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A NEW CANDONINAE GENUS (CRUSTACEA: OSTRACODA) FROM  
SUBTERRANEAN WATERS OF QUEENSLAND, WITH A CLADISTIC ANALYSIS OF  
THE TRIBE CANDONOPSINI

IVANA KARANOVIC

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*Pioneercandonopsis hancocki* gen. nov., sp. nov. was collected from subterranean waters of Pioneer Valley, Queensland, and it is the first subterranean ostracod from this state. The new genus belongs to the tribe Candonopsini Karanovic, in press b, which also includes *Candonopsis* Vávra, 1891, *Caribecandona* Broodbakker, 1983, and *Cubacandona* Broodbakker, 1983. Characteristics of the hemipenis and prehensile palps suggest that *Pioneercandonopsis* is more closely related to the latter two genera than to *Candonopsis*. A cladistic analysis based on two sets of morphological characters was performed on all 32 species of the tribe Candonopsini, with *Cryptocandona dudichi* (Klie, 1930) chosen as outgroup taxon. Resulting cladograms support a monophyletic origin for the Candonopsini and close phylogenetic relationship between the new genus and *Caribecandona* and *Cubacandona*. □ *Pioneercandonopsis*, new genus, Candonopsini, Candoninae, cladistic analysis.

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A total of 19 freshwater free-living ostracods are known from Queensland (Sars, 1889; De Deckker, 1978, 1979, 1981, 1983; De Deckker & McKenzie, 1981) and all are surface water inhabitants. The subterranean ostracod fauna of Queensland is completely unexplored. Recently, the Queensland Department of Natural Resources and Mines started an extensive sampling of the subterranean waters of Pioneer Valley. I had the opportunity to examine these samples and discovered the new ostracod described in this paper. This is the first subterranean ostracod recorded from Queensland and is also the 10th ostracod genus described from Australian subterranean waters. The other 9 genera are from groundwaters of Western Australia (Karanovic & Marmonier, 2003; Karanovic, 2003a, b, in press a, b). All 10 genera belong to the Candoninae Kaufmann, 1900. This subfamily has 11 extant genera in Australia (10 endemic, plus *Candonopsis* Vávra, 1891), with an additional 20 genera worldwide.

Initially, the Candoninae was divided into tribes Namibcypridini Martens, 1992 with two genera, and Candonini Kaufmann, 1900 containing 16 genera (Martens, 1992). However, discovery of a highly diverse Candoninae fauna in WA, with striking morphological features, necessitated revision of the Candoninae with the aim of better understanding the phylogenetic

relationships between genera. Karanovic (in press a, b) described the *Humphreyscandonini* Karanovic, in press a, and Candonopsini Karanovic, in press b. The former tribe includes 7 genera known only from subterranean waters of the Pilbara region (WA), while the Candonopsini encompasses *Candonopsis*, *Caribecandona* Broodbakker, 1983, and *Cubacandona* Broodbakker, 1983. The new genus from Queensland is assigned to this tribe.

The Candonopsini contains 32 Recent species. *Candonopsis* is the largest, with 24 species, and is divided (Karanovic, in press b) into *Candonopsis s. str.* and *Abcandonopsis* Karanovic, in press b. The latter subgenus is an Australian endemic with 3 subterranean species: 2 from Kimberley and one from the Murchison Region (Karanovic, in press b). *Candonopsis s. str.* has 5 species in Australia, 4 endemic to subterranean waters of the Murchison Region (Karanovic & Marmonier, 2002). The remaining *Candonopsis* species are in Europe, South America and Africa. *Cubacandona* and *Caribecandona* are less diverse and have more restricted distributions. *Cubacandona* was represented only by the type species, *C. cubensis* (Danielopol, 1978), from Cuba (Danielopol, 1978, 1980), but Karanovic (in press b) assigned *Candonopsis* species from South America to that genus. All 3 species of *Caribecandona* are found

in subterranean waters of the West Indies (Broodbakker, 1983).

*Cubacandona* and *Caribecandona* share 3 very important morphological characteristics: 2 extensions of the lateral lobe of hemipenis, almost symmetrical prehensile palps and a very short terminal segment of the mandibular palp. In contrast, *Candonopsis* has only 1 extension of the lateral lobe, extremely asymmetrical prehensile palps and a long terminal segment of the mandibular palp. With respect to these characteristics, the new genus is more closely related to the Central and South American genera than it is to *Candonopsis*, but shares several setal reductions with the subgenus *Abcandonopsis* and some other *Candonopsis* s. str. species. To test the phylogenetic relationships in the Candonopsini, a cladistic analysis was performed. This analysis was based on species-level taxonomy, because this is more likely to represent evolutionary relationships (Walker-Smith & Poore, 2001) and included all 32 species of the tribe.

#### MATERIAL AND METHODS

**TAXONOMIC METHODS.** Samples were collected with haul-nets (mesh size 250 or 350 µm) from bores. Haul-nets are actually simple plankton nets of a different size suitable for the bore, which can range from 30-180 mm in diameter. Weighed nets were lowered down into the bore with one bottle screwed on its distal part then hauled through the water column, usually a number of times. Animals were stained with the 'Rose Bengal' dye, for easier sorting.

For observation under the light microscope, ostracods were dissected in a mixture of distilled water and glycerol (1:1) with fine entomological needles (mark 000). Dissected appendages were mounted in Faure's medium and observed using a Leica DMLS brightfield compound microscope with C-plan achromatic objectives. All drawings were prepared using a drawing tube attachment on the same microscope. For the Scanning Electron Microscopy (SEM), soft parts were taken from their valves and then dehydrated in a graded series of ethanol: 70%, 80%, 95% and 100%. In each of the grades, soft parts were left for about 15 minutes. The carapace was kept in the 100% ethanol for only a few minutes. After that, the soft parts and carapace were mounted on a SEM stub using double-sided adhesive tape. All samples were sputter coated with gold and observed under the LEO FEG VPSEM microscope with in-lens detectors, working distance

between 2-6mm, and accelerating voltage between 2-5kV.

In the systematics, the length of all segments was measured along the midline, and length ratios are presented beginning with the proximal segment. Appendage terminology follows Martens (1998), while chaetotaxy of all limbs follows Broodbakker & Danielopol (1982), revised for the antenna by Martens (1987). I follow Martens' (1987) terminology except that the shortest claw on the male terminal segment is considered homologous with the female GM claw, while the longest one is homologous with the female Gm claw. Setae on the third thoracopod are labeled according to Meisch (1996), while setae on the antennula are labeled according to Karanovic (in press c). Lobes on the hemipenis are designated according to Danielopol (1969). In front of the abbreviations for the setae on the endopodal segments of the 3rd thoracopod and setae on the 1st thoracopod, the letter 'T' was added so that they are not confused with abbreviations for the hemipenis given below.

**ABBREVIATIONS.** a - lateral lobe on hemipenis; A1 - antennula; A2 - antenna; CB1, CB2 - setae on the antennular coxobasis; b - medial lobe on hemipenis; d1, d2, dp - setae on the basal segment of the third thoracopod; En1-6 - endopodal segments of the antennula; En a, b, c, d - endopodal setae on the antennula; Ex1, 2 - exopodal setae on the antennula; Fu - furca; G1, G2, G3, GM, Gm - antennal claws; H - height; L - length; LV - left valve; Md - mandibula; Mxl - maxillula; QM - Queensland Museum; RV - right valve; Ta, Ta', Tb, Td - setae on the first thoracopod; Te, Tf, Tg, Th1, Th2, Th3 - setae on endopodal segments of the third thoracopod; T1, T2, T3 - first, second and third thoracopods; t1, t2 - medial setae on the second endopodal segment of the antenna; W - width; WAM - Western Australian Museum; Y, ya, y1, y2, y3 - aesthetascs; z1, z2, z3 - apical setae on the second endopodal segment of the antenna.

**CLADISTIC METHODS.** A total of 32 species of the Candonopsini are included in the cladistic analysis, while *Cryptocandona dudichi* (Klie, 1930) was chosen as an outgroup taxon. According to Baltanás et al. (2000), *Cryptocandona* Kaufmann, 1900 represents a primitive lineage in the Candoninae. All known species of *Cryptocandona* have the highest number of setae found in the Candoninae on the A1, A2, and all thoracopods, which makes them

closely related to the Candonopsini. However, the characteristics of Md, the prehensile palps, furca and hemipenis exclude *Cryptocandona* from the Candonopsini and the genus is placed in the Candonini (Martens, 1992). *Cryptocandona dudichi* was chosen because it was recently redescribed in detail (Namiotko et al., 2001) and both sexes are known.

The morphological characters used in this analysis were selected from information in the literature. Characters were polarised so that the outgroup taxon values all remained zero. This gives the least increase in the length of the overall cladogram (Kitching et al., 1998). The '0' state also means a plesiomorphic character state, while '1' means an apomorphy. Unknown or missing values are coded '-'. Only the carapace shape and the total number of the A1 segments were multistate characters (with states 0, 1, and 2); all other characters used in this analysis were binary. Carapace shape was coded as a non-additive (representing unordered multistate character as a linked series of binary character) character, while the total number of segments on A1 was coded as additive (representing ordered multistate character as a linked series of binary characters).

Two data matrices were created, characters coded, optimised and weighted using the computer program WinClada, version 1.00.08 (Nixon, 2002), and then analyzed using NONA, version 2 (Goloboff, 1999). All 24 characters from the first data matrix were analyzed as equally weighted, using the heuristic and the Ratchet Island Hopper searches with the WinClada default parameters. For the heuristic search the default parameters are: hold 100; mult\*1; hold/1 (hold 100 trees in memory, perform tree bisection and reconstruction (TRB) branch swapping on 1 random additional replicates and hold 1 starting tree in memory). For the Ratchet Island Hopper search the default parameters are: 200 replications; 1 tree to hold; 3 characters to sample; 10 random constraint level and amb-poly= (amb- collapses a branch if the ancestor and descendant have different states under same resolutions of multistate characters or of '-'; poly=treats trees as collapsed). Characters in the second data matrix were weighted so that the highest weight (1) was given to the characters from 0-15. Those were characters of the tribe, genera, subgenera, and some characters of the species groups. Characters 16-27 were weighted 0.75, majority of these are homoplastic. The lowest value (0.5) was given to the characters from 28-33, i.e. to the carapace shape and to the almost all ambiguous

characters. When analysing with the Ratchet Island search the same default parameters were used, while for the Heuristic search the following options were chosen: hold 10000; mult\*100; hold/10. On all trees obtained unsupported branches were collapsed and characters were optimised using the fast optimisation option in WinClada.

#### REFERENCE SOURCES FOR THE OUTGROUP AND INGROUP TAXA (\*indicates original paper is a reference source).

1. *Cryptocandona dudichi* (Klie, 1930): Namiotko et al. (2001);
2. *Candonopsis (Abcandonopsis) aula* Karanovic, in press b\*;
3. *C. (A.) indoles* Karanovic, in press b\*;
4. *C. (A.) williamsi* Karanovic & Marmonier, 2002\*: Karanovic (in press b);
5. *C. (Candonopsis) africana* Klie, 1944\*: Rome (1962); Martens (1984);
6. *C. (C.) anteroarcuata* Rome, 1962\*;
7. *C. (C.) boui* Danielopol, 1978\*: Danielopol (1980);
8. *C. (C.) bujukuensis* Löffler, 1968\*
9. *C. (C.) dani* Karanovic & Marmonier, 2002\*;
10. *C. (C.) hummelincki* Broodbakker, 1983\*;
11. *C. (C.) kingsleii* (Brady and Roberston, 1870): Petkovski (1977)
12. *C. (C.) kimberleyi* Karanovic & Marmonier, 2002\*;
13. *C. (C.) mareza* Karanovic & Petkovski, 1999\*;
14. *C. (C.) murchisoni* Karanovic & Marmonier, 2002\*;
15. *C. (C.) nama* Daday, 1913\*;
16. *C. (C.) navicula* Daday, 1910\*: Klie (1935); Rome (1962); Karanovic (in press b);
17. *C. (C.) putealis* Klie, 1932\*;
18. *C. (C.) scourfieldi* Brady, 1910: Petkovski & Meisch (1995);
19. *C. (C.) solitaria* Vávra, 1895\*: Klie (1936)
20. *C. (C.) sumatrana* Klie, 1932\*: Harding (1962); Victor & Fernando (1978); Karanovic (in press b);
21. *C. (C.) tenuis* (Brady, 1886)\*: Sars (1896); Karanovic and Marmonier (2002);
22. *C. (C.) thienemanni* Schäfer, 1945\*;
23. *C. (C.) trichota* Schäfer, 1945\*;
24. *C. (C.) urmila* Gupta, 1988\*;
25. *C. (C.) westaustraliensis* Karanovic & Marmonier, 2002\*;
26. *Cubacandona cubensis* (Danielopol, 1978\*): Danielopol (1980); Broodbakker (1983);
27. *C. anisitsi* (Daday, 1905)\*: Klie (1930);
28. *C. columbiensis* (Méhes, 1913)\*;
29. *C. falclandica* (Vávra, 1898)\*;
30. *Caribecandona trapezoidea* Broodbakker, 1983\*;
31. *C. auricularia* Broodbakker, 1983\*;
32. *C. ansa* Broodbakker, 1983\*.

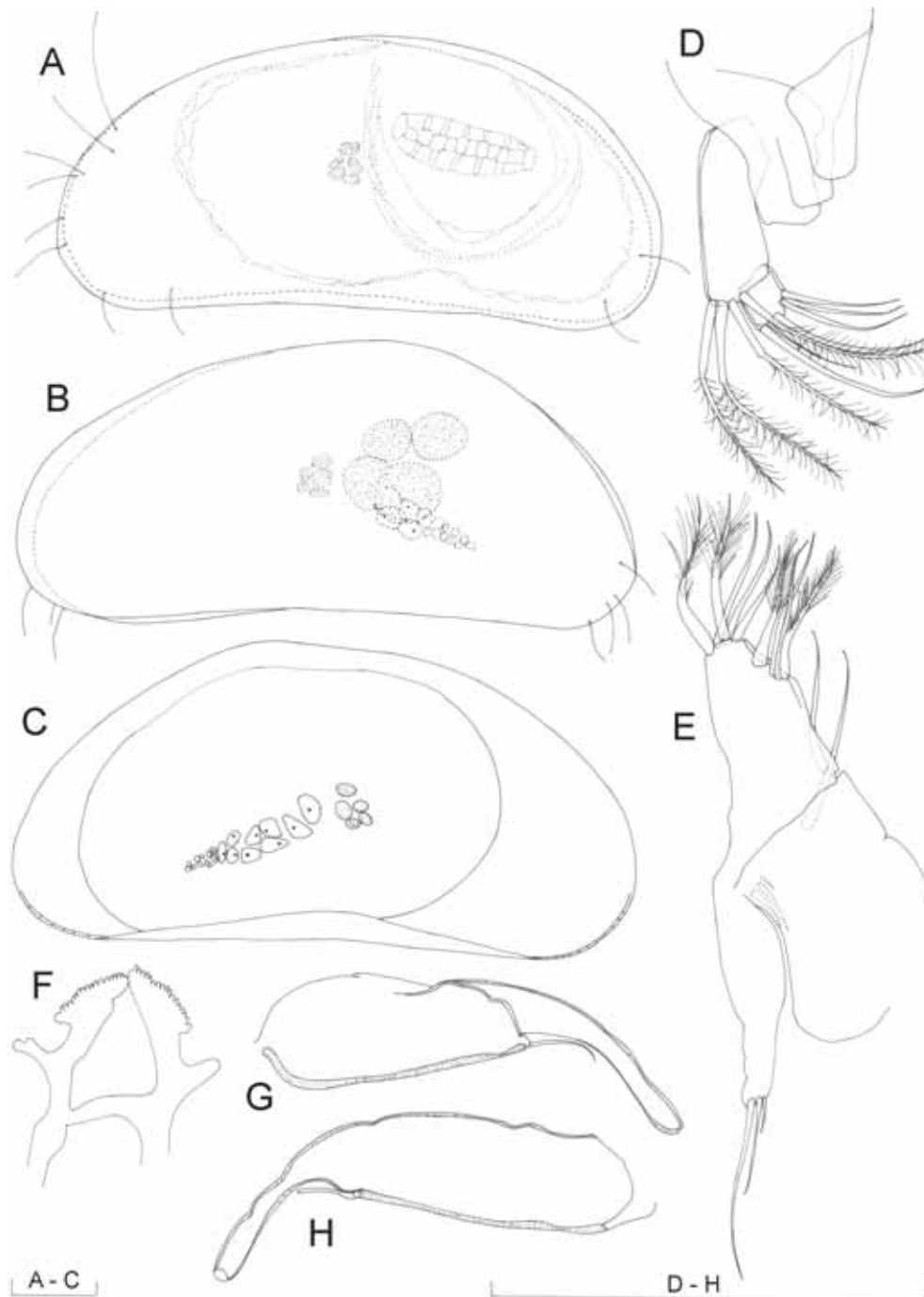


FIG. 1. *Pioneercandonopsis hancocki* gen. et sp. nov. A, G, H, Holotype (♂); B-F, Allotype (♀). A, carapace, lateral view from the left side; B, carapace, lateral view from the left side; C, LV, internal view; D, Mx1 palp and three endites; E, T1; F, rake-like organ; G, left prehensile palp; H, right prehensile palp. Scales=0.1mm.



## SYSTEMATICS

Family CANDONIDAE Kaufmann, 1900  
 Subfamily CANDONINAE Kaufmann, 1900  
 Tribe CANDONOPSINI Karanovic, in press b

**Pioneercandonopsis** gen. nov.

TYPE SPECIES. *Pioneercandonopsis hancocki* sp. nov.

ETYMOLOGY. Prefix *Pioneer* (after the Pioneer Valley, Queensland where the species was collected) and the genus name *Candonopsis*. Gender feminine.

DIAGNOSIS. Carapace subreniform, surface smooth (Fig. 5A,B). Calcified inner lamella narrow posteriorly, wider anteriorly. Muscle scar imprints typical for Candoninae, although poorly visible. A1 4-segmented. Segments En2, En3, En4 and En5 fused. Small suture and seta En3a between En3 and En4. A2 in females with 4-segmented endopod, while 5-segmented in males. Male sexual bristles (t2 and t3). Claws G1 and G3 male A2 reduced into setae; z1 and z2 transformed into claws, former one considerably shorter; z3 seta-like (Fig. 5C). Md with 6 rays in vibratory plate. Md-palp 4-segmented; second segment with 1 seta externally, 3+2 setae in bunch internally; penultimate segment with 3 setae extero-distally. Terminal segment of Md-palp with broadly fused central claw (Fig. 5D); L:W of same segment equals 1.1:1. Mx1 palp with rectangular terminal segment, and with 6 appendages. T1 with symmetrical palps, subterminal sclerified structures thin, only 1 well developed, another 1 very small and hardly visible (Fig. 2D). T2 5-segmented, basal segment without any seta. T3 5-segmented; basal segment with all setae (dp, d1 and d2); setae Te and Tg present, while seta Tf missing; terminal segment with 2 long (Th2 and Th3) and 1 short seta (Th1). Fu without posterior seta, anterior setae present (Fig. 5F), both claws present and long. Hemipenis with all lobes developed. Lobe 'a' with 2 extensions: 1 dorsal and 1 distal; dorsal much smaller than distal. Lobe 'h' small and rounded; lobe 'b' with 1 ventral, finger like part. Part 'g' very poorly sclerified. Zenker's organ with 7 whorls of spines. Genital field rounded, without extensions.

**Pioneercandonopsis hancocki** gen. et sp. nov.  
(Figs 1-5)

ETYMOLOGY. For Peter Hancock, Department of Natural Resources and Mines who collected the material.

MATERIAL. Holotype ♂ (dissected on slide, QM W27255), allotype ♀ (dissected on slide, QM W27256);

paratype ♂ (dissected on slide, WAM C33460); paratype ♂ and 2 paratype ♀ (all on SEM stub, WAM C33461); 1 paratype ♂, 3 paratype ♀ and 15 juveniles (nauplius larvae) (all in a test tube in 70% ethanol, QM W27257); 1 paratype ♂, 2 paratype ♀ and 15 juveniles (nauplius larvae) (all in a test tube in 70% ethanol, WAM C33462).

TYPE LOCALITY. Australia, Queensland, Pioneer Valley, Bore No. 125004B, 148°35'24"E; 21°08'39"S; 26 June 2003; collector P. Hancock.

DESCRIPTION. Holotype (♂). Carapace subreniform in lateral view (Fig. 1A). L of carapace 0.69mm. Dorsal margin evenly arched with greatest H slightly behind middle, equaling 46.5% of L. Posterior and anterior margins broadly rounded, frontal slightly wider. Ventral margin straight. Inner calcified lamella anteriorly =26% of total L, while posteriorly =12% of total L. Marginal pore canals short, straight, dense. Valve surface smooth, covered only with long sparse hairs (small pits visible on Fig. 5B are caused by the SEM, and they are not characters of the species). Carapace decalcified due to poor conservation.

A1. 4-segmented. Exopod reduced in 2 very long setae (Ex1 and Ex2) both longer than L of all endopodal segments combined. Only CB1 seta present, while CB2 absent. Endopod of 3 segments. Segments E2, En3, En4 and En5 fused. En1 with seta En1a. On fused segments only seta En3a. Segment En5 with 1 long seta (En5a) 2 short setae (En5b, En5c). External  $\alpha$ -seta very short. Terminal segment with long seta En6b, while both En6c and En6d short. Aesthetasc ya 3.38 times longer than terminal segment. L ratio of endopodal segments 1.4:2.6:1.

A2 (Fig. 2C). Endopod 5-segmented. Exopod of plate with 1 long and 2 short setae. Males bristles (t2 and t3). Claws G1 and G3 reduced into setae: former one 3.45 times longer than terminal segment, latter one 2.6 times longer than same segment. Claw G2 1.56 times longer than first endopodal segment. Setae z1 and z2 transformed into claws: z1 0.8, while z2 1.55 times longer than first endopodal segment; z3 seta-like and 2 times longer than terminal segment. Claw Gm very long, 1.44 times longer than first endopodal segment, GM only as long as terminal segment. Aesthetasc Y 0.5 times longer than first endopodal segment.

Md. Vibratory plate with 6 rays. Palp 4-segmented. First segment internally with 2 long and 1 short plumed setae. Alpha seta not observed. Second segment internally with 3 setae in bunch, plus 1 additional seta, while beta seta

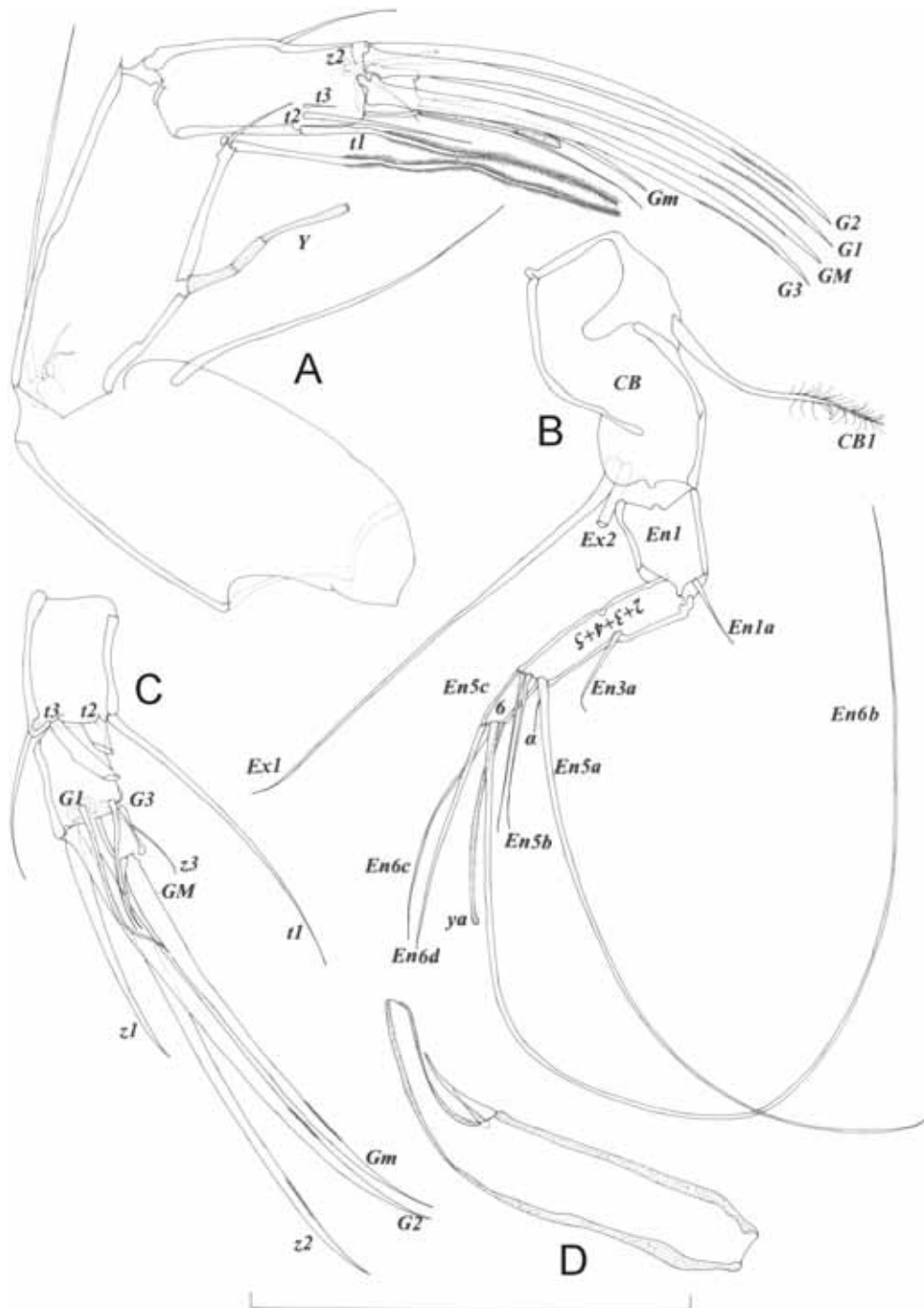


FIG. 2. *Pioneercandonopsis hancocki* gen. et sp. nov. A, B, Allotype (♀); C, Holotype (♂); D, Paratype (♂, 0.71mm, WAM C33460). A, A2; B, A1; C, 3 distal segments of A2; D, left prehensile palp. Scale=0.1mm.

not observed. Externally same segment with 1 seta not reaching distal end of penultimate segment. Third segment of Md-palp extero-distally with 3 subequally long setae; distally with 2 setae (1 of which being gamma seta) and 2 setae intero-distally. Terminal segment almost as long as wide. Terminal, central claw broadly fused with segment and distally plumed. Terminal segment with one additional weak claw externally and one seta internally.

*Mxl*. Palp 2-segmented. First segment only slightly dilated distally, and with 4 setae, all plumed. Terminal segment rectangular, with 6 appendages: 2 claws and 4 setae.

*T1*. Palps symmetrical (Fig. 1G, H); fingers long and slightly hook-shaped.

*T2* (Fig. 4C). 5-segmented. Basal segment without any seta. First endopodal segment with 1 very short seta, 2nd segment bare, penultimate segment with only 1 seta. Terminal segment with 2 short setae and claw which 1.2 times longer than 3 distal segments combined. Claw serrated.

*T3*. 5-segmented. Basal segment with dp, d1 and d2 setae. Seta *Te* present, while seta *Tf* absent. Penultimate segment with seta *Tg*. Terminal segment with 2 long and 1 short seta, L ratios of 3 setae equal 1:1.7:2.4. All setae terminally plumed. Endopodal segments 2 and 3 each with 3 rows of fine setae.

*Fu* (Fig. 3A). Posterior seta absent. Anterior seta very small and hardly visible. L ratios of anterior furcal margin, anterior and posterior claws equal 1.2:1:1. Claws serrated, ramus curved. Furcal attachment (Fig. 4D).

*Hemipenis* (Fig. 4A). Lobe 'a' with 2 extensions: dorsal 1, finger-like and small, distal 1 big, rounded and chitinised around margin. Lobe 'h' small and rounded. Lobe 'b' rounded dorsally, ventrally with small, finger-like part. Part 'g' very poorly sclerified. Inner tube coiled 2 times, ejaculatory process indistinct.

*Zenker's organ* (Fig. 4B). Of 5+2 whorls of spines.

Allotype (♀). Carapace L=0.7mm. Very similar to male, subreniform but with more pronounced point of the greatest H, which equals 0.48% of L (Fig. 1B, C).

*A2* (Fig. 2A). Endopod 4-segmented. Three t-setae present. Seta *z1* absent. Claws G1, G2 and G3 long, 1.4 times longer than first endopodal segment; GM 1.3 times longer than first endopodal segment, while Gm 5 times longer than terminal segment.

*Rake-like organ* (Fig. 1F). With numerous (17 and 18) small teeth.

*T1* (Fig. 1E). With *Tb* and *Td* setae and 3 setae in vibratory plate. Setae *Ta* and *Ta'* not observed.

*Fu and genital field* (Fig. 3B). L ratios of anterior furcal margin, anterior and posterior claws equal 1.3:1.26:1. Claws serrated. Genital field rounded and without any extensions.

*A1* (Fig. 2B); *Md* (Fig. 3C); *Mxl* (Fig. 1D); *T2* and *T3* (Fig. 4E) same as in male.

*Variability*. Except a small variation in the carapace length, no other variability was noticed.

#### CLADISTIC ANALYSIS

Using the heuristic search, the computer program NONA produced 5 equally parsimonious trees after the analysis of the first data matrix (Table 1). The same results were obtained with the Ratchet Island Hopper search. All trees were 43 steps long with the consistency index,  $Ci=60$ , and retention index,  $Ri=79$ . On 3 cladograms, the Candonopsini was subdivided into 2 clades: one containing *Cubacandona*, *Caribecandona* and *Pioneeracandonopsis*, and supported with synapomorphies of characters 12 and 23; the other containing all 24 species of *Candonopsis* and defined by the synapomorphy of character 11. One such tree (Fig. 6) is also a consensus tree. The strict consensus of all 5 trees was 53 steps long, with  $Ci=49$  and  $Ri=67$ , and it was less informative. The tree in Fig. 6 clearly defined *Candonopsis* (with both subgenera) and *Caribecandona* as monophyletic groups. *Pioneeracandonopsis* and each of the *Cubacandona* species appeared as separate branches (clades) in the Candonopsini.

Characters and their coding corresponding to the Table 1 matrix are as follows:

0, surface: smooth (0), ornamented (1); 1, lateral view: symmetrical (0), asymmetrical (1); 2, dorsal view: LV=RV (0), LV>RV (1); 3, total number of segments on A1: seven (0), six (1), four (2); 4, En2a seta: present (0), absent (1); 5, male sexual bristles: present (0), absent (1); 6, *z1* seta in males: long (0), short (1); 7, G2 claw in females: shorter than G1 (0), as long as G1 (1); 8, number of setae on second segment of Md-palp: two (0), one (1); 9, number of strong claws on terminal segment of Md-palp: two (0), one (1); 10, type of fusion of terminal claw on Md-palp: narrow (0), broad (1); 11, L:W ratio of terminal segment of Md-palp: less than 3:1 (0), more than 3:1 (1); 12, prehensile palps: asymmetrical (0), symmetrical (1); 13, subterminal sclerified structures on prehensile palps: both well developed (0), only one well



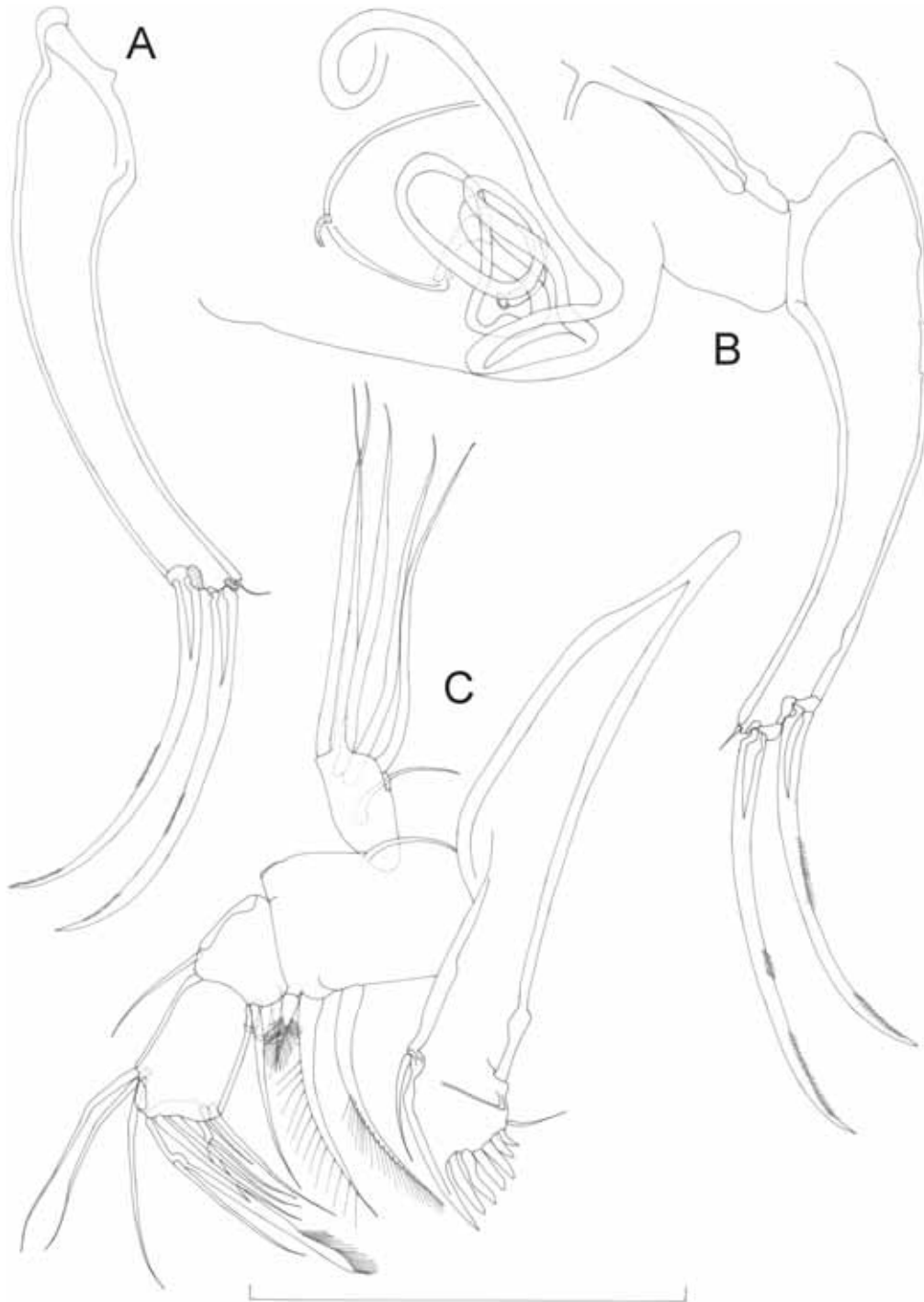


FIG. 3. *Pioneercondonopsis hancocki* gen. et sp. nov. A, Holotype (♂); B, C, Allotype (♀). A, Fu; B, Fu and genital lobe; C, Md. Scale=0.1mm.

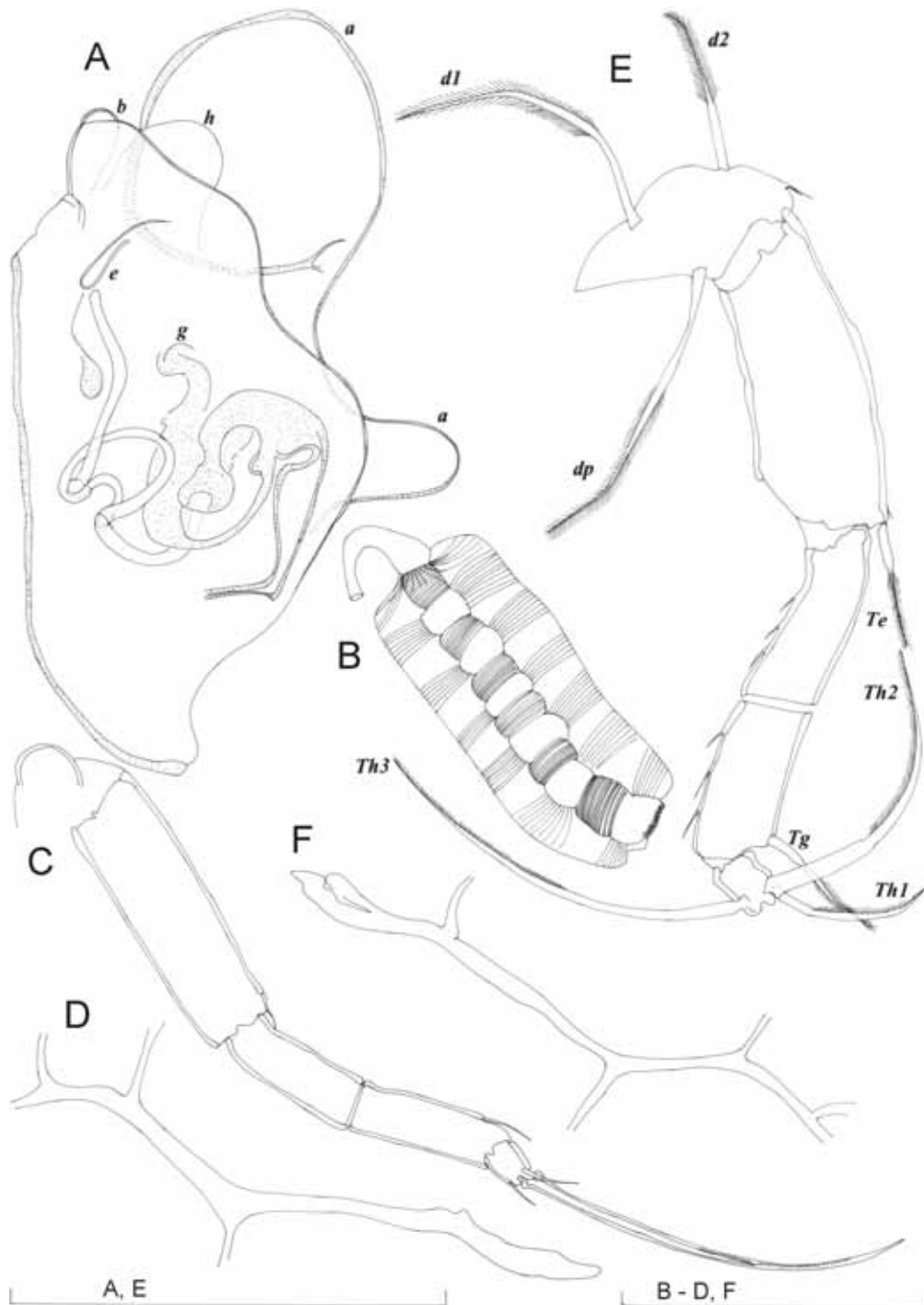


FIG. 4. *Pioneercondonopsis hancocki* gen. et sp. nov. A-D, Holotype (♂); E-F, Allotype (♀). A, hemipenis; B, Zenker's organ; C, T2; D, Furcal attachment; E, T3; F, Furcal attachment. Scales=0.1mm.

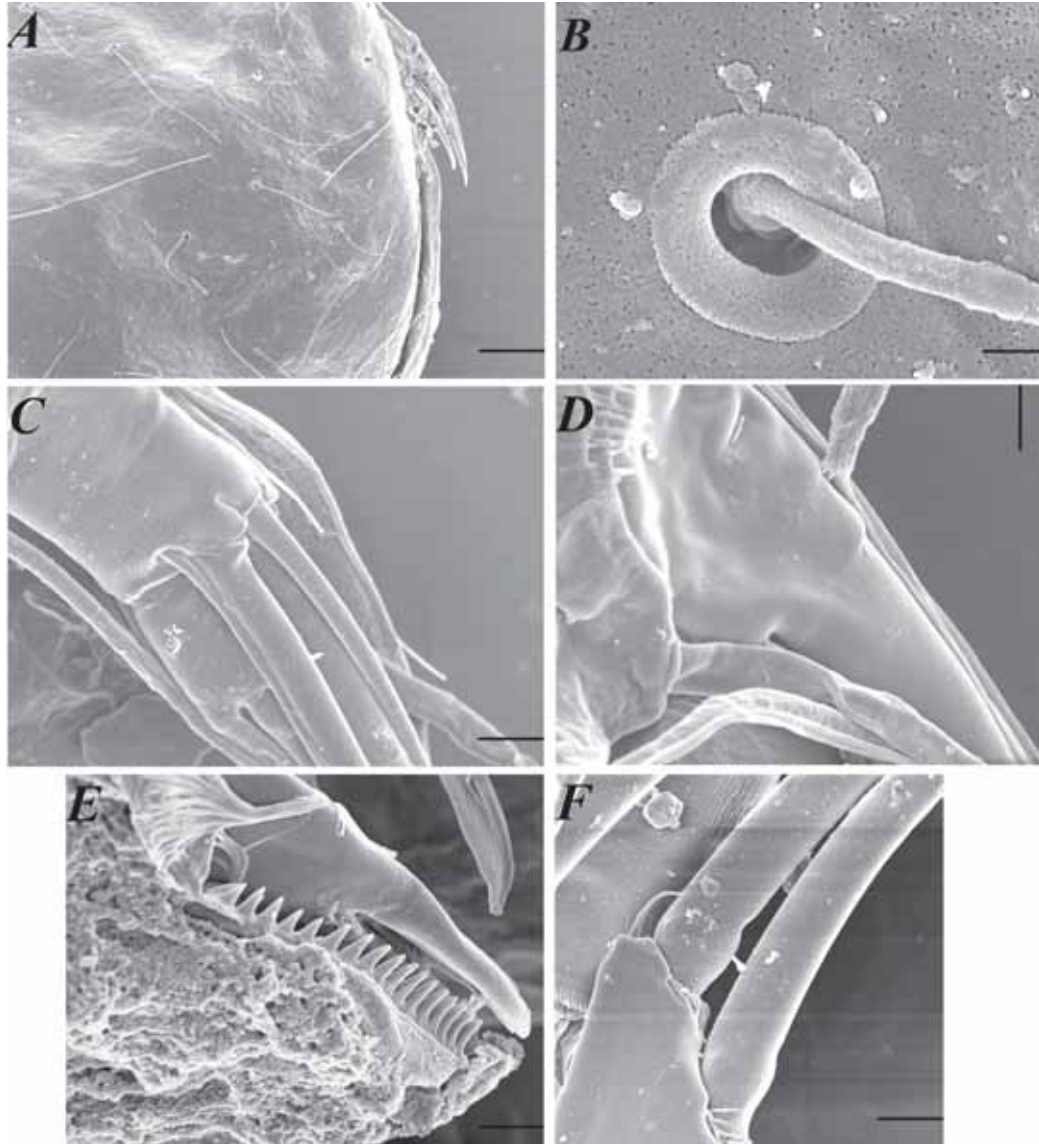


FIG. 5. Scanning Electron Microphotographs. *Pioneercondonopsis hancocki* gen. et sp. nov. A, B, E, Paratype (♀, 0.68mm, WAMC33461); C, D, F, Paratype (♂, 0.72mm, WAMC33461). A, carapace surface, frontal part; B, seta on the carapace surface; C, detail of A2; D, detail of terminal segment of Md palp; E, rake-like organ; F, detail of Fu. Scales: A=11.2µm; B=666.6nm; C=4.9µm; D=3.2µm; E=3.69µm; F=5.6µm.

developed (1); 14, basal seta on T2: present (0), absent (1); 15, seta on second segment T2: present (0), absent (1); 16, Td2 seta: present (0), absent (1); 17, Te seta: present (0), absent (1); 18, Tf seta: present (0), absent (1); 19, number of short setae on terminal segment T3: two (0), one (1); 20, posterior furcal seta: present (0), absent (1); 21, posterior furcal claw: well developed

(0), reduced (1); 22, spines on furcal claws: absent (0), present (1); 23, number of 'a' lobe extensions: one (0), two (1); 24, internal hemipenis ducts: not coiled (0), coiled (1).

The heuristics analysis of the weighed characters from the second data matrix (Table 2)

TABLE 1. Data matrix for the species of the tribe Candonopsini and the outgroup. Characters correspond to the Fig. 6.

Taxon	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
<i>Cryptocandona dudichi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>C. (A.) aula</i>	0	0	1	0	1	0	1	1	0	1	1	1	-	-	1	0	1	1	1	1	1	1	0	-	-
<i>C. (A.) indotes</i>	0	0	1	0	1	-	-	1	0	1	1	1	-	-	1	1	1	1	1	1	1	0	0	0	1
<i>C. (A.) willami</i>	0	0	1	0	1	0	1	1	0	1	1	0	1	1	0	1	1	1	1	1	1	0	0	0	1
<i>C. (C.) africana</i>	0	0	0	0	1	0	1	1	0	1	1	0	1	0	0	0	0	0	0	1	1	0	1	0	1
<i>C. (C.) anteroarcuata</i>	0	0	0	0	1	0	1	1	0	1	1	0	1	0	0	0	0	0	0	1	1	0	0	0	1
<i>C. (C.) boui</i>	0	0	0	0	1	0	1	0	0	1	1	0	1	0	0	0	0	0	0	1	1	0	0	0	1
<i>C. (C.) bujukuensis</i>	0	0	0	0	1	0	1	1	0	1	1	0	1	0	0	0	0	0	0	1	1	0	1	0	1
<i>C. (C.) dani</i>	0	1	0	0	1	0	1	1	0	1	1	0	1	0	0	0	0	0	0	1	1	0	1	0	1
<i>C. (C.) hummelincki</i>	0	0	0	0	1	-	-	1	0	1	1	1	-	-	0	0	0	0	0	1	1	0	1	-	-
<i>C. (C.) kingslei</i>	0	0	0	1	0	1	1	0	1	1	0	1	0	0	0	0	0	0	1	1	0	0	0	0	1
<i>C. (C.) kimberleyi</i>	1	0	0	0	1	0	1	1	0	1	1	0	1	0	0	0	0	0	1	1	0	1	0	1	1
<i>C. (C.) marea</i>	0	0	0	0	1	0	1	0	0	1	1	0	1	0	0	0	0	0	0	1	1	0	0	0	1
<i>C. (C.) marchisoni</i>	0	1	0	0	1	0	1	1	0	1	1	0	1	0	0	0	0	0	0	1	1	0	1	0	1
<i>C. (C.) namu</i>	0	0	0	0	1	0	1	1	0	1	1	0	1	0	0	0	0	0	0	1	1	0	1	0	1
<i>C. (C.) navicula</i>	0	0	0	0	1	-	-	1	0	1	1	1	-	-	0	0	0	0	0	1	1	0	1	-	-
<i>C. (C.) putealis</i>	0	0	0	0	1	0	1	1	0	1	1	0	1	0	0	0	0	0	0	1	1	0	1	0	1
<i>C. (C.) scourfieldi</i>	0	0	0	0	1	0	1	0	0	1	1	0	1	0	0	0	0	0	0	1	1	0	0	0	1
<i>C. (C.) solitaria</i>	0	0	0	0	1	0	1	1	0	1	1	0	1	0	0	0	0	0	0	1	1	0	1	0	1
<i>C. (C.) sumatrana</i>	0	0	0	0	1	0	1	1	0	1	1	0	1	0	0	0	0	0	0	1	1	0	1	0	1
<i>C. (C.) tenuis</i>	0	0	0	0	1	0	1	1	0	1	1	0	1	0	0	0	0	0	0	1	1	0	1	0	1
<i>C. (C.) thienemanni</i>	0	0	0	0	1	0	1	1	0	1	1	0	1	0	0	1	0	0	1	1	1	0	0	0	1
<i>C. (C.) trichota</i>	0	0	0	0	1	-	-	1	0	1	1	1	-	-	0	0	0	0	0	1	1	0	0	-	-
<i>C. (C.) urmilae</i>	0	1	0	0	1	0	1	0	0	1	1	0	1	0	0	0	0	0	0	1	1	0	0	0	1
<i>C. (C.) westaustraliensis</i>	1	0	0	0	1	0	1	1	0	1	1	0	1	0	0	0	0	0	0	1	1	1	0	0	1
<i>Cub. cubensis</i>	0	0	0	0	1	1	1	-	0	1	0	1	0	1	0	0	1	1	0	1	1	0	0	1	0
<i>Cub. anisitsi</i>	0	0	0	0	1	0	1	1	0	1	0	1	0	0	0	1	0	0	1	1	0	0	1	0	1
<i>Cub. columbiensis</i>	0	0	0	0	1	0	1	1	0	0	0	1	0	0	0	1	0	1	1	1	0	0	1	0	1
<i>Cub. falcandica</i>	0	0	0	0	1	0	1	1	0	1	1	0	0	1	0	0	1	0	0	1	1	0	0	1	0
<i>Carib. trapezoides</i>	0	1	0	1	1	0	1	1	0	1	1	0	1	0	0	0	0	0	0	1	1	1	0	1	0
<i>Carib. auricularia</i>	0	1	0	1	1	0	1	1	0	1	1	0	1	0	0	0	0	0	0	1	1	1	0	1	0
<i>Carib. ansa</i>	0	1	0	1	1	0	1	1	0	1	1	0	1	0	0	0	0	0	0	1	1	1	0	1	0
<i>Pioneer. hancocki</i>	0	0	0	2	1	0	1	1	1	1	0	1	1	1	1	0	0	1	1	1	1	0	0	1	1

revealed 8849 equally parsimonious trees with  $L=21$ ,  $Ci=80$  and  $Ri=90$ . The strict consensus of all trees had the same length,  $Ci$  and  $Ri$  values. On the other hand, the Ratchet Island Hopper analysis found only one most parsimonious tree, presented in the Fig. 7. This tree also had  $L=21$ ,  $Ci=80$  and  $Ri=90$ , and it is very similar to the strict consensus of 8849 trees except that it better resolves the relationships in the *Candonopsis* clades.

Characters and their coding corresponding to the Table 2 matrix are as follows:

0, Posterior furcal seta: present (0), absent (1); 1, number of strong claws on terminal segment of Md-palp: two (0), one (1); 2, type of fusion of strong claws on terminal segment of Md-palp: narrow (0),

wide (1); 3, z1 seta in males: long (0), short (1); 4, number of short setae on terminal segment T3: two (0), one (1); 5, number of 'a' lobe extensions: one (0), two (1); 6, number of segments on T3: five (0), four (1); 7, subterminal sclerified structures on prehensile palps: both well developed (0), only one well developed (1); 8, L: W ratio of terminal segment of Md-palp: less than 3:1 (0), more than 3:1 (1); 9, dorsal view:  $LV=RV$  (0),  $LV>RV$  (1); 10, total number of segments on A1: seven (0), six (1), four (2); 11, number of setae on second segment of Md-palp: two (0), one (1); 12, lateral view: symmetrical (0), asymmetrical (1); 13, spines on furcal claws: absent (0), present (1); 14, En2a seta: present (0), absent (1); 15, G2 claw in females: shorter than G1 (0), as long as G1 (1); 16, basal seta on T2: present (0), absent (1); 17, seta on second endopodal segment of T2: present (0), absent (1); 18, Td2 seta: present (0), absent (1); 19, Tf seta: present (0), absent (1); 20, Te seta: present (0), absent (1); 21, Ta' seta: present (0), absent (1); 22, number of setae on A2 penultimate segment externally: two (0), one (1); 23, prehensile palps: asymmetrical (0), symmetrical (1); 24, internal hemipenis ducts: not coiled (0), coiled (1); 25, posterior furcal claw: well developed (0), reduced (1); 26, male sexual bristles: present (0), absent (1); 27, surface: smooth (0), ornamented (1); 28, carapace shape: subtriangular (0), subreniform (1), subtrapezoidal (2); 29, posterior margin: narrower than anterior (0), wider or equal to anterior (1); 30, CB2 seta: present (0), absent (1); 31, En2d seta: present (0), absent (1); 32, En3b seta: present (0), absent (1); 33, En4b seta: present (0), absent (1).

## DISCUSSION

The Candonopsini has at least 2 evolutionary branches: 1 with *Candonopsis* Vávra, 1891, and the other with *Caribecandona*, *Cubacandona* and *Pioneercandona*. The first branch, presented as a separate clade in all cladograms



TABLE 2. Data matrix for the species of the tribe Candonopsini and the outgroup. Characters correspond to the Fig. 7.

Taxon	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	
<i>Cr. dudichi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>C. (A.) aula</i>	1	1	1	1	1	0	0	-	1	1	0	0	0	0	1	1	1	0	1	1	1	1	1	-	1	1	0	0	1	1	1	1	1	1	1
<i>C. (A.) indoles</i>	1	1	1	-	1	-	0	-	1	1	0	0	0	0	1	1	1	1	1	1	1	1	1	1	-	1	0	-	0	1	1	1	1	1	1
<i>C. (A.) williamsi</i>	1	1	1	1	1	0	0	1	1	1	0	0	0	0	1	1	1	0	1	1	1	1	1	1	0	1	0	0	0	1	1	0	1	1	1
<i>C. (C.) africana</i>	1	1	1	-	1	0	0	1	1	0	0	-	0	1	-	-	-	0	0	0	0	-	-	0	1	0	0	0	1	1	-	-	-	-	-
<i>C. (C.) anteroarc.</i>	1	1	1	1	1	0	0	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0
<i>C. (C.) houi</i>	1	1	1	1	1	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	-	1	0	1	0	0	0	1	1	0	1	1	1
<i>C. (C.) bujukuensis</i>	1	1	1	1	1	0	0	1	1	0	0	-	0	1	-	1	-	0	0	0	0	-	0	0	1	0	0	0	1	1	-	-	-	-	-
<i>C. (C.) dani</i>	1	1	1	1	1	0	0	1	1	0	0	0	1	1	1	1	0	0	0	0	0	0	0	1	0	1	0	0	0	1	1	0	0	0	0
<i>C. (C.) hummelincki</i>	1	1	1	-	1	-	0	-	1	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	-	-	0	-	0	1	1	0	1	0	0
<i>C. (C.) kingslei</i>	1	1	1	1	1	0	0	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	1	0	0	0	1	1	0	0	0	0
<i>C. (C.) kimberleyi</i>	1	1	1	1	1	0	0	1	1	0	0	0	0	1	1	1	0	0	0	1	0	1	1	0	1	0	0	1	2	0	0	1	1	0	0
<i>C. (C.) marea</i>	1	1	1	1	1	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0
<i>C. (C.) murchisoni</i>	1	1	1	1	1	0	0	1	1	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	1	0
<i>C. (C.) nama</i>	1	1	1	1	1	0	0	1	1	0	0	0	0	1	-	1	0	0	0	0	0	-	0	0	1	0	0	0	1	1	-	-	-	-	-
<i>C. (C.) navicula</i>	1	1	1	-	1	-	0	-	1	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	-	-	0	-	0	1	1	0	0	0	0
<i>C. (C.) putealis</i>	1	1	1	-	1	0	0	1	1	0	0	-	0	1	-	1	-	0	0	0	0	-	1	0	1	0	0	0	1	1	-	-	-	-	-
<i>C. (C.) scourfieldi</i>	1	1	1	1	1	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	1	0	1	0	0
<i>C. (C.) solitaria</i>	1	1	1	-	1	0	0	1	1	0	0	-	0	1	-	-	-	0	0	0	0	-	-	0	1	0	0	0	1	1	-	-	-	-	-
<i>C. (C.) sumatrana</i>	1	1	1	-	1	0	0	1	1	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0
<i>C. (C.) tenuis</i>	1	1	1	1	1	0	0	1	1	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0
<i>C. (C.) thienemanni</i>	1	1	1	1	1	0	0	1	1	0	0	0	0	0	0	-	1	-	0	1	0	0	-	-	0	1	0	0	0	0	0	-	-	-	-
<i>C. (C.) trichota</i>	1	1	1	-	1	-	0	-	1	0	0	0	0	0	-	1	-	0	0	0	0	-	-	-	-	0	-	0	0	0	-	-	-	-	-
<i>C. (C.) urmilae</i>	1	1	1	1	1	0	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	-	1	0	1	0	0	0	1	1	-	1	1	0
<i>C. (C.) westaustral.</i>	1	1	1	1	1	0	0	1	1	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	1	1	0	1	1	1	0	0	1	1	
<i>Cub. cubensis</i>	1	1	1	1	1	0	1	0	0	0	0	0	0	0	1	-	0	0	1	0	1	-	1	1	0	0	1	0	2	1	0	1	1	0	
<i>Cub. anisitsi</i>	1	1	1	-	1	1	0	0	0	0	-	0	0	-	-	-	0	-	0	0	-	-	1	0	0	-	0	2	1	-	-	-	-	-	
<i>Cub. columbiensis</i>	1	0	0	1	1	1	0	0	0	0	0	0	0	-	1	-	0	1	-	0	-	1	1	0	0	0	0	1	1	-	-	-	-	-	
<i>Cub. fulclandica</i>	1	1	1	-	1	1	0	0	0	-	0	0	-	0	-	1	-	0	-	0	0	-	-	1	0	0	0	1	1	-	-	-	-	-	-
<i>Car. trapezoidea</i>	1	1	1	1	1	0	1	0	0	1	0	1	0	1	1	0	0	0	0	0	0	0	1	1	0	1	0	0	2	0	0	1	0	0	
<i>Car. auricularia</i>	1	1	1	1	1	0	1	0	0	1	0	1	0	1	1	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	1	0	0
<i>Car. ansa</i>	1	1	1	1	1	0	1	0	0	1	0	1	0	1	1	0	0	0	0	0	0	0	1	1	0	1	0	0	2	0	0	1	0	0	
<i>Pioneer. hancocki</i>	1	1	1	1	1	0	1	0	0	2	1	0	0	1	1	1	1	1	1	1	0	1	1	1	1	1	0	0	0	1	1	1	1	1	1

(Figs 6, 7), is defined with a long terminal segment on the Md-palp, a synapomorphy of all 24 Recent species of *Candonopsis*. In addition, all species are characterised with 2 symplesiomorphies: the asymmetrical prehensile palps, and only 1 extension of the lobe 'a' on the hemipenis. However, compared with other Candoninae the palps and the hemipenis in *Candonopsis* are very characteristic and have little in common with other Candoninae. Within *Candonopsis* several distinct clades occur on all resulting cladograms. The largest is defined by one synapomorphic character (presence of a spine on the furcal claws), and it includes almost

all African, the only Central American and almost all Australian species of *Candonopsis s. str.* This correlates with Klie's (1932) zoogeographical groupings of the species based on the appearance of the furcal claws, in which almost all species from the tropics and subtropics have a spine at least on one of the furcal claws, while European species have both claws spineless. The exceptions are 1 species from Lake Tanganyika (*C. anteroarcuata* Rome, 1962) and 1 from the Murchison Region (*C. westaustraliensis* Karanovic & Marmonier, 2002). The Australian species has, in addition, a reduced posterior furcal claw. *Abcandonopsis*



Karanovic, in press b is a clade defined by only 1 autapomorphic character - asymmetrical valves in dorsal view. All other features of this subgenus are homoplastic. For example, the 3 known species of *Abcandonopsis* have many setal reductions that are also recorded in *Pioneer-candonopsis hancocki* sp. nov., *C. (C.) thienemanni* Schafer, 1945 and *C. (C.) kimberleyi* Karanovic & Marmonier, 2002. Because all these species are subterranean inhabitants, some of the setal reductions may well be stygomorphies. A clade containing *Candonopsis (C.) scourfieldi* Brady, 1910; *C. (C.) boui* Danielopol, 1978, *C. (C.) urmila* Gupta, 1988; and *C. (C.) mareza* Karanovic & Petkovski, 1999 is supported with the symplesiomorphic state of the character number 7, i.e. a short claw G2 on the female A2. This claw is long in all other representatives of the tribe. The smallest clade in *Candonopsis* includes Australian *C. (C.) murchisoni* Karanovic & Marmonier, 2002 and *C. (C.) dani* Karanovic & Marmonier, 2002. Although, the connecting character (asymmetry of the valves in the lateral view) is homoplastic in the tribe, and it is found in all *Caribecandona* species, and in *C. (C.) urmila* Gupta, 1988, the two Australian species are indeed more closely related to each other than either is to any other representative of *Candonopsis* (Karanovic & Marmonier, 2002).

The second branch in *Candonopsini* is supported with 2 synapomorphic characters: 2 extensions of the lobe 'a' on the hemipenis, and almost symmetrical prehensile palps. Also, all species have a small terminal segment of the Md-palp. *Pioneer-candonopsis* is a clade defined by 2 autapomorphies: 4-segmented A1 and only 1 seta externally on the second segment of the Md-palp. The reduction of A1 segments more closely relates *Pioneer-candonopsis* to *Caribecandona* than to *Cubacandona*. However, in the former genus, A1 is 6-segmented, the posterior furcal claw is reduced and the valves are asymmetrical in the lateral view. The new genus and two genera from South and Central America occur as a monophyletic clade in Fig. 6, but in Fig. 7, the clade does not include *Cubacandona cubensis* (Méhes, 1913) or *C. anisitsi* (Daday, 1905). According to Méhes' (1913) drawings, *C. cubensis* has 2 strong claws on the terminal segment of the Md-palp, which gives it an isolated position in the tribe. *Cubacandona anisitsi* stands apart because it has both subterminal sclerified structures well developed (Daday, 1905).

*Cubacandona columbiensis* and *C. anisitsi*, together with about a dozen other species of the *Candonopsini*, are insufficiently described. Because of this, many characters are unknown (and coded '-') in the second data matrix (Table 2) and in the cladistic analysis treated as ambiguous. Many ambiguous characters and a great number of homoplasies in the tribe *Candonopsini* produced confusing cladograms. Therefore, characters from the second data matrix (Table 2) were weighted in accordance to their taxonomic importance. The resulting cladogram (Fig. 7) is very similar to the one obtained after the analysis of the first data set (Fig. 6). The difference is that some newly introduced characters (chaetotaxy of the A1, A2 and T1) better resolve phylogenetical relationships in the *Candonopsis* clades. This suggests that a better understanding of the morphology of the insufficiently described taxa would certainly contribute to the cladogram resolution. However, both trees correlate with the present systematics of the tribe *Candonopsini* with the exception of the genus *Cubacandona*, which seems to be a polyphyletic genus.

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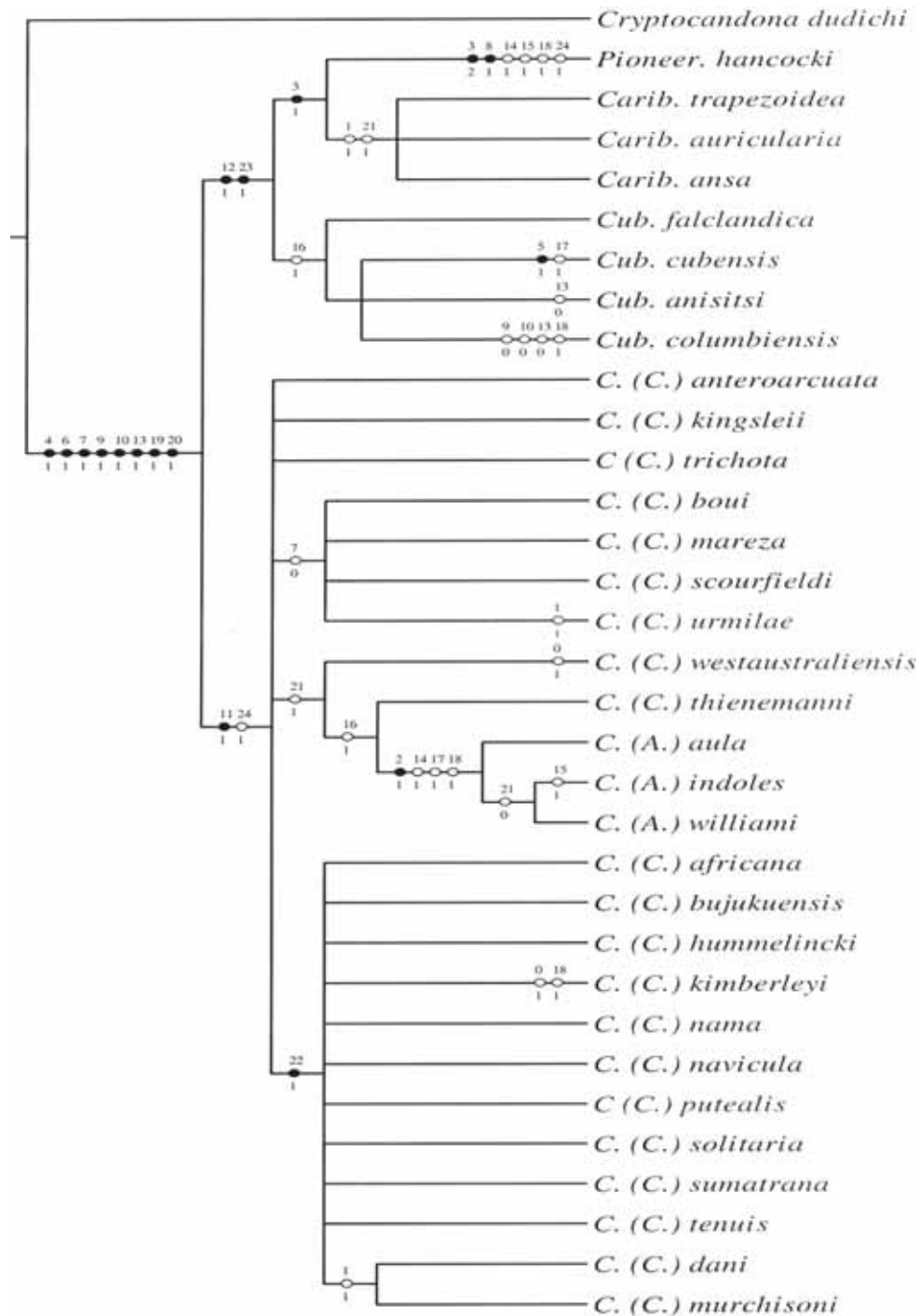


FIG. 6. Cladogram of the tribe Candonopsini based on 24 characters. Number above the hash-marks correspond to the character, numbers below are character states. Black dots are apomorphies, white dots are homoplasies.

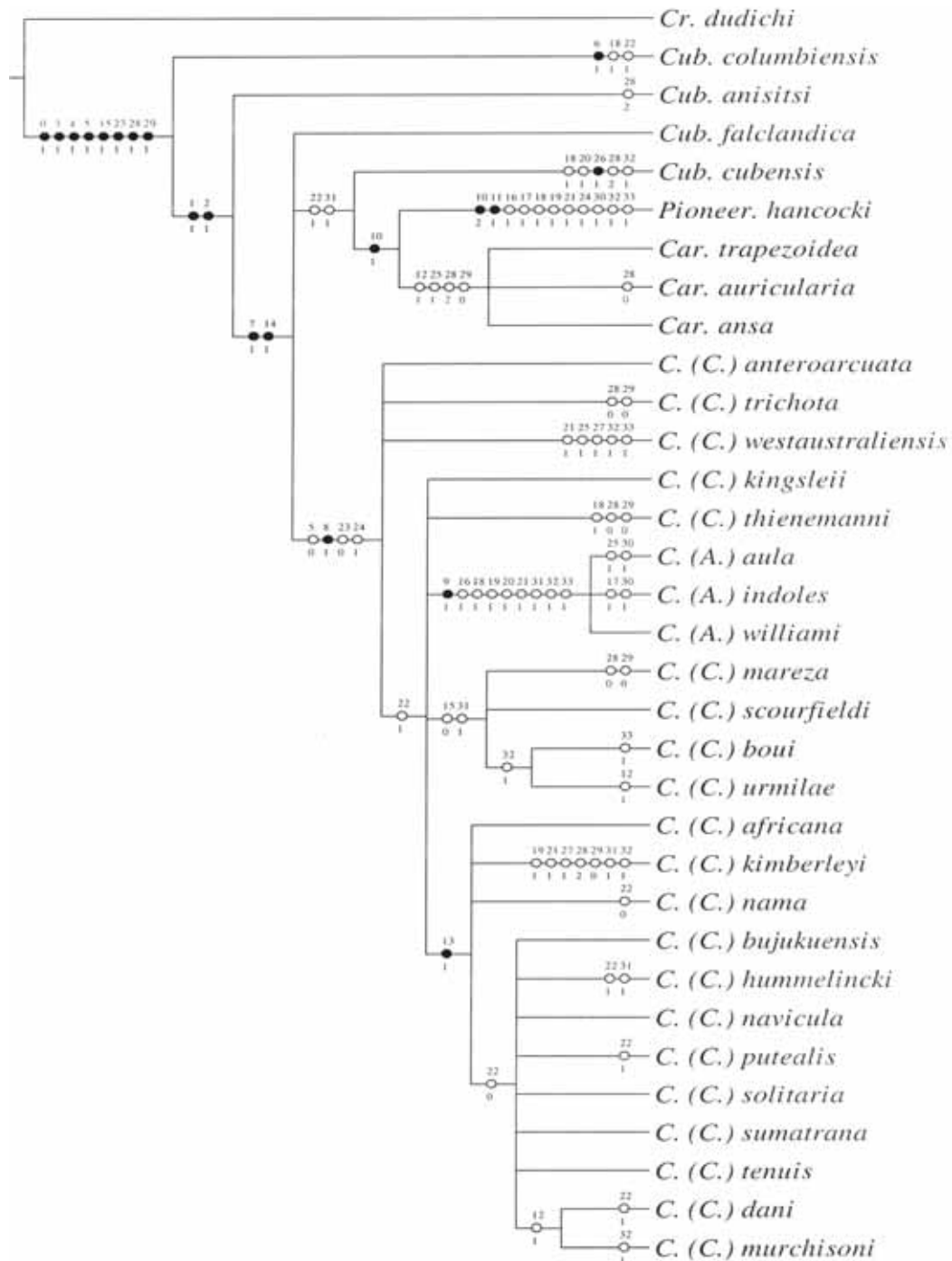


FIG. 7. Cladogram of the tribe Candonopsini based on 33 weighted characters. Number above the hash-marks correspond to the character, numbers below are character states. Black dots are apomorphies, white dots are homoplasies.

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