Population Dynamics of the New Zealand Geoduck, *Panopea zelandica,* in Golden Bay, New Zealand

A Master's Thesis by Adam Slater

Submitted to the Auckland University of Technology (2018) in partial fulfillment of the requirements of the degree of Master of Science.

This thesis is dedicated to my partner and fiancée, Ella.

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1. **Abstract**

Geoduck (genus *Panopea*) are a large and commercially significant marine clam in the phylum Mollusca, which are distributed throughout the world with *Panopea zelandica* being found in New Zealand (Quoy & Gaimard, 1835). Aquaculture NZ set a target of $1 billion by the year 2025 (Aquaculture NZ, 2005) and *Panopea zelandica* is one of two species identified to achieve this goal. Advancement and expansion of the existing geoduck fishery are obviously instrumental in achieving this target and hence there must be a more thorough understanding of population dynamics, stock structure, and potential effects of harvesting upon a population (Gribben & Heasman, 2015) to create a sustainable growth in the *P. zelandica* fishery. Despite the comparatively large amount of literature available on farmed and hatchery-raised geoduck in NZ, information and studies performed on wild *Panopea zelandica* remain relatively sparse.

It was the goal of this thesis to investigate stock structure, harvesting efficiency and components of productivity of *Panopea zelandica* in the Collingwood area of FMA7. Water depth was the strongest predictor of geoduck density as well as a highly significant association (p-value = 0.00038) between grain size and density. We found a normally distributed group of size classes and our ages ranged from 4 to 33 years old. We found an estimated instantaneous mortality (Z) of 0.209 with an L_{inf} of 127.5mm and a growth rate (k) of 0.110. We found a total [effectively virgin] parent biomass of 1,334kg with an average density of 0.062km/m^2 and a CV of 0.205 and found show-factors of 15.9 to 30.8% *sensu* Gribben, Helson & Millar (2004). Our results were broadly comparable with previous studies.

Future research could investigate sex ratios and the effect of protandric development on population harvesting as well as the effect of sediment type on siphon colour, the implementation of crossdating and perhaps investigating the viability of SONAR technology into biomass surveys.

This thesis has contributed to the overall understanding of population dynamics, stock structure and other components of the *P. zelandica* identified by previous publications as being important focal points for research as well as outlining possibilities for future work.

2. **Attestation of Authorship**

I hereby declare that this submission is my own work and that, to the best of my knowledge and belief, it contains no material previously published or written by another person (except where explicitly defined in the acknowledgements), nor material which to a substantial extent has been submitted for the award of any other degree or diploma of a university or other institution of higher learning.

Signed, Adam Keith Slater.

3. Acknowledgments

Firstly, my primary supervisor and mentor Lindsey has guided me through some difficult personal and professional times whilst maintaining an almost superhuman level of patience with my postgraduate apprenticeship. This thesis would not have been accomplished without his support, guidance, and knowledge and I will be grateful for many a year to come. My secondary supervisor, Armagan had a door that was always open and assisted greatly in the final stages of this document. It's been a few years in the writing of this and I like to think of Lindsey and Armagan as good friends – though, not quite peers! Paul Graham has played a large role in my completion of this thesis – he has required consistent updates on my progress and given good motivation in the way only a best friend can! Russell Millar has also been important in providing me with assistance regarding the rabbit warren that is biostatistics as well as Nick Garrett from AUT helping with this and with structuring the document. Le Viet Dung of AUT and the Cawthron Institute also generously provided geoduck shell specimens for the calibration of the annual growth rings and for this I thank him. The administrative staff of AUT Sciences – Brid, Winnie and Sawi also managed to put up with [sometimes] frustrating requests from me. Angelina and Beibei of the postgraduate office of AUT also provided help along the way as well as providing friendly consults and much-needed support towards the end of my work. The laboratory technicians (especially Saida and Jinan!) and laboratory manager Sonya also deserve gratitude for providing me with access and assistance in the practical endeavors. Kind thanks to Dan Breen with the help he provided on GIS mapping. Glenn Farrington must also be thanked for his encouragement – especially towards the end. Geoff, Grant, Rob and David of PZL Harvesters for the impetus and financial backing for the project as well as some good laughs and ribbings along the way. Special thanks to Seafood Innovations Ltd. and Mike Mandeno for funding the study without which it would not have been possible. My parents – endless and loyally supportive well into my adult years. Lastly, I would like to thank my partner and fiancée Ella. She has been the light at the end of the tunnel during trying times, has stuck with me through thick and thin and been a rock for several years of postgraduate study and work and without her loving support, I'm not sure this would have been possible.

4. **Introduction**

Geoduck (genus *Panopea*) are a large marine clam in the phylum Mollusca and family Hiatellidae, which are distributed throughout the world where they inhabit intertidal and subtidal sedimentary habitats of up to 100m for some species (Jamison et al, 1984) and are the largest burrowing infaunal bivalve known (Goodwin & Pease, 1987.) Upon larval settlement, they burrow into the substrate at depths of up to 1m where they remain for the entirety of their adult lives) in fact, their name “geoduc[k]” is potentially derived from the Nisqually phrase for “dig deep” (Gordon, 1996.) Their morphology is rather distinct due primarily to their large size of both the shell, which can be as long as 20cm and their very large and elongated siphons - which can be up to 1m long and are too cumbersome to retract into the shell like other Bivalvia, and with which they use to filter plankton from the water. Geoduck in New Zealand consists of two species; *Panopea smithae* (Powell, 1979) which is not important commercially and inhabits rather deeper water (110-130m) and coarser substrates than the apparently more common and commercially significant *P. zelandica* (Quoy & Gaimard, 1835), also known as the deepwater clam or *hohehohe* (Strickland, 1990.)

Geoduck are extremely long-lived animals with individuals of P. *generosa* reaching a maximum recorded age of 168 years old (Orensanz, Hand, Parma, Valero & Hilborn, 2004) and typically reach maturity around 4 years old. Adult geoduck are sexually distinct and also appear to exhibit protandric development, with males dominating the smaller size classes and females becoming increasingly prevalent as they reach their maximum size (Gribben & Creese, 2003.) Despite the large size of female ovaries and the vast amounts of oocytes they contain, geoduck are dribble spawners and typically release their reproductive material annually during a spawning event where they release approximately 1-2 million eggs (Goodwin & Pease, 1989) during warmer months and this event appears to be driven by water temperature changes; this is also supported by the influence of latitudinal gradients in temperature on spawning time in the New Zealand geoduck (Gribben, Helson & Jeffs, 2004.) After fertilization and early development occurring in the water column, geoduck attach themselves to substrates using byssal threads until they reach approximately 2mm in shell length (Goodwin & Pease, 1989.) They use these byssal threads to act as parachutes, both as single individuals or as an aggregation of up to 100 individuals, (Vadopalas et al. 2012) to travel with water currents (King, 1986) until, presumably, they reach an area favourable to further growth and then bury into the substrate (Le et al., 2016) (iii), where they remain for the entirety of their adult lives. Growth appears to be rapid until ten to twelve years of age (Gribben & Creese, 2005) whereupon the increase in overall length slows markedly with shell thickness and body mass continuing to increase thereafter (Goodwin & Shaul, 1984.)

Fisheries are a vital source of nutrition and protein for hundreds of millions of people globally; in fact, world per capita fish consumption was at its highest levels ever, 20kg, in the year 2014 (FAO, 2016.) This increasing trend looks set to continue based upon 2015 data and total world fishery production is projected to expand to approximately 200 million tonnes in the year 2025 (FAO, 2016.) and Asia is expected to increase its share of this production more markedly, increasing from 70 to 73%. Food security is increasingly an issue for populations around the world and with the human population projected to increase to 9.7 billion by the year 2050, many international organisations, experts and industries have identified the growth of fisheries production to contribute as sources of essential amino acids and essential fatty acids for a burgeoning global population, (FAO, 2016.)

Nutrition obtained specifically from marine [as well as freshwater] sources has been credited with allowing human brain evolution to proceed to the level exhibited in modern humans (Cunnane & Stewart, 2010) with levels of docosahexaenoic acid (DHA), the principle omega-3 fatty acid in the brain, being a key driver of human physical (Byrd-Bredbenner et al., 2016) and brain health (McNamara & Carlson, 2006) with low levels being linked to increased incidences of decreased metabolic health and heightened neuro- and psychopathology. Increased consumption of shellfish and clams, in particular, should be encouraged as they are especially good sources of the essential fatty acid DHA as well as essential amino acids, iron, zinc, copper and vitamin B12 and would be in line with dietary recommendations set forth by the United Nations. (FAO, 2016.)

Total global capture fisheries production in the year 2014 was 93.4 million tonnes; (FAO, 2016) marine captures represented 87.3% of the total, and inland fisheries made up the remainder; China has remained by far the largest producer followed by Indonesia, the USA and Russia (FAO, 2016.) Alaska pollock or *Theragra chalcogramma* became the top-ranked species in terms of total production overtaking the Peruvian anchovy or *Engraulis ringens* which has been by far the highest ranked species since a major El Nino event in 1998 (FAO, 2016.) Persons employed in primary fisheries production globally stands at 56.6 million, with 84% engagement in the global sector based in Asia. Asia also represents by far the largest proportion of global fishing fleets with 75.1% of the total followed by Africa (14.7%) and Latin America (6%.) Global trade export values in the year 2017 stand at an estimated USD 153.5 million with the FAO Fish Price Index increasing over 50% since the period of 2002-04 and now stands at 152 (FAO, 2018.)

The state of the world’s marine fish stocks has remained overall unimproved; 31.4% of all fish stocks are estimated as being overfished, fully fished stocks at 58.1% and underfished at 10.5% (FAO, 2016.) Percentages of total fisheries that are underfished have decreased markedly since the 1970s as well as overfished stocks approximately tripling since the same period – the ten most productive species globally are fully fished and therefore have no potential to increase production (FAO, 2016) and therefore, to keep pace with increasing global demand for fisheries products and maintain food security, new fisheries must be developed.

Whilst there are ten extant species within the genus *Panopea*, only five are important commercially; *Panopea abbreviate* which is endemic to the southwestern Atlantic (Valenciennes, 1839), *Panopea globosa* which is principally found in the Sea of Cortez (Dall, 1898), *Panopea generosa* which has a distribution from Alaska waters south to California Baja (Gould, 1850), *Panopea japonica* which is distributed mainly in northern China, Japan and the Korean Peninsula (Adams, 1850) and *Panopea zelandica* which is found here in New Zealand (Quoy & Gaimard, 1835) with the overwhelming majority of exports going to eastern Asia and China in particular.

Geoduck is a high-end, luxury food item most popular in hot pot, quick fry and sashimi style applications in Hong Kong and South China, however, it appears to be popular across eastern Asia and Japan. It commands high prices on par with Alaskan king crab and its main competition in seafood markets are other high-end live seafood such as abalone/paua, Australian lobster, and crab. Despite this, however, the market remains short of product as supply growth from traditional sources cannot increase in line with demand. Continued growth in the Chinese currency and economy would support higher prices for perceived luxury products as well as the penetration of the product into new markets developed in northern China and interior Chinese regions (Canada Fisheries & Oceans, 2012.)

Other studies on bivalves in New Zealand have contributed to the growth of the sector, such as White et al. (2012), with Aquaculture New Zealand setting an ambitious target of $1 billion by the year 2025 (Aquaculture NZ, 2005). Aquaculture NZ has identified two species of which development of their commercial exploitation would be key to meeting this aforementioned lofty goal; *Ostrea chiliensis* or the flat oyster (Philippi, 1844) and *Panopea zelandica*. In order to ensure the Aquaculture New Zealand target is reached and in addition to developing new markets and customers, maximizing the market penetration of *Panopea zelandica* and utilisation by current end users is vital. To do so, advancement and expansion of the current and existing fishery are paramount and hence there must be a more thorough understanding of stock structure, productivity and potential effects of harvesting upon a population (Gribben & Heasman, 2015.)

The most important factor affecting the quality, grading and therefore the price a geoduck commands on the market is the colour of the siphon; siphons that are whiter or lighter in colour command higher prices and anecdotally, this difference in colour appears to be linked to the substrate that the individual lives in (PZL Harvesters, unpubl.) Other factors include the texture of the flesh, which is hard to gauge externally, as well as shell thickness, total weight, and the ratio of meat-to-shell. (Canada Fisheries & Oceans, 2012.)

Individual Transferable Quotas (ITQ) are an example of a fisheries management catch-share where a regulatory body sets forth a species-specific Total Allowable Catch (TAC) within a framework of other parameters such as a season; globally 148 fisheries are managed under ITQs and have been utilized to great extent in Iceland, Australia and, in particular, New Zealand. No other country has used ITQs so broadly as New Zealand (QMS system) and in doing so, our method of regulating ITQs is largely considered a success story, despite the changes to the system since its beginnings in 1986 (Lock & Leslie, 2007.)

Introduced in legislation in 1986, The Quota Management System (QMS) is composed of several Quota Management Areas (QMA) which are delineated by the boundaries of 10 Fishery Management Areas (FMAs) which comprise New Zealand’s Exclusive Economic Zone (EEZ.) In order to retain more precise control over stock levels and Maximum Sustainable Yield (MSY), FMAs that share similar populations and population dynamics are controlled together under the QMS utilizing stock distribution and biological information held at the time of acceptance of the species into the QMS. New Zealand has 98 species or species groups managed under 642 separate stocks under the QMS (MPI, 2018.)

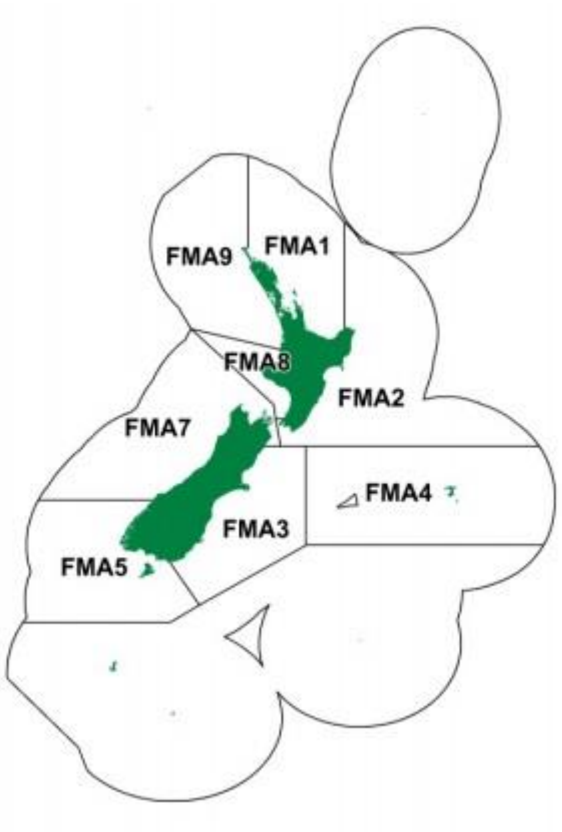

Figure 1. Fishing Management Areas of New Zealand. (Source: MPI)

The TAC is composed of recreational, customary allowances and Total Allowable Commercial Catch (TACC.) Quota holders can own an amount of the quota available for a given fishery in the form of shares; for any given fish stock, there are always 100,000,000 shares. Every calendar year, quota holders are allotted an Annual Catch Entitlement (ACE) which is determined by the proportion of their quota and the given TACC for that year; ACE can be traded and sold throughout a year, however, fishers must ensure they have enough ACE to cover the fish harvested or they may face financial penalties (MPI, 2018.) Fisheries scientists and managers receive information from fishers with monthly harvest returns and catch, effort and landings returns for each trip; Licensed Fish Receivers (LFRs) also submit monthly returns with amounts and types of fish received over the previous month and the fishers that provided those fish. A marine species can comprise of spatially and biologically distinct populations and therefore, management of their fishery at larger geographic levels (i.e. nationally) may not be feasible and requires the use of Quota Management Areas (QMAs) which can cover a fraction of a single or multiple of the ten FMAs that exist within NZ’s EEZ.

Central to effective and sustainable fisheries management is information on stock structure, recruitment, population dynamics and potential harvesting effects upon a population, however, there is little available on this on *P. zelandica*. Due to the low exploitation levels of *P. zelandica* [even within the main commercially significant area], however, it is likely that the stocks have remained in what is effectively a virgin and pristine state (MPI, 2017.)

Geoduck are harvested by divers using underwater breathing apparatus and a hydraulic jet to liquefy the substrate around the geoduck to allow extraction with minimal damage – the geoduck are located by observing firstly the indentations made by their siphon holes and therefore, the location of the individual (MPI, 2017).

Geoduck densities in North America are calculated using established methods that include counting the siphon holes through which geoduck filter feed. Problematically, not all geoduck "show" their siphon holes at the same time and thus could lead to an erroneous population estimate (Hand & Dovey, 1999). This is solved by the use of a "show-factor" which is the number of geoduck siphons that are visible or can be felt versus the total number of individuals present in a given area and is expressed in the formula, $S = n / N$, where S = show factor, n = the number of visible geoduck shows within a defined area and N = the absolute number of harvestable geoduck present within the area (Gribben, Helson & Millar, 2004). In Washington, "show plots" are utilised at sites to estimate the show factor and entails permanently marked subtidal areas in which N is known due to repeated tagging studies and n is obtained from divers counting all visible geoduck as if they were completing a standard survey (Campbell, Yeung, Dovey & Zhang, 2004). The number of geoduck that "show" their siphon holes is variable upon different environmental and physiological factors; with more showing during the summer months during periods of feeding and breeding (Campbell, Harbo & Hand, 1998) and when local water currents are not overly severe with no mechanical disturbances of the bottom due to events such as storm activity (Goodwin, 1977), (Campbell et al., 1996).

Some of the show factors used in the major geoduck fisheries are 0.90 in British Columbia (Campbell, Yeung, Dovey & Zhang, 2004), 0.73 in Washington (Bradbury, Sizemore, Rothaus & Ulrich, 2000) and 0.80 in SE Alaska (Rumble, Hebert & Siddon, 2012). Gribben, Helson & Millar (2004) suggest that the North American methodology for estimating geoduck populations is, indeed, transferrable to *Panopea zelandica*Worldwide production quantities of the Pacific geoduck in the year 2016 stands at 23,465.111t (FAO, 2018), however, NZ production and harvesting of geoduck has largely been limited to the Golden Bay area and has remained in relative infancy since its inception in 1988. This operation began under a special permit and continued at a relatively low level for several years (Breen, 1994) and faltered before the introduction of the species into the QMS in 2006. The TAC stands at 40.5t with 31.5t of TACC and 9t allotted for other sources of mortality such as storm events or bycatch;

recreational and customary fisheries for *P.* zelandica are estimated to be very small or nonexistent. The landings from PZL7 during the 2015-16 period are only 20% of the TACC (MPI, 2017) and the largest landing of geoduck since 1993 occurred in the 2011-2012 period (10.885t) in PZL 7 was a fraction of even the smallest annual landing of *P. zelandica* under the 1988-1993 special permit fishery.

Whilst a large body of scientific literature on the Pacific geoduck (*Panopea generosa*) and its related fishery, comparatively little exists on its New Zealand counterpart, *Panopea zelandica* with the seeming majority existing on farmed and aquacultured geoduck. Studies relating to geoduck aquaculture in NZ are: Adams et al. (2012), Gribben, Millar & Jeffs (2012), Le, Alfaro & King (2014), Le et al. (2016), Le et al. (2016 ii), Le et al. (2016 iii), Le et al. (2017) Le et al. (2017 ii) and Le et al. (2017 iii). Dung Viet Le recently completed his Ph.D. on the cultivation of *P. zelandica* at AUT in 2016 and his research has yielded several papers, which are outlined here.

Adams et al. (2012) investigated the cryopreservation and fertility of *P. zelandica* gametes and found that, on average, unfrozen sperm from serotonin injection had a slightly higher fertility with fresh oocytes than sperm from thermal shock. The addition of bovine serum albumin improved sperm fertility by 30% and sperm frozen in either 10% dimethyl sulfoxide or 10/15% propylene glycol gave the highest fertilization rates post-thawing. Concluding, they stated that further work will include the optimization and development of cryopreservation methods for both gametes and larvae, the longevity of gametes and a larval assay to assess subsequent development.

Gribben, Millar & Jeffs (2014) investigated the fertilisation success of *P. zelandica*. The effects of sperm concentration, gamete age and contact time on the fertilisation success using an extended-Vogel-Czihak-Chang-Wolf model. Fertilization rates peaked at 70%, with the proportion of fertilized eggs decreasing rapidly at sperm concentration levels below the optimal. The paper suggests that should commercial hatcheries ensure that the kept broodstock are in ripe condition and use sperm that is less than 30 minutes old, optimal fertilisations can be expected at sperm densities of 10^{2}-10^{3} sperm □L^{-1} at contact times of 5-10 minutes.

Le, Alfaro & King (2014) examines the effects of different temperature and feeding regimes upon the broodstock of *P. zelandica*. Their results indicate that there was no significant difference of temperature or feeding regime upon wet or dry weights for geoduck for the first 36 days, however, there was a general increasing trend for both wet and dry weights with increasing feeding rations at both medium (11-12^{o}C) and high (16-17^{o}C) temperatures. At the lower temperature treatments (7-8^{o}C), a different pattern was observed with the medium feeding regime resulting in the highest wet and dry weights for geoduck; these weights were similar to the reference group grown in pond water. They note that, interestingly, the reference group grown in pond water resulted in the highest wet and dry weights, however, they reached this after the conclusion of the experiment and concluded that whilst the nutrients were sufficient for development, there was a missing “trigger.” The authors recommend that two-year-old *P. zelandica* be conditioned in pond water for a month and then in low or medium temperature seawater at the medium level feeding regime for optimal gametogenesis.

Le et al. (2016) (i) investigated the effect of daily hypoxia treatments on respiration, aerobic scope and oxygen regulation of both fed and starved groups of *P. zelandica*. They found that the critical partial pressure of oxygen was approximately 4 kPa for all groups; respiration rates for small fed geoduck decreased with decreasing levels of oxygen down to mild hypoxia; all starved geoduck and large-sized fed geoduck maintained respiration with decreasing oxygen down to mildly hypoxic levels but all groups suffered decreased respiration at severely hypoxic levels. The overall conclusion of the study is that larger geoduck maintain respiration, aerobic scope and oxy-regulatory capacity under hypoxic conditions and a variety of oxygen gradients better than smaller ones and therefore, to maximise growth potential of cultivated *P. zelandica*, smaller individuals must be kept in areas that remain normoxic at all times, with larger ones having the possibility to be moved into sites that experience periodic hypoxia at a safer time.

Le et al. (2016) (ii) focuses on examining the embryonic development of *P. zelandica* embryos at 15^{o}C and 35 ppt as well as the optimal sperm: egg ratios for hatchery fertilization conditions. The optimal sperm: egg ratio was under 500:1 with eggs developing the first and second polar bodies within 15-20 and 50-55 minutes after fertilization. The blastula appeared at approximately 8 hpf and gastrulation occurred at 12-18 hpf. The mid-stage trochophore had an apical plate with an apical tuft and the D-stage veliger appeared at 45 hpf. They conclude that their observations and measurements will serve as the basis for future analyses of *P. zelandica* embryogenesis.

Le et al. (2016) (iii) presented the effects of neuroactive compounds on the larval metamorphosis of *P. zelandica*. Two batches of hatchery-reared larvae were exposed to acetylcholine chloride, epinephrine hydrochloride, and excess potassium ions – none of these pharmacologically active compounds increased the proportion of metamorphosed individuals and despite being used extensively in other species, in some cases caused significant mortality. The authors postulate that this may indicate that the larval physiology and development of geoduck differs from other Bivalvia with perhaps evolving distinct chemoreceptor patterns that facilitate metamorphosis under environmentally favourable conditions and conclude that further research should focus on identifying the cues that may induce metamorphosis in *P. zelandica* such as sediment characteristics and surface biofilm.

Le et al. (2017) (i) determined the allometric coefficients of the respiration rate and clearance rate in *P. zelandica*. These coefficients were approximately and respectively 0.73 and 0.62 for respiration rate and clearance rate; there was a negative linear allometric relationship between respiration and clearance rates with tissue dry weight.

Le et al. (2017) (ii) established the temperature window that resulted in the widest aerobic scope for the New Zealand geoduck and did so in order to optimize cultivation procedures for farmed *P. zelandica*. They found that juvenile geoduck had a narrower thermal optimum compared to young adult individuals (15-19^{o}C vs 11-19^{o}C), however, temperatures higher than 19^{o}C reduced the aerobic scope for both juvenile and adult geoduck individuals.

Le et al. (2017) (iii) explored the biochemical composition of *P. zelandica* broodstock conditioned under different temperature and feeding regimes; broodstock were exposed to nine factorial treatment combinations of temperature (7.5, 11.5 and 16.5^{o}C) and feeding regimes (10,000, 50,000 and 100,000 cells mL-1 of a 1:1 mixture of *Tisochrysis lutea* and *Chaetoceros muelleri*. Glycogen, protein, lipid and fatty acid contents of both the flesh and viscera was measured at the commencement of the experiment (day 0), day 36 and day 73 with the glycogen, protein and lipid analyses indicating that geoduck within all treatments had achieved a positive energy balance except those with the highest temperature and lowest nutrient concentration combination. The study also revealed that two omega-3 and one omega-6 fatty acids were important contributors to development; eicosapentaenoic acid (omega-3), docosahexaenoic acid (omega-3) and arachidonic acid (omega-6).

Le et al. (2017) (iv) studied the physiological, morphological and behavioural characteristics throughout the larval developmental process. Larvae were reared in a flow-through system at 17^{o}C and 35 ppt and were fed continuously with marine algae and the behavior and morphology of the larvae were described using video, photomicrographs and scanning electron microscopy. Larval development from the first D-veliger took 16-19 days and metamorphosis occurred over a wide range of shell lengths, from 300 to 375 µm. Increase in shell length was linear over time and the ingestion rate followed a power law with time and this ingestion rate was closely correlated with the development of the alimentary system.

A larger and more recent amount of literature exists on farmed and hatchery-raised geoduck in NZ; information and studies performed on wild *Panopea zelandica* remain relatively sparse. This literature (Breen, 1991; Breen, Gabriel & Tyson, 1991; Breen, 1994; Gribben & Creese, 2003; Gribben & Hay, 2003; Gribben, Helson & Millar, 2004; Gribben, Helson and Jeffs, 2004; Gribben & Creese, 2005; Gribben, Gribben & Heasman, 2015) is outlined as follows:

Breen (1991) is a report to the Ministry of Agriculture and Fisheries (MAF) to advise on the management of the geoduck fishery. It provides an overview of the *P. zelandica* fishery in general with a description of the fishery that existed at that time, a review of the existing fishery, a summary of the research that existed until 1991 such as stock structures, growth, reproduction, recruitment, biomass estimates, yield estimates, models and importantly, mortality. The report then continues to outline the management implications for the fishery as well as research implications.

Breen, Gabriel & Tyson (1991) outlines estimates of age, mortality, growth, and reproduction of *P. zelandica* from Golden Bay. Age of individuals was assessed by counting internal growth rings from acetate peels taken from samples obtained from commercial catches. These acetate peels were created from polished and etched sections of the umbo region. Whilst these age rings were not validated, the technique was based upon a validated technique used in North America for a similar clam, *P. generosa* and has subsequently been validated on *P. zelandica*. Their results show that the maximum growth ring count was 34 with the expansion in shell length appearing to be rapid until age 10, whereupon it slows. The natural mortality rate was approximately 0.20. While they carried out a histological examination of gonads in 200 geoduck, this was of limited use as all samples were taken in just one season. Every individual taken in March appeared to have spawned recently and were developing gametes at the time of the study. The sex ratio was not significantly different from 1:1.

Breen (1994) is another report to MAF Fisheries to advise on management and sustainable fishing patterns of *P. zelandica* populations in New Zealand. It builds upon information outlined in Breen (1991) and sets forth management implications for the fishery. Sustainable yields of 2-4% of unfished parent biomass were recommended, as productivity is relatively low. These estimates are similar to those of *P. generosa* and the model used for the British Columbian fishery suggest very little risk either of the population falling below 20% of the unfished parent biomass or of the fishery being unable to harvest its prescribed quota, due to low densities. The expected mean biomass after 50 years is 70% of virgin parent biomass and the minimum is estimated at approximately 64%. This model is considered rather conservative; however, it has only considered the consequences of constant fishing patterns. Pulse fishing appears to have limited usefulness for these clams. In practice, populations are likely to be pulse fished or harvested in patterns that vary annually. Pulse fishing is thought to have no impact on mean catches in fisheries with low to medium quotas, however, in fisheries with high quotas pulse fishing reduces the propensity of the fishery to take the target catch. This model assumes that only the target catch is taken; any wasteful removal of geoduck (such as individuals that are darker due to sediment type and age) and then discarded would heighten the quota being taken.

Paul Gribben completed a Ph.D. on various aspects of geoduck ecology and biology which led to 6 published papers. Gribben & Creese (2003) investigated protandry in *P. zelandica* from specimens obtained in Kennedy Bay on the Coromandel and Shelly Bay in Wellington from mid-1999 to early 2001. Internal growth rings were used to determine the age at sexual maturity and further used to construct von Bertalanffy growth curves for both sexes in both populations. 50% of individuals were estimated to be mature at approximately 55 to 57mm in shell length at both locations. Length-frequency analysis of individuals from Kennedy Bay suggests that females become more common as shell length increases, with significantly more females existing in the larger size classes in both populations. Protandry for a large amount of *P. zelandica* is likely due to all individuals maturing into males in their third year of life. Similar growth rates in both sexes in both populations means that the differences in growth rates were not responsible for the observed sex-ratios.

Gribben & Hay (2003) examined the larval development of *P. zelandica*. The development of the larvae was illustrated through measurements of shell morphometry using video image analysis, photomicrographs and scanning electron microscopy. Gametes were stripped from sexually mature individuals and the eggs fertilised with a diluted sperm solution. The developing larvae were then kept at 17^{o}C with +/- 1^{o}C variation. These fertilised eggs transitioned into trochophores in under 12 hours and to the D-stage larvae (105.3µm in shell length) within 24 hours. These then completed larval settlement after 16 days at around 247µm in shell length. Measurements were made of shell morphology including length, height, hinge length, anterior end length, umbo height, and umbo length are all considered adequate descriptors of larval development. The relative ease of the spawning and rearing of *P. zelandica* in this study suggests that the development of commercial hatchery technology warranted further investigation. This is currently taking place at the Cawthron Institute in Nelson.

Gribben, Helson & Millar (2004) investigated whether the North American methodology used for determining population abundance estimates is transferable to New Zealand's *P. zelandica*. Line transects were used in Kennedy Bay and in Wellington Harbour. Both sites were restricted to less than 17m in water depth; geoduck in Kennedy Bay were found from 4-8 metres in water depth whereas the population in Wellington occurred from 4-16 metres. Analysis of sediment samples indicates that *P. zelandica* is found in similar habitats to *P. generosa.* Experiments to determine how many geoduck are visible at a given point in time (Show/no-show factors). There was no significant difference in the show-factor with regard to season or tidal height. Thus, a mean show-factor of 0.914 was used to adjust the density estimates from both populations which gave mean densities of 0.058 geoduck/m^2 in Kennedy Bay and 0.489 geoduck/m^2 in Wellington Harbour, and coefficients of variation were generally less than 0.2. The density estimates for *P. zelandica* are much lower than those reported for *P. generosa.* The authors suggested that more research should be conducted on diver variability on counts of geoduck, the role that geoduck occurring deeper than 17m perform and the effects of fertilization success upon densities.

Gribben, Helson & Jeffs (2004) examined the reproductive cycle of *P. zelandica* in Kennedy Bay and Shelly Bay. Standard histological analysis, measurements of oocyte diameter and gonadosomatic indices were determined in order to outline the chronology of gametogenic development and spawning with sex ratios and sexually mature size also being assessed at both locales. Gametogenesis in both populations began in late autumn with spawning beginning during spring and late summer at Kennedy Bay and Shelly Bay, respectively. It was posited that latitudinal gradients in temperature were influential when populations spawned as both populations spawned when local water temperatures reached approximately 15^{o}C. Monthly mean oocyte values and gonadosomatic indices closely mirrored the patterns found in the histological analysis of the reproductive cycle but the monthly mean number of eggs also indicated a small proportion of spawning may begin earlier than indicated by histological examination. Sex ratios were equal in Shelly Bay, however, in Kennedy Bay, there were significantly more males proportionally with this being attributed to a large cohort of small males present in Kennedy Bay. Males in both locales matured earlier than females.

Gribben & Creese (2005) outlined the age, growth, and mortality of *P. zelandica* at Kennedy Bay and Shelly Bay. Annual growth rings from polished shell sections were used to estimate age, growth rates and mortality of *P. zelandica* at both sites. Individuals from Kennedy Bay ranged from 2 to 34 years of age whilst individuals from the population in Shelly Bay ranging from 3 to 85 years of age. There was a significant difference in shell length growth rates between the two sites, however, the typical rapid growth in length during the first 10-12 years with minimal subsequent growth was found in both populations. Growth in terms of weight continues to around 12-13 years of age before finally tapering off. Estimated maximum drained weights of individuals from Kennedy Bay (275.5g) than in Shelly Bay (223.1g) and there was also a significant difference in the relationship between shell length and weight between the two populations. The width of the siphon holes was considered a reasonable predictor of shell length of individuals from Kennedy Bay. Estimates of natural mortality were very low (0.02-0.12 proportion per year.) This study was the first to confirm that shell bands in *P. zelandica* are deposited annually and can, therefore, be used to age individuals. With the low estimated rates of natural mortality and the longevity of *P. zelandica*, fishery management will need to consider the feasibility of the commercial harvest of *P. zelandica.*

Gribben & Heasman (2015) focuses on examining the development of the small fishery that has existed since the late 1980s for *P. zelandica*. This study confirms that, despite low capture rates, *P. zelandica* exhibits several traits similar to those of the Pacific geoduck or *P. generosa* that make it amenable to fisheries expansion and development. The largest impediments to developing a sustainable fishery for the New Zealand geoduck were identified as the potential bias of overharvesting female geoducks due to the functional protandry exhibited by *P. zelandica* and the simple lack of information on actual populations and the low densities and natural mortality of known populations. The 2017 MPI plenary on *P. zelandica* also states that no estimate of fishery parameters, abundance, biomass or yield estimates exist for any geoduck stocks in New Zealand but suggests that with realistic management constraints, 2-4% of virgin biomass might be an appropriate MSY based on the findings of Breen (1994.)

5. **Aims**

To make informed and responsible decisions regarding the development of a new fishery or to establish new quota limits, information on the existing fishery must be obtained including stock structure, components of productivity and the potential effects of harvesting on this population (Gribben & Heasman, 2015) and whilst a comparatively large body of scientific work exists on P. *zelandica*'s cousins, it is clear that there is a relative sparsity of literature relating to wild NZ geoduck and especially geoduck in this particular geographic locale. It is the goal of this thesis to investigate the population dynamics of *Panopea zelandica* in the Collingwood area of FMA7, Golden Bay and contribute to the knowledge of geoduck in NZ with the following specific objectives:

1) To estimate biomass.
2) To investigate diver efficiency and the show-factor.
3) To predict recruitment and estimate mortality.
4) To examine sediment characteristics and their relation to density.

6. **Methods**

6.1 Study Area

This study was conducted in the northern part of Golden Bay, inside Fisheries Management Area PZL7. The delineation of this area was determined in consultation with PZL Harvesters Ltd. and broadly based on historical fishing effort and anecdotal information on the distribution of geoduck in Golden Bay. As no formal surveys have been carried out in these areas, the outer boundaries of the beds were not known, although preliminary surveys in the northern (Collingwood) indicate that high density of geoduck extends far beyond the traditionally fished beds. The survey area extended from MLWS to the 10m contour and consisted of 21,554,077m^2.

To randomize site selection, points were generated within a polygon encompassing the study area and then transformed into GPS coordinates and plotted over a map. Points that were outside of the delineated area or within 100m of previously chosen study sites were rejected. From here, the first fifty random points were then selected (C1-C50.)

All the transects from the 50 sites allocated to the Collingwood area were sampled between 25/09/2014 and 29/08/2015.

6.2 Equipment

The vessel used in this work was the *Takapu* (Registration No. 901062). The *Takapu* is 12.5m in length, 4.3m in width and 15 tonnes powered by a Caterpillar 3208 V8 diesel engine. The latitude and longitude of each waypoint were fixed by a Simrad CP44 GPS plotter with the depth of each site confirmed by a Navman depth sounder. Using New Zealand Hydrographic Authority Tide Predictions (LINZ, 2014; LINZ, 2015), recorded depths were transformed to chart datum depths *sensu* White et al. (2012) or the formula provided by the Australian Hydrographic Service of the Royal Australian Navy. This formula is:

$$h = h1 + (h2 - h1)[(\cos A + 1)/2] \text{ where } A = \Delta([(t - t1)/(t2 - t1)] + 1) \text{ radians}$$

Note 1: On falling tides (h2 – h1) will be negative.

Note 2: t, t1, and t2 are in decimal hours.

A 13hp Honda petrol motor runs the compressor supplying the diver with surface supplied air through a modified pony bottle (with enough air for approximately 20 minutes of bottom time in the case of equipment malfunction) and standard dive regulator, the water pump for the “stinger” and the alternator. 80PSI of water pressure is given at the diver’s end of the stinger.

6.3 Survey Technique Using Modified Fishing Procedures

Under normal fishing procedures, the fisher has 100m of hose that is played out over the back of the boat. The fisher enters the water and runs out from the boat to the length of the hose and fishes back along the hose towards the boat. Each geoduck found (by locating its siphon hole, is fished by placing one hand on the siphon hole, while applying the water jet (stinger) next to the animal, liquefying the sand and allowing the fisher to extract the animal and place it in a catch bag. When a geoduck is extracted the stinger creates a plume of sediment that makes it impossible to locate adjacent animals, so the fisher must then move out of the plume to find the next geoduck. When the bag is full, the fisher follows the hose back to the boat and connects the full bag to a weighted line, collects an empty bag from the line and proceeds with more fishing.

We modified a fishing procedure to allow quantification of the fishing effort. Transects were delineated by running out the water hose (80m) and worked back along the hose (towards the boat) for 50m, with the skipper monitoring the diver’s progress for safety. Where detectable water current was present the direction of the particular transect line was approximately into the direction of the current to facilitate sediment clearance from the line of travel along the transect. Surveying was abandoned when a) the sea became too rough to carry out surveys, b) if the underwater visibility was too low to fish or c) for the safety of boat or crew. Transects were also abandoned if the hose moved during the fishing due to being dragged by the boat.

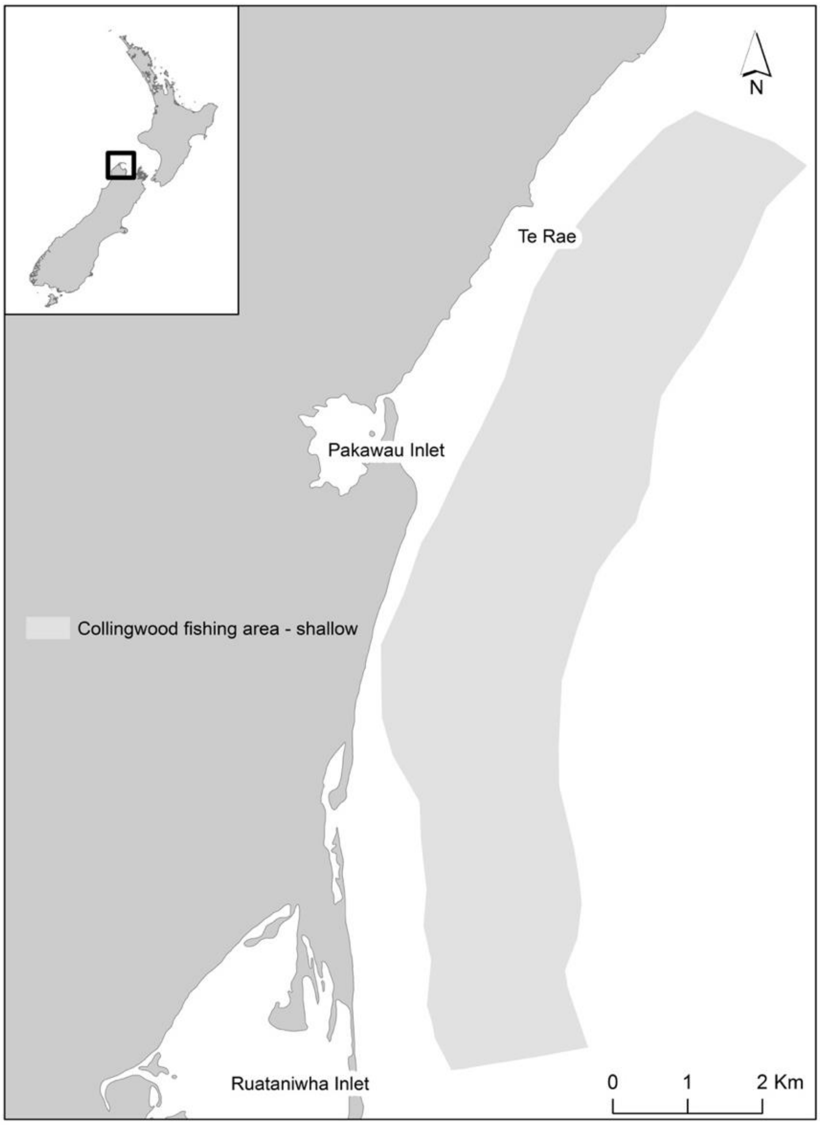

Figure 2. Map of Collingwood study area (delineated in light grey)

6.4 Biomass Estimation

At each location (C1-C50), two transects, each 50m long and 1m wide, were fished, making for a total of 100m^2 searched per site. Every geoduck landed in these transects was measured (maximum anterior-posterior length) to the nearest mm with vernier calipers (*sensu* Gribben and Creese 2005) and these measurements then tabulated and all geoduck encircled with a rubber band in order to minimize water loss in transit to the licensed fish receiver (LFR). The total weight of all geoduck collected from each transect were then weighed at the LFR in Tarakohe. These weights were then tabulated and the biomass calculated.

6.5 Productivity Components, Growth and Mortality

At each location (C1-C50), two transects, each 50m long and 1m wide, were fished, making for a total of 100m^2 searched per site. Every geoduck landed in these transects was measured (maximum anterior-posterior length) to the nearest mm with vernier calipers (*sensu* Gribben and Creese 2005). The total weight of all geoduck collected from each transect was weighed at the licensed fish receiver (LFR) in Tarakohe.

[Up to] The first five individual geoduck were collected from the bottom of the catch bag, i.e. the first five to be fished, these animals were labeled and kept for aging by examining the growth rings in the shells as in previous studies (Breen, 1991; Gribben and Creese, 2005). After drying the shells, we cut a section through the umbo using a Dremel 3000 Variable Speed Rotary Tool and Diamond wheel (Figure 3). We then mounted this cut section onto a glass slide using heated glue on an Analite SH1 hot plate (Figure 4) and allowed the glue and mounted section to then harden. (Only the right-hand side of the shells were used to complete this work, in keeping with tradition; in the case of damage to the right-hand side shell, the left-hand side was used.) The sections were then ground and polished on a Gemmasta Faceting Machine (Figure 6) to the desired thickness (Figure 7) – several trial runs were conducted on test shells prior to the commencement of the study to ensure the optimal thickness was known and easily achieved. These ground and polished sections were then viewed and photographed with a compound microscope – a Leica DM2000 and Leica software (Figure 8). All the images were minimally post-processed to enhance blacks, white and contrast before printing and annual growth rings counted by two independent observers.

Figure 3. Dremel 3000 with diamond saw attachment used to cut the shells.

Figure 4. The hot plate used to melt the CrystalBond adhesive and thus mount the sample section to the slide.

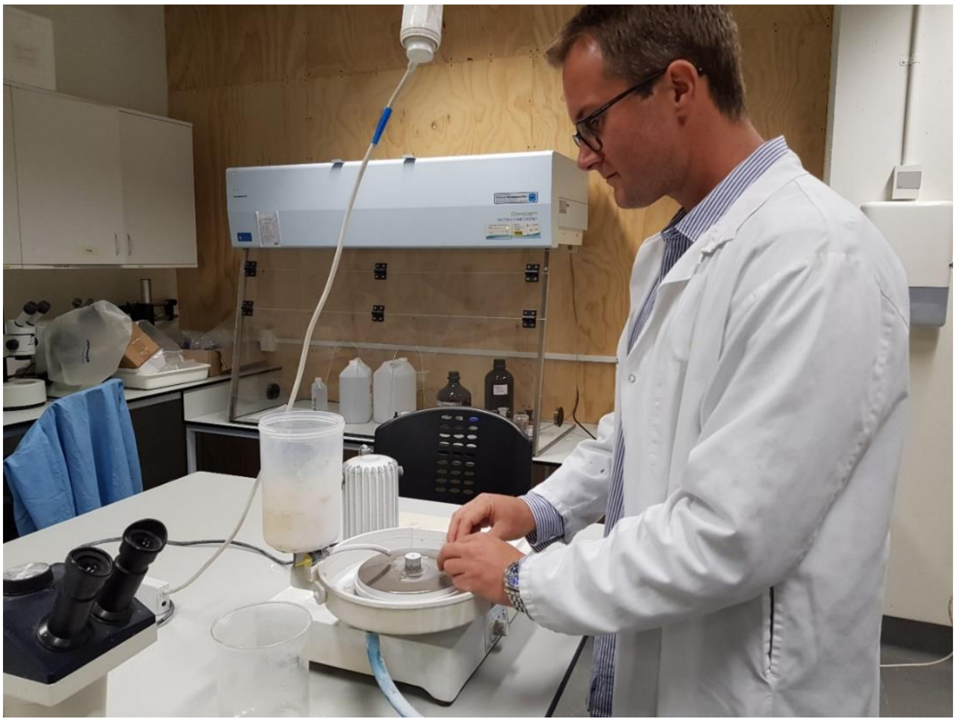

Figure 5. Grinding of mounted sample using polishing wheel.

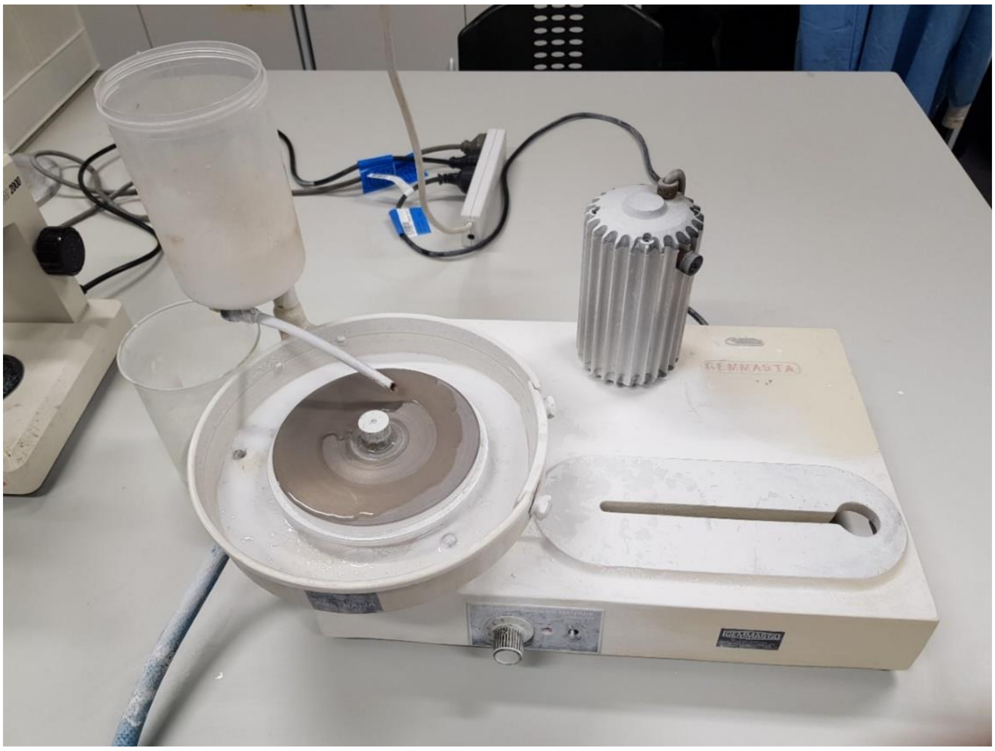

Figure 6. The Gemmasta polishing wheel used to polish the samples to the desired thickness with the water input device visible.

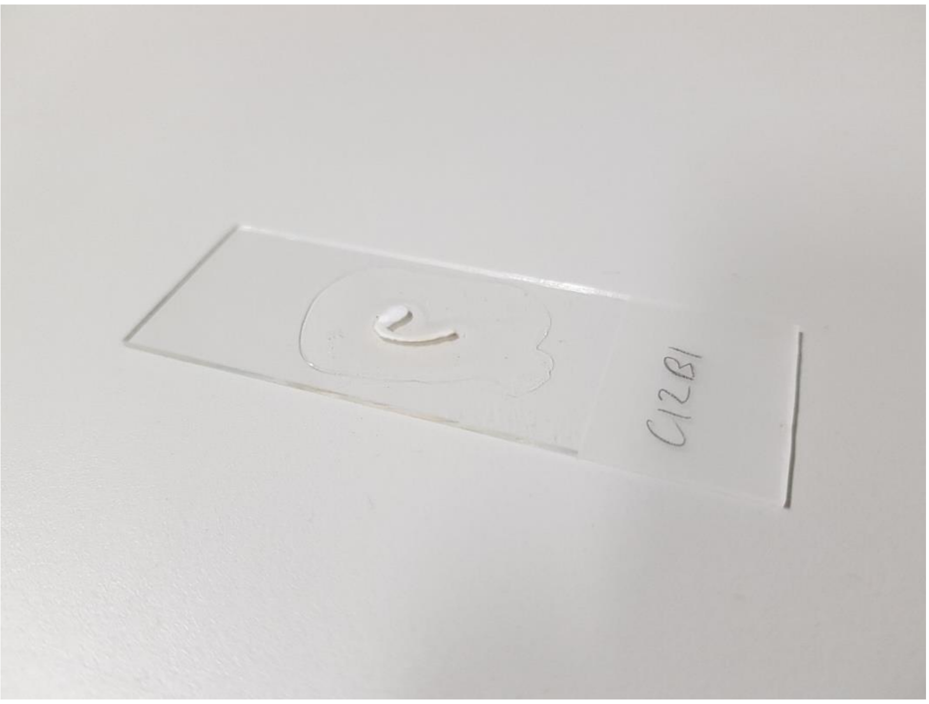

Figure 7. Example of a mounted and polished sample “C12B1” to desired thickness.

Figure 8. Leica DM2000 microscope and associated computer hardware for imaging analyses.

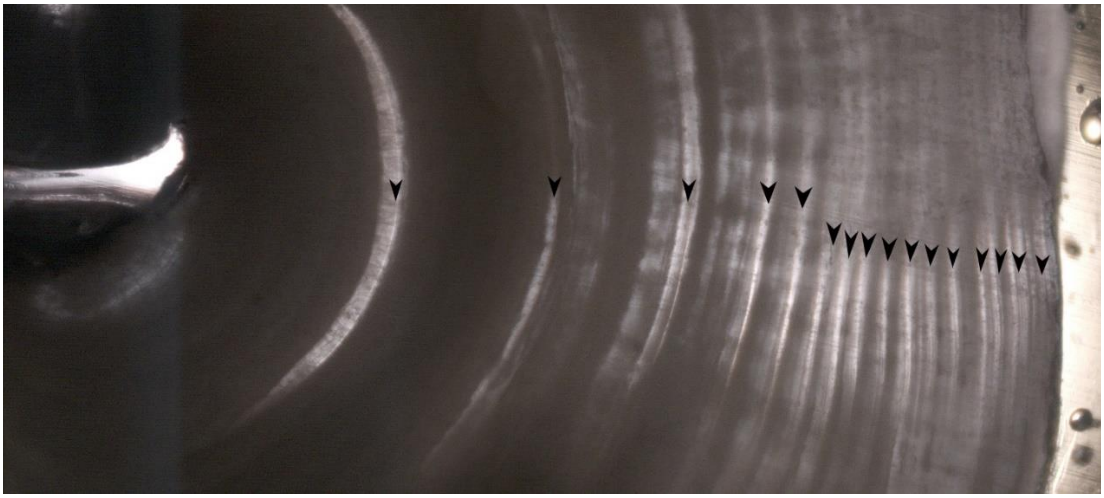

Figure 9. Sample with marked annual growth rings.

As mentioned previously, before the commencement of the above steps and the study proper, we performed several “test runs” on geoduck individuals that did not form part of our sample. This was done in order to practice the procedure and lessen potential errors with the study sample as there are only a finite number of attempts possible at aging each individual (due to there being only two shells) and as always, errors and breakages occur. We were also fortunate to have shell samples of P. zelandica individuals that had been cultured at the Cawthron Institute and were there known to be four years old (supplied by Le Viet Dung of Cawthron Institute and AUT.) We analysed four of these as above to calibrate that we were, in fact, finding the year one ring and that the rings we were counting were indeed annual ones.

6.6 Diver Efficiency

Two sites in the Collingwood area (Pakawau) at depths of approximately 6.5 m were haphazardly chosen for the experiments. At site 1, six 50m transects were laid and at site 2, four 50m transects were laid. These transects were marked out by placing a stake into the sediment at the start of the transect playing out a line for 50m and attaching it to another stake. A float was attached to the end of the transect so it could be located again. Once all the transects were marked out and on day one, each transect was fished (all visible fish were collected) 50cm either side using the water jet as outlined in the survey methods above, but instead of using the water hose at the transect, the marked-out lines were used instead. For the next 4 days, each transect was re-surveyed on SCUBA by two divers, searching for all visible geoduck siphon indentations and marking each one with a labeled 15cm length of No.4 galvanised wire. At the end of this period, this was tabulated and the efficiency was calculated.

6.7 Sediment Characteristics

At each site (C1-C50), a marked sediment jar was used to take a sediment sample of uniform volume at the start of both transects and delivered to the surface before the fishing survey began. These jars were then packed and frozen for storage and transport. Each sediment sample was then processed for 4 hours through a sediment sorter machine (Figure 10) and categorized into 4mm, 2mm, 1mm, 500um, 250um, 125um, 67um and <67um size classes (Figure 11) whereupon each size class for each sample was then collected and dried to constant weight in a drying oven at 50°C (approximately 72 hours.) Each size class weight for each sample was then converted to a percentage proportion of the total sample and then categorized as a sediment type.

It should be noted that before the commencement of the above steps and the study proper, we performed several “test runs” on using the sorter machinery, the procedure, drying oven and the dimensions of the drying vessels in order to hasten the time taken to process samples and minimize any error that might occur. The drying temperature of 50°C was chosen in order to not denature any proteins present in the sediment sample that might alter the mass proportion of any samples with a higher percentage of these.

Figure 10. Machinery used to process sediment sample in the centre of the image. Seven sieves were held and rotated through water.

Figure 11. Example of one of the seven sieves used to separate sediment samples. (500 microns.)

6.8 Geographical Information System Mapping

GPS data was imported (WGS1984 coordinate system) as well as depth data generated along with density and imported this into ArcGIS 10.6 as class features. We then created density “bubbles” within the outline of the study area using Spatial Analyst Tools.

6.9 Statistical methodology

The 50 locations were randomly chosen within the study area, and hence average density and its standard error were calculated using the standard formula for normal samples. Density of geoduck was modelled as quasi-Poisson. This models expected density on the log scale (multiplicative effects) and also assumes standard deviation in observed density is proportional to expected density. Analyses of morphometry used nonlinear modelling, assuming lognormal errors. All analyses were performed in the R language.

7. Results

7.1 Biomass

The smallest measured geoduck individual within the dataset was 69mm in shell length and the largest was 153mm. Transect total biomass ranged from 0.0015kg/m^2 to 0.39kg/m^2.

In total 665 individual geoduck were collected and landed in the 100 transects (Figure 12 and Table 1), totaling 311kg green weight. The average density across all transects was 0.062 kg/m^2, with a CV of 0.205. With the total Collingwood area measuring 21,554,077m^2, this gives a total [virgin] parent biomass of 1,334kg.

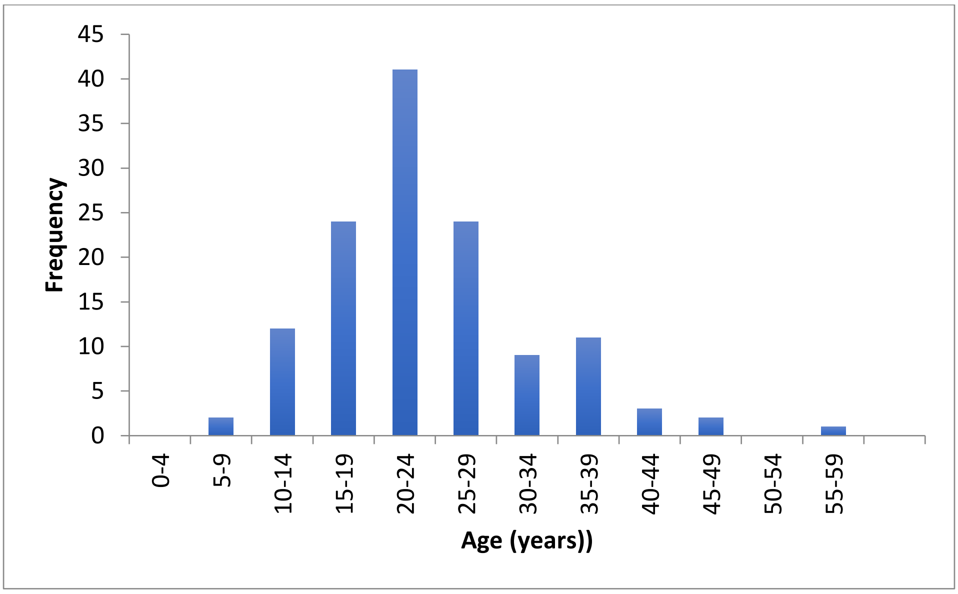

Figure 12. Age-class frequencies across the sample.

The distribution of age class frequencies appears to be normally distributed, with potentially a very slight positive skew. This could be, however, the result of a few outliers.

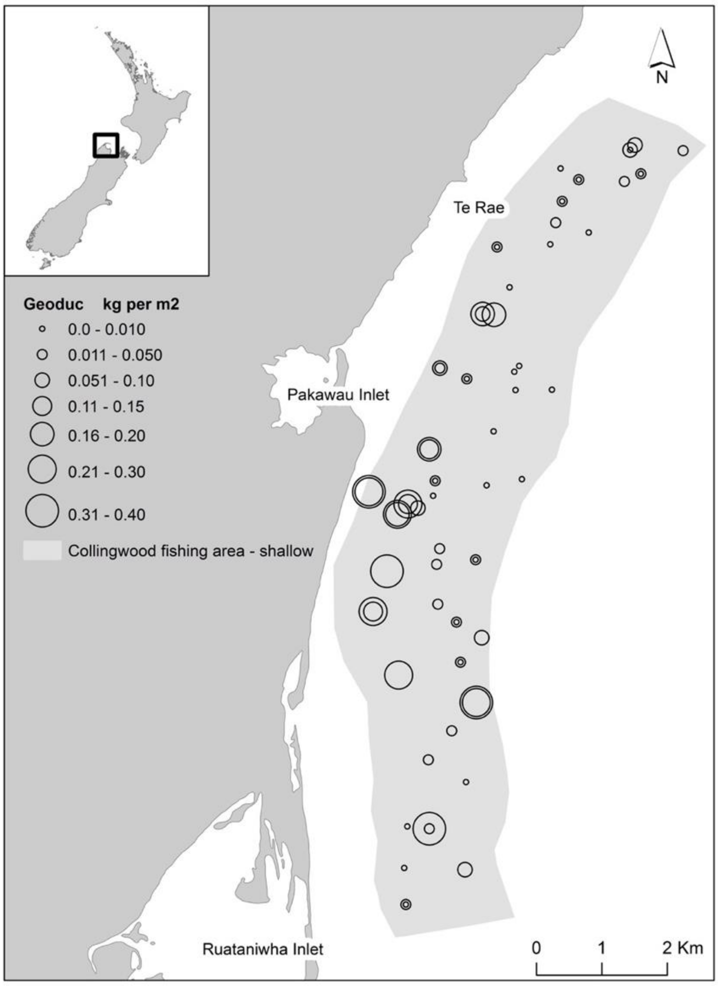

Figure 13. Distribution of geoduck in the Collingwood area

Chart datum depth was the strongest predictor of density with a predicted density of approximately 0.15kg/m2 occurring at slightly shallower than 4m datum depth (Figure 14).

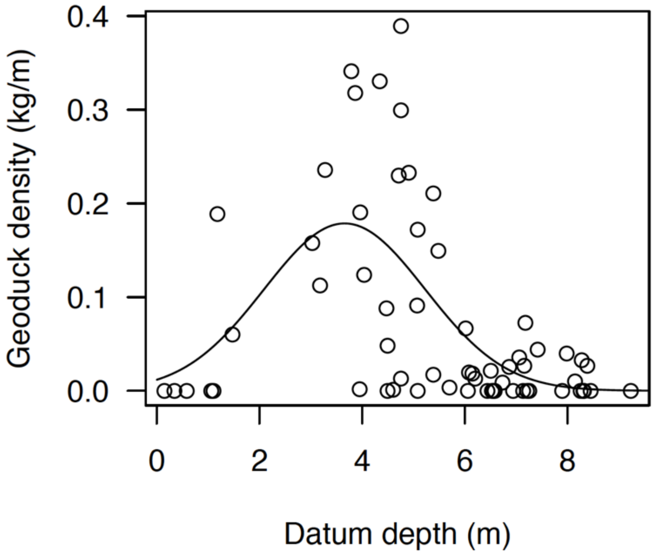

Figure 14. Relationship of *Panopea zelandica* density (kg m^{-2}) to datum depth (m)

There is also a highly significant association between grain size and density (p-value of 0.00038) (Figure 4). Standard error was 0.205. Grain size was expressed using the Krumbein phi, where phi = -log$_2$(diameter). For every unit increase in phi (i.e., grain size diameter becoming finer by a factor of 2), density is reduced by 54%. The model that includes both depth and grain size as covariates explains 51% of the variation in density.

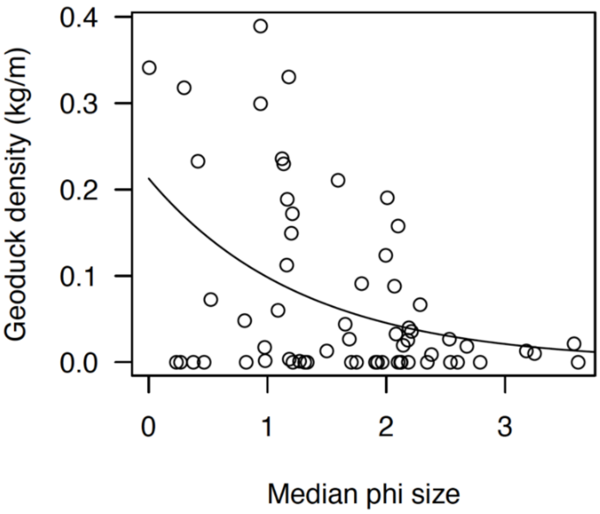

Figure 15. Relationship of *Panopea zelandica* density (kg m^{-2}) to median sediment grain size (phi) in FMA7.

7.2 Productivity Components, Growth and Mortality

All 665 geoduck collected were measured (ranging from 69 to 153mm, with an average of 112mm) (Figure 16). The youngest geoduck aged was 4 years old and the oldest age-determined individual was 33 years old. The distribution of size class frequencies appears to be normally distributed, with minimal skew and the unimodal nature of the length-frequency data would suggest a single age class.

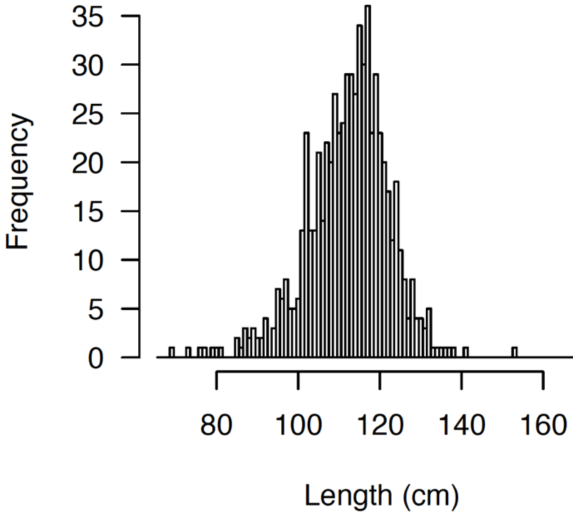

Figure 16. Frequency of Shell Length Classes (mm) of *Panopea zelandica* in FMA7.

The estimated instantaneous mortality Z (inclusive of both natural mortality and fishing mortality) is 0.209 (SE 0.047). Estimated annual mortality is 0.189 (SE 0.042). In this analysis, the first 8 age classes were removed since there is aged-based selectivity bias.

A von Bertalanffy growth curve fitted to the aged individuals estimated (Figure 17) a L_{inf} of 127.5mm (SE 4.8mm), growth rate (K-value) of 0.11 (SE 0.027) and an age-at-length-zero of -4.24 years (SE 2.15.)

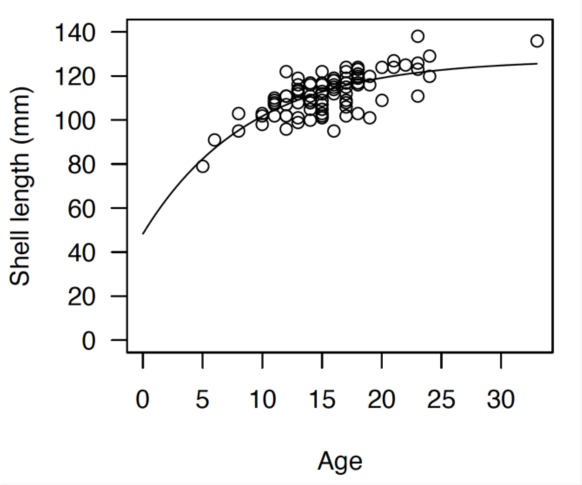

Figure 17. Von Bertalanffy Growth Model (VBGM) of shell length (mm) to age (years) of *Panopea zelandica* from FMA7.

7.3 Diver Efficiency

The mean efficiency of fishing on day one was just 22% (Table 2). A double bootstrap was implemented to obtain a confidence interval. This includes the between transect variability in show proportions by resampling both transects, and clams within transects. The 95% bootstrap confidence interval was 15.9 to 30.8%. There was no statistically significant relationship (p = 0.3) between the density of geoduck per square metre and the efficiency (Figure 18). NB. Table 2 “Fished” column also stands for Day 1, as Day 1 was the only day that was “fished.”

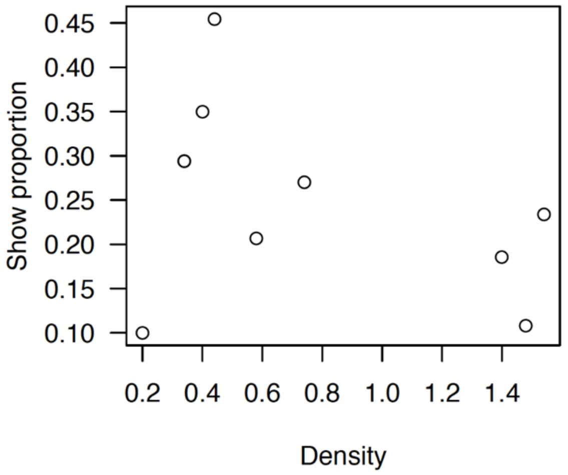

Figure 18. Relationship of show proportion to density (kg m^{-2}) of *Panopea zelandica* in FMA7.

Table 1. Percentage efficiency over a 5 day period.

Site	Trans.	Fished	Day 2	Day 3	Day 4	Day 5	Total	% Eff.
1	1	5	4	4	1	3	17	29.41
	2	10	5	2	4	1	22	45.45
	3	5	6	3	1	2	17	29.41
	4	6	5	8	6	4	29	20.69
	5	1	4	1	2	2	10	10.00
	6	7	6	4	1	2	20	35.00
2	1	13	23	18	12	4	70	18.57
	2	8	18	25	15	8	74	10.81
	3	18	20	27	7	5	77	23.38
	4	10	15	5	4	3	37	27.03

7.4 Sediment Characteristics

Median phi size ranged from approximately 4 to just close to 0 for Golden Bay. That is, the substrate would be classified as very fine sand (62.5µm-125µm) through to coarse sand (0.5-1mm) according to the Wentworth scale.

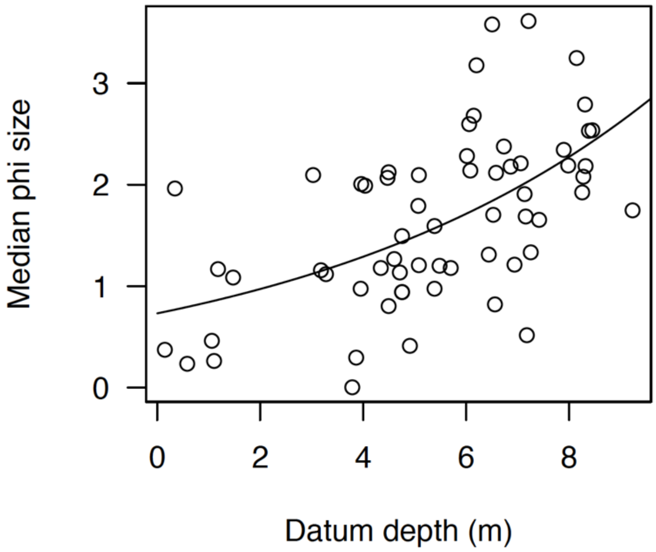

Figure 19. Relationship of datum depth of sampled *Panopea zelandica* to median sediment grain size (phi) in FMA7

Phi is estimated to increase by 15.22% for every metre increase in datum depth. That is, in terms of grain size, there is a reduction in diameter of 10.01% for every metre depth increase (Figure 19).

8. Discussion

8.1 Biomass Estimation

Gribben, Helson and Millar (2004) found densities of 0.058 geoduck/m^2 in Kennedy Bay and 0.489 geoduck/m^2 in Shelly Bay with Gribben & Creese (2005) showing mean maximum drained wet weights of 275.5g in Kennedy Bay and 223.1g in Shelly Bay. This could be calculated to give 0.016kg/m^2 average densities for Kennedy Bay and 0.109kg/m^2 for Shelly Bay compared with our average density of 0.062kg/m^2. and so, accounting for water lost in draining, the Collingwood area appears to have similar or higher densities than Kennedy Bay and Shelly Bay. Our Coefficient of Variation (CV) of 0.205 is fairly typical of a biomass survey and is similar to results obtained by Gribben, Helson & Millar (2004). Differences in density could be explained by local environmental and productivity factors as well as Shelly Bay being a part of PZL1; a fishing management area that has seen no landings since these studies were performed whereas Collingwood, in PZL7, has seen 43.7 t in landings in between the course of the aforementioned studies and our surveying (2004-2015.) Gribben et al. (2004) also gives caution to potential fisheries managers in harvesting geoduck due to the relatively low densities of *P. zelandica* found in the study, however, given our densities were relatively high, this population of geoduck may not suffer as rapid depletion as potentially heralded in Gribben, Helson & Millar (2004). Other Bivalvia experience high recruitment even when their spawning biomass is depressed (Hancock, 1973), however, no investigation of any relationship of this nature has been performed on *P. zelandica*.

Our investigation into the relationship between depth and geoduck density yielded similar results to other studies; Gribben et al. (2004) found peak geoduck densities at comparable depths to our own. Gribben et al. (2004) suggest that biofilm may function as a settlement cue for geoduck similar to other marine bivalves and Le et al. (2017) has postulated that the settlement cues may be quite different to other genera and, indeed, unique to geoduck.

8.2 Productivity Components, Growth and Mortality

Traditional methods for dating Bivalvia involves the examination and counting of external rings on the individual's surface (Richardson & Walker, 1991), however, this method is not suitable for all species due to such rings being difficult to distinguish with first-year depositions, the growth rings being packed together more closely as the individual's growth slows down later in life (Richardson et al., 1993) and some external rings being missing in some growth years in some *Panopea* species, notably *P. abbreviata* (Morsan & Ciocco, 2004.)

Accurate mortality and growth estimations are based on the assumption that the growth rings being counted in geoduck are indeed annual. The annual growth bands deposited by geoduck have been shown to be the formation of a dissolution of calcium carbonate due to anaerobic metabolism during periods of winter inactivity in both *P. abrupta* (Shaul & Goodwin, 1982) and *P. abbreviata* (Morsán & Ciocco, 2004). Whilst Breen (1991) presents estimated ages in *P. zelandica* that have not been validated, we validated that the depository growth rings were annual by aging several individuals of known age and adding to the strong evidence of annual deposition shown by Gribben & Creese (2005).

The use of internal bands suggested by Thompson et al. (1980) to more accurately determine age due to the clarity of deposition being more easily read than external bands has been explored and utilized by a multitude of studies (Palacios et al., 1994) (Cerrato, 2000) however, similar problems still exist in that first-year depositions have been difficult to validate and despite the increased clarity of deposition of internal bands over than external growth bands, longer-lived individuals can be underestimated.

Some studies (Black et al., 2008) utilize crossdating to further solidify age data and this is particularly useful, especially for longer-lived individuals (Black et al., 2008), which are more likely to influence growth and mortality data. However, any errors in the aging of individuals within our study is likely to underage individuals which would mean that our results, whilst not infallible, are conservative by nature and keep any resulting detrimental effects on fishery exploitation to a minimum. Dendrochronology has demonstrated for nearly a century that individuals and populations from a single [or even multiple] locations exhibit synchronous growth in line with local environmental conditions. These factors include temperature, precipitation, and river discharge and show that environmental processes can have a mechanistic effect on growth (Helser, Lai & Black, 2012.) The same is true of many marine organisms, with dendrochronology techniques being used to age biogenous calcium carbonate structures that are laid down annually and respond mechanically to local environmental conditions. This has been done in coral (Correge, 2006), fish (Black et al., 2008) and other Bivalvia (Butler et al., 2009) and also, in *Panopea*. The longevity of members of *Panopea* genus is useful in creating paleoclimatic reconstructions of local environmental conditions [such as temperature (Black et al., 2009), (Goman et al., 2008), upwelling (Killingley & Berger, 1979) and productivity (Marchitto et al., 2000)] that were present during the lifetime of the individual and thus influenced the mechanistic growth of individuals and local populations. This relationship has also been used in reverse to analyse the effects of variables upon the mechanistic growth of geoduck.

The size and age data generated by this study have been used for comparison with the age-weight growth curve and natural mortality data used largely in the study of geoduck sustainability of Breen (1994) and the results of other studies are broadly comparable to our's. Our maximum age (33 years) is extremely similar to the 34 years old found in Breen (1994) and with the maximum of 34 years from the Kennedy Bay population from Gribben & Creese (2005) but contrasting with the maximum of 85 years from the Shelly Bay population described in the same 2005 study; these authors state that Kennedy Bay and Golden Bay both represent relatively high energy and exposure coastal bay environments compared to the benign and sheltered nature of Shelly Bay with this suggesting that local environmental characteristics are important in determining growth and age of *P. zelandica*. Breen and Shields (1983) suggest that shell length of *P. generosa* increases when exposure to wind and wave energy decreases and our results appear to be relatively consistent with this, given the relative shelter to the prevailing westerly winds and wave exposure of the Pakawau area and Golden Bay in general.

Our instantaneous mortality (Z) of 0.209 (SE 0.047) is similar to Breen's 1991 (upon which the current management is based) instantaneous mortality M (0.20) and contrasts with Gribben & Creese's (2005) natural mortality being lower at between 0.05 and 0.07 (Kennedy Bay) and 0.02 to 0.04 (Shelly Bay), a key difference being that our mortality (Z) is instantaneous mortality determined from both natural causes and fishing.

Breen's 1991 natural mortality rate of 0.14 was based on a maximum age of 34 years with the assumption that 1% of any cohort would grow to maximum age; 40 age classes were simulated and after 40 years, all clams were assumed to have died. We assumed non-variable rates of natural mortality from year-to-year and did not operate under the arbitrary assumption of 1% survival to maximum age.

Higher estimates of growth (k) are expected when studied populations are composed of larger proportions of younger individuals (Hoffman et al., 2000); When estimating recruitment, Breen (1994) used only animals 8 years or older for recruited biomass; we also did the same when estimating mortality as there appears to be an aged-based selectivity bias and thus our growth rate (k) is reliable.

Our growth rate (k) of 0.1123 appears to somewhat smaller than other species found in the Aragon-Noriega et al., (2015) with this publication suggesting that this could be due to primary productivity differences, local environmental conditions or simply differences that are known to exist between populations. The growth rates for the two spatially distinct populations published in Gribben & Creese (2005) were significantly different and this supports findings by Aragon-Noriega et al., (2015).

Furthermore, the mechanistic relationships established in previously mentioned dendrochronological studies have been used in reverse to estimate the strength of different environmental effects on the growth of *Panopea generosa*; Helser, Lai & Black (2012) showed that whilst larger-scale processes such as the Pacific Decadal Oscillation (PDO) has a significant impact on the growth of geoduck, the variability in growth is largely explained by sea surface temperatures (SSTs) and random year events with SSTs corresponding largely with latitudinal gradients in temperature.

It should also be noted that comparisons with other studies based on the VBGM may not be as applicable as the use of VBGMs to represent geoduck growth has been criticised (Haddon, 2001) and suggestions that the multimodel approach is more favourable (Burnham & Anderson, 2002). Our study removed the first 8 age-classes to account for the sampling bias evident in the sampling; smaller individuals are likely to be missed during harvesting and therefore introduce an age and size-based sampling bias which leads to unrealistic lengths-at-age-zero and inaccurate growth rates (k) (Hoffman et al. 2000). Our study gives smaller growth rates (k) than other studies mentioned previously and is therefore likely to be more conservative and less inclined to lead to the fishery of *P. zelandica* being managed as a species with higher turnover.

We found a maximum theoretical length of 127.5mm with standard error 4.75mm. K value (growth rate) of 0.112 year^{-1} annually, standard error of 0.027. T_0 of -4.23 with a standard error of 2.15. Given our standard errors, our results are not dissimilar to other findings by Breen (1991) that found a maximum theoretical length of 116.5mm, K=0.16 year^{-1} and t_0 of -3.80 years and 111.5mm (Kennedy Bay) and 103.6mm (Shelly Bay) from Gribben & Creese (2005.) Our maximum observed length of 141mm is somewhat larger than the largest individual (127mm) found by Gribben & Robert (2005) as was our maximum theoretical length (L_{inf}) (127.5mm) compared with their 111.5.mm. Our rapid increase in growth of shell length and subsequent tapering off after 10-12 years of age appears to be consistent with Breen (1991) as well as Gribben & Creese (2005.) Compared to North American and other species, our maximum lengths are smaller and Aragón-Noriega & Rodríguez-Domínguez (2015) state the primary production differences in local areas could be the difference; northern hemisphere species such as *P. generosa* are based in one of the world's most productive fisheries areas whereas *P.*

zelandica is located within a relatively poor one. It is widely known that food availability and temperature are linked to size and growth in Bivalvia, however, no samples or data were taken in order to investigate these relationships in *P. zelandica* more fully and this could be a focus for future work.

Other studies in *Panopea* species other than *P. generosa* and *P. zelandica* have shown similar growth differences in different populations; Morsán et al. (2010) found that two *P. abbreviata* populations differed in asymptotic size across a thermohaline boundary and postulate that temperature and salinity clearly are likely to be causes of this. Morsán & Ciocco (2004) attributed to the seasonal cycle of translucent and opaque deposition of calcium carbonate to be linked to the seasonal change in metabolism due to lower temperatures and food availability.

Despite our modeling being more accurate than previous studies, the use of only one model (even if it is considered the best model to be used) can lead to biased point estimation and false evaluations (Katsaevakis, 2006) and therefore future studies might include multimodel inferences to estimate growth parameters as a more accurate method. However, in previous studies such as Zaidman & Morsán (2015), the VBGM was the best model used in all but two of the locations and given that their growth and asymptotic lengths were similar to our own, it is the opinion of this study that use of the VBGM was justified and the results generated to be robust.

The catch-curve analyses used by Breen (1991), as well as Gribben & Creese (2005), operate under two assumptions; firstly, recruitment rates are approximately constant during the time that aged geoduck were recruited and secondly, mortality is similar for all age classes. Gribben & Creese (2005) concluded that catch-curve analyses may not be appropriate for estimating natural mortality in geoduck with Millar (2015) suggesting general linear mixed modeling (GLMM) is superior in predicting mortality due to the inclusion of recruitment involving annual variation and substantial variability known to exist in population dynamics (Myers et al, 1995.) Breen's 1991 estimate of mortality was rejected due to spatial and temporal variability in recruitment being rather high; our estimates of mortality are likely to be more accurate and reliable given the improved method of estimation specifically including annual variation in recruitment, and this has significant implications for the management of the fishery. Gribben & Creese (2005) suggest that due to low natural mortality and longevity of *P. zelandica*, fisheries managers will need to be cautious in commercially harvesting geoduck in NZ. Our findings, however, suggest a much higher instantaneous mortality and less longevity; this advocates a higher sustainable yield of biomass due to a higher turnover rate.

Breen’s 1994 study shows, that at a 6% quota, doubling M from 0.1 to 0.2 resulted in more than doubling the mean recruited biomass.

8.3 Diver Efficiency

Geoduck densities in North America are adjusted by the use of established methods that include counting the siphon holes through which geoduck filter feed. Problematically, not all geoduck “show” their siphon holes at the same time and thus could lead to an erroneous population estimate (Hand & Dovey, 1999).

This is solved by the use of a “show-factor” which is the number of geoduck siphons that are visible or can be felt versus the total number of individuals present in a given area and is expressed in the formula, $S = n / N$, where S = show factor, n = the number of visible geoduck shows within a defined area and N = the absolute number of harvestable geoduck present within the area. In Washington, “show plots” are utilised at sites to estimate the show factor and entails permanently marked subtidal areas in which N is known due to repeated tagging studies and n is obtained from divers counting all visible geoduck as if they were completing a standard survey (Campbell, Yeung, Dovey & Zhang, 2004). The number of geoduck that “show” their siphon holes is variable upon different environmental and physiological factors; with more showing during the summer months during periods of feeding and breeding (Campbell, et al., 1998) (i) and when local water currents are not overly severe with no mechanical disturbances of the bottom due to events such as storm activity (Goodwin, 1977), (Campbell et al., 1996). Some of the show factors used in the major geoduck fisheries are 0.90 in British Columbia (Campbell, Yeung, Dovey & Zhang, 2004), 0.73 in Washington (Bradbury, Sizemore, Rothaus & Ulrich, 2000) and 0.80 in SE Alaska (Rumble, Hebert & Siddon, 2012). Gribben, Helson & Millar (2004) investigated the use of show-factors in assessing geoduck populations in New Zealand and found a mean show-factor of 0.914.

Gribben et al. (2004) performed the show-factor experiments for five days with a single experienced geoduck diver, as did our study, under the assumption that no geoduck would remain hidden for more than five days. However, Gribben et al. (2004) had high show-factors on any given day (with 71-100% showing) whereas our study showed low overall efficiencies, with a show-factor of only 22% on day one which is consistent with the findings of other studies, such as Campbell et al. (1998) (ii), that state that not all siphon holes are visible at any one time. It could possibly be argued that, perhaps, our show proportions were smaller due to the higher densities that we encountered, however, our results also show that there is no significant relationship between density and the number of geoduck siphons showing. Gribben et al. (2004) states the reason for any geoduck in their study not being counted being due to the diver inadvertently missing siphon holes or due to low visibility; they employed a method of counting geoduck where they were not extracted, citing high mortality rates when the extracted individuals are attempted to be resettled. However, our show-factor experiments and entire study were based on a modified fishing method where the geoduck were fully extracted using a weighted diver on the bottom and using a pressurized water hose to obtain the geoduck, thus releasing sediment into the water column and lowering visibility, potentially lowering our show-factor relative to Gribben et al. (2004) and is more indicative of the show proportion that will be encountered in the commercial harvesting of this species. Given that our experiments were still finding geoduck that were not showing after day 5, our efficiency and show proportion estimates are already, by nature, conservative.

Puget Sound, for example, uses a show-factor to adjust density estimates to give the fishery's managers a conservative estimate of true harvestable biomass (Gribben et al. 2004, Bradbury et al. 2000). Gribben et al. (2004) also conclude that, indeed, methods for estimating biomass and importantly here in particular, that the use of show-factors employed in the North America geoduck fisheries is transferable to New Zealand's *P. zelandica*. As previously mentioned, our study results show that there was no statistically significant relationship ($p = 0.3$) between the density of geoduck per square metre and the efficiency of geoduck found – the proportion of geoduck showing at any given time is independent of density of geoduck present and this is an important consideration for management of the fishery.

Employing the upper confidence interval of 30.8% efficiency of the survey effort as a multiplier to the estimated parent biomass of 1,334t in the Collingwood area, one would obtain an adjusted parent biomass of 4331.17t and in using the lower confidence interval of 15.9%, a parent biomass of 8389.94t would be achieved after adjustment for show proportion. Due to the inherently conservative nature of the show proportion experiments and the very conservative upper confidence interval of 30.8%, it is reasonable to suggest an adjustment of 23.35% to the parent biomass, giving a true and adjusted parent biomass of 5,713.1t.

The 2017 PZL plenary (2017) states that due to low levels of exploitation of *P. zelandica* stocks, they are still effectively in a virgin state and this is important when it comes to estimating MSY. Breen (1994) suggesting a maximum sustainable yield of 2-

4% of virgin biomass, which in application to our adjusted parent biomass of 5,713.1t, gives TACCs of 114.26t and 228.52t, respectively. In line with the conservative show-factor adjustment for biomass, it is the recommendation of this study that an MSY of 3% is utilized, giving a new TACC of 171.4t in PZL7. Breen 1994's modeling of the effect of variables such as harvesting rates on the population and biomass of *P. zelandica* states small risk to the population at 3% yields with the risk to the fishery remains zero until above 3% MSY. The effects of pulse fishing, which may be performed inadvertently by fishers, is negligible with respect to changes in biomass, the risk to the fishery/population and minimum biomass, especially from 0-3% MSY.

With the current TACC for PZL7 standing at 23.1t, this gives an increase of 148.3t and with prices for live weight exported geoduck reportedly reaching as high as $35 per kg, an increase of this magnitude could potentially bring in millions of dollars of revenue annually, employment and follow-on effects into the Golden Bay region with the resulting expansion of the fishery.

8.4 Sediment Characteristics

The effect of sediment type on infaunal Bivalvia biology is well documented; Hernandez-Otero et al. (2014) found that out of several variables, the percentage of mud in the substrate was the most significant predictor of size variability. Furthermore, previous research on *P. generosa* has illustrated that there is a relationship between sediment type and shell length.

We found that, unlike the findings of Gribben, Helson & Millar (2004), P. *zelandica* in Collingwood appear to prefer sediments with a larger diameter than those of the aforementioned study. Our highest densities occurred in sediment aggregates characterized as very coarse sand with the density dropping off as median phi size increases (and the sediment aggregate diameter becomes finer.) These differences may simply be a reflection of the diverse range of habitats geoduck occur in rather than a strict habitat preference or this could be linked to both depth and exposure as these are known to have effects upon particle size aggregates.

Hoffman et al. (2000) found that high rates of growth are associated with individuals associated with finer particle substrate aggregates, whereas lower growth rates were associated with coarser particle aggregates; according to our results, *P. zelandica* were found within aggregates consisting of more coarse particles - our growth rates being somewhat lower than in other studies is consistent with Hoffman et al. (2000) in this regard.

8.5 Other Considerations

Due to practical and safe diving constraints, our sampling did not extend to 15m (such as in Gribben et al. 2004), however, there is a slight indication to suggest that our figures may contain a bimodal relationship with respect to depth and density similar to the aforementioned study. Gribben et al. (2004) sampled to 15m water depth and found a bimodal depth-density relationship with distributions clumping at 6-8m and 10-15m. Other studies such as Gribben et al. (2004) have suggested that, as part of a sustainable fishery allowance, there be a “depth sanctuary” established (at which no harvesting could occur) that could act as a reservoir for genetic input and recruitment. Due to the practical nature of commercial harvesting [in its current state] as seen in our depths sampled, this may be easily passed in the legislature, due to the amenability of commercial fishers, such as PZL Harvesters.

Gribben and Creese (2005) suggest that, due to the width between paired surface siphon holes being a reasonable predictor of shell length, it could possibly be used as a less invasive method of estimating recruitment rather than the typical methods. It is important to note, however, that in their study they experienced much higher show proportions than in our results and it is likely that with such variability in show-factors, the predictive nature of paired siphon hole width is less reliable.

There appears to be locally determined effects on growth in geoduck and growth parameters such as growth rate (k) vary between populations (Gribben & Creese, 2005, Slater et al, this issue). Given that small differences in growth rates (k), how these affect the outcomes of the VGBM, and therefore have tangible implications for the management of a fishery (Hoffman et al. 2000) it is the opinion of this study that, perhaps, separate *P. zelandica* populations be managed under the assumption that their growth rates and, indeed, other estimates of productivity are possibly different. This, however, would require future research into to what degree populations of *P. zelandica* are distinct.

Suarez-Moo et al. (2016) showed that, in *P. generosa*, there was large genetic homogeneity and little genetic difference between populations in locations hundreds or thousands of kilometres apart; they state their findings are consistent with a single management regime encompassing both Canada, the USA, and Mexico. Gribben & Hay (2003) showed that *P. zelandica* larvae spontaneously settled after 16 days which appears to be vastly different to the pelagic larval durations of *P. generosa* of 42-47 days, however, the spatial dispersal barriers and distances would appear to be somewhat less than the northeast Pacific. If *P. zelandica* was similar in having large-scale genetic homogeneity like *P. generosa*, it could have implications for the way our fisheries are managed as seemingly unrelated populations could essentially function as one genetic stock, however, more research is necessary into the genetic reservoir of *P. zelandica* as well as the basic locations of populations around the country. The role of epigenetics in the role of inheritance has become increasingly understood recently; simply because an array of populations is genetically homogenous does not lead to epigenetic similarity. With fisheries management being based on practical outcomes, the interaction between the genome of *P. zelandica* and its environment and the inheritance of epigenetic modifications resulting in phenotypic differences between populations becomes increasingly important. One population may be epigenetically unique to another, with such unique characteristics as growth rates and therefore, may warrant being managed as a unique fishery yet still receive genetic input from another fishery being managed under its own unique management area under the QMS.

8.6 Limitations, Improvements and Future Research

Despite our best efforts to account for bias, nevertheless, some exist. Firstly, there is size-based selectivity bias. Accurate sampling is critical to obtaining reliable growth, mortality and recruitment data, therefore, in the future potentially a more thorough sampling method may be utilized in order to get a more fully representative sample. The suitability of different methods of doing this should be investigated; dredging is potentially worth and Vanblaricom et al. (2015) hints at minimal damage to infaunal communities as the result of other seemingly invasive techniques, however, whether the results of this study are applicable to the harvesting methods utilized in New Zealand would require further determination. There is also the potential development of SONAR techniques currently being assessed at the Auckland University of Technology.

Despite our faith in our aging methods in this study, Black et al. (2005) note that it is relatively easy to incorrectly estimate the age of geoduck, especially in the oldest individuals. Black et al. (2008) also suggest that using crossdating, a method borrowed from dendrochronology, can establish more accurate production-age data due to the growth synchronization in response to environmental conditions changing across calendar years. Estimating longevity in long-lived animals such as geoduck depends largely upon having very old individuals present in the sample; a sample size on thousands of individuals in Bureau et al. (2002) yielded a maximum age of 168 in *P. abrupta*, however, our sample of 668 individuals had a maximum age of 33 years old. It is likely that *P. zelandica* is simply a shorter-lived species inhabiting different latitudes and different environmental and oceanic zones.

Dendrochronology has demonstrated for nearly a century that individuals and populations from a single [or even multiple] locations exhibit synchronous growth in line with local environmental conditions. These factors include temperature, precipitation, and river discharge and show that environmental processes can have a mechanistic effect on growth (Helser, Lai & Black, 2012.) The same is true of many marine organisms, with dendrochronology techniques being used to age biogenous calcium carbonate structures that are laid down annually and respond mechanically to local environmental conditions. This has been done in coral (Correge, 2006), fish (Black et al., 2008) and other Bivalvia (Butler et al., 2009) and also, in *Panopea*. The longevity of members of *Panopea* genus is useful in creating paleoclimatic reconstructions of local environmental conditions [such as temperature (Black et al., 2009), (Goman et al., 2008), upwelling (Killingley & Berger, 1979) and productivity (Marchitto et al., 2000)] that were present during the lifetime of the individual and thus influenced the mechanistic growth of individuals and local populations. This relationship has also been used in reverse to analyse the effects of variables upon the mechanistic growth of geoduck. It would prove interesting to investigate the effects of such local environmental conditions upon the growth of *Panopea zelandica* populations and could potentially be used to further validate age-growth data. It is an interesting potential area for future research – with the possibility of paleoclimatic reconstructions of areas around New Zealand for which few records exist.

There is also the possibility of a depth-based selection bias; we did not sample below 12m due to the constraints of safe commercial diving practices. It could be posited that it may be worthwhile to sample below this depth, however, it would require the reconstruction of our sampling method and would be likely to introduce its own issues and limitations in the applicability of the data into the survey.

Budget constraints did not lend themselves to conducting sexing of our geoduck samples or other genetic work, however, potential future studies could examine the potential effects of the functional protandry exhibited in geoduck and whether this creates a selection bias that would lead to overharvesting geoduck of increasing size and therefore, proportionally more females removed from the reproductive population. While Gribben & Creese (2003) investigated protandry in *P. zelandica* in both Kennedy and Shelly Bay, future work should explore the potential effects of protandry in harvesting bias and the possible effects on the fishery in PZL 7.

Potential future studies could examine the potential effects of this protandry and whether this creates a selection bias that would lead to overharvesting geoduck of increasing size and therefore, proportionally more females removed from the reproductive population. Whilst this may be a concern, the implied fisheries management implications of a *potential* harvesting bias may be difficult to implement; a maximum size would require the resettlement of individuals into the substrate and given the high mortality rates in doing so, this may not be feasible. In addition to this, in the potential event of establishing size limits, it is unlikely that commercial fishers would be willing or even able to perform measurements such as this due to practical considerations; leading to significant negative consequences for the management of the fishery – this could be potentially solved via the creation of depth harvesting refugia.

It is the recommendation of this study that, in order to take measures to create a sustainable fishery and that in light of the limitations of this study with respect to *Panopea zelandica*'s functional protandry, that a harvesting sanctuary potentially be created past 12m water depth in order to keep a reproductive population intact. This recommendation is in line with the recommendations of Gribben & Heasman (2015).

One minor but easy-to-implement improvement to the study would include the individual wet weight of each geoduck being determined in addition to transect weights in order to more accurately estimate age-growth data and morality.

Other future work could include the potential for investigating the anecdotal evidence of a relationship between siphon colour and conditioning and sediment type; whiter and better-conditioned siphons in the geoduck fetch higher prices in the market and this would obviously be important in growing the value of the *P. zelandica* fishery and contributing to meeting Aquaculture NZ's 2025 target.

This thesis contributes to the current body of knowledge on *P. zelandica*. We investigated poorly understood areas identified by Breen (1991), Gribben & Creese (2003), Gribben et al. (2004), Gribben & Creese (2005), Gribben & Heasman (2015) and the Ministry for Primary Industry (2016) as well as discussing potential limitations and management problems described by the previous studies. Furthermore, we have identified and posited potential biases, issues and possible future research in *P. zelandica* fisheries and populations in New Zealand for the future.

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10. Appendix 1 - Summary statistics from geoduck survey

Transect	N	Aged	kg/m2
C01A			0
C01B			0
C02A	4	4	0.0270
C02B	5	5	0.0427
C03A			0
C03B	1	1	0.0101
C04A			0
C04B			0
C05A	3	3	0.0247
C05B	4	4	0.0328
C06A			0
C06B			0
C07A			0
C07B			0
C08A	2	2	0.0184
C08B	1	1	0.009
C09A	6	5	0.0543
C09B	12	5	0.0914
C10A	24	5	0.2332
C10B	25	5	0.2298
C11A	1	1	0.0092
C11B			0
C12A	5	5	0.044
C12B	2	2	0.0246
C13A			0
C13B			0
C14A	3	3	0.0256
C14B	4	4	0.036
C15A	1	1	0.0015
C15B	7	4	0.0544
C16A			0
C16B	1	1	0.0034
C17A	17	5	0.1904
C17B	11	5	0.124
C18A	5	5	0.0398
C18B	3	3	0.023
C19A	2	2	0.0174
C19B	40	5	0.3246
C20A	24	5	0.204
C20B	40	5	0.3304
C21A	5	5	0.0558
C21B	17	5	0.189
C22A	4	4	0.0331
C22B			0
C23A	2	2	0.0219
C23B	2	2	0.0134
C24A	1	1	0.0134
C24B	2	1	0.0246
C25A	5	4	0.0404
C25B	3	3	0.0266

Transect	N	Aged	kg/m2
C26A	10	4	0.0794
C26B	11	4	0.0726
C27A	6	5	0.0593
C27B	6	4	0.0669
C28A	16	5	0.195
C28B	14	5	0.158
C29A	1		0.002
C29B	1	1	0.0236
C30A	24	5	0.2356
C30B	11	4	0.1125
C31A	6	5	0.0604
C31B	4	4	0.0396
C32A	19	4	0.2164
C32B	15	5	0.1724
C33A	1	1	0.0105
C33B			0
C34A	1		0.0076
C34B			0
C35A			0
C35B			0
C36A			0
C36B	4	4	0.0484
C37A			0
C37B	2	2	0.0196
C38A	1	1	0.0072
C38B			0
C39A			0
C39B			0
C40A			0
C40B			0
C41A	29	5	0.3178
C41B	30	5	0.3414
C42A			0
C42B	1	1	0.0108
C43A	2	2	0.0215
C43B			0
C44A			0
C44B			0
C45A	11	5	0.0881
C45B	11	5	0.0983
C46A			0
C46B			0
C47A	4	3	0.0296
C47B	1	1	0.0038
C48A			0
C48B			0
C49A	42	5	0.2996
C49B	48	5	0.3895
C50A	21	5	0.2106
C50B	13	5	0.1493

11. Appendix 2 – Location of transects

Transect	Longitude	Latitude
C01A	172.719536	-40.589162
C01B	172.719536	-40.589162
C02A	172.701478	-40.614827
C02B	172.701478	-40.614827
C03A	172.704408	-40.616977
C03B	172.704408	-40.616977

Transect	Longitude	Latitude
C04A	172.71035	-40.594133
C04B	172.71035	-40.594133
C05A	172.740274	-40.56057
C05B	172.740274	-40.56057
C06A	172.69655	-40.641433
C06B	172.69655	-40.641433
C07A	172.714756	-40.599874
C07B	172.714756	-40.599874
C08A	172.696283	-40.6508
C08B	172.696283	-40.6508
C09A	172.708352	-40.618864
C09B	172.708352	-40.618864
C10A	172.695267	-40.6233
C10B	172.695267	-40.6233
C11A	172.713628	-40.587003
C11B	172.713628	-40.587003
C12A	172.701789	-40.608171
C12B	172.701789	-40.608171
C13A	172.69605	-40.646417
C13B	172.69605	-40.646417
C14A	172.699898	-40.633462
C14B	172.699898	-40.633462
C15A	172.731945	-40.560468
C15B	172.731945	-40.560468
C16A	172.709204	-40.6006
C16B	172.709204	-40.6006
C17A	172.700202	-40.59626
C17B	172.700202	-40.59626
C18A	172.701313	-40.610054
C18B	172.701313	-40.610054
C19A	172.700008	-40.641719
C19B	172.700008	-40.641719
C20A	172.707477	-40.626628
C20B	172.707477	-40.626628
C21A	172.708676	-40.580068
C21B	172.708676	-40.580068
C22A	172.705016	-40.621776
C22B	172.705016	-40.621776
C23A	172.731026	-40.564248
C23B	172.731026	-40.564248
C24A	172.720215	-40.569144
C24B	172.720215	-40.569144
C25A	172.7036	-40.63

C25B	172.7036	-40.63
C26A	172.705604	-40.646648
C26B	172.705604	-40.646648
C27A	172.698387	-40.603294
C27B	172.698387	-40.603294
C28A	172.710466	-40.580157
C28B	172.710466	-40.580157
C29A	172.723848	-40.563999
C29B	172.723848	-40.563999
C30A	172.691282	-40.615677
C30B	172.691282	-40.615677
C31A	172.701922	-40.586537
C31B	172.701922	-40.586537
C32A	172.695161	-40.604037
C32B	172.695161	-40.604037
C33A	172.733626	-40.563332
C33B	172.733626	-40.563332
C34A	172.720998	-40.562651
C34B	172.720998	-40.562651
C35A	172.700791	-40.601825
C35B	172.700791	-40.601825
C36A	172.706163	-40.587826
C36B	172.706163	-40.587826
C37A	172.70112	-40.600038
C37B	172.70112	-40.600038
C38A	172.705813	-40.636145
C38B	172.705813	-40.636145
C39A	172.725393	-40.57034
C39B	172.725393	-40.57034
C40A	172.719349	-40.571746
C40B	172.719349	-40.571746
C41A	172.693483	-40.610855
C41B	172.693483	-40.610855
C42A	172.710979	-40.572047
C42B	172.710979	-40.572047

Transect	**Longitude**	**Latitude**
C43A	172.707431	-40.609507
C43B	172.707431	-40.609507
C44A	172.714404	-40.586298
C44B	172.714404	-40.586298
C45A	172.732717	-40.559876
C45B	172.732717	-40.559876
C46A	172.713807	-40.58919
C46B	172.713807	-40.58919

C47A	172.721233	-40.566603
C47B	172.721233	-40.566603
C48A	172.712915	-40.576891
C48B	172.712915	-40.576891
C49A	172.690706	-40.60132
C49B	172.690706	-40.60132
C50A	172.696825	-40.602812
C50B	172.696825	-40.602812

12. Appendix 2 – Raw data on collected shells. Time of collection, depth of transect (corrected for tide height), length of shell, weight of dewatered flesh, total green weight of entire transect and weight of each valve after cleaning and drying to constant weight.

Transect	Number	Time	Depth (m)	size (mm)	flesh (kg)	total wt (kg)	LHS Valve (g)	RHS Valve (g)
C01A		1536	8.31			0		
C01B		1545	8.25			0		
C02A	1	1144	7.16	102	0.125	1.35	0.01846	0.01861
C02A	2	1144		114	0.235		0.03362	0.03187
C02A	3	1144		95	0.105		0.03034	0.03029
C02A	4	1144		105	0.205		0.03215	0.03209
C02B	1	1159	7.39	105	0.185	2.135	0.03049	
C02B	2	1159		102	0.195		0.02927	0.02825
C02B	3	1159		120	0.21			
C02B	4	1159		120	0.205		0.04424	0.04299
C02B	5	1159		103	0.13		0.02951	0.02675
C03A		1300	7.94			0		
C03B	1	1315	8.15	101	0.22	0.505	0.03206	0.02939
C04A		1238	7.25			0		
C04B		1248	7.21			0		
C05A	1	1042	8.49	95	0.135	1.235	0.01495	0.0134
C05A	2	1042		117	0.22		0.03813	0.04148
C05A	3	1042		102	0.245		0.028	0.02832
C05B	1	1025	8.28	118	0.25	1.64	0.03009	0.0294
C05B	2	1025		103	0.15		0.02233	0.0222
C05B	3	1025		100	0.22		0.01635	
C05B	4	1025		98	0.14			0.01514
C06A		1041	0.58			0		
C06B		1050	0.56			0		
C07A		1510	9.17					
C07B		1518	9.23					
C08A	1	1019	6.15	113	0.175	0.92	0.02995	0.03197
C08A	2	1019		116	0.31			
C08B	1	1322	6.14	124		0.45	0.0381	0.0392
C09A	1	1105	4.79	111	0.18	2.715	0.02853	0.02685
C09A	2	1105		116	0.23		0.0342	0.03342
C09A	3	1105		114	0.185		0.03664	0.03794
C09A	4	1105		116	0.19		0.03325	0.03147
C09A	5	1105		118	0.225		0.03264	0.03333
C09A	1	1105		118				
C09B	1	1125	5.07	129	0.215	4.57	0.03747	0.04092

Transect	Number	Time	Depth (m)	size (mm)	flesh (kg)	total wt (kg)	LHS Valve (g)	RHS Valve (g)
C09B	2	1125		110	0.14		0.02392	0.02483
C09B	3	1125		109	0.195		0.03713	0.03729
C09B	4	1125		107	0.17		0.02287	0.02313
C09B	5	1125		109	0.145		0.01428	0.01347
C09B		1125		109				
C09B		1125		120				
C09B		1125		112				
C09B		1125		102				
C09B		1125		115				
C09B		1125		109				
C09B		1125		0				
C10A	1	1258	4.91	96	0.22	11.66	0.0226	0.02215
C10A	2	1258		117	0.225			0.0227
C10A	3	1258		116	0.28			0.02881
C10A	4	1258		111	0.24		0.02961	0.02982
C10A	5	1258		109	0.195		0.02463	0.02464
C10A		1258		107				
C10A		1258		99				
C10A		1258		112				
C10A		1258		107				
C10A		1258		106				
C10A		1258		108				
C10A		1258		117				
C10A		1258		105				
C10A		1258		110				
C10A		1258		106				
C10A		1258		112				
C10A		1258		131				
C10A		1258		119				
C10A		1258		117				
C10A		1258		97				
C10A		1258		109				
C10A		1258		113				
C10A		1258		88				
C10A		1258		112				
C10B	1	1325	4.71	114	0.22	11.49		0.03016
C10B	2	1325		122	0.23		0.02908	
C10B	3	1325		101	0.165		0.0215	0.02132
C10B	4	1325		118	0.23			0.02917
C10B	5	1325		109	0.17			0.02816
C10B		1325		110				
C10B		1325		106				
C10B		1325		91				

Transect	Number	Time	Depth (m)	size (mm)	flesh (kg)	total wt (kg)	LHS Valve (g)	RHS Valve (g)
C10B		1325		135				
C10B		1325		115				
C10B		1325		112				
C10B		1325		106				
C10B		1325		119				
C10B		1325		117				
C10B		1325		133				
C10B		1325		123				
C10B		1325		102				
C10B		1325		116				
C10B		1325		121				
C10B		1325		115				
C10B		1325		116				
C10B		1325		97				
C10B		1325		116				
C10B		1325		109				
C10B		1325		102				
C11A	1	1338	6.73	111	0.25	0.46		0.03007
C11B		1348	6.67			0		
C12A	1	1623	7.42	117	0.23	2.2	0.03312	0.03457
C12A	2	1623		113	0.225		0.0346	0.03453
C12A	3	1623		119	0.185		0.04445	0.0424
C12A	4	1623		112	0.26		0.03955	0.03828
C12A	5	1623		108	0.2		0.03803	0.03694
C12B	1	1640	7.21	127	0.38	1.23	0.04017	0.03963
C12B	2	1640		116	0.395		0.03981	0.04047
C13A	1	0913	1.06			0		
C13B	1	0922	1.10			0		
C14A	1	1222	6.86	124	0.1736	1.28	0.03069	0.02908
C14A	2	1222		117	0.206		0.0327	0.0351
C14A	3	1222		102	0.1389		0.03047	0.03044
C14B	1	1236	7.06	121	0.2124	1.8	0.0339	0.0348
C14B	2	1236		127	0.1344		0.0286	0.0321
C14B	3	1236		126	0.1724			0.0362
C14B	4	1236		108	0.2209		0.0454	0.0464
C14C	1	1217	6.59	112	0.19	0.92		
C14C	2	1217		121	0.19			
C14D	1	1230	6.50	108	0.155	0.775		
C14D	2	1230		115	0.14			
C15A	1	1114	4.60	79	0.05	0.075		
C15B	1	1114		97	0.135	2.72	0.01144	0.0143
C15B	2	1114		119	0.225		0.02779	0.02767
C15B	3	1114		123	0.22		0.03364	0.03269

Transect	Number	Time	Depth (m)	size (mm)	flesh (kg)	total wt (kg)	LHS Valve (g)	RHS Valve (g)
C15B	4	1114		113	0.235		0.02965	0.03013
C15B	5	1114		122	0.24		0.04134	0.03937
C15B		1114		87				
C15B		1114		96				
C16A		0920	8.32			0	0.03982	0.03827
C16A		1148	10.68			0		
C16B	1	0956	8.13	103	0.1133	0.17	0.0197	0.0189
C16B		1157	10.67			0		
C17A	1	1658	3.96	121	0.315	9.52		0.03434
C17A	2	1658		108	0.255			0.03932
C17A	3	1658		138	0.2		0.0225	0.0235
C17A	4	1658		111	0.215		0.0355	0.0346
C17A	5	1658		111	0.42		0.03881	
C17A		1658		122				
C17A		1658		115				
C17A		1658		113				
C17A		1658		123				
C17A		1658		114				
C17A		1658		122				
C17A		1658		113				
C17A		1658		115				
C17A		1658		115				
C17A		1658		99				
C17A		1658		118				
C17A		1658		117				
C17B	1	1713	4.04	115	0.245	6.2		
C17B	2	1713		122	0.26		0.0382	0.03916
C17B	3	1713		112	0.265		0.0405	0.0398
C17B	4	1713		125	0.29		0.0274	0.0269
C17B	5	1713		119	0.3		0.0274	0.0269 ?^
C17B		1713		102				
C17B		1713		124				
C17B		1713		107				
C17B		1713		111				
C17B		1713		110				
C17B		1713		125				
C18A	1	1550	7.98	102	0.305	1.99	0.03261	0.03257
C18A	2	1550		91	0.155		0.0159	0.01514
C18A	3	1550		109	0.205		0.03564	0.03459
C18A	4	1550		117	0.225		0.04407	0.04651
C18A	5	1550		105	0.21		0.02116	0.02101
C18B	1	1600	7.98	99	0.205	1.15	0.02135	0.02268
C18B	2	1600		103	0.15		0.02306	0.02265

Transect	Number	Time	Depth (m)	size (mm)	flesh (kg)	total wt (kg)	LHS Valve (g)	RHS Valve (g)
C18B	3	1600		119	0.29		0.0368	0.03767
C19A	1	1000	5.39	106	0.175	0.87	0.02757	0.02761
C19A	2	1000		112	0.16			0.02578
C19B	1	1010	4.40	113	0.255	16.23		0.0349
C19B	2	1010		108	0.185			
C19B	3	1010		112	0.295		0.02424	0.02419
C19B	4	1010		102	0.15		0.02662	0.02706
C19B	5	1010		106	0.18		0.02082	0.02163
C19B		1010		108				
C19B		1010		119				
C19B		1010		100				
C19B		1010		112				
C19B		1010		109				
C19B		1010		108				
C19B		1010		108				
C19B		1010		105				
C19B		1010		119				
C19B		1010		118				
C19B		1010		115				
C19B		1010		107				
C19B		1010		105				
C19B		1010		110				
C19B		1010		99				
C19B		1010		89				
C19B		1010		95				
C19B		1010		118				
C19B		1010		115				
C19B		1010		105				
C19B		1010		116				
C19B		1010		107				
C19B		1010		100				
C19B		1010		116				
C19B		1010		116				
C19B		1010		115				
C19B		1010		118				
C19B		1010		89				
C19B		1010		88				
C19B		1010		101				
C19B		1010		104				
C19B		1010		124				
C19B		1010		89				
C19B		1010		109				
C19B		1010		125				

Transect	Number	Time	Depth (m)	size (mm)	flesh (kg)	total wt (kg)	LHS Valve (g)	RHS Valve (g)
C20A	1	1540	4.44	113	0.235	10.2	0.02944	0.02953
C20A	2	1540		108	0.21			0.03001
C20A	3	1540		113	0.255		0.02602	0.02647
C20A	4	1540		104	0.21		0.03294	0.0329
C20A	5	1540		115	0.22		0.02103	0.02102
C20A		1540		107				
C20A		1540		109				
C20A		1540		113				
C20A		1540		110				
C20A		1540		97				
C20A		1540		120				
C20A		1540		128				
C20A		1540		123				
C20A		1540		110				
C20A		1540		111				
C20A		1540		102				
C20A		1540		85				
C20A		1540		98				
C20A		1540		107				
C20A		1540		105				
C20A		1540		119				
C20A		1540		116				
C20A		1540		118				
C20A		1540		121				
C20B	1	1600	4.34	113	0.124	16.52	0.02636	0.0264
C20B	2	1600		115	0.225		0.03204	
C20B	3	1600		114	0.19		0.03116	0.03207
C20B	4	1600		99	0.16		0.01415	0.01484
C20B	5	1600		102	0.195		0.02427	0.02686
C20B		1600		116				
C20B		1600		118				
C20B		1600		101				
C20B		1600		121				
C20B		1600		101				
C20B		1600		107				
C20B		1600		116				
C20B		1600		107				
C20B		1600		132				
C20B		1600		101				
C20B		1600		105				
C20B		1600		112				
C20B		1600		103				
C20B		1600		102				

Transect	Number	Time	Depth (m)	size (mm)	flesh (kg)	total wt (kg)	LHS Valve (g)	RHS Valve (g)
C20B		1600		97				
C20B		1600		98				
C20B		1600		110				
C20B		1600		119				
C20B		1600		110				
C20B		1600		114				
C20B		1600		110				
C20B		1600		112				
C20B		1600		97				
C20B		1600		117				
C20B		1600		110				
C20B		1600		110				
C20B		1600		122				
C20B		1600		107				
C20B		1600		110				
C20B		1600		117				
C20B		1600		111				
C20B		1600		98				
C20B		1600		113				
C20B		1600		113				
C20B		1600		116				
C21A	1	1257	0.69	110	0.32	2.79	0.0348	0.035
C21A	2	1257		113	0.235		0.037	0.0381
C21A	3	1257		127	0.28		0.03339	
C21A	4	1257		130	0.235		0.03576	
C21A	5	1257		119	0.19			0.02992
C21B	1	1310	1.18	112	0.22	9.45	0.03393	0.0384
C21B	2	1310		128	0.235			0.0293
C21B	3	1310		121	0.215		0.02728	0.02486
C21B	4	1310		116	0.23		0.03553	0.0366
C21B	5	1310		128	0.265			0.0322
C21B		1310		123				
C21B		1310		101				
C21B		1310		113				
C21B		1310		105				
C21B		1310		117				
C21B		1310		118				
C21B		1310		117				
C21B		1310		115				
C21B		1310		115				
C21B		1310		111				
C21B		1310		117				
C21B		1310		118				

Transect	Number	Time	Depth (m)	size (mm)	flesh (kg)	total wt (kg)	LHS Valve (g)	RHS Valve (g)
C22A	1	1400	8.36	101	0.165	1.655	0.02938	0.02909
C22A	2	1400		115	0.234		0.04254	0.04144
C22A	3	1400		107	0.15		0.03096	0.0307
C22A	4	1400		90	0.135		0.02309	0.02331
C22B		1411	8.45			0		
C23A	1	1230	6.04	117	0.32	1.095	0.03501	0.03487
C23A	2	1230		109	0.33		0.02799	0.02953
C23B	1	1245	6.20	115	0.27	0.67	0.03075	0.03141
C23B	2	1245		112	0.2		0.03278	0.03169
C24A	1	1120	4.76	121	0.335	0.67	0.03785	
C24B	1	1132	4.67	125	0.275	1.23	0.03304	0.03473
C24B	2	1132		134	0.305		0.03227	0.0344
C25A	1	1508	8.40	101	0.155	2.02	0.0284	0.02776
C25A	2	1508		114	0.195		0.02793	
C25A	3	1508		105	0.18		0.02472	0.02646
C25A	4	1508		109	0.185		0.03174	0.03167
C25A	5	1508		115	0.175			
C25B	1	1528	8.38	112	0.225	1.33	0.03023	0.02879
C25B	2	1528		111	0.175		0.02685	0.02663
C25B	3	1528		110	0.25		0.03362	0.03357
C26A	1	0825	7.09	113	0.18	3.97		0.03673
C26A	2	0825		107	0.16			
C26A	3	0825		107	0.17			0.02711
C26A	4	0825		103	0.135		0.02478	
C26A	5	0825		90	0.105		0.01159	0.01227
C26A		0825		104				
C26A		0825		102				
C26A		0825		115				
C26A		0825		107				
C26A		0825		112				
C26B	1	0838	7.18	103	0.19	3.63	0.02477	0.02544
C26B	2	0838		101	0.16			
C26B	3	0838		100	0.135		0.02029	0.01942
C26B	4	0838		103	0.16			0.02844
C26B	5	0838		94	0.1		0.01764	
C26B		0838		105				
C26B		0838		109				
C26B		0838		110				
C26B		0838		106				
C26B		0838		103				
C26B		0838		109				
C27A	1	0934	5.95	115	0.245	2.965	0.0407	0.04074
C27A	2	0934		111	0.25			0.03785

Transect	Number	Time	Depth (m)	size (mm)	flesh (kg)	total wt (kg)	LHS Valve (g)	RHS Valve (g)
C27A	3	0934		118	0.2			0.03575
C27A	4	0934		117	0.21			0.04
C27A	5	0934		116	0.2			0.03831
C27A		0934		111				
C27B	1	0947	6.02	129	0.425	3.345	0.03772	0.03968
C27B	2	0947		132	0.4			
C27B	3	0947		124	0.325			
C27B	4	0947		104	0.26		0.03168	
C27B	5	0947		101	0.285		0.03571	0.03528
C27B		0947		103				
C28A	1	1359	3.11	120	0.28	9.75	0.0256	0.0276
C28A	2	1359		120	0.28		0.02404	0.02347
C28A	3	1359		112	0.32		0.02853	0.02637
C28A	4	1359		115	0.3		0.0471	0.0445
C28A	5	1359		120	0.325		0.0364	0.0353
C28A		1359		111				
C28A		1359		122				
C28A		1359		114				
C28A		1359		119				
C28A		1359		114				
C28A		1359		114				
C28A		1359		113				
C28A		1359		116				
C28A		1359		126				
C28A		1359		121				
C28A		1359		122				
C28B	1	1412	3.03	120	0.215	7.9	0.02996	0.03
C28B	2	1412		102	0.24		0.0336	0.03269
C28B	3	1412		124	0.355		0.0448	0.04635
C28B	4	1412		123	0.265		0.03815	
C28B	5	1412		120	0.26			
C28B		1412		122				
C28B		1412		114				
C28B		1412		115				
C28B		1412		118				
C28B		1412		120				
C28B		1412		105				
C28B		1412		125				
C28B		1412		132				
C28B		1412		107				
C29A	1	1000	3.95	69		0.1		
C29B	1	1010	3.92	117	0.255	1.18		
C30A	1	1356	3.28	119	0.24	11.78		

Transect	Number	Time	Depth (m)	size (mm)	flesh (kg)	total wt (kg)	LHS Valve (g)	RHS Valve (g)
C30A	2	1356		120	0.245			
C30A	3	1356		106	0.19			
C30A	4	1356		123	0.195			
C30A	5	1356		128	0.275			0.04225
C30A		1356		76				
C30A		1356		117				
C30A		1356		120				
C30A		1356		124				
C30A		1356		102				
C30A		1356		109				
C30A		1356		116				
C30A		1356		116				
C30A		1356		114				
C30A		1356		111				
C30A		1356		114				
C30A		1356		123				
C30A		1356		113				
C30A		1356		121				
C30A		1356		106				
C30A		1356		111				
C30A		1356		107				
C30A		1356		112				
C30A		1356		96				
C30B	1	1409	3.18	121	0.27	5.625		0.03171
C30B	2	1409		118	0.25		0.0391	0.0392
C30B	3	1409		114	0.265		0.03143	0.03056
C30B	4	1409		105	0.135		0.02334	0.02331
C30B	5	1409		121	0.16			0.03205
C30B		1409		77				
C30B		1409		121				
C30B		1409		120				
C30B		1409		117				
C30B		1409		115				
C30B		1409		130				
C31A	1	1509	1.47	101	0.25	3.02		0.0238
C31A	2	1509		113	0.33			0.03449
C31A	3	1509		115	0.265		0.03102	
C31A	4	1509		102	0.175			0.02807
C31A	5	1509		107	0.235		0.04065	0.0406
C31A		1509		170				
C31B	1	1519	1.44	118	0.22	1.98	0.02475	
C31B	2	1519		109	0.23		0.02913	
C31B	3	1519		121	0.245			

Transect	Number	Time	Depth (m)	size (mm)	flesh (kg)	total wt (kg)	LHS Valve (g)	RHS Valve (g)
C31B	4	1519		108	0.21		0.04141	0.04086
C32A	1	1541	4.44	109	0.23	10.82		0.02656
C32A	2	1541		122	0.285		0.02783	0.02839
C32A	3	1541		110	0.24			
C32A	4	1541		108	0.21			0.03397
C32A	5	1541		108	0.21		0.02001	0.01949
C32A		1541		108				
C32A		1541		105				
C32A		1541		103				
C32A		1541		109				
C32A		1541		120				
C32A		1541		119				
C32A		1541		120				
C32A		1541		117				
C32A		1541		125				
C32A		1541		122				
C32A		1541		132				
C32A		1541		104				
C32A		1541		113				
C32A		1541		117				
C32B	1	1355	5.08	94	0.15	8.62	0.01538	0.01563
C32B	2	1355		114	0.215			
C32B	3	1355		116	0.29			0.0287
C32B	4	1355		112	0.325			
C32B	5	1355		125	0.245		0.03628	0.03573
C32B		1355		128				
C32B		1355		120				
C32B		1355		102				
C32B		1355		118				
C32B		1355		121				
C32B		1355		106				
C32B		1355		130				
C32B		1355		125				
C32B		1355		117				
C32B		1355		116				
C33A	1	1342	7.01	104	0.28	0.525	0.02134	0.02094
C33B		1350	6.94			0		
C34A	1	1038	0.20	116	0.225	0.38		
C34B	1	1049	0.15			0		
C35A		1011	6.54			0		
C35B		1022	6.58			0		
C36A	1	1548	4.50			0		
C36B	1	1557	4.50	105	0.345	2.42		0.03621

Transect	Number	Time	Depth (m)	size (mm)	flesh (kg)	total wt (kg)	LHS Valve (g)	RHS Valve (g)
C36B	2	1557		117	0.36		0.02998	
C36B	3	1557		113	0.225			0.02964
C36B	4	1557		127	0.28		0.03951	0.0395
C37A		1048	6.06			0		
C37B	1	1100	6.08	104	0.19	0.98	0.03014	0.0289
C37B	2	1100		117	0.265	0	0.03444	0.03502
C38A	1	1148	7.95	109	0.18	0.36	0.02647	0.02644
C38B		1158	7.90			0		
C39A		1200	6.56			0		
C39B		1212	6.56			0		
C39B		1212				0		
C40A		0830	5.08			0		
C40B		0850	5.01					
C41A	1	1458	3.86	116	0.255	15.89	0.04504	0.03292
C41A		1458	3.86	114				
C41A	2	1458		117	0.235			0.0296
C41A	3	1458		128	0.325			0.04306
C41A	4	1458		124	0.295		0.03545	0.03224
C41A	5	1458		123	0.295		0.03379	
C41A		1458		117				
C41A		1458		132				
C41A		1458		114				
C41A		1458		122				
C41A		1458		112				
C41A		1458		119				
C41A		1458		129				
C41A		1458		110				
C41A		1458		113				
C41A		1458		123				
C41A		1458		115				
C41A		1458		95				
C41A		1458		137				
C41A		1458		111				
C41A		1458		120				
C41A		1458		128				
C41A		1458		94				
C41A		1458		125				
C41A		1458		114				
C41A		1458		111				
C41A		1458		105				
C41A		1458		130				
C41A		1458		123				
C41B	1	1510	3.79	115	0.285	17.07	0.03804	0.03449

Transect	**Number**	**Time**	**Depth (m)**	**size (mm)**	**flesh (kg)**	**total wt (kg)**	**LHS Valve (g)**	**RHS Valve (g)**
C41B	2	1510		136	0.265			0.04981
C41B	3	1510		124	0.23			
C41B	4	1510		126	0.3		0.04567	0.04316
C41B	5	1510		122	0.205		0.03514	0.03623
C41B		1510		153				
C41B		1510		124				
C41B		1510		115				
C41B		1510		107				
C41B		1510		124				
C41B		1510		119				
C41B		1510		105				
C41B		1510		120				
C41B		1510		117				
C41B		1510		128				
C41B		1510		117				
C41B		1510		124				
C41B		1510		116				
C41B		1510		123				
C41B		1510		122				
C41B		1510		113				
C41B		1510		113				
C41B		1510		118				
C41B		1510		115				
C41B		1510		115				
C41B		1510		119				
C41B		1510		106				
C41B		1510		126				
C41B		1510		119				
C41B		1510		111				
C42A		1627	0.34			0		
C42B	1	1636	0.37	119	0.23	0.54	0.02901	0.02972
C43A	1	1434	6.50	120	0.265	1.075	0.04579	0.045
C43A	2	1434		117	0.29		0.03753	0.03948
C43B		1449	6.56					
C44A		1436	6.53			0		
C44B		1449	6.44			0		
C45A	1	1150	4.47	95	0.125	4.405	0.01116	0.01181
C45A	2	1150		87	0.065			0.00668
C45A	3	1150		126	0.22		0.01387	0.01432
C45A	4	1150		96	0.145		0.04012	0.03958
C45A	5	1150		124	0.255		0.04195	0.04073
C45A		1150		100				
C45A		1150		125				

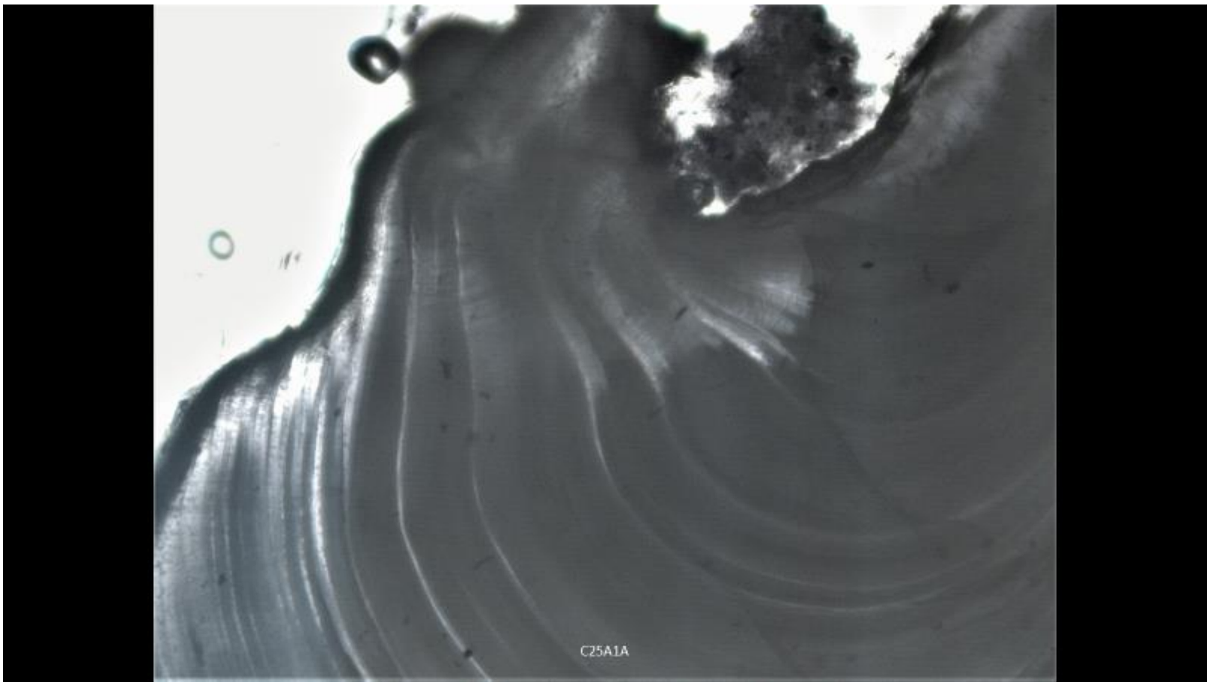
Transect	Number	Time	Depth (m)	size (mm)	flesh (kg)	total wt (kg)	LHS Valve (g)	RHS Valve (g)
C45A		1150		124				
C45A		1150		118				
C45A		1150		100				
C45A		1150		115				
C45B	1	1202	4.62	124	0.285	4.915	0.04316	0.04549
C45B	2	1202		141	0.27		0.04598	0.04737
C45B	3	1202		73	0.035		0.00453	0.00457
C45B	4	1202		114	0.165		0.03091	0.03157
C45B	5	1202		131	0.3			
C45B		1202		122				
C45B		1202		122				
C45B		1202		117				
C45B		1202		92				
C45B		1202		122				
C45B		1202		0				
C46A		1309	7.20			0		
C46B		1320	7.14			0		
C47A	1	1419	5.70	112	0.255	1.48	0.03022	0.02863
C47A	2	1419		121	0.325		0.02959	0.02955
C47A	3	1419		92	0.15		0.01487	0.01512
C47A	4	1419		80	0.095		0.00555	0.00482
C47B	1	1419		81	0.115	0.19	0.00613	0.00704
C48A		0910	4.20					
C48B		0930	4.24					
C49A	1	1120	4.76	104	0.1138	14.98		0.0203
C49A	2	1120		120	0.1403		0.03427	0.034
C49A	3	1120		111	0.177		0.0347	0.0346
C49A	4	1120		116	0.1616		0.0349	0.0339
C49A	5	1120		115	0.1654		0.0288	0.0304
C49A		1120		109				
C49A		1120		119				
C49A		1120		119				
C49A		1120		112				
C49A		1120		111				
C49A		1120		118				
C49A		1120		108				
C49A		1120		106				
C49A		1120		121				
C49A		1120		117				
C49A		1120		112				
C49A		1120		111				
C49A		1120		112				
C49A		1120		92				

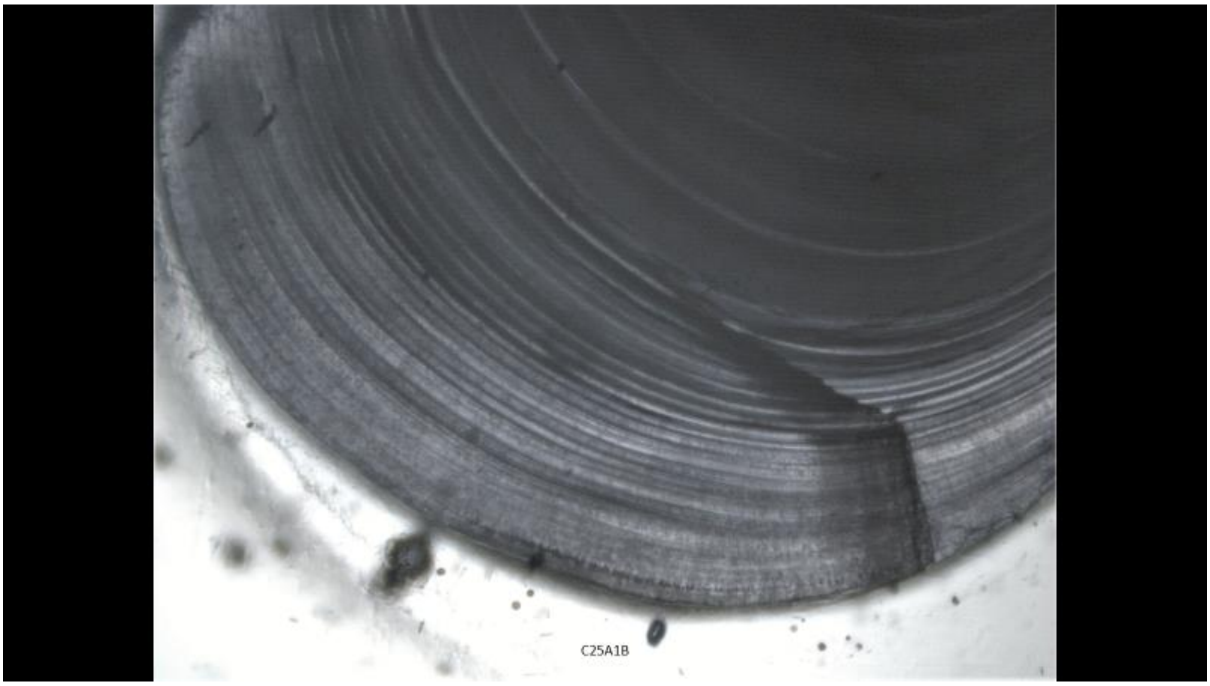
Transect	Number	Time	Depth (m)	size (mm)	flesh (kg)	total wt (kg)	LHS Valve (g)	RHS Valve (g)
C49A		1120		118				
C49A		1120		119				
C49A		1120		126				
C49A		1120		119				
C49A		1120		119				
C49A		1120		97				
C49A		1120		103				
C49A		1120		114				
C49A		1120		108				
C49A		1120		116				
C49A		1120		117				
C49A		1120		108				
C49A		1120		112				
C49A		1120		119				
C49A		1120		116				
C49A		1120		121				
C49A		1120		114				
C49A		1120		87				
C49A		1120		108				
C49A		1120		103				
C49A		1120		96				
C49A		1120		109				
C49A		1120		106				
C49B	1	1200	4.76	115	0.1739	19.475	0.0307	0.0302
C49B	2	1200		112	0.1643		0.0315	0.0326
C49B	3	1200		86	0.1516		0.0312	0.0296
C49B	4	1200		104	0.1688		0.0347	0.0346
C49B	5	1200		111	0.1075		0.0283	0.0284
C49B		1200		104				
C49B		1200		124				
C49B		1200		119				
C49B		1200		119				
C49B		1200		124				
C49B		1200		107				
C49B		1200		113				
C49B		1200		105				
C49B		1200		115				
C49B		1200		113				
C49B		1200		117				
C49B		1200		112				
C49B		1200		120				
C49B		1200		117				
C49B		1200		113				

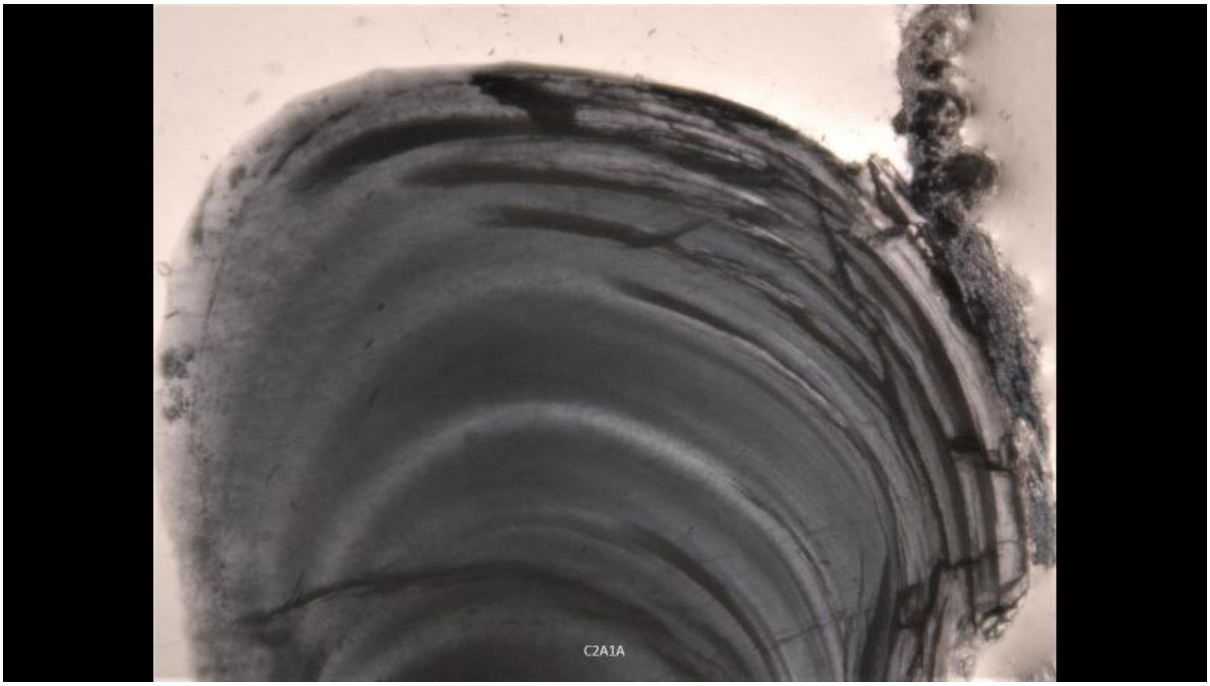
Transect	Number	Time	Depth (m)	size (mm)	flesh (kg)	total wt (kg)	LHS Valve (g)	RHS Valve (g)
C49B		1200		109				
C49B		1200		102				
C49B		1200		114				
C49B		1200		113				
C49B		1200		116				
C49B		1200		104				
C49B		1200		116				
C49B		1200		110				
C49B		1200		102				
C49B		1200		105				
C49B		1200		110				
C49B		1200		109				
C49B		1200		107				
C49B		1200		114				
C49B		1200		105				
C49B		1200		110				
C49B		1200		114				
C49B		1200		109				
C49B		1200		110				
C49B		1200		102				
C49B		1200		107				
C49B		1200		95				
C49B		1200		118				
C49B		1200		85				
C49B		1200		108				
C49B		1200		104				
C49B		1200		98				
C49B		1200		96				
C50A	1	0854	5.39	118	0.3	10.53	0.0413	0.0467
C50A	2	0854		112	0.205			0.03106
C50A	3	0854		111	0.24			0.03354
C50A	4	0854		109	0.26		0.03574	
C50A	5	0854		102	0.105		0.01875	0.01834
C50A		0854		106	0.245			0.03918
C50A		0854		126	0.225			0.03576
C50A		0854		114	0.25		0.0326	
C50A		0854		119	0.205		0.02008	0.02102
C50A		0854		110	0.32			0.0292
C50A		0854		120	0.22			0.03938
C50A		0854		119				
C50A		0854		108				
C50A		0854		117				
C50A		0854		125				

Transect	Number	Time	Depth (m)	size (mm)	flesh (kg)	total wt (kg)	LHS Valve (g)	RHS Valve (g)
C50A		0854		114				
C50A		0854		117				
C50A		0854		102				
C50A		0854		104				
C50A		0854		115				
C50A		0854		113				
C50B	1	0854		92	0.15	7.465		
C50B	2	0908	5.48	126	0.37			
C50B	3	0908		101	0.12			0.01931
C50B	4	0908		124	0.275			
C50B	5	0908		121	0.25		0.0455	0.046
C50B		0908		121	0.28			0.04909
C50B		0908		97	0.11			0.01819
C50B		0908		95	0.26			0.04815
C50B		0908		129	0.27			0.03512
C50B		0908		114	0.175		0.01555	0.0158
C50B		0908		120				
C50B		0908		131				
C50B		0908		111				

13. Appendix 3 – Shell aging figures



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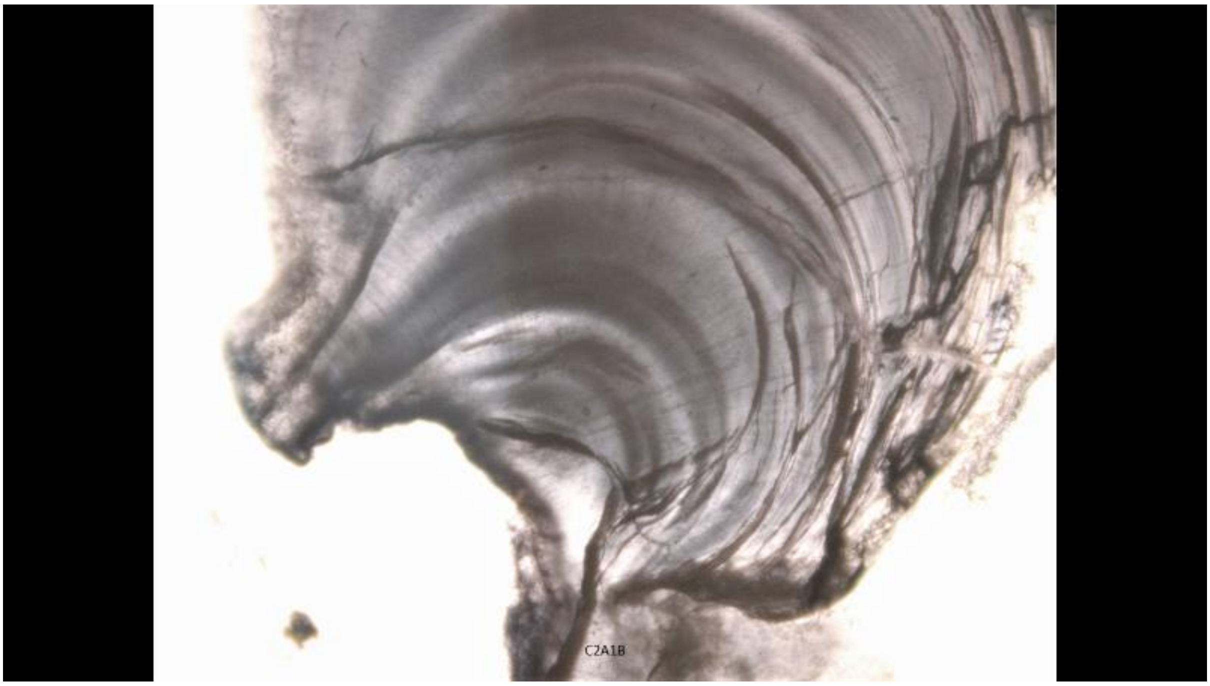
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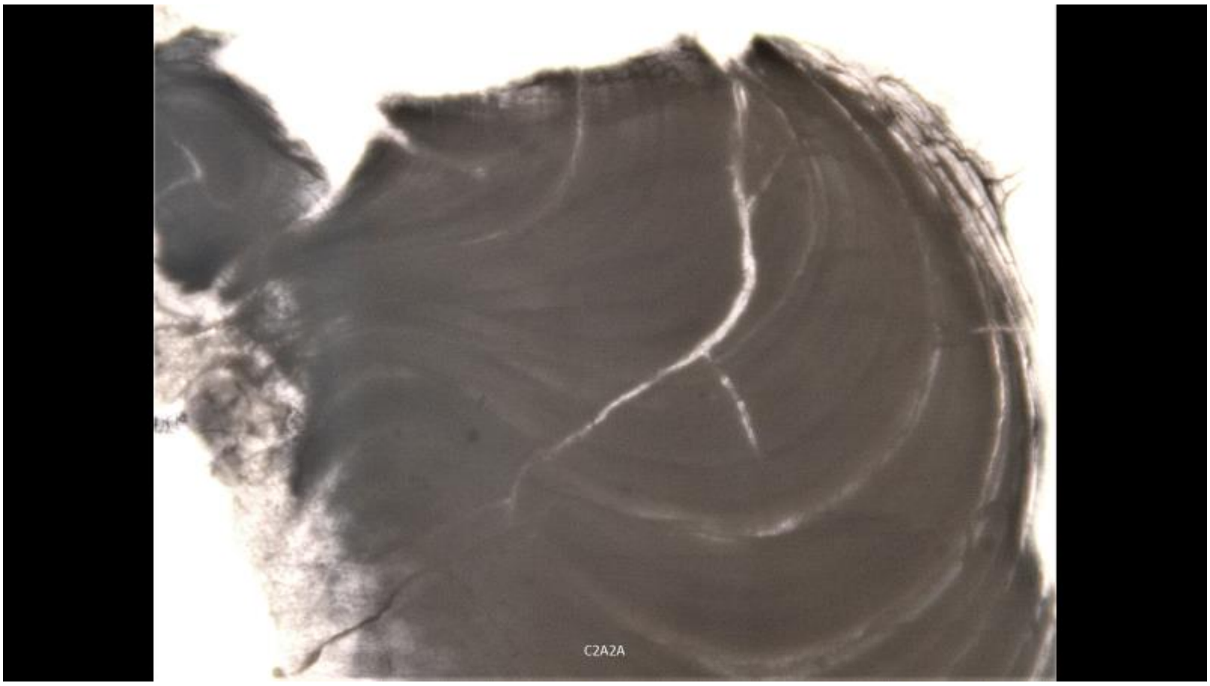
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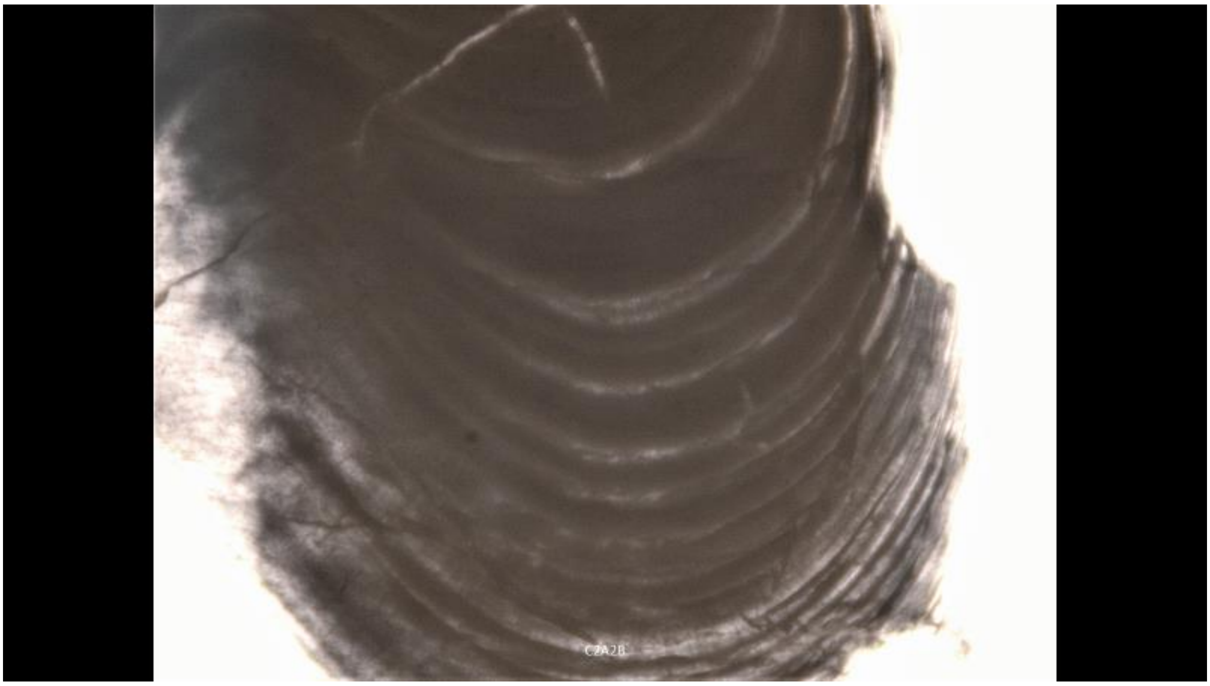
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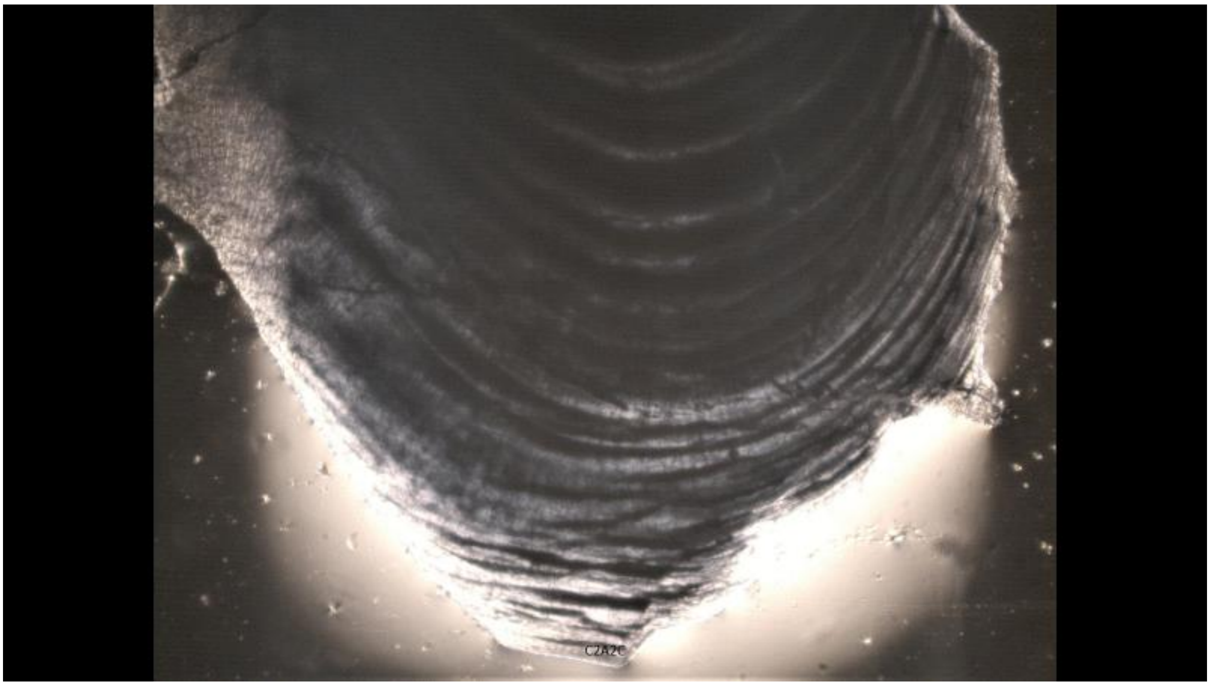
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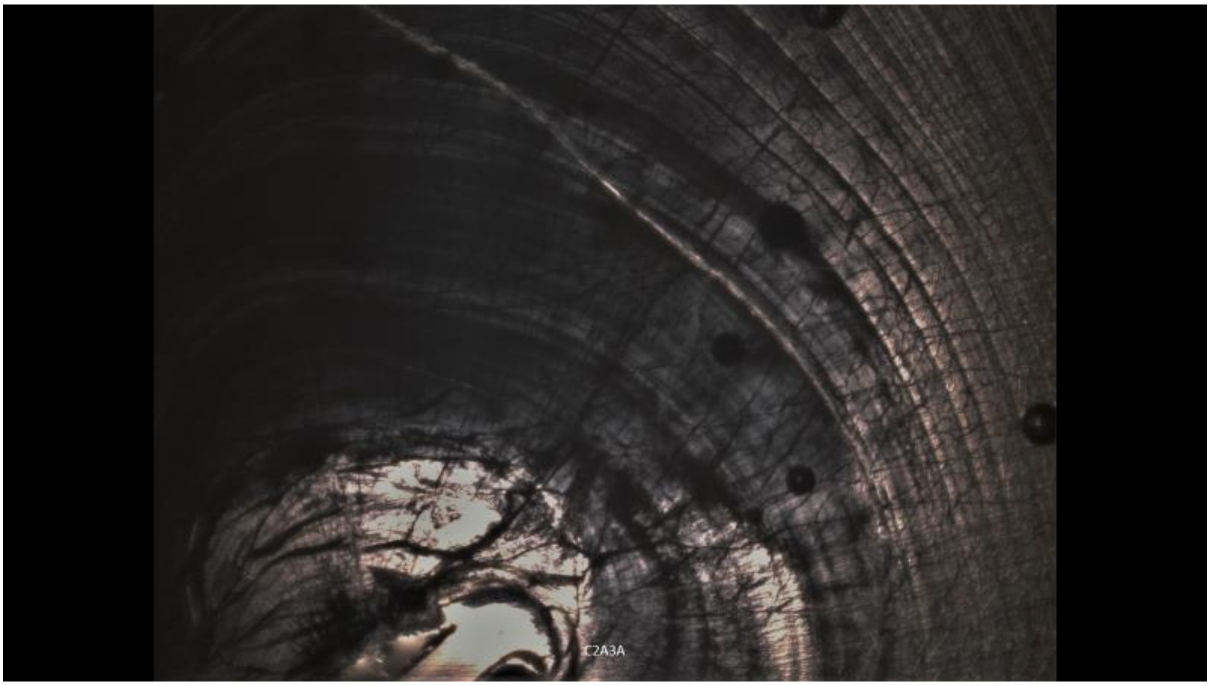
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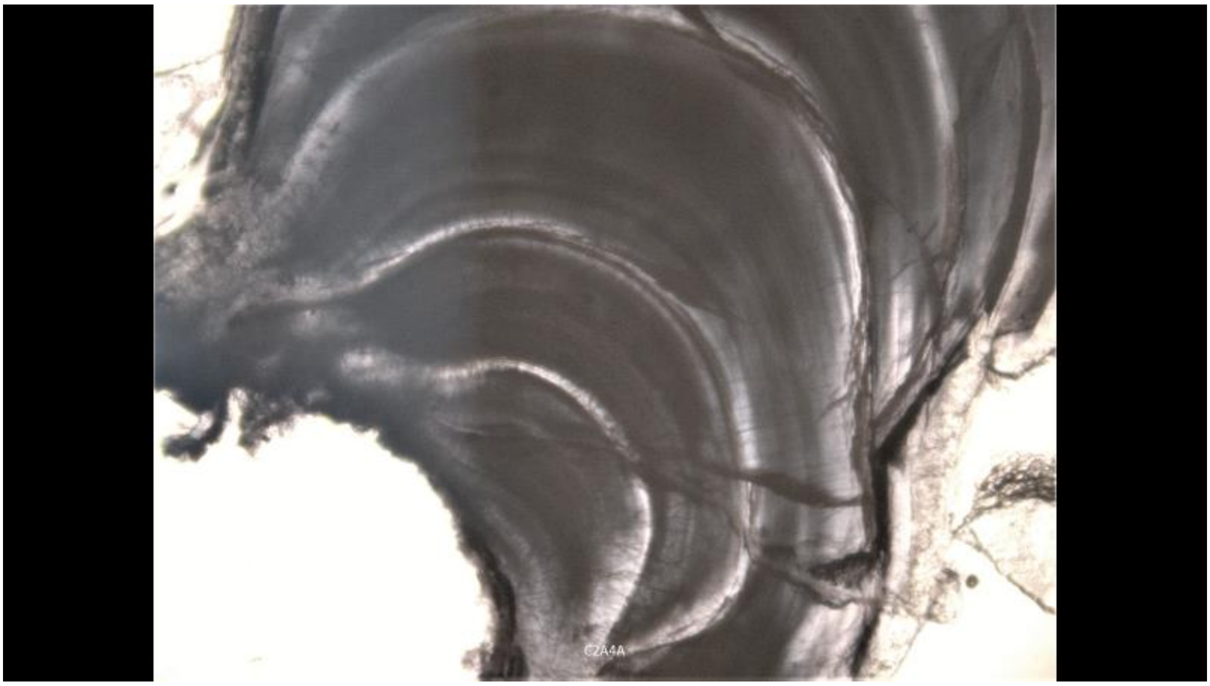
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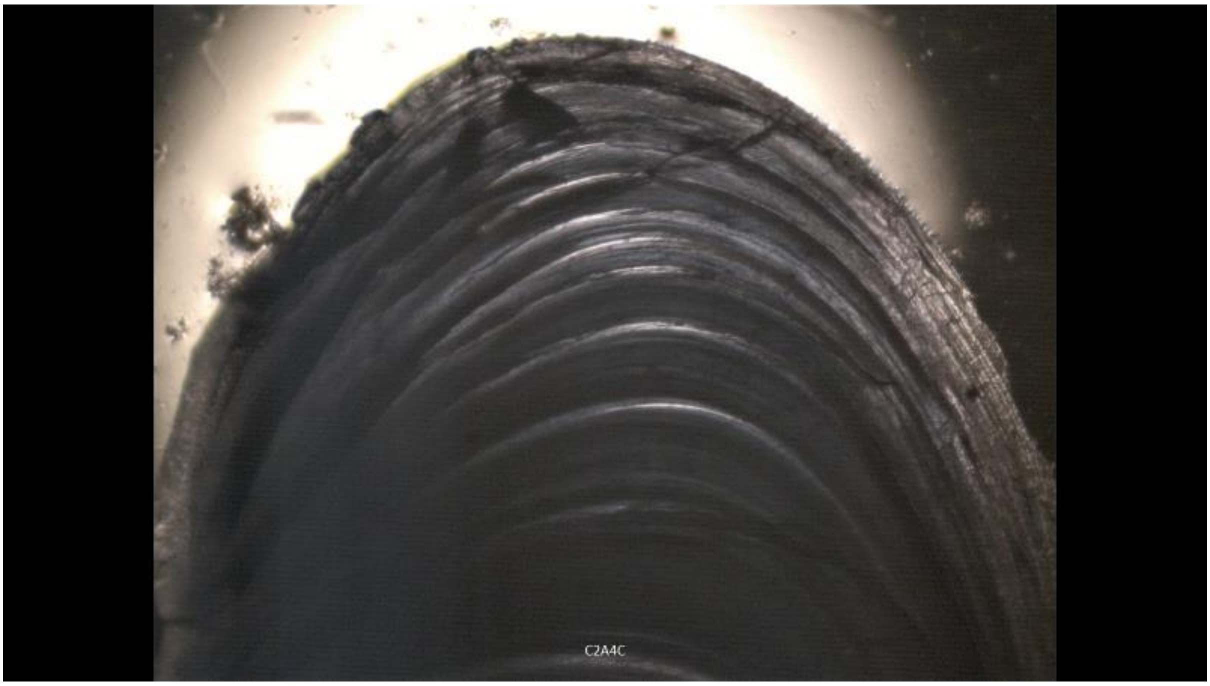
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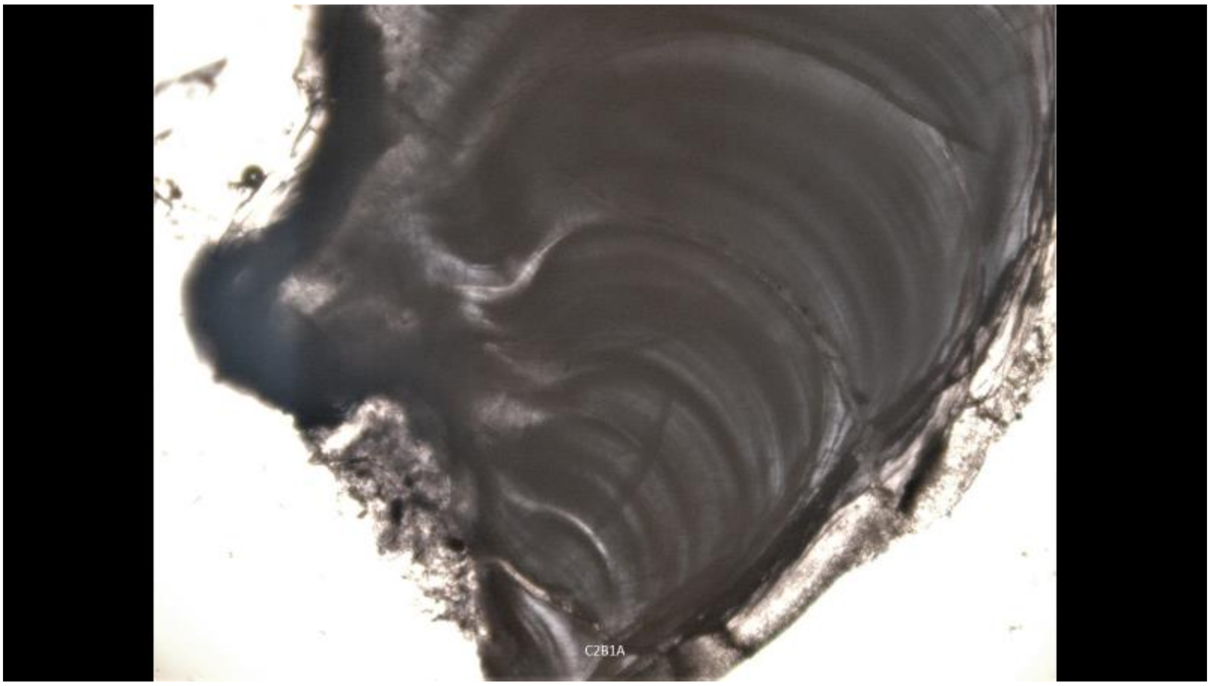
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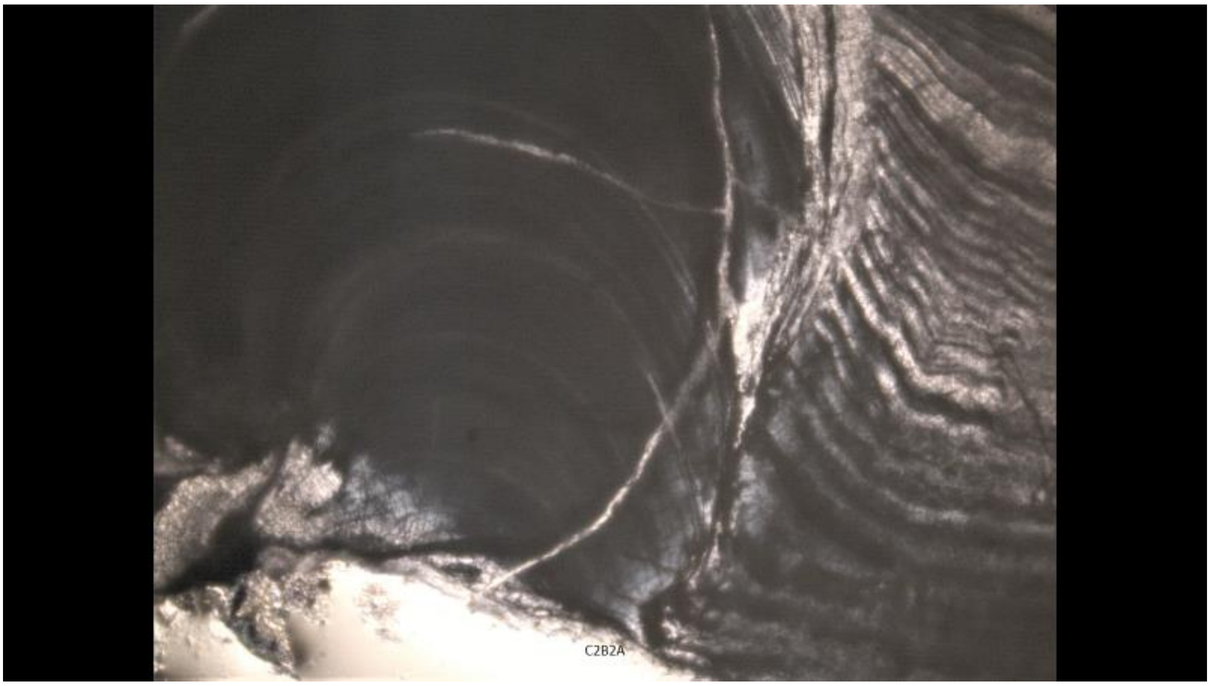
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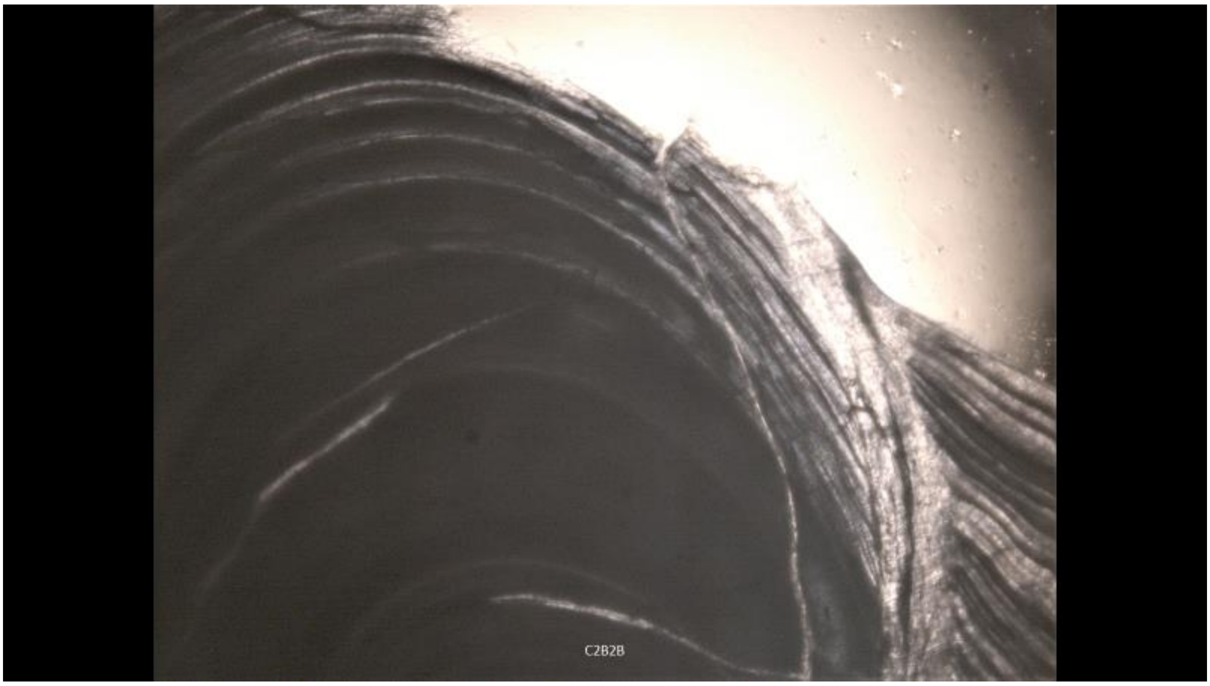
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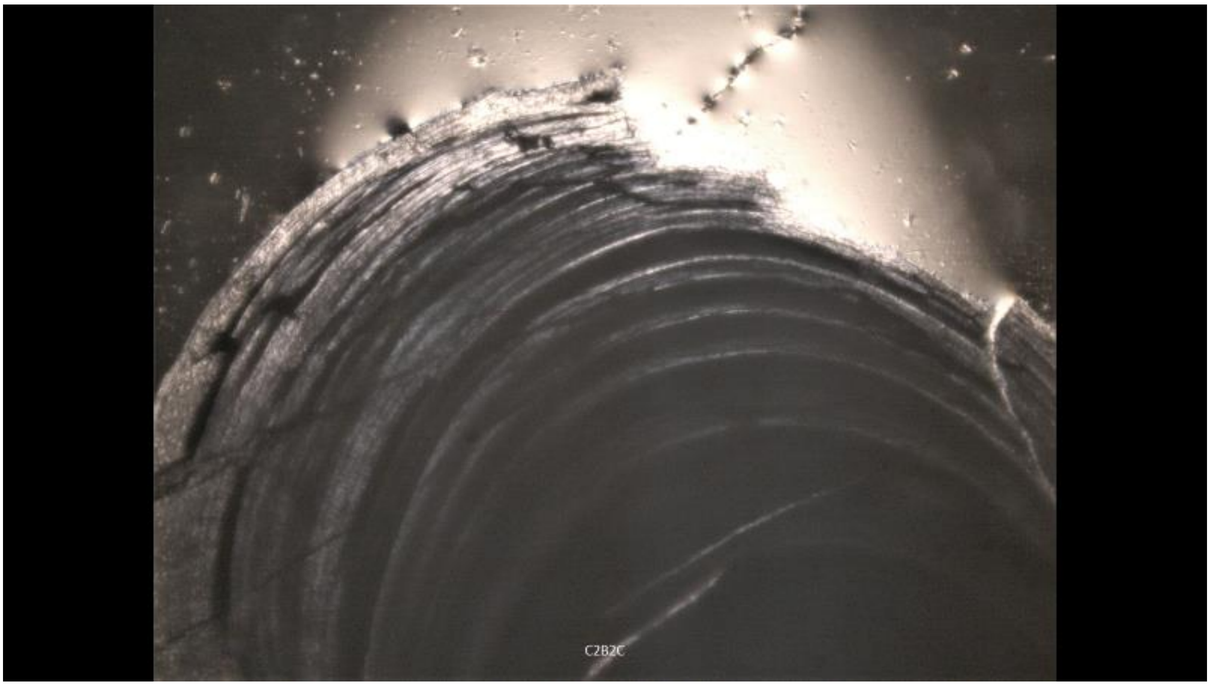
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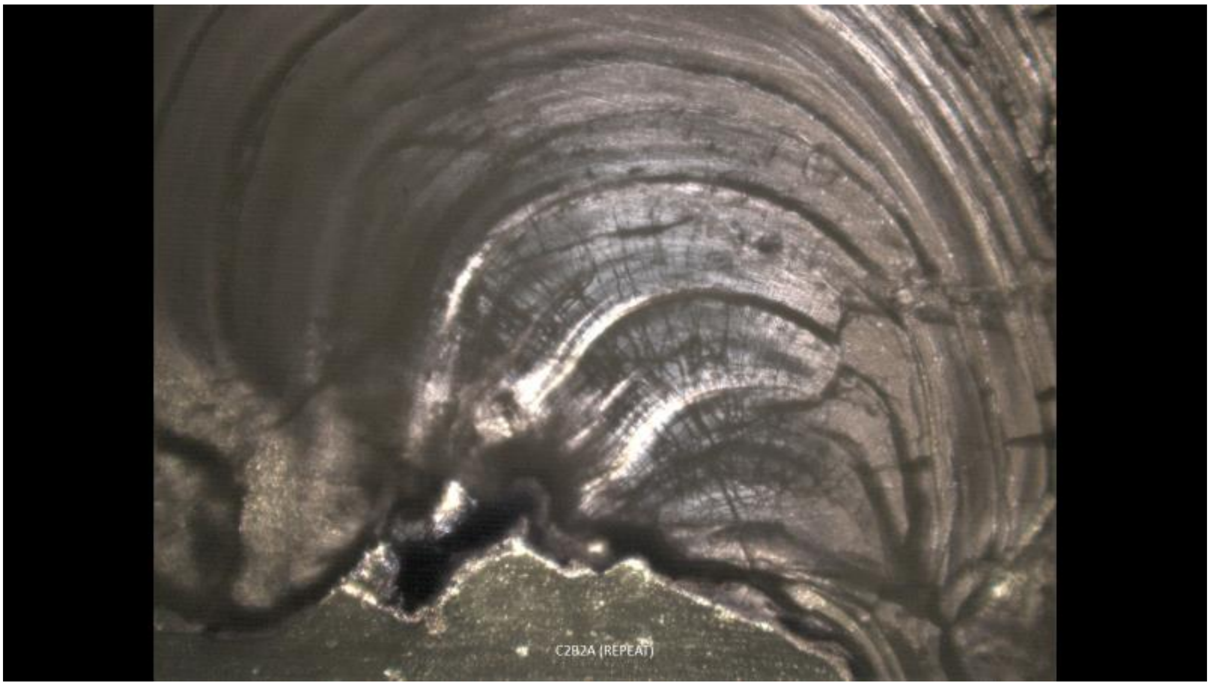
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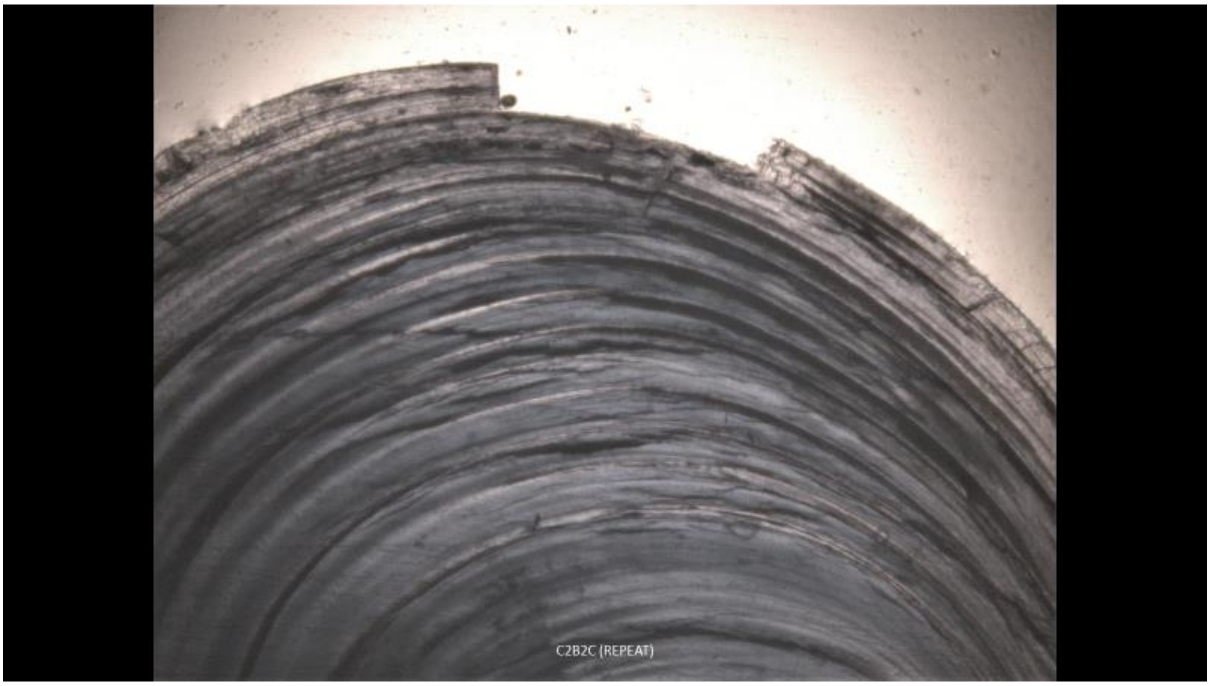
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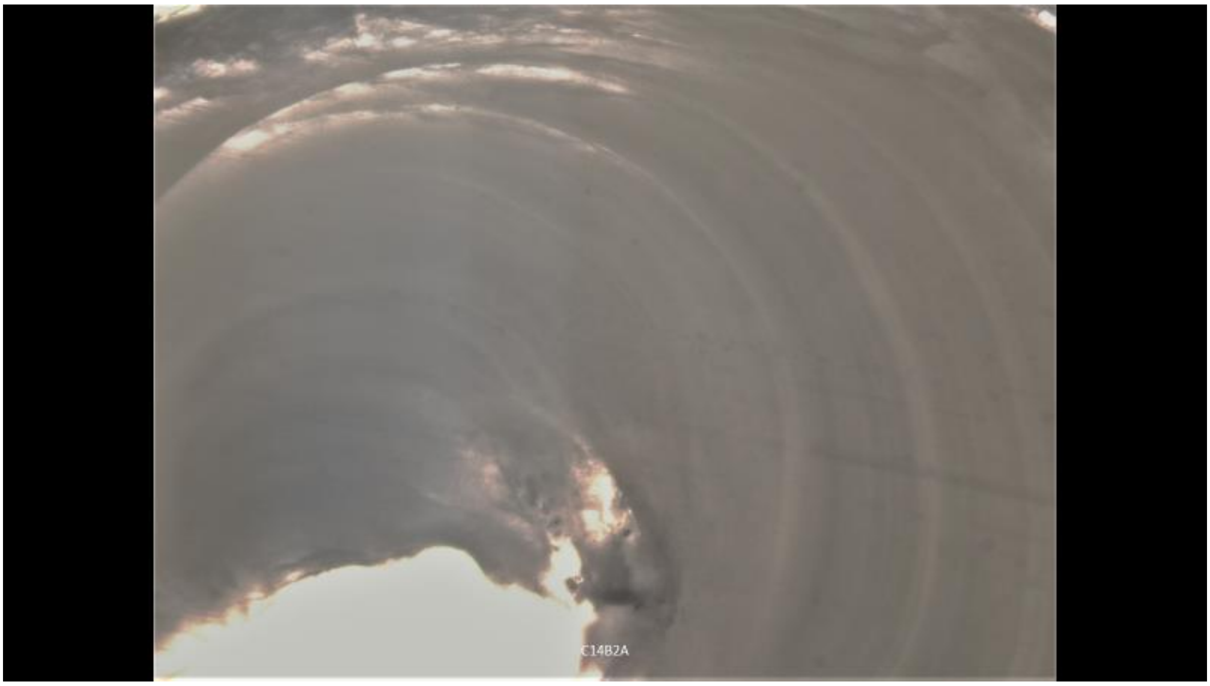

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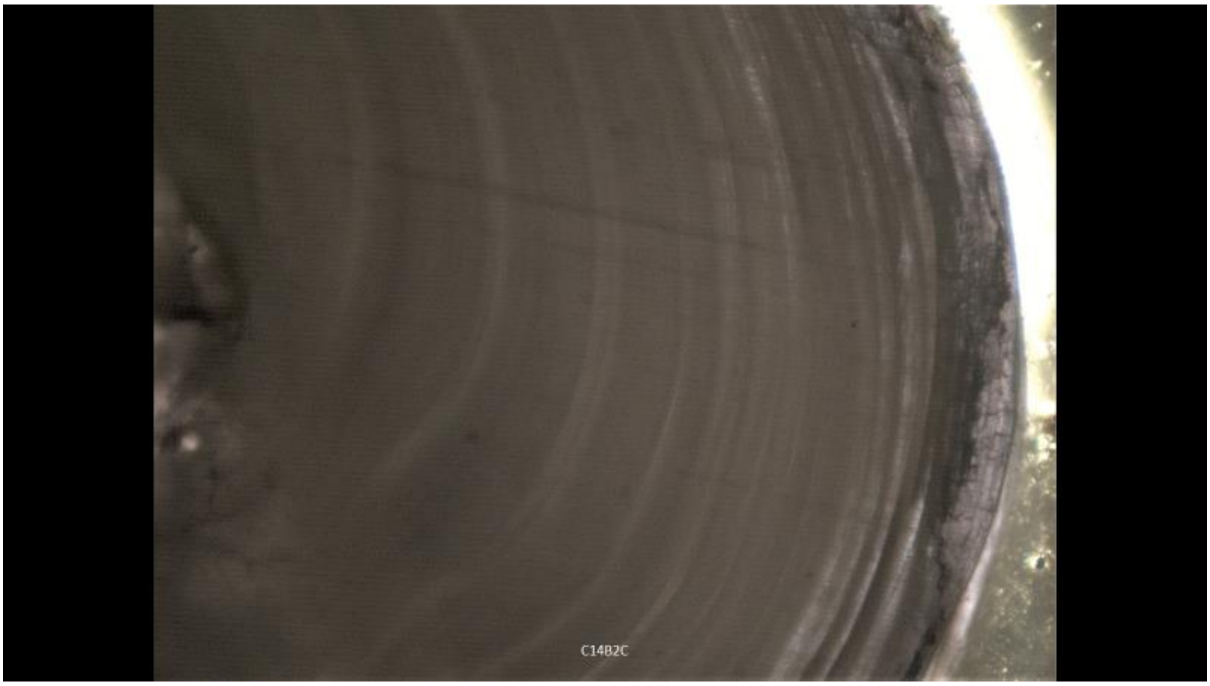
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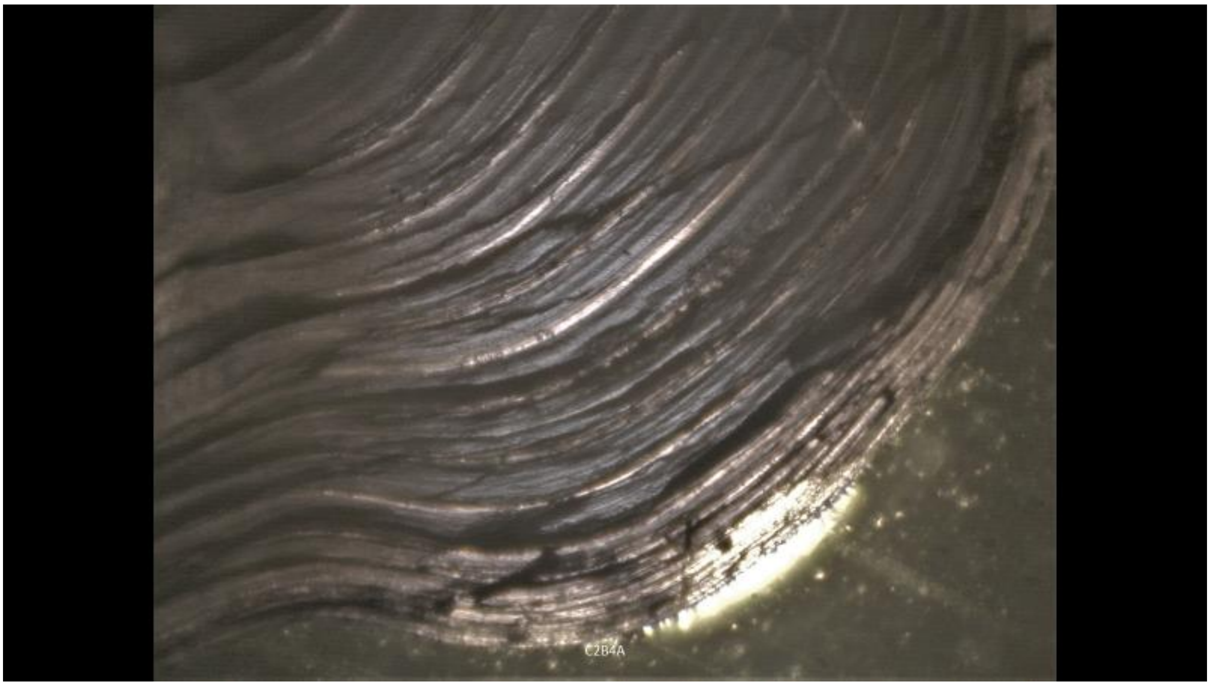
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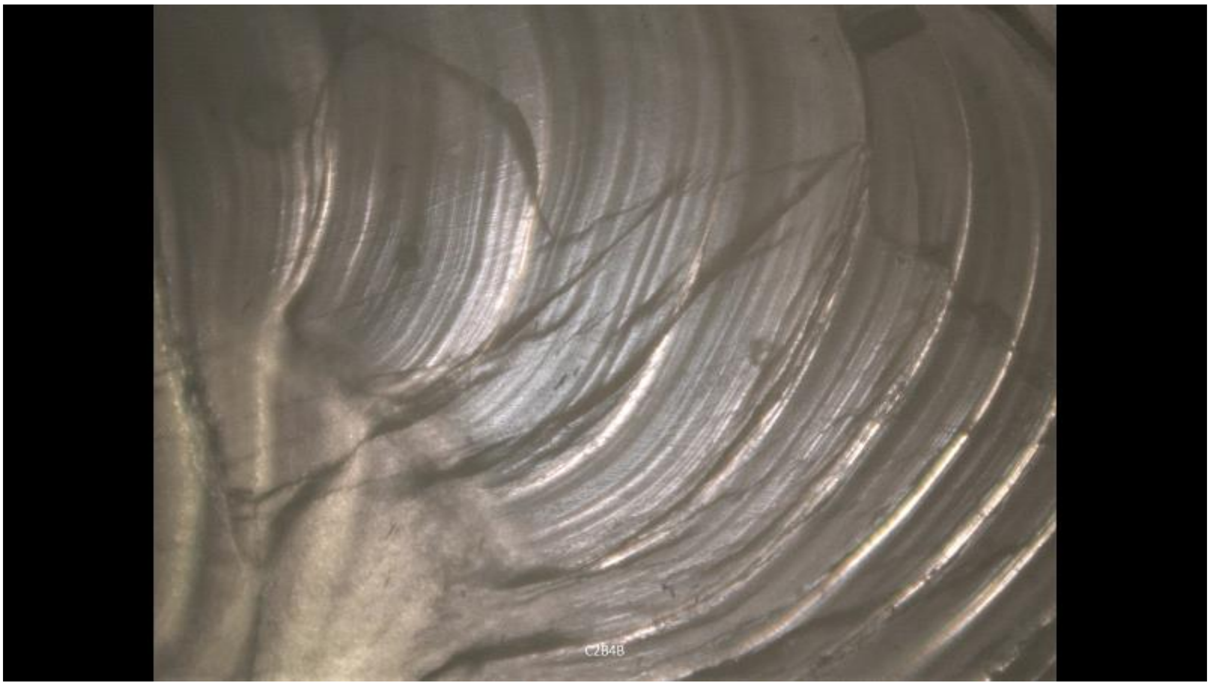
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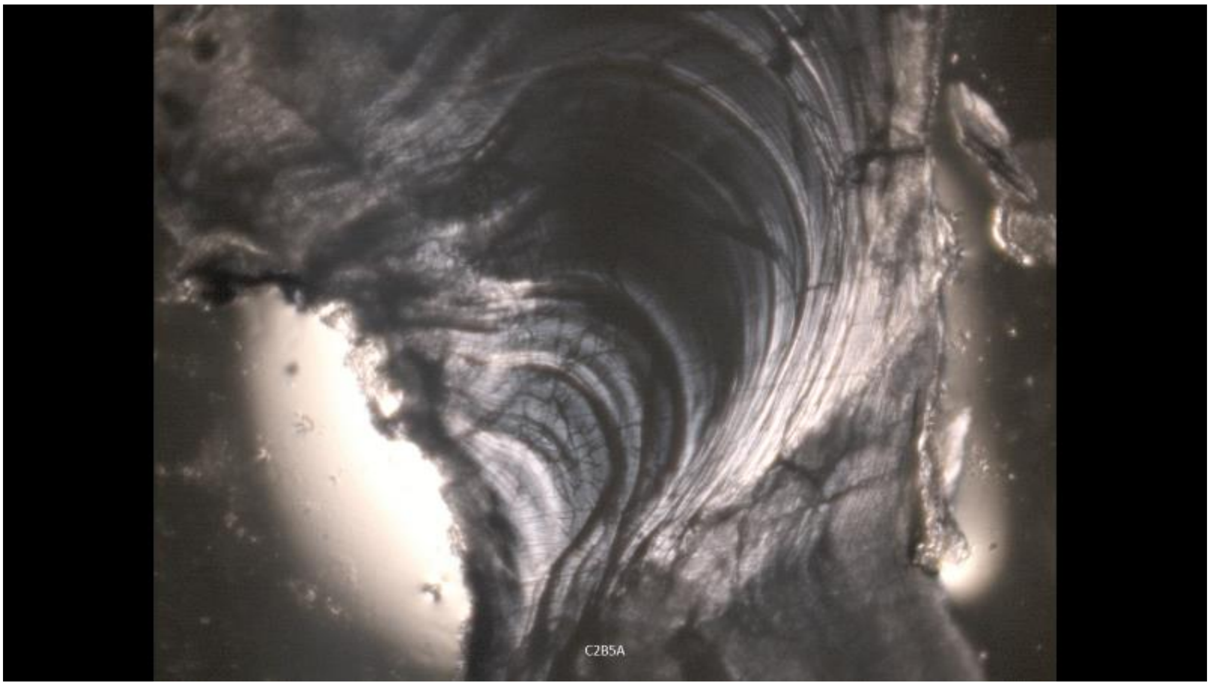
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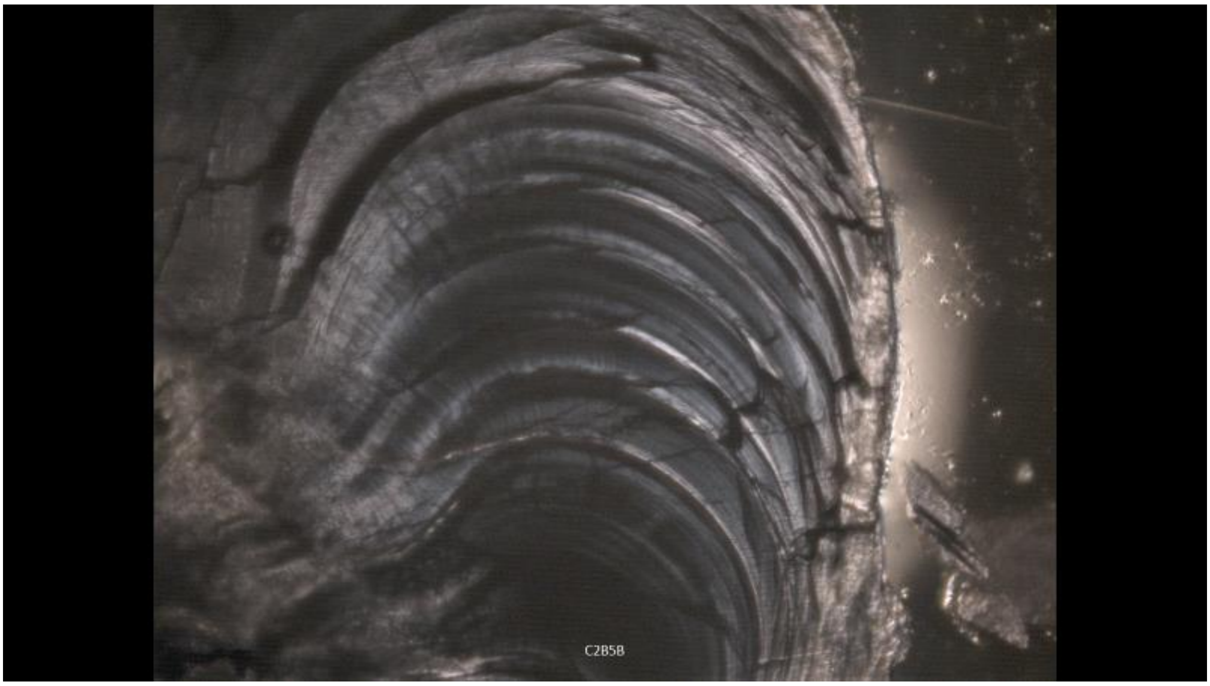
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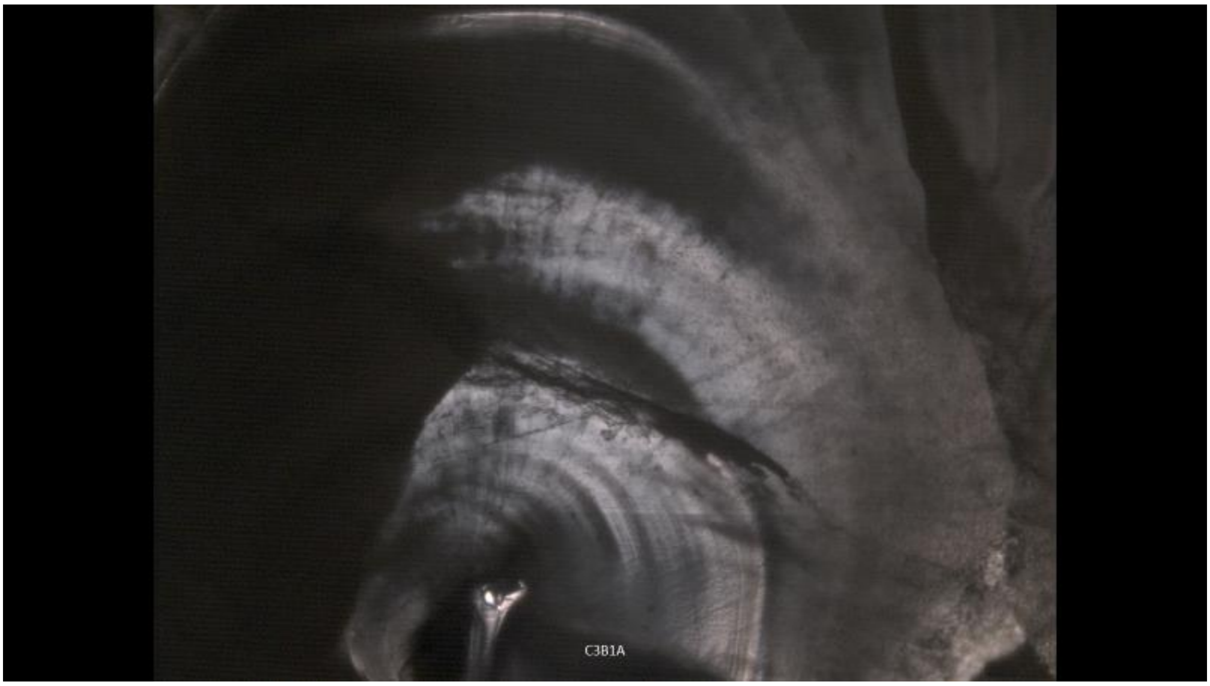
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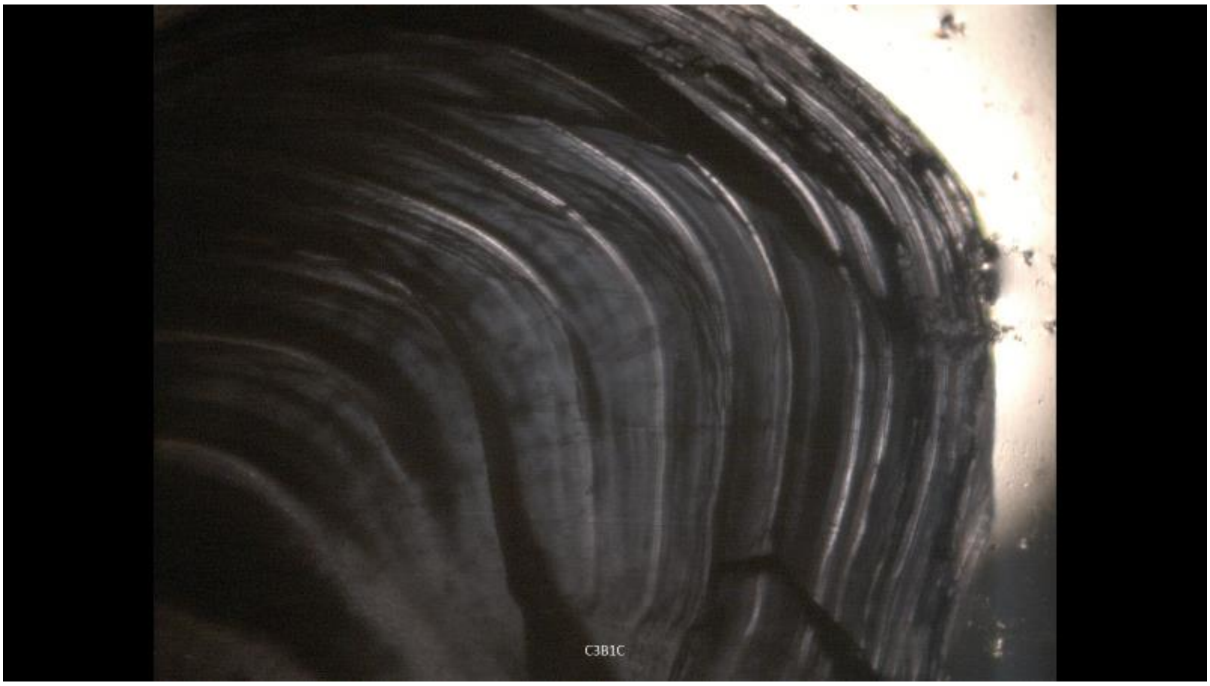
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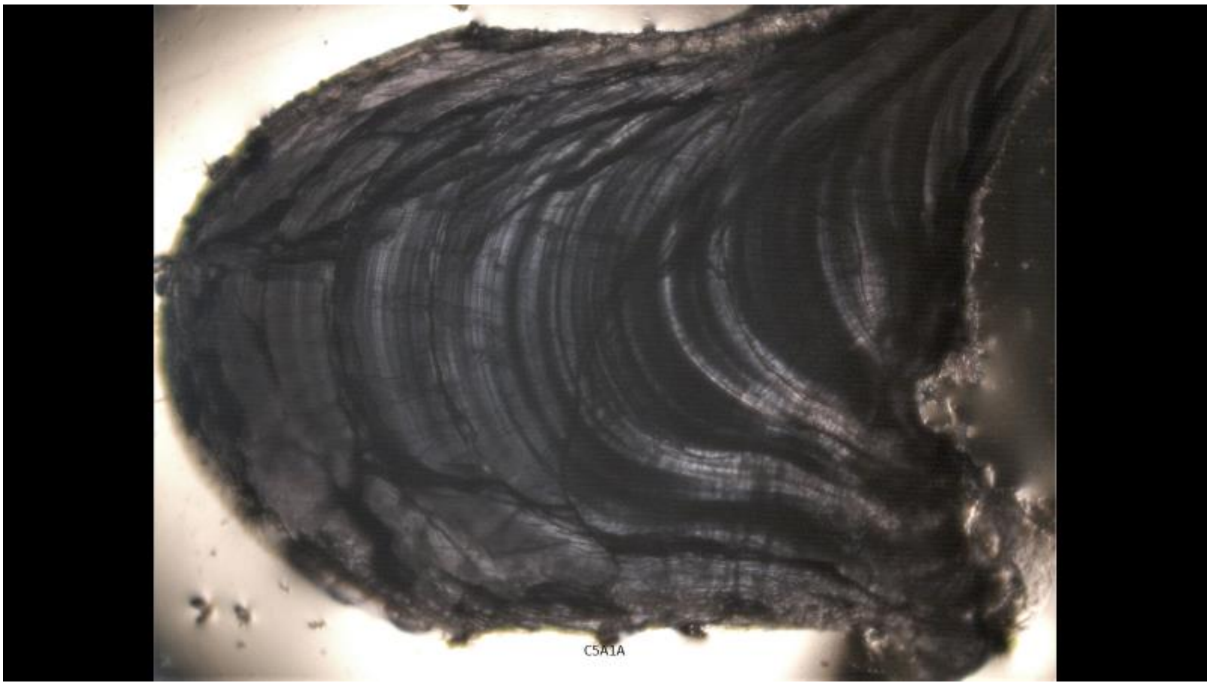
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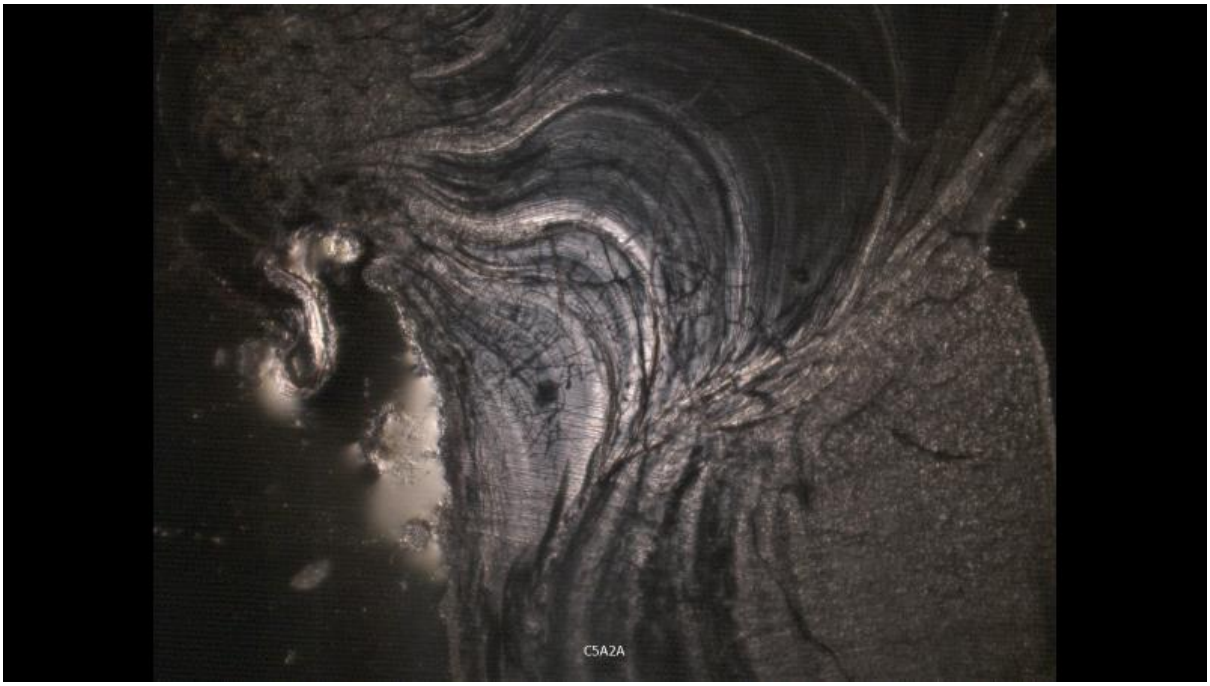

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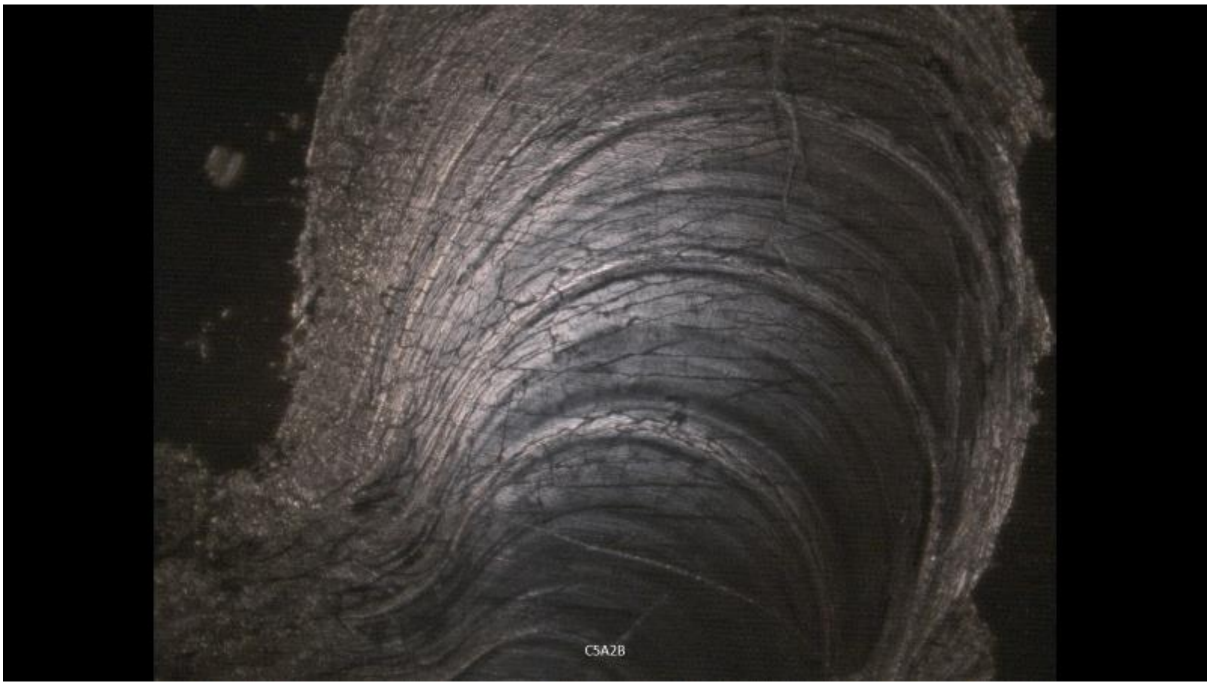

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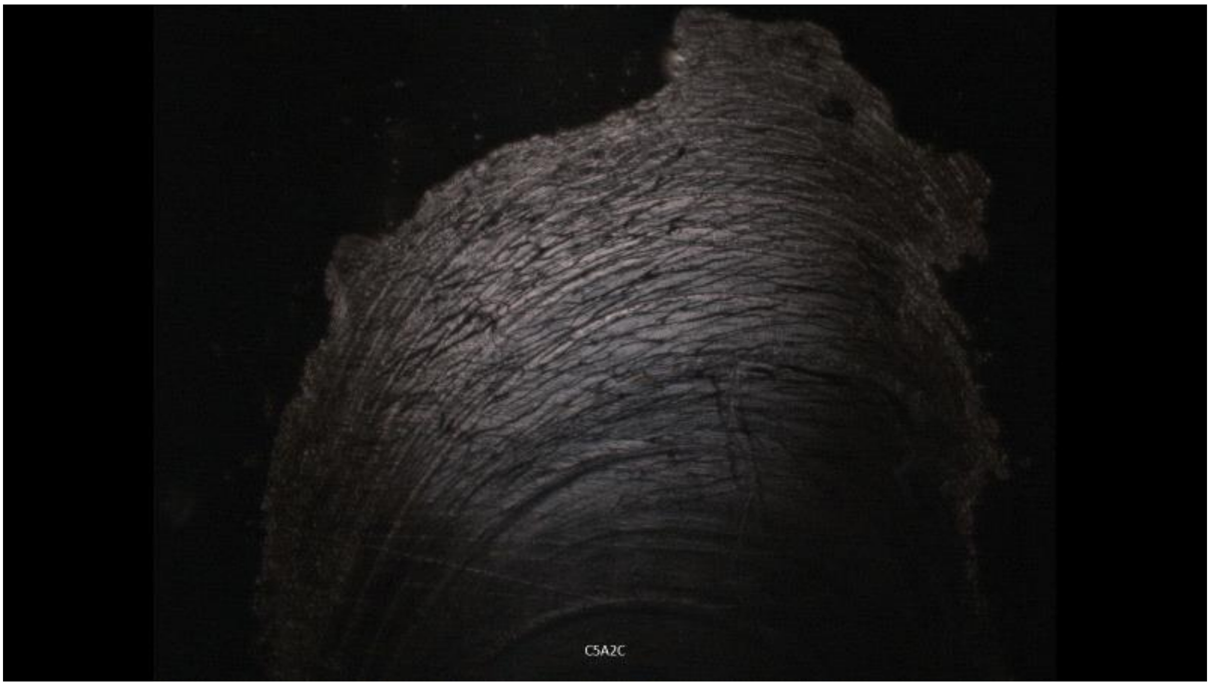
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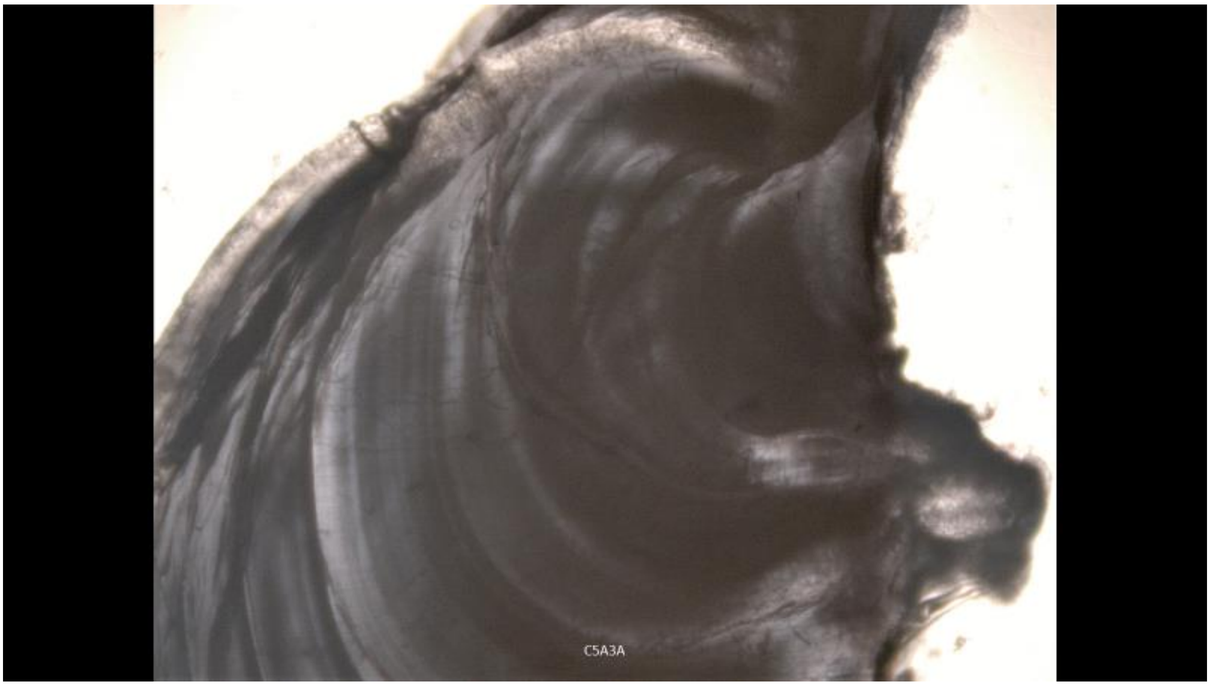
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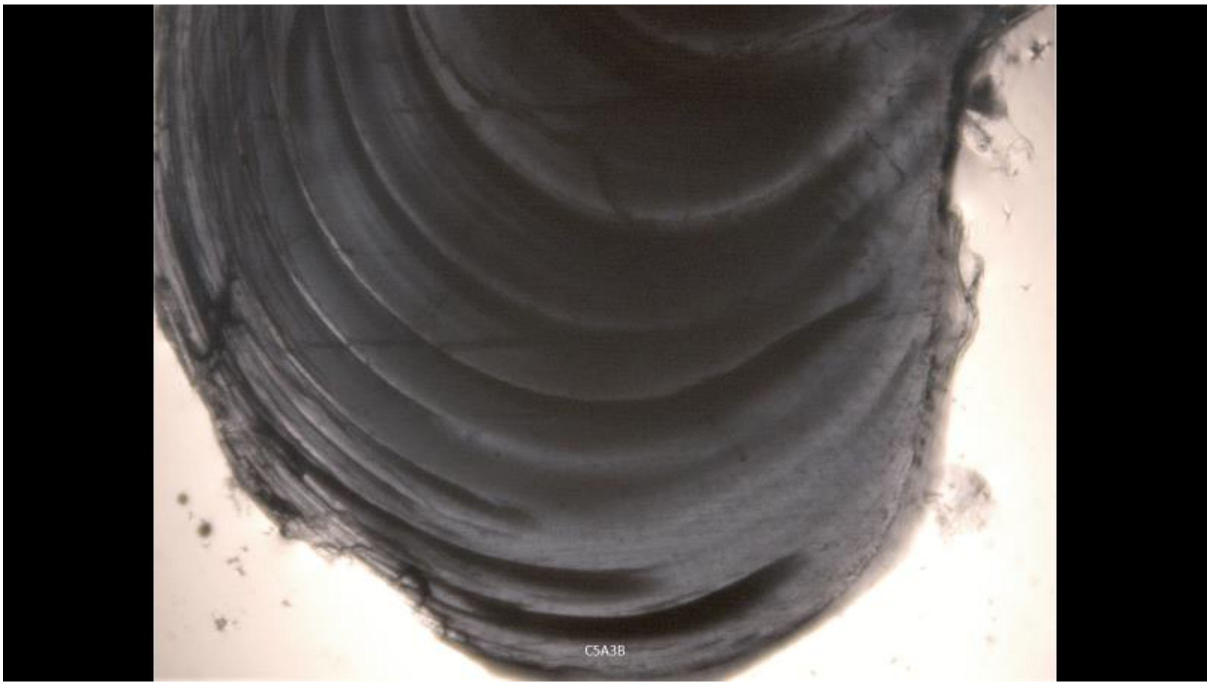
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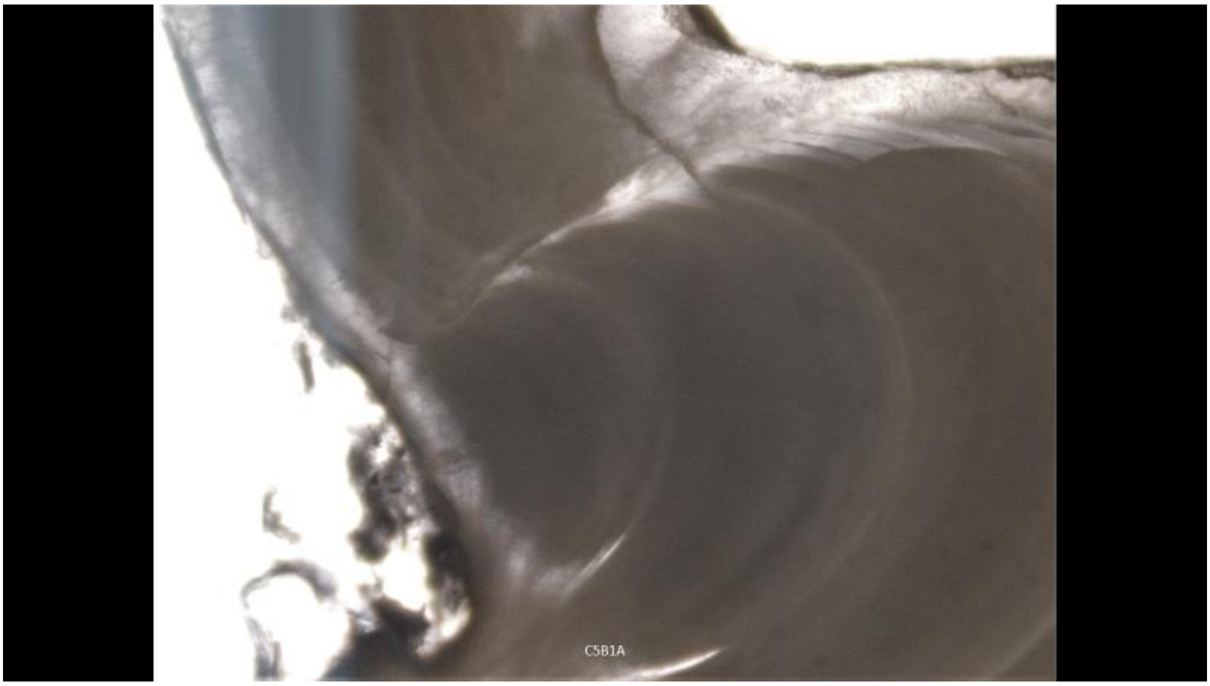
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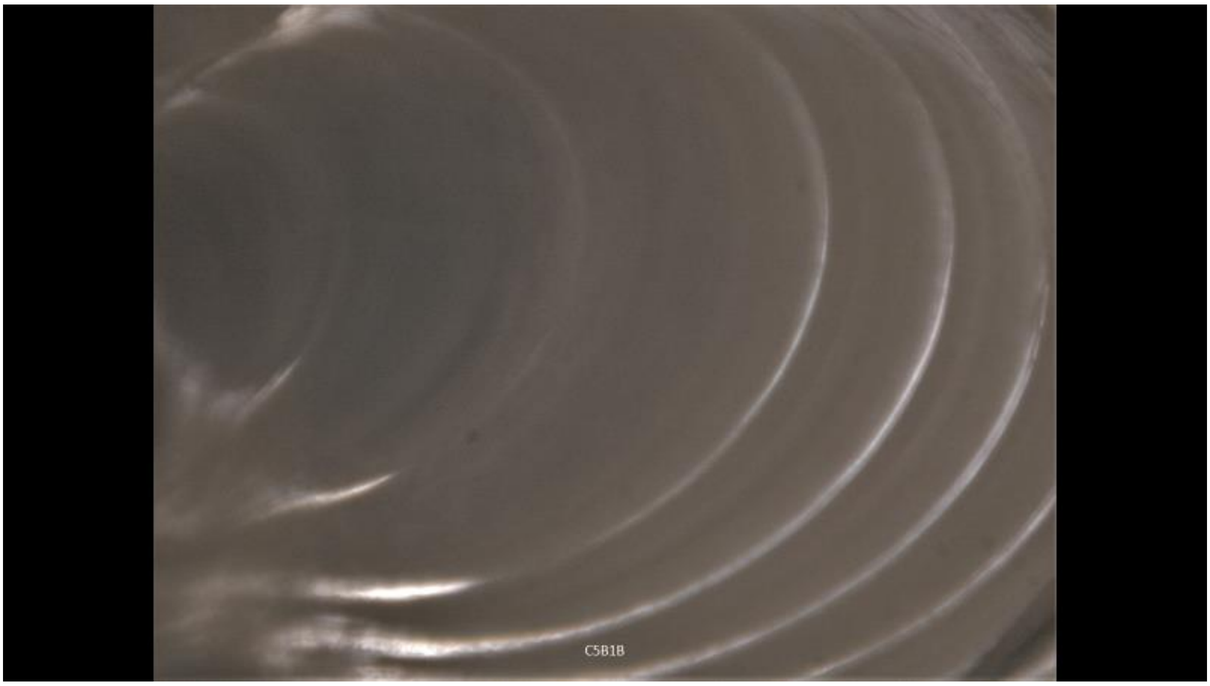
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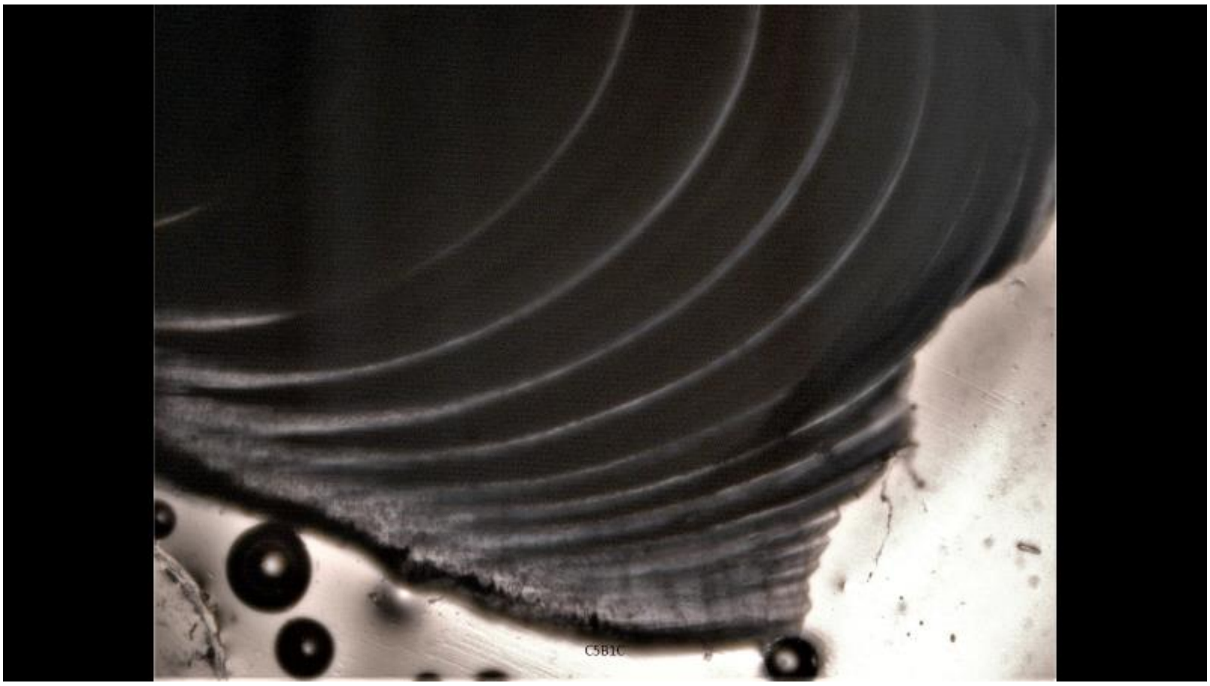
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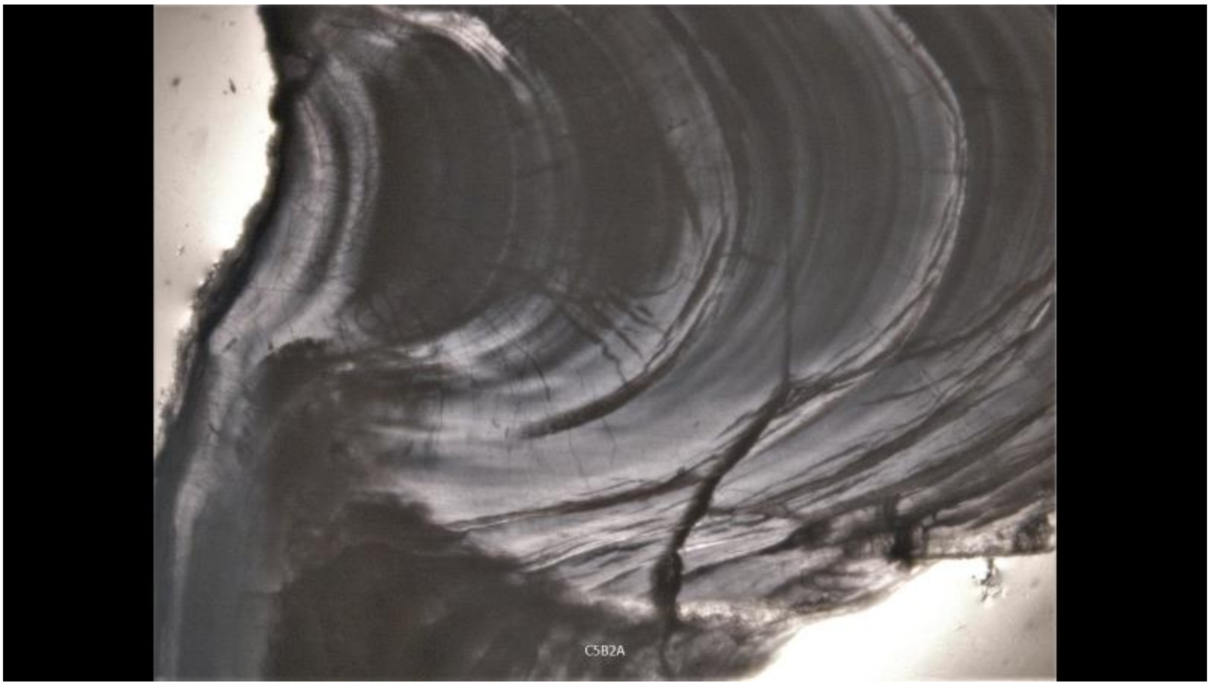
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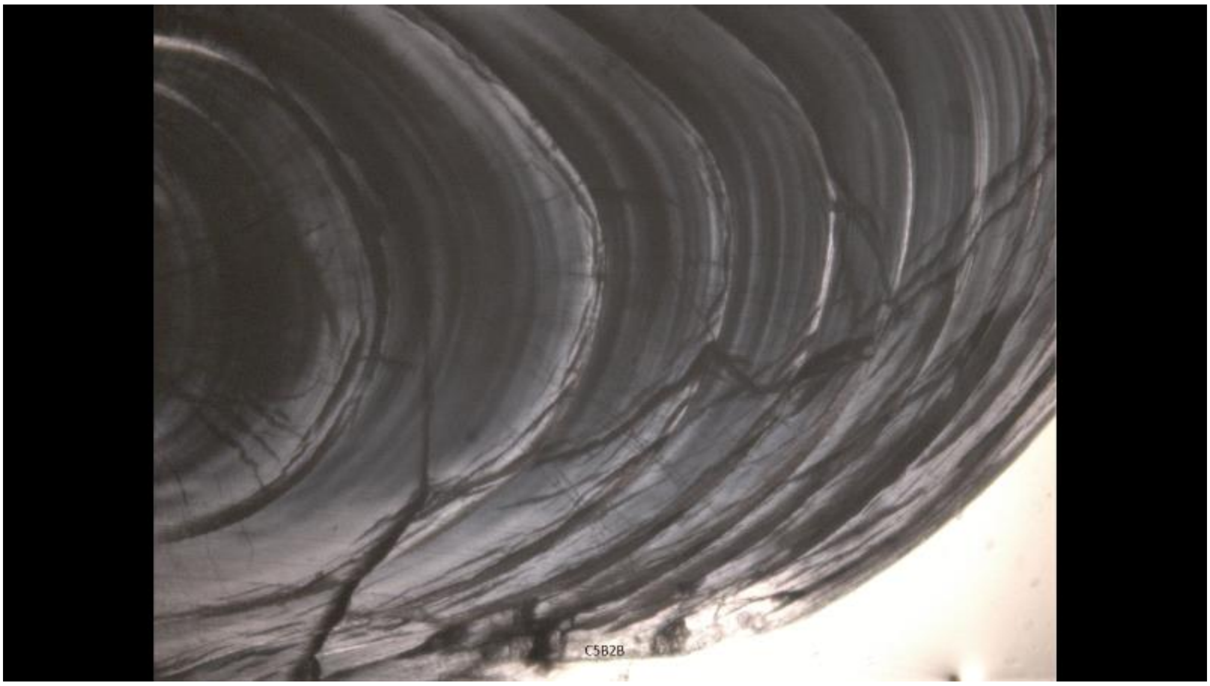
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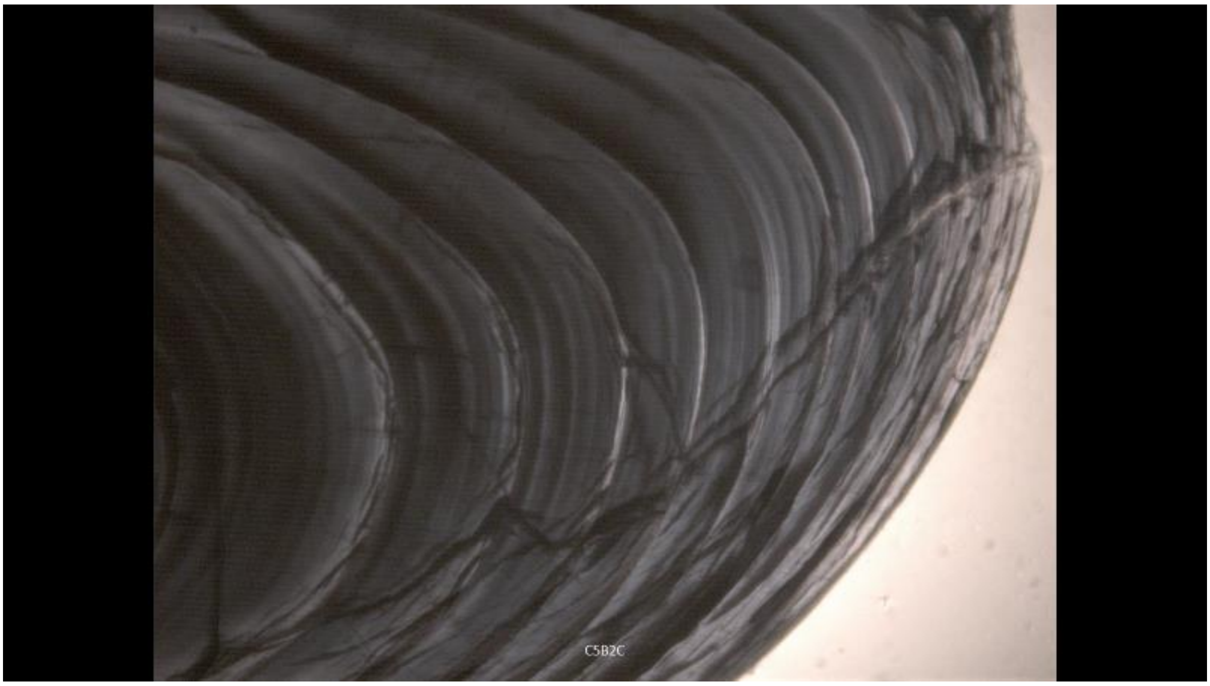
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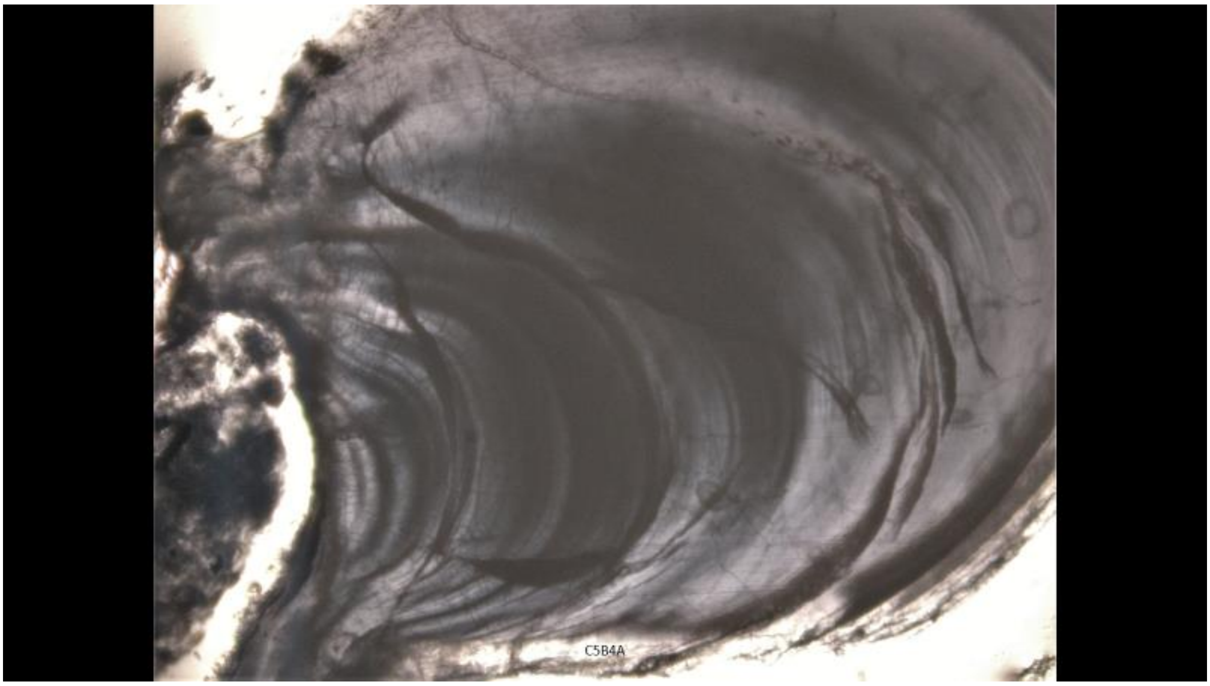
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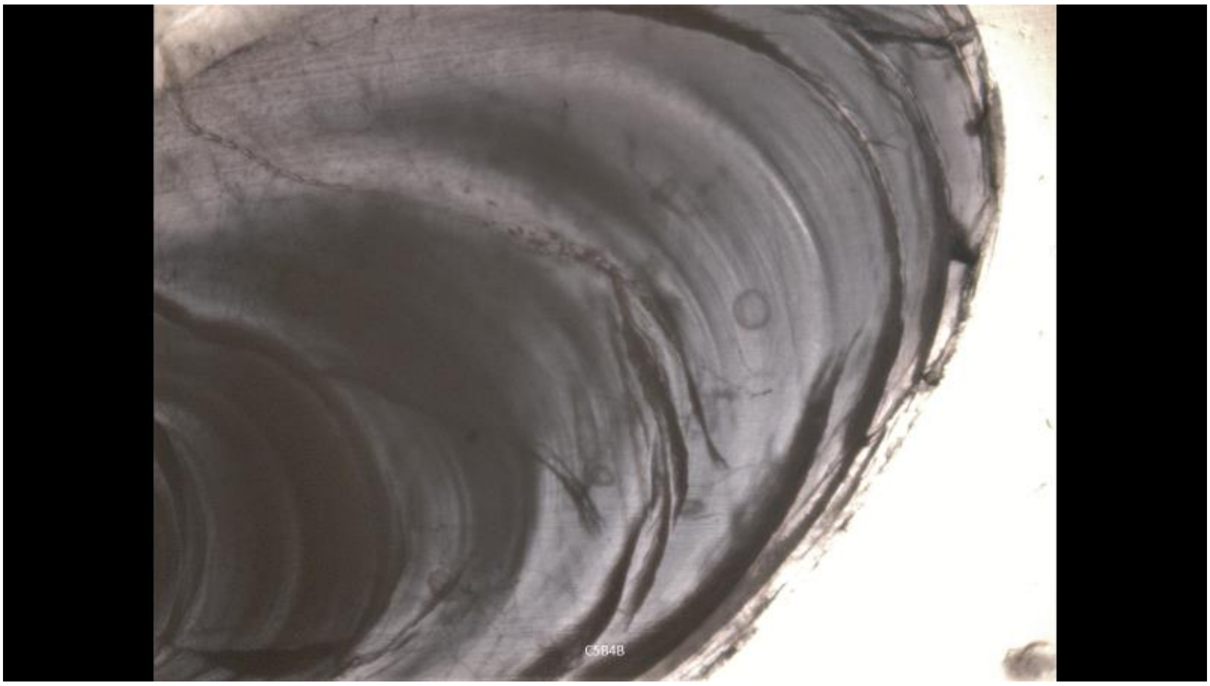
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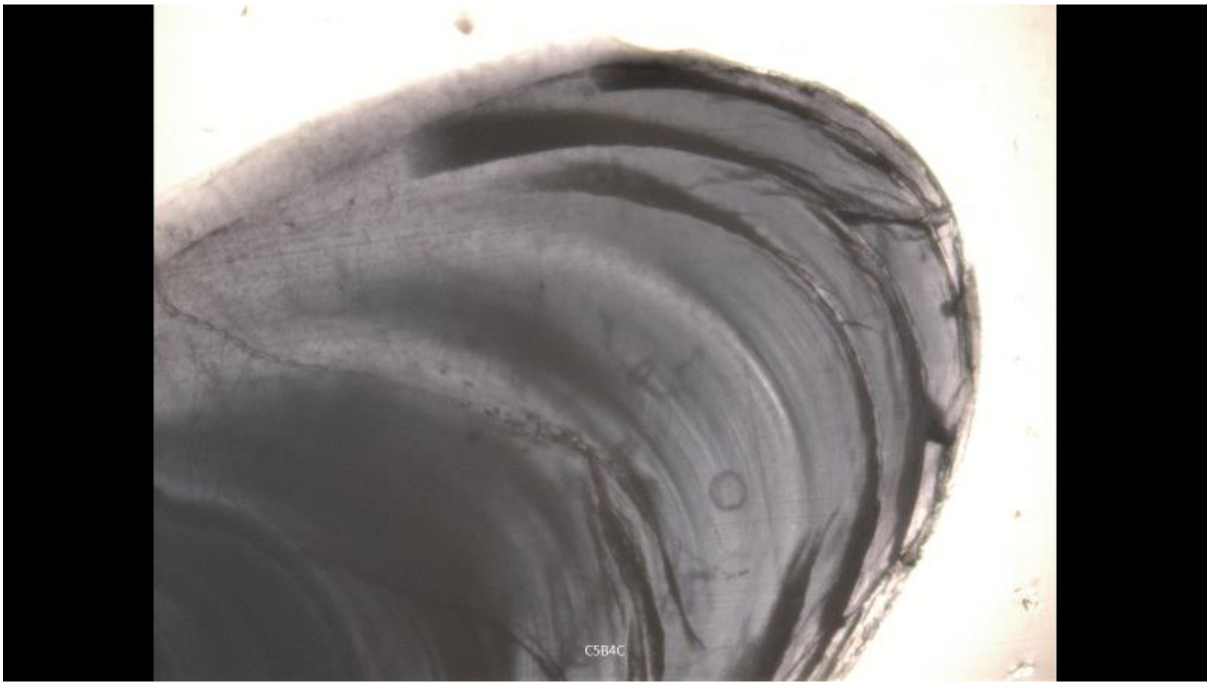
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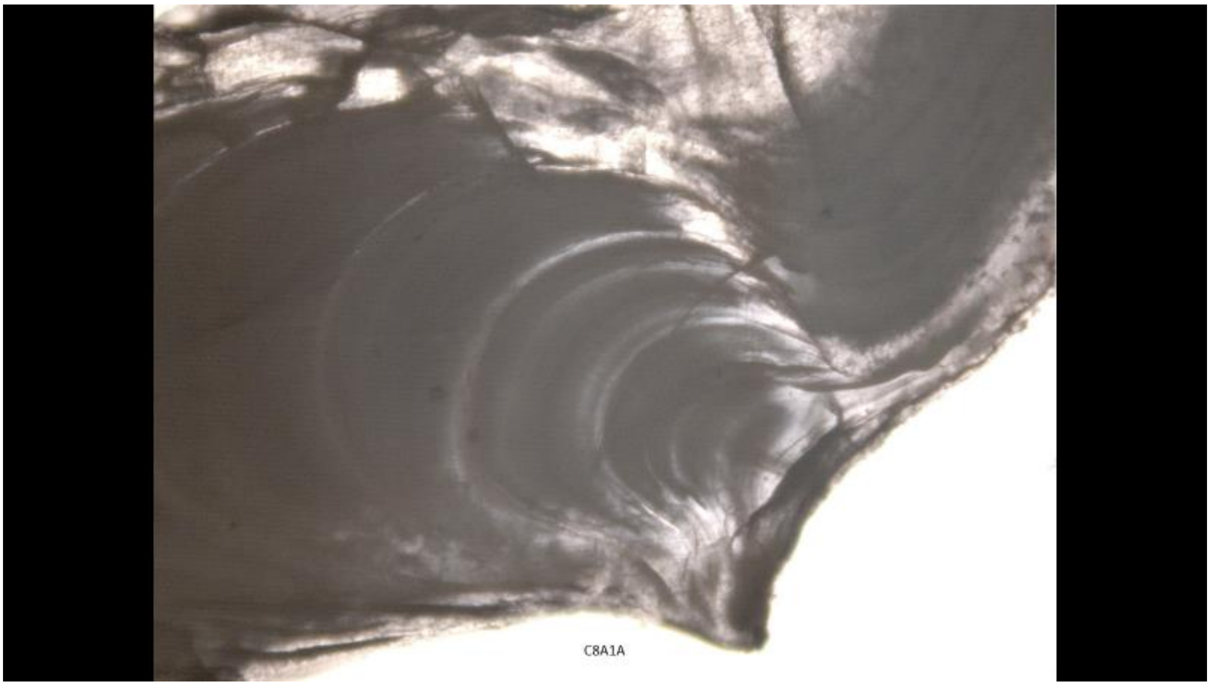
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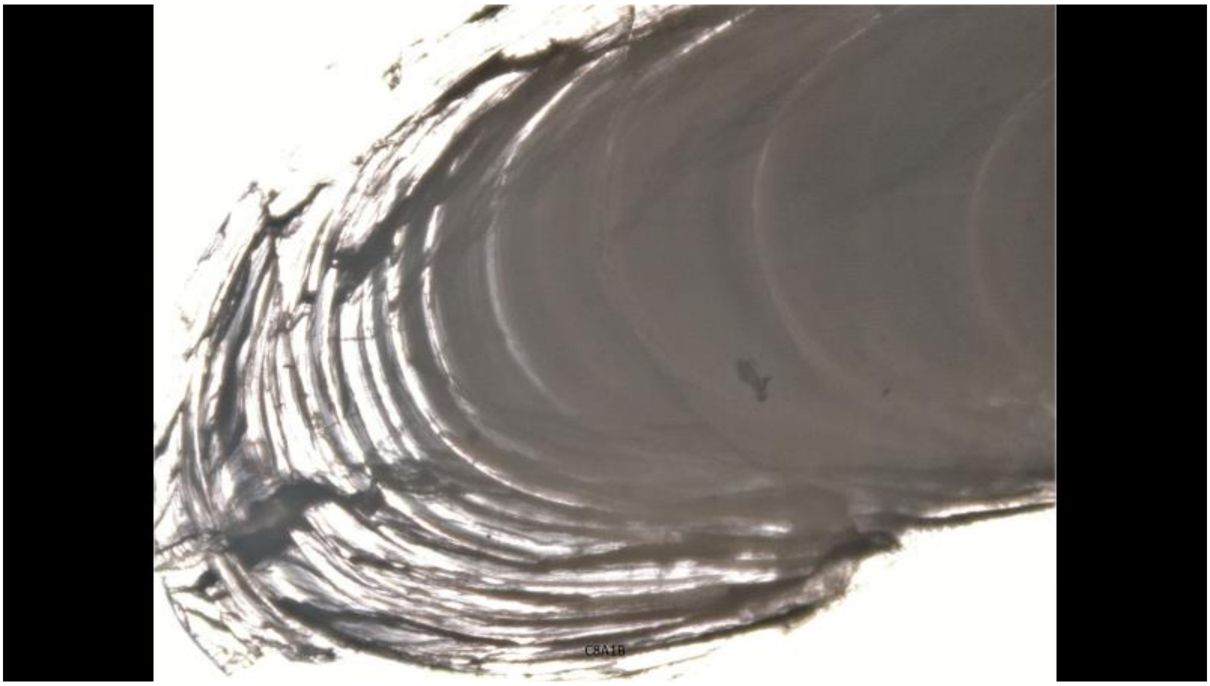
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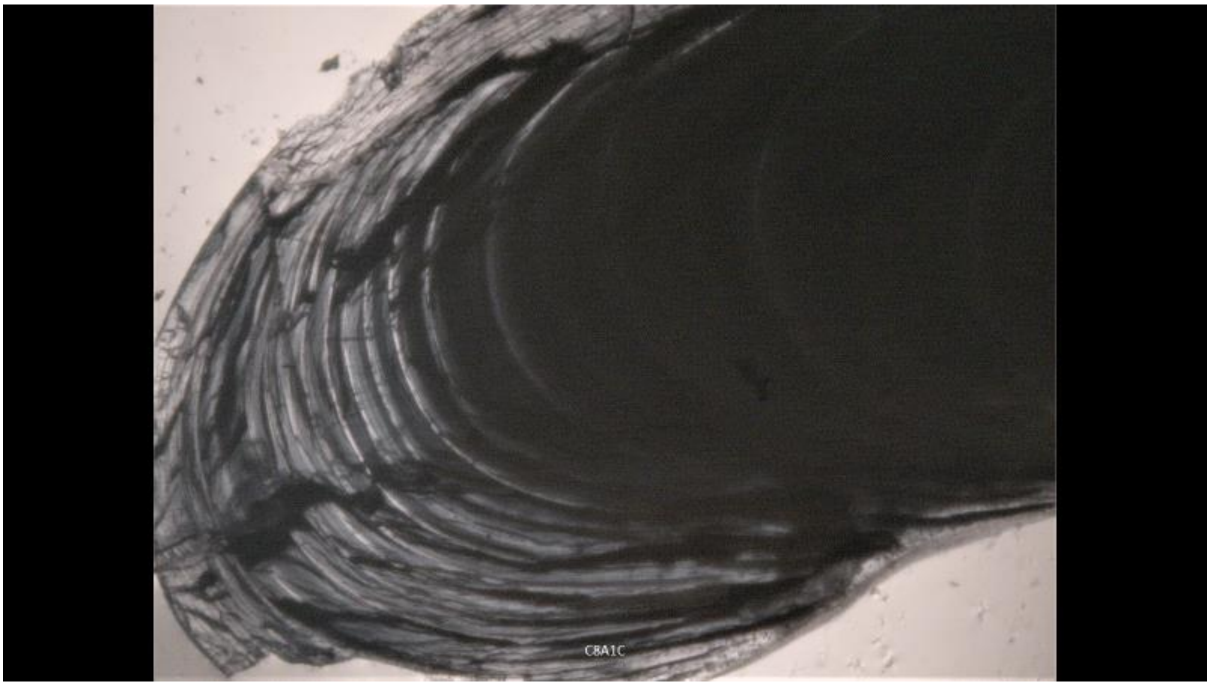
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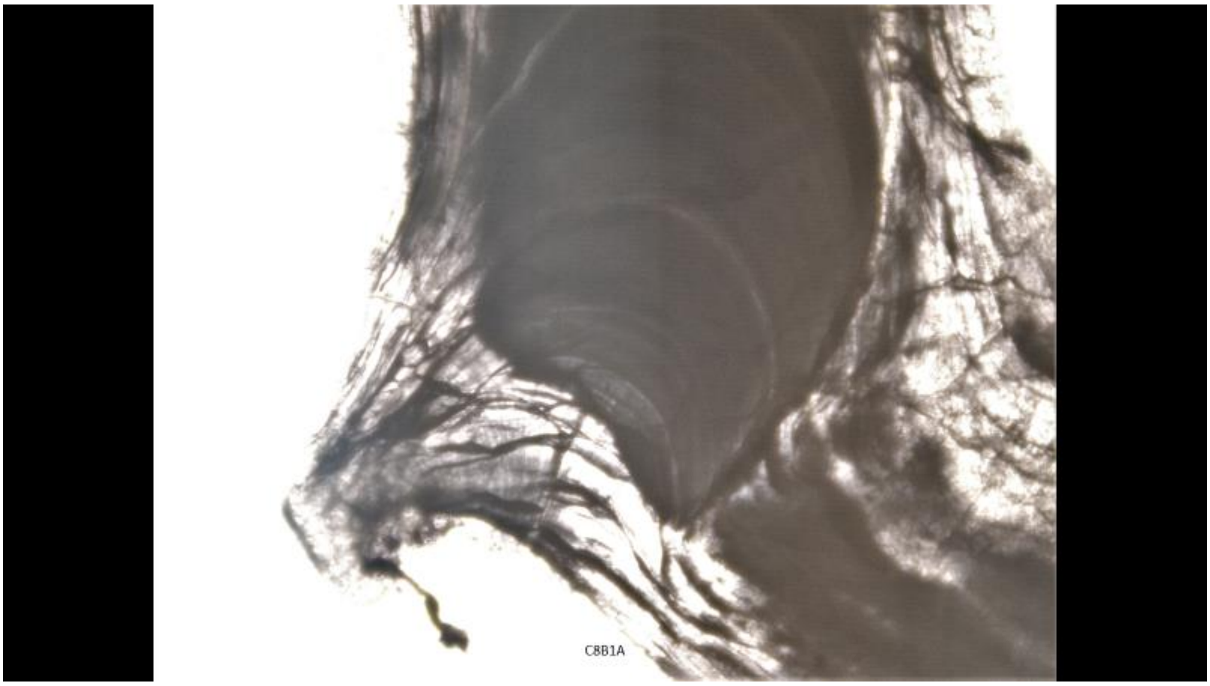
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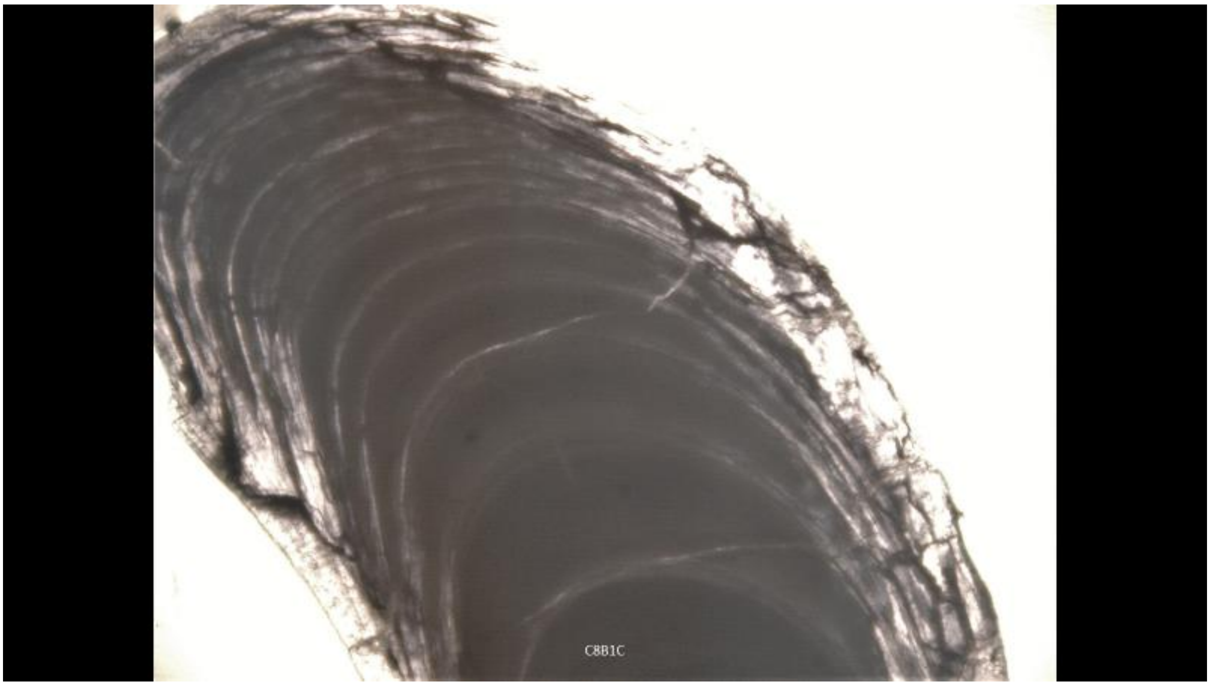
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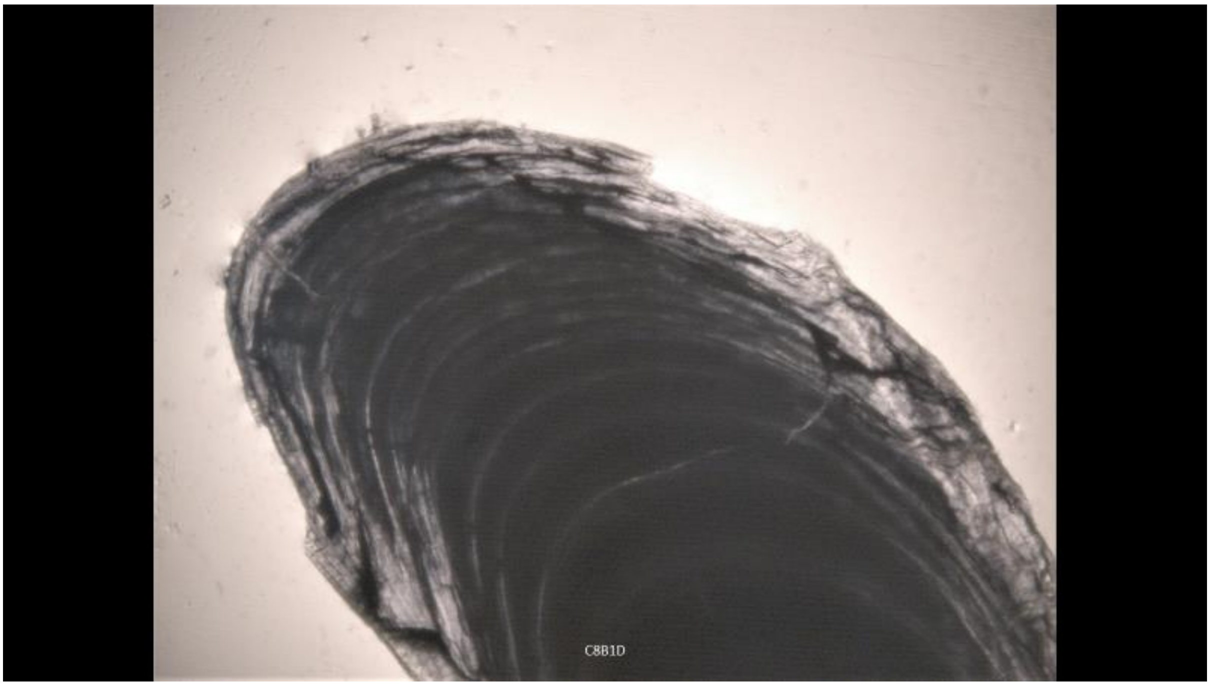
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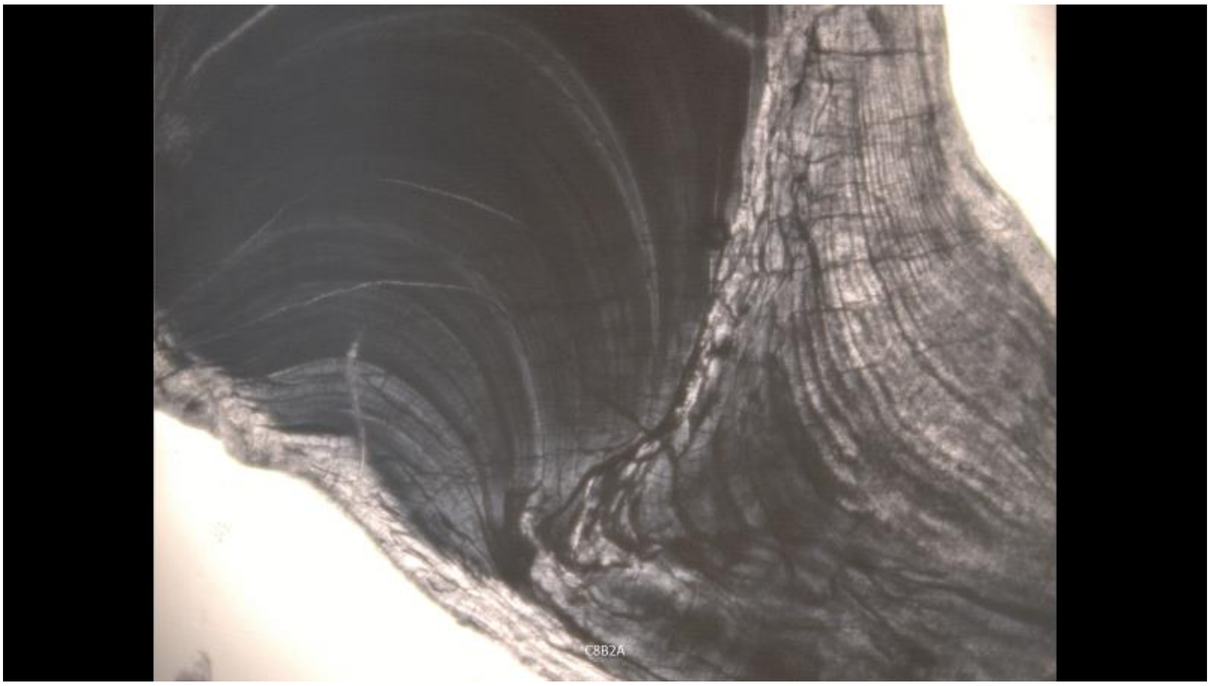
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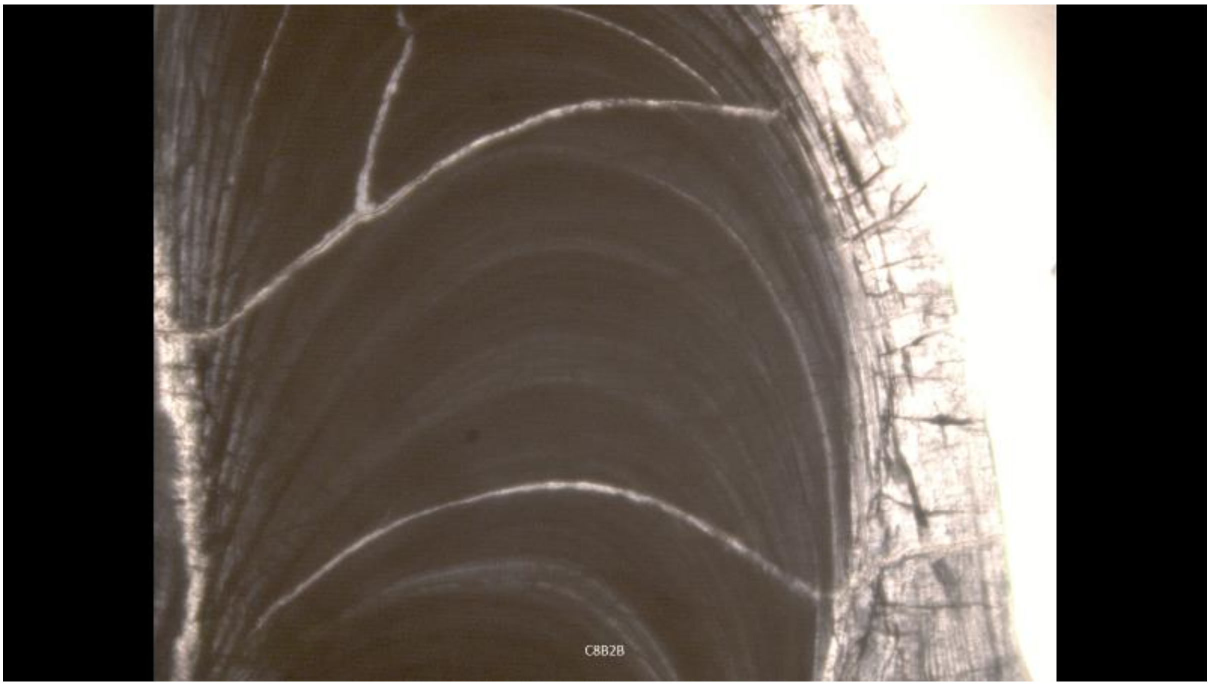
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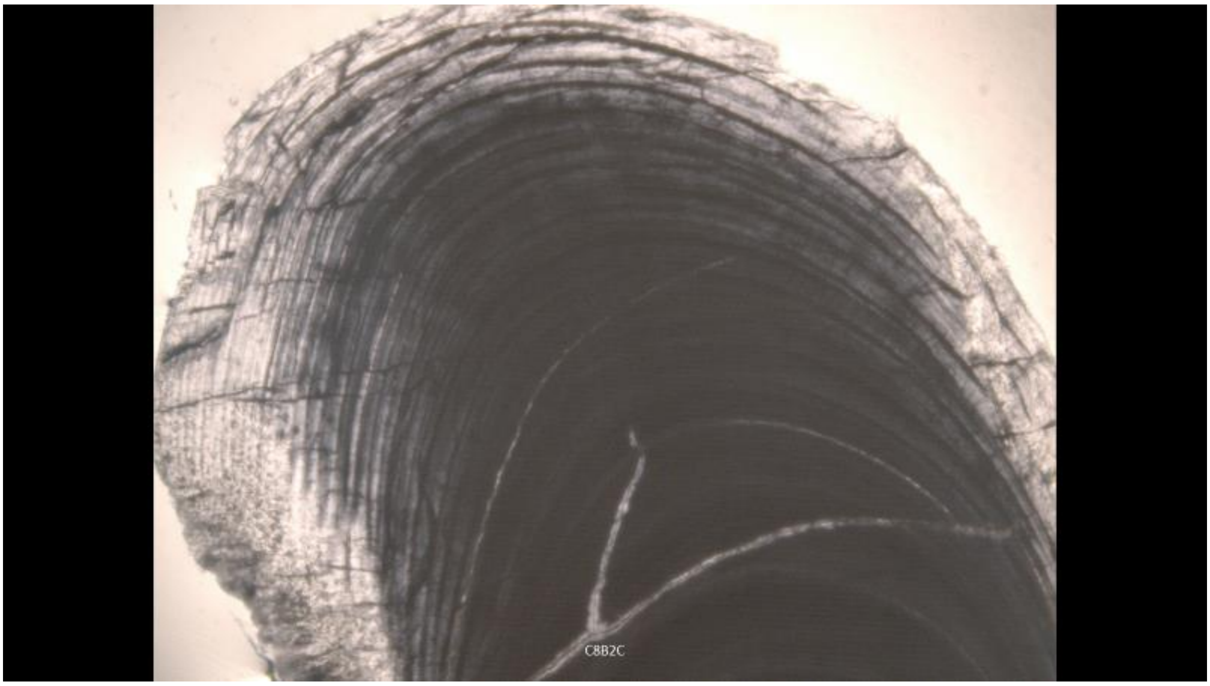
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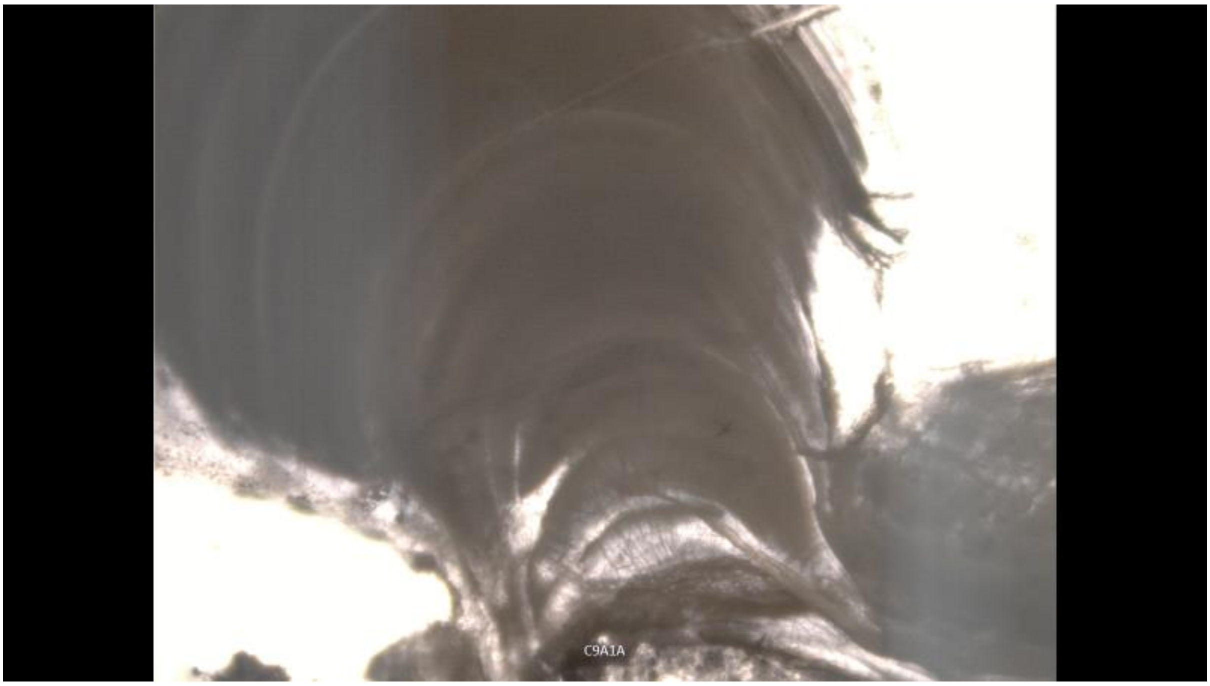
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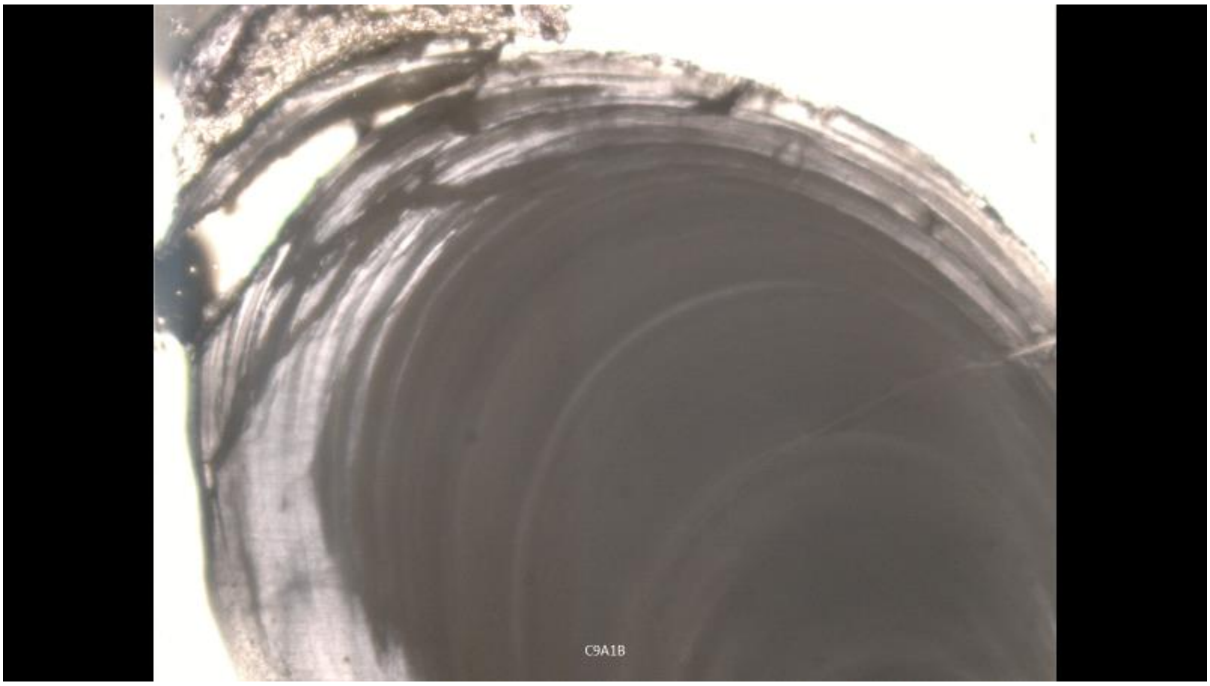
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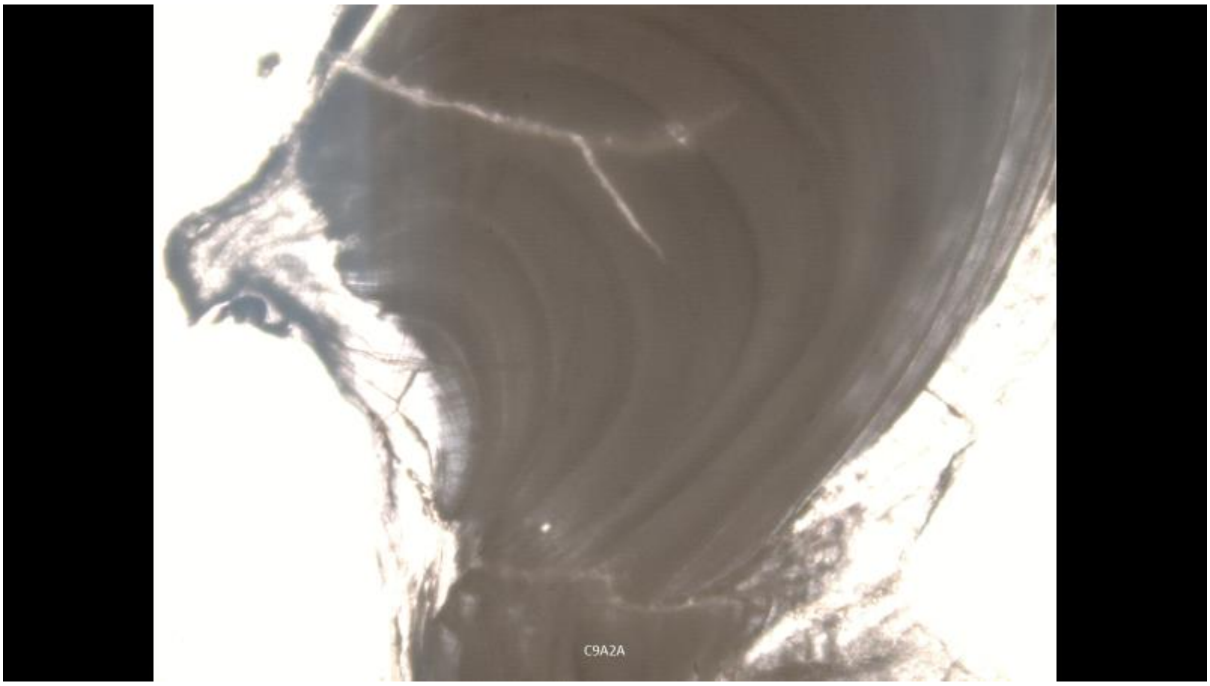
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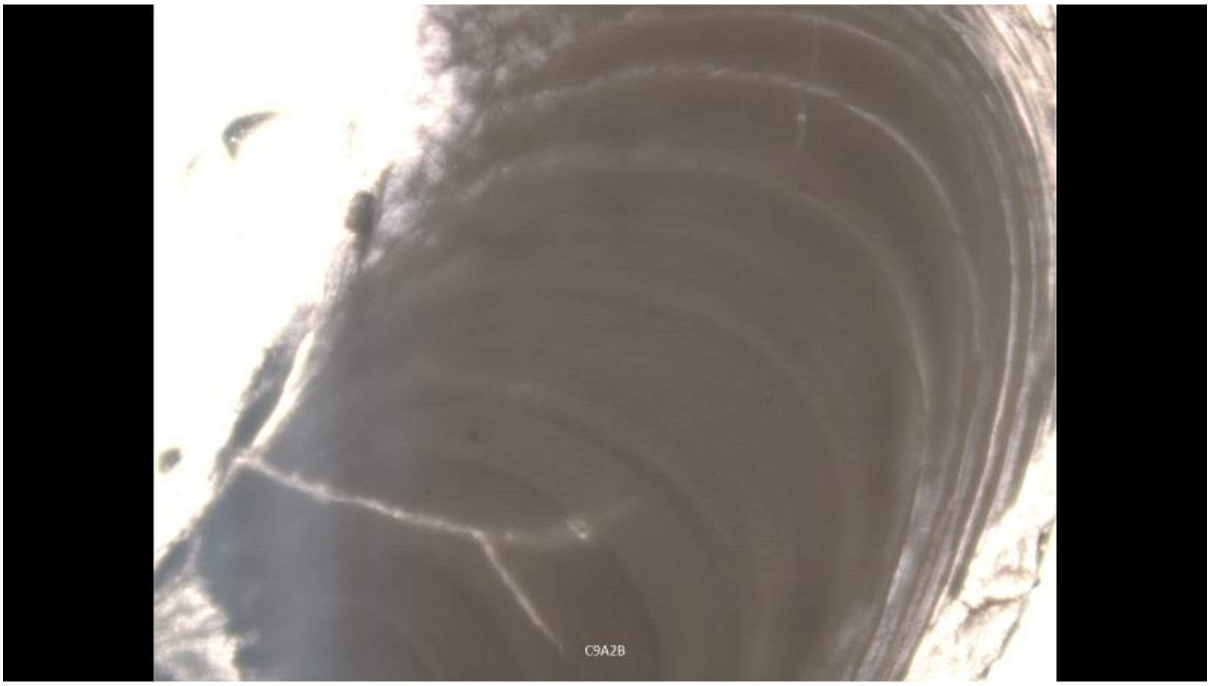
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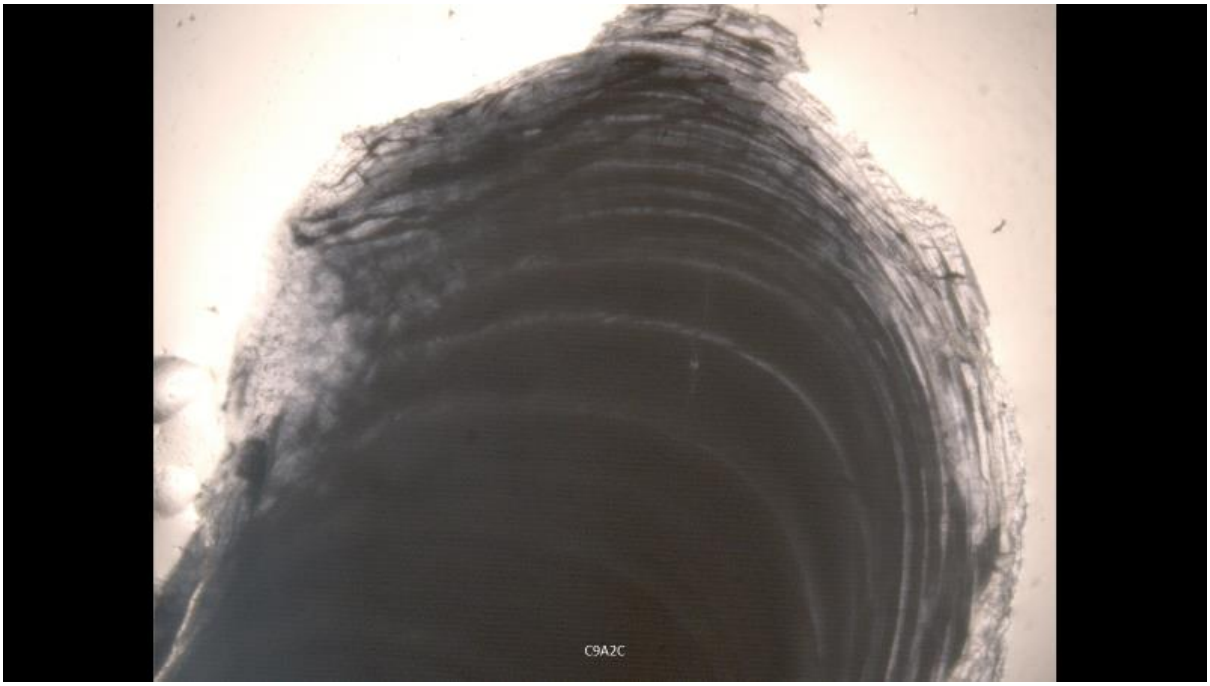
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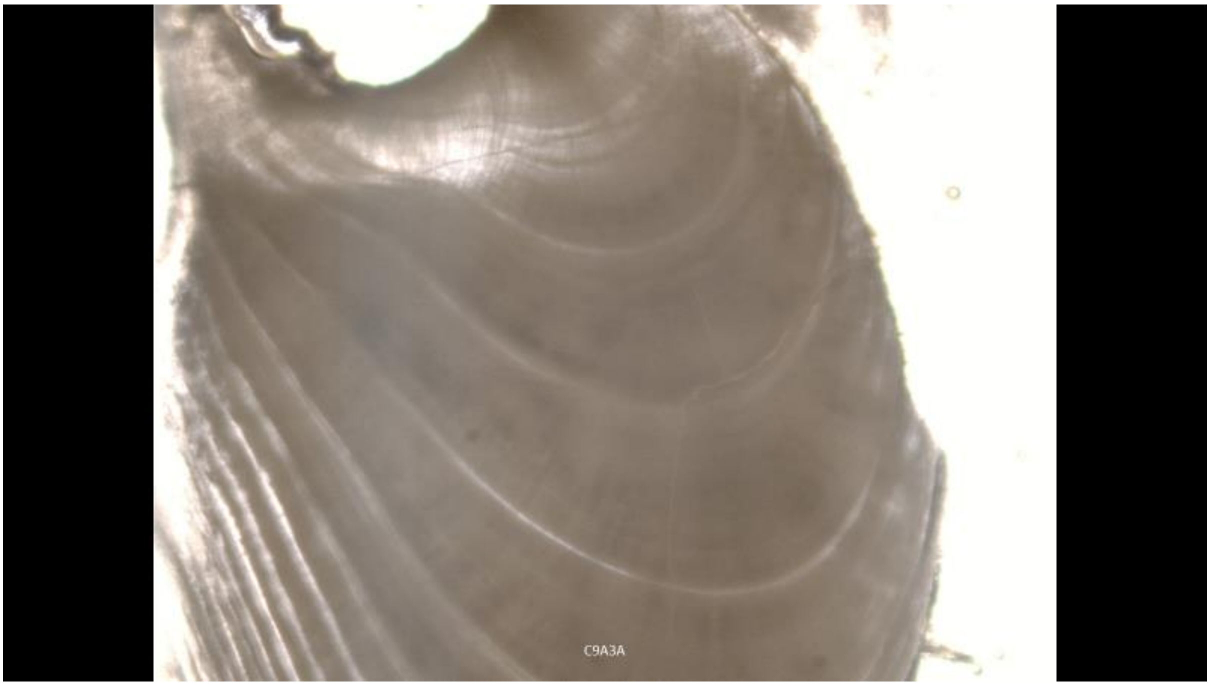
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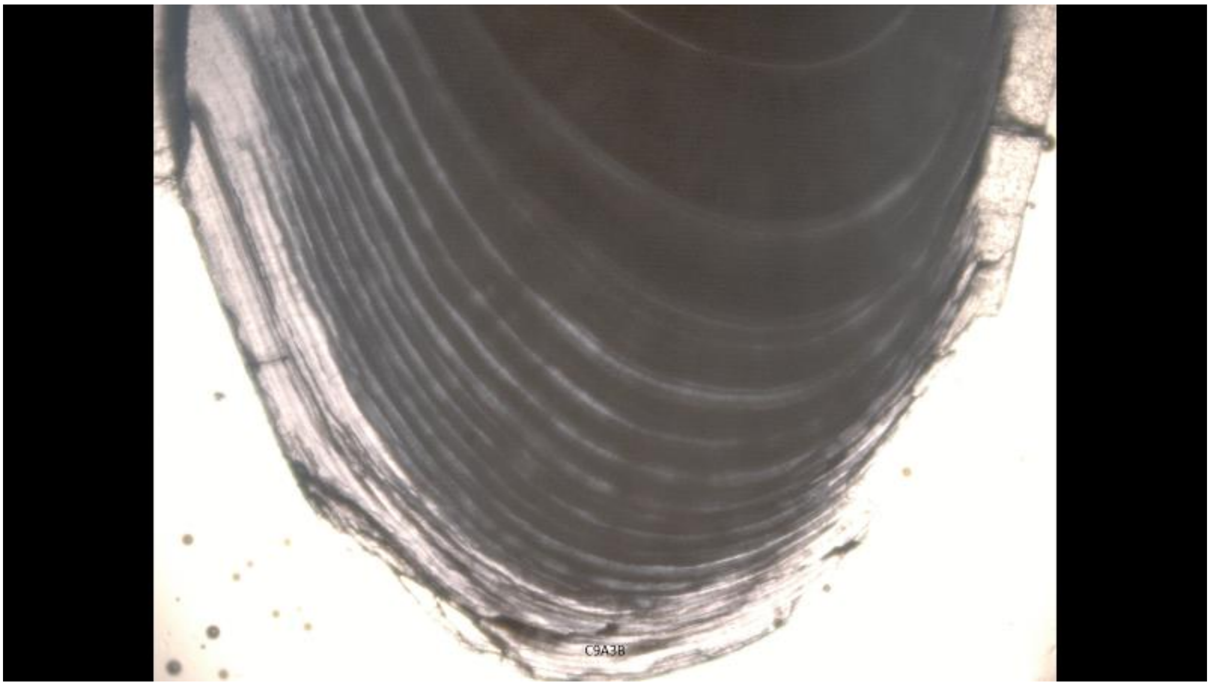
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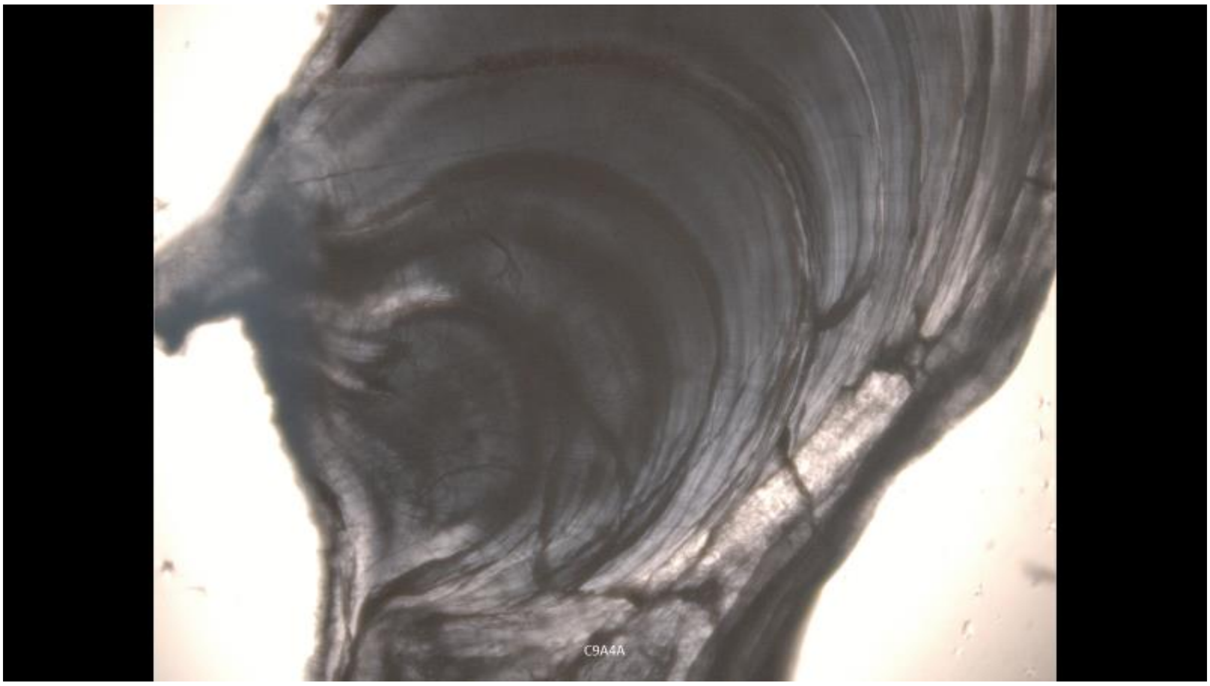
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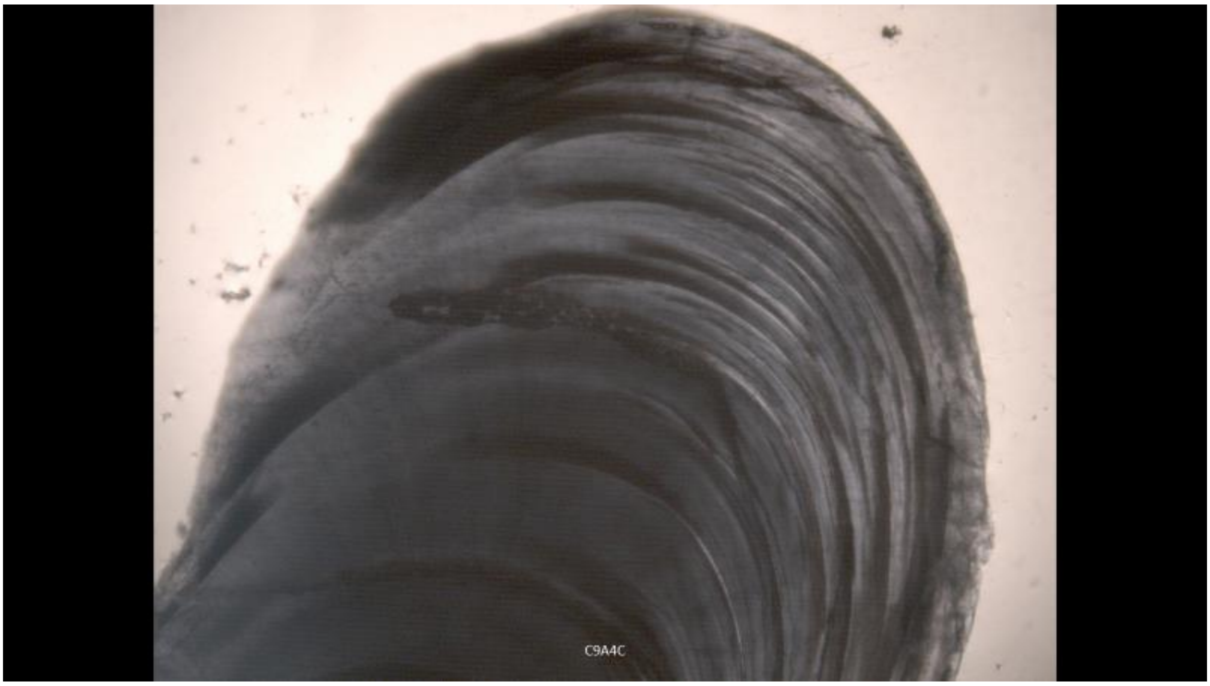
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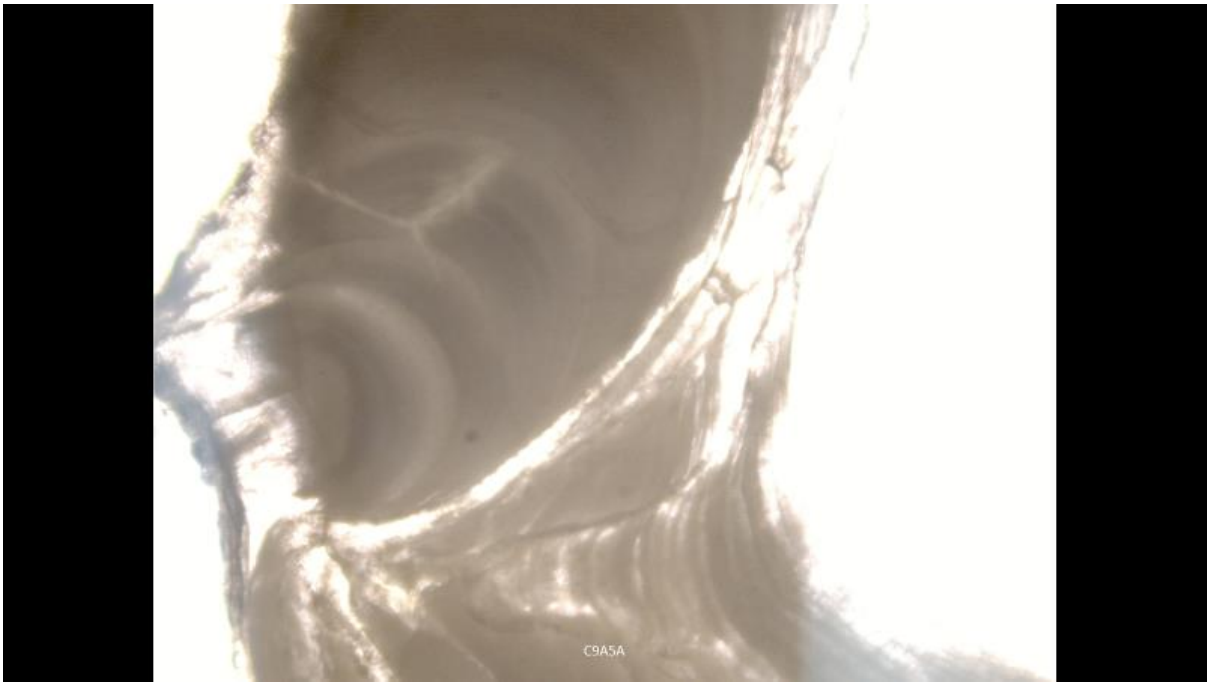
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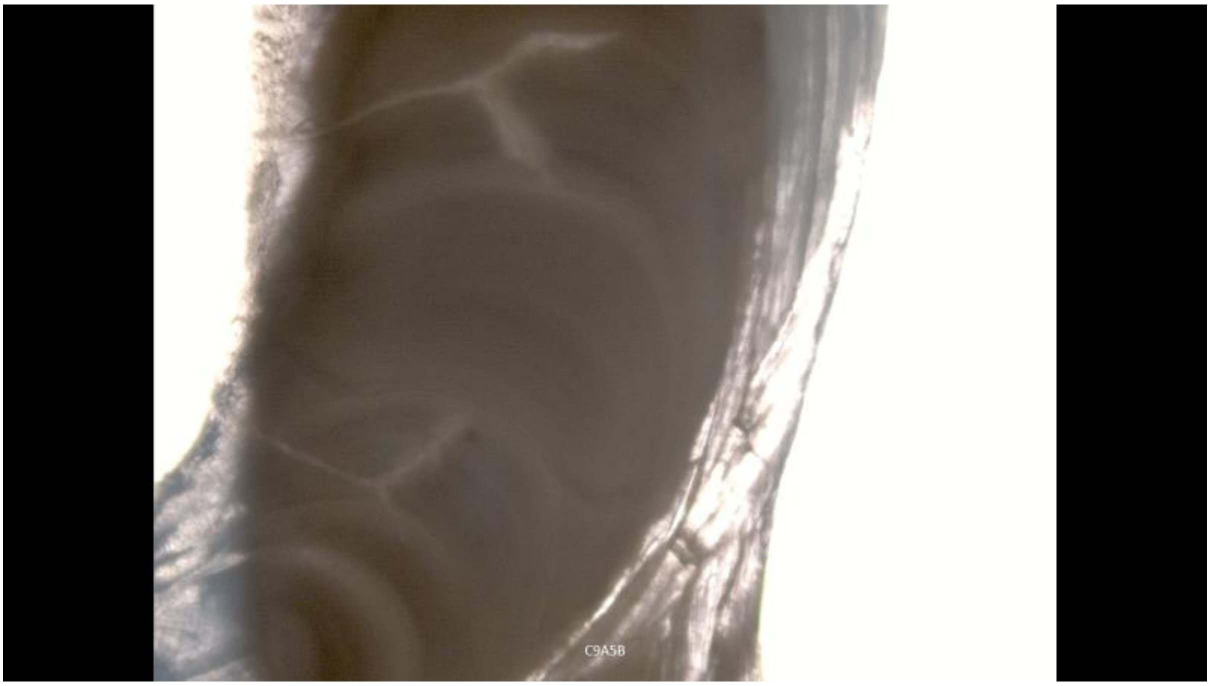
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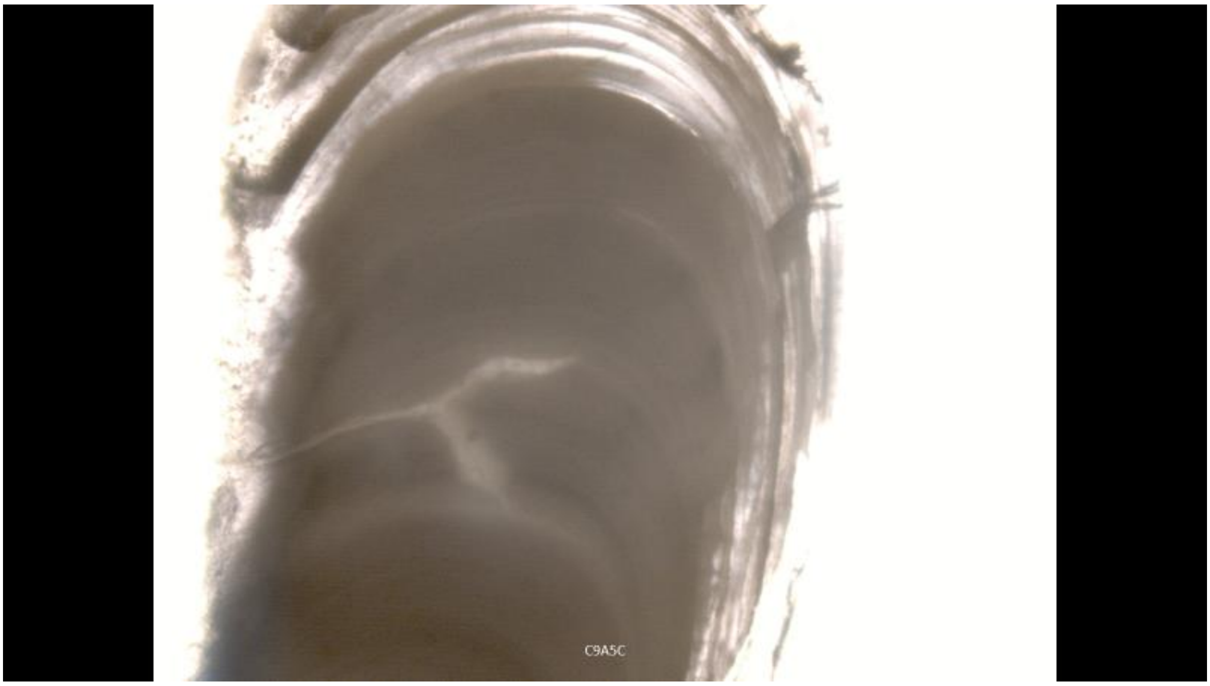
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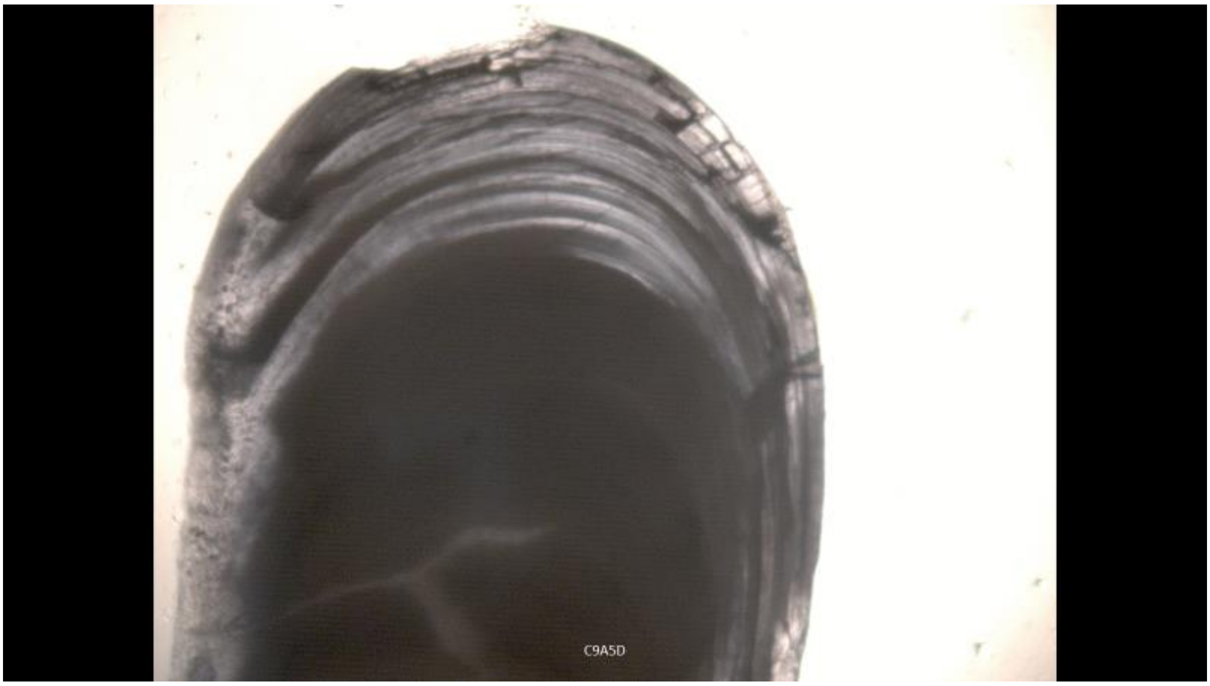
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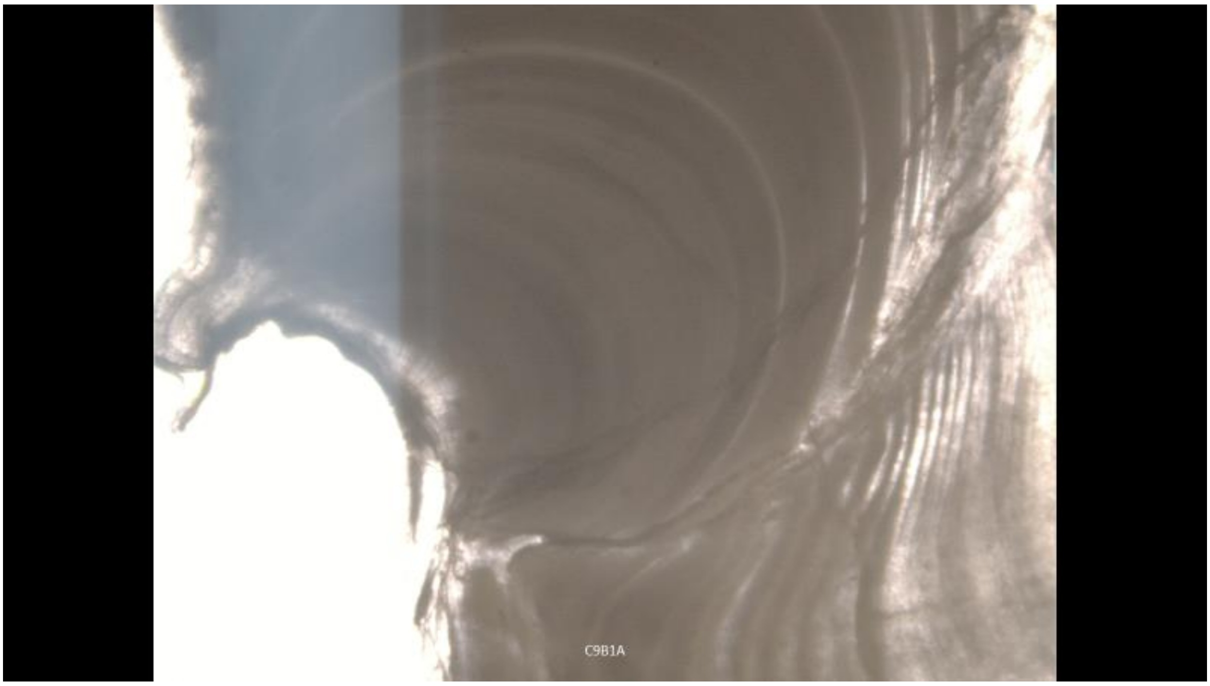
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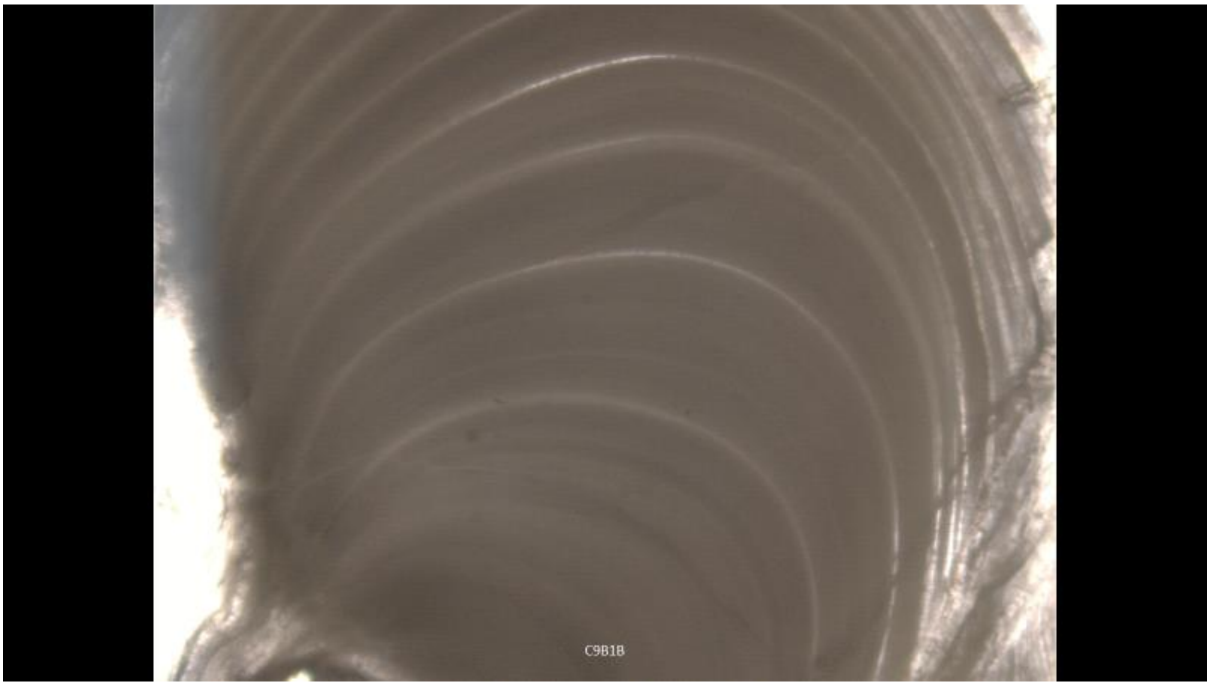
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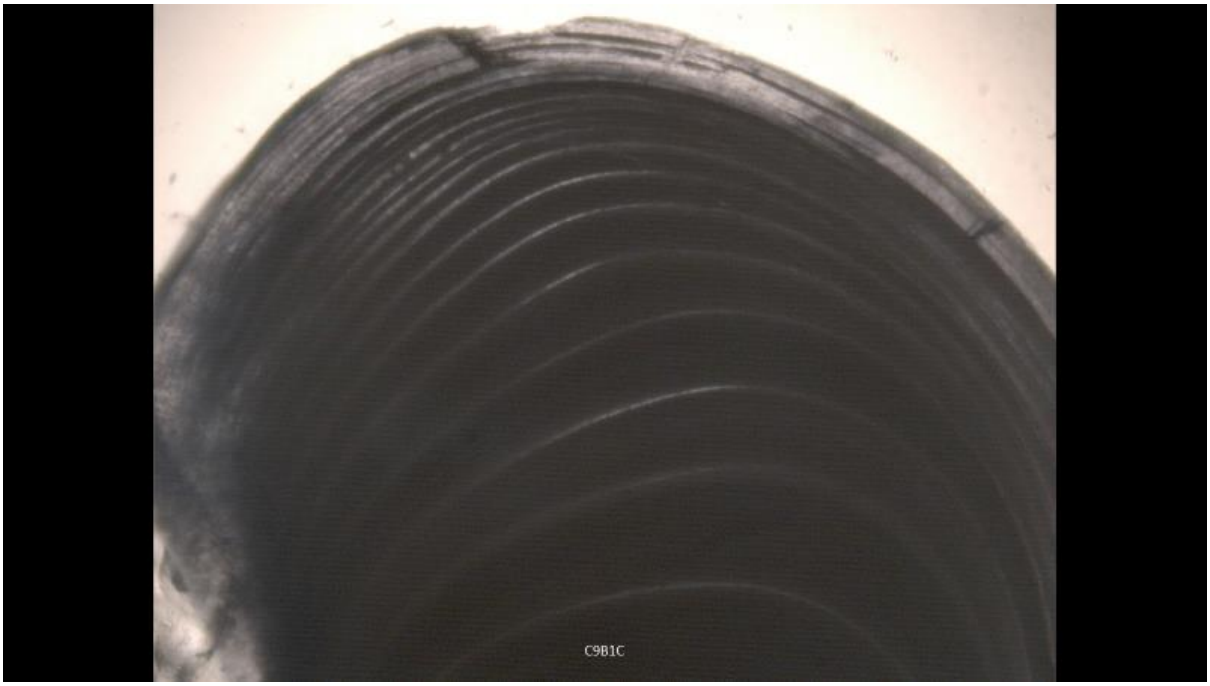
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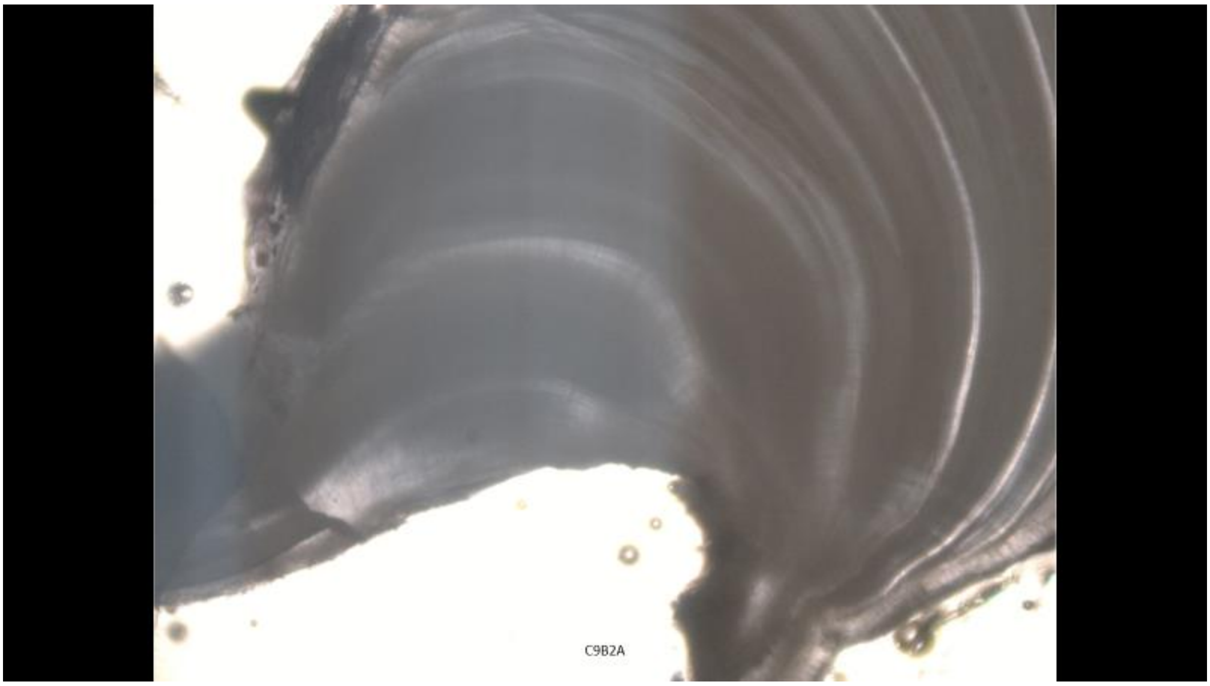
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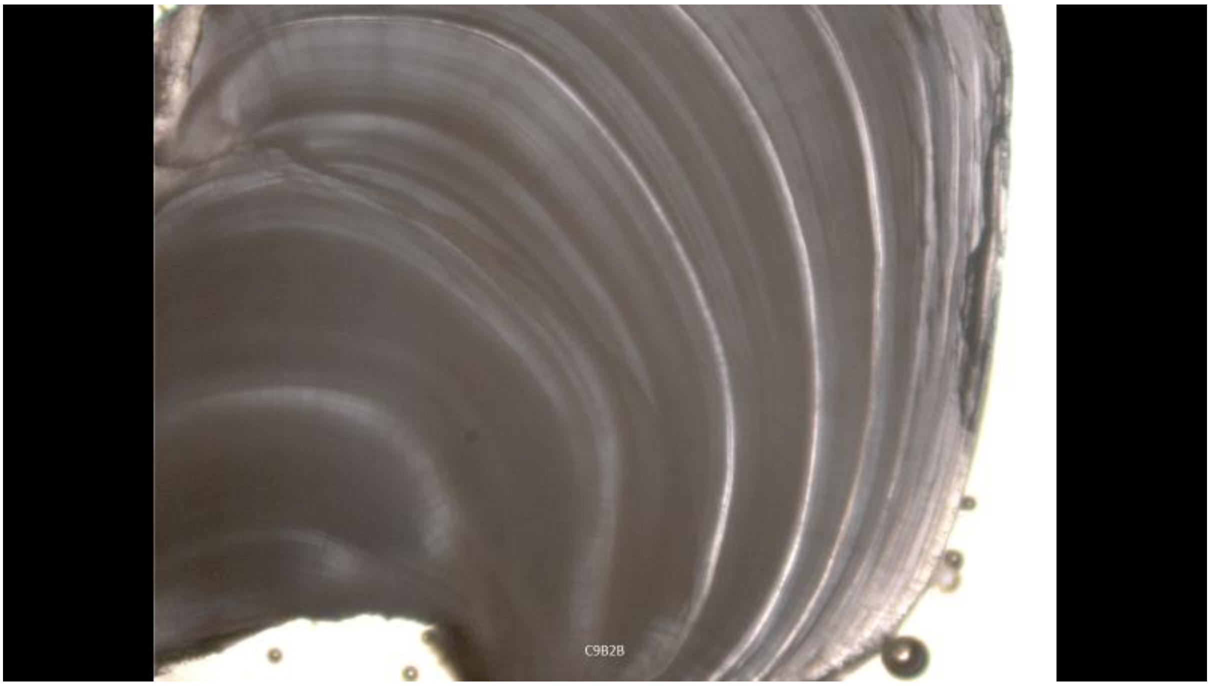
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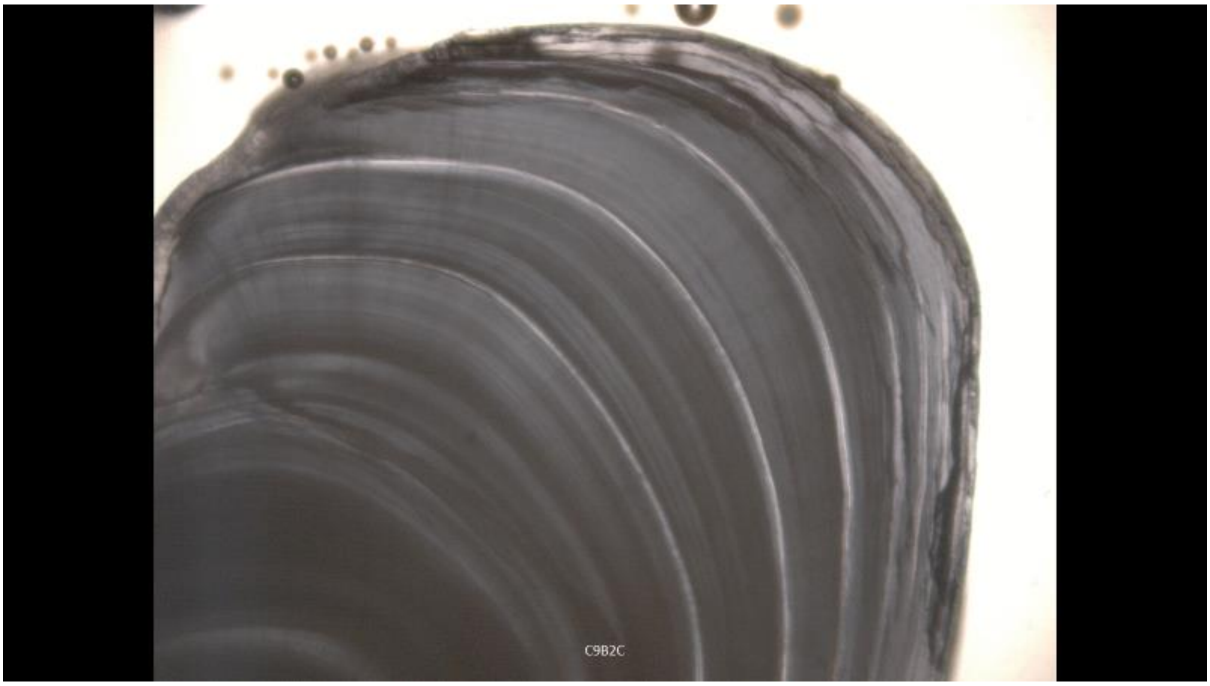
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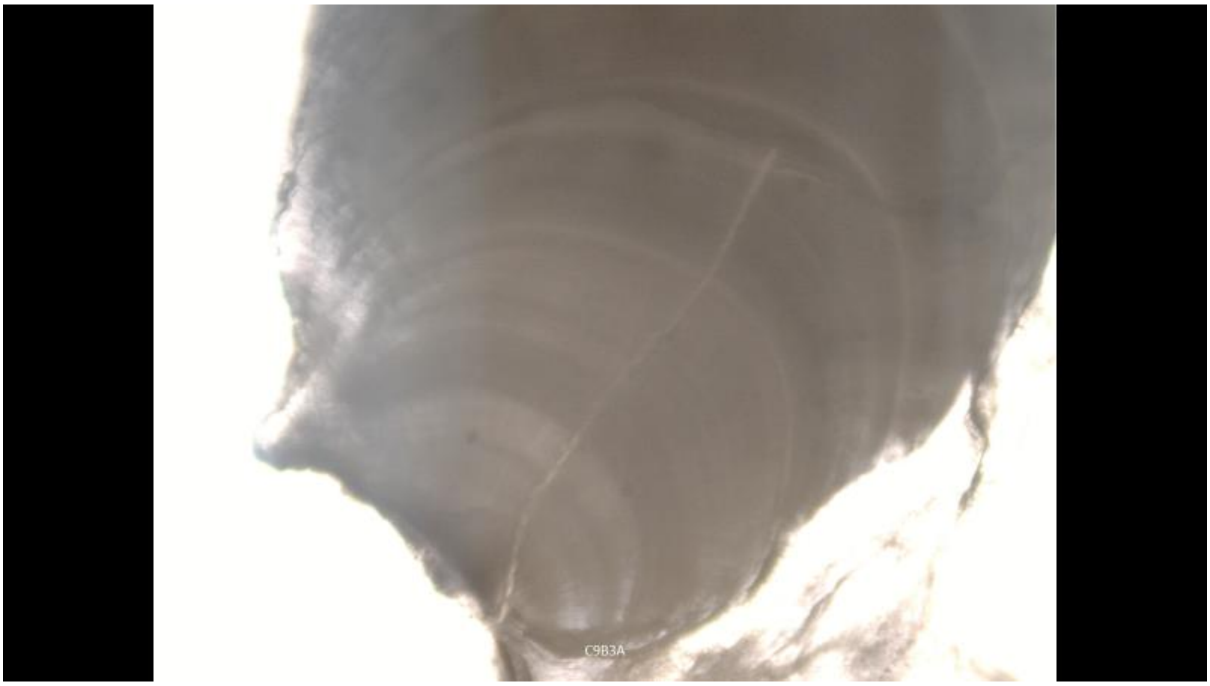
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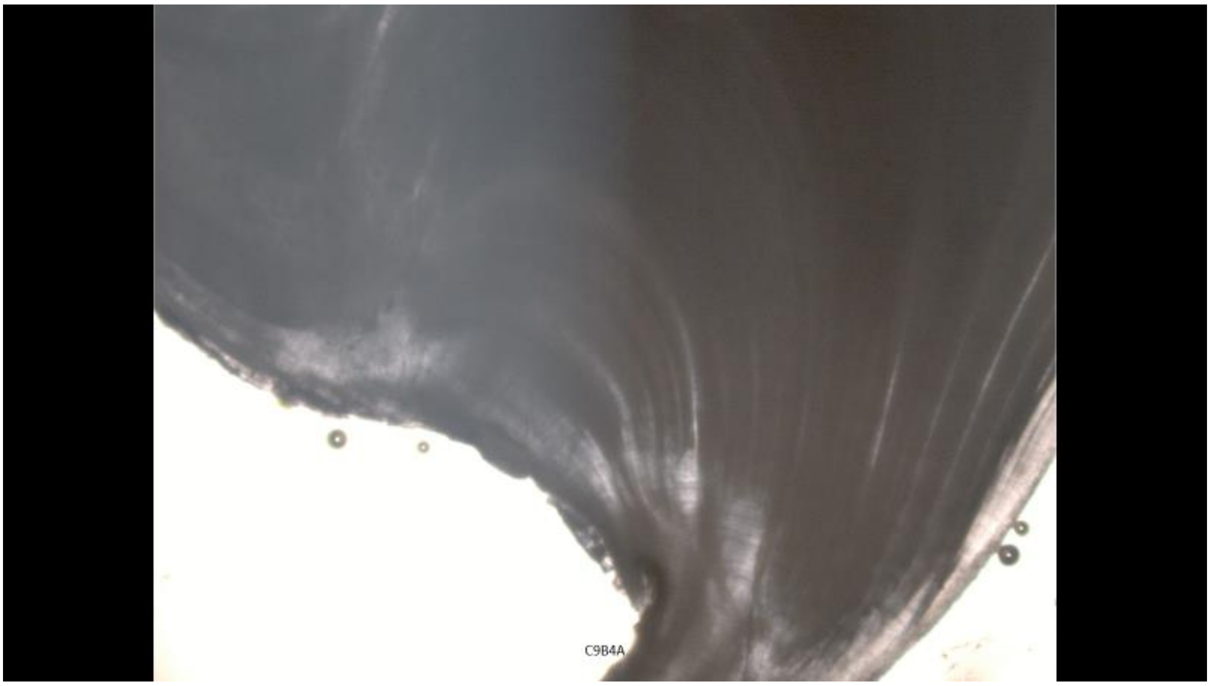
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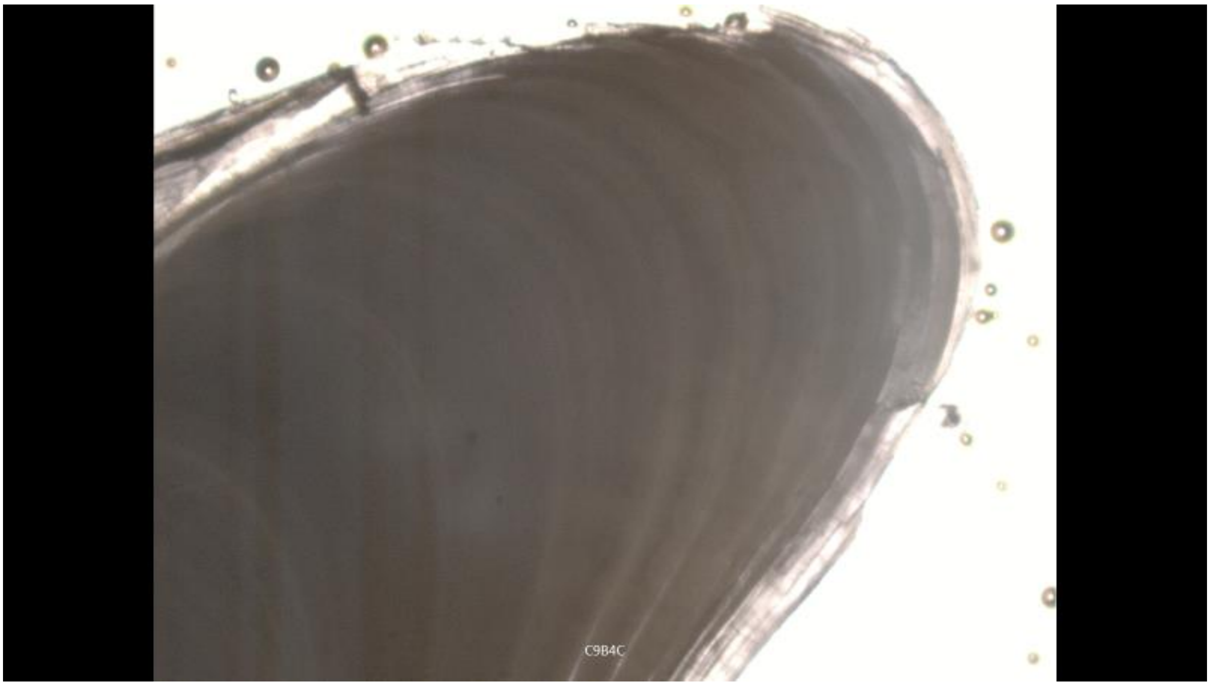
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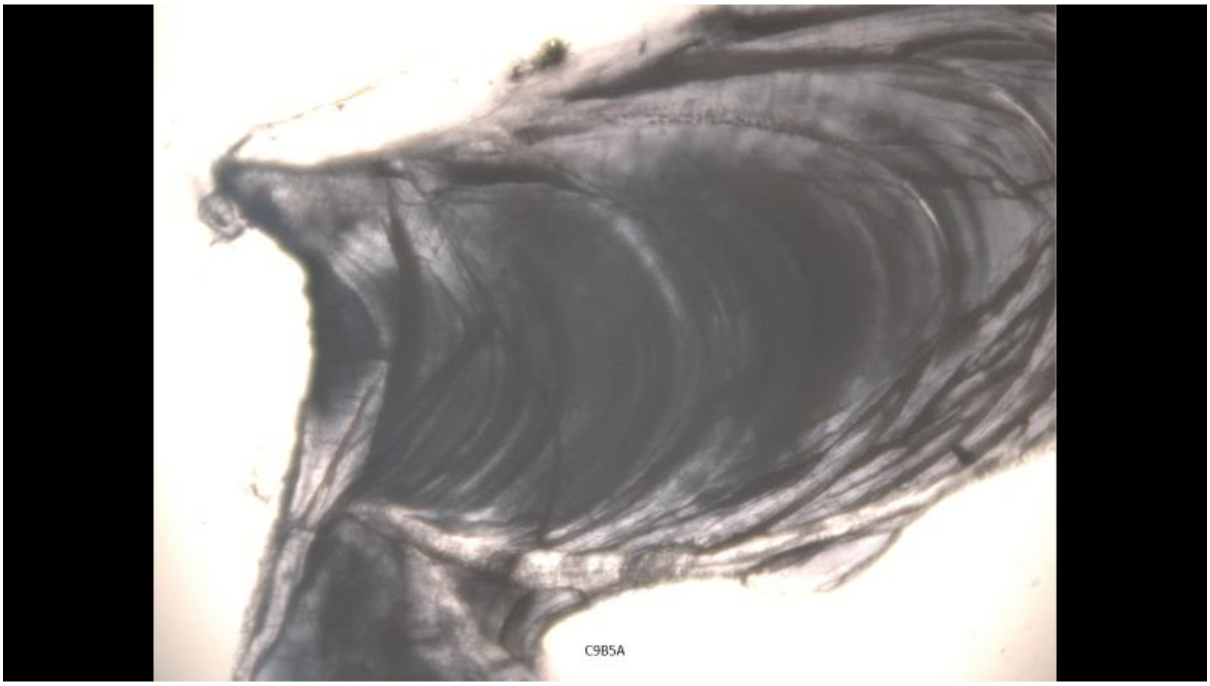
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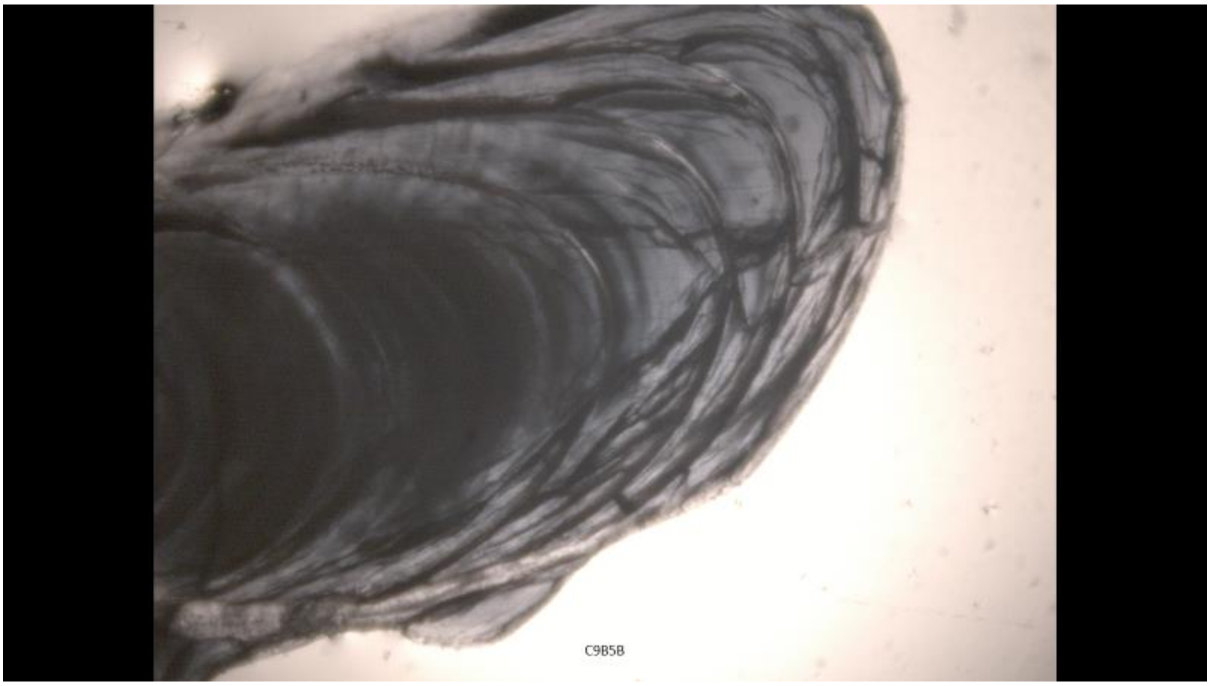
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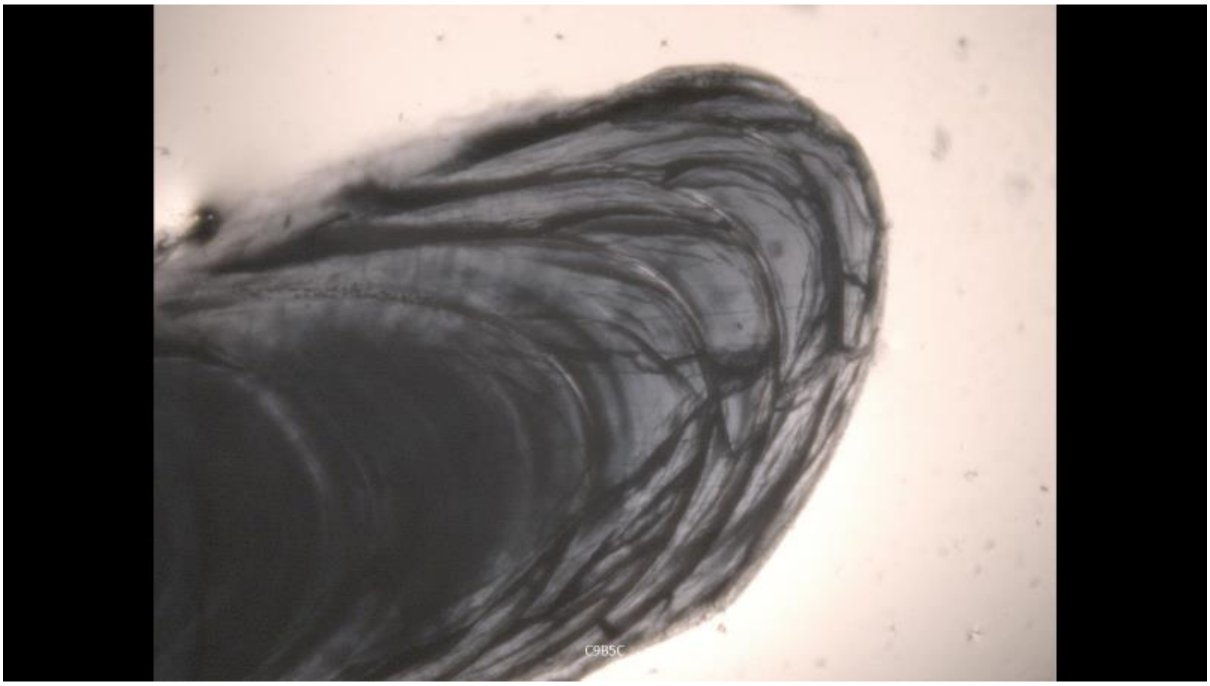
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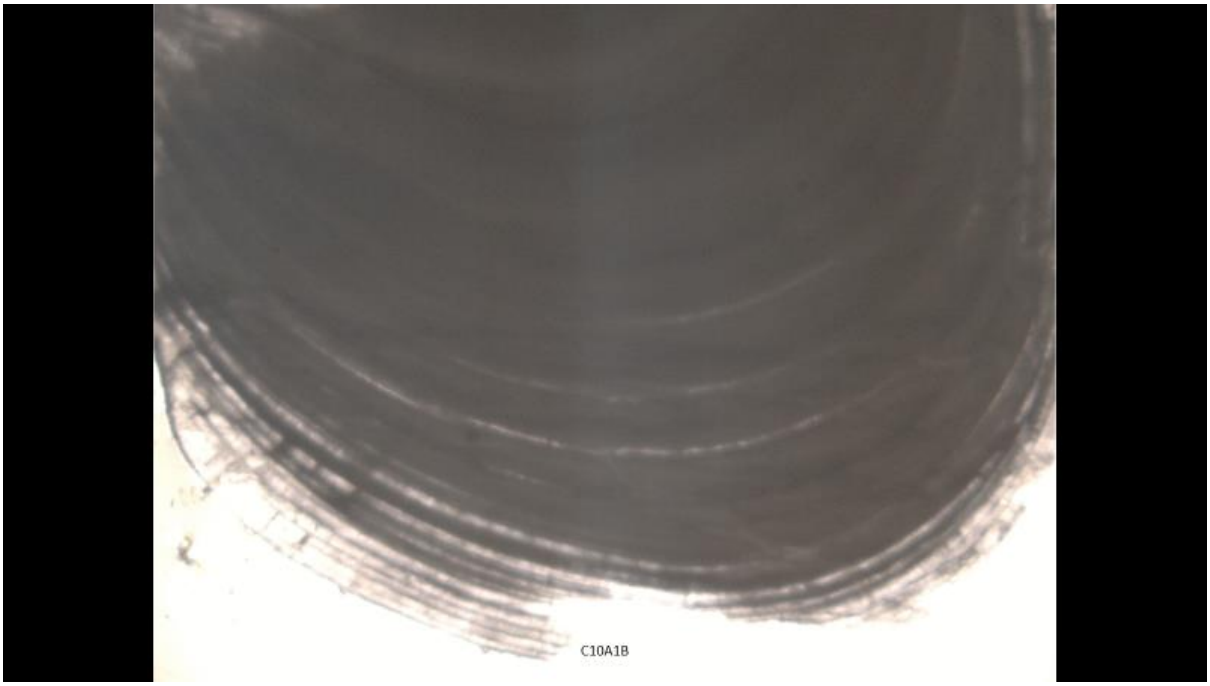
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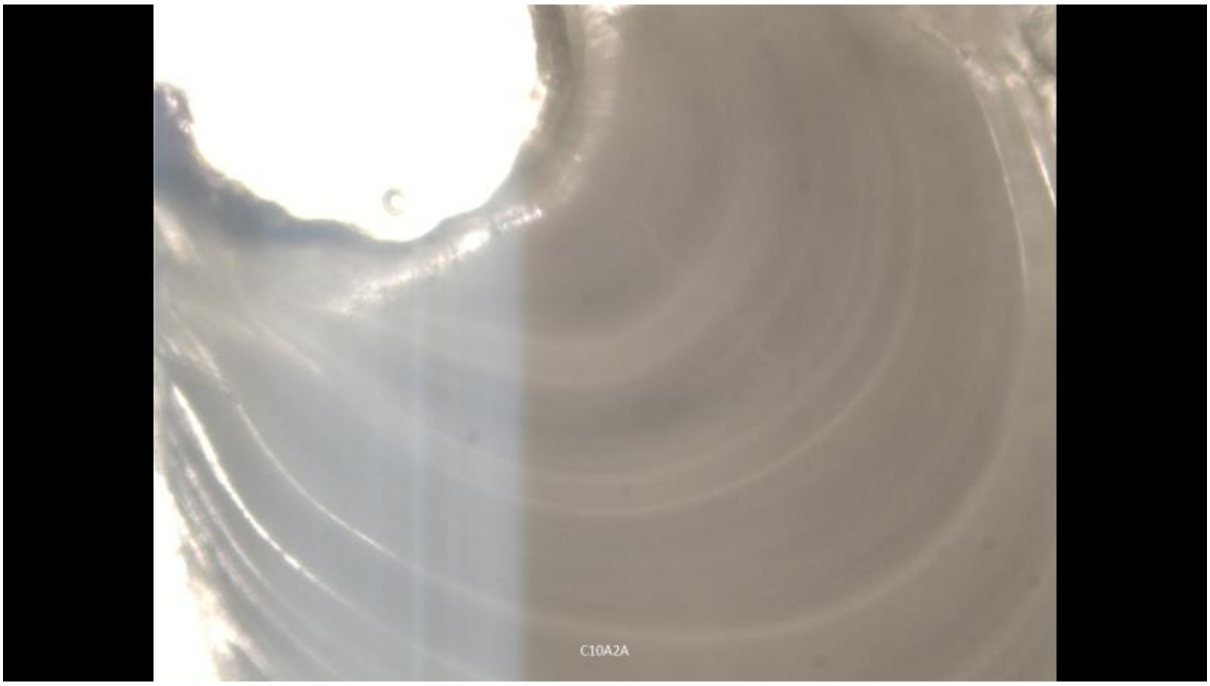
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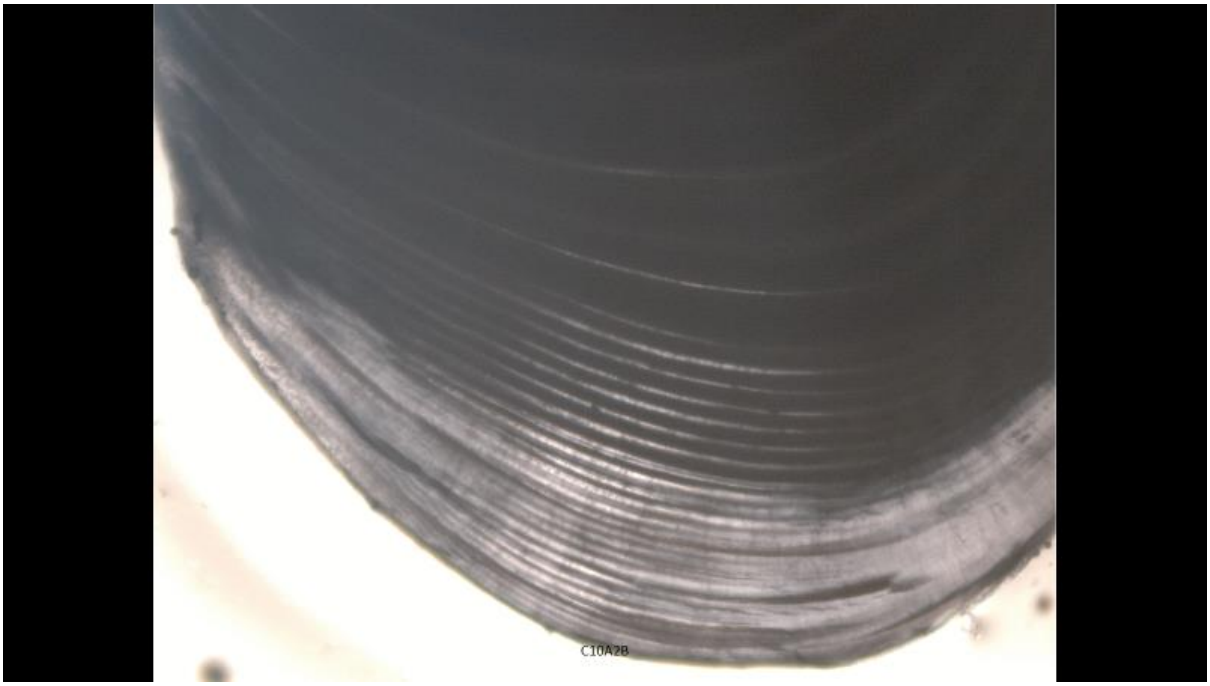
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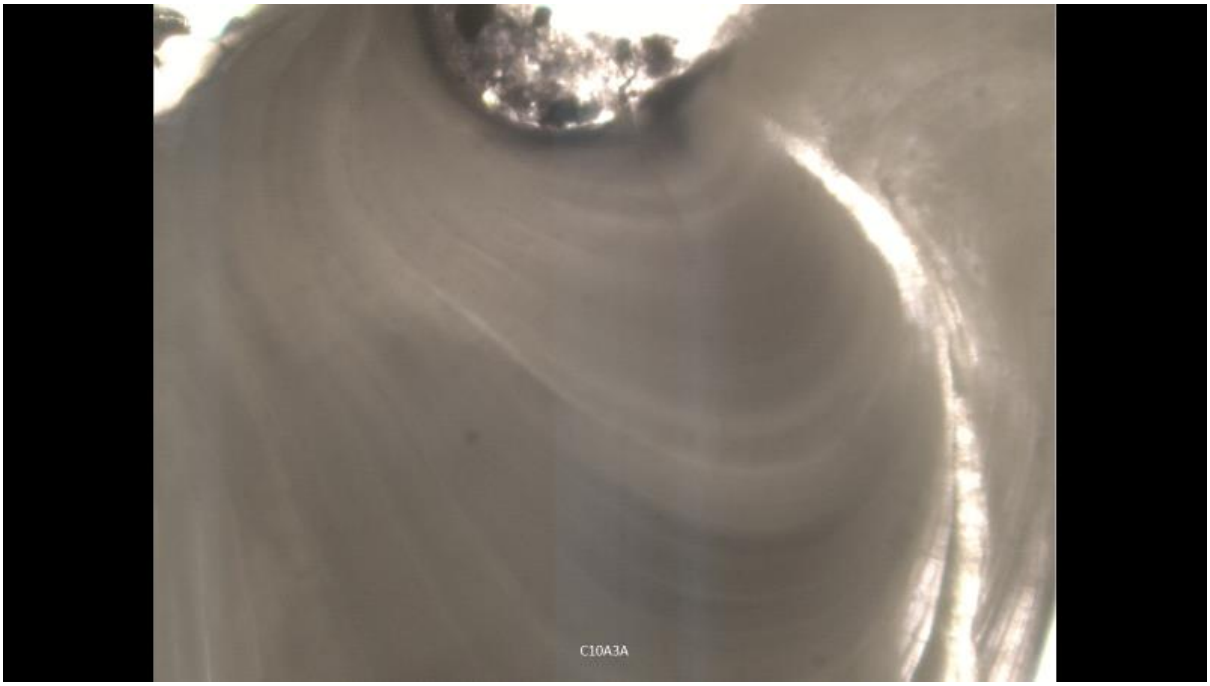
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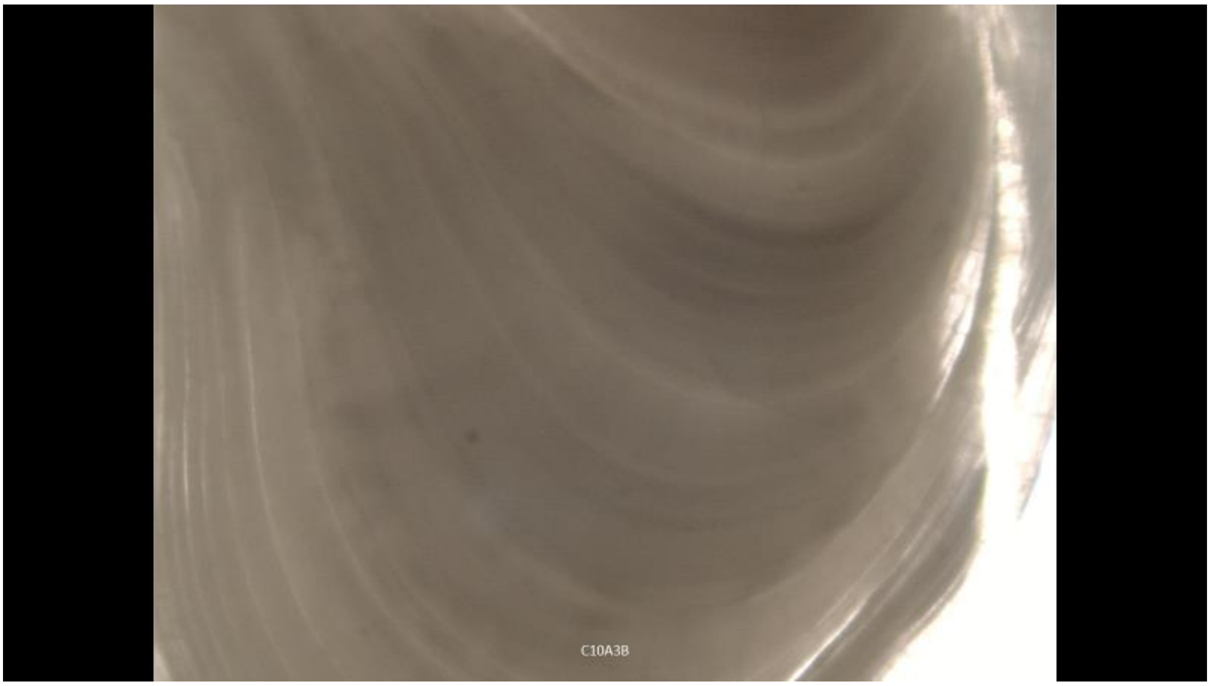
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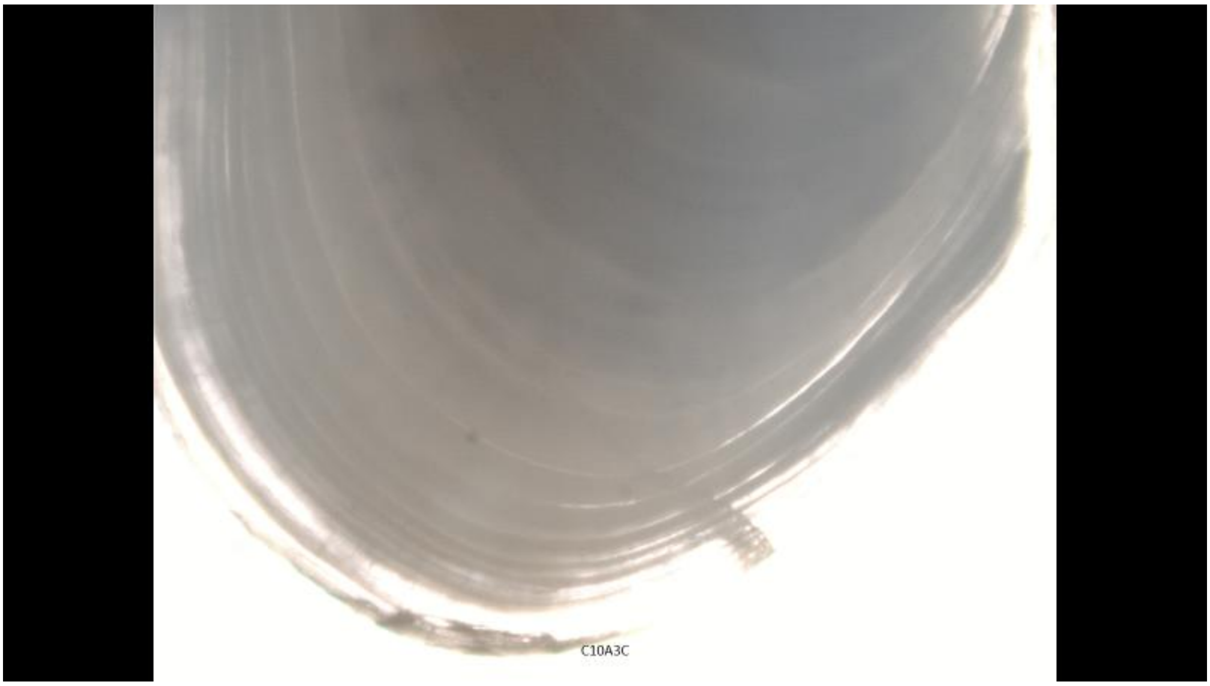
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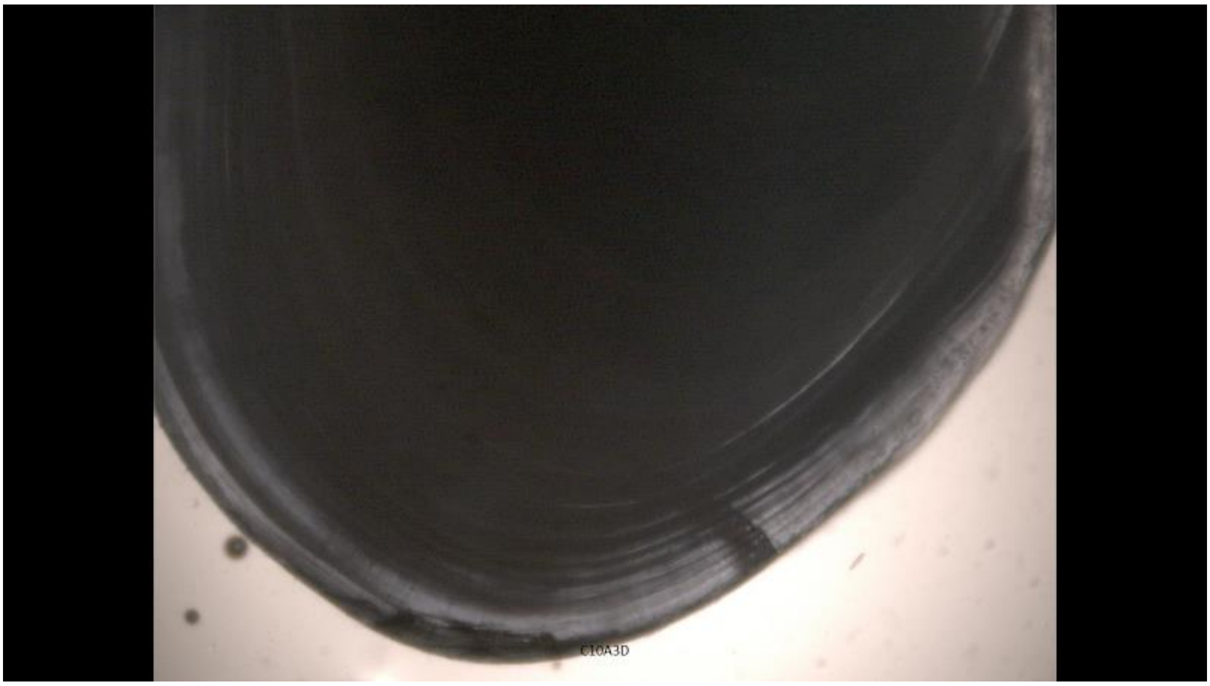
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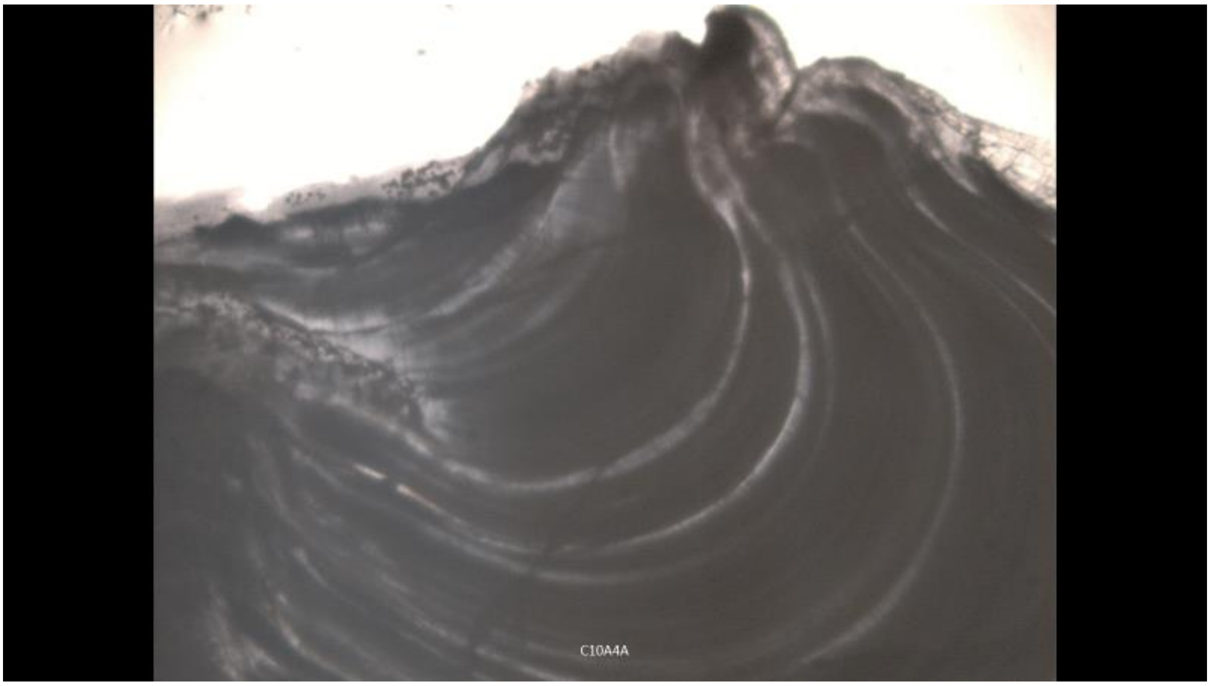
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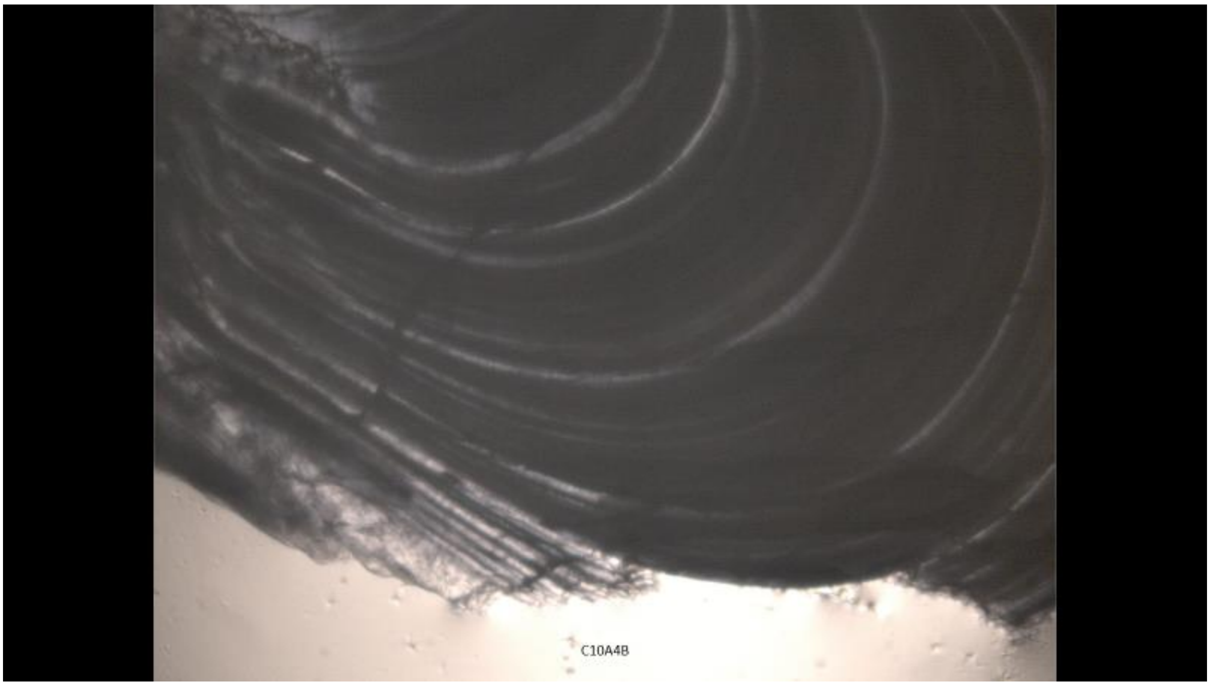
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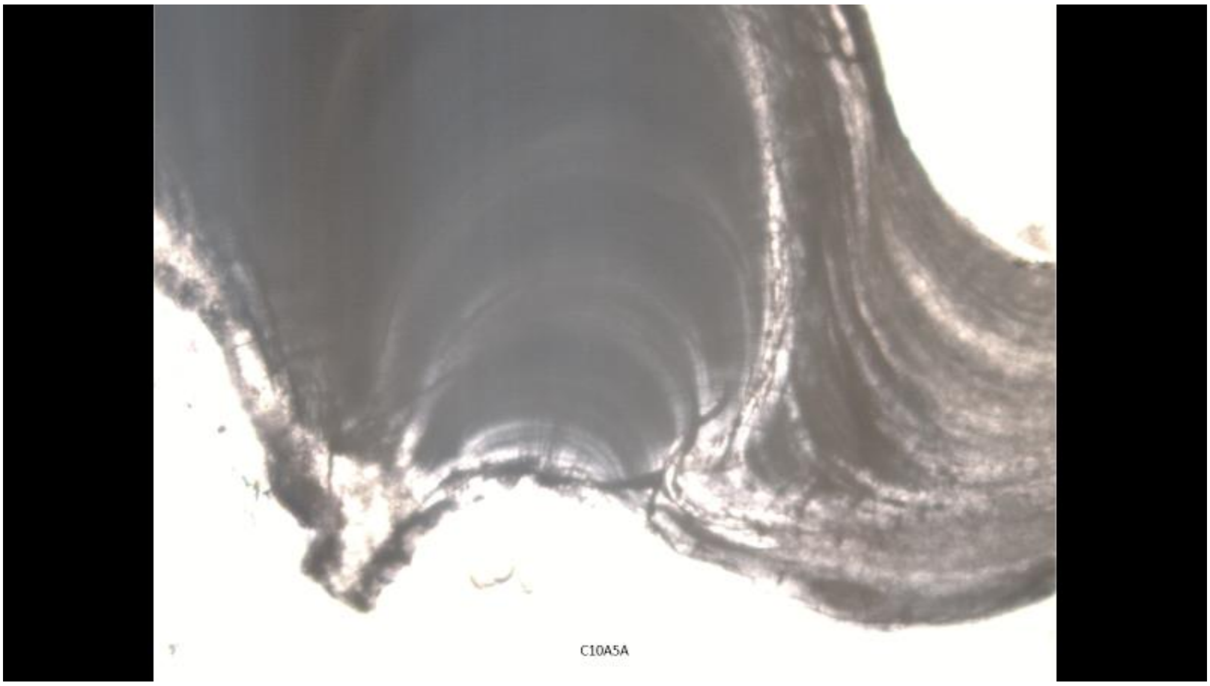
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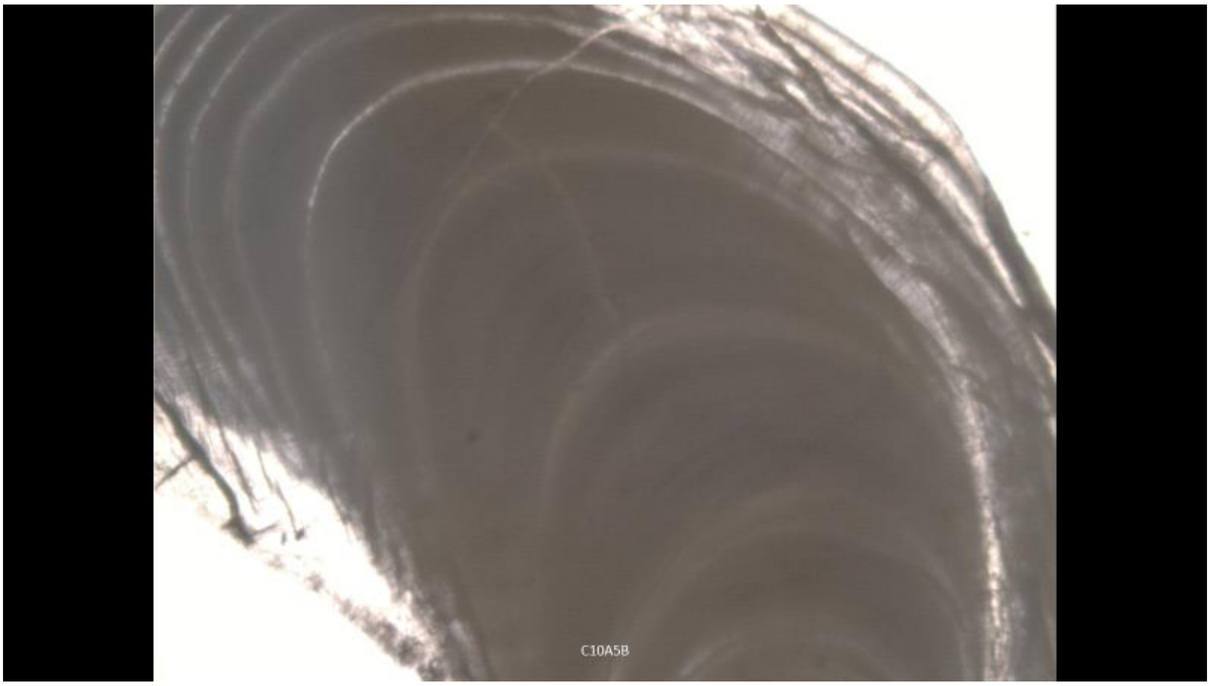
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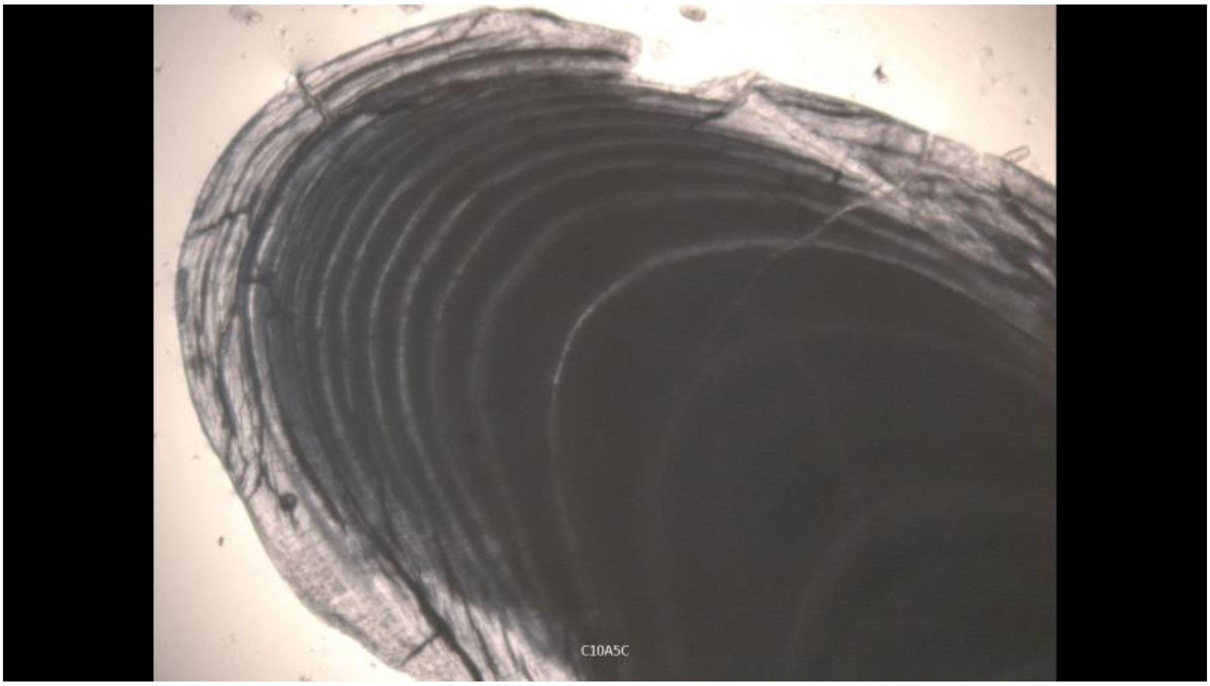
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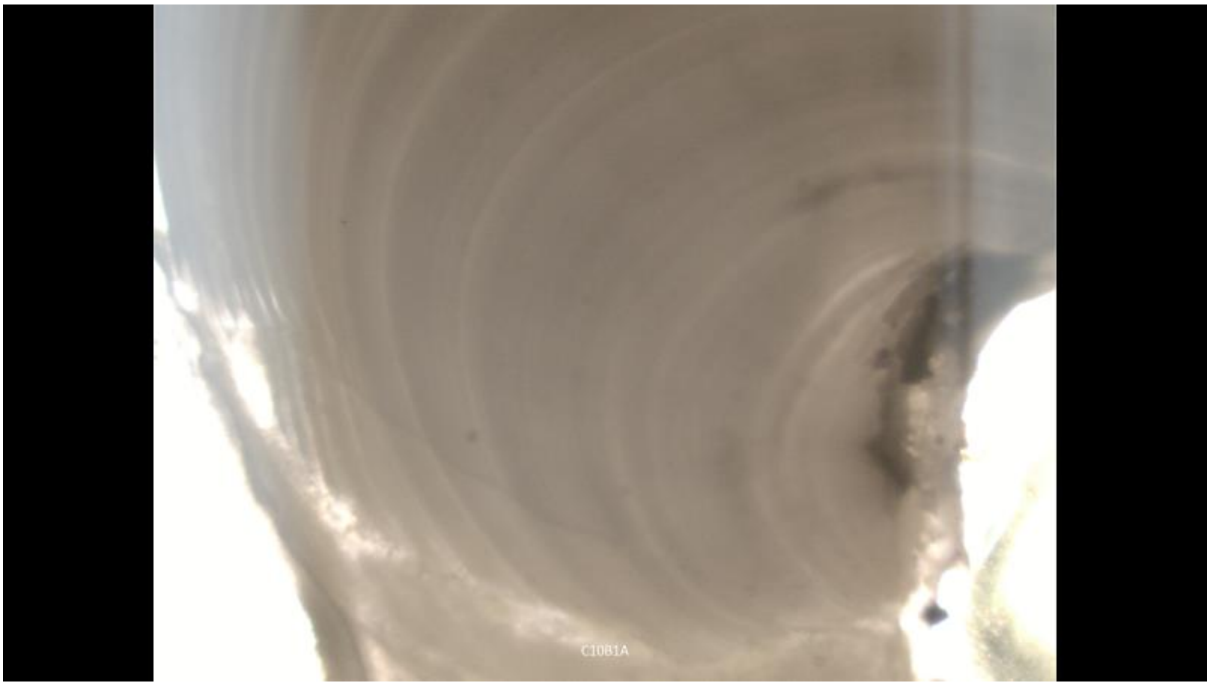
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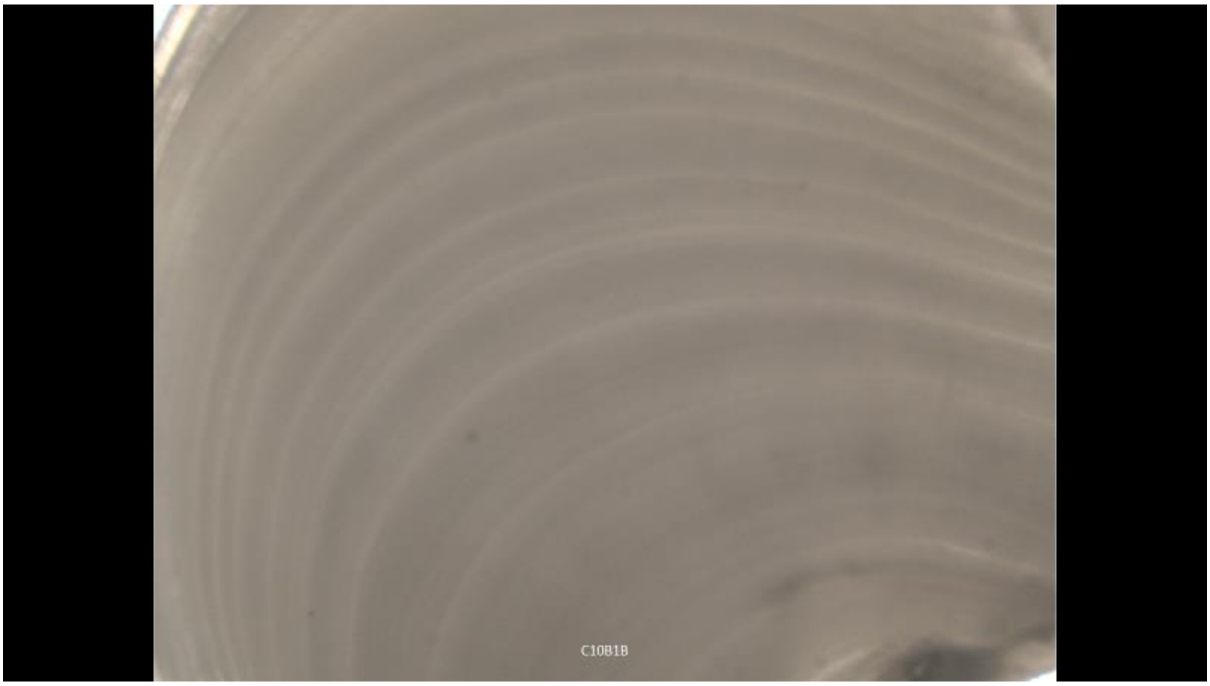
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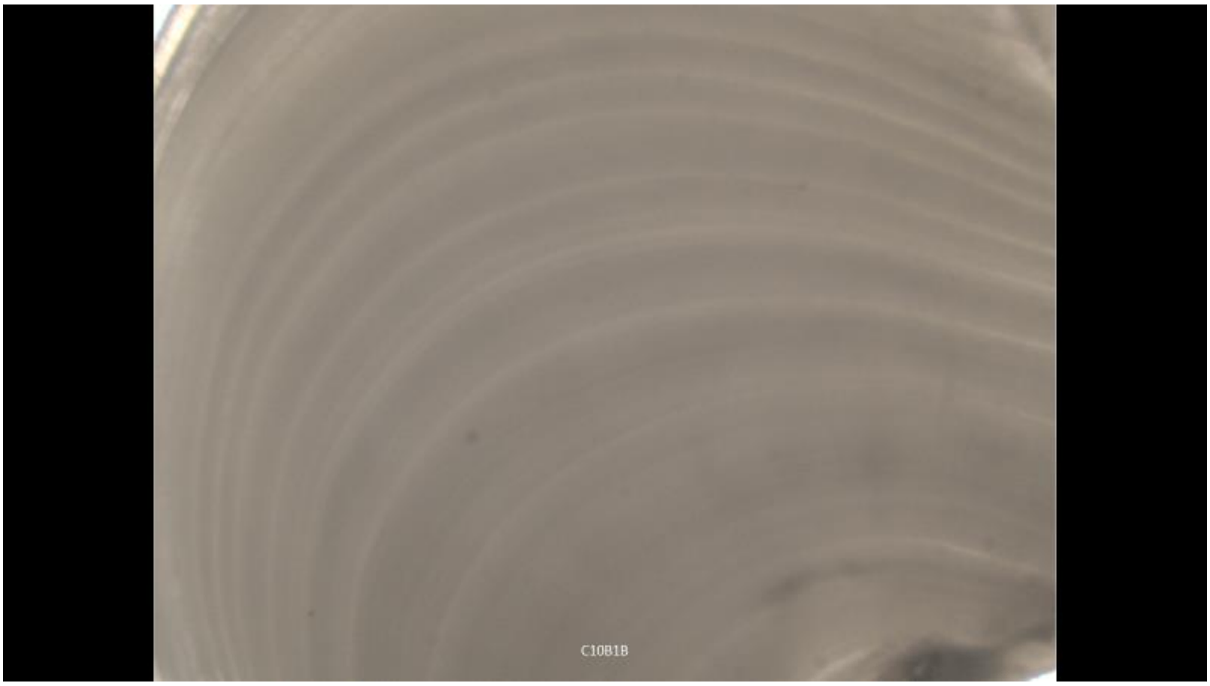
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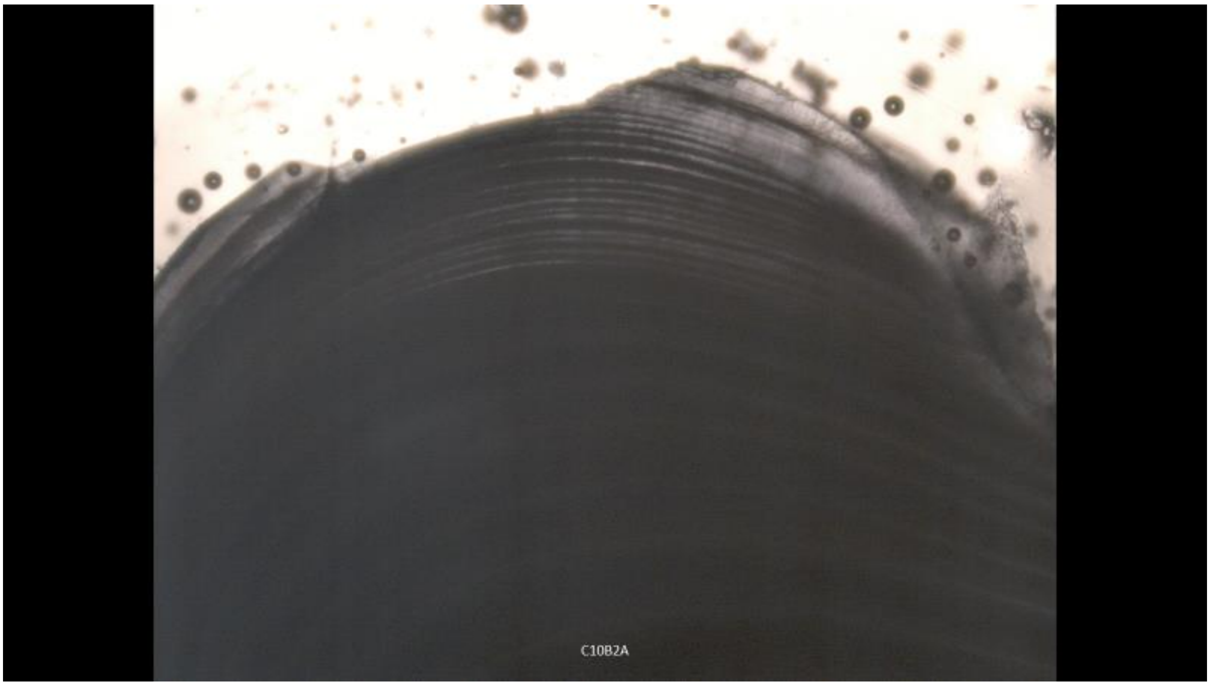
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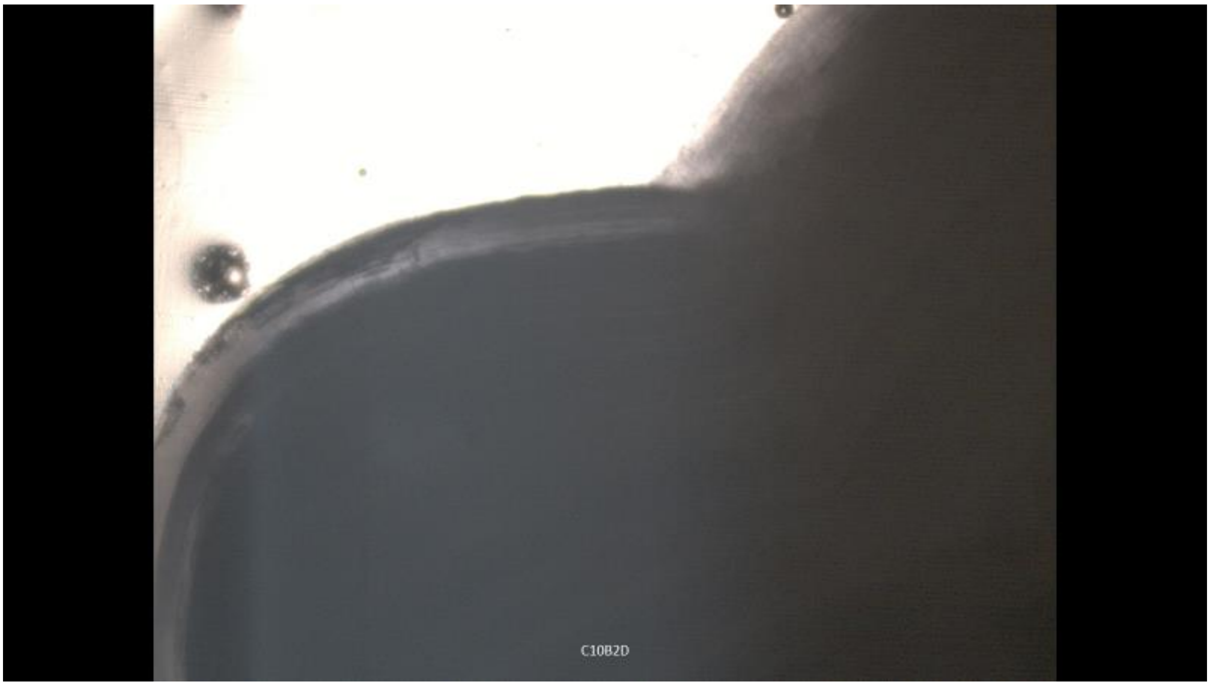
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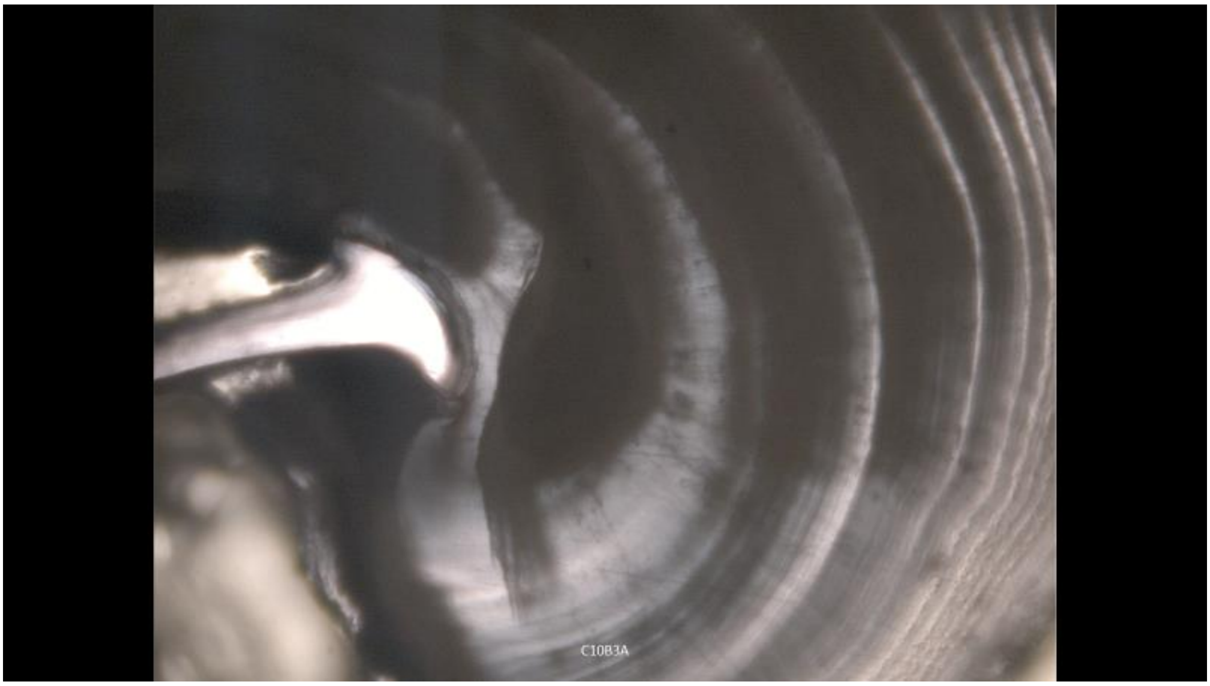
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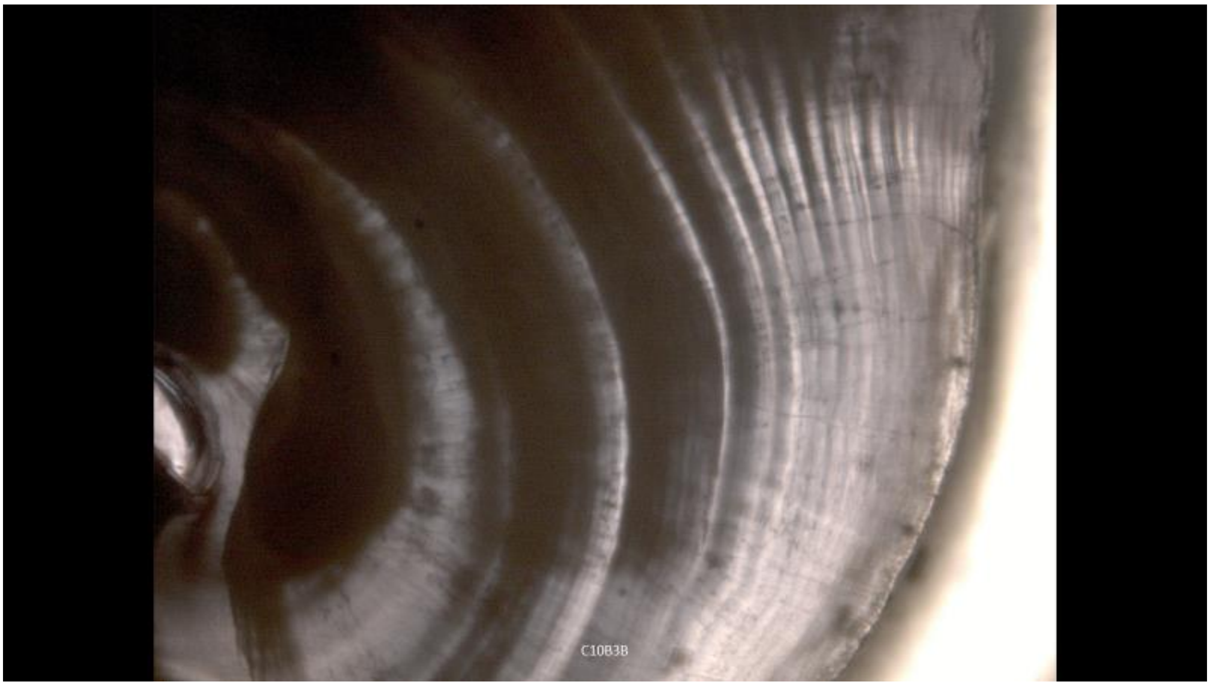
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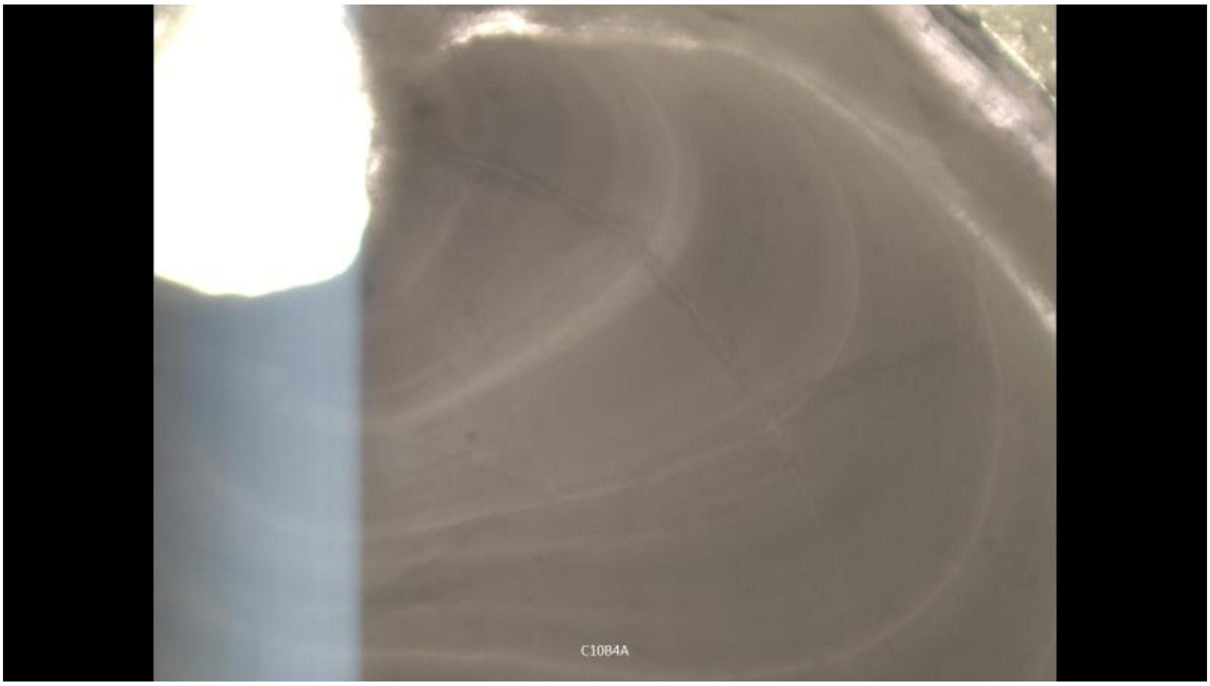
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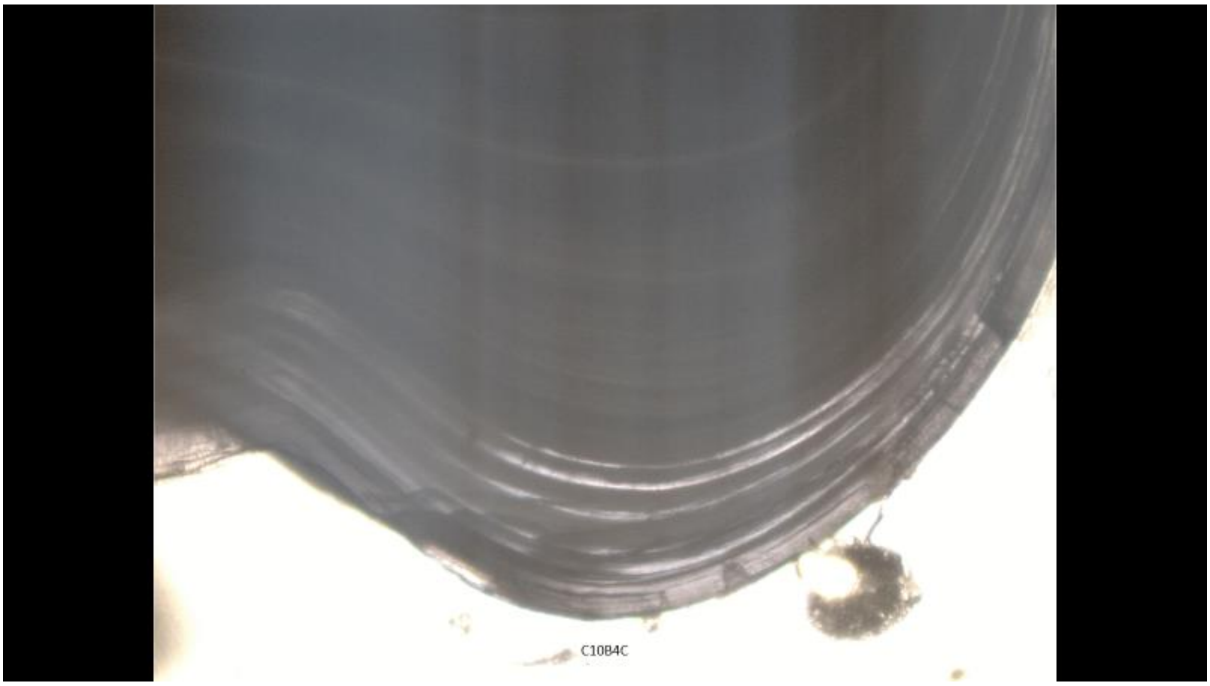
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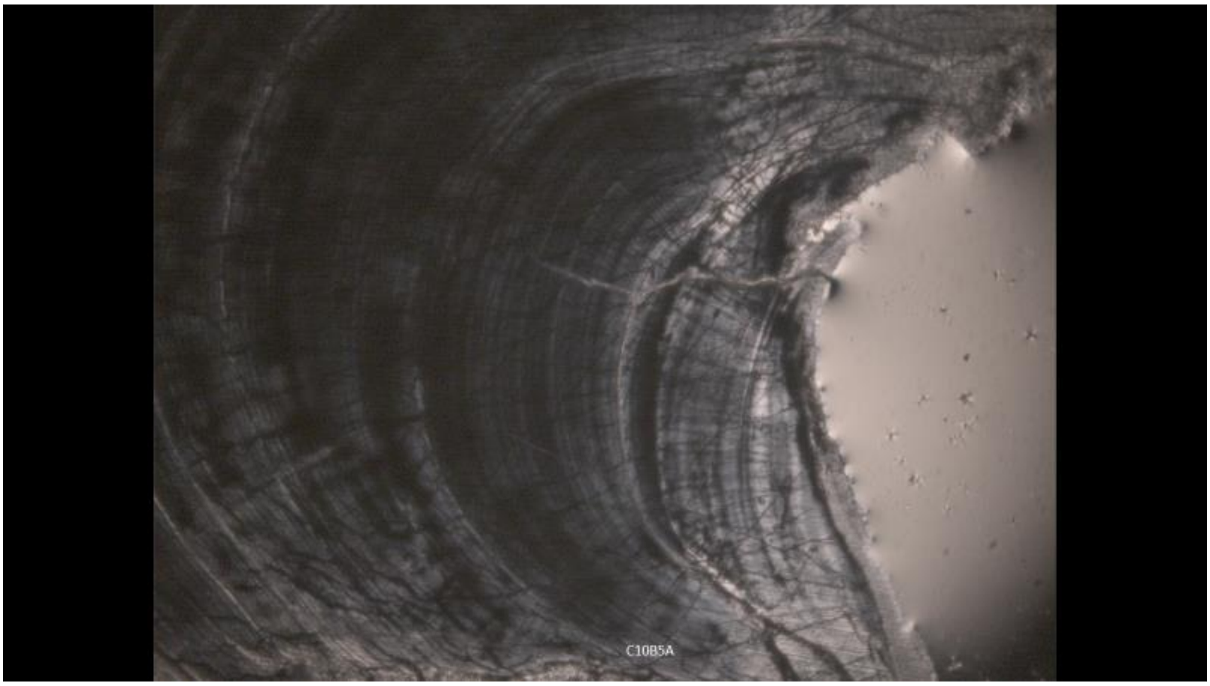
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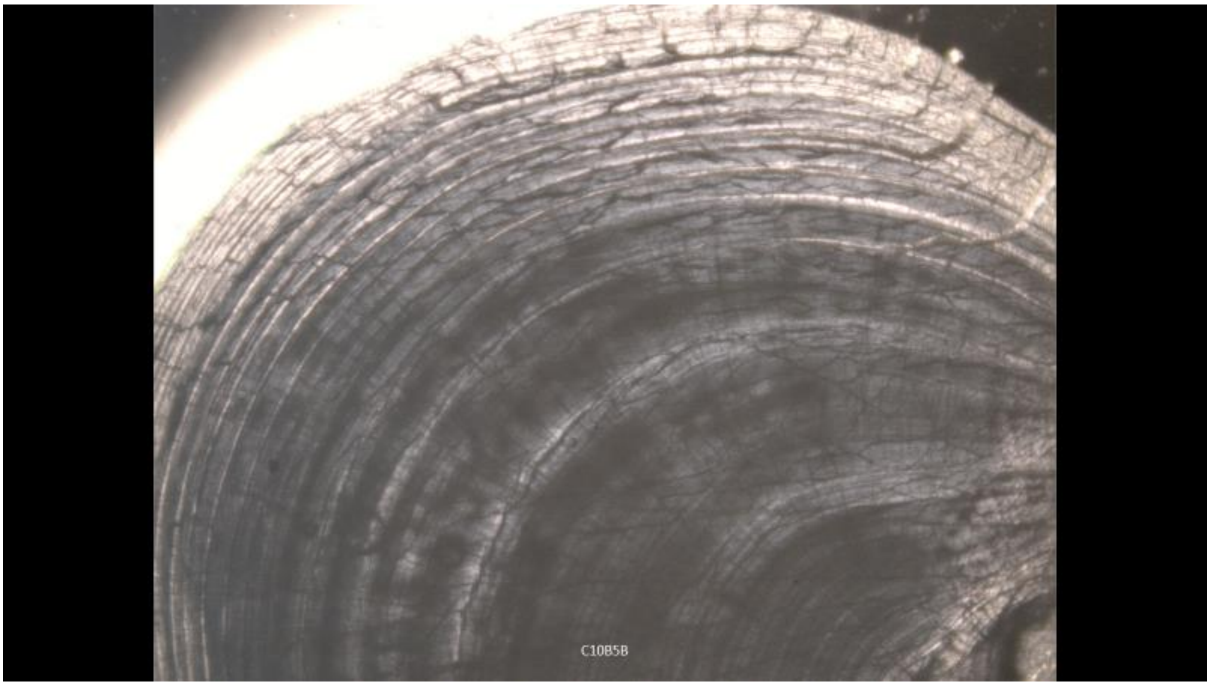

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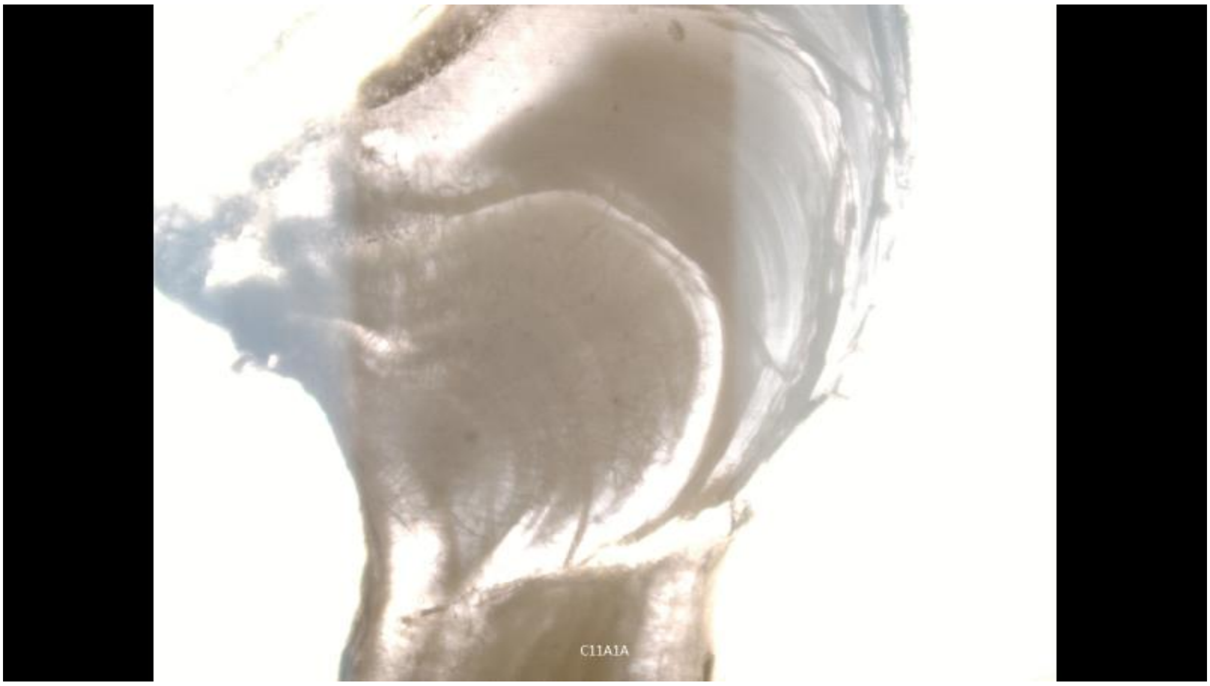

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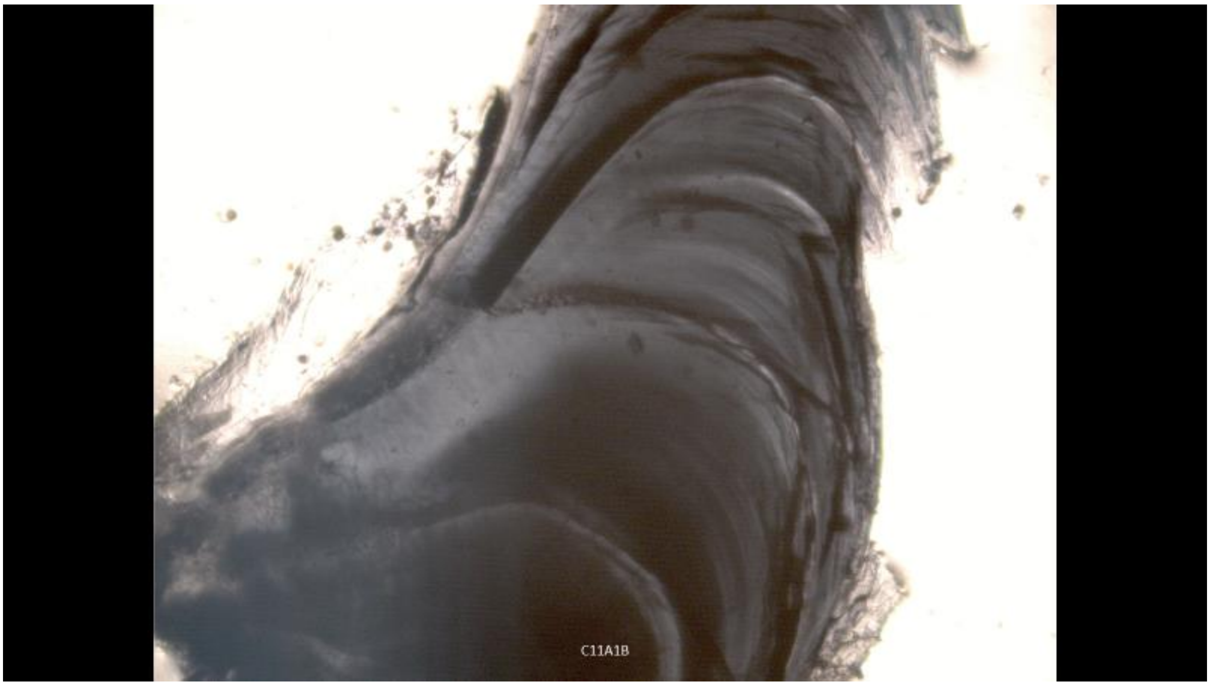
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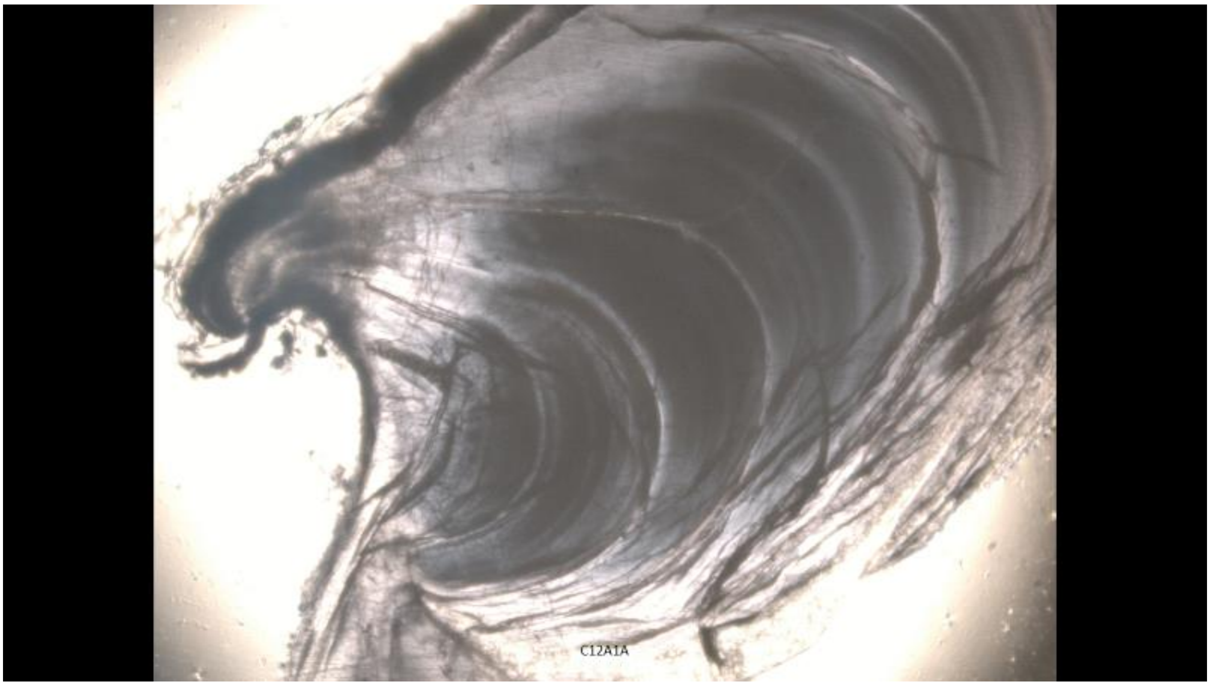
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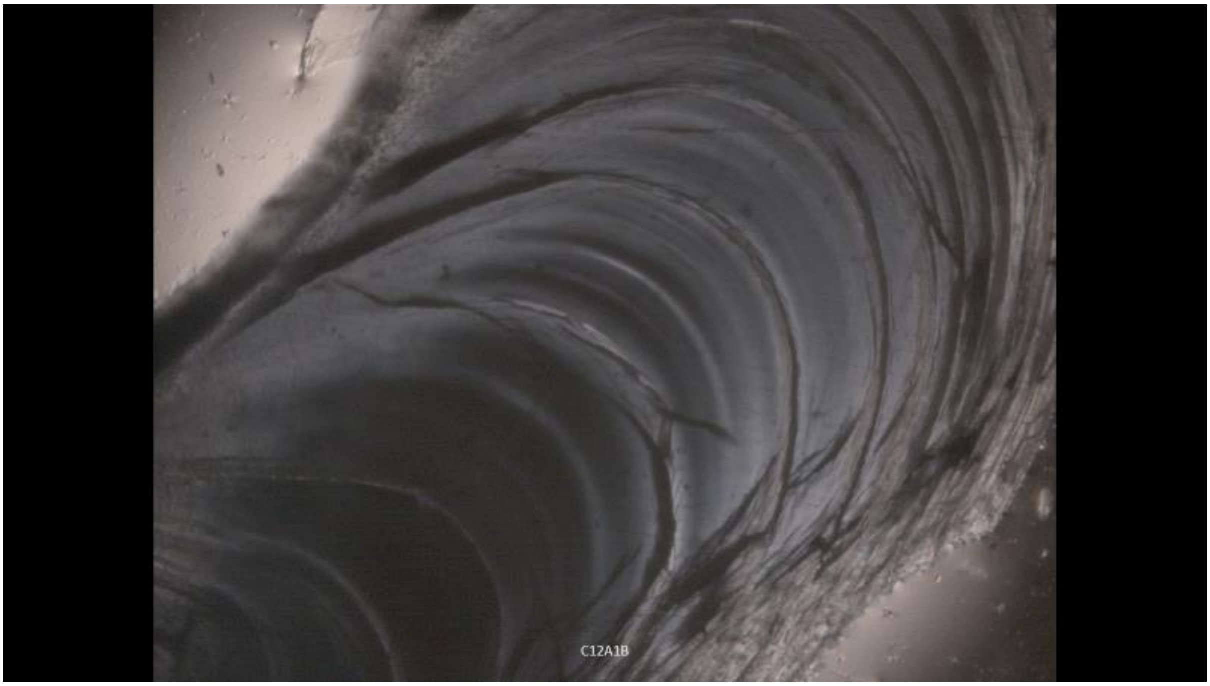
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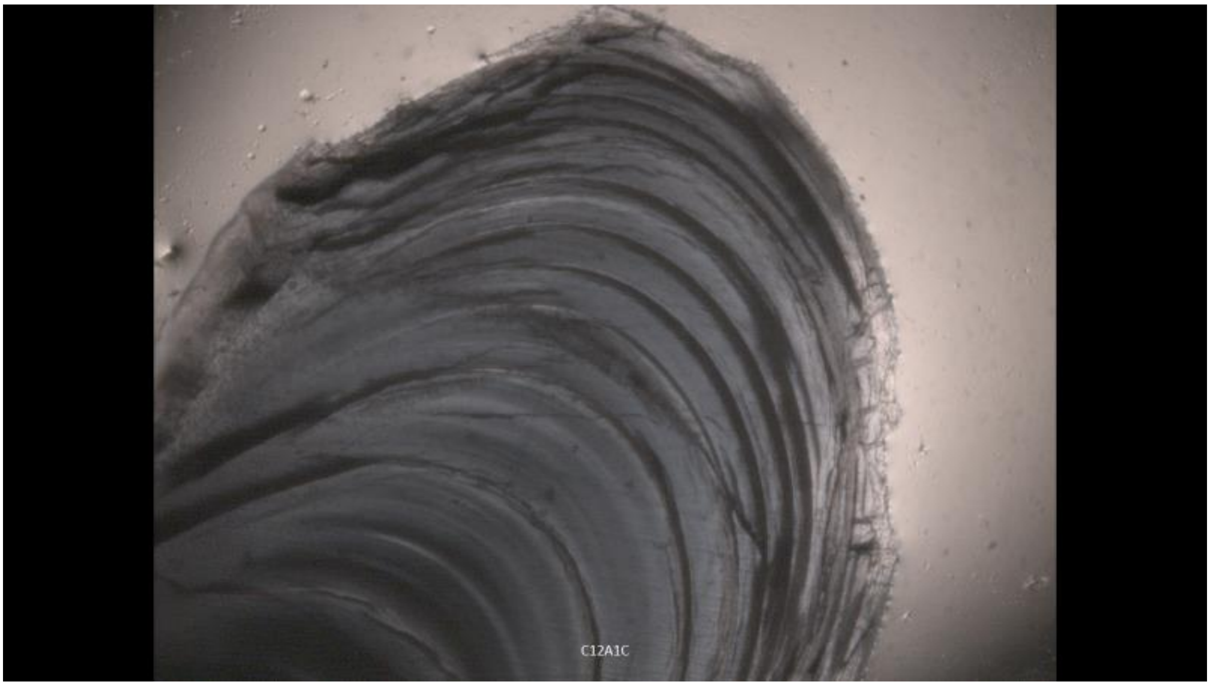
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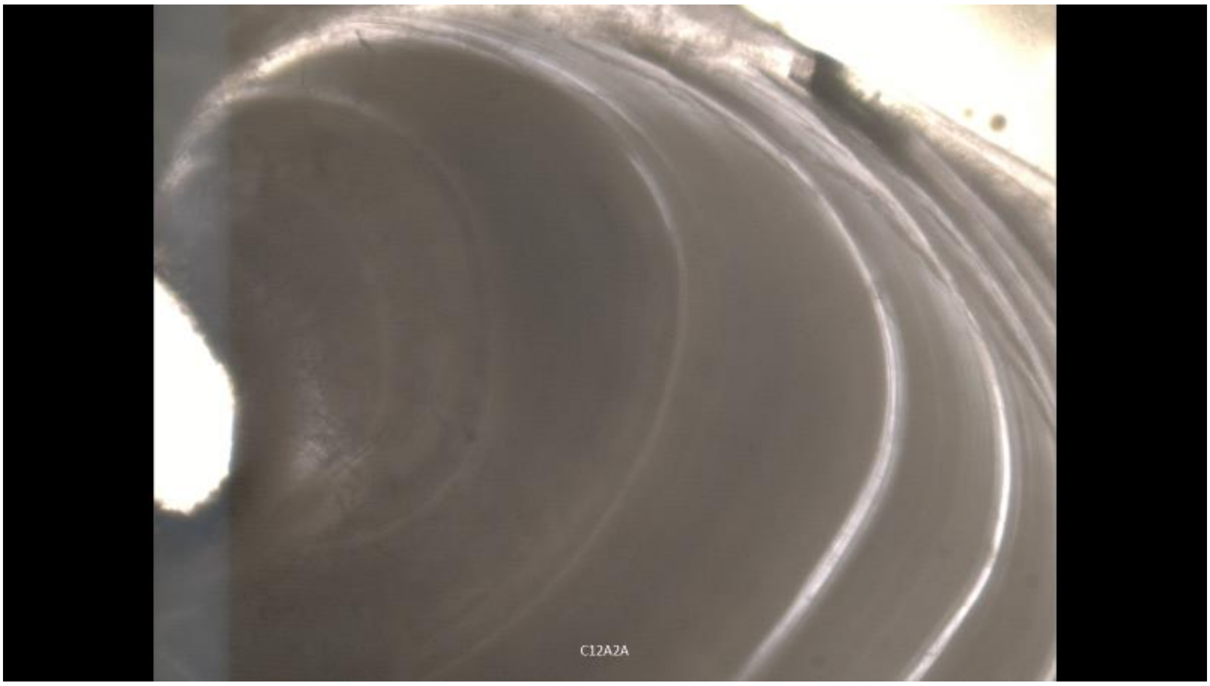
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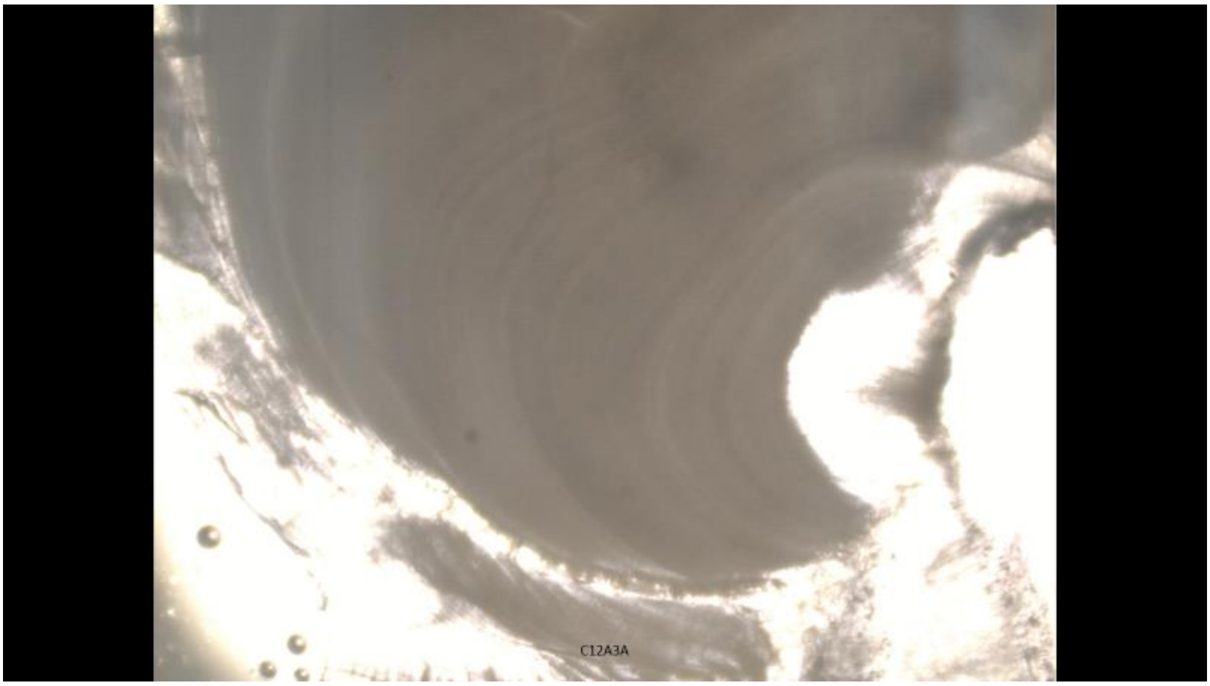
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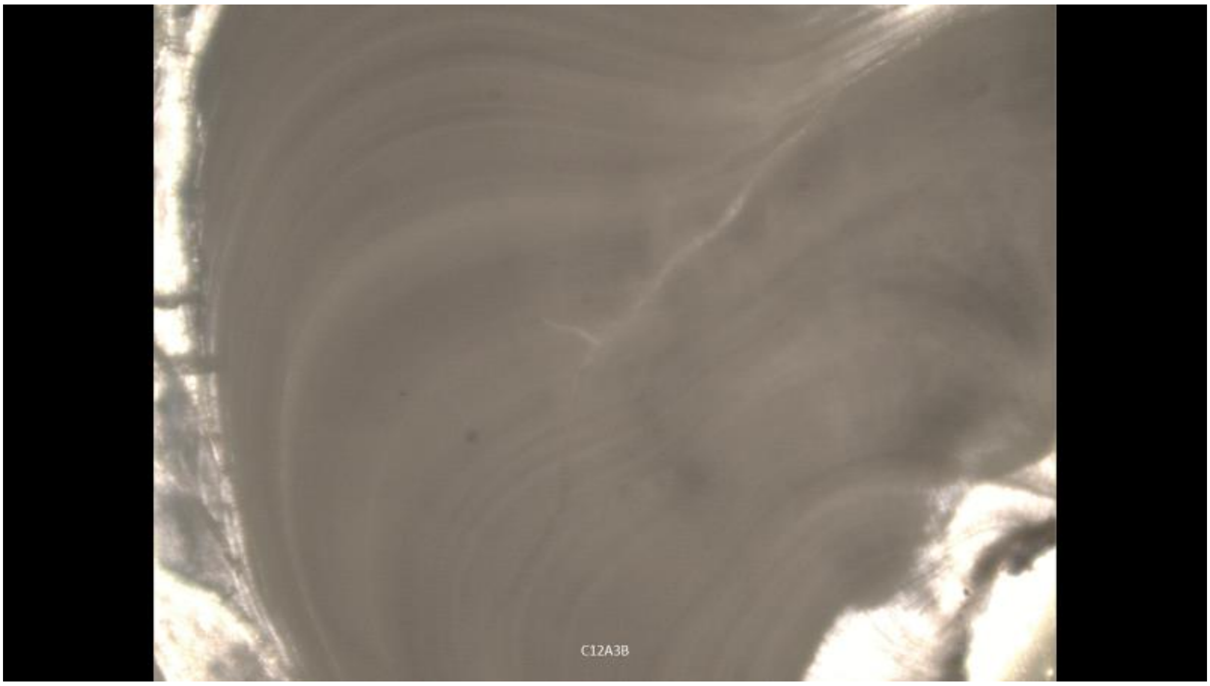
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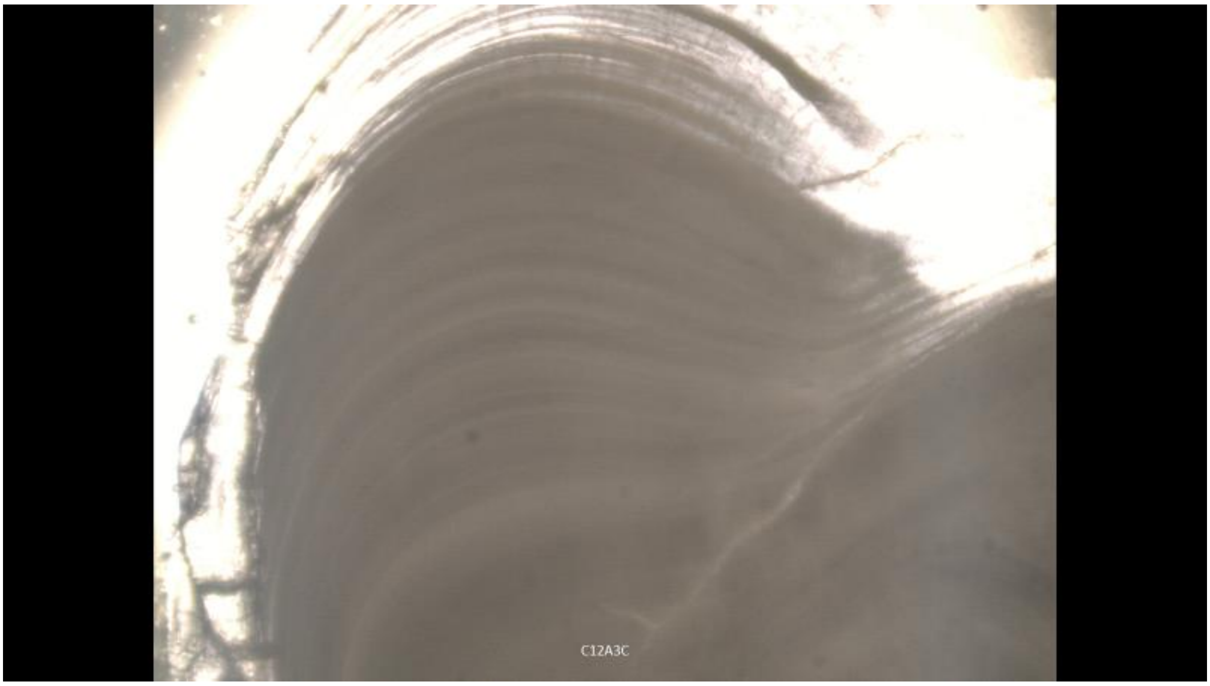
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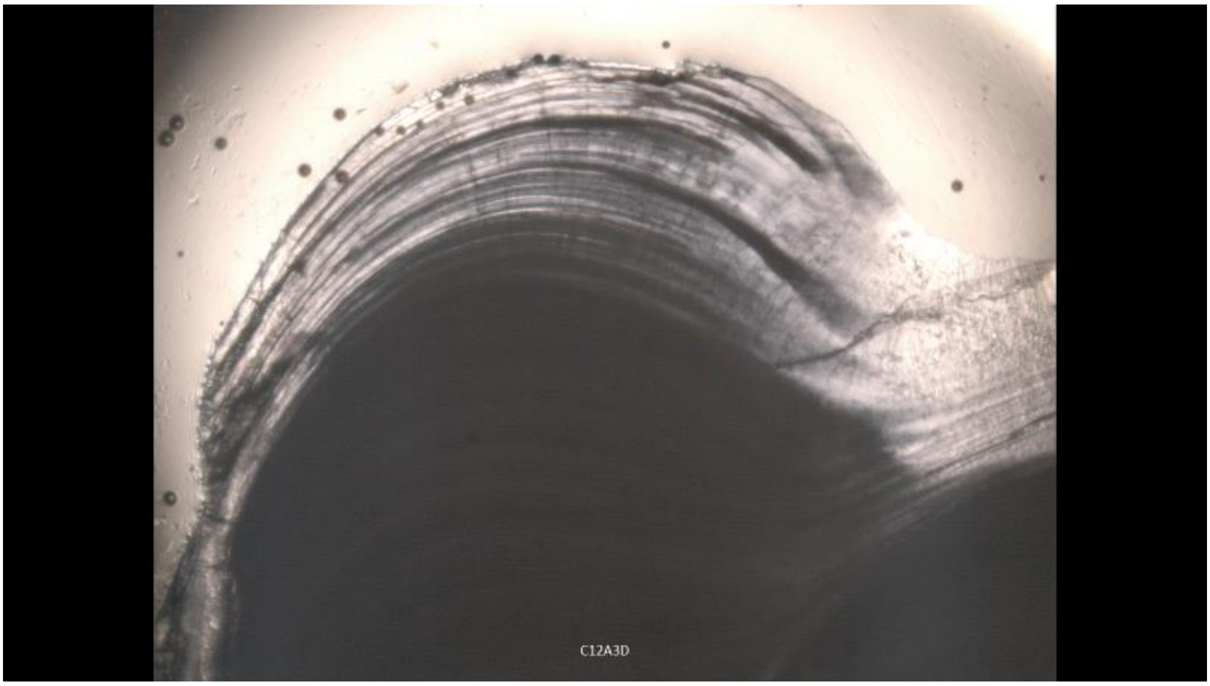
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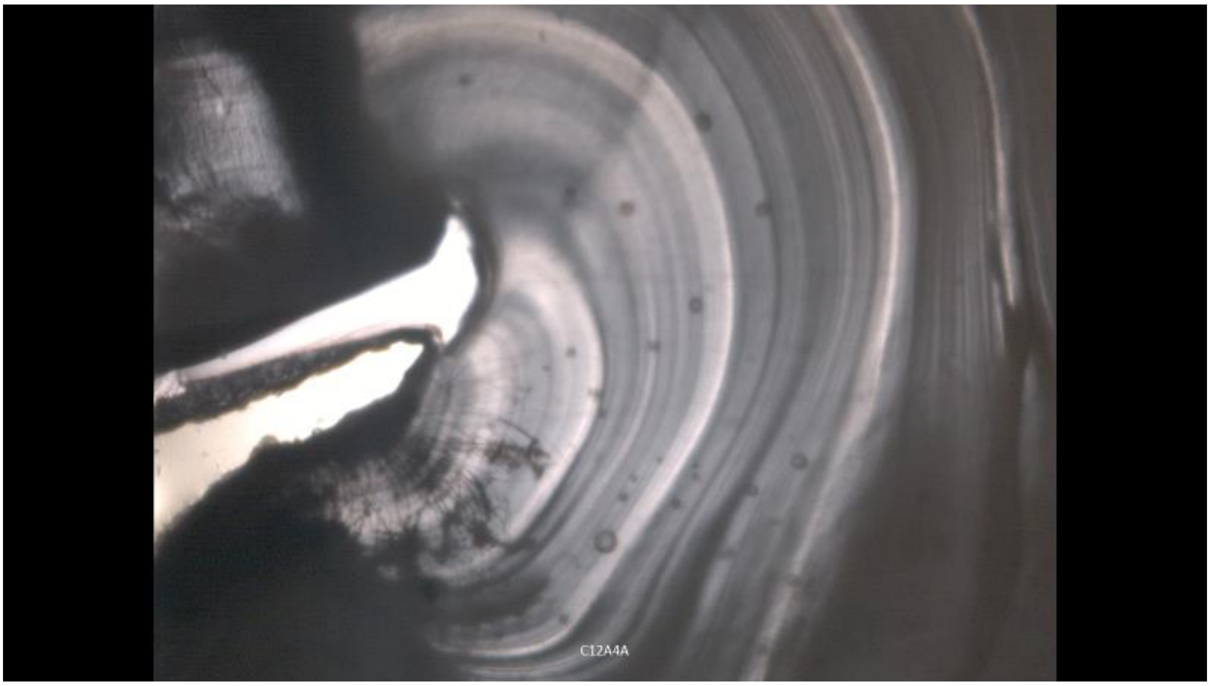
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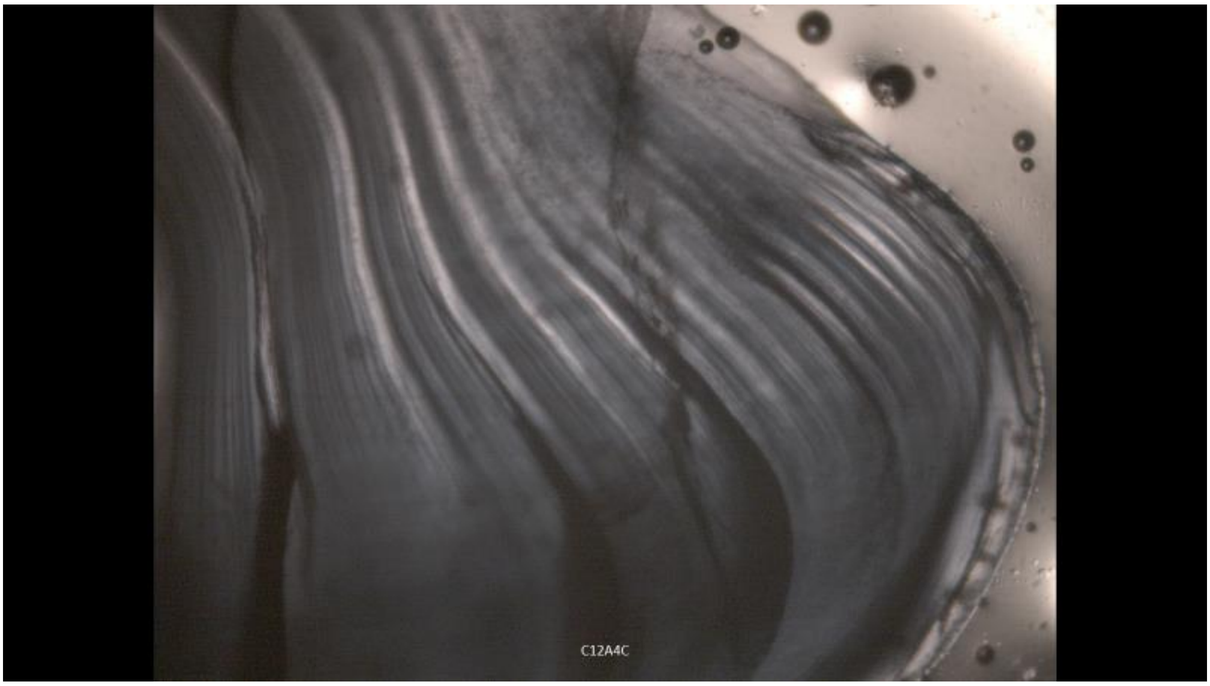
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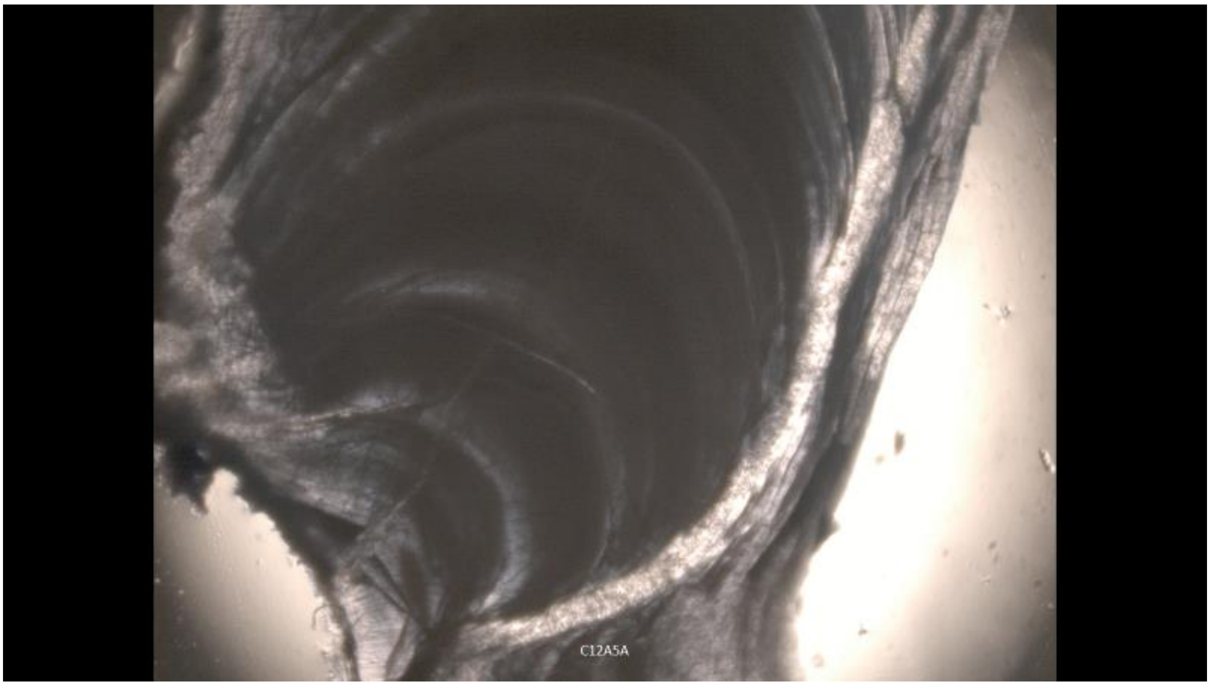
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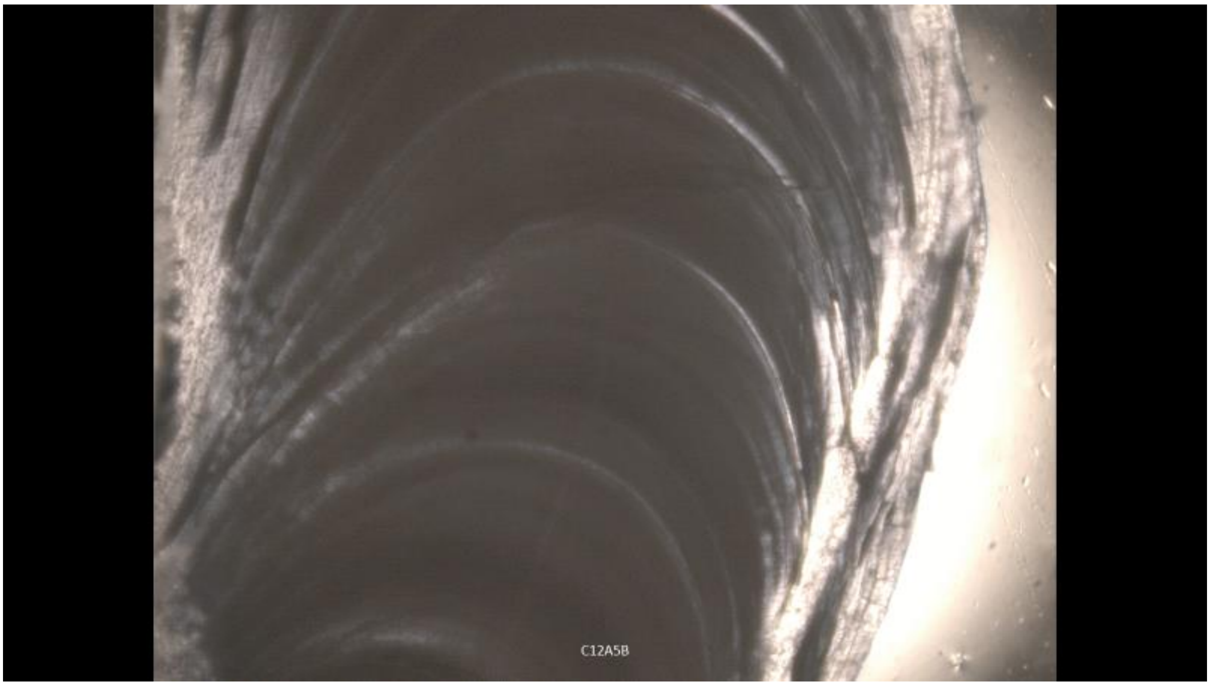
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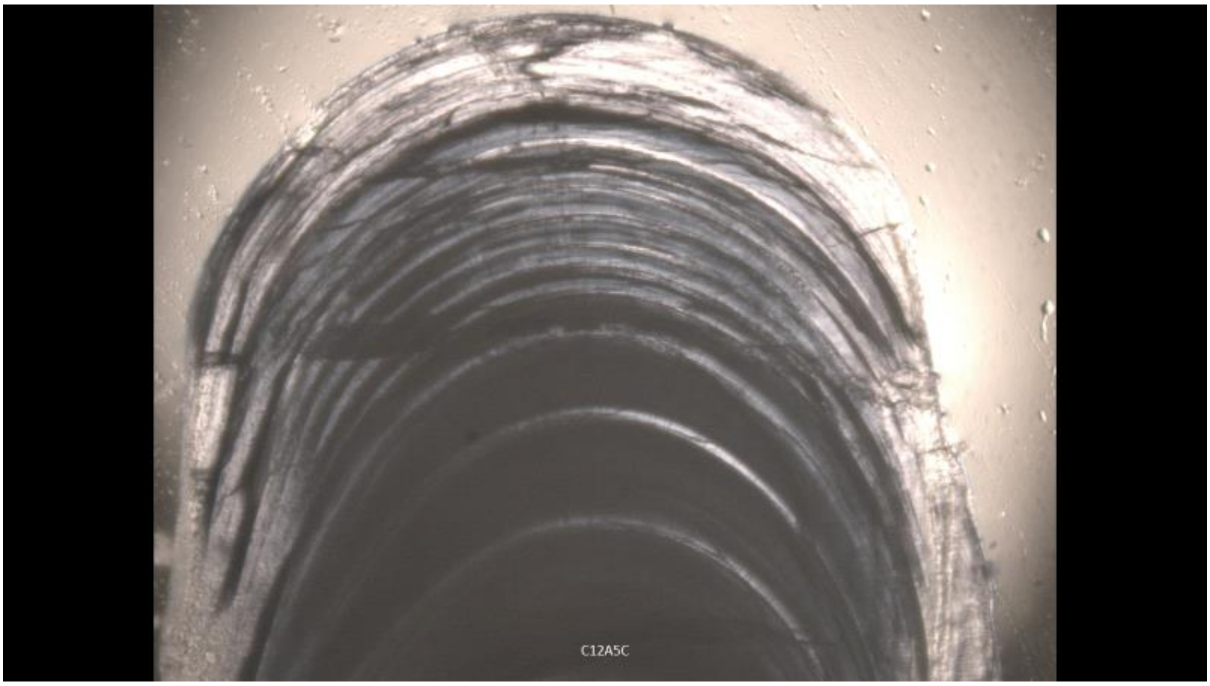
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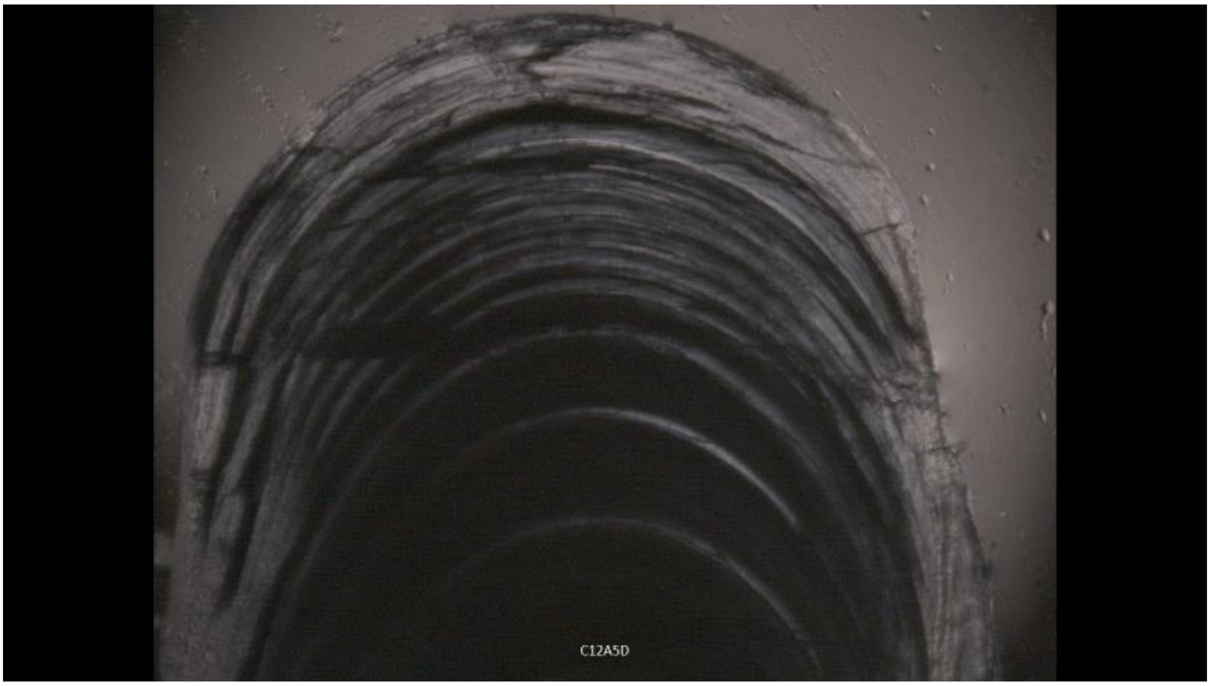
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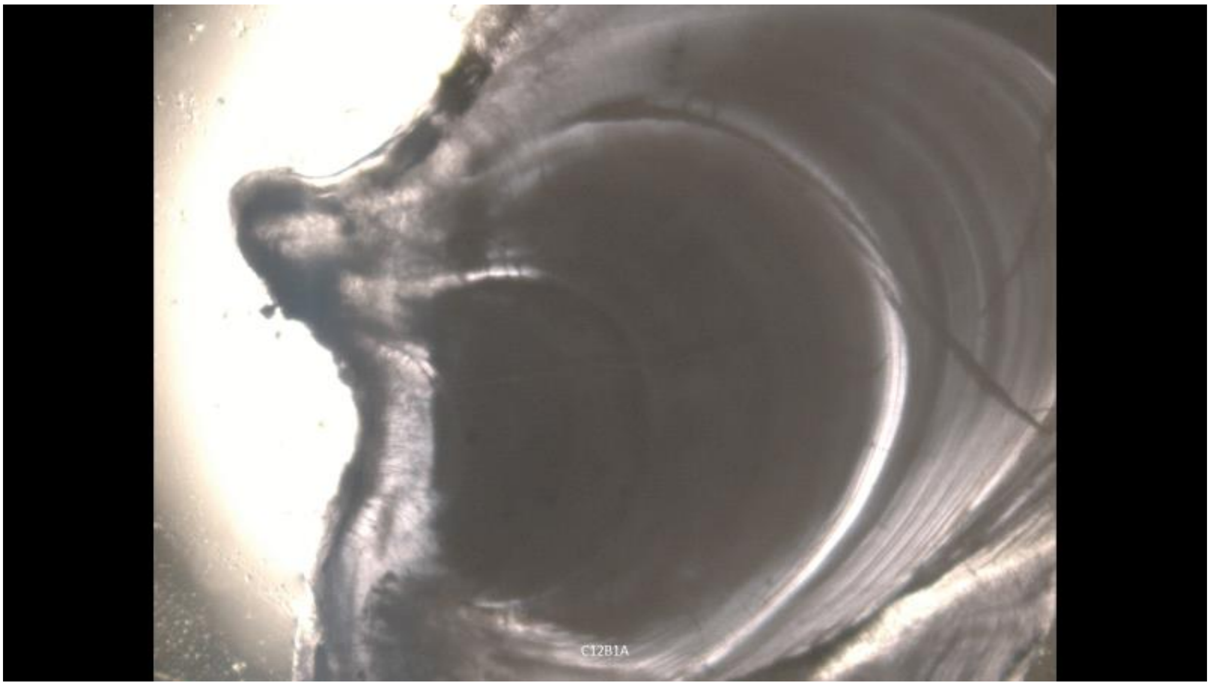
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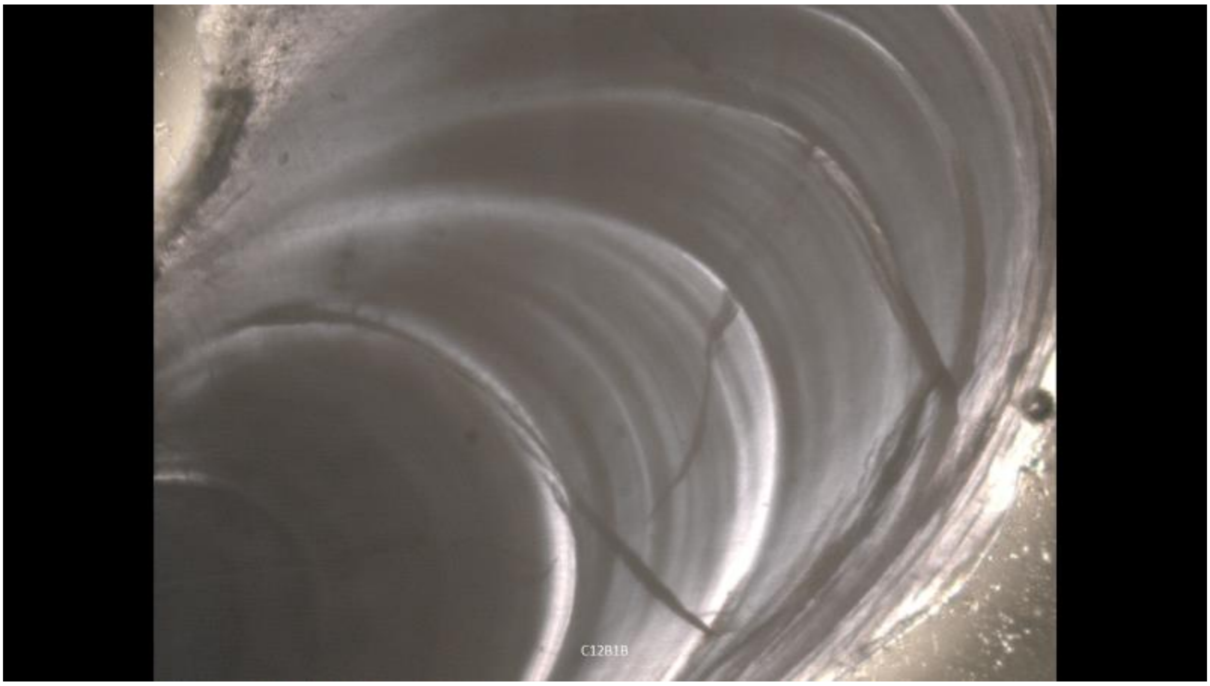
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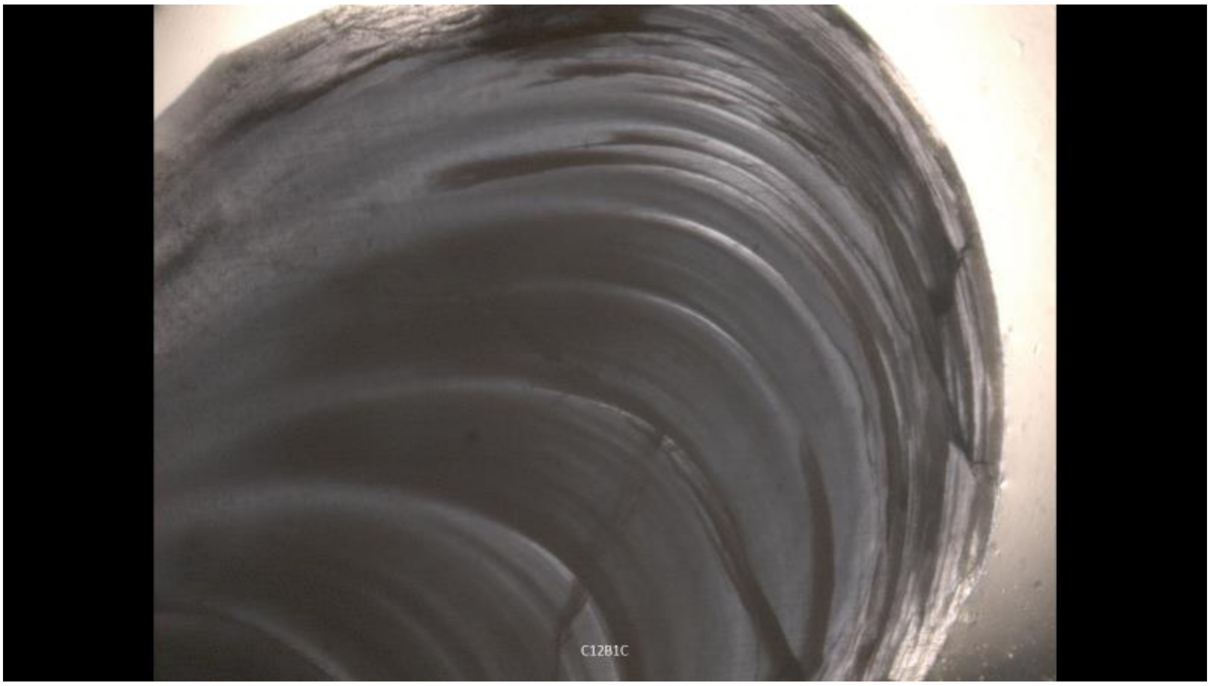
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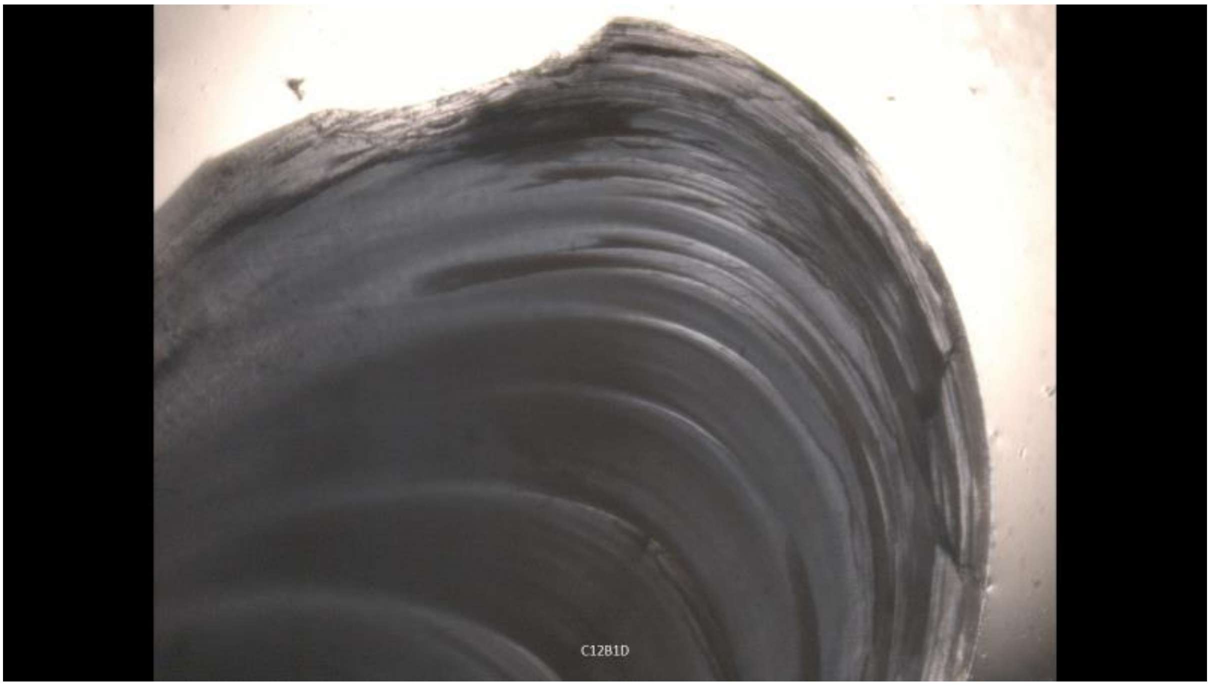
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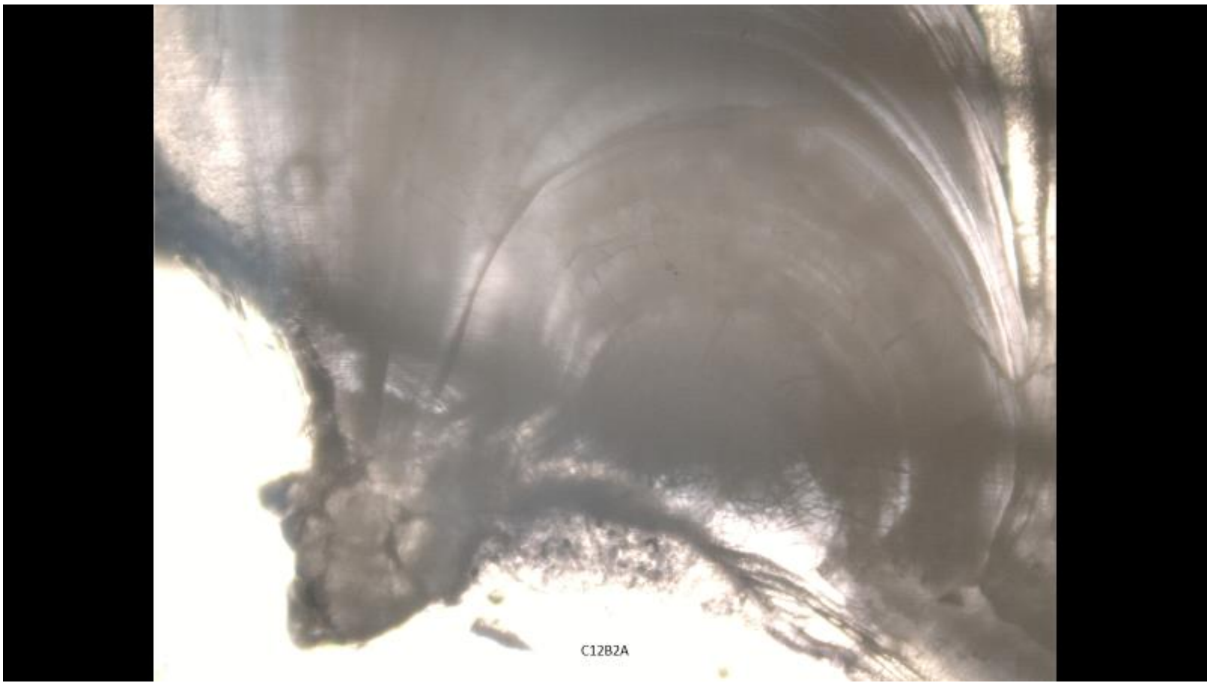
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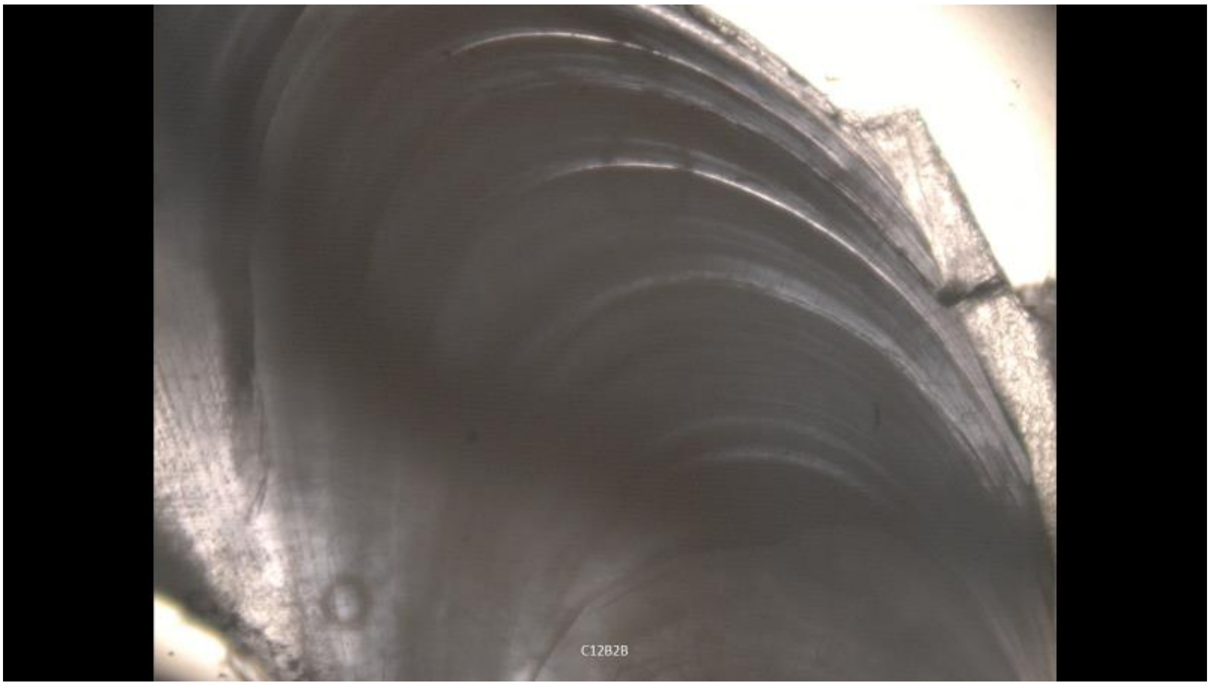
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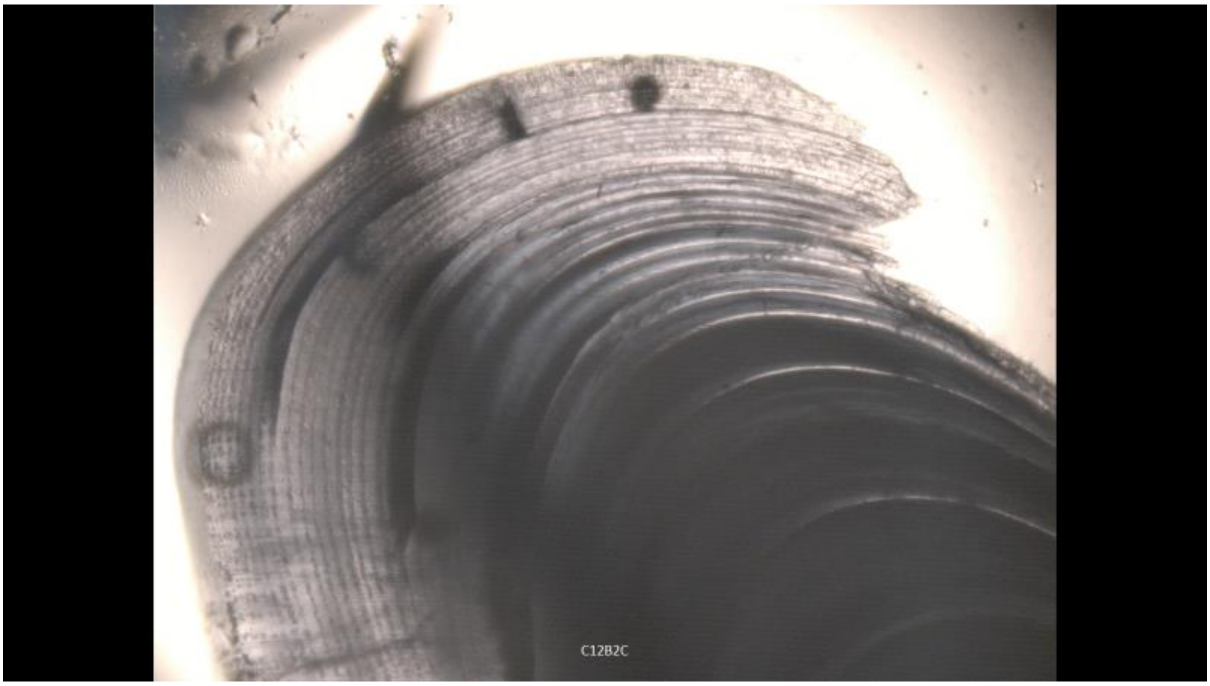
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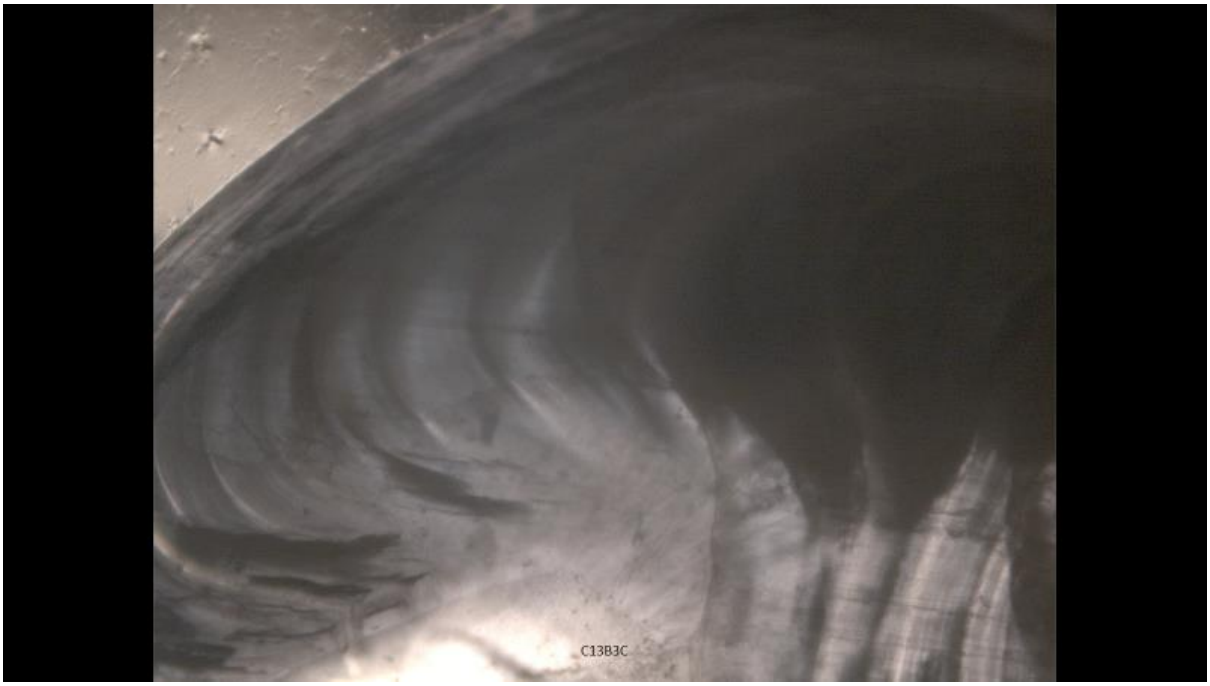
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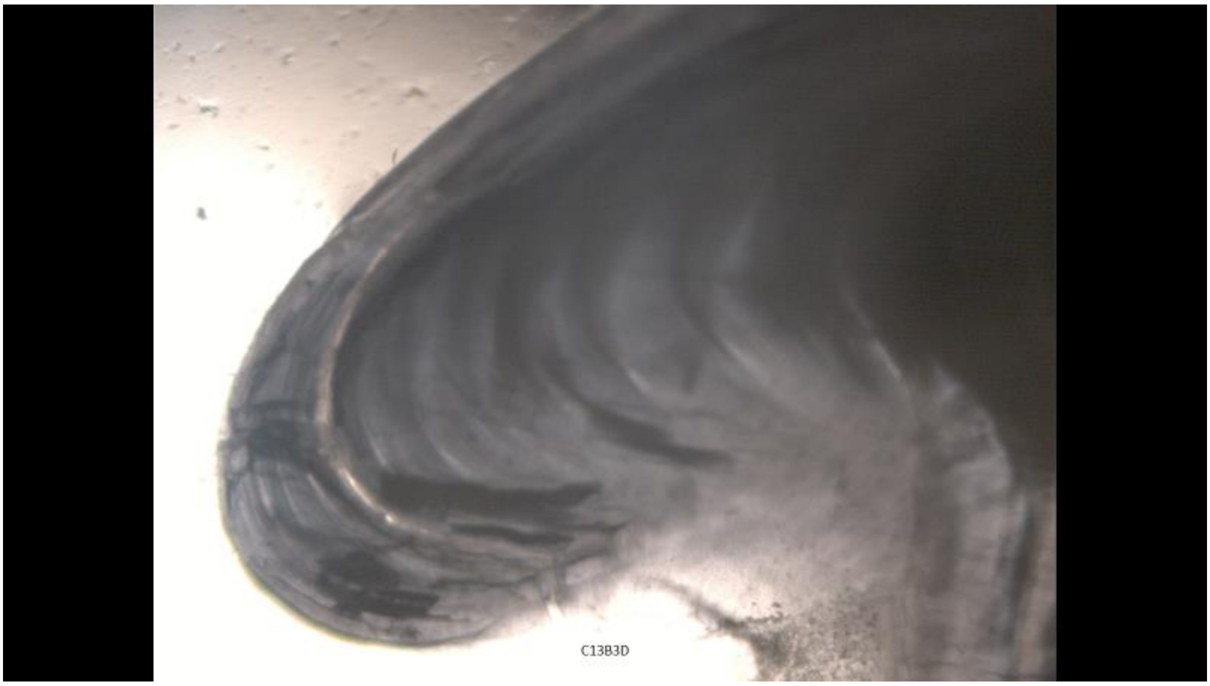
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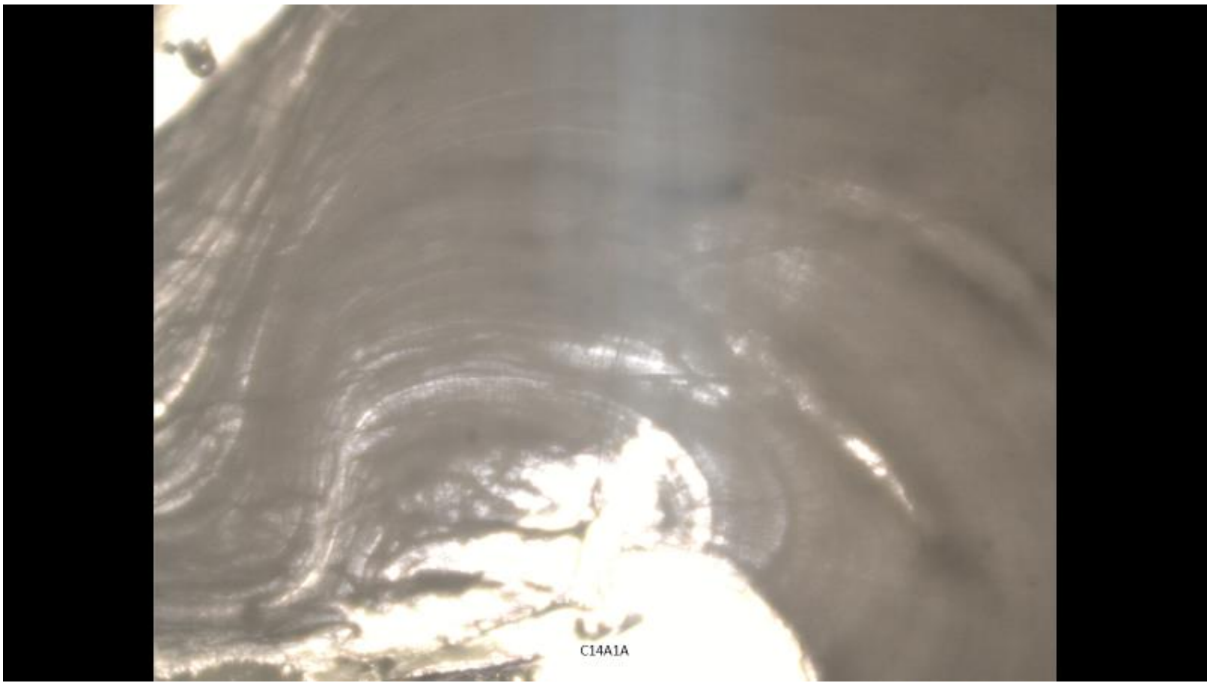
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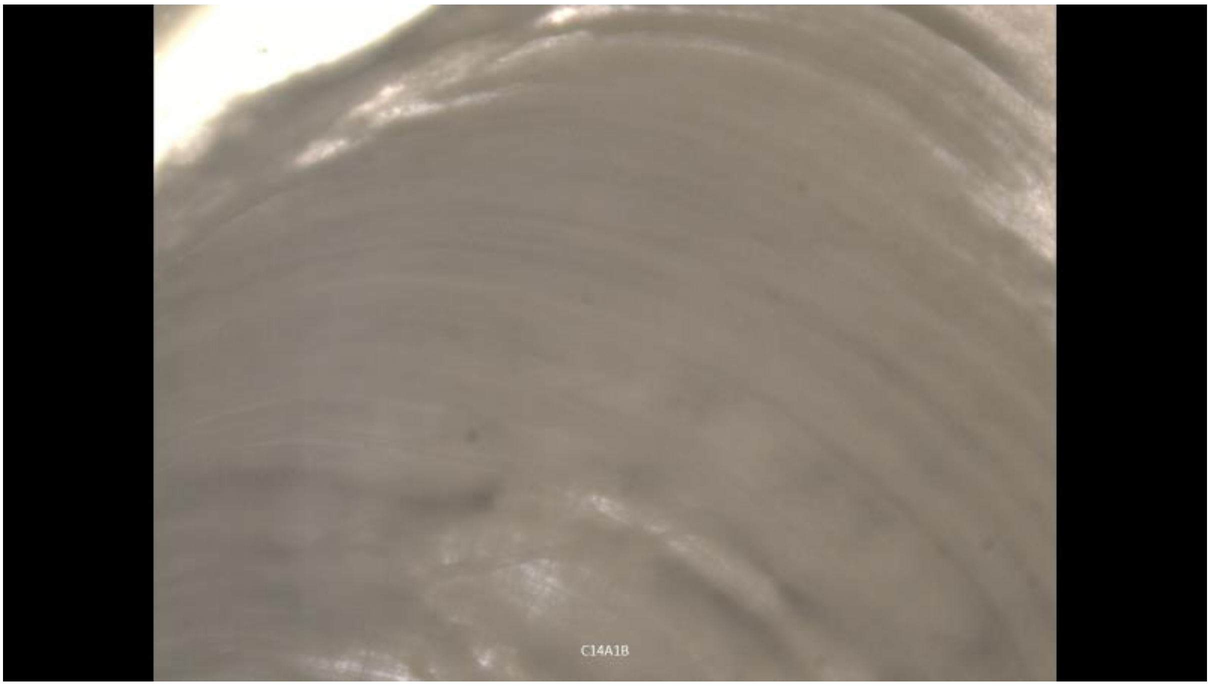
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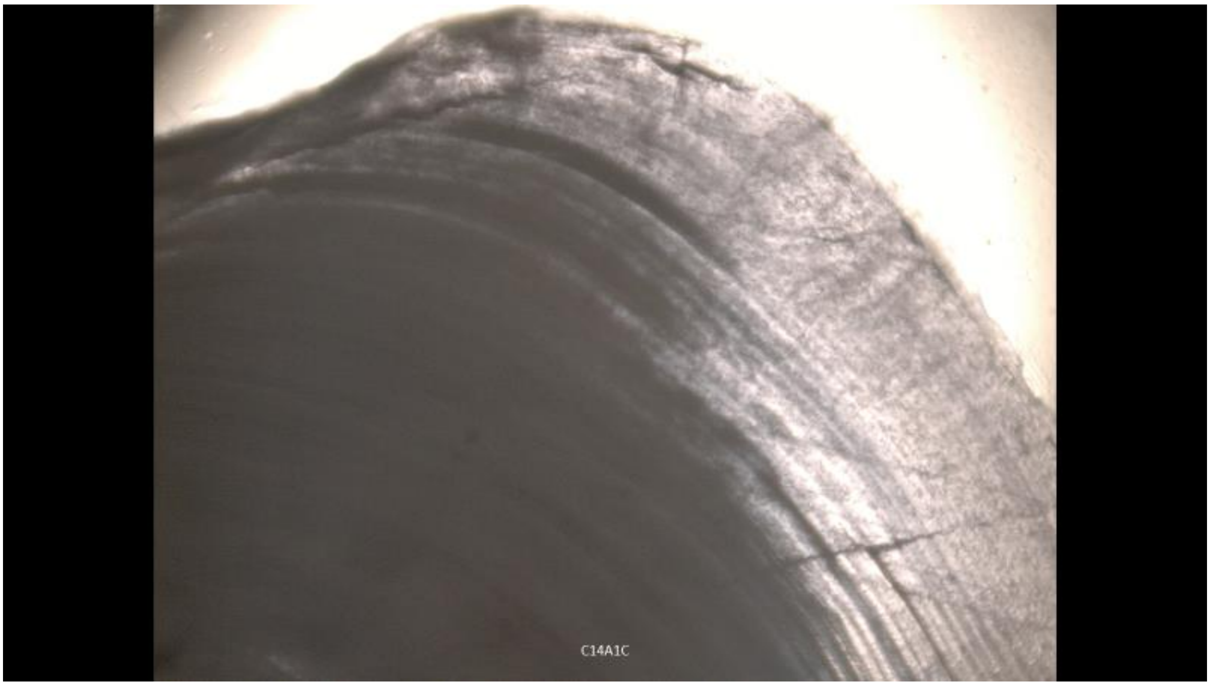
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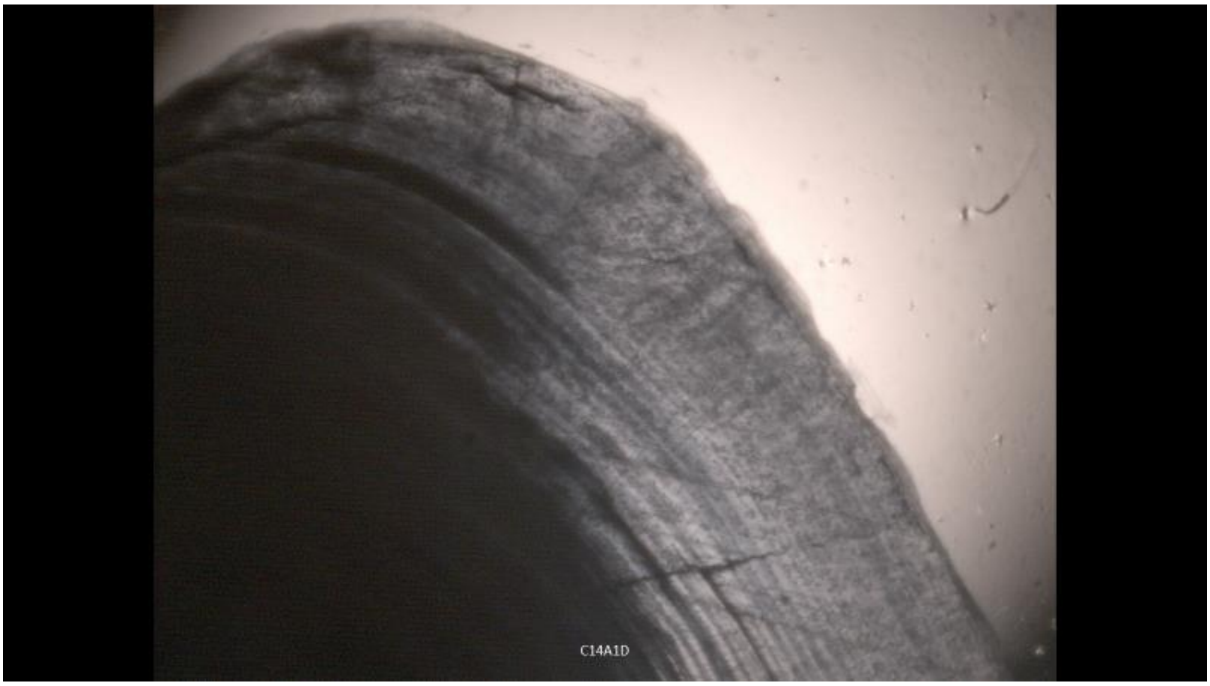
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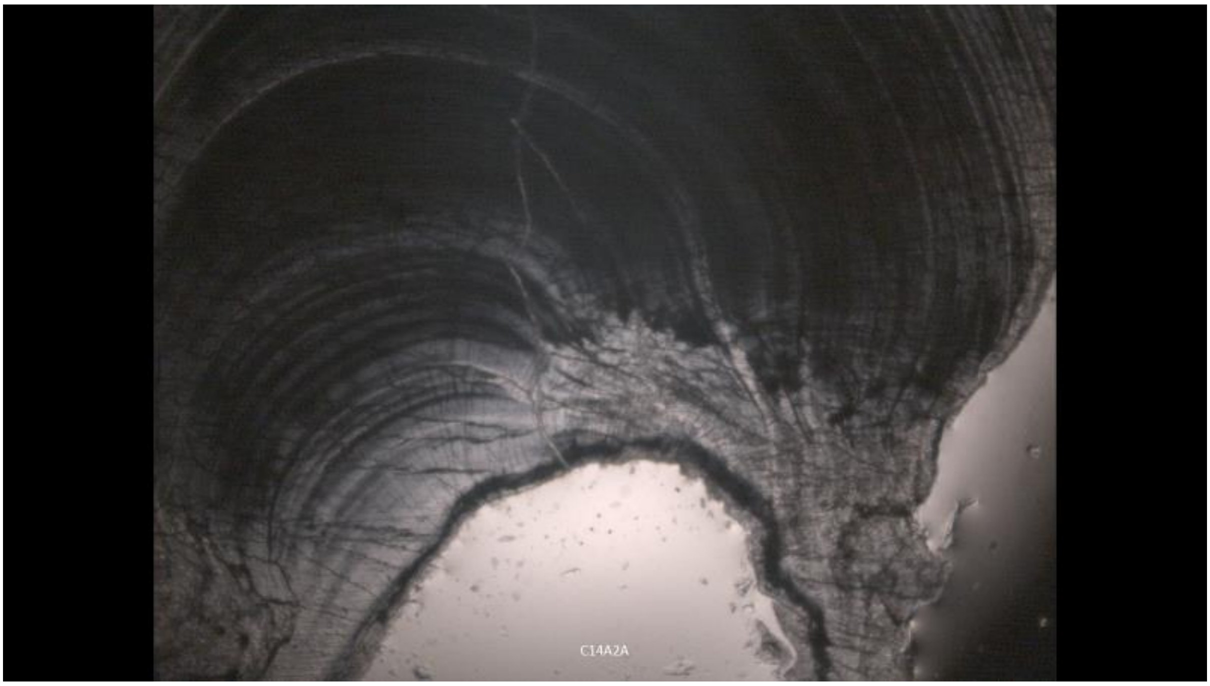
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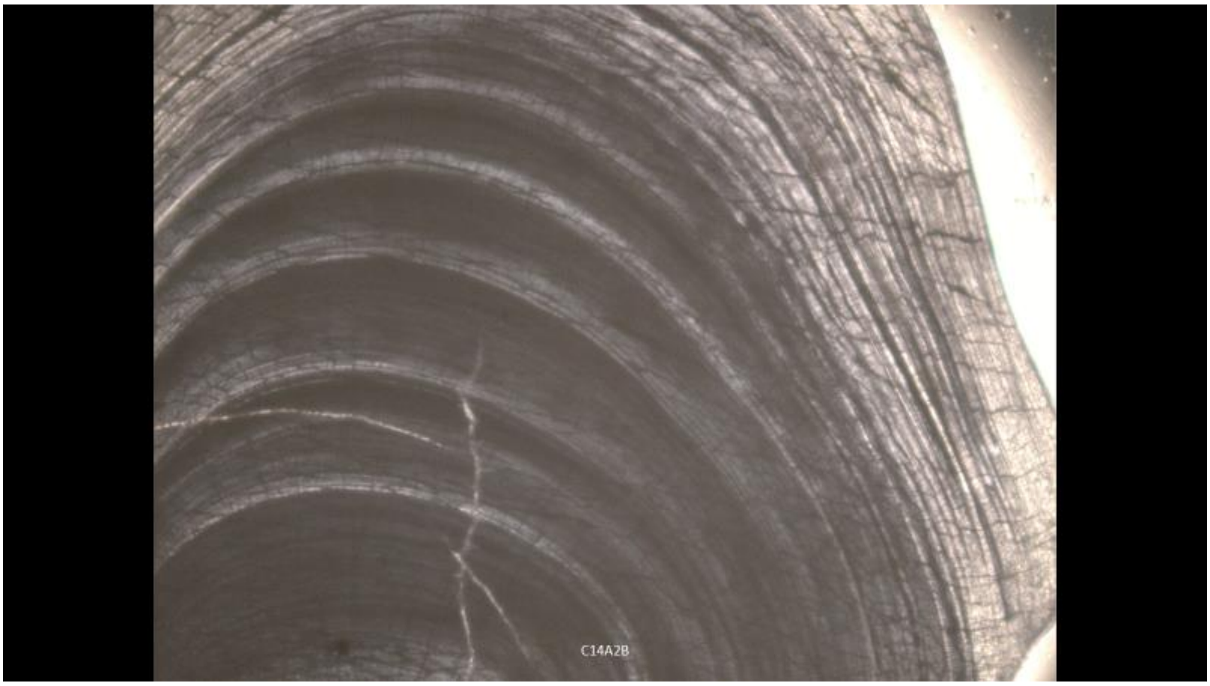
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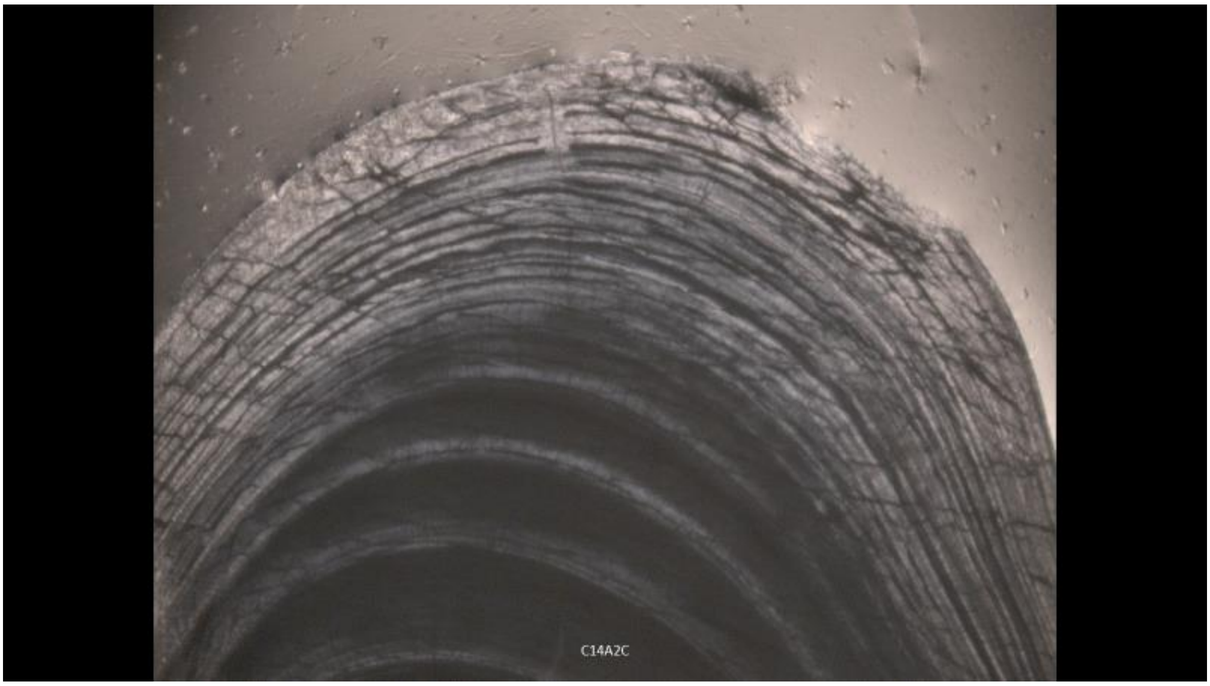
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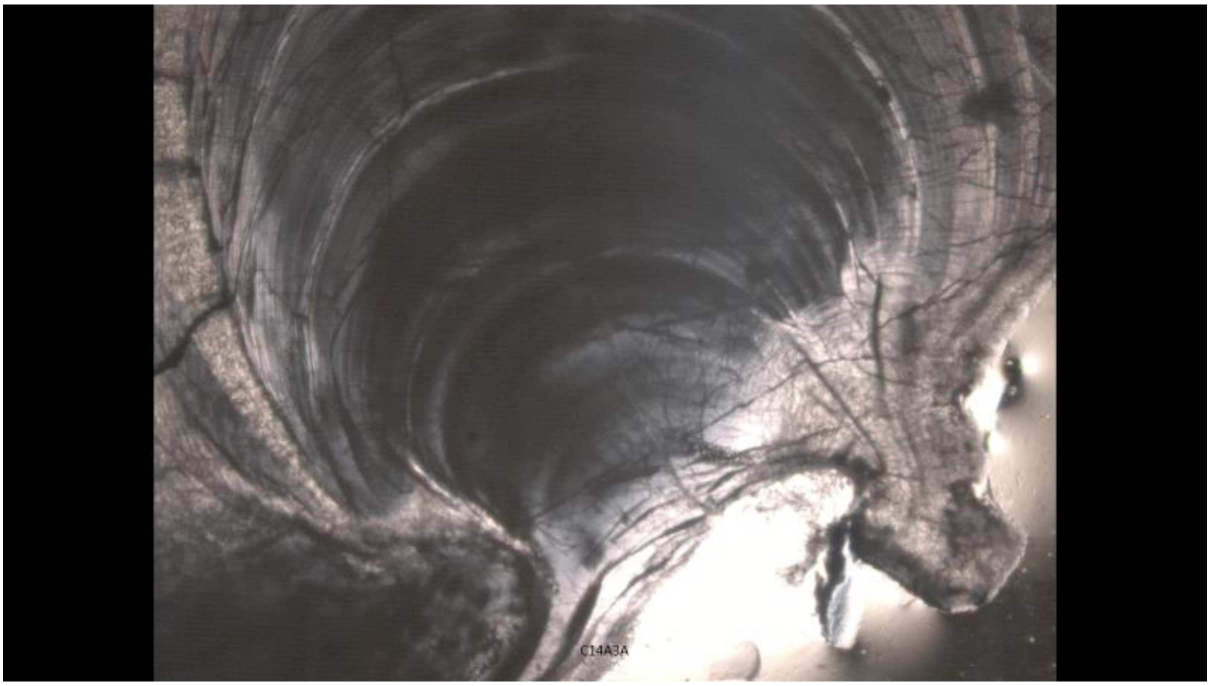
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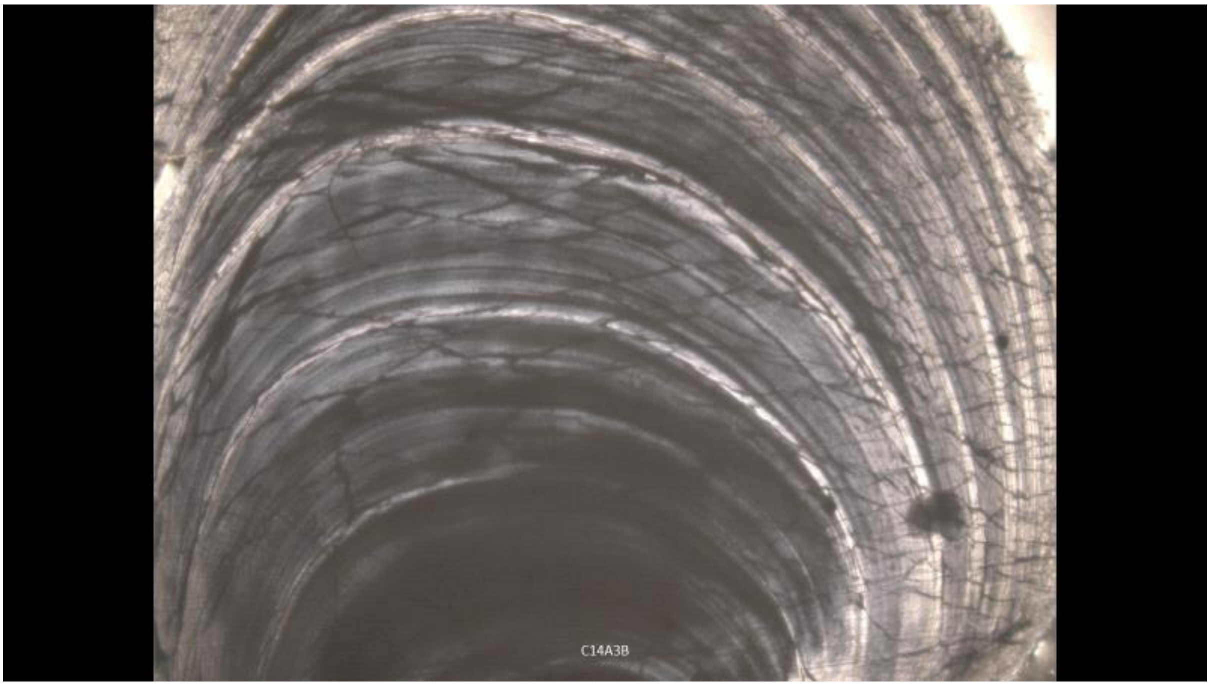
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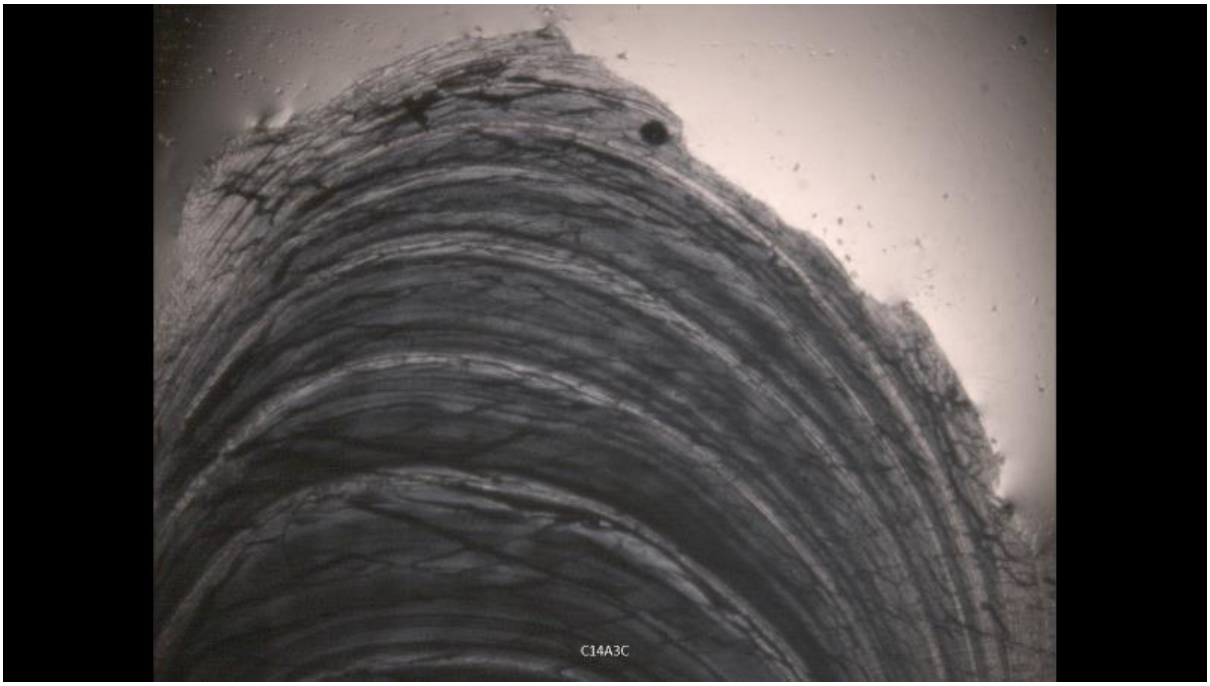
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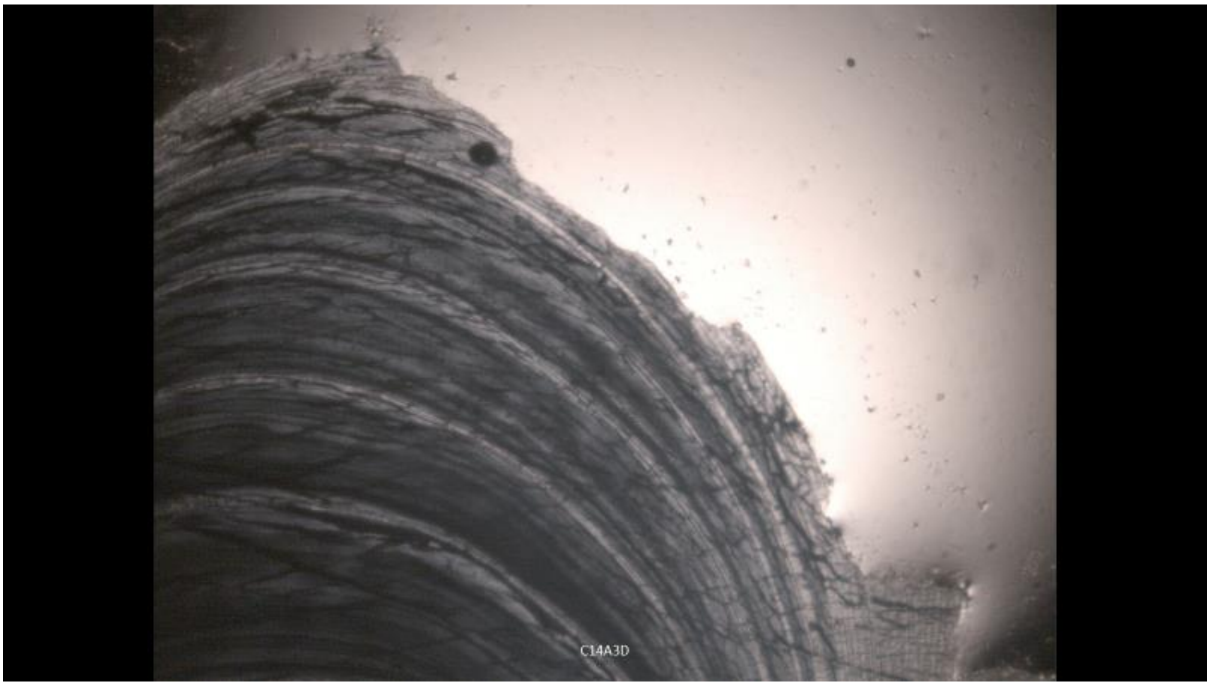
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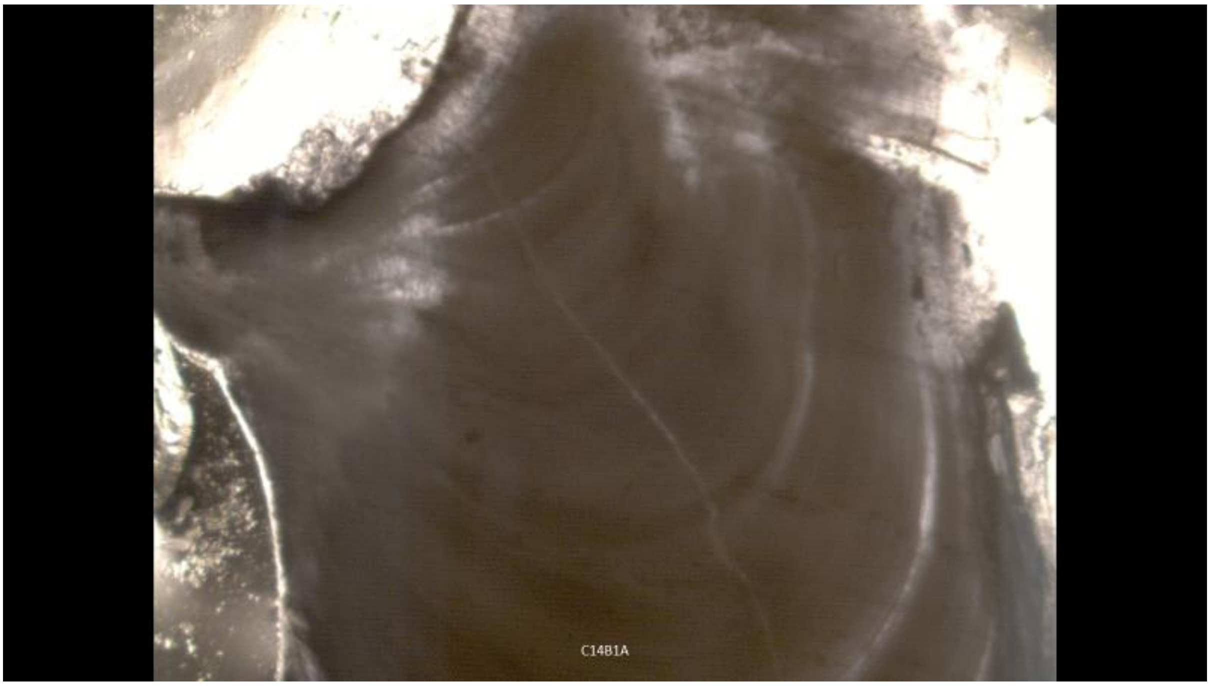

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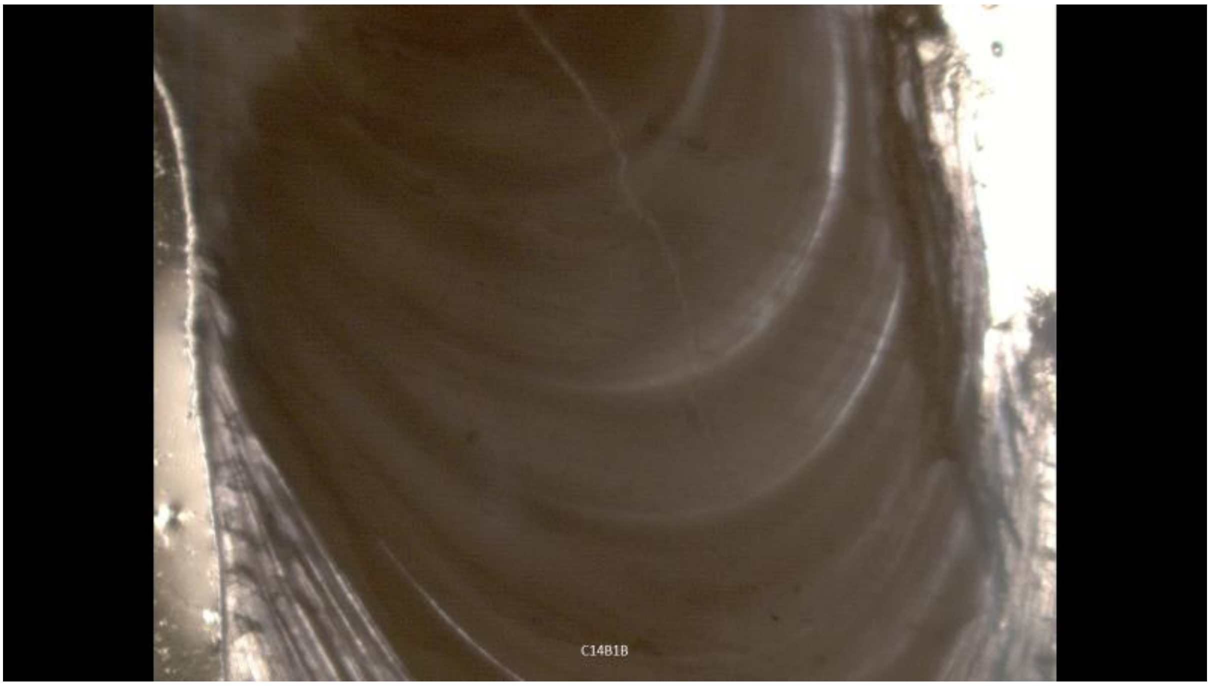

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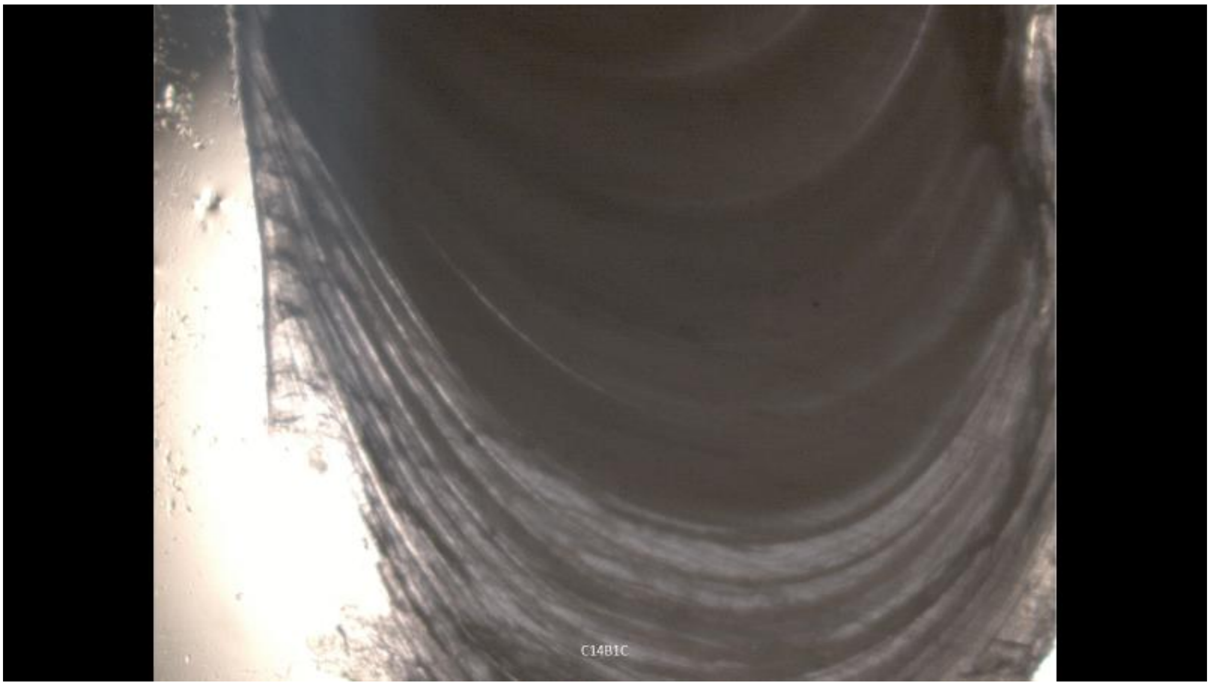
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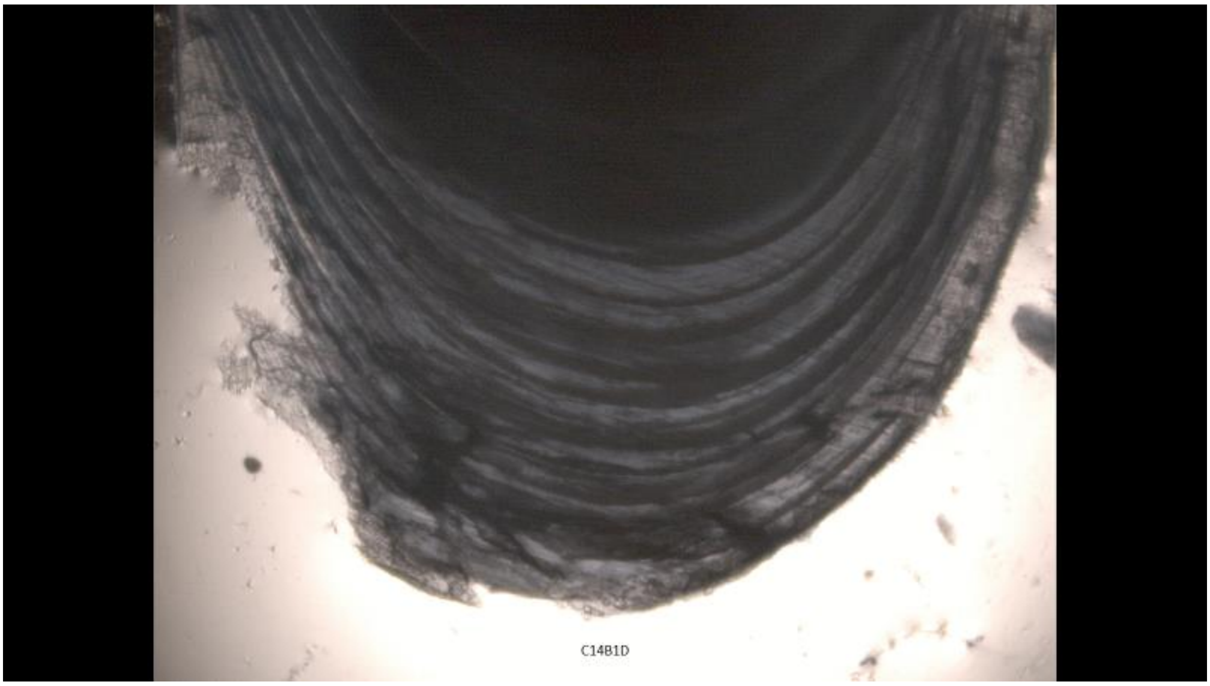
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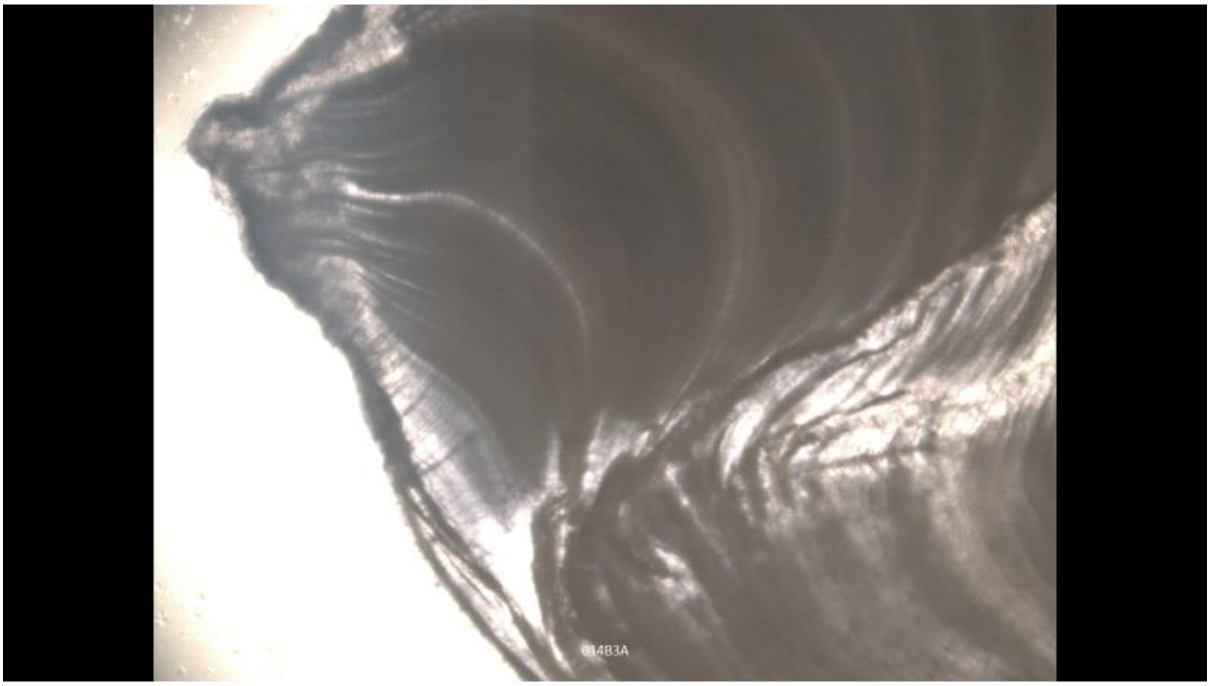
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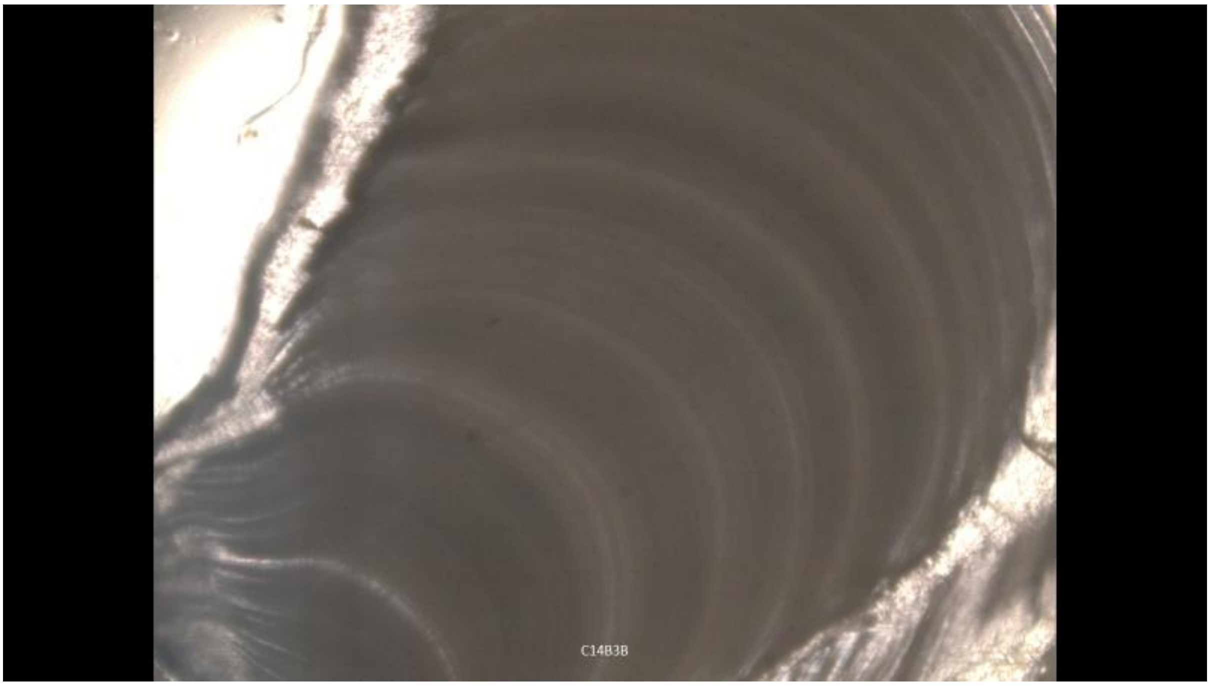
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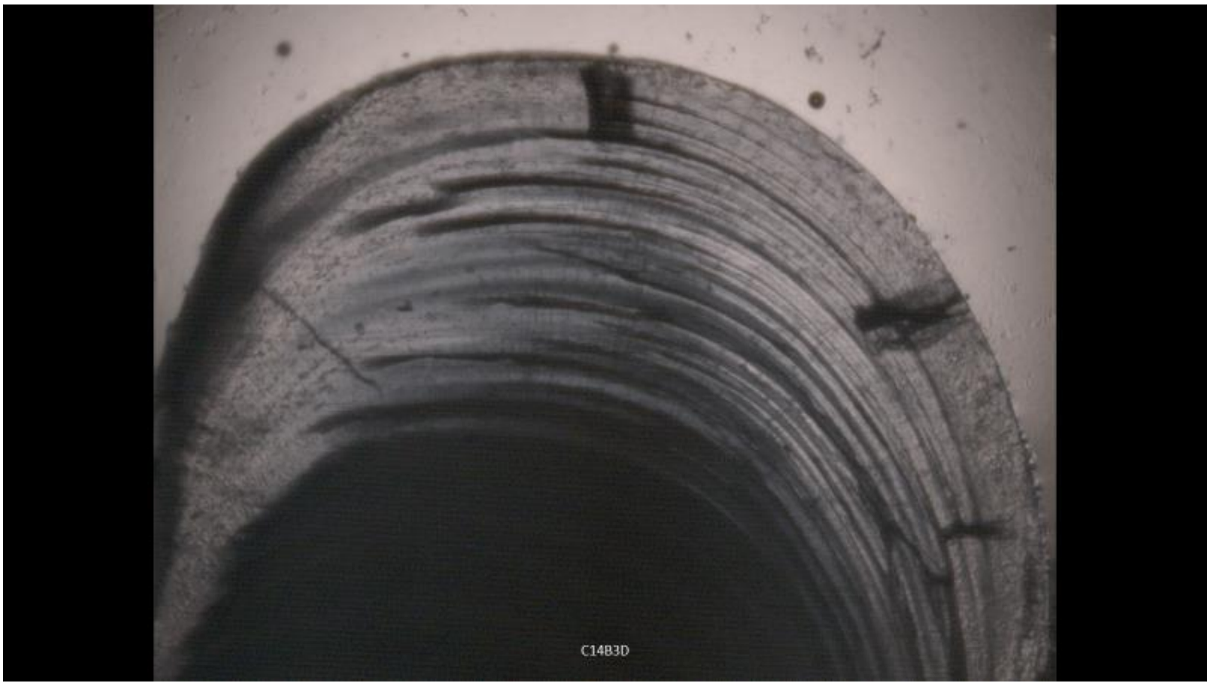
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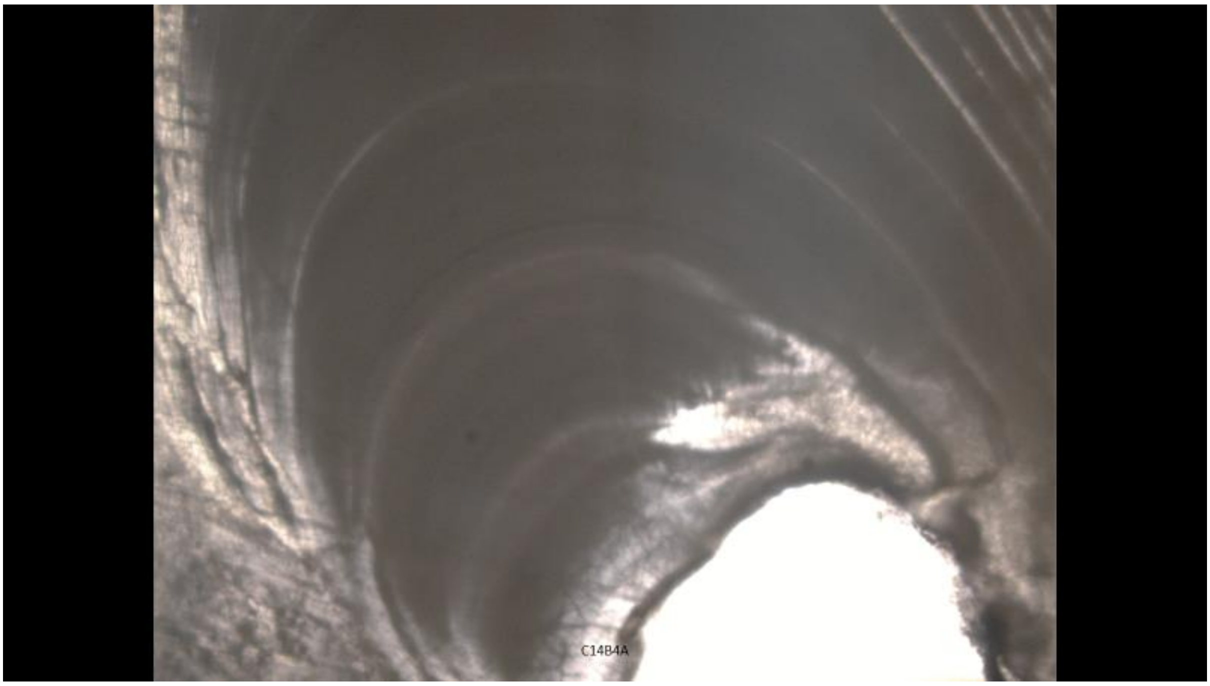
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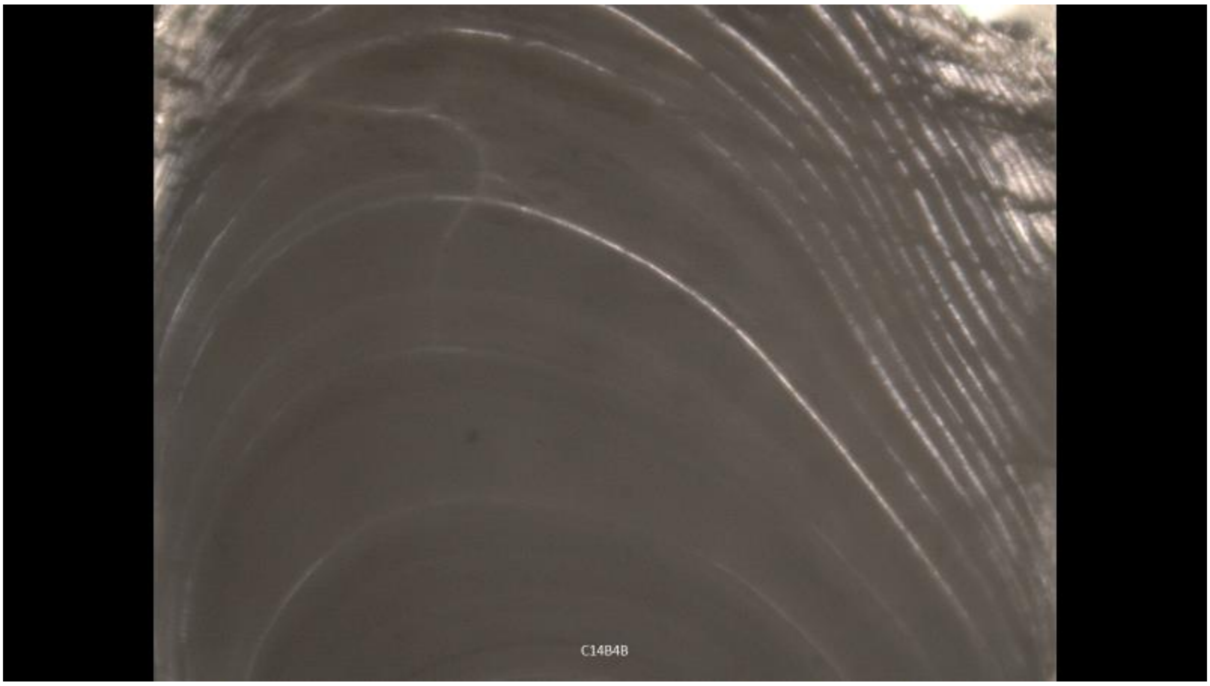
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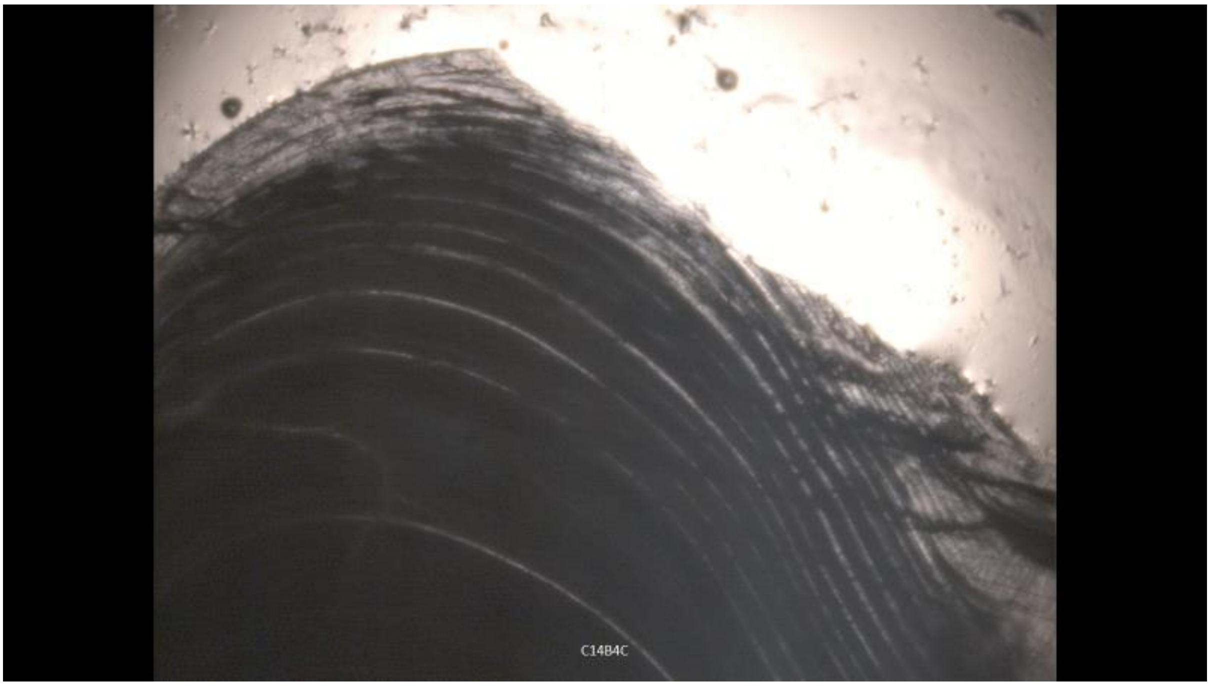
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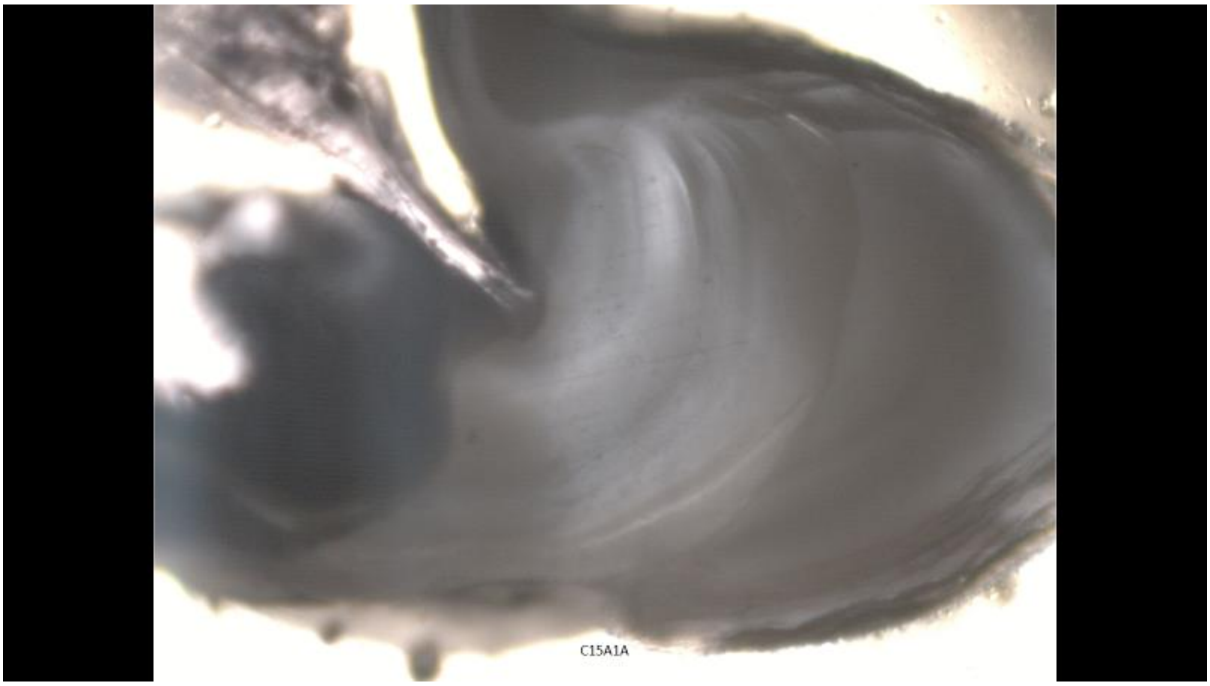
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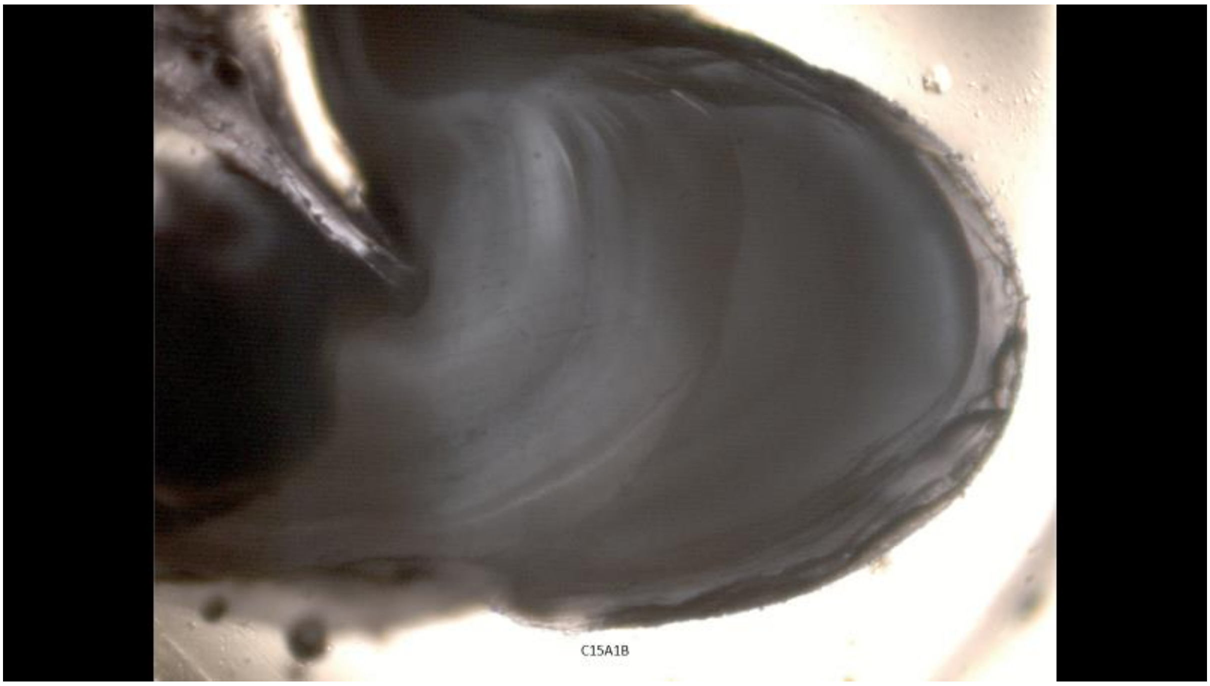
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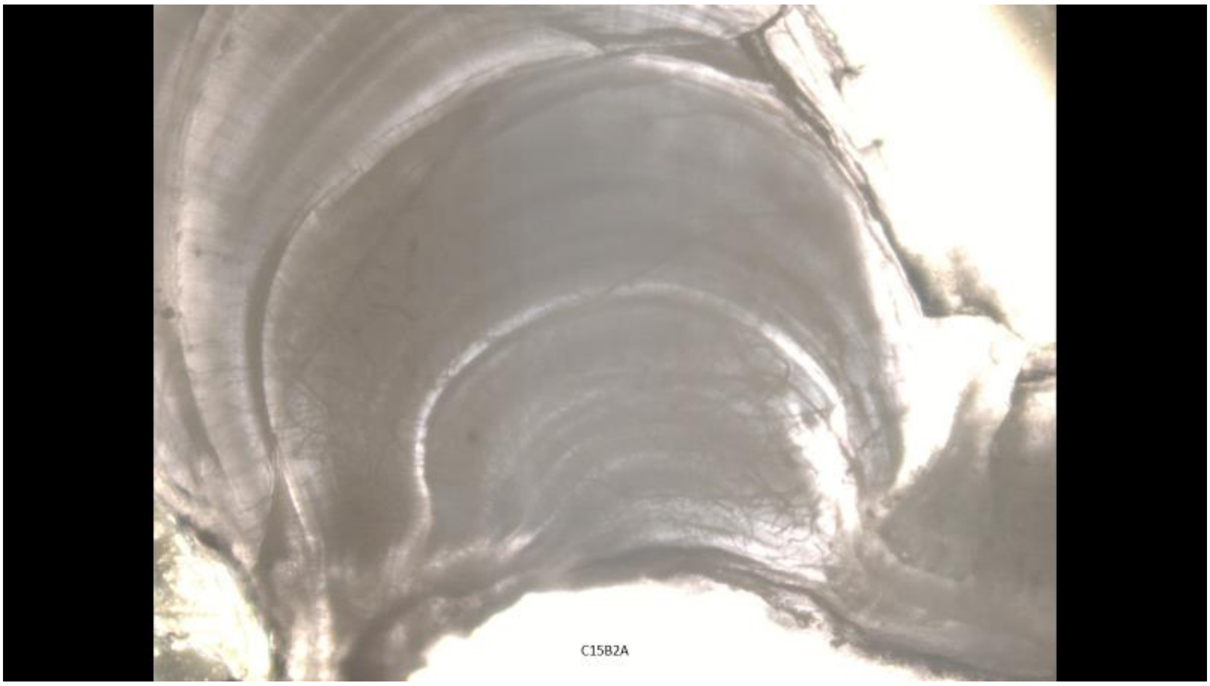
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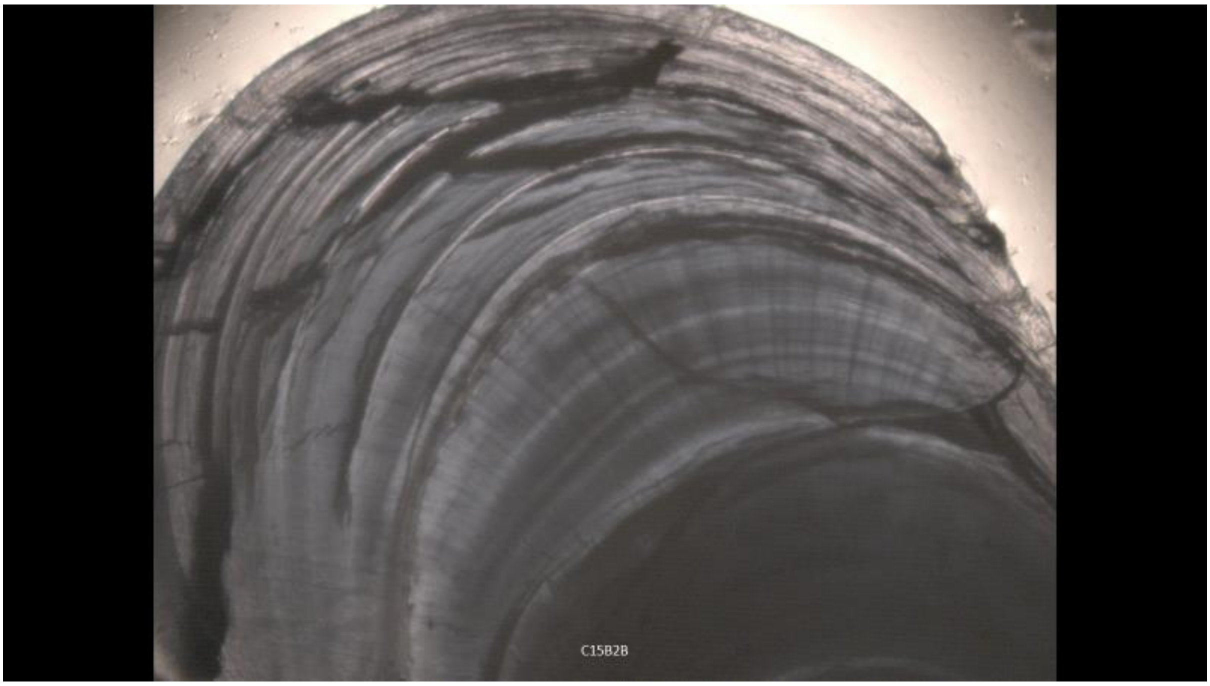
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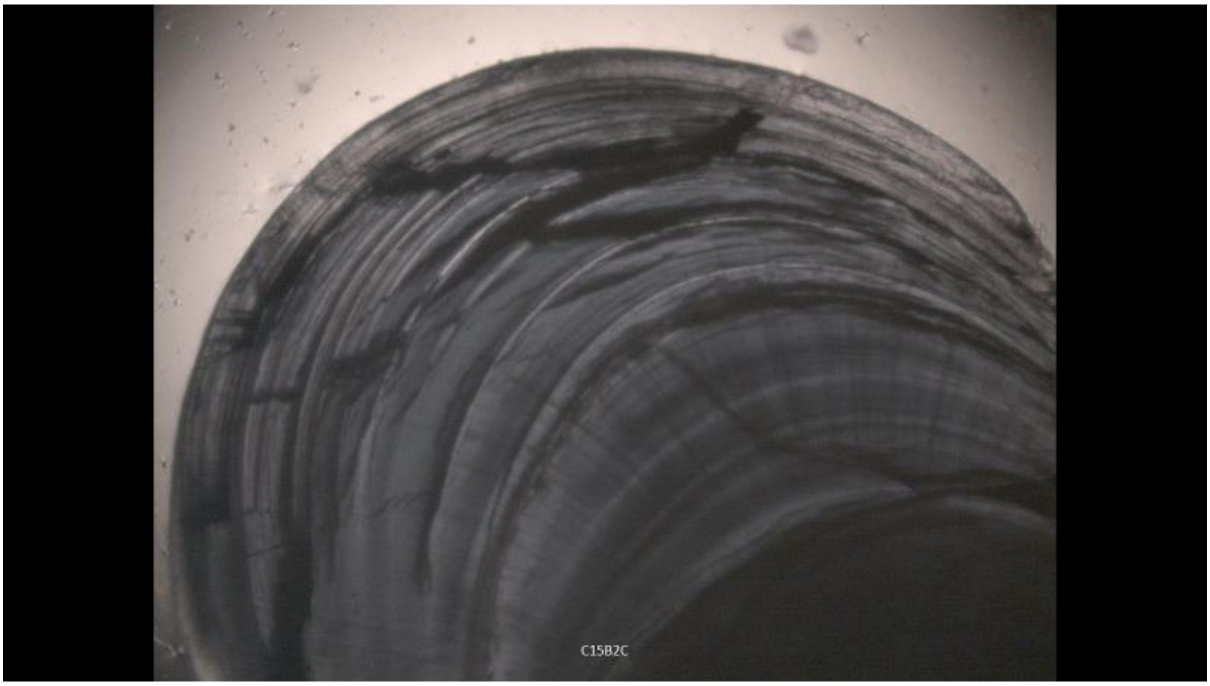
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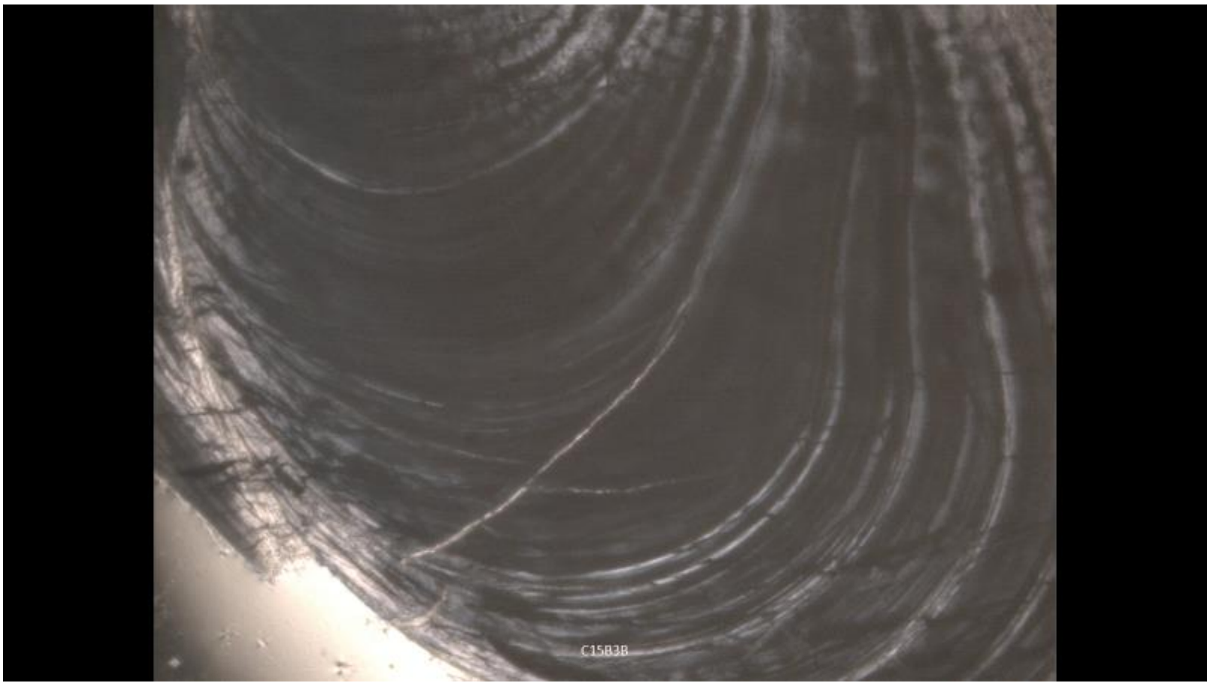
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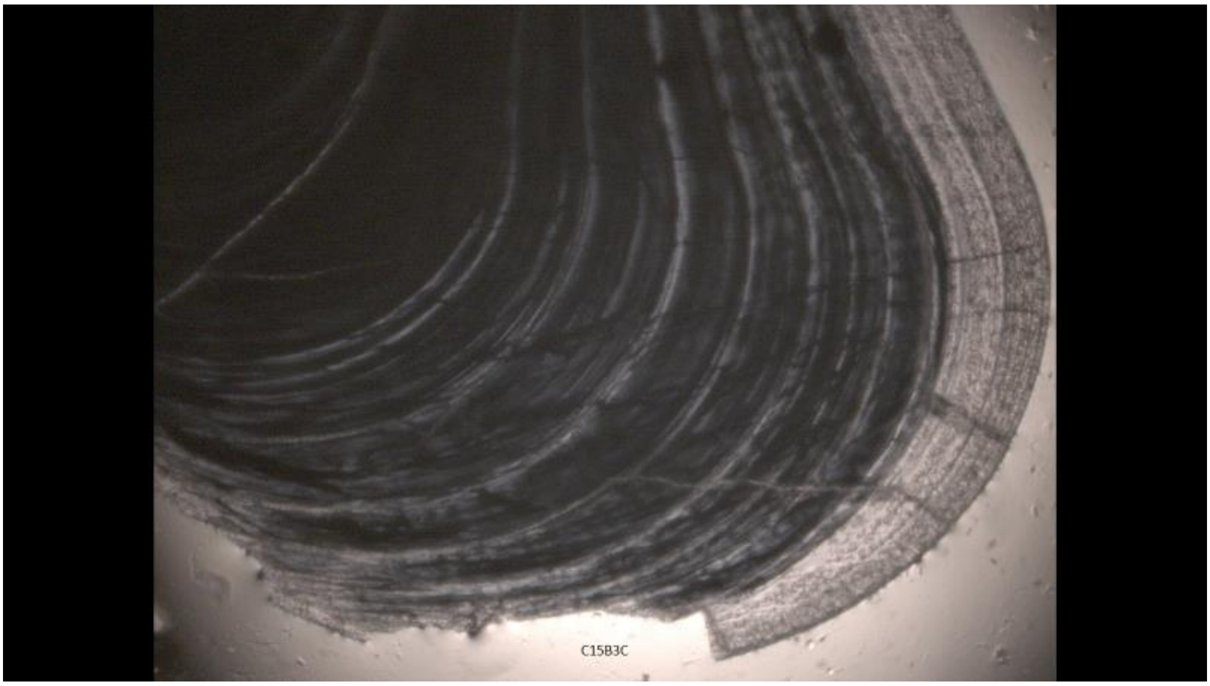
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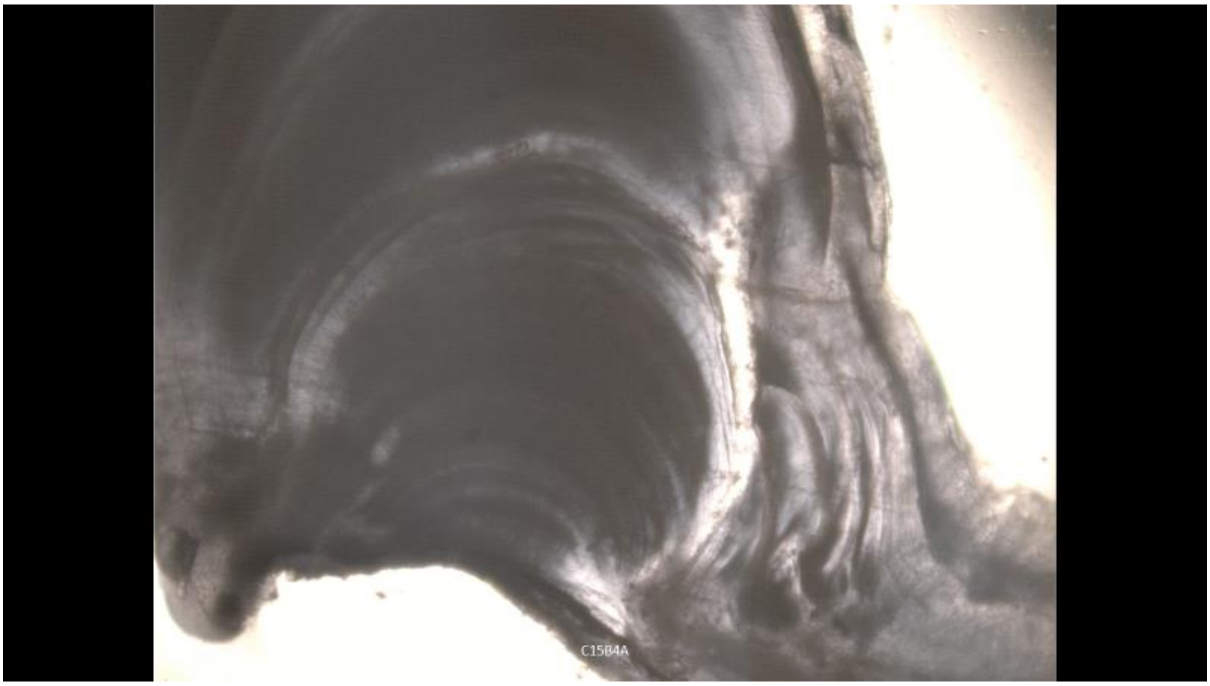
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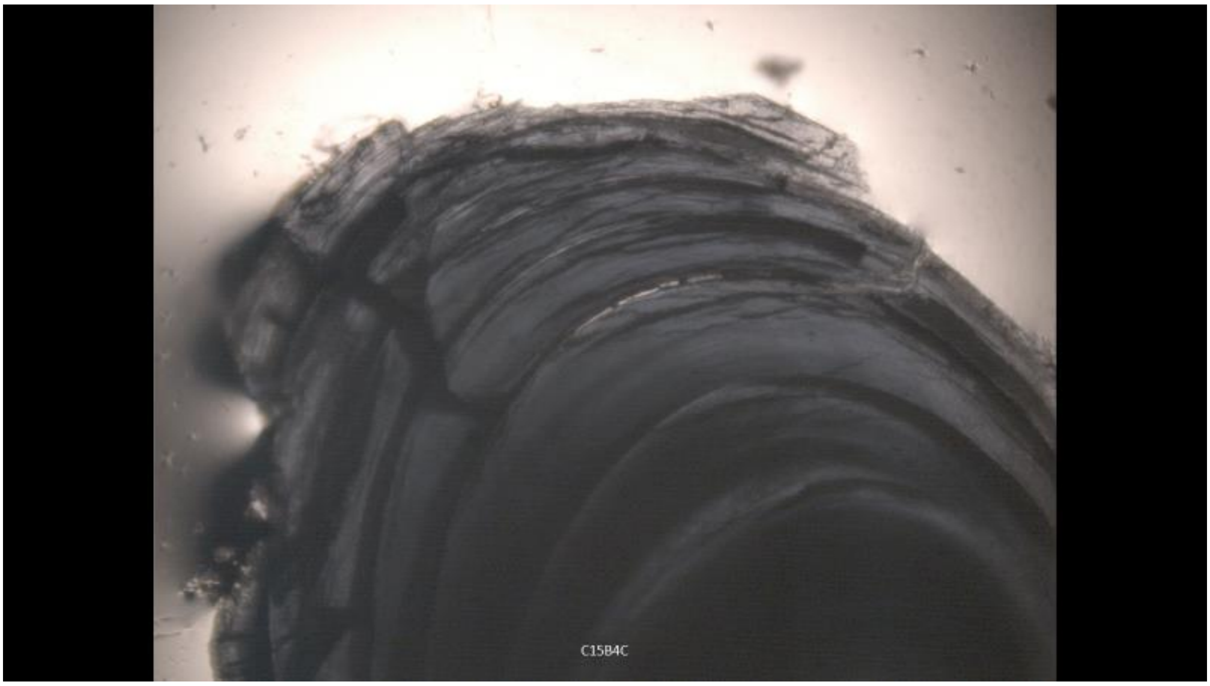
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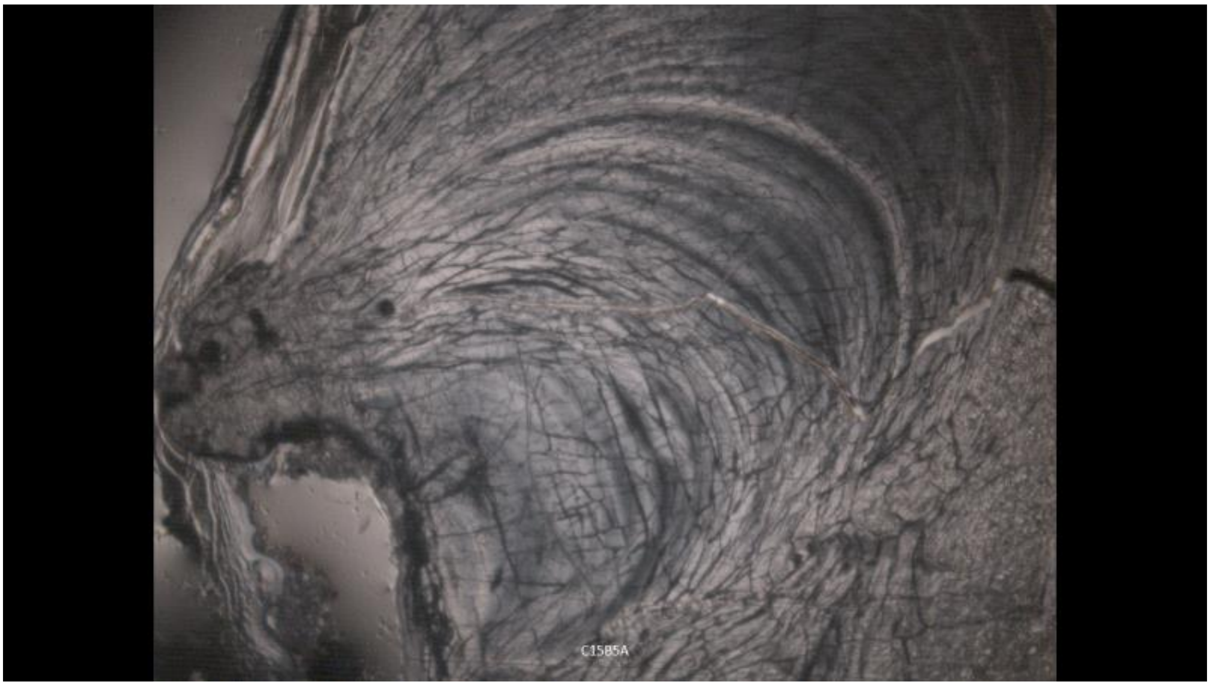
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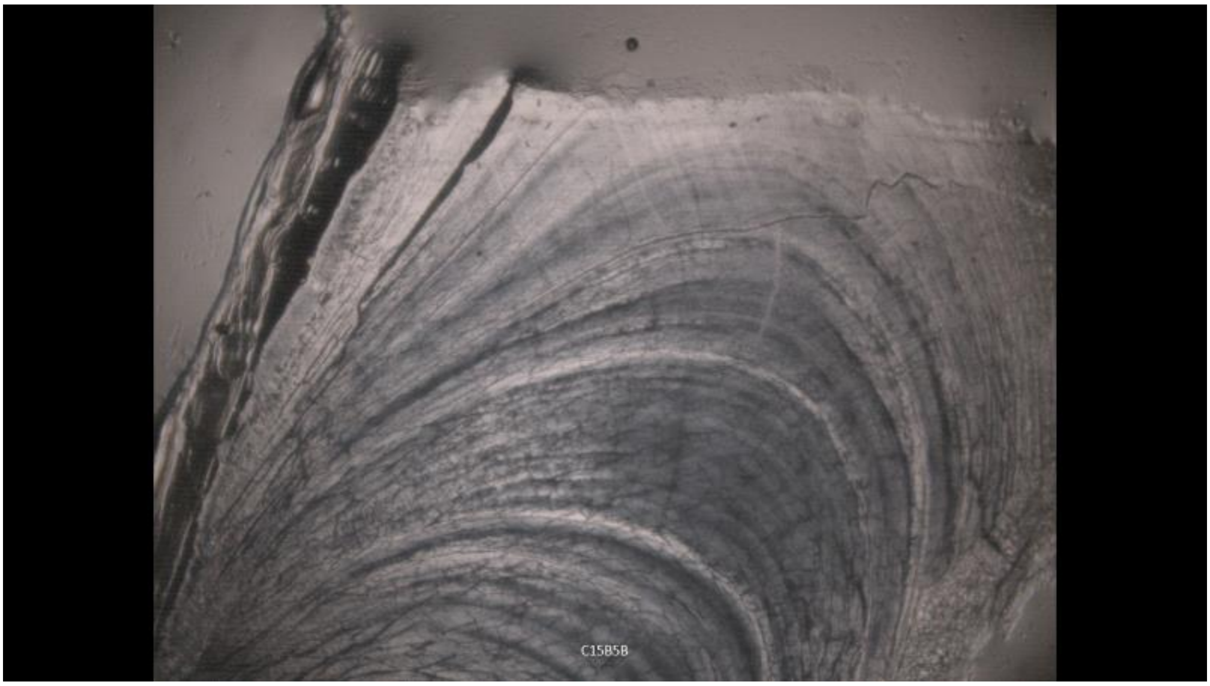
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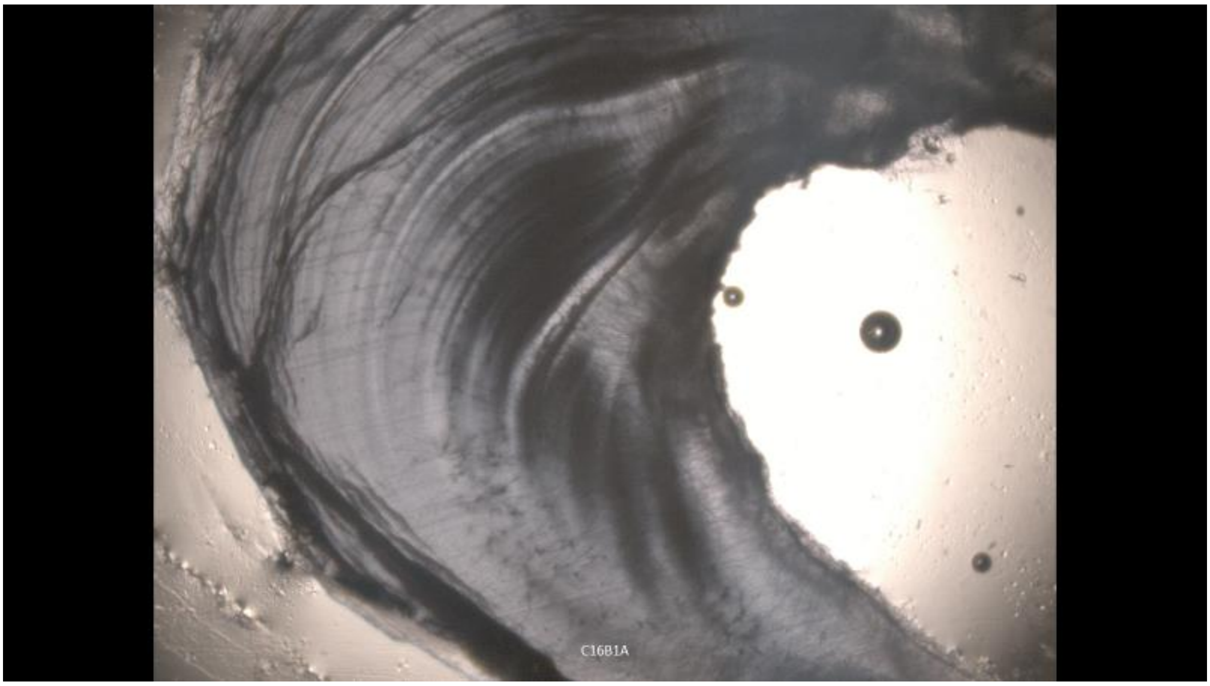
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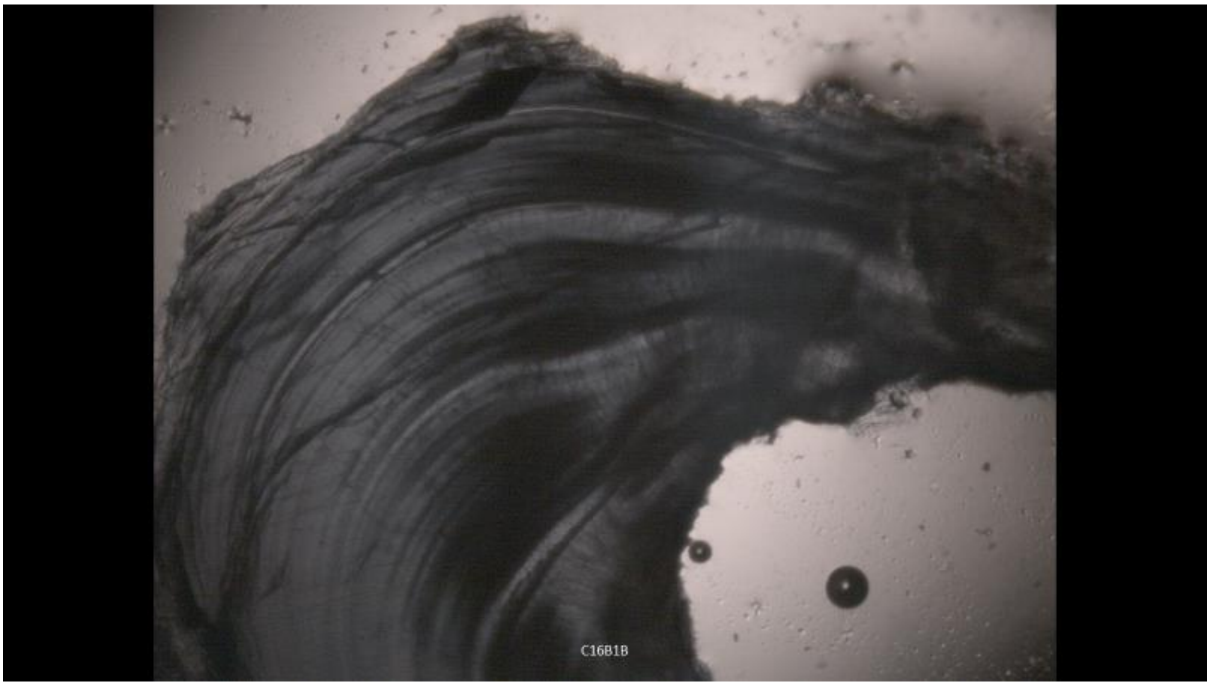
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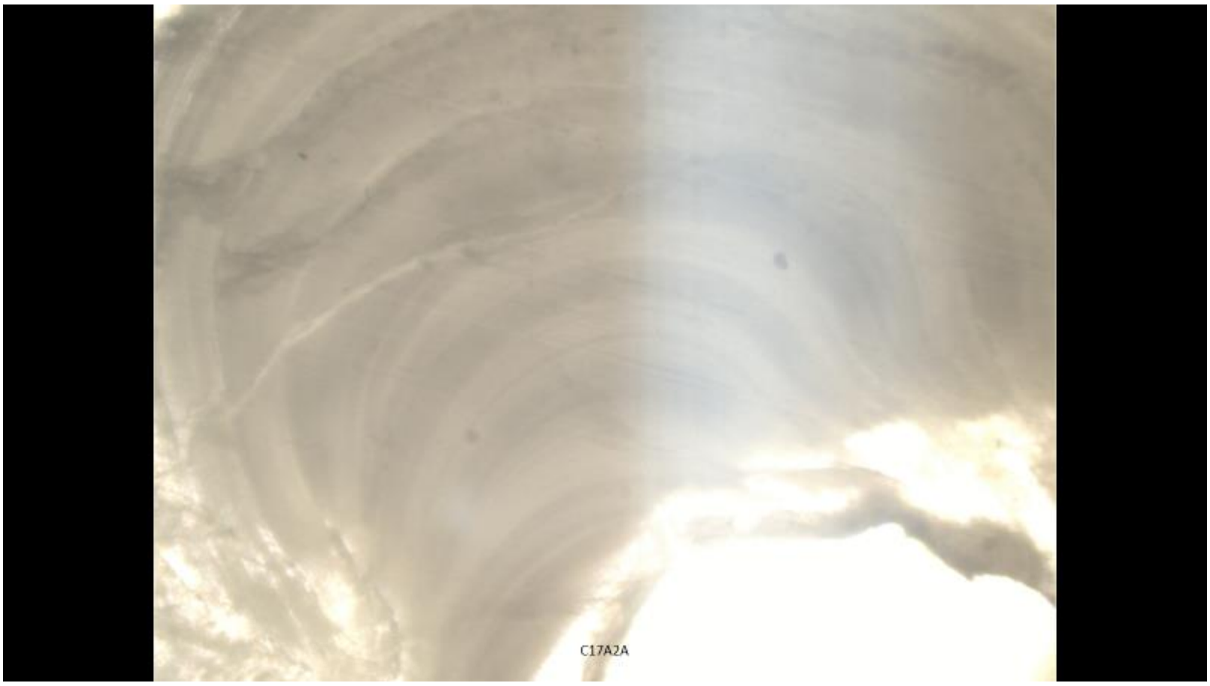
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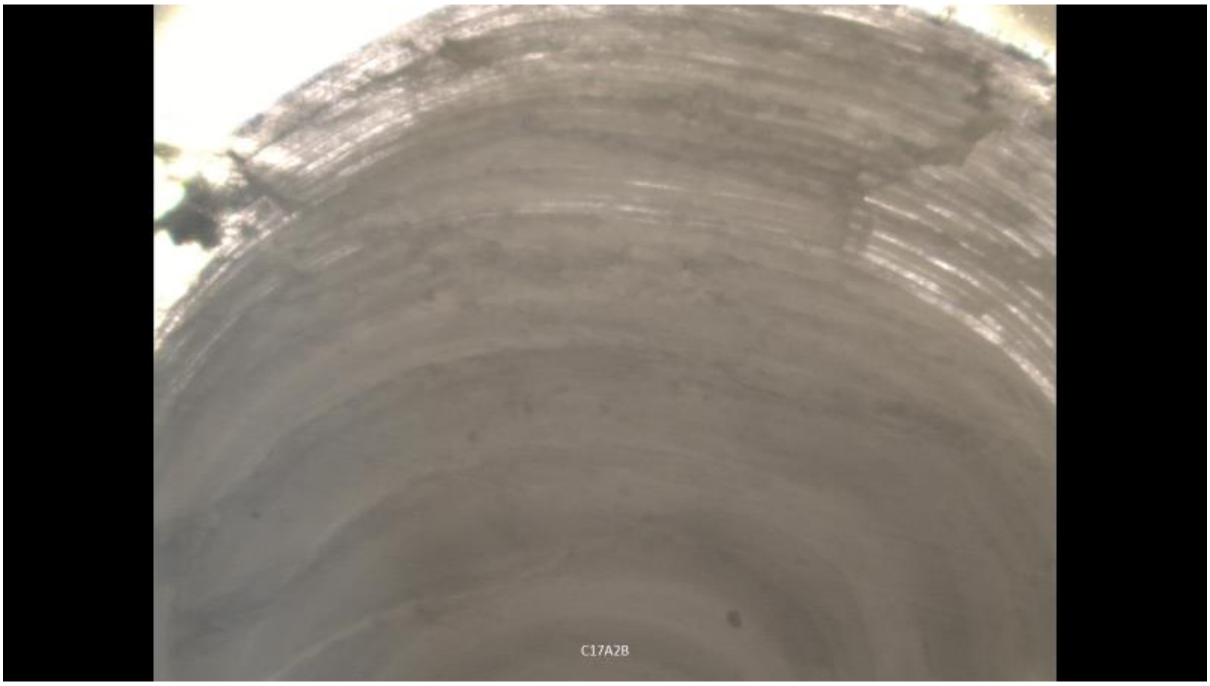
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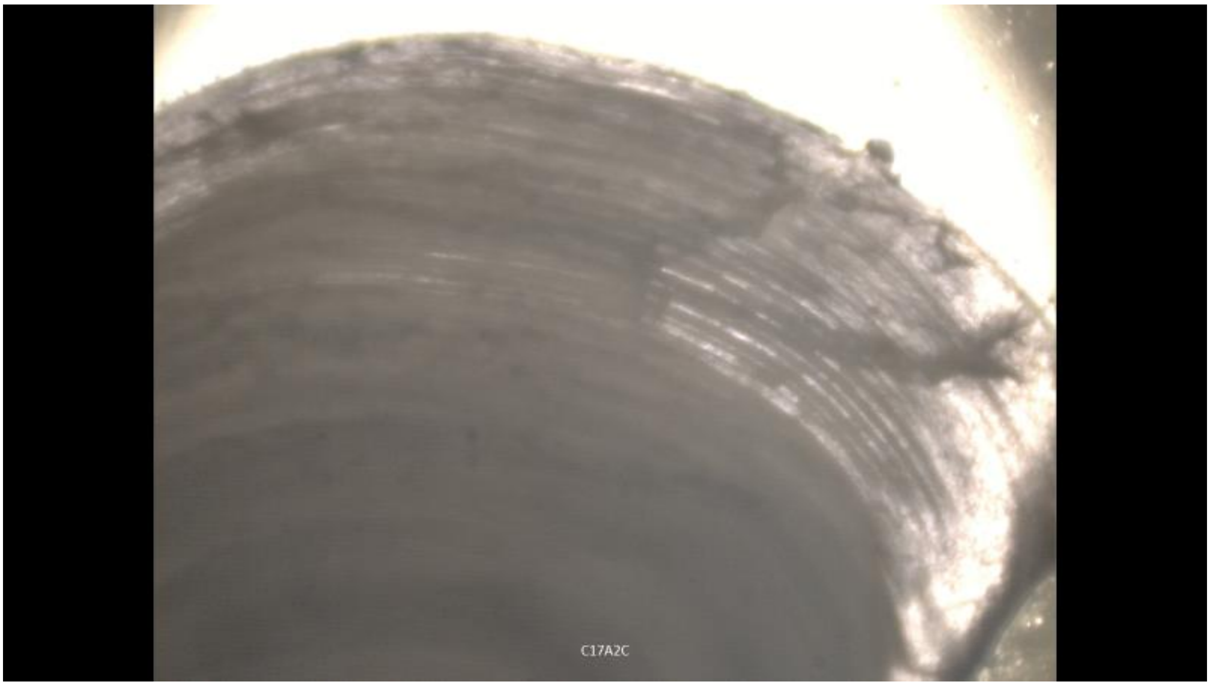
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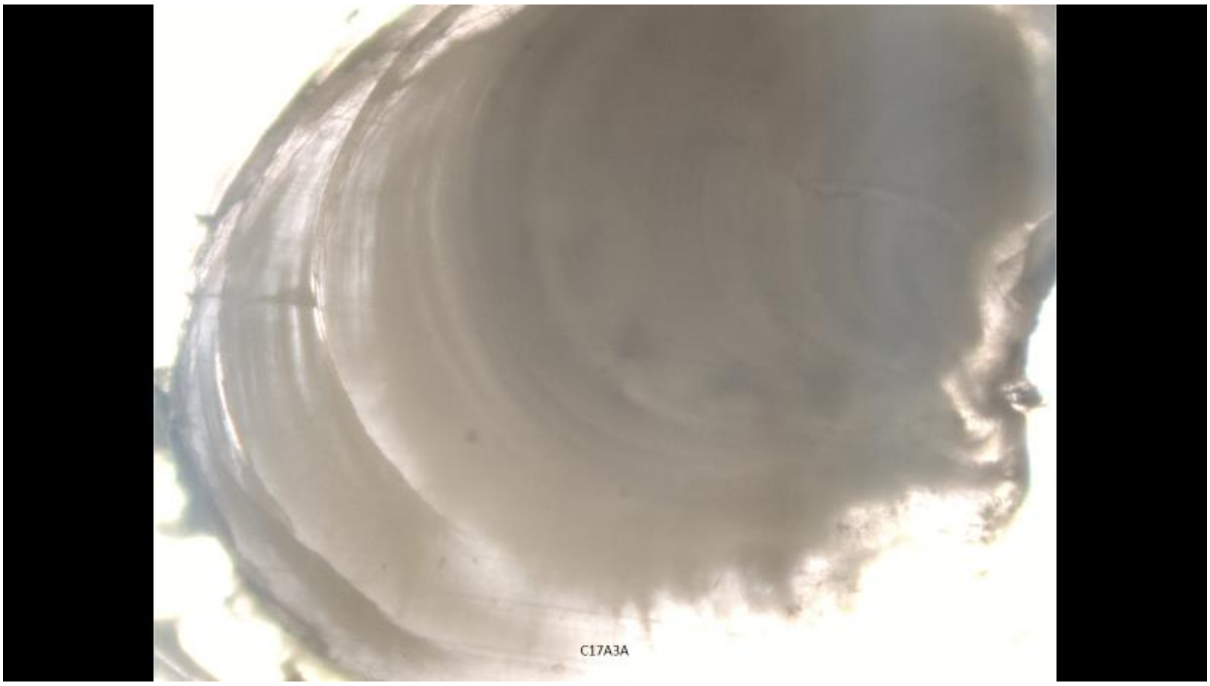
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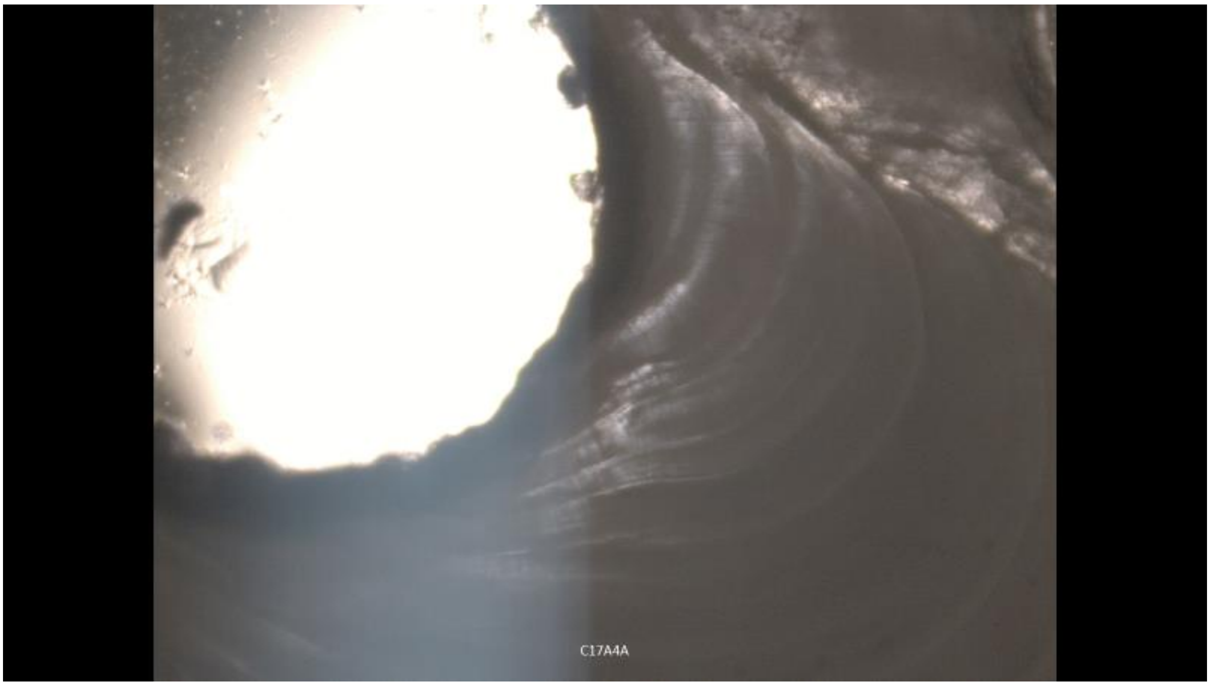
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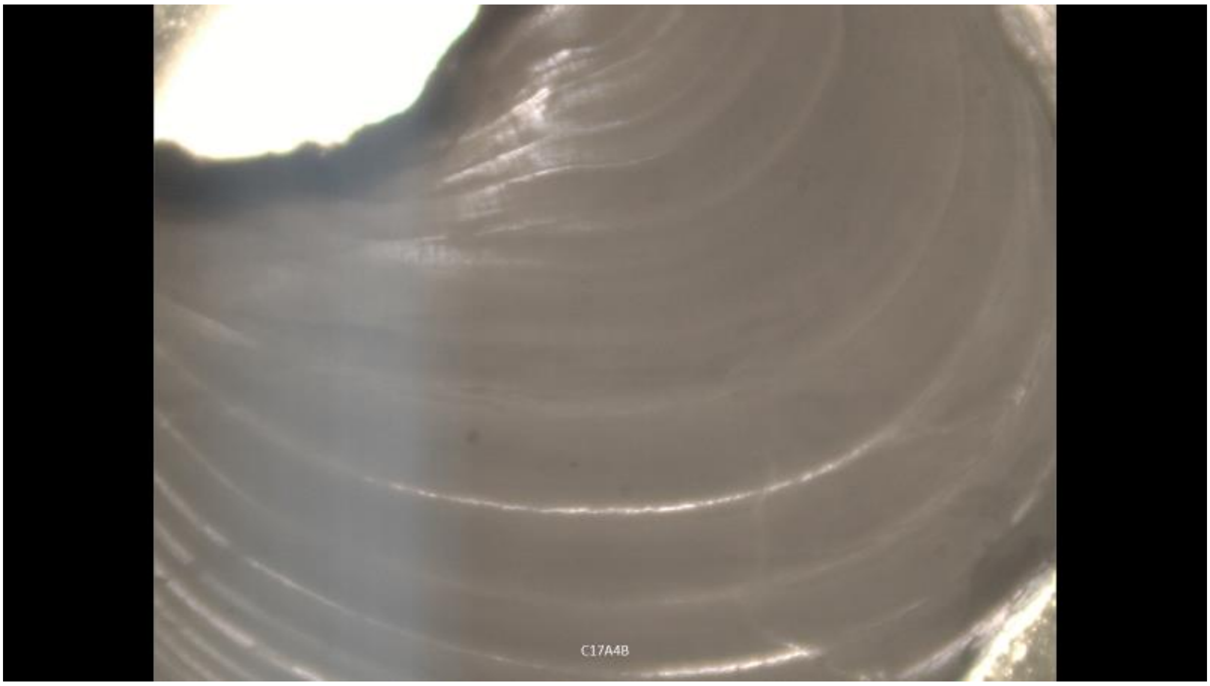
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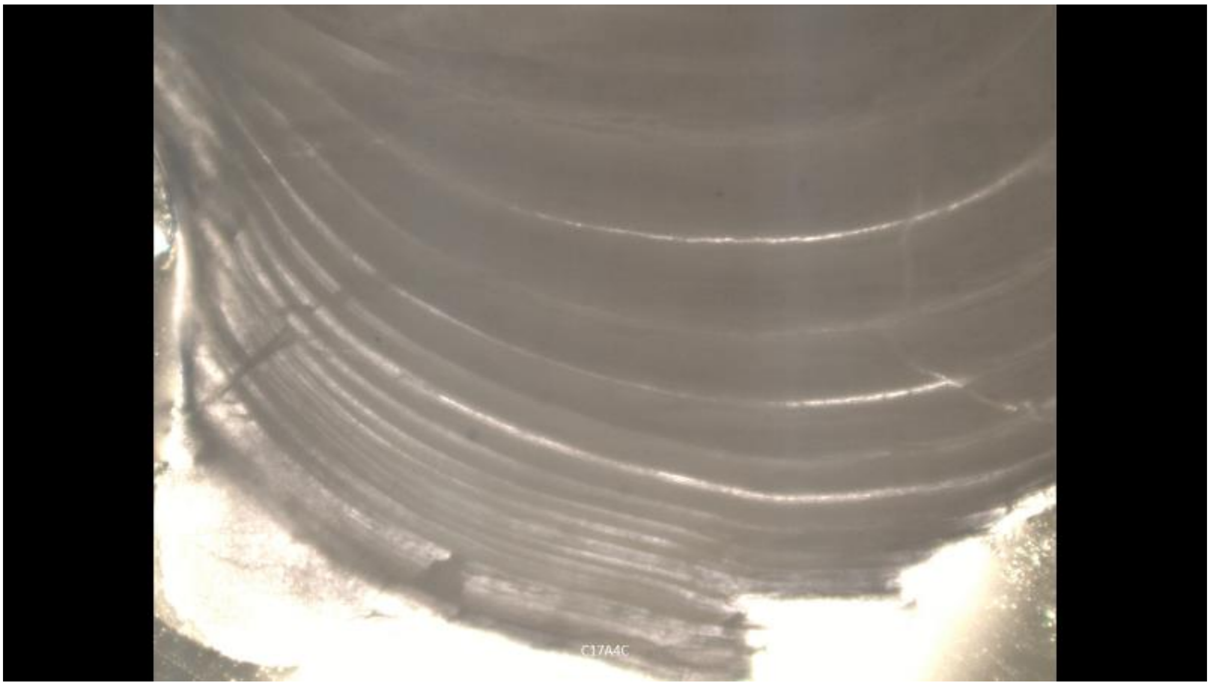
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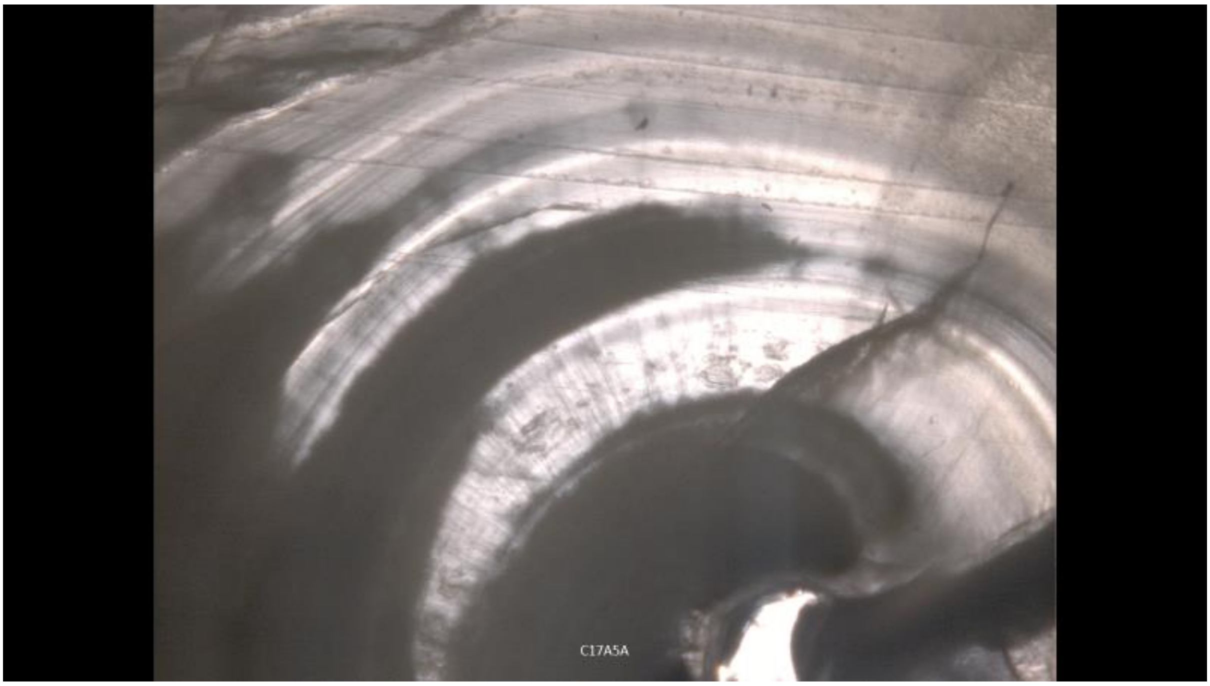
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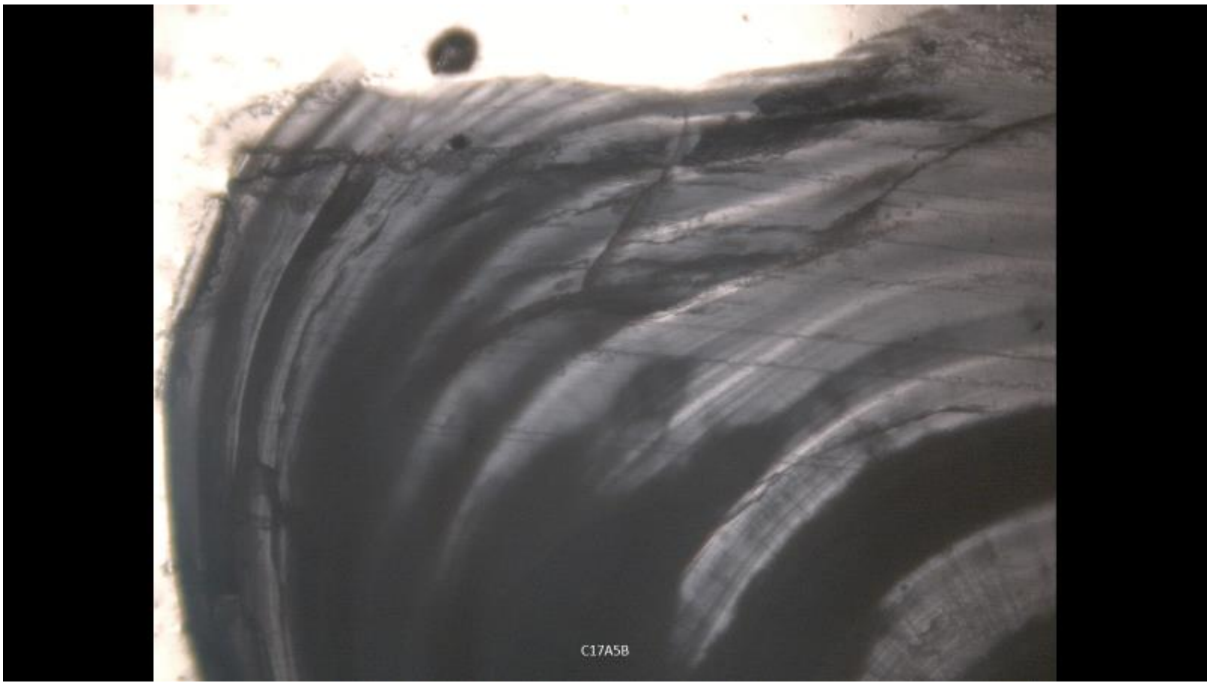
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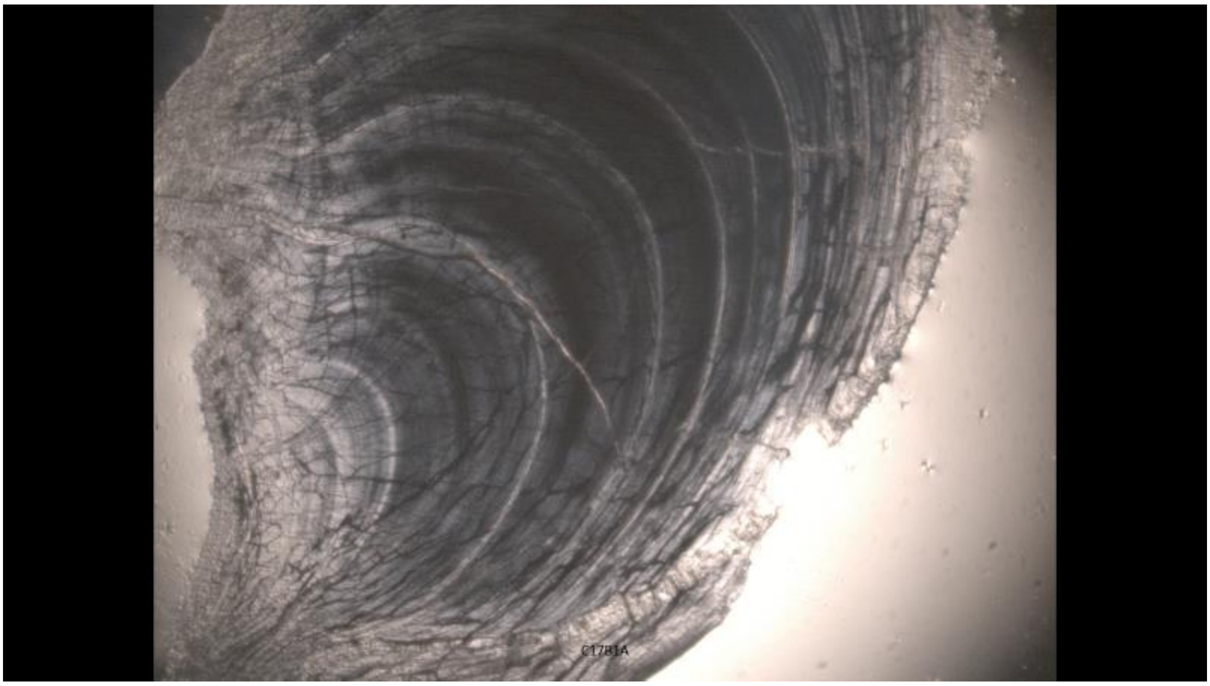
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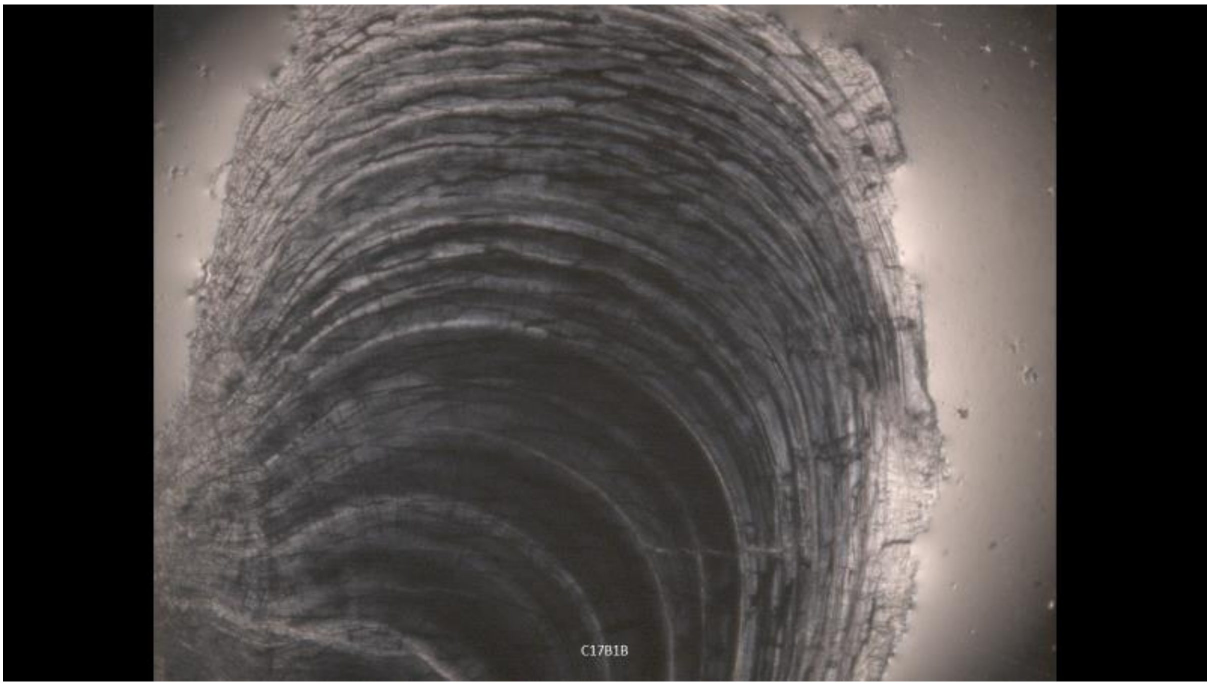
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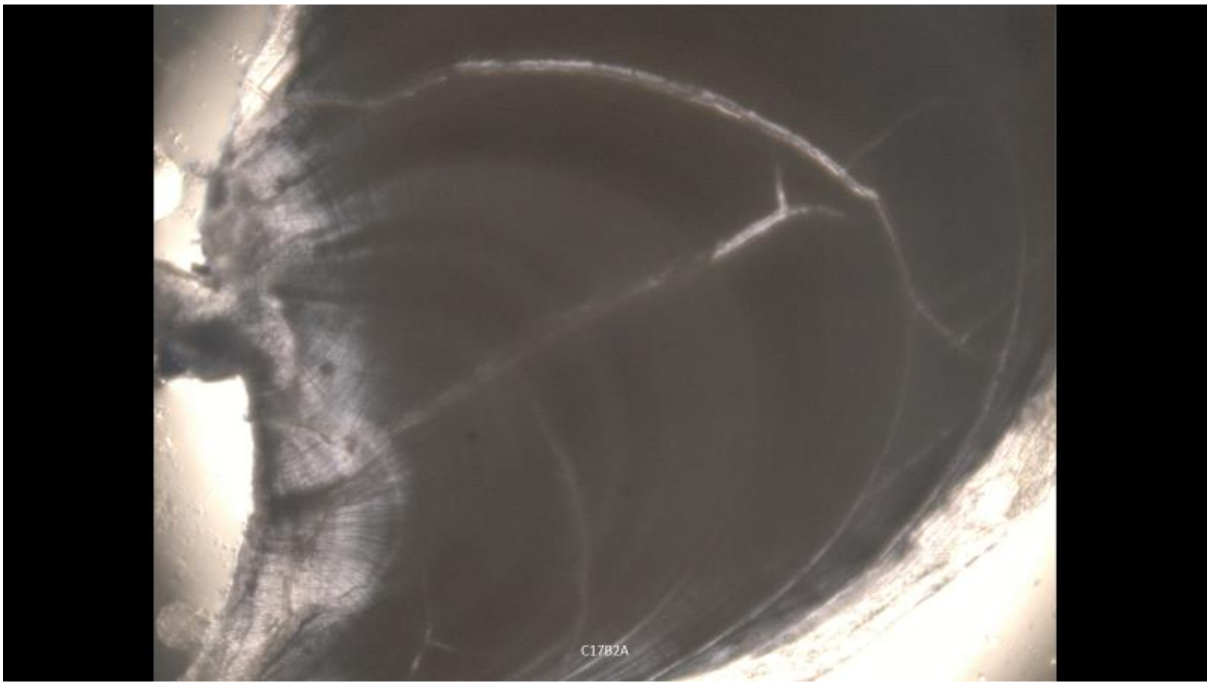
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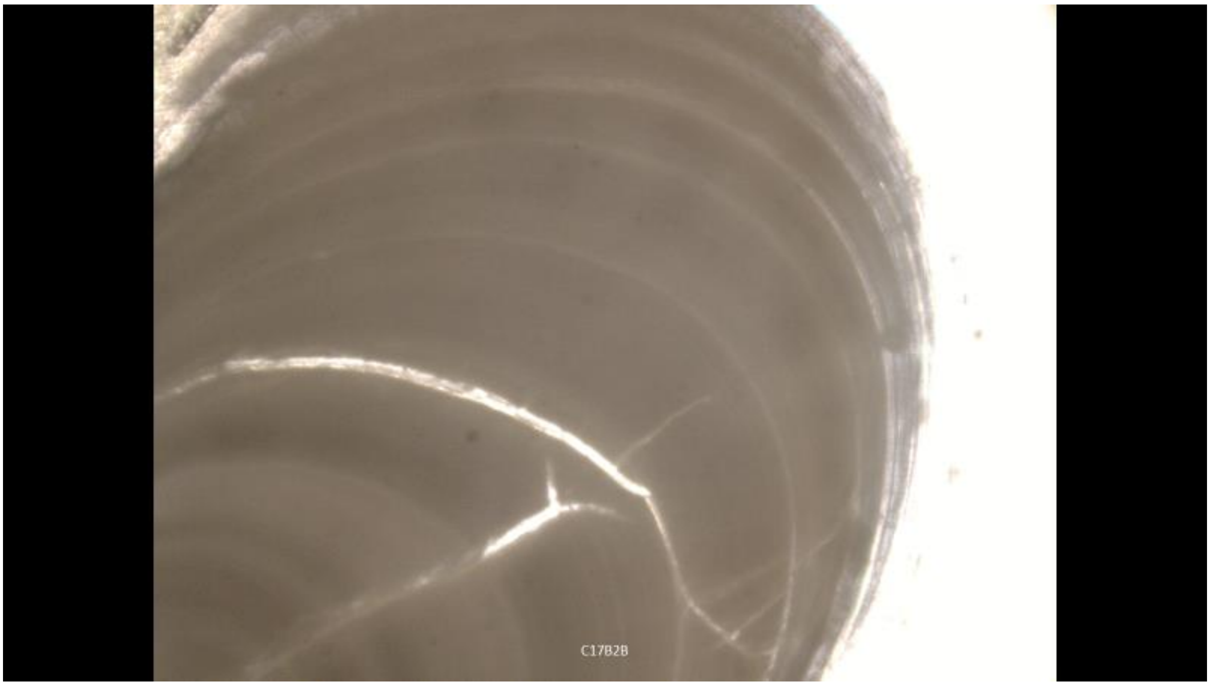
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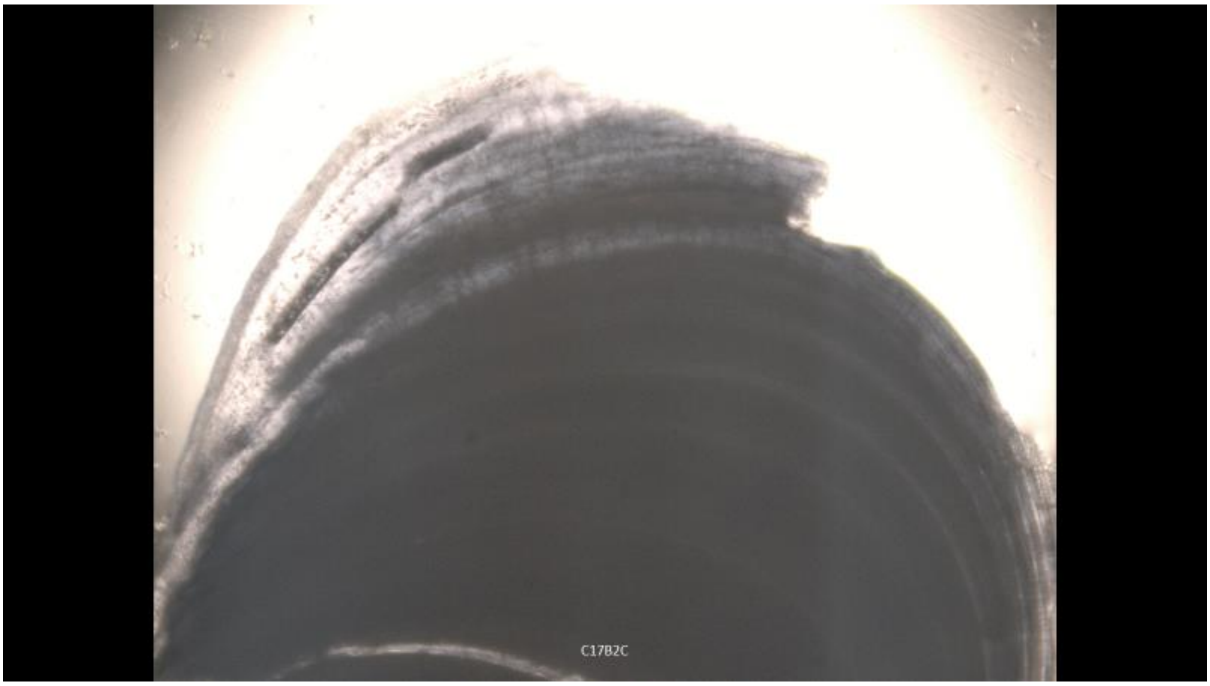
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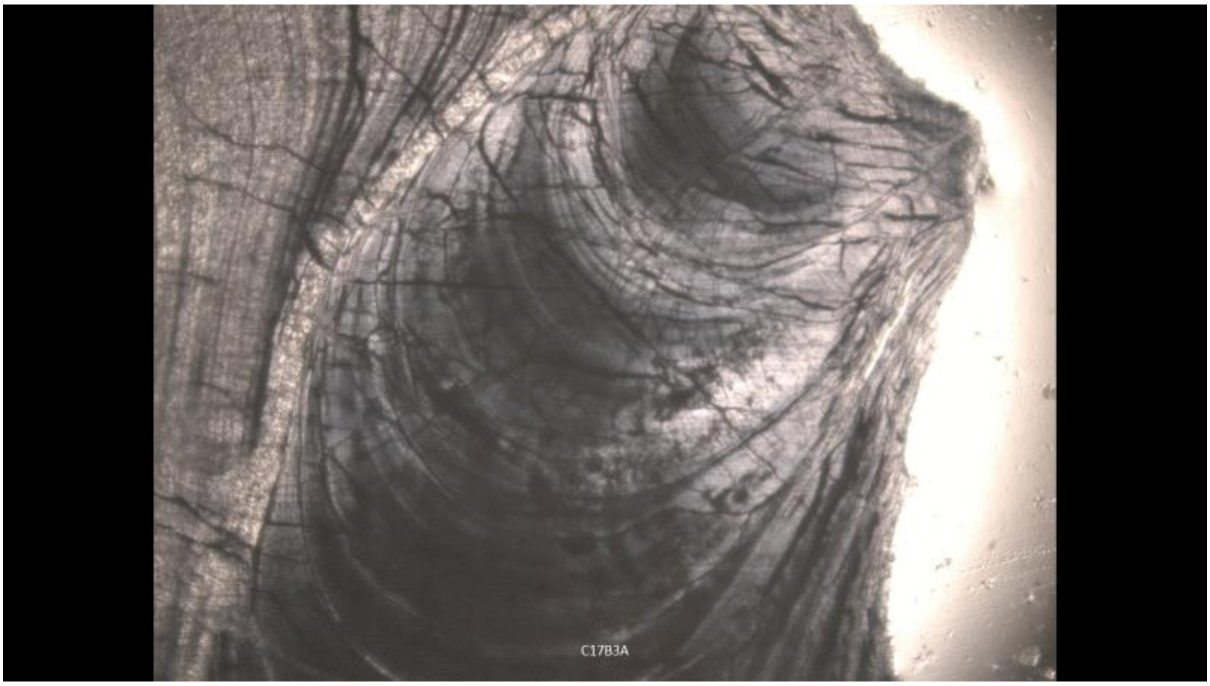
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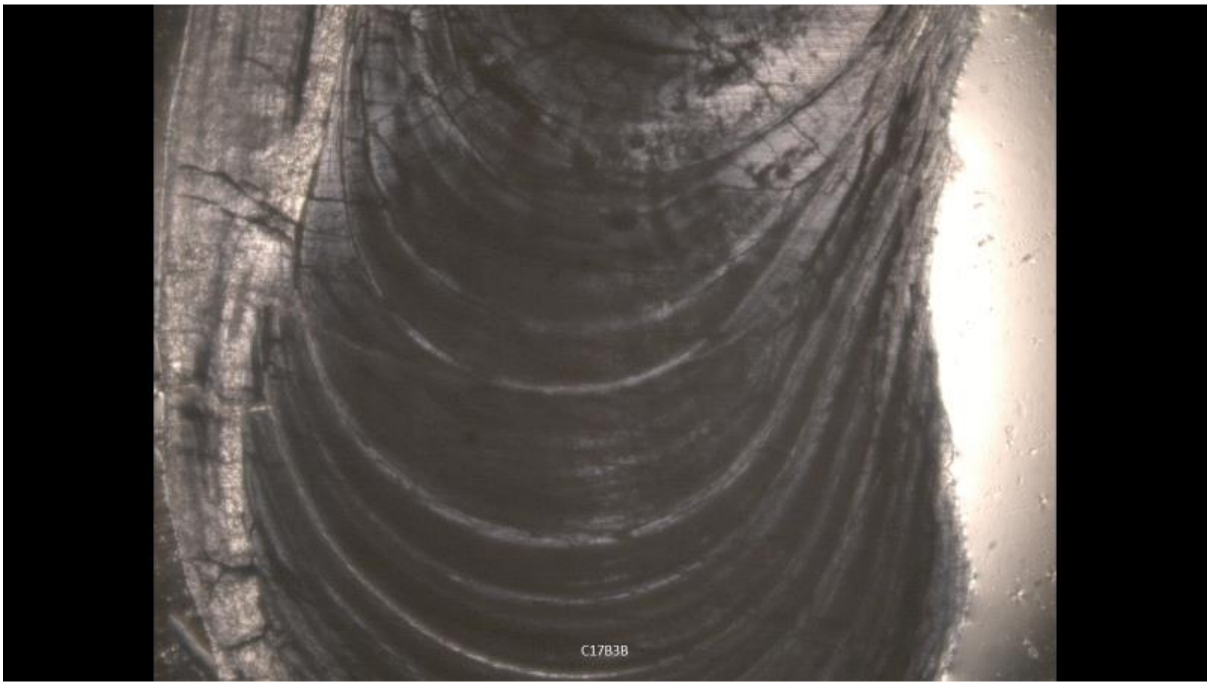
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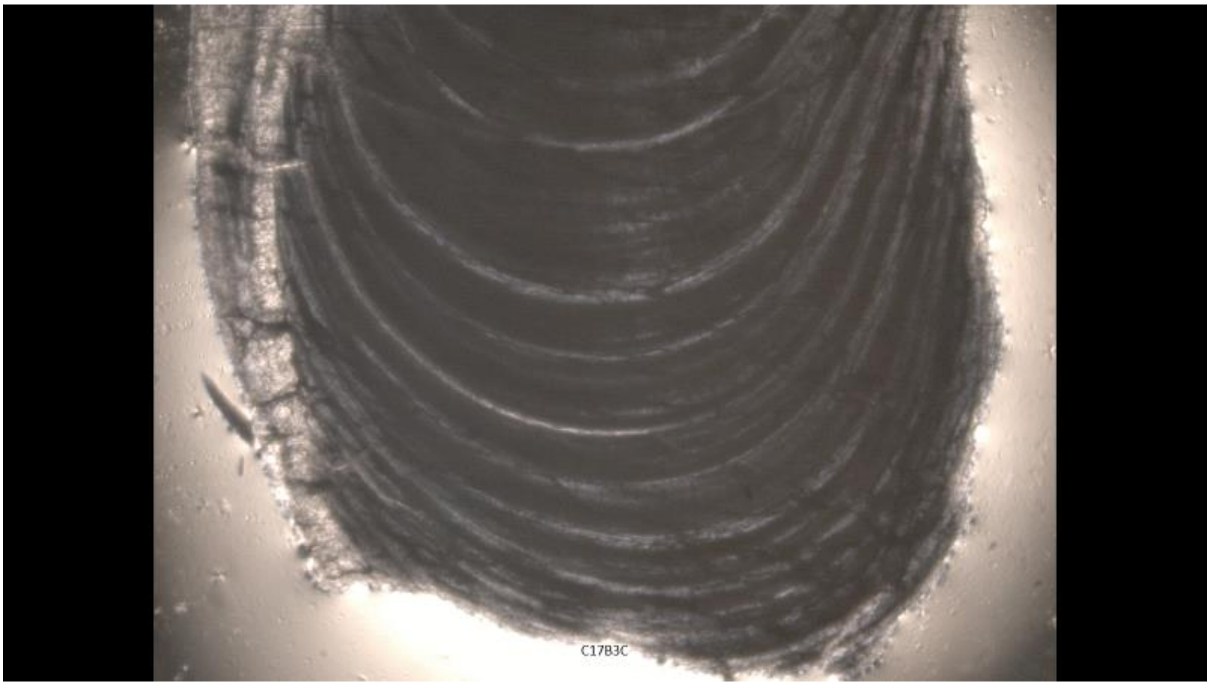
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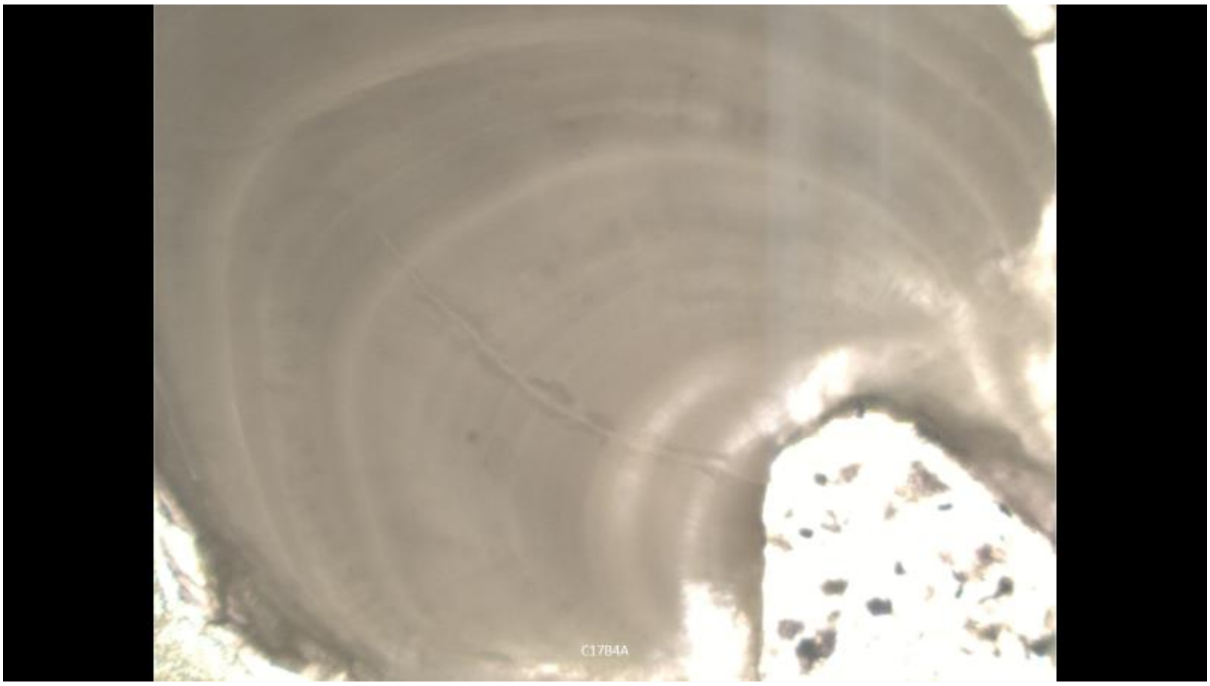
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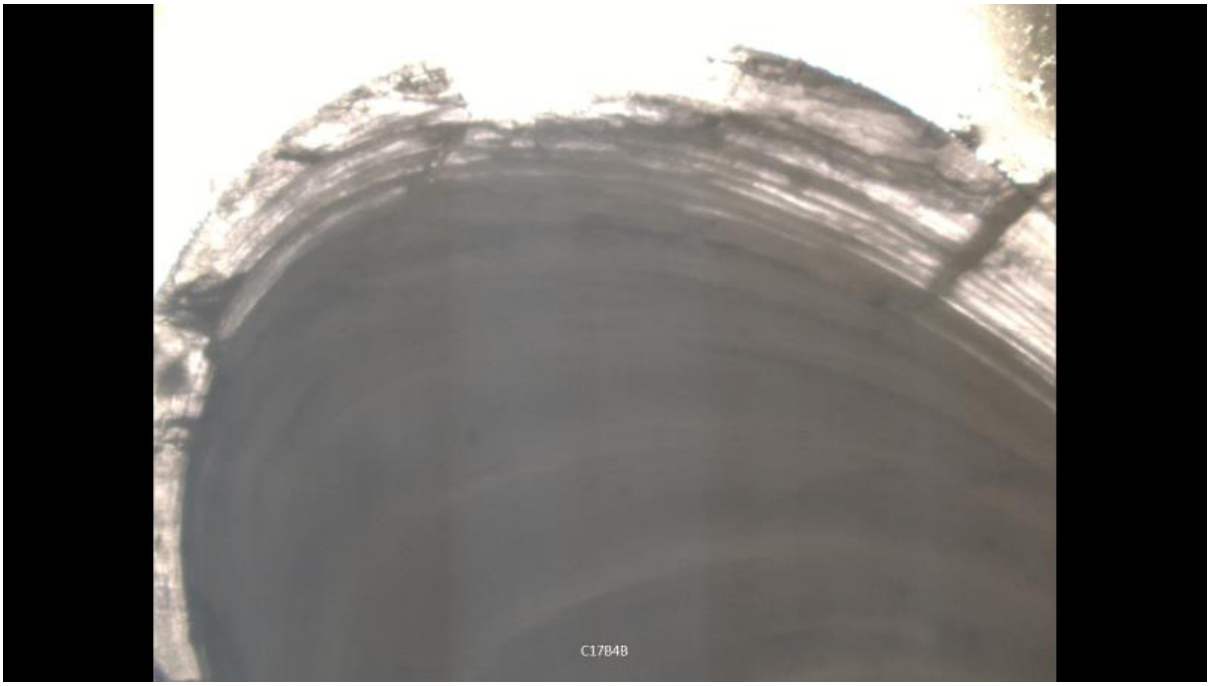
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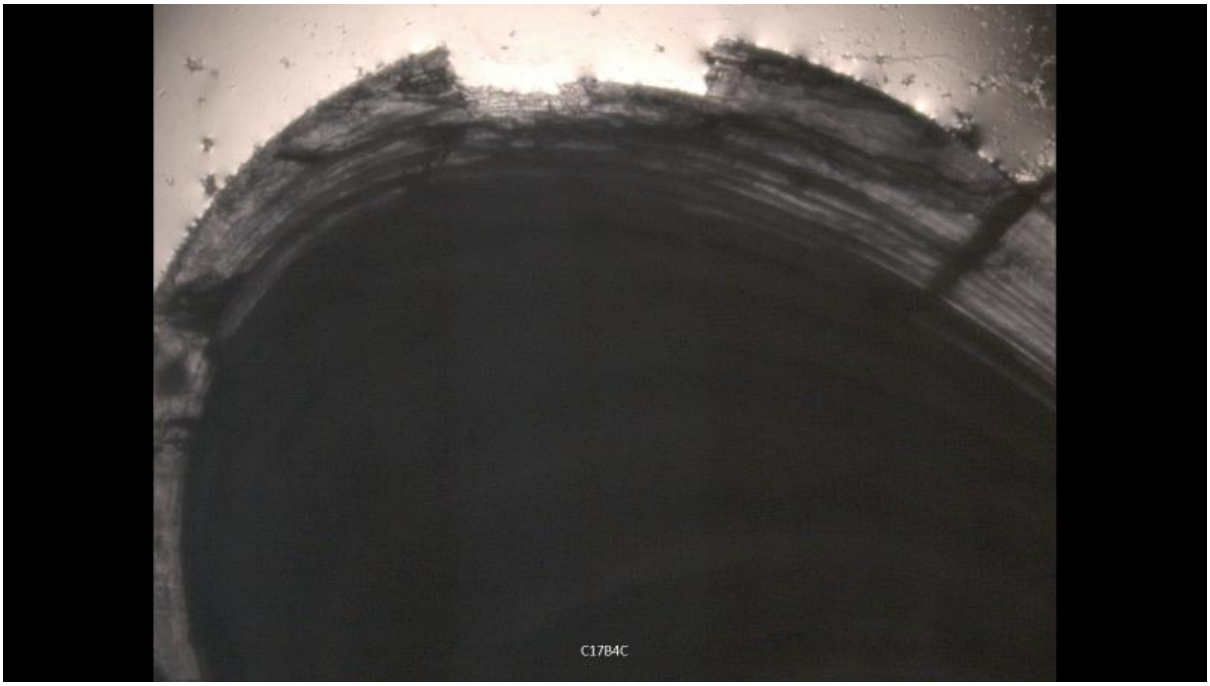
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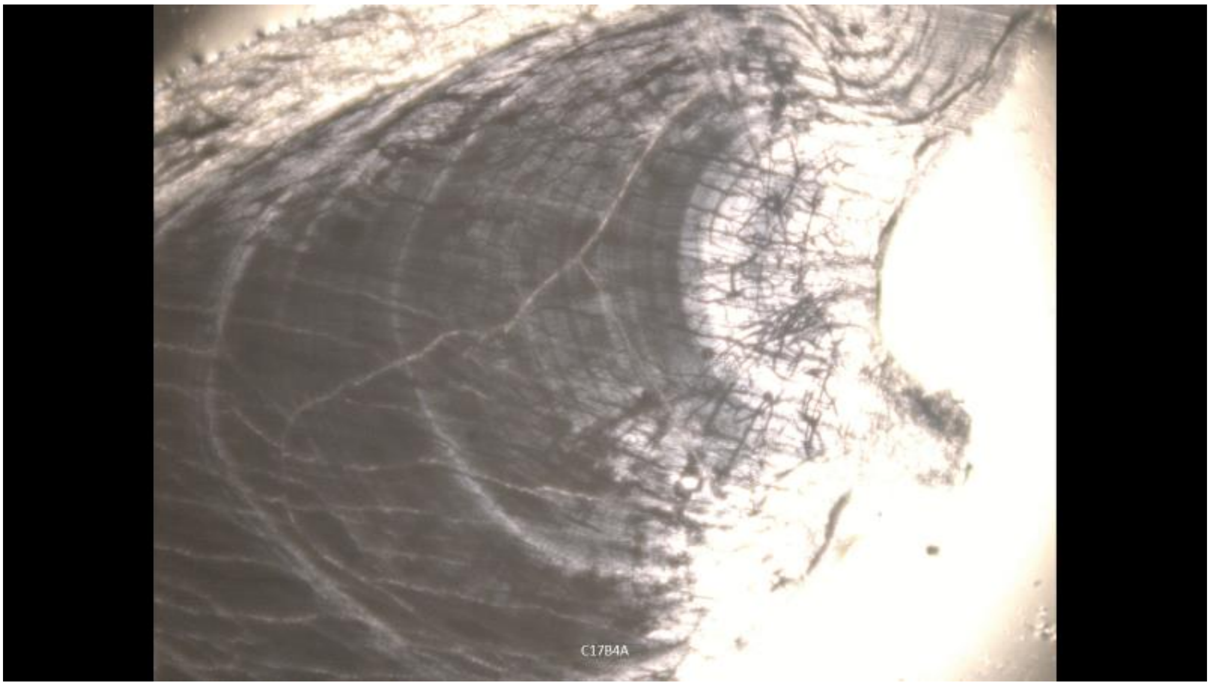
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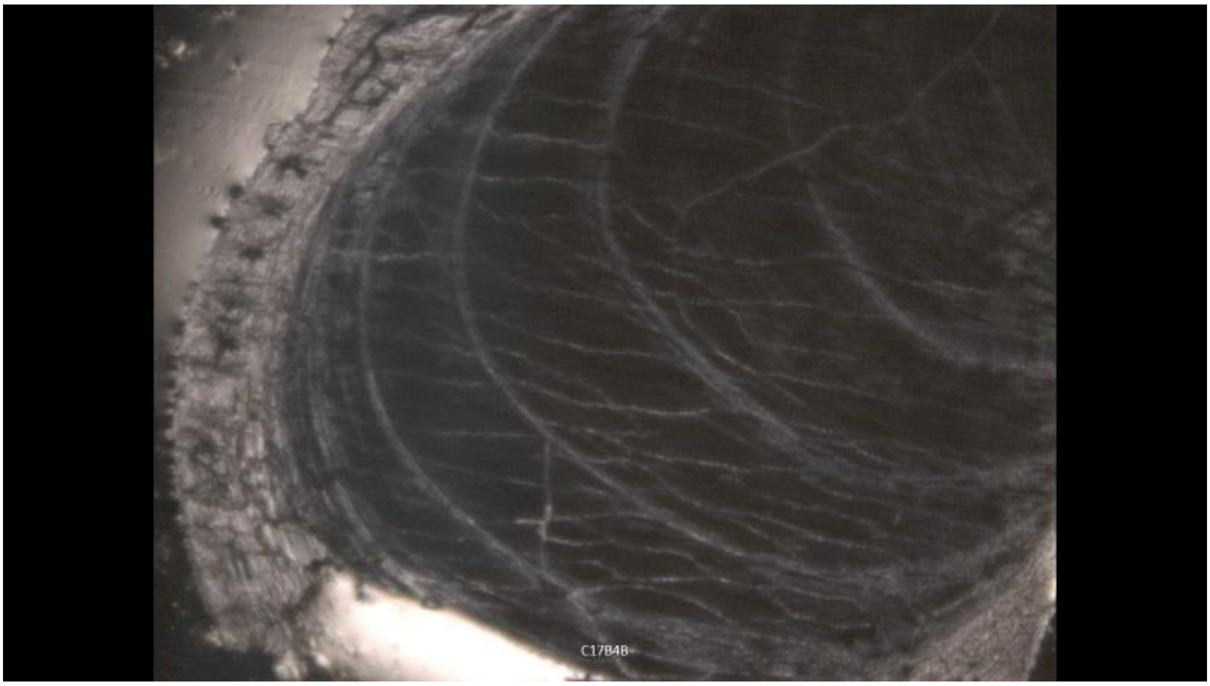
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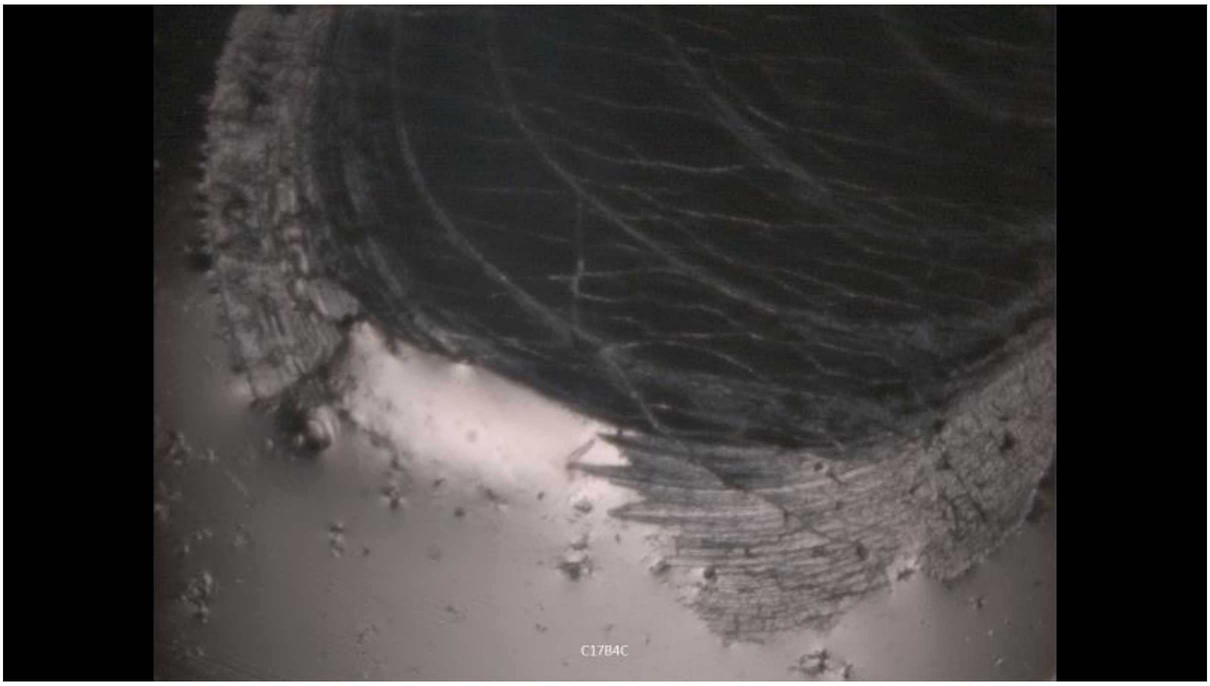
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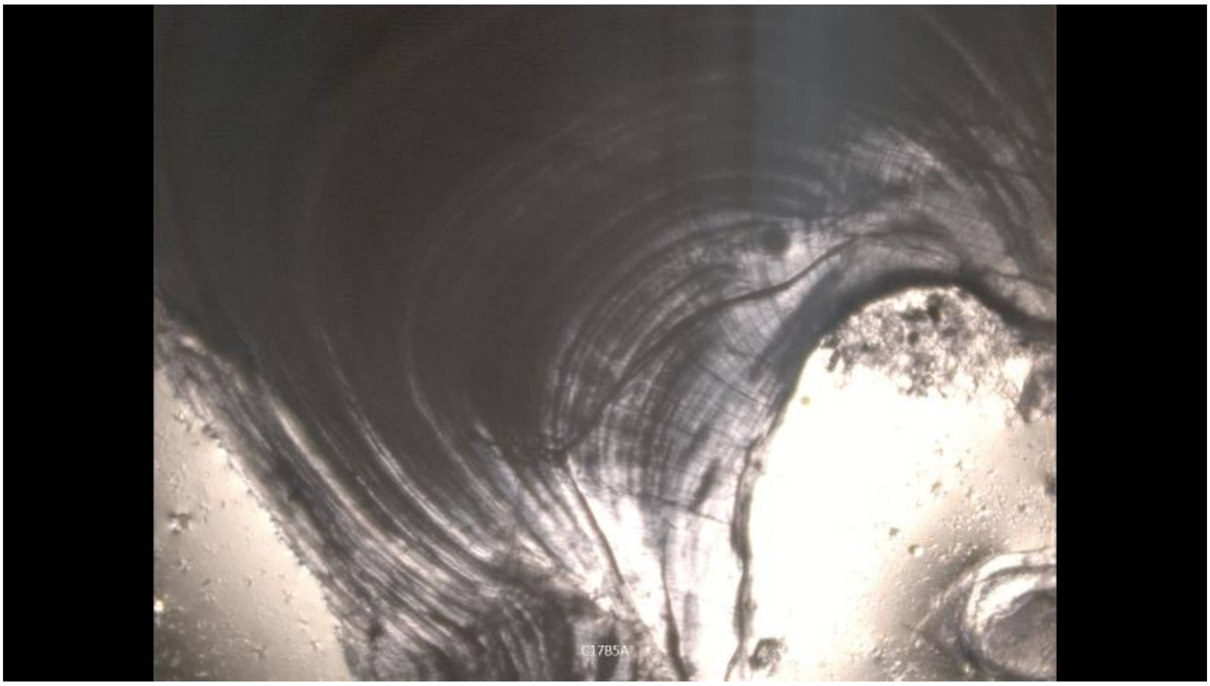
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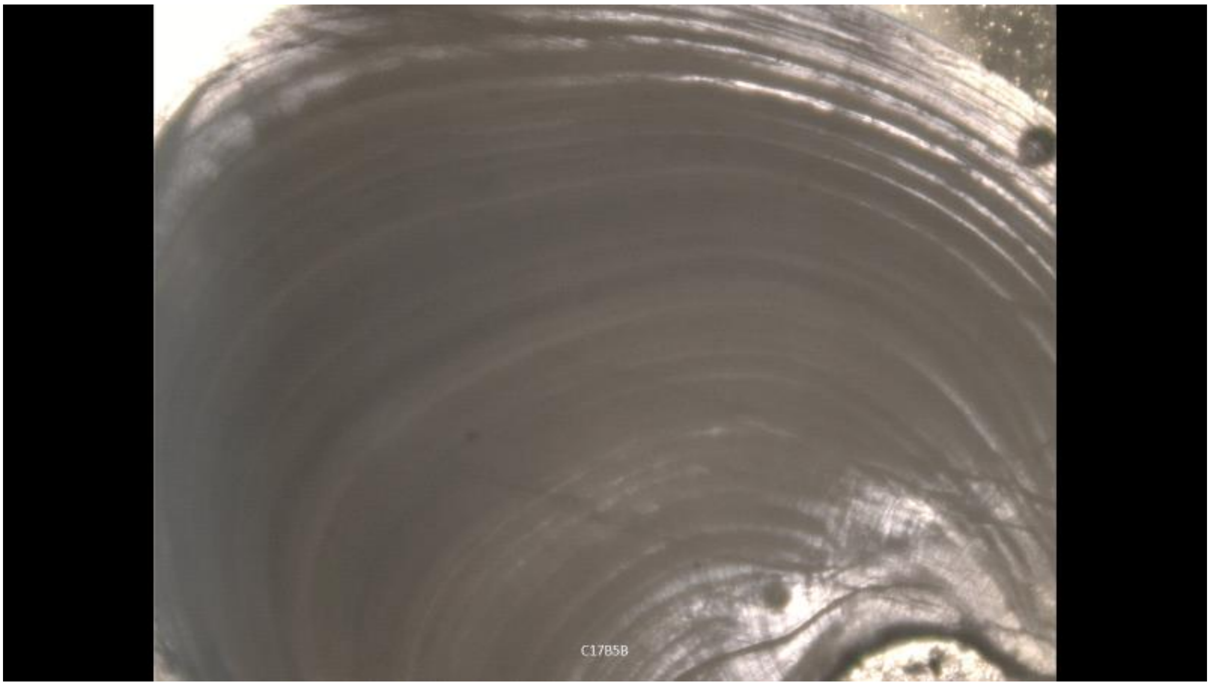
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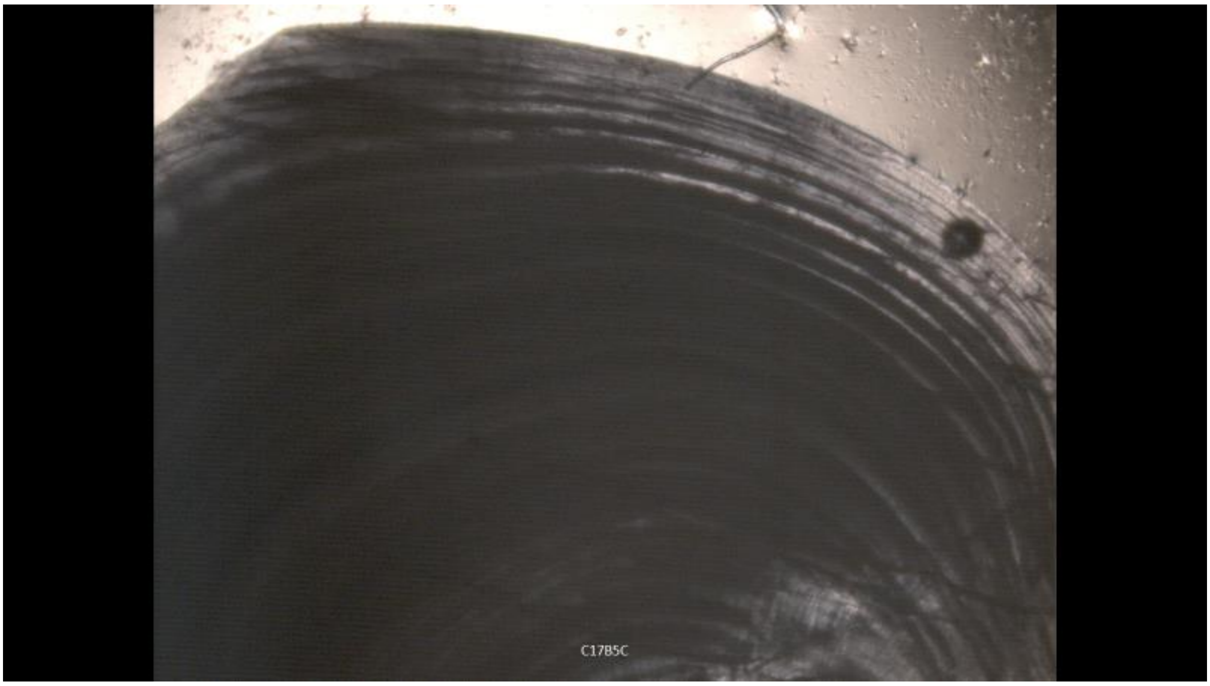
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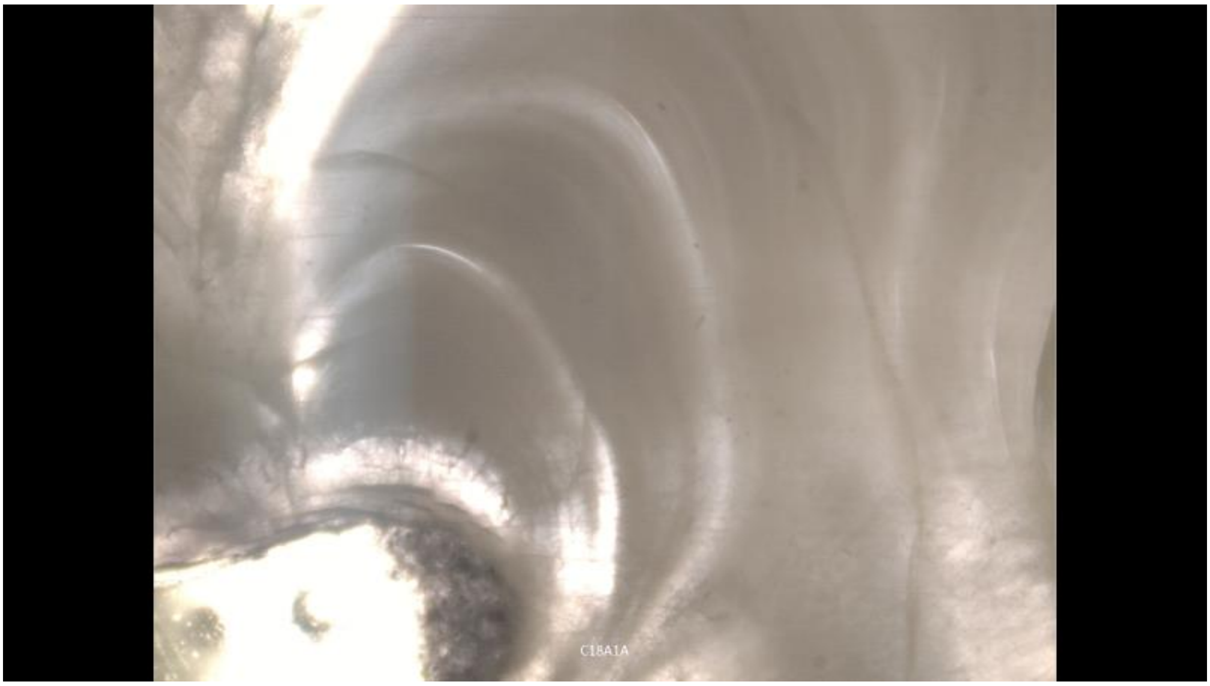
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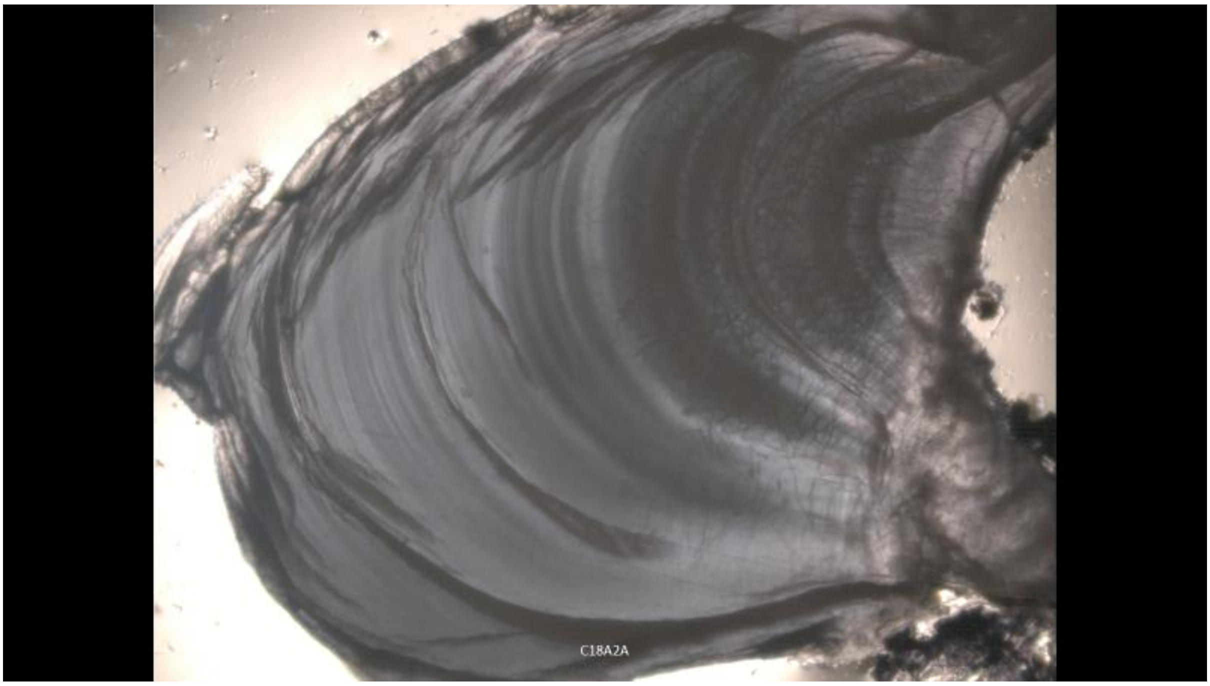
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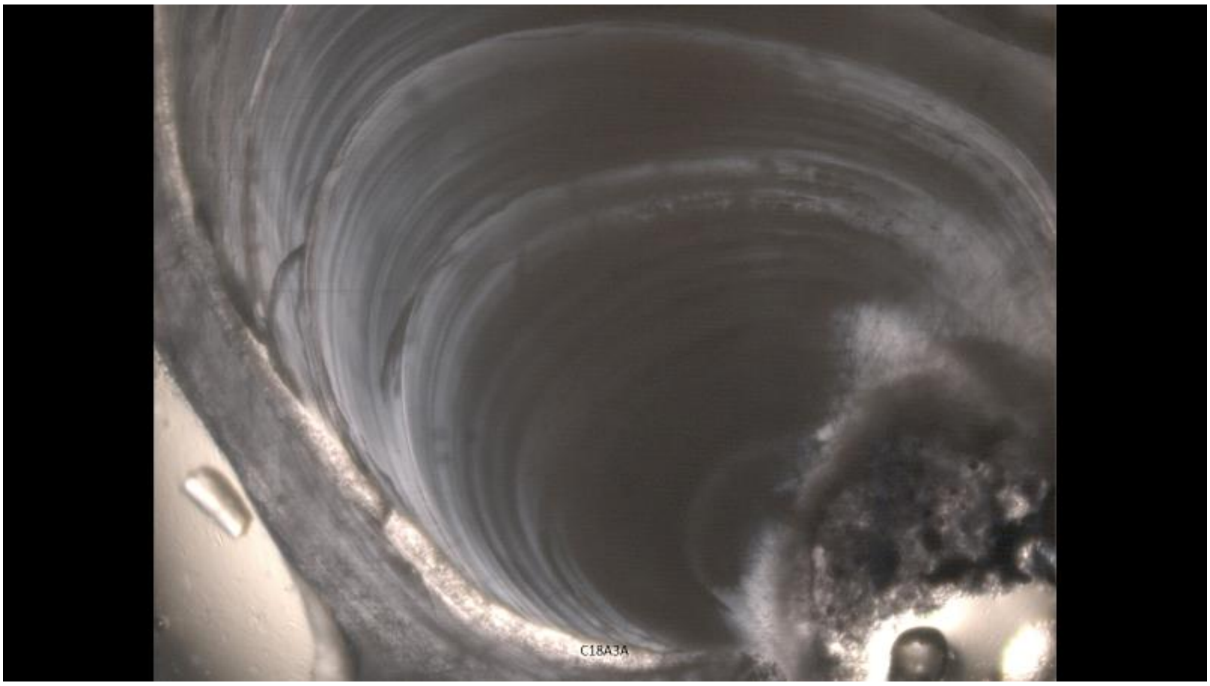
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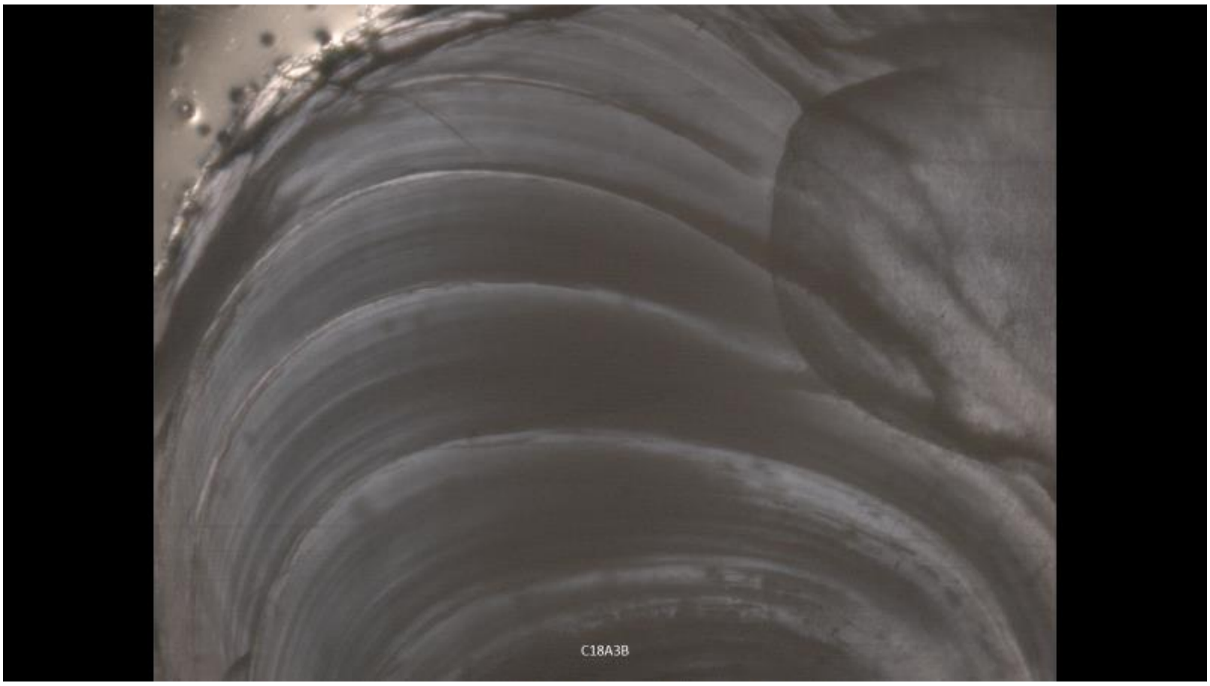
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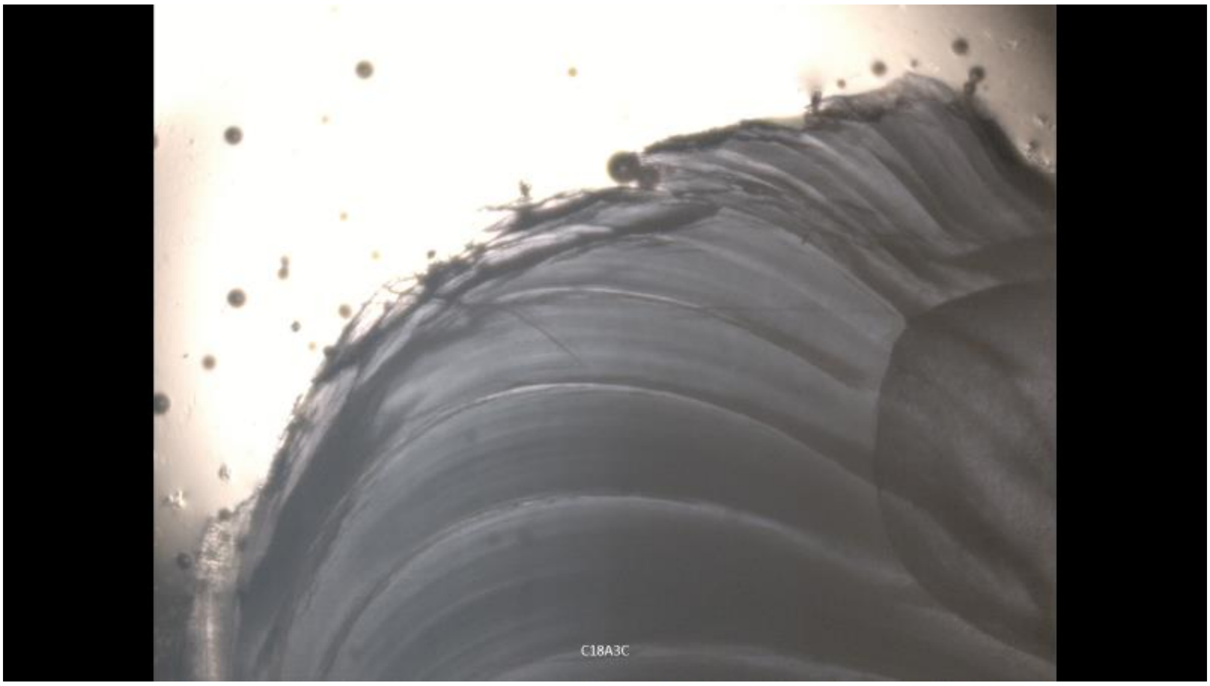
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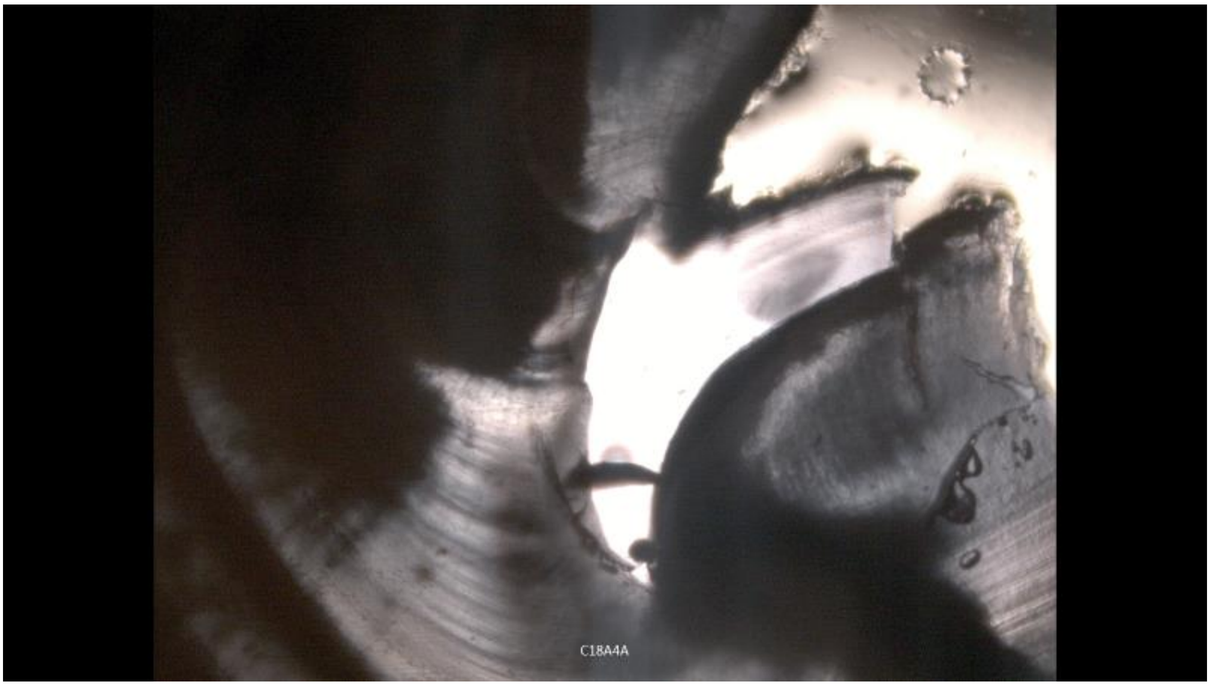

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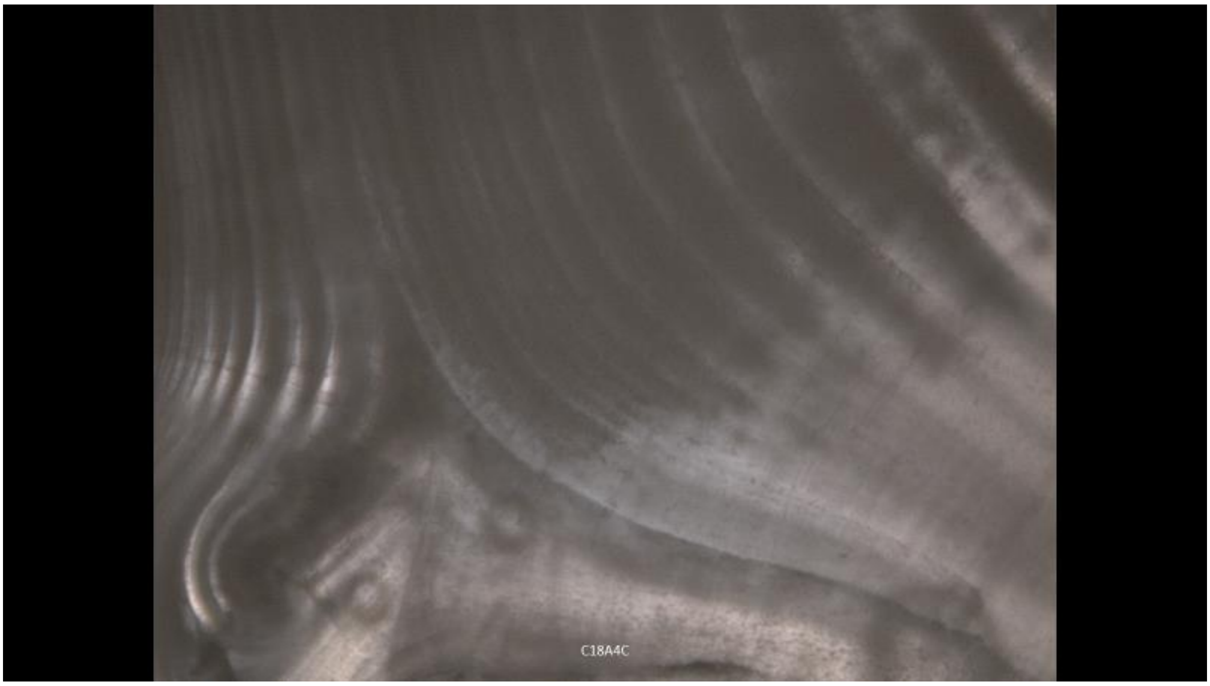
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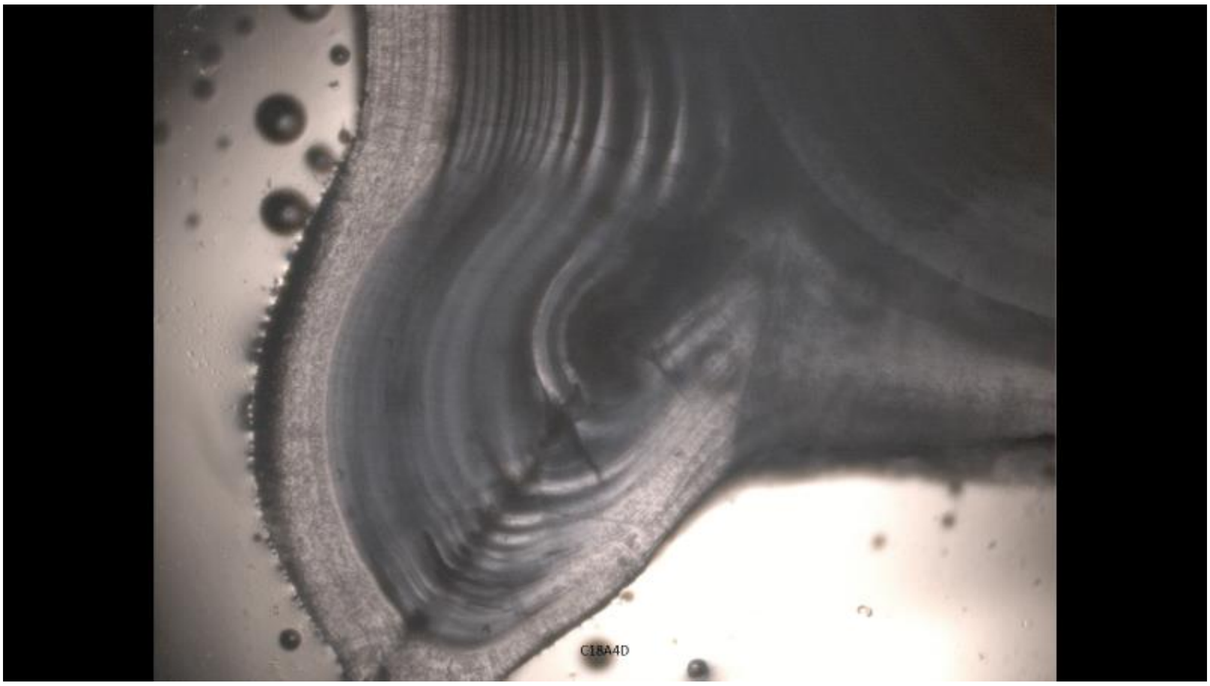
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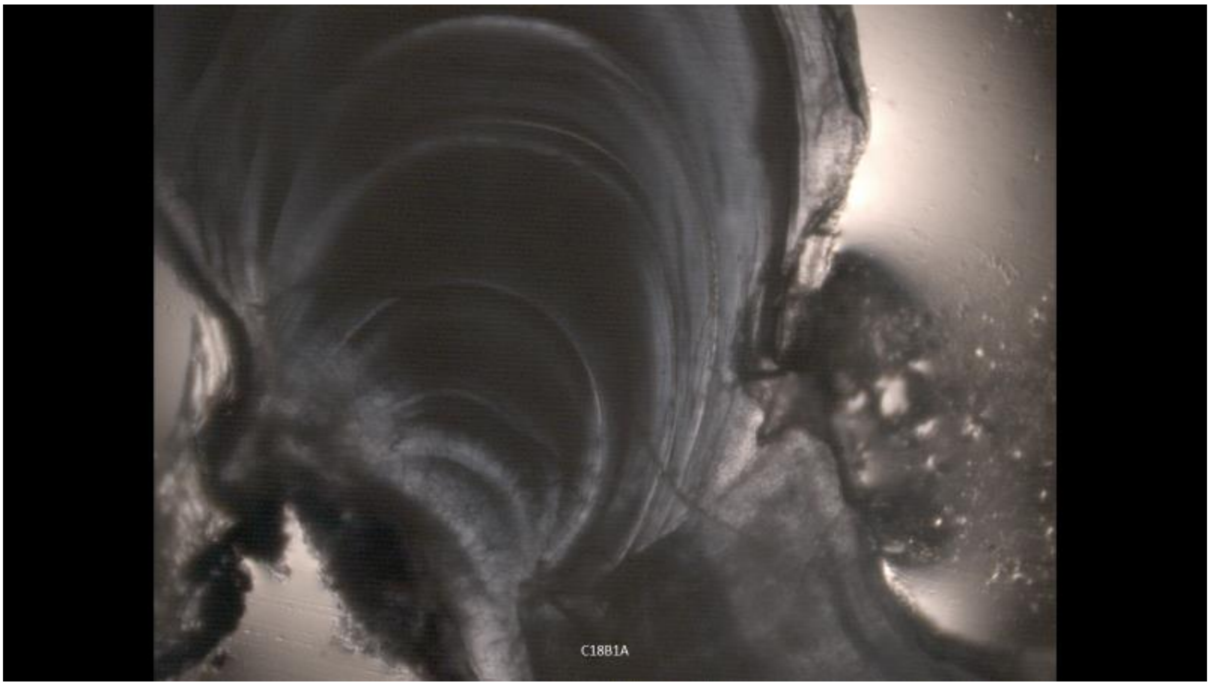
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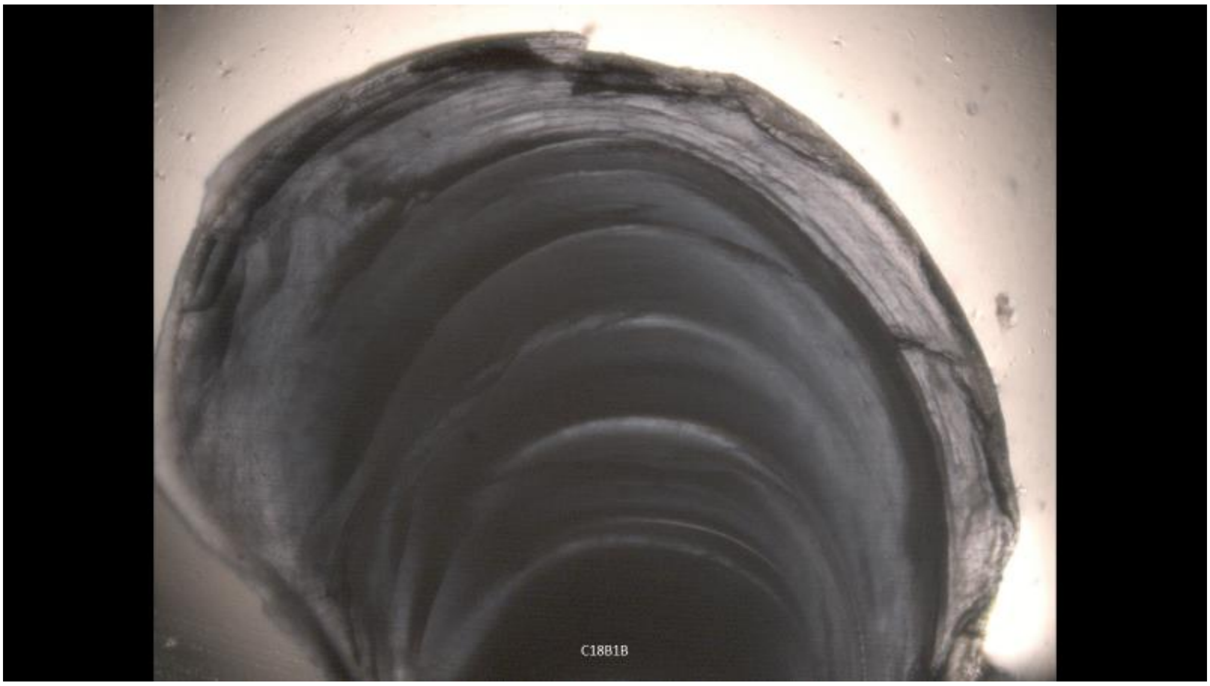
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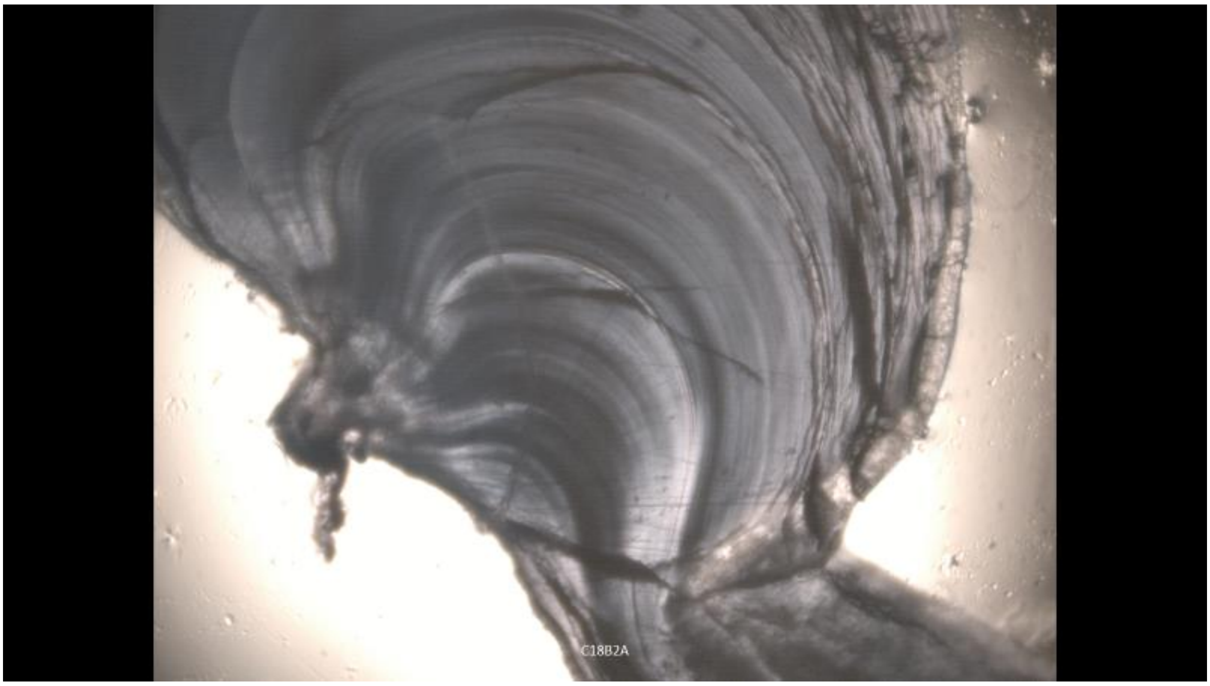
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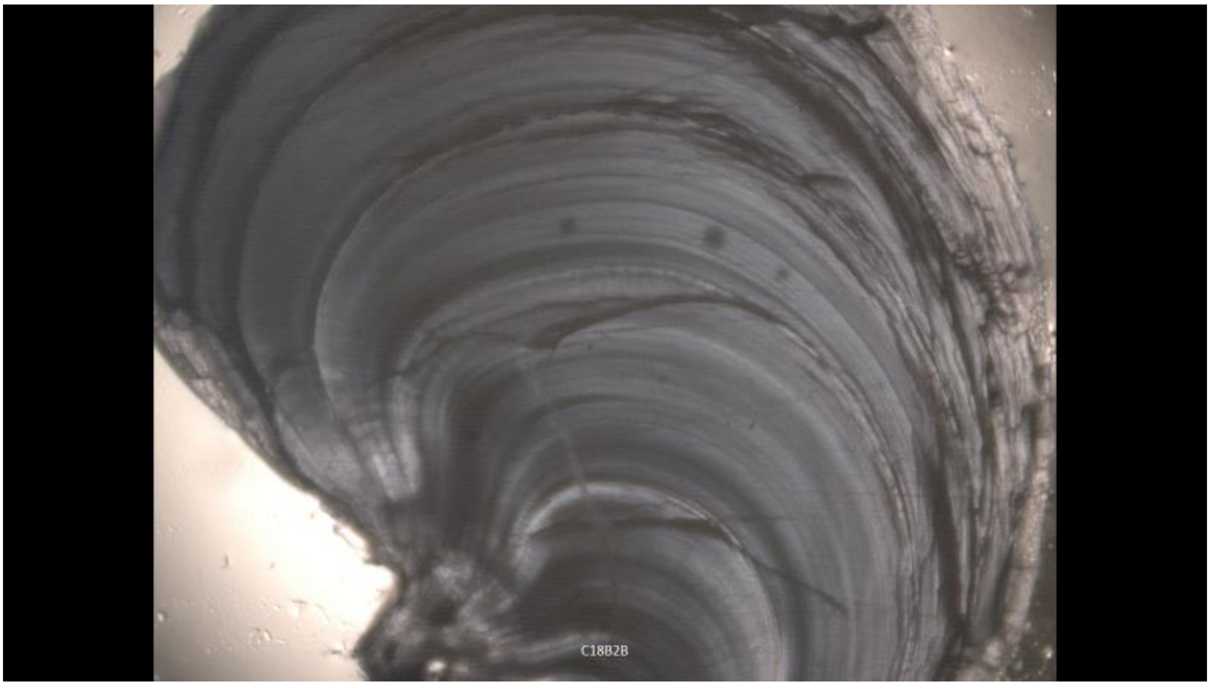
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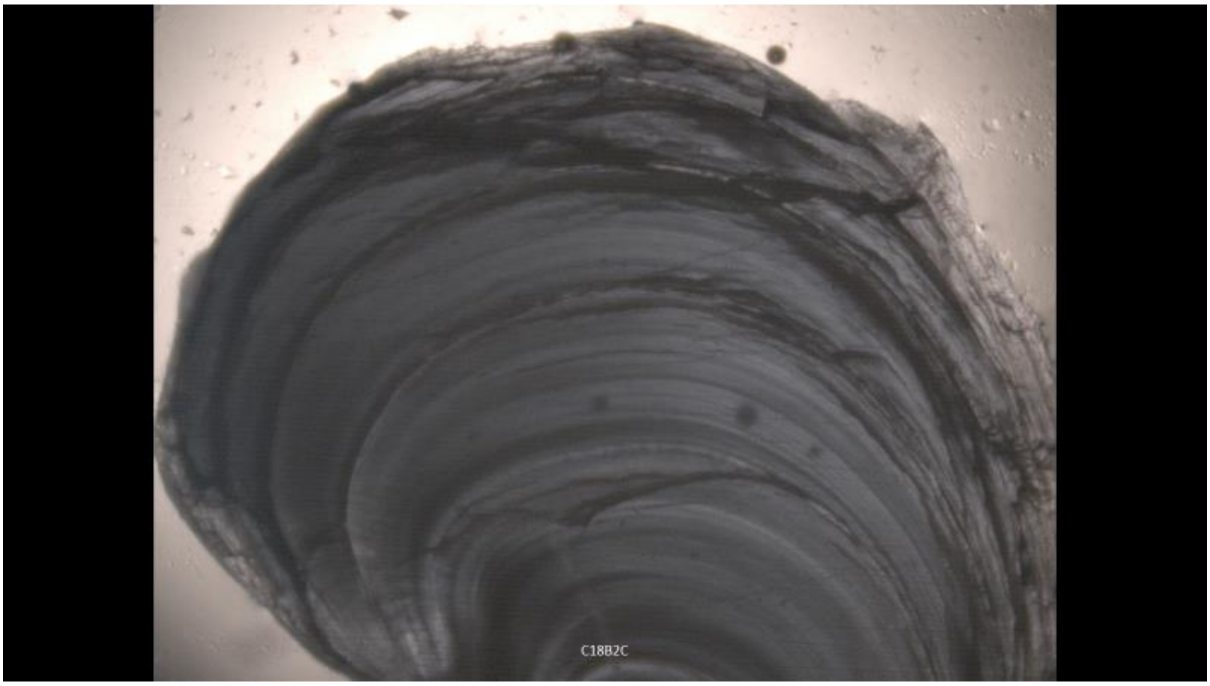
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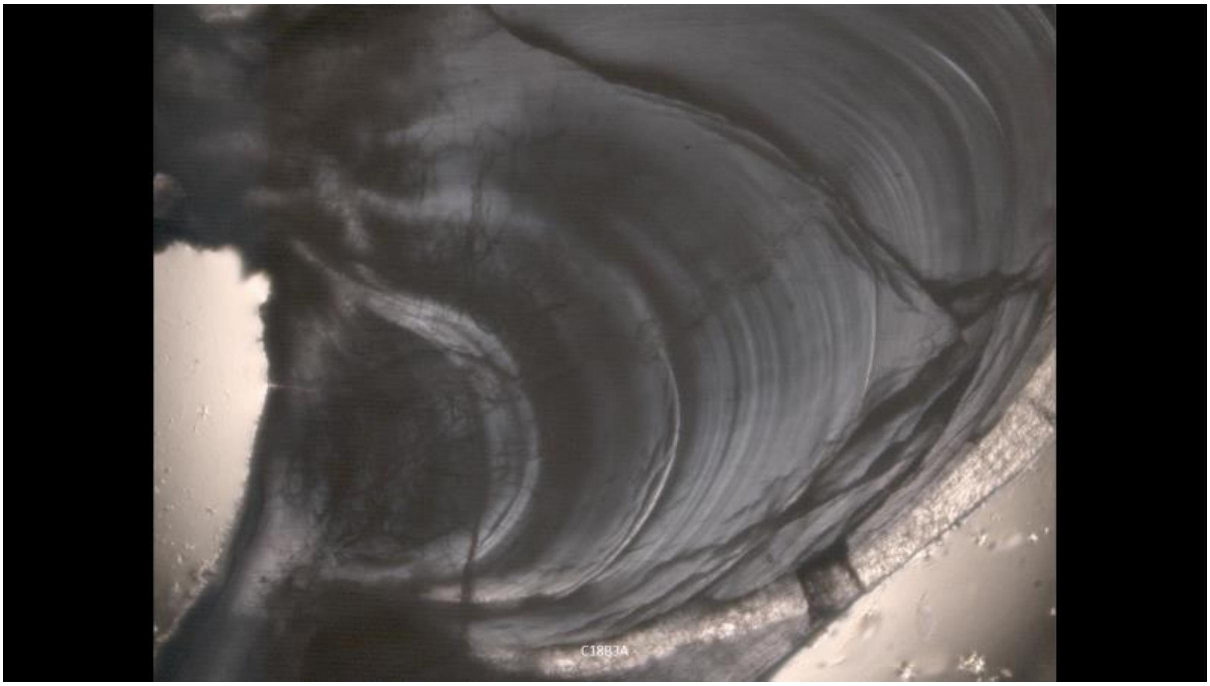
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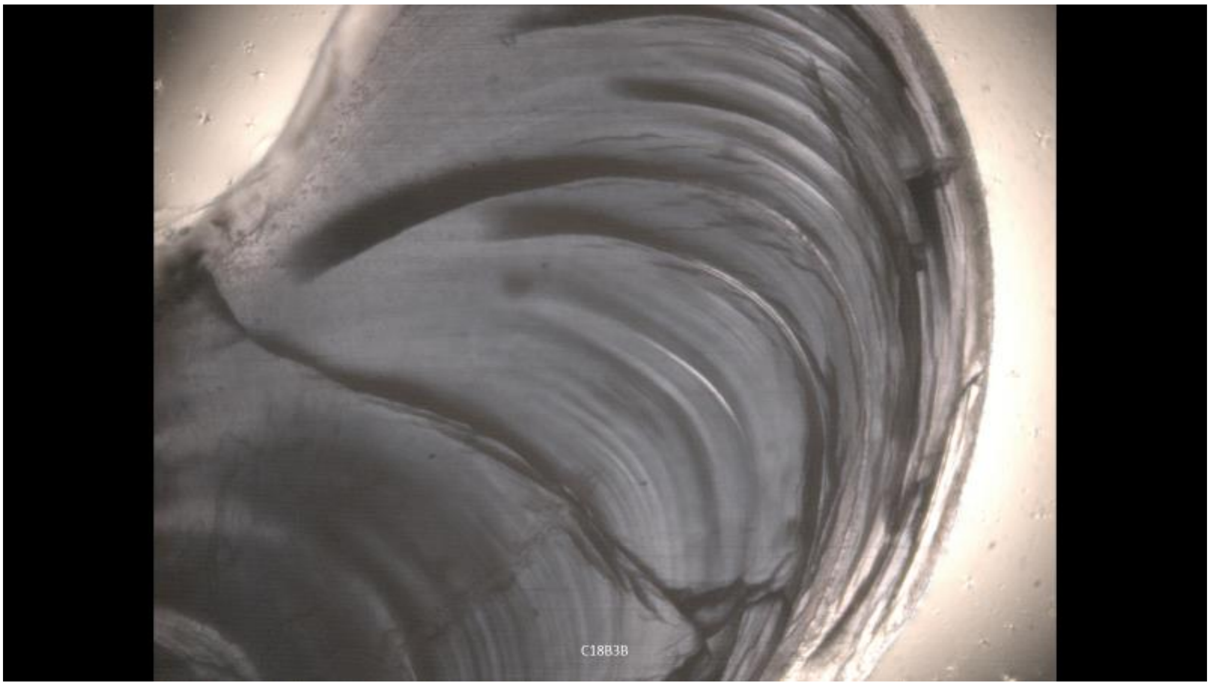
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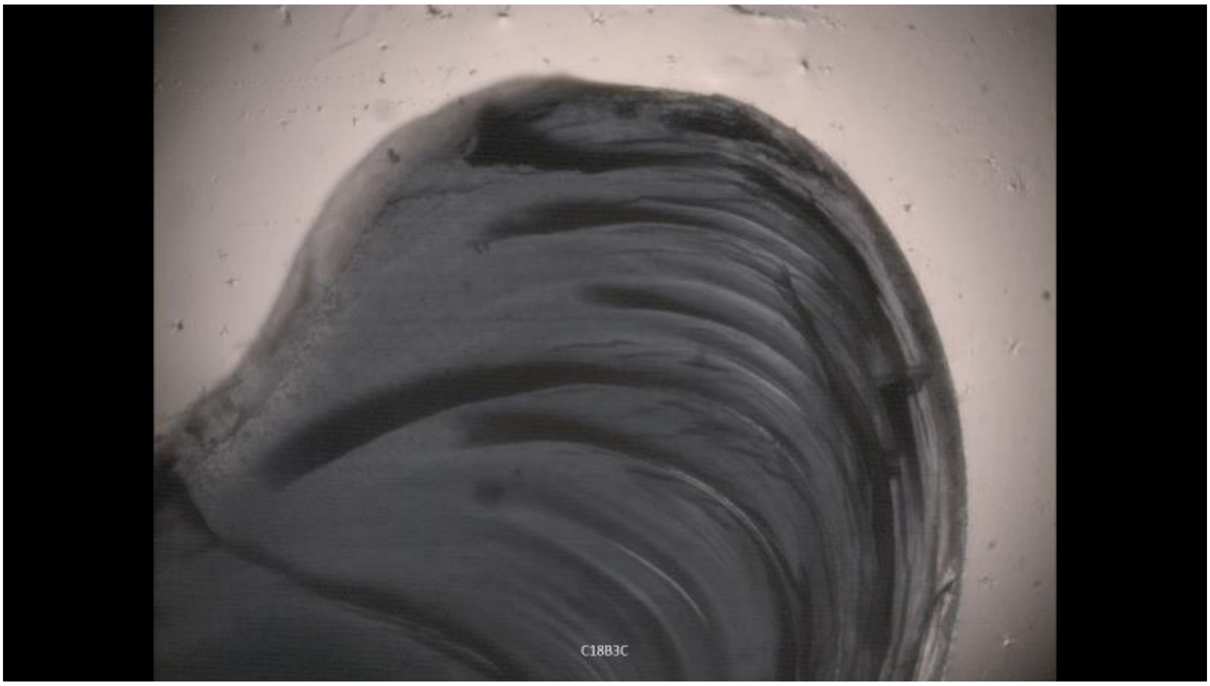
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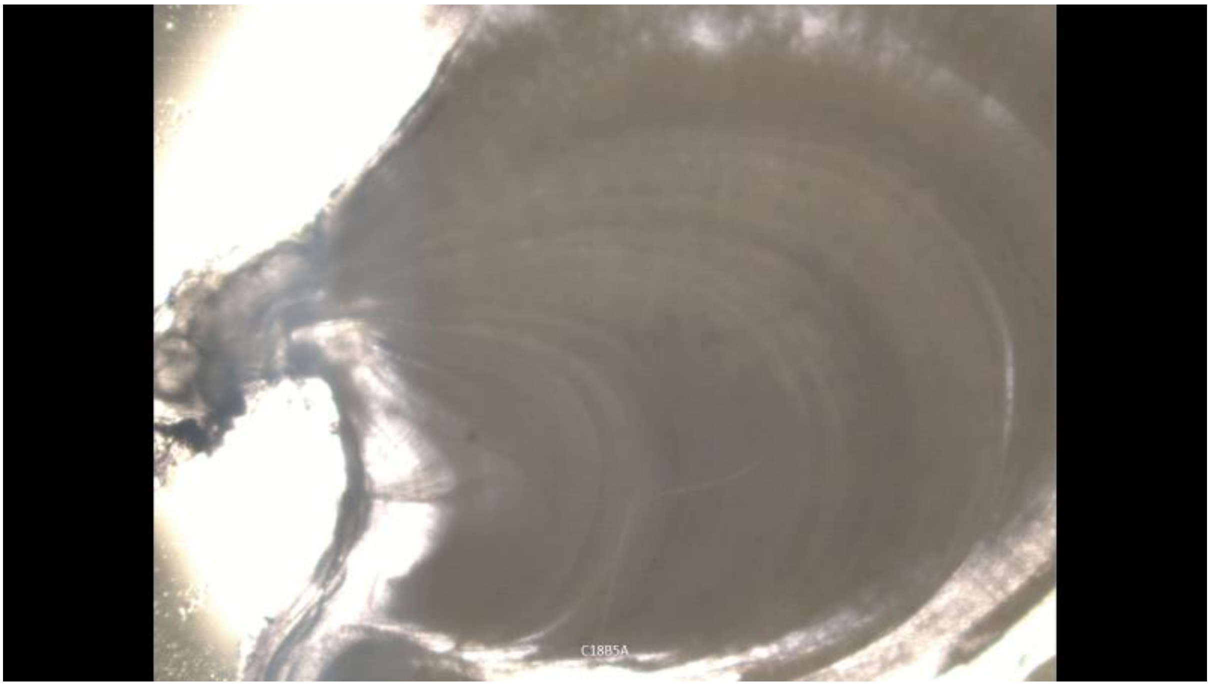
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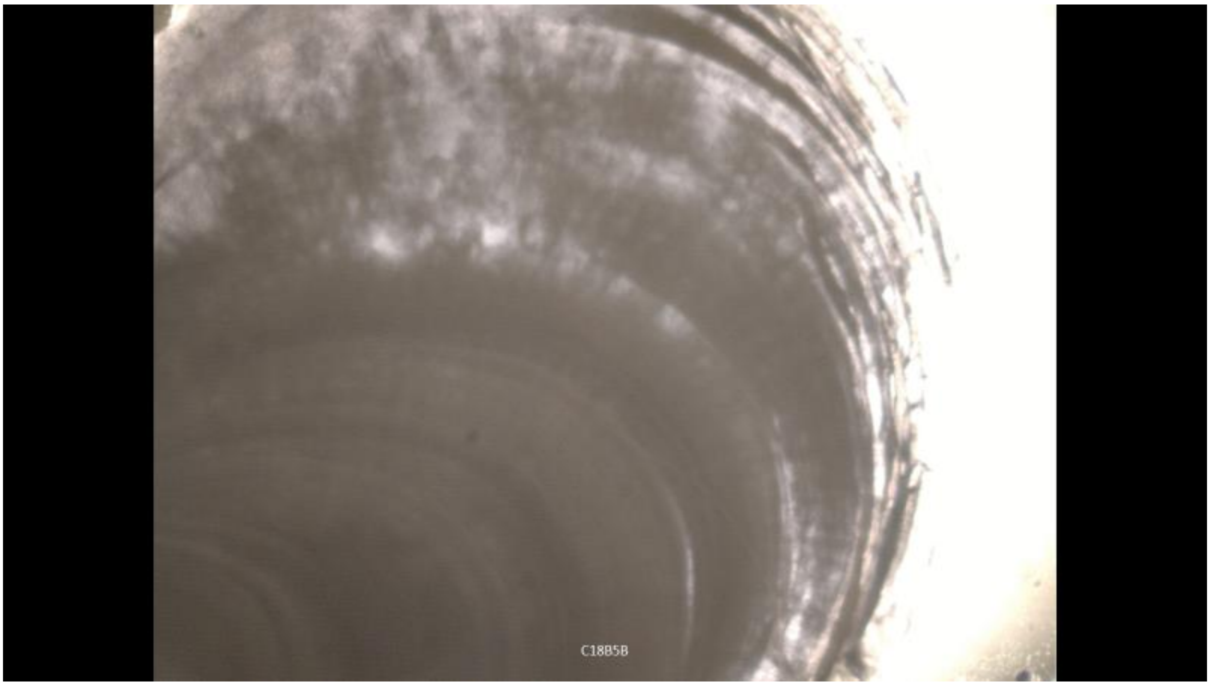
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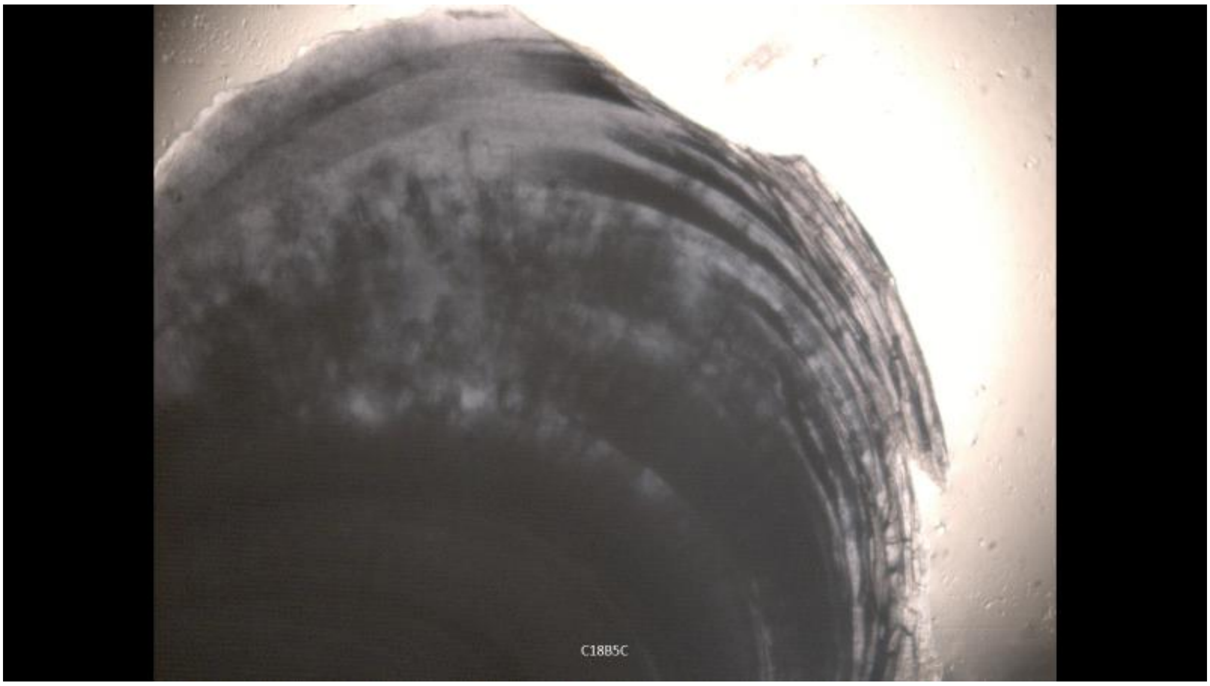
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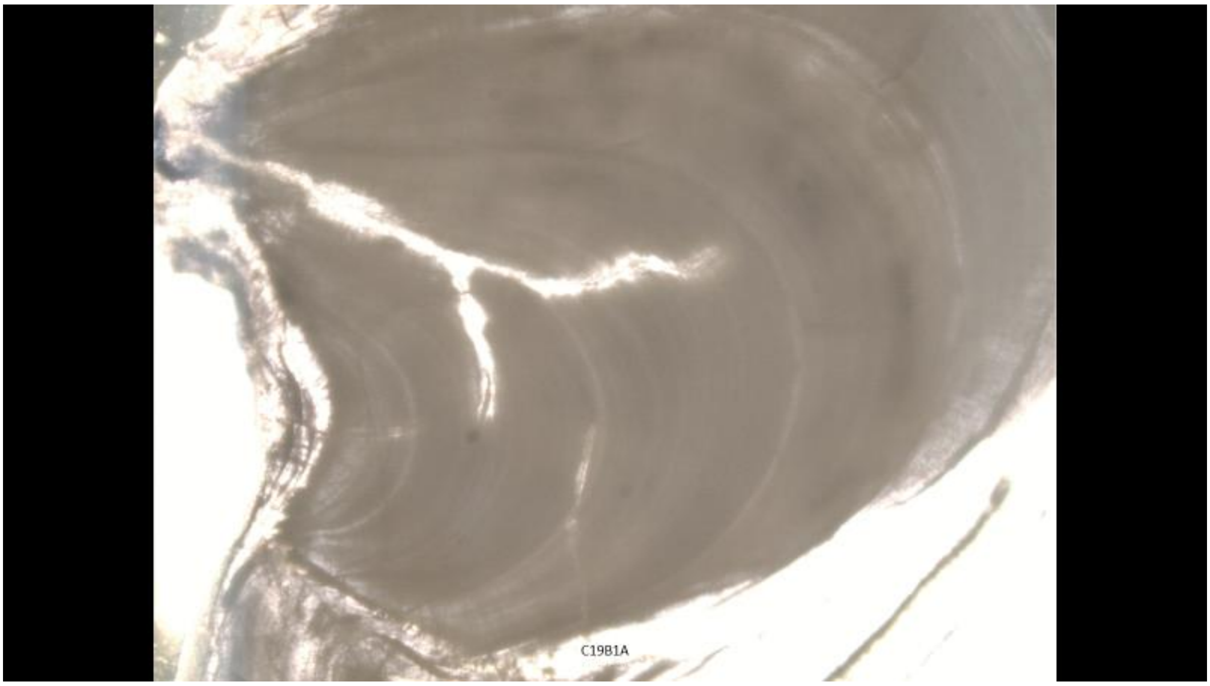
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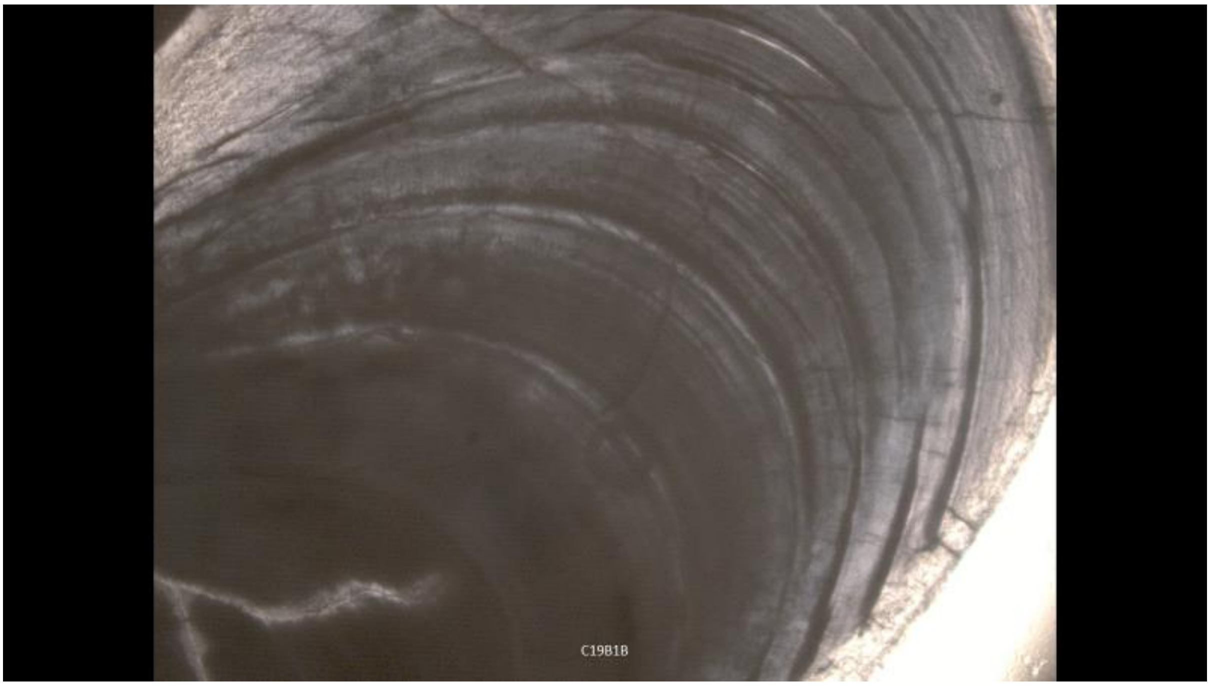
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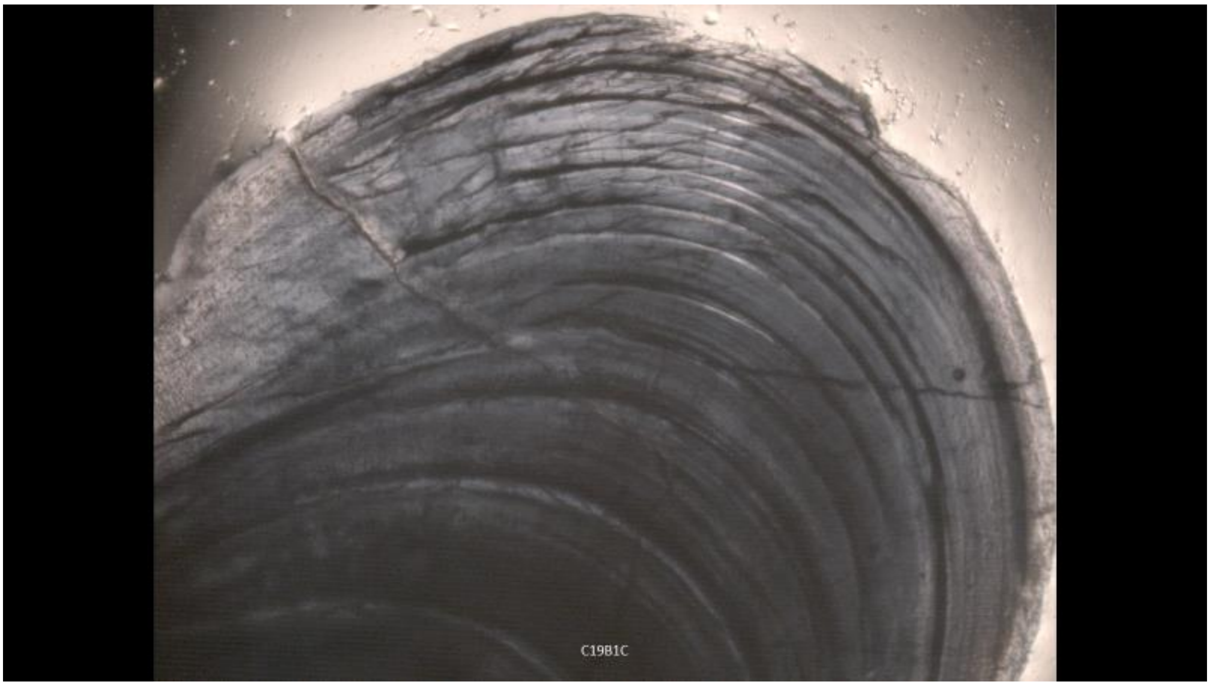
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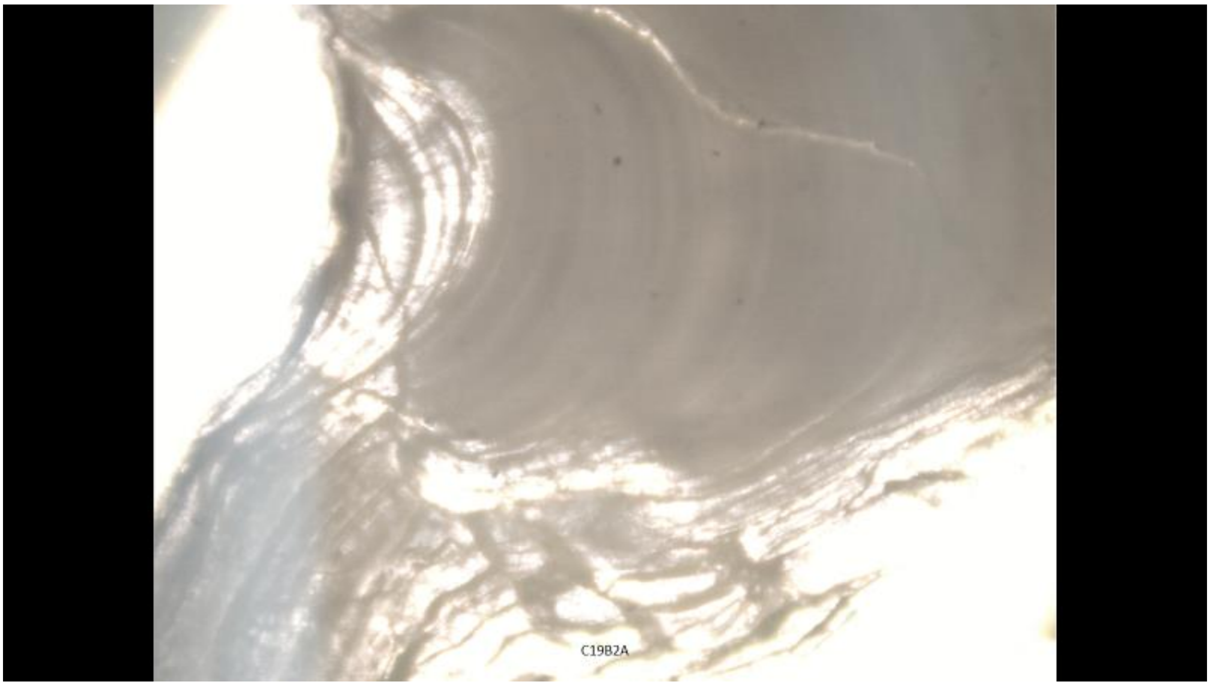
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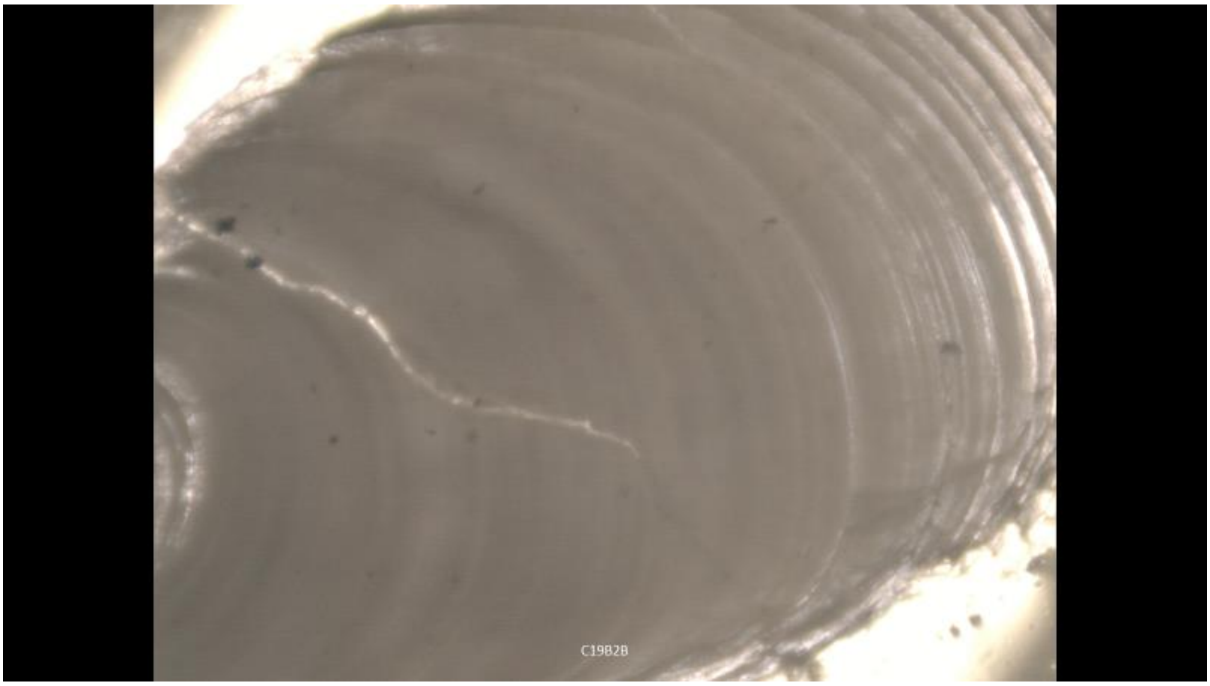
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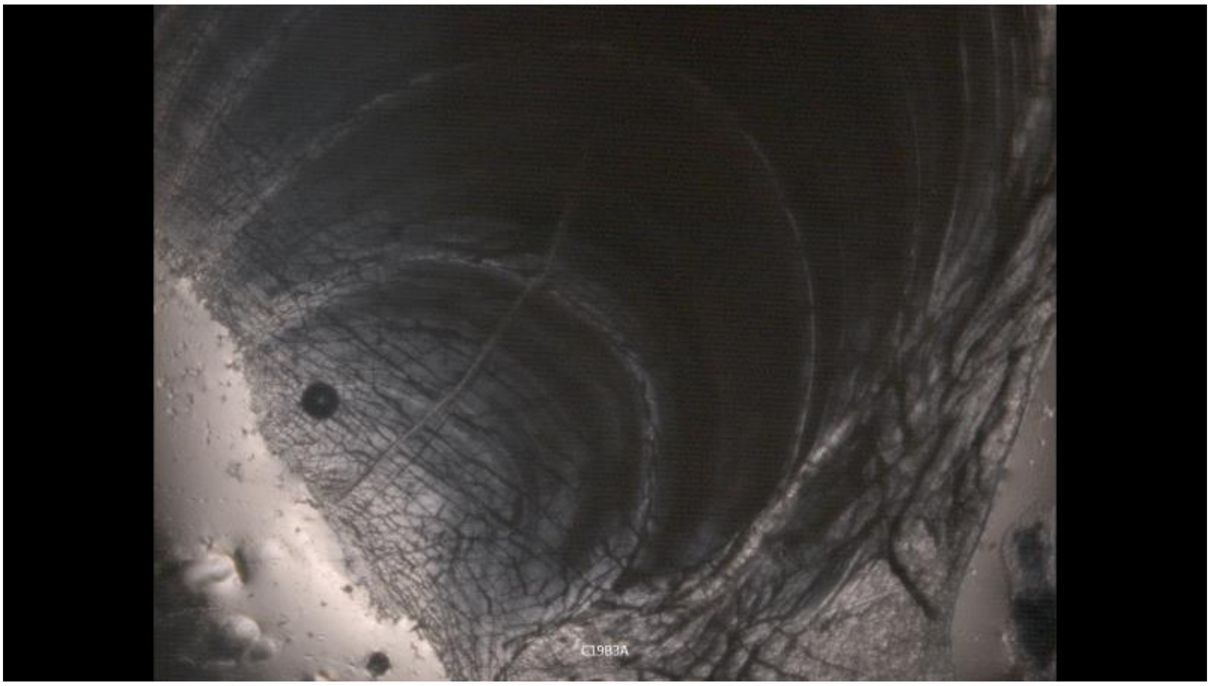
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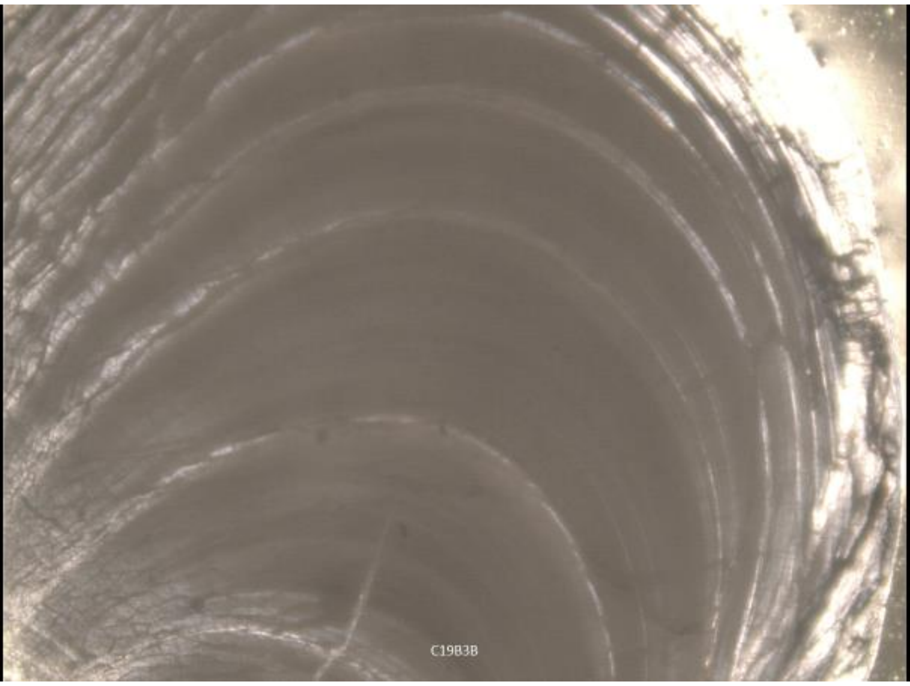
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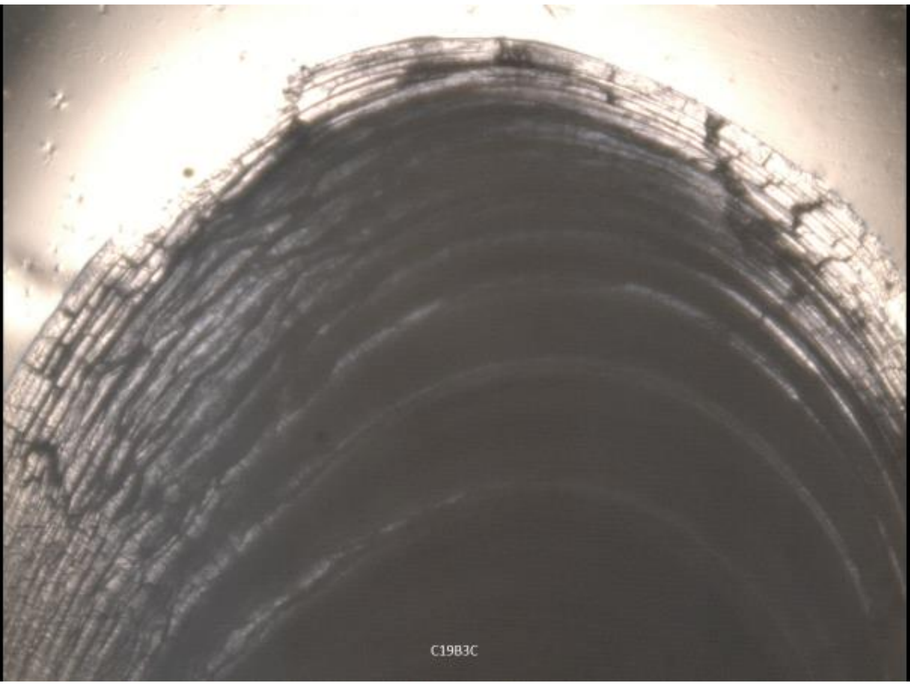
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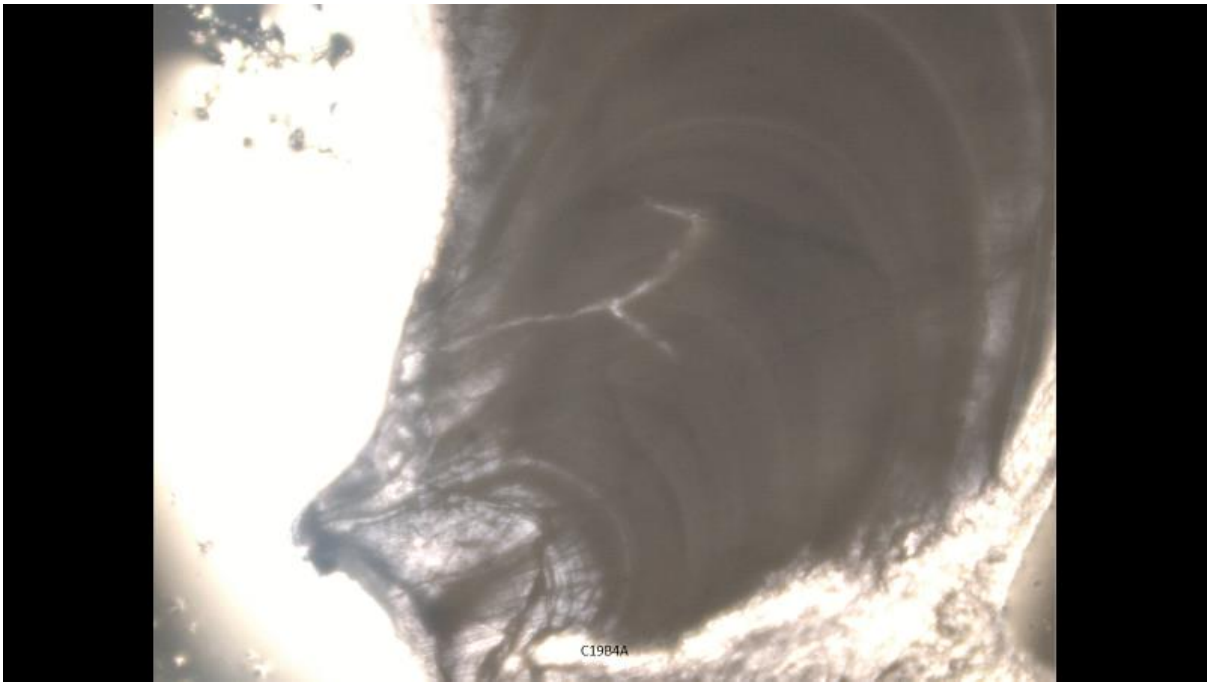
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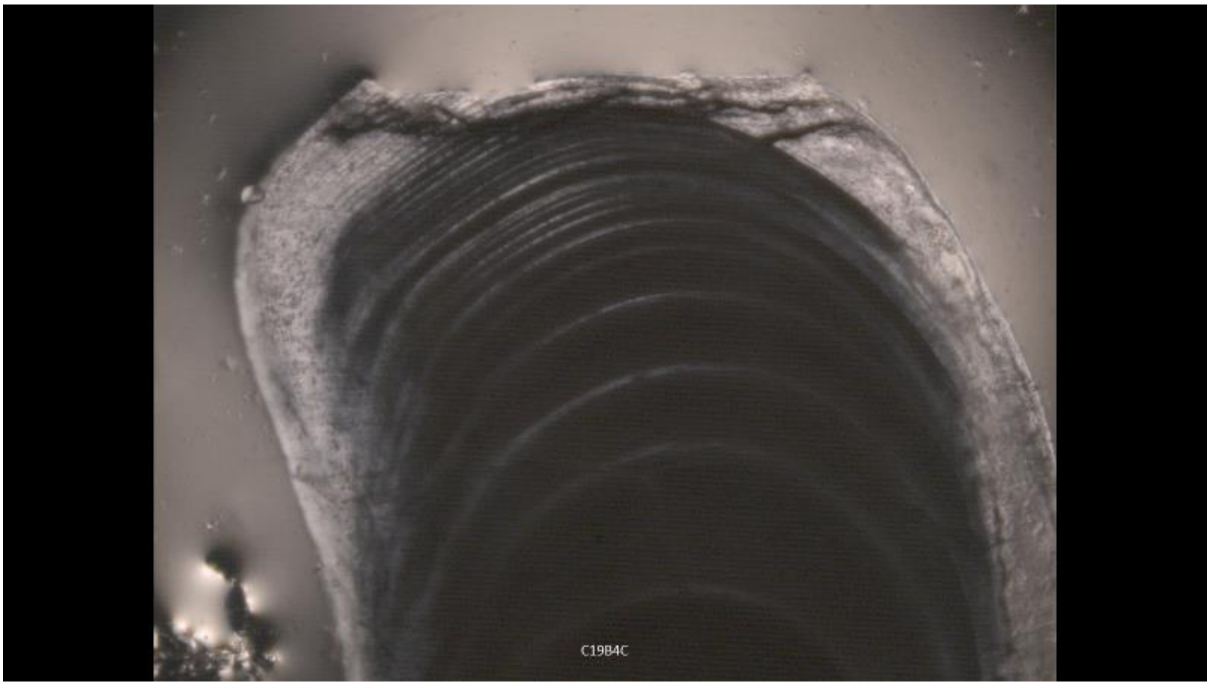
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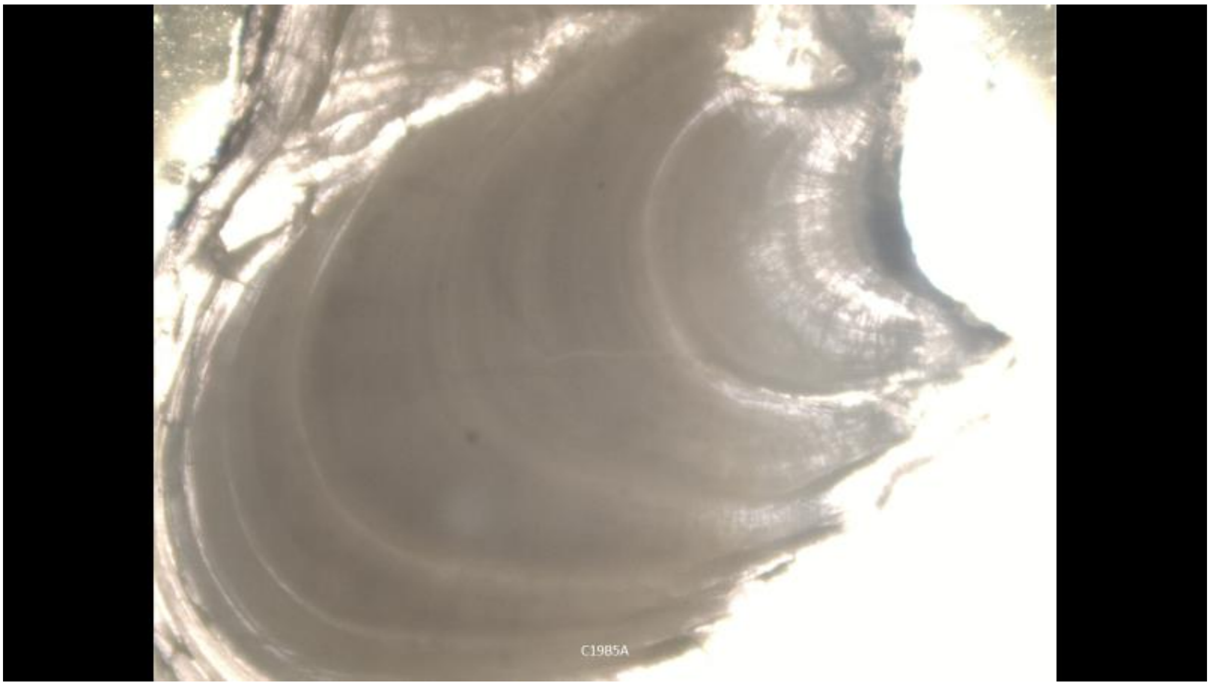
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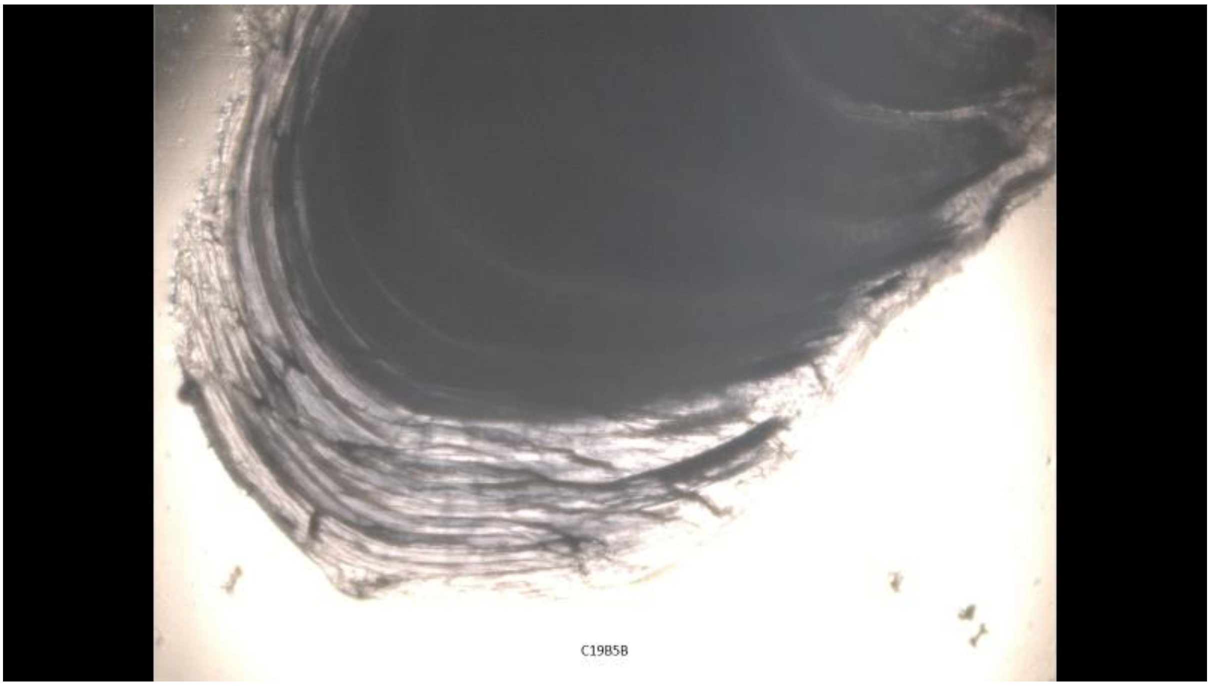
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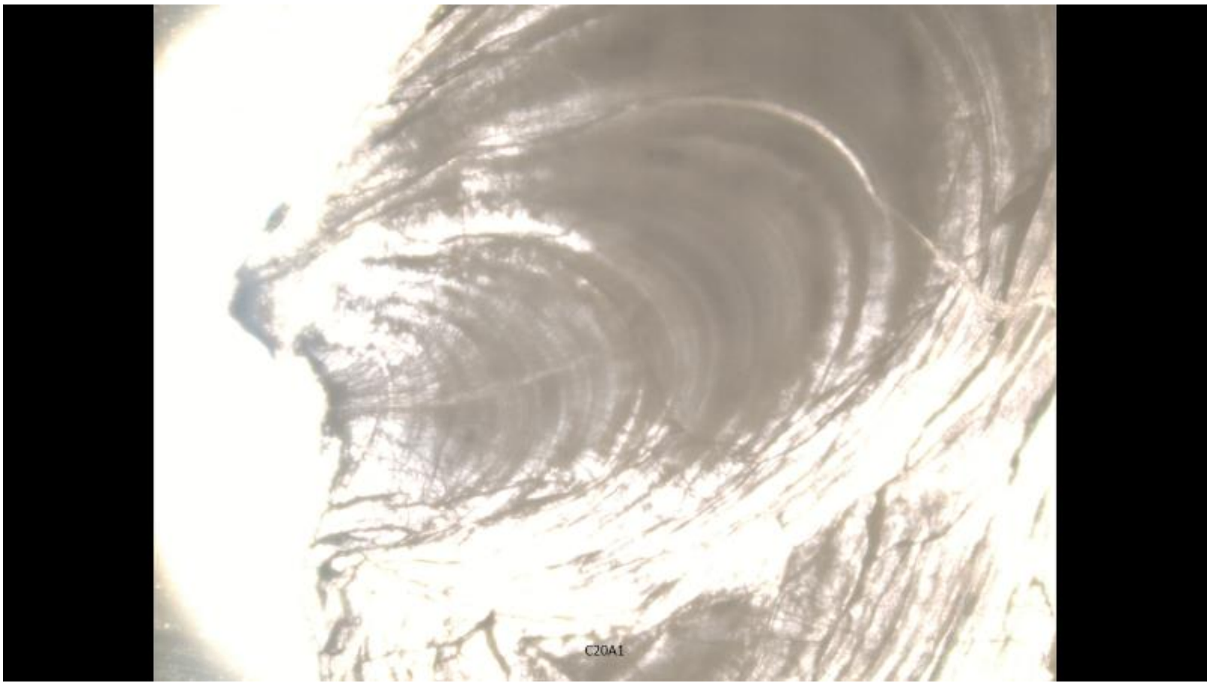
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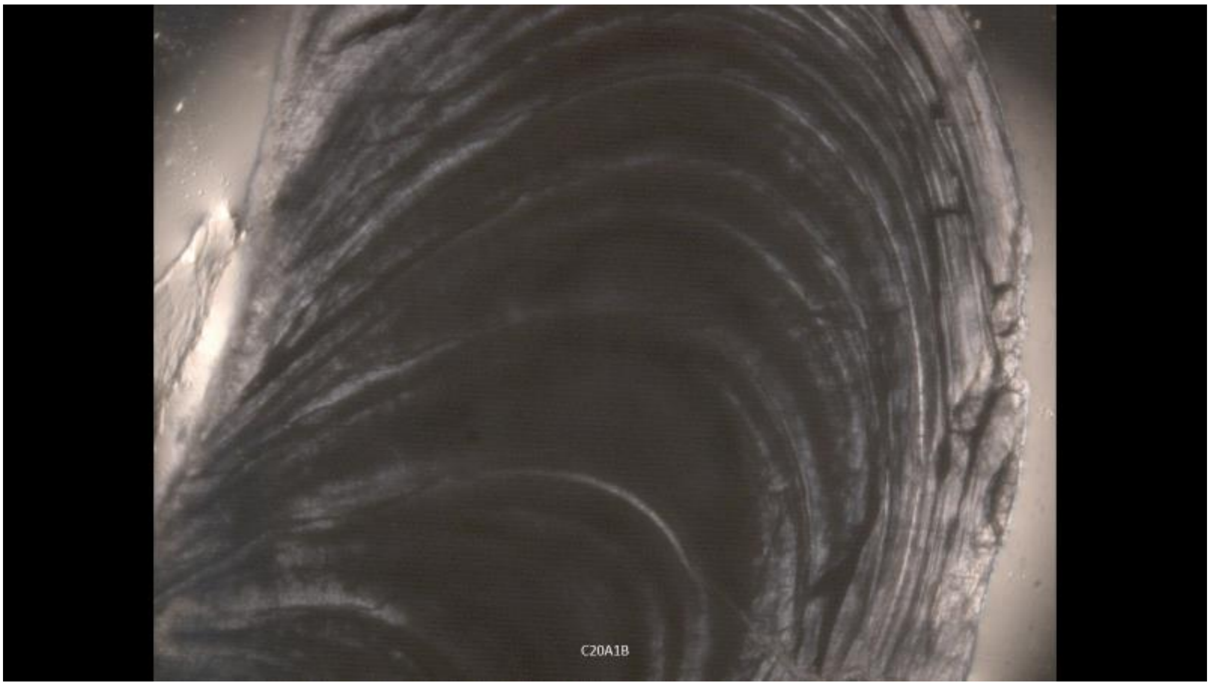

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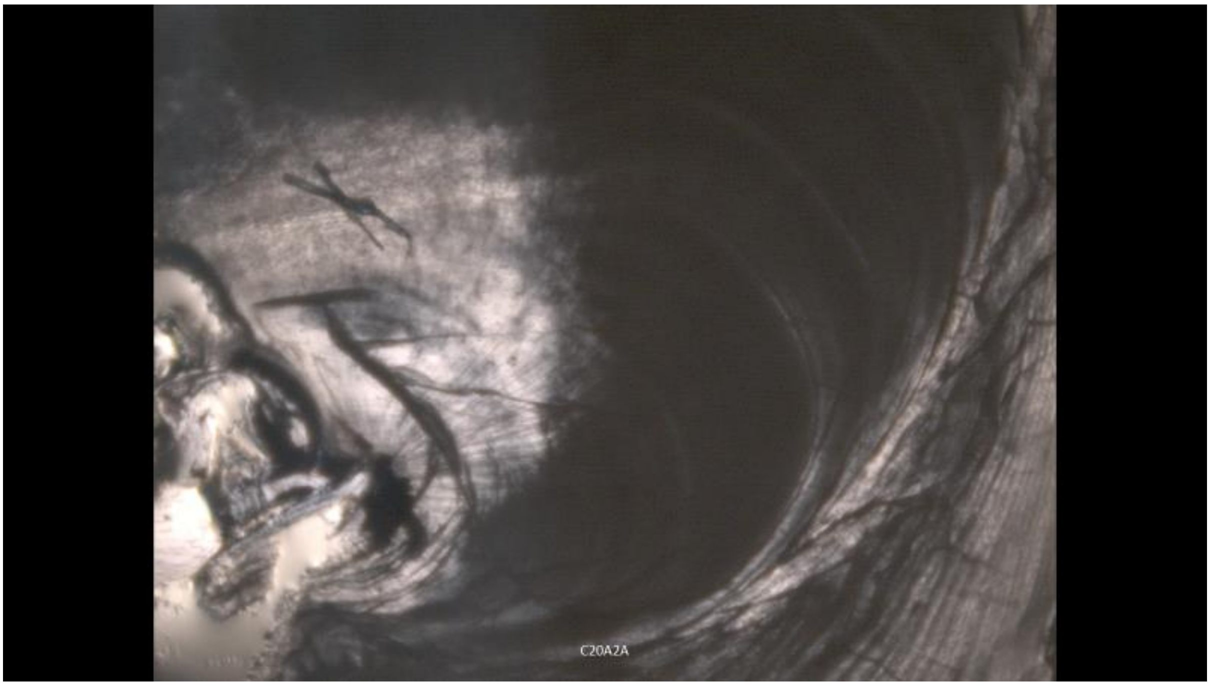
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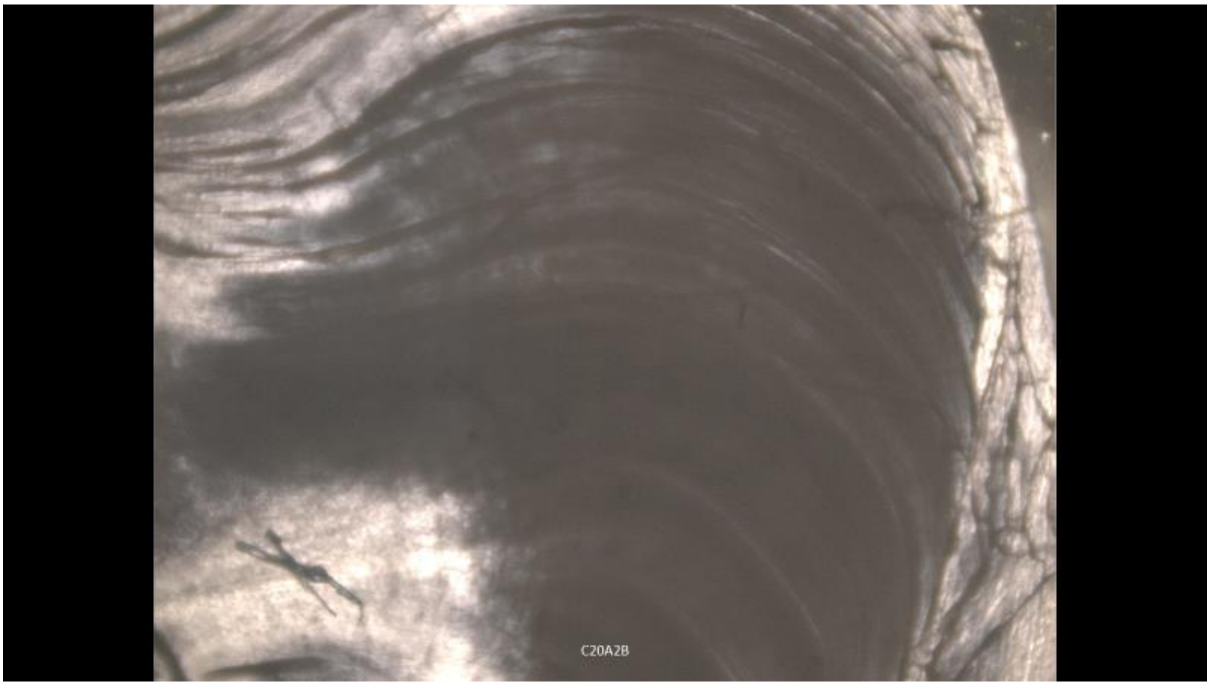
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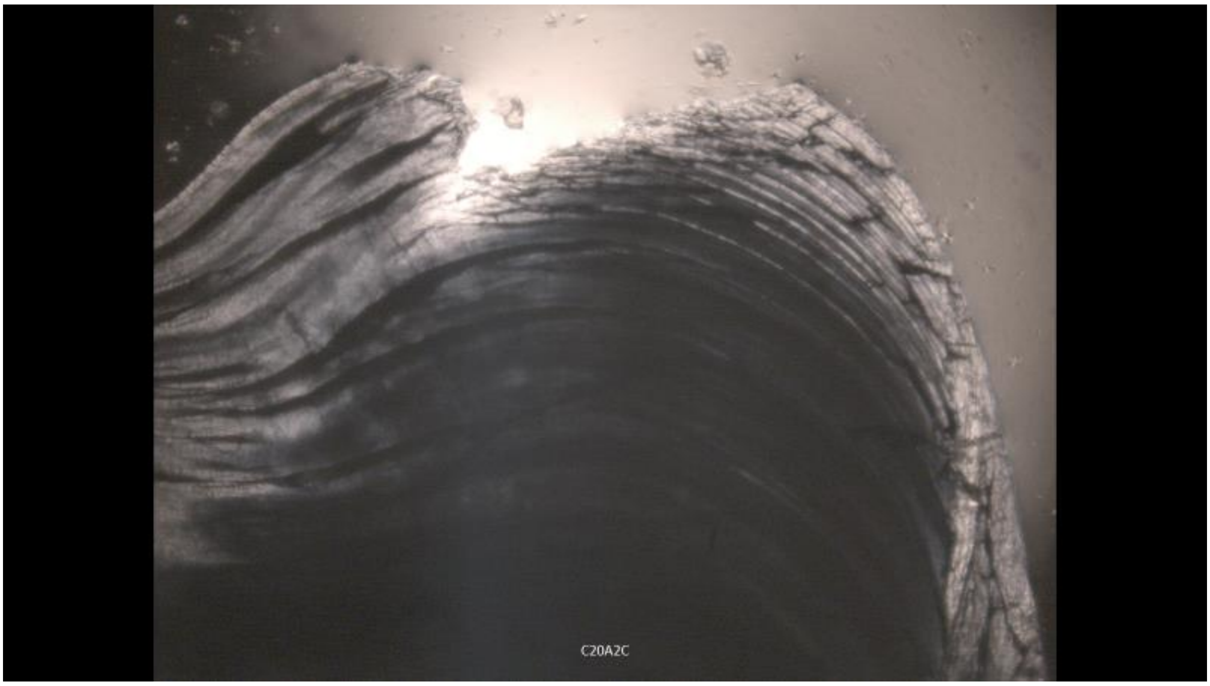
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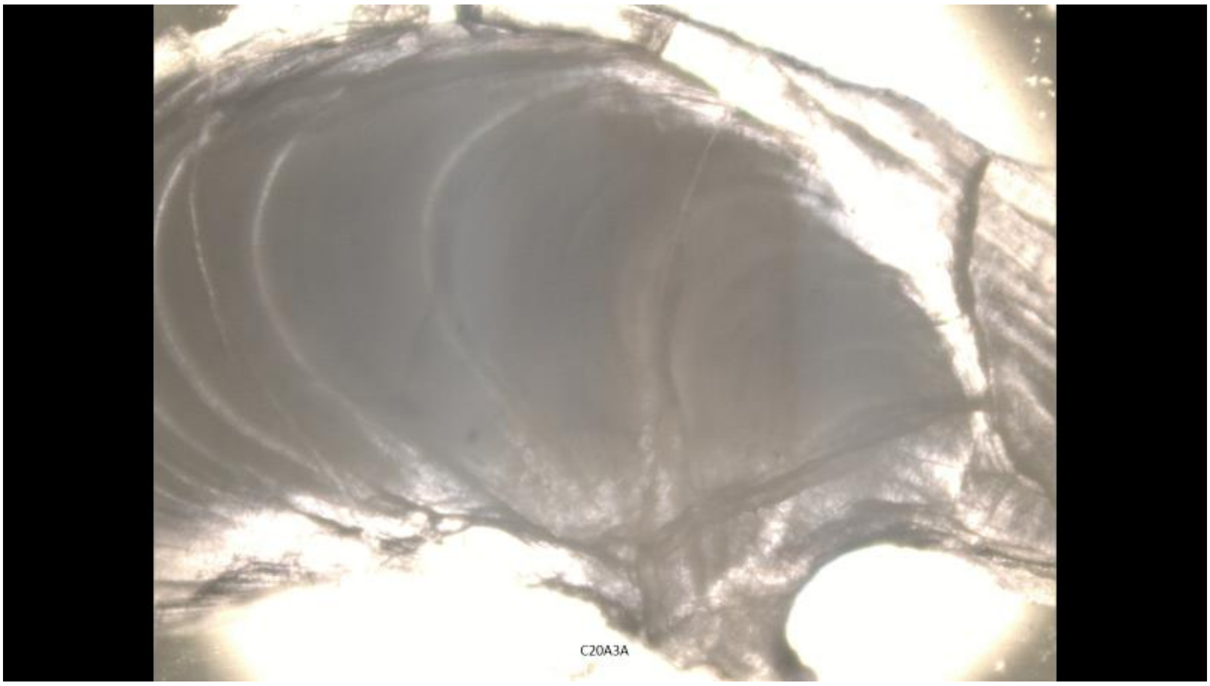
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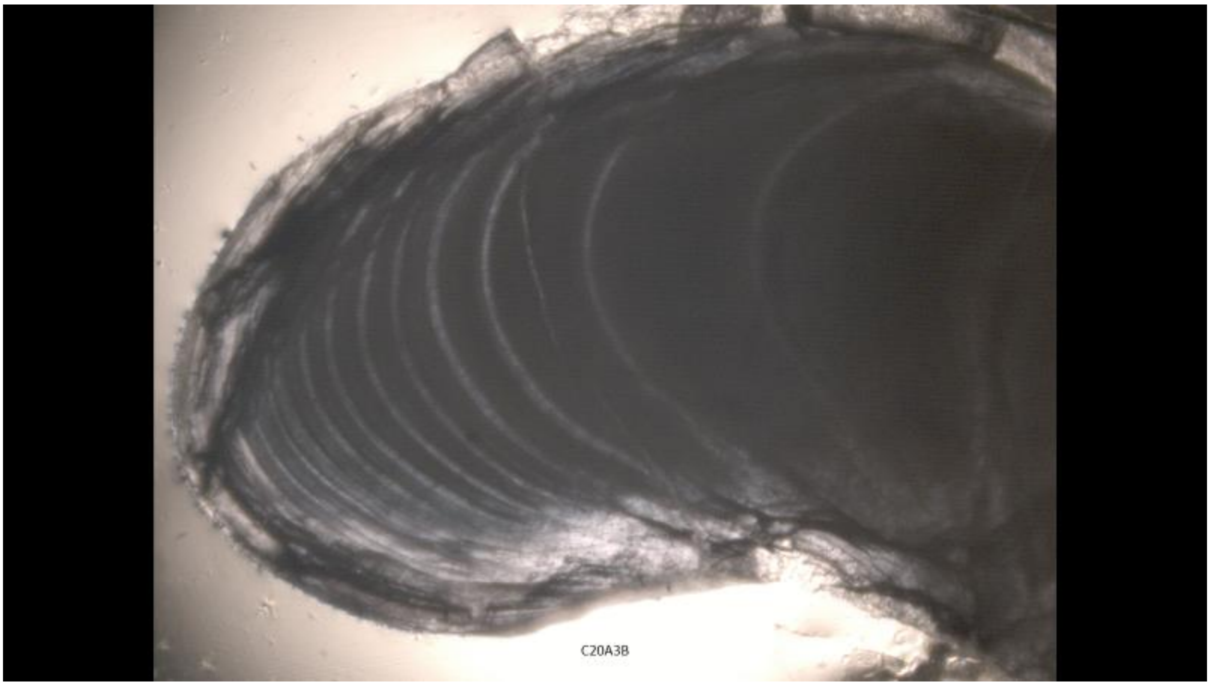
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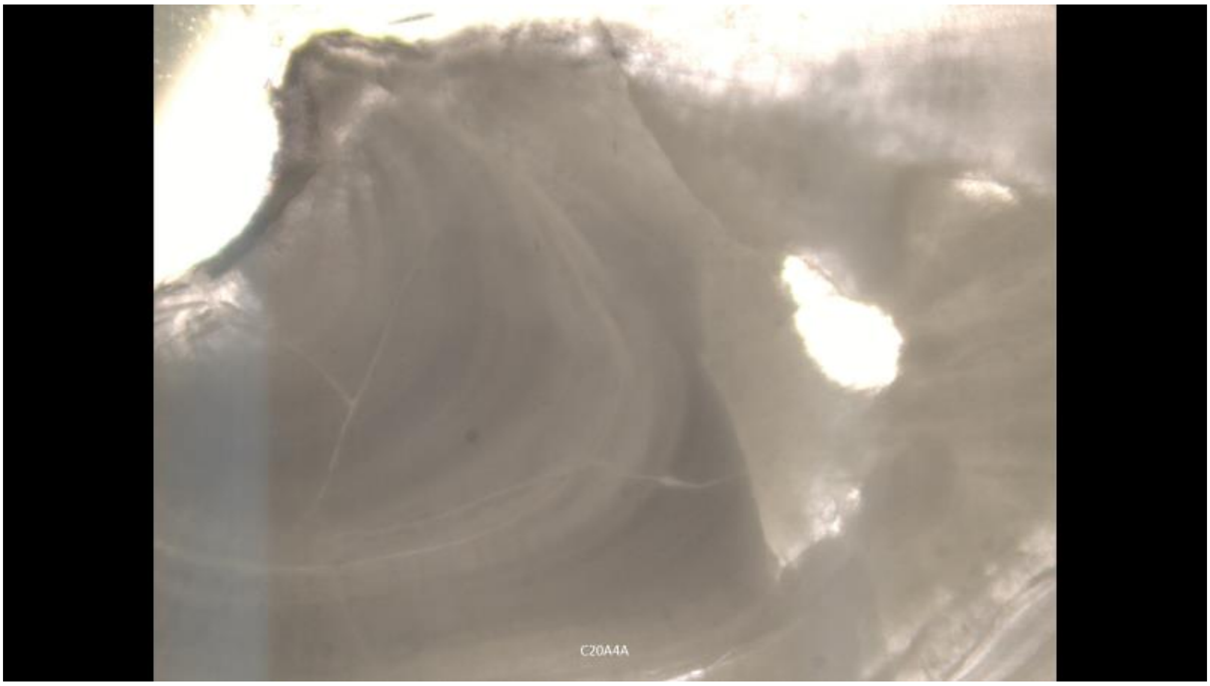
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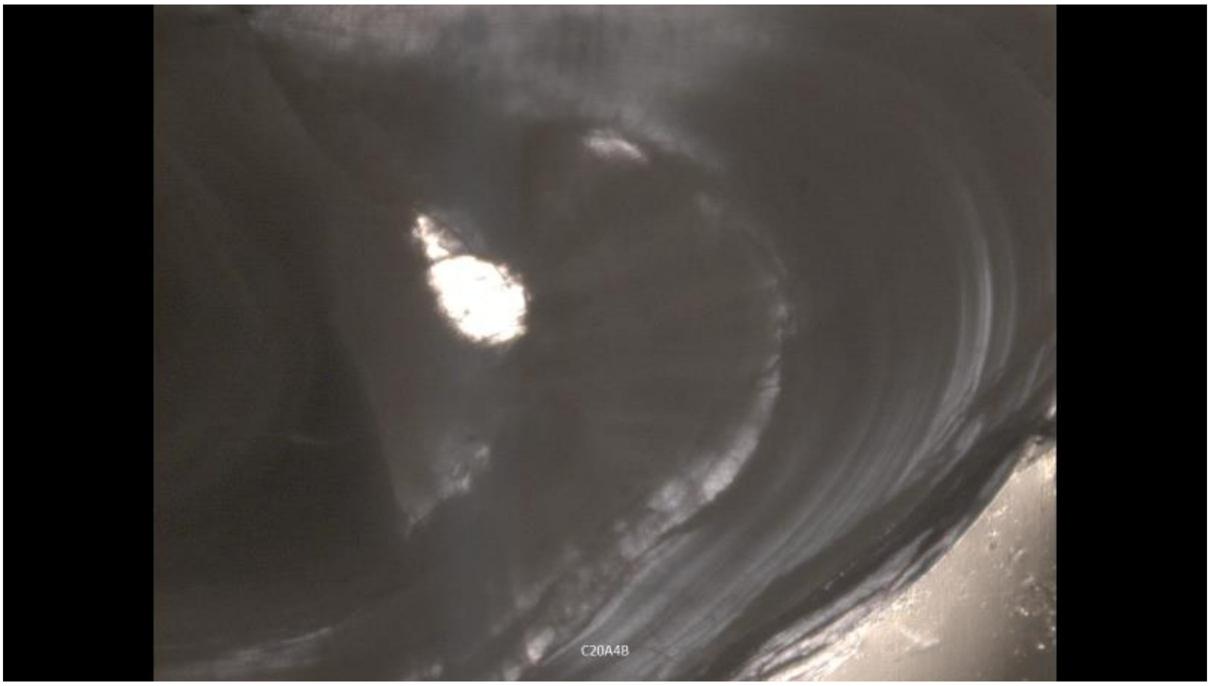
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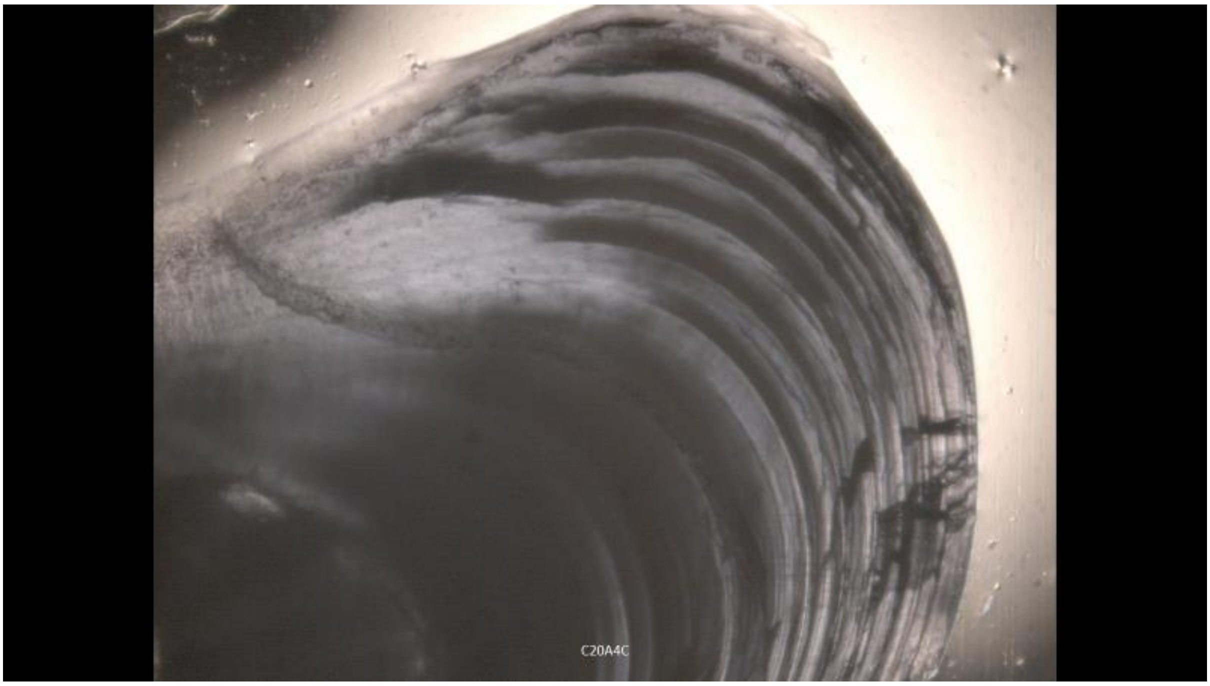
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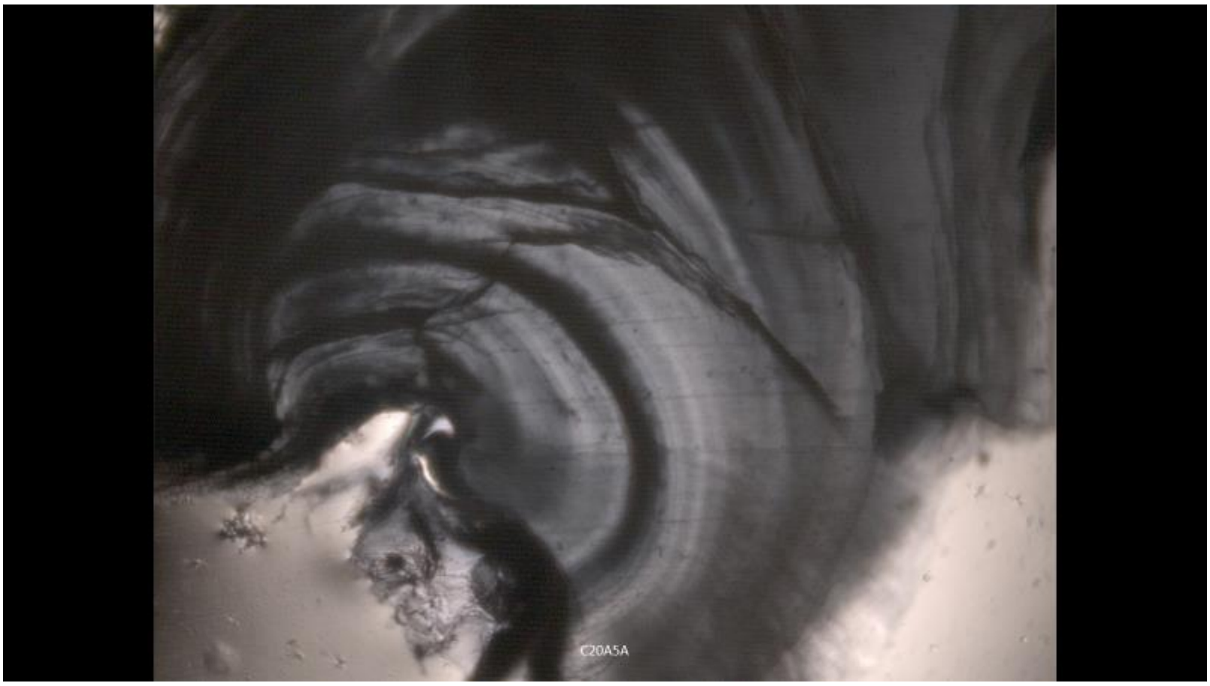
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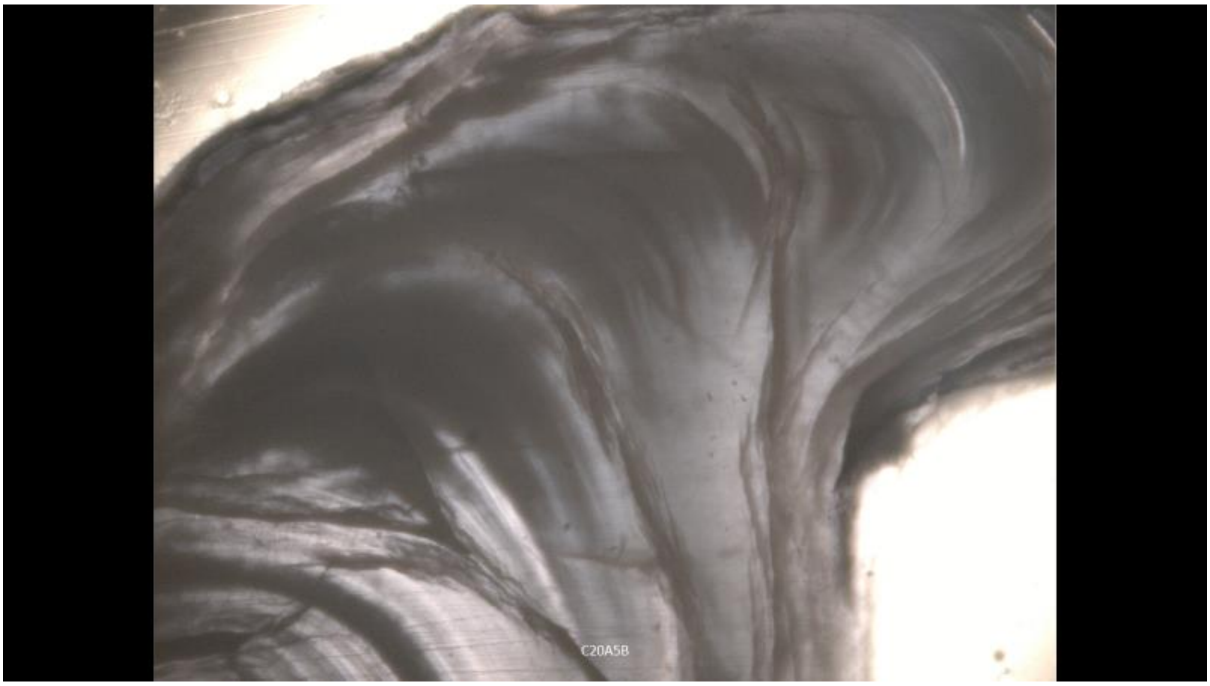
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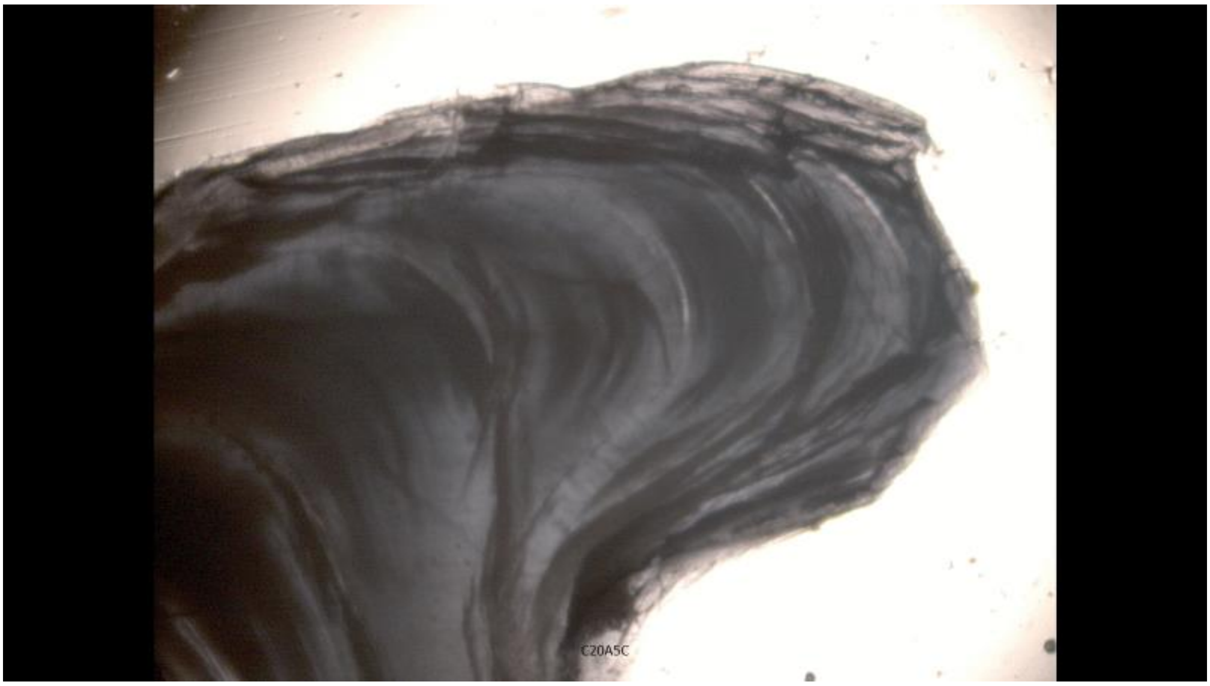

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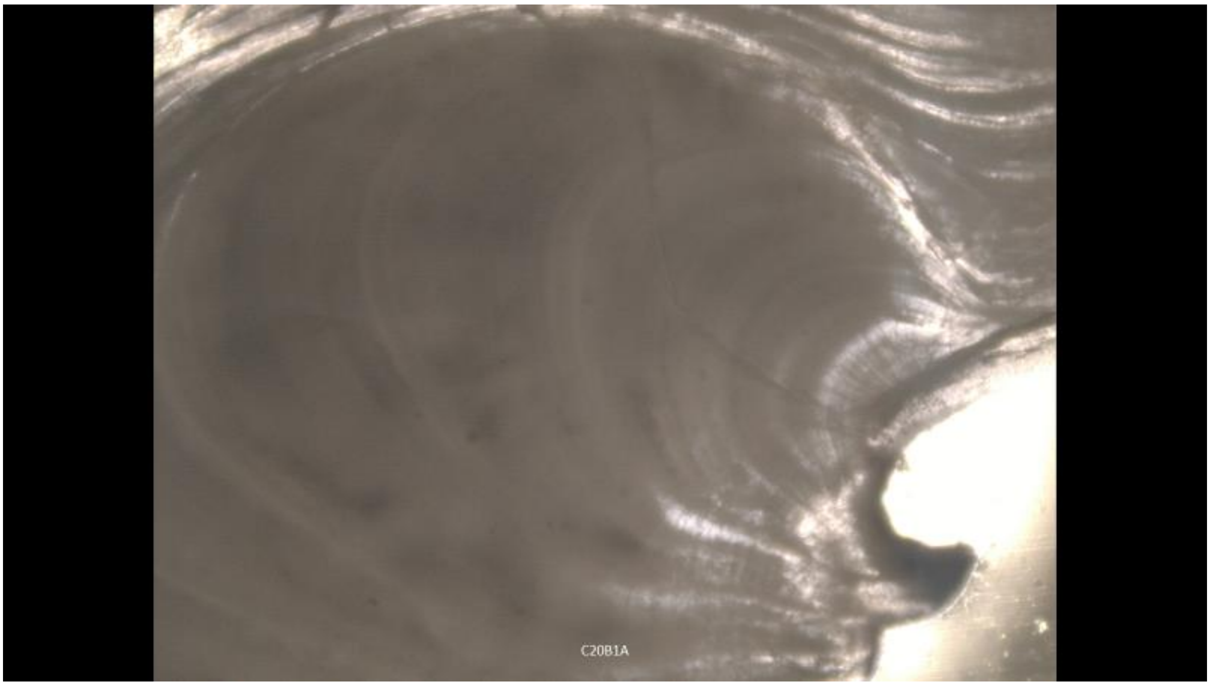

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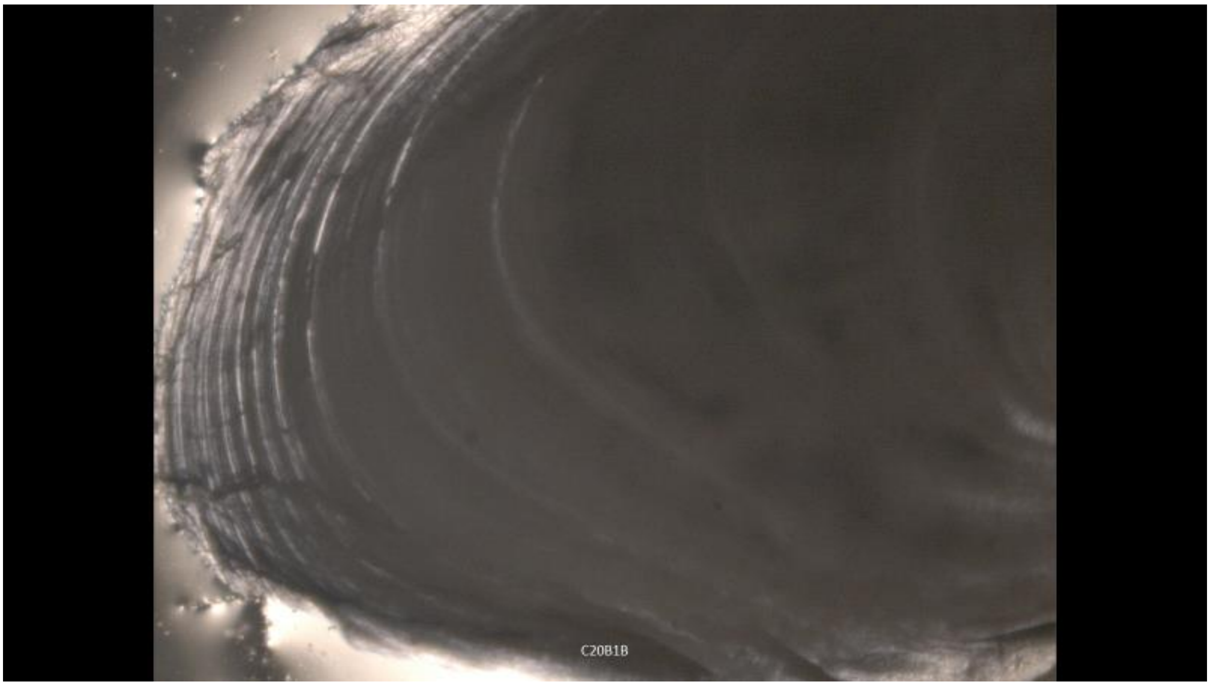
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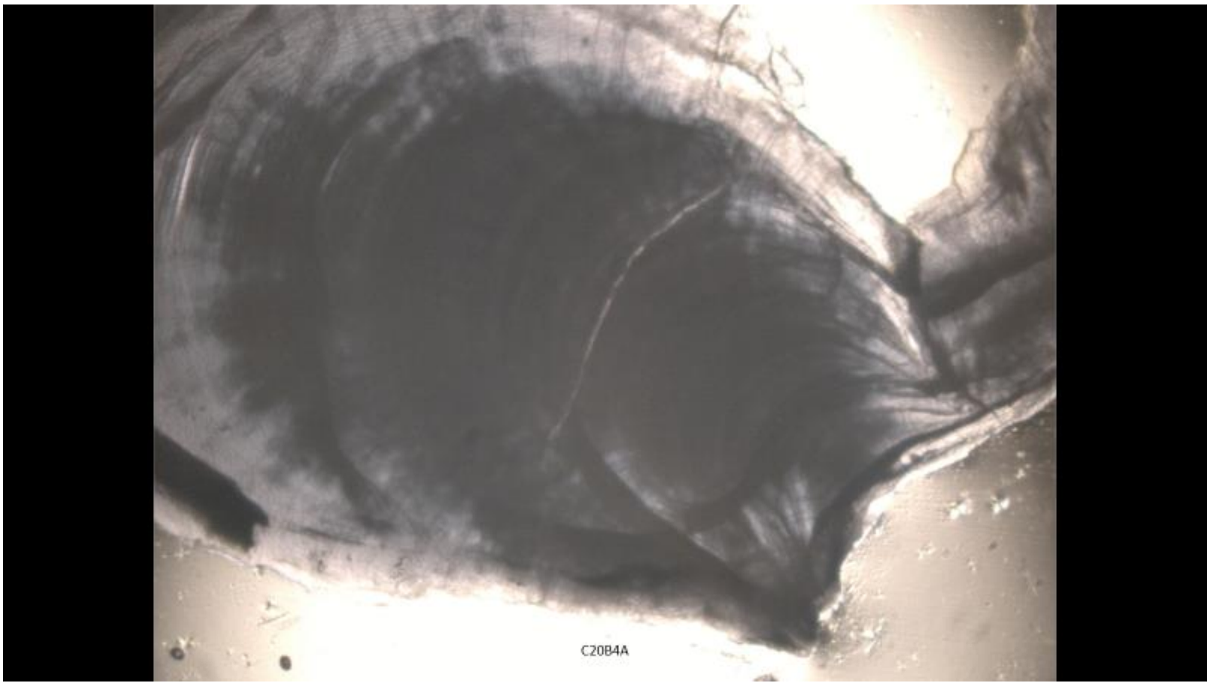
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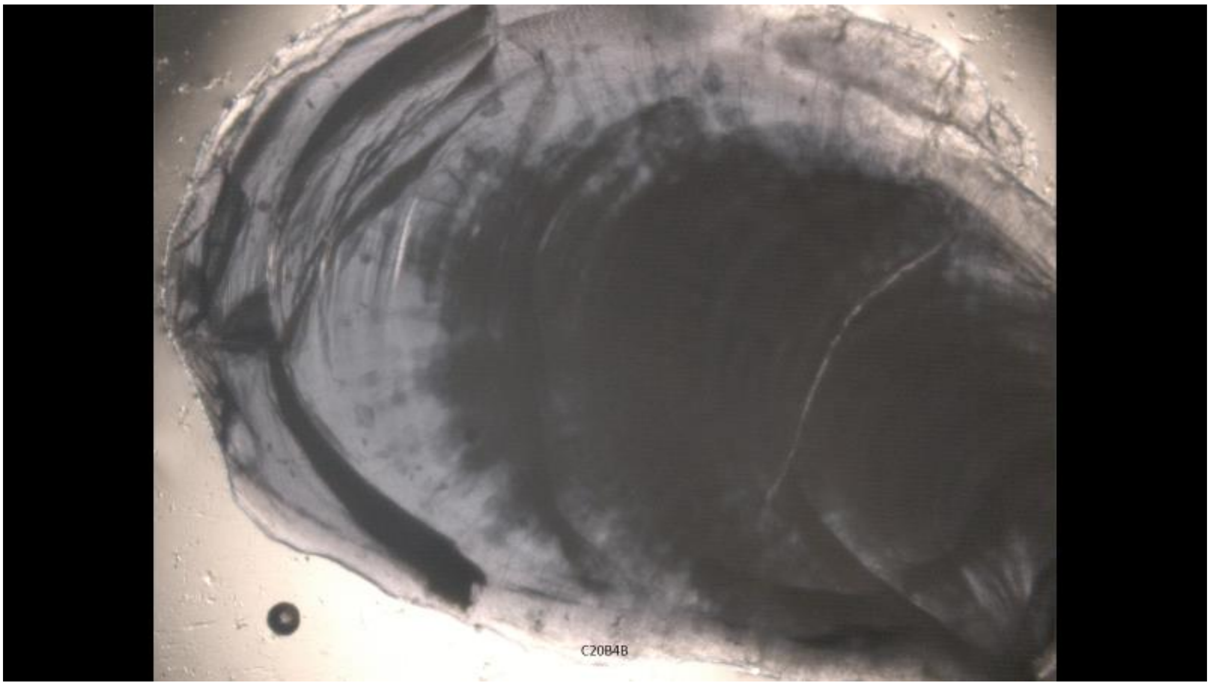
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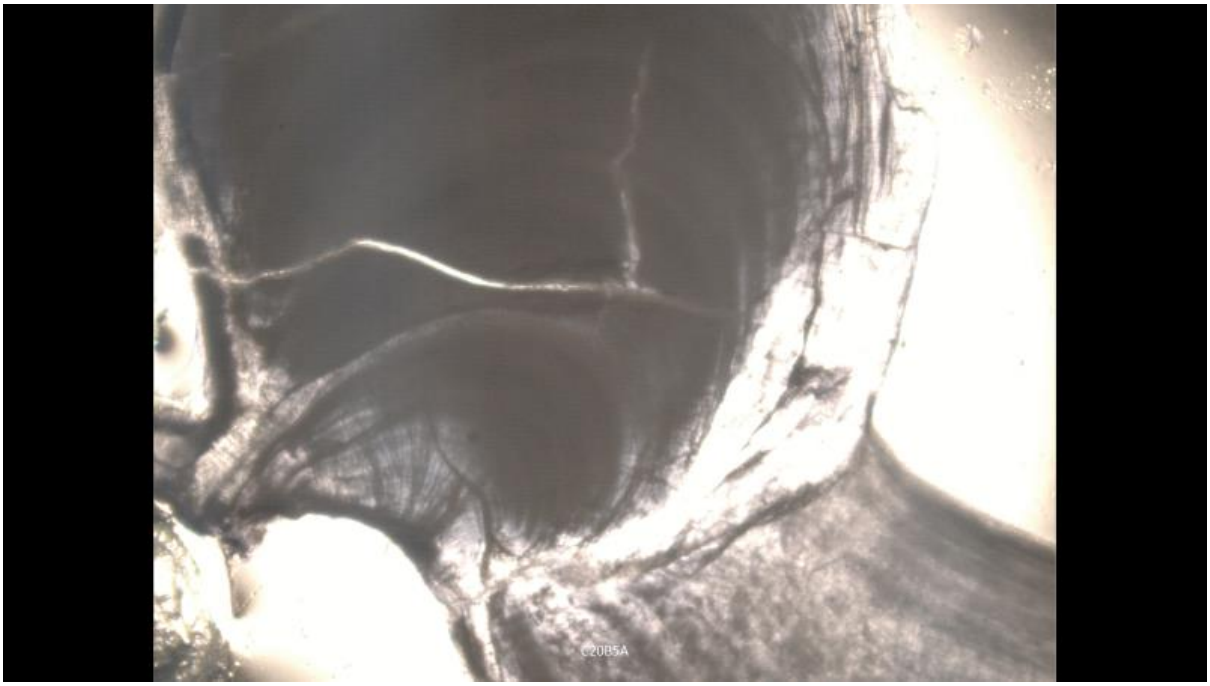
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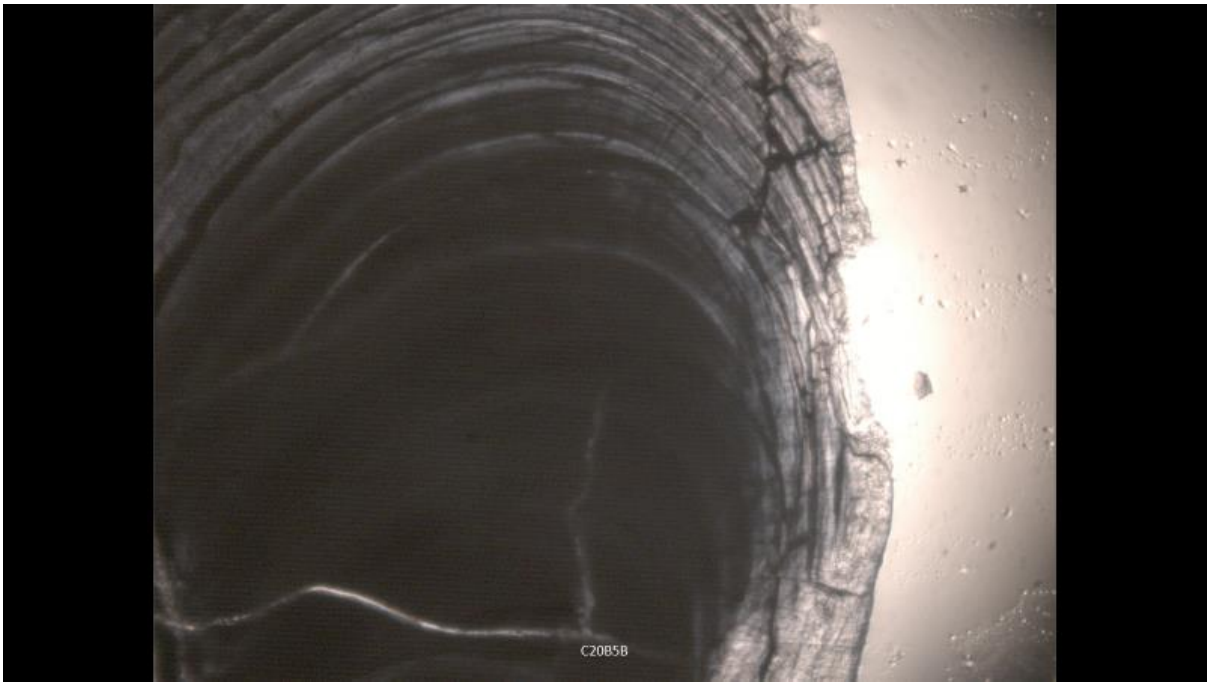
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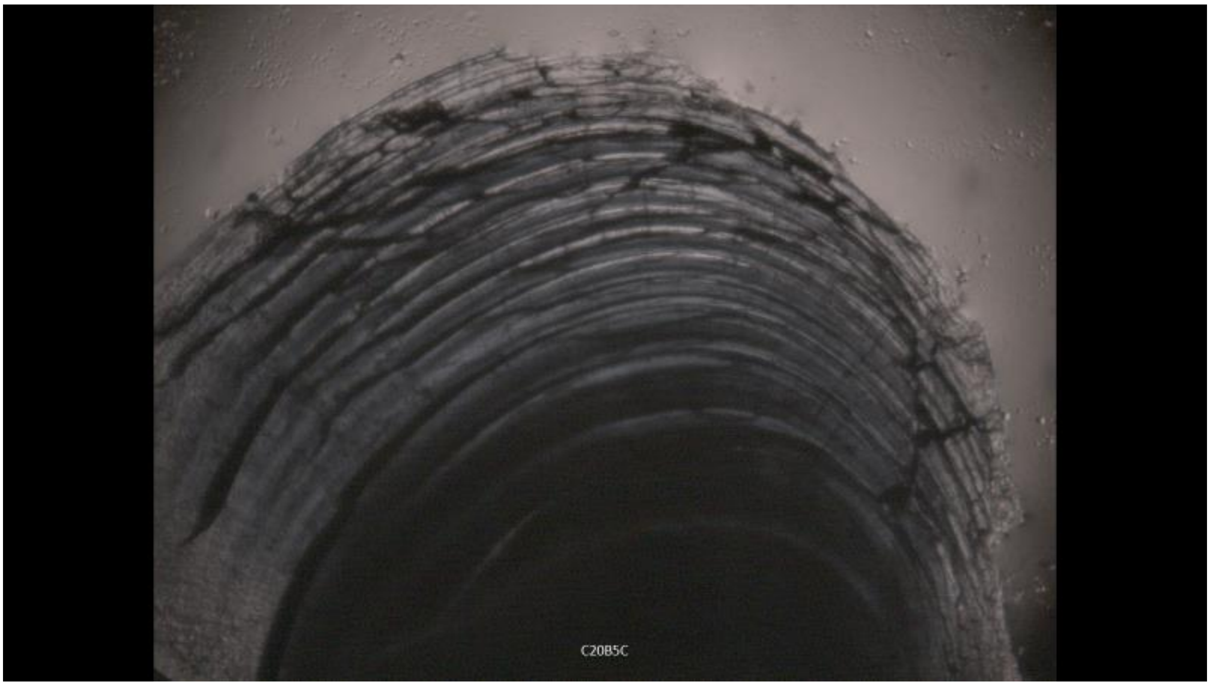
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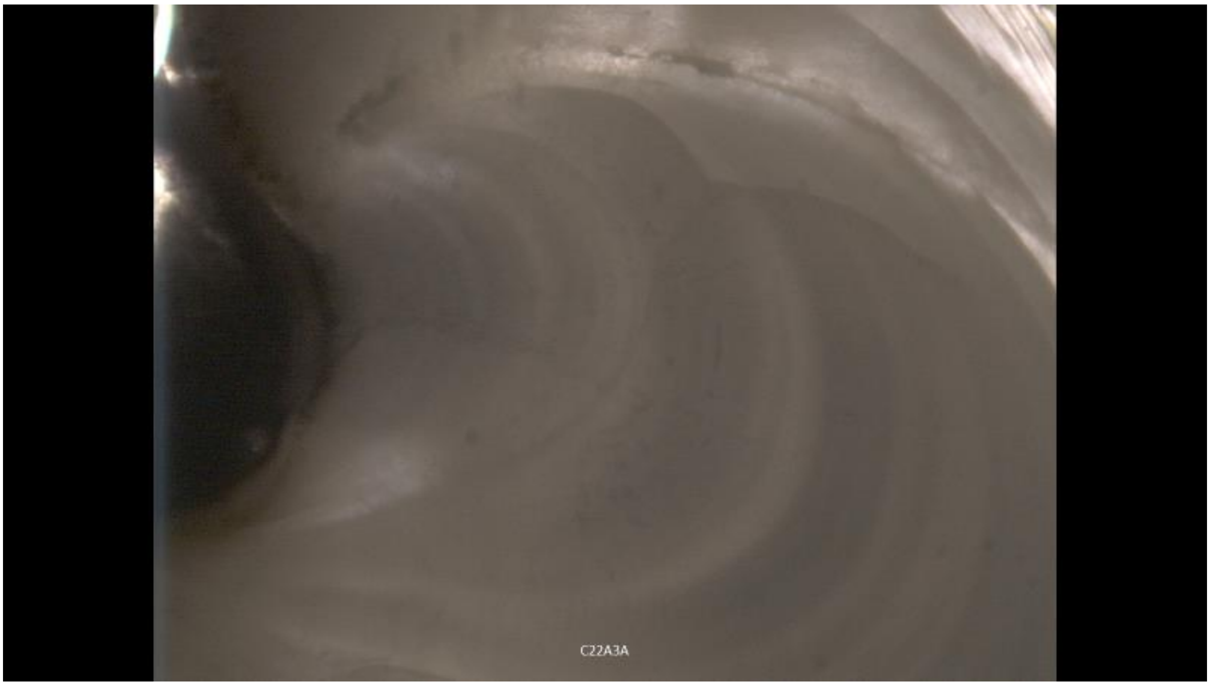
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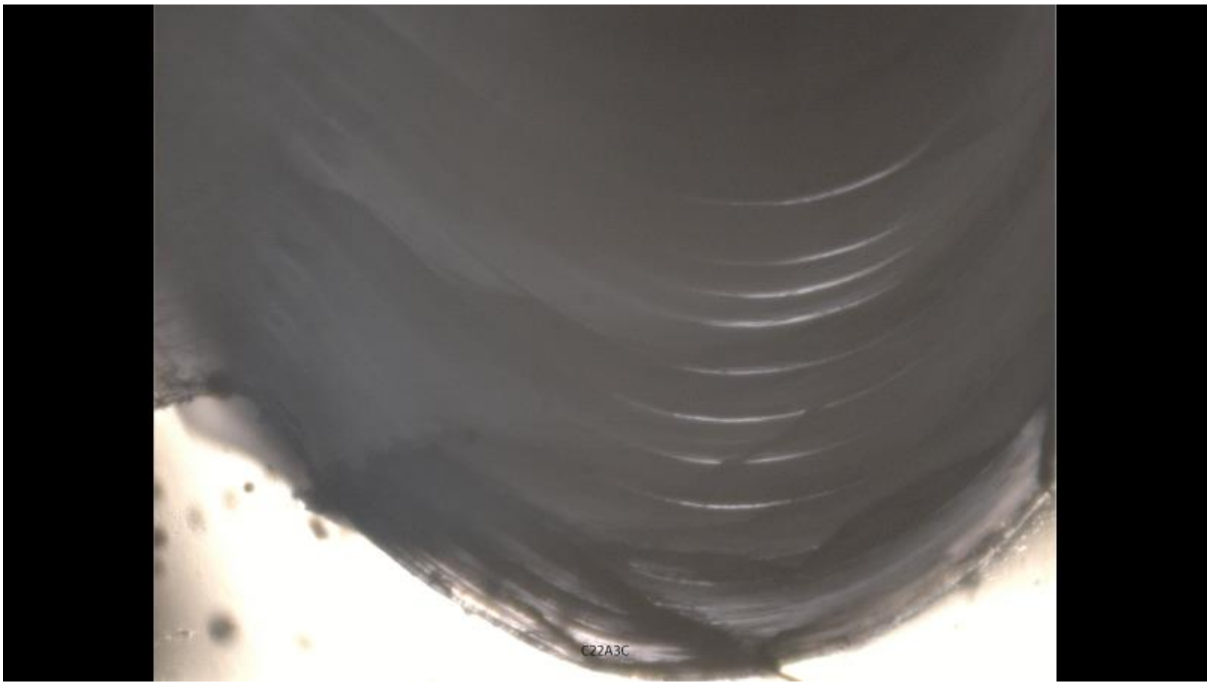
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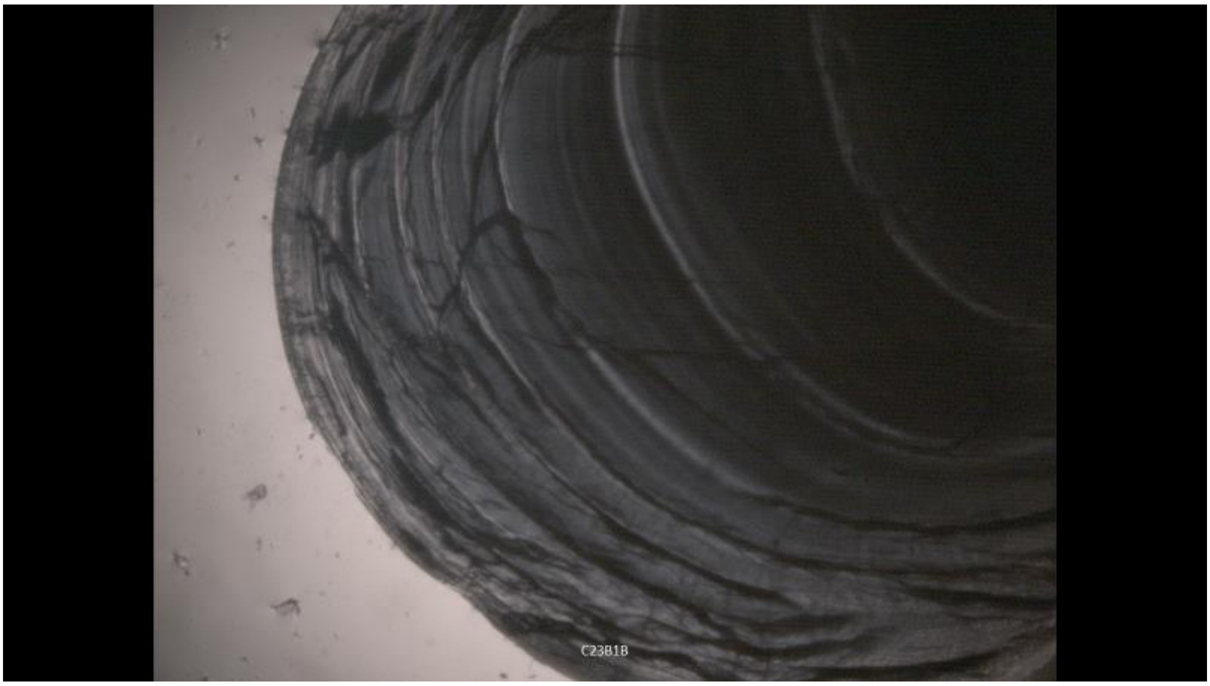
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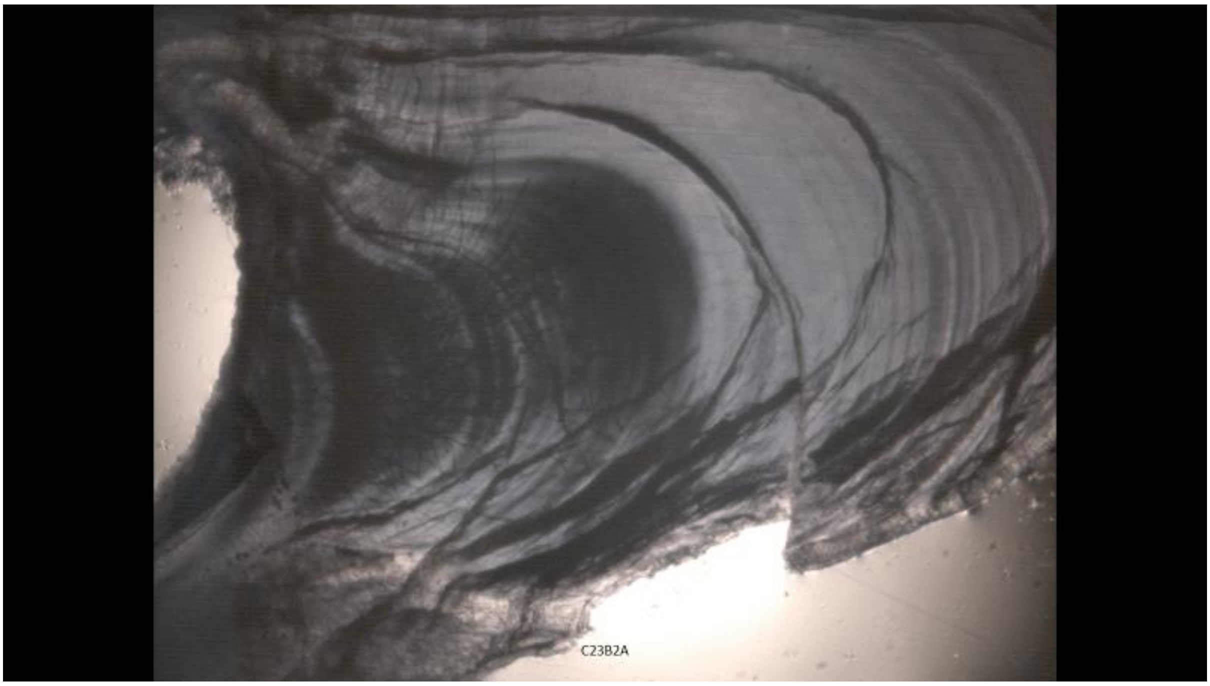
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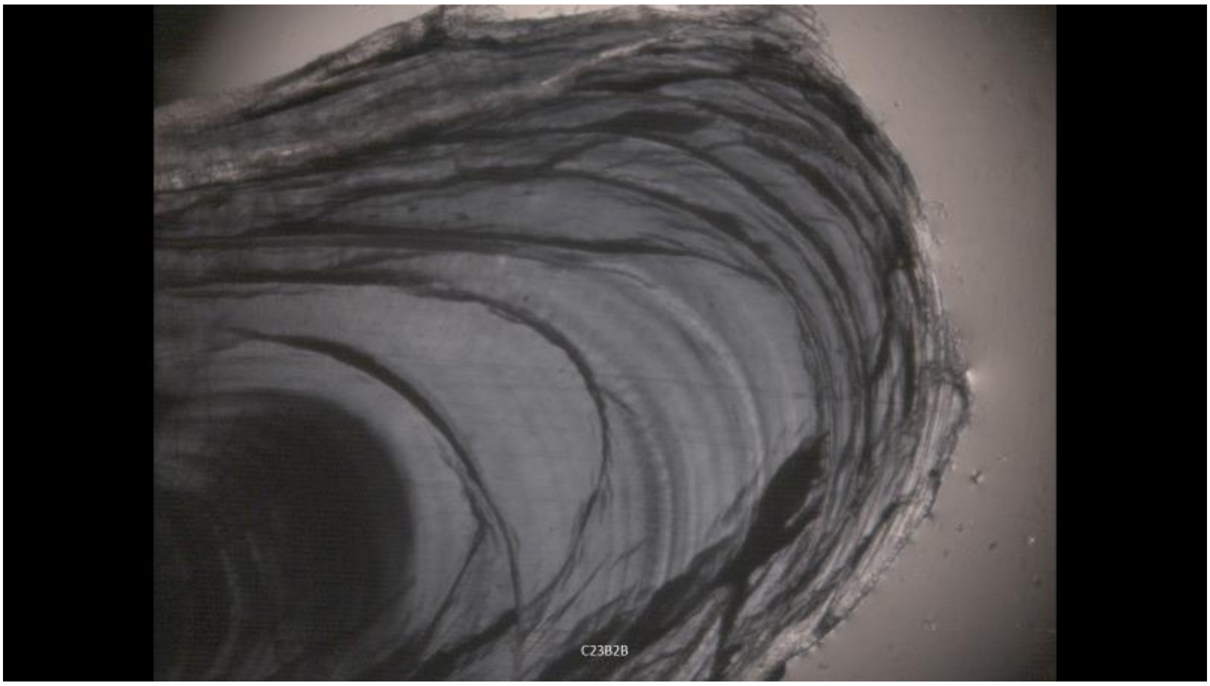
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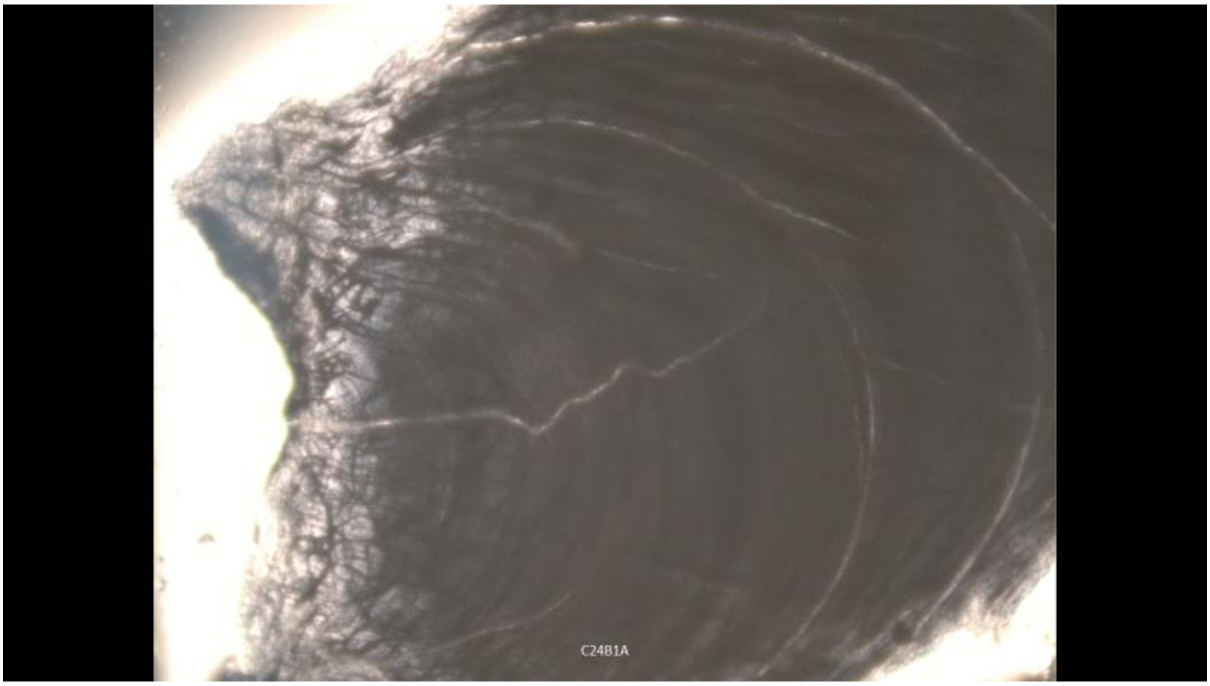
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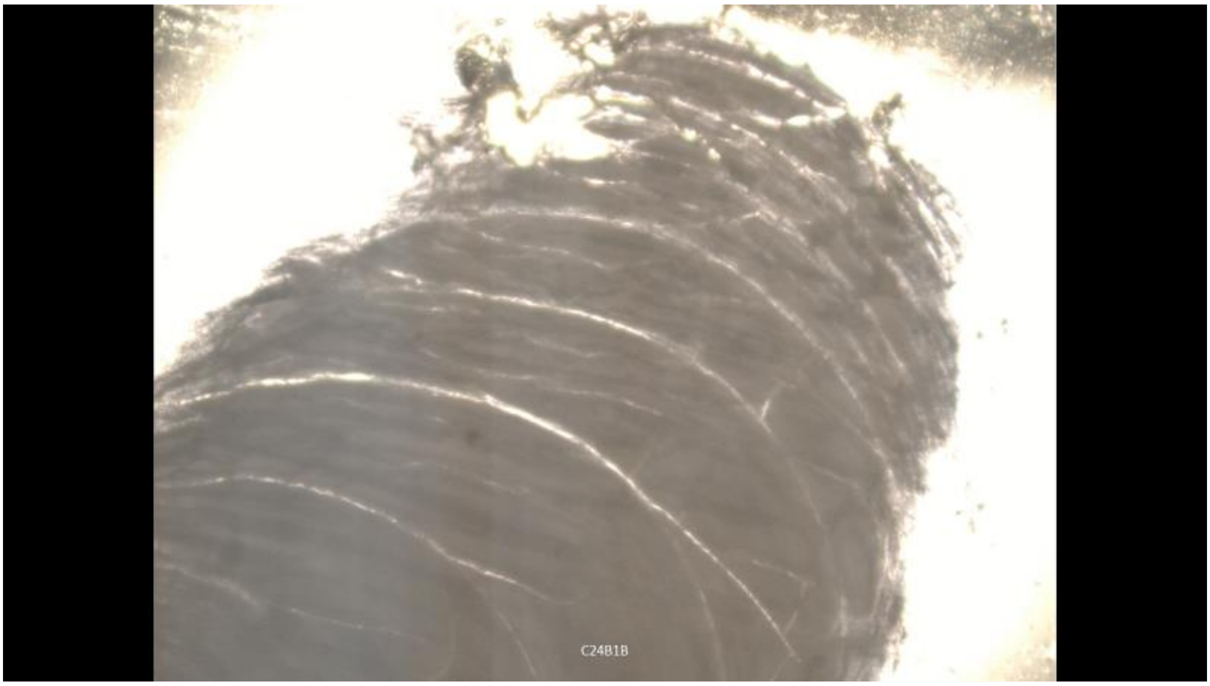
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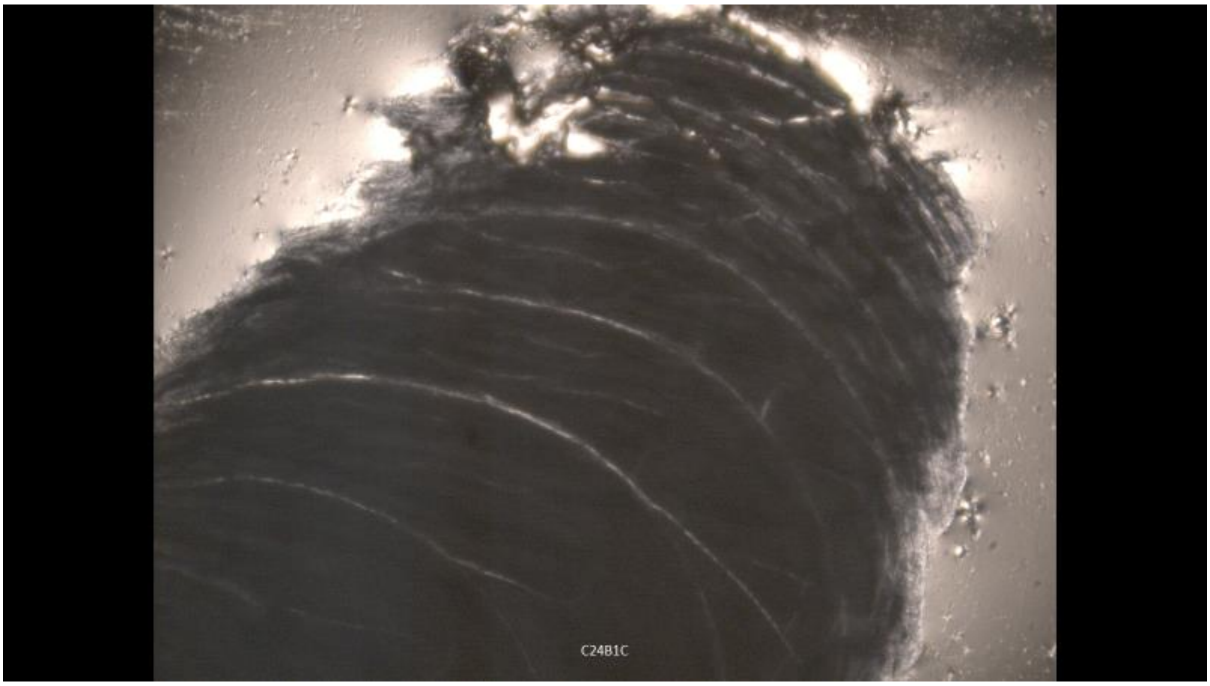
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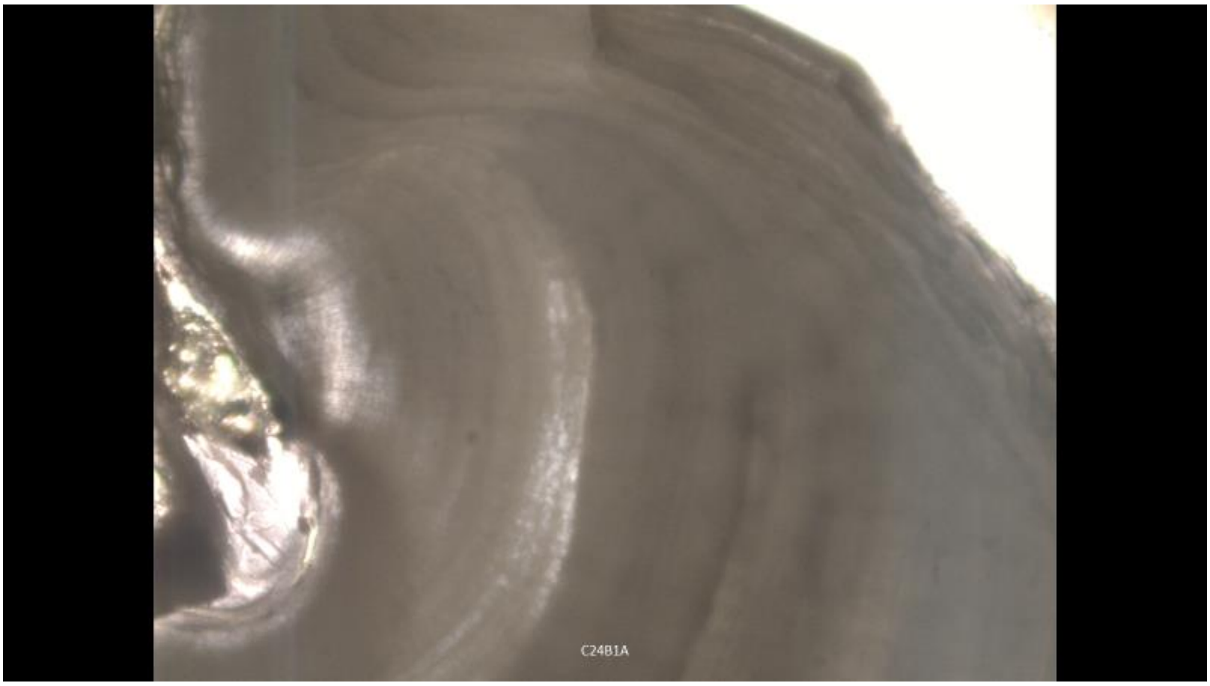

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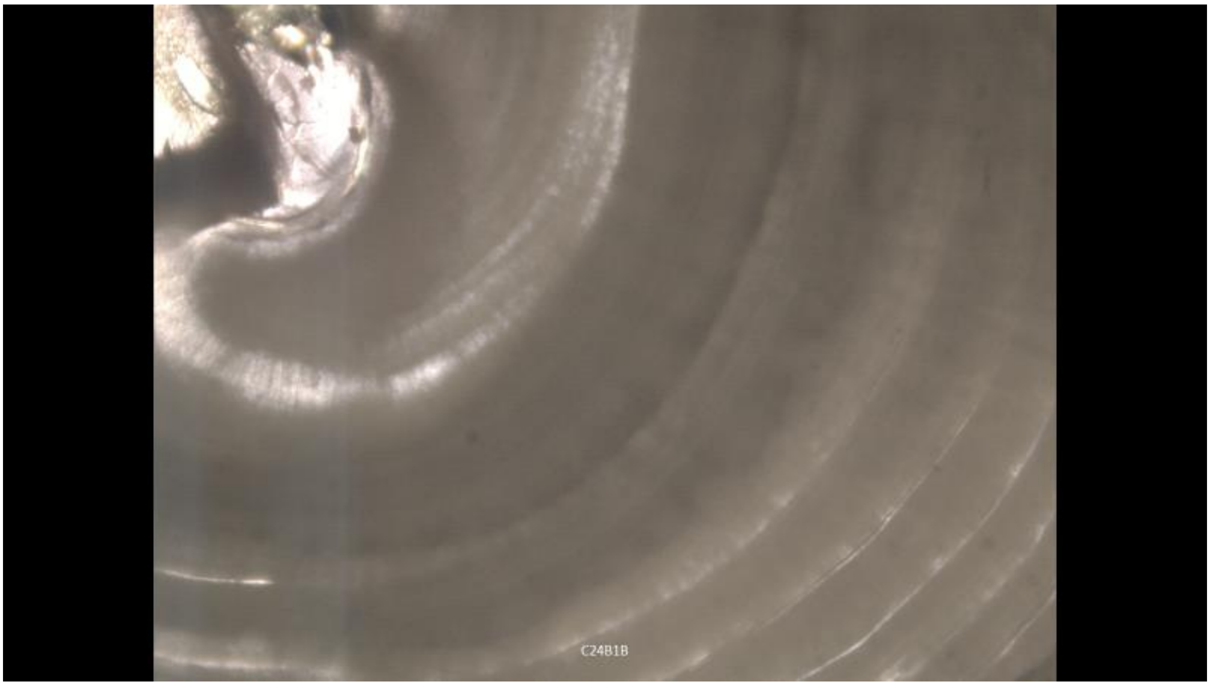

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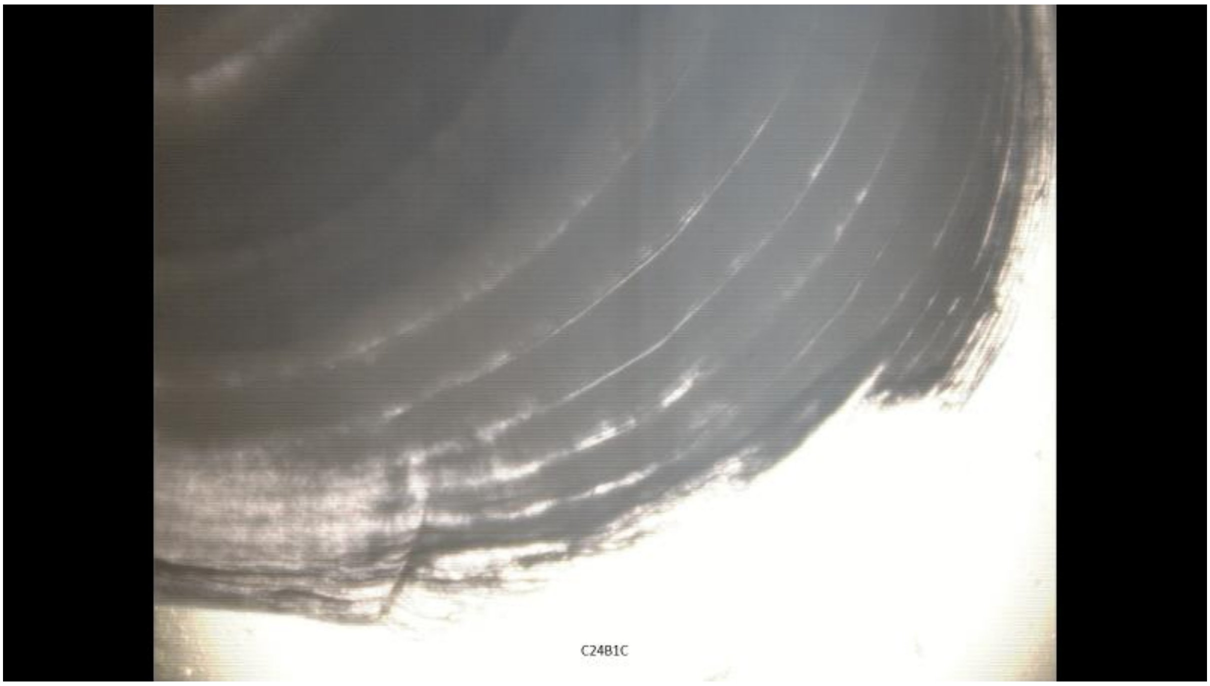
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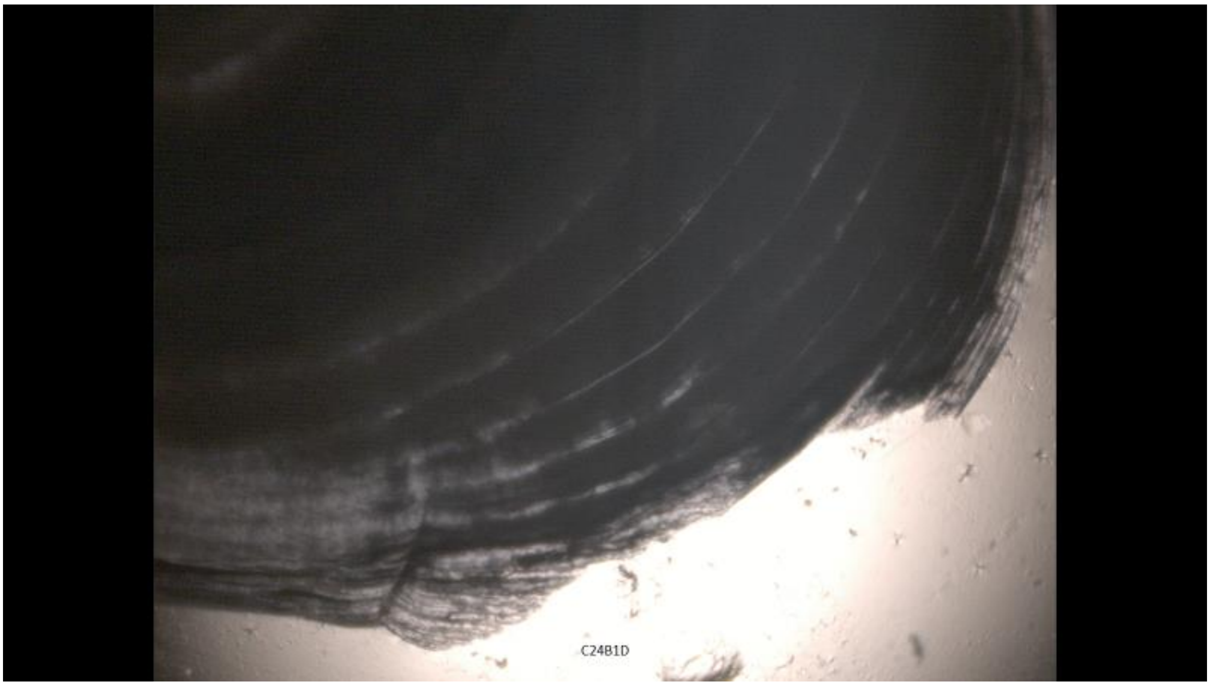
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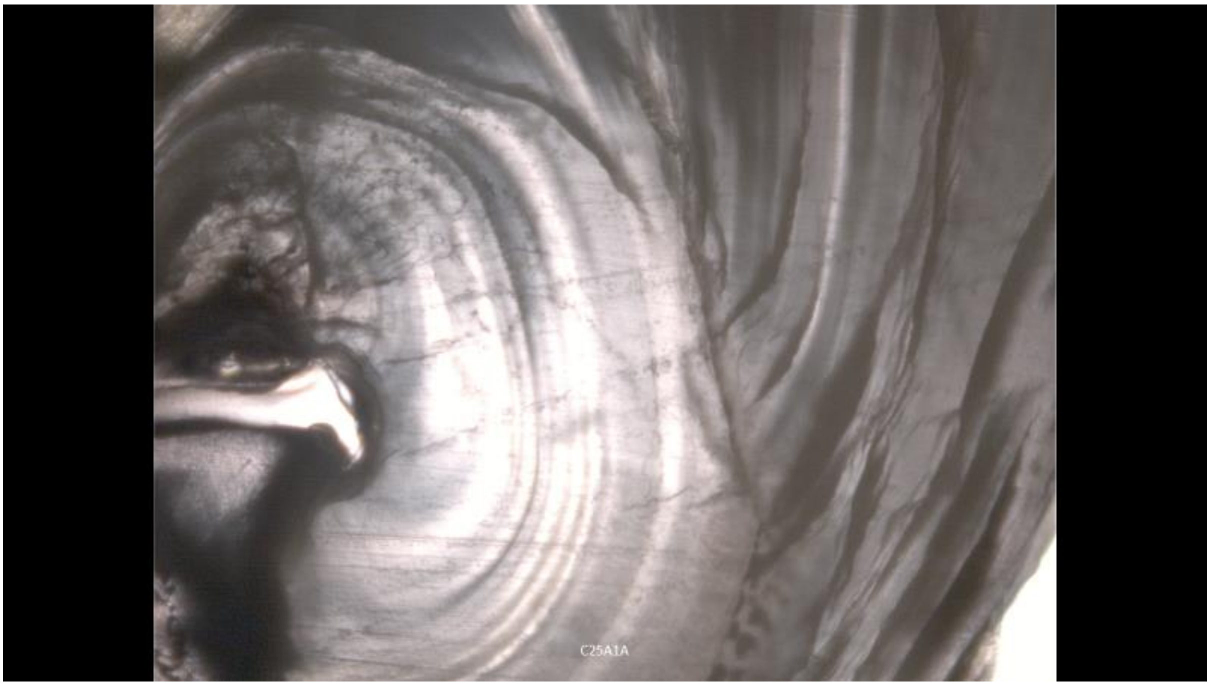
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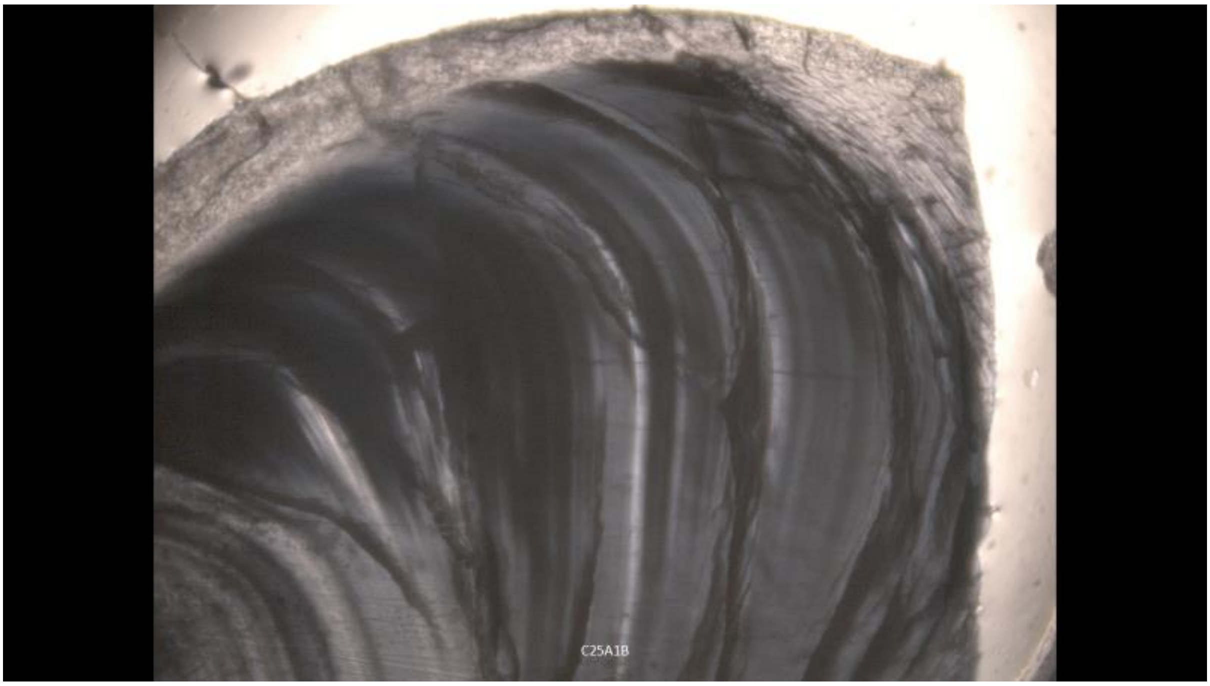
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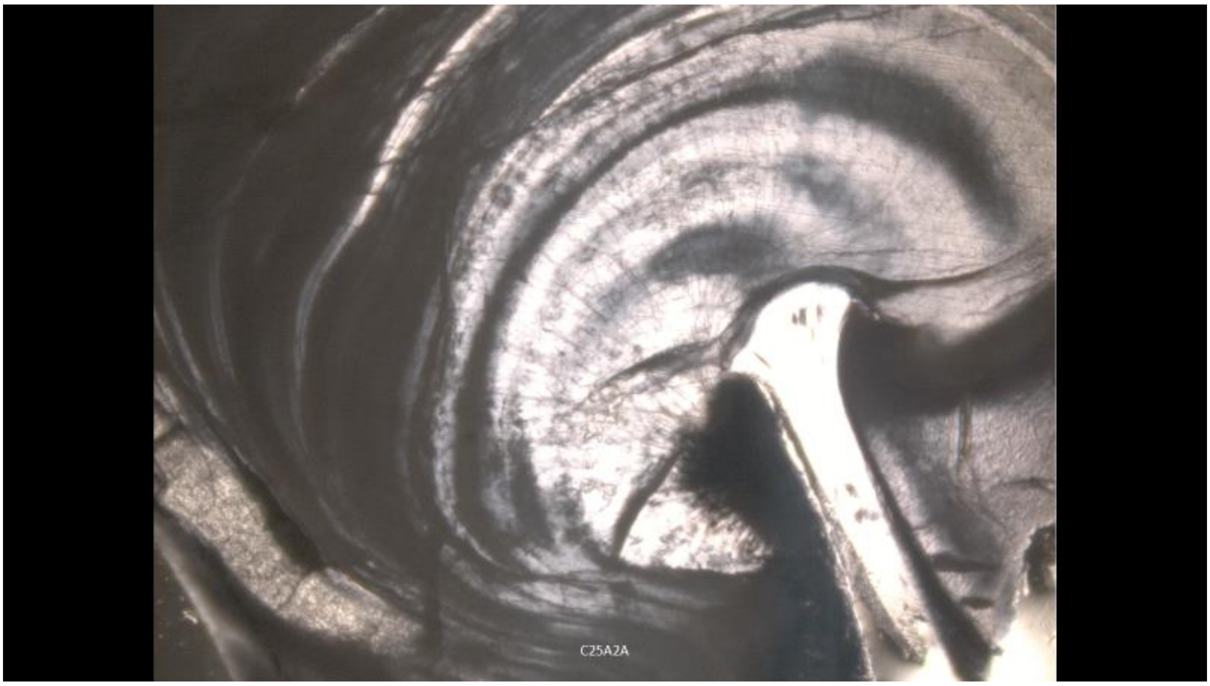
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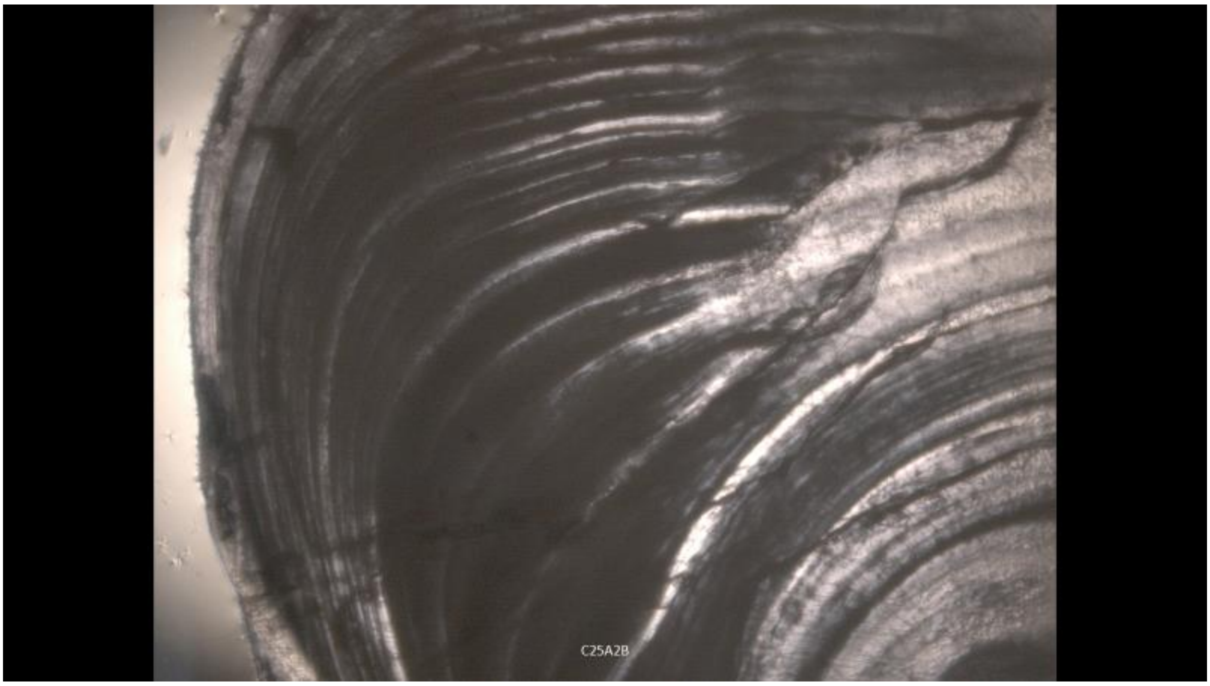
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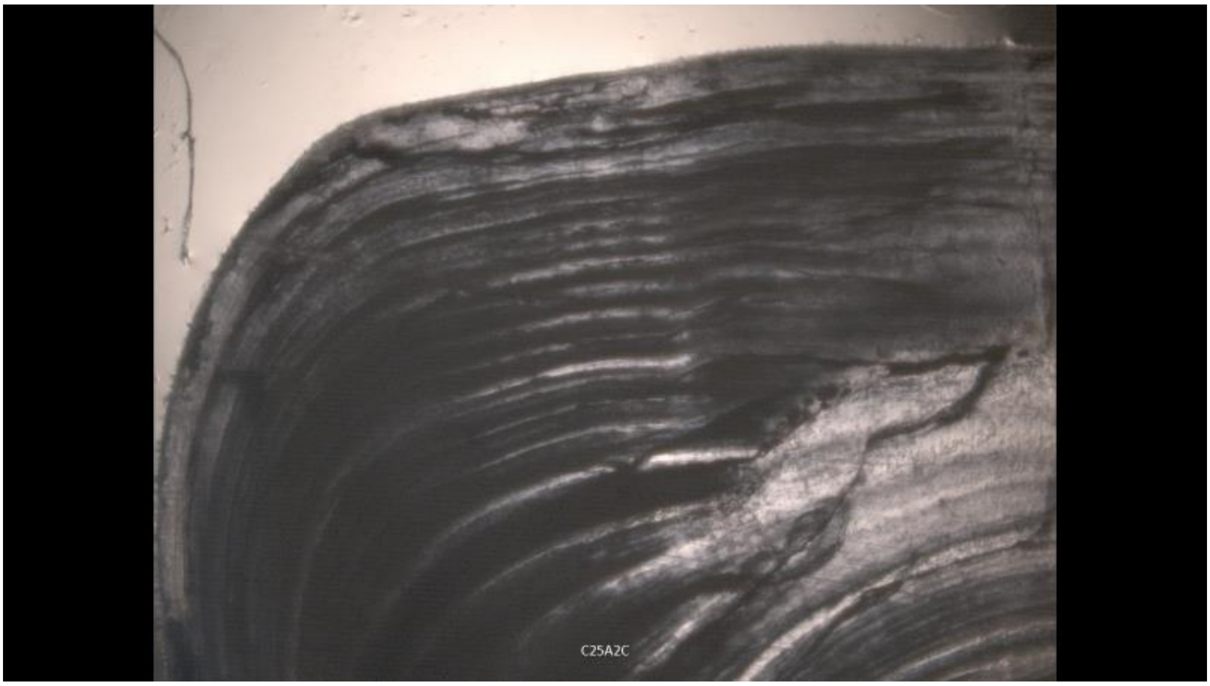
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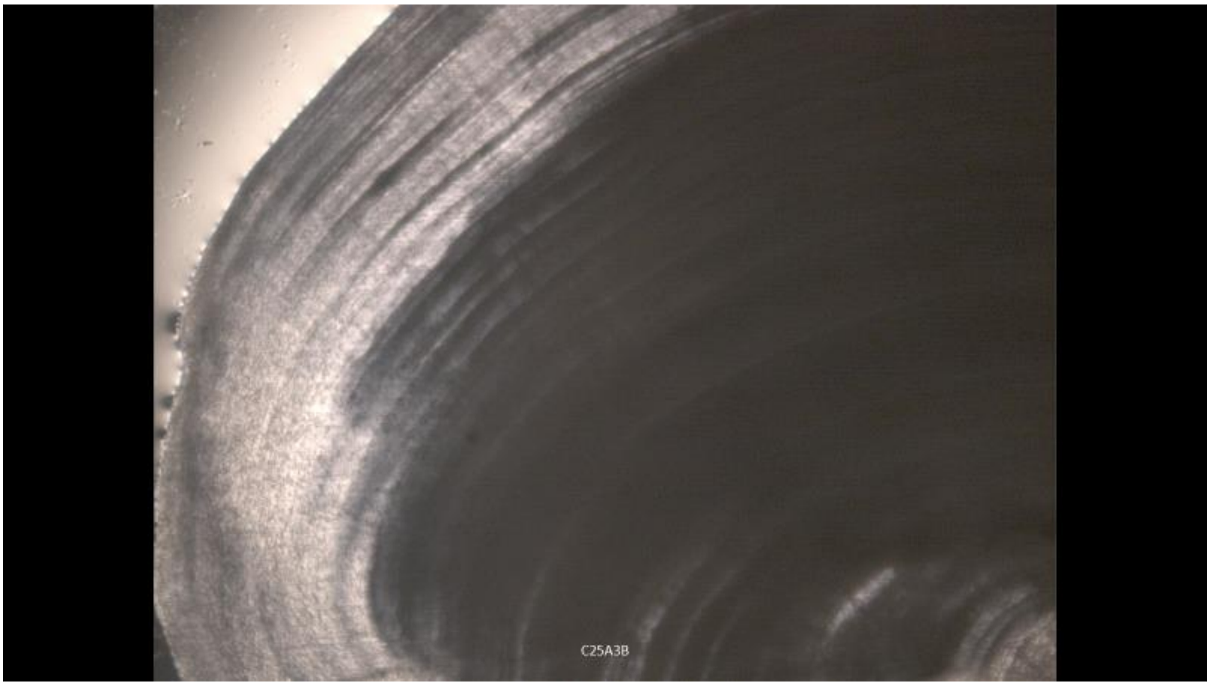
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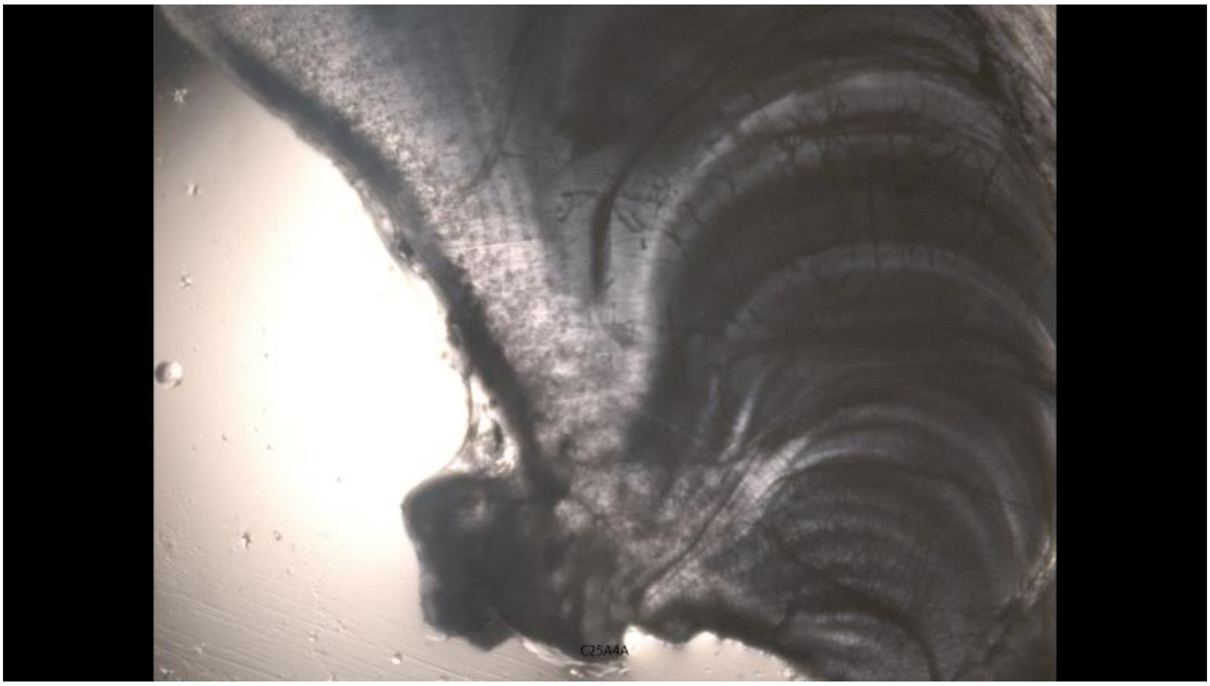
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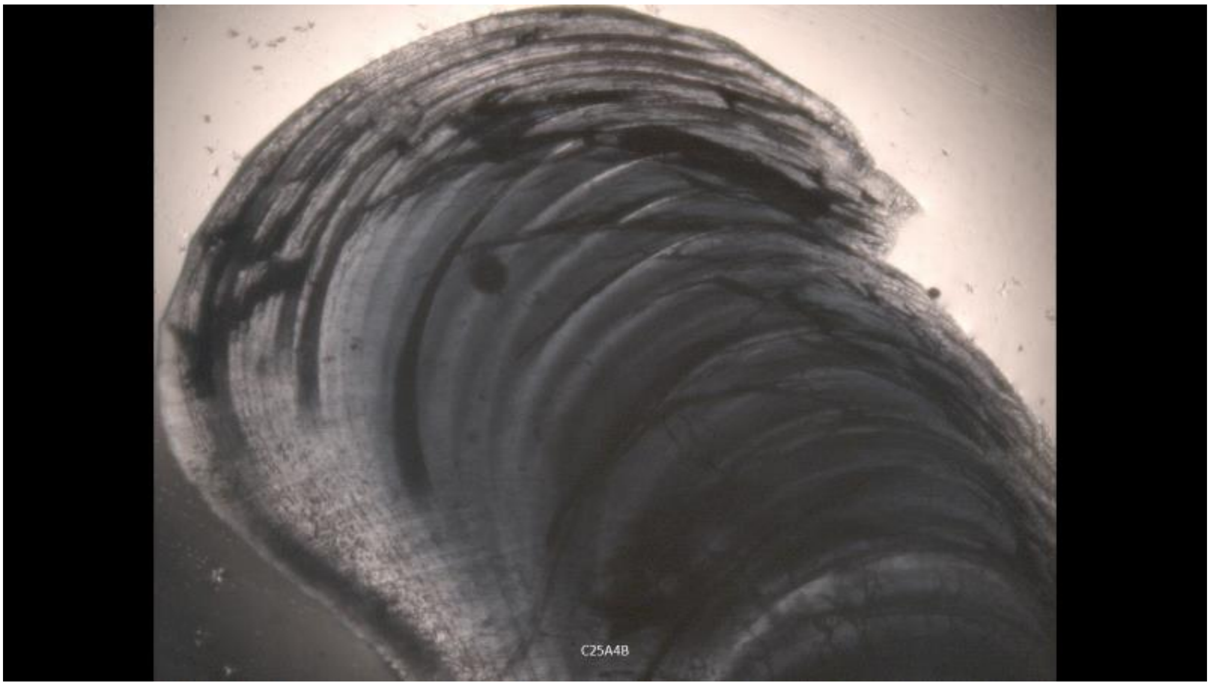
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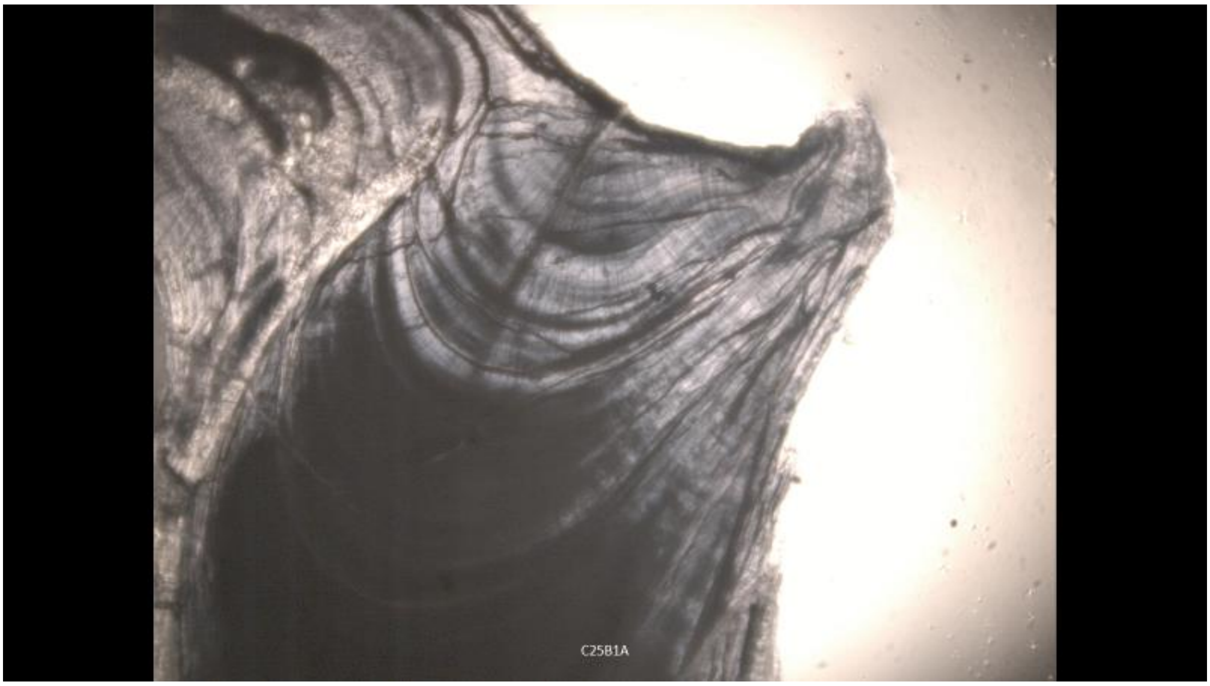
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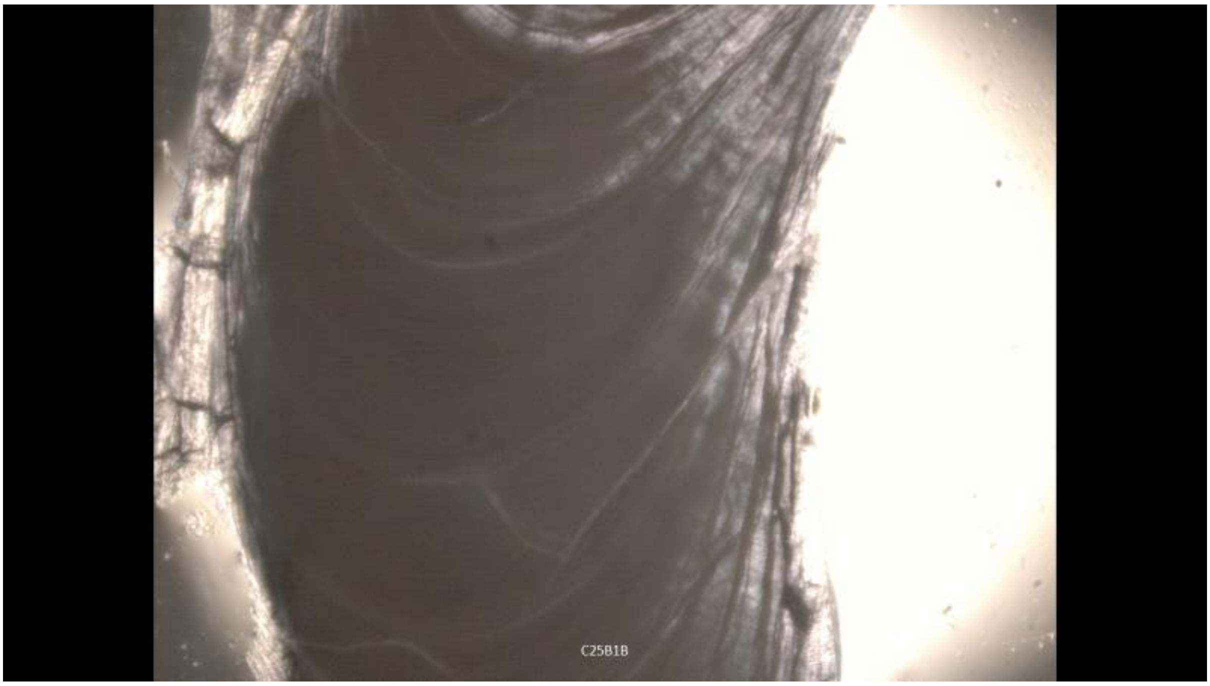
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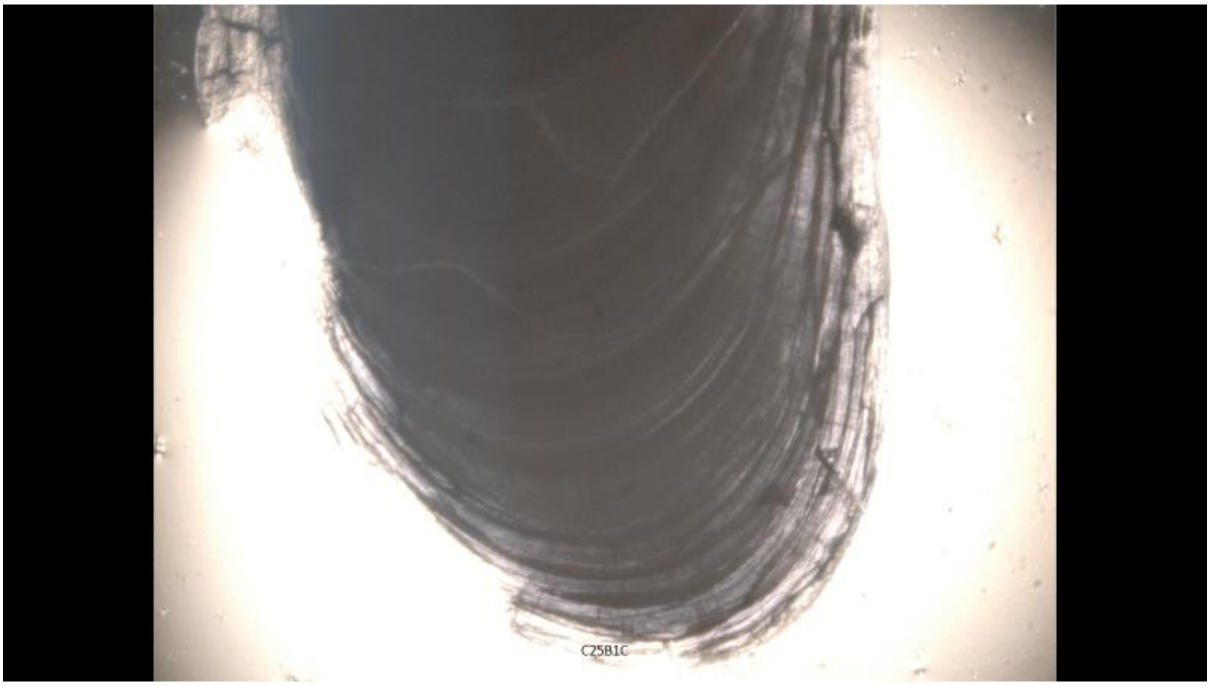
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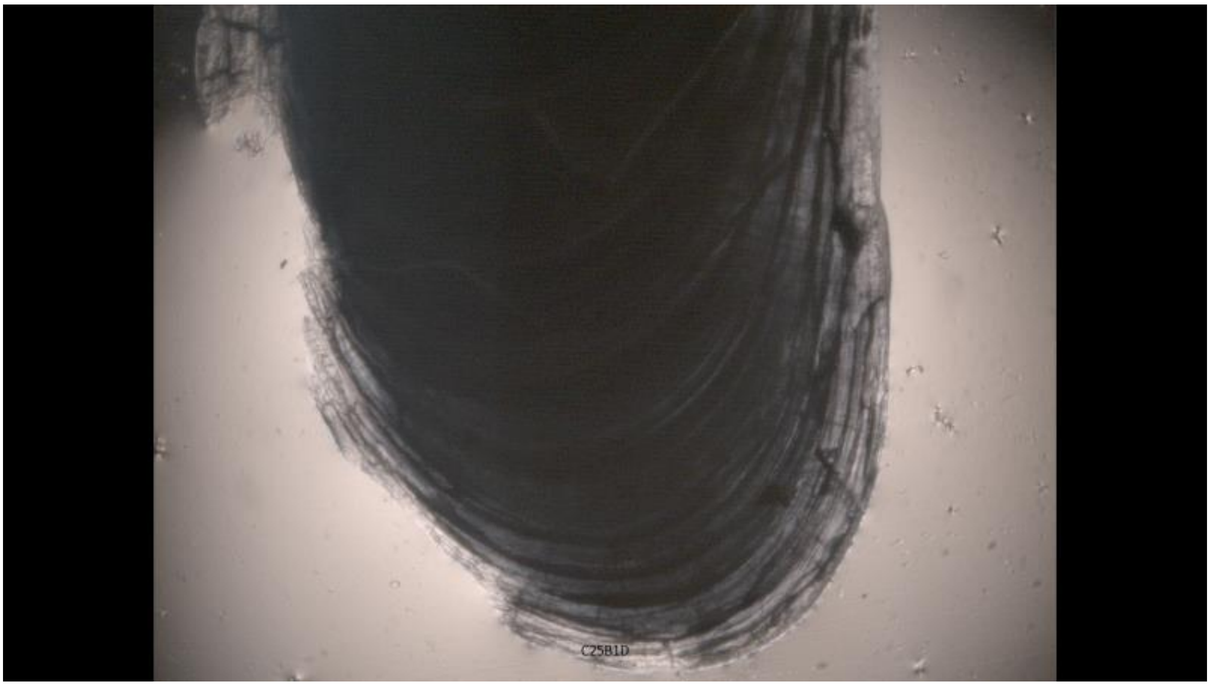
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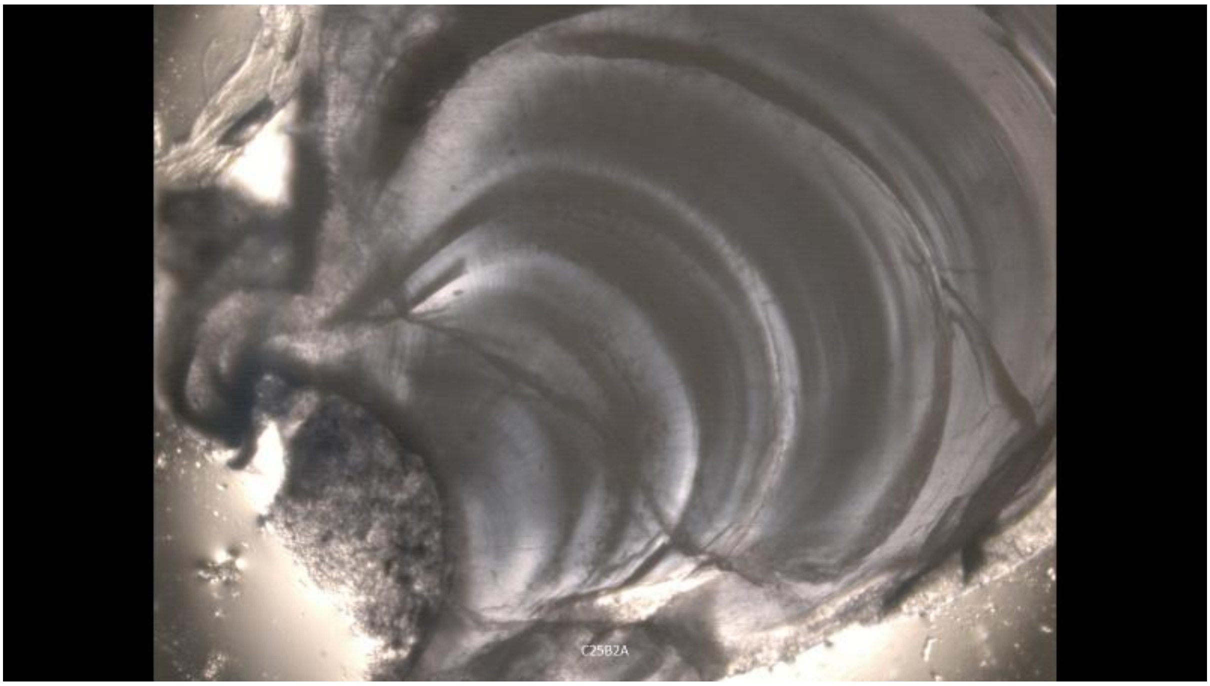
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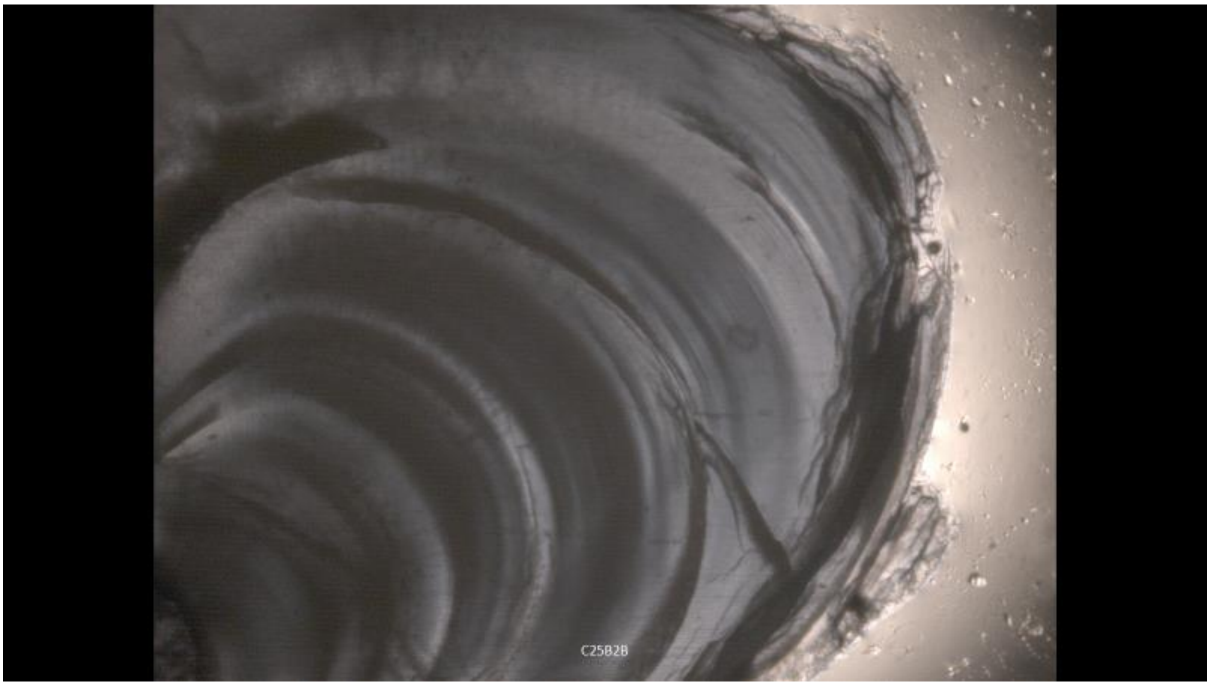
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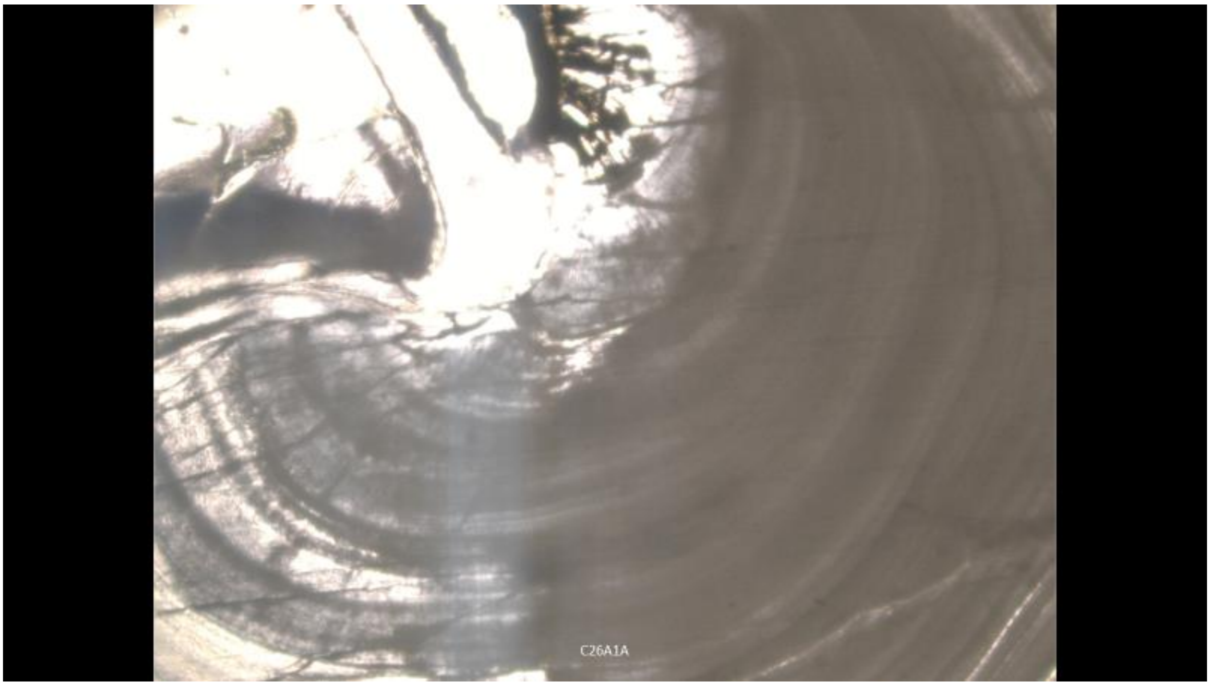
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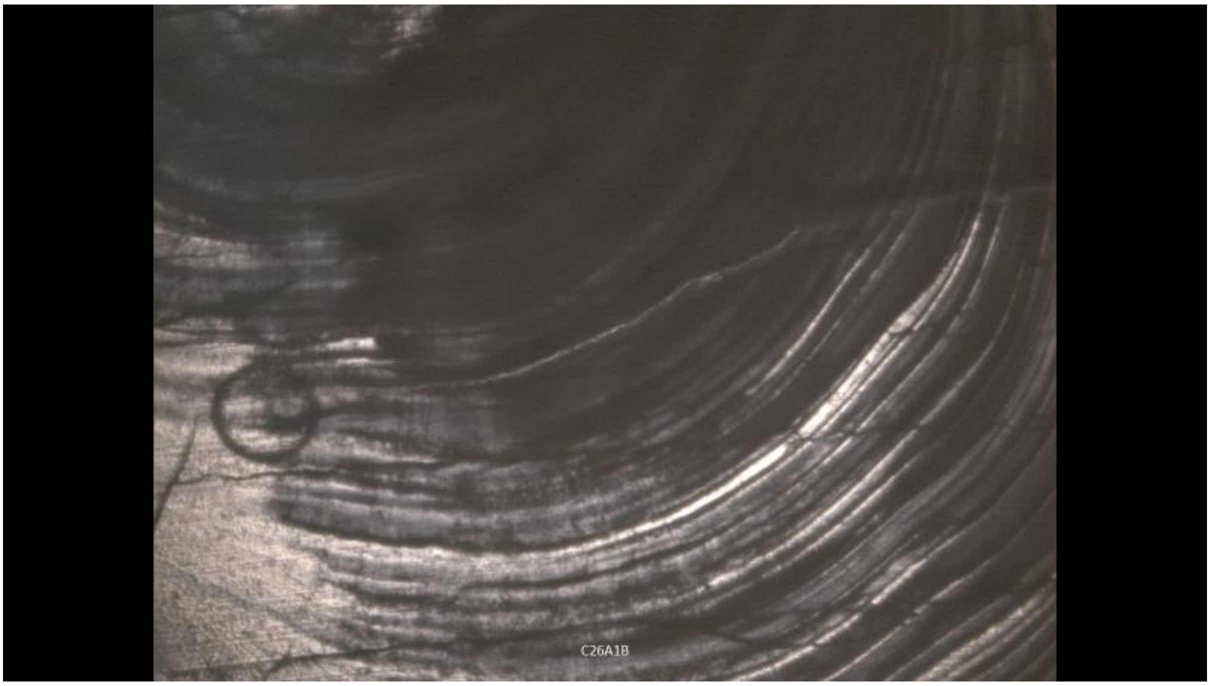
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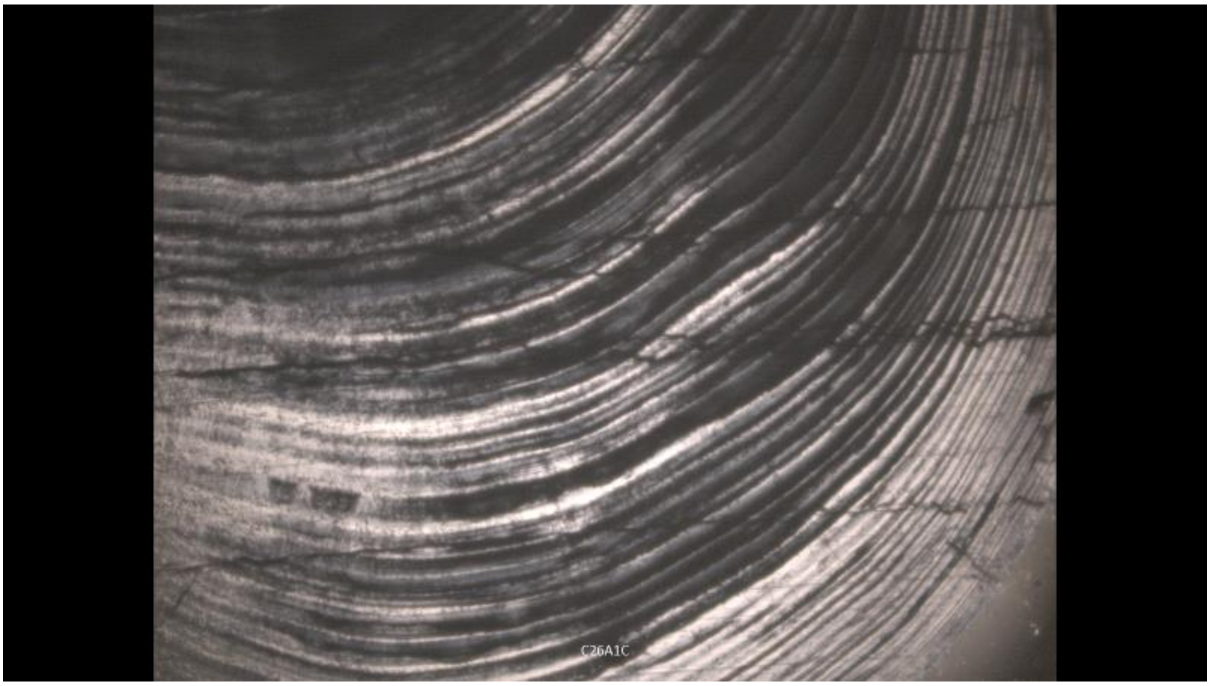
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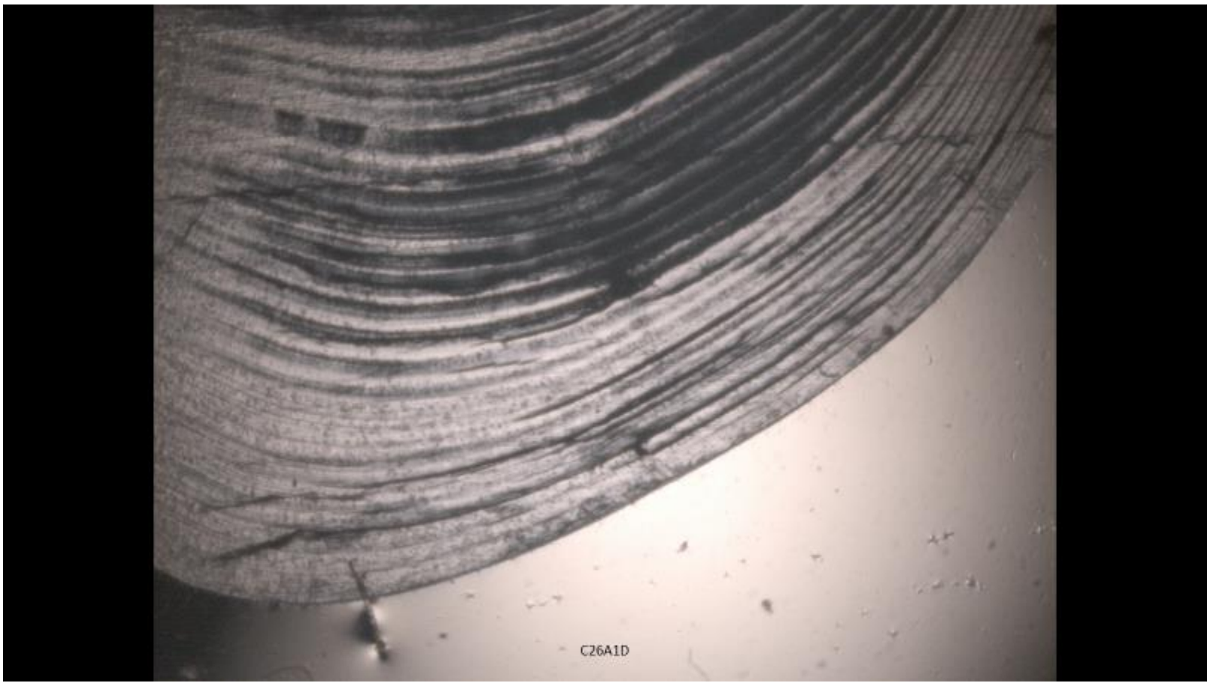
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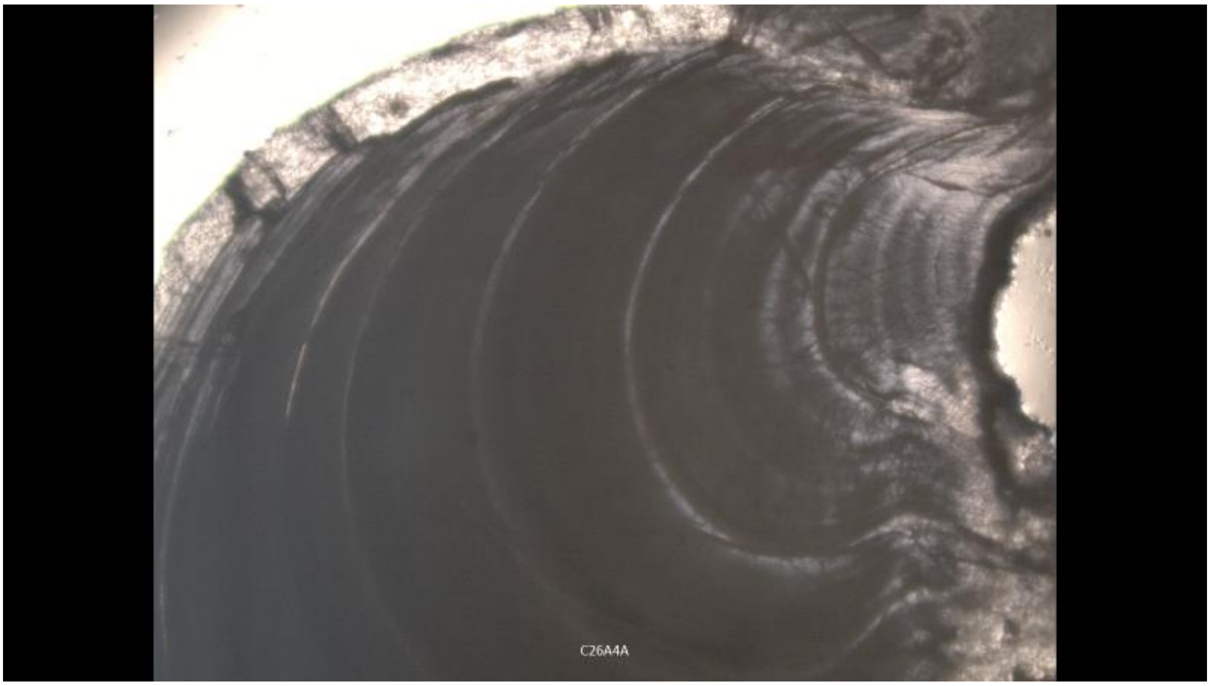
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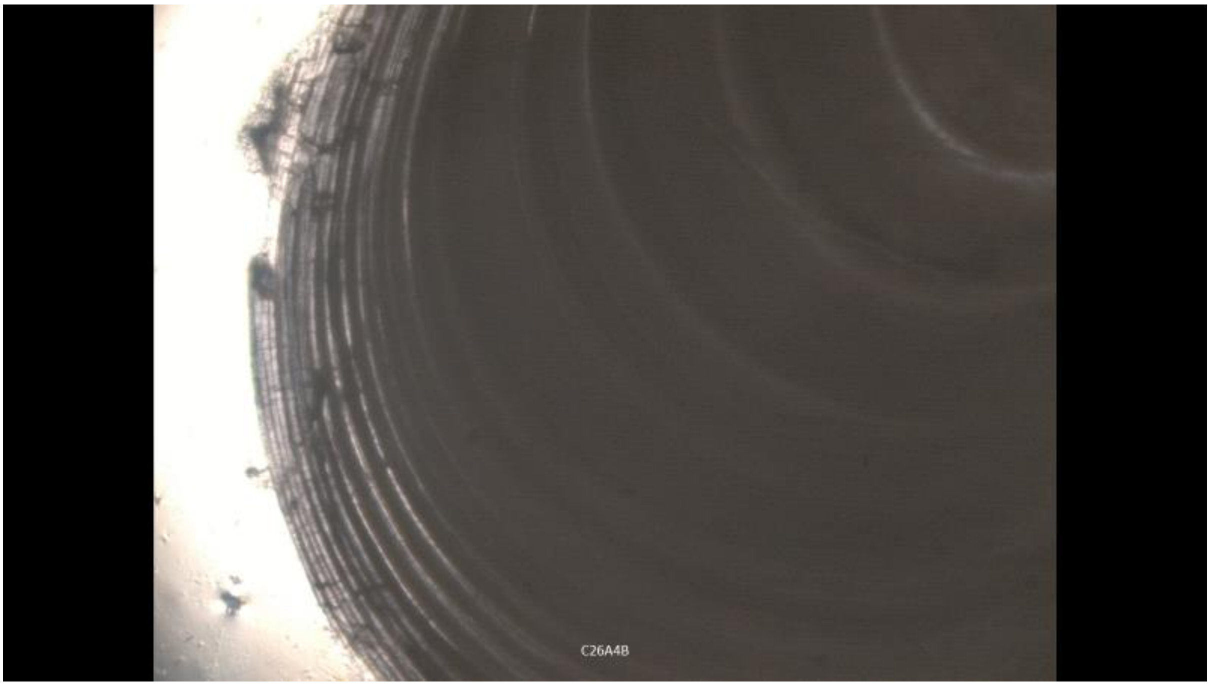
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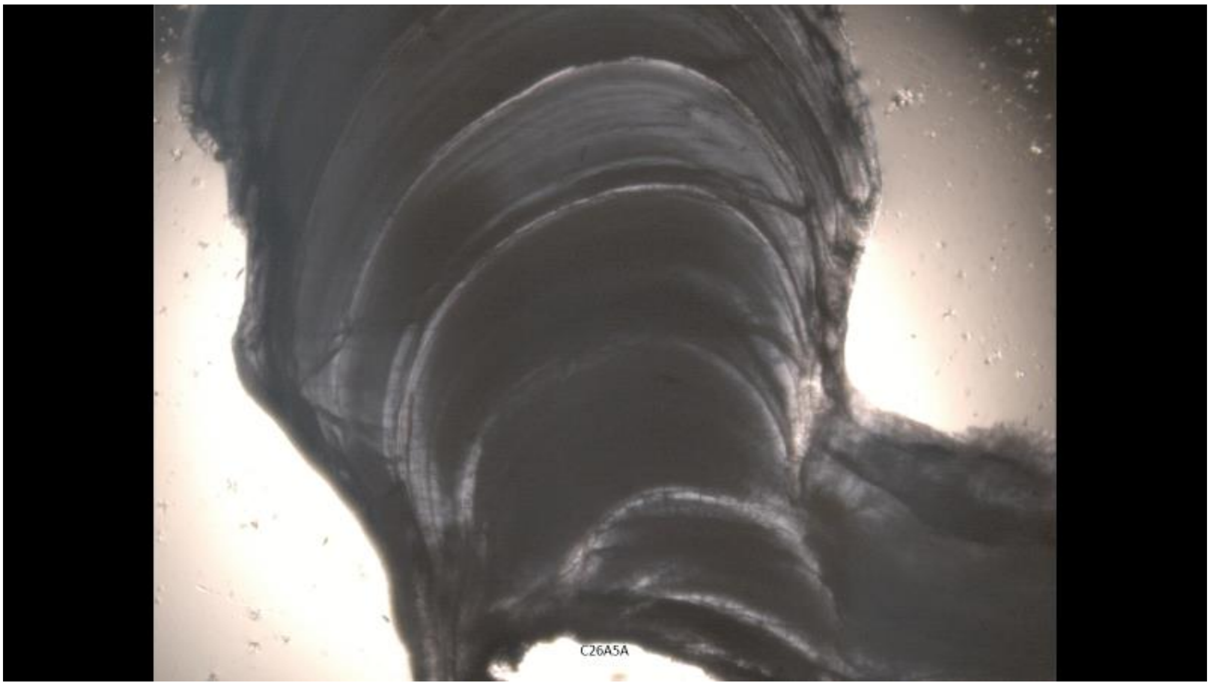
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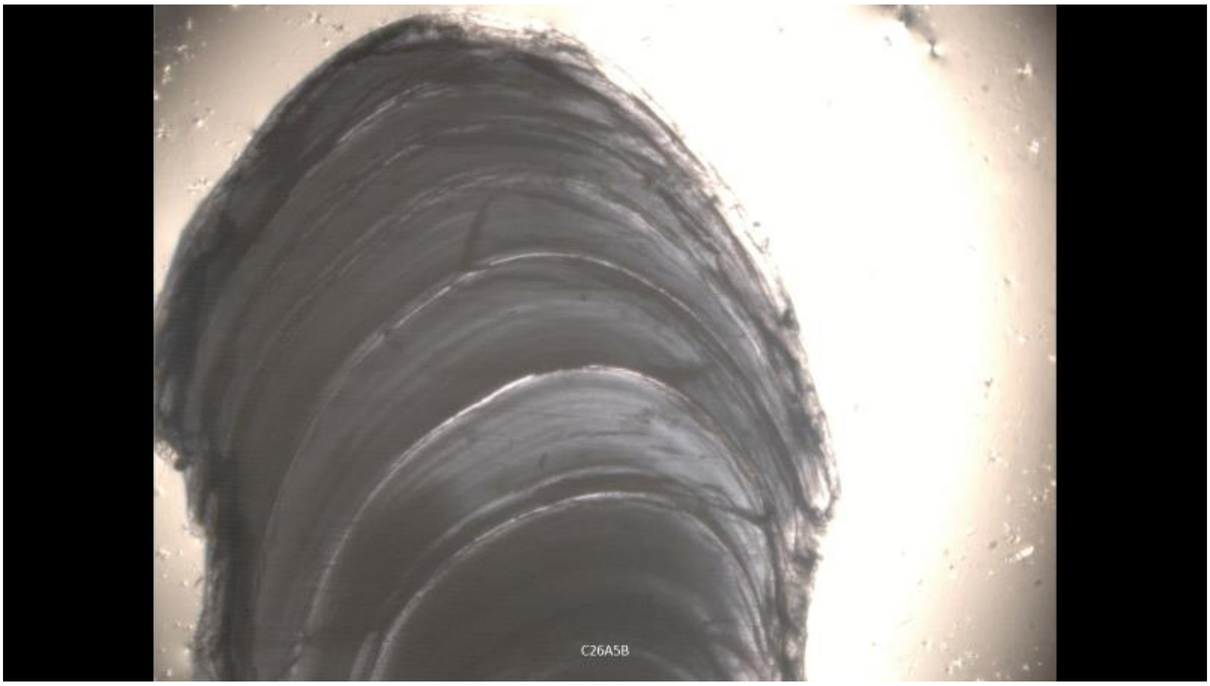
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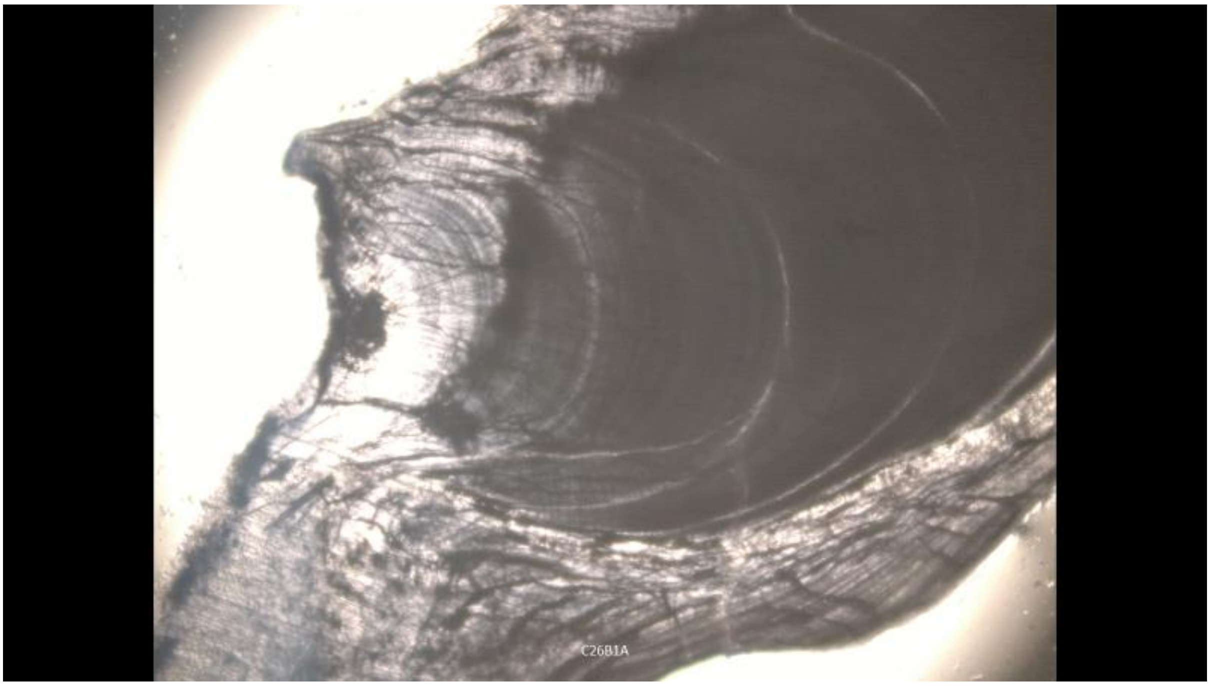
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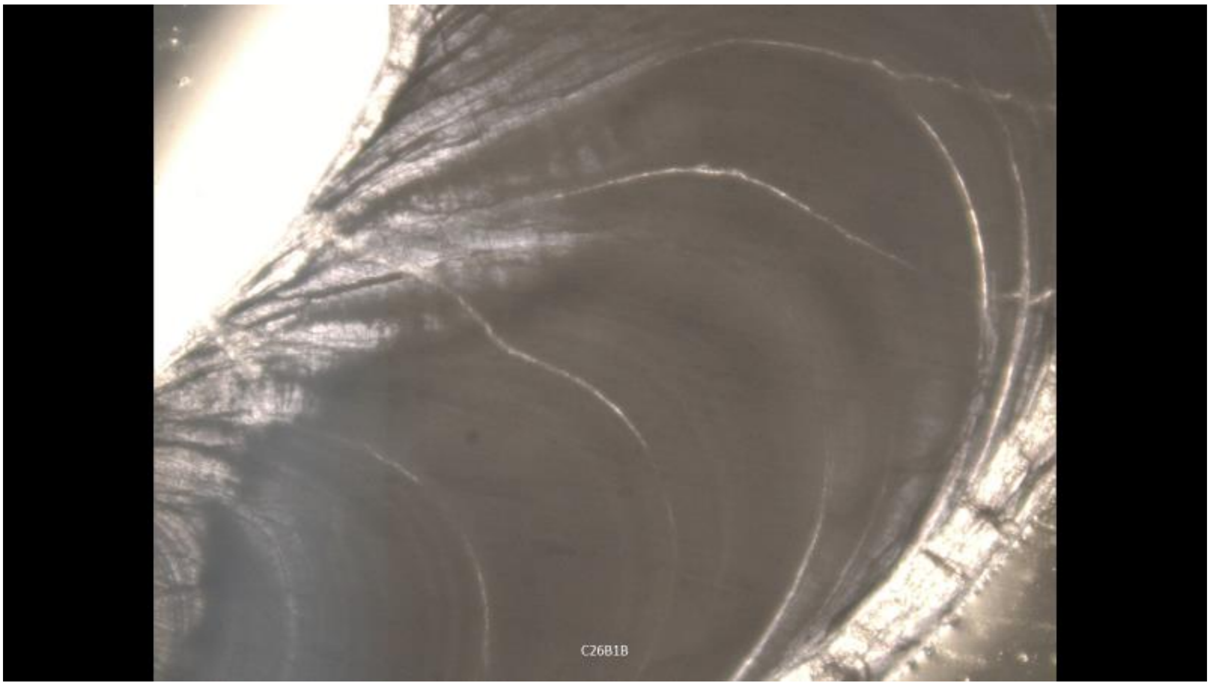
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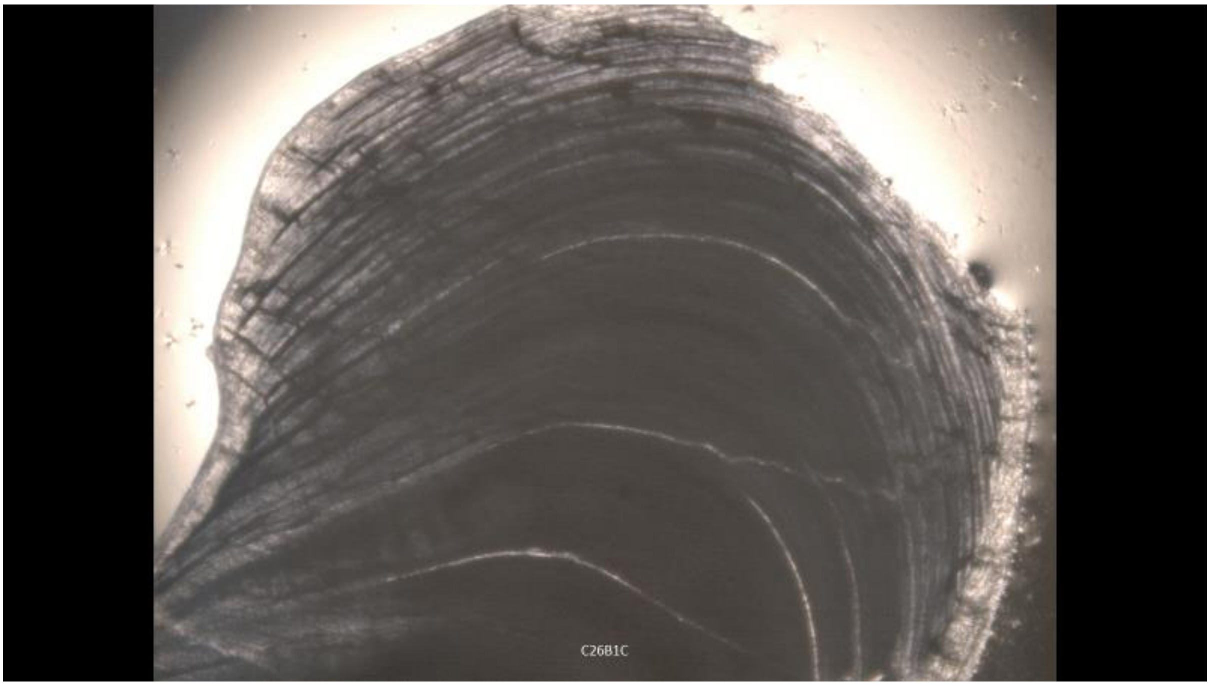
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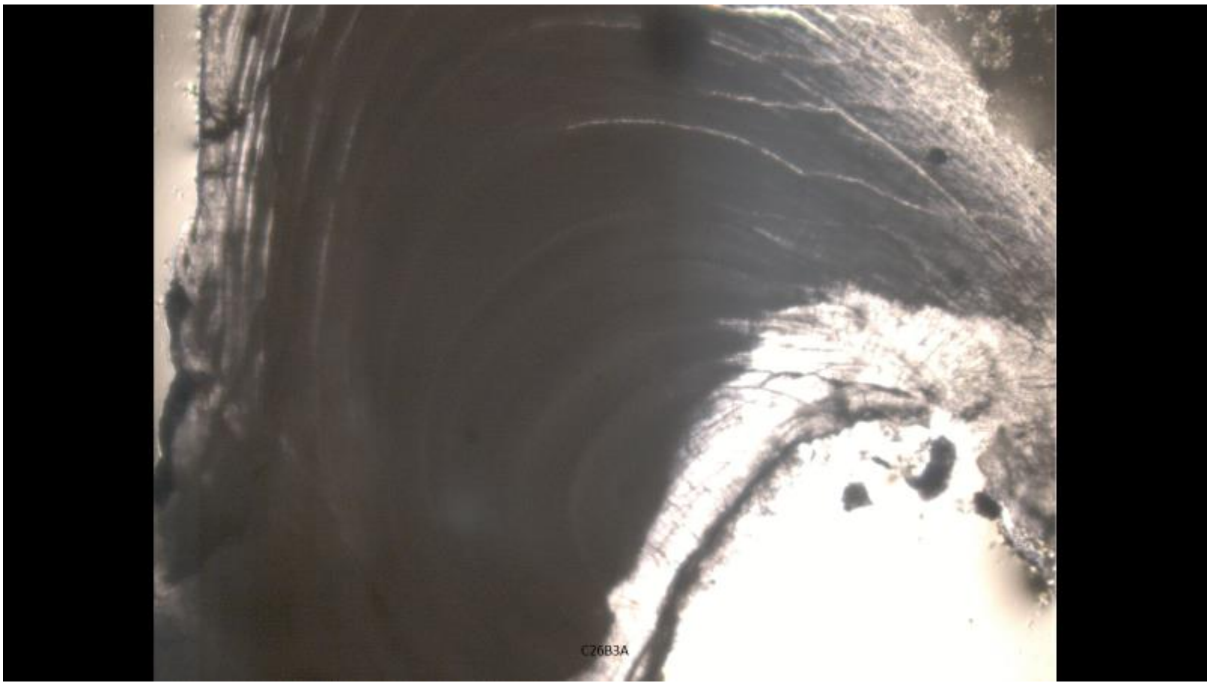
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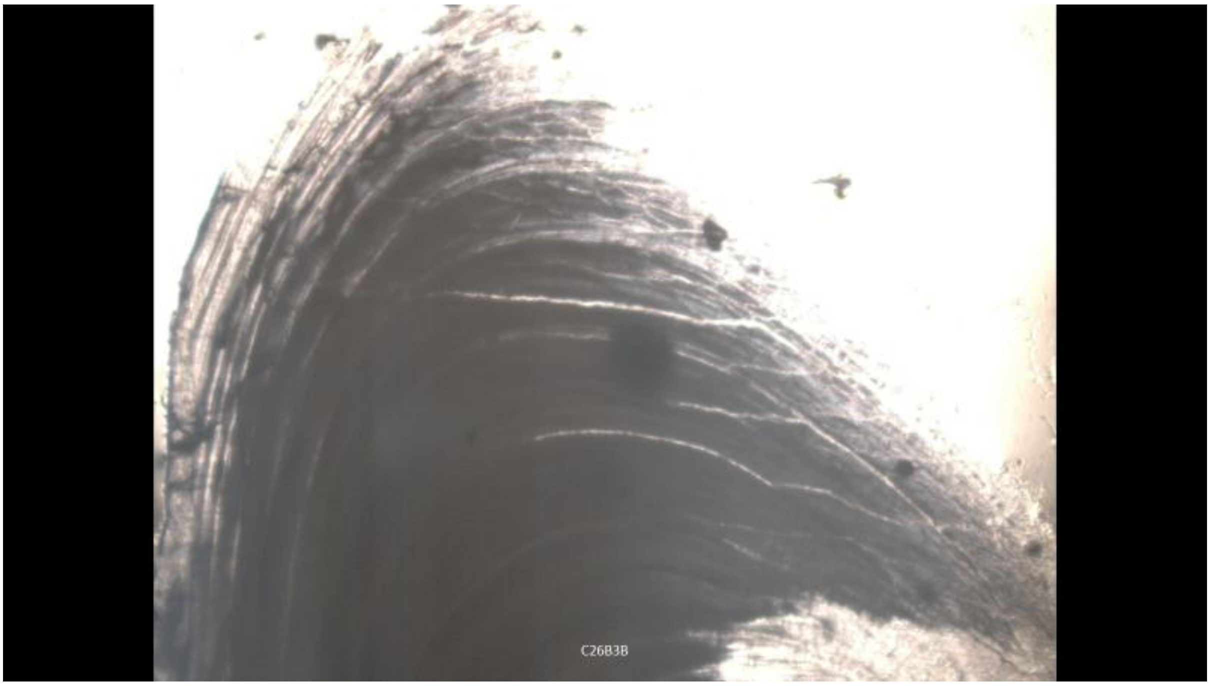
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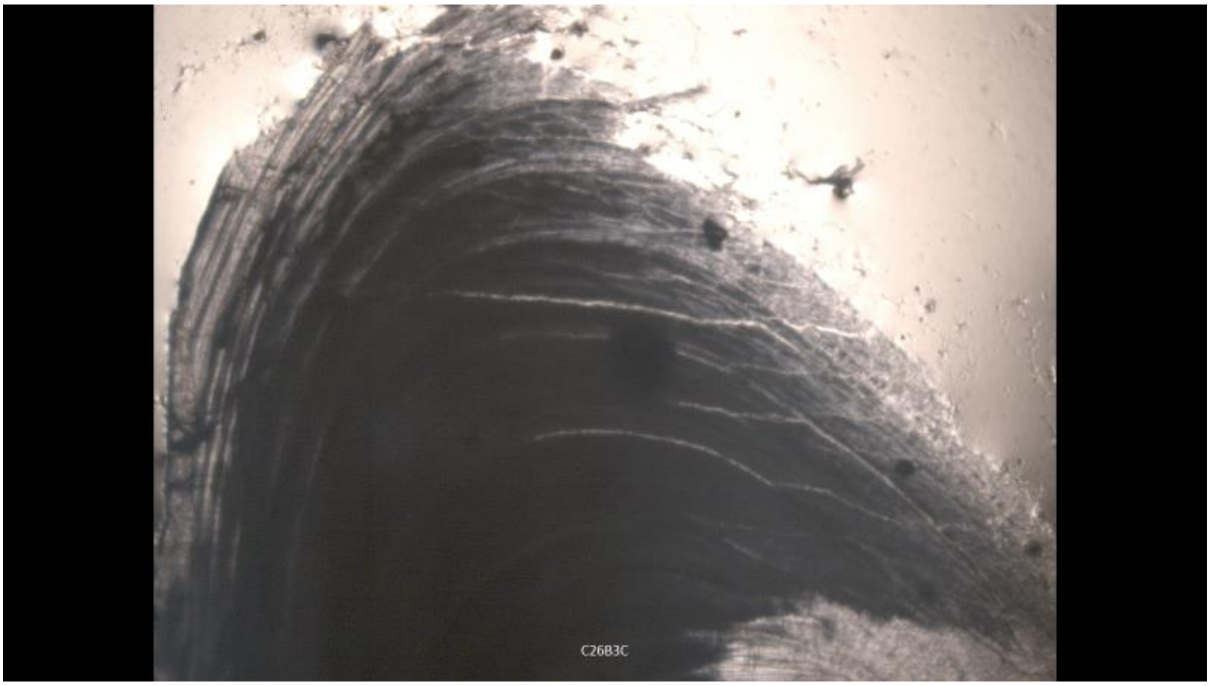
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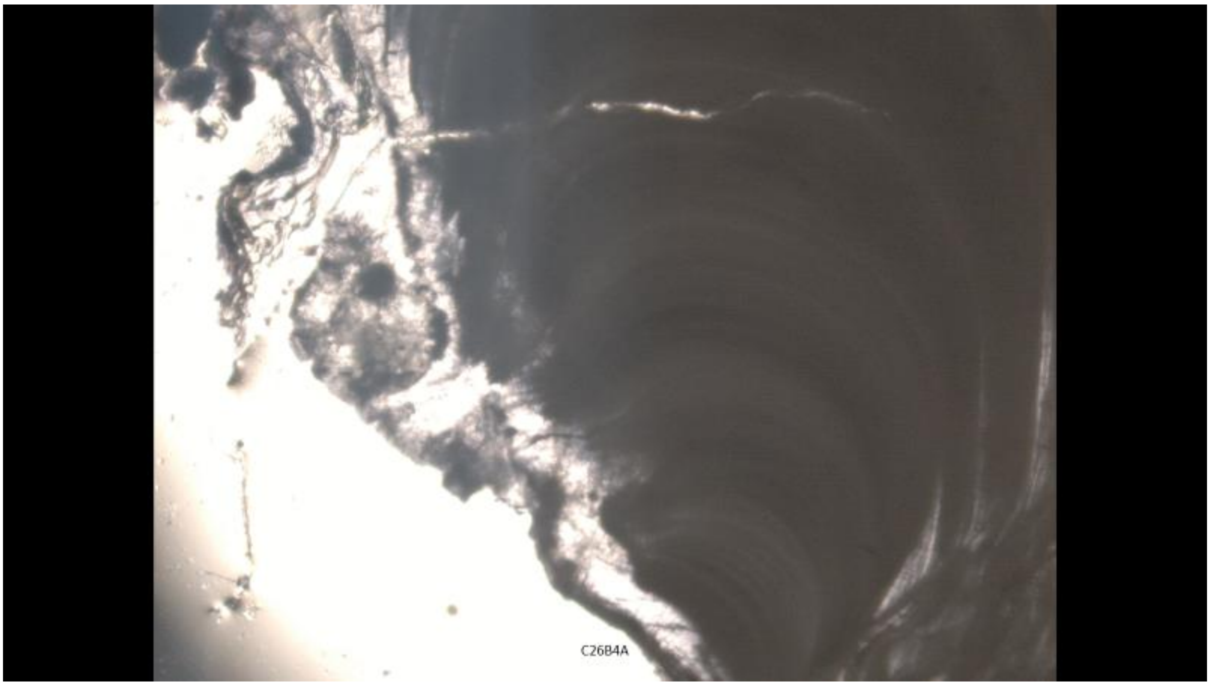
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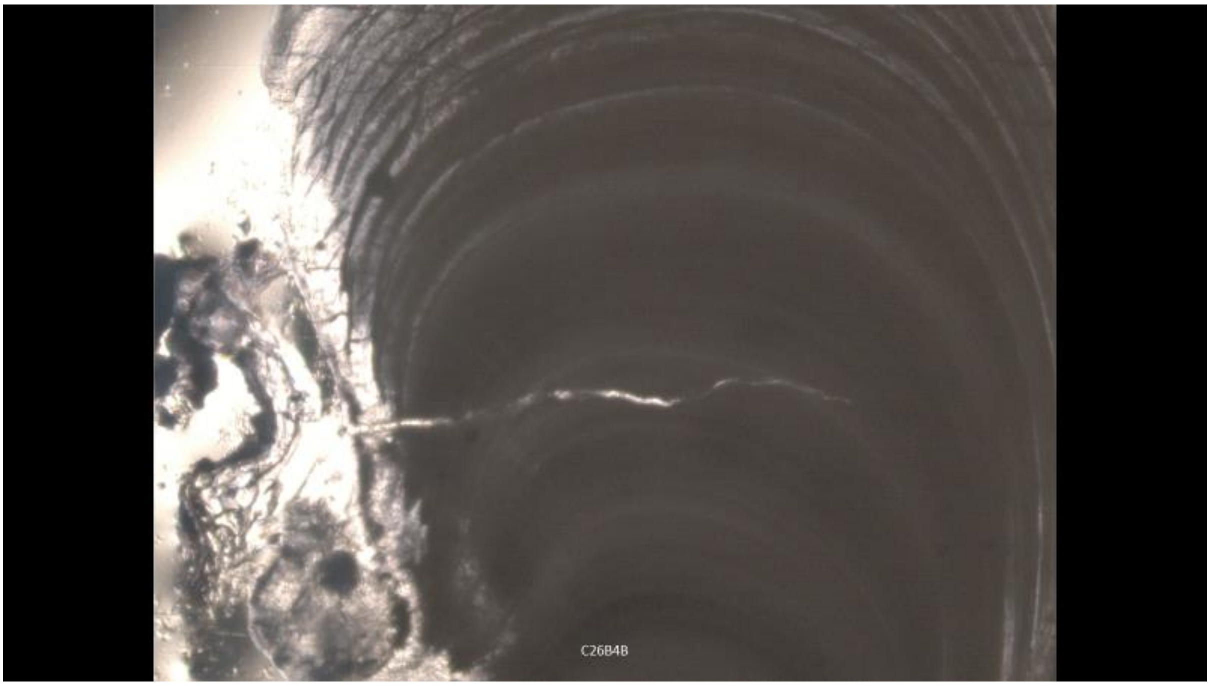
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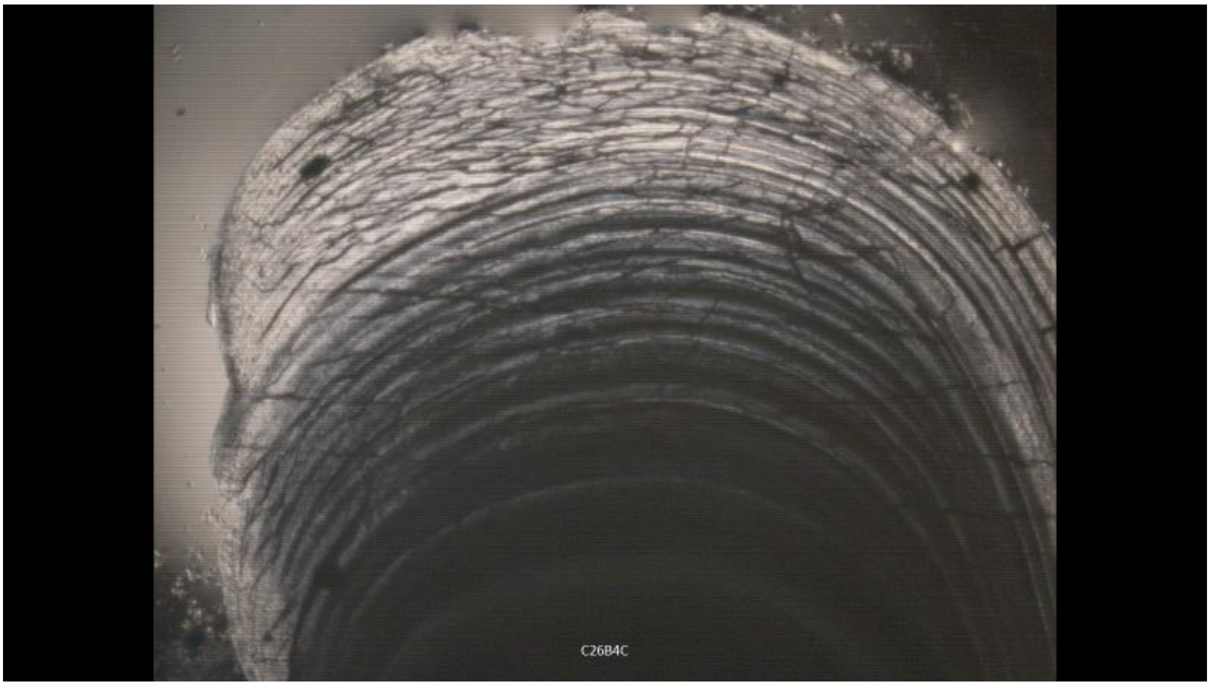
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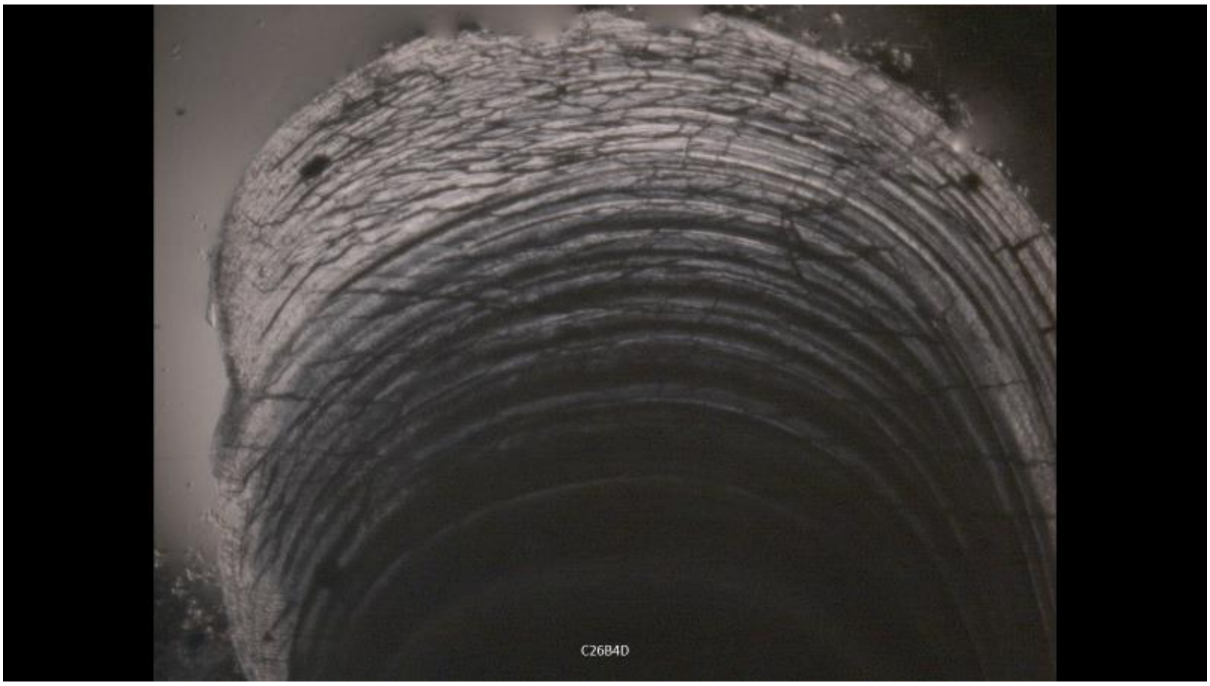
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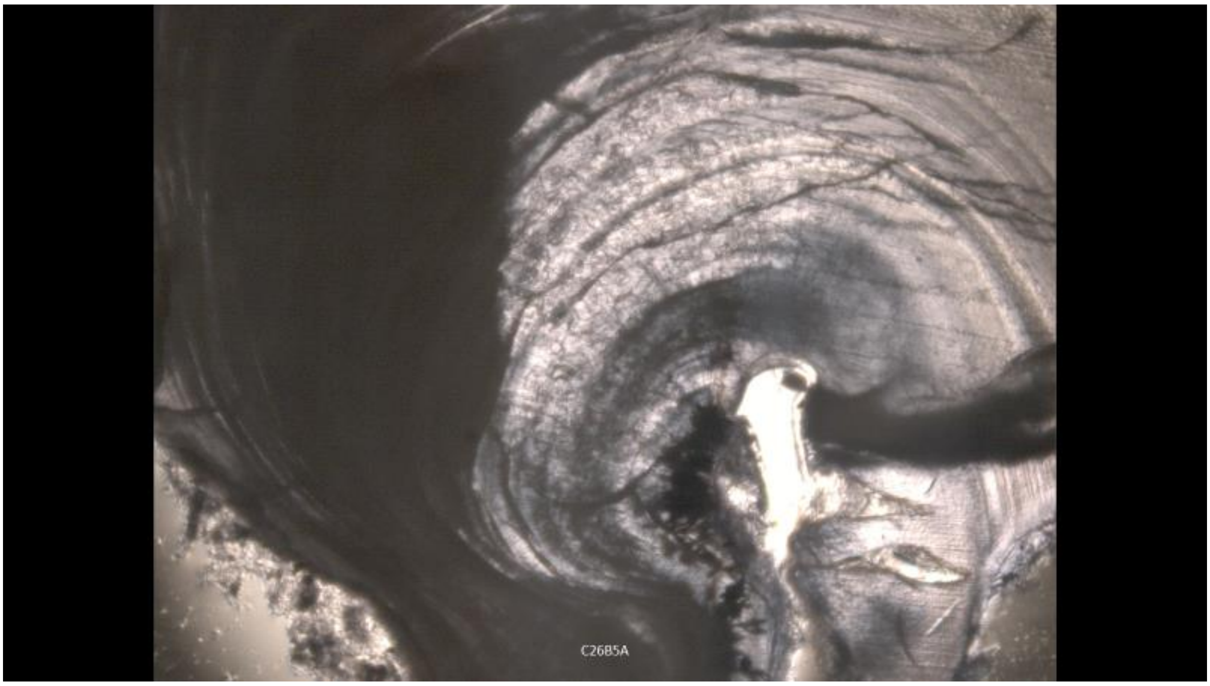
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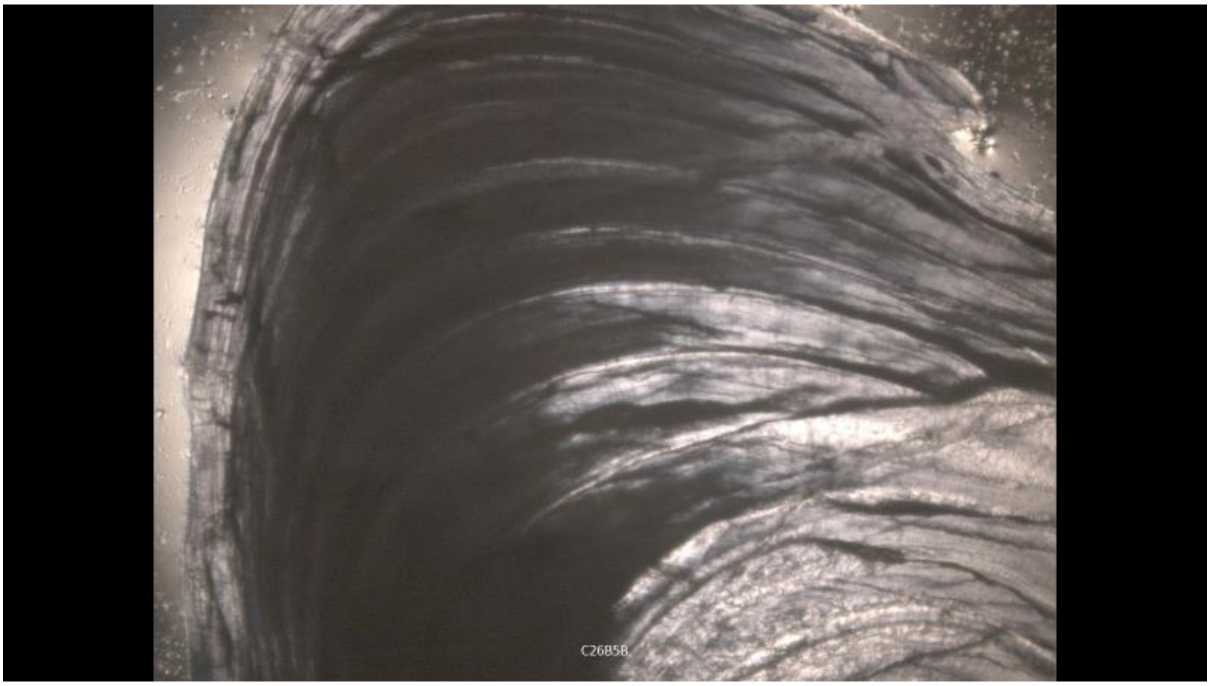
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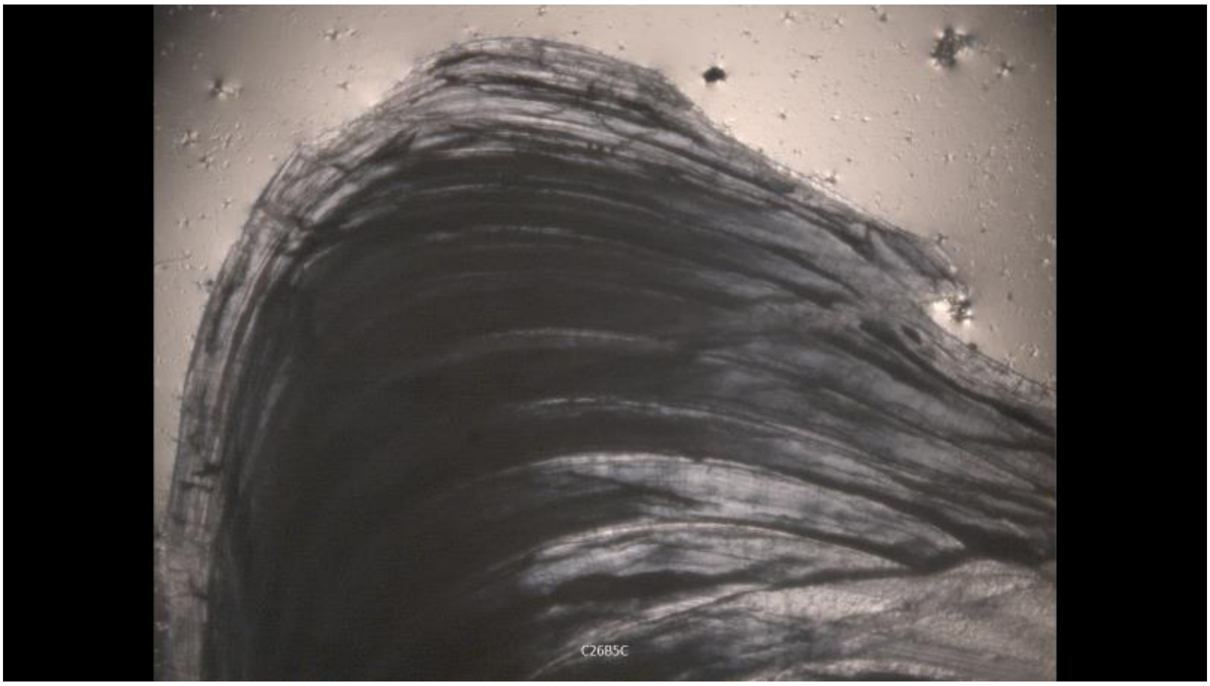
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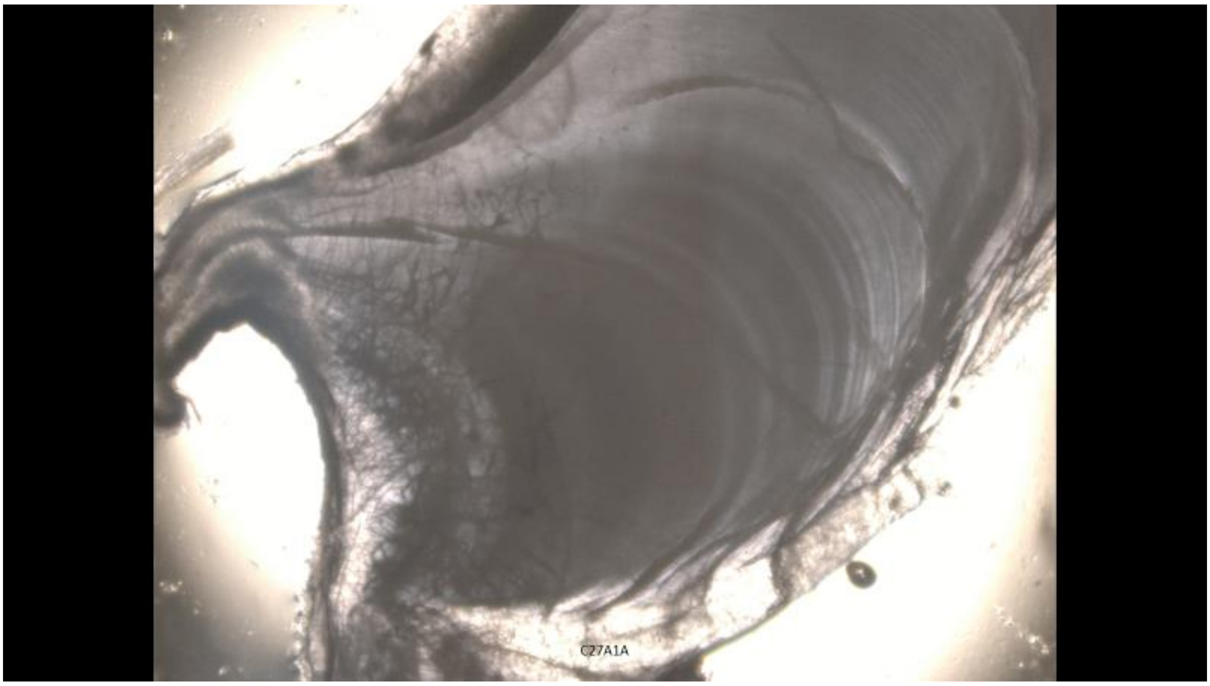
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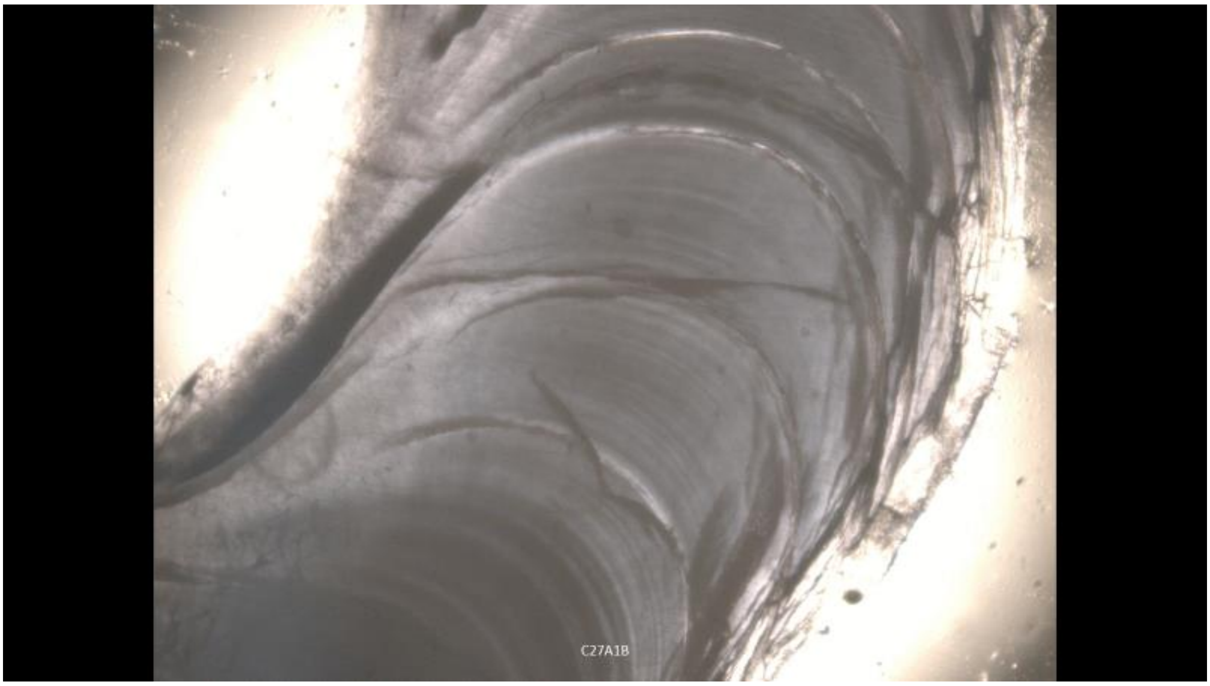
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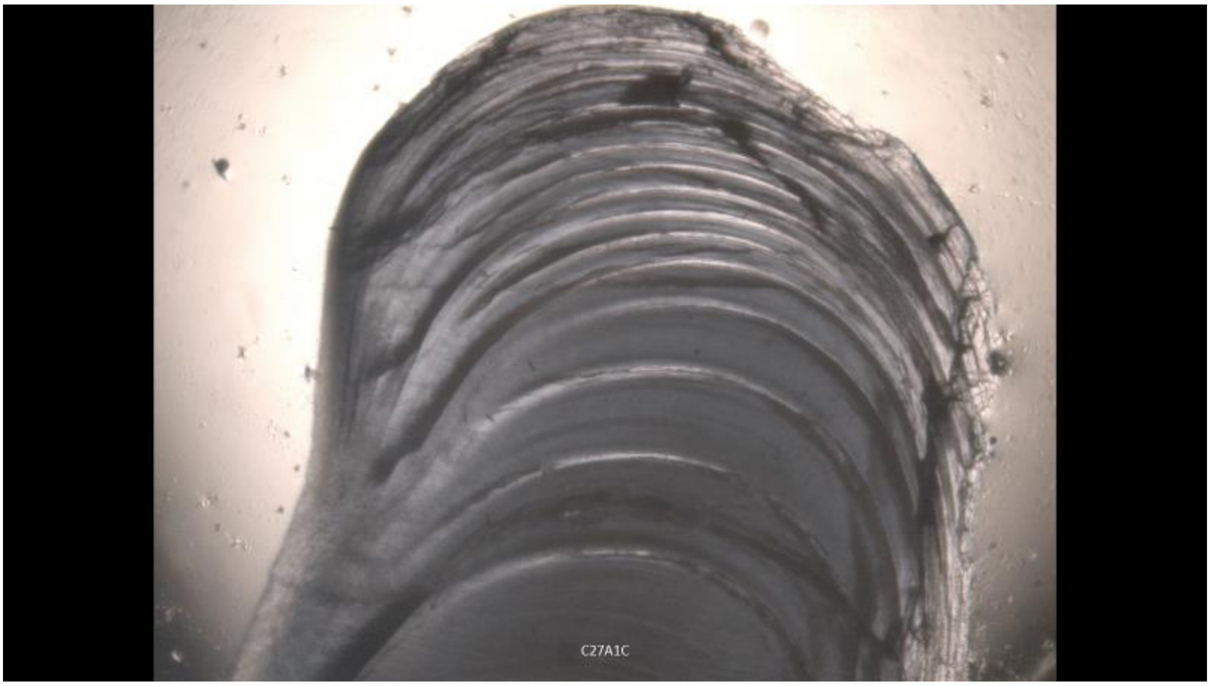
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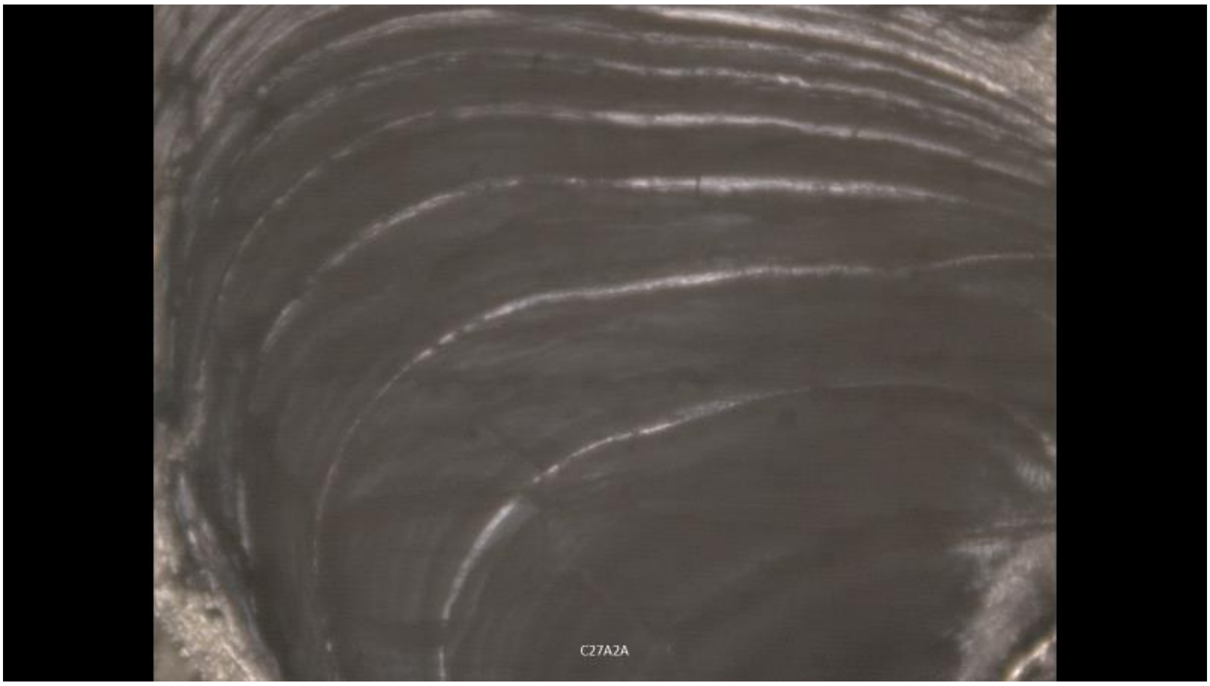
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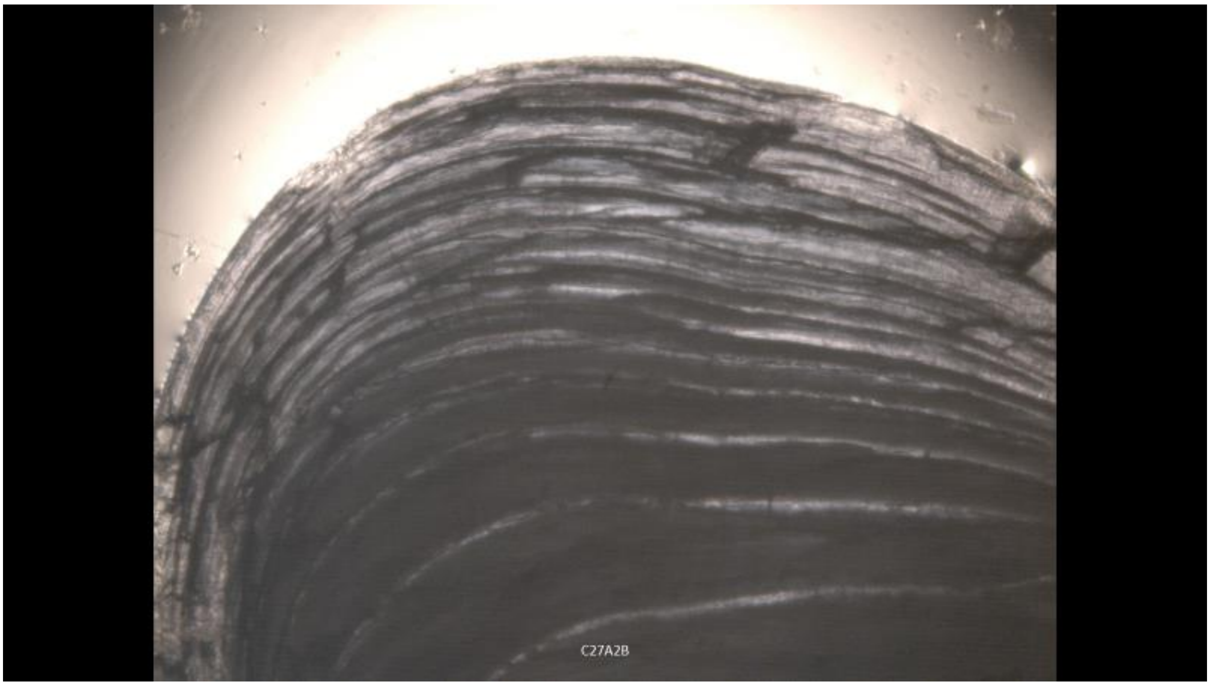
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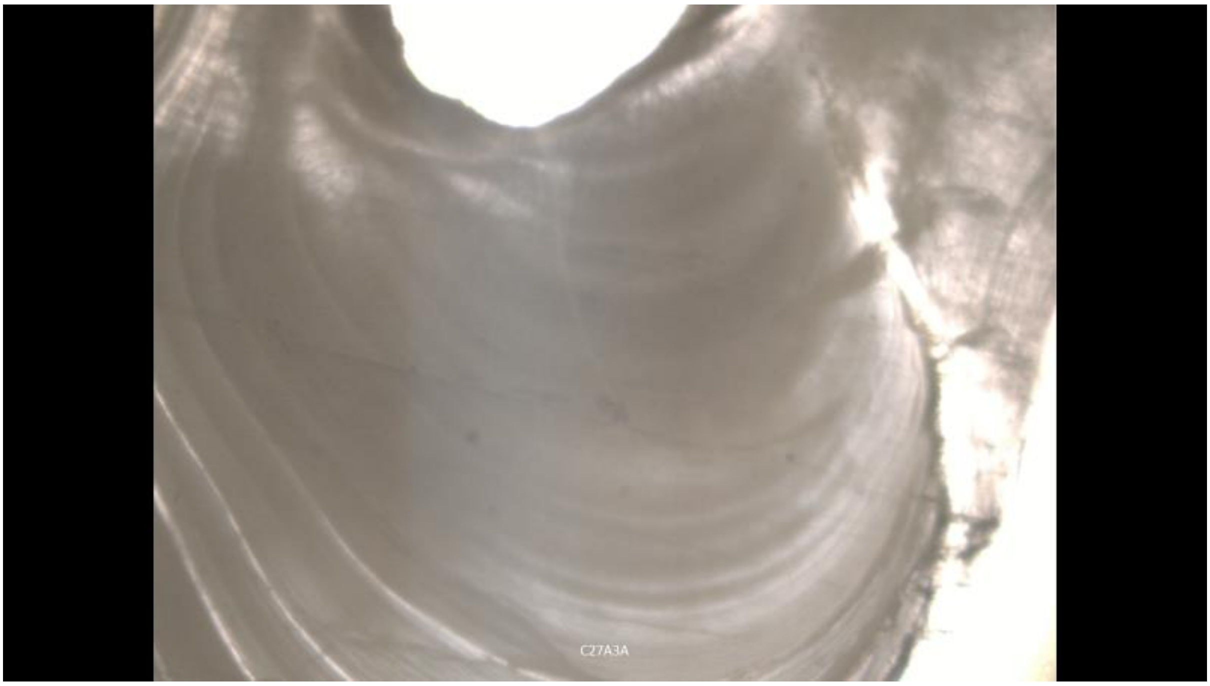
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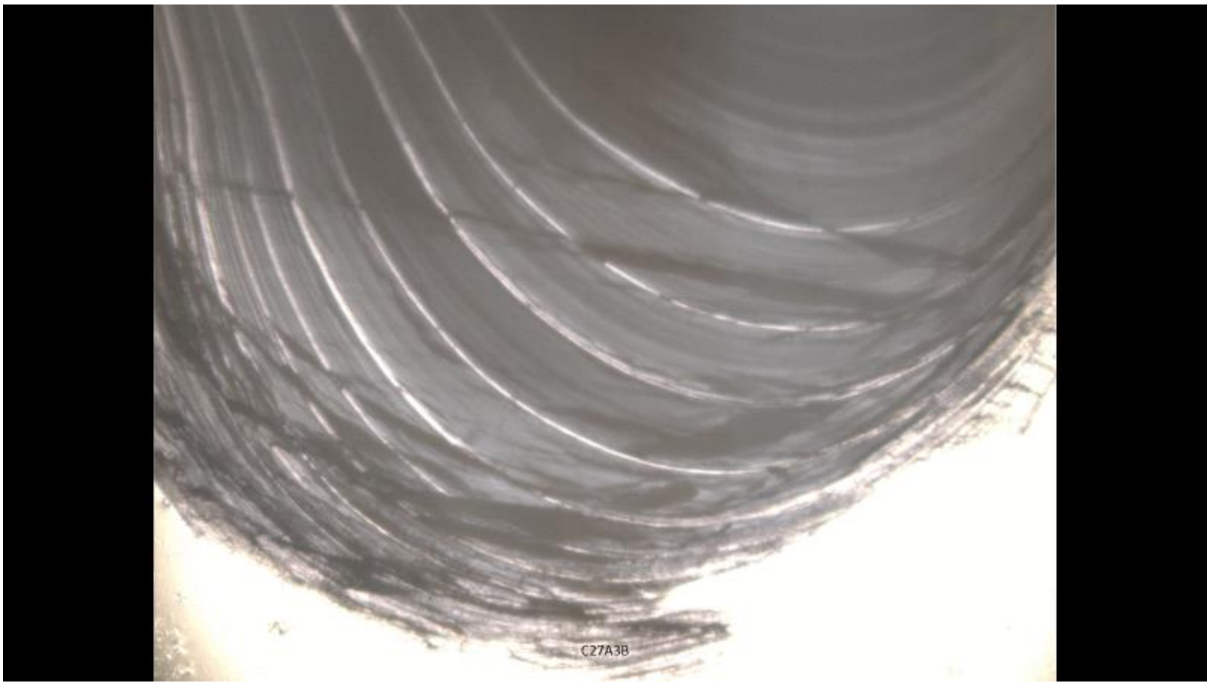
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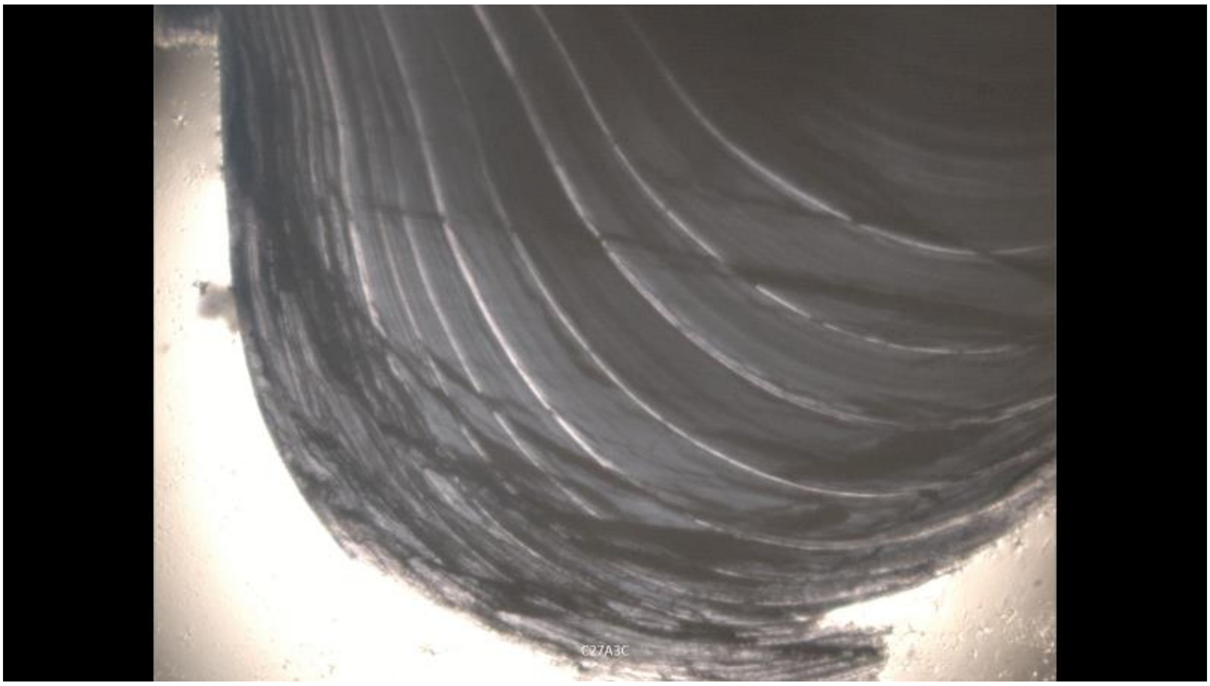
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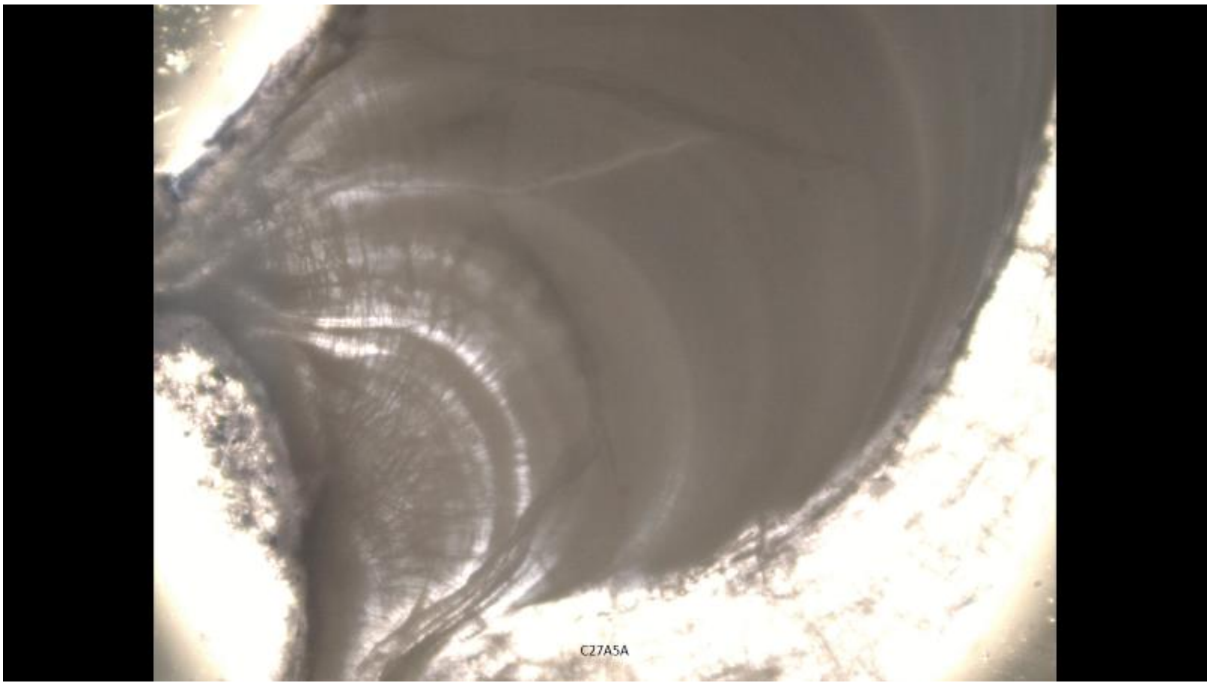
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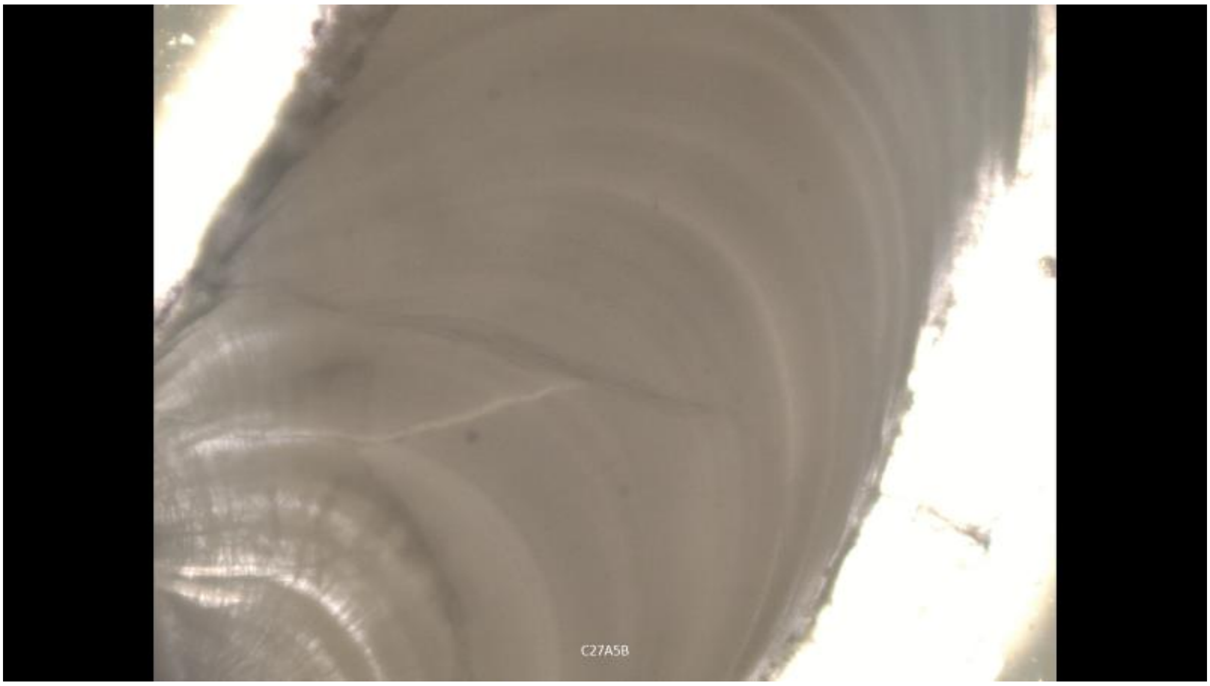
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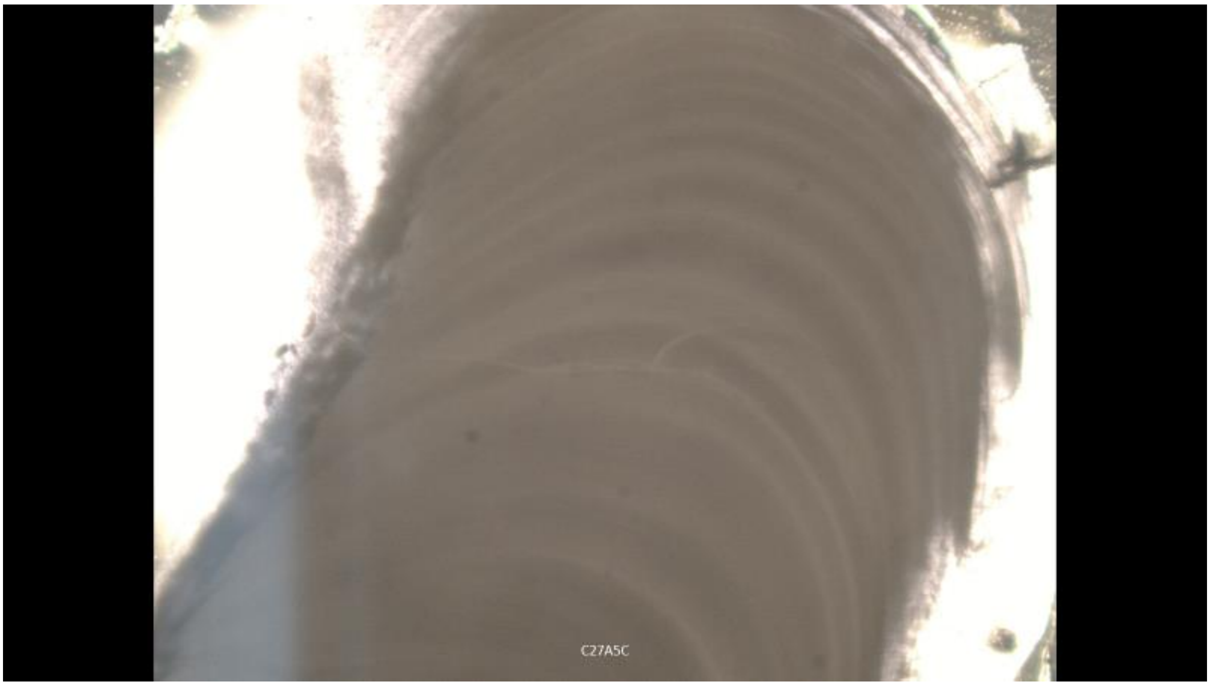
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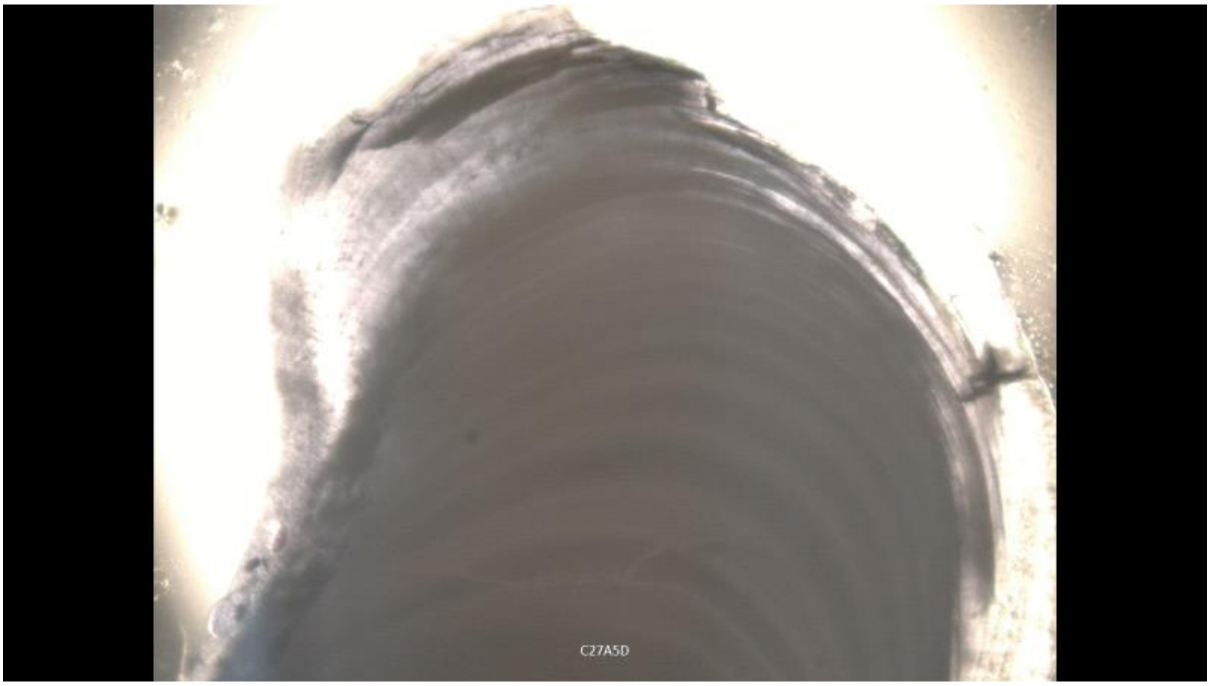
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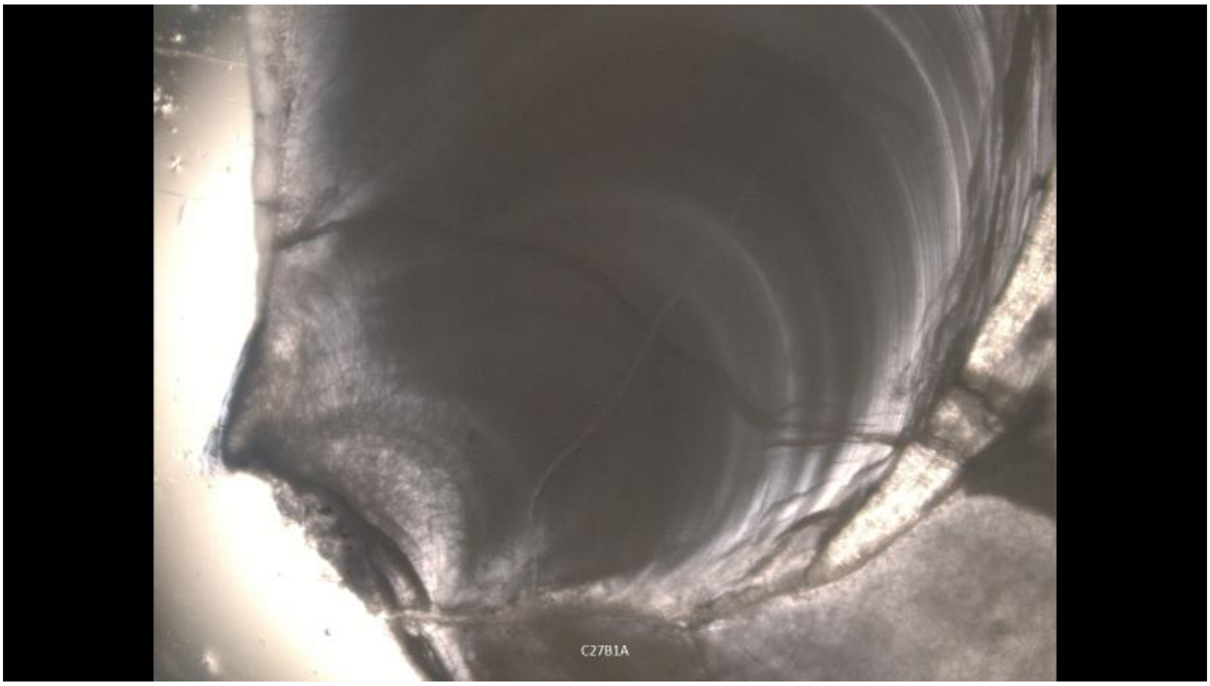

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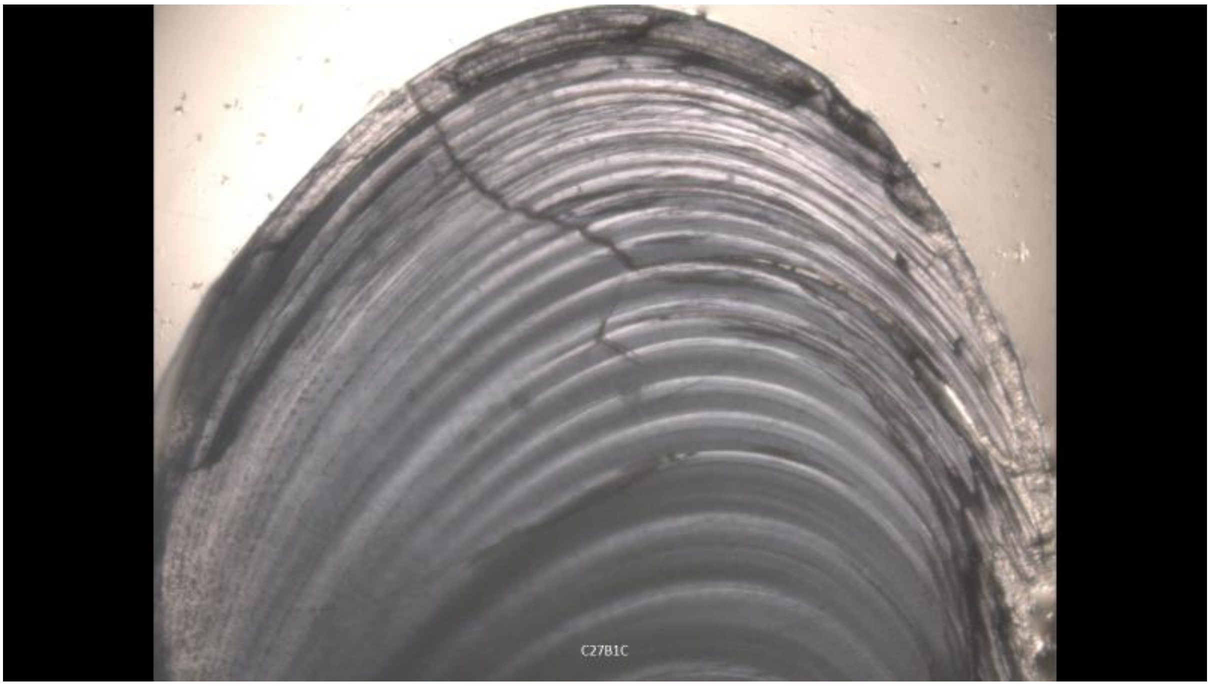
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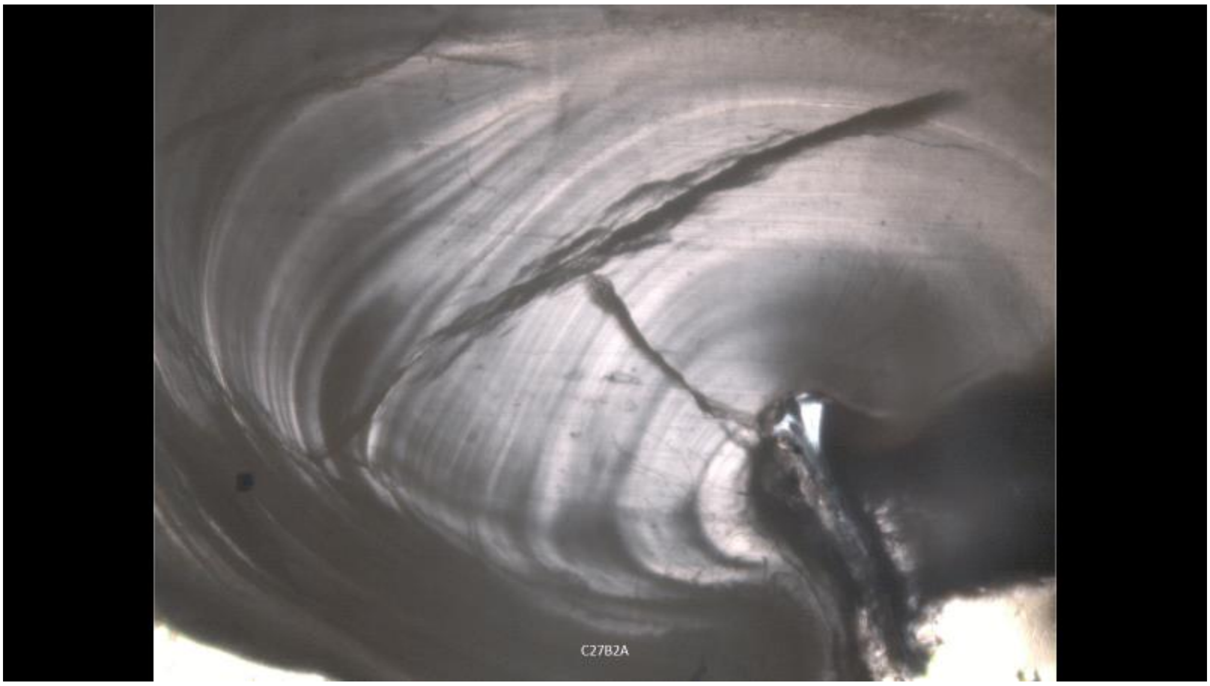
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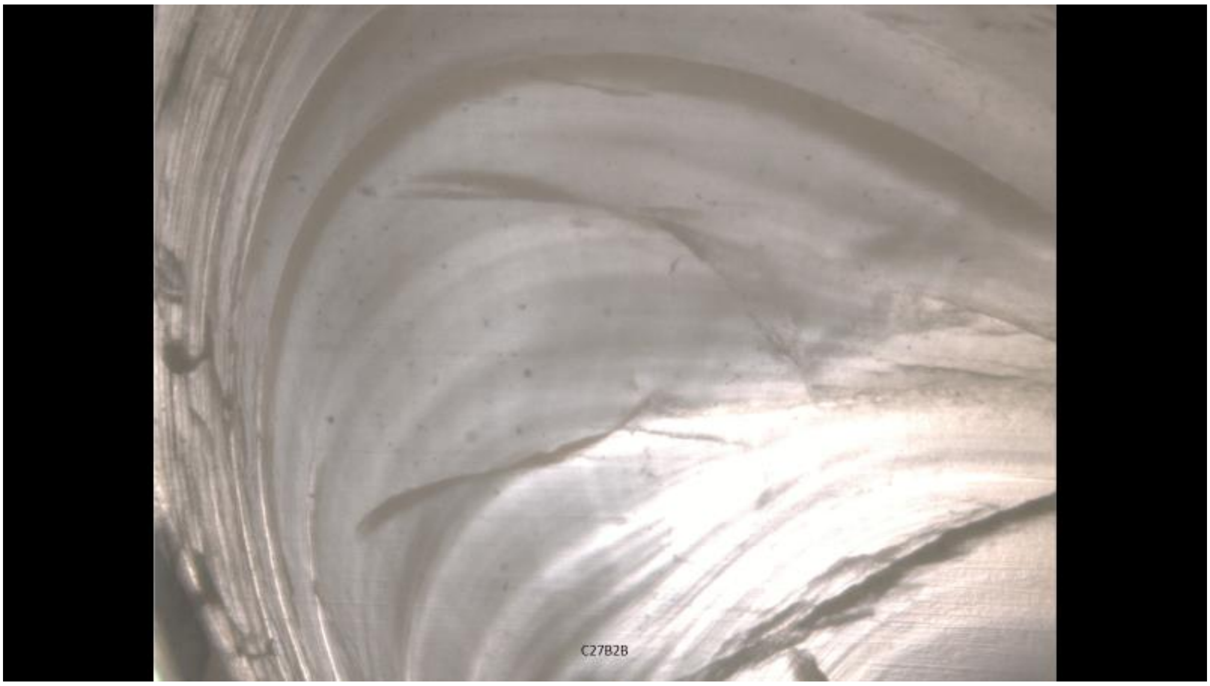
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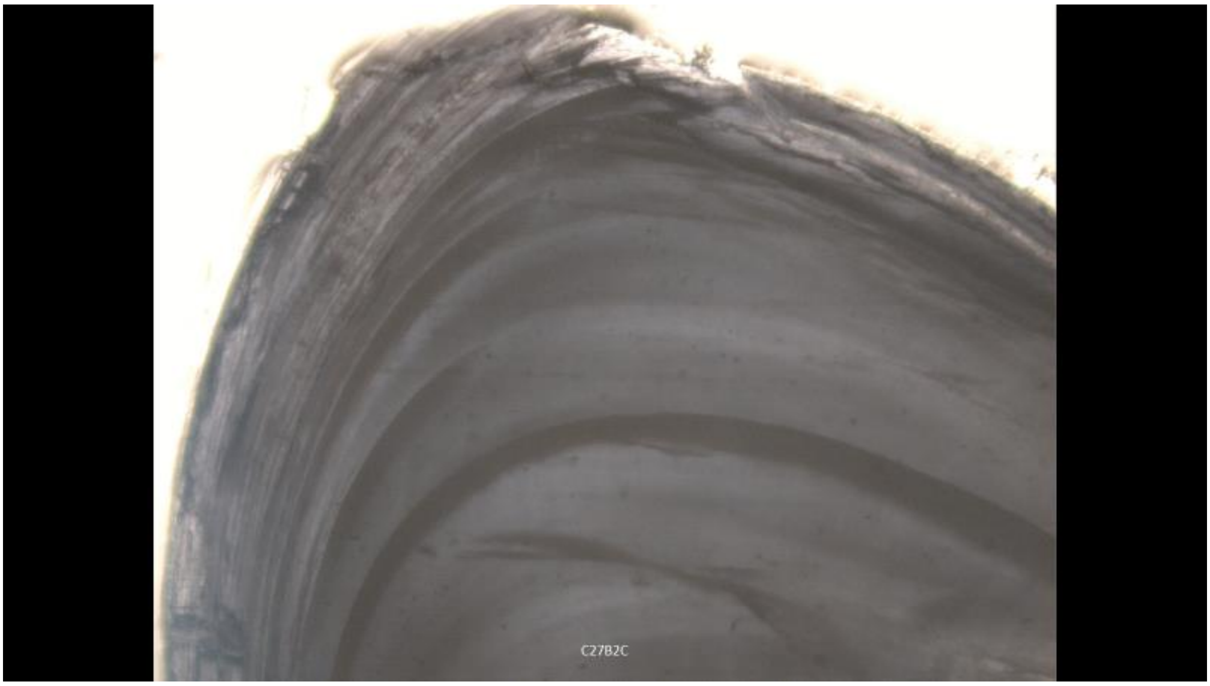
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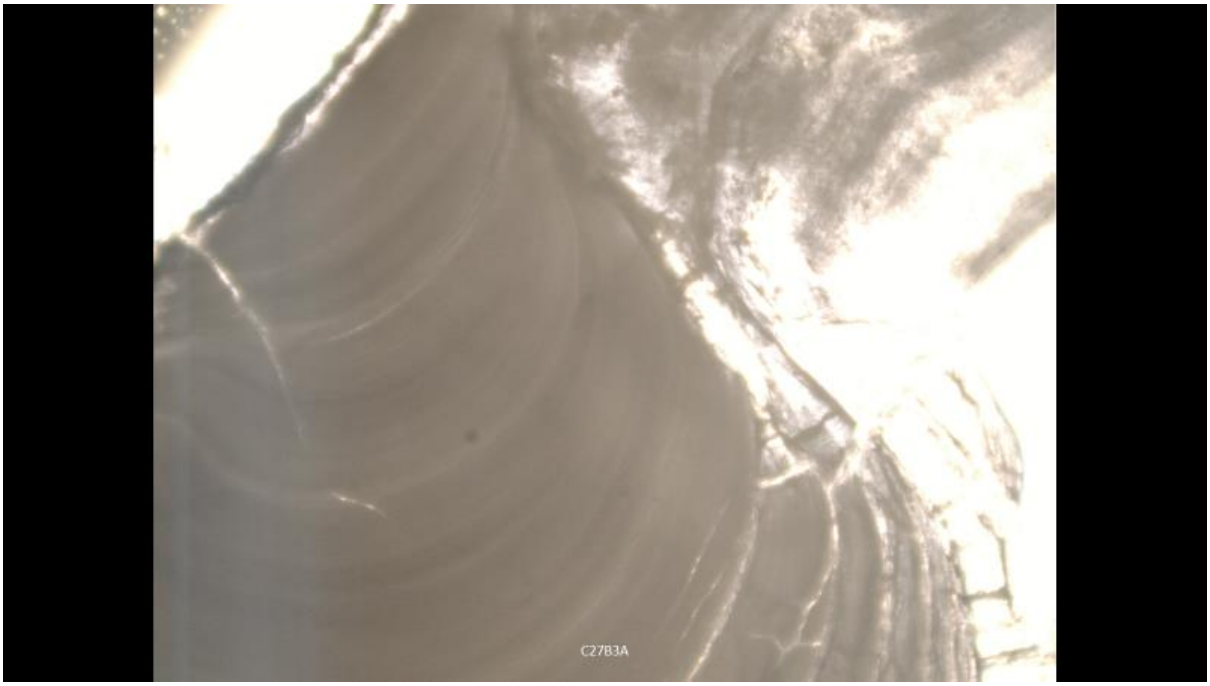
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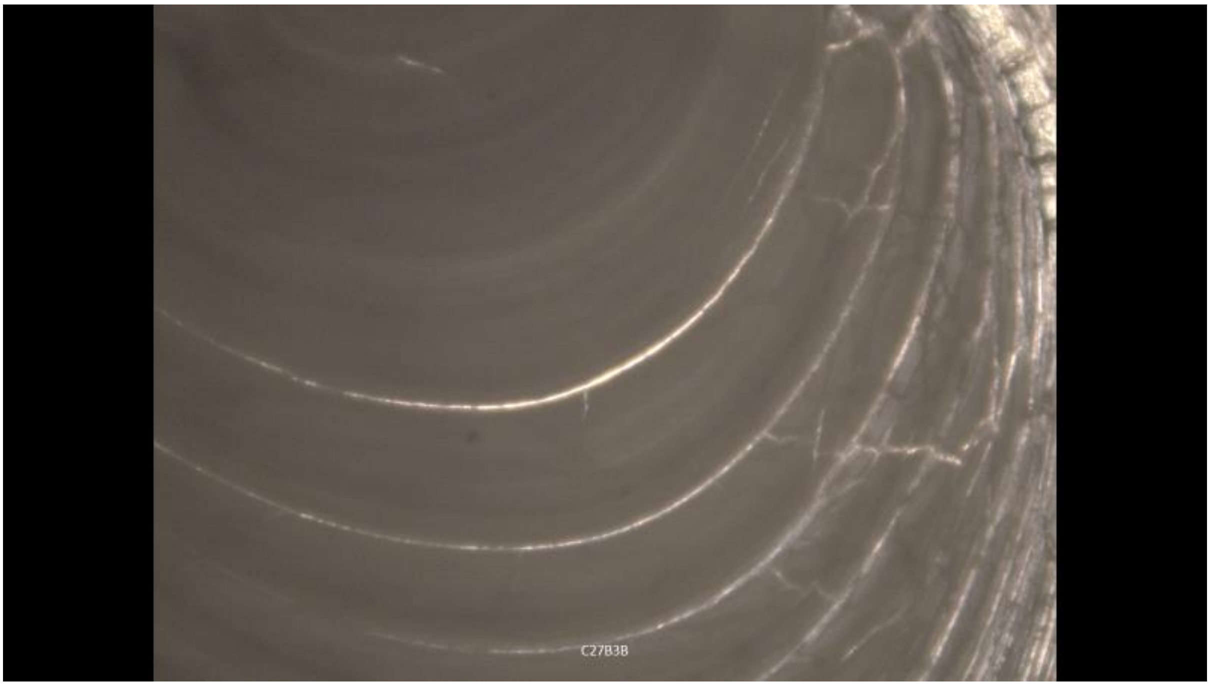
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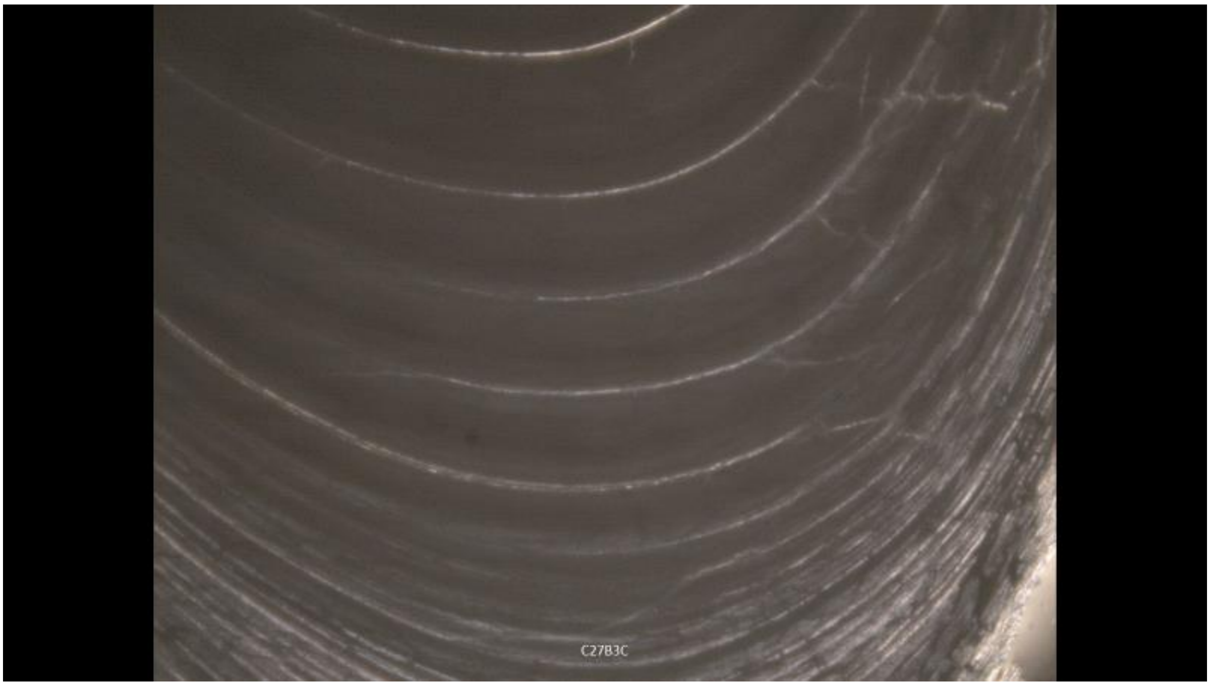
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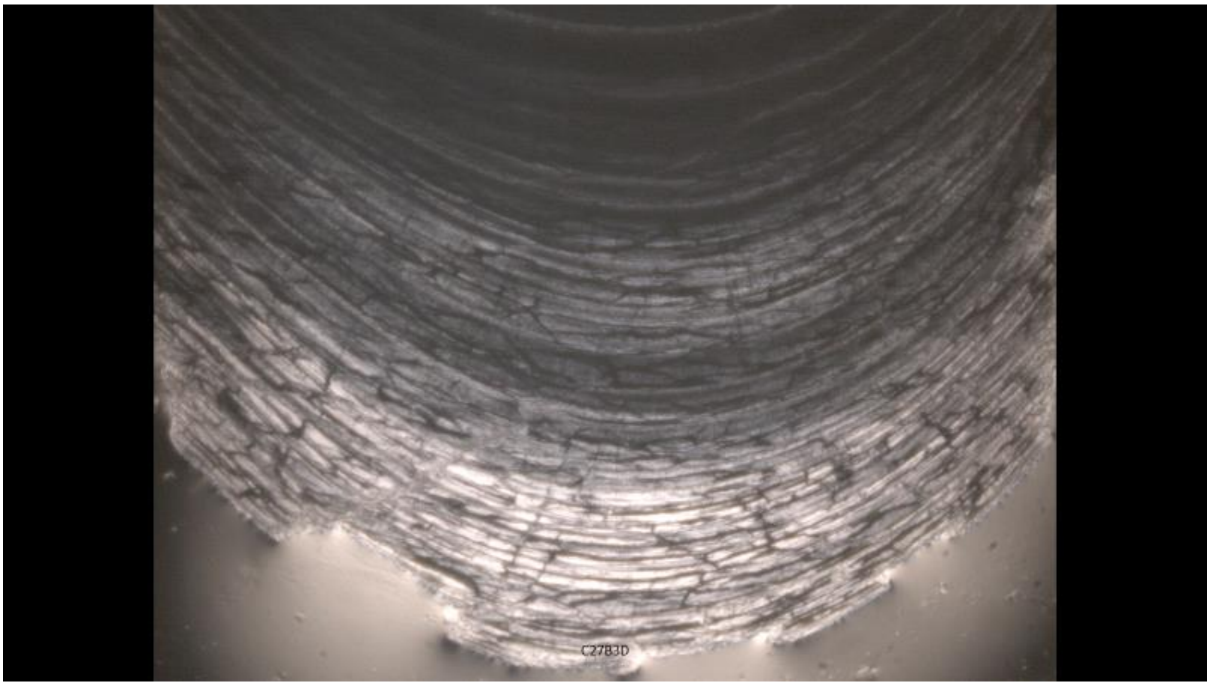
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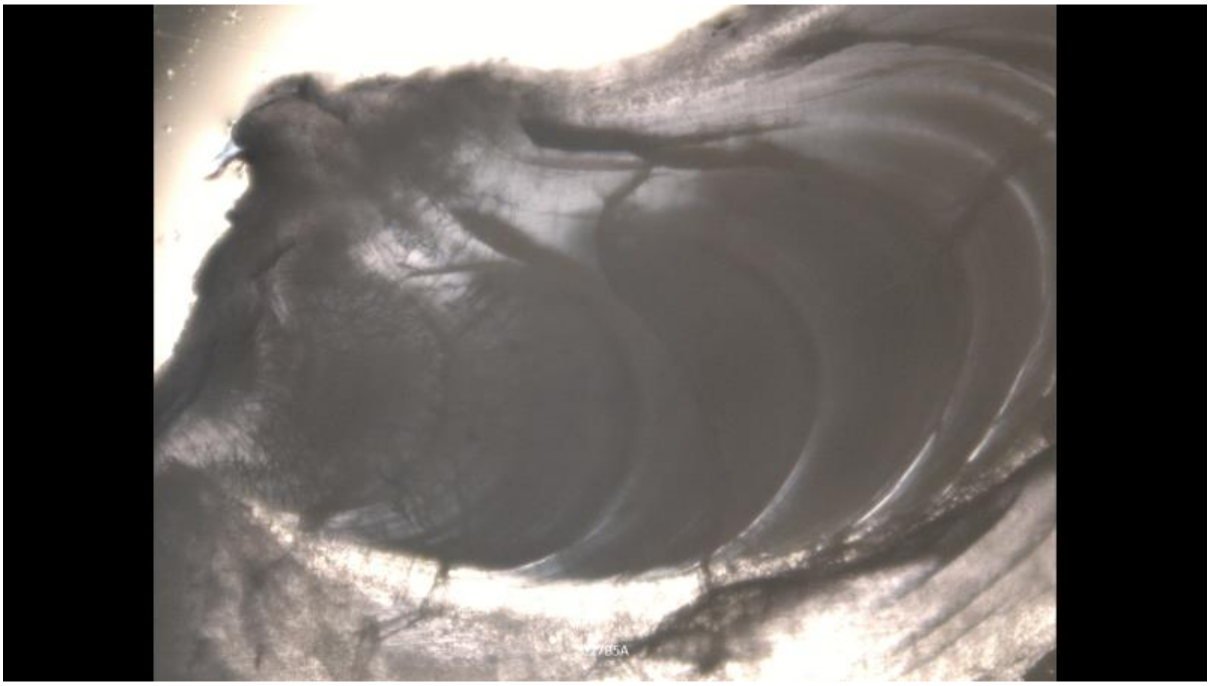
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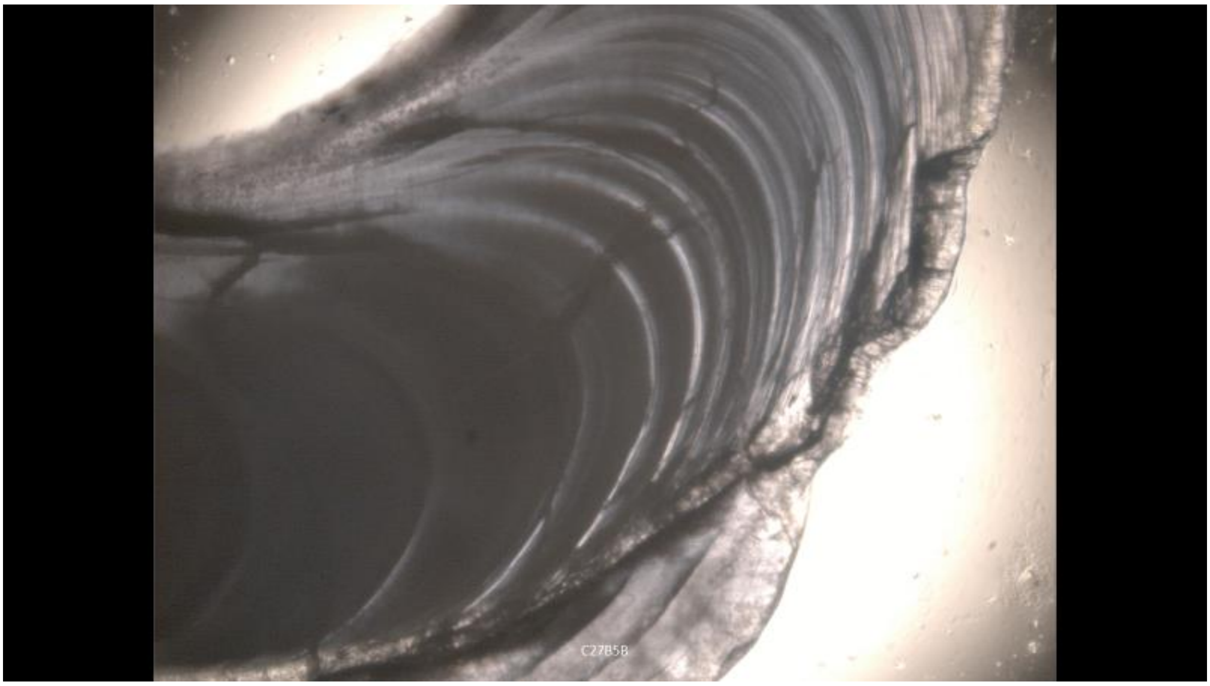
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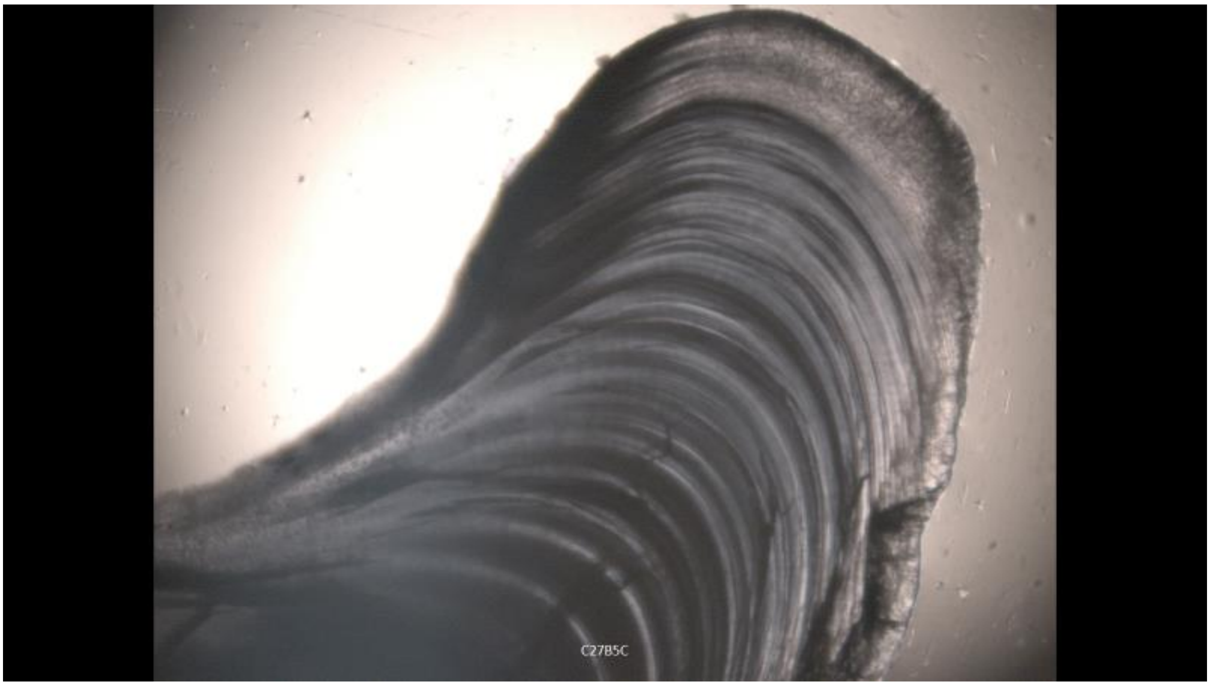
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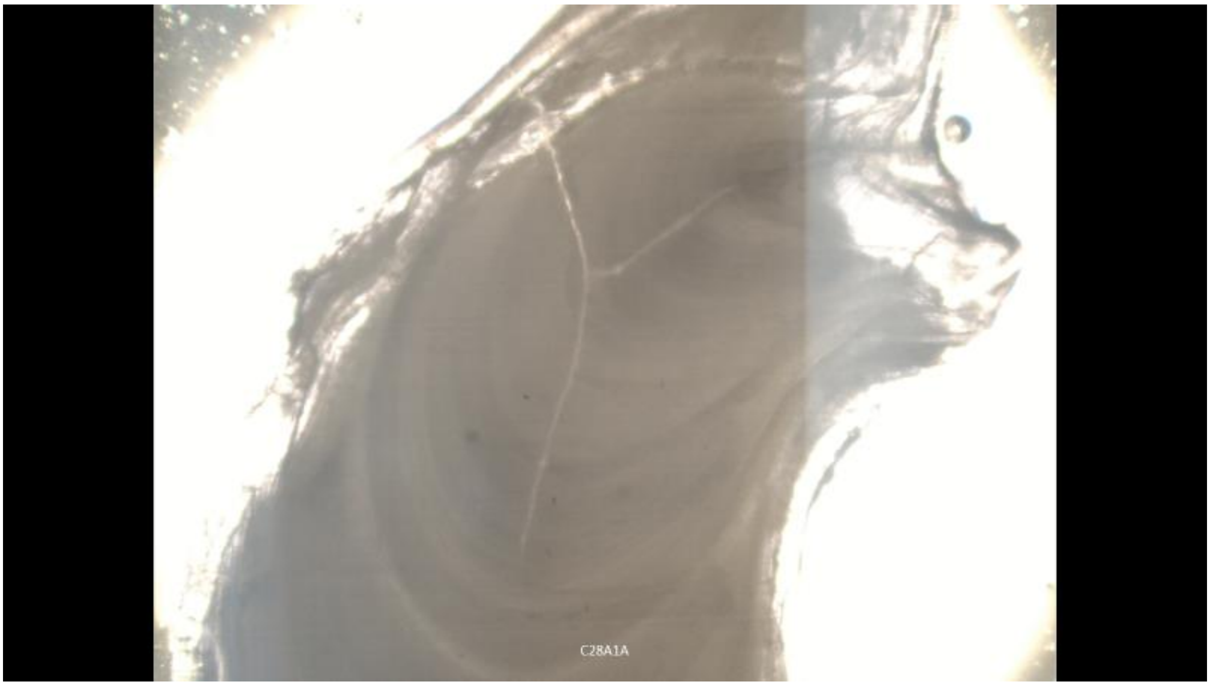
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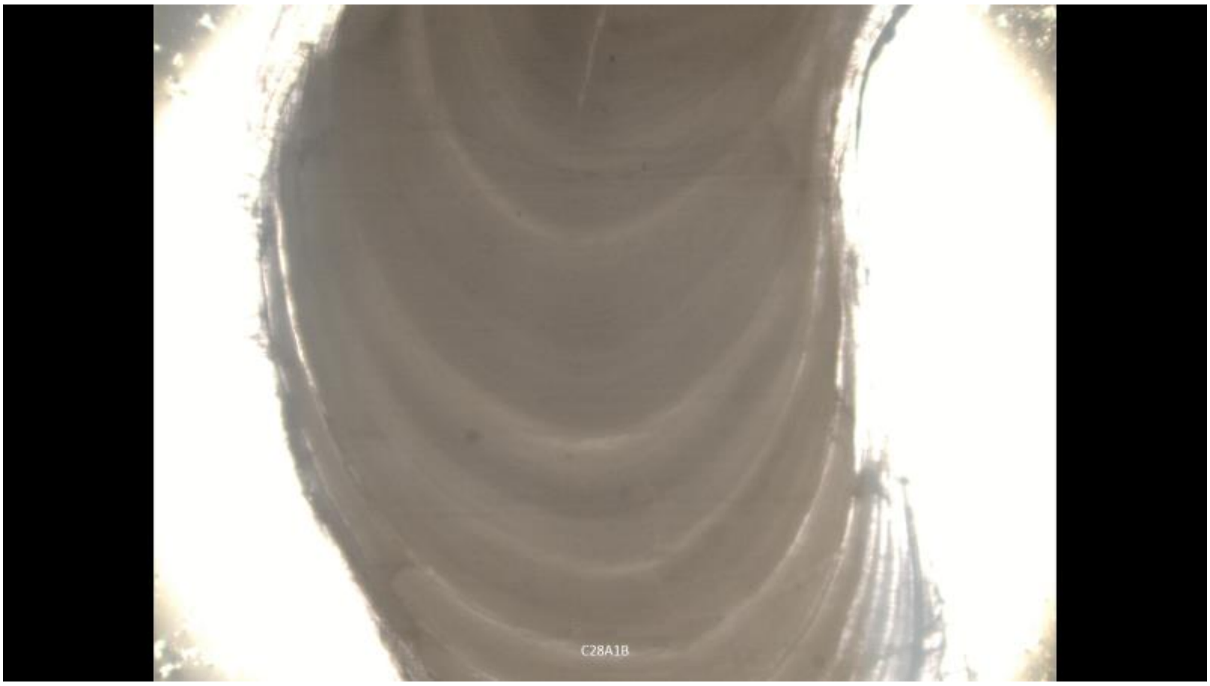
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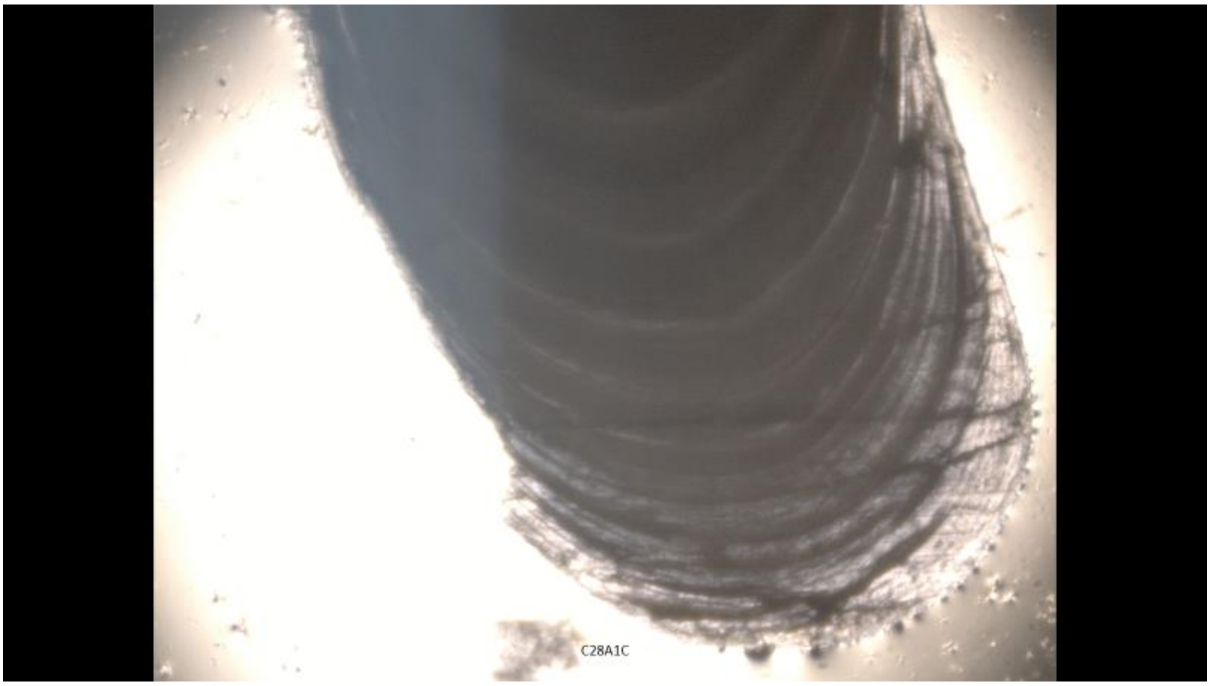
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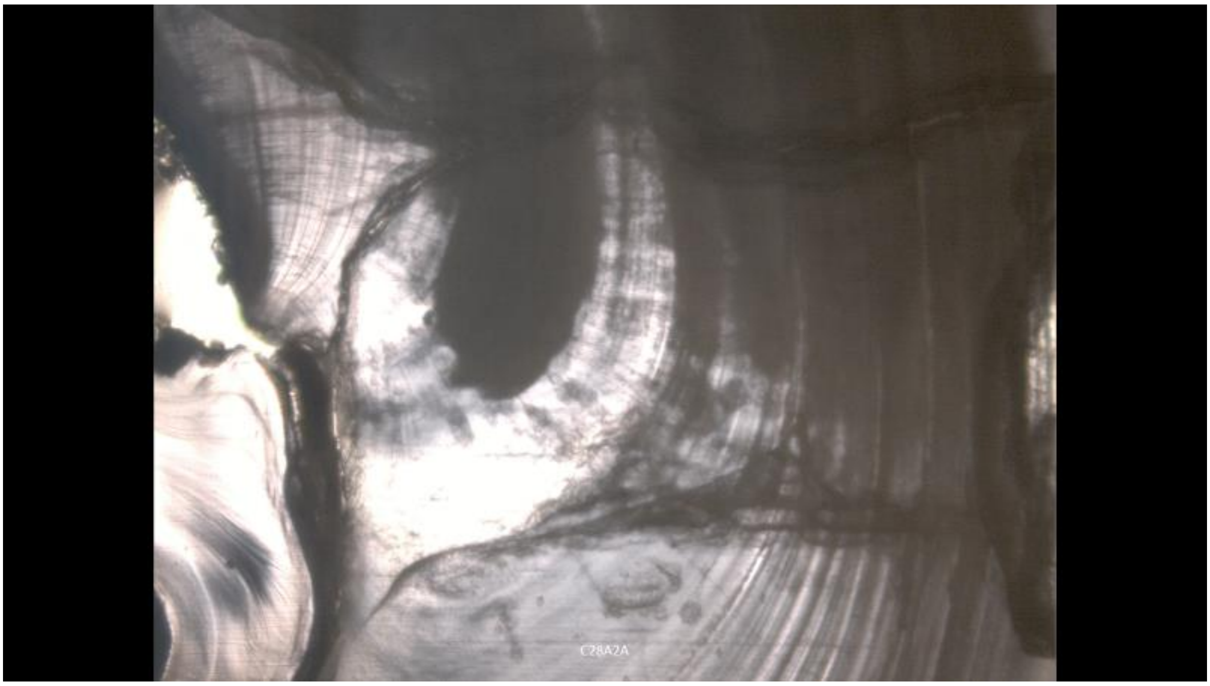
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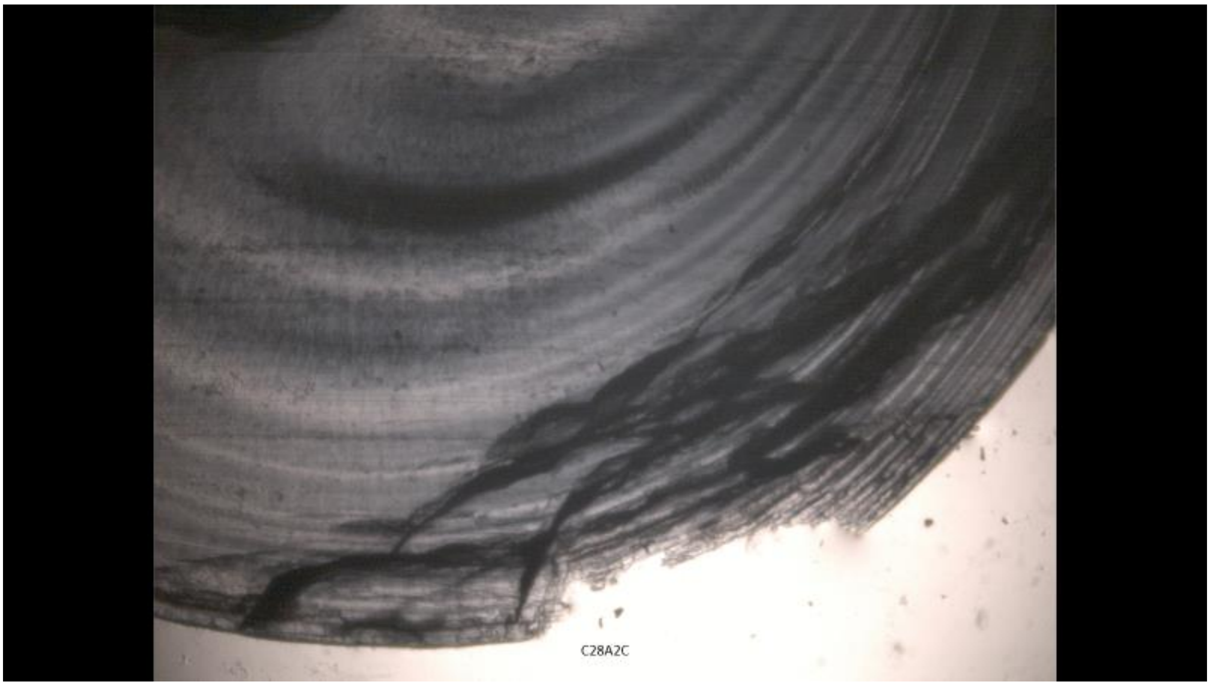
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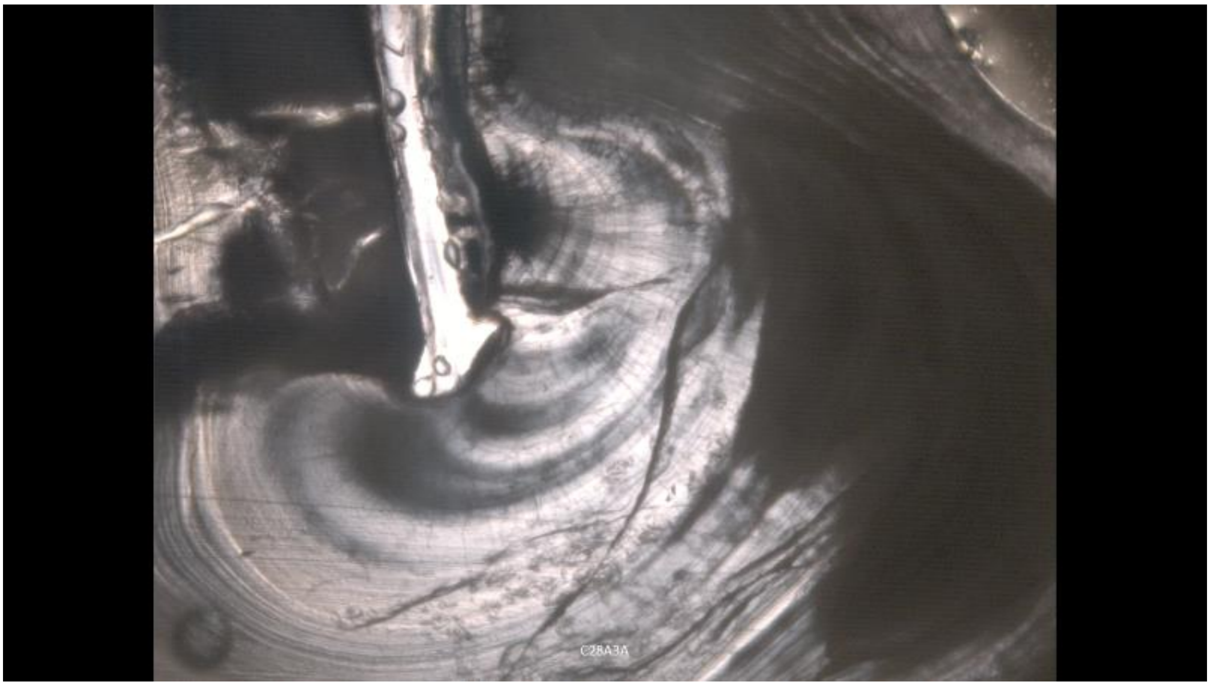
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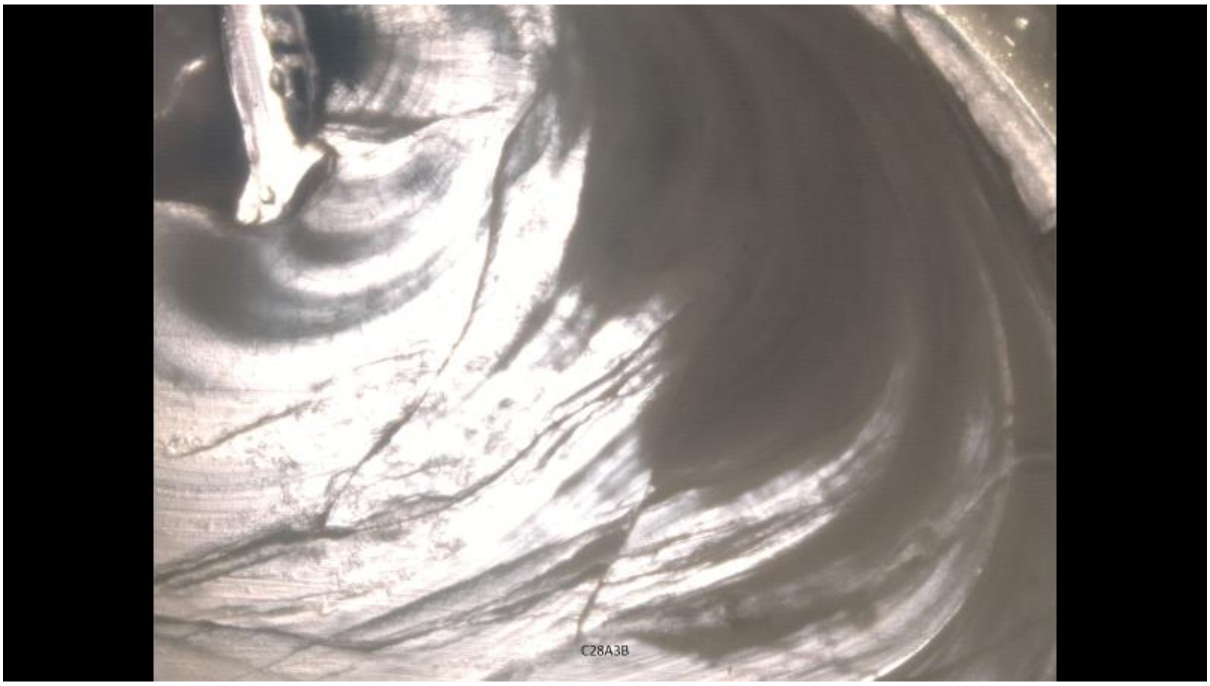
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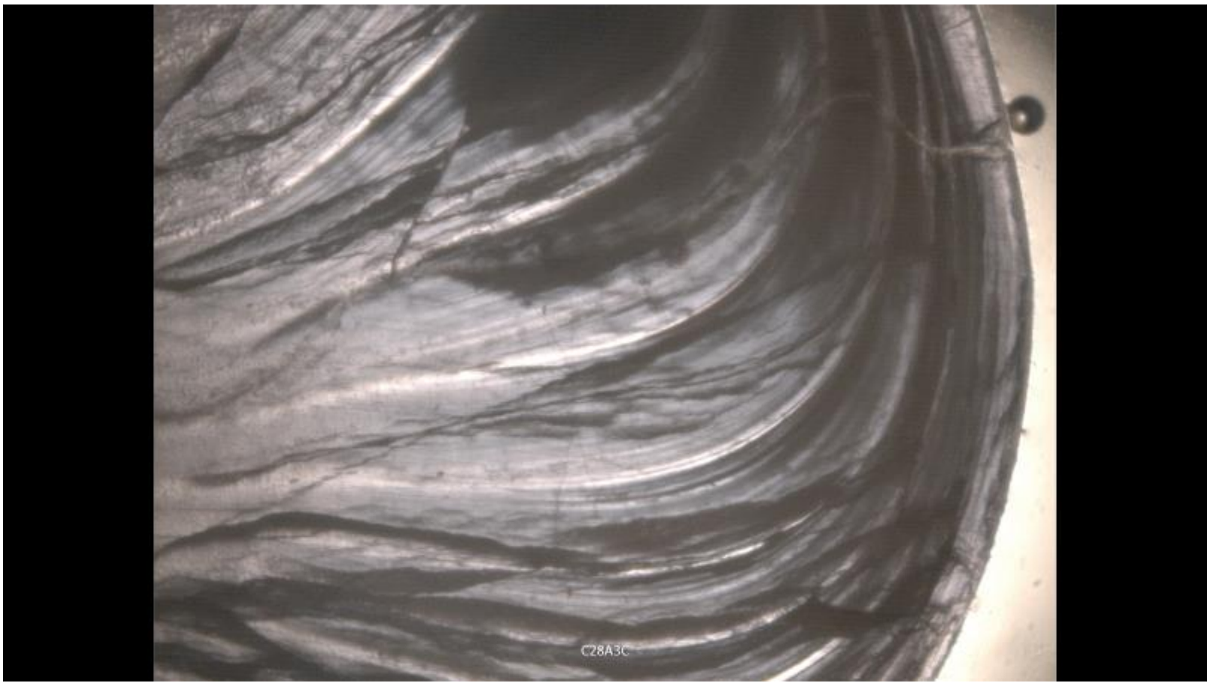
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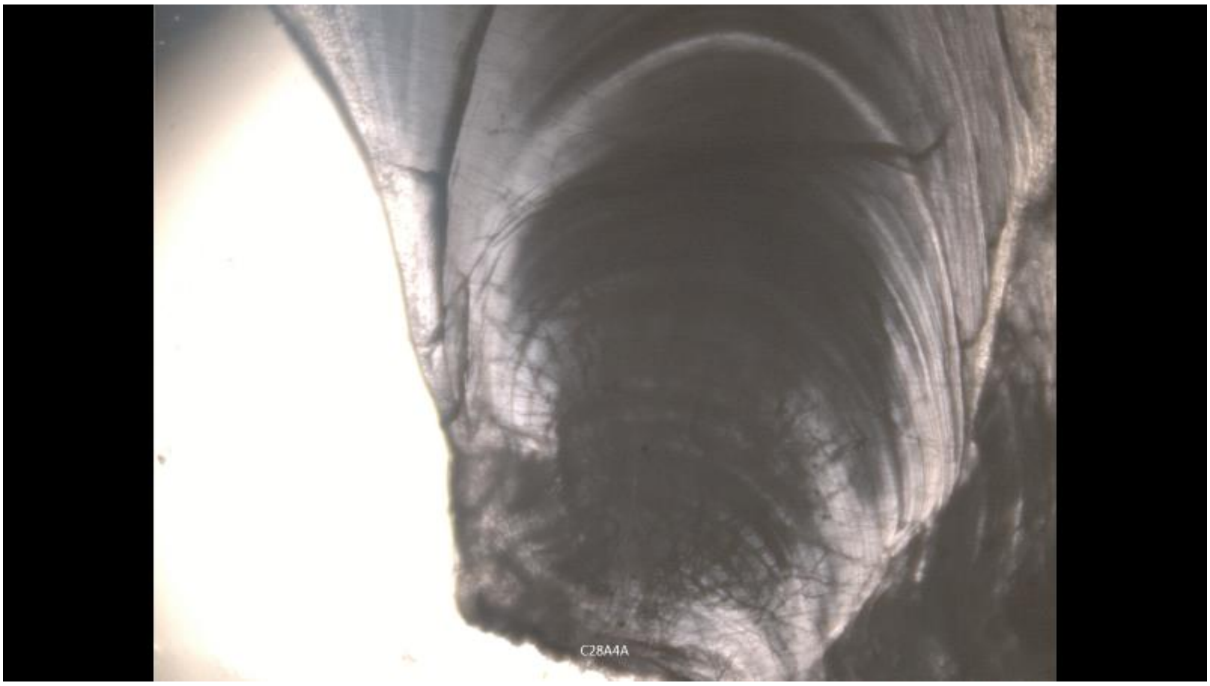
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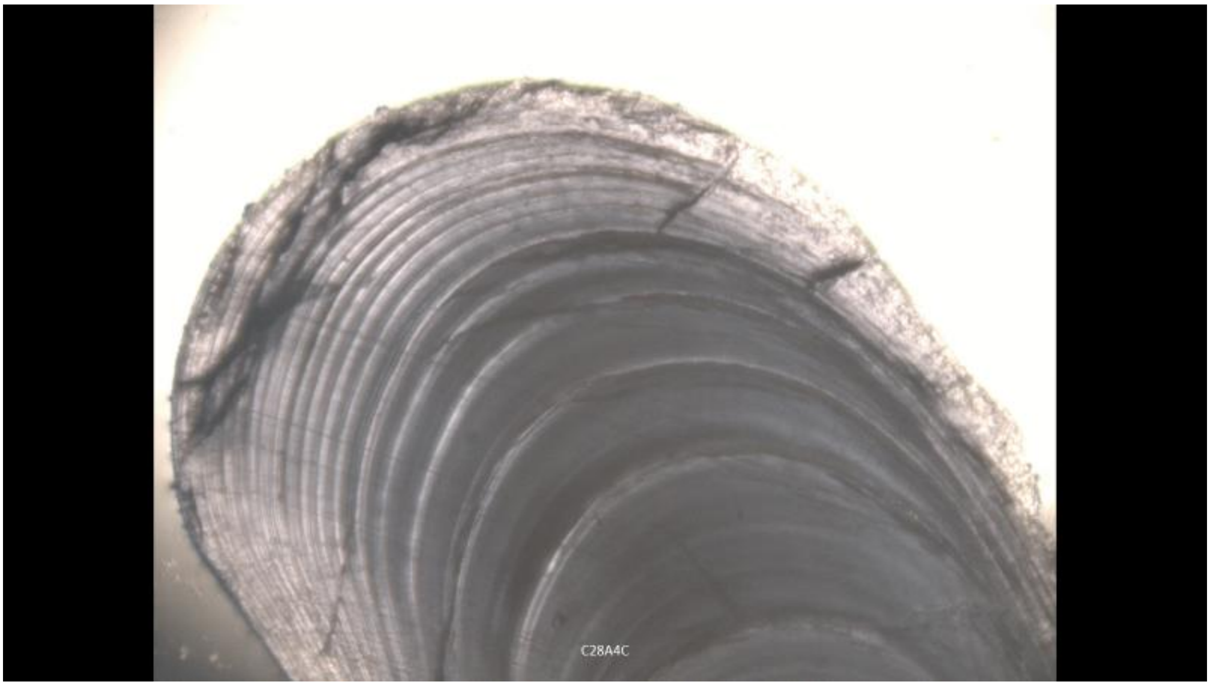
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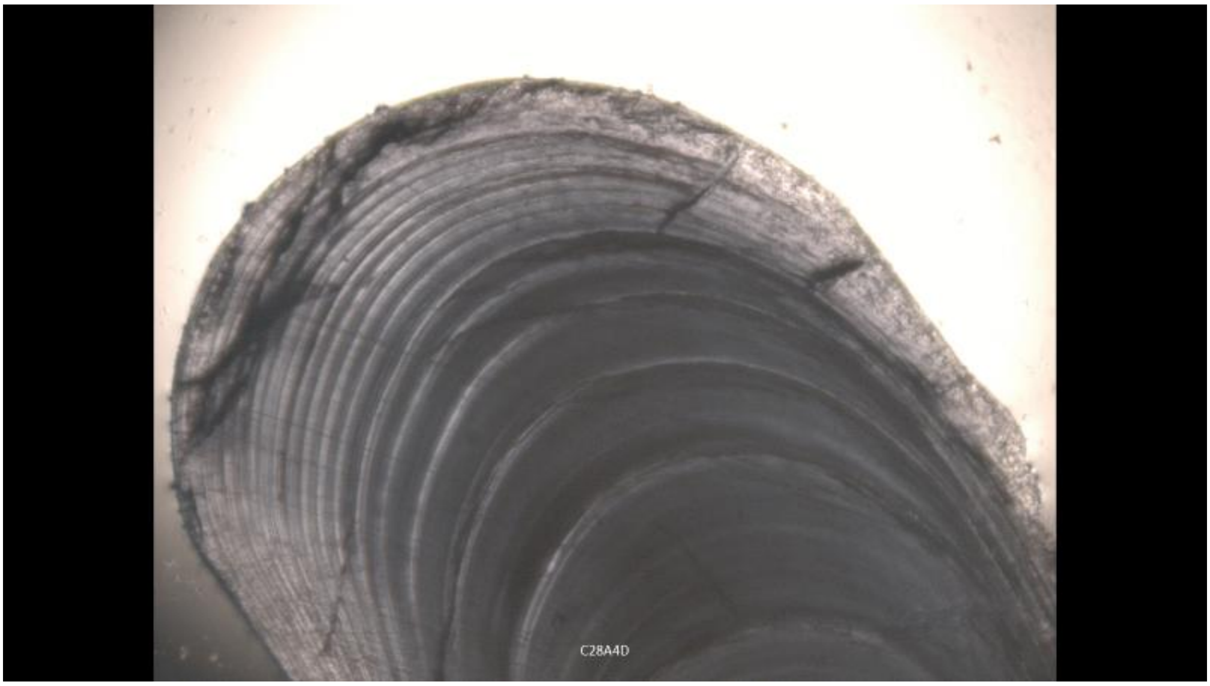
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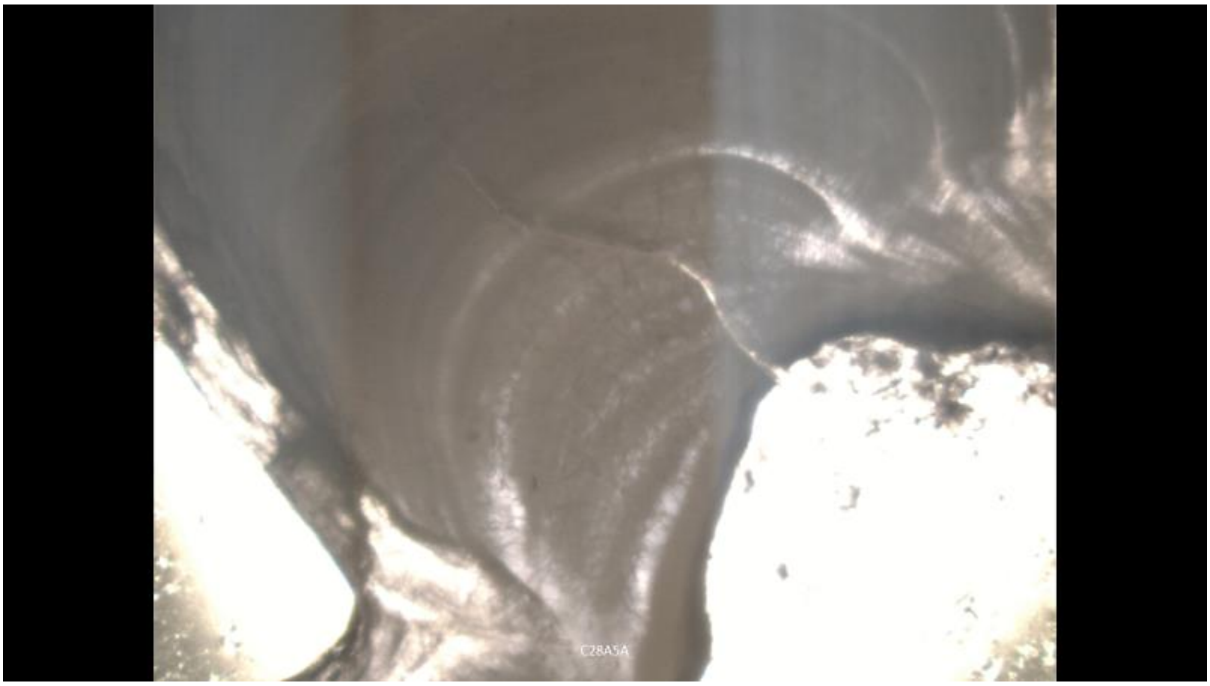
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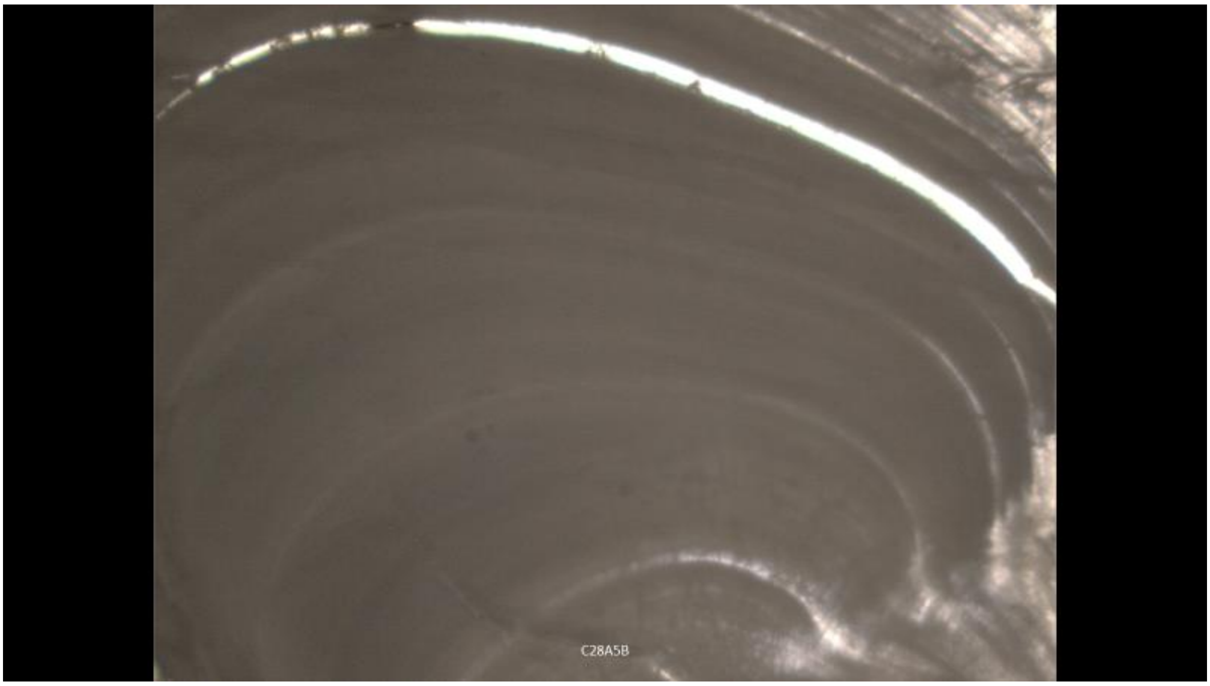
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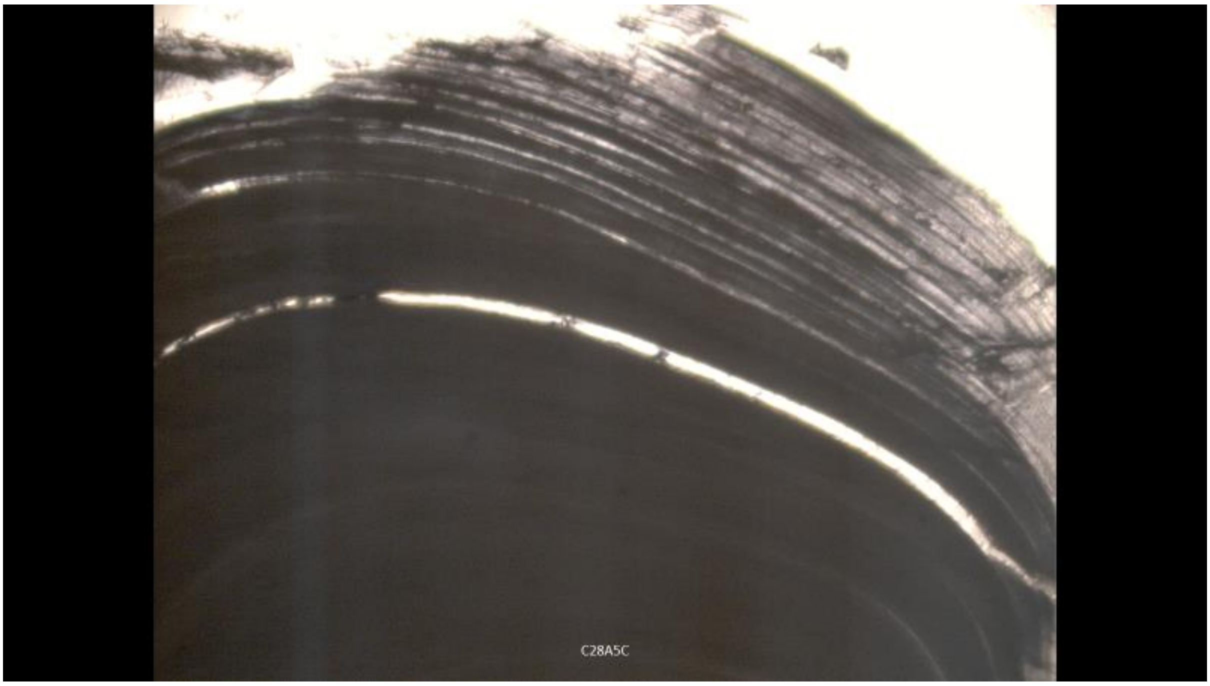
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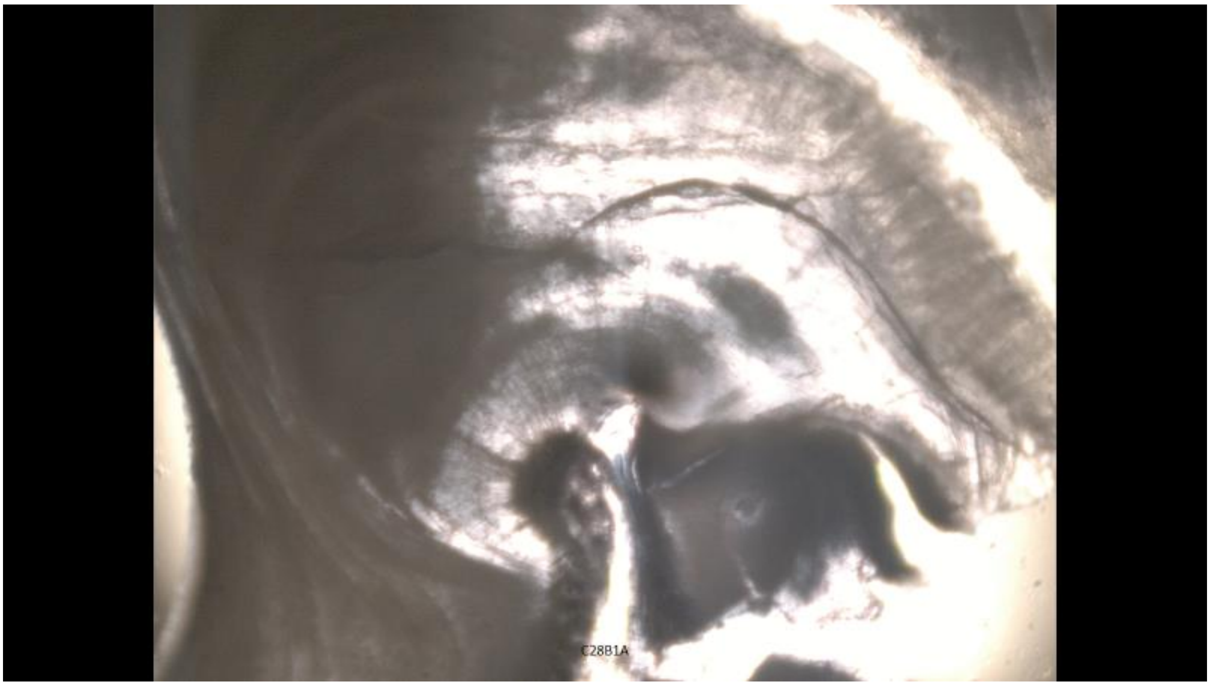
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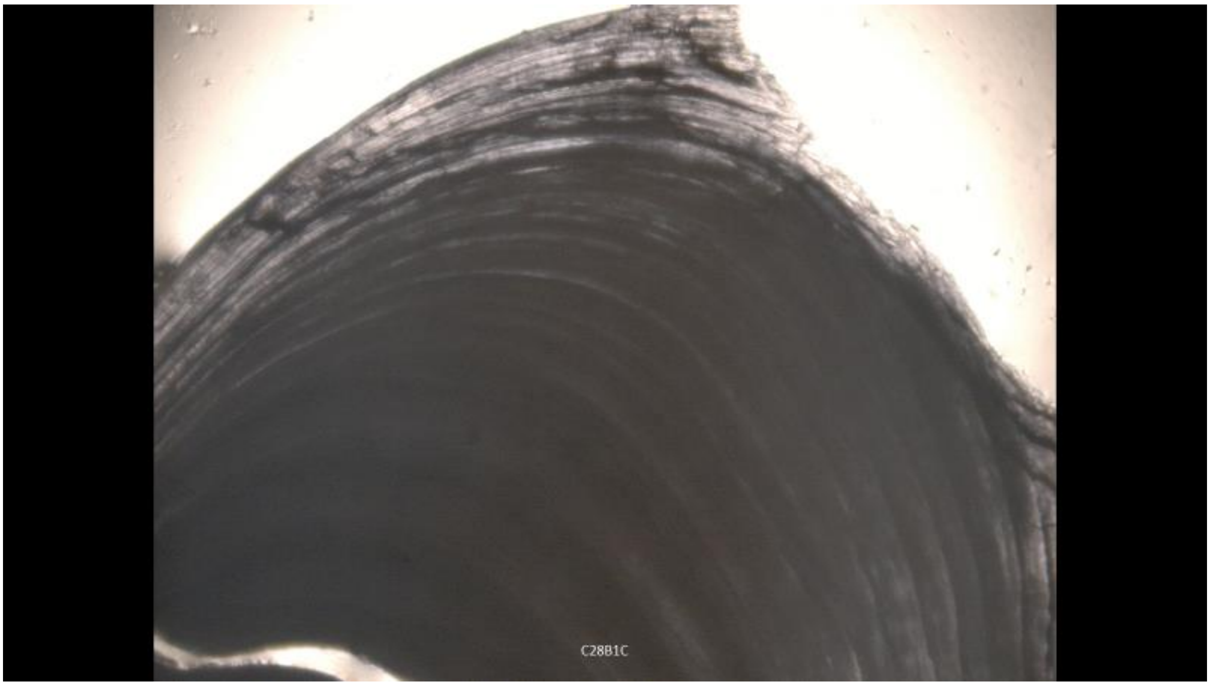
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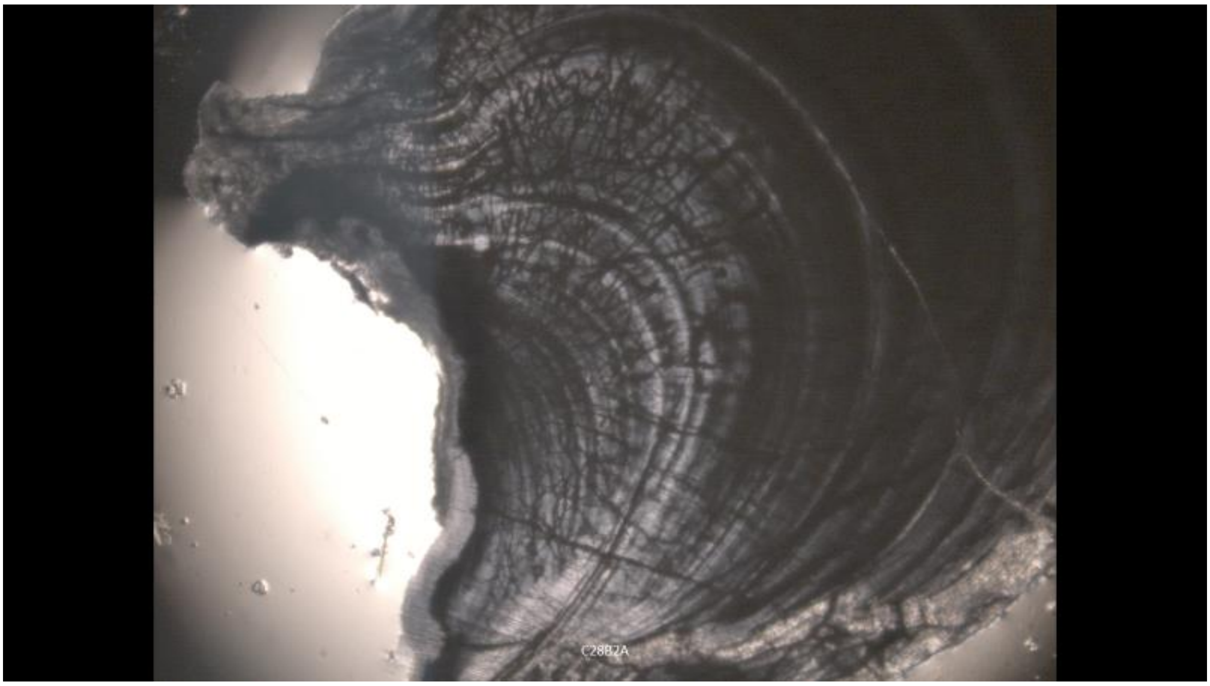
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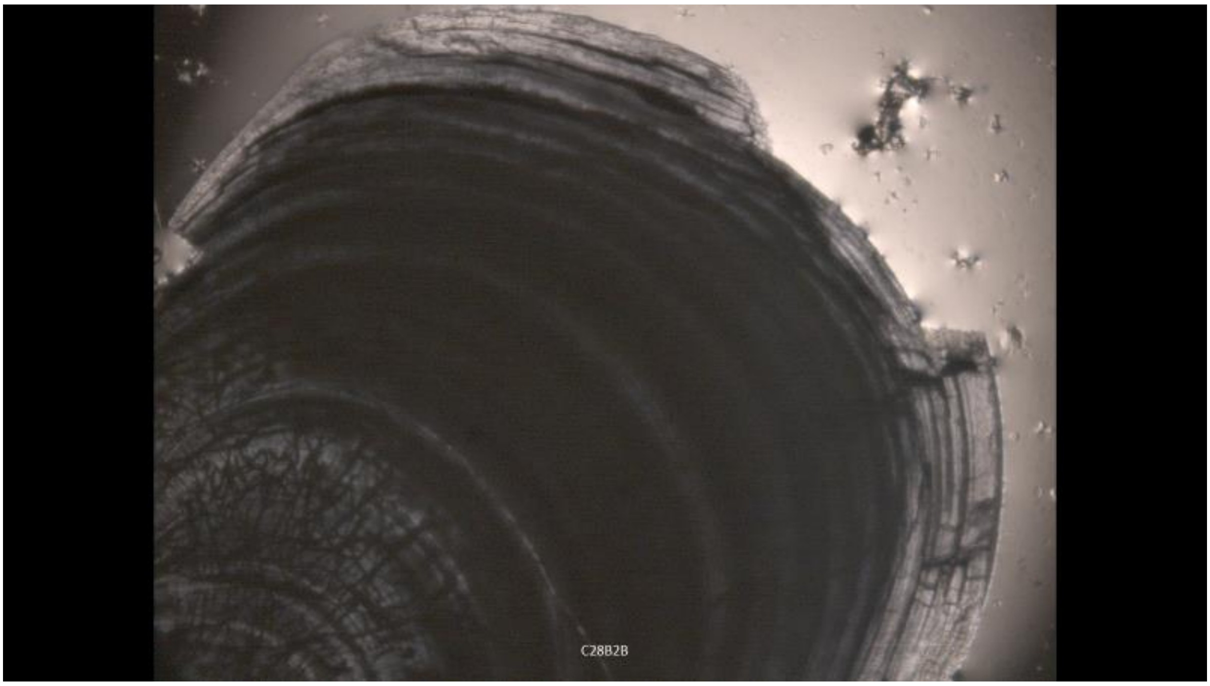
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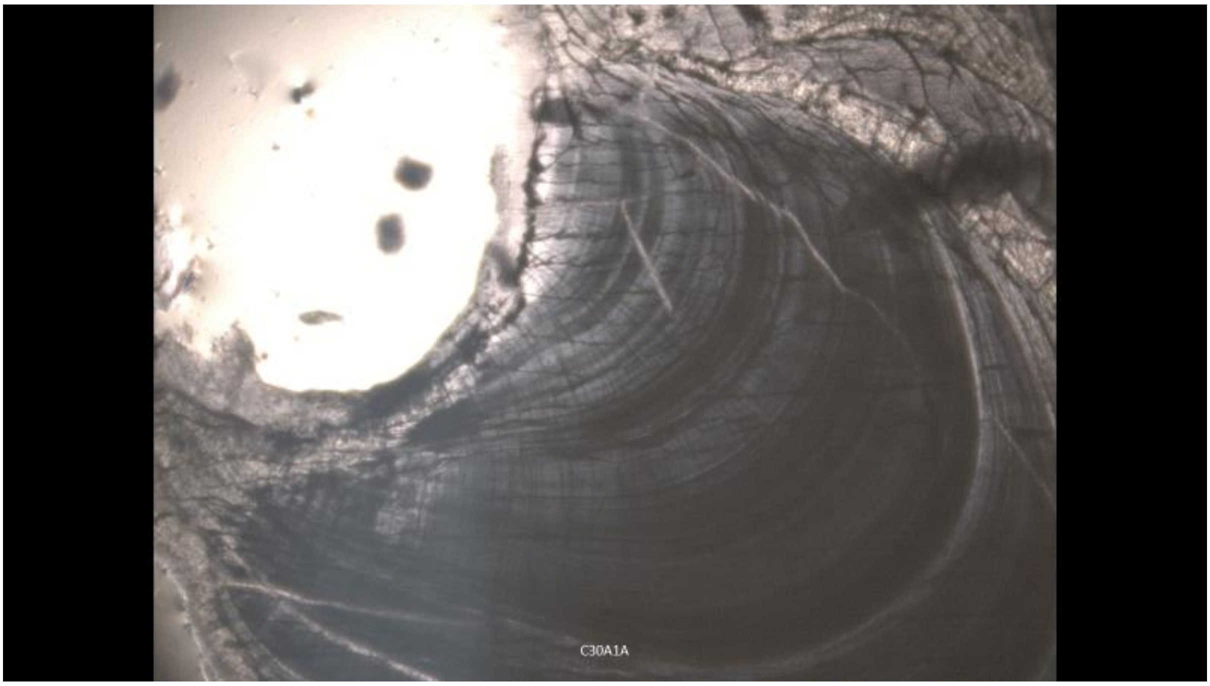
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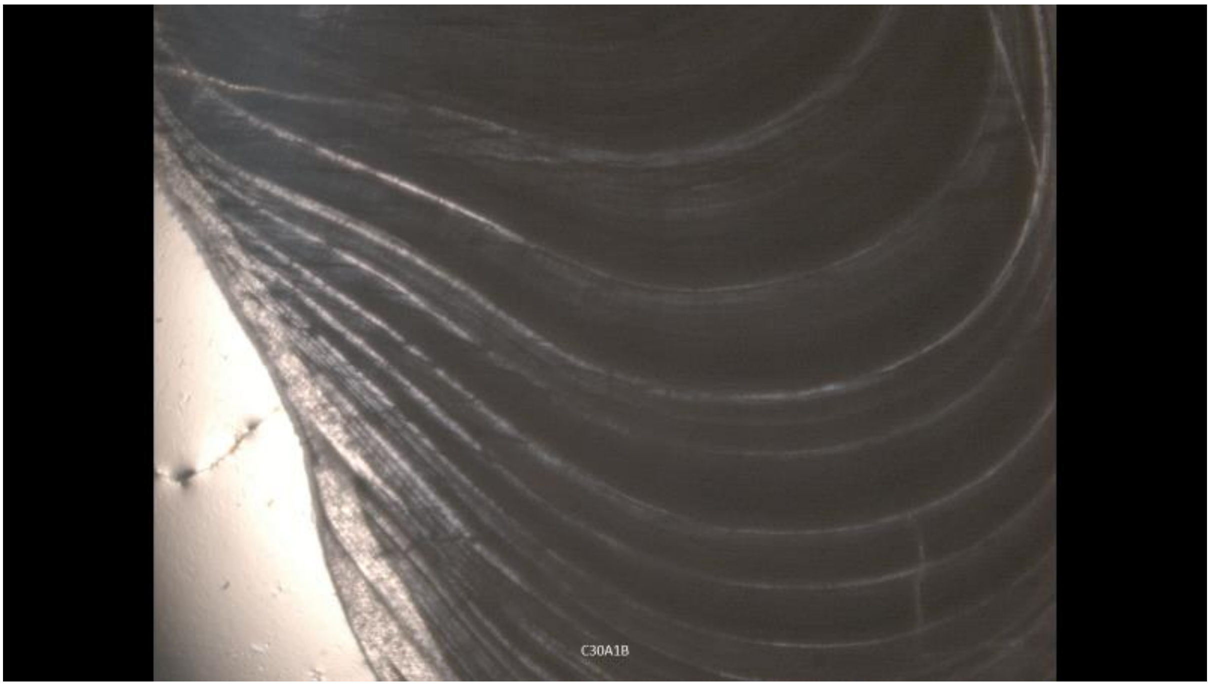
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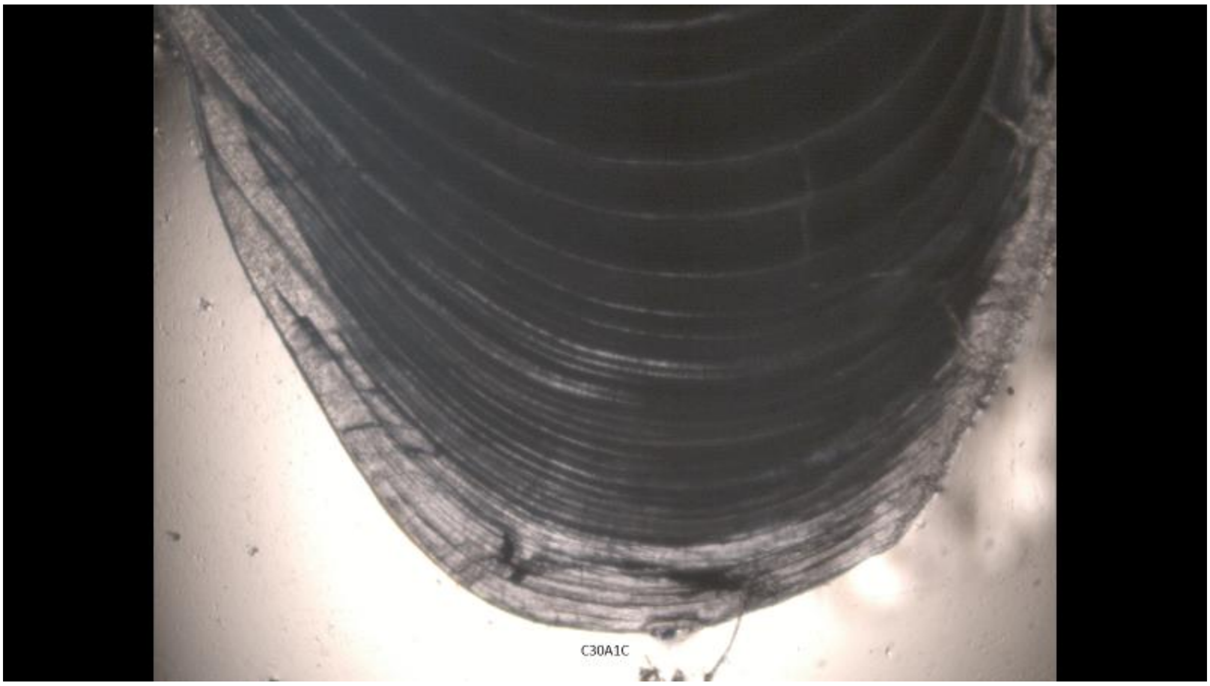
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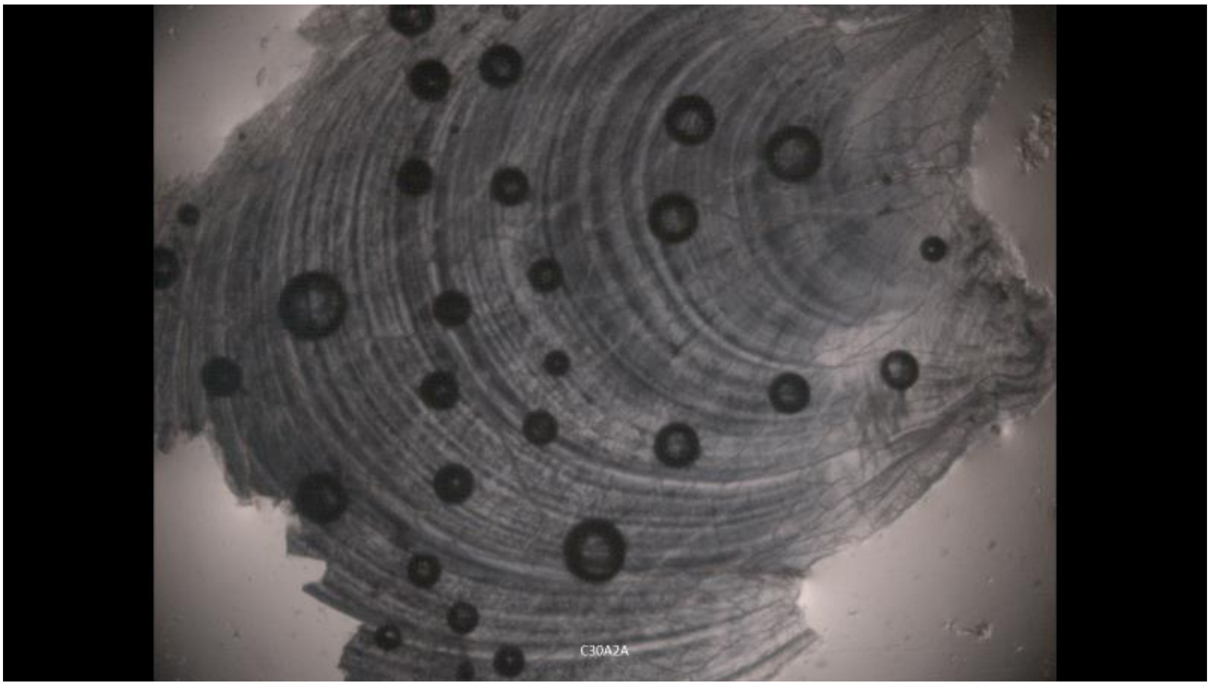
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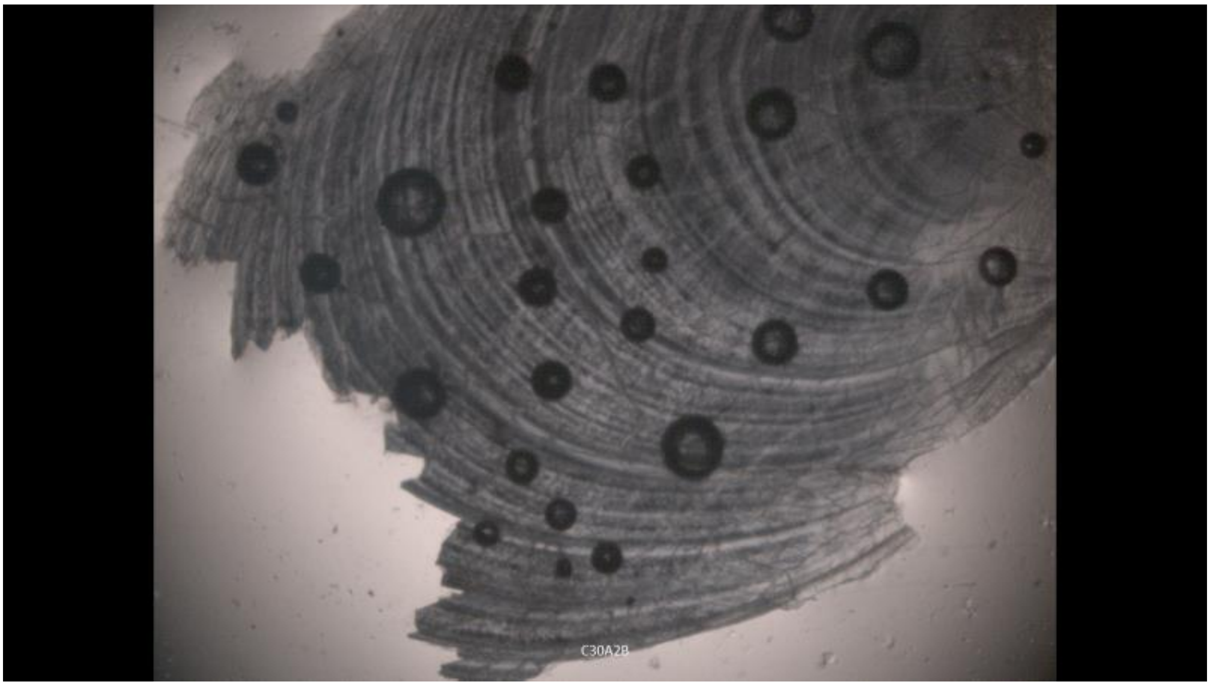
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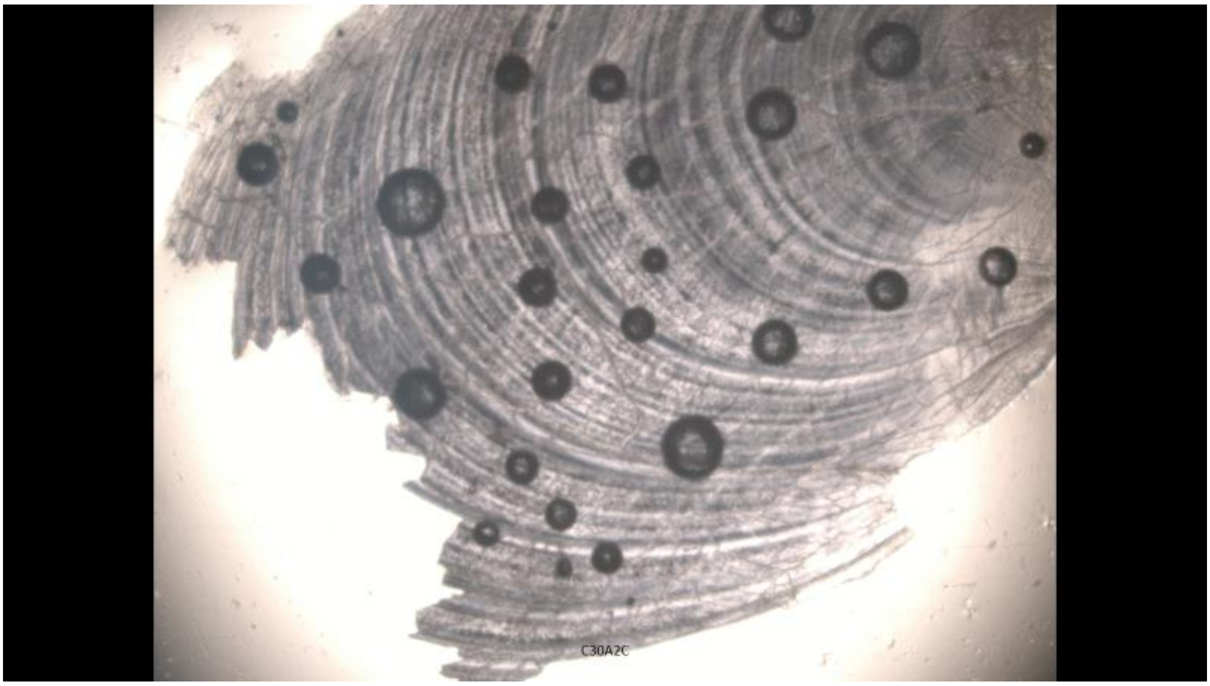
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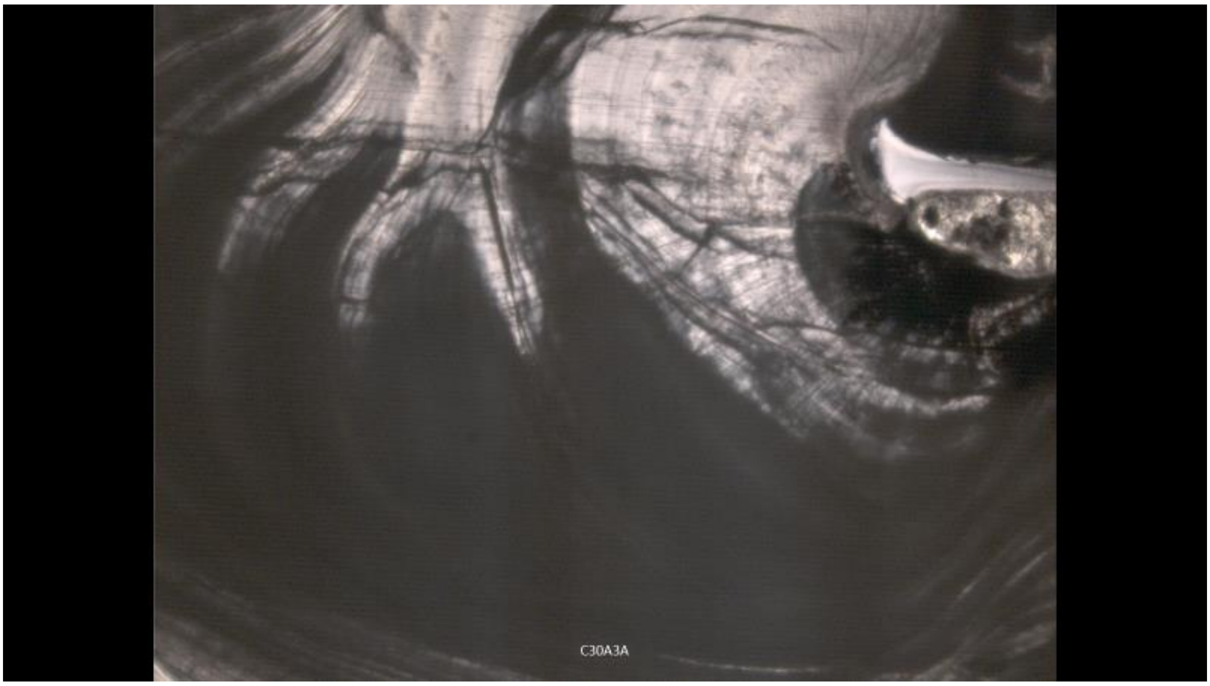
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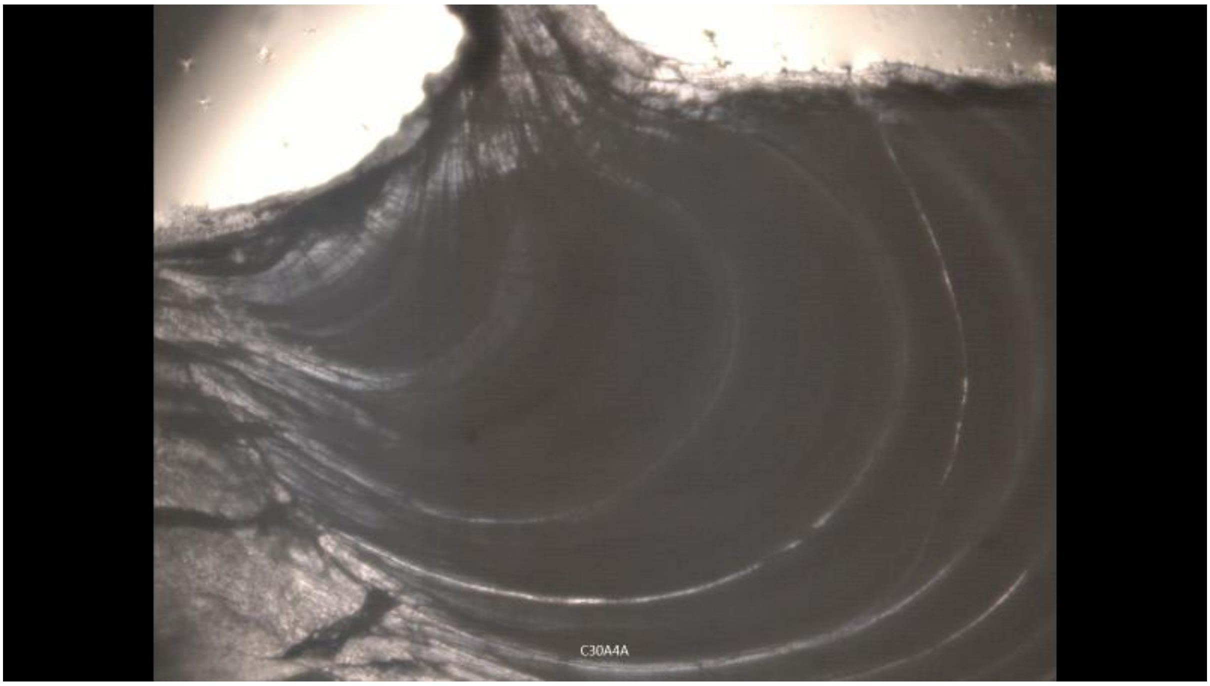
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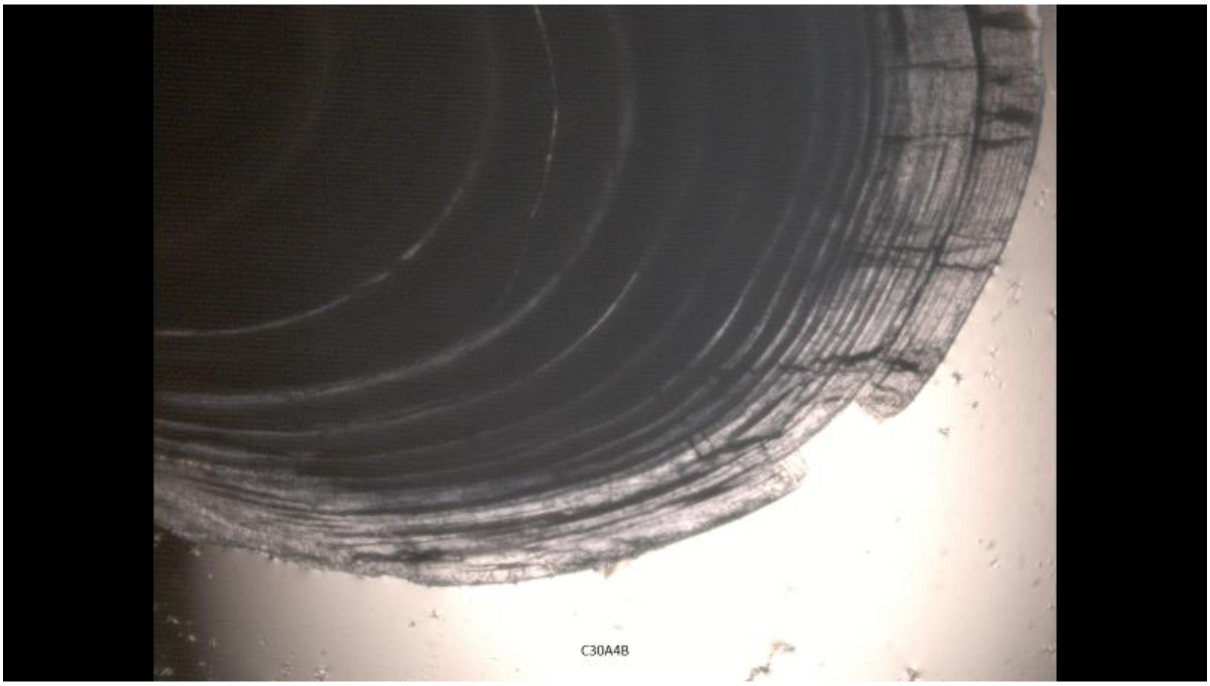
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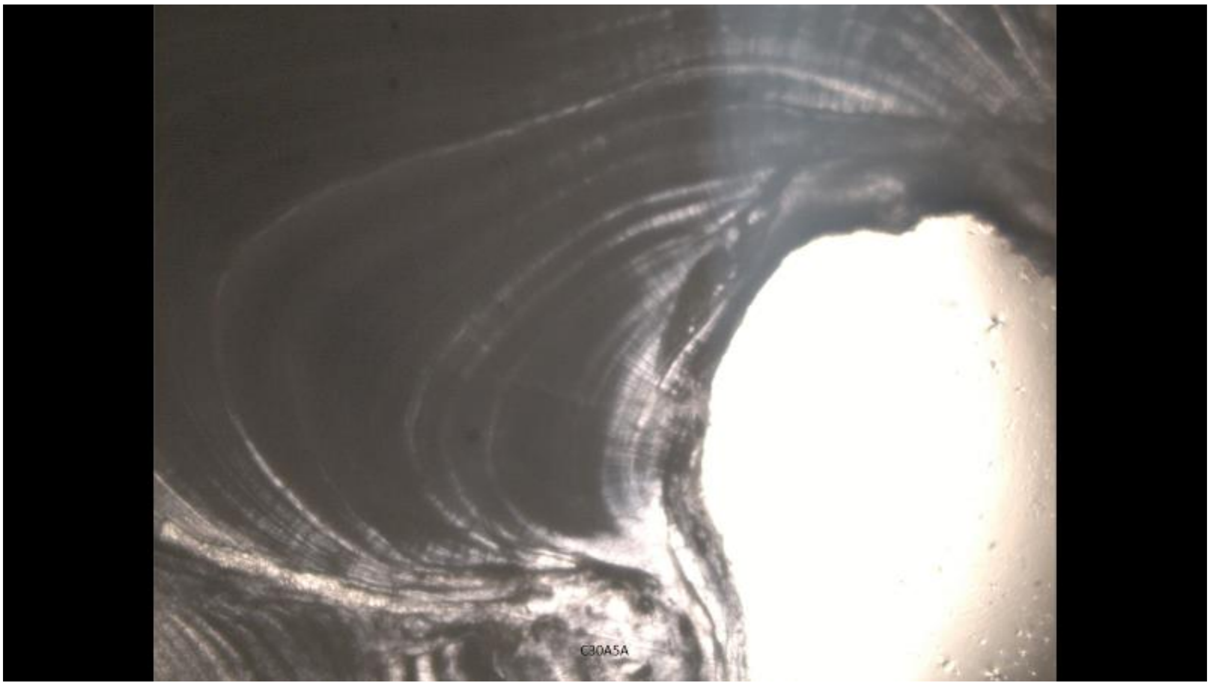
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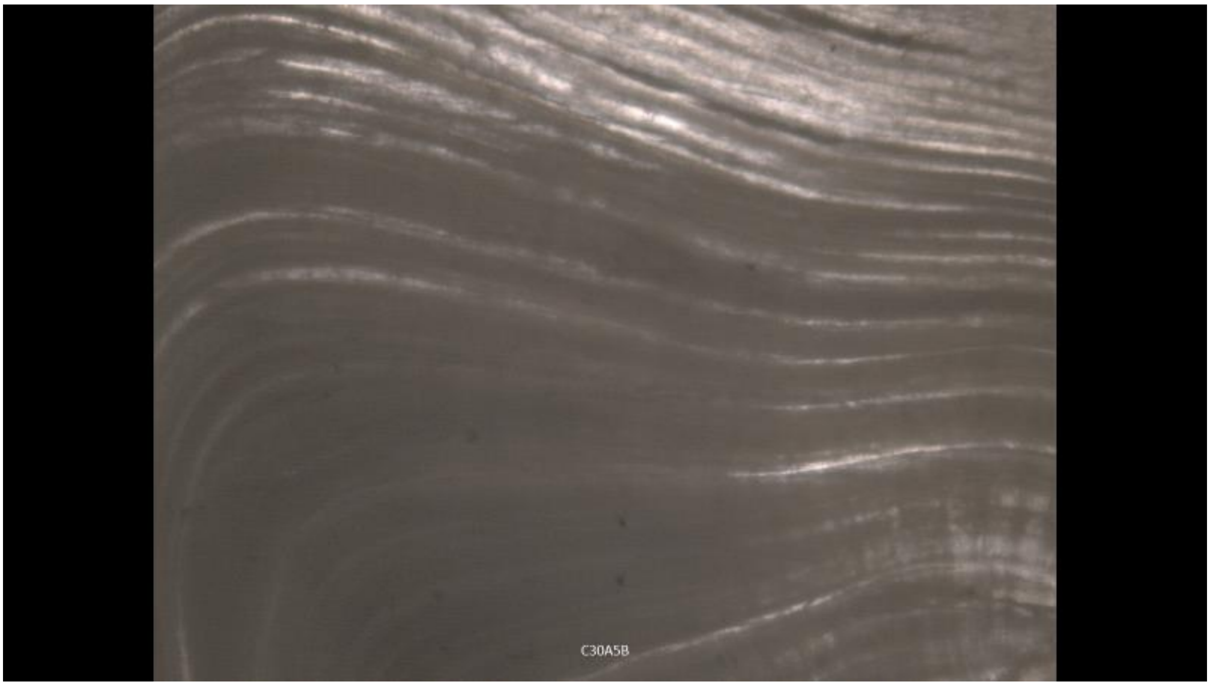
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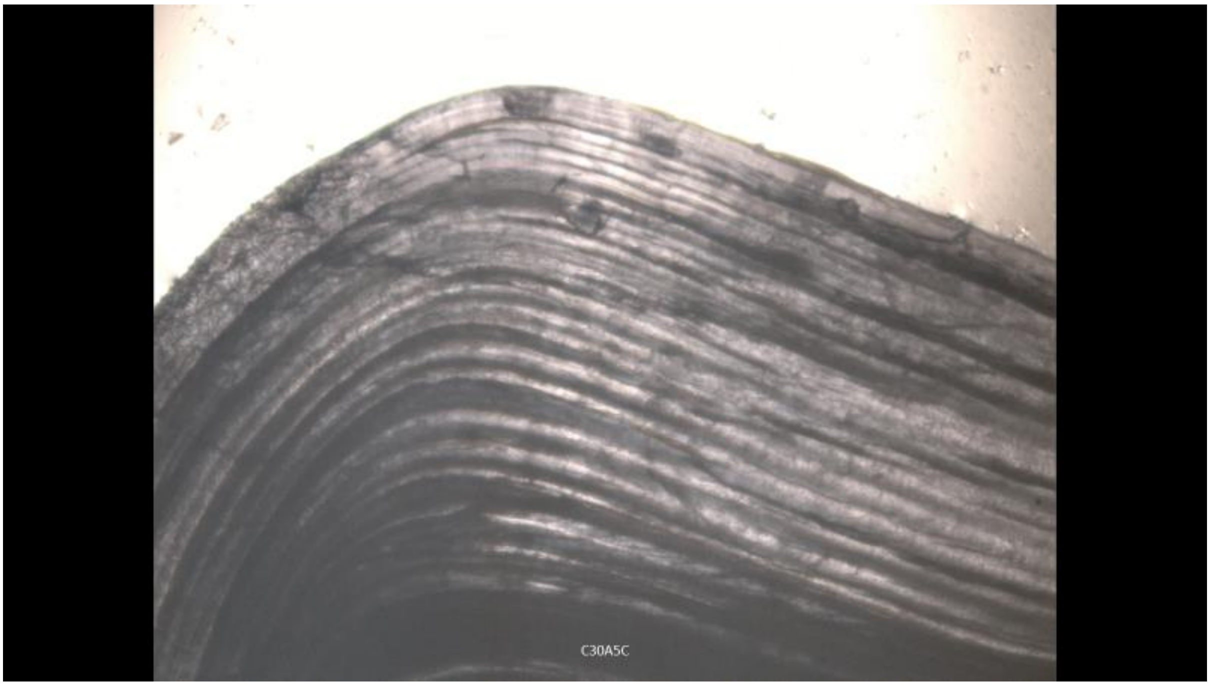
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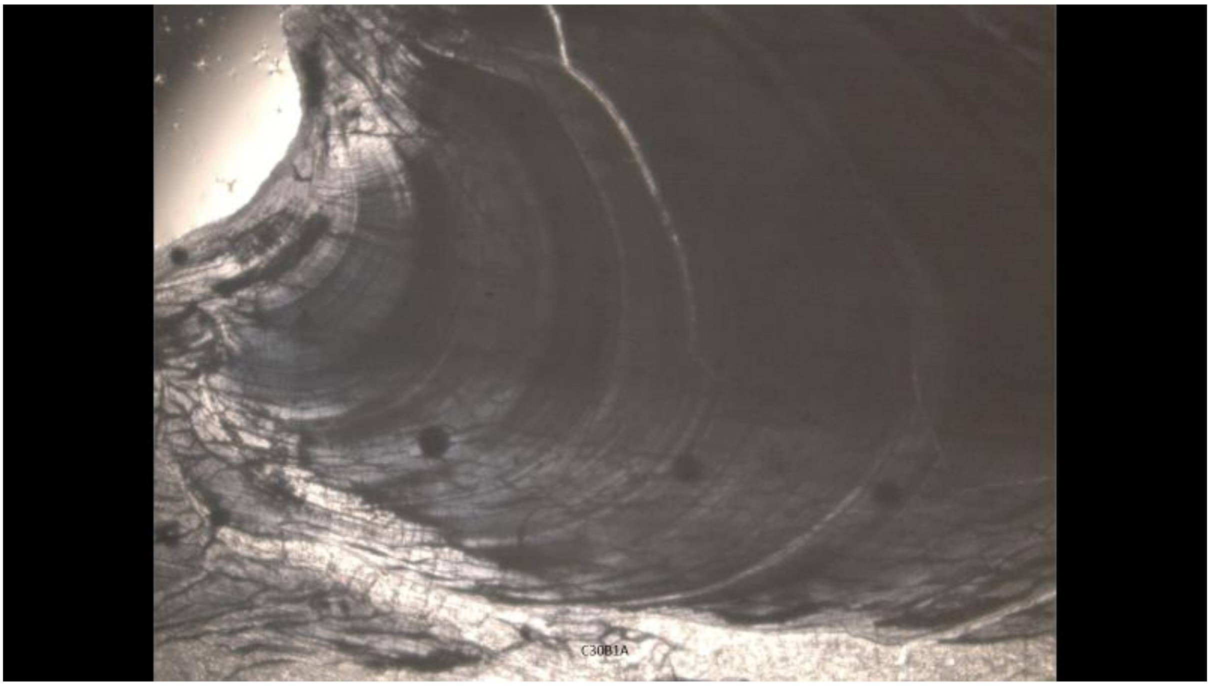
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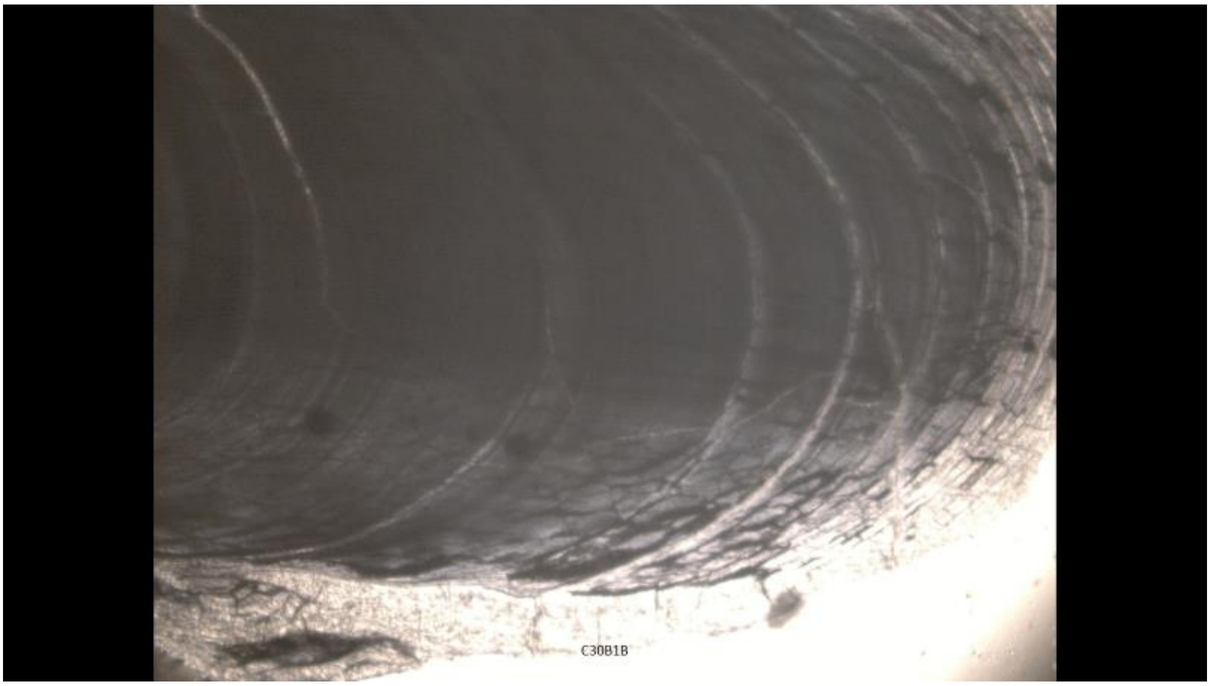
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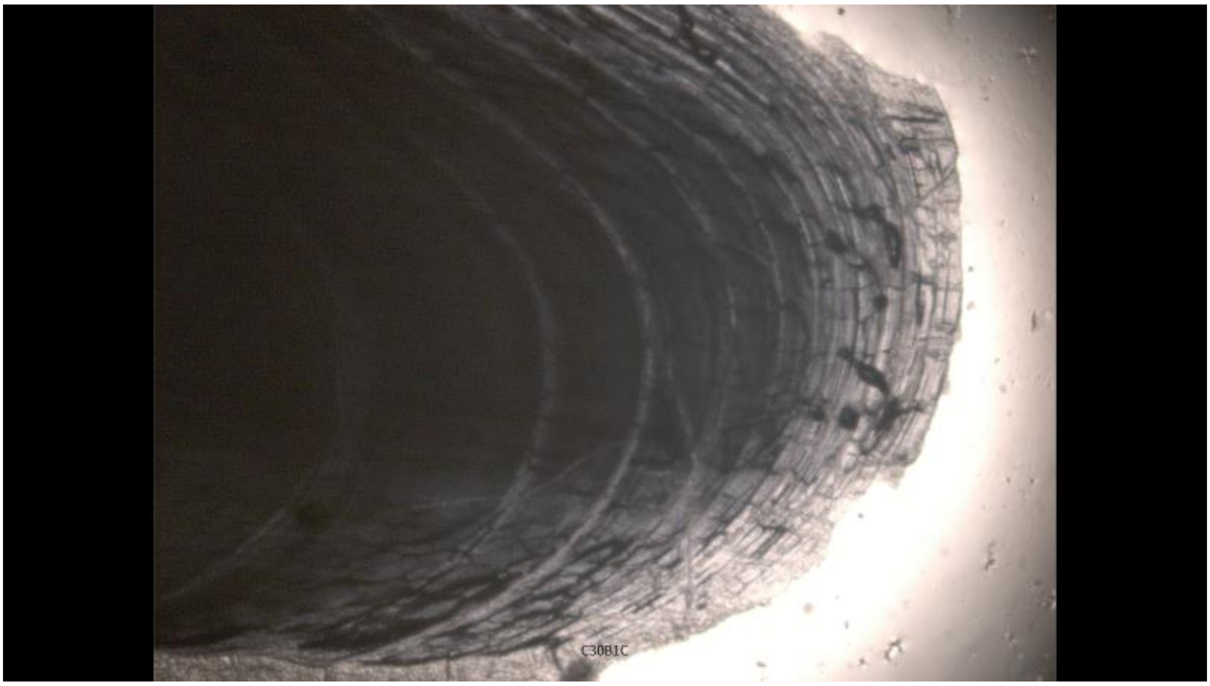
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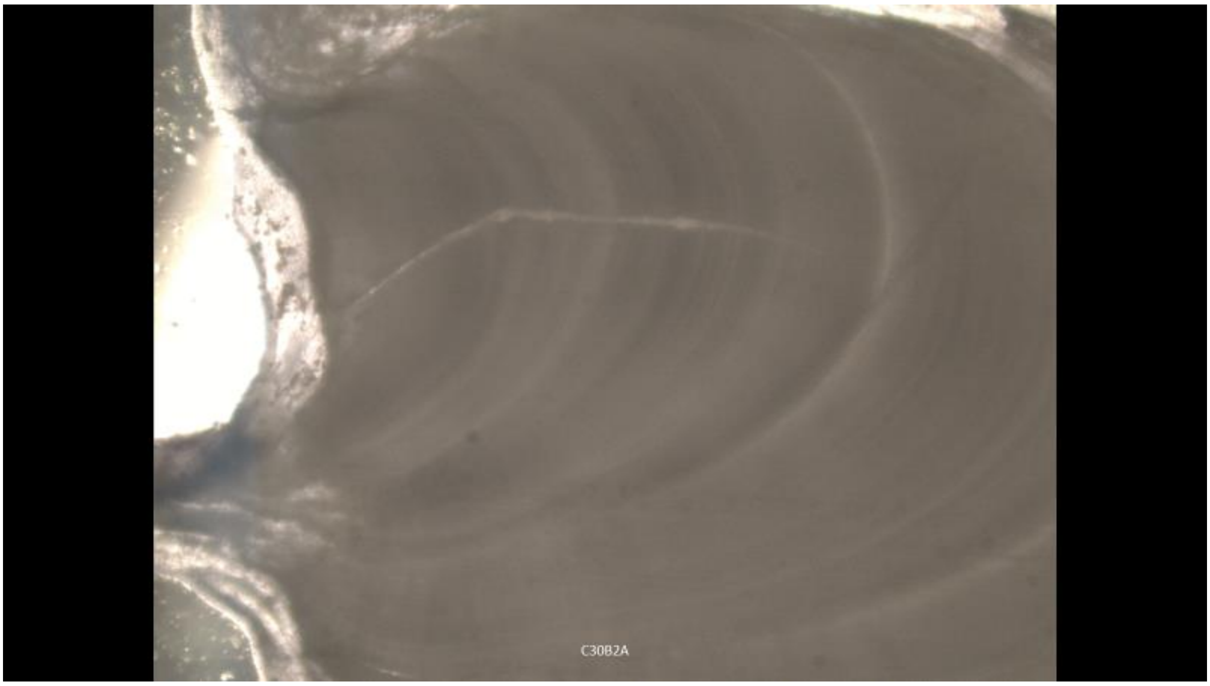
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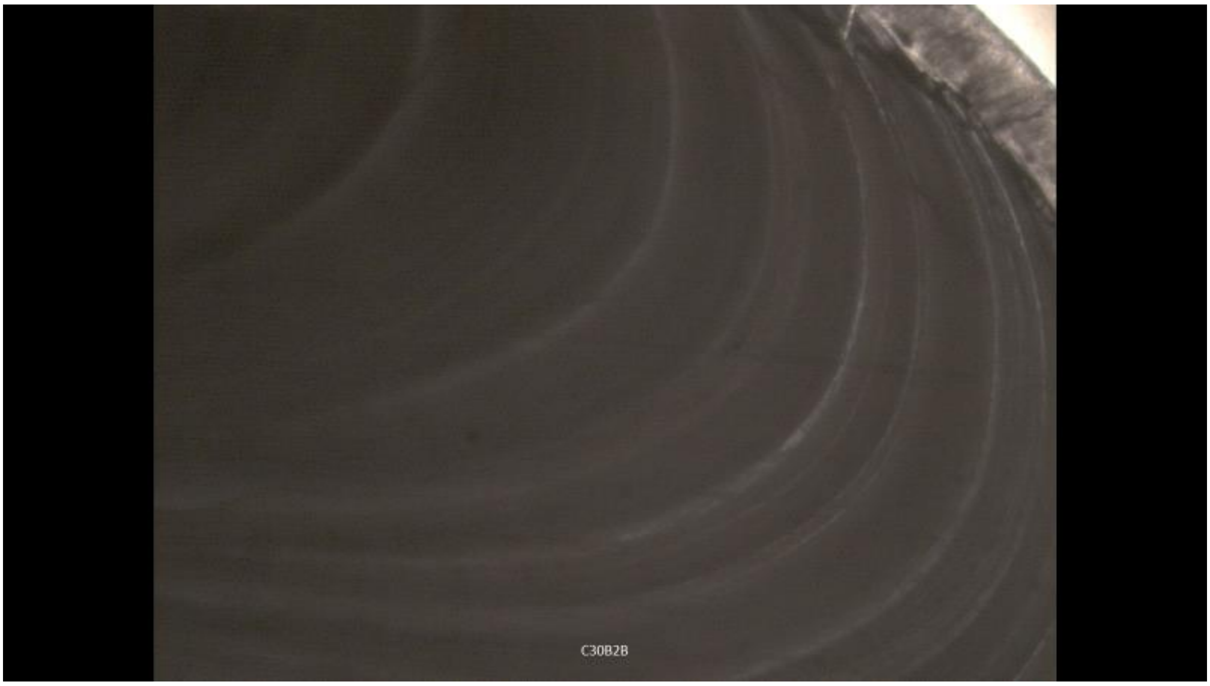
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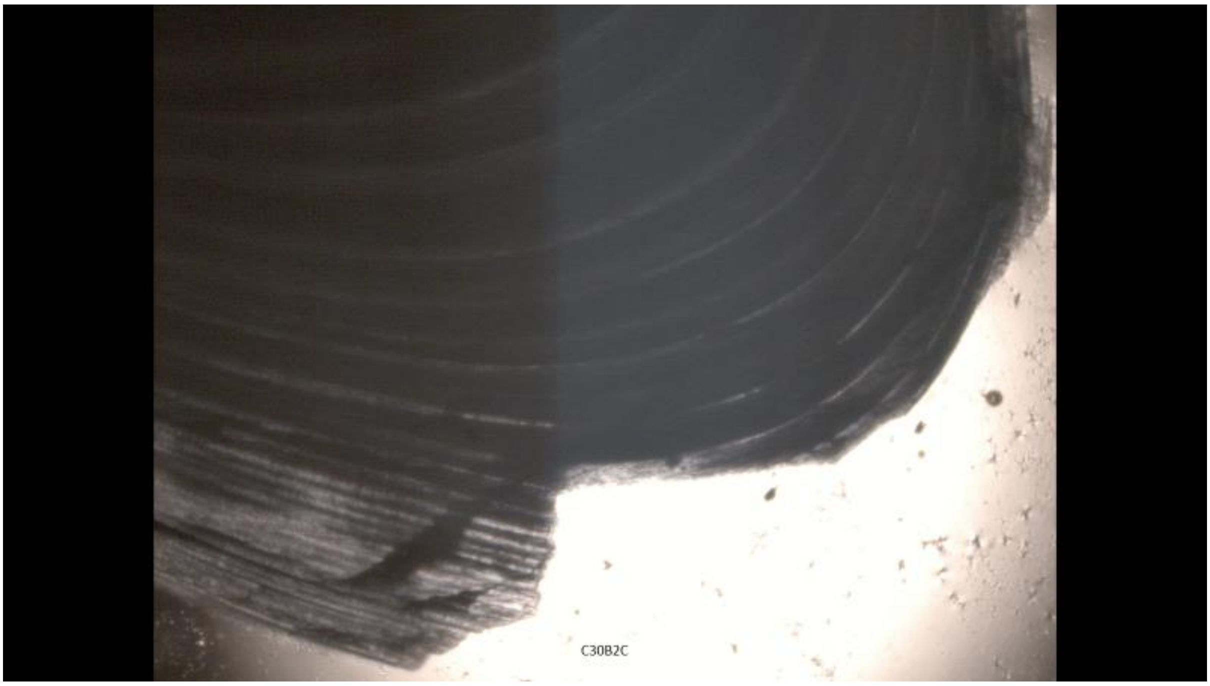
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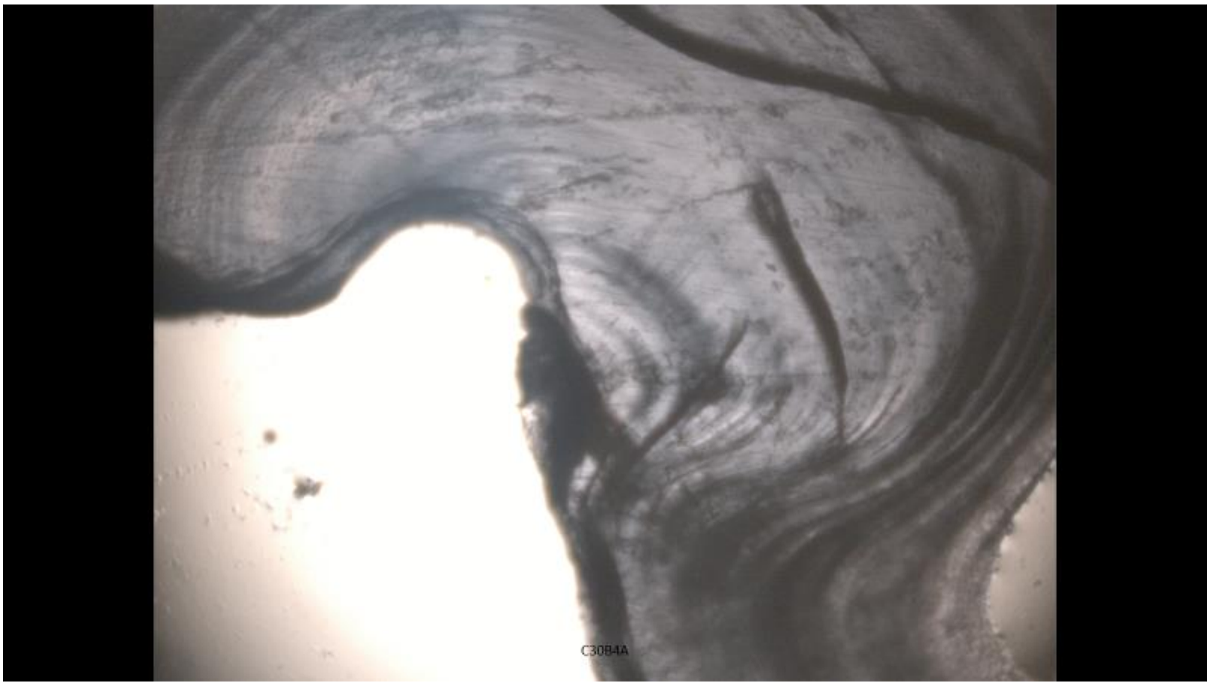
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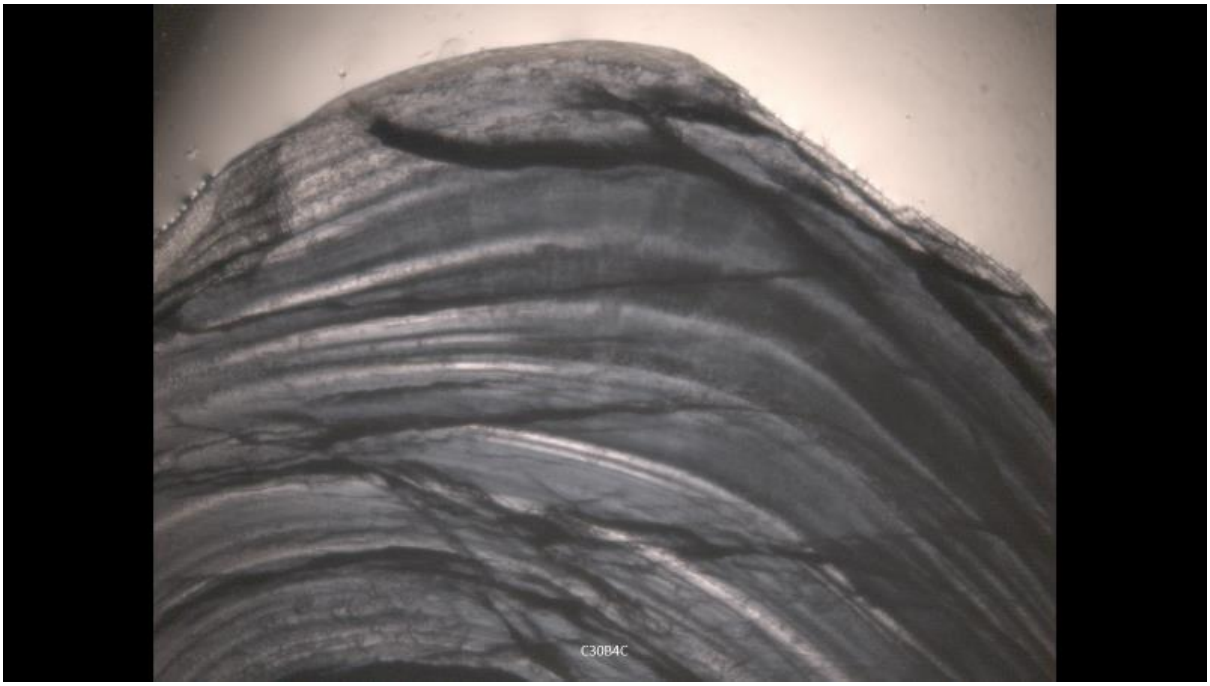
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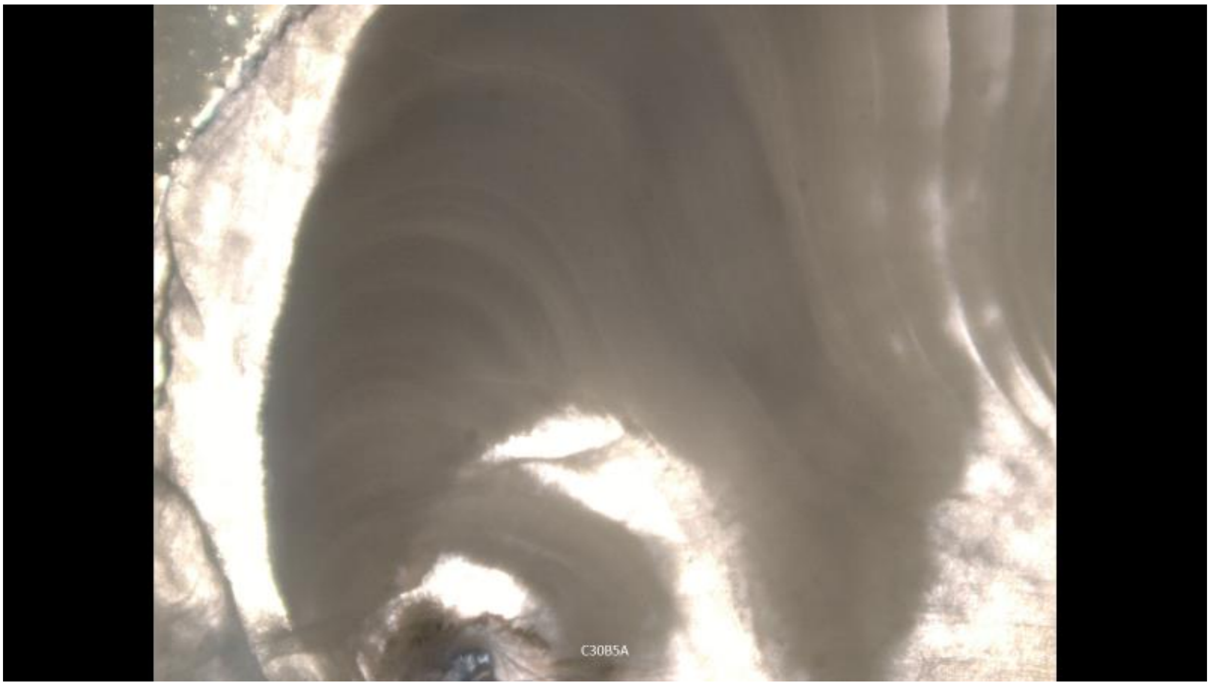
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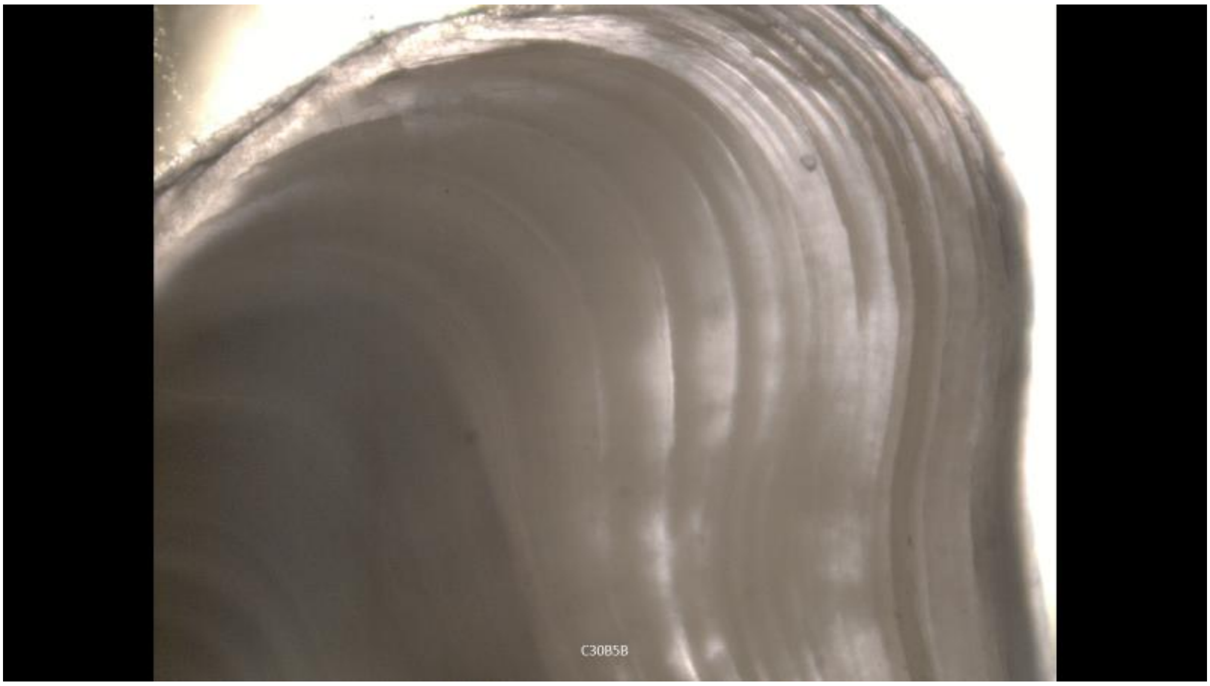
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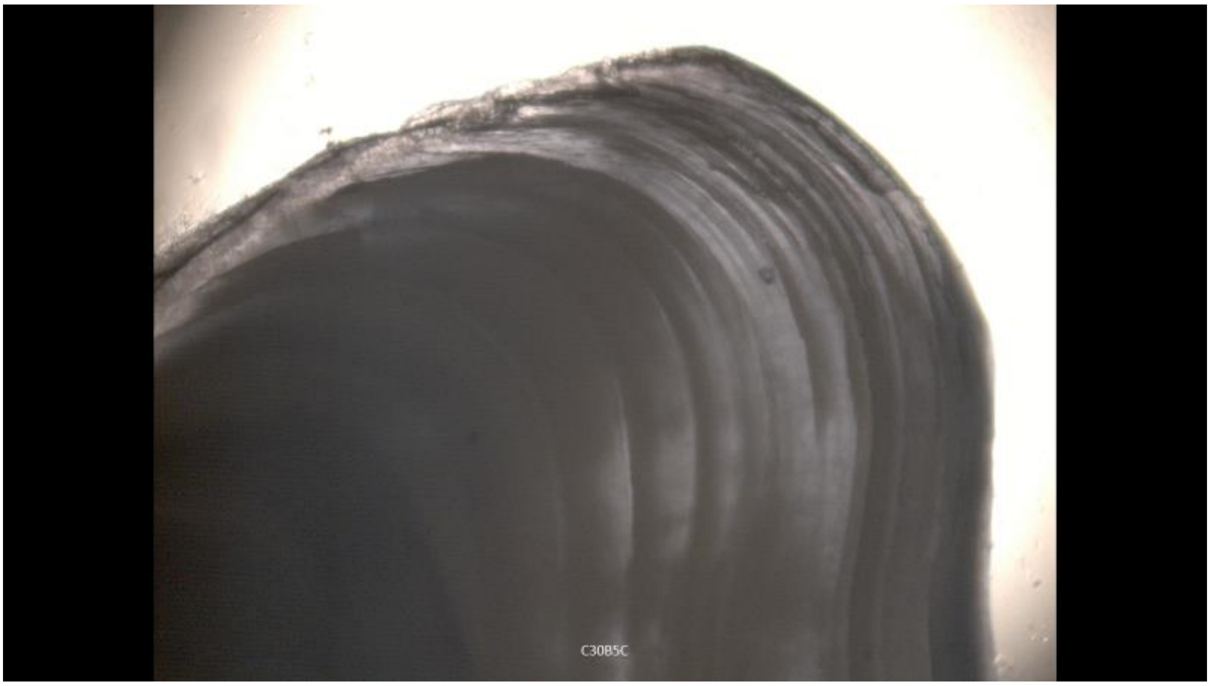
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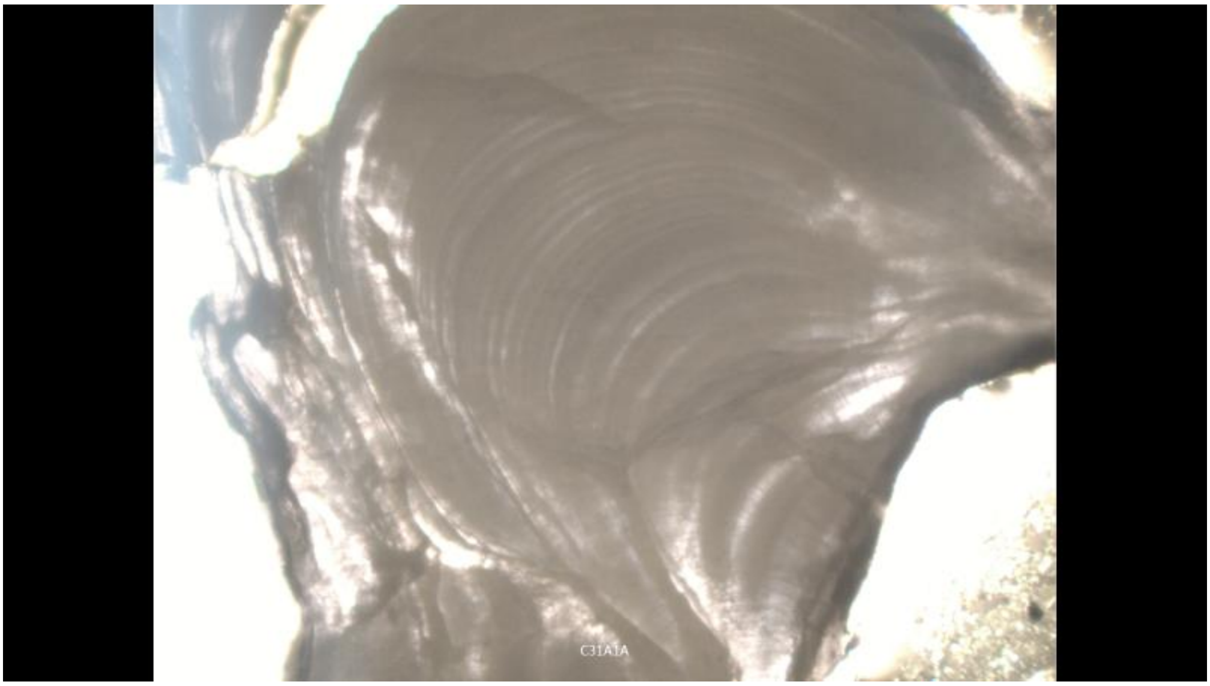
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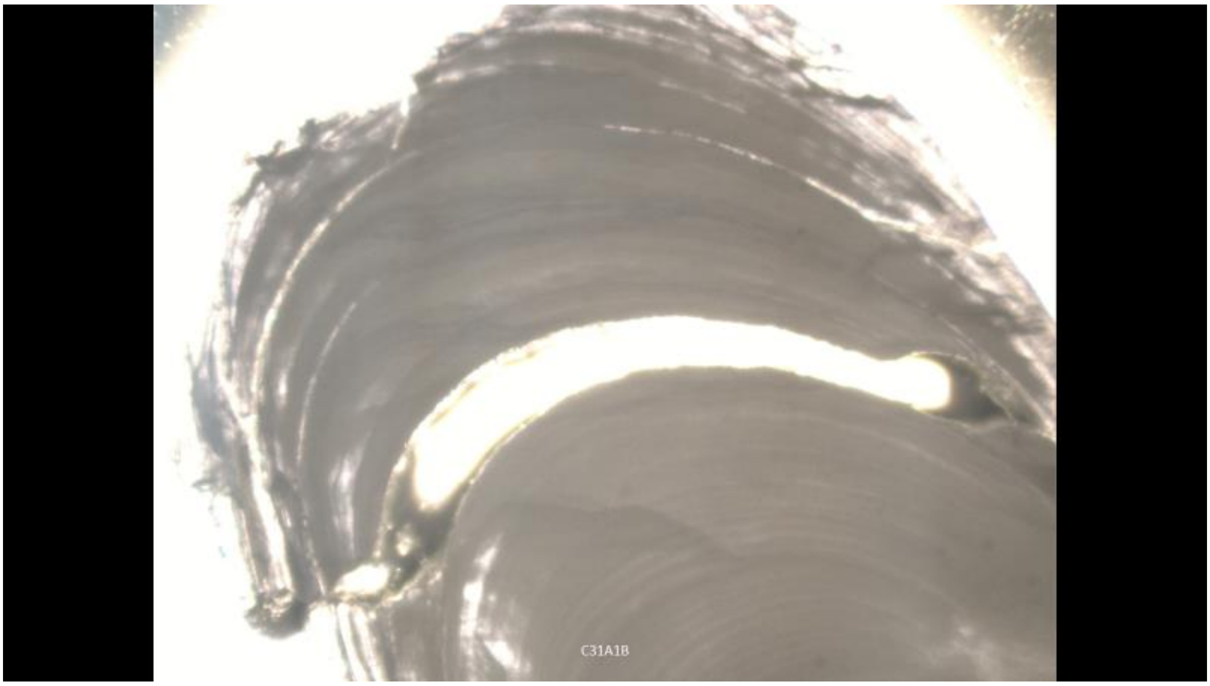
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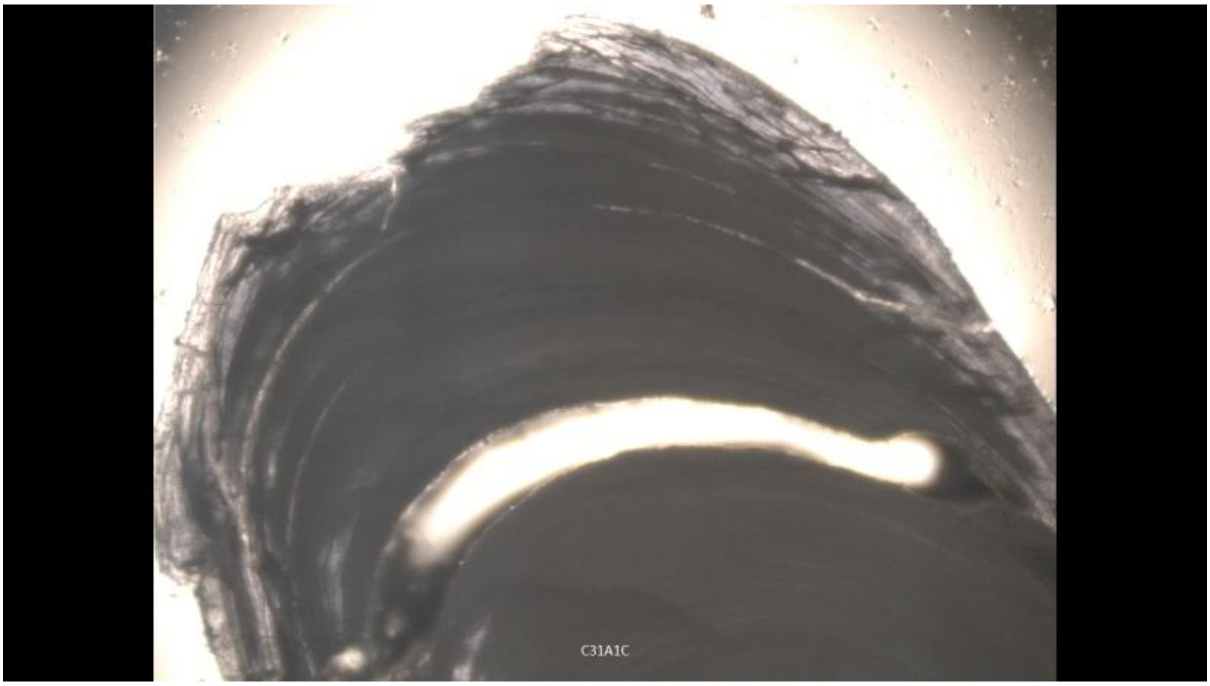
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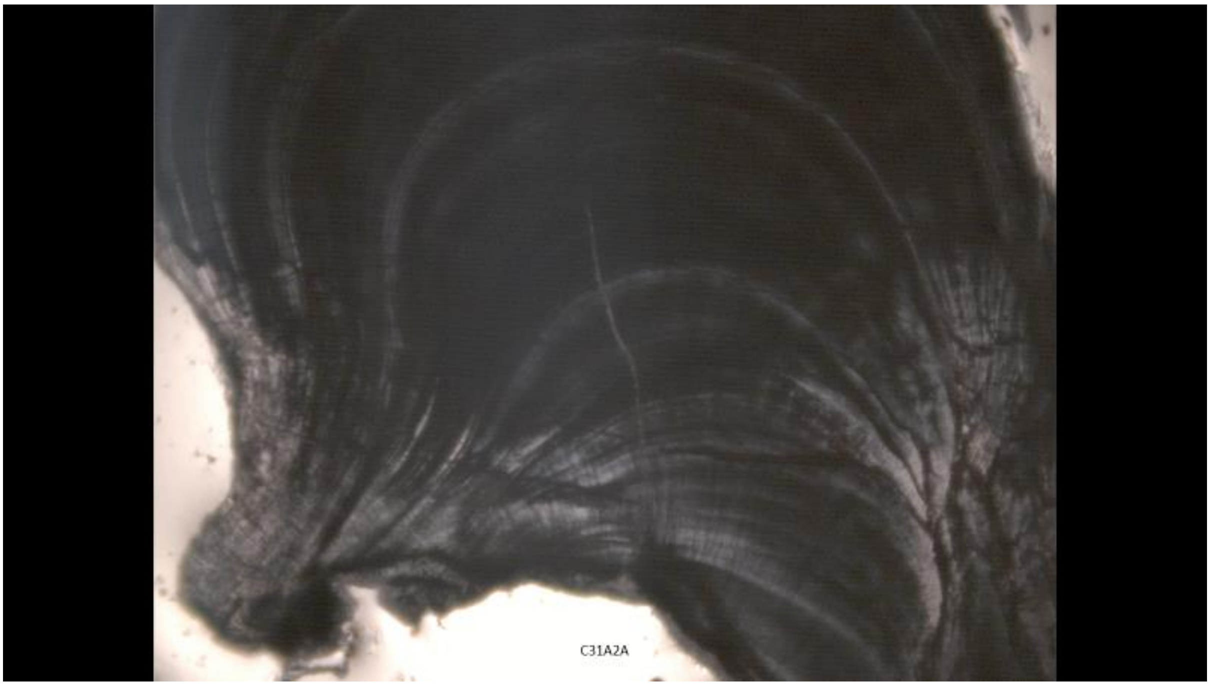
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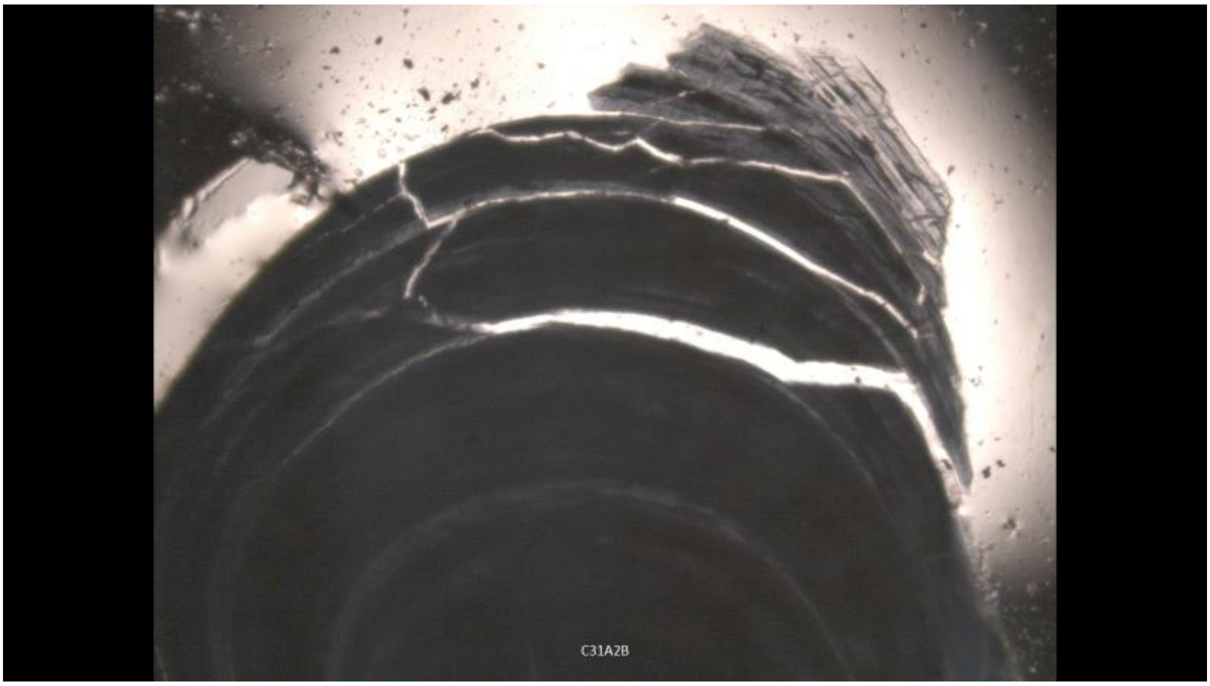
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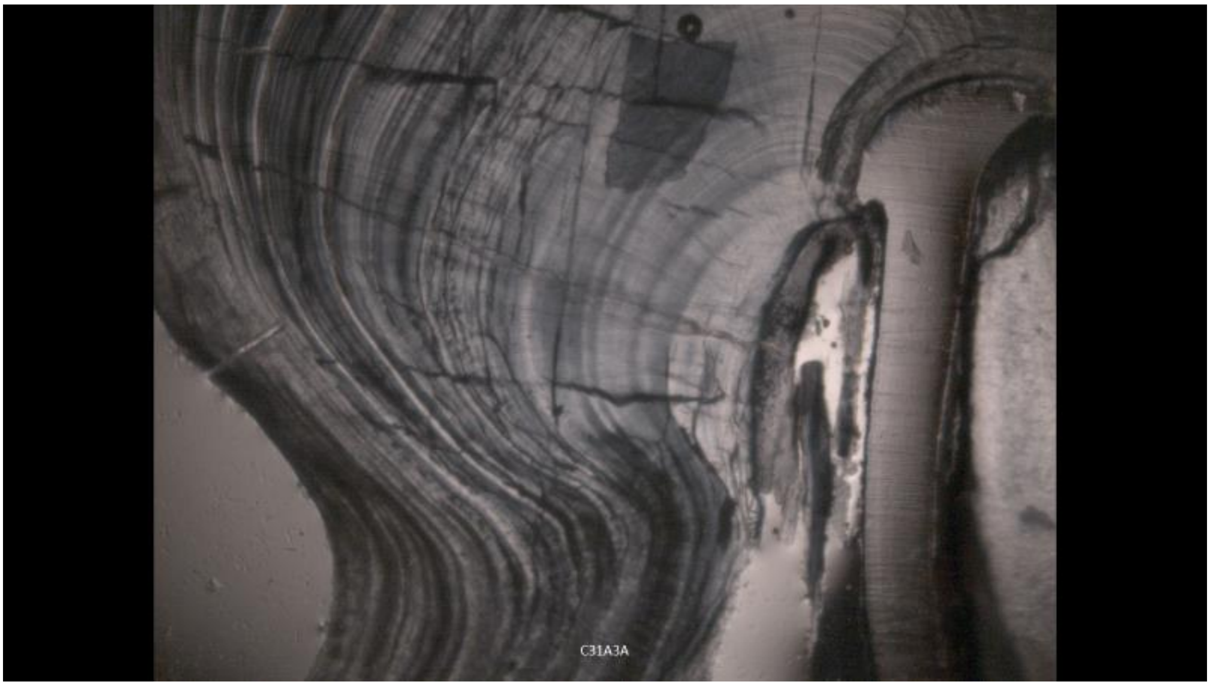
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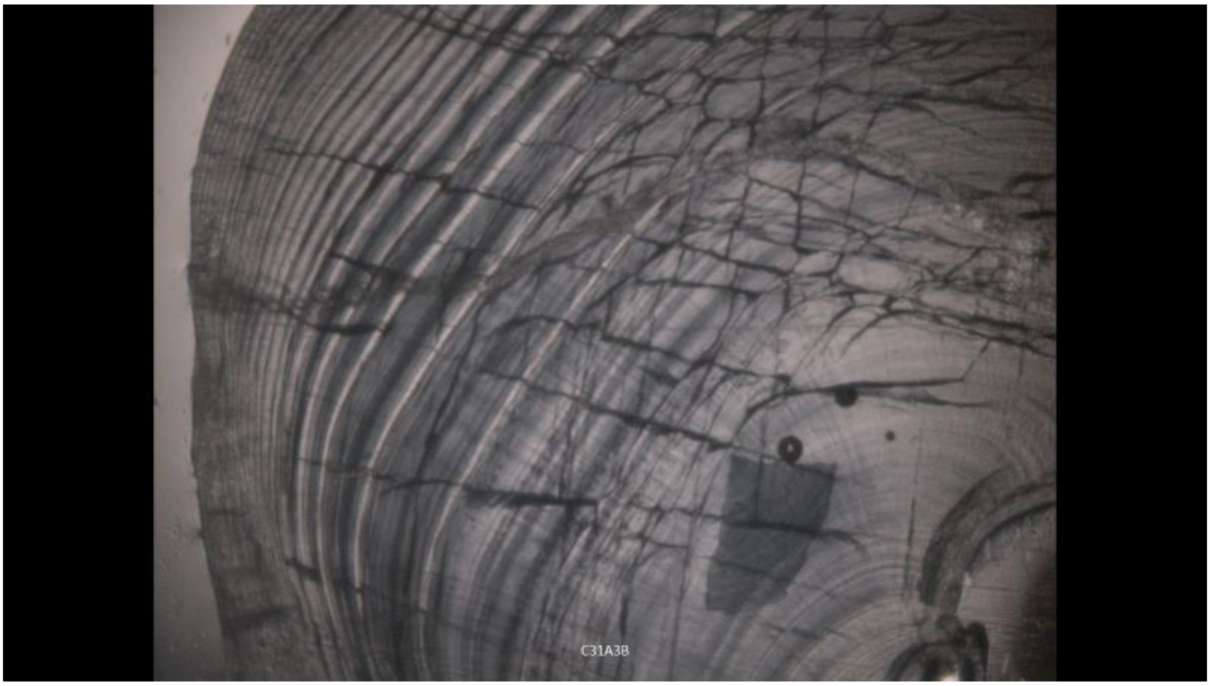
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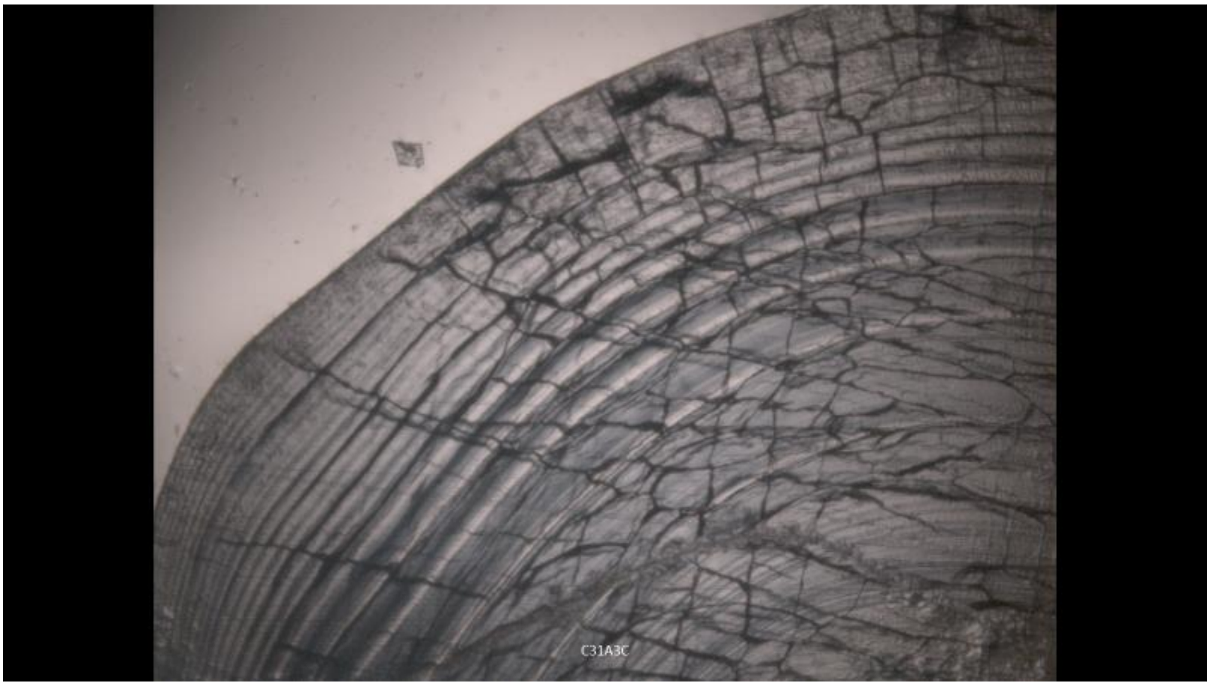
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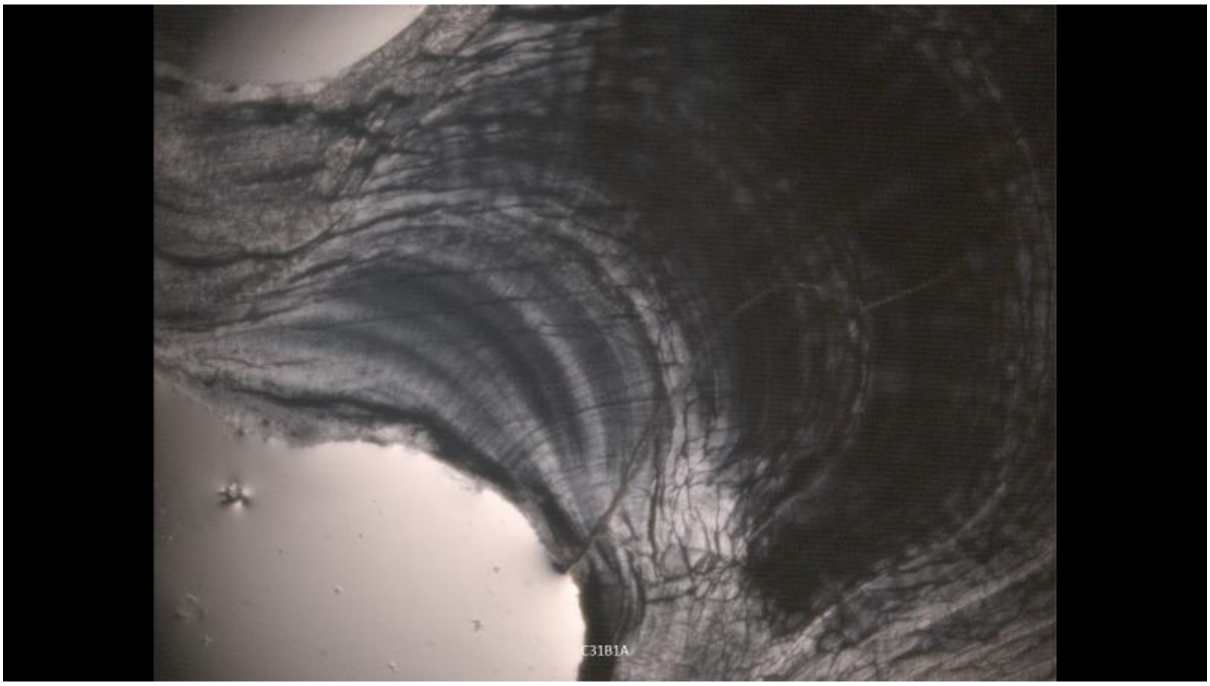
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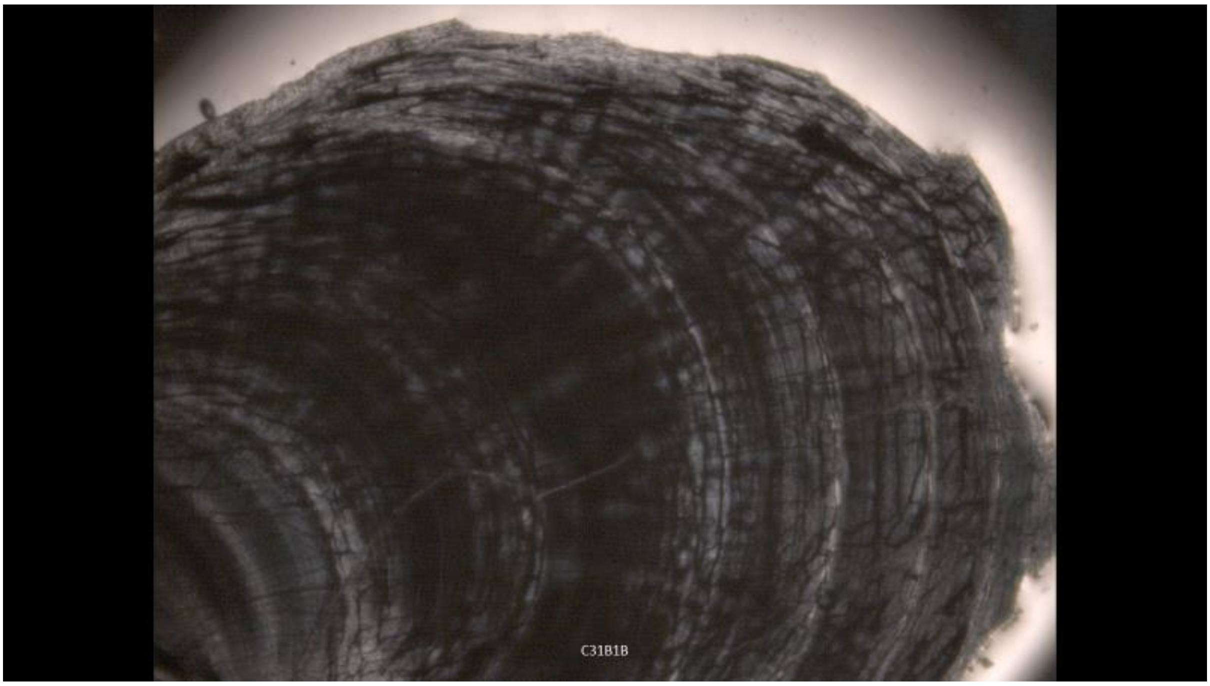
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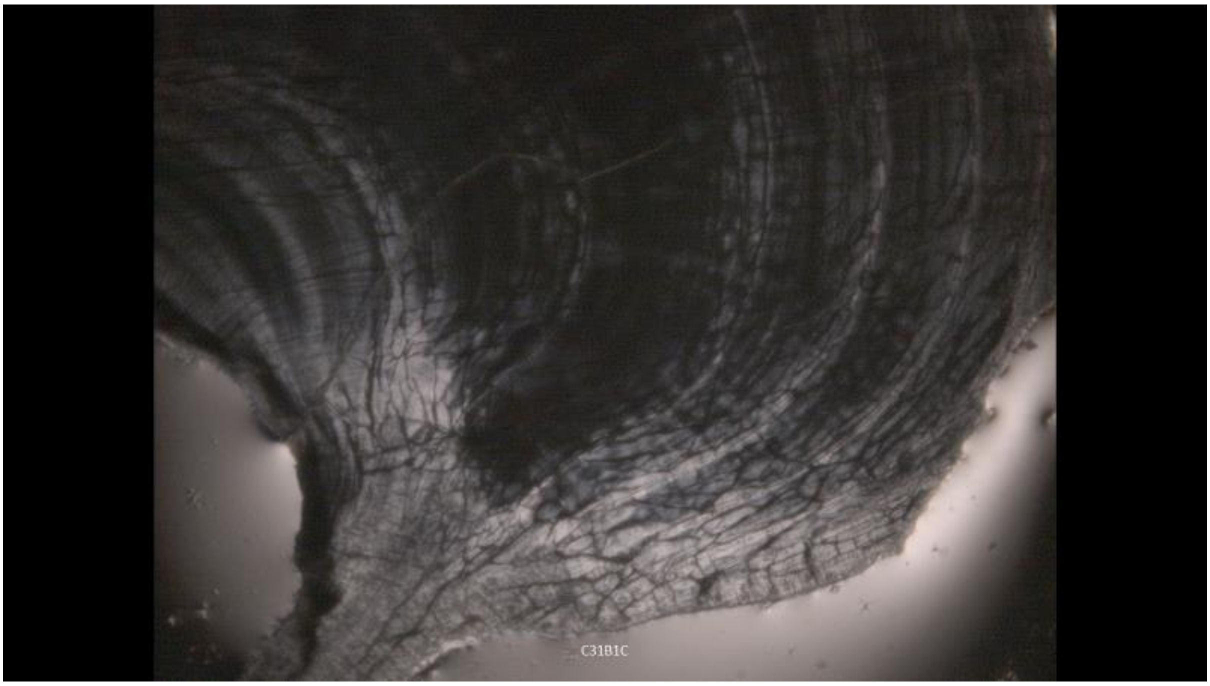
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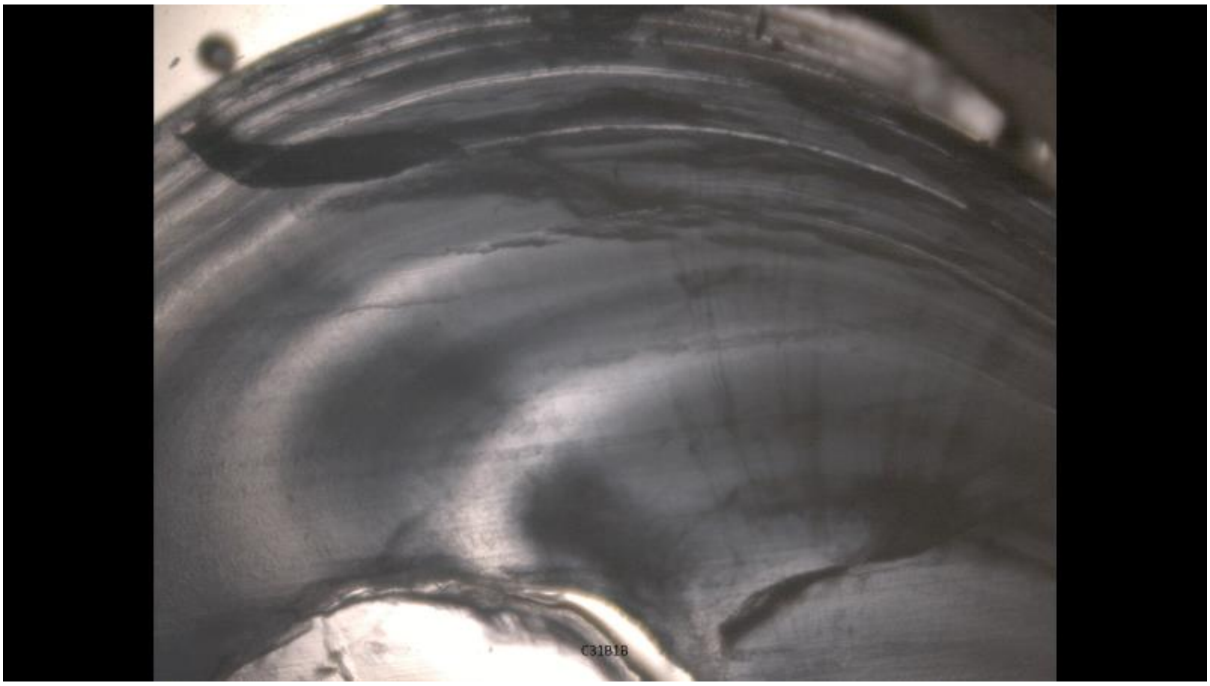
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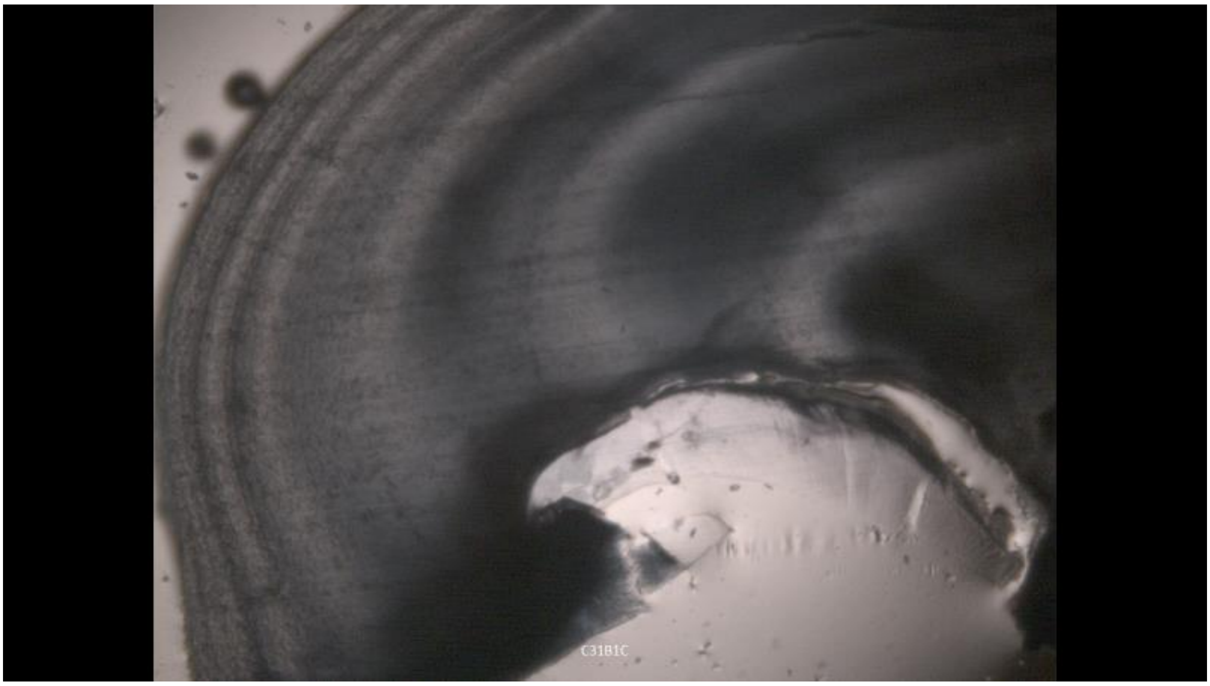
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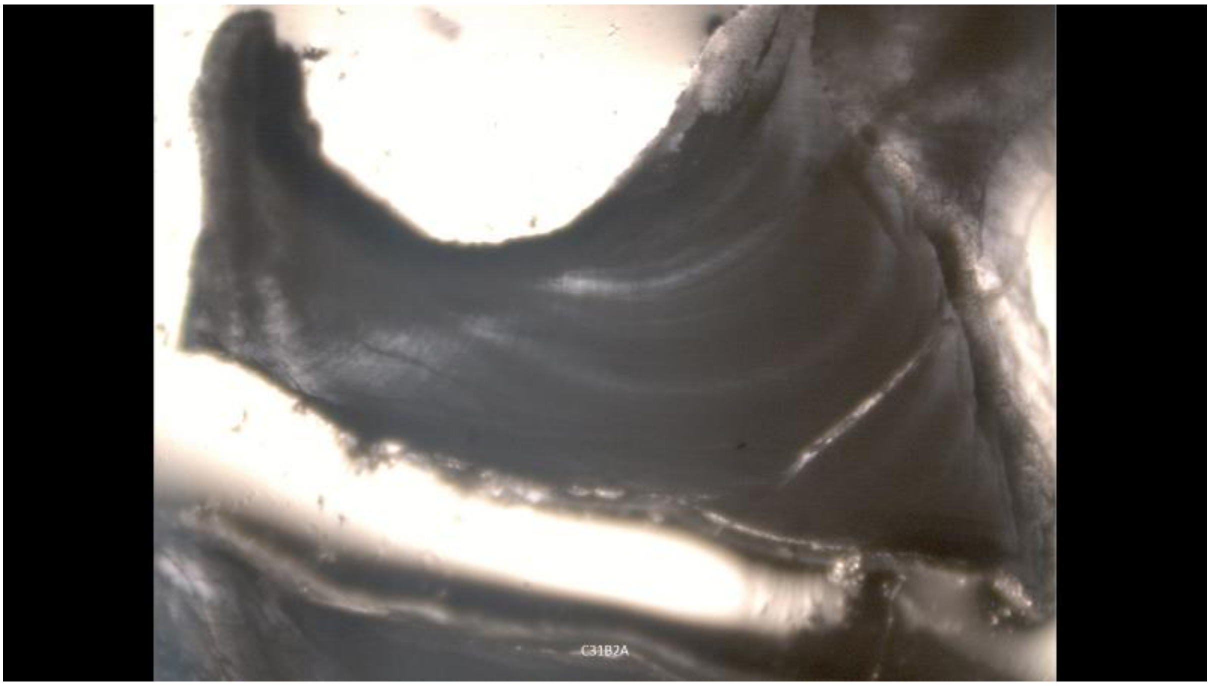
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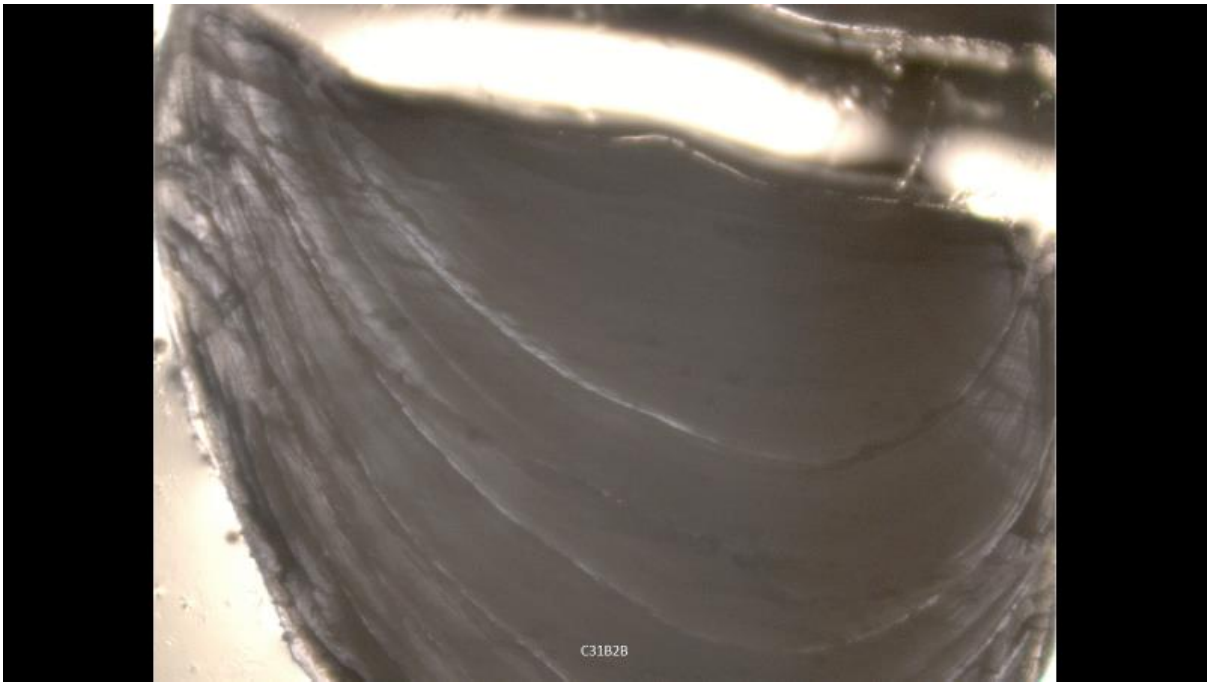
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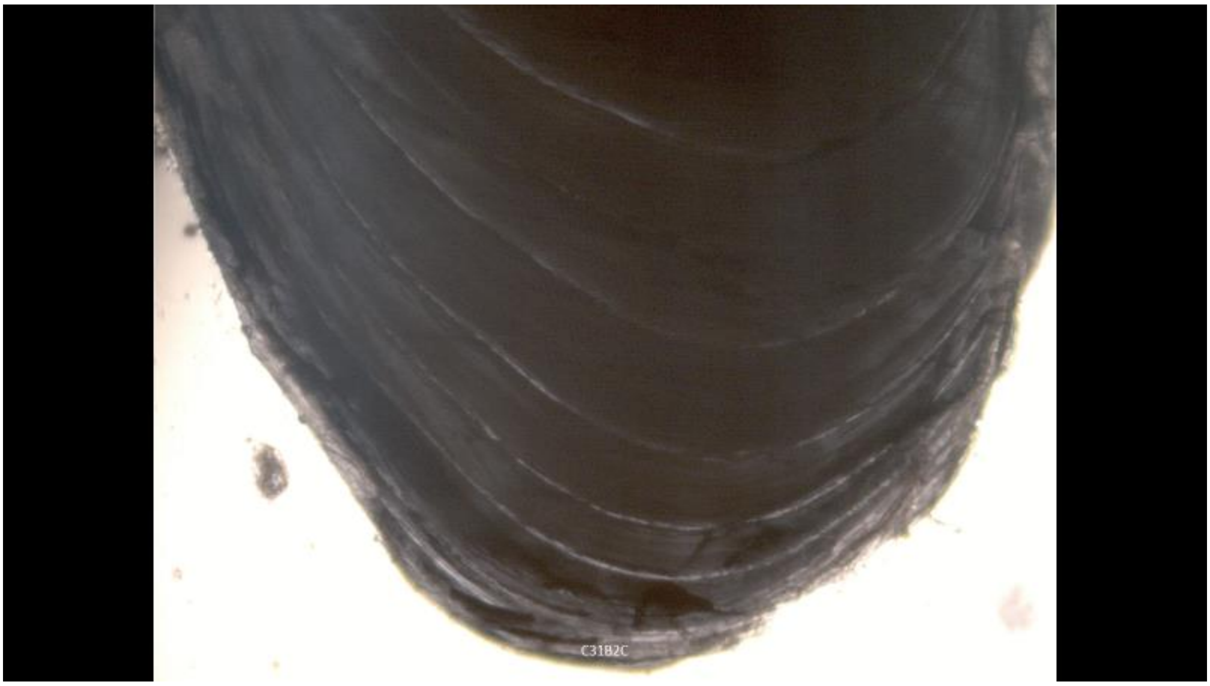
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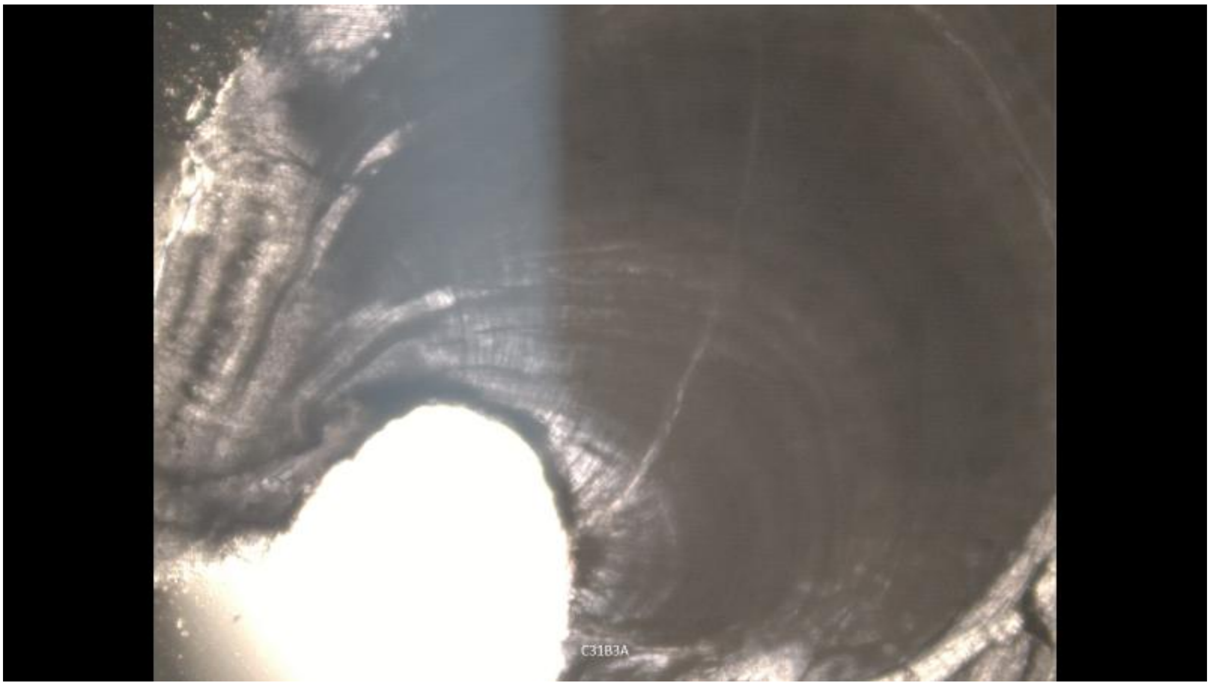
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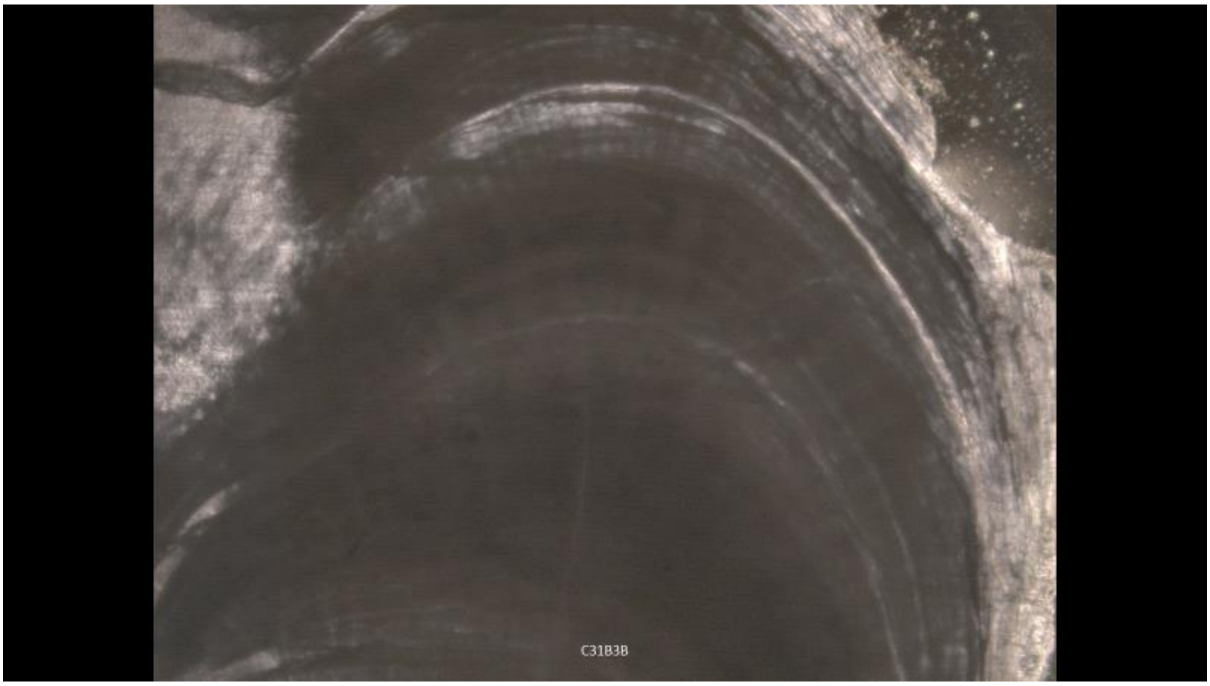
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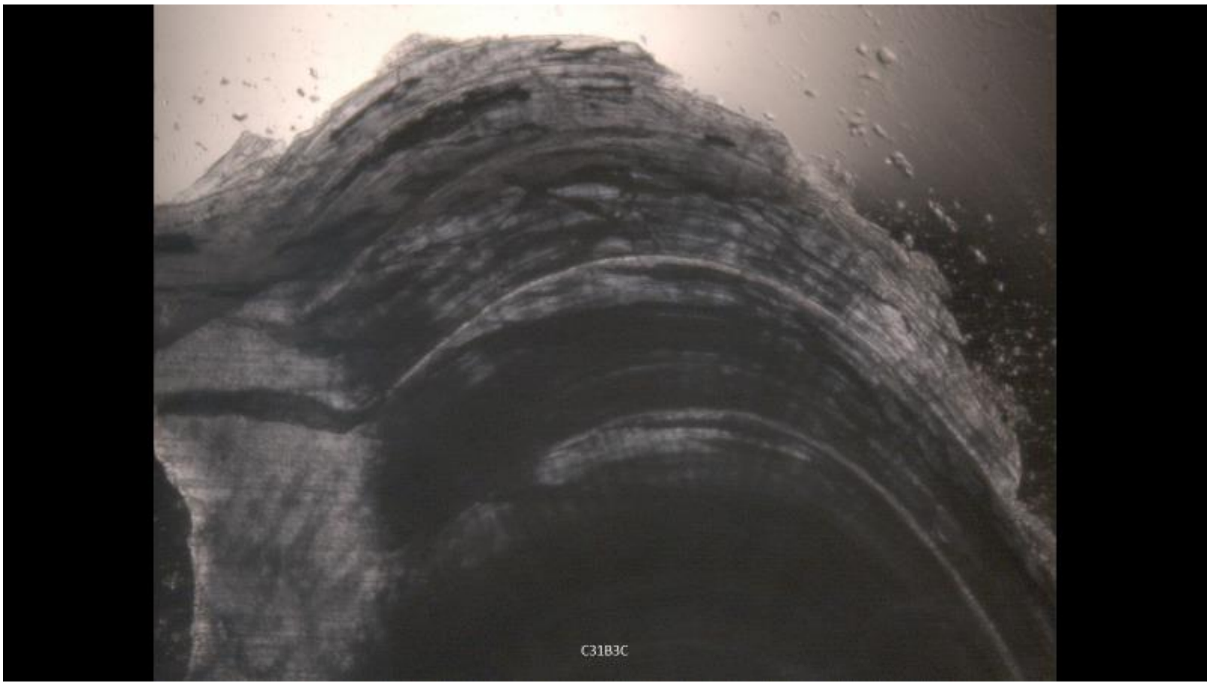
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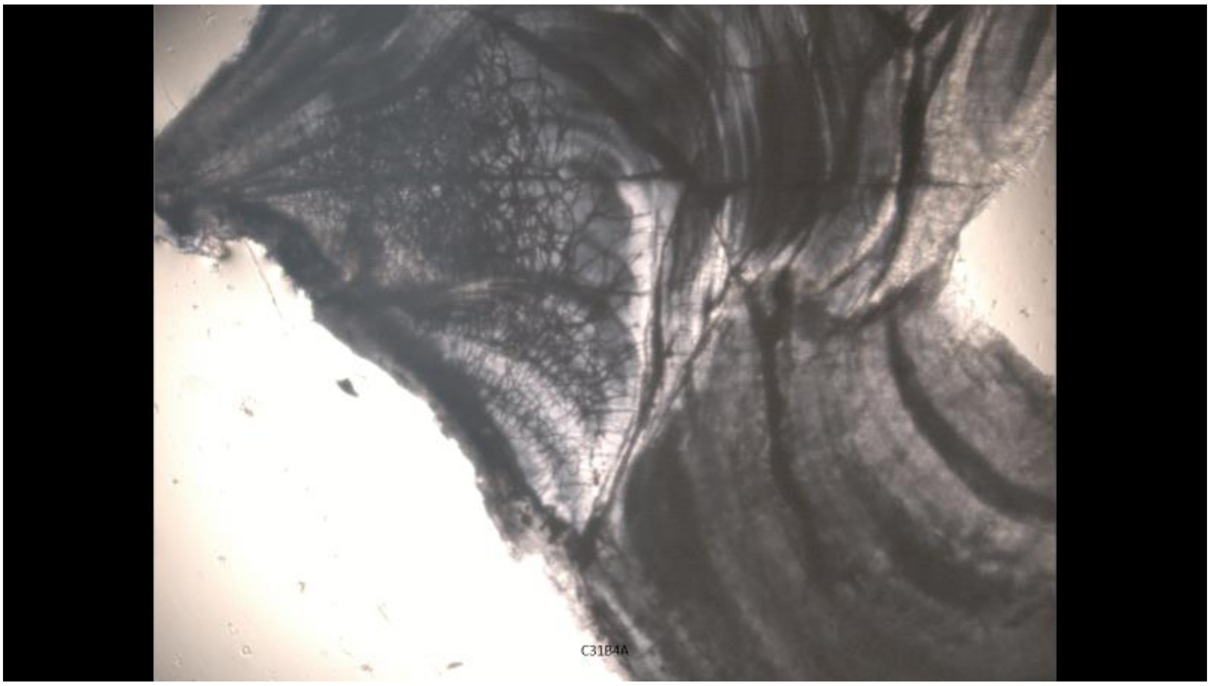
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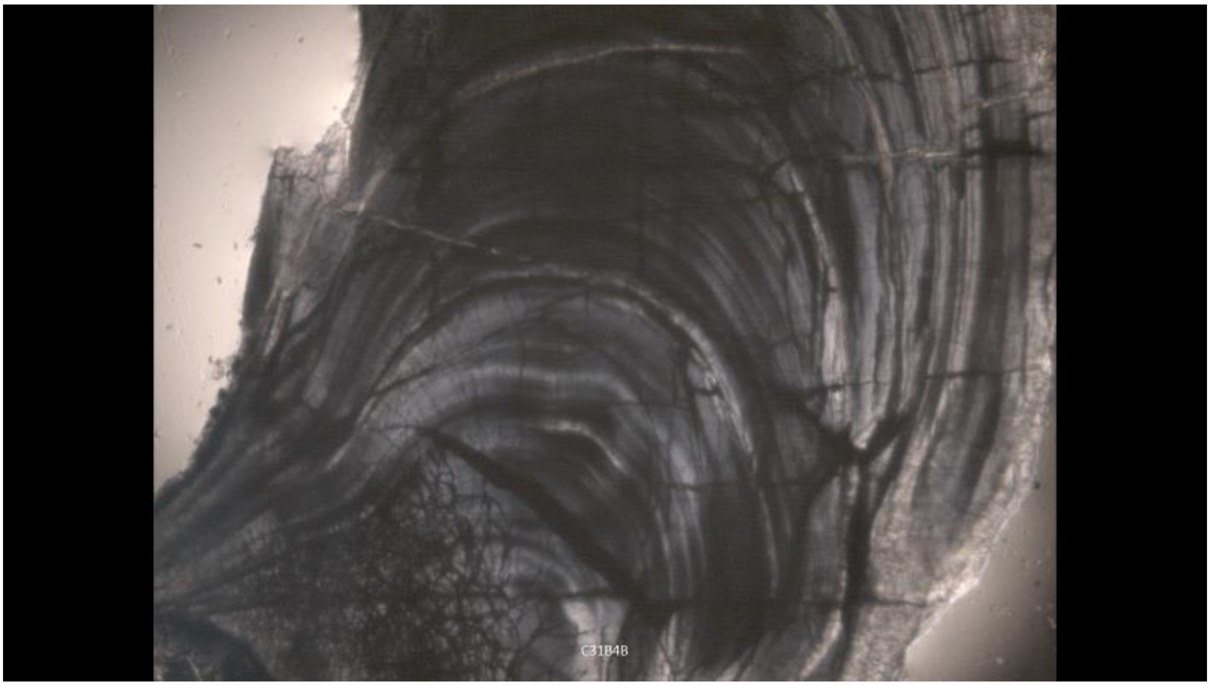
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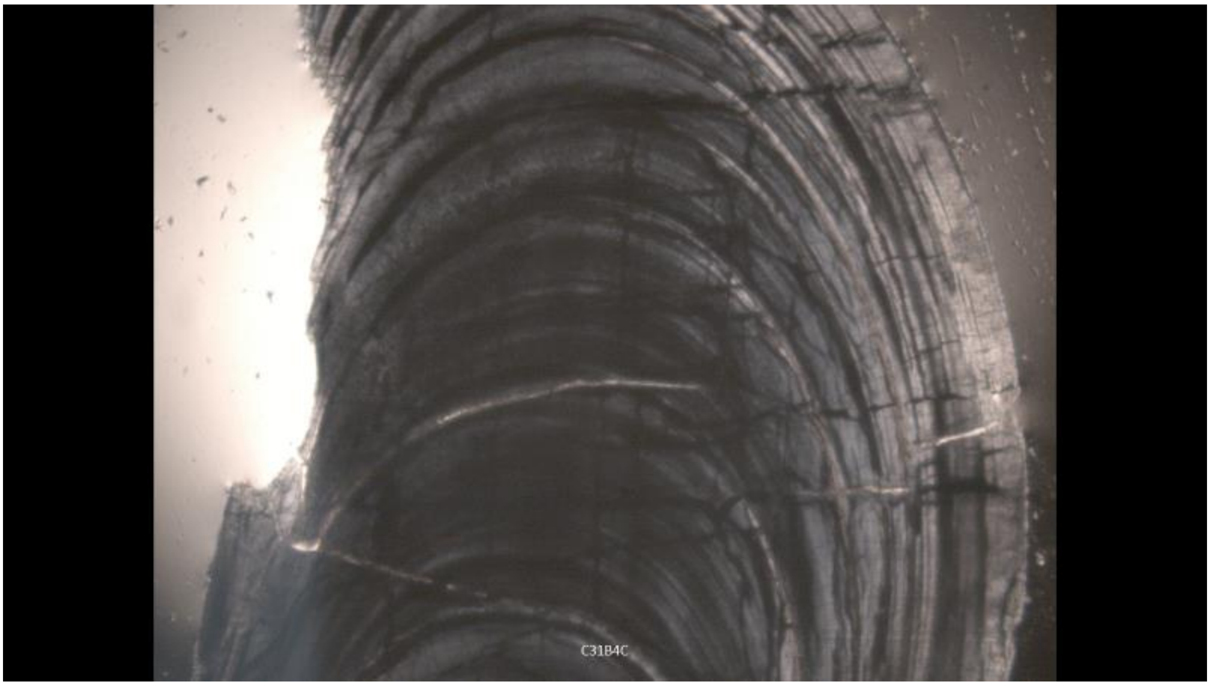
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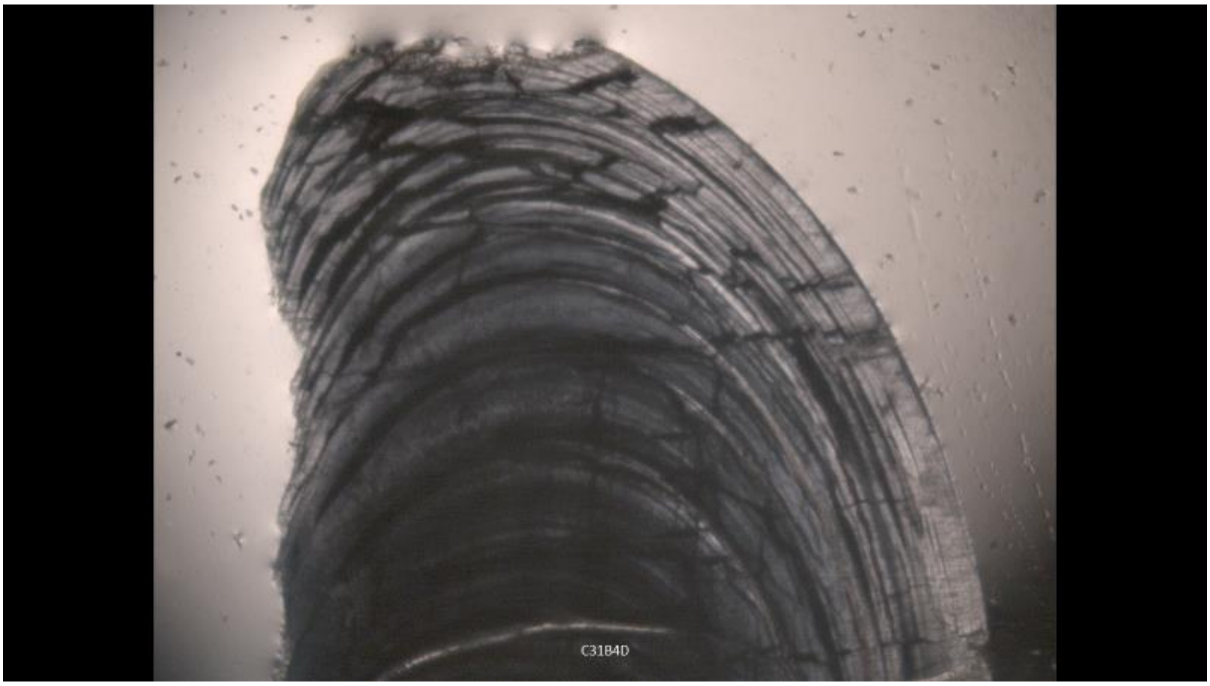
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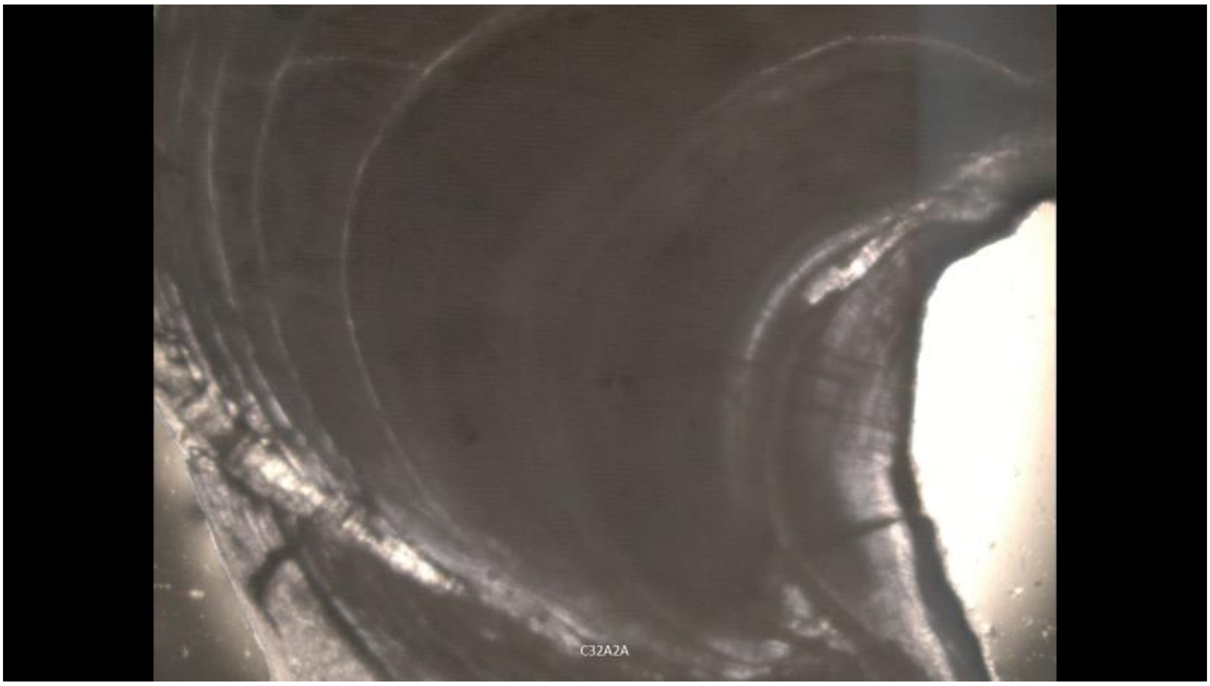
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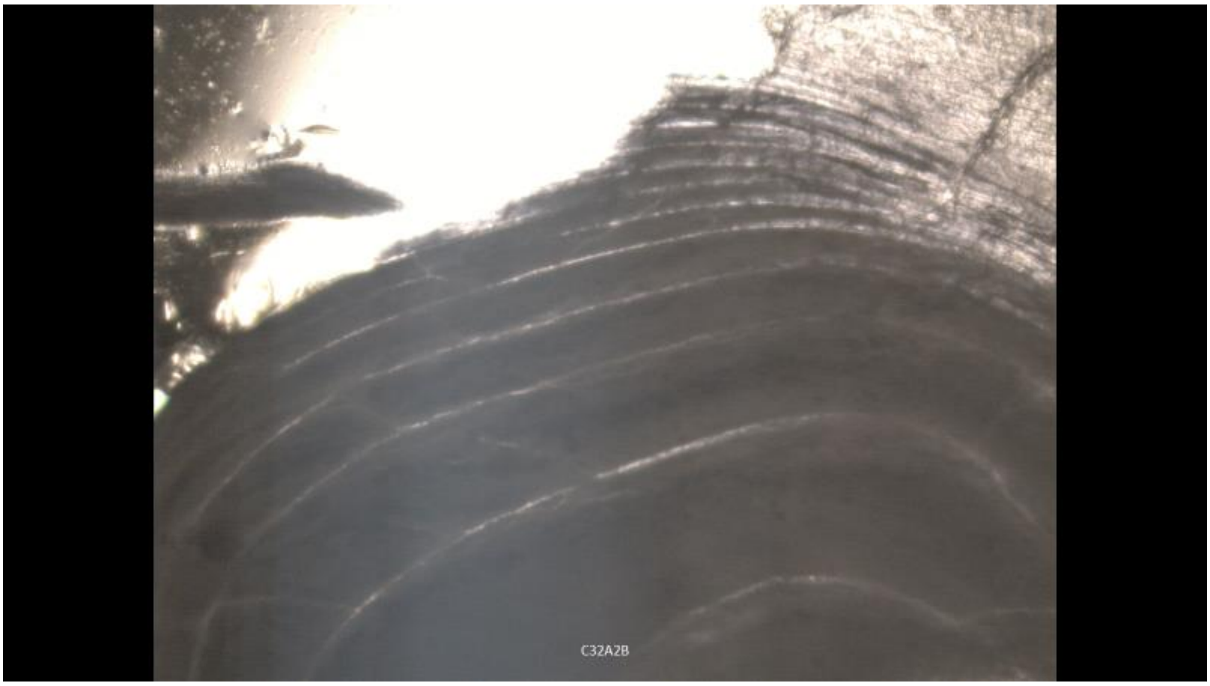
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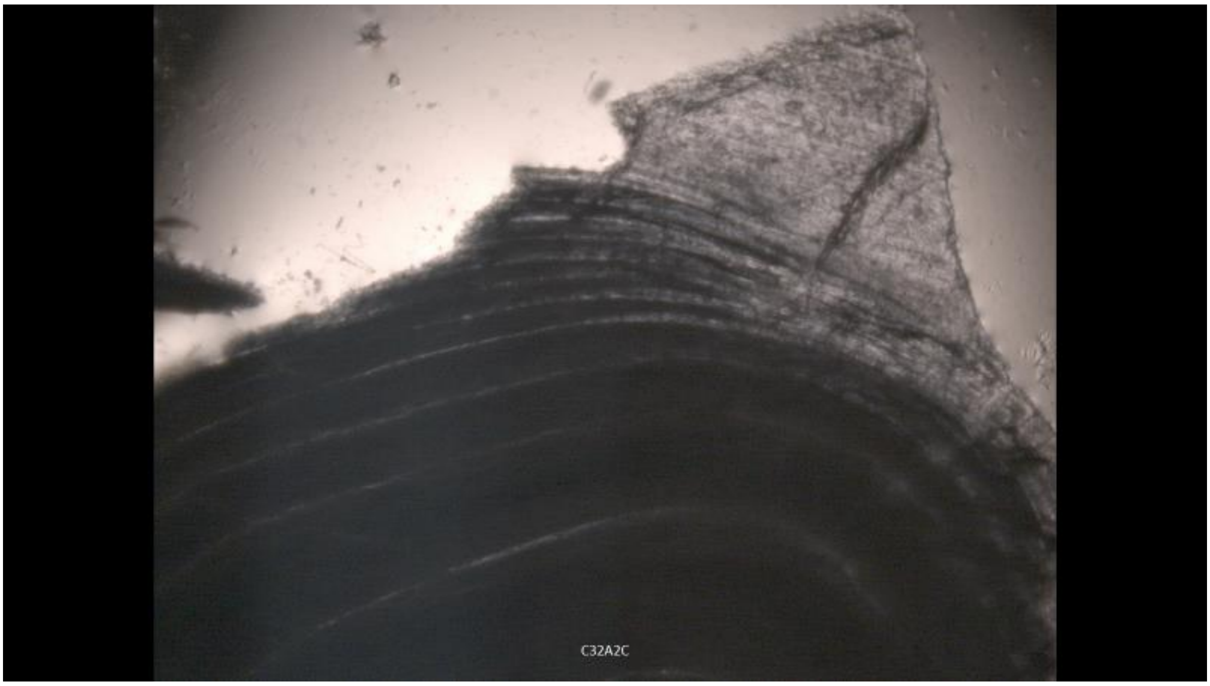
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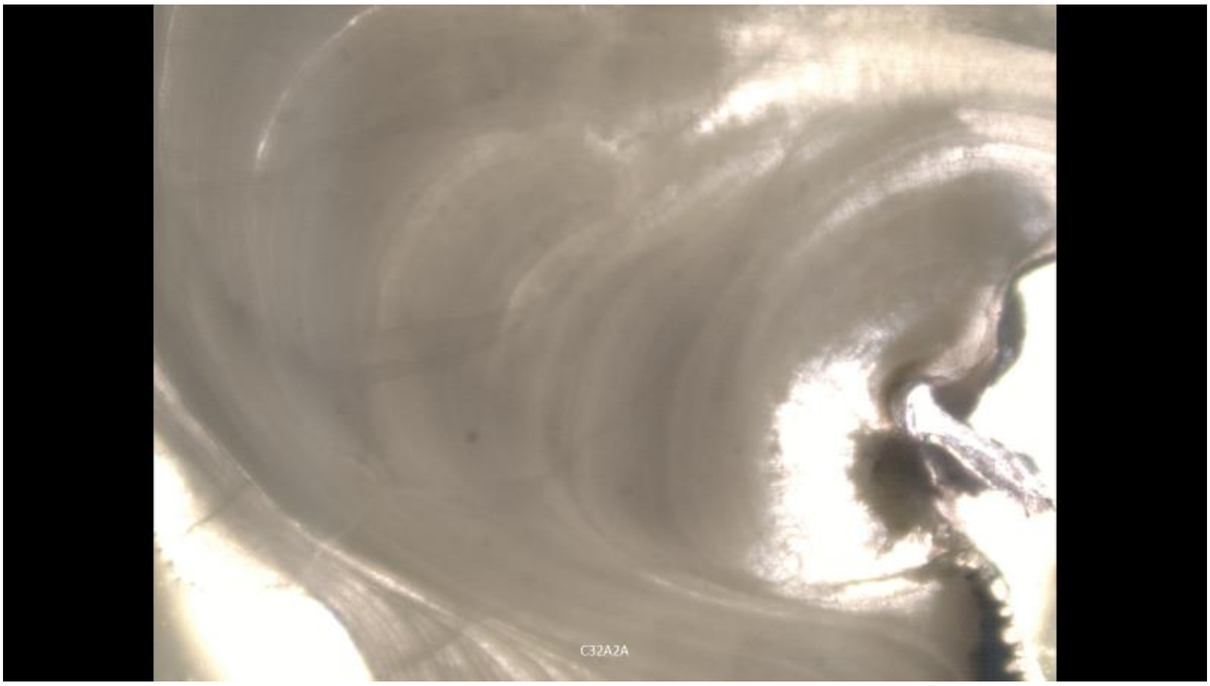
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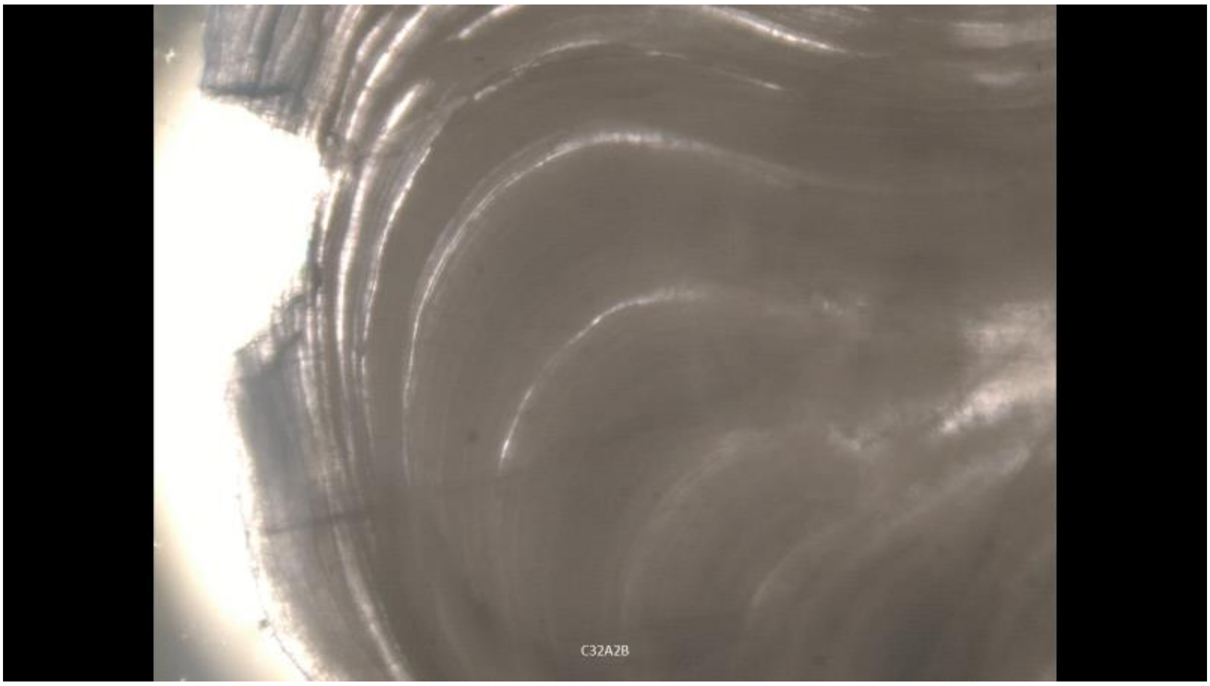
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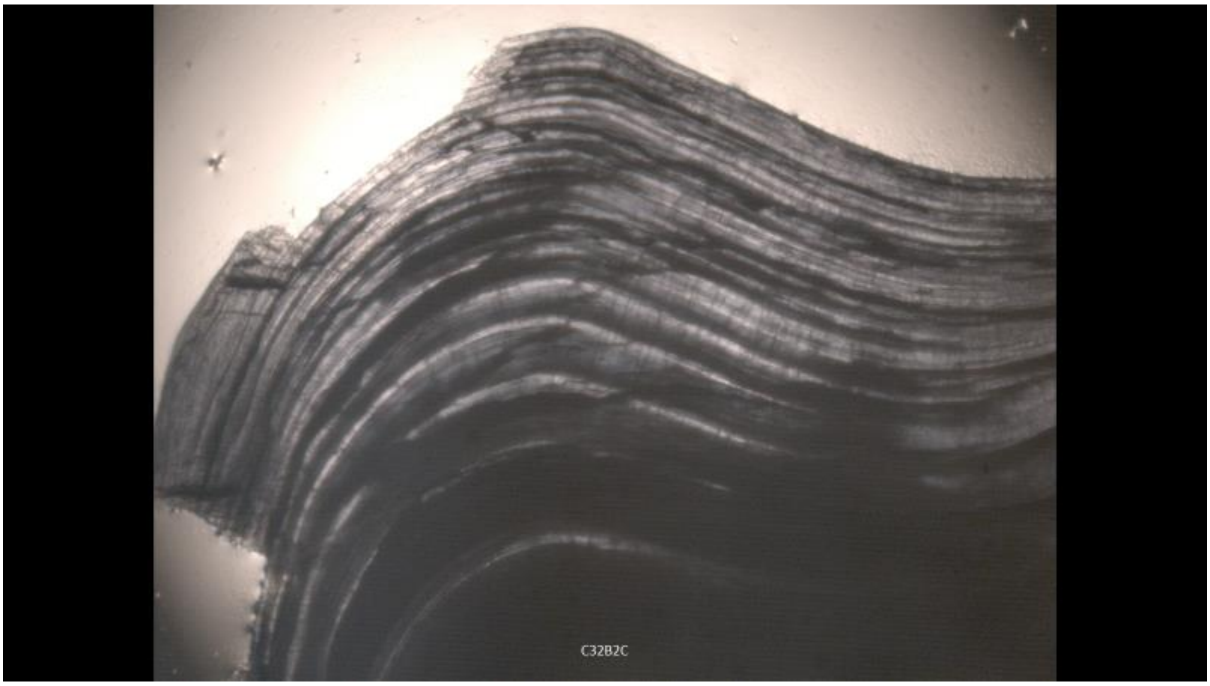
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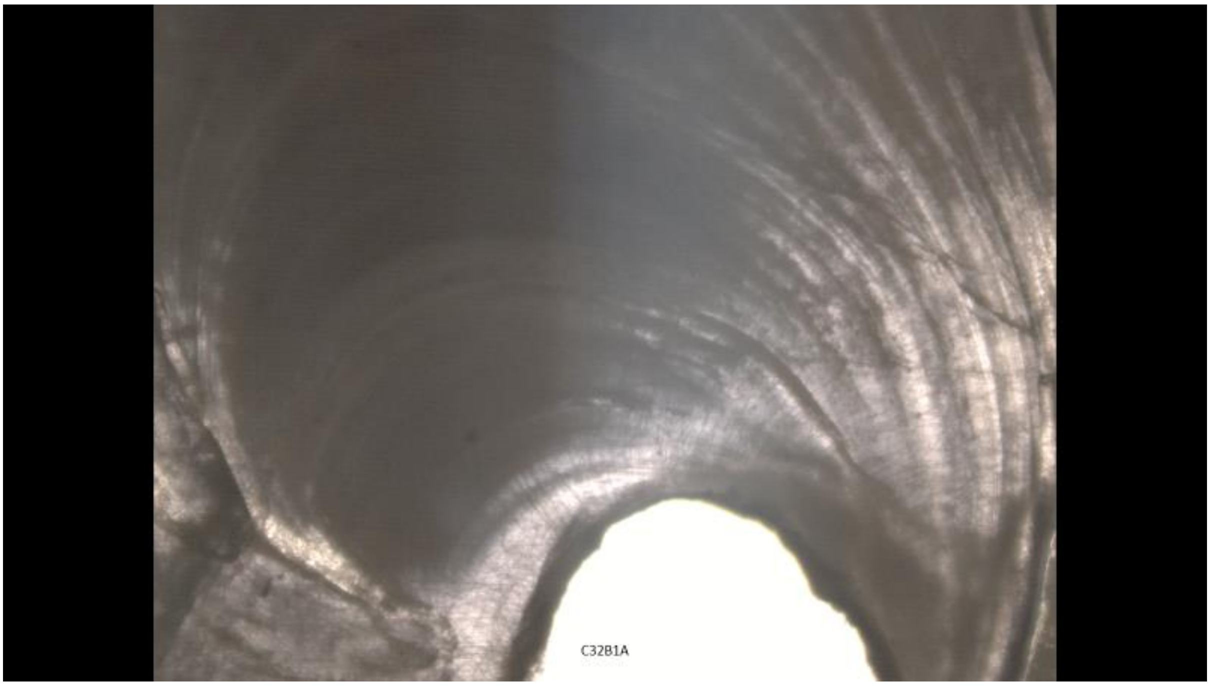
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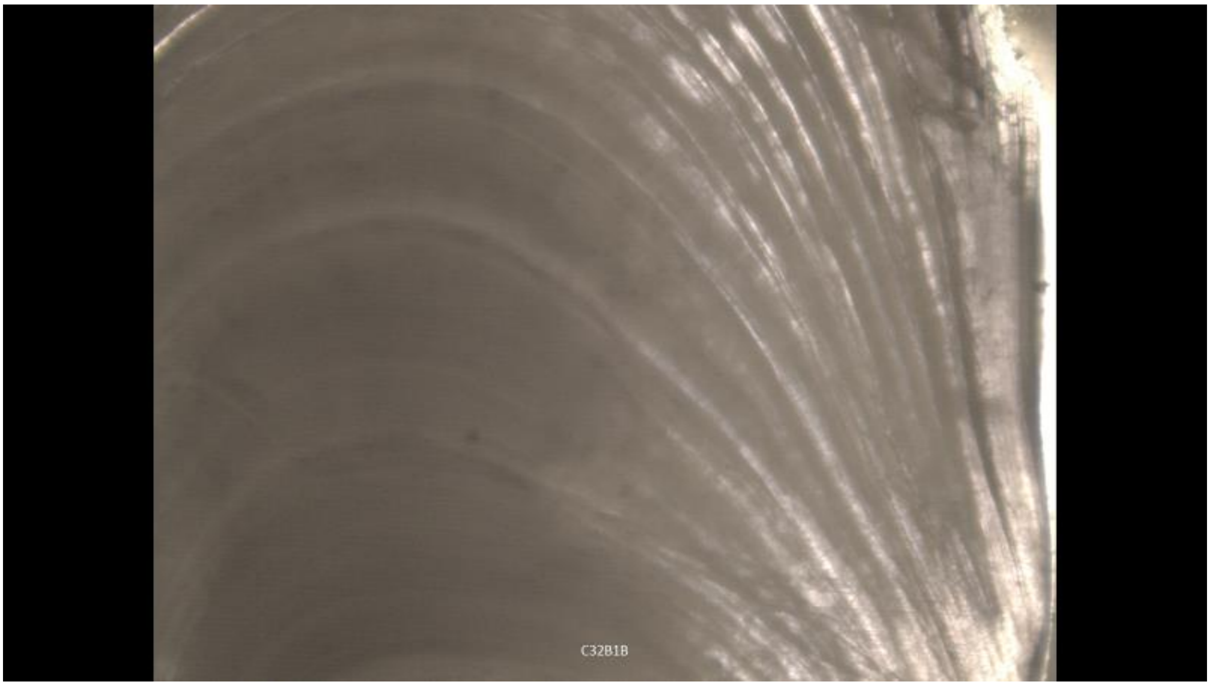
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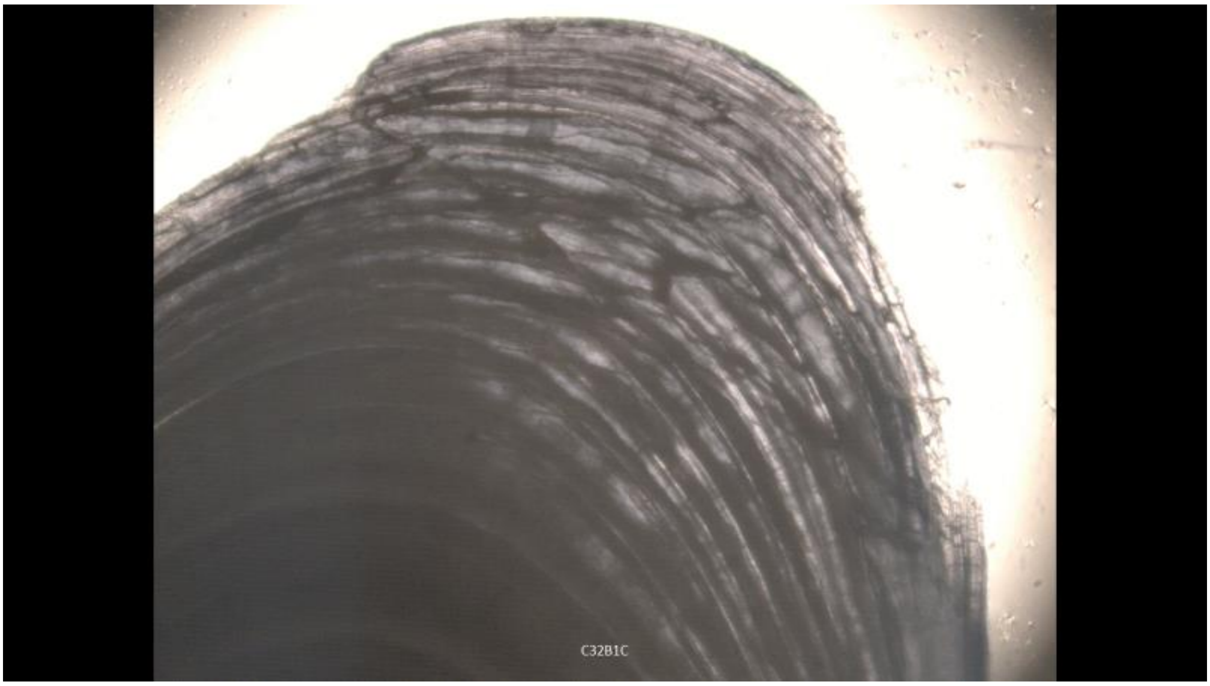
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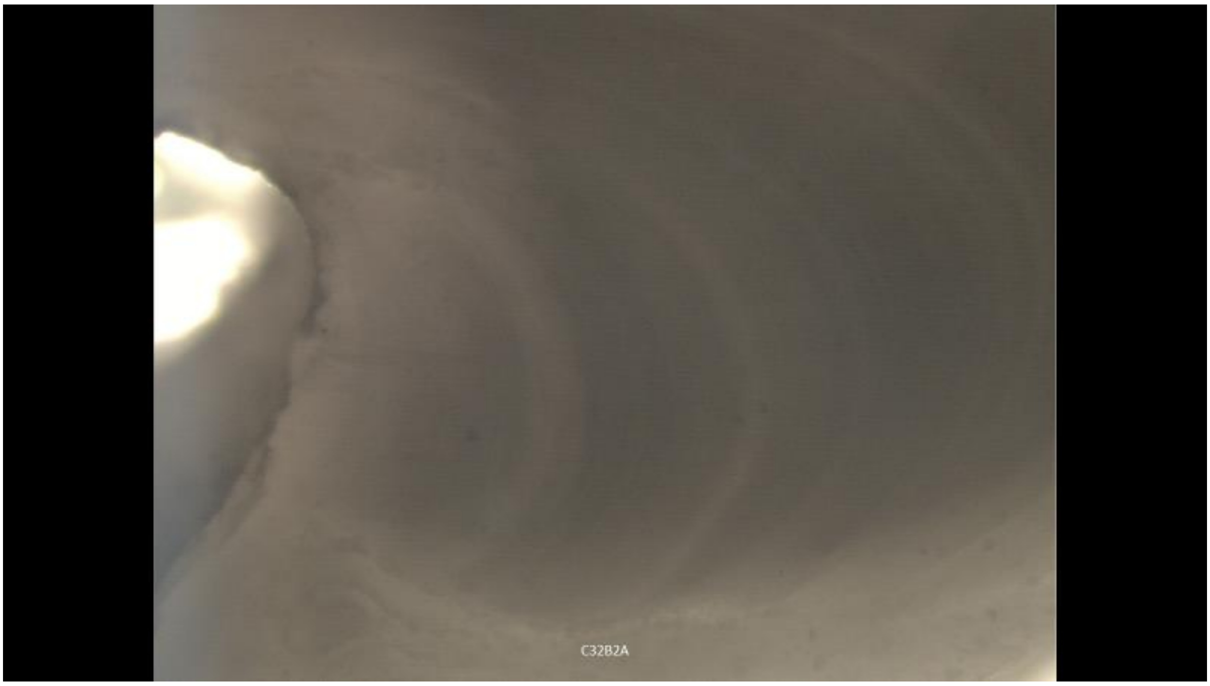
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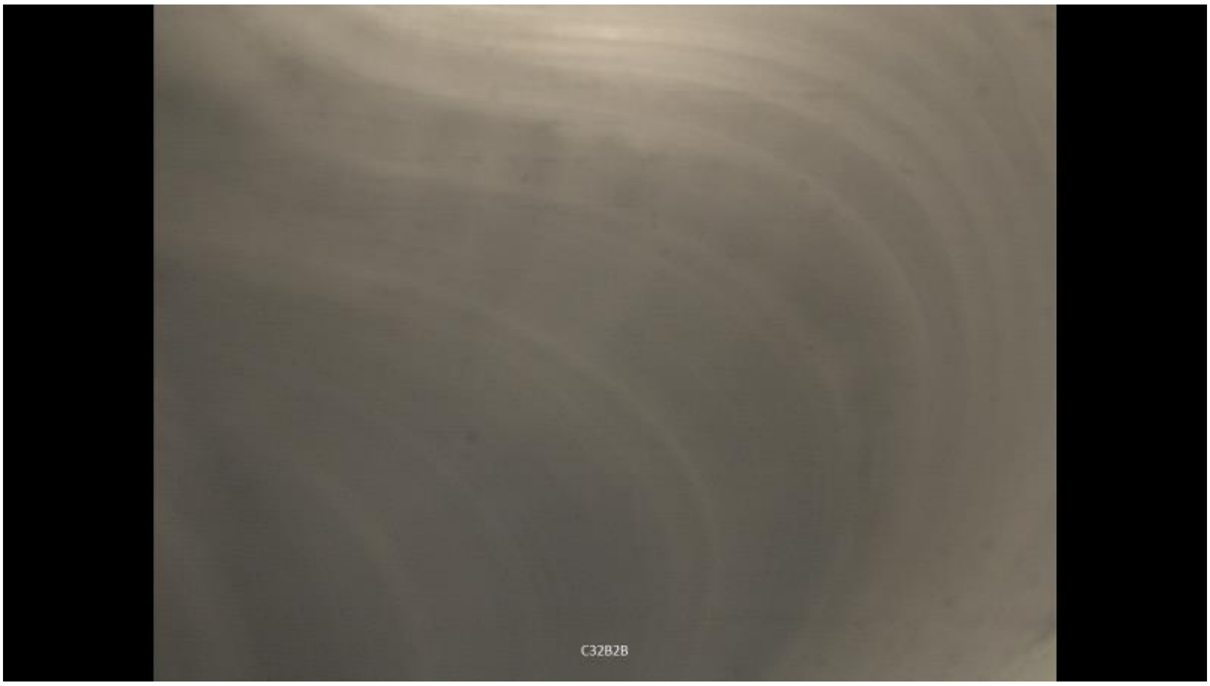
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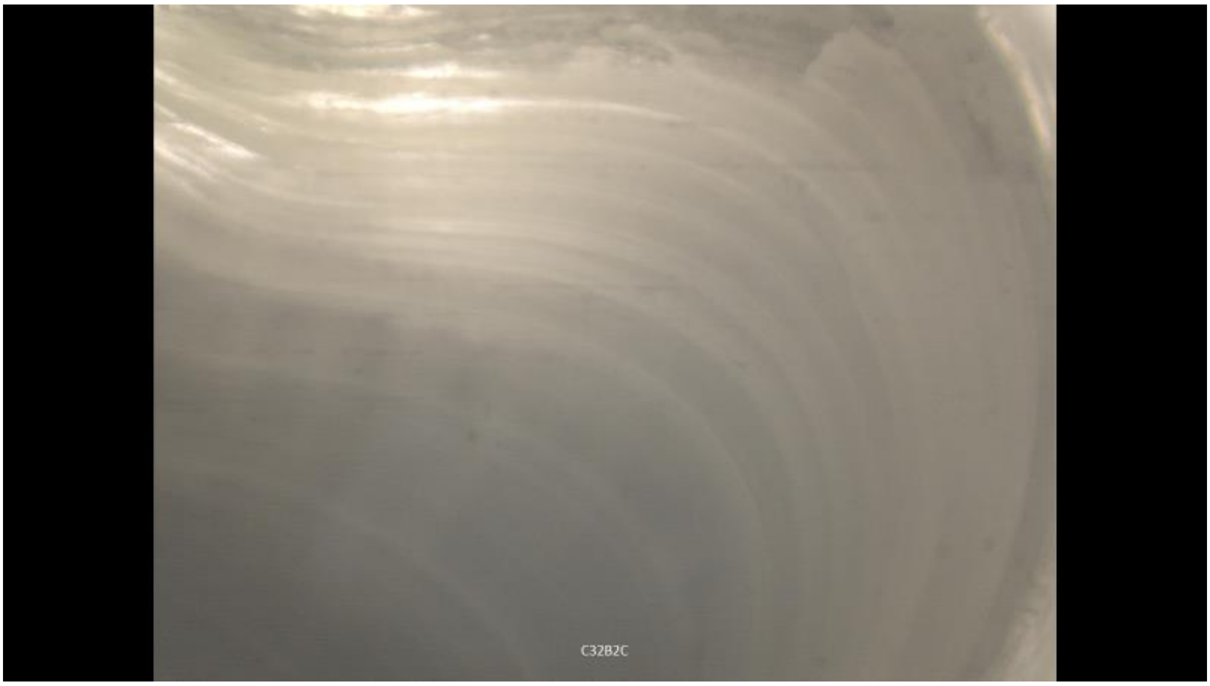
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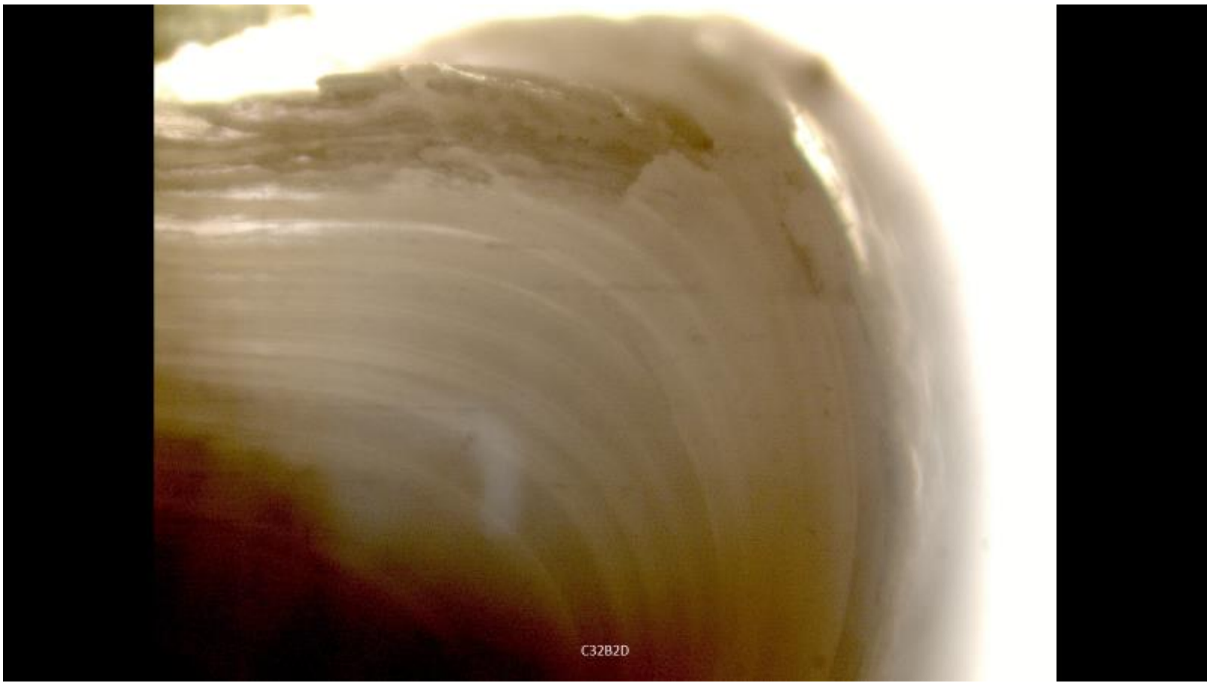
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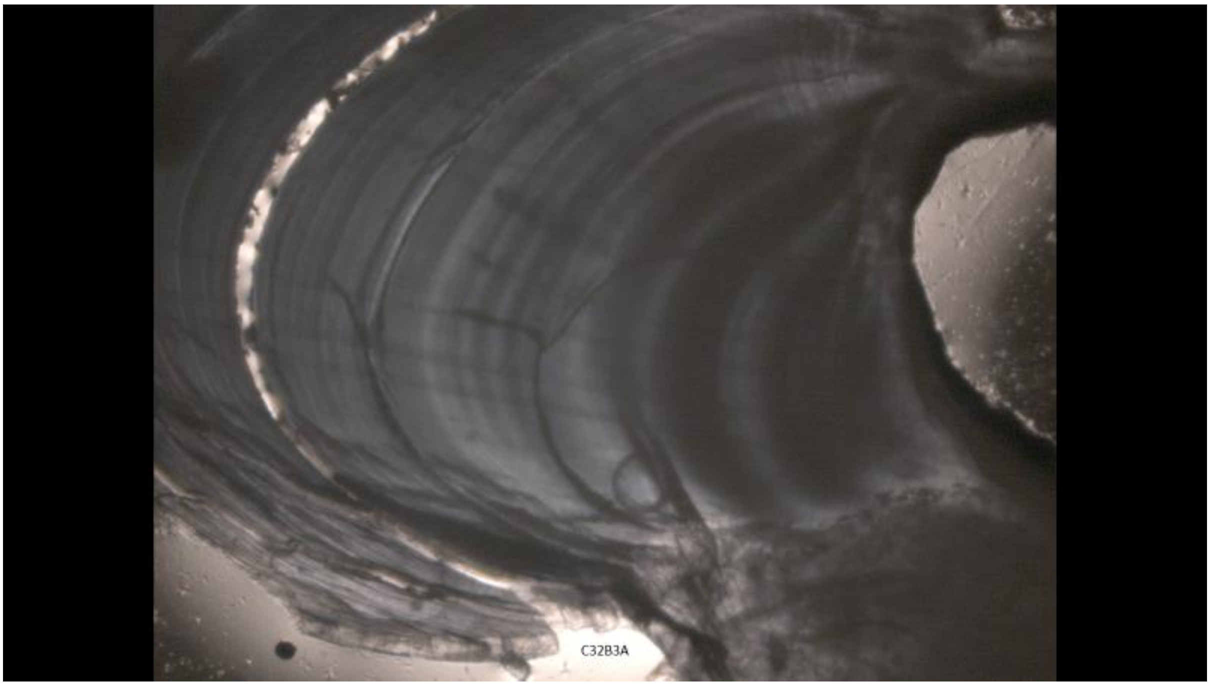
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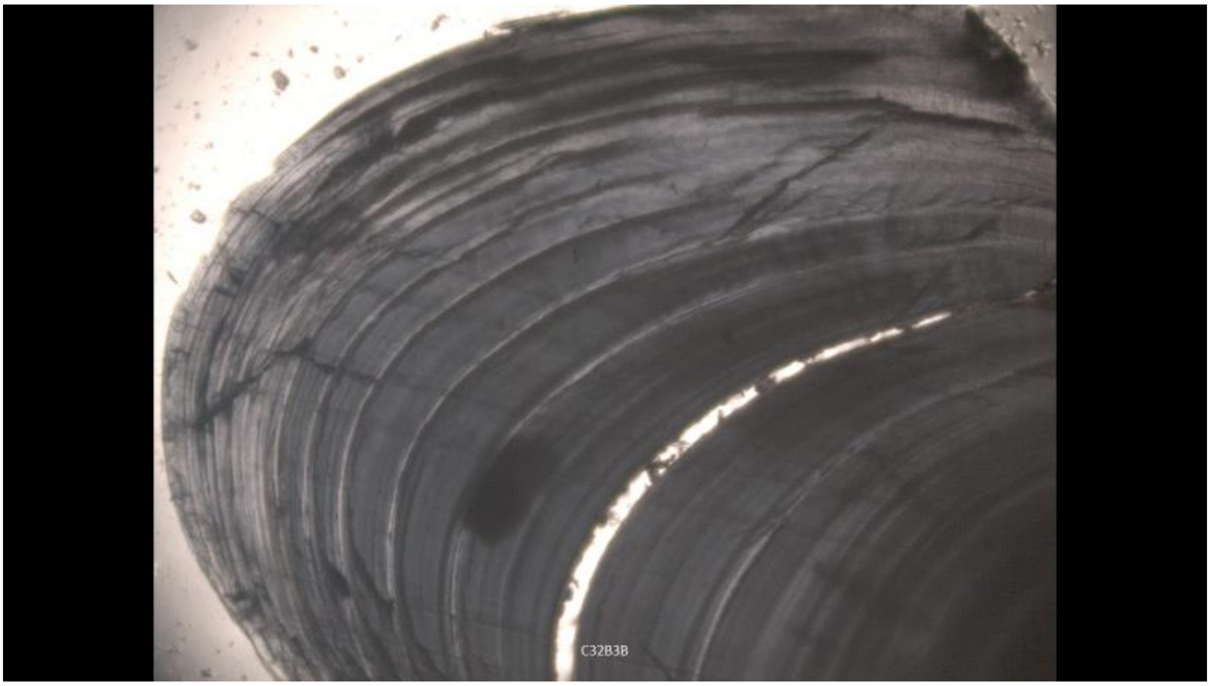
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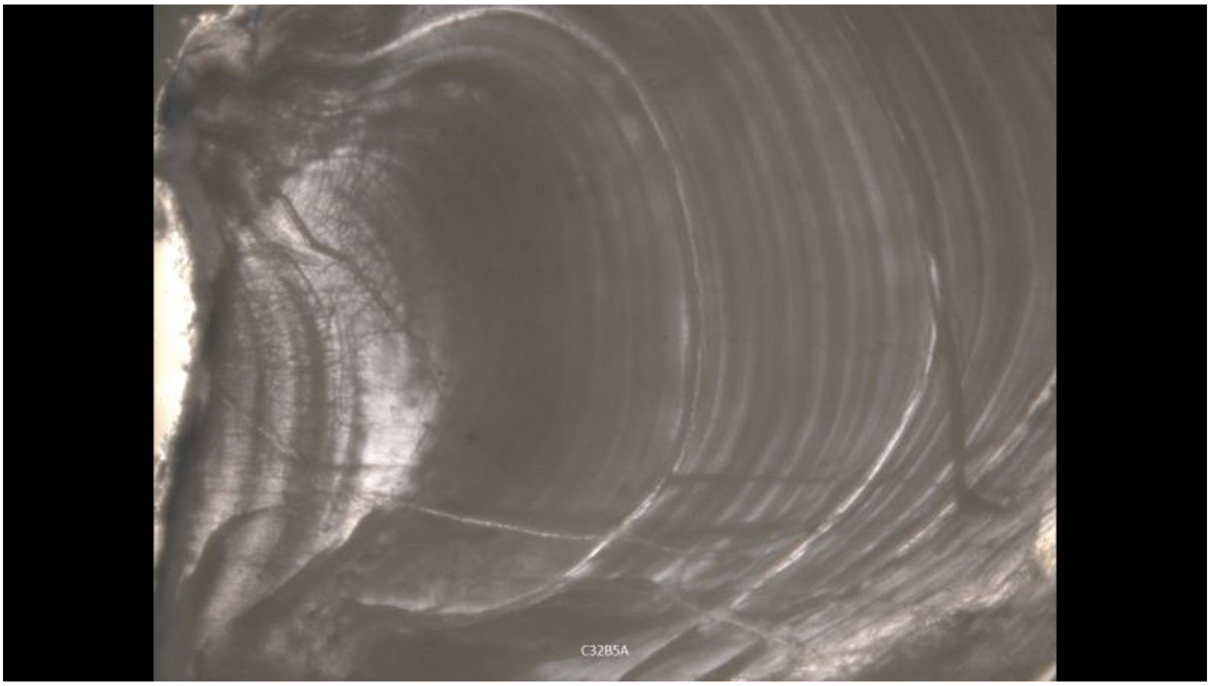
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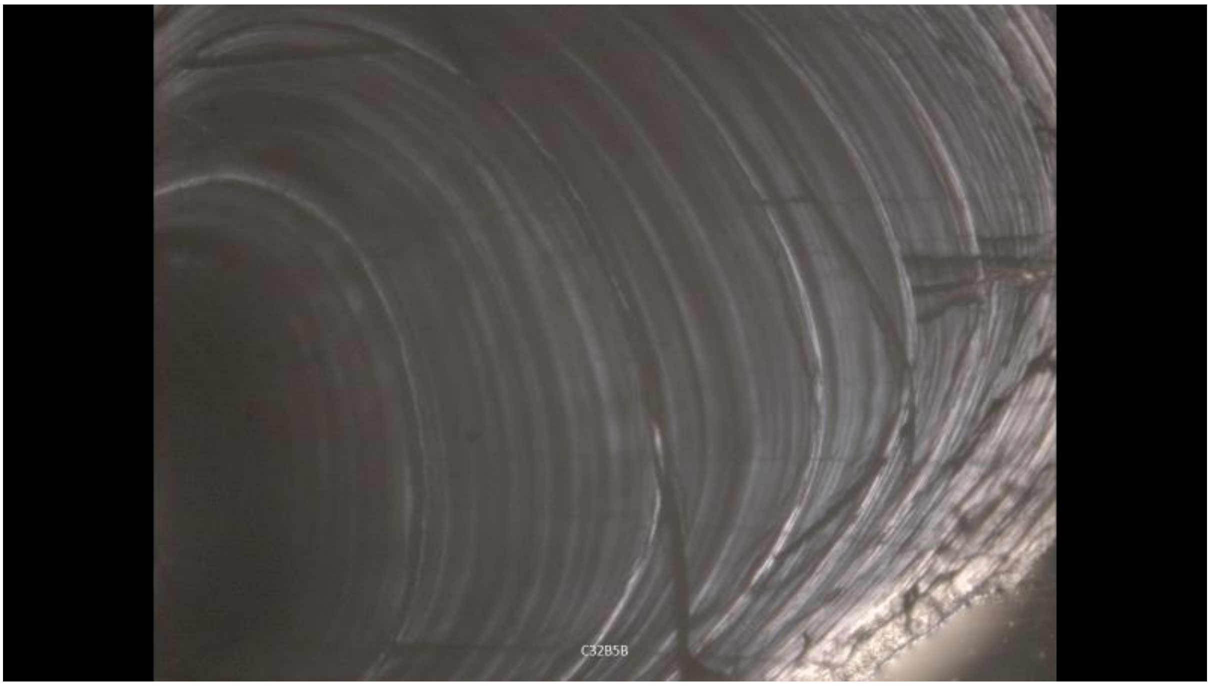
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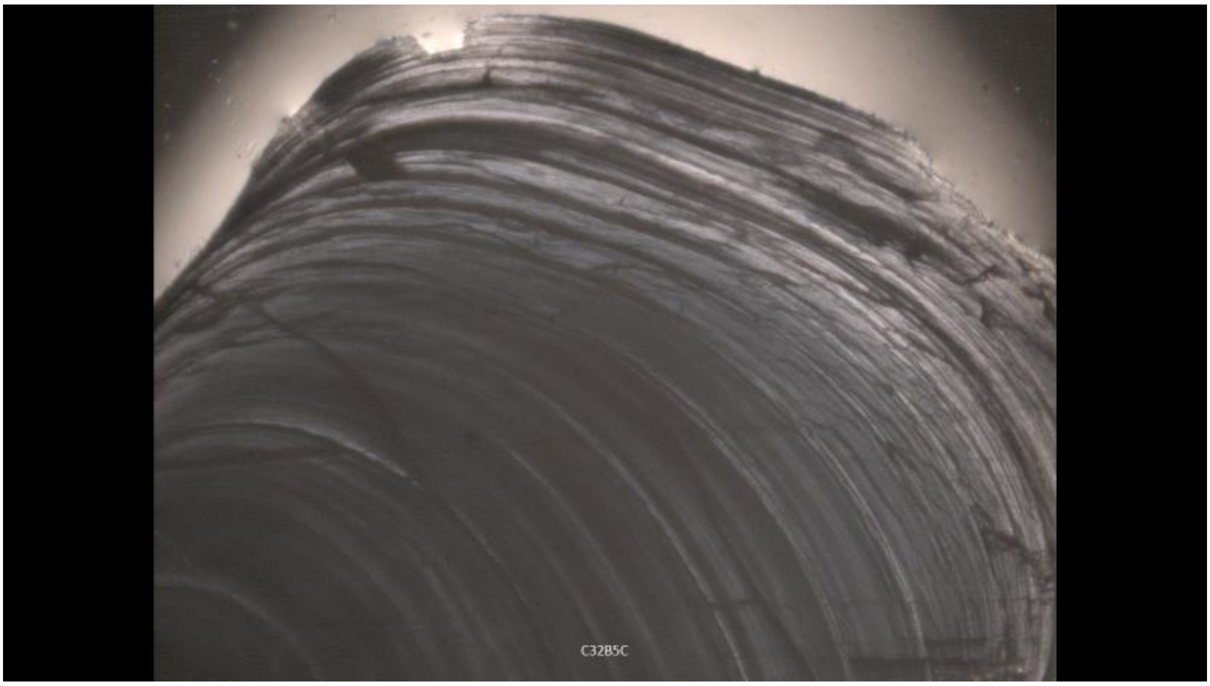
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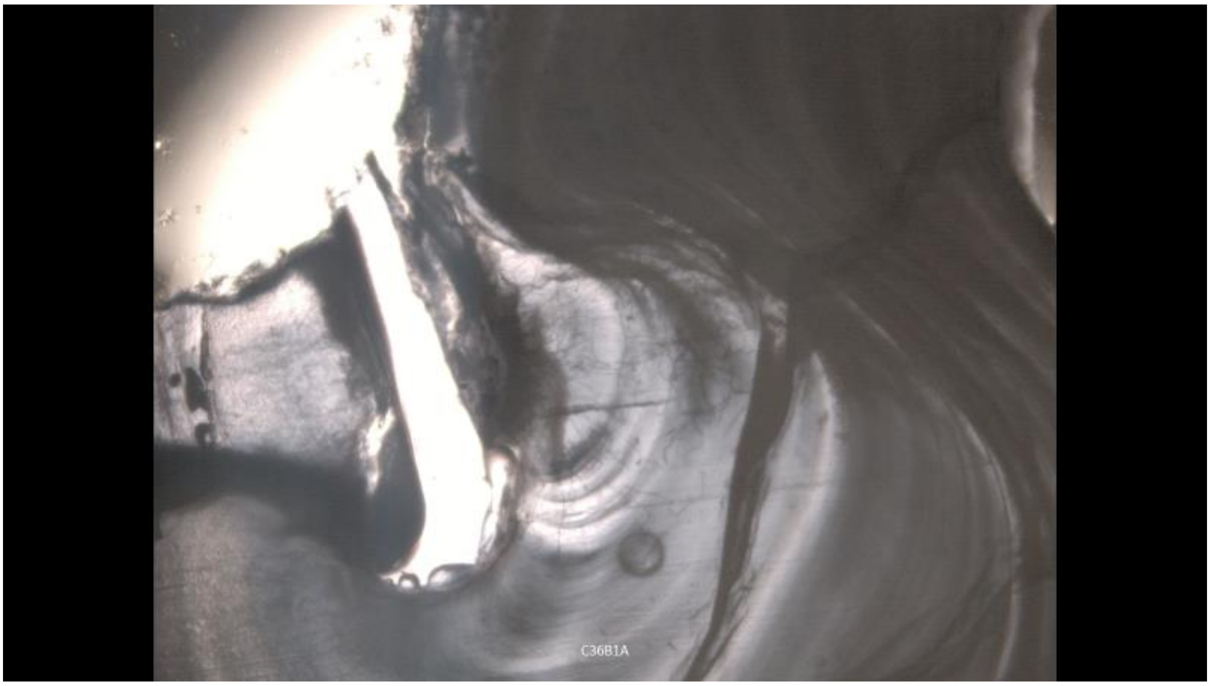
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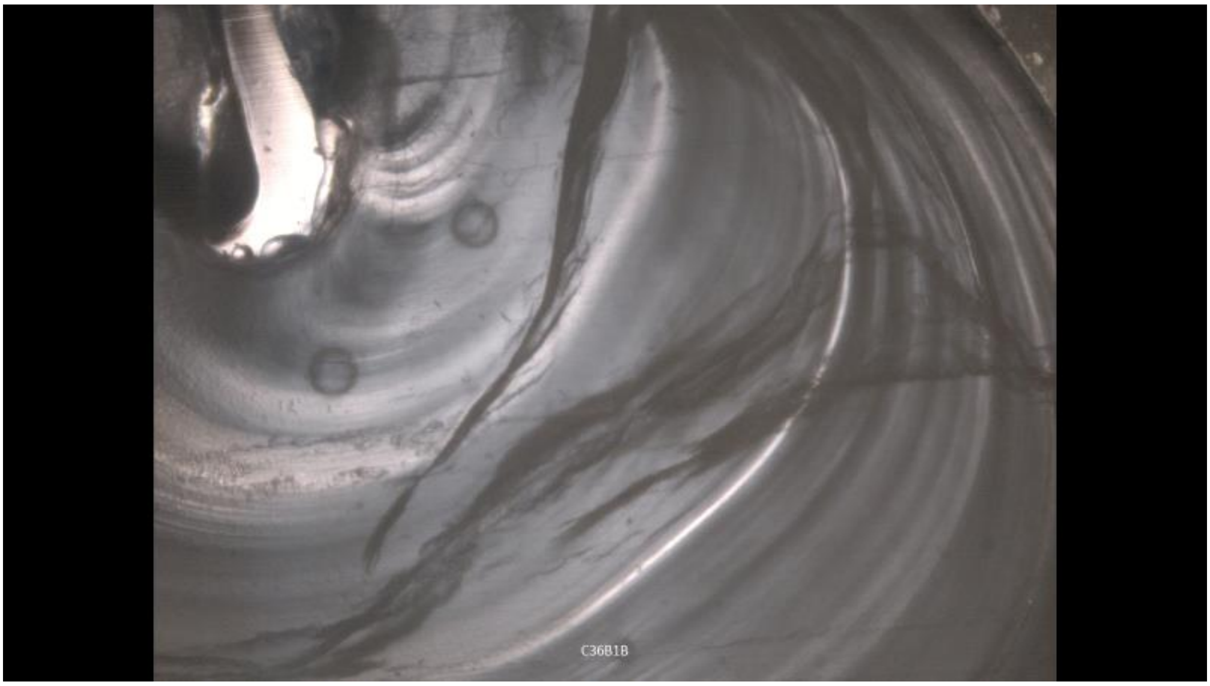
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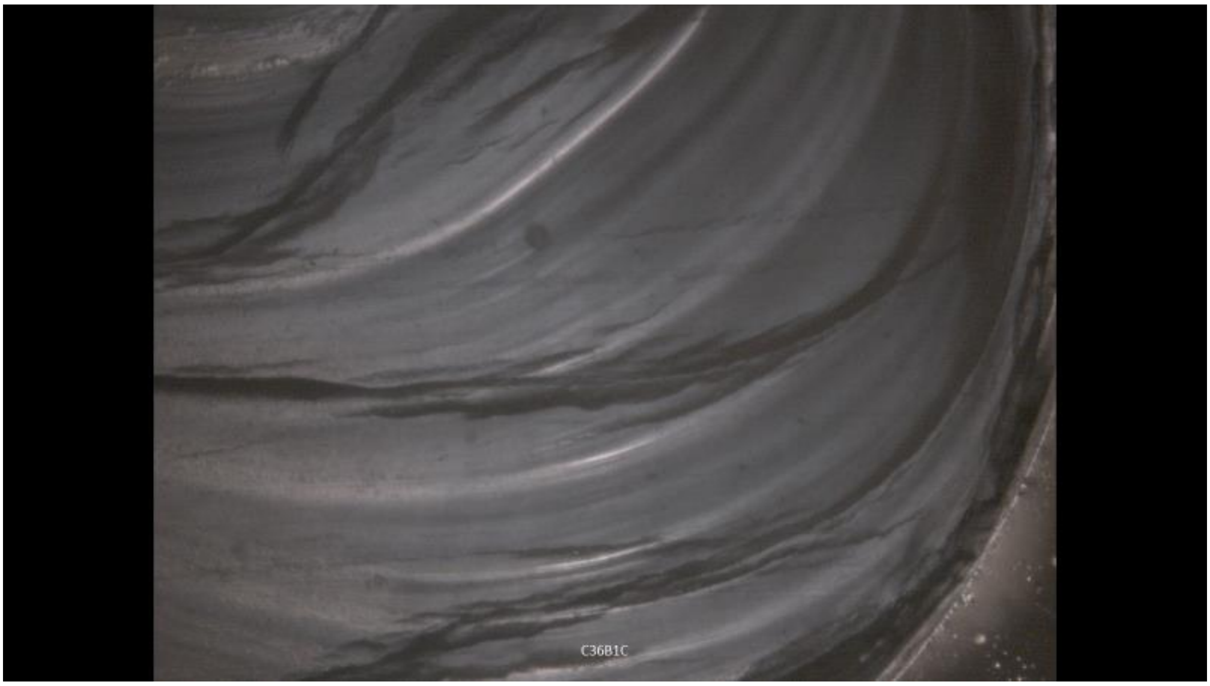
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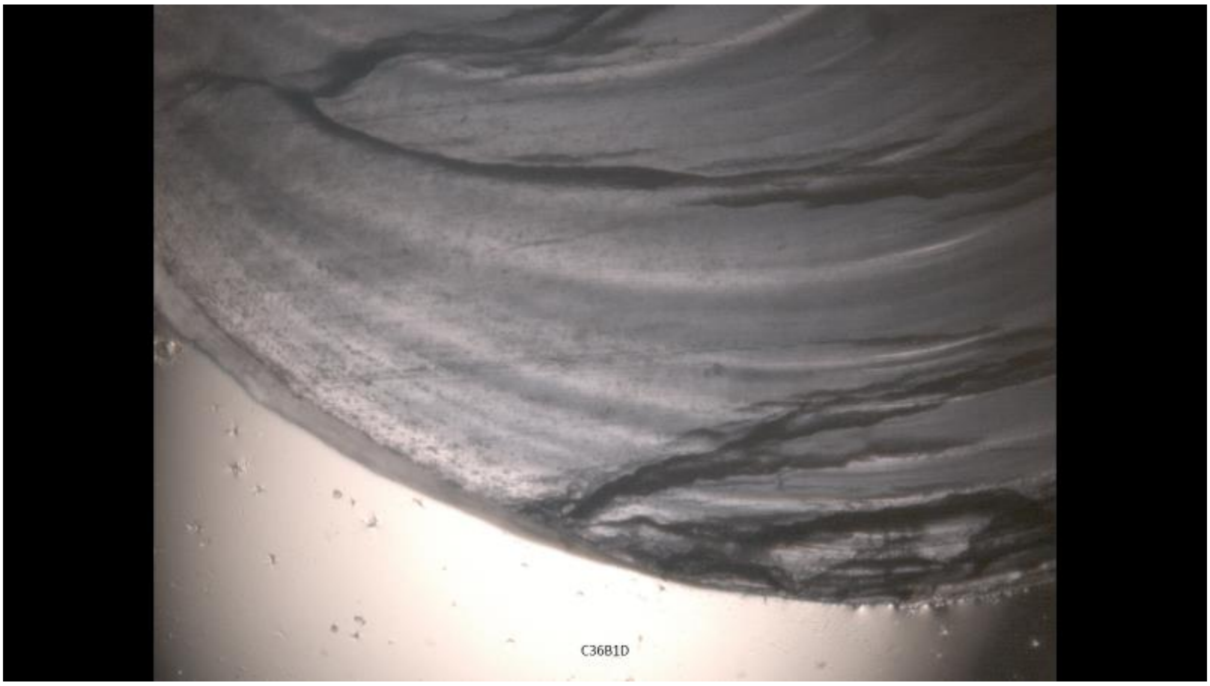
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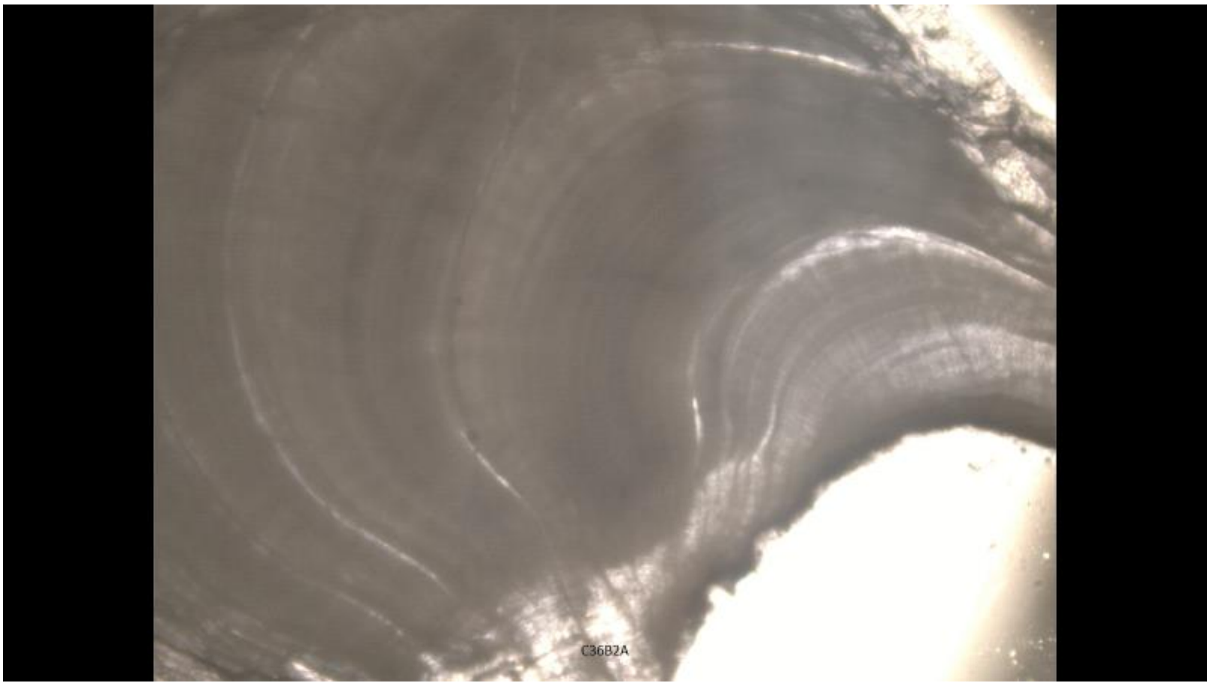
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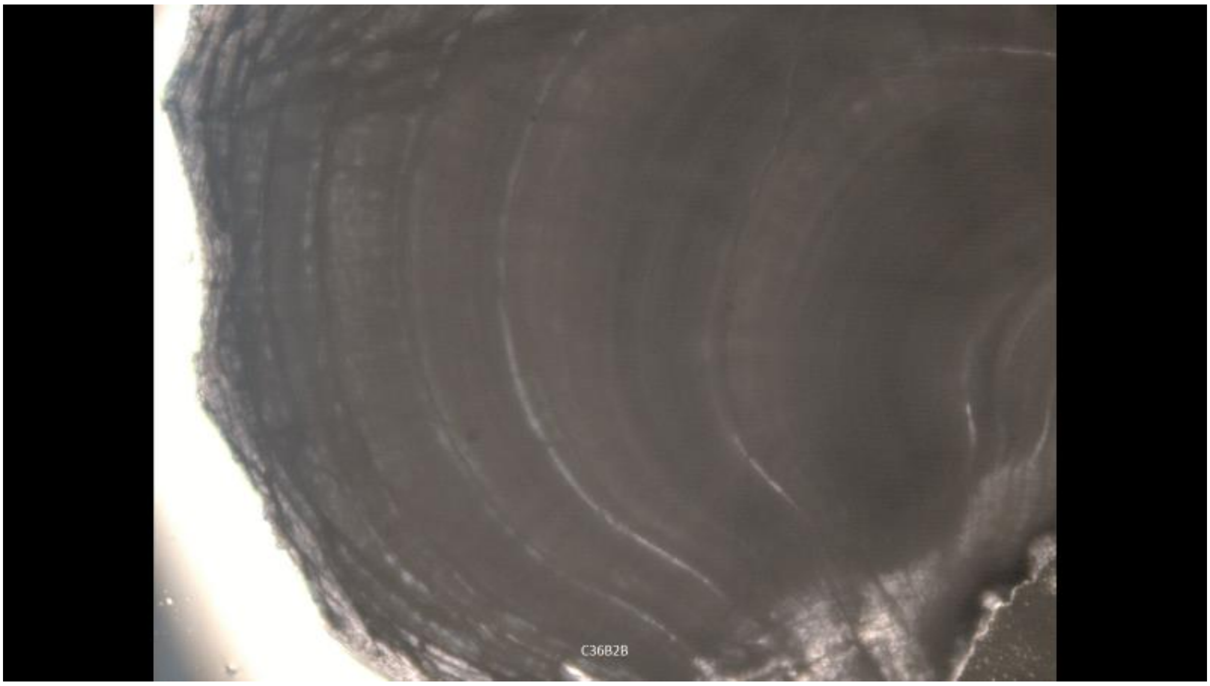
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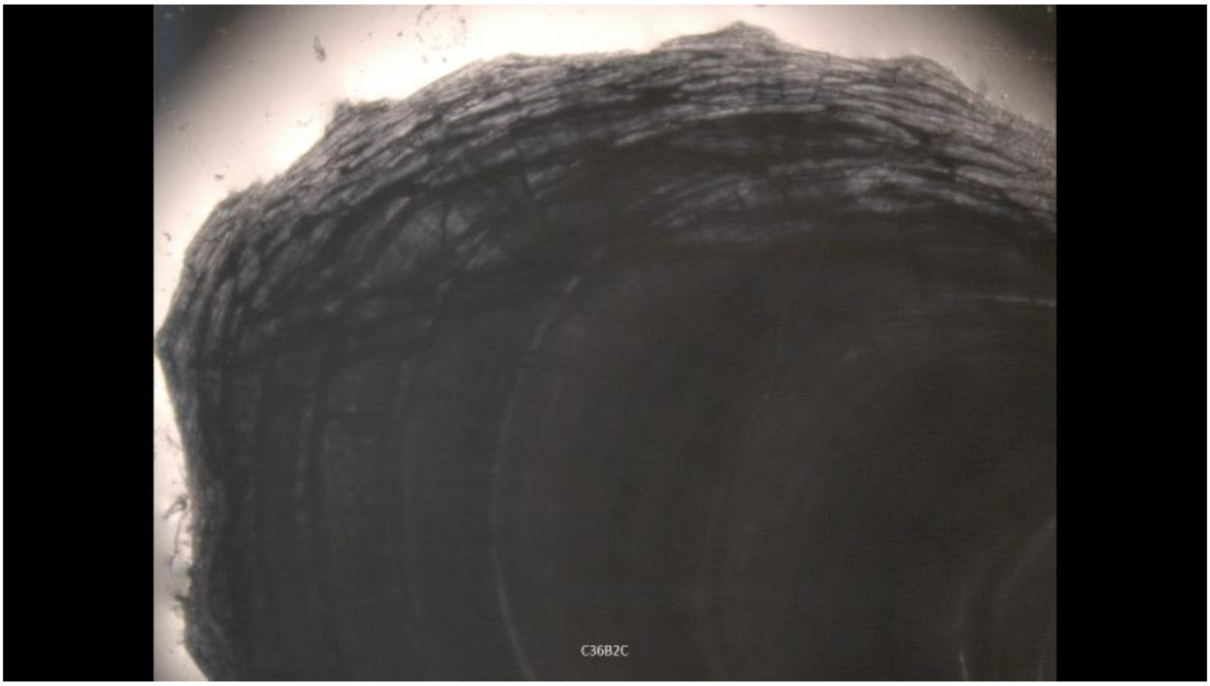
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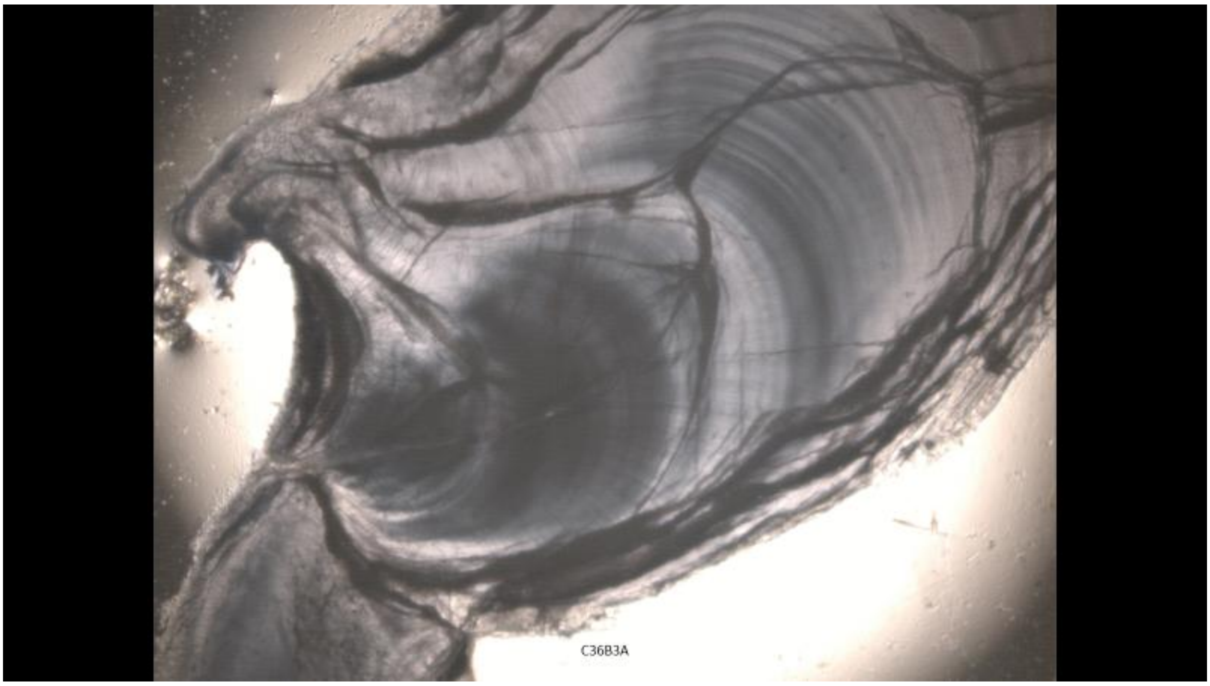
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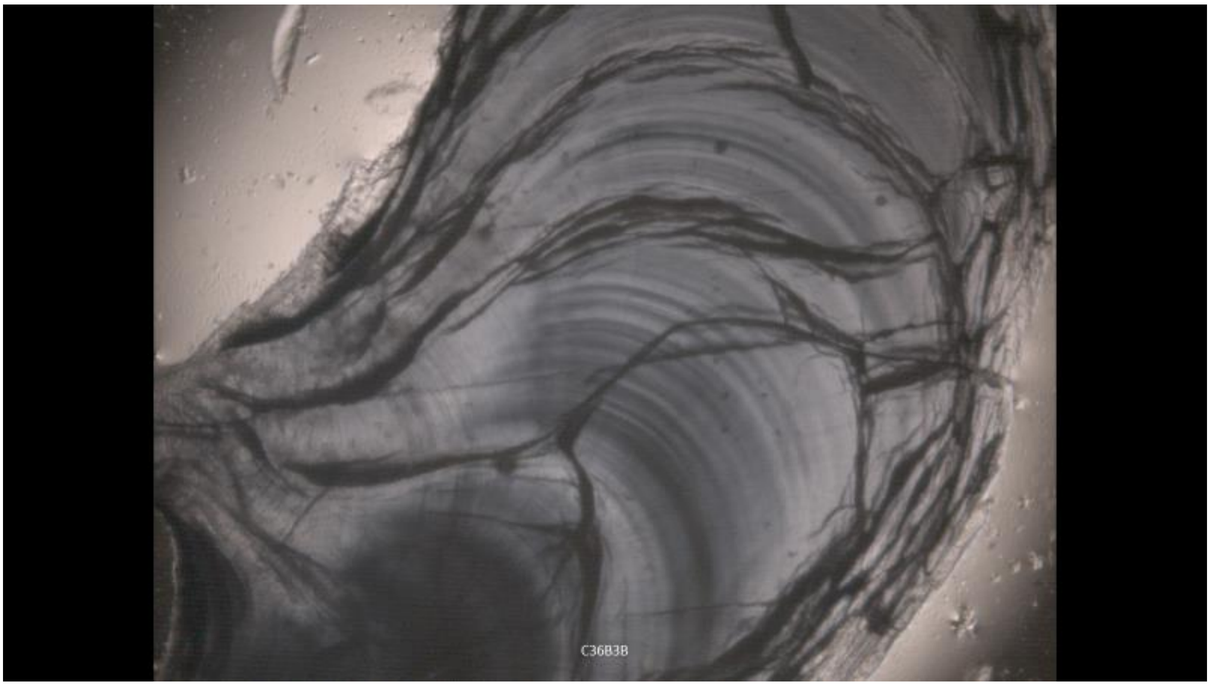
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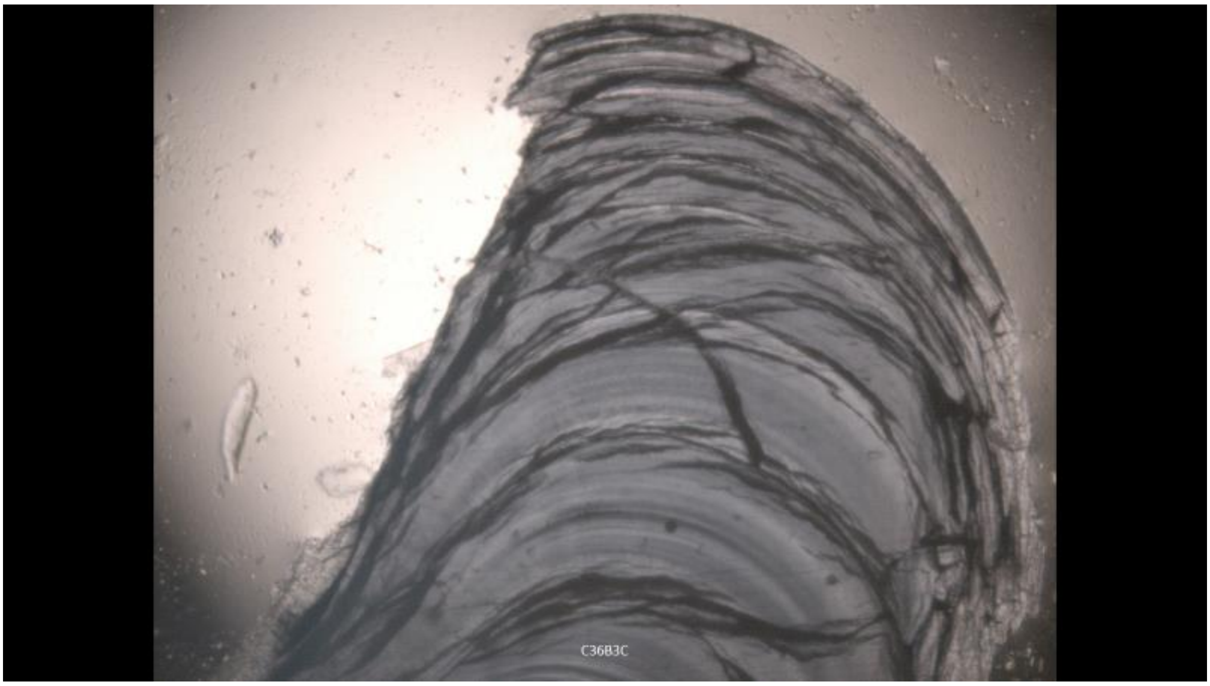
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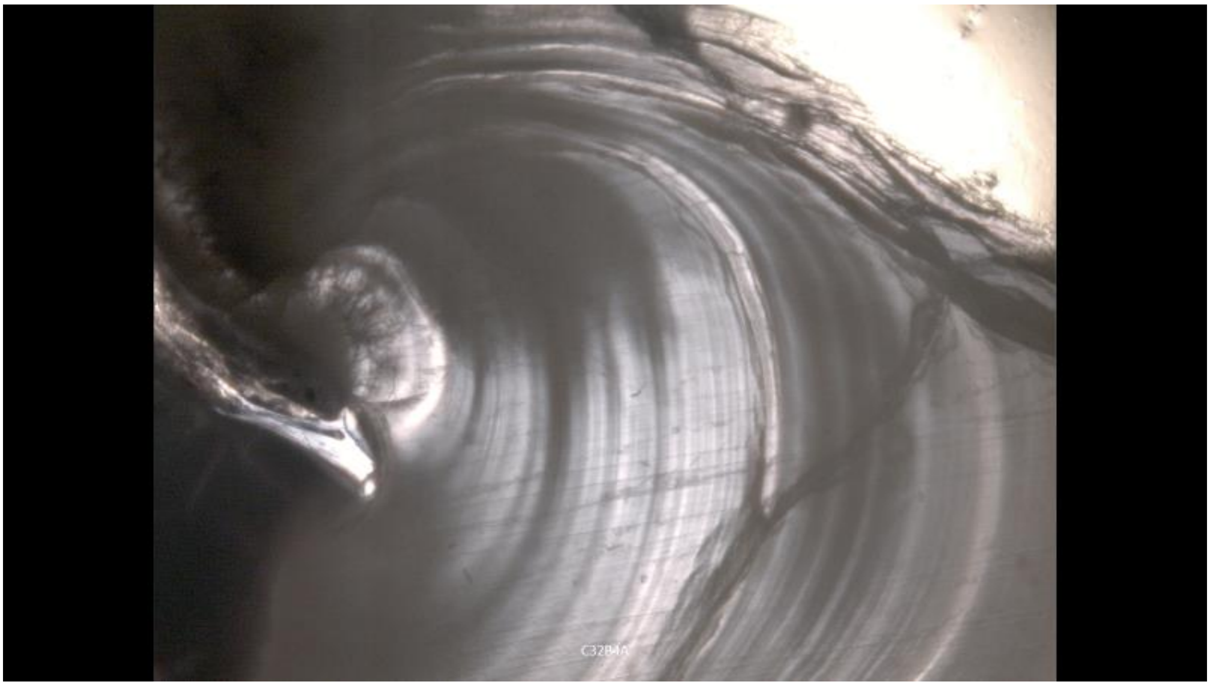
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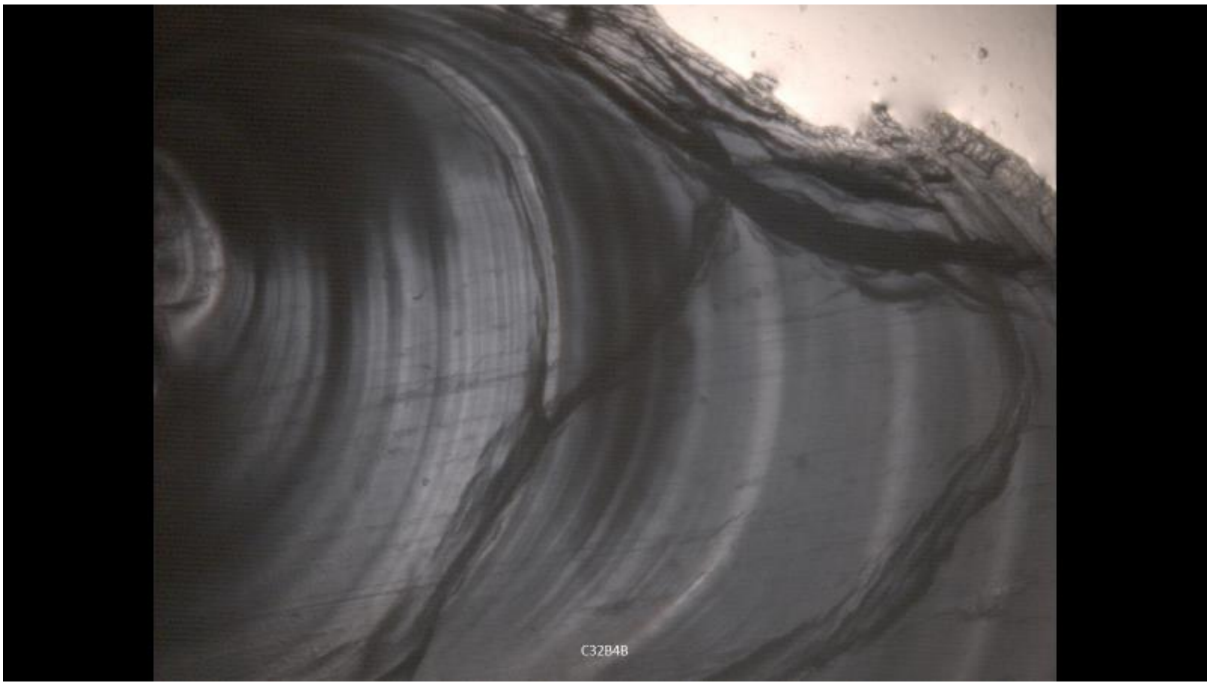
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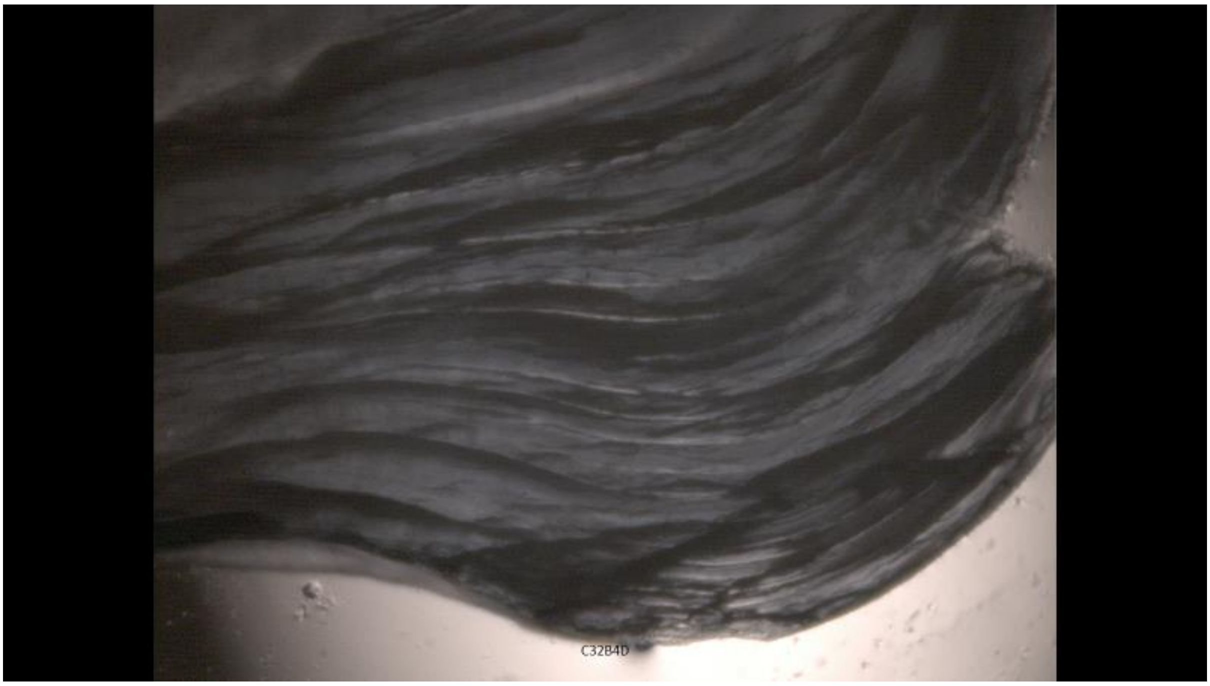
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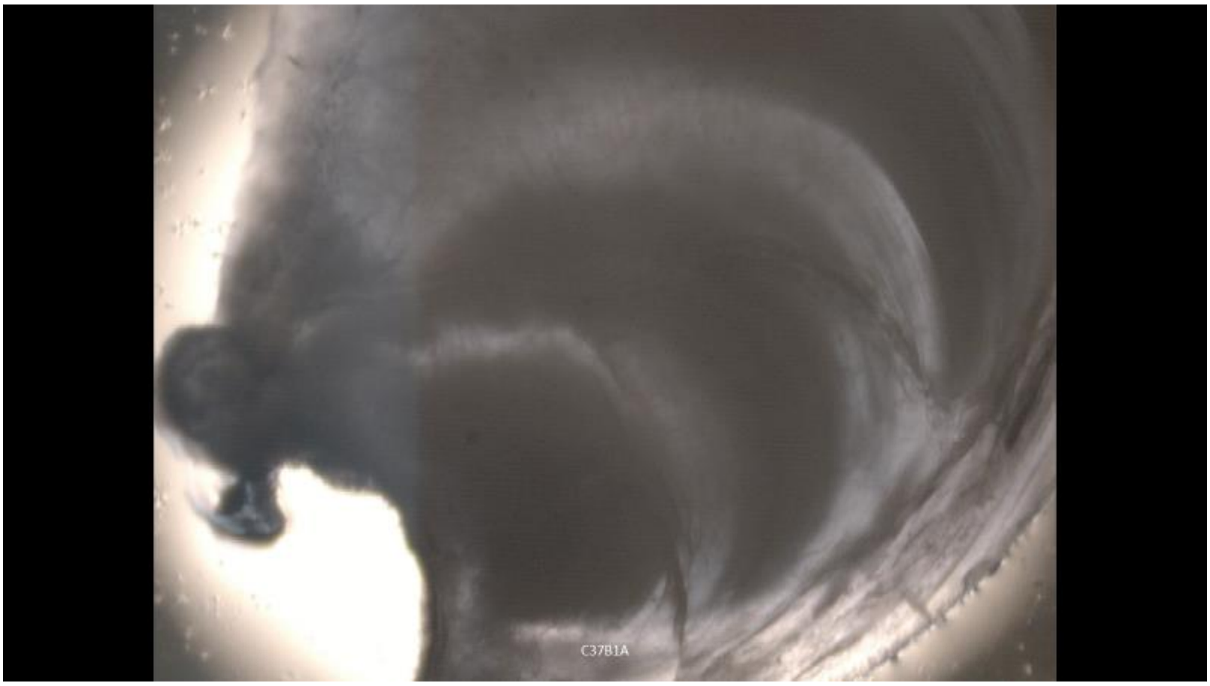
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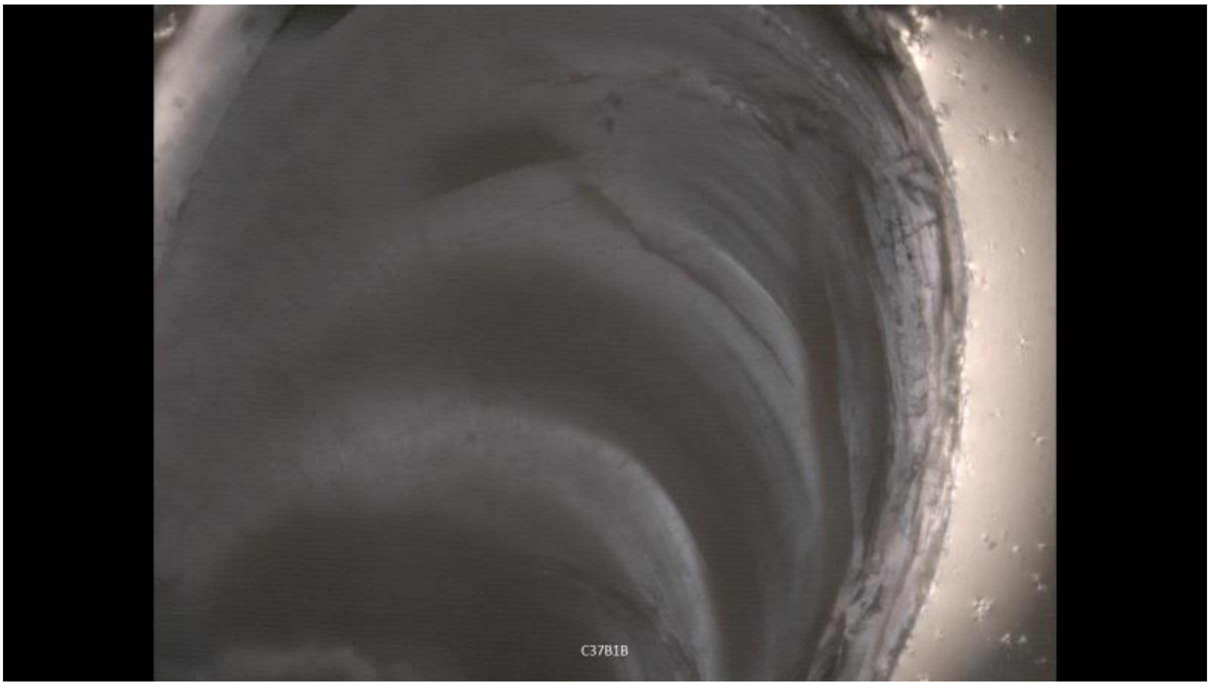
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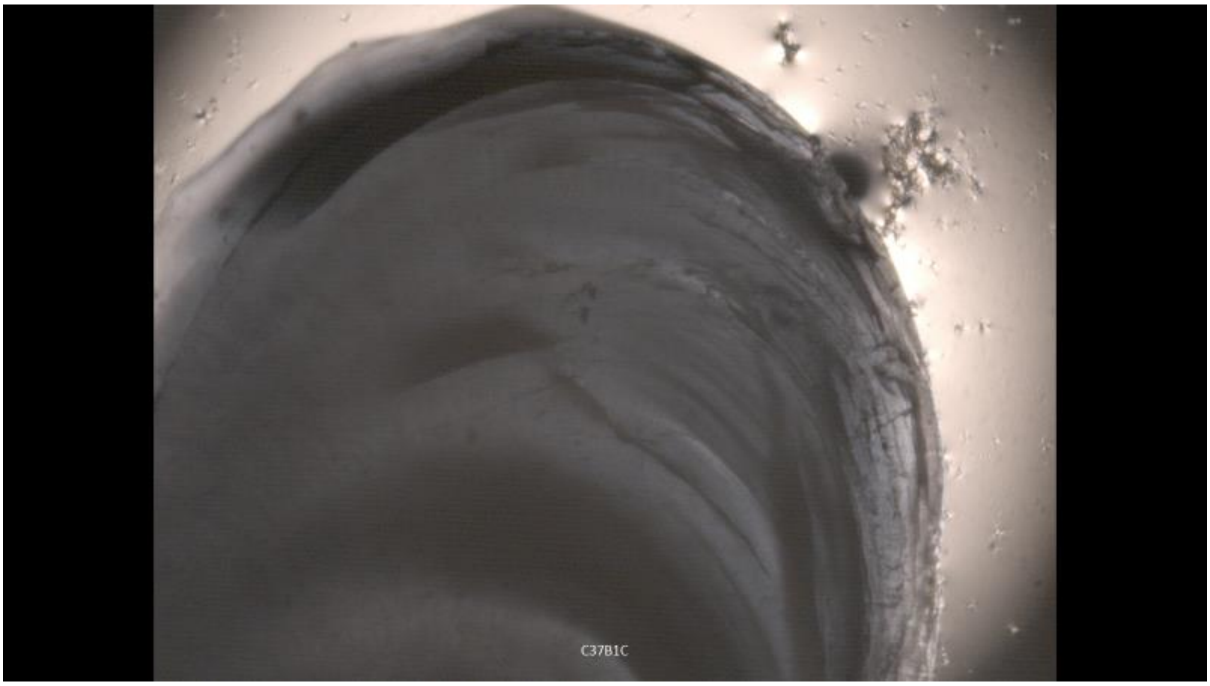
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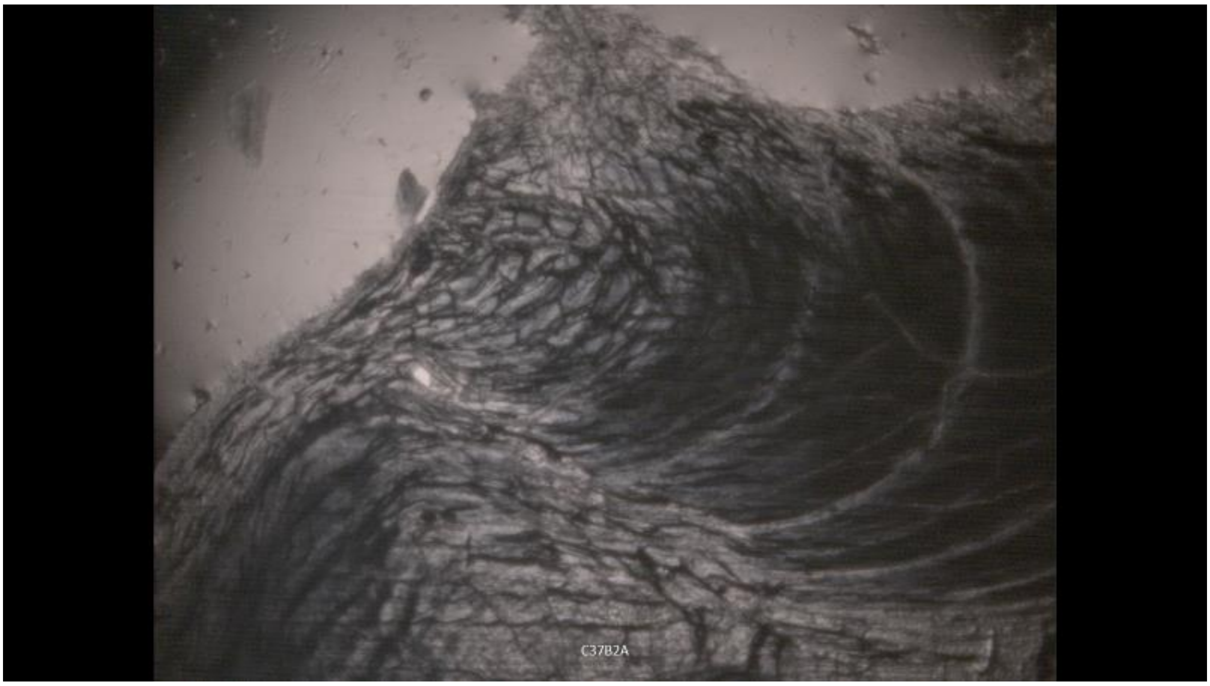
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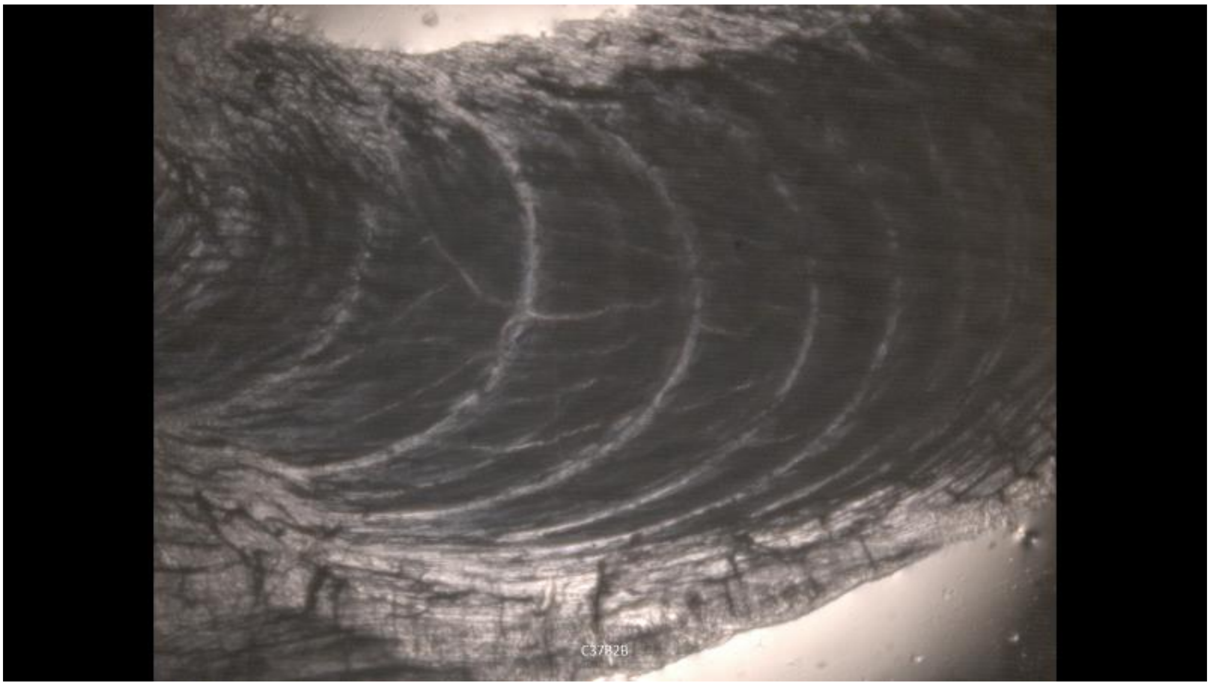
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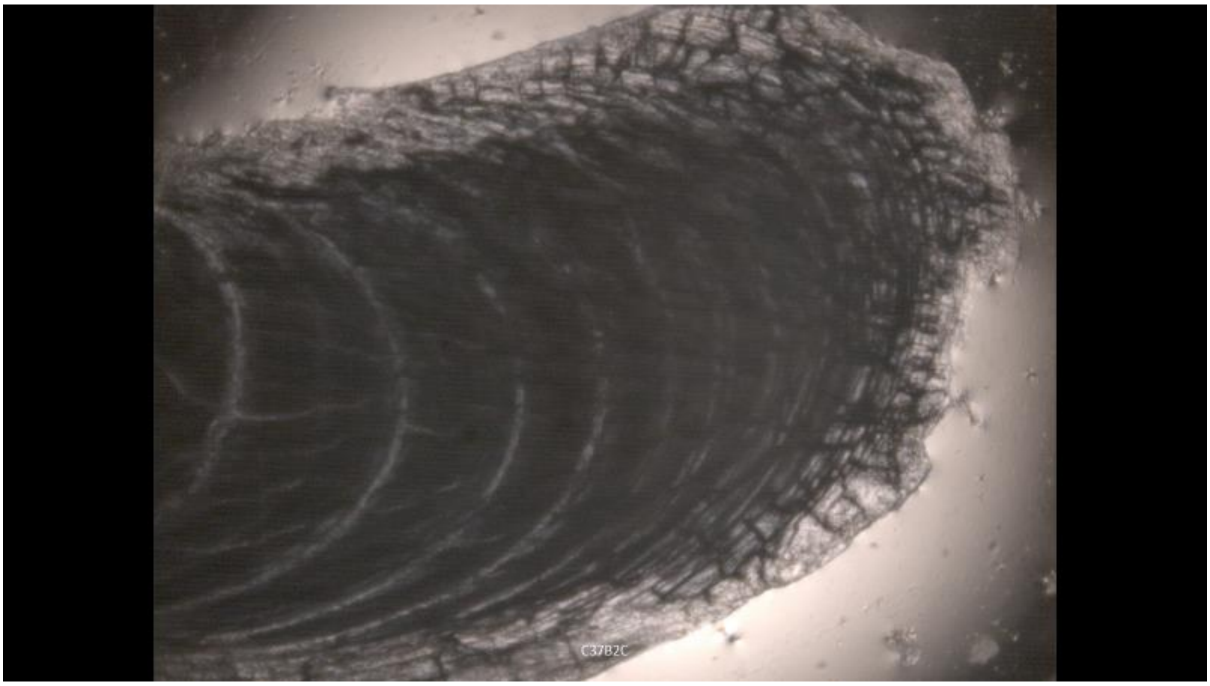
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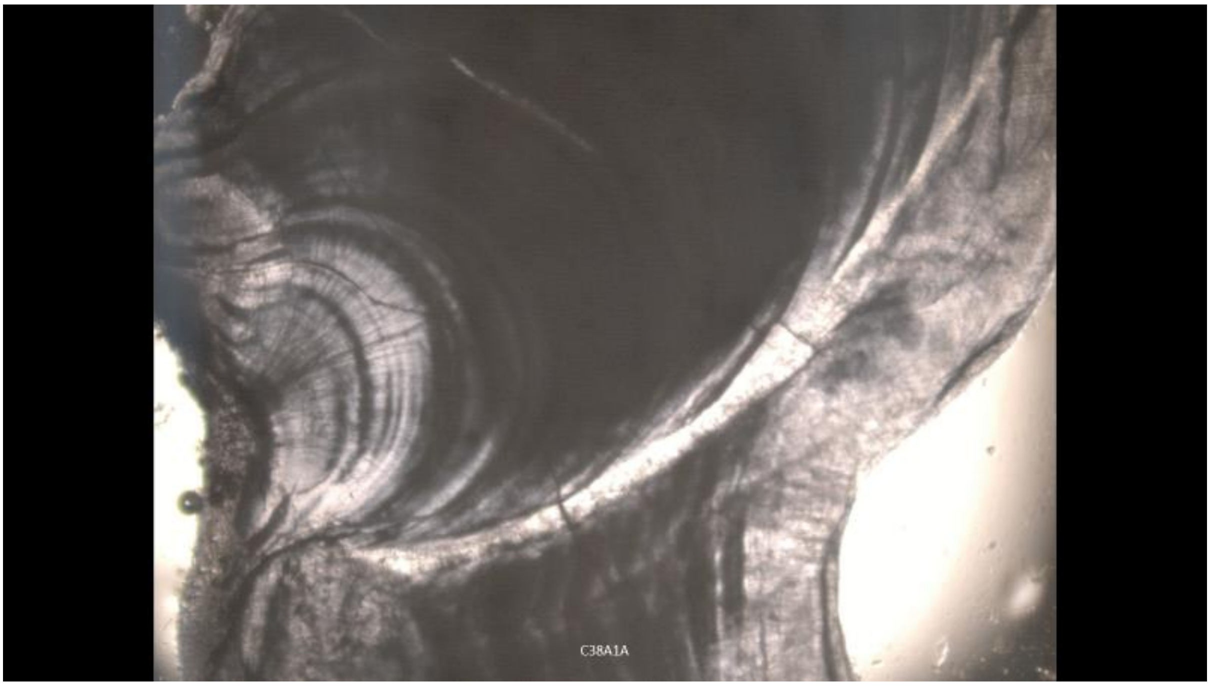
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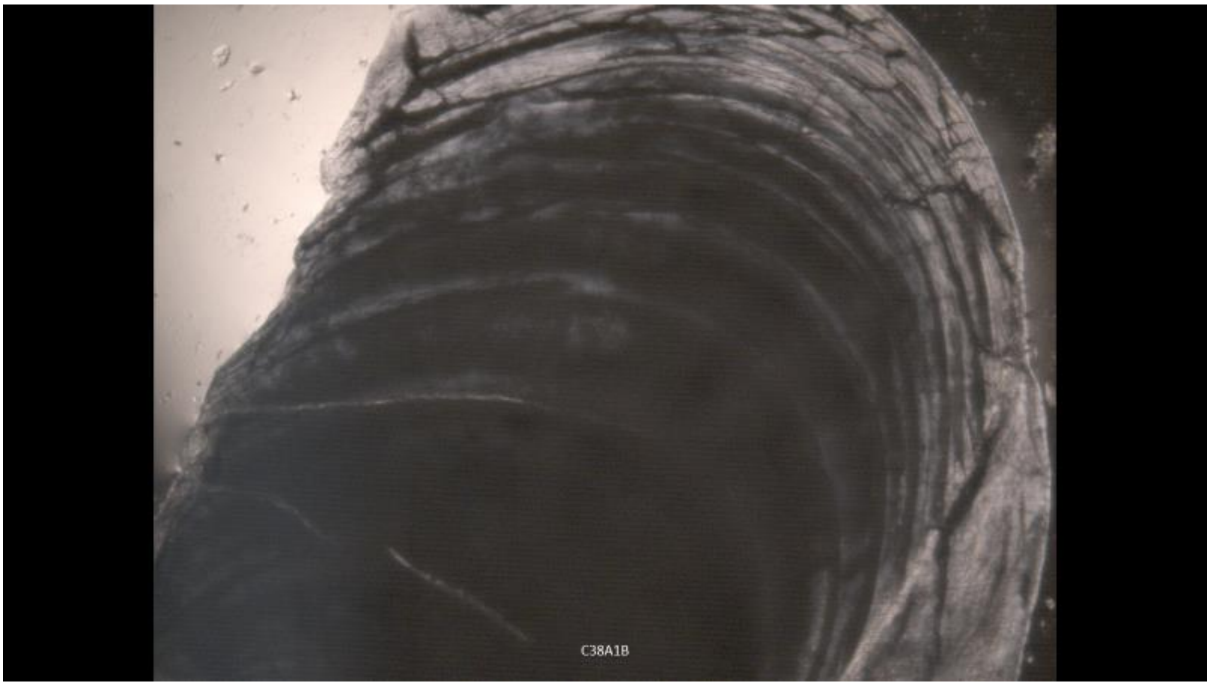
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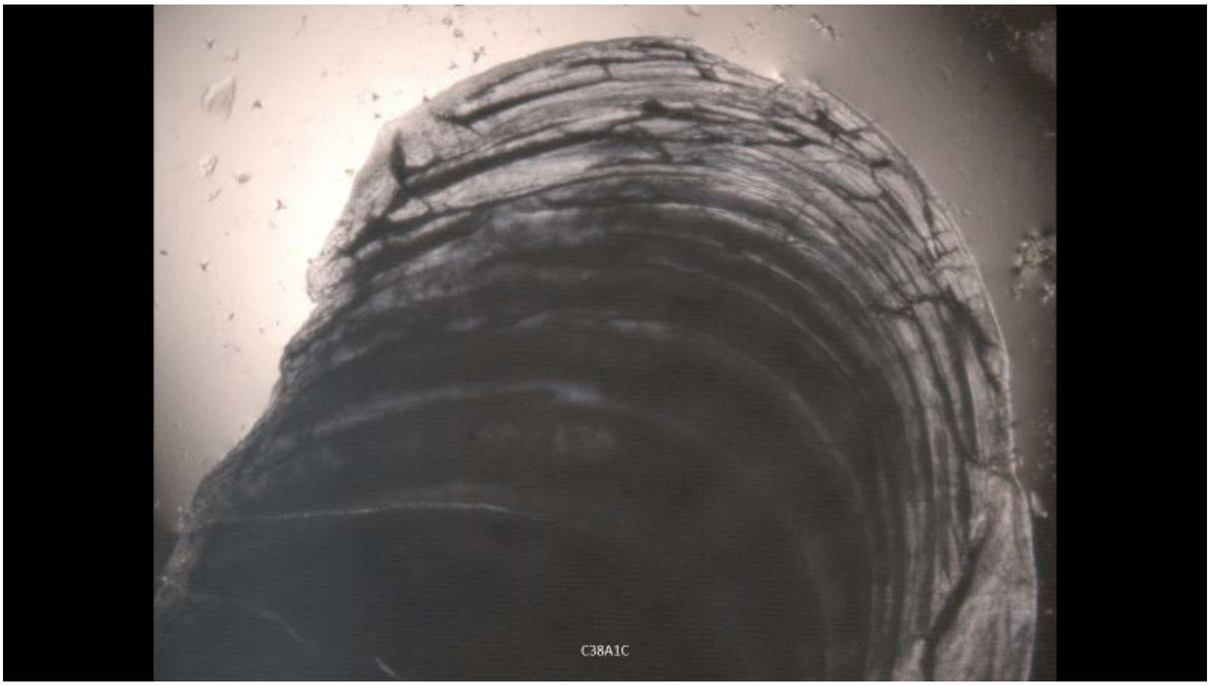
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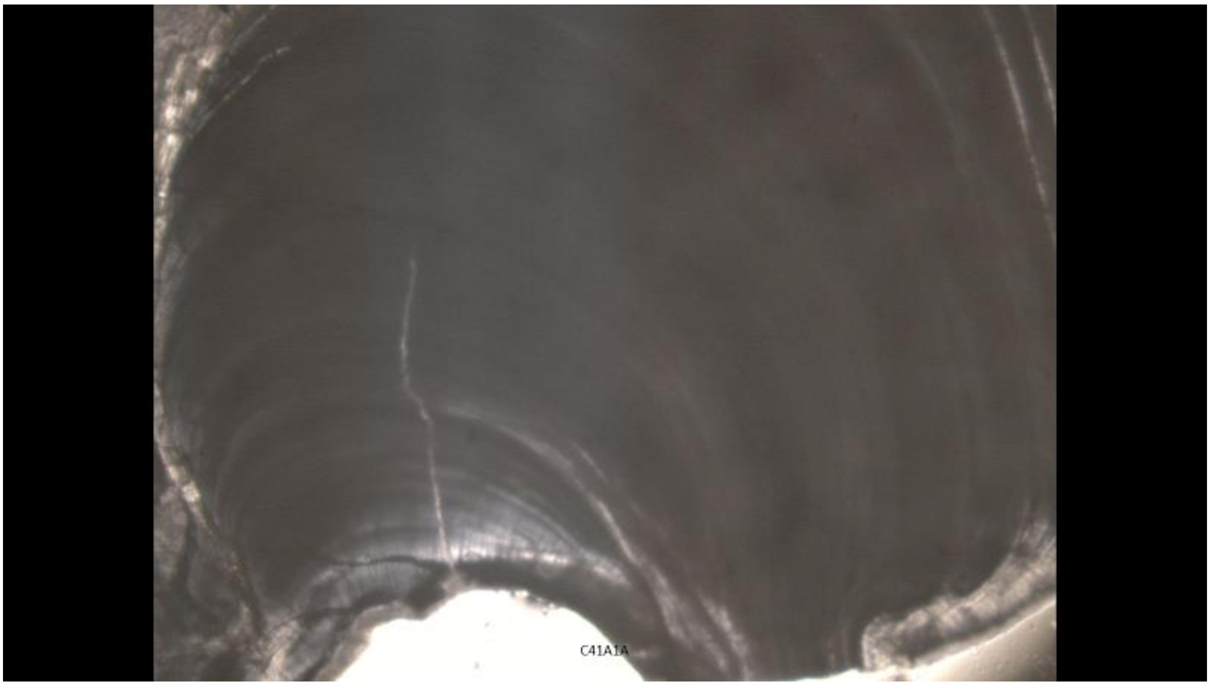
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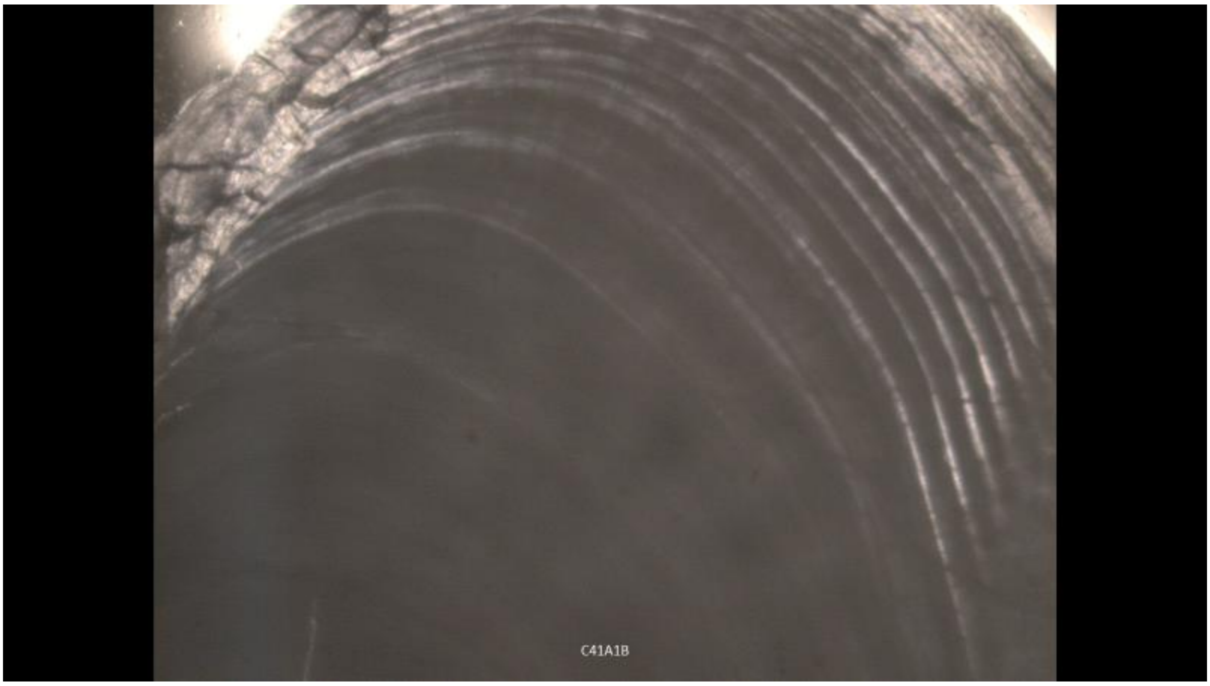
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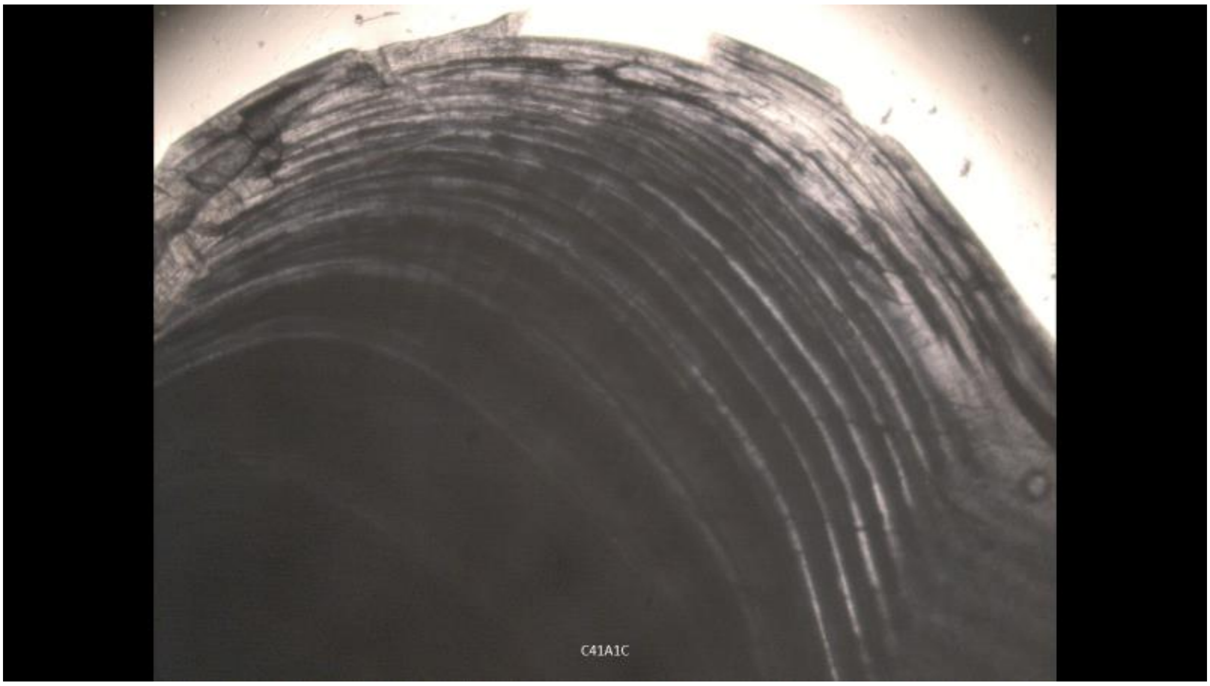
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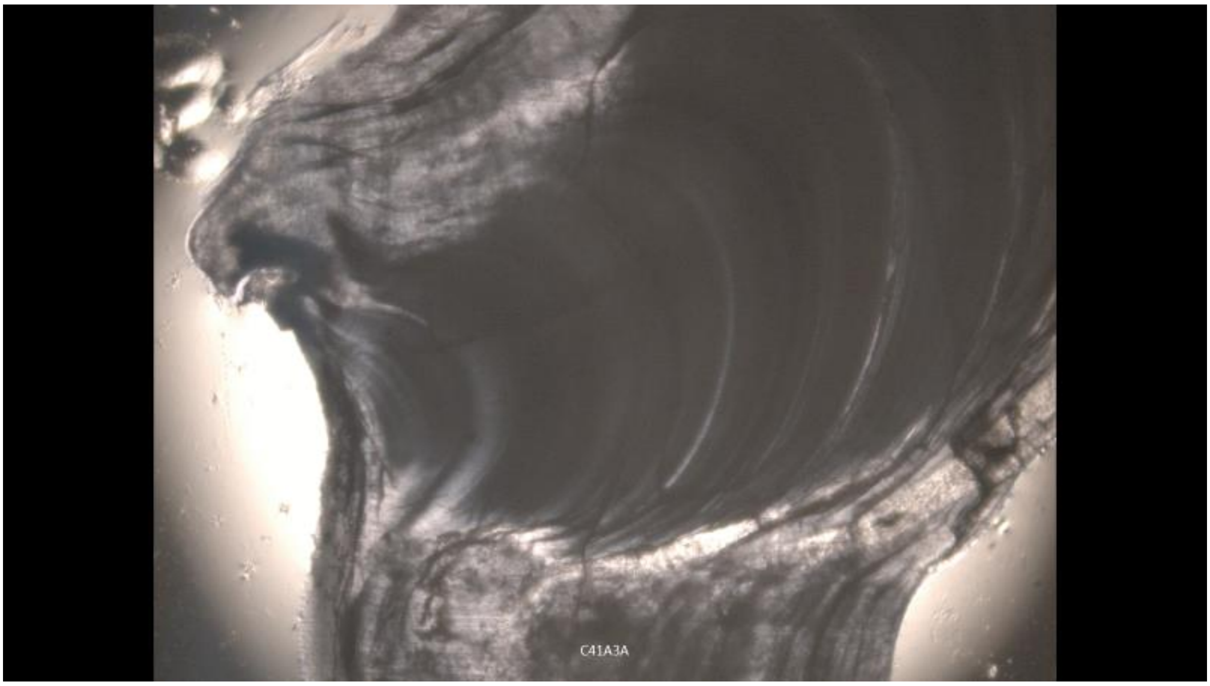
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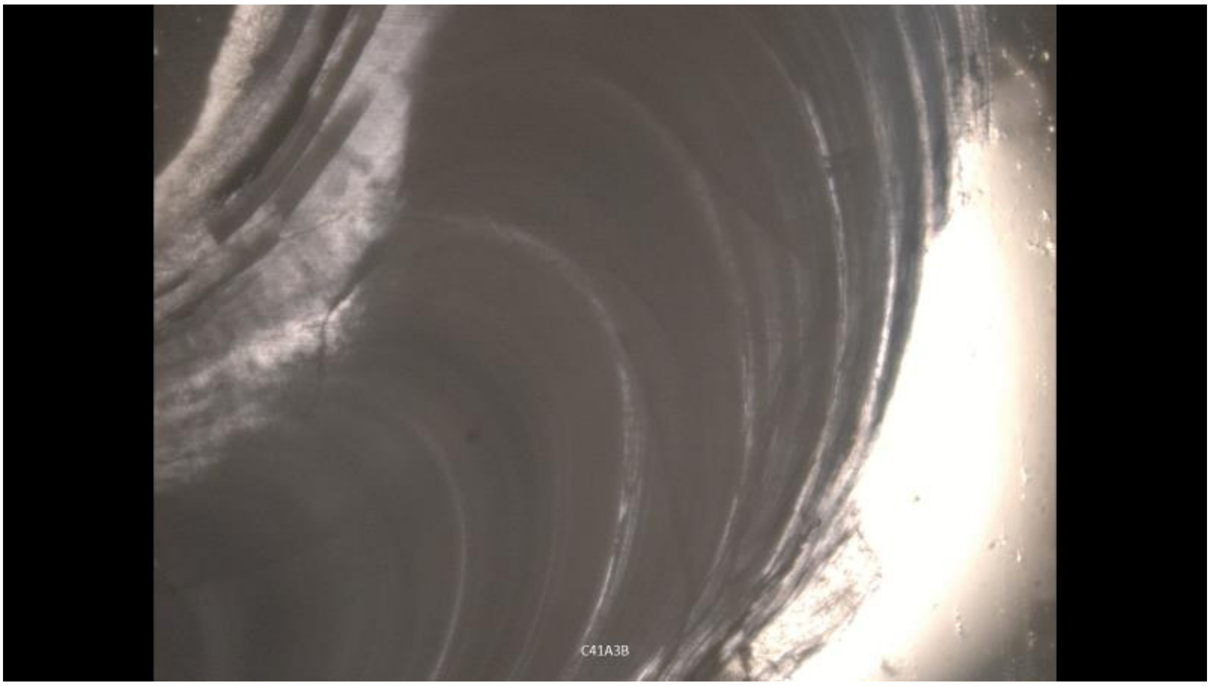
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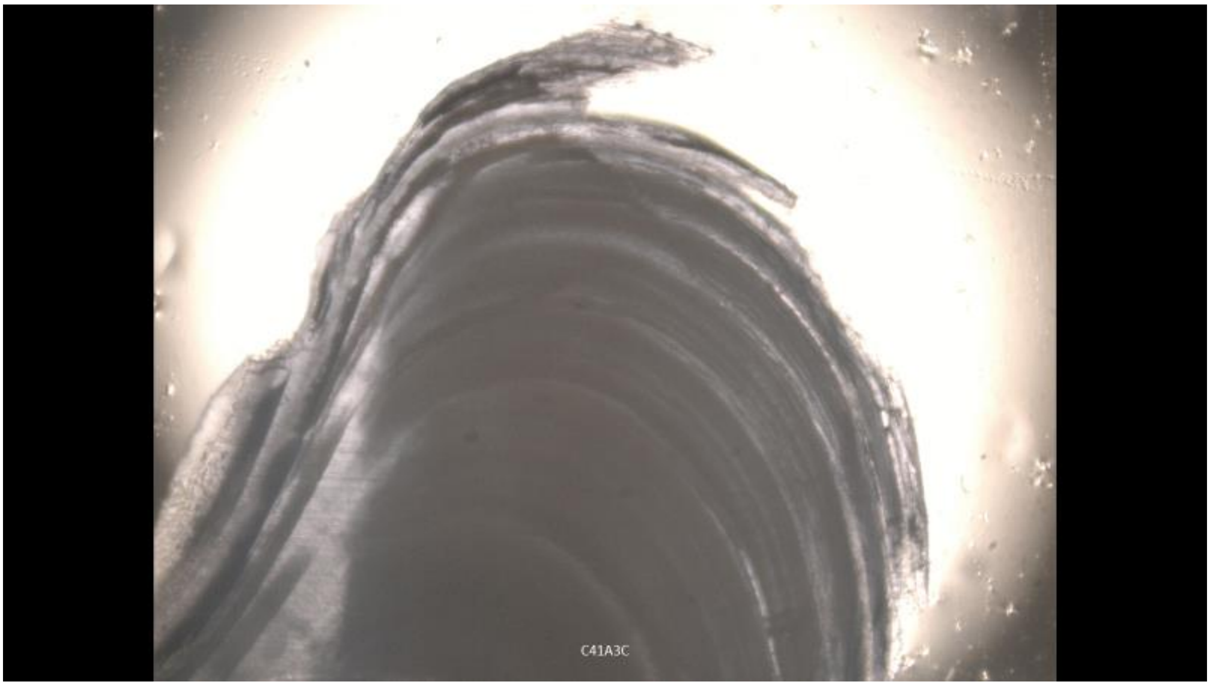
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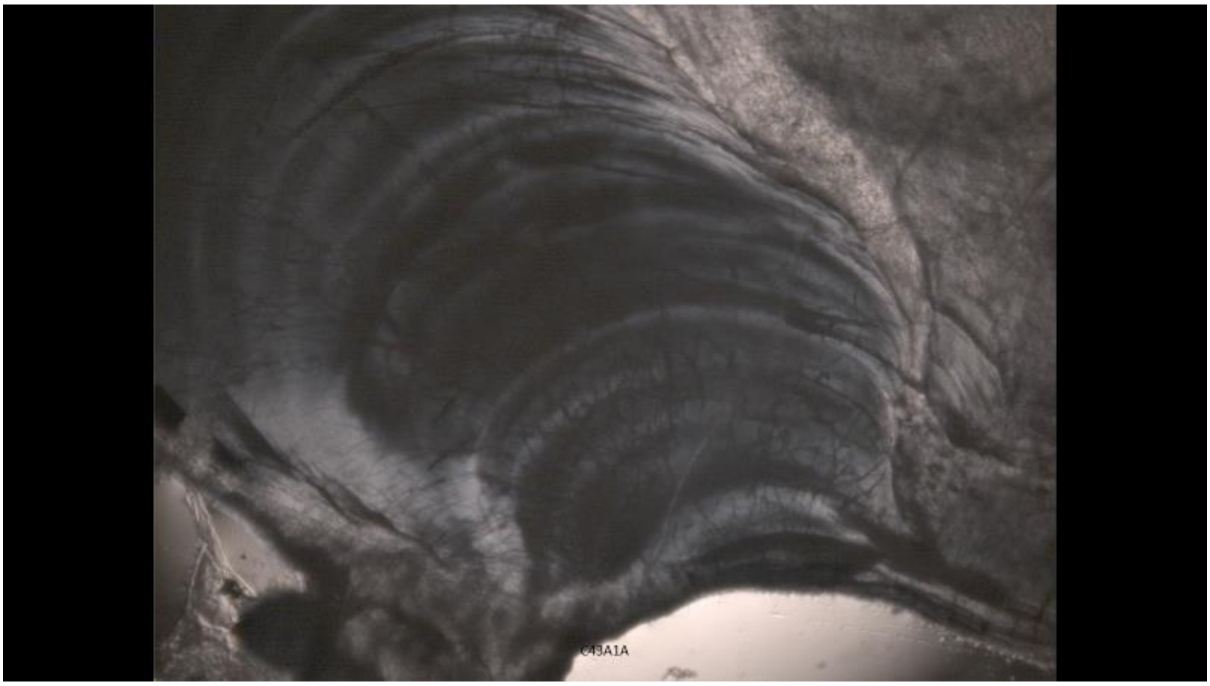
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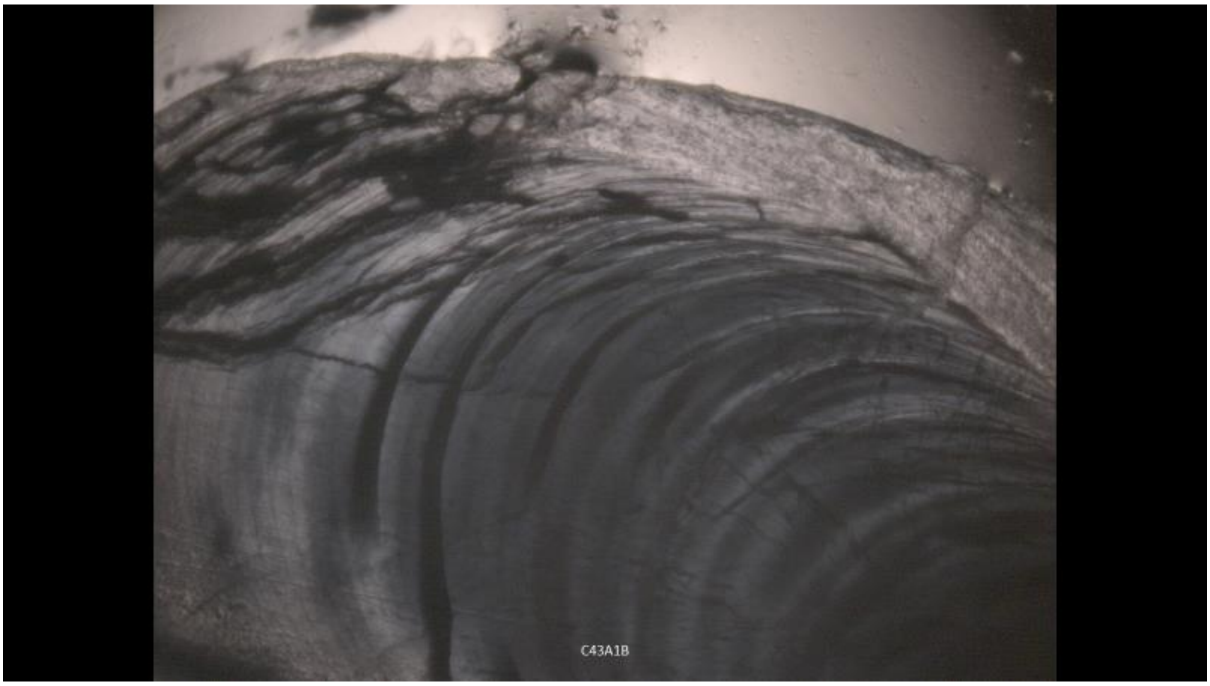
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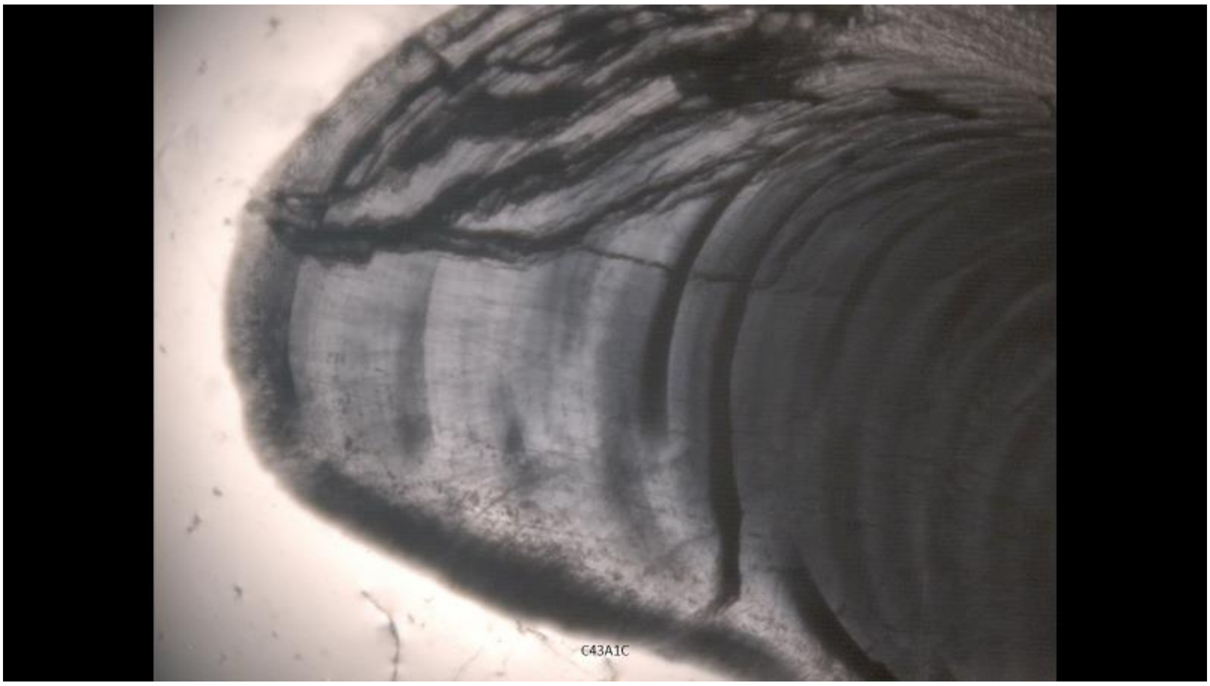
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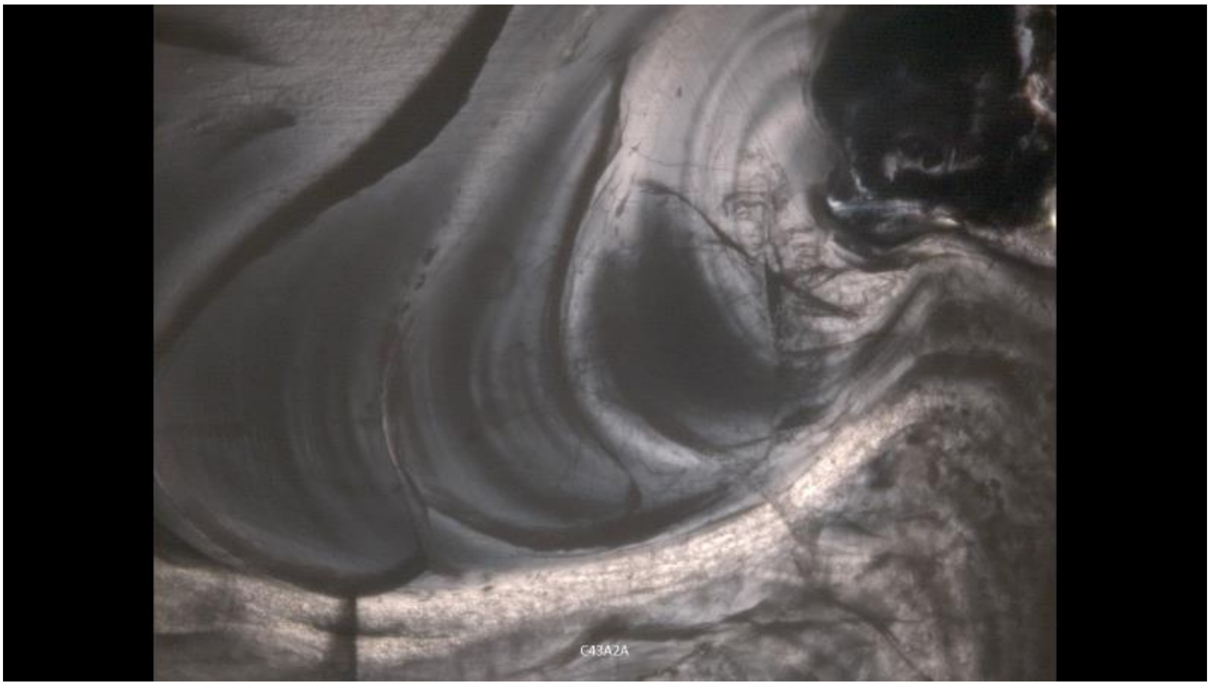
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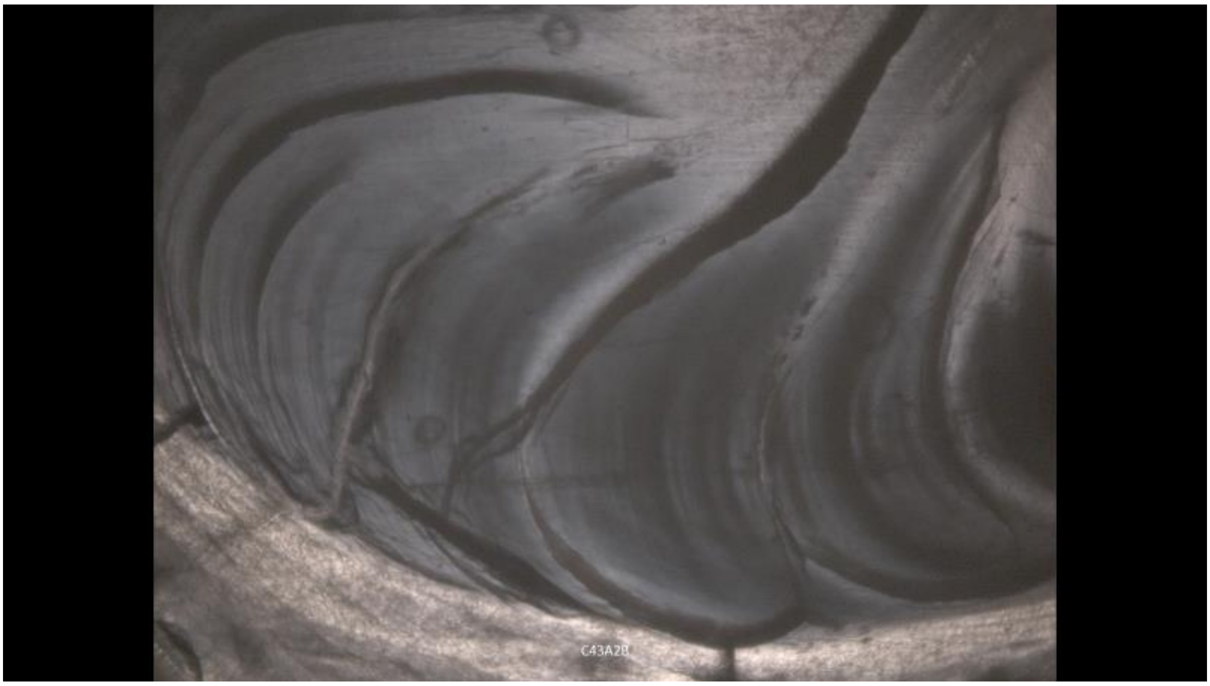
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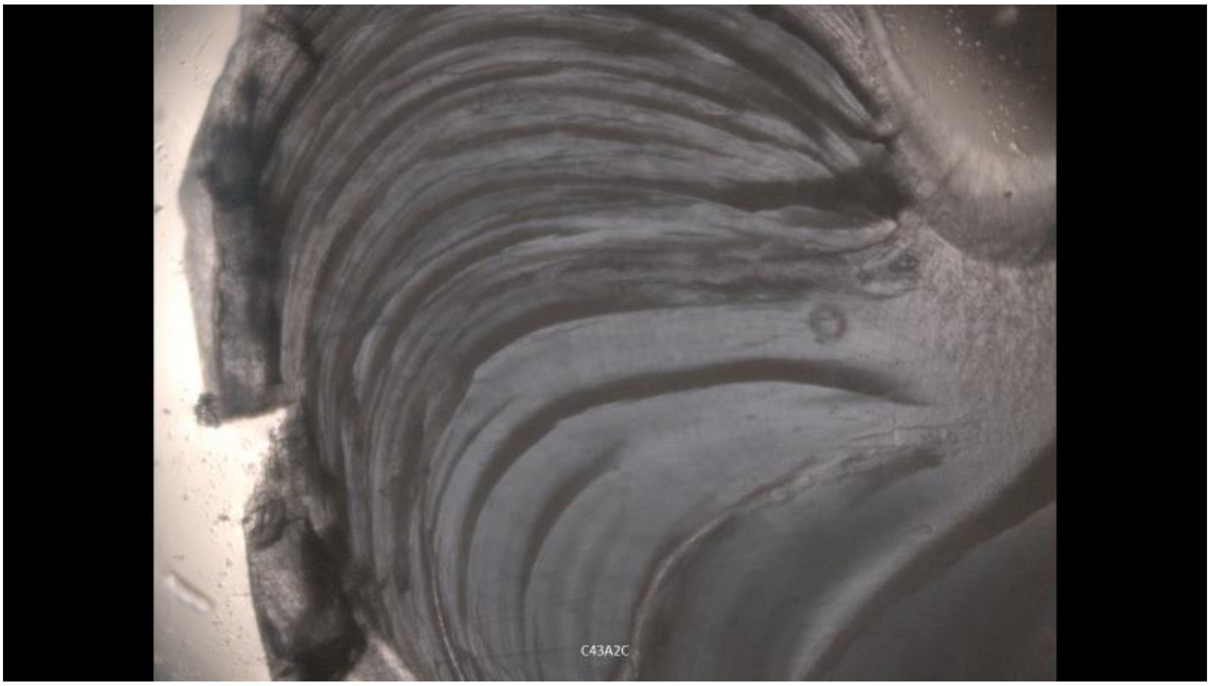
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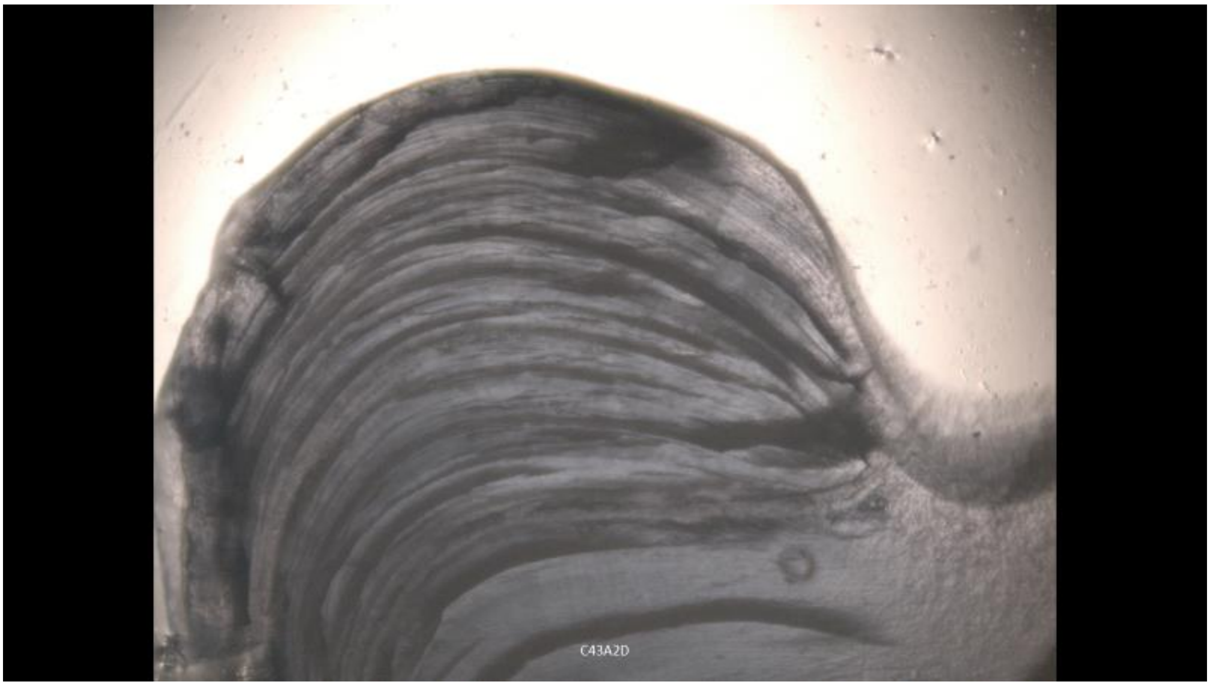
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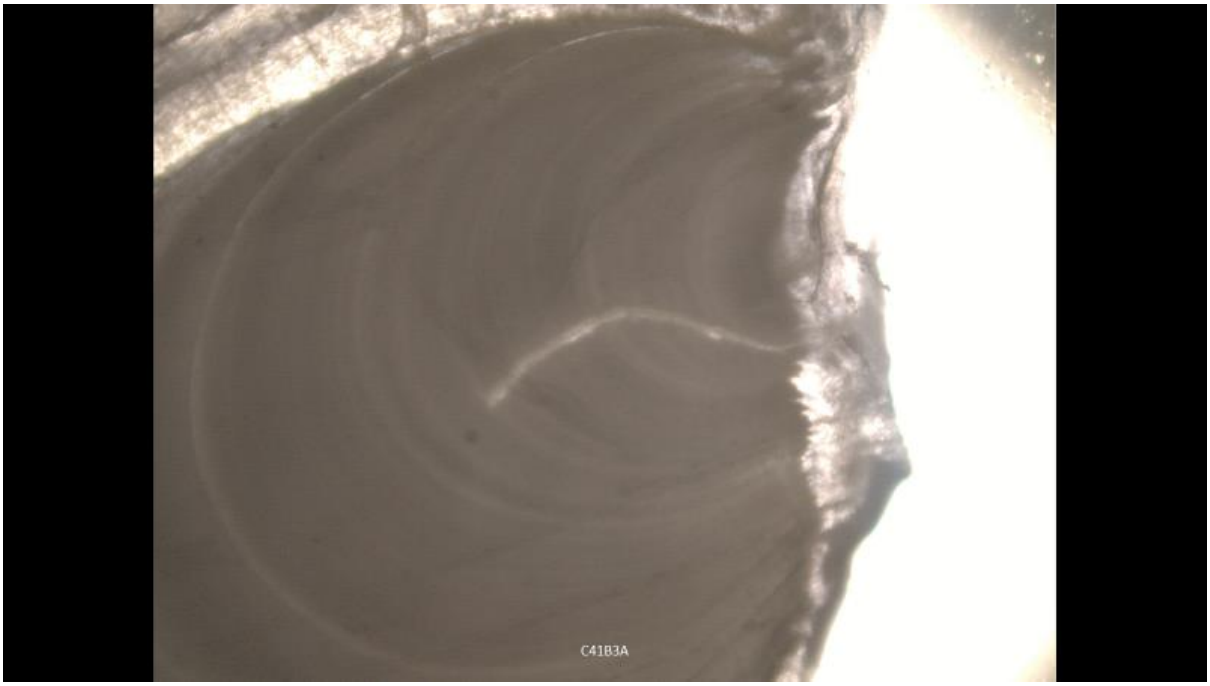
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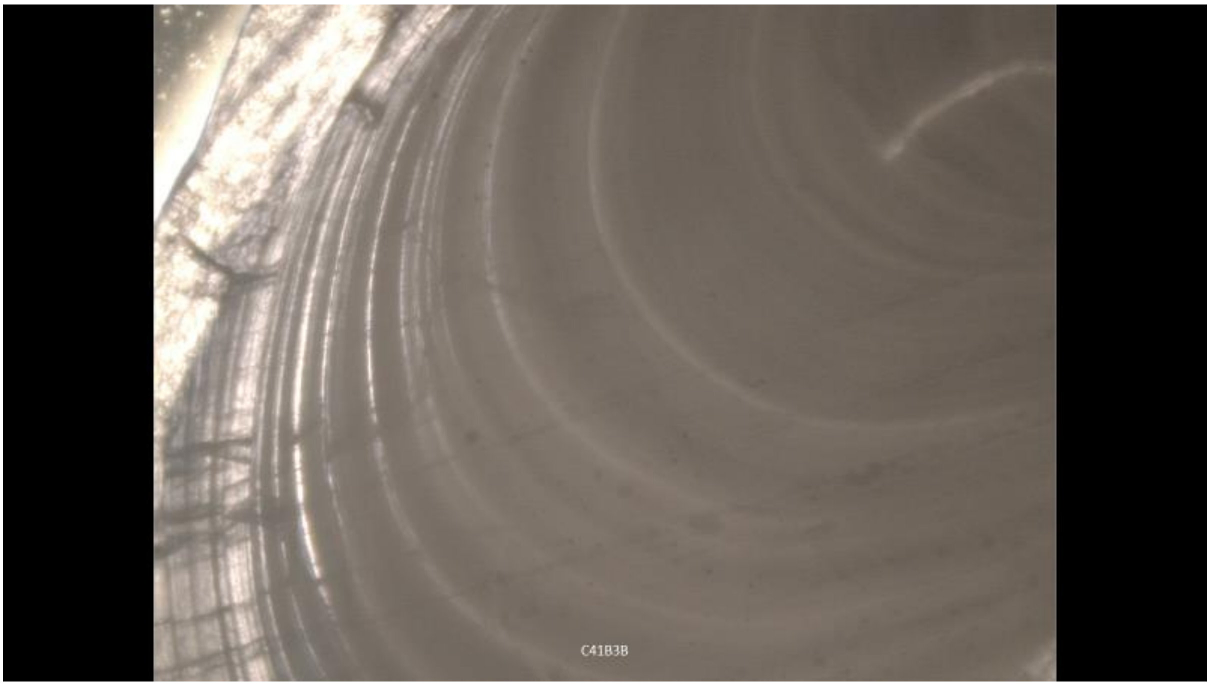
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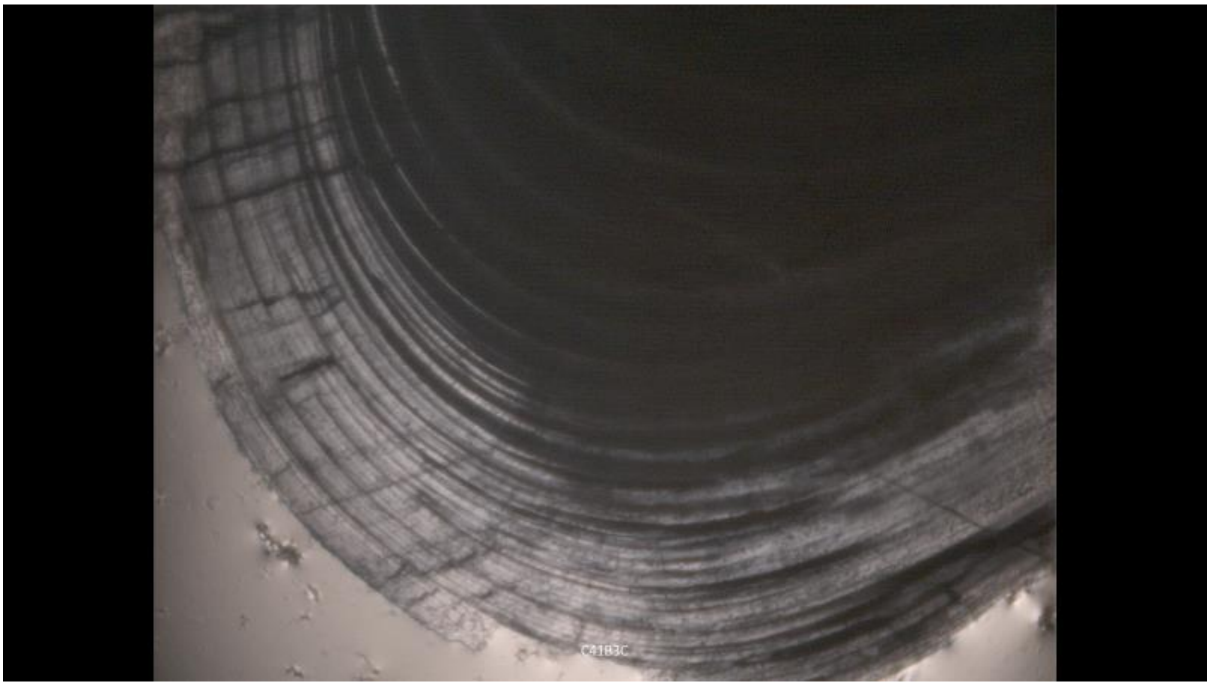
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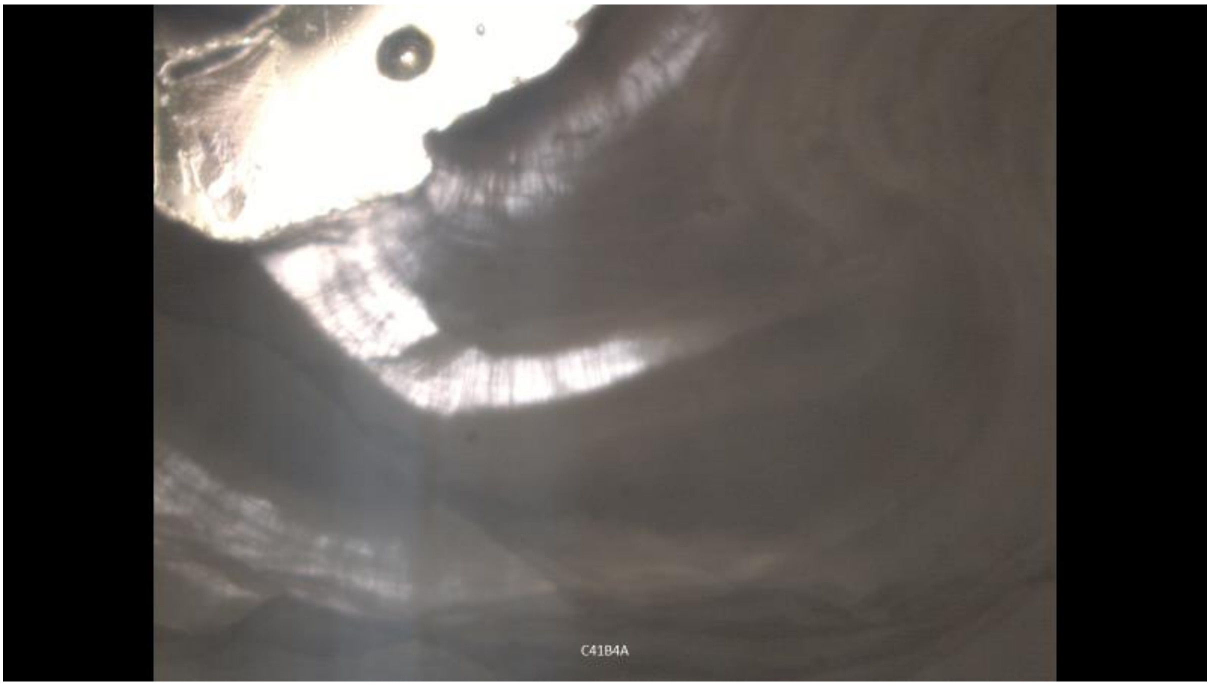
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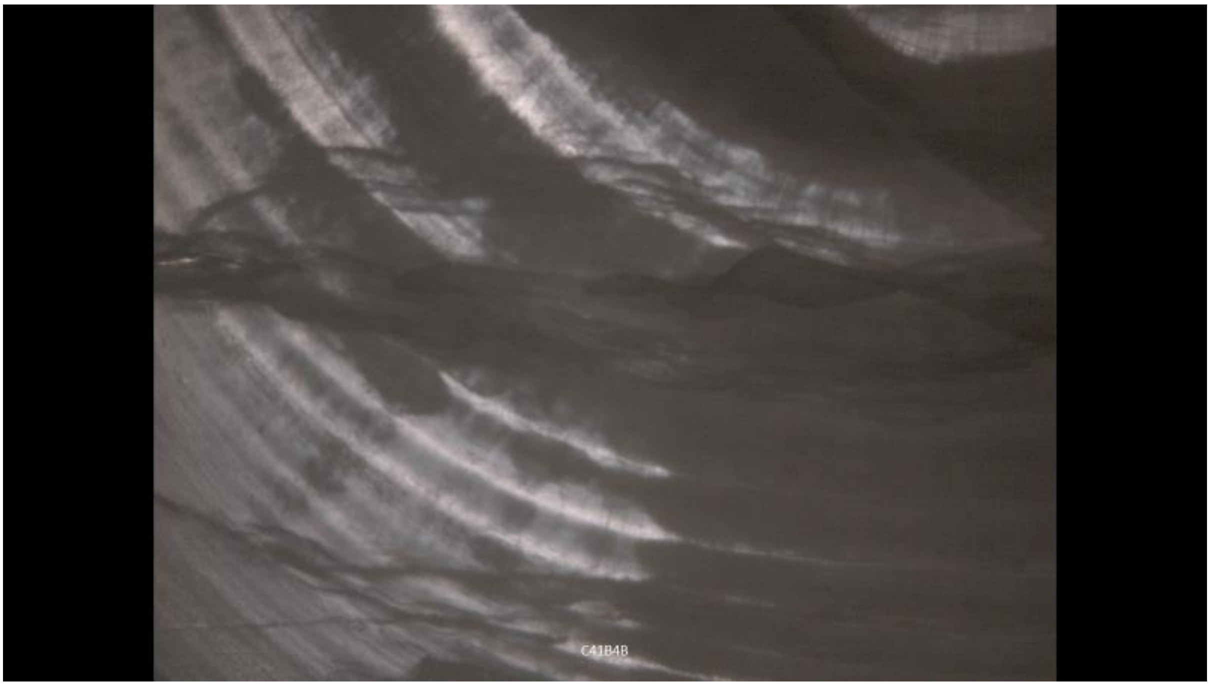
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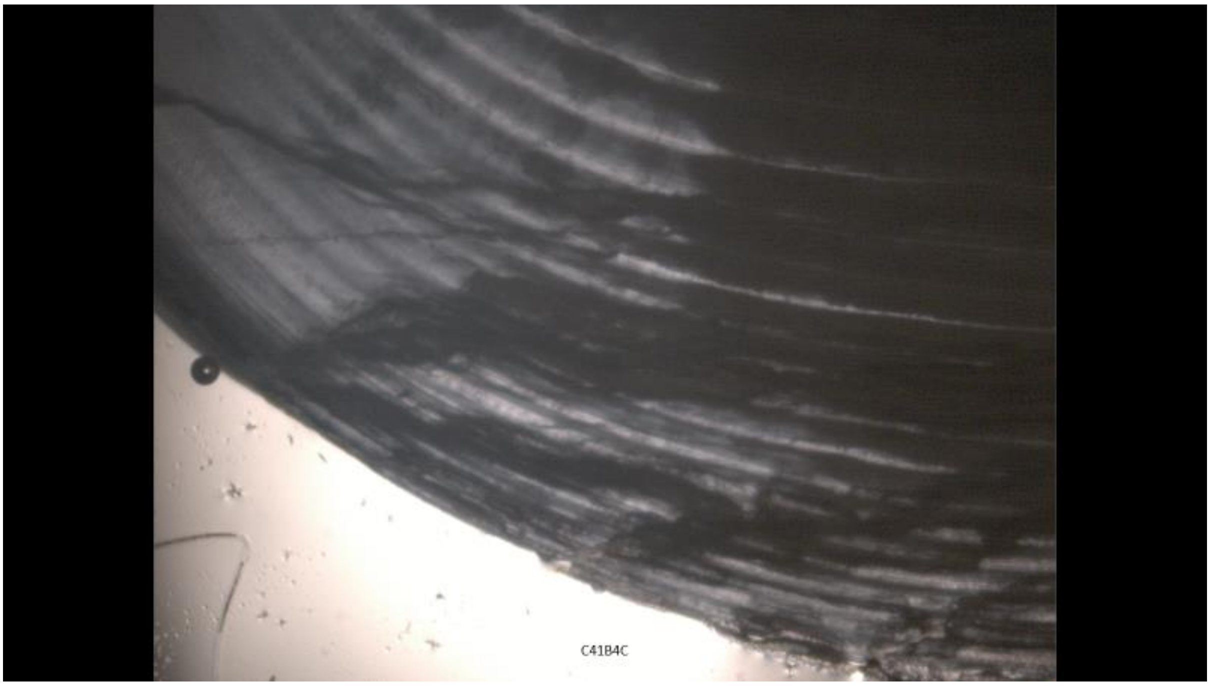
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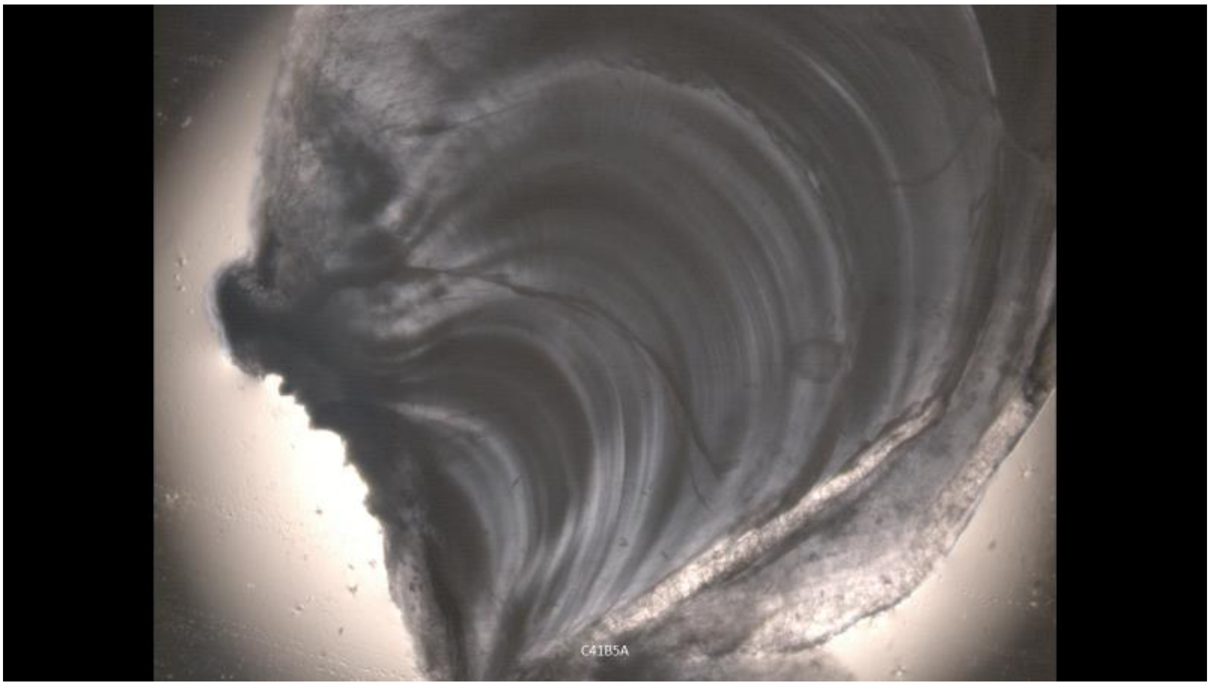
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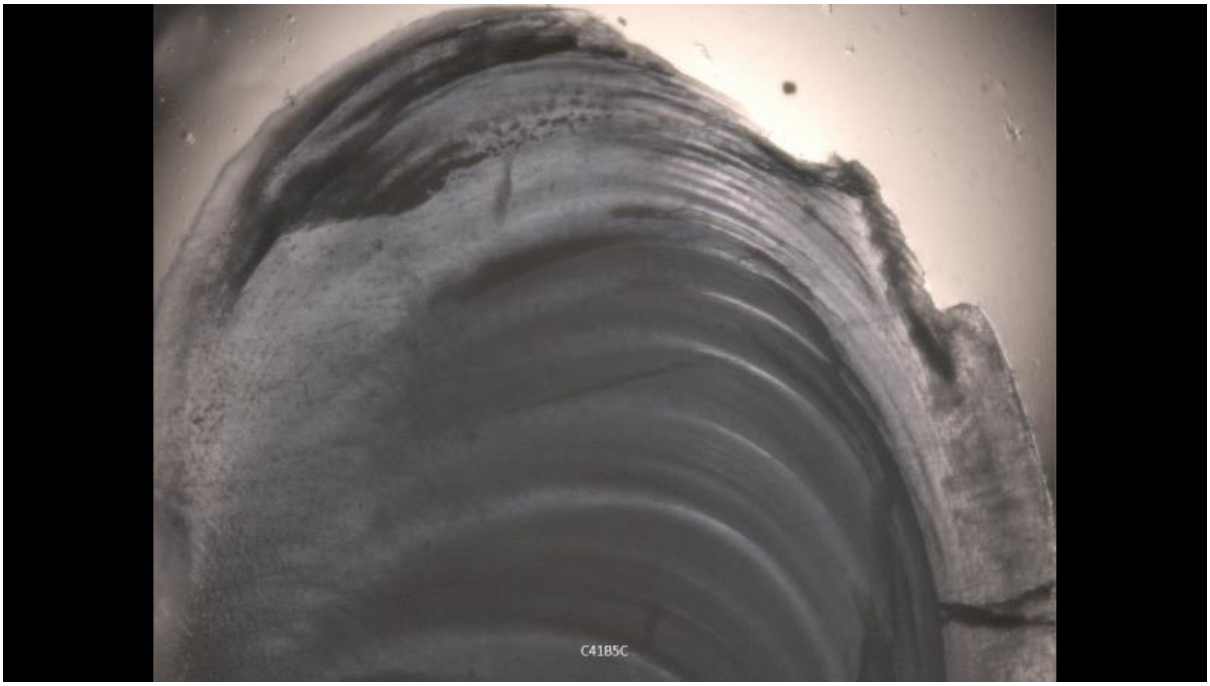
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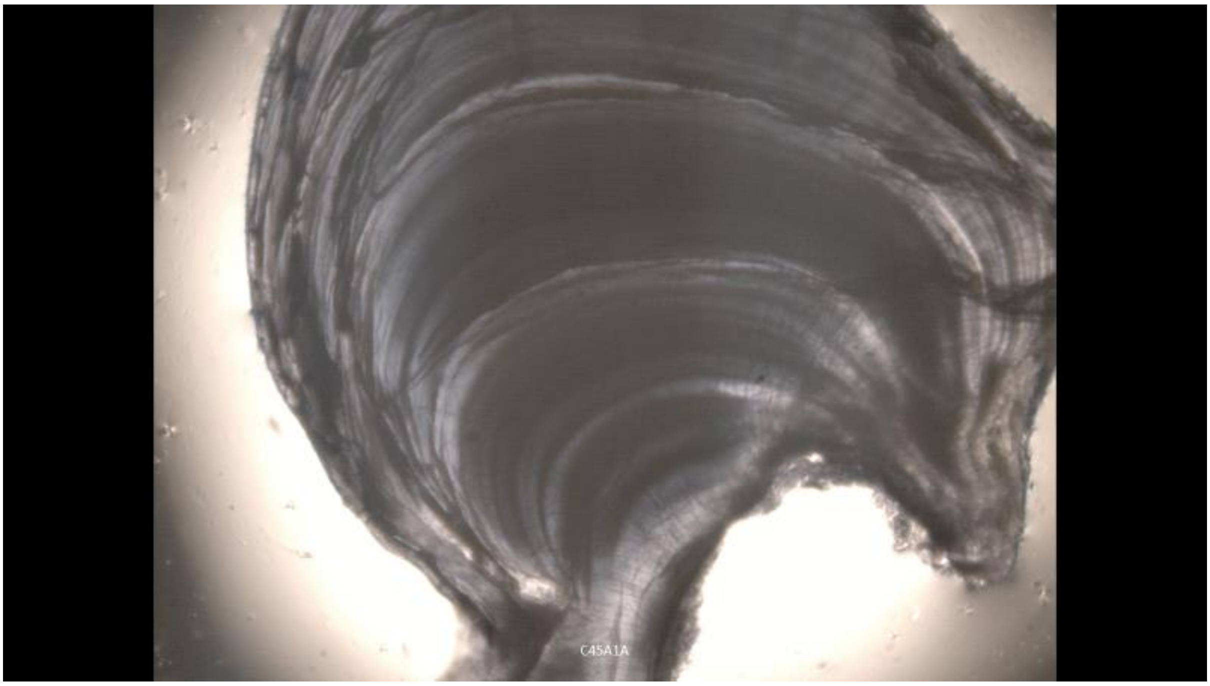
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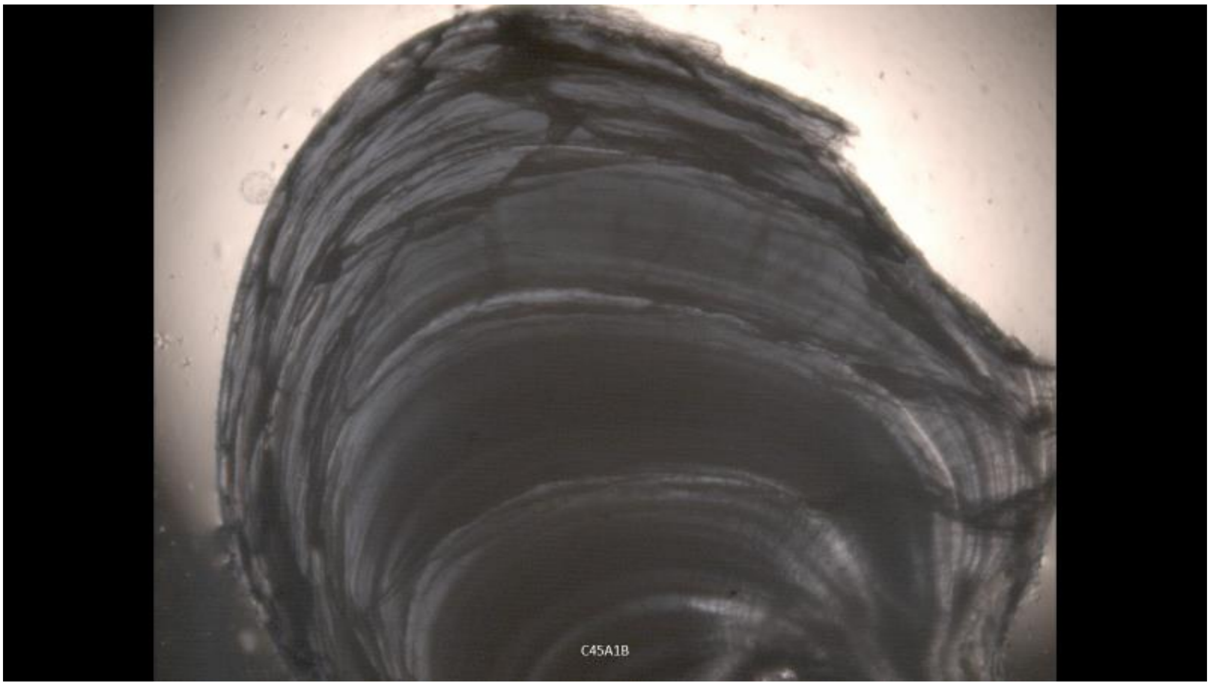
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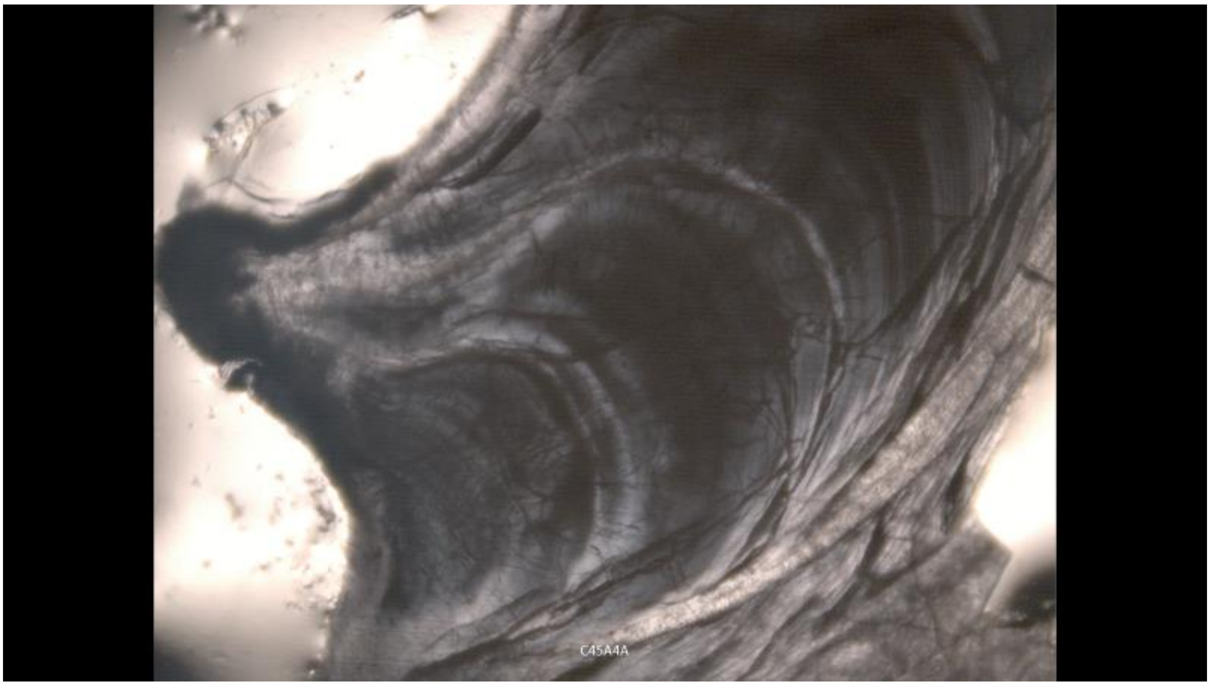
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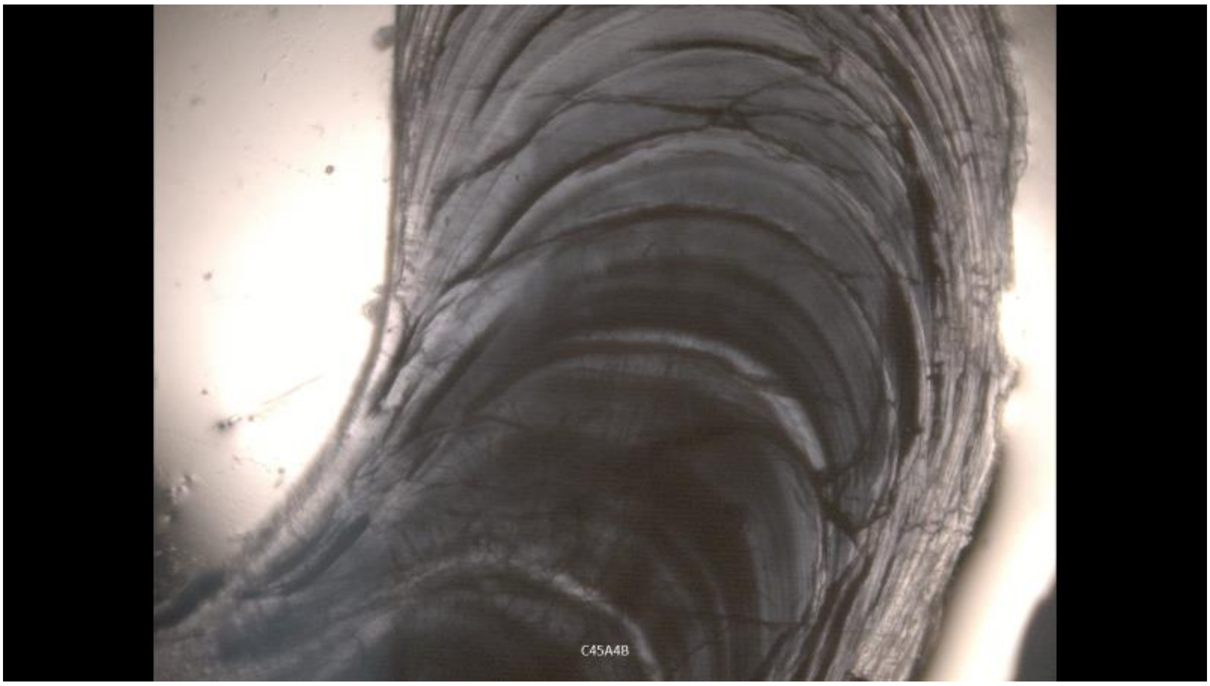
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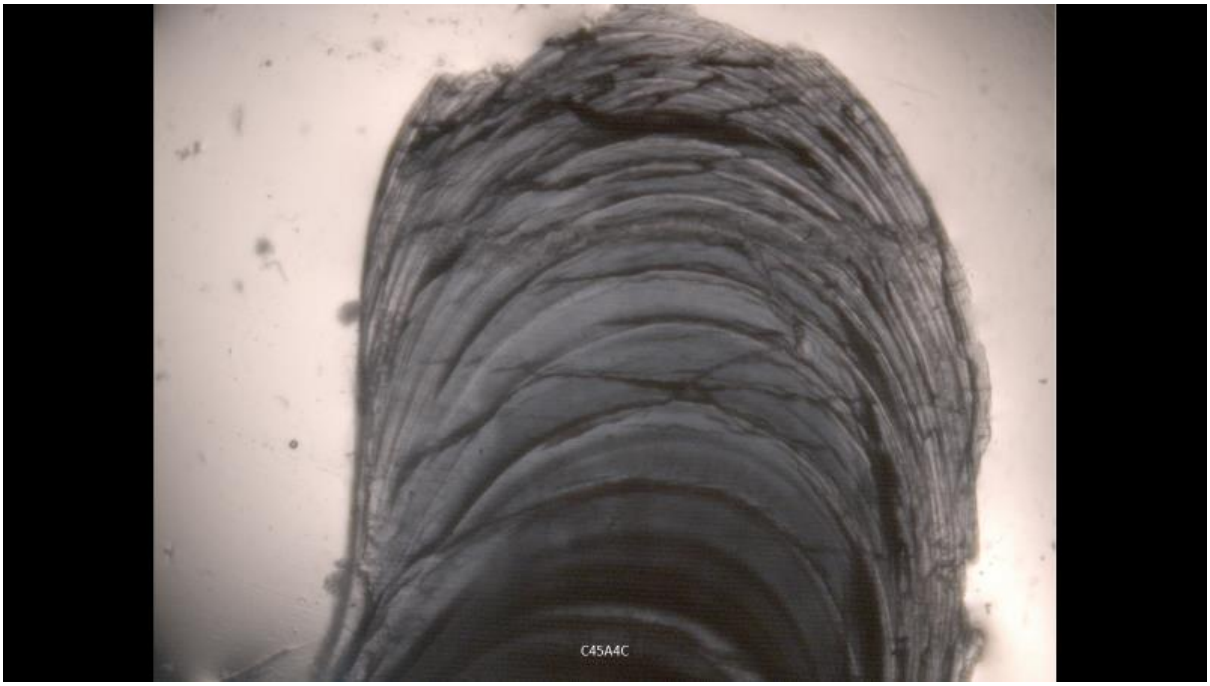
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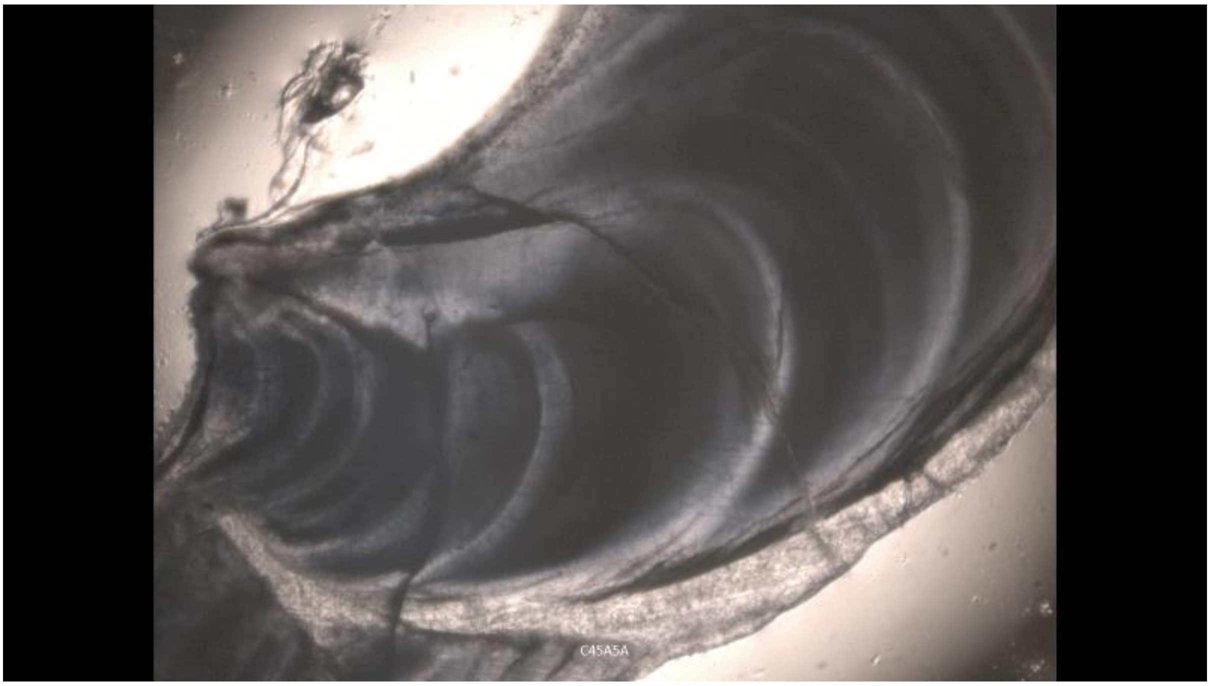
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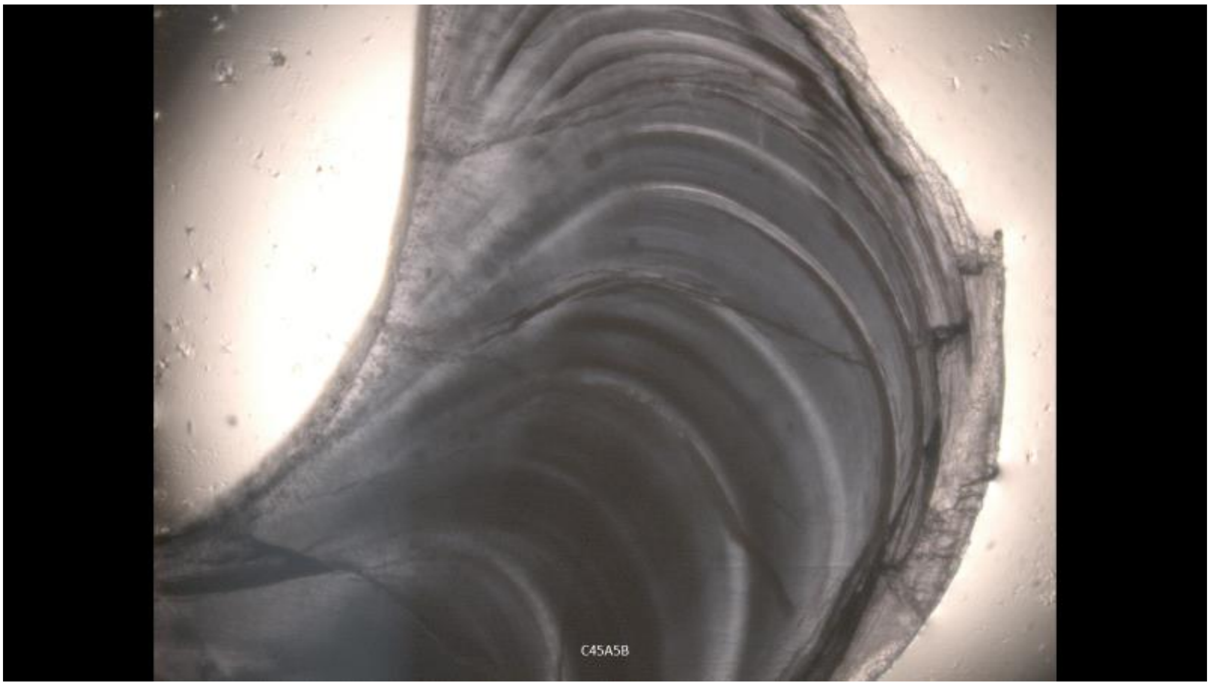
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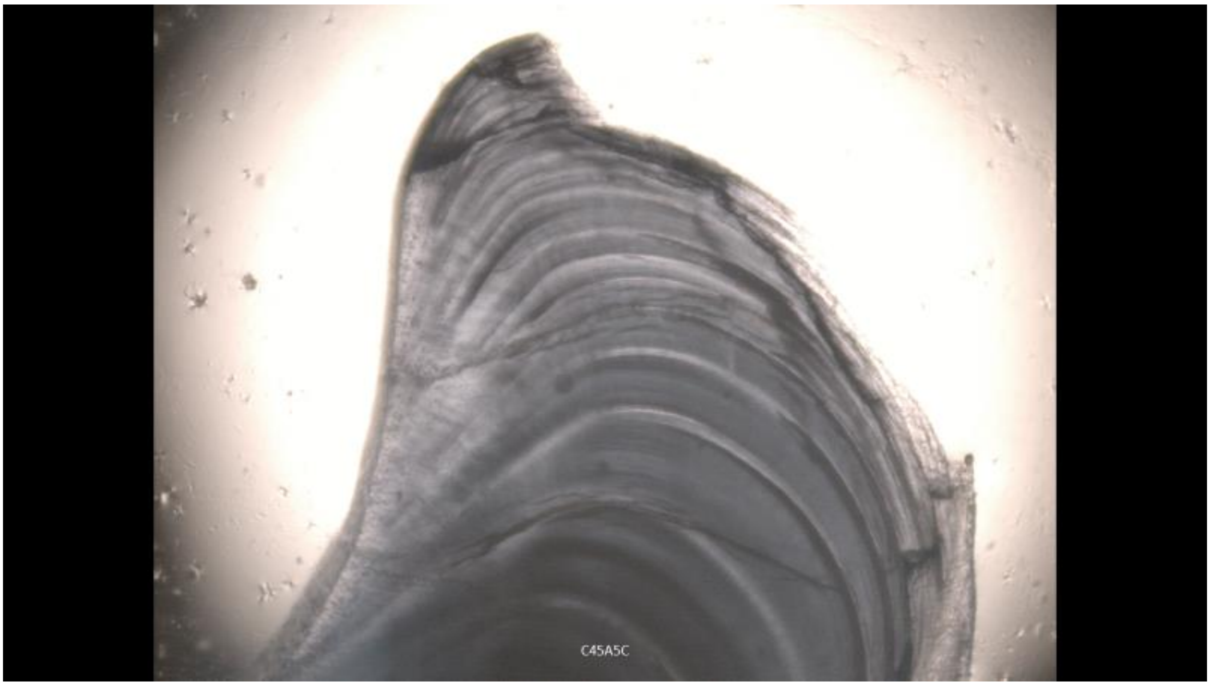
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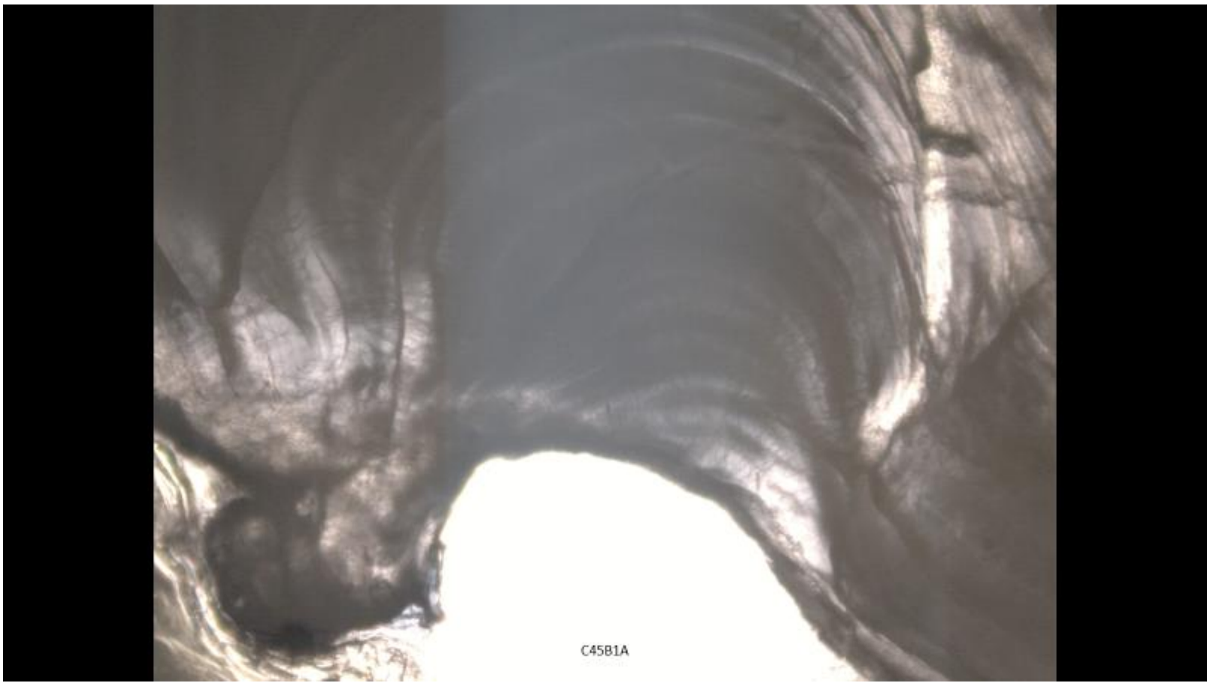
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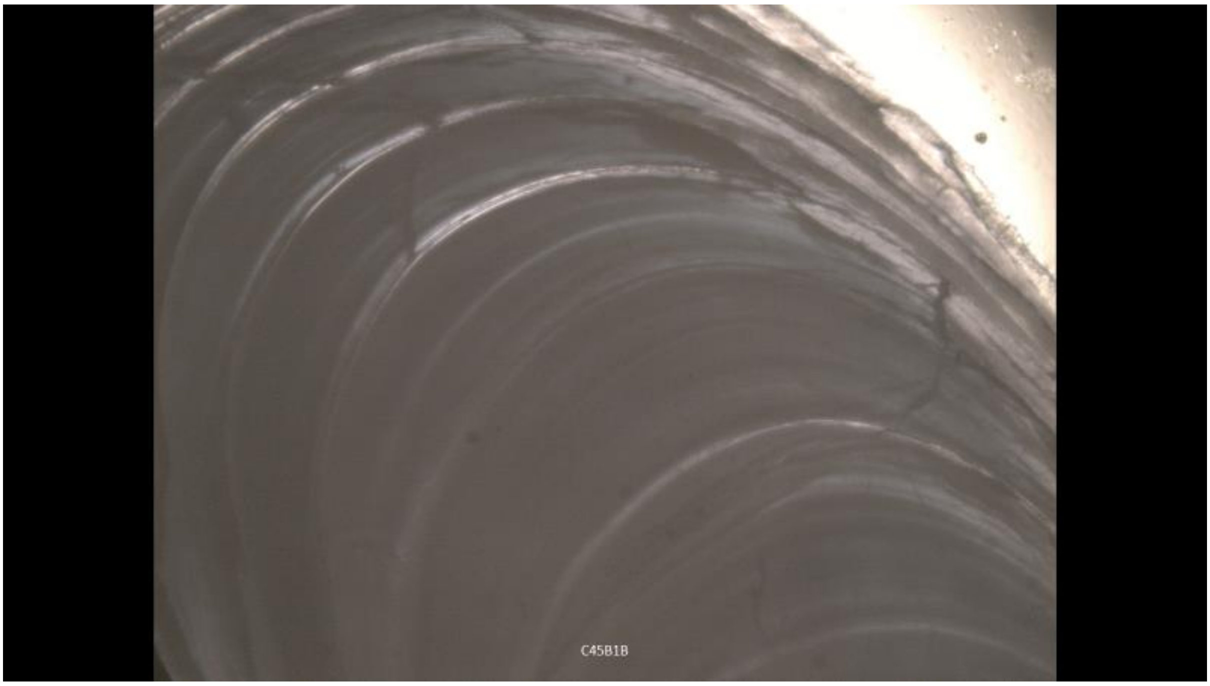
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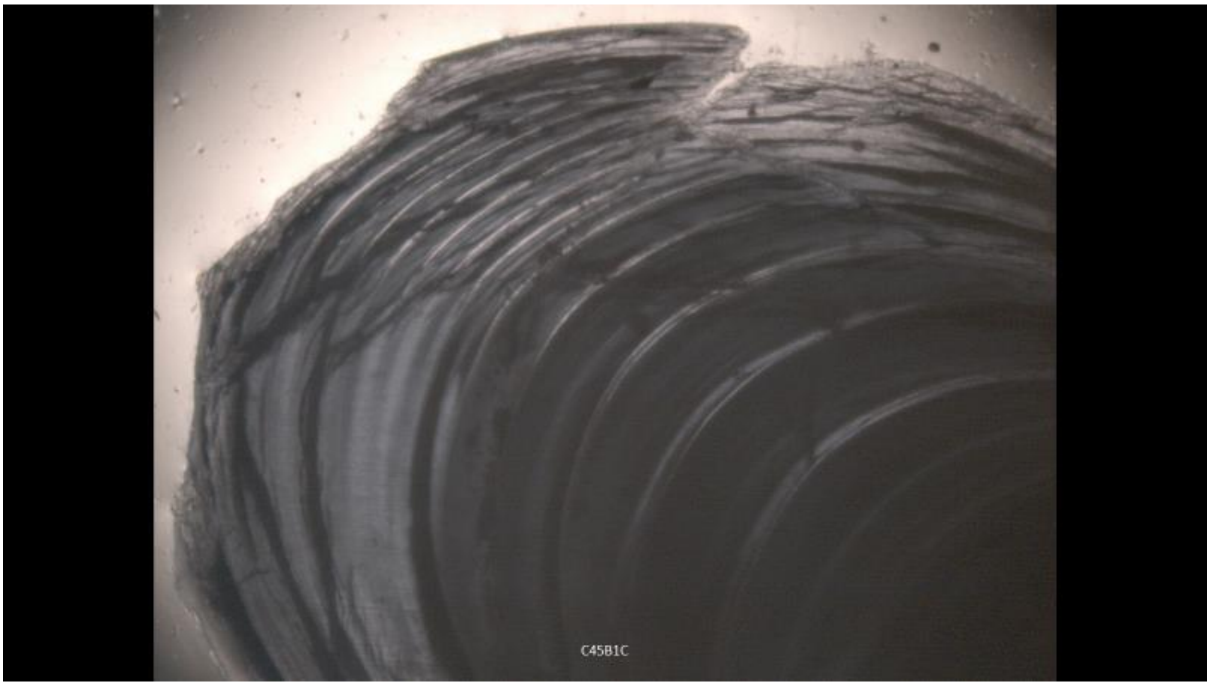
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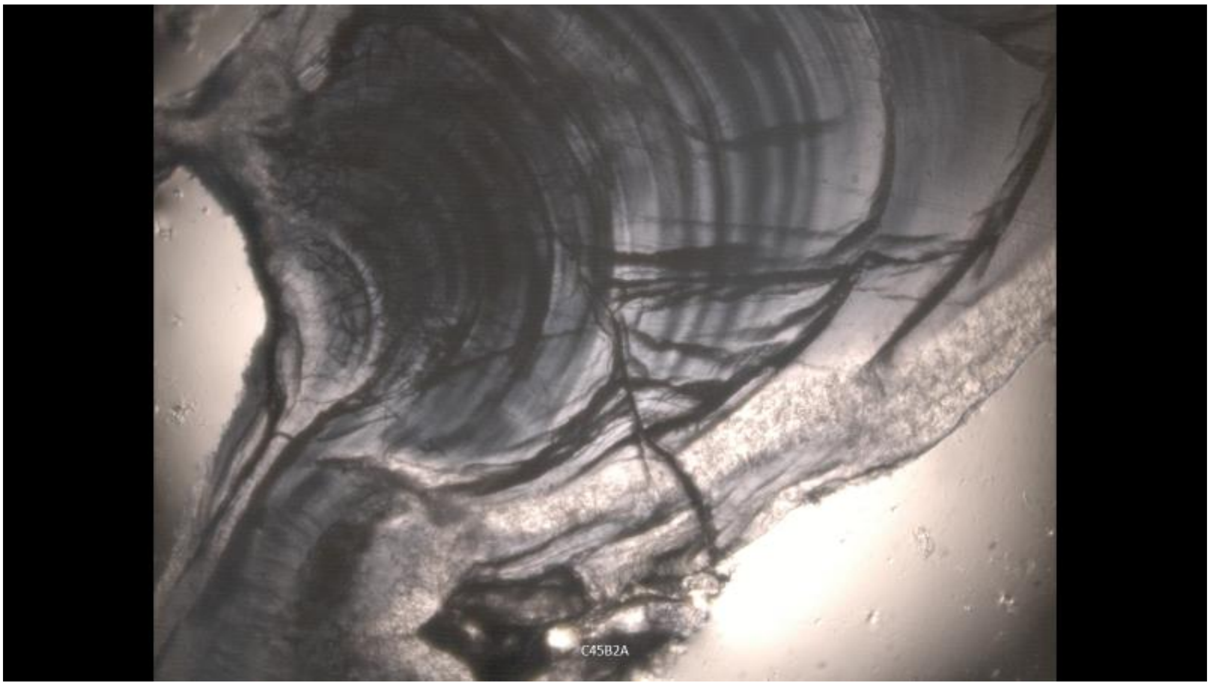
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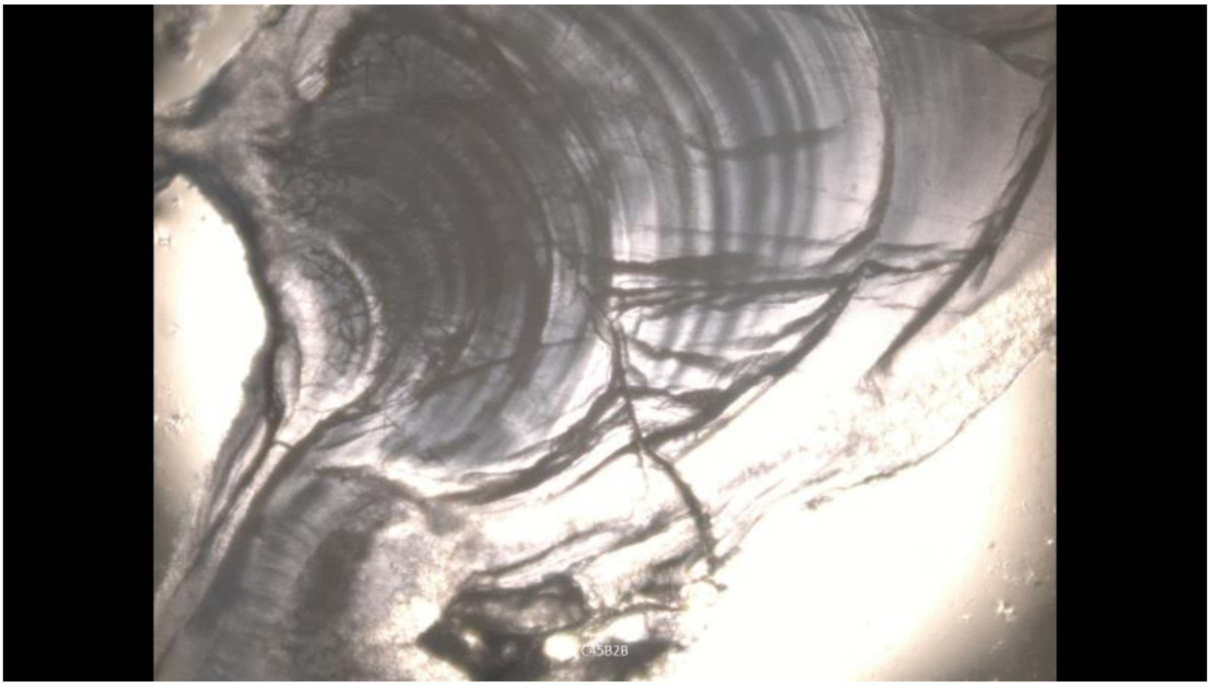
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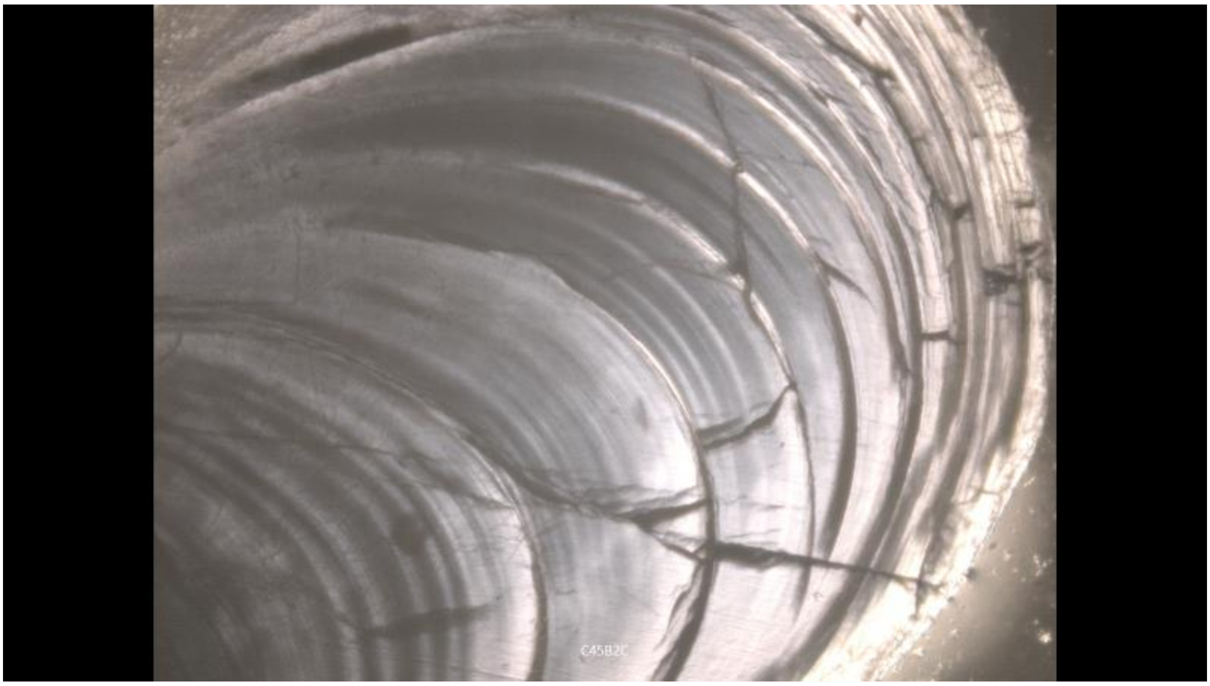
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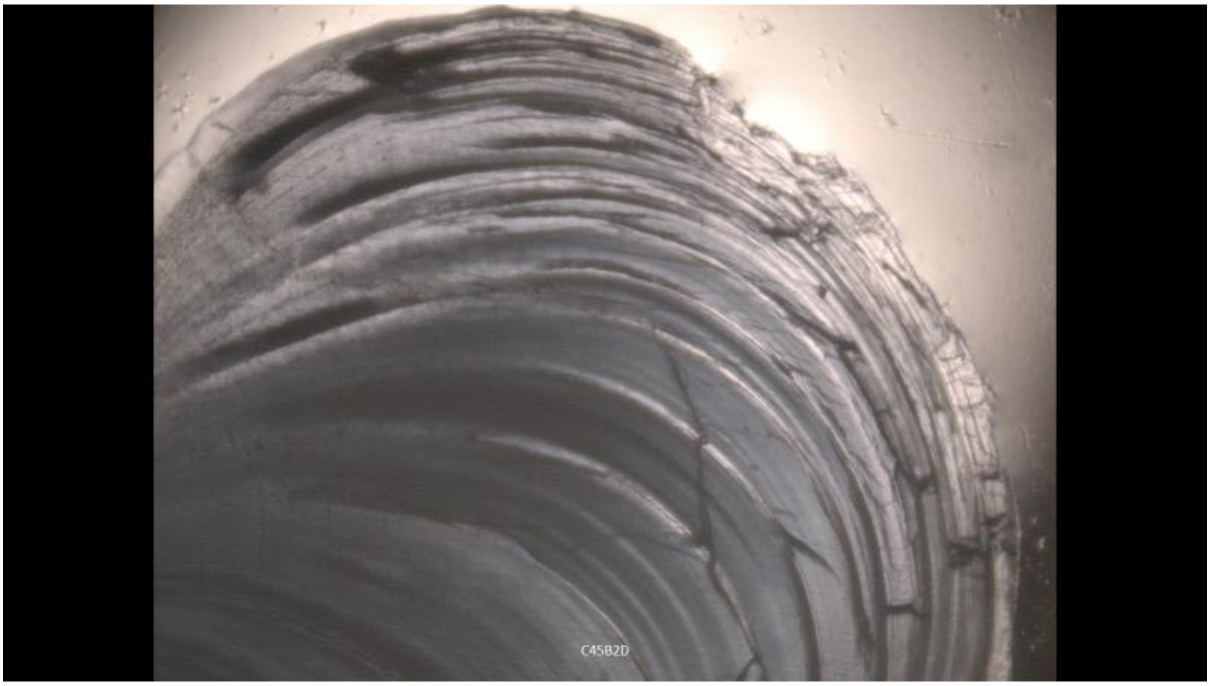
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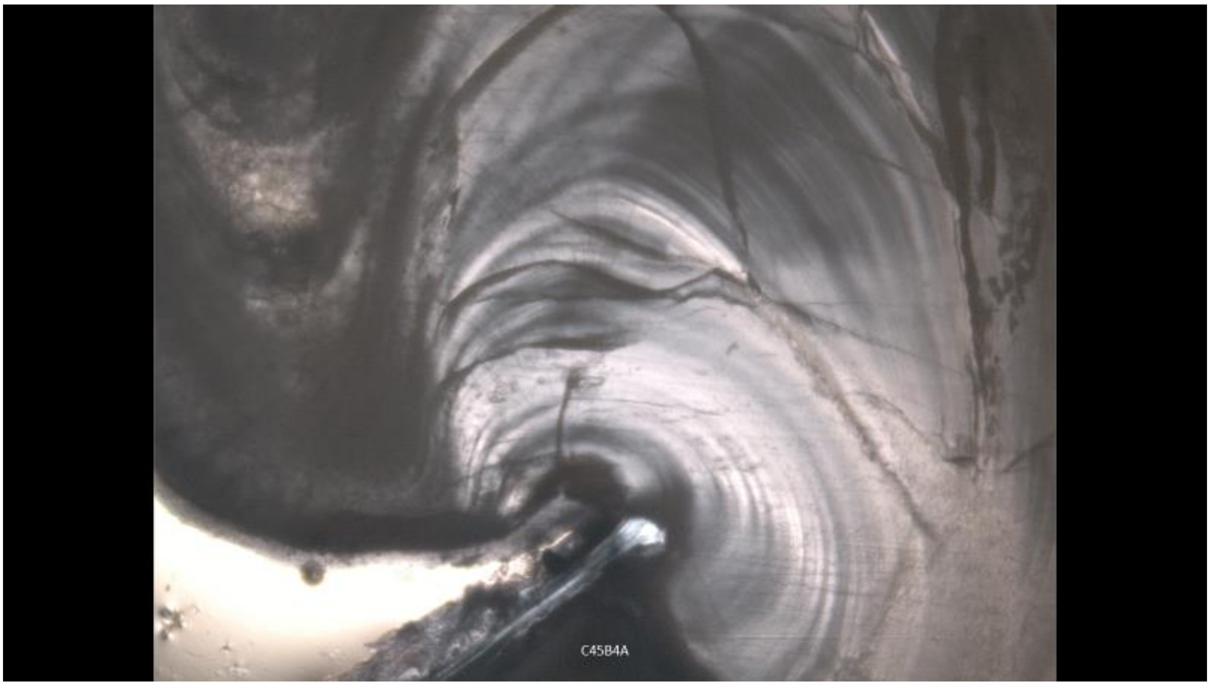
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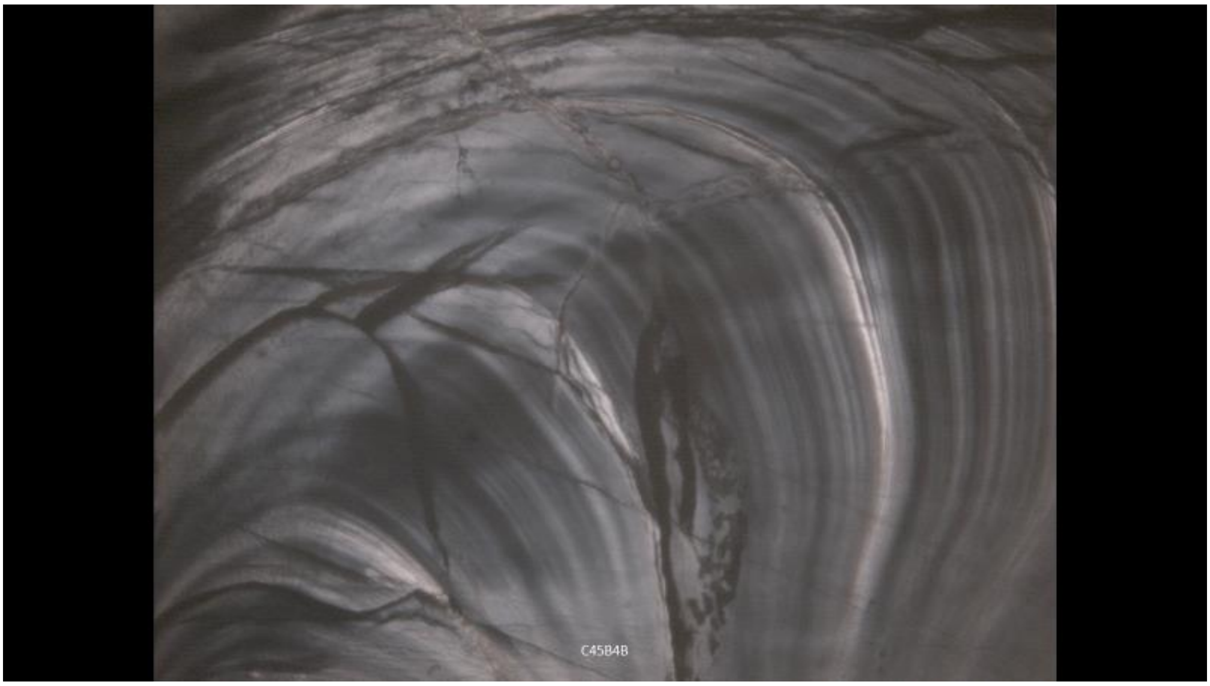
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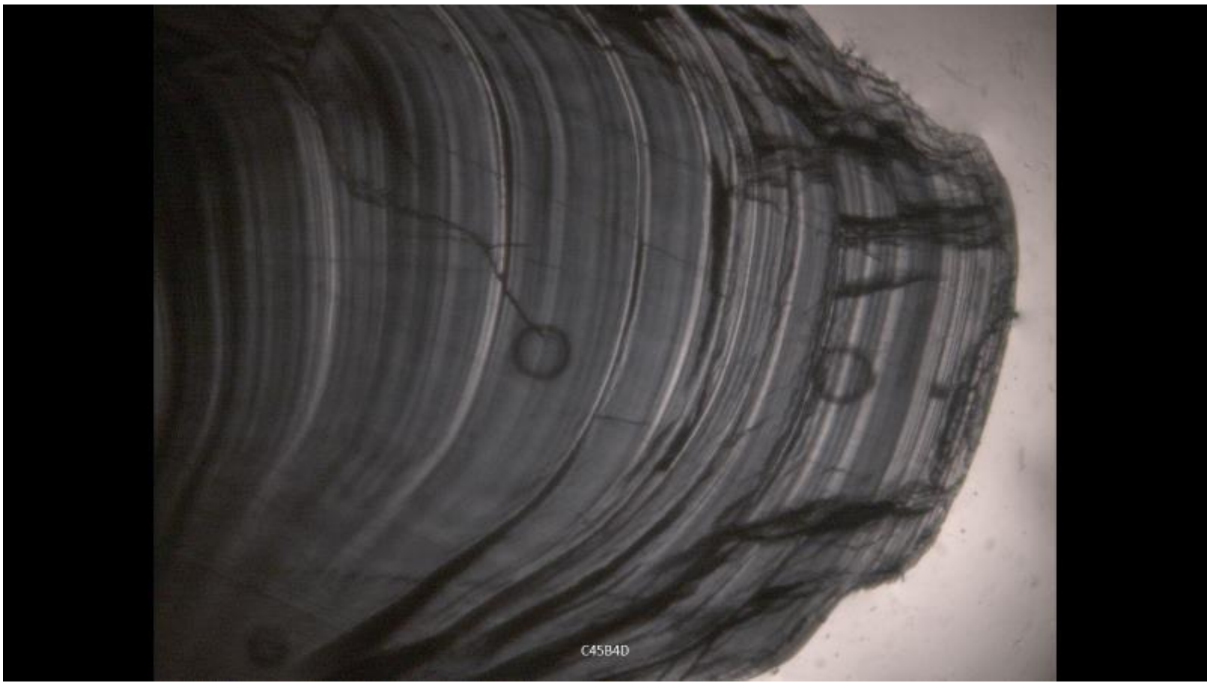
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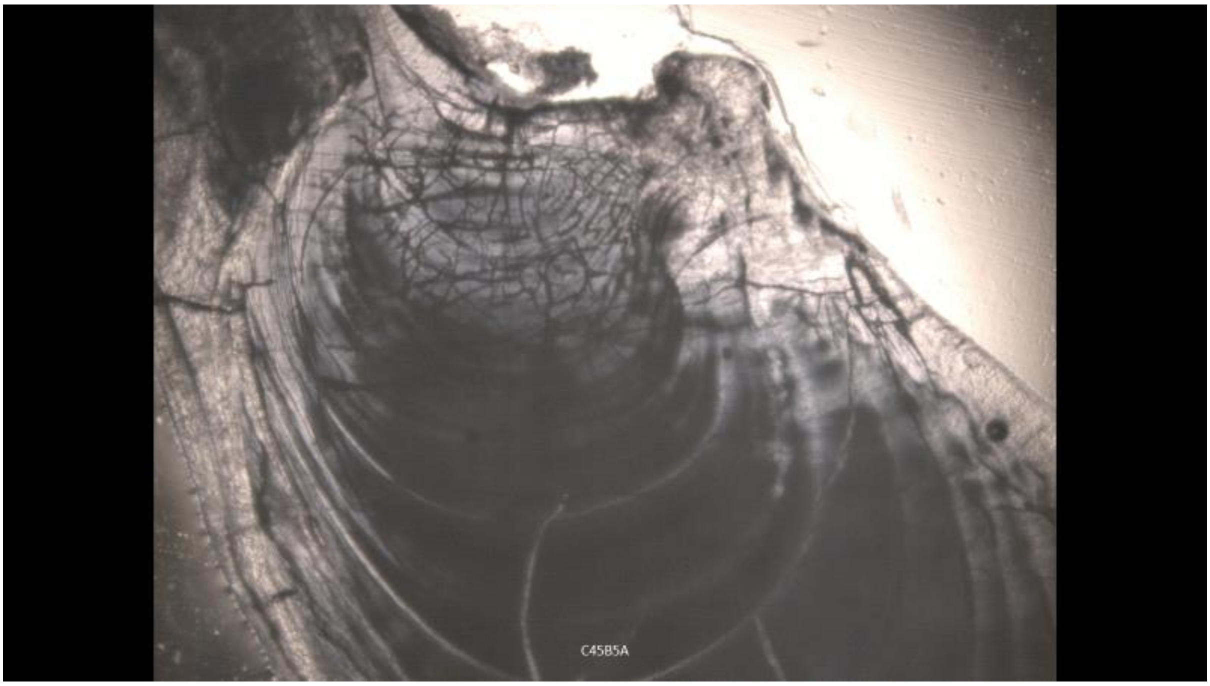
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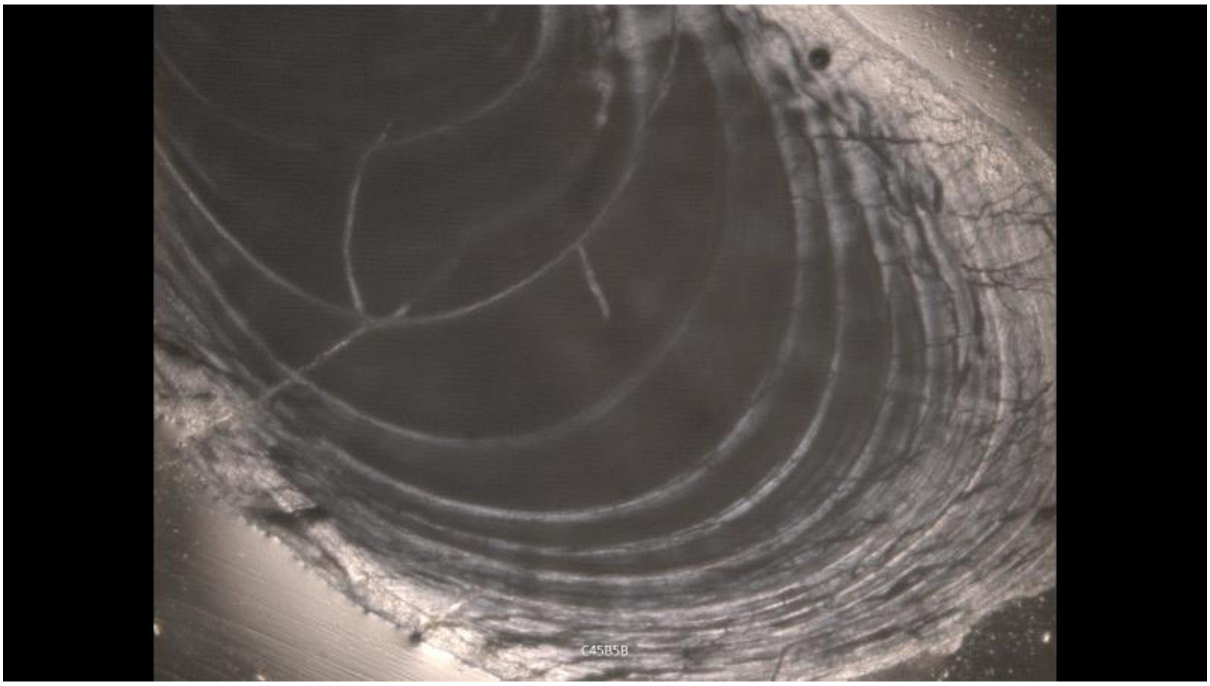
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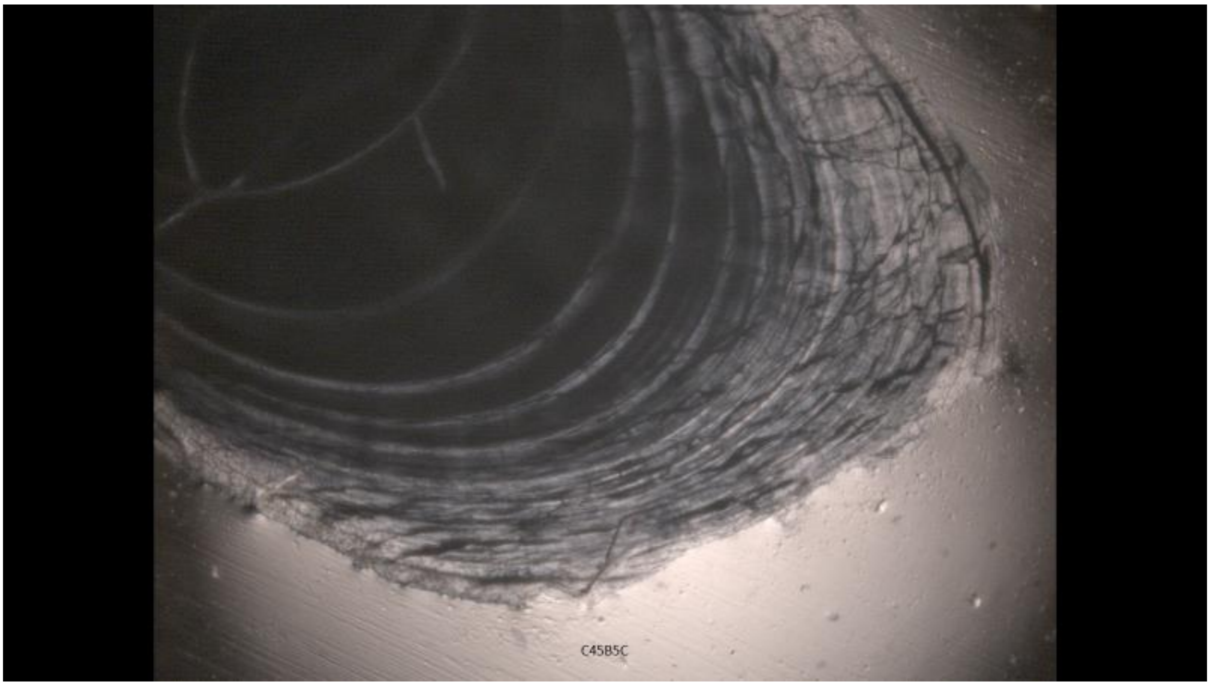
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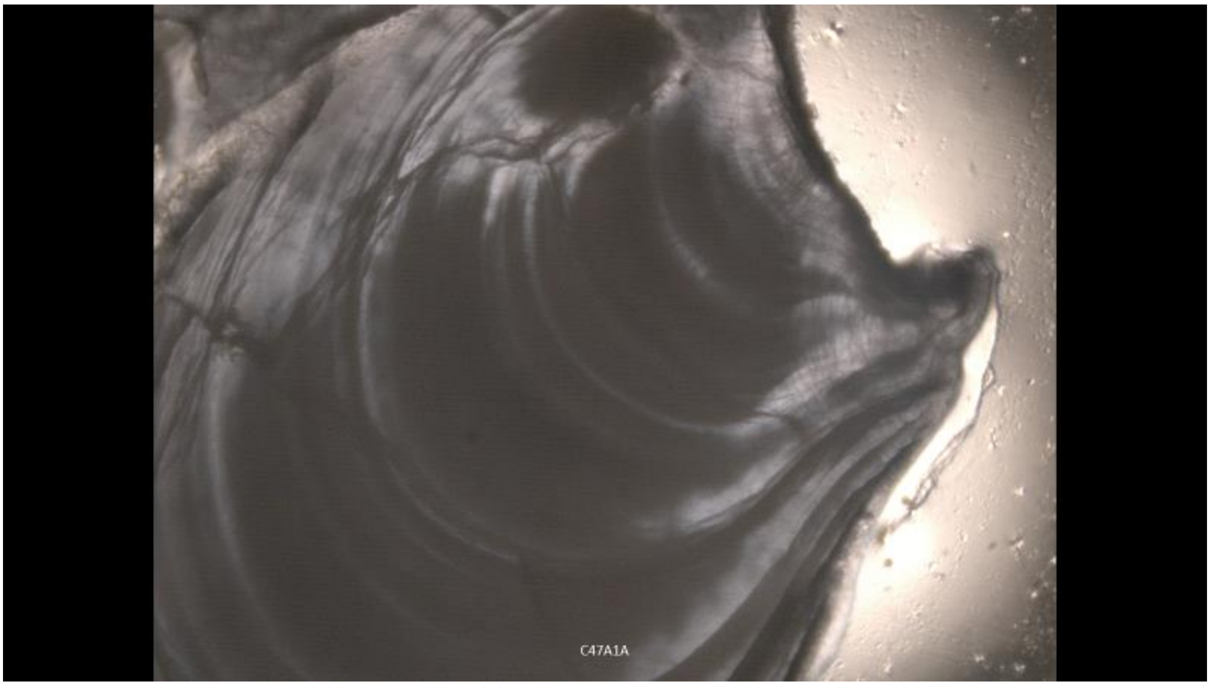
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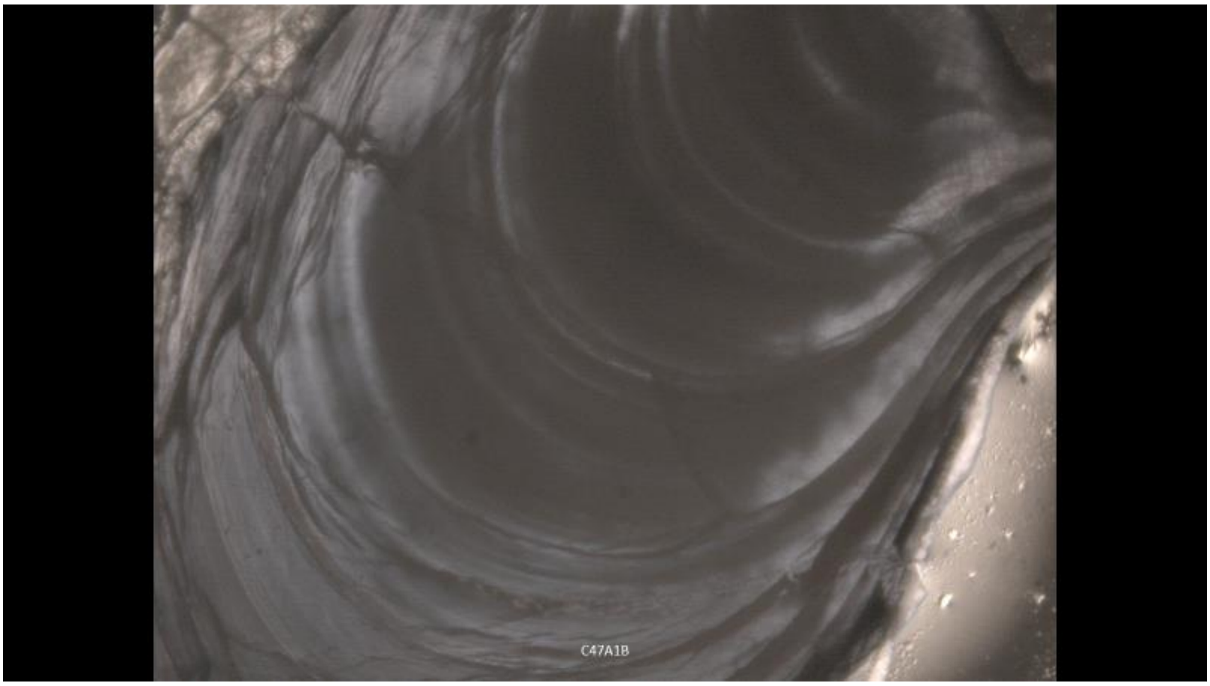
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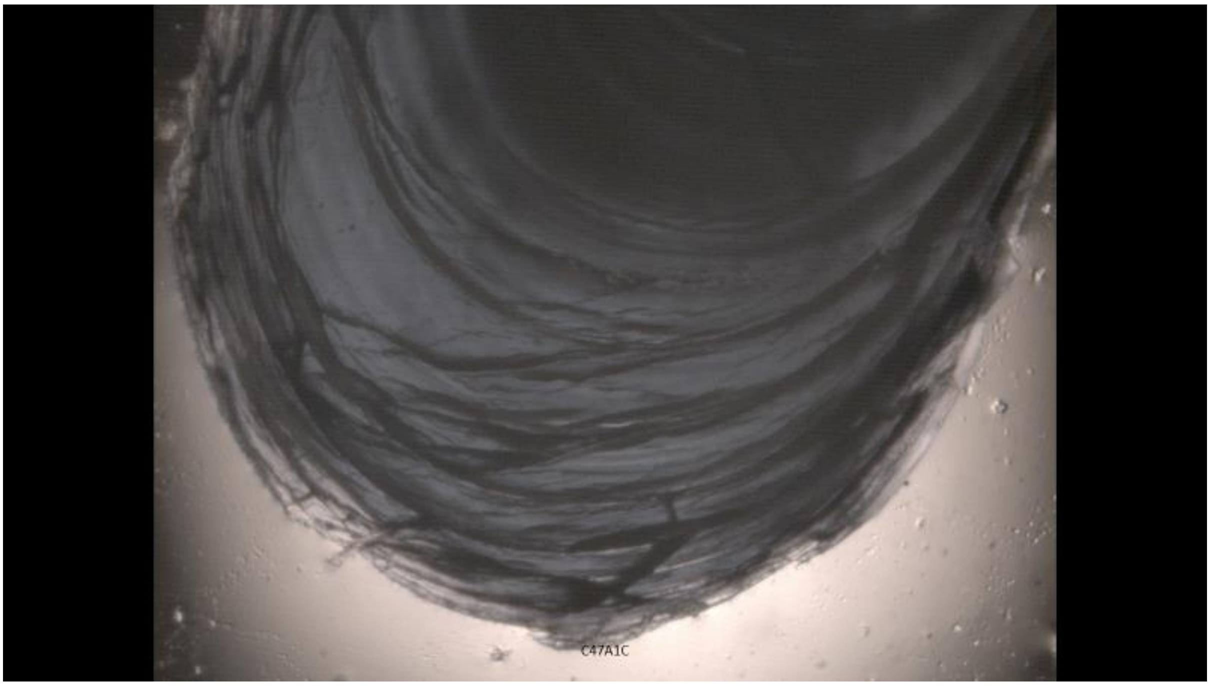
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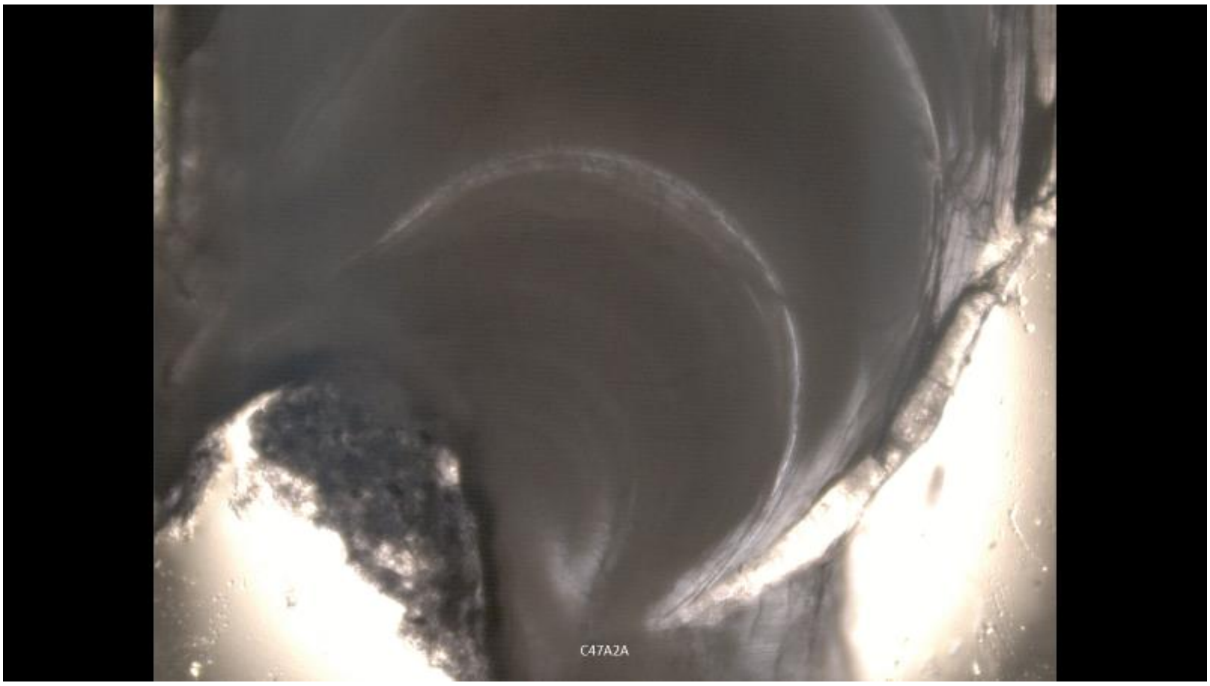
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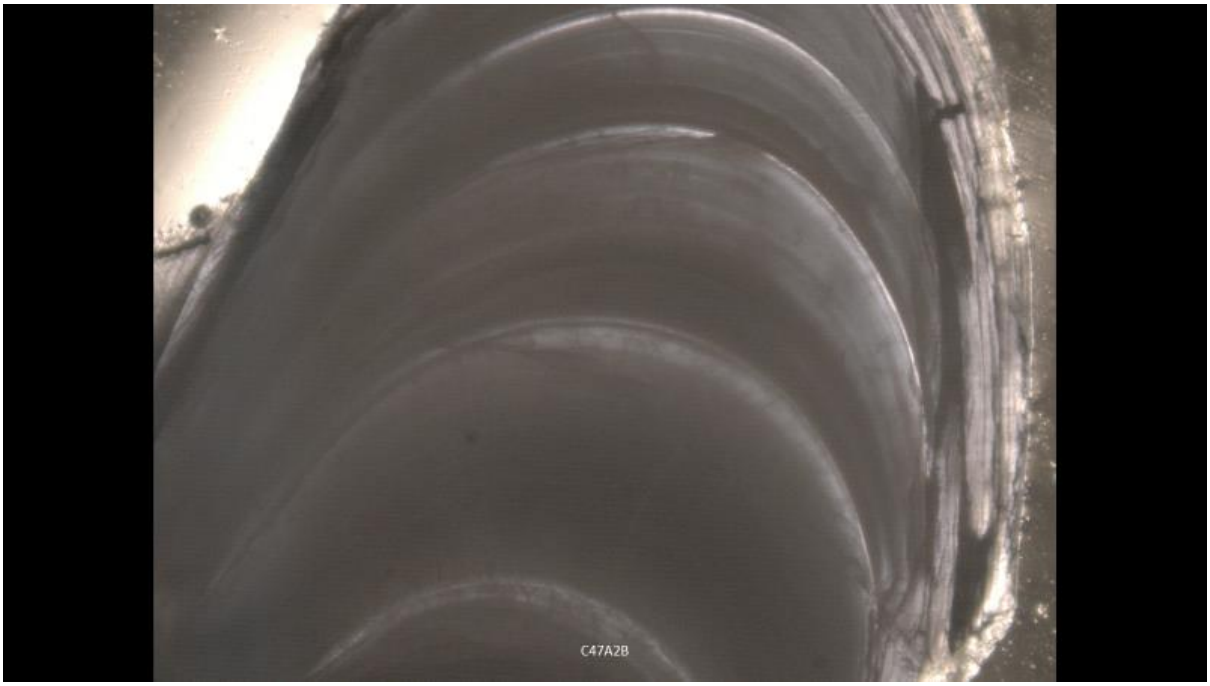
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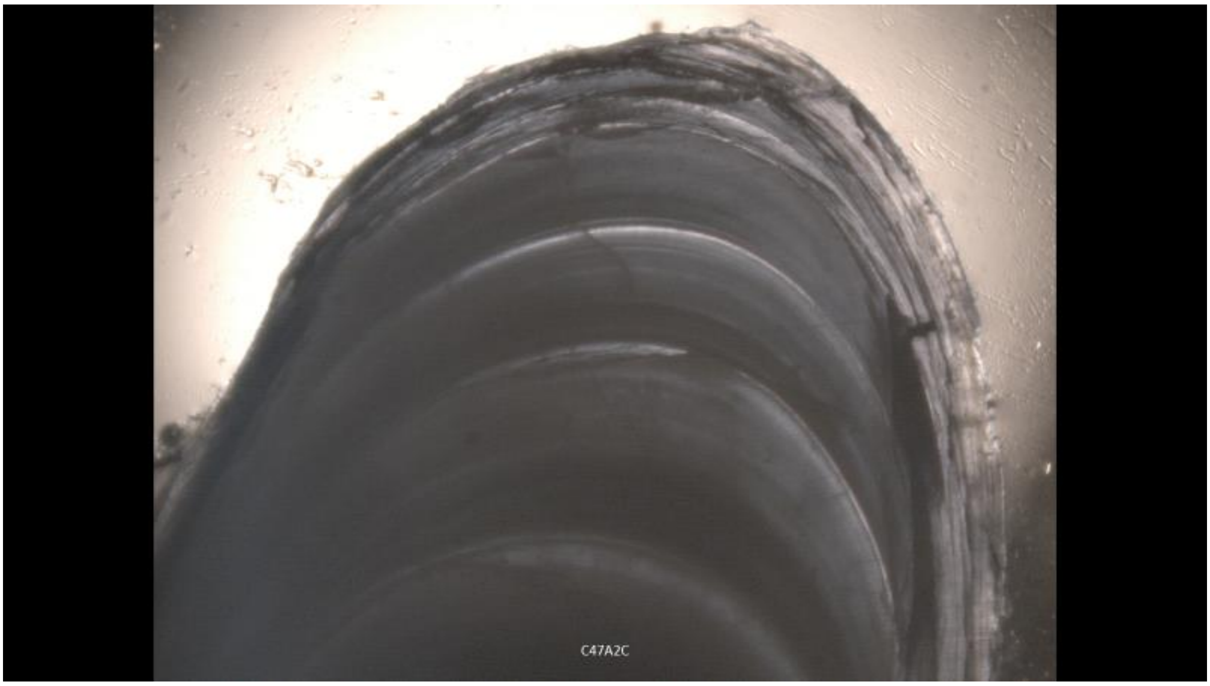
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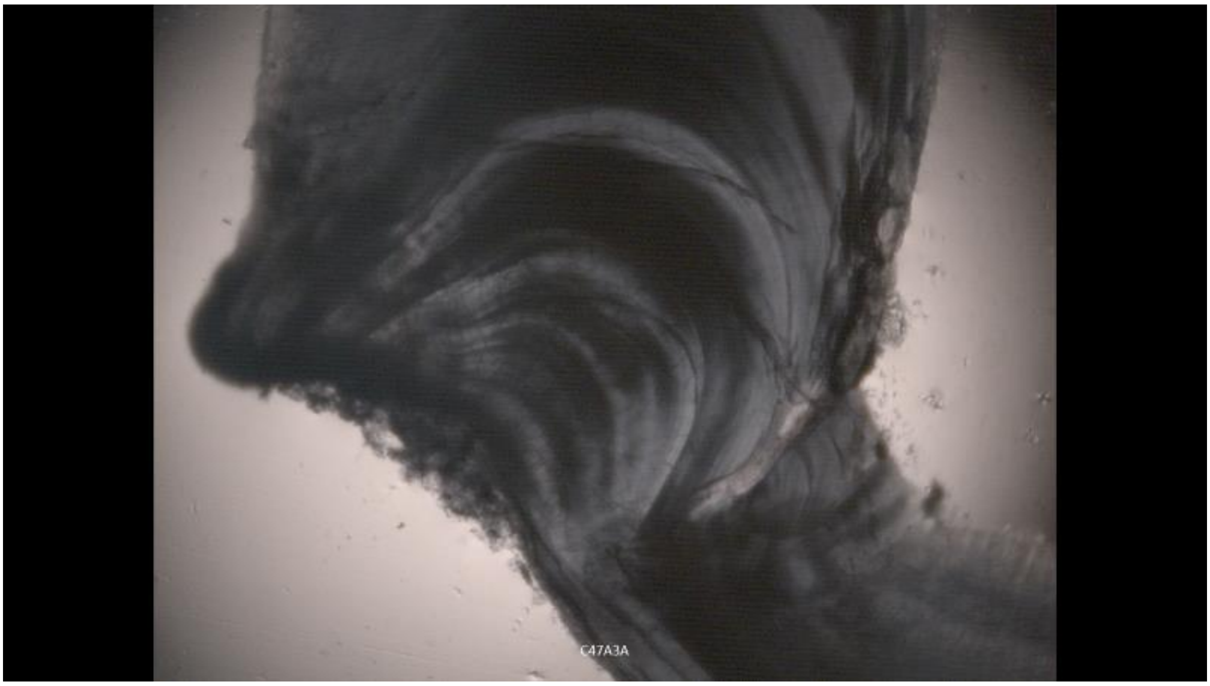
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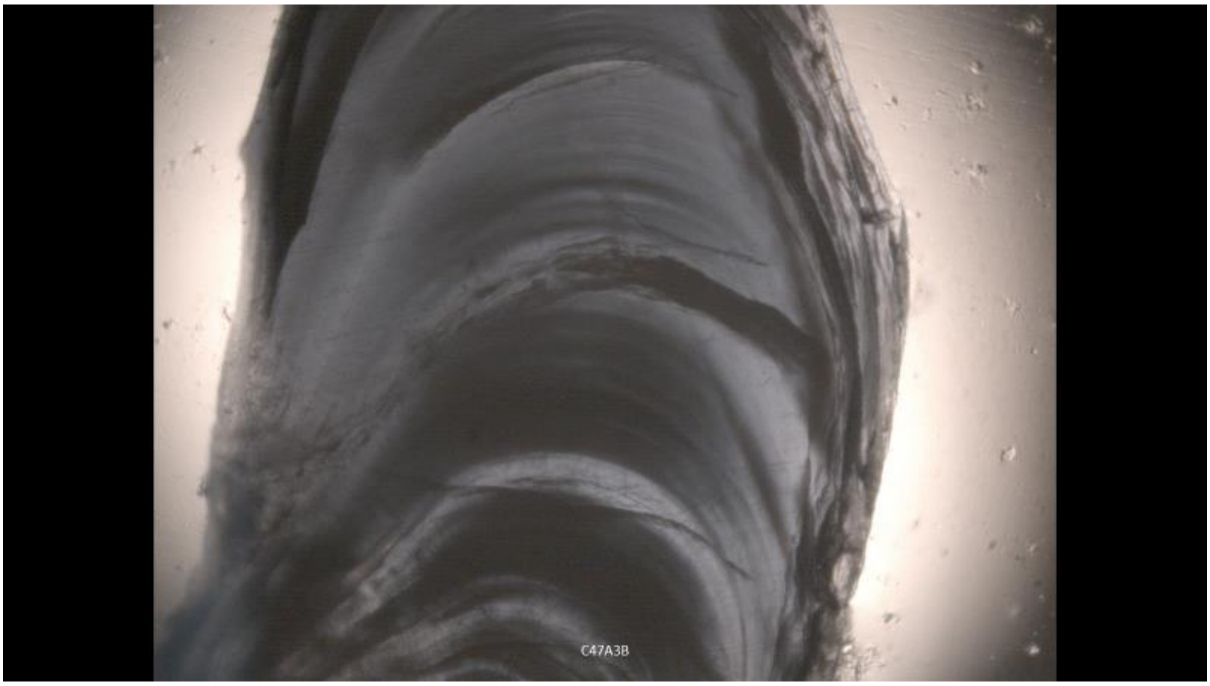
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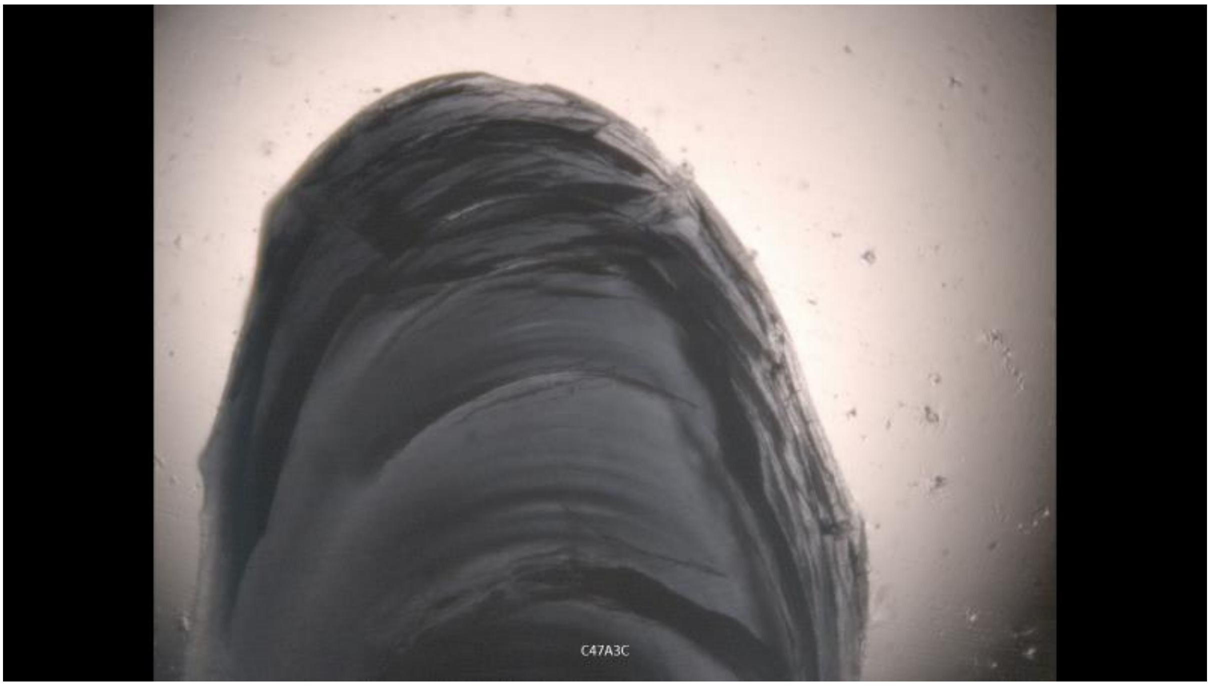
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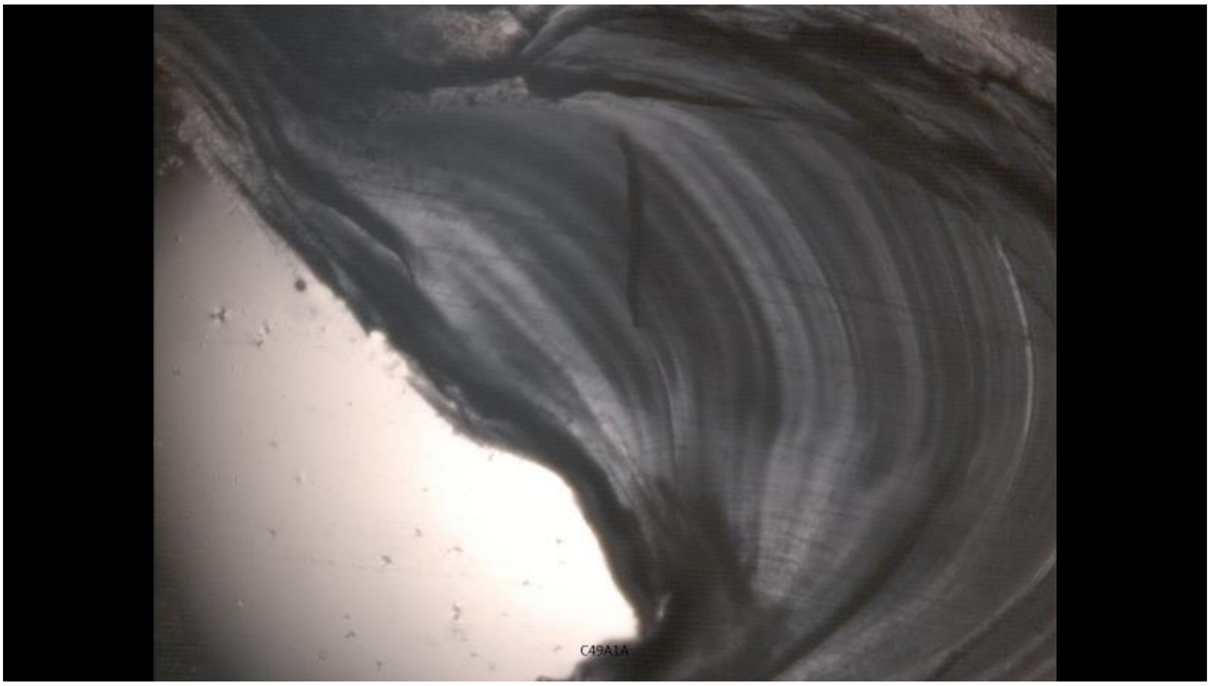
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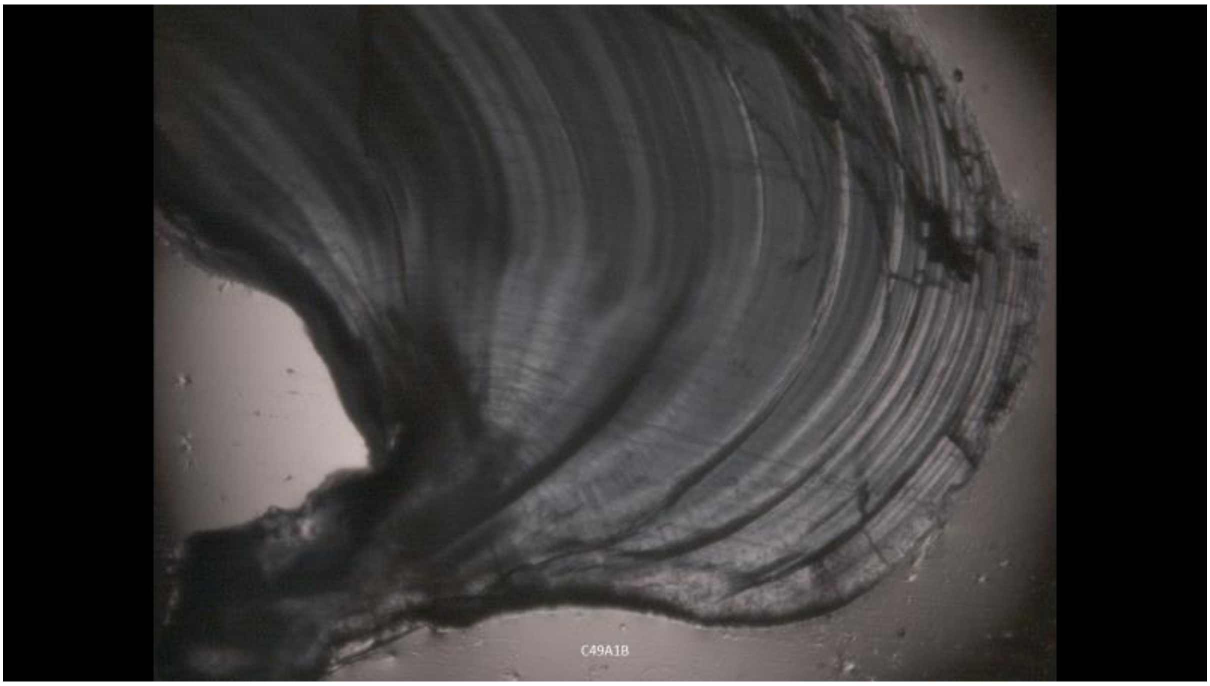
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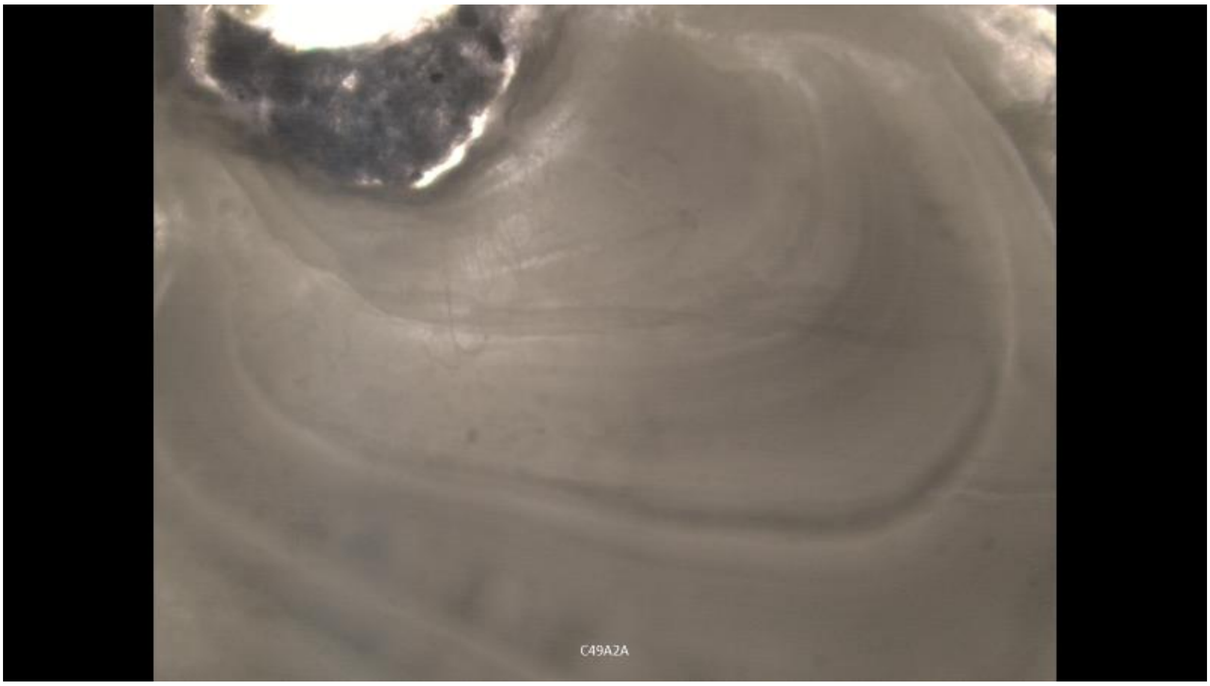
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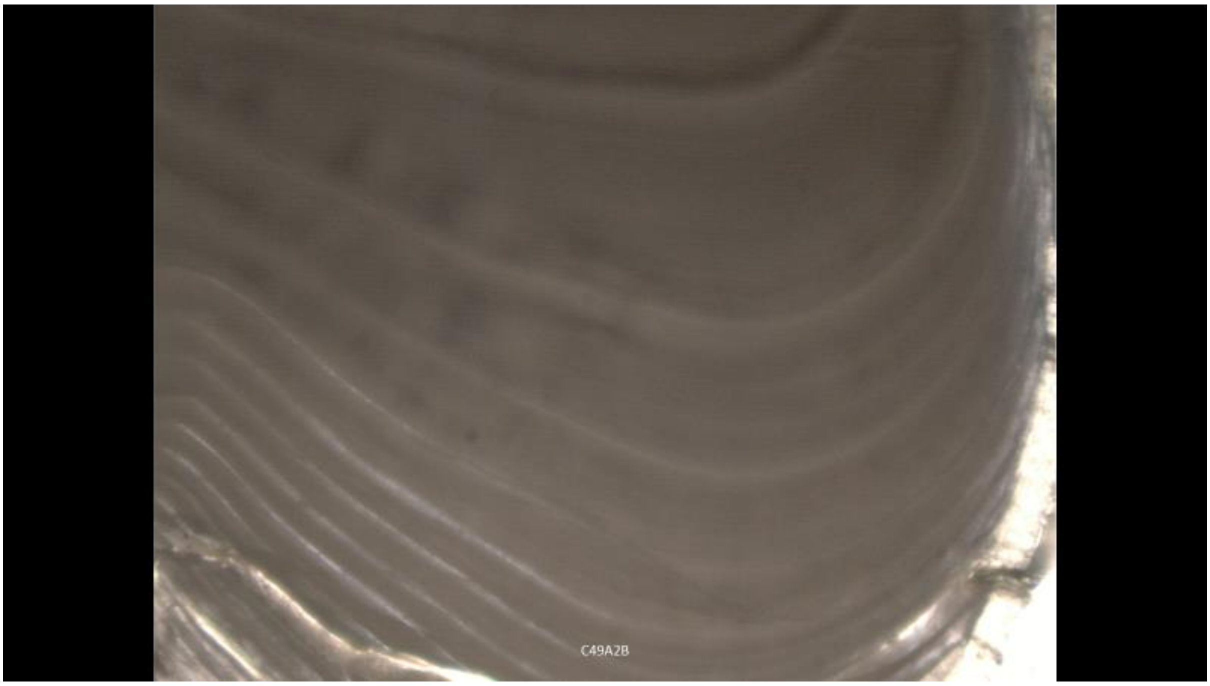
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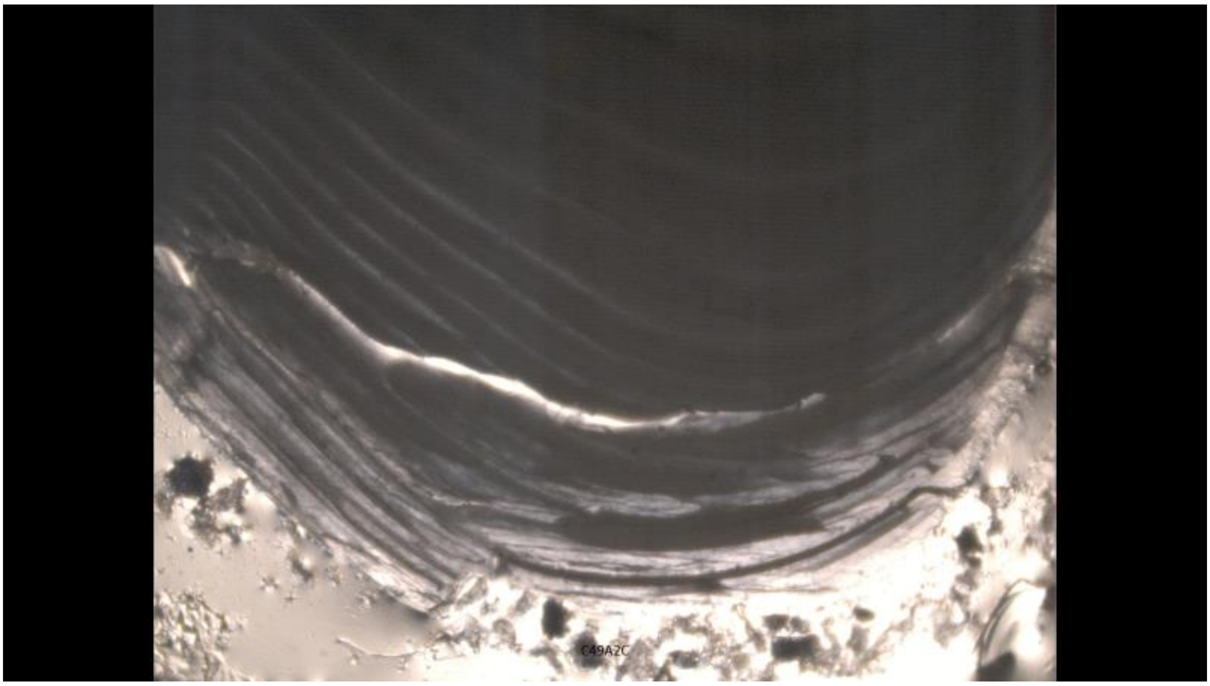
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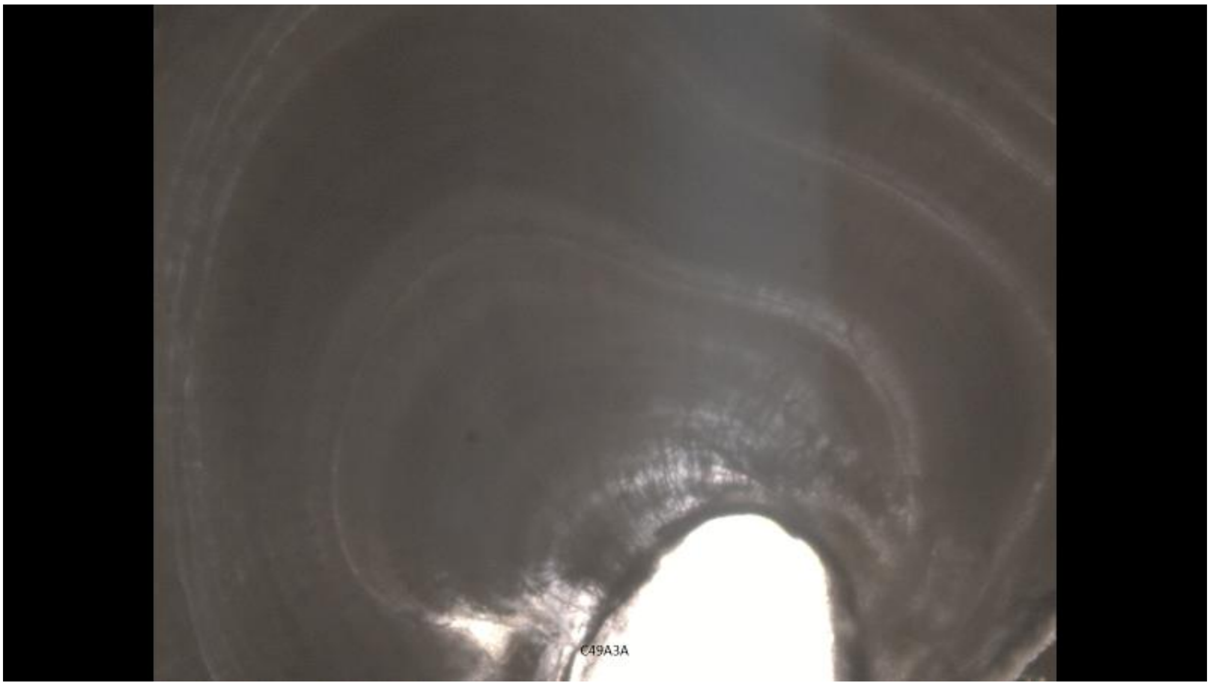
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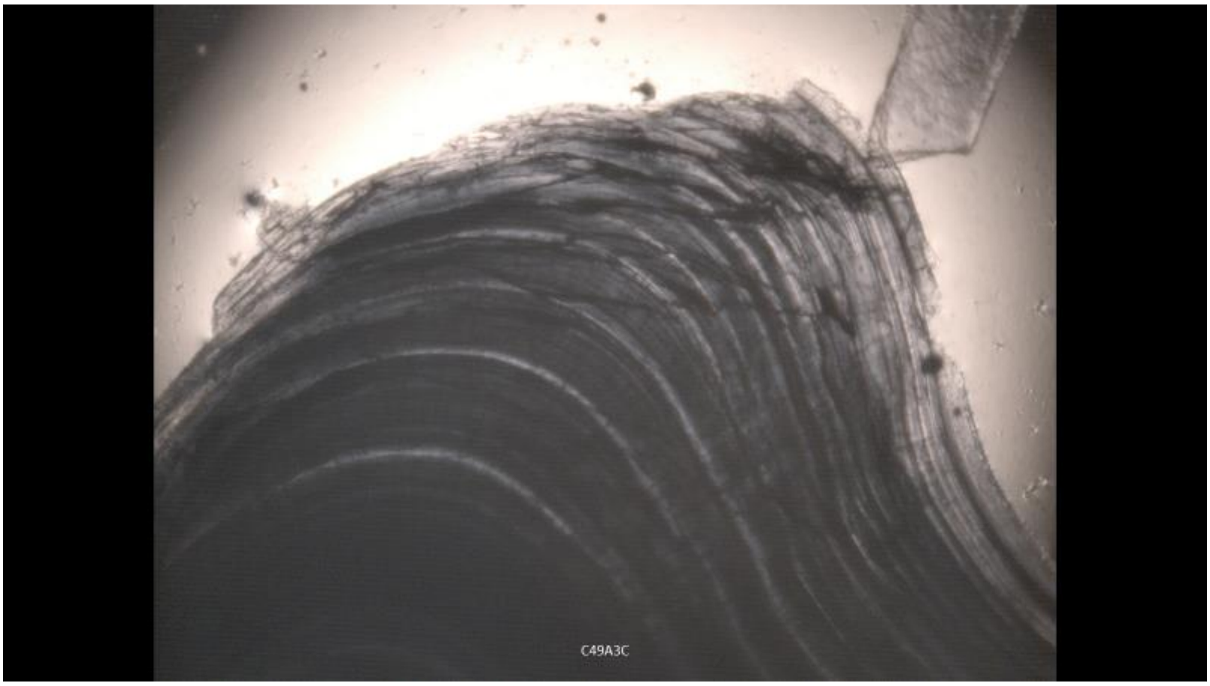
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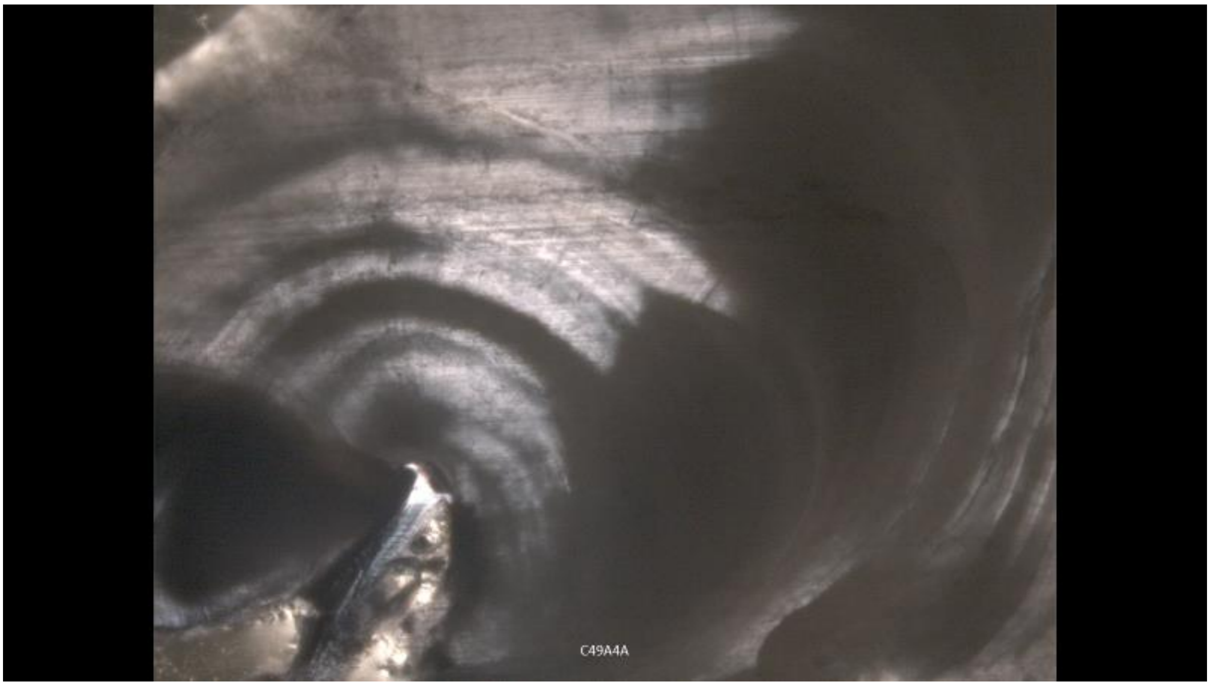
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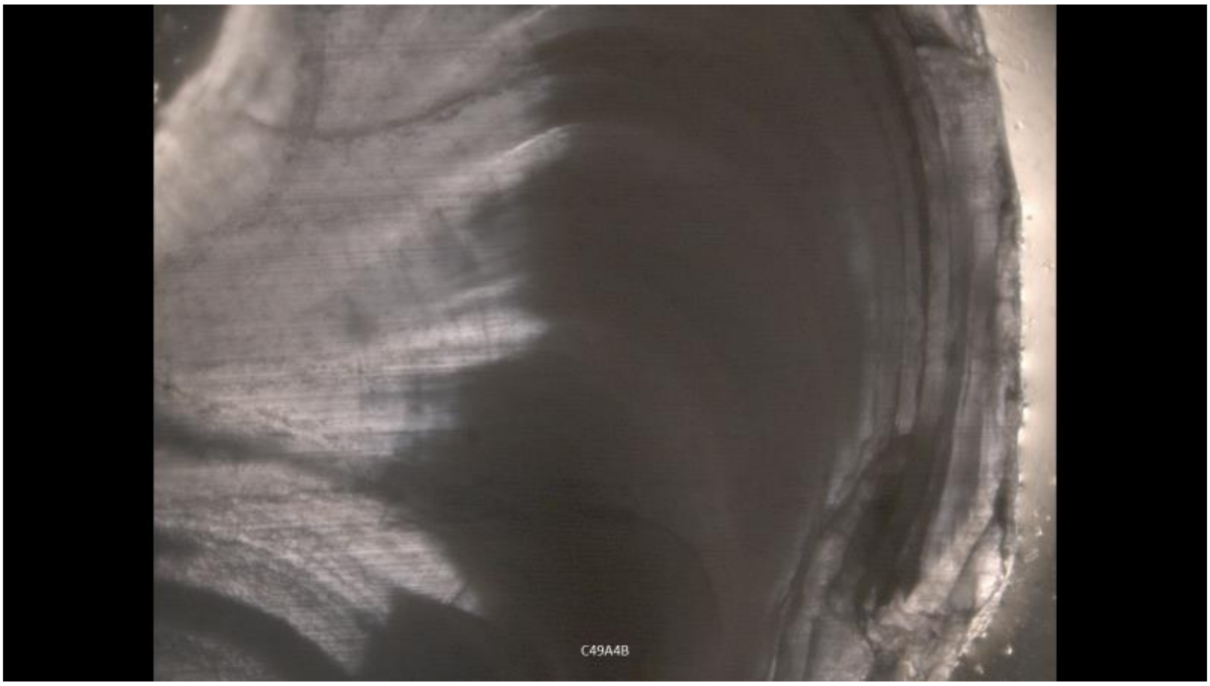

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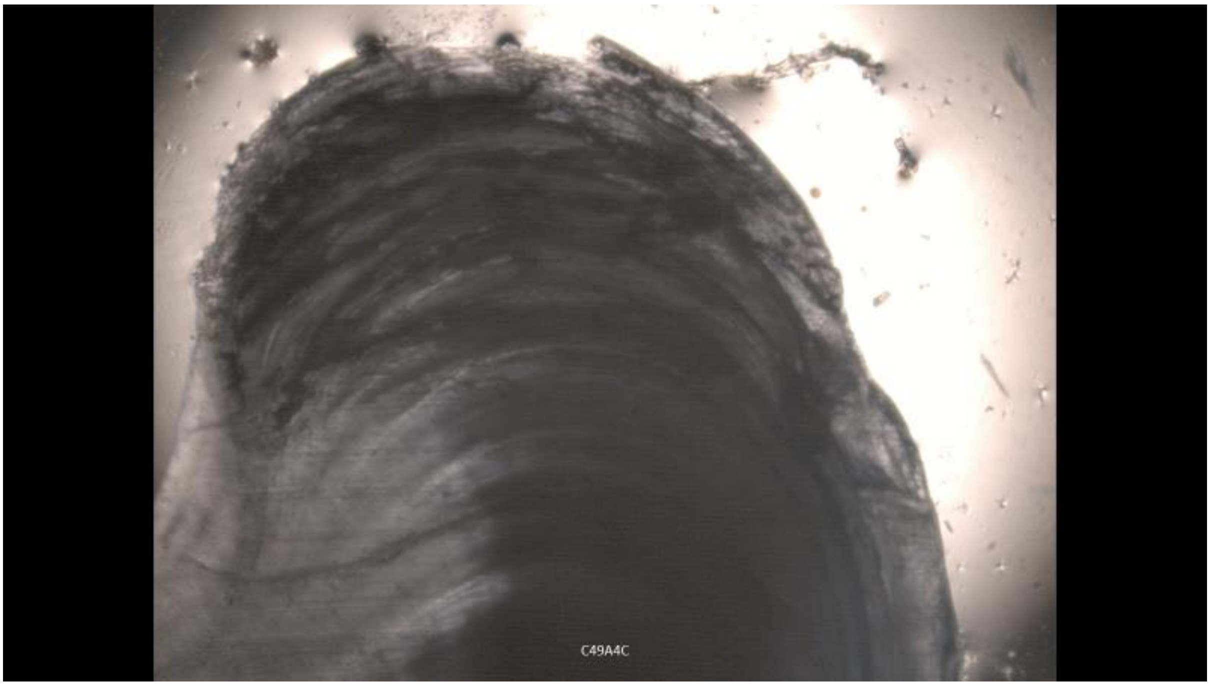

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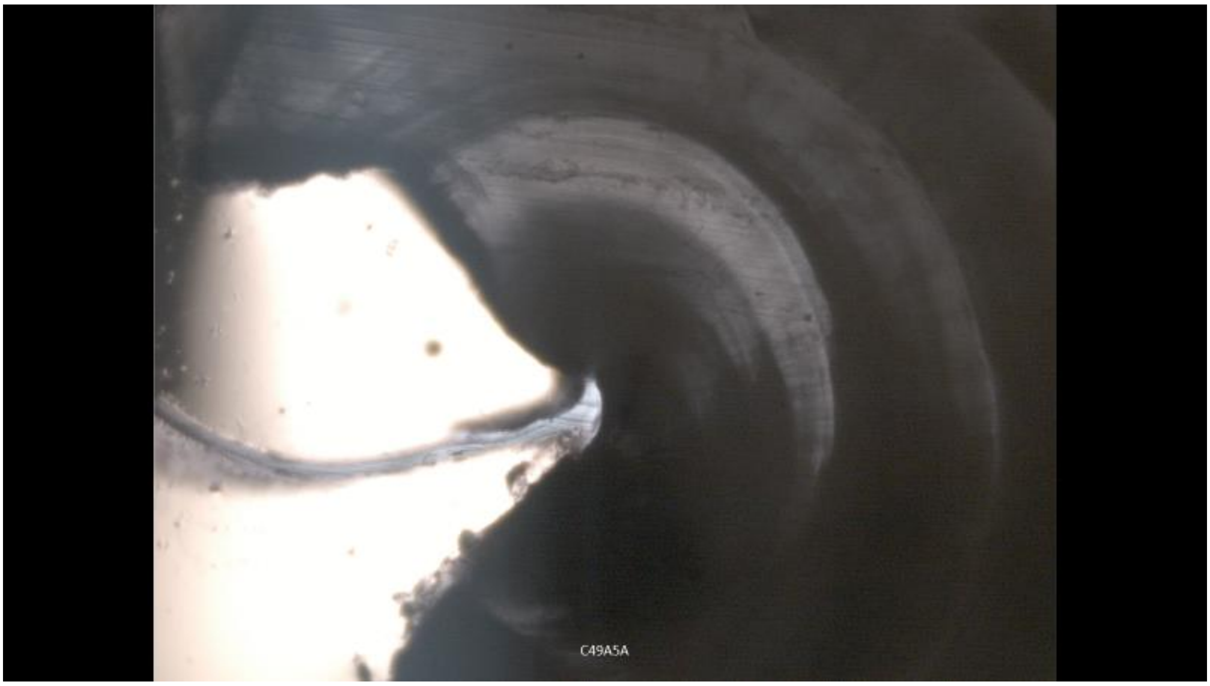
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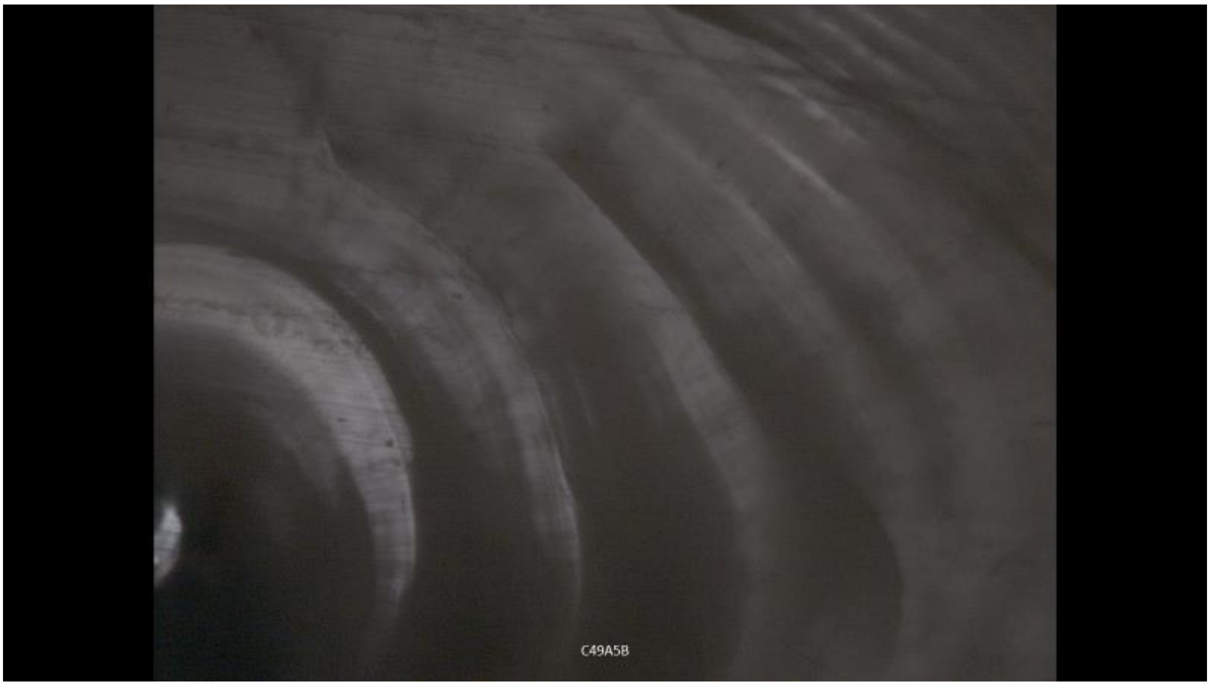
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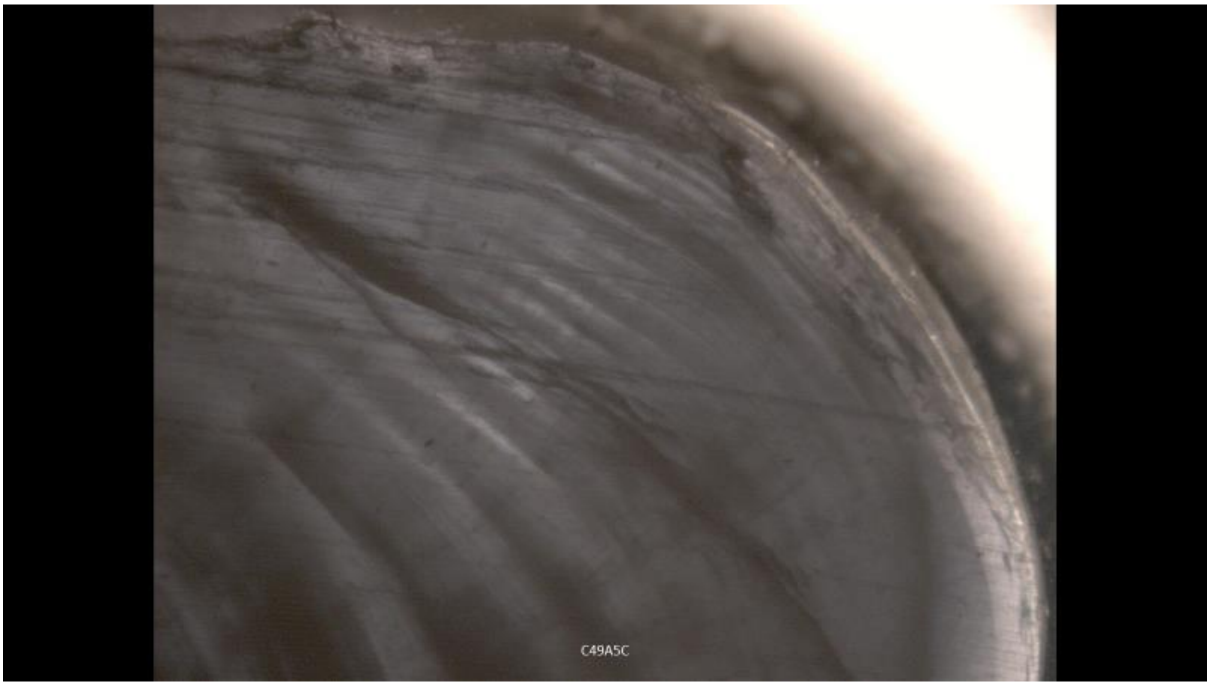
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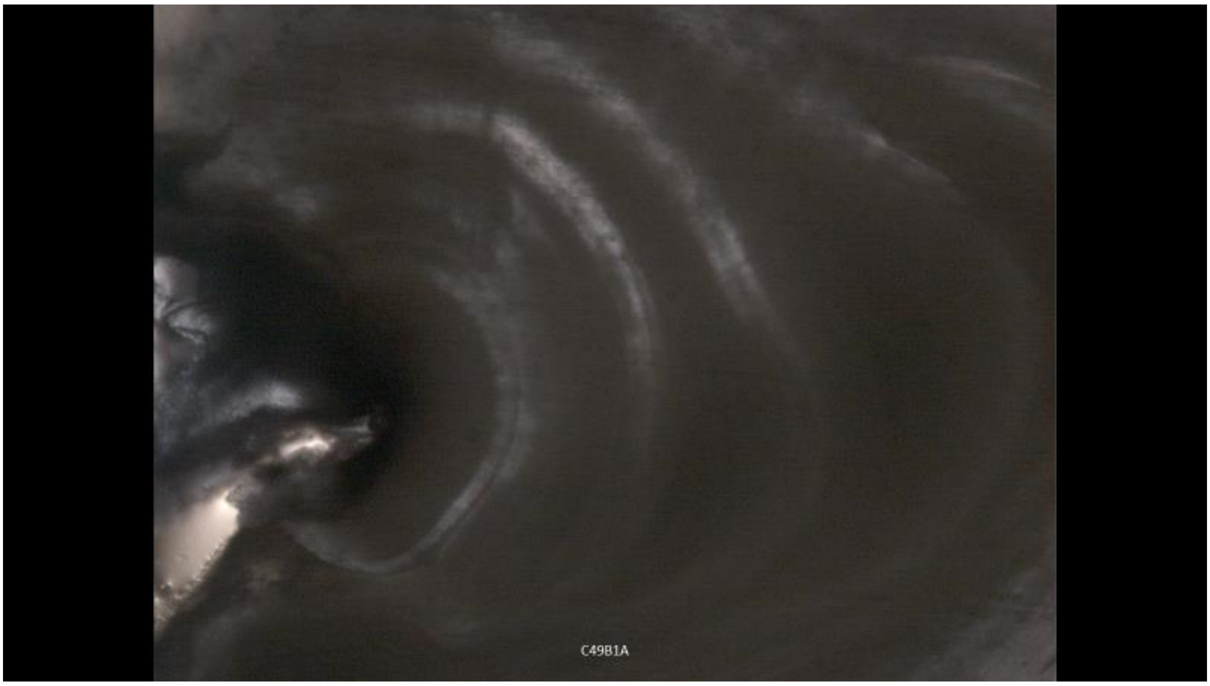
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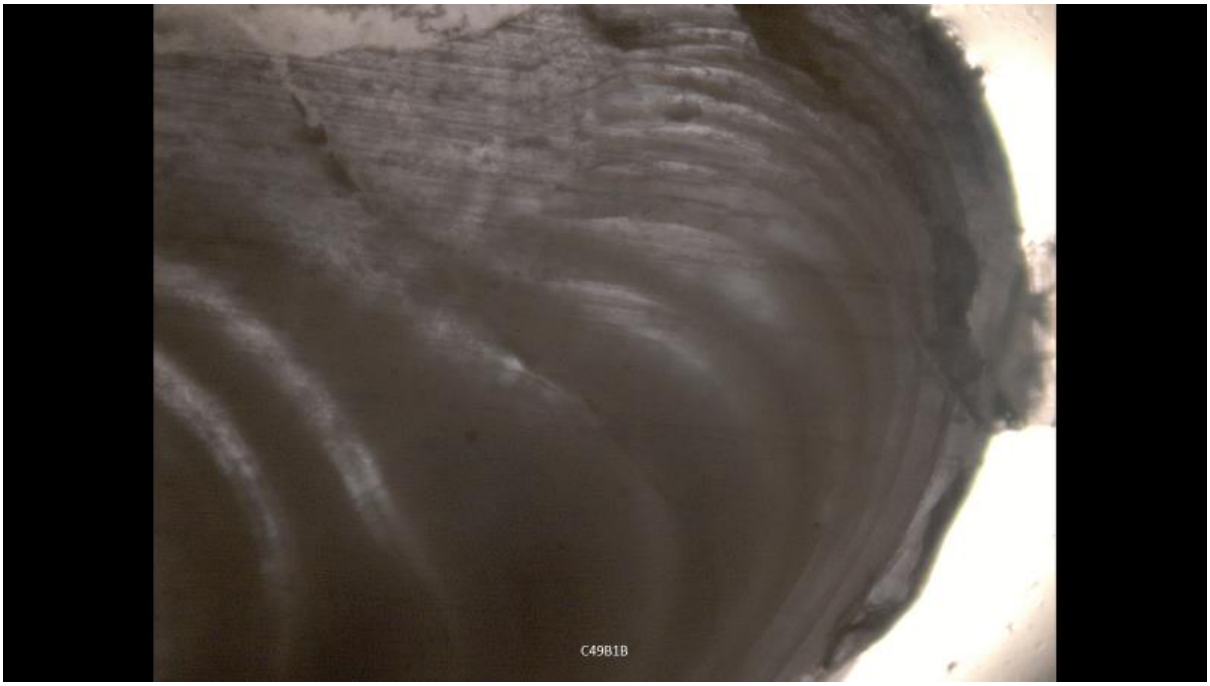
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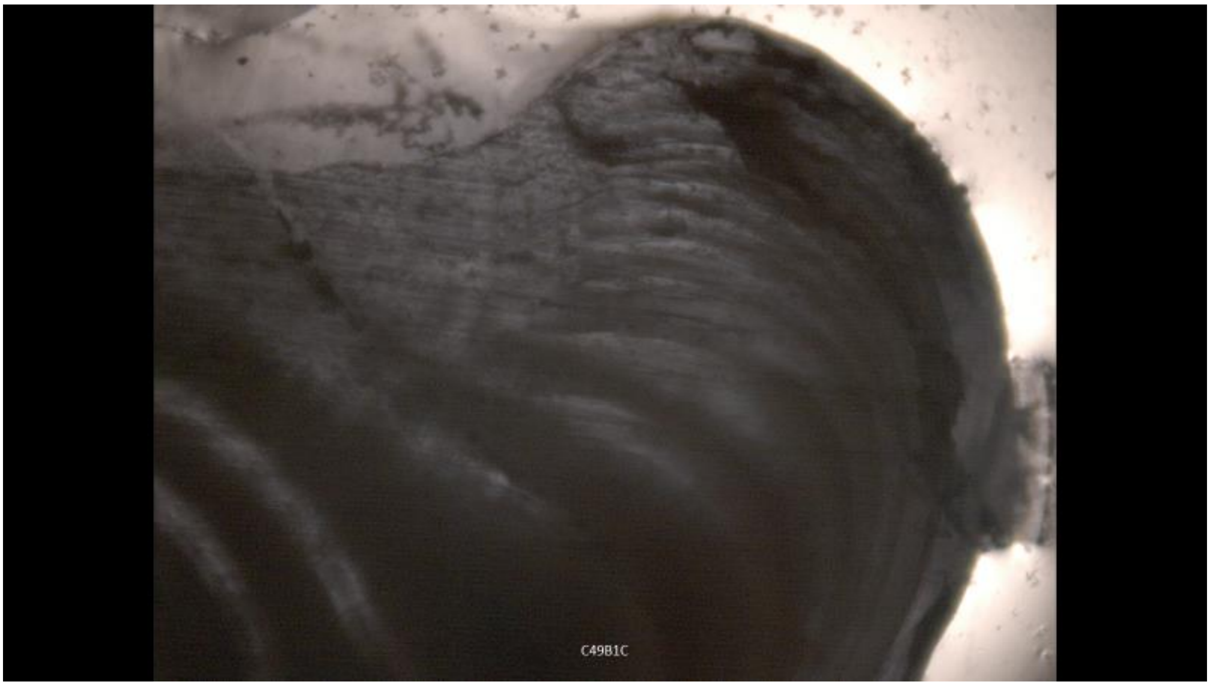
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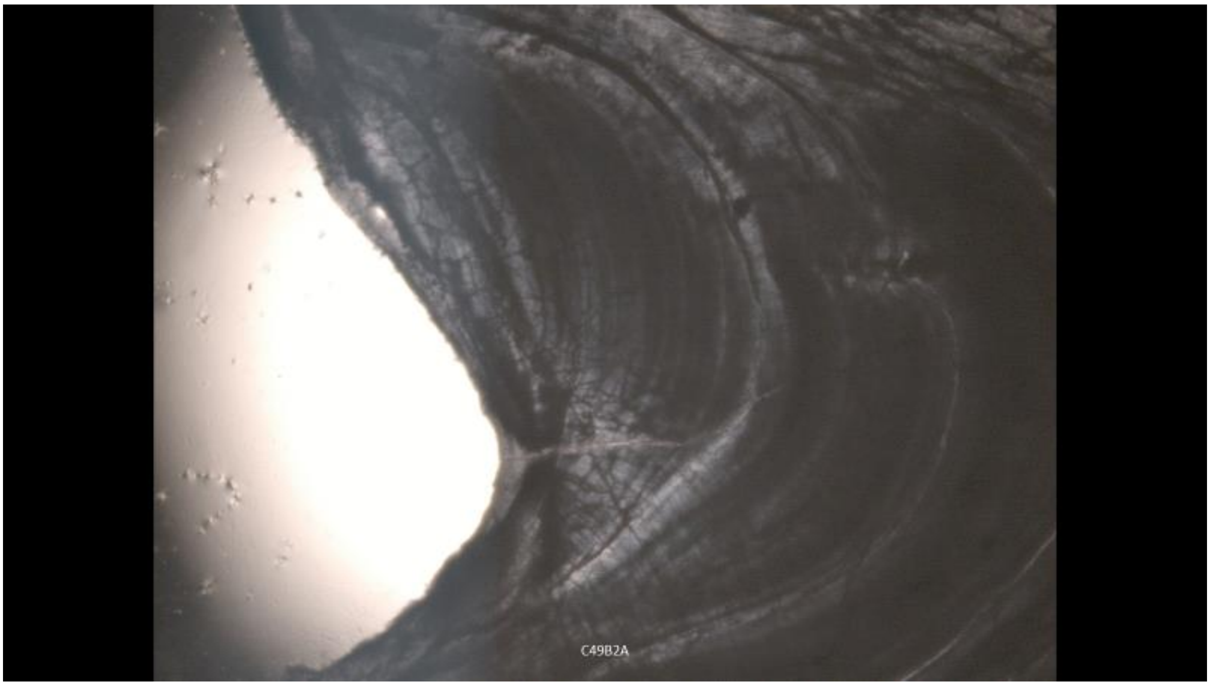
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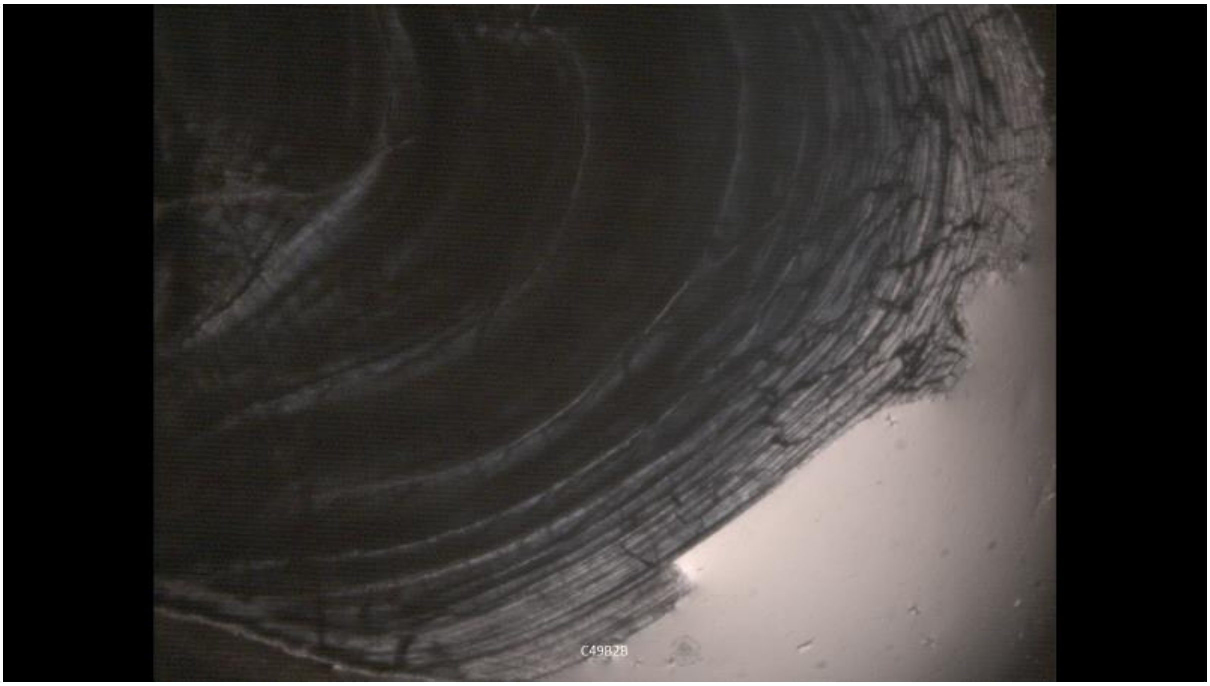
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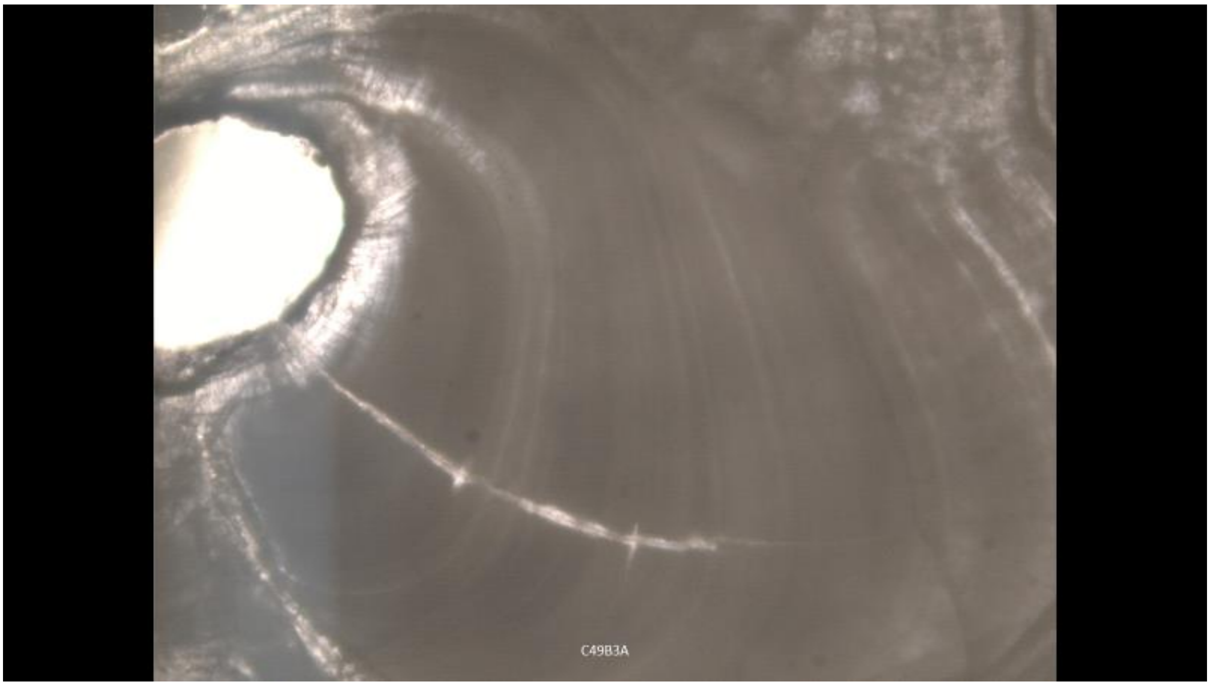
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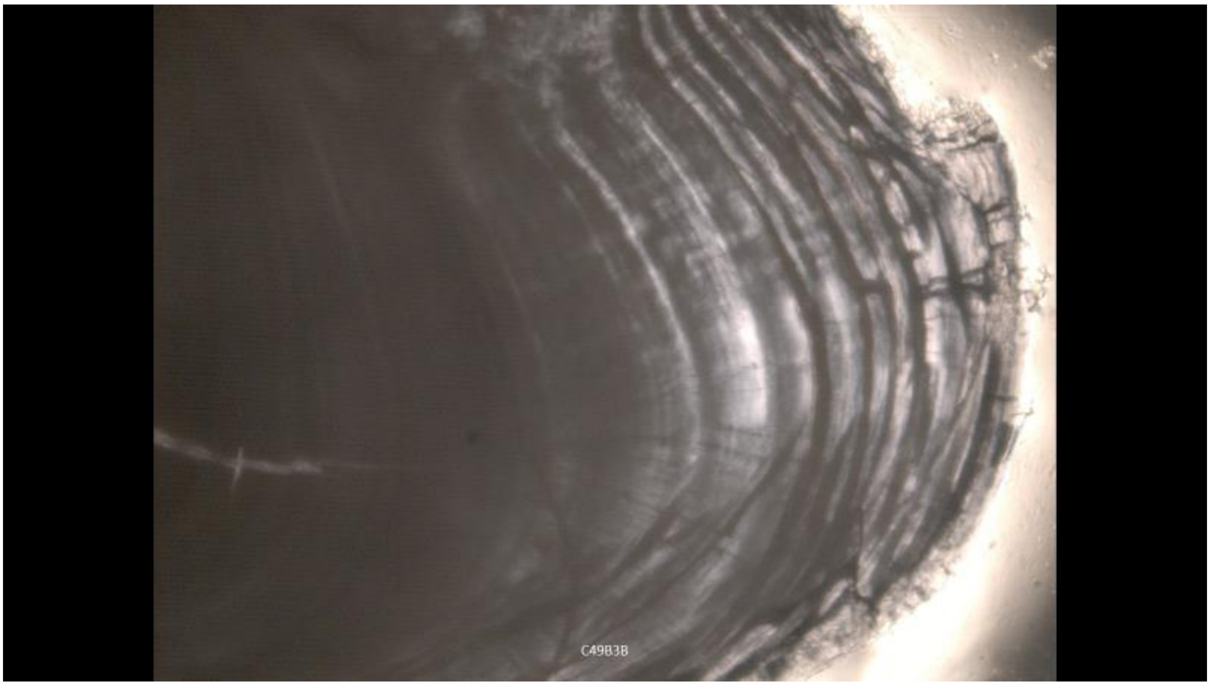
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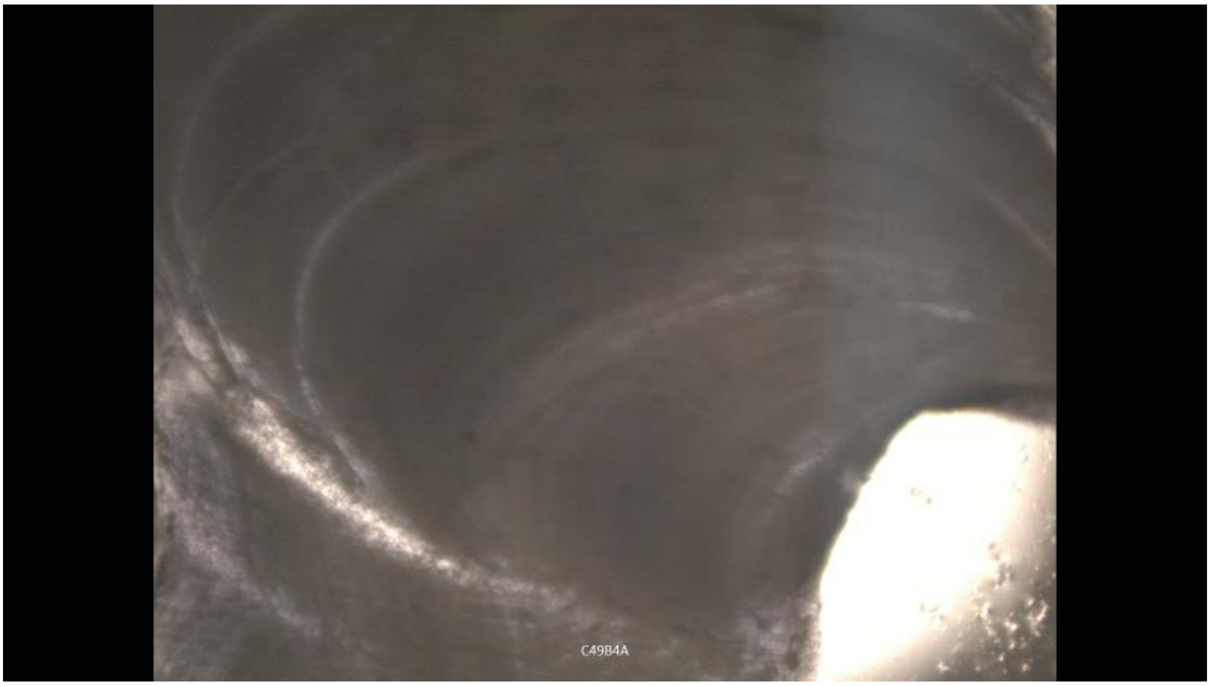
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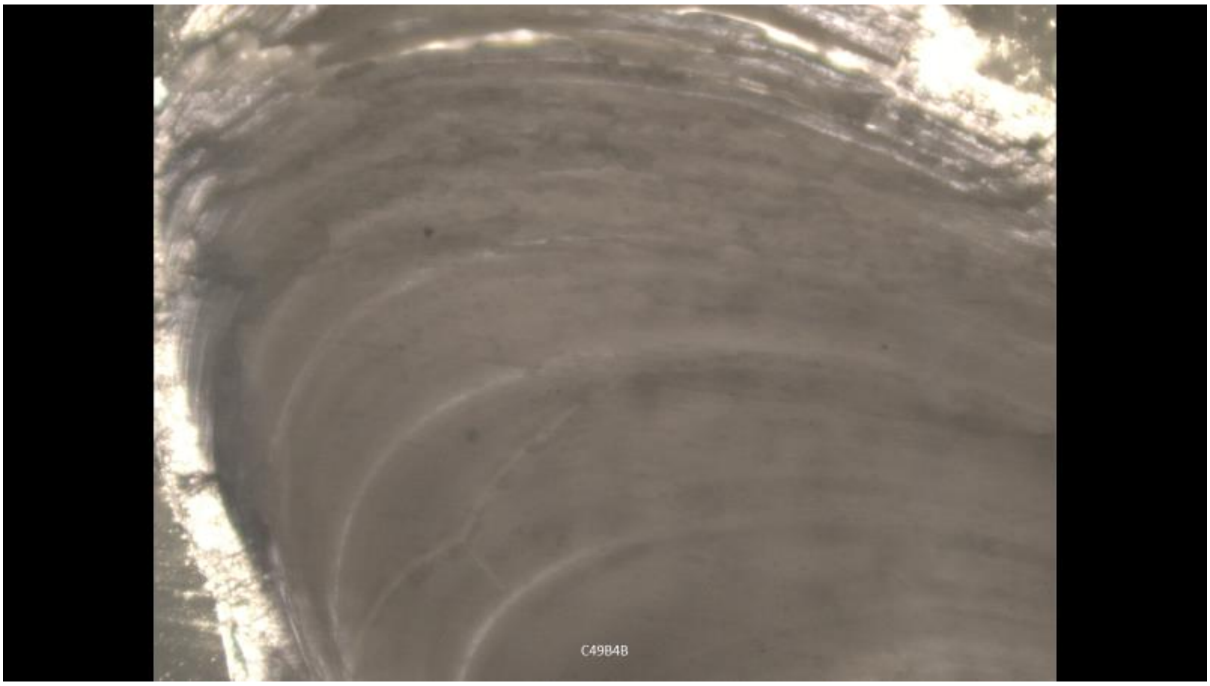
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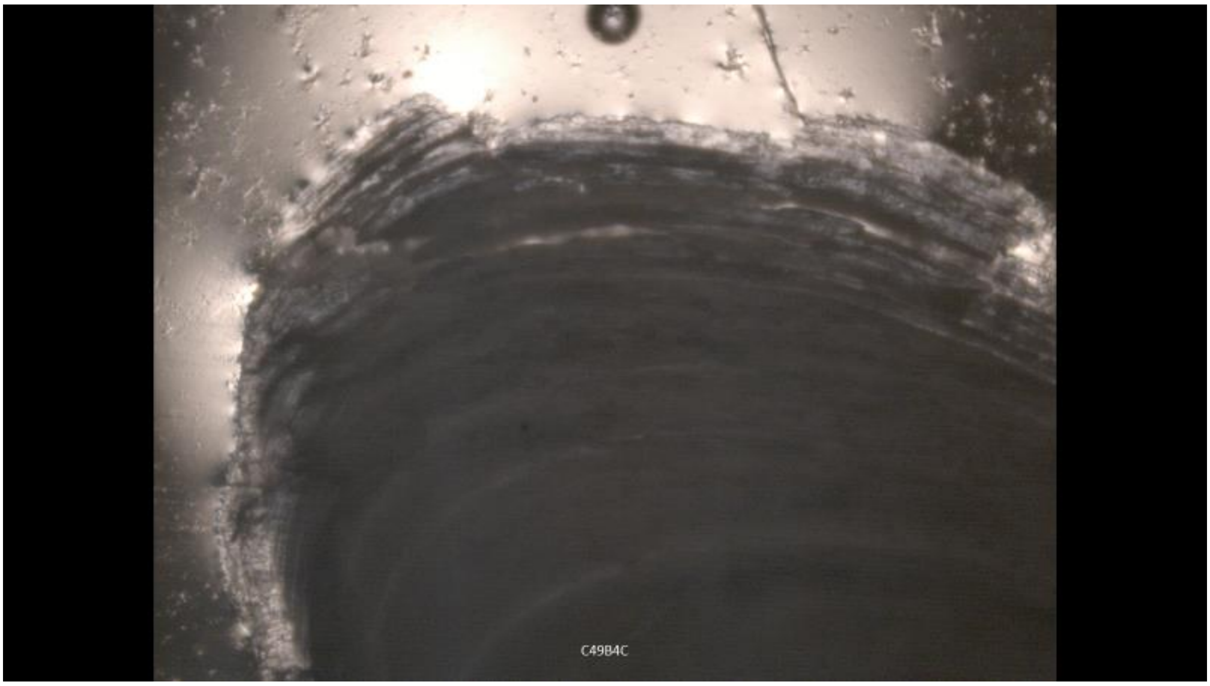
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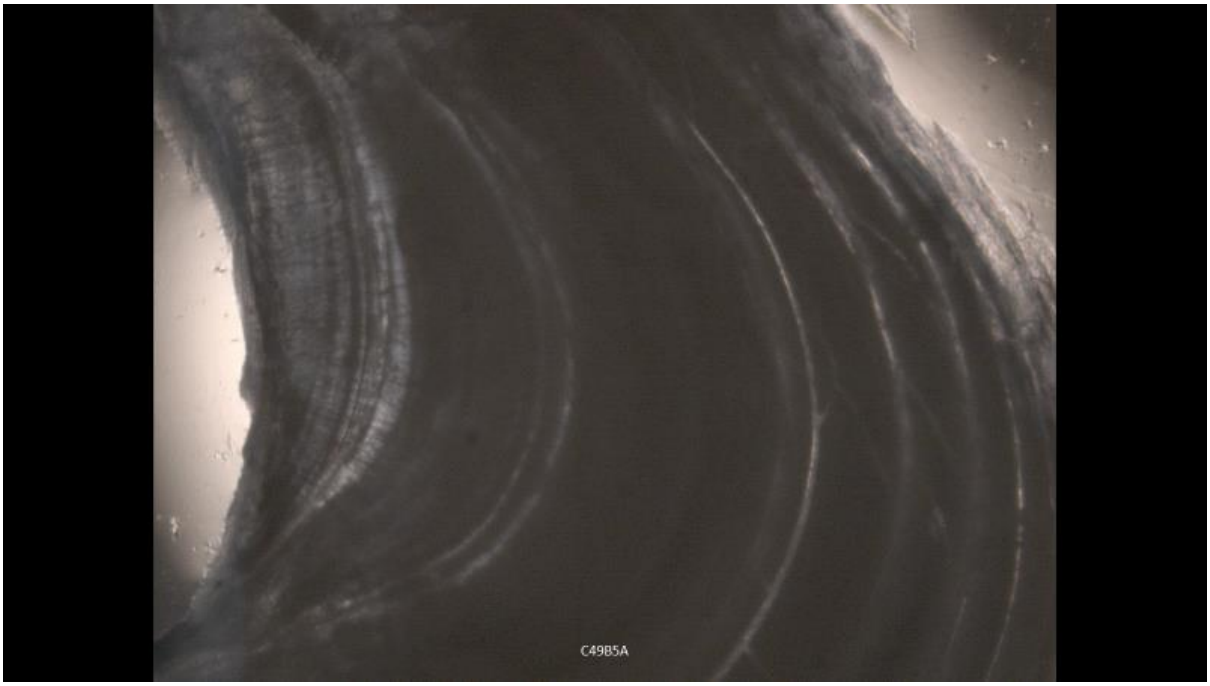
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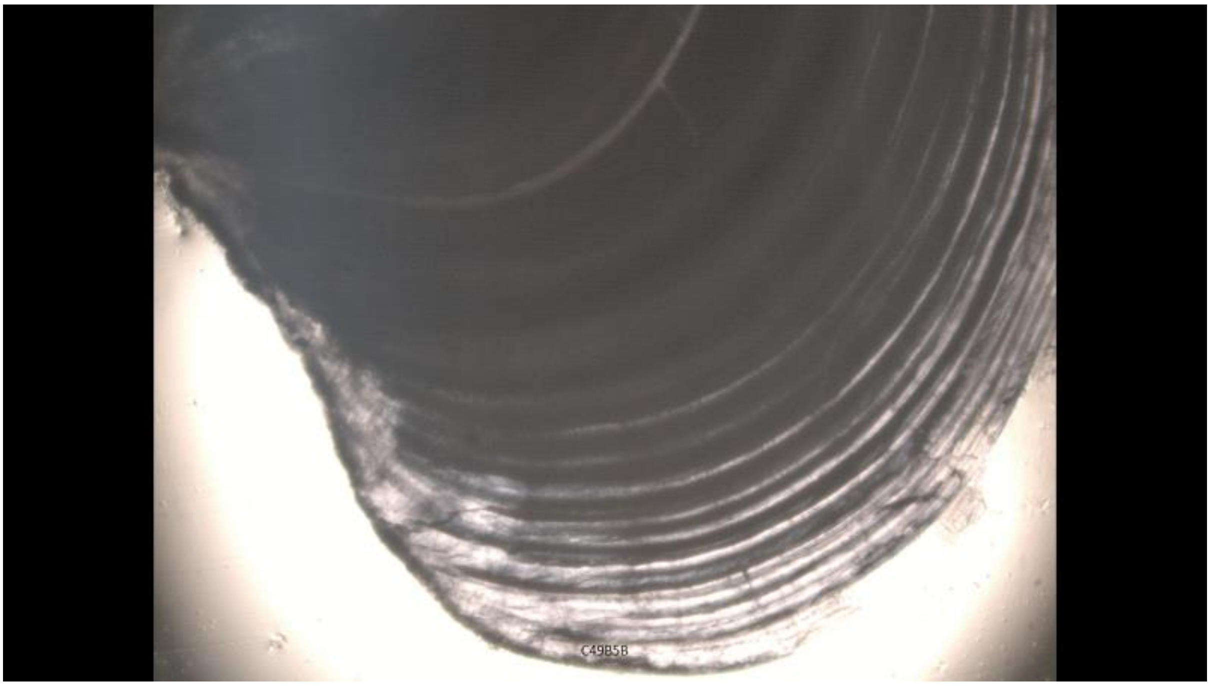
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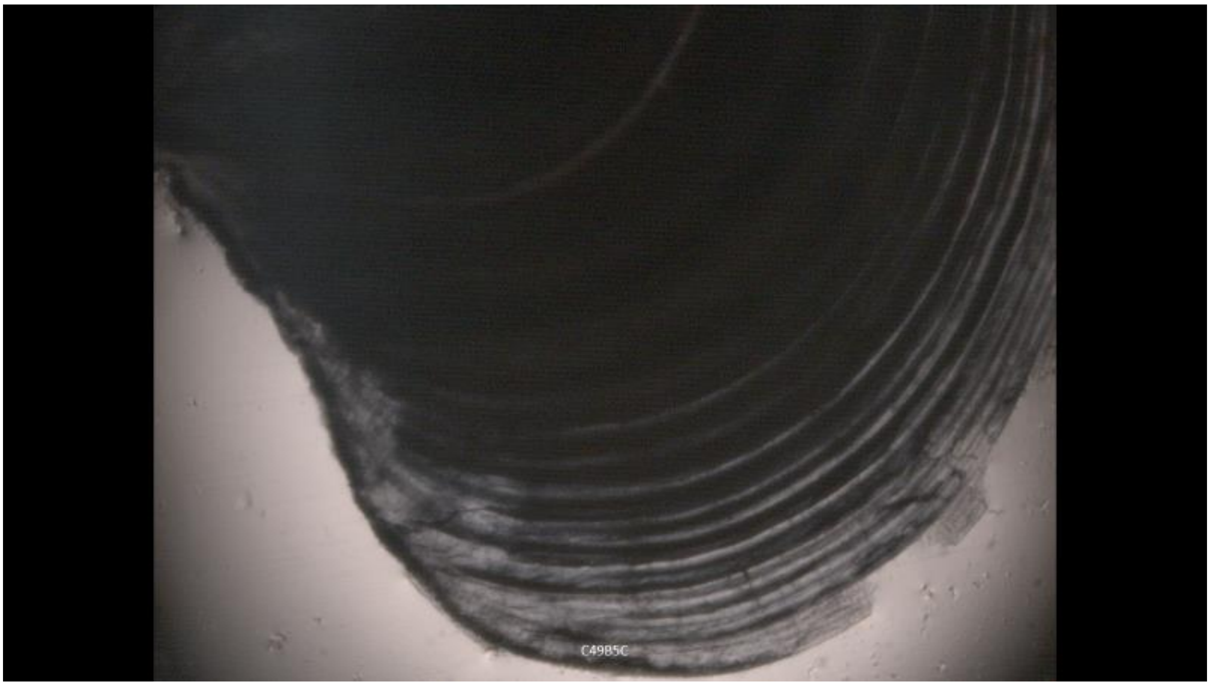
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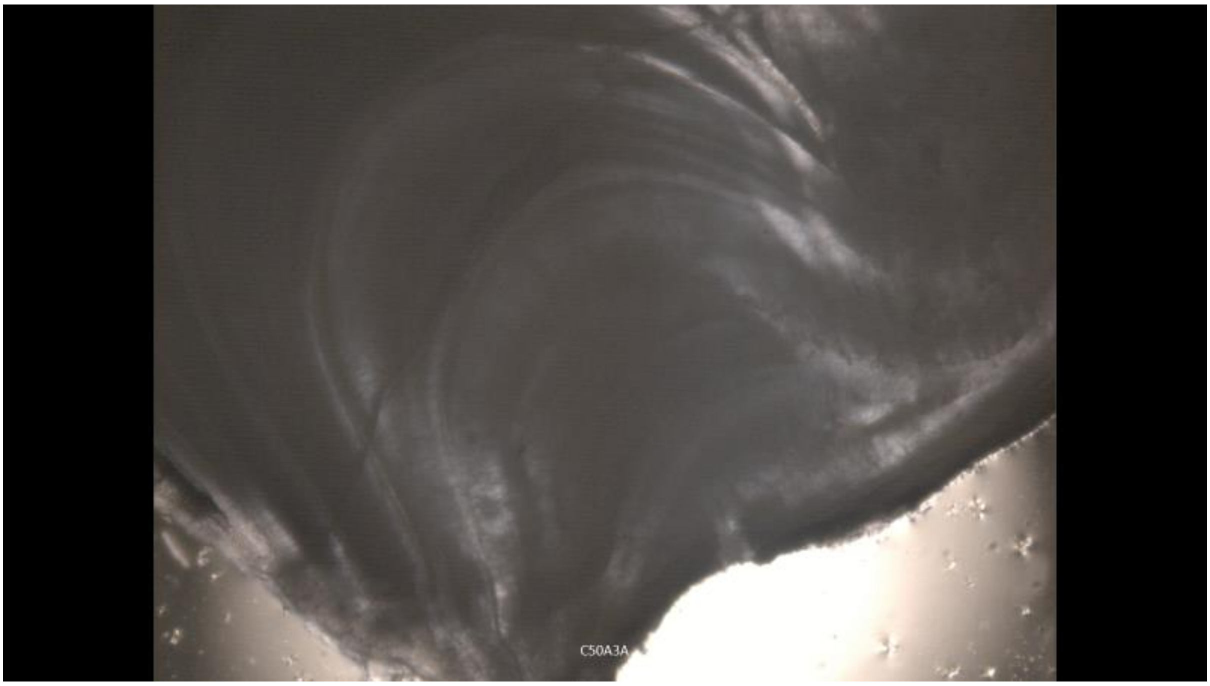
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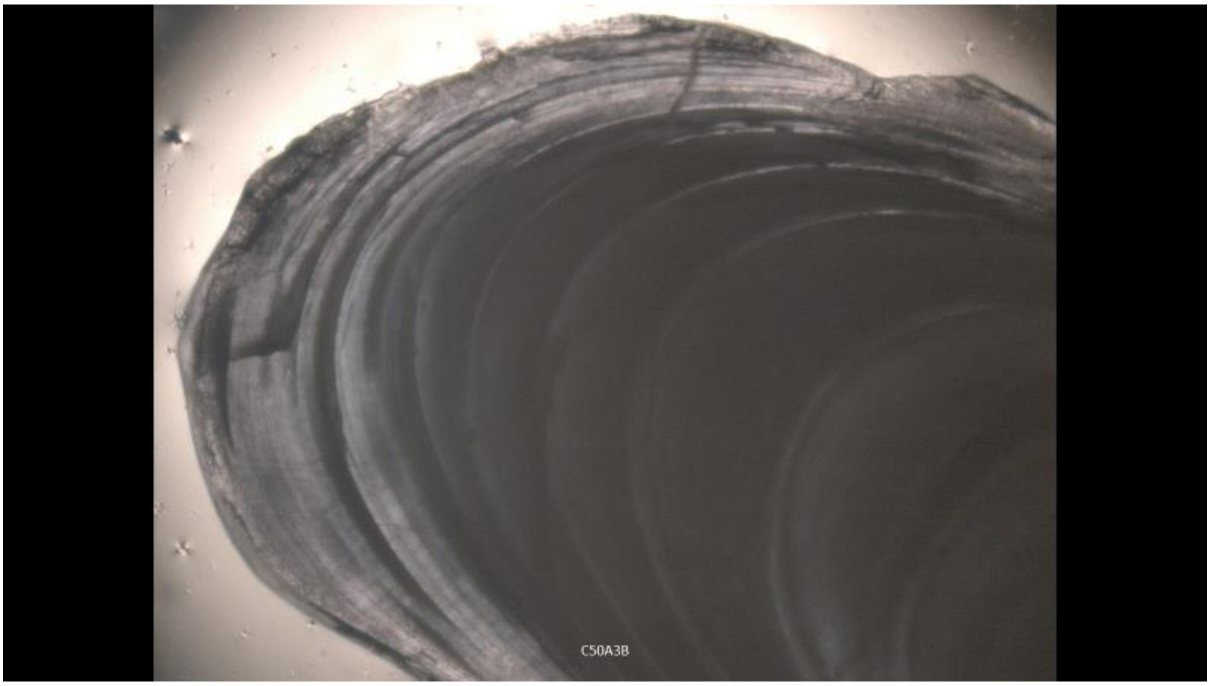
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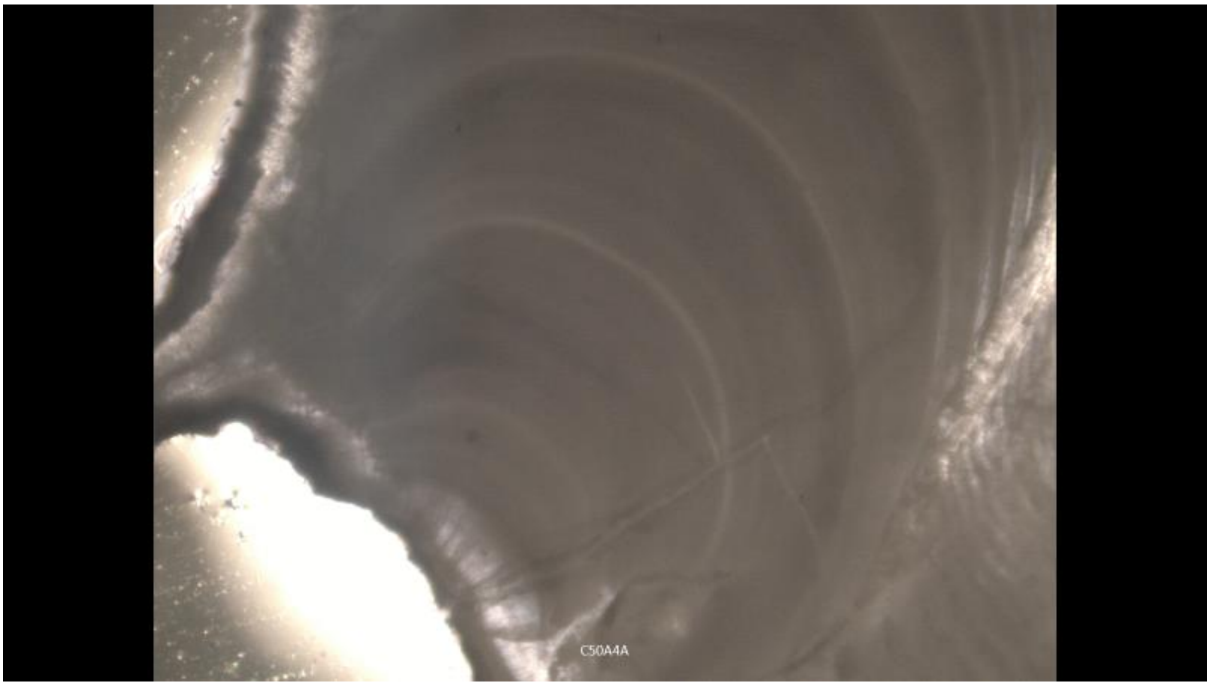
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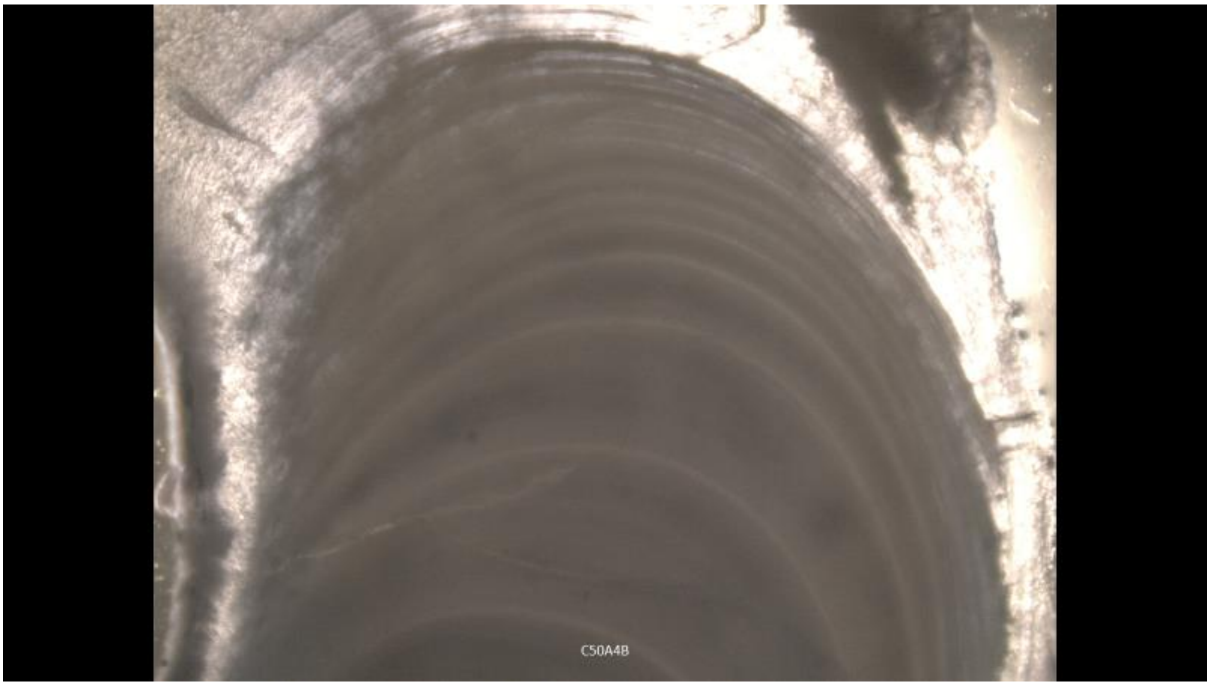
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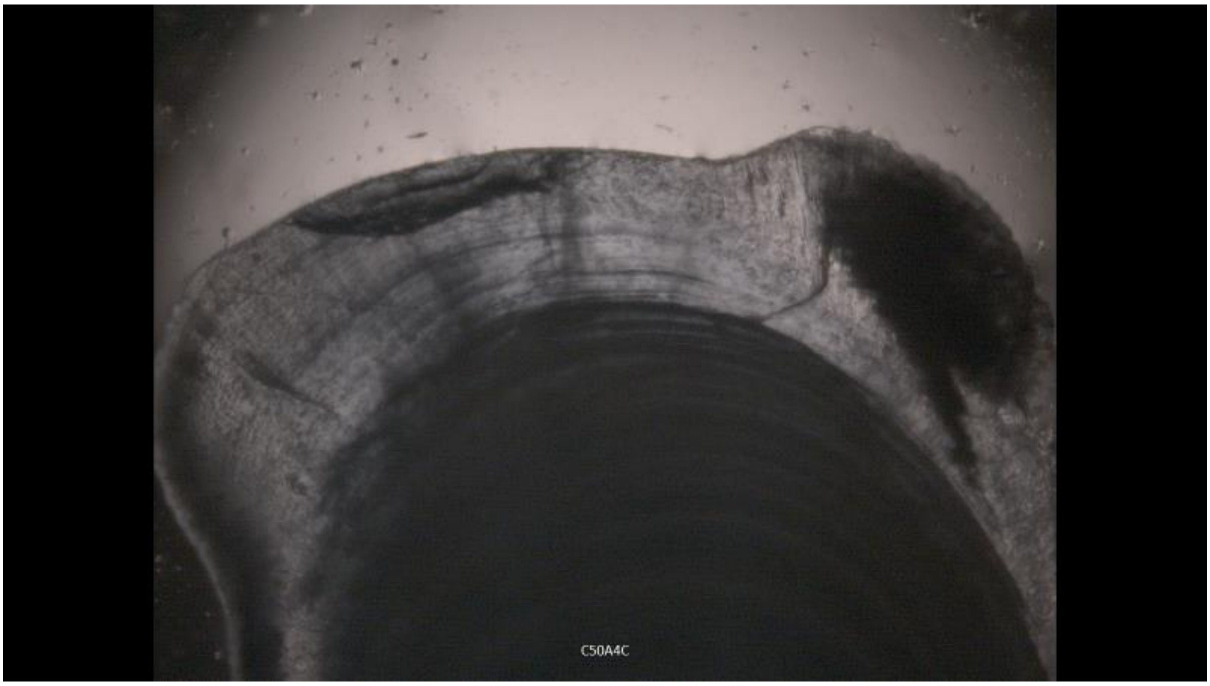
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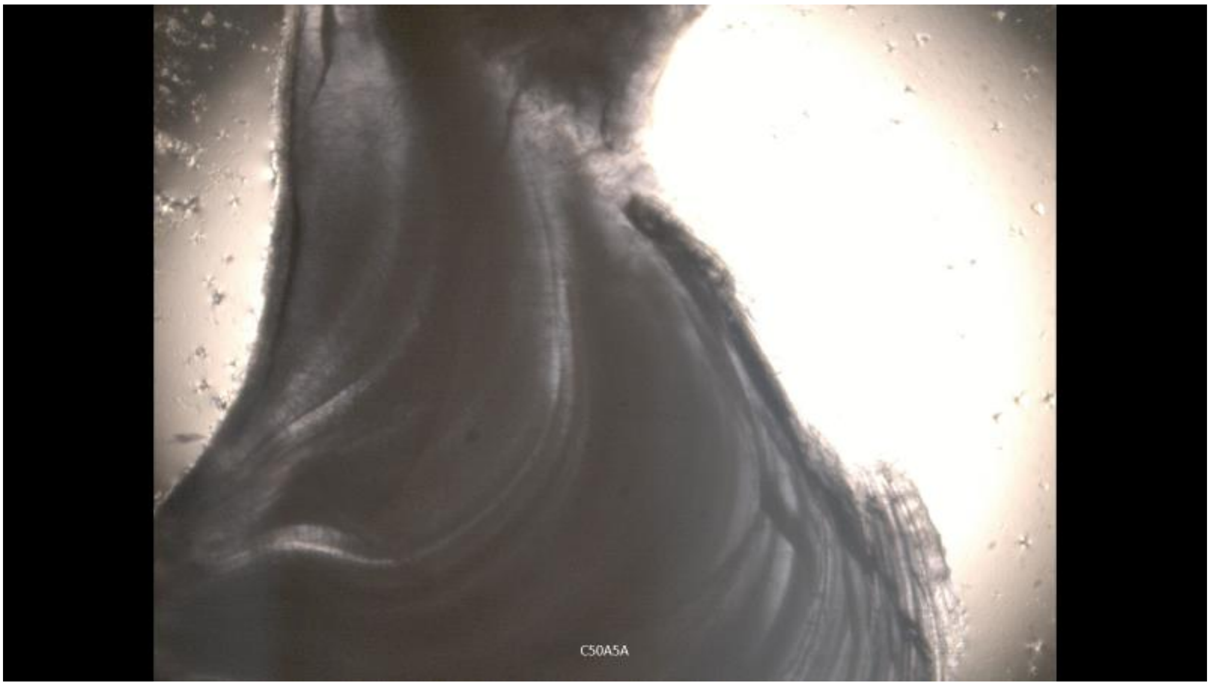
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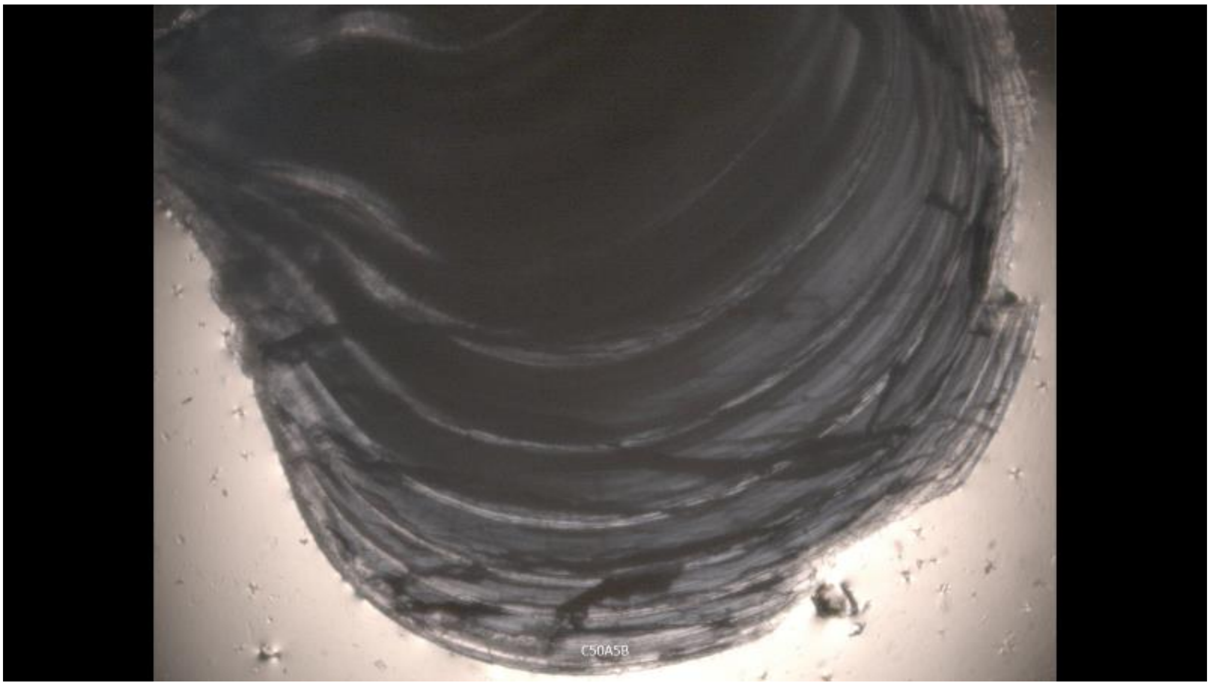
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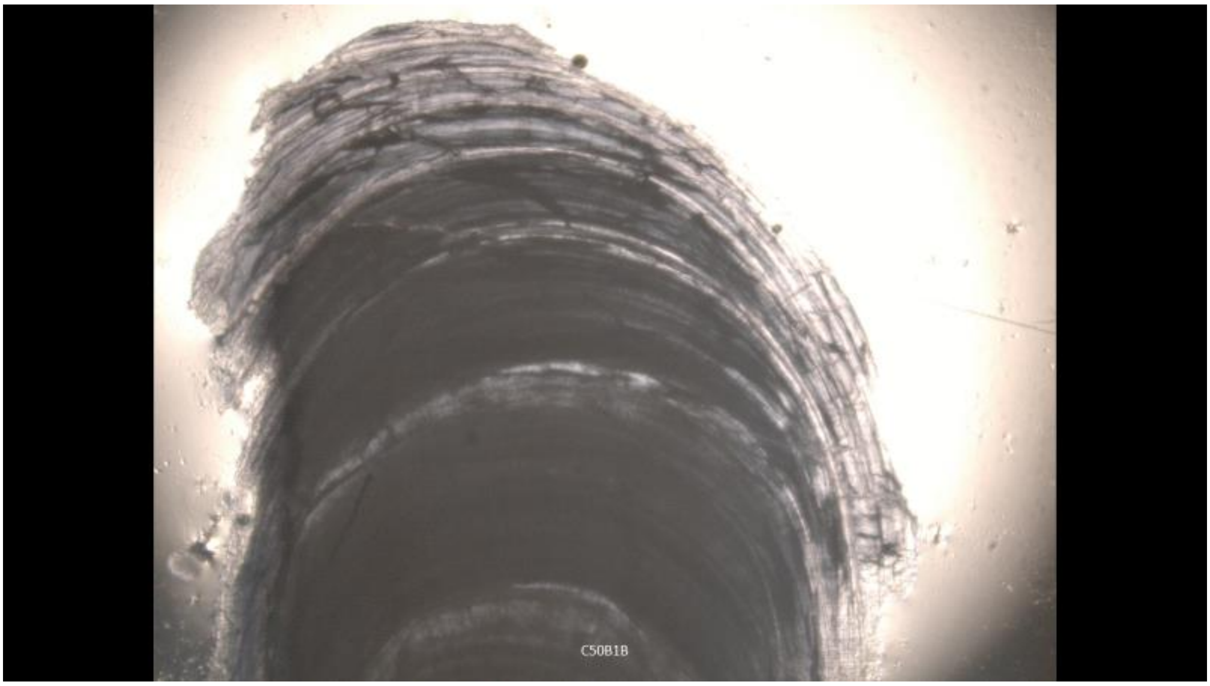
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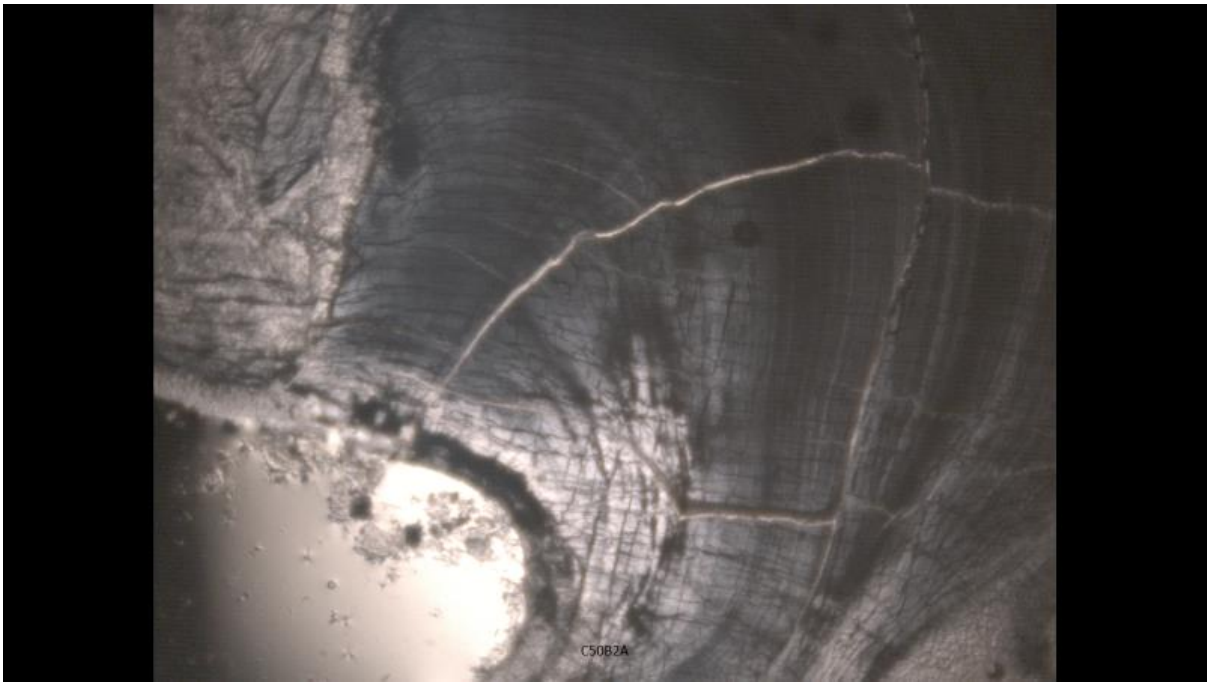
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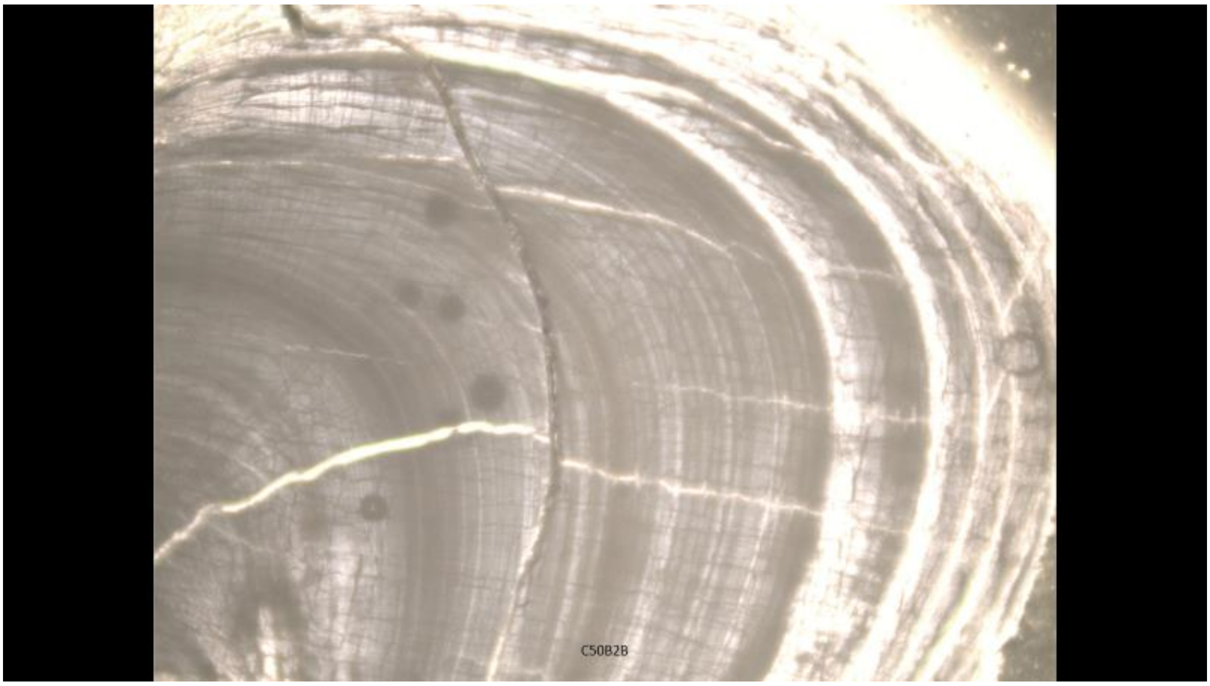
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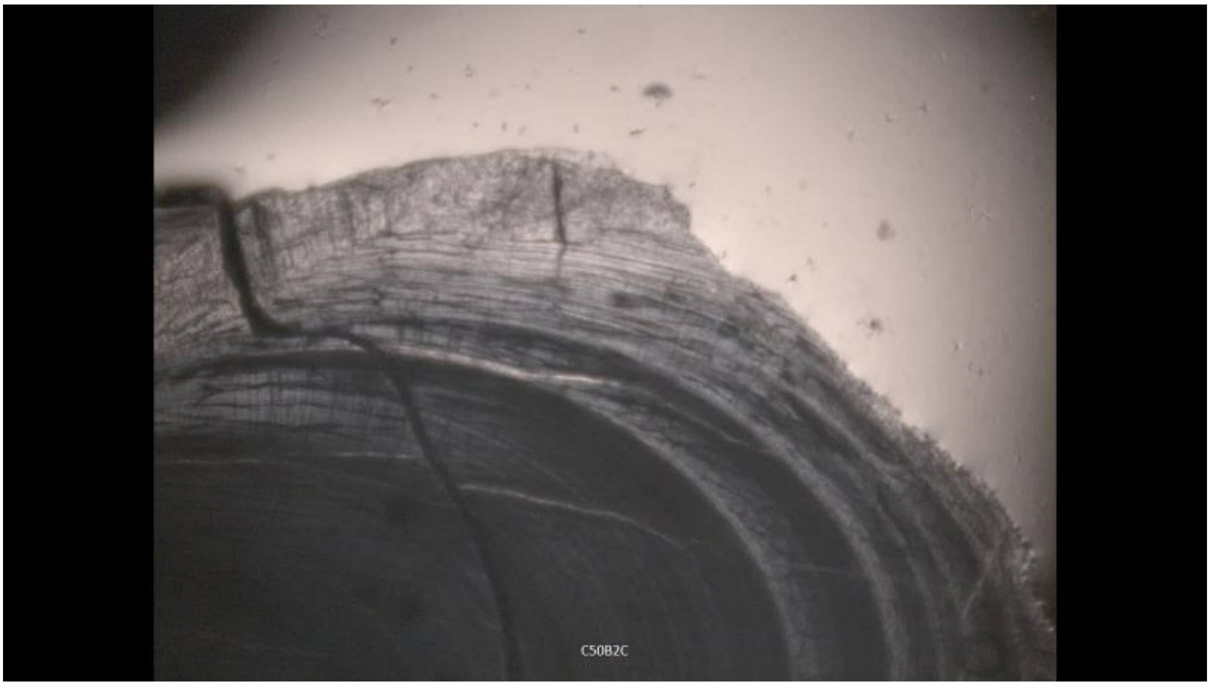
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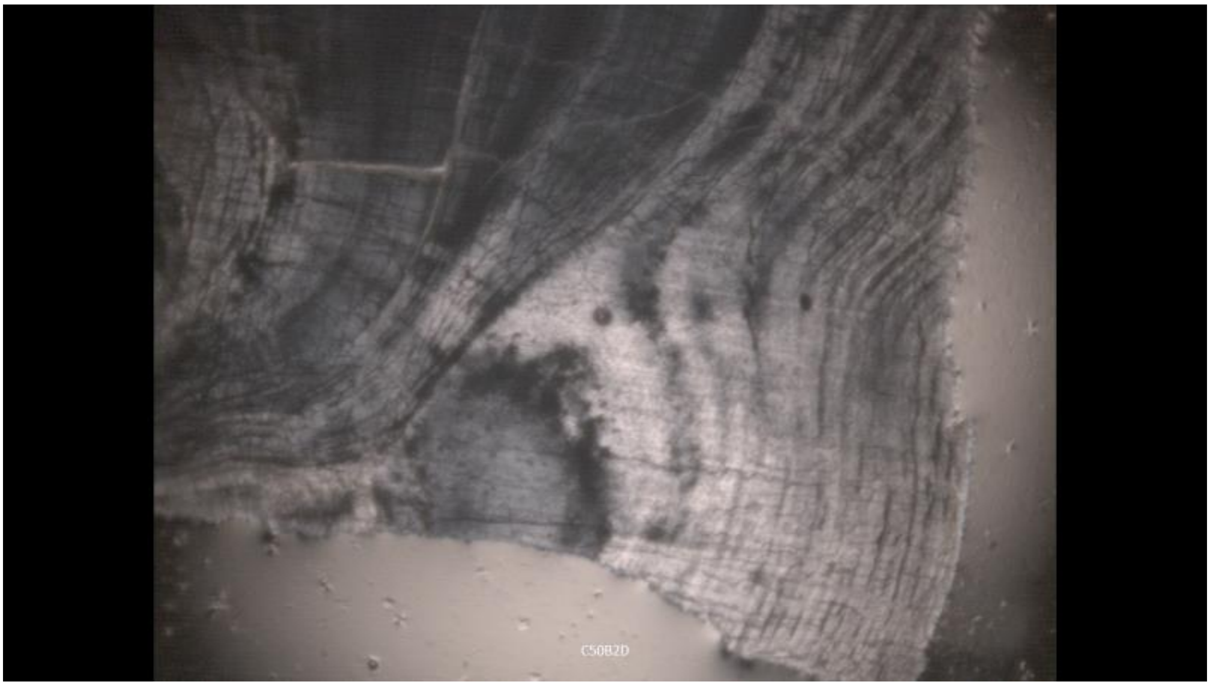
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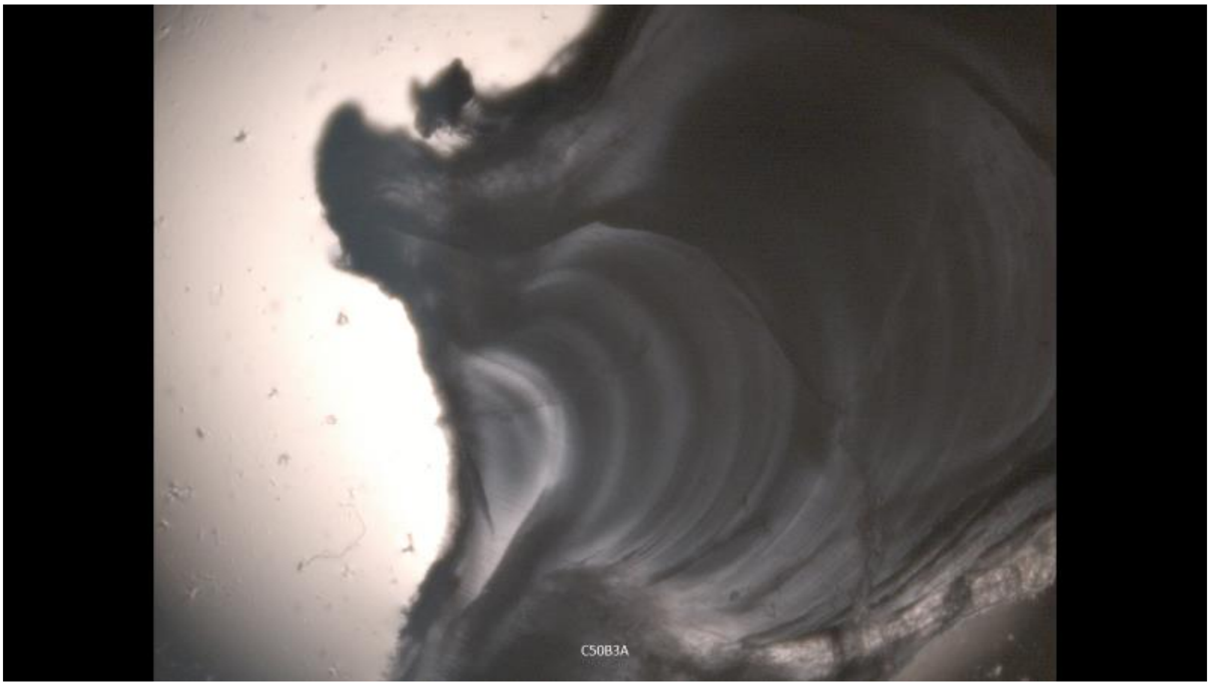
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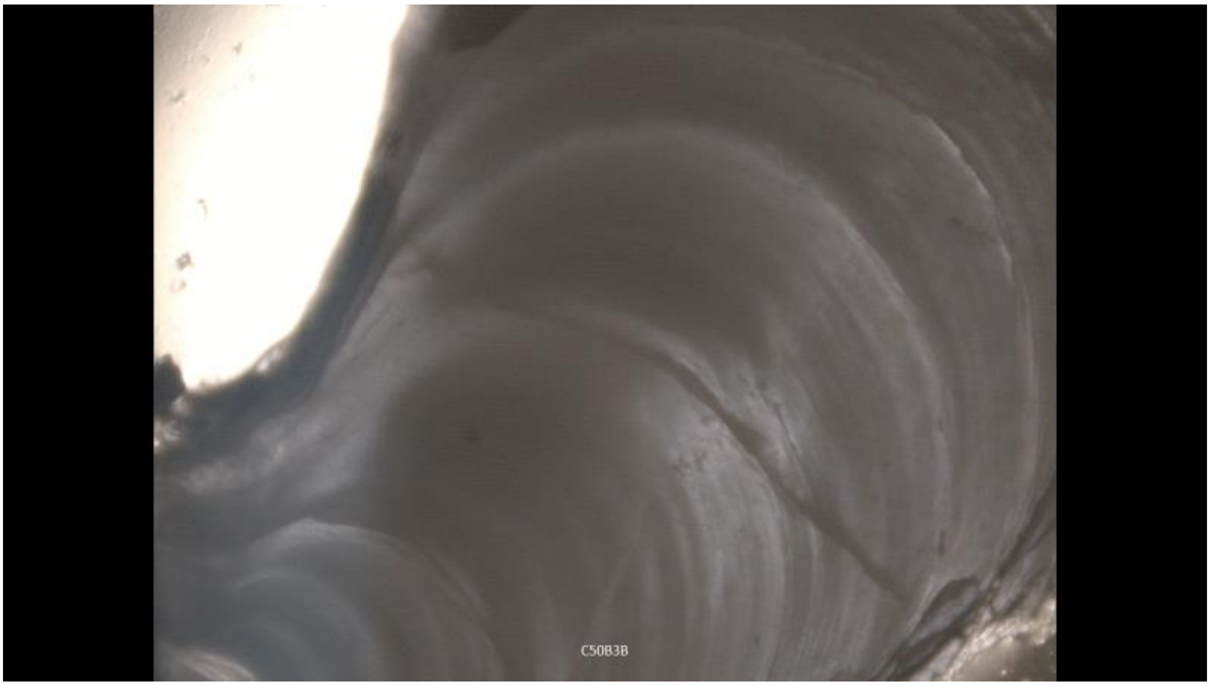
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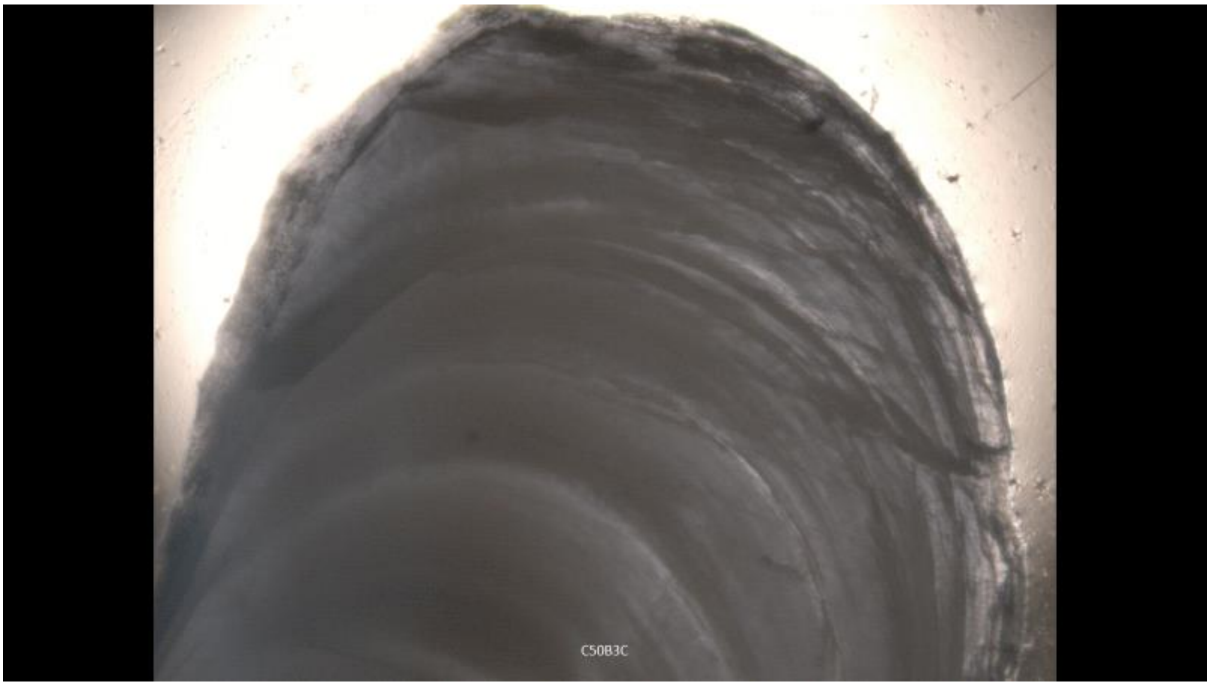
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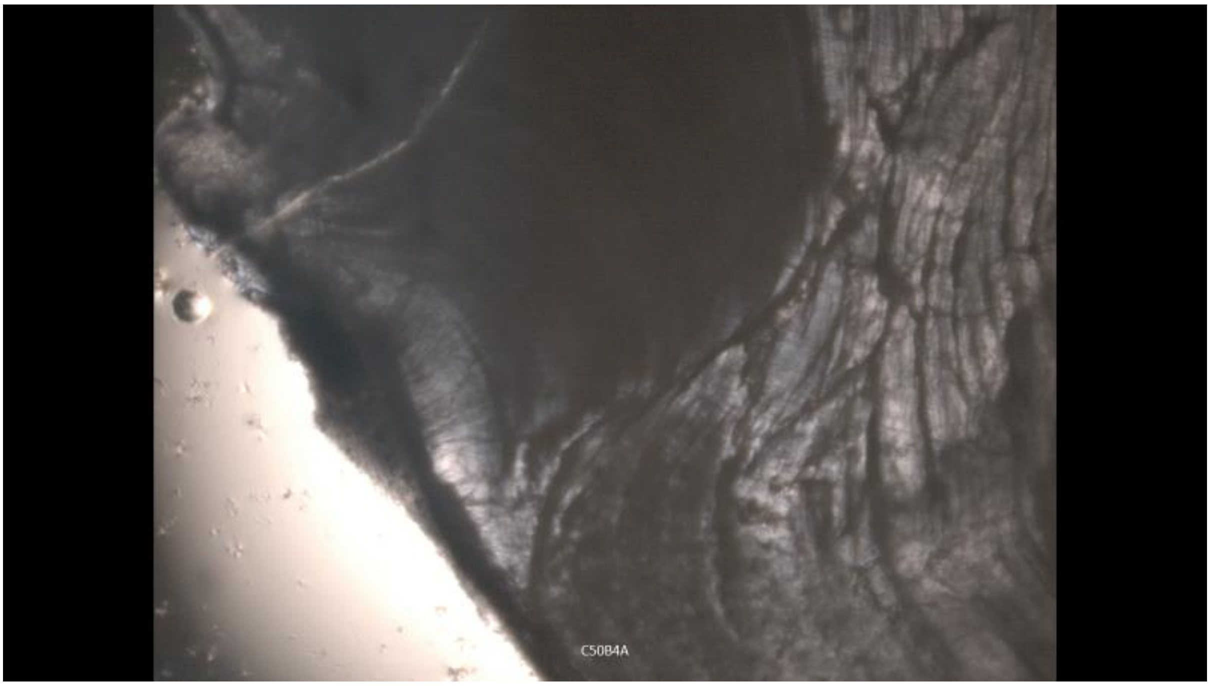
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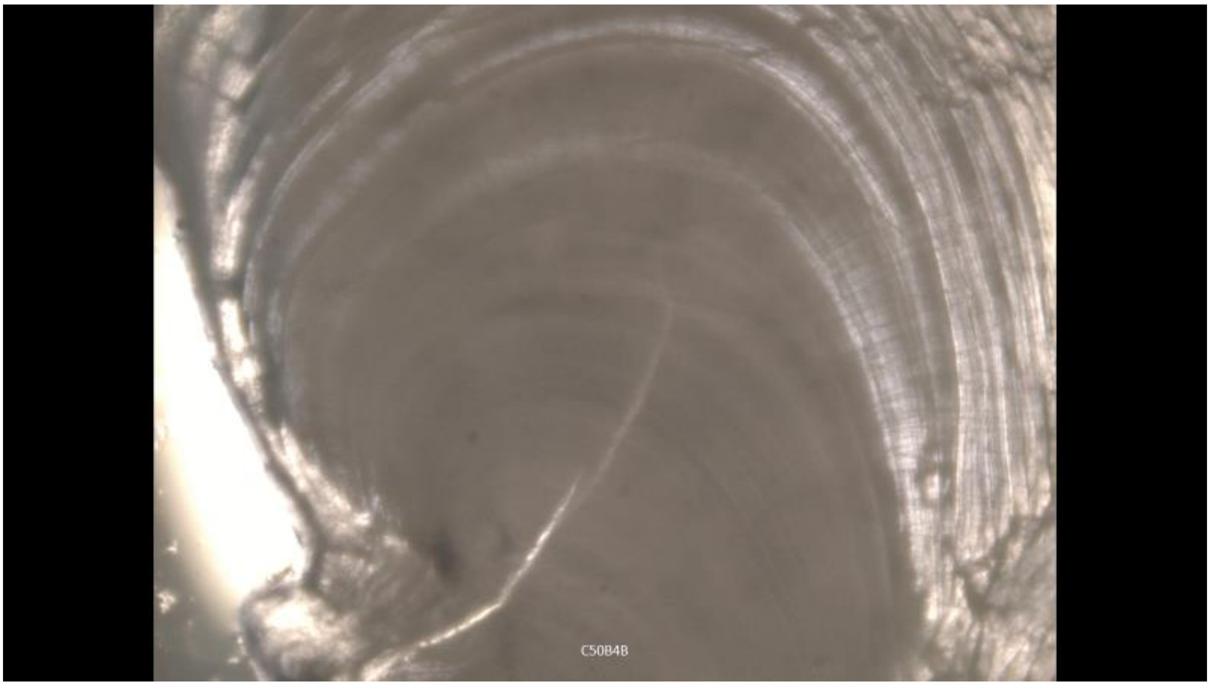
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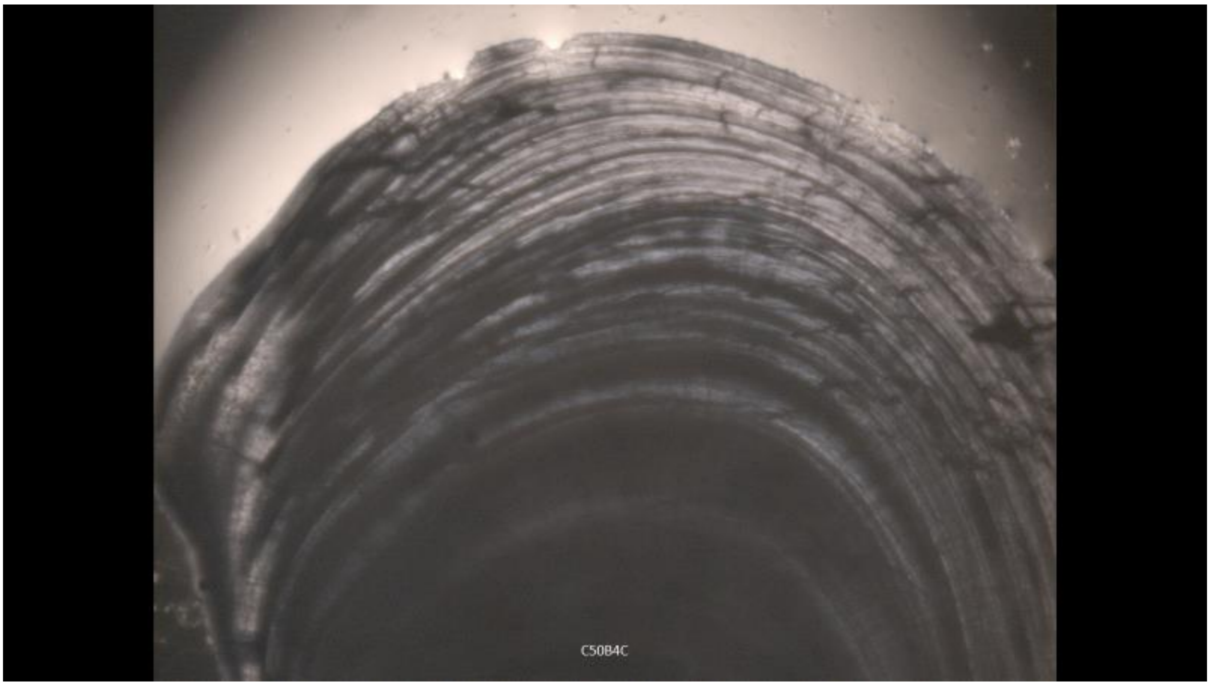
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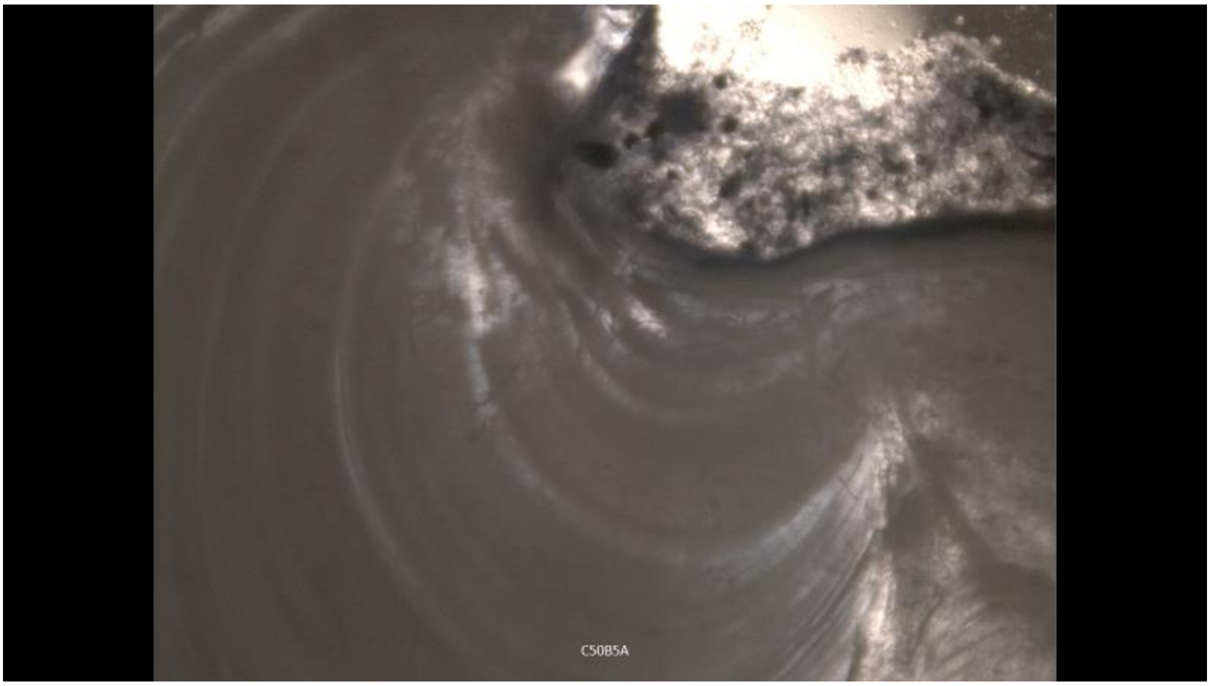
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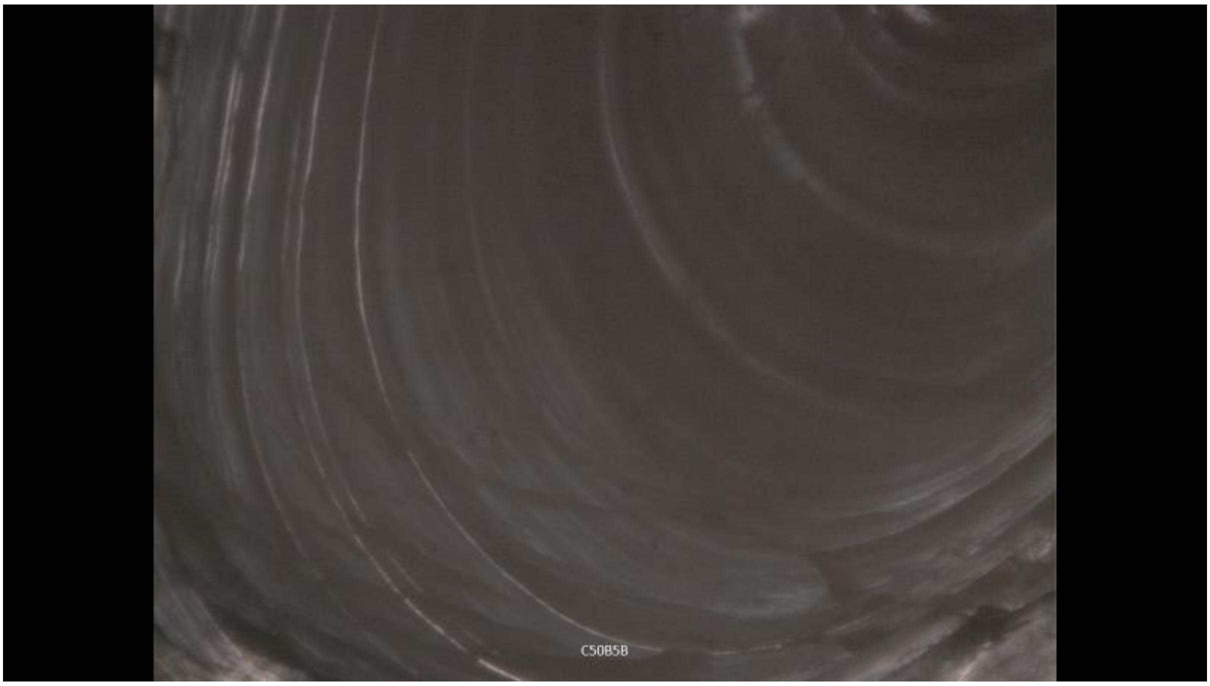
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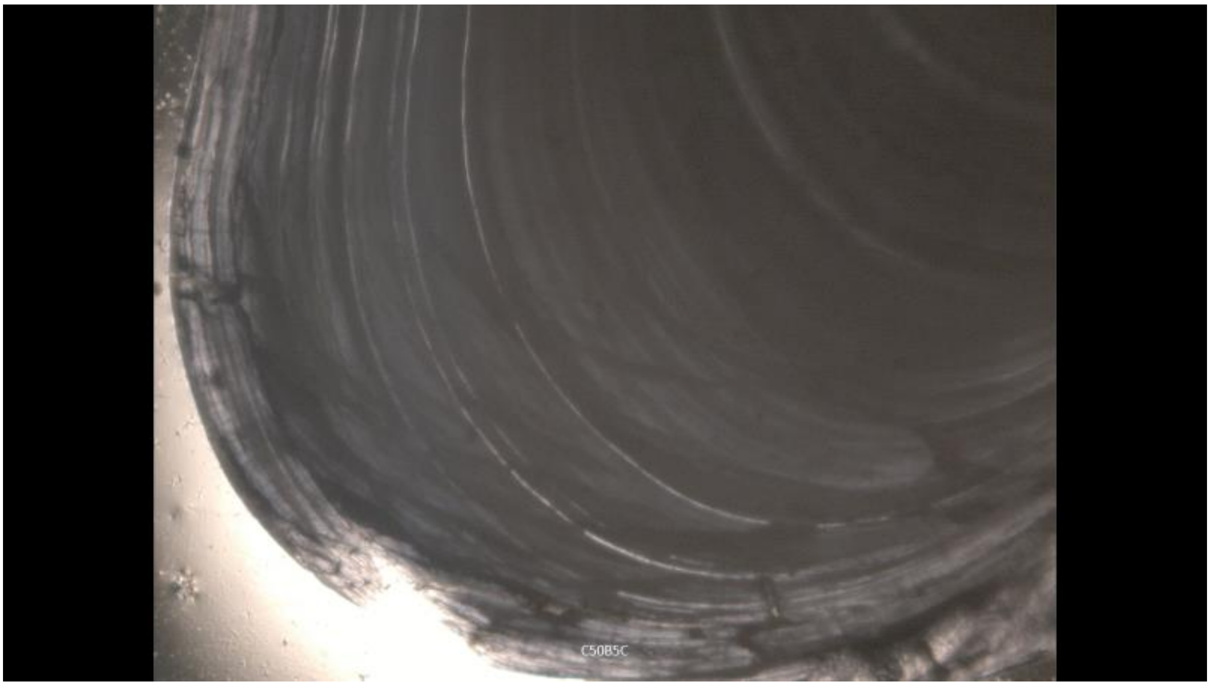
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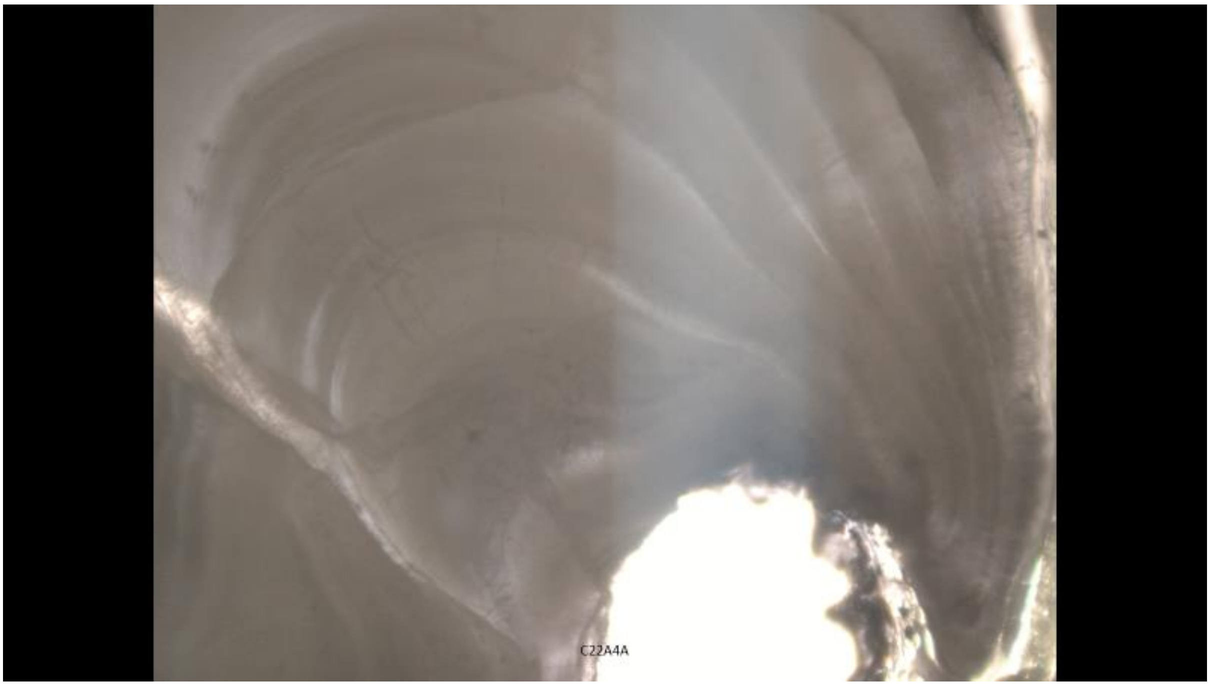
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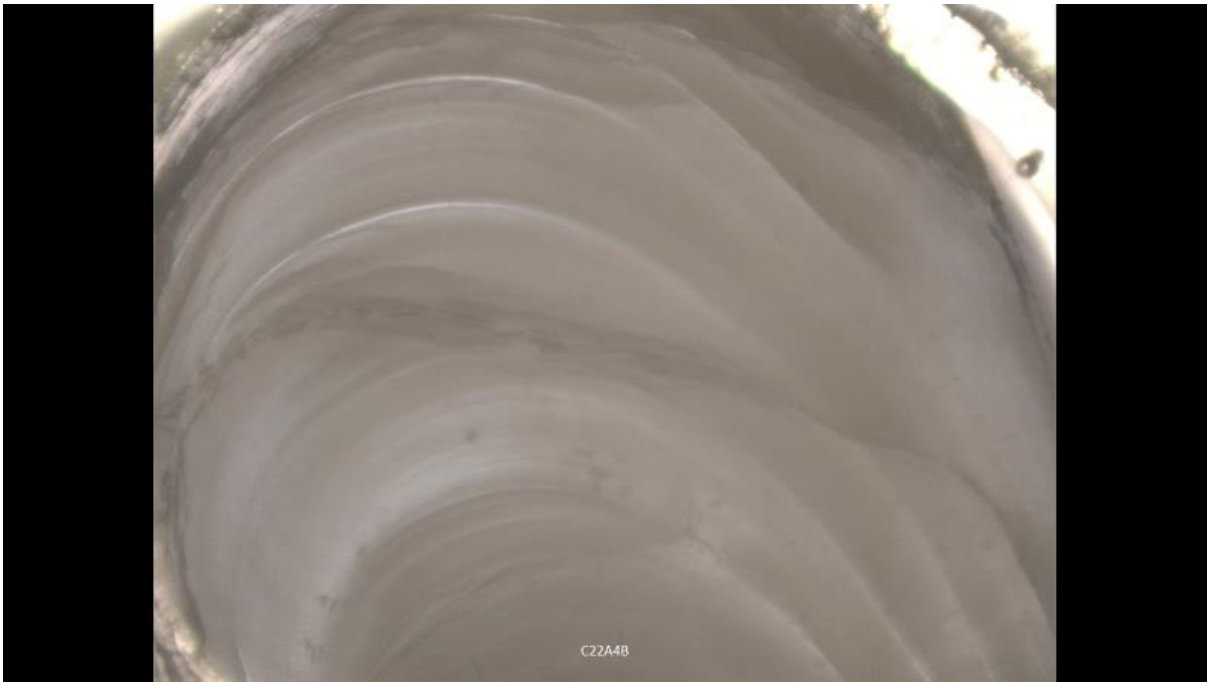
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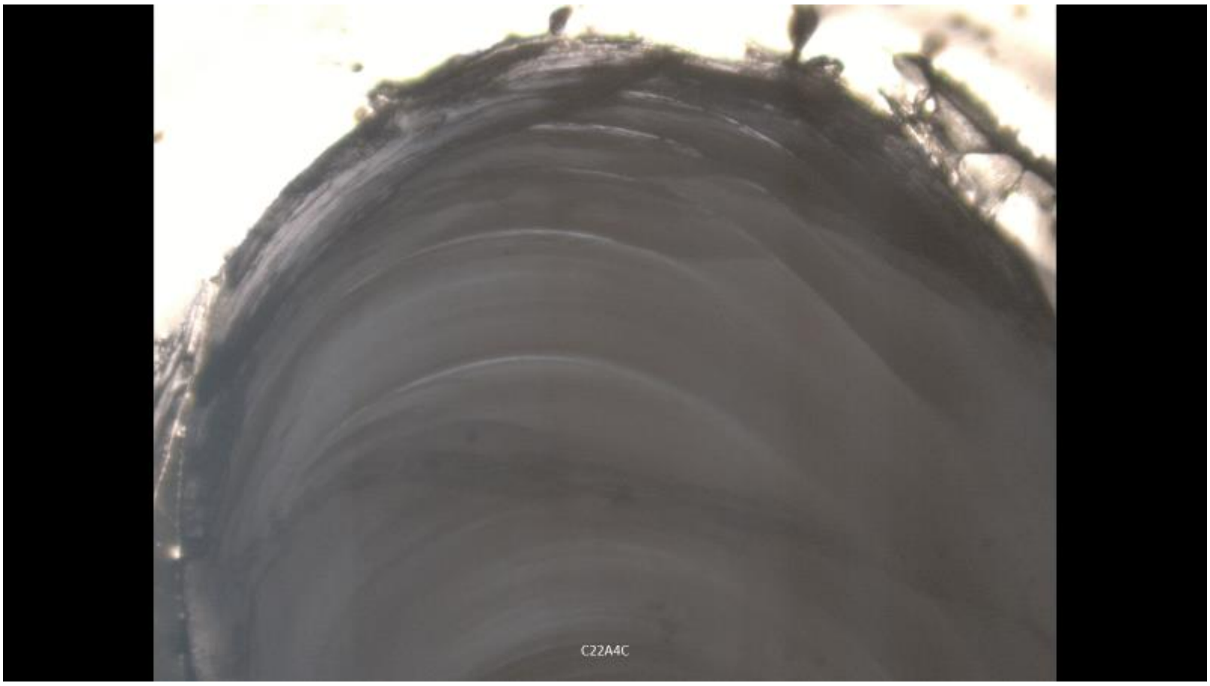
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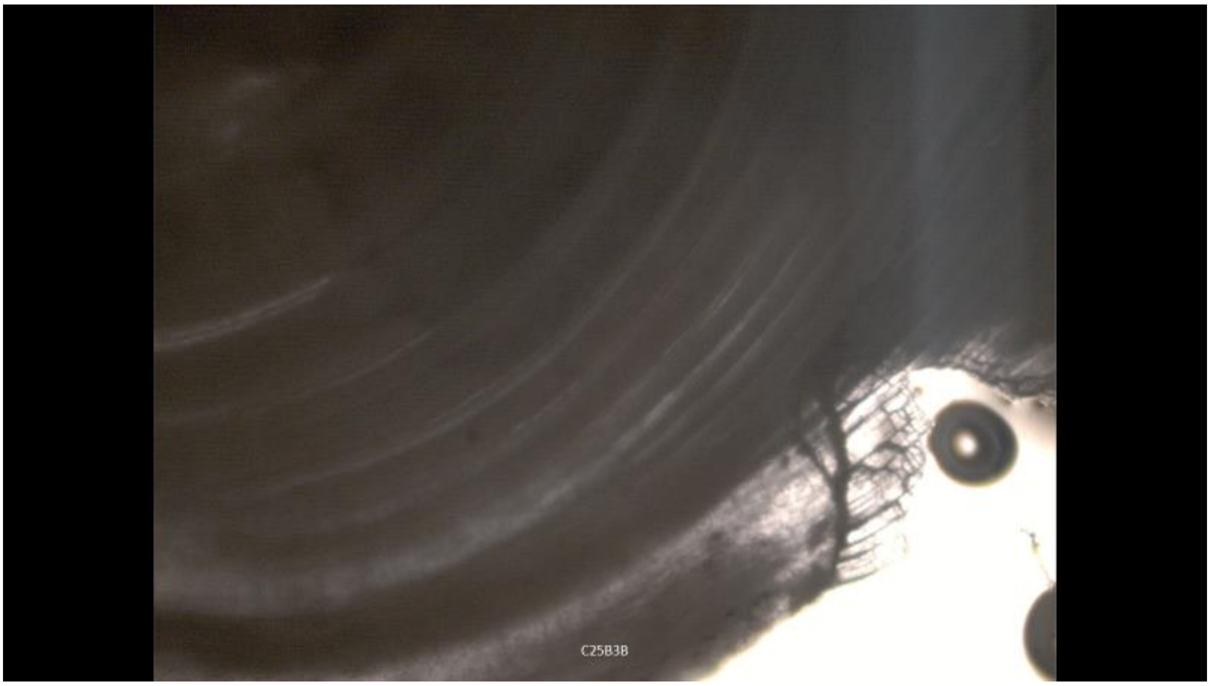
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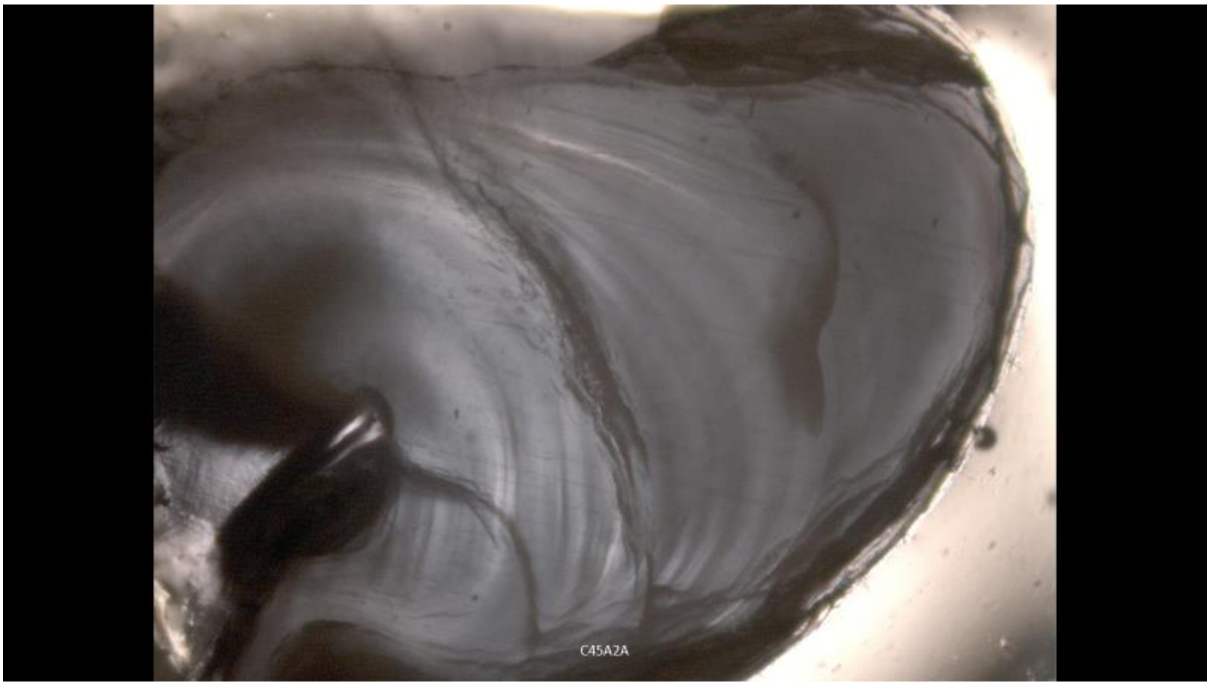
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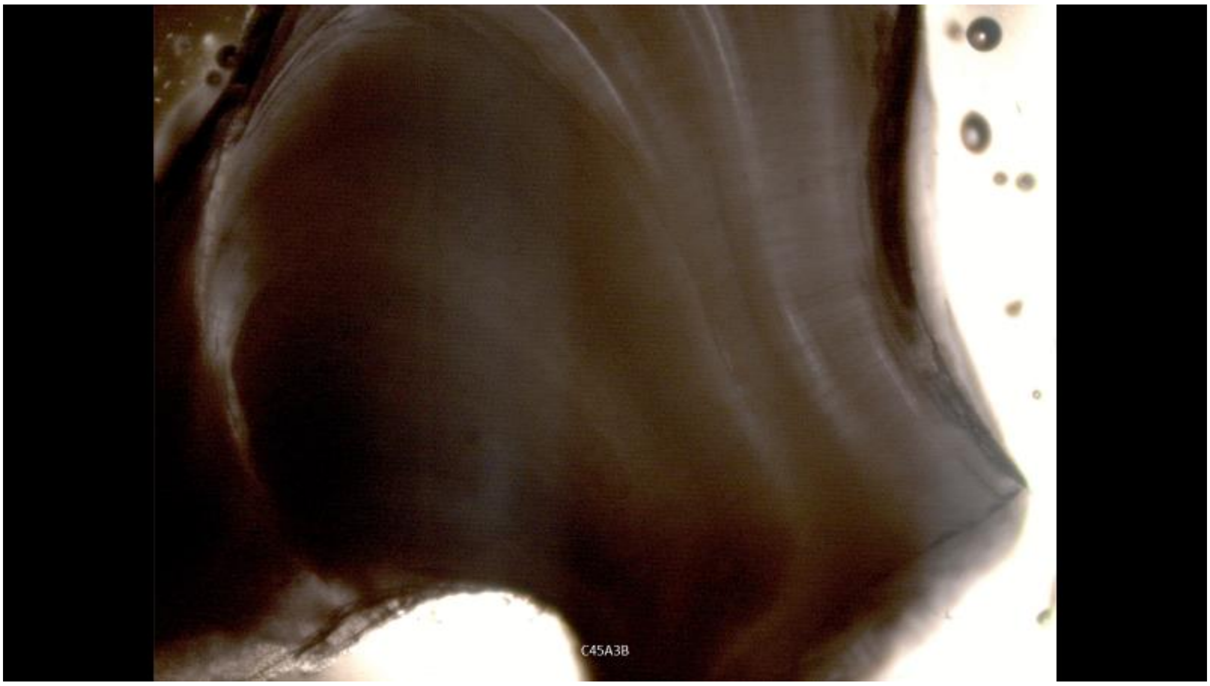
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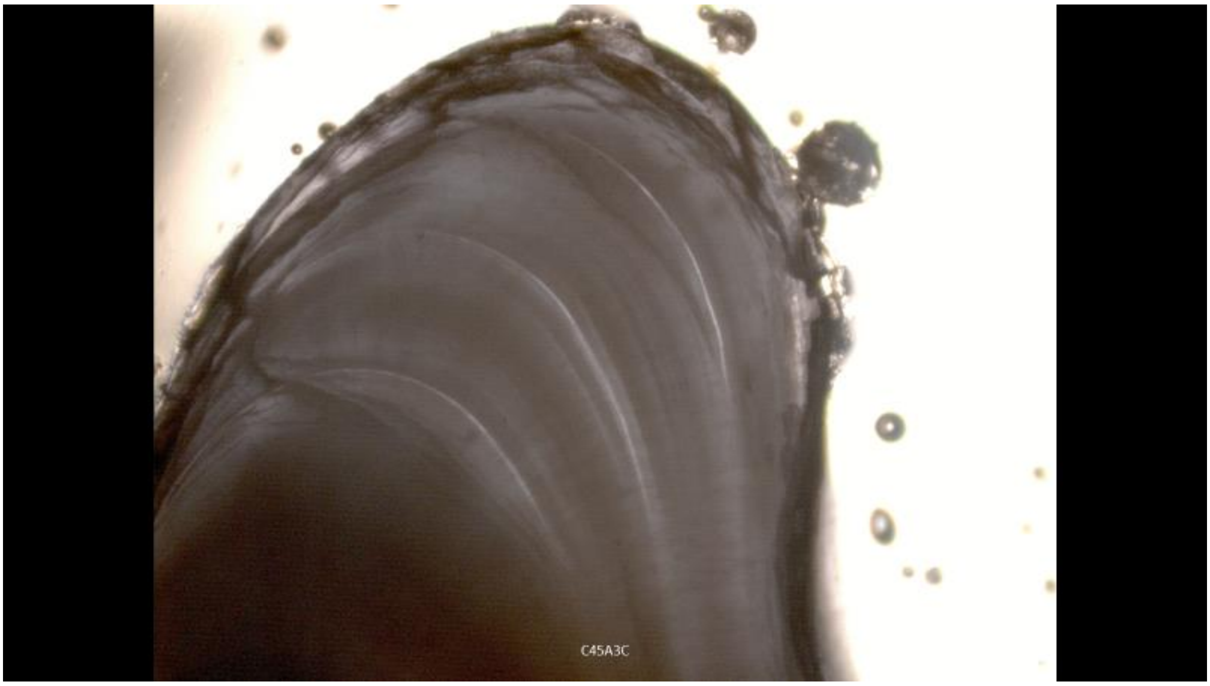
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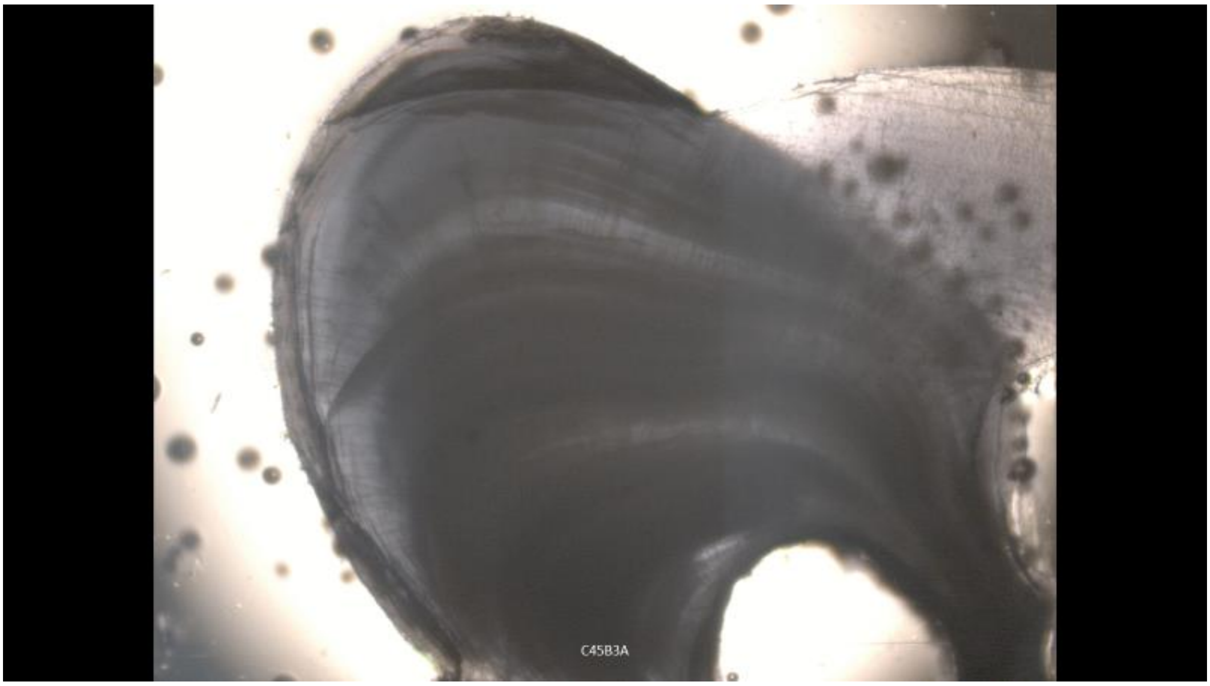
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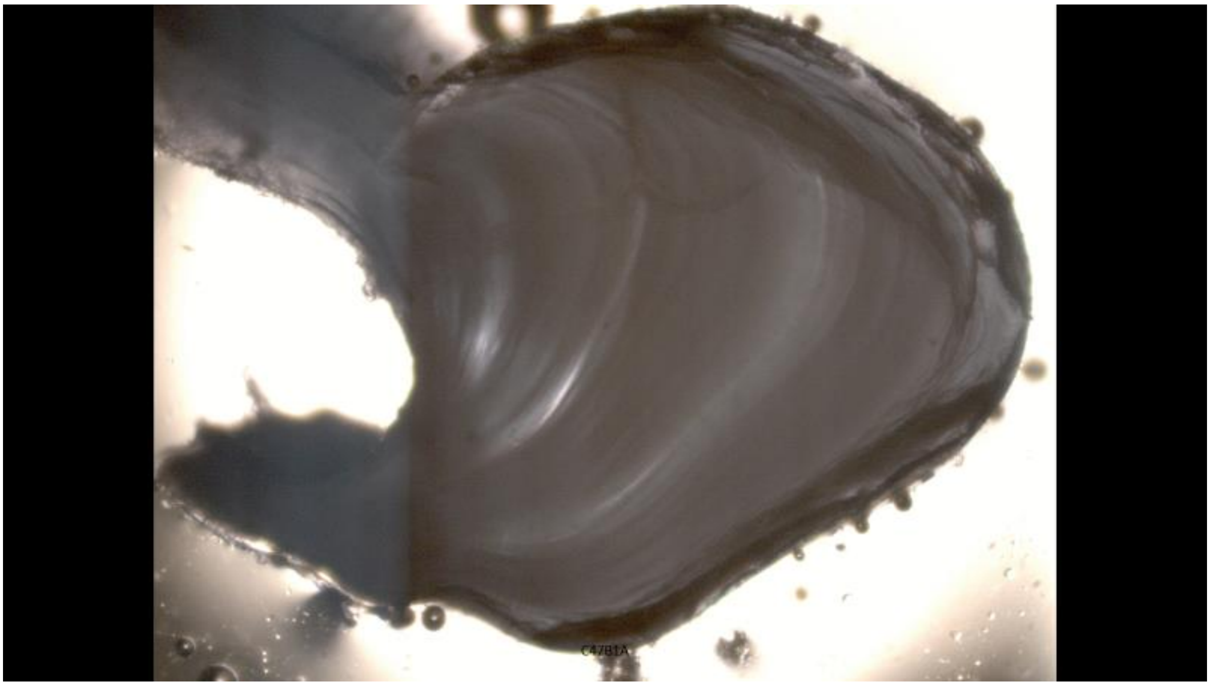
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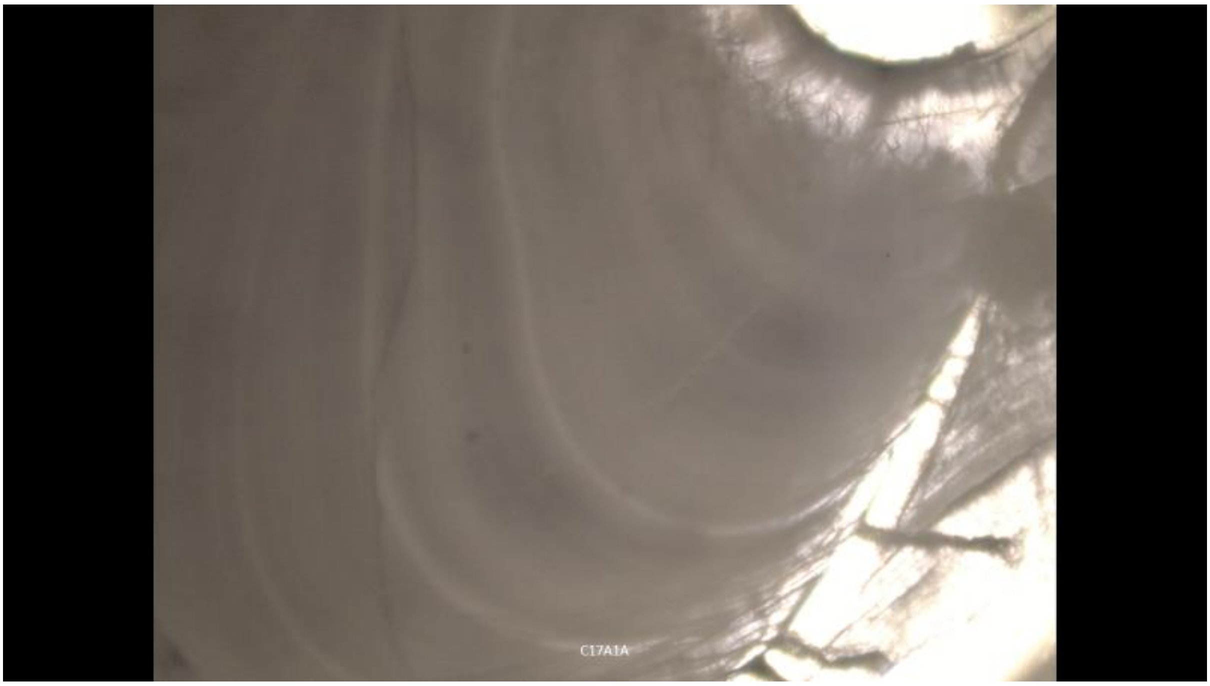
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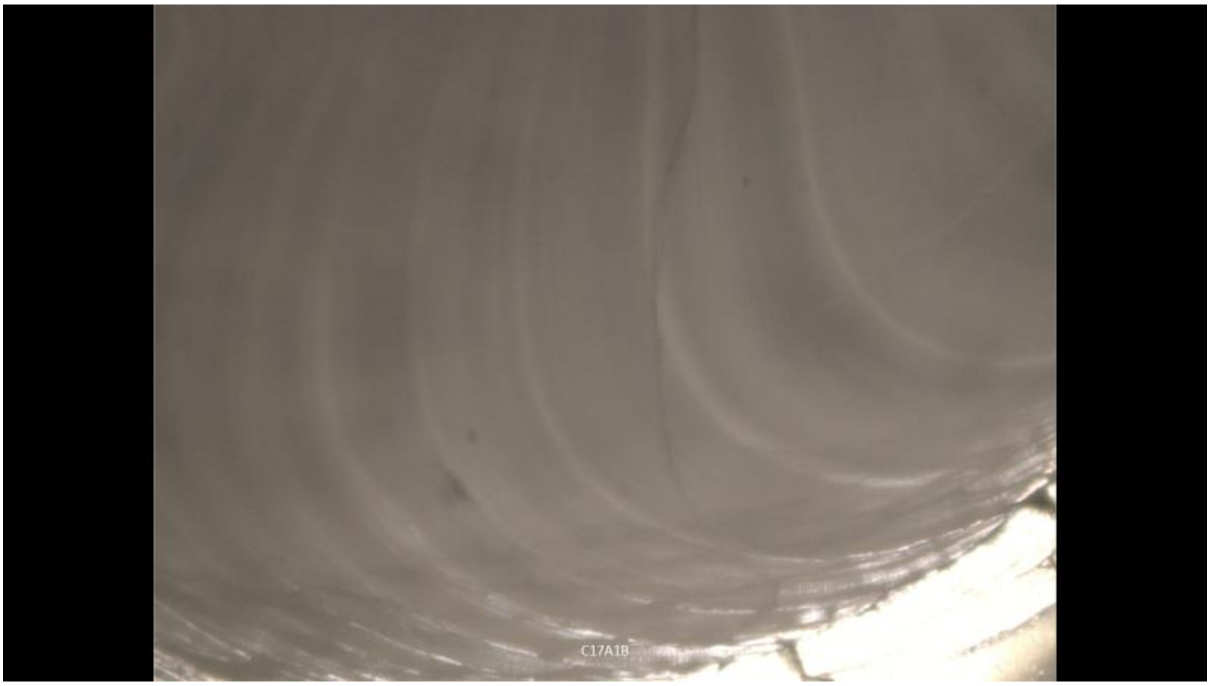
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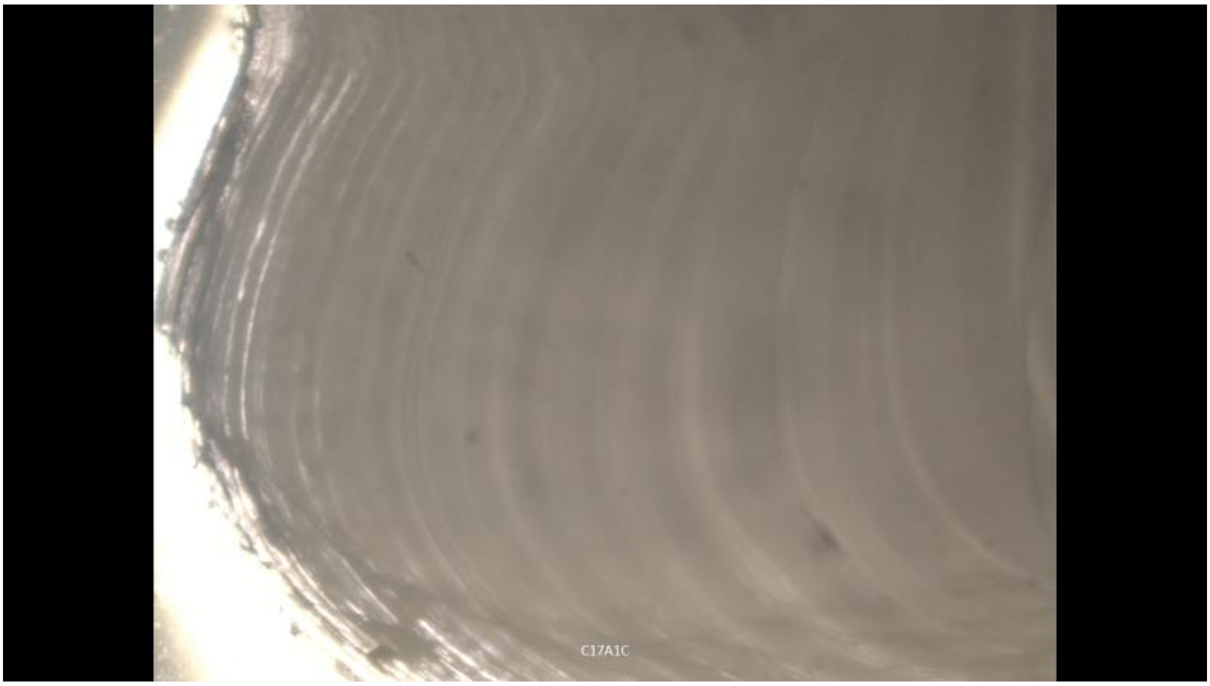
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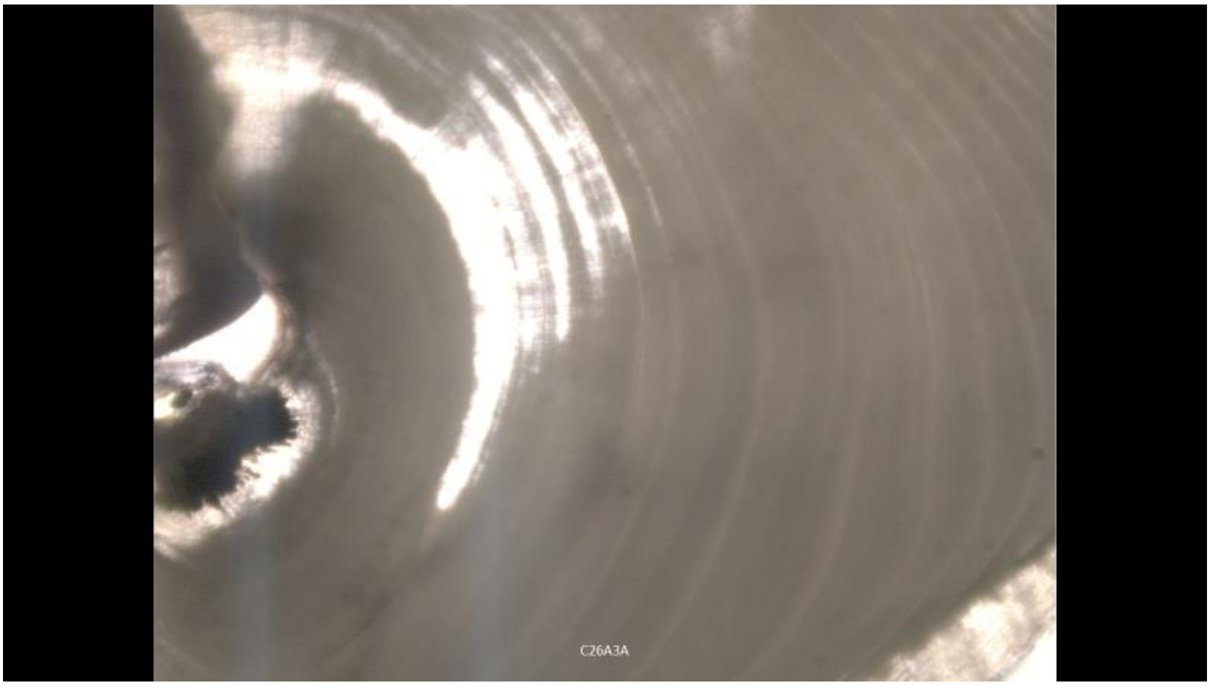
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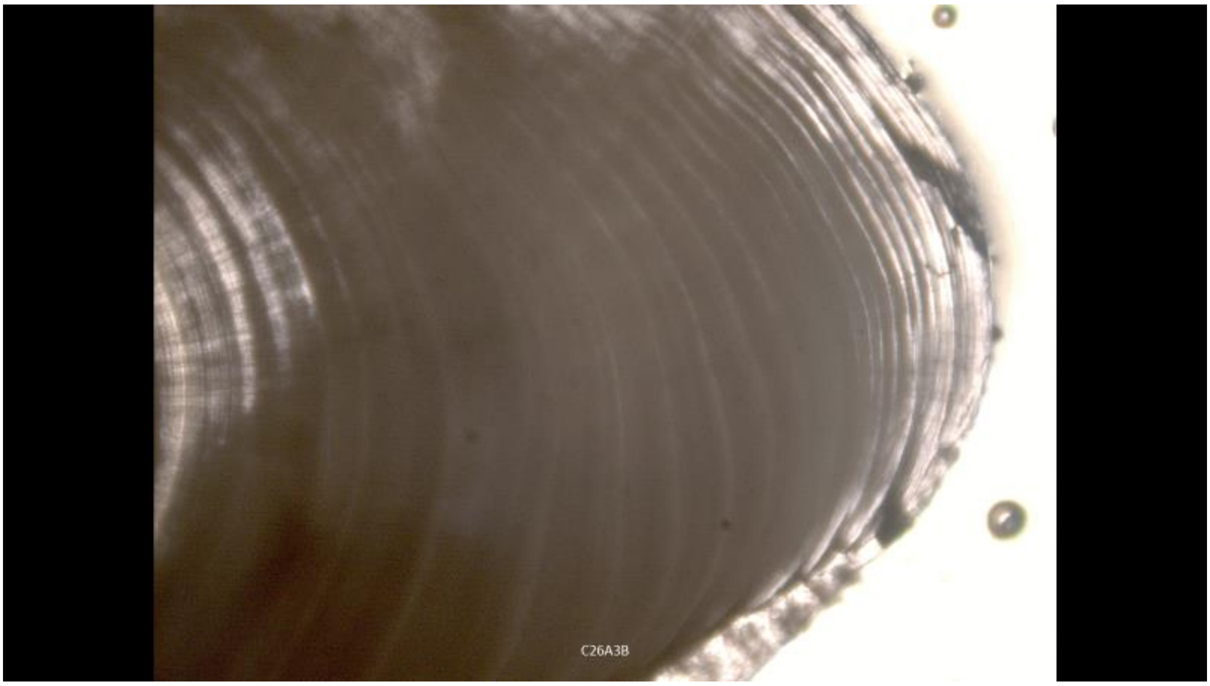
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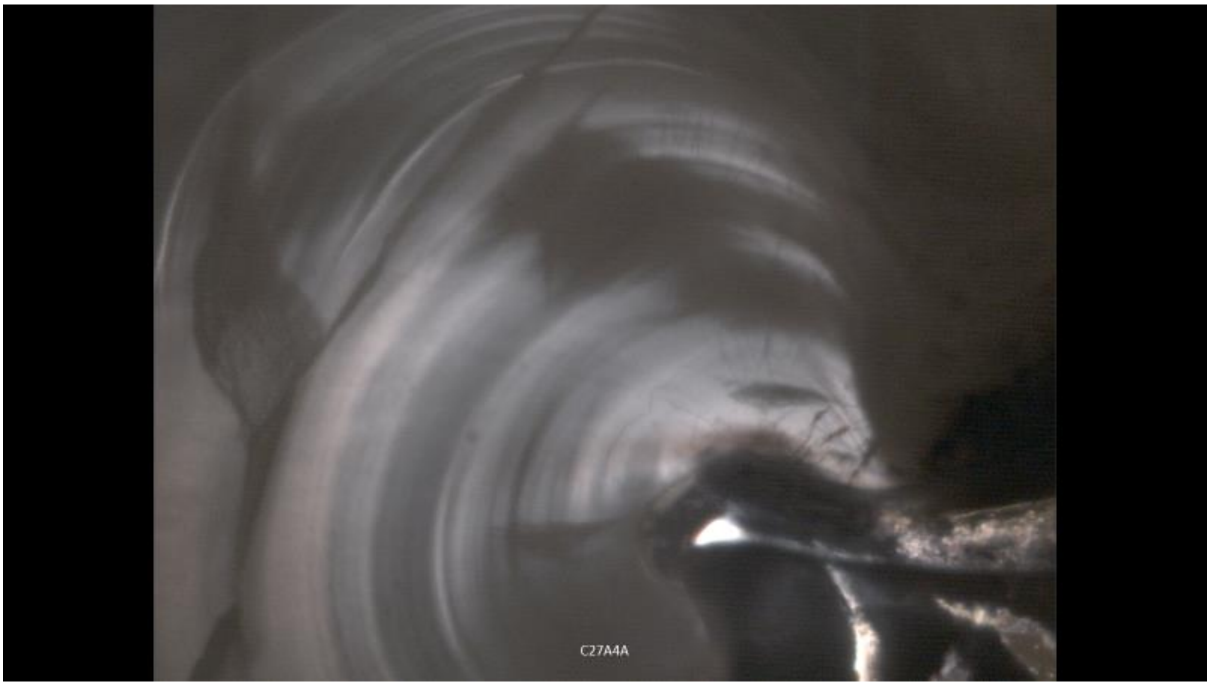
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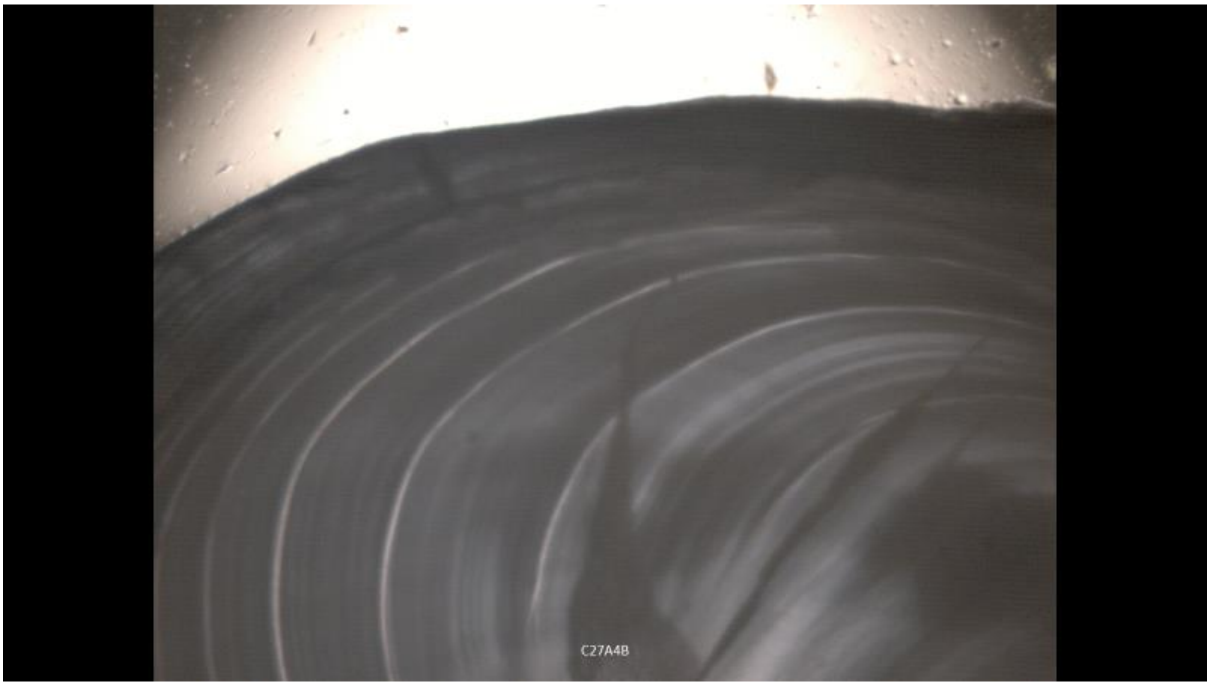
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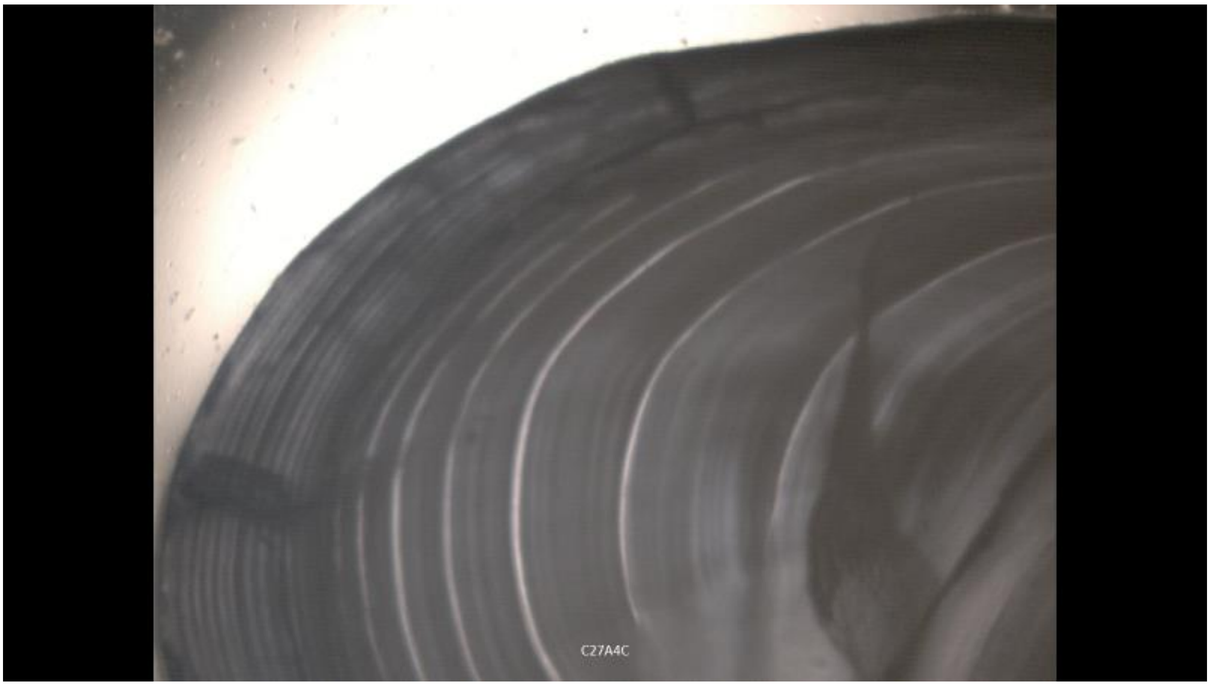
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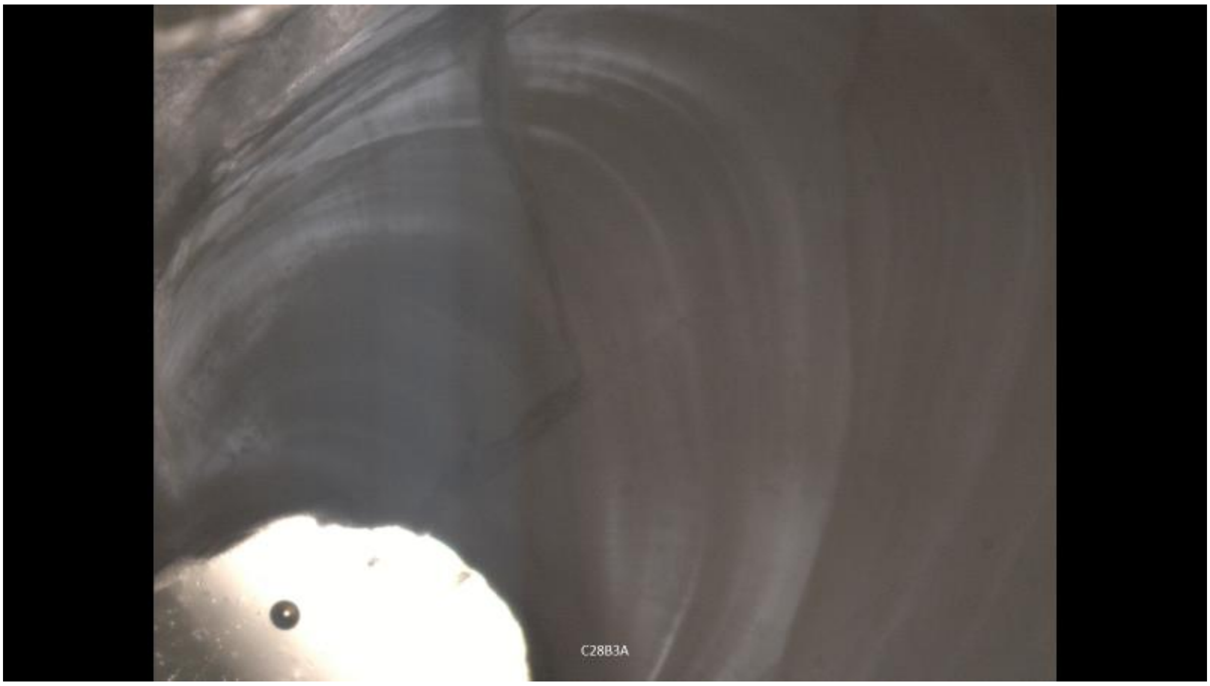
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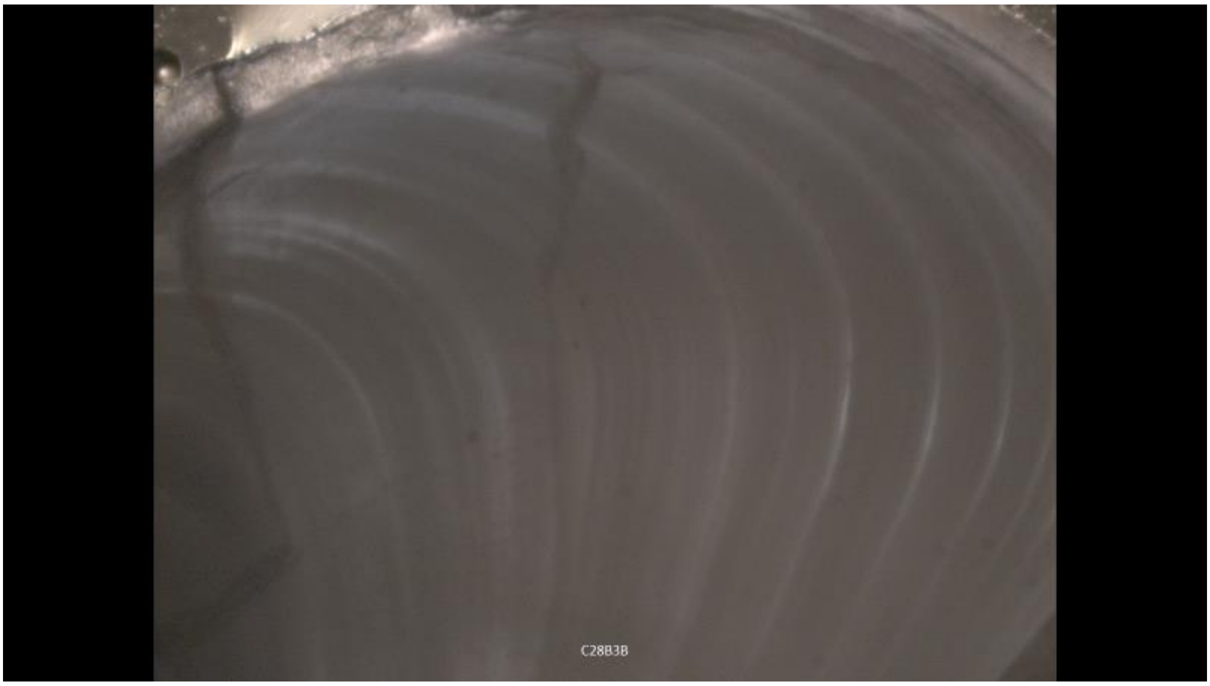
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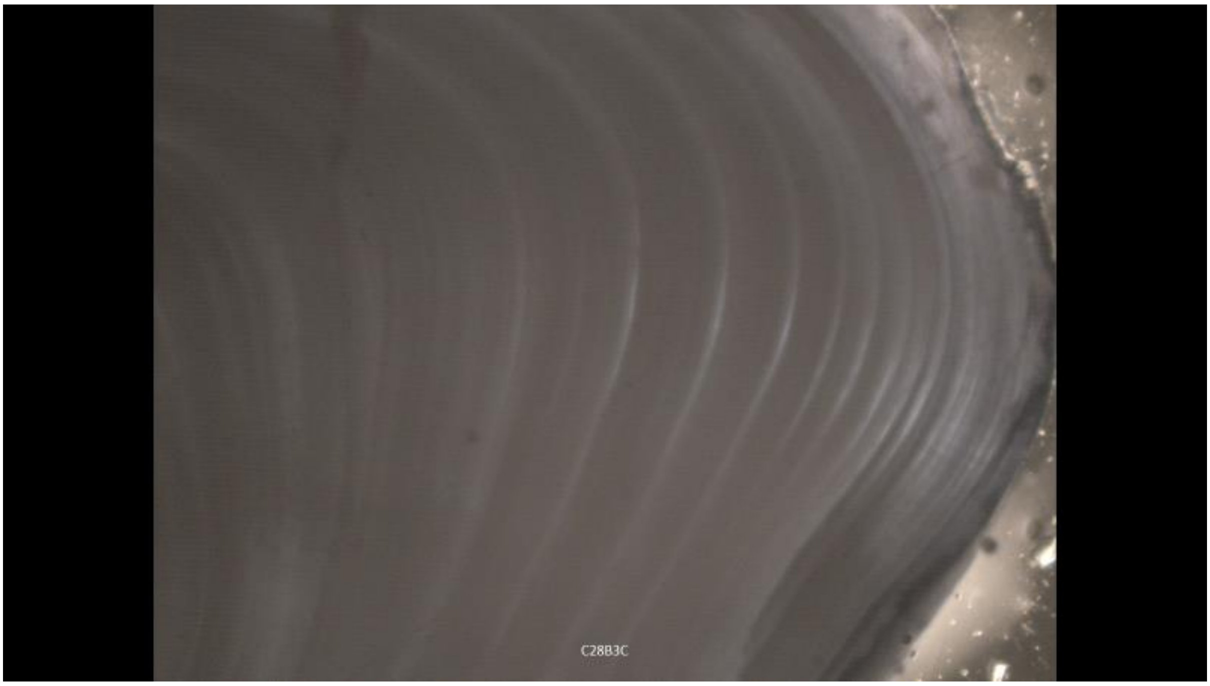
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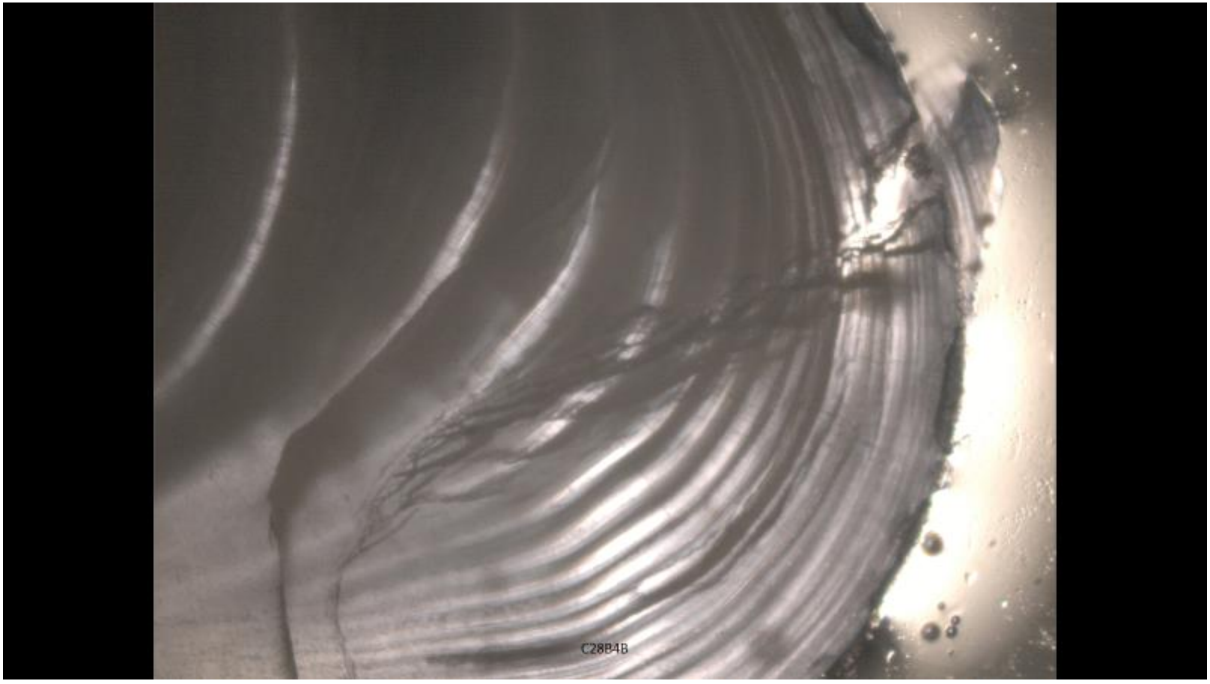
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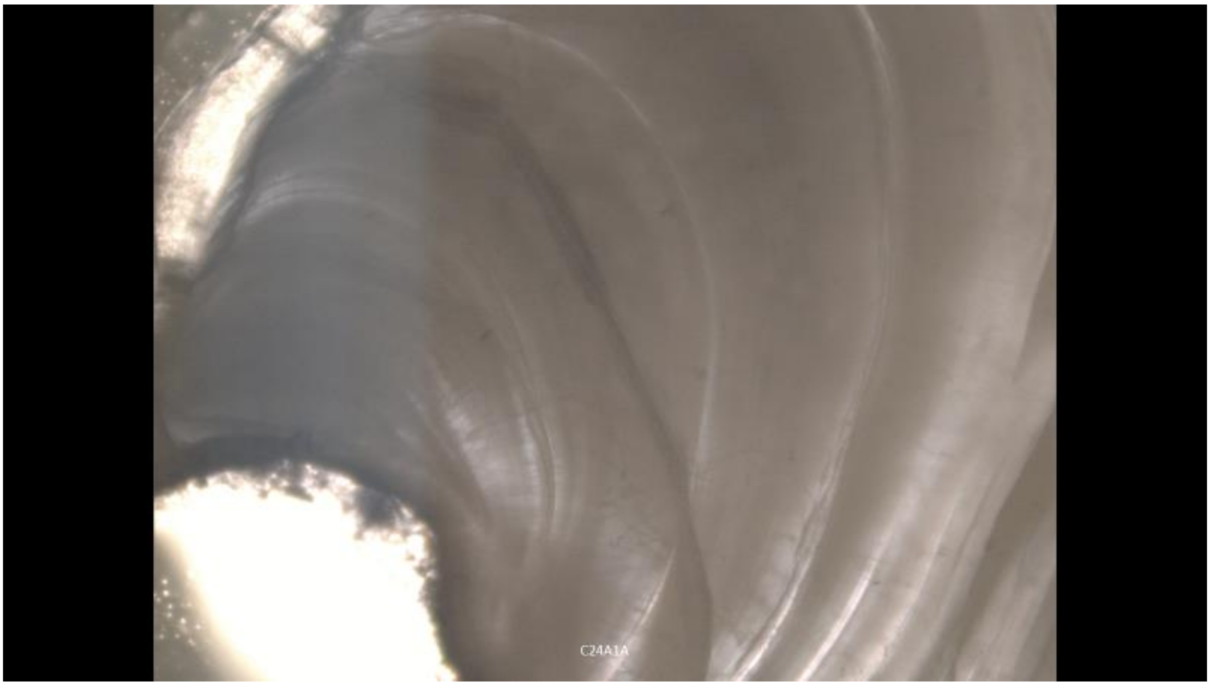
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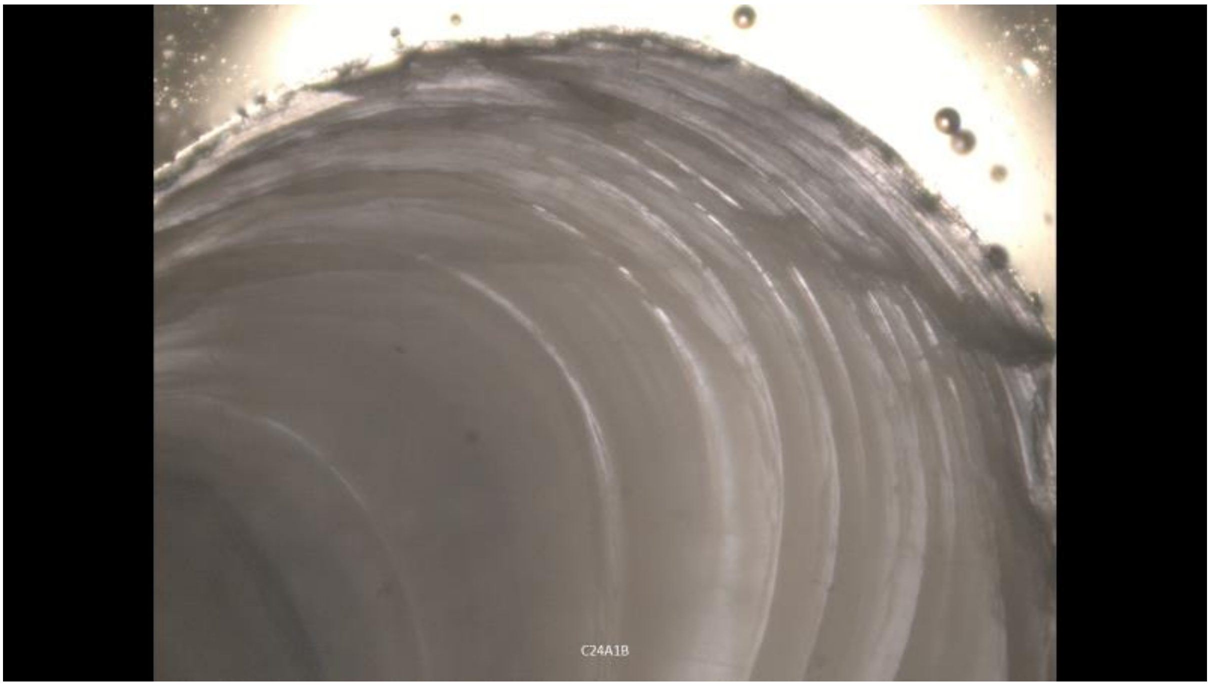
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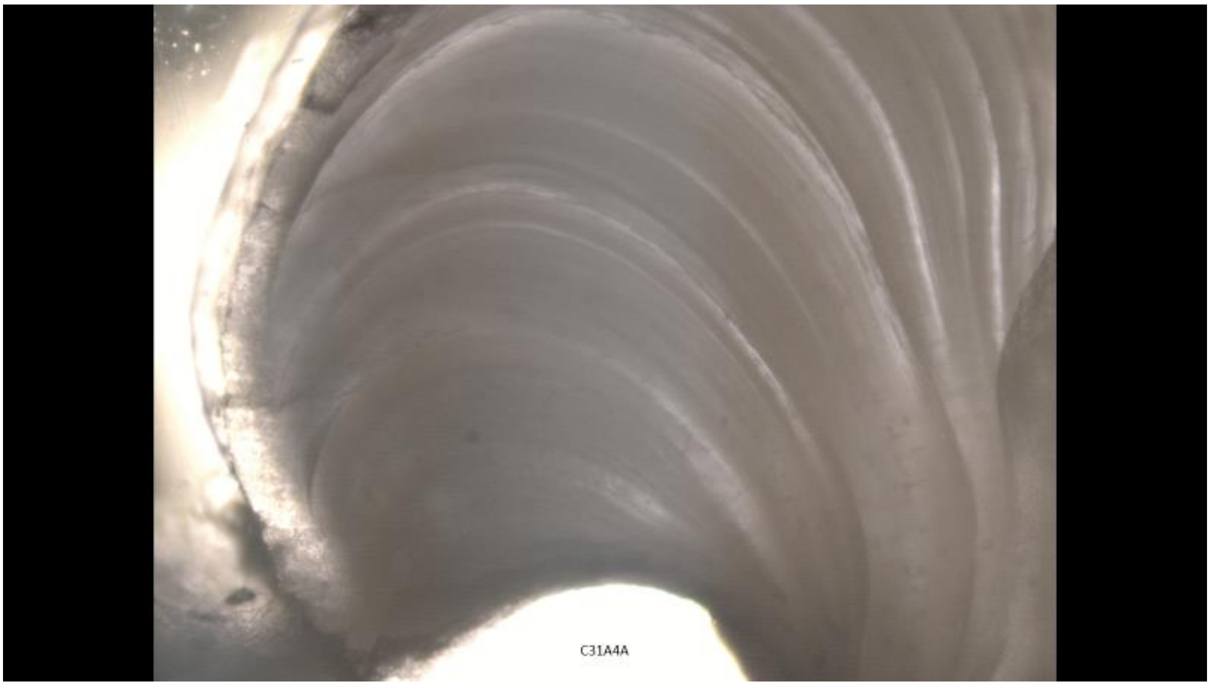
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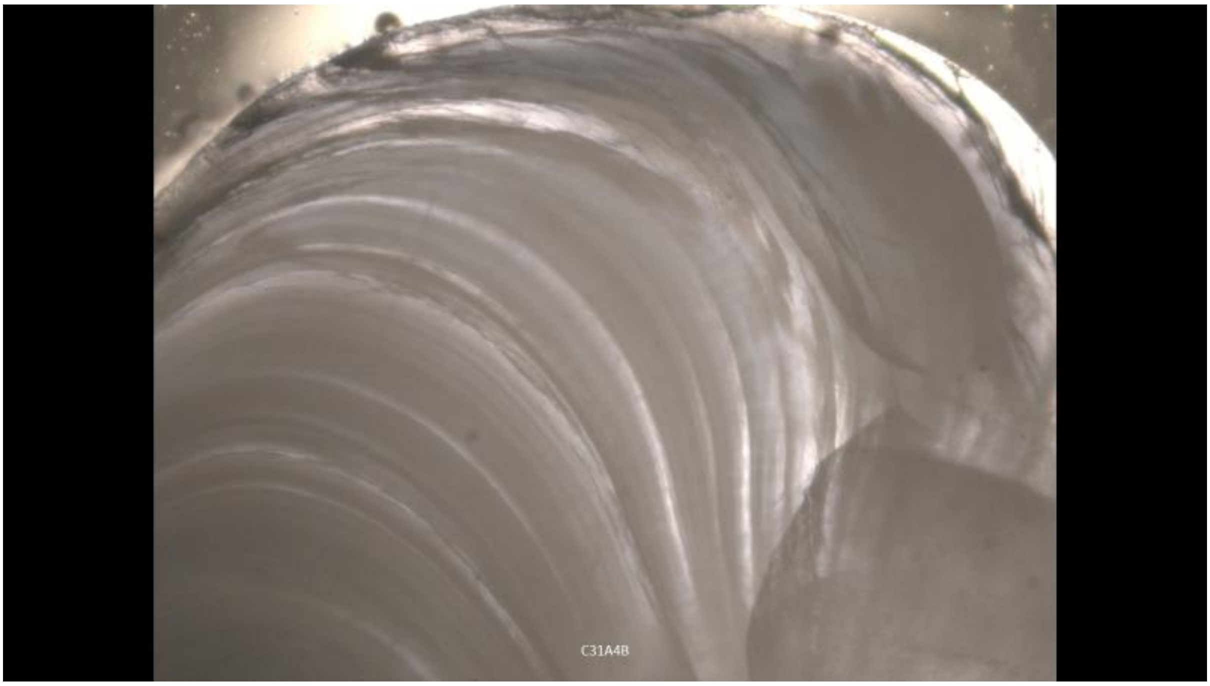
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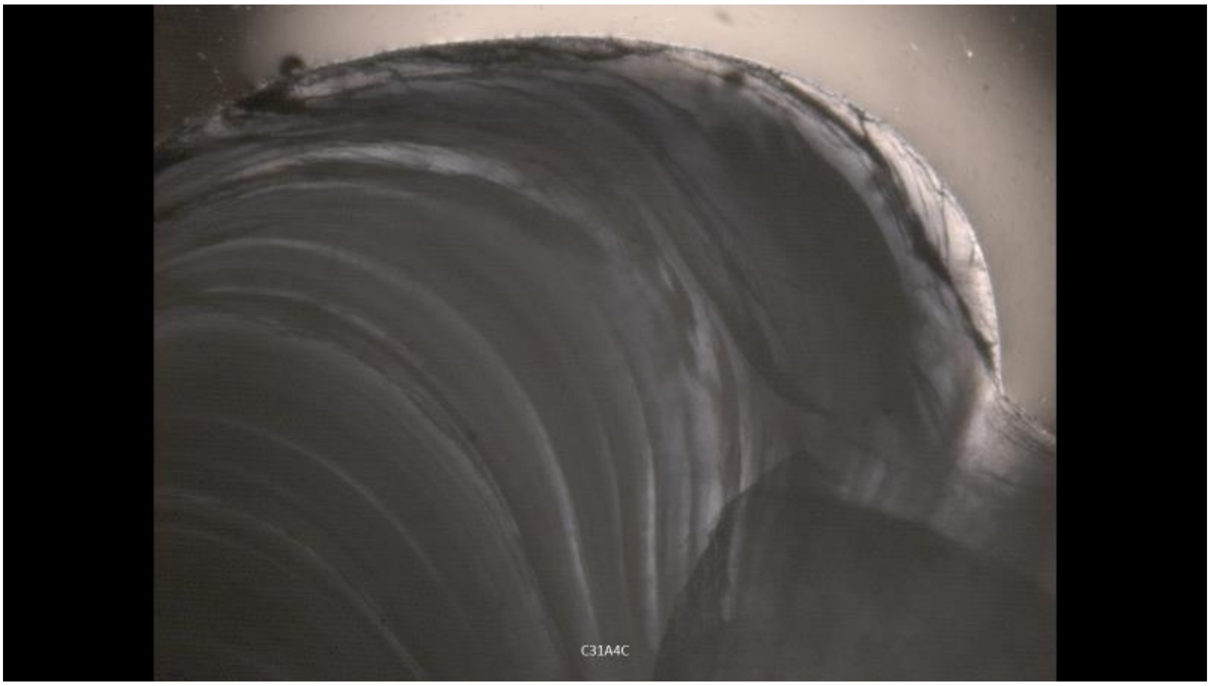
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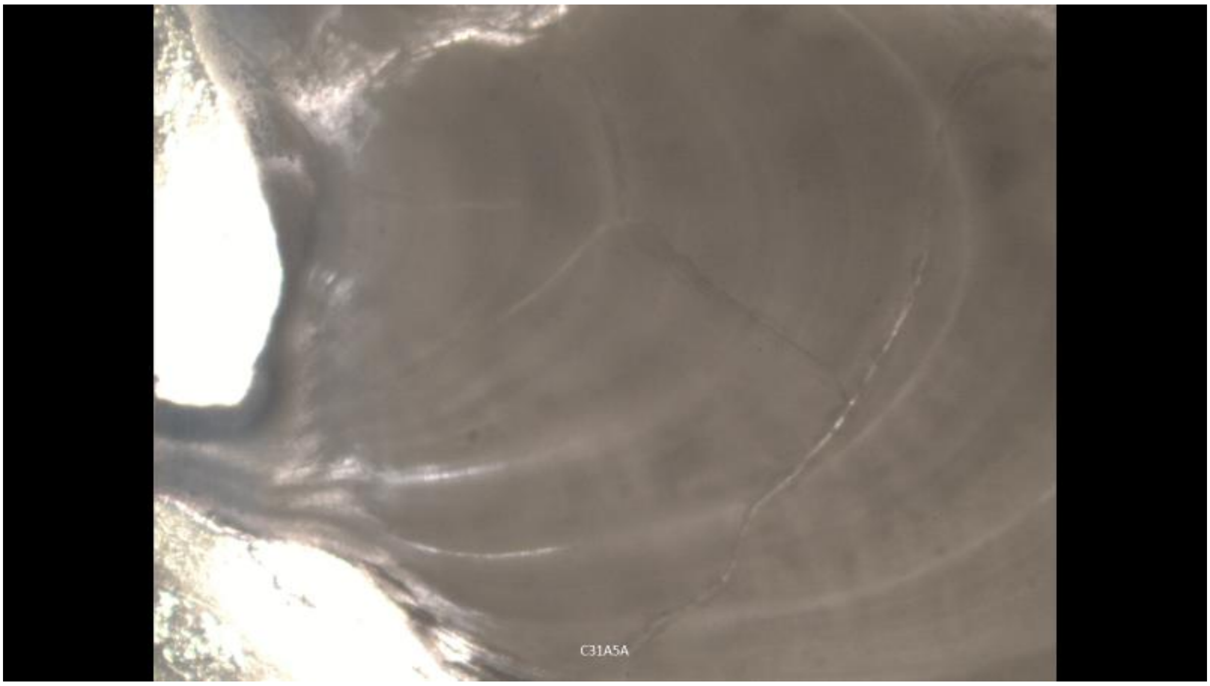
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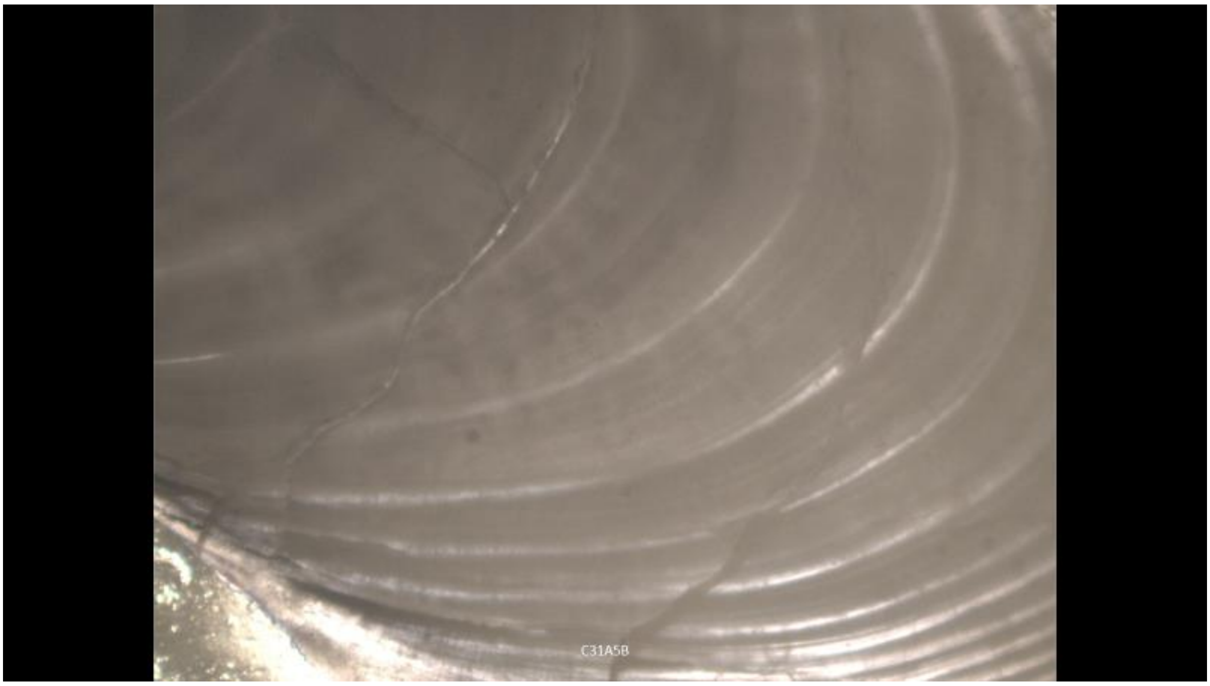
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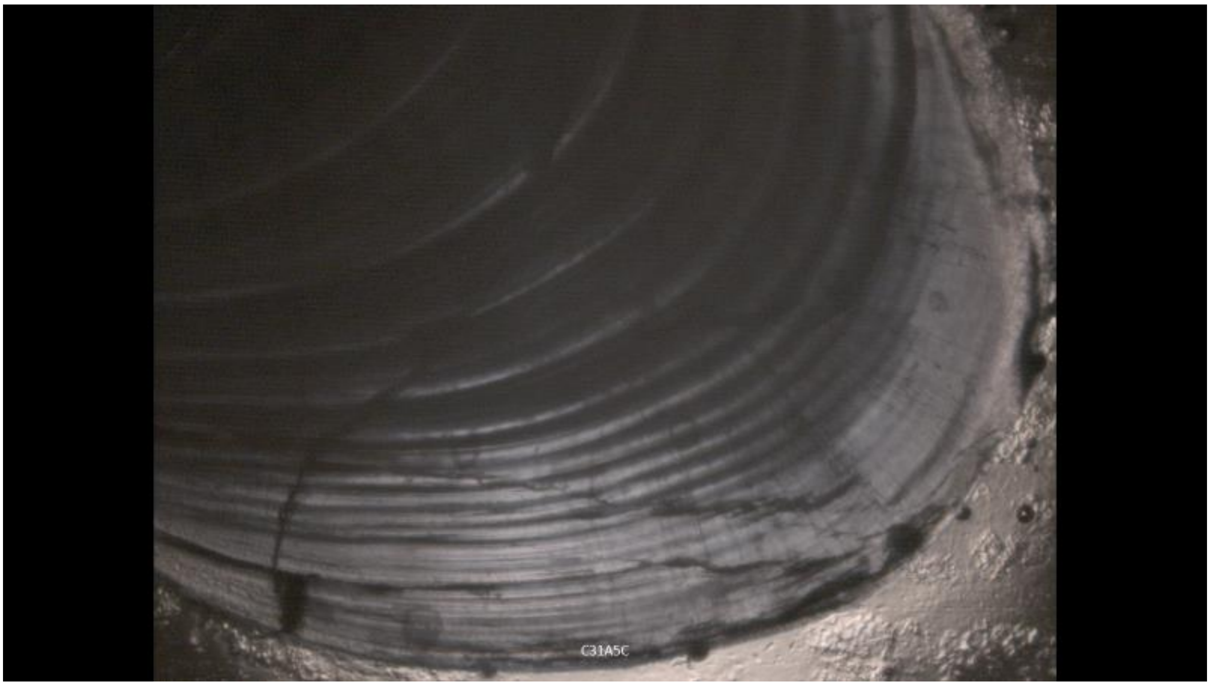
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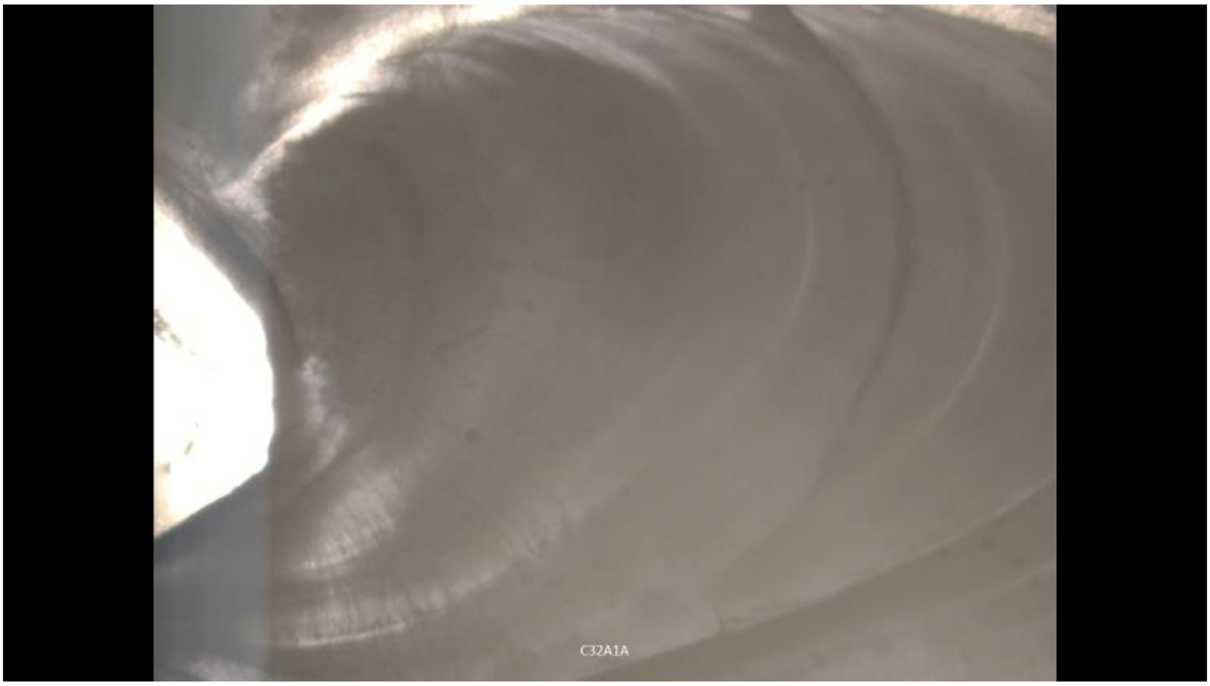
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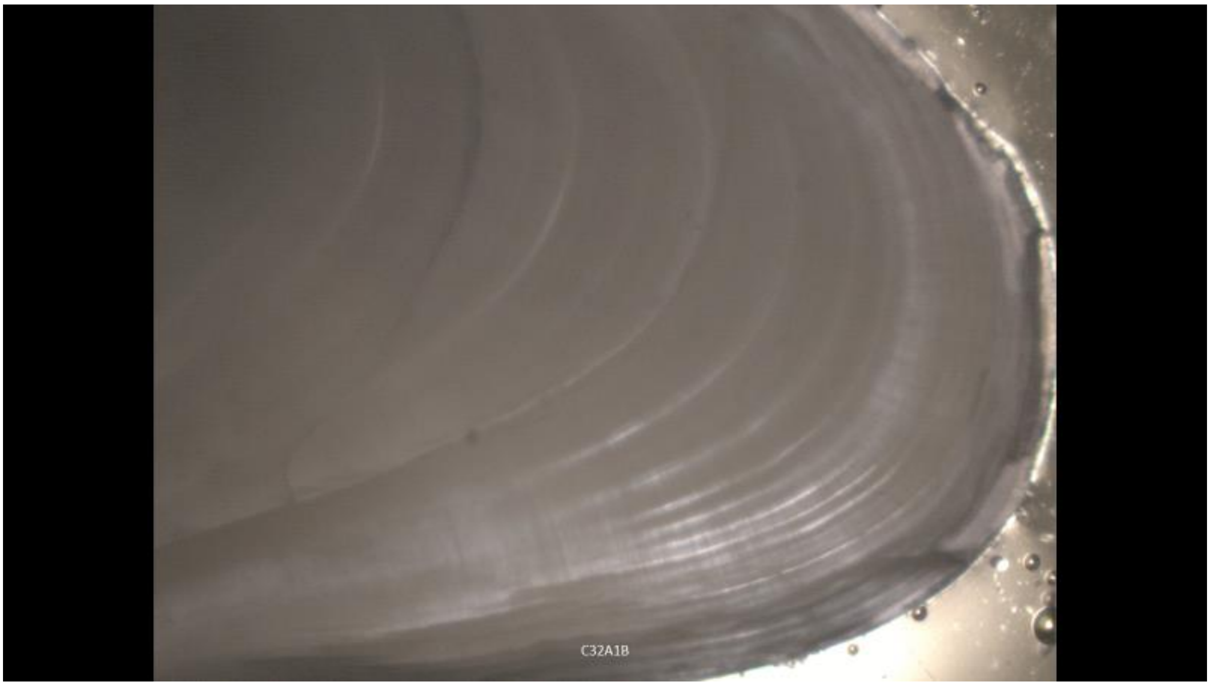
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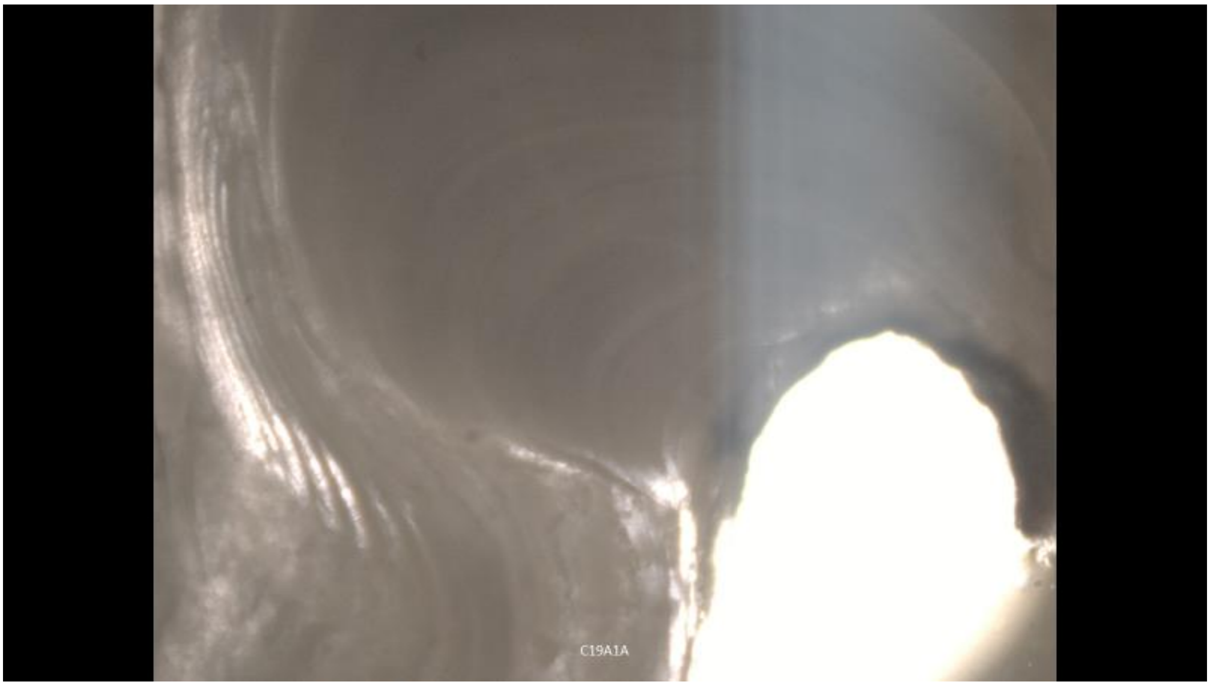
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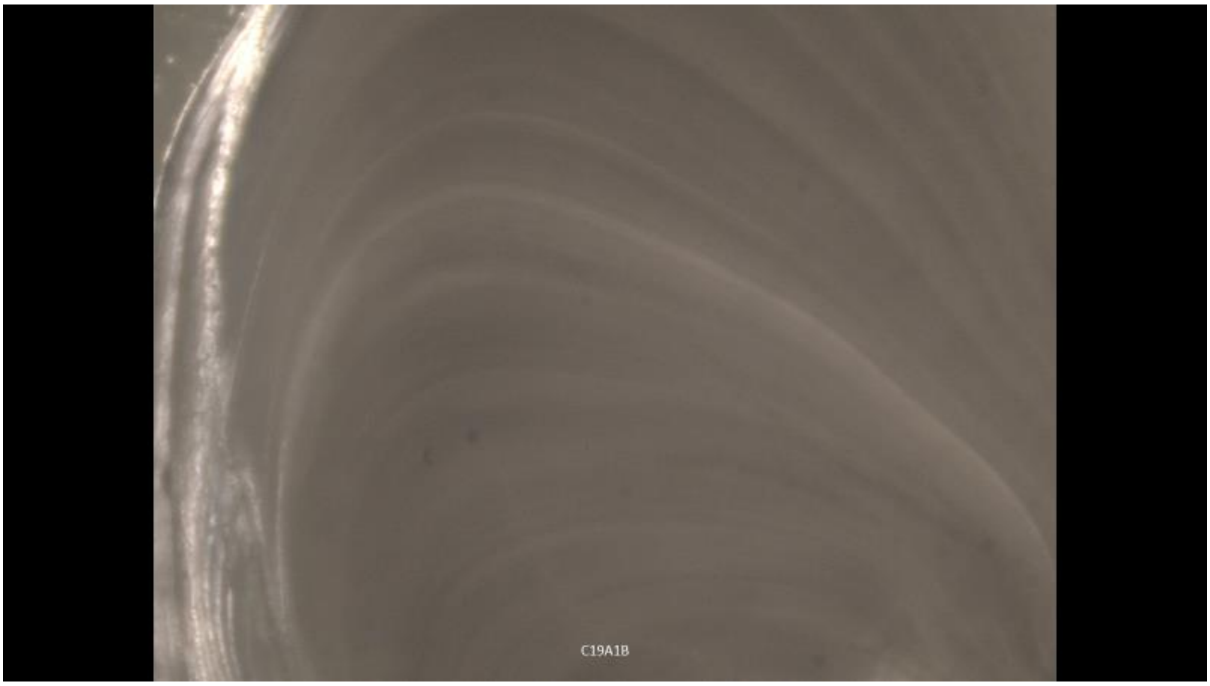
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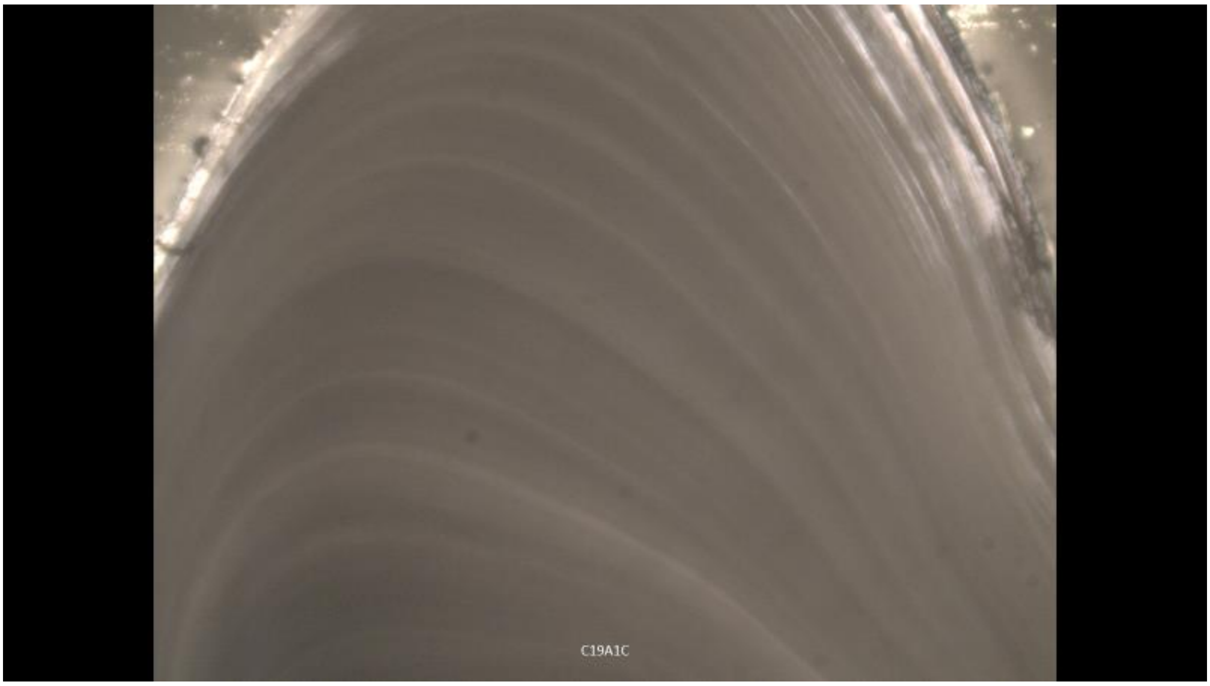
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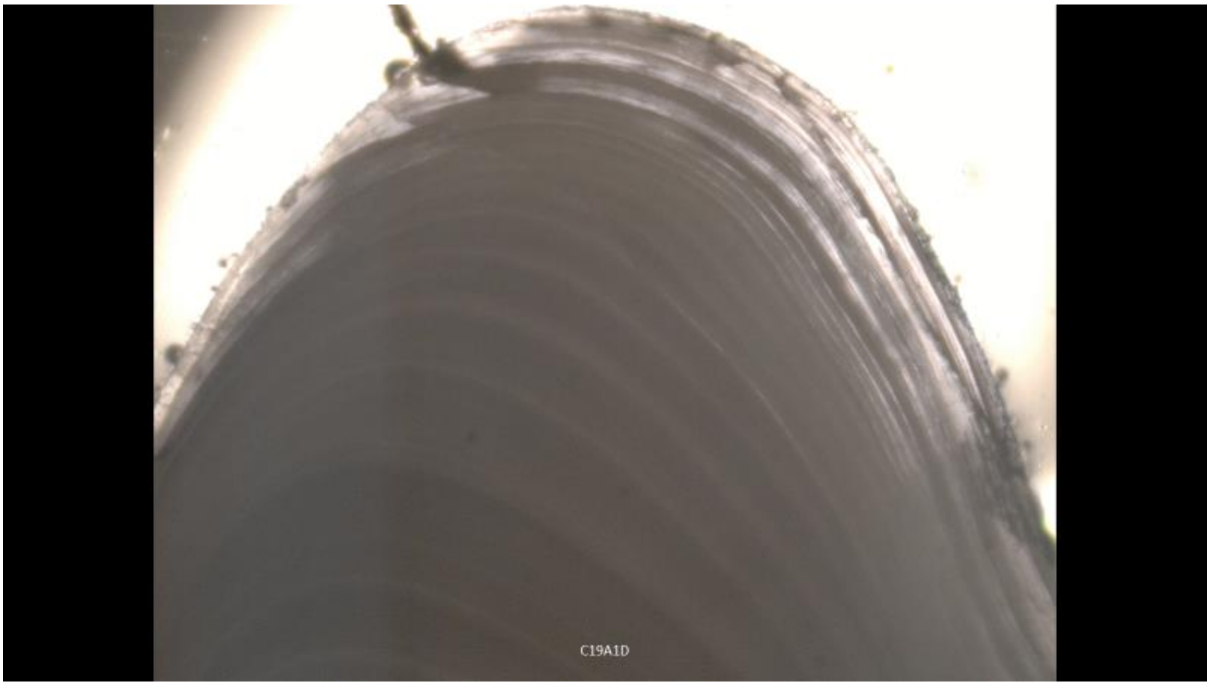
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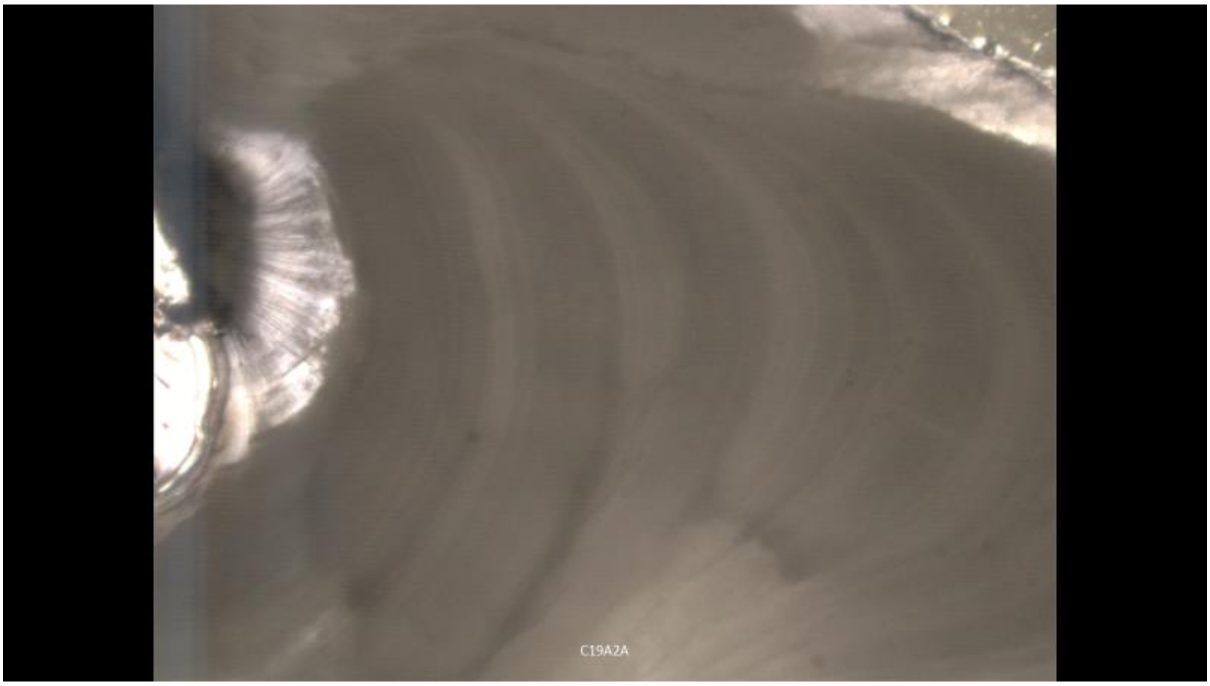
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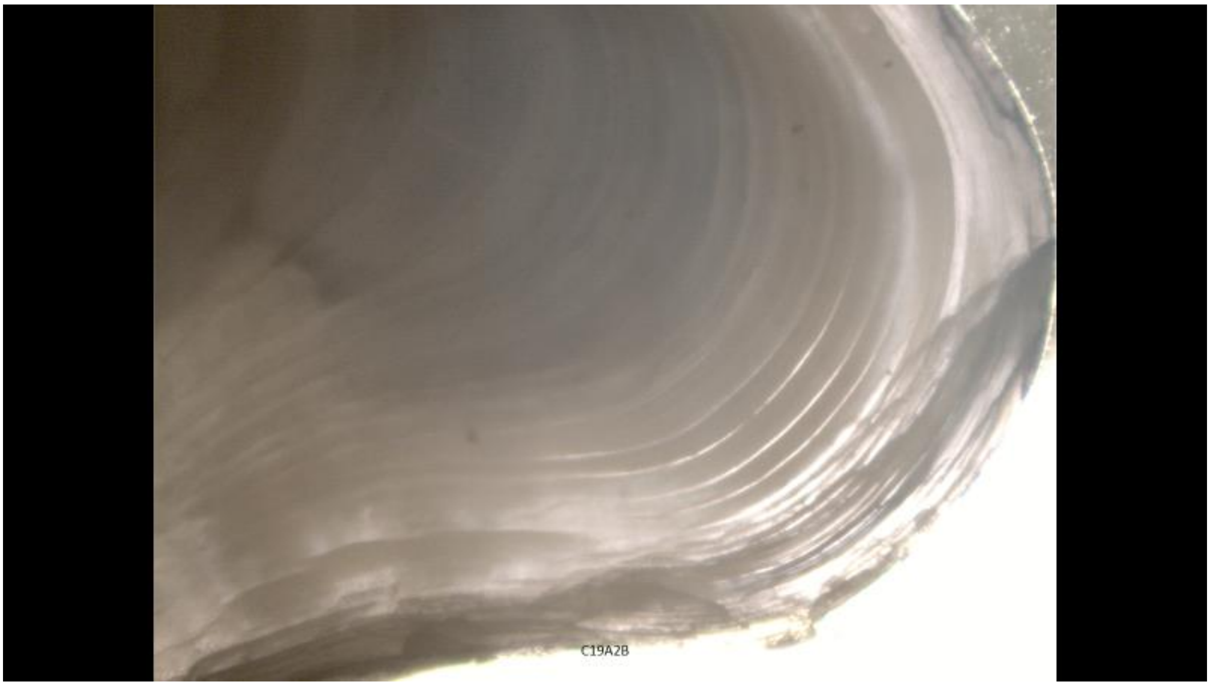
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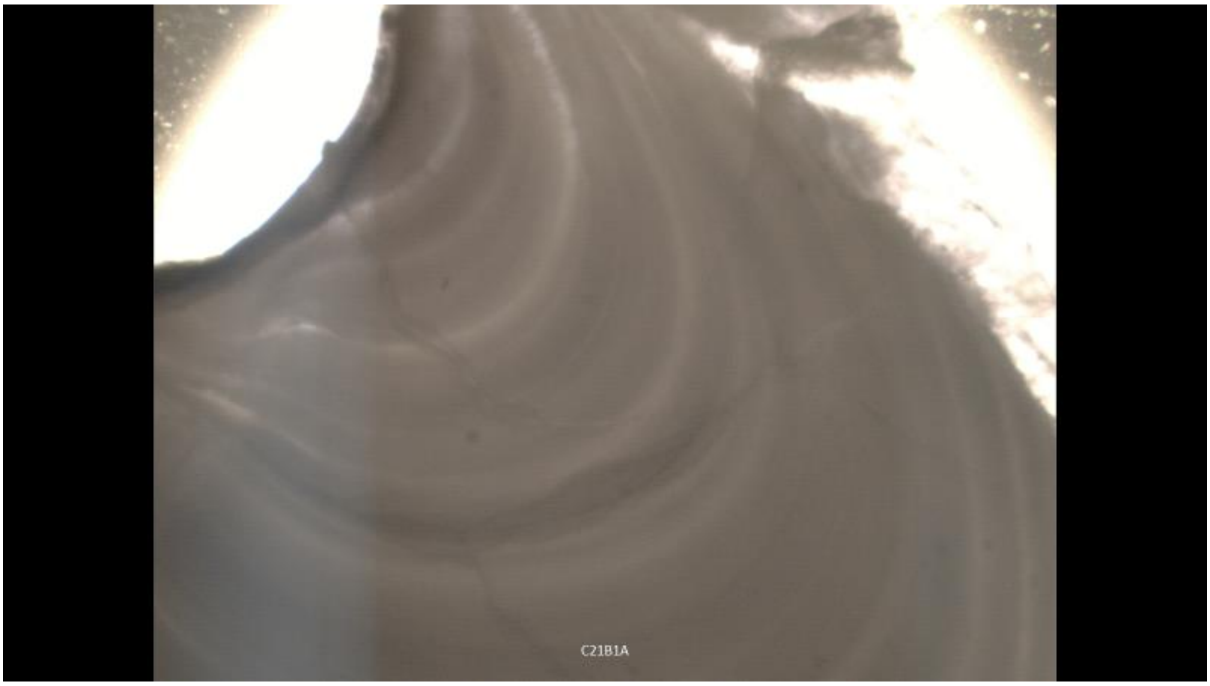
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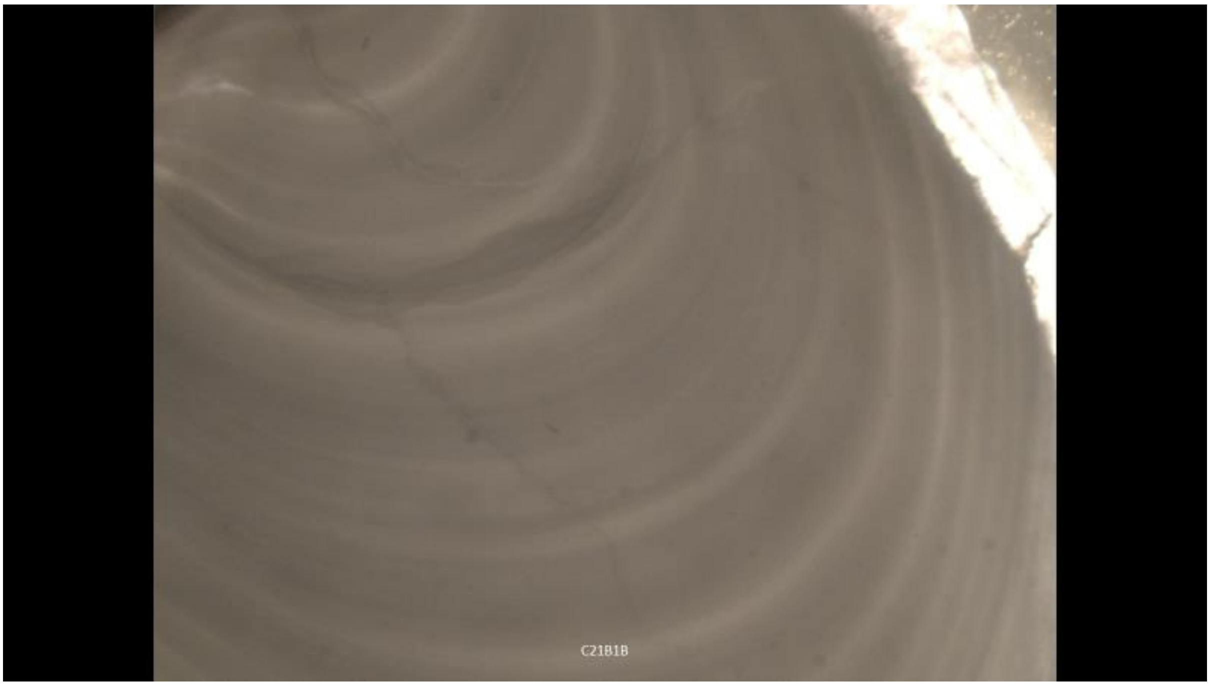
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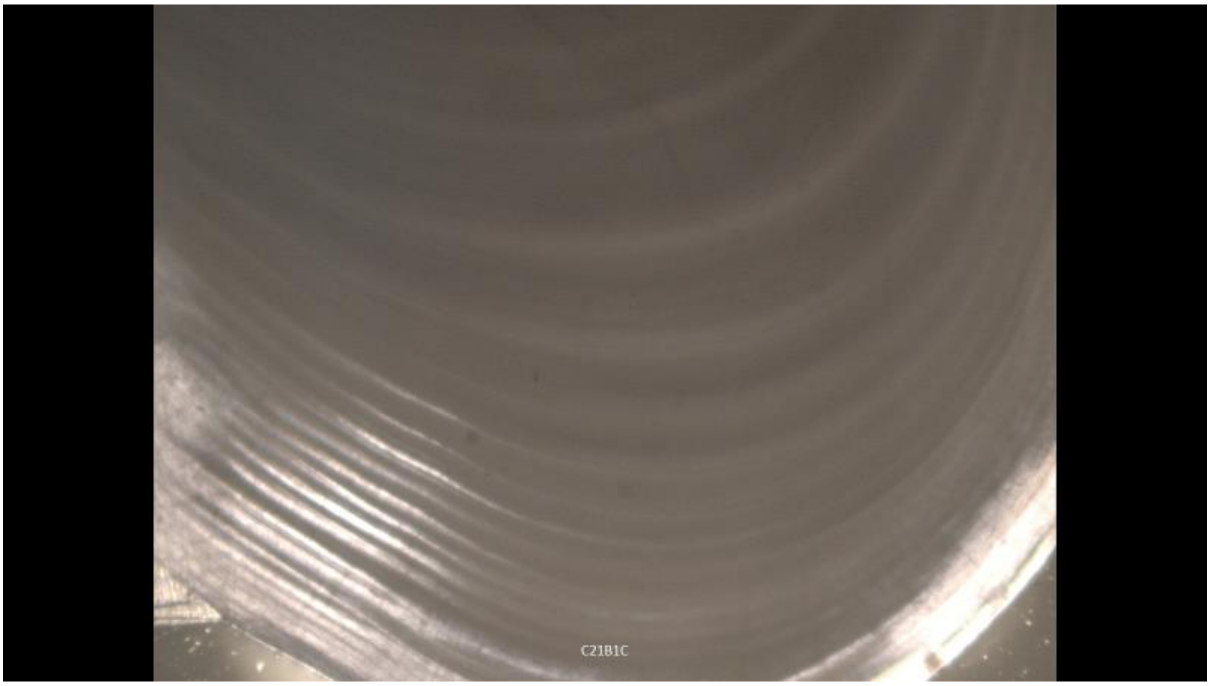
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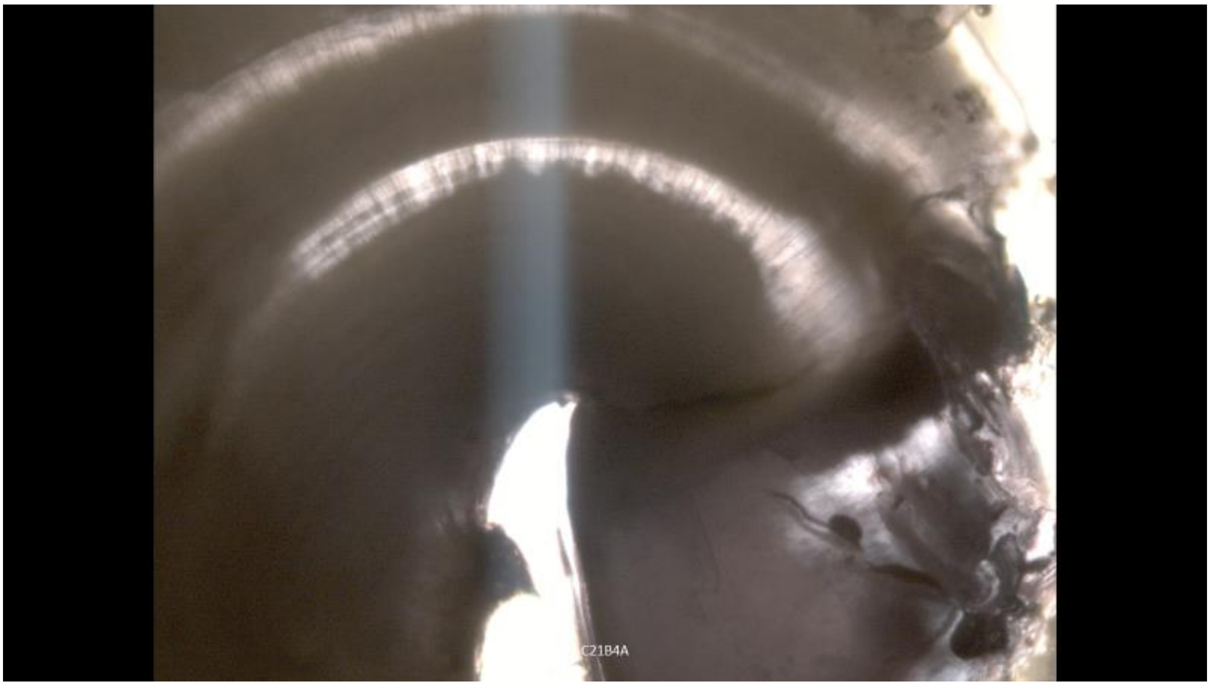
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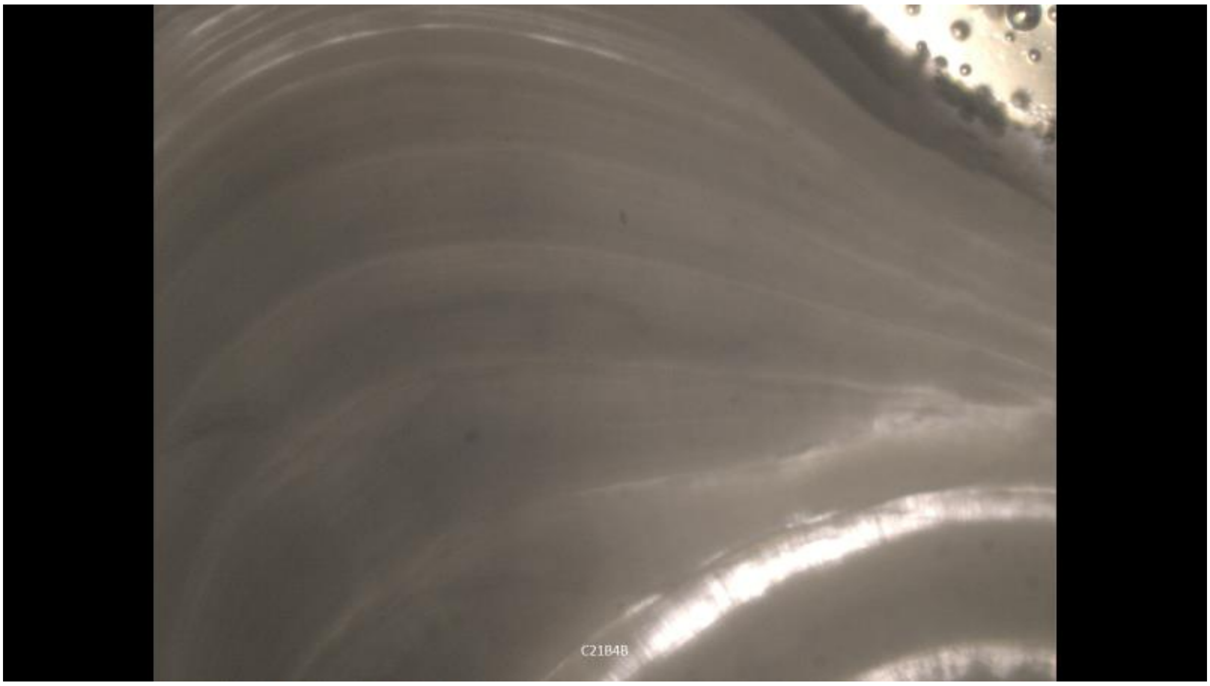
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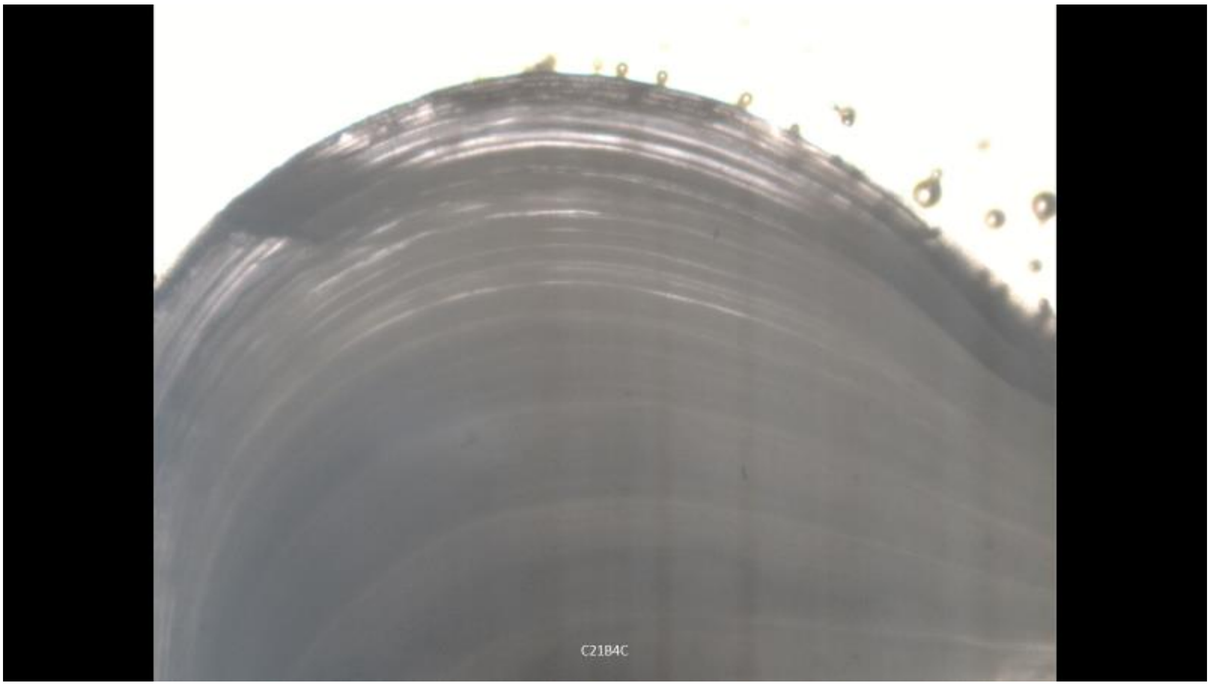
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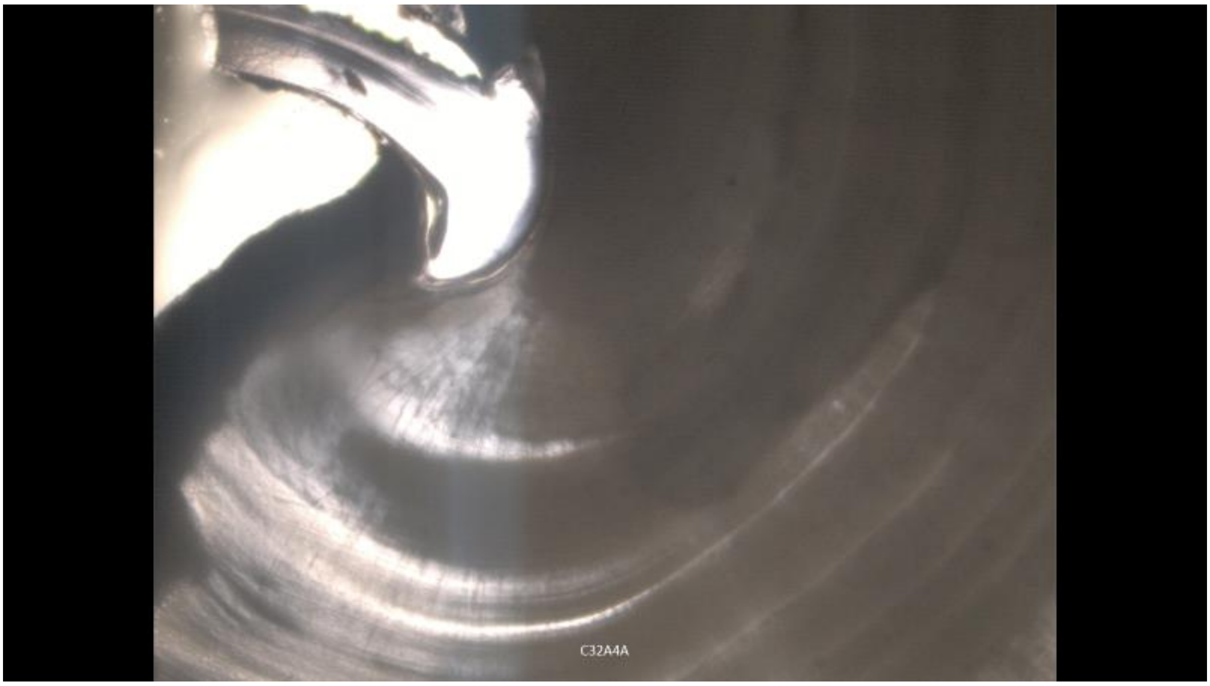
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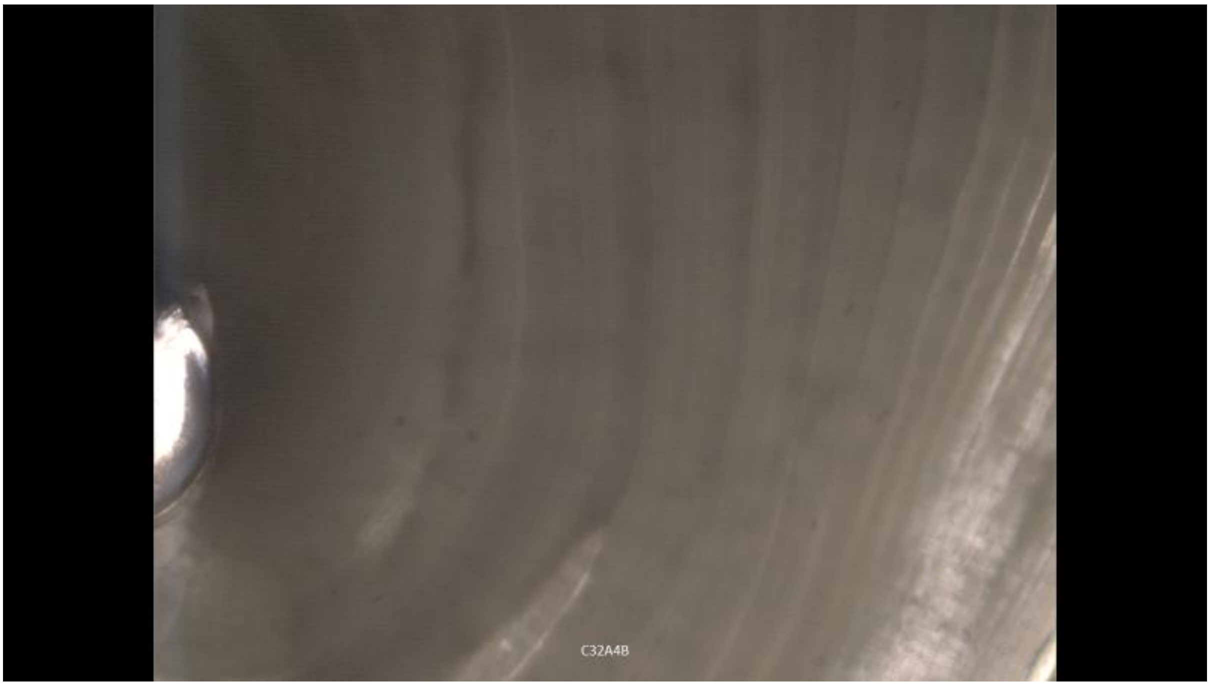
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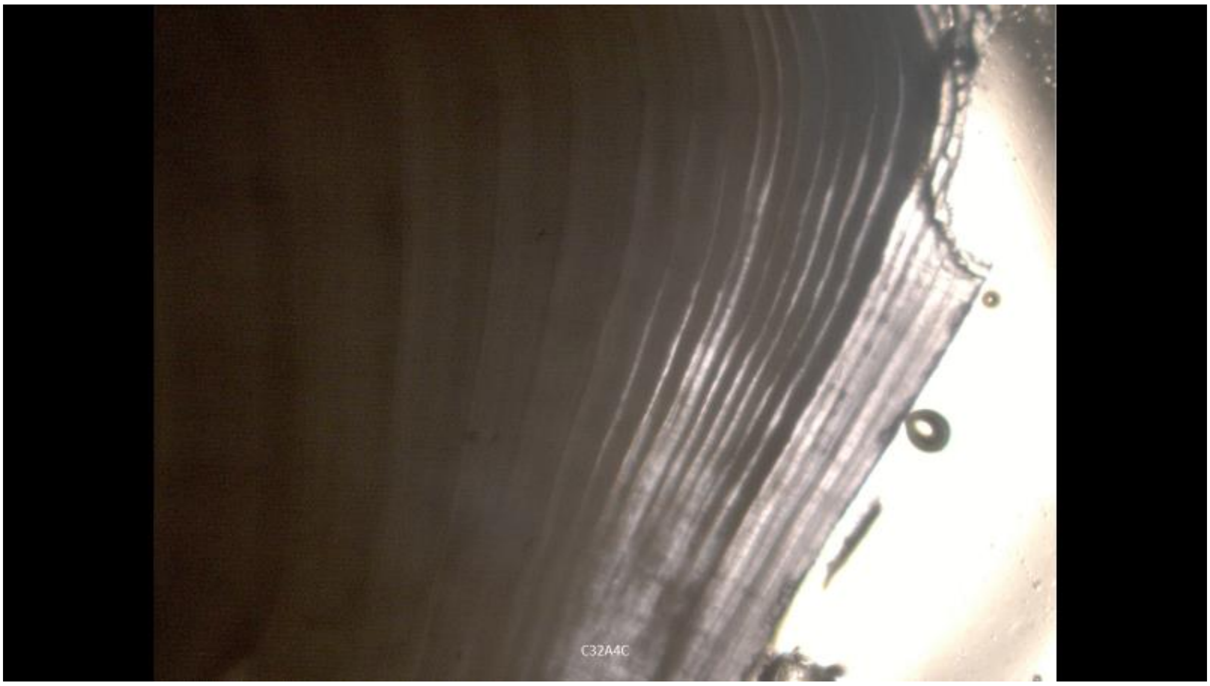
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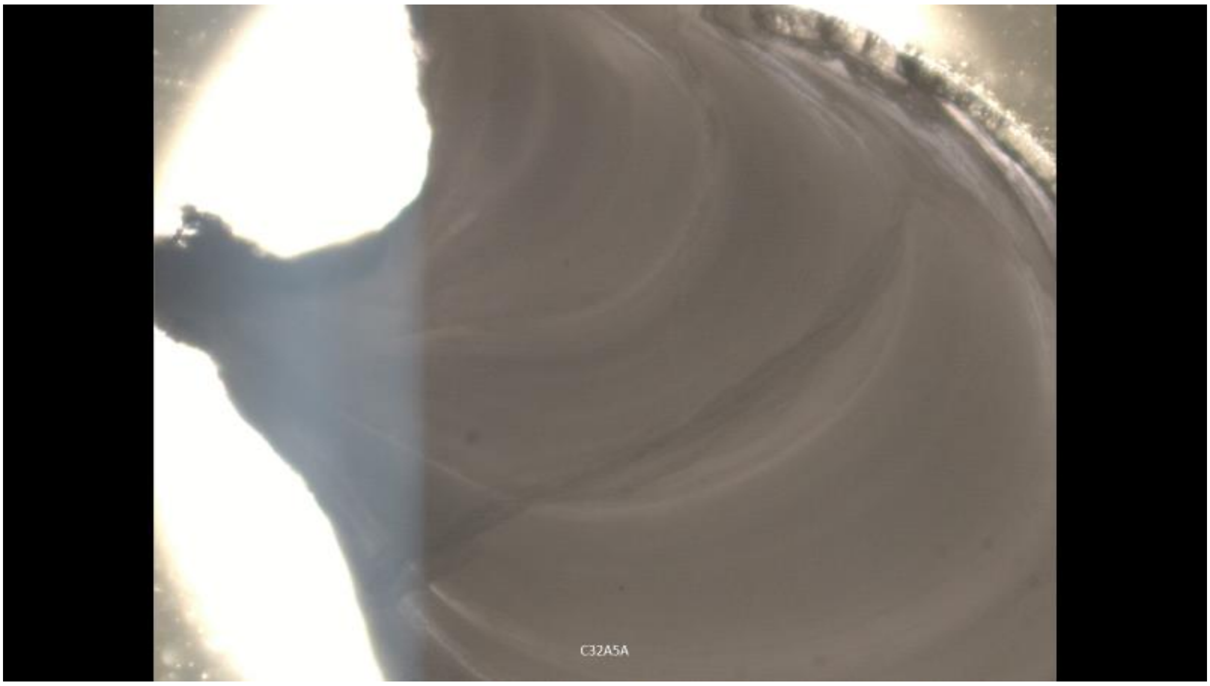
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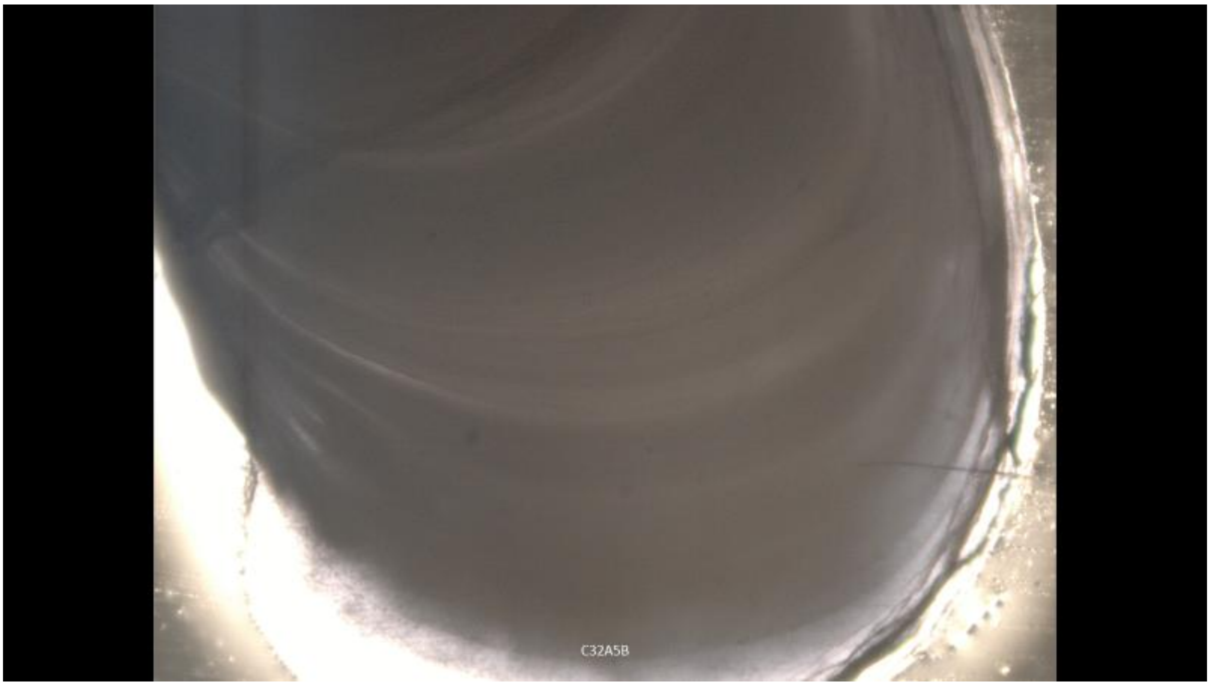
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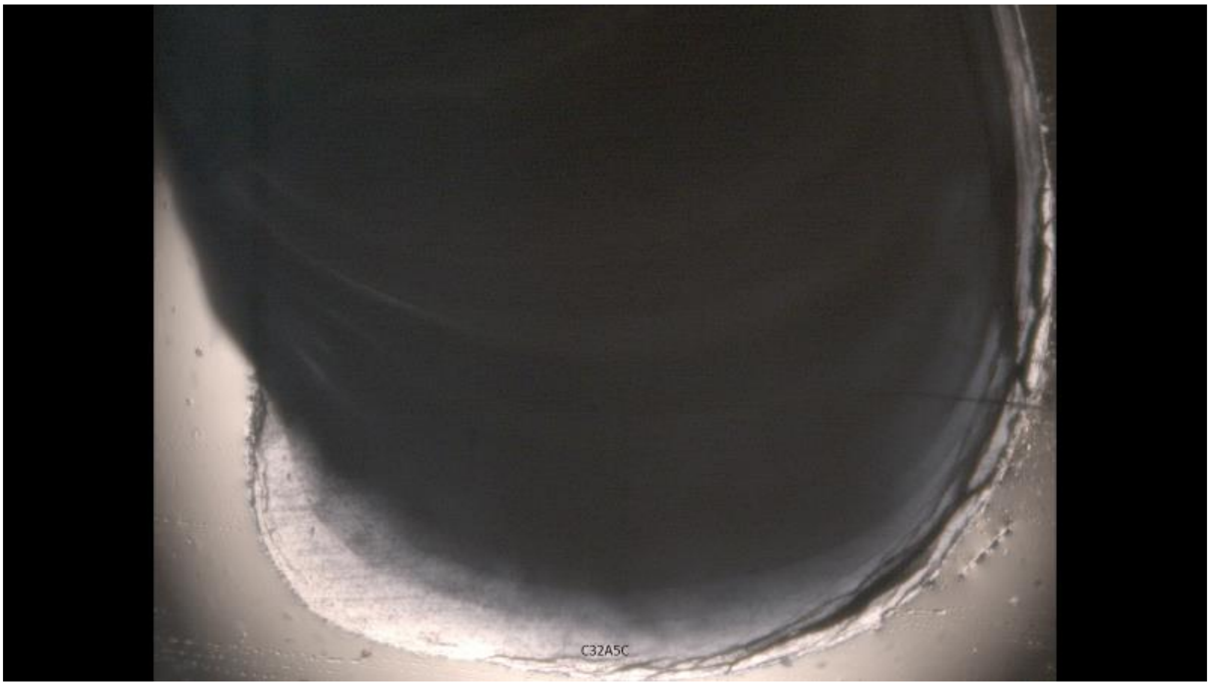
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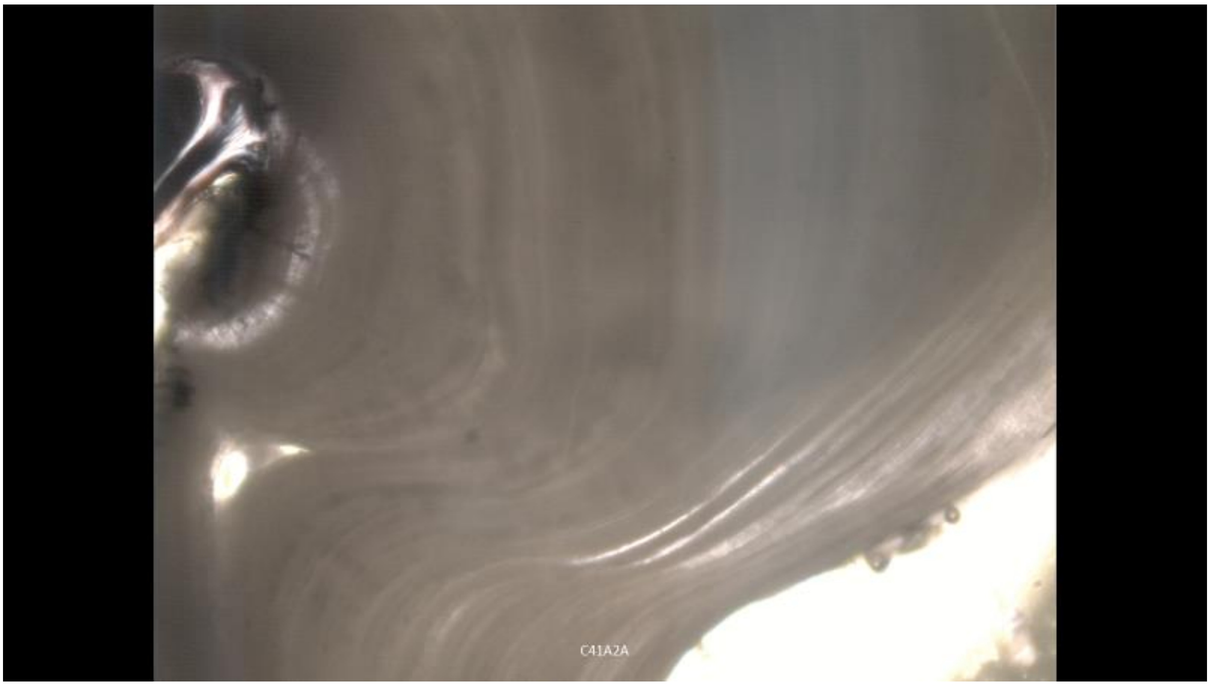
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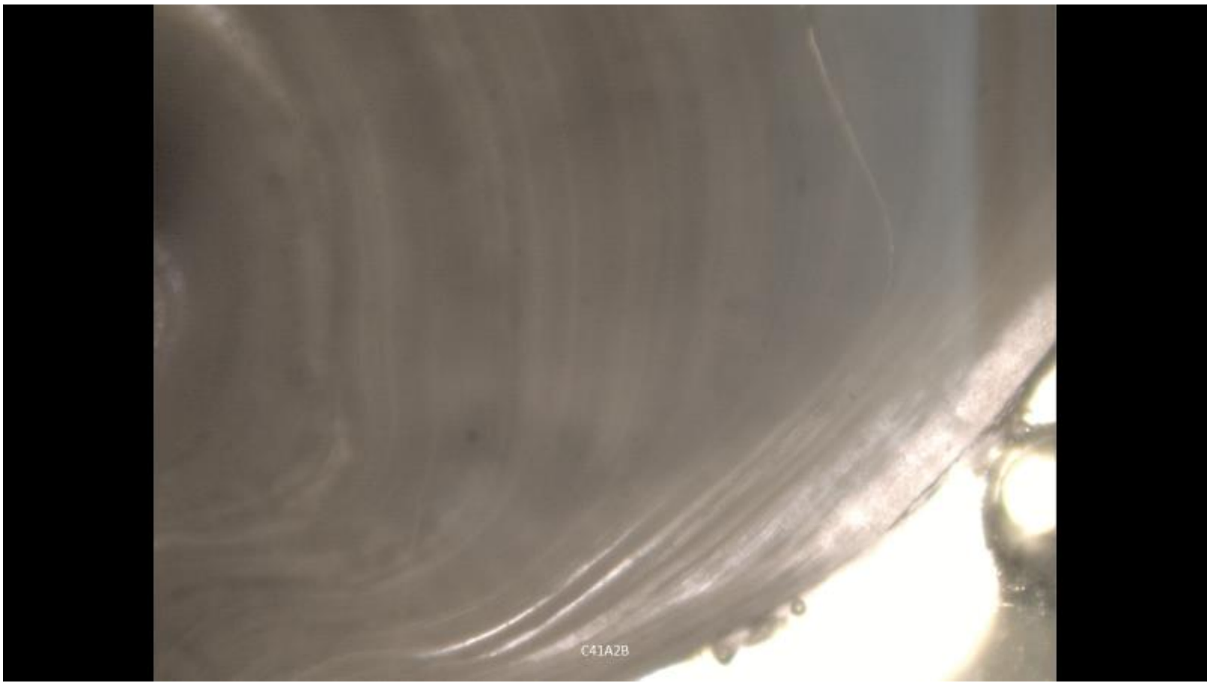
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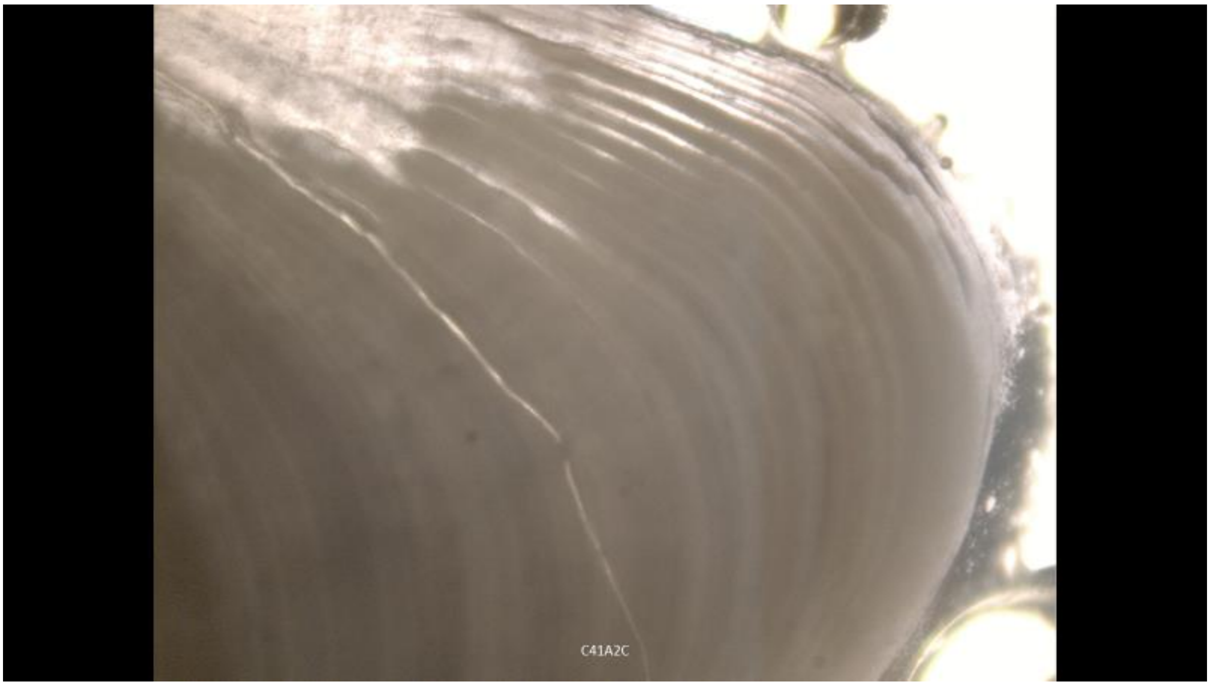
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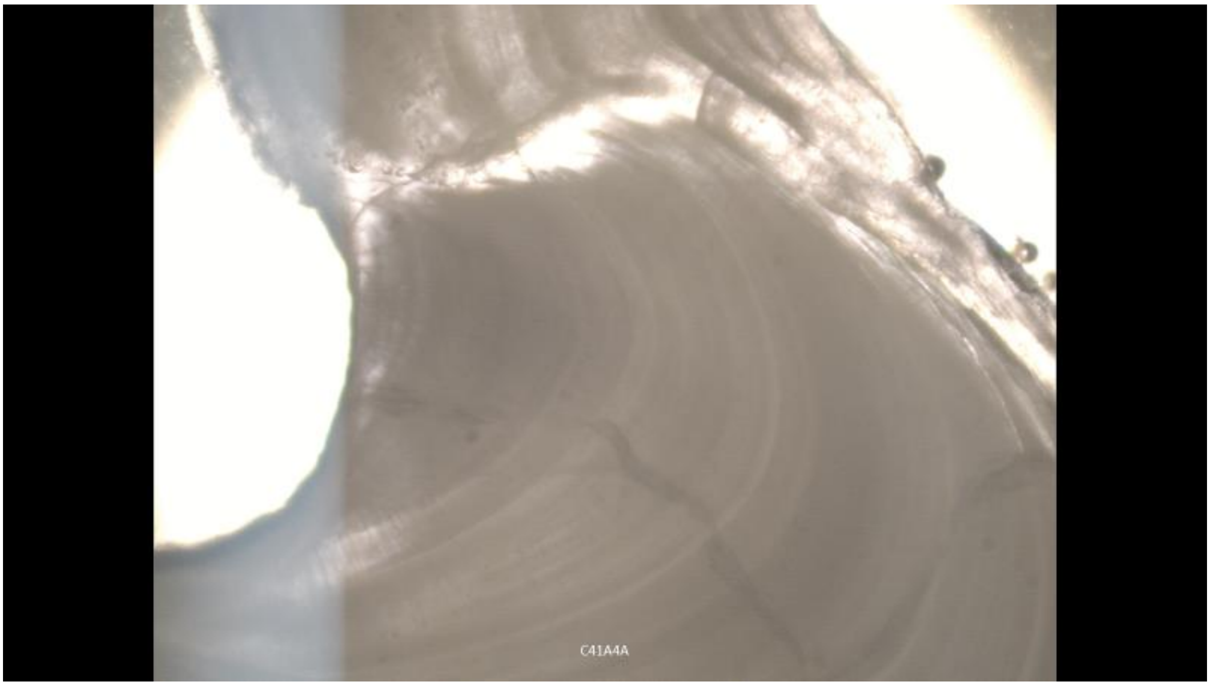
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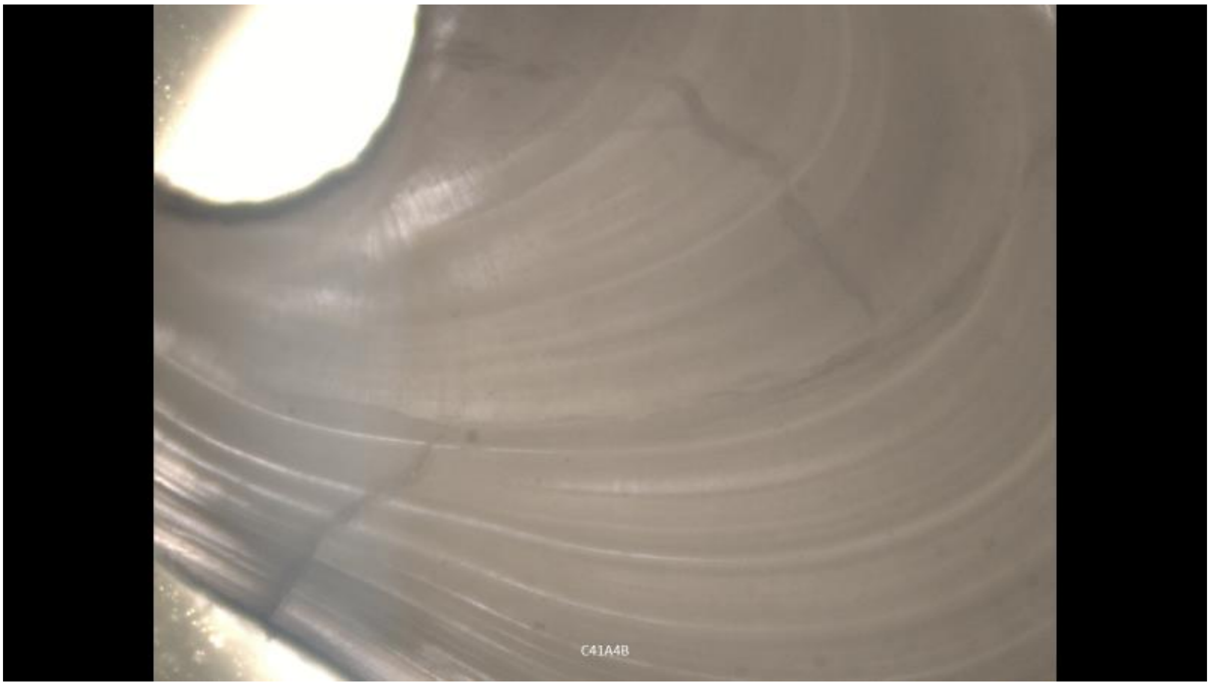
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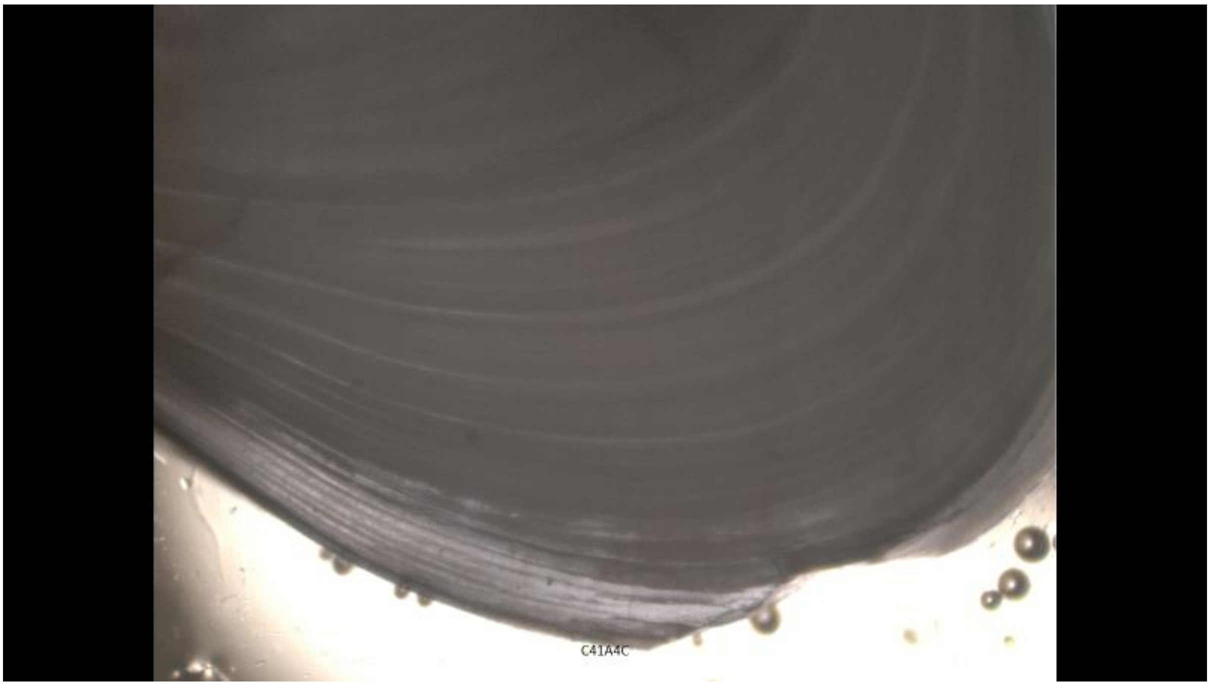
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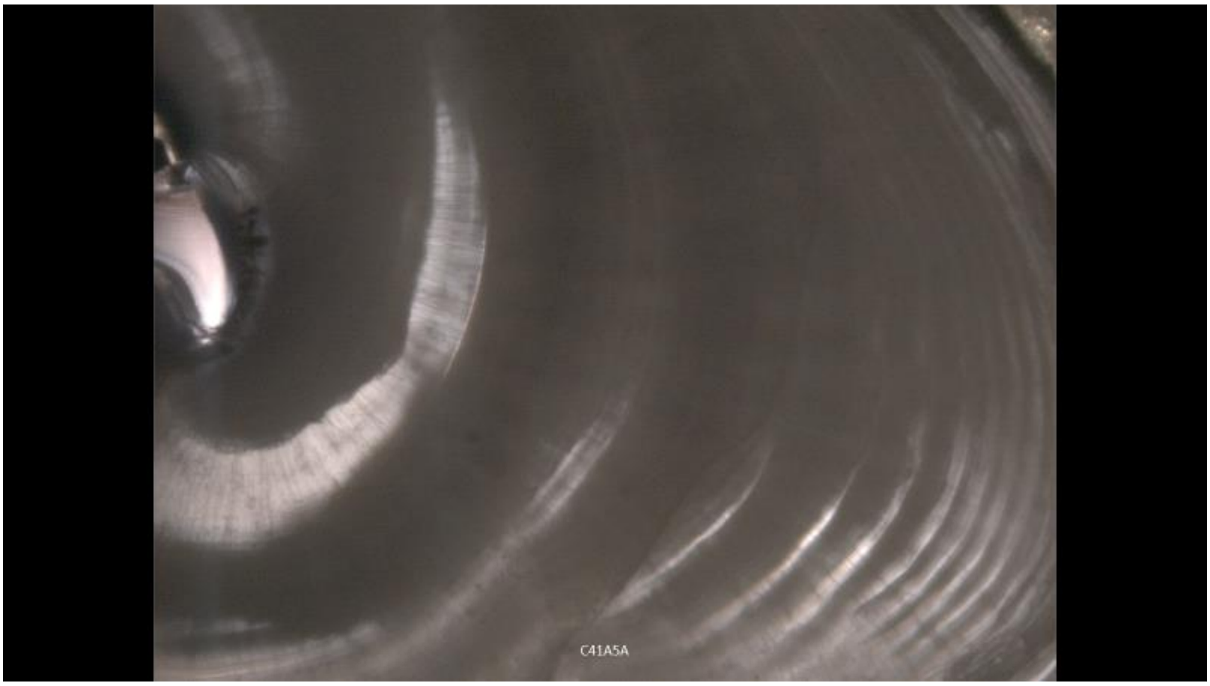
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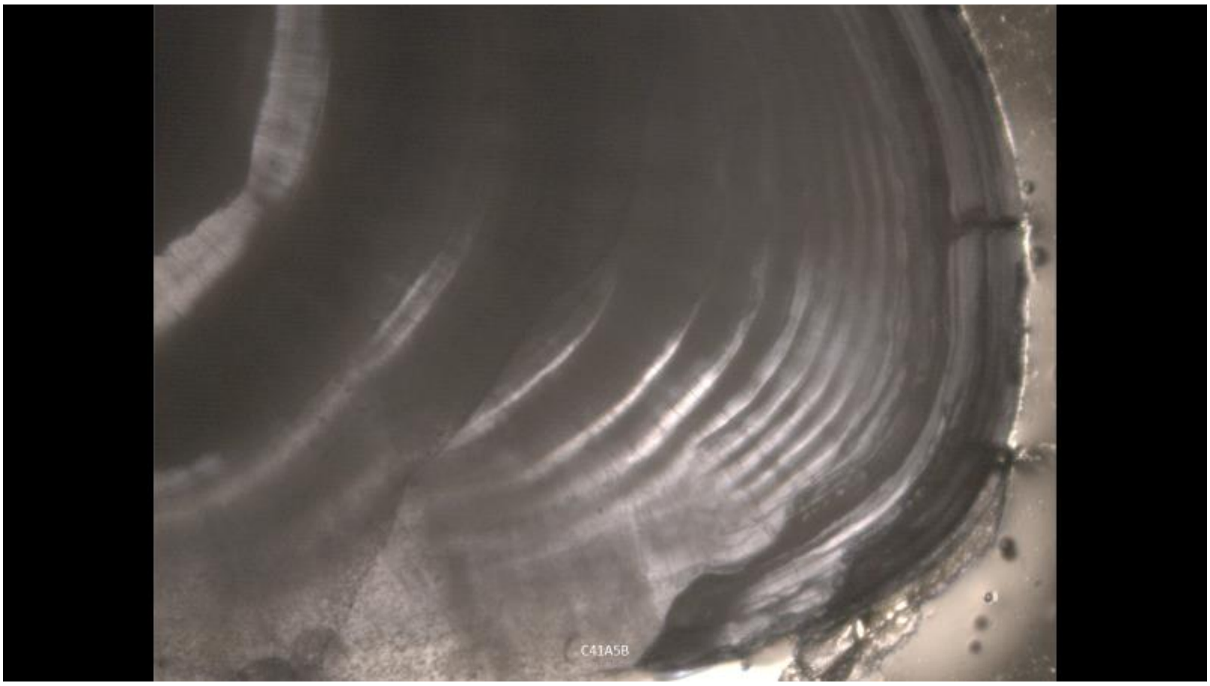
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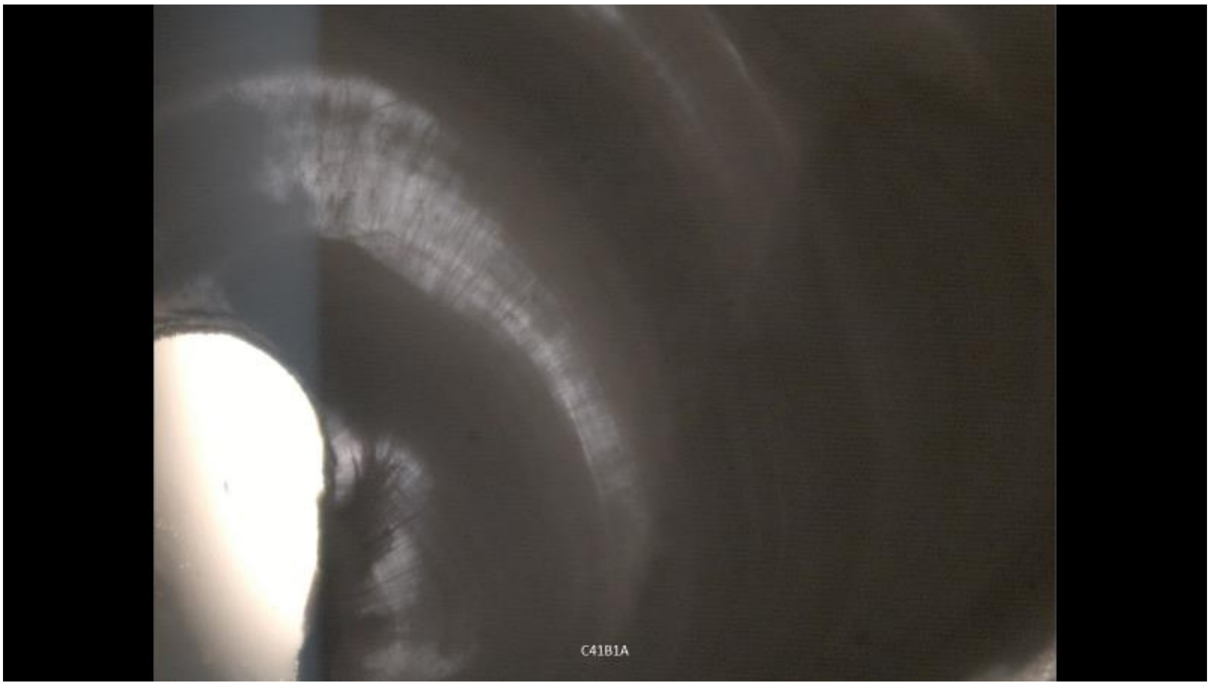
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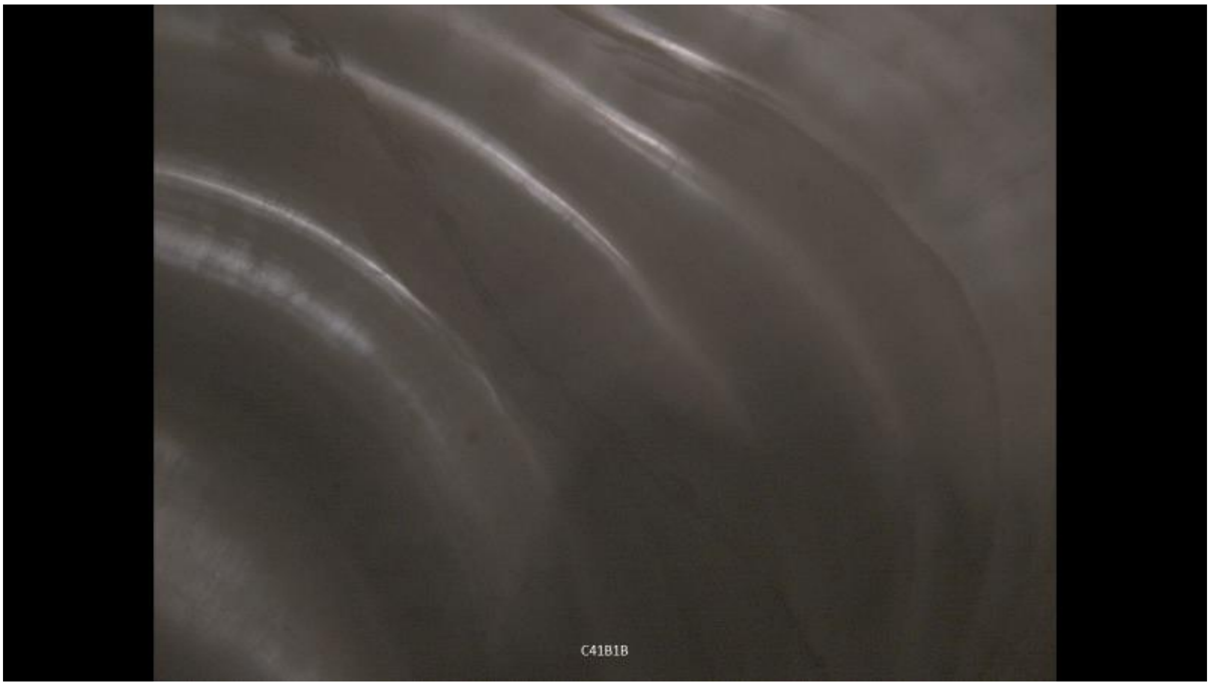
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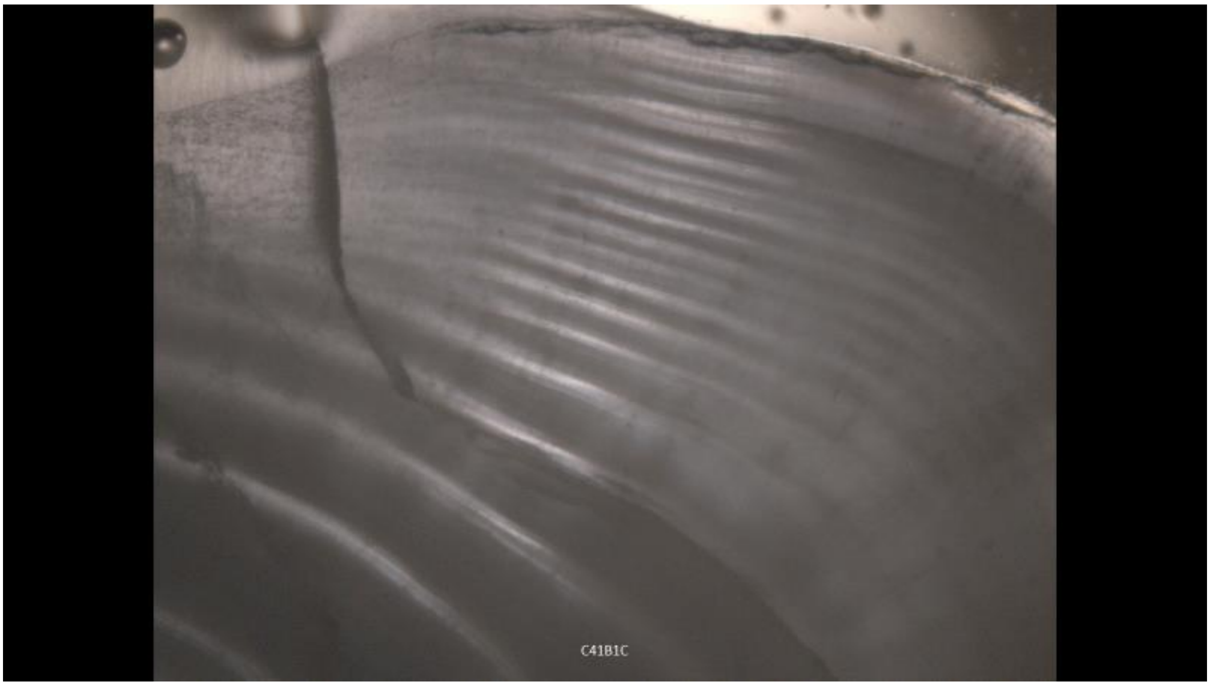
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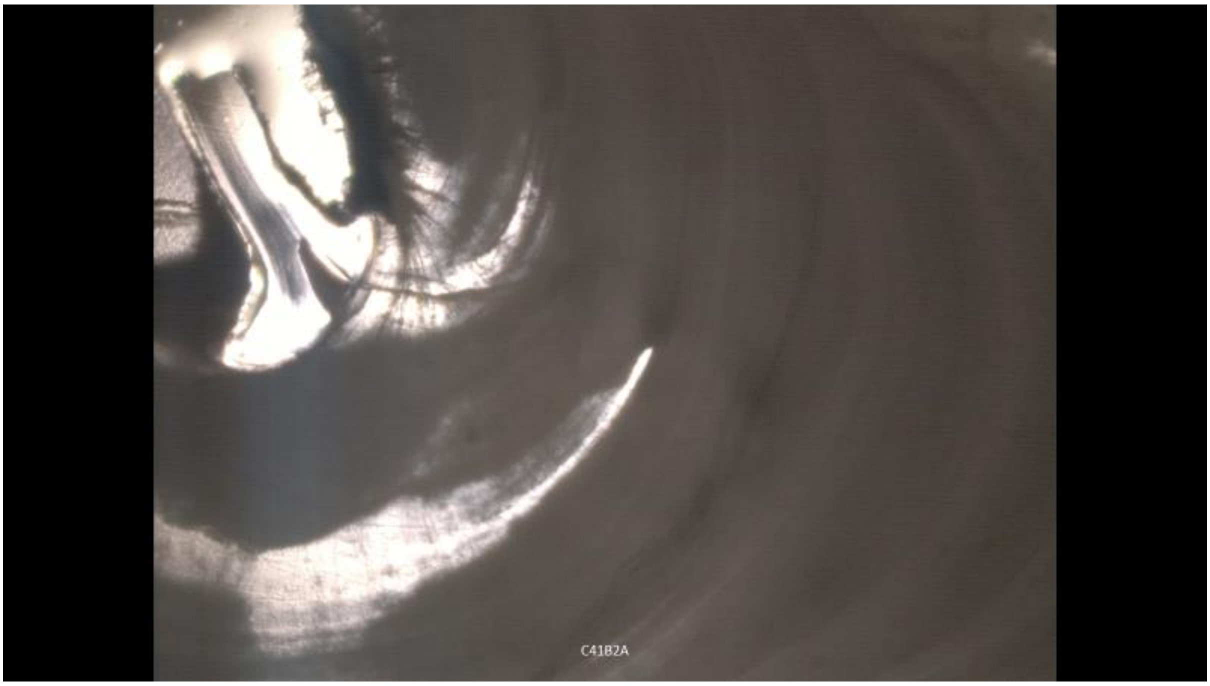
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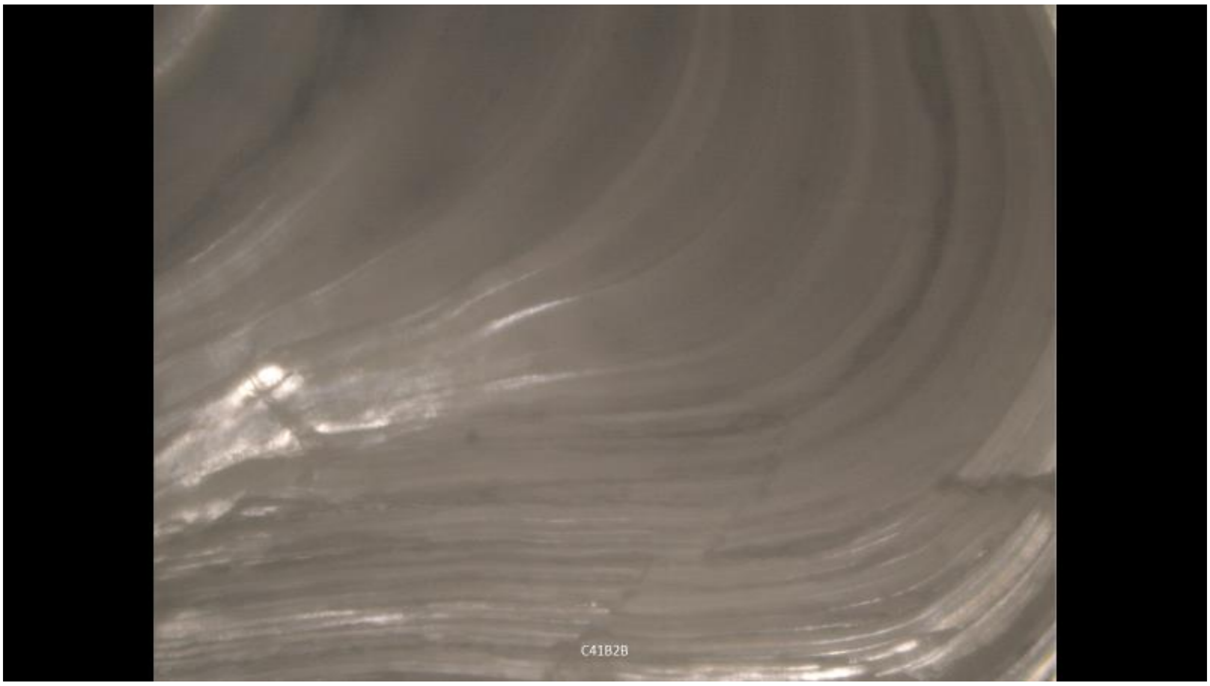
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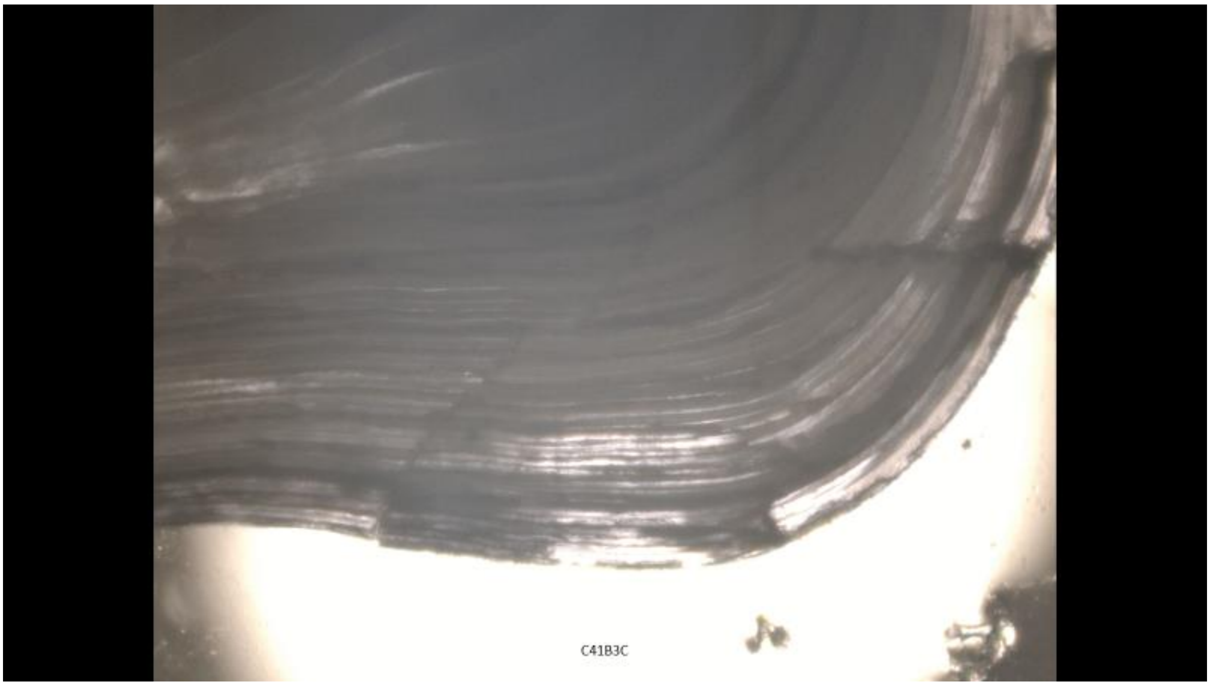
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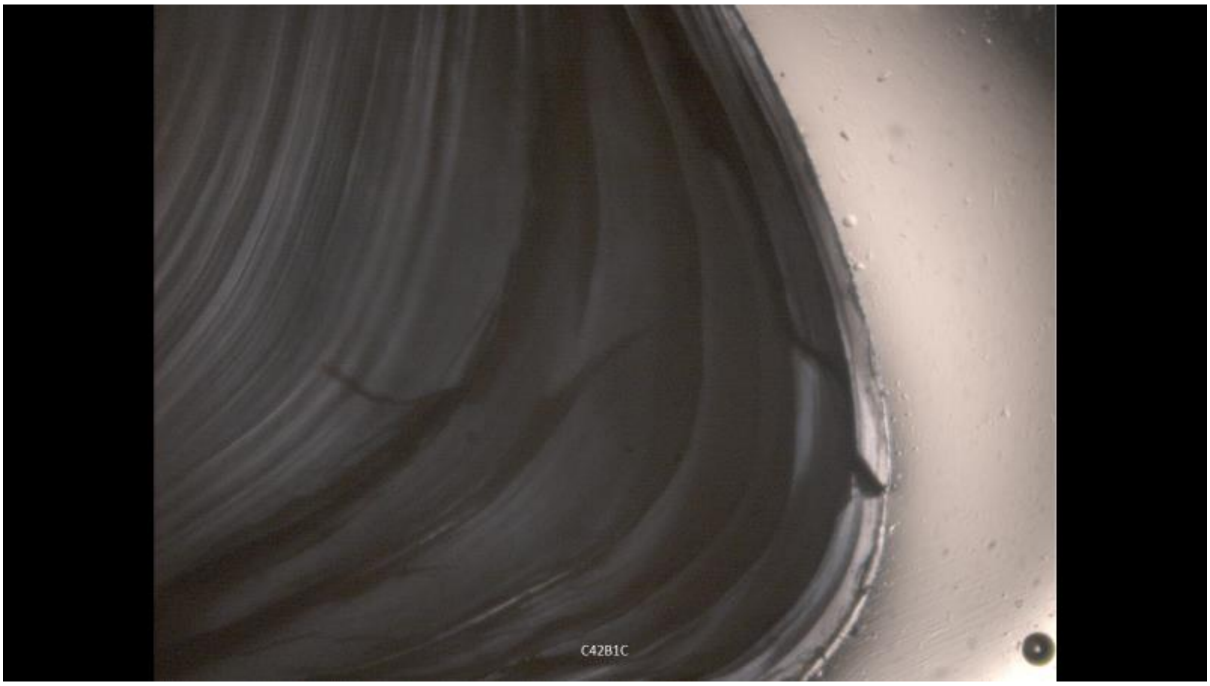
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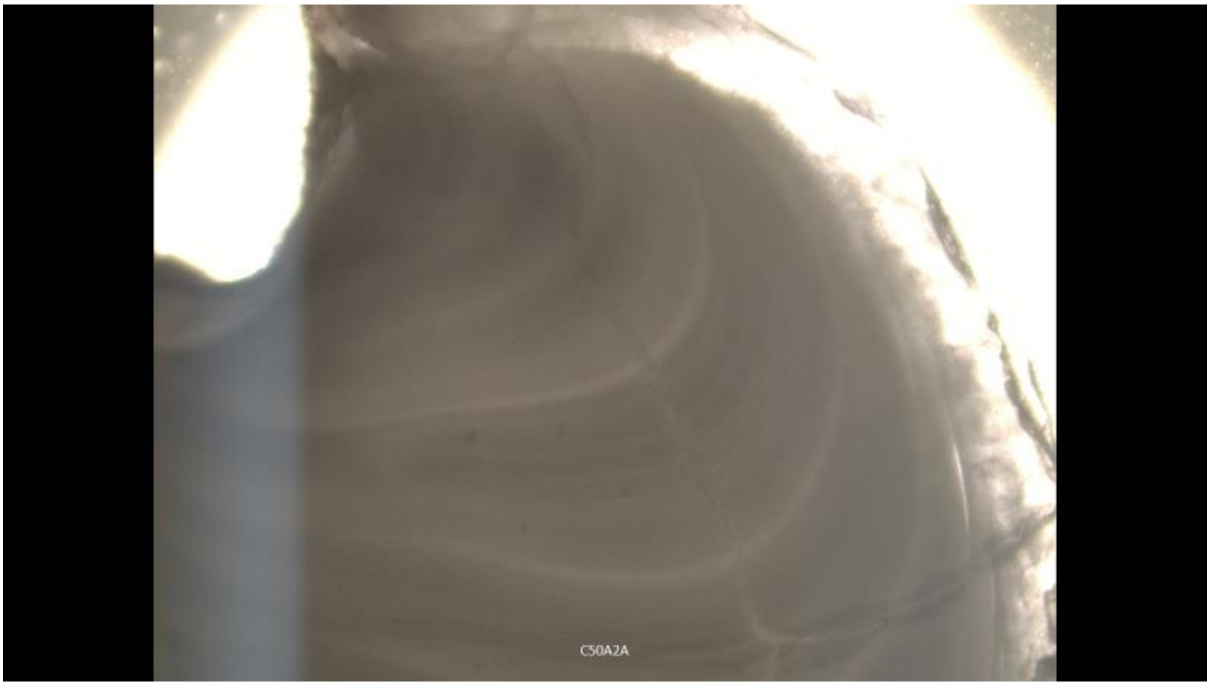
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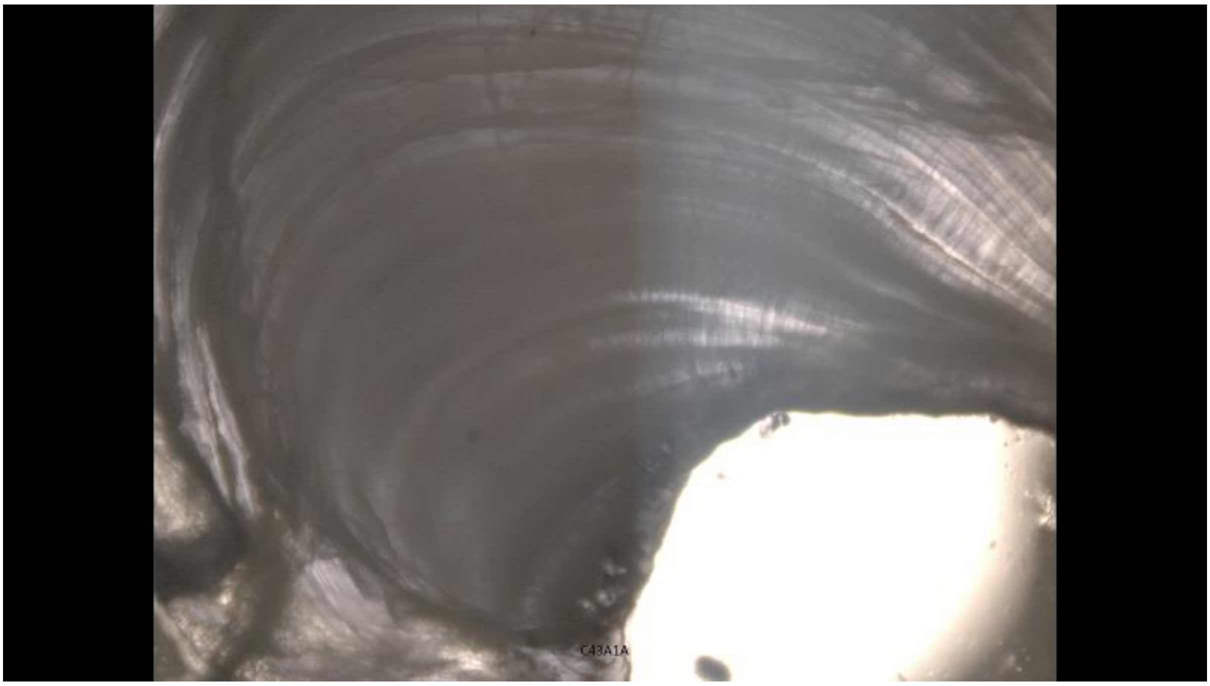
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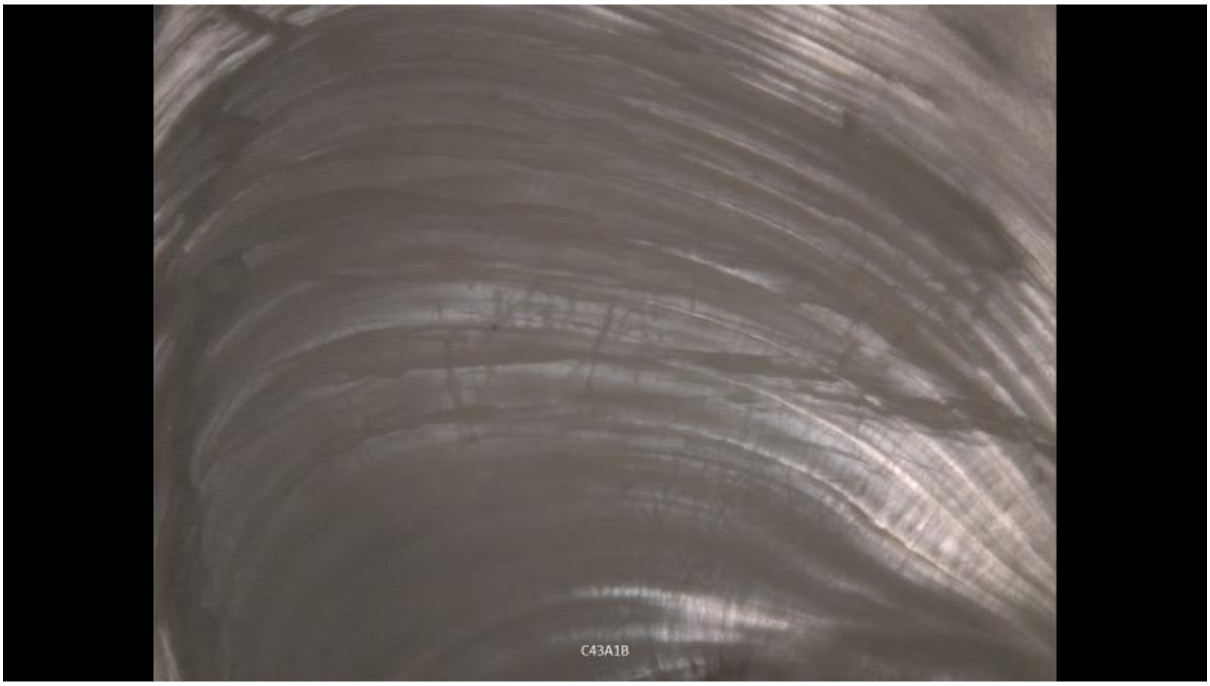
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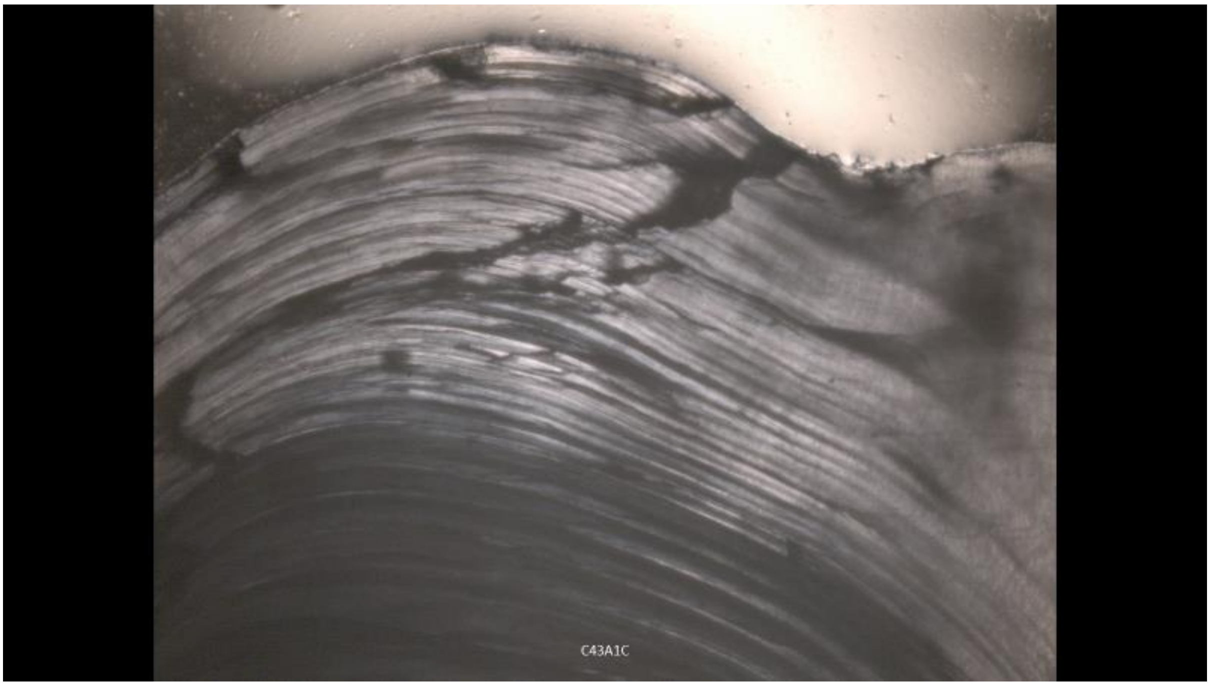
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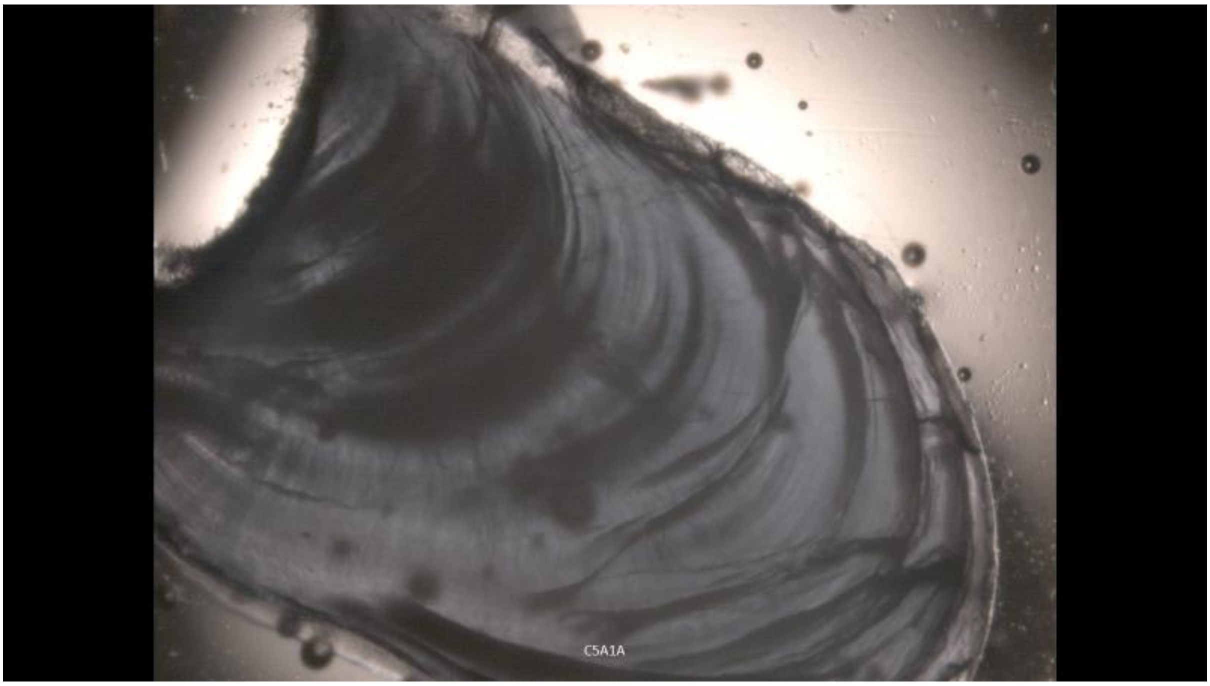
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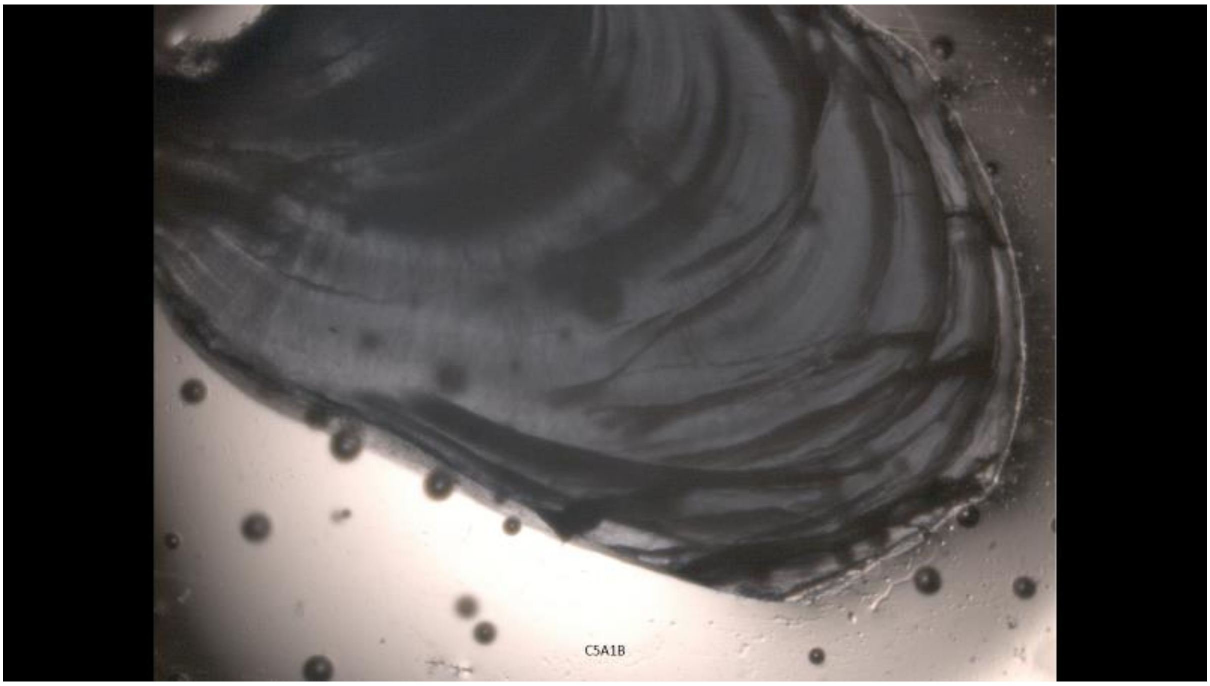
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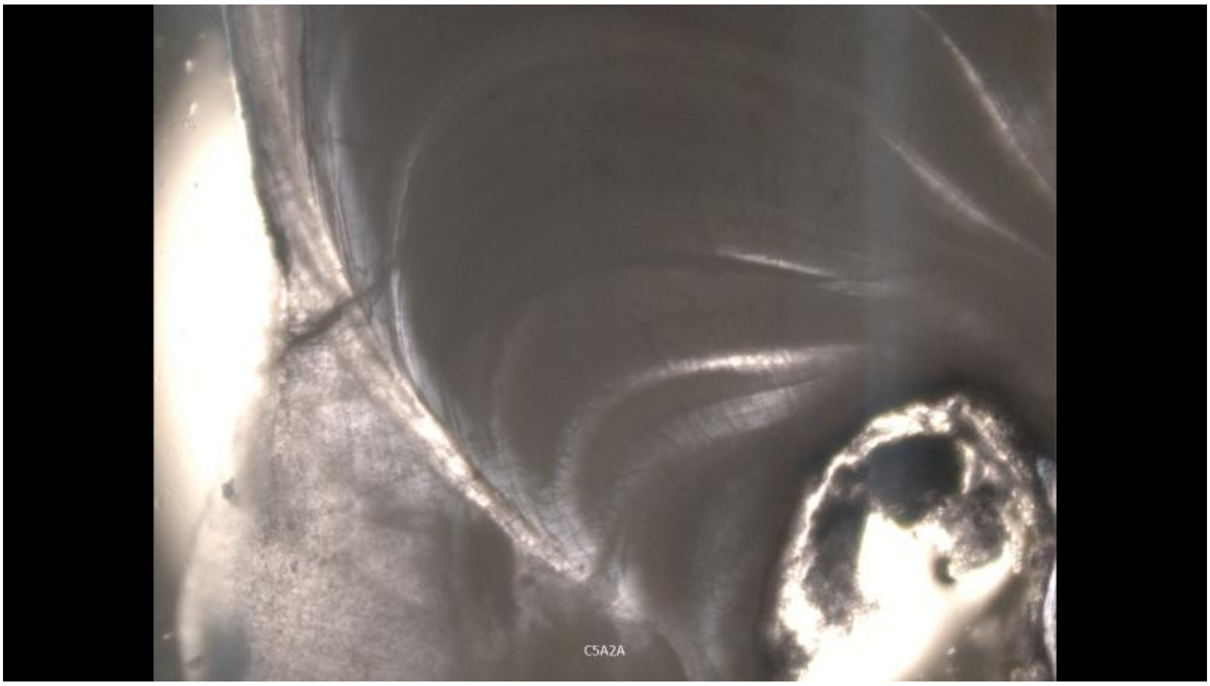
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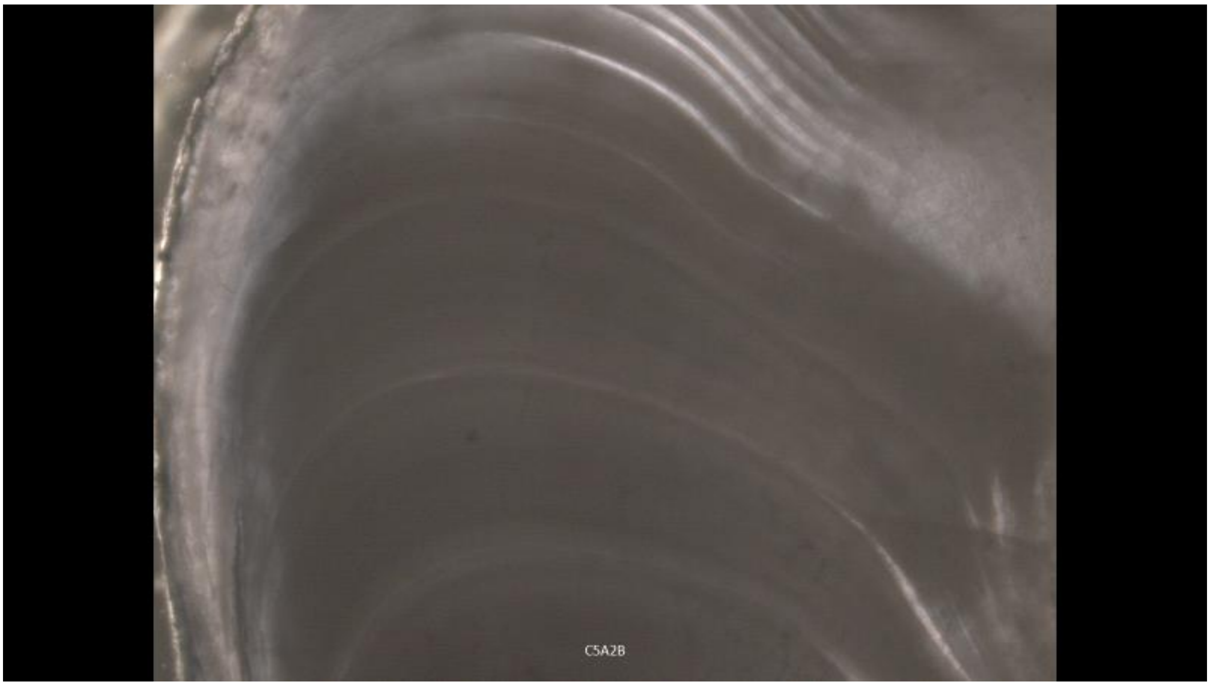
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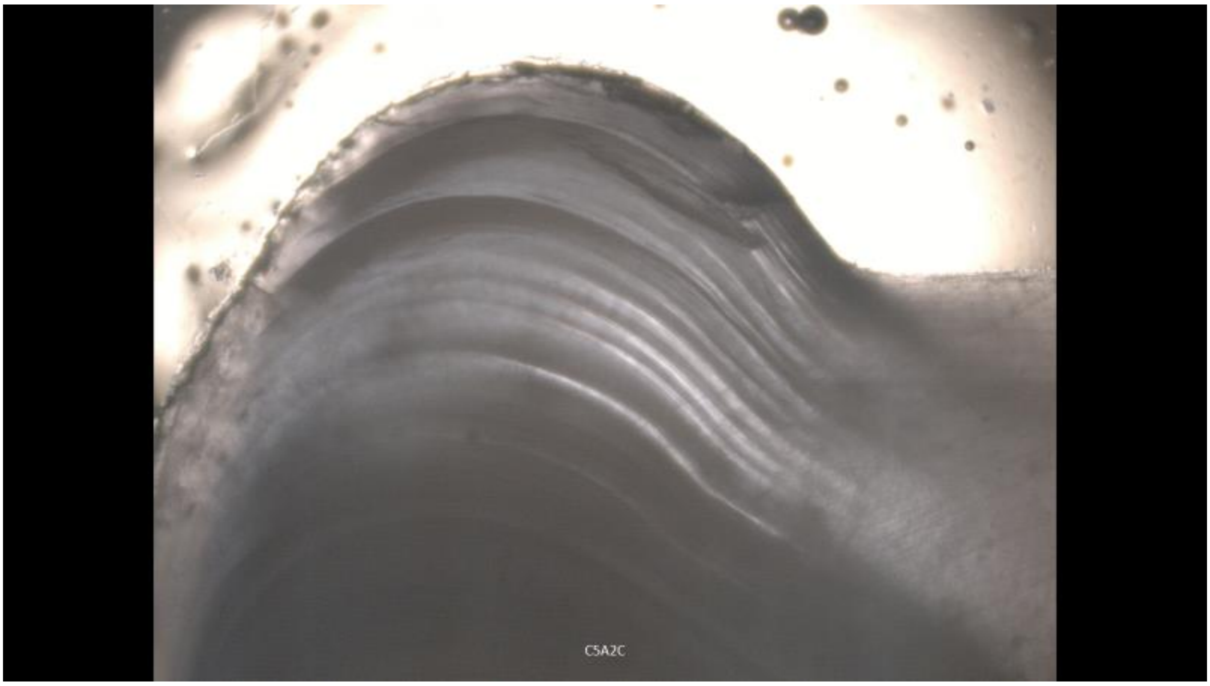
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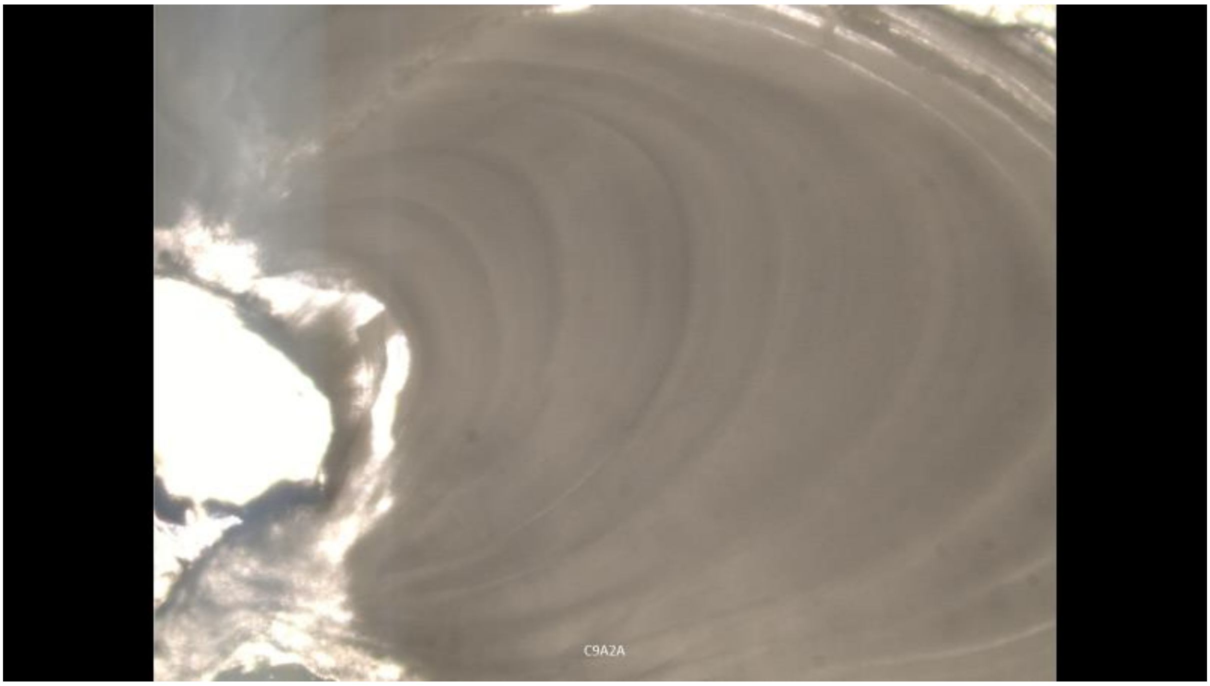

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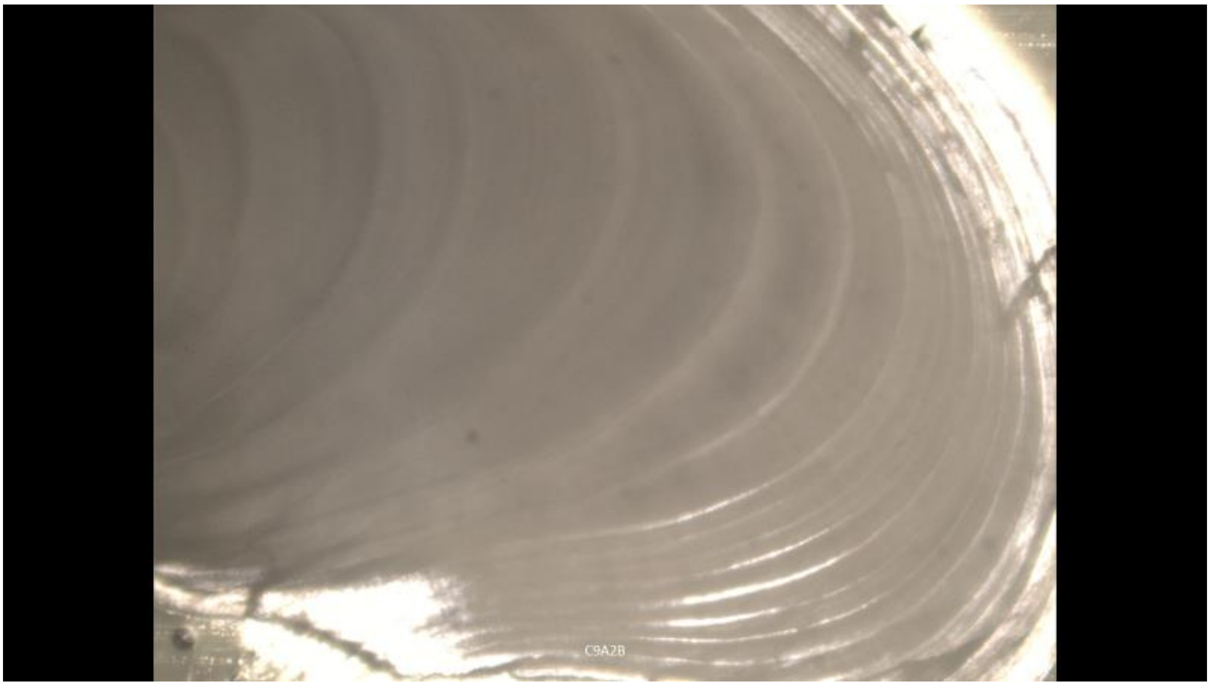

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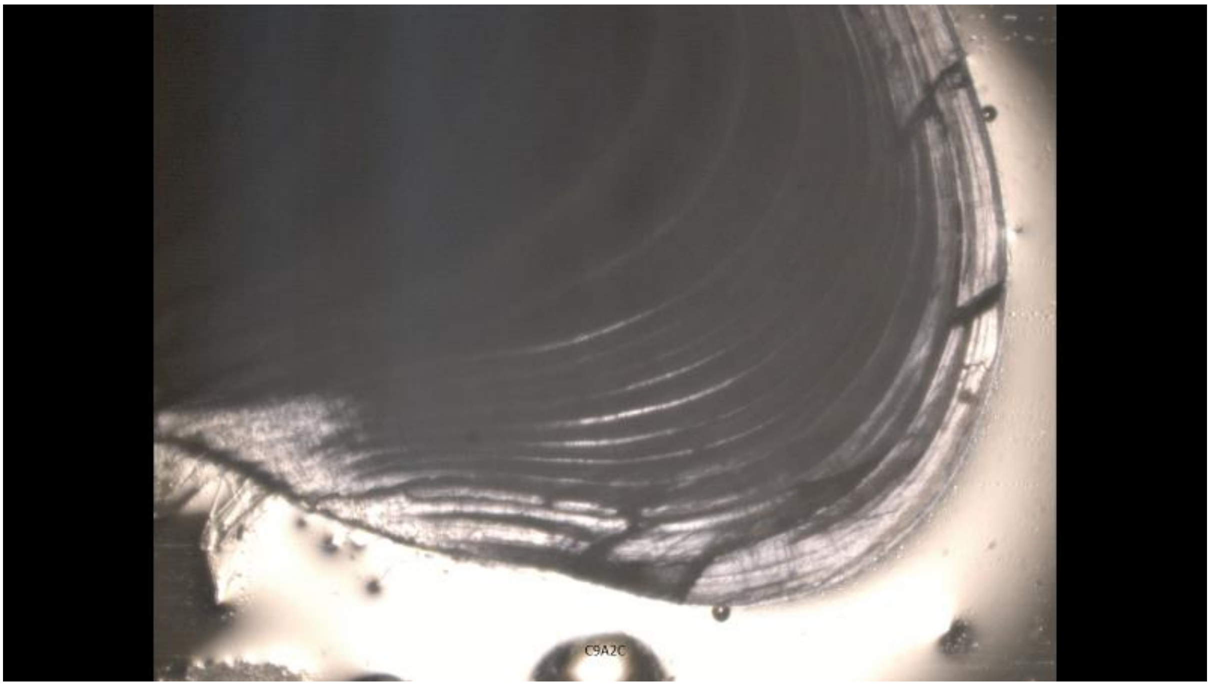
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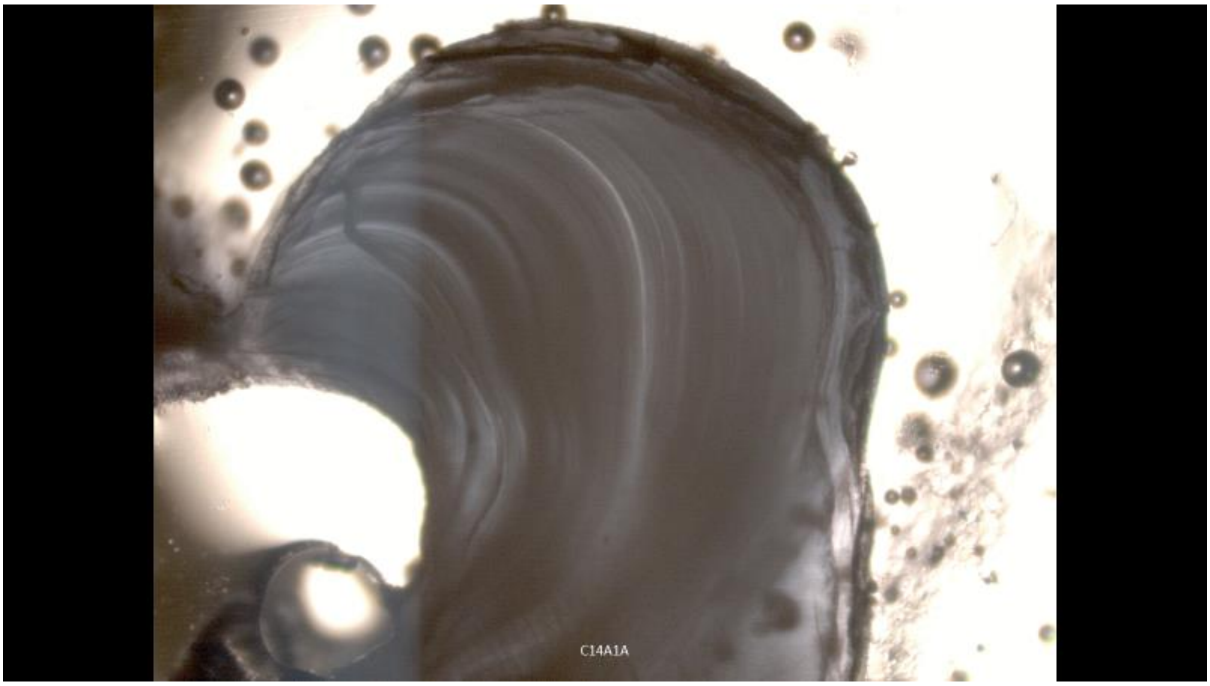
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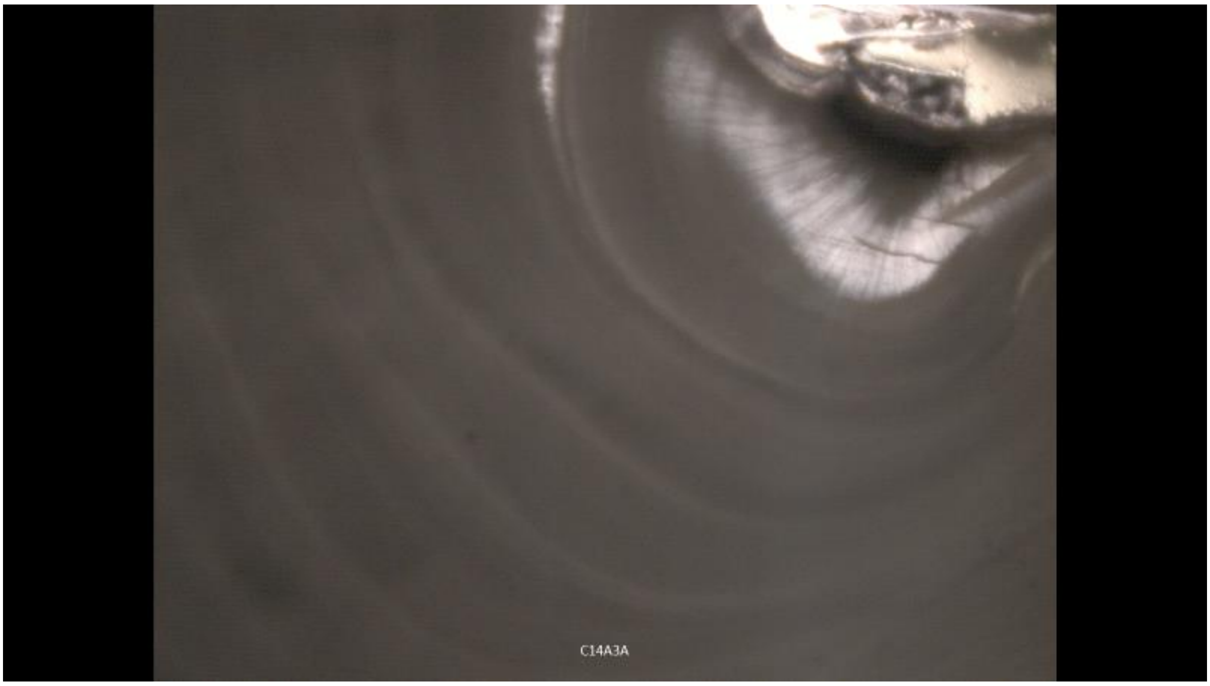
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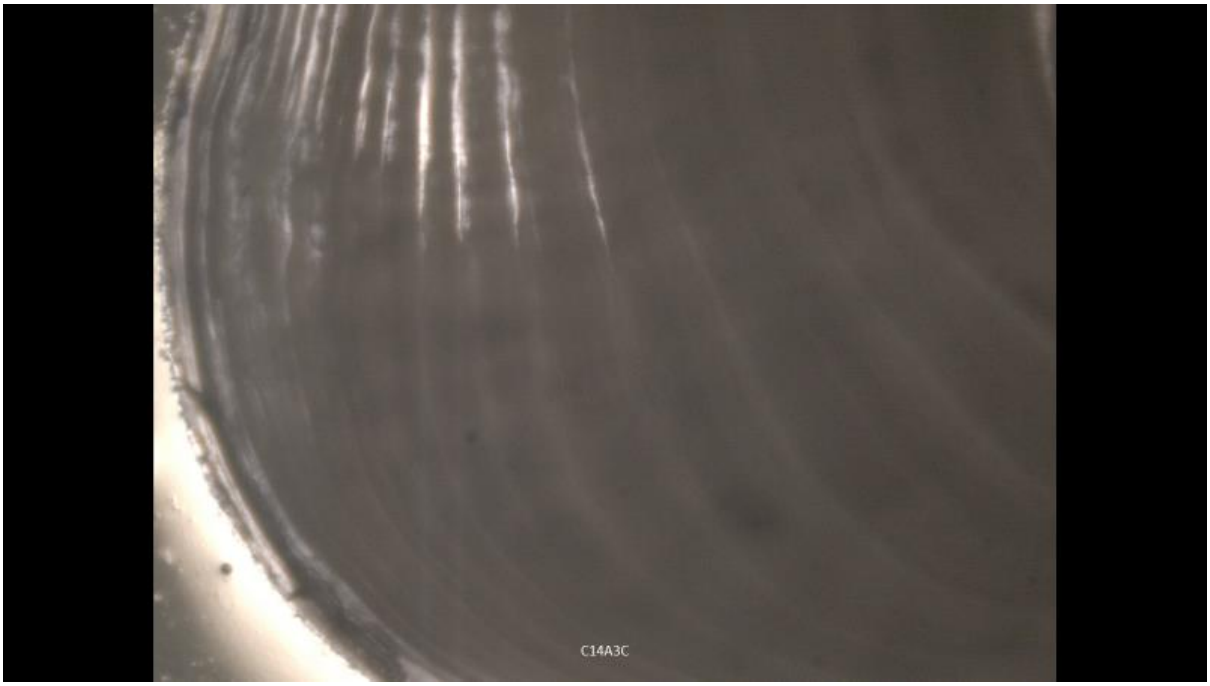
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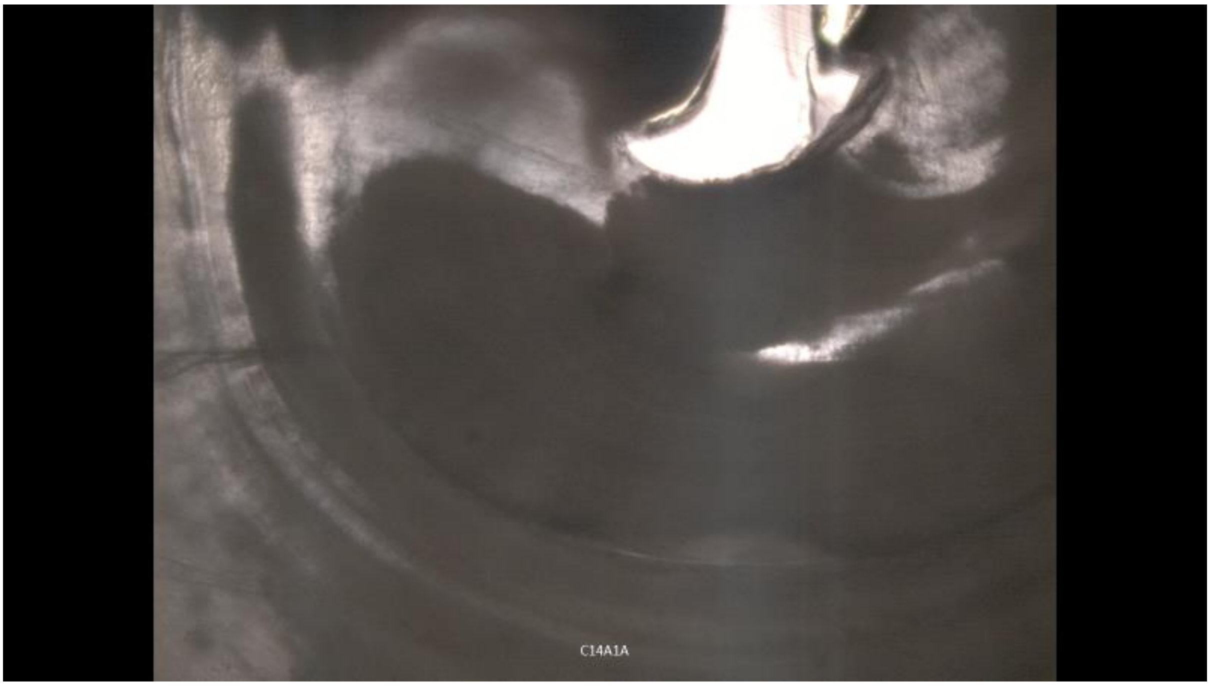
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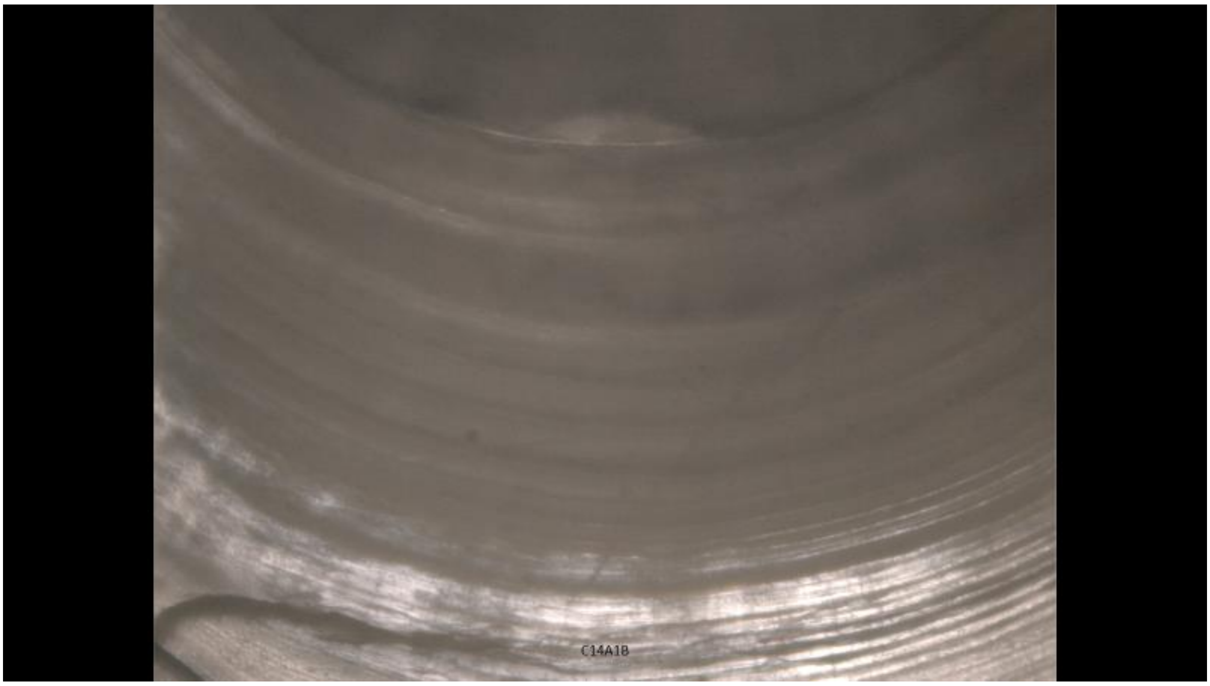
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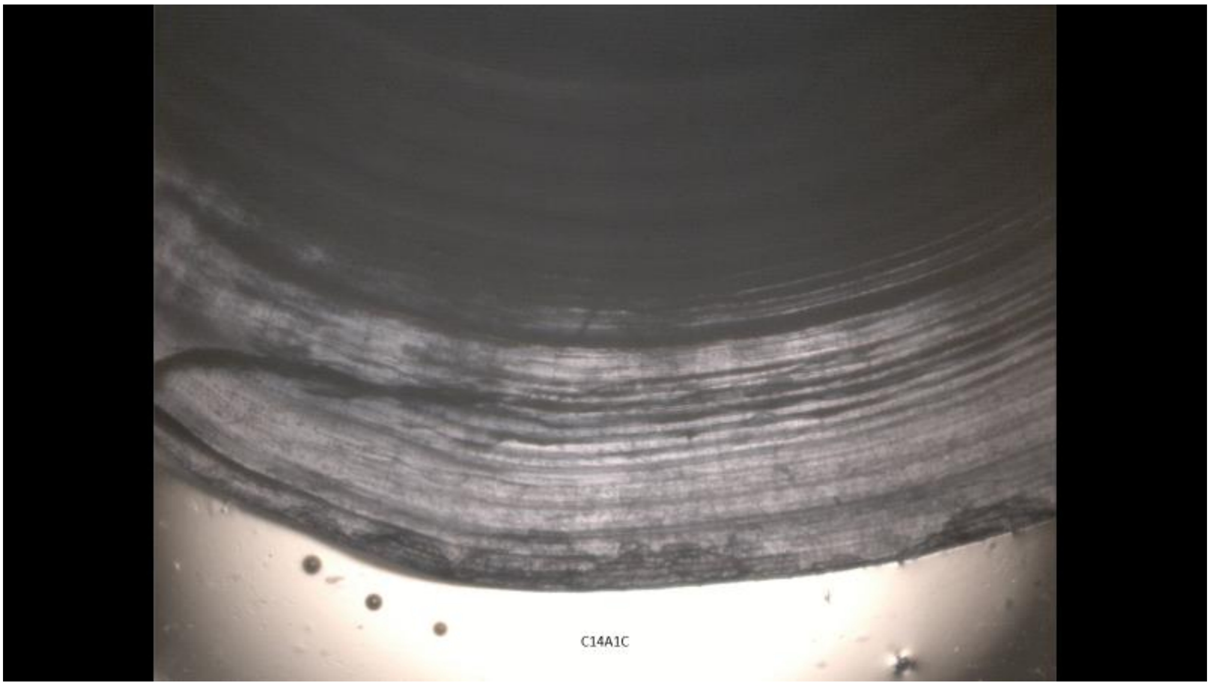
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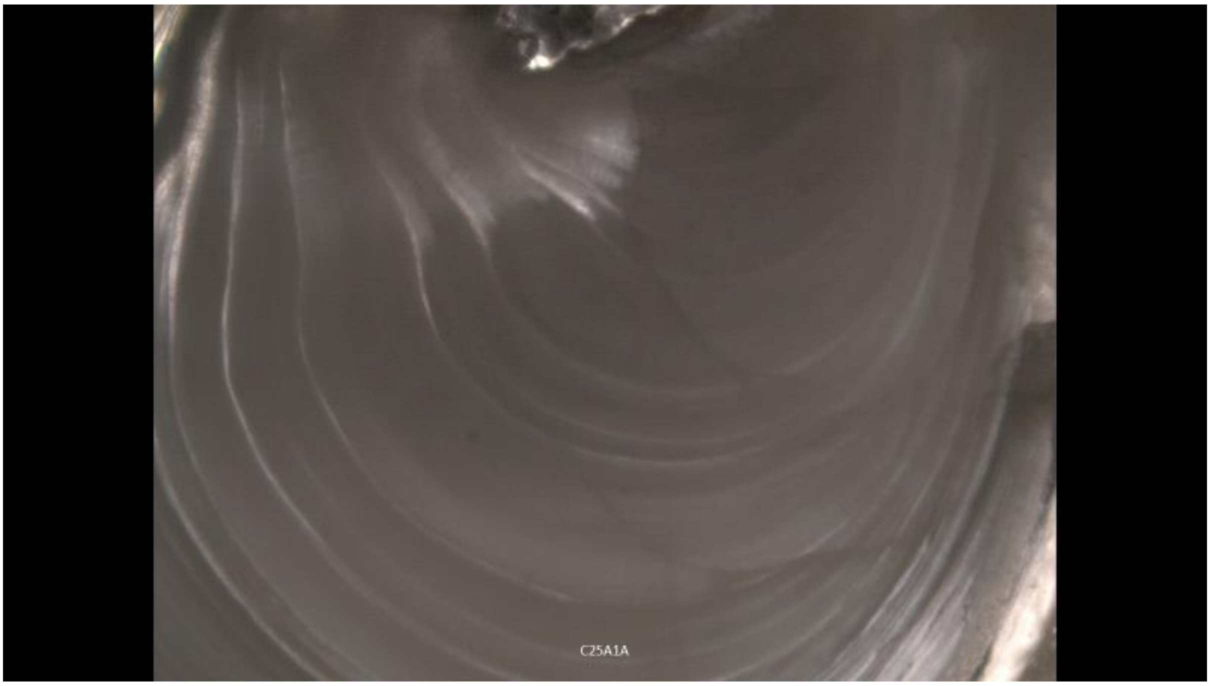
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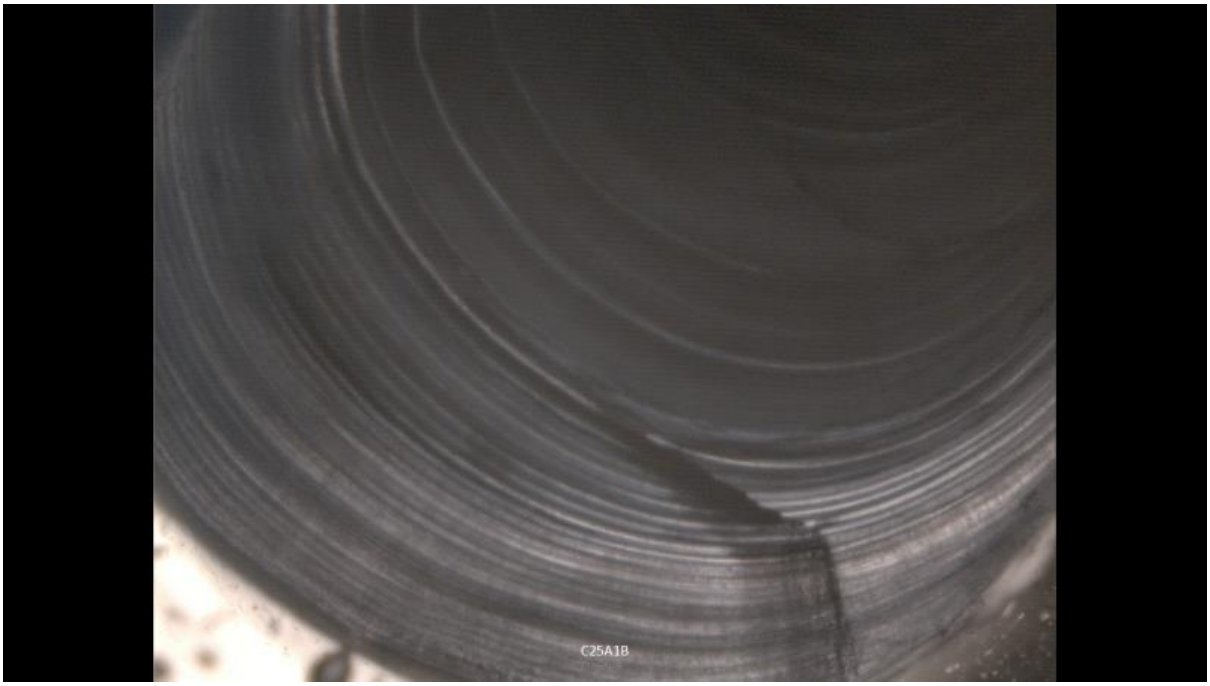
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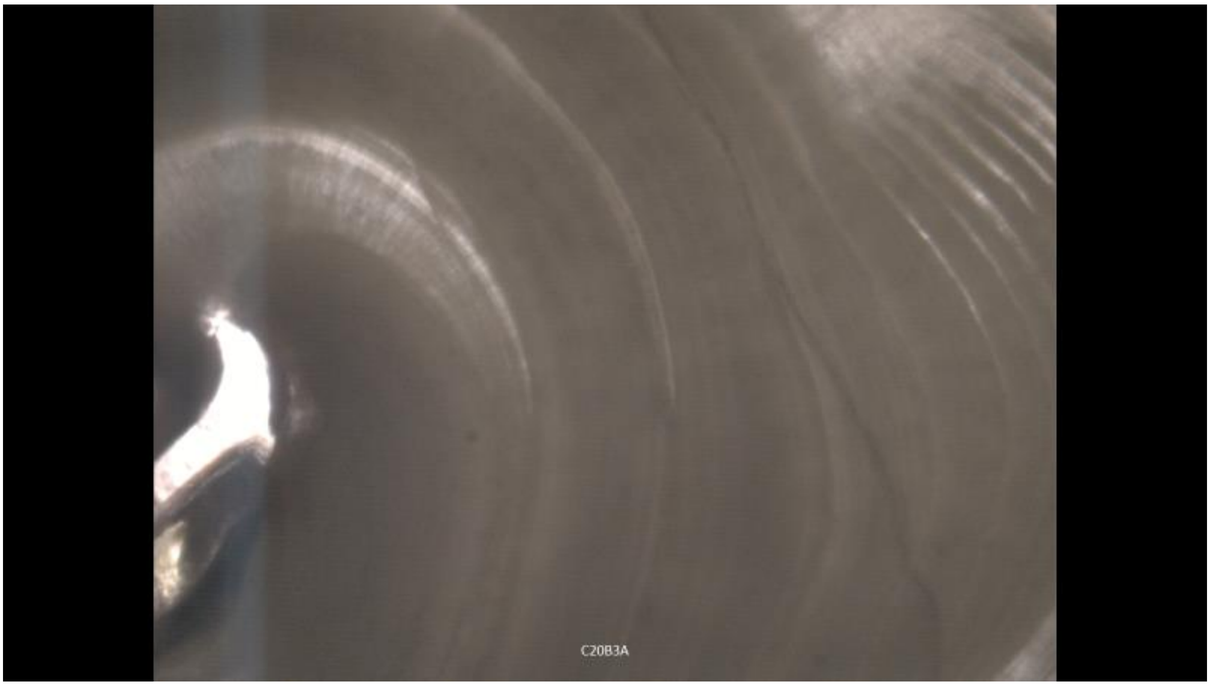
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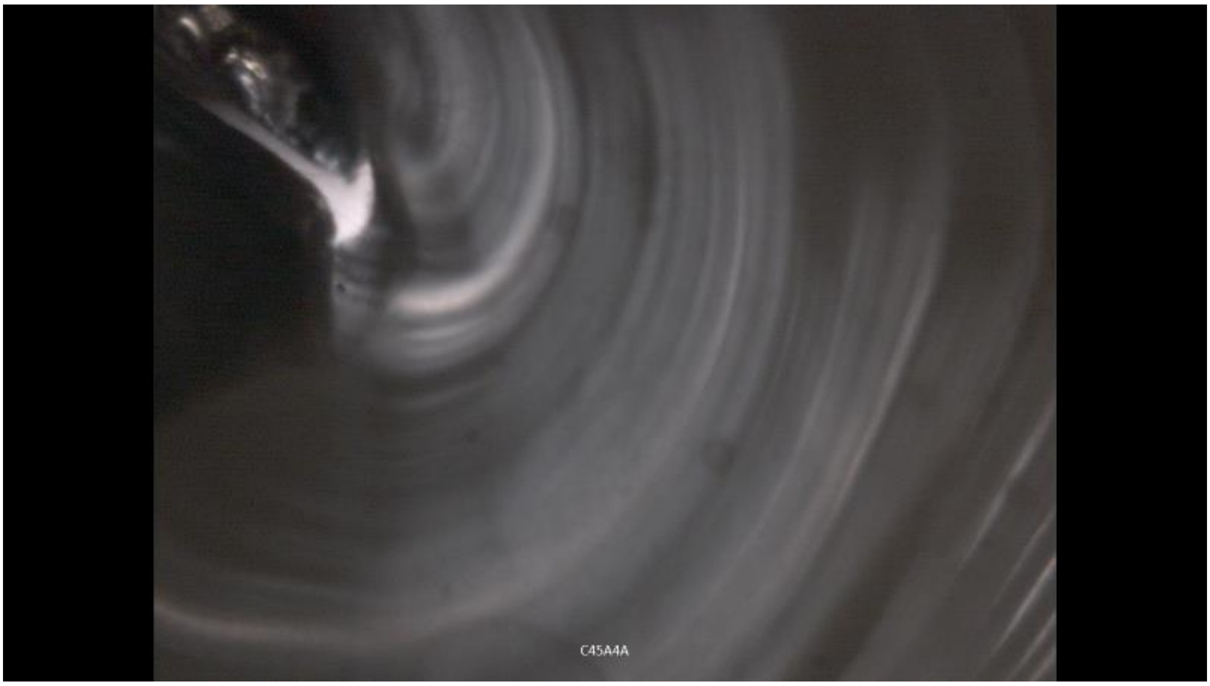
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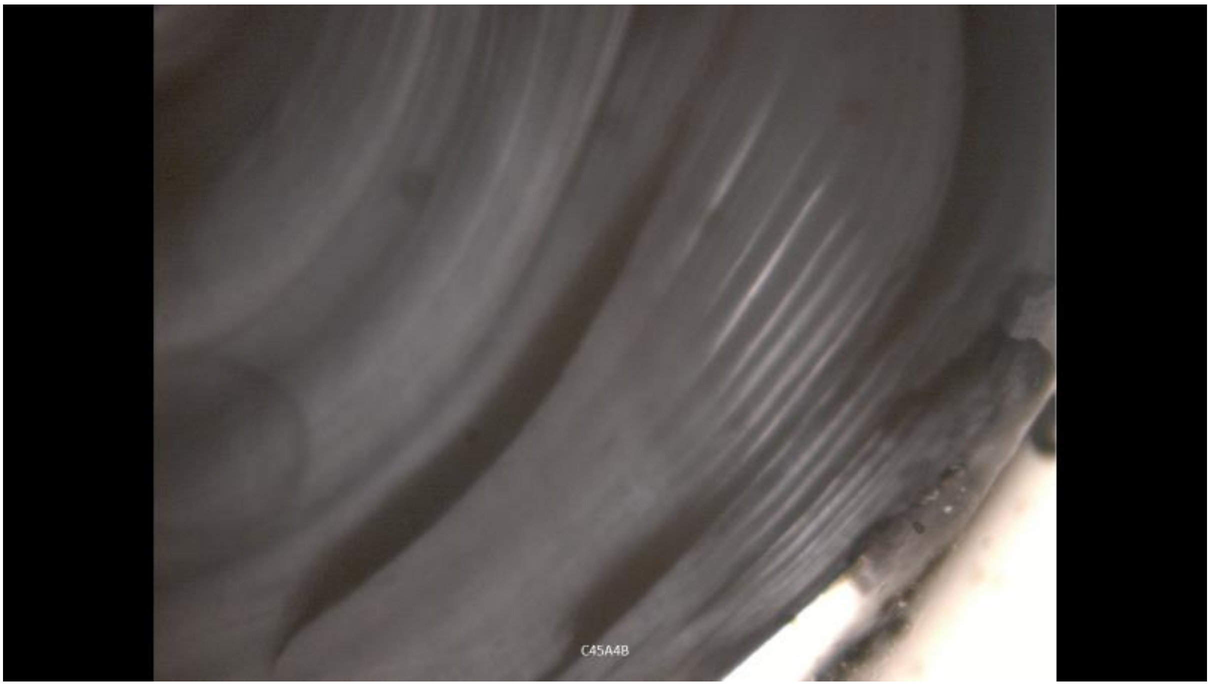
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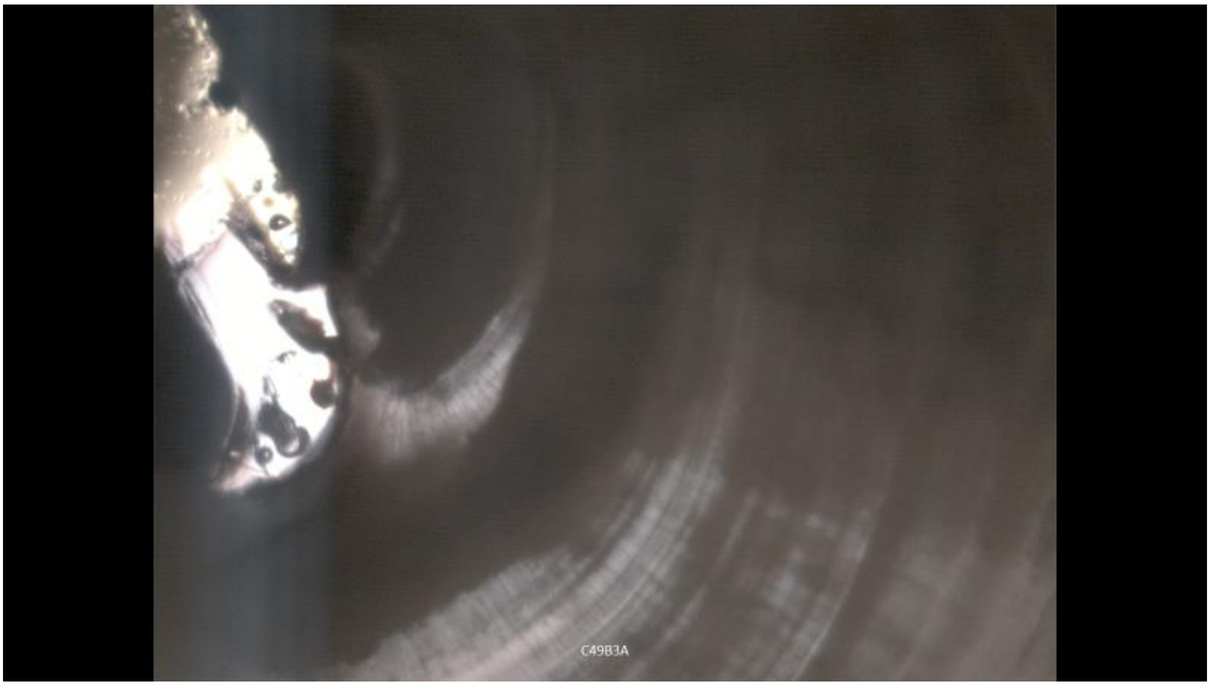
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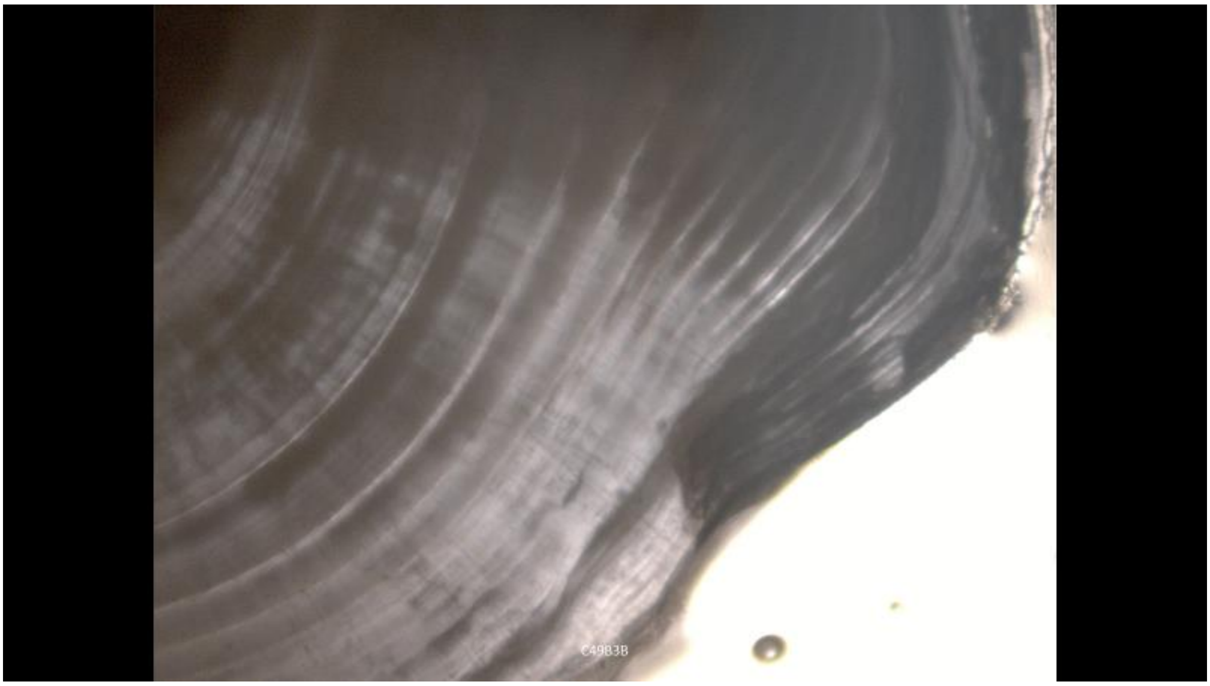
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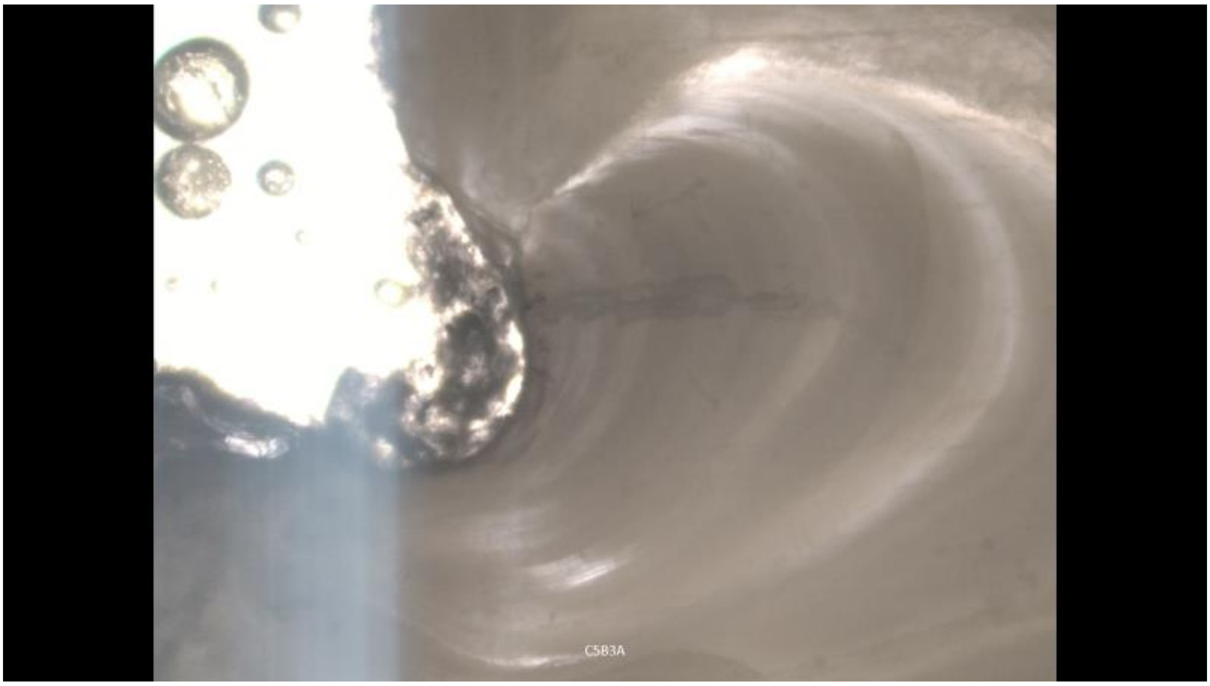
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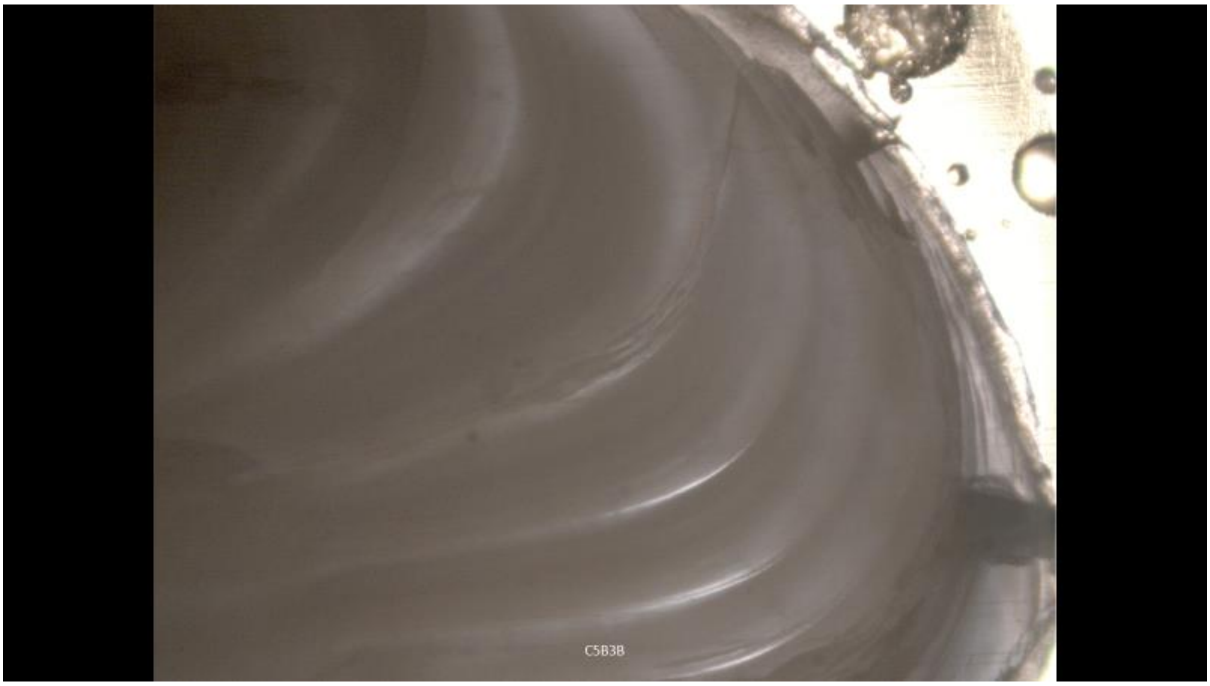
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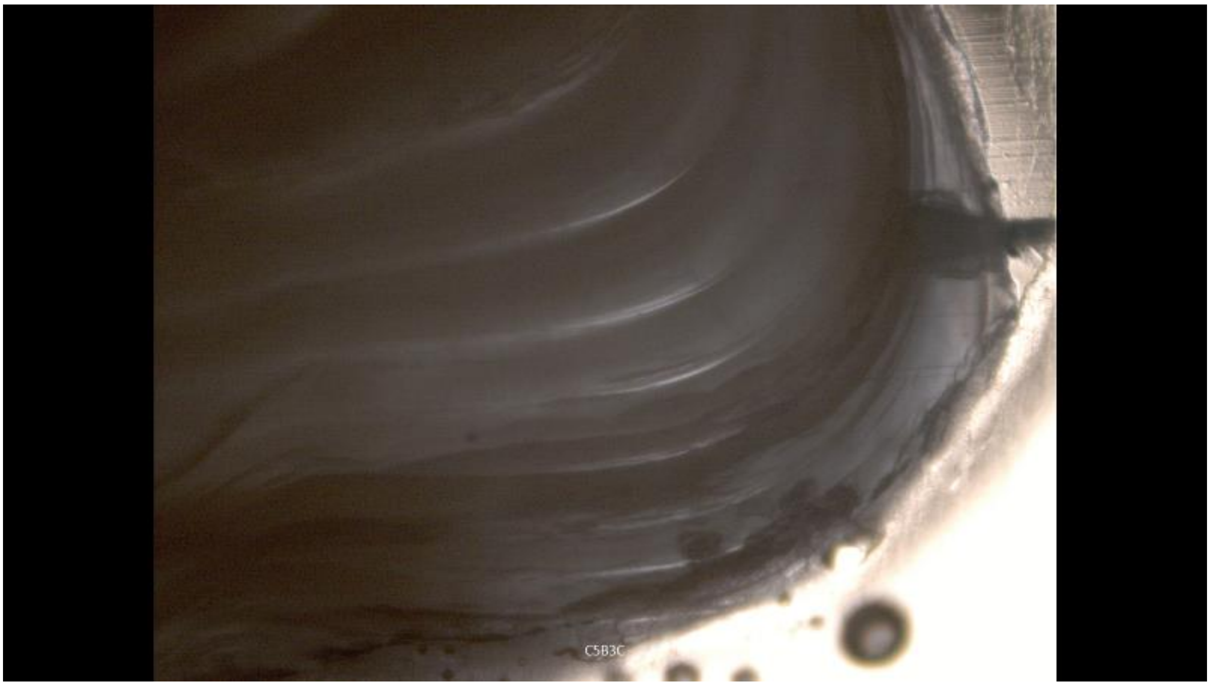
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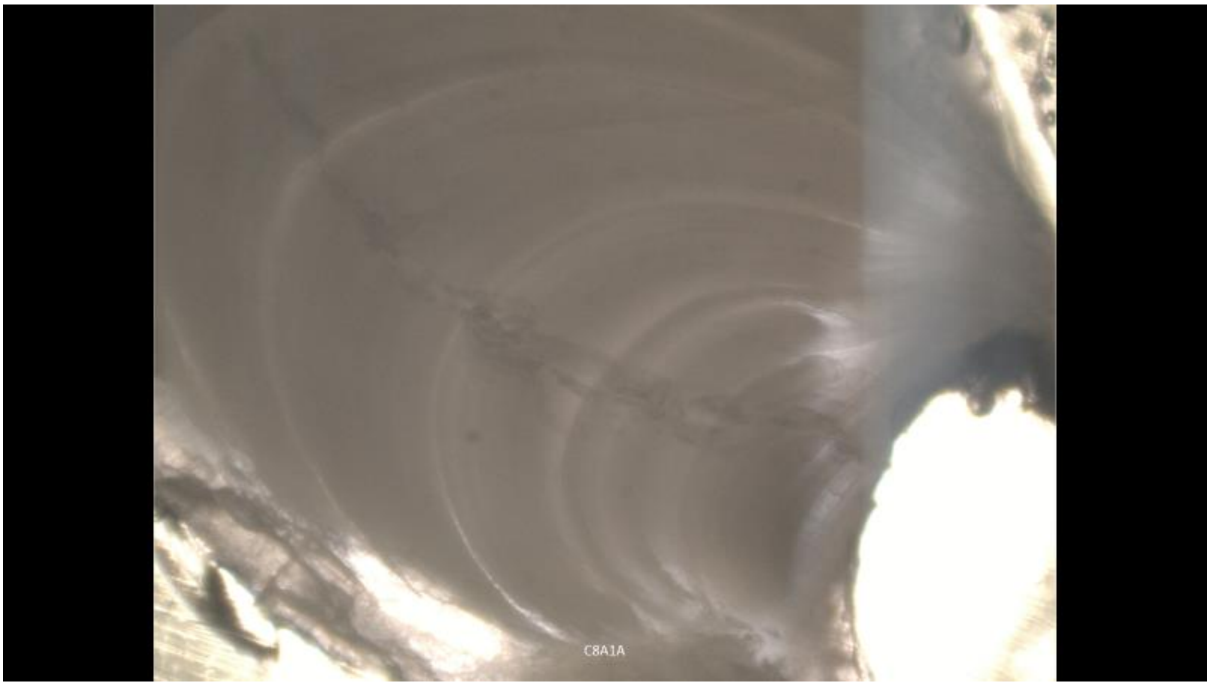
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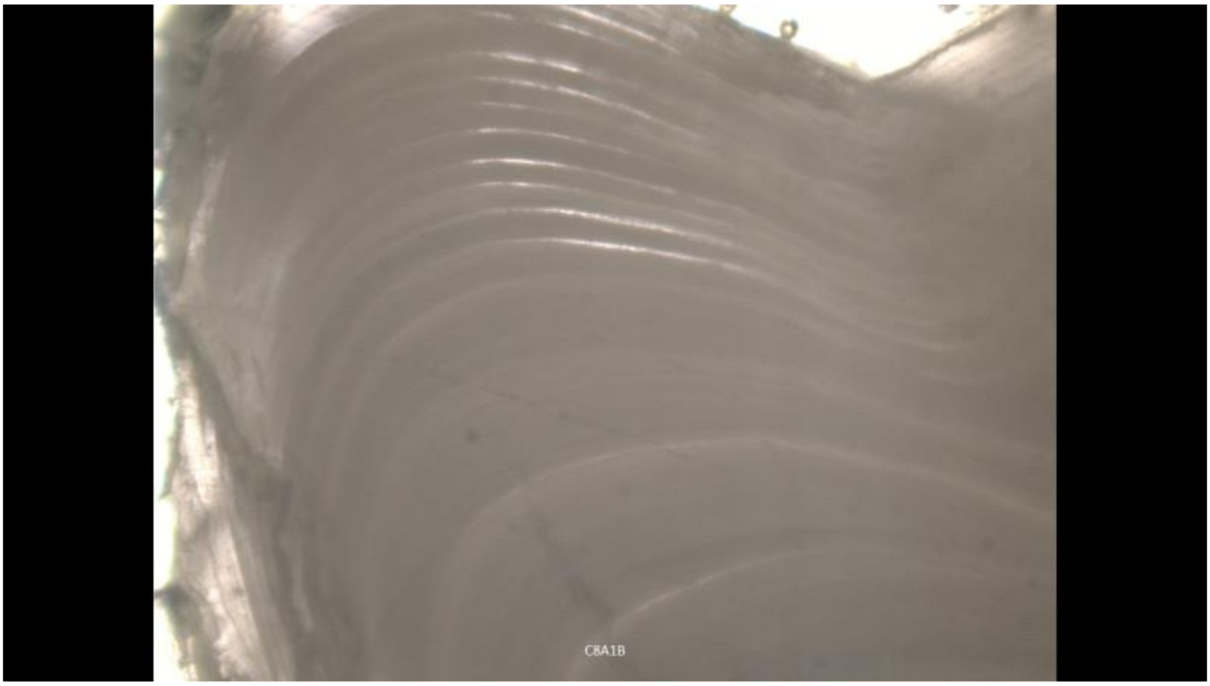
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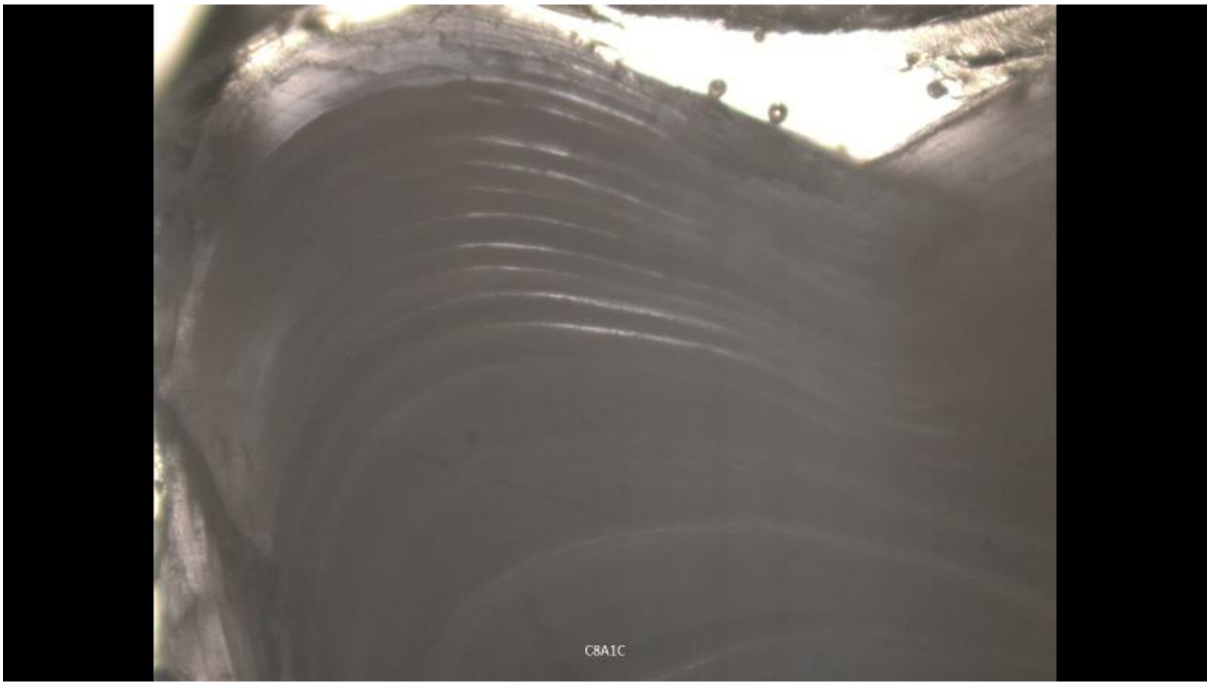
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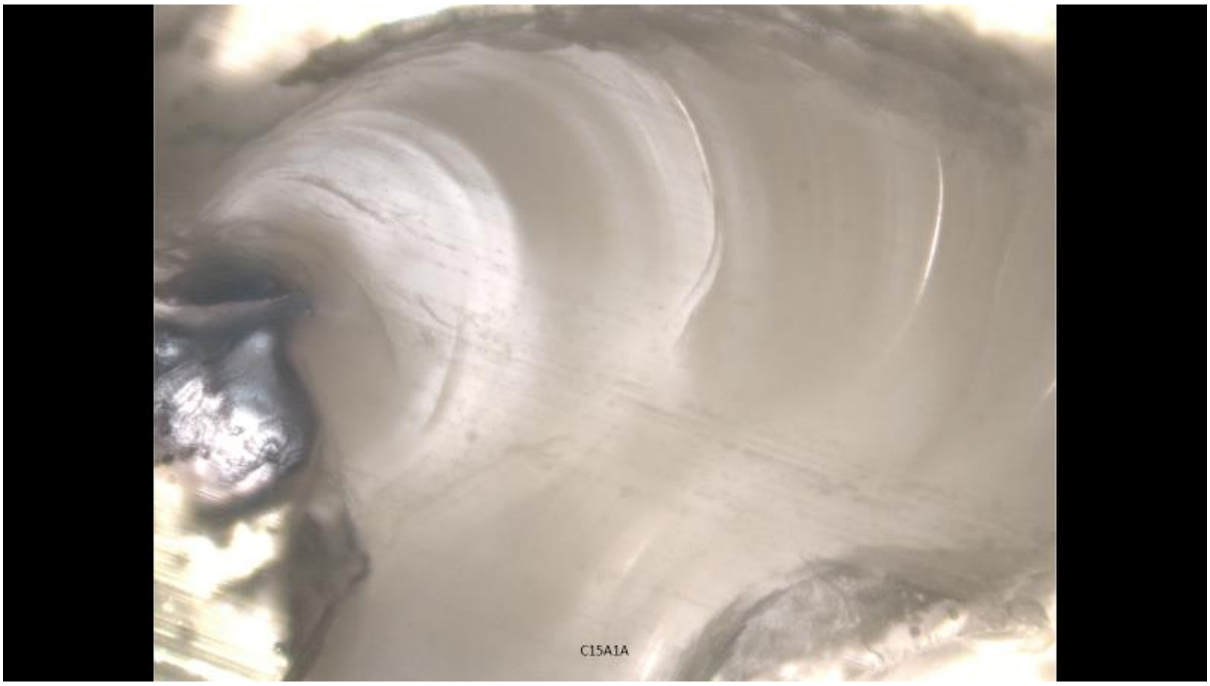
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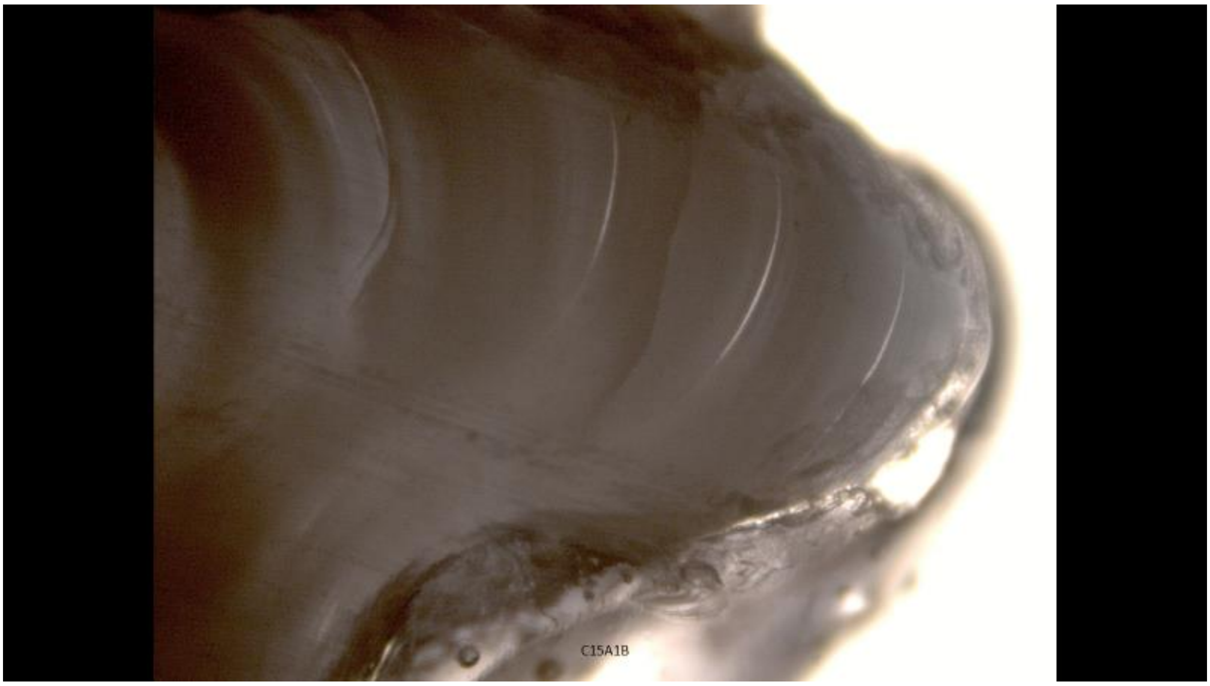
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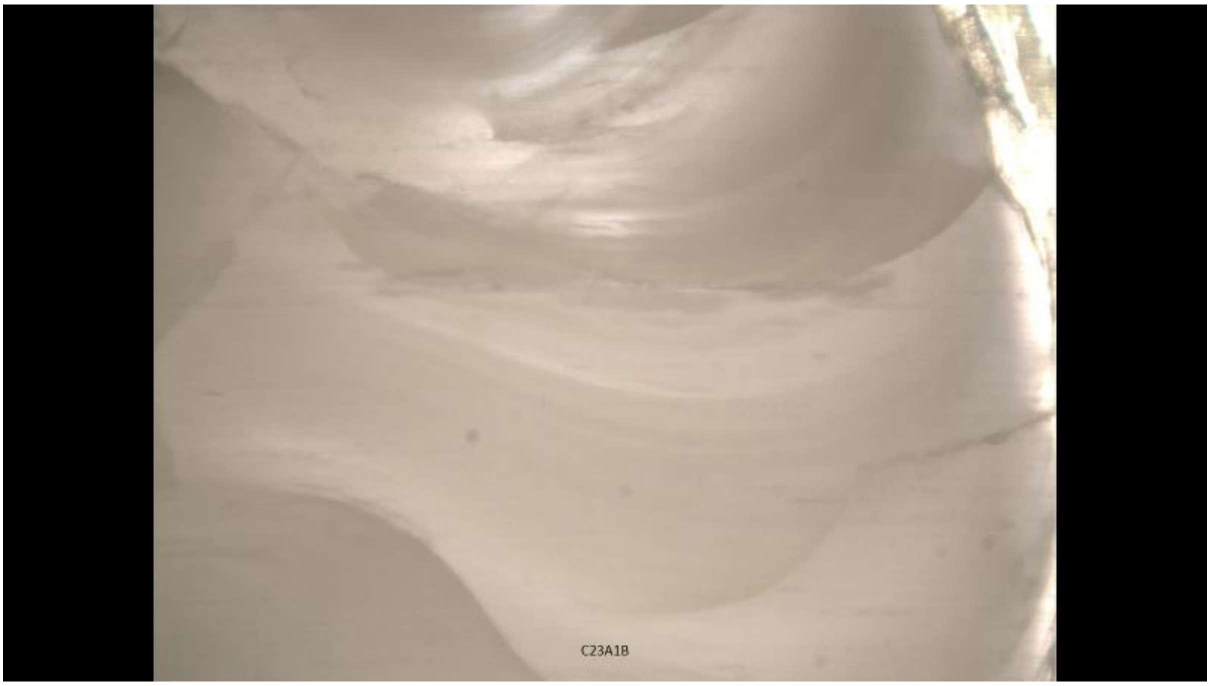
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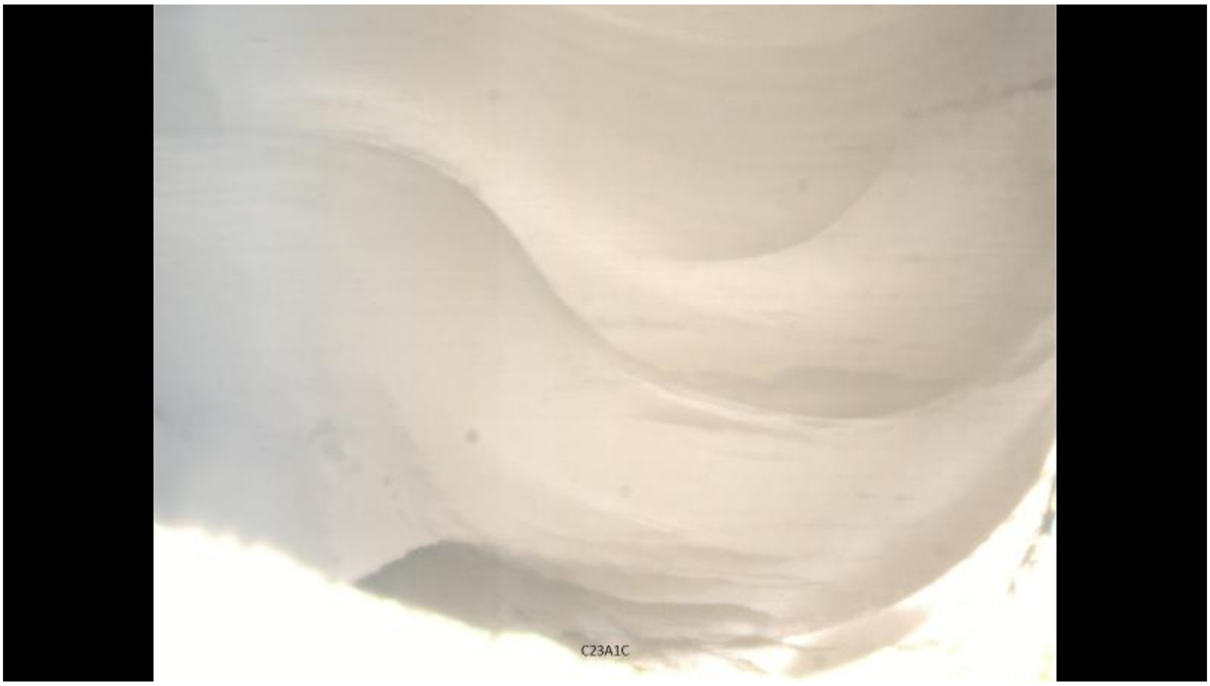
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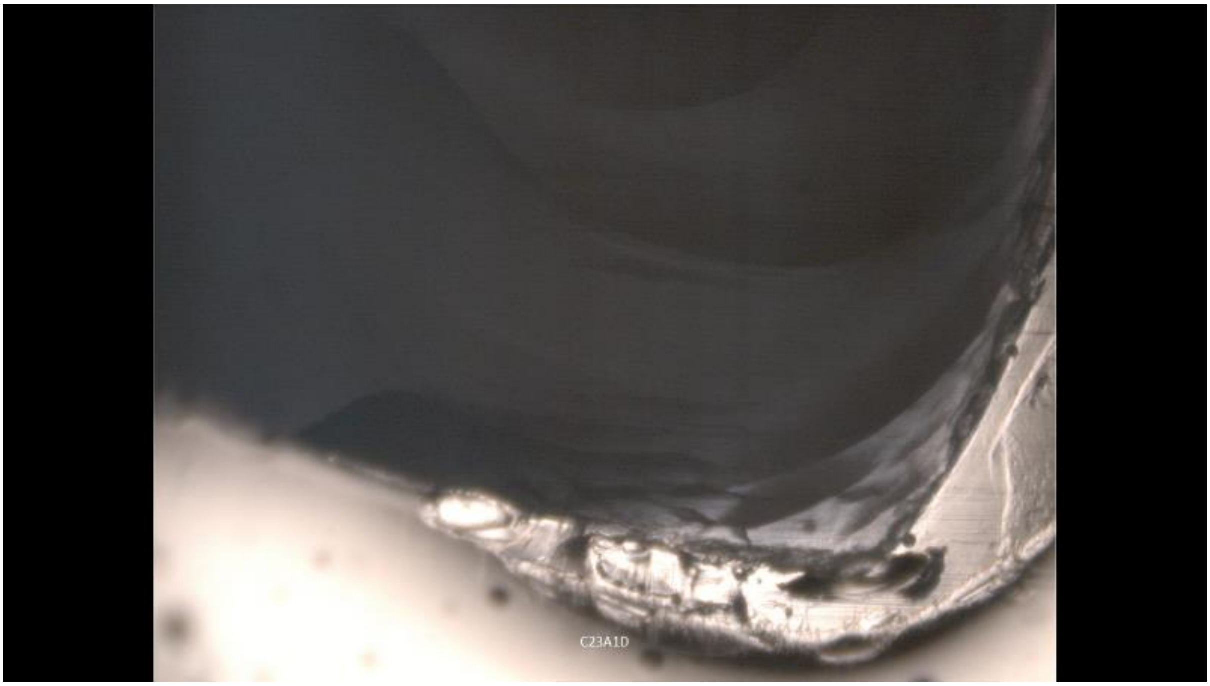
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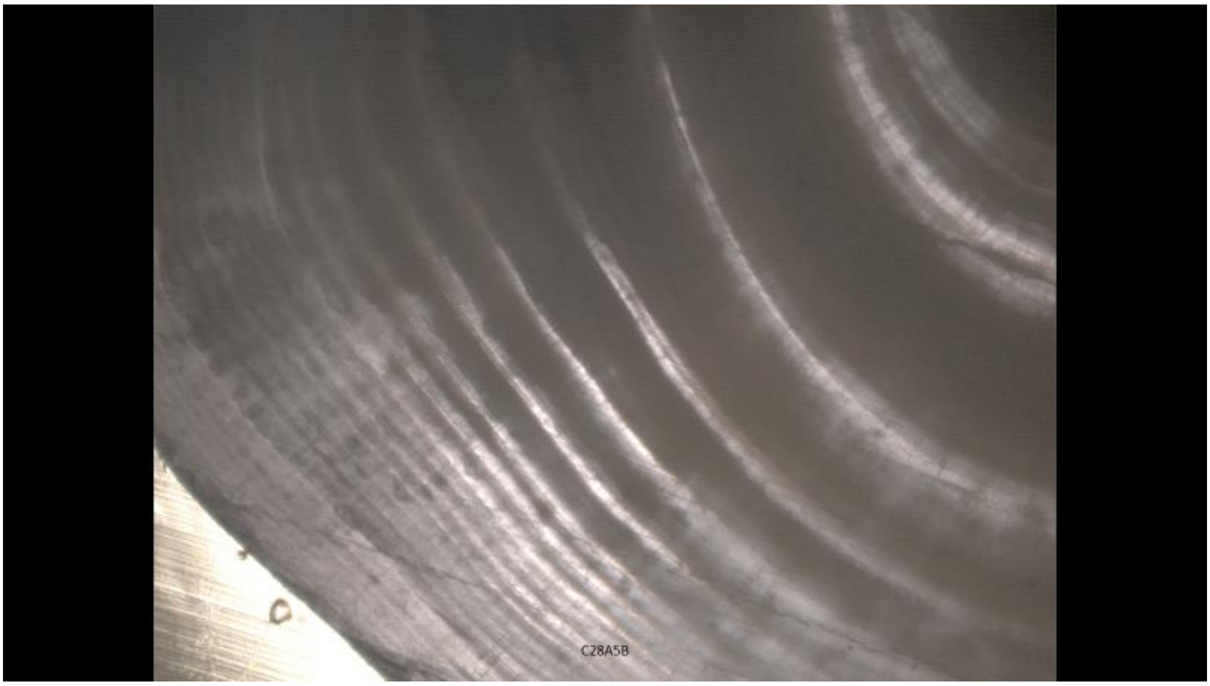
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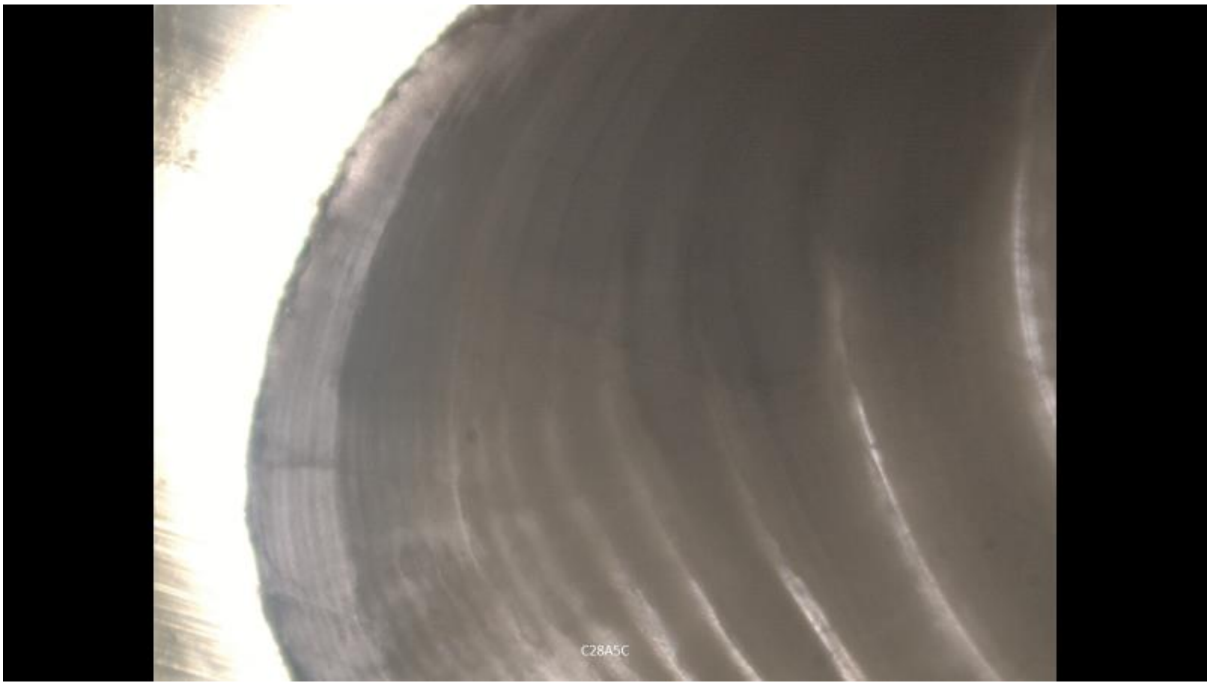
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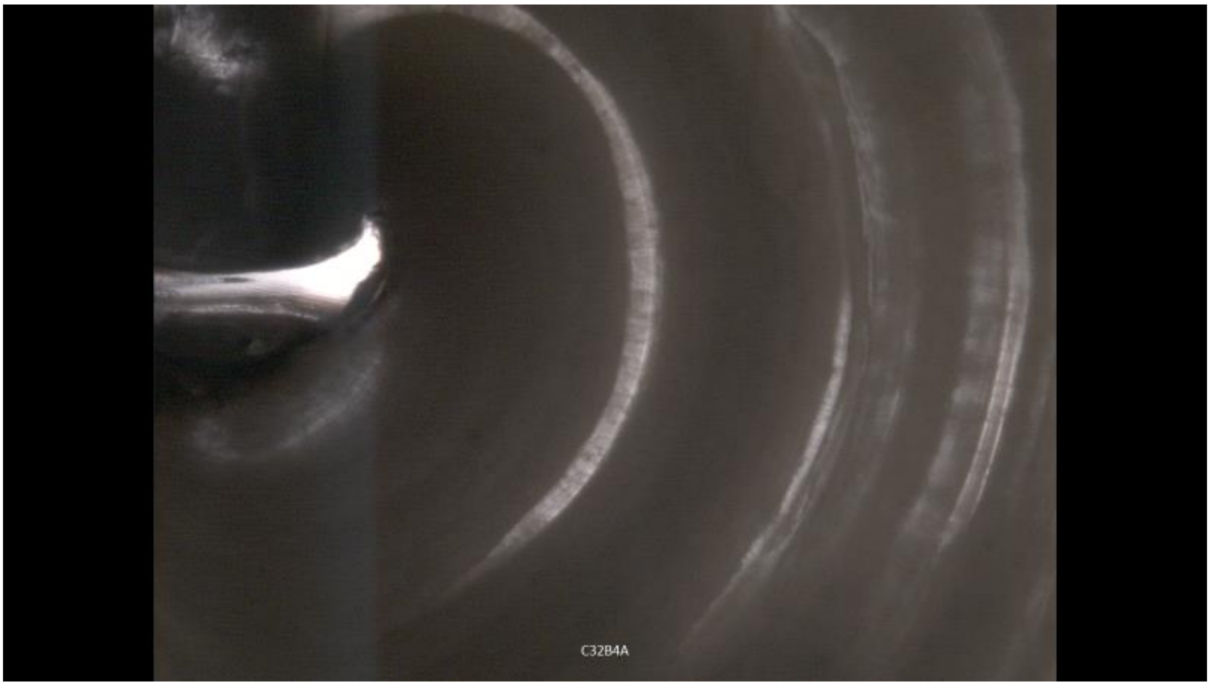
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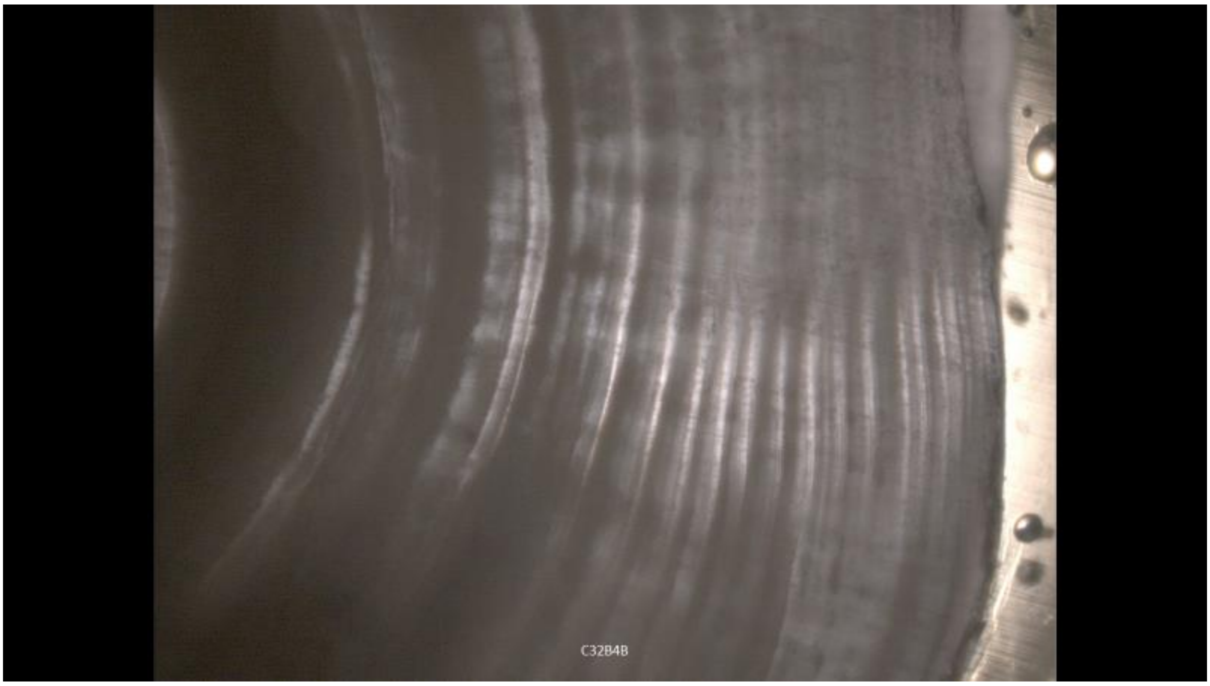
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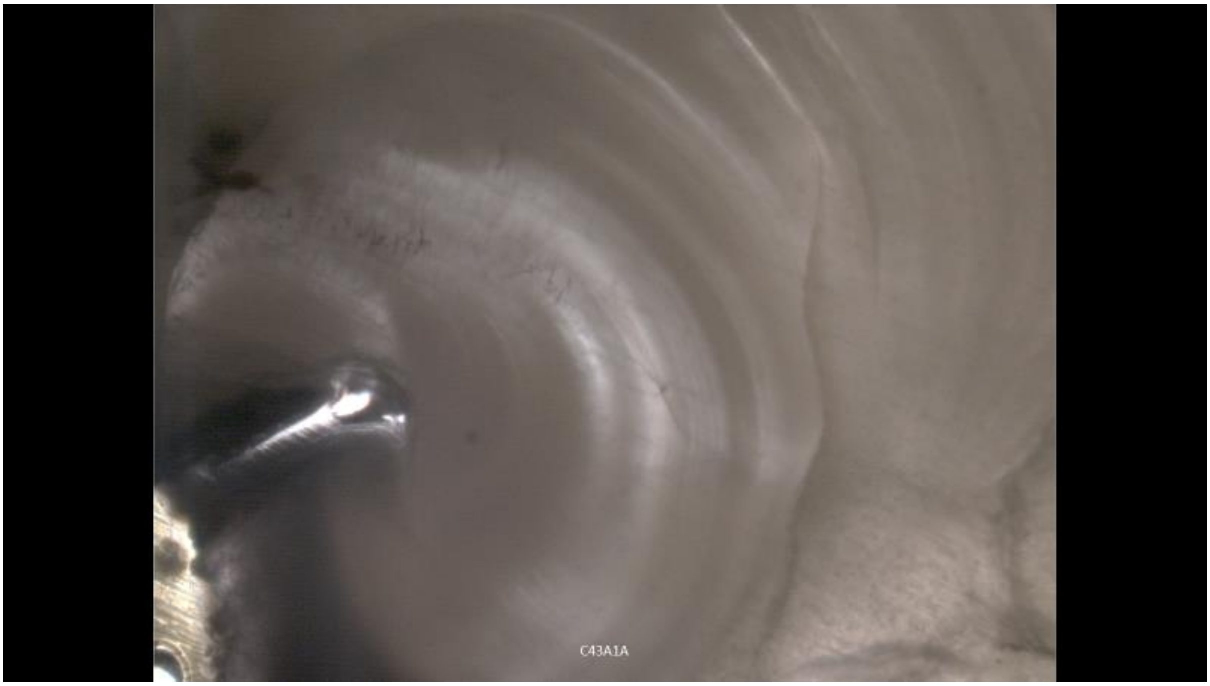
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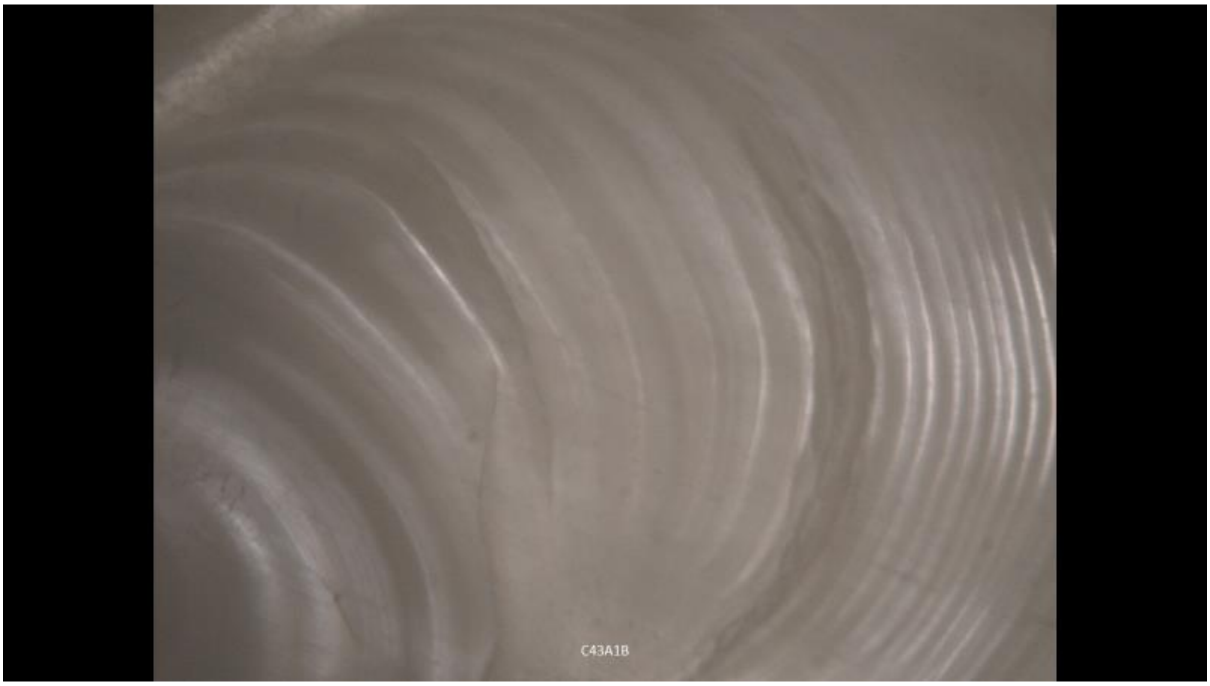
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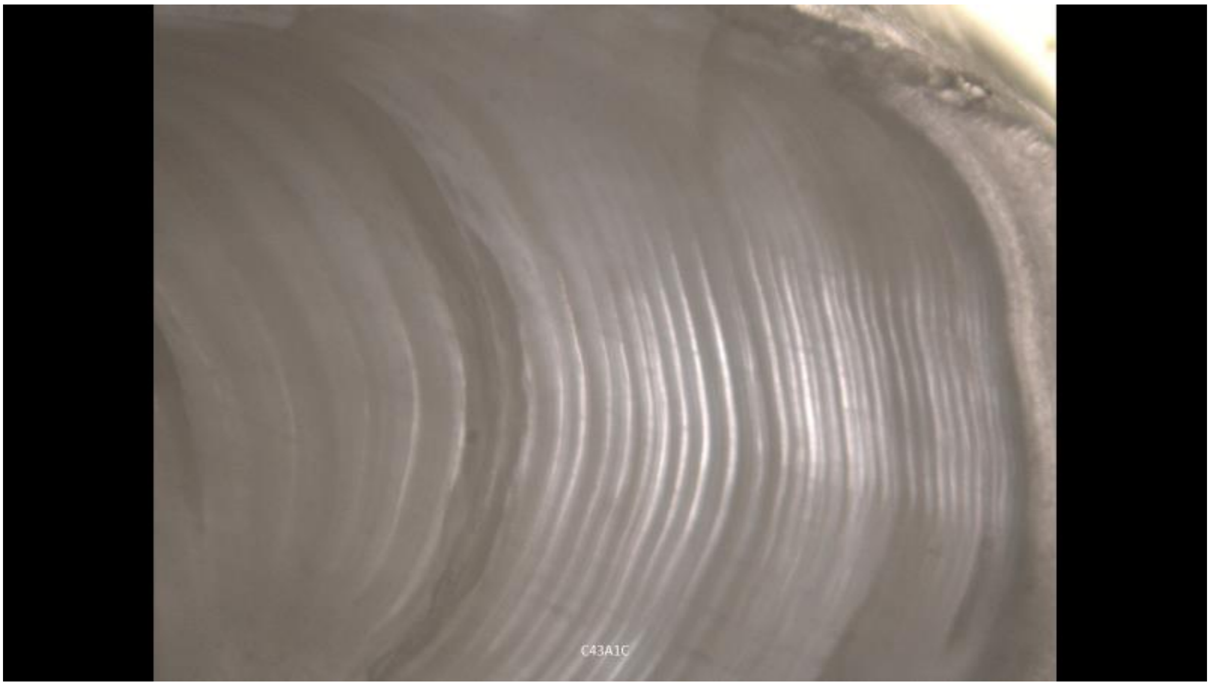
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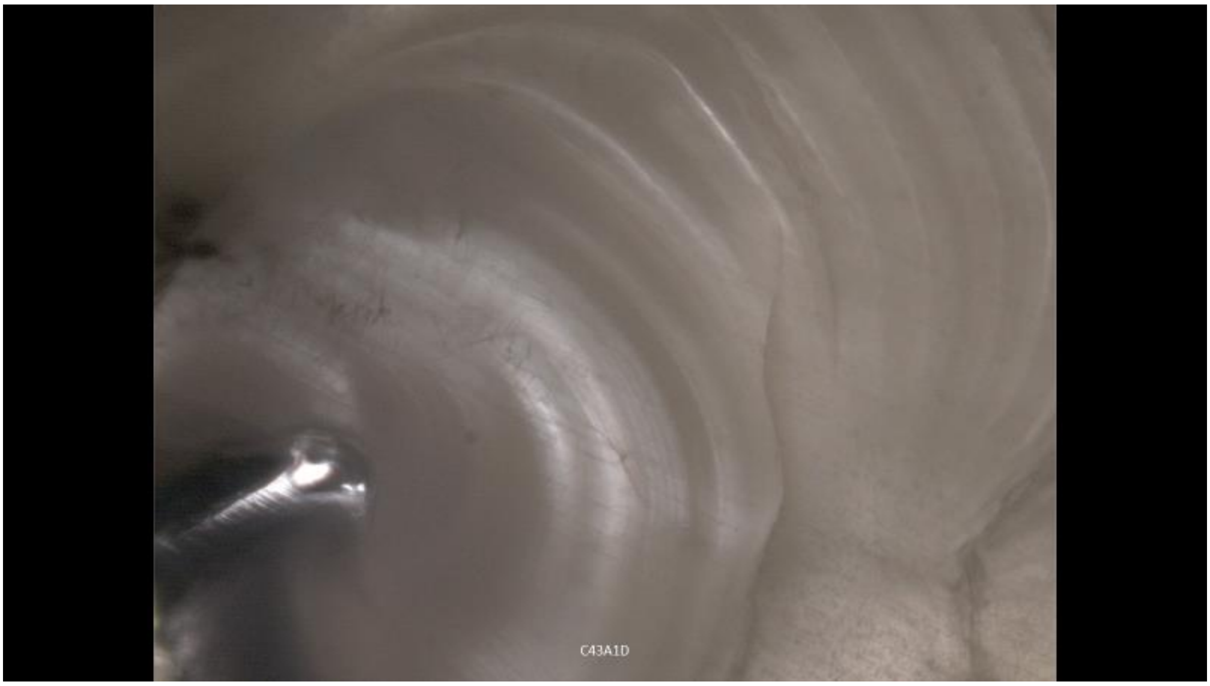
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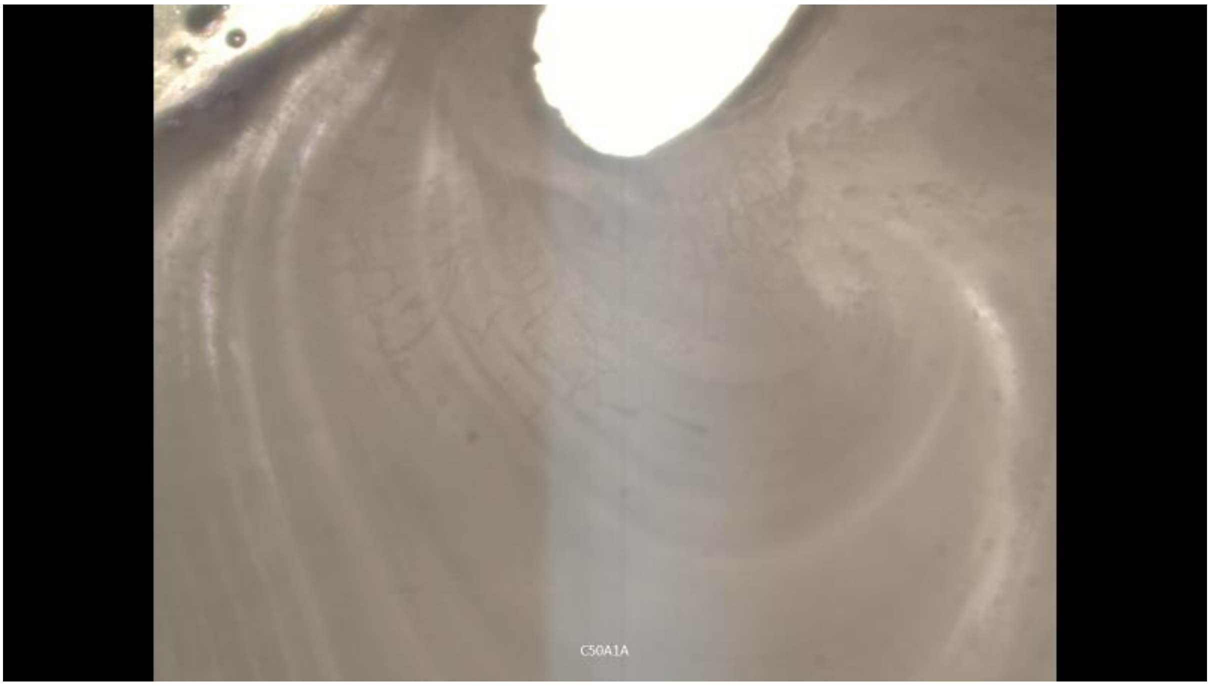
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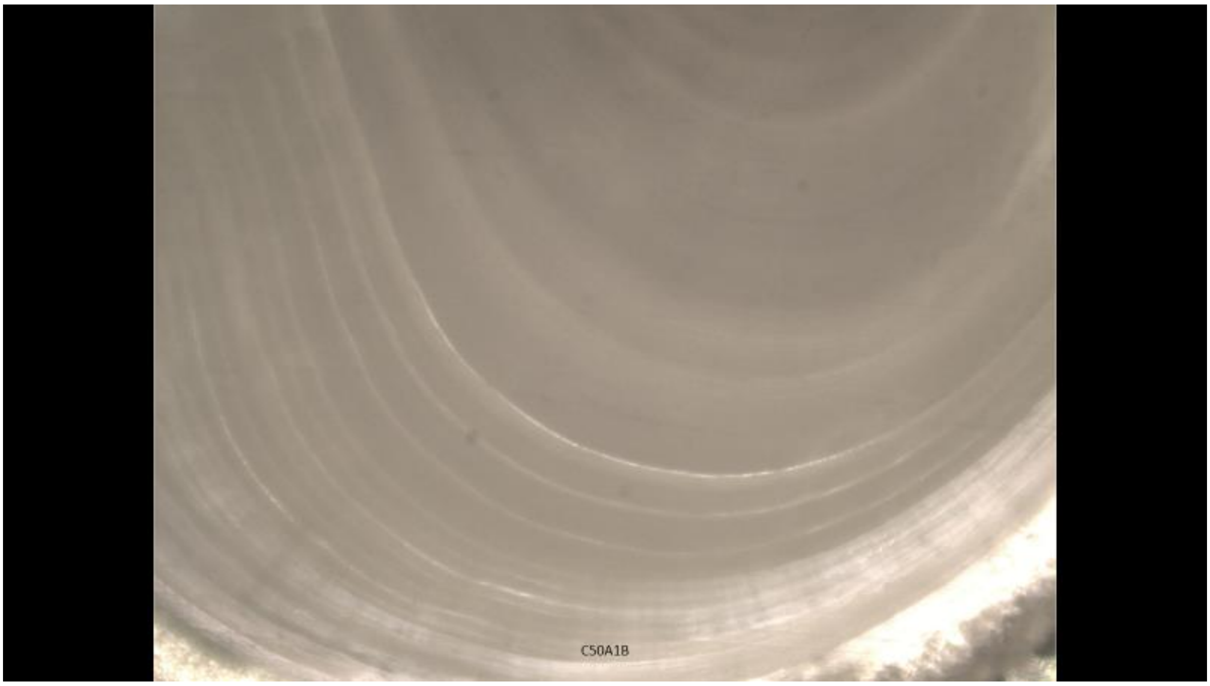
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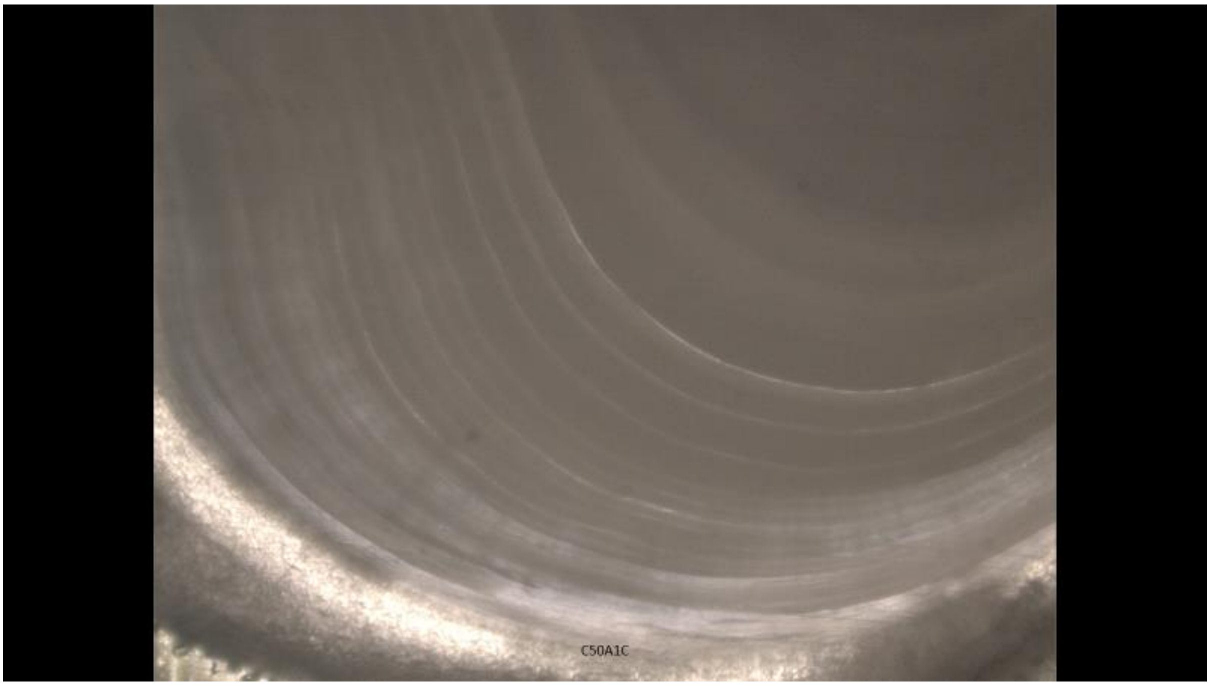
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