

CHAPTER 5:

GENERAL DISCUSSION

5.1. Polystome diversity

The parasitic world is everywhere, diverse, and creative. When looking at a springbok, a biologist may imagine the power of natural selection shaping host-predator interactions that pushed the limits of its running abilities (van As *et al.*, 2012). A parasitologist will see an amazing bag for parasites. Moreover a parasite is not a worm or a bacterium anymore. It may be a plant, an insect or a fish (Begon *et al.*, 2006). From the feather of birds to the deepest benthic mollusc, parasites are able to survive and perform wondrous life cycles (Begon *et al.*, 2006; Hickman *et al.*, 2004; Roberts & Janovy, 2009; van As *et al.*, 2012).

For centuries, parasitology has been seen as a field of research apart from the rest of biological concerns. This is possibly due to its intimate link with medical and veterinary professions (Begon *et al.*, 2006). As a result parasitology remained as a distinctive discipline that provided additional but non-fundamental knowledge. Indeed, a compulsory dependent life style has been supposed to represent only a regression of the evolutionary history. However, it has been clearly demonstrated that parasitism is not a regression, rather it is an active evolution of life (Hall, 1999; Price, 1980). Studying host-parasite models could provide valuable insights in understanding our living world, especially in the disciplines of developmental and evolutionary biology (Price, 1977).

Developmental biology recently focused on parasite models to address the question of phenotypic modulations that may occur along a parasitic life-cycle. For instance, the sole genetic information of parasitic flatworms may provide up to five different phenotypes from the egg to the adults in order to achieve transmission (Stearns, 1989). Furthermore, the extraordinary ability of parasites to display plastic strategies to match small but rapid variation in host ecology, physiology and distribution, has been documented (Reece *et al.*, 2009). The deviation of the ontogenetic routes within parasitic lineage compared to their most phylogenitically remote neighbours offers the opportunity to understand the molecular processes behind the evolution of developmental programs (Olson & Littlewood, 2002). Because molecular methods are universal, the growing field of developmental biology involving parasites will undoubtedly extend our current knowledge on regulation pathways and tissue differentiation for the next years (Olson & Littlewood, 2002).

On the other hand, parasites developed the curiosity of evolutionary biology to understand the proximate causes of their success. Why so many parasitic species? One may argue that a biotic environment is much more heterogeneous than an abiotic one (Begon *et al.*, 2006; Hickman *et al.*, 2004; Roberts & Janovy, 2009; van As *et al.*, 2012). Because host individuals are dispersed, enabling them to adapt and evolve, the dependent parasitic world should be submitted to drastic and various selective pressures enhancing speciation (Reece *et al.*, 2009; van As *et al.*, 2012). A fundamental issue is to understand how the rates of speciation between free and parasitic species may differ.

However, we still lack experimental data to understand the links between host and parasite population dynamics in natural environment (Begon *et al.*, 2006; Hickman *et al.*, 2004; Roberts & Janovy, 2009; van As *et al.*, 2012). One such group of parasites that serve as a perfect model for parasitological studies is the polystomes.

Within the class of the Monogenea (Platyhelminthes), the family Polystomatidae radiated onto tetrapod hosts and are known from the Australian lungfish, frogs, salamanders, caecileans, freshwater turtles and the hippopotamus (Badets & Verneau, 2009; Bakke, 2009; Bentz *et al.*, 2006; Du Preez *et al.*, 2010; Hickman *et al.*, 2004; Littlewood *et al.*, 1997; Morrison & Du Preez, 2012; Roberts & Janovy, 2009; Verneau *et al.*, 2009; Whittington, 1998). Polystomes are usually host specific and display a direct life-cycle, which facilitates host to host parasite transmission in aquatic environments (Badets & Verneau, 2009; Bakke, 2009; Bentz *et al.*, 2006; Du Preez *et al.*, 2010; Hickman *et al.*, 2004; Littlewood *et al.*, 1997; Morrison & Du Preez, 2012; Roberts & Janovy, 2009; Verneau *et al.*, 2009; Whittington, 1998). Because biological and reproductive patterns encountered within amphibians are more diverse than in any other group of terrestrial vertebrates, a large diversity of strategies ranging from ovoviviparity to developmental plasticity may have been shaped within polystomes to counteract changes in host ecology. Thereby it is very likely that life-history traits of hosts may account for the diversity of polystome transmission patterns.

The first platyhelminth parasite reported as a parasite of an amphibian, was a trematode discovered by Swammerdam as far back as 1737. The first monogenean from an anuran was discovered in 1758 by Roesel von Rosenhof (Prudhoe & Bray, 1982). Zeder (1800) claimed that this parasite was in fact *Polystoma integerrimum* (Frölich, 1971). Van Beneden proposed, as early as 1858, that trematodes be separated into two groups. Carus (1863) was given credit as the first person to use the term "Monogenea" (Yamaguti, 1963). The Monogenea and Digenea were seen as orders of the Class Trematoda. At a "Round Table" meeting in Warsaw, Poland in 1978, it was decided to elevate the original epithet "Monogenea" to the level of Class (Boeger & Kritsky, 1993). The overwhelming majority of polystomes (62%) are found in anuran hosts, followed by chelonian hosts (32.6%) (Figure 5.1). Only a few species are known from the remaining hosts namely salamanders (3%), caecilians (1.2%), the Australian lungfish (0.6%) and the hippopotamus (0.6%).

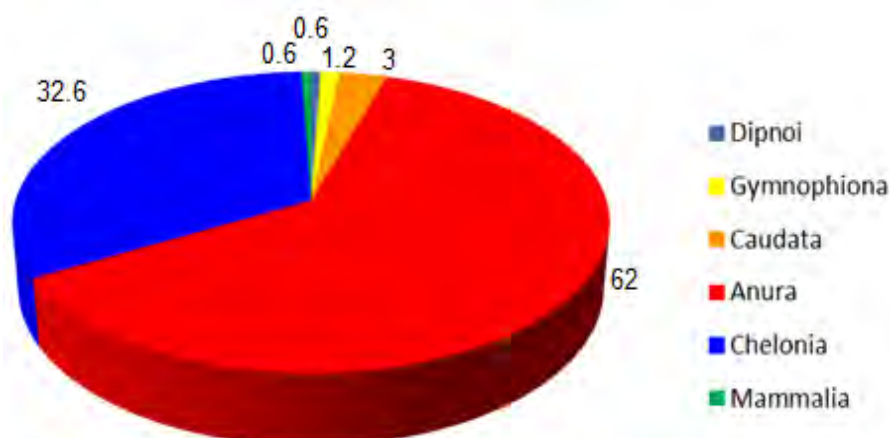


Figure 5.1: Pie chart showing the respective proportions of polystomes parasitising different host groups.

Since the first polystome was discovered several spikes in the number of parasites described were noted. By studying the parasites presented in chapter 2 it is evident that the discovery of new polystomes received a boost in the decade 1930-1940. In this period equal numbers of anuran and chelonian polystomes were described (Figure 5.2) and mainly from the Nearctic and Oriental Realms followed by the Palearctic (Figure 5.3). In the 1940's and 1950's the interest in polystomes declined (Figure 5.2). In the 1950's the focus was more in the Nearctic Realm and in the 1950's to 1960's the focus shifted to the Ethiopian Realm. During this period the first polystomes were discovered from the Neotropical Realm (Figure 5.3). From 1970 until 2000 a dramatic increase in the number of newly described species was observed. This focus was mainly the result of French researchers focussing on central and West Africa followed by the Oriental and Neotropic Realms (Figures 5.2 & 5.3).

Thus this study, by producing a reference document for all known polystome species, endeavours to simplify obtaining information on polystomes as well as to aid in clearing up any uncertainties regarding the identification of certain polystome species as information on polystomes is scattered and in various languages in sometimes poorly known journals or journals that have been discontinued.

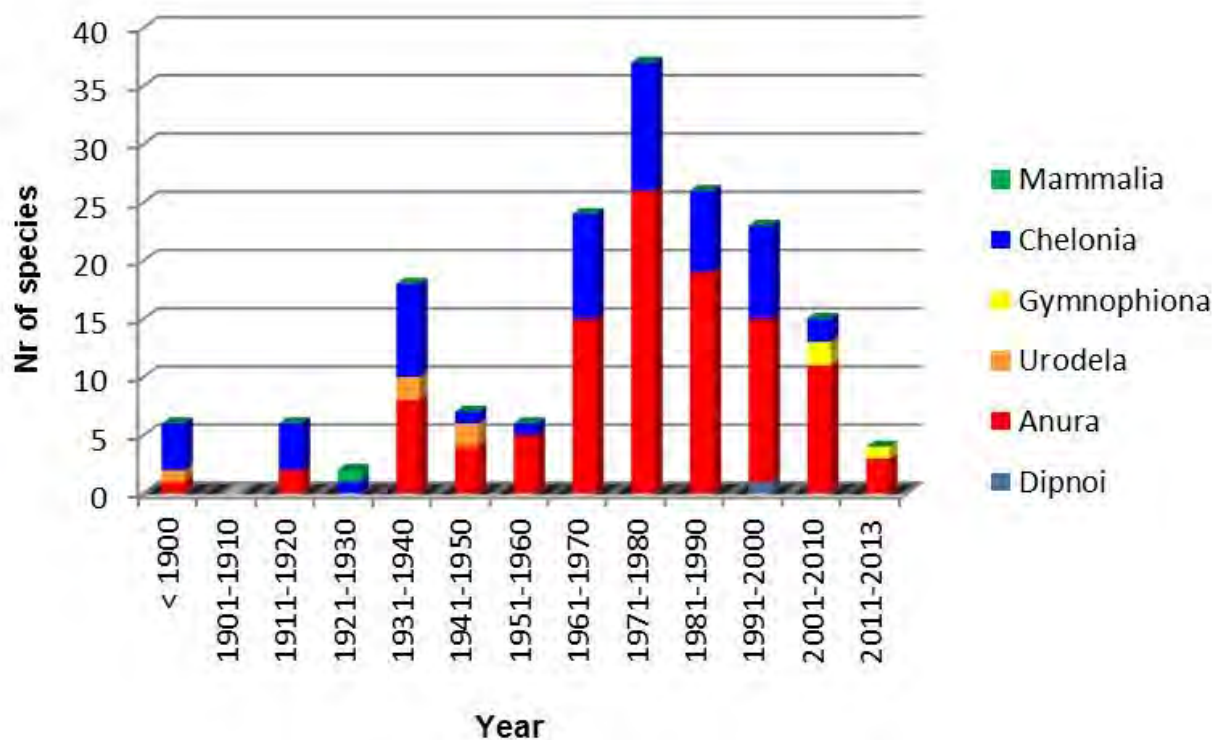


Figure 5.2: Graphical representation of newly discovered polystome species from 1900 to 2013 in the various host species they parasitize.

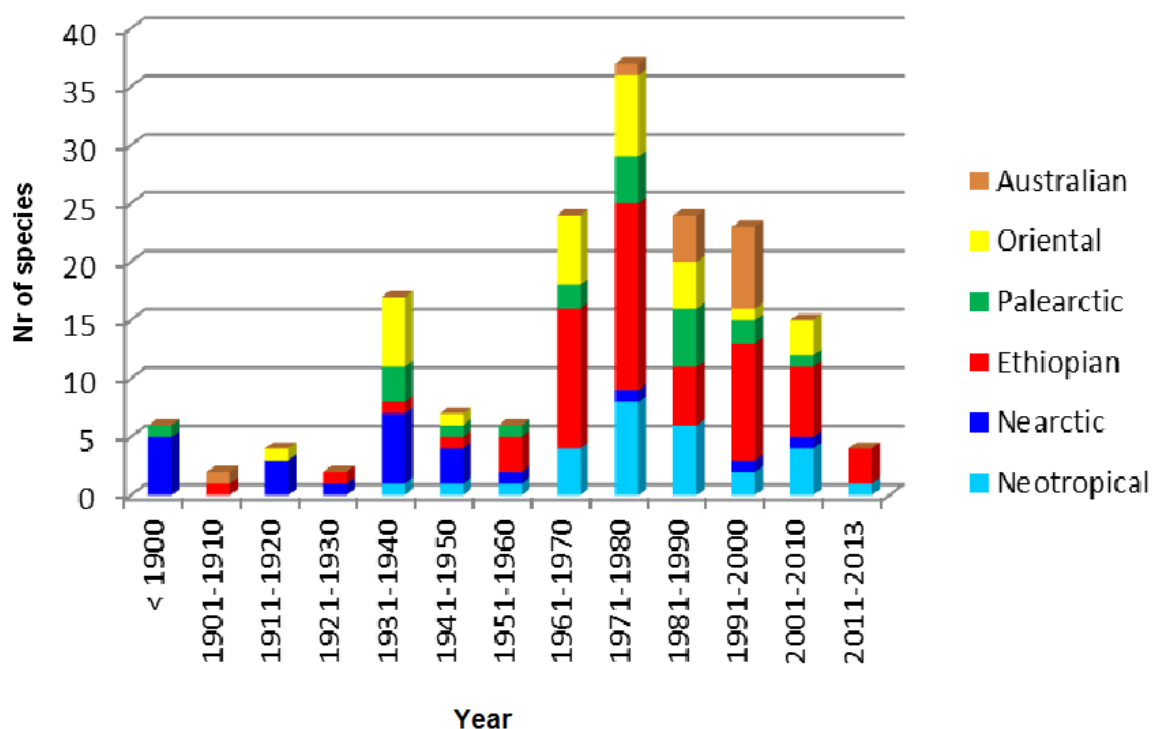


Figure 5.3: Graphical representation of newly discovered polystome species from 1900 to 2013 in the various realms in which they are found to occur

5.2. Description of a new *Polystomoidella*

Molecular studies in collaboration with Olivier Verneau from University of Perpignan, France revealed that the polystomes collected by Louis Du Preez from *Pseudemys nelsoni* belongs to a as yet undescribed species. A draft description of this species was included. In order to comply with the International Code of Nomenclature for Zoology, a species name is not suggested herein but will be when this paper is submitted for publication to a peer reviewed journal.

5.3. Intestinum variation

Polystomatidae are similar in appearance with all polystomes having a pyriform body shape, a false oral sucker, uterus, ovary, vitellaria, testis, an intestinal tract and a haptor containing hamuli, marginal hooks and suckers. There are however characteristics with which these parasites can be distinguished from one another, including the size, shape, position and/or number of hamuli, ovary, uterus, testes, pharynx, suckers and hooks.

Among polystomatids the shape of the intestinum vary significantly and several authors commented upon the value thereof as taxonomic characteristic (Aisien & Du Preez, 2009; Stunkard; 1916; Tinsley, 1974a). This study attempted to evaluate intestinum shape as taxonomic characteristic in the

hope that it would assist in the description of new species. Sanguivorous polystomes have more complex intestinal tracts and contains haematin, while mucus and epithelial tissue feeding polystomes show a far more simple intestinal shape, with the majority showing an absence in diverticula as well as anastomoses.

Based on the degree of branching, number of diverticulae and whether anastomoses are present, a set of nine intestine forms were identified. These findings will be refined and published in the open literature with the expectation that future descriptions will refer to this intestine classification.