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Extraordinary New Subterranean Isopods (Peracarida: Crustacea) from the Kimberley Region, Western Australia

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ABSTRACT. A new genus and two new species of fresh water isopods from ground waters of the Kimberley region of West Australia are described. This new genus cannot be immediately assigned to an isopod suborder or family because its unique combination of characters encompass many plesiomorphies, as well as synapomorphies with the 'Flabellifera' *sensu lato*. These features include free pleonites that are subequal except for an enlarged fifth pleonite, broad natatory pleopods, genital pores on medial extensions of the coxae, five pairs of oostegites, true coxal plates, an antennal protopod of three articles, and a rudimentary second flagellum on the antennula. One of the new species, well represented in one sample, is iteroparous and breeds continuously during the winter months. Because the type localities are from limestone fossil reefs not exposed to the marine environment since the Devonian period, these isopods may be remnants of an ancient freshwater stock. Name changes of some setal types are proposed.

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During 1988, one of us (WFP) explored fresh water habitats in parts of the Kimberley Region of Western Australia, and made several incidental collections of small crustaceans from a pool in a limestone cave and in several springs issuing from limestone. This material contained odd, swimming isopods that, in their natural habitat, looked like syncarid crustaceans. Preliminary inspection suggested that these animals were related to phreatoicidan isopods. Subsequent study, however, has revealed that these specimens represent a novel taxon that cannot be comfortably classified in any suborder of the Isopoda. This paper provides a detailed description

of two species of the new taxon, a preliminary evaluation of its morphological features, and a discussion of its possible affinities and biogeography. The following description of the genus provides features of potential phylogenetic significance. A diagnosis and phylogenetic definition, however, will be provided with a natural classification estimated using cladistic techniques (research in progress). The combination of character states possessed by this new taxon may have a significant impact on interpretations of the phyletic relationships of isopods, recently evaluated using cladistic techniques by Brusca & Wilson (1991). Because this research is still in

progress, the precise classification of this new taxon is left undecided. Nevertheless, this taxon may be distinct from all other isopods at the subordinal level.

Methods and Terminology

Field collections were made using a hand sieve in three localities (K1, K2, K5) and a dip net in one (K10). Temperature, pH and conductivity (in s cm^{-1} at 25°C) were recorded from each site. The field pH meter was not functioning well and consequently the recorded pH must be regarded as only approximate. Ellaway *et al.* (1990) describe the water chemistry of the region from which the samples were obtained. The material was fixed in 8% formalin buffered with excess NaHCO_3 .

The following descriptions use the same descriptive methods, terminology, and format as described in Wilson (1989), except for the setal forms discussed below. In the phylogenetic discussion, "higher isopods" refers to the non-basally derived groups of the Isopoda: Oniscidea (including *Celoboriscidae*), Valvifera, Anthracidea, Eriopodidae,

setal decorations. We agree with Oshel & Steele (1988) who argue that the use of "spine" to describe setae confounds the ontogenetic and phylogenetic origins of both structures. Herein "spine" will be used *only* for simple epidermal outgrowths. Poore (1991) gives a similar opinion.

Taxonomy

Tainisopus n.gen.

Type species. *Tainisopus fontinalis* n.sp.

Etymology. *Tainisopus* refers to the flattened, elongate and flexible body of this new isopod genus. The name is derived from the Greek word *tainia* ('ribbon' or 'band'), and the Greek combining forms *iso* ('like'), and *pus* ('foot'), which together can be construed to mean 'ribbon isopod'.

Description. Isopoda with elongate, dorsoventrally flattened body having substantial lateral as well as

setules distally) on 2 distal articles; dorsal condyle short, rounded and curved.

All pereopods with coxal plates (as defined by Brusca & Wilson, 1991); coxal plates of pereopods I-III completely or partially fused to produced and flattened lateral margins of body; coxal plates of pereopods IV-VII freely articulated with body dorsally along broad insertions. Coxal plate of pereopod VII of male covering most of ventral surface of pereonite 7, with penes attaching to posteromedial projections of coxa. Pereopods I-III subchelate and prehensile, with robust toothed sensillate setae on ventral margins of propodus (PI), carpus (PI-III), and merus (PI); coxae of pereopods I-III fused to lateral margins of body. Pereopods IV-VII with fewer robust sensillate setae on ventral margins and more walking leg-like. Fully-functional oostegites on coxae of pereopods I-V.

Pleopods I-V similar in shape. Pleopodal protopods broad with wide lateral margins bearing elongate sensillate setae, and medial projections bearing several curved setulate setae. Pleopodal exopods broad, rounded, with 2 large distinct articles, with many marginal plumose setae. Exopods of pleopod V covering anus. Endopod of pleopod I (both sexes) small, narrow, shorter than exopod, bluntly pointed or rounded distally, with medial setae. Endopod of male pleopod II elongate, longer than exopod, broad at base, narrowing to bluntly pointed tip having cuticular combs on medial margin. Endopods of pleopods III-V in male and of pleopods II-V in female shorter than exopod, completely lacking setae, trilobed, with central lobe thickest.

Uropods only slightly flattened, with broad elongate protopod having robust sensillate setae on lateral and medial margins and distally rounded rami. Endopod larger than exopod, both furnished with robust sensillate setae.

Remarks. *Tainisopus* differs from all other described isopods as currently defined in having the following characters. The antennula bears a rudimentary secondary flagellum, and the antenna has a basal article on the protopod, making it three-articled. Both of the features are found in other isopods (*Flabellifera sensu stricto* and *Asellota*, respectively), but no other isopod has both together. The penes are born on triangular medial projections of coxa of pereopod VII. This unusual feature may not occur in other isopods, although it could be related to the penial forms in the *Asellota* (Just & Poore, 1992). The flabelliferan-like features include broad natatory pleopods, a pereopodal tagmosis of three anterior grasping limbs and four posterior ambulatory limbs (see Brusca & Wilson, 1991), true coxal plates with the three anterior coxae fused to body. However, because these are generalised features found in many families, they do not advise us on the correct classification of *Tainisopus*. The detailed form of the pleopodal endopods is also unusual and not precisely typical of

any other isopod group.

Tainisopus fontinalis n.sp.

Figs 1-8, 13, 14

Etymology. *Fontinalis*, meaning 'from a spring' (Latin), refers to the habitat where this species was collected.

Type material. HOLOTYPE, large preparatory female, body length (bl) 8.2 mm, not dissected, left uropod missing one ramus. Australian Museum catalogue number (AM) P40752.

PARATYPES. Illustrated and/or dissected specimens: copulatory male, bl 6.7 mm (P40753); copulatory male, bl 6.1 mm (P40754); copulatory male, bl 7.4 mm (P40755); brooding female, bl 7.0 mm (P40756); preparatory female, bl 6.0 mm (P40757); brooding female, bl 6.5 mm (P40758); 29 specimens, AM P40759, 5 specimens AM P38513. PARATYPE female, deposited at Northern Territory Museum, Darwin (from AM P38513). PARATYPE female deposited at Museum of Victoria, Melbourne, registration number J23755 (from AM P40759).

Type locality. WFP Station K1 (see Fig.14). Small unnamed spring, north-east side of Oscar Range, Kimberley Region, West Australia. Collected by WFP, 30 June 1988. 4.3 km north-west of Elimberrie Spring, 17°39'S 125°01'E (Leopold Downs, 1:100,000 series, 136477). A small spring flowing as a narrow trickle into a small, slow flowing stream up to about 1 m wide. Slope about 2°. Water depth 1-2 cm, clear, pH about 7.8, conductivity 560, water temp. 26°C (air temp. 30°C). Filamentous green algae and roots. Substrate limestone boulders on mud and silt. In small gully with rain forest trees and shrubs. Some cattle damage. [Ellaway *et al.* (1990) give the following data for 9 May 1988 for what is assumed to be the same spring (their station 5):- temp. 27°C (air 31.5°C), pH 7.27, conductivity 460].

Habitat. Washed from algae and/or roots at spring head.

Distribution. Known only from type locality, an unnamed spring near the northern end of the Oscar Ranges.

Diagnosis. Pleotelson rounded distally with distinct gap between distal 2 major sensillate setae. Endopod of female pleopod I length 0.57 exopod length. Outer lobes of maxilla with 7 comb setae (each seta with row of regular flattened denticles).

Description. Body lengths as follows: brooding females 6.5-7.0 mm; preparatory females 5.7-8.3 mm, early preparatory female 5.1 mm; juvenile females 46.0-65.5 mm; copulatory males 6.1-7.4 mm; precopulatory male 4.4 mm; juvenile males 47.0-54.5 mm; manca 33.5-35.5 mm.

Head (Fig.2C,E) freely articulating with pereonite 1, with presumed (blind) eyelobes lateral to insertion of antennae. Length 0.82 width; head dorsal surface length 1.5-1.7 first pereonite medial length. Anterior margin medially concave, with anterolateral flattened

projections covering insertions of antennae. Dorsal surface oval, covered with scattered fine setae, demarcated from lateral surface by thin cuticular ridge. Antennular insertions closely spaced medially. Interantennular ridge narrow, terminating ventrally in rounded frontal projection vertically adjacent to clypeus. Clypeus rounded, nearly as broad as space including antennal insertions, with narrow socket for mandibular articulation. Labrum distally rounded, setose on anterior and ventral sides, only slightly asymmetrical.

Pereon (Fig.1). Total body length 4.8-6.1 width measured at pereonite 3. Medial length 0.41 body length. Pereonite 1 laterally longer than subequal pereonites 2-7. Pereonite 7 shorter than proceeding segments. Dorsal surfaces of each segment with 2 transverse rows of simple setae, just behind anterior

segment and at posterior margin; tiny hair-like setae most dense at lateral margins. Dorsal surfaces of each segment with 1 or 2 thin transverse cuticular ridges.

Pleon (Figs 1,3A,D). All segments articulated flexibly, having ability to rotate in both vertical and transverse axes; pleotelson especially free in transverse axis with possible rotations approaching 90° driven by strong muscles in pleonite 5. Medial length 0.43 body length. Segments increasing in medial length posteriorly; pleonites 1-5 medial length - pleon length ratios: 0.11, 0.11, 0.13, 0.13, 0.22. Pleotelson medial length 0.39 pleon length; length 0.97 width. Dorsal setal distributions on free pleonites similar to that of pereon, with 2 rows of larger simple setae on each segment. Pleotelson with scattered dorsal simple setae, posterolateral margins with 6 larger, more robust sensillate setae and 16 small simple (nonsensillate)

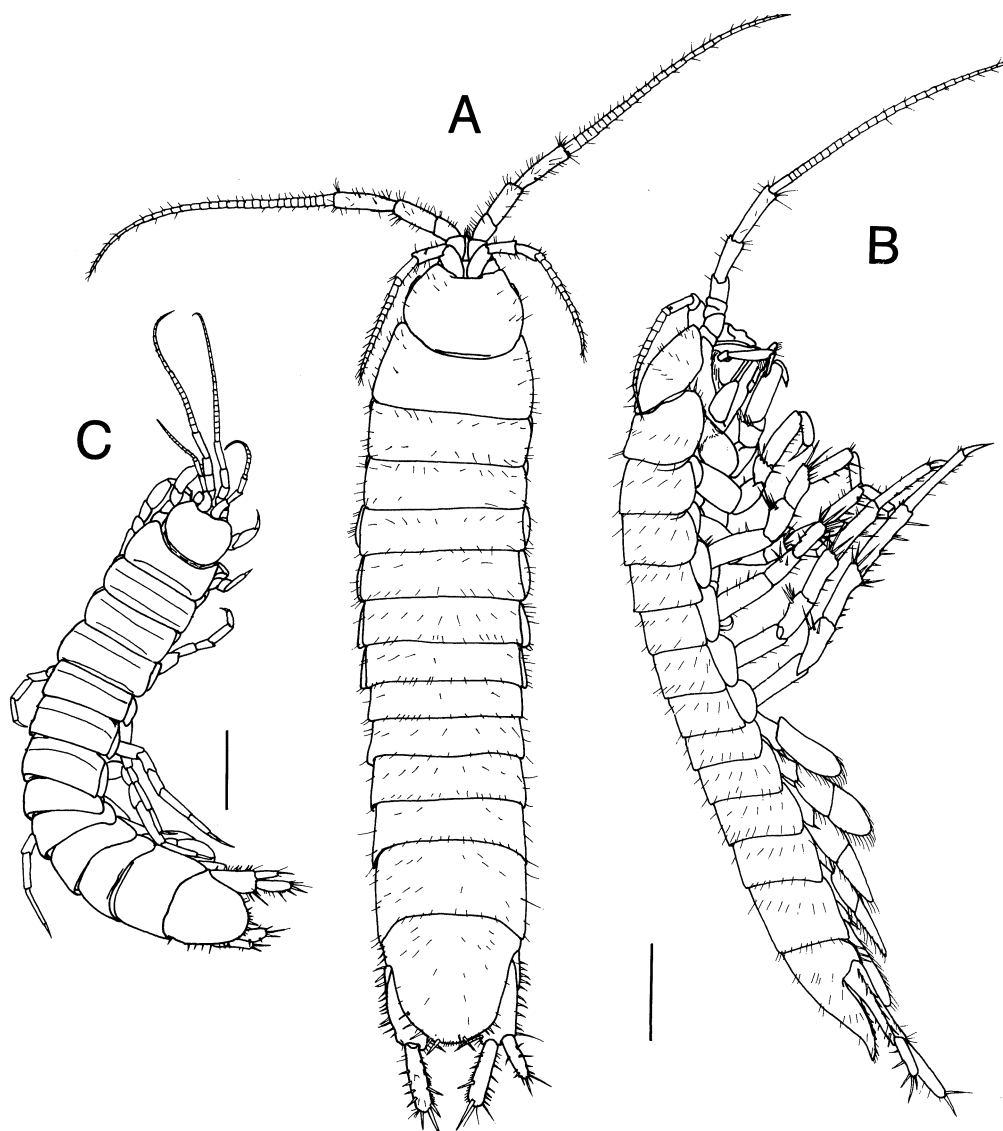


Fig.1. *Tainisopus fontinalis* n.gen., n.sp. A-B, holotype preparatory female, Australian Museum catalogue number (AM) P40752, dorsal and lateral views. C, paratype copulatory male, AM P40755, dorsal view. Scale bars = 1 mm.

tooth-like setae: 2 largest terminal sensillate setae separated by distinct space occupied by only small simple tooth-like setae. Pleon lacking dorsal transverse ridges.

Antennula (Figs 1,2A-C) not sexually dimorphic, curving laterally and posteriorly in most specimens. Length 0.22-0.24 body length, with 16-18 articles in adults. Article 1 strongly curved laterally, with few simple setae, and with cuticular scales on medial margin. Articles 2-3 shorter than article 1, decreasing in length distally. Article 3 lacking penicillate setae. Well-defined remnant of second flagellum on anteromedial margin of article 3, with several large setae and at least 1 penicillate seta. Basal flagellar article 4 with penicillate setae, shorter than either protopodal

article 3 or main flagellar article 5. More distal articles having simple setae and aesthetascs on distal margins. No more than 2 aesthetascs on each article with most having only 1, proximal and distal articles lacking aesthetascs. Aesthetascs consisting of narrow proximal peduncle, enlarged thin distal part, and distal tip with tiny pore.

Antenna (Figs 1,2C-D). Length 0.57 body length, with 31-38 articles in adults. Articles 1-3 subequal, with few simple setae, but with many cuticular combs and scales. Article 3 with tiny circular scale surrounded by articular membrane, adjacent to papillose structure. Article 4-6 longer than basal articles, increasing in length distally. Flagellum length 0.6 total antenna length.

Mandibles (Fig.4). Body of mandible robust and

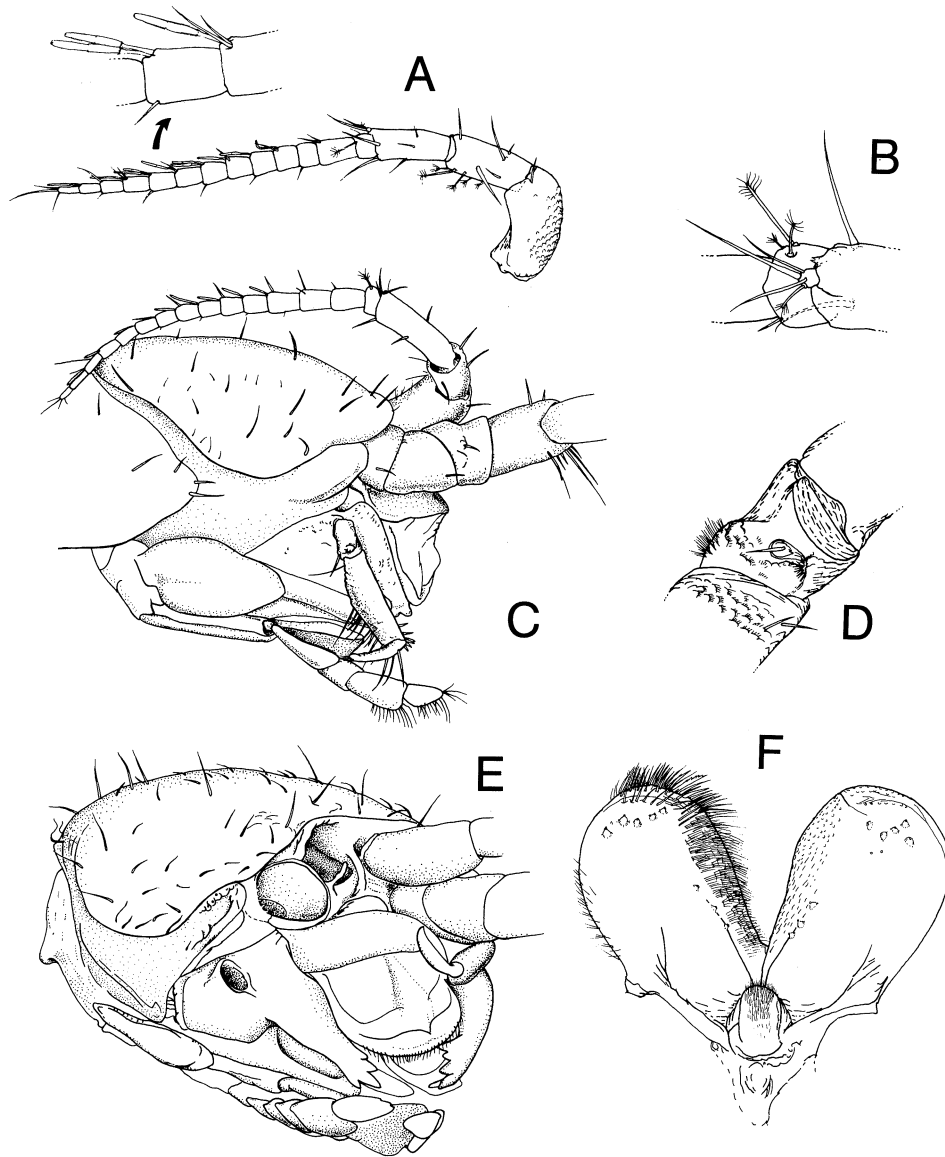


Fig.2. *Tainisopus fontinalis* n.gen., n.sp. A, left antennula, dorsal view. B, left antennula, enlargement of accessory flagellum on article 3. C, lateral view of intact head. D, antenna, enlargement of article 3 showing reduced antennal scale. E, frontal oblique view of head, antennula, antenna and mandibular palp removed. F, paragnaths, ventral view, setae omitted on left side. A-B, D-E from copulatory male, AM P40753; C from holotype female, AM P40752; F from paratype female, AM P40757.

broad; articular axis (defined by line between dorsal condyle and posterior extension of mandible) at approximately right angles to incisor process. Incisor processes with 4 teeth, with second tooth from ventral side largest and most projecting; 2 dorsal teeth shortest and more rounded. Left lacinia robust, somewhat flattened and curved, with 3 teeth. Right lacinia resembling modified and fused members of spine row but with broad rounded base and 4 denticulate terminal subspines curling in posteromedial direction. Spine row with 6 denticulate members on right side and 7 on left; posteriormost spine smaller than more anterior members and on left side distinctly set apart from more distal row members. Molar process short, broad, distal margin on

dorsal and posterior with many small denticles and many fine setae; distal triturating surface flat, irregularly granular or denticulate. Dorsal condyle rounded, hook-like, articulating with head in rounded socket on lateral edge of clypeus. Palp approximately same length as body of mandible; articles 2-3 with many denticulate or setulate setae on distal ends and cuticular combs covering opposing surfaces; article 3 only slightly curved, projecting laterally at right angle from article 2.

Maxillula (Fig.5A,B). Outer lobe with 12 robust setae; 5 medial setae with strong posteromedial directed teeth. Inner lobe with 4 large densely setulate setae and 2 small simple setae. Inner and outer margins of both

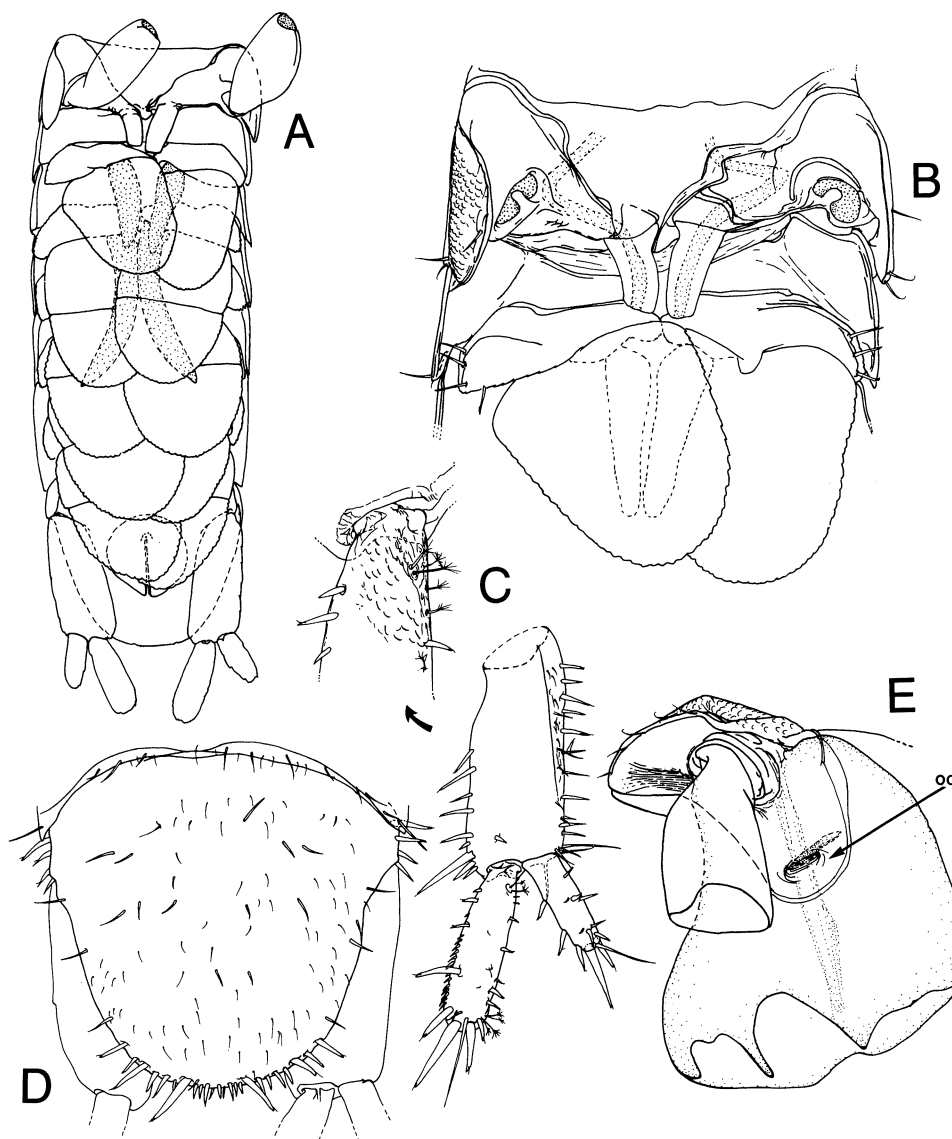


Fig.3. *Tainisopus fontinalis* n.gen., n.sp. A, ventral view of posterior pereon, pleonites and pleotelson showing form of penile papillae and pleopod arrangement. B, enlargement of genital area from A. C, right uropod and enlargement of basal area of uropodal protopod (upper left), dorsal view, drawn *in situ*. D, pleotelson, dorsal view, detail of uropods omitted. E, posteroventral oblique view of pereonite 5 and oostegite, brooding female, medial part of coxa seen through oostegite, showing medial position of oopore (indicated by arrow and oo), pereopod V truncated. A-B from paratype male, AM P40754; C-D from holotype female, AM P40752; E from paratype brooding female, AM P40756.

lobes with fine hair-like setae.

Maxilla (Fig.5C). Lobes short and robust. Inner lobe distal and medial surface densely covered with setulate and spinulate setae: 3 large medial setulate setae; 13 outer more distal setae in 2 rows (5 in ventral row, 8 in dorsal row) with both spinules and setules.

Maxilliped (Fig.5D,E). Basis elongate and narrow, width at either base of palp or at endite 0.2 length. Endite with 4 coupling hooks; distal tip with 9-11 robust radially plumose setae, 3-4 subdistal smooth setae, and 1 squat lightly setulate seta on medial corner. Dorsal longitudinal ridge of basal endite with 6 setulate setae, and with extremely fine, hair-like setae along proximal section, especially below palp. Palp wider than endite, palp article 3 width 1.3 basis width. Palp articles 3 and 4 with 18-27 and 14-24 simple setae, respectively. Palp article 5 with 17-25 simple setae, single most distal seta

with single row of setules. Epipod broad, rounded, width 0.78 length, with cuticular combs on ventroproximal surface and on lateral margin; distomedial margin with extremely fine, hair-like setae.

Pereopod I (Fig.6A). Length 0.22-0.32 body length, not sexually dimorphic, distinctly subchelate with major hinge between propodus and dactylus. Dactylus distal tip with 1 primary claw and tiny denticulate accessory claw, separated by elongate, stiff sensillum and simple seta. Propodus robust and broad, much longer than carpus, with 9-10 robust bidenticulate sensillate setae. Carpus short, triangular with 3-4 robust bidenticulate sensillate setae. Merus short, trapezoidal with 3 robust bidenticulate sensillate setae on ventral side, and 6 elongate bisetulate setae on dorsal side. Basis approximately as long as ischium, merus, and carpus combined, with lateral flange and elongate

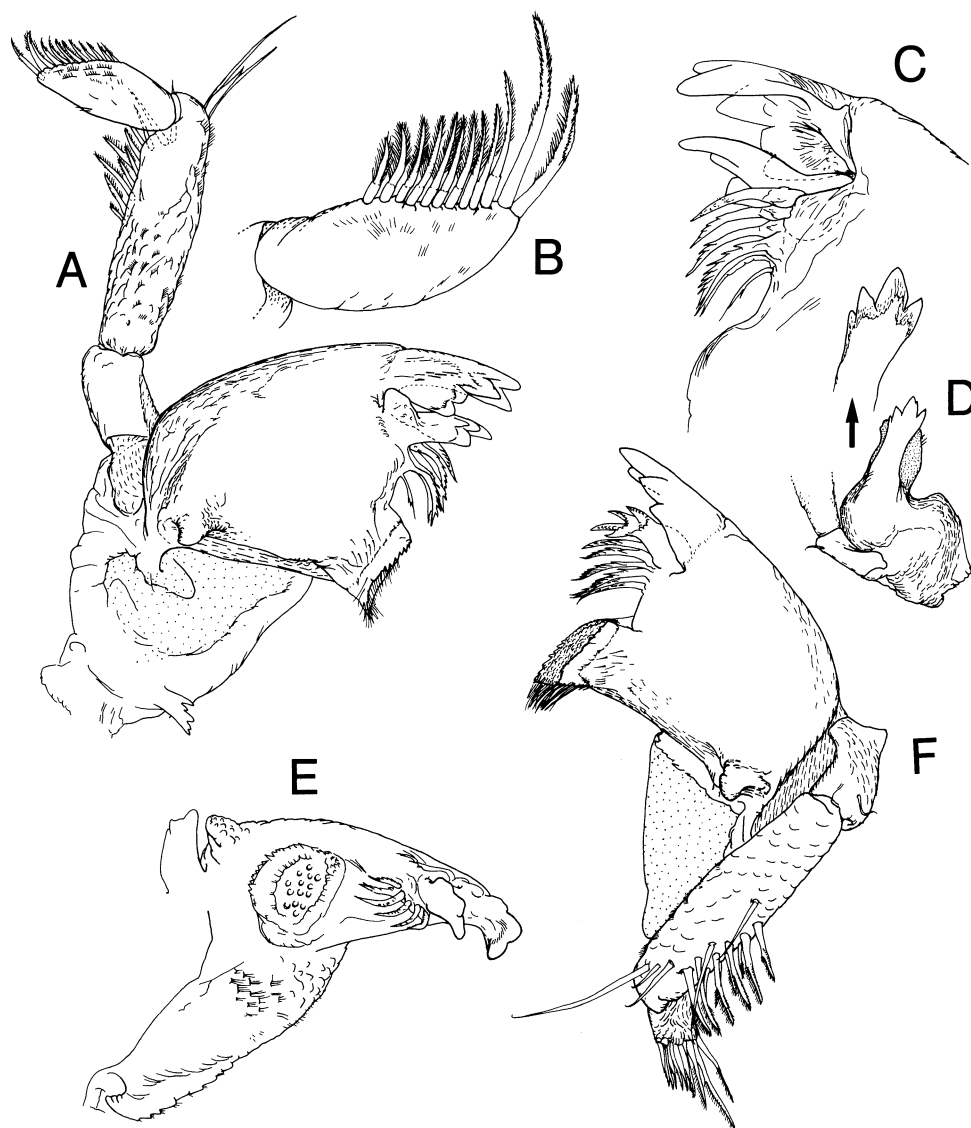


Fig.4. *Tainisopus fontinalis* n.gen., n.sp. Mandibles from paratype female, AM P40757. A, left mandible, dorsal view. B, right palp article 3, anterior view. C, left incisor process, lacinia mobilis and spine row, ventral view. D, right mandible, anterior view with enlargement of incisor process. E, left mandible, medial view, palp omitted. F, right mandible, dorsal view.

depression on anterior face for retraction of distal parts of limb. Coxa completely fused to pereonite 1 in both sexes.

Pereopods II-III (Fig.6B-D). Lengths 0.28-0.35, 0.29-0.36 body length, respectively. Not sexually dimorphic, moderately subchelate with major hinge between carpus and propodus. Dactylar distal tips each with one primary claw and tiny denticulate accessory claw, separated by elongate, stiff sensillum and simple seta; subdistal medial side of dactyli with 3 sensilla. Propodus elongate but shorter than carpus, with 2-4 small denticulate sensillate setae on ventral margin. Carpus robust and elongate, with approximately 16 robust bidenticulate sensillate setae on ventral margin. Merus with dorsal triangular projection bearing row of 4-5 elongate setulate setae. Basis with lateral flange and elongate depression on anterior face for retraction of distal parts of limb. Coxa of pereopod II completely fused to tergite 2; coxa of pereopod III ventrally fused to tergite 3, dorsally with distinct line of articulation,

approximately half width of tergite.

Pereopod IV (Fig.7A). Ambulatory, not prehensile or subchelate, length 0.27-0.36 body length. Dactylar distal tip with primary claw, small denticulate accessory claw and single thick sensillum; subdistal medial side of dactylus with 3 sensilla. Carpus and propodus elongate, not robust, with 3-4 and 9 sensillate setae on medial margins, respectively. Ischium and merus with group of elongate sensillate setae on distodorsal projections. Basis with lateral-facing groove for retraction of ischium and merus. Coxa nearly as broad as tergite, with free tergal articulation and distinct lateral projection or plate.

Pereopod V-VII (Fig.7B-D). Broadly similar to pereopod VI, but increasing in length posteriorly: lengths 0.29-0.36, 0.033-0.43, 0.37-0.49 body length, respectively. Dactylar distal tip with primary claw, small denticulate accessory claw and single thick sensillum; subdistal medial side of dactyli with 3 sensilla. Carpi and propodi elongate, not robust, with 3-8 and 12-14 sensillate setae on medial margins, respectively.

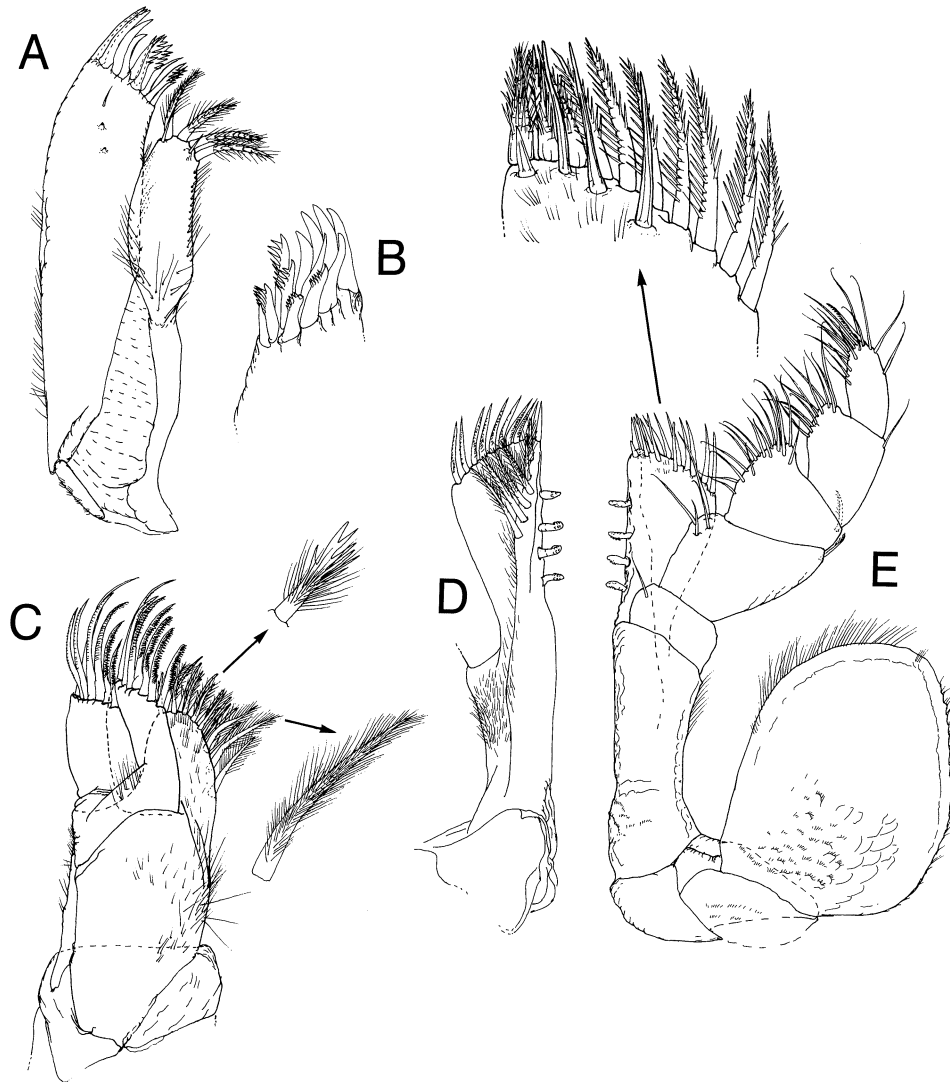


Fig.5. *Tainisopus fontinalis* n.gen., n.sp. Mouthparts from paratype female, AM P40757. A-B, right maxillula, dorsal view of whole limb and enlarged medial view of outer lobe. C, right maxilla with enlargements of setae from inner lobe. D-E, left maxilliped, dorsal view of endite and ventral view.

Ischium and merus with group of elongate sensillate setae on distodorsal projections. Basis with shallow posterior-facing groove for partial retraction of ischium and merus. Coxa as broad as tergite, with free tergal articulation and with distinct lateral projection or plate.

Pleopods (Fig.8). All similar in size and shape, covering entire ventral surface of pleotelson when retracted. Length/body length ratios: 0.10-0.12, 0.13-0.15, 0.14-0.16, 0.15-0.17, 0.13-0.15, respectively, females with proportionately longer pleopods. Protopods of pleopods I-V with broad insertions, expanded lateral plates bearing 3-6, 9-10, 9-13, 12-14, 13-18 elongate distally setulate sensillate setae, respectively. Protopods with medial projections bearing 2-3 robust setae with distal hooked tip and row of setules, overlapping with counterparts on

opposite side (coupling setae). Exopods broad, covering smaller endopods, with distinct cuticular scales or sculpturing on anterior (or ventral) surface. Exopods of pleopods I-V with fringe of 31-40, 36-50, 40-60, 43-60, 40-56 biplumose setae, respectively; proximolaterally inserted setae shorter and with fewer setules than distally and medially inserted setae. Exopod of pleopod I of both sexes lacking division between proximal and distal segments; suture line only on anterior (or ventral) face in pleopods II-V. All exopods with medial ridge following medial margin approximately two thirds length so that cross section of exopod resembling flattened wedge with deepest part medially. Endopods of pleopods I-II various depending on sex. Endopod of male pleopod I simple, flattened, narrow, elongate, length 0.71 exopod length, widest just distal to narrow insertion, with single

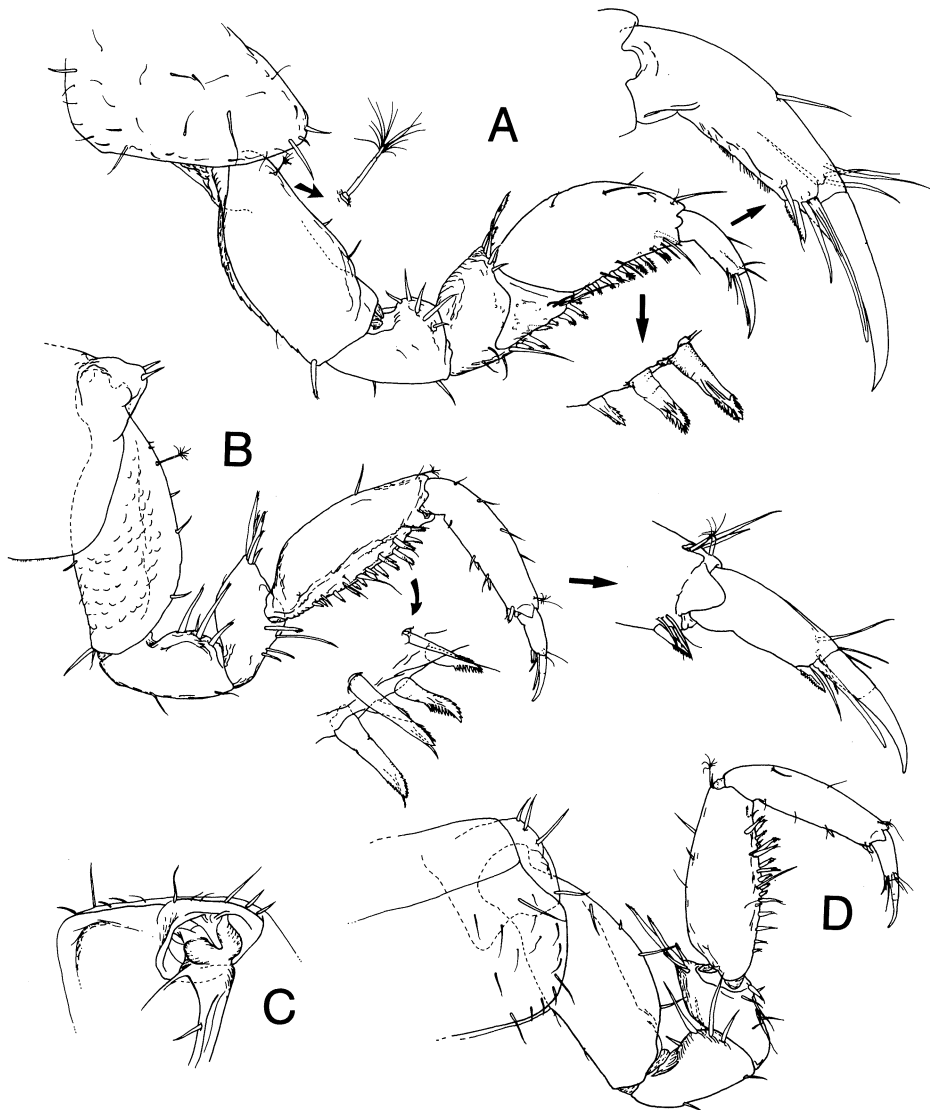


Fig.6. *Tainisopus fontinalis* n.gen., n.sp. Right pereopods I-III from paratype male, AM P40753. A, pereopod I, with enlargements of dactylus and proximal end of setal row on propodus. B, pereopod II, with enlargements of dactylus and distal end of setal row on carpus. C-D, ventrolateral view of coxa of pereopod III and lateral view of pereopod III.

distal biplumose seta and cuticular hairs on medial and distolateral margin. Endopod of female pleopod I similar with single distal plumose seta, but shorter, length 0.59 exopod length. Endopod of male pleopod II elongate, length subequal to exopod length, medioventral margin of distal tip with denticulate ridge and distomedial margin with minute cuticular hairs. Male endopods of pleopods III-V and female endopods of pleopods II-V similar: inserting approximately midway between exopodal insertion and medial margin, expanding into 3 distinct lamellae approximately 0.4-0.6 length of exopod; dorsal and ventral lamellae simple and flat; middle lamella thicker, folded into roughly transverse curved ridges, highest density of folding proximally.

Uropods (Figs 1,3A,C). Length 0.41-0.45 pleon medial length. Protopod longer than broad, approximately wedge shaped in cross-section with deepest part on

lateral side, sensillate setae on both medial and lateral margins. Exopod shorter than endopod, length 0.48 protopod length, with sensillate setae distally and on margins. Endopod approximately oval in cross section, length 0.78 protopod length, with several different setal types: medial margin with proximal and distal groups of penicillate setae, all margins with sensillate setae becoming large distally, medial margin with row of 8-15 small tooth-like simple setae; distal tip with thin elongate simple setae.

Remarks. Much of the variation in the proportional lengths of various body parts is caused by variation in the body length. Compared to some specimens, the holotype female is axially compressed. If a length-width ratio of another individual is multiplied by the holotype's width, its length could be near 10 mm, rather than 8.2 mm. This disparity suggests that both the width

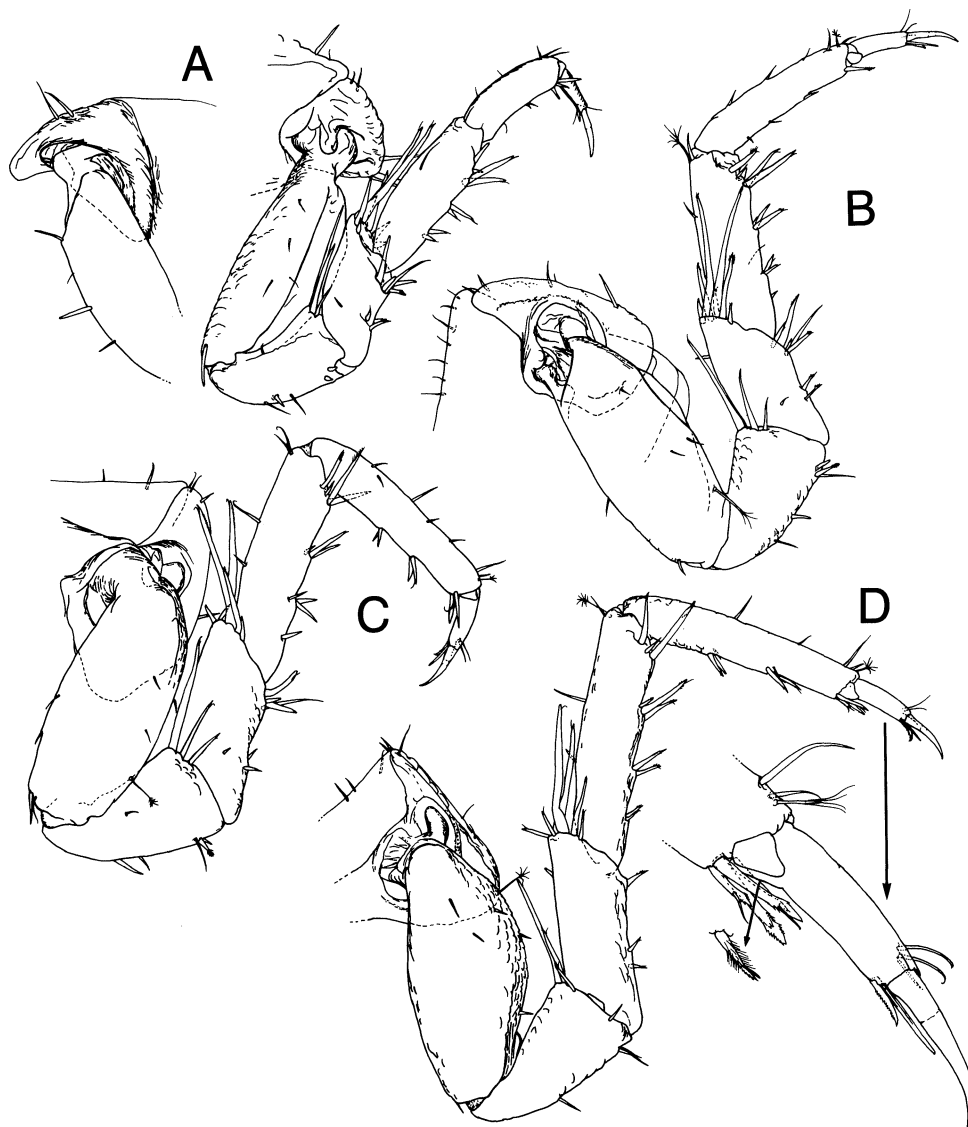


Fig.7. *Tainisopus fontinalis* n.gen., n.sp. A-D, right pereopods IV-VII, in lateral view but rotated anteriorly, from paratype male, AM P40753. A, pereopod VI including anterior view of coxa. D, pereopod VII with enlargement of dactylus.

and the length contain significant individual or preservation-dependent variation. Consequently, ratios using body length cannot be diagnostic. Variation in the body segments appears to be a function of the relative compression or expansion of both the pereon and pleon, which may be a function of preservation. The holotype was chosen because it seemed the most undamaged by preservation. Despite this apparent variation due to preservation or other sources, the lengths of these specimens compared to their developmental states show consistent patterns (see "Population Biology" below).

***Tainisopus napierensis* n.sp.**

Figs 9-12

Etymology. *Tainisopus napierensis* refers to the Napier Range where this species was collected.

Type material. HOLOTYPE. Large preparatory female, body length 8.35 mm, appendages dissected off right side after intact specimen illustrations were made. AM P40760. No other specimens available.

Type locality. WFP Station K10 (see Fig.14). Outer pool of Napier Downs Cave (= Old Napier Cave or local name Lake Cave), Napier Ranges, Kimberley Region, West Australia. Collected by WFP, 3 July 1988, 17°14'S 124°38'E (Lennard, 1:100,000 series, 745945). Flood prone, still pool in outer part of cave with some roots. Water depth up to 1 m, clear, pH about 7.66, conductivity 260, water temp. 20°C. Substrate limestone rock, some boulders with gravel, sand, mud and silt. Attyiid shrimps common. [Ellaway *et al.* (1990) give the following data for 9 May 1988 for what is assumed to be the same pool:- temp. 26.5°C (air 31.5°C), pH 7.93, conductivity 273].

Habitat. The specimen was caught with a net in the pool where it was swimming with attyiid shrimps.

Distribution. Known only from the type locality.

Diagnosis. Pleotelson obtusely pointed distally without large gap between distal two major sensillate setae. Endopod of female pleopod I length 0.28 exopod length. Outer lobes of maxilla with 9 comb setae.

Description of holotype female, differences from *T. fontinalis*. *Body features* (Figs 9, 11C). Body

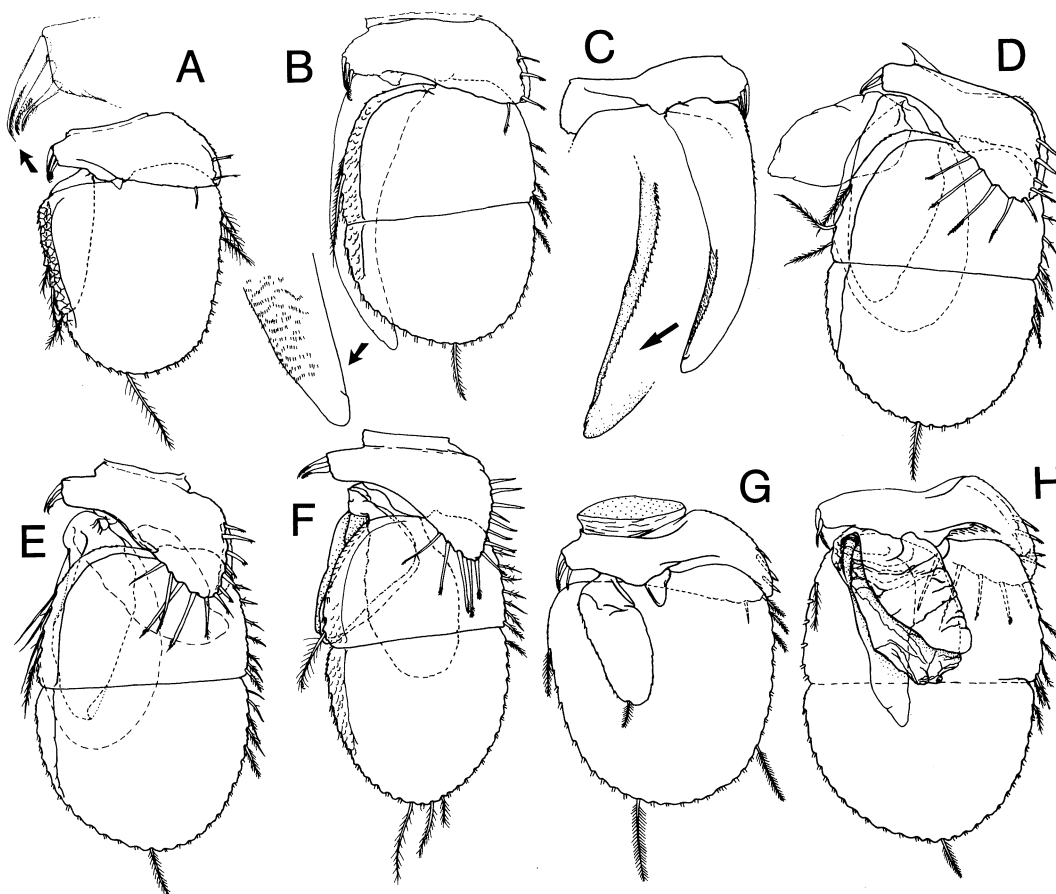


Fig.8. *Tainisopus fontinalis* n.gen., n.sp. A-F, left pleopods I-V from paratype male, AM P40753. A, pleopod I with enlargement of medial coupling setae. B, pleopod II, with enlargement of endopod distal tip, ventral view. C, endopod of pleopod II, with enlargement of distal tip, dorsal view. G-H, left pleopods I-II, dorsal view, from brooding female, AM P40758.

length 5.2 width measured at pereonite 3. Head length 0.85 width. Pereon medial length 0.43 body length. Pleon medial length 0.45 body length. Pleonites 1-5 medial length - pleon length ratios: 0.10, 0.10, 0.14, 0.12, 0.19. Pleotelson medial length 0.36 pleon length; pleotelson length 1.03 width. Pleotelson tip with 7 large sensillate setae and 13 small nonsensillate setae (using bilateral symmetry as a guide, the odd numbers suggest that an average specimen of same size may have 8 large and 12 small, or 6 large and 14 small setae).

Antennula (Fig.9) Length 0.25 body length, with 18-19 articles.

Antenna (Fig.9). Length 0.55 body length, with 36-38 articles. Flagellum length 0.57 total antenna length.

Mandibles. Spine row with 5 denticulate members on right side, 6 on left.

Maxilla (Fig.10A). Inner lobe with 3 large medial radially setulate setae; 18 more distal setae in 2 rows (7 in ventral row, 11 in dorsal row) with both spinules and radially arranged setules.

Maxilliped (Fig.10B). Basis width at either base of palp or at endite 0.22 length. Endite distal tip with 13 robust radially plumose setae, 4 subdistal smooth setae, and 1 squat lightly setulate seta on medial corner. Dorsal longitudinal ridge of basal endite with 5 radially setulate setae. Palp articles 3-5 with 44, 34, 25 medial simple setae, respectively. Epipod width 0.81 length.

Pereopods (Figs 9B,11A). Propodal and carpal

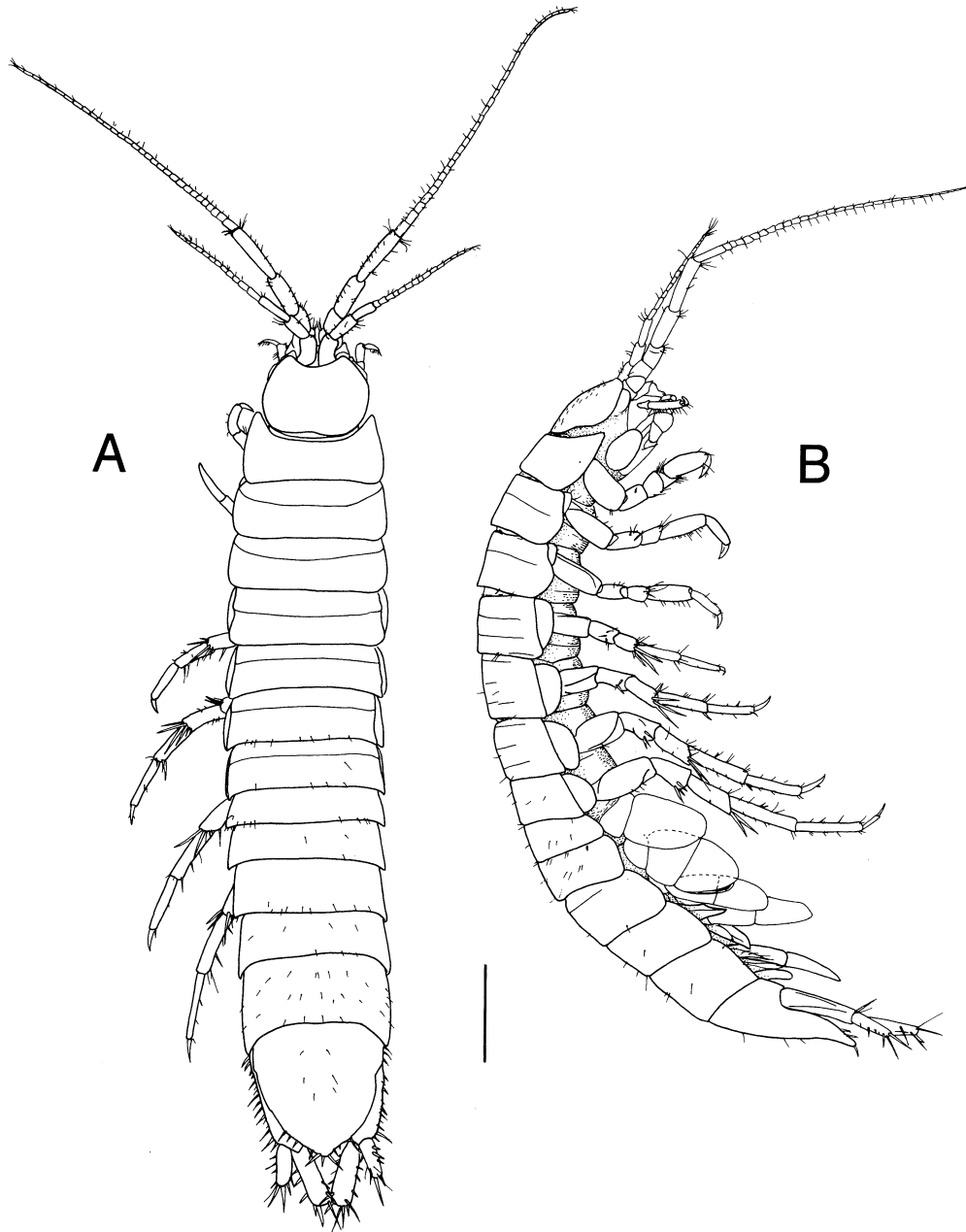


Fig.9. *Tainisopus napierensis* n.sp. Holotype, AM P40760. A-B, dorsal and lateral views. Scale bar = 1 mm.

ventral margins of pereopod I with 11 and 4 robust bidenticulate sensillate setae, respectively. Carpus of pereopods II-VII with 18, 18, 13, 15, 17, 16 robust bidenticulate sensillate setae on ventral margin, respectively.

Pleopods (Fig.12). Flattened lateral plate of protopods I-V with 6, 11, 11, 14, 18 distally setulate sensillate setae, respectively. Exopods of pleopods I-V with 41, 50, 59, 64, 59 fringing biplumose setae, respectively.

Uropod (Fig.11B). Length 0.18 body length; length 0.40 medial pleon length. Exopod length 0.44 protopod length, with sensillate setae distally and on margins. Endopod length 0.80 protopod length; distomedial margin with 11 small tooth-like simple setae.

Remarks. *Tainisopus napierensis* is imperfectly

described owing to the availability of only one specimen, the holotype. Although it is not described as fully as *T. fontinalis*, the holotype was fully dissected on one side and comparisons were made between the two species. We feel justified in erecting this new species because the features that differ between the two species are constant in *T. fontinalis*, indicating that these features are also likely to be relatively constant in *T. napierensis*. The species level distinctness of these two forms, however, should be considered a hypothesis to be tested by the recovery of additional material of both species.

Tainisopus napierensis is most easily identified by its subangular pleotelson tip with no obvious gap between the large terminal sensillate setae. Because the pleotelson form is reasonably constant in *T. fontinalis*, this species should also be consistent for this feature,

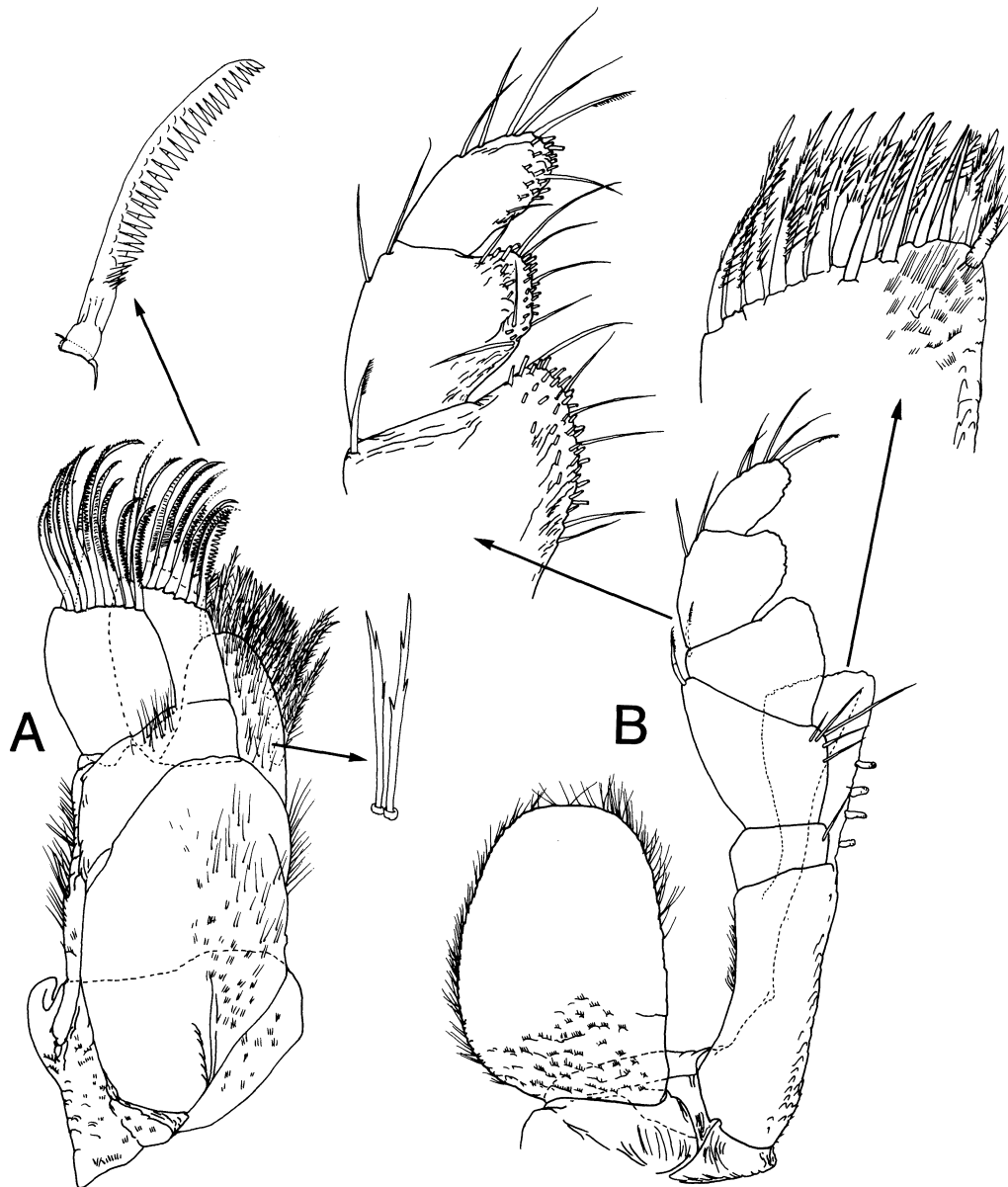


Fig.10. *Tainisopus napierensis* n.sp. Holotype, AM P40760. A, right maxilla with enlargement of comb seta from middle lobe and fine setae from inner lobe. B, right maxilliped, with enlargement of endite distal tip and setae on palp segments 3-5, most setae truncated.

assuming the species concept is correct. This hypothesis and its alternative (conspecific geographic variation in *T. fontinalis*) can be tested by the acquisition and study of variation in more specimens. The setal counts of the pereopods and pleopods are essentially identical to that of similar-sized specimens of *T. fontinalis*, suggesting at least a sister group relationship between the two species. Many ratios of measurements show small differences between the two species, although most are unlikely to be statistically significant. In *T. napierensis*, the maxillipeds have more large setae than in *T. fontinalis*, although the setal counts vary allometrically in the latter species. The number of comb setae on the outer lobes of maxillae, however, do not vary in adults of sizes of 6 to 9 mm in *T. fontinalis*; therefore, a count of nine comb setae on the outer maxillary lobes of *T. napierensis* appears to be a useful diagnostic character. The endopod of the female pleopod I in *T. fontinalis* is consistently larger than in *T. napierensis*, allowing this character to also be used in the diagnosis.

Tainisopus spp.

Material. Single damaged preparatory female, body length approximately 6.6 mm, missing most of pleotelson and one uropod, more anterior parts of body and pereopods intact from WFP station K2, AM P40779. Single intact female, WFP station K5.

Localities. WFP Station K2 (see Fig.14). Unnamed spring, north-east side of Oscar Range, Kimberley Region,

WA. Collected by WFP, 30 June 1988. 1.2 km south-east of Elimberrie Spring, 17°40.08'S 125°03'E (Leopold Downs, 1:100,000 series, 179452). A small spring flowing as a small trickle into a slow flowing stream 0.5-1 m wide, 1-3 cm deep. Slope about 5-10°. Clear, pH about 7.14, conductivity 500, water temp. 28.5°C (air temp. 31°C). No aquatic vegetation except some roots. Substrate limestone boulders on sand, mud and silt. Few trees and *Pandanus*. Some cattle damage.

WFP Station K5 (see Fig.14). Elimberrie Spring, north-east side of Oscar Range, Kimberleys Region, WA. Collected by WFP, 1 July 1988. 17°39.83'S, 125°02.5'E (Leopold Downs, 1:100,000 series, 179452). A small spring with its outlet pooled and fed to a tank by a pipe. The clear, still water in the pool at the head of the spring is about 10 cm deep. Clear, pH about 6.7, conductivity 550, water temp. 24°C (air temp. 29°C). No aquatic vegetation except some roots. Substrate limestone boulders and sand. Small trees provide a partial canopy.

Habitat. Washed from roots at spring head.

Distribution. Springs near the northern end of the Oscar Ranges.

Remarks. A single damaged female specimen, recovered from WFP station K2, is clearly unlike either *T. fontinalis* and *T. napierensis*. Because of the current uncertainty of its classification, this specimen is only provisionally assigned to *Tainisopus*. Furthermore, the generic description was not modified to account for this specimen, which differs in several important points. The pereopods are longer and less differentiated than in *T. fontinalis* and *T. napierensis* where the change between pereopod III to pereopod IV is substantial. This

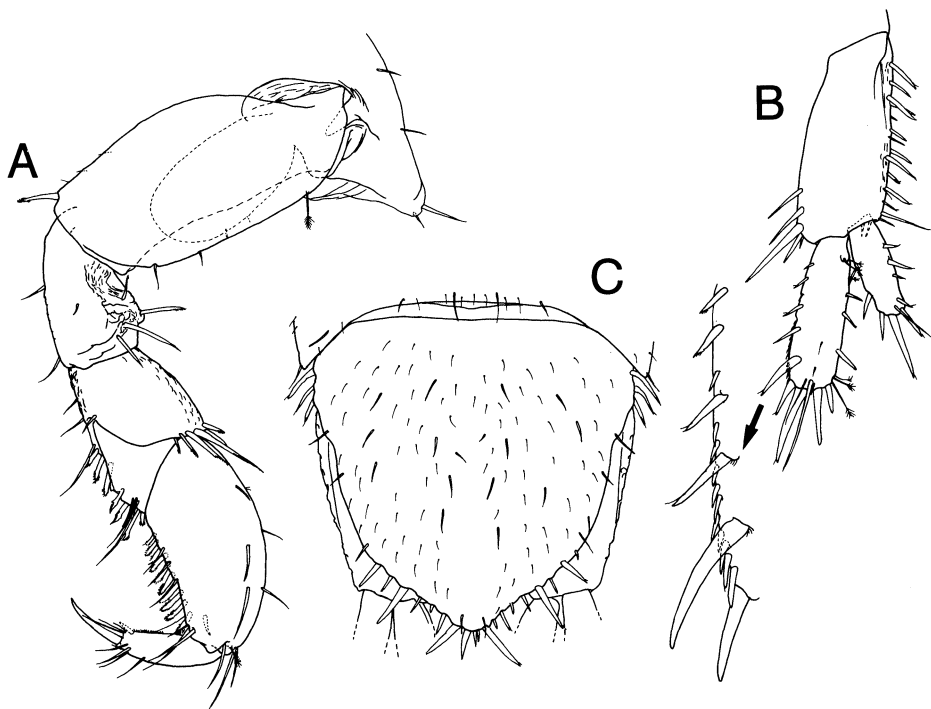


Fig.11. *Tainisopus napierensis* n.sp. Holotype, AM P40760. A, right pereopod I, lateral view. B, right uropod, with enlargement of setal rows on medial side of endopod. C, pleotelson, dorsal view.

specimen seems to lack the endopods of the pleopods, and instead has a thickened region of the medial part of the exopod. The uropods and pleotelson tip are also much more setose. A new genus-level taxon may be necessary to classify this specimen. Another specimen of *Tainisopus* from WFP station K5 was discovered after this paper was completed. It, too, appears to be a different species based on its setation, but is more similar to *T. fontinalis* and *T. napierensis*.

Discussion

Relationships. *Tainisopus* is unusual because it bears no apomorphies (that we recognise) that unquestionably ally this taxon with any of the established isopod suborders. Some possible hypotheses of classification within the existing subordinal system

are as follows.

1. "*Tainisopus* is a derived phreatoicidean". Presumed synapomorphies driving this hypothesis are the enlarged pleonite 5, equality of the other pleonites and all pleopods, the general shape of the uropods, presence of multiple lobes on the pleopodal endopods (found in the hypsimetopine phreatoicideans). All other features not agreeing with known phreatoicideans are considered derived features within the suborder.

2. "*Tainisopus* is a member of the asellotan-microcerberid clade". Features central to this hypothesis are three distinct protopodal articles of the antenna, clear remnants of the antennal scale on article 3, and an arrangement of the male penes and coxae of pereopod VII similar to that found in possibly early-derived Asellota (Just & Poore, 1992). In the cladograms of Brusca & Wilson (1991), the antennal characters exhibit a reversal throughout the Peracarida, and become synapomorphies of the asellotan-microcerberidan clade.

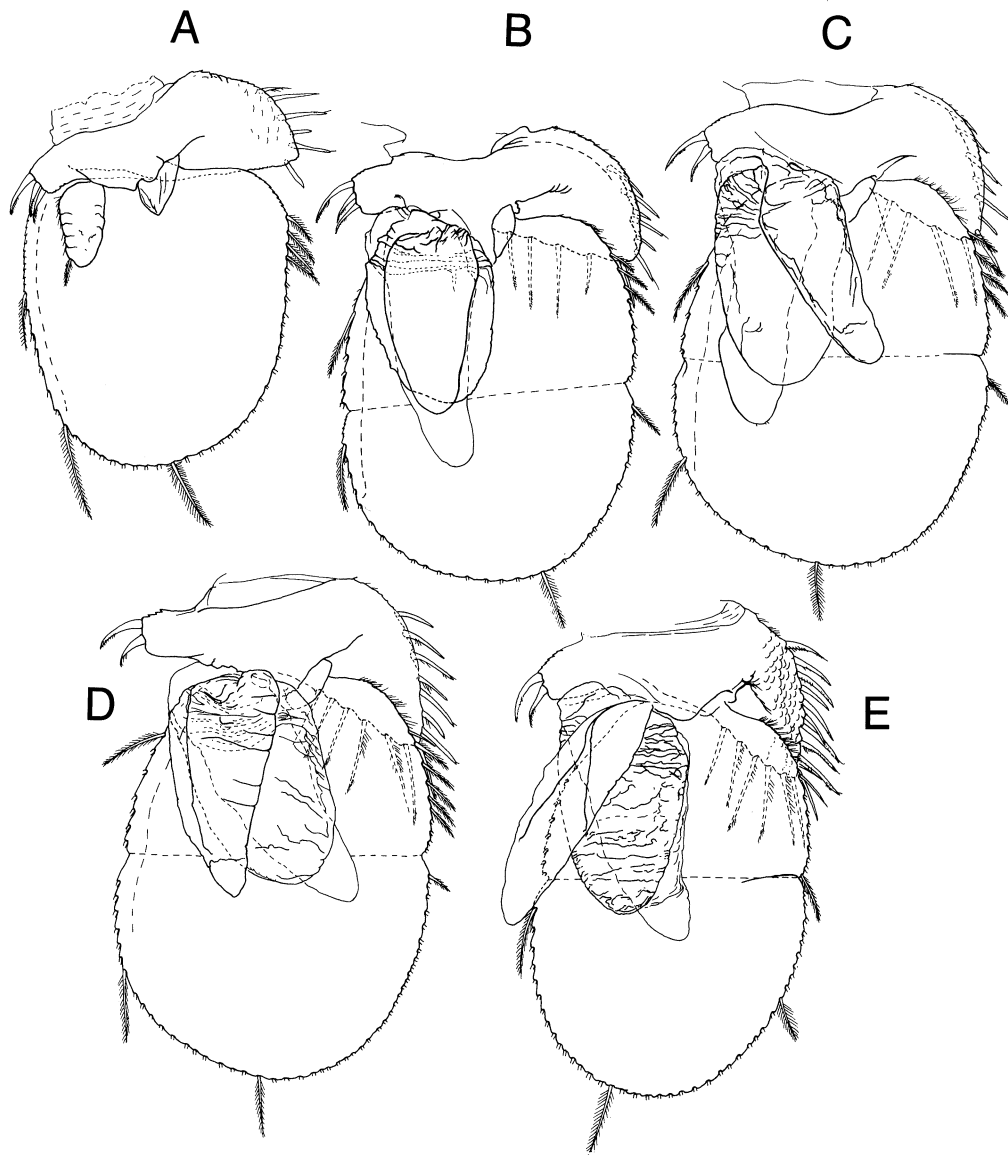


Fig.12. *Tainisopus napierensis* n.sp. Holotype, AM P40760. A-E, pleopods I-V, dorsal view.

If these features are interpreted as apomorphies, then they would argue for inclusion of *Tainisopus* into the same clade. This, however, is a fairly weak hypothesis and is included here to allow comparison with the potentially important morphologies.

Other possible hypotheses are more difficult to interpret because the relationships of the higher Isopoda are currently not well understood (Brusca & Wilson, 1991). Therefore, we shall primarily confine ourselves to addressing these two hypotheses on the basis of character analysis, rather than a more concrete cladistic treatment. The main point of our argument may be summarised with the statement "Neither hypothesis can be true because (i) supposedly derived characters of *Tainisopus* may be plesiomorphies or at least shared with other taxa at the ordinal level and (ii) *Tainisopus* shares synapomorphies with the higher isopods, not seen in the phreatoicideans and asellotes".

The enlarged pleonite 5 of *Tainisopus* has been regarded as a synapomorphy of the Phreatoicidea (Nicholls, 1943). Other taxa also have an enlarged pleonite 5: Limnoriidae, Lynseidae, and Anthuridea (where the pleonites are distinctly separate). Other isopod groups may have an enlarged pleonite 5, although not as a frequent or defining trait. Many isopod taxa have subequal pleonites (where they are distinct), and this is the common state in all potential outgroups (Mictacea, Tanaidacea, Spelaeogriphacea). Consequently, this feature must be regarded as equivocal on relationships with the Phreatoicidea until a full reanalysis of the Isopoda is completed.

The "lacinia" on the right mandible (see Dahl & Hessler, 1982 for a detailed discussion of its derivation) could be a synapomorphy of the amphisisopids and *Tainisopus*, because Nicholls (1943) felt this was a useful character to define the Amphisisopidae. A right lacinia most similar to that of *Tainisopus*, however, is found in the Holognathidae (early derived Valvifera; see Brusca, 1984; Poore & Lew Ton, 1990). Lacinia-like spines on the right mandible are common among the Valvifera and Serolidae (G.C.B. Poore, personal communication). The typical phreatoicidean right lacinia is a flat toothed structure, rather different from the multispined right lacinia of *Tainisopus*. Moreover, the produced and often doubled spine row of the Phreatoicidea is unusual among the isopods (research in progress) and is quite unlike the more plesiomorphic morphology seen in *Tainisopus*. We conclude that the right lacinia is not a synapomorphy shared between the phreatoicideans and *Tainisopus*.

Multiple endopodal rami on pleopods III-V of *Tainisopus* may be a feature shared with some phreatoicideans, *Phreatoicoides* and *Hypsimitopus* in particular, although this is a variable feature in these taxa (Knott, 1975). Other isopods are also known to have multiple gill-like structures on the pleopods (Bathynomus, Bopyridae, Cymothoidae). The multiple

rami could possibly be a special response to low oxygen tensions found deep subterranean waters but, more likely, an increase in pleopodal gill surface may be a response to increased activity and greater oxygen demand due to active swimming, not seen among the lower isopods, Asellota and Phreatoicidea. This feature seems equivocal for determining relationships, or may be an autapomorphy of *Tainisopus*.

The organisation of the pleotelson, although bearing some similarity between *Tainisopus* and phreatoicideans in the shape of the uropods, shows a substantial departure in morphoclines. *Tainisopus* has a broad and flat telsonic region (plesiomorphic, as in potential outgroups Mictacea or Spelaeogriphacea). The phreatoicidean pleotelson, however, is greatly modified for an amphipod-like pushing function, being vaulted and reflexed posteroventrally. If the *Tainisopus* pleotelson is in the same morphocline as the phreatoicidean pleotelson, then the *Tainisopus* form must be the earlier derived of the two. Associated with the pleotelson shape, the dorsoventrally flattened shape of the body is a standard feature of all isopods, and could easily be obtained directly from isopod ancestors, while the vaulted and elongate body form of the phreatoicideans is derived and not seen in any potential isopod outgroups.

A basal article in the antennal protopod is found in *Tainisopus*, Asellota and Microcerberidea. Although the analysis by Brusca & Wilson (1991) forces this feature to be a synapomorphy of the latter two taxa, this basal article may be an ancestral feature because it is also found in some Mysidacea. Authors have claimed that Amphipods and Cumacea have a three-articled protopod (e.g., Dahl & Hessler, 1982:134). Amphipods and Cumacea, however, lack a scaphocerite or scale to define the position of the third propodal article, therefore rendering segmental homologies equivocal. The basal article's apparent absence in most Peracarida may be regarded as i) multiple loss events, ii) a derivation of the Isopoda earlier than most other peracarid groups, or iii) insufficient data as seen in Cumacea and Amphipoda. A rudimentary antennal basal article is also present in some hypsimetopine phreatoicideans (research in progress). Because the basal antennal article is found in at least four major isopod taxa as well as some mysids, it appears to be a plesiomorphic feature within the isopods, and possibly in other peracarids. Other key taxa, such as the Mictacea and the Spelaeogriphacea, have not been carefully studied for basal article remnants, so perhaps we do not have the full story.

The morphology of the seventh pereonite and the male penes (Fig.3A,B) could be an apomorphy shared with the Asellota. Just & Poore (1992) show that the asellotan penes are derived from a coxal position: species of the genus *Vermectias* has a thin sclerite that connects the coxa with the penes. In *Tainisopus*, however, the coxal connection to the penes is broad and triangular, such that much of the ventral surface of the seventh pereonite appears to be composed of the coxa of

pereopod VII. Many higher isopods have ventral surfaces of coxal origin (Brusca & Wilson, 1991), and the expanded articulations of the coxae seen in *Tainisopus* may be a step in this direction. The penial morphology of *Tainisopus* may be intermediate between i) the primitive condition where the penes are on the coxae, ii) the asellotan condition where the penes are 'pinched off' still fully functional coxae, and iii) a more derived isopod condition where the coxae expand to cover the ventral surface, thereby carrying the genital pores medially and rendering the coxa-body articulation inflexible.

The broad coxa of pereopod V of the female also bears the oopore (Fig.3E), although it also has a fully developed oostegite, unlike the Phreatoicidea. A recent review of isopod female genitalia (Wilson, 1991) has suggested that the position of the isopod oopore on the ventral surface might have developed in a variety of ways, either as part of the lateral movement of the ventral coxal plate, or as a preliminary disassociation from the coxa and then a later penetration of the ventral coxal plate as it migrates medially over the ventral surface. In the Asellota, the oopore has become disassociated from the still movably articulated coxa. *Tainisopus* clearly has retained the primitive condition, found also in *Bathynomus* (unpublished observations), where the oostegite is still intimately associated with the coxa. The fifth pereonite coxa of the female, like the other pereonite's coxae, has become more intimately associated to the ventral surface and is not completely mobile. The coxae of *Bathynomus* seems to be much more mobile and freely articulated.

In conclusion, the above features militate against *Tainisopus* being members of the phreatoicidean clade. The diagnosis of the Phreatoicidea, currently a compact group, would have to be considerably diluted to include *Tainisopus*. The synapomorphies of the Phreatoicidea that are not shared with *Tainisopus* are as follows: pleotelson vaulted with uropods rotated ventromedially; pleotelson strongly flexed ventrally with a dorsally recurved tip (secondarily uncurved in ground water taxa); proximal and distal segments of pleopodal exopods, when separate, with narrow articulation; mandibular spine row on distinct medially projecting lobe; antenna with basal article of the protopod reduced or absent; antennula lacking rudiment of a second flagellum. Moreover, *Tainisopus* is also clearly not an asellotan. It lacks the specialised copulatory structures, such as the female spermathecal duct (cuticular organ), and modified pleotelson that defines the Asellota (Wilson, 1991; Brusca & Wilson, 1991). No asellotan can swim with its pleopods, while *Tainisopus* is a good swimmer. In many respects, the Asellota are highly derived compared to other isopods, and *Tainisopus* shares none of their specialisations. The features that *Tainisopus* shares with the asellotans (as discussed above) are probably plesiomorphies.

Therefore, we conclude that *Tainisopus* can be neither a phreatoicidean nor an asellotan.

Unfortunately, the best classification is not immediately obvious because *Tainisopus* lacks specific synapomorphies of other isopod suborders. The generalised mouthparts are unlike the derived features seen in any of the higher isopod suborders ('Flabelliferan' families, Anthuridea, Epicaridea, Gnathiidea, Oniscidea + Calabozoidea, Valvifera), except for perhaps the Sphaeromatidae or some Oniscidea (disregarding the lack of a mandibular palp in the latter). We suspect that *Tainisopus* may have evolved prior to the evolutionary divergence of these suborders. The similarity of all body segments suggests a fair amount of generality, and therefore *Tainisopus* seems to retain presumed ancestral forms for any higher isopod.

Furthermore, the possession in *Tainisopus* of derived features common to all higher isopods is suggestive of an early derivation with the higher isopods. Such synapomorphies include the presence of true coxal plates and a pereopodal tagmosis (3-4, not 4-3: see Brusca & Wilson, 1991) similar to that seen in the Cirolanidae or other derived isopods. *Tainisopus* also has five pereopodal oostegites, while Phreatoicidea and Asellota never have more than four. Most higher isopods, from Cirolanidae to Epicaridea, have five pereopodal oostegites (a sixth may appear on the maxilliped), with some taxa having more; these (e.g., Cymothoidae) can be considered special apomorphies. Broad, strongly natatory pleopods are shared between *Tainisopus* and the higher isopods, while the phreatoicideans and asellotes are either poor swimmers, do not swim at all, or do so secondarily using their pereopods. A homology study of these and other characters in all isopods (research in progress) will recommend the most probable classification for *Tainisopus*.

Population biology. On a comparative basis, the body length measurements of the relatively undamaged specimens reveal the approximate size structure of *T. fontinalis* (Fig.13). The mancae present in the sample were of the latest stage (instar 3, showing a rudimentary pereopod VII), indicating that the young are released from the brood pouch at a size just below 2 mm. Sexual differentiation is apparently present by the fourth instar, and sexual maturity in both sexes is reached at a length of approximately 5.5 to 6 mm. There appears to be at least two different sizes of fully preparatory females (5.5-6.5 mm and 7.5-8.4 mm), with a distinct gap of brooding females in between (6.5-7.0 mm). Therefore, this species is iteroparous, with alternating preparatory and brooding instars in the females. The fully copulatory males cover a large size range, indicating that they continue to moult after reaching maturity, and also may breed several times. The presence of most life stages in this one sample suggests that breeding occurs almost continuously at this time of the year (June), despite the sample occurring at the beginning of the dry season. Continuous breeding, however, is common in subterranean animals, and the population at station

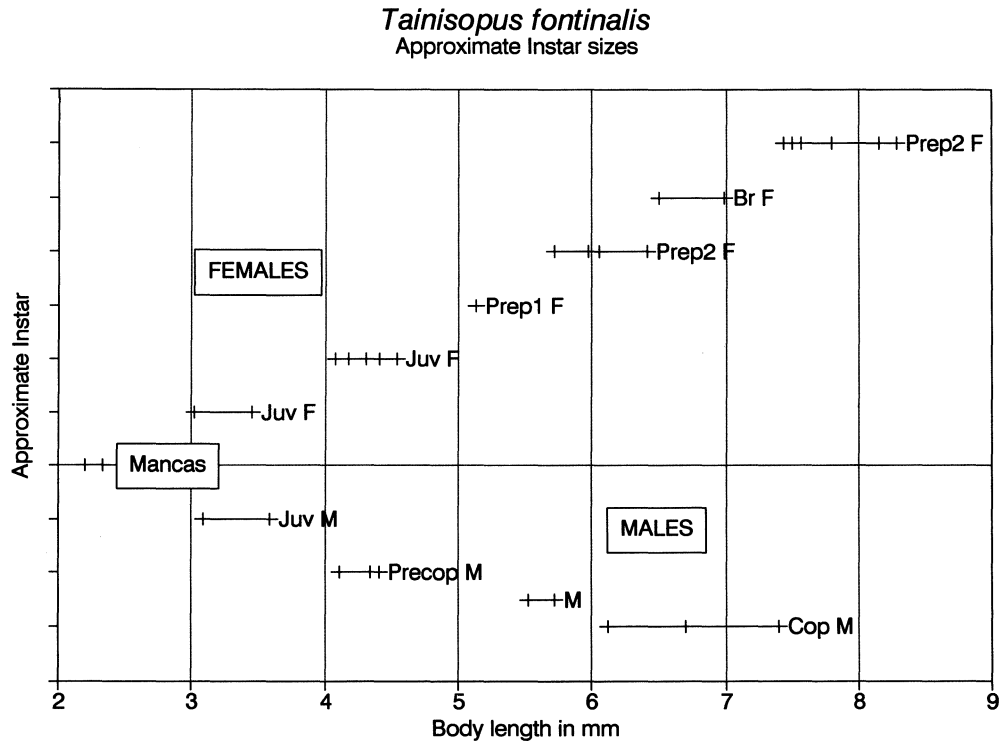


Fig.13. Approximate population size structure from sample K1 of *Tainisopus fontinalis* n.gen., n.sp. Horizontal bars mark the size ranges within approximate instars, and vertical ticks mark individual size measurements. Abbreviations used in figure: Br - brooding; Cop - copulatory; F - female; Juv - juvenile; M - male; Precop - precopulatory; Prep1 - early preparatory; Prep2 - fully preparatory or copulatory.

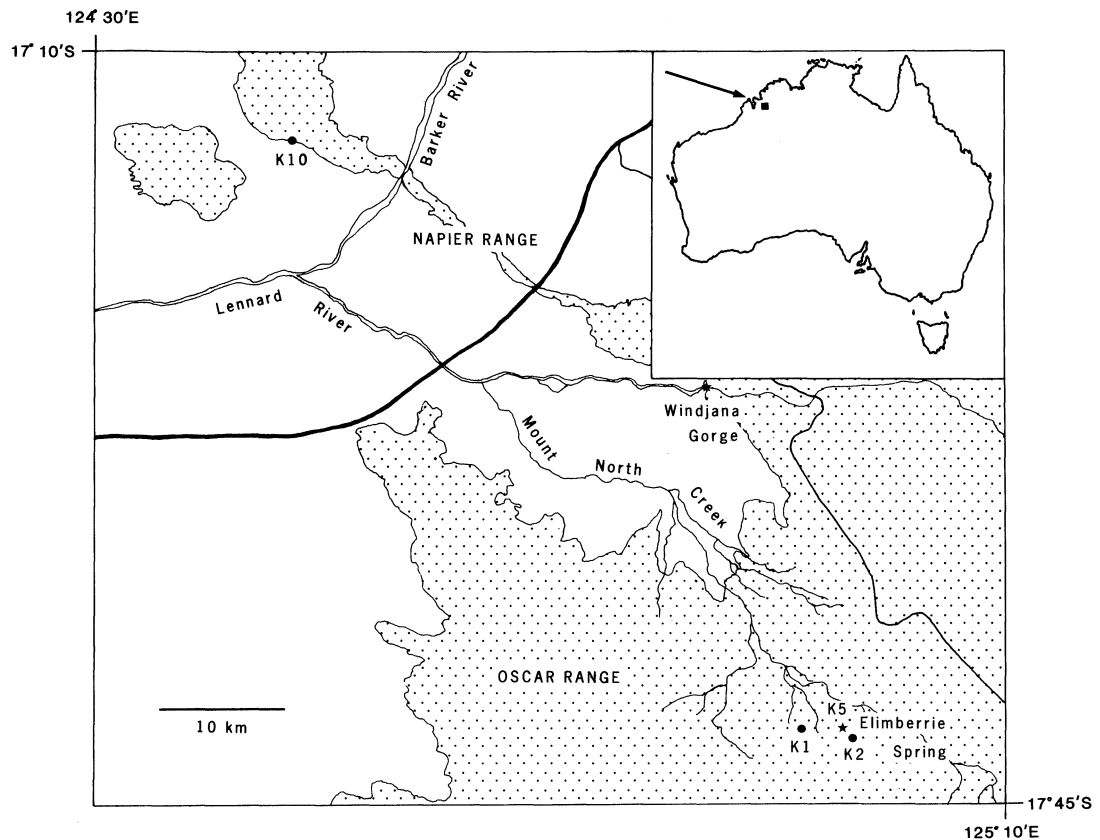


Fig.14. Map of *Tainisopus* localities in the Oscar and Napier Ranges, Kimberley Region, West Australia. In upper right inset, the arrow and small filled square indicates the Australian location of the map.

K1 is evidently largely subterranean.

Biogeography. The Kimberley Region has a tropical savanna climate with about 380 mm of rainfall in the southern part to about 890 mm in the northern part. Most of the rain falls between December and March, the region being arid with high evaporation for the remainder of the year. Ellaway *et al.* (1990) state that of the 650 mm annual rainfall in the region in which our material was obtained, 85% falls in the December-March period. Consequently all rivers except the lower reaches of the Ord River and spring fed streams in the Kimberley Plateau stop flowing in the winter months and even large water holes and most springs are only semipermanent (Dow & Gemuts, 1969). Water flow was presumably even more reduced during the arid Pleistocene glacials (e.g., DeDeckker, 1986). Under conditions of extreme aridity, aquatic invertebrates with poor dispersal powers probably only survived in subterranean water or springs fed from significant subterranean sources. With this in mind a survey of springs of parts of the Kimberley was carried out, primarily to collect molluscs and crustaceans. Of the numerous habitats collected, the four from which material is recorded in this paper (Fig.14) were the only ones to reveal unusual 'locally endemic' macrocrustaceans.

Tainisopus species are blind and may breed continuously, so this genus is clearly part of the Kimberley subterranean fauna. The limestone hills in which the springs and cave containing the isopods are found (see Fig.14) are Devonian coral reefs formed in a small embayment occupying the western edge of the Kimberley. No marine transgressions in this area have occurred since the Devonian (Veevers, 1984). Thus *Tainisopus* is not derived from a immediate marine ancestor, but is most likely of ancient freshwater stock. The only other relictual freshwater isopods known from Australia are mostly found in the south western and south eastern areas. The exceptions, however, are interesting. *Phreatomerus latipes* (Chilton, 1922) is an unusual relict phreatoicoidean restricted to one group of artesian springs in northern South Australia (Ponder, 1986). *Eophreatoicus kershawi* Nicholls, 1926 has been found in a small pool at Sandstone Bluff (about 12°S 133°30'E), in Arnhem Land, NT (Nicholls, 1926, 1943). These species may be remnants of a period when Australia was more extensively covered with temperate rain forest and freshwater habitats were more prevalent. Owing to their highly restricted and patchy distribution, these isopods are among the Australian fauna's most potentially endangered invertebrate species (cf. Ponder, 1986). The difficulty of sampling in the Kimberley and in Arnhem Land of the Northern Territory, however, suggests that more collecting in these areas may uncover new species of these interesting relicts. The karst ground water system of the Oscar and Napier Ranges (Ellaway *et al.*, 1990) may also provide additional undiscovered habitats for *Tainisopus*.

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