

**TAXONOMIC RE-EXAMINATION OF *CAMBAROIDES* (DECAPODA: CAMBARIDAE) WITH A RE-DESCRIPTION OF *C. SCHRENCKII* FROM SAKHALIN ISLAND RUSSIA AND PHYLOGENETIC DISCUSSION OF THE ASIAN CAMBARIDS BASED ON MORPHOLOGICAL CHARACTERISTICS**

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ABSTRACT

Within the freshwater crayfish genus *Cambaroides*, there has been taxonomic uncertainty as to the population from Sakhalin Island, Russia, represent *Cambaroides schrenckii* (Kessler, 1874) or whether it warrants full recognition as *C. sachalinensis* Birstein and Winogradov, 1934. Detailed morphological examination of specimens from Sakhalin, combined with molecular analysis of the mitochondrial 16S rRNA and COI genes, has shown that they can be regarded as *C. schrenckii*. We also provide detailed information on the geographic distribution, life history, and habitat of this little known species. Morphology of the epistome, merus of the third maxilliped, and the male second pleopod has phylogenetic importance for freshwater crayfishes in the Northern Hemisphere (Astacidae and Cambaridae in Asia and North America). These morphological features are described and illustrated in detail for four species of *Cambaroides* (Asian Cambaridae), and compared with all representative genera in Astacidae and American Cambaridae. Members of *Cambaroides* share the same features, and the male second pleopod of *Cambaroides* has a unique character within Astacidea. This indicates the Asian Cambaridae are monophyletic, and separate from the American cambarid clade, which is consistent with previous molecular data.

KEY WORDS: *Cambaroides*, mitochondrial gene, morphology, phylogeny, Sakhalin

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INTRODUCTION

Freshwater crayfish of Astacidea, including the superfamilies Astacoidea (Astacidae and Cambaridae) and Parastacoidea, are one of the most well-studied taxa of the Crustacea and have been used traditionally as model organisms in zoology since the work of Huxley (1896) and Stebbing (1893). The genus *Cambaroides* within the Cambaridae still has an unsolved taxonomic issue. Starovogotov (1995) suggested that *C. schrenckii* could be divided into two species, *C. schrenckii* and *C. sachalinensis*. The former species occurs in the Amur River basin and the latter only in northern Sakhalin Island. However, Fitzpatrick (1995) disagreed with this concept and suggested that *C. sachalinensis* is a junior synonym of *C. schrenckii*. These two taxonomic studies examined morphology and distributional ranges based on a limited set of specimens deposited in a few museums. Starovogotov (1995) focused on the morphology of the rostrum and telson and, in contrast, Fitzpatrick (1995) suggested that while the male first pleopod could be a reliable diagnostic character, the rostrum and telson show geographical variation in species of *Cambaroides*. To clarify this taxonomic controversy we carried out a detailed morphological examination together with molecular analyses.

To date, there is no confident consensus for the monophyly of Astacida, as has been suggested from a number of

morphological and molecular studies (Scholtz, 1999; Rode and Babcock, 2003; Sinclair et al., 2004). Scholtz (1999, 2002) and Crandall et al. (2000) provided evidence for a single invasion into freshwater in the stem lineage of the freshwater crayfish. However, their distributions are disjunct, with the astacid species distributed in northwestern America and Europe and the cambarid species in far-east Asia (the Asian Cambaridae, or the genus *Cambaroides*) as well as eastern North America (the American Cambaridae). This enigmatic distribution pattern has been the subject of systematic and phylogenetic debate for the Northern Hemisphere for more than a century (Huxley, 1896; Ortmann, 1902; Hobbs, 1988; Scholtz, 1999, 2002; Crandall et al., 2000; Schram, 2001).

Certain characters (epistome, merus of third maxilliped, and male second pleopod) reflect phylogeny for the freshwater crayfishes (Astacidea) in the Northern Hemisphere (Ents, 1914; Bott, 1950). Our analyses demonstrated that the shape of male second pleopod in *Cambaroides* shows a very unique character among the world's crayfish, suggesting that this group is monophyletic and are an isolated clade from the American Cambaridae. Thus, the phylogenetic position of *Cambaroides* should be re-assessed in greater detail.

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## MATERIALS AND METHODS

Fifteen specimens, males of 45.9 mm (Male No. 1), 39.5 mm, 38.6 mm, 38.5 mm and 34.0 mm (Male No. 2), 31.8 mm, 28.1 mm, 26.9 mm, 26.2 mm, 26.1 mm, 24.5 mm, 21.4 mm and 21.3 mm (Male No. 3) in POCL and females of 44.7 mm and 29.8 mm (Female No. 1) in POCL, respectively, from the Lake Sladokoe, Northern Sakhalin, Russia were collected by a hand net on 1 to 15 August 2009, 14 to 25 October 2009, 20 to 26 June 2010, and 5 to 25 September 2010 used for observation. We recorded notes on the colors of each live individual, with color photographs being taken immediately after capture. The specimens were then fixed in 10% formalin, except for three specimens that were preserved in 70% ethanol for DNA extraction. The POCL of these individuals was 45.9 mm and 38.5 mm, representatively, for the males, and 29.8 mm for the female.

Abbreviations used in the text are: ANSP, Academy of Natural Sciences of Philadelphia, PA, USA; POCL, post-orbital carapace length; TCL, total carapace length; TL, total length; USNM, National Museum of Natural History, Washington, DC, USA.

In addition to the above specimens, further observations were conducted for the epistome, third maxilliped and second pleopod for the following specimens, covering all genera of Astacidae, as well as Form I males of the American Cambaridae. *Astacus astacus* (Linnaeus, 1758), POCL 44.6 mm (from Helsinki, Finland on 10 August 1954, USNM 175999); *Austropotamobius pallipes* (Lereboullet, 1859), POCL 25.3 mm (from Kent, England, date unknown, USNM 147261); *Pacifastacus leniusculus* (Dana, 1852), POCL 51.0 mm (from Lake Shikaribetsu, Hokkaido Prefecture, Japan on 1 October 2009), *Cambarellus montezumae* Saussure, 1857, POCL 12.8 mm (from Flalpm, Mexico in 1899, ANSP 1562); *Barbicambarus cornutus* (Faxon, 1884), POCL 42.9 mm (from Allen County, KY, USA on 17 July 1984, USNM 209259); *Bouchardina robisoni* Hobbs, 1977, POCL 10.3 mm (from Nevada County, AR, USA on 27 April 1991, USNM 218493); *Cambarus bartonii* (Fabricius, 1798), POCL 24.8 mm (from Clinton County, OH, USA on 22 March 1940, ANSP 4291); *Distocambarus carlsoni* Hobbs, 1983, POCL 22.9 mm (from Greenville County, SC, USA on 13 November 1982, USNM 207837); *Fallicambarus devastator* Hobbs and Whiteman, 1987, POCL 42.3 mm (from Angelina County, TX, USA on 13 April 1987, USNM 220098); *Faxonella clypeata* (Hay, 1899), POCL 16.4 mm (from Dooly County, GA, USA on 7 April 1978, USNM 148668); *Hobbseus promimens* (Hobbs, 1966), POCL 11.9 mm (from Hale County, AL, USA on 15 April 1974, USNM 145403); *Orconectes durrelli*, Bouchard and Bouchard, 1995, POCL 22.0 mm (from Wayne County, TN, USA on 22 April 1978, ANSP-CA 4638); *Procambarus clarkii* (Girard, 1852), POCL 41.0 mm (from Kamakura, Kanagawa Prefecture, Japan on 22th Sep. 2009); *Troglocambarus maclanei* Hobbs, 1942, POCL 11.2 mm (from Alachua Co., Florida, USA on 20th Mar. 1941, USNM 131725); *Cambaroides dauricus* (Pallas, 1772), POCL 20.2 mm (from the Amur side channel, Mal'shevskii Zaliv, near Peteropavlovka, Russia on 17th July 2007); *Cambaroides schrenckii* (Kessler, 1874, 1876), POCL 18.6 mm (from the Amur side channel, Mal'shevskii Zaliv, near Peteropavlovka, Russia on 17th July 2007); *Cambaroides similis* (Koelbel, 1892), POCL 20.3 mm (from Milyang, Kyongsangnam-do, South Korea on 5th May 2002); *Cambaroides japonicus* (De Haan, 1841), POCL 26.5 mm (from Sapporo, Hokkaido Prefecture, Japan on 25th July 2008).

Measurements were recorded to the nearest 0.1 mm using a digital caliper, and the number of denticles on the opposable margin of fingers was counted at the widest portion of the line of denticles. Terminology of the second pleopod was based on Bott (1950).

Three individuals (labeled C1-C3) from Sakhalin, Russia were analysed to verify their identity using mitochondrial DNA sequences. The total DNA was isolated from muscle tissue from a leg segment of each individual by using a phenol-chloroform extraction protocol (Kocher et al., 1989). The nuclear 16S rRNA gene fragment was amplified using 16SmF (5'-GCGAA CGGGTGAGTAACG-3') and 16SmR (5'-CCTCCCTTACGGGTTAGAA-3') primers (Masuzawa et al., 2004), while the cytochrome c oxidase subunit I (COI) gene fragment was amplified using LCO 1490 (5'-GGTCAACAAATCATAAGATATTGG-3') (Folmer et al., 1994) and CoxREV (5'-ACTCCCACARATATTGTAA-3') (Braband et al., 2006) primers. The PCR reaction mixture (25  $\mu$ l) contained PCR buffer (with 1.5 mM MgCl<sub>2</sub>), 200  $\mu$ M of each dNTP, 25  $\mu$ M of each primer, 0.625 U of *Taq* polymerase and 0.5  $\mu$ l of the DNA template. The amplification program for analysis of the 16S rRNA gene fragment consisted of an initial denaturation step of 3 min at 94°C, then 35 cycles of 45 s at 94°C, 45 s at 48°C (16S) or 50°C (COI) for annealing and 45 s at 72°C, followed by a final extension for 5 min at 72°C. PCR products were purified with

Exonuclease I and Shrimp Alkaline Phosphatase, with incubation for 1 h at 37°C followed by 20 min at 80°C. Purified products were then sequenced using both primers and BigDye Terminator 3.1 Cycle Sequencing Kit on capillary sequencer. Sequences were truncated to 428 bp (16S) and 457 bp (COI) and analyzed with the software package MEGA version 5.05 (Tamura et al., 2011). The Kimura-2-parameter (K-2-P) model was used to calculate average pairwise divergences between studied individuals and the reference sequences of species of the genus *Cambaroides*: *C. schrenckii*, *C. dauricus*, *C. similis* and *C. japonicus* (GenBank acc. nos 16S: DQ666835, DQ666837, DQ666841, DQ666839; COI: AY820882, AY820883, AY820880 and AY820881, respectively) (Ahn et al., 2006; Braband et al., 2006). Neighbour-joining trees (based on 2-P model) were constructed using the software MEGA version 5.05 (Tamura et al., 2011) (Fig. 6).

## SYSTEMATICS

Redescription of *Cambaroides schrenckii* (Kessler, 1874)

Figs 1-4, Table 1

Russian name: Sakhalin Rechnoi Rak, or Rechnoi Rak

Diagnosis.—Body and eyes pigmented, eye large (adult diameter  $X = 2.3$  mm,  $SD = 0.5$ , range = 1.5-2.9,  $N = 11$ , mean  $\pm$   $SD$  POCL  $34.4 \pm 9.6$  mm, range 21.3-45.9). Carapace subcylindrical, dorsal and lateral surfaces with numerous tufted seta punctuations; sections (width/depth) averaging 1.1-1.5 times wider than deep ( $X = 1.3$ ,  $SD = 0.2$ ,  $N = 11$ ). Rostrum not sharply acuminate or blunt triangular; margins slightly thickened, lacking spines or tubercles, tip reaching distal margin of antennal scale and extending beyond ultimate podomere of antennular peduncle; floor (dorsal surface) of rostrum convex, median carina complete absent; rostrum comprising 18.0-27.0% ( $X = 24.1\%$ ,  $SD = 3.6$ ,  $N = 11$ ) of TCL. Areola 1.2-2.0 times longer than wide ( $X = 1.8$ ,  $SD = 0.3$ ,  $N = 11$ ), occupying 19.6-32.7% ( $X = 29.4$ ,  $SD = 5.5$ ,  $N = 11$ ) of TCL and 25.9-41.6% ( $X = 38.0$ ,  $SD = 6.8$ ,  $N = 11$ ) of POCL, with long tufted setal punctuations. Suborbital ridge and postorbital ridge poorly defined dorsally, caudal end very weak, without spines. Suborbital angle obtuse. Single, strong cervical spine on each side of carapace; cervical groove uninterrupted. Antennal scale 2.1-2.7 ( $X = 2.4$ ,  $SD = 0.2$ ,  $N = 11$ ) times as long as broad, widest at midlength; mesial margin with long plumose setae, lateral margin thickened, terminating in large, corneous sharp spine, tip of which reaching midlength of antennule peduncle and extending beyond ultimate podomere of antennule peduncle. Epistome with subovate cephalic lobe bearing cephalomedian projection and slightly curved zygoma. Pleura of second to fifth pleomere with subtriangular to pointing apex. Endopod and exopod of uropod with submedian dorsal ridge and caudolateral spines.

Chela with scattered, long, tufted setal punctuations on entire surface; palm inflated, 1.2-1.5 ( $X = 1.4$ ,  $SD = 0.1$ ,  $N = 11$ ) times wider than deep, width 0.9-1.3 ( $X = 1.1$ ,  $SD = 0.1$ ,  $N = 11$ ) times length of mesial margin, fixed finger with longitudinal ridges on dorsal and ventral surfaces, flanked each side by row of small punctuations; mesial margin of fixed finger with single row of 2-12 tubercles (usually 3-5). Length of dactylus 1.3-1.5 ( $X = 1.4$ ,  $SD = 0.1$ ,  $N = 11$ ) times length of mesial margin of palm, very slightly curved mesially, dactylus with weak longitudinal ridges dorsally and ventrally, flanked each side by row of small punctuations; opposable surface with 2-5 prominent tubercles (usually 3-5).

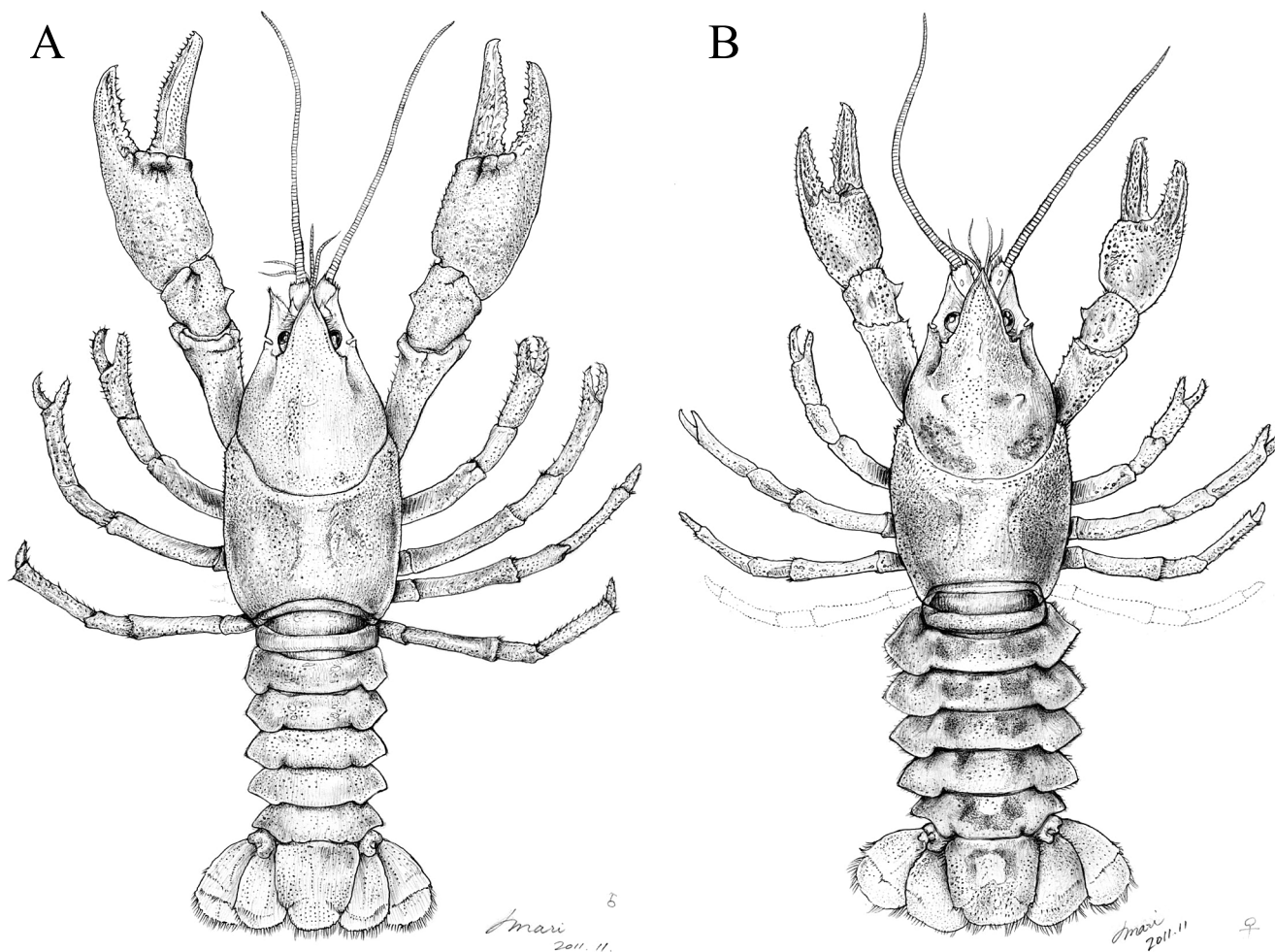


Fig. 1. *Cambaroides* from Lake Sladokoe, Sakhalin, Russia. A, male (left 4th pereiopod loss) (POCL 38.5 mm); B, female (5th pereiopods lost) (POCL 29.8 mm) (Female No. 1), October 2009.

Hooks on ischia of second and third pereiopods in males simple and rounded, reaching or beyond basio-ischical articulation. Gonopods of adult male (based on male lectotype; Fig. 4) symmetrical in caudal aspect, bases not contiguous; tip extending to posterior edge of basis of second pereiopod when pleon is flexed. In ventral aspect, apex directed cephalodistally at nearly  $30^\circ$  to axis of shaft, with strong endopod and propod. Adult male gonopods with "juvenile suture" (Fig. 4A-B). Proximal part of gonopods subcylindrical in cross section, becoming subtriangular distally. Sperm groove situated along mesial face of endopod, shallow and narrow, open between mesial process and central projection, ending in relatively blunt tips (Fig. 4C-F). Apex of gonopod sclerotized with more corneous distal part; lateral and mesial parts swollen; single small boss at midwidth on cephalodistal margin; cephalic margin with three straight, subacute, stout spines of subequal length directed cephalodistally and with mesial, centrocaudal, and centrocephalic processes, length of three processes about one-tenth of apex; blade-like caudal process at midwidth on cephalodistal margin of apex, width about one to three times width of apex. Total length of

gonopod 27.9% of TCL (35.3% of POCL) (based on male No. 1; Fig. 4A).

Annulus ventralis (based on female No. 1; Fig. 3C) immovable, symmetrical and rounded in outline, as long as wide; preannular plates transversely subdivided into subtriangular plates, slightly depressed middle section of posterior part with very shallow fossa without sinus; postannular sclerite subtriangular, medially situated single large convex, about 1.5 times as wide as long, width about two-thirds of annular plate.

For measurements of some representative specimens, see Table 1.

Description.—(Male No. 1 from Lake Sladokoe, Sakhalin Island). Body and eye pigmented, eye 2.9 mm in diameter. Cephalothorax (Fig. 2C-D) subcylindrical; thoracic section of carapace depressed (maximum width 1.5 times depth), dorsal and lateral sections of carapace with tufted setal punctuations, cephalic and lateral parts densely covered with slightly tufted setal punctuations; cephalic section of carapace covered laterally with very small, squamous tubercles. Areola 2.0 times as long as wide, occupying 32.7% of TCL (41.4% of POCL) and covered with short tufted setal punc-

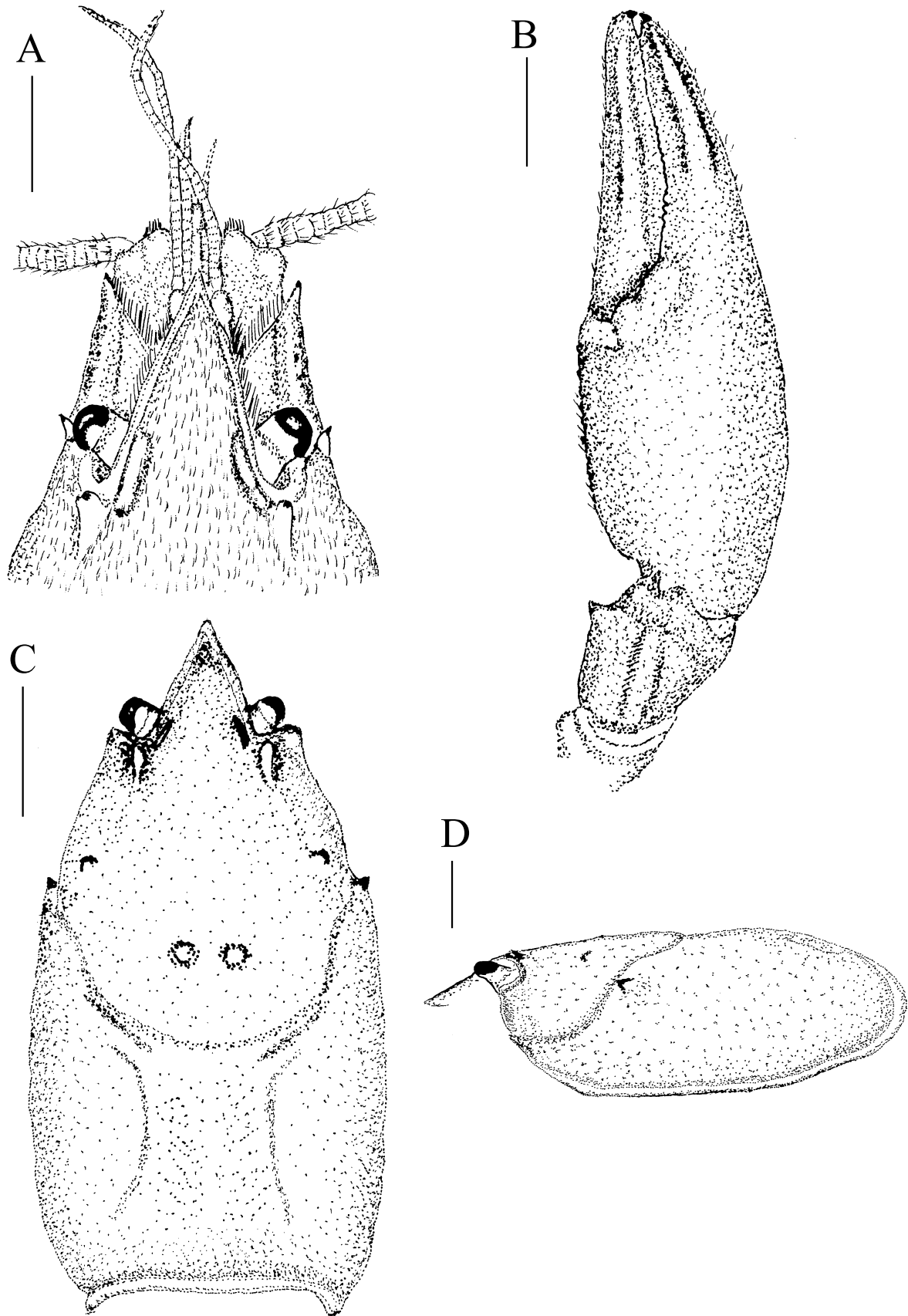


Fig. 2. *Cambaroides schrenckii*: all from male No. 1. A, dorsal view of rostrum; B, dorsal view of distal podomeres of right cheliped; C, dorsal view of carapace; D, lateral view of carapace. Scale bars = 2 mm.

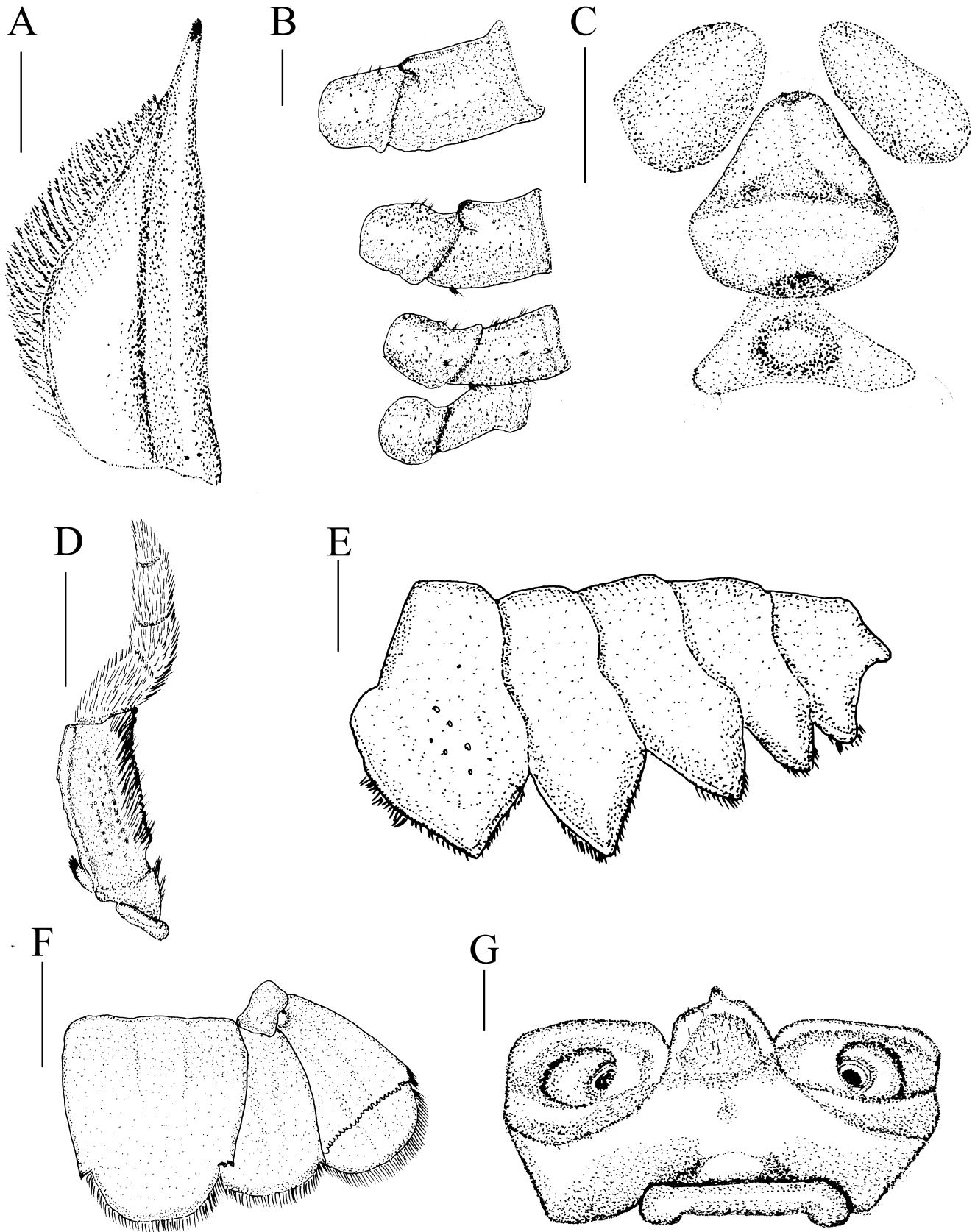


Fig. 3. *Cambaroides schrenckii*: all from male No. 1, except C from female No. 1. A, dorsal view of antennal scale; B, proximal podomeres of pereopods 2-4; C, annulus ventralis with antecedent sternite; D, ventral view of third maxilliped; E, lateral view of second to sixth pleonal somites; F, dorsal view of right uropod and telson; G, epistome and base of antennae. Scale bars = 2 mm.

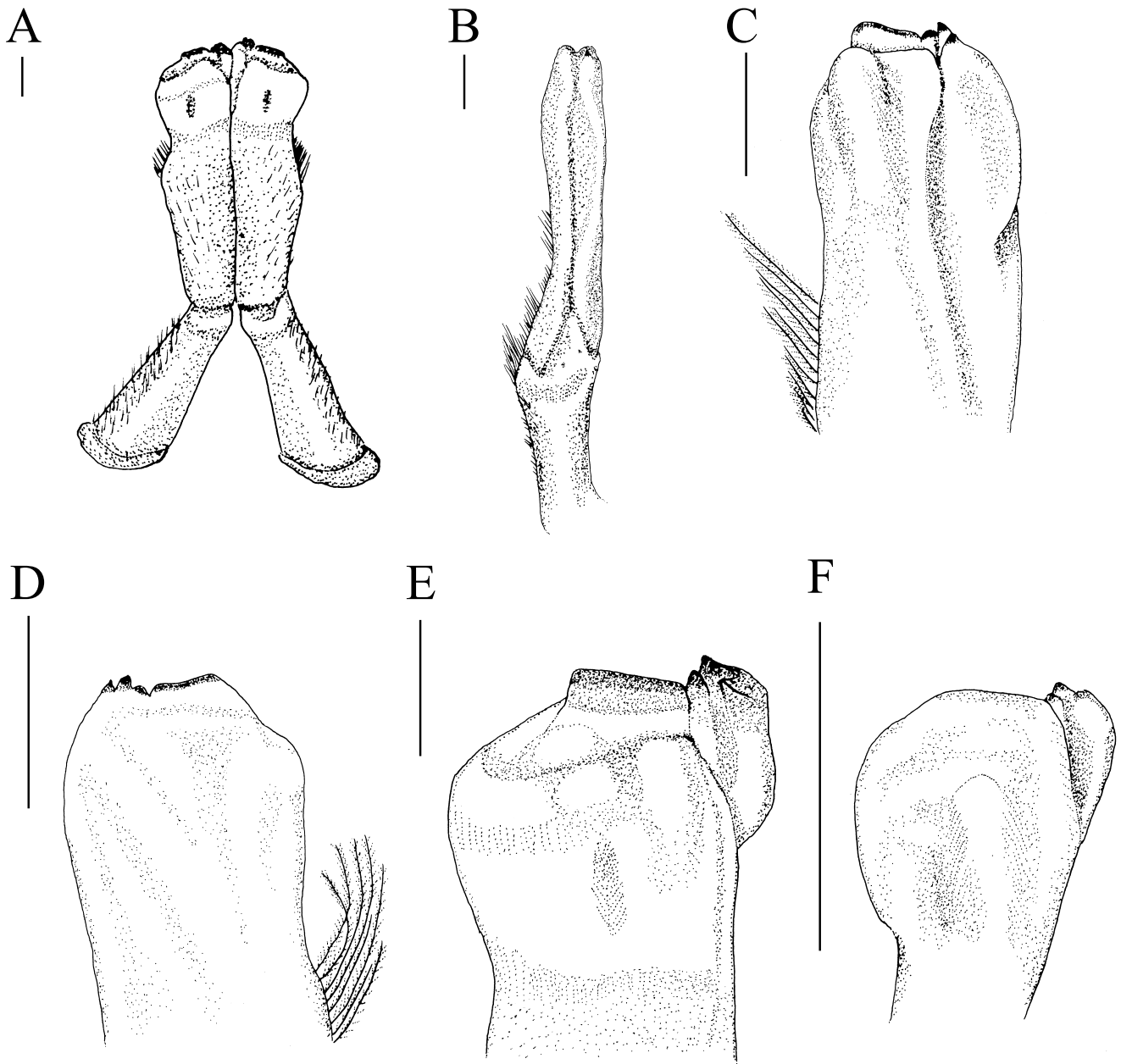


Fig. 4. *Cambaroides schrenckii*: all from male No. 1, except E from male No. 2, F male No. 3. A, dorsal view of in situ gonopods (first pleopod); B, mesial view of gonopod; C, ventral view of distal portion of gonopod; D, lateral view of distal portion of gonopod; E, ventral view of distal portion of gonopod; F, ventral view of distal portion of gonopod. Scale bars = 2 mm.

tuations. Branchiocardiac grooves feebly defined, reaching just caudal to midlength of areola. Rostrum (Fig. 2A) bluntly triangular and terminating in acute, dorsally directed apex, reaching distal margin of antennal scale and slightly beyond distal margin of ultimate podomere of antennular peduncle, occupying 24.8% of TCL (31.4% of POCL); floor of rostrum moderately convex, entire surface densely covered with tufted setal punctuations, median carina absent and with narrowly thickened margin lacking marginal tubercles or spines; ventral keel of rostrum without setae or spines; poorly defined suborbital ridge visible to base of rostrum in dorsolateral aspect, without tubercles; postorbital ridge very weak, without spines; suborbital angle obtuse without tuber-

cles. Stout cervical spine and small hepatic spine on each side of carapace; cervical groove uninterrupted; branchiostegal spine obtuse; dorsocaudal part of gastric area with two rounded bosses.

Antennal scale (Fig. 3A) 2.1 times as long as wide, greatest width at midlength; lateral margin thickened, with blunt spine; tip extending as far as distal margin of rostrum and beyond distal margin of ultimate podomere of antennular peduncle; lamella approximately 1.5 times as long as wide, with attenuated distal margin and broadly curved mesial margin proceeding obliquely to base.

Abdomen shorter than carapace; abdominal pleura (Fig. 3E) distinctly tapering to ventral apex, surface with

Table 1. Measurements (mm) of specimens of *Cambaroides schrenckii* from Sakhalin.

	Male No. 1	Male No. 2	Female No. 1
<b>Carapace</b>			
Total length	58.1	45.0	38.9
Postorbital length	45.9	34.0	29.8
Length cephalic section	38.5	30.5	25.5
Width	31.1	24.0	21.4
Depth	21.2	16.9	15.3
<b>Areola</b>			
Length areola	19.0	8.8	12.2
Width areola	9.6	7.1	6.0
<b>Rostrum</b>			
Length	14.4	8.1	10.5
<b>Antennal scale</b>			
Length	9.4	8.5	7.1
Width	4.4	3.2	3.0
<b>Pleon</b>			
Length	56.1	45.2	44.1
Width	23.0	19.4	23.1
<b>Cheliped</b>			
Length of lateral margin of chela	57.0	36.0	25.2
Length of mesial margin of chela	22.2	14.0	8.9
Width of palm	17.0	12.5	9.5
Depth of palm	13.9	8.4	6.5
Length of dactylus	28.4	20.0	13.6
Length of carpus	15.2	10.8	8.8
Width of carpus	11.4	8.3	6.1
Length of dorsal margin of merus	26.2	18.5	13.3
Depth of merus	12.7	7.5	6.3
<b>Gonopod</b>			
Length	16.2	13.3	N/A

long tufted setal punctuations, less on tergites and absent from articular surfaces. Proximal podomere of uropod (Fig. 3F) with caudomedian tubercle on medial lobe; endopod of uropod with caudolateral spine; cephalic and caudal sections of exopod of uropod with broad median ridge, bearing spine at transverse flexure, former on right side with row of denticulate spines and single middle articulated sublateral spine. Telson (Fig. 3F) with single (right 2) fixed, corneous spine at each caudolateral corner of cephalic section; lateral margin slightly tapering to flat caudal margin.

Epistome (Fig. 3G) with symmetrical, subovate cephalic lobe bearing prominent rounded cephalomedian projection; most of margins evenly thickened lateral corners, with sparse setae; floor (ventral surface) of lobe covered with short tufted setal punctuations, cephalic half of lobe slightly concave and caudal half of lobe convex; lobe constricted at base, with transverse basal sulcus; strong oblique arms leading to central shallow depression of body, with shallow centromedian fovea; lamella with truncate lateral corner, devoid of setae; zygoma thick, slightly arched, cephalic margin flanked by usual pits.

Third maxilliped (Fig. 3D) with tip of endopod reaching distal margin of penultimate podomere of antennal peduncle; basal podomere of exopod very hirsute, tip reaching one-fifth of ischium of endopod; lateral margin of ischium with

raised rib, flanked on mesial side by row of small punctuations; mesial half more coarsely punctuated, having long, stiff bristles obscuring all but proximal margin, distolateral corner slightly produced in subacute spine; mesial margin of ischium with array of irregular denticles. Right mandible with incisor armed with denticles.

Total chela length 98.1% of TCL (124.2% of POCL); palm (Fig. 2B) 3.4 times wider than long, 1.2 times wider than deep; mesial margin of right palm bearing row of small tubercles, dorsal surface of palm with very long tufted setal punctuations, becoming denser laterally and cephalically; ventral surface of palm with fewer and smaller tufted setal punctuations than other surfaces, lacking tubercles, lateral and mesial portions depressed, scattered with tufted setal and small punctuations; articular ridge strong, proximal margin well defined. Fingers of cheliped lacking gap, fixed finger moderately flattened, covered by small, long tufted setal punctuations; dorsomedian ridges defined, flanked each side by punctuate groove with proximal depression; ventral surface with poorly defined median ridge, flanked by row of small punctuations; opposable surface with single row of 12 small tubercles, most basal tubercle much larger than others. Dactylus of chela 1.3 times as long as mesial margin of palm, occupying 49.8% of total chela length; dorsal surfaces of dactylus with rounded ridge, flanked each side by punctuated groove; mesial surface bearing single row of very small denticulate tubercles; ventral surface with poorly defined longitudinal ridge, flanked each side by row of small punctuations, proximal area moderately depressed; opposable surface with dorsal row of four tubercles or denticles, third from base largest.

Carpus of cheliped (Fig. 2B) 1.3 times as long as wide, 0.7 times length of mesial margin of palm; dorsal surface with shallow, wide, slightly oblique sulcus, dorsolateral and dorsomesial surfaces of sulcus densely punctuated; mesial surface of carpus with long, blunt subdistal spine; ventral surface with single shallow longitudinal groove, and large blunt distolateral, distomedian and distomesial spines. Merus of cheliped 2.1-times longer than greatest depth, length 45.1% of TCL (57.1% of POCL); dorsal surface with single large subdistal spine and denticulate tubercles along much of dorsomedian ridge, ventrolateral ridge with 2 (left 3) acute spines; ventromesial ridge with 9 (left 7) acute spines; ischium with 3 (left 0) small ventral tubercles.

Hook on ischia of second and third pereopods (Fig. 3B) simple, oblique, rounded, more rounded in third one, tip overreaching basio-ischial articulation, not opposed by tubercle on basis. Coxa of fifth pereopod with caudomesial genital papilla (gonopore). Coxae of pereopods and sternites with dense, long, tufted setae.

Gonopods (Fig. 4A-F) as described in "Diagnosis."

**Morphological Variation.**—In addition to those addressed in the "Diagnosis," the following variations are noticed depending on localities. Samples from the present study have a lancet shape rostrum (Fig. 2A) and truncate telson (Fig. 3F). However, specimens from Amur River, Ussuri River, and Sungari River in mainland Russia have a slightly acuminate rostrum and a triangular telson (Starovogotov, 1995). Morphology of the rostrum and the telson is thus

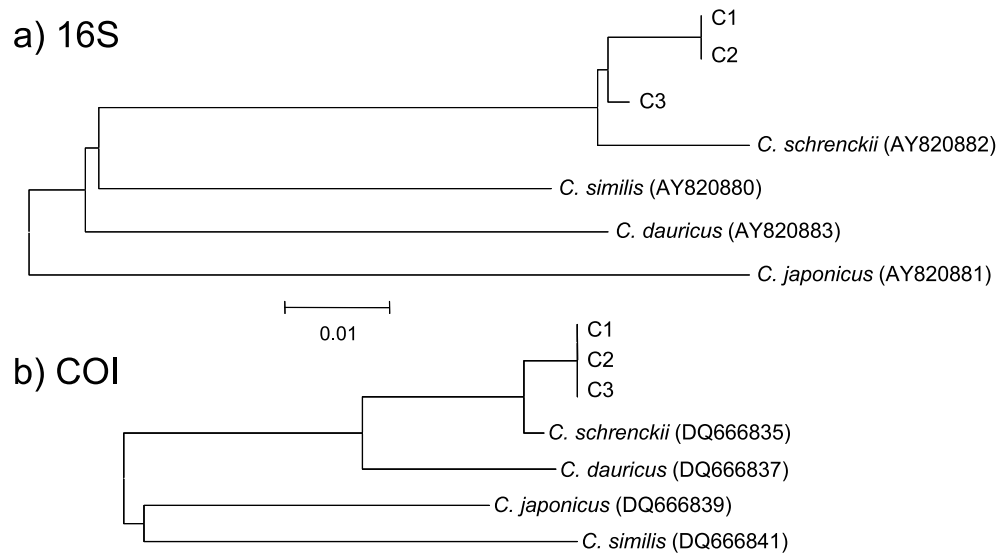


Fig. 5. Neighbor-joining trees showing patterns of the mitochondrial 16S rRNA (a) and COI (b) gene similarities between the three samples collected from Lake Sladokoe, Sakhalin Island, Russia (C1-C3) and four other species of *Cambaroides*; *C. schrenckii* (from Amur side channel, Mal'shevskii Zaliv, near Peteropavlovka, Russia), *C. dauricus*, *C. similis* and *C. japonicus*.

different between populations in rivers in mainland Russia and Sakhalin Island.

The lateral and mesial parts of the apex of the first pleopod are noticeably swollen (Male No. 2, Fig. 4E), but in male No. 1 from Lake Sladokoe, Sakhalin, it is only swollen (Fig. 4C-D).

## DISCUSSION

### Taxonomic Status of the Sakhalin Crayfish

Starovogotov (1995) suggested that the shapes of the rostrum and telson, which are regarded as taxonomically diagnostic of the members of *Cambaroides*, differ between the Amur River basin and Sakhalin populations. However, Fitz-

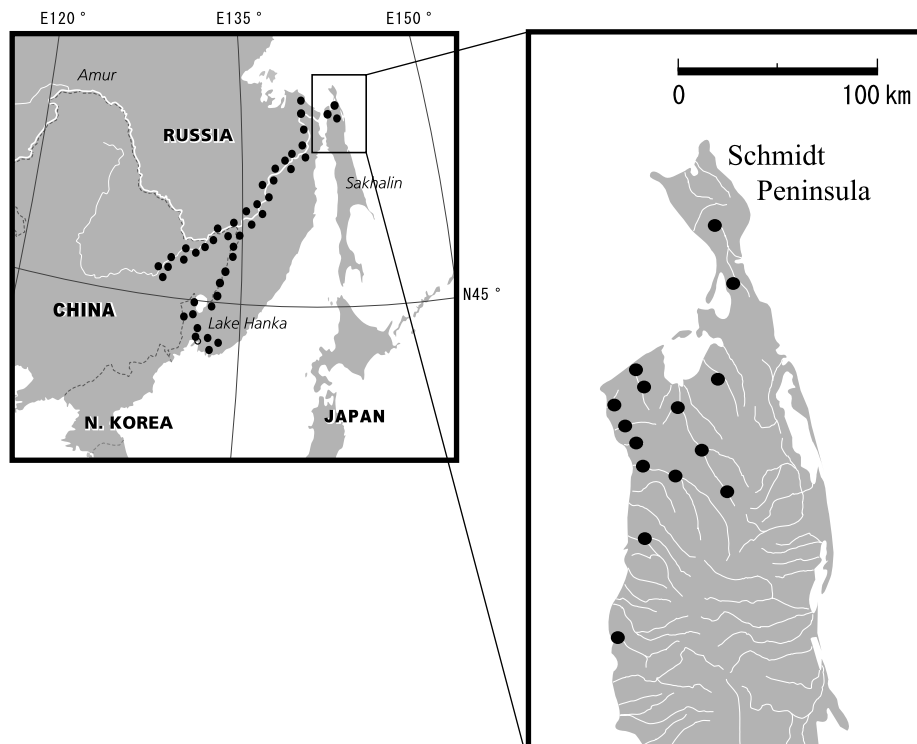


Fig. 6. Known distribution range of *Cambaroides schrenckii* (based on Basarukin and Klitin, 1997; Birstein, 1940; Labay, 1996, 1998, 1999, 2003, 2005; Labay and Shtyrts, 1996; Shtyrts and Labay, 1995, 1997; Zhivoglyadova and Labay, 2003).



patrick (1995) dismissed these differences, noting that *Cambaroides* shows geographical variation in these features. Recent taxonomic studies on the *Cambaroides* revealed that the morphology of the first pleopod could be an important diagnostic character, while features of the rostrum and telson are less important due to intra-specific variation (Kawai and Fitzpatrick, 2004; Kawai and Min, 2005). Based on the morphology of the first pleopod, *Cambaroides* found in Sakhalin are identified as belonging to *C. schrenckii*.

Our molecular analyses have shown that the individuals examined share the same 16S haplotype and two COI haplotypes with 1.1% divergence (Fig. 5). The average pairwise divergences between the individuals from Sakhalin and the reference sequences of *C. schrenckii* were 0.7% (16S) and 2.2% (COI), which corresponds to levels of intraspecific variations found in a closely related species *C. japonicus* (according to sequences available from GenBank and I. Koizumi, unpublished data), and other cambarid species (Fetzner and Crandall, 2001). In contrast, the genetic divergences between the specimens analyzed here and the second most closely related species, *C. dauricus*, were much higher, showing 3.9% (16S) and 10.8% (COI), respectively. The mtDNA data therefore confirm the previous conclusion based on morphological data, that the specimens from Sakhalin, Russia belong to *C. schrenckii*.

Thus, the morphological differences seen in the rostrum and telson between populations from the Amur River and Sakhalin are regarded as geographical variation within a single species, *C. schrenckii*.

**Notes on Geographic Distribution, Life History, and Habitat of *Cambaroides schrenckii* Geographical Range.**—This species has been found in the Lower Amur River, Ussuri River, Songhua (= Sungari) River, and the northern part of Sakhalin Island, Russia. The distribution of *C. schrenckii* in northern Sakhalin is as follows: northern limit, 54.4°0.7'N, 142.5°7.5'E in the Schmidt Peninsula; southern limit, 51.5°9.7'N, 141.4°6.5'E; and western limit 53.6°2.2'N, 143.6°0.3'E (Fig. 6). This range coincides with the Down Segment of the Paleomur River, 7500-12 000 years ago (Labay, 2007).

**Color.**—Ground color of dorsal and lateral surfaces of cephalothorax and tail fan dark brown to chocolate brown, ventral surface light brown (Fig. 7D). Dorsal and lateral surfaces of cheliped brown, ventral surface dark yellow. Dorsal and lateral surfaces of abdomen and ventrolateral pleura dark brown; tergites paler. Dorsal part of gonopods of adult male light brown, apical lobe amber.

**Habitat and Life History Traits.**—The habitat of *C. schrenckii* seems to be restricted to remarkably lentic water in flats and open rivers, dead channels or lakes (Fig. 7A-B). They live in mesotrophic or oligotrophic conditions, with the bottom sediment composed of silt or sand and usually covered with detritus and vegetation snags. One-year juveniles live in shallower areas (depth 0.2-0.4 m) of lakes, where emergent plants or sub-emergent plants dominate. Individuals of 2 years old were observed in channels at depths of 0.5-0.8 m.

The apex of the first pleopod in 2-year-old males does not show any corneous structure (Fig. 4F). Maturation in this

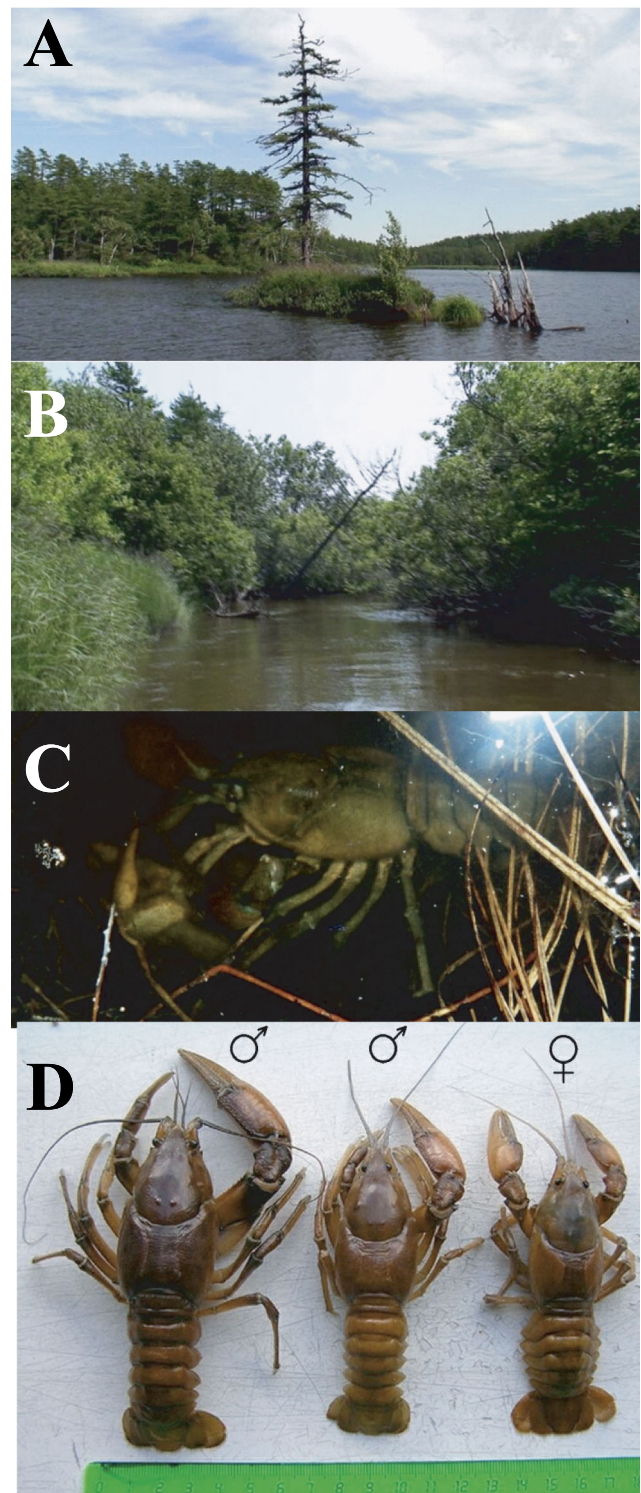


Fig. 7. (A, B) Habitat of *Cambaroides schrenckii* in Lake Sladokoe, North Sakhalin, Russia, August 2009; (C) mating of *C. schrenckii* in anonymous lake on Cape Lah, October 2009; (D) color of live specimens from Lake Sladokoe (D) (Photo by V. S. Labay). This figure is published in colour in the online edition of this journal, which can be accessed via <http://booksandjournals.brillonline.com/content/1937240x>.

species starts at 3 years as the apex of the male first pleopod poses a corneous structure (Fig. 4E). Mature individuals inhabit banks of large rivers or lakes deeper than 1 m.

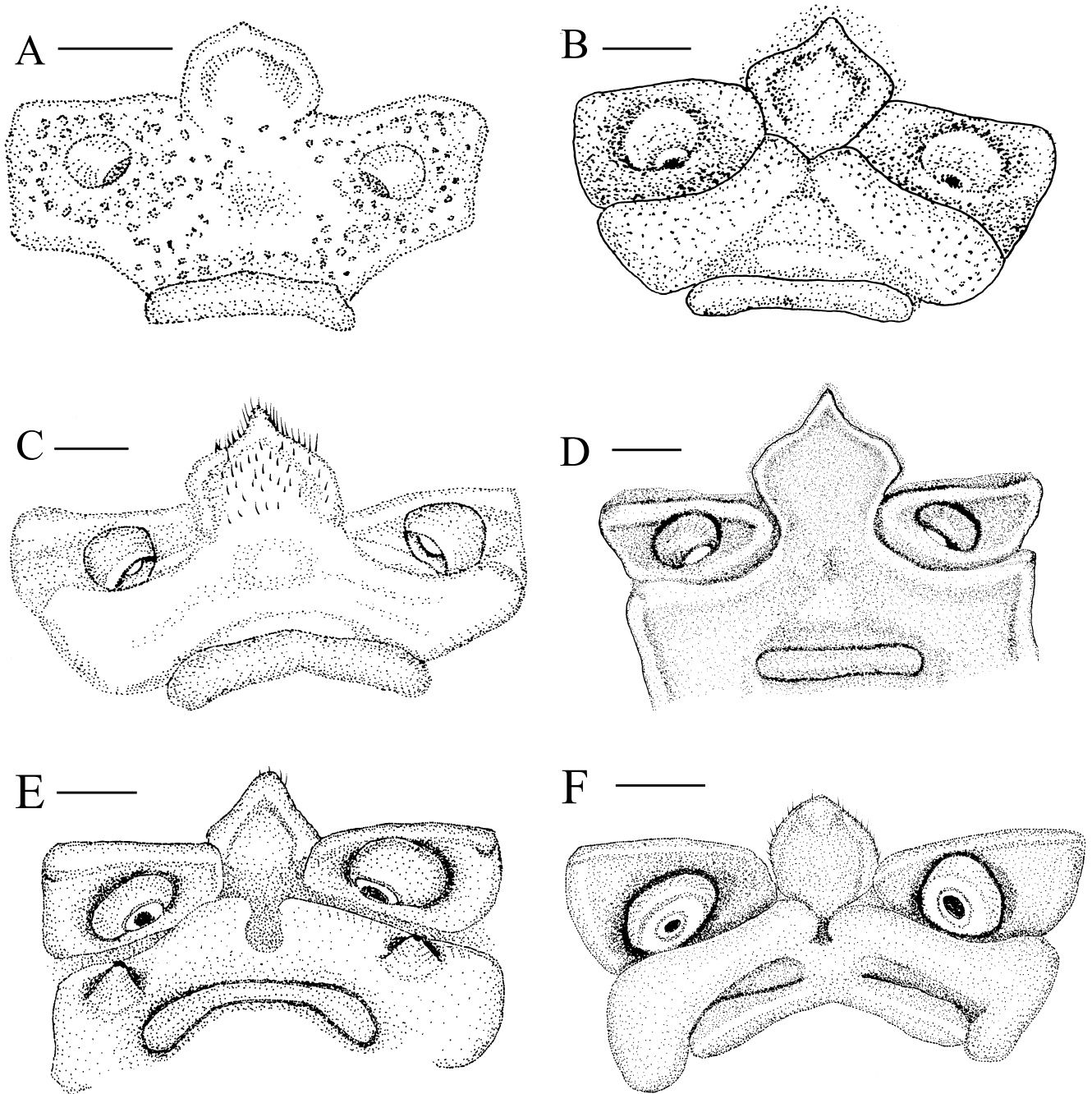


Fig. 8. Epistome and base of antennae in Asian Cambaridae and Astacidae. A, *Cambaroides schrenckii*; B, *C. dauricus*; C, *C. similis*; D, *C. japonicas*; E, *Astacus astacus*; F, *Pacifastacus leniusculus*. Scale bars = 2 mm.

Mating behavior of this species was observed at nighttime in mid-October at a depth less than 0.5 m in an un-named lake, Cape Lah, Sakhalin, Russia (Fig. 7C). Females bear 100-125 eggs per year and hatching of the eggs may occur in April or May of the next year, after frozen and/or snowed habitats are uncovered in spring. Longevity of this species may be 4-5 years.

Form alternation or cyclic dimorphism in the first pleopod is observed in adult males of the American Cambaridae, whereas it is absent in Astacidae. Payne (1996) noted that form alternation of adult males occurs in association with

the sexual activity, in which males show the first form (Form I) in the breeding season and then molt into a non-breeding status, second form (Form II). Upon return of the breeding season, Form II males molt and revert back to Form I. The Form I males could be recognized by the presence of corneous terminal elements on the first pleopods while it is completely absent in Form II males. The first pleopod of all adult male specimens from Sakhalin, possessed a corneous element (Fig. 4C-E), suggesting the absence of form alternation as known in *C. japonicus* and *C. similis* (cf.,

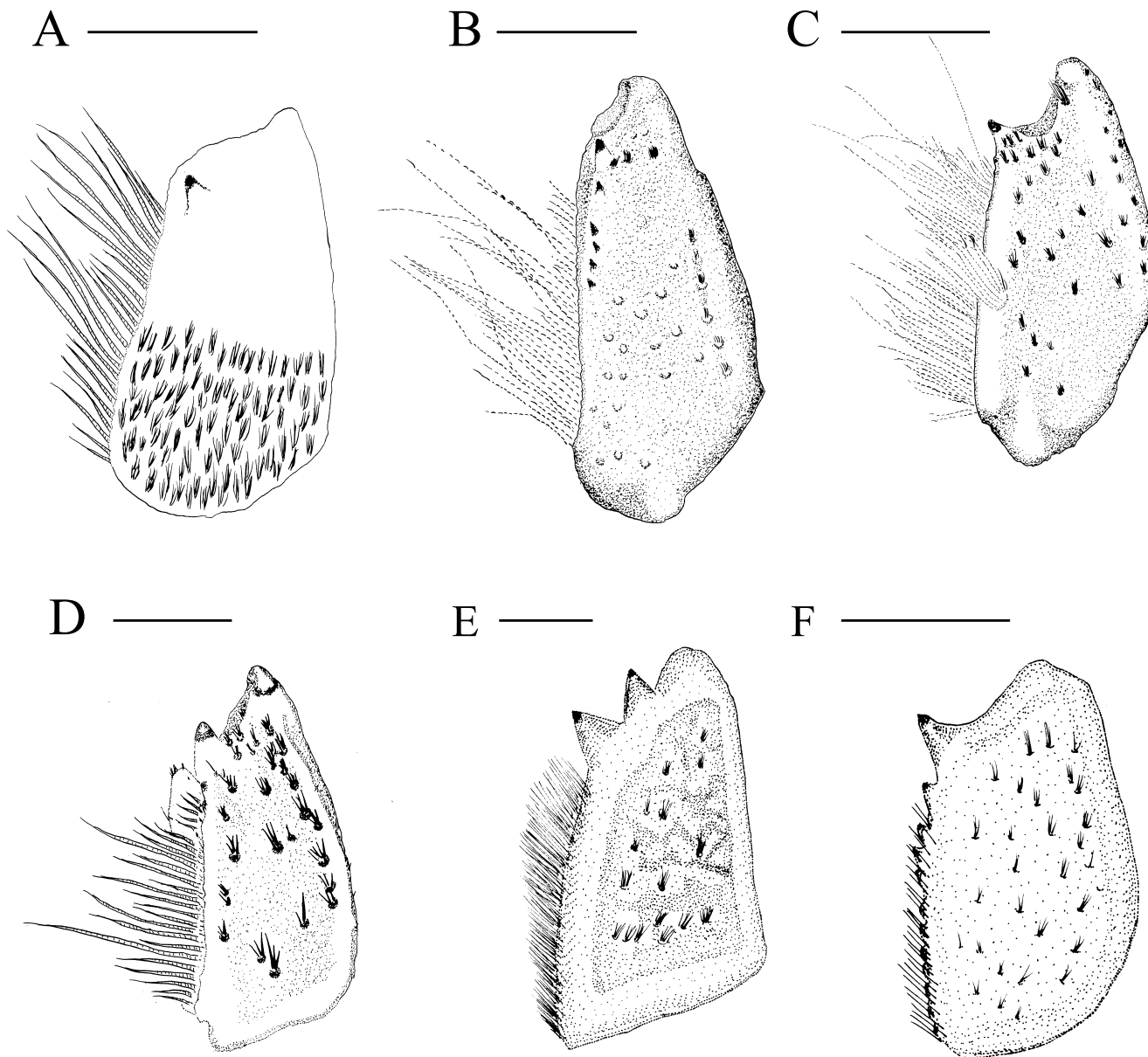


Fig. 9. Merus of third maxilliped in Asian Cambaridae and Astacidae. A, *Cambaroides schrenckii*, tufted setal punctuations on cephalic half of merus of third maxilliped omitted; B, *C. dauricus*; C, *C. similes*; D, *C. japonicus*; E, *Astacus astacus*; F, *Pacifastacus leniusculus*. Scale bars = 2 mm.

Kawai and Saito, 2001; Kawai and Fitzpatrick, 2004; Kawai and Min, 2005).

#### Morphological Characteristics in *Cambaroides*

The morphology of the epistome, third maxilliped and second pleopod of *Cambaroides* confirms their phylogenetic relationships among crayfishes in the Northern Hemisphere (Ents, 1914; Bott, 1950). *Astacus astacus* in Europe has spines or ridges posterior to a renal papilla, whereas *P. leniusculus* in North America lacks these features (Fig. 8E-F); *A. astacus* has a large mesiodistal spine along the mesial margin of the merus on the third maxilliped, however, a large mesiodistal spine with a row of spines is present in *P. leniusculus* (Fig. 9E-F). The exopod of the second pleopod of *A. astacus* does not reach the terminal end of the endopod,

but the exopods of *O. durelli* does reach the distal tip of endopod (Fig. 11A, L).

All four species of the Asian Cambaridae (genus *Cambaroides*) were compared for these three features. This analysis revealed that all members of *Cambaroides* share the following features in common: epistome with subovate cephalic lobe bearing rounded cephalomedian projection, cephalic half of lobe slightly concave and caudal half of lobe convex; strong oblique arms leading to central shallow depression of body; lamella with truncated lateral corner lacking tubercles and without spines or ridges posterior to renal papilla (Fig. 8A-D); merus of third maxilliped with row of long setae along mesial margin and large mesiodistal spine, mesial margin rarely having row of spines, dorsal surface scattered with tufted setal punctuation (Fig. 9A-D). Male second pleo-

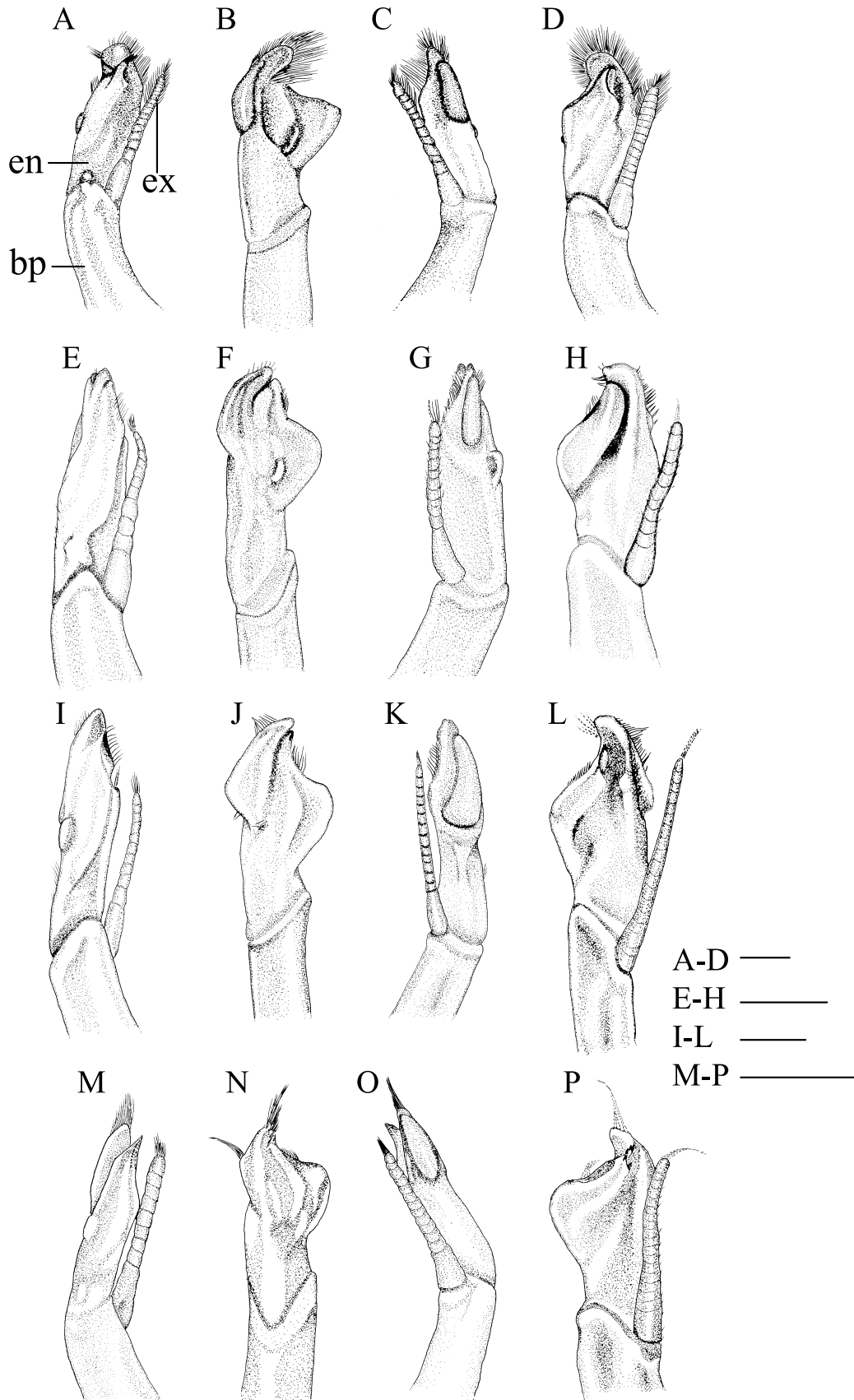


Fig. 10. Dorsal, mesial, ventral and lateral view of the male second pleopod, respectively, of (A-D) *Cambaroides schrenckii*, (E-H) *Cambaroides dauricus*, (I-L) *Cambaroides similis* and (M-P) *Cambaroides japonicas*. bp, basis; en, endopod; ex, exopod. Scale bars = 2 mm.

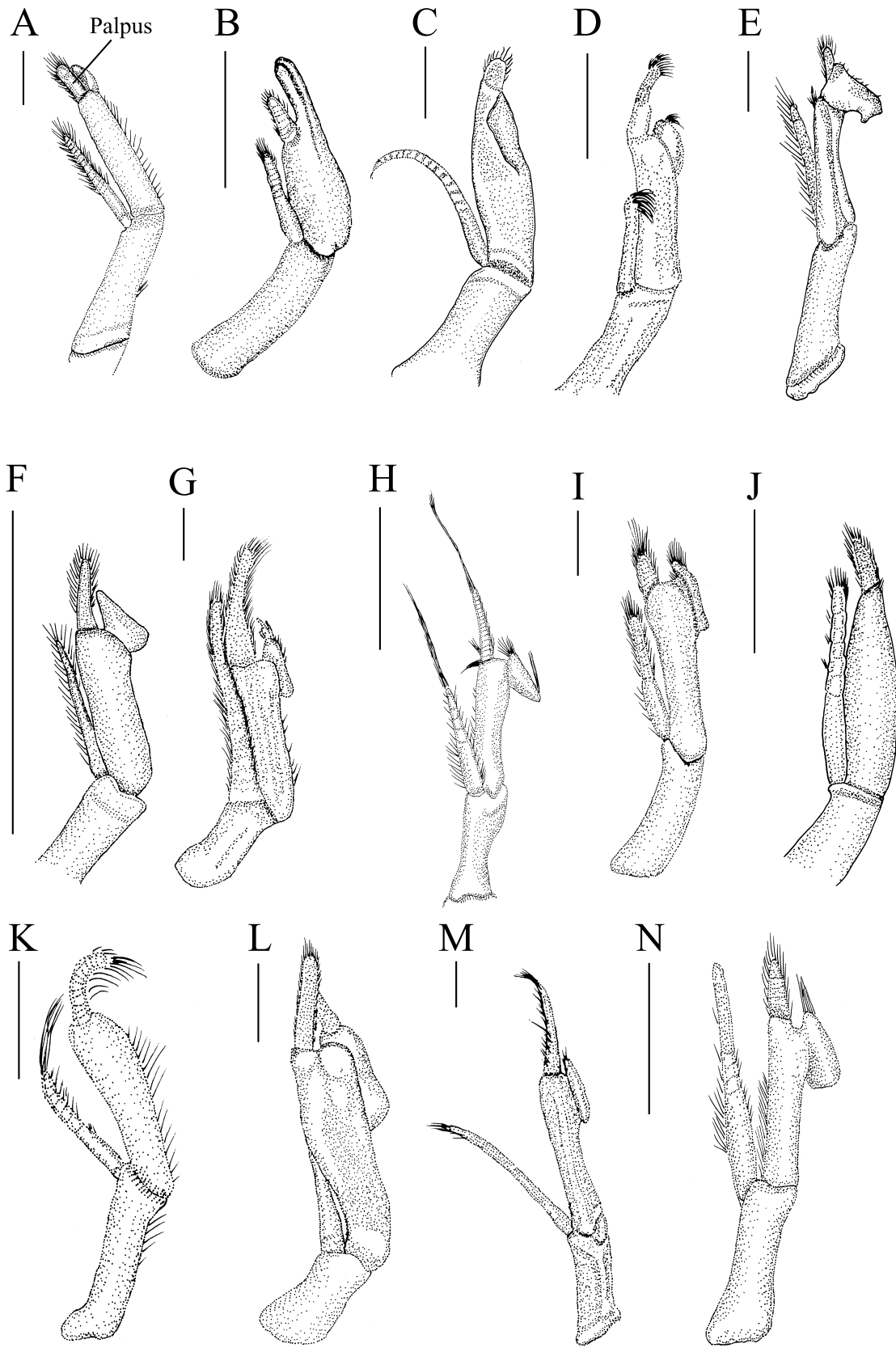


Fig. 11. Ventral view of second pleopod in Astacidea and Cambaridae: A, *Astacus astacus*; B, *Austroptamobius pallipes*; C, *Pacifastacus leniusculus*; D, *Cambarellus montezumae*; E, *Barbicambarus cornutus*; F, *Bouchardina robisoni*; G, *Cambarus bartonii*; H, *Distocambarus carlsoni*; I, *Fallicambarus devastator*; J, *Faxonella clypeata*; K, *Hobbseus prominens*; L, *Orconectes durelli*; M, *Procambarus clarkii*; N, *Troglocambarus maclanei*. Pa, palp. Scale bars = 2 mm.

pod with stout endopod and basipod divided by deep suture and angled at approximately 30–45°; terminal tip of exopod not reaching end of endopod, terminal tip of endopod with rolled element and borne on subtriangular lobe, without exopod or palp such as in astacid and American cambarid members (Fig. 10).

This morphological similarity in all four members of *Cambaroides* suggests that this group is monophyletic. The morphology of the gill and mandible also reflects the phylogeny of the crayfish (Laguarda, 1961; Bouchard, 1977), and the members of *Cambaroides* share the same features (Kawai, 2012). The results of morphological analyses are congruent with molecular data (16S rRNA and 12S rRNA, and COI) (Crandall et al., 2000; Ahn et al., 2006; Braband et al., 2006).

#### Discussion on Systematic Status of *Cambaroides*

The second pleopod is only developed in the crayfishes of the Northern Hemisphere (Astacidae and Cambaridae) (Hobbs, 1942). However, the palpi of the second pleopods are lacking in *Cambaroides* (Asian Cambaridae) when compared with other genera of Astacidae and the American Cambaridae (Figs. 10 and 11). Similarly, the lack of a pleurocoxal lappet (= pendant) on the gills in *Cambaroides* has been regarded as a unique character among the crayfish (Astacida) (Hobbs, 1988; Kawai, 2012).

After mating, females of *Cambaroides schrenckii* have the spermatophore attached on the surfaces of the annulus ventralis for 5 or 6 months during the winter season. A similar spermatophore attachment time is also known in other members of *Cambaroides* (see Kawai and Saito, 2001; Kawai and Min, 2005). In contrast, the storage period of the spermatophore in most other crayfishes appears to be much shorter (usually a few weeks) (e.g., Guan and Wiles, 1999). Thus, this reproductive trait of *Cambaroides* appears to be unique among Astacidae and Cambaridae (Hobbs, 1977).

Schram (2001) and Scholtz (1999) examined the phylogeny of Decapoda from a paleontological aspect and also discussed the evolutionary history of crayfish. It seems obvious that the origins of the modern crayfishes in the Northern Hemisphere can be traced back to Triassic times. If the modern distributions of Astacidae and Cambaridae are plotted on a paleogeographic map of the Triassic, the apparent anomalies from the modern continental positions begins to disappear, and the geographic range of the primitive *Cambaroides* is isolated from the ancestors of Astacidae and American Cambaridae (Scotese, 1997; Schram, 2001).

As already noted, molecular analyses have demonstrated that *Cambaroides* is a separate (possibly basal) clade from the North American cambarids and the European astacids (Crandall et al., 2000; Ahn et al., 2006; Braband et al., 2006). These morphological and molecular data suggest a separate familial status for the Asian genus *Cambaroides* may be warranted: Cambaroididae.

Finally, based on the result of present paper, a list of valid species is given below:

- Cambaroides dauricus* (Pallas, 1772)
- Cambaroides japonicus* (De Haan, 1841)
- Cambaroides schrenckii* (Kessler, 1874)
- Cambaroides similis* (Koelbel, 1892)

*Cambaroides wladivostokiensis* Birsyein and Vinogradov, 1934

*Cambaroides koshewnikowi* Birstein and Vinogradov, 1934

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