REVIEW OF THE CLAM SHRIMP FAMILY LYNCEIDAE STEBBING, 1902 (BRANCHIOPODA: CONCHOSTRACA), IN THE AMERICAS

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ABSTRACT

The North, South, and Central American species of the Lynceidae Stebbing are reviewed. Morphological characters that distinguish the family, including several not previously known or not recognized as being of familial importance, are illustrated and discussed. Of the three known genera in the family, only two, *Lynceus* Müller and *Paralimnetis* Gurney, are known from North, Central, and South America; the genus *Lynceiopsis* Daday, known only from Africa, is described and discussed for comparative purposes. Taxonomic characters that can be reliably used to identify American species are primarily those of the male first thoracopods (claspers) and head region (rostrum). All American species are redescribed, with two exceptions. The validity of two species, *Lynceus tropicus* and *L. rotundirostris*, is questioned on the basis of the poor condition of type material and inadequate original descriptions. One new species of *Paralimnetis* Gurney is described from Texas. A key to the American species is included.

Among the extant conchostracan families, the family Lynceidae Stebbing, 1902, containing *Lynceus, Lynceiopsis,* and *Paralimnetis,* is unique in several respects. Whereas all other clam shrimps have a variable number of growth lines on the valves of the carapace and a well-developed caudal furca (=cercopods; see Bowman, 1971; Schminke, 1976), lynceids have a smooth carapace lacking growth lines (with the possible exception of an undescribed Siberian form illustrated by Linder, 1945) and the telson is greatly reduced with no furca or dorsal abdominal spines. In addition, males have only the first pair of legs modified as subchelate claspers (although the second pair may be modified to various degrees in *Lynceiopsis* and *Paralimnetis*), whereas all other conchostracans except the monotypic Cyclestheriidae have the first two pairs of the male so modified (Belk, 1982). Several authors (e.g., Tasch, 1969; Pennak, 1978; Kaestner, 1970) have noted that the head is not entirely covered by the carapace, but this is not true for all members of the family (see Martin *et al.,* 1986, and Fig. 1*b*). The family has been the source of much taxonomic confusion. The name Lynceidae and the genus *Lynceus* have been applied in the past to certain cladocerans (e.g., see Rathbun, 1905), and the clam shrimps that now belong to *Lynceus* were treated as *Limnetis* for many years (see discussion in Mattox, 1959).

The genus *Lynceus* Müller, 1776, is known from ephemeral ponds or streams and occasionally lakes throughout most of North America, Europe, and Asia (Tasch, 1969; Mattox, 1957, 1959; Straškraba, 1965). Belk (1982) noted that species occur on all continents except Antarctica. The exact number of species is unknown, and it is likely that some of the 31 species listed in Table 1 will be synonymized. Daday (1927) listed 15 species of *Lynceus* in his monograph of the Conchostraca, but it is unclear to what extent intraspecific variation may account for differences among his supposed species. Since Daday's paper, new species have been described from India (Gurney, 1930; Royan and Alfred, 1971; Battish, 1981), Madagascar (Gauthier, 1936), Arabia (Harding, 1941), and Europe (Botnariuc, 1947) (see Table 1). For North America, Packard (1883) listed four species (as the genus *Limnetis* Lovén): *L. brachyurus* Müller (as *L. gouldii* Baird), *L. mucronatus* (Packard), *L. brevifrons* (Packard), and *L. gracilicornis* (Packard). Unfortunately, many of the characters employed by Packard (1883) (and also Daday, 1927) appear to be variable. An additional problem is that Packard apparently was not careful in his written descriptions of the species, and often produced illustrations inconsistent with his verbal accounts. Lynch (1964), in a vitriolic attack on Packard's monograph, stated that ". . . responsibility for the confusions must be attributed to A. S. Packard, whose descriptions are not only deficient in requisite taxonomic

Table 1. Known species of the conchostracan family Lynceidae[1].* = occurs in the Americas.

Species	Range	Source
Lynceus aequatorialis Daday, 1927*[2]	Venezuela	Daday, 1927
L. andronachensis Botnariuc, 1947	Romania	Šrámek-Hušek *et al.*, 1962
L. bicarinatus Barnard, 1924	Namibia	Barnard, 1924
L. biformis (Ishikawa, 1895)	Japan	Ishikawa, 1895
L. bouvieri Daday, 1927[2]	eastern Africa	Daday, 1927
L. brachyurus Müller, 1776*	Holarctic	Straškraba, 1965
L. brevifrons (Packard, 1877)*	North America	Mattox, 1959
L. caecus (Joseph, 1882)[3]	northern Yugoslavia	Daday, 1927
L. dauricus Thiele, 1907	southern Russia, Mongolia	Daday, 1927; Brtek *et al.*, 1984
L. decaryi Gauthier, 1936	Madagascar	Gauthier, 1936
L. denticulatus Gurney, 1930	southern India	Gurney, 1930
L. dovei Daday 1927[2]	Madagascar	Daday, 1927
L. gracilicornis (Packard, 1871)*	North America	Martin *et al.*, 1986
L. indicus Daday, 1927[2]	eastern India	Daday, 1927
L. jeanneli Daday, 1913b	eastern Africa	Daday, 1913b
L. lobatsianus Barnard, 1929	Botswana	Barnard, 1929
L. macleayanus (King, 1855)	Australia	Daday, 1927
L. mandsuricus Daday, 1927[2]	Manchuria, China	Daday, 1927
L. massaicus Thiele, 1907	eastern Africa	Daday, 1927
L. mucronatus (Packard, 1875)*	North America	Packard, 1875
L. pachydactylus Barnard, 1929	South Africa	Barnard, 1929
L. rotundirostris (Daday, 1902)*	Patagonia	Daday, 1927
L. rotundus Thiele, 1907	Madagascar	Daday, 1927
L. serratus Royan and Alfred, 1971	southern India	Royan and Alfred, 1971
L. simiaefacies Harding, 1941	southwest Arabia	Harding, 1941
L. tatei (Brady, 1886)	Australia	Daday, 1927
L. triangularis Daday, 1927[4]	South Africa	Daday, 1927
L. tropicus Daday, 1927*[2]	Venezuela	Daday, 1927
L. truncatus Barnard, 1924	Namibia	Barnard, 1929
L. vasishti Battish, 1981	Punjab, India	Battish, 1981
L. wahlbergii (Lovén, 1847)[5]	central Africa	Daday, 1927
Lynceiopsis perrieri Daday, 1912a	western Africa	Daday, 1927
Lynceiopsis sanctijohanni Thiery, 1986[6]	Chad, Africa	Thiery, 1986
Paralimnetis rapax Gurney, 1931*	Paraguay	Gurney, 1931
Paralimnetis mapimi Maeda-Martinez, 1987*	Mexico	Maeda-Martinez, 1987
Paralimnetis texana, new species*	Texas	This study

[1] Many names no longer in use can be found in the synonymy of *L. brachyurus*. Additionally, *Lynceus eremia* Spencer and Hall is a junior synonym of *L. tatei*, and *Lynceus madagascariensis* Thiele is a junior synonym of *L. rotundus* (Ján Brtek, personal communication). To our knowledge, this completes the list of all previously used names in the family.
[2] Name originally used in 1913 (Daday, 1913c); the species were not described or illustrated until 1927 (see Forró and Brtek, 1984).
[3] Probably = *L. brachyurus*; see Daday, 1927.
[4] Listed as Wolf "in litteris" by Daday (1927). We agree with Forró and Brtek (1984) who, noting it was only a manuscript name in Wolf, believe authorship should go to Daday, who originally described and figured the species.
[5] Barnard (1929: 248) suggested this name will always be in doubt and should not be used.
[6] Originally as *L. sancti-johanni*; hyphen here removed according to Article 31(d)(i) of the International Code of Zoological Nomenclature, third edition.

detail, but are so filled with errors, contradictions, and indeterminate data, that practically no statement or illustration can be accepted without verification by examination of specimens," and later, "His monograph, indeed, provides almost perfect examples of all the errors, obscurities, and insufficiencies to be avoided in zoological taxonomy. . . ." A second problem involves the deposition of type material. Packard left no type series for any conchostracans (or for many other taxa as well), and according to Geiser (1933) the type locality listed by Packard often was incorrect. Adding to the confusion is the fact that Eugene Daday, a prolific writer who described over 400 new crustacean taxa (see Forró, 1982; Forró and Brtek, 1984), frequently described the same species as "new" in different journals and in different years. Because of these deficiencies, many of the popular works that deal with fresh-water American crustaceans (e.g., Mattox, 1959; Pennak, 1978; Fitzpatrick, 1983) contain erroneous information regarding the species of *Lynceus* and other clam shrimp.

The genus *Lynceiopsis* was described by Daday (1912a, see also 1927) to accom-

modate *Lynceiopsis perrieri* from West Africa. The distinguishing character of *Lynceiopsis* is the modified and enlarged second male thoracopod. To the best of our knowledge, the type species has not been reported subsequently, although a second species of *Lynceiopsis* has now been described from Chad, Central Africa (Thiery, 1986). The genus is not known to occur in the Americas, but is included here for comparative purposes.

Gurney (1931), apparently unaware that Daday had recognized *Lynceus* Müller as the senior synonym of *Limnetis* Lovén, and also unaware that Daday (1912a, b, 1927) had established the new genus *Lynceiopsis,* erected the genus *Paralimnetis* to contain an unusual species from South America, a species that like *Lynceiopsis perrieri* Daday has an enlarged and modified second male thoracopod. Gurney's new species, *Paralimnetis rapax,* has never since been collected; a second species, *P. mapimi,* has recently been reported from Mexico (Maeda-Martinez, 1987) and we describe a third species herein.

Despite the fact that many characters employed by early workers for separating members of the Lynceidae have proven to be variable and taxonomically unreliable, the species in the Americas can be recognized easily. Of primary importance in identification is the morphology of the male first thoracopod. The present paper reviews the species of the family Lynceidae known from the Americas. In addition to redescribing distinguishing characters of the male first thoracopod and head region, we comment on morphological variability, geographic range, and natural history where known. One new species of *Paralimnetis* Gurney is described from North America (Texas).

Materials and Methods

Lynceid conchostracans were examined from most of the known collecting localities in the United States, Mexico, and Canada. Additional specimens were loaned by the following persons or institutions: Dr. Geoffrey Boxshall, British Museum of Natural History (*Paralimnetis rapax*); Dr. László Forró, Hungarian Museum of Natural History (*Lynceiopsis perrieri* and *Lynceus rotundirostris*); Dr. Jacques Forrest, National Museum of Natural History, Paris (*Lynceus tropicus*); Mr. Guido Pereira, University of Maryland (*Lynceus aequatorialis*). Although we attempted to consult all known published reports of the family, the synonymies are restricted to papers that include at least one of the following criteria: (1) descriptions or redescriptions of species, (2) taxonomic discussion, (3) name changes, (4) figures, and (5) keys to identification. Although females of all species were examined, we did not illustrate female characters because we feel that positive identification depends on examination of males. The abbreviation DB in brackets refers to the branchiopod collections of Dr. Denton Belk in San Antonio, Texas. All illustrations were made with the aid of a camera lucida attached to a Wild M-5 stereoscope. Measurements were made of valve length, height, and depth as defined by Saunders and Wu (1984). Specimens used for scanning electron microscopy (SEM) were prepared following procedures outlined by Felgenhauer (1987), but without postfixation in osmium tetroxide.

Results

General Morphology and Terminology

Several workers have commented on the unusual morphology of the family Lynceidae compared to that of other extant conchostracan families. In a recent redescription of *Lynceus gracilicornis* Packard, Martin *et al.* (1986) noted that some character states of that species may occur in all members of the family; this uncertainty stemmed from the few thorough descriptions existing for other members of the Lynceidae. After having examined members of all lynceid genera, we can now comment on and increase the known familial characters.

The carapace is globose, nearly circular in lateral view, and devoid of an umbo, growth lines, or (with one known exception) external ornamentation (Fig. 1*a*). The dorsal border is recessed into a deep longitudinal groove, within which is the hinge that joins the valves. Although the valves interlock, as in such truly bivalved animals as many ostracods, they are not entirely separate but are continuous (fused) for a short interval along the dorsal border (Fig. 2*a, b*). Often the posteroventral borders of the valves diverge, creating a slight flange (Fig. 2*c*). The head region, or rostrum, is large relative to the rest of the body (see Fig. 1*b, c*) and is inflated and filled with two anterior lobes of the hepatopancreas (Fig. 1*d*). A well-developed supportive marginal ridge, the fornix, is always present (Fig. 1*c, d*). The compound eyes are distinct but may be very close together. The midline of the head region has a simple or bifurcate dorsal rostral carina, which may extend to the anterior border of the head region or terminate just short of it. The posterior termination of this

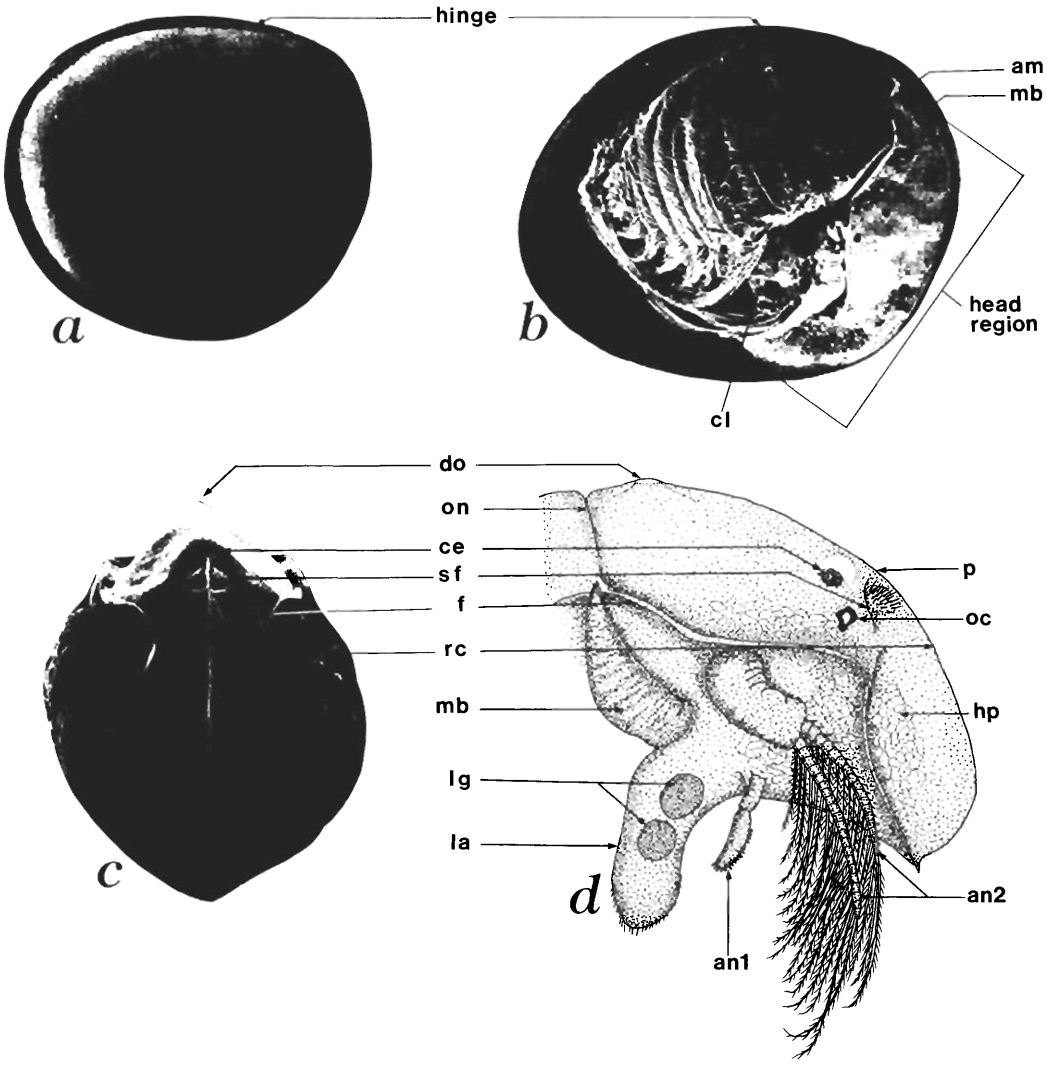


Fig. 1. External morphology of the Lynceidae. *a,* lateral view of right valve, *Lynceus aequatorialis,* ×40; *b,* lateral view of *Lynceus brachyurus* with right valve removed, ×33; *c,* frontal view of *L. aequatorialis* removed from shell, ×45; *d,* schematic illustration of head region (corresponding to bracketed area shown in *b*) of a typical lynceid, not drawn to scale. Abbreviations: am = adductor muscle; an1 = first antenna; an2 = second antenna; ce = compound eye; cl = male clasper; do = dorsal organ; f = fornix (supportive ridge); hp = lobes of hepatopancreas; la = labrum; lg = labral glands; mb = mandible; oc = ocellus (naupliar eye); on = occipital notch; p = frontal pore (see Fig. 2); rc = rostral carina; sf = setose field.

carina separates two distinct fields of simple setae, termed olfactory setae or sensory setae by various authors (Figs. 1*c, d,* 2*d, e,* see also Martin *et al.,* 1986). Between and slightly posterior to these fields of setae is a pore or pit (Fig. 2*d, e*) that apparently opens into a space just above the compound eyes; its function is not known. Posterior to this pore, and in the midline of the head region, is a small oval dorsal organ similar to that described for larval decapods by Barrientos and Laverack (1986). This organ in lynceids (Fig. 2*f, g*) differs from that seen in larval decapods in that there is no central pore, although there is a slight central elevation (Fig. 2*f,* central arrow), and there is no elevation or tubercle in the center of the peripheral bumps. The dorsal organ is located on a slight elevation of the head cuticle just anterior to the occipital notch (Fig. 1*c, d*). Below and slightly anterior to the setose fields is an internal "naupliar eye" or ocellus

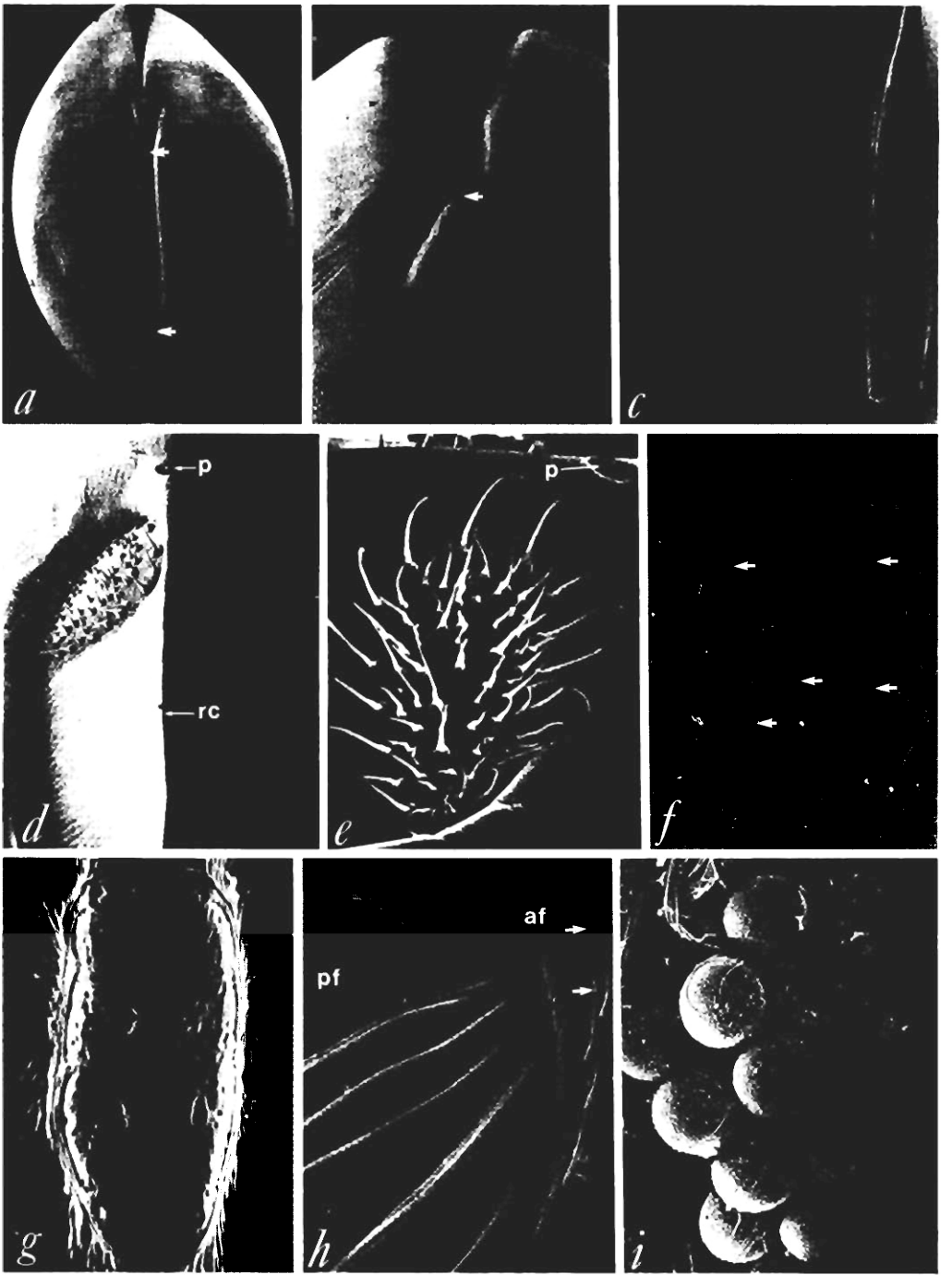


Fig. 2. Scanning electron microscopy (SEM) of selected lynceid familial characters. *a,* dorsal view of shell of *Lynceus gracilicornis*; valves are contiguous between arrows, ×30, anterior end uppermost; *b,* close-up of area corresponding to upper arrow in *a, L. gracilicornis,* ×110; *c,* posteroventral border of carapace of *Lynceiopsis perrieri* showing "flange" of valve and minutely toothed valve border, ×90; *d,* head region of female *L. gracilicornis* with frontal pore (p), rostral carina (rc), and paired setose fields, ×135; *e,* one of the setose fields shown in lateral view with rostral carina uppermost, p = frontal pore, ×175; *f,* dorsal organ of female *L. gracilicornis* with 5 small raised areas indicated by arrows (see text), ×950; *g,* dorsal organ of female *Paralimnetis mapimi,* ×650; *h,* second antenna of *L. gracilicornis* with spines of anterior flagellum (af) indicated by arrows, pf = posterior flagellum, ×200; *i,* eggs of *L. mucronatus,* ×160.

(Fig. 1*d*) that appears to be birefringent under light microscopy and has a central light-reflecting region; the shape and location of this structure vary within a species, and it is often not visible in preserved specimens.

The first antenna (Fig. 1*d*) is always small and two-segmented, with the distal segment oval and tipped with short setae of presumably olfactory function. The second antenna is large and natatory; the anterior flagellum bears short dorsal spines (Fig. 2*h*, arrows). Within the large labrum are two oval glands (Fig. 1*d*). The mandibles are large and serrate on the distal border (see Martin, 1988).

The thoracic appendages (thoracopods) of the Lynceidae are foliaceous, setose, and divided into an exopod, epipod, and endopod. The endopod is subdivided into several endites (Fig. 3*a*), which have been referred to in various ways by many authors. The proximal endite differs morphologically and functionally from the remaining endites and is often referred to as the coxal lobe; the other endites are numbered sequentially in a distal direction (e.g., Martin *et al.*, 1986). For simplicity we treat the endites equally, numbering all of them, including the coxal lobe, from proximal to distal (Fig. 3*a*). In females, the dorsal lobe of the exopod is elongated in thoracopods 9 and 10 and functions in retaining the egg mass. In the male, the first thoracopod is a large subchelate appendage that grasps the shell of the female during mating (Fig. 3*b*).

Derivation of the male clasper is uncertain. It appears that endite 3 has become greatly enlarged, with one of the other endites (endite 6) modified into a corresponding movable finger (Botnariuc, 1947; Fryer, 1987). Endites 4 and 5 are reduced to small palplike processes on the posterior-facing side of the enlarged endite 3 (Fig. 3*b*). In all species the posterior face of endite 3 bears few to many stout spines that may be serrate or otherwise modified and in some cases are species-specific. The movable finger of the clasper lies in a slight depression between rows of setae on the anterior face of endite 3 and the setae and stout spines on the posterior face of endite 3 (see Fig. 8*h*).

In *Paralimnetis* the immovable part of the clasper (endite 3) is larger relative to the head region than in *Lynceus*, and is swollen or globose (Fig. 3*c*). In both *Paralimnetis* and the African genus *Lynceiopsis* the second male thoracopod is also modified, but in a much different manner. In *Paralimnetis* the protopod is greatly enlarged and, opposite the endites of the endopod, bears a large hooked projection that we term the "protopodal complex" (Fig. 3*d*, *e*). The endopodal endites are unusual in that one of them, which we believe is a modified endite 6, terminates in a small distal hook, whereas another one (endite 5) is enlarged and sclerotized. Endite 4 is thick and subdivided into seven or eight sclerotized crenulations, each with a single distal seta. In *Lynceiopsis* the second thoracopod terminates in a large, thick, lobed process that may be the result of the fusion of endites 4 and 5 (Fig. 3*f*). Under light microscopy the distal lobe appears to bear small circular depressions that must be subcuticular because they can not be seen under SEM (Fig. 15*f*).

In all lynceids the terminal pair of trunk appendages is modified ventrally as a subanal plate (the opercular lamellae) that extends backward beneath the telson. In females, an extension of the posterolateral trunk somites, termed the lamina abdominalis or dorsal lamina, protrudes laterally to hold the egg mass; the shape of this extension is apparently species-specific. Both of the above characters have been used in previous taxonomic treatments of the family.

The eggs are always spherical with a smooth or slightly granulate outer shell (Fig. 2*i*); they are never highly sculptured as in some other clam shrimp families (e.g., Limnadiidae).

Systematic Account

Family Lynceidae Stebbing, 1902

Conchostraca with large, smooth, globose carapace, its valves lacking growth lines and an umbo, and both joined in elongate dorsal depression. Head region bearing distinct fornix, sharp longitudinal "rostral" carina and paired setose fields just anterior to compound eyes; rostral carina bearing small median pore between paired oval setose fields. Hepatopancreas extending into head region and into proximal part of large labrum; labrum with 2 internal oval glandular bodies. Mandibles robust and obviously serrate. Second maxilla reduced or absent. First thoracopods in male modified as prehensile

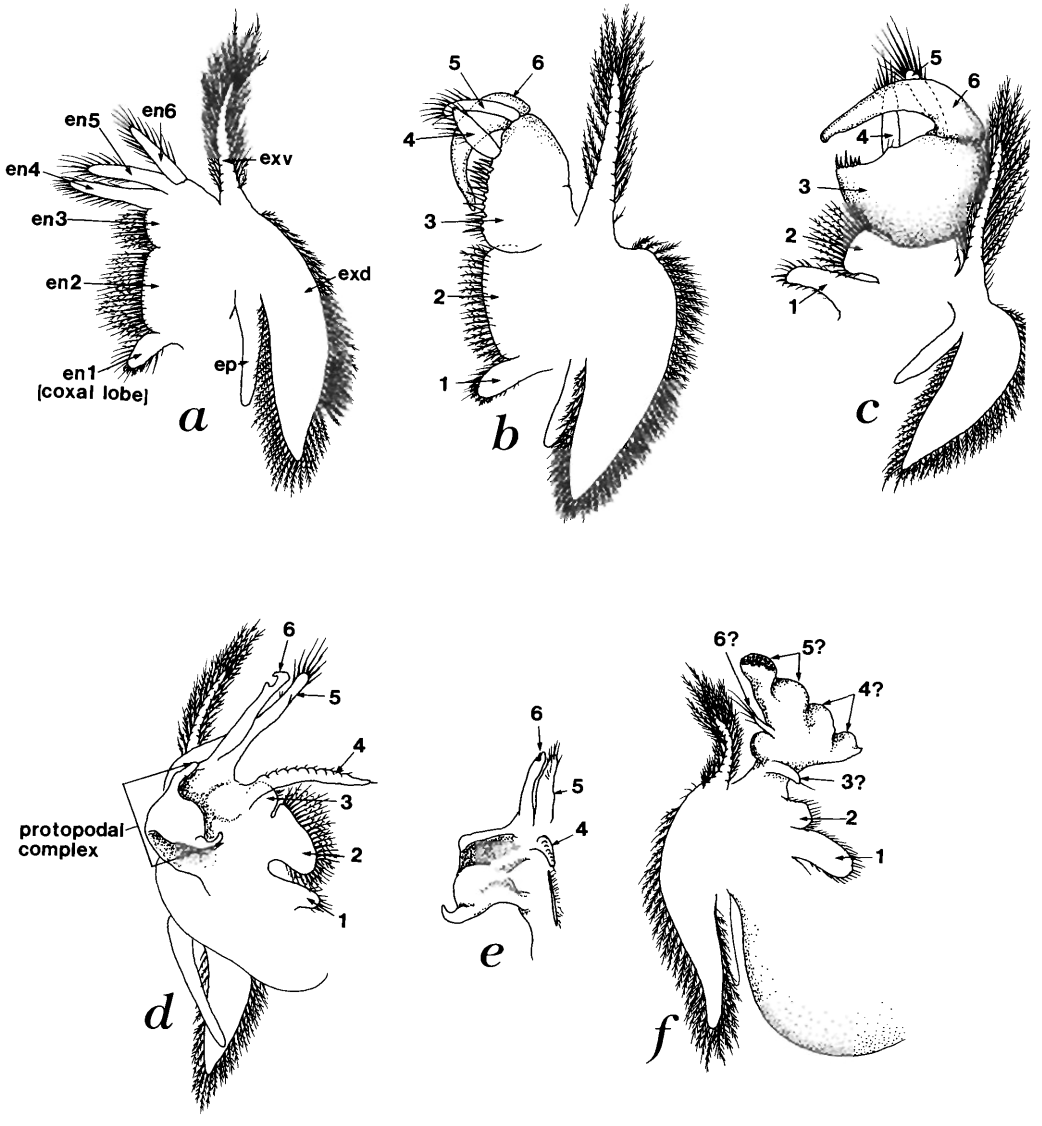


Fig. 3. Lynceid thoracopod morphology. *a,* typical thoracopod with endites (en) numbered and with epipod and exopod marked; *b,* typical male first thoracopod in *Lynceus*; note flattened endite 3; *c,* typical male thoracopod in *Paralimnetis*; note swollen endite 3 and reduced basal endites; *d,* strongly modified male second thoracopod of *Paralimnetis* with protopodal complex bracketed; *e,* same thoracopod as in *d* but turned 90°; *f,* male second thoracopod of *Lynceiopsis perrieri,* endite numbering uncertain. Abbreviations: ep = epipod; exv = ventral lobe of exopod; exd = dorsal lobe of exopod; labels in *a* apply to all other figures as well. Arabic numerals in *b–f* refer to endites (en) as marked in *a.*

subchelate claspers, second pair usually unmodified (*Lynceus*; the exception is *L. aequatorialis*) or enlarged and greatly modified (*Paralimnetis* and *Lynceiopsis*) but never terminating in subchelate clasper. Anal segment reduced, with delicate telsonal filaments but no caudal furca. Dorsolateral area of posterior segments lacking spiniform protuberances. Penultimate segment with appendages modified to form ventral flat opercular lamellae that extend posteriorly beneath anal somite. Female with posterolateral lamina for holding egg mass. Vas deferens in male extending through anal segment and opening on either side of anus [according to Linder (1945); Sars (1896) believed that the external male openings were in the same location as in females (base of

thoracopod 11)]. Eggs spherical, outer shell smooth or slightly granulate, never highly sculptured.

Genera: *Lynceus* Müller, 1776; *Lynceiopsis* Daday, 1912; *Paralimnetis* Gurney, 1931.

Key to Males of Genera and Species of the Family Lynceidae in the Americas

(*Lynceus rotundirostris* and *L. tropicus*, for which males are undescribed, are not included.)

1. Second male thoracopod unmodified and similar to posterior thoracopods or, if modified (*L. aequatorialis*), without a protopodal complex on either right or left appendage (see Fig. 3) and lacking small hook on tip of endite 6; rostral carina entire, not bifurcate at level of frontal constriction of head region ..... (*Lynceus*) 2
– Second male thoracopod obviously modified, with a protopodal complex on either right or left appendage (never both) and with small hook on tip of endite 6 on either right or left appendage; rostral carina bifurcate at about level of frontal constriction of head region ..... (*Paralimnetis*) 6
2. Male right and left claspers approximately equal in size and shape 3
– Male right and left claspers strongly dimorphic 5
3. Male rostrum truncate in lateral view and with minute setae on concave distal surface; movable finger (endite 6) of male clasper much shorter than immovable finger, not reaching to distal end; distal palp (endite 5) of clasper twice length of proximal palp (endite 4) ... *Lynceus brevifrons*
– Male rostrum not truncate in lateral view, lacking minute setae on distal rostral border; movable finger of male clasper equal in length or exceeding length of immovable finger; distal palp (endite 5) of clasper less than twice length of proximal palp (endite 4) 4
4. Male clasper with small spinelike process extending distally from immovable finger at base of movable finger and with small, smooth bump on outer border of movable finger; last abdominal appendage of male with obvious stout upturned hooklike process .... *Lynceus mucronatus*
– Male clasper without spinelike process extending distally from immovable finger; outer border of movable finger smoothly curving, lacking bump; last abdominal appendage of male similar to preceding ones, without upturned hooklike process ..... *Lynceus brachyurus*
5. Major clasper with large "backward" directed process approximately equal in size and length to distal part of movable finger; second male thoracopod modified, unlike posterior ones .. .. *Lynceus aequatorialis*
– Major clasper lacking "backward" directed projection; second male thoracopod similar to posterior ones ..... *Lynceus gracilicornis*
6. Movable finger of major clasper lacking protrusion on outer surface; male minor second thoracopod (without protopodal complex) without hook on tip of endite 6 ..... *Paralimnetis rapax*
– Movable finger of major clasper with distinct outward protrusion at about level of proximal endite; male second thoracopod with hook on tip of endite 6 on right and left sides 7
7. Movable finger of major clasper with smooth, small outward protrusion at about level of distal palp (endite 5) ..... *Paralimnetis mapimi*
– Movable finger of major clasper with large, sharp outward protrusion at about level of distal palp (endite 5) ..... *Paralimnetis texana*

Genus *Lynceus* Müller, 1776

Second male thoracopod similar to posterior ones or, if modified (*L. aequatorialis*), never with hooklike process on protopodite (protopodal complex; see *Paralimnetis*) or large distal lobed process (see *Lynceiopsis*). Rostral carina usually entire, i.e., without bifurcating; rarely bifurcate (never in any American species).

Lynceus brachyurus Müller, 1776
Figs. 4, 6*a–c*

Lynceus brachyurus Müller, 1776: 2392.—Müller, 1785: 69, pl. 8, figs. 1–12.—Daday, 1927: 8 (594), figs. 147a–o, 148a–s, 149a–r, 150a–z, 151a–p.—Pratt, 1935: 378 (key), fig. 510.—Mattox, 1939: 645, pl. 5.—Mattox, 1957: 367, fig. 11.—Mattox, 1959: 580 (key), fig. 26.3.—Straškraba, 1962: 169 (key), 170.—Straškraba, 1965: 205, figs. 1–3.—Pennak, 1978: 344 (key), figs. 228, 229C, 234D, 243A, 243B.—Saunders and Wu, 1984: 6–8, figs. 4–6, 23 (map).

Hedessa Sieboldi.—Liévin, 1848: 4.

Hedessa brachyura.—Siebold, 1849: 198 (as cited by Daday, 1927; we have not been able to locate this reference).

Limnetis brachyurus.—Grube, 1853: 73, pl. 5–7.—Sars, 1896: 117, pl. 18, figs. 1–8, pl. 19, figs. 1–16, pl. 20, figs. 1–19.

Limnetis brachyura.—Lilljeborg, 1877: 18.

Limnetis gouldii.—Baird, 1862: 149, pl. 15, figs. 7a–c.—Packard, 1877: 173, fig. 11d.—Packard, 1883: 298 (key), 299, figs. 1, 3d, pl. 2, figs. 1–6, pl. 26, figs. 4, 4a, b, pl. 29, fig. 9.—Dodds, 1915: 276, fig. 19.—Pearse, 1918: 672 (key).

Limnetis zichyi.—Daday, 1901: 435, pl. 18, figs. 11–15, pl. 19, figs. 1–9.

Lynceus acutirostris.—Daday, 1912b: 726 (nomen nudum).

Lynceus acanthorhynchus.—Bowkiewicz, 1923: 1, pl. 1, figs. 1–7.

Lynceus brachiurus var. *Zichyi.*—Botnariuc, 1947: 92, figs. 4a, 19 (larva), pl. 8.

Material Examined.—[DB 233], Coconino County, Arizona, natural soil depression pond named Lake #1 in Sitgreaves National Forest, about 56.4 km east of Payson on south side of Az 260, collected by D. Belk, 4 June 1974; [DB 373], Czechoslovakia, Kralovsky Chlmec, southeast Slovakia, collected by J. Brtek, 3 June 1970; [DB 157], Coconino County, Arizona, Crane

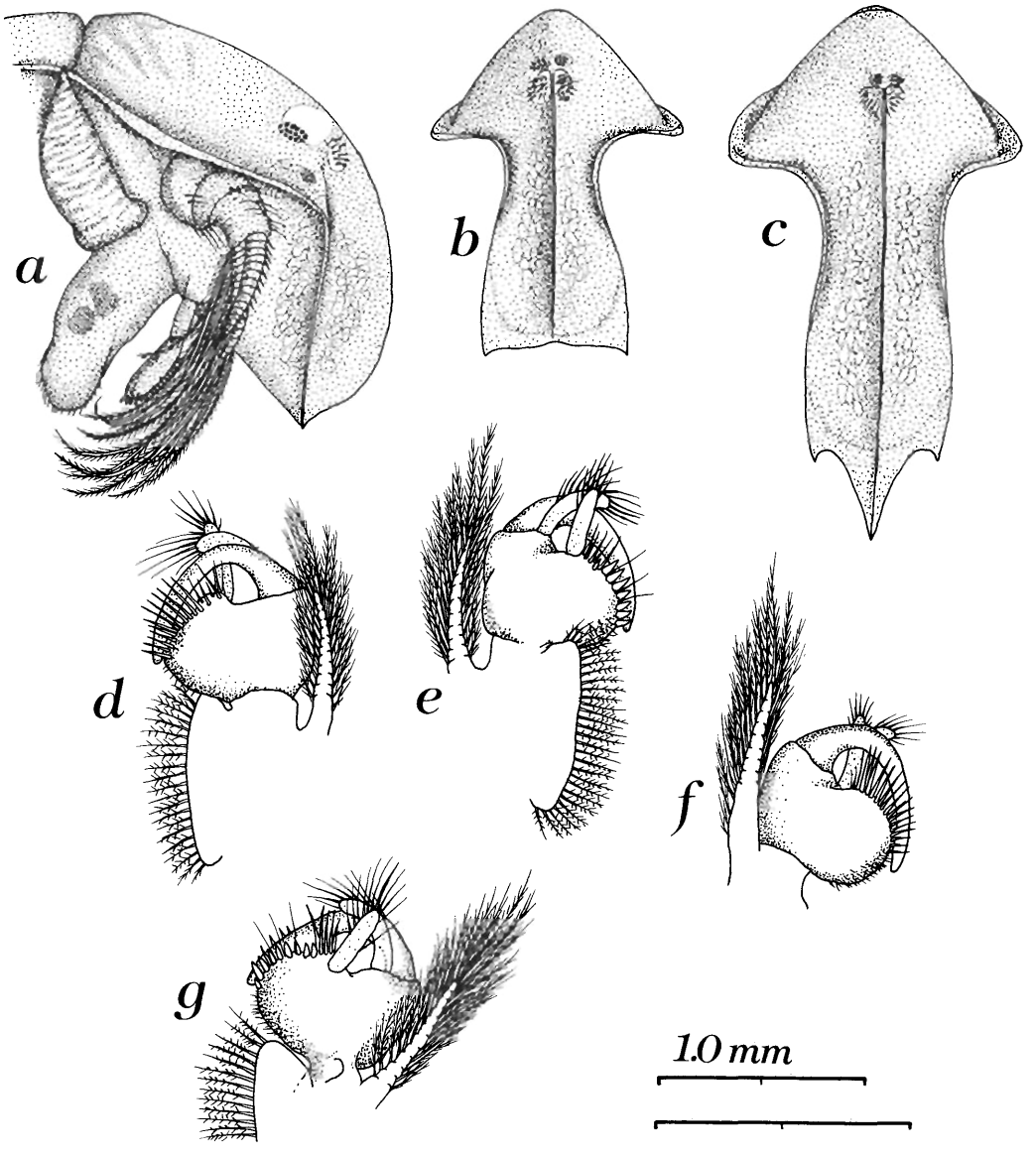


Fig. 4. *Lynceus brachyurus* Müller. *a,* lateral view of head region, male; *b,* frontal view of head region, male; *c,* frontal view of head region, female; *d,* anterior face of right first thoracopod (clasper); *e,* posterior face of same; *f,* anterior face of left clasper; *g,* posterior face of same. Upper scale bar applies to *a–c,* lower bar to *d–g.*

Lake on east side of Az 67, 26.6 km south of Jacob Lake, Kaibab National Forest, collected by D. Belk, 10 June 1973; [DB 172], Coconino County, Arizona, centermost of Three Lakes lakes in Jacob Lake section of Kaibab National Forest, collected by D. Belk, 14 June 1973; [DB 732], Clearwater County, Minnesota, small pond at Lake Itasca Biological Station (University of Minnesota), near the old ice house, Itasca State Park, collected by G. A. Cole, 21 July 1966.

Type locality.—Unknown.

Measurements.—Variable, usually 2–4 mm. Straškraba (1965) gave a range of 2.2–4.0 mm (females) and 1.5–2.5 mm (males), depending on locality of the population (Blatna versus southern Slovakia, Czechoslovakia). In North America, Saunders and Wu (1984) gave the following measurements: females, 2.4–3.0 mm length, 2.1–2.7 mm height; males, 2.3–4.9 mm length, 2.0–4.3 mm height. Retallack and Clifford (1980) recorded lengths up to 4.1 mm in Canada.

Description.—Male rostrum variable, usually truncate in frontal view, with anterolateral corners often slightly produced and with median frontal indentation (Figs. 4*a,*

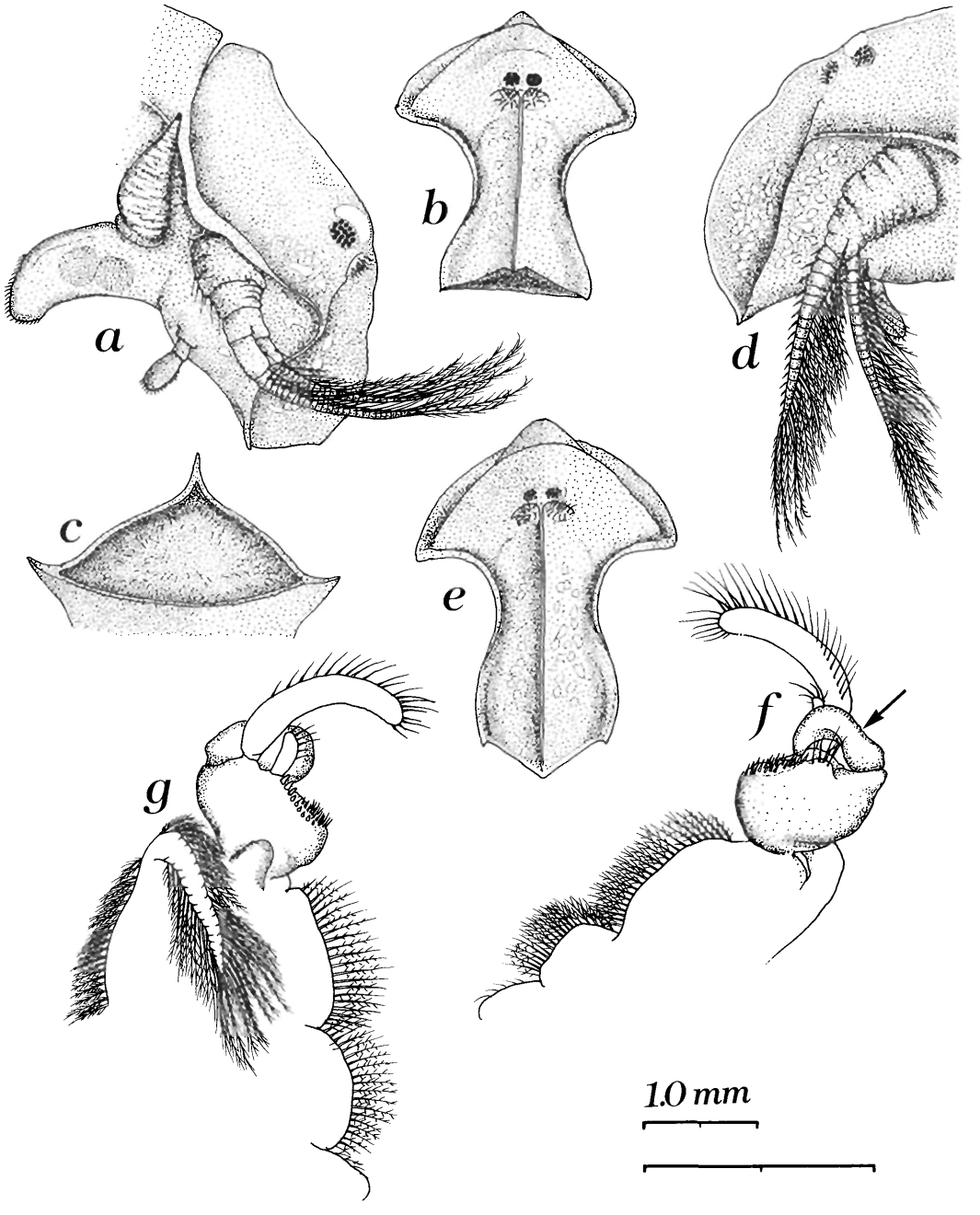


Fig. 5. *Lynceus brevifrons* (Packard). *a,* lateral view of head region, male; *b,* frontal view of head region, male; *c,* ventral view of distal tip of head region, male; *d,* lateral view of head region, female; *e,* frontal view of head region, female; *f,* anterior face of male clasper, arrow indicates movable finger (endite 6); *g,* posterior face of same. Upper scale bar applies to *a–e*; lower bar applies to *f, g.*

b, 6*a*), rarely tridentate with center projection long and acute and thus similar to female (see also Valtonen, 1966). Female rostrum with acute anterolateral borders and acute medial projection giving rostrum a tridentate appearance (Figs. 4*c,* 6*b*). Both male and female rostrum with border of short fringing setae best observed under

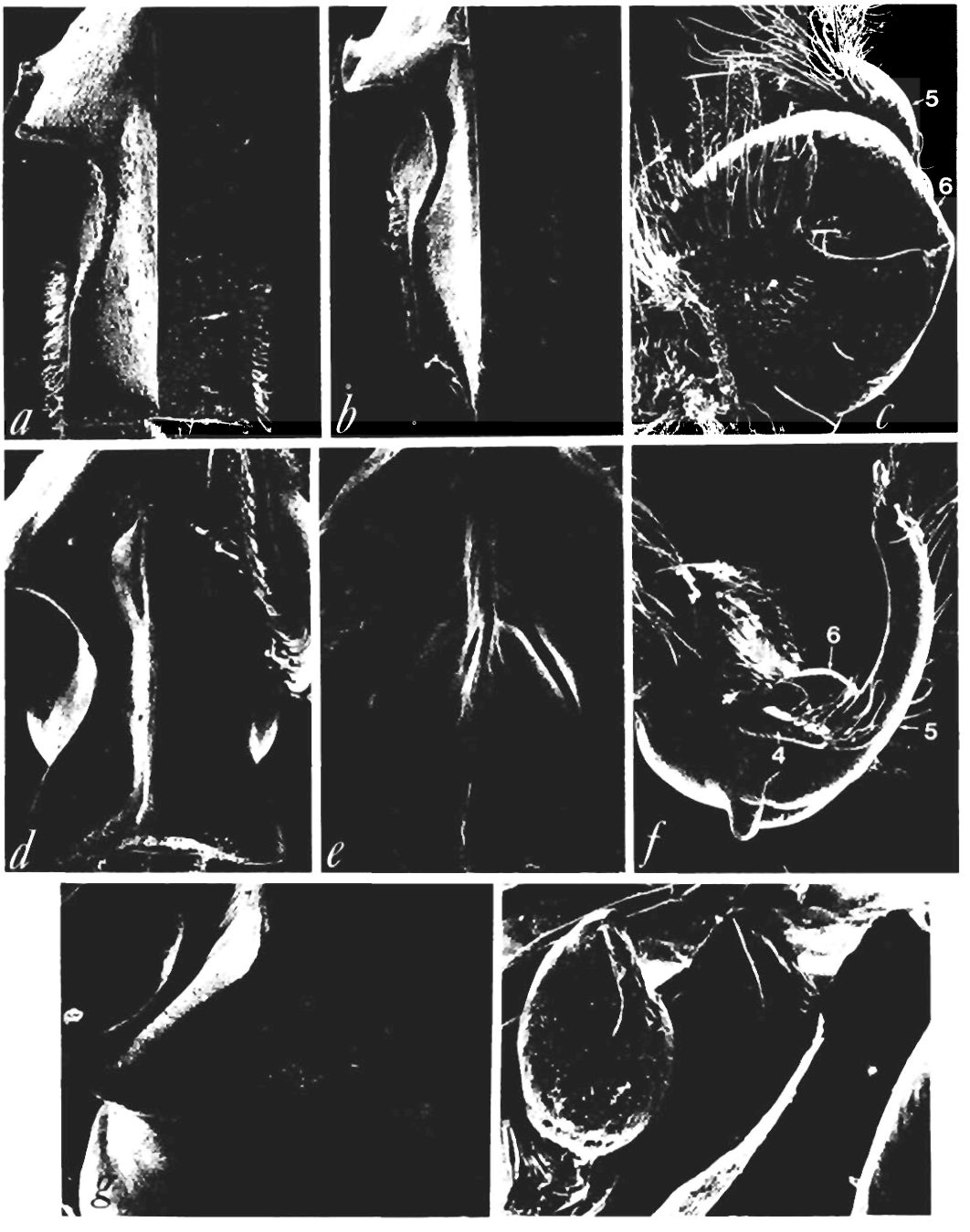


Fig. 6. SEM of selected characters of *L. brachyurus* and *L. brevifrons. Lynceus brachyurus*: *a,* frontal view of male, ×70; *b,* frontal view of female, ×50; *c,* male clasper, anterior face, ×170. *Lynceus brevifrons: d,* frontal view of male, ×50; *e,* frontal view of female, ×45; *f,* male clasper, posterior face, ×110; *g,* distal truncate border of male head region, ×80; *h,* stout carinate spines of clasper indicated by stout arrow in *f.* Arabic numerals refer to endites; see Fig. 3.

scanning electron microscope (Fig. 6*a, b*). Right and left claspers equal in size and shape; movable finger of clasper thin, sickle-shaped, and gently curving (Figs. 4*d–g*, 6*c*), extending beyond setose margin of immovable finger (endite 3); posterior surface of immovable finger (endite 3) with long pappose setae and row of shorter, stout, serrate spines near clasping edge and with short setae on proximal swollen part of endite (Fig. 6*c*).

Distribution.—Holarctic; known from Europe, Asia, and North America (Saunders and Wu, 1984). In Canada, *L. brachyurus* is reported from Quebec (Baird, 1862; Packard, 1883), Alberta (Johansen, 1921), Yukon Territory (Johansen, 1922), and Ontario (Johansen, 1923). In the United States, *L. brachyurus* is reported from Illinois, Massachusetts, New Hampshire, New York, and Rhode Island (Packard, 1883); Alaska (Johansen, 1922); Saint Paul Island, Pribilof Islands (Daday, 1927: 23); Colorado and Michigan (Pearse, 1913; Dodds, 1917; Saunders and Wu, 1984); Oregon (Coopey, 1946); California (Wootton and Mattox, 1958); Indiana (Eberly, 1971), and North Dakota (personal communication, James F. Saunders III, specimens UCM 1944, University of Colorado Museum). Mattox (1959) listed Ohio and Washington, for which we have been unable to locate additional published reports. We add Arizona and Minnesota.

Natural History.—Retallack and Clifford (1980) recorded a life cycle of about 118 days (from April to August; summer temperatures as high as 28°C with daily fluctuations of 17°C) in Canada. Sars (1896) described feeding behavior. At the southern end of the North American distribution, in Arizona, *L. brachyurus* occurs only above 1,800 m. Belk (personal observation) observed, as did Johansen (1922) for Ontario populations, that this species has bright green eggs.

Remarks.—This species is widespread and morphologically variable. Daday (1927) and Straškraba (1962) described several distinct "variants" of *L. brachyurus*, some of which were originally considered separate species. The forms recognized by Daday (1927) were *typicus, zichyi,* and *isorhynchus.* To these Straškraba (1962) added *acanthorynchus* (described as a new species by Bowkiewicz, 1923) and a new variant, *isoacanthorhynchus.* North American specimens are the "true" *brachyurus,* given no other name by Daday, with the exception of the specimens from the Pribilof Islands, which according to Daday (1927) are *typicus*; we have not seen these. Daday (1927) considered *L. mucronatus* a synonym of *L. brachyurus,* but the former species is valid (see later). Rostral morphology appears plastic and is known to change during ontogeny (see Valtonen, 1966). Straškraba (1965) illustrated and discussed the variability of the rostrum in European populations. Because of the morphological variability and geographic range of the species, it is possible that some of the species in Table 1 will eventually be synonymized with *L. brachyurus.* Fortunately, the morphology of the claspers seems to vary only slightly and can be used as a reliable taxonomic character.

Lynceus brevifrons (Packard, 1877)
Figs. 5, 6*d–h*

Limnetis brevifrons Packard, 1877: 172, fig. 11c.—Packard, 1883: 298 (key), 301, figs. 3c, 4–6, pl. 26, figs. 5, 5a, pl. 27, figs. 1–3.

Lynceus brevifrons.—Daday, 1927: 101 (687), figs. 170a, b.—Pratt, 1935: 379 (key).—Mackin, 1939: 46 (key).—Mattox, 1959: 580 (key), fig. 26.2.—Pennak, 1978: 344 (key).—Saunders and Wu, 1984: 5, figs. 1–3, 23 (map).

Material Examined.—[DB 204], 1 ♂, 2 ♀♀, Apache County, Arizona, temporary pond on Long-H Ranch (about 32 km north of Saint Johns, Arizona), collected by G. A. Cole, M. C. Whiteside, August, 1964; [DB 733], 1 lot, Tergo County, Kansas, farm pond about 2.4 km north and 5.6 km east of Voda, collected by T. Edmonds, 17 June 1975.

Type Locality.—In pools near Ellis, Kansas (Packard, 1877).

Measurements.—Packard (1883) described this as the "largest species known" and gives an average size of 4 mm length, 3.5 mm breadth; larger ones were 6 × 5 mm. Saunders and Wu (1984) gave the following data: males, 4.2–5.0 mm length, 3.5–4.5 mm height, 2.7–3.5 mm depth; females, 3.9–5.1 mm length, 3.9–4.65 mm height, 3.0–3.45 mm depth. Arizona specimens were even larger; male, 5.9 mm length, 5.4 mm height; females, 5.9–6.8 mm length (height not measured).

Description.—Male rostrum (Figs. 5*a–c*, 6*d, g*) sharply truncate in lateral and frontal views, slightly concave on distal border; distal border covered with minute setae visible under high magnification (Fig. 6*g*). Female rostrum (Figs. 5*d,e*, 6*e*) not truncate, with 2 lateral and 1 medial acute projections vis-

ible in frontal view. Male right and left claspers equal in size and shape; movable finger (endite 6) of clasper (Fig. 5*f*, arrow) very short relative to immovable part of clasper (endite 3), not reaching outer margin of endite 3; posterior distal border of immovable finger (endite 3) with unusual stout carinate setae (Fig. 6*f, h*); distal palp (endite 5) at least twice length of proximal palp (endite 4) and extending well beyond movable finger.

Distribution.—Kansas, Colorado, New Mexico, and Mexico (Mattox, 1959; Sublette and Sublette, 1967; Oldham, 1978; Saunders and Wu, 1984); Texas (Moore, 1965; Sublette and Sublette, 1967); and Arizona (this paper).

Natural History.—Moore (1965) reported *L. brevifrons* from three localities in Texas, all of which were very turbid playa ponds, and noted the following branchiopods in the same locations: *Leptestheria compleximanus, Caenestheriella setosa,* and *Eocyzicus concavus* (Conchostraca); *Streptocephalus texanus, Streptocephalus similis,* and *Thamnocephalus mexicanus* (Anostraca); and *Triops longicaudatus* (Notostraca) (see Moore, 1965, for details of species occurrences and additional limnological data). Sublette and Sublette (1967) also found *L. brevifrons* in turbid, hard-water playa lakes during warm times of the year.

Remarks.—This large species is easily distinguished by the truncate rostrum (in lateral view) of males. In the several other species that have been described as having a truncate rostrum, the rostrum appears truncate only in frontal view and not in lateral view (compare Figs. 4*a* and 5*a*). The slightly concave and lightly setose surface of the truncate part of the rostrum is not known for any other American species. Furthermore, there is no other American species in which the movable finger of the clasper is as short relative to the swollen hand of the clasper (endite 3); the stout carinate setae on the posterior distal surface are also unique. However, a similar rostrum occurs in the Indian species *Lynceus denticulatus* (see Gurney, 1930) and in the Romanian species *L. andronachensis* (see Botnariuc, 1947; Botnariuc and Orghidan, 1953). The latter species also has a very short movable finger on the clasper (and thus is similar to *L. brevifrons*) but differs from all other lynceids in having a spine on the posterolateral outer surface of the carapace. A final character unique to *L. brevifrons* is the distal palp (endite 5), which is much longer than endites 4 or 6 (the claw) and extends beyond the movable finger by more than the length of the proximal palp.

Lynceus gracilicornis (Packard, 1871)
Fig. 8*a–d*

Limnetis gracilicornis Packard, 1871: 113.—Packard, 1874: 618.—Packard, 1883: 298 (key), 302, fig. 3b.—Pearse, 1918: 672 (key).

Lynceus gracilicornis.—Daday, 1927: 89 (675), fig. 166.—Pratt, 1935: 379 (key).—Mattox, 1959: 580 (key).—Pennak, 1978: 344 (key).—Martin *et al.*, 1986: 221, figs. 1–8.—Martin, 1988: figs. 1E, 2F, H, I, 4D–F, 5E, 6B–F, 7A–C, E, 10, 11A, B, 12.

Material Examined.—[DB 263], Comal County, Texas, pools in dry creekbed, Maurice Clark Ranch, collected by D. Belk, 4 June 1982; [DB 598], Blanco County, Texas, natural depression north side of Ranch Road 1323, 1.1 km east of Sandy, collected by D. Belk, 7 November 1984; [DB 654], Gillespie County, Texas, pond east of Ranch Road 2323, 13.8 km north of US87, collected by D. Belk, 29 October 1985; [DB 655], Llano County, Texas, pond east of Ranch Road 2323, 22 km north of US87, collected by D. Belk, 29 October 1985; [DB 533], Brunswick County, North Carolina, Country Club Woods Pond in Wilmington about 1 km northwest of NC132 and Randall Drive, collected by A. McCrary, 4 September 1981; Leon County, Florida, temporary pond, Trailer Park off Highway 90 (see Martin *et al.*, 1986), several large lots, collected by J. Martin and B. Felgenhauer, April 1984, April 1987.

Type Locality.—Bosque County, Texas; incorrectly listed by Packard (1883) as Waco, Texas; see Geiser (1933) and Martin *et al.* (1986).

Measurements.—Up to 6.0 mm length (Martin *et al.*, 1986); usually somewhat smaller.

Description.—See Martin *et al.* (1986).

Distribution.—Known from the type locality and from Blanco, Comal, Gillespie, and Llano Counties, Texas; Leon County, Florida (Martin *et al.*, 1986); Brunswick County, North Carolina (McCrary, 1984).

Natural History.—Known from warm tannic pools in north Florida from April through the summer (Martin *et al.*, 1986) and as late as mid-September. The only other crustacean present was an anostracan, *Streptocephalus seali* Ryder.

Remarks.—The only illustration of *L. gracilicornis* in Packard's (1883) monograph is a frontal view of a male (his fig. 3*b*) showing a broad flat rostral border. The species was

next illustrated by Daday (1927), who drew a more or less trilobed female rostrum, slightly indented male rostrum, and dimorphic claspers. Daday's description thus differs from the verbal description and single illustration of Packard. We have examined specimens from localities in Blanco, Comal, Gillespie, and Llano Counties, on the eastern edge of the Edwards Plateau region of Texas. These sites are within 240 km of the type locality in Bosque County, Texas (see Geiser, 1933). The Texas specimens are probably true *L. gracilicornis,* and are fairly similar to the species from Florida (Fig. 8*a–d*) described by Martin *et al.* (1986). There are slight differences between the Texas and Florida specimens, and between the Florida specimens and the description of Daday (see Martin *et al.,* 1986). In both localities the male rostrum is always distally truncate in frontal view (Fig. 8*a*), but the female rostrum is apparently extremely variable. Florida females collected in 1987 possessed a truncate rostrum essentially identical to that seen in males, whereas females collected in 1984 have a produced, rounded distal rostral border (Fig. 8*b*). The illustrations of the male claspers in Martin *et al.* are slightly misleading in that endite 5 appears to arise from the movable finger of the clasper, rather than from the distal border of endite 3 (see Fig. 8*d*).

Among the known North American species of *Lynceus, L. gracilicornis* most closely resembles the widely distributed *L. brachyurus.* The two species differ in clasper and rostral morphology, with *L. brachyurus* having a rostrum produced in the female into a long acute process with anterolateral projections and having male right and left claspers of similar size and shape. In *L. gracilicornis* the clapsers are strongly dimorphic. The only other American species with dimorphic claspers is *L. aequatorialis* (see later). The minor clasper of *L. gracilicornis* is unremarkable and similar to that seen in *L. brachyurus,* whereas the major clasper is large and somewhat angular (Fig. 8*c,d*).

Lynceus mucronatus (Packard, 1875)
Figs. 7, 8*e–h*

Limnetis mucronatus Packard, 1875: 311 [as *Lymnetis,* typographical error].—Packard, 1877: 172, figs. 11a, 12.—Packard, 1883: 298 (key), 300, fig. 2, pl. 1, figs. 1–6.—Pearse, 1918: 672 (key).

Lynceus mucronatus.—Daday, 1927: 8 (594) (as synonym of *L. brachyurus*).—Mattox, 1959: 581 (key).—Pennak, 1978: 344 (key).

Material Examined.—[DB 561], Alberta, Canada, pond northeast of Calgary, collected by K. A. L. Reading, 15 May 1983; [DB 567], British Columbia, Canada, ephemeral pond 12.9 km southeast of Merritt on Princeton Highway, collected by K. A. L. Reading, 21 May 1983.

Type Locality.—"Several small prairie pools from a hundred yards to a half mile or so wide, exactly on the Boundary line, 49°N, just on the west bank of Frenchman River, Montana" (Packard, 1875, from letter to Packard by E. Coues).

Measurements.—4 mm length, 3 mm breadth (Packard, 1883); up to 3.7 mm length (Retallack and Clifford, 1980).

Description.—Male rostrum (Fig. 7*a,b*) truncate or slightly convex in frontal view; anterolateral corners with small acute projection. Female rostrum (Figs. 7*c, d,* 8*e*) with acute medial and lateral projections; rostral margin between these projections either strongly concave (resembling typical *L. brachyurus* as in Fig. 4*c*) or slightly convex (Figs. 7*d,* 8*e*). Right and left claspers equal, with acute distally directed projection on endite 3 near base of movable finger and with small distinct knob on movable finger at point where finger bends sharply back against endite 3 (Figs. 7*e, f,* 8*f, g*). Male terminal abdominal appendage with strong, sclerotized, hooklike projection curved dorsally (Fig. 7*g*).

Distribution.—Frenchman River, Montana (Packard, 1875); Sounding Creek, east central Alberta, Canada (Retallack and Clifford, 1980); Alberta, Canada (Mattox, 1959); British Columbia, Canada (this paper). Packard (1877) reported a large number of specimens, all female, in pools at Ellis, Kansas, associated with *L. brevifrons.* He wrote "... the species is so easily recognized by the mucronate, tridentate front of the female head, that I think no mistake has been made in the identification of the Kansas specimens." Our preceding discussions document the highly variable nature of the rostral characters. We strongly suspect misidentification and thus reject this disjunct record. This is the Kansas record noted in Oldham (1978).

Natural History.—Known to occur with *Lepidurus* in Montana (Packard, 1875, 1883). Retallack and Clifford (1980) recorded a life cycle of about 60 days and densities of 48/l in saline prairie streams of

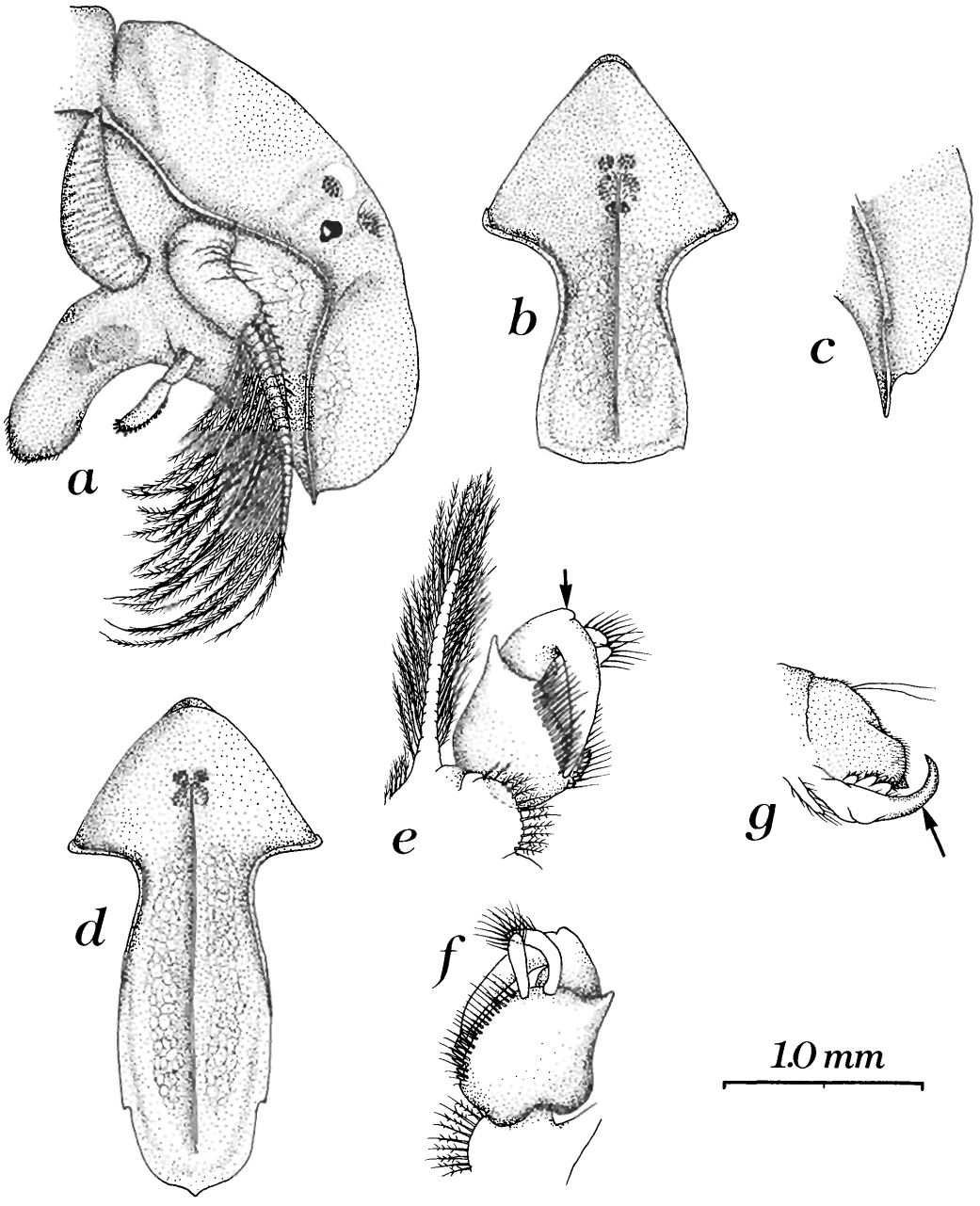


Fig. 7. *Lynceus mucronatus* (Packard). *a,* lateral view of head region, male; *b,* frontal view of head region, male; *c,* lateral view of tip of head region, female; *d,* frontal view of head region, female; *e,* anterior face of male clasper with dorsal protuberance of endite 6 (movable finger of clasper) indicated by arrow; *f,* posterior face of male clasper; *g,* lateral view of male posterior segment and terminal appendage showing large sclerotized upturned hooklike process (arrow).

Alberta; the cycle of *L. brachyurus,* which was sympatric, was noted to be about twice as long. Other sympatric Crustacea recorded by Retallack and Clifford included anostracans (6 species), another conchostracan (*Cyzicus mexicanus*), the notostracan *Lepidurus couesii,* and 21 species of cladocerans. There were also several potential predators, including fish, coexisting for part of the year with the branchiopods.

Fig. 8. SEM of selected characters of *L. gracilicornis* and *L. mucronatus*. *Lynceus gracilicornis*: *a,* frontal view of male, ×45; *b,* frontal view of female, ×40; *c,* major clasper, anterior face, ×150; *d,* same, posterior face, ×140. *Lynceus mucronatus*: *e,* frontal view, female, ×50; *f,* male clasper, anterior face, with distinguishing characters indicated by arrows (see text), ×95; *g,* same, posterior face, ×95; *h,* ventral view of clasper showing endite 6 between rows of setae and stout spines on posterior face, ×220. Arabic numerals refer to endites; see Fig. 3.

Remarks.—Because of errors in the illustrations of Packard (1883) (see Lynch, 1964), Daday (1927), and later Straškraba (1965: 208) considered this species a junior synonym of *L. brachyurus*. The two species are easily distinguished by the clasper, which in *L. mucronatus* has a distinct knob on the distal border of the clasper base (endite 3) and also on the movable finger of the clasper (endite 6) (see Fig. 8*f*, arrows). The life histories of the two species also differ (Retallack and Clifford, 1980), and the strong, sclerotized upturned hooklike projection on the terminal appendages of males of *L. mucronatus* (described by Mattox, 1959) is unmistakable (Fig. 7*g*).

Lynceus rotundirostris (Daday, 1902)

Lynceus rotundirostris Daday, 1902: 286, figs. 10–17.—Daday, 1927: 94 (680), fig. 167a–l.

Material Examined.—Holotype, 1182/1, 1203/1901, Patagonia, 1 ♀, collected by F. Silvestri, 24 December 1899, collections of the Hungarian Museum of Natural History.

Type Locality.—Amenkelt, Patagonia, 45°S, 70°W.

Measurements.—6.5–7.0 mm length, 5.2–5.5 mm height, 4 mm width (Daday, 1927); our measurement of damaged right valve 6.6 mm length.

Description.—See Remarks.

Distribution.—Known only from the type locality, Patagonia (Daday, 1902, 1927).

Natural History.—Nothing known.

Remarks.—The single known specimen is in very poor condition. The rostrum is damaged and the carapace is not intact. The dorsal border of the carapace, illustrated by Daday (1927) as having a distinct umbo, has been torn away and is not in the vial. It is difficult, without either a male or an intact female, to assign this very large specimen to any known species or to state definitely that it is distinct from any other species. Verification of the validity of this species must await discovery of the male or at least an intact female.

Lynceus tropicus Daday, 1927

Lynceus tropicus Daday, 1927: 97 (683), fig. 168a–i.

Material Examined.—Holotype (Bp 521), Muséum National d'Histoire Naturelle, Paris, presumably female (body missing).

Type Locality.—Guanaparo, Venezuela.

Measurements.—2.8 mm length, 2.7 mm height, 2.2 mm width (Daday, 1927). Our measurements of the holotype agree, with the exception of the length, which we found to be 3.0 mm.

Description.—See Remarks.

Distribution.—Known only from the type locality.

Natural History.—Nothing known.

Remarks.—This species was described from a single female that differed, according to Daday (1927), from *L. aequatorialis* and *L. rotundirostris* only in the shape of the telson and in the morphology of the ventral carapace border. The holotype (the only existing specimen) is not intact. Both valves are present, but the body has been removed and its location is unknown. Because so many characters, including valve morphology, are known to be variable, positive verification of the validity of the species must await discovery of the male or an intact female. The type locality (Guanaparo, Venezuela) could not be located on modern maps of Venezuela. It is possible that Daday meant Guarapana, in northwest Venezuela; this is the locality indicated in Fig. 17.

Lynceus aequatorialis Daday, 1927
Figs. 9, 10

Lynceus aequatorialis Daday, 1927: 79 (665), fig. 163a–u.

Material Examined.—[DB 651], Mantecal, State of Apure, Venezuela, 1 lot, collected by G. Pereira; [DB 816] Arichuna Road, State of Apure, Venezuela, 1 lot, collected by G. Pereira.

Type Locality.—Between the Rio Apure and Rio Arauca, Venezuela.

Measurements.—2.6–2.88 mm length, 2.3 mm height, 2 mm depth (Daday, 1927); our specimens were as follows: females, 2.3–2.9 mm length, 2.0–2.5 mm height; males, 2.3–2.5 mm length, 2.2–2.3 mm height.

Description.—Male and female rostrum (Figs. 9*a–c*, 10*a*) similar, with distal border truncate and slightly concave in frontal view; rostral carina entire (not bifurcate); claspers strongly dimorphic; major clasper (which may be right or left) with large posteriorly directed "hammerlike" projection extending from movable finger (Figs. 9*d,e*, 10*b,c*); left clasper with smaller smoothly curving movable finger (Figs. 9*f, g*, 10*d*); second thoracopod on same side as major clasper modified (Figs. 9*h*, 10*e*) with fourth, fifth, and sixth endites slightly sclerotized, endite 5 with distally directed lobes that are mi-

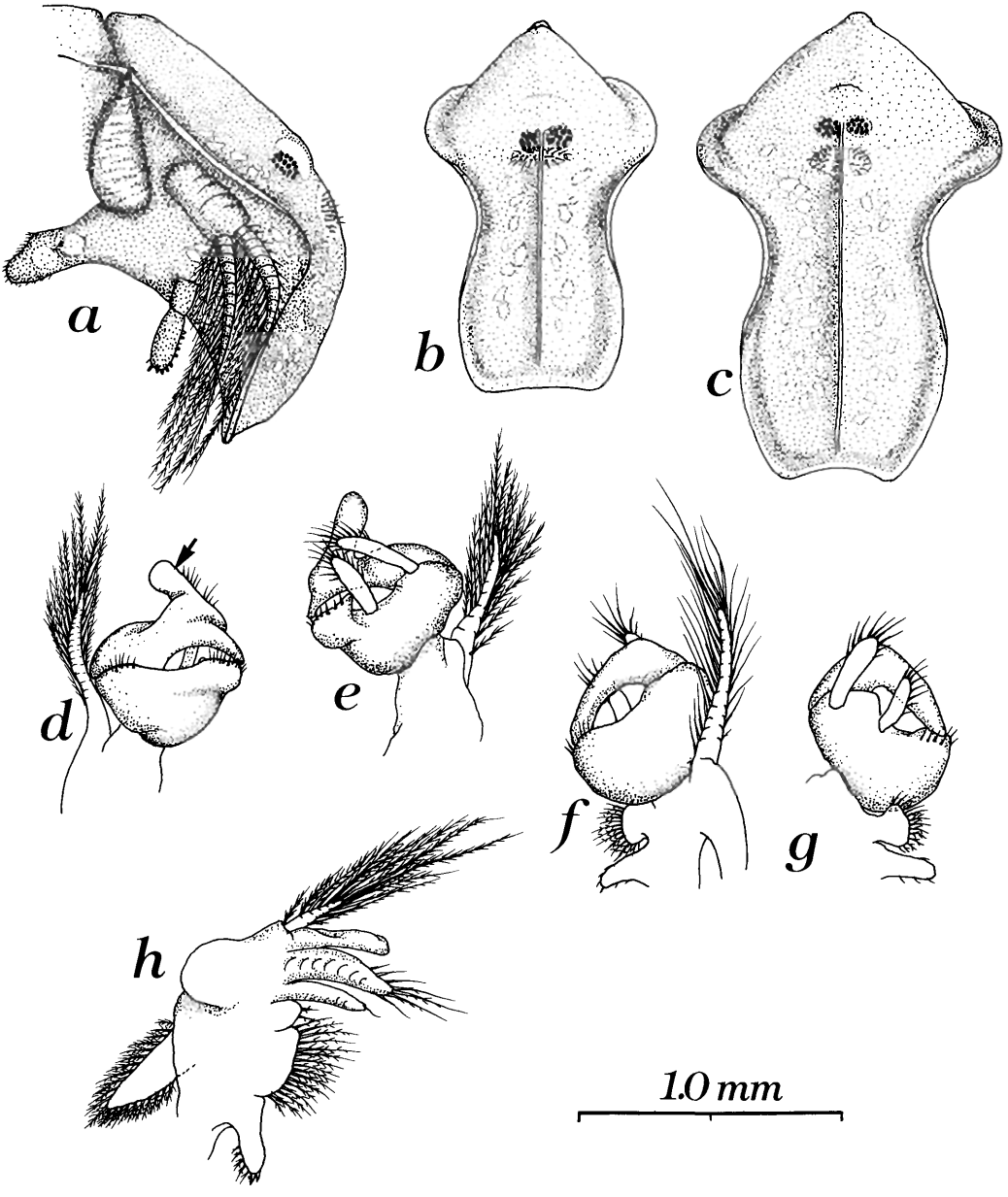


Fig. 9. *Lynceus aequatorialis* Daday. *a,* lateral view of head region, male; *b,* frontal view of head region, male; *c,* frontal view of head region, female; *d,* anterior face of major (left) clasper, with distinguishing posteriorly directed prominence indicated by arrow; *e,* posterior face of major clasper; *f,* anterior face of minor (right) clasper; *g,* posterior face of minor clasper; *h,* modified male second thoracopod.

nutely serrate under high magnification (Fig. 10*e, f*).

Distribution.—Between 69° and 70°E and at about 7°N, between the equator and the Tropic of Cancer (Daday, 1927).

Natural History.—Nothing known.

Remarks.—*Lynceus aequatorialis* is described here, rather than in alphabetical order, because of the many similarities to species in the genus that follows. Although the rostral carina is not bifurcate (as it is in *Paralimnetis*), the second thoracopod is modified and is somewhat similar to the

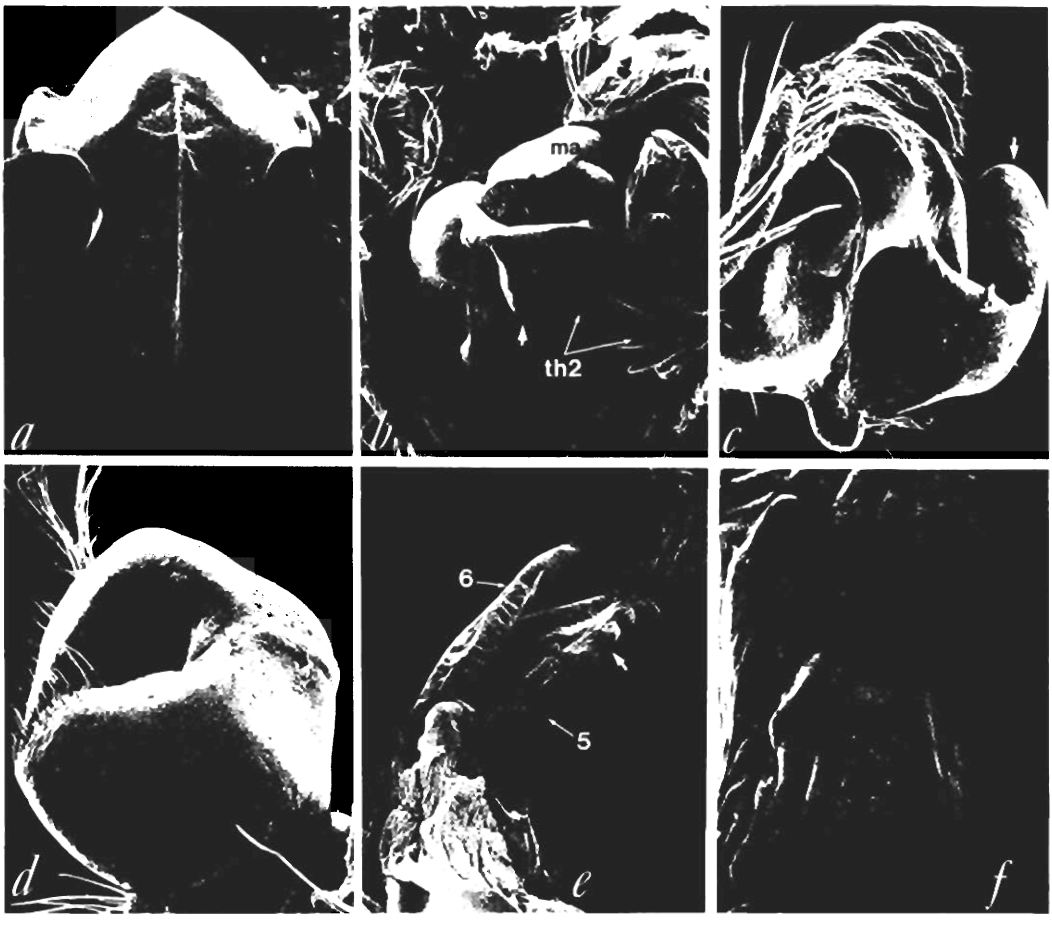


Fig. 10. SEM of selected characters of *L. aequatorialis*. *a*, frontal view of male, ×60; *b*, male claspers in situ with posteriorly directed prominence indicated by stout arrow and with second thoracopod identified, anterior end is at top, ×70; *c*, major clasper ("open" end toward bottom of photo, hinge at top), note large hammer-like distal prominence (arrow), ×160; *d*, minor clasper, anterior face, ×180; *e*, modified second male thoracopod with sclerotized bumps on endite 5 (arrow), ×130; *f*, high magnification of sclerotized bumps indicated by arrow in *e*. Abbreviations: ma = major clasper, th2 = second thoracopod. Arabic numerals refer to endite numbers, see Fig. 3.

second thoracopod of *Paralimnetis* and *Lynceiopsis*. Endites 4, 5, and 6 are modified, but in this species endite 5, rather than endite 4, is divided into blunt lobes; there is no protopodal complex. Other differences are apparent under SEM; the proximal border of each lobe on endite 5 of *L. aequatorialis* is minutely serrate, whereas these are all smooth in *Paralimnetis*. An Arabian species, *Lynceus simiaefacies*, also has a modified second thoracopod (Harding, 1941).

Paralimnetis Gurney, 1931

Rostral carina bifurcate. First male thoracopod very large and globose, relatively larger than in *Lynceus*. Protopod of second male thoracopod modified on right or left side as large sclerotized hooklike projection. Distal tip of endite 6 with minute hook on one or both sides of second thoracopod.

Paralimnetis rapax Gurney, 1931
Fig. 11

Paralimnetis rapax Gurney, 1931: 272, figs. 17–24.

Material Examined.—One male (holotype), British Museum (Natural History), no. 1928.2.23.21-23.

Type Locality.—"Pool at Makthlawaiya, 11 xii 26," Paraguay, 23°25′S, 58°19′W (Gurney, 1931).

Measurements.—"Nearly circular; length 4 mm; greatest height 3.4 mm" (Gurney, 1931; our measurements agree).

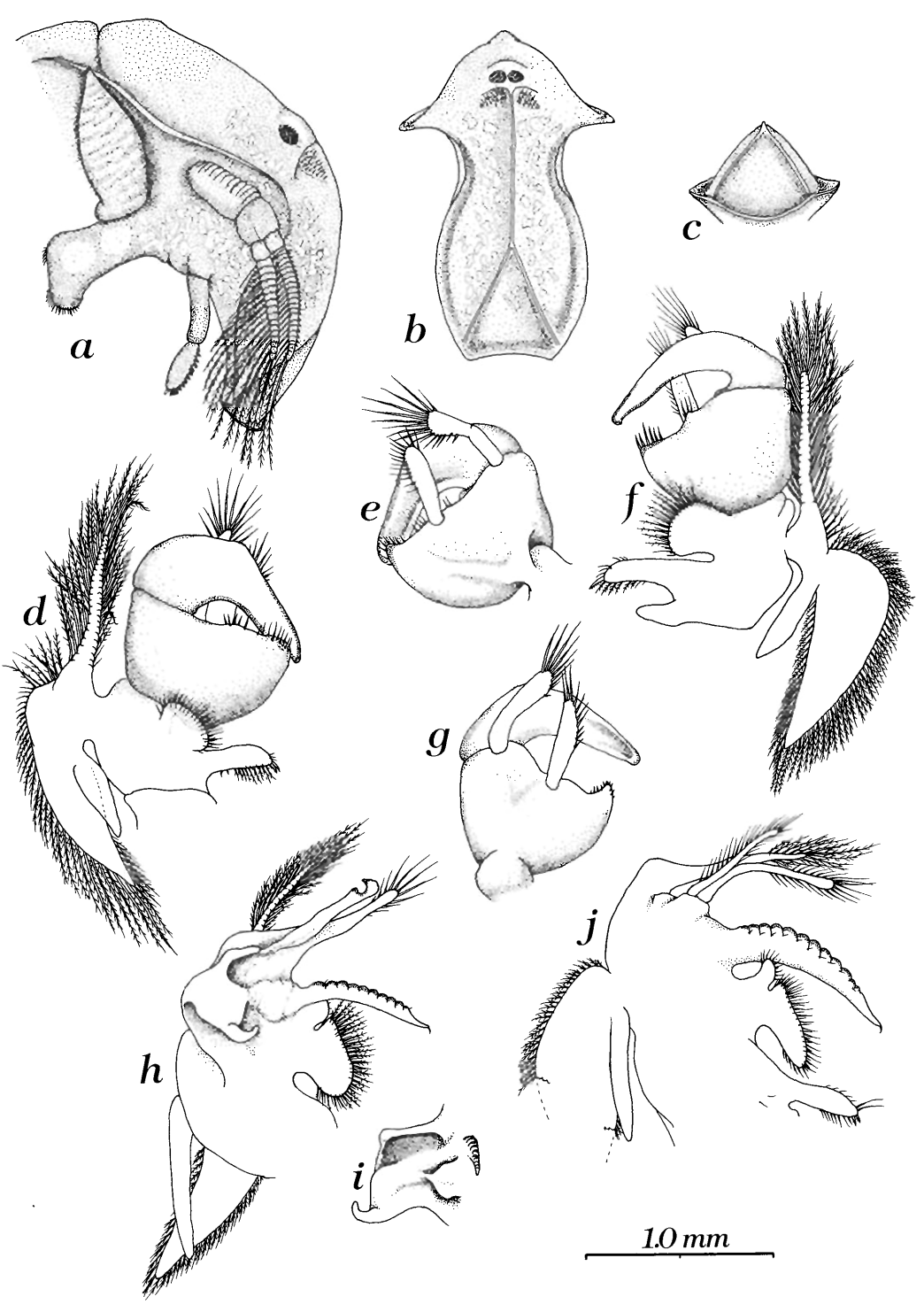


Fig. 11. *Paralimnetis rapax* Gurney, male holotype. *a,* lateral view of head region; *b,* frontal view of head region; *c,* ventral view of tip of head region; *d,* anterior face of major (left) clasper; *e,* posterior face of major clasper; *f,* anterior face of minor (right) clasper; *g,* posterior face of minor clasper; *h,* modified second thoracopod of right side with protopodal complex; *i,* protopodal complex turned 90°; *j,* modified second thoracopod of left side; note absence of hooks on distal endites.

Description.—Male rostrum (female not seen) with slightly concave distal border (Fig. 11*a–c*); rostral carina bifurcate and almost reaching distal border of rostrum; left clasper (Fig. 11*d,e*) slightly larger and with sharp bend at about level of endite 4; right clasper (Fig. 11*f, g*) thinner and without distinct sharp bend; male second left thoracopod (Fig. 11*h, i*) with large protopodal complex and with minute hook on distal tip of endite 6; endite 4 with rounded sclerotized lobes, each bearing minute seta; male second right thoracopod (Fig. 11*j*) similar to left but without protopodal complex and without hook on tip of endite 6.

Distribution.—Known only from the type locality.

Natural History.—Nothing known.

Remarks.—This species apparently has been reported only once (Gurney, 1931). The second male thoracopod resembles that of *Lynceus aequatorialis* in that it has one endite modified with small sclerotized bumps. However, endite 4 is modified in *P. rapax,* whereas endite 5 is modified in *L. aequatorialis.* The fine structure of the bumps also differs, as discussed under *L. aequatorialis.*

Paralimnetis mapimi Maeda-Martinez, 1987

Figs. 12, 14*a–c*, 15*e*

Paralimnetis mapimi Maeda-Martinez, 1987: 67, figs. 1, 2.

Material Examined.—[DB 639], El Socorro, Durango, Mexico, 1 lot, collected by A. M. Maeda, 20 September 1985 (paratypes).

Type Locality.—Bolson de Mapimi in Chihuahua and Durango, Mexico.

Measurements.—2.43–3.14 mm length, 2.16–2.81 mm height, 2.05–2.92 mm depth (Maeda-Martinez, 1987); our specimens as follows: males, 2.2–2.8 mm length, 1.9–2.2 mm height; females, 2.6–2.9 mm length, 2.4–2.6 mm height.

Description.—Rostrum similar in both sexes, distally truncate in frontal view (Figs. 12*a–d,* 14*a,b*), broader in male; rostral carina bifurcate, extending almost to distal border of rostrum; left clasper larger than right, with distinct projection at about level of endite 5 (Fig. 12*e, f*) and with markedly undulating borders on movable finger and immovable finger (Figs. 12*e,* 14*c,* arrows); minor (right) clasper with smoothly curving outer margin on movable finger (Fig. 12*g,h*); second thoracopod as in *P. rapax* but with larger endite 5, slightly different protopodal complex, and with hook on tip of endite 6 on both right and left second thoracopods (Figs. 12*i–k,* 15*e*).

Distribution.—Known only from the type locality.

Natural History.—Nothing known.

Remarks.—*Paralimnetis mapimi* is similar to *P. rapax* in many characters, but is distinguished by the distinct protrusion of the major clasper. In *P. rapax* the movable finger bends sharply but does not possess any protrusion; there is a distinct, low protrusion where this finger bends in *P. mapimi.* In addition, the tip of the sixth endite of the second male thoracopod, which bears a minute hook in *P. mapimi,* is unmodified in *P. rapax.*

Paralimnetis texana, new species

Figs. 13, 14*d–f*, 15*a–d*

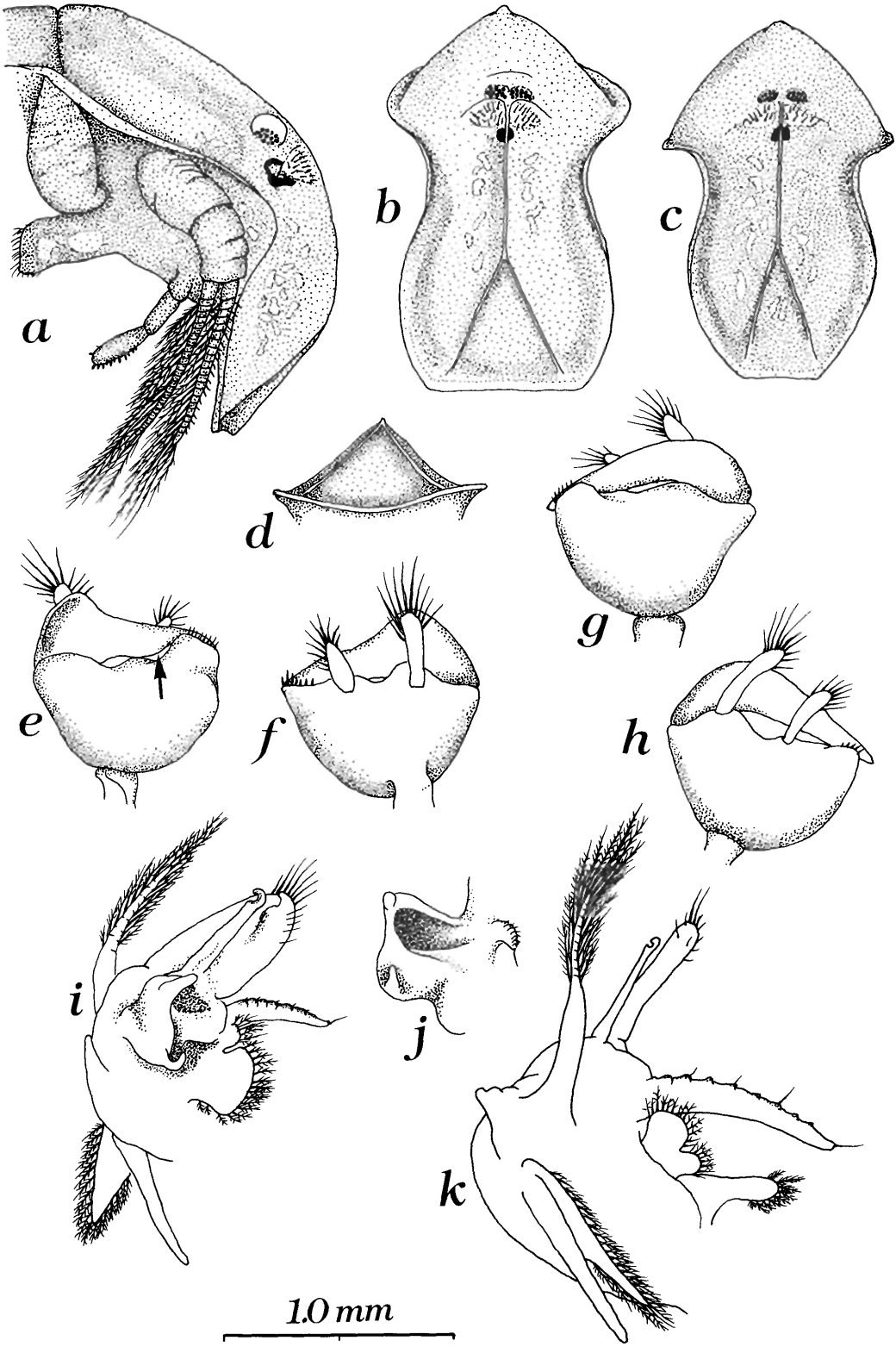
Material Examined.—[DB 605], Llano County, Texas, natural drainage dammed by road, east side of Ranch Road 2323, 8 km south of Texas Highway 16 at Llano, 1 lot, collected by D. Belk, 7 November 1984, holotype (USNM 234415) and paratypes (USNM 234416) from this lot deposited at the National Museum of Natural History, Smithsonian Intitution; [DB 252], Llano County, Texas, roadside ditch between south side of Texas 29 and railroad tracks, 13.4 km east of Texas 16 at Llano, 1 lot, collected by D. Belk, 14 June 1978.

Type Locality.—Llano County, Texas, east side of Ranch Road 2323, 8 km south of Texas Highway 16 at Llano (30.8°N, 98.5°W).

Measurements.—Males, 2.7–2.9 mm length, 2.5–2.7 mm height; females 2.7–3.2 mm length, 2.4–2.9 mm height.

Description.—Rostrum (Figs. 13*a–d,* 14*d,e* 15*a,b*) of male and female similar, broadly truncate and slightly concave anteriorly, slightly broader in male; rostral carina bifurcate; male with very large and strongly dimorphic claspers; larger (left) clasper (Figs. 13*e, f,* 14*f*) with sharp projection (Figs. 13*e,* 14*f,* arrows) at about level of endite 5; minor clasper (Fig. 13*g,h*) with smoothly curving movable finger lacking sharp projection. Male second left thoracopod (Figs. 13*i,* 15*c*) as in *P. mapimi* but with slight differences in hooklike lobe of the protopodal complex; male right second thoracopod as in *P. mapimi,* with hook on tip of endite 6 (unlike *P. rapax*).

Distribution.—Known from two ponds near the city of Llano in Llano County, Texas.


a
b
c
d
e
f
g
h
i
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1.0 mm

Natural History.—Occurs in central Texas ponds with the anostracans *Streptocephalus texanus* and *Branchinecta packardi* and the notostracan *Triops longicaudatus.*

Remarks.—*Paralimnetis texana* closely resembles the Mexican *P. mapimi.* The distinguishing character is the presence of a large, acute spinelike projection on the outer border of the movable finger in *P. texana.* In *P. mapimi* there is a low and rounded projection here, but never a projection as large or as sharp as in *P. texana.* Moreover, the border of the movable clasper finger, which is strongly undulating in *P. mapimi,* has only a slight undulation along the closing edge of the movable finger. Additional minor differences can be seen in the morphology of the protopodal complex of the two species (compare Fig. 15*d* with Fig. 15*e*).

Genus *Lynceiopsis* Daday, 1912

Rostral carina bifurcate. Male claspers thin, nonglobose, dimorphic. Second male thoracopod strongly modified but lacking protopodal hooklike process known for *Paralimnetis.* Distal endites of second thoracopod fused into large 4-lobed process bearing circular knob on one end and small sharp knob on other. Endite 4 not modified into thick, multilobed process seen in *Paralimnetis.*

Lynceiopsis perrieri Daday, 1912
Figs. 15*e*, 16

Lynceiopsis perrieri Daday, 1912a: 410, fig. 2.—Daday, 1912b: 726.—Daday, 1913a: 198, fig. 2.—Daday, 1927: 106, figs. 171a–o, 172a–g.

Material Examined.—1913-164, Collectio Dadayana Phyllopoda: I/C-191, Hungarian Museum of Natural History, Afrique occidentale, Simbidissi.

Type Locality.—Niger River Valley, west-central Africa.

Measurements.—Males, 1.7–3.0 mm length, 1.6–2.8 mm height, 1.7–2.0 mm width; females, 1.9–3.0 mm length, 1.8–2.5 mm height, 2.0 mm width (Daday, 1927). Our specimens fell within these ranges.

Description.—Rostrum similar in both sexes, rostral carina bifurcate, frontal border slightly concave; claspers strongly dimorphic, not inflated; larger clasper (Fig. 16*e, f*) with wide movable finger bearing small protuberance near base; minor clasper unremarkable; second male thoracopod on same side as larger clasper (usually left side) modified distally with large 4-lobed swelling hooklike on dorsalmost lobe and circular and smooth on ventralmost lobe (Figs. 15*f,* 16*g–i*); smooth circular ventralmost lobe appearing to have small indentations under light microscopy but smooth under SEM (compare Figs. 15*f,* 16*h*); posteroventral margin of carapace slightly bifurcate creating longitudinal flange (Fig. 2*c*).

Distribution.—Tropical, near 15°N, between 1–2°E, between equator and Tropic of Cancer, West Africa (Daday, 1927).

Natural History.—Nothing known.

Remarks.—Although this genus is not known in the Americas, we include it here for comprison with *Paralimnetis.* The two genera are similar in the possession of a bifurcate rostral carina and a strongly modified second male thoracopod. However, the second thoracopod of *Lynceiopsis* lacks the protopodal complex seen in *Paralimnetis* and has a large 4-lobed process at the distal end; this is true not only for *Lynceiopsis perrieri* but for the recently described *Lynceiopsis sanctijohanni* from Chad (see Thiery, 1986, figs. 5–7).

Discussion

Affinities of the American Species

Of the American species of *Lynceus,* only two, *L. gracilicornis* and *L. aequatorialis,* possess dimorphic male first thoracopods. The two species are easily distinguished by the hammerlike clasper and modified second male thoracopod in *L. aequatorialis.* In *L. brachyurus, L. brevifrons,* and *L. mucronatus,* the right and left claspers are of ap-

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Fig. 12. *Paralimnetis mapimi* Maeda-Martinez. *a,* lateral view of head region, male; *b,* frontal view of head region, male; *c,* frontal view of head region, female; *d,* ventral view of tip of head region, male; *e,* anterior face of major (left) clasper; *f,* posterior face of major clasper; *g,* anterior face of minor (right) clasper; *h,* posterior face of minor clasper; *i,* male second thoracopod, right side; *j,* protopodal complex of same; *k,* male second thoracopod, left side; note hooklike tip of endite 6.

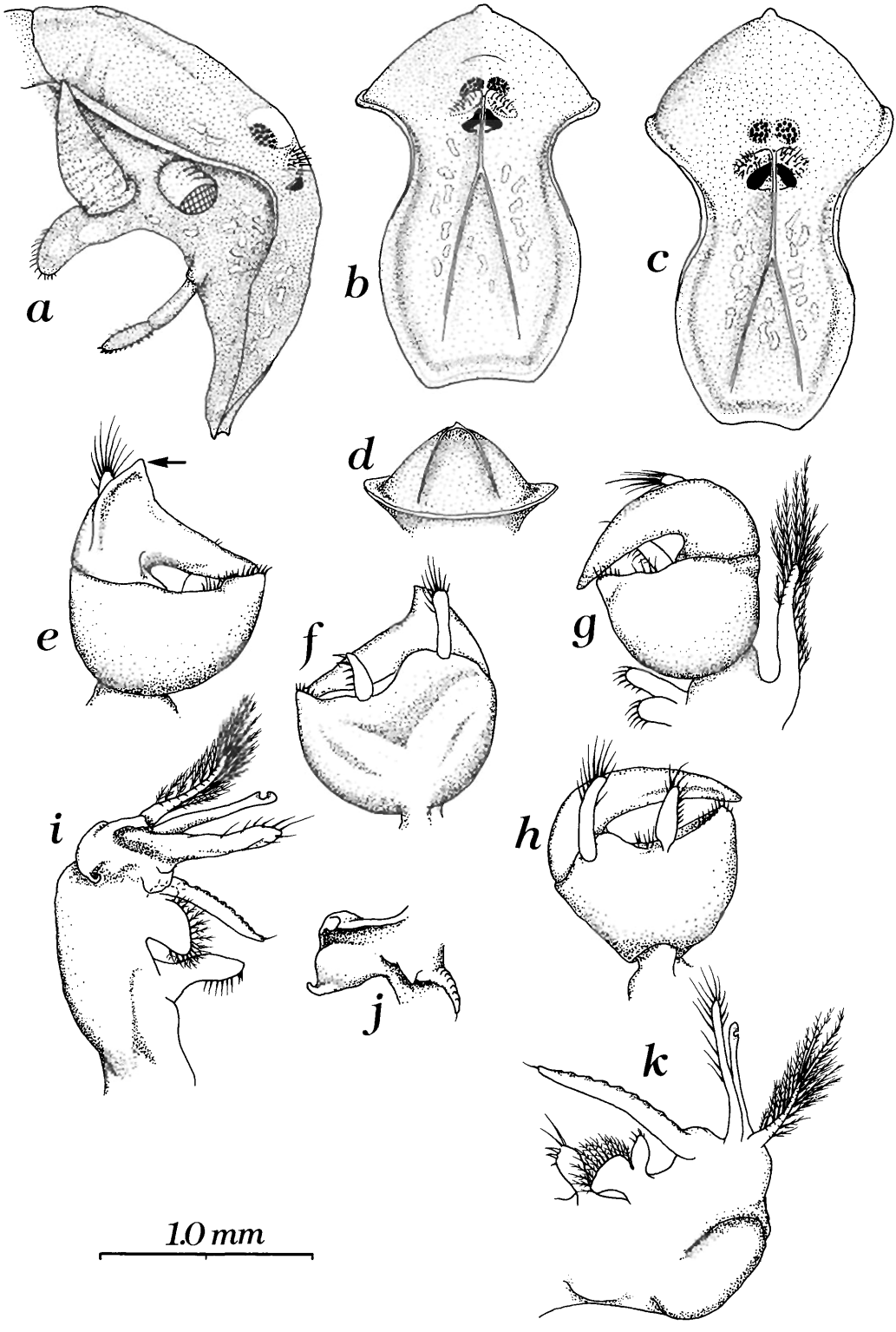

Fig. 13. *Paralimnetis texana,* new species. *a,* lateral view of head region, male; *b,* frontal view of head region, male; *c,* frontal view of head region, female; *d,* ventral view of tip of head region, male; *e,* major (left) clasper, sharp projection shown by arrow, anterior face; *f,* major clasper, posterior face; *g,* minor (right) clasper, anterior face; *h,* minor clasper, posterior face; *i,* second thoracopod with protopodal complex; *j,* protopodal complex turned 90°; *k,* second thoracopod lacking protopodal complex (left side).

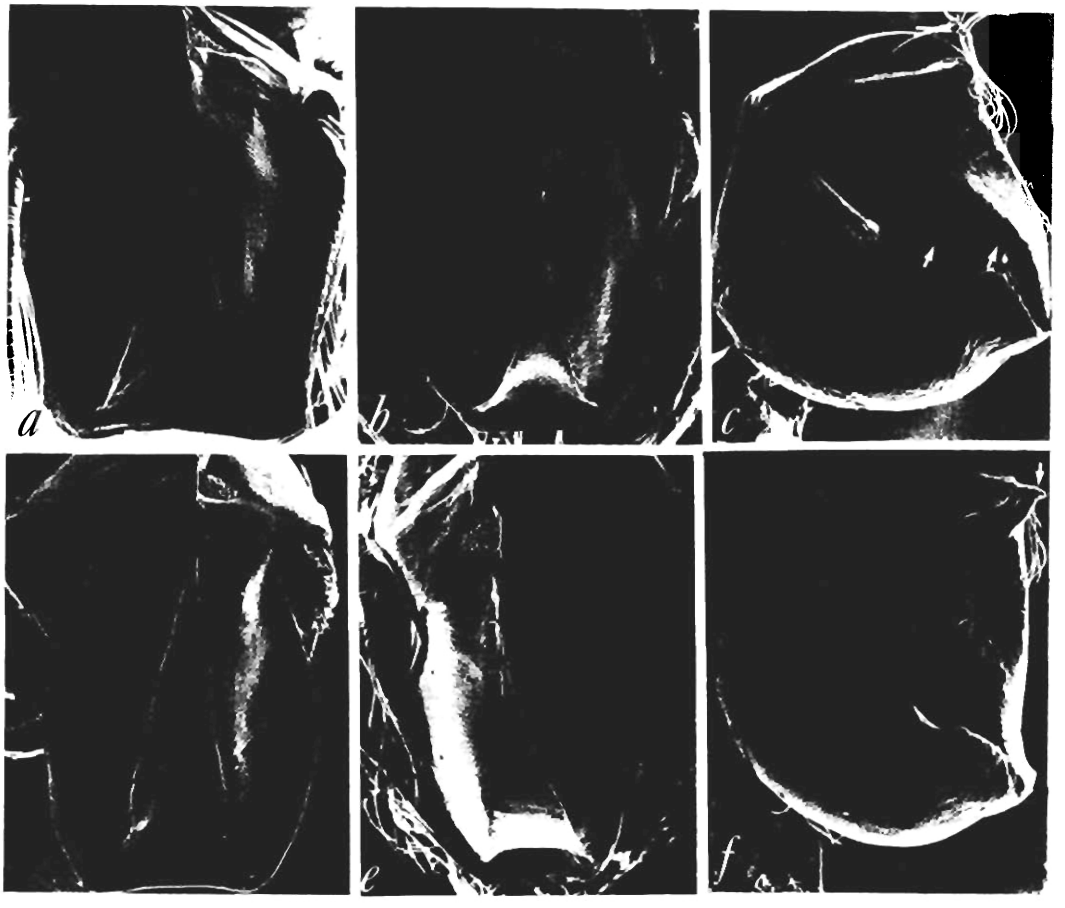

Fig. 14. SEM of selected characters of *P. mapimi* and *P. texana*. *Paralimnetis mapimi*: *a*, frontal view of male, ×85; *b*, frontal view of female, ×85; *c*, anterior face of major clasper, ×120. *Paralimnetis texana*: *d*, frontal view of male, ×80; *e*, frontal view of female, ×75; *f*, anterior face of major clasper, ×95. Note sinuous border of movable finger of clasper in *c*, and acute distal prominence in *f* (arrows).

proximately equal size and shape. These three species also are fairly easy to recognize, especially the unusual *L. brevifrons*. Daday (1927) felt that male clasper dimorphism warranted a division within the family, and he established the subgenera *Lynceus* and *Eulynceus* to accommodate species with equal or dimorphic claspers, respectively. This distinction is probably not important, since among species with dimorphic claspers there is no consistency in which clasper is the larger, and there are no other characters uniting the species. It is unlikely that *L. gracilicornis* and *L. aequatorialis*, species that by Daday's scheme would be united in the subgenus *Eulynceus*, are as closely related as *L. gracilicornis* is to either *L. brachyurus* or *L. mucronatus*. The large and inflated clasper of *L. aequatorialis* and the modified second thoracopod of that species are more reminiscent of members of *Paralimnetis*, with which *L. aequatorialis* may be allied.

Geographic Distribution

The possibility that *Lynceiopsis* and *Paralimnetis* are closely related and reflect an original Gondwana distribution is attractive, but must be tempered by the realization that conchostracan dispersal may be rapid with resulting distributions widespread; present distributions (Fig. 17) may be misleading. It is also possible that the two genera are not closely related, but rather have evolved a modified second thoracopod independently, as have at least two species

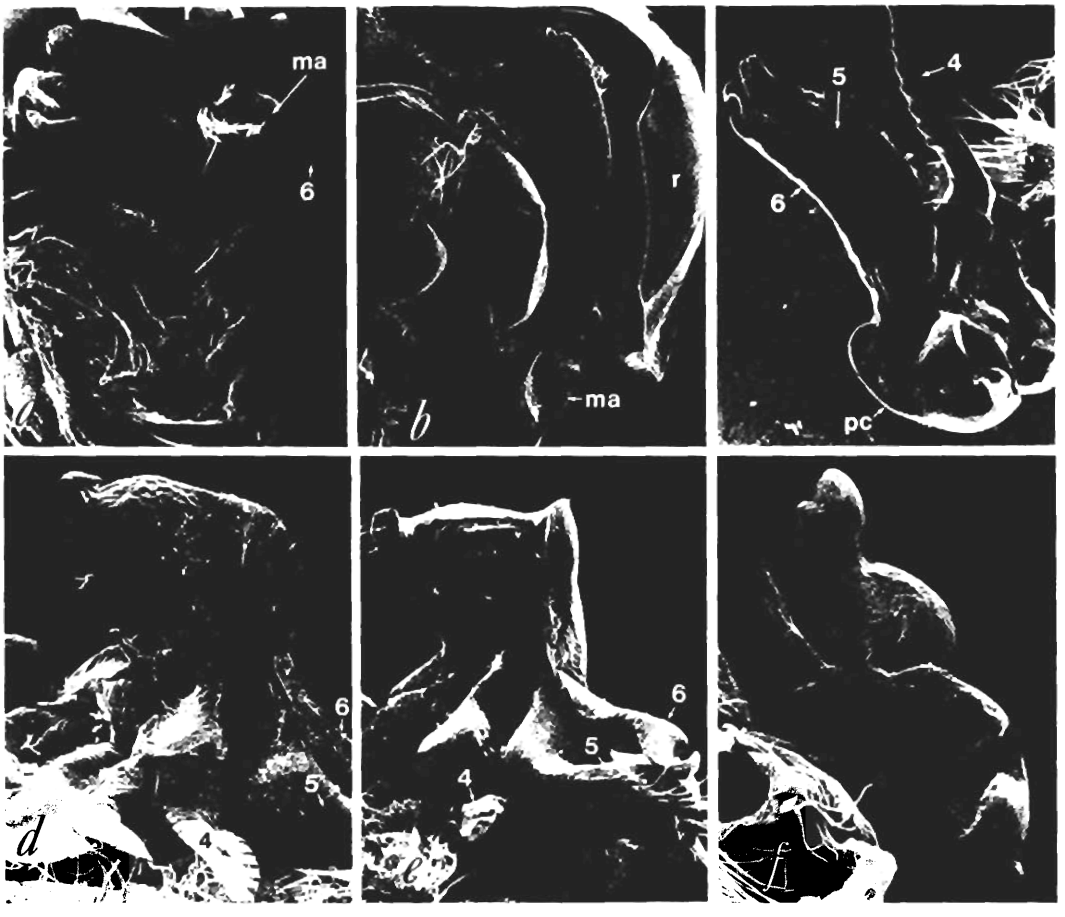

Fig. 15. SEM of selected characters of *P. texana, P. mapimi,* and *Lynceiopsis perrieri. Paralimnetis texana*: *a,* ventral view of male with major clasper (ma) endite 6 of second thoracopod indicated, ×55; *b,* lateral view of anterior region, ×65; *c,* modified male second thoracopod showing endites (numbered) and protopodal complex (pc), ×110; *d,* protopodal complex turned 90° to face viewer, ×170. r = rostrum, pc = protopodal complex. *Paralimnetis mapimi*: *e,* protopodal complex oriented as for *d* for comparison, ×190. *Lynceiopsis perrieri: f,* distal end of male modified second thoracopod, ×130.

of *Lynceus* (*L. aequatorialis* and *L. simiaefacies*; see Remarks under *L. aequatorialis*). Because the second thoracopod in *Lynceus* is unmodified, it is probable that *Lynceus* is the oldest of the three genera. *Lynceus aequatorialis* appears to be somewhat intermediate between *Lynceus* and *Paralimnetis,* since the second thoracopod of *L. aequatorialis* is slightly modified and the clasper is thick and globose (and thus more like *Paralimnetis*) relative to most species of *Lynceus.* Although the second thoracopod is modified in both *Paralimnetis* and *Lynceiopsis,* the modifications are different, and it is difficult to envision a transformation from one to the other. Lynceid distributions are poorly known. Some species are known from a single location, whereas others (e.g., *Lynceus brachyurus*) are nearly cosmopolitan. It is probable that most species are more widespread than currently reported, and knowledge of lynceid distributions will doubtless increase with further investigation. A recent example is the finding of *L. gracilicornis* in Florida and North Carolina, extending the known range from Texas. Because our knowledge of distributions is so incomplete, it would be premature to draw any biogeographic and/or phylogenetic conclusions on the basis of known geographic distributions.

Lynceid Morphology and Classification

Several workers have noted that lynceids differ markedly from other families of the Conchostraca. Salient characters serving to

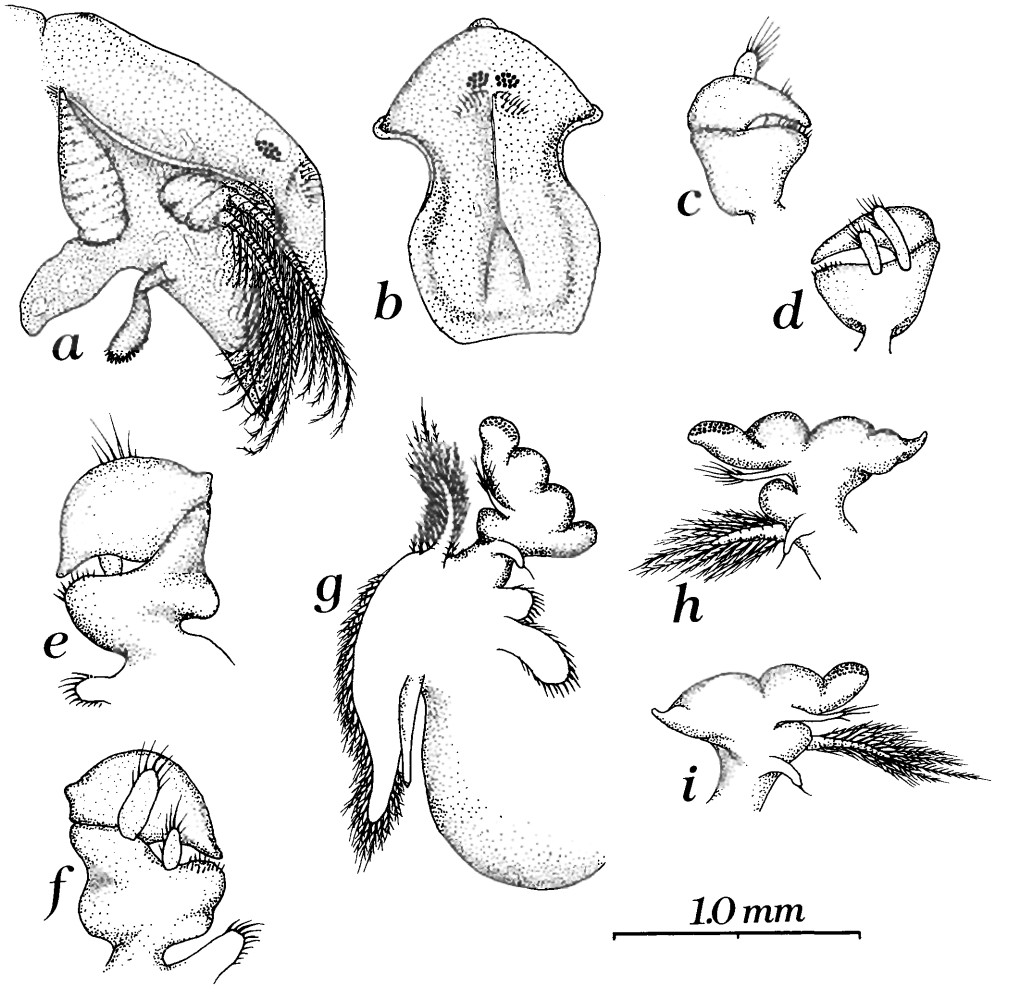

Fig. 16. *Lynceiopsis perrieri* Daday. *a,* lateral view of head region, male; *b,* frontal view of head region, male; *c,* anterior face of minor (left) clasper; *d,* posterior face of minor clasper; *e,* anterior face of major (right) clasper; *f,* posterior face of major clasper; *g,* modified second thoracopod of left side; *h,* same appendage, turned slightly to show hooked end of lobed region; *i,* different specimen with modified second thoracopod on right side, distal region only.

separate the family are the cruciform head of the larvae, spherical carapace lacking growth lines or umbo, hingelike joining of the two valves, low number of trunk somites, absence of caudal furca or dorsal abdominal spines, two-segmented first antenna, opercular lamellae, female abdominal lamellae, and strongly serrate mandibles. Several of these characters were thought by Linder (1945) to be "larval characters" (i.e., paedomorphic). Carapace shape, as an example, is known to change with ontogeny in lynceids (e.g., see Sars, 1896, plate 17; Retallack and Clifford, 1980) and in other families of the Conchostraca (e.g., Anderson, 1967, for the Limnadiidae), and growth lines are absent in early developmental stages of other families (e.g., Sars, 1896, for *Limnadia lenticularis*). Strenth and Sissom (1975), in a study of postembryonic development, stated that growth lines in *Eulimnadia texana* appear related to the number of molts, and Vidrine *et al.* (1987) provided direct evidence from observations on a natural population that number of growth lines is related to age and increase in size. The low number of trunk segments and absence of dorsal abdominal spines and caudal furcae could possibly reflect neotenous or paedomorphic development (suggested by Linder, 1945), since several species outside the Lynceidae pass through stages of develop-

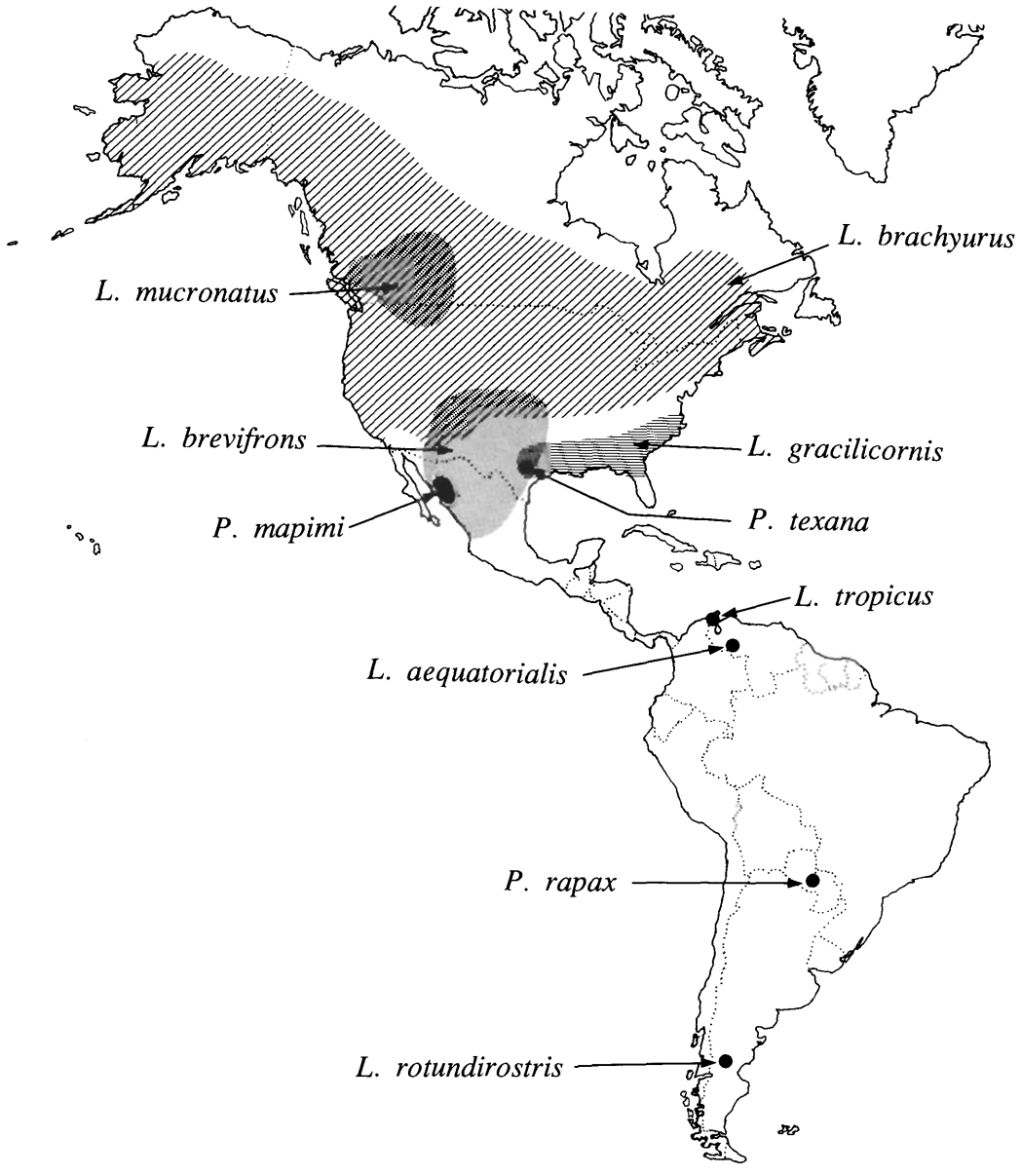

Fig. 17. Estimate of geographic distribution of species of the Lynceidae in the Americas; see species accounts for more precise data. Location of *Lynceus tropicus* assumes that Daday (1927) meant Guarapana rather than Guanaparo, a name that could not be located on currently used maps of Venezuela. All ranges are slightly exaggerated to approximate probable distributions; see text.

ment in which dorsal spines and caudal furcae are absent, whereas adults of these species possess spines and furcae. However, such spines appear very early in the development of other branchiopods, such as ctenopod and anomopod cladocerans and the clam shrimp genus *Cyclestheria* (Geoffrey Fryer, personal communication).

Linder (1945) also proposed a possible phylogenetic affinity between lynceids and the Notostraca. While the former explanation (paedomorphosis) is of moderate interest, the latter (relationship to notostracans), if true, is significant and could well necessitate a reexamination of phylogeny within the Branchiopoda. Some of our observations have a bearing on these two purported explanations. Calman (1909) noted that in the Notostraca a small pit maintains a connection between an inner space above

the compound eye and the outside environment. This pit is similar to that seen in the Lynceidae (Fig. 2*d*). However, we have now found this pit in other families of the Conchostraca (J. W. Martin, unpublished) and it can no longer be argued that lynceids and notostracans alone possess this pit. The carapace hinge of lynceids resembles that of some ostracods, with a distinct median depression between the valves and interlocking edges of the dorsal valve border (although the two valves are still contiguous; see Fig. 2*a,b*). The hinge structure of *Lynceus* would *not* be expected if lynceids are more closely related to notostracans than to other clam shrimps. The simple folding of the carapace into two valves, seen in all other conchostracan families, is much closer to what one would expect in an intermediate form. It seems likely that the carapace has arisen more than once in the Branchiopoda (see also Fryer, 1987). The form of the maxillary gland has been called similar to that of the Notostraca, or intermediate between notostracans and other clam shrimps (Cannon and Manton, 1927). We do not see this distinction, since the gland in lynceids (see Martin, 1988) is no more elongate than in certain limnadiids. Fryer (1987) feels that the shape of this gland reflects only the available space beneath the carapace and is of no phylogenetic importance. The triturating surface of the lynceid mandible (see Martin, 1988) is similar to that of the notostracans, which also possess a large mandible with few large distal denticles. However, the muscular system (and the function) is totally different, and the resemblance is only a superficial one (Geoffrey Fryer, personal communication).

Lynceids possess a suite of characters found in no other conchostracan or any other member of the Branchiopoda. The most obvious of these are the setose sensory fields, true hinge on the carapace, and opercular lamellae on the penultimate segment. The lower number of trunk somites, and the consistency of this number (12), are also unique to lynceids in all of the Branchiopoda. Linder (1945) noted that "one must find the fixation of the number in the Lynceidae significant, and this impression is stressed by the fact that the segment series here finishes with a segment bearing a specialized structure, the opercular lamella, a kind of ending [to] the series that is unknown in all other Branchiopoda." The larger head region, while serving to separate the lynceids from the other clam shrimps, differs mostly in size and only slightly in form and function (it is capable of protruding outside the carapace valves). It is unfortunate that our observations could not confirm Linder's (1945) belief that the vas deferens passes through the anal somite of the male, rather than emptying at the base of a posterior thoracopod as believed by Grube (1853) and Sars (1896). If Linder is correct, then lynceids are unique in this respect, since the genital opening of all other clam shrimps is on the eleventh somite.

Many of the Branchiopoda, such as some cladocerans (see Calman, 1909; Frey, 1959), possess an anterior "dorsal organ" or "adhesive organ" near the posterior head region. In the conchostracan family Limnadiidae this organ, which we do not believe is homologous to that of cladocerans, is produced and pedunculate and often referred to as a frontal organ. The dorsal organ of the Lynceidae may be homologous to that of the limnadiids, since it is found in the same location, and therefore distinguishes the family Lynceidae further from the Notostraca, which have no such organ. However, functions and homologies of the various "dorsal organs" in branchiopods are uncertain at best.

The separation of the lynceids into a tribe or suborder (Laevicaudata) apart from all other conchostracans (Spinicaudata) by Linder (1945), followed by Tasch (1969), is easily justified. Fryer (1987) has clearly recognized the degree to which lynceids differ from other conchostracans, and he includes additional characters, such as the arrangement of the antennary muscles, that distinguish the lynceids (Laevicaudata) from other clam shrimps. Because of the many fundamental differences between the two groups, Fryer suggested that the Laevicaudata and Spinicaudata be raised to ordinal level, and that the taxon Conchostraca be rendered invalid. By documenting several of the unique lynceid characters in all genera and many species, our study lends support to Fryer's proposal.

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Addendum

The following publication, which contains additional records of *Lynceus brachyurus* and *L. mucronatus* from Canada, came to our attention too late to be incorporated into the text.

Chengalath, R. 1987. Bibliographia invertebratorum aquaticorum Canadensium, volume 7. Synopsis speciorum. Crustacea: Branchiopoda.—National Museum of Natural Sciences, Ottawa, Canada. Pp. i–v, 1–119.