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Studies of male sexual tubes in hermit crabs (Crustacea: Decapoda: Anomura: Paguroidea). III. Morphology of the sexual tube in *Catapagurus sharreri* A. Milne-Edwards, 1880 (Paguridae)

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ABSTRACT

This study, the third of a multi-part series on male sexual tubes in hermit crabs, the external morphology of the tube of the western Atlantic *Catapagurus sharreri* A. Milne-Edwards, 1880 is documented using scanning electron microscopy. The male of this species has an unpaired right sexual tube that is long (more than five coxal lengths), and curves externally and upwardly around the pleon, ending at about the mid-dorsal surface of the pleon. The tubes are subcylindrical, flexible, lack a cuticular ridge, and terminate in an opening surrounded by a dorsal beak-like and a ventral rounded lip. Setation on the tubes consist of short, simple, and relatively sparse setae, more numerous near the distal portion of the tube and gonopore. The tube is of cuticular origin, and represents an extension of the calcified right coxa. The morphology of the tip of the tube, with similar to the tip of an elephant trunk, is particularly intriguing and possibly represents a character shared with other species of *Catapagurus* A. Milne-Edwards, 1880. The tube of *C. sharreri* is compared with those documented for other species in previous parts of this series, the marine pagurid *Micropagurus acantholepis* (Stimpson, 1858), and the semi-terrestrial coenobitids *Coenobita perlatus* H. Milne Edwards, 1837 and *C. clypeatus* (Fabricius, 1787). The evolution of highly diverse sexual tubes in 63.6% of the genera of Paguridae that are known to have them, continues to raise intriguing questions for future study.

Key Words: External reproductive morphology, gonopores, spermatophores, SEM

INTRODUCTION

In the previous two parts of this study series, the external and internal morphology of the male sexual tubes, specialized structures for sperm transfer, in three species of hermit crabs, one of the family Paguridae, *Micropagurus acantholepis* (Stimpson, 1858), and two of the semi-terrestrial family Coenobitidae, *Coenobita perlatus* H. Milne Edwards, 1837 and *C. clypeatus* (Fabricius, 1787), were documented in detail using SEM and histological techniques (Tudge & Lemaitre, 2004, 2006). As discussed in these studies and by Lemaitre & McLaughlin (2003), the sexual tubes of paguroids are more complex and diverse than previously thought, and have played a significant role in the systematics of Paguroidea since they were first reported 180 years ago by H. Milne Edwards (1837). The tubes are found on the coxae of the fifth pereopods,

and to date have been found to be of two types: 1) heavily calcified prolongations of the coxae as in coenobitids and some paguroids, or 2) external prolongations of the vas deferens from one, or both of, the male gonopores, with often a chitinous sheath that is cuticular in structure, as in many paguroids.

The structure and variety of shapes, and paired or unpaired condition of the sexual tubes in males of many species of Paguridae is remarkable. The species of a good number of genera of this family have membranous, chitinous, or weakly calcified sexual tubes of varying lengths and strengths on one or both coxae (McLaughlin, 2003; Tudge *et al.*, 2012). Moreover, the number of known pagurid genera with species having sexual tubes in males has increased dramatically in the last three decades. Of the 88 currently known genera of Paguridae worldwide (Lemaitre *et al.*, 2017), 56 or 63.6% have males with sexual tubes, a large

percentage that suggests the presence of tubes is a significant evolutionary adaptation that may have contributed to the success and diversification of this family of hermit crabs. Yet, as noted by Lemaitre & McLaughlin (2003) and Tudge & Lemaitre (2004, 2006), knowledge of the morphology and function of pagurid sexual tubes remains superficial, and for the most part limited to often sketchy illustrations generally showing only external features used in taxonomic studies (e.g., de Saint Laurent-Dechancé, 1966; de Saint Laurent, 1968a, b, c, 1969, 1970a, b; Forest & de Saint Laurent, 1968; García-Gómez, 1983, 1994; Ingle, 1993; McLaughlin, 1997, 2003, 2004; Forest *et al.*, 2000; Asakura, 2001). Given the uniqueness of the male sexual tubes of paguroids, much more detailed anatomical information is needed in order to better comprehend their biological function during reproduction as well as their evolutionary significance.

In this third part of a study series of the male sexual tube of hermit crabs, we used scanning electron microscopy (SEM) to study the gross anatomy of the sexual tube in the male of *Catapagurus sharreri* A. Milne-Edwards, 1880, a species of Paguridae that is found abundantly in moderately deep waters (80–500 m) of the western Atlantic, and ranging from the northeastern coast of the United States, Gulf of Mexico, and the Caribbean, to Brazil (Felder *et al.*, 2009). This species is one of 24 known in the worldwide genus *Catapagurus* A. Milne-Edwards, 1880, of which only *C. sharreri* and *C. gracilis* occur in the western Atlantic. The species of *Catapagurus* are characterized, along with other anatomical characters, by the males having a prominent sexual tube on the coxae of the fifth pereopod (McLaughlin 2003, 2004). Given the increased interest in hermit crab reproductive morphology and the use of these male secondary sexual structures to investigate phylogenetic relationships (Tudge, 1991, 1999a, b; Jamieson & Tudge, 2000; Manjón-Cabeza & García Raso, 2000; Hess & Bauer, 2002), this basic descriptive information of the sexual tubes of *C. sharreri* should be useful to provide context and data for future investigations.

MATERIALS AND METHODS

Morphological terminology for the male sexual tubes follows the previous two parts of this series (Tudge & Lemaitre, 2004, 2006). General pagurid anatomical terminology is according to McLaughlin (2003), including the protocol suggested therein for describing the length of the sexual tube. The shield length, measured in millimeters, is the standard measurement reported for paguroids to indicate relative size, and is taken from the tip of the rostrum to the midpoint of the posterior margin of the shield.

Male specimens of *C. sharreri* came from the preserved collections of the National Museum of Natural History, Smithsonian Institution, Washington DC (USNM), as follows: three males, shield length 5.0–8.0 mm, USFC Albatross, station 2245, south of Nantucket Shoals, Massachusetts, United States, 179 m, 26 September 1884 (USNM 8693); one male, shield length 4.0 mm, USFC *Albatross*, station 2418, 33°20'00"N, 77°05'00"W, off Cape Fear, North Carolina, USA, 165 m, 2 April 1885 (USNM 9865). The specimens were originally preserved in formalin and subsequently stored in 70% ethanol. Undamaged and complete (with all appendages) males with intact sexual tubes and the surrounding coxal area were selected for dissection and observation from each of these large USNM lots containing multiple specimens of the same species. The selected specimens were manually cleaned under a dissecting microscope, using a sable brush and then sonicated for 20 s in a Rapidograph ultrasonic cleaner (Crest Ultrasonics, Ewing Township, NJ, USA). Specimens were dehydrated in a graded ethanol series (75%, 95%, 2 × 100% at 5 min intervals). The second change to 100% ethanol made

immediately before the critical point drying to ensure that all water was removed. Critical point drying was performed for 2.5 h using a Bal-Tec CPD 030 critical point dryer (Columbia Nano Initiative, New York, NY, USA). Samples were then mounted on large, single stubs using carbon-impregnated sticky tabs, and placed in an oven to allow for the specimens to completely adhere to the tabs. Specimens were initially coated in a Cressington sputter coater (Cressington Scientific, Watford, UK) with gold palladium for 180 sec. Sputter coating was repeated three times, for 2.5 min each time, to ensure that the entire specimen was covered. Specimens were stored in a vacuum desiccator. Micrographs were taken using a Leica scanning electron microscope (Leica Microsystems, Wetzlar, Germany), at 10–20 kV. The stubs with the dissected sexual tubes used for SEM remain deposited in the USNM.

RESULTS

The sexual tube in *Catapagurus sharreri* consists of a long tubular extension on the coxa of the fifth right pereopod directed towards the exterior, then curving and directed straight upward and again curved slightly over the dorsal side of the pleon, ending at about the mid-dorsal level of the pleon (Fig. 1). The tube is weakly calcified but is still relatively flexible. Occasionally the left coxae of the fifth pereopod may have a small membraneous papilla (Fig. 2D, E) produced on the gonopore and partially obscured by dense

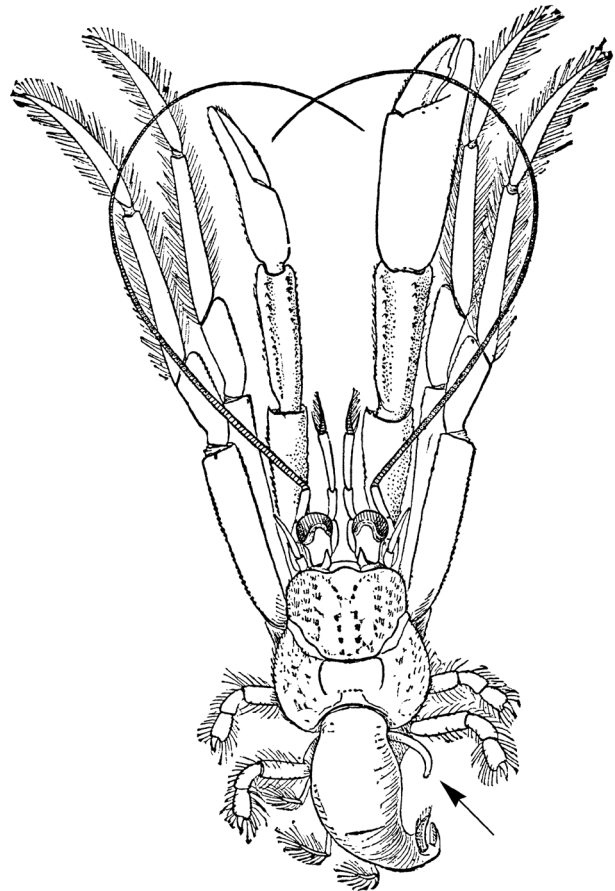


Figure 1. Male of *Catapagurus sharreri* (shield length ~6.7 mm) in dorsal view, showing conspicuous sexual tube on right side of pleon (arrow). Modified from Smith, 1884: pl. 4, Fig. 2.

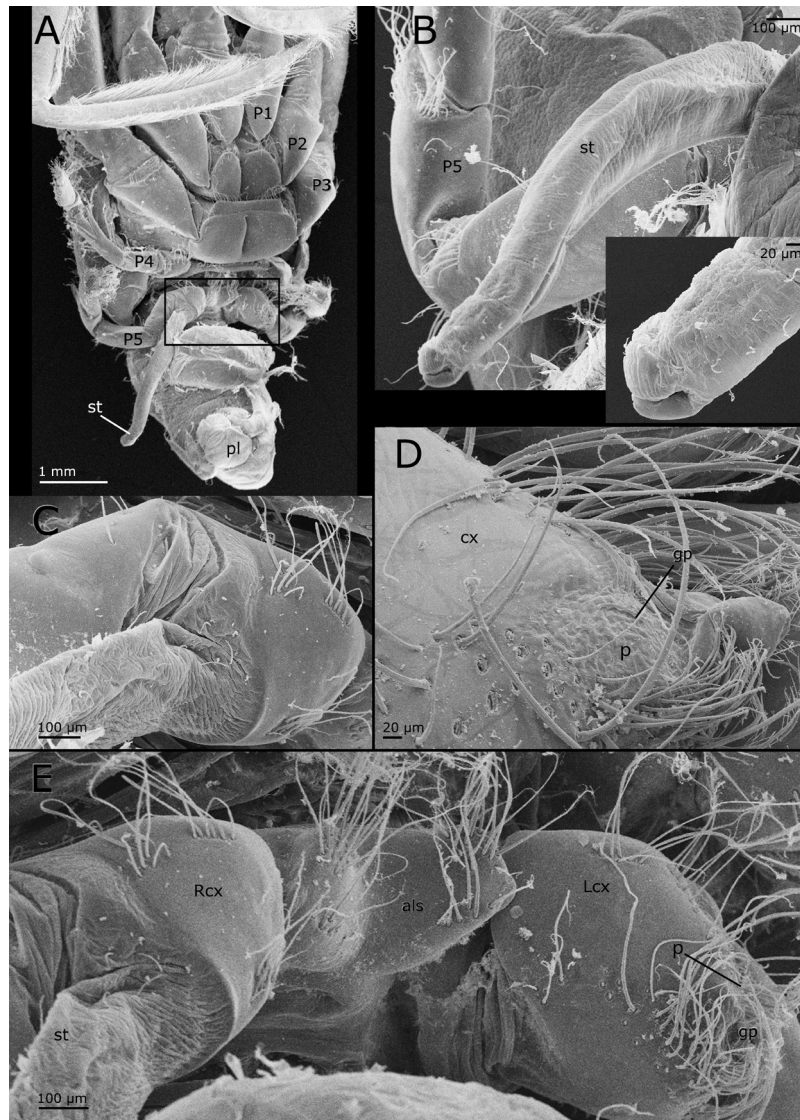


Figure 2. SEM micrographs of sternal region of *Catapagurus sharreri* with sexual tubes of two males (USNM 9865 and USNM 8693), all in ventral view. Sternum, proximal portions of pereopods with sexual tube on coxa of right fifth pereopod, and pleon (rectangle indicates enlargement in Fig. 2E) (USNM 9865) (A); enlargement of sexual tube in relation to fifth pereopod, with inset showing detail of distal portion of sexual tube (USNM 9865) (B); basal portion of sexual tube emanating from coxa of right fifth pereopod (USNM 8693) (C); enlargement of gonopore and setation on coxa of left fifth pereopod (USNM 8693) (D); enlargement of sternite XIV and coxae of fifth pereopods (rectangle in Fig. 2A), showing left gonopore with papilla and membrane, and right coxae with basal portion of sexual tube (E). ALS, anterior lobe of sternite XIV; GP, gonopore; LCX, left coxa; P, papilla; P1–5, pereopods; PL, pleon; RCX, right coxa; ST, sexual tube.

setation. This papilla, which does not appear to totally occlude the left gonopore, has no anatomical similarities with the right sexual tube.

The sexual tube is cylindrical, long (> 5 coxal lengths), extending from the right gonopore of the coxa of the fifth pereopod, to approximately the distal end of the merus of the same pereopod (Fig. 1, 2A). The tubes range in size from 2,372 μm to 2,818 μm from the distal tip to the base of the coxa, and from 2,186 μm to 2,545 μm if the coxa is included. The coxa therefore comprises a range of approximately 7% to 12% of the total tube length (Figs. 2A, 3). Compared to the shield length, the tubes range from 31.8% to 54.6% the length of the shield. The width of the tube ranges from 133 μm to 244 μm at the coxa (Fig. 2C), and from 85 μm to 172 μm (Fig. 3) distally near the tip.

In the specimens used for SEM observations, the sexual tube is directed laterally from the coxa and then curves dorsally (Figs. 1, 2A). In some male specimens not used for SEM observations, the tube can occasionally extend laterally and then curve away from the pleon. The tip of the tube can vary in morphology, sometimes ending in a slit with two lips (Fig. 2B), or ending in a part resembling the tip of an elephant trunk with a long beak-like lip and a short, rounded lip (Fig. 3, 4B). There are setae at or near the tip in all cases (Fig. 4A, B). The tip indicates clearly the presence of a lumen throughout the tube.

The tube appears divided by a groove into two distinct portions along its length: one section is smooth and another is wrinkled (Figs. 2B, 3, 4C–F). The latter portion appears to be more flexible, and can be flattened, swollen, or curved, and wraps around the smooth, more rigid portion of the tube (Figs. 3, 4C–F). There is

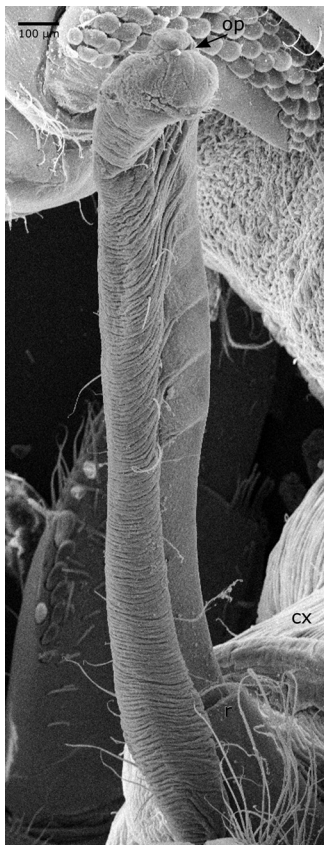


Figure 3. SEM micrograph of entire male sexual tube of *Catapagurus sharrieri* (USNM 8693) viewed from the anterior end of the crab, showing setation and morphology of tip. CX, coxae (of right fifth pereopod); OP, opening.

no apparent cuticular ridge. A more or less irregular row of well-spaced, short setae is present on the wrinkled portion and parallel to the dividing groove (Figs. 3, 4D, E).

There are short, simple setae scattered along the tube, with their density increasing distally and near the gonopore. A short transverse, more or less irregular, row of short setae is present subdistally on the tip (Fig. 4A, B). The right and left fifth coxae have relatively dense simple setae near the edges of the gonopores (Fig. 2C–E). These simple setae are longer than those found on the sexual tube itself. The setation on the left and right coxae are similar except around the gonopores. The left gonopore is obscured by dense setation around the margins, whereas on the right gonopore the surface around the margins or base of the tube is nearly barren (Fig. 2C–E).

The left fifth coxa is slightly larger than the right coxa with the sexual tube. The left gonopore is located subdistally, and has a slight protrusion or papilla (Fig. 2D, E).

No spermatophores were observed inside the tubes of the specimens examined with SEM, although under a dissection microscope they were frequently visible through the semi-transparent tube membrane in other male specimens examined in preserved USNM collections.

DISCUSSION

The presence of setae along the length of the tube, and the morphology of the tube, suggest that in *C. sharrieri* the tube is cuticular in

origin, and thus represents an extension of the calcified right coxa rather than an exterior prolongation of the vas deferens. It would appear that the cuticular margins of the right gonopore have been extended into a long sexual tube that is flexible, somewhat calcified, and with setae. Whether or not this coxal extension stands alone, or functions as a sheath to a prolonged vas deferens can only be determined by histological examination of the tube.

The presence of a lumen or interior channel in the tube of *C. sharrieri* is demonstrated by the presence of a mouth-like opening at the tip of the tube, as well as by the observations in preserved male specimens of spermatophores within the semi-transparent tube. As previously suggested for other paguroids, the sexual tubes of *C. sharrieri* must also function in the delivery of spermatophores to the female (Tudge & Lemaitre, 2004, 2006).

The tip of the tube of *C. sharrieri* has a puzzling, perhaps unique morphology, which appears to be similar to that illustrated in some species of *Catapagurus* (e.g., McLaughlin, 1997, 2004; Asakura, 2001). The tube ends in an opening surrounded by two lips, one of which is typically longer and beak-like, somewhat similar to the tip of an elephant trunk. In other species of *Catapagurus*, the tip has been described as distally “forked” (Asakura, 2001; McLaughlin, 2002). A somewhat similar, beak-like tip morphology has also been illustrated by de Saint Laurent (1968a: 73: fig 39) for the sexual tube of the pagurid *Decaphyllus junquai* de Saint Laurent, 1968a. Exactly how the lips function in *C. sharrieri* or *D. junquai* can only be speculated at this point. The lips could serve to open and close the terminal opening, they could serve some special function during spermatophore transfer, or serve as grasping structures. Observations of the female gonopore structure of preserved specimens of *C. sharrieri* fail to shed any light on the possible role of the sexual tube during spermatophore transfer because the female gonopores are unmodified from the typical paguroid arrangement of two symmetrical pores, one on each left and right third pereopods, without any elevation above the coxal surface.

When comparing the sexual tube of *C. sharrieri* with those in other species thus far investigated in our series, there are more morphological differences than similarities. The tubes of the marine *C. sharrieri* and the semi-terrestrial species of *Coenobita* (see Tudge & Lemaitre, 2006) have different characteristics that can be attributed to different habitat adaptations. In the former, the tube is unpaired, present on the right side only, long and flexible, and the opening has lip-like margins, whereas in the latter the tubes are paired and symmetrical, short, strongly calcified (not flexible), and the openings have thickly setose margins. The sexual tube is unpaired in the pagurid *Micropagurus acantholepis*, present on the left side only, consists of a thick, one-and-a-half coiled tube of limited flexibility, has a prominent cuticular ridge, and a small pore with a small lip around it (see Tudge & Lemaitre, 2004). In contrast, the unpaired tube of *C. sharrieri* is present on the right side only, it is curved around the side to the dorsal surface of the pleon, not coiled, a cuticular ridge is absent, and the opening has prominent lips, one of which is usually distinctly larger and beak-like.

This study, albeit presenting only some basic external morphological observations at the microscopic level, further highlights that sexual tubes in paguroids are complex, diverse structures that can differ in various anatomical characteristics and degree of symmetry. Among the Anomura, comparable sexual tubes are known outside the Paguroidea only in Aeglidae (Moraes et al., 2016), although they remain understudied. How and why these sexual tubes have evolved in such diversity, particularly among the Paguridae, continues to be a puzzle and a topic in need of further study. In the notable absence of any comparable morphological differences in female gonopore structure, the exact role of sexual tubes can only be determined by observing *in vivo* the sexual behavior and the process of spermatophore transfer.

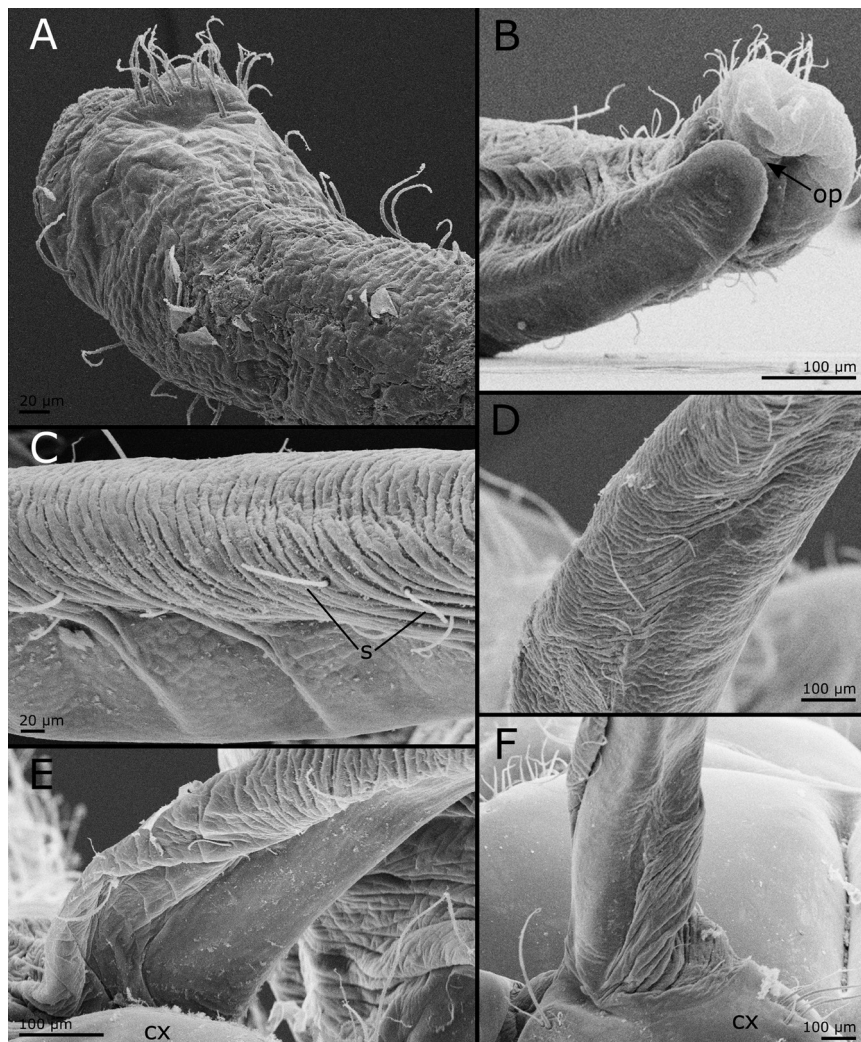


Figure 4. SEM micrographs of different parts of the sexual tube of two males of *Catapagurus sharreri* (USNM 8693 and USNM 9865). Distal portion showing subdistal transverse row of setae dorsally (USNM 8693) (A); distal portion showing beak-like and rounded lips at opening of tube (USNM 8693) (B); enlargement of lateral surface showing smooth and wrinkled regions with simple setae (USNM 8693) (C); same at lower magnification (USNM 9865) (D); close-up of basal portion showing smooth and wrinkled regions (USNM 9865) (E); same at lower magnification (USNM 8693) (F). CX, coxa; OP, opening; S, simple setae.

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