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A histological study of the protracted dismantling of the spent (Sertoli-only) shark spermatocyst post-spermiation: Insight from species with or without testis-associated lymphomyeloid tissue

Leon Mendel McClusky[1] | Julius Nielsen[2]

[1]Anatomy Section, Department of Health & Care, Faculty of Health Sciences, UiT The Arctic University of Norway, Campus Narvik, Narvik, Norway

[2]Greenland Institute of Natural Resources, Nuuk, Greenland

Correspondence
Leon Mendel McClusky, Anatomy section, Department of Health & Care, Faculty of Health Sciences, UiT The Arctic University of Norway, Campus Narvik, Lodve Langesgate 2, 8514 Narvik, Norway.
Email: leon.mcclusky@uit.no

Abstract

Sertoli cells of sharks are non-permanent components of the spermatocyst that they share exclusively with only one germ cell stage. After spermiation, all Sertoli cells, and thus the whole spent cyst, are disposed of in an area adjacent to the spermatozoal spermatocysts, that is, the resorption zone (RZ). Differences in the histology and magnitude of the RZ of the mature blue shark and Greenland shark correlate with differences in how spent cysts are dismantled. In the blue shark's RZ, the spent cyst's Sertoli nuclei were synchronously and stepwise fragmented into pyknotic bodies that were eventually resorbed in a whorl in the RZ interstitium. Conversely, cyst dismantling in the Greenland shark, that also lacked a spatially definitive RZ, revealed redundancy. One mode entailed the sloughing of the bulky Sertoli nuclei through an indistinct cyst–ductule transition area into its attached collecting ductule. A second mode entailed the asynchronous, progressive fragmentation of the bulky Sertoli nuclei into membrane-enclosed pyknotic bodies. Both these modes solely entailed an internally coordinated demise of the spent cyst and whose basal lamina remained intact almost right to the end. Whatever the underlying mechanisms of these differences, these findings nonetheless reveal species-specificity in the clearing up of the elasmobranch testicular parenchyma after the completion of a round of spermiogenesis. One consideration is the blue shark's expansive immune cell augmented RZ, that adjoins the animal's bone marrow equivalent tissue. The notable finding of a second conspicuous Sertoli cell type in the Greenland shark's spent cysts is also discussed.

KEYWORDS
pyknotic bodies, Sertoli cell degeneration, shark, spent cysts

1 | INTRODUCTION

The Sertoli cell is, by virtue of its presence in the germinal compartment, indispensable for the developmental advance of spermatogonial, spermatocyte and the different spermatid stages during spermatogenesis (Griswold & McLean, 2006). The spermatogenic tubules that comprise the testes of higher vertebrates (amniotes; reptiles, birds and mammals) aptly display the essence of this indispensableness with the Sertoli cells constituting a permanent cellular backbone of the tubular wall during which successive germ cell cohorts are layered from base to lumen in the cytoplasmic folds of the Sertoli cells (Franca et al., 2016; Yoshida, 2016). The very first report of a rare instance of Sertoli cell death, namely that occurring in a bird species, the European Starling (Young et al., 2001), not surprisingly elicited much debate about the broader implications of the loss of this anchoring cell in the amniote seminiferous epithelium (Beltrán-Frutos et al., 2022). Subsequent reports of similar deaths in other amniote species (Islam et al., 2012; Jenkins et al., 2007; Martínez-Hernández et al., 2020; Seco-Rovira et al., 2014) prompted the latter review to conclude that the Sertoli cell kinetics of vertebrates are probably far more dynamic than previously thought (Beltrán-Frutos et al., 2022). The extent and mechanisms of these Sertoli deaths, not to mention the disposal of the corpses of these large-bodied cells, have eluded systematic research inquiry, in part, due to the swiftness of mammalian cell kinetics to maintain tissue integrity and the complex organization of the amniote testis. This, together with timely updates to streamline concepts pertaining to the different pathways of cell death observed in the testes (Allan et al., 1992; Koji & Hishikawa, 2003) and generally in the cells and tissues of higher vertebrates (Dini et al., 1996; Elmore et al., 2016), adds to the difficulties to understand the life cycle of this conserved supporting cell in the germinal compartment.

In contrast, the germinal compartment in the testes of anamniotes (fish and amphibians) is assembled de novo with each round of spermatogenesis (Yoshida, 2016). In these lower vertebrates, each germ cell stage is sequestered right from its conception with its own set of co-developing Sertoli cells that derive from somatic cell precursors, to form a germinal unit called a spermatocyst (França et al., 2015; Pudney, 1995; Yoshida, 2016). In newly assembled cysts of old vertebrates such as elasmobranchs (sharks and rays), the same somatic cell precursors are recruited in the simultaneous construction (at one end of the cyst) of the germinal clone's future exit passageway (i.e. collecting ductule) that only becomes patent upon the release (i.e. spermiation) of the spermatozoa from the cyst (McClusky, 2018; Park et al., 2013). Thus, the conclusion of spermatogenesis in the spermatogenically active elasmobranch manifests as the appearance of numerous spent (Sertoli cell-only) cysts among the spermatozoal cysts. These empty cysts will eventually be dismantled and resorbed in an area in the testicular parenchyma, termed the resorption zone (RZ).

Knowledge gleaned from the study of spermatogenesis that is conserved from sharks to mammals (Callard, 1991) can supplement and extend basic concepts of the hitherto poorly understood life cycle of the higher vertebrate Sertoli prototype. It was previously reported that Sertoli cell degeneration in the spent cysts of both the blue shark and thresher shark resolves ultimately as single masses of pyknotic bodies scattered among otherwise unperturbed spermatozoal cysts (McClusky, 2013, 2022). To date, nothing else is known about the progressive onset of cytoarchitectural changes in the elasmobranch spent cyst and any concomitant changes in the surrounding interstitium of the RZ. The very first study to mention the fate of the elasmobranch Sertoli cells post-spermiation was that of the spotted ray (Prisco et al., 2002). However, the latter study neither described the type of cell death nor did the accompanying electron micrographs offer any insight regarding the mechanism of these presumed Sertoli cell deaths, all of which raises questions about whether these species differences may concern differences in the testicular organization of elasmobranchs in general (Pratt, 1988).

Here we provide evidence from two shark species with a similar testicular organization, but whose protracted process of the dismantling of the germ cell-less, expendable germinal compartment is species-specific. This paper also discusses novel findings of the prominent display of a second Sertoli cell type in the Greenland shark spent cyst.

2 | MATERIALS AND METHODS

2.1 | Animals

The blue shark (*Prionace glauca)* and Greenland shark (*Somnosius microcephalus)* are apex predators in temperate and tropical waters, and the Arctic and northern North Atlantic, respectively. The two sexes of *P. glauca* congregate on the continental shelf off southern New England (USA) during the summer months for purposes of mating (Pratt, 1979) after which they depart in October towards warmer waters. Considering the status of *P. glauca* and *S. microcephalus* as near-threatened and vulnerable species, respectively, it is imperative therefore that opportunities which provide access to tissues be fully utilized as year-round investigations into the life cycle of these species are hampered by a lack of specimens. The testicular tissues of *P. glauca* were harvested from moribund mature specimens ($n = 7$) whose morphometrics were previously reported (McClusky & Sulikowski, 2014). Briefly, they were landed by recreational fishermen participating in sports-fishing tournaments over the summer months near Portland (Maine, USA) in late August–September. All subsequent handling and dissections of *Prionace* were conducted under the auspices of attending fisheries scientists from the National Oceanic and Atmospheric Administration Fisheries Service, Narragansett, RI, USA.

As for the adult *S. microcephalus* reported here, these were part of a previous study (Nielsen et al., 2020), with the testicular tissues sourced from specimens captured off Greenland as follows: (A) freshly harvested testes from two specimens that were unintended bycatch during the annual fish surveys of the Greenland Institute of Natural Resources and followed all national laws and regulations of

the Government of Greenland, and (B) a donated archival collection of histology preparations from 13 specimens (from 1959 to 1961) captured from commercial seal boats by the late professor emeritus Bjørn Berland (Norwegian Fisheries Research Institute). This valuable archival material includes paraffin blocks and a set of 50 histology slides of a range of dissected tissues, including testicular fragments fixed in either 70% alcohol, formol or Bouin's fixative. Owing to the latter's superior fixation qualities, only slides with Bouin's fixed testicular fragments were selected for further scrutiny.

2.2 | Histology and microscopy

Of the archival collection, only six slides containing sections of randomly dissected Bouin's fixed testicular fragments were deemed useful. As these excessively thick sections (10 μm) also had numerous artefacts, a reflection of that era's microtomy standards, one paraffin block with the largest testicular fragment was identified, melted down and the fragment re-embedded and processed for routine histology. Regarding the other freshly dissected testes: slices 5–7 mm thick were cut transversely and midway along the length of the elongated testes, fixed for 24–48 h in 10% buffered formalin and stored in 70% ethanol until processing for routine histology and stained with haematoxylin and eosin (H&E). Slides were viewed and photographed with a Leica DMLS brightfield microscope fitted with a Visicam 5.0 digital camera.

3 | RESULTS

Spent (spermiated) cysts of the blue shark displayed various histoarchitectures (Figure 1). Recently formed spent cysts were typically found adjacent to or in the vicinity of mature spermatozoal cysts and were discernible by their large, peripherally located Sertoli cell nuclei (Figure 1a). The other histoarchitectures reflected spent cysts each at a different stage of the gradual, synchronous fragmentation of the Sertoli nuclei; contiguous cysts show some key stages of the process Figure 1b. The final stage resolved as pyknotic Sertoli bodies that were subsequently encircled in a whorl by the RZ's constituent cells (Figure 1b). An appropriate plane of

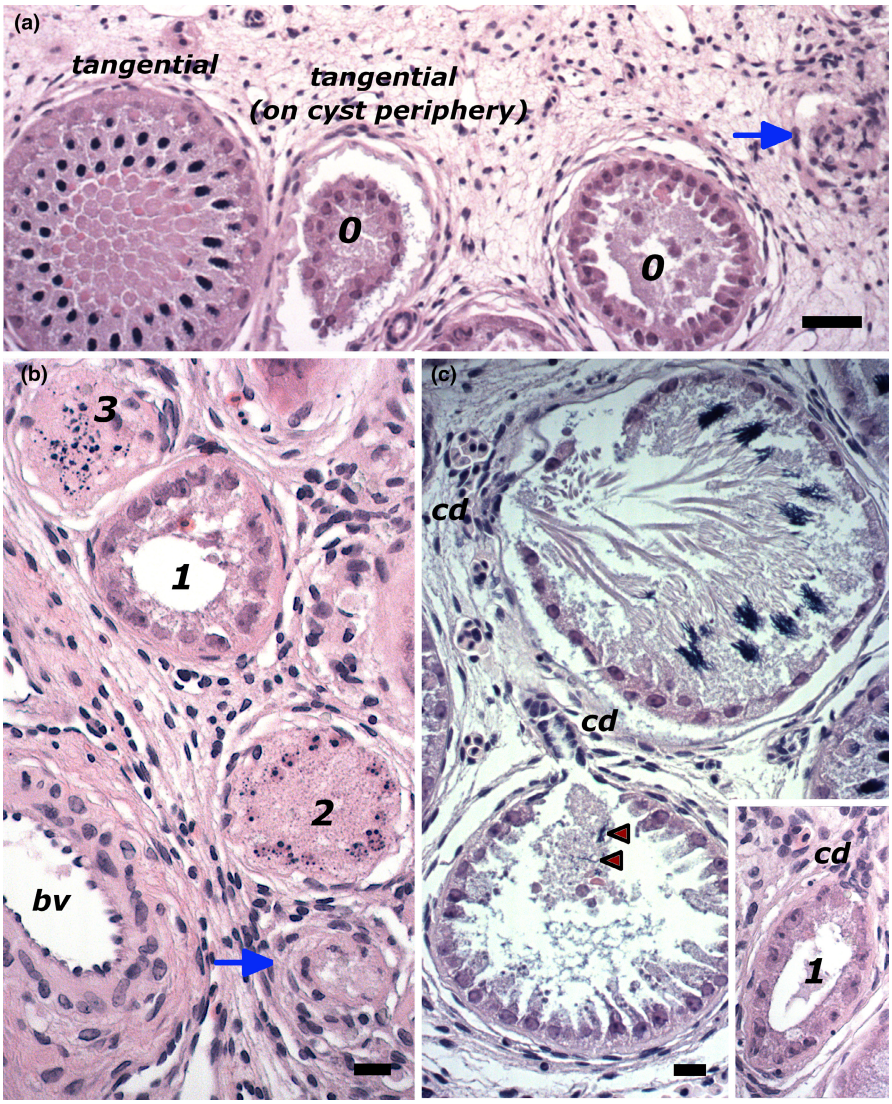

FIGURE 1 Dismantling of spent cysts in the blue shark testis. The expansive resorption zone (RZ) that consists of connective tissue, is scattered with spent cysts in various stages (0 → 3) of the synchronous fragmentation of the Sertoli nuclei that ultimately resolves as pyknotic bodies (a, b). A whorl indicates the site in the RZ where the pyknotic bodies were finally resorbed (blue arrow). Appropriate planes of sectioning showing a spermatozoal cyst (top) in the process of spermiation and a newly spermiated cyst (bottom) still with fragments of residual spermatozoa (red arrowheads). The cyst periphery immediately adjacent to the cyst opening is lined by flat cells of the cyst–ductule transition. *Inset*: A major change after spermiation, namely the loss of at least more than half its volume. Note the presence of bulky Sertoli nuclei directly at the cyst opening. bv, blood vessel; cd, collecting ductule. Bars: a = 50 μm; b, c = 20 μm.

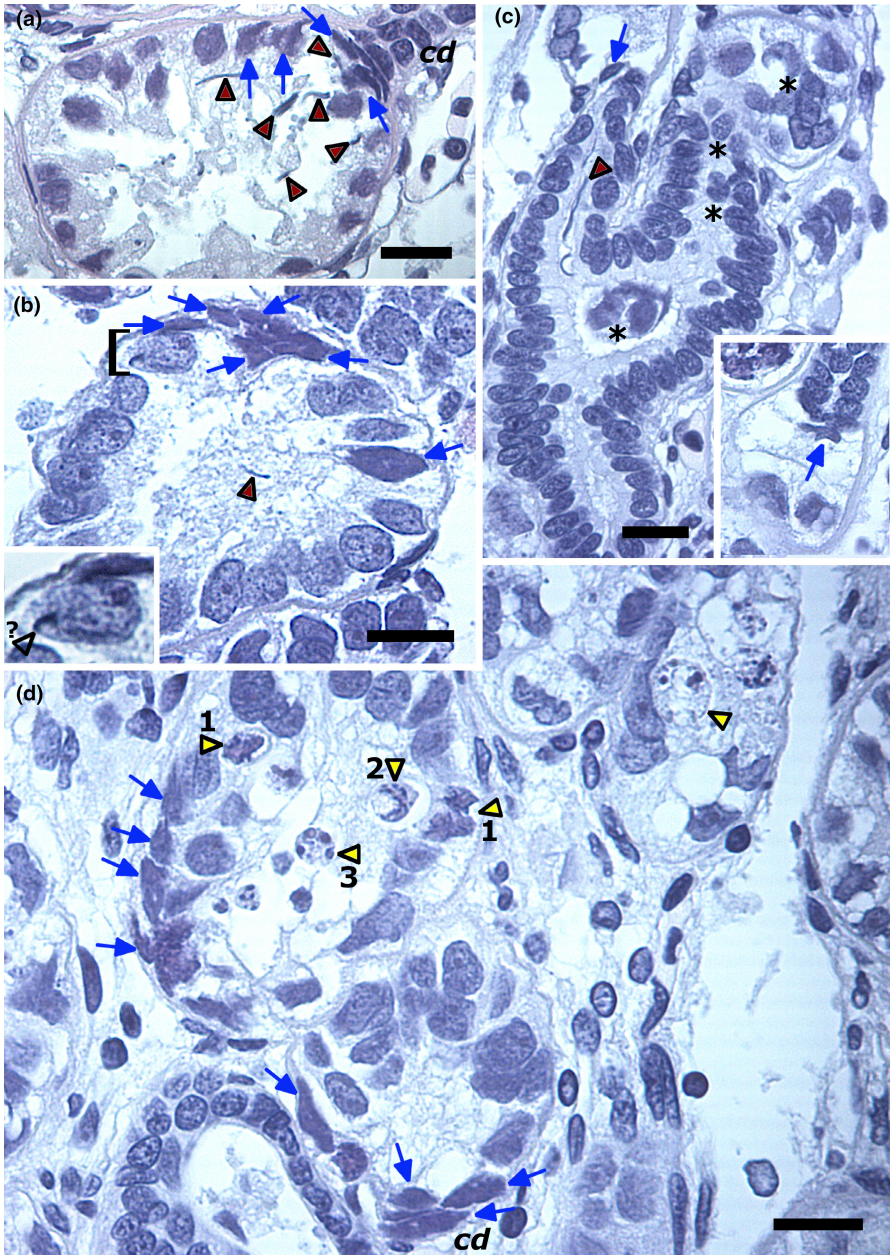

FIGURE 2 Dismantling of spent cysts in the Greenland shark testis. (a) The cyst–ductule transition is characterized by slender strongly basophilic cells, some of which are in the process of migrating into the cyst (blue arrows). Debris of residual sperm (red arrowheads) in the lumen indicate that this is a recently spermiated cyst. (b) A slightly older spent cyst almost devoid of the latter debris. Appropriate tangential sectioning shows the peripheral expansion (around the cyst opening) of the slender strongly basophilic cells that gradually enlarge and transform into a second type of Sertoli cell (blue arrows). *Inset*: Close examination of the highlighted area (bracket). Material strongly resembling a fragment of the sperm head (open arrowhead) lies separate from the highly indented Sertoli nuclear compartment. (c) In this greatly shrunken cyst, a distinct transition area is less clear, in part, due to bulky Sertoli nuclei (asterisks) that are sloughed into the collecting ductule that contains residual sperm (red arrowhead). The latter simultaneously implies very recent spermiation. *Inset*: the conclusion of the latter is an empty sac-like structure with its basal lamina still intact. (d) In contrast, other old spent cysts reveal the progressive fragmentation (1 → 3) of one to three bulky Sertoli nuclei at a time into membrane-enclosed pyknotic bodies (yellow arrowheads) all while the basal lumina remains intact. Note the sparse histologically, unremarkable interstitium. Bar = 20 μm.

sectioning through a newly spermiated cyst revealed the open cyst–ductule transition area, and flat cells lining the opening into the collecting ductule (Figure 1c).

In contrast, the testicular parenchyma of the spermatogenically active Greenland shark lacked a clearly demarcated RZ, and its interstitium was histologically unremarkable, with the spent cysts often bordering directly on each other (Figure 2). The cyst–ductule transition of a very recently spermiated cyst often displayed heterogeneity owing to the aggregation of slender strongly basophilic cells, some of which were in the process of migrating into the cyst to become a second type of Sertoli cell (Figure 2a). The latter developments were more overtly displayed in older spent cysts devoid of residual sperm and related debris. These older spent cysts clearly revealed the cytoarchitectural differences between the nuclei of the second Sertoli cell type and the cyst's original bulky Sertoli cells (Figure 2b). In contrast, other older spent cysts revealed sloughing of the bulky Sertoli nuclei into the collecting ductule that sometimes still showed evidence of the very recent release of spermatozoa (Figure 2c). Sloughing culminated in a spent cyst resembling an empty sac with only its basal lamina still intact (Figure 2c). A scattering of collecting ductules disclosed evidence of this mode of the disposal of spent cysts.

However, a common mode of the dismantling of the spent cysts appeared, what at first glance, seemed like variably sized old spent cysts containing a scattering of membrane-enclosed pyknotic bodies (Figure 2d). Scrutiny of the latter together with the subtle changes observed in the adjoining Sertoli nuclei informed of their protracted fragmentation, one to three bulky Sertoli nuclei at a time. The second Sertoli cell type was only infrequently observed in the latter type of spent cysts.

4 | DISCUSSION

Novel findings from vertebrates near the base of the phylogeny offer insight into the demise of the vertebrate Sertoli cell when it constitutes an expendable population of cells post-spermiation. Consistent with the slow and progressive nature of cell kinetics in sharks (McClusky, 2020, 2022), evidence is herewith provided that the fragmentation of the spent cyst's Sertoli nuclei is likewise protracted in the blue shark and Greenland shark.

The species-specificity of the synchronous (blue shark), and asynchronous (Greenland shark) fragmentation of the spent cyst's Sertoli nuclei and the clearing of the pyknotic Sertoli bodies is noteworthy. In the blue shark, the singular mass of pyknotic bodies is disposed of in the form of a whorl in the RZ interstitium. In contrast in the Greenland shark, the process advances a few Sertoli cells at a time towards the formation of membrane-enclosed pyknotic bodies with the rest of the Sertoli nuclei and cyst basal lamina still intact. These Sertoli nuclear deaths in spent cysts that in both species resolve as crisp pyknotic masses, differ markedly from the purported diffuse Sertoli cell degeneration with no evidence of electron dense masses in an ultrastructural study of the spotted ray's spent cysts (Prisco et al., 2002).

A second novel finding in this study concerns the phenomenon, only in the Greenland shark, of a second mode to dispose of spent cysts, namely the sloughing of the spent cyst's Sertoli nuclei into the collecting ductule. The plethora of cross- and longitudinal sectioned profiles of collecting ductules in the blue shark's extensive RZ do not provide the slightest indication of this alternative mode for the disposal of the Sertoli nuclei. Though not unusual among fishes since sloughing of Sertoli cells also occurs in an atherinomorph teleost, *Horaichthys setnai* (Grier, 1984), the broader functional significance though of these differences in the elimination of expendable Sertoli cell-only cysts between two migratory shark species that both have diametric testes, is nevertheless intriguing. The latter notion stems from the similarities the blue shark and Greenland shark display with regards to the lengthy retention of another type of Sertoli cell-only cyst typically seen in spermatogenically inactive individuals of both species (McClusky, 2013; McClusky, Nielsen and Christiansen, unpublished observations). In the blue shark, these Sertoli-only cysts accumulate as a thick band, and in place of spermatozoal cysts, long after the completion of spermiation, because of the gradual and complete Sertoli cell phagocytic clearing of the previous round of spermatogenesis's aborted spermiogenesis.

A third novel finding (Greenland shark) pertains to some spent cysts whose site of attachment to the collecting ductule features slender strongly basophilic cells. Appropriate tangential sectioning of these cysts shows the peripheral expansion of the latter cells around the cyst opening and their migration into the cyst concomitant with their transformation into a second type of Sertoli cell. Unlike in a freshly formed spermiated cyst that still contains residual sperm and debris, this second Sertoli cell type is conspicuous in its expansion around the cyst opening and location deeper into the Greenland shark's older spent cysts (that are notably also devoid of residual sperm or related debris). This microanatomical change is reminiscent of the mammalian testis that features a transition area (i.e. terminal segment) between the seminiferous tubule and the rete testis and that is lined by modified Sertoli cells known to phagocytize unwanted and degenerated spermatozoa before they exit the tubular environment (Murakami et al., 1988; Osman, 1978; Sinowatz et al., 1979). These mammalian Sertoli cells have been speculated to act as a second 'line of filtration' for unwanted sperm (Osman, 1978).

In conclusion, differences in the histology and magnitude of the RZ interstitial tissue of the mature blue shark and Greenland shark correlate with differences in how spent (spermiated) cysts, and in essence the Sertoli cell nuclei, are dismantled. A possible explanation may pertain to the blue shark's leukocyte augmented RZ. The latter arises from the variable immigration of leukocytes from the blue shark's massive bone marrow equivalent tissue (termed the epigonal organ) that is affixed to the mature pole of the testis and specifically to the RZ (McClusky & Sulikowski, 2014). The potent phagocytic activity of the elasmobranch's epigonal cells has been demonstrated in vitro (Walsh & Luer, 1998). It is therefore intriguing that the disintegration of cyst basal lamina during the dismantling of the blue shark's spent cysts is concomitant with the synchronous pyknotic fragmentation of its Sertoli nuclei and encircling of the latter in a whorl-like manner by the RZ's constituent cells. None of the testes of the Greenland sharks examined in the present study revealed any traces of an epigonal organ, which is consistent with the first report of its absence in this species (Fange & Mattison, 1981). This, together with the absence of a well-defined RZ, correlates with redundancy and the internal, gradual demise of older spent cysts whose basal lamina remains intact, even with only one or two normal-looking Sertoli nuclei still left to be disposed of. At the very least, these findings in the blue shark and Greenland shark reveal that the clearing up of the elasmobranch testicular parenchyma after the completion of a round of spermiogenesis is species-specific.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no competing interests in this work.

DATA AVAILABILITY STATEMENT

The data supporting the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Leon Mendel McClusky https://orcid.org/0000-0003-0127-6415

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