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A short history of beer brewing

Alcoholic fermentation and yeast technology over time

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A s far back as we can retrace history, beer has always been an important part of human life: it was and still is a valuable food staple that has been constantly improved and adapted to human needs. For most of the time, intoxication was not the main purpose and could only be achieved to a limited extent, if at all, given that beer had a low alcohol content for most of human history. Instead, beer, owing to its specific ingredients and characteristics—alcohol, carbon dioxide and a low pH value was often the only safe liquid to drink when clean water was rare.

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In addition, beer and other fermented foods are an important source of essential vitamins, such as vitamin B or riboflavin, trace elements and other health-promoting ingredients. Especially for poorer people who mainly lived on bread or porridge, supplementing their diet with beer was beneficial to their health. Beer was also an important staple for certain professions, such as seafarers, who had to live of vitamin-poor foodstuffs for longer times. Not surprisingly, many seafaring nations contributed to the spread and improvement of beer brewing (Fig 1).

Fermented drinks—often the only safe liquid in ancient times

It required some resources and technological developments, however, to proceed from a random fermentation as it takes place in ripe or fallen fruit, to the 'controlled' brewing process that turns malt into alcohol. The most important factor was a reliable supply of suitable grains, which likely began between 9,500 and 6,000 BC when humans founded greater settlements in the Fertile Crescent in the Middle East, along the Nile in Africa and the flood plains of the Yangtze and Yellow Rivers in China and domesticated plants and animals. This semi-secure food supply, as well as the new, predominantly plant-based diet, had an impact on the human oral flora, microbiome of the digestive system and thereby the immune system. It is also possible that the amylases in human saliva became more selective and more efficient in response (Meußdoerffer & Zarnkow, 2014).

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This provided another important factor for brewing: a reliable method for converting cereal starch into sugar. There is evidence from every continent that, indeed, chewing grain and salivating was, and in some cases such as chicha, still is an integral part of beer-making. This was eventually replaced with a more controlled malting process using water and solar energy: adding water starts germination of the cereal seeds which converts the stored starch into usable sugars. Drying the germinating seeds or heating them over fire provided the third precondition: the drying stops the germination and makes the malt fermentable.

From a biotechnology point of view, this is where it gets interesting, as the alcoholproducing yeasts are of course the most important factor in producing beer with pleasant characteristics. These yeasts are likely also a product of human civilisation and domestication since alcohol-producing yeasts are a rarity among microorganisms. When humans began to live in close contact with domesticated animals and pests, animal bacteria and viruses adapted to infect humans: some of the most dangerous human pathogens evolved that way. Other useful microorganisms adapted as well to take advantage of new foods, such as cereal porridge or milk. Lactic acid bacteria, for example, lost pathogenic genes and specialised in the utilisation of lactose. Similarly, yeasts evolved to better metabolise various sugars into alcohol, which is a protective mechanism by converting the temporary sugar overhang of ripe fruits into a compound that many competing microorganisms are not able to utilise. The baking and brewing yeast Saccharomyces cerevisiae in particular evolved the ability to utilise malt sugar, which is one of the rarest sugars in the wild (Meußdoerffer & Zarnkow, 2014). Theodor Schwann, a pioneer of fermentation science, thus first classified this organism as a 'sugar fungus' (Saccharomyces) in 1836 (Smith, 2012).

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Yeast related Yeast related product product Substrate Product QUALITY DIVERSITY Long before antiquity Random or inoculated spontaneous Fermentations happen in daily life fermentation of substrate to fermented beverages 6000-3000 BCE Oldest breweries found in Göbleki Tepe (Turkey), Knowledge about fermentation through Abydos (Egypt) and (macroscopic) observation: other places Continuation of ferments/suspension/ sediment 14th-16th century S. pastorianus is propably described for the first time Knowledge about fermentation through as bottom fermenting yeast microscopic observation: · Continuation of microorganism or yeast mixtures 1680 Antonie van Leeuwenhoek discovers yeast cells under the microscope for the Knowledge about fermentation through first time IME pure cultures: 1883 Continuation of pure brewery yeast strains Emil Christian Hansen invents the pure culture procedure. Worldwide 'triumph' of · Selection and breeding of yeasts with S. pastorianus specific characteristics Optimisation of yeast management 19th-20th Restriction to a few high performance Modern microbiology was strains founded and yeast is briefly examined Utilisation of the biological diversity of End of 20th yeast strains beginning of 21st century Progressive characterisation Various scientific projects to Targeted use of a wide variety of yeast encode genomes and brew characteristics of new and strains for the development of different EMBO 'old' yeast strains product types with different aroma profiles and product characteristics

Figure 1. Beer brewing over time.

The most important discoveries and developments during a history of 10,000 years of brewing beer.

There is also evidence that humans have controlled yeast evolution. As we did with plants and animals, we also domesticated microorganisms—at first rather unconsciously—to produce healthy food. Thus, the foundation of today's biotechnology was laid back in the first large settlements millennia ago. Nevertheless, it took thousands of years before humans were able to identify microorganisms, such as yeast, as individual organisms, let alone isolate them.

Ingredients of ancient beer: starch, amylolytic enzymes and yeast

Even without the knowledge of what actually converts sugar into alcohol, brewers soon developed an understanding of which additives-such as oak bark, fruits, honey or fruit juices-were suitable for initiating fermentation and producing pleasant aromas. Many fruit acids lower the pH of the wort and have an additional bacteriostatic effect. Grapes, where they existed, were particularly suitable and indeed archaeological findings of early beers from ancient breweries show traces of grapes. Such findings also show that the spectrum of cereal cultivation shifted in Mesopotamia to emmer and barley and that fermentations were started using leftover bread or sourdough. The yeast-rich liquid from the fermentation vessel or must was mixed with flour to make a dough and dried to keep the yeast fit until the next fermentation. Bread and beer, two foods in perfect symbiosis, thus developed into two of the most important characteristics of civilisation (Meußdoerffer & Zarnkow, 2014; Hutzler, 2021).

Given the much cheaper price compared to wine, the better availability of raw materials, but primarily the advantage of being able to store malt and grain, beer quickly became the more important beverage. Centralised breweries were established in every larger settlement to produce beer at a consistent quality for a large number of people at low cost. As wine has always been significantly more expensive than beer, it was the choice of the rich and the authorities, especially in areas without viticulture. The climate has had a major influence: wine cultivation is more efficient in warmer regions and during warmer periods to produce more and stronger wine as the sugar content of the grapes increases with warmer climate. In cold areas or during periods the cultivation of cold-tolerant cereals with short growing seasons or winter cereals still yields sufficient raw materials for brewing (Unger, 2013; Meußdoerffer & Zarnkow, 2014). However, brewing beer in a warm climate is more difficult because fermentation proceeds faster and more uncontrolled, the risk of infection by beer spoilage organisms increases and shelf-life decreases. It was therefore an extraordinary achievement by the first brewers in the Fertile Crescent and ancient Egypt to develop and improve the fermentation process to mass-produce beer with a consistent quality.

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Yet, many of the processes and characteristics that have made modern beer so successful were established later in the colder areas in Northern Europe. Nordic ethnic groups are often more associated with extensive bouts of intoxication through fiction and literature, but they were also highly conscientious craftsmen and brewers and exerted a significant influence on beer production. Still, the spiritual intoxication through psychoactive substances from alkaloid plants was indeed an integral part of many rituals of the Norsemen although evidence of such rites can also be found among other populations from Egyptians to Aztecs. Many of the plants used were revered as sacred and magical.

One of these plants was hop (Unger, 2013), an important component of beers in some regions from today's Northrhine-Westphalia, Belgium and the Netherlands in the form of grut beers. The grut—the 'fermentum'—is a 'ready-made mixture' of all the raw materials needed to initiate beer fermentation. It mainly contained beer spice, such as gale, swamp brier, yarrow and a consortium of yeasts and other microorganisms, and people had to buy it from the

regional grut lord. Grut therefore refers to both the brewing material and the brewing right (Unger, 2013; Verberg, 2018).

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The great disadvantage of grut beers is their short shelf life. Thus, beginning in the 14th and increasingly in the 15th century, hop beers replaced grut beers. The advantages are obvious: it is much cheaper because hops, unlike the grut ingredients, can be cultivated and grown almost everywhere. In addition, hop beers have a much longer shelf-life and their production is easier to standardise. The bitter substances from hop have antimicrobial properties and suppress the growth of potentially harmful germs while yeasts and other fermentation-relevant microorganisms increasingly adapted to hop. Despite these advantages, the adoption and spread of hop beer were slow. One reason was the resistance of landowners-lords, towns and private individuals-who profited from the sale of beer wort. Their attempts to ban hop beer however failed (Unger, 2013; Meußdoerffer & Zarnkow, 2014; Verberg, 2018).

Improvements in brewing technology from medieval to modern times

With the onset of the Little Ice Age in the 15th century, colder temperatures prevailed and fermentation proceeded slower. As a result, the taste of the beers produced was not so obtrusively 'solvent-like' and the growth of 'souring' and other harmful microorganisms was better controlled by the brewer. It is therefore no coincidence that many important innovations, such as the lager brewing that dominates until today, were invented during the cold periods at the beginning of the 16th century (Meußdoerffer & Zarnkow, 2014).

There is also the first evidence from this period of a 'bottom-fermenting' yeast, which found its way into brewing along the mountain range in Southern Germany and Bohemia. In contrast to its top-fermenting relative, this new yeast strain *Saccharomyces* pastorianus was able to ferment wort at lower temperatures between 7 and 10°C. Top-fermenting yeast float in the liquid during fermentation owing to their sprout structures and the entrapped CO₂ bubbles, while the smaller cell groups of S. pastorianus veast sink to the bottom (Narziß & Back, 2009). Today we know that S. pastorianus is a hybrid of *S. cerevisiae* and *S. eubayanus*. The question of where the latter originated has not been answered satisfactorily vet and is the subject of much speculation and extensive scientific work. The appearance of S. pastorianus also led to disputes with bakers, who were not satisfied with its fermentation performance and insisted that only top-fermenting yeast should be used. However, it was not possible to keep S. cerevisiae and S. pastorianus apart until it became possible to better control the fermentation temperature (Meußdoerffer & Zarnkow, 2014).

Domesticated yeast strains determine taste

Brewers in ancient times were dependent on the climate and ambient temperature as well as spontaneous fermentation before the establishment of centralised breweries and cooling strategies. Spontaneously fermented beers are naturally very variable in quality and taste and sometimes even undrinkable if infections of wild yeasts or souring bacteria, especially in the warmer months of the year, spoiled the beer. Over time though, people started to use the 'sediment' in the fermentation vessel to start the next brew as they realised that this improved the quality of the beer. As a result, each brewery 'domesticated' and evolved its unique yeast strains.

However, until the end of the Middle Ages, brewing was still largely empirical, and the existence and function of the organisms involved unknown. Fermentation was regarded as a natural force and practical brewing knowledge was passed down from generation to generation. Monasteries played an important role in that regard, as they kept meticulous records of the brewing activities. Starting in the late Middle Ages, many alchemists took a heightened interest in the causes of fermentation. In 1674, the Dutch naturalist Antoni van Leeuwenhoek (1632-1723) first discovered and described microorganisms under the microscope. Around 1680, he was also the first to observe yeast which he had isolated from fermentation substrate. Indeed, yeast was the first microorganism to be studied by scientists, owing to its large cells and economic importance (Unger, 2013; Meußdoerffer & Zarnkow, 2014; Methner *et al*, 2019).

But it was not until the middle of the 19th century that several scientists independently recognised yeast as the fermenting organism. It was a time when the natural sciences in general expanded rapidly not just by generating an enormous body of knowledge but also applying said knowledge for practical purposes. Further research into alcoholic fermentation laid the scientific foundations for studying cellular metabolism, especially the function of enzymes. Theodor Schwann's (1810-1882) experimental work of 1837 on fermentation that demonstrated that yeast was a living organism provided a model for later research in microbial physiology (Smith, 2012).

The Danish botanist Emil Christian Hansen (1842-1909) and the German hygienist Robert Koch (1843-1910) founded 'yeast inbreeding' by isolating individual cells and propagating them in the laboratory under germ-free conditions. This was the beginning of the 'pure' cultured yeasts and made it possible for the first time to start microbiologically clean fermentations. Hansen had been investigating the so-called 'beer disease' as an employee of the Carlsberg Laboratory since 1878. He also isolated wild yeasts and found that only a few yeast strains were suitable for brewing. Louis Pasteur recognised the role of acidifying bacteria in spoiling and souring beer. He was also the first to distinguish between aerobic and anaerobic life: '... fermentation is always associated with the life of the yeast cell, but without oxygen' (Smith, 2012).

At the end of the 19th and into the following century, the decoding of glycolysis and new insights into fermentation metabolism allowed a more precise control of the brewing process via temperature or pH value. Yeast management was decisively improved, and there was lively competition for pure yeast strains, which, along with other advances, were often the subject of industrial espionage. Theoretical and practical brewing knowledge was classified as company secrets and only passed on with caution (Meußdoerffer & Zarnkow, 2014). British brewers were much further ahead technologically than their colleagues on the continent: the German Brewer Gabriel Sedlmayr (1811–1891), for example, brought back a saccharometer from an educational trip to England.

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New apprenticeships emerged that spread the knowledge of process technology and microbiology which helped to professionalise the 'job' of beer brewer. In England, Robert Warington was probably the first professional brewery chemist who was employed by Truman, Hanbury and Buxton in 1831. In the early 1860s, Johann Carl Lermer was employed as the first 'brewery chemist of a bottom-fermenting brewery' at the Schwechater brewery in Vienna. With the establishment of brewing technology institutes-for instance Weihenstephan, Berlin or Löwen-the knowledge of brewing spread rapidly to a wider audience. In 1865, Carl Lintner (1828-1900) ushered in the era of academic brewing education at the Landwirtschaftliche Centralschule in Freising, Germany, with a Brauer-Cursus (Brewers' Course). Many of his students left for the USA, where they founded some of the largest breweries in the world: Pabst and Anheuser-Busch were each already producing well over 1,000,000 hl at the turn of the 20th century (Meyer, 2015).

Modern brewing—a balance between high tech and traditional knowledge

During the world wars, it was more important to supply the population with food, but with the economic growth after the second world war, taste and brand became increasingly important. But catering to a broader consumer base with recognisable brand names and taste also meant the beers became more homogeneous and lacked unique flavour characteristics. The global economic crisis in the 1970s accelerated this impoverishment of variety as many smaller breweries had to shut down. In the USA, only 89 breweries were left in 1978. Today, the US Brewers Association lists more than 9,000 breweries, including microbreweries and taprooms (Brewers Association, 2022).

At the same time, the craft brewing movement, which began in the USA, distanced itself from the classic lagers and mass-produced beers in terms of taste and production. This trend has now taken over other countries with traditional breweries and complements the diversity of flavours in every brewing nation. Nowadays, the use of larger amounts of hops in so-called IPA beers, alternative raw materials and other food additives create an enormous variety of beers. Alternative yeast strains and fermentative microorganisms play a major role too (Kurtzman et al, 2011). In contrast to traditional breweries, which have cultivated their own brewhouse yeast strains for decades or even centuries, many of these new breweries rely on dry yeasts, liquid or frozen preparations from yeast centres and strain collections. Some traditional and experimental breweries use spontaneous fermentation and have built their own culture collections over years to cater to a new market that appreciates unique flavours. The potential of these strain collections is tremendous and more and more breweries dare to work with new/old yeasts to create innovative products such as non-alcoholic beers via maltose-negative yeast strains (Methner et al, 2019).

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These developments have countered the 'impoverishment' of the brewing yeast variety. This had already been a criticism when yeast breeding was established in 1883: that brewers did not leverage the evolutionary forces of mixed fermentations for the sake of reproducibility and quality. Since, it is the duty of research institutes to ensure and generate diversity. One way to achieve this is using the tools of modern molecular biology—in fact, *S. cerevisiae* was the first genetically modified organism used in the food sector (Kurtzman *et al*, 2011)—and the Yeast 2.0 project now offers unprecedented opportunities to further manipulate the organism to generate new fermentation strains. This, however, does not always find acceptance among consumers or in countries with strict laws regarding the use of genetically modified organisms in food production. On the other hand, the hunt for new yeast strains in natural environments (Hutzler, 2021) and experiments with mixed fermentations in the laboratory or in pilot projects taps into the enormous natural diversity and the evolutionary forces to give brewers new yeast strains to produce new varieties of beer. From a basic food staple in the ancient cities of Mesopotamia, Egypt and China, beer brewing has continually evolved over millennia to offer consumers an unprecedented variety of tastes and flavours.

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The authors declare that they have no conflict of interest.

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