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What is the importance of zoonotic trichomonads for human health?

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Trichomonads are common parasites of many vertebrate and invertebrate species, with four species classically recognized as human parasites: *Dientamoeba fragilis, Pentatrichomonas hominis, Trichomonas vaginalis*, and *Trichomonas tenax*. The latter two species are considered human-specific; by contrast, *D. fragilis* and *P. hominis* have been isolated from domestic and farm mammals, demonstrating a wide host range and potential zoonotic origin. Several new studies have highlighted the zoonotic dimension of trichomonads. First, species typically known to infect birds and domestic mammals have been identified in human clinical samples. Second, several phylogenetic analyses have identified animal-derived trichomonads as close sister taxa of the two human-specific species. It is our opinion, therefore, that these observations prompt further investigation into the importance of zoonotic trichomonads for human health.

The trichomonad lineage in phylum Parabasalia

Trichomonads are anaerobic, flagellated protists belonging to the large and diverse groups Trichomonadea and Tritrichomonadea of phylum Parabasalia [1]. They are characterized by the presence of three to five anterior flagella, hydrogenosomes – hydrogen-producing organelles corresponding to anaerobic versions of mitochondria [2], a parabasal body (a large Golgi), and a complex cytoskeleton. A few species have been isolated from environmental samples and may represent free-living species; however, the majority of species form symbiotic interactions (see Glossary) with various animal hosts. Among the parasitic trichomonads, several species inhabit the oral, digestive, and urogenital tracts of invertebrate and vertebrate hosts, including livestock, pets, and humans.

Historically, phylum Parabasalia was divided into two groups based on morphological characteristics; however, the recent inclusion of molecular data recovered six groups: Trichomonadea, Tritrichomonadea, Hypotrichomonadea, Cristamonadea, Spirotrichonymphea, and Trichonymphea [3]. The Trichomonadea, Tritrichomonadea, and Hypotrichomonadea are of primary concern to parasitologists; however, the evolutionary relationships within and between these groups are unclear [4]. Several molecular phylogenies have attempted to resolve these evolutionary relationships using phylogenetic markers such as ribosomal RNA (rRNA) and protein coding genes (Figure 1), which give inconsistent phylogenies [4,5].

Four species of trichomonad are considered human parasites: *Trichomonas vaginalis* (found in the urogenital tract) [6], *Trichomonas tenax* (localized to the oral cavity) [7], and *Pentatrichomonas hominis* and *Dientamoeba fragilis* (located in the digestive tract) [8,9]. Only one species has well-established pathogenic potential: *T. vaginalis*, the cause of the most prevalent non-viral sexually transmitted infection in humans, trichomoniasis [10]. Only *T. vaginalis* and *T. tenax* are considered human-specific, with the former characterized by the richest, although still limited, epidemiology data [11], but very little is known about the latter. *P. hominis* and *D. fragilis* can cause gastrointestinal symptoms in some patients, such as abdominal pain and diarrhea [8,12], *D. fragilis* has also been proffered as a potential causative agent of irritable bowel syndrome (IBS) [13,14], but debate surrounds its pathogenicity, infection route, and epidemiology [15]. In addition, several trichomonad species are of veterinary importance, such as the avian pathogens *Trichomonas gallinae*, *Tetratrichomonas gallinarum*, and *Histomonas meleagridis* [16–19], and *Tritrichomonas foetus*, the causative agent of a venereal disease in cattle [20]. This extensive host range, along with the isolation of *D. fragilis* [21] and *P. hominis* [22] from various animal hosts, suggests that certain species of trichomonads may exhibit the characteristics of zoonoses. Although the question of zoonotic trichomonads has been considered for some years (e.g., [23,24]), recent results from several different sources have highlighted this potential. Here we summarize the clinical and phylogenetic studies that suggest a zoonotic potential for trichomonads, discuss their implications for human health, and the next steps required for investigation into their epidemiology, pathobiology and evolution.

New evidence supports the zoonotic potential of trichomonads

Human trichomonad infections are not body site-specific

The four trichomonad species recognized as human parasites were initially thought to be site-specific [25] (Table 1). However, various clinical studies have shown that they can

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Glossary

Commensal: : a form of symbiosis between two organisms where one derives benefit, whereas the other is unaffected. Some gut trichomonads are thought to represent commensals.
Disease incidence: : the number of new disease cases that occur in a population for a given time period (typically per year).
Dysbiosis: : an imbalance of the microbiota (the microbial populations at a particular body site of an animal host) that leads, or predisposes, the host to disease conditions [60].
Emerging infectious disease: : outbreaks of previously unknown diseases or known diseases that show an increase in incidence, expansion in geographical range, or spread to a new population. Emerging infections can be caused by previously unknown or undetected infectious agents, newly evolved strains, environmental changes, and changes in human demography [51]. A recent review found that over 60% of human emerging infectious diseases are zoonotic in origin [53]. Examples include influenza, HIV/AIDS, and severe acute respiratory syndrome (SARS) coronavirus.
Intermediate host: : a host in or on which a pathogen spends a part of its life, usually a transition period, but does not reach sexual maturity.
Mutualism (mutualist): : a form of symbiosis between two organisms in which both benefit from the relationship. Some gut parabasalids from termites are thought to represent mutualists [80].
Opportunistic: : a potential pathogen that typically does not cause disease in a healthy host, but can in particular situations cause disease, for example, owing to the compromised immune system (e.g., attributable to AIDS, chemotherapy, or malnutrition) of the host. Lung trichomonads represent probable opportunistic infections – see main text.
Parasitic (parasite): : a non-mutual symbiosis between two species where one, the parasite, benefits at the expense of the other, the host. Parasites typically do not kill their hosts but exploit them for resources necessary for their survival. Obligate parasites cannot complete their life cycles and reproduce without a suitable host.
Pathogenic (pathogen): : a broad term that refers to the ability of an organism to cause disease. It is typically used to describe an infectious agent or microorganism, such as a bacterium, protist, virus, etc., that causes disease in its host. Some pathogens, for example, protists *Acanthamoeba* spp. and *Naegleria fowleri* and fungi *Aspergillus* spp. are free-living species thriving in the environment and occasionally infect humans, often in an opportunistic manner in compromised hosts [59].
Pathogenicity: : the ability of a pathogen to overcome host defenses and cause disease.
Re-emerging infectious disease: : the reappearance of a historically known infectious disease after a significant decline in incidence. Acquired resistance of pathogens to antimicrobial medications is an important factor in the re-emergence of many diseases. Examples include West Nile virus, cholera, MRSA (methicillin-resistant *Staphylococcus aureus*).
Reservoir: : the habitat or host that harbors an infectious agent, where it can live, grow, and multiply. Reservoirs can include humans, animals, and serve as a source of potential disease outbreaks.
Symbiosis: : a close and often long-term relationship between two or more different biological species. These relationships can be obligate or facultative, mutualistic, commensalistic, or parasitic.
Transmission: : the passing of an infectious agent from one host to another host. Direct transmission routes include: physical contact, contact with a contaminated environment or surface, airborne transmission, and fecal–oral transmission. Indirect transmission routes involve another organism such as an insect vector or intermediate host.
Vector: : an organism that carries and transmits a pathogen from an infected individual to another individual.
Virulence: : a property of a pathogen, such as specific structural elements or biochemical compounds commonly called virulence factors that cause a reduction in host fitness or damage to the host. It is now recognized that virulence is multifactorial and involves characteristics of both the pathogen and its host, which influence the outcome of their interaction and hence the observed virulence (e.g., an opportunistic pathogen in immunocompromised patients) [59].
Zoonosis: : an infectious organism, such as a bacterium, virus, parasite, or fungus, transmissible between wildlife or domesticated animals and humans. Examples include: (i) the Lyme disease bacterium *Borrelia* transmitted to humans by ticks from a natural reservoir in rodents; (ii) the malaria parasite *Plasmodium knowlesi* transmitted by *Anopheles* vectors that causes malaria in monkeys and humans; and (iii) *Cryptosporidium parvum*, a parasite found in cats, dogs, and farmed animals and transmitted as a cyst in contaminated water, food, or through the fecal–oral route. Zoonoses are the leading cause of emerging infectious diseases worldwide, responsible for devastating disease outbreaks, mortality, and serious socioeconomic consequences [21,56,79].
Zoonotic potential: : the potential for infectious diseases of wildlife or domestic animals to be transmitted to humans.

also be found in atypical locations. For example, *T. tenax*, a commensal of the human mouth found in patients with poor oral hygiene [7], has been identified by microscopic and molecular methods in the upper and lower respiratory tracts [26,27]. One possibility that could account from this 'aberrant' location is inhalation of the parasite from the oral cavity into the respiratory tract. However, in some cases where *T. tenax* was identified in the respiratory tract, no parasites were found in the mouth [26]. Other human trichomonad species have also been identified in the respiratory tract including the sexually transmitted species *T. vaginalis* [28,29] and the gut parasite *P. hominis* [30], which suggests that these species too can proliferate outside their usual body sites.

At least five species of trichomonad, including *P. hominis*, *T. tenax*, *T. vaginalis*, *T. foetus*, and *T. gallinarum*, have been identified in the human respiratory tract and as causative agents of pulmonary trichomoniasis (Table 1). They have been found in up to 60% of patients with *Pneumocystis* pneumonia (PcP) and in up to 30% of patients with acute respiratory distress syndrome (ARDS) [31]. Because trichomonads are microaerophilic it is unlikely that they initiate and cause these diseases themselves, but may represent secondary and opportunistic infections that could exacerbate symptoms and prolong illness [23]. These trichomonad respiratory infections seem to depend upon: (i) the presence of bacteria on which to feed and (ii) local anaerobic conditions caused by PcP or ARDS-associated infections [32] but not necessarily upon immunosuppression, because drugs against PcP consistently cure patients of pulmonary trichomonosis and, in one study, treated ARDS patients were not found to be immunocompromised [25]. Thus, the presence of an increasing number of distinct trichomonads in a broader range of clinical samples from patients with diverse diseases, such as AIDS, rheumatoid arthritis, prostate cancer, pulmonary infections (empyema and pneumonia in addition to PcP and ARDS), and digestive conditions such as diarrhea and IBS [33–35], is becoming increasingly apparent. Indeed, the frequency of pulmonary trichomonosis infections may be higher than reported because transformation of parasites from the motile, pear-shaped stage to the amoeboid stage renders microscopic identification in clinical samples difficult [31], highlighting the importance of molecular data to identify such infections [25].

Non-human species of trichomonad have been isolated from clinical samples

Trichomonads were thought to have strict host specificity [25]; however, trichomonad parasites not previously reported as infecting humans have recently been found in human clinical samples (Table 1). For example, parasites belonging to the genus *Tritrichomonas* can be isolated from the reproductive tract of cattle (*Tritrichomonas foetus*), the nasal mucosa and intestine of pigs (*Tritrichomonas suis*), and the intestine of non-human primates (*Tritrichomonas mobilensis*) [20]. Another example is *T. foetus*, historically considered specific to cattle [25,36]. Nonetheless, experimental cross-infections of the parasites between pigs and cattle in addition to analysis of molecular data suggest that these three species should be considered

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