JOURNAL OF CRUSTACEAN BIOLOGY, 1(1): 105–122, 1981

THERMOSPHAEROMA MILLERI AND *T. SMITHI*, NEW SPHAEROMATID ISOPOD CRUSTACEANS FROM HOT SPRINGS IN CHIHUAHUA, MEXICO, WITH A REVIEW OF THE GENUS

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ABSTRACT

Thermosphaeroma milleri is described from 3 hot springs in northwestern Chihuahua, and *T. smithi* is described from Balneario San Diego in central Chihuahua. Supplemental descriptive notes are given for *Thermosphaeroma thermophilum*, from Socorro, New Mexico, and its status as an endangered species is briefly discussed. A key is given for all 5 species of *Thermosphaeroma*, and the probable origin of the genus from marine ancestors is considered. The presence of flabelliferans in hot springs and their absence in freshwater streams, ponds, and lakes is attributed to their inability to compete with most species of larval insects.

Three species of the isopod genus *Thermosphaeroma* Cole and Bane 1978 (Sphaeromatidae) have been described from hot springs in the American Southwest and Mexico: *T. dugesi* (Dollfus 1893) from Ojo Caliente, Aguascalientes, Mexico, *T. thermophilum* (Richardson 1897) from Socorro, New Mexico, and *T. subequalum* Cole and Bane 1978 from two springs in Boquillas Canyon, Big Bend National Park, Brewster Co., Texas. During their studies of Mexican desert-spring pupfishes, Drs. Robert A. Miller and Michael L. Smith, University of Michigan, collected the two additional species of *Thermosphaeroma* from the state of Chihuahua, Mexico, described below, raising the known species of the genus to five. *T. thermophilum* has been described only briefly, and I take this opportunity to add some descriptive notes.

Sphaeromatidae White, 1847
Dynameninae, new name

Hansen (1905) divided his subfamily Sphaerominae into three groups: Platybranchiatae, Hemibranchiatae, and Eubranchiatae. With the elevation of the subfamily to family, the groups achieved the rank of subfamilies, and Hurley and Jansen (1977) recognized the subfamilies Platybranchiatinae, Hemibranchiatinae, and Eubranchiatinae. However, under Article 11(e) of the ICZN, these names are not available as family-group names, since none is based on a contained genus. Hemibranchiatinae contains the type-genus of the family, *Sphaeroma*, and becomes Sphaeromatinae. I propose selection of *Dynamene* Leach 1814, the oldest of the 10 genera included by Hansen in the Eubranchiatae, as the type-genus of the subfamily Dynameninae, to replace Eubranchiatinae. Hansen included 12 genera in his Platybranchiatae, but since I am not concerned herein with this group, I do not propose a subfamily name for it.

Thermosphaeroma Cole and Bane, 1978

Thermosphaeroma Cole and Bane, 1978: passim [synonymy, diagnosis]. Type-species, by original designation, *Sphaeroma dugesi* Dollfus, 1893. Gender neuter.

Diagnosis.—Mouthparts not reduced in adult ♀. Maxilliped palp 5-merous, segments 2–4 with strongly produced inner lobes; endite with 1 retinaculum. Maxilla

2 exopod with 11 long (10 robust, 1 slender) and 1–2 short apical spines; exopod with 4 apical plumose setae. Pereopods very hirsute. Penes separate to base. Pleopod 3 exopod 2-merous; other pleopod rami undivided, including pleopod 5 exopod. Branchial folds weak or absent on pleopod 4 exopod. Appendix masculina variable, from straight and not exceeding apex of endopod to sinuous and extending past apex. Exopod of pleopod 5 with 2 scabrous swellings, a round to oval terminal swelling and a reniform swelling on distal part of lateral margin. One pleonite, without lateral sutures, anterior to pleotelson. Pleotelson similar in both sexes, rounded posteriorly, without terminal notch or slit. Uropod rami smooth, relative lengths varying according to species (modified from Cole and Bane, 1978).

Remarks.—*Thermosphaeroma* exhibits some features that are unusual for the Dynameninae. In most members of the subfamily the telson is at least emarginate apically and usually has a notch or slit leading to a foramen. Other characters unusual for the subfamily are the absence of incomplete lateral sutures on the free pleonite, the poor development of branchial folds on the pleopod 4 exopod, and the undivided exopod of pleopod 5. This combination of unusual features makes it difficult to deduce the relationships and possible origin of *Thermosphaeroma*, a subject considered later herein.

KEY TO THE SPECIES OF *THERMOSPHAEROMA*

1. Exopod of uropod distinctly longer than endopod .... *T. smithi*
– Exopod of uropod subequal in length to uropod or distinctly shorter 2
2. Exopod and endopod of uropod subequal in length; lacinia of left mandible 2-cuspate .... *T. subequalum*
– Exopod of uropod distinctly shorter than endopod; lacinia of left mandible 3-cuspate 3
3. Apex of endopod of uropod angular .... *T. dugesi*
– Apex of endopod of uropod rounded 4
4. Pleotelson evenly and broadly rounded; exopod of uropod about 0.6 length of endopod; appendix masculina of ♂ pleopod 2 curving laterad, longer than endopod .... *T. thermophilum*
– Pleotelson with slightly concave margins just anterior to narrowly rounded apex; exopod of uropod more than 0.7 length of endopod; appendix masculina of ♂ pleopod 2 straight, about as long as endopod .... *T. milleri*

Thermosphaeroma milleri, new species
Figs. 1–3, 8d, 9d, 10d

Material Examined.—MEXICO. Chihuahua, from 3 springs around Ejido Rancho Nuevo in the arid Bolsón de los Muertes, about 36 km W of Villa Ahumada: Ojo El Medio, leg. M. L. Smith and B. Chernoff, 2 June 1979, ♂ holotype, USNM 181123. Ojo de las Varas, leg. M. L. Smith and B. Chernoff, 2 June 1979, 1 ♂ paratype, 10.4 mm, 1 ♀ paratype, 8.7 mm, USNM 181124. Ojo de Carbonera, leg. R. R. Miller, M. L. Smith, and E. Marsh, 28 May 1978, 7 ♂ paratypes, 8.5, 9.0, 9.3, 9.4, 10.2, 10.7, 11.5 mm; 1 ♀ (juv. ♂ ?) paratype, 7.5 mm, USNM 181125.

Etymology.—Named for Dr. Robert R. Miller, University of Michigan.

Description.—Length up to 11.5 mm. Body broad, about 0.6× as wide as long. Pereonites and pereopods more hirsute than in other species. Sides of pereon subparallel; pereon widening only slightly posteriorly. Pleotelson narrowly rounded at apex; lateral margins concave just anterior to apex. Clypeus moderately long, slightly convex, anterior margin evenly curved. Antenna 1 flagellum 5–7-merous (6-merous in most specimens). Antenna 2 flagellum 11–14-merous, last 4 segments minute. Mandible incisors and lacinia 3-cuspate; right spine-row with 7 spines (1st 3 with common peduncle), left spine-row with 5 spines. Maxilla 1 outer ramus with 10 long spines, a central setiform spine, and 2 short dentiform spines. Pereopods densely setose; opposable margin of propus densely armed

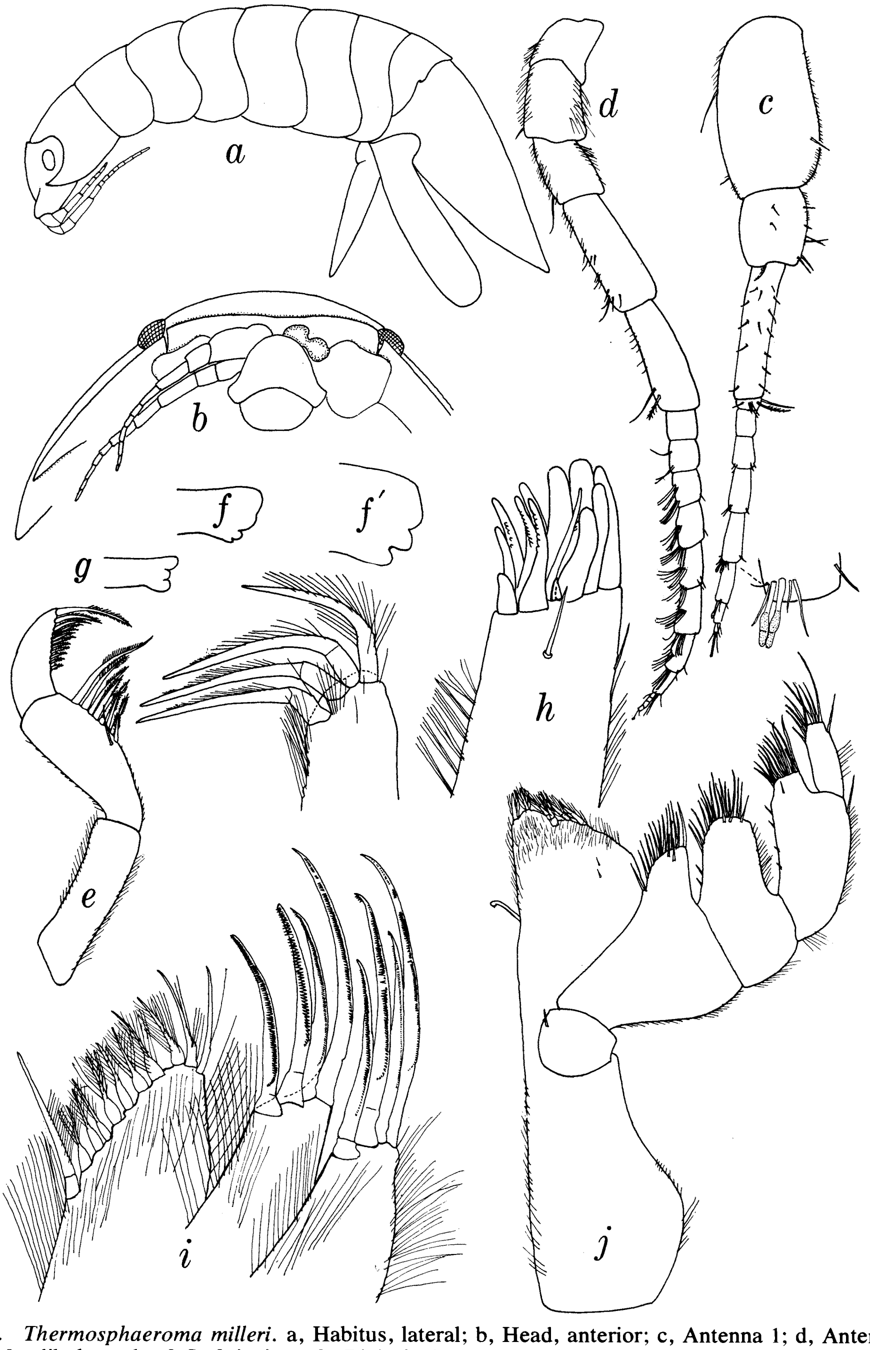

Fig. 1. *Thermosphaeroma milleri*. a, Habitus, lateral; b, Head, anterior; c, Antenna 1; d, Antenna 2; e, Mandibular palp; f, Left incisor; f′, Right incisor; g, Left lacinia; h, Maxilla 1; i, Maxilla 2; j, Maxilliped.

Fig. 2. *Thermosphaeroma milleri*. a, Pereopod 1; b, Pereopod 2; c, Pleopod 1; d, Pleopod 2, ♂; e, Apex of appendix masculina.

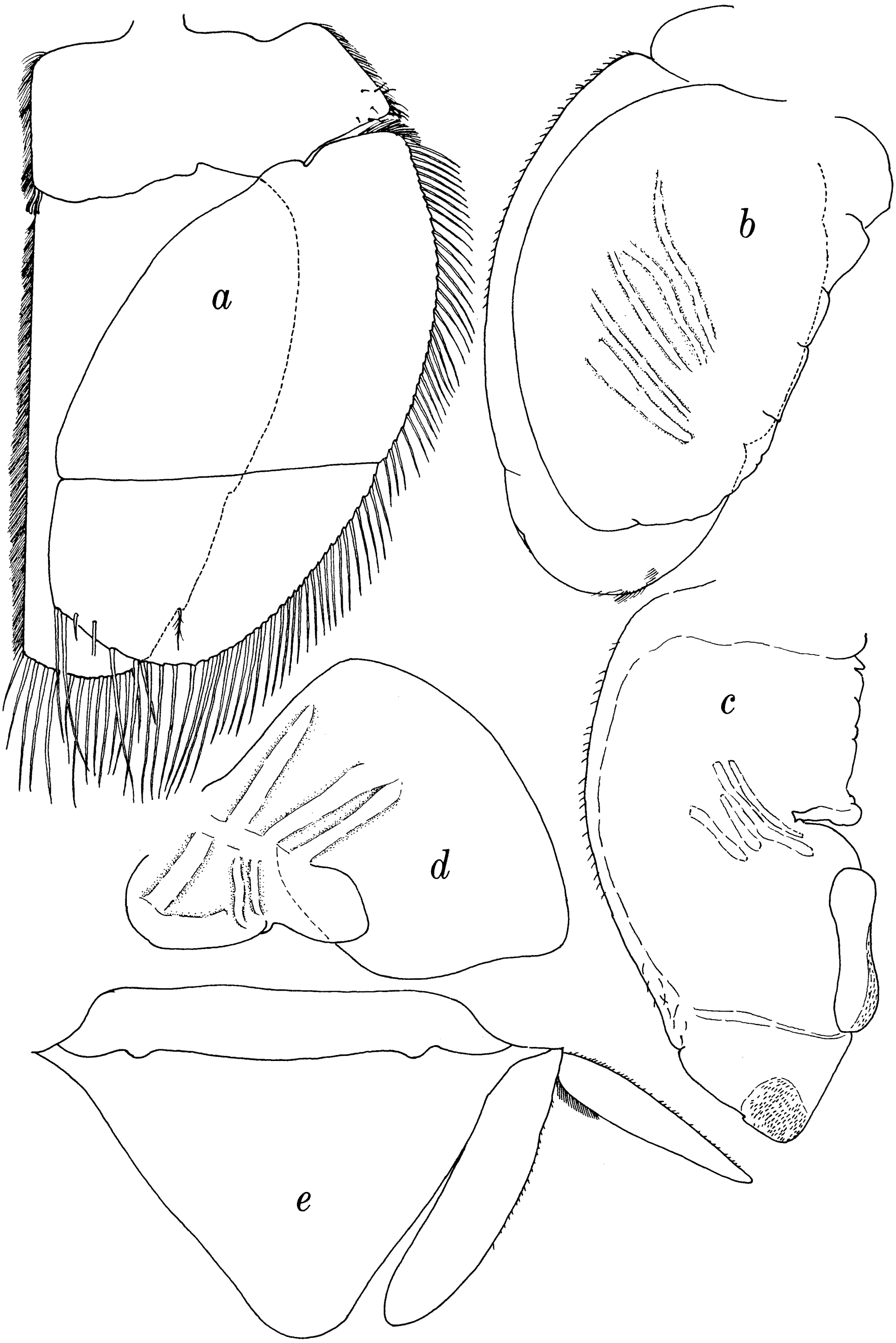

Fig. 3. *Thermosphaeroma milleri.* a, Pleopod 3; b, Pleopod 4; c, Pleopod 5 exopod; d, Pleopod 5 endopod; e, Pleotelson and uropod, dorsal.

with cylindrical spinules. Appendix masculina cylindrical, curving slightly laterad, not quite reaching distal margin of pleopod 2 endopod. Pleopod 5 exopod with narrow incision on lateral margin proximal to reniform swelling. Exopod of uropod more than 0.7 × length of endopod, apex pointed, curving slightly laterad; endopod with rounded apex.

Remarks.—*T. milleri* is similar to *T. dugesi,* but can be distinguished by the concave subterminal margins of the pleotelson and the rounded apex of the uropodal endopod.

Habitat.—The three springs inhabited by *T. milleri* form part of an isolated cluster of springs in northwestern Chihuahua. Ojo El Medio and Ojo de las Varas (about 0.5 and 1.0 km N of Ojo de Carbonera respectively) are ponds resulting from the impoundment of springs for irrigation purposes. Water rises through quicksand in each spring and is clear and fresh. Vegetation is sparse and consists of filamentous algae and submerged hummocks of grass. At Ojo de las Varas isopods were found in a seine after fishing in a pond (about 20 × 40 m, 0.5 m deep) over mud and sand. Water temperature was 27.1°C on 2 June 1979. At Ojo El Medio isopods were taken in a seine in water about 0.5 m deep over mud and sand. Water temperature on 2 June 1979 was 28°C.

Ojo de Carbonero is the only spring that has not been highly modified. Water rises from a complex of spring-heads and flows about 100 m as a shallow brook (10 cm deep) before entering an irrigation system. The main spring is about 3.7 m wide; many lateral springs are about 0.6 m wide; water depth in both is about 1 m. Substrates include gravel, silt, mud, and bedrock. The sparse vegetation consists of filamentous green algae, *Chara, Nasturtium,* "cress," and submerged grass. Water temperature on 28 May 1978 and 6 June 1979 was 27°C.

Thermosphaeroma smithi, new species
Figs. 4–6, 8e, 9e

Material Examined.—MEXICO, Chihuahua, Balneario San Diego (about 37 km E Ciudad Chihuahua): leg. Jerry Landye 1971, ♂ holotype, USNM 181119 and 100+ ♂ ♀ paratypes, USNM 181120. Irrigation ditch downstream from hotel, leg. M. L. Smith and B. Chernoff, 26 May 1979, 8 ♂, 3 ♀ paratypes, USNM 181121. Stream and springs just below hotel, leg. M. L. Smith and B. Chernoff, 26 May 1979, 61 ♂ ♀ paratypes, USNM 181122.

Etymology.—Named for Dr. Michael L. Smith, University of Michigan.

Description.—Length up to 11.7 mm. Body broad, about 0.5× as wide as long. Pereopods hirsute, pereonites much less so than in *T. milleri.* Pereon gradually widening posteriorly, widest at pereonite 7. Pleotelson somewhat less narrowly rounded at apex than in *T. milleri,* lateral margins not concave just anterior to apex. Clypeus shorter than in *T. milleri,* anterior margin nearly straight. Antenna 1 flagellum with up to 9 segments. Antenna 2 flagellum with up to 14 segments; last 3–4 segments minute. Mandible incisors 2-cuspate, with a large rounded cusp occupying most of incisor and a small accessory cusp; lacinia with 3 subequal cusps; right spine-row with 6 spines, left spine-row with 5 spines. Maxilla 1 outer ramus with 10 long spines, a central setiform spine, and a single short dentiform spine. Opposable margin of propus of pereopods smooth, without spinules. Appendix masculina sinuous, narrowing distally, extending beyond apex of pleopod 2 endopod. Pleopod 5 with broad V-shaped incision on lateral margin proximal to reniform swelling. Uropod dimorphic, exopod longer than endopod, apex pointed and curved slightly laterad in ♀, blunter and straight in ♂; endopod apex angular and slightly curved laterad in ♀, broadly rounded in ♂.

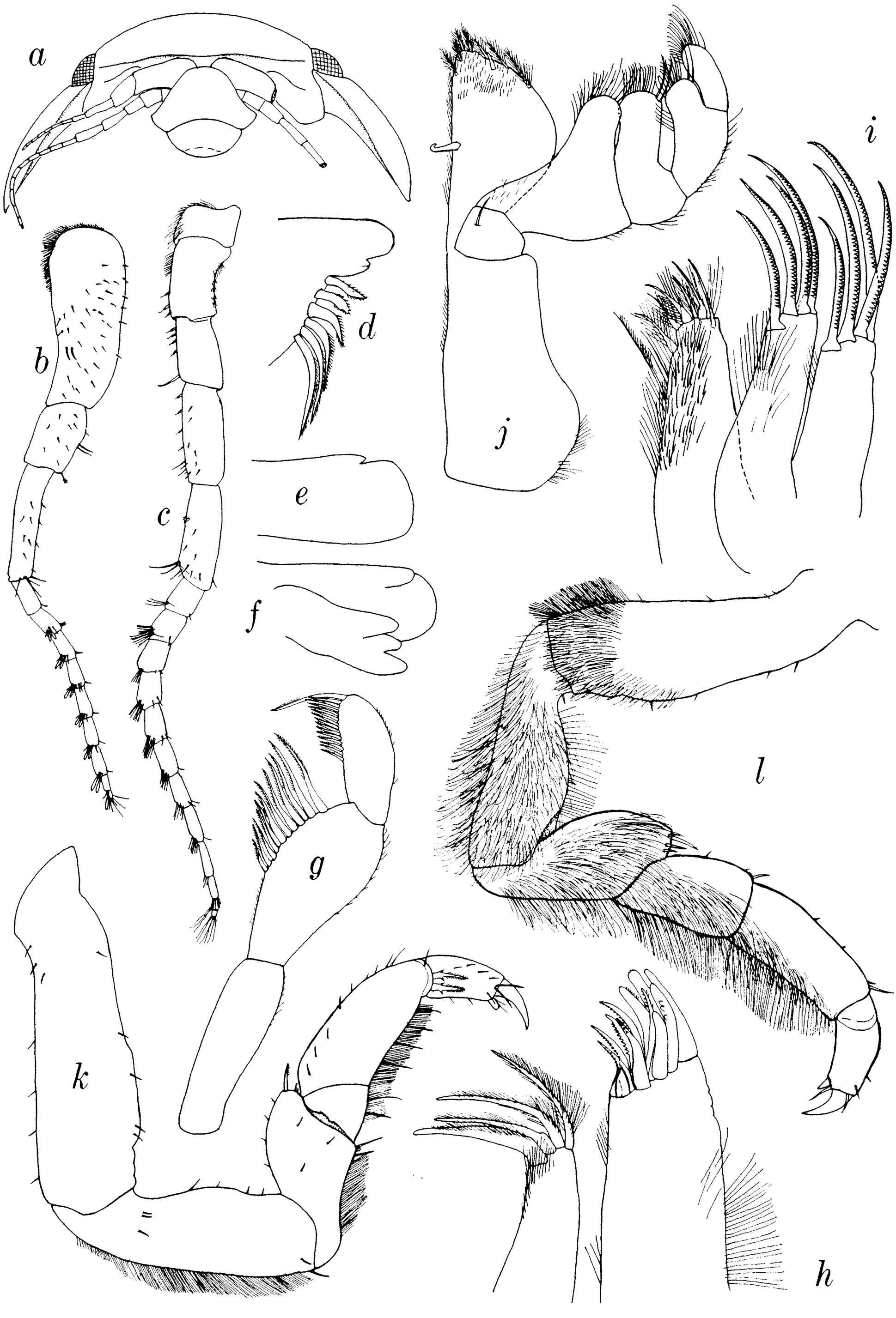

Fig. 4. *Thermosphaeroma smithi*. a, Head, ventral; b, Antenna 1; c, Antenna 2; d, Right mandible, incisor and spine-row; e, Incisor, right mandible; f, Incisor and lacinia, left mandible; g, Mandibular palp; h, Maxilla 1; i, Maxilla 2; j, Maxilliped; k, Pereopod 1.

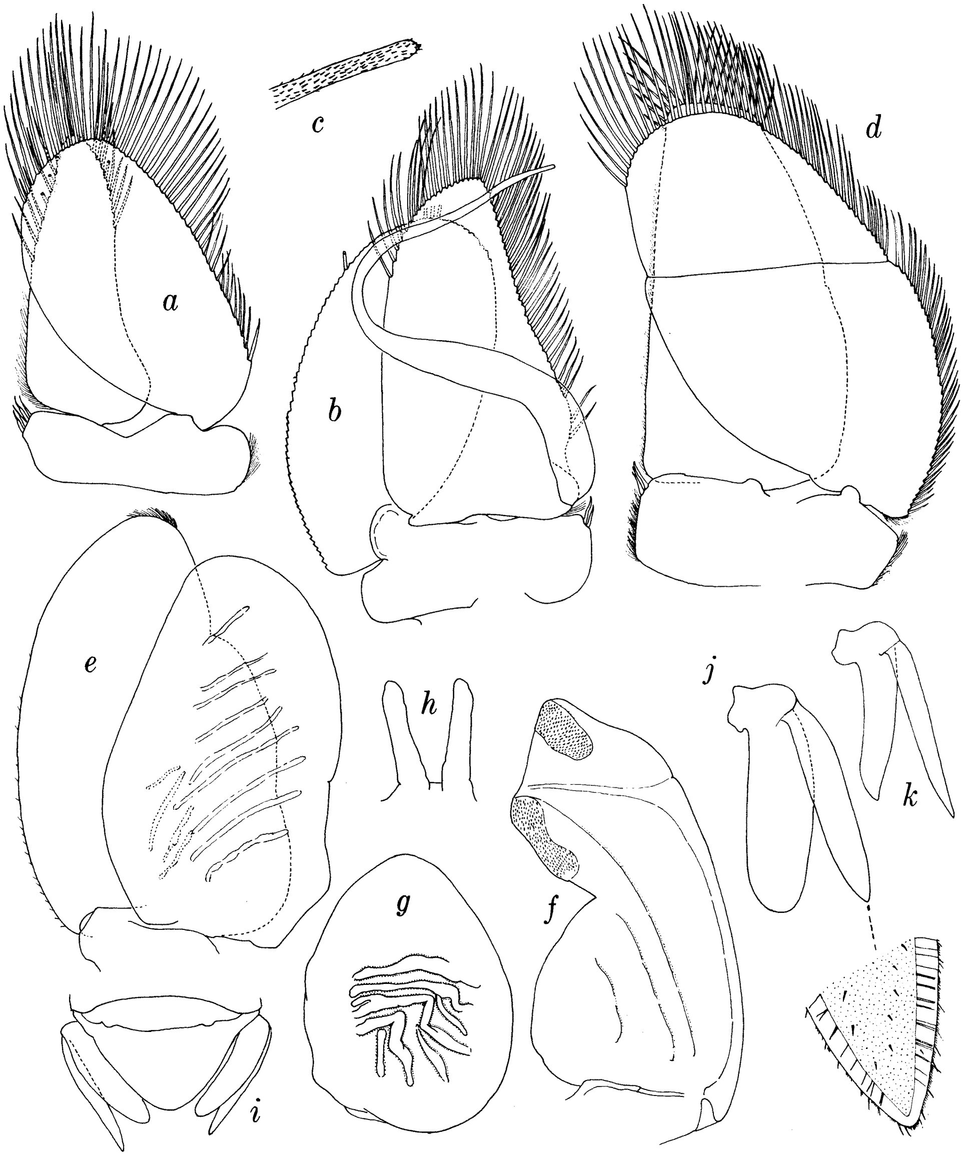

Fig. 5. *Thermosphaeroma smithi.* a, Pleopod 1; b, Pleopod 2, ♂; c, Apex of appendix masculina; d, Pleopod 3; e, Pleopod 4; f, Pleopod 5 exopod; g, Pleopod 5 endopod; h, Penes; i, Pleotelson and uropods, dorsal, ♂; j, ♂ uropod, ventral; k, ♀ uropod, ventral.

Remarks.—*T. smithi* is Cole and Bane's (1978: 228) "undescribed member of the genus from Chihuahua [that] has a sharply-pointed [uropodal] exopod, 1.5× the endopod length and held at right angles to it." It is the only known species in which the exopod exceeds the endopod in length and can be distinguished readily by this character alone. The sexual dimorphism in the uropodal rami is also unique for the genus. The exopod:endopod ratio tends to be greater in females, but there is considerable overlap (Fig. 6). The exopod sometimes is held at right angles to the endopod.

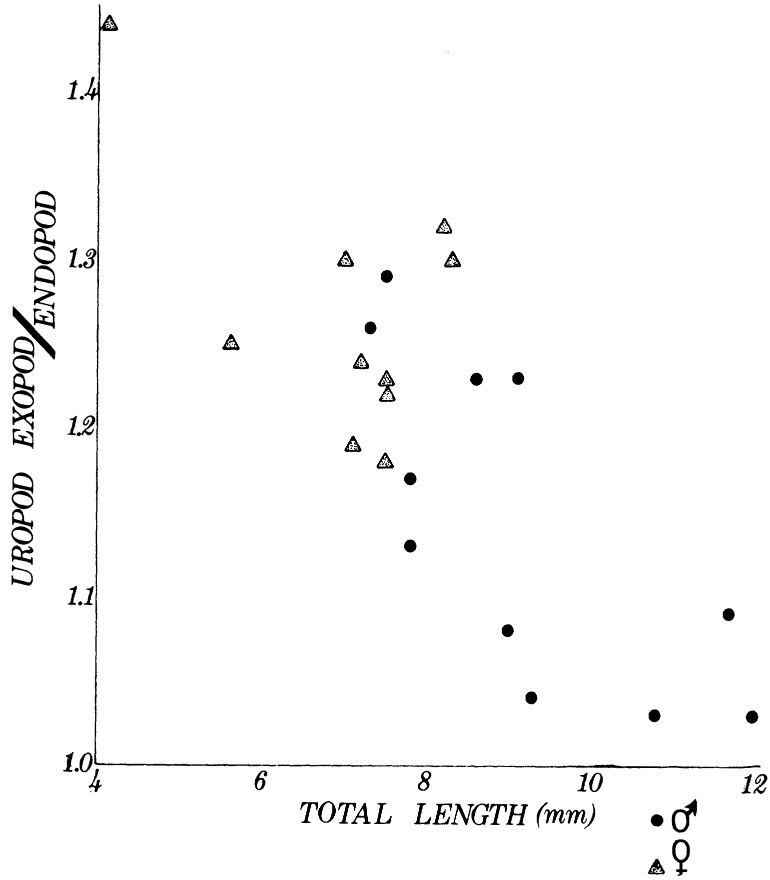

Fig. 6. Relative lengths of exopod and endopod of uropod in *Thermosphaeroma smithi.*

Males are much more numerous than females in the samples. Of 56 specimens picked at random from the Landye sample, 40 were male and 16 were female, a ratio of 2.5:1. None of the females carried eggs or young, and none had oostegites. Possibly the brooding females had taken refuge and escaped collection.

Habitat.—At Balneario San Diego water comes from about 15 small spring-heads (<0.5 m in depth or diameter) that empty into a creek about 1 m wide and less than 0.5 m deep. Water temperatures ranged from 32.1–43.8°C in different parts of the stream and springs on 26 May 1979. *T. milleri* was found in the spring-head (43.8°C) and on the silt bottoms of pools or along banks (32.1–43.4°C) where they completely covered the substrate in some places. They were not found on loose sand or where the current was significant.

Thermosphaeroma dugesi (Dollfus)
Figs. 7g, 8a, 9a, 10a

Sphaeroma dugesi Dollfus, 1893: 15, figs. 1, 2.—Richardson, 1904: 24.
Exosphaeroma dugesi.—Richardson, 1905: 295–296, figs. 313–314.—Brues, 1924: 415.—Van Name, 1936: 449–450, fig. 280.—Rioja, 1951: 351–365, figs. 1–39 (on pls. 1–5).
Thermosphaeroma dugesi.—Cole and Bane, 1978: 223, 228.

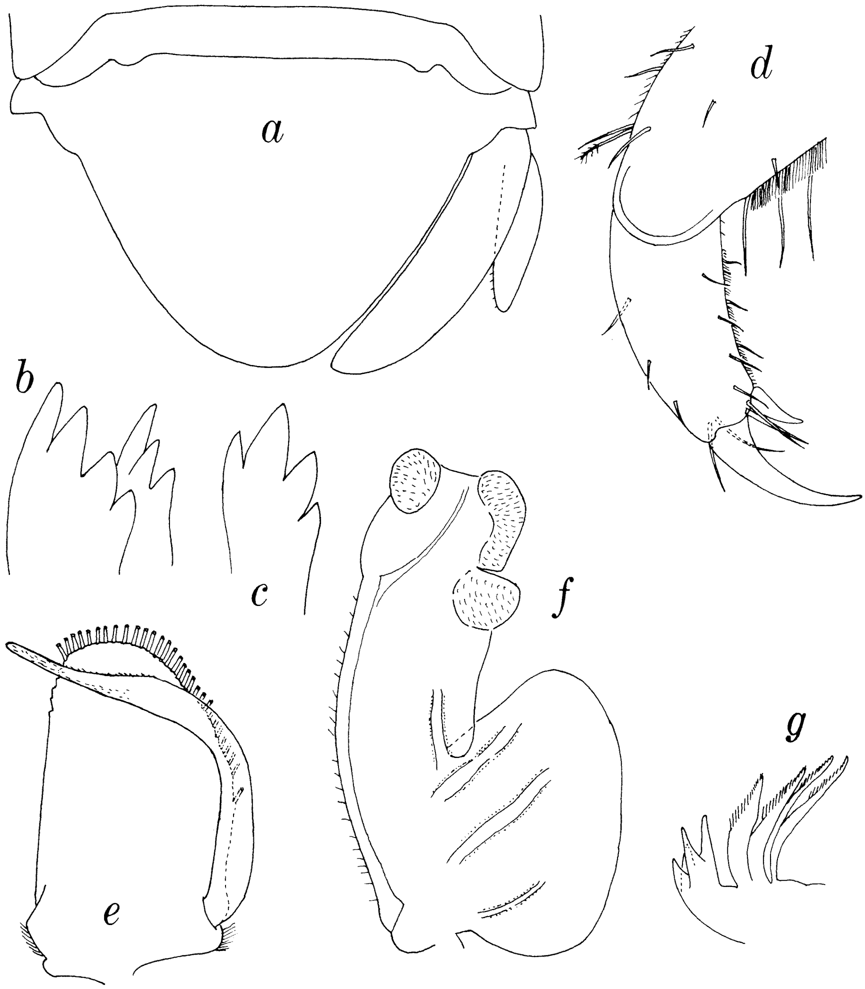

Fig. 7. a–f, *Thermosphaeroma thermophilum*. a, Pleotelson and uropod, dorsal; b, Left incisor and lacinia; c, Right incisor; d, Pereopod 1, distal part; e, Pleopod 2 endopod, ♂; f, Pleopod 5 exopod; g, *Thermosphaeroma dugesi*, spine row of right mandible.

Material Examined.—Prof. A. Dugés sent 3 collections from the type-locality to the Smithsonian Institution. He also sent specimens to A. Dollfus who described the species. Dates of collection are not indicated on the labels of the vials, but they were received 26 January 1888 (USNM 15334, 16 specimens), 24 July 1894 (USNM 18492, 7 specimens), and 11 July 1899 (USNM 23045, 13 specimens). Curiously the 1888 sample, identified by Harriet Richardson as *Sphaeroma dugesi* Dollfus, was catalogued in 1890, about 3 years before publication of Dollfus's description.

Type-locality.—Ojo Caliente, Aguascalientes, Mexico.

Etymology.—Named for the collector, Professor Adrien Dugés.

Diagnosis.—Length up to 14 mm. Body about 0.55× as wide as long. Pleotelson evenly rounded. Antenna 1 flagellum 7–9-merous; antenna 2 14-merous. Incisors and lacinia of mandible 3-merous; right spine-row with 7 spines (1st 3 with common peduncle), left spine-row with 5 spines. Maxilla 1 outer ramus with 10 long spines (5 pectinate, 5 smooth), a central setiform spine, and 2 short dentiform spines. Appendix masculina sinuous, extending well beyond apex of pleopod 2 endopod. Pleopod 5 exopod with narrow elongate reniform swelling; notch proximal to swelling rudimentary. Endopod of uropod distinctly longer than exopod, ending in angle at distolateral corner.

Remarks.—*T. dugesi* differs from *T. subequalum* in having a uropodal endopod that is longer rather than equal to the endopod and with a rounded apex with an angular corner rather than a truncate apex. *T. milleri* differs in its pleotelson shape and the round, cornerless apex of its uropodal endopod. A full description of *T. dugesi* with excellent illustrations is given by Rioja (1951).

Habitat.—I have no information on the habitat other than it is a warm spring with a temperature of more than 35°C.

Thermosphaeroma thermophilum (Richardson)
Figs. 7a–f, 8b, 9b, 10b

Sphaeroma thermophilum Richardson, 1897: 465–466; 1900: 223; 1904: 24.
Exosphaeroma thermophilum.—Richardson, 1905: 294–295, figs. 311, 312.—Cockerell, 1912: 49.—Giambiagi, 1922: 236.—Brues, 1924: 415.—Van Name, 1936: 450, fig. 281.—Rioja, 1951: 351–352.—Chace *et al.*, 1959: 874, fig. 31.5.
Exosphaeroma termophilum [sic].—Rioja, 1951: 364–365.
Thermosphaeroma thermophilum.—Cole and Bane, 1978: 228.

Material Examined.—Two samples collected 8 June 1938 by Leslie Hubricht: from Evergreen Ranch Spring, 3.5 mi W Socorro, New Mexico, water temperature 31°C, 630+ specimens; from City Spring, 3.5 mi W Socorro, water temperature 34°C, 430+ specimens.

Type-locality.—Warm spring, a few miles W of Socorro, Socorro Co., New Mexico.

Description.—Length up to 13 mm. Body about 0.5× as wide as long. Pereonites sparsely hirsute. Sides of pereon subparallel; pereon widening very gradually posteriorly. Pleotelson broadly and evenly rounded, without ventral shelf. Clypeus relatively short; anterior margin curving, tending to be slightly angular at midlength. Antenna 1 flagellum 7–8-merous. Antenna 2 flagellum 11–12-merous. Mandible incisors 4-cuspate, lacinia 3-cuspate; right spine-row with 6 spines, left with 5 spines. Maxilla 1 outer ramus with 10 long spines (6 pectinate, pointed, 4 flat, smooth, with truncate tips), 1 central spiniform seta, and 1 short dentiform spine. Setation of pereopods less dense and setae shorter than in other species of *Thermosphaeroma*. Appendix masculina curving laterally and reaching past apex of pleopod 2 endopod, but not recurving as in *T. dugesi, T. subequalum,* and *T. smithi*. Pleopod 5 exopod sometimes with incision dividing reniform swelling, proximal half of exopod produced into prominent lateral lobe. Endopod of uropod nearly 2 × length of exopod, apex rounded.

Remarks.—The broadly rounded pleotelson lacking a ventral shelf, and the short uropodal exopod immediately identify *T. thermophilum*.

Habitat.—The exact locality was not given by Richardson, but the present population of about 2,400 individuals lives within the water system of an abandoned bathhouse called "The Evergreen" (Stanley, 1950), which is supplied with water from Sedillo Spring. It seems likely that in the past *T. thermophilum* also inhabited two nearby springs, Cook and Socorro. The present population occupies two small pools, 20–26 cm in depth, totalling about 7 m in length, and two runs (total length about 39 m) below each pool. Water temperatures are 31–32°C.

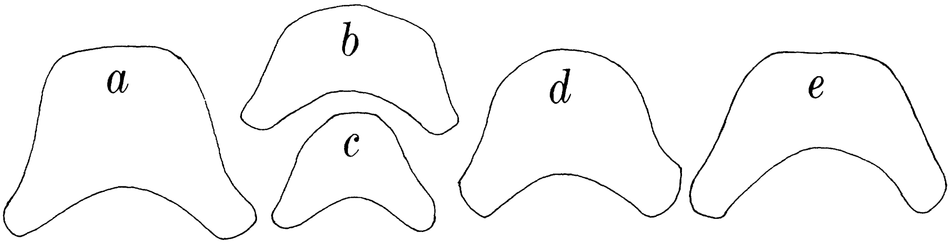

Fig. 8. Clypei of species of *Thermosphaeroma*. a, *T. dugesi*; b, *T. thermophilum*; c, *T. subequalum*; d, *T. milleri*; e, *T. smithi*.

Endangered Status.—*T. thermophilum* was classified as an endangered species by the State of New Mexico in February 1978 and by the U.S. Fish and Wildlife Service on 27 March 1978 (43 Federal Register 9612). It is the only crustacean so-classified under the provisions of the Endangered Species Act of 1973. The major threat to the species is loss of habitat. The source of the original spring has been capped and most of the flow diverted to the Socorro city water supply. Only a limited amount of water flows into "The Evergreen," and it can be shut off by a readily accessible valve. The habitat is on private land, and at present steps cannot be taken to secure continuation of the flow of water or protection of the habitat from contamination or other damage.

Captive populations have been established at the University of New Mexico and at the Rio Grande Zoo, both in Albuquerque. The New Mexico Game and Fish Department has prepared a plan to protect *T. thermophilum* which included enhancing and expanding the habitat at Sedillo Spring and establishing introduced populations at other suitable localities.

(The above has been extracted from the unpublished, "Technical review draft of Socorro isopod recovery plan," by the New Mexico Game and Fish Department.)

Thermosphaeroma subequalum Cole and Bane
Figs. 8c, 9c, 10c

Thermosphaeroma subequalum Cole and Bane, 1978: 223–228, figs. 1–3.

Material Examined.—Holotype and 7 paratypes.

Type-locality.—Hot spring near Boquillas Canyon, Big Bend National Park, Brewster Co., Texas.

Etymology.—Referring to the subequal lengths of the uropod rami.

Diagnosis.—Length 8.15 mm. Body about 0.5× as wide as long. Pleotelson evenly rounded. Antenna 1 flagellum 9-merous; antenna 2 flagellum 11-merous. Right incisor of mandible 3-cuspate, left incisor 4-cuspate; lacinia 2-cuspate; right spine-row with 7 spines, left spine row with 5 spines. Maxilla 1 outer ramus with 10 long spines (5 pectinate, 5 smooth), a central setiform spine, and 2 short dentiform spines. Appendix masculina sinuous, extending well beyond apex of pleopod 2 endopod. Pleopod 5 exopod with broad, shallow excavation proximal to reniform swelling. Uropods subequal in length, reaching beyond apex of telson; exopod pointed, curving slightly laterad at apex; endopod apex truncate, with round-angular lateral corner.

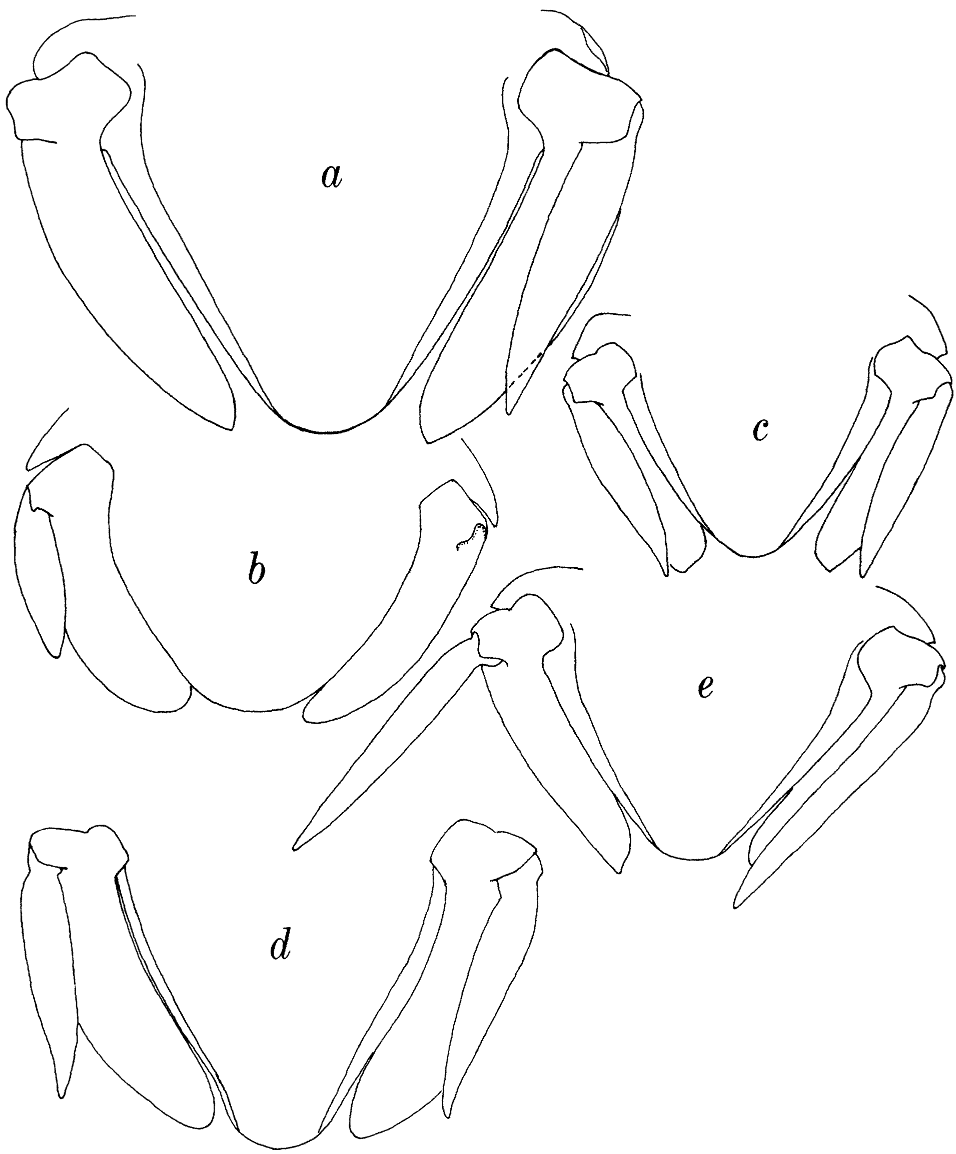

Fig. 9. Pleotelson and uropods, ventral, of species of *Thermosphaeroma*. a, *T. dugesi*; b, *T. thermophilum*; c, *T. subequalum*; d, *T. milleri*; e, *T. smithi*.

Remarks.—The subequal lengths of the uropod rami and the shape of the endopod apex distinguish this species from its congeners.

Habitat.—*T. subequalum* is known from two springs near Boquillas Canyon and a site on the Rio Grande Village Nature Trail. Water temperatures at the localities range from 32 to 35°C.

Origin of Thermosphaeroma.—Isopods of the family Spaeromatidae are, with few exceptions, inhabitants of marine or brackish waters. A few species, e.g. *Gnorimosphaeroma insulare* (Van Name, 1940) (synonym *G. oregonensis luteum*

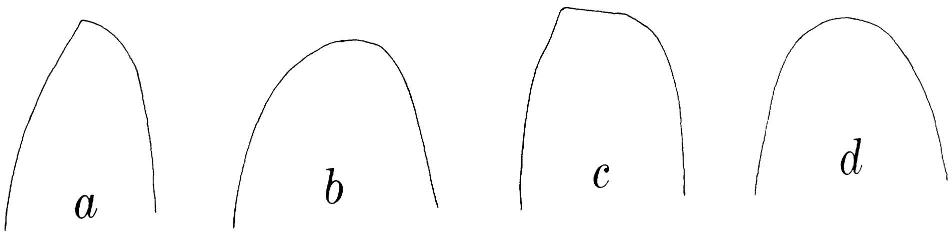

Fig. 10. Apices of right endopods, dorsal, of species of *Thermosphaeroma*. a, *T. dugesi*; b, *T. thermophilum*; c, *T. subequalum*; d, *T. milleri*.

Menzies 1954, =*G. luteum* Menzies, see Riegel 1959b, Hoestlandt, 1977), inhabit freshwater parts of coastal streams above tidal influences, and also the lower brackish parts of such streams. Despite its ability to live in fresh water for extended periods and to regulate osmotically (Riegel, 1959a), *G. insulare* and species in comparable habitats such as *G. chinense* (Tattersall, 1921) are not fully adapted to the freshwater environment.

The ancestors of *Thermosphaeroma* must be sought among species of marine sphaeromatids, more specifically among the Dynameninae. The unusual features of *Thermosphaeroma* make such a search difficult, and no likely candidates can easily be found among known western Atlantic Recent Sphaeromatidae.

It is probable that the ancestral stock of *Thermosphaeroma* inhabited the marine embayment that covered most of central and eastern Mexico, southern Texas, and most of New Mexico during the middle to late Mesozoic. As the embayment regressed at the end of the Cretaceous and thereafter, the ancestral sphaeromatids would have been stranded in continental freshwaters (Fig. 11). Analysis of fossil floras shows development of a progressively drier climate during the Tertiary, but the emergence in the area of regional deserts of extreme heat and aridity occurred only during interglacial times, and especially after the Wisconsin glaciation (Axelrod, 1979). The confinement of ancestral *Thermosphaeroma* to hot springs and its evolution into the several species is probably a recent event.

The Restricted Occurrence in Freshwater of Flabellifera

Flabelliferan isopods in general, not just the Sphaeromatidae, have been unsuccessful in establishing themselves in "normal" epigean freshwater habitats of the kind occupied, for example, by asellid isopods and gammaridean amphipods. Excluding coastal streams, freshwater habitats of flabelliferans fall into three categories:

1. Parasites of freshwater fishes, or more rarely shrimps. This group includes about 15 species in the family Cymothoidae living on freshwater fish hosts in South America (Van Name, 1936) and a few cymothoid species in Africa, Indonesia, China, Japan, Korea, and far-eastern Siberia. In the family Aegidae, *Alitropus typicus* Milne-Edwards has been reported from freshwater localities in Sumatra, Borneo, Thailand, Ceylon, and India, either free-living or from the gills of fishes (for summary see Ingle and Fernando, 1963). Aegids are all fish parasites, but leave their hosts after feeding, hence free-living records do not conflict with their being considered parasites. In Queensland and New South Wales, Australia, two species of *Austroargathona* (Argathonidae) parasitize freshwater shrimps of the genera *Macrobrachium, Atya,* and *Paratya* (Riek, 1953, 1966). Finally, three freshwater species of *Tachaea* (Corallanidae) parasitize freshwater

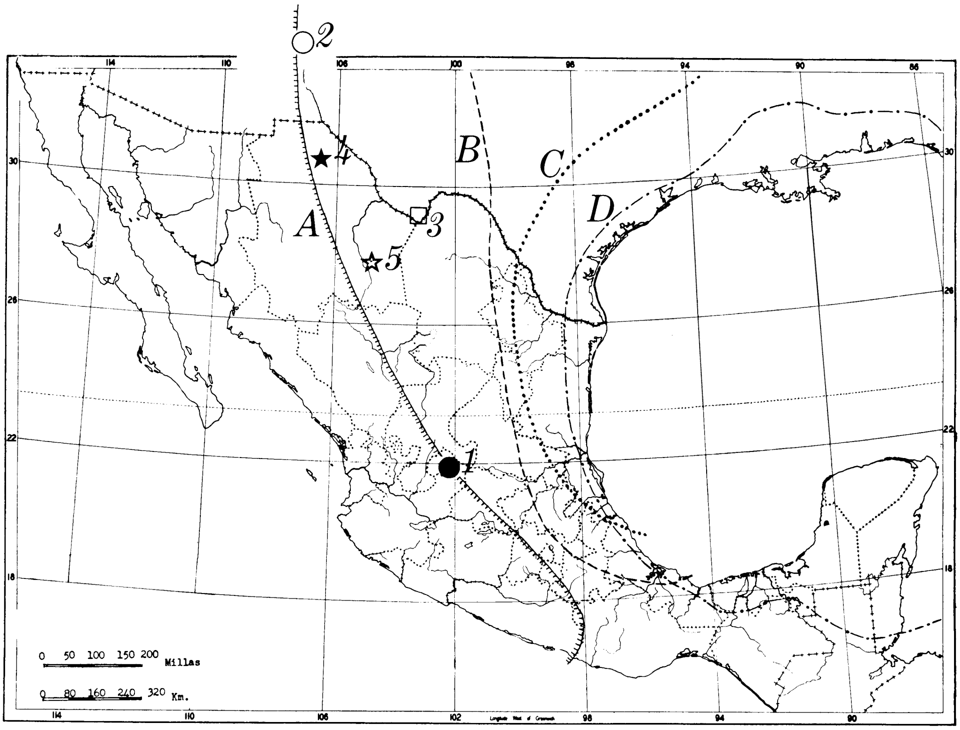

Fig. 11. Known distribution of species of *Thermosphaeroma*. 1, *T. dugesi*; 2, *T. thermophilum*; 3, *T. subequalum*; 4, *T. milleri*; 5, *T. smithi*. Boundaries of marine embayments are indicated for A, Maastrichtian (Upper Cretaceous); B, Paleocene; C, Eocene; D, Miocene (from Axelrod, 1979, fig. 26).

cyprinoid fishes in Java and Sumatra (Weber, 1892; Nierstrasz and Marees van Swinderen, 1931), the canals of a freshwater sponge in Calcutta (Stebbing, 1907), and the carapace of freshwater shrimps in China (Tattersall, 1921).

2. Subterranean species, mostly inhabiting caves. A map summarizing the world distribution of subterranean Cirolanidae is given by Monod (1975). Recently discovered cirolanids not included are *Mexilana saluposi* Bowman (1975) from San Luis Potosi, Mexico, and *Arubolana imula* Botosaneanu and Stock (1978) from Aruba, an island in the Leeward Group of the Lesser Antilles. Subterranean Sphaeromatidae have not been found in the New World, but several species of the genera *Caecosphaeroma* and *Monolistra* are widely distributed in karst areas of France and Northern Italy-Yugoslavia respectively (Vandel, 1964; Sket, 1964).

3. Isopods occurring in hot springs. These include only the five species of *Thermosphaeroma* discussed previously herein.

In attempting to explain the restricted occurrence of Flabellifera in freshwater habitats, two questions need to be considered: 1. What factors have enabled them to successfully colonize caves and hot springs and to become parasites of freshwater fishes? 2. What factors have deterred them from gaining footholds in normal epigean freshwater habitats? Proposed answers to these questions follow.

1. It is generally agreed that the parasitic isopod families (Cymothoidae, Aegidae, Corallanidae, Argathonidae) evolved from cirolanid-like ancestors (Menzies, Bowman, and Alverson, 1955). Cirolanids are primarily scavengers, but

readily attack fish that are injured or confined by nets or traps. The evolutionary path from scavenger to parasite is well-travelled. However, freshwater fish parasites probably evolved from marine ancestors that were already parasitic.

Free-living cirolanids have no obvious preadaptations for a troglobitic existence. However, given a cave with a niche available for an aquatic scavenger-predator and a cirolanid with access to the cave, there is no reason to doubt that the cirolanid would come to occupy this niche unless excluded by a better adapted competitor. Cave cirolanids do not differ basically from their epigean relatives except for the loss of eyes and pigmentation, and must occupy similar niches.

There is no obvious evidence for preadaptation to the high temperatures of hot springs among the Sphaeromatidae, and it seems likely that *Thermosphaeroma* gradually evolved a tolerance to high temperatures concomitant with the increase in environmental temperature.

2. In considering why the Flabellifera have been excluded from normal epigean freshwater habitats, we must look for a cause or causes than can be invoked for all flabelliferans—marine, parasitic, hypogean, and thermophilic. There appear to be no physical attributes of freshwater habitats that would prevent flabelliferans from adapting to them and becoming members of freshwater communities. Physical properties of hypogean waters and waters bathing a freshwater fish parasite are fundamentally similar to those of other bodies of fresh water. Hence biotic factors must be involved, and the question to be considered is, "What non-parasitic animal group commonly occurs in freshwater except caves and hot springs, but not (or rarely) in the ocean, and fills a niche similar to that of flabelliferans?" The answer is clear: various kinds of predaceous aquatic insects or insect larvae. Eleven of the 30–35 orders of insects contain species that are aquatic or semiaquatic (Pennak, 1978). Of the 13 orders included in Pennak's (1978) manual, 8 contain species that are at least partly predaceous. I suggest that Flabellifera are excluded from normal freshwaters because they are unable to compete successfully with aquatic insects and insect larvae.

Aquatic insects are rarely found in caves. Vandel (1964) lists only two families of Coleoptera: Dytiscidae, with about half a dozen species from Europe, Africa, and Japan, and Dryopidae, with one species from the Congo. Hypogean Flabellifera have little or no competition from insects.

Flabelliferan freshwater fish parasites also are free from competition by insects, none of which, to my knowledge, parasitize fishes. Perhaps the greatest advantage of parasitism to an isopod is the shelter and protection that it obtains from this relationship, rather than the nutrition. Adult Cymothoidae probably do not feed, and the host may be more valuable as a protected habitat than as a food source. This would not apply to the Aegidae, in which the adult leaves the fish after taking a blood meal.

Acknowledgements

I am grateful to Dr. Robert R. Miller and Dr. Michael L. Smith for sending collections of the new species from Chihuahua and for providing detailed information on the collection localities. Dr. Gerald A. Cole kindly sent me the largest sample of *T. smithi*.

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RECEIVED: 8 July 1980.

ACCEPTED: 18 August 1980.

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