New localities are reported to detail the distributions of the order Siphonophorida and the family Siphonophoridae in the southwestern and southcentral United States, and northern Mexico. The northernmost sites are in Los Angeles County, California; Yavapai County, Arizona; and Coryell County, Texas. The Siphonorhinidae is represented by only one genus and species, *Ilacme plenipes* Cook & Loomis, known only from northern San Benito County, California, the northernmost ordinal record. Congenetic status is confirmed for *Siphonacme lytoni* Cook & Loomis, in Arizona, and *S. pseustes* (Chamberlin), in Sonora, Mexico; *Californizonium Verhoeff* is synonymized under *Siphonacme* Cook & Loomis. Diagnostic illustrations are presented for *I. plenipes, S. lytoni* and *pseustes*, and *Siphonophora limitare* Loomis and *texascolens* Chamberlin & Mulaik.

The order Siphonophorida, containing the diplopods with the most segments and legs, occurs primarily in east Asia and the Western Hemisphere, with minor representation, the family Nematozoniidae, in South Africa (Hoffman 1980). The two principal families, Siphonorhinidae and Siphonophoridae, occur in both areas, but the former is represented by only one genus and species in the New World, *Ilacme plenipes* Cook & Loomis. The Siphonophoridae is widespread on Caribbean islands and in South and Central America, and ranges northward into the southwestern and southcentral United States (Shelley 1995). Its representatives are difficult to study because of their small, narrow bodies and the minuteness and structural uniformity of the male genitalia; consequently, I conduct only a minimal analysis of the two known genera and four species in the United States and northern Mexico, providing diagnostic illustrations of the type specimens and summarizing other generic records. The distinctions of these from species occurring farther south is beyond the scope of this contribution, the major purpose of which is to define the northern distributional limits of the order and family. I therefore accept the current generic assignments and the validity of *Siphonacme* Cook & Loomis, which can only be assessed in a family revision; *Californizonium Verhoeff* is considered a synonym of *Siphonacme*.

The Siphonophoridae clusters in three areas of the United States (Fig. 14): southern California, Arizona, and central and southern Texas. This pattern suggests three northward expansions from Mexico, each possibly correlating with a separate genus. The known Mexican records correlate with the areas in Arizona and Texas; no samples are available from.
Baja California, but siphonophorids should be expected there, particularly in mountains like the Sierra Juarez and San Pedro Martir. The Los Angeles County, California, and Yavapai County, Arizona, localities are near the same latitude and are the northernmost for the family. The northernmost ordinal record is the one known locality of *I. plenipes*, in northern San Benito County, California.

Fourteen of the 23 unreported siphonophorid localities are caves in Texas, which have been investigated preferentially because of the research focus at the TMM (see abbreviations below). Siphonophorids appear to be especially cryptic in epigean environments, at least in the United States; with all the millipede sampling that has occurred between Texas and southern California in the past 60 years only nine new samples exist from surface habitats. This suggests that the arthropods cluster and that one must not only investigate the right habitat but also fortuitously dislodge the one or few rocks or logs that shelter them. With typically hundreds of rocks/logs at potential sites, the probability of discovering siphonophorids is low and apparently chiefly a matter of chance. The resultant dearth of specimens and the inherent difficulties in studying siphonophorids are reasons why decades will probably elapse before their taxonomy is significantly advanced. In the interim, narrowly focused regional studies are the only feasible contributions. Acronyms of sources of preserved study material are as follows:

CAS - California Academy of Sciences, San Francisco.
FSCA - Florida State Collection of Arthropods, Gainesville.
LACMNH - Los Angeles County Museum of Natural History, Los Angeles, California.
NMNH - National Museum of Natural History, Smithsonian Institution, Washington, D. C.
SWRS - Southwest Research Station, Portal, Arizona.
TMM - Texas Memorial Museum, University of Texas, Austin.
UAZ - Entomology Department, University of Arizona, Tucson.
VMNH - Virginia Museum of Natural History, Martinsville.
WAS - Private collection of W. A. Shear, Hampden-Sydney, Virginia.

LITERATURE REVIEW

The history of the Siphonophorida in the United States and northern Mexico begins with the proposal of *Siphonophora pseustes* by Chamberlin (1923), for a form collected along the Gulf of California, Sonora, Mexico. Cook & Loomis (1928) recognized that the order was unknown from the United States and erected *Siphonacme* for *S. lyttoni*, a new species in the central Arizona desert that seemingly could not be accommodated by *Siphonophora* Brandt; on the basis of Chamberlin's description they transferred *Siphonophora pseustes* into *Siphonacme*. Cook & Loomis also erected *Illacme* for *I. plenipes*, a new species from San Benito County, California. Eight years later, Loomis (1936) proposed *Siphonophora limitare* for specimens from Brownsville, Cameron County, Texas, and recorded *Siphonacme lyttoni* from Prescott, Yavapai County, Arizona, and the Chiricahua Mountains, Cochise County, in the southeastern corner of the state. Omitting *Siphonacme*, Verhoef (1941) published a key to siphonophorid genera in which he proposed *Californizonium* for *Siphonophora pseustes*. Chamberlin & Mulaik (1941) proposed *Siphonophora texascolens* for specimens from Kerr, Bandera, and Kendall counties, Texas, and the first author (Chamberlin 1946) recorded this species from Laguna Madre, near the type locality of *S. limitare*. Loomis (1963) reported *S. limitare* from Bastrop County, Texas, about 100 mi (160 km) east of the type locality of *S. texascolens*, and suggested that the names might be synonymous since each species had been
recorded near the other's type locality. Loomis (1966, 1968a) reported unidentified species of *Siphonophora* from three localities near Monterrey, Nuevo León, Mexico: Huasteca Canyon in the Sierra Madre Oriental, Chipinque Mesa, and Horsetail Falls.

In addition to these accounts, siphonophorids are cited in five listings. Chamberlin & Hoffman (1958) summarized the taxa in the United States, omitting the Laguna Madre record of *Siphonophora texacoisens*; Buckett (1964) included *I. plenipes* in his list of California diplopods; and Loomis (1968b) included *Siphonacme pseustes* in his Mexican/Central American checklist, disregarding *Californizonium* and the other relevant genera proposed by Verhoeff (1941). The final pertinent publications are by Jeekel (1971) and Hoffman (1980), who included the genera in the "Nomenclator" and "Classification," respectively; the latter author also transferred *Illacme* into the Siphonorhinidae.

**Key to Families of the Siphonophorida**
(adapted from Hoffman [1990])

Head prolonged into acuminate rostrum; antennae nearly straight, 5th and 6th antennomeres with distal, circular, sensory pits (Figs. 4, 7, 8, 11).....................Siphonophoridae

Head pyriform to subtriangular; antennae distinctly elbowed between 3rd and 4th articles, without sensory pits (Fig. 1)..........................................................Siphonorhinidae

**Family Siphonorhinidae**

**Genus Illacme** Cook & Loomis


Type species: *Illacme plenipes* Cook & Loomis, 1928, by original designation.


Distribution: Known only from northern San Benito County, California (Fig. 14).

Species: One is known; others are anticipated in southern California, Mexico, and Central America.

Remarks: Until other siphonorhinids are discovered in the Western Hemisphere, the diagnostic features of *Illacme*, and which aspects of the gonopods hold significance at the generic level, will remain unknown. At present, the family characters of the head and antennae diagnose *Illacme* in the New World.

*Illacme plenipes* Cook & Loomis

Figs. 1-3.


Type specimens: Male holotype (NMNH), one male and three female paratypes (FSCA) and two female paratypes (VMNH) collected by O. F. Cook, 27 November 1926, near the divide between Salinas and San Juan Bautista, San Benito County, California.

Diagnosis: With the characters of the genus and family; also characterized by the minute, leg-like anterior gonopods and by the three-branched ultimate podomere of the posterior
Figs. 1-3. Illacme plenipes holotype. 1, head, right antenna, and collum, dorsal view. 2, left anterior gonopod, medial view. 3, posterior gonopods, caudal view. Setaion omitted from all illustrations of the head. Scale line for fig. 1 = 0.50 mm; line for figs. 2-3 = 0.25 mm.
gonopods (Figs. 1-3).

Ecology: According to Cook & Loomis (1928) numerous specimens were discovered under a "rather large stone" in a valley with oak trees.

Remarks: Illacme plenipes has not been recollected and is known only from the original colony of type specimens: The present illustrations are the first for the genus and species, and the crossing of the ultimate podomeres of the posterior gonopods may be an artifact of the dissection. Both pairs of gonopods are extremely small, even smaller than the dissecting pin, and I could not determine the in situ configuration of the posterior pair, which extends anteriad between the anterior appendages. As noted by Hopkin and Read (1992), I. plenipes enjoys the distinction of being the millipede with the most segments (192) and legs (750 total, 375 pairs), these numbers being slightly higher than those for Siphonophora millepeda Loomis, from Tobago, which has 190 segments (Loomis 1934) and, if I calculated correctly, 742 legs (371 pairs). Accordingly, I. plenipes also has the most legs and segments of any known myriapod and arthropod, the centipede with the most legs and segments being Gonibregmatus plurimipes Chamberlin (1920) (Geophilomorpha: Gonibregmatidae), from the Fiji Islands, with 191 segments and leg pairs (382 legs total). Illacme plenipes has one more segment than G. plurimipes, but these are dissegmental representing fusion of alternate embryonic somites; I. plenipes therefore has 384 metameres, as opposed to 191 for the chilopod. For the benefit of future students I quote Cook & Loomis' (1928) concluding observation of I. plenipes: "The living animals were nearly white, moved very slowly, and rolled themselves into regular, close spiral coils when disturbed, the coils with three or four turns."

Family Siphonophoridae

Genus Siphonacme Cook & Loomis


Type species: Of Siphonacme, Siphonacme lyttoni Cook & Loomis, 1928, by original designation; of Californizonium, Siphonophora pseustes Chamberlin, 1923, by monotypy.

Diagnosis: Anterior gonopods with five podomeres, ultimate and penultimate articles fused; posterior gonopods entire.

Distribution: Yavapai and Cochise counties, Arizona, to central coastal Sonora, Mexico.

Species: Two.

Remarks: Cook & Loomis (1928) correctly observed that the distal article of the anterior gonopod is nearly straight, "as long or longer than the combined lengths of the preceding podomeres." Other ostensibly diagnostic characters of Siphonacme - the relatively short, slender, abrupt rostrum and the slender posterior gonopod with the distal article as long or longer than the preceding articles combined - are either illusory or applicable also to the Texas species, currently assigned to Siphonophora. The rostrum is proportionately equivalent in all New World siphonophorids that I have examined, extending to the level of the 6th antennomere. As Californizonium was erected specifically for Siphonophora pseustes, it falls as a synonym of Siphonacme, the third oldest siphonophorid genus-group name in the Western Hemisphere behind Siphonophora Brandt, 1837, and Siphonocybe Pocock, 1903, erected for species in Puerto Rico and Trinidad, respectively. Siphonacme is thus the oldest generic name for continental forms and, if distinct from Siphonophora and Siphonocybe, could have numerous synonyms.
Figs. 4-7. Siphonacme spp. 4-6. S. lyttoni holotype. 4, head, antennae, and collum, dorsal view. 5, right anterior gonopod, medial view. 6, posterior gonopods, caudal view. 7, S. pseustes holotype, head, antennae, and collum, dorsal view. Scale lines for figs. 4 and 7 = 0.50 mm; line for figs. 5-6 = 0.25 mm.
Siphonacme lyttoni Cook & Loomis

Figs. 4-6


Type specimens: Male holotype (NMNH) and three female paratypes (VMNH) collected by H. F. & E. M. Loomis, 1 March 1925, at the summit between Superior & Miami, probably along US highway 60, ca. 1.25 mi (2.0 km) N Gila/Pinal County line, Arizona; one male and two female paratypes (FSCA) collected at same site by L. R. Lytton and O. F. Cook, 27 November 1924.

Diagnosis: Collum and tergites relatively narrow, only slightly wider than head (Fig. 4).

Ecology: The type specimens were encountered under large stones on loose soil in an open area without vegetation (Cook & Loomis 1928).

Remarks: The number of segments varies greatly. According to Cook and Loomis (1928) males possessed from 78-108 segments, while female segment numbers varied from 88-121. The present gonopod illustrations (Figs. 5-6) are the first for S. lyttoni, and two or more congeneric species could occur in Arizona.

Siphonacme pseustes (Chamberlin)

Fig. 7

Siphonophora pseustes Chamberlin, 1923: 400, 402, figs. 30-33.

Type specimen: Male holotype (CAS) collected by J. C. Chamberlin, 7 July 1921, along San Pedro Bay on the Gulf of California, ca. 68.7 mi (110 km) SSW Hermosillo and 21.8 mi (35 km) NW Guaymas, Sonora, Mexico.

Diagnosis: Collum and tergites relatively broad, much wider than head (Fig. 7).

Remarks: According to Chamberlin (1923), the holotype possesses 124 segments. The gonopods have been dissected and are lost, so we must rely on Chamberlin's illustration (1923, fig. 33) of the anterior gonopod for specific details. The drawing is at low magnification (75x) but does show the same general podomere configuration as S. lyttoni, particularly the fusion of the distal two articles, and confirms that pseustes and lyttoni are congeneric. I directly compared the types, and they differ in body proportions, the tergites of S. pseustes being much broader relative to the head. Its rostrum and antennae are not slightly longer, nor is the first segment more emarginate, these being other distinctions cited by Cook & Loomis (1928). Because of the dramatic difference in body proportions, I recognize both forms at the specific level.

Siphonacme sp.

To fully detail the known generic distribution in the United States, I report below all additional samples of Siphonacme, which are plotted on the map (Fig. 14). The Prescott and Chiricahua Mountains literature records of S. lyttoni (Loomis 1936) also are plotted here, but the latter is supplanted by the definite records from Cochise County, the first of which was discovered under damp boards near a building. These literature records were not based on a comparison of gonopods with the type of S. lyttoni, the only sure way to render a determination.
Figs. 8-13. *Siphonophora* spp. 8-10, *S. limitare* holotype. 8, head, antennae, and collum, dorsal view. 9, right anterior gonopod, medial view. 10, posterior gonopods, caudal view. 11-13, *S. texascens*, topotypical male from Kerr County, Texas. 11, head, antennae, and collum, dorsal view. 12, left anterior gonopod, medial view. 13, posterior gonopods, caudal view. Scale lines for figs. 8 and 11 = 0.50 mm; line for figs. 9-10 and 12-13 = 0.25 mm.

Genus Siphonophora Brandt


Type species: Siphonophora portoricensis Brandt, 1937, by monotypy.

Diagnosis: Anterior gonopods with six podomeres, ultimate and penultimate articles separate; posterior gonopods entire or apically bifurcate.

Distribution: Central Texas to southern Nuevo León and Tamaulipas, Mexico.

Species: Two are recognized in the United States; others may exist among the unidentified specimens.

Remarks: The oldest genus-group name in the order and family, Siphonophora may have numerous synonyms among the nine names that are available for New World forms. The generic synonymy provides the original citation of Brandt (1837) and all those for the area of study. In lieu of erecting a new genus, I accept the current generic assignment of Siphonophora for the two Texas species, because the gonopod differences with the Arizona/Sonora species are considered significant at the generic level. Almost surely, the Texas species are not congeneric with S. portoricensis, in which the distal three podomeres of the anterior gonopods are fused (Shelley 1995), and the diagnosis presented here is for the generic category that covers the Texas species and not for Siphonophora. Proposing new genera is inadvisable under present knowledge of the family, and the Texas species may be referable to another established genus like Linzonion Attems (1951), which was established for Siphonophora mexicana Humbert & Saussure, in Vera Cruz, Mexico, and reasonably proximate to south Texas. Other proximate genera are Yucataniun and Guatemaliun, both proposed by Verhoeff (1941), for forms in the Yucatan Peninsula of Mexico and Guatemala, respectively.

Siphonophora limitare Loomis

Figs. 8-10


Type specimen: Male holotype (NMNH) collected by H. S. Barber on an unknown date in Brownsville, Cameron County, Texas. According to Loomis (1936) one additional male and three females were collected along with the holotype; their location is unknown.

Diagnosis: Ultimate podomere of anterior gonopod apically rounded and relatively narrow, about half as wide as base of article; ultimate podomere of posterior gonopod entire (Figs. 8-10).

Distribution: Known definitely from Kendall and Cameron counties. Data for the former sample, designated as paratypes of S. texascolens, are as follows: Kendall Co., exact location unknown, M, 3F, December 1939, S. & D. Mulaik (NMNH).

Remarks: According to Loomis (1936), segment number varies from 68-78 in males and 44-63 in females.
**Siphonophora texascogens** Chamberlin & Mulaik

Figs. 11-13


Type specimens: Male holotype and female allotype (NMNH) collected by S. & D. Mulaik, on an unknown date in August 1939, at Raven Ranch, ca. 12 mi (19.2 km) S Kerrville, off TX hwy. 173 north of Camp Verde, Kerr County, Texas; one male and three female paratypes (NMNH) taken by same collectors on an unknown date in December 1939 at an unknown site in Kendall County. The holotype is in poor condition, as the internal viscera on the anteriormost legs and segments, including the gonopods, have shrunk and detached from the exoskeleton. Dissection is thus impossible because the gonopods consist solely of fragile exoskeleton that is easily distorted and torn. I broke off a piece of sternite that holds the anterior gonopods but could not be certain of the apical configuration. The only available male paratype, from Kendall County, is a specimen of *S. limitare*, but the gonopods of a topotypical male from Kerr County exhibit a different configuration. I therefore exercise the right of first reviser and assign the name *texascolens* to this form.

Diagnosis: Ultimate podomere of anterior gonopod apically flat and broad, nearly as wide distally as basally; ultimate podomere of posterior gonopod distally bifid (Figs. 11-13).

Remarks: The male topotype possesses 90 segments. The records from Bandera County (Chamberlin & Mulaik 1941) and Laguna Madre, Cameron County (Chamberlin 1946), are not based on gonopod comparisons and are plotted as unknown species in figure 14.

*Siphonophora sp.*

To fully detail the known generic distribution in the United States and northern Mexico, I report below all additional, unidentified samples of *Siphonophora*, which are plotted on figure 1. Most samples from the United States are from caves, which are attractive to surface organisms because their cool, moist environments contrast markedly with the surface heat and aridity of Texas. Siphonophorids may be expected in most Texas caves between Coryell County and the Rio Grande; the precise locations of those in Bell, Bexar, Coryell, Llano, Travis, and Williamson counties are unknown.

Undetermined Siphonophoridae

To completely detail distributions in the United States, I record here two unidentifiable samples that are not proximate to a described species; generic assignment is unknown.


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**LITERATURE CITED**


Shelley: Siphonophorida


ADDENDUM

As the manuscript was going to press, I discovered a sample of siphonophorids from Baja California Sur among unsorted material at the Essig Museum of Entomology, University of California at Berkley, which definitely establishes the order and family from this part of Mexico. The sites are incorporated into the map (fig. 14); collection data are as follows:

**MEXICO**: Baja California Sur: *Sierra Laguna*, ca. 17 mi (27.2 km) ENE Todos Santos, 3M, 2F, 2 juveniles, 12-18 December 1979, C. E. Griswold, J. T. Doyen, W. Tschinkel.

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