WHAT IS *NEPA HOFFMANNI* (HETEROPTERA: NEPIDAE)? MALE GENITALIA HOLD THE ANSWER, AND DELIMIT SPECIES GROUPS

S. L. Keffer,[1] J. T. Polhemus,[2] and J. E. McPherson[1]

[1]Department of Zoology, Southern Illinois University,
Carbondale, Illinois, 62901
[2]University of Colorado Museum, 3115 S. York St.,
Englewood, Colorado 80110

Abstract.—*Nepa hoffmanni* Esaki is different somatically from its congeners; therefore, we here examine its generic assignment by comparing the male genitalia of *N. hoffmanni, N. cinerea* Linnaeus, *N. sardiniensis* Hungerford, and *N. apiculata* Uhler. Three diagnostic genitalic character states were found for the four taxa confirming *hoffmanni*'s membership in *Nepa*. In addition, internal genitalic structures clearly delimit two species groups within *Nepa*: an *apiculata* group composed of *N. apiculata* and *N. hoffmanni,* and a *cinerea* group composed of *N. cinerea* and *N. sardiniensis.* Finally, we hypothesize that internal genitalic characters can be used to delimit waterscorpion genera.

Esaki concluded his 1925 description of *Nepa hoffmanni* with four diagnostic characters for his new species. Compared to the two other species then in the genus *Nepa,* i.e., *N. cinerea* Linnaeus and *N. apiculata* Uhler, *N. hoffmanni* was much larger, had stouter legs (particularly the forelegs), a much shorter caudal respiratory siphon, and a relatively shorter abdomen (p. 314), characteristics that would seem to ally *hoffmanni* with *Telmatotrephes* Stål rather than *Nepa* (Lansbury, 1972a; Keffer et al., 1989). Currently, there are five species in *Nepa* (*N. apiculata,* eastern North America; *N. cinerea* with eight recognized subspecies, Europe, North Africa and northeast Asia; *N. hoffmanni,* northeast Asia; *N. remyi* Poisson, Morocco; *N. sardiniensis* Hungerford, Corsica and Sardinia) (Poisson, 1961; Tamanini, 1973) and *hoffmanni* differs somatically from all its congeners. Therefore, we here assess the generic assignment of *N. hoffmanni* by comparing its male genitalia with those of other *Nepa* species.

Ivor Lansbury, the preeminent taxonomist of the Nepidae over the last two decades, laid the groundwork for this study with his 1967 work on male Australian Nepidae. He later figured the male genitalia of other nepid genera in various revisionary works (1972a, b, 1973a, b, 1974a, b, 1978). Other workers who have figured male waterscorpion genitalia include Hamilton (1931), Larsen (1938), Kumar (1961) and De Carlo (1968).

MATERIALS AND METHODS

Specimens of *N. hoffmanni* from Japan; *N. cinerea* from Finland, Portugal and Morocco; *N. sardiniensis* from Sardinia; and *N. apiculata* from Illinois were dissected (*N. remyi* was not seen). The technique followed in the dissections was that of Lansbury (pers. comm.). Abdomens of relaxed specimens were immersed in dimethyl

sulfoxide and then washed in alcohol. The outer margins of ventral laterotergites six and seven were cut with iridectomy scissors and then levered away, exposing the genital capsule. The apodemes attaching the capsule to the respiratory siphons were cut and the capsule then pulled free with spatulate forceps. After soaking in 10% KOH at room temperature for 24 hours the capsule was rinsed in glacial acetic acid and distilled water. The internal genitalic structures were exposed by cutting the capsule along one lateral margin and then severing the apodemes holding the internal structures to the inner capsule wall. In order to see the innermost structures it was then necessary to cut away one phallothecal plate and half of the anterior diverticulum of the internal genitalia (see below for description of terms). The genitalia were cleared in clove oil and drawings were prepared using a 10 × 10 ocular grid.

In the figures that accompany the text *N. cinerea, N. hoffmanni,* and *N. apiculata* are illustrated. *N. sardiniensis* is not figured because its male genitalia was found to be nearly identical with all the *N. cinerea* specimens.

RESULTS

Genital capsule. Lansbury has described waterscorpion genitalia as a "box within a box within a box" (pers. comm.). The outermost box is the genital capsule shown in lateral (Figs. 1–3), dorsal (Figs. 4–6), and ventral (Figs. 7–9) views. Two differences were found to occur between the four taxa. First, the anal cone (ac) of *N. hoffmanni* is constricted distally in dorsal view (Fig. 4), a condition not found in *N. sardiniensis, N. cinerea* (Fig. 5) or *N. apiculata* (Fig. 6). Second, the distal hook of the paramere (p) in *N. hoffmanni* (Fig. 7) and *N. apiculata* (Fig. 9) lies at a right angle to the long axis of the paramere and extends medially beneath the paramere's ventral edge while in *N. cinerea* (Fig. 8) and *N. sardiniensis* the hook lies mostly in the longitudinal plane of the paramere. *N. remyi,* the one *Nepa* species not seen in this study, also has the *cinerea* type paramere (Poisson, 1961, pp. 635–637).

Internal genitalia. Within the genital capsule is the second "box" which consists of a set of structures called by Lansbury the internal genitalia. All four taxa exhibit a high degree of uniformity in the arrangement of their internal genitalic structures (Figs. 10–12). An anterior diverticulum (ad) is short and heavily sclerotized. A median phallotheca (ph) is comprised laterally of heavily sclerotized phallothecal plates (pp). Dorsal to the phallotheca, paired basal plates (bp) are connected medially by a bridge (not shown in lateral view). Paired lateral arms of the basal plates (labp) curve around the anterior end of the phallotheca and posterior end of the anterior diverticulum and unite ventrally in a lamina ventralis (lv) which extends caudad. The lateral arms are clearly bipartite in all four taxa with the ventral and dorsal parts joined by membrane. Bipartite lateral arms have not been reported elsewhere in the Nepidae. This character state is thus diagnostic for these species. All four taxa have a large ejaculatory duct (ed) which passes beneath the anterior diverticulum and between the lateral arms and then into the phallotheca. Caudally, in all four taxa a membranous posterior diverticulum (pd) is framed laterally by sclerotized secondary struts (ss) which emanate from inside the phallotheca and extend to the distal margin of the posterior diverticulum. In no other species of the Nepidae thus far studied do secondary struts reach the distal margin of the posterior diverticulum. This character state constitutes a second diagnostic feature for these four *Nepa* species.

Two internal genitalic character state differences are evident. In *N. hoffmanni* (Fig.
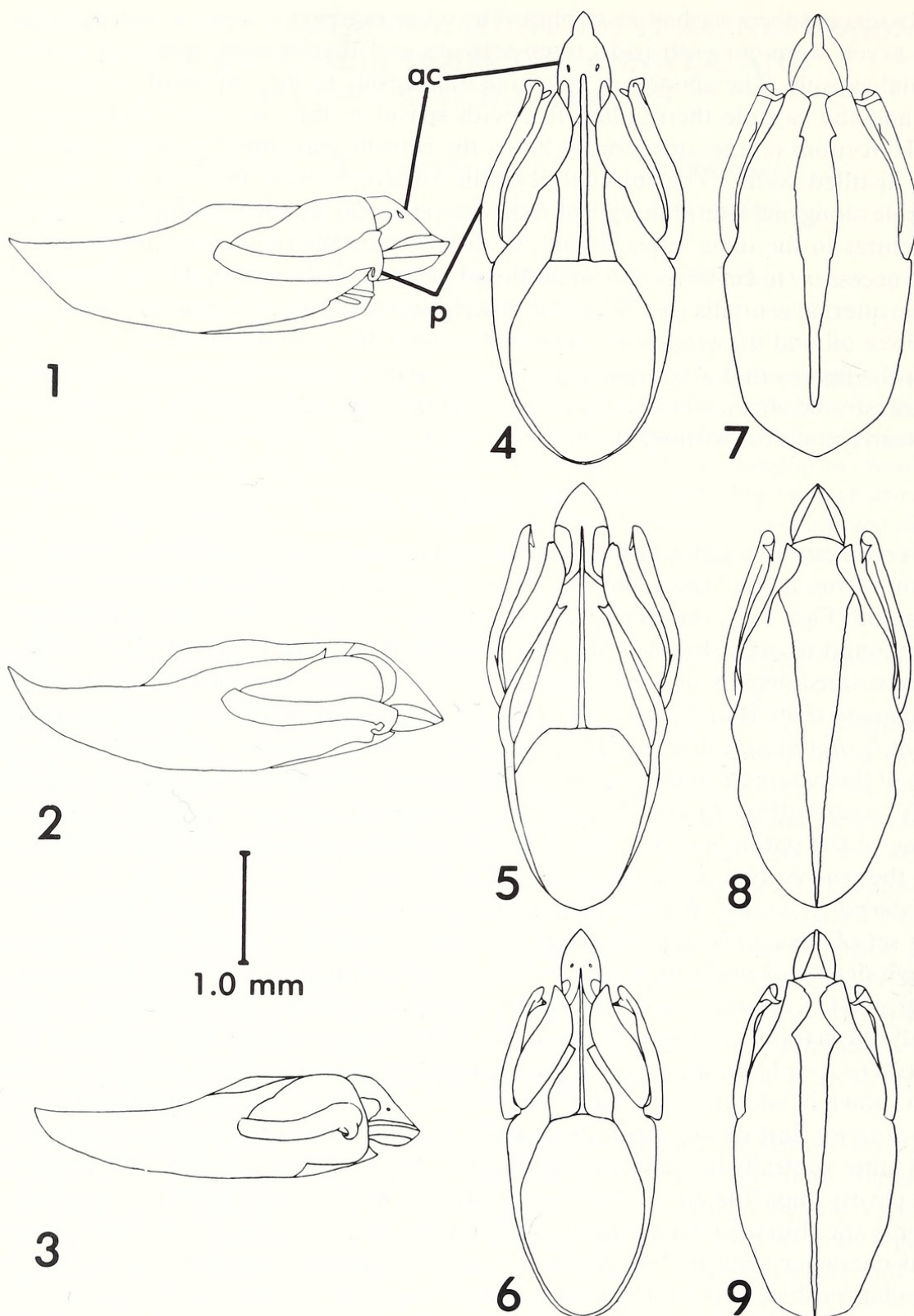
Abbreviations used in the figures.   ac, anal cone; ad, anterior diverticulum; bp, basal plates; bvr, break in the vesical rod; cs, central strut; e, endosoma; ed, ejaculatory duct; er, ejaculatory reservoir; labp, lateral arms of the basal plate; lv, lamina ventralis; p, paramere; pcs, process of the central strut; pd, posterior diverticulum; ph, phallotheca; pp, phallothecal plate; slr, sclerotized lever rods of the vesica; ss, secondary strut; v, vesica; vr, vesical rod.

10) and *N. apiculata* (Fig. 12) the dorsal margin of the posterior diverticulum is always shorter in lateral view than that of the anterior diverticulum while in *N. sardiniensis* and *N. cinerea* (Fig. 11) the dorsal margin of the posterior diverticulum is always longer. In *N. hoffmanni* and *N. apiculata* the posterior diverticulum ventrally descends well beneath the ventral margins of the exposed secondary struts. In contrast, the posterior diverticulum ventrally of *N. cinerea* and *N. sardiniensis* descends only partially beneath the ventral margins of the secondary struts.

Endosoma and ancillary structures. By removing the phallothecal plate and anterior diverticulum from one side of the internal genitalia, one reveals the innermost "box" of the male genitalia, a rather bewildering array of single and paired structures (Figs. 13–15) termed by Lansbury the endosoma and ancillary structures. In all four taxa a single median central strut (cs) is attached caudally to the lamina ventralis (lv) by membrane. Basally, the central strut is broadened into paired symmetrical processes (pcs). Above these processes are the paired secondary struts (ss). The cephalic end of the central strut is joined to the ejaculatory reservoir (er) which in all four taxa is broadly triangular. The vesica (v) is enclosed in an inverted U-shaped vesical rod (vr) which in all four species is bipartite. Bipartite vesical rods are not found elsewhere in the Nepidae and this is, therefore, a third diagnostic character state for the four *Nepa* species. Paired sclerotized lever rods of the vesica (slr) are attached anteriorly to the vesical rod, and from there descend into the phallotheca forming a deep (*hoffmanni* and *apiculata*) or shallow (*cinerea* and *sardiniensis*) concavity before ascending to the anterodorsal margin of the posterior diverticulum. The lever rods then descend to the dorsolateral margins of the posterior diverticulum and become thinner and very lightly sclerotized. They then extend posteriorly, meeting medially just distal and ventral to the upturned apex of the posterior diverticulum. The vesica and vesical rods are enclosed in a hyaline endosoma (e) which extends from the posterodorsal margin of the anterior diverticulum to the upturned apex of the posterior diverticulum and is attached variously to the central strut, the sclerotized lever rods, and the posterior diverticulum.

Differences between the four taxa occur in the shape and composition of the vesical rods. In *N. hoffmanni* (Fig. 13) and *N. apiculata* (Fig. 15) the break in the vesical rod (bvr) occurs in the posterior diverticulum, ventral to the secondary struts in *hoffmanni* and dorsal to the secondary struts in *apiculata*. The vesical rod anterior to the break is sinuate, descending into the phallotheca and then to the posterior diverticulum. Posterior to the break the rod ascends in, and then emerges from, the posterior diverticulum and ends simply. In *N. cinerea* (Fig. 14) and *N. sardiniensis* the break in the vesical rod occurs at the phallotheca/posterior diverticulum border. Anterior to the break the rod is straight, posteriorly it is shallowly concave, and distally the rod ends in a spear-shape. In all *Nepa* species examined the anterior section of the vesical rod is heavily sclerotized and rigid. Posteriorly, the vesical rods

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Figs. 1–9. Genital capsule. Lateral view: 1. *N. hoffmanni.* 2. *N. cinerea.* 3. *N. apiculata.* Dorsal view: 4. *N. hoffmanni.* 5. *N. cinerea.* 6. *N. apiculata.* Ventral view: 7. *N. hoffmanni.* 8. *N. cinerea.* 9. *N. apiculata.*
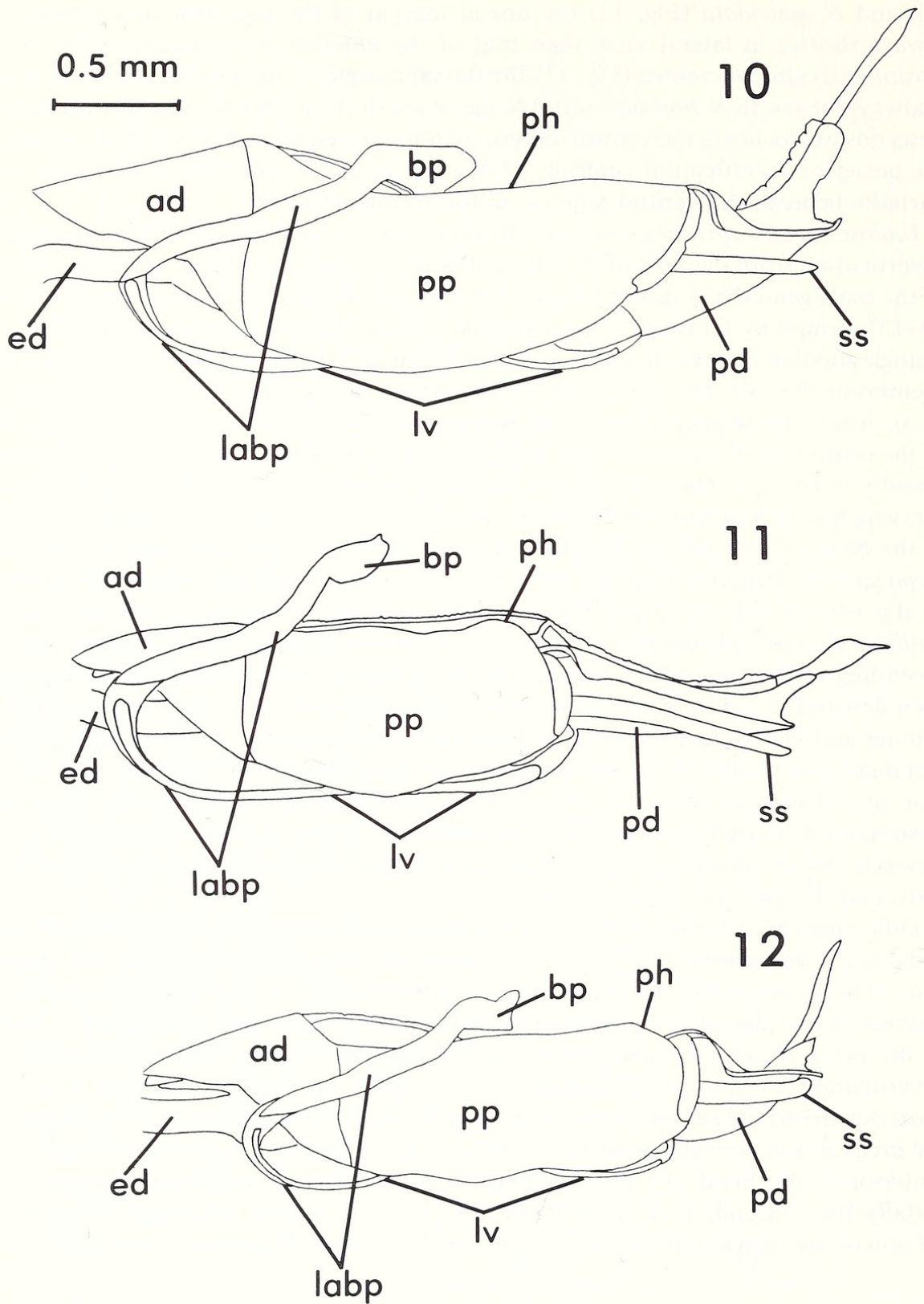
Figs. 10–12. Lateral view of internal genitalia. 10. *N. hoffmanni* 11. *N. cinerea*. 12. *N. apiculata*.
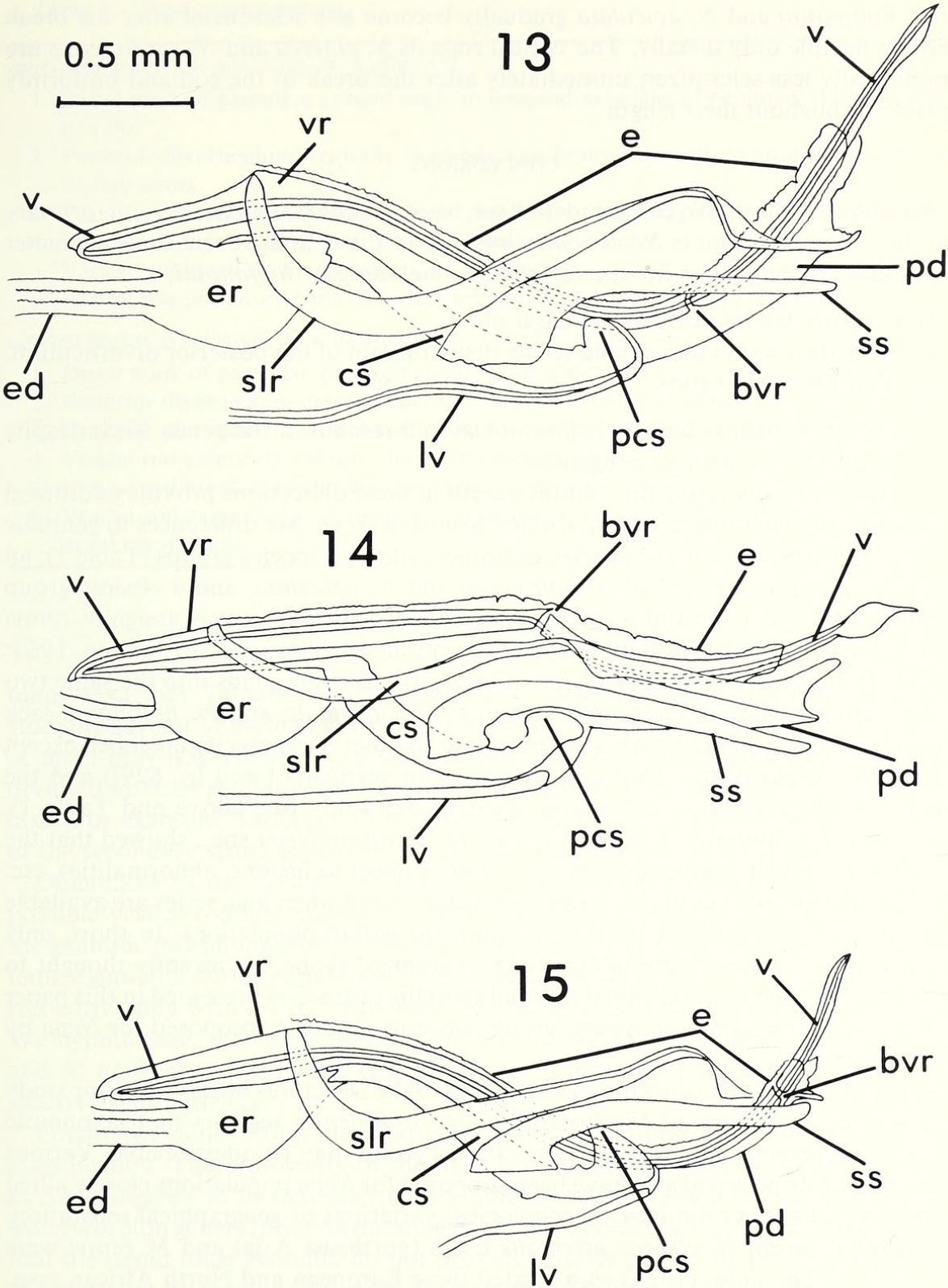
Figs. 13–15. Lateral view of endosoma and ancillary structures. 13. *N. hoffmanni*. 14. *N. cinerea*. 15. *N. apiculata*.

of *N. hoffmanni* and *N. apiculata* gradually become less sclerotized after the break and are flexible only distally. The vesical rods in *N. cinerea* and *N. sardiniensis* are dramatically less sclerotized immediately after the break in the rod and uniformly flexible throughout their length.

CONCLUSIONS

Amidst this mass of genitalic detail we have, of course, answered our primary question, namely, what is *Nepa hoffmanni*? These dissections reveal three character states that are diagnostic for species of *Nepa* including *N. hoffmanni*:

1) Bipartite lateral arms of the basal plate.
2) Secondary struts that extend to the distal margin of the posterior diverticulum.
3) Bipartite vesical rods.

We therefore conclude that *N. hoffmanni* should remain in the genus *Nepa* despite somatic differences with its congeners.

In addition to answering our central question, these dissections provide additional taxonomic information regarding species groups in *Nepa*. Six differences in genitalic structure clearly separate the species examined into two species groups (Table 1): an *apiculata* group composed of *N. hoffmanni* and *N. apiculata,* and a *cinerea* group composed of *N. cinerea* and *N. sardiniensis*. We can also tentatively assign *N. remyi* to the *cinerea* group because the shape of its paramere is *cinerea*-like (Poisson, 1961: 635–637). Poisson, in his 1961 review of *Nepa,* divided the genus into the same two species groups using differences in antennae (*N. apiculata* and *N. hoffmanni* lack lateral lobes on the penultimate segment while all other *Nepa* species are lobed except *N. cinerea dollfusi* Esaki which has the last two segments fused [p. 629]) and the same differences in paramere shape noted in our study (see above and Table 1). Subsequently, Tamanini, in a 1973 review of European *Nepa* spp., showed that the antennae of a given species are quite variable, subject to fusions, abnormalities, etc. Thus, antennae are of doubtful taxonomic value except when long series are available to establish a "normal" or most common form within populations. In short, only one of Poisson's species group characters, paramere shape, is currently thought to be valid. Thus, the five additional internal genitalic characters presented in this paper confirm and strengthen the species group concepts originally proposed for *Nepa* by Poisson.

The high degree of uniformity of internal genitalic structures observed in our study between the specimens of *N. cinerea* and *N. sardiniensis* suggests that taxonomic differences currently recognized in the *cinerea* group may be questionable. Various species and subspecies names have been proposed for *Nepa* populations closely allied to *cinerea,* all based on minor morphological variations or geographical separation. All of these except *N. cinerea orientalis* Esaki (northeast Asia) and *N. remyi* were reviewed by Tamanini (1973) who treated these European and North African taxa, with the exception of *sardiniensis,* as subspecies of *cinerea*; these include the nominate subspecies *cinerea* Linnaeus (northern Europe), *dollfusi* (Morocco), *major* Bergevin (Morocco), *meridionalis* Poisson (southeast Europe, Algeria, Tunisia), *minor* Puton (Mediterranean region), *poissoni* Tamanini (Pyrenees, southeastern Spain) and *seurati* Bergevin (southern Italy, Sicily, Tunisia, Tripolitania). Earlier Poisson (1961) provided analysis of roughly the same group of taxa; in this work he treated as species

Table 1. *Nepa* species groups.

apiculata group: *N. apiculata, N. hoffmanni*

1. Distal hook of paramere at right angle to longitudinal plane of paramere (Poisson, 1961, p. 629).
2. Posterior diverticulum ventrally descends significantly beneath ventral margins of secondary struts.
3. Posterior diverticulum with dorsal margin shorter than that of anterior diverticulum.
4. Vesical rod anteriorly sinuate, descends into phallotheca.
5. Vesical rod break occurs in posterior diverticulum.
6. Vesical rod posteriorly: gradually less sclerotized, flexible distally only, ends simply.

cinerea group: *N. cinerea, N. sardiniensis,* (*N. remyi?*)

1. Distal hook of paramere in longitudinal plane of paramere.
2. Posterior diverticulum descends partially beneath ventral margins of secondary struts.
3. Posterior diverticulum with dorsal margin longer than that of anterior diverticulum.
4. Vesical rod anteriorly straight, dorsal in phallotheca.
5. Vesical rod break at phallotheca/posterior diverticulum border.
6. Vesical rod posteriorly: abruptly less sclerotized, uniformly flexible throughout length, distal spear-shape.

many taxa that Tamanini later relegated to subspecies status. Nico Nieser, after studying several of these taxa from southeastern Europe, suggests (in litt.) that some of them may not warrant even subspecies status. It is possible that analysis of individual internal genitalic structures may help clarify the status of the *cinerea* group taxa. For example, Tamanini (1973) noted a difference in the posteroventral shape of the secondary struts between *N. c. cinerea* and *N. sardiniensis* (p. 259).

Differences in the vesical rod morphology of the two species groups suggests a possible vesical rod/spermathecal lock-and-key effect. Larsen, in his 1938 study of the genitalic morphology of *N. cinerea,* illustrated the conformation of the male and female genitalia during copulation. His figure 26 (p. 63) shows the break in the vesical rod correlating with a 180° switchback in the spermatheca (see also fig. 18, p. 56). We hypothesize, therefore, that the more distal vesical rod breaks in *N. apiculata* and *N. hoffmanni* will match correspondingly more distal switchbacks in their respective spermathecae.

Finally, we believe that our study has important implications for waterscorpion classification. The uniformity of the male genitalia across divergent external forms in *Nepa* suggests to us that internal genitalic characters may be useful in delimiting waterscorpion genera, notwithstanding Lansbury's (1967:647; 1974b:226) contention that the nepid male genitalia do not provide reliable subfamily or tribal characters in the genera he studied. We intend to test our hypothesis in forthcoming revisions of nepid genera.

our study would not have been possible without the help of Dr. Lansbury who very generously shared his dissection protocol with the senior author.

Specimens examined were provided by the following: Southern Illinois University Entomological Collection (*N. apiculata*), Polhemus Collection (University of Colorado Museum at Englewood) (*N. hoffmanni, N. cinerea,* and *N. sardiniensis*), and Dr. Nico Nieser, Tiel, The Netherlands (*N. cinerea*). We also thank Dr. Nieser for sharing his assessment of certain European subspecies of *N. cinerea*.

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