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Revision of the Genus *Holonuncia* Forster (Arachnida: Opiliones: Triaenonychidae) with Description of Cavernicolous and Epigean Species from Eastern Australia

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ABSTRACT. The genus *Holonuncia* Forster and the type species *H. cavernicola* Forster are redescribed. One new combination is established: *H. seriata* (*Nuncia*) (Roewer, 1915). *Holonuncia seriata* and *H. tuberculata* (Roewer, 1915) are redescribed and ten new species described: *H. sussa, H. dewae, H. francesae, H. katoomba, H. weejasperensis, H. dispar, H. recta, H. hamiltonsmithi, H. kaputarensis* and *H. enigma.* Allozyme electrophoresis resolves some species boundary problems. Morphological adaptations to cave life include leg attenuation, depigmentation and eye regression but not loss. The distribution of the genus in eastern mainland Australian caves is illustrated.

HUNT, G.S., 1992. Revision of the genus *Holonuncia* Forster (Arachnida: Opiliones: Triaenonychidae) with description of new cavernicolous and epigean species from eastern Australia. Records of the Australian Museum 44(2): 135–163.

Species of *Holonuncia* Forster are the most widely distributed cavernicolous harvestmen in eastern mainland Australia (Fig.1). Apart from notes on cavernicolous adaptations (Hunt, 1972), no work has been done on the group since Forster (1955) described the type species from Jenolan Caves. Surface species in the genus occur across virtually the entire range of the genus, unlike the situation with the largely cavernicolous Tasmanian genus *Hickmanoxyomma* in which the single known surface species is confined to a small part of the generic range (Hunt, 1990).

Materials and Methods

Type material of all nominal species has been examined and reassessed. The following abbreviations are used to indicate the present location of material examined:

AM – Australian Museum, Sydney (usually denoted by the registration number prefix KS); ANIC – Australian National Insect Collection, CSIRO, Canberra; FIS – Forschungsinstitut Senckenberg, Frankfurt am Main; SAM – South Australian Museum,

Adelaide.

Official numbers for caves (e.g., J31) follow Matthews (1985). Terminology and methods of measurement follow Hunt (1990) except that lateral plate becomes dorsolateral plate in conformity with Martens (1986). Tergal areas are abbreviated to TA1, etc.; coxa of leg I is coxa I, etc.

Other abbreviations are: SL – scute length, CW – carapace width, PFL – pedipalp femur length, AI and AIV – astragalus I and IV lengths, CI and CIV – calcaneus I and IV lengths, MI – metatarsus I length, FIV – femur IV length, CSL – cheliceral second segment length. In general CW is used as an indication of body size as it is less subject to variation due to physiological state. Methods for allozyme electrophoresis are given at the end of the paper. Tables referred to throughout the text are listed in the Appendix.

Triaenonychidae Soerensen

Triaenonychinae Soerensen

Remarks. *Holonuncia* belongs to an assemblage of eastern Australian genera which includes *Equitius, Paranuncia, Odontonuncia, Hickmanoxyomma* and at least three undescribed genera. Their male genitalia are of the basic form that Martens (1986) ascribes to Australian and New Zealand Triaenonychidae: a well developed ventral plate (Fig.3) bearing sensory setae which is joined to the glans basally and is apparently embryologically related to it; a mid-dorsal plate, similarly derived; and dorsolateral plates on each side embryologically related to the truncus.

It seems that Martens is correct in considering this penis configuration as plesiomorphic for the Triaenonychidae, and that various apomorphic configurations in the family can be derived by the

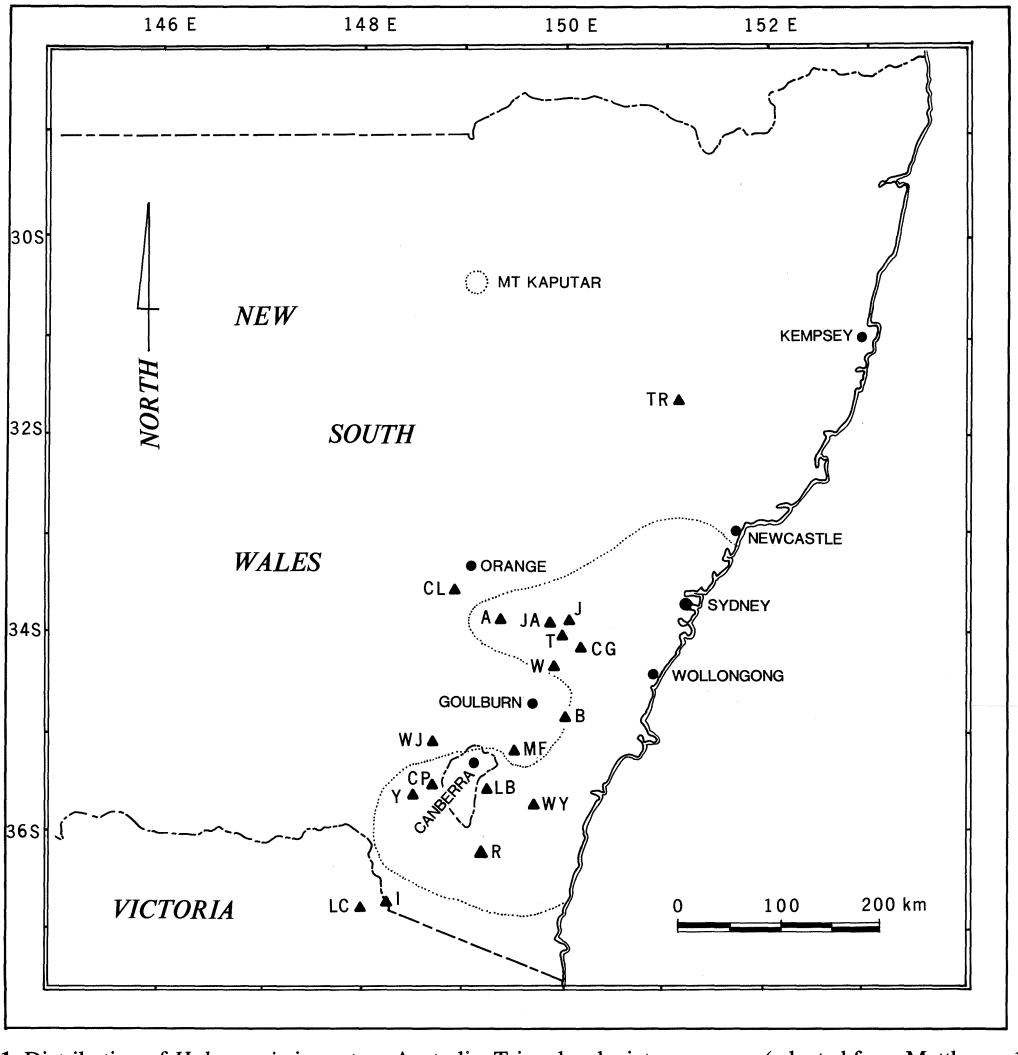

Fig.1. Distribution of *Holonuncia* in eastern Australia. Triangles depict cave areas (adapted from Matthews, 1985); A = Abercrombie; B = Bungonia; CG = Colong; CL = Cliefden; CP = Cooleman Plain; I = Indi; J = Jenolan; JA = Jaunter; L = Limestone Creek; LB = London Bridge; MF = Mount Fairy; R = Rosebrook; T = Tuglow; TR = Timor; W = Wombeyan; WJ = Wee Jasper; WY = Wyanbene; Y = Yarrangobilly. Dotted lines indicate approximate known distribution of surface species.

reduction or loss of one or more of these plates. He is not correct in implying that this plesiomorphic condition characterises Australian Triaenonychidae. The genus *Lomanella*, for example, shows extreme reduction in plates which parallels that in some North American and Japanese taxa (Hunt & Hickman, in press).

It is possible that the penis of *Holonuncia* and similar genera is the most plesiomorphic form for triaenonychids possessing the full complement of plates. The glans is relatively simple, lacking the accessory processes which occur in some other genera, for example *Cluniella* and *Mestonia*. The mid-dorsal plate is of relatively simple morphology compared with the elaborately folded structures typical of many genera like *Nunciella, Calliuncus* and *Leionuncia*. The ventral plate is generally of conservative form without the conspicuous modifications possessed by some taxa including *Cluniella ornata* Forster.

I have regarded possession of a ventral notch in calcaneus 1 of males as a strong generic character, but revision of *Holonuncia* has qualified this view, at least for this genus. Two species at the southern limits of distribution, namely *H. recta* n.sp. and *H. hamiltonsmithi* n.sp. (and a more problematic species from the Sydney region, *H. enigma*), lack a notch despite possessing synapomorphies indicating monophyly with other *Holonuncia* spp. Presence or absence of a notch is considered relevant at the species group level in *Holonuncia*.

Male genital morphology is normally useful in establishing species boundaries within a genus. *Holonuncia*, however, generally has a penis of conservative morphology making the task difficult for some species. Electrophoresis was used to help elucidate some boundaries (results reported and discussed at end of paper).

All populations of *Holonuncia* which inhabit caves show at least some degree of morphological modification to cave life. Such 'troglomorphies' include depigmentation, eye regression but not loss, leg attenuation, reduced sclerotisation, and reduction in size and number of dorsal spines/tubercles. *Holonuncia sussa* n.sp. from Colong Caves is the most highly troglomorphic species; *H. dewae* n.sp. from Wombeyan Cave, somewhat less so. These two species appear to be obligate cavernicoles, or troglobites.

Unlike the situation with *Hickmanoxyomma* (Hunt, 1990), *Holonuncia* frequently has surface representatives in the genus in close proximity to caves, a situation similar to that reported by Forster (1965) for New Zealand cavernicolous *Nuncia* and *Hendea*. Forster considered the cave populations to be different species from those on the surface. In *Holonuncia*, however, it was frequently difficult to judge whether cave populations were conspecific with adjacent or nearby surface populations. In these cases, conspecificity was assumed. Briggs (1971) recognised both surface and cave populations of the north American triaenonychid *Zuma acuta*, basing his judgement on the degree of morphological similarity when troglomorphic variations are excluded. It would be interesting to extend electrophoretic studies to quantify gene flow between surface and cave populations of *Holonuncia*. The potential exists to determine which surface species gave rise to the cavernicolous forms, and whether there have been multiple invasions of particular cave systems, as may be the case at Jenolan, Colong and Bungonia Caves.

Holonuncia Forster, 1955

Holonuncia Forster, 1955: 388.

Type species. *Holonuncia cavernicola* Forster, 1955 by original designation.

Diagnosis. Eyemound rising immediately behind anterior margin. Anterior margin with a few tubercles on each side, rarely naked. TA3 with mesial pair of enlarged tubercles or small spines; sternum long and thin, spiracles partly obscured by bridging tubercles of coxa IV, free lateral sclerites absent. Chelicera without a proximal boss. Pedipalp femur with a proximoventral, unevenly trifid spine, most distal or second most distal retroventral spine strong. Calcaneus of leg I of male usually with notch. Ventral plate of penis narrow, usually only slightly wider than glans, with 3 inferior and 1 (rarely 2) superior seta on each side; ventral plate with a proximal hollow in which bases of proximal inferior setae are usually set; mid-dorsal plate as wide as or narrower than glans, subequal to or shorter than ventral plate, weakly bifid, with terminal bifurcations not strongly curved and not supporting the glans laterally; glans with distodorsal denticles.

Redescription. Eyemound rising immediately behind anterior margin, rounded or canaliculate or with a short simple spine or tubercle. Anterior margin below with 5 inter-appendage projections; above with a few small tubercles on each side or rarely naked. Scutal groove distinct mesially; the 5 tergal areas marked by faint tergal grooves and by tubercles/granules or rows of same, mesial pair on TA3 largest. Ninth abdominal tergite fused with anal plate; free lateral sclerites absent. Sternum long and narrow; genital operculum rounded; spiracle abutting coxa IV and slightly obscured by bridging tubercles. First segment of chelicera without a proximal boss, with prodistal spine. Pedipalp usually much larger in male; femur with proximoventral trifid spine with main shaft and 2 weaker accessory processes; most distal or second most distal of retroventral spines strong, subequal to most proximal retroventral spine; 2 prodistal spines on both femur and patella; tibia with 3 or 4 retro- and 3 proventral spines; tarsus with 3 large pro- and retroventral spines; claw movable. Proximal fusion of coxae II and III marked by suture; coxa II with labial process; coxa I with distal proventral compound, but not clavate, spine. Leg femora armed only with small granules; calcanei less than 0.35 length

of astragalus; calcaneus I of male with notch or notch lacking, astragali with pseudosegmentation. Male tarsus I with 4-5 segments, female 3; distitarsi I and II with 2 and 3-4 segments; adult claw of legs III and IV with 1 pair of short lateral branches. Ventral plate of penis narrow, usually only slightly wider than glans, with 3 inferior and 1-2 superior setae on each side, median cleft depth 0.2-0.5 plate length; ventral plate with a proximal hollow, best seen in lateral view, in which bases of proximal inferior setae are usually set; mid-dorsal plate simple in form, subequal to glans in width, subequal to or shorter than ventral plate, weakly bifid, with terminal bifurcations not strongly curved and not supporting the glans laterally; glans with distodorsal denticles, lacking accessory processes.

Comments. *Holonuncia* is apparently closely related to *Equitius* Simon and *Paranuncia* Roewer, though some of the similarities in genital structure may be symplesiomorphies. Synapomorphies for *Holonuncia* are distodorsal denticles on the stylus, and the proximal hollow in the ventral plate.

Distribution. South eastern mainland Australia: known southern limit is Limestone Creek Caves in the Victorian Alps; northern limit in the coastal ranges is at Timor Caves near Murrurundi, New South Wales; outlier to the north-west in the Nandewar Ranges via Narrabri.

Key to Males of Species in Genus *Holonuncia* Forster

1. Calcaneus I with ventral notch (Fig.4,B-D) 2

—— Calcaneus I straight 11

2. Eyemound with a small median spine (Fig.9A) 3

—— Eyemound rounded, at most with small median granule 5

3. Notch in calcaneus 1 tiny (Fig.15K) ..... *H. kaputarensis* n.sp.

—— Notch in calcaneus 1 large 4

4. Penis ventral plate widest basally (Fig.10H); anterior margin of carapace with large spines tending to be directed forward (Fig.10A) ..... *H. katoomba* n.sp.

—— Ventral plate widest sub-distally (Fig.6G); spines on anterior margin not tending to be directed forward ..... *H. francesae* n.sp.

5. Anterior margin naked (Fig.5,A-B) ..... *H. sussa* n.sp.

—— Anterior margin with spines, tubercles or granules 6

6. Ventral plate with 2 superior setae on each side (Fig.12J) ..... *H. dispar* n.sp.

—— Ventral plate with 1 superior seta on each side 7

7. Notch in calcaneus I shallow, depth less than 0.3 remaining calcaneus width (Fig.11K); collected in Wee Jasper Caves ..... *H. weejasperensis* n.sp.

—— Depth of notch in calcaneus I greater than 0.3 remaining calcaneus width (Fig.4D); not collected in Wee Jasper Caves 8

8. Anterior margin usually with 2 tubercles or granules on each side; collected in Wombeyan Caves ..... *H. dewae* n.sp.

—— Anterior margin usually with more than 2 tubercles/ granules; not collected in Wombeyan Caves 9

9. Proximal retroventral spine on pedipalp tibia reduced to a blunt granule and retroventral spines 3 and 5 closer together than spines 1 and 3 (Fig.8E), spine 4 often lacking ..... *H. tuberculata* (Roewer)

—— Proximal retroventral spine small but usually not reduced to a granule and distance between spines 3 and 5 similar to 1 and 3 (Fig.7F), spine 4 usually present 10

10. Tarsus I usually with 5 articles (Fig.7H); stylus of penis narrowest subdistally (at about 0.7 stylus length) (Fig.7J) ..... *H. seriata* (Roewer) n.comb.

—— Tarsus 1 usually with 4 articles; stylus of penis narrowest at about 0.5 stylus length (Fig.3J) ..... *H. cavernicola* Forster

11. Tarsus 1 with 3 articles, carapace width less than 2 mm ..... *H. enigma* n.sp.

—— Tarsus 1 with greater than 3 articles, carapace width greater than 2 mm 12

12. Stylus very broad basally, very narrow subdistally (Fig.14J); collected in Limestone Creek Caves, Victoria ..... *H. hamiltonsmithi* n.sp.

—— Stylus only slightly broader basally than sub-distally (Fig.13F) ..... *H. recta* n.sp.

Holonuncia cavernicola Forster, 1955

Figs 2-4

Holonuncia cavernicola Forster, 1955: 389-390.

Type material. New South Wales, HOLOTYPE, male, KS6912 (old no. K13022), Jenolan Caves, 33°49'S 150°02'E, label "W.J.R. det.", no other data. PARATYPE male, KS6914 (old no. K12570), Jenolan Caves, no other data.

Additional material examined. Jenolan Caves: KS 5077, Chifley Cave (J-2M), on flowstone, M. Gray, 13 Dec. 1979, 2 juveniles; KS 17829, Imperial Cave (J-4M), M.R. Gray, 25 Oct. 1987, 1 female; KS 19033, Devils Coachhouse (J-165A), Jenolan Caves Fauna Survey, in thick litter in flood bypass to west side, G. Smith and L. Wheeler, 12 Dec. 1987, 1 male; KS 19048, Hennings Cave (J-39), entrance chamber, Jenolan Caves Fauna Survey, wandering over floor, G. Smith and L. Wheeler, 13 Dec. 1987, 1 female; KS 19049, Cerberus Cave, Jenolan Caves Fauna Survey, Cave Guides, May 1988, 1 male; KS 19050, McKeowns Hole (J-68), Jenolan Caves Fauna Survey, on old bat guano in lower section of cave, M. Gibian, 19 Mar. 1988, 2 juveniles; KS 21401, cave in Southern Limestone, B. Dew, 25 July 1964, 2M; KS 21402, small cave in Southern Limestone, Speleological Club, 26 Sept. 1970, 1 female; KS 21403, cave in Southern Limestone, on guano, B. Dew, 3 Sept. 1970, 1 male; KS 21404, Temple of Baal Cave (J-9M), under rock, dark zone, G.S. Hunt, 1970, 1 female; SAM, BS2184, Paradox Cave (J-48), E. Hamilton-Smith, 2 Jan. 1973, 2 juveniles; SAM BS2185, same data, 1 male. Boyd Plateau via Jenolan Caves (epigean): KS 21438, Mount Edwards, 33°59'S 150°03'E, under log, G.S. Hunt, Apr. 1971, 1 male; KS 23153, Mount Wiburd, 33°50'S 150°02'E, 1400 m, inside log, G.S. Hunt, 10 Jan. 1973, 1 male; KS 23154, Mount Wiburd, G.S. Hunt, 20 Sept. 1969, 1 female; KS 23155, Mount Wiburd, under log, G.S. Hunt, 6 June 1971, 2 males, 1 female; KS 23156, Budthingeroo Creek, 33°54'S 150°02'E, G.S. Hunt, 24 Feb. 1973, 1 female; KS 23157, Budthingeroo Creek, G.S. Hunt, 11 June 1971, 1 female; KS 23158, Mount Emperor, 33°59'S 150°08'E, G.S. Hunt, 11 Jan. 1973, 1 male; KS 23159, Mount Edwards, headwaters of Council Creek, 33°50'S 150°03'E, G.S. Hunt, 29 Jan. 1971, 1 male; KS 23160, Green Gully, 32°47'S 149°41'E, M.R. Gray, 18 June 1971, 2 female; KS 23161, Gillespies Lookout near Mount Boss, 33°11'S 152°24'E under log, G.S. Hunt, 5 Dec. 1971, 1 male. McKeown's Creek valley Jenolan Caves, 33°49'S 150°02'E (epigean): KS 21406, on surface under logs, G.S. Hunt, 15 Apr. 1972, 3 male; KS 23162, under wood beside creek, G.S. Hunt, 20 Sept. 1969, 1 juvenile. Cavernicolous material from Tuglow Caves (KS 23165, KS 23166, SAM BS 2008, BS2009) and epigean material from Mount Shivering, south of Kanangra Walls (KS 23163), Oberon Prison Farm (KS 23164), Mulgoa (KS 21416), and Glenbrook (KS 21417) are tentatively assigned to this species.

Diagnosis. Prominent notch in calcaneus I; anterior margin with at least 3 prominent tubercles on each side; stylus in ventral view narrowest at about 0.5 its length and expands gradually without marked subapical constriction, in lateral view terminal flexure short and thick.

Redescription. MALE (Jenolan Caves population). *Body:* SL 3.83-4.45 (4.24), CW 2.74-3.08 (2.91)(n=5). Background colour of dorsum orange; pigmentation pattern (KS17829) as figured, intensity highly variable in different specimens. Eyemound rising at about 50° from anterior margin, about 0.5 as high as long; rounded in profile, unarmed except at most for tiny granule; eyes reduced. Anterior margin with 3-5 tubercles on each side. TA3 with pair of mesial tubercles tending to enlarge to small spines in many specimens; distribution of other tubercles and granules as figured. Coxosternal region as figured; genital operculum longer than wide; spiracle partly obscured by coxa IV. *Chelicerae:* CSL 2.17-2.40 (2.31). Prodistal spine on first segment moderately large; second segment spines as figured. *Pedipalps:* PFL 2.51-2.96 (2.79). Gracile; ratio PF:CW 0.86-1.00 (0.93). Femur with row of 5 mediodorsal spines size order 4,3,2,5,1, largest in distal half; 5-6 retroventral spines size order 1,5,3,2=4,6. Proximal accessory denticle on proximoventral trifid spine moderately developed, distal denticle weak. Tibia with 4 retroventral spines, spine 1 about 0.5 length spine 2, spine 4 much greater than 0.5 spine 3. *Legs*: long, FIV 4.10-4.92 (4.31), ratio FIV:CW 1.39-1.98 (1.54); calcaneus long, ratio CI:AI 0.18-0.25(0.22). Tarsus IV dorsally with 2 large setae placed at about 0.25 and 0.75; lateral branches inserted at about 0.4 on claw; Tarsal formula: 4-rarely 5(2),11-15(3-4),4,4. *Genitalia:* ventral plate with 1 superior and 3 inferior setae on each side, about 1.7 as long as wide, slightly wider than base of stylus, median notch about 0.3 plate length and not reaching level of bases of inferior setae. Mid-dorsal plate reaching beyond bases of superior setae but not reaching level of distal margin of ventral plate; terminal cleft shallow, depth about 0.75 narrowest width of plate. Stylus basally about 0.8 ventral plate width, viewed ventrally tapers gradually to its narrowest point at about 0.5 its length, and expands gradually without a marked subapical constriction; in lateral view, distal flexure short and thick, width about 0.5 length; distodorsal denticles inconspicuous and not set in longitudinal grooves.

FEMALE. Similar to male except: body smaller, SL 3.47-3.76 (3.61)(n=5), CW 2.27-2.30 (2.29); pedipalps relatively shorter, PFL 1.97-2.01 (1.99), spines more slender, short spines longer, proximal accessory denticle of trifid spine weaker. Tarsal formula:3-4(2),9-15(3-4),4,4.

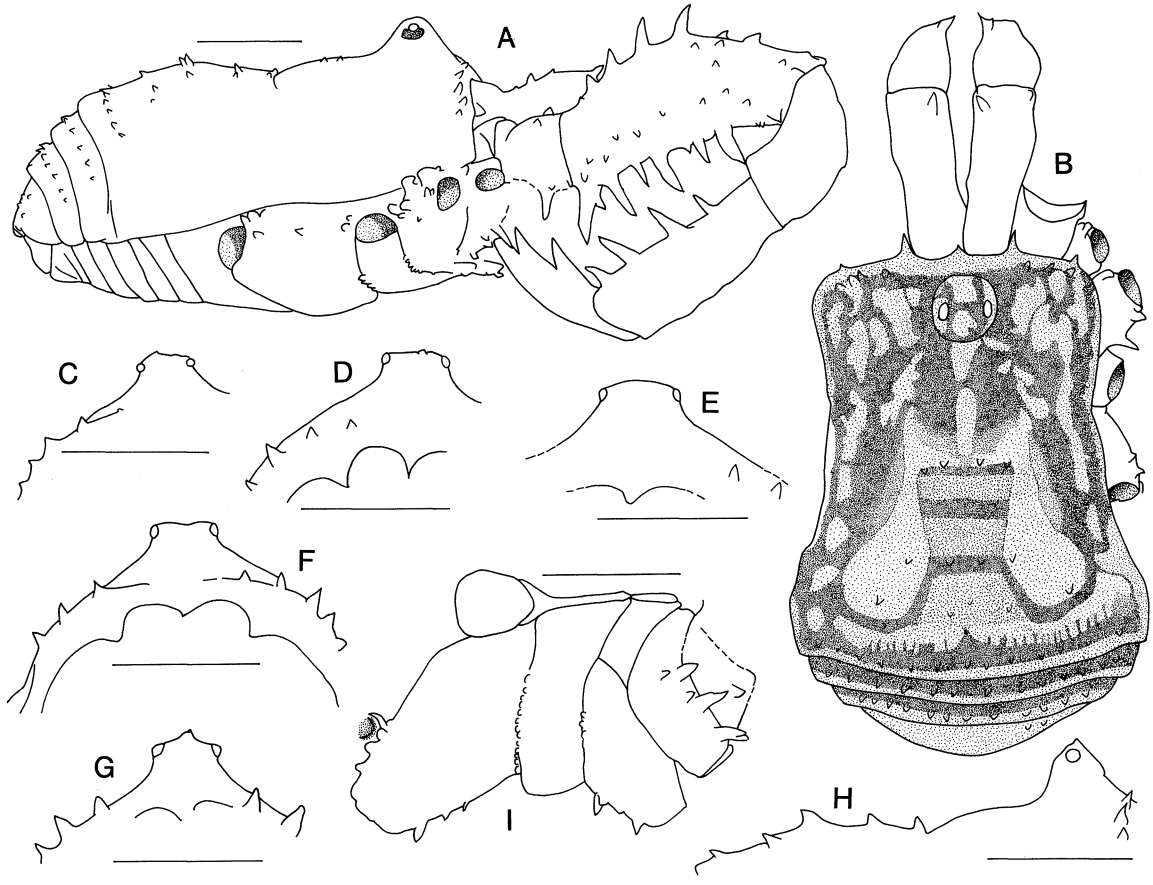

Fig.2. *Holonuncia cavernicola* Forster. A = body, lateral (KS19033); B = dorsum, relatively pigmented specimen, Imperial Cave, KS17829; C-G = eyemound and anterior spination, frontal; C-F = Jenolan Caves; C = holotype, D = KS19033, E = KS19049, F = KS17829, G = Mulgoa specimen, KS21416; Mulgoa specimen, lateral; I = coxisternal region, KS19033. All males. Scale bars = 1.0 mm.

Variation. Eyemound varies from canaliculate in a few specimens, rounded in most, to carrying a short spine in the Mulgoa population. Scute spination is subdued and legs relatively more elongate in holotype compared with most specimens. Mean relative leg length only slightly less for surface than for cave specimens. Pigmentation and eye size vary between cave and surface populations but also within the cave population(s).

Comments. One of Forster's male paratypes (K41749, Yarrangobilly Caves) lacks a notch in calcaneus I and belongs to *H. recta* n.sp. Surface populations at Jenolan and on the adjacent Boyd Plateau have an identical penis to cave populations of *H. cavernicola* and agree closely in other respects except eyes are normal in size and mean relative leg length is less (mean FIV:CW 1.30 compared to 1.54). These means are comparatively close, however the mean for the related *H. sussa* and *H. dewae* being respectively 2.35 and 2.09. Surface and cave populations of *H. cavernicola* are tentatively assigned to the same species. Variation in eyemound form noted above may indicate the presence of more than one species. For example, individuals at Jenolan Caves with a canaliculate eyemound may belong to a separate species

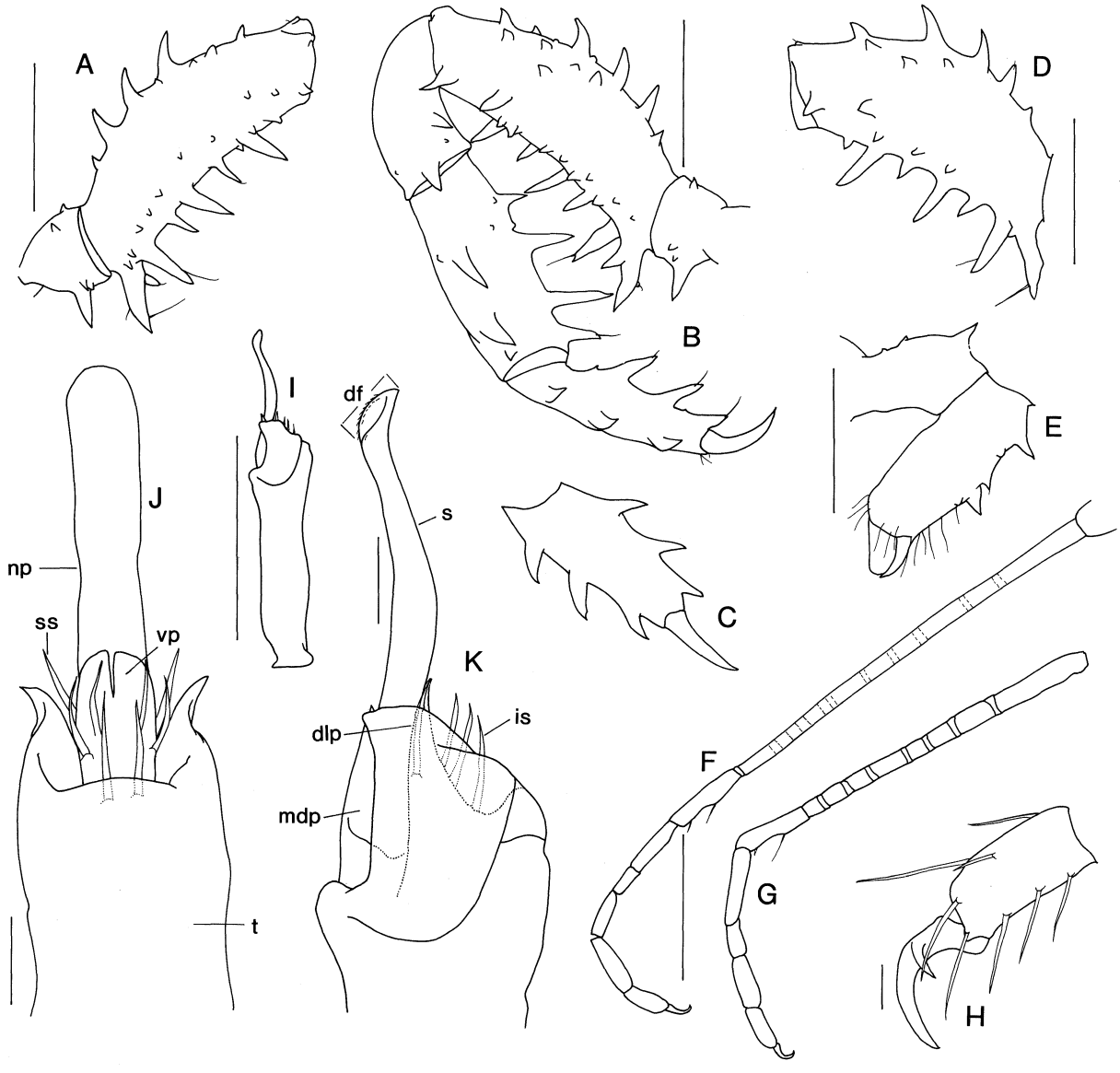

Fig.3. *Holonuncia cavernicola* Forster. D = female, others male; A-C, E-F = holotype. A = pedipalp femur, retrolateral; B = pedipalp, prolateral; C = pedipalp tarsus, ventral; D = pedipalp femur, prolateral, KS21402; E = chelicera, retrolateral; F-G = metatarsus and tarsus of leg I, retrolateral; G = epigean specimen, Boyd Plateau, KS21438; H = distal article of tarsus IV and claw with larger setae; I-K = penis, BS2185, I = entire, lateral, J = ventral, K = lateral. df = distal flexure, dlp = dorsolateral plate, is = inferior seta, mdp = mid-dorsal plate, np = narrowest point, s = stylus, ss = superior seta, t = truncus, vp = ventral plate. Scale bars: H, J-K = 0.1 mm, others = 1.0 mm.

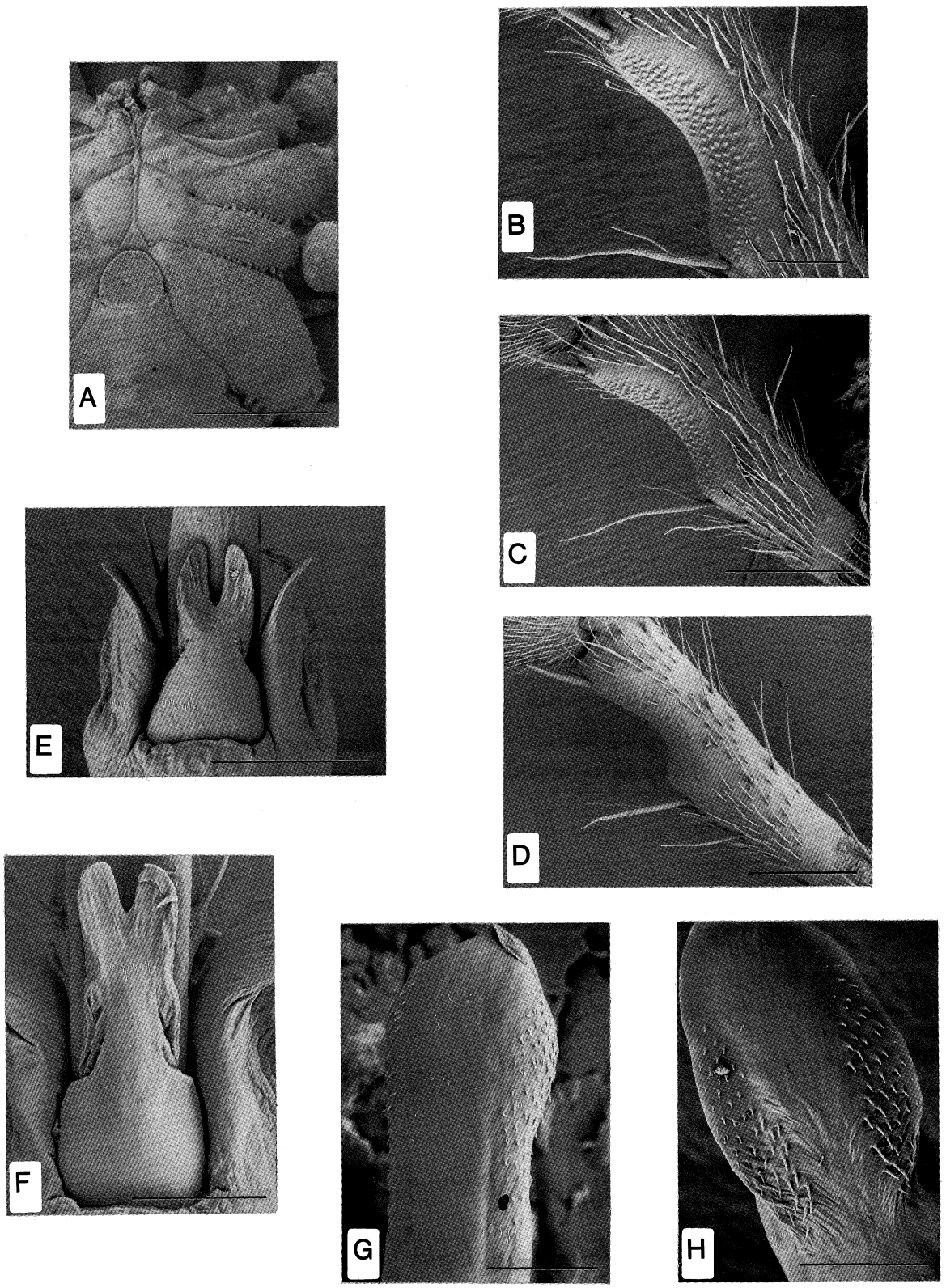

Fig.4. *Holonuncia* spp. A-C, F-G = *H. cavernicola Forster*; D-E, F = *H. seriata* (Roewer). A = coxisternal region; B-D = notch in calcaneus I, B = ventrolateral, C-D = prolateral; E-F = dorsal plate of penis; G-H = distodorsal denticles on stylus. Scale bars: A = 1.0 mm, B,F = 100 μm, C-E = 200 μm, G-H = 50 μm.

related to *H. sussa* which has such an eyemound. Allozyme electrophoresis would be useful in determining whether more than one species is present and whether gene flow occurs between cave and surface populations.

On the basis of penis form, *H. cavernicola* is most closely related to *H. sussa* and *H. dewae*.

Natural history. Cavernicolous individuals of *H. cavernicola* have usually been taken from the dark zone of caves. Surface individuals tend to be found deep in the core of large rotten logs (Hunt, 1979), in contrast to *Equitius doriae*, a common species in a related genus living in the same general habitat. *Equitius doriae* is easily found resting beneath even small logs and has never been collected beyond the entrance zone of caves. Surface populations of *H. cavernicola* may thus be 'preadapted' to cave life, or because of microhabitat preferences may have evolved in similar fashion to their cavernicolous relatives.

Distribution. New South Wales: Jenolan Caves area, both in caves and on the surface.

Holonuncia sussa n.sp.

Fig.5

Type material. New South Wales, Colong Caves: HOLOTYPE, male, AM KS 21439. PARATYPES: KS 21441, 1 female; KS21439, 2 females; SAM BS1292, K. Davey, 12 Jan. 1966, 1 male.

Diagnosis. Located in Colong Caves, eyemound 0.3 as high as long, eyes tiny, anterior margin without prominent tubercles or granules.

Description. MALE. Similar to *H. cavernicola* (cave population) except in the following. SL 2.75-3.55(n=2), CW 1.97-2.34. Eyemound rising slightly behind anterior margin at an angle of about 30°, only about 0.3 as high as long, canaliculate and smooth, eyes tiny; anterior margin and carapace smooth, TA1-4 smooth, at most with 1 or 2 small mesial granules in each. CSL 1.56-1.98. PFL 1.92-2.24, ratio PFL:CW 0.97-1.00; pedipalp femur with 4 mediodorsal spines in proximal half size order 3=4,2,1, and 6 retroventral spines size order 1,3=5,2,4=6; proximal accessory denticle on trifid spine weak, distal lacking but its seta present; spine 1 on retroventral margin of tibia less than 0.5 spine 2. Legs relatively longer, FIV 4.97-5.10, ratio FIV:CW 2.18-2.52, mean ratio MI:CW 1.66, calcaneus relatively longer, mean ratio CI:AI 0.25; tarsal claw and its lateral branch very slender; tarsal formula 4(2),14-16(3-4),4,4. Genitalia very similar to *H. cavernicola*.

FEMALE. Differs from male as in *H. cavernicola*; small distal accessory denticle present on trifid spine; tarsal formula 3(2),12-13(3),4,4.

Comments. *Holonuncia sussa* is most closely related to *H. dewae* but differs in its low profile eyemound and lack of tubercles on the anterior margin. A female, probably of *H. cavernicola* or *H. seriata*, has also been collected in Colong Caves but is readily distinguished from *H. sussa* by its more heavily spined dorsum and larger eyemound and eyes. This sympatry supports the view that *H. sussa*, the most troglomorphic species in *Holonuncia*, is genetically isolated from its surface congeners.

Etymology. The specific epithet is a latinised acronym of the Sydney University Speleological Society (SUSS) which has been responsible for much of the exploration and early faunal studies of the Colong Cave system, and of which I have been a member for almost 30 years.

Natural history. The species is apparently a troglobite.

Distribution. New South Wales: Colong Caves.

Holonuncia dewae n.sp.

Fig.6

Type material. New South Wales, Wombeyan Caves, 34°06'S 150°08'E: HOLOTYPE male, KS 23168, Basin Chamber, Basin Cave (W-4). PARATYPES: Basin Cave: KS 23169, G.S. Hunt, 1 June 1964, 1 male, 7 females; KS 23170, B.B. Dew, Nov. 1963, 1 female; KS 23171, B.B. Dew, 18 Apr. 1964, 2 juveniles. Fig Tree Cave (W-148): KS 21437, G.S. Hunt, 2 June 1964, 1 male, 1 female; KS 23172, G.S. Hunt, 2 June 1964, 1 juvenile; KS 23173, on guano, 30 Oct. 1965, 1 female, 1 juvenile. Bullio Cave (W-2): KS 23174, on flowstone, G. Smith, 16 Sept. 1979, 1 male, SAM BS1261, E. Hamilton-Smith, 27 Feb. 1966, 4 males, 3 females

Diagnosis. Located in Wombeyan Caves, pale orange in colour, calcaneus I with prominent notch; anterior margin with at most 2 prominent tubercles; lateral branches of tarsal claw IV inserted at about 0.5 claw length.

Description. MALE. Similar to *H. cavernicola* (cave population) except in the following. SL 3.31-4.18(3.68)(n=9), CW 2.34-2.86(2.54); body colour light orange with faint pigmentation pattern, slightly darker lateral to eyes; eyemound above eyes slightly conical, never canaliculate, eyes more reduced; anterior margin armed above with 2-3 tubercles/granules on each side, if 3 only 2 are conspicuous; tubercles/granules on dorsum slightly smaller. CSL 1.93-2.43(2.04). Pedipalps relatively longer, PFL 2.29-2.92(2.47), ratio PFL:CW 0.92-1.02(0.98). Legs relatively much longer, FIV 4.97-5.61(5.30), ratio

FIV:CW 1.82-2.40(2.09), metatarsi and tarsi very attenuated, mean ratio MI:CW 1.53; lateral branches inserted at about 0.5 length of tarsal claw of leg IV; tarsal formula 4(2),12-20(3),4,4. Stylus narrower basally, about 0.6 ventral plate width.

FEMALE. Differs from male as in *H. cavernicola*; CW 2.19-2.43(2.36)(n=4), PFL 1.92-2.16(2.05), FIV 4.88-5.12(5.02); tarsal formula 3(2),14-15(3),4,4.

Comments. The structure of the penis demonstrates that *H. dewae* is very closely related to *H. cavernicola* but differs from Jenolan cave specimens by the shape of the eyemound and tarsal claw on leg IV, and the tendency to have fewer tubercles/granules on the anterior margin and to have relatively longer legs. I had originally thought that the Wombeyan animals belonged in *H. cavernicola*. However, in addition to the slight morphological differences, it is probable that *H. dewae* is isolated from both surface and cave populations of *H. cavernicola*. *Holonuncia seriata* occurs in intervening country, at least at Mount Werong, and may well occur on the surface at Wombeyan.

Etymology. The specific epithet honours the late Miss Barbara Dew who was among the first Australian biospeleologists. It was on one of her field trips to Basin Cave, Wombeyan that I saw and collected my first

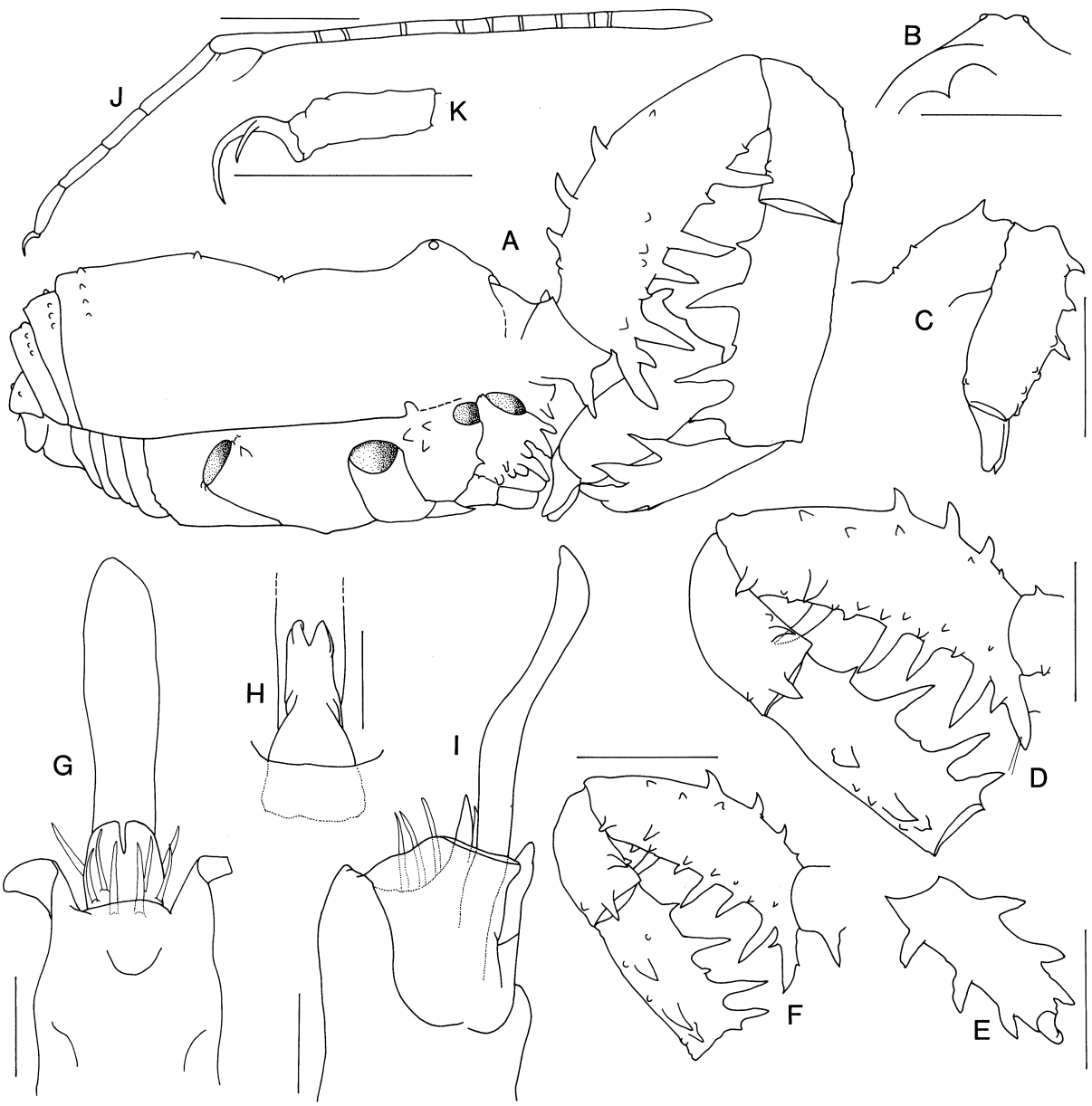

Fig.5. *Holonuncia sussa* n.sp. F = female, others male. A-E = holotype. A = body, lateral; B = eyemound, frontal; C = chelicera, retrolateral; D,F = pedipalp except tarsus, prolateral; E = pedipalp tarsus, ventral; G-I = penis, G = ventral, H = dorsal plate, I = lateral; J = metatarsus and tarsus of leg I, retrolateral; I = distal article of tarsus IV and claw. Scale bars: K = 0.5 mm, G-I = 0.1 mm, others = 1.0 mm.

harvestmen, an experience which led to my interest in the group.

Natural history. The species appears to be troglobitic.

Distribution. New South Wales: several caves at Wombeyan.

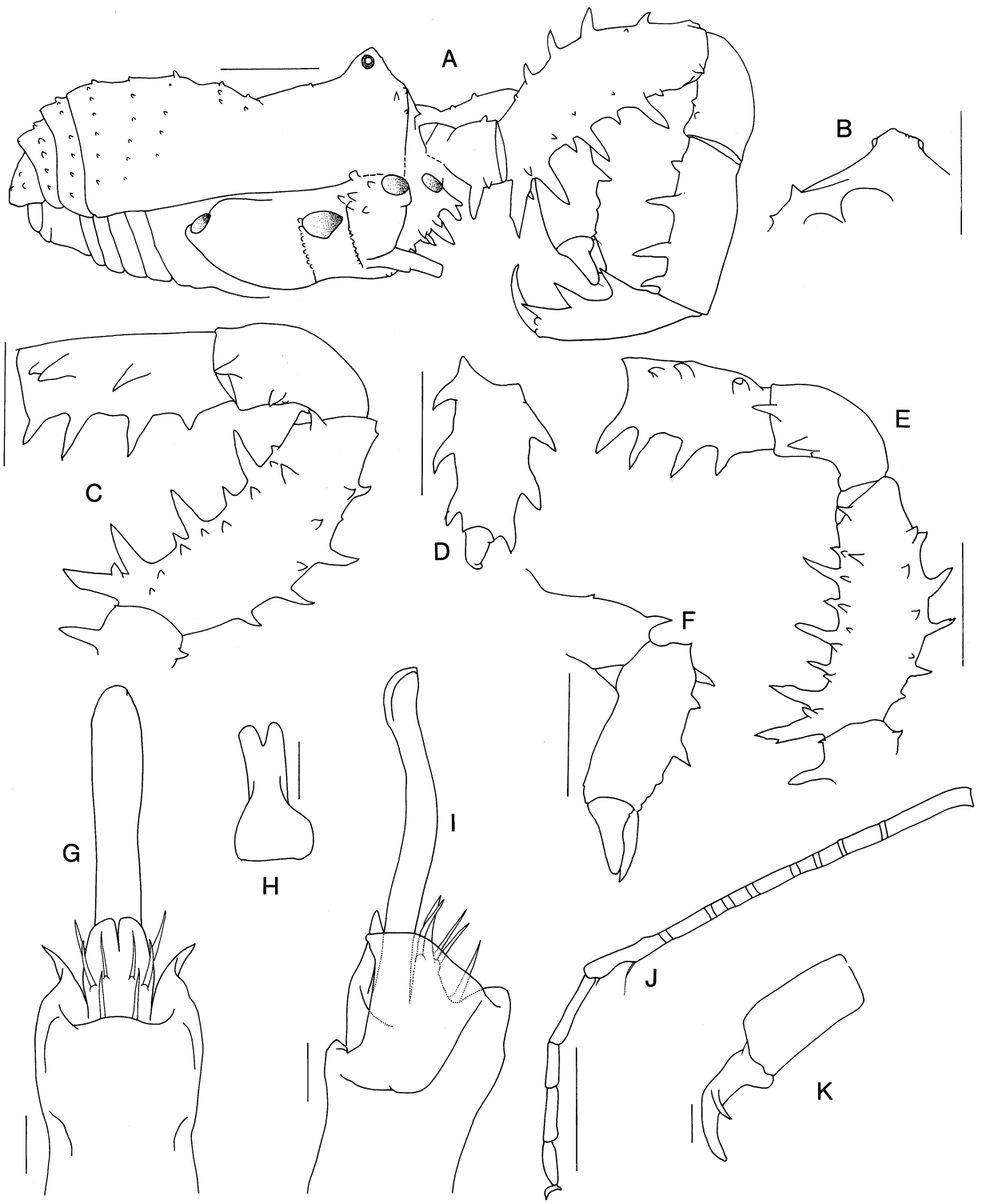

Fig.6. *Holonuncia dewae* n.sp. E = female, others male, KS21437. A = body, lateral; B = eyemound and anterior spination, frontal; C,E = pedipalp except tarsus, prolateral; D = pedipalp tarsus, ventral; F = chelicera, retrolateral; G-I = penis, G = ventral, H = dorsal plate, I = lateral; J = metatarsus and tarsus of leg I, retrolateral; K = distal article of tarsus IV and claw. Scale bars: G-I, K = 0.1 mm, others = 1.0 mm.

Holonuncia seriata (Roewer, 1915), n.comb.

Figs 4,7

Nuncia seriata, Roewer, 1915: 82-83.–Roewer, 1923: 593-4.

Type material. New South Wales: HOLOTYPE, female, Mount Murray, Roewer coll. no. 1020, no other data.

Additional material examined. New South Wales: Mount Murray near Robertson, 34°33'S 150°38'E: KS 19758, 650 m, closed forest, under rock, G.S. Hunt, 29 June 1987, 1 male; KS 19759, closed forest, under rotting wood, G.S. Hunt, 3 Jan. 1987, 2 females. The Gib, Mittagong, 34°05'S 149°56'E: KS 21408, under logs and rocks, G.S. Hunt, 24 Oct. 1987, 1 male, 2 females. Mount Werong, 34°05'S 149°56'E: KS 21436, near pluviometer, under logs, G.S. Hunt, 3 July 1972, 1 male; KS 21407, same data, 1 male, 2 juveniles. Plateau on Taralga Wombeyan Caves Road near Wombeyan, 34°22'S 149°49'E: KS 23175, under log, G.S. Hunt, 28 July 1989, 1 female. Bungonia Caves, 34°50'S 150°04'E: KS0648, Hogans Hole cave (B5), dark zone, D. Rothery, 15 Jan. 1977, 2 males; SAM BS0915, Fossil Cave (B4), B.P. Moore, 14 Mar. 1964, 2 males, 1 female. Other Bungonia Caves material is KS 21422, KS23180-3.

Redescription. MALE (Mount Murray, Mittagong population). Similar to *H. cavernicola* (cave population) except in following. Body slightly larger, CW 3.07-3.23(n=2), eyemound more elevated above eyes, eyes not reduced, tubercles/granules on TA1-5 slightly larger. CSL 2.70-2.87. Pedipalp and its spines more robust, PFL 2.94-2.99, ratio PF:CW 0.93-0.96; femur with row of 6 mediodorsal spines (size order 3=4,2,6,1=5) and 5 large retroventral spines (size order 1,5,3,4,2); spine 1 of tibia less than 0.5 length spine 2. Legs shorter, FIV 3.32-3.66, ratio FIV:CW 1.08-1.13; mean ratio MI:CW 0.91; calcaneus relatively longer, mean ratio CI:AI 0.33; tarsal formula: 5(2),11-12,4,4. Penis with ventral plate about 1.4 as long as wide, median notch about 0.25 plate length setae; mid-dorsal plate terminal cleft moderately deep, depth subequal to plate width; stylus viewed ventrally tapers gradually to narrowest point at about 0.7 its length, expands abruptly, is then constricted and expands apically; viewed laterally distal flexure long and narrow, width about 0.2 length; distodorsal denticles set in dorsolateral grooves.

FEMALE. Differs from male as in *H. cavernicola*. Tarsal formula: 3(2),10-13(3),4,4.

Variation. The Bungonia Caves population has relatively longer legs (mean FIV:CW 1.57 compared to 1.10), smaller eyes and less pigmentation than surface individuals.

Comments. Roewer (1915) sexes the type as a male, but it is a female. The population(s) in Bungonia Caves are tentatively assigned to this species. Electrophoretic study should help clarify relationships. A single female collected in Odyssey Cave has much longer legs than specimens from other caves. This cave is in a different limestone bed from most other caves in the Bungonia karst, connection being made below the water table by water flowing through fissures in intervening non-limestone strata (Jennings, 1972). It is therefore possible that this specimen represents a different, more troglomorphic species which is isolated from the other species in the Bungonia karst.

Specimens (KS23208, 21421, 19753-4) from the Budawang Ranges, south-west of Nowra, are morphologically very similar to *H. seriata*, but also resemble closely the specimens from Tomerong, near Nowra, which. on the basis of electrophoresis, probably represent a different species. The Budawang Ranges and Nowra are south of the Shoalhaven River while the type locality of *H. seriata* is to the north. Description of this putative new species will await further study of populations south of the Shoalhaven.

Distribution. New South Wales: plateaux country northwards from the Shoalhaven River to Mittagong and Mount Werong, both surface and caves.

Holonuncia tuberculata (Roewer, 1915)

Fig.8

Neonuncia tuberculata Roewer, 1915: 107-108.–Roewer, 1923: 605-6.
Holonuncia tuberculata.–Forster, 1955: 388, 390.

Type material. New South Wales: LECTOTYPE, male (here designated), New South Wales, Roewer coll. no. 1038, no other data, FIS. PARALECTOTYPE, female, same data, FIS.

Additional material examined. New South Wales: Royal National Park, 34°08'S 151°04'E: KS6666, Sydney University Zoology, 8 July 1972, 1 male, 1 juvenile; KS 21410, near Waterfall, under log, rainforest, S. McAuley, Apr. 1964, 1 male; KS 23177, Mascord Collection, R. Mascord, 2 July 1966, 1 female.

Diagnosis. Tarsus 1 of male with 4 segments, retroventral spines 3 and 5 on pedipalp close together (spine 4 may be lacking), retroventral spine 1 of pedipalp tibia reduced to a small granule.

Redescription. MALE. Similar to *H. cavernicola* (cave population) except in following. CW 2.48-2.72(n=4), eyes not reduced, pedipalp and its spines more robust, ratio PF:CW 0.77-0.88(0.83); femur with row of 6 mediodorsal spines size order 4,3,2,6,5,1 and 6 retroventral spines size order 5,1,3,2,4=6, spines 3 and 5 close together; retroventral spine 1 of tibia reduced to a granule. Legs shorter, FIV 2.67-3.5(3.01), ratio FIV:CW 1.08-1.12(1.10); mean ratio CI:AI 0.29; tarsal formula: 4(2),9-11(3),4,4. Penis with ventral plate about 1.7 as long as wide, median notch about 0.2 plate

length; mid-dorsal plate terminal cleft moderately deep, depth subequal to plate width; stylus viewed ventrally tapers gradually to narrowest point at about 0.7 its length and then expands apically, viewed laterally distal flexure long and narrow, width about 0.2 length; distodorsal denticles set in dorsolateral grooves.

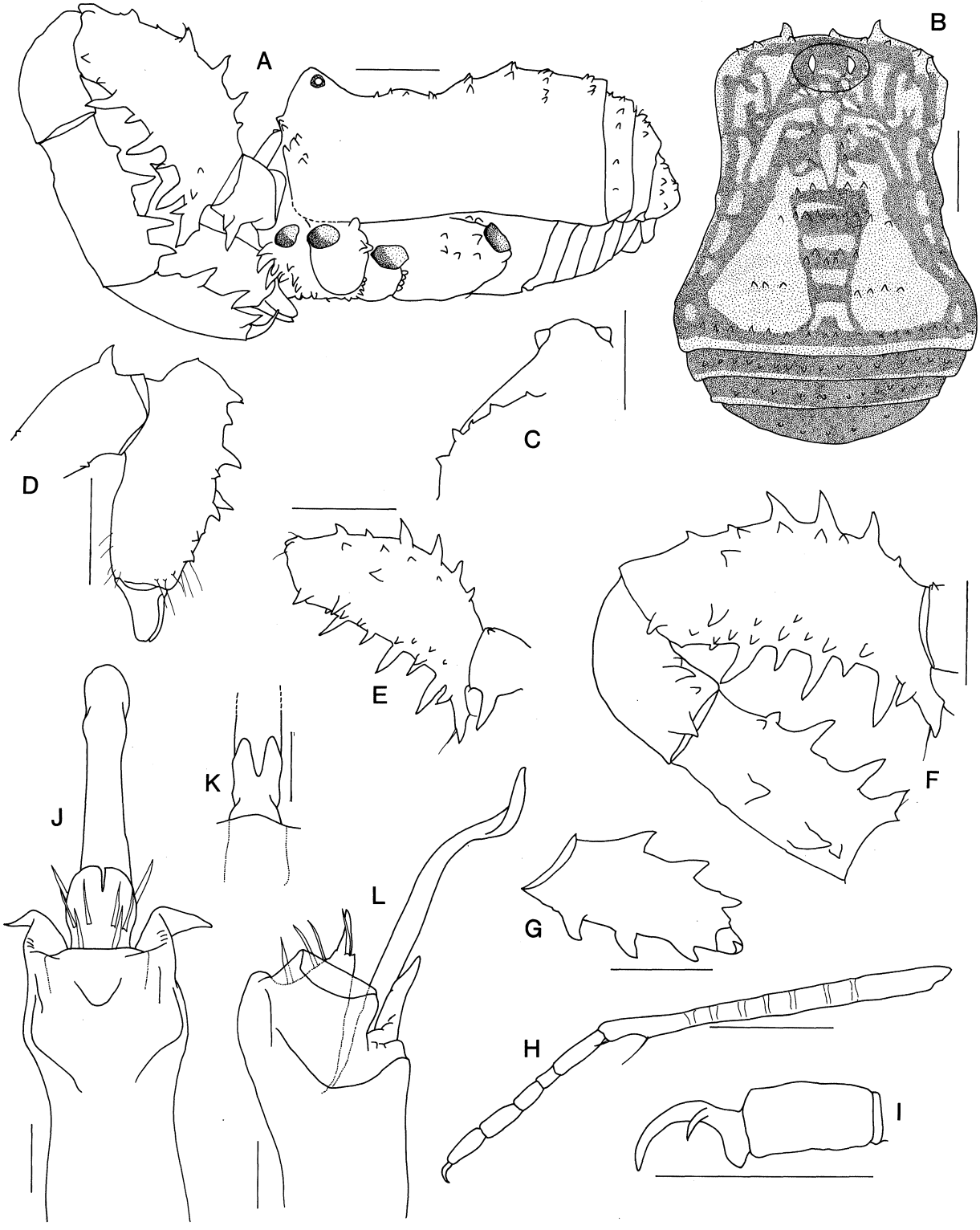

Fig.7. *Holonuncia seriata* (Roewer). E = holotype female, others male, KS19758. A = body, lateral; B = dorsum; C = eyemound and anterior spination, frontal; D = chelicera, retrolateral; E = pedipalp femur, prolateral; F = pedipalp except tarsus, prolateral; G = pedipalp tarsus, ventral; H = metatarsus and tarsus of leg I, retrolateral; I = distal article of tarsus IV and claw; J-L = penis, G = ventral, H = dorsal plate, I = lateral. Scale bars: I = 0.5 mm, J-L = 0.1 mm, others = 1.0 mm.

FEMALE. Differs from male as in *H. cavernicola* except that retroventral spine 1 on tibia remains granule sized in female. Tarsal formula: 3(2),10(3),4,4.

Comments. Forster (1955) placed this species in *Holonuncia* though he did not redescribe it. Roewer (1915, 1923) records the type locality as "Neu-Sud-Wales". Comparison of the lectotype male, particularly using pedipalp and genital structures, with specimens of known provenance indicates the species occurs in rainforest patches along coastal New South Wales between Port Hacking and the Shoalhaven River. This species differs from *H. seriata*, which occurs on plateaux areas immediately west of the coastal strip occupied by *H. tuberculata*, by the close spacing of retroventral spines 3 and 5 on the pedipalp femur, the small size of retroventral spine 1 on the tibia (though Mount Werong population of *H. seriata* has similar

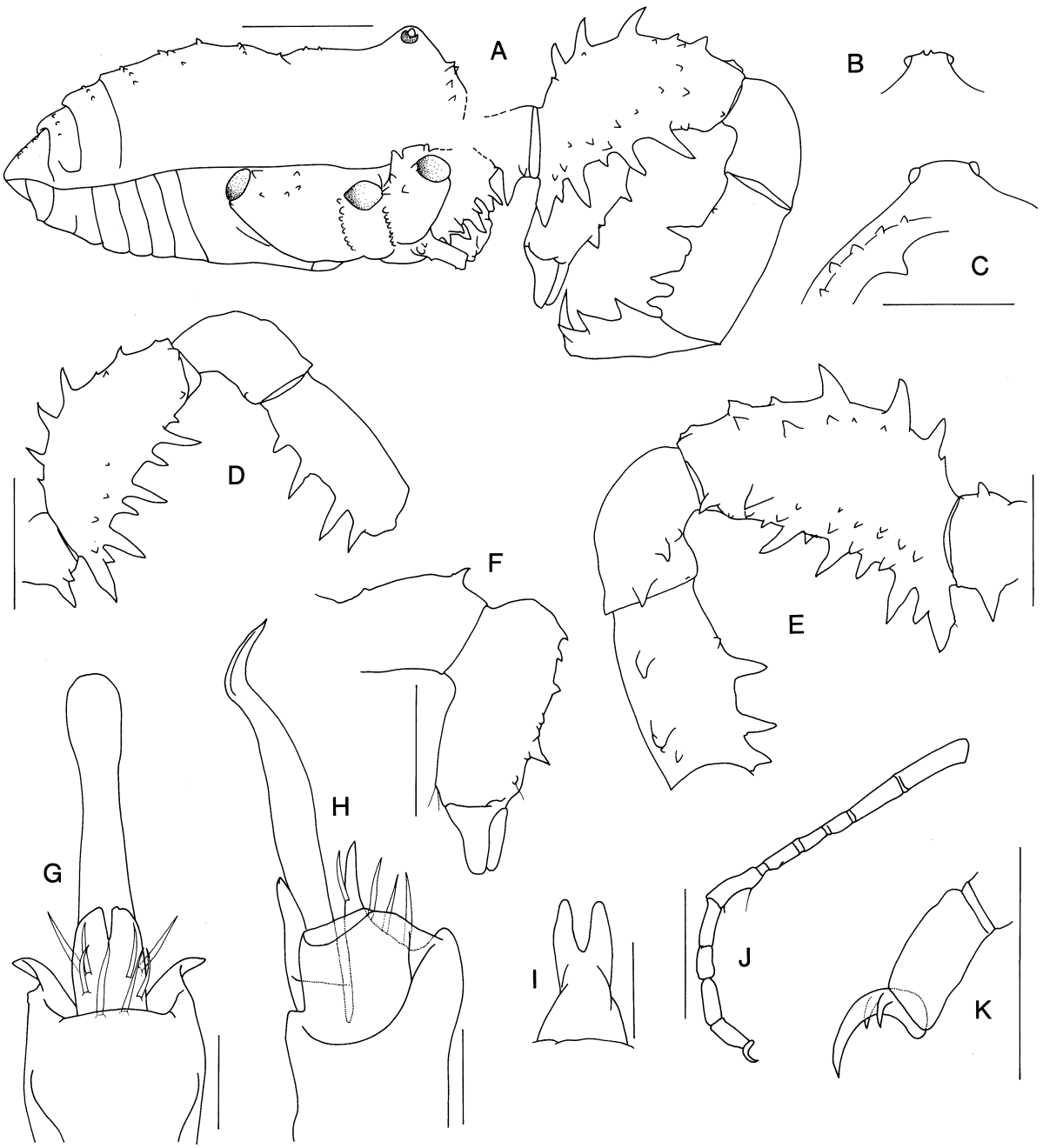

Fig.8. *Holonuncia tuberculata* (Roewer). B,D = paralectotype female, A,J-K = KS6666, others lectotype male. A = body, lateral; B-C = eyemound and anterior spination, frontal; D = pedipalp except tarsus, retrolateral; E = pedipalp except tarsus, prolateral; F = chelicera, retrolateral,; G-I = penis, G = ventral, H = lateral, I = dorsal plate; J = metatarsus and tarsus of leg I, retrolateral; K = distal article of tarsus IV and claw. Scale bars: G-I = 0.1 mm, K = 0.5 mm; other = 1.0 mm.

condition for this latter character), and four rather than a usual five segments in tarsus I.

Distribution. New South Wales: Royal National Park and south to Jamberoo Mountain.

Holonuncia francesae n.sp.

Fig.9

Type material. New South Wales: HOLOTYPE, male, KS 14251, Gordon (Sydney suburb), 33 44'S 151 09'E, in litter, C Horseman, 28 Mar. 1984. PARATYPES: type locality: KS 10122, KS 10125, KS 10271, KS 10575, KS 10888, KS 12376, KS 12387, KS 12407, KS 12418, KS 12438, KS 12641, KS 13297, KS 13332, KS 13465, KS 13568, KS 13579, KS 13751, KS 14043, KS 14049, KS 14255, KS 14408, KS 14750, KS 21458, KS 23186, KS 23187, KS 23188, pit-trapping program, 1982-4, C. Horseman and M.R. Gray, total 20 males, 14 females. Pymble reserve, Blackbutt Creek 33°45'S 151°09'E: KS 23193, under wood, G.S. Hunt, 5 July 1970, 1 male, 1 female. St Ives beside Ku-ring-gai Creek, 33°44'S, 151°10'E: KS 23196, under rotting wood in bush, G.S. Hunt, 3 Aug. 1969, 3 males, 6 females; KS 21409, KS 23206, under wood and stones, moist conditions, G.S. Hunt, 26 July 1969, 1 male, 2 females, 9 juveniles. Killara, 33°45'S 151°10'E: KS 23197, beside Arterial Road, under wood, very moist, G.S. Hunt, 24 Aug. 1969, 1 male, 2 female; KS 23203, 76 Rosebery Road, under small rocks in moist conditions, G.S. Hunt, 15 June, 1964, 1 female; KS 23204, same data, 1 male, 2 females; Ryde, Malvina High School, 33°48'S 151°06'E: KS 23189, under sandstone, G.S. Hunt, 3 June 1970, 1 male, 1 female; KS 23190, under rock moist conditions at edge of bush, G.S. Hunt, 22 May 1969, 1 female; KS 23191, same data, 1 Apr. 1969, 1 male, 3 females. Willoughby, 33°47'S 151°13'E: KS 23192, in bush beside rubbish tip, under log, G.S. Hunt, 2 Aug. 1969, 1 male; KS 23205, Gore Creek, M.R. Gray, July 1988, 1 male, 1 juvenile. Mosman, 51 Parriwi Road, 33°50'S 151°15'E: KS 23194, in garden at base of bananas, G.S. Hunt, 9 Aug. 1964, 3 males; KS 23195, under rock, G.S. Hunt, 28 Mar. 1988, 1 male. Greenwich, beside Gore Creek, 33°54'S 151°11'E: KS 23198, in cavity in moist log, G.S. Hunt, 27 July 1969, 2 females; KS 23199, under bark at base of *Angophora*, G.S. Hunt, 10 Aug. 1968, 1 male; KS 23200, under rock, G.S. Hunt, 29 July 1969, 2 juveniles. Narrabeen, 33°44'S 151°18'E: KS 23201, Middle Creek, Wakehurst Parkway, rainforest, G.S. Hunt, 13 June 1970, 1 female; KS 6670, downstream from Oxford Falls, Wakehurst Parkway, rainforest, G.S. Hunt, 1 Feb. 1982, 2 males, 1 female. North Curl Curl, 33°47'S 151°18'E: KS 23202, F.J. Beeman, 19 Aug. 1956, 1 male. Bargo, 34°17'S 150°35'E: KS 21411, 17.5 km south of Pheasants Nest Bridge, under log, G.S. Hunt, 24 Oct. 1987, 1 male; KS 23213, Tea Tree Hollow, north boundary Wirrimbirra Sanctuary, under canopy of leaves of Black Bog Rush, D. Wilson, 16 Aug. 1969, 1 male; KS 23214, same data, G.S. Hunt, 16 Aug. 1969, 3 females. south side Razorback Ridge near Camden, 34°03'S 150°42'E: KS 23215, under moist rotting wood in rainforest-like conditions beside tributary Racecourse Creek, G.S. Hunt, 17 Aug. 1969, 1 male, 3 juveniles.

Other material examined. New South Wales: Blue Mountains National Park, 18 km east of Woodford, 33°44'S 150°33'E, KS 6667 low open forest heath, under logs, M.R. Gray, 17 Apr. 1974, 1 male, 1 female. Royal National Park, 34°08'S 151°04'E: KS 13818, beside creek near end of Wallamarra track, under logs, rainforest, G.S. Hunt, 10 Jan. 1984, 1 female; KS 21412, M.R. Gray, July 1970, 1 male. Bilpin, 33°30'S 150°31'E: KS 16565, G.S. Hunt, 12 May 1986, 1 male. Between Bilpin and Kurrajong Heights, 33°32'S 150°38'E: KS 21418, dry sclerophyll, 1 male, 1 juvenile. St Albans via Wisemans Ferry, 33°18'S 150°59'E: KS 21413, beside creek in hilly country, G.S. Hunt, 20 Dec. 1969, 1 male. Watagan Mountains, 32°57'S 151°14'E: KS 21414, G.S. Hunt, no date, 2 male.

Diagnosis. Calcaneus I with notch, eyemound with short spine, largest mediodorsal spine on pedipalp femur in distal half, ventral plate of penis widest subdistally.

Description. MALE. Similar to *H. cavernicola* (cave population) except in following. Mean body size slightly smaller, CW 2.51-3.03(2.84)(n=5). Eyemound armed with a short spine; eyes not reduced. CSL 2.17-2.66(2.40); second segment of chelicera more spinose distodorsally. PFL 2.25-2.90(2.67), PFL:CW 0.87-0.98(0.92); pedipalp femur with 5-6 mediodorsal spines size order 5,4,3,6,2,1 and 5 retroventral spines size order 1=5,3,2,4; distal accessory denticle on trifid spine relatively strong; retroventral spine 1 on tibia less than 0.5 spine 2. FIV 3.84-4.40, FIV:CW 1.36-1.53(1.45), mean CI:AI 0.26; tarsal formula 4-5(2),10-12(3),4,4. Genitalia very similar to *H. seriata*.

FEMALE. Differs from male as in *H. cavernicola*; tarsal formula 3(2),9-10(3),4,4.

Variation. The shape of the dorsal plate varies (Fig.9I-K). The ventral plate cleft is somewhat deeper in the St Albans specimen.

Comments. The species is closely related to *H. seriata* and *H. tuberculata* but differs in having a spine on the eyemound.

A specimen carrying a spine on the eyemound and occurring south of the Shoalhaven River (near Nowra) is electrophoretically more similar to *H. francesae* from the Sydney region than the specimens without a spine with which it is in sympatry. Specimens bearing the spine also occur further south, for example, KS3842 and KS 2620 from Kioloa State Forest near Batemans Bay. The Shoalhaven River has proved a significant barrier for some taxa, for example in the related genus *Equitius* (Hunt, 1985). Populations south of the Shoalhaven and carrying an eyemound spine are considered to belong to a new, as yet undescribed species, with affinities to *H. francesae* whose distribution lies well to the north of the River. This undescribed species is sympatric with another undescribed species resembling *H. seriata* (see allozyme electrophoresis discussion below).

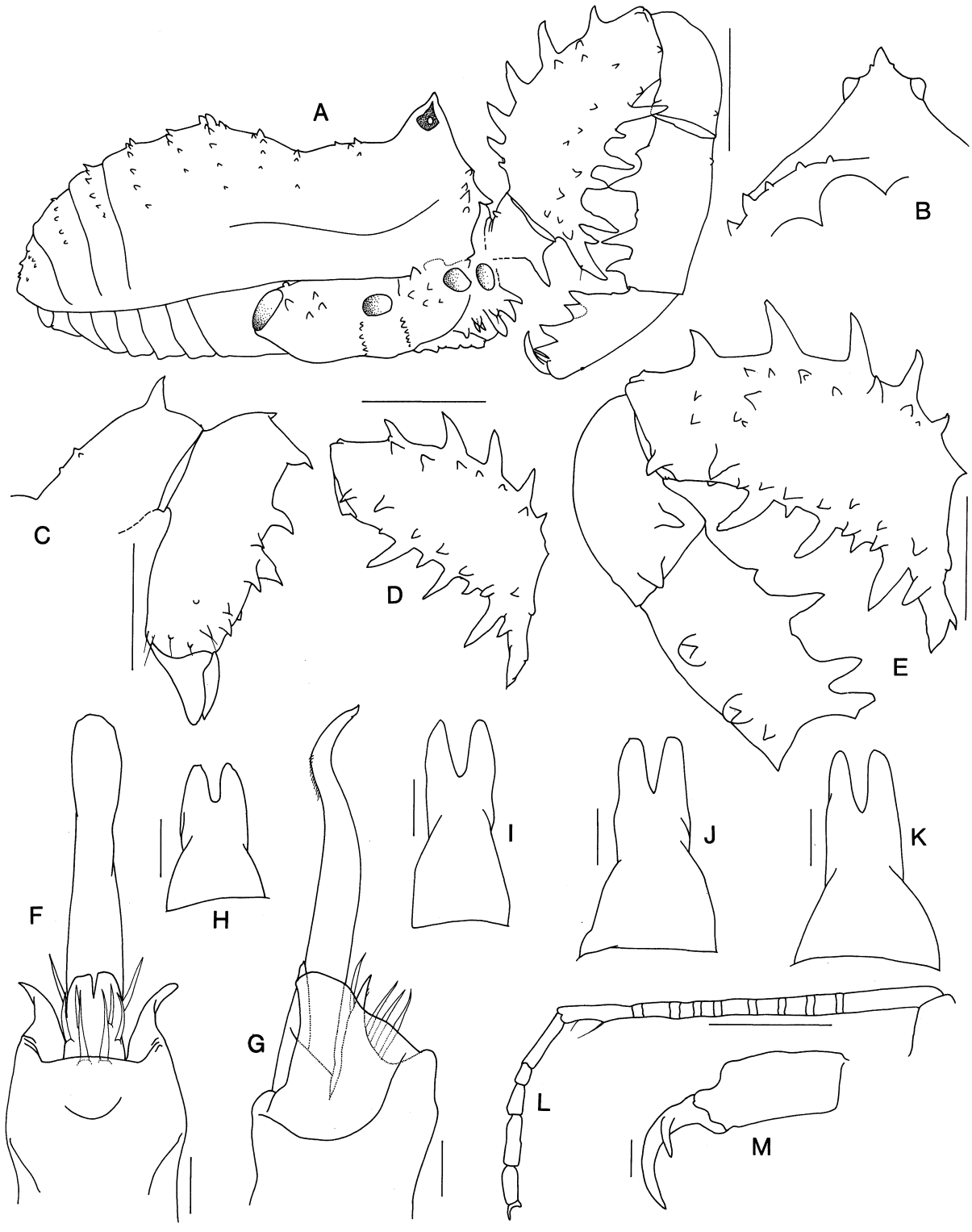

Fig.9. *Holonuncia francesae* n.sp. D = female, KS14750, A = holotype male, F-H = male, KS13332, others = male, KS13579. A = body, lateral; B = eyemound and anterior spination, frontal; C = chelicera, retrolateral; D = pedipalp femur, prolateral; E = pedipalp except tarsus, prolateral; F-H = penis, F = ventral G = lateral, H = dorsal plate; I-K = dorsal plate *ex* Pheasants Nest Bridge near Bargo, Saint Albans and Wattagan Mountains; L = metatarsus and tarsus of leg I, retrolateral; M = distal article of tarsus IV and claw. Scale bars: F-K, M = 0.1 mm, others = 1.0 mm.

Etymology. The specific epithet acknowledges the patience of my wife, Frances, whose support has made much of my research possible. Appropriately, the species occurs in our semi-natural garden in Mosman, a suburb of Sydney.

Natural history. In an extensive pit-fall sampling program at the type locality, males outnumbered females by approximately 4 to 1, indicating they were more ambulatory. This may be associated with reproductive activity.

Distribution. New South Wales: Sydney region, from Royal National Park in the south to Watagan Mountains in the north, and westwards to Bargo, and to Woodford and Bilpin in the Blue Mountains.

Holonuncia katoomba n.sp.

Fig.10

Type material. New South Wales, Katoomba, 33°43'S 150°19'E: HOLOTYPE, male, KS 21415, no other data; PARATYPE, male, KS 23179, no other data.

Diagnosis. Notch in calcaneus I of male prominent, eyemound with a small spine, anterior margin with 7-8 tubercles/granules on each side which tend to be directed forward, ventral plate of penis widest basally.

Description. MALE. Similar to *H. cavernicola* (cave population except in the following. Body larger, CW 2.64-3.06(n=2). Eyemound armed with a short spine, eyes not reduced; anterior margin armed with 7-8

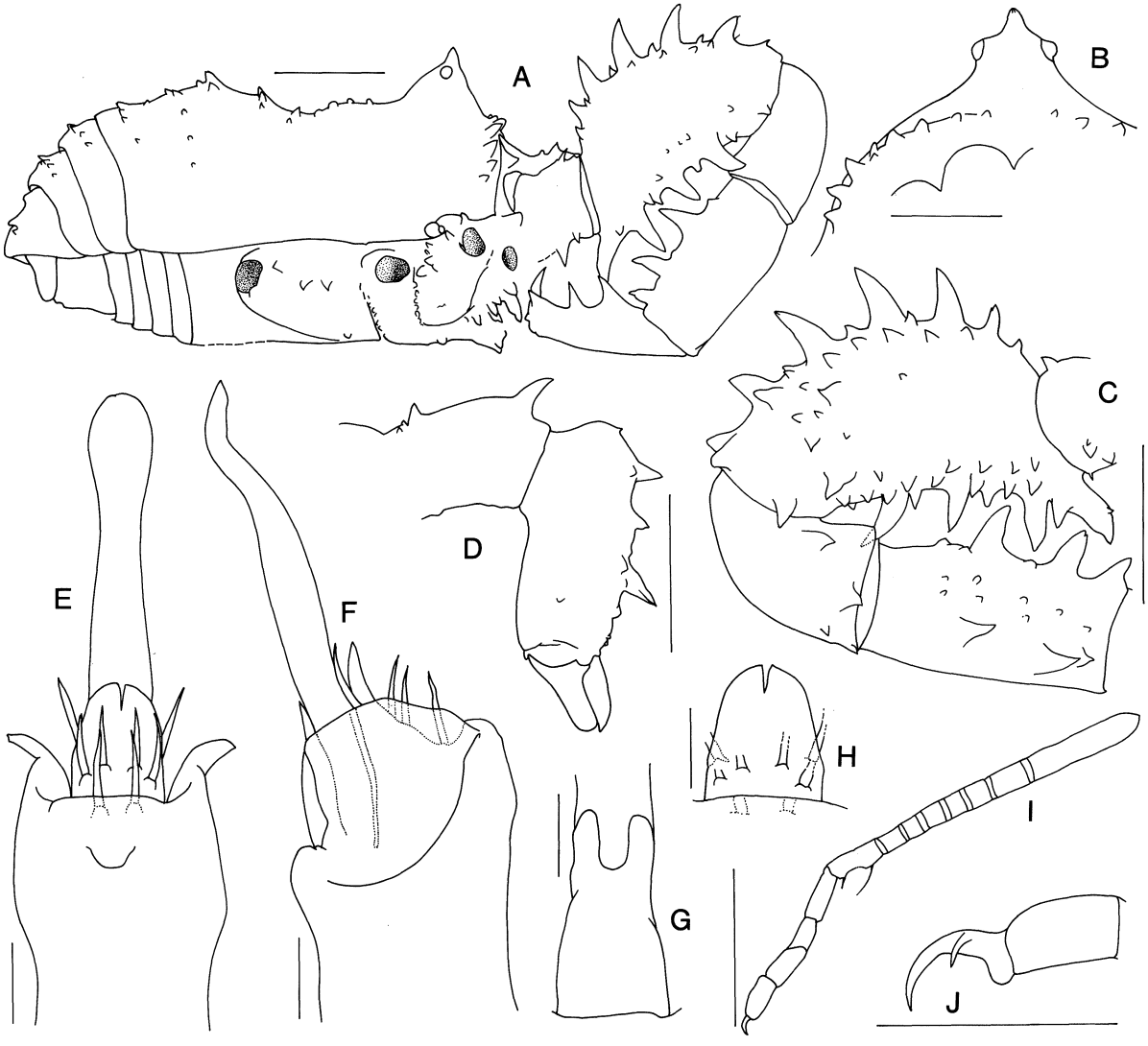

Fig.10. *Holonuncia katoomba* n.sp. A-G = holotype male; H-J = male, KS21415. A = body, lateral; B = eyemound and anterior spination, frontal; C = pedipalp except tarsus, prolateral; D = chelicera, retrolateral; E-G = penis, E = ventral, F = lateral, G = dorsal plate; H = ventral plate shape; I = metatarsus and tarsus of leg I, retrolateral; M = distal article of tarsus IV and claw. Scale bars: E-H = 0.1 mm; J = 0.5 mm; others = 1.0 mm.

tubercles/granules on each side which tend to directed forward. Mesial spines on TA3 larger. CSL 1.98-2.19, second segment robust, mid-dorsal spine much longer than proximodorsal spine. Pedipalp femur short and robust, PFL 2.27-2.47, PFL:CW 0.81-0.86; femur with 5-6 mediodorsal spines size order 5,4,3,6,2,1; 5 retroventral spines size order 1 or 5,3,2=4; proventral surface more spinous; spine 1 on tibia reduced to granule, venter of tibia granular. Legs short, FIV 3.06-3.23, FIV:CW 1.06-1.16; mean CI:AI 0.23; tarsal formula 4(2),9-10(3),4,4. Ventral plate of penis broadest basally, 1.5 as long as wide, 1.5 wider than base of glans, median cleft shallow, about 0.2 plate length; mid-dorsal plate cleft wide but depth only about 0.66 width of plate; stylus viewed ventrally tapers to narrowest point at about 0.75 its length and distally expands smoothly, viewed laterally distal flexure long, width about 0.2 its length; distodorsal denticles set in dorsolateral grooves.

Comments. *Holonuncia katoomba* has a localised distribution near the western periphery of the range of *H. francesae*, the species to which it is closely related. It differs in a more spinose anterior margin, and in the shape of the ventral and dorsal plates.

Etymology. The specific epithet is a noun in apposition and is the name of the type locality, Katoomba.

Distribution. New South Wales: Katoomba, Blue Mountains.

Holonuncia weejasperensis n.sp.

Fig.11

Type material. New South Wales, Wee Jasper Caves, 35°08'S 148°40'E: HOLOTYPE, male, ANIC, Humidicrib Cave (WJ-34), E. Holm, 19 May 1987. PARATYPES: KS 1531, Dip Cave (WJ-1), dark zone, M. Marx, 7 May 1978, 1 male, 1 female; KS 16256, cave 6.5 km south of Wee Jasper, J.H. Webb, 4 Jan. 1956 1 male.

Diagnosis. Wee Jasper Caves, notch in calcaneus I shallow, pedipalp femur with 6 mediodorsal spines.

Description. MALE. Similar to *H. cavernicola* (cave population) except in the following. Body tends to be smaller, CW 2.3 (n=1). CSL 1.90. PFL 2.27, PFL:CW 0.99; femur with 6 mediodorsal spines size order 3=4,2,1=5=6 and 6 retroventral spines size order 1=3=3,2 or 4,6. Legs tend to be relatively longer, FIV 4.00, FIV:CW 1.74, calcaneus relatively longer CI:AI 0.29, notch in calcaneus I long and shallow; lateral branches on tarsal claw of leg IV inserted at about 0.5 claw length; tarsal formula 4(2),11-13,4,4. Ventral plate of penis about 1.3 as long as wide, median notch deep, about 0.5 plate length. Dorsal plate terminal cleft moderately deep, depth subequal to plate width; stylus similar to *H. seriata.*

FEMALE. Differs from male as in *H. cavernicola.* Tarsal formula: 3(2),12-17(3),4,4.

Comments. *Holonuncia weejasperensis* is closely related to *H. seriata* which occurs in surface and cave habitats in the coastal ranges north-east of Wee Jasper. It differs from cavernicolous *H.seriata* in having a long, shallow notch in calcaneus of leg I. Humidicrib cave was chosen as the type locality as there has been research on its bat colony (Hall *et al.*, 1975) and it is less subject to recreational use than Dip Cave.

Etymology. The specific epithet refers to Wee Jasper Caves in which the species occurs.

Natural history. The species appears to be a troglobite.

Distribution. New South Wales: Wee Jasper Caves.

Holonuncia dispar n.sp.

Fig.12

Type material. New South Wales, Budawang Ranges, Quiltys Mountain, 35°22'S 150°03'E. HOLOTYPE, male, KS21419, under rocks in rainforest beside Kilpatrick Creek, eastern side of mountain, G.S. Hunt, 17 Apr. 1969. PARATYPE, female, KS 21435, same data.

Diagnosis. Notch in calcaneus I of male shallow; ventral plate of penis wide, almost twice as wide as base of glans, and equipped with 2 superior setae.

Description. MALE. Similar to *H. cavernicola* (cave population) except in the following. SL 3.85. Colour pattern of dorsum has faded in preservation. Eyemound shortly conical in anterior view, eyes not reduced. Anterior margin with smaller tubercles; granules on carapace posterior to eyes lacking; mesial tubercles on TA3 smaller; genital operculum more round. CSL 2.45. Pedipalp and its spines more robust, PFL 2.70; size order mediodorsal spines on femur 3=4,2,1,5, size order retroventral spines 5,1=3,2,4; proximal retrolateral spine on tibia blunt. Legs relatively short; notch in calcaneus shallow; tarsal formula 4(2),12(3),4,4. Ventral plate of genitalia with 2 superior and 3-4 inferior setae, about as wide as long, almost twice as wide as base of glans, notch about 0.25 plate length; mid-dorsal plate terminal cleft moderately deep, depth subequal to plate width; stylus viewed ventrally with apical expansion more clearly defined, viewed laterally wider basally, distal flexure long and narrow, width about 0.25 length; distodorsal denticles

set in dorsolateral grooves; dorsolateral plate broad distally.

FEMALE. Differs from male as in *H. cavernicola*. Carapace with 2 granules posterior to eyes; calcaneus of similar length to that in male; tarsal formula 3(2),11(30,4,4).

Comments. The affinities of this species are uncertain but, on the basis of stylus shape, it appears more closely related to *H. seriata* than to *H. cavernicola*. The male is readily separated from *H. seriata* by the shallow notch and the two superior setae on the penis ventral plate. It is sympatric with a species of *Holonuncia* which is similar morphologically to, but distinct electrophoretically from, *H. seriata*. Females of *H. dispar* cannot be differentiated with certainty from this sympatric species. Because *H. dispar* appears to be rare, an unusual female having a calcaneus of similar length to the male was selected as a female for this species. Verification of this choice is needed.

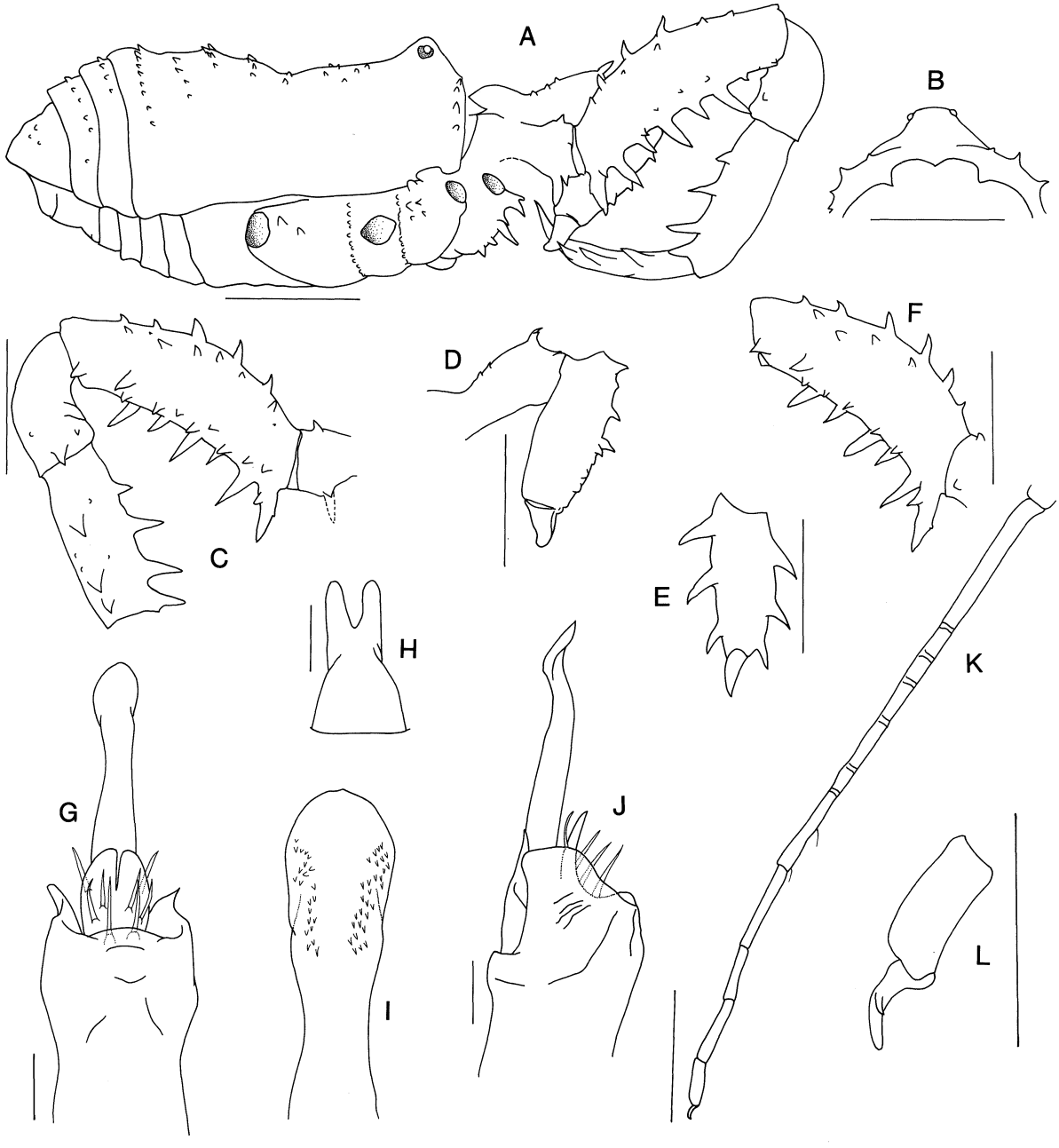

Fig.11. *Holonuncia weejasperensis* n.sp. F = female; others = holotype male. A = body, lateral; B = eyemound and anterior spination, frontal; C = pedipalp except tarsus, prolateral; D = chelicera, retrolateral; E = pedipalp tarsus, ventral; F = pedipalp femur, prolateral; G-J = penis, G = ventral, H = dorsal plate, I = distodorsal part of stylus; J = penis, lateral; K = metatarsus and tarsus of leg I, retrolateral; L = distal article of tarsus IV and claw. Scale bars: G-H,J = 0.1 mm, I = terminal part of G enlarged; L = 0.5 mm, others = 1.0 mm.

The asymmetrical presence, in the single male available, of four inferior setae on one side of the ventral plate and the usual three on the other suggests the possibility that the presence of two superior setae, albeit symmetrical, may be due to a somatic abnormality. However, the shallow notch and the fact that two superior setae is a consistent character in some species of the closely related *Hickmanoxyomma* (Hunt, 1990) suggest that *H. dispar* is a valid species and not an abherrent form of the more common species in sympatry with it.

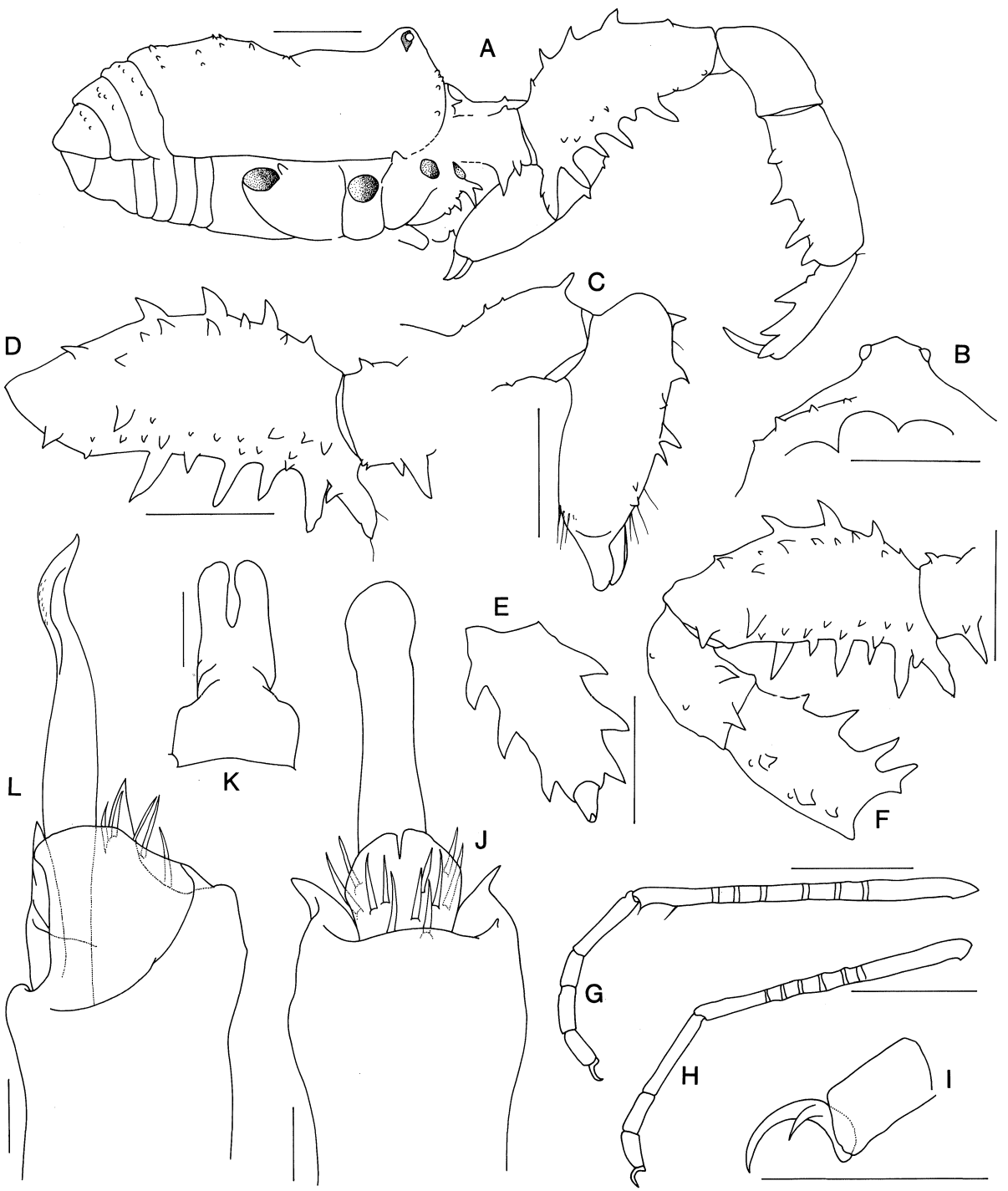

Fig.12. *Holonuncia dispar* n.sp. F,H = female, KS21435; others = holotype male. A = body, lateral; B = eyemound and anterior spination, frontal; C = chelicera, retrolateral; D = pedipalp femur, prolateral; E = pedipalp tarsus, ventral; F = pedipalp except tarsus, prolateral; G-H = metatarsus and tarsus of leg I, retrolateral; I = distal article of tarsus IV and claw; J-K = penis, J = ventral, K = dorsal plate, L = lateral. Scale bars: J-L = 0.1 mm, I = 0.5 mm, others = 1.0 mm.

Etymology. The specific epithet refers to the unusual male genital features of this species.

Distribution. New South Wales: rainforest at the base of Quiltys Mountain, Budawang Ranges.

Holonuncia recta n.sp.

Fig.13

Type material. Australian Capital Territory: HOLOTYPE, male, KS21426, Mount Murray, near Jacks Creek just upstream of Yaouk Trail, open eucalypt forest, under log, 800 m, G.S. Hunt, 21 Apr. 1987. PARATYPES: KS14327, Tidbinbilla Nature Reserve, M. R. Gray, 9 Mar. 1978, 1 male; KS21427, same data, 1 female; KS21429, same data, 1 female; ANIC, Blundels, F. J. Gay, 7 Mar. 1958, 1 male; Bulls Head, under log, 19 Nov. 1958.

Other material examined. New South Wales: Yarrangobilly Caves, 35°43'S 148°30'E: Paratype male *H. cavernicola*, KS 6913. Stead. KS5703, Grotto Cave (Y-30), K. Keck, 3 Jun. 1980, 1 female; KS23211, cave, G. Butler, June 1957, 1 female; Eyrie Cave (Y-3E), M.R. Gray, 31 Oct. 1980, 1 male; SAM BS1912, un-named cave, G. Middleton, 27 Jan. 1970, 2 males; KS23212, on surface, near creek behind 'power house', under log, G.S. Hunt, 4 Apr. 1988, 1 female. Cooleman Plains: River Cave (CP-6), G. Smith, 15 Apr. 1979, 1 female. ?London Creek: ANIC, label indistinct, 1 male. Brown Mountain: ANIC, rainforest, berlesate no. 24, about 800 m, R.W. Taylor and R.J. Bartell, 11 Apr. 1967, 1 male.

Diagnosis. Calcaneus I without notch, carapace width greater than 2 mm, stylus without strong expansion near its base.

Description. MALE. Similar to *H. cavernicola* (cave population) except in the following. Body large, CW 3.18-3.57(3.32)(n=4). Eyemound tends to slope more gradually posteriorly than anteriorly, eyes not reduced; genital operculum about as wide as long. CSL 2.68-3.05(2.89), dorsal spines and tubercles on second segment strong, spine placed at about 0.3 strong. PFL 3.01-3.60(3.28), ratio PFL:CW 0.95-1.01(0.99). Pedipalp femur with row of 6 mediodorsal spines size order 3=4,2,1,5=6; size order of retroventral spines 1=3=5,2,4; proximal accessory denticle on trifid spine strong; prolateral surface more spinose; retroventral spine 1 on tibia less than 0.5 length spine 2, proventral spine 3 weak, less than 0.5 length spine 2. Legs relatively short, FIV 3.86-4.46(4.24), ratio FIV:CW 1.21-1.33(1.26), mean MI:CW 0.98; calcaneus I without notch, mean CI:AI 0.27; tarsal formula 4(2), 10-15(3),4,4. Genitalia similar to *H. seriata*.

FEMALE. Differs from male as in *H. cavernicola* except that calcaneus 1 without conspicuous dimorphism; tarsal formula 3(2),9-11(3),4,4.

Variation. The specimens from Yarrangobilly Caves are smaller, CW 2.68-3.17(2.85)(n=4), and show some troglomorphy including eye reduction and leg attenuation, FIV:CW 1.70-1.81(1.76). The median cleft in the ventral plate is deeper, about 0.5 plate length and the plate is somewhat broader. The surface specimens from Brown Mountain to the east tend to have a prominent flange on the dorsolateral plate. The specimen from London Creek has a slightly canaliculate eyemound.

Comments. This species appears most closely related to *H. hamiltonsmithi* which also lacks a notch and inhabits the same general region of Australia. It differs from the latter species in spination of the anterior margin and the shape of the stylus. Despite having a straight calcaneus I, *H. recta* also appears closely related to *H. seriata* and *H. weejasperensis*.

The differences between surface populations and the cave populations at Yarrangobilly are suggestive of genetic isolation and perhaps specific difference. Allozyme work would help resolve this problem. KS21425 from Piccadilly Circus, Brindabella Range, has a notch in calcaneus I and belongs to a different species. As the male genitalia were lost, the species remains undescribed.

Etymology. The specific epithet refers to the straight calcaneus I of the male.

Distribution. South-east New South Wales and Australian Capital Territory.

Holonuncia hamiltonsmithi n.sp.

Fig.14

Type material. Victoria, Limestone Creek Caves, 36°50'S 148°05'E. HOLOTYPE, male: SAM N1992233, Sheehans Cave (LC-5), E. Hamilton-Smith, 11 Mar. 1972. PARATYPES: SAM, same data, 1 female; SAM BS2205, Cave LC-1Q, E. Hamilton-Smith, 11 Mar. 1972, 2 females.

Diagnosis. Limestone Creek Caves, calcaneus I without notch; glans very broad above base, very narrow subapically.

Description. MALE. Similar to *H. cavernicola* (cave population) except in the following. Body (1 specimen) smaller, CW 2.24. Eyemound rising at about 45° from slightly behind anterior margin, armed with a very short spine; anterior margin unarmed above except for 3 small granules; genital operculum about as wide as long. CSL 1.74. PFL 1.86, PFL:CW 0.83. Pedipalp femur with row of 6 mediodorsal spines size order 4,3,2,1,5=6; size order of retroventral spines 1,3=5,2=4; distal accessory denticle on trifid spine lacking; retroventral spine 1 on tibia weak, 0.5 spine

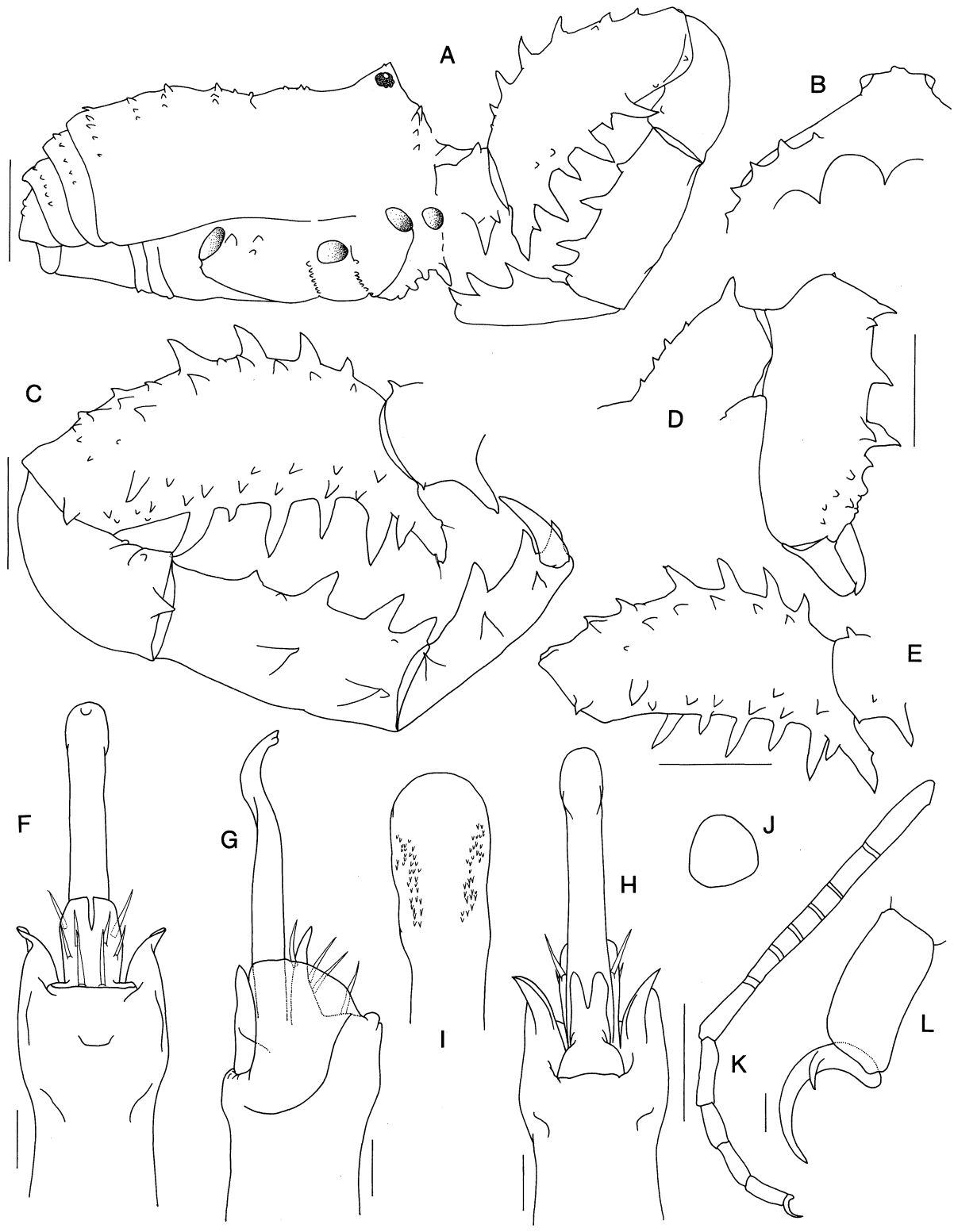

Fig.13. *Holonuncia recta* n.sp. E = female, KS21427, others = holotype male. A = body, lateral; B = eyemound and anterior spination, frontal; C = pedipalp except tarsus, prolateral; D = chelicera, retrolateral; E = pedipalp femur, prolateral; F-I = penis, F = ventral, G =lateral, H = dorsal, I = distodorsal part of stylus; J = genital operculum; K = metatarsus and tarsus of leg I, retrolateral; L = distal article of tarsus IV and claw. Scale bars: F-H = 0.1 mm, I = terminal part of H enlarged; L = 0.1 mm, others = 1.0 mm (J same scale as A).

2, FIV 3.81, FIV:CW 1.70; calcaneus I without notch, relatively long, CI:AI 0.36; lateral branch of tarsal claw IV inserted at about 0.5 claw length; tarsal formula 4(2),10-12(3),4,4. Ventral plate about as long as wide, median cleft about 0.5 plate length; in dorsal and ventral view glans somewhat narrow basally, broadens, constricts to a very narrow neck at about 0.7 glans length, termination similar to *H. seriata.*

FEMALE. Differs from male as in *H. cavernicola* except that body larger, CW 2.54-2.76(n=3), tubercles on anterior margin slightly more developed, distal accessory denticle present on trifid spine; calcaneus 1 without dimorphism; tarsal formula 3(2),11-14(3),4,4.

Variation. The size difference between the male specimen and three females may be due to sample size.

Comments. This species appears most closely related to *H. recta* which also lacks a notch in calcaneus I. I cannot determine whether specimens (females - SAM BS1731, BS1735) from nearby Indi Caves belong to this species, *H. recta*, or to a third species.

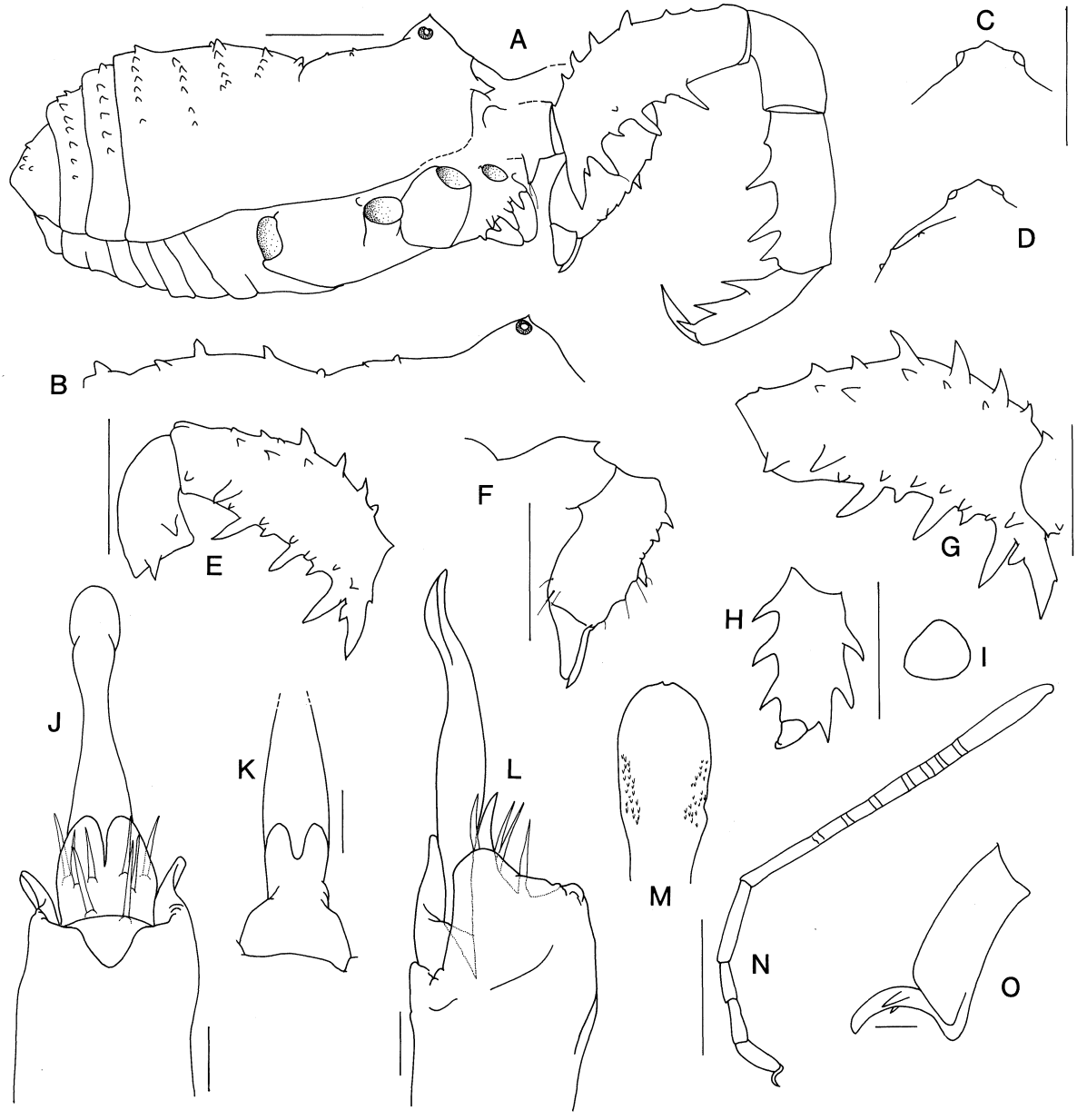

Fig.14. *Holonuncia hamiltonsmithi* n.sp. B,C,G = female, BS2205; others = holotype male. A = body, lateral; B = dorsal profile of scute; C-D = eyemound and anterior spination, frontal; E,G = pedipalp femur, prolateral; F = chelicera, retrolateral; H = pedipalp tarsus, ventral; I = genital operculum; J-M = penis, J = ventral, L =lateral, K = dorsal plate, M = distodorsal part of stylus; N = metatarsus and tarsus of leg I, retrolateral; O = distal article of tarsus IV and claw. Scale bars: J-L = 0.1 mm, M = terminal part of J enlarged; O = 0.1 mm, others = 1.0 mm (I same scale as A).

Etymology. The specific epithet acknowledges the contribution that Elery Hamilton-Smith has made to Australian biospeleology, including collection of the specimens for this species.

Distribution. Limestone Creek Caves in northern Victorian Alps.

Holonuncia kaputarensis n.sp.

Fig.15

Type material. New South Wales, Nandewar Ranges via Narrabri, 30°15'S 150°15'E. HOLOTYPE, male: Mount Kaputar National Park near Mount Kaputar turnoff, under log, field no. 2337, M.R. Gray and C. Horseman, 23 Feb. 1983.

Diagnosis. Notch in calcaneus I of male short and shallow, eyemound armed with spine, median cleft in penis ventral plate deep, greater than 0.5 plate length, distodorsal denticles on stylus large.

Description. MALE. Similar to *H. cavernicola* (cave population) except in the following. CW 2.50 (n=1). Eyemound rising at about 70° from anterior margin, armed with a short spine, eyes not reduced; carapace lacking granules behind eyemound; TA1-5 slightly more tuberculate, mesial spine on TA1 larger than spine on TA2. CSL 1.87. PFL 2.13, PFL:CW 0.85; pedipalp femur with 5 mediodorsal spines size order 2=3,1,4,5 and 5 retroventral spines size order 1,3=4,2,5; retroventral spine 1 on tibia reduced to a denticle, tibia granulate ventrally. Calcaneus I short, CI:AI 0.15; notch very shallow. FIV 3.86, FIV:CW 1.54; tarsal formula 4(2),11(3),4,4. Width of ventral plate subequal to length, cleft deep, greater than 0.5 plate length and reaching almost to level of bases of distal pair of inferior setae; dorsolateral plate very broad, in lateral view obscuring mid-dorsal plate, in ventral view basal part broad and tapering abruptly to short lamina part; glans narrowest basally, broad apically; dorsal denticles larger, fewer and placed more terminally than in *H. cavernicola*.

Comments. Genital structure suggests a closer relationship to *H. enigma* than to other *Holonuncia* spp. *H. kaputarensis* is the most northerly record of the genus. The species is probably endemic to the Nandewar Ranges, an isolated 18.5 Ma volcanic mountain block which still retains moist habitat despite being surrounded by relatively dry alluvial plains. Two females of an undescribed *Holonuncia* sp. have been collected in the Warrumbungle Ranges, another isolated volcanic mountain block south-west of the Nandewars.

Etymology. The specific epithet refers to the type locality, Mount Kaputar.

Distribution. Mount Kaputar, and probably other moist regions of the Nandewar Ranges.

Holonuncia enigma n.sp.

Fig.16

Type material. New South Wales, northern suburbs of Sydney. HOLOTYPE, male: KS10577, Gordon, 33°52'S 151°12'E, pitfall trap in litter, field no. 2294, C. Horseman, 1 Jan. 1983. PARATYPES: KS13475, Gordon, pitfall trap in litter, C. Horseman, 1 Nov. 1983, 1 male; KS13323, same data, 12 Oct. 1983, 1 male; KS21445, Pymble area, G.S. Hunt, no date, 4 females; KS21446, St Ives, beside Ku-ring-gai Creek, under rotting wood, G.S. Hunt, 3 Aug. 1969, 1 male; KS19892, Lane Cove, Stringy Bark Creek, near Epping Road, under log, G.S. Hunt, Oct. 1988.

Diagnosis. Notch absent in calcaneus 1 of both sexes, retroventral spine 4 on pedipalp femur usually bifid, retrodistal spines 1 and 2 on pedipalp tarsus with thick bases, 3 segments in tarsus 1 and 6-7 in tarsus II of both sexes, dorsolateral plate of penis with lamina part visible only in dorsal view and not rising above level of the broad, finely denticulate basal part.

Description. MALE. This species differs in many respects from *H. cavernicola* (cave population): colour is yellow-orange with pigmentation pattern as figured; body small, CW 1.60 (n=1); eyemound rising at about 70° from anterior margin but sloping more gently posterior to eyes; eyes normal. Carapace lacking mesial granules posterior to eyes; mesial tubercles on TA3 not enlarged into spines; genital operculum width subequal to length. CSL 1.12, second segment of chelicera dorsally with large spines in distal half. PFL 1.35, PFL:CW 0.84; pedipalp femur with 7 mediodorsal spines size order 3=4=5,2,6=7,1 and 5 retroventral spines size order 4,1,3,2,5; spine 4 usually unevenly bifid; tibia granulate ventrally, retroventral spine 1 reduced to granule; retroventral spines 1 and 2 on tarsus thick at base. Legs short, FIV 1.52, FIV:CW 0.95; calcaneus I not notched below, CI:AI 0.18; tarsus IV dorsally with very large seta at about 0.4; tarsal formula 3(2),6-7(3),4,4. Ventral plate of penis about as wide as long, tendency for proximal pair of inferior setae to arise in a hollow is weak; dorsolateral plates broad and low, in lateral view obscuring base on mid-dorsal plate but not base of superior setae, basal part of plates enlarged and finely denticulate, lamina part of plate only visible in dorsal view and not rising above level of basal part; mid-dorsal plate cleft shallowly triangular; in ventral view glans narrowest basally, expanding gradually to about 0.66 and then expanding abruptly, in lateral view terminally bifurcate; distodorsal denticles larger and fewer than in *H. cavernicola*, similar in size to *H. kaputarensis*.

FEMALE. The female is very difficult to distinguish

from the male without lifting the genital operculum. There tend to be 4 subequal retrolateral spines on the tibia (3 in male), and spine 1 tends to be relatively larger. There is no dimorphism in tarsal segmentation, tarsal formula 3(2),6-7(3),4,4.

Variation. Accessory branch to retroventral spine 4 is sometimes lacking.

Comments. A monotypic genus was contemplated for this species but it is placed in *Holonuncia* on the basis of two synapomorphies: distodorsal denticles on the glans, and proximal inferior setae inserted in a hollow in ventral plate (though this is weakly

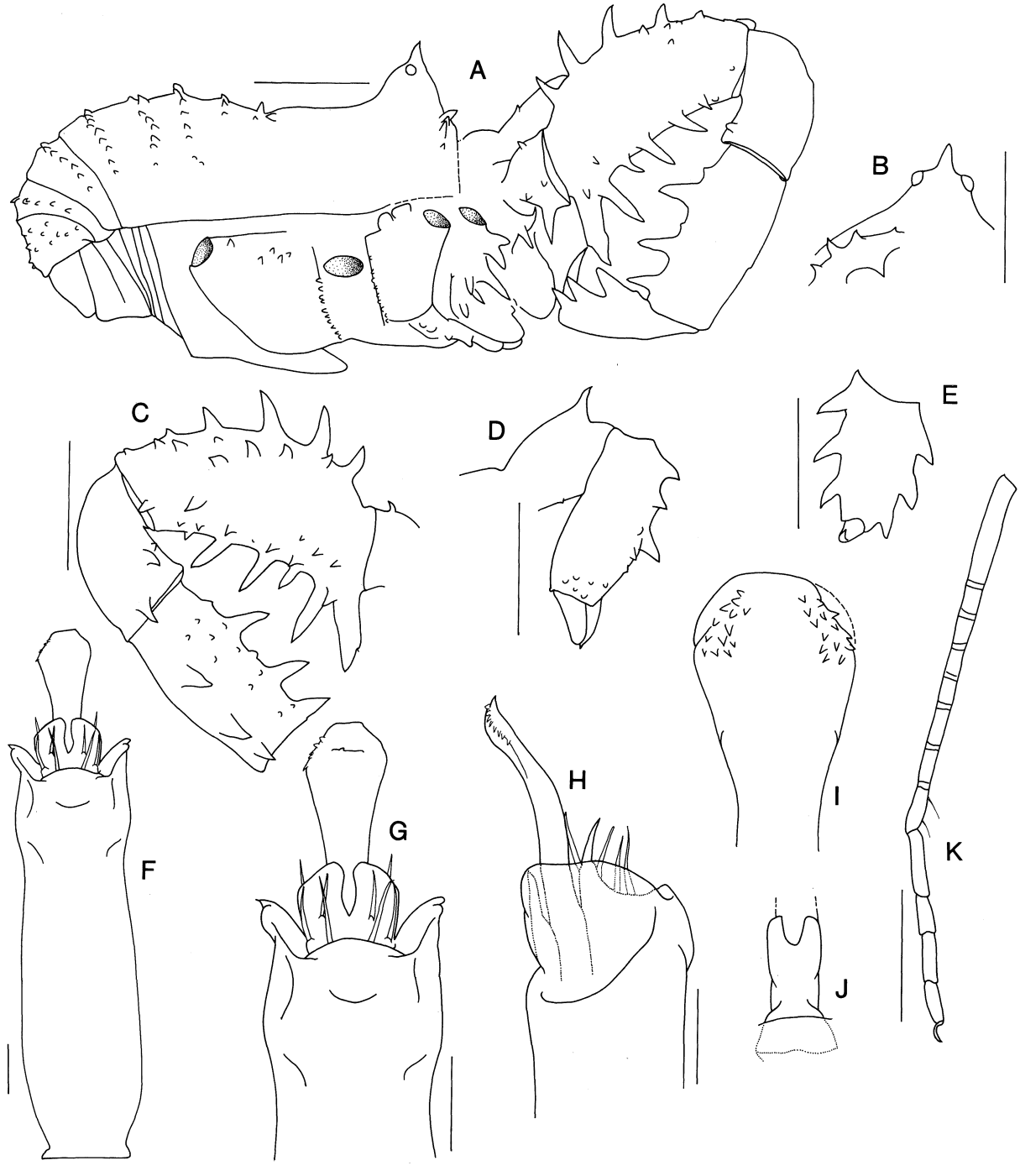

Fig.15. *Holonuncia kaputarensis* n.sp. Holotype male. A = body, lateral; B = eyemound and anterior spination, frontal; C = pedipalp except tarsus, prolateral; D = chelicera, retrolateral; E = pedipalp tarsus, ventral; F-I = penis, F = entire, G = ventral, H =lateral, J = dorsal plate, I = distodorsal part of stylus; J = genital operculum; K = metatarsus and tarsus of leg I, retrolateral. Scale bars: F-H,J = 0.1 mm, I = terminal part of G enlarged; others = 1.0 mm.

developed in this species). Generic placement will need to be revised should further, similar species be found.

Etymology. The specific epithet is a noun in apposition which underscores the peculiar nature of this species, particularly relating to aspects of genital morphology and the lack of sexual dimorphism in tarsus I segmentation.

Natural history. This species is probably more common in ground litter than its congeners.

Distribution. Northern suburbs of Sydney - valleys

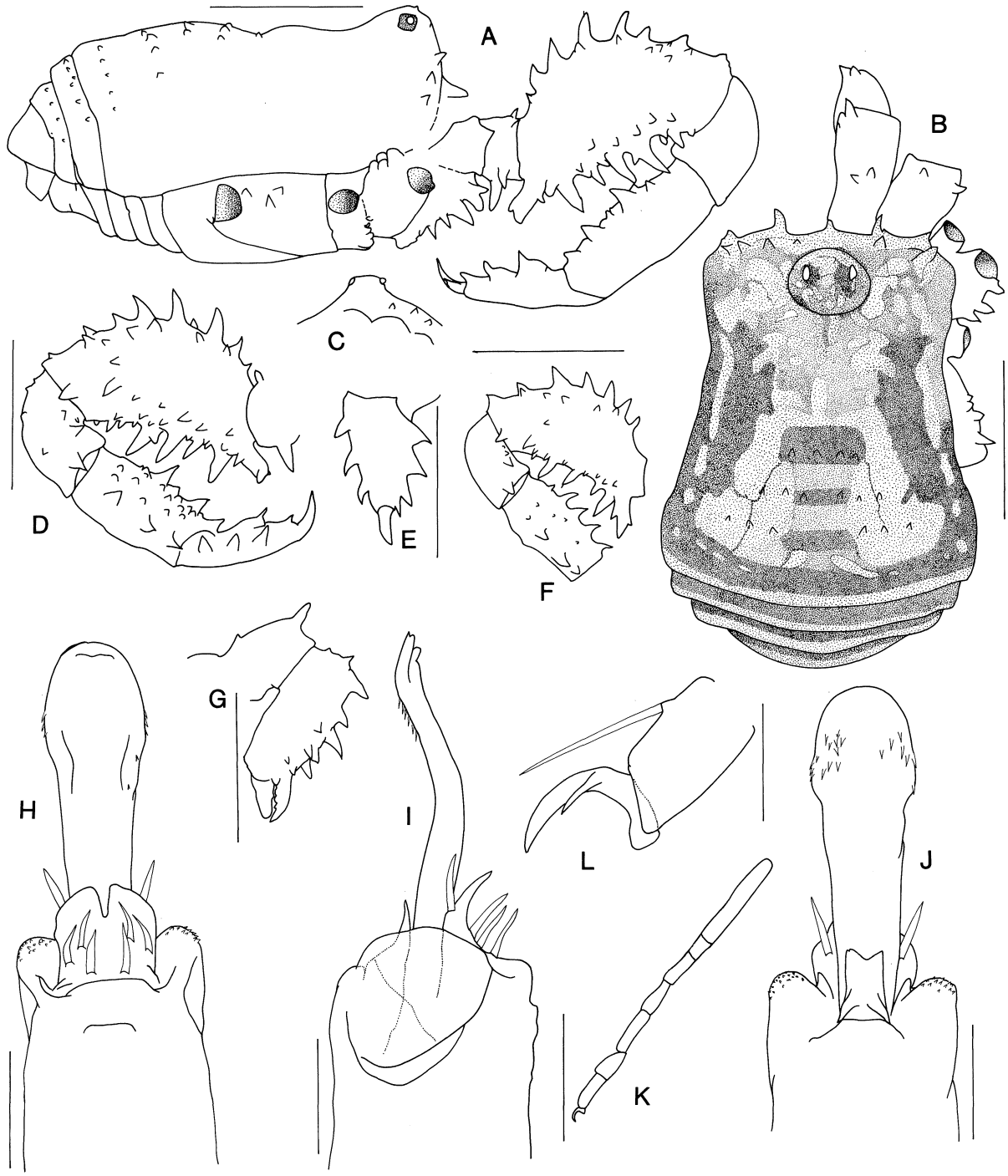

Fig.16. *Holonuncia enigma* n.sp. C,F = female, KS21445; others = male, KS10577. A = body, lateral; B = dorsum; C = eyemound and anterior spination, frontal; D = pedipalp, prolateral; E = pedipalp tarsus, ventral; F = pedipalp except tarsus, prolateral; G = chelicera, retrolateral; H-J = penis, H = ventral, J = dorsal I = lateral; K = metatarsus and tarsus of leg I, retrolateral; L = distal article of tarsus IV and claw with largest seta. Scale bars: H-J,L = 0.1 mm, others 1.0 mm.

in Hawkesbury Sandstone.

Other Cavernicolous Records

Holonuncia has been recorded from several other cave areas in New South Wales (Fig.1). Lack of males or doubts about identity have meant that some species descriptions have been deferred.

Three females have been collected in Timor (Isis River) Caves near Murrurundi, north of the Hunter River. They probably belong to a new species as other cavernicolous species occur south of the Hunter, a barrier implicated in the speciation of other harvestmen (Hunt, 1985). The females collected from Cliefden Caves, near Carcoar, have a canaliculate eyemound similar to that in *H. sussa*. These caves are distant from caves to the east (Fig.1), and so these specimens probably represent a new species. Similarly, the female specimens from the relatively isolated Abercrombie Caves may well belong to a new species. A sample lacking males has been collected from the Indi Caves in the Snowy Mountains on the New South Wales-Victorian border. The two males available from Wyanbene Cave near Braidwood have genitalia similar to *H. seriata* but, as the species occurs south of the Shoalhaven River, it may belong to a new species identified by electrophoresis (see below), or to a separate cavernicolous species.

Electrophoretic Study

A limited electrophoretic study was used to help resolve species boundary problems in *Holonuncia*. A study of the entire group was not practical so *H. seriata* and *H. francesae*, n.sp. were chosen. The latter possessed a short spine on the eyemound and four rather than five articles in tarsus I. However, the significance of these small differences was unclear in view of the seeming constancy of male genitalic characters. In addition, specimens from south of the Shoalhaven River (Sassafras and Tomerong) which had two morphologies resembling *H. francesae* and *H. seriata*, were chosen for comparison.

Methods and materials. Samples of *Holonuncia* spp. were collected at four sites: Ku-ring-gai Creek, St Ives; The Gib, Mittagong; Sassafras (between Nowra and Nerriga); and 3 km south of Tomerong. *Holonuncia* is closely related to *Equitius*, so samples from two nominal species, *E. doriae* (*ex* Mittagong) and *E. spinatus* (3 populations), were included for comparison. Specimens were held at -80°C until required. Variation at 20 enzyme loci (Table 1) was interpretable in a consistent Mendelian fashion. Electrophoretic methods for Titan III cellulose acetate plates and data analysis follow Colgan (1986), Richardson *et al.* (1986) and Ponder *et al.* (in press).

Results and discussion. Genetic distances are reported in Table 3 and summarised in Figure 17. A computer printout of allele frequencies for each population is available in the Australian Museum Library.

Although genetic distances are not final arbiters of specific status, the following conclusions are suggested by the data:

1. *H. francesae* n.sp. is a separate species from *H. seriata* (Roewer) despite the similarity in male genitalia. Fixed differences occur for AP-1, GPD, GOT-1, HK, TPI, and GPI. These differences contribute to a much greater genetic distance

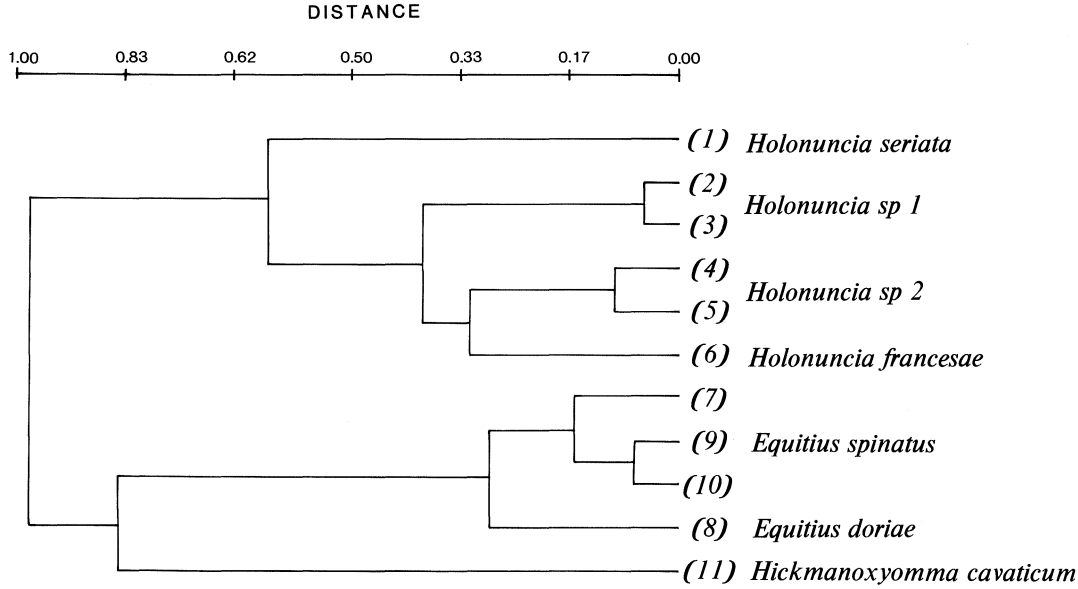

Fig.17. Distance tree based on genetic distances between selected populations of *Holonuncia, Equitius* and *Hickmanoxyomma*. Coefficient is Nei genetic distance. Numbers in parentheses refer to populations numbered in Table 2.

separating *H. francesae* n.sp. and *H. seriata* than that separating *E. doriae* and *E. spinatus* (Table 3; Fig.17).

2. *Holonuncia* sp.1 is morphologically very similar to *H. seriata* apart from having 4 articles in tarsus 1, but is genetically more similar to *H. francesae* (which also possesses 4 articles). In fact, this species was listed in "material examined" under *H. seriata* before electrophoretic analysis was undertaken. Material in the collection from Quiltys Mountain, Budawang Ranges, may belong to *Holonuncia* sp.1. Fixed differences between *Holonuncia* sp.1 and *H. seriata* occur for MDH-2, PGM, PK-2, TPI, FDP-1, and FDP-2. Again, the genetic distance between *H. seriata* and this new species is greater than that between the two *Equitius* spp.

3. *Holonuncia* sp.2 is sympatric with *Holonuncia* sp.1 near Tomerong (south of the Shoalhaven River) but is genetically more similar to *H. francesae* from the Sydney region (north of the Shoalhaven River) which it also resembles in carrying a small spine on the eyemound. Fixed differences between *H. francesae* and *Holonuncia* sp.2 occur for GPD, TPI, GPI and FDP-2. The distance between *H. francesae* and *Holonuncia* sp.2 is comparable to that between the two *Equitius* species. Fixed differences between the sympatric *Holonuncia* spp. 1 and 2 occur for GOT-2, PGM, PK-2 and TPI.

4. On the basis of the limited genetic distance data in this study, *Equitius* appears more closely related to *Hickmanoxyomma* than either is to *Holonuncia*, despite the fact that *Equitius* and most *Holonuncia* spp. possess a similar notch in calcaneus I.

Sample sizes of *Holonuncia* spp. 1 and 2 were small (Table 2). Description of these species will await the study of further material south of the Shoalhaven River to gauge both morphological and electrophoretic variation.

ACKNOWLEDGMENTS. This research was conducted with the assistance of an Australian Biological Resources Study grant. I also wish to thank the Directors of museums for making their collections available and the many speleologists for their essential efforts in collecting specimens from caves. Dr Dan Bickel and Dr Don Colgan have commented on the manuscript, while Ms Judy Thompson has helped with SEM work and specimen registration. Ms Grace Serkowski ran and scored the gels for electrophoresis, while Dr Don Colgan analysed the data. Mr Roger Springthorpe assisted with illustrations and Mr Gerard Clark with a computer program which assisted measurements.

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APPENDIX

Table 1. Enzymes scored in electrophoretic analyses.

Enzyme (E.C. Number)	Code	Alleles
Alkaline phosphatase (3.1.3.1)	AP-1	4
Malate dehydrogenase (1.1.1.37)	MDH-1	2
	MDH-2	3
Alanine aminotransferase (2.6.1.2)	GPT	1
Alpha-glycerophosphate dehydrogenase (1.1.1.8)	GPD	2
Fumerase (4.2.1.2)	FUM	3
Glyceraldehyde-3-phosphate dehydrogenase (1.2.1.12)	GA3PDH	1
Aspartate aminotransferase (2.6.1.1)	GOT-1	4
	GOT-2	2
Phosphoglucomutase (2.7.5.1)	PGM	7
Hexokinase (2.7.1.1)	HK	2
Pyruvate kinase (2.7.1.40)	PK-2	2
6-phosphogluconate dehydrogenase (1.1.1.44)	6PGDH	4
Triosephophosphate isomerase (5.3.1.1)	TPI	3
Mannosephophosphate isomerase (5.3.1.8)	MPI	2
Glucosephophosphate isomerase (5.3.1.9)	GPI	5
Fructose diphosphatase (3.1.3.11)	FDP-1	3
	FDP-2	3
Isocitrate dehydrogenase (1.1.1.42)	IDH-1	3
	IDH-2	3

Table 2. Populations and sample sizes used for electrophoretic analysis.

Species	Population (No.)	Sample Size
Holonuncia seriata	The Gib, Mittagong (1)	3
Holonuncia sp. 1	Tomerong (2)	1
Holonuncia sp. 1	Tomerong (3)	1
Holonuncia sp. 2	Tomerong (4)	1
Holonuncia sp. 2	Sassafras (5)	1
H. francesae	St Ives (6)	4
Equitius spinatus	Johns River (7)	5
E. doriae	The Gib, Mittagong (8)	4
E. spinatus	Sandbar, Smiths Lake (9)	11
E. spinatus	The Grandis, Bullahdelah (10)	6
Hickmanoxyomma cavaticum	Mystery Creek Cave, Ida Bay (11)	2

Table 3. Genetic distances between *Holonuncia* spp., *Equitius* spp. and *Hickmanoxyomma cavaticum*. Nei Unbiased Genetic Distance above diagonal, Rogers Genetic Distance below. Numbers in parentheses refer to taxa numbered in Table 2.

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)
(1)	****	0.57	0.48	0.48	0.67	0.80	0.61	0.69	0.77	0.87	1.11
(2)	0.65	****	0.05	0.29	0.36	0.50	1.23	0.92	1.04	1.07	0.89
(3)	0.61	0.22	****	0.29	0.36	0.50	1.23	0.92	1.03	1.07	0.89
(4)	0.61	0.50	0.50	****	0.11	0.32	0.87	0.69	0.84	0.98	0.77
(5)	0.69	0.55	0.55	0.32	****	0.32	1.14	0.92	1.07	1.12	0.99
(6)	0.73	0.62	0.62	0.52	0.52	****	1.21	0.83	1.24	1.42	0.76
(7)	0.65	0.82	0.82	0.74	0.80	0.81	****	0.23	0.09	0.17	0.75
(8)	0.70	0.78	0.78	0.71	0.78	0.75	0.45	****	0.25	0.36	0.68
(9)	0.71	0.79	0.79	0.74	0.80	0.82	0.30	0.46	****	0.05	0.83
(10)	0.74	0.80	0.80	0.78	0.81	0.86	0.39	0.54	0.23	****	0.93
(11)	0.80	0.76	0.76	0.73	0.79	0.72	0.70	0.67	0.73	0.76	****