# The history of mesowear: A review

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Here we review published mesowear data from the year 2000 to November 2019 (211 publications, 707 species, 1396 data points). Mesowear is a widely applied tooth wear technique that can be used to infer a herbivore's diet by scoring the height and sharpness of molar tooth cusps with the naked eye. Established as a fast and efficient tool for paleodiet reconstruction, the technique has seen multiple adaptations, simplifications, and extensions since its establishment, which have become complex to follow. The present study presents a detailed review of all successive changes and adaptations to the mesowear technique, providing a template for the application of each technique to the research question at hand. In addition, the array of species to which mesowear has been applied, along with the equivalent recorded diets have been compiled here in a large dataset. This review provides an insight into the metrics related to mesowear publication since its establishment. The large dataset overviews whether the species to which the various techniques of mesowear are applied are extant or extinct, their phylogenetic classification, their assigned diets and diet stability between studies, as a resource for future research on the topic.

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## ABSTRACT

Here we review published mesowear data from the year 2000 to November 2019 (211 publications, 707 species, 1396 data points). Mesowear is a widely applied tooth wear technique that can be used to infer a herbivore's diet by scoring the height and sharpness of molar tooth cusps with the naked eye. Established as a fast and efficient tool for paleodiet reconstruction, the technique has seen multiple adaptations, simplifications, and extensions since its establishment, which have become complex to follow.

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## KEY WORDS

tooth wear, diet reconstruction, herbivore, dietary proxy, palaeodiet

## INTROCUCTION

Tooth wear can be measured on different physiological scales, from the microscopic (2D microwear (Walker et al., 1978) and 3D dental microtexture analysis (Schulz et al., 2013a)) to the macroscopic (mesowear, absolute wear (Ackermans et al., 2019; Fortelius and Solounias, 2000)), informing us about a specimens' or a species' dietary signal. Within tooth wear, attrition to the tooth's enamel surface caused by tooth-on tooth contact is generally the main cause of wear in animals with a browsing diet. The soft nature of a browse-based diet causes opposing teeth to wear themselves, as the diet itself does not provide resistance (Sanson, 2006). Abrasion on the other hand, is caused by internal or external abrasives, which wear tooth material upon contact (Janis, 2008). Grasses contain large amounts of internal opaline silicates that wear tooth enamel when chewed repetitively (Baker et al., 1959), and, grazing animals generally tend to feed close to the ground in open habitats, where plants become covered in external abrasives, e.g. dust and grit (Janis and Fortelius, 1988). It is still debated whether tooth wear is mainly caused by phytoliths (Lucas et al., 2013; Sanson et al., 2007; Xia et al., 2015) or external abrasives (Damuth and Janis, 2011; Healy, 1967; Hummel et al., 2011; Merceron et al., 2016), and which is the main driver in the evolution of hypsodonty, though the general agreement is that both types of abrasives contribute at least somewhat to tooth wear and thus to the evolution of hypsodonty (Kaiser et al., 2013; Williams and Kay, 2001). Historically, tooth wear patterns have been of interest for age determination, using the visual aspect of the tooth's surface (Grant, 1982), using a technique that has been called "macrowear", and confusingly, "meso-wear" in the past. It is important to note that, while this "macrowear" is a species-specific technique - applicable to a variety of species from bears (Stiner, 1998) to manatees (Gonzalez-Socoloske et al., 2018) - this technique is solely applicable when estimating age based on wear, and does not provide information on diet.

In the current review, mesowear is referred to as a series of techniques using a semi-quantitative method to evaluate tooth wear visible on the tooth profile with the naked eye. The original mesowear technique was introduced by Fortelius and Solounias (2000) (Table 1), as a method to reconstruct general paleodiets of fossil ungulates by observing the macroscopic wear on their molars. An abrasion-attrition wear gradient is used to assign dietary categories to herbivores, with browsers generally showing a more attrition-based wear pattern, and grazers a more abrasion-dominated pattern (Fortelius and Solounias, 2000). This technique, also called "mesowear I" (Solounias et al., 2014), was established to represent the average diet of a species from a certain location. As such, in terms of dietary signal length, mesowear serves as a midway point between the unworn shape of a tooth representing a general diet on the evolutionary scale (*i.e*. herbivore or carnivore), and microscopic wear, representing a specimen's last few meals (Grine, 1986). At the establishment of the technique, selenodont- (*i.e.* cow) or trilophodont-type (*i.e.* mastodon) molars were the target teeth for mesowear, applied by observing "*the buccal edges of the paracones and metacones of upper molars"* with the naked eye or at low magnification (Fig.1). As a direct consequence, mesowear is a fast, inexpensive technique for diet determination. Molar cusp relief or occlusal relief (OR) are defined in the original publication as "*the relative distance between cusp height and inter-cusp valleys*, with low OR related to the high abrasion typical of the grazer diet. Cusp shape (CS) is therein defined by "*the apex of the cusp being described as sharp, rounded or blunt"*, using the maxillary M2 as the tooth of reference. Applying these variables allows dietary reconstruction based on the percentage of sharp, round, or blunt cusps; alongside the percentage of high relief. Mesowear I was developed using a database of 64 extant species (Annex 1), and was succinctly applied to six fossil species of known diet to test its strength, followed by a blind test on 20 specimens of *Hippotherium* (Kaiser et al., 2000) (Table1, Annex 1).

In the original mesowear method described above, the sharper of the two molar cusps was scored on a wide variety of taxa, noting that the choice of cusp was not critical. This hypothesis has been confirmed by Ackermans et al. (2018) in a feeding experiment on goats, though significant inter-cusp differences have been detected in rhinoceroses (Taylor et al. 2013) and certain equids (Taylor et al., 2016). The authors also note the importance of scoring at least 10- and ideally 20-30 specimens per species and/or locality for a reasonable approximation of the score, though on palaeontological specimens, rudimentary dietary assumptions are sometimes made using a single tooth, as complete specimens are rare. Although the initial assumption was that mesowear remains relatively stable throughout an individual's life (when very young or very old specimens are excluded), Rivals et al. (2007a) later established the idea that mesowear varies based on initial crown height and is different throughout an animal's lifetime.

Further adaptations were made to the original mesowear technique (for more details, see Table 1), expanding it to more teeth (Franz-Odendaal and Kaiser, 2003; Kaiser and Fortelius, 2003), and adapting the method to specific taxa (Butler et al., 2014; Fraser and Theodor, 2010; Kropacheva et al., 2017; Purnell and Jones, 2012; Saarinen and Karme, 2017; Saarinen et al., 2015; Taylor et al., 2013; Ulbricht et al., 2015). Some, deeming OR a redundant measure, simplified mesowear by only using categories of CS (Mihlbachler and Solounias, 2006; Widga, 2006), while others simplified the technique by combining OR and CS into a single score (Croft and Weinstein, 2008; Kaiser, 2009; Rivals and Semprebon, 2006) – these simplified versions of the original mesowear technique were deemed "mesowear II" by Solounias et al. (2014). Further simplifications include a "mesowear ruler" system (Mihlbachler et al., 2011) (Fig. 2), and a "mesowear angle" system (Saarinen et al., 2015). Mesowear also has an extended version, where intermediate stages were added to the original mesowear categories and a more complex combined score was created to provide more detail (Winkler and Kaiser, 2011) (Table 1, Fig. 1). "Mesowear III" or "inner-mesowear" was implemented by Solounias et al. (2014) (Fig. 3), where scoring the inner enamel band of the tooth aimed to record a more precise signal, and represent a shorter timeframe. Mesowear III has been applied in six other studies since it was established (Annex 1), but has been tested experimentally once, and results did not show more precision than traditional mesowear when both techniques were applied to the same dataset (Stauffer et al., 2019).

Traditionally, mesowear has either been scored directly on the specimens' teeth, on resin casts, or on photographs of the specimen's teeth (Fortelius and Solounias, 2000). More recent studies, however, have used 3D models of wear facets (Hernesniemi et al., 2011), or scored mesowear directly onto 3D reconstructions from CT scanned skulls of live animals (Ackermans et al., 2018). Various microscopy techniques have also been used as a means of scoring mesowear on smaller specimens such as conodonts (Purnell and Jones, 2012), lagomorphs, and rodents (Kropacheva et al., 2017; Ulbricht et al., 2015).

The many iterations and addendums to the original mesowear technique can create confusion regarding the category of mesowear best applied (Viranta and Mannermaa, 2014), and the interpretation of corresponding results (Díaz-Sibaja et al., 2018). The aim of this review was to therefore create a body of reference with precise definitions and short explanations for each variation of the mesowear technique, to facilitate future applications. An overview of current dental wear techniques exists (Green and Croft, 2018), but the current study provides a more detailed and widely understandable overview of the history and progression of the mesowear technique in particular. For this purpose, Table 1 lists all major amendments to the original mesowear technique - including the various versions of mesowear I, II and III – along with a short description and the scoring system used, thus hoping to ease comprehension of the available techniques and promote enhance comparability of studies.. In addition, a dataset was created reuniting the dietary classifications of all species to which the mesowear technique has been applied thus far, including specimen type, phylogenetic classification, and diet, as a readily accessible resource for future research (Annex 1).

## METHODS

Publications were cited using the search term "mesowear" in Google Scholar (n=1150), PubMed (n=25), ResearchGate (n=230), and Web of Science (n=142), for every year from 2000 until the present (11 November 2019). After removing duplicates and non-relevant studies (using the terms "mesowear" or "macrowear" to describe wear on the macroscopic scale, without referring to the Fortelius and Solounias (2000) mesowear technique), n=211 publications analysed. Book chapters, PhD, MSc thesis, and conference proceedings were included if they contained otherwise unpublished original mesowear data.

Diets in Annex 1 are indicated as shown in the corresponding references. A "various" diet indicates a diet change for the same species within the publication (different localities or time periods). A species without an assigned diet represents the lack of a diet indication or mesowear score within the text. An "experimental" diet represents studies in which experimental diets were fed to animals in controlled environments. When a study measured both mesowear and microwear (or another dietary proxy) and the indicated diets diverged, the diet determined by mesowear scoring was reported here. If species were listed with multiple entries within a single study an average was made. If within a study mesowear was scored but the diet was not defined, a diet was assigned according to the mesowear score reported in the publication and previous research regarding the respective technique. Extant and extinct specimens were classified as either “wild”, “captive” (zoo, or experimental specimens), archaeological (excavated in an archaeological context as defined by the original publication, designated “extant**” in Annex I) or fossil (fossil specimens of extant species designated “extant*” in Annex 1). When a palaeontological specimen’s identification could not be established to the species level, the specimen was designated as “fossil” in Annex 1. For simplicity of analysis, mesowear techniques are designated mesowear I, II, III, or a combination thereof in Annex 1. Extended or simplified versions are only noted in the case of the “mesowear ruler”, “mesowear angle”, “mesowear I and II – extended”, and all taxon-specific techniques. Data was arranged using pivot tables in Microsoft Excel (version 16.26) for graphic representation and interpretation.

Although mesowear can vary within species at different localities or different points in time, the constancy of diets assigned to a species using mesowear was assessed using the dataset assembled in the present study. It should be noted that the extreme variability between publications makes this a very coarse measure, however, it may either serve as an indication of the consistency of a species’ diet, or as an indication of the difficulty to consistently assign a score to the species. When species were scored in more than one publication, a simple metric was devised: the percentage of the species’ main diet across publications was plotted against the number of publications scoring the species – in this case a higher main-diet percentage, alongside a high publication count indicated a more robust diet. This was measured using the dataset from Annex 1 including all types of diets, as well as using a simplified version of this dataset excluding all but the “grazer”, “browser”, and “mixed-feeder” diets (Fig. 7b).

## RESULTS

The data collected (Annex 1) shows that, when ordering the data by publication, 55% of all publications score exclusively extinct specimens, while 17% apply mesowear to solely extant species. Five percent of publications score solely extant- archaeological or fossil specimens; while 10% score a mix of extinct and extant specimens, the rest scoring combinations of the above (Fig. 5a). Only four publications applied mesowear to captive - including experimental - animals representing roughly 2% of all studies. With regards to diet, the mixed diet is most highly represented among all species (33%) as it covers a large spectrum, followed by the browser diet, at 26% (Fig. 7a).

When ordering the data by technique and publication, “mesowear I” on its own was scored in 37% of studies, followed by “mesowear II” (21%), “mesowear ruler” (14%), and “mesowear I and II” (9%), the rest using a combination thereof, or taxon-specific techniques (Fig. 6a). Most taxon-specific techniques were only used once in their original publication, with the exception of “mesowear adapted for Proboscidea”, used in nine publications and “mesowear adapted for Conodonta” used in four. This fits within a statement from the original mesowear study, stating that “*care should be taken not to lose the generality of the method, since restricting it to a single, morphologically uniform group will serve to limit the choice of recent species available for comparison”*.

Out of the 211 publications analysed, 17 studies scored over 20 species, with the highest number of species being 85 (Solounias et al., 2013). Placental mammals were overwhelmingly scored (95%), though they were surprisingly not the only class of animals to which mesowear was applied. Butler et al. (2014) adapted mesowear to marsupials, and Purnell and Jones (2012) applied mesowear to fossil conodonts (Table 1), a technique which was also applied to elasmobranches

(McLennan, 2018). When sorted by order, artiodactyls were most represented (63%), followed by perissodactyls (26%) (Fig. 4). Overall, out of 707 species (excluding “sp.”), *Equus* was by far the most scored genus, with 109 counts, followed by *Tragelaphus* with 38 counts, and *Cervus* at 37 counts. At the species level, *Cervus elaphus* was most commonly scored, with 19 counts, followed by *Equus ferus* (18 counts). In total, 177 species were scored in more than one publication, meaning that about 75% of species were only scored once (Annex 1).

In part because of the number of times it is represented in the dataset and because of its extreme hypsodonty, the species with the most robust unchanging diet is *Equus ferus,* with 95% diet robustness within 20 publications (Fig. 7b).

## DISCUSSION

Although one may envision more sophisticated or precise methods of palaeodietary reconstruction, it is important to remember that the original goal of the mesowear technique was to provide a fast and cost-effective way of determining diets for a large number of species. It has been thoroughly tested for this purpose and is extremely efficient in determining diet on a coarse scale. The array of mesowear measurement techniques stemming from the original method have their respective pros and cons. If the technique is too simplified, we run the risk of hiding more subtle variations in diet. The “mesowear ruler technique” was originally designed for use on horses (Mihlbachler et al., 2011) but was later applied to other species without adaptation or further tests of robustness (e.g. López-García et al., 2012; Rivals, 2012). Additionally, adapting the technique to species with very specific tooth morphology, such as proboscideans (Saarinen et al., 2015), adds the advantage of being able to score diets for these species, but this can only be reliabily reached through copious amounts of testing. Fine-tuning mesowear to every taxon runs the risk of tarnishing the main goal of mesowear, that is being fast and cost efficient, and most importantly, the creation of so many techniques reduces comparability between studies. Ideally, if the majority of studies applied the extended version of mesowear (Winkler and Kaiser, 2011), from which mesowear I scores can be easily deduced, this would enable higher comparability between studies, all while remaining a quick and easy technique.

The “dietary robustness measure” established here may be coarse, however, it provides a different approach in investigating dietary robustness. It also represents the number of species scored within a single publication, demonstrating some species have been scored in over ten separate publications. Providing an overview of the variability in mesowear scoring may allow for a re-balance of mesowear application in future studies, by increasing reproducibility and reducing repeated measures, e.g. on species with high dietary robustness.

Since the creation of the mesowear technique, the number of publications per year, as well as the type of publication (paleontological or not) has grown until around 2010, with a roughly even distribution between non- and purely- palaeontological publications (Fig. 5b). The type of mesowear technique applied over the years also varies, and the number of publications applying solely “mesowear I” appears to decline over time as it becomes part of a combination of techniques, while the use of taxon-specific techniques increases (Fig. 6b). Mesowear remains an essential asset for dietary reconstruction and has become more frequently applied in combination with other dietary proxies such as microwear or isotopic data, to provide a more accurate representation of diet over different timescales, though these proxies are rarely in accordance, and the development of wear on different scales remains to be investigated (Ackermans et al., in prep.-b).

A precise understanding of dietary timescales requires the establishment of a baseline, to be used as a reference in defining the length of a dietary signal. In the case of mesowear, very few publications investigate mesowear experimentally (Ackermans et al., 2018; Kropacheva et al., 2017; Solounias et al., 2014; Stauffer et al., 2019) due to the cost and time required for long-term animal experiments. Because of this, the duration of the dietary signal represented by mesowear remains widely unknown. The few experimental tests of mesowear that can be considered long-term seem to indicate this proxy as representing more of a general lifetime signal, at least in small ruminants (Ackermans et al., in prep.-a on sheep for 17 months; Ackermans et al., 2018 on goats for 6 months). However, it is impossible to experimentally recreate the variations of nature, and the comparison of the aforementioned results to those where mesowear shows more seasonal effects (Kaiser and Schulz, 2006; Marom et al., 2018; Schulz et al., 2013b) requires further investigation. A better understanding of the timescale represented by mesowear can only improve the precision of dietary reconstructions, all while furthering our understanding of the dental wear and dietary habits of extant species.

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**COMPETING INTERESTS**

The author declares no competing interests

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**Table 1: Additions and adaptations to the original mesowear technique - ordered by mesowear technique and date.**

**Figure 1. I: Mesowear features used for scoring in the original study from Fortelius and Solounias (2000), described in more detail as "CM" in II, from Taylor et al. (2016).**
I: A: *Capra hircus*, high OR, sharp CS
B: *Cervus duvaucelli,* mesodont, high OR, round CS
C: *Odocoliaus virginianus,* brachydont, high OR, sharp CS
D: *Equus ferus caballus*, hyperhypselodont, low OR, blunt CS
E: *Kobus ellipsiprymnus*, high OR, round CS
F: *Acelaphus busephalus*, low OR, blunt CS
II: CM: Description of cusp shape categories for the classical mesowear method by Fortelius and Solounias (2000); EM: enhanced mesowear method established by Winkler and Kaiser (2011).

**Figure 2. Wear stages of mesowear III, from Solounias et al. (2014).**

**Figure 3. Wear stages of the mesowear ruler representing average mesowear score and crown height index, from Mihlbachler et al. (2011).**

**Figure 4: Percentage of taxonomic orders represented within a mesowear dataset from 2000 to November 2019.** Data sorted by specimen

**Figure 5a. Specimen status of samples represented within a mesowear dataset from 2000 to November 2019.** Data sorted by number of publications.

**Figure 5b. Yearly amount of publications scoring mesowear on paleontological specimens versus non-paleontological specimens between 2000 and November 2019*.**

**Figure 6a. Proportion of techniques employed within a mesowear dataset from 2000 to November 2019.** Data sorted by number of publications.

**Figure 6b. Yearly amount of the different techniques used to score mesowear between 2000 and November 2019*.** Data sorted by number of publications.

**Figure 7a. Percentages of diets represented within a mesowear dataset from 2000 to November 2019.** Data sorted by number of publications.

**Figure 7b. Dietary robustness of species represented in a mesowear dataset from 2000 to November 2019.** Dietary robustness is a measure represented by the percentage of a species' main diet throughout publications, plotted against the number of publications featuring the species. Size of marker indicates the number of species per point (minimum 1, maximum 14). Grey markers indicate multiple species (and multiple diets), green markers represent grazers, brown markers represent browsers, and brown and green pattern markers represent mixed diets.

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## Table 1(on next page)

Table 1: Additions and adaptations to the original mesowear technique - ordered by mesowear technique and date.

**Table 1: Additions and adaptations to the original mesowear technique - ordered by mesowear technique and date.**

| Technique | Reference | Description | Scores |
|---|---|---|---|
| Original mesowear - Mesowear I | (Fortelius and Solounias, 2000) | -Using the naked eye or x10 magnification<br>-Scoring only sharpest buccal cusp of maxillary M2<br>-Last molar in occlusion and M1 shape similar to M2<br>-Percentage of high relief and Percentage of sharp, round and blunt cusps | OR: low, high<br><br>CS: blunt, round, sharp |
| Mesowear I – Adapted for Equidae | (Kaiser and Fortelius, 2003) | Method extended to all apices on maxillary P4-M3 in equids | Original mesowear |
| Mesowear I | (Franz-Odendaal and Kaiser, 2003) | Method extended to maxillary M3, and mandibular M2 in ruminants | Original mesowear |
| Mesowear I – Adapted for Lagomorpha | (Fraser and Theodor, 2010) | “Cusp relief” combined with “buccal shearing crush wear” on maxillary and mandibular P4-M2 – resulting in 5 dietary classes | 1: 45° enamel-dentine relief with no additional wear - highly folivorous<br>2: 45° enamel- dentine relief with buccal shearing crush wear - leaves & woody materials<br>3: 45° enamel-dentine relief with buccal shearing crush & phase II wear - leaf, twig, & fruit diet<br>4: 90° enamel-dentine relief with no additional wear - open area grazers<br>5: 90° enamel-dentine relief with buccal shearing crush wear - open area browsers |
| Mesowear I – Adapted for Conodonta | (Purnell and Jones, 2012) | Scored on P1 elements | |
| Mesowear I – Adapted for Leporines & Murines | (Ulbricht et al., 2015) | Classical mesowear on the maxillary M1- M2, and mandibular p3 in *leporinae* and distal side of the maxillary M1 and mandibular m1 in *murinae* | Original mesowear |
| Mesowear I – Adapted for voles | (Kropacheva et al., 2017) | Maxillary M1-M2, mandibular m1 | Occlusal relief 1-7<br>Lateral facet development 1-3 |
| Mesowear II - “Mesowear ruler” | (Mihlbachler et al., 2011) | Simplified score using gauges and a seven-point system | Combined score 0-6 |
| Mesowear II - “Mesowear ruler” | (Wolf et al., 2012) | additional intermediate scores | Combined score 0-13<br>in increments of 0.5 |
| “Mesowear angles” – Adapted for Proboscidea | (Saarinen et al., 2015) | “*Mean mesowear angles of three central lamellae in occlusion”*<br>on all except deciduous teeth | Mean mesowear angle<br>< 106°: C3-plant based diet<br>> 130°: C4-plant based diet (grazer) |

| | | | |
|---|---|---|---|
| “Mesowear angles” – Adapted for Xenarthra | (Saarinen and Karme, 2017) | All molariform teeth | For *Xenarthra, Folivora*: Mean mesowear angle:<br>60°-85°: fruit browsers<br>75°-100°: leaf browsers<br>100-132°: mixed-feeders<br>132°-150°: grass dominated mixed-feeders<br>150°-190°: grazers<br><br>For X*enarthra, Cingulata*:<br>60°-100°: carnivore, insectivore, omnivore, possibly browsers<br>100°-125°: browse-dominated mixed-feeders & herbivorous omnivores<br>125°-152°: grass-dominated mixed-feeders<br>152°-190°: grazers |
| Mesowear II | (Mihlbachler and Solounias, 2006) | Simplified score, only proportion of sharp cusps | Proportion of sharp cusps:<br>40-100%: Clean browser<br>20-40%: Mixed feeders:<br>0-20%: Grazer |
| Mesowear II “quantitative mesowear” | (Widga, 2006) | Interval measurements of cusp and saddle heights to calculate cusp relief | Index of cusp relief:<br>Low ICR: grazer<br>High ICR: browser |
| Mesowear II | (Rivals and Semprebon, 2006) | Simplified score combining OR and CS | 0: high relief & sharp cusps<br>1: high relief & round cusps<br>2: low relief & round cusps<br>3: low relief & blunt cusps |
| Mesowear II | (Kaiser, 2009) | | 0: high relief & sharp cusps<br>1: high relief & round cusps<br>2: low relief & sharp cusps<br>3: low relief & round cusps<br>4: low relief & blunt cusps |
| Mesowear II | (Rivals et al., 2009) | | 0: high relief & sharp cusps<br>1: high relief & round cusps<br>2: low relief & round cusps<br>2.5: low relief & sharp cusps<br>3: low relief & blunt cusps |
| Mesowear II | (Croft and Weinstein, 2008) | | 0: high relief & sharp cusps<br>1: high relief & round cusps<br>2: low relief & round cusps<br>2.5: low relief & sharp cusps<br>3: high/low relief & blunt cusps |
| Mesowear II | (Fraser et al., 2014) | Method extended to mandibular p4-m3 for ruminants | 1: high relief & sharp cusps<br>2: high relief & round cusps<br>3: high relief & very round cusps<br>4: low relief & round-blunt cusps<br>5: low relief & flat-blunt cusps |
| Mesowear II – Adapted for Marsupialia | (Butler et al., 2014) | Use of classical mesowear and a combined score on the maxillary left maxillary molars, scoring sharpest buccal cusp | Combined score as in (Kaiser et al., 2009) |
| Mesowear I & II – Expanded | (Winkler and Kaiser, 2011) | Intermediate stages added to original and combined score | OR: low, high-low, high, high-high.<br>CS: blunt, round-round, round, round-sharp, sharp.<br>Combined score 1-17 |
| Mesowear I and II - Expanded, | (Taylor et al., 2013) | Expanded version and combined score on maxillary P2-M2. | Combined score 1-11 |

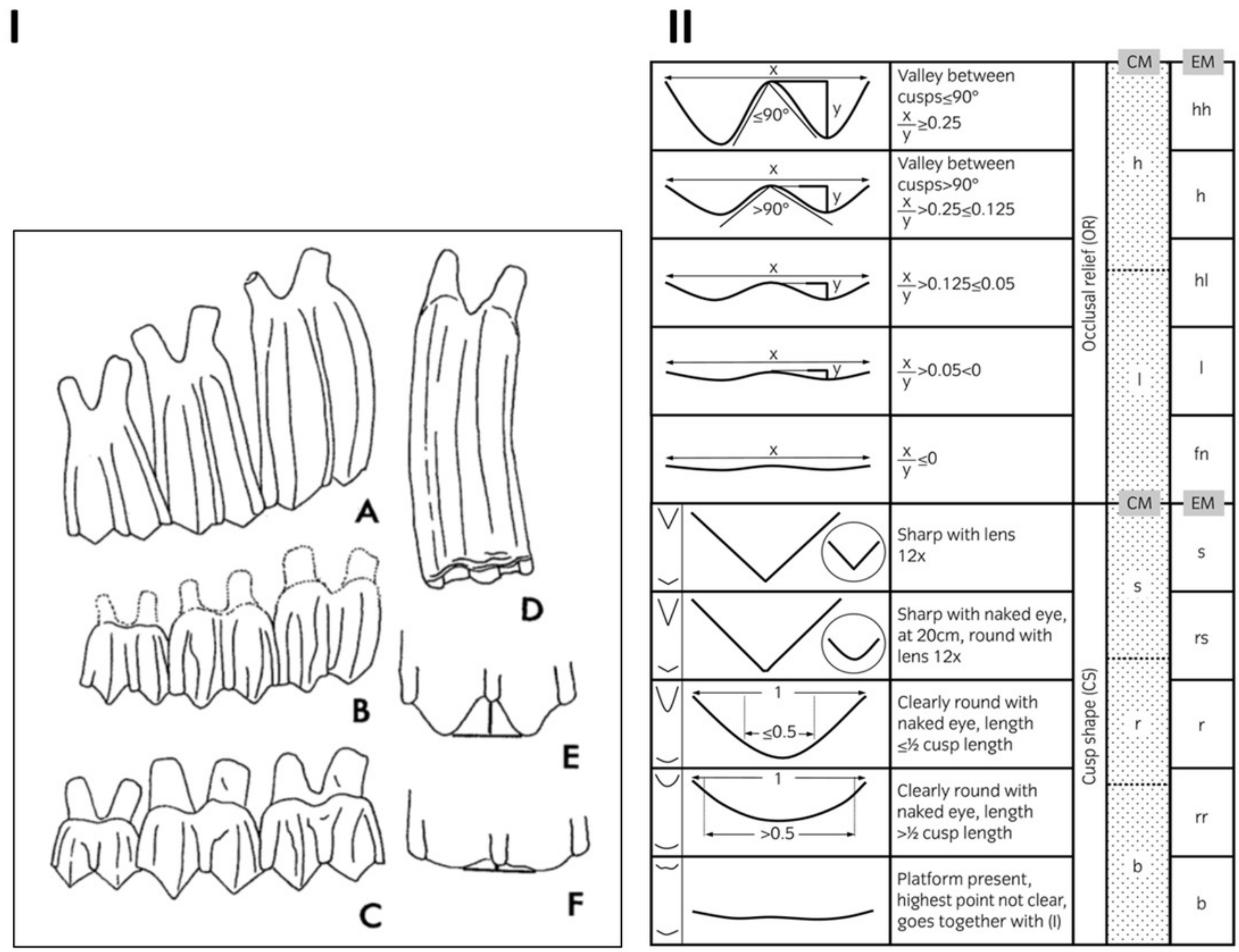
| |
|---|
| Adapted for Rhinocerotidae |

| | | | |
|---|---|---|---|
| Mesowear III – “Inner mesowear” | (Solounias et al., 2014) | Scores the second enamel band, using a stereo-microscope. Mesial side, distal side and junction point are scored separately. | Enamel band wear states:<br>1: ideal browser<br>2-3: intermediate<br>4: ideal grazer<br>Junction point score 1-4 |

# Figure 1

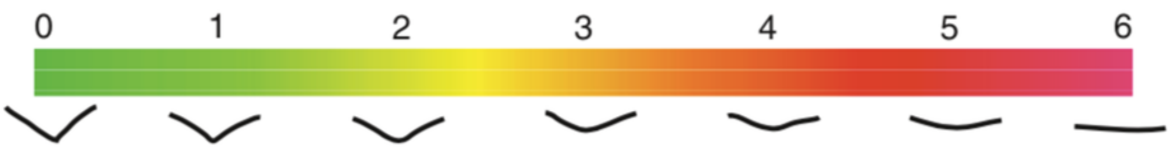
Figure 1. I: Mesowear features used for scoring in the original study from Fortelius and Solounias (2000) , described in more detail as “CM” in II, from Taylor et al. (2016) .

I: A: *Capra hircus*, high OR, sharp CS B: *Cervus duvaucelli,* mesodont, high OR, round CS C: *Odocoliaus virginianus,* brachydont, high OR, sharp CS D: *Equus ferus caballus*, hyperhypselodont, low OR, blunt CS E: *Kobus ellipsiprymnus*, high OR, round CS F: *Acelaphus busephalus*, low OR, blunt CS II: CM: Description of cusp shape categories for the classical mesowear method by Fortelius and Solounias (2000) ; EM: enhanced mesowear method established by Winkler and Kaiser (2011) .


I
II
A
B
C
D
E
F
Valley between cusps≤90° x/y≥0.25
≤90°
Valley between cusps>90° x/y>0.25≤0.125
>90°
x/y>0.125≤0.05
x/y>0.05<0
x/y≤0
Occlusal relief (OR)
CM
EM
hh
h
hl
l
fn
Sharp with lens 12x
Sharp with naked eye, at 20cm, round with lens 12x
Clearly round with naked eye, length ≤½ cusp length
Clearly round with naked eye, length >½ cusp length
Platform present, highest point not clear, goes together with (l)
Cusp shape (CS)
s
rs
r
rr
b
≤0.5
>0.5

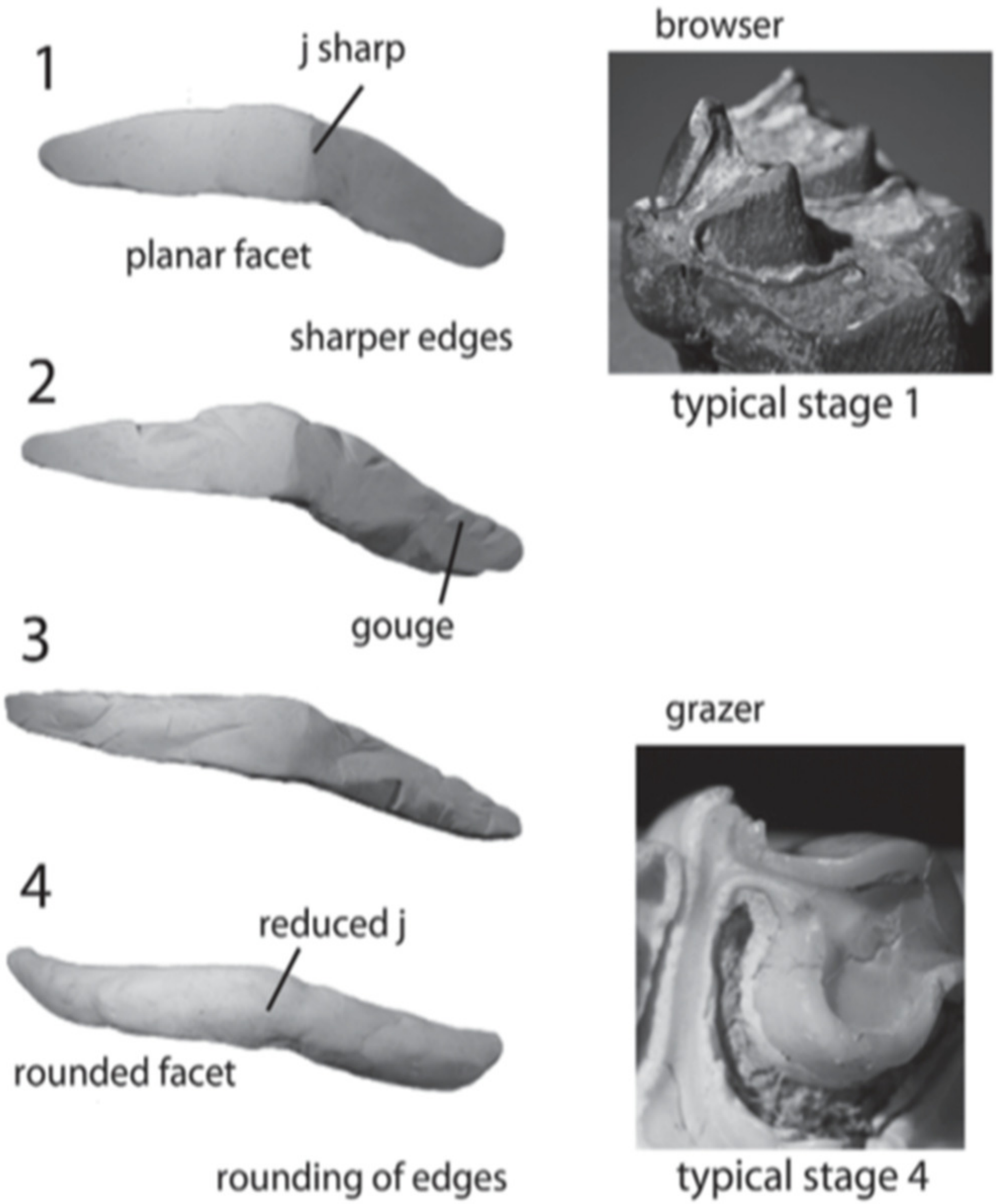
# Figure 2

Figure 2. Wear stages of mesowear III, from Solounias et al. (2014) .



# Figure 3

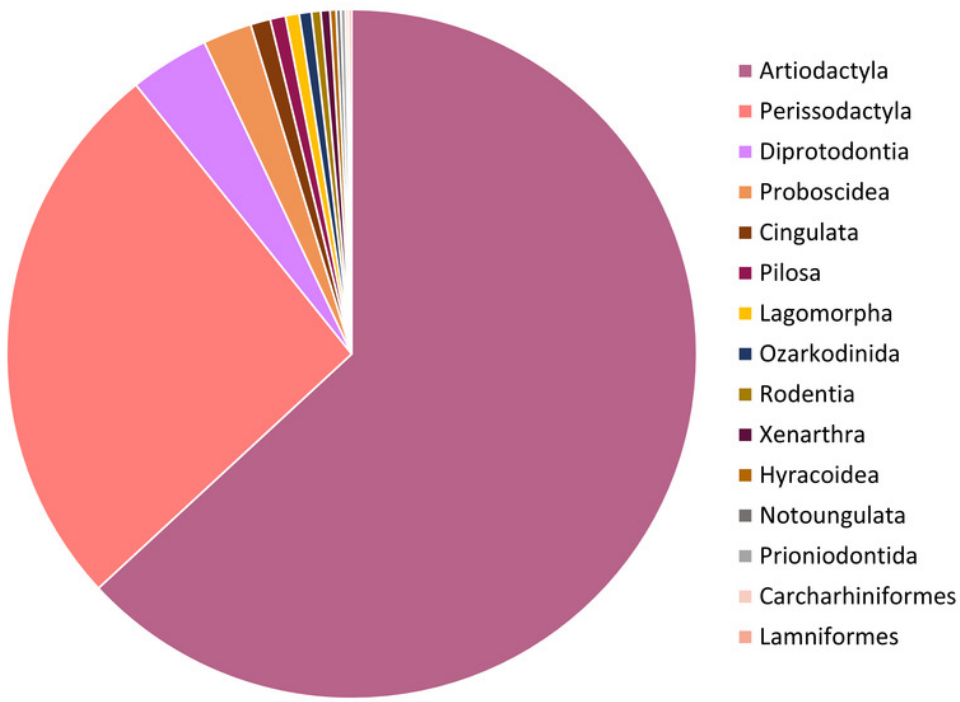
Figure 3. Wear stages of the mesowear ruler representing average mesowear score and crown height index, from Mihlbachler et al. (2011) .


1
j sharp
planar facet
sharper edges
2
gouge
3
4
reduced j
rounded facet
rounding of edges
browser
typical stage 1
grazer
typical stage 4

# Figure 4

Figure 4: Percentage of taxonomic orders represented within a mesowear dataset from 2000 to November 2019.

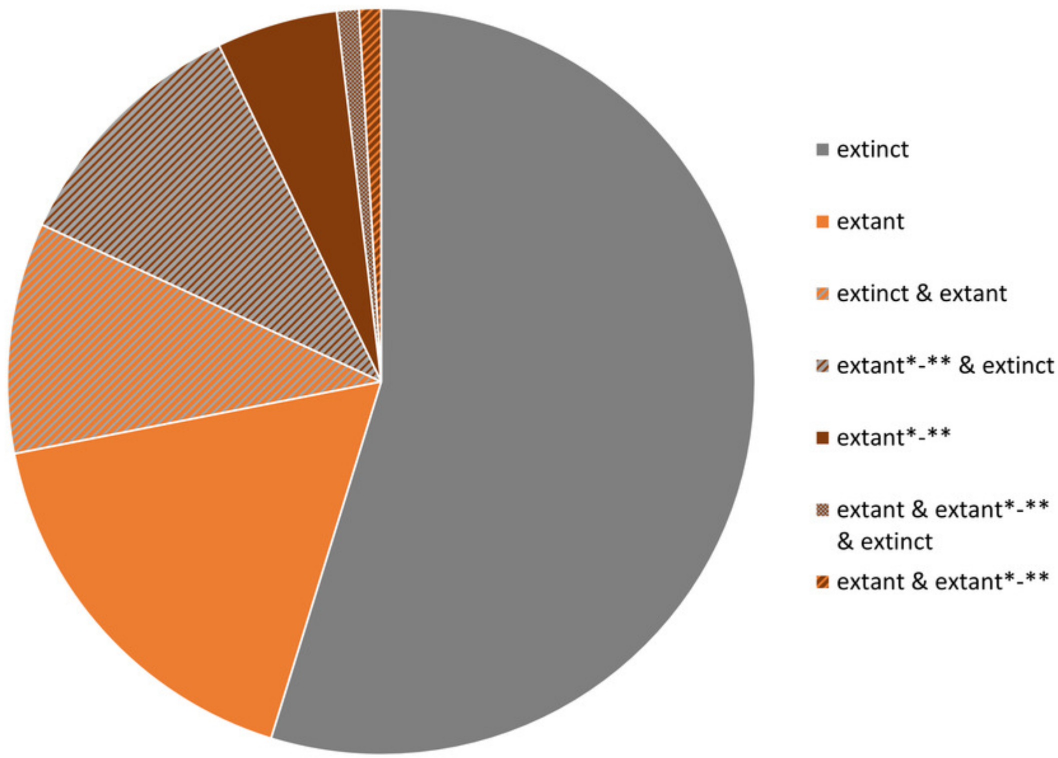
Data sorted by specimen



# Figure 5

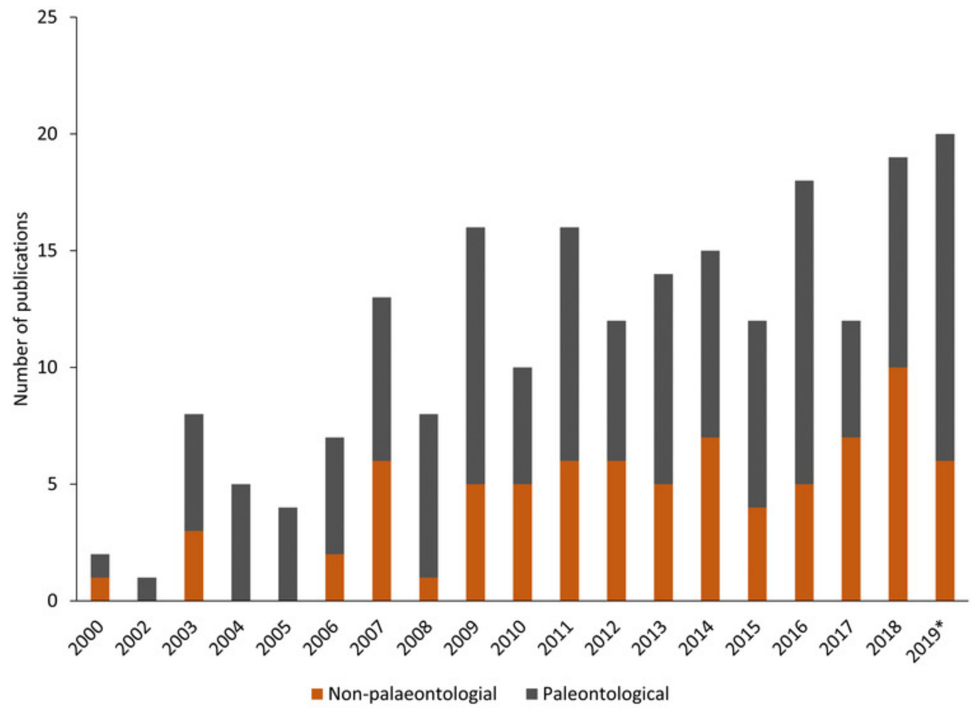
Figure 5a. Specimen status of samples represented within a mesowear dataset from 2000 to November 2019.

Data sorted by number of publications



# Figure 6

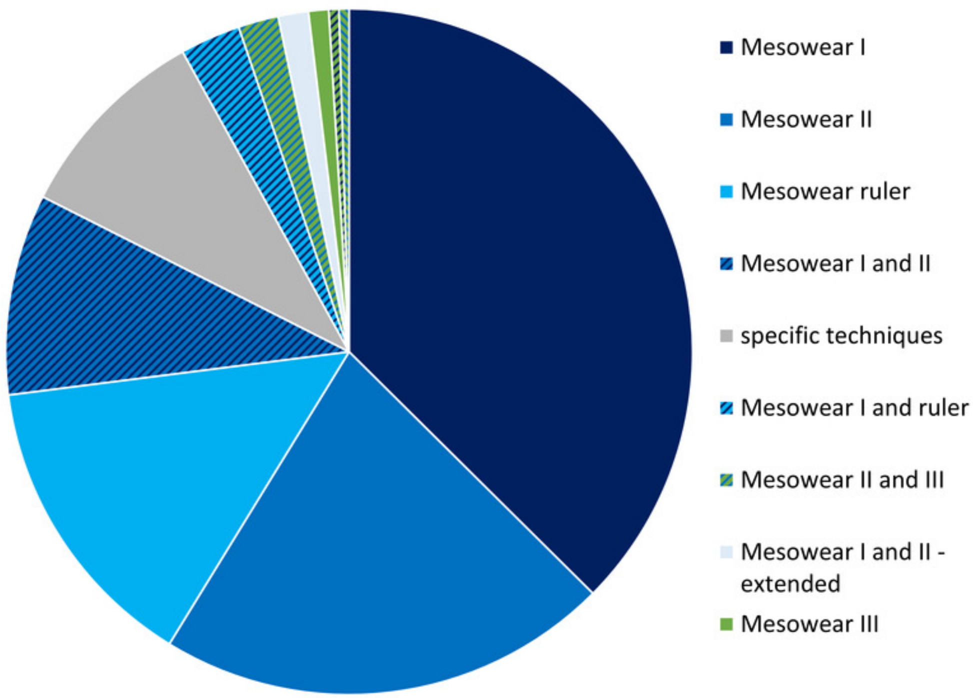
Figure 5b. Yearly amount of publications scoring mesowear on paleontological specimens versus non-paleontological specimens between 2000 and November 2019*.



# Figure 7

Figure 6a. Proportion of techniques employed within a mesowear dataset from 2000 to November 2019.

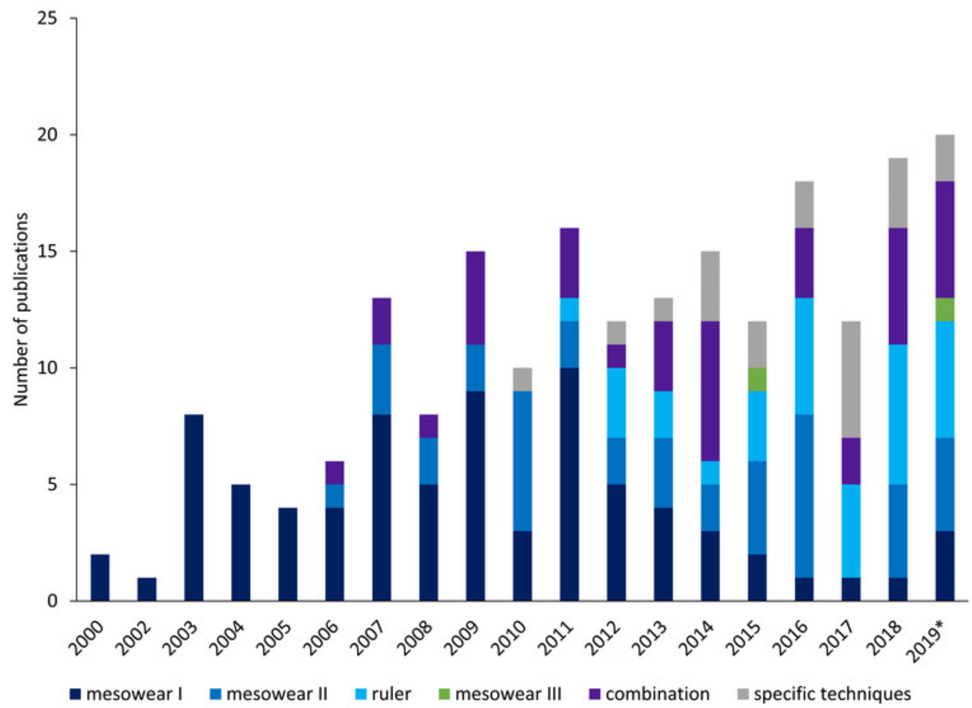
Data sorted by number of publications.



# Figure 8

Figure 6b. Yearly amount of the different techniques used to score mesowear between 2000 and November 2019*.

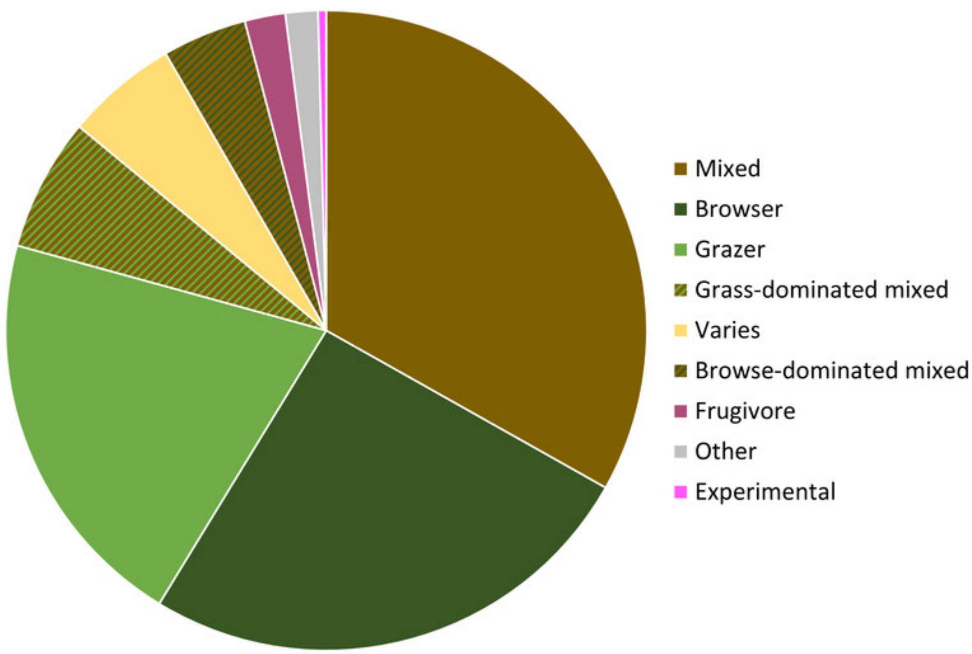
Data sorted by number of publications.



# Figure 9

Figure 7a. Percentages of diets represented within a mesowear dataset from 2000 to November 2019.

Data sorted by number of publications.



# Figure 10

Figure 7b. Dietary robustness of species represented in a mesowear dataset from 2000 to November 2019.

Dietary robustness is a measure represented by the percentage of a species' main diet throughout publications, plotted against the number of publications featuring the species. Size of marker indicates the number of species per point (minimum 1, maximum 14). Grey markers indicate multiple species (and multiple diets), green markers represent grazers, brown markers represent browsers, and brown and green pattern markers represent mixed diets.