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## Three new species of *Tharybis* (Crustacea: Copepoda: Calanoida: Tharybidae) from benthopelagic waters of the Pacific Ocean

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**Abstract:** Three new benthopelagic species of *Tharybis* are described from two localities in the Pacific Ocean: *T. pseudomegalodactyla* near Kona, Hawaii; *T. juhlae* near Kona, Hawaii, and from Volcano 7; *T. shuheiiella* from Volcano 7. The new species are distinguished from known species by the shapes of the genital complex of the female and the segments of the first and fifth leg, and the setation of maxilla 1, maxilla 2 and maxilliped. There are now 25 nominal species of *Tharybis*. A distally vaulted praecoxal lobe of maxilla 1 is proposed as a synapomorphy for species of *Tharybis*; other possible synapomorphies are discussed.

**Key words:** *Tharybis*, new species, Pacific Ocean, morphology, synapomorphies

### Introduction

Sars (1902) established the genus *Tharybis* for *T. macrophthalma* which was collected with a dredge at 100 fathoms in the Christiania Fjord off Norway. Sars noted that this new genus and species, and its new family did not exhibit gender dimorphism in antenna 1 or the oral limbs, and that a fifth leg is present in females. Sars also noted the similarity of its maxilla 2 [which Sars called first maxilliped] to species of Phaennidae, particularly *Phaenna*, and mentioned that the first enditic lobe of maxilla 1 is large.

Since Sars (1902), sixteen calanoid species, often associated with the sea floor, have been described as species of *Tharybis*: *T. sagamiensis* Tanaka, 1960; *T. fultoni* Park, 1967; *T. asymmetrica* Andronov, 1976; *T. megalodactyla* Andronov, 1976; *T. minor* Schulz, 1981; *T. magna* Bradford & Wells, 1983; *T. angularis* Schulz, 1995 (in Schulz & Beckmann 1995); *T. crenata* Schulz, 1995 (in Schulz & Beckmann 1995); *T. inaequalis* Bradford-Grieve, 2001; *T. inflata* Andronov, 2002; *T. lauta* Andronov, 2002; *T. macrophthalmoida* Andronov, 2002; *T. scaura* Andronov, 2002; *T. tuberosa* Andronov, 2002; *T. tumidula* Andronov, 2002. Schulz (1981) moved three species to *Tharybis* without comment: *T. neptuni* (Cleve 1905) originally described as a species of *Scolecithricella*; *T. altera* (Grice & Hulsemann 1970) and *T. compacta* (Grice & Hulsemann 1970)

both originally described as species of *Undinella*. Bradford et al. (1983), also without comment, suggested moving *T. paraincertus* (Grice & Hulsemann 1965) and *T. macrocephalon* (Grice & Hulsemann 1970) both originally described as species of *Xanthocalanus*. Schulz & Beckmann (1995) moved *T. groenlandica* which Tupitzky (1982) described as a species of *Xanthocalanus* to *Tharybis*, and removed *T. paraincertus* (Grice & Hulsemann 1965) and *T. macrocephalon* (Grice & Hulsemann 1970) from *Tharybis*. However, Schulz & Beckmann did not state to which genus *T. paraincertus* or *T. macrocephalon* belong, nor did they provide synapomorphies for *Tharybis*. We have chosen to retain both species in *Tharybis* at this time. Andronov (2002) placed *T. crenata* Schulz, 1995 in synonymy with *T. groenlandica* and *T. minor* Schulz, 1981 in synonymy with *T. asymmetrica* Andronov, 1976, but without examining type specimens of the species whose name was synonymized. Finally, Ohtsuka et al. (1998) re-described specimens of *T. magna* which differ from the original description, but without observing the type specimens.

In this paper, we describe three new species of *Tharybis* and discuss possible synapomorphies for the genus. We continue to recognize all of Schulz's species until a careful comparison has been made of the type specimens. With three new species here, there are presently 25 nominal species in the genus *Tharybis*.

## Materials and Methods

Specimens from Kona, Hawaii, were collected in seawater flowing from a flexible plastic pipe maintained by Natural Energy Laboratory of Hawaii Authority near Kona, Island of Hawaii, 19°43'27.01"N, 156°04'35.46"W (pipe intake 1 m diameter at depth off 600 m about 30 m from the bottom) on 6 July 1997. These specimens may have been in the collecting net for up to 12 hours prior to fixation with 4% formaldehyde. Few internal tissues remain in these specimens, some exoskeletal structures are missing, and the prosome often is broken. Specimens collected from Volcano 7 (13°23'N; 102°27'W, dive 2145, D7, N4; dive 2146, D8, N8; and dive 2147, D9, N4, N8) in the eastern tropical Pacific Ocean by the submersible ALVIN 1–5 m above bottom depths of 1291–1316 m, 2945–3010 m, 2973–2992 m, respectively, in November 1988 were fixed at depth of capture with gluteraldehyde. Their exoskeleton and internal tissues appear intact. Ferrari & Markhaseva (1996, 2000a) give further details about collections from Volcano 7 and Hawaii, respectively. In the laboratory, specimens from both localities were preserved in 0.5% propylene phenoxylol/4.5% propylene glycol/95.0% de-ionized freshwater. During examination, specimens were cleared in steps through 50% lactic acid/50% de-ionized freshwater to 100% lactic acid, stained by adding a solution of chlorazol black E dissolved in 70% ethanol/30% de-ionized freshwater, and examined with bright-field and with differential interference optics. Drawings were made with a camera lucida. Dissected and undissected specimens are preserved in 70% ethanol/30% de-ionized freshwater. Specimens are deposited in National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

Thoracic somites are Th1–7. Prosome is cephalic somites 1–5 plus thoracic somites 1–6; urosome is thoracic somite 7 plus all abdominal somites. Cephalic appendages are abbreviated A1=antenna 1; A2=antenna 2; Mn=mandible; Mx1=maxilla 1; Mx2=maxilla 2. Appendages on thoracic somites are Mxp=maxilliped (thoracopod 1); P1–5=swimming legs 1–5 (thoracopods 2–6). Re is exopod; Ri is endopod. The caudal ramus is CR. The length of the whole animal is measured from the anterior edge of the cephalon to the posterior edge of the caudal ramus, and does not include that part of the prosome which overlaps the genital complex. Designations of appendage segments follow Ferrari (1995) and Ferrari & Markhaseva (2000a). The coxa of the maxilliped of copepods is the distal setiferous lobe on the calanoid syncoxa; the remaining three setiferous lobes belong to the praecoxa (Ferrari & Ivanenko 2001; Ferrari & Dahms 1998). Articulating armament elements of appendages are termed setae regardless of their location, morphology or degree of rigidity. Two setae and one aesthetasc on a segment of antenna 1 are designated 2+1; “?” indicates that a setal element was broken so that its identity could not be determined and only the scar at the location of attachment of the seta was observed. Setules are epicuticu-

lar extensions of a seta; denticles are epicuticular extensions of an appendage segment; spinules are epicuticular extensions of a somite.

## Taxonomy

### *Tharybis pseudomegalodactyla* new species

#### Figures 1–6, 15A

Holotype: dissected female 1.44 mm (USNM 1027385); prosome 1.12 mm, urosome 0.32 mm from eastern tropical Pacific Ocean 1–5 m above Volcano 7 (dive 2146, D8, N8). Paratypes: 1 dissected male 1.16 mm and 1 dissected female (body lost, slides with oral parts and swimming legs, (USNM 1027386), collection data same as holotype; 1 dissected female 1.38 mm (USNM 1027387) from Volcano 7 (dive 2147, D9, N8); 2 dissected females (1.32 and 1.24 mm) and 1 dissected and 1 undissected male (1.12 and 1.22 mm) (USNM 1027388) from Volcano 7 (dive 2147, D9, N4).

*CVI Female.* Total length 1.24–1.44 mm. Prosome 3.0–3.5 times longer than urosome. Cephalon, Th1 and Th2 fused. Th5 and Th6 fused ventrolaterally (Fig. 1A). Dorsally cephalon rounded anteriorly (Fig. 1B). Laterally posterior corners of prosome rounded (Fig. 1A); in dorsal view obtusely triangular (Fig. 1D), reaching at least to the mid-length of genital complex. Posterior edge of urosome somite 2 with epicuticular fringe best seen in dorsal view (Fig. 1D). Genital complex slightly asymmetrical; in dorsal view small swelling on the left side slightly more pronounced than swelling on right (Fig. 1D, F, G).

Rostrum (Fig. 1C): 2 thin filaments.

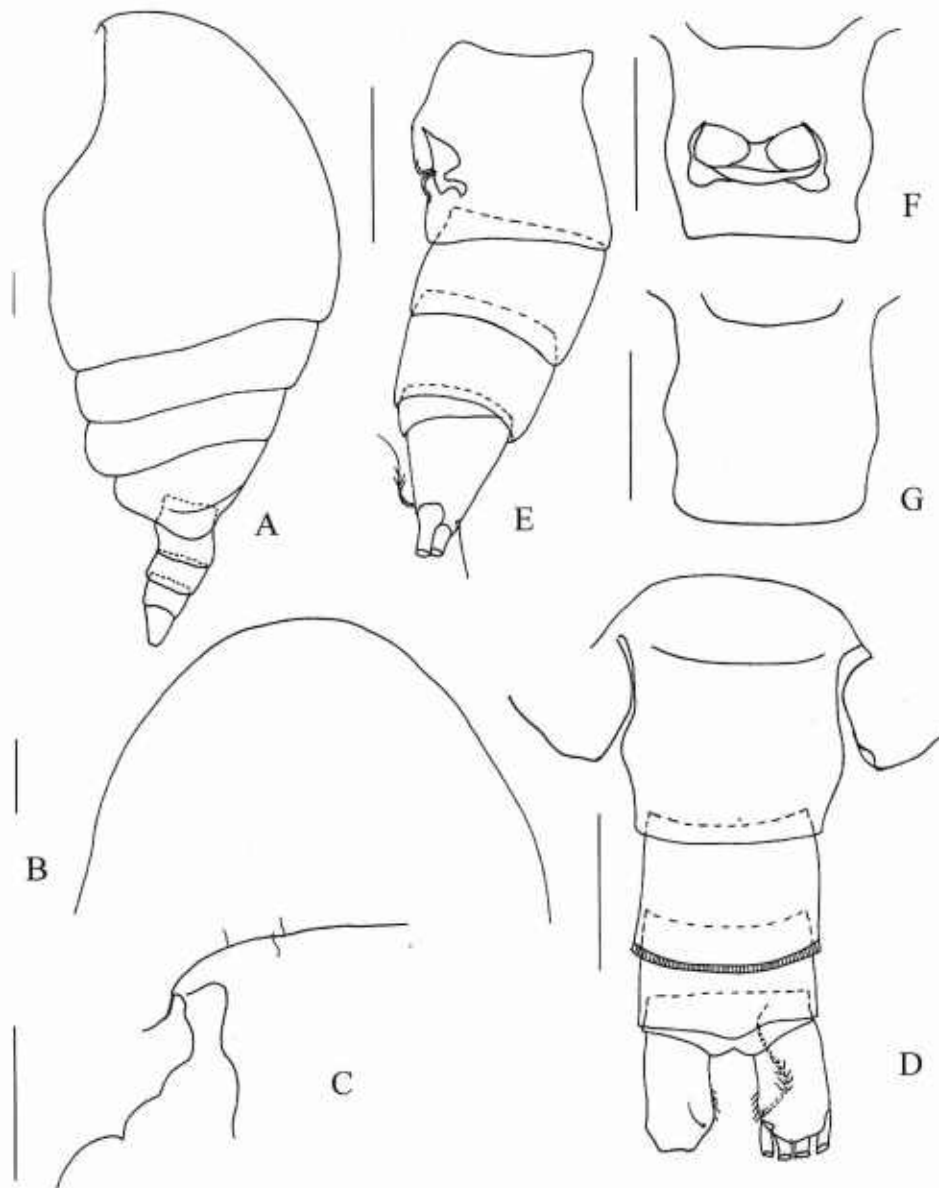
A1 (Fig. 2A): reaching the posterior end of Th4 and of 24 articulated segments: with groups of setae: 3, 6+1, 2+1, 2, 2+1, 2, 2+1, 4+1, 1, 1, 1+1, 1, 2+1, 1, 1, 1, 2, 1+1, 1, 1, 2, 2, 2, 4+1.

A2 (Fig. 2B): coxa with 1 small seta; basis with 2 setae. Ri 2-segmented; proximal segment with 2 setae and row of small denticles distally; distal segment with 14 (6 terminal and 8 sub-terminal setae). Re 7-segmented (2nd and 3rd segments from basis incompletely articulated) with 0, 0 (+1), 1, 1, 1, 1, 3 setae.

Mn (Fig. 2C, D): coxa with row of stiff denticles originating along medial edge of gnathobase; basis with 3 setae. Ri 2-segmented, proximal with 2 setae and distal with 9 setae. Re indistinctly segmented apparently with 1, 1, 1, 1 and 2 setae.

Mx1 (Fig. 2E): praecoxal endite vaulted distally, with 9 terminal, 4 posterior and 1 anterior setae; coxal endite with 3 setae; proximal and distal basal endites with 4 and 3 setae respectively. Ri with 7 setae (2+2+3); Re with 3 setae and exite with 7 setae.

Mx2 (Fig. 3): proximal praecoxal endite with 4 setae; distal with 3 setae. Proximal coxal endite with 3 setae, posterior seta a poorly-sclerotized, sensory seta without se-



**Fig. 1.** *Tharybis pseudomegalodactyla*, new species. Female. A, habitus, lateral; B, anterior part of cephalon; C, rostrum, left lateral; D, posterior corners of prosome and urosome, dorsal; E, urosome, left lateral; F, genital complex, ventral; G, genital complex, dorsal. Figures B, C, D from holotype; A, E, F, G from paratypes. Scale lines 0.1 mm.

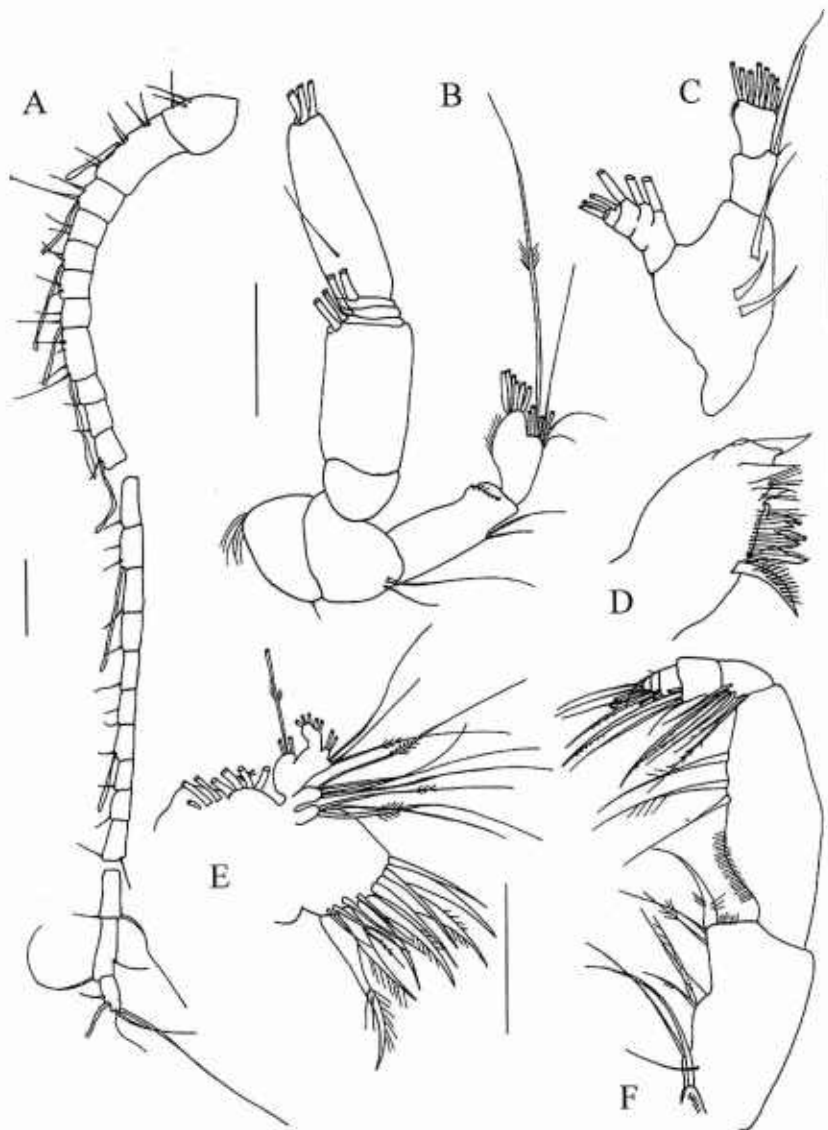
tules; distal coxal endite with 3 setae, including 1 thick spine-like seta. Proximal basal endite with 4 setae, 1 poorly sclerotized sensory seta without setules, and 3 well sclerotized seta with setules. Distal basal lobe plus Re with 8 sensory setae; 5 brush-like and 3 worm-like.

Mxp (Fig. 2F): syncoxa with 1 seta on proximal lobe; 2 setae on middle lobe; 3 setae on distal lobe; coxal lobe with 3 setae and distal hairs; all setae sclerotized. Basis with row of stiff hairs proximally, 3 setae on unattenuated proximal lobe and 2 setae on distal lobe. Ri of 5 articulated segments with 4, 4, 3, 4 and 4 setae.

P1 (Figs. 4A, 15A): coxa without seta. Basis with small lateral seta and medial seta; latter seta part of organ of Von Vaupel Klein along with thumb-like knob on Ri (Fig. 15A);

distal edge of knob smooth with 4–6 denticles on anterior face. Ri 1-segmented with 3 medial and 2 terminal setae. Re 3-segmented, proximal with 1 lateral seta, middle with 1 medial and 1 lateral seta, distal with 3 medial, 1 terminal, 1 lateral seta; lateral seta on proximal segment exceeds the base of terminal seta and lateral seta on middle segment covers at least one third length of lateral seta on distal segment.

P2 (Fig. 4B): coxa with medial seta. Basis without seta. Re 3-segmented, proximal with 1 medial and 1 lateral seta, middle with 1 medial and 1 lateral seta, distal with 4 medial, 1 terminal and 3 lateral setae. Proximal and distal segments with groups of small surface denticles. Medial segment with row of small denticles distally. Ri 2-segmented,



**Fig. 2.** *Tharybis pseudomegalodactyla*, new species. Female. A, antenna 1; B, antenna 2; C, mandibular palp; D, mandibular gnathobase; E, maxilla 1; F, maxilliped. Figure B from holotype; figures A, C–F from paratypes. Scale lines 0.1 mm.

proximal with 1 medial seta, distal with 2 medial, 2 terminal and 1 lateral setae. Proximal and distal segments with groups of small surface denticles.

P3 (Fig. 4C): coxa with medial seta. Basis without seta. Re 3-segmented, proximal with 1 medial and 1 lateral seta, middle with 1 medial and 1 lateral seta, distal with 4 medial, 1 terminal and 3 lateral setae. Proximal and distal segments with groups of surface denticles. Medial segment with row of small denticles distally. Ri 3-segmented, proximal with 1 medial seta, middle with 1 medial seta, distal with 2 medial, 2 terminal and 1 lateral seta. Middle and distal segments with groups of surface denticles.

P4 (Fig. 4D): coxa with medial seta. Basis without seta. Re 3-segmented, proximal with 1 medial and 1 lateral seta, middle with 1 medial and lateral seta, distal with 4 medial, 1 terminal and 3 lateral setae. Medial segment with row of small denticles distally. Distal segments with group of sur-

face denticles. Ri 3-segmented, proximal with 1 medial seta, middle with 1 medial seta, distal with 2 medial, 2 terminal and 1 lateral seta. Middle and distal segments with groups of surface denticles.

P5 (Fig. 4E, F): 3-segmented; coxa and basis unarmed. Re (distal segment)  $3.2\times$  as long as wide [length along medial face to width at origin of seta] with 1 articulated medial seta, slightly curved, with setules,  $4.5\times$  as long as wide [width at base to height at tip] and 2 spine-like attenuations, terminal with denticles.

CR (Fig. 1D): 4 large, terminal setae, 1 small mediodorsal seta and 1 small ventral setae.

*CVI Male.* Total length 1.12–1.22 mm. Prosome 2.2–2.7 times longer than urosome. Cephalon and Th1 fused. Th1–Th2 separate dorsally. Th5–Th6 fused (Fig. 5A, B). Posterior corners of prosome rounded laterally and dor-

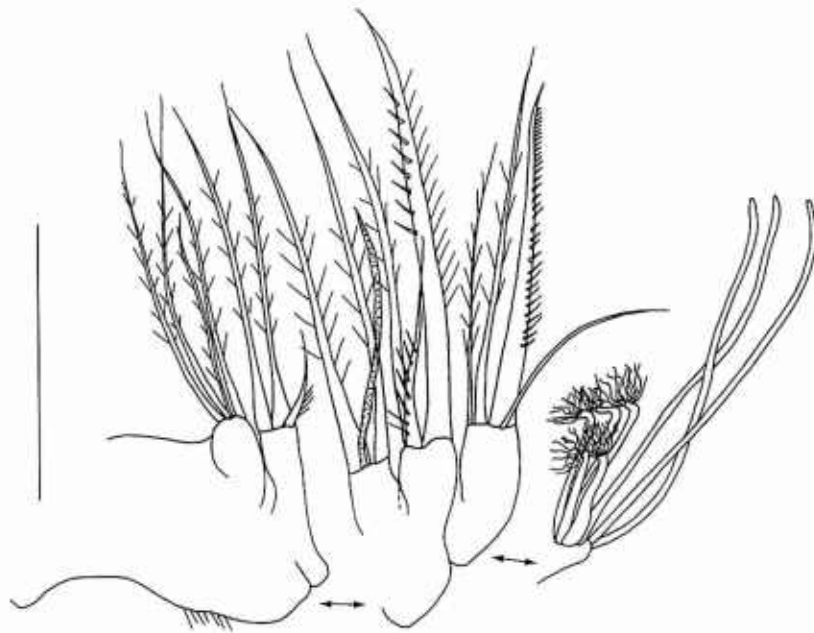


Fig. 3. *Tharybis pseudomegalodactyla*, new species. Female. Maxilla 2. From holotype. Scale line 0.1 mm.

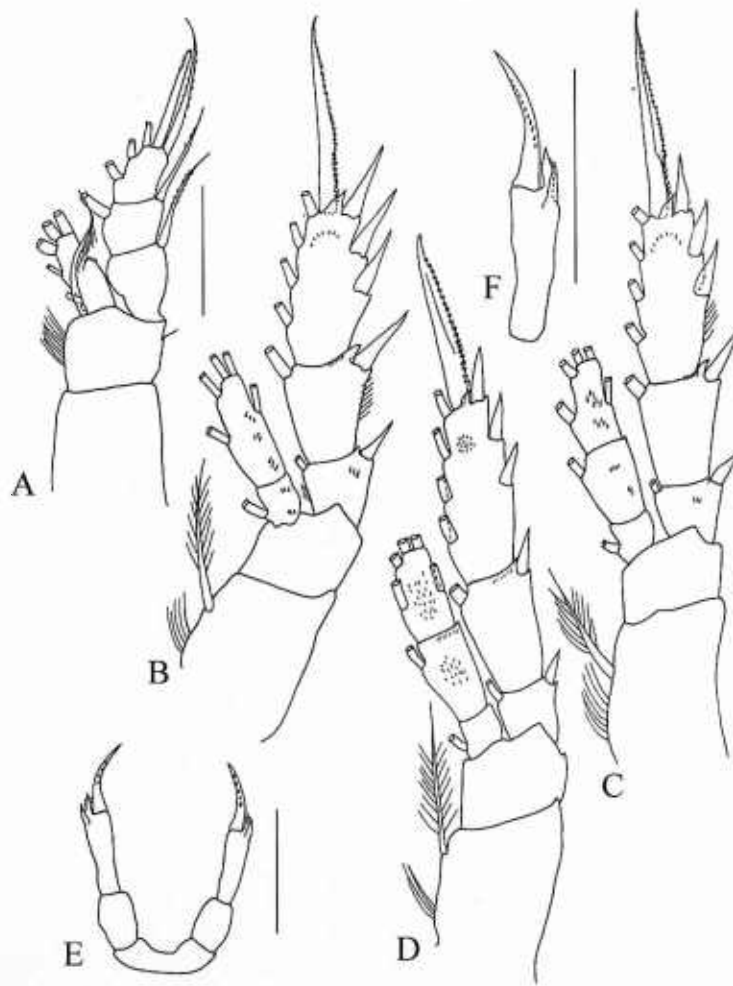
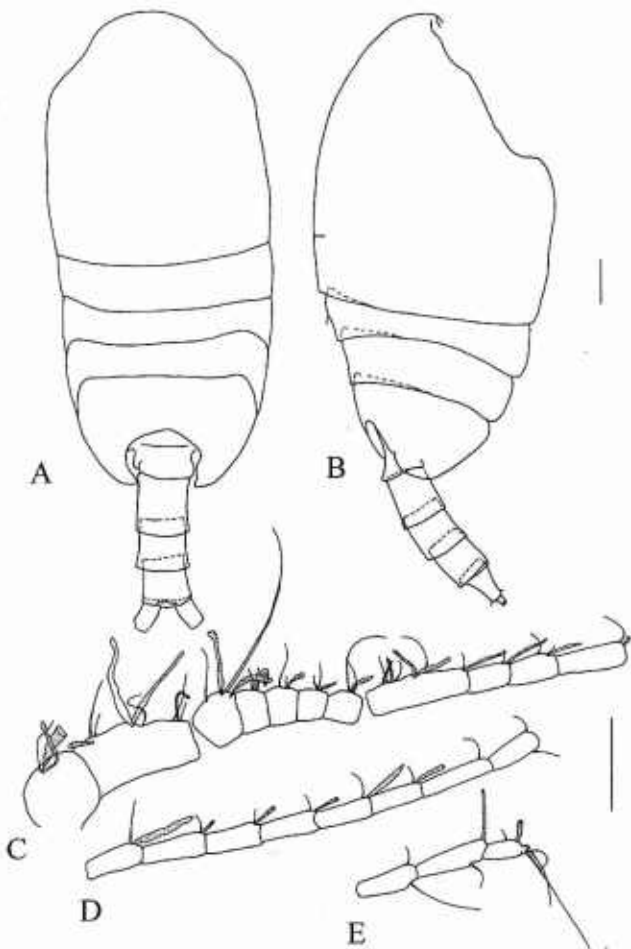
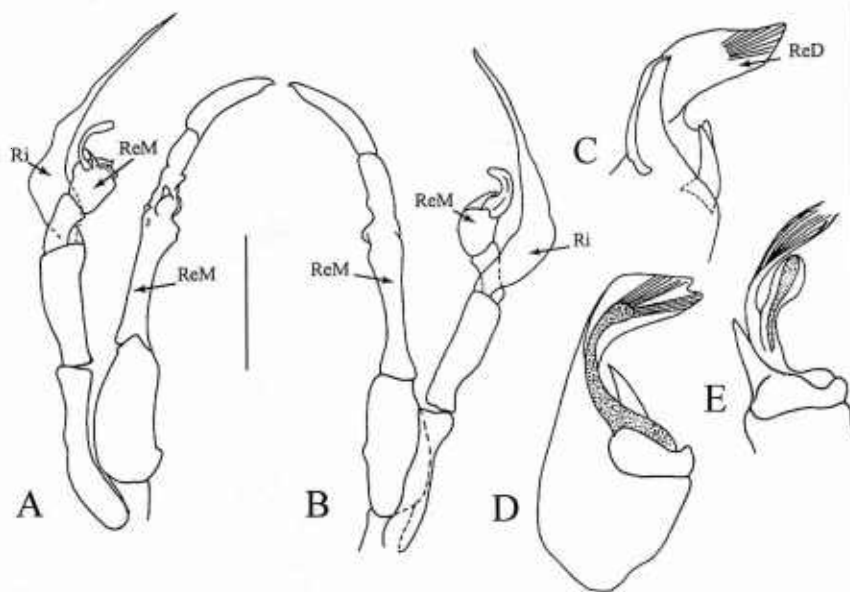


Fig. 4. *Tharybis pseudomegalodactyla*, new species. Female. A, P1, posterior; B, P2, posterior; C, P3, posterior; D, P4, posterior; E, P5; F, P5 Re3. Figures A, B, C, D from paratypes, Figs. E, F from holotype. Scale line 0.1 mm.



**Fig. 5.** *Tharybis pseudomegalodactyla*, new species. Male. A, habitus, dorsal; B, habitus, lateral; C, right antenna 1, articulated segments 1–11; D, right antenna 1, articulated segments 12–19; E, right antenna 1, articulated segments 20–22. From paratype. Scale lines 0.1 mm.



**Fig. 6.** *Tharybis pseudomegalodactyla*, new species. Male. A, B, P5 in different views; C–E, left P5 Re3 in different views. ReM is middle segment of exopod; ReD is distal segment of exopod; Ri is endopod. From paratype. Scale lines 0.1 mm.

sally. Genital opening on left.

Rostrum (Fig. 5B): 2 small filaments.

A1 (Fig. 5C–E): right of 22 articulated segments: with groups of setae: 1+2, 5+4, 2+2, 2+1, 2+1, 2+1, 2+1, 4+5, 1+1, 2+1, 1+1, 1+1, 1+1, 1+1, 1+1, 1+1, 1+1, 1, 2, 2, 2, 4+1. Left A1 of 23 articulated segments; segment apparently homologous to the 18th of the right A1 appears divided into 2 segments in left A1 with the proximal segment lacking seta.

A2: as for female, except for basis with 1 seta.

Mn: as for female, except for Ri2 with 8 setae.

Mx1: as for female except for praecoxa lacking anterior seta and exite with 8 setae.

Mx2, Mxp and P1–P2 as for female.

P3–P4: as for female except surface denticulation less dense.

P5 (Fig. 6A–E): right leg uniramal 4-segmented; Re 2-segmented, Re1 with several knob-like attenuations along middle of segment. Left leg biramal, Ri 1-segmented falciform, thin, narrowing distally. Re 3-segmented; middle segment with distal flange around proximal part of distal segment; distal segment with flange around 2 terminal attenuations.

#### Etymology

The name recognizes a general similarity of the species to *Tharybis megalodactyla* Andronov, 1976.

#### Remarks

Female and male specimens have been assigned to the same species based on their co-occurrence, and identical number and kind of sensory setae on maxilla 2 and the maxilliped. Females of *T. pseudomegalodactyla* share several features with females of *Tharybis magna* Bradford,

1983 (in Bradford & Wells 1983) and *Tharybis megalodactyla* Andronov, 1976. The new species shares with *T. megalodactyla* a leg 5 of similar general shape, 5 brush-like sensory setae on the basis plus ramus of maxilla 2; it differs from *T. megalodactyla* by the asymmetrical genital complex (symmetrical in *T. megalodactyla*), larger size (1.10–1.24 mm *T. megalodactyla*), and curved seta on P5 (straight in *T. megalodactyla*). *Tharybis pseudomegalodactyla* shares with *T. magna* an asymmetrical genital complex with more pronounced bump on the left side, similar leg 5, and all setae sclerotized on the syncoxa of the maxilliped, as recently redescribed by Ohtsuka et al. (1998). *Tharybis pseudomegalodactyla* is distinguished from *T. magna* by the presence of 5 brush-like sensory setae on the basis plus ramus of maxilla 2 and 8 transformed setae in total (*T. magna* has 6 brush-like sensory setae and 9 transformed setae in total) and smaller size (*T. magna* is 1.50–1.70 mm). Males of *T. pseudomegalodactyla* differ significantly in the structure of leg 5 from males of the above mentioned two species as well as from males all known species of *Tharybis*. Males of *T. pseudomegalodactyla* differ from *T. megalodactyla* which has knob-like attenuation on the proximal exopodal segment of the right leg 5 and in the shape of the left endopod which is curved significantly. Males of the new species are distinguished from *T. magna* which has a knob-like attenuation on the distal segment of the right leg 5 and a distal segment of the left exopod without flanges (Bradford & Wells 1983); this also is the case for *T. altera*, *T. asymmetrica*, *T. compacta*, *T. groenlandica* and *T. minor*. *Tharybis fultoni*, *T. macrophthalmia* and *T. inaequalis* have a complicated distal left Re, but the shape of the distal segment of the right exopod of leg 5 is more complex than that of *T. pseudomegalodactyla*.

### *Tharybis juhlae* new species

#### Figures 7–12, 15C

Holotype: female 1.69 mm; prosome 1.28 mm, urosome 0.41 mm collected 6 July 1997 near Kona, Island of Hawaii, 19°43'27.01"N, 156°04'35.46"W (USNM 1027390). Paratypes: 4 dissected females (1.42, 1.59, 1.61 and 1.63 mm) whose lengths could be accurately measured and 4 undissected females. One dissected male, total length 1.36 mm (same data as holotype) (USNM 1027391); 2 dissected males (1.42, 1.48 mm) from Volcano 7 (dive 2145, D7, N4) (USNM 1027392).

*CVI Female.* Total length 1.42–1.69 mm; prosome 3.0–3.4 times longer than urosome; cephalon and Th1 fused, Th1 and Th2, Th4–Th5 fused dorsally, in lateral view both arthrodistal membranes present (Fig. 7A, C). Posterior corners of prosome rounded in lateral view (Fig. 7A, C) and triangular in dorsal view (Fig. 7B), reaching to mid-length of genital complex. Urosomites with epicuticular fringe (Fig. 7B, C). Genital complex symmetrical, nearly as long as following 2 urosomites together, with low dorsal

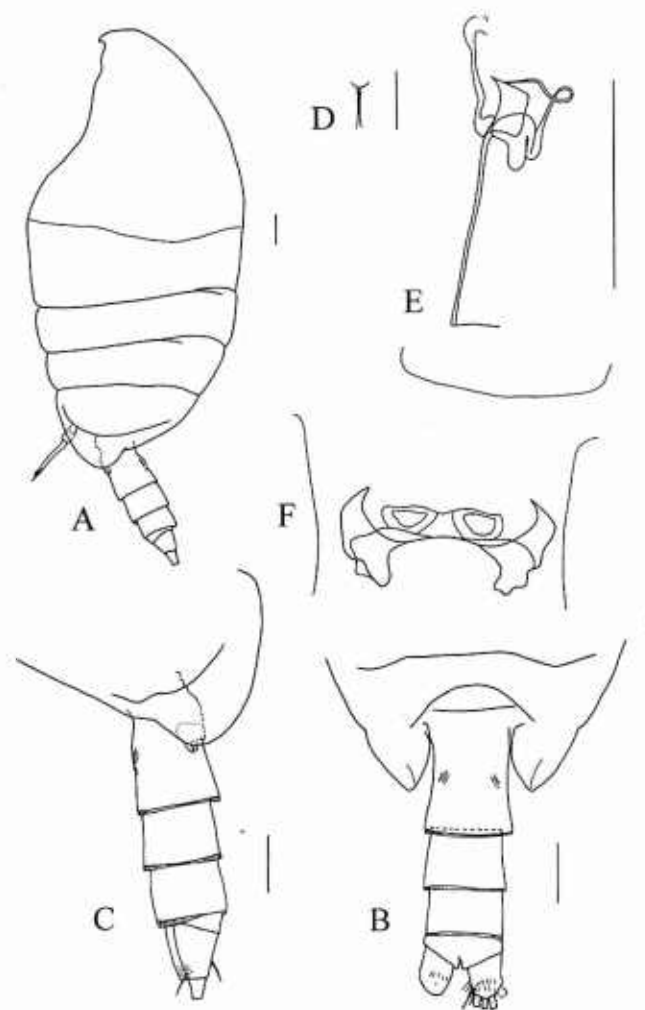


Fig. 7. *Tharybis juhlae*, new species. Female. A, habitus, left lateral; B, posterior corners of prosome and urosome, dorsal; C, same, right lateral; E, genital field, left lateral; F, genital field, ventral. From paratypes. Scale line 0.1 mm.

knob laterally at about mid length (Fig. 7A, C). Genital field in the anterior part of genital complex (Fig. 7E, F).

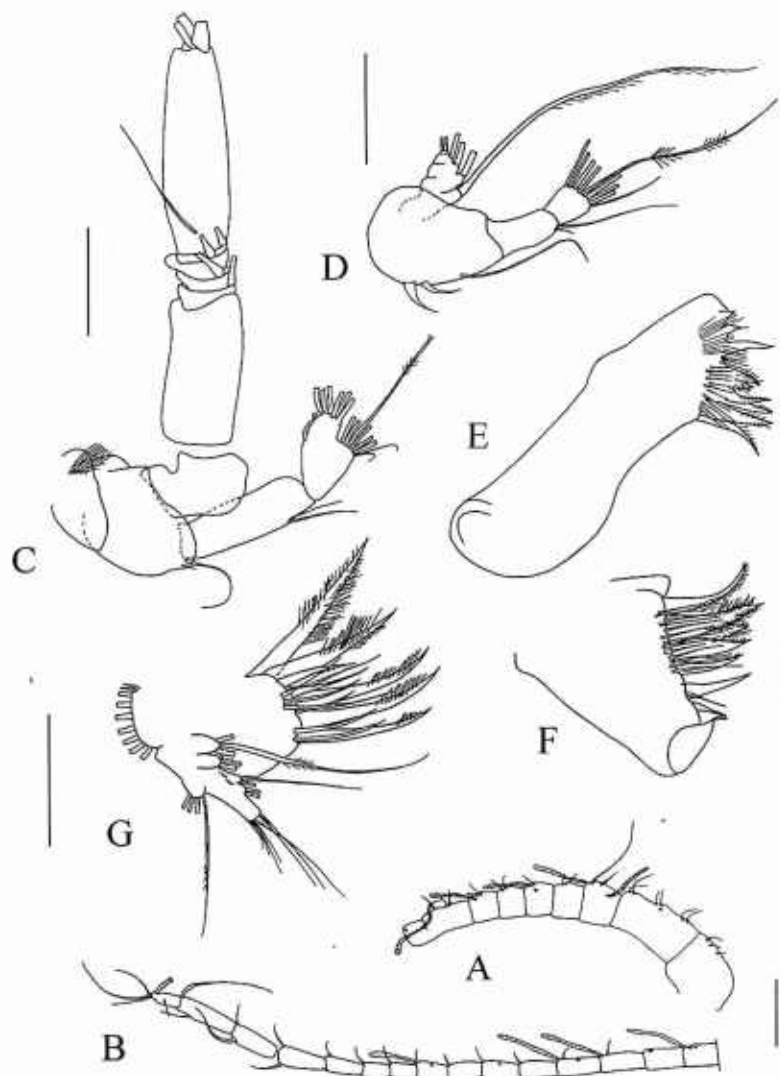
Rostrum: 2 thin filaments (Fig. 7D).

A1 (Fig. 8A, B): reaching to the end of Th3; 24 articulated segments with groups of: 3, 6, 2+2, 2, 1+1+?, 2, 2+1, 4+1, ?, ?+1, ?, 1+1, 1+1+?, 1, 1+?, 1, 1+1+?, 1, 1, 1, 2, 2, 2, 4+1 setae.

A2 (Fig. 8C): coxa without seta; basis with 2 setae. Ri 2-segmented; proximal segment with 2 setae and distal with 14 (6 terminal and 8 subterminal setae). Re 8 segmented with 0, 0, 1, 1, 1, 1, 1, 3 setae.

Mn (Fig. 8D–F): coxal gnathobase with row of stiff hairs; basis with 3 setae. Ri 2-segmented; proximal segment with 2 setae, and distal with 9 setae. Re indistinctly segmented apparently with 1, 1, 1, 1 and 2 terminal setae.

Mx1 (Fig. 8G): praecoxal endite vaulted distally with 10 terminal, 3 posterior and 1 anterior setae; coxal endite with 3 setae, proximal and distal basal endites with 4 setae and 3 setae respectively. Ri with 2, 2, 5 setae; Re with 4 setae and



**Fig. 8.** *Tharybis juhlae*, new species. Female. A, antenna 1, articulated segments 1-9; B, antenna 1, articulated segments 10-24; C, antenna 2; D, mandibular palp; E, mandibular gnathobase; F, cutting edge of mandibular gnathobase; G, maxilla 1. From paratype. Scale lines 0.1 mm.

exite with 9 setae.

Mx2 (Fig. 9A, B): proximal praecoxal endite with 4 setae; distal with 3 setae. Proximal coxal endite with 3 setae; distal coxal endite with 3 setae, of them 1 thick, spine-like. Proximal basal endite with 4 setae, distal basal lobe plus Re with 5 brush-like, 3 worm-like and 1 sclerotized seta, latter with sparse setules.

Mxp (Fig. 9C): syncoxa with 1 seta on proximal lobe, 2 setae on middle lobe, 3 setae on distal lobe, coxal lobe with 3 setae and distal hairs; all setae sclerotized. Basis with row of stiff hairs proximally, 3 setae on unattenuated proximal lobe and 2 setae on distal lobe. Ri of 5 articulated segments with 4, 4, 3, 4 and 4 setae.

P1 (Figs. 10A, 15C): coxa without seta. Basis with a medial seta curved back upon itself, degree of curvature varies (compare Fig. 10A with Fig. 15C); organ of Von Vaupel Klein with pronounced thumb-like knob on Ri; distal edge

of knob smooth, without ornamentation on anterior face, with long, thin denticles behind the knob extending toward distal margin of endopod (Fig. 15C). Re 3-segmented, proximal with 1 lateral seta, middle with 1 medial and 1 lateral seta, distal with 3 medial, 1 terminal, 1 lateral seta; lateral seta on proximal segment reaches the base of terminal seta and lateral seta on middle segment reaches nearly the mid-length of lateral seta on distal segment.

P2 (Fig. 10B): coxa with medial seta; basis without seta. Re 3-segmented, proximal with 1 medial and 1 lateral seta, middle with 1 medial and lateral seta, distal with 4 medial, 1 terminal and 3 lateral setae. Distal segment with group of small surface denticles. Ri 2-segmented, proximal with 1 medial seta, distal with 2 medial, 2 terminal and 1 lateral setae. Distal segment with groups of small surface denticles.

P3 (Fig. 10C): coxa with medial seta; basis without seta.



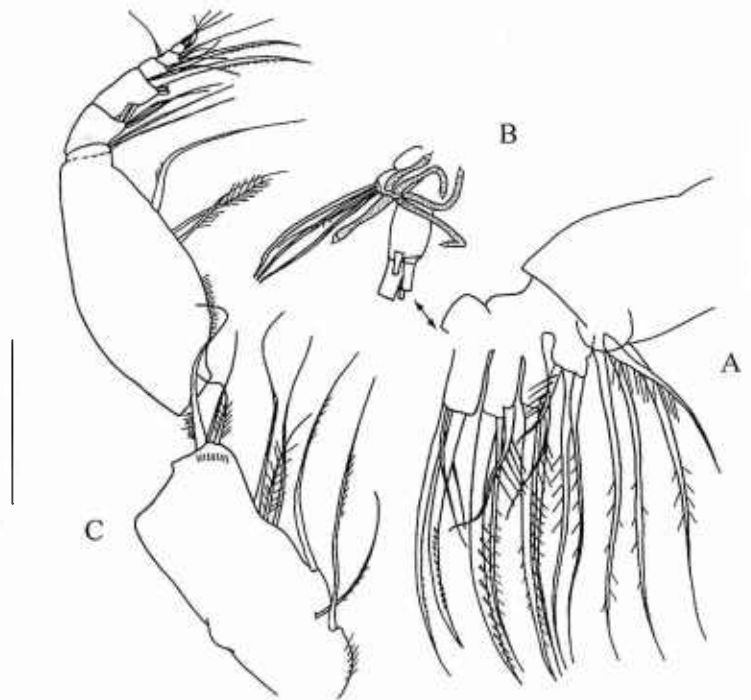


Fig. 9. *Tharybis juhlae*, new species. Female. A, maxilla 2 (without distal basal lobe and Re); B, maxilla 2, distal basal lobe plus Re. From paratypes. Scale line 0.1 mm.

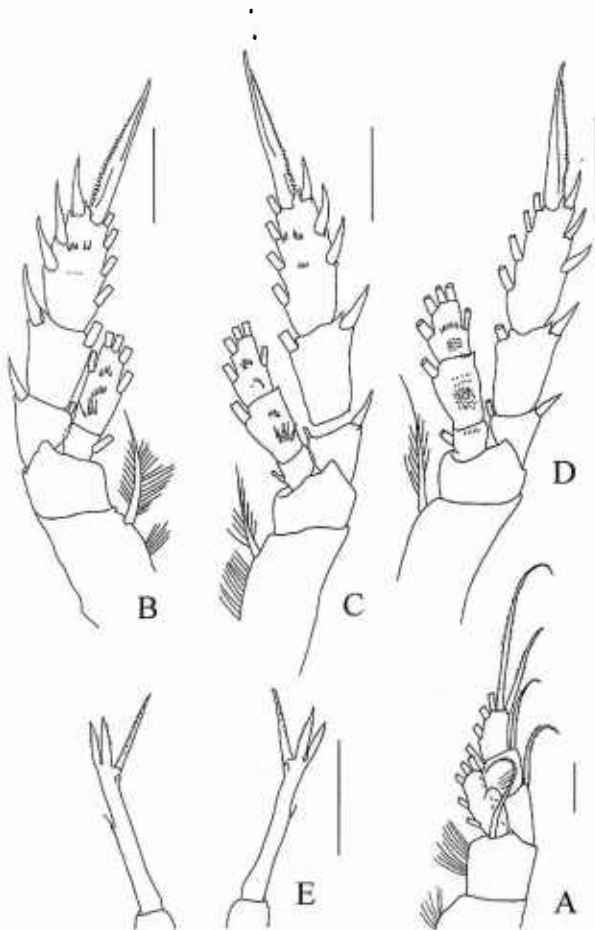


Fig. 10. *Tharybis juhlae*. Female. A, P1; B, P2; C, P3; D, P4; E, P5. From paratypes. Scale lines 0.1 mm.

Re 3-segmented, proximal with 1 medial and 1 lateral seta, middle with 1 medial and lateral seta, distal with 4 medial, 1 terminal and 3 lateral setae. Distal segment with groups of surface denticles. Ri 3-segmented, proximal with 1 medial seta, middle with 1 medial seta, distal with 2 medial, 2 terminal and 1 lateral seta. Middle and distal segments with groups of surface denticles.

P4 (Fig. 10D): coxa with medial seta; basis without seta. Re 3-segmented, proximal with 1 medial and 1 lateral seta, middle with 1 medial and lateral seta, distal with 4 medial, 1 terminal and 3 lateral setae. Ri 3-segmented, proximal with 1 medial seta, middle with 1 medial seta, distal with 2 medial, 2 terminal and 1 lateral seta. All segments with groups of surface denticles.

P5 (Fig. 10E): 3-segmented; coxa and basis unarmed. Re [distal segment]  $6.5\times$  as long as wide [length along medial face to width at origin of seta] with 1 small lateral seta at mid-length and 1 terminal, medial seta with setules,  $10.5\times$  as long as wide [width at base to height at tip], 2 spine-like attenuations with denticles, and lobe at base of terminal seta.

CR (Fig. 7B, C): 4 large terminal setae, very small dorsal and small ventral seta; dorsal surface with small denticles.

*CVI Male*. Total length 1.36–1.48 mm; prosome 2.3–2.8 times longer than urosome. Cephalon and Th1–Th2 fused, Th5–Th6 fused dorsally (Fig. 11A). Posterior corners of prosome rounded in lateral view, in dorsal view slightly asymmetrical (Fig. 11C). Genital opening on left. Anal somite small, often obscured by somite anterior to it (Fig. 11C, D).

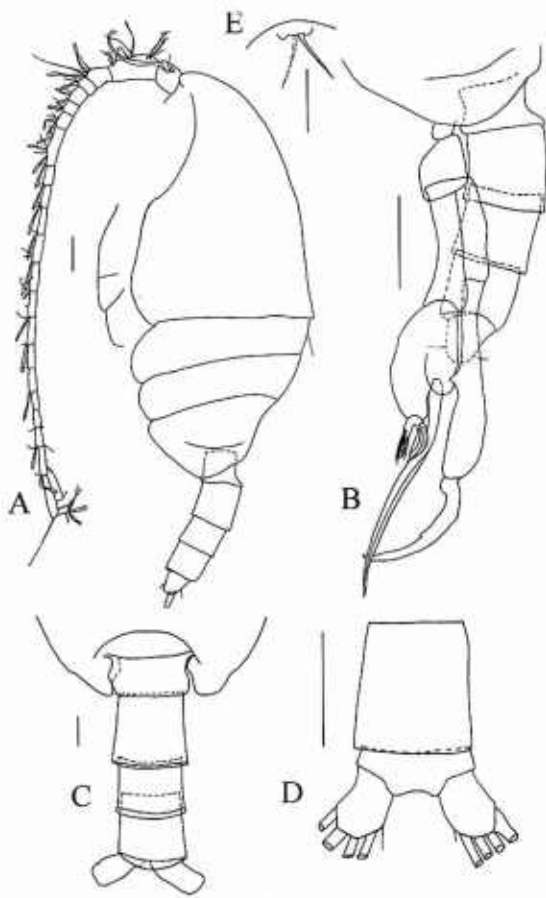


Fig. 11. *Tharybis juhlae*, new species. Male. A, habitus, left lateral; B, posterior corners of prosome, urosome and P5; C, posterior corners of prosome and urosome; D, fourth somite of urosome and anal somite; E, rostrum. From paratype. Scale lines 0.1 mm.

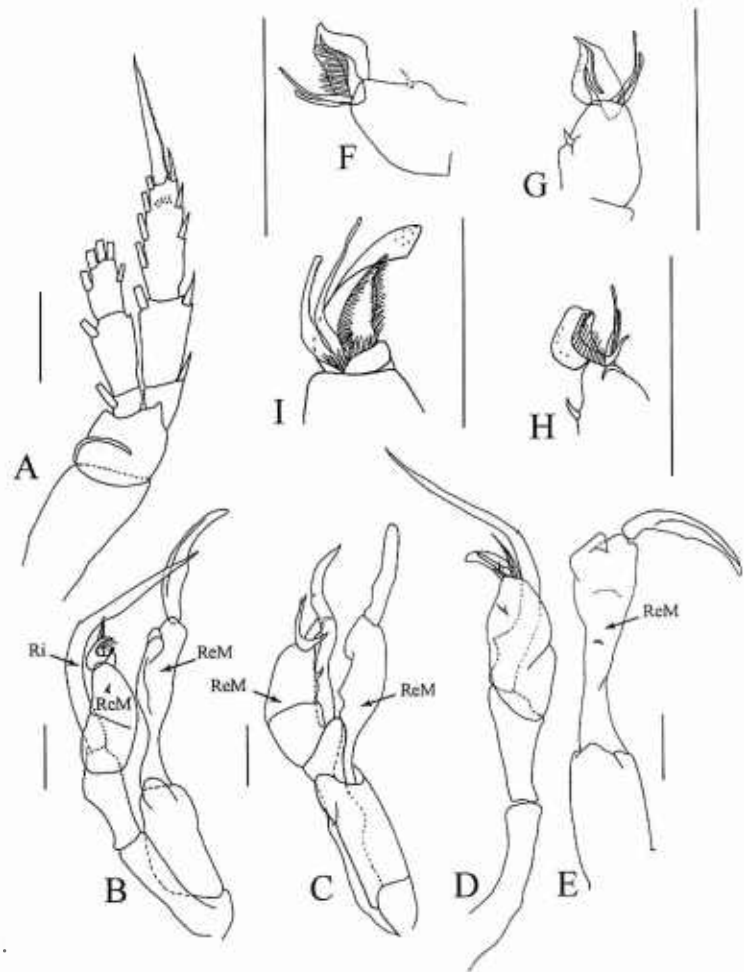


Fig. 12. *Tharybis juhlae*, new species. Male. A, P4; B-E, P5 different views; F-I, left Re3 P5. ReM is middle segment of exopod; Ri is endopod. From paratypes. Scale line is 0.05 mm for I; and 0.1 mm for all other figures.

Rostrum (Fig. 11E): 2 filaments.

A1 (Figs. 11A, 15B): right of 22 articulated segments; with groups of setae: 1+1, 5+4, 2+2, 2+1, 1+2, 2+1, 2+2, 4+4, 1+1, 2+1, 1+1, 2+1, 2+1, 2+1, 1+1, 2, 1+1, 1, 2+1, 2, 2, 4+1. Left A1 of 23 articulated segments; segment apparently homologous to the 18th of the right A1 appears divided into 2 segments in left A1 with the proximal segment lacking seta (see Fig. 15B).

A2: as for female.

Md: as for female, except for Ri2 with 8 setae.

Mx1: as for female except proximal praecoxal endite without anterior seta and coxal exite with 7 setae.

Mx2, Mxp and P1-P2 as for female.

P3: as for female except sparser surface denticulation.

P4: as for female except semicircular chitinous ridge at basipod (Fig. 12A).

P5 (Figs. 11B, 12B-I): right uniramous, Re 2-segmented. Left biramous, Ri 1-segmented falciform; Re 3-segmented; middle segment with spine-like attenuation; distal segment complex with 2 digitiform appendages and a flange with denticles along its base and around its edges.

### Etymology

The species name honors Dr. Hildegard Juhl who has curated the MONOCULUS Copepod Library at the University of Oldenburg in Germany since its inception.

### Remarks

Female and male specimens have been assigned to the same species based on their co-occurrence and identical number and kind of sensory setae on maxilla 2 and the maxilliped. Females of *Tharybis juhlae* differ from all other species of the genus in the shape of genital complex which is very long in dorsal view (nearly as long as two following somites), and has a knob visible in lateral view. It shares with *T. macrophthalma*, *T. fultoni*, *T. macrocephalon*, *T. paraincertus* and *T. macrophthalmoida* a lateral seta (or attenuation) at mid-length of the distal segment of leg 5. Males differ from all other *Tharybis* males in the general morphology of leg 5 and particularly in the presence of spine-like attenuation on the second exopodal segment of the left leg 5.

*Tharybis shuheiella* new species

## Figures 13, 14 and 15D

Holotype: female 1.36 mm; prosome 1.03 mm, urosome 0.33 mm collected 6 July 1997 near Kona, Island of Hawaii, 19°43'27.01"N, 156°04'35.46"W (USNM 1027393).

*CVI Female.* Total length 1.36 mm. Prosome 3.1 times longer than urosome. Cephalon and Th1 fused; Th5 and Th6 fused (Fig. 13A, B). Dorsally cephalon rounded anteriorly. Laterally, posterior corners of prosome rounded but with slight indentation at level of genital complex (Fig. 13B, D); in dorsal view posterior corners of prosome obtusely triangular (Fig. 13E), reaching only slightly past the anterior articulation of the genital complex. Genital complex asymmetrical with bump on the right side slightly more pronounced than bump on left (Fig. 13A). Genital opening defined by thick cuticular ridges ventrally and postero-ventrally (Fig. 13D, E). Anal somite not visible dorsally (Fig. 13A).

Rostrum (Fig. 13C): 2 small flaps; filaments may have been damaged or lost.

A1: damaged; proximal 15 segments remain on right limb and proximal 10 segments remain on left limb; setation similar to *T. pseudomegalodactyla*.

A2: similar to *T. pseudomegalodactyla*.

Mn: similar to *T. pseudomegalodactyla*.

Mx1: similar to *T. pseudomegalodactyla* except proximal praecoxal lobe without anterior seta; exite damaged.

Mx2 (Fig. 14A): similar to *T. pseudomegalodactyla* except posterior seta on proximal coxal lobe poorly sclerotized and without well-sclerotized setules present on corresponding seta of the praecoxal and distal coxal lobes. Distal basal lobe plus Re with 9 sensory setae, 6 brush-like and 3 worm-like (Fig. 14A).

Mxp: syncoxa with 1 poorly-sclerotized seta on proximal lobe; 1 of 2 setae on middle lobe poorly-sclerotized; 1 of 3 setae on distal lobe poorly-sclerotized (Fig. 14B).

P1 (Figs. 14C, 15D): Re with lateral seta of proximal and middle segment, and terminal seta of distal segment curved proximally away from the ramus. Organ of Von Vaupel

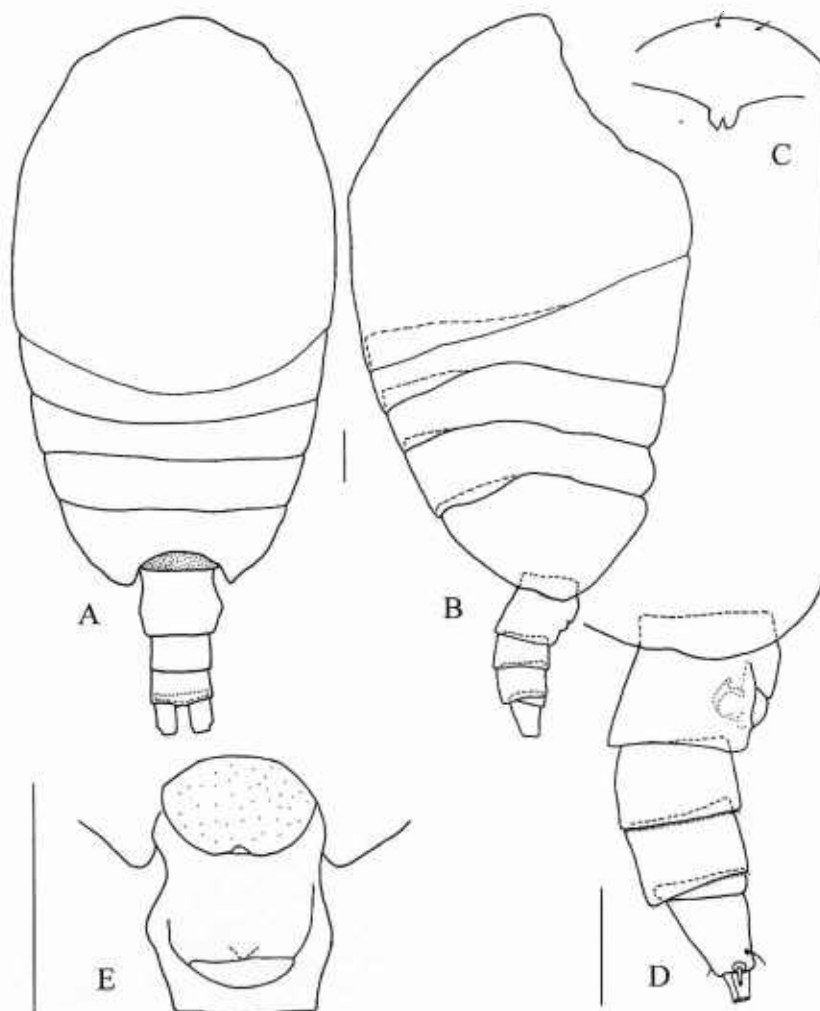


Fig. 13. *Tharybis shuheiella*, new species. Female. A, habitus, dorsal; B, habitus, right lateral; C, anterior cephalon, ventral; D, urosome, right lateral; E, genital complex, ventral. From holotype. Scale lines 0.1 mm.

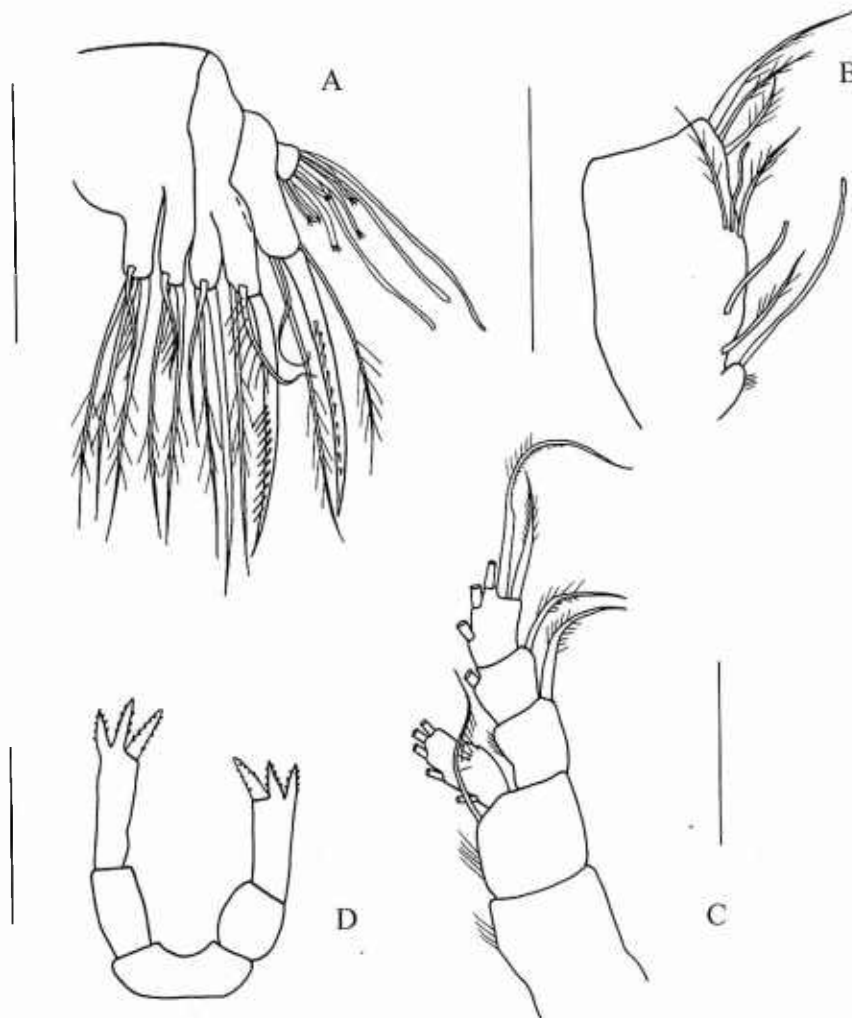


Fig. 14. *Tharybis shuheiella*, new species. Female. A, maxilla 2; B, syncoxa of maxilliped; C, P1, anterior; D, P5, anterior. From holotype. Scale lines 0.1 mm.

Klein a shallow thumb-like knob on endopod with several denticles on anterior face and uneven distal edge; medial seta of basis with a slight curve at tip.

P2-4: similar to *T. pseudomegalodactyla*.

P5 (Fig. 14D): 3-segmented. Coxa and basis unarmed; Re (distal segment) with 1 articulated medial seta with setules, and 2 spine-like attenuations with denticles. Slightly asymmetrical. Right limb: basis  $2.0\times$  as long as wide [length along medial face to width at distal end]; Re  $2.7\times$  as long as wide [length along medial face to width at origin of seta]; medial seta  $3.5\times$  as long as wide [width at base to height at tip]. Left limb: basis  $1.7\times$  as long as wide; Re  $1.9\times$  as long as wide; medial seta  $3.8\times$  as long as wide.

CR: 4 terminal setae, 1 small ventral seta and dorsal seta, several setae broken.

CVI male: unknown.

#### Etymology

The species name honors Prof. Dr. Shuhei Nishida of the Ocean Research Institute, University of Tokyo, for his elu-

cidation of the structure and function of unusual organs unique to marine copepods.

#### Remarks

The female of *T. shuheiella* shares only with *T. juhlae* a lateral seta of the proximal and middle segment, and the terminal seta of distal segment of swimming leg 1 curved proximally away from the ramus. The lateral seta of the proximal, middle, and distal segment of *T. paraincertus* differ in that they are curved toward the ramus (Grice & Hulsemann 1965, Fig. 13C). The female of *T. shuheiella* shares with *T. macrophthalmoidea*, *T. pseudomegalodactyla*, *T. tumidula* and *T. magna* [as illustrated by Ohtsuka et al. (1998, Fig. 8D) but not illustrated from the type (Bradford & Wells 1983, Fig. 4C)] has a genital complex with a swelling on the right side and on the left side; the swelling on the right side of *T. shuheiella* is more pronounced; the swelling on the left side of *T. pseudomegalodactyla*, and *T. magna* is more pronounced. The situation of the other two species is unclear. *Tharybis sagamiensis*, *T.*

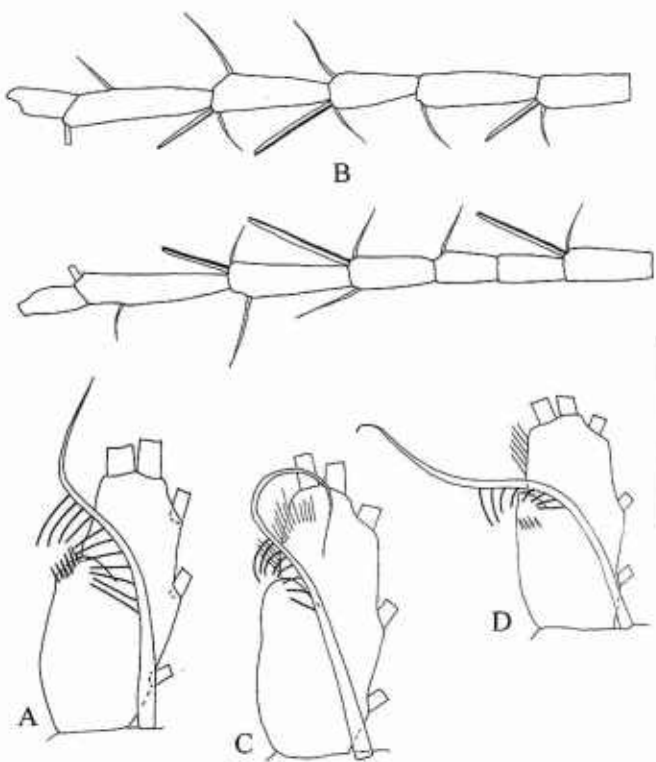


Fig. 15. A, organ of Von Vaupel Klein of female of *Tharybis pseudomegalodactyla*, new species; B, last 6 articulating segments of right antenna, medial down (above) and last 7 articulating segments of left antenna 1, medial up (below) of *Tharybis juhlae*, new species (seta on distal segment not drawn); C, organ of Von Vaupel Klein female of *Tharybis juhlae*, new species; D, organ of Von Vaupel Klein female of *Tharybis shuheiella*, new species. Scale line 0.1 mm.

*minor*, *T. angularis*, *T. crenata*, and *T. inequalis* share with *T. shuheiella* 6 brush-like and 3 worm-like setae on the distal basal lobe plus ramus of maxilla 2. No species except *T. shuheiella* has an unsclerotized seta on the first and on the second praecoxal lobe of the maxilliped.

### Discussion

Despite the statement by Sars (1902) that antenna 1 of *Tharybis* does not exhibit gender dimorphism, two recent studies suggest that some species may show a gender dimorphism in segment number. The three segments of antenna 1 proximal to the terminal segment which have a distal seta on both sides of the segment, in effect in a lateral and medial position, serve as reference segments in this discussion of this limb. The antenna 1 of the female of *T. minor* is illustrated with 24 segments (Schulz 1981: abb. 1E); the two segments immediately proximal to the three reference segments are unarmed. The male has 22 segments with no unarmed segments proximal to the reference segments (Schulz 1981: abb. 2I). For *T. inequalis* gender dimorphism is manifested in an asymmetry of the male; Bradford-Grieve (2001: Fig. 4A) illustrates the female an-

tenna 1 with 23 segments and no unarmed segments proximal to the reference segments. The male antenna 1 has 21 segments on the right side with no unarmed segments proximal to the reference segments (Bradford-Grieve 2001: Fig. 7A). The left antenna 1 apparently has 22 segments [not completely illustrated]; the second segment proximal to the reference segments is unarmed. The phenomenon reported here for *T. pseudomegalodactyla* and *T. juhlae* (Fig. 15B) is similar to the latter example of Bradford-Grieve (2001), although the total number of segments of antenna 1 of the two new species differs from *T. inequalis*. This unarmed segment cannot be related to the Roman numeral system of Huys & Boxshall (1991). While some segments of the calanoid antenna 1 begin development without a seta (Ferrari & Benforado 1998), the Roman numeral adult segments (Huys & Boxshall 1991) are defined by setation. The segment in question here bears no setae.

Synapomorphies for *Tharybis* remain elusive. However, the shape of the praecoxal lobe of maxilla 1 may be informative. In an anterior or posterior view, the general shape of the praecoxal lobe of maxilla 1 of most calanoid copepods is trapezoidal. The long parallel side bears the medial setae and the short parallel side attaches to the shaft of the segment; the convergent sides are proximal and distal. For many species of *Tharybis*, the distal surface is illustrated as vaulted giving the lobe a more robust outline than is general for calanoids and contributing to its description as large or strong (Bradford et al. 1983; Andronov 2002). However, distal vaulting awaits confirmation for many *Tharybis* species.

Bradford (1973) was the first to emphasize the kind [worm-like or brush-like] and number of modified setae associated with the ramus of maxilla 2 in families that are now called bradfordian: Diaxiidae, Phaennidae, Scolecitrichidae and Tharybidae [with Parkiidae established later]. The ultrastructure of worm-like and brush-like setae in a few species has been elucidated and a chemosensory function to facilitate detritivory has been proposed by Nishida & Ohtsuka (1997). Within *Tharybis*, variability has been observed in number, seven to nine with recent publications stating eight or nine (Ohtsuka et al. 1998; Andronov 2002), and in kind, including a sclerotized seta (Ferrari & Markhaseva 1996) (see Table 1). If nine setae are assumed present on the ancestral *Tharybis*, and worm-like and brush-like setae are transformed from sclerotized setae, then three worm-like, five brush-like, one sclerotized might be considered ancestral with three worm-like, six brush-like the first derivative, and three worm-like, five brush-like the second derived state, assuming the same seta has been lost among all species with only eight setae. However, nine transformed setae also are known from genera of the bradfordian families Phaennidae and Scolecitrichidae (Ferrari & Markhaseva 2000b,c) so that it is doubtful that this state will prove to be a synapomorphy for *Tharybis*. Because most of these setae are poorly sclerotized and originate from a very small section of the limb, multiple observations

**Table 1.** Species - name, mx2 - number of worm-like-brush-like-sclerotized setae on the second lobe of basis plus ramus of maxilla 2, total - number of setae on basis plus ramus, mxpd - number of setae on the three praecoxal lobes of the maxilliped (1w=one worm-like seta; 1br=one brush-like seta), source - of information.

Species	mx2	Total	mxpd	Source
<i>T. pseudomegalodactyla</i>	3-5-0	8	1-2-3	Here
<i>T. juhlae</i>	3-5-1	9	1-2-3	Here
<i>T. shuheiiella</i>	3-6-0	9	1(w)-2(1w)-3(1w)	Here
<i>T. macrophthalma</i>	3-5-1	9	1-2-3(1br)	Here; Ferrari & Markhaseva (1996)
<i>T. sagamiensis</i>	3-6-0	9	1-2-3(1br)	Tanaka (1960)
<i>T. fultoni</i>	3-5-1	9	1-2-3	Here; Park (1967)
<i>T. asymmetrica</i>	3-5-0	8	?	Andronov (2002)
<i>T. megalodactyla</i>	3-5-0	8	?	Andronov (2002)
<i>T. minor</i>	3-6-0	9	1-2-3(1br)	Schulz (1981)
<i>T. magna</i>	3-5-0	8	1-2-3	Bradford & Wells (1983)
<i>T. angularis</i>	3-6-0	9	1-2-3(1br)	Schulz & Beckmann (1995)
<i>T. crenata</i>	3-6-0	9	1-2-3(1br)	Schulz & Beckmann (1995)
<i>T. inaequalis</i>	3-6-0	9	1-2-3(1w?)	Bradford-Grieve (2001)
<i>T. inflata</i>	3-5-0	8	?	Andronov (2002)
<i>T. lauta</i>	3-5-0	8	?	Andronov (2002)
<i>T. macrophthalmoida</i>	4-4-0	8	?	Andronov (2002)
<i>T. scaura</i>	3-5-0	8	1-2-3	Andronov (2002)
<i>T. tuberosa</i>	3-5-0	8	?	Andronov (2002)
<i>T. tumidula</i>	3-5-0	8	?	Andronov (2002)
<i>T. neptuni</i>	3-5-0	8	1-2-3	Cleve (1905); Andronov (2002)
<i>T. altera</i>	3-4-0	7	1-2-3	Grice & Hulsemann (1970)
<i>T. compacta</i>	3-5-0	8	0-1-3(1br)	Grice & Hulsemann (1970)
<i>T. paraincertus</i>	5-2-0	7	0-2-3	Grice & Hulsemann (1965)
<i>T. macrocephalon</i>	3-5-0	8	1-1-3(1br)	Grice & Hulsemann (1970)
<i>T. groenlandica</i>	3-5-0	8	?	Andronov (2002)

will continue to be invaluable.

Recent publications (Schulz & Beckmann 1995; Ferrari & Markhaseva 1996; Bradford-Grieve 2001) suggest variability within *Tharybis* in the kind of setae associated with the third praecoxal lobe of the syncoxa of the maxilliped (the single coxal lobe is the distal lobe of the syncoxa; the third praecoxal lobe is proximal to that lobe). One of three setae on *T. angularis*, *T. crenata*, *T. sagamiensis*, *T. minor*, *T. compacta*, and *T. macrophthalma* is brush-like rather than sclerotized, or on *T. inaequalis* otherwise sensory. Sensory setae are found in several positions on the syncoxa of the maxilliped of other taxa (Ohtsuka et al. 1998; Ferrari & Markhaseva 2000b,c; Markhaseva & Schnack-Schiel 2003), so that it is doubtful that this state will prove to be a synapomorphy for *Tharybis*.

Most *Tharybis* species have two terminal attenuations and a terminal, medial seta on the distal segment [exopod] of the female's fifth leg. *Tharybis macrophthalma*, *T. macrophthalmoida* and *T. fultoni* have two terminal attenuations, a terminal, medial seta, plus a lateral seta (or attenuation) at mid-length of the distal segment. *Tharybis macrocephalon* and *T. paraincertus* have an attenuation terminally, a medial seta, a lateral seta, and a lateral seta at mid-length of the distal segment. However, Andronov (2002) has observed *T. asymmetrica*, *T. macrodactyla*, *T. neptuni* and *T. scaura* dimorphic for the presence or not of a lateral

seta/attenuation, so it is doubtful that this state will prove to be a synapomorphy for *Tharybis*. At present, then, the distal vaulting of the first enditic lobe of maxilla 1 is the only synapomorphy which might be proposed for the genus.

### Acknowledgements

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### Literature Cited

- Andronov, V. N. 1976. Novye vidy roda *Tharybis* (Copepoda, Tharybidae) iz yugo-vostochnoi Atlantiki. [New species of the genus *Tharybis* (Copepoda, Tharybidae) from the south-east Atlantic] *Zoologicheskii Zhurnal* **55**: 1903-1905. (in Russian with extensive English summary)
- Andronov, V. N. 2002. Veslonogie rachki rodov *Diaixis* Sars, 1902, *Parundinella* Fleminger, 1957, *Undinella* i *Tharybis* Sars, 1902 (Copepoda: Calanoida). [The calanoid copepods (Crustacea) of the genera *Diaixis* Sars, 1902, *Parundinella* Fleminger, 1957, *Undinella* Sars 1900 and *Tharybis* Sars, 1902] *Arthropoda Selecta* **11**: 1-80. (in Russian with extensive English summary)

- Bradford, J. M. 1973. Revision of family and some generic definitions in the Phaennidae and Scolecithricidae (Copepoda: Calanoida). *N. Z. J. Mar. Freshw. Res.* **7**: 133–152.
- Bradford, J. M., L. Haakonssen & J. B. Jillett 1983. The marine fauna of New Zealand: pelagic calanoid copepods: families Euchaetidae, Phaennidae, Scolecithricidae, Diaixidae, and Tharybidae. *Mem. N. Z. Oceanogr. Inst.* **90**: 1–150.
- Bradford, J. M. & J. B. J. Wells 1983. New calanoid and harpacticoid Copepoda from beneath the Ross Ice Shelf, Antarctica. *Polar Biol.* **2**: 1–15.
- Bradford-Grieve, J. M. 2001. A new species of benthopelagic copepod of the genus *Tharybis* (Calanoida: Tharybidae) from the upper slope, north-eastern New Zealand. *N. Z. J. Mar. Freshw. Res.* **35**: 421–433.
- Cleve, P. T. 1905. The plankton of the South African seas. I. Copepoda. *Mar. Investigations S. Africa* **3**: 177–210.
- Ferrari, F. D. 1995. Six copepodid stages of *Ridgewayia klausruetzleri*, a new species of calanoid copepod (Ridgewayiidae) from the barrier reef in Belize, with comments on appendage development. *Proc. Biol. Soc. Wash.* **108**: 180–200.
- Ferrari, F. D. & A. Benforado 1998. Setation and setal groups on antenna 1 of *Ridgewayia klausruetzleri*, *Pleuromamma xiphias*, and *Pseudocalanus elongatus* (Crustacea: Copepoda: Calanoida) during the copepodid phase of their development. *Proc. Biol. Soc. Wash.* **111**: 209–221.
- Ferrari, F. D. & H.-E. Dahms 1998. Segmental homologies of the maxilliped of some copepods as inferred by comparing setal numbers during copepodid development. *J. Crust. Biol.* **18**: 298–307.
- Ferrari, F. D. & V. N. Ivanenko 2001. Interpreting segment homologies of the maxilliped of cyclopoid copepods by comparing stage-specific changes during development. *Org. Divers. Evol.* **1**: 113–131.
- Ferrari, F. D. & E. L. Markhaseva 1996. *Parkius karenwishnerae*, a new genus and species of calanoid copepod (Parkiidae, new family) from benthopelagic waters of the eastern tropical Pacific Ocean. *Proc. Biol. Soc. Wash.* **109**: 264–285.
- Ferrari, F. D. & E. L. Markhaseva 2000a. *Griceus buskeyi*, a new genus and species of calanoid copepod (Crustacea) from benthopelagic waters off Hawaii. *Proc. Biol. Soc. Wash.* **113**: 78–88.
- Ferrari, F. D. & E. L. Markhaseva 2000b. *Brachycalanus flemingeri* and *B. brodskyi*, two new calanoid copepods (Crustacea) from benthopelagic waters of the tropical Pacific. *Proc. Biol. Soc. Wash.* **113**: 1064–1078.
- Ferrari, F. D. & E. L. Markhaseva 2000c. *Grievella shanki*, a new genus and species of scolecitrichid calanoid copepod (Crustacea) from a hydrothermal vent along the southern East Pacific Rise. *Proc. Biol. Soc. Wash.* **113**: 1079–1088.
- Grice, G. D. & K. Hulsemann 1965. Abundance, vertical distribution and taxonomy of calanoid copepods at selected stations in the north-east Atlantic. *J. Zool., London* **146**: 213–262.
- Grice, G. D. & K. Hulsemann 1970. New species of bottom-living calanoid copepods collected in deep water by the DSRV Alvin. *Bull. Mus. Comp. Zool., Harvard University* **139**: 185–227.
- Huys, R. & G. A. Boxshall. 1991. *Copepod Evolution*. The Ray Society, Randon, 468 pp.
- Markhaseva, E. L. & S. B. Schnack-Schiel 2003. New and rare calanoid copepods from the Great Meteor Seamount, North Eastern Atlantic. *Ophelia* **57**: 107–123.
- Nishida, S. & S. Ohtsuka 1997. Ultrastructure of the mouthpart sensory setae in mesopelagic copepods of the family Scolecithricidae. *Plankton Biol. Ecol.* **44**: 81–90.
- Ohtsuka, S., I. Takeuchi & A. Tanimura 1998. *Xanthocalanus gracilis* and *Tharybis magna* (Copepoda: Calanoida) rediscovered from the Antarctic Ocean with baited traps. *J. Nat. Hist.* **32**: 785–804.
- Park, T. 1967. Two new species of calanoid copepods from the Strait of Georgia, British Columbia, Canada. *J. Fish. Res. Bd. Can.* **24**: 231–242.
- Sars, G. O. 1902. Copepoda Calanoida, Parts V & VI, Scolecithricidae, Stephidae, Tharybidae, Pseudocyclopiidae. *Account Crust. Norway* **4**: 49–72, pls. 33–48.
- Schulz, K. 1981. *Tharybis minor* sp. n. (Copepoda: Calanoida: Tharybidae) aus dem nordwestafrikanischen Auftriebsgebiet mit Anmerkungen zur Gattung *Tharybis* Sars. *Mitteil. Hamburg. Zoolog. Mus. Inst.* **78**: 169–177. (in German with English summary)
- Schulz, K. & W. Beckmann 1995. New benthopelagic tharybids (Copepoda: Calanoida) from the deep North Atlantic. *Sarsia* **80**: 199–211.
- Tanaka, O. 1960. The pelagic copepods of the Izu region, Middle Japan. Systematic account VI. Families Phaennidae and Tharybidae. *Pub. Seto Mar. Biol. Lab.* **8**: 85–135.
- Tupitsky, V. V. 1982. Novyi glubokovodnyi vid roda *Xanthocalanus* (Copepoda, Calanoida) iz Grenlandskogo morya. [A new deep-water species of the genus *Xanthocalanus* (Copepoda: Calanoida) from the Greenland Sea]. *Zoolog. Zhur.* **61**: 297–299. (in Russian with English summary)