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Dynamic in vitro gastric digestion behaviour of camel milk

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ABSTRACT

This study investigated the dynamic in vitro gastric digestion behaviour of camel milk. Coagulum that was retainable in the stomach was not formed during the digestion of camel milk, whereas bovine milk reconstituted to the same protein concentration (2.9%, w/w) underwent pronounced gastric coagulation into structured clots. During early digestion, the camel milk formed small particles, resulting from its weak coagulation, that were preferentially emptied from the stomach. These particles became more compact and spherical in the first hour of digestion and then gradually decreased in size. Protein analysis indicated that the main camel milk proteins were digested in the order α_{S1}-casein > β-casein > α-lactalbumin, which may have been modulated by the decreasing pH during the dynamic gastric digestion. This unique coagulation behaviour of camel milk resulted in its rapid gastric digestion and emptying, which may have nutritional implications.

1. Introduction

Camels are the fifth most important dairy animals in the world (following dairy cattle, buffalos, goats and sheep). In 2020, over 3.1 million tons of camel milk were produced globally and there were 38.0 million camels; this population is projected to increase (FAOSTAT http://www.fao.org/faostat/en). Central African, Gulf Cooperation Council and Central Asian countries are the primary home of the main camel species (dromedary and Bactrian). Camels are not ruminants; unlike other major dairy animals that belong to the animal family *Bovidae* (suborder Ruminantia), camels belong to the animal family *Camelidae* (suborder Tylopoda).

The proximate composition of camel milk is comparable with that of bovine milk. The protein, fat and carbohydrate contents of camel milk are in the ranges of 2.7 to 4.8%, 3.1 to 4.2% and 4.1 to 4.8%, respectively (Hailu et al., 2016b; Mohamed, Nagy, Agbaba, & Kamal-Eldin, 2021). Camel milk is produced throughout the year because of the long lactation period of female camels (Nagy et al., 2013). Previous studies have demonstrated that camel milk and its products have some unique nutritional features, such as being richer in bioactive proteins and vitamin C among common animal milks, and various biological activities (e.g., antidiabetic, anticancer and anti-autistic activities) (Abou-Soliman, Awad, & Desouky, 2020; Ayoub, Palakkott, Ashraf, & Iratni, 2018; Ho, Zou, & Bansal, 2022; Mohamed, Ayyash, & Kamal-Eldin, 2022).

During the early stages of gastric digestion, ruminant milks (e.g., bovine, ovine and caprine) are known to restructure into a coagulum that is retainable in the stomach and is normally referred to as "curds" or "clots" (Li et al., 2022a; Roy, Ye, Moughan, & Singh, 2021; Ye, Cui, Dalgleish, & Singh, 2016); it results from the preferential hydrolysis of κ-casein by pepsin, which destabilises the casein micelles similar to the milk-clotting action of rennet (Huppertz & Chia, 2020; Li, Ye, & Singh, 2021; Ye et al., 2019b). Some researchers have suggested that camel milk forms softer curds in the stomach, which is associated with its poor gelation properties upon acidification or renneting (Berhe, Seifu, Ipsen, Kurtu, & Hansen, 2017; Roy, Ye, Moughan, & Singh, 2020). The poor gelation/coagulation properties of camel milk have been attributed to the large casein micelles (~380 nm), the low κ-casein content (~3.5%), and the high proportion of β-casein in camel milk (Baig, Sabikhi, Khetra, & Shelke, 2022; Hailu et al., 2016b; Mohamed et al., 2022).

Relative to other dairy animal species, the understanding of the gastric digestive behaviour of camel milk and its impact on digestive kinetics is lacking. Interestingly, a recent study reported that camel milk, but not bovine milk, formed a curd under static in vitro infant digestion (Zou et al., 2022). However, the camel and bovine milk used in this study were diluted to 1.2% protein concentration with water. The authors attributed the finding to the higher dilution of bovine milk that more extensively solubilised the colloidal

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calcium phosphate (CCP), which is important for the gastric coagulation of milk (Huppertz & Lambers, 2020; Wang et al., 2023). To the best of our knowledge, the gastric digestion behaviour of camel milk has not been studied in a (semi-)dynamic gastric digestion model, which is the optimal system for investigating structural changes and the kinetics of nutrient release during gastric digestion (Li et al., 2021; Mulet-Cabero et al., 2020a).

This study investigated the gastric digestion behaviour of camel milk in a dynamic in vitro gastric digestion system, the human gastric simulator (HGS) (Kong & Singh, 2010). Using the HGS, previous studies have demonstrated the gastric coagulation behaviour of ruminant milks (Li et al., 2022a; Roy et al., 2021; Ye, Cui, Dalgleish, & Singh, 2017), which well resembled that found in a piglet model (Roy et al., 2022). In the present study, the structural changes, the gastric emptying of proteins and lipids and the protein hydrolysis during the gastric digestion of camel milk were investigated. The results would demonstrate whether camel milk displays a unique digestion behaviour among the commercially available animal milks, which may have further nutritional implications.

2. Materials and methods

2.1. Materials

The camel milk powder (from Al Ain Farms, United Arab Emirates) contained 26 g fat, 26 g protein, 41 g carbohydrate and 926 mg calcium per 100 g, according to the available nutritional information. A bovine milk powder (29 g fat, 24 g protein, 38 g carbohydrate and 819 mg calcium per 100 g) was purchased from a supermarket in Palmerston North, New Zealand, as a control sample for comparisons of the curd formation behaviour, pH profile and particle size during digestion. The milk powders were reconstituted to 2.9% (w/w) protein in reverse osmosis water and were stirred for 30 min before being stored at 4 °C overnight to ensure complete hydration. The casein: total protein ratio was 80.3% for the bovine milk and 73.0% for the camel milk, as determined using a Milkoscan FT1 (Foss Electric, Denmark). Porcine pepsin (P7000, Sigma–Aldrich, St. Louis, MO, USA) with a determined activity of 541 U mg^{-1} was used for gastric digestion.

2.2. Dynamic in vitro gastric digestion

The digestion experiment was conducted using the HGS as described previously for other ruminant milks (Li et al., 2022a, 2022b; Pan et al., 2021). Simulated salivary fluid (SSF) (without amylase) and electrolyte simulated gastric fluid (SGF) (1.25× concentrated, pH 1.5) were prepared as described by Brodkorb et al. (2019). Prior to the digestion experiment, 200 g milk was warmed to 37 °C in a water bath. The SSF was added at an amount equal to the dry weight of the milk to simulate the oral phase of digestion, as recommended by Mulet-Cabero et al. (2020a). This mixture was then added to the gastric chamber of the HGS. To simulate the basal amount of SGF in the fasted stage, 20 mL of SGF (1× concentration, pepsin activity 2000 U mL^{-1}) was added immediately before the start of gastric digestion. The gastric digestion was performed at a controlled temperature of 37 °C for 240 min. During the digestion process, two pumps on the HGS controlled the addition of the 1.25× concentrate of electrolyte SGF, pepsin and $CaCl_2$ solution to reach an addition rate of the SGF (1× concentration, pepsin activity 2000 U mL^{-1}) of 2.5 mL min^{-1}. Rollers moved along four sides of the stomach chamber to simulate the peristaltic movement in the stomach at a frequency of 3 times per minute. Gastric digesta were emptied every 20 min at a rate of 3 mL min^{-1} through a 1-mm sieve to mimic gastric sieving. The gastric content that was retained after the simulated gastric sieving, if any, is referred to as the gastric milk coagulum or milk clots.

2.3. Characterisation of digestion samples

The pH of the digesta emptied from the gastric chamber at 20-min intervals was measured using a CyberScan pH 510 (Eutech Instruments, Singapore). Samples were taken at certain time points (20, 60, 120, 180 and 240 min) for further analysis. Photographs and confocal laser scanning microscopy (CLSM) images of the samples at different stages of gastric digestion were taken as described by Ye et al. (2017). In the CLSM images, proteins are displayed in green and lipids are displayed in red.

The particle size distribution of the freshly emptied digesta was determined using a MasterSizer 2000 (Malvern Instruments Ltd., Malvern, UK). The concentrations of fat and crude proteins (including proteins and peptides, nitrogen conversion factor = 6.38) were determined using the Mojonnier method and the Dumas method, respectively (Li et al., 2022b).

To understand the processes of protein emptying and degradation during digestion, digesta samples emptied from the gastric chamber were analysed using sodium dodecyl sulphate polyacrylamide gel electrophoresis (SDS-PAGE); 16.5% Tris-Tricine precast gels (Criterion™, Bio-Rad Laboratories, Hercules, CA, USA) were used for the analysis and were used according to the manufacturer's instructions. A molecular mass marker Precision Plus Protein Dual Xtra Prestained Protein Standard (2–250 kDa, Bio-Rad Laboratories) was loaded with the samples. The camel milk proteins were identified according to previous studies (Khulal, Ghnimi, Stevanovic, Rajkovic, & Cirkovic Velickovic, 2021; Zou et al., 2022). The digesta samples collected at different digestion times were diluted with the sample buffer to an equal protein concentration of 1 mg mL^{-1}. In addition, to better understand the phase separation behaviours during early digestion, selected samples (digesta at 20 and 60 min of digestion) were separated into three fractions by centrifugation at 3800 × *g* for 20 min: (i) a cream fraction on the top; (ii) a clear serum fraction in the middle; (iii) a solid sediment fraction at the bottom. SDS-PAGE was conducted on these fractionated samples. The SDS-PAGE gels were scanned using a Gel Doc XR+ system and the Image Lab 5.2.1 software (Bio-Rad Laboratories).

The gastric digestion experiment of the camel milk was repeated three times from sample preparation to digesta analyses. Error bars in the figures indicate standard deviations.

3. Results and discussion

3.1. Structural changes of camel milk during dynamic gastric digestion

Fig. 1 compares the camel milk and the bovine milk after 60 min of gastric digestion. Interestingly, no coagulum was retained in the stomach for the camel milk (following sieving through a 1-mm sieve) throughout the dynamic digestion process (Fig. 1A). In contrast, the bovine milk reconstituted to the same protein concentration underwent pronounced coagulation and a large number of clots were formed (Fig. 1B), some of which survived the whole gastric digestion of 240 min, as widely demonstrated for different ruminant milks in previous studies (Li et al., 2022a; Mulet-Cabero, Mackie, Wilde, Fenelon, & Brodkorb, 2019; Ye et al., 2017).

The absence of a coagulum that was retained in the stomach indicated that all of the camel milk components were able to be emptied throughout the gastric digestion process. The CLSM images showed that protein aggregates with loose structures were found in the emptied camel milk digesta at 20 min of gastric digestion (Fig. 2), similar to the time taken for ruminant milks to

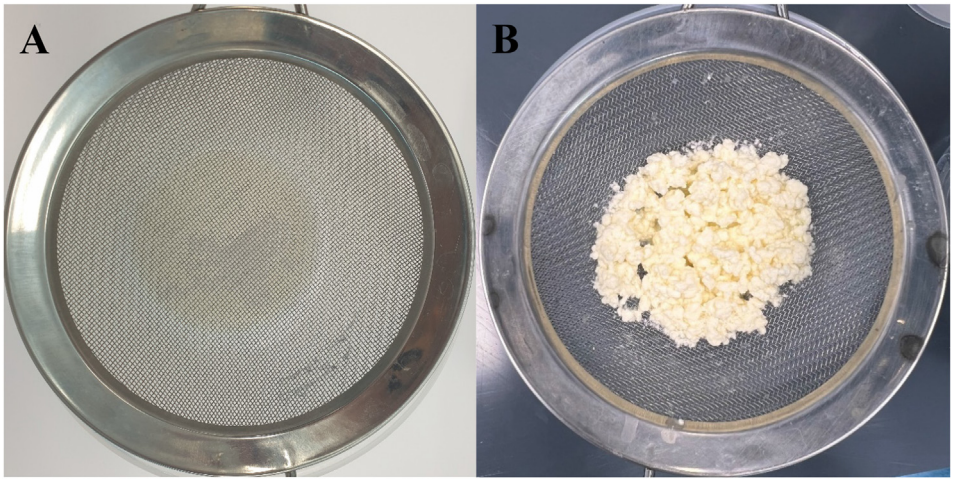

Fig. 1. Gastric contents retained (simulated gastric sieving through a 1-mm sieve) after 60 min of digestion of (A) reconstituted camel milk and (B) reconstituted bovine milk in the human gastric simulator.

coagulate in previous studies (Li et al., 2022a; Ye et al., 2017). It appeared that protein coagulation occurred during the digestion of camel milk, but to a much lower extent than for other ruminant milks. In addition, some fat globules were loosely associated with the protein structures at 20 min of digestion, whereas others were independently present in the aqueous phase. The digesta emptied at 60 min consisted of large particles that were more compact and spherical than at 20 min, and most of the fat globules were embedded in the protein particles. At 120 min of digestion, the emptied digesta contained compact particles that were similar to those found at 60 min but were smaller in size. Virtually, all fat globules were closely associated with the protein particles or covered by a layer of protein. From 120 to 240 min, there were no apparent changes in the structure of the emptied particles except for a slight decrease in their size.

3.2. Particle size distribution in the emptied digesta

The particle size distributions of the emptied digesta of camel milk and bovine milk at different stages of gastric digestion are exhibited in Fig. 3. Before digestion, the particle size distribution of both types of milk had three populations, which probably represented the casein micelles, homogenised fat globules and some insoluble particles, in the increasing order of particle size. The first population of casein micelles peaked at approximately 275 nm and 209 nm for camel and bovine milk, respectively, agreeing with

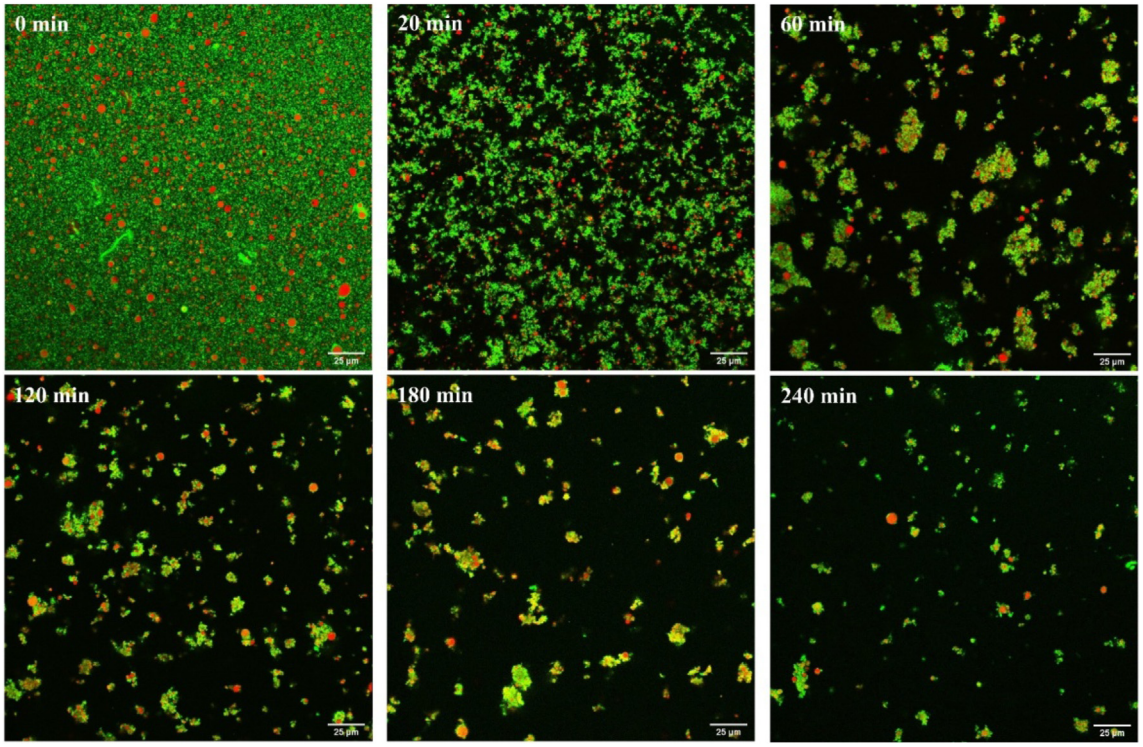

Fig. 2. Confocal laser scanning microscopy images of the digesta emptied at different stages of the dynamic gastric digestion of reconstituted camel milk.

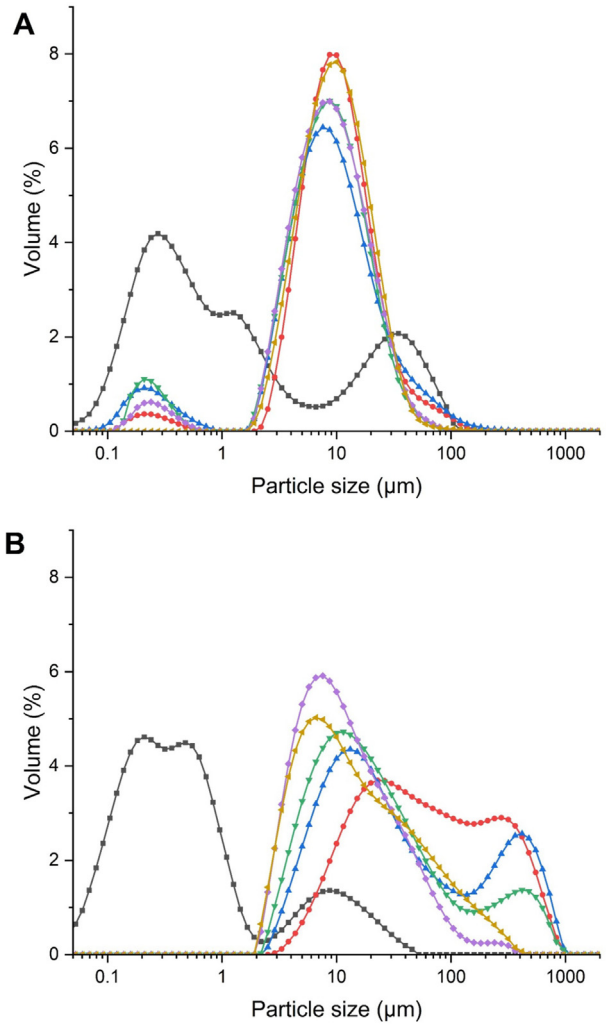

Fig. 3. Particle size distributions of reconstituted camel milk (A) and reconstituted bovine milk (B) and their respective digesta emptied at different stages of dynamic in vitro gastric digestion: ■, 0 min; ●, 20 min; ▲, 60 min; ▼, 120 min; ◆, 180 min; ◀, 240 min.

reports that camel milk has a markedly larger casein micelle size (Baig et al., 2022; Hailu, Hansen, Seifu, Eshetu, & Ipsen, 2016a). Comparison of the second population at around 1 μm indicated that the bovine milk was slightly more intensively homogenised than the camel milk during powder processing. For the last population, previous studies have reported that insoluble particles of similar size presented after reconstitution from powders (Baldwin, 2010; Toikkanen, Outinen, Malafronte, & Rojas, 2018). The size of these particles in the reconstituted camel milk was larger than those in the bovine milk.

For all the camel milk digesta samples, the main population of particles was consistently centred at around 10 μm, which largely matched the size of the particles observed in the CLSM images (Fig. 2). In comparison with the digesta emptied from 120 min onwards, the digesta emptied at both 20 and 60 min of digestion had wider particle size distributions towards the larger side, into the 30–100 μm range. The wider particle size distributions of the camel milk digesta emptied at 20 and 60 min (Fig. 3A) probably represented the larger aggregate structures found in the confocal images (Fig. 2). Besides the population at 10 μm, a small population probably representing the casein micelles are present in most digesta samples, suggesting that they were not incorporated into the larger particles.

In contrast, the bovine milk digesta (Fig. 3B) contained much larger particles (up to 1000 μm) than the camel milk digesta from 20 min of digestion, which then gradually decreased over time. It is important to note that this particle size analysis only included the digesta emptied through the simulated gastric sieving of 1 mm and did not include the larger clot structures in the stomach chamber, like those presented in Fig. 1. The gastric sieving of 1 mm explains why the particle size in the digesta reached the maximum of 1000 μm. In addition, unlike the camel milk digesta, no particle population of the casein micelles at around 0.2 μm was found in any bovine milk digesta, further indicating the greater tendency for coagulation of bovine milk than camel milk.

3.3. Discussion of the weak gastric coagulation of camel milk

Based on the structural and particle size analyses (Figs. 1–3), pepsin-induced coagulation of the camel milk occurred, but to a much lower extent than for the bovine milk or other ruminant milk digested under similar conditions, in which larger clots were formed and were retained in the stomach (Li et al., 2022a; Ye et al., 2017). This gastric digestion behaviour of camel milk is unique among the milks of major dairy animal species, and is probably associated with its weak coagulation properties upon renneting and acidification (Baig et al., 2022; Berhe et al., 2017; Hashim, Khalil, & Habib, 2009; Ho et al., 2022).

Previous studies attributed the poor coagulation and gelation properties of camel milk to its lower casein:whey protein ratio and larger casein micelle size compared with ruminant milks (Baig et al., 2022; Berhe et al., 2017; Hailu et al., 2016a). In the present study, we also found that the camel milk has a lower proportion of caseins in total proteins (73.0%) and a larger casein micelle size (~275 nm) than the bovine milk (80.3% and ~209 nm, respectively). The lower casein:whey protein ratio would limit gastric coagulation because casein micelles are the primary building blocks of the clot matrix whereas whey proteins can retard the coagulation process (Mulet-Cabero et al., 2020b; Yang et al., 2023; Ye et al., 2016). The smaller casein micelle size of bovine milk (compared with ovine and caprine milk) was suggested to contribute to its stronger gastric coagulation, similar to the effect of casein micelle size on rennet-induced coagulation (Glantz et al., 2010; Li et al., 2022a). Interestingly, goat milk, which displayed weaker gastric coagulation than bovine milk (Li et al., 2022a; Maathuis, Havenaar, He, & Bellmann, 2017; Ye, Cui, Carpenter, Prosser, & Singh, 2019a), has a casein:whey protein ratio and a mean casein micelle size that are in between those of bovine milk and camel milk (Roy et al., 2020). Some characteristics that influence the gastric coagulation behaviour of milk appear to apply generally to the milk of different dairy species.

Besides protein composition and casein micelle size, the camel milk has a lower fat:protein ratio than the bovine milk (Section 2.1), which would contribute to a stronger gastric coagulation as the inclusion of more lipid was reported to result in a weaker coagulum (Mulet-Cabero et al., 2020b). The size of the homogenised fat globules and insoluble particles (the 2nd and the 3rd peak in Fig. 3) was larger in the camel milk than in the bovine milk, the effects of which on gastric coagulation are unclear. However, the insoluble particles probably did not play a critical role considering the major change in particle size distribution during digestion was the near-complete shift of the populations of casein micelles and fat globules to those of large particles ≥10 μm (Fig. 3).

3.4. Gastric emptying and pH profile

The concentrations of fat and crude protein (including proteins and peptides) in the emptied camel milk digesta are presented in Fig. 4A. At 20 min of digestion, the protein and fat contents in the

digesta were similar to those in the original milk, despite being diluted by the addition of SSF and SGF. This indicated that the fat and proteins in the camel milk were preferentially emptied during the early stages of digestion, probably because of their aggregation into particles (Fig. 2) that descended to the bottom of the gastric chamber. From 60 min of digestion, the concentrations of crude protein and fat decreased gradually, as expected. The overall higher concentration of crude proteins than of fat in the digesta suggested that creaming occurred during digestion, as also found during the (semi-)dynamic digestion of other animal milks (Li et al., 2022b; Mulet-Cabero et al., 2019).

The pH profile during the dynamic gastric digestion of camel milk was inverse-S shaped (Fig. 4B). The pH reduction was slow initially (from 0 to 60 min), accelerated to a near linear reduction from 60 to 120 min and then slowed down towards the end of digestion. In comparison, the pH during the digestion of the bovine milk had a quicker initial decrease in the first 60 min, which then slowed down during 60 to 120 min, before accelerating again towards the end. The pH profile during the digestion of reconstituted bovine milk resembles that of homogenised and heated bovine milk (Ye et al., 2017).

The shape of the pH profile during dynamic gastric digestion (under constant rates of SGF addition and gastric emptying) can indicate the pattern of gastric coagulation and the breakdown of

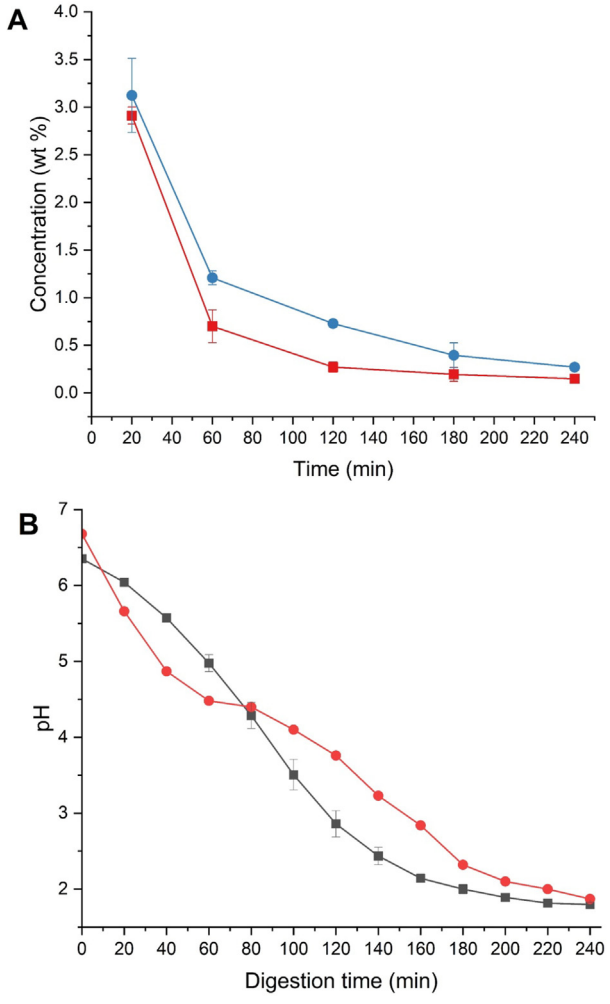

Fig. 4. Concentrations (A) of fat (■) and crude protein (●) emptied during the dynamic gastric digestion of camel milk and pH profiles (B) of the digesta emptied during the digestion of camel milk (■) and bovine milk (●).

ingested foods at different stages of digestion. Generally, strong coagulation of proteins results in faster pH reduction due to the depletion of buffering components in the gastric liquid phase. In contrast, the breakdown and emptying of proteins typically coincide with a stage of slow pH reduction because more proteins can contribute to the buffering capacity of the liquid gastric chyme. The weak coagulation of camel milk probably contributed to the slower pH decrease during early digestion than the bovine milk (Fig. 4B) because most proteins, the major buffering component in camel milk, readily resist pH changes in the aqueous environment. The inverse-S-shaped pH curve observed for camel milk was similar to those during the digestion of sodium caseinate, which did not coagulate into a large coagulum by the pepsin hydrolysis of κ-casein during early digestion (Wang, Ye, Lin, Han, & Singh, 2018).

The pH profile during the early stages of digestion (Fig. 4B) helps in understanding the mechanism behind the structural changes in camel milk (Fig. 2). Protein aggregation occurred in the camel milk at 20 min of gastric digestion when the pH was 6.0, simultaneous with the pronounced coagulation of bovine milk (Fig. 3B), suggesting that it probably also resulted from the hydrolysis of κ-casein by pepsin that causes the gastric coagulation of ruminant milk (Ye et al., 2019b). The particle structure in the camel milk digesta shifted from loose at 20 min to more compact and spherical at 60 min (Fig. 2). This may have resulted from the reduced negative charge on the proteins from 20 to 60 min of digestion, as the pH decreased from 6.0 to 4.9 (Fig. 4B), promoting further fusion of the particle structure (Fig. 2). The dissolution of CCP from the casein micelles as the pH decreased may have also played a part. Also, probably resulting from the charge neutralisation as the pH decreased, the protein-covered fat globules were more incorporated into the particles from 60 min of digestion, as previously reported by Li et al. (2022b). The reduction in the particle size from 60 min (Fig. 3) to the later stages of digestion probably arose from the increased pepsin activity and the greater protein hydrolysis at pH below 4.0 (Piper & Fenton, 1965). However, the persistence of protein particles in the digesta (Fig. 2) and the population of particles at around 10 μm (Fig. 3) until 240 min of digestion suggested that some peptides were rather resistant to pepsin hydrolysis and were able to maintain the structure of small particles; this has also been demonstrated during the digestion of goat milk (Li et al., 2022b).

3.5. SDS-PAGE profiles

SDS-PAGE profiles of camel milk digesta emptied at different gastric digestion time points are presented in Fig. 5A. The bands at just below 15 kDa are labelled as α-lactalbumin (Fig. 5) based on the double-band pattern of this protein identified by Zou et al. (2022). The digesta emptied at 20 min had a nearly identical protein profile to that of undigested camel milk, except for the small peptide bands appearing at below 10 kDa, which indicated minor proteolytic action of pepsin. The digesta emptied at 60 min was composed mainly of α-lactalbumin, with faint traces of other whey proteins, caseins and peptides. Almost no intact proteins remained from 120 to 240 min of digestion, with only traces of small peptides (<5 kDa) being visible. The persistence of α-lactalbumin at 60 min and its disappearance after 120 min of digestion in camel milk is in agreement with studies on ruminant milks; that is, the susceptibility of α-lactalbumin to pepsin hydrolysis is pH dependent, and is markedly higher at pH values below 3.5–4 (Li et al., 2021, 2022b; Miranda, Hazé, Scanff, & Pélissier, 1989; Roy et al., 2021).

Key changes appear to have occurred during the early stages of digestion, as indicated by the considerable changes in particle structure (Fig. 2) and protein profile (Fig. 5A) from 20 to 60 min of digestion. To better illustrate the changes that occurred during this period, we separated the digesta sampled at 20 and 60 min into

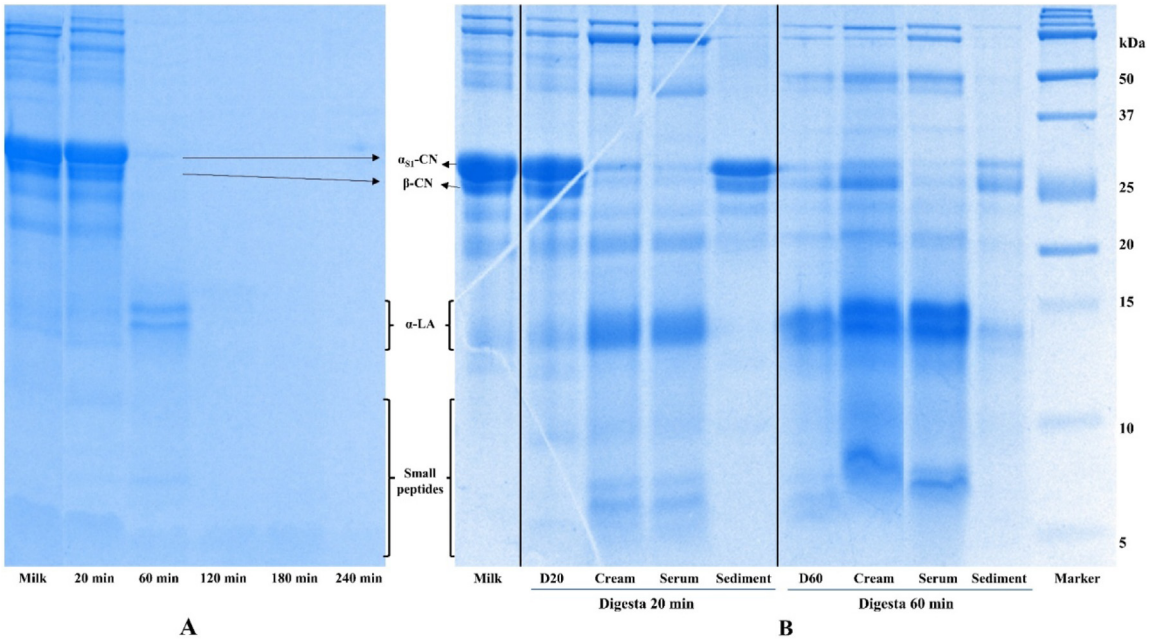

Fig. 5. SDS-PAGE profiles of (A) the digesta emptied at different stages of the gastric digestion of camel milk and (B) different fractions (separated by centrifugation) of the digesta collected at 20 and 60 min of digestion. CN, casein; α-LA, α-lactalbumin; D20, unfractionated digesta at 20 min; D60, unfractionated digesta at 60 min.

three fractions by mild centrifugation (3800 × *g* for 20 min): a cream fraction, a serum fraction and a solid sediment fraction (as described in Section 2.3). The SDS-PAGE profiles of these fractions are presented in Fig. 5B. At 20 min of digestion, the cream and serum fractions had similar protein profiles, being abundant in whey proteins of higher molecular mass (e.g. lactoferrin, serum albumins and milk fat globule membrane proteins), α-lactalbumin and peptides at 5–10 kDa. They also contained small amounts of caseins, which were slightly more abundant in the cream than in the serum. This could be explained by the homogenised fat globules covered by milk proteins, including the casein micelles. The sediment in the 20-min digesta consisted of mostly intact caseins at similar ratios to those in the undigested camel milk.

At 60 min of digestion, the β-casein band became more abundant than the α_{S1}-casein band in all three fractions (Fig. 5B), indicating a faster rate of hydrolysis of α_{S1}-casein than of β-casein from 20 to 60 min of digestion. Along with the observation that α-lactalbumin persisted for longer during digestion (Fig. 5A), the camel milk proteins were hydrolysed in the order α_{S1}-casein > β-casein > α-lactalbumin during the dynamic gastric digestion. This may have resulted from different proteolytic specificities of pepsin on camel milk proteins at different pH values, which has yet to be elucidated.

The cream fraction of the digesta at 60 min was still largely similar in protein profile to the serum fraction, but contained more caseins and a peptide band at around ~8 kDa; the latter was not found in any other samples (Fig. 5B). As discussed in Section 3.4, the binding affinity between the caseins and the protein-covered fat globules probably increased as the pH decreased, which could have resulted in the higher proportion of caseins in the cream fraction. The unique peptide at around ~8 kDa in the cream fraction indicated that these peptides were formed during 20–60 min of digestion and that they were preferentially associated with the fat globules. Interestingly, the sediment at 60 min of digestion contained bands at around 13 kDa, which were absent in the sediment at 20 min of digestion (Fig. 5B). The nature of these bands is unclear. We speculate that they were hydrophobic peptides produced from pepsin hydrolysis. In ruminant milks, the gastric milk clots and particles contain hydrophobic peptides, such as para-κ-CN (~14–15 kDa) (Li et al., 2022b; Pan et al., 2021; Roy et al., 2021). The shift in the composition of the proteins and peptides of the sediment from 20 to 60 min of digestion (lower α_{S1}-casein:β-casein ratio and the presence of new peptide bands at ~13 kDa) may have also contributed to the simultaneous changes in the structures of the emptied particles (Fig. 2).

4. Conclusions

In contrast to bovine milk, camel milk displayed a very weak tendency to coagulate during dynamic gastric digestion; no coagulum was retained in the stomach throughout the gastric digestion process. Instead, camel milk formed small particles at 20 min of digestion that were composed mainly of caseins, which were preferentially emptied from the stomach chamber. From 20 to 60 min of digestion, the structure of the particles became more compact and spherical and α_{S1}-casein was more digested than β-casein. The neutralisation of negative charges on the proteins and the dissolution of CCP as the pH decreased, as well as the altered protein and peptide compositions, were probably responsible for the structural shift of the particles. The association of fat globules with the protein particles also appeared to increase as the pH decreased during gastric digestion. From 60 to 120 min onwards, the particle size of the emptied digesta decreased and then stabilised and no intact proteins remained, indicating a high overall rate of gastric digestion and emptying. This study demonstrated the different gastric digestion behaviour of camel milk in comparison with common ruminant milks. Its rapid gastric emptying and digestion resulting from its weak gastric coagulation may have unique nutritional and functional implications.

Declaration of competing interest

None.

Data availability

Data will be made available on request.

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