



A new species of *Thermosphaeroma* Cole & Bane, 1978 (Isopoda: Sphaeromatidae) from a thermo-mineral spring in northern Jalisco (Chihuahuan Desert, Mexico), with an assessment of the conservation status of the species of *Thermosphaeroma*

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ABSTRACT

We describe a new species of *Thermosphaeroma* Cole & Bane, 1978 discovered in a thermo-mineral spring in the Mexican state of Jalisco, within the Mexican Plateau subprovince of the Chihuahuan Desert. This species represents the ninth known in the genus and the eighth identified in Mexico to date. Alongside morphological characteristics, the distinctiveness of the new taxon is corroborated by a molecular phylogeny of the genus based on mitochondrial *cytochrome c oxidase* DNA sequences. Diagnostic features of the new species include elongated rami of the uropods, each extending at least to the distal margin of the pleotelson, and marked sexual dimorphism in uropods, with the female endopod being significantly longer than that of the male. We surveyed all known species localities to evaluate the conservation status of its populations. We unfortunately document the loss of four species presumed extinct due to excessive groundwater extraction resulting from declining aquifer levels and anthropogenic alterations to their habitats.

KEYWORDS: biogeography, COI gene, conservation, Crustacea, endangered and extinct species, genetic fingerprinting, Mexican Plateau, thermal springs

INTRODUCTION

The family Sphaeromatidae Latreille, 1825 is predominantly marine and represents one of the most diverse and species-rich groups of isopod crustaceans. Their occurrence in continental waters is incidental, as only eight of the 99 recognized genera within the family include strictly freshwater species. Of these eight genera, six are entirely non-marine. Europe is home to the stygobitic genera *Caecosphaeroma* Dollfus, 1896, which includes two species; *Monolistra* Gerstaecker, 1856, comprising 21 species; and the monotypic *Merozoon* Sket, 2012. Two additional strictly freshwater genera are found only in New Zealand: *Bilistra*

Sket & Bruce, 2004, with three species, one of which is epigeal and two are cave-dwelling, and the monotypic *Makaraspheara* Bruce, 2005, inhabiting coastal rivulets (Sket, 1986, 2012; Sket & Bruce, 2004; Bruce, 2005; Prevorčnik *et al.* 2010). *Thermosphaeroma* Cole & Bane, 1978 is confined to thermo-mineral springs in northern Mexico and the southern United States, with eight epigeal species. The two genera of Sphaeromatidae that have representatives in both marine and freshwater habitats are the northern Pacific genus *Gnorimosphaeroma* Menzies, 1954, which includes nine freshwater species out of a total of 27 (Tomikawa *et al.*, 2023), and

Exosphaeroides Holdich & Harrison, 1983, with one freshwater species out of three (Boyko et al., 2025).

In addition to *Monolistra* from the Dinaric karst, *Thermosphaeroma* stands out as a diversified taxon in inland waters, with all of its species occurring far from the coast and mostly isolated from fluvial systems. This genus, endemic to southern North America, occupies a narrow ecological niche, consisting of desert springs with water temperatures reaching up to 44°C, but typically ranging 25–35°C (Bowman, 1981; De la Maza-Benignos et al., 2012). Bowman (1981) hypothesized that *Thermosphaeroma* species are relicts of ancient seas that were stranded far inland during episodes of coastline regression. Indeed, their distribution aligns closely with a narrow band of territories that were once covered by epicontinental seas between the Upper Cretaceous and the Paleocene (Bowman, 1981: fig. 11).

It is noteworthy that two presumed freshwater sphaeromatid fossil taxa from Mexican deposits may belong to the phylogenetic lineage of *Thermosphaeroma*, given the rarity of freshwater sphaeromatids and the fact that both fossils originate from the geographic region where this genus is currently found. *Sphaeroma burkartii* Bárcena, 1876, was described from Neogene continental deposits in Jalisco, Mexico; however, Vega et al. (2022) suggested that it is more likely a terrestrial isopod (Oniscidea, Crinocheta) rather than a true sphaeromatid. More recently described is *Jaliscosphaera pliocenica* García-Vázquez, Alvarado-Ortega & Vega, 2023, a monotypic sphaeromatid genus identified in Pliocene lacustrine volcanic ash deposits in Jalisco. Notably, we do not rule out the possibility that this taxon might actually represent a fossil *Thermosphaeroma*, despite the fact that the poorly preserved remains exhibit morphological features compatible with this genus.

We describe a new species of *Thermosphaeroma* from a thermo-mineral spring located in the Mexican state of Jalisco, within the Mexican Plateau subprovince of the Chihuahuan Desert as defined by Morrone et al. (2022). This species represents the ninth known in the genus and the eighth described from Mexico to date. In addition to morphological characters, this new taxon is also supported by a molecular phylogeny of the genus based on mitochondrial *cytochrome c oxidase* DNA sequences.

MATERIALS AND METHODS

Study site and sampling procedures

Samples were collected using a hand-held plankton net attached to an extendable handle, both in open water and among submerged vegetation, in the thermal baths of El Montecillo. This is a thermo-mineral spring approximately 55 m long and 50 m wide, with a maximum depth of 150 cm. It is located 6 km southeast of Belen del Refugio, Teocaltiche, Jalisco state, Mexico (21°30.475'N, 102°22.939'W; 1,750 m). The mean annual atmospheric temperature of this locality is 18.4°C. The spring is surrounded by riparian vegetation, including species of Poaceae, Lythraceae, and Fabaceae. The water is jade green in appearance, alkaline (pH 9.4), and slightly warm (30.3°C). No other aquatic fauna, such as mollusks or fish, were found.

Specimens were preserved in 95% ethanol immediately after collection (Martin, 2016). Those selected for morphological examination were immersed in pure lactic acid for 2 d to digest

internal tissues and soften the cuticle, thereby facilitating dissection and subsequent microscopic analysis. Drawings were made using a camera lucida mounted on a Leica DM2500 microscope (Leica Microsystems, Wetzlar, Germany), equipped with Nomarski differential interference contrast optics.

The material has been deposited in the National Crustacean Collection, Institute of Biology, Universidad Nacional Autónoma de México (CNCR), Mexico City.

Phylogenetic analysis

Molecular analysis was conducted to examine the taxonomic differences among species. Four species were included in the analysis: *T. jalisciensis* sp. nov., *T. subequalum* Cole & Bane, 1978, *T. smithi* Bowman, 1981, and *T. macrura* Bowman, 1985. The absence of fresh or well-preserved material suitable for DNA extraction prevented molecular analysis of the other species.

DNA extraction was performed by first rinsing the collected specimens with distilled water, drying them at room temperature, and placing them in a mortar pre-frozen in dry ice (approximately –96°C). Specimens were combined with 500 µl of 1M NaOH and 10% SDS solution. The macerate was thawed at room temperature, centrifuged at 10,000 rpm for 2 min, and the supernatant recovered. Two volumes of absolute ethanol and NaCl (5M) were added to the supernatant, and the mixture stored at –20°C for 2 d to precipitate nucleic acids. The samples were then centrifuged at 13,000 rpm for 5 min. Ethanol was decanted, and the sample was washed with one volume of cold 70% ethanol (mixed by inversion and centrifuged at 13,000 rpm for 2 min). After decanting and evaporating the ethanol, the samples were resuspended in 30 µl of ultrapure water, previously heated to 37°C, and incubated for 20 h.

We used the polymerase chain reaction (PCR) (Saiki et al., 1988) to amplify a 405 bp fragment of the mitochondrial *cytochrome c oxidase* subunit I (COI). Using the complete mitochondrial genome of the isopod *Ligia oceanica* (Linnaeus, 1767) GenBank accession [DQ442914](#) as a template, primers were designed (F12: 5'–GCN TTY CCT CGR ATR AAT AAY AT–3'; R122: 5'–CTT CCT TTT TAC CAG CCT CTT GCC T–3'). The amplification conditions consisted of an initial denaturation step at 95°C for 3 min, followed by 40 cycles of 95°C for 30 s, 53°C for 30 sec, and 72°C for 30 sec, with a final extension at 72°C for 5 min. PCR products were purified using NucleoSpin PCR clean-up (Takara Bio USA, San Jose, CA, USA), according to the manufacturer's instructions, and were sequenced in both forward and reverse directions at the BioMed Sequencing Core Facility (Seattle Biomedical Research Institute, Seattle, WA, USA).

Nucleotide sequences were edited and manually adjusted using BioEdit ver. 7 (Hall, 1999). Additional sequences of *Cassidinidea lunifrons* (Richardson, 1901) (GenBank accession [OQ322833](#), [OQ323015](#), [OQ323325](#), and [OQ323456](#)) from the *Dynamenella* Hansen, 1905 lineage following Wetzter et al. (2018), as well as sequences of *Dynamene bidentata* (Adams, 1800) (GenBank accession [MK505853](#)) and *D. magnitorata* Holdich, 1968 (GenBank accession [MK505859](#)) were included as outgroups. Sequence alignment was performed using MAFFT ver. 7 (Katoh et al., 2019), and the data matrix was trimmed to equal length. The best evolutionary model was selected using

JModelTest2 (Darriba *et al.*, 2012), based on the Akaike information criterion (AIC), with the best model being HKY+I ($I = 0.582$). Bayesian phylogenetic inference was performed with MrBayes ver. 3 (Huelsenbeck & Ronquist, 2001). Two independent runs were conducted with 4 Markov chains, each running for one million generations, sampled every 1,000 generations. The congruence of parameters from the two independent runs was evaluated using MrBayes ver. 3 and Tracer ver. 1.7 (Rambaut *et al.* 2018) after the 25% burn-in samples. A consensus topology was constructed with the remaining trees (Huelsenbeck & Ronquist, 2001) and visualized using iTOL ver. 7 (Letunic & Bork, 2021). Bootstrap support values for each node were estimated using MEGA ver. 11 (Tamura *et al.*, 2021) with a maximum likelihood (ML) analysis, employing the estimated evolutionary model, based on 1,000 replicates.

Distribution and conservation status of *Thermosphaeroma*

We visited the type localities of all described *Thermosphaeroma* species as well as other sites where the presence of the genus has been documented (Wilson, 2008; Rocha-Ramírez *et al.*, 2012), and additional water bodies identified by local residents near these locations. In each thermal spring, pH and temperature were recorded using a YSI EcoSense pH10A tester (YSI, Yellow Springs, OH, USA). Collected specimens were identified using taxonomic keys (Schotte, 2000) and by comparing their morphological characters with specimens deposited in museum collections (USNM, Invertebrate Zoology Collections, National Museum of Natural History, Washington DC, USA; CNCR, National Crustacean Collection, Institute of Biology, Universidad Nacional de México, Mexico City).

TAXONOMY

Order Isopoda Latreille, 1816

Suborder Sphaeromatidea Wägele, 1989

Family Sphaeromatidae Latreille, 1825

Genus *Thermosphaeroma* Cole & Bane, 1978

Thermosphaeroma jaliscensis sp. nov.

(Figs. 2–6)

Diagnosis: *Thermosphaeroma* with conspicuously sexually dimorphic uropods, displaying both rami equal or longer than distal margin of pleotelson in both sexes, but female exopod much longer than in males. Pleopod I sexually dimorphic, sexes differing in ornamentation of proximal outer margin of exopod: margin densely setulose with stout, irregularly multi-denticulate spine in males, margin smooth, with stout bi-serrate spine in females.

Material examined: El Montecillo thermal baths, SE of Bélen del Refugio, Teocaltiche, Jalisco, Mexico, 21.30.475°N, 102.22.939°W, 1,750 m altitude (Fig. 1), 6 November 2013, temperature 30.3°C, pH 9.4, coll. C. Pérez-Amezola, G. Cortez, L. García and A. Botello; 21 December 2014, coll. A. Botello and P. Pantoja. Preserved in 70% ethanol in single vial (CNCR 37081).

Comparative material examined: *Thermosphaeroma dugesi* (Dollfus, 1896), type series specimens (USNM 18492, 23045);

T. thermophilum (Richardson, 1897), type series specimens (USNM 19609); *T. subequalum* Cole & Bane, 1978, type series specimens (USNM 170588, 170589, 290275) and CNCR 37080; *T. milleri* Bowman, 1981, type series specimens (USNM 181123, 181124, 181125); *T. smithi* Bowman, 1981, type series specimens (USNM 181119, 181120, 181121, 181122, 250879) and CNCR 37079; *T. cavicauda* Bowman, 1985, type series specimens (USNM 227044, 227045); *T. macrura* Bowman, 1985, type series specimens (227046, 227047, 1086769) and CNCR 37078); *T. mendozai* Schotte, 2000, type series specimens (USNM 291485, 1106239) and CNCR 37077.

Etymology: Species name refers to the Mexican state of Jalisco, where it is found.

Description (for both sexes unless otherwise indicated): Body (Fig. 2) with sparsely set black chromatophores, up to 16 mm long, ~2.3× longer than wide, parallel-sided, apparently not capable of conglobation. Head (Fig. 3A) anterior margin simple, without incision or transverse ridges, short, simple rostrum between separate antennule bases. Eyes circular with black pigmentation, clearly faceted with ommatidia, placed posterolaterally on pedestal (Fig. 3A).

Pereonites with posterior margin not raised (Fig. 2). Pleon comprising completely incorporated pleonites 1–5 (five pairs of pleopods detach together with the corresponding composite somite in dissections), covered laterally by overlapping coxal plate 7 (Fig. 5E, G). Pleotelson with evenly rounded distal margin (Fig. 5E, G).

Epistome clearly visible in dorsal view (Fig. 3A) although not dorsally covering insertion of antennules or antennae, slightly concave lateral margins, deeply excavated distally, rounded lateral lobes (Fig. 4A). Labrum globose, distal margin and posterior surface densely setulose (Fig. 4A). Paragnaths (not figured) normal; inner lobes wanting.

Antennule (Fig. 3B) with peduncle segments not flattened or expanded, up to 10-articulate flagellum. Relative length of peduncle segments 1–3 as 100:43:56. Proximal peduncle segment reflexed, articulating proximoventrally to head, about 2.4× longer than wide, concave posterior margin; tuft of long setules on proximoventral margin of segment (Fig. 3B). Second peduncle segment ~1.6× as long as broad, straight margins; third peduncle segment long, slender, ~3.5× longer than wide, only 38% width of proximal segment of peduncle. Flagellum shorter than 2 proximal segments of peduncle combined; pair of aesthetascs on each of articles except on distalmost 2, with 1 aesthetasc each, two most proximal devoid of aesthetascs.

Antenna (Fig. 5A) peduncle segments 1–5 relative length 52:77:59:100:84; proximal segment with tuft of long setules on both margins. Flagellum much longer than peduncle, up to 16-articulate.

Left mandible (Fig. 4B) with 4-cuspidate incisor and 3-cuspidate lacinia; spine row comprising 5 strong recurved pappose elements implanted on common pedestal; molar (not figured) columnar, ordinary; palp (Fig. 4C) 3-segmented, segments progressively shorter towards distal portion; proximal segment much longer than second segment, with single simple seta subdistally; second segment with row of 10 strong bipinnate setae along medial margin; distal segment with row of 12 strong

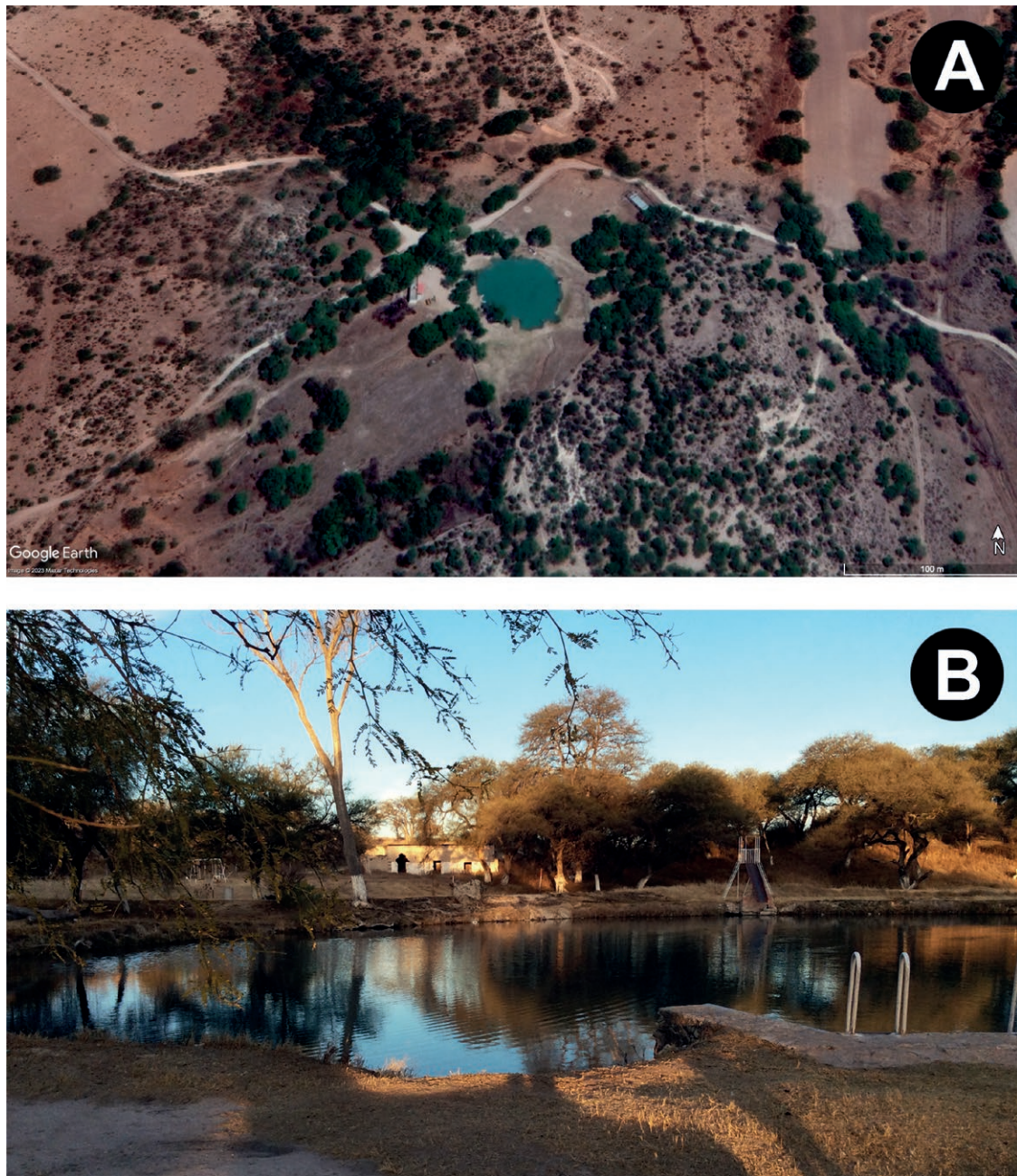


Figure 1. *Thermosphaeroma jaliscensis* sp. nov. aerial view. Google Earth, image Maxar Technologies, 2023 (A); type locality (B).

bipinnate setae along medial margin, distalmost seta much longer than rest.

Right mandible (Fig. 4D, E) as left counterpart except for spine row of 5 elements, of which distalmost (lacinia?) trifid, strongly denticulate.

Maxillule exopod (= outer plate) (Fig. 4F) with 6 pectinate spines, 2 smooth, simple spines (innermost reduced), single seta, and 3 strong spatulate spines all distal; reduced penicillate seta disposed subdistally on segment (Fig. 4F). Endopod (= inner plate) (Fig. 4G) with 4 strong recurved setae ornamented disposed distally, reduced, conical simple seta subdistally. Integument of both segments of maxillule covered with densely set transverse rows of long spinules (not figured).

Maxilla (Fig. 4H) middle and lateral lobes each with 4 strong curved comb-like spines; medial lobe with 3 short simple spines, 5 short, strong recurved pappose setae, and long bipectinate pappose seta.

Maxilliped (Fig. 6A) basal endite with 7 pappose and 3 bipinnate strong short setae; single recurved coupling hook with denticulate tip (Fig. 6B) on posterior surface. Palp segments 2–4 each with densely setose distomedial lobe; segment 5 slender, blunt, ~3× longer than wide and shorter than preceding segment, densely setose distomedially and with long flanged terminal seta.

Pereiopod I carpus comparatively shorter than pereiopods II–VII, unarmed and partially incorporated into propodus, and merus with fewer pectinate spines on distolateral angle (Fig. 5B, C vs. 5D).

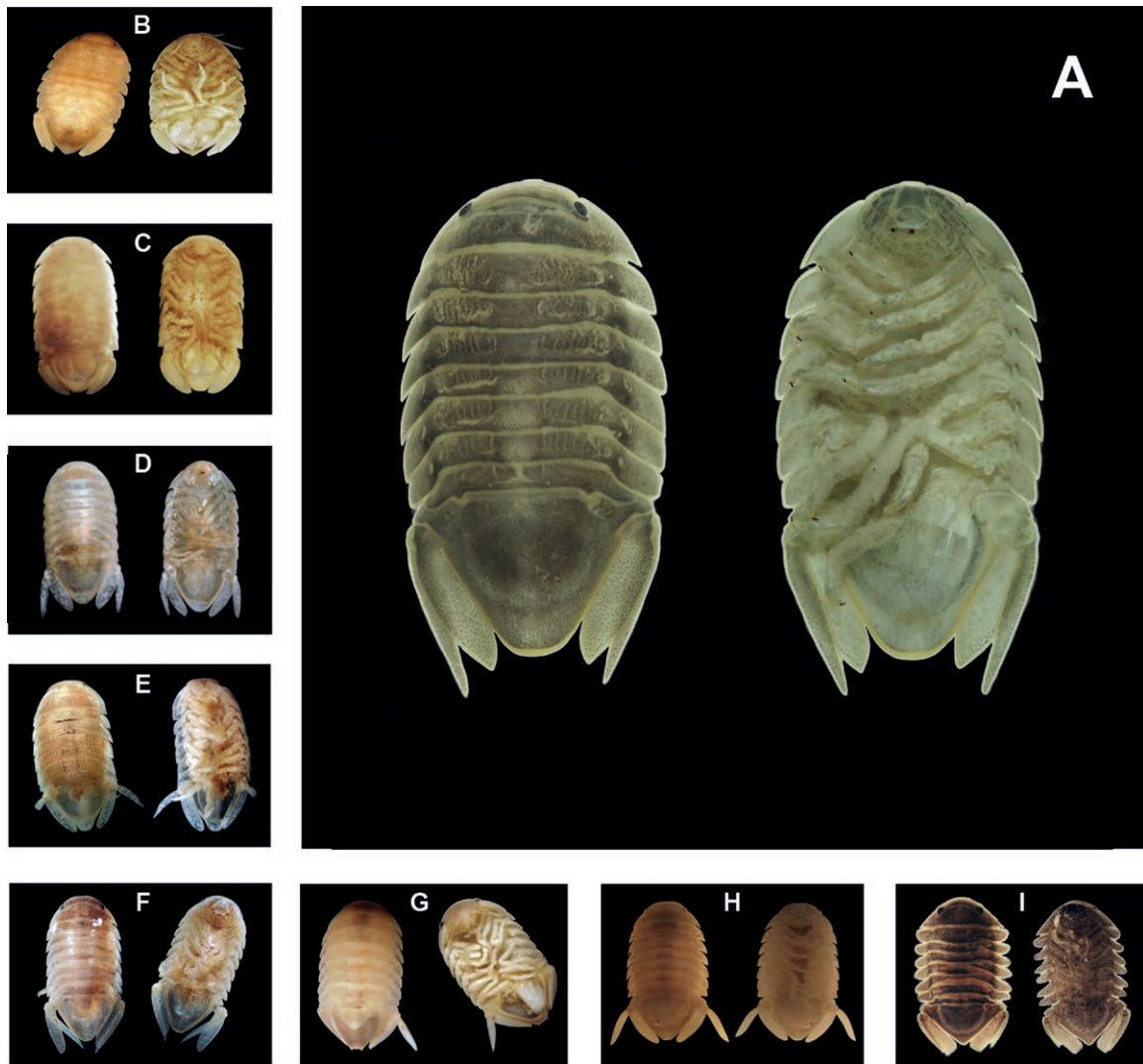


Figure 2. General aspect of males of *Thermosphaeroma* species: *T. jaliscensis* **sp. nov.**, dorsal and ventral view (CNCR 37081) (A); *T. dugesi* (USNM 18492) (B); *T. thermophilum* (USNM 19609) (C); *T. subequalum* (USNM 170588) (D); *T. milleri* (CNCR 181123) (E); *T. smithi* (USNM 181119) (F); *T. cavicauda* (USNM 227044) (G); *T. macrura* (USNM 227046) (H); *T. mendozai* (USNM 291485) (I). USNM, National Museum of Natural History, Washington DC, USA; CNCR, Colección Nacional de Crustáceos, Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City.

Pereiopods II-VII similar. All pereiopods ischium-to-propodus densely setulose.

Penes (Fig. 3C) simple, $\sim 4.5\times$ longer than broad.

Pleopod I sexually dimorphic, sexes differing in ornamentation of proximal outer margin of exopod: margin densely setulose with stout, irregularly multi-denticulate spine in male (Fig. 3D, E), margin smooth with stout bi-serrate spine in female (Fig. 3F). Distomedial angle of protopod with 4 short stout serrate coupling hooks.

Pleopod II sexually dimorphic. Male (Fig. 3G) differing from female (not figured) in recurved, S-shaped appendix masculina inserted proximally on medial margin of endopod; inner face of appendix covered with densely-set spinules; appendix much longer than corresponding endopod. Distomedial angle of protopod with 4 short stout serrate coupling hooks.

Pleopod III (Fig. 3H) exopod apparently 2-segmented due to clear presence of transverse suture. Distomedial angle of protopod with 4 short, stout, serrate spines.

Pleopod IV (Fig. 6C) with both rami having oblique branchial folds, those on exopod comparatively reduced. Distomedial angle of protopod unarmed. Exopod outer margin bilobed, proximal lobe not protruding beyond distal lobe.

Pleopod V (Fig. 6D) endopod with oblique branchial folds. Distomedial angle of protopod unarmed. Exopod with 3 wart-like bulges covered with imbricated scales; more proximal bulge reniform, other 2 sphaereoidal, placed as close to each other as to appear like a bilobed process.

Uropods sexually dimorphic. Male (Fig. 5E, F; see also Fig. 2) with both rami subequal in length and as long as pleotelson. Female (Fig. 5G; see also Fig. 2) with exopod much longer than endopod and conspicuously outreaching distal margin of pleotelson.

Remarks: The new species displays two features rarely reported in other congeners. The rami of both uropodal rami are elongated, each reaching at least the distal margin of pleotelson. Then uropods

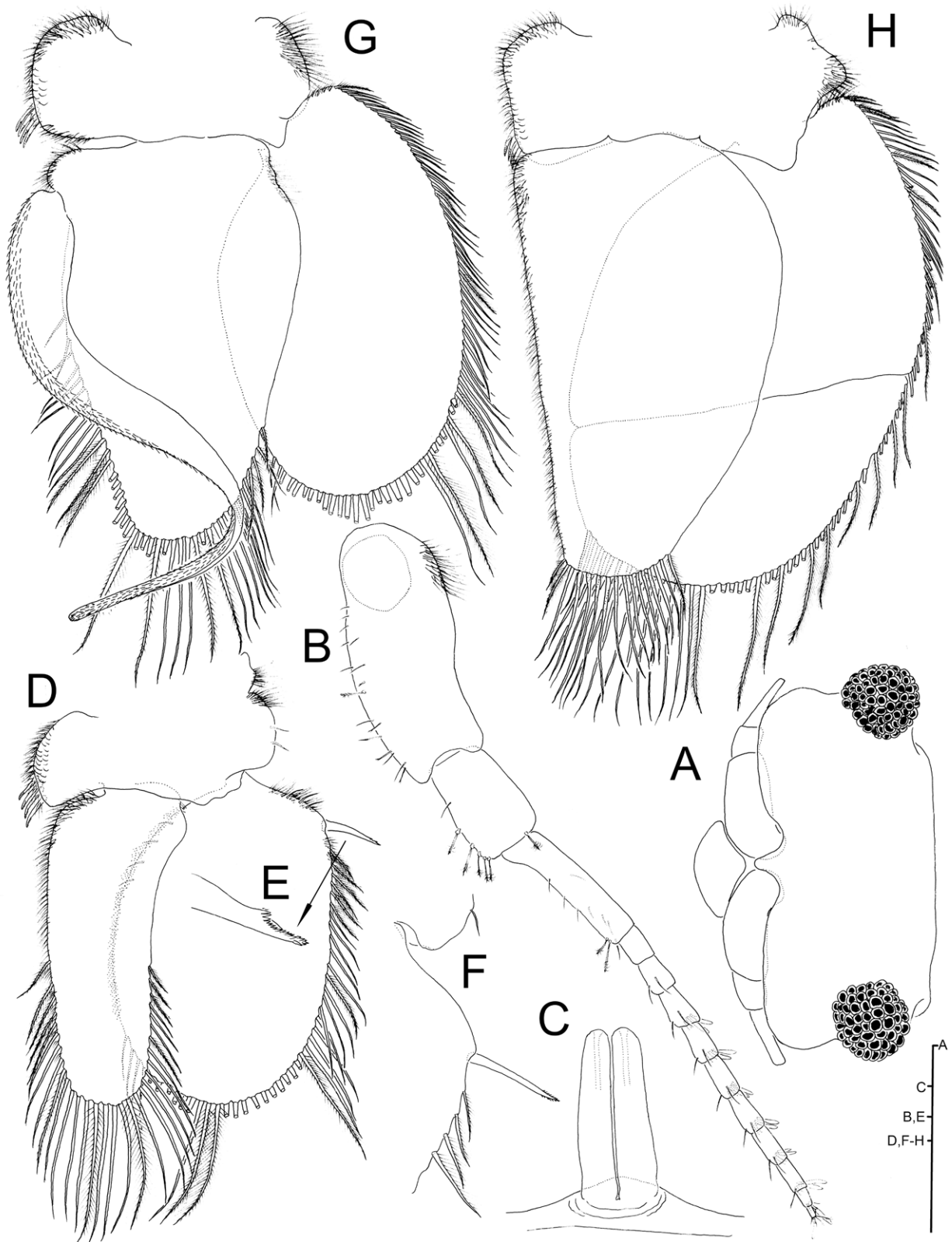


Figure 3. *Thermosphaeroma jaliscensis* **sp. nov.**: male syntypes. (A); head showing eyes, rostrum and epistome, dorsal view (B); left antennule, anterior (C); penes (D); right male pleopod I, posterior (E); inset of distal part of spine on proximo-lateral margin of exopod of latter (F); inset of proximo-lateral margin of exopod of female pleopod I (G); right male pleopod II, posterior (H); right pleopod III, posterior. Scale bars: A = 2.0 mm; B, D, G, H = 0.4 mm; C = 1.0 mm; E = 0.1 mm; F = 0.2 mm.

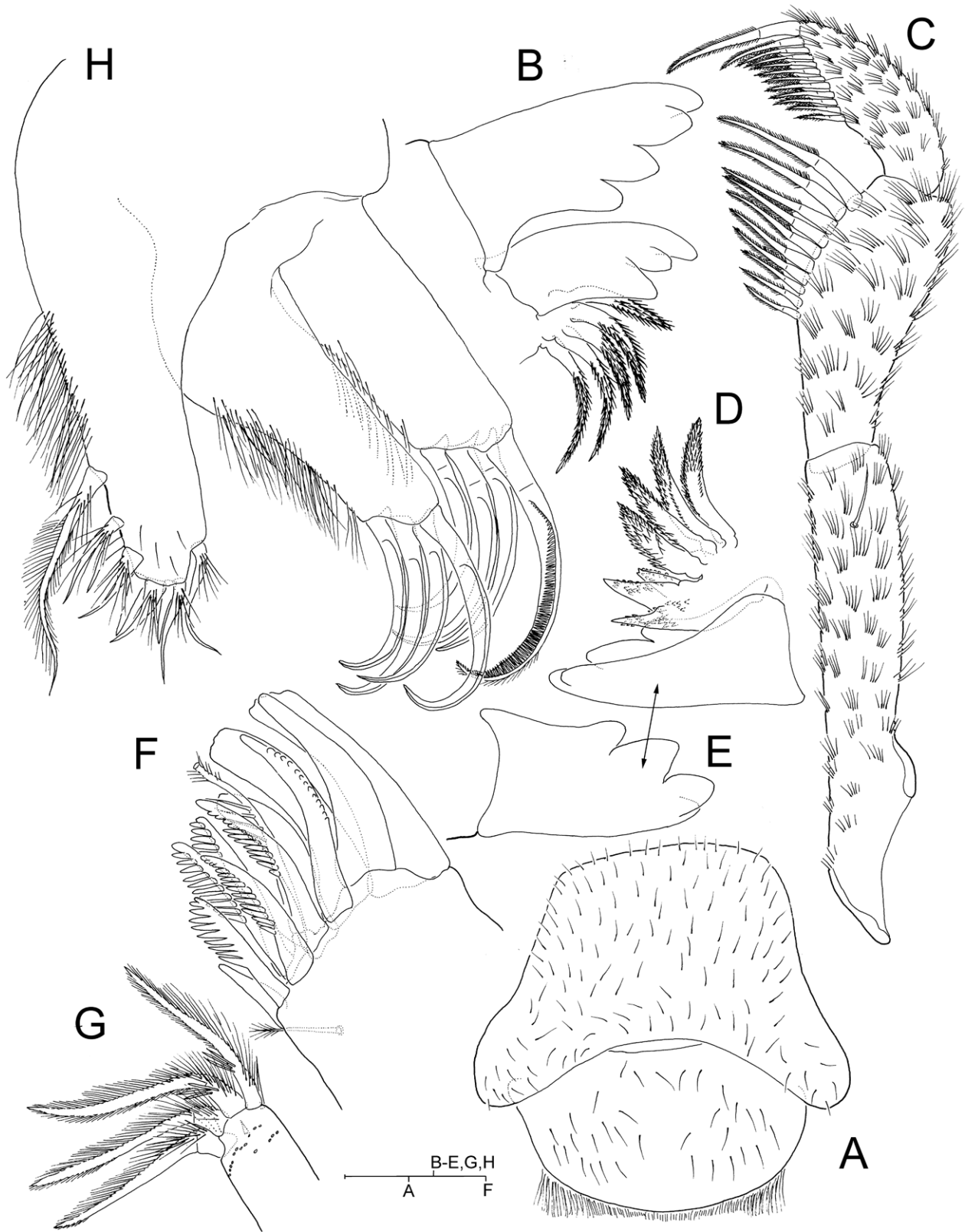


Figure 4. *Thermosphaeroma jaliscensis* sp. nov.: male syntype (A). Labrum and epistome (B); inset of distal portion of left mandible (C); left mandibular palp (D); istal portion of right mandible (E); inset of incisor of latter (F); distal portion of lateral lobe of maxillule (G); distal portion of medial lobe of maxillule (long spinules on surface of segment omitted in figure, where only scars of their insertions are represented) (H); maxilla (all strong curved setae on middle and lateral lobes similar and comb-like, but only outermost on lateral lobe represented with complete ornamentation). Scale bars: A = 0.2 mm; B–H = 0.1 mm.

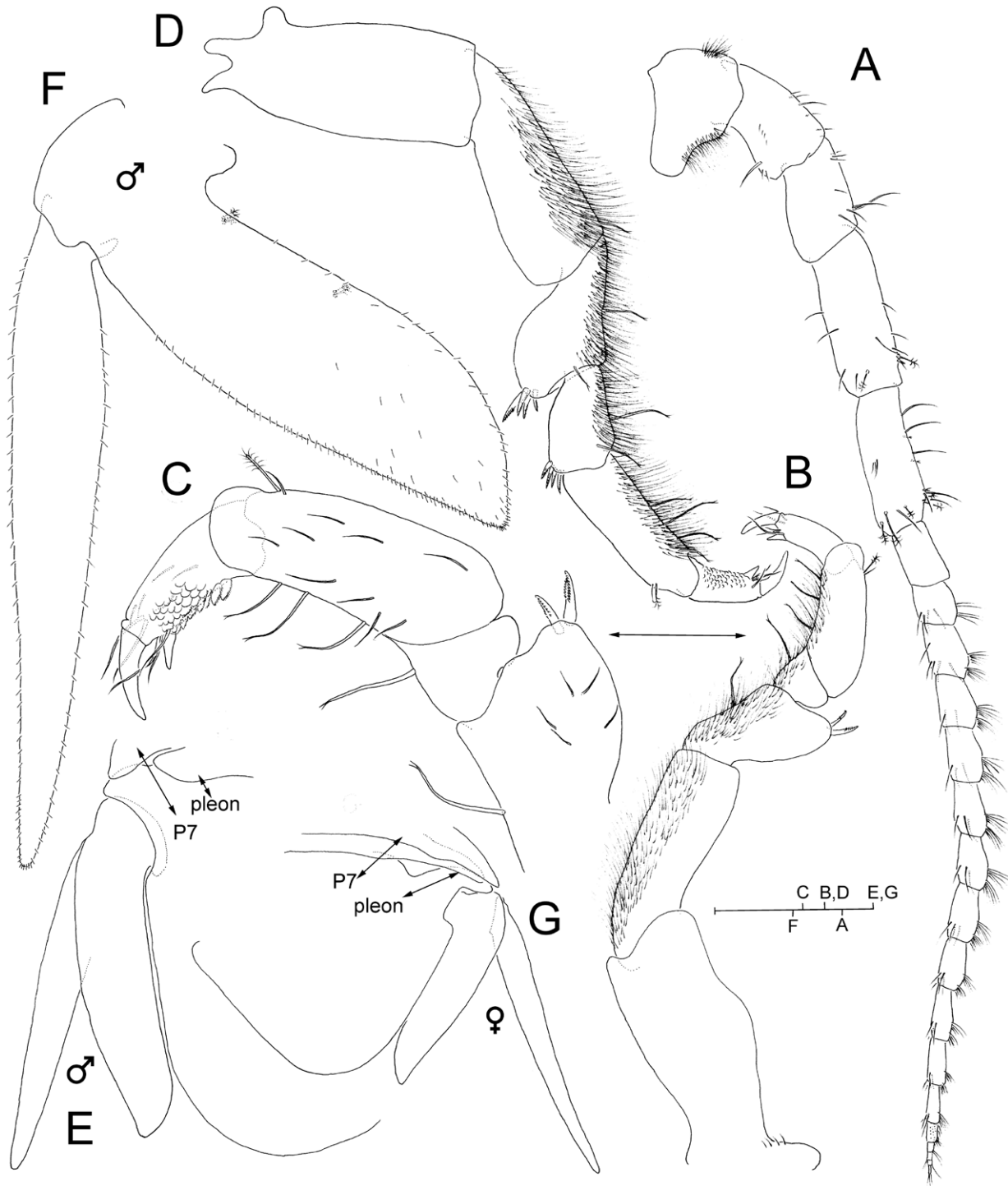


Figure 5. *Thermosphaeroma jaliscensis* sp. nov.: male syntype (A–F), female syntype (A). Left antennule (B); left pereopod I (C); inset of merus-dactylus of latter (D); left pereopod II (E); male pleotelson, dorsal (F); male right uropod, ventral (G); female pleotelson, dorsal. (P7: pereopod VIII). Scale bars: E, G = 1.0 mm; B, D, F = 0.5 mm; A = 0.4 mm; C = 0.2 mm.

are sexually dimorphic, with the female endopod much longer than in the male (Fig. 5E, G). This feature was previously recorded only in *Thermosphaeroma smithi*, but not as extreme as in the new species. The latter species can nevertheless be distinguished from the new species by their mandibular incisors, which are spatulate but strongly dentate in the new species (Bowman, 1981).

The new species also displays sexual dimorphism in pleopod I. The male exopod (Fig. 3C, D) has a setulose proximal outer margin and with a modified spine, whereas this margin is devoid of setules and displays an ordinary spine in the female (Fig. 3E). A sexually-dimorphic pleopod I has apparently not been recorded previously in any other congener.

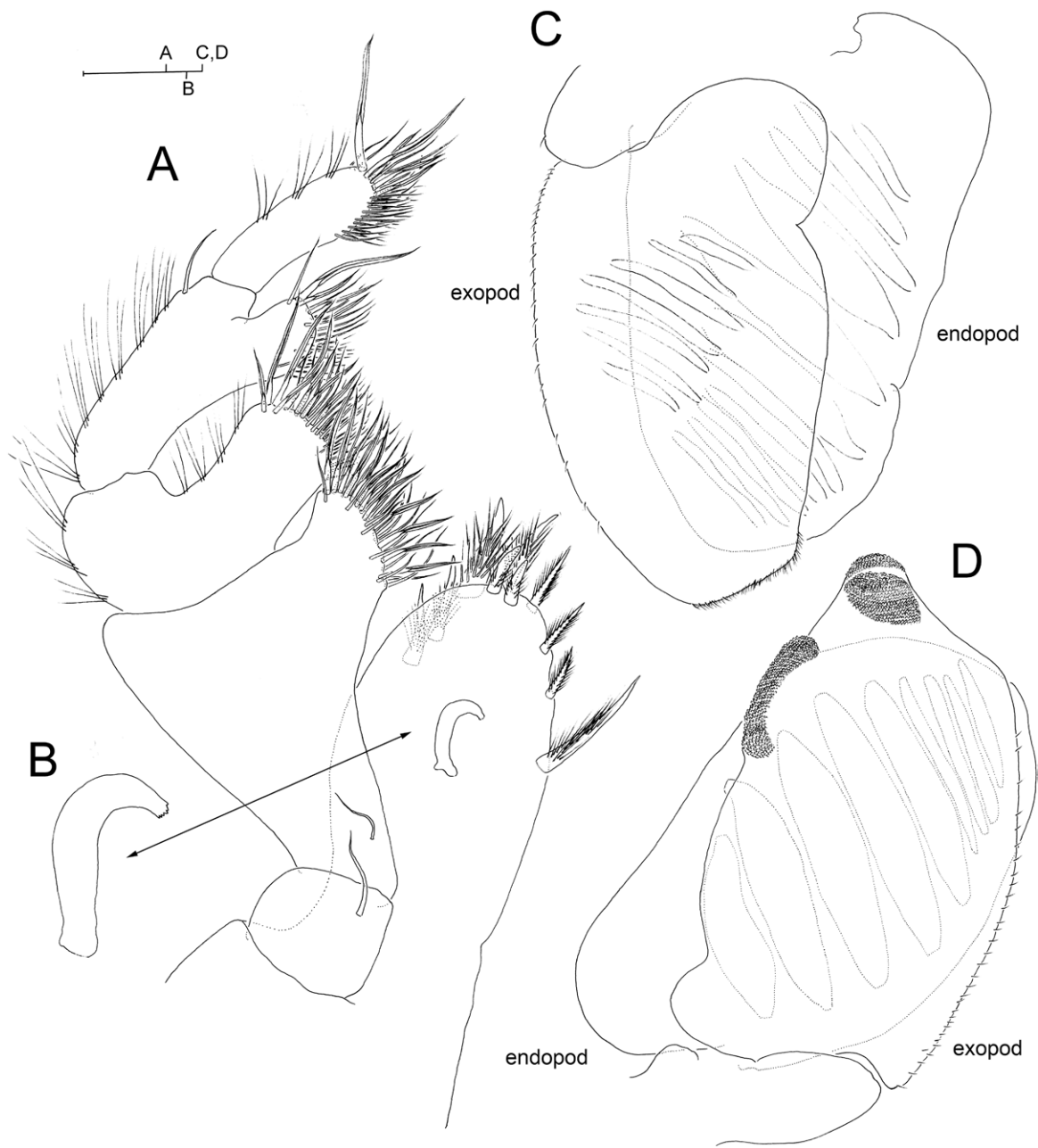


Figure 6. *Thermosphaeroma jalisciensis* **sp. nov.**: male syntype (A). Right maxilliped, posterior (B); inset of coupling hook on latter (C); right pleopod IV, anterior (D); right pleopod V, anterior. Scale bars: B = 0.05 mm; A = 0.1 mm; C, D = 0.5 mm.

Phylogenetic analyses

The well supported Bayesian included *T. jalisciensis* **sp. nov.**, *T. subequalum*, *T. smithi*, and *T. macrura* and was rooted with *Dynamene magnitorata* and *Cassinidea lunifrons* (Fig. 7). *Thermosphaeroma smithi* and *T. macrura* re sister taxa, which together are sister to *T. subequalum* with *T. jalisciensis* **sp. nov.** The maximum intraspecific divergence was 0.99%, whereas the average interspecific nucleotide divergence ranged from 5.2% between *T. smithi* and *T. macrura*, to 19.9% between *T. jalisciensis* **sp. nov.** and *T. macrura* (*T. jalisciensis*, *T. subequalum* 19.7%; *T. jalisciensis*, *T. smithi* 18.9%; *T. jalisciensis*, *T. macrura* 19.9%; *T. subequalum*, *T. smithi* 8.7%; *T. subequalum*, *T. macrura* 5.2%; *T. smithi*, *T. macrura* 10.6%).

Historical and current distribution of *Thermosphaeroma*

All *Thermosphaeroma* species are distributed within the biogeographic province of the Chihuahuan Desert, with the northernmost species being *T. thermophilum*, found in New Mexico, USA at 32°N, and the southernmost *T. jalisciensis* **sp. nov.** at 21°N (Fig. 8). Although all type localities were surveyed, only five of the nine thermal springs currently contain *Thermosphaeroma* species. These five aquatic habitats offer suitable environmental conditions for the species (Schotte, 2000), with temperatures of 27–44°C (Bowman, 1981) and an alkaline pH of 8.4–9.4 (Table 1). These springs can be considered thermal, as their water temperature is approximately 12°C higher than the atmospheric temperature (Springer *et al.*, 2008).

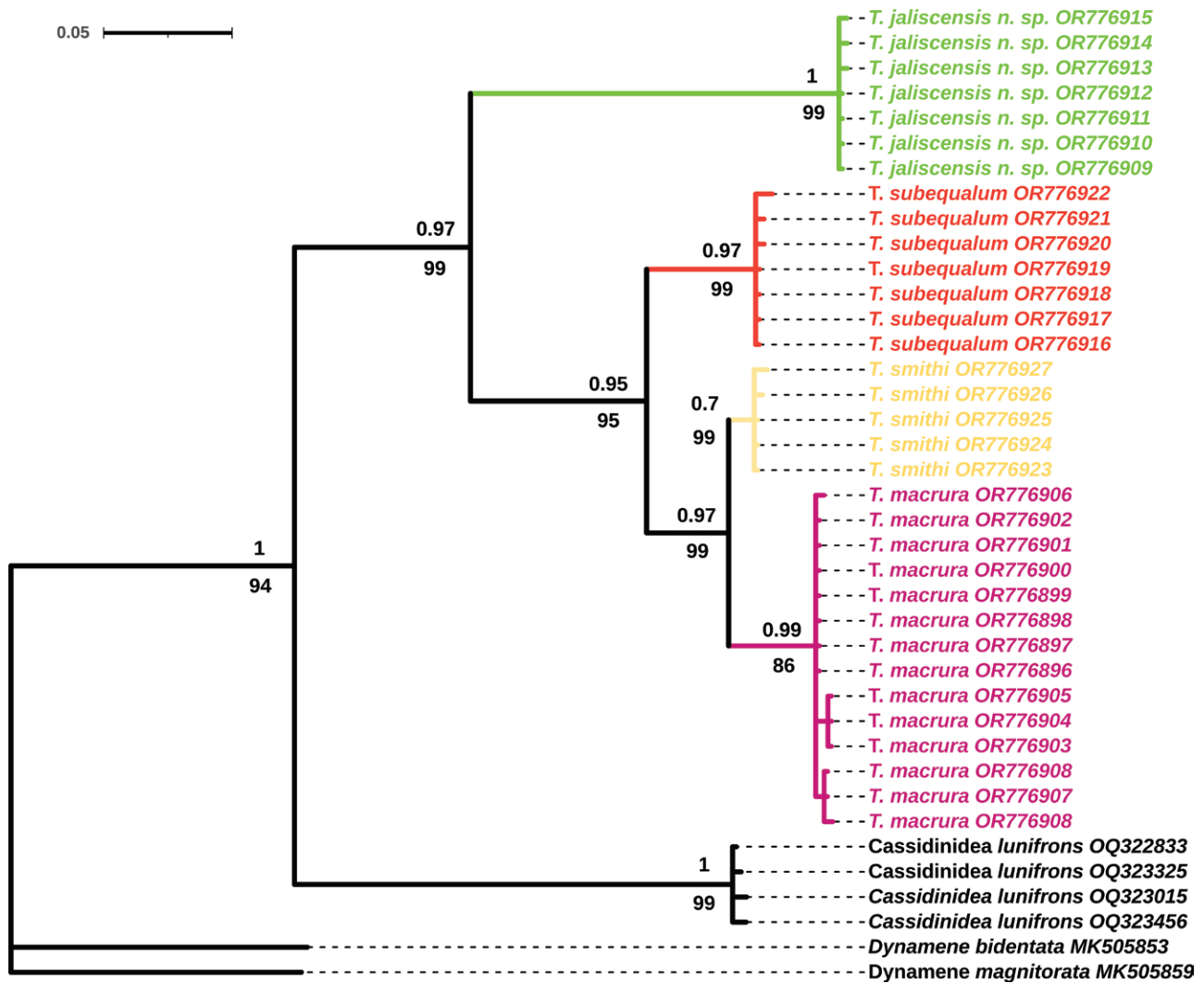


Figure 7. Bayesian inference tree based on Hasegawa-Kishino-Yano model constructed (+I, parameter = 0.582). Posterior probability is shown in the upper part of nodes and Bootstrap support (maximum likelihood 1,000 replicates consensus) in the lower.

Thermosphaeroma dugesi (Dollfus, 1896). The exact type locality of this species remains uncertain, as the original description by Dollfus (1896) and the specimens from the holotype and type series (USNM 18492) only specify the location as “Ojo Caliente” in “Aguascalientes, Mexico.” Two potential springs have been proposed as the type locality (M. Silva-Briano, personal communication), having been visited by C. Pérez-Amezola, G. Cortez, L. García, and A. Botello in December 2014: 1) Ojo Caliente, Calvillo, Aguascalientes (21.87256°N, 102.67732°W; 1,746 m altitude). This small spring has been modified, with water currently emerging from a polyvinyl chloride (PVC) pipe embedded in a concrete wall used for laundry. The flow creates a small stream that also receives wastewater from nearby houses. Local residents have long reported the presence of aquatic isopods in this spring, but they also noted that the spring dried up some years ago, prompting the construction of extraction wells. 2) Ojo Caliente, Aguascalientes City. This spring has been entirely modified for use as a thermal bath. Employees report that the original spring dried up several years ago but recently resumed flow, creating a small adjacent pool. No aquatic isopods were observed at this location during the visit. Both springs have

experienced significant anthropogenic modifications, and the lack of detailed historical records makes it challenging to confirm the exact type locality. Further research and historical data are required to resolve this uncertainty.

Thermosphaeroma thermophilum (Richardson, 1897). The type locality of this species, is Sedillo Spring (32.02278°N, 106.5629°W; 1,508 m altitude), near Socorro, New Mexico. The locality was visited by C. Pérez-Amezola, M. C. Camacho-Hernández, and A. Botello in April 2015 for photographic documentation and location confirmation, as the species was declared “Extinct in the Wild” by the International Union for Conservation of Nature and Natural Resources (IUCN) in 1996 (IUCN; <https://www.iucnredlist.org/species/21741/9315891>).

The site consisted of two small concrete pools connected by a pipe discharging into pools used for recreational bathing. Sedillo Spring has undergone significant anthropogenic modifications since the early 20th century to supply water to the city of Socorro, leading to repeated population bottlenecks. The native population became extinct in August 1988 when a valve controlling the spring’s water flow was blocked. Although water flow



Figure 8. Geographical distribution of the species of *Thermosphaeroma*.

Table 1. Temperature and pH of localities of species of *Thermosphaeroma*. Atmospheric mean temperatures for Mexican localities provided by CONAGUA (National Water Commission; <https://smn.conagua.gob.mx/es/climatologia/temperaturas-y-lluvias/resumenes-mensuales-de-temperaturas-y-lluvias>). Data for USA localities from NOAA (National Oceanic and Atmospheric Administration; <https://forecast.weather.gov>). NA, not available.

Species	Water temperature (°C)	pH	Atmospheric mean temperature (°C)	References
<i>T. cavicauda</i>	29	NA	16.9	Bowman, 1985
<i>T. dugesi</i>	35	NA	19.4	Dollfus, 1896
<i>T. jalisciensis sp. nov.</i>	30	9.4	18.4	herein
<i>T. macrura</i>	25–32	9.3	19.4	Bowman, 1985; herein
<i>T. mendozai</i>	29–30	8.8	16.3	Schotte, 2000; herein
<i>T. milleri</i>	27–28	NA	17.5	Bowman, 1981
<i>T. smithi</i>	32–44	8.4	20.3	Bowman, 1981; De la Maza-Benignos <i>et al.</i> , 2012; herein
<i>T. subequalum</i>	32–35	9.4	19.4	Cole & Bane, 1978; herein
<i>T. thermophilum</i>	30–33	NA	16	Summers, 1976; Lang <i>et al.</i> , 2006

was restored in September 1988, efforts to reintroduce a population of isopods maintained in captivity at the University of New Mexico were unsuccessful.

Controlled propagation of the species began at the Socorro Isopod Propagation Facility (SIPF) in 1990. A captive population has been successfully maintained at the Albuquerque Biological Park in New Mexico since 1998, ensuring the species survival in captivity (United States Fish & Wildlife Service; <https://ecos.fws.gov/ecp/species/2470>).

Thermosphaeroma subequalum Cole & Bane, 1978. The type locality, on the Rio Grande Village Natural Trail (29.17656°N, -102.951622°W; 558 m altitude), was surveyed to corroborate the presence of this species by C. Pérez-Amezola, G. Cortez, L. García, and A. Botello in December 2014. Numerous individuals were observed at a depth of approximately 10 cm, within a sandy substrate and clear water with a temperature of 32°C and a pH of 9.4.

This species is documented to have nine populations along the Mexico-USA border, with seven in springs on the USA side and

two on the Mexican side, both of which flow into the Rio Bravo in Mexico (Rio Grande in the USA) (Rodríguez *et al.*, 2009). The species is found in the Big Bend National Park, Texas, a designated protected area, and inhabits the Ocampo Flora and Fauna Protection Area on the Mexican side (Secretaría de Medio Ambiente y Recursos Naturales, 2015).

Thermosphaeroma milleri Bowman, 1981. Originally described from specimens collected at three springs in Ejido Rancho Nuevo, Chihuahua (Ojo El Medio, Ojo de las Varas, and Ojo Carbonera; 30.583333°N, 106.875278°W; 1,120 m altitude) was visited by C. Pérez-Amezola, G. Cortez, L. García, and A. Botello in November 2013. No specimens were found during the visit, with only depressions marking the locations of the dried-up springs remaining. Bowman (1981) noted that these water bodies were used for irrigation at the time of collection, which was corroborated by locals, who reported that the springs had dried up around the late 1990s. Guided by local residents and the original description, nearby thermal springs were surveyed, but no populations of this species were found.

The desiccation of these springs is linked to aquifer exploitation. Chihuahua has 61 aquifers, including the Flores Magón-Villa Ahumada aquifer, which supplied water to the three surveyed localities. This aquifer is among the ten most heavily exploited in the state, supporting agriculture and urban centers (Comisión Nacional del Agua; <https://sigagis.conagua.gob.mx/gas1/sections/Edos/chihuahua/chihuahua.html>). The Mexican Government declared this aquifer under “strict regulation” in 1957, yet water extraction has continued unabated. Although the exact number of wells tapping the aquifer is unknown, it is likely increasing. In 2012, for instance, a Mennonite community purchased 59,000 hectares in the municipalities of Chihuahua and Villa Ahumada, initiating the drilling of deep wells (Cervantes-Rendón *et al.*, 2020). Consequently, the aquifer now has an annual deficit exceeding 70 million m³ (Diario Oficial de la Federación; https://www.dof.gob.mx/nota_detalle.php?codigo=5398033&fecha=25/06/2015#gsc.tab=0, 2015).

Thermosphaeroma smithi Bowman, 1981. The type locality is the Balneario San Diego de Alcalá thermal spring, Chihuahua, Mexico (28.590556°N, 105.55°W; 1,150 m altitude), was visited by C. Pérez-Amezola, G. Cortez, L. García, and A. Botello in November 2013. Despite its use as a tourist and recreational site, the spring still harbors isopods. The water temperature was recorded as 32–39°C, with a pH of 8.4. The isopods were observed at a depth of 30 cm in clear water with a sandy bottom. Conservation efforts for this species include a collaborative agreement between the World Wide Fund for Nature (WWF) and the area’s owner. The agreement outlines mechanisms and strategies for monitoring and conservation. The management plan associated with this agreement highlights *T. smithi* as an endemic and conservation-priority species, alongside other micro-endemic aquatic species, including the pupfish *Cyprinodon pachycephalus* Minckley & Minckley, 1986, the poeciliid *Gambusia zarskei* Meyer, Schories & Scharlt, 2010, and the gastropods *Tryonia chuviscarae* Hershler, Liu & Landye, 2011 and *T. minckleyi* Hershler, Liu & Landye, 2011 (De la Maza-Benignos *et al.*, 2012). The plan remained active until 2020, supporting habitat conservation through education programs and water resource management, but a significant reduction in the habitat has been

noted due to declining water levels (PRONATURA Noreste; https://pronaturanoreste.org/wp-content/uploads/2024/11/Informe-anual-2023_compressed.pdf).

Thermosphaeroma cavicauda Bowman, 1985. The species was described from material collected in a pond fed by a spring approximately 0.6 km west of La Laguna, Durango state (24.173611°N, 104.638611°W, 1,880 m altitude) was visited by C. Pérez-Amezola, G. Cortez, L. García, and A. Botello in November 2013. The spring appears to have dried up permanently.

Several factors may have contributed to the desiccation of the spring. The locality lies within the San Pedro hydrological basin in southern Durango, which is the only basin in the Mexican Plateau that drains into the Pacific Ocean. Soil erosion caused by logging activities, along with the low recharge rate of the aquifer, attributed to insufficient infrastructure and low precipitation, are likely contributing factors to the spring’s desiccation (Comisión Nacional del Agua, 2009).

Thermosphaeroma macrura Bowman, 1985. The species was originally described from a tributary spring of the Río Conchos south of the municipality of Julimes, Chihuahua. The locality was visited by C. Pérez-Amezola, G. Cortez, L. García, and A. Botello in November 2013. At this site, a spring channel crossing part of the municipality was identified (28.423333°N, 105.433333°W; 1,122 m altitude) flowing through public thermal baths where isopods were present. The recorded water temperature at the spring was 32°C, the water used to fill the thermal resort pools at 25°C, with a pH of 9.3.

The geothermal springs of Julimes were designated as a wetland of biological importance (Ramsar Convention on Wetlands; <https://rsis Ramsar.org/ris/2201>) in 2013 and were registered by the Mexican government as an Environmental Management Unit (UMA) (PRONATURA Noreste; https://conanp.gob.mx/conanp/dominios/ramsar/docs/sitios/FIR_RAMBSAR/Chihuahua/Manantiales_Geotermiales_de_Julimes/Manantiales_Geotermiales_de_Julimes.pdf). The management plan for this area, where *T. smithi* is found, also includes the locality of El Pandeño, the home to *T. macrura* along with other micro-endemic aquatic species, such as the pupfish *Cyprinodon julimes* De la Maza-Benignos & Vela Valladares, 2009 and the gastropods *Tryonia julimensis* Hershler, Liu & Landye, 2011, and *Trytonia* sp. (De la Maza-Benignos *et al.*, 2012). The conservation program, active until 2020 in collaboration with the civil association Amigos del Pandeño, successfully preserved these species despite a noticeable decline in water levels at the locality (PRONATURA Noreste; https://pronaturanoreste.org/wp-content/uploads/2024/11/Informe-anual-2023_compressed.pdf).

Thermosphaeroma mendozai Schotte, 2000. The species is found in a site known as Ojo Vareleño (30.4°N, 107.983333°W; 1,497 m altitude), a shallow spring where water is channeled to supply two pools and a pond used for fish breeding. The locality was visited by C. Pérez-Amezola, G. Cortez, L. García, and A. Botello in September 2012, May 2013, February 2014, and January 2024 when isopods were observed on a gravel substrate in flowing water, with temperatures of 29–30°C and a pH of 8.8.

Ojo Vareleño is the only known spring inhabited by a species of *Thermosphaeroma* that lacks formal legal protection. Although the spring was historically used to supply water to the town of Casas Grandes, Chihuahua and is currently used as a recreational

Table 2. Status of *Thermosphaeroma* species listed in the IUCN Red List of Threatened Species (1996) (IUCN; <https://www.iucnredlist.org/search?query=thermosphaeroma&searchType=species>).

Species	IUCN status
<i>T. cavicauda</i>	Critically Endangered
<i>T. dugesi</i>	Critically Endangered
<i>T. macrura</i>	Critically Endangered
<i>T. milleri</i>	Endangered
<i>T. smithi</i>	Critically Endangered
<i>T. subequalum</i>	Least concern
<i>T. thermophilum</i>	Extinct in the Wild

site, it does not appear to be significantly overexploited or modified at present.

Conservation status of *Thermosphaeroma*

The International Union for Conservation of Nature (IUCN) Red List of Threatened Species (<https://iucn.org/resources/conservation-tool/iucn-red-list-threatened-species>) has assessed six of the eight described species, categorizing them under varying levels of threat, except for *T. subequalum*, which is classified as Least Concern (Table 2) and *T. mendozai*, described after 1996 the last IUCN evaluation (Schotte, 2000) (IUCN; <https://www.iucnredlist.org/search?query=thermosphaeroma&searchType=species>). In the US, only *T. thermophilum* is protected under the U.S. Fish & Wildlife Service, holding the status of Endangered (USFWS; <https://www.fws.gov/federal-register-file/final-determination-endangered-status-socorro-isopod>); however, it is classified as Extinct in the Wild by the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (IUCN; <https://www.iucnredlist.org/species/21741/9315891>). None of the *Thermosphaeroma* species are under any legal protection status in Mexico according to national environmental protection regulations (Secretaría de Medio Ambiente y Recursos Naturales; <https://www.dof.gob.mx/normasOficiales/4254/semarnat/semarnat.htm>).

DISCUSSION

Thermosphaeroma comprises nine species, each of which exhibits a microendemic distribution (*sensu* Borgwerth *et al.*, 2024), where each species is typically restricted to a small body of freshwater with particular environmental characteristics regarding temperature and pH. Wilson & Humphrey (2020) suggested that the richness of microendemic species in freshwater isopods can be explained by their occurrence in biogeographic regions with stable geomorphology and climate, where these lineages are likely to diverge, particularly in permanent water bodies such as springs and groundwater. Moreover, the fact that they exhibit internal fertilization, a characteristic feature of Peracarida (Dick *et al.*, 1998; Horváthová *et al.*, 2017), allows them to maintain stable populations even during periods of declining water levels. This, in turn, results in a low capacity for dispersal and recruitment of these populations.

The Chihuahuan Desert contains many shallow water bodies and springs that have undergone processes of isolation and

connectivity, resulting in a diverse range of ecological niches for aquatic fauna such as fishes and crustaceans (Rocha-Ramírez *et al.* 2009). Furthermore, other aquatic species exhibit similar distribution patterns and are sympatric with the *Thermosphaeroma* fauna, such as pupfishes of the genus *Cyprinodon* Lacepède 1803 (e.g. *C. pachycephalus* sympatric with *T. smithi*, or *C. julimes* sympatric with *T. macrura*). Although it has been hypothesized that *Cyprinodon* diverged and invaded the basins of the Conchos and Bravo rivers much more recently, during the Neogene (Echelle *et al.*, 2005), in contrast to the proposed invasion of freshwater habitats by the *Thermosphaeroma* ancestor as suggested by Bowman (1981) during the Paleocene.

Several factors contribute to the habitat loss of *Thermosphaeroma*, specifically the decline in aquifer levels, including salt-water intrusion, subsidence, and reduced rainfall (Kidd, 2002), in addition to the overexploitation of both surface and subterranean water bodies, which have been utilized for human needs since pre-Columbian times (Sorroche-Cuerva, 2022). Temperature is the main limiting factor for species adapted to thermal springs (Schotte, 2000). As such, habitat modification, along with geographical isolation and human overexploitation, constitutes an increasing risk of extinction for microendemic aquatic fauna (Wilson, 2008). The geothermal springs in the southern USA and northern Mexico are nevertheless located in isolated and biologically understudied regions. It is possible that species of *Thermosphaeroma* and other sympatric species adapted to such water bodies have not yet been discovered, so it is necessary to generate predictive distribution models based on the environmental characteristics of these species, as well as to increase collection efforts.

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