered setae; segment 5, overlap by segment 4 variable; segment 6 not posteriorly spinose. Peraeopod. 5-7: segment 2 production variable; segment 4 not posterodistally spinose;

segment 5 with a cluster of spines posterodistally at least on peraeopod 5; segment 6 not strongly expanded anteriorly; dactyl not facially serrated, posterior (outer) margin not cusped distally, anterior (inner) margin, setation variable. Urosome: segment with dorsal pair of erect setae. Pleopods: very short, each with 2 coupling hooks. Uropod 1: ramal not cusped below the apical spine group. Uropod 3: peduncle mid-ventrally setose, without mid-dorsal spines, but with a crown of spines around the dorso-distal rim and a cluster of setae disto-laterally; outer ramus not setose mid-dorsally, tipped by a basally immersed, dorsally recurved spine and associated seta and serrations, cusps variable, but never as on Jassa. Telson: each corner with a pair of cusps accompanied by setae (2 long, simple, and 2 short, plumose) but not spines.

ADULT FEMALE. Body length at maturity 2.7-9.6 mm. Brood plates broad, setae well separated, abundant. Antenna 2: peduncle, posterior filter setae long, not shortening with age. Gnathopod 2: segment 6 much larger and different in shape from segment 6 of gnathopod 1, palm concave, defined by a single medial spine and without a thumb; dactyl tip apposing the defining angle and spine, dactyl cusps strong. Peraeopod 3: segment 2 somewhat broader than in the male.

VARIATION: Antenna 2 peduncular setal change appears to be similar to that of Jassa, with the male setae shortening at presumed maturity and the female's remaining long. Male gnathopod 2 thumbing is not homologous, however, because the thumb develops at the defining spine rather than

distal to it. Consequently the thumb's setation pattern is quite different.

TYPE SPECIES: Jassa wandeli Chevreux, 1906

INCLUDED SPECIES AND SUBSPECIES: Pleojassa wandeli (Chevreux, 1906), P. multidentata multidentata (Schellenberg, 1931), P. multidentata orientalis n. subsp., P. lowryi n. sp., and P. moori n. sp.

REMARKS: The males of P. wandeli and P. multidentata produce a long thumb if sufficiently larger than the adult female and thus would superficially appear to be a Jassa. Distinguishing features are a single spine defining the palm of gnathopods 1 and 2, and hence different thumb setation, closure of the second gnathopods's dactyl at, rather than distal to, the defining spine, lack of a gnathopod 2 gill, reduced pleopods, and lack of a double cusp on the uropod 3 outer ramus.

KEY TO WORLD SPECIES OF PLEOJASSA

- 1a. Uropod 1, posteroventral peduncular spinous process as long as the outer ramus. Gnathopod 1, segment 5 without a seta at the anterodistal junction of segment 6 (Fig. 11G). Female gnathopod 2, palmar setae not densely plumose 1. P. moori n.sp.
- 1b. Uropod 1, posteroventral peduncular spinous process 1/2 to 3/4 the length of the outer ramus. Gnathopod 1, segment 5 with a single seta or cluster of setae at the anterodistal junction of segment 6 (Fig. 11E,F). Female gnathopod 2, palm bearing abundant plumose setae (Fig. 11I,J) 2
- 2a. Peraeopods 3 and 4, segment 5 fully overlapped by segment 4 (Fig. 11C). Female body size at maturity 3.2 to 4.2 mm. Gnathopod 2, segment 6, palm densely plumose in both sexes; adult male palm defined by a small "hook" but not by a long thumb (Fig. 11M)..
..... 2. P. lowryi n.sp.
- 2b. Peraeopods 3 and 4, segment 5 1/2 to 3/4 overlapped by segment 4 (Fig. 11D). Female body size at maturity 5.9 to 9.6 mm. Gnathopod 2, segment 6, only the female palm densely plumose; adult male palm defined by a long thumb (Fig. 11L) 3
- 3a. Female gnathopod 2, segment 6, dactylar hinge tooth shallow (Fig. 11I). Antenna 2, large male and female, posterior margin of segment 5 and flagellum plumose (Fig. 11A).... 3. P. vandell (Chevreux, 1906)

Fig. 11. Pleojassa. A, B, antenna 2; C, D, peraeopod 3; E-G, gnathopod 1; H-J, gnathopod 2, adult female; K-N, gnathopod 2, male (K, N, juvenile; L, M, adult). A, P. wandeli; B, P. moori, adult male; C, P. lowryi; D, P. moori; E, P. wandeli; F, P. multidentata multidentata; G, P. moori; H, P. multidentata orientalis; I, P. wandeli; J, P. multidentata multidentata; K, P. multidentata multidentata; L, P. wandeli; M, P. lowryi; N, P. multidentata orientalis; Views H, J, K, M, N lateral; all others medial. Views K, M, N, all setae but those at the palmar angle omitted. Scale 0.1 mm.

- 3b. Female gnathopod 2, segment 6 hinge tooth deep (Fig. 11 H,J).
 Antenna 2, large male and female, posterior margin of segment 5
 and flagellum not plumose (Fig. 11B) 4
- 4a. Gnathopod 1, segment 5 with a cluster of setae at the anterodistal
 junction of segment 6 (Fig. 11F). South Georgia.....
4.1. P. multidentata multidentata (Schellenberg, 1931)
- 4b. Gnathopod 1, segment 5 without a cluster of setae at the
 anterodistal junction of segment 6 (Fig. 11G). Macquarie Island...
4.2. P. multidentata orientalis n. subsp.

1. PLEOJASSA MOORI n.sp.

Figs. 11, 46, 47, 48

ADULT MALE. Holotype: Length 4.0 mm. Antenna 1: lacking. (Male, 3.1 mm, antenna 2 overlapped by antenna 1 to midway along segment 5). Antenna 2: segment 5 bearing a few simple setae only, these about as long as those of the juvenile; flagellum 3 segments, segment 1 75% of full flagellum length. Mandible: palp segments 2 and 3 without a dorsal fringe of setae; raker spines 3 right, 4 left. Maxilla 1: palp without setae at the base of segment 1; segment 2 with 1 row of facial setae. Gnathopod 1: coxal margins, anterior 92% of dorsal length; ventral margin straight; segment 2, anterior and posterior margins each with a single seta distally; segment 5, posterior lobe 47% of anterior margin length, without an anterodistal setal cluster; segment 6, palm broadly convex, defining spine central. Gnathopod 2: coxal margins, anterior 65% and posterior 61% of ventral length; ventral margin straight; segment 5 1/4 the length of segment 6; segment 6, 2 hinge teeth, palm sparsely setose throughout, defined by a single strong spine, this not associated with a discrete thumb-like extension from the palm. Peraeopod 3: segment 2 slender, anterior margin shallowly convex; segment 4, anterior margin setose only distally, segment width two thirds of length; segment 5 a third overlapped by segment 4; segment 6 width 44% of length. Peraeopods 5-7: slender, setae and spines sparse, segment 2 not posterodistally produced; segment 4 not spinose. Uropod 1: peduncle, posteroventral spinous process underlying 88% of the inner ramus, inner and outer ramus with 1 and 3 mid-dorsal spines respectively. Uropod 2: peduncle,

posteroventral spinous process underlying 21% of the inner ramus. Uropod 3: inner ramus not mid-dorsally spinose.

CONDITION: Without antennae 1, right antenna 2 or left peraeopod 3. Remaining right appendages, telson and mouthparts slide mounted. Remaining left appendages with the carcass.

ADULT FEMALE. Allotype: Length 4.2 mm. Antenna 2: only slightly longer than antenna 1, segment 5 without plumose setae, simple filter setae about twice the length of those of the adult male. Gnathopod 2: segment 6 without a hinge tooth, palm 40% of the posterior margin; setae not so dense as to obscure the palm's shape.

CONDITION: Without antennae 1 and right peraeopod 6. Right antenna 2 and gnathopod 2 slide mounted. Other appendages with the carcass.

VARIATION: Body length at maturity: male to 4.0 mm, female 2.9-4.2 mm. The male's antenna 2 lengthens allometrically during maturation and the setae shorten. Change in the female is isometric. Gnathopod 2 development is isometric in both sexes. There is no thumb production although in the male the hinge tooth enlarges and the palm lengthens (Fig. 47,48).

TYPE MATERIAL: Holotype, male (BMNH), registration no. 1987:511, station no. 13(244), South Orkney Islands: Signy Island: Billie Rocks (60°43'S, 45°38'W), 4 March 1965, diver collection of Lithothamnium, Desmarestia

anceps, D. chordalis, Ascoseira mirabilis, Rhodophyceae, Porifera, and Polyzoa off solid rock inclined at 65⁰, 3.1-3.4 m depth, M. H. Thurston, collector. Allotype, female (BMNH), registration no. 1987:512, same location. Paratypes, approximately 200 specimens, registration no. 1969:768 (part), same location.

OTHER MATERIAL (excluded from type series): approximately 900 specimens from the South Orkney Islands (Signy Island) (BMNH) and 1 juvenile from South Georgia (ZMUH).

REMARKS: Table 5 summarizes obvious differences between P. moorl and P. lowryi.

CONFIRMED LITERATURE: Thurston (1974b), as Jassa falcata form 3.

ETYMOLOGY: In appreciation of Dr. Geoff Moore's great contribution to our knowledge of the systematics, ecology and behaviour of amphipods and of his assistance in locating specimens for this study.

Table 5. Morphological differences between Plecojassa moori and P. lowryi

Character	P. moori	Character State P. lowryi
Body length at maturity		
female range	2.9 - 4.2	2.7 - 5.1
male maximum	4.0	5.3
Antennae 1 & 2		
shape	slenderer, longer	stouter, shorter
setation	sparsely setose	densely setose
Antenna 2		
development	lengthens, setae sparser and shorter (male only)	develops plumose setae (both sexes)
Gnathopod 1		
segment 2, medial margin, spination	not spinose	spinose along most of its length
segment 5, anterodistal setae, presence	absent	present, short
segment 6, palm shape	broader, convex	slender, nearly straight
Gnathopod 2		
segment 5, length relative to segment 6	1/4	less than 1/4
segment 6, female, palm, length in relation to posterior margin	less than 1/2	more than 1/2
setation, abundance	sparse	dense
type	simple	plumose
segment 6, adult male, hinge tooth, shape	split in two	shallowly bifid
defining angle, shape	not produced	produced into a hook
setation, abundance	sparse	dense
type	simple	plumose
Peracopods 3 & 4		
segment 5 overlap		
by segment 4	1/2	3/4
Peracopods 5-7		
segment 2, shape	slender	stout
setation, abundance	sparse	moderately dense
spination, abundance	sparse	moderately dense
Propod 1		
posteroventral peduncular process, length in relation to outer ramus	equal	3/4

2. PLEOJASSA LOWRYI n.sp.

Figs. 11, 46, 47, 48

ADULT MALE. Holotype: Length 5.3 mm. Without antenna 1. (Paratype, male, 3.8 mm, antenna 2 overlapped by antenna 1 to the end of segment 5). Antenna 2: segment 5 and flagellum, posterior margin bearing abundant plumose setae, simple filter setae interspersed, these sparser and shorter than in the juvenile; flagellum 3 segments, segment 1 86% of full flagellum length. Mandible: raker spines 4 right, 6 left. Gnathopod 1: coxal margins, anterior 112% of dorsal length; ventral margin straight; segment 2, antero-medial margin with a row of short, spine-like setae, antero-lateral and posterior margins setose only distally; segment 5, posterior lobe 42% of anterior margin length, setal cluster short, 16% of the anterior margin length; segment 6 narrow, palm nearly straight, defining spine proximal of centre. Gnathopod 2: coxal margins, anterior 48% and posterior 70% of ventral length; ventral margin convex; segment 5 less than a quarter the length of segment 6; segment 6, hinge tooth triangular, shallowly bifid, palm densely plumose throughout, defined by a single minute spine at the end of a short hook-like protuberance. Peraeopod 3: segment 2 slender, anterior margin straight; segment 4, anterior margin setose centrally and distally, central setae less than 1/4 segment width, segment width 73% of length; segment 5 three quarters to fully overlapped by segment 4; segment 6 width 58% of length. Peraeopods 5-7: stout, segment 2 of peraeopod 7 posterodistally produced; segment 4, posterior margin with a row of spines. Uropod 1: peduncle, posteroventral spinous process underlying

39% of the inner ramus, inner and outer rami with 3 and 5 mid-dorsal spines respectively. Cusps ventral to the apical spine group. Uropod 2: peduncle, posteroventral spinous process underlying 17% of the inner ramus.

CONDITION: Without antennae 1, right antenna 2, right peraeopods 5 and 6, and both peraeopods 7. Remaining right appendages, telson, and mouthparts slide mounted. Remaining left appendages with the carcass.

ADULT FEMALE. Allotype: Length 5.1 mm. Antenna 1: overlapping antenna 2 to the end of segment 5; segment 5, posterior margin with long filter setae and a few plumose setae distally; flagellum, posterior margin with a few plumose setae proximally and brush setae distally. Gnathopod 2: segment 6 without a hinge tooth, palm 58% the length of the posterior margin, setae plumose, so abundant as to obscure the palm's shape.

CONDITION: Without left peraeopod 7.

VARIATION: Body length at maturity: male to 5.3 mm, female 2.7-5.1 mm. Antenna 2 plumosity is a feature of adulthood. Gnathopod 2 palm plumosity intensifies with age, but is present to some degree in the juvenile, especially the male.

TYPE MATERIAL: Holotype, male (AM), type no. P34948, station no. SA-3417, New Zealand: The Snares: Rima Islet (48°07'S, 166°38'E), from barnacles encrusted with sponge, in a crevice in the Durvillea zone, G.

D. Fenwick, collector. Allotype, female (AM), type no. P37922, same location. Paratypes, 5 adult males, 25 adult females, and 163 juveniles (AM), type no. P37923, same location.

OTHER MATERIAL: Two juveniles from The Snares: Alert Stack (Al.), catalogue no. P.34949, station no. SA-3456, from algae below the Durvillea zone to 7m, G. D. Fenwick, collector.

REMARKS: The gnathopod 1, segment 2 spination is not homologous to that of J. alonsoae, J. justii, J. fenwicki, and J. hartmannae because it is medial instead of lateral. Readily recognizable differences between P. lowryi and P. moori are listed in Table 5.

ETYMOLOGY: In gratitude to Dr. Jim Lowry (Australian Museum) for assistance in locating Southern Hemisphere material and in interpreting biogeography.

3. PLEOJASSA WANDELI (Chevreux, 1906) new combination

Figs. 11, 12, 46, 47, 48

Jassa wandeli Chevreux, 1906, 94-99, Figs. 54-56: 1913, 181, Fig. 61

Jassa falcata: (form 1) Thurston, 1974a, 46-47: 1974b, 101-102

ADULT MALE. (Not type; BMNH 1969:735:39 station 10(95): South Orkney Islands: Signy Island: Billie Rocks, 5 March 1965, M. H. Thurston, collector). Length 9.8 mm. Antenna 2: overlapped by antenna 1 to midway along segment 5; segment 5 and flagellum, posterior margin covered in a mass of plumose setae; simple setae absent; flagellum 3 segments, the last half the length of the second; segment 1 87% of full flagellum length. Mandible: raker spines 4 right, 5 left. Gnathopod 1: coxal margins, anterior 113% of dorsal length; ventral margin straight; segment 2, anterior margins with a few fine setae spaced along their length, posterior margin with a single distal seta; segment 5, posterior lobe 50% of anterior margin length, anterodistal setal cluster short, 39% of the anterior margin length; segment 6, palm convex, defining spine proximal of centre. Gnathopod 2: coxal margins, anterior 21% and posterior 83% of ventral length, ventral margin straight; segment 5 less than a quarter the length of segment 6, posterior lobe without a distal seta; segment 6, palm, hinge tooth rectangular, shallowly bifid centrally, setae sparse but spread throughout the palm, thumb 36% of segment 6 length, distally squared, posterior margin straight, with clusters of setae subapically, and 3 groups posteriorly, and with 1 minute defining spine at its tip. Peraeopod 3: coxa, greatest depth at the centre; segment 2, anterior

Fig. 12. Pleojassa wandeli. Lectotype, juvenile male 6.0 mm. Ile Booth-Wandel, Antarctica, 10 December, 1904. Adult, male 1, 9.8 mm; juvenile male 2, 6.3 mm; female, 9.6 mm. Billie Rocks, Signy Island, South Orkney Islands, station no. 10(95), 5 March 1965. Note the thumbed cuticle within the juvenile male 2 gnathopod 2. Lateral views: whole body, maxillae 1 and 2; dorsal view: telson; all other views medial. Appendages are of the lectotype unless indicated otherwise. Scale 0.1 mm.

margin straight; segment 4, anterior marginal setae in discrete, well spaced clusters, about a third the segment width, segment width 61% of length; segment 5 44% overlapped by segment 4; segment 6, width 56% of length. Peraeopods 5-7: setae and spines moderately abundant, segment 2 posterodistally produced, segment 4 not spinose. Uropod 1: peduncle, posteroventral spinous process underlying 38% of the inner ramus, inner and outer rami with 7 and 13 mid-dorsal spines respectively. Uropod 2: peduncle, posteroventral spinous process underlying 10% of the inner ramus. Uropod 3: inner ramus with 2 dorso-medial spines in addition to the single apical spine.

CONDITION: Without the left peraeopod 5. Right appendages, telson and mouthparts slide mounted. Remaining appendages with the carcass.

ADULT FEMALE. (Not type; same location as for the adult male). Length 9.6 mm. Antenna 2: segment 5, posterior margin with long simple setae mainly, but interspersed with a few plumose setae. Gnathopod 2: coxal margins, anterior 56% and posterior 94% of ventral length, ventral margin convex; segment 6, hinge tooth strongly pronounced, palmar setae densely plumose throughout, so much so as nearly to obscure the shape of the palm.

CONDITION: With all appendages. Right appendages, telson, and mouthparts slide mounted. Left appendages with the carcass.

VARIATION: Body size at maturity: male to 10.8 mm, female 5.9-9.6 mm. In juveniles and in the adult female the antenna 2 is much shorter (about the same length as antenna 1). The filter setae on segment 5 shorten with maturity, to be infused with dense plumose setae. These plumose setae appear also in the female, but less abundantly. In the female the appearance of plumose setae is not accompanied by shortening and disappearance of the filter setae. In both sexes plumose setae are evident at 5.5 mm body length or greater. Male gnathopod 2 development is illustrated in Figs. 47 and 48. The shape of the dactyl margin changes with maturity in the male, but not in the female. In juveniles and females the inner margin is straight. In the adult male it is curved and proximally produced.

TYPE MATERIAL: Lectotype (here designated), male (MHNP), catalogue no. Am.2630(1), Antarctica: Booth-Wandel Island, 10 December 1904, among sponges at low tide, Expédition Antarctique Française (1903-1905). Paralectotypes, 4 juveniles, same location.

OTHER MATERIAL (excluded from type series): Approximately 140 specimens from the Signy Island (South Orkney Islands), South Georgia, Visikoi Island (South Sandwich Islands), Deception Island (South Shetland Islands), Petermann Island, Pourquoi Pas Island, and Kerguelen (BMNH, MHNP, ZMUH, ZMUO, D. Bellan-Santini).

REMARKS: Pleojassa wandeli resembles P. multidentata in thumb development and overall appearance. The latter can be distinguished by

the shorter seta at the anterodistal junction of segments 5 and 6 on gnathopod 1, lack of antenna 2 plumosity in the adult, denser plumosity of the gnathopod 2 palm in the female and juvenile, more pronounced hinge tooth, and pronounced uropod 2 peduncular process.

4. PLEOJASSA MULTIDENTATA (Schellenberg, 1931)

Jassa multidentata Schellenberg, 1931, 251-253, Fig. 131

4.1. PLEOJASSA MULTIDENTATA MULTIDENTATA

Figs. 11, 46, 47, 48

ADULT MALE. (Not type; ZMHB 22.962, South Georgia, Swedish Antarctic Expedition): Length 3.0 mm. Antenna 2: overlapped by antenna 1 to midway along segment 5; antenna 2, segment 5 bearing simple setae only, these less than half the length of those of the juvenile; flagellum 3 segments, segment 1 86% of full flagellum length. Mandible: raker spines 4 right, 6 left. Gnathopod 1: coxal margins, anterior 110% of dorsal length, ventral margin shallowly convex; segment 2, anterior and posterior margins not setose; segment 5, posterior lobe 49% of anterior margin length, anterodistal setal cluster short, 18% of the anterior margin; segment 6, palm convex, defining spine proximal of centre. Gnathopod 2: coxal margins, anterior 30% and posterior 72% of ventral length, ventral margin convex; segment 5 less than 1/4 the length of segment 6, posterior lobe with a short distal seta; segment 6, hinge tooth large, triangular, not bifid, palmar setae sparse throughout, thumb 30% of segment length, distally squared, tip with a minute defining spine, both inner and outer margins setose, posterior margin straight. Peraeopod 3: coxa, greatest depth posterior of centre; segment 2, anterior margin shallowly concave; segment 4, anterior margin with 2 clusters of setae, these setae shorter than segment width, segment width

95% of length; segment 5 69% overlapped by segment 4; segment 6, width 36% of length. Peraeopods 5-7: setae and spines moderately abundant, segment 2 posterodistally produced; segment 4 not spinose. Uropod 1: peduncle, posteroventral spinous process underlying 38% of the inner ramus, inner and outer rami with 12 and 7 mid-dorsal spines respectively. Uropod 2: peduncle, posteroventral spinous process underlying 27% of the inner ramus. Uropod 3: inner ramus with two spines in addition to the single apical spine.

CONDITION: Without left antennae 1 and 2 flagella, right and left peraeopod 7, and right uropod outer ramus. Right appendages, both uropods 1, telson, and mouthparts slide mounted.

ADULT FEMALE. Lectotype (here designated): Length 7.7 mm. Antenna 2: segment 5 without plumose setae. Gnathopod 2: segment 6, hinge tooth pronounced, anterior margin crenulated, palmar setae dense throughout, sufficiently so to obscure the palm's shape.

CONDITION: Ovigerous. Without left peraeopods 3, 6 and 7, and right peraeopods 4-7.

VARIATION: Body length at maturity: male to 8.0 mm, female 6.0-9.1 mm. The number of antennal segments is constant over age and sex. Sexual maturation in the male is marked by shortening of the second antennal setae and a change in the shape of the second gnathopod palm (Figs.

47,48). The dactyl's inner margin also changes shape from evenly convex to proximally expanded and sinuous.

TYPE MATERIAL: Lectotype, female (ZMUH), catalogue no. K-8028, station 7813, South Georgia: Royal Bucht: Moltke Hafen (54°30'58"S, 36°0'45"W), 1883, Deutsche Polar Comm., K. von den Steinen, collector. Paralectotypes, 4 mature females, 16 immatures, K-8017, K-8019, K-8021 (ZMUH).

OTHER MATERIAL: 21 specimens from South Georgia collected during the Swedish Antarctic Expedition of 1901-1903 (NRS, ZMHB).

REMARKS: Pleojassa multidentata multidentata differs from P. multidentata orientalis in the shape of the gnathopod 2 palm (both sexes) (Figs. 11 and 46), and by possessing a cluster of short setae at the anterodistal margin of gnathopod 1, segment 5.

In his type description of Jassa multidentata, Schellenberg (1931) notes having examined specimens from the Swedish Museum of Natural History (collected in 1902, during the Discovery Expedition, from four locations in South Georgia), and from the Hamburg Museum (from South Georgia, but locations and collection dates not specified). I have examined three of the Swedish collections (Nos. 3676, 3677, and 3678), and four of the Hamburg collection (Nos. K-8017Am K-8019, K-8021, and K-8028). The Swedish specimens comprise two immature males and one adult, ovigerous female. The University of Hamburg specimens comprise sixteen unsexed immatures and five adult females. Since Schellenberg was curator

of the Hamburg collection, I herein limit type designation to the Hamburg material, selecting the 7.7 mm adult female of K-8028 as lectotype. The only other collection known to me (ZMHB) comprises one adult male, four adult females, and thirteen unsexed immatures.

4.2. PLEOJASSA MULTIDENTATA ORIENTALIS n.subsp.

Figs. 11, 46

ADULT FEMALE. Holotype: Length 9.8 mm. Antenna 2: overlapped by antenna 1 to the end of segment 5; segment 5, posterior margin bearing long simple setae only, without plumose setae; flagellum 3 segments, segment 1 89% of the full flagellum length. Mandible: raker spines, number not measured. Maxilla 1: palp without setae at the base of segment 1, segment 2 with 1 row of facial setae. Gnathopod 1: coxal margins, anterior 140% of dorsal length; ventral margin straight; segment 2, anterior margins with a few short setae distally, ventral margin not setose; segment 5, posterior lobe 59% of anterior margin length, without an anterodistal setal cluster; segment 6, palm convex, defining spine proximal of centre. Gnathopod 2: coxal margins, anterior 44% and posterior 73% of ventral length; ventral margin straight; segment 5 less than 1/4 the length of segment 6; segment 6, hinge tooth large and triangular, not anteriorly bifid, palmar setae plumose, distributed throughout the palm, but not so dense as to obscure the palm's shape, palmar angle acute, with a single, minute spine at its corner; dactyl, inner margin slightly sinuous. Peraeopod 3: coxa, greatest depth posterior of centre; segment 2, anterior margin shallowly convex; segment 4, anterior marginal setae in well separated clusters, central setae, length 1/2 or less the segment width, segment width 72% of length; segment 5 42% overlapped by segment 4; segment 6, width 48% of length. Peraeopods 5-7: setae and spines moderately abundant, segment 2 posterodistally produced; segment 4 not spinose. Uropod 1: peduncle,

posteroventral spinous process underlying 52% of the inner ramus, inner and outer rami with 15 and 12 mid-dorsal spines respectively. Cusps ventral to the apical spine group. Uropod 2: peduncle, posteroventral spinous process underlying 42% of the inner ramus. Uropod 3: inner ramus with 2 spines mid-dorsally in addition to the single apical spine.

CONDITION: Without right peraeopod 7. Right antenna 1, flagellum lacking terminal segments.

JUVENILE MALE. Allotype: Length approximately 6.5 mm; head to end of segment 6, 3.9 mm. Antenna 2: segment 5, filter setae half or less the length of those in the female, interspersed with plumose setae. Gnathopod 2: as in the female, but palm less densely setose and dactyl inner margin straight.

CONDITION: Without body segments posterior of segment 6, antennae 1 flagella, left antenna 2 distal flagellum, right antenna 2, left peraeopods 5-7, and right peraeopods 5 and 7.

VARIATION: Body length at maturity: male unknown, female to 9.8 mm. The male is 2/3 the size of the holotype female (judging by relative difference in head length), yet plumose setae are present on the male's antenna 2 and lacking on the female's. This suggests that, as in P. wandeli, larger females would have plumose setae. Due to lack of material, male gnathopod 2 development is unknown; it can be assumed to resemble that of P. multidentata multidentata.

TYPE MATERIAL: Holotype, female, ovigerous (AM), type no. P34955, station no. MA-147, Macquarie Island: Gorilla Head Rock, southeast corner (54°29'S, 158°58'E), 23 December 1977, in a small Durvillea antarctica holdfast, 8 m. Allotype, juvenile male (AM), type no. P37924, same location. Paratype, juvenile female (AM), type no. 37925, same location.

REMARKS: Noted under P. multidentata multidentata

ETYMOLOGY: In reference to the eastern location of the subspecies.

4. JASSA Leach, 1814

Jassa Leach, 1814, p. 433: Stebbing, 1906, p. 652-653: Chevreux and Fage, 1925, p. 343, 344: Schellenberg, 1942, p. 208: Gurjanova, 1951, p. 906, 907: Barnard, 1969, p. 279: 1973, p. 25: Lincoln, 1979, p. 548

ADULT MALE. Body length at maturity 2-22 mm. Head lobe: squared, but with the dorsal angle more acute and the ventral angle lobe more broadly rounded. Antenna 1: accessory flagellum 2 segments, the second minute, only the second segment setose. Antenna 2: stouter and longer than antenna 1, especially in the male, the long filter setae becoming shorter and sparser at maturity and in many species developing short plumose setae as well; flagellum with at least two of its distal segments bearing posteriorly curved spines, first segment considerably longer than any of the distal segments. Mandible: palp segments 2 and 3 with or without a dorsal fringe of setae. Maxilla 1: inner plate bearing a few short fine setae, palp with one or more rows of setae. Gnathopod 1: coxa rectangular; segment 6 with 3 medioproximal defining spines (arranged in medial-lateral-medial sequence); dactyl with or without facial striations. Gnathopod 2: coxa deeper posteriorly, with a gill; segment 2, filter setae, when present, simple or finely barbed, and located on the anterolateral flange only; segment 5 less than $1/4$ segment 6 length; segment 6 with a triangular, shallowly bifid tooth below the dactyl hinge and a larger thumb incised at the last molt from the posterior margin of the palm distal to the 3 palmar defining spines (or associated setae if spines absent), inner margin of thumb not setose, outer margin with 3-4

discrete clusters; dactyl shorter than segment 6, extending beyond the thumb to rest against the thumb's posterior margin when closed, inner margin expanded at the location of the hinge tooth or more centrally and acutely as a tooth into the palmar incision, dactyl cusps reduced to small buttons interspersed with a few short setae. Peraeopod 3: coxa usually deepest posterior of centre; segment 2 slenderer at maturity, margins more parallel than convex; segment 4 half to fully overlapping segment 5, anterior margin bearing numerous setae in clusters or singly; segment 6 not posteriorly spinose. Peraeopods 5-7: segment 2 of at least one of peraeopods 5-7 posterodistally produced; segments 4 and 5, posterior margin not spinose; segment 6 variably expanded; dactyl usually not facially striated, posterior (outer) margin not cusped distally, anterior (inner) margin bearing a seta only at the unguis. Urosome: segment 1 bearing a pair of erect setae dorsally. Pleopods: well developed, usually with 2 coupling hooks each. Uropod 1: rami with or without a fringe of cusps below the apical spine group. Uropod 3: peduncle mid-ventrally setose, without spines mid-dorsally, but with a crown of 2 clusters of spines around the dorso-distal margin and a cluster of setae distolaterally; outer ramus not setose mid-dorsally, tipped by a basally immersed, dorsally recurved spine, a short seta at the spine's insertion, 2 large cusps and many additional minute cusps. Telson: each corner with a pair of cusps accompanied by setae (1 long, simple and 2 short, plumose) but without spines.

ADULT FEMALE. Body length at maturity 2-21 mm. Brood plates broad, setae abundant. Antenna 2: peduncle, posterior filter setae long, not

shortening with age. Gnathopod 2: segment 6 much larger and different in shape from segment 6 of gnathopod 1, palm concave, defined by a tight cluster of 3 spines (2 medial, 1 lateral - these not lost with age) but without a thumb; dactyl fitting into a depression between the palmar angle and spines, inner margin cusps much smaller than those of the gnathopod 1 dactyl. Peraeopod 3: segment 2 broadly expanded, margins convex.

VARIATION: There are certain developmental changes in Jassa that are common to a majority of species. In females, these changes are isometric, but in males, certain parts of the antenna 2, gnathopod 2, and peraeopods 3-4 may develop allometrically at or just prior to maturity. Development is discussed in section 3.1.6. Many species develop plumose setae on the posterodistal margin of the second antenna's segment 5 and posteroproximal margin of the flagellum. This occurs in both sexes, as a function of size rather than maturity; thus large juveniles may have abundant plumose setae but small adults may have few. Since the modal size of maturity less in females than in males, fewer females exhibit antenna 2 plumosity. Other changes to the second antenna such as reduction in length of the simple filtering setae and gross lengthening of the segments are unique to the males.

More spectacular is the change in morphology of the male's second gnathopod. As maturity is approached the coxa shallows anteriorly and the antero- and postero-ventral margins become increasingly angular. The sixth segment enlarges to about 1 1/2 to 2 times the size of the female's. Then at the last molt the palm is incised to produce a

pronounced thumb that arises distally to the palmar defining spines. In most species the three defining spines are reduced in the thumb stage, and absent if the individual is large; however, in a few species the spines enlarge and are produced onto a ledge. The defining spines are always present in the juvenile male and at any stage of maturity in the female. The male's thumb shape varies with body size, but its position on the segment is bimodally distributed as a minor or major form. Species differentiation on the basis of thumb appearance is highly unreliable unless individuals of the same stage are compared. The dactyl also changes shape at maturity, becoming more curved or sinuous. In all species the male's dactyl becomes increasingly proximally expanded with age, but the location of expansion may vary: in the minor form of some species the expansion is acute and tooth-like, and is located more distally so as to fill the palmar incision; in all other minor forms and in all major forms the expansion is shallower, broader, and located more proximally against the hinge tooth. Females of some species sport a dactyl expansion but this is never as acute as in the male. Commonly in both sexes the dactyl cusps become sparser and less acute with age.

Associated with the male's thumb production is a reduction in size of the spinning gland in the second segment of pereopods 3 and 4. This change is most obvious in large species. The glands of the female do not decline at maturity. Setation intensity of segment 4 also increases at maturity in some species, particularly in the male.

There are some interspecific differences in posterior appendage morphology but intraspecific variation is not usually sexually dimorphic.

TYPE SPECIES: Cancer (Gammarus) falcatus Montagu, 1808

INCLUDED SPECIES: Jassa falcata (Montagu, 1808), J. ingens (Pfeffer, 1888), J. herdmani (Walker, 1893), J. pusilla (Sars, 1895), J. marmorata Holmes, 1903, J. alonsoae n. sp., J. borowskyae n. sp., J. carltoni n. sp., J. fenwicki n. sp., J. gruneri n. sp., J. hartmannae n. sp., J. justi n. sp., J. morinoti n. sp., J. myersi n. sp., J. oclairi n. sp., J. shawi n. sp., J. slatteryi n. sp., J. stauderi n. sp., and J. thurstoni.

REMARKS: Jassa has traditionally been the recipient for species that produce a thumb on the second gnathopod's sixth segment. Jassa produces its thumb distally to the palmar defining spines; in all other species the thumb develops at the spines. Other distinctive features of Jassa are the medial-lateral-medial sequence of the defining spines and double cusping of the uropod 3 outer ramus.

Stebbing (1906), Chevreux and Fage (1925), and Schellenberg (1931) erroneously placed Jassa in the family Jassidae. This name is preoccupied by a family of insects in the Rhynchota (Hemiptera). Shoemaker (1942) noted this and shifted Jassa to the Ischyroceridae.

Sexton and Reid (1951) have traced the nomenclatural history of the genus. Leach (1814) erected Jassa for two species, J. pulchella and J. pelagica. The latter has since been transferred to Parajassa Stebbing, 1899. At that time Leach noted that "Cancer Gammarus falcatus of Montagu, Lin. Trans. vol. ix. tab. 5. fig. 2 seems referable to this genus". Leach (1814) also established the genus Podocerus, with type species P. variegatus. According to Sexton and Reid (1951), "Walker

(1899, p. 394) found, on reexamining Leach's type specimens of P. variegatus (reg. no. 295 a-f) that at least two species were represented 'one being apparently the female or young of P. falcatus (Mont.)'. Currently only two of the original six syntypes remain, 295b and 295d. Each is Podocerus variegatus. It is not known from Sexton and Reid's account who was the first to synonymize Jassa with Podocerus, but the latter name held until Stebbing (1899) re-erected Jassa. Stebbing (1899, 1906) believed that J. pulchella should be held as type to Jassa, with J. falcata indeterminate, but both Sars (1894) and Walker (1895 and 1899) considered J. pulchella to be synonymous with J. falcata. J. pulchella continued to appear in publications as a distinct species as recently as Gurjanova (1951) but since Sexton and Reid's (1951) full synonymy of all species of Jassa under J. falcata it has been disregarded, and J. falcata has been deemed type species for the genus.

Table 6 lists the species that at one time or other were considered a member of Jassa, along with their current nomenclatural status.

Table 6. Nomenclatural disposition of species referred to as Jassa or Jassa falcata by other taxonomists.

First Name	Current Name
<u>Cancer</u> (<u>Gammarus</u>) <u>falcatus</u> Montagu, 1808	<u>Jassa falcata</u>
<u>Podocerus</u> <u>variegatus</u> Leach, 1814	syntypes 295b and 285d were <u>Podocerus</u>
<u>Jassa</u> <u>pelagica</u> Leach, 1814	<u>Parajassa pelagica</u>
<u>Jassa</u> <u>pulchella</u> Leach, 1814	<u>Jassa falcata</u>
<u>Podocerus</u> <u>capillatus</u> Rathke, 1843	<u>Parajassa pelagica</u> (Leach, 1814)
<u>Podocerus</u> <u>calcaratus</u> Rathke, 1843	whereabouts of type unknown
<u>Cratophium</u> <u>validum</u> Dana, 1852	type lost according to Dr. J. L. Barnard, USNM; was possibly <u>J. marmorata</u>
<u>Gammarus</u> <u>orientalis</u> Dana, 1852	types lost according to Dr. J. L. Barnard, USNM
<u>Podocerus</u> <u>monodon</u> Heller, 1866	<u>Ischyrocerus monodon</u>
<u>Podocerus</u> <u>californicus</u> Boeck, 1872	whereabouts of types unknown
<u>Podocerus</u> <u>australis</u> Haswell, 1880	types lost
<u>Podocerus</u> <u>minutus</u> Sars, 1882	<u>Jassa pusilla</u> (Sars, 1894)
<u>Podocerus</u> <u>ingens</u> Pfeffer, 1888	<u>Jassa ingens</u>
<u>Podocerus</u> <u>cumbrensis</u> Stebbing and Robertson, 1891	<u>Microjassa cumbrensis</u>
<u>Podocerus</u> <u>hoecki</u> Stebbing, 1888	syntypes examined were <u>Ischyrocerus</u>
<u>Jassa</u> <u>punctata</u> (see Della Valle, 1893)	whereabouts of types unknown
<u>Podocerus</u> <u>ornatus</u> Miers, 1875	syntypes examined were <u>Podocerus</u> , not <u>Jassa</u>

Podocerus tristanensis Stebbing, 1888

Podocerus oclius Bate, 1862

Jassa goniamera Walker, 1903

Jassa lilipuna Barnard, 1970

Jassa barnardi Stephensen, 1949

Jassa dentex Czerniavski, 1868
(Bate, 1862)

Jassa odontonyx (Sars, 1894)

Podocerus falcatifformis Sowinski, 1898

Podocerus frequens Chilton, 1883

Parajassa tristanensis

Plumulojassa oclia

Hemijassa goniamera

Neoischyrocerus lilipuna

Ventojassa barnardi

Plumulojassa oclia

Jassa pusilla
(Sars, 1894)

has not been transferred
to Ischyrocerus,
Parajassa,
or Ventojassa; maybe
to Podocerus?

Ventojassa frequens

KEY TO WORLD SPECIES OF JASSA

- 1a. Gnathopod 2, anterolateral margin of segment 2 with a row of setae along its length (Figs. 13 A,C,D,E) 2
- 1b. Gnathopod 2, segment 2, setae absent or, if present, microscopic (Fig. 13B) 14

- 2a. Gnathopod 1, anterolateral margin of segment 2 with a row of short setae along its length (Fig. 14A). Southern Hemisphere 3
- 2b. Gnathopod 1, segment 2 without a row of short setae along the length of the anterolateral margin (if setae present, these are minute, or confined to the anterodistal corner) (Figs. 14B-H). Mainly Northern Hemisphere 6

- 3a. Peraeopods 5-7, segment 6 anteroproximally expanded, spines thick (Fig. 15E) 1. J. fenwicki n.sp.
- 3b. Peraeopods 5-7, segment 6 not expanded anteroproximally, spines thin (Fig. 15F) 4

- 4a. Gnathopod 1, segment 5 without a seta at the anterodistal junction with segment 6 (Figs. 14B,E,H). Gnathopod 2, female and non-thumbed male, palm concave, defining angle acute (Fig. 16N).....
..... 2. J. justii n.sp.
- 4b. Gnathopod 1, segment 5 with a seta or cluster of setae (may be minute and slightly lateral or medial) at the anterodistal junction with segment 6 (Figs. 14A,C,D,F), palm variable..... 5

Fig. 13. Jassa. Gnathopod 2, adult male. A, J. staudei; B, J. falcata; C, J. slatteryi; D, J. borowskyae; E, J. oclairi; F, J. morinói; G, J. carltoni; H, J. myersi; I, J. ingens. Views F, G, and I of palmar area, only thumb setae shown. Views A, C, D, F, G, and I lateral, others medial. Scale 0.1 mm.

Fig. 14. Jassa. Gnathopod 1. A, J. alonsoae, male; B, J. falcata, male; C, J. borowskyae, female; D, J. shawi, juvenile male; E, J. staudei, female; F, J. slatteryi, female; G, J. thurstoni, male; H, J. pusilla, female. View H lateral, all others medial. Scale 0.1 mm.

Fig. 15. Jassa. A-D, peraeopod 3; E-G, peraeopod 7; H, I, uropod 1; J, K, uropod 3; L, M, telson. A, J. borowskyae; B, J. myersi; C, J. ingens; D, J. oclairi; E, J. fenwicki; F, J. staudei; G, J. ingens; H, J. falcata; I, J. shawi; J, J. falcata; K, J. borowskyae; L, J. morinoi; M, J. slatteryi. Views F, H, I, J, K, L, M lateral, others medial. Scale 0.1 mm.

- 5a. Gnathopod 2, female and non-thumbed male, palmar angle shallow, giving the palm a sinuous appearance (Fig. 16M). Gnathopod 2, segment 6, thumbed male, posterior margin of thumb sinuous (Figs. 43-46)..... 3. J. alonsoae n.sp.
- 5b. Gnathopod 2, female and non-thumbed male, palmar angle acute, giving the palm a concave appearance (Fig. 16P). Gnathopod 2, segment 6, thumbed male, posterior margin of thumb straight or shallowly concave..... 4. J. hartmannae n.sp.
- 6a. Gnathopod 2, juvenile male, juvenile female, and adult female, palm of segment 6 appearing straight or sinuous (Fig. 16O). Gnathopod 1, segment 5 without a seta at the anterodistal junction of segment 6 (Figs. 14B,E,H)..... 5. J. gruneri n.sp.
- 6b. Gnathopod 2, juvenile male, juvenile female, and adult female, palm of segment 6 usually concave (Fig. 16A) (if sinuous, then segment 5 of gnathopod 1 with a long seta at the anterodistal junction of segment 6 (Figs. 14C,F).....7
- 7a. Gnathopod 1, segment 5 without setae at the anterodistal junction of segment 6 (Fig. 14B,E,F) 6. J. staudei n.sp.
- 7b. Gnathopod 1, segment 5 with seta(e) at the anterodistal junction of segment 6 (seta(e) usually slightly medial, minute (Fig. 14D) or long (Figs. 14 C,F) 8
- 8a. Gnathopod 1, segment 5, seta(e) at the anterodistal junction with

Fig. 16. Jassa. Adult female gnathopod 2 palm morphology. A, J. marmorata; B, J. morinói; C, J. slatteryi; D, J. carltoni; E, J. myersi; F, J. staudei; G, J. oclairi; H, J. borowskyae; I, J. shawi; J, J. pusilla; K, J. falcata; L, J. herdmani; M, J. alonsoae; N, J. justí; O, J. gruneri; P, J. hartmannae; Q, J. thurstoni; R, J. ingens. Setae omitted. All views lateral. Scale 0.1 mm.

- segment 6 short, slightly lateral (Figs. 14D)
 7. J. marmorata Holmes, 1903
- 8b. Gnathopod 1, segment 5, seta(e) at the anterodistal junction with
 segment 6 long, slightly medial or dorsal (Fig. 14C,F) 9
- 9a. Uropod 1, ventral peduncular spinous process at least 1/4 to 1/2 the
 length of the shortest ramus (Fig. 15H) 10
- 9b. Uropod 1, ventral peduncular spinous process vestigial (Fig. 15I)...
 13
- 10a. Gnathopod 2, segments 2 and 6, anterior marginal setae abundant,
 plumose (Fig. 13E). Mandibular palp, segment 2 with a fringe of
 setae on the dorsal margin (Fig. 17F) 8. J. oclairi n.sp.
- 10b. Gnathopod 2, segments 2 and 6, anterior marginal setae less
 abundant, and simple, or microscopically pectinate (Fig. 13C).
 Mandibular palp, segment 2 without a fringe of setae on the dorsal
 margin (Fig. 17H) 11
- 11a. Telson, tip bearing apical setae in addition to the usual setae at
 each lateral cusp (Fig. 15L). Gnathopod 2, segment 6, large thumbed
 male, posterior margin expanded around the defining spines (Fig. 13
 F) 9. J. morinof n.sp.
- 11b. Telson, tip without apical setae, only with the usual setae at each
 lateral cusp (Fig. 15M). Gnathopod 2, segment 6, large thumbed
 male, posterior margin without defining spines, or not expanded
 around the spines if spines present (Figs. 13C,G) 12

Fig. 17. Jassa. A-E, antenna 2; F, H, mandible; G, I, maxilla 1. A, J. slatteryi, adult male; B, J. shawi, juvenile male; C, J. falcata, adult male; D, J. pusilla, adult female; E, J. herdmani, adult male; F, J. falcata; H, J. pusilla; G, J. staudei; I, J. ingens. Views B, D, G, H, I lateral; all others medial. Scale 0.1 mm.

- 12a. Large thumbed male, antenna 2 with plumose setae on the posterodistal margin of peduncular segment 5 and flagellum segment 1 (Fig. 17A). Gnathopod 2, segment 6, thumb tip acute; defining spines absent (although present in smaller, thumbed adults) (Fig. 13C). Female, gnathopod 2, segment 6, palmar angle more distal from the defining spines; spines tightly clustered (Fig. 16C). Gnathopod 1, segment 6, large male or female, palm straight or slightly concave (Fig. 14F) 10. J. slatteryi n.sp.
- 12b. Large thumbed male, antenna 2 setae simple or microscopically pectinate (Fig. 17B). Gnathopod 2, segment 6, thumb tip angled posteriorly (Fig. 13G). Female, gnathopod 2, segment 6, palmar angle close to the defining spines; spines more separated and sequential (Fig. 16D). Gnathopod 1, segment 6, large male or female, palm evenly convex (Fig. 14G).....11. J. carltoni n.sp.
- 13a. Antenna 2, large adult male or female, posterior margin of peduncle segment 5 and flagellum segment 1 bearing plumose setae (Fig. 17A). Gnathopod 2, segment 2, anterior marginal setae abundant (Fig. 13D); male segment 6, thumb larger, setae proximal to, but not at the apex of, the thumb tip (Fig. 13D). Gnathopod 2, segment 6, female, palm concave, palmar angle close to the defining spines (Fig. 16H). Peraeopods 3 and 4, male, coxa deeper than wide (Fig. 15A)..... 12. J. borowskyae n.sp.
- 13b. Antenna 2, large adult male or female, antennal setae simple or microscopically pectinate, but not plumose (Fig. 17B). Gnathopod 2,

segment 2, anterior marginal setae sparse (Fig. 13H); male segment 6, thumb very small, setae nearly at the thumb tip (Fig. 13H). Gnathopod 2, segment 6, juvenile and adult female, palm straight or slightly sinuous (Fig. 16E). Peraeopods 3 and 4, male, coxa wider than deep (Fig. 15B) 13. J. myersi n.sp.

14a. Peraeopods 5-7, segment 6 anteriorly expanded, spines thick (Fig. 15G). Peraeopods 3 and 4, segment 4 about twice the length of segment 6 (Fig. 15C). Gnathopod 2, segment 6, male and female, defining spines extended on a protuberance (Figs. 13I, 16R). Maxilla 1 with a cluster of setae at the base of the palp (Fig. 17I). Body size at maturity 15 mm or more (female), 19 mm or more (male) 14. J. ingens (Pfeffer, 1888)

14b. Peraeopods 5-7, segment 6, anterior margin not centrally expanded (Fig. 15F), spines not especially strong. Peraeopods 3 and 4, segment 4 less than twice the length of segment 6 (Figs. 15A,B,D). Gnathopod 2, segment 6, male and female, defining spines, if present, not on a protuberance (Figs. 13B, 16I,J,K,L,Q). Maxilla 1 without a cluster of setae at the base of the palp (Fig. 17C). Body size at maturity less than 9 mm (female), 11 mm (male)..... 15

15a. Uropod 1, peduncle, posteroventral spinous process short, about 1/8 the length of the outer ramus (Fig. 15I). Northeastern Pacific coast 15. J. shawi n.sp.

15b. Uropod 1, peduncle, posteroventral spinous process normal, 1/3-1/2

- the length of the outer ramus (Fig. 15H). Southern Hemisphere and North Atlantic 16
- 16a. Gnathopod 1, segment 5 with a cluster of setae at the anterodistal junction of segment 6 (Fig. 14G); coxa large, broadly produced anteriorly (Fig. 14G). Gnathopod 2, segment 6, female and non-thumbed male, palm sinuous (Fig. 16Q). Southern Hemisphere....
..... 16. J. thurstoni n.sp.
- 16b. Gnathopod 1, segment 5 without setae at the anterodistal junction of segment 6 (Figs. 14B,H); coxa smaller, not broadly produced anteriorly (Figs. 14B,H). Gnathopod 2, segment 6, female and non-thumbed male, palm concave (Figs. 16 I,J,K,L). North Atlantic.. 17
- 17a. Mandibular palp, segment 2, dorsal margin fringed with setae Fig. 17F). Antenna 2, flagellum stout (Fig. 17C) 18
- 17b. Mandibular palp, segment 2, dorsal margin without a fringe of setae (Fig. 17H). Antenna 2, flagellum slender (Fig. 17D).....
..... 17. J. pusilla (Sars, 1895)
- 18a. Antenna 2, adult male and female, posterior margin of segment 5 and flagellum segment 1 bearing plumose setae (these absent in small juveniles) (Fig. 17C). Uropod 3, inner ramus bearing 1-2 spines centrally in addition to the usual apical spine (Fig. 15J). Gnathopod 2, segment 6, female, palmar angle bulbous, more distal to the defining spines (Fig. 16K)..... 18. J. falcata (Montagu, 1808)

- 18b. Antenna 2, adult male and female, posterior margin of segment 5 and flagellum segment 1 without plumose setae (Fig. 17E). Uropod 3, inner ramus without central spines (Fig. 15K). Gnathopod 2, segment 6, female, palmar angle acute, more proximal to the defining spines. (Fig. 16L) 19. J. herdmanni (Walker, 1893)

1. JASSA FENWICKI n.sp.

Figs. 15, 45

ADULT MALE. Holotype: Length 7.4 mm. Antenna 2: overlapped by antenna 1 to the full length of peduncular segment 5; segment 5, posterior margin bearing long filter setae proximally and shorter brush setae distally; flagellum 4 segments, the last minute, segment 1 63% of full flagellum length. Mandible: palp segments 2 and 3 without a dorsal fringe of setae; rake spines 3 right, 4 left. Maxilla 1: palp without setae at the base of segment 1, segment 2 with 1 row of facial setae. Gnathopod 1: coxal margins, anterior 100% of dorsal length; ventral margin sinuous; segment 2, anterior margin with a fringe of strong spine-like setae; posterior margin with a seta proximally and another at the junction with segment 3; segment 5, posterior lobe 36% of anterior margin length, without an anterodistal setal cluster; segment 6, palm straight; dactyl cusped along most of the posterior margin, without facial striations. Gnathopod 2: coxal margins, anterior 29% and posterior 52% of ventral length; ventral margin straight; gill small; segment 2, anterolateral flange with 12 short, simple setae (setae less than 1/4 segment width); segment 5, posterior lobe with a minute distal seta; segment 6, anterior margin with short setae proximally (setae about 1/4 segment 2 width), hinge tooth triangular and shallowly bifid, palmar setae more abundant at the hinge tooth area, thumb 26% of segment 6 length, distally squared, posterior margin evenly concave, defining setae well separated, not accompanied by spines; dactyl, inner margin strongly expanded at the location of the hinge tooth. Peraeopod 3: coxa, greatest depth posterior

of centre; segment 2, anterior margin fairly straight; segment 4, anterior marginal setae single and well separated, length not more than $1/4$ segment width, segment width 94% of length; segment 5 fully overlapped by segment 4; segment 6, width 80% of length. Peraeopods 5-7: segment 6, anterior margin proximally expanded, spines strong, concentrated in the area of expansion; dactyl without facial striations. Pleopods: with 2 coupling hooks. Uropod 1: peduncle, posteroventral spinous process underlying 52% of the inner ramus, inner and outer ramal with 4 and 6 mid-dorsal spines respectively, not terminating in a fringe of cusps ventral to the apical spine group. Uropod 2: peduncle, posteroventral spinous process underlying 14% of the inner ramus. Uropod 3: outer ramus with 2 sequential, closely approximated cusps proximal to the basally immersed, dorsally recurved spine, minute serrations in the area of the cusps, and a single seta originating at the insertion of the recurved spine; inner ramus with only the single apical spine. Telson: setose only at the lateral cusps.

CONDITION: Without right antennae 1 and 2. Other right appendages, telson, and mouthparts slide mounted. Left appendages with the carcass.

ADULT FEMALE. Unknown.

VARIATION: Only the single specimen is known.

TYPE MATERIAL: Holotype, male (AM), type no. P34951, New Zealand: The

Snares: Punui Bay ($48^{\circ}07'S$, $166^{\circ}38'E$), 21 January 1977, among red algae, 0 to -2 m, G. D. Fenwick, collector.

REMARKS: J. fenwicki is allied to J. alonsoae, J. justi, and J. hartmannae in possessing a fringe of short, spine-like setae along the anterior margin of the second segment of gnathopod 1. The expanded sixth segment of peraeopods 5-7 with accompanying strong spines is distinctive (Fig. 15E). Only in J. ingens does this also occur (Fig. 15C), but here the expansion is localized distally and quite unlike that of J. fenwicki. The two are likely to be convergent adaptations. The male's gnathopod 2 thumb is distinctive (Fig. 45). The large dactyl expansion is similar to that of J. ingens. Segment 6 of peraeopods 3 and 4 is notably short and stout.

ETYMOLOGY: Named for Dr. G. D. Fenwick in appreciation of his generous assistance in this and my previous work on the Amphipoda.

2. JASSA JUSTI n.sp.

Figs. 16, 42, 44, 45

ADULT MALE. Holotype: Length 8.5 mm. Antenna 2: overlapped by antenna 1 to about 2/3 along peduncular segment 5; segment 5, posterior margin bearing long filter setae, these as long as in the juvenile; flagellum of 4 segments, segment 1 82% of full flagellum length. Mandible: palp segments 2 and 3 without a dorsal fringe of setae; raker spines 3 right, 4 left. Maxilla 1: palp without setae at the base of segment 1, segment 2 with 1 row of facial setae. Gnathopod 1: coxal margins, anterior 70% of dorsal length, ventral margin straight; segment 2, anterior margin with a fringe of short, spine-like setae, posterior margin with a single cluster at the junction of segment 5; segment 5, posterior lobe 45% of anterior margin length, without an anterodistal setal cluster; segment 6, palm convex; dactyl cusped along most of the posterior margin. Gnathopod 2: coxal margins, anterior 32% and posterior 48% of ventral length, ventral margin straight; gill moderately large; segment 2, anterolateral flange with 16 short, spine-like setae (setal length less than 1/4 segment width); segment 5, posterior lobe with a minute distal seta; segment 6, anterior margin with short setae proximally (setal length about 1/4 the width of segment 2), hinge tooth triangular, anteriorly shallowly bifid, palmar setae concentrated in the hinge tooth area, thumb 20% of segment 6 length, distally rounded, posterior margin evenly concave to the defining setae, setae closely approximated, accompanied by 3 spines; dactyl, inner margin strongly expanded at the location of the hinge tooth. Peraeopod 3: coxa, greatest depth posterior of centre;

segment 2, anterior margin straight; segment 4, anterior marginal setal clusters well separated, with 1-2 setae in the middle clusters, setal length about 1/2 segment width, segment width 89% of length; segment 5 fully overlapped by segment 4; segment 6, width 73% of length. Peraeopods 5-7: segment 6 not expanded anteriorly; dactyl without facial serrations. Pleopods: with 2 coupling hooks. Uropod 1: peduncle, posteroventral spinous process underlying 54% of the inner ramus, inner and outer rami with 5 and 8 mid-dorsal spines respectively, terminating in a fringe of cusps ventral to the apical spine group. Uropod 2: peduncle, posteroventral spinous process underlying 5% of the inner ramus. Uropod 3: outer ramus with 2 oppositely arranged cusps proximal to the basally immersed, dorsally recurved spine, small serrations in the area of the cusps, and single seta originating at the insertion of the recurved spine; inner ramus with only the single apical spine. Telson: setose only at the lateral cusps.

CONDITION: Without right peraeopod 7.

ADULT FEMALE. Allotype: Length 6.9 mm. Antenna 2: segment 5 without plumose setae. Gnathopod 1: coxa, ventral margin straight. Gnathopod 2: coxal margins, anterior 45% and posterior 60% of ventral length; ventral margin shallowly convex; segment 6, hinge tooth pronounced, palmar setae not abundant, palmar angle rounded, not close to the defining spines; dactyl, inner margin broadly convex, tip fitting into a depression at the defining spines.

CONDITION: Ovigerous, with all appendages.

VARIATION: Body length at maturity: male to 8.5 mm, female 5.1-7.1 mm. Although only one thumbed male is known, the large size of the second gnathopod with a rather short, distally originating, spine bearing thumb, suggests that the male is a minor form (Fig. 45). The shape of the juvenile gnathopod 2 palm is distinctive (Fig. 44).

TYPE MATERIAL: Holotype, male (AM), type no. P34953, station no. MA-10, Macquarie Island: Garden Bay ($54^{\circ}29'S$, $158^{\circ}58'E$), 20 November 1977, J. K. Lowry and D. S. Horning, collectors, among mixed red and green algae on rocky bottom, -3 m. Allotype, female, type no. P37920, same location. Paratypes, 2 adult females, 7 juveniles, type no. P37921, same location.

OTHER MATERIAL (excluded from type series): 5 adult females and 60 juveniles from New Zealand (Kaikoura), Australia (Careel Bay, Pittwater) MacQuarie Island, South Georgia and South Chile (Isla Navarino) (AM, ZMHB, NMNS).

REMARKS: J. justi shares the gnathopod 1, segment 2 setal fringing with J. alonsoae, J. fenwicki, and J. hartmannae. Like J. fenwicki and J. gruneri, the pereopod 3 and 4 segment 6 is quite short and stout. Unique to J. justi is the arrangement of uropod 3 outer ramus cusps: opposite, rather than sequential.

CONFIRMED LITERATURE: Fenwick (1976), as Jassa falcata.

ETYMOLOGY: Named for Dr. Jean Just in recognition of his contribution to the systematics of amphipods and of his support for this study.

3. JASSA ALONSOAE n.sp.

Figs. 14, 16, 18, 42-45

ADULT MALE. Holotype: Length 11.1 mm. Antenna 2: overlapped by antenna 1 to midway along peduncular segment 5; segment 5 bearing simple setae only, these less than 1/2 the length of the juvenile's; flagellum 5 segments, the last minute, segment 1 59% of flagellum length. Mandible: palp segments 2 and 3 without a dorsal fringe of setae; raker spines 3 right, 4 left. Maxilla 1: palp without setae at the base of segment 1, segment 2 with 1 row of facial setae. Gnathopod 1: coxal margin, anterior 110% of dorsal length, ventral margin straight; segment 2, anterolateral flange with a row of short setae along its length, posterior margin with setae only at the distal angle; segment 5, posterior lobe 58% of anterior margin length, anterodistal setal cluster short, 32% of the anterior margin length; segment 6, palm convex; dactyl without facial striations, cusped along most of the posterior margin. Gnathopod 2: coxal margins, anterior 50% and posterior 46% of ventral length; ventral margin slightly sinuous; gill small; segment 2, anterolateral flange with 21 moderately long, simple setae (setae nearly 1/2 segment width); segment 5, posterior lobe with a short distal seta; segment 6, anterior margin with short setae proximally (setae shorter than those on segment 2), hinge tooth triangular, anteriorly bifid, palmar setae sparse but spread throughout, thumb 20% of segment 6 length, distally squared, posterior margin expanded at the thumb but not at the defining setae, defining setae not separated, not accompanied by spines; dactyl, inner margin broadly expanded at the location of the hinge tooth.

Fig. 18. Jassa alonsoae. Adult male, major form. From Sexton and Reid (1951), plates 27-29. x58.

Peraeopod 3: coxa, greatest depth posterior of centre; segment 2, anterior margin shallowly concave; segment 4, some central setae nearly as long as segment width, segment width 116% of length; segment 5 73% overlapped by segment 4; segment 6, width 58% of length. Peraeopods 5-7: segment 6 not expanded anteriorly; dactyl without facial striations. Pleopods: with 2 coupling hooks. Uropod 1: peduncle, posteroventral spinous process underlying 39% of the inner ramus, inner and outer rami with 8 marginal spines each, terminating in a fringe of cusps ventral to the apical spine group. Uropod 2: peduncle, posteroventral spinous process underlying 11% of the inner ramus. Uropod 3: outer ramus with 3 sequential cusps proximal to the basally immersed, dorsally recurved spine, smaller cusps or spines nearby, and a single seta originating at the insertion of the recurved spine; inner ramus with only the single apical spine. Telson: setose only at the lateral cusps.

CONDITION: With all appendages.

ADULT FEMALE. Allotype: Length 9.8 mm. Antenna 2: segment 5 without plumose setae. Gnathopod 1: coxa, ventral margin straight. Gnathopod 2: coxal margins, anterior 50% and posterior 86% of ventral length; ventral margin slightly sinuous; segment 6, hinge tooth not particularly pronounced, palmar setae moderately dense throughout but not so abundant as to obscure the shape of the palm, palmar angle shallow and fairly distal of the defining spines, thereby giving the palm a sinuous appearance; dactyl, inner margin shallowly expanded proximally, tip

fitting into a depression between the palmar angle and the defining spines.

CONDITION: With all appendages.

VARIATION: Body length at maturity: male 3.4-11.1 mm, female 7.1-10.1 mm. The number of segments on the second antennal flagellum varies with body length with a range of 5-7 (the last minute), measured in both males, females and juveniles. The larger value is found only in the largest animal, regardless of sexual maturity. There is considerable variation in setation within the species which seems to be size related. In large animals the first gnathopod's segment 2 flange has pronounced spine-like setae along its margin. On the second gnathopod flange the setae are abundant and long. The anterior margin of pereopods 3 and 4 are also well clothed in setae. The second antenna sports a dense pack of brush setae on the posterior margin of the flagellum. In small animals the setation is much less pronounced, both in abundance and length.

Small specimens of J. alonsoae resemble Jassa hartmannae in their setation pattern, but the two species differ in the shape of the second gnathopod. In females and non-thumbed males the palm is sinuous in J. alonsoae and concave in J. hartmannae. The posterior margin of the adult male's thumb differs in similar fashion: in J. alonsoae it is sinuous, while in J. hartmannae it is straight or shallowly concave (Figs. 43-45). Although the range of maturity of the two species overlaps, J. hartmannae

was found mature at 3.5 to 4.5 mm body length, while most specimens of J. alonsoae were not mature until 7 mm or greater.

In J. alonsoae the shape of the second gnathopod dactyl changes at maturity: in the female and juvenile male, the inner margin is straight or, if body size is large, shallowly expanded proximally (Figs. 16, 42, 44); in the minor form adult male the dactyl is curved and the expansion is more pronounced as a tooth extending into the palm (Fig. 43); in the major form the expansion peaks at the hinge tooth and the dactyl is more concave posteriorly (Fig. 45). The palmar defining spines are lost in the larger major form males. Occasionally the number of spines may differ from the usual 3. On the uropod 3 outer ramus the number of cusps may sometimes be reduced to 1, with the accessory cusps or spines being accentuated.

TYPE MATERIAL: Holotype, male (ZMUH), type no. K-33619 (ex-catalogue no. K-8017a), station no. 7804, South Georgia (54°30'58"S, 36°0'45"W), 16 January 1884, Deutsche Polar Comm., K. von den Steinen, collector. Allotype, female (ZMUH), type no. K-33635, same location. Paratypes, 31 males, 26 adult females, and 18 immature females (ZMUH), type nos. K-33627, K-33636, K-33637, and K-33616, same location.

OTHER MATERIAL (excluded from type series): 436 specimens from southern Argentina, Tierra del Fuego, Southern Chile, Falkland Islands, South Georgia, Tristan da Cunha, Kerguelen, Auckland Islands, Macquarie Island and the Snares (AM, NRS, NMNS, ZMHB, ZMUH, ZMUO, G. Alonso).

REMARKS: There is no other species that has the combination of setose second segment of the gnathopod 2, sinuous palm, and presence of a setal cluster at the anterodistal junction segments 5 and 6 on gnathopod 1. Possibly Stephensen's (1927) "Jassa pulchella" is J. alonsoae. Although the specimens referred to therein were not available, other specimens taken at the same location (Auckland Islands: Carnley Harbour) by Stephensen four days later were J. alonsoae.

CONFIRMED LITERATURE: Schellenberg (1931) and Alonso (1980) as J. falcata, Stephensen (1949) as J. pulchella, and Sexton and Reid (1951) as the Large Polar Form of J. falcata.

ETYMOLOGY: Named after Dr. Gloria Maria Alonso, who kindly lent me the specimens referred to in her publication.

4. JASSA HARTMANNAE n.sp.

Figs. 16, 42, 43, 45

ADULT MALE. Holotype: Length 4.5 mm. Antenna 2: overlapped by antenna 1 to about $3/4$ along the length of peduncular segment 5; segment 5, posterior margin bearing simple filter setae only, these about as long as those of the juvenile; flagellum 4 segments, the last minute, segment 1 36% of the flagellum length. Mandible: palp segments 2 and 3 without a dorsal fringe of setae; raker spines 3 right, 4 left. Maxilla 1: palp without setae at the base of segment 1, segment 2 with 1 row of facial setae. Gnathopod 1: coxal margins, anterior 100% of dorsal length; ventral margin slightly concave; segment 2, anterior margin fringed with short spine-like setae, posterior margin with a single setal cluster at the junction with segment 3; segment 5, posterior lobe 42% of anterior margin length, without an anterodistal setal cluster; segment 6, palm straight; dactyl cusped along most of the posterior margin, without facial striations. Gnathopod 2: coxal margins, anterior 32% and posterior 58% of ventral length; ventral margin sinuous; gill very small; segment 2, anterolateral flange with 11 short, simple setae (setae about $1/4$ segment width); segment 5, posterior lobe without a distal seta; segment 6, anterior margin with short setae proximally (setae about $1/4$ segment 2 width), hinge tooth triangular, shallowly bifid, palmar setae confined to the hinge tooth area, thumb 21% of segment 6 length, distally squared, posterior margin shallowly concave to the defining setae, defining setae closely approximated and accompanied by 3 spines; dactyl, inner margin expanded at the location of the hinge tooth. Peraeopod 3:

coxa, greatest depth posterior of centre; segment 2, anterior margin straight; segment 4, anterior margin with single, evenly spaced setae about 1/3 the segment width, segment width 90% of length; segment 5 90% overlapped by segment 4; segment 6, width 63% of length. Peraeopods 5-7: lacking (in paratype, segment 6 not expanded anteriorly; dactyl without facial striations). Pleopods: with 2 coupling hooks. Uropod 1: peduncle, posteroventral spinous process underlying 50% of the inner ramus, inner and outer rami with 4 and 5 marginal spines respectively, terminating in a fringe of cusps ventral to the apical spine group. Uropod 2: peduncle, posteroventral spinous process underlying 14% of the inner ramus. Uropod 3: outer ramus with 2 sequential, closely approximated cusps proximal to the basally immersed, dorsally recurved spine, smaller cusps in the area of the large cusps, and a single seta originating at the insertion of the recurved spine; inner ramus with only the single apical spine. Telson: setose only at the lateral cusps.

CONDITION: Without left and right peraeopods 5-7. Remaining right appendages, telson, and mouthparts slide mounted.

ADULT FEMALE. Allotype: Length 3.6 mm. Antenna 2: segment 5 without plumose setae. Gnathopod 1: coxa, ventral margin straight. Gnathopod 2: coxal margins, anterior 47% and posterior 94% of ventral length; ventral margin straight; segment 6, hinge tooth pronounced, palmar setae not abundant, palmar angle acute, distal, but close to the defining spines; dactyl, inner margin shallowly expanded at the position of the hinge

tooth, tip fitting into a depression between the palmar angle and the defining spines.

CONDITION: Ovigerous. Without left peraeopods 4-7 and right peraeopods 5-7. Right antenna 2, gnathopods 1 and 2, peraeopod 3, and uropods 1-3 slide mounted.

VARIATION: Body length at maturity: male 3.1-4.5 mm, female 3.6 mm. The minor form has a toothed dactyl (Fig. 43); the major does not (Fig. 45). All thumbed males have defining spines; however, these are not strongly pronounced as in J. ingens or J. morinot, so they may be lost in larger males.

TYPE MATERIAL: Holotype, male (AM), type no. P34950, station no. SA-3492, New Zealand: The Snares: Senecio Pool (48°07'S, 166°38'E), 6 January 1977, from Lessonia variegata holdfast, 1.5 m, G. D. Fenwick, collector. Paratypes, 2 adult males, type no. P37919, same location. Allotype, female (USNM), type no. USNM 235008, accession no. 149461, station no. E973 (J. L. Barnard station NZ-8), New Zealand: South Island: Dunedin: St. Clair (45°50'S, 170°20'E), formalin wash of algae, especially of pterocladians or streblocladians, heavy turf Celidium-Bostrychia, and several specimens of Pyura sp., J. L. Barnard, collector. Paratypes, 1 adult male, 2 ovigerous females, 9 juveniles, type no. USNM 235009, same location.

REMARKS: J. hartmannae is a very small bodied species. It falls in with the J. alonsoae, J. justi, J. fenwicki group in having a fringe of short setae along the anterior margin of the gnathopod 1, segment 2. The lack of a seta on the anterodistal junction of the gnathopod 1, segments 5 and 6, and the fringe of short setae on the gnathopod 2, segment 2 distinguish this from sympatric species.

CONFIRMED LITERATURE: Barnard (1972), as J. falcata.

ETYMOLOGY: Named in honour of Dr. G. Hartmann, who lent numerous specimens for this study.

5. JASSA GRUNERI n.sp.

Figs. 16, 42

JUVENILE MALE. Holotype: Length 2.1 mm. Antenna 2: overlapped by antenna 1 to the end of segment 5; segment 5, posterior margin bearing simple filter setae only; flagellum 5 segments, the last minute, segment 1 39% of full length. Mandible: palp segments 2 and 3 without a dorsal fringe of setae; raker spines 3 right, 4 left. Maxilla 1: palp without setae at the base of segment 1, segment 2 with 1 row of facial setae. Gnathopod 1: coxal margins, anterior 100% of dorsal length; ventral margin convex; segment 2, anterior margin with a single seta at the junction of segment 3, posterior margin with a single longer seta mid-distant; segment 5, posterior lobe 60% of anterior margin length, without an anterodistal setal cluster; segment 6, palm convex; dactyl cusped along most of the posterior margin, without facial striations. Gnathopod 2: coxal margins, anterior 80% and posterior 90% of ventral length; ventral margin convex; gill medium; segment 2, anterolateral flange with 2 simple filter setae about 1/4 segment width; segment 5, posterior lobe with a long distal seta; segment 6, anterior margin with short setae proximally (setae about 1/4 segment 2 width), hinge tooth triangular, not obviously bifid, setae sparse throughout, palm shallow, appearing sinuous; appearance of thumb unknown, palm defined by 3 spines; dactyl, inner margin straight. Peraeopod 3: coxa, greatest depth posterior of centre; segment 2, anterior margin broadly convex; segment 4, anterior margin with 1 seta centrally and a cluster of 2 distally, central seta about 1/3 segment width, segment width 125% of length; segment 5 fully

overlapped by segment 4; segment 6, width 80% of length. Peraeopods 5-7: segment 6 not expanded anteriorly; dactyl with 3 rows of facial striations. Pleopods: with 2 coupling hooks. Uropod 1: peduncle, posteroventral spinous process underlying 43% of the inner ramus, inner and outer rami with 2 and 0 marginal spines respectively, terminating in a fringe of cusps ventral to the apical spine group. Uropod 2: peduncle, posteroventral spinous process underlying 11% of the inner ramus. Uropod 3: outer ramus with 2 sequential, closely approximated cusps proximal to the basally immersed, dorsally recurved spine, small serrations in the area of the cusps, and a single seta originating at the insertion of the recurved spine; inner ramus with only the single apical spine. Telson: setose only at the lateral cusps.

CONDITION: Without right antenna 1, right and left peraeopods 6 and 7. Right appendages, left pleopods, uropods, telson and mouthparts slide mounted.

ADULT FEMALE. Allotype: Length 3.2 mm. Antenna 2: segment 5 without plumose setae. Gnathopod 1: coxa, ventral margin convex. Gnathopod 2: coxal margins, anterior 69% and posterior 88% of ventral length; ventral margin shallowly convex; segment 6, hinge tooth moderately pronounced, palmar setae moderately abundant, but not obscuring the palm's shape, palmar angle shallow, distal, but not abutting the 3 strong defining spines, thus giving a sinuous appearance; dactyl, inner margin straight, tip fitting into a depression between the palmar angle and the defining spines.

CONDITION: Ovigerous. With all appendages. Right appendages slide mounted.

VARIATION: Body length at maturity: female 3.2 mm. The adult male is unknown, so no evaluation of gnathopod 2 development can be made. Some paratypes bore more setae on the gnathopod 2, segment 2 flange, and more spines on the uropod 1 outer ramus. Antenna 2 segment number and gnathopod 1 and 2 palm shape remained the same.

TYPE MATERIAL: Holotype, male (NMNS), catalogue no. NMCC1987-1077, accession no. 1978-287, Tasmania: Hobart Harbour (42°50'S, 147°20'E), 8 November 1978, 3-5 m depth, scuba, algal washes, Graham Edgar, collector. Allotype, female (NMNS), catalogue no. NMCC1987-1078, same location. Paratypes, 4 ovigerous females, 6 juveniles, catalogue no. NMCC1987-1079, same location.

REMARKS: The juvenile male's and adult female's second gnathopod palm is very shallow, resembling the sinuous palms of J. alonsoae, J. thurstoni and J. ingens. Like J. fenwicki and J. justi, the sixth segment of pereopods 3 and 4 is quite stout. This is the only species of Jassa that has striated pereopod 5-7 dactyls.

ETYMOLOGY: Named in appreciation of the assistance given to this work by Dr. H. -E. Gruner of the University of Berlin.

6. JASSA STAUDEI n.sp.

Figs. 13-17, 19, 20, 42-45, 51.

ADULT MALE. Holotype: Length 6.0 mm. Antenna 2: overlapped by antenna 1 to midway along segment 5; segment 5, posterior margin bearing a mixture of plumose and simple setae, simple filter setae about the length of those of the juvenile; flagellum stout, tip damaged (paratype, male, 5.1 mm, 3 segments (the last minute), segment 1 76% of full length). Mandible: palp segments 2 and 3 without a dorsal fringe of setae; raker spines 2 right, 3 left. Maxilla 1: palp without setae at the base of segment 1, segment 2 with 1 row of facial setae. Gnathopod 1: coxal margins, anterior 78% of dorsal length; ventral margin concave; segment 2, anterior and posterior margins with a single seta at the distal angle; segment 5, posterior lobe 46% of anterior margin length, without a setal cluster at the anterodistal junction of segment 6; segment 6, palm convex; dactyl with 2 rows of facial striations, cusped along most of the posterior margin. Gnathopod 2: coxal margins, anterior 28% and posterior 56% of ventral length; ventral margin slightly concave; gill small; segment 2, anterolateral flange with 12 long, simple setae (setae as long as the segment width); segment 5, posterior lobe with a long distal seta; segment 6, anterior margin with long setae proximally (setae as long as on segment 2), hinge tooth triangular, anteriorly shallowly bifid, setae confined to the hinge tooth area, thumb 34% of segment 6 length, distally squared, posterior margin indented at the thumb setae and slightly expanded at the defining setae, defining setae not separated, not accompanied by spines; dactyl, inner margin broadly

Fig. 19. Jassa staudei. Holotype, adult male, major form, 6.0 mm; allotype, adult female, 5.5 mm; paratypes, adult male 1 minor form, 5.1 mm; adult male 2, minor form, 4.2 mm. Broken Islands, north side of Wouwer Island, Barkley Sound, Vancouver Island, British Columbia, 27 June 1976. Lateral views: whole body, maxilla 1; dorsal view: telson; all other views medial. Appendages are of the holotype unless indicated otherwise. Scale 0.1 mm.

expanded at the location of the hinge tooth. Peraeopod 3: coxa, greatest depth posterior of centre; segment 2, anterior margin slightly concave; segment 4, anterior margin, some central setae as long as segment width, segment width 79% of length; segment 5 fully overlapped by segment 4; segment 6, width 56% of length. Peraeopods 5-7: segment 6 not expanded anteriorly; dactyl without facial striations. Pleopods: with 2 coupling hooks. Uropod 1: peduncle, posteroventral spinous process underlying 37% of the inner ramus, inner and outer rami with 3 and 6 mid-dorsal spines respectively, rami terminating in a fringe of cusps ventral to the apical spine group. Uropod 2: peduncle, posteroventral spinous process underlying 5% of the inner ramus. Uropod 3: outer ramus with 2 sequential, closely approximated cusps proximal to the basally immersed, dorsally recurved spine (left outer ramus, distal cusp bifid), minute serrations in the area of the cusps, and a single seta originating at the insertion of the recurved spine; inner ramus with only the single apical spine. Telson: setose only at the lateral cusps.

CONDITION: Right appendages, both uropods 3, telson and mouthparts slide mounted; right antenna tip and maxilliped 1 damaged; carcass without left antennae 1 and 2, peraeopod 7 or uropod 2 rami.

ADULT FEMALE. Allotype: Length 5.5 mm. Antenna 2: segment 5 without plumose setae. Gnathopod 1: coxa, ventral margin straight. Gnathopod 2: coxal margins, anterior 31% and posterior 73% of ventral length; ventral margin slightly concave; segment 6, hinge tooth pronounced, palmar setae moderately dense throughout but not obscuring the palm's shape, palm

concave, palmar angle acute, distal, but close to the defining spines; dactyl, inner margin straight, tip fitting into a depression between the palmar angle and the defining spines.

CONDITION: Brooding young. Right appendages, telson and mouthparts slide mounted; carcass with left appendages.

VARIATION: Body length at maturity: male 3.5-11.4 mm, female 4.6-7.6 mm. The number of second antennal segments in adults may sometimes be less than 3 (the last minute). Plumose setae appear on the antenna 2 flagellum and distal part of segment 5 in large males and females. Concurrent with such development is reduction in number and length of simple setae on segments 4 and 5 of the male; those on the female's second antennae remain long. Minor form thumbed males have a pronounced tooth on the dactyl (Fig. 43) which fits into the palmar incision; in major form males the dactyl expansion is broader and more proximal to the hinge (Fig. 45), thus imparting a different shape to the palm. The palmar spines are present in smaller thumbed males (both minor and major), but disappear in males of both forms. Unlike the female, the shape of the juvenile male's palm changes with size, so that in large subadults an indication of a thumb is visible (Fig. 44). Occasionally specimens may be found with 2 or 4 palmar defining spines on the segment 6 of gnathopods 1 or 2. The uropod 3 cusping may also vary (Fig. 19, 20), although 2 is the usual number.

TYPE MATERIAL: Holotype, male (NMNS), catalogue no. NMCC1987-1074,

Fig. 20. Jassa staudei. Uropod 3, tip of outer ramus. x1200.

accession no. 1976-157, station no. B7, Canada: British Columbia: Vancouver Island: Barkley Sound: Broken Group: north side of Wouwer Island ($48^{\circ}51.06'N$, $125^{\circ}21.08'W$), 27 June 1976, dip net scrape of Phyllospadix and various unspecified algae on bedrock at low water level, temperature about $12^{\circ}C$, salinity above 32 ppt, E. L. Bousfield, collector. Allotype, female (NMNS), catalogue no. NMCC1987-1075; same location. Paratypes, 5 adult males, 179 adult females, 207 immatures (NMNS), catalogue no. NMCC1987-1076, same location.

OTHER MATERIAL: Several thousand specimens from Alaska (northernmost record: Seward), British Columbia (mainland, Queen Charlotte Islands, Vancouver Island outer coast), Washington (San Juan Island, Cape Flattery), Oregon and California (southernmost record: Morro Bay) (BCPM, LACM, NMNS, UAM, USNM, P. Shaw, P. Slattery).

REMARKS: Of all species of Jassa, J. staudel has the longest setae along the anteroproximal margin of the second gnathopod segment 6. This feature is distinctive in both sexes and at all ages. Jassa staudel can also be distinguished from co-occurring congeners by its lack of a setal group on the anterodistal margin of the gnathopod 1, segment 5 (also a feature that does not vary with sex or age). It can be most easily mistaken for J. marmorata, whose segment 5 seta(e) are very short and slightly lateral, and thus easily overlooked. The stout, plumose antennae 2, the 3 segmented flagellum (appearing 2 segmented under low magnification), the long, dense setae on the gnathopod 2, segment 2 and the well developed peduncular spinous process on uropod 1 are additional

characters which, in combination, distinguish J. staudel from sympatric congeners.

CONFIRMED LITERATURE: Chess (1979), as J. falcata.

ETYMOLOGY: In honour of Dr. Craig P. Staude, University of Washington, Friday Harbor Marine Lab, who has long promoted the study of amphipods and considerably expanded our knowledge of Pacific North American species.

7. JASSA MARMORATA Holmes, 1903

Figs. 16, 21, 22, 42-45

Jassa marmorata Holmes, 1903, 289: 1904, 511-513: Shoemaker, 1930, 128: Lincoln, 1979, 552, fig. 265 a-j: Arresti et al., 1986, 117, fig. 15

Jassa falcata: Chevreux and Fage, 1925, 345-346, figs. 352-353: Shoemaker, 1942, 2-3: Sexton and Reid, 1951, 29-91 (Broad Form only): Bousfield, 1973, 190-191, plate 58.2

ADULT MALE. Neotype (here designated): Length 6.7 mm. Antenna 2: overlapped by antenna 1 to about 3/4 along segment 5; segment 5, posterior margin bearing long simple setae proximally and short brush setae distally; simple filter setae as long as those of the juvenile; flagellum 3 segments, the last minute, segment 1 81% of full length. Mandible: palp segments 2 and 3 without a dorsal fringe of setae; raker spines 2 right, 3 left. Maxilla 1: palp without setae at the base of segment 1, segment 2 with 1 row of facial setae. Gnathopod 1: coxal margins, anterior 120% of dorsal length; ventral margin straight; segment 2, anterior and posterior margins with a few short setae at the distal angle; segment 5, posterior lobe 41% of anterior margin length, anterodistal setal cluster at the junction of segment 6 short and slightly lateral, 5% of the anterior margin length; segment 6, palm convex; dactyl cusped along most of the inner margin, without facial striations. Gnathopod 2: coxal margins, anterior 25% and posterior 59% of ventral length; ventral margin straight; gill small; segment 2, anterolateral flange with 14 long, simple filter setae (setae more than

Fig. 21. Jassa marmorata. Adult male, major form, and adult female. Whole body and female gnathopod 2 from Bousfield (1973); all other appendages from Lincoln (1979).

3

Microl

1/2 the segment width); segment 5, posterior lobe with a minute distal seta; segment 6, anterior margin with short setae proximally (setae about 1/3 segment 2 width), hinge tooth triangular, anteriorly shallowly bifid, setae confined to the hinge tooth area, thumb 37% of segment 6 length, distally squared, posterior margin slightly indented at the thumb setae and slightly expanded at the location of the defining setae, defining setae well separated, not accompanied by spines; dactyl, inner margin broadly expanded at the location of the hinge tooth. Peraeopod 3: coxa, greatest depth posterior of centre; segment 2, anterior margin slightly concave; segment 4, anterior marginal setae clustered proximally but single distally and covering the full length, as long or longer than the segment width, segment as wide as long; segment 5 fully overlapped by segment 4; segment 6, width 50% of length. Peraeopods 5-7: segment 6 not expanded anteriorly; dactyl without facial serrations. Pleopods: with 2 coupling hooks. Uropod 1: peduncle, posteroventral spinous process underlying 36% of the inner ramus, inner and outer rami with 5 and 6 mid-dorsal spines respectively, terminating in a fringe of cusps ventral to the apical spine group. Uropod 2: peduncle, posteroventral spinous process underlying 5% of the inner ramus. Uropod 3: outer ramus with 2 sequential, closely approximated cusps proximal to the basally immersed, dorsally recurved spine, minute serrations in the area of the cusps, and a single seta originating at the insertion of the recurved spine; inner ramus with only the single apical spine. Telson: apex rounded, setose only at the lateral cusps.

CONDITION: With all appendages but the right peraeopod 3.

ADULT FEMALE. (Same location as for neotype). Length 5.3 mm. Antenna 2: segment 5 with brush and simple setae as in the male. Gnathopod 1: coxa, ventral margin straight. Gnathopod 2: coxal margins, anterior 46% and posterior 92% of ventral length; ventral margin straight; segment 6, hinge tooth pronounced, palmar setae moderately dense throughout but not so dense as to obscure the palm's shape, palmar angle acute, distal, but close to the defining spines; dactyl, inner margin straight, tip fitting into a depression between the palmar angle and defining spines.

CONDITION: Brood plates setose, but not ovigerous. With all appendages.

VARIATION: Body size at maturity: male 4.0-7.1 mm, female 3.2-6.2 mm. The antenna 2 flagellum may occasionally be 4 segmented (the last segment minute). In larger individuals the brush setae on antenna 2 and the setae on pereopods 3 and 4, segments 2 and 4 are more abundant. In large juvenile males that are close to adult stage a small indentation appears where the thumb will be excised (Fig. 44). Defining spines are still present in small thumbed males but absent in larger animals. Occasionally the number of palmar spines may be 2 or 4.

TYPE MATERIAL: Neotype, male (NMNS), catalogue no. NMCC1987-1067, accession no. 1984-112, U.S.A.: New York: Brooklyn: Jamaica Bay Wildlife Refuge: Barren Islands Marina (40°35'N, 73°55'W), early July 1984, amongst hydroids and Ulva just below water level on a floating dock, B. Borowsky, collector.

OTHER MATERIAL (excluded from type series): several thousand specimens from the U.K., Denmark, Sweden, West Germany (Helgoland), France, Spain, Italy, China, U.S.S.R. (Peter the Great Bay), Australia (Port Jackson, Tasmania), New Zealand (South Island), Algeria, Senegal, Gambia, Namibia, South Africa, Brazil, Chile, Cuba, Bahama Islands, U.S.A. (California, Oregon, Washington, Alaska, Texas, Florida, Georgia, South Carolina, North Carolina, Virginia, Maryland, Delaware, New Jersey, New York, Connecticut, Rhode Island, Massachusetts, New Hampshire, Maine), Canada (New Brunswick, Nova Scotia, Prince Edward Island, Newfoundland, British Columbia) (AM, BMNH, CAS, LACM, MHNP, NMNS, NRS, RSME, SAMC, TAMU, UCT, ZMUH, USNM, VIMS, ZMUC, K. Anger, G. Diviacco, E. Gonzalez, S. Ishimaru, G. Krapp-Schickel, M. Ledoyer, P. G. Moore, P. Shaw).

REMARKS: Jassa marmorata most closely resembles J. stauderi, but differs in having shorter setae on the anterior margin of the gnathopod 2, segment 6 and by possessing a short, slightly lateral seta on the anterodistal junction of segments 5 and 6 on the first gnathopod. The second antenna in both sexes is stout, the flagellum possessing 3 segments (although the last is minute); however, the long simple setae on segments 3-5 do not shorten in the male as they do in many species of Jassa (including J. stauderi) and the plumose setae that develop on segments 5 and flagellum are less feathery. Although J. marmorata does not approach as great a body size as does J. stauderi, the male's second gnathopod can be enormous (Fig. 7). Unlike J. stauderi, penultimate juveniles show a small indentation where the thumb will develop (Fig. 44), but minor form adult males never exhibit dactyl toothings (Fig. 43).

Fig. 22 shows the cusps and accessory setae on the telson. This arrangement is typical of all species of Jassa. The frilled tip of the larger setae arising proximal to each cusp suggests a sensory function different from that of the short plumose setae.

It is possible that Podocerus validus (Dana, 1852) (= Cratophium validum) and Podocerus australis Haswell, 1880 are synonymous with J. marmorata, making the former the senior synonym. Specimens from the British Museum were indeed J. marmorata; however, no types could be found. These specimens had been collected at a later time than the first described, and they had been identified by other than the original authors of P. validus and P. australis. Thus the connection between J. marmorata, P. validus, and P. australis is tenuous, and the authors' descriptions and illustrations of the types are of no help in assigning relationship. It is recommended, therefore, that P. validus and P. australis be considered as "nomina oblita".

CONFIRMED LITERATURE: Jassa marmorata has often been mistaken in the literature for J. falcata. Sexton and Reid's (1951) "Broad Form" is, in fact, J. marmorata. Confirmed reports from this area and elsewhere, as J. falcata, are Reid (1951), Daro (1970), Watling and Maurer (1970), Relini et al (1977), Cognetti et al (1979), Diviacco (1979a, 1979b, 1980, 1981, 1983), Diviacco and Relini (1981), Ledoyer and Meniouf (1983), and Borowsky (1983, 1985). Specimens provided by K. Anger as being representative of those used in the life history study of J. falcata by Nair and Anger (1979, 1980) were, in fact, a mixture of J. marmorata (mainly) and J. falcata. Indeed, the world-wide

Fig. 22. Jassa marmorata. Telson. A, cusps and associated setae. B, tip of long seta arising proximally to each cusp. x2000.

B **A**

distribution of J. marmorata would make suspect the identification of any native Jassa from heavily populated areas (see Biogeography and Ecology sections).

8. JASSA OCLAIRI n.sp.

Figs. 13, 15, 16, 23, 42-45

ADULT MALE. Holotype: Length 7.7 mm. Antenna 2: overlapped by antenna 1 only to the proximal 1/4 of segment 4; segment 5, posterior margin nearly asetose, without plumose setae, simple filter setae minute; flagellum 4 segments, the last minute, segment 1 70% of full length. Mandible: palp segment 2 with a dorsal fringe of setae; raker spines 2 right, 3 left. Maxilla 1: palp without setae at the base of segment 1, segment 2 with 1 row of facial setae. Gnathopod 1: coxal margins, anterior 85% of dorsal length; ventral margin straight; segment 2, anterior and posterior margins with a few short setae at the distal angle; segment 5, posterior lobe 38% of anterior margin length, anterodistal setal cluster long, 43% of the anterior margin length; segment 6, palm convex; dactyl cusped along most of the posterior margin, without facial striations. Gnathopod 2: coxal margins, anterior 32% and posterior 68% of ventral length; ventral margin convex; gill small; segment 2, anterolateral flange with 35 long, plumose setae (setae 3/4 segment width); segment 5, posterior lobe with a single minute, distal seta; segment 6, anterior margin with abundant plumose setae proximally (setae about 40% the width of segment 2); hinge tooth triangular, anteriorly shallowly bifid, setae relatively confined to the hinge tooth area; thumb 14% of segment 6 length, distally squared, posterior margin evenly concave to the defining setae and slightly expanded at the location of the defining setae, setae quite closely approximated, accompanied by 3 spines; dactyl, inner margin centrally toothed.

Fig. 23. Jassa oclairi. Holotype, adult male, minor form, 7.7 mm; allotype, adult female, 7.6 mm; paratypes, juvenile male 1, 7.1 mm; juvenile male 2, 14.1 mm. Square Bay, Amchitka Island, Alaska, 21 September 1969. Adult male, major form, 11.6 mm. Snipe Bay, Alaska, 8 July 1975. Lateral views: whole body, maxilla; dorsal view: telson and uropod 1; other views medial. Scale 0.1 mm. Appendages are of the holotype unless indicated otherwise.

Peraeopod 3: coxa, greatest depth posterior of centre; segment 2, anterior margin concave; segment 4, anterior marginal setae clustered throughout, as long or longer than the segment width, segment width 60% of length; segment 5 a little less than fully overlapped by segment 4; segment 6, width 64% of length. Peraeopods 5-7: segment 6 not expanded anteriorly; dactyl without facial striations. Pleopods: with 2 coupling hooks. Uropod 1: peduncle, posteroventral spinous process underlying 38% of the inner ramus, inner and outer rami with 9 and 16 mid-dorsal spines respectively, terminating in a fringe of cusps ventral to the apical spine group. Uropod 2: peduncle, posteroventral spinous process underlying 6% of the inner ramus. Uropod 3: outer ramus with 2 sequential, closely approximated cusps proximal to the basally immersed, dorsally recurved spine, minute serrations in the area of the cusps, and a single seta originating at the insertion of the recurved spine; inner ramus with only the single apical spine. Telson: setose only at the lateral cusps.

CONDITION: Without peraeopod 5; right appendages, left peraeopod 5, telson and mouthparts slide mounted; remaining left appendages with the carcass.

ADULT FEMALE. Allotype: Length 7.6 mm. Antenna 2: segment 5 and flagellum bearing abundant plumose setae. Gnathopod 1: coxa, ventral margin straight. Gnathopod 2: coxal margins, anterior 39% and posterior 81% of ventral length; ventral margin slightly sinuous; segment 6, hinge tooth pronounced, palmar setae moderately dense throughout but not so

dense as to obscure palm's shape, palmar angle acute, and distal, but close to the defining spines; dactyl, inner margin sinuous, tip fitting into a depression between the palmar angle and defining spines.

CONDITION: Ovigerous. Right appendages, telson and mouthparts slide mounted; left appendages with the carcass.

VARIATION: Body length at maturity: male 6.9-11.8 mm, female 6.1-9.8 mm. The antenna 2 develops in a unique fashion: in the juvenile male and adult female it is stout and densely clothed in plumose setae; however, in thumbed males these setae are lost and the peduncle and flagellum elongate markedly. Also notable in the male is a lengthening and increasing concavity of the posterior margin of segment 4 on pereopods 5-7. Penultimate males do not exhibit an indication of a thumb. Minor form males have a toothed dactyl and defining spines; in the major form the dactyl is broadly expanded and the defining spines are lacking.

TYPE MATERIAL: Holotype, male (NMNS), catalogue no. NMCC1987-1071, accession no. 1976-30, station no. CT02069, C-16, U.S.A.: Alaska: Anchitka Island: Bering Sea: Square Bay ($51^{\circ}27.2'N$, $179^{\circ}11.5'E$), 21 September 1969, amongst algae (Laminaria longipes holdfasts, Clathromorphum sp.) and sponges (Halicondria panicea and Scypha compressa) on exposed coast rocky shore, C. E. O'Clair, collector. Allotype, female (NMNS), catalogue no. NMCC1987-1072, same location. Paratypes, 2 adult males, 6 adult females, 143 juveniles (NMNS), catalogue no. NMCC1987-1073.

OTHER MATERIAL (excluded from type series): 7 adult males, 39 adult females and approximately 150 juveniles from Alaska (Aleutian Islands and Gulf of Alaska) and British Columbia (Georgia Strait: Cortes Island) (UAM, NMNS).

REMARKS: Jassa oclairi is distinctive in bearing abundant plumose setae along the anterior margin of the antennae and gnathopod 2 and the posterior margin of pereopods 5-7 (large juvenile male and adult male only). The combination of stout antennae 2, dorsally setose mandibular palp segment 2, long seta on the anterodistal margin of gnathopod 1, segment 5, long and abundant plumose setae on the appendages, well developed postero-ventral peduncular process on uropod 1, relatively large body size, and northern distribution, will serve to distinguish J. oclairi of any age from other North Pacific species of Jassa. A list of species found along with J. oclairi at the type location is available from C. E. O'Clair.

CONFIRMED LITERATURE: O'Clair (1977) as Jassa sp.

ETYMOLOGY: Named for Mr. C. E. O'Clair, who collected this species and generously provided habitat data and additional specimens.

9. JASSA MORINOI n.sp.

Figs. 13, 15, 16, 42-45

ADULT MALE. Holotype: Length 5.6 mm. Antenna 2: overlapped by antenna 1 only to the end of segment 5; segment 5, posterior margin bearing long filter setae only, these more than the length of the juvenile's; flagellum 5 segments, the last minute, segment 1 48% of full length. Mandible: palp segments 2 and 3 without a dorsal fringe of setae; raker spines 2 right, 3 left. Maxilla 1: palp without setae at the base of segment 1, segment 2 with 1 row of facial setae. Gnathopod 1: coxal margins, anterior 100% of dorsal length; ventral margin straight; segment 2, anterior and posterior margins with only a few short setae at the distal angle; segment 5, posterior lobe 53% of anterior margin length, anterodistal setal cluster long, 73% of the anterior margin; segment 6, palm shallowly concave; dactyl cusped along most of the posterior margin, without facial striations. Gnathopod 2: coxal margins, anterior 75% and posterior 156% of ventral length; ventral margin straight; gill small; segment 2, anterolateral flange with 9 short, simple setae (setae about 1/4 segment width); segment 5, posterior lobe without a distal seta; segment 6, anterior margin with a few short setae proximally (less than 1/4 segment 2 width), hinge tooth triangular, anteriorly shallowly bifid, setae concentrated at the hinge tooth area, thumb 21% of segment 6 length, distally acute, posterior margin sinuous, curving in at the thumb and defining setae, defining setae quite closely approximated, accompanied by 3 spines, both located on the underside of a pronounced shelf; dactyl, inner margin shallowly expanded at the location of the

hinge tooth. Peraeopod 3: coxa, greatest depth posterior of centre; segment 2, anterior margin fairly straight; segment 4, anterior marginal setae about 1/3 the segment width, segment width 110% of length; segment 5 fully overlapped by segment 4; segment 6, width 56% of length. Peraeopods 5-7: segment 6 not expanded anteriorly; dactyl without facial serrations. Pleopods: with 2 coupling hooks. Uropod 1: peduncle, posteroventral spinous process underlying 32% of the inner ramus, inner and outer rami with 4 and 5 mid-dorsal spines respectively, terminating in a fringe of cusps ventral to the apical spine group. Uropod 2: peduncle, posteroventral spinous process underlying 6% of the inner ramus. Uropod 3: outer ramus with 2 sequential, closely approximated cusps proximal to the basally immersed, dorsally recurved spine, minute serrations in the area of the cusps, and a single seta originating at the insertion of the recurved spine; inner ramus with only the single apical spine. Telson: setose at both the apex and at the lateral cusps.

CONDITION: With all appendages. Right appendages, telson and mouthparts slide mounted. Left appendages with the carcass.

ADULT FEMALE. Allotype: Length 5.8 mm. Antenna 2: segment 5 without plumose setae. Gnathopod 1: coxa, ventral margin straight. Gnathopod 2: coxal margins, anterior 40% and posterior 80% of ventral length; ventral margin shallowly convex; segment 6, hinge tooth pronounced, palmar setae moderately dense throughout but not so dense as to obscure the palm's shape, palmar angle acute, distal, but fairly close to the defining

spines; dactyl, inner margin expanded at the hinge tooth, tip fitting into a depression between the palmar angle and defining spines.

CONDITION: Ovigerous. With all appendages. Right appendages, telson and mouthparts slide mounted; left appendages with the carcass.

VARIATION: Body length at maturity: male 2.0-5.9mm, female 2.1-5.0mm. The antenna 2 flagellum segment number may vary between 3 and 5 (the last microscopic). Larger males have a slightly concave or straight gnathopod 1 palm; in juveniles and females the palm is convex.

TYPE MATERIAL: Holotype, male (H. Morino), Japan: Wakayama Prefecture: Tanabe Bay: Bansho-no-hana Point (33°42'N, 135°20'E), 17 March 1971, on Sargassum microcanthum at low intertidal level, H. Morino, collector. Allotype, female (H. Morino), same location. Paratypes 7 adult males, 3 adult females, 1 juvenile, same location.

OTHER MATERIAL (excluded from type series): approximately 850 specimens from southern France, northern Yugoslavia, Japan, Senegal, South Africa, British Columbia (west Vancouver Island), California, Oregon and Washington (LACM, MHNP, NMNS, SAMC, UCT, ZMUH, USNM, S.-I. Ishimaru, G. Krapp-Schickel, and M. Ledoyer).

REMARKS: Jassa morinoi closely resembles J. slatteryi and J. carltoni in having rather short, sparse setae on the anterior margin of the gnathopod 2, segments 2 and 6, and a long, slightly medial seta or setal cluster at

the junction of segments 5 and 6 on gnathopod 1. Unique to J. morinoi, however, is the development of setae at the dorsal tip of the telson. The gnathopod 2 morphology of each species also differs at maturity in either sex (Figs. 16, 43 and 45). In J. morinoi the palmar defining spines are strong and are produced from a ledge in very large males. Most other species of Jassa lose their defining spines when large. The spine pronunciation is evident even in the juvenile (compare J. morinoi and J. slatteryi juveniles, Figs. 42 and 44). Both J. morinoi and J. slatteryi have stouter antennae 2 than J. carltoni, but J. morinoi never develops plumose setae while J. slatteryi does.

CONFIRMED LITERATURE: Barnard (1969), as J. falcata thick form.

ETYMOLOGY: Named for Dr. H. Morino, who contributed to the development of amphipod taxonomy in Japan, and assisted in locating specimens for this study.

10. JASSA SLATTERYI n.sp.

Figs. 13-17, 24, 25, 42-45

ADULT MALE. Holotype: Length 5.1 mm. Antenna 2: overlapped by antenna 1 only to about midway along segment 5; segment 5, posterior margin bearing short, finely plumose brush setae, long filter setae lacking; flagellum 4 segments, segment 1 66% of full length. Mandible: palp segments 2 and 3 without a dorsal fringe of setae; raker spines 2 right, 3 left. Maxilla 1: palp without setae at the base of segment 1, segment 2 with 1 row of facial setae. Gnathopod 1: coxal margins, anterior 138% of dorsal length; ventral margin straight; segment 2, anterior and posterior margins with a single seta at the distal angle; segment 5, posterior lobe 40% of anterior margin length, anterodistal setal cluster long, 73% of the anterior margin length; segment 6, palm shallowly concave; dactyl cusped along most of the posterior margin, without facial striations. Gnathopod 2: coxal margins, anterior 41% and posterior 74% of ventral length; ventral margin sinuous; gill moderately large; segment 2, anterolateral flange with 17 short, simple filter setae (setae about 1/4 segment width); segment 5, posterior lobe without a distal seta; segment 6, anterior margin with a few short setae proximally (setae less than 1/4 segment 2 width); palm, hinge tooth triangular, anteriorly shallowly bifid, setae concentrated at the hinge tooth area; thumb 23% of segment 6 length, distally acute, posterior margin concave to the thumb setae and then fairly straight thereafter, defining setae well separated, not accompanied by spines; dactyl, inner margin shallowly expanded at the location of the hinge tooth. Peraeopod 3: coxa, greatest depth posterior

Fig. 24. Jassa slatteryi. Holotype, adult male, major form, 5.1 mm; allotype, adult female, 4.1 mm. Moss Landing Harbor, California, 4 July 1986. Intersex 1, 4.6 mm and 5.6 mm, Tanabe Bay, Wakayama Prefecture, Japan, 17 March 1971. Lateral views: whole body, intersex 4.6 mm left gnathopod 2, intersex 5.2 mm right gnathopod 2, and maxilla 1; dorsal view: telson; all other views medial. Scale 0.1 mm unless indicated otherwise. Appendages are of the holotype unless indicated otherwise.

Fig. 25. Jassa slatteryi. Variation in morphology of the antenna 2 and gnathopod 2 with body size. Paratype, juvenile male 1, 2.7 mm; paratype juvenile male 2, 4.5 mm; paratype adult male 3, minor form, 3.5 mm; holotype, adult male 4, major form, 5.1 mm. Moss Landing Harbor, California, 4 July 1986. Medial view: antenna 2; lateral view: gnathopod 2. Scale 0.1 mm.

of centre; segment 2, anterior margin relatively straight; segment 4, anterior marginal setae nearly as long as segment width, segment width 85% of length; segment 5 fully overlapped by segment 4; segment 6, width 45% of length. Peraeopods 5-7: segment 6 not expanded anteriorly; dactyl without facial striations. Pleopods: with 2 coupling hooks. Uropod 1: peduncle, posteroventral spinous process underlying 27% of the inner ramus, inner and outer rami with 4 and 5 mid-dorsal spines respectively, terminating in a fringe of cusps ventral to the apical spine group. Uropod 2: peduncle, posteroventral spinous process underlying 5% of the inner ramus. Uropod 3: outer ramus with 2 sequential, closely approximated cusps proximal to the basally immersed, dorsally recurved spine, serrations in the area of the cusps, and a single seta originating at the insertion of the recurved spine; inner ramus with only the single apical spine. Telson: setose only at the lateral cusps.

CONDITION: In the process of molting. Without the left peraeopod 7. Right appendages, telson and mouthparts slide mounted. Left appendages with the carcass.

ADULT FEMALE. Allotype: Length 4.1 mm. Antenna 2: segment 5, posterior margin with long filter setae, without plumose setae. Gnathopod 1: coxa, ventral margin straight. Gnathopod 2: coxal margins, anterior 52% and posterior 86% of ventral length; ventral margin straight; segment 6, hinge tooth pronounced, palmar setae moderately dense throughout but not so dense as to obscure the palm's shape, palmar angle acute and distal, but fairly close to the defining spines; dactyl, inner margin shallowly

expanded at the hinge tooth, tip fitting into a depression between the palmar angle and the defining spines.

CONDITION: Ovigerous. With all appendages. Right antenna 2, gnathopods 1 and 2 slide mounted.

VARIATION: Large males and females possess plumose setae on the antenna 2, segment 5 and flagellum, but smaller animals, whether adult or not, lack them. In concert with the development of plumose setae in the male is enlargement of the peduncle (especially segment 4) and shortening of the simple filter setae. No such change occurs in the female. The plumose setae are more brush-like as in J. marmorata than feathery as in J. stauderi. They readily trap detritus and so may seem more plumose than they actually are. The gnathopod 1 palm becomes less convex with age in both sexes. Gnathopod 2, segment 6 development in the male is illustrated in Figs. 47 and 48. Changes in dactyl shape are evident as well. Intersexes have been found in this species, but only in California, at Eureka, Morro Bay, and Santa Ynez.

TYPE MATERIAL: Holotype, male (NMNS), catalogue no. NMCC1987-1068, accession no. IZ1986-057, station no. C9, U.S.A.: California: Monterey County: Moss Landing Harbor ($36^{\circ}48'N$, $121^{\circ}47'W$), 4 July 1986, amongst filamentous red algae and hydroids just below water level on a floating dock, K. E. Conlan, collector. Allotype, female, catalogue no. NMCC1987-1069, same location. Paratypes, 11 adult males, 12 adult females, 18 juveniles and 3 intersexes, catalogue no. NMCC1987-1070.

OTHER MATERIAL (excluded from type series): approximately 1000 specimens from northern France, South Korea, Japan, Australia, (Tasmania, Sydney and Hobart), New Zealand (South Island), South Africa, Brazil, Chile, Mexico (Baja California), Alaska (Gulf), British Columbia (lower mainland and Vancouver Island), Oregon and California (AM, BMNH, LACM, MHNP, NMNS, NRS, SAMC, UAM, USNM, ZMUC, E. Gonzalez, J.-S. Hong, H. Morino, and P. Slattery).

REMARKS: Jassa slatteryi, J. morinoi, and J. carltoni are very similar and small juveniles are indistinguishable. At later stages the three species can be distinguished by their antenna 2 and gnathopod 2 morphology (see remarks on J. morinoi). Although collection localities are very close, there is no record of any of the three species co-occurring on the same substrate.

CONFIRMED LITERATURE: Barnard and Reish (1959), Reid (1951) and Hong (1983), as J. falcata. Conlan (1988) as J. falcata California form. J. falcata thick form of station 38-D-3 (Barnard, 1969) is J. slatteryi; thick forms of other stations are J. morinoi.

ETYMOLOGY: Named in appreciation of the generous support to this and many other projects of the National Museum of Natural Sciences given by Peter N. Slattery through his ecological and taxonomic research in California and Northern Alaska.

11. JASSA CARLTONI n.sp.

Figs. 13, 16, 42, 44, 45

ADULT MALE. Holotype: Length 2.9 mm. Antenna 2: overlapped by antenna 1 only to the end of segment 5; segment 5 bearing long, simple filter setae only, these sparse and about 1/2 the length of the juvenile's; flagellum 5 segments, the last minute, segment 1 45% of full length. Mandible: palp segments 2 and 3 without a dorsal fringe of setae; raker spines 2 right, 3 left. Maxilla 1: palp without setae at the base of segment 1, segment 2 with 1 row of facial setae. Gnathopod 1: coxal margins, anterior 91% of dorsal length, ventral margin straight; segment 2, anterior and posterior margins with a single seta at the distal angle; segment 5, posterior lobe 53% of anterior margin length, anterodistal setal cluster 73% of the anterior margin; segment 6, palm convex; dactyl cusped only on the posterior of the margin, without facial striations. Gnathopod 2: coxal margins, anterior 32% and posterior 53% of ventral length, ventral margin straight; gill small; segment 2, anterolateral flange with 8 short, simple filter setae (setae about 1/3 segment width); segment 5, posterior lobe without a distal seta; segment 6, anterior margin with short setae proximally (setae about 1/4 segment 2 width), hinge tooth triangular, anteriorly shallowly bifid, setae confined to the hinge tooth area, thumb 27% of segment 6 length, distally squared, posterior margin concave to the thumb setae, then straight to the defining setae; dactyl, inner margin shallowly expanded at the location of the hinge tooth. Peraeopod 3: coxa, greatest depth posterior of centre; segment 2, anterior margin straight; segment 4, anterior marginal

setae $1/3$ to $1/2$ the segment width, segment width 107% of length; segment 5 fully overlapped by segment 4; segment 6, width 43% of length. Peraeopods 5-7: segment 6 not expanded anteriorly; dactyl without facial striations. Pleopods: with 2 coupling hooks. Uropod 1: peduncle, posteroventral spinous process underlying 25% of the inner ramus, inner and outer rami with 3 mid-dorsal spines each, terminating in a fringe of cusps ventral to the apical spine group. Uropod 2: peduncle, posteroventral spinous process underlying 7% of the inner ramus. Uropod 3: outer ramus with 2 sequential, closely approximated cusps proximal to the basally immersed, dorsally recurved spine, minute serrations in the area of the cusps, and a single seta originating at the insertion of the recurved spine; inner ramus with only the single apical spine. Telson: setose only at the lateral cusps.

CONDITION: Without antennae 1, left antenna 2, right and left peraeopods 5-7. Remaining right appendages slide mounted. Remaining left appendages with the carcass.

ADULT FEMALE. Allotype: Length 2.4 mm. Antenna 2: segment 5 without plumose setae. Gnathopod 1: coxa, ventral margin straight. Gnathopod 2: coxal margins, anterior 42% and posterior 100% of ventral length; ventral margin convex; segment 6, hinge tooth fairly shallow, palmar setae sparse, palmar angle acute but shallow, distal, but fairly close to the defining spines; dactyl, inner margin straight, tip fitting into a depression between the palmar angle and defining spines.

CONDITION: Not ovigerous. Without peraeopods 5-7. Right antenna 2 and gnathopod 2 slide mounted. Remaining appendages on the carcass.

VARIATION: Body length at maturity: male 2.2-2.9 mm, female 2.1-3.4mm. The number of gnathopod 1 palmar defining spines is usually 3, rarely 2. The juvenile and female bear longer, more abundant simple filter setae on the posterior margin of antenna 2. Male gnathopod 2 development is illustrated in Figs. 42-45.

TYPE MATERIAL: Holotype, male (LACM), type no. _____, J. L. Barnard station no. 42-T-5, U.S.A.: California: San Luis Obispo County: Montana de Oro State Park: Hazard Canyon Reef (35°10'N, 12°50'W), 8-9 December 1961, formalin-seawater wash of Egretta holdfasts at low intertidal level, J. L. Barnard, collector. Allotype, female (LACM), type no. _____, same location. Paratypes, 10 adult and 1 juvenile female, type no. _____, same location.

OTHER MATERIAL (excluded from type series): California: Corona del Mar (stations 46-K-1, 46-K-2) and La Jolla (stations 45-R-1 and 45-W-5) (LACM).

REMARKS: Jassa carltoni is closest among eastern Pacific species of Jassa to J. slatteryi and J. morinoti. Differences between the three are discussed in the sections for the latter species. Jassa carltoni is the smallest of the three, yet both sexes bear a larger, stouter gnathopod 2. The male's thumb tip is more squared than in the other two species. All

known J. carltoni adult males possess palmar defining spines, but it cannot be predicted what may happen in larger adults. The defining spines are not on a pronounced ledge as in J. morinot, yet are not reduced as in J. slatteryi. In both sexes of J. carltoni the spines seem more separated as well.

ETYMOLOGY: Named for Dr. James T. Carlton, in appreciation of his assistance in interpreting the biogeography of Jassa.

12. JASSA BOROWSKYAE n.sp.

Figs. 13-16, 26, 42-45

ADULT MALE. Holotype: Length 4.5 mm. Antenna 2: overlapped by antenna 1 only to the upper third of segment 5; segment 5, posterior margin bearing plumose setae on the distal half, simple filter setae minute or lacking; flagellum 4 segments, segment 1 73% of full length. Mandible: palp segments 2 and 3 without a dorsal fringe of setae; raker spines 2 right, 3 left. Maxilla 1: palp without setae at the base of segment 1, segment 2 with 1 row of facial setae. Gnathopod 1: coxal margin, anterior 114% of dorsal length, ventral margin shallowly concave; segment 2, anterior and posterior margins with only a few short setae at the distal angle; segment 5, posterior lobe 40% of anterior margin length, anterodistal setal cluster long, 95% of the anterior margin length; segment 6, palm convex; dactyl cusped along most of the posterior margin, without facial striations. Gnathopod 2: coxal margins, anterior 33% and posterior 69% of ventral length; ventral margin straight; gill large; segment 2, anterolateral flange with 21 long, simple setae (setae more than 1/2 segment width); segment 5, posterior lobe without a distal seta; segment 6, anterior margin with short setae proximally (setae about 1/3 the width of segment 2), hinge tooth triangular, anteriorly shallowly bifid, setae confined to the hinge tooth area, thumb 24% of segment 6 length, distally acute, posterior base defined by 3 spines and associated setae; dactyl, inner margin broadly expanded at the palmar incision. Peraeopod 3: coxa, greatest depth posterior of centre; segment 2, anterior margin convex; segment 4, anterior marginal setae up to 3/4

Fig. 26. Jassa borowskyae. Holotype, adult male, minor form, 4.5 mm; allotype, adult female, 5.0 mm. Brady's Beach, Barkley Sound, Vancouver Island, British Columbia, 26 June 1976. Juvenile male, 4.3 mm; adult male 1, major form, 5.0 mm. Point Grenville, Washington, 22 July 1966. Thumbed new cuticle is shown under the outer cuticle of the juvenile male. Lateral views: whole body, uropod 3, maxillae 1 and 2, maxilliped, right mandible; dorsal view: telson; other views medial. Appendages are of the holotype unless noted otherwise. Scale 0.1 mm.

the segment width, segment width 100% of length; segment 5 fully overlapped by segment 4; segment 6, width 60% of length. Peraeopods 5-7: segment 6 not expanded anteriorly; dactyl without facial striations. Pleopods: with 2 coupling hooks. Uropod 1: peduncle, posteroventral spinous process short, underlying 10% of the inner ramus, inner and outer rami with 3 and 4 mid-dorsal spines respectively, rami terminating in a fringe of cusps ventral to the apical spine group. Uropod 2: peduncle, posteroventral spinous process underlying 4% of the inner ramus. Uropod 3: outer ramus with 2 sequential, closely approximated cusps proximal to the basally immersed, dorsally recurved spine, minute serrations in the area of the cusps, and a single seta originating at the insertion of the recurved spine; inner ramus with only the single apical spine. Telson: setose at both the apex and the lateral cusps.

CONDITION: Right appendages, both uropods 3, telson, and mouthparts slide mounted; carcass with all left appendages.

ADULT FEMALE. Allotype: Length 5.0 mm. Antenna 2: segment 5 with a few plumose setae distally. Gnathopod 1: coxa, ventral margin slightly concave. Gnathopod 2: coxal margins, anterior 30% and posterior 100% of ventral length, ventral margin convex; segment 6, hinge tooth pronounced, palmar setae moderately dense throughout, palm concave, palmar angle acute, distal but close to the defining spines; dactyl, inner margin straight, tip fitting into a depression distal to the defining spines.

CONDITION: Ovigerous. Right appendages, both uropods 3, telson, and mouthparts slide mounted; carcass with remaining appendages, except pereopods 3 and 6.

VARIATION: Body length at maturity: male 2.8-7.7 mm, female 3.2-5.6 mm. The number of second antennal segments may sometimes be less than 4 (the last minute). As in J. stauderi, plumose setae appear on the antenna 2 distal segments in larger males and females. The male's second antenna lengthens more than in J. stauderi and the filter setae disappear. Thus antenna 2 change is intermediate to J. stauderi and J. oclairi. Most thumbed males retain the juvenile's palmar defining spines; however, the largest males have a broader, more squared thumb and lack defining spines (Fig. 45).

TYPE MATERIAL: Holotype, male (NMNS), catalogue no. NMCC1987-1064, accession no. 1976-157, station B5, Canada: British Columbia: Vancouver Island: Barkley Sound: Brady's Beach (48°49.08'N, 125°08.3'W), 26 June 1976, dip net scrape of Phyllospadix, kelp and other brown algae on boulders embedded in the sand beach at low water level, temperature about 13°C, salinity above 32 ppt, E. L. Bousfield, collector. Allotype, female (NMNS), catalogue no. NMCC1987-1065, same location. Paratypes, 3 adult females, 1 juvenile female, 2 juvenile males (NMNS), catalogue no. NMCC1987-1066, same location.

OTHER MATERIAL (excluded from type series): approximately 900 specimens from the U.S.S.R. (Peter the Great Bay), Alaska (northernmost record:

Unimak Island: Izembek Lagoon), British Columbia (outer Vancouver Island only), Washington (outer coast only), Oregon and California (southernmost record: Cayucos). (BCPM, VAM, USNM, ZIL, P. Shaw).

REMARKS: Jassa borowskyae is stout and setose, therein most closely resembling J. staudei, J. shawi and J. oclairi among sympatric congeners. Two characters combined differentiate it from all sympatric species: a very short uropod 1 peduncular spinous process and a long setal cluster on the anterodistal margin of the gnathopod 1, segment 5. Both features are unaffected by sex or age. Other, more subtle characters may be useful: in both sexes, smaller size of segment 6 on gnathopod 2; in the male, lack of pre-thumbings, lack of toothings on the dactyl, tendency to retain defining spines, and a shorter thumb; in the male's second antennae, enlargement at maturity, shortening of the simple setae and development of plumose setae and consistently 4 segmented flagellum. Collection records suggest that J. borowskyae is restricted to exposed coast.

ETYMOLOGY: Named in recognition of the contribution to our understanding of the role of the male thumb in Jassa made by Dr. Betty Borowsky and in appreciation of her generous personal assistance in expanding the horizon of this study beyond the confines of systematics.

13. JASSA MYERSI n.sp.

Figs. 13, 15, 16, 42-45

ADULT MALE. Holotype: Length 5.8 mm. Antenna 1: lacking (in male, 4.5 mm, J. L. Barnard station 39-K-1, antenna 2 overlapped by antenna 1 to midway along segment 5). Antenna 2: segment 5 bearing short filter setae only, without plumose setae, simple setae only about 1/4 shorter than those of the juvenile's, flagellum 5 segments, the last minute, segment 1 82% of full length. Mandible: palp segments 2 and 3 without a dorsal fringe of setae; raker spines 2 right, 3 left. Maxilla 1: palp without setae at the base of segment 1, segment 2 with 1 row of facial setae. Gnathopod 1: coxal margins, anterior 65% of dorsal length, ventral margin straight; segment 2, anterior and posterior margins with a few short setae distally; segment 5, posterior lobe 34% of anterior margin length, anterodistal setal cluster short, 34% of the anterior margin; segment 6, palm straight; dactyl cusped along most of the margin, without facial striations. Gnathopod 2: coxal margins, anterior 29% and posterior 34% of ventral length, ventral margin straight; gill small; segment 2, anterolateral flange with a few short, simple setae (setae less than 1/4 segment width); segment 5, posterior lobe without a distal seta; segment 6, anterior margin with a few short setae proximally (less than 1/4 segment 2 width), hinge tooth triangular, anteriorly shallowly bifid, setae concentrated around the hinge tooth area; thumb 6% of segment 6 length, distally rounded, thumb setae nearly at the tip, 2 of the 3 clusters of defining setae accompanied by spines; dactyl, inner margin broadly expanded at the location of the hinge tooth. Peraeopod 3: coxa,

greatest depth posterior of centre; segment 2, anterior margin convex; segment 4, anterior marginal setae less than $1/4$ the segment width, segment width 92% of length; segment 5 fully overlapped by segment 4; segment 6, width 75% of length. Peraeopods 5-7: lacking (male, 4.5 mm, segment 6 not expanded anteriorly; dactyl without facial striations). Pleopods: with 2 coupling hooks. Uropod 1: peduncle, posteroventral spinous process underlying 6% of the inner ramus, inner and outer rami with 4 and 6 mid-dorsal spines respectively, terminating in a fringe of cusps ventral to the apical spine group. Uropod 2: peduncle without a posteroventral spinous process. Uropod 3: outer ramus with 2 sequential, closely approximated cusps proximal to the basally immersed, dorsally recurved spine, minute serrations in the area of the cusps, and a single seta originating at the insertion of the recurved spine; inner ramus with only the single apical spine. Telson: lacking (male, 4.5 mm, setose at both the apex and at the lateral cusps).

CONDITION: Without antenna 1, peraeopods 5-7, right uropod 3, telson, right maxilla 1 and both maxillae 2. Right appendages, telson, and mouthparts slide mounted.

ADULT FEMALE. Allotype: Length 4.4 mm. Antenna 2: segment 5 without plumose setae. Gnathopod 1: coxa, ventral margin straight. Gnathopod 2: coxal margins, anterior 35% and posterior 60% of ventral length, ventral margin straight; segment 6, hinge tooth pronounced, palmar setae sparse, palmar angle shallow, distal to, but well separated from, the defining spines; dactyl, inner margin shallowly expanded at the location of the

hinge tooth, tip fitting into a depression between the palmar angle and defining spines.

CONDITION: Brood plates setose but not ovigerous. Without left antenna 1, right antenna 2 and pereopods 5-7.

VARIATION: Body length at maturity: male 4.5-5.8 mm, female 3.1-4.4 mm. The number of antenna 2 segments varies from 2 to 4. The usual number of defining spines on gnathopods 1 and 2 is 3. Male gnathopod 2 development is illustrated in Fig. 13. The gnathopod 1 palm is straight in both sexes; however, it becomes shallowly excavate in larger males.

TYPE MATERIAL: Holotype, male (LACM), type no. , station no. 39-H-2, U.S.A.: California: Santa Barbara County: Goleta: Coal Oil Point ($34^{\circ}26'N$, $119^{\circ}50'W$), 2 July 1961, from mixed collection on rock surfaces in Phyllospadix zone at low intertidal level, J. L. Barnard, collector. Allotype, female (LACM), type no. , same location. Paratypes, 1 adult male, 5 adult females, juveniles (LACM), type no. , same location.

OTHER MATERIAL (excluded from type series): 6 adult males, 20 adult females and 95 juveniles from California: Goleta, Coal Oil Point (J. L. Barnard stations 39-H-1, 39-K-1), Santa Cruz Island, southwest shore of Snugglers Cove (J. L. Barnard station 1660), Corona del Mar (J. L. Barnard station 46-A-4), La Jolla (J. L. Barnard stations 45-A-1 and 45-

A-5) and four unspecified locations (J. L. Barnard stations 9, 11, 17 and 18) (LACM).

REMARKS: Certain features at first glance suggest that J. myersi is not a member of Jassa: the very short male thumb which is seemingly (but not actually) tipped by setae, the long, shallow female gnathopod 2 palm, and the very shallow but wide coxae. However the other body parts are overwhelmingly Jassa-like: strong antenna 2 with reducing setal length in the male at maturity, gnathopod 1 shape and 3 (rarely 4) spine count, typical spine arrangement on the gnathopod 2 with distally produced thumb and subapical thumb setae in the male, expanded peraeopod 3-4 segments 2 and 4 with well produced segment 4, and typical uropod 3 uncination. All males encountered had broad peraeopod 3-4 segment 2, suggesting that, if development is similar to other species of Jassa, these males were not at maximum size for the species. Segment 6 is somewhat broader than in other Northern Hemisphere species, a feature that appears in the Southern Hemisphere J. fenwicki and J. gruneri. In common with the Southern Hemisphere J. alonsoae, J. gruneri, J. thurstoni and J. ingens, the female and juvenile male gnathopod 2 palm is shallowly defined, giving a sinuous appearance.

CONFIRMED LITERATURE: J. L. Barnard (1969) as Jassa falcata thick form.

ETYMOLOGY: Named in appreciation of the interest and assistance given to this study by Dr. Alan Myers, University College, Cork, Ireland.

14. JASSA INCENS (Pfeffer, 1888)

Figs. 13, 15-17, 42-45, 52

Podocerus ingens Pfeffer, 1888, 131-137, plate III, fig. 1Jassa ingens: Stebbing, 1906, 653-654; Schellenberg, 1931, 248-250, fig. 129; Thurston, 1974a, 47; 1974b, 99-100

ADULT MALE. Lectotype (here designated): Length 22.1 mm. Antenna 2: overlapped by antenna 1 to midway along segment 5; segment 5, simple filter setae minute, without plumose setae; flagellum 7 segments, segment 1 38% of full length. Mandible: palp segments 2 and 3 with a dorsal fringe of setae; raker spines 10 right, 11 left (in female, 19.2 mm). Maxilla 1: palp with a cluster of setae at the base of segment 1, segment 2 with 2 rows of facial setae. Gnathopod 1: coxal margins, anterior 120% of dorsal length, ventral margin slightly sinuous; segment 2 with short spine-like setae along the anterior margin and clusters of longer setae centrally and distally on the posterior margin; segment 5, posterior lobe 38% of anterior margin length, anterodistal setal cluster long, 32% of the anterior margin; segment 6, palm convex; dactyl cusped along most of its length, without facial striations. Gnathopod 2: coxal margins, anterior 33% and posterior 60% of ventral length, ventral margin sinuous; gill moderately large; segment 2, anterolateral flange setae minute and spine-like; segment 5, posterior lobe with a cluster of long setae; segment 6, anterior margin with clusters of short setae proximally (setae 1/2 or less than the width of segment 2), hinge tooth triangular and shallowly bifid, setae mostly confined around the hinge tooth area,

thumb 14% of segment 6 length, distally squared, posterior margin sinuous, strongly expanded at the location of the defining setae, defining setae not separated, accompanied by 3 spines; dactyl, inner margin strongly but broadly produced at the position of the hinge tooth. Peraeopod 3: coxa, greatest depth posterior of centre; segment 2, anterior margin concave; segment 4, anterior marginal setae shorter than segment width, segment width 69% of length; segment 5 81% overlapped by segment 4; segment 6, width 66% of length. Peraeopods 5-7: central part of segment 6 expanded anteriorly, spines strong; dactyl without facial striations. Pleopods: with 4-5 coupling hooks (in the female, 19.2 mm). Uropod 1: peduncle, posteroventral spinous process underlying 42% of the inner ramus, inner and outer rami with 11 and 16 mid-dorsal spines respectively, without terminal fringe of cusps ventral to the apical spine group. Uropod 2: peduncle, posteroventral spinous process underlying 12% of the inner ramus. Uropod 3: outer ramus with 2 sequential cusps proximal to the basally immersed, dorsally recurved spine, smaller cusps and serrations in the area of the cusps, and a single seta originating at the insertion of the recurved spine; inner ramus with only the single apical spine. Telson: setose only at the lateral cusps.

CONDITION: With all appendages. Left uropod 1 without tip of inner ramus.

ADULT FEMALE. (Not type; BMNH 1969:723:7 station no. 46 (1929), South Orkney Islands: Signy Island: Factory Cove: Berntsen Point, 15 April

1964, M. H. Thurston, collector.) Length 19.2 mm. Antenna 2: segment 5 without plumose setae. Gnathopod 1: coxa, ventral margin straight. Gnathopod 2: coxal margins, anterior 38% and posterior 70% of ventral length, ventral margin sinuous; segment 6, hinge tooth shallow, palmar setae moderately abundant throughout, but not so dense as to obscure the palm's shape, palm sinuous, palmar angle shallow and distal from the defining spines; 3 defining spines on the tip of a protuberance, as in the male; dactyl, inner margin slightly expanded anteriorly, tip fitting into a deep depression between the palmar angle and defining spines.

CONDITION: Without left pereopods 4 and 5. Right appendages, telson and mouthparts slide mounted. Remaining appendages with the carcass.

VARIATION: Body length at maturity: male 19.6-24.1 mm, female 15.3-20.8 mm. The number of second antennal segments in adults varies from 7 to 9 (the last often minute). Immature males have second antennal setation similar to that of the female; at maturity the setae shorten and the segments elongate allometrically (Fig. 52). Coincident with the male's thumb production is an allometric increase in the second gnathopod's sixth segment. Lengthening is isometric in the female. Although the palmar spines are smaller in the largest males, they have never been found lacking. This, and their pronounced location, suggest a functionality at maturity.

TYPE MATERIAL: Lectotype, male (ZMUH), type no. K-8017, South Georgia:

Royal Bucht: Moltke-Hafen (54°30'58"S, 36°0'45"W), 16 January 1884, Deutsche Polarstat. 1882/83, K. von den Steinen, collector.

OTHER MATERIAL: 141 specimens from the South Sandwich Islands (Candlemas Island), South Orkney Islands (Signy Island) and South Georgia (BMNH, ZMHB, ZMUH, ZMUC, ZMUO).

REMARKS: Jassa ingens is the largest species of Jassa, the female maturing at 15 mm or more. The expanded sixth segment on peraeopods 5-7 is distinctive, even in the young.

15. JASSA SHAWI n.sp.

Figs. 14-17, 27, 44

SUBADULT MALE. Holotype: Length 6.8 mm. Antenna 2: overlapped by antenna 1 to about $3/4$ along segment 5; segment 5, simple filter setae long, without plumose setae; flagellum 4 segments, the last minute, segment 1 60% of full length. Mandible: palp segments 2 and 3 without a dorsal fringe of setae; raker spines 2 right, 4 left. Maxilla 1: palp without setae at the base of segment 1, segment 2 with 1 row of facial setae. Gnathopod 1: coxal margins, anterior 71% of dorsal length, ventral margin straight; segment 2, anterior and posterior margins with a short seta at the distal angle; segment 5, posterior lobe 43% of anterior margin length, without a distal setal cluster at the anterior margin; segment 6, palm convex; dactyl cusped along most of the posterior margin, without facial striations. Gnathopod 2: coxal margins, anterior 35% and posterior 51% of ventral length, ventral margin straight; gill small; segment 2, anterolateral flange without a fringe of setae; segment 5, posterior lobe with a minute distal seta; segment 6, anterior margin without setae proximally, hinge tooth triangular, anteriorly shallowly bifid, setae confined to the hinge tooth area, thumb shape of adult unknown, juvenile with 3 defining spines; dactyl, inner margin broadly but shallowly produced at the location of the hinge tooth. Peraeopod 3: coxa, greatest depth posterior of centre; segment 2, anterior margin slightly convex; segment 4, anterior marginal setae less than $1/2$ segment width, segment width 93% of length; segment 5 71% overlapped by segment 4; segment 6, width 78% of length. Peraeopods 5-7: segment 6 not

Fig. 27. Jassa shawi. Holotype, juvenile male, 6.8 mm; allotype, adult female, 5.6 mm. Bamfield, Barkley Sound, Vancouver Island, British Columbia, 24 June 1976. Lateral view: whole body; dorsal view: telson; other views medial. Appendages are of the holotype unless indicated otherwise. Scale 0.1 mm.

expanded anteriorly; dactyl without facial striations. Pleopods: with 2 coupling hooks. Uropod 1: peduncle, posteroventral spinous process short, underlying 10% of the inner ramus, inner and outer rami with 3 and 4 mid-dorsal spines respectively, terminating in a fringe of cusps ventral to the apical spine group. Uropod 2: peduncle, posteroventral spinous process underlying 3% of the inner ramus. Uropod 3: outer ramus with 2 sequential, closely approximated cusps proximal to the basally immersed, dorsally recurved spine, minute serrations in the area of the cusps, and a single seta originating at the insertion of the recurved spine; inner ramus with only the single apical spine. Telson: setose only at the lateral cusps.

CONDITION: Right appendages, telson and mouthparts slide mounted; without left gnathopod 1 and left peraeopods 5-7.

ADULT FEMALE. Allotype: Length 5.6 mm. Antenna 2: segment 5 without plumose setae. Gnathopod 1: coxa, ventral margin straight. Gnathopod 2: coxal margins, anterior 46% and posterior 81% of ventral length, ventral margin convex; segment 6, hinge tooth pronounced, palmar setae moderately dense throughout, but not so dense as to obscure the palm's shape, palmar angle acute, distal, but close to the defining spines; dactyl, inner margin proximally expanded, tip fitting into a depression between the palmar angle and defining spines.

CONDITION: Brood plates setose but not ovigerous. With all appendages.

VARIATION: Insufficient material is available to assess variation.

TYPE MATERIAL: Holotype, male (NMNS), catalogue no. NMCC1987-1133, accession no. 1976-157, station no. 81, Canada: British Columbia: Vancouver Island: Barkley Sound: Bamfield Marine Station, 24 June 1976, on settling block suspended from floating dock at the water's surface, approximately 13°C and 30 ppt, E. L. Bousfield, collector. Allotype, 5.6 mm, catalogue no. NMCC1987-1134, same location.

OTHER MATERIAL (excluded from type series): 1 ovigerous female and 2 juveniles from La Jolla, California, J. L. Barnard station 45-W-5, 11-13 November 1962, 32°50'N, 116°30'W, amongst calcareous sponge under a rocky ledge in a surge channel at low water level (LACM).

REMARKS: Jassa shawi lacks long setae on the anterior margin of segments 2 and 6 on gnathopod 2, lacks a seta at the anterodistal junction of segments 5 and 6 of gnathopod 1, and has a reduced uropod 1 peduncular process. No other species has this combination of characters. There is no adult male known. Judging by the appearance of the second antenna and gnathopod, the subadult holotype is a penultimate juvenile. Lack of plumose setae in the subadult and in the adult female suggests that this will be the condition of the adult male.

ETYMOLOGY: Named for Mr. P. Shaw in appreciation of his generous assistance to many aspects of this work.

16. JASSA THURSTONI n.sp.

Figs. 14, 16, 43, 45

ADULT MALE. Holotype: Length 5.9 mm. Antenna 2: (paratype, male, 6.0 mm, overlapped by antenna 1 only to the end of segment 5); segment 5, posterior margin bearing long filter setae only, without plumose setae; simple filter setae somewhat shorter than those of the female; flagellum 6 segments, segment 1 33% of full length. Mandible: palp segments 2 and 3 without a dorsal fringe of setae; raker spines 4 right, 4 left. Maxilla 1: palp without setae at the base of segment 1, segment 2 with 1 row of facial setae. Gnathopod 1: coxal margins, anterior 207% of dorsal length, ventral margin shallowly convex; segment 2, anterior margin with a short seta distally, posterior margin without setae centrally; segment 5, posterior lobe 63% of anterior margin length, anterodistal setal cluster short, 24% of the anterior margin length; segment 6, palm deeply convex; dactyl cusped along most of the posterior margin, without facial striations. Gnathopod 2: coxal margins, anterior 50% and posterior 59% of ventral length, ventral margin straight; gill small; segment 2, anterolateral flange with a few minute setae only; segment 5, posterior lobe with a short distal seta; segment 6, anterior margin with a few short setae proximally, palm, hinge tooth triangular, anteriorly shallowly bifid, setae restricted to the hinge tooth area, thumb 23% of segment 6 length, distally squared, posterior margin straight, defining setae accompanied by 3 spines; dactyl, inner margin strongly expanded at the position of the hinge tooth. Peraeopod 3: coxa, greatest depth central; segment 2, anterior margin shallowly concave; segment 4,

anterior marginal setae in well separated clusters, central setae 1/2 the segment width or less, segment width 59% of length; segment 5 65% overlapped by segment 4; segment 6, width 55% of length. Peraeopods 5-7: segment 6 not markedly expanded anteriorly; dactyl without facial striations. Pleopods: with 2 coupling hooks. Uropod 1: peduncle, posteroventral spinous process underlying 50% of the inner ramus, inner and outer rami with 6 and 4 mid-dorsal spines respectively, not terminating in a fringe of cusps ventral to the apical spine group. Uropod 2: peduncle, posteroventral spinous process underlying 16% of the inner ramus. Uropod 3: outer ramus with 2 sequentially arranged cusps proximal to the basally immersed, dorsally recurved spine, a mass of serrations proximodorsal to the recurved spine and a single seta originating at its insertion; inner ramus with only the single apical spine. Telson: setose only at the lateral cusps.

CONDITION: Without antennae 1 and right peraeopods 5-7. Right appendages, telson and mouthparts slide mounted. Remaining left appendages with the carcass.

ADULT FEMALE. Allotype: Subadult. Length 3.7 mm. Antenna 2: segment 5 without plumose setae. Gnathopod 1: coxa, ventral margin convex. Gnathopod 2: coxal margins, anterior 71% and posterior 76% of ventral length, ventral margin convex; segment 6, hinge tooth moderately pronounced, shallowly bifid, palmar setae sparse, palmar angle shallow, considerably distal of the defining spines; dactyl, inner margin evenly

convex, tip fitting into a depression between the palmar angle and the defining spines.

CONDITION: Without left antennae, right antenna 1, left peraeopod 3, and left and right peraeopods 5-7.

VARIATION: Body length at maturity: male 5.9-6.0 mm, female 5.4-6.5 mm. The gnathopod 1 coxa is unusually deep and produced anterodistally in the male, but shorter in the female.

TYPE MATERIAL: Holotype, adult male (BMNH), registration no. 1969:761:2, station no. 44 (1218), South Orkney Islands: Signy Island: Paal Harbour (60°43'S, 45°38'W), 5 February 1965, anchor dredge over mud at 20-25 m depth, M.H. Thurston, collector. Allotype, female (BMNH), same location as for the holotype. Paratypes, one adult male (BMNH), registration no. 1969:763:1, station no. 52 (2085), South Orkney Islands, Signy Island: Outer Islet-Observation Bluff, 14 September 1964, Agassiz trawl over gravel and sand, sand with some rock, algae on rocks, 20 m depth, M.H. Thurston, collector; one adult female (BMNH), registration no. 1969:762:3, station no. 50 (AT 76), Berntsen Point-Bare Rock, 16 October 1964, Agassiz trawl over gravel and sand, some rocks with Desmarestia anceps and Phyllogigas grandifolius, 5-10 m depth, M.H. Thurston, collector; one adult female (BMNH), registration no. 1907.6.6.414-415, Ross Sea: Flagon Pt., Discovery Expedition, 23 January 1903.

OTHER MATERIAL (excluded from type series): 1 ovigerous female and 3 juveniles from South Georgia and between South Georgia and the Falkland Islands, collected during the Swedish Antarctic Expedition of 1901-1903 (NRS).

REMARKS: Jassa thurstoni has unusually wide and square coxae 1-4, particularly in the male. Unlike most other species of Jassa, coxae 1 and 2 are about as deep as coxae 3 and 4. The antennae are also very long, antenna 2 being hardly stouter than antenna 1 and non-sexually dimorphic. However the apparent lack of variation may be an artifact of lack of specimens. The palm of the female and juvenile male's gnathopod 2 is sinuous.

CONFIRMED LITERATURE: As Jassa falcata form 2 in Thurston (1974b).

ETYMOLOGY: Named for Dr. M.H. Thurston in appreciation of his contribution to our knowledge of Antarctic Amphipoda.

17. JASSA PUSILLA (G. O. Sars, 1894)

Figs. 14, 16, 17, 28, 29, 42-45

Podocerus minutus Sars, 1882, 112, plate 6, fig. 6Podocerus pusillus Sars, 1894, 596-597, plate 213, fig. 1: Walker, 1895, 314Podocerus odontonyx Sars, 1894, 597-598, plate 213, fig. 2 (new synonymy)Jassa pusilla: Stebbing, 1906, 655: Chevreux and Fage, 1925, 346, 347, fig. 354Jassa dentex (Czerniavski, 1868): Stebbing, 1906, 655: Chevreux and Fage, 1925, 348, 349, fig. 356: Gurjanova, 1951, 910, 911, fig. 631

ADULT MALE. (Not type; ZMUO, reg. no. F.13359, Norway: Risør, G. O. Sars, collector). Length 4.1 mm. Antenna 2: overlapped by antenna 1 to about $3/4$ along segment 5; segment 5, posterior margin without plumose setae, simple setae about $3/4$ the length of those of the juvenile; flagellum 4 segments, the last about $1/2$ the length of the $1/3$, segment 1 53% of full length. Mandible: palp segments 2 and 3 without a dorsal fringe of setae; raker spines 3 right, 4 left. Maxilla 1: palp without setae at the base of segment 1, segment 2 with 1 row of facial setae. Gnathopod 1: coxal margins, anterior 145% of dorsal length, ventral margin straight; segment 2, anterior margin with a few minute setae; segment 5, posterior lobe 46% of anterior margin length, without an anterodistal setal cluster; segment 6, palm convex; dactyl cusped along the majority of the posterior margin, without facial striations. Gnathopod 2: coxal margins, anterior 44% and posterior 56% of ventral

Fig. 28. Jassa pusilla. Paralectotype, adult female 1, F.10562 (ZMUO); adult female 2 (length unknown), F.10564; adult male 1, major form (length unknown), F.10563; adult male 2, minor form (length unknown), F.10565. Hammerfest, Norway (date unknown). Adult female 3, 4.7 mm, F. 13359. Risør, Norway (date unknown). Lateral views: whole body, maxilla 1, right and left mandibles; dorsal view: telson; all other views medial. Scale 0.1 mm.

Fig. 29. Jassa pusilla. Male gnathopod 2 palm morphology. Juvenile male, A, 3.3 mm; adult males, minor form, C, 2.8 mm, D, 3.2 mm and E, 3.3 mm; adult males, major form, B, 3.3 mm, F, 3.2 mm, G, 4.0 mm, H, 3.7 mm, I, 4.0 mm and J, 4.1 mm. Risör, Norway (date unknown), catalogue no. F. 13359 (ZMUO). Scale 0.1 mm.

length, ventral margin straight; gill small; segment 2, anterolateral flange without filter setae; segment 5, posterior lobe with a minute distal seta; segment 6, anterior margin without setae proximally, hinge tooth triangular, anteriorly shallowly bifid, setae confined to the hinge tooth area, thumb 27% of segment 6 length, distally bifid, posterior margin straight, defining setae well separated, not accompanied by spines. Peraeopod 3: coxa, greatest depth posterior of centre; segment 2, anterior margin straight; segment 4, anterior marginal setae $1/2$ or less than the segment width; segment 5 80% overlapped by segment 4; segment 6, width 44% of length. Peraeopods 5-7: segment 6 not expanded anteriorly; dactyl without facial striations. Pleopods: with 2 coupling hooks. Uropod 1: peduncle, posteroventral spinous process underlying 28% of the inner ramus, inner and outer rami with 4 and 2 mid-dorsal spines respectively, terminating in a fringe of cusps ventral to the apical spine group. Uropod 2: peduncle without a posteroventral spinous process. Uropod 3: outer ramus with 2 sequential, closely approximated cusps proximal to the basally immersed, dorsally recurved spine, minute serrations in the area of the cusps, and a single seta originating at the insertion of the recurved spine; inner ramus with only the single apical spine. Telson: setose only at the lateral cusps.

CONDITION: With all appendages. Right appendages, telson and mouthparts slide mounted.

ADULT FEMALE. (Not type; ZMUO, reg. no. F.13359, Norway: Risør: G. O. Sars, collector. Length 4.7 mm. Antenna 2: segment 5 without plumose

setae. Gnathopod 1: coxa, ventral margin convex. Gnathopod 2: coxal margins, anterior 65% and posterior 96% of ventral length, ventral margin straight; segment 6, hinge tooth pronounced, palmar setae sparse, palmar angle acute, distal, but close to the defining spines; dactyl, inner margin proximally expanded, tip fitting into a depression between the palmar angle and defining spines.

CONDITION: Without left pereopods 5 and 7. Right appendages, left pereopod 6, telson and mouthparts slide mounted. Remaining appendages with the carcass.

VARIATION: Body length at maturity: male 2.8-4.5 mm, female 2.8-4.7 mm. The number of antenna 2 flagellum segments occasionally may vary by 1. Male gnathopod 2 development is illustrated in Figs. 42-45. Minor form adults have a pronounced tooth on the dactyl and the thumb is apically squared. Major forms have a broader, more proximal dactyl expansion and bifid thumb tip. Subadults can have a pronounced thumb but this is short, acute, and more distal than in the adult. Large thumbed subadults probably transform into a major form adult. Sars (1894) suspected that Podocerus odontonyx was synonymous with J. pusilla, and this is confirmed here: the former is a minor form, the latter a major form.

TYPE MATERIAL: Lectotype (here designated), male (ZMUO), reg. no. F.10562. Norway: Hammerfest (71°N, 23.9°E), date unknown, G. O. Sars, collector. Paralectotypes (ZMUO), reg. no. F.10563 and F.10564.

OTHER MATERIAL: approximately 300 specimens from England, Norway, the Faeroe Islands, Northern France and U.S.A. (off Cape Hatteras, South Carolina, off central Georgia and off Newport, Rhode Island) (BMNH, MHNP, NRS, ZMUB, USNM, UTM, ZMUC, ZMUO).

REMARKS: The lectotype is not described here because it was slide mounted by G.O. Sars, and the characteristics of some appendages were obliterated by overlap of other appendages. Jassa pusilla is a smaller, slenderer species than the two other species that are indigenous to Europe endemics, J. falcata and J. herdmani. It can be readily distinguished from these species by its lack of dorsal setae on the mandibular palp segment 2. The major form male has a distinctive bifid thumb on its second gnathopod, segment 6 (Figs. 28, 29, 45). The second antennae of J. pusilla are never as stout as those of J. falcata and J. herdmani and never bear plumose setae. Although J. pusilla has been found in collections of J. falcata and J. herdmani, it is generally a deeper dweller. More often J. pusilla has been found with Plumulojassa ocia. There are several records of J. pusilla associated with crabs, an infrequently documented feature of Jassa (Chevreux and Fage, 1925; Jones, 1948; Moore, 1984).

Jassa odontonyx (Sars, 1894) is the minor form of J. pusilla, and the name is herein submerged. The male syntype, F.10565 Mp. 41 (ZMUO, slide mount) is herein established lectotype of J. odontonyx, and F. 10566 Mp. 41 the paralectotypes (Norway: Hammerfest, 180m, G. O. Sars, collector). F.10566 is a slide mount of 4 specimens: two J. pusilla males, one J. pusilla female and one Ischyrocerus. The Ischyrocerus is not part of the

type series. The lectotype could not be scored for numerical analysis because it had been mounted on a thick slide by Sars, thus preventing viewing of mouthparts and structures at high magnification.

Although described as Podocerus minutus by G.O. Sars in 1882, Sars (1894, p. 596) changed the name to P. pusillus "To avoid confusion with Ischyrocerus minutus Lilljeb., in case the latter genus should not be accepted...." Since this species has been referred to as P. pusillus, and Jassa pusilla subsequently, I suggest that minutus be considered "nomen oblitum".

CONFIRMED LITERATURE: Although specimen identifications have not been confirmed, it is probable that the accounts of J. pusilla by Jones (1948) and Moore (1984) are correct because of the relatively great depth at which the specimens were taken (Jones) and the recognized difference of this species from its regional congeners (Moore).

18. JASSA FALCATA (Montagu, 1808)

Figs. 13-17, 30, 31, 42-45

Cancer (Gammarus) falcatus Montagu, 1808, 100, t.5, fig. 2Podocerus falcatus: Bate, 1857, 148: Sars, 1895, 594-595, pl. 212Jassa pulchella Leach, 1814, 433: Gurjanova, 1951, 908-909, fig. 628Jassa falcata: Leach, 1814, 433: Sexton and Reid, 1951 (part of Narrow Form), 42, plate 4, figs. 1-3, plate 18, figs. 12b, e: Lincoln, 1979, 550, figs. 263 a,b, 264

ADULT MALE. Holotype redescription: Length 6.3 mm. Antenna 2: overlapped by antenna 1 only to about 3/4 along segment 5; segment 5, posterior margin bearing plumose setae along the full length, simple filter setae lacking; flagellum 6 segments, the last minute, segment 1 35% of full length. Mandible: palp segment 2 with a dorsal fringe of setae; raker spines 4 right, 5 left. Maxilla 1: palp without setae at the base of segment 1, segment 2 with 1 row of facial setae. Gnathopod 1: coxal margins, anterior 108% of dorsal length, ventral margin straight; segment 2, anterior and posterior margins with a few short, thin setae; segment 5, posterior lobe 47% of anterior margin length, without an anterodistal setal cluster; segment 6, palm slightly concave; dactyl cusped along most of the posterior margin, with a row of facial striations. Gnathopod 2: coxal margins, anterior 26% and posterior 61% of ventral length, ventral margin convex; gill large; segment 2, anterolateral flange without filter setae; segment 5, posterior lobe without a distal seta; segment 6, anterior margin without setae

Fig. 30. Jassa falcata. Holotype, adult male, minor form, 6.3 mm. Torcross, South Devon, England (date unknown). Lateral views: whole body, left mandible, left maxilla 1, right uropods 1-3; dorsal view: telson; other views medial. Scale 0.1 mm.

Fig. 31. Jassa falcata. Adult male, major form, 5.7 mm, lectotype 296e of Jassa puchella. Devon, England (date unknown). The tip of the thumb on gnathopod 2 had been damaged while the animal was alive. Adult male 1, major form, 11.2 mm; juvenile male 2, 7.4 mm; adult male 3, major form, 6.2 mm; juvenile male 4, 4.5 mm; and adult female, 7.0 mm. Stoer Bay, Sutherland, Scotland, 22 October 1937. Developing new cuticle is shown in the gnathopod 2 of the juvenile male 2, not yet at the terminal molt. Lateral view: whole body; all other views medial. Appendages are of the lectotype unless indicated otherwise. Scale 0.1 mm.

proximally, hinge tooth triangular, anteriorly bifid, setae sparse but not particularly confined to the hinge tooth area, thumb 16% of segment 6 length, distally squared, posterior margin smoothly concave to the defining setae, setae closely approximated and accompanied by 3 spines; dactyl, inner margin with a strongly pronounced protuberance extending into the palmar incision. Peraeopod 3: coxa, greatest depth posterior of centre; segment 2, anterior margin nearly straight; segment 4, anterior marginal setae $1/3$ to $1/2$ segment width, segment width 88% of length; segment 5 nearly fully overlapped by segment 4; segment 6, width 45% of length. Peraeopods 5-7: segment 6 not expanded anteriorly; dactyl without facial striations. Pleopods: with 2 coupling hooks. Uropod 1: peduncle, posteroventral spinous process short, underlying 50% of the inner ramus, inner and outer rami with 8 and 6 mid-dorsal spines respectively, terminating in a fringe of cusps ventral to the apical spine group. Uropod 2: peduncle, posteroventral spinous process underlying 12% of the inner ramus. Uropod 3: outer ramus with 2 sequential, closely approximated cusps proximal to the basally immersed, dorsally recurved spine, many small additional cusps in the area of the two major cusps, and a single seta originating at the insertion of the recurved spine; inner ramus with 2 medial spines in addition to the single apical spine. Telson: setose only at the lateral cusps.

CONDITION: Rehydrated from original dry mount. Right appendages, telson and mouthparts slide mounted.

ADULT FEMALE. (Not type; ZMUC, Scotland: Sutherland: Stoer Bay, 22 October 1937, D. M. Reid, collector). Length 7.0 mm. Antenna 2: segment 5, posterior margin with long filter setae proximally and plumose setae distally. Gnathopod 1: coxa, ventral margin slightly concave. Gnathopod 2: coxal margins, anterior 38% and posterior 49% of ventral length, ventral margin straight; segment 6, hinge tooth pronounced, palmar setae moderately dense throughout, but not so dense as to obscure the palm's shape, palmar angle bulbous, distal to and fairly distant from the defining spines; dactyl, inner margin straight, tip fitting into a depression between the palmar angle and defining spines.

CONDITION: Without left peraeopods 5-7. Right appendages, telson and mouthparts slide mounted. Remaining appendages with the carcass.

VARIATION: Body length at maturity: male 3.1-11.6 mm, female 3.8-6.6 mm. Both males and females develop plumose setae on the posterior margin of the antenna 2 peduncle segment 5 and flagellum segment 1. The length of the simple filter setae declines to zero in the male and near zero in the female, but only on segment 5; segment 4 setae remain long. The number of flagellum segments is usually 6 but may be 5 (these appearing to be 5 and 4 at low magnification, as the last segment is difficult to distinguish). The shape of the male's gnathopod 1 palm changes with age from convex to straight to slightly concave; the female's remains convex. Male gnathopod 2 development is illustrated in Figs. 42-45. The position where the adult's thumb will originate is evident in larger subadult males. Minor forms have a toothed dactyl (Figs. 30, 43). The uropod 3

inner ramus usually sports 1 or 2 medial spines; however, in smaller individuals these may be absent.

TYPE MATERIAL: Holotype, male (BMNH), type no. 603a, England: South Devon: Torcross (50°13'N, 3°40'W), date unknown, G. Montagu, collector.

OTHER MATERIAL: Approximately 2000 specimens from the U.K., Ireland, Iceland, Norway, Faeroe Islands, West Germany (Helgoland), France, Northern Spain and Portugal (BMNH, MHNP, NRS, RSME, ZMUB, UHSM, USNM, IITM, ZMUC, K. Anger, G. Krapp-Schickel, J. C. Marques, P. G. Moore).

REMARKS: Jassa falcata, J. herdmanni, and J. pusilla are sympatric. J. falcata is generally a shallower dweller than J. pusilla but J. herdmanni can be found on the same substratae with J. falcata. Jassa falcata and J. herdmanni can be readily differentiated from J. pusilla by checking for dorsal setae on the mandibular palp segment 2 (present in J. falcata and J. herdmanni, absent in J. pusilla). Jassa falcata differs from J. herdmanni in antenna 2 setation (plumose setae in larger males and females on peduncle segment 5 and flagellum segment 1; never plumose setae in J. herdmanni), antenna 2 flagellum segment number (maximum 7 in J. falcata, 6 in J. herdmanni), the male's gnathopod 1 palm shape (shallowly concave in J. falcata, broadly convex in J. herdmanni), male and female gnathopod 2 palm shape (Figs. 16, and 42-45), and uropod 3 inner ramus spination (1-2 medial spines in J. falcata, none in J. herdmanni). Overall, J. falcata appears slenderer and matures at a smaller body size than does J. herdmanni.

Sars (1894) was the first to recognize J. pulchella as synonymous with J. falcata, although he mistakenly considered that J. falcata was sexually immature and J. pulchella fully adult. The holotype of J. falcata is a minor form adult male. The male syntype of Jassa pulchella, BMNH 296e, 5.7 mm, which is the major form adult, is herein designated lectotype for the series 296a-g.

CONFIRMED LITERATURE: There has been a considerable amount written about J. falcata which most likely mistakenly deals with other species of Jassa. J. falcata is actually restricted to northeastern Atlantic waters. Sexton and Reid (1951) were mistakenly dealing with 4 species: J. falcata and J. herdmanni as their "Narrow Form", J. marmorata as their "Broad Form" and J. alonsoae as their "Large Polar Form." Specimens sent by K. Anger as being representative of the specimens described in Nair and Anger's (1979, 1980) life history studies of J. falcata were in actuality a mix of J. marmorata (majority) and J. falcata (minority). Specimens described by Arresti et al. (1986) as J. falcata were actually a mix of J. falcata, J. herdmanni, and J. marmorata. Specimens described by Marques (1984) were a mix of J. herdmanni (mainly) and J. falcata. The Podocerus falcatus listed by Walker (1895) were also a mixture of these two species. Although Moore (1973, 1984) recognized the differences between J. falcata and J. marmorata, he was unaware that J. herdmanni could be a common co-inhabitant of J. falcata populations. It is therefore recommended that literature references to J. falcata, outside of those confirmed herein, be considered invalid unless the specimens to which they refer have been re-identified using the information provided

herein.

19. JASSA HERDMANI (Walker)

Figs. 16, 17, 32, 42-45

Podocerus herdmani Walker, 1893, 78, 79, fig. 13; Walker, 1895, 314, 315Jassa falcata: Sexton and Reid, 1951 (partor Narrow Form), 35-38, 42, 43, plates 6-8, plate 10, 2a-d, plate 12, 7a-c, plate 18, 12 a,c,d, plate 19

ADULT MALE. Neotype (here designated): Length 6.0 mm. Antenna 2: overlapped by antenna 1 only to about $3/4$ along segment 5; segment 5 and flagellum, posterior margin without plumose setae, simple filter setae about $1/2$ the length of those of the juvenile; flagellum 5 segments, the last minute, segment 1 45% of full length. Mandible: palp segment 2 with a dorsal fringe of setae; raker spines 4 right, 5 left. Maxilla 1: palp without setae at the base of segment 1, segment 2 with 1 row of facial setae. Gnathopod 1: coxal margins, anterior 98% of dorsal length, ventral margin sinuous; segment 2, anterior and posterior margins with only a few minute setae; segment 5, posterior lobe 50% of anterior margin length, without an anterodistal setal cluster; segment 6, palm convex; dactyl cusped along most of the posterior margin, with 2 rows of facial striations. Gnathopod 2: coxal margins, anterior 28% and posterior 50% of ventral length, ventral margin sinuous and convex; gill small; segment 2, anterolateral flange without long filter setae; segment 5, posterior lobe without a distal seta; segment 6, anterior margin without setae proximally, hinge tooth triangular, anteriorly shallowly bifid, setae throughout the palm, thumb 18% of segment 6 length, distally squared, posterior margin evenly concave to the location of the defining

Fig. 32. Jassa herdmani. All views of males unless indicated otherwise (from Sexton and Reid, 1951). x58.

setae, setae quite closely approximated, accompanied by 3 spines; dactyl, inner margin with a strongly pronounced protuberance extending into the palmar incision. Peraeopod 3: coxa, greatest depth posterior of centre; segment 2, anterior margin sinuous, not broadly convex; segment 4, anterior marginal setae single and evenly spaced, $1/3$ to $1/2$ segment width, segment width 87% of length; segment 5 fully overlapped by segment 4; segment 6, width 55% of length. Peraeopods 5-7: segment 6 not expanded anteriorly; dactyl without facial striations. Pleopods: with 2 coupling hooks. Uropod 1: peduncle, posteroventral spinous process underlying 40% of the inner ramus, inner and outer rami with 4 and 7 mid-dorsal spines respectively, terminating in a fringe of cusps ventral to the apical spine group. Uropod 2: peduncle, posteroventral spinous process underlying 5% of the inner ramus. Uropod 3: outer ramus with 2 sequential, closely approximated cusps proximal to the basally immersed, dorsally recurved spine, additional numerous small cusps proximally, and a single seta originating at the insertion of the recurved spine; inner ramus with only the single apical spine. Telson: setose only at the lateral cusps.

CONDITION: With all appendages. Right appendages, telson, and mouthparts slide mounted; carcass with all left appendages.

ADULT FEMALE. (Not type; NMNS 121986-041, England: Plymouth: Langstone Harbour, 26 March 1986, R. J. Trott, collector). Length 7.2 mm. Antenna 2: segment 5 without plumose setae distally. Gnathopod 1: coxa, ventral margin straight. Gnathopod 2: coxal margins, anterior 39% and posterior

83% of ventral length, ventral margin slightly convex; segment 6, hinge tooth pronounced, palmar setae moderately dense throughout, but not so dense as to obscure the palm's shape, palmar angle acute, distal but fairly close to the defining spines; dactyl, inner margin straight, tip fitting into a depression between the palmar angle and defining spines.

CONDITION: Without left peracopod 7.

VARIATION: Body length at maturity: male 3.3-9.5 mm, female 4.9-7.3 mm. Most specimens have a 5 segmented antenna 2 flagellum (which appears 4 segmented, as the terminal segment is minute). Smaller specimens may have 4 segments and larger specimens 6. The filter setae on the antenna 2 posterior margin become shorter in adult males but are never absent and never replaced by plumose setae. Male gnathopod 2 development is illustrated in Figs. 42-45. Minor forms have a toothed dactyl, the tooth being more pronounced in small minors. As in most other species of Jassa the defining spines are present in smaller majors and minors but disappear in larger members of either form. Spine loss never occurs in juveniles, and never in females of any age.

TYPE MATERIAL: Neotype (here designated), male (BMNH), 1925.9.8.1686, England: Isle of Man: Port Erin (54°5'N, 4°45'W), November 1892, A. O. Walker, collector.

OTHER MATERIAL: Approximately 1500 specimens from the U.K., Denmark, Netherlands, northern and southern France, northern Spain, northern

Portugal, Algeria and Gambia (BMNH, MHNP, NMNS, RSME, ZMUH, USNM, ZMUC, ZMIK), M. Ledoyer and J. C. Marques).

REMARKS: Features that differentiate J. herdmani from its closest congeners J. falcata and J. pusilla are discussed in the remarks section for J. falcata. The neotype was selected from A. O. Walker's collection which he described in 1895 as Podocerus herdmani. The type, from Laxey Bay, Isle of Man, is not in Walker's collection at the British Museum (Natural History) and is assumed to have been lost. The proximity in location, collecting time, collector and gnathopod 2 appearance (both are minor forms) were deciding factors in the selection of the Port Erin specimen as neotype. Jassa herdmani has been found co-occurring with J. falcata, J. pusilla and J. marmorata.

CONFIRMED LITERATURE: Since J. herdmani is sympatric with J. falcata and can be easily confused with it, especially if immature, it is quite possible that some of the literature on J. falcata actually pertains to J. herdmani. Descriptions of J. falcata by Arresti et al. (1986) and Marques (1984) and of the Narrow Form of J. falcata by Sexton and Reid (1951) were actually based on a mixture of the two species.

5. PLUMULOJASSA n.g.

ADULT MALE. Maximum body length 4.0 mm. Head lobe: triangular, apically acute. Antenna 1: accessory flagellum 1 segment. Antenna 2: slightly stouter than antenna 1 but hardly longer, filter setae somewhat shorter, never with plumose setae; flagellum with at least the last two segments bearing posteriorly curved spines, first segment considerably longer than any of the following segments. Maxilla 1: inner plate bearing a few short, fine setae. Gnathopod 1: coxa rectangular; segment 6 with 3 defining spines (medial-lateral-medial), these mid-distant along the palm. Gnathopod 2: coxa deeper posteriorly; segment 2, anterolateral and anteromedial margins clothed in long plumose setae; segment 5 less than $1/4$ segment 6 length; segment 6, palm with a broad, trifid hinge tooth, defined by two narrow, apically acute teeth, these reaching nearly to the depth of the hinge tooth, thus giving the palm a transverse appearance, neither tooth appearing dramatically at the last molt; dactyl shorter than segment 6, inner margin slightly sinuous, tip reaching beyond the posterior defining tooth; dactyl, cusps reduced to small buttons interspersed with a few short setae. Peraeopod 3: coxa deepest at the centre; segment 2 not slenderer at maturity, margins convex; segment 4 over-lapping segment 5, anterior margin bearing a series of single plumose setae; segment 6 not posteriorly spinose. Peraeopods 5-7: at least one segment 2 posterodistally produced; segments 4 and 5, posterior margin not spinose; dactyl, posterior (outer) margin not cusped distally, anterior (inner) margin bearing a seta only at the unguis. Urosome: segment 1 bearing a pair of setae dorsally. Uropod 3: peduncle mid-

ventrally setose, without mid-dorsal spines, but with a crown of 2 clusters of spines around the dorsodistal margin, and a small cluster of setae distolaterally; outer ramus not setose mid-dorsally, tipped by a basally immersed, dorsally recurved spine, a single seta at the spine's point of immersion and a dorsal cluster of minute cusps proximal to the spine, none of these cusps particularly larger than the other. Telson: cusps accompanied by setae (1 long, single and 2 short, plumose) but without spines.

ADULT FEMALE. Body length at maturity 3.1-4.0 mm. Brood plates broad, setae abundant. Antenna 2: posterior filter setae long, not shortening with age. Gnathopod 1: segment 2 not flanged, without plumose setae. Gnathopod 2: segment 6 much larger and different in shape from segment 6 of gnathopod 1 but differing only in the following respects from the adult male: size slightly smaller, hinge tooth bifid, distal palmar tooth more central, proximal tooth little more than an acute expansion, bearing a large, single medial defining spine; dactyl, inner margin straight, tip apposing the defining spine.

TYPE SPECIES: Podocerus ocius Bate, 1862 (monotypy).

ETYMOLOGY: The name refers to the abundant plumose setae on the anterior legs, particularly gnathopod 2, which makes this genus unmistakable, even at young stages.

PLUMULOJASSA OCIA (Bate, 1862) new combination

Fig. 33, 34, 46-48

Podocerus ocius Bate, 1862, 257: Bate and Westwood, 1862, 450: Della Valle, 1893, 448, 449, tav. 14, figs. 11-27

Jassa ocius: Stebbing, 1906, 655

Jassa ocia: Chevreux and Fage, 1925, 347, 348, fig. 355: Gurjanova, 1951, 909, 910, fig. 630: Lincoln, 1979, 554, fig. 266 g-j

ADULT MALE. Neotype (here designated): Length 3.5 mm. Antenna 2: overlapped by antenna 1 to the end of segment 5; segment 5, simple setae as long as those of the juvenile; flagellum 4 segments, the last minute, segment 1 71% of full length. Mandible: palp segments 2 and 3 without dorsal fringe of setae; raker spines 2 right, 3 left. Maxilla 1: palp without setae at the base of segment 1, segment 2 with 1 row of facial setae. Gnathopod 1: coxal margins, anterior 100% of dorsal length, ventral margin shallowly concave; segment 2 flanged both anteriorly and posteriorly, anterior margin fringed with long plumose setae laterally and medially, ventral margin with a few plumose setae throughout; segment 5, posterior lobe 58% of anterior margin length, anterodistal setal cluster long, 67% of anterior margin; segment 6, palm convex, defined by 3 spines; dactyl cusped along most of the inner margin, without facial striations. Gnathopod 2: coxal margins, anterior 24% and posterior 59% of ventral length, ventral margin convex; gill absent; segment 5, posterior lobe with a short, distal seta; segment 6, anterior margin with a few individual plumose setae proximally (setae about the width of

Fig. 33. Plumulojassa oia. Adult male. A, gnathopod 1; B, gnathopod 2; C, peraeopod 4; D, head and gnathopods; E, peraeopod 6. Views A-C, and E from Lincoln (1979). View D from the original description of Podocerus dentex Czerniavski, 1868.

Fig. 34. Plumulojassa ocia. Tip of right uropod 1 inner and outer rami,
showing the fringe of cusps on the apex of the outer ramus. x5000.

segment 2); hinge tooth rectangular, trifid, palm and lateral face clothed in long plumose setae, palm with 2 defining teeth, each bearing plumose setae proximally but not apically, neither accompanied by a defining spine, defining teeth 14% (distal) and 17% (proximal) of segment 6 length. Peraeopod 3: segment 4, setae 1/2 segment width, segment width 75% of length; segment 5 45% overlapped by segment 4; segment 6 50% of length. Peraeopods 5-7: segment 6 not markedly expanded anteriorly; dactyl without facial striations. Pleopods: long, each with 2 coupling hooks. Uropod 1: peduncle, posteroventral spinous process underlying 36% of the inner ramus, inner and outer rami with 0 and 2 mid-dorsal spines respectively, terminating in a fringe of cusps ventral to the apical spine group (Fig. 35). Uropod 2: peduncle, posteroventral spinous process underlying 5% of the inner ramus. Uropod 3: inner ramus tipped with a single spine, without spines mid-dorsally.

CONDITION: Without right antenna 2, left peraeopods 5-7 and right peraeopods 5. Remaining right appendages, telson and mouthparts slide mounted. Remaining left appendages with the carcass.

ADULT FEMALE. (Not type; MHNP An. 2664, France: Loire-Atlantique: Le Croisic, E. Chevreux, collector). Length 3.5 mm. Antenna 2: segment 5 without plumose setae distally. Gnathopod 1: coxa, ventral margin straight. Gnathopod 2: coxal margins, anterior 27% and posterior 87% of ventral length, ventral margin convex.

CONDITION: Ovigerous. Without right antenna 2 and left pereopods 6 and 7. Remaining right appendages slide mounted. Remaining left appendages with the carcass.

VARIATION: Body length at maturity: male to 4.1 mm, female 2.4-4.0 mm. Sexual dimorphism in Plumulojassa ocla is confined to difference in density of plumosity and slight difference in gnathopod 2 segment 6 shape (Figs. 46-48). As in all the Ischyroceridae studied here the female's coxae are somewhat deeper and less divergent, and the gnathopod 2 is somewhat smaller than the male's. Unlike Jassa, both sexes develop a thumb in the gnathopod 2 palm, but this develops isometrically. The extension at the defining spine is considered to be an acute production of the palm, rather than a second thumb. The position of the palmar thumb is sex and age variable, being closer to the palm's definition in older males. Large males also lose their single long defining spine. The dactyl's inner margin becomes slightly sinuous in older males. The female and juvenile are less densely plumose than the male and lack the flange on segment 2 of gnathopod 1.

TYPE MATERIAL: Neotype, male (BMNH), registration no. 1987-514, England: Cornwall: Scilly Isles: St. Agnes: St. Wenna's Cove, west side (49°50'N, 6°20'W), 1 August 1973, extreme low water spring, R. Parslow, collector.

OTHER MATERIAL: Sixty-six specimens from the U.K. (Jersey), France

(English Channel, Bay of Biscay and Mediterranean coasts), Spain (Bay of Biscay) and Portugal (Atlantic coast).

REMARKS: Of Northern Hemisphere ischyrocerids, Plumulojassa is more similar to Parajassa than to Jassa in the way that it develops. The purpose of the appendage plumosity is speculative. Since the setae occur in both sexes, only at the front of the animal, and laterally more than medially, they may be used for feeding, by capturing particles that escape the coarser net formed by the fan of antennal setae. Plumulojassa ocia has been recorded from Laminaria holdfasts (Jones, 1948), sponges (Chevreux and Fage, 1925; Jones, 1948) and the surface and coelomic fluid (fluid of the respiratory "cloaca"?) of sea cucumbers (Vader, 1973). The plumose setae could perhaps be used to blot up detritus particles that had settled on the host.

Jassa dentex (Czerniavski, 1868), which was previously placed with Jassa ocia by Della Valle (1893) and with Jassa odontonyx (now synonymous with J. pusilla) by Stephensen (1942) is unmistakably Plumulojassa ocia (Fig. 33D). Unlike the species of Jassa, P. ocia is so distinctive that records of the distribution and ecology of this species are probably taxonomically correct (e.g. Heller, 1866; Walker, 1895; Jones, 1948; Bellan-Santini and Ledoyer, 1973; Moore, 1984; Marques, 1984; Marques and Bellan-Santini, 1985; Arresti et al, 1986).

According to Joan Ellis (BMNH), "I have not found the type(s) of this species, nor any evidence that it was ever in the BMNH collection, in spite of Bate's (1862) indication to the contrary. Also, in 1895 A. O. Walker (Ann. Mag. Nat. Hist. (6) 15:473) stated that the specimen was not

in the collection that Bate presented to the Museum. I suppose one must assume that the type material of Jassa ocia is lost." (personal communication, 31 July 1984). A neotype is accordingly erected herein.

6. HEMIJASSA Walker, 1907

Hemijassa Walker, 1907, 38

ADULT MALE. Body length at maturity 13-18 mm. Head lobe: squared, angles acute. Antenna 1: accessory flagellum 2 segments, the second minute, only the second segment setose. Antenna 2: stouter and longer than antenna 1, the filter setae progressively shorter from segment 4 proximally to segment 5 distally; flagellum with all but the first segment bearing spines on the posterior margin, first segment considerably longer than any of the following segments. Maxilla 1: inner plate bearing a few short, fine setae. Gnathopod 1: coxa rectangular; segment 6 with 4 defining spines, these proximal of centre. Gnathopod 2: coxa not deeper posteriorly; segment 2, filter setae simple or finely barbed and located on the anterolateral flange only; segment 5 less than $1/4$ segment 6 length; segment 6 with a pronounced triangular, multiply incised tooth below the dactyl hinge, and a larger acute thumb with 3 minute palmar defining spines at its tip, thumb setose on both inner and outer margins, not markedly increasing in size at any one molt; dactyl shorter than segment 6, inner margin not expanded, tip resting on the tip of the thumb or between the thumb's anterior margin and the palm; dactyl cusps reduced to small buttons interspersed with a few short setae. Peraeopods 3 and 4: coxae rectangular; segment 2 not slenderer at maturity, margins more parallel than convex; segment 4 slightly overlapping segment 5, anterior margin bearing discrete clusters of setae; segment 6 not posteriorly spinose. Peraeopods 5-7: at least one segment

2 posterodistally produced; segments 4 and 5, posterior margin not spinose; dactyl without facial serrations, posterior (outer) margin not cusped distally, anterior (inner) margin bearing a row of setae along its length. Urosome: segment 1 bearing a pair of setae dorsally. Uropod 3: peduncle setose and spinose mid-ventrally, without spines mid-dorsally, but with a crown of 2 clusters of spines around the dorsodistal margin, and a cluster of setae distolaterally; outer ramus not setose mid-dorsally, tipped by a basally immersed, dorsally recurved spine and minute serrations dorsally, but without cusps. Telson: each corner with a pair of cusps and accompanying setae (1 long, simple and 2 short, plumose) but without spines.

ADULT FEMALE. Body length at maturity 14-20 mm. Brood plates broad, setae abundant. Antenna 2: peduncle, posterior filter setae long, not shortening with age. Gnathopod 2: segment 6 and dactyl much larger and different in shape from that of the male. Peraeopods 3 and 4: segment 2 slender as in the male.

TYPE SPECIES: Jassa goniamera Walker, 1903 (monotypy).

REMARKS: Walker first suggested the genus name in 1903 but decided to place his new species (goniamera) under Jassa. In 1907 he formally erected the genus for H. goniamera but taxonomists appear to have disregarded this change and have continued to assign H. goniamera to Jassa. Subsequently Sexton and Reid (1951) submerged the genus and species under Jassa falcata. Hemijassa is formally re-erected here.

HEMIJASSA GONIAMERA (Walker, 1903)

Figs. 35, 46-50

Jassa goniamera Walker, 1903, 61, 62, pl. 11, figs. 98-107 (part, according to Thurston (1974b), specimens less than 5 mm long are Parajassa georgiana): Stebbing, 1906, 739: Schellenberg, 1931, 253: Thurston, 1974b, p. 100

Hemijassa goniamera Walker, 1907, 38

Jassa falcata: Sexton and Reid, 1951, 72, 75, 77-78, 81-83, 85, 86

ADULT MALE. Lectotype (here designated): Length 18.3 mm. Antenna 2: overlapped by antenna 1 to midway along segment 5; segment 5, posterior marginal setae very short and simple, minute compared with those of the juvenile; flagellum 8 segments, the last 1/2 the size of the second last, segment 1 46% of full length. Mandible: palp segments 2 and 3 with a dorsal fringe of setae; raker spines 6 right, 8 left. Maxilla 1: palp without setae at the base of segment 1; segment 2 with many scattered rows of facial setae. Gnathopod 1: coxal margins, anterior 72% of dorsal length, ventral margin straight; segment 2, anterior margin with a fringe of long setae laterally, vertical setae just as long and wide ranging, but more scattered; segment 5, posterior lobe 47% of anterior margin length, anterodistal setal cluster short, 25% of the anterior margin length; segment 6, palm convex, defined by 4 spines; dactyl cusped along the full length, without facial striations. Gnathopod 2: coxal margins, anterior 87% and posterior 100% of ventral length, ventral margin straight; gill large; segment 2, anterolateral flange with a row of long,

Fig. 35. Hemijassa goniamera. Lectotype, adult male, 18.3 mm; paralectotypes, juvenile male, 6.1 mm, and adult female, 19.9 mm. Cape Adare, McMurdo Sound, Antarctica, 5 November 1902, Southern Cross Expedition. Lateral views: whole body, juvenile male, female antenna ?, and left mandible; dorsal view: telson, and uropod 3; other views medial. Appendages are of the adult male unless indicated otherwise. Scale 0.1 mm.

simple filter setae (setae about 1/2 segment width); segment 5, posterior lobe with a cluster of distal setae; segment 6, anterior margin with a series of clusters of short setae proximally (setae about 1/2 segment 2 width). Pleopods: long, pleopod 3 with 8 coupling hooks. Uropod 1: peduncle, posteroventral spinous process underlying 41% of the inner ramus, inner and outer rami with 12 and 13 mid-dorsal spines respectively, not terminating in a fringe of cusps ventral to the apical spine group. Uropod 2: peduncle, posteroventral spinous process underlying 25% of the inner ramus.

CONDITION: Left antenna 1, tip of flagellum missing, without left pereopod 7. Right appendages, telson and mouthparts slide mounted.

ADULT FEMALE. Paralectotype: Length 19.9 mm. As in the genus description.

CONDITION: With all appendages. Right appendages, telson and mouthparts slide mounted.

VARIATION: Body length at maturity: male to 17.6 mm, female 13.8-19.9 mm. Hemijassa goniamera exhibits sexual dimorphism in the antenna 2. The antenna 2 development is much like that in species of Jassa, with the filter setae shortening and the segments lengthening allometrically. The female's antenna 2 lengthens isometrically and the setae remain long. Gnathopod 2 morphology and development are both unlike that of Jassa. The "thumb" arises at, rather than distal to, the palmar defining spines,

and occurs in both sexes. Its growth is gradual, rather than metamorphic (Figs. 49 and 50). In effect, the "thumb" could be considered homologous to the ledge that develops at the defining spines in Jassa morinot and J. ingens, and thus bears no homology to the Jassa thumb at all. The lack of difference in pereopod 3 and 4, segment 2 shape is also suggestive of a different sexual life style.

TYPE MATERIAL: Lectotype, male (BMNH), registration no. 1987:515, Antarctica: Ross Sea: McMurdo Sound: Cape Adare ($71^{\circ}17'S$, $170^{\circ}14'E$), "Southern Cross" Expedition, 5-10 November 1902, A. O. Walker, collector. Paralectotypes, 5 adult males, 9 adult females, 6 juvenile males and 10 juvenile females, registration no. 1902.11.5:6-10 (part), same location.

OTHER MATERIAL: Twenty-eight specimens from South Shetland Islands (Clarence Island), South Sandwich Islands (Visikoi Island) Weddell Sea Graham Region (Cape Norvegia), Adélie Land, Commonwealth Bay and the Ross Sea McMurdo Sound (Cape Adare, Coulman Island, Flagon Point) (AM, BMNH, ZMUC, D. Bellan-Santini).

3.1.4. Sex- and age-related variation in *Jassa* and comparison with outgroup species

Secondary sex change in male *Jassa* is most marked in the second gnathopod's grasping area (propod and dactyl) and occurs to a lesser extent in the first gnathopod, antenna 2, and in the bases of pereopods 3 and 4.

3.1.4.1. Sexual development of the second gnathopod

3.1.4.1.1. Changes in live *Jassa marmorata*

Fig. 36 illustrates the change seen by Sexton and Reid (1951) in the second gnathopod of four captive males of *Jassa marmorata*. The palms of young juveniles were found to be similar in both sexes until after the development of the primary sex characters. Then the palm of the male became less convex in successive molts, taking on, as they termed it, a "cut across" shape. At the last molt, thumb production marked the start of the male's sexual activity.

4

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Fig. 36. Jassa marmorata, male. Morphological changes in the second gnathopod upon approaching and reaching adulthood in four individuals of differing size. Figures from Sexton and Reid (1951), as Jassa falcata, Broad Form. From top to bottom row, plate 16 specimen 10, plate 21 specimen 14 (2), plate 15 specimen 9, and plates 13 and 14 specimen 8. All figures x58.

JUVENILE

SUBADULT

ADULT

3.1.4.1.2. Adult male dimorphism

To assess intraspecific variation in morphology of the second gnathopod, plots were made of the position of the thumb's origin for all species of Jassa for which sufficient specimens were available (J. stauderi, J. slatteryi, J. marmorata, J. falcata, J. morinói, J. herdmani, and J. alonsoae). For all species it was found that the adult males differentiated into two groups: a minor form, in which the thumb originated distally, and a major form, in which the thumb originated proximally. Fig. 37 shows this result for J. stauderi and J. slatteryi. Figs. 38 and 39 show coincident difference in thumb and segment 6 length. Minor form individuals are smaller bodied and have a shorter segment 6 and a smaller thumb than major form individuals of the same body size. Furthermore, the species themselves differentiate into two groups, these defined by the proportion and size relation of the two forms. In the type 1 group (here defined), comprising J. stauderi, J. marmorata, and J. falcata, the minor form is rare and always small sized. In the type 2 group, comprising J. slatteryi, J. morinói, J. herdmani, and J. alonsoae, the minor form is common, and although smaller than the major form on average, spans as great a size range. Repeated collection from populations of J. stauderi, a type 1 species, over time (Fig. 40) and latitude (Fig. 41) demonstrates that the proportion, morphology and size range of the males, although variable, consistently conforms to type 1.

Fig. 37. Male Jassa staudei (left) and Jassa slatteryi (right). Scatter plot and histogram of thumb position as a function of the second gnathopod's segment 6 length. Jassa staudei collected at Friday Harbor Marine Lab, 2 October 1984. Jassa slatteryi from various locations.

Fig. 38. Male Jassa staudei (left) and Jassa slatteryi (right). Scatter plot and histogram of thumb length as a function of body length. Jassa staudei collected at Friday Harbor Marine Lab over the dates plotted in Fig. 40. Jassa slatteryi from various locations.

Fig. 39. Male Jassa staudei (left) and Jassa slatteryi (right). Scatter plot and histogram of the second gnathopod's segment 6 as a function of body length. Jassa staudei collected at Friday Harbor Marine Lab, 2 October 1984. Jassa slatteryi from various locations.

Fig. 40. Jassa staudei, male. Gnathopod 2, segment 6 thumb length. Temporal collections from the east pressure head tank, Friday Harbor Marine Lab, San Juan Island, Washington. Plots show most or all thumbed males and most similarly sized juveniles.

Fig. 41. Jassa staudei, male. Thumb length as a function of body length. Geographic variation. From top to bottom: Barkley Sound, B.C., 27 June 1976, low intertidal; Friday Harbor, Washington, 2 October 1984, east pressure head tank; Point Delgada, California, 5 June 1986, shallow subtidal; Albion Cove, California, 29 June 1978, 20 m depth.

Bamfield, BC
48°50'N

Friday Harbor, Wash.
48°32'N

Pt. Delgada, Calif.
40°02'N

Albion Cove, Calif.
39°15'N

3.1.4.1.3. Interspecific differences in morphology

Figs. 42-45 illustrate, respectively, the male's second gnathopod palm and dactyl shape in the small juvenile, minor form adult, large juvenile, and major form adult of Jassa. The species have been illustrated at as closely equivalent developmental stages as possible. Using Sexton and Reid (1951) for guidance, the small juvenile (Fig. 42) would be considered to be at an antepenultimate or penultimate molt to the minor form (Fig. 43). The large juvenile (Fig. 44) would be penultimate to the large major form (Fig. 45). The small juvenile's second gnathopod (Fig. 42) is similar in size and shape to that of the female (Fig. 16). In the large juvenile (Fig. 44), the location of the adult's thumb apex is indicated, or in some species a small thumb is present. The dactyl, too, is different, being more sinuous on the inner face. Dactyl sinuosity is also a feature of the adult female. Dactyl expansion is most pronounced in the major form adult (Fig. 45). In many species (J. staudei, J. oclairi, J. pusilla, J. falcata, J. alonsoae and J. hartmannae), the minor form adult has a different dactylar shape. In these, the expansion is more acute and distal to the hinge, so that the apex projects into the palm, rather than resting against the hinge tooth. Toothing is a consistent feature of the minor form for those species that exhibit this character. Such toothing never occurs in the major form. Each species of Jassa is distinctive in the range of morphological variation that it encompasses. These interspecific differences are most pronounced at the upper end of the size scale, that is, in the major form adult (Fig. 45). The longest thumb is developed by major forms of J.

Fig. 42. Jassa. Male gnathopod 2 palm shape in the small juvenile. MAR, J. marmorata; MOR, J. morinói; SLA, J. slatteryi; CAR, J. carltoni; MYE, J. myersi; STA, J. staudei; OCL, J. oclairi; BOR, J. borowskyae; PUS, J. pusilla; FAL, J. falcata; HER, J. herdmani; ALO, J. alonsoae; JUS, J. justí; GRU, J. gruneri; HAR, J. hartmannae; ING, J. ingens. Small juvenile state unknown for J. shawi (SHA), J. thurstoni (THU), and J. fenwicki (FEN). All setae but those at the defining spines omitted. All views lateral. Scale 0.1 mm.

Fig. 43. Jassa. Male gnathopod 2 palm shape in the minor form adult. Codes as in Fig. 42. State unknown for J. carltoni, J. shawi, J. justi, J. gruneri, and J. fenwicki. All setae but those on the thumb omitted. All views lateral. Scale 0.1 mm.

Fig. 44. Jassa. Male gnathopod 2 palm shape in the large juvenile. Individuals of several species have a large thumbed cuticle inside. Codes as in Fig. 42. State unknown for J. gruneri, J. hartmannae, J. thurstoni, and J. fenwicki. All setae but those in the thumb area omitted. All views lateral. Scale 0.1 mm.

Fig. 45. Jassa. Male gnathopod 2 palm shape in the major form adult. Codes as in Fig. 42. State unknown for J. shawi and J. gruneri. All setae but those in the thumb area omitted. All views lateral. Scale 0.1 mm.

falcata, the shortest by J. myersi, the widest by J. marmorata, J. stauderi and J. oclairi. A thumb with indented tip is unique to J. pusilla; one with strong defining spines extending from a ledge marks J. morinoti or J. ingens.

When using sexually variable appendages for identification it is essential to determine the effect of maturation on morphology and establish how sexual change develops, and then to compare specimens at equivalent developmental state. Failure to do so was the cause of Sars' (1894) erroneous separation of J. odontonyx from J. pusilla (the former is actually the minor form of the latter), and of Leach's (1814) confusion of J. falcata with J. pulchella (the former is the minor form of the latter). It is recommended that, in future, new species descriptions of Jassa be based on major form adult males. This has been done whenever possible for new species erected herein and for exemplars used for numerical analysis. Table 7 lists the developmental status for the male types of all species of Jassa.

Table 7. Developmental status of male types of Jassa.

Species	Juvenile		Adult	
		Minor	Major	Unknown
<u>J. marmorata</u>			X	
<u>J. morinot</u>			X	
<u>J. slatteryi</u>			X	
<u>J. carltoni</u>			X	
<u>J. myersi</u>				X
<u>J. staudel</u>			X	
<u>J. borowskyae</u>		X		
<u>J. oclafri</u>		X		
<u>J. shawi</u>	X			
<u>J. pusilla</u>			X	
<u>J. falcata</u>		X		
<u>J. herdmani</u>		X		
<u>J. alonsoae</u>			X	
<u>J. justii</u>				X
<u>J. gruneri</u>	X			
<u>J. fenwicki</u>			X	
<u>J. hartmannae</u>			X	
<u>J. thurstoni</u>			X	
<u>J. ingens</u>				X

3.1.4.1.4. Comparison with changes in outgroup species

Figs. 46-48 compare second gnathopod palm shapes in adult females, and juvenile and adult males of the outgroup species. Fig. 48 shows that Pleojassa lowryi, Pleojassa moori, Microjassa claustris, Ischyrocerus sp., and the unnamed ischyrocerid (IGE) do not produce a thumb at all. In Hemijassa goniamera, Ventojassa barnardi, Parajassa pelagica, and Plumulojassa ocia, the adult female's palm of each species (Fig. 46) resembles that of its male (Fig. 48). It is only in Microjassa cumbrensis, Neoischyrocerus lilipuna, Pleojassa wandeli, and Pleojassa multidentata that the second gnathopods are sexually dimorphic. In Microjassa and Neoischyrocerus, the female's second gnathopod does not differ from the first gnathopod. Only in the two species of Pleojassa do the male's and female's second gnathopods differ at maturity as they do in Jassa. Despite the similarity in sexual dimorphism, the second gnathopod of all species of Jassa differ from all outgroup species, including Pleojassa, in three ways. (1) In Jassa the thumb originates distal to the palmar defining spines; in the outgroup species the thumb arises at the spines. (2) The thumb's setation pattern is distinctive and consistent within Jassa, comprising a pair of clusters on the thumb (one lateral, one medial) and three clusters deriving from the defining spines; the thumb's tip and inner margin lack setae. In the outgroup species, the thumb's setae, if clustered, do not group in such a pattern; the thumb tip and inner margin are setose as well. (3) The palmar defining spines in Jassa are strong, three in number, and always present in the female, juvenile male, and small adults, but in most species are

Fig. 46. Adult female gnathopod 2 palm shape in Pleojassa wandeli (WAN), P. m. multidentata (MMU), P. m. orientalis (MOE), P. lowryi (LOW), P. moori (MOO), Hemijassa goniamera (GON), Ventojassa barnardi (BAR), Parajassa pelagica (PEL), Plumulojassa ocia (OCI), and Ishyroceridae n.g. (IGE). All setae omitted. All views lateral. Scale 0.1 mm.

Fig. 47. Juvenile male gnathopod 2 palm shape in outgroup species. Codes as in Fig. 46, with the addition of Microjassa cumbrensis (CUM), Neoischyrocerus lilipuna (LIL), Microjassa claustris (CLA), and Ischyrocerus sp. (ISP). All setae but those on the thumb and dactyl omitted. All views lateral. Scale 0.1 mm.

Fig. 48. Adult male gnathopod 2 palm shape in outgroup species. Codes as in Figs. 46 and 47. All setae but those on the thumb and dactyl omitted. All views lateral. Scale 0.1 mm.

lost in the larger adult. In outgroup species, the spines differ in number, or if the same number, are minute.

3.1.4.1.5. Interspecific differences in development

In Figs. 49 and 50 the size relationship of thumb and segment 6 length is compared for the males of type 1 and 2 species of Jassa (J. staudei and J. slatteryi) against P. wandeli and H. goniamera. The plots for J. staudei and J. slatteryi illustrate the development of all other species of Jassa; the plot for P. wandeli exemplifies that seen in the sexually dimorphic outgroup species (P. multidentata and M. cumbrensis--insufficient specimens were available for N. lilipuna), while the plot for H. goniamera exemplifies the pattern seen in all other outgroup species that produce a thumb. Two differences in development are evident. (1) In J. staudei, J. slatteryi, and P. wandeli, the male does not produce a thumb until after it exceeds the mature female in body size. In H. goniamera, thumbing occurs at less than the female's maturation size. (2) In J. staudei, J. slatteryi, and J. wandeli, thumb development is determinate. In H. goniamera, thumb development is indeterminate. (3) In J. staudei and J. slatteryi, the largest non-thumbed juvenile exceeds the adult female in body size. This is not the case for P. wandeli. (4) In J. staudei and J. slatteryi, the juvenile lacks a thumb. In some other species of Jassa, a small thumb is evident in larger penultimates (Fig. 44). In P. wandeli (and P. multidentata), however, the thumb is progressively incised over several molts before lengthening allometrically at the last molt. Thus the development of P. wandeli and P. multidentata seems intermediate between that of Jassa and the other outgroup species that have a thumb (M. cumbrensis excluded).

Fig. 49. Male gnathopod 2, segment 6 thumb length as a function of body length, plotted for the juvenile and adult male of Jassa staudei, J. slatteryi, Pleojassa wandeli, and Hemijassa goniamera. Hemijassa goniamera is not differentiated by maturity because growth is indeterminate. Zero values are not included in the regression calculation. Juveniles with an internal thumbed cuticle visible (i.e., penultimate) are indicated by a half closed circle. Values are standardized on the x axis by range of female maturity; on the y axis by range of thumb length.

Fig. 50. Male gnathopod 2, segment 6 length as a function of body length, plotted for the juvenile and adult male of Jassa staudei, J. slatteryi, Pleojassa wandeli, and Hemijassa goniamera. Hemijassa goniamera is not differentiated by maturity because growth is indeterminate. Zero values are not included in the regression calculations. Values standardized on the x axis by range of female maturity; on the y axis by range of thumb length.

Table 8. Comparison of sexual size relationships at maturity for Jesse and outgroup species. A dash indicates insufficient specimens. An asterisk indicates that male growth is indeterminate, thus preventing identification of maturation point.

Species	Smallest adult male	Smallest adult female	Largest adult male	Adult male size range
	Largest juvenile	Largest juvenile	Largest adult female	Adult female size range
	male (%)	female (%)	(%)	(%)
<u>J. marmorata</u>	54.0	105.4	132.9	179.8
<u>J. morinot</u>	46.4	-	118.3	128.5
<u>J. slatteryi</u>	47.4	68.5	129.0	129.2
<u>J. myersi</u>	-	-	132.1	-
<u>J. staudel</u>	62.9	96.5	142.9	134.8
<u>J. borowskyae</u>	54.0	84.4	138.9	203.3
<u>J. oclairi</u>	-	105.8	120.3	-
<u>J. pusilla</u>	57.9	-	-	-
<u>J. falcata</u>	35.9	-	142.5	-
<u>J. hardmani</u>	35.5	93.1	116.3	230.0
<u>J. alonsoae</u>	26.6	80.6	126.3	198.0
<u>J. ingens</u>	-	91.1	116.0	-
<u>P. wandell</u>	70.5	67.0	112.1	113.4
<u>P. m. multidentata</u>	-	102.9	-	-
<u>P. lowryi</u>	*	93.7	108.4	*
<u>P. moori</u>	*	100.0	94.1	*
<u>H. gnaniere</u>	*	77.6	88.3	*
<u>P. ocia</u>	*	117.2	102.0	*
<u>V. bernardi</u>	*	142.7	92.8	*
<u>Ischyrocerus</u> sp.	*	78.0	128.7	*
<u>P. pelagica</u>	*	74.6	101.1	*
<u>Ischyroceridae</u> n.g.	*	76.9	87.5	*
<u>M. cumbrensis</u>	55.5	-	133.3	262.5

sufficient specimens were available. In species where the male's state of maturity can be inferred from morphology (Jassa, P. wandeli and P. multidentata), maturation occurs at 27% to 71% of the body size of the largest juveniles. By contrast, in the female, the smallest adult is at least 67% of the largest juvenile in size. The males of Jassa achieve a greater maximal size than do the females, and the size range at maturity markedly exceeds the female's as well. In most of the outgroup species the maximal size differs less between the sexes.

3.1.4.2. Sexual development of the second antenna

In Jassa the second antennae bear pairs of long, regularly arranged filter setae on the posterior margin of segments 3 to 5 and clusters of short brush setae on the flagellum (Fig. 17). The filter setae are stiff and sparsely plumose, and the brush setae are scaled around a posterior groove (Fig. 51). The flagellum also bears a pair of posteriorly hooked spines at the junction of each segment (Fig. 51A). The first antennae are entirely equipped for filtering. The second antennae have a dual role: filtering in the proximal region and scraping detritus distally. The setation pattern and second antennal size are similar in both sexes until about the time of physiological maturity. Then in the male the filter setae shorten and the antennae enlarge. Species differ in the amount of each. No such change occurs in the female of any species. Antennal lengthening is most marked in the males of J. borowskyae, J. oclairi, and J. ingens. In J. slatteryi the male's second antennae grow to twice the width of the female's. Fig. 52 plots change in length for J. ingens. The purpose of the change in the male is unknown. The second antennae are prodded into crevices and other amphipods' tubes, and are the main appendage for assessing another amphipod on encounter. Antennal enlargement may be useful for agonistic encounters. Setal reduction may be necessary for streamlining the antennae for sexual assessment, may be a response to lesser metabolic requirement, or may indicate altered feeding method.

Many, but not all species of Jassa exhibit a setal change with increased body size, which is not sexually dimorphic. This is the

Fig. 51. Jassa staudei. Antenna 2, tip of flagellum. A, adult female; B, magnification of A, arrow showing the same seta; C, subadult male; D, magnification of C, arrow showing the same seta. A and C x1200; B and D x4700.

303
Fig. 52. Jassa ingens. Antenna 2 segment 5 length as a function of body length at different growth stages in the male and female.

production of plumose setae along the lateral and posterior margins of the segment 5 and flagellum (Fig. 51C). Figs. 51C and D suggest that the plumosity develops as a lengthening and spreading of the brush setae scales. Plumosity first appears on the first segment of the flagellum, but spreads onto peduncular segment 5, a region which did not previously sport brush setae. Setal change is related to size, not maturity, so that small thumbed males may lack the plumose setae, while large juveniles may be abundantly clothed. Plumose setae also develop in females, but only in the largest individuals. Since a female's mean size at maturity is smaller than a male's, relatively fewer females than males will be found with plumose second antennae. The development of plumose setae may be a consequence of changed metabolic need. Such would allow a partitioning of feeding strategies, whereby larger individuals depend increasingly on detritus. Species that do not produce plumose setae have more abundant flagellum spines.

All species of Pleojassa and Hemijassa exhibit antennal setal alteration similar to that of Jassa, but such change does not occur in phenetically more distinct outgroup species. Parajassa pelagica is sexually dimorphic in antennal setation but the change occurs over different parts of the antenna and involves different setae.

Fig. 53 shows segment 5 lengthening in P. wandeli. There is less shift in size than in J. ingens.

Fig. 53. Pleojassa wandeli. Antenna 2 segment 5 length as a function of body length in the juvenile and adult male.

3.1.4.3. Sexual development of the third and fourth peraeopod basis

The peraeopod 3 and 4 bases (segment 2), which hold the spinning gland, are more slender in the thumbed male than in the juvenile male. By contrast, in the female, the basis is broadly convex at any age. This relation holds in all species of Jassa, although it is more obvious in larger species. Pleojassa wandeli and P. multidentata also exhibit this shape change, but species with indeterminate growth do not.

3.2. Behavior

3.2.1. Tube building

Table 9 illustrates the propensity for tube building in Jassa marmorata and J. slatteryi. Nearly all adult females and two thirds of the juveniles constructed tubes during overnight isolation in a seawater system at Moss Landing Marine Lab, California. Seventeen of nineteen individuals which were offered either Ulva or a hydroid as substrate built their tube amongst the hydroid. All four individuals which were offered a choice of a branching red alga or Ulva selected the red alga. Not one built its tube on the glass surface. In the two cases where an adult male constructed a tube, the tube was thinner (more translucent) and it covered only half the body. The tube was constructed by glueing hydroid perianths or algal blades around the amphipod's body with the webbing spun from the tips of the third and fourth peraeopod dactyls. The tube was as long as the body, open ended, and translucent. If detritus was available it was incorporated into the tube mesh. If no biotic substrate was provided, the tube was attached to the container. In a strong, unidirectional current, the tube was vertical to the substrate, the animal facing the current with antennae extended. Where there was little current, the tube was horizontal, and the animal swept the area at either end with its antennae.

Table 9. Number of individuals of Jassa marmorata and J. slatteryi constructing a tube after isolation in a seawater system with native substrate after twenty-two hours. Total number observed is in parentheses.

Adult male	Adult female	Juvenile
2* (7)	17 (18)	4 (6)

* tube partially built, covering only head to pereopod segment 5.

3.2.2. Feeding

Species of Jassa filter suspended particles and scrape settled detritus with their antennae and first gnathopods. The antennae are well adapted for filtering and scraping. Each antenna bears long, scaled setae which, when expanded, filter a 180° radius around the head. The flagellum of the second antennae bears a pair of posteriorly hooked spines on each segment. The first gnathopods bear strong pectinate setae on the medial face of segments 3 to 6 for capturing food, cleaning the antennae, and delivering material to the mouthparts. The second gnathopods are used in food manipulation but are brought into action less often than the first pair. In strong currents the antennae are held in a passive filter feeding mode, and the tips of the antennae are flicked to the mouthparts at regular intervals. In slow moving water the second antennae are prodded onto the surrounding substrate, or extended for filtering and frequently cleaned by the mouthparts and first gnathopods. The mandibular palp also has a cleaning function. Its setae reach the proximal and medial margins of the antennae.

Field collected animals have a green digestive tract, indicating that phytoplankton are a major food source. Laboratory observed animals ate brine shrimp larvae, but did not actively search for them. J. falcata has been observed capturing nematodes while exploring a lab substrate (Boero and Carli, 1979). Nagle (1968) found crustacean remains and ostracods in the stomachs of J. marmorata collected from eelgrass.

The mouthparts work in concert to macerate the food and to move the material to the esophagus. The inner plates of the maxilliped macerate

laterally and the first maxillae move in synchrony. The second maxillae move antero-posteriorly, moving the food from the maxillipeds through the first maxillae to the mandibles. The mandibles bear both incisors and molars. While they move latero-medially, the upper lip moves antero-posteriorly, with the result that the food moves back to the esophagus.

Animals observed in static water were found regularly to reverse ends in their tubes. The pleon was held folded under the thorax, the pleopods beating continuously. Purchase on the tube wall was gained by the three pairs of posterior peraeopods and by the uropods. In a feeding mode the animal extended itself from the tube to the end of the second peraeon segment.

3.2.3. Locomotion

Although Jassa has been collected in plankton (Stebbing and Fowler, 1904; Schellenberg, 1926; Boero and Carli, 1979), it is most frequently benthic. Animals observed among the fouling biota of a floating dock or in large aquarium holding tanks were found to walk more often than swim. Animals captured and released a meter from a floating dock invariably returned directly to the dock, no matter whether the release location was shaded or in full sunlight. In the swimming mode, the body was held straight with all four antennae extended anteriorly. Movement was effected by pleopod beating. In walking, the first antennae were directed forward, the second perpendicularly, each prodding the substrate during progression. The substrate was grasped by the gnathopods and peraeopods 5-7. The third and fourth peraeopods lack spines or hooked dactyls for purchase. Their function seemed to be fully given to tube building.

3.3. Ecology

3.3.1. Habitat type

Table 10 lists the collection information for Jassa and the outgroups. All species are tube builders, colonizing hard substrates, hydroids, bryozoans, filamentous algae, sponges, kelp holdfasts and eelgrass roots in well circulated waters of moderate to high salinity. For the well sampled species, differences in exposure and depth range are probably correct. Thus, J. borowskyae, J. morinoi, J. oclairi and J. pusilla are probably restricted to exposed coasts and J. pusilla to deeper water. Females of J. marmorata, J. slatteryi, J. staudei, J. falcata and J. alonsoae are ovigerous in both summer and winter. Spotty records for other species are due to uneven collection. Although the body size in Jassa spans 22 mm, there is no species difference in size with latitude. Such clinal variation may, however, occur intraspecifically. Table 11 is a record of instances where species were found proximally, co-habiting the same substrate. Intersexes, suggestive of hybridization, have been found in Southern Californian harbors where J. slatteryi and J. marmorata co-occur. Sexton and Reid (1951) induced intersexes in J. marmorata by inbreeding. When the three cosmopolitan species are deleted from consideration, it is notable that no two species of the same adult male developmental type have been found to co-occur.

Species	Substrate	inorganic	organic	Coast exposed protected	Temperature range (°C)	Salinity range (‰)	Depth range (m)	Months female ovigerous	Body length at maturity (mm)	
									minimum	maximum
								J F M A M J J A S O N D		
<i>J. bronckhaae</i>	bedrock, pebble and boulder beaches		hydroids, bryozoans, filamentous algae, eelgrass	X	8.5-16.6	31-34	low intertidal to -5	X X X X	X	3.2 7.7
<i>J. ocellari</i>	bedrock, boulders		keelp holofests	X	10.5	27.6	intertidal and subtidal	X X X X		6.2 11.6
<i>J. shawi</i>	bedrock, settling block		calcareous sponges	X	15	30	intertidal	X	X	2.9 6.8
<i>J. pusilla</i>	bedrock, sand beach		hydroids, sponges, filamentous algae, polychaete tubes, <u>Secorchiza</u> bulbs, crab carapace	X	-	-	-8 to -500	X	X	2.8 4.8
<i>J. talcote</i>	bedrock, floats		bryozoans, coralline algae, <u>Ceramium</u> , <u>Polysiphonia</u> , <u>Gelidium</u> , <u>Laminaria</u> holofests	X	cold	high	intertidal to -400	X X X X X X		3.2 11.7
<i>J. herdmanni</i>	bedrock, ship bottom, oil & gas platform, buoys, floating wood, settling plates, aquaculture cage, reef		sponges, filamentous algae, <u>Laminaria</u> holofests	X	-	-	intertidal to -8	X X X	X X	3.3 9.5
<i>J. alonsoae</i>	-		filamentous algae, keelp holofests, spider crabs	X	-	-	intertidal to -150	X X X	X X X X	3.4 12.8
<i>J. just</i>	bedrock		sponges, bryozoans, tunicates, filamentous algae, eelgrass, keelp holofests	X	-	-	-3 to -14	X		3.5 8.5
<i>J. gruneri</i>	-		-	X	-	-	-3 to -5		X	3.2 5.2
<i>J. lenaicki</i>	-		red algae	X	-	-	0 to -2			7.4 7.4
<i>J. hartmannae</i>	bedrock		heavy turf algae, keelp holofest	X	-	-	intertidal to X -1.5			3.1 4.5
<i>J. thurstoni</i>	-		-	X	-	-	-7 to -140	X	X	5.9 6.5

Species	Substrate		Coast	exposed protected	organic	Temperature range (°C)	Salinity range (‰)	Depth range (m)	Months female ovigerous	Body length at maturity (mm)	
	inorganic									minimum	maximum
<u>J. ingens</u>	bedrock		X	X	hydroids, sponges, filamentous algae, kelp holdfasts	-	-	0.6 to -75	X X	15.1	26.1
<u>P. sandell</u>	bedrock			X	hydroids, sponges, bryozoans, kelp holdfasts, filamentous algae	-	-	-16 to -30	X X X X	5.9	10.8
<u>P. multidentata</u> <u>multidentata</u>				X	kelp holdfasts	-	-	-1.2 to -15	X	5.5	8.0
<u>P. multi-</u> <u>dentata</u> <u>orientalis</u>	bedrock			X	<u>Durvillaea</u> <u>antarctica</u> holdfast	-	-	-8		-	9.8
<u>P. gonlamere</u>	-			X	-	-	-	-20 to -342	X	6.9	8.8
<u>P. lewisi</u>	bedrock			X	sponges, <u>Durvillaea</u> holdfasts	-	-	-	X	2.5	5.3
<u>P. neoni</u>	bedrock			X	hydroids, sponges, bryozoans, kelp holdfasts, filamentous algae	-	-	-	X X X X	2.9	4.2
<u>N. liliipuna</u>	-			X	<u>Sargassum</u> , coral, <u>Ulva</u> , fleshy algae, coralline algae	-	-	intertidal to -4	X X	1.8	2.1
<u>P. ocia</u>	bedrock			X	sponges, coralline algae	-	-	intertidal to -11	X	3.1	4.0
<u>V. barnardi</u>	bedrock			X	-	-	-	-5 to -40	X	2.3	4.5

Table 11. Co-occurrence of conspecifics in Jassa (X). Adult male breeding type is given in parentheses. Possibility of hybridization is indicated by an asterisk. Species codes are described in Table 3.

[illegible]

3.3.2. Algal dwelling amphipod associates

A survey of amphipods on the exposed rocky shores and on floating harbor docks of the Pacific North American coast yielded species of Jassa in a variety of locations. Jassa borowskyae occurred exclusively on the exposed coast; J. stauderi was found on both exposed and semi-protected shore; J. slatteryi was most eurytopic, inhabiting exposed coast, protected shore, and well populated harbors. All three species were found on a variety of substrates: sponges, hydroids, roots of Phyllospadix, kelp holdfasts, and numerous species of filamentous and more coarsely branched algae. The dominant Atlantic North American species, J. marmorata, was found in high numbers, but only in harbors on the Pacific coast of North America. Sometimes it occurred on the same substrate as J. slatteryi, but more often with the tube dweller Corophium and a caprellid as co-dominants.

A survey of algal specificity among amphipods was made at Sunset Bay, Oregon, and at nearby Charleston Harbor on 8 July 1986 (Tables 12 and 13). Jassa stauderi was found only once, in a mixture of Odonthallia flocculosa and Microcladia coulteri, along with five other tube dwellers and seven nestlers. The high density of suspension feeders is attributed to the strong water movement at both locations. Jassa slatteryi was found at Sunset Bay also, but among the roots of Phyllospadix scouleri and among the branches of Hedophyllum sessile. Jassa marmorata occurred exclusively at Charleston Harbor. No species of Jassa was as widespread as the tube dweller Aoroides columbiae or the nestlers Atylus levidensus, Parallorchestes sp., or Hyale (Protohyale) frequens. The low intertidal

Table 12. Survey of algal dwelling amphipods from the exposed rocky intertidal region of Sunset Bay, Coos County, Oregon (stations A-L) and nearby Charleston Harbor (station M). Codes: N, nestler; T, tube dweller; B, borer. The stations are described in Table 13.

Species	Dwelling type	Station											
		A	B	C	D	E	F	G	H	I	J	K	L
<u>Jassa staudel</u>	T				X								
<u>Jassa slatteryi</u>	T			X						X			
<u>Jassa marmorata</u>	T												X
<u>Amphithoe sectimanus</u>	T		X	X	X								
<u>Amphithoe simulans</u>	T							X	X				X
<u>Amphithoe valida</u>	T												X
<u>Aoroides columbica</u>	T		X	X	X			X	X	X			
<u>Microjassa</u> sp. b	T				X								
<u>Corophium acherusicum</u>	T				X								X
<u>Photis brevipes</u>	T												X
<u>Photis</u> sp.	T				X								
<u>Ischyrocerus anguipes</u>	T		X	X									
<u>Ischyrocerus</u> sp. 1	T		X		X			X	X				
<u>Ischyrocerus</u> sp. 2	T												X
<u>Ischyrocerus</u> sp. near <u>pervus</u>	T										X		
<u>Atylus levidensus</u>	N		X	X	X	X		X					
<u>Pontogeneia</u> sp.	N		X	X	X			X			X		X
<u>Oligochinus</u> sp.	N									X			
<u>Calliopliella pratti</u>	N				X								
<u>Calliopliella</u> sp.	N										X		
<u>Parapleustes nautilus</u>	N				X			X					
<u>Parapleustes</u> sp. near <u>nautilus</u>	N			X									
<u>Parapleustes</u> den	N												X
<u>Parallorchestes</u> sp.	N		X	X	X	X		X	X	X			
<u>Hyale (Prothyale)</u> <u>frequens</u>	N		X		X		X	X				X	X
<u>Hyale (Apothyale) anceps</u>	N					X							
<u>Hyale</u> sp. S	N						X						X
<u>Hyale</u> sp.	N									X			
<u>Tritella laevis</u>	N				X								
<u>Tritella pinnana</u>	N			X				X	X				
<u>Caprella drepanochir</u>	N												X
<u>Najna</u> sp. near <u>lessoniophila</u>	B									X			

Table 13. Algal substrate and elevation of collection at Sunset Bay and Charleston Harbor. Sunset Bay collection was from exposed rocky shore. Charleston Harbor collection was from a floating dock.

Station	Species	Depth (m above (+) or below (-) chart datum)
A	<u>Phyllospadix scouleri</u>	-0.2
B	<u>Phyllospadix scouleri</u>	-0.2
C	<u>Phyllospadix scouleri</u>	+0.3 and -0.5
D	<u>Odonthallia flocculosa</u> & <u>Microcladia coulteri</u>	-0.5
E	<u>Odonthallia flocculosa</u> & <u>Corallina vancouveriensis</u>	+2.0
F	<u>Rhodomela larix</u>	+0.7
G	<u>Rhodomela larix</u>	-0.5
H	<u>Gracilaria sjoestedtii</u>	-0.3
I	<u>Hedophyllum sessile</u>	-0.5
J	<u>Hymenena multiloba</u>	-0.5
K	<u>Cladophora</u> sp.	-0.3
L	<u>Leathesia difformis</u>	+2.0
M	<u>Enteromorpha interstitialis</u> & <u>Polysiphonia</u> sp.	just below the water surface

zone is probably a suboptimal habitat for Pacific coast species of Jassa. Records of greatest abundance are for subtidal situations (Chess, 1979; this study). Jassa marmorata cannot withstand any emersion at all (Borowsky, pers. comm.). Only J. falcata has been found intertidally. Here individuals were observed clambering along damp crevices and under air dried algae at mid-intertidal level.

3.4. Biogeography

The distribution of each species of Jassa is mapped in Figs. 54-59. The distribution of Jassa's sister group, Pleojassa, is shown in Fig. 60, and that of the remaining secondary outgroup species (P. oia, N. lilipuna, V. barnardi, and H. goniamera) in Fig. 61. It is evident from Fig. 54 that Jassa and its relatives are notably absent from tropical waters. The latitudinal range is temperature controlled, so that the Gulf Stream enables an extended northern distribution on the Scandinavian coast, while the cold Arctic Oyashio and Labrador currents prevent a more northerly range on the eastern coasts of the USSR and Canada, respectively.

Three species of Jassa occur world-wide; the other sixteen are restricted to one hemisphere or the other. The cosmopolitan species penetrate further into the tropics than do the more restricted species. Of the nine Northern Hemisphere species, six are endemic to the North Pacific and three to the North Atlantic. The high Pacific diversity may prove to be greater still when more collections are made in the West Pacific. Only three collections from the West Pacific were available for this study. On the other hand, the North Atlantic has been intensively collected over this and the last century. Since species of Jassa are shallow water inhabitants, it is unlikely that further species will be found here. However, with extended use of submersibles, the known range of deeper dwelling rock wall colonizers like J. pusilla may be considerably expanded. Data on Southern Hemisphere species are derived mainly from the Antarctic expeditions of Walker (1903), Chevreux (1906

Fig. 54. Distribution of Jassa, all species combined (map from Lincoln et al., 1982).

Fig. 55. Distribution of species Jassa occurring world-wide.

Fig. 56. Distribution of species of Jassa restricted to the North Pacific.

Fig. 57. Distribution of species of Jassa restricted to the North Atlantic.

Fig. 58. Distribution of circum - Antarctic species of Jassa.

Fig. 59. Distribution of species of Jassa with restricted ranges in the Southern Hemisphere.

Fig. 60. Distribution of species of Pleojassa.

Fig. 61. Distribution of the secondary outgroup species, Plumulojassa ocia, Neoschyrocerus lilipuna, Ventojassa barnardi, and Hemijassa goniamera.

and 1913), Schellenberg (1931), Stephensen (1949), Thurston (1974a,b) and Alonso (1980), and from material housed in a variety of museums (AM, NMNS, NRS, SAMC, UST, USNM, ZMHB, ZMUH, and ZMUO). Lack of collection (or of collection availability) is probably the cause of the apparently sparse records for Jassa in the Southern Hemisphere (Fig. 54). Suitable habitat for Jassa probably occurs on the west coast of South America, the south and west coasts of Africa, and the south coast of Australia. Inferences on the dispersal and speciation of Southern Hemisphere species is therefore necessarily tentative. Of the seven species found there, four are known to have a broad range and three are known from only a few proximate locations. The restricted species were found in accessible habitats (intertidal or shallow subtidal areas). Thus their apparent endemicity may be real, although their actual local range may be greater than that shown.

Pleojassa occurs entirely in the Southern Hemisphere (Fig. 60). So too do the more distant outgroup species, Hemijassa goniamera and Ventojassa barnardi (Fig. 61). Plumulojassa ocia covers a range that is similar to, but more restricted than that of J. falcata, J. herdmani, and J. pusilla (Fig. 57). Neoischyrocerus lilipuna is a tropical species, occurring in the Hawaiian, Cook, and Society Islands.

3.5 Hypotheses of phylogeny

Wagner parsimony and compatibility analyses were applied to six data sets having the following characteristics: (1) a single species representative of each genus; (2) the species of (1), with all species of Pleojassa and Microjassa added; (3) all secondary outgroup species with four randomly chosen species of Jassa as in (3); (4) the most distant primary outgroup species, all secondary outgroup species, and the same species of Jassa, with J. ingens added; (5) all species of Jassa, with three species of the secondary outgroup; (6) the species of (5), with sexually dimorphic characters removed. Thus data sets 1-4 were established to examine relationships within the secondary outgroup, and sets 5 and 6 to assess relationships within Jassa. As in the phenetic analyses, the primary outgroup species must be considered simply as benchmarks for the ingroup and secondary outgroup, because their characteristics were not fully resolved.

Since the entry order of species was changed ten times, some orders generated trees of slightly different length. Therefore a consensus was drawn on the topologies of the shortest trees. Table 14 summarizes the characteristics of the data sets and their consensus trees. Wagner parsimony analysis always produced trees of more similar topology than did compatibility analysis. For data sets 1-3, each of the ten Wagner runs produced the same shortest tree. There was more agreement between the trees produced by parsimony and compatibility when the data sets were small (data sets 1 and 2). However, reduction of data set 5 by removing sexually dimorphic characters did not produce a similar effect. It

Table 14. Characteristics of the six data subsets for cladistic analysis.

Data set	Outgroup	No. species	No. characters	Analysis method ^a	No. steps in shortest tree (% of no. characters factored)	No. most parsimonious/ compatible trees	Consensus between trees ⁺ (%)	Consensus between methods (%)
1	IGE	10	95	P C	175	7 28	100 85.7	85.7
2	IGE	14	98	P C	199	3 33	100 86.2	63.6
3	GON LIL BAR	12	79	P C	184	4 98	100 83.2	89.0
4	IGE	15	84	P C	212	11 10	92.4 60.9	54.5
5	WAN GON BAR	22	115	P C	224	12 100	78.5 67.1	10.5
6	WAN GON BAR	22	86	P C	242	50 200	70.4 70.4 ^{**}	5.2

^a P: Parsimony, C: compatibility

⁺ Calculated as proportion of total number of nodes that can possibly be in common.

^{**} Average of 2 concenses produced on 100 trees each.

caused a slight increase in consensus between compatibility trees, but a decline in consensus between Wagner parsimony trees. The number of steps on the shortest trees produced by Wagner parsimony was considerably greater (145% to 242%) than the minimum number possible if all characters were congruent.

3.5.1. Relationships in the secondary outgroup

Fig. 62 shows the consensus trees produced from data set 1. Here, each genus is represented by a single species: Jassa by J. falcata (FAL), Pleojassa by P. wandeli (WAN), Neoischyrocerus by N. lilipuna (LIL), Microjassa by M. cumbrensis, Ischyrocerus by Ischyrocerus sp. (ISP), Plumulojassa by P. ocia (OCI), Parajassa by P. pelagica (PEL), Ventojassa by V. barnardi, and the root of the Ischyroceridae by ICE. The consensus tree for the shortest trees produced by Wagner parsimony is shown at the top left, that for compatibility at the top right, and a consensus of the two consensus trees at bottom centre. The numbers on the forks of the trees indicate the number of times the group consisting of the species above and to the right of that fork occurred in the trees. The same topology emerged in all seven of the shortest trees produced by Wagner parsimony. Under compatibility analysis there was only disagreement on relations within the group of more derived genera (Jassa, Pleojassa, Neoischyrocerus, and Microjassa). Both methods agreed in setting Hemijassa, Plumulojassa, and Parajassa basal, and Ventojassa next to the root, ICE.

Thirteen of the ninety-five characters in data set 1 are fully congruent with the Wagner parsimony phylogeny, and fifteen are fully congruent with the compatibility phylogeny. Their state changes are mapped on Figs. 63 (parsimony) and 64 (compatibility), and they are described in Table 15. The characters range from the anterior, middle, and posterior regions of the body. The second gnathopod is more heavily represented because it is the most variable appendage. Ten of the

Fig. 62. Consensus trees for data set 1: a single species representative of Jassa (FAL) and Pleojassa (WAN), with LIL, CUM, ISP, GON, OCI, PEL, BAR, and ICE. The outgroup is ICE. Species codes are described in Table 3.

WAN
 "
 7—FAL
 "
 " LIL
 " "
 " 7—CUM
 " "
 7—7—ISP
 "
 7—GON
 "
 " OCI
 " "
 7—7—PEL
 "
 " BAR
 "
 L—IGE

Wagner parsimony - 7 trees

WAN
 "
 14—FAL
 "
 " LIL
 " "
 " 14—CUM
 " "
 28—28—ISP
 "
 28—OCI
 "
 28—PEL
 "
 28—GON
 "
 " BAR
 "
 L—IGE

Compatibility - 28 trees

ICE
 "
 " BAR
 " "
 " " GON
 " " "
 " " " ISP
 " " " "
 " " " " CUM
 " " " " "
 " " " 2—2—LIL
 " " " "
 " " " " WAN
 " " " "
 " " 1—2—2—FAL
 " " "
 " " " PEL
 " " "
 L—2—1—OCI

Combined Wagner parsimony consensus
and compatibility consensus - 2 trees

347
Fig. 63. Wagner parsimony consensus tree of Fig. 62 with state transitions mapped for non-homoplasious characters. Species codes are described in Table 3.

PARSIMONY

Fig. 64. Compatibility consensus tree of Fig. 62 with state transitions mapped for non-homoplasious characters. Species codes are described in Table 3.

COMPATIBILITY

Table 15. Characters non-homoplasious for the generic phylogenies produced by Wagner parsimony analysis (Fig. 63) or compatibility analysis (Fig. 64) of data set 1. The character states are ordered from plesiomorphic to apomorphic, as polarized by the ischyrocerid, IGE.

20. Maxilla 1, male or female, inner plate with: fine setae plus apical spine; fine setae; no setae.
34. Gnathopod 1, segment 6, male or female, palmar defining spines located: distal to centre; proximal to centre; central.
44. Gnathopod 2, segment 2, male, anterolateral flange, setae located: on the flange and medial face; on the flange only.
45. Gnathopod 2, segment 2, male or female, anterior setae, modal length: 11 to 29; 1.
51. Gnathopod 2, segment 6, male, hinge tooth: absent; present.
58. Gnathopod 2, segment 6, male, thumb setation type: inner margin setose; inner margin not setose, outer marginal setae individual; inner margin not setose, outer marginal setae clustered into developmentally constant groups (thumb cluster and defining clusters). (The latter two states are equally derived).
68. Gnathopod 2, dactyl, male, inner margin shape: not proximally expanded; proximally expanded.
72. Gnathopod 2, dactyl, male, inner marginal setae, length: minute; as long as dactyl width.
73. Gnathopod 2, dactyl cusps, male, size: as large as the juvenile's; reduced, minute.
87. Peraeopods 5-7, segment 2, male or female, at least one of these produced posterodistally: no; yes.
98. Uropod 1, inner ramus, male or female, percentage of length underlain by ventral peduncular spinous process: 100; 88-73; 54-25; 16-6.
100. Uropod 1, male or female, rami terminating in a ventral fringe of cusps: no; yes.
101. Uropod 2, inner ramus, male or female, percentage of length underlain by ventral spinous process: 64; 27 to 21; 17 to 0.
103. Uropod 3, peduncle, male or female, number of mid-dorsal spines: 0; 1; 17. (The latter two states are equally derived).
109. Uropod 3, outer ramus, male or female, number of major cusps: 1; 2; 3.

123. Gnathopod 2, segment 6, female, palm shape: clearly concave; broad outline convex but with some shallow concavity; evenly convex.
125. Gnathopod 2, segment 6, female, palm shape: similar to adult male or hardly differing; markedly different.
130. Gnathopod 2, segment 6, female, number of defining spines differs from the male's: no; yes.

characters (20, 45, 58, 68, 87, 98, 103, 123, 125, and 130) are non-homoplasious for both phylogenies. Assuming monophyly for Jassa and Pleojassa, five of these characters (20, 34, 58, 103, and 125) would remain non-homoplasious with the addition of all other species of these genera. An additional three characters (44, 51, and 72) would stand by these criteria for the Wagner parsimony tree, and one additional character (109) would stand for the compatibility tree.

3.5.2. Relationships within Pleojassa

Fig. 65 shows the phylogenies produced by expanding data set 1 to include Microjassa claustris and all species of Pleojassa. I will not dwell on M. claustris, since this species was not fully resolved. For Wagner parsimony analysis, three runs produced the shortest tree, and the topology of each is identical. The compatibility trees were more variable in topology. Both methods set Pleojassa wandeli, P. multidentata, and P. lowryi together with Jassa falcata. Pleojassa moori was grouped with the genus by Wagner parsimony, but separated from it by compatibility analysis.

Figs. 66 and 67 show phylogenies with additional species of Jassa added. The trees are not strictly comparable because changes were made to species representation at the base of the tree. In Fig. 66, the species of Pleojassa are graded by Wagner parsimony, but grouped as a monophyletic unit by compatibility. The species set in Fig. 67 suggest a graded relationship by both analyses. The addition of Jassa ingens (ING) to the representatives of Jassa has caused Hemijassa goniamera (CON) to be moved into the Jassa unit. This is a body size effect, caused by the two species possessing a number of characters that are invariant in the other species. Addition of the full suite of species from Jassa would perhaps draw J. ingens closer to Jassa, as exhibited by the phenetic results, since J. ingens possesses the characters that define Jassa and exclude Hemijassa.

The four members of Pleojassa are defined by a number of characters that are not possessed by any species of Jassa: single spine defining the

Fig. 65. Consensus trees for data set 2: all primary and secondary outgroup species with J. falcata (FAL). The species were rooted on ICE. Species codes are described in Table 3.

Fig. 66. Consensus trees for data set 3: five randomly chosen species of Jassa (HER, JUS, MYE, BOR, and THU), and Pleojassa (MMU, WAN, LOU, and MOO) as ingroup, with GON, LIL, and BAR as outgroup. Species codes are described in Table 3.

5

Metro

Fig. 67. Consensus trees for data set 4: the species of data set 3, with Jassa ingens (ING) added and Neoschyrocerus lilipuna replaced by Plumulojassa ocia (data set 4). The species were rooted on IGE. Species codes are described in Table 3.

```

GON
"
11-ING
"
11-THU
"
"      JUS
"
"      " MYE
"      "
11-11-BOR
"
11-HER
"
7-MMU
"
10-WAN
"
7-LOW
"
10-MOO
"
11-LIL
"
11-OCI
"
9-BAR
"
L-IG

```


palm of gnathopods 1 and 2, palmar angle and thumb development at, rather than distal to the defining spine, lack of a second gnathopod gill, spinose fifth segment of peraeopods 5-7, reduced pleopods, and differently structured third uropod outer ramus. Each of these characters is shared with at least one outgroup member, and this explains why the four species are not always differentiated as a monophyletic genus.

3.5.3. Relationships within Jassa

Fig. 68 shows the consensus trees produced by analysis of the full set of species in Jassa, rooted on Pleojassa wandeli, Hemijassa goniamera, and Ventojassa barnardi. These three species were selected for rooting because their characteristics were fully resolved, and they varied in distance from the ingroup (see Section 3.1.2.). Figs. 62-67 indicate that either Pleojassa or Hemijassa could be considered the sister group of Jassa, while Ventojassa is more distant. Fig. 69 shows the results of analysing the same species, with their sexually dimorphic characters deleted. These are the same characters that were removed for phenetic analysis. The relationships suggested by Wagner parsimony in particular are similar to those found phenetically (Figs. 2-5).

The grouping of J. stauderi with J. marmorata is based on similarity in shape of the male's first gnathopod, possession of long setae on the anterior margins of the second and sixth segment, presence or absence of a minute seta at the junction of the first gnathopod's fifth and sixth segment, and development of plumose setae on the second antenna at maturity. The relationship of J. oclairi and J. borowskyae is also close. These species produce short thumbs, but they otherwise closely resemble J. stauderi and J. marmorata.

Another common subgroup is that including J. slatteryi, J. morinot, J. myersi, and J. carltoni. These species are more slender and generally less setose than are the species of the J. stauderi group. They commonly share a long setal cluster at the first gnathopod segment 5-6 junction. It is not known what the function of this setal cluster is. It brushes

Fig. 68. Consensus trees for data set 5: all characters, for all species of Jassa, rooted on WAN, GON, and BAR. Species codes are described in Table 3.

Fig. 69. Consensus trees for data set 6: non-sexually dimorphic characters for all species of Jassa, rooted on WAN, CON, and BAR. Species codes are described in Table 3.

against the mouthparts and antennae during gnathopod movement, and so may have a cleaning or sensory function. The setal length is age invariant, and is sometimes the only key character usable for immature specimens.

The consistent pairing of J. shawi with J. pusilla may be due to lack of a stronger relation to other species and to lack of information on the male adult characteristics of J. shawi. Both species are not particularly setose, lack a seta at the first gnathopod's fifth segment, and lack the cluster of setae on the dorsal margin of the mandibular palp's second segment that is common to J. falcata and J. herdmani. The latter species are sympatric with J. pusilla, although J. pusilla occurs at greater depth (see Biogeography and Ecology Sections). J. falcata and J. herdmani are very similar when juvenile, but diverge when subadult. The females remain divergent at maturity, but the males converge on thumb morphology.

The Southern Hemisphere species group together in both the phenetic analyses (Figs. 2-5) and Wagner analyses (Figs. 68 and 69). Jassa alonsoae, J. justi, J. fenwicki, and J. hartmannae share a uniquely derived character that is otherwise found only in the outgroup Ischyrocerus sp. This is the presence of a row of short spine-like setae along the anterior margin of the second gnathopod's second segment. Jassa fenwicki and J. thurstoni share a similar setal arrangement on the segment's posterior margin. The second gnathopod palms of J. gruneri, J. thurstoni and J. ingens are all shallow and sinuous, rather than deeply concave, as in the Northern Hemisphere species (J. myersi excepted, but this species is closer to the Northern Hemisphere species in other features). J. fenwicki, J. thurstoni, and J. ingens are the only species

of Jassa to lack the minute cusps that fringe the ventro-distal margin of the first and second uropods.

Restriction in specimen choice for J. carltoni, J. myersi, J. gruneri, J. fenwicki, J. hartmannae, and J. thurstoni resulted in lack of scores for some characters. Thus I have less confidence in assessing the finer relationships of these species than in the abundantly available Northern Hemisphere species.

The unusual features of J. ingens have been noted previously. The phenetic (Figs. 2 and 3) and Wagner analyses (Figs. 68 and 69) set J. ingens closest to J. thurstoni. The common thumb morphology (short thumb and mounting of the defining spines onto a ledge) caused the grouping of J. ingens with J. morinai (Fig. 68) by compatibility criteria.

4. DISCUSSION

4.1. The importance of classification

"The need for some system of classification is absolute, for it is only by first naming organisms and then grouping them in recognizable categories that one can begin to sort out and understand the vast array that exists." (Stale, 1980).

A classification facilitates the identification of species. A classification also provides a key to a species' literature. Its classes may have common properties about which biologists can make generalizations; and it may represent phylogenetic hypotheses of relationship (Warburton, 1967).

The relevance of classification to biologists is well illustrated by the impact that reclassifying Jassa will have on our interpretation of past studies. Table 16 summarizes the non-, or semi- taxonomic literature on Jassa (by the latter term I mean regional surveys that may have included morphological description but did not have a revisionary intent). Of the forty-seven studies known (and there are probably more, since Jassa is readily encountered), ninety-one percent of the authors assigned the species to J. falcata. On borrowing and examining the specimens from twenty-six of these studies, I ascertained that ninety-three percent of the identifications required change as a consequence of systematic revisions made herein. Forty percent of the changes required splitting the identifications into more than one species. The failure to discriminate species appeared to result from confusing J. herdmanni with J. falcata, or of not expecting J. marmorata to occur with the local species.

Table 16. Species identifications for Jassa in primarily non-taxonomic studies. My identifications, marked by an asterisk, are confirmed (specimens examined); others are likeliest species (assuming correct generic identification).

Author	Subject	Identification	
		Author's	Mine
Ebling et al. (1948)	kelp fauna - Scotland	<u>J. falcata</u>	<u>J. falcata</u> and/or <u>J. herdmani</u>
Jones (1948)	rocky shore amphipods - Isle of Man	<u>J. falcata</u>	<u>J. falcata</u> and/or <u>J. herdmani</u>
Sexton and Reid (1951)	reproductive behavior - Plymouth, England	<u>J. ocla</u>	<u>P. ocla</u>
		<u>J. falcata</u> Narrow Form	<u>J. falcata</u> ¹ and <u>J. herdmani</u> ¹
		<u>J. falcata</u> Broad Form	<u>J. marmorata</u> ¹
		<u>J. falcata</u> Large Polar Form	<u>J. alonsoae</u>
Bousfield (1952)	amphipods of Atlantic Canada	<u>J. falcata</u>	<u>J. marmorata</u> ¹
Stock and Bloklender (1952)	amphipod dispersal by drifting - Holland	<u>J. dentex</u>	<u>J. falcata</u>
		<u>J. falcata</u>	and/or
		<u>J. sp.</u>	<u>J. herdmani</u>
Kenny and Haysom (1962)	rocky shore ecology - Macquarie Island	<u>J. falcata</u>	<u>J. lowryi</u> ¹ and <u>J. justl</u> ¹
		<u>J. marmorata</u>	<u>J. marmorata</u>
Wynne-Edwards (1962)	castes	<u>J. falcata</u>	<u>J. falcata</u> and/or
			<u>J. herdmani</u>
			<u>J. marmorata</u>
Nagle (1968)	epibiota of macro- epibenthic plants	<u>J. falcata</u>	<u>J. marmorata</u>
Culpepper (1969)	colonization of offshore settling plates - Gulf of Mexico	<u>J. falcata</u>	<u>J. marmorata</u> ¹
Daro (1970)	amphipods associated with the polychaete <u>Polydora ciliata</u> - Belgium	<u>J. falcata</u>	<u>J. marmorata</u> ¹
Bellan-Santini (1972a,b)	marine invertebrates of Terre Adélie, Antarctica	<u>J. falcata</u>	<u>H. goniamera</u> ¹
Moore (1973, 1984, 1986)	amphipods of kelp holdfasts - West Scotland	<u>J. falcata</u>	<u>J. falcata</u> and/or <u>J. herdmani</u>
		<u>J. ocla</u>	<u>P. ocla</u>
		<u>J. falcata</u>	<u>J. justl</u> ¹
Fenwick (1976)	amphipods of <u>Caulerpa</u> <u>brownii</u> -Kalkoura, New Zealand	<u>J. falcata</u>	<u>J. justl</u> ¹
Relini et al. (1977)	colonization of offshore settling plates - Italy	<u>J. falcata</u>	<u>J. marmorata</u> ¹
O'Clair (1977)	rocky shore ecology - Northern Alaska	<u>Jassa sp.</u>	<u>J. oclairi</u> ¹

Author	Subject	Identification	
		Author's	Mine
Vader (1978)	amphipods associated with echinoderms - Banyuls, France	<u>J. ocla</u>	<u>P. ocla</u>
Boero and Carilli (1979)	behavior - Italy	<u>J. falcata</u>	<u>J. falcata</u> and/or <u>J. herdmani</u> <u>J. marmorata</u>
Carlton (1979)	marine invertebrate introductions - Pacific North America	<u>J. falcata</u>	<u>J. marmorata</u> *
Chess (1979)	seafloor colonization induced by upwelling - Northern California	<u>J. falcata</u>	<u>J. staudei</u> *
Diviacco (1979a,b, 1983)	colonization of cooling water pipes of an electric power station - Italy	<u>J. falcata</u>	<u>J. marmorata</u> *
Kamenskaya (1979)	biology of <u>Jassa</u>	<u>J. falcata</u>	<u>J. marmorata</u> * and <u>J. borowskyae</u> *
Nair and Anger (1979, 1980)	population dynamics and biochemical composition - Helgoland, West Germany	<u>J. falcata</u>	<u>J. marmorata</u> * <u>J. falcata</u> *
Reish and Barnard (1979)	coastal pollution - Southern California	<u>J. falcata</u>	<u>J. slatteryi</u> <u>J. morinot</u> , <u>J. marmorata</u> <u>J. marmorata</u>
Diviacco (1980)	colonization of settling plates - Genoa harbor	<u>J. falcata</u>	<u>J. marmorata</u>
Nelson (1980)	reproduction patterns - New England	<u>J. falcata</u>	<u>J. marmorata</u>
Diviacco (1981), and Diviacco and Reilini (1981)	amphipods of Orbetello Lagoons - Italy	<u>J. falcata</u>	<u>J. marmorata</u>
Borowsky (1983, 1985)	reproductive behavior - New York	<u>J. falcata</u>	<u>J. marmorata</u> *
Ledoyer and Menioul (1983)	distribution around Marseilles, France in relation to pollution	<u>J. falcata</u>	<u>J. marmorata</u> * <u>J. slatteryi</u> * <u>J. herdmani</u> *
Marques (1984), Marques and Bellan-Santini (1985), and Bellan-Santini and Ledoyer (1972)	rocky shore amphipods - Portugal	<u>J. falcata</u>	<u>J. falcata</u> * and <u>J. herdmani</u> *
Southgate and Myers (1985)	colonization of off-shore gas platforms - Irish Sea	<u>J. ocla</u> <u>J. falcata</u>	<u>P. ocla</u> * <u>J. falcata</u> and/or <u>J. herdmani</u> *
Witman (1985) and Sebens (1986 a,b)	rocky shore ecology - New England	<u>J. falcata</u>	<u>J. marmorata</u> and/or <u>J. pusilla</u>

Author	Subject	Identification	
		Author's	Mine
Arresti et al. (1986)	rocky shore amphipods -Spain	<u>J. falcata</u>	<u>J. marmorata</u> , ^a
			<u>J. falcata</u> and <u>J. hardmani</u> ^a
Kaandorp (1986)	rocky shore ecology - Northwest France	<u>J. ocla</u>	<u>P. ocla</u>
		<u>J. falcata</u>	<u>J. falcata</u> and/or
		<u>J. dentex</u>	<u>J. hardmani</u>
Costello and Myers (1987)	amphipods of sponges- Southwest Ireland	<u>J. falcata</u>	<u>J. falcata</u> and/or
			<u>J. hardmani</u>
Franz (1987)	population dynamics - New York	<u>J. marmorata</u>	<u>J. marmorata</u> ^a

4.2. Characteristics of classification

"Simpson (1961) has argued that taxonomy, like many other sciences, is a combination of science and art. For example, tempering vertical with horizontal classification, dividing a gradually evolving lineage into species, deciding how much interbreeding is permissible before two populations are included in the same species, the assignment of category rank above the species level, choices between alternative ways of classifying the same phylogeny, balancing splitting and lumping tendencies, and the inductive inferences by which phylogenies are inferred are all to some extent part of the art of taxonomy." (Hull, 1970).

The intent of taxonomy over the past three decades has been to reduce the amount of art by making procedures more explicit. This has been applied not only to phenetics and cladistics, but to evolutionary classification as well (Stuessy, 1987). Evolutionary classification attempts to describe a composite of phylogeny, such as is shown in Fig. 70. My approach in developing the classification of Jassa and its outgroups has been to synthesize phenotypic resemblance with what is known of the biology of the group. The classification is seemingly more reasonable than its predecessor's, because I have attempted to maximize stability, informativeness, naturalness, and predictivity (Warburton, 1967; Hull, 1970; Bock, 1977; Archie, 1984; Sneath and Hansell, 1985). My classification seems stable under substitution of characters and outgroups. The classification is informative, because it is based on a large number of characters. It is, I hope, natural, because it accounts for variation induced by differences in sex and age. The classification is also predictive: we can be confident that a new species of Jassa would be colonial, prefer stable substrates, live in well mixed, high salinity waters, and the males may delay functional maturity to the last molt, and

Fig. 70. The components of phylogeny (from Stuessy, 1987, Fig. 5).

FIG. 5. Diagram of dimensions contained within phylogeny (after Stuessy 1983, with permission of the publisher and editor of SIDA).

assort into different mating strategies.

4.3. Species: the fundamental unit of evolution

"Species are the real units of evolution, they are the entities which specialize, become adapted, or which shift their adaptation. And speciation, the production of new gene complexes capable of ecological shifts, is the method by which evolution advances. The species truly is the keystone of evolution..." (Mayr, 1942).

And what is a species? "Species are groups of interbreeding natural populations that are reproductively isolated from other such groups." (Mayr, 1969). "... individuals are members of the same species if their genes can descend through the generations to unite in the same individual under natural conditions (Futuyma, 1979, from Simpson, 1961). And further, "a species is a lineage (or a closely related set of lineages) which occupies an adaptive zone minimally different from that of any other lineage in its range and which evolves separately from all lineages outside its range" (Van Valen, 1976). Thus species are real, cohesive, and independent groups of individuals, behaving as evolutionary and adaptive units. According to Hull (1976), they have all the properties of individuals: the relation which an organ has to an organism is the same as the relation which an organism has to its species. Higher taxa, if monophyletic at the species level, have spatio-temporal continuity, but they lack the cohesiveness of species. Organisms are not the units of evolution, because not enough change can take place before they cease to exist.

Speciation often occurs when geographically isolated populations diverge under selection for adaptation to their environments (Mayr, 1963), or as a response to differential success in sexual and social competition (West-Eberhard, 1983). Over time, species may appear as a

smeary continuum of gradual change, only definable because the awkward intermediates are dead (Dawkins, 1986).

The instability in the taxonomy of Jassa has resulted from differences in opinion as to what denotes a species. Sexton and Reid (1951) merged previously defined species because two of them "interbred". Sexton and Reid set themselves on shaky ground because they failed to establish that the interbreeding produced viable offspring capable of successful propagation. But if they had, would this have been sufficient grounds for their actions? Definitely they did not have evidence to synonymize all species. They did not establish that all previously named species successfully interbred, and they did not establish that any of the species did so in nature. Even if some individuals did interbreed, it is the amount of crossing and the degree of viability and fertility of the offspring that matter (Hull, 1970). My analysis has gone no further than Sexton and Reid's in establishing reproductive isolation. What I have done differently, is to examine a large number of specimens, of all species described, over a much broader range of morphological variation. I have assessed that variation for the effect of age and sex, and then classified the specimens by characters that were unaffected by either. Then I have drawn the inference that the morphological differences seen between the groups is what one would expect to find between two reproductively isolated populations. I have sought biological evidence for discreteness by searching for morphological intermediacy and character displacement where congeners co-occur. The species so defined are morphospecies, but I predict that they indeed will be proven to be biological species.

4.4. Jassa: species characteristics

The following discussion of species characteristics can now be made in light of the reclassification of Jassa.

4.4.1. Population dynamics, community structure, competition, and predation

Species of Jassa may be found aggregating on man-made structures so densely that the term 'fouling organism' is an apt description. Jassa marmorata has been recorded at a density of up to 500,000/m² on floating docks in New York (Franz, 1987, and unpubl. data), at greater than 200,000/m² on buoys in Peter the Great Bay (Sea of Japan) (Kamenskaya, 1979), and at up to 72,000/m² in Helgoland (Nair and Anger, 1979). This amounts to a wet weight biomass of up to 1500 g/m² (Kamenskaya, 1979). Jassa marmorata has also been found in large numbers on offshore buoys, settling plates, and oil and gas platforms (Bousfield, 1952; Pequegnat and Pequegnat, 1968; Culpepper, 1969; Relini et al., 1977), in power plant cooling pipes (Diviacco, 1977a,b, 1983), and in seawater aquaria (pers. obs.). In more natural habitats, J. marmorata has been found in dense colonies among the tubes of the polychaete Polydora ciliata (Daro, 1970; Kaandorp, 1986), and on the distal blades of eelgrass (Nagle, 1968). It is not particularly specific in its preference for algae (Ledoyer and Menioui, 1983), although Nagle (1968) reported it absent from algal epiphytes and Borowsky (pers. comm.) observed greater abundance in hydroids than in Ulva. Ulva is strongly avoided by the

herbivorous amphipod Gammarus palustris (Borowsky and Borowsky, 1987a). There is evidence to suggest that some tubicolous amphipods preferentially reside in algae that are avoided by fish predators (Hay et al., 1987).

Because of its ubiquity, J. marmorata has been studied more extensively than any other species. Franz (1987, and unpubl. data) followed a population of J. marmorata on floating docks at New York and observed five overlapping generations. Summer cohorts lived approximately three months. Fall cohorts overwintered, releasing offspring in April. Summer individuals grew faster and reproduced at smaller size than did winter cohorts.

In studying an undifferentiated mixture of J. marmorata and J. falcata (my identification), Nair and Anger (1979) observed that females lived, on average, 2.4% to 3.6% longer than males in the laboratory. Mortality during growth declined steadily from hatching to adulthood. The growth rate was higher in early molt juveniles, and greater in males than in females. Growth was faster at higher temperatures. Molt number was also flexible. Animals underwent fewer molts at higher temperatures, and males molted fewer times than females. Females produced three to four broods of twenty to forty offspring each. The eggs were incubated from eight to sixteen days. Upon hatching, the juveniles left the brood pouch ten to thirty hours later. Higher lipid reserves in females than males allowed better survival for females in the face of starvation.

Jassa marmorata frequently co-occurs with Caprella equilibra, Caprella dilatata, Stenothoe valida, Elasmopus rapax, and Corophium insidiosum (Daro, 1970; Diviacco, 1979a,b). Nagle (1968) noted an inverse relation

of abundance with Caprella geometrica and Paracaprella pusilla. Ledoyer and Menioui (1983) noted a negative association with Ericthonius brasiliensis. Both relations were thought to be current induced: J. marmorata occurring in calmer areas than the caprellids, but in faster moving waters than Ericthonius. Ericthonius occurs on siltier substrates than does Jassa. It also penetrates the tropics, while Jassa does not (pers. obs.).

In studying the structure of a rocky subtidal community in New England, Witman (1985) found a species of Jassa with Ischyrocerus anguipes, Corophium bonellii, and Ampithoe rubricata amongst kelp beds. Witman's Jassa may be J. marmorata, or the deeper dwelling J. pusilla. While the Modiolus bed provided its inhabitants refuge against sea urchin predation, Jassa was unable to attain any abundance here, inhabiting instead the kelp bed below. When the kelp bed was denuded by sea urchins one year, Jassa was displaced and did not return afterwards.

At a neighbouring location north of Cape Cod, Sebens (1986b) found Jassa, along with Corophium bonellii, in abundance among the tubes of the terebellid polychaete, Nicolea zostericola. Judging by the shallower depth (5-7m), this Jassa was more likely J. marmorata. Although less abundant in winter months, this mixture of species recurred through the three and a half years of study. Earliest colonizers on cleared rock were the serpulid polychaete Spirorbis, encrusting bryozoans, a red crustose alga, and erect hydroids and bryozoans. Subsequently, the tube dwellers rapidly covered the red crustose alga and most of the bryozoans. However they were poor competitors against the slower growing tunicates Dendrodoa, Molgula, and Aplidium. Sebens (1986b) considers that the

tubicolous species exemplify the "fugitive - dominant" mechanism for co-existence with superior competitors.

Another instance of rapid colonization and disappearance was seen in the North Pacific in Jassa staudei. Chess (1979) found a density of up to 128,000/m² carpeting the sea floor at the onset of the spring - summer upwelling at Albion Cove, in northern California. Co-existing with huge numbers of other amphipods, including Microjassa claustris and Metacaprella kennerleyi, Jassa staudei apparently subsisted largely on diatoms. Density fell drastically when the upwelling and phytoplankton bloom diminished at the end of summer.

Jassa is probably frequently preyed upon by fish. Sebens (1986b) noted fishes, especially the wrass, Tanigolabrus adspersus, picking at the rock walls colonized by Jassa. Their gut contents showed significant numbers of amphipods (the species were not identified). Chess (1979) noted that the amphipod tube mat in northern California was a major food source for benthic fishes during the upwelling period. Some of the specimens that I examined came from fish stomachs: J. slatteryi from unidentified fish, and J. staudei from Oligocottus snyderi.

No species of Jassa is tolerant of water low in oxygen or salinity. Ledoyer and Menoui (1983) found that Jassa (possibly J. marmorata, J. slatteryi and/or J. herdmanni) declined in density around a sewage outfall on the Mediterranean coast of France. However Reish and Barnard (1979) found that Jassa (likely J. marmorata, J. slatteryi and/or J. morinot) was an early colonizer after pollution abatement in Los Angeles Harbor. The broad range of J. marmorata throughout North America's Atlantic

seaboard suggests that J. marmorata is relatively more eurytopic than the less widely ranging species.

4.4.2. Sexual dimorphism and reproduction

Jassa has the following characteristics: (1) at least some species occur in dense aggregations; (2) the females and functionally immature males tend to reside in their tubes, but the thumbed adults abandon their tubes to search out and mate with receptive females; (3) although there is a burst of reproduction in spring and a decline in winter, reproduction occurs asynchronously, year-round; (4) reproduction is not cued to a precise signal such as lunar periodicity, as may be the case in sediment dwellers, like the Ampeliscidae, Phoxocephalidae, and Pontoporeiidae (Bousfield, pers. comm.); (5) both sexes mate more than once, but the time investment for a female is nearly a whole molt cycle, while that for a male is only the female's period of receptivity (four to five days (Borowsky, 1985)); and (6) adult females are rarely found to be lacking eggs. The combined effect of a polygynous mating system, asynchronous reproduction, and sole female care would be to bias the operational sex ratio toward the males. That is, at any one time there are likely more functionally mature males searching out females than there are receptive females available. A consequence of strong male-male competition is to delay maturity to the last molt (Trivers, 1972). Fewer functionally mature males means less competition, and less exposure to the dangers of predation and dislodgement. With the females breeding asynchronously, there is a chance for a small number of males to control many females, one after the other. Thus any male feature that would increase the chance of mating success or to achieve social dominance would be selected for. In Jassa, this may be the male's thumb. The thumb

does not enhance a male's grasp on the substrate (Borowsky, 1985). Neither is it simply a by-product of excising palmar tissue in order to achieve greater gnathopod size (Fig. 71), since the thumbed gnathopod's area is still greater than that of a non-thumbed gnathopod. In agonistic encounters, the thumb does not appear to be used as a weapon or a means to dislodge the opponent, as it is in horned beetles (Eberhard, 1980, 1982). I would suggest that the male's thumb is a hindrance, since it makes the palmar length so much greater. The thumb seems to act as a signal of dominance to the non-thumbed male, and, possibly, of sexual intent to the female (Borowsky, 1985). Since the result of an agonistic encounter between thumbed males is a function of body size, one might expect sexual selection to favor a small bodied male producing a disproportionately large thumb, if thumb size were the marker for body size. In fact, the opposite was seen: the minor form male's thumb was smaller than the major's at equivalent body size.

I suggest that the major and minor forms have alternative reproductive strategies. No behavioral hypothesis can be tested without the live animal. However, I would like to speculate on what might be expected of Jassa under such mating systems.

Krebs and Davies (1987) set three hypotheses for the occurrence of alternative strategies within a species.

(1) The alternative strategy is a temporal condition in a changing environment. A different morphology is assumed, and a different strategy played, depending on the situation. Three-spined stickleback males exemplify this strategy. To female sticklebacks, males with bright throats are more attractive than males with dull throats. But red

Fig. 71. Nassa marmorata, male. Weight of paper outlines of the gnathopod 2, segments 6 and 7, as a function of body length.

throated males are more susceptible to predation. In deeper water, most males are red throated; in shallow water, where a red throat is conspicuous to predators, most males are dull. Thus there is a trade-off, with both morphs being advantageous in different environments (McPhail, 1969; Semler, 1971; Moodie, 1972). In Jassa, it is possible that different morphologies are favored in different situations. If, for instance, minor form males were acting as immatures, and therefore were more cryptic than major forms, they would be better protected from predators than the major form. Thus where predation was intense, a major form would be at a disadvantage. The temporal data for Jassa staudel, which is a type 1 species, suggests that it does not change to the type 2 form depicted by J. slatteryi (Fig. 40). As well, the type 1 situation is seen in all four geographic collections (Fig. 41). The Friday Harbor population is protected from fish predation, while the other three are not. The Albion Cove population, which may have been under strong predation pressure (Chess, 1979), has a greater proportion of minor form males. Thus environmental conditions may affect the relative proportions of each type in Jassa as well. The notable point, however, is that in each location the plots are still type 1, not type 2.

(2) Making the best of a bad situation. In the type 1 species of Jassa, the minor form male comprises a small portion of the total of adult males. The minor forms are the smallest of the group, have a shorter thumb than expected for a major form male, and (in several species), have a toothed dactyl. The minor form may be simply making the best of its situation. It will have a limited chance at successfully guarding a female against other large bodied males. A better strategy would be to

act unobtrusively, and mate surreptitiously when the dominant male is otherwise occupied. The thumb would signal reproductive intent to the female, and be advantageous in encounters with juvenile males, but its shortness would be less visible to a major form male. The dactyl tooth may be an additional sexual signal specific to the minor form.

(3) Evolutionarily stable strategy. In the type 2 species of Jassa, the minor form is about as abundant as the major form, and overlaps it in size to a greater degree than in type 1 species. This suggests that the pay-off for a minor form may be greater in type 2 species than in type 1 species. In this situation, the pay-off for one strategy depends on what others in the population are doing (Krebs and Davies, 1987). It is an advantage to be a sneak if there are not too many other sneaks. Conversely, it is an advantage to be a major form if there are fewer major form competitors. Such occurs in coho salmon, where a percentage of the males mature early (the jacks) and sneak copulations at spawning (Gross, 1985).

For species of Jassa in which there are sufficient males to suggest a particular strategy, the minor forms encompass about the same range in morphology, whether type 1 or type 2. Thus, of the species that exhibit dactyl toothing in the minor form, two are type 1 and two are type 2. Curiously, species of the same type are not known to co-occur unless introduced (as in J. falcata and J. marmorata). Howden (pers. comm.) and Eberhard (1982) have found that small, short horned male beetles are better dispersers than large bodied, long horned males. The former also emerge and are active earlier in the season than the latter. Neither characteristic may be advantageous to Jassa, however, since rafting or

currents would presumably disperse either form equally well, and mating occurs year-round.

Considering the Amphipoda as a whole, the extension of a protuberance or incision of a thumb in the male is a common phenomenon throughout Jassa's superfamily, the Corophioidea, but rare elsewhere (Table 17). It is in these genera that alternative mating strategies may be seen as well. The Podoceridae, Caprellidae and Stenothoidae, which are nestlers, often co-occur with Jassa. A similar form of sexual dimorphism may relate to a similar mating style, whereby male dominance is established and the female is attended when receptive. Thumbing does not occur in males that carry receptive females around until they molt (e.g., most Gammaroidea and Talitroidea). Sexual dimorphism in males that carry is less than in males that attend. In species that mate synchronously (e.g., Phoxocephalidae, Ampeliscidae, and Pontoporeidae), dimorphism is of a different kind. Here, the swimming appendages and sensory organs enlarge in the male, presumably to assist mate capture while swarming (Bousfield, pers. comm.).

Table 17. Incidence in the gammaridean Amphipoda of incision of the palm of the male's sixth segment of gnathopod 2 to produce a thumb.

Superfamily	Family	Genus
Corophioidea	Isaeidae	<u>Microprotopus</u>
		<u>Eurystheus</u>
		<u>Podoceropsis</u>
		<u>Photis</u>
	Amphithoidae	<u>Amphithoe</u>
		<u>Cymadusa</u>
	Aoridae	<u>Lembos</u>
	Ischyroceridae	<u>Jassa</u>
		<u>Pleojassa</u>
		<u>Parajassa</u>
		<u>Hemijassa</u>
		<u>Ventojassa</u>
		<u>Neolishyrocerus</u>
		<u>Microjassa</u>
Caprelliidea	Podoceridae	<u>Dulichia</u>
	Caprellidae	<u>Caprella</u>
		<u>Aeginella</u>
		<u>Podocerus</u>
Leucothoidea	Stenothoidae	<u>Metopa</u>
Melitoidea	Melitidae	<u>Elasmopus</u>
Talitroidea	Talitridae	<u>Talorchestia</u>

4.4.3. Dispersal

At least some species of Jassa readily disperse by rafting. Stock and Bloklander (1962) frequently encountered Jassa among algae, floating wood, rubber, and cork fishing floats washed ashore on the Dutch coast. Several species of Jassa have been found fouling boat bottoms (Table 10). Relini et al. (1977), Reish and Barnard (1979), and Southgate and Myers (1985) all noted the high similarity of the fauna colonizing offshore structures to harbor faunas, and speculated that the fauna had been carried out on ships' hulls. It is not known, however, whether Jassa can survive the scour induced by waves, water turbulence, and the ship's speed. Short passages may well be possible, but trans-oceanic transport seems less probable, especially if it were to involve movement through low salinity and/or tropical water. A gentler mechanism would be transport in ships' seawater ballast. Carlton (1985) suggests that survival in seawater ballast is quite possible, particularly in shorter voyages where temperature change is not great. Medcof (1975, as quoted by Carlton, 1979), found that a variety of planktonic crustaceans, polychaetes, and chaetognaths survived a 14.5 day passage from Taganoura, Japan to Twofold Bay, New South Wales, Australia. Carlton (1985) cites several instances of plankton survival in seawater ballast carried over long periods (up to 30 days) and broad temperature escalation (up to 15°C change). The potential of seawater ballast for introducing species has been greatly enhanced by increased usage of clean (rather than oil contaminated) seawater, increased vessel speed, and shortening of

shipping distance on the opening of the Suez and Panama canals (Carlton, 1985).

Jassa may also be dispersed through hitch-hiking on oyster shells. Carlton (1979) attributed the oyster industry with introducing as many of Pacific North America's exotic species as did shipping. He designated 160 species from 11 phyla as introduced, Jassa being one. One of the characteristics of an introduced species is that it is generally well established in harbors but is excluded from open coasts (Carlton, 1979). Taking this as a guide, I suggest that the cosmopolitan distributions of J. marmorata, J. slatteryi, and J. morinoi (Fig. 55) are a recent phenomenon, caused by man. Jassa marmorata occurs on both exposed coast and protected harbors in Atlantic North America, and co-occurs there with no other species (J. pusilla, although sympatric, is deeper). Elsewhere, J. marmorata is only known from well populated areas. In my survey of the rocky shores of Pacific North America, J. marmorata was abundant in harbors from Victoria, B.C. to Morro Bay, California, yet never occurred on open coast. This would suggest an Atlantic North American origin for J. marmorata. Both J. slatteryi and J. morinoi occur on Pacific North American open coast, but have never been found with J. marmorata in Atlantic North America. European waters have been thoroughly collected, yet J. slatteryi and J. morinoi have only appeared in areas well frequented by man. This would argue, therefore, for an origin in Pacific waters. The temperate coasts of South America and Africa are possible centers of origin, but too little is known of their regional fauna to speculate.

Man-induced dispersal is less likely a factor in the distribution of the narrowly ranging species (Figs. 56-59). The propensity for inhabiting areas subject to strong water flow (Ebling et al., 1948; Jones, 1948; Kenny and Haysom, 1962; Moore, 1973, 1984, 1986; Fenwick, 1976; Chess, 1979; Borowsky, 1983, 1985; and Table 10) predisposes Jassa to dispersal by currents, either by rafting, or among the plankton. Barriers to establishment would be unsuitable substrate (beaches), low salinity water (estuaries), tropical (and arctic ?) water, great depth (probably levels below the euphotic zone), nutrient poor, highly enriched, or poorly oxygenated water (eg. around sewage outfalls), competition, and predation.

Judging by the major current patterns (Fig. 54), one could expect quite different amphipod faunas existing today on either side of South America and South Africa. The Coriolis effect would enhance the northward dispersal of Jassa along their west coasts, but hinder it on their east coasts.

4.4.4. Hypotheses of phylogeny

Wagner parsimony analyses of the full character set (Fig. 68) and compatibility analysis on both the full, and the non-sexually dimorphic characters (Figs. 68 and 69) favor Pleojassa as the sister group to Jassa. Wagner analysis on the non-sexually dimorphic characters favor Hemijassa as the sister group. The uncertainty is caused by Jassa ingens (compare Figs. 62, 65, and 66 with Fig. 67), which, presumably because of its large size, shares more characters with Hemijassa than with Pleojassa. However, I have noted elsewhere that J. ingens is closer to Jassa than to any of the outgroup species.

Phenetically, Pleojassa is closer than Hemijassa to J. ingens. In addition, the type of sexual dimorphism and male thumb development exhibited by Pleojassa wandeli and P. multidentata is similar to that of J. ingens, while that of Hemijassa is quite different. The balance of evidence seems therefore to favor Pleojassa as the sister group to Jassa.

Fig. 72 shows the Jassa section of the cladogram produced by Wagner parsimony analysis of the full character set (Fig. 68). The characters that vary within Jassa (other than autopomorphies) are mapped. Their states and polarities, as deduced from the outgroup arrangement of Fig. 68, are described in Table 18. This suggests that character evolution in Jassa has been overwhelmingly restricted to the part of the body that extends from the tube. The only changes elsewhere are seen in the third and fourth peraeopods, and in the first uropod. The difference in peraeopod segment 4 overlap may relate to a difference in method of tube

Fig. 72. Wagner parsimony consensus tree of Fig. 68 with state transitions mapped for all synapomorphic characters variable within Jassa. Species codes are described in Table 3.

Table 18. Characters other than autapomorphies defining the species relations in Fig. 72. The character states are ordered from plesiomorphic to apomorphic, using Ventojassa as the most distant outgroup, Hemijassa as the next-most, and Pleojassa as the sister group. Characters 5 to 100, and 136 to 141 were measured on a male; characters 100 to 129 were measured on a female.

5. Antenna 2, segment 5, adult male, simple filter setae half or more the length of the juvenile's or female's; less than half.
6. Antenna 2, segment 5 and proximal part of flagellum developing setae that differ in morphology from those of the juvenile: no; yes.
7. Antenna 2, flagellum, number of segments (the last minute): 6; 3; 2; 1; 0.
9. Antenna 2, flagellum, segment 1, proportion of full flagellum length: 22 to 28; 35 to 53; 59 to 90.
10. Antenna 2, segment 5, overlap by antenna 1: greater than or equal to a third; less than a third.
17. Left mandible, number of raker spines: 6; 2; 1; 0.
25. Gnathopod 1, coxa, ventral margin sinuous: no; yes.
26. Gnathopod 1, segment 2, anterolateral marginal setae: absent or a few at the distal angle; covering the majority of the length and short and spiny; covering the majority of the length and long, simple; covering the majority of the length and long, plumose.
27. Gnathopod 1, segment 2, mid-posterior margin, setae (ignoring those at distal angle): 1-2 short; absent.
33. Gnathopod 1, segment 6, palm shape: convex; straight; concave.
35. Gnathopod 1, dactyl, number of rows of facial serrations: 0; 2.
38. Gnathopod 2, coxa, anterior length (residual, regressed on char. 40): 14.0 to 3.8; 2.2 to -9.0.
41. Gnathopod 2, coxa, ventral margin shape: convex; straight; sinuous.
43. Gnathopod 2, segment 2, anterolateral flange, number of setae: 0 to 1; 5 to 22; 44.
45. Gnathopod 2, segment 2, anterior setae, modal length (micrometer units X500): 1; 2 to 5; 11 to 29.
47. Gnathopod 2, segment 5, dorsal length (residual, regressed on char. 49): 15.1; 10.3 to 3.0; 0.8 to -3.4; -5.3 to -5.9; -9.8 to -12.9.
48. Gnathopod 2, segment 5, posterior lobe, length of setae (micrometer units X500): 13-3; 1; 0.

54. Gnathopod 2, segment 6, species with a thumb, thumb length (residual, regressed on char. 49): -11.4 to -6.7; -3.1 to 2.2; 4.4 to 16.8.
56. Gnathopod 2, segment 6, thumb development plot: type 2; type 1.
57. Gnathopod 2, segment 6, thumb tip, shape: acute; squared or rounded; indented.
59. Gnathopod 2, segment 6, defining spines in the larger adult males: present but reduced in length; present, more pronounced than in the juvenile; lost (latter two states equally apomorphic).
62. Gnathopod 2, segment 6, species with 3 defining spines (char. 61, state 3) that lose these when larger (char. 59, state 2), distance between defining setae: 13-15; 9; 6; 4-2; 0.
66. Gnathopod 2, segment 6, species with type 2 setation (char. 55, state 1), thumb length in largest subadult: 18-10; 3-1; 0.
69. Gnathopod 2, dactyl, inner margin, species with determinate growth (char. 55, state 1), minor forms with pronounced tooth extending into the palmar incision: no; yes.
79. Peraeopod 3, segment 4, anterior marginal setae, modal number per cluster: 1; 2; 3; 4.
83. Peraeopod 3, segment 5, proportion of length overlapped by segment 4: 65-81; 100.
98. Uropod 1, inner ramus, percentage of length underlain by ventral peduncular spinous process: 54-25; 16-6.
100. Uropod 1, rami terminating in a ventral fringe of cusps: no; yes.
126. Gnathopod 2, segment 6, distance of hinge tooth from intra-palmar angle (or defining spines if no palmar angle) (residual, regressed on char. 122): -16.8; -8.0 to -3.7; -1.7 to 0.7; 2.0 to 5.3; 14.5 to 15.2.
128. Gnathopod 2, segment 6, intra-palmar angle, distance to nearest defining spine: at; 1/3 of palm's length away; just distal of.
129. Gnathopod 2, segment 6, intra-palmar angle, shape: shallow and wide; pronounced, rounded; pronounced, acute; pronounced, squared (latter two states are equally apomorphic).
136. Gnathopod 2, dactyl, inner margin, shape: evenly convex or straight; proximally expanded.
139. Gnathopod 2, segment 6, anteroproximal setal group: absent; present.

141. Cnathopod 1, segment 5, anterodistal setal cluster: present;
absent.

spinning. Conlan and Bousfield (1982a) noted a difference in segment 4 expansion in amphipods, which are tube building amphipods also. Species with broadly expanded segments, such as Peramphithoe humeralis and P. lessoniophila, were found to roll kelp blades around themselves (Jones, 1971). Species with slender segments (e.g., Ampithoe lacertosa and A. valida) built their tubes by locating pre-existing folds of algae, or by fastening two blades together (Heller, 1968). Thus, those with more expanded segments were more powerful in algal manipulation.

The difference in first uropod cusping may relate to tube adherence or to cleaning. The urosome can be curved below the animal, the uropod spines then scraping detritus off the head, antennae and gnathopods.

The characters that are species distinctive, no matter what the age or sex, occur on the second antennae, mandible, both first and second gnathopods, third and fourth pereopods, and first uropods (characters 7, 9, 16, 17, 26, 27, 35, 43, 45, 47, 48, 79, 83, 98, 100, 126, 128, 129, 139, and 141 in Appendix Table 1). Males of Southern Hemisphere species diverge more in sexually dimorphic features than in non-sexually dimorphic characters. Northern Hemisphere species show the reverse. Species recognition may involve a combination of visual, tactile, and chemical cues. Vision is important for agonistic communication in various decapods (Brusci and Dunham, 1987), and pheromones have been implicated in sexual recognition in amphipods (Borowsky, 1984; Borowsky et al., 1987; Borowsky and Borowsky, 1987b). Thus, Southern Hemisphere species may base species recognition on mating behavior and secondary sexual characteristics. Northern Hemisphere species may require species recognition at an earlier age, and in either sex. The difference may

signify a divergence in mating behavior, and may be a consequence of a greater degree of sympatry and more recent divergence in the Northern Hemisphere.

Of the thirty-four synapomorphic characters plotted on Fig. 72, only one fully supports the phylogeny without a reversal or independent origin. This is character 17, the mandible raker spine number. However, despite the high amount of homoplasy, there is strong consensus on most portions of the tree topology (Fig. 68).

Taking either Hemijassa or Pleojassa as the sister group sets the origin of Jassa in the Southern Hemisphere. Invoking parsimony as a criterion for tree selection, the Wagner trees of Figs. 68 and 69 require fewer hypotheses than the compatibility trees for surmounting major barriers like the equator (Table 19) and the Central American land bridge (Table 20). Without invoking anthropochory, chances for dispersal across (or vicariance by) the warm water equatorial barrier probably have not occurred since the last period of oceanic cooling eleven thousand years ago (Brown and Gibson, 1983). Opportunities for dispersing between tropical Atlantic and Pacific Oceans would have been lost when North and South America were joined. Estimates for closure range from 2 to 5.7 million years ago (Lessios, 1981). Currently, no species of Jassa is known from Central America. In order for Jassa to have survived dispersal through the Panama gap, either the Central American waters would have had to have been cooler than they are now or the ancestor warm water adapted. Disjunct populations either side of a major barrier may result from a vicariant event. Here, erection of the barrier (Isthmus of Panama and warmer equatorial water) would bisect a continuous population, resulting

Table 19. Number of trans-equatorial speciation events hypothesized for Jassa by the consensus trees of Figs. 68 and 69, assuming origin in the Southern Hemisphere.

Fig. no.	Description	Analysis	No. of speciations across the equator	No. of hypothetical ancestors	Proportion (%)
68	All characters	Parsimony	3	19	15.8
		Compatibility	9	19	47.4
69	Non-sexually dimorphic characters	Parsimony	3	19	15.8
		Compatibility	4	19	21.1
		Compatibility	5	19	26.3

Table 20. Number of trans-North American speciation events hypothesized for Northern Hemisphere lineages of Jassa by the consensus trees of Figs. 68 and 69.

Fig. no.	Description	Analysis	No. of speciations between North Atlantic and North Pacific	No. of hypothetical ancestors in Northern Hemisphere lineages	Proportion (%)
68	All characters	Parsimony	2	11	18.2
		Compatibility	3	7	42.9
69	Non-sexually dimorphic characters	Parsimony	2	11	18.2
		Compatibility	2	9	22.2
		Compatibility	4	10	40.0

in local extinction, regression poleward, divergence, and speciation.

Although there are no fossils of the Amphipoda older than Upper Eocene (about 45 million years BP), Bousfield (1983) has speculated, on the basis of fossil evidence for related orders, that the Amphipoda originated in the Triassic (232 - 195 MYBP) and that the ancestor of all the Ischyroceridae occurred at some time during the Tertiary (65 - 22.5 MYBP). When the ancestor of all extant species of Jassa actually occurred is, of course, unknown. Ross (1972) (cited in Pielou, 1979), states that "... it takes at least 30,000 years of isolation for [an insect] population to evolve into a species." Yet many of the Hawaiian species of Drosophila arose in just a few thousand years (Futuyma, 1979). Ferris et al. (1976) (cited in Pielou, 1979) determined that an extant species of nematode had existed for at least 100 MY. Futuyma (1979) states that most species do not persist more than about 6 million years. Haldane (1957) (cited in Futuyma, 1979) calculated that it would take, on average, about three hundred generations for complete genetic change at one locus, and about three hundred thousand generations for complete genetic change at one thousand loci. On this basis it might take five hundred thousand years for new species to evolve by gradual allele replacement.

The cladogram of Fig. 72 suggests that Jassa originated in cold Antarctic waters. There were two trans-equatorial dispersals: an earlier one, from which radiated the northeastern Atlantic J. falcata group and J. herdmani, and a second one, from which radiated the northeastern Pacific species, the (originally) northwestern Atlantic J. marmorata, and the pan- North Atlantic J. pusilla. According to Stanley (1984), it is common to find the oldest animal species in cold water, because they have

been buffeted less by past mass extinctions caused by global water cooling. According to Bousfield (pers. comm.), pleustid amphipods, which are algal dwellers like Jassa, show a similar northward evolution, but unlike Jassa, have radiated into the Arctic. Being a younger group than the pleustids, Jassa may radiate into the Arctic in time.

The cold Antarctic distribution of J. ingens (Fig. 59) resembles that of Pleojassa wandeli (Fig. 60) and Hemijassa goniamera (Fig. 61). The cladistically more distant Ventojassa barnardi occurs in warmer water. This suggests that the sister group to Jassa (whether Hemijassa or Pleojassa) originated as the world oceans progressively cooled during the Paleogene (65MYBP - 26MYBP) (Kennett, 1983). Although the Antarctic ice cap may not have formed until the middle Miocene, 14MYBP, Antarctica was cold enough to form an ice sheet as early as 39MYBP (Kennett, 1983). It was about this time that the ancestor leading to Jassa ingens might have originated. Significantly, Ventojassa barnardi, Hemijassa goniamera, and all species of Pleojassa do not occur intertidally, while all species of Jassa (with the exception of J. pusilla) can be found intertidally or shallow subtidally (Table 10). The diversity of biotic substrates for tube attachment (algae, sponge, hydroid) must be considerably greater for shallow species, while deep dwellers may have more free rock substrate available. Thus, competition for space may have increased with habitation of shallower areas, and delayed male maturation would have been selected for.

Opportunity for circum-Antarctic dispersal would have been greatly enhanced once the Antarctic Circumpolar Current became established about 30MYBP (Kennett et al, 1974). This would also have allowed dispersal

northward, as arms of the Antarctic Circumpolar Current ran along the west coast of Africa (today's Benguela Current) and South America (today's Humboldt Current). Either current could have taken an ancestor of J. falcata and J. herdmani to the North Atlantic, but lack of either species on the North American coast argues for dispersal via the Benguela Current. With the oceans cooling throughout the Paleogene (Kennett, 1981), the tropics may not have presented as formidable a barrier to Jassa as they apparently do today.

Although J. falcata and J. herdmani broadly overlap in distribution today, J. falcata ranges further north and J. herdmani further south. Centres of speciation could have been British or Scandinavian for J. falcata and Mediterranean for J. herdmani. The Mediterranean Sea was a much larger body of water then than it is now (Sclater and Tapscott, 1979). J. falcata and J. herdmani can be found cohabiting the same algae, but one always exceeds the other in abundance. Both species lack the fringe of setae along the second gnathopod's segment 2 and 6 anterior margins. Both bear an unusual fringe of setae on the dorsal margin of the mandibular palp's second segment. The function of these setal arrangements is not known. The mandibular setae curve laterally, suggesting that they may be used in cleaning the inner surfaces of the antennae. The gnathopod setal fringe may assist in funneling water movement along the sternum and over the gills.

While Jassa was diverging in the Northern Hemisphere, speciation was continuing in the Southern Hemisphere. The temperate distribution of J. gruneri, J. hartmannae (Fig. 59), J. alonsoae, J. fenwicki, and J. justi (Fig. 58) suggests that these species are less capable of withstanding

cold than are J. thurstoni and J. ingens. Speciation may have occurred during the Pliocene, when global temperatures became warmer than they had during the Paleogene (Kennett, 1983). Currently J. alonsoae, J. fenwicki, and J. justi broadly overlap in distribution (Fig. 58), while J. hartmannae and J. gruneri are restricted to southern New Zealand and The Snares. Unique to J. alonsoae, J. justi, J. hartmannae, and J. fenwicki is the spine row along the anterior margin of the first gnathopod's second segment.

Fig. 72 suggests that a second invasion of the Northern Hemisphere led to radiation in the Atlantic and Pacific. Here the equatorial barrier may have been crossed on the Pacific coast of South America. With the two Americas separated, the Peru Current may have extended further north, crossing through the Panamanian gap into the Gulf of Mexico. Dispersal around the Americas presumably could have occurred any time between the late Paleocene and late Pliocene while the land bridge was submerged (Guyer and Savage, 1986). Dispersal could have occurred in a clockwise direction, around the Atlantic and Pacific gyres.

Jassa pusilla may have been the first species of Jassa to populate the Atlantic coast of North America, with J. marmorata arriving much later. Currently, J. pusilla is sympatric with J. marmorata, J. falcata, and J. herdmani, but occupies a greater depth zone. Its occupation of European shores may have occurred subsequent to colonization by the ancestor of J. falcata and J. herdmani, dispersal being aided by the Gulf Stream.

Twice as many species of Jassa are known from North America's Pacific coast than from its Atlantic coast. Such is typical for all gammarid amphipods: the Pacific coast supports twice the diversity, and more

endemic families than the Atlantic (Bousfield, 1981). The disparity holds for most other marine fauna as well (Briggs, 1970). The difference results from the physical, meteorological, and oceanographic attributes of each coast. The Northeastern Pacific coast is uniformly steep and rocky, and is frequently dissected by deep fords and rapidly inflowing rivers. Upwelling supports a high diversity of food groups. Lack of intrusion of cold Arctic water results in a benign climate, suitable to stenotopic inhabitants. By contrast, the Atlantic coast of North America is rocky to the north, but smoother and lower lying to the south. The broad expanse of beaches and lagoons in the southern US may prevent inhabitation by Jassa, except adventitiously on man-made structures. Both coastal water salinity and temperature are more variable on the Atlantic coast than on the Pacific coast (29 to 36 ‰ and 0 to 30 °C on the Atlantic coast, as opposed to 31 to 34 ‰ and -1 to 20 °C on the Pacific coast of North America) (Gross, 1972). Thus the Atlantic coast presents a smaller range of suitable coastline for Jassa, and physico-chemical conditions that prevent the development of stenotopy. Between twenty and sixty degrees North, the Atlantic coast of North America is divisible into three zoogeographic provinces (Arctic, Newfoundland to Cape Hatteras, and the Caribbean), while the Pacific coast of North America is divisible into six provinces (Arctic, Aleutian, Oregonian, California, Cortez, and Mexican) (Briggs, 1974; Brusca and Wallerstein, 1979). Some provinces are faunistically more distinct than others. The Florida peninsula is not a significant zoogeographic barrier, while the Baja California peninsula is (Briggs, 1970). The major currents running along the temperate Atlantic coast of North America are the northeasterly

flowing Gulf Stream along the south coast, and the cold Labrador current flowing southward from the Arctic (Fig. 54). The Labrador current effectively stops dispersal of J. marmorata northward (Fig. 55). The Pacific coast of North America receives the southward flowing California current and the nearshore, northerly flowing Davidson current which surfaces in winter (Brusca and Wallerstein, 1979). Farther north is the northward flowing Aleutian current. None of the endemic Pacific species of Jassa extend as far south as does J. marmorata on the Atlantic coast. However, the Pacific species range considerably farther north.

The ecological data for North Pacific species is not sufficiently refined to suggest ways in which differences in habitat could have effected speciation. There is some differentiation based on exposure. Jassa oclairi, J. morinot, and J. shawi are only known from exposed coasts, while J. stauderi and J. slatteryi are found in protected bays and harbors as well. The restricted northern range of J. oclairi suggests an Alaskan origin, perhaps as a glacial relict. J. carltoni and J. myersi may be warmer water relicts, now limited in range to the southern limit of the temperate North Pacific. The most recently derived species, J. stauderi and J. marmorata, may have originated after the emergence of the Panamanian landbridge bisected the range of their circum- North American ancestor. Jassa stauderi is not as widespread as is J. marmorata, but does occur in a wide range of habitats, and like J. marmorata, succeeds in invading aquaria.

Jassa marmorata seems to be the most successful of all species of Jassa. It has penetrated further into the tropics than any other species of Jassa. It is the sole member of the genus to occupy shallow Atlantic

North America, and in harbors it may outnumber all other amphipods in abundance. Jassa marmorata has now succeeded in traversing major barriers and dispersing to other temperate shores, and may have displaced native residents wherever there has been broad disruption by man.

5. CONCLUSIONS

Jassa is not a monotypic genus, as claimed by Sexton and Reid (1951), but comprises a diverse group of nineteen species. These species are distinctive among the Ischyroceridae by having the following characters. (1) Both first and second antennae bear long filter setae, but the second antennae are pediform in most, and their setation changes at adulthood. (2) The palm of the first and second gnathopods is defined by three closely approximated spines, positioned in medial-lateral-medial order. (3) The second gnathopod of both sexes is large and differs in shape from the first gnathopod. In the male the palm is incised between dactyl hinge and defining spines to produce a (usually) long, narrow thumb; the defining spines disappear in most species if the animal is sufficiently large, but the associated clusters of setae remain in a distinctive pattern. In the female, the palm is concave or sinuous, but the shape remains unchanged throughout life. (4) The fifth, sixth, and seventh pereopods lack spines on the posterior margin of the fourth and fifth segments. (5) Both the dorsum of the urosome segment 1 and the telson have a pair of dorsally projecting setae which probably sense proximity of the body to the tube. (6) The third uropod is distinctive in lacking spines in the mid-dorsal region of the peduncle, and bearing a pair of cusps and a basally immersed, dorsally recurved spine on the outer ramus.

Six species that were previously assigned to Jassa have been transferred to other genera as follows: J. wandeli and J. multidentata to Pleojassa, J. goniamera to Hemijassa, J. barnardi to Ventojassa, J. lilipuna to Neoischyrocerus, and J. ocia to Plumulojassa. Seventeen new

species and one new subspecies have been recognized. Finally, Jassa odontonyx has been synonymized with J. pusilla, and J. dentex with Plumulojassa oia. J. pulchella has been confirmed as being synonymous with J. falcata.

Analysis of morphological change in relation to body size has supported the observations of Borowsky (1983 and 1985) on live Jassa marmorata that the males of all species of Jassa delay thumb production to the last molt. That thumbing signifies functional maturity has been established elsewhere by Borowsky (1985). I suggest that the delay in male breeding is caused by a male biased operational sex ratio, which has resulted from coloniality, a polygynous mating system, asynchronous female receptivity, and sole parental care by the female. The observed divergence of males into a minor or major form at the time of thumbing can also be expected under such mating conditions. In the type 1 species of Jassa, the alternative mating strategy seems to be an effort to make the best of a bad situation when small. In the type 2 species, the mating strategies may be frequency dependent and evolutionarily stable. Prolific breeding, ready availability, and propensity for establishing colonies in lab aquaria are characteristics that should make Jassa a desirable subject for experimental analysis.

Species of Jassa are restricted to shallow cold temperate or Antarctic marine coasts. Seven species reside in the Southern Hemisphere, nine species are restricted to the Northern Hemisphere, and three others have probably been secondarily dispersed by man to the Southern Hemisphere. The typically high diversity of North Pacific marine biota is reflected in Jassa. Six species of Jassa are restricted

to the North Pacific, and another two are suspected to have originated there. By contrast, the North Atlantic supports three indigenous species, plus an additional cosmopolitan species whose origin is hypothesized to be Northeastern Atlantic. Range differences can be attributed to the effect of temperature, depth, and exposure. There may be some difference in substrate preference as well, but better documentation of substrate, and more precise sampling must be made by collectors in the future.

Character evolution in Jassa has been predominantly restricted to the portion of the body that extends from the tube. Males of Southern Hemisphere species diverge more in sexually dimorphic than in non-sexually dimorphic characters. The reverse is true for Northern Hemisphere species. Thus, Southern Hemisphere species may not recognize conspecifics until the time of mating; Northern Hemisphere species may require species recognition at an earlier age. These differences may be partly the result of there being a greater amount of sympatry among Northern Hemisphere species.

Cladistic analysis by Wagner parsimony showed a greater consensus among equally short trees than did compatibility analysis on the trees generated by the largest cliques. The overall trend seen by comparing the secondary outgroup species to Jassa is of increasing sexual dimorphism, and of delay in the male's reproduction to the final molt. This is culminated in Jassa by divergence into alternative reproductive strategies.

Wagner parsimony required fewer hypotheses of transgression of major barriers like the tropics and the Panama gap. Using Wagner parsimony, it

is hypothesized that Jassa originated in the Southern Hemisphere from an ancestor common to Pleojassa in the mid-Tertiary, and twice succeeded in traversing the tropical barrier, probably by dispersing on currents to the North. Additional species of Jassa may still be found along relatively poorly studied cold water coasts, such as occur in eastern Asia, the USSR, northwest and southwest Africa, southeast and southwest South America, Antarctica, South Australia, and on the many small cold water islands of both hemispheres.

6. REFERENCES

- Alonso, G. 1980. Anfipodos de la Ria Deseado (Santa Cruz-Argentina). 1.
-Contribuciones Cientificas CIBIMA 175: 1-15.
- Archie, J.W. 1984. A new look at the predictive value of numerical
classifications. -Systematic Zoology 33: 30-51.
- Arresti, A., J. C. Iturrondobeitia, and A. Rallo. 1986. Contribucion al
conocimiento faunistico y ecologico del orden Amphipoda en al Abra de
Bilbao (C. Vasca). -Cuadernos de Investigacion Biologica (Bilbao) 9:
89-125.
- Barnard, J. L. 1961. Gammaridean Amphipoda from depths of 400 to 6,000
metres. -Galathea Report 5: 23-128.
- , 1962. Benthic marine Amphipoda of Southern California:
Families Aoridae, Photidae, Ischyroceridae, Corophiidae, Podoceridae.
-Pacific Naturalist 3: 1-72.
- , 1969. Gammaridean Amphipoda of the rocky intertidal of
California: Monterey Bay to La Jolla. -Bulletin of the U.S.
National Museum 258: 1-230.
- , 1970. Sublittoral Gammaridea (Amphipoda) of the Hawaiian
Islands. -Smithsonian Contributions to Zoology 34: 1-286.
- , 1972. The marine fauna of New Zealand: algae-living littoral
Gammaridea (Crustacea Amphipoda). New Zealand Oceanographic
Institute Memoir No. 62: 1-216.
- , 1973. Revision of Corophiidae and related families
(Amphipoda). -Smithsonian contributions to Zoology 151: 1-27.
- , and M. M. Drummond. 1981. Three corophioids (Crustacea:
Amphipoda) from Western Port, Victoria. -Proceedings of the Royal

- Society of Victoria 93: 31-41.
- , and D. J. Reish. 1959. Ecology of Amphipoda and Polychaeta of Newport Bay, California. -Allan Hancock Foundation Occasional Papers 21: 1-106.
- Bate, C. S. 1857. A synopsis of the British edriophthalmous Crustacea. Part 1. Amphipoda. -Annals of the Magazine of Natural History (Series 2) 19: 135-152.
- , 1862. Catalogue of the specimens of amphipodous Crustacea in the collection of the British Museum, London. Printed by Order of the Trustees by Taylor and Francis, London, Publisher. Pp. 1-399.
- , and J. O. Westwood. 1862. A history of British sessile-eyed Crustacea. Volume 1, parts 4-10. John Van Voorst, London. Pp. 145-480
- Bellan-Santini, D. 1972a. Amphipodes provenant des contenus stomacaux de trois espèces de poissons Nototheniidae récoltés en Terre Adélie (Antarctique). -Téthys 4(3): 683-702.
- , 1972b. Invertébrés marins des XIIème et XVème expéditions Antarctiques Françaises en Terre Adélie. 10. Amphipodes Gammariens. -Téthys Supplement 4: 157-238.
- , and M. Ledoyer. 1972. Inventaire des Amphipodes Gammariens récoltés dans la région de Marseille. -Téthys 4(4): 899-934.
- , 1973. Gammariens (Crustacea Amphipoda) des Iles Kerguelen et Crozet. -Téthys 5(4): 635-708.
- Bock, W. J. 1977. Foundations and methods of evolutionary classification. -In: M.K. Hecht, P.C. Goody and B.M. Hect, eds., Major patterns in vertebrate evolution. Pp.851-895. Plenum Press, New York.
- Boeck, A. 1872. De Skandinaviske og Arktiske Amphipoder Part 1. -

Christiania 1-160.

Boero, F., and A. Carli. 1979. Observations on the behaviour of the amphipod Jassa falcata. -Bolletino del Museo Civico Storia Naturale di Verona 6: 147-153 [in Italian].

Bonnier, J. 1896. Edriophthalmes: Résultats scientifiques de la campagne du "Caudan" dans le Golfe de Gascogne. -Annales de l'Université de Lyon 26: 527-689.

Borowsky, B. 1983. Reproductive behavior of three tube-building peracarid crustaceans: The amphipods Jassa falcata and Ampithoe valida and the tanaid Tanais cavolinif. -Marine Biology 77: 257-263

-----, 1984. Effects of receptive females' secretions on some male reproductive behaviors in the amphipod crustacean Microdeutopus gryllotalpa. -Marine Biology 84: 183-187.

-----, 1985. Differences in reproductive behavior between two male morphs of the amphipod crustacean Jassa falcata Montagu. -Physiological Zoology 58(5): 497-502.

-----, C. E. Augelli, and S. R. Wilson. 1987. Towards chemical characterization of waterborne pheromone of amphipod crustacean Microdeutopus gryllotalpa. -Journal of Chemical Ecology 13(7): 1673-1680.

-----, and R. Borowsky. 1987a. Feeding by the salt marsh amphipod, Gammarus palustris, on Ulva and Enteromorpha. Abstract 285. -American Zoologist 27(4): 55A.

-----, 1987b. The reproduction behaviors of the amphipod crustacean Gammarus palustris (Bousfield) and some insights into the nature of their stimuli. -Journal of Experimental Marine

- Biology and Ecology 107: 131-144.
- Bousfield, E. L. 1952. Zoological investigations in the Maritime Provinces. -In: Annual report of the National Museum of Canada for the Fiscal Year 1950-51. Pp. 188-194. National Museum of Canada Bulletin No. 126.
- , 1973. Shallow-water Gammaridean Amphipoda of New England. Cornell University Press, Ithaca and London. Pp. 1-312.
- , 1981. Evolution in north Pacific coastal marine amphipod crustaceans. Pp. 69-89. In: G.G.E. Scudder and J.L. Reveal, eds., Proceedings of the Second International Congress of Systematics and Evolutionary Biology. Pp. 69-89. Vancouver, British Columbia.
- , 1983. An updated phyletic classification and palaeohistory of the Amphipoda. In: F. F Schram, ed., Crustacean phylogeny. Pp. 257-277. A. A. Balkema, Rotterdam.
- Briggs, J. C. 1970. A faunal history of the North Atlantic Ocean. - Systematic Zoology 19: 19-34.
- , 1974 Marine zoogeography. McGraw-Hill, New York. Pp. 1-475.
- Brown, J. H., and A. C. Gibson. 1983. Biogeography. The C. V. Mosby Company, St. Louis. Pp. 1-643.
- Brusca, R. C., and B. R. Wallerstein. 1979. Zoogeographic patterns of idoteid isopods in the Northeast Pacific, with a review of shallow water zoogeography of the area. -Bulletin of the Biological Society of Washington 3: 67-105.
- Bruski, C. A., and D. W. Dunham. 1987. The importance of vision in agonistic communication of the crayfish Orconectes rusticus L: An analysis of bout dynamics. -Behavior 103 (1-3): 83-107.

- Carlton, J. T. 1979. History, biogeography, and ecology of the introduced marine and estuarine invertebrates of the Pacific coast of North America. -Ph.D. thesis. University of California, Davis. Pp. 1-904.
- , 1985. Transoceanic and interoceanic dispersal of coastal marine organisms: the biology of ballast water. -*Oceanography and Marine Biology Annual Review* 23: 313-37.
- Chess, J. R. 1979. High densities of benthic amphipods related to upwelling on the northern California coast. -*Coastal Oceanography and Climatology News* 1(3): 31.
- Chevreaux, E. 1900. Amphipodes provenant des campagnes de l'Hirondelle, 1885-1888. -*Résultats des campagnes scientifiques accomplies sur son yacht par Albert I^{er}, Prince souverain de Monaco* 16: 1-195.
- , 1906. Crustacés Amphipodes. -*In*: *Expédition Antarctique Française (1903-1905) commandée par le Dr. Jean Charcot. Sciences naturelles: Documents scientifiques.* Pp. 1-100. Masson et Cie, Paris.
- , 1913. Crustacés Amphipodes. -*In*: *Deuxième Expédition Antarctique Française (1908-1910) commandée par le Dr. Jean Charcot. Sciences naturelles: Documents scientifiques.* Pp. 79-186. Masson et Cie, Paris.
- and L. Fage. 1925. Amphipodes. -*Faune de France* 9: 1-488.
- Chilton, C. 1883. Further additions to our knowledge of the New Zealand Crustacea. -*Transactions and Proceedings of the New Zealand Institute* 15: 69-86.
- Clark, C., and D. J. Curran. 1986. Outgroup analysis, homoplasy, and global parsimony: a response to Maddison, Donoghue, and Maddison. -

- Systematic Zoology 35(3): 422-426.
- Cognetti, G., P. Tongiorgi, and A. M. Bonvicini-Pagliai. 1979. La biologia marina e la gestione della fascia costiera. Attidella Societa Toscana di Scienze Naturali Processi Verbali e Memorie Serie B 86, supplement: 312-315.
- Conlan, K. E. 1988. Phenetic and cladistic methods applied to a small genus (Corophioidea: Ischyroceridae: Microjassa) and a larger outgroup. -Crustaceana, Supplement 13: 143-166.
- , and E. L. Bousfield. 1982. The amphipod superfamily Corophioidea in the Northeastern Pacific region. Family Amphithoidae: Systematics and distributional ecology. -National Museum of Natural Sciences (Ottawa) Publications in Biological Oceanography 10: 41-73.
- Costello, M. J., and A. A. Myers. 1987. Amphipod fauna of the sponges Halichondria panicea and Hymeniacidon perleve in Lough Hyne, Ireland. -Marine Ecology-Progress Series 41: 115-121.
- Culpepper, T. J. 1969. A taxonomic and ecological study of selected benthonic gammarid Crustaceans from the Northeastern Gulf of Mexico. -Ph.D. thesis, Texas A&M University. Pp. 1-141.
- Czerniavski, V. I. 1868. Materialia and zoographiam ponticam comparatam. Trudy Russkikh Estestvoispytatelei v S. -Peterburge Session 1 (Zool.): 17-36.
- Dahl, E., H. Emanuelsson, and C. Von Mecklenburg. 1970. Pheromone transport and reception in an amphipod. -Science 170:739-740.
- Dawkins, R. 1986. The blind watchmaker. W. H. Norton and Company, New York and London. Pp. 1-332.

Dawkins, R. 1986. The blind watchmaker. W. H. Norton and Company, New York and London. Pp. 1-332.

Dana, J. D. 1852. United States exploring expedition during the years 1838, 1839, 1840, 1841, 1842 under the command of Charles Wilkes, U.S.N. Volume XIII. Crustacea. United States Exploring Expedition. Pp. 1-1618.

Daro, M. H. 1970. L'association des amphipodes et des Polydora ciliata à la côte Belge. -Netherlands Journal of Sea Research 5(1): 96-100.

Della Valle, A. 1893. Gammarini del Golfo di Napoli. -Fauna u. Flora des Golfes von Neapel und der angrenzenden meeresabschnitte. Berlin. 20: 19-48.

Diviacco, G. 1979a. Amphipods of fouling (sic) in the conduits of the electrical power station of Torvaldaliga (Civatavecchia). -Atti della Societa Toscana di Scienze Naturali Processi Verbali e Memorie Serie B, Supplement 86: 312-315.

-----, 1979b. I crostacei anfipodi del fouling nella centrale termoelettrica di Vado Ligure (Savona). -Bollettino del Museo e degli Istituti Biologici dell'Universita di Genova 47: 93-99.

-----, 1980. Osservazioni sui crostacei anfipodi del porto di Genova. -Memorie di Biologia Marina e di Oceanografia, Supplement. 10: 387-388.

-----, 1981. Ecologia e distribuzione dei crostacei anfipodi nella Laguna di Orbetello. -Bollettino del Museo Civico di Storia Naturale di Verona 7: 303-317.

-----, 1983. Osservazioni sui crostacei anfipodi della centrale termoelettrica di Torvaldaliga. -Natura-Societa Italiana di

- Scienze Naturale, Museo Civico di Storia Naturale e Acquario
Civico, Milano 74 (1-2): 83-95.
- , and G. Relini. 1981. Gli anfipodi della Laguna di Orbetello. -
Quaderni del Laboratorio di Tecnologia della Pesca 3(1): 283-291.
- Donoghue, M. J., and P.D. Cantino. 1984. The logic and limitations of the
outgroup substitution approach to cladistic analysis. -Systematic
Botany 9(2): 192-202.
- , and W. P. Maddison. 1986. Polarity assessment in phylogenetic
systematics: a response to Meacham. -Taxon 35(3): 534-545.
- Eberhard, W. G. 1980. Horned beetles. -Scientific American 242(3): 166-
182.
- , 1982. Beetle horn dimorphism: making the best of a bad lot.
The American Naturalist 119: 420-426.
- Ehling, F.J., J. A. Kitching, R. D. Purchon, and R. Bassindale. 1948. The
ecology of the Lough Ine Rapids with special reference to water
currents. 2. The fauna of the Saccorhiza canopy. -Journal of Animal
Ecology 17: 223-244.
- Eck, R. V., and M. O. Dayhoff. 1966. Atlas of protein sequence and
structure 1966. National Biochemical Research Foundation, Silver
Spring, Md.
- Farris, J. S. 1982. Outgroups and parsimony. -Systematic Zoology 31(3):
328-334.
- Felsenstein, J. 1973. Maximum likelihood and minimum-steps methods for
estimating evolutionary trees from data on discrete characters. -
Systematic Zoology 22: 246-249.

- , 1978. Cases in which parsimony or compatibility methods will be positively misleading. -Systematic Zoology 27(4): 401-410.
- , 1979. Alternative methods of phylogenetic inference and their interrelationship. -Systematic Zoology 28: 49-62.
- , 1981. A likelihood approach to character weighting and what it tells us about parsimony and compatibility. -Biological Journal of the Linnean Society 16: 183-196.
- , 1985. Confidence limits on phylogenies: an approach using the bootstrap. -Evolution 39(4): 783-791.
- Fenwick, G. D. 1976. The effect of wave exposure on the amphipod fauna of the alga Caulerpa brownii. Journal of experimental marine Biology and Ecology 25: 1-18.
- Franz, D. R. 1987. Population dynamics of a marine fouling community amphipod Jassa marmorata. Abstract 177. -American Zoologist 27(4): 36A.
- Futuyma, D. J. 1979. Evolutionary biology. Sinauer Associates, Incorporated, Mass. Pp. 1-565.
- Gower, J. C. 1971. A general coefficient of similarity and some of its properties. -Biometrics 27: 857-874.
- Griffiths, C. L. 1977. Deep-sea amphipods from west of Cape Point, South Africa. -Annals of the South African Museum 73(4): 93-104.
- Gross, M. G. 1972. Oceanography. A view of the earth. Prentice-Hall, Incorporated, Englewood Cliffs, New Jersey. Pp. 1-581.
- Gross, M. R. 1985. Disruptive selection for alternative life histories in salmon. -Nature 313: 47-48.

- Gurjanova, E. F. 1951. Gammaridea of the seas of the USSR and adjacent waters. -Fauna SSSR 41: 1-1031. [in Russian].
- Guyer, C. and J. M. Savage. 1986. Cladistic relationships among Anoles (Sauria: Iguanidae). Systematic Zoology 35(4):509-531.
- Haswell, W. A. 1880. On some additional new genera and species of amphipodous crustaceans. -Proceedings of the Linnean Society of New South Wales 4: 319-350.
- Hay, M. E., J. E. Duffy, and C. A. Pfister. 1987. Chemical defense against different marine herbivores: are amphipods insect equivalents? -Ecology 68(6): 1567-1580.
- Heller, C. 1886. Beiträge zur näheren kenntniss der Amphipoden des Adriatischen Meeres. -Denkschriften der Akademie der Wissenschaften. Wien. 26(2): 1-57.
- Heller, S. P. 1968. Some aspects of the biology and development of Amphithoe lacertosa (Crustacea: Amphipoda). -M.Sc. thesis, University of Washington, Seattle.
- Heppner, J. B., and G. Lamas. 1982. Acronyms for world museum collections of insects, with an emphasis on Neotropical Lepidoptera. - Bulletin of the Entomological Society of America 28(3): 305-313.
- Holmes, S. J. 1903. Synopses of North American invertebrates. 18. The Amphipoda. -American Naturalist 37: 267-292.
- , 1904. The Amphipoda of southern New England. -Bulletin of the Bureau of Fisheries 24: 457-529.
- Hong, J. -S. 1983. Three tube-building amphipods from experimental plates in Deukryang Bay in the southern coast of Korea. -Korean Journal of Zoology 26(2): 135-153.

- Hull, D. L. 1970. Contemporary systematic philosophies. -In: R. F. Johnston, P. W. Frank, and C. D. Michener, eds., Annual review of ecology and systematics. Volume 1. Pub. Annual Reviews Incorporated, 4139 El Camino Way, Palo Alto, California. Pp. 10-54.
- , 1976. Are species really individuals? -Systematic Zoology 25(2):174-191.
- Jones, L. G. 1971. Studies on selected small herbivorous invertebrates inhabiting Macrocystis canopies and holdfasts in southern California kelp beds. -In: W. J. North, ed., The biology of giant kelp beds (Macrocystis) in California. Nova Hedwigia 32: 343-367.
- Jones, N. S. 1948. The ecology of the Amphipoda of the south of the Isle of Man. -Journal of the Marine Biological Association of the United Kingdom 27(2): 400-439.
- Kaandorp, J. A. 1986. Rocky substrate communities of the infralittoral fringe of the Boulonnais coast, NW France: a quantitative survey. -Marine Biology 92: 255-265.
- Kamenskaya, O. E. 1979. Some data on the biology of Jassa falcata (Montagu) (Amphipoda, Gammaridea) in the Sea of Japan. -In: The ecology of the bottom population of the shelf zone. Pp. 104-107. Oceanography Institute, Academy of Sciences, USSR. [In Russian].
- Kennett, J. P. 1983. Paleo-oceanography: global ocean evolution. -Reviews of Geophysics and Space Physics 21(5): 1258-1274.
- , R. E. Houtz, P. B. Andrews, A. R. Edwards, V. A. Gostin, M. Hajos, M. A. Hampton, D. G. Jenkins, S. V. Margolis, A. T. Owenshine, and K. Perch-Nielson. 1974. Development of the Circum-Antarctic Current. -Science 186: 144-147.

- Kenny, R., and N. Hayson. 1962. Ecology of rocky shore organisms at Macquarie Island. -Pacific Science 16: 245-263.
- Kluge, A. G., and J. S. Farris. 1969. Quantitative phyletics and the evolution of anurans. -Systematic Zoology 18: 1-32.
- Krebs, J. R., and N. B. Davies. 1987. An introduction to behavioural ecology. Blackwell Scientific Publications, Oxford. Pp. 1-389.
- Kröyer, H. N. 1838. Grönlands Amphipoder. -Kjöbenhavn (Kongelige) Danske videnskabernes Selskab Afh. VII: 229-326.
- Leach, W. E. 1814. Crustaceology. -The Edinburgh Encyclopaedia 7(2): 385-437.
- Ledoyer, M. 1979. Les gammariens de la pente externe du grand recif de Tuléar (Madagascar) (Crustacea Amphipoda). Memorie del Museo Civico di Storia Naturale di Verona (II^a Serie). Sezione Scienze Della Vita. No.2. Pp. 1-150.
- , and M. Menioni. 1983. Considerations sur la repartition du gammarien (Crustacea, Amphipoda) Jassa falcata (Montagu, 1808). - Bulletin de L'Institut Scientifique, Rabat, 7: 93-114.
- Lessios, H. A. 1981. Divergence in allopatry: molecular and morphological differentiation between sea urchins separated by the isthmus of Panama. -Evolution 35(4): 618-634.
- Lincoln, R. J. 1979. British marine Amphipoda: Gammaridea. British Museum (Natural History), London. Pp. 1-657.
- , G. A. Boxshall, and P. F. Clark. 1982. A dictionary of ecology, evolution and systematics. Cambridge University Press, Cambridge. Pp. 1-298.

- Maddison, W. P., M. J. Donoghue, and D. R. Maddison. 1984. Outgroup analysis and parsimony. -Systematic Zoology 33(1): 83-103.
- Marques, J. C. 1984. Contribuição para o conhecimento sistemático e ecológico dos anfípodes (Crustacea-Amphipoda) do litoral Português. Primeiro inventário do espécies (Gammaridea e Caprellidea). Trabalho de síntese apresentado para prestação de provas de aptidão científico - pedagógica. Coimbra. Pp. 1-71.
- , and D. Bellan-Santini. 1985. Contribution a l'étude systematique et ecologique des amphipodes (Crustacea - Amphipoda) des côtes du Portugal. Premier inventaire des espèces (Gammariens et Caprelliens). -Ciência Biológica (Portugal) 5: 299-351.
- Mayr, E. 1942. Systematics and the origin of species. -Columbia University Press, New York. Pp. 1-334.
- , 1963. Animal species and evolution. Harvard University Press, Cambridge. Pp. 1-797.
- , 1969. Principles of systematic zoology. McGraw-Hill, New York. Pp. 1-428.
- McPhail, J. D. 1969. Predation and the evolution of a stickleback, Gasterosteus. -Journal of the Fisheries Research Board of Canada 26: 3183-3208.
- Meacham, C. A. 1986. More about directed characters: a reply to Donoghue and Maddison. -Taxon 35: 538-540.
- Metropolis, N., A. W. Rosenbluth, M. N. Rosenbluth A. H. Teller, and E. Teller. 1953. Equation of state calculations by fast computing machines. -Journal of Chemical Physics 21: 1087-1092.

- Miers, E. J. 1875. Descriptions of new species of Crustacea collected at Kerguelen's Island by the Rev. A. E. Eaton. -Annals of the Magazine of Natural History 16(4): 73-76.
- Milne Edwards, H. 1830. Extrait de recherches pour servir à l'histoire naturelle des crustacés amphipodes. -Annales des Sciences Naturelles Zoologie et Biologie Animale 20: 353-399.
- Montagu, G. 1808. Description of several marine animals found on the south coast of Devonshire. -Transactions of the Linnaean Society London 9: 81-114.
- Moodie, G. G. E. 1972. Predation, natural selection and adaptation in an unusual three spined stickleback. -Heredity 28: 155-167.
- Moore, P. G. 1973. The larger Crustacea associated with holdfasts of kelp (Laminaria hyperborea) in North-East Britain. -Cahiers de Biologie Marine 14: 493-518.
- , 1984. The fauna of the Clyde Sea Area Crustacea: Amphipoda. - Occasional Publication No.2. University Marine Biological Station, Millport, Isle of Cumbrae. Pp. 1-74.
- , 1986. Levels of heterogeneity and the amphipod fauna of kelp holdfasts. -In: Moore, P. G., and R. Seed, eds., The ecology of rocky coasts. Pp. 274-289. Columbia University Press, New York.
- Nagle, J. S. 1968. Distribution of the epibiota of macroepibenthic plants. -Contributions in Marine Science 13: 105-144.
- Nair, K. K. C., and K. Anger. 1979. Experimental studies on the life cycle of Jassa falcata (Crustacea, Amphipoda). -Helgolander wissenschaftliche Meeresuntersuchungen 32: 444-452.

- , 1980. Seasonal variation in population structure and biochemical composition of Jassa falcata (Crustacea, Amphipoda) off the island of Helgoland (North Sea). -Estuarine and Coastal Marine Science 11: 505-513.
- Nelson, W. G. 1980. Reproductive patterns of gammaridean amphipods. -Sarsia 65(2): 61-71.
- O'Clair, C. E. 1977. Marine invertebrates in rocky intertidal communities. -In: The environment of Amchitka Island, Alaska. Pp. 395-449. Technical Information Center, Energy Research and Development Administration.
- Pequegnat, W. E. and L. H. Pequegnat. 1968. Ecological aspects of marine fouling in the northeastern Gulf of Mexico. Texas A&M Research Foundation, A&M Project 286-6, Reference 68-22T. Pp. 1-80.
- Pfeffer, G. 1888. Die Krebse von Süd-Georgien nach der Ausbeute der Deutschen Station 1882-83. [1887-88]. -Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten 5: 75-142.
- Pielou, E. C. 1979. Biogeography. Wiley-Interscience. New York. Pp.1-351.
- Rathke, H. 1843. Beitrage zur fauna Norwegens. Crustacea. -Novorum Actorum Academiae Caesarae Leopoldino -Carolinae Naturae Curiosorum 12(1): 63-98.
- Reid, D. M. 1951. Report of the Amphipoda (Gammaridea and Caprellidea) of the coast of tropical West Africa. -Atlantide Report 2: 189-291.
- Reish, D. J., and J. L. Barnard. 1979. Amphipods (Arthropoda: Crustacea: Amphipoda). -In : Hart, C. W. Jr., and S. L. H. Fuller, eds., Pollution ecology of estuarine invertebrates. Pp. 345-379. Academic Press, New York.

- Relini, G., C. N. Bianchi, G. Diviacco, and R. Rosso. 1977. Fouling di alcune piattaforme offshore del mari Italiani VI: Anfipodi e policheti. -Bollettino dei Musei e degli Istituti Biologici dell Università di Genova 45: 105-121.
- Sars, G. O. 1882. Oversigt af Norges Crustaceer med foreløbige Bemærkninger over de nye eller mindre bekjendte Arter. - Forhandlinger i Videnskabselskabet i Kristiana 18: 1-124.
- , 1894. An account of the Crustacea of Norway, with short descriptions and figures of all the species. Christiania and Copenhagen. Pp. 473-671.
- , 1895. An account of the Crustacea of Norway, with short descriptions and figures of all the species. Part 31/32 Appendix. Pp. 673-711. -Suppl. 1-8. Cammermeyers, Christiania and Copenhagen.
- Say, T. 1817. On a new genus of Crustacea, and the species on which it was established. -Journal of the Academy of Natural Sciences, Philadelphia 1: 49-52.
- Schellenberg, A. 1926. Die gammariden der deutschen Südpolar-Expedition 1901-1903. Deutsch südpolar-Expedition 18: 235-414.
- , 1931. Gammariden und Caprelliden des Magellangebietes, Suedgeorgiens und der Westantarktis. Further Zoological Results of the Swedish Antarctic Expedition 2(6): 1-290.
- , 1942. Die Tierwelt Deutschlands. Krebstiere oder Crustacea; IV, Flohkrebse oder Amphipoda. -Tierwelt Deutschlands 40: 1-252.
- Selater, J. G., and C. Tapscott. 1979. The history of the Atlantic. - Scientific American 240(6): 156-174.

- Sebens, K. P. 1986a. Community ecology of vertical rock walls in the Gulf states. -In: Moore, P. G., and R. Seed, eds., The ecology of rocky coasts. Pp. 346-371. Columbia University Press, New York.
- , 1986b. Spatial relationships among encrusting marine organisms in the New England subtidal zone. -Ecological Monographs 56(1): 73-96.
- Semler, D. E. 1971. Some aspects of adaptation in a polymorphism for breeding colours in the three-spined stickleback (Gasterosteus aculeatus L.). -Journal of Zoology (London) 165: 291-302.
- Sexton, E. W., and D. M. Reid. 1951. The life-history of the multiform species Jassa falcata (Montagu) (Crustacea Amphipoda) with a review of the bibliography of the species. Journal of the Linnean Society of London Zoology 42(283): 29-91.
- Shoemaker, C. R. 1930. The Amphipoda of the Cheticamp expedition of 1917. -Contributions to Canadian Biology and Fisheries 5(10): 221-359.
- , 1942. Amphipod crustaceans collected on the Presidential Cruise of 1938. -Smithsonian Miscellaneous Collections 101(11): 1-52.
- Simpson, G. G. 1961. Principles of animal taxonomy. Columbia University Press, New York. Pp. 1-147.
- Sneath, P. H. A. and R. I. C. Hansell. 1985. Naturalness and predictivity of classifications. -Biological Journal of the Linnean Society 24: 217-231.
- Sokal, R. R. and C. D. Michener. 1958. A statistical method for evaluating systematic relationships. -University of Kansas Science Bulletin 38: 1409-1438.

- Southgate, T., and A. A. Myers. 1985. Mussel fouling on the Celtic Sea Kinsale field gas platforms. -Estuarine, Coastal and Shelf Science 20: 651-659.
- Sowinski, W. 1898. Les Crustacées superieures (Malacostraca) de Bosphor. Mémoires de la Société des Naturalistes de Kiev. Pp. 1-72.
- Stace, G. 1980. Plant taxonomy and biosystematics. Edward Arnold, London. Pp. 1-279.
- Stanley, S. M. 1984. Mass extinctions in the ocean. -Scientific American 250(6): 64-72.
- Stebbing, T. R. R. 1888. Report of the scientific results of the voyage of H.M.S. Challenger during the years 1873-76. -Zoology Vol. 29. Neill and Company, Edinburgh. Pp. 1-1739.
- , 1899. On the true Podocerus and some new genera of amphipods. Annals of the Magazine of natural History (Series 7) 3: 237-241.
- , 1906. Amphipoda 1: Gammaridea. Das Tierreich, vol.21. Verlag von Friedländer und Sohn, Berlin. Pp. 1-806.
- , and G. H. Fowler. 1904. Biscayan plankton. Part II. Transactions of the Linnean Society of London. Zoology. 10: 2.
- , and D. Robertson. 1891. On four new British Amphipoda. - Transactions of the Zoological Society of London 13: 31-42.
- Stephenson, K. 1927. Papers from Dr. Th. Mortensen's Pacific Expedition 1914-1916. 40. Crustacea from Auckland and Campbell Islands. Videnskabelige Meddeleser fra dansk naturhistorisk Forening 83: 289-390.
- , 1942. The Amphipoda of N. Norway and Spitsbergen with adjacent waters. Tromsø Museums Skrifter 3(4): 363-526.

- , 1944. Crustacea Malacostraca, VIII: (Amphipoda IV). -Danish Ingolf-Expedition 3(13): 1-51.
- , 1949. The Amphipoda of Tristan da Cunha. Results of the Norwegian Scientific Expedition to Tristan da Cunha 1937-1938. No. 19. -I Kommissjon Hos Jacob Dybwad, Oslo. Pp. 1-61.
- Stock, J. H., and A. E. M. H. Bloklander. 1952. Notes on adventive Amphipoda (Crustacea, Malacostraca) on the Dutch coast. -Beaufortia 10: 1-10.
- Stuessy T. F. 1987. Explicit approaches for evolutionary classification. -Systematic Botany 12(2): 251-262.
- Thomas, J. D., and R. W. Heard. 1979. A new species of Cerapus Say, 1817 (Crustacea: Amphipoda) from the northern Gulf of Mexico, with notes on its ecology. -Proceedings of the Biological Society of Washington 92(1): 98-105.
- Thurston, M. H. 1974a. Crustacea Amphipoda from Graham Land and the Scotia Arc, collected by operation Tabarin and the Falkland Islands dependencies survey, 1944-59. -British Antarctic Survey Scientific Reports No. 85. Natural Environment Research Council, London, England. Pp. 1-89.
- , 1974b. The Crustacea Amphipoda of Signy Island, South Orkney Islands. -British Antarctic Survey Scientific Reports, No. 71. Natural Environment Research Council, London, England. Pp. 1-127.
- Trivers, R. L. 1972. parental investment and sexual selection. -In: B. Campbell, ed., Sexual selection and the descent of man, 1971-1981. Pp. 136-179. Aldine, Chicago.

- Vader, W. 1978. Associations between amphipods and echinoderms. -*Astarte* 11: 123-134.
- Van Valen, L. 1976. Ecological Species, multi-species, and oaks. -*Taxon* 25: 233-239.
- Walker, A. O. 1893. The marine zoology of the Irish Sea. -*Proceedings and Transactions of the Liverpool Biological Society* 7: 535.
- , 1895. Revision of the Amphipoda of the L.M.B.C. District. -*Proceedings and Transactions of the Liverpool Biological Society* 9: 287-320.
- , 1899. Podocerus and Jassa of Leach. -*Annals of the Magazine of Natural History (Series 7)* 3: 394-395.
- , 1903. Amphipoda of the 'Southern Cross' Antarctic expedition. -*Journal of the Linnean Society of London Zoology* 29: 38-64.
- , 1907. Crustacea. III. Amphipoda. National Antarctic Expedition 1901-1904, Natural History, Vol. 3. -*Zoology and Botany* 3: 1-39.
- Warburton, F. E. 1967. The purposes of classification. -*Systematic Zoology* 16: 241-245.
- Watling, L., and D. Maurer. 1970. Marine shallow water amphipods of the Delaware Bay area, USA. -*University of Delaware Contribution* 63: 251-266.
- Watrous, L. E. and Q. D. Wheeler. 1981. The out-group comparison method of character analysis. -*Systematic Zoology* 30(1): 1-11.
- West-Eberhard, M. J. 1983. Sexual selection, social competition, and speciation. *The Quarterly Review of Biology* 58(2): 155-183.
- Witman, J. D. 1985. Refuges, biological disturbance, and rocky subtidal

community structure in New England. -Ecological Monographs 55(4):
421-445.

Wynne-Edwards, V. C. 1962. Animal dispersion in relation to social
behaviour. -Oliver and Boyd, Edinburgh and London. Pp. 1-653.

7. APPENDIX

Character descriptions and their scores for numerical analysis are given in Tables A1 and A2, following.

Table A1. Characters scored for phenetic and cladistic analysis. Codes used in the cladistic analyses are in parenthesis. Characters 1-11, 14-30, 32-52, 54, 57, 58, 60, 62, 64, 65, 67, 68, 70-118 and 138-141 were scored on an adult male, major form; characters 12, 13, 31, 53, 55-56, 59, 61, 63 and 69 on numerous males of various developmental stages; character 66 on a large subadult male; and characters 119-137 on a large adult female.

1. Body length, adult male: reference measure, therefore not analysed.
2. Head lobe shape: triangular (0); squared or upper and lower lobes of differing acuity (1).
3. Antenna 1, accessory flagellum, number of segments (the last minute): 5 (0); 4 (1); 2 (2); 1 (3).
4. Antenna 1, accessory flagellum setose midway along the segment (0); distally only (1).
5. Antenna 2, segment 5, adult male, simple filter setae half or more the length of the juvenile's or female's (0); less than half (1).
6. Antenna 2, segment 5 and proximal part of flagellum developing setae that differ in morphology from those of the juvenile: no. (0); yes (1).
7. Antenna 2, flagellum, number of segments (the last minute): 3 (0); 4 (1); 5 (2); 6 (3); 7 (4); 8 (5); 10 (6).
8. Antenna 2, flagellum spines: absent (0); on the terminal segment only (1); on more than one segment (2).
9. Antenna 2, flagellum, segment 1, proportion of full flagellum length: 22 to 28 (0); 35 to 53 (1); 59 to 90 (2).
10. Antenna 2, segment 5, overlap by antenna 1: greater than or equal to a third (0); less than a third (1).
11. Antenna 2, segment 5, width (residual, regressed on char. 1): 5.9 to -5.2 (0); -8.8 (1).
12. Antenna 2 sexually dimorphic: no (0); yes (1).
13. Antenna 2 morphology markedly altered at the thumbed state: no (0); yes (1).
14. Mandibular palp, segment 2, dorsal margin, setae: single (0); clustered or absent (1).
15. Mandibular palp, segment 2, dorsal margin, setae: clustered (0); single or absent (1).
16. Mandibular palp, segment 3, mid-dorsal margin, setae: absent (0);

present (1).

17. Left mandible, number of raker spines: 3 (0); 4 (1); 5 (2); 6 (3); 8 (4); 11 (5); 12 (6).
18. Maxilla 1, palp, segment 2, facial setae arranged: in a single row (0); in several rows or scattered (1).
19. Maxilla 1, palp, segment 1, setal cluster at its base: absent (0); present (1).
20. Maxilla 1, inner plate with: fine setae plus apical spine (0); fine setae (1); no setae (2).
21. Gnathopod 1, segment 2, anteromedial margin with: a few setae or none at all (0); a row of spines (1).
22. Gnathopod 1, coxa, anterior margin length (residual, regressed on char. 1): -10.9 to 7.9 (0); 12.9 to 14.7 (1).
23. Gnathopod 1, coxa, shape: rectangular (0); round (1).
24. Gnathopod 1, coxa, ventral margin length (residual, regressed on char. 1): -16.5 (0); -6.6 to 9.7 (1); 14.8 (2).
25. Gnathopod 1, coxa, ventral margin sinuous: no (0); yes (1).
26. Gnathopod 1, segment 2, anterolateral marginal setae: absent or a few at the distal angle (0); covering the majority of the length and short and spiny (1); covering the majority of the length and long, simple (2); covering the majority of the length and long, plumose (3).
27. Gnathopod 1, segment 2, mid-posterior margin, setae (ignoring those at distal angle): absent (0); 1-2 short (1); many short (much shorter than segment width) and over most of the length (2); a few long and simple (much longer than segment width) (3); a few long and plumose (4).
28. Gnathopod 1, segment 5, anterodistal setal cluster, length (residual, regressed on char. 29): -5.5 to 4.9 (0); 11.9 (1).
29. Gnathopod 1, segment 5, anterior margin, length: reference measure, therefore not analysed.
30. Gnathopod 1, segment 5, posterior margin, length (residual, regressed on char. 29): -3.4 to -2.2 (0); -15.2 (1).
31. Gnathopod 1, segment 6, palm, modal number of defining spines: 1 (0); 3 to 4 (1).
32. Gnathopod 1, segment 6, width at the defining spines (residual, regressed on char. 1): -9.5 (0); -6.5 to -5.1 (1); -3.5 to 7.2 (2).

33. Gnathopod 1, segment 6, palm shape: convex (0); straight (1); concave (2).
34. Gnathopod 1, segment 6, palmar defining spines located: proximal to centre (0); central (1); distal to centre (2).
35. Gnathopod 1, dactyl, number of rows of facial serrations: 0 (0); 1 (1); 2 (2); 4 (3); 10 (4).
36. Gnathopod 1, dactyl, facial serrations arranged: parallel to the dactyl margin (0); angled to the dactyl margin (1).
37. Gnathopod 1, dactyl cusps: on majority of length (0); half length (1); distal only (2).
38. Gnathopod 2, coxa, anterior length (residual, regressed on char. 40): 14.0 to 3.8 (0); 2.2 to -9.0 (1); -16.6 (2).
39. Gnathopod 2, coxa, ventral length: reference measure, therefore not analysed.
40. Gnathopod 2, coxa, posterior length: reference measure, therefore not analysed.
41. Gnathopod 2, coxa, ventral margin shape: convex (0); straight (1); sinuous (2).
42. Gnathopod 2, species with a gill, length (residual, regressed on char. 1): 35.9 to 35.0 (0); 8.8 to -10.6 (1).
43. Gnathopod 2, segment 2, anterolateral flange, number of setae: 0 to 1 (0); 5 to 22 (1); 44 (2).
44. Gnathopod 2, segment 2, anterolateral flange, setae located: on the flange and medial face (0); on the flange only (1).
45. Gnathopod 2, segment 2, anterior setae, modal length: 1 (0); 2 to 5 (1); 11 to 29 (2).
46. Gnathopod 2, segment 2, anterior setae: simple (0); plumose, barbs short (1); plumose, barbs long (2).
47. Gnathopod 2, segment 5, dorsal length (residual, regressed on char. 49): 15.1 (0); 10.3 to 3.0 (1); 0.8 to -3.4 (2); -5.3 to -5.9 (3); -9.8 to -12.9 (4).
48. Gnathopod 2, segment 5, posterior lobe, length of setae: 28 (0); 13-3 (1); 1 (2); 0 (3).
49. Gnathopod 2, segment 6, length: reference measure, therefore not analysed.
50. Gnathopod 2, segment 6, species with anteroproximal setae, modal setal length (residual, regressed on char. 49): -13.5 to 4.5 (0);

10.1 (1).

51. Gnathopod 2, segment 6, hinge tooth: absent (0); present (1).
52. Gnathopod 2, segment 6, hinge tooth shape: rectangular (0); triangular (1).
53. Gnathopod 2, segment 6, hinge tooth sculpture: always single (0); at some stage bifid (1); at some stage multiplyincised (2).
54. Gnathopod 2, segment 6, species with a thumb, thumb length (residual, regressed on char. 49): -11.4 to -6.7 (0); -3.1 to 2.2 (1); 4.4 to 16.8 (2).
55. Gnathopod 2, segment 6, thumb development plot: juvenile and adult hardly overlap in body length (0); juvenile and adult overlap by 60% or more (1).
56. Gnathopod 2, segment 6, thumb development plot: type 2 (0); type 1 (1).
57. Gnathopod 2, segment 6, thumb tip, shape: acute (0); squared or rounded (1); indented (2).
58. Gnathopod 2, segment 6, thumb setation type: inner margin setose (0); inner margin not setose, outer marginal setae individual (1); inner margin not setose, outer marginal setae clustered into developmentally constant groups (thumb cluster and defining clusters) (2).
59. Gnathopod 2, segment 6, defining spines in the larger adult males: unaltered from juvenile state (present or absent) (0); present, more pronounced than in juvenile (1); present but reduced in length (2); lost (3).
60. Gnathopod 2, segment 6, defining spine located: subapical to thumb tip (0); at apex of thumb (1); at thumb base (2).
61. Gnathopod 2, segment 6, juvenile, number of defining spines: 0 (0); 1 (1); 2 (2); 3 (3).
62. Gnathopod 2, segment 6, species with 3 defining spines (char. 61, state 3) that lose these when larger (char. 59, state 2), distance between defining setae: 0 (0); 2-4 (1); 6 (2); 9 (3); 13-15 (4).
63. Gnathopod 2, segment 6, defining spine length (measured in juvenile if lost when larger): moderate (0); long (1); minute (2).
64. Gnathopod 2, segment 6, species with type 2 setation (char. 58), thumb shape: not expanded at thumb setae (0); expanded at thumb setae (1).
65. Gnathopod 2, segment 6, palmar setae located: along full length, as or more abundant than in juvenile (0); full length, less abundant

- than in juvenile (1); concentrated at hinge tooth (2).
66. Gnathopod 2, segment 6, species with determinate growth. (char. 55, state 1), thumb length in largest subadult: 18-10 (0); 3-1 (1); 0 (2).
 67. Gnathopod 2, segment 6, distance from thumb base (inner margin) to end of segment 6 (residual, regressed on char. 49): no discrete breaks, therefore deleted for cladistics.
 68. Gnathopod 2, dactyl, inner margin shape: not proximally expanded (0); proximally expanded (1).
 69. Gnathopod 2, dactyl, inner margin, species with determinate growth (char. 55, state 1), minor forms with pronounced tooth extending into the palmar incision: no (0); yes (1).
 70. Gnathopod 2, dactyl, tip apposing: thumb tip (0); thumb inner margin (1); thumb outer margin (2).
 71. Gnathopod 2, dactyl, length relative to segment 6 length: shorter than (0); as long as or longer than (1).
 72. Gnathopod 2, dactyl, inner marginal setae, length: minute (0); as long as dactyl width (1).
 73. Gnathopod 2, dactyl cusps, size: as large as the juvenile's (0); reduced, minute (1).
 74. Peraeopod 3, coxa, maximum dorsoventral length (residual, regressed on char. 1): 23.0 (0); 10.5 to -15.9 (1); -33.2 (2).
 75. Peraeopod 3, coxa, greatest dorsoventral length located: equally anterior and posterior of centre (0); centre (1); posterior of centre (2).
 76. Peraeopod 3, segment 2 slenderer at maturity: no (0); yes (1).
 77. Peraeopod 3, segment 4, anterior marginal setae located: along full margin (0); distally only (1).
 78. Peraeopod 3, segment 4, anterior marginal setae distributed: clustered (0); individually (1).
 79. Peraeopod 3, segment 4, anterior marginal setae, nodal number per cluster: 1 (0); 2 (1); 3 (2); 4 (3).
 80. Peraeopod 3, segment 4, anterior marginal setae, nodal length (excluding distal cluster), (residual, regressed on char. 81): -9.1 to 3.1 (0); 4.7 to 11.1 (1).
 81. Peraeopod 3, segment 4, maximum width: reference measure, therefore not analysed.

82. Peraeopod 3, segment 4, length: reference measure, therefore not analysed.
83. Peraeopod 3, segment 5, proportion of length overlapped by segment 4: 25-45 (0); 65-81 (1); 100 (2).
84. Peraeopod 6, maximum width (residual, regressed on char. 85): -2.9 to 2.1 (0); 5.4 (1).
85. Peraeopod 6, maximum length: reference measure, therefore not analysed.
86. Peraeopod 3, segment 6, posterior margin spinose: no (0); yes (1).
87. Peraeopods 5-7, segment 2, at least one of these produced posterodistally: no (0); yes (1).
88. Peraeopods 5-7, segment 4, posterior margin spinose: no (0); yes (1).
89. Peraeopods 5-7, segment 5, posterodistal margin spinose: no (0); yes (1).
90. Peraeopods 5-7, segment 6, anterior margin shape: not markedly expanded or expanded proximally (0); markedly expanded centrally (1).
91. Peraeopods 5-7, segment 6, anterior margin shape: not markedly expanded or expanded centrally (0); markedly expanded proximally (1).
92. Peraeopods 5-7, dactyl, number of rows of facial serrations: 0 (0); 1 (1); 2 (2); 3 (3).
93. Peraeopods 5-7, dactyl, outer margin distally cusped: no (0); yes (1).
94. Peraeopods 5-7, dactyl, anterior marginal setae located: distally (0); along full length (1).
95. Pleopod length: long (0); reduced (1).
96. Pleopod 3, number of coupling hooks: 2 (0); 3 (1); 5 (2); 8 (3).
97. Prosopod 1, dorsum, pair of setae: absent (0); present (1).
98. Propod 1, inner ramus, percentage of length underlain by ventral peduncular spinous process: 100 (0); 88-73 (1); 54-25 (2); 16-6 (3).
99. Propod 1, inner ramus, number of mid-dorsal spines (residual, regressed on char. 1): -3.4 to 3.4 (0); 6.3 (1).
100. Propod 1, rami terminating in a ventral fringe of cusps: no (0); yes (1).
101. Propod 2, inner ramus, percentage of length underlain by ventral

- spinous process: 0 to 17 (0); 21 to 27 (1); 64 (2).
102. Uropod 3, peduncle, mid-ventrally setose or spinose: no (0); yes (1).
103. Uropod 3, peduncle number of mid-dorsal spines: 0 (0); 1 (1); 4 (2); 17 (3).
104. Uropod 3, peduncle, number of groups of distal crown spines: 2 (0); 1 (1); 4 (2).
105. Uropod 3, peduncle with ventrolateral setal cluster: no (0); yes (1).
106. Uropod 3, outer ramus with dorsal fringe of setae: no (0); yes (1).
107. Uropod 3, outer ramus terminated in basally immersed, dorsally recurved spine: no (0); yes (1).
108. Uropod 3, outer ramus, cusps: absent (0); minute, all one size (1); a few large, many minute (2).
109. Uropod 3, outer ramus, number of major cusps: 1 (0); 2 (1); 3 (2).
110. Uropod 3, outer ramus, cusps spaced: well separated (0); proximate (1).
111. Uropod 3, outer ramus, cusps located: opposite (0); sequential (1).
112. Uropod 3, outer ramus, distolateral setal cluster: absent (0); present (1).
113. Uropod 3, outer ramus, dorsodistal setal cluster: absent (0); present (1).
114. Uropod 3, inner ramus, mid-dorsal spines: 0 = absent; 1 = present.
115. Telson, number of spines accompanying each cusp group: 3 (0); 1 (1); 0 (2).
116. Telson, number of cusps per group: 1 (0); 2 (1); 3 (2).
117. Telson, apically setose: no (0); yes (1).
118. Telson, apical shape: transverse (0); acute (1).
119. Body length, adult female: reference measure, therefore not analysed.
120. Gnathopod 2, brood plate, maximum width (residual, regressed on char. 119): no discrete group, therefore deleted for cladistic

analysis.

121. Gnathopod 2, brood plate, number of setae (residual, regressed on char. 119): no discrete group, therefore deleted for cladistic analysis.
122. Gnathopod 2, segment 6, length: reference measure, therefore not analysed.
123. Gnathopod 2, segment 6, palm shape: evenly convex (0); broad outline convex but with some shallow concavity (1); clearly concave (2).
124. Gnathopod 2, segment 6, hinge tooth: absent (0); present (1).
125. Gnathopod 2, segment 6, palm shape: similar to adult male or hardly differing (0); markedly different (1).
126. Gnathopod 2, segment 6, distance of hinge tooth from intra-palmar angle (or defining spines if no palmar angle) (residual, regressed on char. 122): -16.8 (0); -8.0 to -3.7 (1); -1.7 to 0.7 (2); 2.0 to 5.3 (3); 14.5 to 15.2 (4).
127. Gnathopod 2, segment 6, species with concave palm (char. 123, state 2), maximum depth of concavity (residual, regressed on char. 122): no discrete groups, therefore deleted for cladistic analysis.
128. Gnathopod 2, segment 6, intra-palmar angle, distance to nearest defining spine: at (0); just distal of (1); 1/3 of palm's length away (2).
129. Gnathopod 2, segment 6, intra-palmar angle, shape: shallow and wide (0); pronounced, rounded (1); pronounced, acute (2); pronounced, squared (3).
130. Gnathopod 2, segment 6, number of defining spines differs from the male's: no (0); yes (1).
131. Gnathopod 2, segment 6, defining spines located: on a marked protuberance: no (0); yes (1).
132. Gnathopod 2, segment 6, palmar defining spines located: medially (0); medially and laterally (1).
133. Gnathopod 2, segment 6, defining spines arranged: well separated (0); clustered (1).
134. Gnathopod 2, segment 6, palmar setae, abundance: not obscuring the palm (0); obscuring the palm (1).
135. Gnathopod 2, dactyl, tip resting in a depression distal to the defining spines: no (0); yes (1).
136. Gnathopod 2, dactyl, inner margin, shape: evenly convex or

straight (0); proximally expanded (1).

137. Gnathopod 2, dactyl cusps, number and size: as numerous and as large as those on gnathopod 1 (0); few and minute (except single cusp adjacent to unguis (1)).
138. Gnathopod 2, gill: present (0); absent (1).
139. Gnathopod 2, segment 6, anteroproximal setal group: absent (0); present (1).
140. Gnathopod 2, segment 6, thumb absent (0); present (1).
141. Gnathopod 1, segment 5, anterodistal setal cluster: present (0); absent (1).

Table A2. Scores for the 141 characters described in Table 3 on the 27 species of Jassa (OTU's 1-27) and the 5 outgroup species (OTU's 28-32).
CHAP: score not transformed and PCHAR: residual.

NO	NAME	AGE	CHAR1	CHAR2	CHAR3	CHAR4	CHAR5	CHAR6	CHAR7
1	SM	11	1	1	1	1	1	1	1
2	MA	11	1	1	1	1	1	1	1
3	TA	11	1	1	1	1	1	1	1
4	CAR	29	1	1	1	1	1	1	1
5	MYE	55	1	1	1	1	1	1	1
6	STA	106	1	1	1	1	1	1	1
7	ROB	77	1	1	1	1	1	1	1
8	JCL	118	1	1	1	1	1	1	1
9	SHA	68	1	1	1	1	1	1	1
10	PUS	41	1	1	1	1	1	1	1
11	FAL	86	1	1	1	1	1	1	1
12	HER	95	1	1	1	1	1	1	1
13	ALO	111	1	1	1	1	1	1	1
14	JUS	85	1	1	1	1	1	1	1
15	MAU	80	1	1	1	1	1	1	1
16	GRU	21	1	1	1	1	1	1	1
17	FEN	74	1	1	1	1	1	1	1
18	NAR	45	1	1	1	1	1	1	1
19	THU	80	1	1	1	1	1	1	1
20	RAM	98	1	1	1	1	1	1	1
21	INC	221	1	1	1	1	1	1	1
22	CON	178	1	1	1	1	1	1	1
23	OW	43	1	1	1	1	1	1	1
24	MOD	40	1	1	1	1	1	1	1
25	ELL	18	1	1	1	1	1	1	1
26	OCI	35	1	1	1	1	1	1	1
27	BAR	42	1	1	1	1	1	1	1
28	ISP	101	1	1	1	1	1	1	1
29	PCL	75	1	1	1	1	1	1	1
30	ICE	61	1	1	1	1	1	1	1
31	CUM	28	1	1	1	1	1	1	1
32	CLA	18	1	1	1	1	1	1	1

OPS	CHAR9	CHAR10	CHAR11	CHAR12	CHAR13	CHAR14	CHAR15	CHAR16	CHAR17
1	81	0	16	1	0	1	1	0	1
2	48	0	12	1	0	1	1	0	1
3	66	0	15	1	0	1	1	0	1
4	45	0	6	1	0	1	1	0	1
5	82	0	12	1	0	1	1	0	1
6	76	0	24	1	0	1	1	0	1
7	75	1	15	1	0	1	1	0	1
8	70	1	28	1	1	1	1	0	1
9	60	1	13	1	1	1	1	0	1
10	53	0	7	1	0	1	1	0	1
11	35	0	13	1	0	1	1	0	1
12	45	0	18	1	0	1	1	0	1
13	59	0	21	1	0	1	1	0	1
14	82	0	17	1	0	1	1	0	1
15	86	0	22	1	0	1	1	0	1
16	39	0	6	1	0	1	1	0	1
17	63	0	15	1	0	1	1	0	1
18	36	0	8	1	0	1	1	0	1
19	22	0	10	1	0	1	1	0	1
20	87	0	22	1	0	1	1	0	1
21	38	0	35	1	0	1	1	0	1
22	4	0	30	1	0	1	1	0	1
23	88	0	14	1	0	1	1	0	1
24	75	0	11	1	0	1	1	0	1
25	37	0	0	1	0	1	1	0	1
26	71	0	4	1	0	1	1	0	1
27	28	0	5	1	0	1	1	0	1
28	52	0	26	1	0	1	1	0	1
29	80	0	18	1	0	1	1	0	1
30	39	0	9	1	0	1	1	0	1
31	53	0	3	1	0	1	1	0	1
32		0		1	0	1	1	0	1

OPS	CHAR18	CHAR19	CHAR20	CHAR21	CHAR22	CHAR23	CHAR24	CHAR25	CHAR26
1	0	0	1	1	30	0	27	1	0
2	0	0	1	0	17	0	20	0	0
3	0	0	1	0	22	0	22	0	0
4	0	0	1	0	10	0	12	0	0
5	0	0	1	0	12	0	23	0	0
6	0	0	1	0	32	0	52	1	0
7	0	0	1	0	22	0	27	0	0
8	0	0	1	0	40	0	40	0	0
9	0	0	1	0	15	0	17	0	0
10	0	0	1	0	18	0	18	0	0
11	0	0	1	0	25	0	28	0	0
12	0	0	1	0	31	0	32	0	0
13	0	0	1	0	34	0	43	0	0
14	0	0	1	0	29	0	29	0	1
15	0	0	1	0	34	0	53	0	0
16	0	0	1	0	8	0	5	0	0
17	0	0	1	0	22	0	23	0	0
18	0	0	1	0	13	0	14	0	1
19	0	0	1	0	34	0	36	0	0
20	0	0	1	0	35	0	32	0	0
21	1	1	1	0	49	0	80	1	0
22	0	0	1	0	48	0	42	0	2
23	0	0	1	0	21	0	20	0	0
24	0	0	1	0	12	0	12	0	0
25	0	0	1	0	13	0	16	0	0
26	0	0	1	0	11	0	11	0	0
27	0	0	1	0	44	0	50	0	0
28	0	0	1	0	28	0	24	0	0
29	0	0	1	0	22	0	17	0	0
30	0	0	1	0	2	0	9	0	0
31	0	0	1	0	1	0	7	0	0
32	0	0	1	0	1	0	7	0	0

CHAR27	CHAR28	CHAR29	CHAR30	CHAR31	CHAR32	CHAR33	CHAR34	CHAR35
1	0	1	17	7	3	22	0	0
2	0	11	15	8	3	15	2	0
3	0	11	15	8	3	17	2	0
4	0	5	7	3	3	8	0	0
5	0	4	12	4	3	13	2	0
6	0		14	7	3	28	0	2
7	0	19	20	8	3	25	1	0
8	0	11	33	13	3	40	0	0
9	0		14	8	3	18	0	0
10	0		11	6	3	12	0	0
11	0		22	8	3	23	2	2
12	0		20	8	3	29	0	2
13	0	10	31	18	3	33	0	0
14	0		20	9	3	25	0	0
15	0	7	38	19	3	29	0	3
16	0		5	3	3	6	0	0
17	1		14	5	3	23	1	0
18	0		12	5	3	13	1	0
19	1	4	21	12	3	18	0	9
20	0	15	30	19	3	29	0	5
21	1		78	22	3	78	0	0
22	2	15	80	28	3	52	0	0
23	0	3	19	8	1	18	0	1
24	3		15	7	1	11	0	2
25	3	2	5	2	3	5	0	1
26	4	4	8	4	3	10	0	0
27	3	2	10	1	1	6	0	2
28	1	5	30	15	3	25	0	1
29	1	7	23	8	3	23	0	6
30	0		18	6	1	8	2	0
31	3		8	2	3	9	0	1
32	0		7	3	3	6	0	1

CHAR36	CHAR37	CHAR38	CHAR39	CHAR40	CHAR41	CHAR42	CHAR43	CHAR44
1	0	13	51	50	1	31	14	1
2	0	12	18	25	1	22	6	1
3	0	18	39	29	2	16	17	1
4	1	6	19	10	1	10	8	1
5	0	12	41	14	1	15	5	1
6	0	27	32	52	2	28	22	1
7	0	15	45	31	2	41	21	1
8	0	27	80	48	2	55	44	1
9	0	13	37	19	1	27	5	1
10	0	14	32	18	1	12	8	1
11	0	13	47	18	1	32	1	1
12	0	17	61	38	2	30	5	1
13	0	35	70	12	2	47	21	1
14	0	19	60	29	1	14	16	1
15	0	15	50	37	2	9	0	1
16	0	8	15	9	0	9	0	1
17	0	14	48	25	1	22	12	1
18	0	10	31	18	2	7	11	1
19	0	26	50	18	1	25	11	1
20	0	10	48	47	1		4	1
21	0	14	148	84	2	88	29	1
22	0	52	80	60	1	120	44	1
23	0	13	27	19	1			1
24	0	15	23	14	0			1
25	0	11	10	10	0	7	8	1
26	0	4	17	10	0		18	9
27	1	12	19	11	0		5	
28	0	80	80	70	0	80	20	1
29	1	17	32	32	1	33	0	
30	0	20	29	11	1	33	6	0
31	0	24	17	10	0	10	0	
32	0	19	15	12	0		18	1

CHAR45	CHAR46	CHAR47	CHAR48	CHAR49	CHAR50	CHAR51	CHAR52	CHAR53
1	1	0	2	1	62	9	1	
2	5	0	4	0	47	3	1	
3	3	0	16	0	45	2	1	
4	4	0	9	0	22	2	1	1
5	2	0	15	0	36	2	1	1
6	29	0	37	1	98	28	1	1
7	13	0	20	0	58	8	1	1
8	43	1	32	4	87	17	1	1
9	1	0	13	1		1	1	1
10	1	0	11	1	30	1	1	1
11	1	0	15	1	60	1	1	1
12	1	0	10	1	75	1	1	1
13	14	0	23	1	83	10	1	1
14	5	0	23	1	80	13	1	1
15			37	1	73	1	1	1
16	2	0	1	1	70	1	1	1
17	5	0	16	1	54	4	1	1
18	4	0	9	0	14	4	1	1
19	1	0	19	0	46	3	1	1
20	1	0	24	0	67	1	1	1
21	1	0	70	13	168	29	0	2
22	28	0	48	28	115	26	0	1
23	1	0	8	3	52	1	0	2
24	1	0	15	7	20	1	0	1
25	1	0	4	0	1	1	0	1
26	1	0	8	5	2	1	0	1
27	1	0	12	1	14	0	0	1
28	1	0	40	11	81	1	0	1
29	1	0	35	5	41	1	0	1
30	1	0	1	1	2	0	0	2
31	1	0	1	1	1	1	0	1
32	1	0	1	1	1	1	0	1

OBS	CHAR6	CHAR7	CHAR8	CHAR9	CHAR10	CHAR11	CHAR12	CHAR13	CHAR14
1	13	1	1	1	1	1	1	1	1
2	9	1	1	1	1	1	1	1	1
3	10	1	1	1	1	1	1	1	1
4	6	1	1	1	1	1	1	1	1
5	2	1	1	1	1	1	1	1	1
6	33	1	1	1	1	1	1	1	1
7	14	1	1	1	1	1	1	1	1
8	16	1	1	1	1	1	1	1	1
9	1	1	1	1	1	1	1	1	1
10	4	1	1	1	1	1	1	1	1
11	3	1	1	1	1	1	1	1	1
12	3	1	1	1	1	1	1	1	1
13	12	1	1	1	1	1	1	1	1
14	12	1	1	1	1	1	1	1	1
15	25	1	1	1	1	1	1	1	1
16	1	1	1	1	1	1	1	1	1
17	14	1	1	1	1	1	1	1	1
18	8	1	1	1	1	1	1	1	1
19	15	1	1	1	1	1	1	1	1
20	24	1	1	1	1	1	1	1	1
21	24	1	1	1	1	1	1	1	1
22	12	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	0
24	0	0	0	0	0	0	0	0	0
25	1	0	0	0	0	0	0	0	0
26	3	0	0	0	0	0	0	0	0
27	3	0	0	0	0	0	0	0	0
28	0	0	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0	0	0
30	0	0	0	0	0	0	0	0	0
31	0	0	0	0	0	0	0	0	0
32	0	0	0	0	0	0	0	0	0

OBS	CHAR63	CHAR64	CHAR65	CHAR66	CHAR67	CHAR68	CHAR69	CHAR70	CHAR71
1	0	0	2	2	17	1	0	2	0
2	0	1	2	1	16	1	0	2	0
3	0	0	2	0	11	1	0	2	0
4	0	0	2	0	5	1	0	2	0
5	0	0	2	0	8	1	0	2	0
6	0	0	2	0	28	1	0	2	0
7	0	0	2	0	14	1	0	2	0
8	0	0	2	0	32	1	0	2	0
9	0	0	2	0	0	1	0	2	0
10	0	0	2	0	17	1	0	2	0
11	0	0	2	0	11	1	0	2	0
12	0	0	2	0	12	1	0	2	0
13	0	0	2	10	27	1	0	2	0
14	0	0	2	3	13	1	0	2	0
15	0	0	2	3	14	1	0	2	0
16	0	0	2	0	8	1	0	2	0
17	0	0	2	0	10	1	0	2	0
18	0	0	2	0	11	1	0	2	0
19	0	0	2	18	37	1	0	2	0
20	0	0	2	15	48	1	0	2	0
21	0	0	2	0	35	1	0	2	0
22	0	0	2	0	4	1	0	2	0
23	0	0	2	0	14	1	0	2	0
24	0	0	2	0	15	1	0	2	0
25	0	0	2	0	32	1	0	2	0
26	0	0	2	0	4	1	0	2	0
27	0	0	2	0	0	1	0	2	0
28	0	0	2	0	0	1	0	2	0
29	0	0	2	0	0	1	0	2	0
30	0	0	2	0	0	1	0	2	0
31	0	0	2	0	0	1	0	2	0
32	0	0	2	0	0	1	0	2	0

OBS	CHAR72	CHAR73	CHAR74	CHAR75	CHAR76	CHAR77	CHAR78	CHAR79	CHAR80
1	0	1	48	2	1	0	1	1	2
2	0	1	28	2	1	0	0	1	4
3	0	1	27	2	1	0	0	1	8
4	0	1	17	2	1	0	0	1	4
5	0	1	20	2	1	0	0	1	4
6	0	1	74	2	1	0	0	1	4
7	0	1	47	2	1	0	0	1	4
8	0	1	64	2	1	0	0	1	4
9	0	1	29	2	1	0	0	1	4
10	0	1	24	2	1	0	0	1	4
11	0	1	48	2	1	0	0	1	4
12	0	1	66	2	1	0	0	1	4
13	0	1	68	2	1	0	0	1	4
14	0	1	40	2	1	0	0	1	4
15	0	1	51	2	1	0	0	1	4
16	0	1	10	2	0	0	0	1	4
17	0	1	34	1	0	0	0	1	4
18	0	1	22	2	0	0	0	1	4
19	0	1	34	1	0	0	0	1	4
20	0	1	51	1	0	0	0	1	4
21	0	1	12	2	0	0	0	1	4
22	0	1	66	0	0	0	0	1	4
23	0	1	21	0	0	0	0	1	4
24	0	1	4	0	0	0	0	1	4
25	0	1	4	0	0	0	0	1	4
26	0	1	16	0	0	0	0	1	4
27	0	1	6	0	0	0	0	1	4
28	0	1	44	0	0	0	0	1	4
29	0	1	34	0	0	0	0	1	4
30	0	1	27	0	0	0	0	1	4
31	0	1	27	0	0	0	0	1	4
32	0	1	27	0	0	0	0	1	4

BIT	CHAR81	CHAR82	CHAR83	CHAR84	CHAR85	CHAR86	CHAR87	CHAR88	CHAR89
1	18	16	100	7	14	0	1	0	0
2	0	0	100	5	9	0	1	0	0
3	1	19	100	4	11	0	1	0	0
4	8	7	100	1	7	0	1	0	0
5	11	12	100	7	9	0	1	0	0
6	12	18	100	11	19	0	1	0	0
7	12	10	100	8	15	0	1	0	0
8	12	18	100	10	19	0	1	0	0
9	7	8	71	7	8	0	1	0	0
10	7	15	80	4	8	0	1	0	0
11	12	13	67	6	14	0	1	0	0
12	12	25	65	9	15	0	1	0	0
13	12	19	73	11	18	0	1	0	0
14	12	19	100	11	18	0	1	0	0
15	19	25	69	8	11	0	1	0	0
16	6	5	100	4	22	0	1	0	0
17	15	18	100	8	5	0	1	0	0
18	9	10	91	5	10	0	1	0	0
19	11	14	65	6	11	0	1	0	0
20	19	31	44	10	18	0	1	0	0
21	16	22	6	18	24	0	1	0	0
22	24	60	45	12	34	0	1	0	0
23	11	10	100	7	12	0	1	0	0
24	6	12	32	4	9	0	1	0	0
25	8	8	38	1	1	1	1	0	0
26	8	8	43	4	8	0	1	0	0
27	8	6	29	5	10	0	0	1	1
28	20	34	29	13	42	1	1	0	0
29	17	11	55	8	15	0	0	0	1
30			10			0	0	0	1
31	5	7	45	3	8	0	1	0	0
32			25			0	1	0	0

BIT	CHAR91	CHAR92	CHAR93	CHAR94	CHAR95	CHAR96	CHAR97	CHAR98	CHAR99
1	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0	0
4	0	0	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0	0
6	0	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0	0
15	0	0	0	0	0	0	0	0	0
16	0	0	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0	0	0
21	0	0	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	0
24	0	0	0	0	0	0	0	0	0
25	0	0	0	0	0	0	0	0	0
26	0	0	0	0	0	0	0	0	0
27	0	0	0	0	0	0	0	0	0
28	0	0	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0	0	0
30	0	0	0	0	0	0	0	0	0
31	0	0	0	0	0	0	0	0	0
32	0	0	0	0	0	0	0	0	0

BIT	CHAR101	CHAR102	CHAR103	CHAR104	CHAR105	CHAR106	CHAR107
1	4	1	5	1	0	2	1
2	4	1	4	1	0	2	1
3	4	1	5	1	0	2	1
4	1	1	7	1	0	2	1
5	4	1	0	1	0	2	1
6	6	1	2	1	0	2	1
7	5	1	4	1	0	2	1
8	9	1	7	1	0	2	1
9	1	1	3	1	0	2	1
10	4	1	0	1	0	2	1
11	8	1	9	1	0	2	1
12	6	1	9	1	0	2	1
13	8	1	1	1	0	2	1
14	5	1	3	1	0	2	1
15	12	0	27	1	0	2	1
16	1	1	11	1	0	2	1
17	1	1	14	1	0	2	1
18	4	1	14	1	0	2	1
19	4	0	1	1	0	2	1
20	1	0	10	1	0	2	1
21	1	0	12	1	0	2	1
22	1	0	13	1	0	2	1
23	1	0	11	1	0	2	1
24	1	0	21	1	0	2	1
25	1	0	1	1	0	2	1
26	1	0	1	1	0	2	1
27	1	0	1	1	0	2	1
28	1	0	1	1	0	2	1
29	1	0	1	1	0	2	1
30	1	0	1	1	0	2	1
31	1	0	1	1	0	2	1
32	1	0	1	1	0	2	1

OBS	CHAR108	CHAR109	CHAR110	CHAR111	CHAR112	CHAR113	CHAR114	CHAR115	CHAR116
1									
2									
3									
4									
5									
6									
7									
8									
9									
10									
11									
12									
13									
14									
15				0					
16									
17									
18									
19									
20									
21		2							
22									
23									
24									
25		3							
26									
27									
28		2							
29									
30									
31									
32	2	3							

OBS	CHAR117	CHAR118	CHAR119	CHAR120	CHAR121	CHAR122	CHAR123	CHAR124	CHAR125
1	0	1	13	28	64	50	2		
2	1	1	16	26	51	53	2		
3	0	1	47	22	77	34	2		
4	0	1	24	13	50	20	2		
5	0	1	44	19	48	17	2		
6	0	1	76	32	9	62	2		
7	0	1	58	42	64	4	2		
8	0	1	86	52	139	4	2		
9	0	1	59	36	69	43	2		
10	0	1	47	25	63	48	2		
11	0	1	66	50	72	38	2		
12	0	1	81	43	85	52	2		
13	0	1	88	50	148	78	2		
14	0	1	64	31	70	82	2		
15	0	1	60	28	71	71	2		
16	0	1	32	14	42	25	2		
17	0	1					2		
18	0	1	36	17	83	33	2		
19	0	1	85	32	70	66	2		
20	0	1	98	54	85	84	2		
21	0	1	142	70	213	196	2		
22	0	1	166	89	178	182	2		
23	0	1	48	26	44	50	2		
24	0	1	4	1	37	31	2		
25	0	1	16	4	10	5	2		
26	0	1	35	17	28	5	2		
27	0	1	45	13	48	26	2		
28	0	1	71	38	77	38	2		
29	0	1	77	23	85	72	2		
30	0	0	66			47	2		
31	0	1	42	15	16	10	2		
32	0	1	15	3	9	10	0		

OBS	CHAR126	CHAR127	CHAR128	CHAR129	CHAR130	CHAR131	CHAR132	CHAR133	CHAR134
1	17	4	1	2	7	0			
2	20	5	1	2	7	0			
3	11	3	1	2	7	0			
4	8	3	1	2	7	0			
5	14	3	2	2	7	0			
6	19	5	1	1	7	0			
7	12	4	1	1	7	0			
8	1	1	1	1	7	0			
9	20	5	1	1	7	0			
10	16	4	1	1	7	0			
11	21	7	1	1	7	0			
12	19	10	1	2	7	0			
13	19	4	1	2	7	0			
14	25	1	1	0	7	0			
15	24	1	1	1	7	0			
16	12	2	1	1	7	0			
17									
18	10	1	1	2	7	0			
19	24	3	2	0	7	0			
20	43	3	2	1	7	0			
21	21	3	2	1	7	0			
22	21	3	2	1	7	0			
23	21	3	2	1	7	0			
24	7	3	1	1	7	0			
25	3	1	1	1	7	0			
26	1	1	1	1	7	0			
27	1	1	1	1	7	0			
28	1	1	1	1	7	0			
29	1	1	1	1	7	0			
30	1	1	1	1	7	0			
31	1	1	1	1	7	0			
32	1	1	1	1	7	0			

OBS	CHAR84	CHAR85	CHAR88	CHAR120	CHAR121	CHAR122	CHAR126	CHAR127
1	-0.2881	0.0188	0.0999	2.1148	18.488	4.8718	-0.8575	-0.3281
2	-0.6356	-2.5808	-0.2530	-1.8354	-14.630	2.5811	3.7033	0.5887
3	-1.2988	0.1011	0.0382	1.0352	17.775	0.8377	-1.2483	-1.8273
4	-1.8748	-0.8882	0.3284	-0.8841	-0.821	4.3143	-5.2853	-2.5787
5	1.3844	-2.8537	-0.3723	-3.1848	-3.287	0.8713	-0.8875	-1.0025
6	2.0583	0.5884	-1.1873	-3.3182	5.842	-6.8377	-1.2143	0.3713
7	0.3814	0.8548	-0.4888	14.8848	20.418	-7.3848	-3.7388	-0.1027
8	1.0583	-1.0374	1.1088	7.8830	32.418	-8.3241	4.3112	2.8453
9	1.3844	-4.218	-1.8588	1.885	5.418	-0.385	2.788	8.7220
10	-1.8358	-0.535	0.6247	1.575	5.832	-0.185	0.888	0.8474
11	-1.2881	-1.873	2.8838	-1.218	-1.820	-8.818	2.818	2.8218
12	1.3814	-1.900	-0.5422	5.834	-3.177	2.052	4.885	5.8708
13	2.0583	-0.883	0.8184	5.883	38.418	-8.325	14.874	-1.1287
14	1.7034	-4.538	-0.8558	-1.448	-8.881	8.317	2.877	1.1458
15	-1.8322	7.148	8.3375	-0.758	3.323	18.517	3.888	2.1458
16	-0.3138	-1.887	-0.2824	-3.274	2.888	1.137	-0.331	-2.7018
17	2.0338	-4.038	-1.3187					
18	-0.3051	-2.881	0.3811	-1.815	18.884	5.848	1.885	-1.8823
19	-2.2888	-1.128	0.5184	1.184	-2.788	10.488	2.587	-1.7782
20	1.3888	0.881	0.2818	10.883	-18.533	-1.281	15.248	-2.2888
21	5.4888	-18.888	-2.8318	-12.881	10.184	8.582	-18.788	-4.8852
22	-1.8883	8.852	0.7074	0.478	-38.812	0.584	3.888	2.1150
23	0.3728	0.828	-1.0781	4.885	-18.344	11.827	-1.857	-1.3281
24	-1.8356	-0.388	-2.3187	-0.375	-18.248	-3.884	-8.888	-0.8522

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