ORIGINAL ARTICLE

A review of nest and egg descriptions for the genus *Myrmeciza*, with the first description of nests and eggs of the dull-mantled antbird (*M. laemosticta*)

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Abstract We review published information on the nests and eggs of members of the polyphyletic genus of antbirds, Myrmeciza, and present the first descriptions of nests and eggs of the Dull-mantled Antbird M. laemosticta, based on three nests found in Costa Rica. We identify three distinct nest architectures within the group: bulky, bottom-supported, open cups of coarse vegetative matter; rim-suspended open cups of neatly woven fine materials; and bulky domed nests made of coarse vegetative materials. The majority of described nests (eight) belong to the first category, but the nests of M. atrothorax and M. hemimelaena have unique architectural characters which may prove to be phylogenetically informative. The nests of M. laemosticta are rim-suspended, open cups made of fibers, similar to those of M. palliata and M. hyperythra. As molecular data suggest that M. hyperythra is more closely related to Schistocichla than to M. laemosticta and M. palliata, these likely represent independent derivations of the rim-suspended architecture. M. melanoceps, M. goeldii, and M. fortis belong to the third architectural group, united by the construction of domed nests similar to hypothesized relatives. We conclude that nest architecture

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J. E. Sánchez · E. Carman Asociación de Ornitólogos Unidos de Costa Rica, 11695-1000 San José, Costa Rica is phylogenetically informative within this group and supports molecular-based hypotheses. However, more nest descriptions are needed for all species, in particular *M. longipes*, *M. berlepschi*, *M. pelzelni*, and *M. disjuncta*; and future descriptions should include architectural details such as the manner in which nests are supported by or attached to their substrate.

Keywords Dull-mantled Antbird · Egg · *Myrmeciza* · Nest · Phylogenetically informative

Zusammenfassung

Eine Übersicht über Nest- und Ei-Beschreibungen der Gattung *Myrmeciza*, mit einer Erstbeschreibung von Nest und Eiern des Grauscheitel-Ameisenvogels (*M. laemosticta*)

Wir stellen veröffentlichte Informationen über Nester und Eier von Mitgliedern des polyphyletischen Gattung der Ameisenvögel, Myrmeciza, zusammen und liefern eine erste Beschreibung von Nestern und Eiern des Grauscheitel-Ameisenvogels M. laemosticta anhand von drei Nestern aus Costa Rica. Wir stellen drei verschiedene Nest-Typen innerhalb der Gruppe fest: massige, aufsitzende, offene Becher aus grobem Pflanzenmaterial; am Rand getragene offene Becher aus ordentlich verwobenem feinen Material; und massige gewölbte Nester aus grobem Pflanzenmaterial. Der Großteil der beschriebenen Nester gehört zur ersten Kategorie, aber die Nester von M. atrothorax und M. hemimelaena weisen einzigartige Baueigenschaften auf, die möglicherweise phylogenetische Rückschlüsse erlauben. Die Nester von M. laemosticta sind am Rand getragene, offene Becher aus Fasern, ähnlich denen von M. palliata und M. hyperythra. Da molekulare Daten darauf hindeuten, dass



M. hyperythra näher mit Arten der Gattung Schistocichla als mit M. laemosticta und M. palliata verwandt ist, stellt diese Bauweise wahrscheinlich eine unabhängige Ableitung von der Architektur anderer am Rand getragener Nest-Typen dar. M. melanoceps, M. goeldii und M. fortis gehören zur dritten Gruppe, die sich durch die Konstruktion gewölbter Nester auszeichnet, ähnlich der der angenommenen Verwandten. Wir schließen daraus, dass Nestarchitektur in dieser Gruppe phylogenetische Informationen bietet, die molekular basierte Hypothesen unterstützt. Allerdings werden mehr Beschreibungen von Nestern für alle Arten benötigt, insbesondere für M. longipes, M. berlepschi, M. pelzelni und M. disjuncta. Zukünftige Beschreibungen sollten Details zur Bauweise enthalten, wie die Art und Weise, in der das Nest auf dem Substrat aufliegt oder befestigt ist.

Keywords Dull-mantled Antbird \cdot Egg \cdot *Myrmeciza* \cdot Nest \cdot Phylogenetically informative

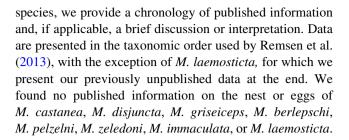
Introduction

As currently defined, the antbird genus *Myrmeciza* includes 22 species of antbirds (Thamnophilidae; (Chaves et al. 2010; Donegan 2012; Remsen et al. 2013). Recent molecular studies (Brumfield et al. 2007; Irestedt et al. 2004; Moyle et al. 2009), along with a growing number of nest descriptions, however, have revealed the now widely accepted view that *Myrmeciza* is polyphyletic (Bravo 2012; Remsen et al. 2013; Ridgely and Tudor 1994; Zimmer and Isler 2003). Records of nest architecture and egg coloration within *Myrmeciza* are, in some cases, unclear or disputed and are scattered throughout the literature, making it difficult to synthesized current knowledge.

Here we review published information on *Myrmeciza* nests and eggs, and we interpret vague descriptions in the light of our own experience with Neotropical bird nests. We also provide the first description of the nests and eggs of *M. laemosticta* from Costa Rica. Nest architecture and other life-history traits are thought to be phylogenetically informative for many groups of birds (Greeney and Port 2010; Miller and Greeney 2008; Sheldon and Winkler 1999; Zyskowski and Prum 1999), including thamnophilids (Restrepo and Londoño 2011). Using recent molecular phylogenies of *Myrmeciza* and related species (Bravo 2012), we examine to what extent nest architecture reflects phylogeny in this polyphyletic group.

Methods

We exhaustively reviewed the literature concerning the reproductive habits of *Myrmeciza* antibrds. For each



Results

White-bellied antbird (M. longipes)

Belcher and Smooker (1936) described nests from Trinidad as "shallow saucer(s) of brown pliable twigs and rootlets, with exteriorly a few light-coloured straw-like stalks, and an inner lining of black material like horsehair" which are "placed upon or set in among (their) supports rather than slung." They stated that nests are generally found ca. 2 m above the ground and that eggs are "dull white in ground-colour, thickly blotched and spotted on the upper part with umber-brown, and underlying clouded markings of lilac-grey," providing measurements for two eggs. This description was repeated by Wetmore (1972), while Robinson et al. (2000) described them as "open cups". Wetmore (1972) gave measurements for four eggs in the British Museum collection, two of which (based on collection date) appear to be those measured by Belcher and Smooker (1936), although Wetmore's measurements do not concur with those previously given. Ffrench (1991) doubted the validity of these records and suggested that they referred to nests of red-crowned ant-tanager (Habia rubica). Although Ffrench (1991) mentioned two nests found by Snow and described eggs of M. longipes as having a "creamy" ground color and "streaked with purplish brown," he failed to provide an alternative nest description. Subsequent authors have also doubted the Belcher and Smooker (1936) description, suggesting that their placement at more than 1 m above the ground rules out their belonging to a Myrmeciza. Although it is clear that a modern, well-documented nest description is needed, neither Zimmer and Isler (2003) nor ourselves are convinced that Belcher and Smooker's (1936) original description was incorrect. Their description of the eggs, both in coloration and size, is consistent with those of other Myrmeciza (and other Thamnophilidae). In addition, the original hand-written (Belcher) label for at least one nest of longipes gives a nest height closer to 1.2 m, rather than the published figure of >2 m (Douglas G. D. Russel, pers. comm.), a height which would be more consistent with related species (see "Discussion").



Chestnut-backed antbird (M. exsul)

Carriker (1910) described the nest and eggs of *M. exsul* from Costa Rica (sspp. *occidentalis* and *exsul*), describing two nests and providing measurements for four eggs. Gross (1926) described a nest with two eggs from Panama (ssp. *exsul*). Eisenmann (1952) describes nests and eggs from Panama. Skutch (ssp. *occidentalis*; 1969) described four nests and provided descriptions and measurements for four eggs. Willis and Oniki (ssp. *exsul*; 1972) described 12 nests and provided measurements for four eggs. Wetmore (ssp. *exsul*; 1972) described a nest "fastened rather insecurely to the upright stems of vines and bushes, hidden by overhanging leaves ... 40 cm above the ground ... built of leaves, leaf fibers, and slender vines, with leaves placed vertically over the sides and bottom of the open cup as support for the lining of long, slender fibers."

Based on our examination of the above references and additional personal experience with nests of this species in Ecuador and Costa Rica, *M. exsul* builds a loosely bound cup of dead vegetative matter supported from below and most frequently set amongst multiple small upright stems or atop many small crisscrossing vines or stems. Most nests have a sparse to well-formed inner lining of dark, flexible fibers.

Ferruginous-backed antbird (*M. ferruginea*)

Haverschmidt (ssp. *ferruginea*; 1962) described and figured a nest and provided measurements for two eggs from Surinam (repeated in Haverschmidt 1968). Stratford (2000) described and figured a nest and two eggs from Brazil.

Both published descriptions of the nests of *M. ferrugi-nea* are of open, leafy cups placed on the ground, and the figures clearly illustrate that nests are bottom-supported and loosely bound together and have an inner lining of flexible fibers.

Scalloped antbird (M. ruficauda)

Buzzetti and Barnett (2003) provided excellent descriptions and illustrations of three nests of *M. ruficauda soror* from Brazil, as well as descriptions and measurements of two eggs. The data from this paper were also presented by Zimmer and Isler (2003). This species clearly builds a bulky open cup of dead vegetative material, supported from the bottom, and placed on or near the ground.

White-bibbed antbird (M. loricata)

The nest and eggs of this species were first described by Euler (1900), who described a single nest and gave descriptions and measurements for two eggs. Nothing further was

reported until Buzzetti and Barnett (2003) provided an excellent description, with figures, of the nest and eggs of *M. loricata* (also given by Zimmer and Isler 2003). What is apparently this same nest was also figured in Buzzetti and Silva (2008). From these descriptions and figures, it is clear that *M. loricata* builds and open, leafy cup, supported from the bottom, and placed on or near the ground.

Squamate antbird (Myrmeciza squamosa)

The first descriptions, with measurements, of the eggs of *M. squamosa* were given by von Ihering (1900). The only nest description, however, appears to be a partial one given by Höfling et al. (1986), cited by Link and Ramírez (2003) and Zimmer and Isler (2003). Based on these authors' interpretations, the nest appears to be an open cup built low to the ground, and (most likely) supported from below.

Magdalena antbird (M. palliata)

Until recently, this species was considered a subspecies of *M. laemosticta* (Chaves et al. 2010). The nest and eggs of *M. palliata* were first described by Willis (1984; as *M. laemosticta*, from Colombia). The eggs were described as white, spotted brown at the larger end and the nest was a "thin cup low in a *Piper* shrub." This cursory description was later re-published by Willis (1988), amending the egg-spot coloration to cinnamon, but with no additional details added.

We interpret Willis's cursory description of a "thincup" as a woven cup of rootlets. Furthermore, we feel the nest is almost certainly rim-suspended, given the openbranched form of most *Piper* species, which would provide little opportunity to support a nest from below. A formal, detailed description of the nest of *M. palliata* is still needed.

Esmeraldas antbird (M. nigricauda)

There is no published nest description for *M. nigricauda*. The eggs are described from a single Ecuadorian clutch (Schönwetter 1967) as "heavily pigmented with a rosy white ground color and reddish brown to dark purple lines and spots in varying amount" (translation by Wetmore 1972). Although the validity of this record is questioned (Wetmore 1972), such a description is consistent with other *Myrmeciza*. We point out, however, that it is also similar to descriptions of eggs for most Thamnophilidae (Zimmer and Isler 2003).

Chestnut-tailed antbird (M. hemimelaena)

The only information on the nest and eggs of this species are from two nests described as open cups built slightly



above the ground, composed of dead leaves (Hennessey 2002). The four eggs contained in these nests were described, but no measurements given. The nests were supported from below by a *Geonoma* sp. palm, and at least partially attached by the rim (see "Discussion").

Black-throated antbird (M. atrothorax)

The first nest description for this species appears to be the "previously unpublished" description of a single nest in French Guiana (ssp. *atrothorax*; by T. Deville and O. Tostain; pers. comm. in Zimmer and Isler 2003). The nest is described as "a cup placed into a clump of sedge, and lined with *Marasmius* fibers [] c. 20 cm over water." Schönwetter (1979) provided measurements of two eggs from Bolivia.

Although the details of nest attachment are not provided in the above description, it seems clear that *M. atrothorax* does not build an enclosed nest. Furthermore, the placement of this nest in a "clump of sedge" suggests that it was a bottom-supported cup.

White-shouldered antbird (M. melanoceps)

Link and Ramírez (2003) provided the first nest and egg description for this species based on one nest and two eggs observed in Colombia, descriptions later repeated by Zimmer and Isler (2003). Subsequently, Greeney et al. (2004) described a single nest with two eggs from Ecuador. Both studies provided egg measurements and described nests as domed and supported by the leaf rachises of palms, located <1 m above the ground.

Goeldi's antbird (M. goeldii)

Parker (1982) described a nest of this species found on the ground from Peru as a "cup of dried leaves and twigs measur(ing) 18 cm in diameter." He described a single egg but provided no further details. Zimmer and Isler (2003) expand upon this description slightly, but provided few additional details other than reporting a nest "near the ground." The only detailed description comes from another nest built on the ground in Peru (Lebbin et al. 2007), described and figured as being built into a mound of leaf litter and being similar to the two nests of *M. fortis* described by Wilkinson and Smith (1997). Lebbin et al. (2007) provided a photograph, description, and measurements for one egg.

The first brief description of a nest of *M. goeldii*, which implies and open cup nest, is likely inaccurate due to the cursory nature of Parker's (1982) examination. It seems likely that nests of this species are indeed loosely formed enclosed nests of leaf litter, as figured by Lebbin et al. (2007).

Plumbeous antbird (*M. hyperythra*)

Londoño (2003) provided the only description of the nest and eggs of Plumbeous Antbird from eastern Peru. The two nests described and figured are pendant, rim-suspended cups, tightly woven of dark fibers and decorated externally with dead leaves. Londoño (2003) also described and provided measurements for four eggs. This description is repeated in Zimmer and Isler (2003), who also describe a similar nest (still under construction) from Brazil.

Sooty antbird (M. fortis)

Apparently the only descriptions of the nest and eggs for this species are those of Wilkinson and Smith (1997) from Peru (ssp. *fortis*), who described two nests built on the ground into mounds of leaf-litter, both with short tunnels leading to spherical chambers neatly lined with interwoven plant fibers. They also described four eggs, but did not provide measurements.

Dull-mantled antbird (M. laemosticta)

With the recent elevation of *M. palliata* to species status (Chaves et al. 2010), the range of *M. laemosticta* is confined to Central America (Costa Rica and Panama), and no data have been published on its breeding biology. Here we describe the nest and eggs of *M. laemosticta* for the first time, based on three nests found in Costa Rica.

On 20 April 2001, J.E.S. and E.C. found a nest with two eggs at Selva, Cartago Province (9°47'N, 83°44'W; 1050 m). Habitat in the area is a mosaic of humid, primary and second-growth forest. The nest and eggs were collected and deposited in the Museo Nacional de Costa Rica, San José (Catalog # 388). The nest was situated 2.5 m from a small creek, 35 cm above the ground in a small shrub (Melastomataceae) growing at the base of a small cliff. The nest (Fig. 1) was built of tightly woven flexible fibers, with those externally being lighter in color than the darker fibers of the poorly defined lining. Externally the nest was lightly decorated with moss, although most may have been brought incidentally with the structural fibers, measuring 125×180 mm at the widest points. It was attached by the sides to several thin vines and branches, with no support below. Internally the cup was almost circular, measuring 73 × 80 mm in diameter (measured at perpendicular angles), and 49 mm deep. The walls of the nest varied from 2.5 to 3.0 cm thick. The two eggs were undeveloped with a pinkish ground color and cinnamon and lavender spots, scrawls and flecks, fairly evenly distributed. They measured 24.4×16.4 and 24.8×16.35 mm and both weighed 3.5 g (Fig. 2).



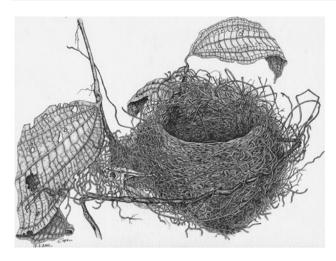


Fig. 1 Drawing of a nest of the Dull-mantled Antbird (Museo Nacional de Costa Rica, San José, Catalog # 388) collected 20 April 2001, Selva, Cartago Prov., Costa Rica



Fig. 3 Nest and complete clutch of the Dull-mantled Antbird photographed 21 May 2011 at San Cristobal, Area de Conservación Guanacaste, Guanacaste Prov., Costa Rica



Fig. 2 Complete clutch of the Dull-mantled Antbird (Museo Nacional de Costa Rica, San José, Catalog # 388) collected 20 April 2001, Selva, Cartago Prov., Costa Rica



Fig. 4 Nearly completed nest of the Dull-mantled Antbird photographed 21 May 2011 at San Cristobal, Area de Conservación Guanacaste, Guanacaste Prov., Costa Rica

On 21 May 2011, H.F.G. found another nest (Fig. 3) with two eggs at San Cristobal, Area de Conservación Guanacaste (10°87′N, 85°39′W; 640 m). Habitat surrounding the nest was humid, mature second growth forest. The nest was 3 m from a small stream, placed 50 cm above the ground in a 1 m tall sapling. Nest materials were as described for the first nest, again with thicker, redder fibers externally, with finer black fibers internally. Many fibers, especially in the outer portion, were very long (30–50 cm) and were twisted and wrapped around two vertical and several horizontal branches of the sapling, suspending the cup between them by 6-7 cm "wings." On one side of the nest, many of the longer fibers were twisted and wrapped into an indistinct ball, nearly the same size as the nest itself. This extra material served to break up the outline of the nest, giving it the overall appearance of disorganized detritus collected naturally. Internally the cup was slightly oblong, 8×7 cm in diameter, and 5 cm deep (measured at the low point between the supporting wings). Externally, excluding the attachment points, the nest was 7.0 cm tall and 8.5 cm in diameter. The walls of the nest were 1.5–2.0 cm thick and tightly woven, allowing little light to pass through. Both eggs were very slightly developed (<1 mm embryos). The eggs (Fig. 3) were white with heavy cinnamon streaking, flecking, and scrawls combined with a few lavender blotches, all markings concentrated at the larger end. They measured 23.5 \times 16.7 and 24.0 \times 16.8 mm, and weighed 3.5 and 3.6 g, respectively. We think that the eggs collected in 2001 were likely described as having a pinkish ground color only because they were still very fresh and not fully calcified.

On the same date, H.F.G. found a third nest (Fig. 4), nearly completely built and lacking only the lining of dark fibers. It was 2 m from a small stream and built 30 cm up



Table 1 Architectural categories of Myrmeciza nests

| Species | Bottom-supported cup | Rim-supported cup | Dome |
|-------------------|----------------------|-------------------|------|
| M. longipes | X | | |
| M. exsul | X | | |
| M. ferruginea | X | | |
| M. ruficauda | X | | |
| M. loricata | X | | |
| M. squamosa | X | | |
| M. palliata | | X | |
| M. laemosticta | | X | |
| M. hemimelaena | X | | |
| M. atrothorax | X | | |
| M. melanoceps | | | X |
| M. goeldii | | | X |
| M. hyperythra | | X | |
| M. fortis | | | X |

Species are listed in taxonomic order following Remsen et al. (2013). Data sources are given under individual species accounts

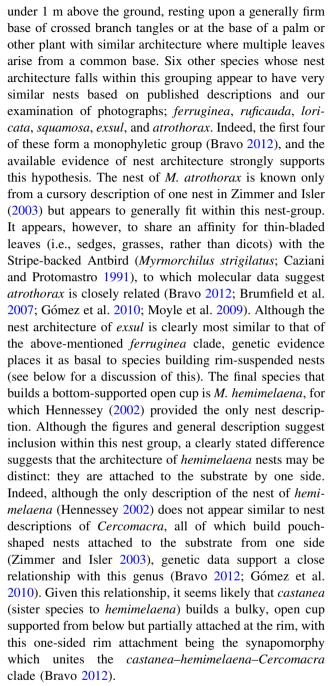
saddled between two horizontal leaf petioles of a 50 cm tall *Dieffenbachia* plant (Araceae). The nest was well-formed and compositionally and architecturally nearly identical to the previous nest, including the large accumulation of extra material to one side.

Discussion

All described eggs of *Myrmeciza* are white with varying amounts of cinnamon and lavender markings. As few eggs have been illustrated in color to allow detailed comparisons, and this description generally applies to most thamnophilid eggs (Zimmer and Isler 2003), we do not discuss eggs any further.

The nests of 14 of the 22 putative *Myrmeciza* species have now been described, allowing us to make a few preliminary conclusions. Based on nest composition, architecture, and placement, the described nests can be divided into three clear groups (Table 1): (a) bottom-supported open cups built of coarse vegetative matter, (b) rim-suspended open cups woven of thin flexible materials, and (c) domed nests build on or near the ground and composed of coarse vegetative matter. Below, we discuss each of these architectures and the possible phylogenetic significance of emerging patterns within the genus.

(a) The most commonly described nest-type within *Myrmeciza* is a bulky, thick-walled, open cup composed of various types of course, dead vegetative matter such as leaves, fibers, and sticks. Placement of these nests, with the possible exception of *M. longipes* (see species account), is



(b) Three species of *Myrmeciza* are now known to build open cups completely suspended by the rim on at least two sides; *palliata*, *laemosticta*, and *hyperythra*. Molecular data show *hyperythra* to be imbedded within *Schistocichla* and unrelated to other *Myrmeciza* (Bravo 2012; Brumfield et al. 2007). Nest architecture is poorly known within *Schistocichla*, but the Spot-winged Antbird (*Schistocichla leucostigma*) builds a rim-suspended cup of thin fibers (ssp. *leucostigma*; H.F.G. unpublished data) that is quite similar to those of all three of the above *Myrmeciza*. Interestingly, Bravo (2012) found *laemosticta*, *palliata*, *nigricauda*, *berlepschi*, and *griseiceps* to form a clade sister to *exsul*,



which clearly builds the "type (a)" nest described above. It is unfortunate that we lack descriptions for the nests of *nigricauda*, *berlepschi*, and *griseiceps*, which may prove to show architectural innovations allowing the evolution from bottom-supported to rim-suspended cups, an architecture that is widespread within the Thamnophilidae (Zimmer and Isler 2003) and has undoubtedly evolved more than once.

(c) The final nest type described within *Myrmeciza* is distinct from the others by being enclosed or domed. All three species known to build domed nests (*melanoceps*, *goeldii*, *fortis*) are related (Bravo 2012; Brumfield et al. 2007). The two other members of this group, *M. zeledoni* and *M. immaculata*, do not have described nests, but the clear prediction is that these species will also build domed nests. Indeed, nests of other genera which are closely related to this clade (*Gymnocichla*, *Percnostola*, *Pyriglena*; Bravo 2012) also build domed nests (e.g., Bradley 2008; Protomastro 2002; Willis 1982).

In conclusion, the nest architecture within the polyphyletic Myrmeciza is largely in concordance with emerging phylogenetic hypotheses. The only possible exception is the bulky, bottom-supported cup nest of M. exsul, a species which is apparently most closely allied to a group which builds rim-suspended nests. Detailed nest descriptions for the remaining members of this clade, however, may explain this apparent inconsistency. For the remaining eight species of Myrmeciza with undescribed nests, we hypothesize that: (1) castanea builds predominantly base-supported nests which are partially attached at the rim similar to hemimelaena or possibly pouch-like nests similar to members of Cercomacra, (2) nigricauda, berlepschi, and griseiceps build open cup nests which are partially or entirely supported by the rim, (3) pelzelni and disjuncta build open cup nests, entirely supported from below and possibly including ribbon-like materials (e.g., grass, leaf strips), although the lack of commonality between loud songs, tail and wing movements, and morphometrics among atrothorax, pelzelni, disjuncta and Myrmochilus (Bravo, pers. comm.) may also be mirrored in nest architecture variation, (4) zeledoni and immaculata build domed nests.

Based on the data presented and reviewed here, it is clear that nest architecture provides phylogenetically informative characters, which support the current hypothesized relationships of *Myrmeciza* antbirds, emphasizing the importance of detailed life-history information for this and other poorly studied groups. Future studies on the nest architecture of these species should pay particular attention to the degree and manner in which nests may be attached, supported, or suspended by their rims. We hope this contribution helps to elucidate important gaps in our knowledge and encourages others to publish information on the nests of these and other poorly known Neotropical birds.

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